

# NORDIC JOURNAL OF BOTANY

## Research

### *Coreomyces* (Laboulbeniales) in Sweden, with two new species

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#### Nordic Journal of Botany

2021: e03323

doi: 10.1111/njb.03323

Subject Editor: Klaus Høiland

Editor-in-Chief: Torbjörn Tyler

Accepted 1 July 2021

Published 15 October 2021

The genus *Coreomyces* (Laboulbeniaceae, Laboulbeniomycetes, Ascomycota) includes minute parasites on water boatmen (Corixidae, Hemiptera, Insecta). This taxonomic study is primarily based on freshly sampled corixids infected by *Coreomyces* from Sweden, although a few samples from Denmark and Turkey were also included. All records were verified using DNA sequence data from the internal transcribed spacer region and large subunit of the nuclear ribosomal DNA repeat region. We recognise four species, two of which are new to science: *Coreomyces confusus* H. Sundb. et al. sp. nov., *C. corixae* Thaxt., *C. dextrorsus* H. Sundb. et al. sp. nov. and *C. macropus* Thaxt. *Coreomyces corixae* is new to Denmark, Sweden and Turkey, while *C. macropus* is new to Denmark and Sweden. *Coreomyces confusus* is morphologically very similar to *C. macropus* and also occupies the same positions on the same host species, although it seems to be less common. *Coreomyces dextrorsus* resembles *C. corixae* morphologically but is usually considerably larger. It infects the same host species as *C. corixae* and also shares one of its positions on the host with *C. corixae*, although it is much more common in its species-specific position. All four species can inhabit two different yet distinct positions on the host. We observe that morphology is affected by the position on the host and that different species sharing the same position on the host tend to be difficult or impossible to separate on morphology only. We conclude that species circumscriptions in *Coreomyces* must be based on the integration of molecular and morphological data.

Keywords: Ascomycota, Corixidae, fungi, oligonucleotide signature, systematics, taxonomy

#### Introduction

Members of the genus *Coreomyces* Thaxt. are small insect–parasitic fungi that belong to the ascomycete order Laboulbeniales (Goldmann and Weir 2018, Haelewaters 2018). *Coreomyces* is the only genus in the order that parasitises water boatmen (Corixidae, Heteroptera, Fig. 1b–c). The genus appears to form the sister group to *Chitinomyces* inside a clade with other genera parasitising aquatic hosts (Goldmann and Weir 2018, Haelewaters 2018). All species in this study are position specific (Majewski 1994, Sundberg et al. 2018a), meaning they are confined to certain spots on the body of



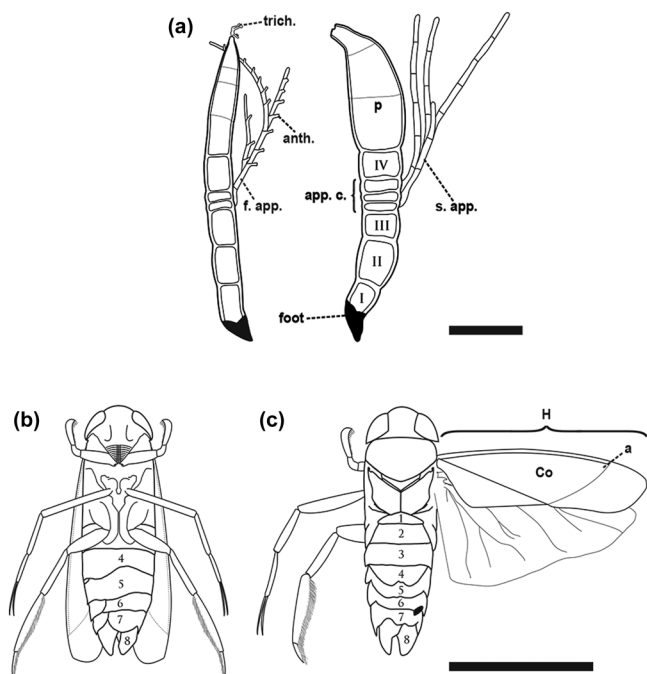


Figure 1. (a) Organisation of the thallus in the genus *Coreomyces*. I–IV = non-appendage-bearing cells of the receptacle, anth. = antheridium (produces spermatia), appc. = appendiculate cells, f. app. = fertile appendages, foot = structure attached to the host, p = perithecium (contains ascospores), s. app. = sterile appendages, trich. = trichogyne (receives spermatia from the antheridia). The thallus on the left is modified from Thaxter 1931. Scale bar = 50  $\mu$ m. (b) Ventral view of a male water boatman. 4–8 = sternites. (c) Dorsal view of a male water boatman. 1–8 = tergites, H = hemelytron, a = apical part of corium, Co = corium.

their host. This spatial confinement seems to be the case for most, if not all, species in the genus, although information is sometimes scarce in old species descriptions (Thaxter 1902, 1905, 1918, 1931, Spegazzini 1917, 1918, Poisson 1929, Lee and Na 2009).

Members of *Coreomyces* are characterised morphologically by a receptacle consisting of a single series of superposed cells (Fig. 1a). In the common case, there are four elongated basal cells, denominated I–IV. The most distal of these (sometimes referred to as the perithecial stalk cell) is separated from the others by a number of flattened cells (appendiculate cells) that carry unilaterally directed, branched or unbranched and hair-like appendages. These appendages may be sterile or fertile, in the latter case carrying antheridia. The arrangement and number of cells in the thallus, however, is somewhat variable both within and between species. In the young thallus there are three or four additional distal cells of the receptacle terminating in a filiform, evanescent primary appendage. The single perithecium develops inside these distal cells, eventually destroying these as it grows. As a consequence, the outer cell walls of the receptacle will enclose the perithecial cell wall rows, preventing them from being observed. The internal perithecial development of *Coreomyces* is unique among the Laboulbeniales (Thaxter 1931, Tavares 1985). In

many other genera of Laboulbeniales, the thallus structure is rather complex, and the size, shape and relative positions of the cells are considered important characters for the discrimination between taxa (Tavares 1985, Santamaria 1998). In the genus *Coreomyces*, on the other hand, cells are few and their organisation is relatively simple. Moreover, important characteristics of the perithecial wall cells are obscured by the internal formation of the perithecium. Species descriptions in *Coreomyces* are largely based on characters such as receptacle and perithecium morphology, colour and size, but also on the number, size and shape of the receptacle cells, including placement of the appendiculate cells. Many of these characters are variable and Thaxter (1931) sometimes expressed doubts about the taxonomic usefulness of such variation.

Since the genus *Coreomyces* was first erected by Thaxter (1902), altogether 21 species have been described (Thaxter 1902, 1905, 1918, 1931, Spegazzini 1917, 1918, Poisson 1929). Only a single species has been described recently (Lee and Na 2009), all others in the early 20th century. Four species of *Coreomyces*, viz. *C. arcuatus*, *C. corixae*, *C. elongatus* and *C. macropus*, have been reported from Europe (Santamaria et al. 1991, Majewski 1994). In a recent study investigating position specificity within *Coreomyces* from Sweden and Denmark (Sundberg et al. 2018a), we came across four species that were found to be distinct on account of variation patterns in sequence data from the internal transcribed spacer (ITS) region, large subunit (nrLSU) and small subunit (nrSSU) of the nuclear ribosomal DNA, as well as the small subunit of the mitochondrial ribosomal DNA. We found a significant correlation between species and position on the host as well as a weak correlation between species and host sex, but did not focus on the taxonomical and nomenclatural aspects. In this study we make use of morphology as well as additional DNA sequence data to review the classification, demonstrate that two out of our four species do not correspond to any previously named taxa, and show that morphology tends to be affected by the position on the host infected by the fungus.

