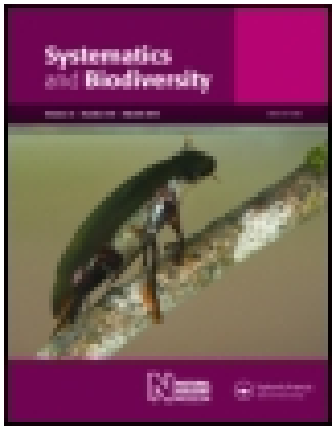

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Revision of Cognettia (Clitellata, Enchytraeidae): re-establishment of Chamaedrilus and description of cryptic species in the sphagnetorum complex

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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 Dózsa-Farkas, 1999, are transferred to *Euenchytraeus*, together with its type *Eu. bisetosus* 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. chlorophilus* Friend, 1913, as well as the type species of *Cognettia*, *Ch. sphagnetorum* s. str. are redescribed, and a neotype is designated for the latter; and the cryptic species *Ch. pseudosphagnetorum* 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.

http://zoobank.org/urn:lsid:zoobank.org:pub:F840CD92-F784-429E-B4BF-3E61F6632A8D

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. Abrahamsen, 1990; Briones et al., 1998; Haimi & Siira-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, 1913a 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*

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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 & Erséus, 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* Claparède, 1861 (today a junior synonym of *Lumbricillus* Örsted, 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. anomala* (Černosvitov, 1928) [originally in *Enchytraeoides*], *C. cognettii* (Issel, 1905) [originally in *Marionina*], *C. glandulosa* and *C. paxi* (Moszyński, 1938) [originally in *Marionina*]. Chalupský (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 Erséus et al. (2005).

Cognettia anomala 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 Chalupský's (1992) *Cognettia* sp. falls within this definition (Martinsson & Erséus, 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. bisetosus* 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 clarae* 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 Erséus (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, Elżbieta Dumnicka). The type of *Enchytraeoides anomala* (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 sphagnetorum, 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. sphagnetorum* 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 online supplemental material, which is available from the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2014.986555) of the material used in Martinsson and Erséus, 2014, with new nomenclature based on this study and some errors corrected.

Newly collected specimens were DNA-barcoded using the mitochondrial cytochrome c oxidase subunit 1 (COI), as described by Martinsson & Erséus (2014); DNA was extracted from a few posterior-most segments, while the rest of each worm was stained with paracarmine and permanently mounted in Canada balsam on slides (see Erséus, 1994), and used for morphological studies. All new worms were matched with COI sequences of *Cognettia sphagnetorum* s. lat. from Martinsson & Erséus (2014), and the matching was visualized by a NeighbourNet network drawn in SplitsTree 4 (Huson & Bryant, 2006).

Unless otherwise mentioned in the descriptions, the morphological information is based on the studied material only, as the four taxa specifically treated in this paper have all been previously classified as one, variable species. As sexually mature specimens are rarely found in these species, all specimens listed in Table 1 were used as the basis 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 sphagnetorum* s. lat. (below referred to as *Chamaedrilus sphagnetorum* s. lat.) already found by Martinsson and Erséus (2014) (Fig. 1). Unfortunately, no species of *Cognettia*/*Chamaedrilus* were found in Smisby, 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. sphagnetorum* complex were found, but neither of them fits the description by Moszyński (1938). At Jelenia Gora, Dolnoślaskie (Poland), the type locality of *Pachydrilus sphagnetorum*, three species of the *C. sphagnetorum* 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.

Species	Spm. No.	Museum voucher no.	Sexual maturity	Collection locality	Coordinates		Leg.	Coll. date	Barcode Acc. no
					N	E			
Ch. sphagnetorum	CE11317	SMNH133623	immature	SE, Närke, Hallsberg, Östansjö	59.0389	15.0186	A. Achurra & C. Erséus	Apr 07 2011	KF672381
Ch. sphagnetorum	CE2337	SMNH133624	immature	SE, Skåne, Sjöbo, Vallarum	55.7371	13.8556	A. Ansebo	May 13 2007	KF672382
Ch. sphagnetorum	CE2339	SMNH133625	immature	SE, Skåne, Sjöbo, Vallarum	55.7371	13.8556	A. Ansebo	May 13 2007	JN260041
Ch. sphagnetorum	CE3890	SMNH133626	submature	SE, Västergötland, Lerum, Aspenäs	57.7761	12.2411	C. Erséus & K. Lundin	Apr 28 2008	KF672383
Ch. sphagnetorum	CE3891	SMNH133627	immature	SE, Västergötland, Lerum, Aspenäs	57.7761	12.2411	C. Erséus & K. Lundin	Apr 28 2008	KF672384
Ch. sphagnetorum	CE3969	SMNH133628	immature	SE, Halland, Kungsbacka, Särö Västerskog	57.505	11.926	P. De Wit	Dec 07 2007	KF672385
Ch. sphagnetorum	CE3970	SMNH133629	immature	SE, Halland, Kungsbacka, Särö Västerskog	57.505	11.926	P. De Wit	Dec 07 2007	KF672386
Ch. sphagnetorum	CE3971	SMNH133630	immature	SE, Halland, Kungsbacka, Särö Västerskog	57.505	11.926	P. De Wit	Dec 07 2007	KF672387
Ch. sphagnetorum	CE3980	SMNH133631	immature	SE, Halland, Kungsbacka, Särö Västerskog	57.505	11.926	P. De Wit	Dec 07 2007	KF672388
Ch. sphagnetorum	CE3981	SMNH133632	immature	SE, Halland, Kungsbacka, Särö Västerskog	57.505	11.926	P. De Wit	Dec 07 2007	KF672389
Ch. sphagnetorum	CE4056	SMNH133633	immature	SE, Blekinge, Olofström, Halen nature reserve	56.2842	14.4911	C. Erséus	Jun 01 2008	KF672390
Ch. sphagnetorum	CE4061	SMNH133634	immature	SE, Småland, Gislaved, 1 km W Bosebo church	57.3019	13.3483	C. Erséus	Jun 01 2006	KF672391
Ch. sphagnetorum	CE4062	SMNH133635	immature	SE, Småland, Gislaved, 1 km W Bosebo church	57.3019	13.3483	C. Erséus	Jun 01 2006	KF672392
Ch. sphagnetorum	CE4063	SMNH133636	immature	SE, Småland, Gislaved, 1 km W Bosebo church	57.3019	13.3483	C. Erséus	Jun 01 2006	KF672393
Ch. sphagnetorum	CE6669	SMNH133637	immature	SE, Västergötland, Vårgårda, Fly	57.9972	12.5873	C. Erséus	Jun 08 2009	KF672394
Ch. sphagnetorum	CE6670	SMNH133638	immature	SE, Västergötland, Vårgårda, Fly	57.9972	12.5873	C. Erséus	Jun 08 2009	KF672395
Ch. sphagnetorum	CE6672	SMNH133639	immature	SE, Västergötland, Vårgårda, Fly	57.9972	12.5873	C. Erséus	Jun 08 2009	KF672396
Ch. sphagnetorum	CE9482	SMNH133640	immature	SE, Norrbotten, Överkalix, Grelsbyn	66.3039	22.8388	C. Erséus	Jun 11 2010	KF672398

