Revision of Cognettia (Clitellata, Enchytraeidae): re-establishment of Chamaedrilus and description of cryptic species in the sphagnetorum complex

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Revision of *Cognettia* (Clitellata, Enchytraeidae): re-establishment of *Chamaedrilus* and description of cryptic species in the *sphagnetorum* complex

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The oligochaete worm, *Cognettia sphagnetorum* (Vejdovský, 1878), is widely used as a model organism in soil biology, and therefore it is important that its taxonomy is firmly established. A previous study based on both mitochondrial and nuclear genetic markers showed that this taxon is an assemblage of at least four species that do not form a monophyletic group. Also the validity of the genus *Cognettia* Nielsen and Christensen, 1959 is subject to debate, since the existence of two putative senior synonyms, *Euenchytraeus* Bretscher, 1906 and *Chamaedrilus* Friend, 1913 has been pointed out. Herein we revise the generic assignment of the species currently placed in *Cognettia*: two species, *C. clarae* Bauer, 1993 and *C. piperi* Christensen and Dóžsa-Farkas, 1999, are transferred to *Euenchytraeus*, together with its type *Eu. bisetosis* Bretscher, 1906, whereas the remaining species, including *Cognettia sphagnetorum*, are being transferred to *Chamaedrilus*. Five species within the *Chamaedrilus sphagnetorum* complex are revised: the type species of *Chamaedrilus*, *Ch. chalupskyi* sp. nov. and *Ch. pseudosphagnetorum*, together with its type *Sphagnetorum* sp. nov. and *Ch. chalupskyi* sp. nov. are described as new to science and discussed against a paratype of *Ch. valeriae* (Dumnicka, 2010) comb. nov. DNA-barcodes are provided for all the named species in the complex except *Ch. valeriae*. A key to the species in the complex is given and the value of different somatic characters for separating and identifying species of *Chamaedrilus* is discussed. No morphological feature seems to distinguish *Ch. sphagnetorum* from *Ch. pseudosphagnetorum*. Thus, for a reliable identification of these species, molecular methods, e.g. DNA barcoding, are recommended.


**Key words**: Annelida, *Cognettia*, DNA barcoding, new species, nomenclature, Oligochaeta, soil fauna

**Introduction**

Genetically distinct and separately evolving lineages of organisms are sometimes classified as the same species, due to their similarity in morphology. Nevertheless, such cryptic lineages may differ in certain ecological and physiological properties (e.g. Hambäck et al., 2013; Sattler et al., 2007; Sturmbauer et al., 1999), but this variation is likely to be ignored if the species taxonomy is not fully resolved (Feckler et al., 2013). The use of inadequate taxonomy makes it almost impossible to interpret and compare results involving such species complexes, as it is not known if the same cryptic species has been investigated.

The oligochaete genus *Cognettia* Nielsen & Christensen, 1959, and especially its type species, *C. sphagnetorum* (Vejdovský, 1878), are common inhabitants of bogs and forest soils in northern Europe, and are often used as model organisms in soil biology (e.g. Abrahamsson, 1990; Briones et al., 1998; Haimi & Siirä-Pietkäinen, 2003; Maraldo et al., 2011). In a DNA-based phylogeny of the family Enchytraeidae (Erséus et al., 2010), the genus was recovered with good support. However, in a more recent molecular study *C. sphagnetorum* turned out to be a non-monophyletic complex composed of at least four well-separated lineages, each justified to be regarded as a separate species (Martinsson & Erséus, 2014). Meanwhile, a nomenclatorial problem regarding the genus *Cognettia* was detected by Schmelz & Collado (2010), with two older names, *Euenchytraeus* Bretscher, 1906 and *Chamaedrilus* Friend, 1913 suggested as senior synonyms. These issues called for a taxonomic revision of *Cognettia*.

The aims of this study were twofold. The first was to discuss the validity and monophyly of the genus *Cognettia*...
as currently defined: following our revision, the majority of species, including *C. sphagnetorum*, are transferred to *Chamaedrilus*, while a few others are transferred to *Euenchytraeus*. The second aim was to revise the taxonomy of the former *Cognettia sphagnetorum* complex by describing the morphology of the four North European species recently recognized by molecular data (Martinsson & Erseus, 2014): a neotype, from the type locality, is designated for *Chamaedrilus sphagnetorum*; *Ch. chlorophilus* Friend, 1913 is redescribed, with the designation of a lectotype; and *Ch. chalupskyi* sp. nov. and *Ch. pseudosphagnetorum* sp. nov. are described as new to science. The poor resolution of the morphological features as compared with the clear genetic differences is briefly discussed.

**Taxonomic background**

Nielsen & Christensen (1959) established the genus *Cognettia* to accommodate five species that had earlier been placed in *Pachydrilus* Claparede, 1861 (today a junior synonym of *Lumbricillus* Orsted, 1844), or *Marionina* Michaelsen, 1890 (in Pfeffer, 1890) or *Enchytraeoides* Roule, 1888 (see Rota et al., 2008 for relevant parts of the complex history of enchytraeid taxonomy and nomenclature). The type species of *Cognettia*, *Pachydrilus sphagnetorum* Vejdovský, 1878, was originally described from a *Sphagnum* bog near Hirschberg (now Jelenia Gora), SW Poland. Ten years later, Michaelsen described another enchytraeid as *P. sphagnetorum* var. *glandulosus* Michaelsen, 1888, from Hamburg, Germany. Both forms (typical *sphagnetorum* and variety *glandulosus*) were transferred by Michaelsen (1889) to *Marionia* (later called *Marionina*). Shortly after this, Michaelsen (1900) considered *Marionina glandulosa* as a good species, and not as a part of *M. sphagnetorum*.