## Material and methods

Following the method described by Sundberg et al. (2018a), corixids were collected from 15 localities in southern Sweden and one in Turkey (Table 1). The corixids were scanned for *Coreomyces* thalli under a dissecting microscope (Olympus SZ-1145). In total, 88 mature thalli were detached from 48 corixids of the genera *Arctocorisa*, *Callicorixa*, *Cymatia* and *Sigara* (Table 1). The position of each thallus on the host was documented with a Moticam 5 camera attached to the dissecting microscope. Each thallus was also measured using the same camera attached to an Olympus BH2 compound microscope equipped with differential interference contrast optics. Images (Fig. 2, 3) were stacked with the software ZereneStacker (Zerene Systems LLC) and adjusted in Adobe Photoshop CC. Individual thalli were measured from the photos taken using the software Motic Images Plus ver. 3.0.

Table 1. *Coreomyces* specimens included in this study with their position on the host species (CV = mid-ventrally on the abdomen, LV = ventrally on the left side of the abdomen, LW = lower side of the margin of the left hemelytron, RD = dorsally on the right side of the abdomen near the margin, RV = ventrally on the right side of the abdomen). Collection sites are identified with coordinates (decimal degrees in the WGS 84 geodetic datum). Sweden and Turkey are abbreviated according to their ISO 3166-1 alpha-3 country codes. GenBank numbers for sequences used in this study are provided, except that sequences shorter than 200 bp (marked 'NA' below) are not accepted by GenBank. Such sequences can be found in the ITS alignment deposited in the Dryad Digital Repository (Sundberg et al. 2021).

Species	Position	Host species	Host sex	Collection date	Collection site	Lat.	Long.	Isolate ID	Genbank ID	Marker
<i>C. confusus</i>	LW	<i>Sigara distincta</i>	male	10/8/2017	SWE, Skåne, Stenhusen	55°46'45.66"	13°21'43.16"	139-6	MN512397	ITS
<i>C. corixae</i>	LV	<i>Arctocoris germari</i>	male	10/20/2014	SWE, Skåne, Lomma	55°40'38.64"	13°03'40.54"	124-1	MN512359	ITS
<i>C. corixae</i>	RD	<i>Callicorixa praeusta</i>	male	10/20/2014	SWE, Skåne, Gladsax	55°34'10.99"	14°16'33.13"	143-1	MN512378	ITS
								143-2	MN512379	
								143-3	MN512380	
								145-5	MN512384	
								145-6	MN512385	
								145-7	MN512386	
								145-8	MN512387	
<i>C. corixae</i>	LV	<i>Cymatia bondsdorffii</i>	male	10/8/2017	SWE, Skåne, Stenhusen	55°46'45.66"	13°21'43.16"	130-1	MN512363	ITS
<i>C. corixae</i>	RD	<i>Sigara distincta</i>	male	10/8/2017	SWE, Småland, Dockrössle	57°40'38.35"	16°27'47.02"	144-3	MN512381	ITS
								144-4	MN512382	
								144-5	MN512383	
<i>C. corixae</i>	LV	<i>Sigara distincta</i>	female	10/20/2014	SWE, Skåne, Lyckehusen	55°44'48.08"	12°58'31.12"	126-2	MN512360	ITS
<i>C. corixae</i>	LV	<i>Sigara distincta</i>	male	10/20/2014	SWE, Skåne, Lyckehusen	55°44'48.08"	12°58'31.12"	128-1	NA	ITS
<i>C. corixae</i>	RD	<i>Sigara distincta</i>	male	10/8/2017	SWE, Skåne, Rolsberga	55°48'19.30"	13°30'48.38"	141-1	MN512373	ITS
								141-2	MN512374	
<i>C. corixae</i>	LV	<i>Sigara distincta</i>	male	10/22/2014	SWE, Skåne, Simrishamn	55°33'25.52"	14°20'15.32"	135-2	MN512364	ITS
<i>C. corixae</i>	RD	<i>Sigara distincta</i>	male	10/22/2014	SWE, Skåne, Simrishamn	55°33'25.52"	14°20'15.32"	135-3	MN512365	ITS
								135-4	MN512366	
<i>C. corixae</i>	LV	<i>Sigara distincta</i>	male	10/8/2017	SWE, Skåne, Stenhusen	55°46'45.66"	13°21'43.16"	135-5	MN512367	ITS
<i>C. corixae</i>	RD	<i>Sigara distincta</i>	male	10/8/2017	SWE, Skåne, Stenhusen	55°46'45.66"	13°21'43.16"	139-2	MN512368	ITS
								139-3	NA	ITS
								139-4	MN512369	
								139-5	MN512347	nrLSU
								127-1	MN512361	ITS
<i>C. corixae</i>	LV	<i>Sigara falleni</i>	female	10/20/2014	SWE, Skåne, Lyckehusen	55°44'48.08"	12°58'31.12"	136-2	NA	
<i>C. corixae</i>	LV	<i>Sigara falleni</i>	male	10/20/2014	SWE, Skåne, Lyckehusen	55°44'48.08"	12°58'31.12"	136-2	NA	
<i>C. corixae</i>	LV	<i>Sigara falleni</i>	female	10/8/2017	SWE, Skåne, Rolsberga	55°48'19.30"	13°30'48.38"	116-1	MN512344	nrLSU
<i>C. corixae</i>	RD	<i>Sigara falleni</i>	male	10/8/2017	SWE, Skåne, Rolsberga	55°48'19.30"	13°30'48.38"	140-2	MN512370	ITS
								140-3	MN512371	
								140-4	MN512372	
								142-1	MN512375	
								142-2	MN512376	
								142-3	MN512377	
<i>C. corixae</i>	LV	<i>Sigara falleni</i>	female	10/8/2017	SWE, Skåne, Skatteborg	55°46'57.86"	13°23'51.25"	129-1	MN512362	ITS
<i>C. corixae</i>	LV	<i>Sigara lateralis</i>	female	10/22/2014	SWE, Skåne, Simrishamn	55°33'25.52"	14°20'15.32"	119-1	MN512354	ITS
<i>C. corixae</i>	LV	<i>Sigara lateralis</i>	female	11/10/2013	TUR, Mugla Province	37°17'17.41"	27°39'14.69"	120-1	MN512355	ITS
								121-1	MN512356	
								122-1	MN512357	
<i>C. corixae</i>	LV	<i>Sigara lateralis</i>	male	11/10/2013	TUR, Mugla Province	37°17'17.41"	27°39'14.69"	123-1	MN512358	ITS
<i>C. corixae</i>	RD	<i>Sigara lateralis</i>	male	11/10/2013	TUR, Mugla Province	37°17'17.41"	27°39'14.69"	147-2	MN512388	ITS
								148-1	MN512389	

(Continued)

Table 1. Continued.

