A survey of bdelloid rotifers from coastal ponds in Southern Norway

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ABSTRACT

We report the results of the first survey of bdelloid rotifers, microscopic aquatic animals, in continental Norway, collected from coastal ponds in the Southern part of the country in Autumn 2021, using a morphological approach in species identification. Out of 25 ponds, 19 bdelloid species were found, ten in water samples and another nine in limno-terrestrial habitats just above the waterline of the ponds. Seven of the species are new records for mainland Norway. Three species could be identified to genus level only and may be novel taxa, not only for Norway but for science: further studies are needed on these animals to clarify their taxonomic identity. We also obtained COI sequences from 194 animals of eight of the species to compare them with what is known in GenBank in a phylogenetic context and confirm the reliability of morphological identification. This data contributes to our understanding of the taxonomic and biogeographic diversity of bdelloid rotifers in Norway. In addition, the newly available sequences increase the coverage of the reference library of bdelloid rotifers for future studies employing DNA metabarcoding.

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INTRODUCTION

Freshwater invertebrates are commonly sampled extensively for biological monitoring programs in large lakes and rivers (Hering *et al.*, 2010; Vitecek *et al.*, 2021). This is especially true in poorly studied Nordic countries like Norway, where biodiversity inventories are often done as part of assays on freshwater fish, or to study the effects of hydropower regulation or acidic precipitation on freshwater fauna (Schartau *et al.*, 2008; Halleraker *et al.*, 2022). These localities are often located in mountain areas in Norway (Brekke *et al.*, 2010) and contain large fish communities that dwell in extensive water catchments. As a result, official biodiversity records of aquatic communities of microscopic invertebrates are heavily biased towards taxa that thrive in the larger (oligotrophic) pelagic masses (Wærvågen and Nilssen, 2003, 2011). This complicates assessing the status for many of the species, which may exclusively use profundal/littoral areas or smaller ephemeral water catchments. Many small ephemeral water bodies are coastal and eutrophic ponds; due to the lack of economic importance, they have been overlooked in major scientific investigations (except for Bjørklund, 2009). When considering the smallest of the invertebrates, the meiofauna (a collective term to consider animals that are generally smaller than 0.5 mm), the situation is even more dire (Zeppilli *et al.*, 2015; Majdi *et al.*, 2020). Sampling small coastal ponds to describe biodiversity of microscopic animals would thus benefit the knowledge of fauna in Norway.

Among the most neglected meiofaunal organisms in biodiversity studies in freshwater habitats are the bdelloid rotifers. The lack of knowledge on these organisms, in addition to the fact that

they are very small like other meiofauna (Artois *et al.*, 2011), is due to the fact that they cannot be fixed, stored, and observed later in the lab like other organisms (e.g. nematodes, copepods, monogonont rotifers), but need to be studied when they are alive and active to allow a reliable identification at species level (Wallace *et al.*, 2006). Bdelloids are a group of rotifers found in aquatic and limno-terrestrial habitats all over the world. There are over 450 described morphological species (Donner, 1965). Bdelloid rotifers are notorious for their exclusively parthenogenetic reproduction (Simion *et al.*, 2021), the ability to survive in dry, harsh environments by entering a state of desiccation-induced dormancy at any life stage (Ricci and Fontaneto, 2009) and for their high proportion of horizontally acquired genes (Wilson *et al.*, 2024), which are unusual features compared to other animals (Gao *et al.*, 2019; Nowell *et al.*, 2024). Furthermore, many bdelloid morphological species seem to occur across different continents and are considered cosmopolitan (Donner, 1965; Segers, 2007). However, a large amount of genetic diversity is known to exist for many morphospecies (Cakil *et al.*, 2021), which can therefore host complexes of cryptic species with more limited distributions (Walczyńska *et al.*, 2024). Without the inclusion of data for DNA taxonomy, species identification could be misleading if based only on morphology (Marrone *et al.*, 2023).

Given that no previous studies focused on species level identification of bdelloids from mainland Norway (Kaya *et al.*, 2010), the aim of this study is to improve our basic knowledge on diversity of bdelloids rotifers in Norway, both at the morphological and at the genetic level, to increase taxonomic and geographic coverage of bdelloids on biodiversity platforms like the Global Biodiversity Information Facility, GBIF (Lane and Edwards, 2007) and to enhance the genetic reference library on repositories of genetic diversity like GenBank (Benson *et al.*, 2012), to be used as a baseline for further studies in the area.