Subsequently, Friend (1913a) described a new species and genus from Derbyshire, England, as *Chamaedrilus chlorophilus*. He regarded this species as close to *Marionina sphagnetorum* and *M. glandulosa*, but also to *Buchholzia appendiculata* (Buchholz, 1863). The original description stated that the spermathecae of *Ch. chlorophilus* were entally attached to the oesophagus, a condition never observed in species of the group recognized as *Cognettia* today (see e.g. Nielsen & Christensen, 1959; Schmelz & Collado, 2010). Later, when transferring both *Marionina sphagnetorum* and *M. glandulosa* from *Marionina* to *Chamaedrilus*, Friend (1919) extended the diagnosis of the genus to include also species with free spermathecae; this paper, however, seems to have been overlooked by most later authors. Friend (1913b) also described *Henlea trisetosa* Friend, 1913, which according to Černosvitov (1937b) he later regarded as the same species as *Ch. chlorophilus*. In a revision of all enchytraeid genera, Welch (1920) claimed that it was impossible to distinguish *Chamaedrilus sensu* Friend (1913a) (i.e. not the extended genus *sensu* Friend, 1919) from *Marionina*. Moreover, both Delphy (1921), who included *Marionina* within *Pachydrilus*, and Černosvitov (1937b), who reinvestigated Friend’s types, regarded *Ch. chlorophilus* as synonymous to *Pachydrilus sphagnetorum*, without discussing the spermathecae-oesophagus connection. Černosvitov (1937b) also mentioned a seemingly unpublished species, ‘E. (*Enchytraeus*) bispermus Friend in lit.’ and concluded that it was identical with *P. sphagnetorum*.

When establishing *Cognettia*, Nielsen & Christensen (1959) did not mention *Chamaedrilus chlorophilus*, they only included the following five species in the genus: *C. sphagnetorum* (type species), *C. anomalala* (Černosvitov, 1928) [originally in *Enchytraeoides*], *C. cognettii* (Issel, 1905) [originally in *Marionina*], *C. glandulosa* and *C. paxi* (Moszyński, 1938) [originally in *Marionina*]. Chalupsky’s (1992), in a study of Swedish enchytraeids, recognized two morphotypes of *C. sphagnetorum* (as Form I and Form II) and an additional unnamed *Cognettia* sp. This last mentioned *Cognettia* sp. was later recognized and reported again from Sweden by Erseus et al. (2005).

*Cognettia anomalala* and *C. paxi* were synonymized with *C. sphagnetorum* by Schmelz & Collado (2010), who thereby broadened the concept of the latter taxon. Dumnicka (2010), on the other hand, regarded these three taxa as separate, in a study that also described *C. valeriae* Dumnicka, 2010 from the Italian Alps. More recently, Schmelz and Collado (2012) noted that *C. valeriae* falls within their definition of *C. sphagnetorum*. Also Chalupsky’s (1992) *Cognettia* sp. falls within this definition (Martinsson & Erseus, 2014).

Not only Friend’s (1919) early inclusion of *Marionina sphagnetorum* and *M. glandulosa* in *Chamaedrilus*, but also Černosvitov’s (1937b) proposed synonymy of *Chamaedrilus chlorophilus* with *M. sphagnetorum* were apparently overlooked by Nielsen and Christensen (1959), when they designated ‘*C. sphagnetorum* (Vejd.)’ as the type species for *Cognettia*. Under the assumption that Friend’s *Chamaedrilus chlorophilus* is closely related to *C. sphagnetorum*, Schmelz & Collado (2010) correctly pointed out that *Chamaedrilus* is a senior synonym to *Cognettia*.

However, Schmelz & Collado (2010) also suggested that an even older genus name had been established for a species likely to belong in the *Cognettia* assemblage. *Euenchytraeus* Bretscher, 1906 was erected for a Swiss alpine species, *Eu. bissetosus* Bretscher, 1906, with nephridia at septum 2/3, an unusual character for enchytraeids. The description was based on immature material and the reproductive systems were not described. This genus was later regarded as a part of *Marionina* by Černosvitov (1937a), who apparently doubted the presence of nephridia at septum 2/3, ’Ausserdem, können insofern Zweifel an der Richtigkeit der Beobachtung Bretschers aufkommen’ (Černosvitov, 1937a, p. 277).
**Euenchytraeus bisetosus** seems to have fallen by the wayside until Schmelz and Collado (2010) synonymized it with *Cognettia clareae* Bauer, 1993, a species also with nephridia at septum 2/3. A third species bearing head nephridia, the Siberian *C. piperi* Christensen and Dózsa-Farkas, 1999, has also been described.

**Materials and methods**

This study is based on parts of the collection analysed by Martinsson and Erzsé (2014), plus new specimens from northern and central Europe, and extant early type materials. Two syntypes of *Chamaedrilus chlorophilus* and a specimen of Friend's unpublished *E. bispermus* were borrowed from the Natural History Museum, London, UK (BMNH) (courtesy, Emma Sherlock), and a paratype of *Cognettia valeriae* was borrowed from the Institute of Nature Conservation, Polish Academy of Sciences, Krakow, Poland (INCPAS) (courtesy, Elzbieta Dumnicka). The type of *Enchytraeoides anomalus* (BMNH 1949.3.1.555) could not be found in the Natural History Museum, where it should be located (E. Sherlock, in lit.). The type localities of *Pachydrilus spagnetorum*, *Marionina paxi* and *Chamaedrilus chlorophilus* were revisited in 2013 by the first author in attempts to obtain fresh worms suitable for DNA-barcoding and morphological studies; unfortunately, only the search for *P. spagnetorum* was successful. Table 1 lists all examined specimens, with locality data and GenBank accession numbers for DNA-barcodes. We also provide an updated list (Table S1, see locality data and GenBank connection for the descriptions. The inclusion of both adult and juvenile worms likely increased the observed intraspecific variation. All measurements and observations were made on preserved and somewhat compressed animals. The material was studied under a compound microscope (Leitz Laborlux K), and sketches were drawn using a camera lucida. The sketches were then used as templates for producing digital illustrations with Adobe Photoshop.

As the posterior parts of the specimens have been used for DNA extraction, the size of the specimens (in preserved condition) are given as the length of the 20 anteriormost segments and the body width at segment XII. The measurements are given as the range followed by the mean ± 1 standard deviation.

The summarized data of distributions are based on our records as well as matches with records in BOLD (Barcoding of Life Data Systems, Ratnasingham & Hebert, 2007). Countries with BOLD records for which no material has been examined by us, are marked with ‘(BOLD)’ in the distribution sections of the descriptions. The Barcode Index Numbers (BIN) (Ratnasingham & Hebert, 2013) are given under Remarks, for respective species. The BIN system clusters sequences to produce operational taxonomic units that are assumed to closely correspond to species (http://www.boldsystems.org).

All new specimens, including the new types, are deposited in the Swedish Museum of Natural History (SMNH), Stockholm, Sweden, except one paratype of *Chamaedrilus chalupskyi* sp. nov. that is deposited in Museo Civico di Zoologia [Civic Museum of Zoology], Rome, Italy (MCZR); all COI barcodes (Table 1) are deposited in GenBank.