Species	Position	Host species	Host sex	Collection date	Collection site	Lat.	Long.	Isolate ID	Genbank ID	Marker
<i>C. corixae</i>	LV	<i>Sigara striata</i>	male	10/21/2014	SWE, Skåne, Barsebäck	55°46'17.90"	12°57'20.09"	117-1	MN512345	nrLSU
<i>C. corixae</i>	LV	<i>Sigara striata</i>	male	10/20/2014	SWE, Skåne, Lyckehusen	55°44'48.08"	12°58'31.12"	125-1	MN512346	nrLSU
<i>C. dextrorsus</i>	RV	<i>Sigara distincta</i>	male	10/8/2017	SWE, Skåne, Lund	55°43'36.08"	13°13'46.63"	134-1	MN512390	ITS
								134-2	MN512349	nrLSU
								134-3	MN512391	ITS
								134-4	MN512392	
								134-5	MN512393	
<i>C. dextrorsus</i>	RV	<i>Sigara distincta</i>	male	10/8/2017	SWE, Skåne, Ringsjö- gården	55°51'12.85"	13°30'48.38"	131-1	MN512348	nrLSU
								132-1	NA	ITS
<i>C. dextrorsus</i>	RV	<i>Sigara distincta</i>	male	10/22/2014	SWE, Skåne, Simrishamn	55°33'25.52"	14°20'15.32"	135-1	NA	ITS
<i>C. dextrorsus</i>	RV	<i>Sigara distincta</i>	male	10/8/2017	SWE, Skåne, Stenhusen	55°46'45.66"	13°21'43.16"	139-1	MN512350	nrLSU
<i>C. dextrorsus</i>	RV	<i>Sigara falleni</i>	male	10/20/2014	SWE, Skåne, Lyckehusen	55°44'48.08"	12°58'31.12"	136-1	MN512394	ITS
								137-1	MN512395	ITS
<i>C. dextrorsus</i>	RD	<i>Sigara falleni</i>	male	10/8/2017	SWE, Skåne, Rolsberga	55°48'19.30"	13°30'48.38"	140-1	MN512396	ITS
<i>C. macropus</i>	CV	<i>Callicorixa praeusta</i>	male	10/20/2014	SWE, Skåne, Gladsax	55°34'10.99"	14°16'33.13"	145-2	MN512400	ITS
								145-3	MN512401	
								145-4	MN512402	
<i>C. macropus</i>	LW	<i>Callicorixa praeusta</i>	male	10/20/2014	SWE, Skåne, Gladsax	55°34'10.99"	14°16'33.13"	145-1	MN512399	ITS
<i>C. macropus</i>	LW	<i>Callicorixa praeusta</i>	male	9/12/2013	SWE, Uppland, Ulva kvarn	59°54'44.93"	17°34'32.16"	156-1	MN512414	ITS
<i>C. macropus</i>	CV	<i>Callicorixa praeusta</i>	male	11/25/2014	SWE, Uppland, Uppsala	59°50'37.86"	17°44'06.50"	162-1	MN512416	ITS
								163-1	MN512417	
								164-1	MN512418	
								167-1	MN512421	
<i>C. macropus</i>	CV	<i>Callicorixa praeusta</i>	male	9/14/2017	SWE, Uppland, Uppsala	59°50'37.86"	17°44'06.50"	165-1	MN512419	ITS
<i>C. macropus</i>	LW	<i>Callicorixa praeusta</i>	female	11/25/2014	SWE, Uppland, Uppsala	59°50'37.86"	17°44'06.50"	154-1	MN512412	ITS
<i>C. macropus</i>	LW	<i>Callicorixa praeusta</i>	male	11/25/2014	SWE, Uppland, Uppsala	59°50'37.86"	17°44'06.50"	167-2	MN512422	ITS
								167-3	MN512423	
<i>C. macropus</i>	LW	<i>Callicorixa praeusta</i>	male	11/19/2014	SWE, Uppland, Uppsala	59°52'01.85"	17°42'45.22"	155-1	MN512413	ITS
<i>C. macropus</i>	CV	<i>Sigara distincta</i>	male	10/8/2017	SWE, Småland, Dockrössle	57°40'38.35"	16°27'47.02"	144-1	MN512398	ITS
								144-2	NA	
<i>C. macropus</i>	LW	<i>Sigara distincta</i>	female	10/8/2017	SWE, Småland, Dockrössle	57°40'38.35"	16°27'47.02"	150-1	MN512352	nrLSU
<i>C. macropus</i>	CV	<i>Sigara distincta</i>	male	10/8/2017	SWE, Skåne, Skatteborg	55°46'57.86"	13°23'51.25"	166-1	MN512420	ITS
<i>C. macropus</i>	LW	<i>Sigara distincta</i>	male	10/8/2017	SWE, Skåne, Skatteborg	55°46'57.86"	13°23'51.25"	151-1	MN512409	ITS
<i>C. macropus</i>	LW	<i>Sigara distincta</i>	male	11/19/2014	SWE, Uppland, Uppsala	59°52'01.85"	17°42'45.22"	158-1	MN512353	nrLSU
<i>C. macropus</i>	LW	<i>Sigara falleni</i>	female	6/13/2017	SWE, Skåne, Lund	55°43'04.04"	13°14'16.44"	146-1	MN512403	ITS
<i>C. macropus</i>	LW	<i>Sigara falleni</i>	female	10/8/2017	SWE, Skåne, Rolsberga	55°48'19.30"	13°30'48.38"	152-1	MN512410	ITS
<i>C. macropus</i>	CV	<i>Sigara semistriata</i>	male	9/12/2013	SWE, Uppland, Ulva kvarn	59°54'44.93"	17°34'32.16"	149-2	MN512405	ITS
								149-3	MN512406	
								149-4	MN512407	
								149-5	MN512408	
<i>C. macropus</i>	LW	<i>Sigara semistriata</i>	female	9/12/2013	SWE, Uppland, Ulva kvarn	59°54'44.93"	17°34'32.16"	160-1	MN512415	ITS
<i>C. macropus</i>	LW	<i>Sigara semistriata</i>	male	9/12/2013	SWE, Uppland, Ulva kvarn	59°54'44.93"	17°34'32.16"	149-1	MN512404	ITS
<i>C. macropus</i>	LW	<i>Sigara striata/dorsalis</i>	female	10/24/2014	SWE, Östergötland, Linköping	58°23'34.98"	15°34'45.37"	153-1	MN512411	ITS

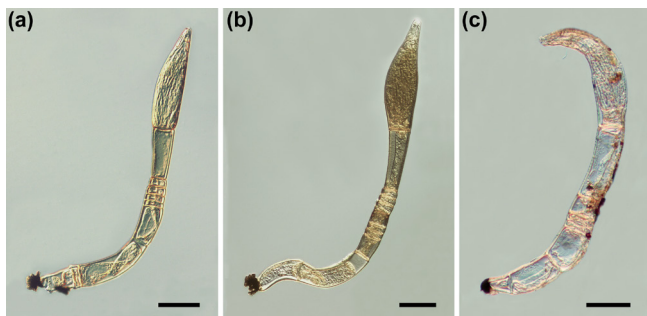


Figure 2. Morphology of *Coreomyces confusus*. (a) Holotype. Thallus from the lower side of the left hemelytron margin of the host, with an extra (appendiculate?) cell with poorly developed lower septum inserted between cell I and II. ID Upl\_1-1 (Sundberg et al. 2018b). (b) Thallus from the lower side of the left hemelytron margin, with two groups of appendiculate cells separated by an extra sterile cell. ID H139-6 (Table 1). (c) Thallus from the midventral position on the abdomen. Branchlets lacking or possibly lost. Note similarity in thallus shape with *C. macropus* occurring in the same position on the host (Fig. 5c). ID Sk\_1-10 (Sundberg et al. 2018b). Scale bars = 50  $\mu$ m.

All measurements of length (individual cells, total length of thallus and perithecium) were made along the longitudinal axis of the thallus, i.e. including any curvature. Measurement values are presented as ‘minimum–median–maximum’ followed by the sample size in brackets, e.g. ‘(n = 26)’. Length/width ratios (L/W) are given for cells I–IV as well as cell IVa when present. Mature ascospores were only measured in *C. dextrorsus*, since they were confined to the inside of the perithecium in the other three species.

