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A relict or new immigrant? The first record of the planorbid *Gyraulus riparius* (Westerlund, 1865) in France

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Abstract. A population of a ramshorn snail species new to the French malacofauna, *Gyraulus riparius* (Westerlund, 1865), has been discovered in the fen surrounding Lake Cerin in southern Jura, eastern France. This population is located more than 450 km south of the previously known localities in Germany, and the species' status as indigenous to France is therefore discussed. A review of palaeontological data show that the species has been recorded in eastern France during cold periods of the Middle and Lower Pleistocene. Furthermore, Lake Cerin is a small lake of glacial origin, located at an altitude of 766 m a.s.l., with little impact from human activities and inhabited by numerous threatened and protected boreo-alpine species. We postulate that this population indicates a wider past distribution, especially in the south, although we cannot exclude the hypothesis of a more recent introduction (natural or anthropic). We propose that *G. riparius* should be treated as a species native to France, as defined by the International Union for the Conservation of Nature, and targeted by a conservation and knowledge programme.

Key words. Jura Mountains, Lake Cerin, Quaternary, palaeomalacology, Planorbidae

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Introduction

Gyraulus riparius (Westerlund, 1865) is a poorly known freshwater gastropod belonging to the hyper-diverse family Planorbidae, which includes about 312 accepted species (Albrecht *et al.* 2006; MolluscaBase 2024). The species geographic range extends in northeastern Europe and Siberia, from southeastern Germany to the Altai Mountains (Welter-Schultes 2012; Glöer 2019). More specifically, the species has been documented in Germany, (i) in the southwest in Baden-Württemberg and Rhineland-Palatinate (Groh & Richling 2009), (ii) in the south in the Danube valley at Reibersdorf Lake, and (iii) in the large lakes in the north (see Glöer 2019 for references), as well as in The Netherlands (Kuiper 1947; Van Bruggen 1957; Gittenberger *et al.* 1998), Poland (Piechocki *et al.* 2016; Czyż *et al.* 2016), Slovakia (Horsák *et al.* 2013), and Hungary (Fehér *et al.* 2006). It is also present around the Baltic Sea in Latvia (Schlesch 1943; Stalazs & Dreijers 2016; Rudzite *et al.* 2018), Lithuania (Zettler 2014; Stalazs & Dreijers 2016), and Estonia (Stalazs & Dreijers 2016). Its northern range includes Denmark (Mandahl-Barth 1949), Finland (Aho *et al.* 1981), and Sweden (Nilsson *et al.* 1998; von Proschwitz 2001), while its eastern range extends through the European part of Russia to western Siberia (Kantor *et al.* 2010; Filippenko 2011; Vinarski *et al.* 2013; Vinarski & Kantor 2018; Pisaryev 2022). In northern Italy, the species has been recorded in Lake Frassino near Verona since 2004, where it is considered to be introduced (Niero 2022).

Gyraulus riparius inhabits standing waters with a dense vegetation, usually in lakes (Glöer 2019), undisturbed pools, oxbow lakes, and wetlands in the floodplains of large lowland rivers (Horsák *et al.* 2013). It is most rarely in rivers (Czyz *et al.* 2016). The species is considered rare, probably because of the rarity of high-quality habitats, with scarce populations throughout most of its range, except in Finland

and the Netherlands. However, the putative rarity of the species may also be partly due to sampling bias related to its small size and similar shell shape to juveniles of *Hippeutis complanatus* (Linnaeus, 1758). Indeed, the shell of *G. riparius* is tiny, 2.3–3.5 mm wide and 0.6–0.8 mm high, with 3½ rapidly increasing whorls; the last whorl is slightly angular at periphery, giving a *Hippeutis*-like shell when viewed in apertural view. However, besides the larger size of the adult shells of *H. complanatus* (4–5 mm wide), *G. riparius* has a last whorl with a less pronounced angular outline and a wider umbilicus. In addition, the umbilical edge of the aperture is inserted on the periphery of the penultimate whorl in *G. riparius*, whereas in *H. complanatus* it is inserted in the middle (Kuiper 1947).

