

The history of an invasion: phases of the explosive spread of the physid snail *Physella acuta* through Europe, Transcaucasia and Central Asia

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Abstract *Physella acuta* (Draparnaud, 1805) is an aquatic pulmonate snail notorious for its high invasive potential. Of New World origin, this species now occurs on all continents. The aim of this study was to trace *P. acuta* dispersal through the Western Palearctic starting from its first arrival in the Old World and to determine possible drivers of this process. A range of literary sources as well as some rich European malacological collections have been consulted to ascertain the dates of the first finding of *P. acuta* in the countries of Europe, Transcaucasia, and Central Asia and to map the most significant localities. The shell characteristics of this species are so distinctive that they almost preclude misidentification and confusion with any native species. This allows one to rely on historical records, including older sources (18th to the first half of the 19th centuries). The earliest reliable records of *P. acuta* in the Old World can be dated to 1742, which implies an earlier date for the first arrival of the species in Europe, possibly in the 17th century. Its introduction may be explained either by accidental dispersal mediated by humans (for example, during transport of exotic plants to European botanical gardens) or by natural causes (long-distance dispersal

from the Americas to Europe). Three successive phases leading to the current invasive range of *P. acuta* in the Western Palearctic can be identified. The species' current Old World range can be viewed as a result of the interaction of natural and anthropogenic factors. The human-mediated drivers of dispersal include canal building, the aquarium trade and, more recently, alteration of natural freshwater habitats.

Keywords Aquarium trade · Invasive species · Eurasia · Human-driven dispersal · Long-distance dispersal

Introduction

Snails (shelled Gastropoda), both terrestrial and aquatic, are a proverbial example of slowness and laziness. Nevertheless, in the last several hundred years, many species of snails have proved to be very successful invaders, able even to cross oceans and continents (Kirschner et al. 1997; Pointier et al. 2005; Gittenberger et al. 2006; Gittenberger 2011; Kappes and Haase 2012). The “100 of the World’s Worst Invasive Alien Species” list (Global Invasive Species Database 2016) contains several species of snails, including the well known invaders *Achatina fulica* Bowdich, 1822 and *Pomacea canaliculata* (Lamarck, 1822). The economic effects of such invasions may be tremendous (Pimentel 2011), but the potential negative impact of non-indigenous molluscs on natural

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ecosystem sustainability and diversity is possibly worse. From a biogeographical point of view, molluscan invasions lead to the homogenization of faunas, extirpation of vulnerable endemic species and alteration of the biotic composition of invaded ecosystems (Cowie 2001; Strayer 2010). A wide range of possible agents for dispersal of snails has been discussed in the literature, including storm winds, other animals and human activities (Valvoglyi 1975; Kappes and Haase 2012; van Leeuwen et al. 2012; Banha et al. 2014; Özgo et al. 2016). One of the most important mechanisms for the spread of freshwater gastropods is the aquarium trade, which has been thought to be the leading factor in human-driven dispersal of such exotic species as the thiarid *Melanoides tuberculata* (Müller, 1774) and the planorbid *Ferrissia fragilis* (Tryon, 1863) (Duggan 2010). This is a relatively recent mode of dispersal as the modern type aquarium dates only from the mid-19th century (Hamlin 1986; Lachapelle and Mistry 2014). Nevertheless, the aquarium trade has been linked to more than 150 species of animals invading natural ecosystems around the world (Chang et al. 2009).

One of the most effective and spectacular invaders among freshwater snails is *Physella acuta* (Draparnaud, 1805), a small air-breathing snail in the family Physidae Fitzinger, 1833. Its generic position is unclear. Different authors have placed it in *Physa* Draparnaud, 1801, *Physella* Haldeman, 1843, *Costatella* Dall, 1870 or *Haitia* Clench and Aguayo, 1932 (see Stadnichenko 1990; Gittenberger et al. 1998; Taylor 2003; Wethington and Lydeard 2007). Here, the binominal name *Physella acuta* is used as being prevalent in works of Old World malacologists. Dillon et al. (2002: 233) nominated this snail as ‘the world’s most cosmopolitan freshwater gastropod’. The aquarium trade is believed to be the primary factor in its dramatic dispersal throughout the world (Duggan 2010). Though *P. acuta* was first described in 1805 from France (Draparnaud, 1805), it is widely accepted that it is not native to Europe, being a species of New World origin (Dillon et al. 2002; Anderson 2003; Taylor 2003; Lydeard et al. 2016). Its rapid spread through Europe may be one of the earliest cases of successful biological invasion resulting from the post-1492 ongoing interactions between the Old World and the Americas. As Bousset et al. (2014: 1771) noted, *P. acuta* ‘can be considered as an excellent biological model for analyzing bioinvasions at a very large geographic scale’. These authors

used a genetic approach to study the invasion history of *P. acuta*. Here, I attempt to reconstruct the same process on the basis of historical records of *P. acuta* in countries of Europe and Central Asia using published reports scattered in the malacological literature of the 19th and 20th centuries as the primary source of information. The distinctive shell characters of *P. acuta* make it easily distinguishable from all native European physid species, which allows one to have faith in the historical records, as misidentifications probably seldom occurred. To my knowledge, Adensamer (1935) in Austria and Feliksiak (1939) in Poland are the only authors to trace the pan-European spread of this species and to map its distribution based on extensive search of the literature. Since their time, nobody has continued and expanded this work, possibly because documentation of new *P. acuta* localities in Europe has occurred so rapidly since the 1950s.