After morphological documentation, DNA sequences were generated following the methods of Sundberg et al. (2018b). We generated new sequences primarily from the internal transcribed spacer (ITS) region or, in some cases,

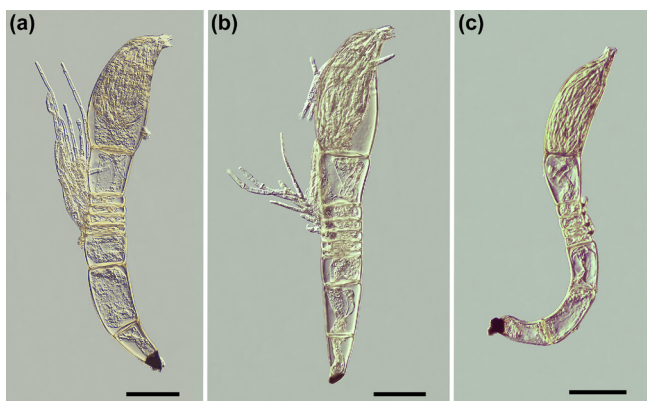


Figure 3. Morphology of *Coreomyces dextrorsus*. (a) Holotype. Thallus of the ventral abdominal form, with sterile branchlets attached to the appendiculate cells. ID H134-4 (Table 1). (b) Thallus of the ventral abdominal form, with sterile branchlets attached to the appendiculate cells. Hyaline ascospores with gelatinous sheaths stick to the perithecium. ID H135-1 (Table 1). (c) Thallus of the dorsal abdominal form. ID H140-1 (Table 1). Scale bars = 50  $\mu$ m.

from the large subunit of the nuclear ribosomal DNA (nrLSU) in case the ITS sequencing failed. New sequences were added to the alignments of Sundberg et al. (2018a) using the ‘--add’ option of MAFFT ver. 7.475 with L-INS-i iterative refinement. Maximum likelihood trees were estimated using IQ-TREE ver. 2.1.2 (Kalyaanamoorthy et al. 2017, Minh et al. 2020). A standard model selection (among models with 1, 2 or 6 rates) was performed and followed by a search for the best tree using default settings except that all nearest neighbour interchange (NNI) branch swaps were explored. The extended ITS and LSU alignments and their corresponding trees have been deposited in the Dryad Digital Repository (Sundberg et al. 2021).

Oligonucleotide signatures of ca 25 base pairs diagnostic to the respective species were included in the descriptions below, in addition to morphological data (Gupta 1998, Zahariev et al. 2018). By ‘diagnostic’ in this context we mean a sequence that is shared by all known sequences of a species but is absent from all other species of *Coreomyces* treated here. Signatures were manually extracted from the ITS1 (because that region is the easiest to sequence) using the parts of our alignment with the best coverage, avoiding internal length variation and repetitive or hypervariable regions. Starting positions assume that the first ITS1 position comes immediately after the GATCATTA motif. Signatures were verified for uniqueness among known DNA sequences of kingdom Fungi by performing a megaBLAST on the fungal nucleotide collection at the the National Center for Biotechnology Information (NCBI) website (<www.ncbi.nlm.nih.gov>).

At present, the only way to sequence individual thalli entails destruction of the thallus. Therefore a light microscopy image was designated holotype for each of the two newly described taxa, which is allowed by Article 40.5 of the ICN (Turland et al. 2018).

Type material of the following species in herbarium FH (The Farlow herbarium, Harvard University) was examined morphologically and compared with our material: *C. arcuatus* Thaxt., *C. bicolor* Thaxt., *C. chinensis* Thaxt., *C. corixae* Thaxt., *C. curvatus* Thaxt., *C. fastigatus* Thaxt., *C. macropus* Thaxt., *C. orientalis* Thaxt., *C. sigmoideus* Thaxt. and *C. subdivisus* Thaxt. Type material of *C. argentinensis* Speg., *C. elongatus* Speg. and *C. italicus* Speg. in herbarium LPS was not available for study and consequently we had to restrict comparisons to descriptions and illustrations in Spegazzini (1917, 1918).

## Results

The ‘orange’ and the ‘red’ species circumscribed by Sundberg et al. (2018a) are described here as new and are named *Coreomyces confusus* and *C. dextrorsus*, respectively. The former most frequently inhabits the lower side of the left hemelytron (forewing) margin in many corixids, the latter most frequently inhabits the right lobe of the 8th sternite, near the inner margin, and on the adjacent middle lobe of the 7th sternite in several corixids. The remaining two *Coreomyces* species in Sundberg et al. (2018a), the ‘blue’

and the ‘green’ species, correspond to *C. macropus* and *C. corixae*, respectively. All four species are described and illustrated below. *Coreomyces macropus* and *C. corixae* are reported here as new to Denmark and Sweden, *C. corixae* also as new to Turkey. The Danish records of the two species are based on the data in Sundberg et al. (2018a). We have also encountered a new host genus for *C. corixae*, the genus *Arctocorisa* (Table 1).

*Coreomyces macropus* and *C. confusus* occur in the same position on the hemelytral margin, and occur rarely in the middle of the 5th sternite on male hosts together with *C. dextrorsus*, where they adopt a different morphology. Observations in the latter, rare position are based on the data of Sundberg et al. (2018a, b). We did not come across any such additional specimens for this study, which is why we do not provide measurements specifically from this position.

Neither *C. corixae* nor *C. dextrorsus* are confined to a single position on their host (Sundberg et al. 2018a). Apart from inhabiting the left ventral side of the abdomen in both host sexes, *C. corixae* is also quite frequently encountered dorsally on the margin of the 6th and 7th tergites in male members of the genera *Callicorixa* and *Sigara*. Likewise, *C. dextrorsus* is rarely encountered on the margin of the 8th tergite in males of the genus *Sigara*. There are distinct morphological differences between thalli of *C. corixae* and *C. dextrorsus* growing ventrally. The scarcity of dorsal *C. dextrorsus*, however, prevents us from saying anything about differences between dorsal forms of the two species.

A total of 76 new ITS and 10 new nrLSU sequences were generated for this study. All nrLSU sequences were identical to alleles reported by Sundberg et al. (2018a) and consequently did not in any way alter the tree reported in Fig. 3c of that paper. Among the new ITS sequences, some represent new alleles and consequently add non-zero branch lengths to the corresponding tree in Fig. 3B of Sundberg et al. (2018a). In the updated tree, generated under a HKY+ $\Gamma$  model with rate heterogeneity across sites approximated using four discrete categories, patristic between-species distances (measured as the sum of internal branch lengths connecting the basal nodes of the species) ranged from 0.113 to 0.334 changes per site, whereas within-species patristic distances (measured as the sum of branch lengths between terminals within a species) ranged from zero to 0.005 changes per site in *C. confusus*, 0.014 in *C. corixae*, 0.003 in *C. dextrorsus* and 0.011 in *C. macropus*. Total branch length summed to 0.448 changes per site.