Described from Sweden and initially attributed to the genus *Planorbis* O.F. Müller, 1773 by Westerlund (1865), the species was successively placed in the genera *Anisus* S. Studer, 1820, *Hippeutis* Charpentier, 1837, *Choanomphalus* Gerstfeldt, 1859, and *Gyraulus* Charpentier, 1837 (see Vinarski *et al.* 2013 for an overview). Based on the structure of the male reproductive system, Starobogatov (1967) created the subgenus *Lamorbis* within the genus *Choanomphalus* with *Planorbis riparius* as type species. Subsequently, Meier-Brook (1983) recognized the taxonomic validity of this subgenus but placed it within the genus *Gyraulus* as a sister group to subgenus *Armiger* W. Hartmann, 1843. The molecular phylogeny approach of planorbids by Albrecht *et al.* (2007) suggests that the genera *Choanomphalus* and *Gyraulus* form separate clades. However, other molecular phylogenetic analyses using mitochondrial and/or nuclear sequences attributed to *G. riparius* (Lorencová *et al.* 2021; Saito *et al.* 2023) do not allow a clear taxonomic assignment within the genus *Gyraulus*.

Gyraulus riparius has never been recorded in the modern French fauna, although paleontological data suggest that the species was present in Alsace (northeastern France) at least 400,000 years ago in alluvial deposits (Wernert & Geissert 1963). However, during opportunistic malacological sampling, one of us (JR) discovered a population in Lake Cerin, in the southern Jura Mountains in eastern France. The aims of this article are (i) to report this discovery, (ii) to review the palaeontological literature, and (iii) to discuss both its native/non-native nature and its conservation status in France.

Material and Methods

Lake Cerin (Fig. 1A) is a small residual lake (*c.* 2,500 m^2) of glacial origin located at an altitude of 766 m a.s.l.; it is immediately surrounded by mires (0.15 km^2) resulting of overgrowing processes (Magny *et al.* 2011). The average annual rainfall is about 1,500 mm, and the average temperature ranges from 0.2 °C in the coldest month to 14.5 °C in the warmest. The current open-water zone, known as the "peat bog eye" (Fig. 1A, B), is 2.5–3.2 m deep, with a constant water level throughout the year (Faussurier 1973). Its pH is alkaline, close to neutral (7.0–7.5) (CEN Rhône-Alpes 2012). Specifically, the natural habitats around the lake consist of a mosaic of intermingled wetlands composed of *Nymphaeion* (EUNIS 2012 code: C1.34), *Caricion lasiocarpae* (EUNIS 2012 code: D2.31), *Cladietum marisci* (EUNIS 2012 code: D5.24), *Rhynchosporion* (EUNIS 2012 code: D2.3H), *Caricetum davallianae* (EUNIS 2012 code: D4.13), *Orchio palustris–Schoenetum nigricantis* (EUNIS 2012 code: D.411). These habitats are home to several threatened and protected boreo-alpine species, such as Varnished Hook-moss (*Hamatocaulis vernicosus* (Mitt.) Hedenäs), Bog Sedge (*Carex limosa* L.), English Sundew (*Drosera anglica* Huds.), or Alpine Bulrush (*Trichophorum alpinum* (L.) Pers.).

This natural site, including the lake and the surrounding natural habitats, is covered by a conservation management plan drawn up by a French NGO (Conservatoire d'espaces naturels Rhône-Alpes or CEN Rhône-Alpes in the following text), which owns or has a management contract for the entire surface of the marshland (National code: FR1506088; International code - Protected Planet: 555739606). It is also included in the European Natura 2000 network of protected areas (site code: FR8201641).

Sampling was carried out on 25 September 2021 and 23 April 2024 in the waterlogged alkaline swamps surrounding the lake (45.7774°N, 005.5615°E) using the wet-sieving method (Horsák 2003). Samples were taken from a small area of approximately 4 m^2 and a total volume of about 10 L of litter was washed (Fig. 1C). The cleaning residue was then filtered through a fine mesh sieve (500 µm) to retain the smallest shells. All molluscs sampled were transported live to the laboratory and then fixed in 70% ethanol. When necessary, they were identified based on diagnostic anatomical features of the reproductive system. Specifically for *G. riparius*, the diagnostic characters from Meier-Brook (1983) and Glöer (2019) were used.