I therefore aimed to identify the dates of the first record of the species in of European and Transcaucasian countries as well as in the republics of the former Soviet Central Asia. On this basis, I tried to shed light on the first steps of *P. acuta* invasion in Europe and to link its observed historical pattern of dispersal to sociocultural factors such as the invention of public and home aquariums in Western Europe in the mid-19th century. Hypotheses regarding the mechanism of dispersal of *P. acuta* from America to Europe are critically re-considered, and some possible cases of occurrence of this snail in Europe prior to its formal taxonomic description in 1805 are discussed.

Materials and methods

Records of *Physella acuta* in the European malacological literature published since 1805 constituted the main source of information. I tried to determine the date of the first reliable finding of this species in each country and to map all occurrences of the snail in Europe that could be significant for reconstruction of the invasion process. In the majority of cases, mention of this species in the older publications was not accompanied by shell illustrations. I therefore took into account all information provided by the author(s) to check the correctness of the species determination. Usually, the verbal description of the shell characters as well as information on habitat made it possible to determine if the identification was

correct. The malacological collection of the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg (ZIN hereafter), was inspected to document the dispersal of *P. acuta* in the southern part of European Russia as well as in Soviet Central Asia. Some earlier but unpublished records of the species in central and eastern Europe were derived from the malacological collection of the Natural History Museum in Vienna (NHMW hereafter). This collection also contains the specimen of *P. acuta* that served as the basis of the formal taxonomic description of the species (the holotype by monotypy) by Draparnaud (1805) (see Vinarski and Eschner 2016).

The extensive synonymy of *P. acuta* (see Taylor 2003: 129–132) has also been taken into account since this species was sometimes mentioned in the past under different names.

My own field observations on invasive populations of *P. acuta* have been carried out in Tunisia and central Kazakhstan (2013), the Volga delta (2015) and Tajikistan (2016).

Records of *P. acuta* in artificial or human-modified waterbodies (e.g. aquariums, tanks in botanical gardens, heated waters of industrial zones) and in outdoor habitats (ponds, rivers and other biotopes with natural thermal regimes) were analyzed and mapped separately.

Results

Dispersal of *P. acuta* through Europe, Transcaucasia and Central Asia since 1805

The dates of the first finding of *P. acuta* in countries of Europe, Transcaucasia and Central Asia are given in Table 1. Table 2 summarizes various authors' views on the European range of the species published between 1841 and 2012. The localities of the records, along with other noteworthy occurrences, in Europe and Transcaucasia are mapped in Fig. 1 and in Central Asia in Fig. 2. No relevant information was found for Albania, Moldova, Serbia and a few others. Below, I provide remarks on the first occurrences and other significant findings of *P. acuta* by country in alphabetical order.

Armenia

Fifteen years after its first recording in Armenia (Akramovsky and Aliev 1961), the species was

actively dispersing through the country and was abundant in some regions (Akramovsky 1976).

Austria

Clessin (1887), in his review of the malacofauna of Austria-Hungary and Switzerland, did not mention this species. There are specimens in NHMW collected in 1925 in Hadersdorf-Weidlingau, Lower Austria (W. Clemm collection) but this finding was not published. The first published record of *P. acuta* in Austria was that of Strouhal (1934), who found it in 1930 in the thermal waters of Bad Villach in Kärnten. Hadersdorf-Weidlingau is another prominent resort with thermal waters and the snails were probably living in these warm springs.

Azerbaijan

The species was first discovered in about 1950, and ten years later had become one of the most abundant snails in the Kura Lowland, second to *Radix auricularia* (Linnaeus, 1758) (Akramovsky and Aliev 1961). It was first found on the Caspian Sea shore in 1985 (Fig. 2).

Belgium

Since 1869, when *P. acuta* was first recorded in Belgium, it has spread over a significant part of the country using river basins and systems of artificial channels (Adam 1960). Adam (1960) dismissed the aquarium trade as the most significant mechanism of *P. acuta* dispersal in Belgium.

Bulgaria

The first records of *P. acuta* were made in 1927–1928 (Table 1). Now this species is widely distributed throughout the country and is abundant (Georgiev 2014).

Belarus

The species is currently known from a restricted number of localities, mostly in artificially heated waterbodies (Laenko 2012) and seems to be rare.

