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Research Article

Separate introductions but lack of genetic variability in the invasive clam *Corbicula* spp. in Swiss lakes

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Abstract

This study documents the spread of the invasive clam *Corbicula* spp. in Switzerland since its first record in the River Rhine in 1995. Clams were newly recorded in several Swiss lowland lakes whose interconnecting rivers have not yet been colonized. We present evidence for separate introductions of an identical haplotype of *Corbicula fluminea* into five lakes in Switzerland in the years 2003–2010 based on the mitochondrial DNA-sequence of the COI in specimens sampled. This suggests passive dispersal of the clam by human activities and/or waterfowl. All but one of the 72 genetically analysed individuals were assigned to a single haplotype FW5 and to the species name *C. fluminea.* Recent records of specimens, which were not genetically analysed, displayed all the shell morphology of *C. fluminea*, confirming the dominance of this clam in Swiss rivers and lakes.

Key words: alien species, DNA sequencing, COI, invasive species, range expansion, *Corbicula*, Switzerland

Introduction

The basket clam *Corbicula fluminea* (Müller, 1774) originating from South-East Asia, was first recorded in Europe in the estuaries of the Dordogne (France) and the Tagus (Portugal) in 1980 (Mouthon 1981), and in the Lower Rhine in The Netherlands in 1985 (Bij de Vaate and Greijdanus-Klaas 1990). In 1991, *C. fluminea* was found near Karlsruhe in the Upper Rhine and, in 1995, the clam was reported near Basel in Switzerland (Rey et al. 2004). It is assumed that transportation by cargo ships is responsible for the rapid spread in the River Rhine (Tittizer 1997, Leuven et al. 2009). Upstream of Basel, where cargo shipping stops, the spread of this invasive clam has been less rapid (Schmidlin and Baur 2007). Early in 2006, *C. fluminea* was only found in the River Rhine from Basel to the confluence of the River Aare (Table 1). At that time, no individuals of *C. fluminea* were found in other rivers connecting the lowland and pre-alpine lakes. However, isolated occurrences of the clam were reported from sites in Swiss lakes and the Austrian part of Lake Constance, indicating independent introductions (P. Stucki pers. communication; Werner and Mörtl 2004).

The rapid spread and persistence of *C. fluminea* throughout Europe, North and South America is related to its high growth rate, early onset of maturity, high fecundity, variety of reproductive strategies (Komaru et al. 1998, Hedke et al. 2008) and its ability to tolerate a wide range of environmental conditions (Mattice and Dye 1976, McMahon, 1983, 2002, Müller and Baur 2011). In the River Rhine, *C. fluminea* reaches densities of up to 10,000 individuals per m^2 (Mürle et al. 2008). *C. fluminea* clogs water intake pipes, electric power plant cooling systems and sewage treatment plants, causing enormous damage (Pimentel et al. 2007). In the U.S.A., costs associated with this clam are estimated to be more than US$ 1 billion per year (OTA 1993). As a dominant species of the macrozoobenthos, *C. fluminea* is involved in sequestering a large proportion of the carbon available for benthic production and consequently altering the ecosystem functioning

(Sousa et al. 2008). The invasive clam decreases the abundance of benthic flagellates, bacteria and diatoms and affects other organisms by bioturbation of sediments (Hakenkamp et al. 2001). Valves of dead *C. fluminea*, however, can increase the surface area and substrate diversity of sandy bottoms resulting in an increase of benthic invertebrates (Werner and Rothhaupt 2007; Schmidlin et al. 2011).