Palynological and lithostratigraphical studies have been carried out at the Cerin lake, using 49 core samples to assess changes in the vegetation and palaeohydrological variations since the end of the Younger Dryas (Ruffaldi 1993; Magny *et al.* 2011). The mollusc assemblages from one of these cores (number TB3; 10 m deep and dated from the Younger

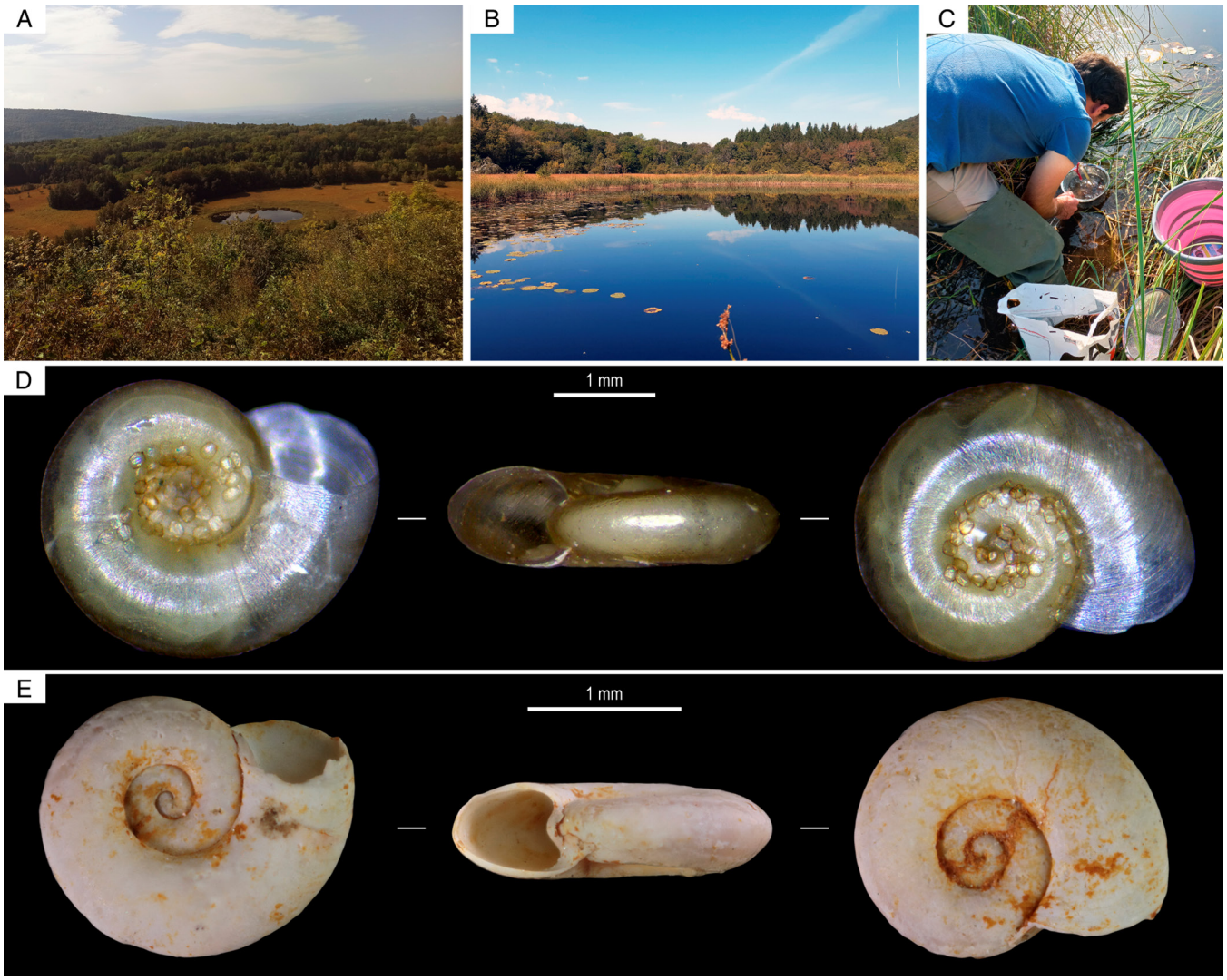

Figure 1. Sampling site and shells of *Gyraulus riparius* (Westerlund, 1865). **A**, view of Lake Cerin and surrounding vegetation. **B**, the open water area also known as the "peat bog eye". **C**, sampling site in the waterlogged alkaline swamps near the "peat bog eye". **D**, shell of *G. riparius* sampled at Cerin Lake, seen from the top, from the aperture and from the bottom side, respectively. **E**, fossil shell of *G. riparius* from the Gelasian (Lower Pleistocene) deposit of Petit-Reversey, Mervans (Bourgogne-Franche-Comté, France; J.J. Puisségur collection).

Dryas to the present) were briefly described in the thesis of Ruffaldi (1993). The corresponding samples have been deposited at the Muséum national d'Histoire naturelle, Paris (MNHN, Jacques Mouthon leg.) and examined by one of us (JR). In addition, the Quaternary fossil occurrences of *G. riparius* have been compiled based on a critical review of the literature and access to the Quaternary Molluscan Database (https://malacologie.in2p3.fr/). The records of this taxa were reviewed for chronological and palaeoclimatic context by checking the type of dating and sedimentary context to provide reliable fossil data.

We follow the taxonomic referential TAXREF v. 17 (Gargominy *et al.* 2024) for all species cited in this paper. The phytosociological classification follows the EUNIS nomenclature (European Nature Information System, https://eunis.eea.europa.eu/).

Results

In the years 2021 and 2024, 12 and four live specimens of *G. riparius* were respectively collected (Figs 1D, 2C), in association with the freshwater gastropods *Anisus leucostoma* (Millet, 1813) ($n = 6$), *Galba truncatula* (O.F. Müller, 1774) ($n = 6$), and *Valvata cristata* O.F. Müller, 1774 ($n = 3$), but also with the terrestrial species *Carychium minimum* O.F. Müller, 1774 ($n = 5$), *Euconulus alderi* (J.E. Gray, 1840) (n