Croatia

Sturany and Wagner (1914) reported *P. acuta* on the Adriatic coast from the Sava River southward to the

Table 1 First records of *Physella acuta* in European, Transcaucasian and Central Asian countries

Country	Date	References
Andorra	1920	Abarca and Suares (1986)
Armenia	1959**	Akramovsky and Aliev (1961)
Austria	1925**	NHMW
	1930**	Strouhal (1934)
Azerbaijan	ca. 1950**	Akramovsky and Aliev (1961)
Belarus	1983**	Naumova et al. (1983)
Belgium	1869**	Kobelt (1880)
Bulgaria	1927–1928**	Wagner (1927), Büttner (1928)
Croatia	1838**	Cantraine (1838)
Czechia	1918	NHMW
	1919*	Beran (2004)
Denmark	1904**	Sell (1905)
Georgia	1910**	Lindholm (1913)
Germany	1895* 1904**	Büttner (1922)
Greece	1869**	Gassies (1870)
Hungary	1926*	Soós (1927)
Ireland	1902*	Green (1902)
Italy	1838–1840**	Cantraine (1838), Villa and Villa (1841), Philippi (1844)
Kazakhstan	1969**	Vinarski et al. (2015)
Kyrgyzstan	ca. 1946**	ZIN
Lithuania	1937*	Schlesch (1937)
Netherlands	1870**	Gittenberger et al. (1998)
Poland	1906*	Feliksiak (1939)
Portugal	1845**	Morelet (1845)
Romania	1955**	Grossu (1955)
Russia (north of the European part)	1908*	Lindholm (1910)
Russia (south of the European part)	1910**	Lindholm (1913)
Slovakia	1954**	Lisický (1991)
Spain	ca. 1845**	Morelet (1845), Graells (1846)
Sweden	1905**	Nilsson (1928)
Switzerland	ca. 1848	Turner et al. (1998)
Tajikistan	ca. 1940**	ZIN
Turkey	1980**	Yildirim et al. (2006)
Turkmenistan	1963**	ZIN
Ukraine	1916**	Beletsky (1918)
United Kingdom (England)	ca. 1860*	Choules (1860)
United Kingdom (Scotland)	1887*	Jenkins (1890)
Uzbekistan	1928**	Lindholm (1929)

* Records from public aquaria, greenhouses of botanical gardens or similar habitats with artificially controlled conditions

** Records from natural waterbodies with no or minimal human impact. No asterisks means that the character of a habitat is unknown

Table 2 The European range of *Physella acuta* according to various authors, 1841–2012

References	Range
Küster (1841)	Spain (near Carthage), France, Italy (Sicily)
Westerlund (1885)	France (including Alsace and Lorraine), Belgium, Spain, Corsica, Sardinia
Büttner (1922)	Portugal, Spain, France, Corsica, Sardinia, introduced to Germany
Adam (1960)	Western and Mediterranean countries of Europe
Illies (1978)	All limnoregions of Europe excluding Fennoscandia
Welter-Schultes (2012)	All Europe except the northern regions of Fennoscandia and of the British Isles