Corbicula fluminalis (Müller, 1774), another basket clam with similar shell morphology, was also introduced to Europe in the past decades (Alf 1992, Bachmann and Usseglio-Polatera 1999). According to the description of the two species, *C. fluminea* has a round shell, whereas *C. fluminalis* has a more saddle-shaped shell (see also Marescaux et al. 2010). Based on morphological analyses, Renard et al. (2000) stated that the two species can be distinguished based on the shape of the shell. In contrast, Pfenninger et al. (2002) showed that the distinction of these species is problematic because an intermediate morphotype occurs. Moreover, examining mitochondrial and nuclear DNA, Pfenninger et al. (2002) and others (Lee et al. 2005; Hedke et al. 2008) found that the two species are not reciprocally monophyletic. These findings suggest that the so far widely used species names (*C. fluminea* and *C. fluminalis*) represent two distinct species with interspecific gene flow or, alternatively, they are a result of an incorrect systematic separation of a single species. A recent paper suggests that the genus *Corbicula* could be considered as a polymorphic species complex (Pigneur et al. 2011). However, Pigneur et al. (2011) did not suggest any change in the taxonomical nomenclature (e.g. synonymization).

According to the rules of taxonomy the actual species names (*C. fluminea* and *C. fluminalis*) are consequently still valid.

Here we present new data on the spread of *Corbicula* in Switzerland. We examined the mitochondrial DNA-sequence of the cytochrome oxidase subunit I (COI) in each specimen sampled in recently colonized lakes in Switzerland and several European rivers. To facilitate comparisons with previous and future genetic studies and to contribute to the needed revision of *Corbicula*, we present the taxonomic species name together with a form and a haplotype code following Pigneur et al. (2011). Thus, *C. fluminea* /form R/haplotype FW5 denotes individual(s) assigned to the species *C. fluminea* (i.e. taxonomical description) to a round (R) form (possible categories are: R: round, S: saddle and Rlc: round light coloured, see Pigneur et al. 2011) and to a mitochondrial haplotype FW5 (see Pigneur et al. 2011).

Methods

First, we compiled the information on the recent range expansion of *Corbicula* in Switzerland between 1995 and 2011 using the following sources: own field observations, personal communications from several researchers and data from unpublished reports.

For the genetic analysis, *Corbicula* samples were obtained from five lakes (four in Switzerland and one from the Austrian part of Lake Constance) and six rivers in Central Europe between 2006 and 2010 (Figure 1, Table 1). Clams were preserved in 70% ethanol and kept at 5°C until analysis. Total DNA was extracted from foot muscle tissue using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Hombrechtikon, CH). A 659-bp fragment of the mitochondrial cytochrome oxidase subunit I (COI) was amplified for 72 specimens using the standard universal primers (see Folmer 1994). Samples were amplified for 40 cycles following the protocol of Pfenninger et al. (2002) after initial incubation at 94°C for 3 min. Sequencing was outsourced to ecogenics GmbH (Zürich-Schlieren, CH; http://www.ecogenics.ch), which uses Applied Biosystems 3100 automated sequencer. Both strands (forward and reverse) were sequenced for all samples. To avoid contaminations between samples, PCR reactions were run at different periods and negative controls were added in each reaction group. Base pairs were checked manually and aligned using CodonCode Aligner version 3.7.1.1 (CodonCode Corporation, Dedham, US). Haplotypes obtained were compared with published COI sequences of *Corbicula* available on GenBank.

Results

The compiled new records demonstrated the further spread of *Corbicula fluminea*/form R in Switzerland since 1995 (Table 1, Figure 1). In the River Aare, *C. fluminea*/form R was found near Wynau, Oftringen, Brugg and Aarau, in the River Reuss near Hünenberg, in the River Suhre