(*continued*)

Table 1. (*Continued*)

Species	Spm. No.	Museum voucher no.	Sexual maturity	Collection locality	Coordinates		Leg.	Coll. date	Barcode Acc. no
Ch. sphagnetorum	CE9483	SMNH133641	immature	SE, Norrbotten, Överkalix, Grelsbyn	66.3039	22.8388	C. Erséus	Jun 11 2010	JN260280
Ch. sphagnetorum	CE9487	SMNH133642	immature	SE, Norrbotten, Överkalix, Grelsbyn	66.3039	22.8388	C. Erséus	Jun 11 2010	JN260186
Ch. sphagnetorum	CE9492	SMNH133643	immature	SE, Norrbotten, Överkalix, Grelsbyn	66.3039	22.8388	C. Erséus	Jun 11 2010	JN260214
Ch. sphagnetorum	CE9605	SMNH133644	immature	SE, Jämtland, Strömsund, Leipikvattnet Lake	64.9325	14.2113	C. Erséus	Jun 16 2010	KF672427
Ch. sphagnetorum	SM8	SMNH139131	immature	SE, Västergötland, Göteborg, Medicinareberget	57.6890	11.9560	S. Martinsson	Feb 2012	**KM874811**
Ch. sphagnetorum	SM10	SMNH139132	immature	SE, Västergötland, Göteborg, Medicinareberget	57.6890	11.9560	S. Martinsson	Feb 2012	**KM874812**
Ch. sphagnetorum	SM37	SMNH139133	immature	SE, Öland, Borgholm, Böda kronopark	57.2700	16.9820	S. Martinsson	Oct 15 2012	**KM874813**
Ch. sphagnetorum	SM40	SMNH139134	immature	SE, Öland, Borgholm, Böda kronopark	57.2700	16.9820	S. Martinsson	Oct 15 2012	**KM874814**
Ch. sphagnetorum	SM84	SMNH139135	immature	PL, Dolnoślaskie, Jelenia Gora, Cieplice	50.8460	15.6650	K. Elliott & S. Martinsson	Jun 14 2013	**KM874815**
Ch. sphagnetorum	**SM87 (N)**	**SMNH TYPE -8682**	immature	PL, Dolnoślaskie, Jelenia Gora, Cieplice	50.8460	15.6650	K. Elliott & S. Martinsson	Jun 14 2013	**KM874818**
Ch. sphagnetorum	SM125	SMNH139136	immature	CZ, Pardubický, Králický Sněžník	50.1499	16.8624	K. Elliott & S. Martinsson	Jun 15 2013	**KM874810**
Ch. sphagnetorum	CE18919	SMNH139137	mature	NO, Telemark, Hjartdal, Kovstulheia	59.8182	8.7222	C. Erséus & B. Williams	13 Jun 2013	**KM874817**
Ch. sphagnetorum	CE21061	SMNH139138	mature	NO, Rogaland, Suldal, Suldalsvatn Lake	59.6220	06.7777	C Erséus & M Eriksson	13 May 2014	**KM874816**
Ch. pseudosphagnetorum	CE3973	SMNH133687	immature	SE, Halland, Kungsbacka, Särö Västerskog	57.505	11.926	P. De Wit	Dec 07 2007	KF672417
Ch. pseudosphagnetorum	CE3974	SMNH133688	immature	SE, Halland, Kungsbacka, Särö Västerskog	57.505	11.926	P. De Wit	Dec 07 2007	KF672418
Ch. pseudosphagnetorum	**CE4023 (P)**	**SMNH TYPE-8686[1]**	mature	SE, Skåne, Vellinge, Skanörs Ljung	55.4011	12.8919	C. Erséus	May 03 2008	KF672419
Ch. pseudosphagnetorum	**CE4024 (P)**	**SMNH TYPE-8687[2]**	mature	SE, Skåne, Vellinge, Skanörs Ljung	55.4011	12.8919	C. Erséus	May 03 2008	KF672420
Ch. pseudosphagnetorum	**CE4025 (H)**	**SMNH TYPE-8685[3]**	mature	SE, Skåne, Vellinge, Skanörs Ljung	55.4011	12.8919	C. Erséus	May 03 2008	KF672421
Ch. pseudosphagnetorum	CE4055	SMNH133692	immature	SE, Blekinge, Olofström, Halen nature reserve	56.2842	14.4911	C. Erséus	Jun 01 2008	KF672422