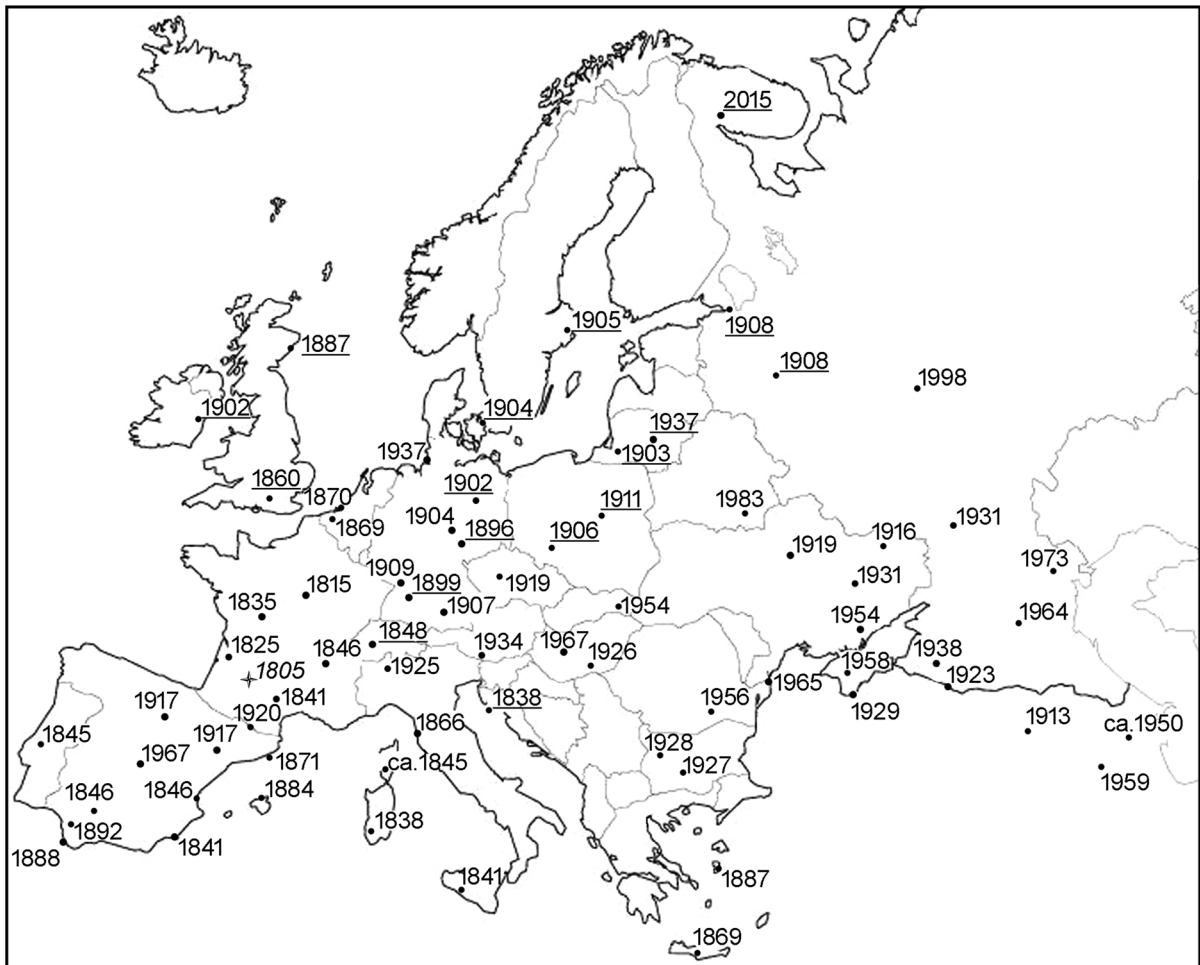


Fig. 1 Localities of dated records of *Physella acuta* in Europe significant for the reconstruction of the invasion process. *Underlined dates* represent records from human-modified waterbodies (e.g. aquariums, tanks in botanical gardens, heated

waters of industrial zones); *non-underlined dates* represent natural water bodies. The *asterisk* indicates the Garonne River, type locality of *P. acuta*

Zrmanja River. Most of this area is now in Croatia. However, the locality mentioned by Cantraine (1838) as “Dalmatie” in his account of the distribution of *P. acuta* probably represents the earliest record.

Czech Republic

According to Beran (2004), the first record was in 1919 in Prague, although specimens collected in 1918

Fig. 2 Localities of dated records of *Physella acuta* of the former Soviet Central Asia significant for the reconstruction of the invasion process (based mainly on unpublished records from ZIN malacological collection)



in Olomouc are present in NHMW. Since 1990, there have been rapidly increasing records in the country, and today it is “the most widely distributed species out of all non-native mollusc species” in the country (Lorencová et al. 2015).

Finland and Norway

Paraense and Pointier (2003) stated that *P. acuta* did not occur in Finland or Norway, but Welter-Schultes (2012) mapped this species in southern regions of Norway, and the IUCN Red List assessment (Van Damme et al. 2012) lists it as introduced to Finland, with no additional information.

France

After its original discovery in 1805 in the Garonne River basin in southern France (Draparnaud, 1805), *P. acuta* was recorded by many French malacologists of the first half of the 19th century (e.g. Férussac 1807; Brard 1815; Goupil 1835). In 1855, Moquin-Tandon (1855: 452) described it as a variable species (with seven varieties as well as the nominotypical variety), the range of which covered almost the entire country, with the exception of the northernmost regions. Essentially the same information was given by Dupuy (1850) and Germain (1931).

Germany

Physella acuta was not known in Germany until the 1890s. Kobelt (1880) and Clessin (1884) did not list it in their surveys of the German malacofauna. The latter believed that the eastern border of its range lay in Alsace. Büttner (1922) gave the exact chronology of the *P. acuta* spread through Germany that allows one to trace the earlier steps of its invasion in the country. The first records were from botanical gardens and other indoor habitats (1895—Leipzig; 1899—Munich; 1899—Tübingen; 1900—Gotha; 1901—Bonn; 1903—Jena; 1904—Dresden). From 1904 it began to be recorded from natural habitats (1904—Passendorf; 1905—Munich; 1907—Cannstadt; 1909—Stuttgart and Spandau and so on). The present range is mainly northern and western parts of the country; it is absent from Bavaria (Glöer 2015).

Georgia

Lindholm (1913) found *P. acuta* in some localities on the Black Sea coast. Kokochashvili (1948) added several new localities in western Georgia, where it was more or less widely distributed. Its current status in Georgia has not been studied but seemingly the species avoids the high mountain regions and is abundant in the Black Sea coast area.

Greece

The first records of *P. acuta* in Greece were in 1870 (Gassies 1870) and 1887 (von Martens 1889) on the islands of Crete, Keos and Ikaria. Today the species is known from various Greek islands and the Greek mainland (Bank 2006).

Hungary

As in Austria, the species was not recorded in Hungary until the 1920s (Soós 1927). Since 1967, it has been recorded in the Hungarian section of the Danube River (Bódis et al. 2012).

Ireland

Green (1902) first reported *P. acuta* in one of the houses in the Dublin Botanic Gardens. However, according to the map of Kerney (1976), there were no records in the entire country, but Anderson (2003) listed a single outdoor locality, as well as confirming the Dublin locality.