**Results**

All newly collected worms group into the four clusters within *Cognettia spagnetorum* s. lat. (below referred to as *Chamaedrilus spagnetorum* s. lat.) already found by Martinsson and Erzsé (2014) (Fig. 1). Unfortunately, no species of *Cognettia*/*Chamaedrilus* were found in Smisy, Derbyshire (England), the type locality of *Chamaedrilus chlorophilus*. In Králický Sněžník, Pardubický (Czech Republic), the type locality of *M. paxi*, two species within the *C. spagnetorum* complex were found, but neither of them fits the description by Moszyński (1938). At Jelenia Gora, Dolnośląskie (Poland), the type locality of *Pachydrilus spagnetorum*, three species of the *C. spagnetorum* complex were found, two of these fit the original description, and a neotype was designated from one of them (see below).

**On the status of Euenchytraeus Bretscher, 1906**

The presence of nephridia at septum 2/3 seems to be a synapomorphy for a small group of enchytraeids,
Table 1. List of material included in this study, with specimen identification numbers, voucher numbers, collection data, GPS coordinates, and GenBank accession numbers for COI barcodes. Specimens in bold indicate type specimens, and the letters in parentheses after the spm no. indicates type status, H = holotype, L = lectotype, N = neotype, P = paratype, PL = paralectotype. Accession numbers in bold are newly generated sequences. Locality data are given in the form of country, province, municipality and locality, GPS coordinates are given as decimal degrees. CZ = Czech Republic, NO = Norway, PL = Poland, SE = Sweden and SK = Slovakia.

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</table>

except those concerning the spermathaecae strongly suggest a close relationship with *Cognettia sphagnetorum* s. lat., as noted by Delphy (1921) and Černosvitov (1937b). In our re-examination of two syntypes of *Chamaedrilus chlorophilus* (whole-mounted on the same slide), whereof one is sexually mature, we were not able to conclude whether the spermathaecae are connected to the oesophagus or not. However, we observed parts of a spermatheca with an ampulla similar to that of a typical *C. sphagnetorum*, and in all other diagnostic traits we found the syntypes to be identical to the lineage referred to as *Cognettia sphagnetorum* Form I by Chalupský (1992) and as *Cognettia sphagnetorum* C by Martinsson & Erséus (2014). Therefore, this lineage is redescribed below as *Ch. chlorophilus*.

Martinsson and Erséus (2014) found this species (as *Cognettia sphagnetorum* C) to be nested within *Cognettia*, in fact as the sister group to *C. glandulosa* s. lat. Thus, it is clear that *Chamaedrilus* is a senior synonym of *Cognettia*. As a consequence, all the 16 species not above transferred from *Cognettia* to *Euenchytraeus* are now to be regarded as members of *Chamaedrilus*.

**Chamaedrilus** Friend, 1913

Type species. *Chamaedrilus chlorophilus* Friend, 1913
Other species. Chamaedrilus anomalus (Černovitov, 1928) comb. nov.; Ch. bisetosus (Christensen & Dózsa-Farkas, 1999) comb. nov.; Ch. chalupskyi sp. nov.; Ch. cognetti (Issel, 1905) comb. nov.; Ch. floridae (Healy, 1996) comb. nov.; Ch. glandulosus (Michaelson, 1888) [as already proposed by Friend, 1919]; Ch. hayachinensis (Nakamura, 2001) comb. nov.; Ch. hibernica (Healy, 1975) comb. nov.; Ch. lapponicus (Nurminen, 1965) comb. nov.; Ch. paxi (Moszyński, 1938) comb. nov.; Ch. pseudosphagnetorum sp. nov.; Ch. quadrosetosus (Christensen & Dózsa-Farkas, 1999) comb. nov.; Ch. sphagnetorum s. str. (Vejdovský, 1987) [as already proposed by Friend, 1919]; Ch. valeriae (Dunnicka, 2010) comb. nov.; Ch. zicsii (Dózsa-Farkas, 1989) comb. nov.

Etymology. According to Friend (1913a): 'Found in earth (Chamae) by the stump of a tree'.

Chamaedrilus sphagnetorum complex

Definition and diagnosis. The Ch. sphagnetorum complex is here defined as species of Chamaedrilus with the following features: at least three pairs of primary pharyngeal glands, sometimes with ventral lobes; no well-developed secondary glands; three chaetae in at least the ventral bundles; no bundles with enlarged chaetae; male pores shifted forward to segments VII–XI.

Morphology-based key to species of the Chamaedrilus sphagnetorum–complex

1. Dorsal blood vessel arising anterior to segment XVI. 2.
2. Dorsal blood vessel arising posterior to segment XVII. 5.

2. First pair of nephridia in septum 4/5; nephridia with efferent duct originating posteriorly on postseptale (Moszyński, 1938, fig. 146). Chamaedrilus paxi

- First pair of nephridia in or posterior to septum 7/8; nephridia with efferent duct originating anterior on postseptale, close to septum (e.g. Fig. 6). 3.

3. Pharyngeal glands 5 pairs, with ventral lobes in the 2 posteriormost pairs. Preclitellar lateral bundles with 2–3 chaetae. Chamaedrilus anomalus

- Pharyngeal glands (2–3)4(–5) pairs, ventral lobes usually absent, if present, only 1 pair. Preclitellar lateral bundles with 2 or 3 chaetae. 4.


- Most preclitellar lateral bundles with 3 chaetae. Pharyngeal glands usually (2–3)4(–5) pairs. Chamaedrilus sphagnetorum s. str. and Ch. pseudosphagnetorum sp. nov.

5. Lateral bundles in II with 2 chaetae, all other bundles with 3 chaetae. Pharyngeal glands (4–)5(–6) pairs, sometimes with ventral lobes in 1–2 pairs; anterior (2–)3(–4) pairs connected dorsally. Chamaedrilus chalupskyi sp. nov.

- Preclitellar lateral bundles, variable with 2 or 3 chaetae. Pharyngeal glands 5 pairs, with ventral lobes in 2–3 pairs; anterior 2 pairs connected dorsally. Chamaedrilus valeriae

No somatic (i.e. non-genital) character useful for separating Ch. sphagnetorum s. str. and Ch. pseudosphagnetorum was found by us. In the studied material, there are some differences in the reproductive system: Ch. sphagnetorum s. str. has its male pores in segment IX, whereas C. pseudosphagnetorum has its male pores in segment VIII. However, if a larger amount of sexually mature material is studied in the future, overlap in this character may be found. In our limited sample of specimens, there are also differences in the spermathecae: our mature individuals of Ch. sphagnetorum have more or less rudimentary spermathecae, while those of Ch. pseudosphagnetorum are more developed; this, however, could be due to the former worms not being fully mature. In any case, for a reliable separation between these two taxa, molecular methods seem to be necessary.