(*continued*)

Table 1. (*Continued*)

Species	Spm. No.	Museum voucher no.	Sexual maturity	Collection locality	Coordinates		Leg.	Coll. date	Barcode Acc. no
Ch. pseudosphagnetorum	SM91	SMNH139143	immature	PL, Dolnośląskie, Jelenia Gora, Cieplice	50.8460	15.6650	K. Elliott & S. Martinsson	Jun 14 2013	**KM874823**
Ch. pseudosphagnetorum	SM93	SMNH139144	immature	PL, Dolnośląskie, Jelenia Gora, Cieplice	50.8460	15.6650	K. Elliott & S. Martinsson	Jun 14 2013	**KM874825**
Ch. pseudosphagnetorum	SM176	SMNH139145	immature	CZ, Pardubický, Králický Sněžník	50.1499	16.8624	K. Elliott & S. Martinsson	Jun 15 2013	**KM874824**
Ch. chalupskyi	**CE11325 (H)**	**SMNH TYPE-8683**[4]	mature	SE, Närke, Hallsberg, Östansjö	59.0392	15.0189	A. Achurra & C. Erséus	Apr 07 2011	KF672399
Ch. chalupskyi	CE1719	SMNH133646	immature	SE, Västergötland, Göteborg, Torslanda	57.7432	11.8135	D. Gustafsson	Apr 19 2006	KF672400
Ch. chalupskyi	CE1720	SMNH133647	immature	SE, Västergötland, Göteborg, Torslanda	57.7432	11.8135	D. Gustafsson	Apr 19 2006	KF672401
Ch. chalupskyi	CE2055	SMNH133648[5]	immature	SE, Västergötland, Göteborg, Torslanda	57.7573	11.8585	D. Gustafsson	Oct 09 2006	KF672402
Ch. chalupskyi	**CE3860 (P)**	**SMNH TYPE-8684**[6]	immature	SE, Västergötland, Lerum, Aspenäs	57.7761	12.2411	C. Erséus & K. Lundin	Apr 28 2008	KF672403
Ch. chalupskyi	CE4035	SMNH133652	immature	SE, Skåne, Ystad, Nyvångsskogen	55.5606	13.8239	C. Erséus	May 31 2008	KF672406
Ch. chalupskyi	CE4036	SMNH133653	immature	SE, Skåne, Ystad, Nyvångsskogen	55.5606	13.8239	C. Erséus	May 31 2008	KF672407
Ch. chalupskyi	CE6153	SMNH133655	immature	SE, Bohuslän, Lysekil, Ingalsröd	58.4338	11.581	C. Erséus, A. Ansebo & M. Johansson	May 27 2009	JN260067
Ch. chalupskyi	CE7712	SMNH133657	immature	SE, Västergötland, Göteborg, S. Guldheden	57.6827	11.9708	C. Erséus, A. Bär & E. Lindqvist,	May 28 2010	JN260116
Ch. chalupskyi	CE7714	SMNH133659	immature	SE, Västergötland, Göteborg, S. Guldheden	57.6827	11.9708	C. Erséus, A. Bär & E. Lindqvist	May 28 2010	JN260273
Ch. chalupskyi	**CE823 (P)**	**MCZR0188**	immature	SE, Västergötland, Götene, Hällekis	58.6189	13.4266	E. Rota & C. Erséus	May 26 2004	KF672410
Ch. chalupskyi	CE8823	SMNH133660	immature	SK, Javorníky Mountains, Štiavnik spring	49.3175	18.4211	J. Schenkova	May 03 2010	JN260151
Ch. chalupskyi	CE9381	SMNH133661	immature	SE, Medelpad, Timrå, Söråker	62.5235	17.4782	C. Erséus	Jun 08 2010	JN260276
Ch. chalupskyi	CE9411	SMNH133663	immature	SE, Ångermanland, Nordmaling, Långed	63.6038	19.6624	C. Erséus	Jun 09 2010	JN260170
Ch. chalupskyi	CE9641	SMNH133665	immature	SE, Gotland, Gotland, Roma	57.5157	18.4579	C. Erséus	Aug 06 2010	JN260227

(*continued*)

Table 1. (*Continued*)