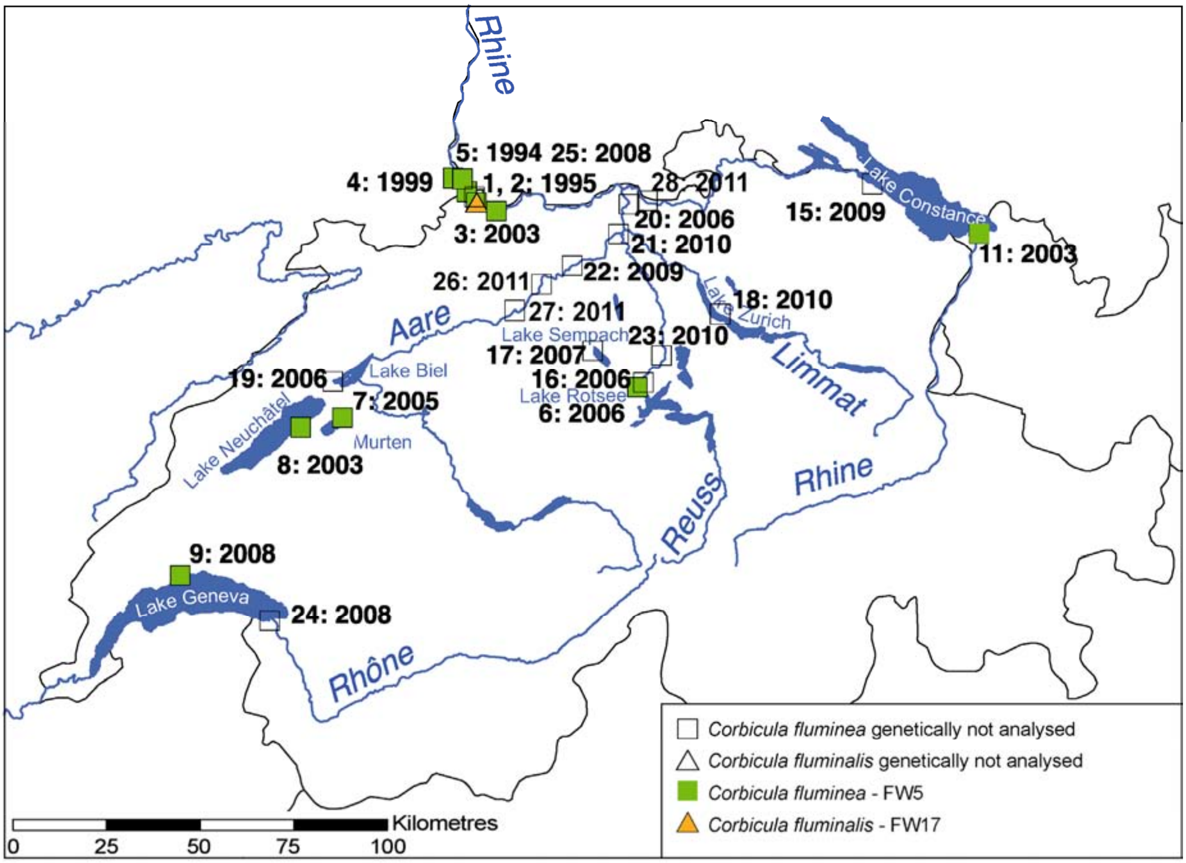

Figure 1. Records of *Corbicula* spp. in Switzerland. Green squares refer to the haplotype FW5, the orange triangle to the haplotype FW17. In this study each individual with FW5 haplotype was assigned to the form R and to the species name *C. fluminea* and each individual with FW17 to the form S and to the species name *C. fluminalis.* Empty squares refer to individuals of *C. fluminea* form R which were not genetically analysed.

near Oberkirch at the outlet of Lake Sempach, in the River Ron near the outlet of the Lake Rotsee, in a side brook of the River Wiese near Basel and in the River Rhine from Basel to Rietheim, a few kilometres upstream of the confluence with the River Aare. Furthermore, the clam was also detected in Lakes Constance (2003), Neuchâtel (2003), Murten (2005), Rotsee (2006), and Biel (2006), Lake Geneva (2008) and Lake Zürich (2010; Table 1B, Figure 1). However, large sections of the interconnecting rivers are not yet invaded by the clam. In the lakes, all records were made close to harbours or canals (Lakes Neuchâtel, Murten, Rotsee, Geneva and Constance). In contrast, one specimen of *C. fluminalis*/form S was exclusively found in the region of Basel in the River Rhine.