METHODS

Sampling

We collected samples from 25 ponds in Southern Norway, Agder county, in the areas of Arendal, Kristiansand, Lista, Mandal and Risør (Tab. 1, Fig. 1). The selection of ponds followed the criteria that they had to be small, between 20 and 500 m^2, situated below 50 m above sea level, isolated from other water catchments, and preferably within 1 km of the nearest marine coastline. Samples consisted of 250 mL of water collected with a plastic bottle directly from the shores, including floating detritus, vegetation, submerged moss and sediment. In addition, samples of dry mosses were collected above the waterline.

Tab. 1. Sampling sites with codes, names, localities, areas, coordinates (WGS84 reference) and sampling dates (MM/DD/YYYY). The bounding box for the sampled ponds is 57.98905-58.76244 N, 6.68723-9.23075 E.

Code	Name	Locality	Area	Latitude	Longitude	Date
A01	Sildevik	Færvik	Arendal	58.43789	8.80740	09/09/2021
A02	Tybakken	Færvik	Arendal	58.46200	8.81362	09/09/2021
A03	Kjørvik	Kongshavn	Arendal	58.50554	8.93708	09/09/2021
A21	Flødevigen	His	Arendal	58.42771	8.75341	09/09/2021
A22	Vesterveien	Hisøy	Arendal	58.43970	8.74216	09/09/2021
A24	Helleskogen	Helleskogen	Arendal	58.51812	8.89206	09/09/2021
K01	Roligheden	Kristiansand	Kristiansand	58.14766	8.02453	09/06/2021
K02	Hamreheia	Kristiansand	Kristiansand	58.14809	8.01582	09/06/2021
K11	Søm	Søm	Kristiansand	58.14109	8.06127	09/06/2021
K12	Høvåg	Høvåg	Kristiansand	58.16454	8.24327	09/06/2021
L11	Loshavn	Loshavn	Lista	58.06732	6.81494	09/07/2021
L12	Lomsesanden N	Farsund	Lista	58.06207	6.78802	09/07/2021
L21	Kviljo	Kviljo	Lista	58.06971	6.68723	09/07/2021
M11	Golfbane vest	Lindesnes	Mandal	58.03941	7.41113	09/08/2021
M12	Golfbane øst	Lindesnes	Mandal	58.03847	7.41524	09/08/2021
M21	Motorveiøya	Mandal	Mandal	58.03011	7.47023	09/08/2021
M22	Valvik sør	Mandal	Mandal	57.98905	7.50469	09/08/2021
M23	Valvik nord	Mandal	Mandal	57.98938	7.50378	09/08/2021
M24	Valvik mini	Mandal	Mandal	57.98927	7.50408	09/08/2021
M25	Tregde	Mandal	Mandal	58.00832	7.56969	09/08/2021
R01	Søndeled	Søndeled	Risør	58.76244	9.07821	09/10/2021
R11	Fiesund	Risør	Risør	58.68353	9.22114	09/10/2021
R21	Sundsveien	Risør	Risør	58.72323	9.19913	09/10/2021
R22	Krantoppen	Risør	Risør	58.72477	9.23075	09/10/2021
R23	Randvik	Risør	Risør	58.70957	9.21910	09/10/2021

Species identification

Animals were sorted and isolated in the field laboratory under a dissecting microscope. All isolated individuals were identified on morphological characters using a compound microscope to species level when possible, if not to genus level. The identification characters for bdelloids are only visible on active individuals (Donner, 1965) and animals were processed immediately after collecting the samples. We identified the first 100 animals isolated from each sample.