Fixation of the name Pachydrilus sphagnetorum Vejdovský, 1878 by neotype designation

Vejdovský’s (1878) original description of Pachydrilus sphagnetorum is brief, and no type material is known. As this is the type species of the genus Cognettia, and referred to as a commonly used model organism in soil biology, it is important that its name is fixed. Therefore a neotype designation is justified. Vejdovský’s original material was from a peat bog near Jelenia Gora in SW Poland. Samples from a wetland, outside Jelenia Gora, that seems to have been a peat bog, but today destroyed by peat harvesting, yielded three genetically identified species within the C. sphagnetorum complex (Table 1). The original description states that P. sphagnetorum has 3–5 chaetae per bundle, but no species of Chamaedrilus, as known today, has more than 4 chaetae per bundle; besides, in his 1879 monograph Vejdovský modified the statement to read: 3 chaetae in dorsal bundles and up to 4 in ventral ones. Chamaedrilus sphagnetorum as viewed in modern literature has only 2–3 chaetae per bundle, indicating that possibly more than one species were present in Vejdovský’s material. Of the three Chamaedrilus species found at Jelenia Gora, only two have 3 chaetae in all bundles, whereas the third species has only two chaetae in preclitellar lateral bundles, and therefore does not fit the original sphagnetorum description. We hereby select C. sphagnetorum A sensu Martinsson & Erséus (2014) to be
the one bearing the name *Ch. sphagnetorum* s. str. It has 3 chaetae per bundle throughout, and it also proved to represent the most common *Chamaedrilus* genotype cluster at the Jelenia Gora site, as well as in all our studied material of *Ch. sphagnetorum* s. lat. Specifically, we designate specimen SM87 (SMNH TYPE-8682) as the neotype of *Pachydrilus sphagnetorum* Vejdovský, 1878; other details are given below.

*Chamaedrilus sphagnetorum* (Vejdovský, 1878) sensu stricto (Figs 2–6)

*Pachydrilus sphagnetorum* Vejdovský, 1878: 304, partim.

*Pachydrilus sphagnetorum*; Vejdovský, 1879: 52, plate 13, figs 1–6, partim.

*Marionina sphagnetorum*; Beddard, 1895: 330, partim.

*Chamaedrilus sphagnetorum*; Friend, 1919: 174, partim.

*Enchytraeoides sphagnetorum*; Bülow, 1957: 85, figs 2–4, partim.

*Cognettia sphagnetorum*; Nielsen and Christensen, 1959: 42, figs 28–29, partim.


*Cognettia sphagnetorum* Form II; Chalupský, 1992: 142, fig. 10 B–C, partim.


*Cognettia sphagnetorum A*; Martinsson & Erséus, 2014.


**Type locality.** Poland: Dolnośląskie, Jelenia Gora, Cieplice (N50.8460, E15.6650). Old peat bog, now destroyed by peat harvesting.

**Additional material.** See Table 1. In total 31 specimens, of which one from Czech Republic, two from Norway, both almost mature, with not fully developed spermathecae, two from Poland and 25 from Sweden, of which one submature.

**Habitat and distribution.** Occurs usually in peaty, wet soils, at the edge of bogs and moors and in forests. Known from Czech Republic, the Netherlands (BOLD), Norway, Poland, Sweden and Scotland (BOLD). Probably
widespread in northern and central Europe, but has been confused with other species in the complex.

**Diagnosis.** Cannot be distinguished from *Chamaedrilus pseudosphagnetorum* sp. nov. by morphological characters, but it is separated from other species in the complex by the combination of 3 chaetae per bundle, (3)4(5) pairs of primary pharyngeal glands that are seldom fused dorsally, and rarely with ventral lobes.

**Description**

**External characters.** Size: length of 20 anteriormost segments 2.58–4.75, 3.03 ± 0.49 mm (n = 19); body width in XII 0.18–0.38, 0.26 ± 0.05 mm (n = 30). Chaetae sigmoid without nodulus, 50–80 μm long, chaetal formula 3–3:3–3; in sexually mature specimens, ventral chaetae missing in IX (segment bearing male pores). In the sexually maturing specimens examined clitellum undeveloped.

**Internal characters.** Brain (Fig. 5) strongly concave posteriorly, slightly concave anteriorly, 125–150 μm long, twice as long as broad. Pharyngeal glands (Fig. 2) (3–4) (–5) pairs, rarely the second pair is fused dorsally, 1–2 pairs occasionally with ventral lobes. Dorsal blood vessel arising in XI–XIII, rarely in X or XIV. First pair of nephridia present at 7/8–10/11; nephridia (Fig. 6) with efferent duct originating antero-ventrally, close to septum; anteseptale consisting of funnel only; postseptale elongate. Chloragogen cells 15–25 μm long. Coelomocytes finely granulated, round to oval, about 20 μm long.

Male genitalia (Fig. 3) paired. Sperm funnel about 210 μm long, 70 μm wide; collar 60–65 μm wide. Vas deferens simple, with several loops, 700 μm long, about 15–20 μm wide. Penial bulb about 70 μm wide, 60 μm long. Male pores in IX. Spermathecae (Fig. 4) paired; pores located slightly below lateral chaetae; duct smooth, 70 μm long, about 20 μm wide; ectal gland 50–70 μm in diameter; ampulla about 110 μm long, with spherical ectal enlargement 50 μm in diameter; spermatheca free, not attached to oesophagus. Spermathecae confined to V. The spermathecae were not fully developed in any of the studied specimens.

**Biology.** Seems to mainly reproduce asexually, mature specimens very rare. Specimens with regenerating heads and/or tails rare. Sexually maturing specimens were found in September (Norway), April (Sweden) and May (Norway).

**Remarks.** The two almost sexually mature specimens from Norway seem to have incompletely developed spermathecae.

*Chamaedilus sphagnetorum* s. str. is represented in BOLD by BIN: AAN1194.

*Chamaedrilus pseudosphagnetorum* sp. nov.