Seventy-one of the 72 individuals that were genetically analysed share the FW5 haplotype (following Pigneur et al. 2011) and could be taxonomically assigned to *C. fluminea* and morphologically to the form R (Table 1A). Thus, 71 *C. fluminea* specimens sampled in Lakes Constance, Neuchâtel, Murten, Rotsee, Geneva and in the Rivers Rigole, Saône, Oder, Elbe, Danube and the Rhine (Basel, Birsfelden and Augst) belong to the group *C. fluminea*/form R/haplotype FW5. One of the two individuals collected in the River Rhine near Birsfelden had a saddle-shaped shell and was assigned to *C. fluminalis*/form S/haplotype FW17 (Table 1A, Figure 2). Thus, individuals with a distinct shell form and discrete haplotype coexist at this locality.

Table 1. A. Locations of *Corbicula* spp. sampling sites, and number of individuals used for the COI analysis, assigned species, forms and haplotypes (in format: species-form-haplotype), year of sampling and year of first record at the locality. **B.** Locations of new records of the species *Corbicula fluminea* in Switzerland (N – number of individuals genetically analysed).

No **A**	Location	Country	Latitude N°	Longitude E°	Year of sampling	N	Assignment	Collector	First record	Reference of first record
1	River Rhine, harbour of Basel	Switzerland	47.589	7.591	2008	1	1 *C. fluminea*-R-FW5	D. Küry	1995	a
2	River Rhine, harbour of Birsfelden	Switzerland	47.561	7.632	2008	2	1 *C. fluminea*-R-FW5 1 *C. fluminalis*-S-FW17	D. Küry	1995	a
3	River Rhine, Augst	Switzerland	47.539	7.714	2006	6	6 *C. fluminea*-R-FW5	S. Schmidlin	2003	b
4	Rigole, Petite Camargue Alsacienne, St. Louis-la-Chaussée	France	47.625	7.534	2006	5	5 *C. fluminea*-R-FW5	S. Schmidlin	1999	c
5	Altrhein, remnant of former River Rhine, Märkt	Germany	47.624	7.572	2006	6	6 *C. fluminea*-R-FW5	S. Schmidlin	1994	d
6	Lake Rotsee near Luzern	Switzerland	47.064	8.304	2008	6	6 *C. fluminea*-R-FW5	P. Steinmann	2006	e
7	Lake Murten near Sugiez	Switzerland	46.955	7.119	2008	6	6 *C. fluminea*-R-FW5	S. Schmidlin	2005	f
8	Lake Neuchâtel near Portalban	Switzerland	46.924	6.952	2006	6	6 *C. fluminea*-R-FW5	S. Schmidlin	2003	g
9	Lake Geneva near Morges	Switzerland	46.503	6.494	2010	6	6 *C. fluminea*-R-FW5	B. Lods-Crozet	2008	h
10	River Saône near Lyon	France	45.797	4.830	2006	6	6 *C. fluminea*-R-FW5	J. Mouthon	1994	i
11	Lake Constance, Rohrspitz	Austria	47.500	9.683	2006	6	6 *C. fluminea*-R-FW5	S. Werner	2003	j
12	River Donau, Schiffmühle Orth near Vienna	Austria	48.123	16.709	2008	4	4 *C. fluminea*-R-FW5	A. Heusler	1999	k
13	River Oder near Frankfurt a. d. Oder	Germany	52.347	14.557	2008	6	6 *C. fluminea*-R-FW5	O. Müller	2007	l
14	River Elbe near Dresden	Germany	51.071	13.700	2008	6	6 *C. fluminea*-R-FW5	K. Schniebs	1998	m
B	New records in Switzerland									
15	Lake Constance near Münsterlingen	Switzerland	47.634	9.246			*C. fluminea*-R	ANEBO	2009	n
16	River Ron, outlet of Lake Rotsee	Switzerland	47.077	8.329			*C. fluminea*-R	H. Vicentini	2006	o
17	River Suhre, outlet of Lake Sempach	Switzerland	47.162	8.121			*C. fluminea*-R	H. Vicentini	2007	o
18	Lake Zürich	Switzerland	47.270	8.634			*C. fluminea*-R	L. De Ventura	2010	p
19	Lake Biel near le Londeron	Switzerland	47.053	7.074			*C. fluminea*-R	P. Stucki	2006	g
20	River Aare, Döttingen	Switzerland	47.568	8.254			*C. fluminea*-R	P. Steinmann	2006	e
21	River Aare, Brugg	Switzerland	47.485	8.214			*C. fluminea*-R	P. Steinmann	2010	e
22	Canal Aare near Aarau power station	Switzerland	47.394	8.029			*C. fluminea*-R	W. Hess	2009	q
23	River Reuss near Hünenberg	Switzerland	47.154	8.400			*C. fluminea*-R	P. Steinmann	2010	e
24	Lake Geneva, Bouveret	Switzerland	46.389	6.859			*C. fluminea*-R	B. Lods-Crozet	2008	h
25	Spittelmattbach near Basel	Switzerland	47.576	7.624			*C. fluminea*-R	D. Küry	2008	r
26	River Aare, Oftringen	Switzerland	47.320	7.898			*C. fluminea*-R	M. Karsai & A. Lanker	2011	this study
27	River Aare, Wynau	Switzerland	47.263	7.806			*C. fluminea*-R	A. Kirchhofer	2011	s
28	River Rhine, near Rietheim	Switzerland	47.614	8.260			*C. fluminea*-R	B. Baur	2011	this study