## Discussion

Sundberg et al. (2018a) demonstrated that the species of *Coreomyces* are more specific to the position on the host than to the host taxon. Previous studies of Laboulbeniales demonstrated that thallus morphology of a species may vary with the thallus position on the host (Goldmann and Weir 2012, Goldmann et al. 2013, Haelewaters 2018). Our results confirm this, but also indicate that different species may adopt a similar or identical morphology when they share the same position

(*C. confusus* and *C. macropus*), or grow in close proximity to each other (the dorsal forms of *C. corixae* and *C. dextrorsus*). Unfortunately, descriptions of species from the early 20th century are sometimes difficult to interpret, because they can be imprecise about the position on the host (as is the case for e.g. *C. corixae*, Thaxter 1902). In many cases, descriptions seem to be based on relatively few thalli from one or a few hosts, often from a single location. Another dilemma is the fact that old type material, often embedded in some medium on a microscope slide, cannot be studied using molecular techniques, which makes the naming of taxa in accordance with existing types a delicate task. In summary, our findings show that circumscriptions of species in *Coreomyces* are difficult based only on morphology, and that taxonomy needs to be based on the integration of molecular and morphological data.

## Taxonomy

***Coreomyces confusus* H. Sundb., S. Ekman & Kruys, sp. nov. Fig. 2a–c**

**Mycobank: MB839336**

A species similar to *C. macropus*, but differing in that the perithecium is  $\pm$  asymmetric with the posterior side bulging and the anterior side less bulging or straight, whereas in *C. macropus* both sides are equal, giving the perithecium a symmetric appearance. Furthermore, cell II in *C. confusus* is mostly of uniform width, or only slightly tapering upwards, and cells II and III are equally wide or nearly so. In *C. macropus* cell II is often distinctly tapering upwards, and cell III is often much narrower than cell II.

**Type:** Fig. 2a (holotype).

### **Etymology**

The epithet reflects that the species is easily mistaken for *C. macropus*.

**Oligonucleotide signature.** *Coreomyces confusus* has the unique signature ATCTYTTTAAGGCTTTAGGAATCGC starting in position 48 of the ITS1.

### **Description**

Hemelytral form. Thallus slender, 402–426–523  $\mu\text{m}$  long from foot to perithecial apex ( $n=3$ ). Upper half  $\pm$  straight. The three basal cells (I–III) usually curved, primarily near the base, resulting in an L- or J-like appearance. Foot  $\pm$  rhizoidal, sometimes two-lobed. Receptacle pale yellowish brown to amber brown. Cell I L/W (including foot) 2.2–2.6–2.6 ( $n=3$ ), elongated, curved to rarely straight and slightly tapering towards the foot. Cell II L/W 2.6–3.0–3.5 ( $n=3$ ), elongated, straight to moderately curved, equal in width or only very slightly tapering upwards. Cell III L/W 1.0–1.5–1.7 ( $n=3$ ), elongated, equal in width to cell II or marginally narrower, straight to slightly curved, equal in width or slightly tapering downwards. Cell IV L/W 2.2–2.3–2.8

( $n=3$ ), straight, elongated and  $\pm$  tapering towards base. Appendiculate cells strongly flattened, 3–4–4 ( $n=3$ ) in number, gradually shorter towards the base and narrower upwards. Branchlets often evanescent or lacking in the mature thallus. No specimens with unbroken branchlets were observed in the material. Perithecium pale yellowish to amber to darker brown, 129–129–159  $\times$  35–38–46  $\mu\text{m}$  ( $n=3$ ). Venter straight, inflated. Posterior side bulging, anterior side less so, rendering the perithecium  $\pm$  asymmetric. The transition between the venter and the neck almost imperceptible and the latter tapers to a rounded apex.

Ventral abdominal form. Thallus distinctly arcuate, 417  $\mu\text{m}$  long from foot to perithecial apex ( $n=1$ ). Receptacle amber coloured. Cell I (including foot) L/W 1.3 ( $n=1$ ). Cell II L/W 1.7 ( $n=1$ ). Cell III L/W 1.2 ( $n=1$ ). Cell IV L/W 0.6 ( $n=1$ ), Cell IVa; L/W 2.8 ( $n=1$ ). Appendiculate cells strongly flattened, 2 ( $n=1$ ) in number, branchlets lacking. Perithecium amber coloured, 159  $\times$  38  $\mu\text{m}$  ( $n=1$ ). Venter only slightly inflated and bent. Transition between the venter and the neck almost imperceptible; the latter extends into a curved beak that tapers to a blunt apex. In all other respects similar to the hemelytral form.

#### Hosts and distribution

We have recorded *C. confusus* on the closely related genera *Callicorixa*, *Paracorixa* and *Sigara* in Sweden and Denmark (Table 1, Sundberg et al. 2018a).

#### Positions on the host

*Coreomyces confusus* occurs on the lower side of the left hemelytron margin, near the apical part of corium, in both host sexes. On male hosts, it has also been found to grow on the central part of the 5th sternite (Sundberg et al. 2018a).

#### Remarks

*Coreomyces confusus* seems rather rare (Table 1, Sundberg et al. 2018a) compared to *C. macropus*, to which it is similar. The two species are very difficult to distinguish morphologically and they also occur in the same positions on the host and in the same environments. We found a single thallus in which cell IVa is present, however this specimen had a malformed perithecium and additional undeveloped septa in the receptacle, and was therefore not included in the study.

*Coreomyces confusus* shares its position with *C. macropus*, but also with a number of other species; the only one previously reported from Europe being *C. elongatus* (Spegazzini 1918, Thaxter 1931). This species was described from Italy and later reported from Germany by Scheloske (1969). It is characterised by an almost straight thallus with an olive-brown colouration and is easily distinguished from our material.

#### *Coreomyces dextrorsus* H. Sundb., S. Ekman & Krays, sp. nov. Fig. 3a–c

#### Mycobank: MB839337

A species similar to *C. corixae*, but with thalli that are larger and paler in colour. *Coreomyces dextrorsus* also differs

in that cell I tapers very distinctly towards the base, cell II is generally more elongate, and the neck more distinct. Both sides of the perithecium are mostly convex in *C. dextrorsus*, whereas the anterior side is often straight or even slightly concave in *C. corixae*.

**Type:** Fig. 3a (holotype).

#### Etymology

The epithet reflects the species most frequent position on the ventral side of the host abdomen, to the right of the middle.

**Oligonucleotide signature.** *Coreomyces dextrorsus* has the unique signature ACATAGATAGCGGGTGGTTTCGCAT ATC starting in position 240 of the ITS1.

#### Description

Ventral abdominal form. Thallus stout, 299–337–363  $\mu\text{m}$  long from foot to perithecial apex ( $n=11$ ), slightly arcuate to  $\pm$  straight. Septa between cells in the receptacle  $\pm$  constricted. Foot triangular/hoof shaped, pointing towards the posterior side. Receptacle pale yellowish, slightly curved away from the posterior (appendage-bearing) side, or  $\pm$  straight. Cell I L/W (including foot) 1.4–1.8–2.0 ( $n=11$ ), distinctly tapering towards the base resulting in a trapezoid shape. Cell II L/W 1.0–1.4–1.8 ( $n=11$ ), curved, elongated, slightly tapering downwards, non to distinctly inflated. Cell III L/W 0.6–0.8–1.0 ( $n=11$ ), straight to moderately curved, slightly flattened to nearly isodiametric, width almost equal throughout its length but sometimes much inflated. Cell IV L/W 0.6–1.0–1.2 ( $n=11$ ),  $\pm$  straight, almost isodiametric or slightly flattened,  $\pm$  tapering towards base, rarely slightly inflated. Appendiculate cells  $\pm$  straight, strongly flattened, 2–4–5 ( $n=11$ ) in number, apically becoming successively longer and bearing (often bountifully) up to 162  $\mu\text{m}$  long, simple or branched sterile branchlets that sometimes are broken off or are lacking. Fertile branchlets not observed. Perithecium 107–128–142  $\times$  38–54–65  $\mu\text{m}$  ( $n=11$ ), pale yellowish, stout,  $\pm$  ovoid/onion-shaped and almost always wider than cell IV. Venter straight in the lower half, slightly bent in the same direction as the receptacle towards the neck. Posterior and anterior sides normally convex, more rarely with a straight anterior side. Neck short, and usually very distinct, distinctly bent and displaced towards the anterior side. Apex truncate with 4 or more papillae or teeth lining the ostiole. Ascospores (Fig. 3b) hyaline, elongated, curved fusiform, 67–69  $\times$  7  $\mu\text{m}$  ( $n=4$ ), two-celled, with a submedian septum. A gelatinous sheet covers the lower cell and is more prominent towards the tip.