DNA amplification

After the morphological identification, DNA was extracted from single identified individuals of bdelloid rotifers in 25 µl of Chelex (InstaGene Matrix; Bio-Rad, Hercules, CA, USA) with

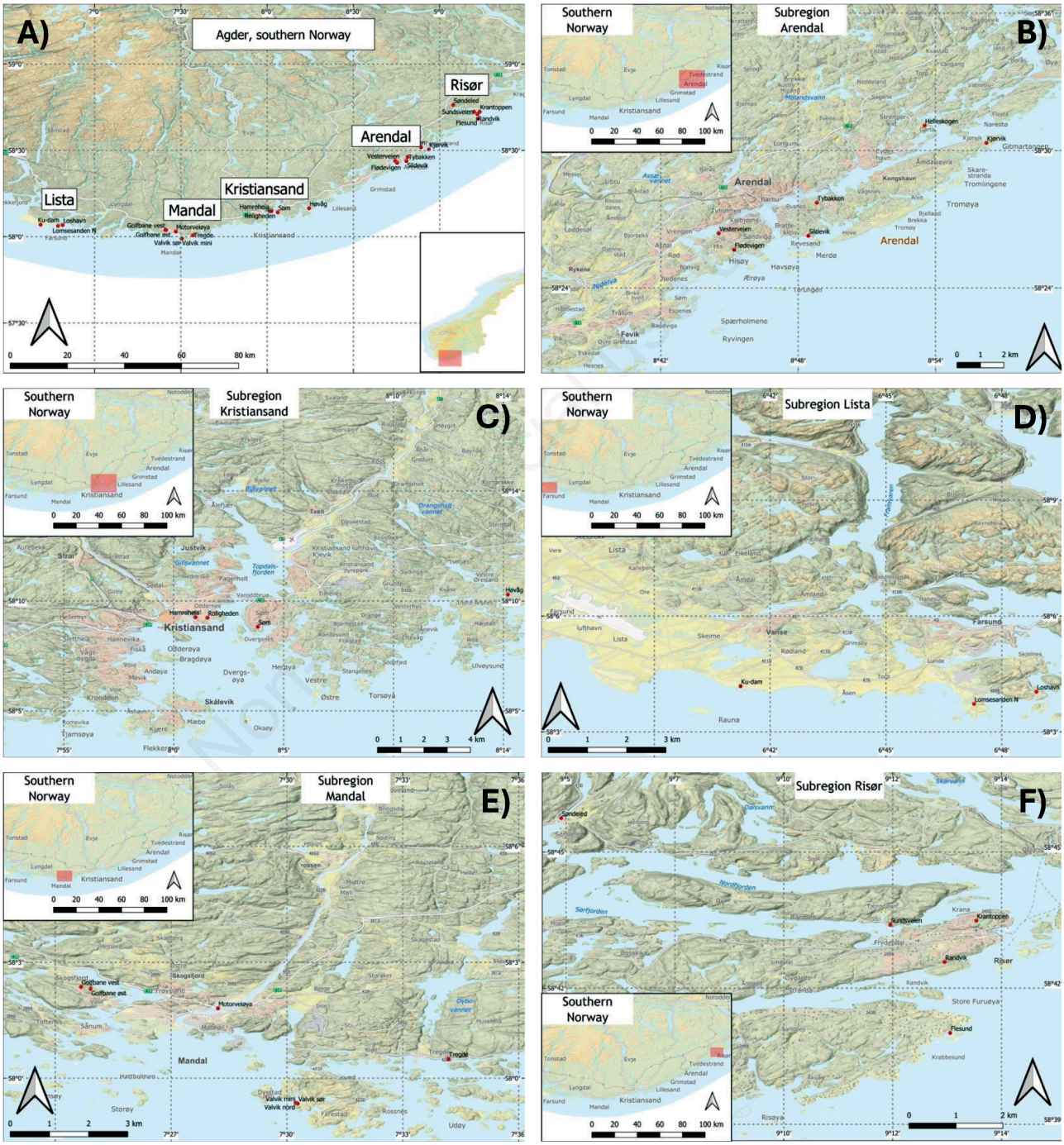

Fig. 1. Maps of sampling areas. A) Localisation of the five sampling localities in Agder, Southern Norway. B-F) Maps of the ponds in the five subregions, listed in alphabetical order: Arendal, Kristiansand, Lista, Mandal, and Risør.