Species	Spm. No.	Museum voucher no.	Sexual maturity	Collection locality	Coordinates		Leg.	Coll. date	Barcode Acc. no
Ch. chalupskyi	CE9647	SMNH133666	immature	SE, Gotland, Gotland, Etelhem	57.3309	18.5061	C. Erséus	Aug 06 2010	JN260230
Ch. chlorophilus	(L)	BMNH 1949.3.1.32	mature	UK, Derbyshire, Smisby	52.76	-1.49	H. Friend	Nov 23 1912	–
Ch. chlorophilus	**(PL)**	**BMNH 1949.3.1.32**	immature	UK, Derbyshire, Smisby	52.76	-1.49	H. Friend	Nov 23 1912	–
Ch. chlorophilus	CE1041	SMNH133667	mature	SE, Halland, Laholm, Hallandsåsen	56.395	13.000	E. Rota, P. De Wit, L. Matamoros, A. Ansebo & C. Erséus,	May 31 2005	KF672411
Ch. chlorophilus	CE2334	SMNH133668	immature	SE, Skåne, Sjöbo, Vallarum	55.7371	13.8556	A. Ansebo	May 13 2007	KF672412
Ch. chlorophilus	CE6492	SMNH133669	immature	SE, Uppland, Österåker, Åkersberga	59.4967	18.2732	C. Erséus	Jun 06 2009	JN260078
Ch. chlorophilus	CE6627	SMNH133670	immature	SE, Uppland, Vallentuna	59.5477	18.2467	C. Erséus	Jun 04 2009	KF672413
Ch. chlorophilus	CE6635	SMNH133671	immature	SE, Södermanland, Nyköping, Näverkvarn	58.6117	16.7598	C. Erséus	Jun 07 2009	KF672414
Ch. chlorophilus	CE6636	SMNH133672	immature	SE, Södermanland, Nyköping, Näverkvarn	58.6117	16.7598	C. Erséus	Jun 07 2009	KF672415
Ch. chlorophilus	CE6678	SMNH133673	immature	SE, Västergötland, Vårgårda, Fly	57.9968	12.587	C. Erséus	Jun 08 2009	KF672416
Ch. chlorophilus	CE6679	SMNH133674	immature	SE, Västergötland, Vårgårda, Fly	57.9968	12.587	C. Erséus	Jun 08 2009	JN260092
Ch. chlorophilus	CE6680	SMNH133675	immature	SE, Västergötland, Vårgårda, Fly	57.9968	12.587	C. Erséus	Jun 08 2009	JN260093
Ch. chlorophilus	CE9408	SMNH133676	immature	SE, Ångermanland, Kramfors, Bönhamn	62.8797	18.4314	C. Erséus	Jun 09 2010	KF672428
Ch. chlorophilus	CE9412	SMNH133677	immature	SE, Ångermanland, Nordmaling, Bönhamn	63.6038	19.6624	C. Erséus	Jun 09 2010	KF672429
Ch. chlorophilus	CE9428	SMNH133678	immature	SE, Västerbotten, Robertsfors. Bygdeå	64.0469	20.8519	C. Erséus	Jun 10 2010	JN260174
Ch. chlorophilus	CE9429	SMNH133679	immature	SE, Västerbotten, Robertsfors, Bygdeå	64.0469	20.8519	C. Erséus	Jun 10 2010	JN260277
Ch. chlorophilus	CE9433	SMNH133680	immature	SE, Västerbotten, Robertsfors, Bygdeå	64.0469	20.8519	C. Erséus	Jun 10 2010	JN260175
Ch. chlorophilus	CE9459	SMNH133681	immature	SE, Norrbotten, Överkalix, S Sandsjärv	66.328	22.7391	C. Erséus	Jun 10 2010	JN260181
Ch. chlorophilus	CE9460	SMNH133682	immature	SE, Norrbotten, Överkalix, S Sandsjärv	66.328	22.7391	C. Erséus	Jun 10 2010	JN260182

(*continued*)

Table 1. (*Continued*)

Species	Spm. No.	Museum voucher no.	Sexual maturity	Collection locality	Coordinates		Leg.	Coll. date	Barcode Acc. no
Ch. chlorophilus	CE9595	SMNH133685	immature	SE, Lappland Vilhelmina, Röberg	65.064	15.0438	C. Erséus	Jun 15 2010	JN260210
Ch. chlorophilus	SM23	SMNH139139	mature	SE, Västergötland, Göteborg, Medicinareberget	57.6890	11.9560	S. Martinsson	Jul 23 2012	**KM874819**
Ch. chlorophilus	SM82	SMNH139140	immature	PL, Dolnośląskie, Jelenia Gora, Cieplice	50.8460	15.6650	K. Elliott & S. Martinsson	Jun 14 2013	**KM874820**
Ch. chlorophilus	SM86	SMNH139141	immature	PL, Dolnośląskie, Jelenia Gora, Cieplice	50.8460	15.6650	K. Elliott & S. Martinsson	Jun 14 2013	**KM874821**
Ch. chlorophilus	CE19033	SMNH139142	immature	NO, Telemark, Kviteseid, Kviteseid Old Church	59.3532	8.5196	C. Erséus & B. Williams	Jun 13 2013	**KM874822**

Changes with respect to Martinsson & Erséus, 2014: [1]Replaces voucher no. **SMNH133689**. [2]Replaces voucher no. **SMNH133690**. [3]Replaces voucher no. **SMNH 133691**. [4]Replaces voucher no. **SMNH133645.** [5]Erroneously given as SMNH133647 in Martinsson & Erséus, 2014. [6] Replaces voucher no. **SMNH133648.**

including *Euenchytraeus bisetosus*, the type species of *Euenchytraeus*, and two other species previously in *Cognettia*, *C. clarae* and *C. piperi*.

Euenchytraeus bisetosus was described as a large enchytraeid (25–30 mm long, 2 mm wide in fixed condition), while specimens of *C. sphagnetorum* s. lat. and other *Cognettia*, including *C. clarae* s. str., are usually much smaller. Both *C. clarae* and *Eu. bisetosus* have only two chaetae per bundle, whereas *C. piperi* has 1–3 chaetae per bundle; the latter species also has a terminal vesicle on the duct of the head nephridia, not observed in the former two taxa. According to Schmelz and Collado (2010), *C. clarae* further differs from other European species of *Cognettia* by having a larger body diameter and softer body wall, as found in species of *Mesenchytraeus* Eisen, 1878. Also *C. piperi* was described as more robust than typical *Cognettia* (Piper et al., 1982). Further, *Cognettia piperi* and *C. clarae* seem to share simpler spermathecae, with ampullae that lack the division into ental and ectal chambers connected by a narrow tube seen in most other species of *Cognettia*.