Dorsal abdominal form. Thallus slender  $\pm$  sigmoid, 338  $\mu\text{m}$  long from foot to perithecial apex ( $n=1$ ), which is close to the median value for the ventral form. Foot hoof like. Receptacle pale yellowish; cell I–III bent away from the posterior side of thallus, elongated and of  $\pm$  the same width; cell IV inflated, constricted at the end that meets the perithecium. Cell I L/W 2.2 ( $n=1$ ). Cell II L/W 2.0 ( $n=1$ ). Cell

III L/W 1.4 (n=1). Cell IV L/W 1.2 (n=1). Appendiculate cells 4 in number (n=1) ± straight, strongly flattened, apically becoming successively longer. Branchlets present, but broken off at the base in the single thallus observed in this study. Perithecium 107 × 38 µm (n=1), slender, slightly curved anteriorly but the posterior side almost straight, neck distinct with a truncated apex and 4 papillae lining the forward pointing ostiole. In all other respects similar to the ventral form.

#### Hosts and distribution

*Coreomyces dextrorsus* was found on members of the closely related genera *Callicorixa* and *Sigara* in Denmark and Sweden (Table 1, Sundberg et al. 2018a).

#### Positions on the host

This species occurs on the anterior half of the right lobe of sternite 8, towards the inner margin, rarely more posteriorly or in the middle of the lobe. It is also found on the middle lobe of sternite 7, adjacent to 8 or on the part of 8 covered by this lobe. On male hosts, it has also been found to grow on the central part of the 5th sternite (Sundberg et al. 2018a). Also encountered near the right margin of tergite 8 close to tergite 7. Infected females seem to be rare, but a single thallus in the same position as in males was encountered in a previous study (Sundberg et al. 2018a).

#### Remarks

*Coreomyces dextrorsus* is closely related to *C. corixae* according to the phylogeny of Sundberg et al. (2018a). They are morphologically very similar in shape, although *C. dextrorsus* is usually considerably larger in all respects and gives a paler impression. *Coreomyces dextrorsus* also differs in that cell I tapers very distinctly towards the base, cell II is generally more elongate, and the neck more distinct. Both sides of the perithecium are mostly convex in *C. dextrorsus*, whereas the anterior side is often straight or even slightly concave in *C. corixae*. The spores of *C. dextrorsus* are considerably larger than the dimensions reported by Santamaria (2003) for *C. corixae* (38–43 µm). Furthermore, the main position of *C. dextrorsus* on its host is clearly distinct from that of *C. corixae*, although a small and rare overlap cannot be completely ruled out. *Coreomyces dextrorsus*, like *C. corixae*, was rarely found dorsally on the right margin of males of the genus *Sigara*. In this position the two species can be hard to separate morphologically. The few observations (n=2) of *C. dextrorsus* occurred, however, in a more posterior position than in *C. corixae* (posterior to the middle of tergite 8). This is the same pattern seen when the two species occupy a ventral position, with *C. dextrorsus* occurring in a more posterior position compared to *C. corixae*.

*Coreomyces dextrorsus* occupies approximately the same position as *C. argentinensis* Speg., *C. chinensis* Thaxt. and *C. subdivisus* Thaxt., which differ from *C. dextrorsus* mainly in their smaller size, overall different shape and in their cell arrangement (Spegazzini 1917, Thaxter 1918).

#### *Coreomyces corixae* Thaxt. (1902, p. 56, as '*C. corixae*')

**Type:** United States, Massachusetts, Middlesex Co., Lexington/Arlington, 'on inferior surface of abdomen of *Corisa kennicotti* Uhler' [= *Hesperocorixa kennicottii*], 1901, C. Bullard (FH 00313593, syntype, seen); Iowa, on '*Corisa* sp.' (FH, syntype, not seen).

**Taxonomic synonym:** *Coreomyces italicus* Spegazzini (1918, p. 321).

**Illustrations:** Fig. 4a–d. Thaxter (1908, Pl. LXXI Fig. 16–18). Picard (1913, Fig. 9). Spegazzini (1918, Fig. 1, as *Coreomyces italicus*). Sugiyama & Hayama (1981, Fig. 1–2, as *Coreomyces italicus*). Majewski (1994, Pl. 20 Fig. 1–13, Pl. 21 Fig. 1–9). Santamaria (2003, Fig. 39a–d).

**Oligonucleotide signature.** *Coreomyces corixae* has the unique signature CTGAAARATGAAGATAAAAATGTTTA starting in position 46 or 47 of the ITS1.

#### Description

Ventral abdominal form. Thallus stout to slender, 158–222–271 µm long from foot to perithecial apex (n=17), slightly to distinctly arcuate, curved away from the posterior (appendage bearing) side, but sometimes ± straight. Cells in the receptacle often inflated with constrictions between them. Foot triangular/hoof-shaped, pointing towards the posterior side. Receptacle pale yellowish brown, usually arcuate, rarely straight. Cell I L/W (including foot) 1.5–1.9–2.2 (n=16), ± square (excluding foot) to rectangular, or slightly tapering towards the base, more rarely inflated. Cell II L/W 0.8–1.1–1.9 (n=17), curved, more seldom straight, mostly ± inflated, nearly isodiametric or slightly elongated, slightly tapering. Cell III L/W 0.5–0.7–1.0 (n=17), straight or very moderately

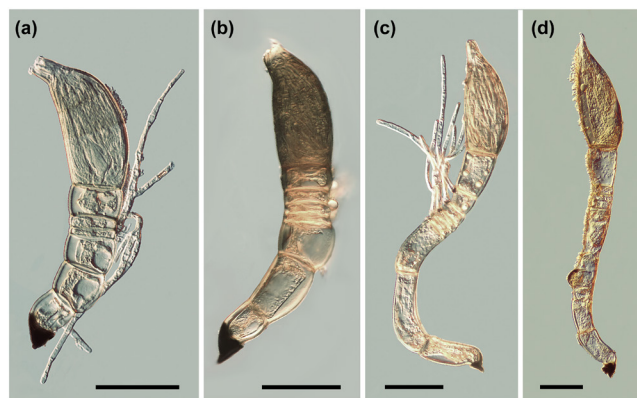


Figure 4. Morphology of *Coreomyces corixae*. (a) Thallus of the common ventral abdominal form, with sterile branchlets attached to the appendiculate cells. ID H129-1 (Table 1). (b) Thallus of the ventral abdominal bicoloured form. ID H126-1 (Table 1). (c) Sigmoid thallus of the dorsal abdominal form, with sterile branchlets attached to the appendiculate cells. ID H145-7 (Table 1). (d) Sigmoid thallus of the dorsal abdominal form with an acuminate apex (possibly with an epibiotic fungus producing conidia, which was not uncommon in our material). ID H135-3 (Table 1). Scale bars = 50 µm.



curved, somewhat flattened or nearly isodiametric, mostly  $\pm$  inflated and sometimes slightly tapering. Cell IV L/W 0.4–0.6–0.7 (n=15),  $\pm$  straight, rectangular or tapering slightly towards base, sometimes inflated, sometimes missing. Appendiculate cells straight, strongly flattened, 1–2–3 (n=17) in number, gradually shorter towards the base and bearing simple or branched sterile branchlets up to 150  $\mu\text{m}$  long. Fertile branchlets are rarely observed. Perithecium pale yellowish brown, or sometimes darker, 78–90–109  $\times$  25–39–58  $\mu\text{m}$  (n=17). As wide as cell IV, or wider. In the latter case  $\pm$  inflated in the lower half giving it a slightly ovoid/onion-like shape. Venter straight, but sometimes slightly bent in the same direction as the lower receptacle, and then often with the posterior side convex and the anterior straight. Neck short,  $\pm$  distinct, distinctly bent and displaced towards the anterior side. Apex truncate with 4–6 papillae lining the ostiole. Rarely the apex is rounded/blunt and then lacks the papillae.

