



Ecrobia ventrosa (Montagu, 1803) (Truncatelloidea: Hydrobiidae) in the interior of Central Germany: identification and faunal history

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ABSTRACT

Numerous Quaternary and subrecent occurrences of brackish water snails (Truncatelloidea: Hydrobiidae, Cochliopidae[?]) have been recorded in northern Central Germany (Thuringia, Saxony-Anhalt). This high concentration of inland occurrences is unparalleled in Central Europe. The Holocene mass occurrences in the Mansfeld Lake region have become particularly well known. Today, brackish water snails are extinct in Central Germany. This makes the discovery of numerous mummified hydrobiid snails in the Regius Collection (Senckenberg Natural History Collections Dresden, Museum of Zoology), which Karl Regius was able to collect alive in 1948/1949 in a side ditch of the Sülze river north-east of Dodendorf, all the more significant. This is the only place in Central Germany where the snails have ever been found alive. This material provided the first opportunity to carry out a reliable identification using molecular genetic methods. Not only was *Ecrobia ventrosa* (Montagu, 1803) confirmed for Central Germany, but also extensive comparisons were made with 33 recent populations of this species from European and North African coasts. These showed that *E. ventrosa* from Dodendorf was most closely related to the populations of the Baltic Sea, the North Sea and the neighbouring Atlantic.

INTRODUCTION

In northern Central Germany, in the surroundings of the Harz Mountains (Thuringia and Saxony-Anhalt), numerous Quaternary and subrecent occurrences of halophilic faunas have been recorded. Most common are brackish water snails (Truncatelloidea: Hydrobiidae, Cochliopidae[?]) and benthic foraminifera, which are normally more likely to be found in marine-influenced habitats (e.g. Martens, 1870; Goldfuss, 1894; Meng *et al.*, 2004; Wennrich *et al.*, 2007; Milker *et al.*, 2023). This high concentration of brackish water faunas in inland areas is unique for Central Europe. These occurrences are linked to saline groundwater and spring water outlets that are fed by the salts of the Zechstein (Permian), the Röt or the Middle Muschelkalk (Triassic) (Balaske, 2012). The mass occurrence of brackish water snails (Hydrobiidae) in the Mansfeld Lakes region (Fauler, Süßer and Salziger See) near Halle (Schmidt, 1856; Martens, 1870; Reinhardt, 1871; Clessin, 1877; Zacharias, 1888; Regel, 1894; Goldfuss, 1894, 1900; Geyer, 1927; Jaekel, 1962; Mania, 1973; Suderlau, 1975; Bank *et al.*, 1979; Meng *et al.*, 2004) (Fig. 1D–F), as well as the Holocene deposits near Artern, Sangerhausen, Magdeburg and the Werra area (Regius, 1950; Jaekel, 1955, 1962; Bössneck *et al.*, 2003) have become particularly well known.

Morphologically, the shells are characterized by strongly curved whorls and a fairly open umbilicus (Fig. 1), which corresponds to ‘typical’ forms of the hydrobiid *Ecrobia ventrosa* (Mon-

tagu, 1803) (see also Böters, 1998; Gittenberger *et al.*, 1998; Götting, 2008; Hoeksema & Raad, 2015; Wigham & Graham, 2017). Therefore, the snails were traditionally assigned to this species or its synonyms, including *Ventrosia ventrosa*, *Hydrobia ventrosa*, *Paludestrina ventrosa* or *Hydrobia stagnalis* (Baster, 1756) (e.g. Martens, 1870; Clessin, 1877; Goldfuss, 1900; Meng *et al.*, 2004; MolluscaBase eds., 2025) despite the general difficulties identifying *Hydrobia*-like taxa based on shell morphology (Muus, 1963; Falsinowski, 1987; also see below). Only Bank *et al.* (1979) claimed to have recognized three shells of the cochliopid *Heleobia stagnorum*, currently *Eupaludestrina stagnorum* (Gmelin, 1791), in addition to dozens of *E. ventrosa* in the collection of the Rijksmuseum van Geologie en Mineralogie, Leiden, in the material from the Mansfeld Lakes.