(Figs 7–11)

**Figs. 7–11. Chamaedrilus pseudosphagnetorum** sp. nov. **Fig. 7.** Anterior part of body, lateral view, indicating size, shape and number of pharyngeal glands. **Fig. 8.** Male genitalia, male pore in segment VIII. **Fig. 9.** Spermatheca. **Fig. 10.** Brain, dorsal view. **Fig. 11.** Nephridium at septum14/15, lateral view. Abbreviations: pb = penial bulb; sa = spermathecal ampulla; sd = spermathecal duct; sf = sperm funnel; sg = spermathecal gland; vd = vas deferens. Scale bars: Fig. 7, 100 μm; Figs 8–11, 50 μm.
**Pachydrilus sphagnetorum** Vejdovský, 1878: 304, partim.

*Pachydrilus sphagnetorum*; Vejdovský, 1879: 52, plate 8, figs 1–6, partim.

*Marionina sphagnetorum*; Beddard, 1895: 330, partim.

*Chamaedrilus sphagnetorum*; Friend, 1919: 174, partim.

*Enchytraeoides sphagnetorum*; Bülow, 1957: 85, figs 2–4, partim.

*Cognettia sphagnetorum*; Nielsen & Christensen, 1959: 42, figs 28–29, partim.


*Cognettia sphagnetorum* Form II; Chalupský, 1992: 142, fig. 10 B–C, partim.


*Cognettia sphagnetorum D*; Martinsson & Erssén, 2014.


**Type locality.** Sweden: Skåne, Vellinge, Skanörs Ljungs Nature Reserve (N55.4011, E12.8919), wet peaty soil in depression on heather moor.

**Paratypes.** SMNH TYPE-8686 (former SMNH133689), CE4023, mature, anterior part; SMNH TYPE-8687 (former SMNH133690), CE4024, mature, anterior part. Same collection data as for holotype.

**Additional material.** See Table 1. In total nine specimens, of which one from Czech Republic, two from Poland and six from Sweden, of which three (the Swedish type specimens) are mature.

**Habitat and distribution.** All studied specimens were collected in *Sphagnum* moss and heather moors. Known from Czech Republic, the Netherlands (BOLD), Poland, Spain (Galicia) (BOLD) and southern Sweden, but probably has a wider distribution in Central Europe.

**Etyymology.** The name refers to its close resemblance to *Ch. sphagnetorum* s. str.

**Diagnosis.** Cannot be distinguished from *Chamaedrilus sphagnetorum* s. str. on morphological characters, but they both are separated from other species in the complex by the combination of 3 chaetae per bundle, and 3–4(−5) pairs of primary pharyngeal glands that are not fused dorsally and lack ventral lobes.

**Description.**

**External characters.** Size: length of 20 anteriormost segments 2.33–3.63, 2.80 ± 0.56 mm (n = 7); body width in XII 0.22–0.39, 0.28 ± 0.06 mm (n = 8). Chaetae sigmoid without nodulus, 45–65 μm long, chaetal formula 3–3:3–3, in sexually mature specimens, chaetae missing in the segment bearing male pores (VIII). In sexually mature specimens examined clitellum undeveloped.

**Internal characters.** Brain (Fig. 10) concave posteriorly, slightly concave anteriorly, 130 μm long, about 60 μm wide. Pharyngeal glands (Fig. 7) 3−4(5) pairs, fifth pair rudimentary if present, glands not connected dorsally, no ventral lobes present. Dorsal blood vessel arising in X–XIV. First pair of nephridia present at 8/9–9/10; nephridia (Fig. 11) with efferent duct originating anteroventrally, close to septum; anteseptale consisting of funnel only; postseptale rounded to elongate. Coelomocytes finely granulated, round to oval, about 20 μm long.

Male genitalia (Fig. 8) paired. Sperm funnel oval, about 140 μm long, 50–70 μm wide, collar 45 μm wide. Vas deferens simple, at least 350 μm long, with several loops, about 6–8 μm wide. Penial bulb about 40 μm long, 50 μm wide. Male pores in VIII. Spermathecae (Fig. 9) paired; pores located slightly below lateral chaetae; duct smooth, 65–75 μm long, about 20 μm wide; ectal gland 45–55 μm in diameter; ampulla long with spherical ectal enlargement 30–40 μm in diameter, followed by a connecting duct, 190–300 μm long, 15–20 μm wide, and a tubular to oval ental chamber; ampulla not attached to oesophagus. Spermatheca confined to V or entering into VI.

**Biology.** Seems to mainly reproduce sexually. Specimens with regenerating heads and/or tails were not found. Sexually mature specimens found in May (Sweden).

**Remarks.** Can only be readily distinguished from *Chamaedrilus sphagnetorum* s. str. on molecular characters. This species has a large genetic variation, and the COI barcodes forms two distinct clusters (obvious in Fig. 1), about 8% different (uncorrected p-distance) from each other. However, Martinsson & Erssén (2014) found no nuclear genetic support for them being more than one species.

*Chamaedrilus pseudosphagnetorum* is represented in ‘BOLD’ by BIN: AAT9506, a sequence cluster that includes the holotype barcode.

**Chamaedrilus chalupskyi** sp. nov.

(Figs 12–15)

*Cognettia* sp.; Chalupský, 1992: 141–142, fig. 9.
Cognettia sp. sensu Chalupský, 1992; Erséus et al., 2005: 186.

*Cognettia sphagnetorum* B; Martinsson & Erséus, 2014.

**Holotype.** SMNH TYPE-8683 (former SMNH133645), CE11325, mature, anterior part. Leg. Ainara Achurra and Christer Erséus, Apr 07 2011; COI barcode, GenBank acc. no. KF672399.


Additional material. See Table 1. In total 16 specimens, of which one from Slovakia and 15 from Sweden, one mature, but with rudimentary male ducts (the holotype).

**Habitat and distribution.** Occurs in wet soils, but also in streams and around springs. Known from Finland (BOLD), Norway, Slovakia and Sweden. Seems to have a Boreo-Alpine distribution.

**Etymology.** Named for Josef Chalupský, who first recognized this form as a separate species, and in honour of his work with the north and central European enchytraeid fauna.

**Diagnosis.** This species can be identified using the following characters: 2 chaetae in lateral bundles in II; pharyngeal glands (4–5)(–6) pairs, 2–4 pairs fused dorsally, 1–2 pairs may have ventral lobes; dorsal blood vessel originates posterior to segment XVI; spermathecae with long duct (210 μm).