Dorsal abdominal form. Thallus differs from thalli in ventral position by being, generally, much longer, 242–306–410  $\mu\text{m}$  (n=26), than the ventral form. The overall thallus shape is  $\pm$  sigmoid (not arcuate or straight as in the ventral form), sometimes to the extent that cells I and II are folded back onto cell III. Receptacle pale yellowish brown. Cell I–II are mostly more elongated than in the ventral form, cell III more similar to that of the ventral form. Cell IV is mostly about as long as wide. Cell I L/W 2.1–2.4–3.0 (n=26). Cell II L/W 1.3–2.2–3.3 (n=26). Cell III L/W 0.7–1.3–2.2 (n=26). Cell IV L/W 0.8–1.0–1.5 (n=26). Appendiculate cells 2–3–6 (n=26) in number, bearing simple or branched sterile branchlets up to 175  $\mu\text{m}$  long. Perithecium pale yellowish brown to amber coloured, 85–96–126  $\times$  26–39–54  $\mu\text{m}$  (n=26), slender to inflated/ovoid, straight or curved. The neck is usually not as distinct as in the ventral form, not displaced or only slightly so. Apex is usually rounded, or sometimes truncated, but always with the ostiole pointing forward. The papillae lining the ostiole are lacking in the rounded form, and seem less pronounced in the truncated form compared to thalli in the ventral position. In all other respects similar to the ventral form.

#### Hosts and distribution

We have encountered *C. corixae* on hosts belonging to the closely related genera *Arctocorisa* (new host genus) *Callicorisa*, *Hesperocorisa* and *Sigara*, as well as on members of the distantly related genus *Cymatia*. We report it here as new to Denmark, Sweden and Turkey (Table 1, Sundberg et al. 2018a). It has previously been reported from countries in Asia, Europe, North and South America (Majewski 1994).

#### Positions on the host

We have come across *C. corixae* on the left half of the ventral side of the abdomen in both host sexes, mainly on sternites 6 and 7, more seldom on sternites 4, 5 and 8. *Coreomyces corixae* is quite frequently also encountered near the right margin of tergite 6 and 7 (and rarely just over the border to 8) in males of the genus *Sigara*.

#### Remarks

The examined thalli are mainly consistent with the descriptions of Spegazzini (1918), Majewski (1994) and Santamaria (2003). However, the type material of Thaxter (1902) differs in being considerably longer, more slender and straight. This may be due to phenotypic plasticity and Majewski's material seems to include specimens closer to Thaxter's in appearance. The thalli we sampled from Turkey agree with the Scandinavian material in most respects, except that our Turkish specimens predominantly have only two appendiculate cells (three in most Scandinavian thalli). This observation, along with minor differences in measurements, could simply be due to the low number of samples as well as that all Turkish thalli come from the same population. In two thalli (from Sweden and Turkey) cell IV was absent.

*Coreomyces corixae* is closely related to *C. dextrorsus* according to the phylogeny of Sundberg et al. (2018a) and is similar in appearance, apart from being generally smaller in all respects. In the material examined it also differs in that cells I and II are nearly square and that cell I does not taper as distinctly. Also, cell IV is generally more flattened. Another difference is that the perithecium is often darker in colour than the receptacle.

*Coreomyces corixae* appears to be cosmopolitan and has been reported from North and South America, Europe and Asia (Santamaria et al. 1991, Majewski 1994). It may turn out to be widely distributed in Europe, since we came across it in both Sweden and Turkey, but further molecular studies should test how far its distribution extends. Given its vast geographical range, *C. corixae* may turn out to be a complex of several similar species. Molecular data from *Hesperomyces virescens*, another species regarded as cosmopolitan (Santamaria et al. 1991), suggest that several species are involved (Haelewaters 2018).

Spegazzini (1918) described a taxon similar to *C. corixae* from Europe as *C. italicus*, but the latter was subsequently synonymised with *C. corixae* by Majewski (1994) and we follow Majewski's synonymization until evidence to the contrary is available. Another similar taxon, *C. bicolor*, was described by Thaxter (1931), who at the same time admitted that it might belong within the variation of *C. corixae*. We have observed two-coloured thalli of *C. corixae* in our material (Fig. 4b), which provides some support for Thaxter's suspicion. From the same animal as *C. bicolor* was described, Thaxter also described the species *C. sigmoideus* Thaxt. This grows on the 'superior surface of the abdomen, on the right side near the base'. The sigmoid shape is also found in two other taxa, likewise dorsal but growing to the left. These are *C. acuminatus* Thaxt. and *C. fastigiatus* Thaxt. They were described from a species of '*Corisa* sp.' from Chile (Thaxter 1918, 1931). A comparison of the morphology of these dorsal species with the dorsal forms of *C. corixae* and *C. dextrorsus* shows that the (sub-)sigmoid shape of the thallus in Thaxter's three species is indeed the shape most common in 'our' species when growing dorsally. Also, the acuminate perithecial apex typical of the Chilean species also occurs in some thalli of the dorsal form of *C. corixae* in our study (Fig. 4). In the case of

*C. acuminatus*, an abundance of *C. corixae* was encountered in the same locality, while *C. acuminatus* and *C. fastigiatus* were unfortunately represented with only one mature thallus each (Thaxter 1918, 1931). For some reason, Thaxter (1918) did not illustrate *C. acuminatus* and he also omitted the species in his later compilation of the genus (1931). It is tempting to speculate that the rarity of Thaxter's dorsal species may have a similar explanation as the dorsal forms in our study, i.e. that they are merely growth forms of species more commonly found in other positions on the host.

### *Coreomyces macropus* Thaxt. (1931, p. 327)

**Type:** Jamaica, Mandeville, 'on the inferior margin of the left hemelytron of *Centrocorixa kollari* Fieb.' 1909, A. E. Wight 1751 (FH 00313596, syntype, seen).

**Illustrations:** Fig. 5a–c. Thaxter (1931, Pl. LIII: Fig. 10). Majewski (1994, Pl. 17 Fig. 1–9, Pl. 18 Fig. 1–11). Santamaria (2003, Fig. 39e).

**Oligonucleotide signature.** *Coreomyces macropus* has the unique signature TGCCAGCGGGTGGTTCGTATTTTG starting in position 243 of the ITS1.