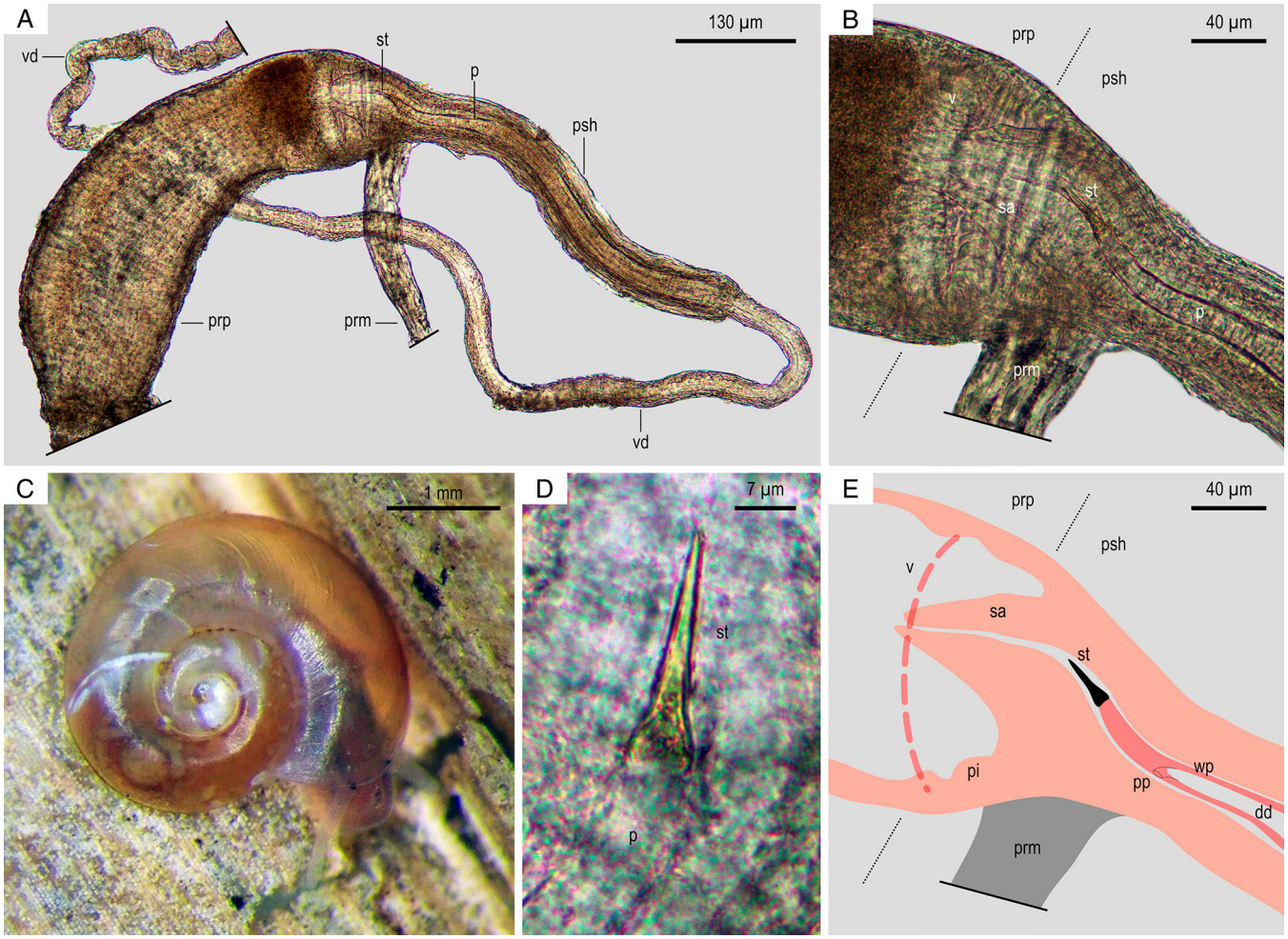

Figure 2. Live specimen and male part of the reproductive system of *Gyraulus riparius* (Westerlund, 1865) from specimens sampled in Lake Cerin (south of the Jura Mountains, eastern France). **A**, view of the male part of the reproductive system. **B**, view of the transition between the penis sheath and preputium. **C**, living specimen sampled on 23/04/2024 in Cerin Lake. **D**, stylet. **E**, schematic view of the transition between the penis sheath and preputium (see **B**). Abbreviations: **dd** ductus deferens, **p** penis, **pi** pilaster, **pp** penis pore, **prm** penis retractor muscle, **prp** preputium, **psh** penis sheath, **sa** sarcobellum, **st** stylet, **vd** vas deferens, **v** velum, **wp** penis wall.

= 2), *Nesovitrea hammonis* (Strøm, 1765) (*n* = 1), *Vertigo antivertigo* (Draparnaud, 1801) (*n* = 2), and *Vertigo pygmaea* (Draparnaud, 1801) (*n* = 8). Count data for these species only refer to the first sampling in 2021.

The study of the anatomical features obtained on three of the sampled specimens of *G. riparius* corresponds well to those reported in the literature (Meier-Brook 1983; Glöer 2019). Here we only show and describe the copulatory apparatus (Fig. 2), which is rarely illustrated in the literature. Penis sheath (psh) narrow, only slightly wider than the vas deferens (vd). Praeputium (prp) is wider but about the same length as the of the penis sheath. Penis retractor muscle (prm) inserts into the terminal part of the penis sheath just before the praeputium emerges. Penis sheath terminated by a sarcobellum (sa) (*sensu* Hubendick 1955; papilla *sensu* Baker 1945), a cone-shaped tissue with a hole through which the stylet (st) passes during copulation. Praeputium with usually one or two muscular pilasters (pi) corresponding to the invagination of the inner epithelium (Meier-Brook 1964, 1983). Presence of a muscular ring (v) (or velum *sensu* Hubendick 1955, or diaphragma *sensu* Meier-Brook 1983) in the proximal part of the praeputium. Penis (p) slender with a stylet (st) at the tip. Penial pore (pp), i.e. the orifice of the ductus deferens (dd), located where the tapering begins and before the stylet. Stylet thin, conical, approximately 25–30 µm in length and 9 µm in diameter at most.