Italy

The first reliable records of *P. acuta* were from Sardinia (Cantraine 1838) and Sicily (Villa and Villa 1841; Philippi 1844). It was unknown in the continental part of the country until 1866, when it was recorded from Pisa (Issel 1866). Now *P. acuta* is among the most abundant and widely distributed species of the Italian malacofauna (Cossignani and Cossignani 1995). The spread of *P. acuta* through Italy is believed to be the cause of significant decline of the indigenous physid snail, *Physa fontinalis* (Linnaeus, 1758) (Cianfanelli et al. 2007).

Kazakhstan

Since 1969 the snail has sporadically been recorded in Kazakhstan (see Fig. 2), including the most recent finding in a semi-desert in the Korgalzhyn Nature Reserve (Vinarski et al. 2015).

Lithuania

The first record was in the Kaunas Botanical Garden in 1937 (Schlesch 1937). However *P. acuta* was not

mentioned in more recent publications on the malacofauna of Lithuania (Zettler et al. 2004; Zettler 2014). Butkus et al. (2014) suggested that it no longer occurs there. (I have no information about *P. acuta* in other Baltic countries of the former USSR, i.e. Latvia and Estonia.)

Netherlands

The first arrival of *P. acuta* in the Netherland is dated as 1870; by 1997 the species was distributed throughout the country, according to the map of Gittenberger et al. (1998).

Poland

In 1906, *P. acuta* was encountered in the botanical garden of Warsaw, which was then part of the Russian Empire (Feliksiak 1939), and later in a heated waterbody in an industrial area near Opole (Oppeln), which was within the borders of the German Empire (Boettger 1913). In the first half of the 20th century, it had been recorded from artificial waterbodies only (Feliksiak 1939). Since the 1950s and especially the 1970s, *P. acuta* has been found frequently in outdoor habitats in Poland, which has been related to industrialization and the consequent modification of natural waterbodies (Alexandrowicz 1986; Strzelec et al. 2006; Spyra and Strzelec 2014).

Portugal

The first record of *P. acuta* in Portugal was that of Morelet (1845). According to Büttner (1922), Spain (see below) and Portugal constitute a part of the initial western Mediterranean range of *P. acuta*. In Portugal the species is quite common. Nobre (1930) gave a long list of localities in different regions. It seems likely that it was present in Portugal well before this, probably well before the first record (Morelet 1845), but research on non-marine molluscs in Portugal started later than in other major European countries such as France and Germany, and the species may have been long unnoticed. The first record in the Azores is dated 1880, which probably reflects its late introduction (Backhuys 1975) or the relatively late start of malacological exploration of the Macaronesian islands.

Russia

The species was found in aquaria in Moscow and Saint Petersburg in 1908 (Lindholm (1910) and on the Black Sea coast of Russia (vicinity of Adler) in 1913 (Lindholm 1913). Several reports from the southern part of European Russia were published in the 1930s to 1970s (Zhadin 1931; Kazannikov 1964; Kudryavtsev and Pirogov 1975). Kudryavtsev and Pirogov (1975) considered its 'natural' range in the USSR to include Central Asia, Transcaucasia, Black Sea maritime territory and the northern Caucasus. Currently, the northernmost locality of *P. acuta* with a natural thermal regime in European Russia is the Kuybyshev Reservoir (middle Volga basin), where it was first discovered in 1998 (Yakovleva et al. 2011). In 2015, it was recorded north of the Arctic Circle, in the Kola Peninsula (northern part of European Russia), in a heated waterbody located at 67°27'43.3"N, 32°26'23.8"E (Nekhaev and Palatov 2016), apparently the northernmost locality of *P. acuta* globally.

In the Urals and Siberia, the species is able to live under artificially warm conditions only; it has been recorded from a few such habitats in the southern part of western Siberia and adjacent areas (Vinarski et al. 2015).

Spain

Morelet (1845) and Graells (1846) were the first to note *P. acuta* in Spain (see Table 1). Its current Spanish distribution was outlined by Abarca and Suares (1986). As for Portugal, it seems likely that the species occurred there well before 1845.

Sweden

Physella acuta was first recorded in Sweden around 1905 in tanks in the Stockholm and Uppsala botanical gardens (Nilsson 1928). It now occurs in several areas in the southern parts of the country (Welter-Schultes 2012).

Switzerland

Neither Clessin (1887) nor Bollinger (1909) included *P. acuta* in their check-lists of the Swiss malacofauna, but Turner et al. (1998) claimed that it was recorded in the country as early as around 1848, in Orbe (north of

Lausanne). The next record (in Geneva) was in 1905 (Turner et al. 1998). It is now widely distributed in lowlands below 820 m above sea level (Turner et al. 1998).

Tajikistan

Numerous records of *P. acuta* in this country have been made since 1940 (ZIN, unpublished). My own field work in Tajikistan in June of 2016 has shown that the snail is quite common and abundant in the entire flat part of the country, but absent in montane areas (above 2500 m above sea level).

Turkey

The species was first recorded in Turkey in 1980, from western Anatolia (Yildirim et al. 2006). Since then it has been found in various regions of both the European and Asian parts of the country, with the exception of eastern Anatolia and the Marmara region (Yildirim et al. 2006).