### Description

Hemelytral form. Thallus slender, 435–477–576  $\mu\text{m}$  long ( $n=14$ ), upper half  $\pm$  straight, lower half  $\pm$  bent towards the posterior side giving the thallus a backward L or J-like shape, rarely slightly sigmoid. Foot  $\pm$  rhizoid, sometimes two-lobed. Receptacle pale yellowish brown to amber brown. The three basal cells (I–III) are usually curved, downward increasingly so; sometimes only cell I is curved and the rest of the receptacle straight; more rarely the whole receptacle is slightly arcuate or sigmoid. Cell I; L/W (including foot) 2.0–2.7–3.0 ( $n=14$ ), elongated, predominantly sharply bent, equally wide or slightly tapering throughout its length. Cell II; L/W 2.5–3.1–3.7 ( $n=14$ ), elongated, straight to moderately curved, often widest in the lower part and tapering upwards, sometimes inflated. Cell III; L/W 1.5–2.4–2.8

( $n=14$ ), elongated, much more narrow than cell II, slightly curved to almost straight, equally wide throughout its length or slightly tapering towards the base. Cell IV; L/W 2.1–2.9–3.7 ( $n=14$ ), straight, elongated,  $\pm$  tapering towards base, sometimes slightly inflated towards the top. Cell IVa; L/W 2.2–2.7–3.0 ( $n=4$ ), similar in shape to cell IV. Cell IVa is present in about one third of the material. Appendiculate cells straight, strongly flattened, 3–4–6 ( $n=14$ ) in number, gradually shorter towards the base and narrower upwards. Branchlets are often evanescent or lacking in the mature thallus. No specimens with unbroken branchlets were observed in the material. Fertile branchlets not observed. Perithecium pale yellowish brown to dark brown, 112–124–152  $\times$  24–34–40  $\mu\text{m}$  ( $n=14$ ). Venter straight, width almost the same as cell IV, sides parallel to distinctly inflated but symmetrical. The transition between the venter and neck is almost imperceptible and the latter tapers to a rounded apex.

Ventral abdominal form. Thallus distinctly arcuate, 344–434–31  $\mu\text{m}$  long from foot to perithecial apex ( $n=15$ ). Receptacle pale yellowish to light amber coloured. Cell I; L/W 1.3–1.6–2.2 ( $n=15$ ). Cell II; L/W 1.7–2.2–2.8 ( $n=15$ ). Cell III; L/W 1.2–1.8–2.4 ( $n=15$ ). Cell IV; L/W 1.4–2.6–3.3 ( $n=15$ ), Cell IVa; L/W 1.8–2.3–2.5 ( $n=4$ ). Appendiculate cells strongly flattened, 1–3–5 ( $n=15$ ) in number, bearing (often lavishly) simple or branched sterile branchlets up to 211  $\mu\text{m}$  long. Fertile branchlets not observed. Perithecium pale yellowish to light amber coloured, 129–143–161  $\times$  29–33–48  $\mu\text{m}$  ( $n=15$ ). Venter slightly to strongly inflated,  $\pm$  straight. Transition between the venter and the neck is almost imperceptible, the latter extends into a curved beak that tapers to a skewed, truncate to blunt apex. In all other respects similar to the hemelytral form.

### Hosts and distribution

We encountered *C. macropus* in Denmark and Sweden (Sundberg et al. 2018a, Table 1), although the species is probably widespread in Europe (Majewski 1994). We recorded the species on *Callicorixa* and *Sigara* (Table 1), but it has previously also been reported on members of *Hesperocorixa* and, from Jamaica, on *Centrocorisa* (Majewski 1994).

### Position on the host

*Coreomyces macropus* occurs on the lower side of the margin of the left hemelytron, near the apical part of corium, in both host sexes, i.e. in agreement with Majewski (1973, 1994). We also found it on the central part of the 5th sternite on male hosts (Sundberg et al. 2018a).

### Remarks

Thaxter's (1931) type material and description of *C. macropus* is quite different from the material examined in this study. Especially the shape of the perithecium differs by having an almost equal width throughout the length of the venter. There are individuals of similar appearance in our material (Fig. 3e) but they are exceptions. Although Thaxter's type material may represent another taxon than the material of this study (and possibly all European material) we follow



Figure 5. Morphology of *Coreomyces macropus*. (a) Thallus from the lower side of the left hemelytron margin. ID H145-1 (Table 1). (b) Thallus from the lower side of the left hemelytron margin, with additional cell IVa just below the perithecium. ID H152-1 (Table 1). (c) Thallus of the ventral abdominal form, with sterile branchlets attached to the appendiculate cells and additional cell IVa. ID H166-1 (Table 1). Scale bars = 50  $\mu\text{m}$ .

other authors (Majewski 1994) and retain the name *C. macropus* for the time being.

*Coreomyces macropus* and *C. confusus* appear in the same position on the host. The two species are difficult to distinguish, but some morphological characters seem to be diagnostic. The perithecium is mostly symmetric in *C. macropus*, but asymmetric with the anterior almost straight and the posterior bulging in *C. confusus*. Cell II is mostly widest in its lower part and tapering upwards in *C. macropus*, whereas in *C. confusus* this cell is mostly equally wide along its entire length, or only very slightly tapering upwards. In *C. macropus*, cell III is mostly much narrower than cell II, whereas in *C. confusus* they are approximately of the same width (or sometimes cell III is slightly narrower than cell II).

*Coreomyces macropus*, like *C. confusus*, grows also on the abdomen, at the centre of the 5th sternite. In our material, thalli in this position are only encountered on male hosts, but neither Thaxter (1931) nor Santamaria (2003) mention anything about host sex. Majewski (1973, 1994), however, states he did not observe any sex-specificity in the genus as a whole. In the abdominal position, *C. macropus* is much different from its hemelytral form. Our description of *C. macropus* from the abdominal position agrees with the description of *C. arcuatus* given by Majewski (1973, 1994), apart from our thalli being generally larger and having a larger span in the number of appendiculate cells. The original description of *C. arcuatus* (Thaxter 1931: Plate LII, Fig. 10), on the other hand, shows less resemblance to our material in terms of size and shape. Thaxter's material is considerably smaller, thallus length 328–352 µm compared to 344–531 µm in our material and also differ from both our material and Majewski's description in the shape of the perithecium. In Thaxter's description the tip of the perithecium taper quite abruptly with a neck-like protrusion, whereas in our material and Majewski's description the perithecium taper smoothly rendering a more beak-like appearance. Both our material (Fig. 5c) and Majewski's illustrations (1994, pl. 19: Fig. 1–10) show more resemblance to Thaxter's illustrations of *C. curvatus* (1905, 1908: Plate LXXI, Fig. 7). Thaxter says in his description (1905) that *C. curvatus* grows on the underside of the left elytron margin, i.e. in the same position as *C. macropus*. This may be a mistake, since Thaxter, on the slide of the type material, stated the position as 'on inf abd.' which we interpret as 'on inferior abdomen'. In Shen et al. (2006), the thalli of what they interpreted as *C. curvatus* were also found growing in the abdominal position. The possible mistake by Thaxter may thus explain that the shape of *C. curvatus* looks like it grows on the abdomen. *Coreomyces curvatus* has been recorded from the United States, Jamaica and China (Thaxter 1931, Shen et al. 2006) and was originally described from the left elytral margin of its host (Thaxter 1905).

Both *C. arcuatus* and *C. macropus* were originally described from the same locality in Jamaica (Thaxter 1931). The European records of *C. macropus* may represent another species than the type from Jamaica, given the more slender perithecium of the latter, the geographic distance and the different climatic conditions. We suggest that the current

understanding of *C. macropus* may turn out to be comprised of a species complex rather than a single species with an inter-continental distribution.

*Acknowledgements* – A special acknowledgement to Tom W. May for valuable input on how to choose images as types.

*Funding* – This research was supported by grants from Kapten Carl Stenholms donationsfond.

## Author contributions

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## Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.fbg79cntw>> (Sundberg et al. 2021).

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