Less well known, however, are the numerous Pleistocene occurrences of brackish water snails in Central Germany (see Wüst, 1902; Geyer, 1927; Mertin, 1940; Zeissler, 1958, 1977; Jaekel, 1962; Mania & Mai, 1969; Mania, 1973, 2000; Bank & Butot, 1984; Meng *et al.*, 2004; Strahl *et al.*, 2010), which have hardly been systematically studied to date.

Ecrobia ventrosa is currently widespread and common along the Atlantic coasts of Europe as well as the coasts of the Mediterranean and the Black Sea (Wilke & Davis, 2000; Vandendorpe *et al.*, 2019). In Central Germany, *E. ventrosa* is now considered extinct (Jungbluth & Knorre, 2008). This makes the discovery of numerous mumi-

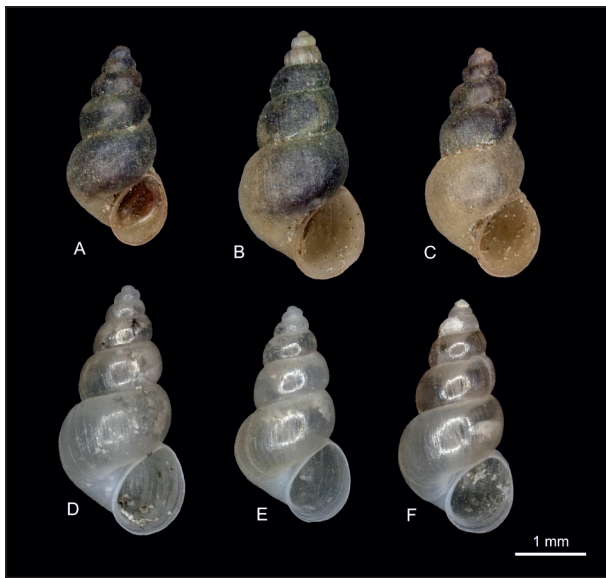


Figure 1. *Ecorbia ventrosa* from Central Germany. **A–C.** Subrecent material from Dodendorf (Saxony-Anhalt) (Regius, 1950). **D–F.** Holocene material from Lake Süßer See (Saxony-Anhalt) (Meng *et al.*, 2004).

fied snails in the Regius collection (Senckenberg Natural History Collections Dresden, Museum of Zoology) of hydrobiids, which Regius (1950) was able to collect alive in a side ditch of the Sülze river northeast of Dodendorf (52°02'35.9"N, 11°37'14.4"E), south of Magdeburg (Saxony-Anhalt), all the more significant (Figs 1A–C, 2). Regius (1950) determined these snails as *Hydrobia stagnalis* in the title and *Paludestrina ventrosa* in the text, respectively, both synonyms of *E. ventrosa*. Despite the numerous and highly abundant occurrences in Central Germany, this is the only locality where this mudsnail has been recorded alive to date. Unfortunately, this population also went extinct soon after its discovery. Regius collected *E. ventrosa* in large numbers in the stagnant water of remnant draining ditches on “algae felt”, for the last time apparently in 1949. The surrounding wasteland had already been meliorated and ploughed into fields in 1934. Investigations of the site near Dodendorf by the authors in 2003, 2021 and 2022 revealed only empty shells, which apparently originated from Holocene floodplain sediments. Exploration of the entire Sülze valley revealed no further evidence of *E. ventrosa*.

Currently, numerous halophytic plants have re-colonized the area around the salt site near Dodendorf as a result of nature conservation measures, but the small bodies of water are heavily eutrophic. Surprisingly, the benthic foraminifera *Entzia macrescens* (Brady, 1870), *Entzia* sp. and *Haplophragmoides manilaensis* Andersen, 1953 were found in large numbers at the site (Milker *et al.*, 2023). The salinities at Dodendorf apparently fluctuate relatively strongly (e.g. between 18.4 psu in October 2022 and 3.5 psu in March 2023) (Milker *et al.*, 2023). Regius (1950) recorded a salinity of 10.9 ‰ (or psu) for the site (October 1949).