Turkmenistan

There are several samples of *P. acuta* collected in 1963 in Turkemistan (ZIN, unpublished). No more recent data on its presence in this country are available.

Ukraine

The first published record of *P. acuta* was that of Beletsky (1918), who found it in 1916 in the vicinity of Kharkov. Another (long unpublished) early finding was in 1919 in the vicinity of Kiev (Son 2007). By 1990, it had become widespread through almost the entire Ukraine, known as *Costatella integra* (Halde-man, 1841) (Stadnichenko 1990).

United Kingdom

The first reliable record of *P. acuta* in the UK was from a water tank in the Royal Botanic Gardens, Kew, near London (Choules 1860). The date of the first appearance of *P. acuta* in outdoor habitats in UK is unknown (Anderson 2003). In the 1900s, the species was still regarded as a dweller of tanks in a few botanical gardens (Williams et al. 1907). Ellis (1926) noted

several additional localities in Britain. By 1976, the species (treated as *Physa* cf. *acuta*) occurred at a number of localities in central and southern England (Kerney 1976), which Anderson (2003) considered to ‘more or less correctly represent the distribution of’ *P. acuta*.

Uzbekistan

The current distribution of *P. acuta* in the former Soviet Central Asia represents the result of its very fast spread from the initial point of invasion situated, perhaps somewhere in the vicinity of Tashkent, the capital of Uzbekistan. This location was the first published occurrence of the snail in Central Asia (Lindholm 1929). By 1950 the species was abundant in Uzbekistan (ZIN, unpublished).

Possible occurrence of *P. acuta* in Europe prior to its description in 1805

It is crucial for this historical study to estimate the time of the first arrival of *P. acuta* in Europe. It probably arrived long before it was described by Draparnaud (1805), since the distribution data published in the first half of the 19th century (Brard 1815; Cantraine 1838; Küster 1841) indicate that by the 1830s its European range was already broad and covered almost the entire Mediterranean region eastward to Croatia (see Table 2). Several hypothetical cases of ancient occurrence of the species in Europe are as follows.

The case of Lister

Martin Lister (1639–1712) was the founder of malacological studies in Great Britain. His works on molluscs include several volumes with detailed descriptions of snails and bivalves occurring in England. Férussac (1807) and Küster (1841) suggested that Lister described *P. acuta* in his treatises *Historia Animalium Angliae* (Lister 1678) and *Historia Conchyliorum* (Lister 1686) and thus became the first European naturalist acquainted with the species. This suggestion also pushes the date of the arrival of *P. acuta* in Europe back to the mid-17th century. However, closer examination of Lister’s works lends no support to this hypothesis. The pictures of shells of assumed *P. acuta* in both books of Lister (1678, pl. 2, fig. 25; 1686, pl. 135, fig. 35) represent a very

generalized view of a physid shell that may well belong to *P. fontinalis*, a native species of Europe. The shell spire in both illustrated specimens is lower than is typical for *P. acuta*. The morphological description (Lister 1678: 142) is very vague and could be applied to almost any species of *Physa* or *Physella*. Besides, Lister (1678) noted that this species was rather abundant in England, especially in small rivers and stagnant waterbodies enriched by vegetation, which seems unlikely for a recently introduced species.

The case of d’Argenville

According to Férussac (1807), *P. acuta* was illustrated in the treatise on conchology written by French designer and collector of curiosities Antoin-Joseph Dézallier d’Argenville (1680–1765). It was published in France three times between 1742 and 1780 under different titles. The first edition (d’Argenville 1742) contains a plate with illustrations of shells of freshwater molluscs, one of which (pl. 31, fig. 6, the farthest right hand shell) almost definitely represents *P. acuta*. In the text, d’Argenville called this species “Buccin à bouche tournée à gauche” (i.e. ‘Buccin [the genus name] with mouth turned to the left’) but gave no detailed description of its shell. Sinistrality (left coiling) is a characteristic trait of Physidae. The shell depicted by d’Argenville has a rather elevated conical spire, typical for *P. acuta* and not for *P. fontinalis*, the native European species. The shell proportions of d’Argenville’s specimen also resemble those in *P. acuta*. Therefore, d’Argenville’s illustration is good evidence of the presence of this species in France 60–70 years before Draparnaud’s (1805) description. Unfortunately, it is unknown where the specimen was collected.

The case of Gualtieri

Evidence of the early occurrence of *P. acuta* in southern Europe also comes from a shell (or shells) once kept in the private museum of Niccolò Gualtieri (1688–1744), a pioneer of conchological studies in Italy. His opus magnum, *Index testarum conchyliorum* (Gualtieri 1742), has been acclaimed as ‘a masterpiece of eighteenth-century illustrated malacological literature’ (Manganelli and Benocci 2011: 74). It includes an illustration of a physid shell (Gualtieri 1742, pl. 5, fig. cc) that may be identified as *P. acuta*. It resembles

the d'Argenville (1742) illustration and, in addition, a conchological diagnosis provided by Gualtieri conforms to the actual shell traits of *P. acuta*. Specifically, Gualtieri mentioned that the shell is white ('albida'), as is the type specimen of *P. acuta* (Fig. 3), which is entirely not typical for any indigenous European physid species.