**Description**

**External characters.** Size: length of 20 anteriormost segments 3.13–4.06, 3.54 ± 0.31 mm (n = 13); body width in XII 0.25–0.41, 0.38 ± 0.05 mm (n = 13). Chaetae sigmoid without nodulus, 70–80 μm long in anterior
segments, slightly longer in posterior segments; chaetal formula 3–3:3–3, but with only 2 chaetae per lateral bundle in II; in sexually mature specimens, chaetae missing in the segment bearing male pores. Clitellum undeveloped.

**Internal characters.** Brain concave posteriorly, slightly concave anteriorly, 160 µm long, about 100 µm wide. Pharyngeal glands (Fig. 12), (4–)5(–6) pairs, sixth pair rudimentary if present, 2–4 anteriormost pairs fused dorsally, 1–2 pairs may have ventral lobes. Dorsal blood vessel arising in XVII–XXVI. First pair of nephridia present at 9/10–11/12; nephridia (Fig. 15) with efferent duct originating antero-ventrally, close to septum; anteseptale consisting of funnel only; postseptale elongate. Chloragogen cells 20–30 µm long. Coelomocytes finely granulated, usually oval, about 30 µm long, concentrated to posterior part of body.

Male genitalia (Fig. 13) paired, but appearing rudimentary, despite the fact that mature spermatozoa are gathered at the inner end of the sperm funnel; sperm funnel small, rounded, 40 µm long, 45 µm wide, collar 10–15 µm wide. Vas deferens simple, with very few loops and only 220–240 µm long; proximal part about 15 µm wide, distal part about 6 µm wide. Penial bulb undeveloped. Male pores in XI. Spermathecae (Fig. 14) paired; pores located slightly below lateral chaetae; duct smooth, 210 µm long, about 15–20 µm wide; ectal gland 40 µm in diameter; ampulla with spherical ectal enlargement 30–40 µm in diameter, followed by a rather short tube connecting to a tubular to spherical ental chamber; ampulla not attached to oesophagus. Spermathecae confined to V or entering into VI.

**Biology.** Main mode of reproduction seems to be by fragmentation. Specimens with regenerating heads and/or tails common. Sexually mature specimens rare and found in April (Sweden).

**Remarks.** When collecting specimens, we noted that this species is generally longer than typical of the other members of the *Ch. sphagnetorum* complex. In Chalupský’s (1992) description the size is given as 20–30 mm long with 85 segments in an adult, and 65–75 segments in unfragmented juveniles. In our only mature individual the male genitalia appear rudimentary and show different proportions than in Chalupský’s description; according to the latter the sperm funnel is 90–100 m wide and 5–6 times longer than wide. Chalupský stated that the male pores were located in segment X in Swedish specimens, but varied between IX–XI in material from Czechoslovakia.

*Chamaedrilus chalupskyi* (represented in ‘BOLD’ by BIN: AAT8926).

*Chamaedrilus chlorophilus* Friend, 1913

(Figs 16–21)

*Chamaedrilus chlorophilus* Friend, 1913: 260, figs 22–23.

*Chamaedrilus chlorophilus*; Černosvitov, 1937b: 205.

**Cognettia sphagnetorum** Form I; Chalupský, *1992: 142*, fig. 10 A.


**Cognettia sphagnetorum** C; Martinsson & Erséus, *2014.*

**Lectotype.** BMNH 1949.3.1.32, mature, whole mounted. Leg. Hilderic Friend, Nov 23 1912. (NOTE: there are two specimens on the slide, the mature, right, specimen is here designated as the lectotype.)

**Parallectotype.** BMNH 1949.3.1.32, immature, whole-mounted together with the lectotype as explained above.

**Type locality.** England: Derbyshire, Ashby-de-la-Zouch, Smisby (N52.76 W1.49).

**Additional material.** See Table 1. In total 23 specimens (two from England, one from Norway, two from Poland and 18 from Sweden), of which three are mature.

**Habitat and distribution.** Occurs in coniferous forests, in soil, peat and needle litter. Seems less moisture dependent than the other species in the complex. Known from England, Finland (BOLD), Germany (BOLD), the Netherlands (BOLD), Norway, Poland, Spain (Galicia) (BOLD) and Sweden.

**Etymology.** Named because of 'the intestine often coloured green or yellow by the living algae on which it feeds' (Friend, 1913a).

**Diagnosis.** Can easily be identified by the combination of only 2 chaetae in precitellar lateral bundles, 3 chaetae in other bundles, (3)4(5) pairs of primary pharyngeal glands, with ventral lobes absent.

**Description**

**External characters.** Size: length of 20 anteriormost segments 1.61–3.17, 2.36 ± 0.43 mm (n = 11); body width in XII 0.18–0.36, 0.26 ± 0.06 mm (n = 18). Chaetae sigmoid without nodulus, 50–65 μm long; chaetal formula 2–3:3–3, rarely 3 chaetae in some precitellar lateral bundles; in sexually mature specimens, either chaetae missing completely in segment bearing male pores, or only ventral chaetae missing in this segment. Clitellum in IX–X when developed.

**Internal characters.** Brain (Fig. 20) strongly concave posteriorly, slightly concave anteriorly, 140 μm long, twice as long as broad. Pharyngeal glands (Fig. 16) (3–)4 (–)5 pairs, not connected dorsally, no ventral lobes present. Dorsal blood vessel arising in IX–XI, rarely in XIV. First pair of nephridia present at 8/9–9/10; nephridia (Fig. 21) with efferent duct originating antero-ventrally, close to septum; anteseptale consisting of funnel only; postseptale rounded to elongate. Chloragogen cells 25–30 μm long. Coelomocytes finely granulated, round to oval, about 20 μm long.

Male genitalia (Fig. 17) paired. Sperm funnel (Fig. 18) oval, about 130 μm long, 70 μm wide; collar 40 μm wide. Vas deferens simple, with several loops, at least 420 μm long, about 7 μm broad. Penial bulb about 30 μm long, 40 μm wide. Male pores in VIII–IX (see Remarks). An internal oval bulb-like structure (function unknown), about 50 μm long, present medially in the segment bearing the male openings, anterior to pores. Spermathecae (Fig. 19) paired; pores located slightly above ventral chaetae; duct smooth, 40–130 μm long, about 15–20 μm wide; ectal gland 40–50 μm in diameter; ampulla with spherical ectal enlargement 30–40 μm in diameter, followed by duct connecting to a spherical ental chamber, with a more or less well developed secondary chamber; ampulla not attached to oesophagus. Spermathecae entering into VI.