Identifying *Hydrobia*-like shells is far from straight-forward, despite the confidence with which such forms are often identified even to species (see Szarowska & Falniowski, 2014). In Europe and the Mediterranean area, there are seven genera occurring in brackish waters sharing the general *Hydrobia*-like morphology: *Hydrobia* W. Hartmann, 1821; *Ecorbia* W. Stimpson, 1865; *Peringia* Paladilhe, 1874; *Adriohydrobia* Radoman, 1977; *Achaiohydrobia* Falniowski, 2021 (all Hydrobiidae); *Eupaludestrina* Mabilie, 1877 (Cochliopidae); and the non-native *Potamopyrgus* W. Stimpson, 1865 (Tateidae). In addition, several of these genera have undergone cryptic speciation, with species not being distinguishable on the basis of shell morphology (e.g. Wilke *et al.*, 2000, 2002; Wilke & Pfenninger, 2002; Haase *et al.*,

2010; Vandendorpe *et al.*, 2019). The Regius material from Dodendorf provides the opportunity to use molecular genetic methods to reliably identify these snails and to carry out extensive comparisons with other European and North African conspecific populations to infer the relationships and origin of the Central German snails.

MATERIAL AND METHODS

We sequenced five and four specimens, respectively, of the following two samples collected by Regius and housed in the Senckenberg Natural History Collections Dresden, Museum of Zoology (SNSD) (Table 1). These are as follows:

- (1) SNSD 31,753: *Paludestrina ventrosa* Mont., “side-ditch of the Sülze river near Dodendorf, in matted filament algae, 1948?” (Regius, 1950), 2,395 mummified specimens.
- (2) SNSD Moll 31,755: *Paludestrina ventrosa* Mont., “from algae-felted side-ditch of the Sülze river near Dodendorf/Magdeburg, Regius, 1949?” (Regius, 1950), 1,002 mummified specimens.

DNA was extracted from nine crushed specimens using the E.Z.N.A Mollusc DNA Kit (Omega Bio-Tek Inc.) according to the manufacturer’s protocol. These extracts are kept in the collection of the AG Vogelwarte in Greifswald (S2725–S2729, S2731–S2734). A 658 bp fragment of subunit I of the mitochondrial cytochrome *c* oxidase subunit I (COI) was amplified with the primers LCO1490 and HCOmod, a modified version of H1298 (Folmer *et al.*, 1994; Zieske *et al.*, 2011). PCRs were carried out in a total volume of 25 µl containing 2.5 µl buffer, 2 µl MgCl₂ (50 mM stock), 0.5 µl dNTPs (10 mM stock), 1 µl BSA (1% stock), 1 µl of each primer, 0.1 µl Taq (Bioline), water and 20–80 ng DNA. The temperature profile started with 3 min of denaturation at 95 °C followed by 40 cycles of denaturation, annealing and extension for 45 s at 95 °C, 45 s at 46 °C and 1 min at 72 °C, respectively, and terminated by a final extension at 72 °C for 5 min. The PCR products were checked on a 1% agarose gel and enzymatically purified with a mix of exonuclease I and shrimp alkaline phosphatase. The cycle sequencing reactions contained each 0.5 µl of AdvancedSeq’s SupreDye v3.1 Cycle Sequencing Kit and HalfBD (Molecular Devices), 0.15 µl primer, 1 µl ADS buffer, 4.85 µl water and 40–80 ng of the PCR product. The products were cleaned with High Prep DTR-DX magnetic beads (MagBio) and sequenced on an ABI 3130xl Genetic Analyser (Applied Biosystems).

Blasting against the nucleotide collection of NCBI’s GenBank identified *Ecorbia ventrosa* as closest match. Hence, all sequences of this species available as of 14 March 2024 were downloaded (Table 1) and aligned with the new ones using ClustalW 1.4 (Thompson *et al.*, 1994) implemented in BioEdit 7.0.5.3 (Hall, 1999). The alignment comprised 638 bp and a total of 82 sequences from 33 localities (Table 1, Figs 2, 3). Based on this alignment, we constructed a statistical parsimony network (TCS; Clement *et al.*, 2002) in PopART 1.7 (Leigh & Bryant, 2015) in order to infer the relationships and origin of the snails from Dodendorf (Table 1, Figs 1A–C, 2, 3).