a: Rey et al. (1997); b: Rey et al. (2004); c: Mosimann (2000); d: Schöll (1995); e: P. Steinmann, pers. comm. f: Fasel (2005); g: P. Stucki, pers. comm.; h: B. Lods-Crozet, pers. comm.; i: Mouthon (1994); j: Werner & Mörtel (2004); k: Fischer & Schultz (1999) (Austria); l: Müller et al. (2007); m: Schöll (1998); n: ANEBO (2011); o: H. Vicentini, pers. comm.; p: L. De Ventura, pers. comm.; q: W. Hess (2009); r: D. Küry, pers. comm.; s: A. Kirchhofer, pers. comm.

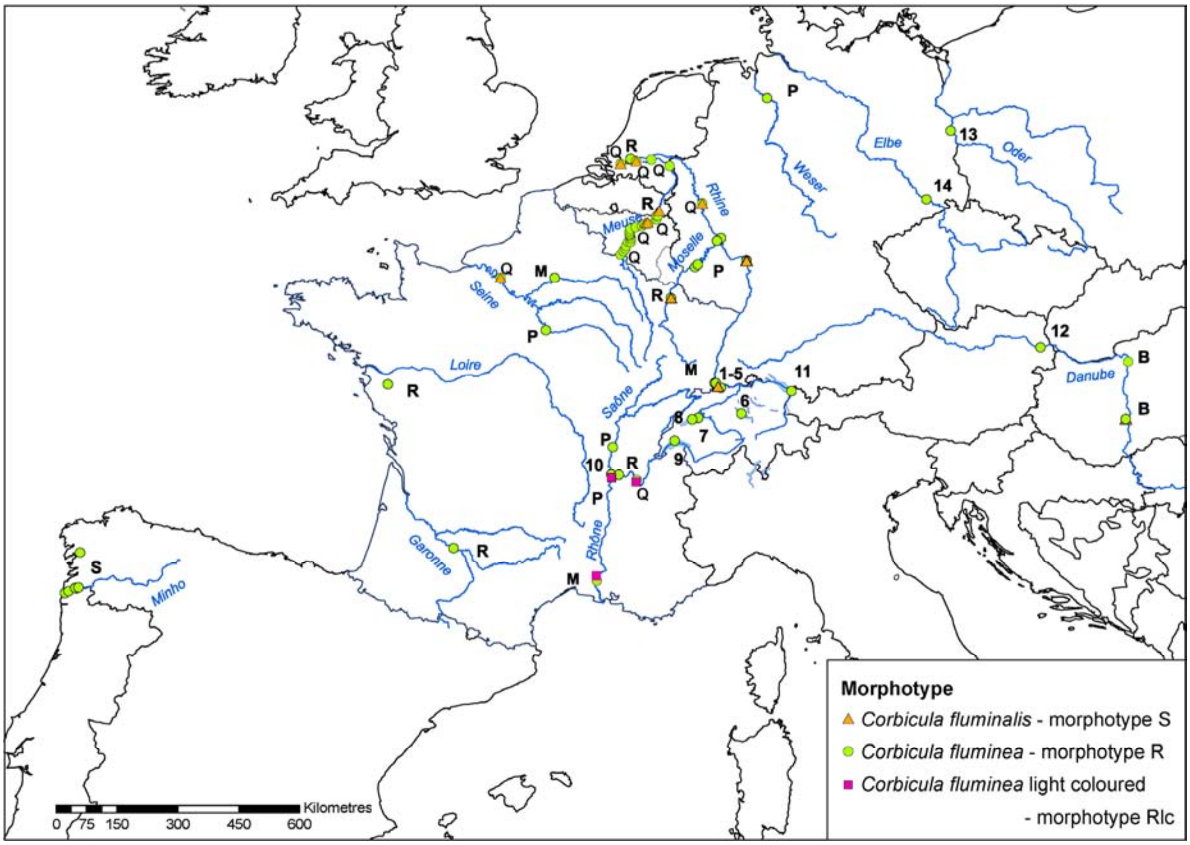

Figure 2 Distribution of *Corbicula* with known haplotypes in Europe (not all sites are shown). Capitals refer to the authors: R: Renard et al. (2000); P: Pfenninger et al. (2002); S: Sousa et al. (2007), B: sequences published by Bódis in Genbank in 2010; M: Marescaux et al. (2010) and combined data from GenBank. Figures (1-14) indicate the sampling sites of the present study (see also Table 1A). Coordinates of additional sampling sites are listed in the Appendix 1.

Discussion

The present study illustrates the most recent spread of *Corbicula* in Switzerland. Clams were newly recorded in several lowland lakes whose interconnecting rivers are not yet colonized. This suggests passive dispersal of the invasive clam by human activities or animal vectors and independent introductions. The transport of pleasure boats from lakes to lakes and from rivers to lakes is the most probable pathway for the introduction of *Corbicula* into the lakes examined. For example, Lake Rotsee is well-known for its international rowing regatta (e.g. the World Championship in 2001). The transport of rowing boats from regatta to regatta increases the probability of introducing *Corbicula* to other water bodies. Recreational boating is generally assumed to contribute to the dispersal of alien species (Burgin and Hardiman 2011).

Passive transport of *Corbicula* by waterfowl is another possible pathway for distant transportation of clams. Lowland lakes in Switzerland serve as resting and feeding places for over-wintering water birds (Keller and Burkhard 2010). During the winter season waterfowl frequently cross Switzerland from Northeast (Lake Constance) to Southwest (Lake Geneva), providing opportunities for passive transportation. A similar range expansion of *Corbicula* has been recorded in lakes in the United States (Thompson and Sparks 1977). There, the spread of the invasive clam was related to the migration corridors of waterfowl. Passive dispersal on bird feet or in feathers seems to be likely due to sticky mucous secretions of juvenile clams, which facilitate attachment (Voelz et al. 1998, Brancotte and Vincent 2002).