The mollusc assemblages from sediment core TB3 at Lake Cerin described in Ruffaldi's thesis do not contain *G. riparius*, which we confirm after careful examination of all the samples housed in the MNHN. According to Ruf-

faldi (1993), 18 species of molluscs were recorded in TB3, including 13 gastropods, such as *Anisus leucostoma*, *Anisus vorticulus* (Troschel, 1834), *Gyraulus albus* (O.F. Müller, 1774), *Gyraulus crista* (Linnaeus, 1758), *Hippeutis complanatus* (Linnaeus, 1758), *Valvata cristata*, and *Valvata piscinalis* (O.F. Müller; 1774).

From our literature review, *G. riparius* appears to be rare in Quaternary non-marine fossil-mollusc assemblages in European alluvial and lacustrine deposits. Fossil occurrences have been documented in Poland from the Late Glacial Period (Kulesza *et al.* 2011) to the Holocene (Alexandrowicz 1987; Alexandrowicz & Żurek 2013; Kurzawska & Kara 2015; Galka *et al.* 2017), Belarus (Eemian: Galka *et al.* 2017) and northern European Russia (Quaternary deposits: Zhadin 1952; Danilovsky 1955). The species has been found in Eemian and Weichselian and Middle Pleistocene deposits in Germany (Mania 1978; Schiermeyer 2000; Olivier Moine personal communication), in the Holocene of Lithuania (Sanko *et al.* 2010), in the Upper Gelasian and Holocene deposits in the Netherlands (Meijer 1989; Meijer in Gittenberger *et al.* 2004), in Czech Republic (Lozek 1964), from the lower Pleistocene (Jánossy & Krolopp 1994) to the Upper Pleistocene (Sumegi *et al.* 2012, 2013) and Holocene (Fukoh 1992) in Hungary, and from the Late Glacial in Ukraine (Hájková *et al.* 2022). Furthermore, *G. riparius* has been identified in fossil sites in France and the United Kingdom that are outside its current known distribution. This species was present during cold periods in eastern France during the Middle Pleistocene in Alsace at Hangebieten (MIS 12: Wernert & Geissert 1963) and the Lower Pleistocene in Bourgogne Franche-Comté at Mervans, Sainte-Marie-la-Blanche, and Levernois (Gelasian: Puisségur 1984, Fig. 1E). In Great Britain, *G. riparius* appeared at two sites during an interglacial phase of the Middle Pleistocene (MIS7: Preece 2003; Preece & White *in* Wenban-Smith *et al.* 2020). Although *G. riparius* is considered to be a cold-resistant species and is regularly found in association with fauna indicative of glacial and late environments, it also occurred during interglacial phases such as the Eemian (Mania 1978; Preece 2003; Sanko *et al.* 2010). Our review of the palaeomalacological literature suggests that the Pleistocene distribution of *G. riparius* was wider and beyond the western limit of its current range.