RESULTS

As already mentioned, the sequence analyses confirmed the identification of the snails from Dodendorf as *Ecorbia ventrosa*. The statistical parsimony network showed three clusters whose centers were separated by two to four mutations, respectively. One cluster was dominated by North European populations, one by samples from the Mediterranean and another contained rather distantly related sequences from southern Europe and Tunisia (note that Ns introduced due to different sequence lengths are being ignored). The nine sequences from Dodendorf were all identical among each

Table 1. GenBank accession numbers, locality data and source publication for the 33 populations (see Fig. 2).

GenBank accession number	Locality	Geographical coordinates	Source
AF118324	1. Orbetello, Italy	42°27'N, 11°13'E	Wilke & Davis (2000)
AF118325			
AF118326			
AF118327			
AF118328			
AF118329	2. Bay of Cadiz, Spain	36°23.62'N, 06°08.25'W	
AF118330			
AF118331			
AF118332			
AF118333			
AF118334	3. Snettisham Lagoon, UK	52°51.8'N, 00°27.6'E	
AF118335			
AF118336			
AF118337			
AF118338			
AF118339	4. Holme Broadwater, UK	52°58.6'N, 00°33.9'E	
AF118340			
AF118341			
AF118342			
AF118343			
AF118344	5. Galgahraun, Iceland	64°28'N, 22°10'W	
AF118345			
AF118346			
AF118347			
AF118348			
AF118349	6. White Sea, Russia	66°19'N, 33°32'E	
AF118350			
AF118351			
AF118352			
AF118353			
AF118354	7. Astrup Bugt, Denmark	56°41'N, 10°13'E	
AF118355			
AF118356			
AF118357			
AF118358			
AF118359	8. Odense Fjord, Denmark	55°30'N, 10°32'E	
AF118360			
AF118361			
AF118362			
AF118363			
AF118364	9. Neustadt, Germany	54°06'N, 10°49'E	
AF118365			
AF118366			
AF118367			
AF118368			
AF118369	10. Boiensdorfer Werder, Germany	54°01.9'N, 11°31.4'E	
AY616137			
KJ406201			
KJ406202			
KJ406203			
KJ406204	11. Lac de Tunis, Tunisia	36°48'28.8''N, 10°15'46.8''E	Kevrekidis et al. (2005)
KX355837			
KX355838			
KX355839			
KX355840			
	12. Kato Xirokhórion, Greece	37°30'30''N, 21°36'52''E	Szarowska & Falniowski (2014)
	13. Constanza, Romania	43°47'46''N, 28°31'02''E	Osikowski et al. (2016)
	14. Greece, Itea, Greece	38°25'37''N, 22°27'22''E	

Table 1. Continued

GenBank accession number	Locality	Geographical coordinates	Source
MN167747	15. Zrce Beach, Croatia	44°32'31.6"N, 14°54'49.7"E	Vandendorpe et al. (2019)
MN167748	16. Small bay of the sea, Croatia	44°32'31.6"N, 14°54'49.0"E	
MN167749	17. Etang de Villepey, France	43°23'53.5"N, 06°43'44.8"E	
MN167750	18. Canal near Etang de Gines, France	43°29'19.3"N, 04°26'35.5"E	
MN167751	19. Spring east of Itea, Greece	38°25'38.3"N, 22°27'20.5"E	
MN167752	20. Bambinello Spring, Italy	40°16'58.8"N, 17°50'16.8"E	
MN167753	21. Laguna di Grado, Italy	45°41'11.4"N, 13°26'13.6"E	
MN167754	22. Po DelSacca di Goro, Italy	44°49'48.0"N, 12°16'12.0"E	
MN167755	23. Saline Ettore Inversa, Italy	37°52'48.0"N, 12°27'00.0"E	
MN167756	24. Near Punta Umbria, Spain	37°15'18.0"N, 07°08'34.8"W	
MN167757	25. Mouth of Torrent de la Borges, Spain	39°43'49.1"N, 03°14'13.9"E	
MN167758	26. Sa Albufereta, Spain	39°51'42.1"N, 03°05'30.5"E	
MN167759	27. Salina San Miguel, Spain	36°27'36.0"N, 06°13'12.0"W	
MN167760	28. Within the Port d'Alcúdia, Spain	39°50'09.6"N, 03°07'04.8"E	
MN167761	29. Southern bank of Lac de Tunis, Tunisia	36°48'29.5"N, 10°15'46.4"E	
MN167762	30. North of Temime, Tunisia	36°47'51.4"N, 11°01'54.8"E	
MN167763	31. Island Djerba, Tunisia	33°49'12.0"N, 11°04'12.0"E	
MN167764	32. Near Braakman Kreek, Netherlands	51°20'08.9"N, 03°44'37.3"E	
PP537618	33. Dodendorf, Germany	52°02'35.9"N, 11°37'14.4"E	This study
PP537619			
PP537620			
PP537621			
PP537622			
PP537623			
PP537624			
PP537625			
PP537626			

Geo-coordinates are given with published accuracy.