The lack of genetic diversity found in *Corbicula* spp. in Switzerland is not unexpected. Other studies reported similar low levels of genetic diversity. For instance, Siripattrawan et al. (2000) recorded a single haplotype in *Corbicula* samples from Michigan and North Carolina, which was genetically distinct from the single haplotype found in specimens collected in Utah and New Mexico. Introduced *Corbicula* populations from temperate, subtropical, and tropical localities in North and South America were also dominated by the same haplotype, demonstrating its wide geographical range (Lee et al. 2005, Hedke et al. 2008). This most widespread lineage is the same both in Europe and America. In Europe, this haplotype occurs from the Iberian Peninsula to the Black Sea (Rhine: Pfenninger et al. 2002; Danube: GenBank sequences provided by Bódis et al. 2011; Loire: Renard et al. 2000; Minho: Sousa et al. 2007). Introductions from a single locality and/or post-colonisation from other introduced populations could partly explain the low genetic diversity found in Europe and North and South America. However, this haplotype is also one of the most common haplotypes in the clam's native range (haplotype FW5; Park and Kim 2003). Introduced individuals of *Corbicula* may reproduce by androgenesis, a relatively rare mode of asexual reproduction (Komaru et al. 1998; Hedtke et al. 2008). This form of reproduction reduces the genetic diversity. However, asexual reproduction is a common means to become invasive despite low genetic diversity (Roman and Darling 2007).

In our study, the only site with a co-existence of two haplotypes (FW5 and FW17) was in the River Rhine near Birsfelden where international cargo shipping is possible. Haplotypes other than FW5 have been recorded at much lower frequency in Europe (Pfenninger et al. 2002). Thus, competitive interactions among different haplotypes should be considered. Darrigran (1991) suggested that clams identified as *Corbicula fluminea*/form R/haplotype FW5 have some competitive advantage over other *Corbicula* species with FW17 haplotype. In the La Plata region of South America, haplotype FW17 has been replaced almost completely by the dominant haplotype FW5 (Darrigran 1991, Lee et al. 2005). Considering the high abundance and wide distribution of haplotype FW5 in Europe and the clam's tolerance to low temperatures (Müller and Baur 2011), it is not surprising to find this haplotype in the newly colonized lakes in Switzerland.

Mitochondrial haplotypes can be unambiguously identified. In our study, haplotypes corresponded to species and forms (*C. fluminea*/form R/haplotype FW5, *C. fluminalis*/form S/haplotype FW17). However, the species status remains uncertain. Specimens collected by Pfenninger et al. (2002) and the sample analysed in this study in the River Rhine harbouring the haplotype FW17 belong to the same lineage as the haplotype IV from the river Rhône analysed by Renard et al. (2000). Interestingly, these individuals with haplotype IV had the round shell form of *C. fluminea* (*C. fluminea*/form R/haplotype FW17, see also Pigneur et al. 2011). Several other studies showed mismatches between operational taxonomic units (OTUs) and operational genetic units (OGUs, Renard et al. 2000; Siripattrawan et al. 2000; Pfenninger et al. 2002; Glaubrecht and Korniushin 2003; Park and Kim 2003), possibly due to androgenesis. Based on findings in freshwater populations of *Corbicula*, Lee et al. (2005) concluded that any systematic interpretation relying exclusively on mitochondrial lineages could be misleading due to discrepancies between mitochondrial and nuclear markers. This highlights the need to analyse both morphological and genetic (mitochondrial and nuclear) variation in future studies.

There is an increasing interest in incorporating genetic analyses into biomonitoring programs (DeWalt 2011). Any discrepancy between OTU- and OGU-based analyses (Pilgrim et al. 2011) requires a detailed consideration of the correspondence between taxonomic and genetic units. In this case, we advocate a parallel assignment of individuals to both an OTU and an OGU until the taxonomic nomenclature incorporates recent evidence of genetic analyses.

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Supplementary material

The following supplementary material is available for this article.

Appendix 1. Locations of *Corbicula* spp. records in Europe.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2012/Supplements/AI_2012_1_Schmidlin_etal_Supplement.pdf