Based on the above-mentioned differences, it seems that this group of taxa (*bisetosus*, *clarae* and *piperi*) are not closely related to *C. sphagnetorum* and other species of *Cognettia*, and therefore should be treated as a separate genus, *Euenchytraeus*. We further believe that the proposed synonymy of *Eu. bisetosus* and *C. clarae* (Schmelz & Collado, 2010) is premature, and we suggest that these two taxa are retained as separate species for the time being. We regard all species of the former *Cognettia* with head nephridia as members of *Euenchytraeus*, which thus now includes *Eu. bisetosus*, *Eu. piperi* (Christensen & Dózsa-Farkas, 1999) comb. nov. and *Eu. clarae* (Bauer, 1993) comb. nov. However, more molecular work on this group is needed, both to establish its position within Enchytraeidae, and to assess the boundaries between these three species.

Chamaedrilus chlorophilus Friend, 1913, and the status of *Chamaedrilus*

Chamaedrilus chlorophilus was regarded as close to *Marionina sphagnetorum* and *M. glandulosa* by Friend (1913a), and therefore he later placed the three of them in *Chamaedrilus* (Friend, 1919). In the original description, *Ch. chlorophilus* had (i) 4–5 pairs of primary pharyngeal glands, sometimes with ventral lobes or secondary glands present on the posterior pairs, (ii) 2–3 sigmoid chaetae per bundle, (iii) brain concave posteriorly and about 1.5 times as long as broad, (iv) the first pair of nephridia present at 9/10, and of the same shape as found in species of *Cognettia*, (v) male pores in segment IX, (vi) sperm funnels 2–4 times longer than broad, and (vii) the spermathecae connected with the oesophagus. All characters

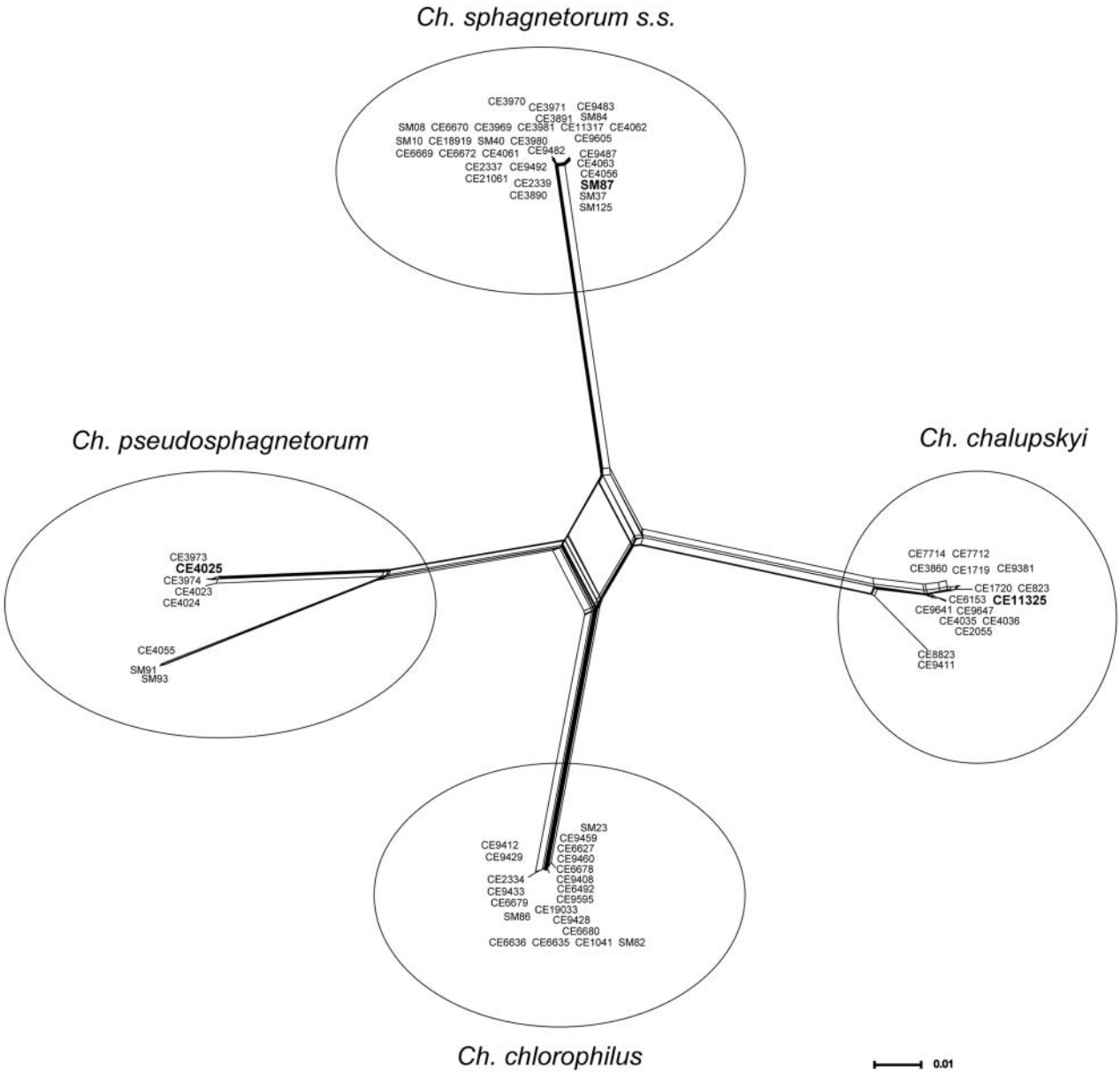


Fig. 1. NeighbourNet network of COI barcodes for specimens of the *Chamaedrilus sphagnetorum* complex included in this study. Specimen numbers in bold indicate holotype and neotype specimens. Scale bar represents uncorrected p-distance.

except those concerning the spermathecae 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* (Černosvitov, 1928) comb. nov.; *Ch. bisetosus* (Christensen & Dózsa-Farkas, 1999) comb. nov.; *Ch. chalupskyi* sp. nov.; *Ch. cognettii* (Issel, 1905) comb. nov.; *Ch. floridae* (Healy, 1996) comb. nov.; *Ch. glandulosus* (Michaelsen, 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, 1878) [as already proposed by Friend, 1919]; *Ch. valeriae* (Dumnicka, 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.
- 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.