Discussion

The discovery of *Gyraulus riparius* in the south of the Jura massif, outside its known current range, raises questions about its French biogeographical and conservation status, but also challenges the true extent of its current global range. Indeed, the new population is at least 435 km distant from the nearest populations in Germersheim, Germany, apart from the introduced Italian population in Lake Fressano, and may therefore represent the westernmost and southernmost edge of its range. Relict or new immigrant, or in other words, native or non-native? That is the key question! The definition of an "introduced" or "native" species is relatively straightforward and based on a dichotomous classification (Essl *et al.* 2018, 2019; Lemoine & Svenning 2022); an introduced species is one that has been introduced by human activity outside its natural range and has the potential to survive and reproduce, and a native species is one within its natural range (see for example definitions by the International Union for Conservation (IUCN) or the Convention on Biological Diversity). However, the criteria for applying these definitions in practice are less clear, due to the variety of considerations, especially where the current and/or historical natural range is poorly known (Essl *et al.* 2018). Crees & Turvey (2015) addressed this issue and proposed a framework that outlines possible subcategories that exist between the current "native/non-native" dichotomy and specifically incorporated Upper Pleistocene and Holocene data. This classification considers a taxon to be native *sensu lato* (see subcategories of Crees & Turvey 2015: table 1 and fig. 1) if it has been continuously present since the Upper Pleistocene or (re)colonised during the Holocene, with or without human influence. In France, palaeontological data indicate that *G. riparius* was present at least during the Lower and the Middle Pleistocene (Wernert & Geissert 1963; Puisségur 1984). At Lake Cerin, *Anisus vorticulus* occurred during the Late Glacial (Ruffaldi 1993) and indicates that environmental conditions were favourable for *G. riparius* during the Lower Dryas (Groh & Richling 2009). Furthermore, in contrast to the situation observed in Lake Fressano, Italy (Nerio 2015), the current high degree of naturalness of Lake Cerin, with minimal anthropogenic influence, limits the potential for accidental introduction by human activities, although this cannot be entirely ruled out (the same applies to a potential (re-) introduction via another non-anthropogenic source, such as birds).

By examining paleontological data over a broader chronological scale than that proposed by Crees & Turvey (2015), we suggest that *G. riparius* is a species native to France. This hypothesis is supported by its occurrence during the Middle Pleistocene in Great Britain (Preece 2003; Preece & White *in* Wenban-Smith *et al.* 2020) and during the Upper Pleisto-

cene in Germany (Mania 1978; Schiermeyer 2000; Olivier Moine personal communication).

Assuming *G. riparius* is native to France, possibly as a glacial relict, it could be classified as Vulnerable under criterion D2 or Near Threatened under criteria B1a+B2a (IUCN 2012), although the Data Deficient category is probably more appropriate, given the poor state of knowledge. Even if this is a recent accidental introduction, we argue that the species does not constitute a threat to the aquatic ecosystem of Lake Cerin, as evidenced by the slow population expansion in Italy since its introduction (Nerio 2015).

A comparison of fossil data and current distributional data suggests that the geographic distribution of *G. riparius* shifted during the Quaternary. Consequently, it is important to consider a broader time scale to gain a more comprehensive understanding of the biogeographic history of this taxon. However, while palaeodata provide a fantastic retrospective palaeobiological view, it is worth bearing in mind that the fossil record contains gaps. Due to their small size and fragility, shells of *G. riparius* may be found in the fossil record in a poor state of preservation. Small, fragile shells have been recovered from sites where the sediment has been meticulously sieved using a fine mesh (500 µm or 1 mm). Consequently, this species' occurrence in the fossil record is contingent upon the application of a specific methodology to find it and suitable sedimentary parameters (e.g. carbonate content and fineness of deposits) that will enhance the likelihood of shell preservation.

The discovery of this population in a lake of glacial origin, far from what is currently thought to be its southern range limit, raises the question of its indigenous status. We argue that this population should not be considered as introduced in the IUCN sense, which would imply its status of "Not Applicable" in the French Red List. *Gyraulus riparius* should be considered a native species in France along with the 691 other species (726 terminal taxa) of French non-marine molluscs, of which 35 are recent introductions (post-1500 AD) (UICN comité français, OFB & MNHN 2021). Finally, we propose here the French vernacular name "la Planorbine des rives" (meaning "Shoreline Ramshorn Snail") to help naturalists and conservationists take better account of this species (Fontaine *et al.* 2011), and we plead that this population should be monitored and its native status investigated using molecular tools. It would be unfortunate if, as in the ironic story in the United Kingdom of the Pool Frog, *Pelophylax lessonae* (Camerano, 1882), its putative native status was only established after its extinction (Beebee *et al.* 2005; Snell *et al.* 2005).

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