the addition of 1 µL of proteinase K, incubating in a shaker at 56°C for 60 min and a final step of 100°C for 10 min. We selected the number of individuals to be sequenced for each species in proportion to the abundance of the species. For each individual, partial cytochrome c oxidase subunit 1 (COI) mitochondrial gene was sequenced following already tested protocols for bdelloid rotifers (Tang *et al*., 2014): a 661 base pairs fragment of the COI gene was PCR amplified using Folmer primers LCOI-1490 and HCOI-2198 (Folmer *et al.*, 1994). Cycle conditions comprised initial denaturation at 95°C for 5 min, followed by 42 cycles of 95°C for 1 min, 40°C for 20 s and 72°C for 50 s, and a final extension step of 72°C for 5 min. Purification and sequencing were performed by an external company. Chromatograms were checked for ambiguous positions using FINCHTV 1.4.0, aligned using MAFFT v7.0 (Katoh *et al.*, 2019) with default settings for a protein coding gene like COI, and visually checked by eye for correct protein coding in Mesquite (Maddison and Maddison, 2018).

Phylogenetic reconstructions

Reconstruction of phylogenetic relationships for each species with DNA data obtained in this study were performed with BEAST 2.6.1 (Bouckaert *et al.*, 2014). The datasets for each species included all the sequences obtained from the survey in Southern Norway, in addition to all haplotypes for the species available from GenBank. Such haplotypes were obtained by downloading from GenBank all available sequences for each species, aligning them using MAFFT v7.0, and removing identical sequences by comparing genetic distances in the R package ape v5.7.1 (Paradis and Schliep, 2019). One alignment was obtained for each species appending the Norwegian sequences and the haplotypes from GenBank. The settings for BEAST were GTR+G+I as evolutionary model, relaxed clock, constant coalescent prior, with estimated parameters for 10 million generations. Burnin was set as 20% for reconstructions that passed the threshold of Effective Sample Size (ESS) >200 for the likelihoods of the tree and coalescent model. Due to the high level of saturation in COI in bdelloids (Tang *et al.*, 2014), which could hinder the accuracy of a combined phylogenetic analysis, we performed separate reconstructions for each species rather than merging all sequences into a single analysis.

Given the high amount of genetic variability in COI in bdelloids, we did not perform any test on DNA taxonomy, but we simply checked whether the DNA sequences from our survey in Southern Norway clustered in monophyletic groups together with sequences of the same morphospecies available in GenBank. In addition, we searched in BLAST for the closest matches and reported the values of uncorrected genetic distances to them.

RESULTS

Overall, 19 bdelloid species were identified. In the water samples from the 25 ponds, 10 bdelloid species were found (Tab. 2). The highest number of five bdelloid species was found in three ponds, whereas in five ponds we did not find any bdelloid. The most common species was *Rotaria rotatoria*, found in 13 of the 25 analysed ponds, followed by *Otostephanos donneri* and *Rotaria macrura* (11 ponds), *Dissotrocha macrostyla* (7 ponds) and *Philodina megalotrocha* (6 ponds); the other five species were found only occasionally.

The other nine species were found in the surrounding dry habitats just above the waterline of the ponds: *Adineta steineri* Bartoš, 1951 in A22, *Adineta vaga* (Davis, 1873) in A21, *Dissotrocha aculeata* (Ehrenberg, 1832) in L11, *Habrotrocha constricta* (Dujardin, 1841) in M21, *Habrotrocha lata* (Bryce, 1892) in A02, *Macrotrachela plicata hirundinella* (Murray, 1892) in M25, *Macrotrachela quadricornifera scutellata* Schulte, 1886 in L11, *Philodina acuticornis* Murray, 1902 in M24, and *Philodina rugosa* Bryce, 1903 in A21.

Two of the taxa identified to genus level, *Habrotrocha* sp. and *Rotaria* sp., did not fit the description of any of the known species, and were found in one population each. The other taxon identified to genus level, *Philodina* sp., revealed characters that could be considered intermediate between different known species. For these three taxa, further studies are currently ongoing. In total, we successfully obtained 194 COI sequences from eight of the species collected in the survey in Southern Norway. For the other species, unfortunately, we failed in obtaining reliable sequences.

Tab. 2. Occurrence of bdelloid species in the 25 analysed ponds, with number of species in each pond in the last row and number of occurrences of each species in the last column.