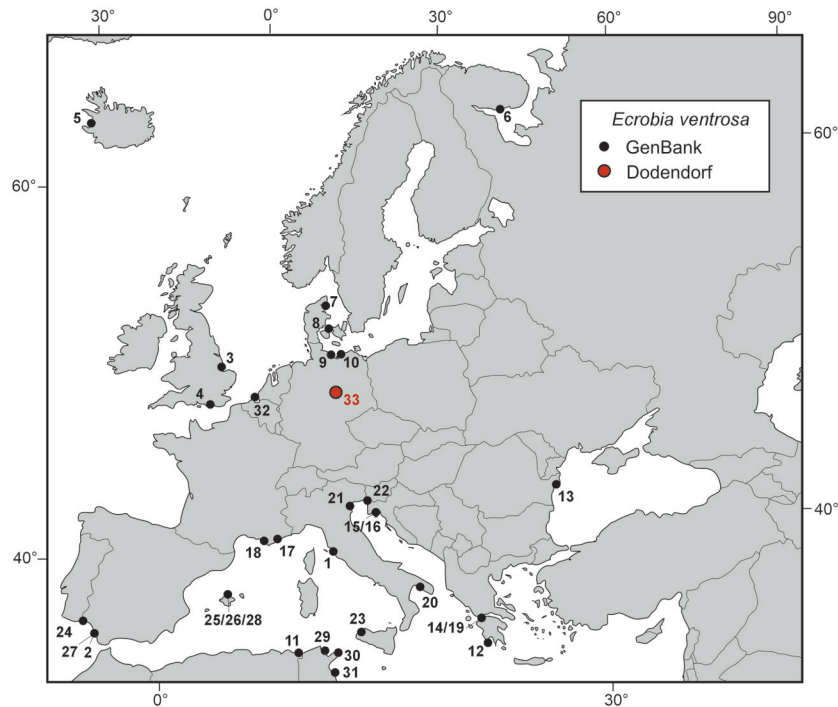


Figure 2. Map showing localities of European and North African GenBank samples of *Ectrobia ventrosa* (see Table 1) used in this study together with Dodendorf in Central Germany.