**Biology.** Main mode of reproduction seems to be by fragmentation. Specimens with regenerating heads and/or tails common. Sexually mature specimens rare and found in May and July (Sweden).

**Remarks.** The lectotype (selected by us) and a second specimen (parallectotype) on the same slide were viewed as part of the original type material by Černosvitov (*1937b*). The slide bears the date ‘31.V.13’, and if this refers to when the two specimens were collected, they may not be part of the first discovered material, but Černosvitov was in a better position than us to judge if these specimens are syntypes, and therefore we designate the only sexually mature specimen of them as the lectotype.

The bulb-like structure anterior to the male pores in the description above is the same structure as the single submedian supernumerary bulb mentioned by Nielsen and Christensen (*1959, p. 43*). As noted by Schmelz & Collado (*2010*), this is the only species in the complex where it is found. Similar bulbs have been reported in at least two other enchytraeid species, viz. Marionina vesiculata Nielsen & Christensen, *1959* and Globulidrilus helgei Christensen & Dózsa-Farkas, *2012*. The function of these bulbs, which may not be homologous structures, is unknown, but they probably play a role during copulation.

In our own, newly collected material, one specimen (CE1041) has two sets of male ducts, one with the pores in VIII and the other with the pores in IX. The other two
sexually mature specimens have only one pair of male ducts, with pores in IX.

This species is represented in 'BOLD' by BIN: AAT8936.

**Comparison with the South European Chamaedrilus valeriae (Dumnicka, 2010) comb. nov.**

**Material studied.** Paratype 'HIGHEST 19/09/00 NB2bis Q1' 1 whole-mounted mature individual.

**Remarks.** Chamaedrilus valeriae was described from the Italian Alps, and it differs from other species within the Ch. sphagnetorum complex by the number of primary pharyngeal glands and ventral lobes, the chaetal formula, shape and size of spermathecae and the position of the male pores (Dumnicka, 2010). Chamaedrilus valeriae shares many characters with Ch. chalupskyi. However, Ch. chalupskyi is a larger species, 20–30 mm long, with 65–85 segments (Chalupsky, 1992), whereas the length of Ch. valeriae is 12–15 mm, with 49–52 segments (Dumnicka, 2010), which is within the range of Ch. sphagnetorum s. lat. given in the literature (Nielsen & Christensen, 1959; Rota, 1995; Schmelz & Collado, 2010). In the original description it is stated that Ch. valeriae has 5 pairs of primary pharyngeal glands, of which the 2 anteriormost pairs are fused dorsally, and ventral lobes are said to be present in 2 segments, VII and VIII. However, in the specimen studied by us ventral lobes are present in 3 segments (VI–VIII). In the north European species in the complex, such lobes are generally absent, only rarely found in Ch. chalupskyi. Moreover, in the paratype studied, the precitellar lateral bundles varyably contain 2 or 3 chaetae, i.e. the bundles contain 2 chaetae in 3 segments and 3 chaetae in 4 segments; and lateral chaetae are missing in IX, as well as in X where the male pores are located. The dorsal blood vessel, not mentioned by Dumnicka, originates in segment XXII in the specimen seen by us. The spermatheca is of the same type as in Ch. chalupskyi, with a long duct and an ampulla with an ectal enlargement followed by a connecting tube that ends in an ental spherical enlargement. We confirm the absence of nephridia in precitellar segments.

Unfortunately, there is no COI barcode available for Ch. valeriae. The species is only known from the Noce Bianco Stream in the Rhaetian Alps, Trentino, Italy.

To summarize, Ch. valeriae appears to be similar to Ch. chalupskyi. For instance, both these taxa have longer spermathecal ducts, and their dorsal blood vessel originates further back than in the other north European species. On the other hand, Ch. chalupskyi is the largest species of them all, whereas Ch. valeriae is a smaller species, of the same size as the other species in the complex. Moreover, the male genitalia of Ch. valeriae are similar to those in the other species, whereas Ch. chalupskyi seems to have simpler (possibly rudimentary) male ducts. Finally, precitellar segments with a mixture of bichaetal and trichaetal lateral bundles are not seen in any of the north European species in the complex. Based on this, we conclude that Ch. valeriae is a valid species, distinct from other species of Chamaedrilus.

**Notes on ‘E. bispermus Friend in lit.’ nom. nud.**

**Material studied.** BMNH 1949.3.1.34 Marionina sphagnetorum Vejd. [E. bispermus Friend in lit.] Netherhall, Derbyshire, Leg. Hilderic Friend, one mature specimen, longitudinally sectioned.

**Remarks.** As noted by Černosvitov (1937b), this specimen falls within the Ch. sphagnetorum complex. The spermathecae are as in the other species of the complex. Due to the condition of the sections it is hard to determine the position of the male pores, but they seem to be in segment VIII or IX, and the chaetae are 3 in all bundles observed. On the basis of the above-mentioned characters, we conclude that this specimen belongs to either Ch. sphagnetorum s. str. or Ch. pseudosphagnetorum. The name E. bispermus was mentioned by Černosvitov (1937b), who referred it to Friend in lit., but it has never been published with a description and does not meet the conditions stated by ICZN (1999, §12 & 13). It is therefore unavailable and should be treated as a nomen nudum.

**Discussion**

**Generic taxonomy of the species previously placed in Cognettia**

In this work we have revised the generic taxonomy of the species previously placed in Cognettia. Three species have been referred to Euenchytraeus, and Chamaedrilus has been found to be a senior synonym of Cognettia, therefore the remaining species should be attributed to Chamaedrilus. An ambition of our revision has been to make the taxonomy of this enchytraeid group more in line with the International Code of Zoological Nomenclature (ICZN, 1999). As often noted (e.g. Brinkhurst & Jamieson, 1971) and by their own admission, Nielsen and Christensen (1959: p. 10) did not always formally follow the rules of the Code. Thus, in spite of all good efforts and merits, their critical revision of Enchytraeidae left the genus-level taxonomy problematic and largely typological (see e.g. Rota et al., 2008). However, using phylogenetic methods to recognize and delimit monophyletic groups based on common descent, will hopefully alleviate some of the problems. Surely this must be done together with
re-evaluation of earlier descriptions and type material, to avoid the introduction of new errors and confusion.