Species	A01	A02	A03	A21	A22	A24	K01	K02	K11	K12	L11	L12	L21	M11	M12	M21	M22	M23	M24	M25	R01	R11	R21	R22	R23	Total
Adineta gracilis Janson, 1893	x																									1
Dissotrocha macrostyla (Ehrenberg, 1838)	x	x	x	x		x	x																		x	7
Habrotrocha sp.														x												1
Otostephanos donneri Bartoš, 1959	x	x	x		x				x	x		x	x	x		x					x					11
Philodina megalotrocha Ehrenberg, 1832									x				x			x					x	x		x		6
Philodina sp.					x					x			x								x					4
Rotaria macrura (Ehrenberg, 1832)				x	x		x	x	x	x			x			x					x			x	x	11
Rotaria rotatoria (Pallas, 1766)	x	x	x							x		x	x	x		x			x		x		x	x	x	13
Rotaria sp.	x																									1
Rotaria tardigrada (Ehrenberg, 1830)																			x			x			x	3
Total	5	3	3	2	3	1	2	1	3	4	0	2	5	3	0	4	0	0	2	0	5	2	1	3	4	

For *Adineta vaga*, we obtained one sequence (GenBank accession number OQ589537), in addition to 504 (merged into 177 haplotypes) from GenBank (Fig. 2A). The Norwegian sequence clustered within the vast diversity of the morphospecies, with an uncorrected genetic similarity of 89.5% to the closest available match in GenBank, from the UK (EF173219).

For *Dissotrocha macrostyla*, we obtained seven sequences (GenBank accession numbers OQ589508-OQ589510, OQ589513-OQ589516), in addition to 40 (merged into 30 haplotypes) from GenBank (Fig. 2B). The Norwegian sequences clustered in four main clades, all within the diversity of the morphospecies. The four clades were also close to already known sequences, ranging from 99.0% similarity to an Italian sequence (DQ656811) to 89.2% to another Italian sequence (KF582500).

For *Macrotrachela plicata hirundinella*, we obtained one sequence (GenBank accession number OQ589610), in addition to five from GenBank for *M. plicata s.l.* (Fig. 2C). The Norwegian sequence clustered as sister to a group of *M. plicata s.l.*, with uncorrected genetic similarity of 88.9% to it (MH251809).

For *Otostephanos donneri*, we obtained four sequences (GenBank accession numbers OQ589511, OQ589512, OQ589602, OQ589603), in addition to six from GenBank (Fig. 2D). The Norwegian sequences clustered within the morphospecies in a clade with a sequence from Italy (EF650595), ranging from 96.1% to 88.2% in similarity to it.

For *Philodina megalotrocha*, we obtained 13 sequences (GenBank accession numbers OQ589685-OQ589697), in addition to 194 (merged into 101 haplotypes) from GenBank (Fig. 2E). The Norwegian sequences clustered within the morphospecies, with a similarity of 95.7% to a sequence from UK (JQ309198).

For *Rotaria macrura*, we obtained 160 sequences (GenBank accession numbers OQ589517-OQ589536, OQ589541-OQ589601, OQ589611-OQ589684, OQ589698-OQ589702), in addition to 12 from GenBank (Fig. 2F). The Norwegian sequences formed two clusters, with a genetic similarity of 94.0% between them, and between 99.4% to a sequence from Italy (DQ656816) to 93.5% to a sequence from UK (EU499848).

For *Rotaria rotatoria*, we obtained four sequences (GenBank accession numbers OQ589538-OQ589540, OQ589605), in addition to 925 (merged into 344 haplotypes) from GenBank (Fig. 2G). The Norwegian sequences fell in three different clusters with high similarity to already known sequences: one at 100.0% with an Italian sequence (DQ656834), one at 99.3% with a sequence from Sweden (JQ309316), and a cluster at 99.6% similarity to another sequence from Sweden (JQ309341).

For *Rotaria tardigrada*, we obtained four sequences (GenBank accession numbers OQ589606-OQ589609), in addition to 29 (merged into 24 haplotypes) from GenBank (Fig. 2H). The Norwegian sequences fell in a clade within the morphospecies, with 96.6% similarity to a sequence from Italy (DQ656869).

DISCUSSION

The species composition of the bdelloid communities found in the coastal ponds in Southern Norway is rather typical for ponds in the Western Palearctic (Donner, 1965). For example, all species from the survey, except for *R. macrura*, were also found in a survey of *Sphagnum* bogs in Switzerland (Fontaneto *et al.*, 2019). Communities of bdelloid species found in lentic water bodies like ponds are indeed quite consistent across Europe and rather different from bdelloid communities found in lotic habitats like streams and limno-terrestrial habitats such as mosses, lichens, and soils (Fontaneto *et al.*, 2006; Majdi *et al.*, 2024).