The case of Maton and Rackett

In 1804, two Englishmen read before the Linnean Society the description of a new British freshwater snail from Hampshire, named, after its formal publication, *Physa rivalis* Maton and Rackett, 1807. Maton and Rackett (1807) referred illustrations in works of three 18th century continental conchologists (Favanne in France, Chemnitz and Schröter in Germany) to their new species. This may mean that *P. acuta* was encountered in Germany more than a century before its first documented finding (see above). According to Westerlund (1885) and some subsequent researchers (Taylor 2003), *P. rivalis* is identical with *P. acuta* and, thus, the species arrived in England much earlier than 1860 when it was found in the Kew Botanical Gardens (Choules 1860). Forbes and Hanley (1853: 145) considered *P. rivalis* a "West Indian species" albeit distinct from *P. acuta*, "a southern Continental species".

In fact, *Physa rivalis* sensu Maton and Rackett may not be a physid as their illustration is of a dextral (right-coiled) shell (Maton and Rackett 1807: pl. 4, Fig. 2), whereas physids all coil sinistrally (left-coiled). Their figure is most likely of a lymnaeid shell. However, in many conchological illustrations of the period dextral shell were represented as sinistral, and vice versa, as the usual technique of engraving required that the plate be a mirror image of the object to be illustrated (Allmon 2007). Nonetheless, this explanation may not be valid for *P. rivalis* since other shells illustrated by Maton and Rackett (for example, the lymnaeid *Stagnicola palustris* illustrated as their pl. 5, fig. 8) were portrayed correctly, not as mirror images.

To summarize, among the four above cases of possible occurrence of *P. acuta* in Europe, only two (d'Argenville, Gualtieri) seem to sustain critical examination. On the basis of its early occurrence in Italy and France, it is possible that the species first appeared in Europe long before its scientific description in 1805, i.e. in the seventeenth century or, maybe,



Fig. 3 The holotype of *P. acuta* from the Draparnaud collection in NHMW. Note that the apex of the shell is broken

even prior to European discovery and settlement of the Americas. This early dating helps to explain the broad Mediterranean range occupied by the 1830s but poses some questions concerning the mechanism of its transatlantic travel from the New World to Europe (see below).

Discussion

The entire process of *P. acuta* dispersal in Europe can be divided into three successive phases driven by different factors either natural or human-mediated.

The first phase of invasion [17th (?)–mid-19th centuries], following initial arrival in Europe, involved the species dispersing and expanding its range throughout the western Mediterranean region eastward to the Balkans. Considering its high invasive potential, this may have taken only 100–150 years. Possibly, natural dispersal mechanisms (such as bird-mediated short distances between lakes and ponds) played the main role in this process, though the initial arrival of *P. acuta* in the Old World was probably due to human activity.

Phylla acuta seems to be one of the first invasive species of New World origin to gain a foothold in Europe after discovery and colonisation of the New World by Europeans in 1492. Human-mediated dispersal is the most frequently invoked mechanism explaining its initial arrival and subsequent rapid spread through Europe and other continents. However, the true pathway by which *P. acuta* arrived in Europe is a matter of debate.

Draparnaud (1805) described *P. acuta* from the Garonne River and its tributaries. Anderson (2003) suggested that this was ‘circumstantial evidence for an introduction since trade in cotton between the eighteenth-century French possessions on the Mississippi and ports in western France, including nearby Bordeaux, had been pursued for most of the latter half of the eighteenth century. The Napoleonic Wars ended this trade and ... the cotton trade switched to British cities ... and certainly resulted in the accidental import of the North American pulmonates’. However, this hypothesis proposes no causal links between the cotton trade and the life habits of aquatic pulmonates.

English authors of the 19th century suggested that *P. acuta* had been introduced to England with plants and other colonial goods, for example the ‘many West-Indian plants ... imported and cultivated in the [botanical] Gardens’ (Jeffreys 1862: 100). This hypothesis does not contradict the suggestion above that the first introduction to Europe may be dated back to the 17th–18th centuries. As early as the end of the 16th century, most universities in Italy and other western European states with strong medical curricula had botanical gardens filled with New World plants as well as European species, and ‘claimed to contain the natural world in microcosm’ (Findlen 2006). The import of exotic plants, including aquatic ones, from the New World to Europe was so common in the 17th century that it has even been reflected in post-modernist fiction (Eco 1995). This may account for the early presence of *P. acuta* in France and Italy starting in the mid-17th century.

However, in my opinion, another, more ‘natural’, mechanism of arrival of this species to the Old World is not excluded. One may suggest that the Macaronesian islands (the Azores, Madeira, the Canary Islands, and Cape Verde) may have served as potential stepping-stones for extremely long-distance dispersal of *P. acuta* from America to Europe.