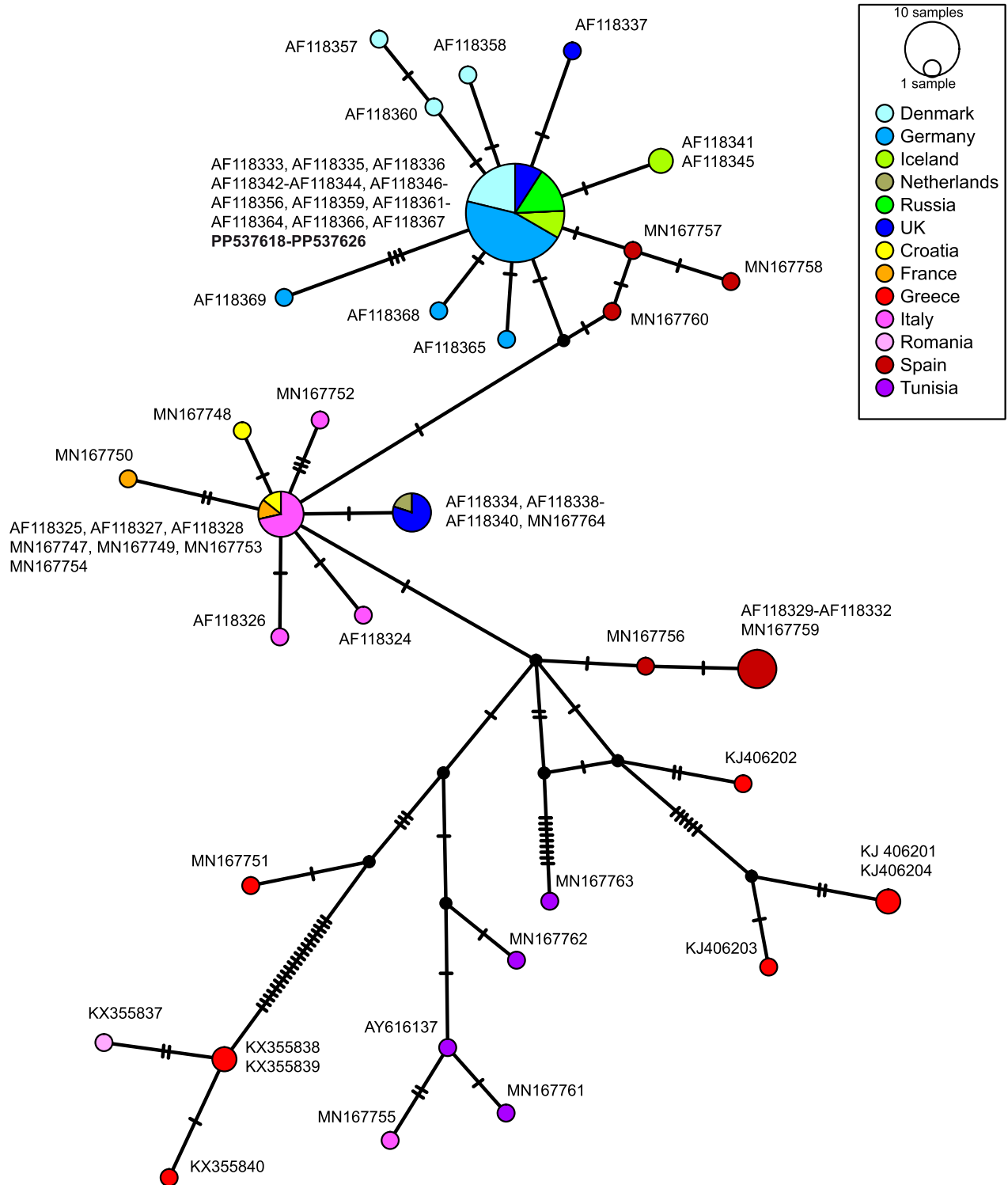


Figure 3. Parsimony network constructed from the GenBank data of *Ecrobia ventrosa* (Table 1) showing the relationships and origin of the snails from Dodendorf in Central Germany.

other as well as identical to sequences from the Baltic coasts of Germany and Denmark, the UK, Russia and Iceland (Fig. 3).

DISCUSSION

The close relationships of the snails from Dodendorf to populations from northern Europe could be expected based on geographic considerations. The nearest occurrences of comparable recent faunas of brackish water snails can be found today in the North and Baltic Seas and on the adjacent Atlantic coasts, including, in addition to *Ecrebia ventrosa*, the hydrobiids *Peringia ulvae* (Pennant, 1777) and *Hydrobia acuta neglecta* Muus, 1963, as well as the Cochliopidae *Eupaludestrina stagnorum* (Bank *et al.*, 1979; Bank & Butot, 1984; Boeters, 1998; Hoeksema & Raad, 2015). An important role in the spread of these snails and other halophilic organisms was probably played by migrating birds (Bairlein *et al.*, 2014; Spina *et al.*, 2022). For the explanation of distribution patterns transport by birds has often been inferred. Anecdotal or experimental evidence is less common, though. Juvenile snails and spawn/eggs in particular adhere well to the plumage and can therefore be transported further distances. Some snails even survive the passage through the gut (e.g. Rees, 1965; Meng *et al.*, 2004; Haase *et al.*, 2010; van Leeuwen & van der Velde, 2012; van Leeuwen *et al.*, 2012; Green *et al.*, 2023; Milker *et al.*, 2023; Saito *et al.*, 2023).