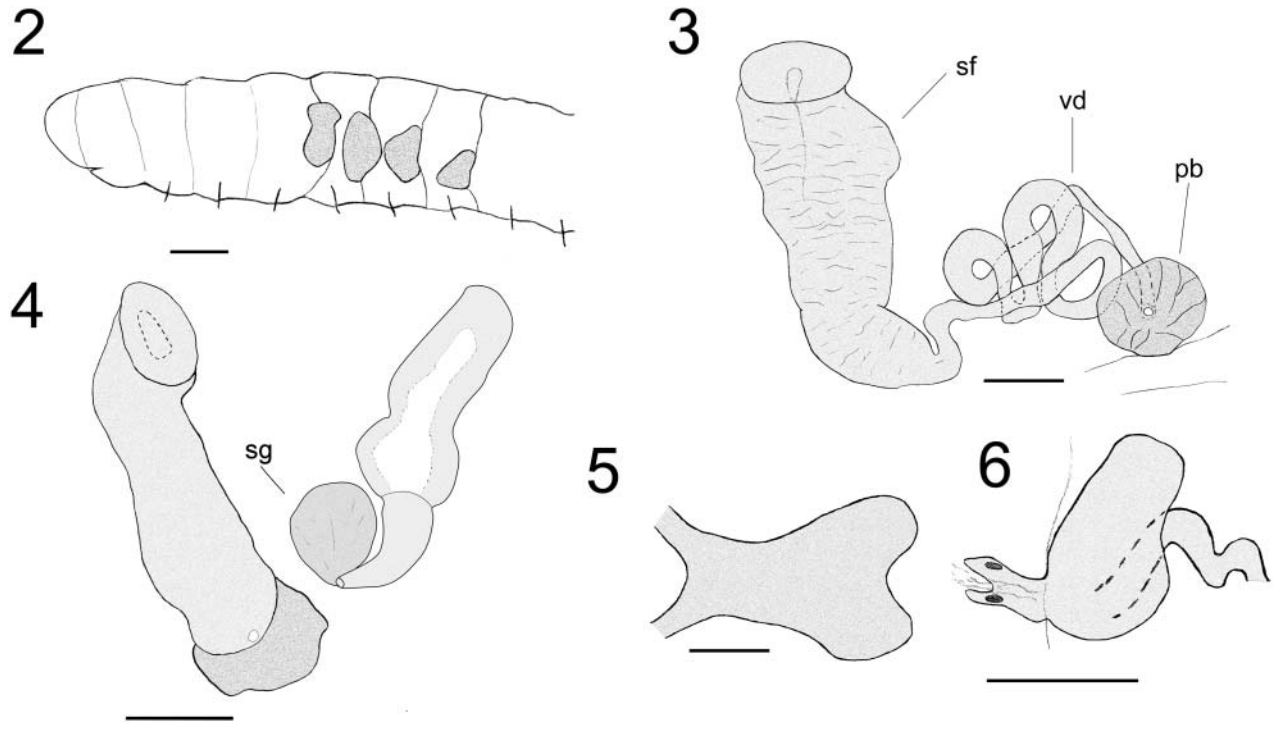
4. Most preclitellar lateral bundles with 2 chaetae. Pharyngeal glands 4 (3−5) pairs, not connected dorsally. *Chamaedrilus chlorophilus*
- Most preclitellar lateral bundles with 3 chaetae. Pharyngeal glands usually (2−3)4(−5) pairs. *Chamaedrilus sphagnetorum* s. str. and *Ch. pseudosphagnetorum* sp. 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



Figs. 2–6. *Chamaedrilus sphagnetorum* (Vejdovský, 1878) s. str. **Fig. 2.** Anterior part of body, lateral view, indicating size, shape and numbers of pharyngeal glands. **Fig. 3.** Male genitalia, male pore in segment IX. **Fig. 4.** Spermathecae from two different specimens, an undeveloped spermatheca to the left, and a more developed spermatheca to the right. **Fig. 5.** Brain, dorsal view. **Fig. 6.** Nephridium at septum 12/13, lateral view. Abbreviations: pb = penial bulb; sf = sperm funnel; sg = spermathecal gland; vd = vas deferens. Scale bars: Fig. 2, 100 μm; Figs 3–6, 50 μm.

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; Kasprzak, 1986: 124, figs 332–334, partim.

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

Cognettia sphagnetorum; Schmelz & Collado, 2010: 79, partim.

Cognettia sphagnetorum A; Martinsson & Erséus, 2014.

Neotype. SMNH TYPE-8682, SM87 immature anterior part. Leg. Kerryn Elliott and Svante Martinsson, Jun 14 2013; COI barcode: GenBank acc. no. KM874818.

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.