Revision of the Ch. sphagnetorum complex

The occurrence of cryptic species is a common and widespread phenomenon (Bickford et al., 2007; Pfenninger & Schwengk, 2007), and not the least among annelid worms (Erséus & Gustafsson, 2009; Nygren, 2014). However, once cryptic species have been detected on the basis of molecular data, morphological support for the species boundaries can often be found (Blanquer & Uriz, 2008). In this study, morphological features support three out of the four lineages suggested to be separate species by the molecular data (Martinsson & Erséus, 2014). This shows the necessity of incorporating DNA also in more classical taxonomic work, both as a more solid base for taxonomic decisions (species delimitation), and for aiding the identification of species; for other clitellate examples, see e.g. Achurra and Erséus (2013); Dózza-Farkas et al. (2012); James et al. (2010); Martinsson, Timm et al. (2013). We communicate about biological organisms using names, and the taxonomical information embedded in them. Therefore it is also important that DNA-barcoding studies (i.e. using COI), which suggest more species than previously known in a studied group, are followed by not only solid molecular studies (i.e. including also nuclear markers), but also by thorough, more classical taxonomical work, describing and formally naming the discovered species (see e.g. Jörger & Schrödl, 2013; Kadereit et al., 2013; Palid & De la Riva, 2007). When molecular and morphological data are used together they reinforce each other, and strengthen the taxonomical hypothesis in a taxonomical feedback loop (Page et al., 2005).

The genetic variation within the species studied here is mostly low, with the exception of Ch. pseudosphagnetorum, in which there are two distinct clusters of mitochondrial COI sequences, separated by an uncorrected p-distance of about 8% (Martinsson & Erséus, 2014). High intraspecific variation in mitochondrial genes has been found within several other clitellate species (see e.g. Achurra & Erséus, 2013; Martinsson et al., 2013; Torres-Leguizamon et al., 2012). This impinges on the discriminating power of DNA-barcoding (using COI), as it may result in an overestimation of the number of species within a group (Dasmahapatra et al., 2010).

By integrating molecular and morphological data, we found four species belonging to the Chamaedrilus sphagnetorum complex in northern Europe. These findings verify Chalupsksý’s (1992) division of Ch. sphagnetorum into two forms. His form I proved to be identical to Ch. chlorophilus and is redescribed, whereas his form II constitutes two morphologically indistinguishable species, Ch. sphagnetorum s. str. and Ch. pseudosphagnetorum. We have also formally described and named his Cognettia sp. as a distinct new species, Chamaedrilus chalupskyi. However, morphology is not enough for the separation of all species in the Chamaedrilus sphagnetorum complex. In particular, there are no morphological characters that clearly distinguish Ch. sphagnetorum s. str. from Ch. pseudosphagnetorum, and thus molecular methods are necessary for their identification. The features most reliable for identification of the other Chamaedrilus species in the complex seem to be the patterns of the chaetae and, to some extent, the pharyngeal glands. Even if genital features are generally found to provide great discriminating power in enchytraeid taxonomy, they are of limited practical use in this case, not only because mature specimens of these species are rare, but also because fully developed spermathecae and male ducts appear very similar in them. Additional material of Chamaedrilus representing a larger geographic range might enable a deeper assessment of the intra- and interspecific morphological variation in the genus, but this must be studied in parallel with molecular data.

We provide a key, to facilitate morphological identification of the species within the Ch. sphagnetorum complex. However, the key is tentative, and should be used with caution. Moreover, it is possible that further cryptic species will be found, within any of the morphospecies described in this work. In addition to the taxa treated in this study, at least two more species fall within the definition of the Ch. sphagnetorum complex, viz. Ch. anomalus and Ch. paxi, both of which show distinctive patterns of pharyngeal glands, chaetal formulae and spermathecal morphologies, plus the male pores located in segment X. According to the original description, Ch. paxi further differs from other species of Chamaedrilus by having nphridia with the efferent duct originating posterior on the postseptale.

Surprisingly, in the species phylogeny of north European Cognettia presented by Martinsson and Erséus (2014, Fig. 4), Ch. sphagnetorum and Ch. pseudosphagnetorum are not sister taxa, despite the fact that they are virtually identical morphologically. Chamaedrilus pseudosphagnetorum was instead found to be the sister to Ch. laponicus Nurminen, 1965. However, these three species do form a well-supported clade, whereas Ch. chalupskyi and Ch. chlorophilus are more closely related to Ch. glandulosus s. lat. than to the other members of the sphagnetorum complex. It is noteworthy that Ch. chlorophilus has the same chaetal formula as Ch. glandulosus, with two chaetae in all lateral preclitellar bundles, while Ch. chalupskyi has two chaetae only in the lateral bundles of II. Chamaedrilus chlorophilus, Ch. sphagnetorum and Ch. pseudosphagnetorum, on the other hand, share their chaetal formula with Ch. laponicus, having three chaetae in all bundles. The chaetal pattern thus seems to be a phylogenetically important character within Chamaedrilus, whereas other characters, such as the length ratio between the spermathecal duct and ampulla, and the pattern of...
pharyngeal glands, do not seem to follow the phylogeny. The spermathecal duct is short in *Ch. pseudosphagnetorum*, *Ch. lapponicus* and *Ch. chlorophilus*, whereas it is long in *Ch. glandulosus* and *Ch. cognettii*, and it seems to be intermediate in *Ch. chalupskyi*. Similarly, for the pattern of pharyngeal glands, a dorsal connection is present in *Ch. cognettii* and *Ch. chalupskyi*, but absent in *Ch. glandulosus*, *Ch. chlorophilus* and *Ch. pseudosphagnetorum*, and rarely present in *Ch. sphagnetorum*.

**Conclusion**

To conclude, *Cognettia* is here invalided and proposed to be divided into two genera. The majority of the species including *C. sphagnetorum* are now placed in *Chamaedrilus*, but at the same time, this common and well known taxon has proven to be a diverse group of enchytraeids, containing at least seven species, only five of which are treated here. Three of the four north European species are distributed widely in Scandinavia, whereas the fourth (*Ch. pseudosphagnetorum*) seems to have its northern distribution limit across southern Scandinavia. Morphological characters are aiding the identification of most species, but cannot be used for the separation of *Ch. sphagnetorum* s. str. and *Ch. pseudosphagnetorum*. Our study thus underlines the importance of using molecular identification in enchytraeid taxonomy.

**Supplemental data**

Supplemental data for this article can be accessed here.

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