It is unclear for how long this sub-recent population has continuously existed in Dodendorf. Is it a relic of a Holocene or even Pleistocene population or has it been founded rather recently (i.e. a few hundred or thousand years ago)? For the Holocene and other sub-recent findings, it may be reasonable to assume that they belong to *E. ventrosa*, too. In the absence of further genetic material, extensive morphometric studies are necessary to clarify this question, though (E. Müller, S. Meng, Wilke & M. Haase, unpubl.). In this context, it should be borne in mind that the Baltic Sea in its present form only developed during the climatic optimum of the Holocene around 8,500 years ago and that large parts of the North Sea were also regularly dry during the Pleistocene and early Holocene. During the Pleistocene, there were even only relatively short-term marine influences in the area (Andrén *et al.*, 2011; Meng *et al.*, 2022, 2024). For the Pleistocene in particular, very different regions of origin of the brackish water snails must therefore also be taken into consideration.

In addition, the numerous climatic fluctuations during the Pleistocene (e.g. under high-cold period conditions, partly with glacial overruns, such as in the Elsterian and Saalian) or in the periglacial area (Weichselian) with permafrost, made it very unlikely that these snails were continuously distributed inland in Central Germany. Therefore, it seems more likely that there have been numerous waves of immigration of possibly different species of brackish water snails, from the North Atlantic region or its neighbouring waters or even from the Mediterranean region since the early Pleistocene. In a research borehole taken near Erdeborn in the area of the former Salziger See (Mansfelder Seen, west of Halle/Saale, Saxony-Anhalt), hydrobiid snails were found not only from the Holocene, but also from the deposits of the Weichselian cold period, albeit with gaps, and above all from the Eemian warm period (Suderlau, 1975). In these cases, the Baltic Sea can hardly be considered area of origin as it did not exist. Marine Pleistocene transgressions in the Baltic Sea region are only known from the Holstein Interglacial (c. 420 ka ago), the Eemian Interglacial (c. 126–115 ka ago) and finally with the Holocene Littorina transgression, which began c. 8,500 years ago (e.g. Meng *et al.*, 2022, 2024). The Pleistocene inland faunas in particular may well have consisted also of endemic, extinct species that no longer have any equivalent in recent faunas (E. Müller, S. Meng, T. Wilke & M. Haase, unpubl.).

Why the Hydrobiidae in Central Germany, ultimately with the species *E. ventrosa*, are extinct today despite the numerous occurrences in the Holocene, often with high abundances, is also un-

clear. Possible scenarios include climatic changes related to the Pleistocene, strongly fluctuating salinities, or the pollution of waters. More concrete evidence can only be found for Dodendorf near Magdeburg. Here, *E. ventrosa* apparently became extinct in the 1950s/1960s due to the drastic transformation of the landscape for agricultural purposes (Regius, 1950). The small-scale occurrences near Artern and Sangerhausen may have suffered a similar fate.

But what about the Mansfeld Lakes near Halle (Saxony-Anhalt)? Despite the large populations of individuals that developed in the Mansfeld Lakes during the Holocene, no living specimens of *E. ventrosa* were ever observed here. Fresh shells were regularly found in the mudflats of the Salziger See, but they did not contain any soft tissue remains (e.g. Goldfuss, 1894). Presumably these shells were relocated from older sediments (e.g. from trench cuts). In a drill core from the Süßer See, for example, numerous fossil shells presumably of *E. ventrosa* dating from the Subboreal were found, which are also excellently preserved with brownish and translucent shells (Fig. 1D–F) (Meng *et al.*, 2004). It is possible that here decreasing salinity led to the extinction of brackish water snails. For optimal population development, *E. ventrosa* requires salinities of at least mesohaline (c. 4–8 psu), perhaps also slightly polyhaline (up to 10 psu) conditions (comparisons Glöer, 2002; Götting, 2008; Wigham & Graham, 2017). However, recently, the Süßer See, e.g. has reached only at best oligohaline salinity values (c. 0.5–1 psu), which in principle almost corresponds to freshwater conditions (e.g. Ule, 1888, 1895; Jaeckel, 1955; Ockert, 1993; Meng *et al.*, 2004). It is therefore likely that many brackish water organisms are unable to exist permanently in the Süßer See today (summarized by Meng *et al.*, 2004).

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AUTHORS' CONTRIBUTIONS

Both authors contributed to the study conception and design, did the data analysis, writing and review of the manuscript.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY

All data generated or analysed during this study are included in this published article.

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