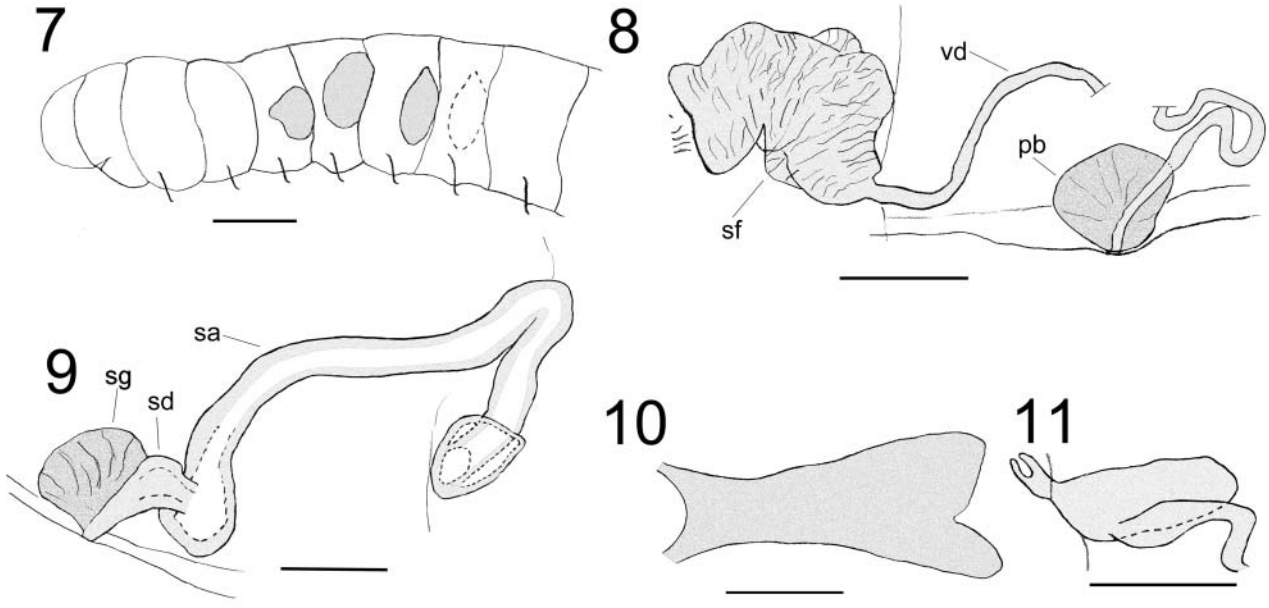
Biology. Seems to mainly reproduce asexually, mature specimens very rare. Specimens with regenerating heads and/or tails rare. Sexually maturing specimens were found in September (Norway), April (Sweden) and May (Norway).

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; Kasprzak, 1986: 124, figs 332–334, partim.

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

Cognettia sphagnetorum; Schmelz & Collado, 2010: 79, partim.

Cognettia sphagnetorum D; Martinsson & Erséus, 2014.

Holotype. SMNH TYPE-8685 (former SMNH133691), CE4025, mature, anterior part. Leg. Christer Erséus, May 03 2008. COI barcode: GenBank acc. no. KF672421.

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.

Etymology. 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).

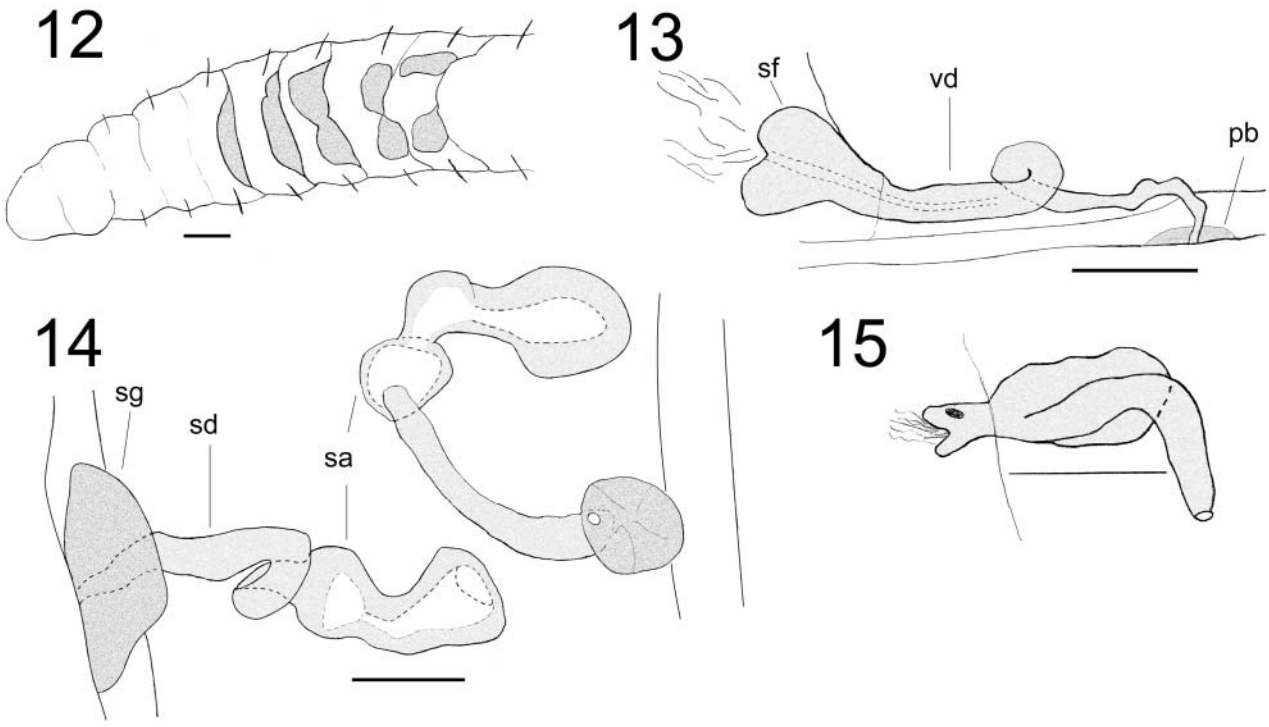
Remarks. Can only be readily distinguished from *Chamaedrilus sphagnetorum* s. str. on molecular characters. This species has a large genetic variation, and the COI barcodes forms two distinct clusters (obvious in Fig. 1), about 8% different (uncorrected p-distance) from each other. However, Martinsson & Erséus (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.