Notwithstanding the expected list of species found in coastal ponds, which is not novel for such habitats in the Western Palearctic, the data from the survey provide seven species as new records for Norway. Previous studies in the country already found *Adineta vaga*, *Dissotrocha aculeata*, *Dissotrocha macrostyla*, *Habrotrocha constricta*, *Habrotrocha lata*, *Philodina megalotrocha*, *Rotaria macrura*, *Rotaria rotatoria*, and *Rotaria tardigrada* among the species found in our survey (Bjørklund, 2009; De Yong *et al.*, 2014). Instead, *Adineta gracilis*, *Adineta steineri*, *Macrotrachela plicata hirundinella*, *Macrotrachela quadricornifera scutellata*, *Otostephanos donneri*, *Philodina acuticornis*, and *Philodina rugosa* are here cited from mainland Norway for the first time. In addition, we could not identify all taxa to species level, and the animals marked as *Habrotrocha* sp., *Philodina* sp., and *Rotaria* sp. may indeed represent novel taxa, not only for Norway but for science. Further analyses are needed on these samples to clarify their taxonomic identity.

Additional more recent records of bdelloids from Norway can be found in the Global Biodiversity Information Facility, GBIF, where a dataset from DNA metabarcoding in eight lakes revealed the presence of *Adineta vaga*, *Dissotrocha aculeata*, *Philodina citrina* Ehrenberg, 1832 and *Philodina megalotrocha* (Majaneva and Grainger, 2022). Even if the authors state that "caution should be exercised when interpreting occurrences of single species" from metabarcoding, these species may indeed exist in those lakes. We found three of the species in our survey, except for *P. citrina*. Another recent study using DNA sequences to identify bdelloid diversity in Norway focused on glaciers in the Northern part of the country (Shain *et al.*, 2024), but only one taxon could be reliably assigned to species level in such data, namely *Philodina flaviceps* Bryce, 1906, not found in our survey.

Another biodiversity platform, iNaturalist, does not provide additional records from Norway, if not for an unidentified species of the genus *Adineta* (https://www.inaturalist.org/ observations/156938896). Other recent studies on rotifers in Norway dealt preferentially with monogonont rotifers and not with bdelloid rotifers, e.g. Wærvågen and Nilssen (2003, 2011). No previous studies focused intensively on species-level identification of bdelloids from mainland Norway and only detailed studies from Svalbard existed so far on bdelloids for Norwegian territories (Kaya *et al.*, 2010).

The use of DNA sequence data to validate species identification from morphology is a useful tool: we indeed confirmed all morphospecies when comparing the data from the survey with sequences of the same marker, namely COI, previously uploaded in GenBank from other parts of the world. A large genetic diversity within each morphospecies was confirmed for bdelloids: we found uncorrected genetic distances up to 12% within the same morphospecies, in line with results from previous analyses (Fontaneto *et al.*, 2009; Tang *et al.*, 2014; Cakil *et al.*, 2021). Thanks to the availability of a reference library in GenBank and the addition of the new sequences from our survey, monitoring of biodiversity of bdelloid rotifers in Norwegian coastal ponds through DNA metabarcoding could now be performed reliably, confirming the usefulness of producing local reference library of the organisms under study for metabarcoding surveys (Garlaschè *et al.*, 2023; Macher *et al.*, 2024).