The overall percentage of endemic taxa in the Atlantic island faunas is very low. The vast majority of invertebrate species have arrived there either from the Americas or from Europe (zur Strassen 1981; Gíslason 2005; Raposeiro et al. 2011) as the result of long-distance dispersal events. Though such events would have been extremely infrequent, their impact on the formation of current biogeographic patterns may have been substantial (de Queiroz 2014).

For instance, the continental malacofauna of the Azores consists of Palearctic species predominantly, but a small group of snails of Nearctic origin also occurs there (Backhuys 1975; Raposeiro et al. 2011). In another group of tiny and non-mobile terrestrial invertebrates, Thysanoptera (Insecta), a small number of Nearctic species is also present in the faunas of the Azores and Madeira (zur Strassen 1981). Recently, long-distance dispersal as a mechanism of transport of another aquatic pulmonate, *Ferrissia fragilis* (Tryon, 1863), from the Americas to the Azores was proposed (Raposeiro et al. 2011).

In my opinion, bird-mediated transoceanic dispersal of *P. acuta* is quite possible, and it may have occupied the European (western Mediterranean) part of its range long before the New World was discovered by Europeans. On the other hand, the occurrence of *P. acuta* in the Old World cannot be very ancient since there is no significant genetic distance or reproductive incompatibility between European and American snails (Dillon et al. 2002; Lydeard et al. 2016). The absence of *P. acuta* in the European fossil record (Lydeard et al. 2016) also indicates its rather late arrival to the Old World. In Europe, remains of it have been found in Recent deposits only (Alexandrowicz 1986).

The second phase of the invasion (mid-19th–mid-20th centuries) was, however, triggered almost exclusively by sociocultural factors. During this phase, *P. acuta* invaded northern and central European countries expanding north and north-east from its initial Mediterranean range. First, intensive canal building took place in industrial countries of Europe in the first half of the 19th century. These canals served as artificial water corridors facilitating spread of various aquatic invertebrates from one river basin to another. Kobelt (1880) and Adam (1960) regarded canals as the primary dispersal route of *P. acuta* from France to Belgium and the Netherlands, which were beyond the initial invasive range of the species. According to

Kobelt (1880), the snails reached Alsace through the Rhine-Rhone canal and then invaded Belgium through the Mosel basin.

Invention of the modern type aquarium was the second trigger of the invasion of northern and central Europe. It was unknown until the mid-1850s, when the first constructions of aquariums with transparent and durable walls were proposed (Taylor 1876; Allen 1976; Hamlin 1986; Lachapelle and Mistry 2014). The first public aquarium in England was opened in Regent's Park in London in 1853 and subsequently private fish tanks became fashionable and decorative objects of the bourgeois home in England, France, Germany, and Russia (Bogdanov 1856; Allen 1976; Lachapelle and Mistry 2014). In the 1850s, the aquarium 'turned into a national craze' in Great Britain (Allen 1976). Freshwater snails, including *P. acuta*, were common and desired inhabitants of these household aquariums, acting both as scavengers (consuming dead leaves and other organic debris) and as food for fish (e.g. Bogdanov 1856; Hibberd 1856; Zolotnitsky 1910; Hamlin 1986).

Apparently, these private aquariums, along with tanks in botanical gardens, constituted the main source of *P. acuta* invading outdoor habitats in warmer regions (e.g. the Black Sea coast; Lindholm 1913) or artificially heated waterbodies in industrial zones (e.g. in Poland; Boettger 1913; Feliksiak 1939). By the 1910s, *P. acuta* occurred in botanical gardens in almost every country of northern and eastern Europe (see Results).

The second phase is also marked by invasion of *P. acuta* into Transcaucasia and Central Asia. It took only 20–30 years for *P. acuta* to become widespread in the vast territory of the former Russian Turkestan (now a group of independent Central Asian states).

The third (mid-20th century–present) phase of dispersal is marked by abundance of *P. acuta* in outdoor habitats in relatively cold countries (England, Netherlands, middle European Russia). By the 2010s *P. acuta* reached trans-polar areas in northern European Russia where it can survive in artificially heated waterbodies. Ongoing human-mediated factors including the aquarium trade (Duggan 2010) and anthropogenic alterations of natural habitats (Strzelec et al. 2006; Spyra and Strzelec 2014) may also be acting in synergy with natural vectors of dispersal, allowing *P. acuta* to expand to cover a virtually pan-European range. Finding the snails in remote and

sparsely populated areas, such as the Central Asian deserts and semi-deserts (Jankowskaja 1972; Vinarski et al. 2015), can hardly be explained by the activities of aquarium owners.

Conclusions

The data collected and discussed above allowed reconstruction of the history of the expansion of the invasive range of *Physella acuta* in Europe, Transcaucasia and Central Asia, from its supposed presence in the Western Mediterranean area in the 17th–18th centuries. The overall duration of the process may be estimated as 300–400 years, though it is not impossible that the first arrival of *P. acuta* in Europe dates back to pre-Columbian time, due to natural, possibly bird-mediated, long-distance dispersal from the New World to Europe. The entire process may be viewed as a product of interaction of diverse environmental and anthropogenic factors, the relative contributions of which varied from one historical phase of the invasion to another.

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