Figs. 12–15. *Chamaedrilus chalupskyi* sp. nov. **Fig. 12.** Anterior part of body, dorsal view, indicating size, shape and number of pharyngeal glands. **Fig. 13.** Rudimentary male genitalia, male pore in segment XI. **Fig. 14.** Spermathecae. **Fig. 15.** Nephridium at septum 11/12, lateral view. . Abbreviations: pb = penial bulb; sa = spermathecal ampulla; sd = spermathecal duct; sf = sperm funnel; sg = spermathecal gland; vd = vas deferens. Scale bars: Fig. 12, 100 μm; Figs 13–15, 50 μm.

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.

Type locality. Sweden**:** Närke, Hallsberg, Östansjö, Ögonakällan Spring Nature Reserve, 2 m downstream of small spring head (N59.0392, E15.0189). Sand and gravel, in small spring-fed stream.

Paratypes. SMNH TYPE-8684 (former SMNH133649), CE3860 immature, anterior part, Sweden: Västergötland**,** Lerum, Aspenäs, *Alnus* swamp E of Seatons strand (N57.7761, E12.2411), somewhat dry land in middle of swamp area, fine sand and soil with *Ranunculus ficaria*, Leg. Christer Erséus and Kennet Lundin, Apr 28 2008. MCZR Oligochaeta 0188, CE823 immature anterior part, Sweden: Västergötland, Götene, Hällekis, lower slope of Kinnekulle, near dirt road to Perstorp (58°37.136'N, 013°25.597'E); edge of *Alnus* swamp with oaks and ferns, wet dark soil, Leg. Emilia Rota and Christer Erséus, May 26 2004.

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.

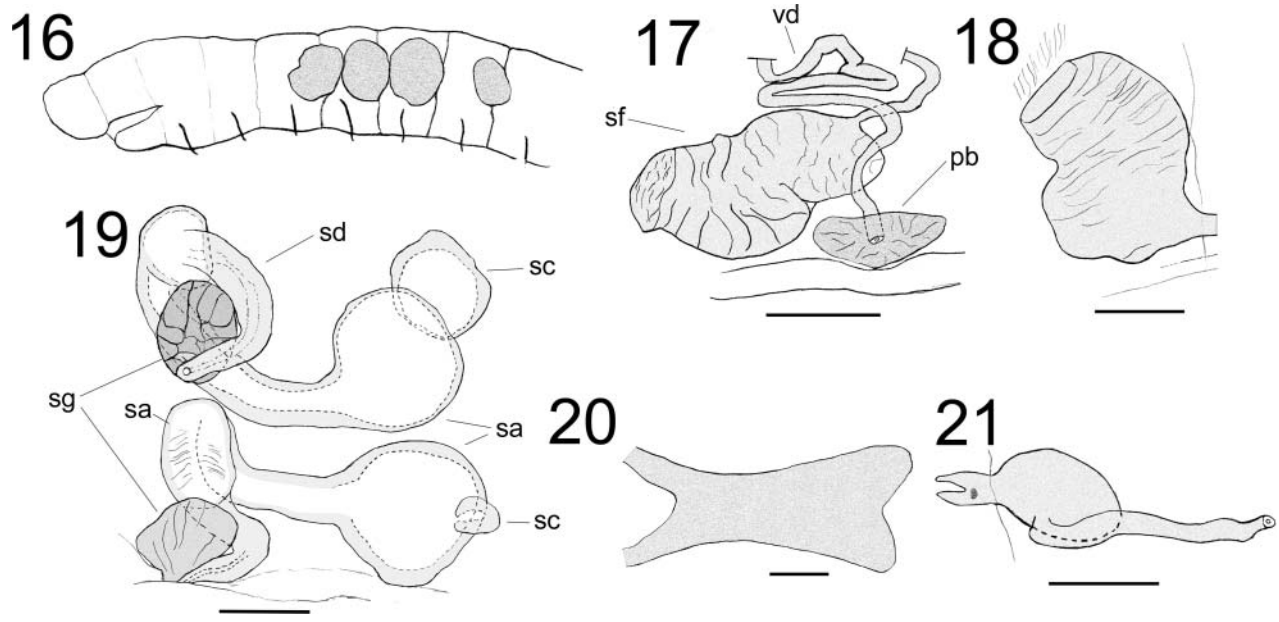
Chamaedrilus chalupskyi (represented in 'BOLD' by BIN: AAT8926).

Chamaedrilus chlorophilus Friend, 1913

(Figs 16−21)

Chamaedrilus chlorophilus Friend, 1913: 260, figs 22−23.

Chamaedrilus chlorophilus; Černosvitov, 1937b: 205.



Figs. 16−21. *Chamaedrilus chlorophilus* Friend, 1913. **Fig. 16.** Anterior part of body, lateral view, indicating size, shape and number of pharyngeal glands. **Fig. 17.** Male genitalia, male pore in IX. **Fig. 18.** Sperm funnel. **Fig. 19.** Spermathecae. **Fig. 20.** Brain, dorsal view. **Fig. 21.** Nephridium at septum 10/11, lateral view. Abbreviations: eg = ectal gland; pb = penial bulb; sa = spermathecal ampulla; sd = spermathecal duct; sc = secondary ental chamber; sf = sperm funnel; sg = spermathecal gland; vd = vas deferens. Scales: Fig. 16, 100 μm; Figs 17−21, 50 μm.

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

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

Cognettia sphagnetorum; Schmelz & Collado, 2010: 79, partim.

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.)

Paralectotype. 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 preclitellar 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 preclitellar 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 (paralectotype) 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 (Chalupský, 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 preclitellar lateral bundles variably 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 preclitellar 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, preclitellar 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 & Schwenk, 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); Dózsa-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; Padial & 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 Chalupský'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 nephridia 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. lapponicus* 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. lapponicus*, 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 invalidated 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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