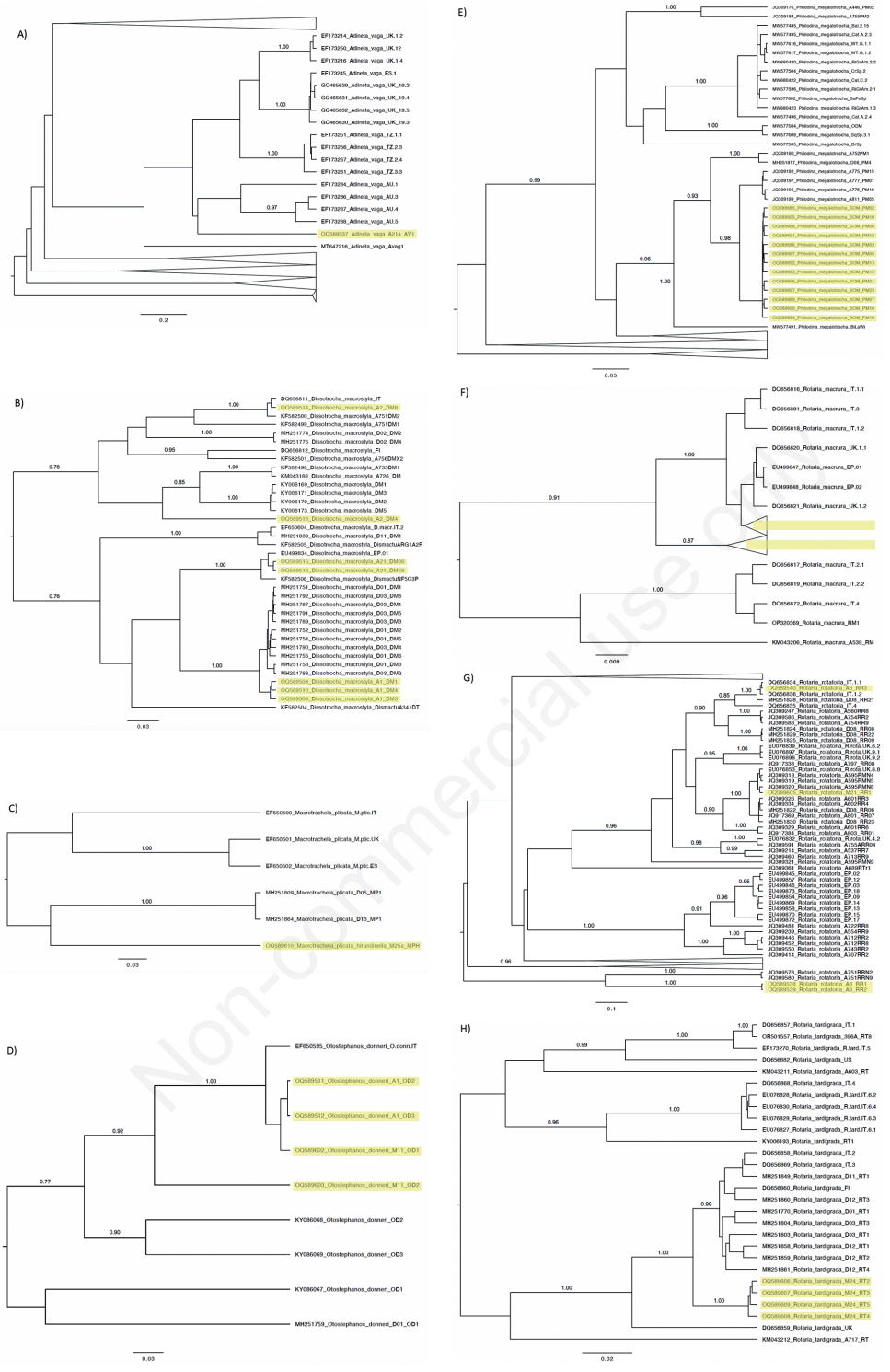

Fig. 2. Phylogenetic relationships of COI sequences from the current survey in Southern Norway (highlighted in yellow) in comparison to the known genetic diversity from GenBank for the eight species for which we obtained DNA sequence data: A) *Adineta vaga*, B) *Dissotrocha macrostyla*, C) *Macrotrachela plicata hirundinella*, D) *Otostephanos donneri*, E) *Philodina megalotrocha*, F) *Rotaria macrura*, G) *Rotaria rotatoria*, H) *Rotaria tardigrada*. Sequences from GenBank are collapsed to haplotype, whereas sequences from the survey in Norway are all kept in the analyses. BEAST reconstructed trees are presented under a GTR+I+G model, with scale bars proportional to substitutions per site. Poster probabilities are reported on branches, but not for short terminal branches and when lower than 0.75. Large clades without any Norwegian sequence were collapsed to improve visibility of the trees. DNA sequences from the survey in Southern Norway are highlighted in yellow; for *R. macrura*, all Norwegian sequences were collapsed in two major clades with little or no variability within each clade.

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