Revision of Phoxinus in France with the description of two new species (Teleostei, Leuciscidae)

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Revision of *Phoxinus* in France with the description of two new species (Teleostei, Leuciscidae)

by

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Abstract. – French minnows of the genus *Phoxinus* are revised based on molecular data (COI and 12S rDNA markers), morphological characters and nuptial colouration patterns. The results delineate six groups of populations, which are recognised as species. *Phoxinus phoxinus* is found in eastern France in the lower and middle Rhine and Seine drainages. *Phoxinus bigerri* occurs in the Adour drainage and populations from the Lake Geneva basin and the upper Rhine drainage are identified as *Phoxinus csikii*. *Phoxinus dragarum*, new species, from the Garonne drainage, is distinguished by its unique nuptial colour pattern (green stripe in Z3 reaching up to the anal fin base and Z4 greenish yellow in male; Z4 green-ochre and black line below in Z5 reaching from the pectoral fin bases to the anal fin base in female), and by an incomplete lateral line generally reaching to a point in front of the anal fin base or just shortly beyond the origin of the last anal fin ray. *Phoxinus fayollarum*, new species, from the Loire drainage, is distinguished by its unique nuptial colour pattern (green bars in Z3 and Z4, Z4 bright yellow, and belly red in male; green stripe in Z3, Z4 yellow-pinkish, and red spots at the pectoral, pelvic and anal fin base in female). Minnows of the Rhône drainage are identified as *Phoxinus septimaniae*. We consider *Pisciculus varius* and *Phoxynus montanus* as *nomben oblitum* and *Phoxinus septimaniae* as *nomen protectum*, and *Leuciscus obtusus* as *incertae sedis* within Leuciscidae.

Key words
Minnows
Phoxinus spp.
Cytochrome oxidase 1
Morphology
Nuptial colouration
Taxonomy

Résumé. – Révision des *Phoxinus* de France avec la description de deux nouvelles espèces (Teleostei, Leuciscidae).

Les vairons français du genre *Phoxinus* sont révisés à partir de données moléculaires (marqueurs du COI et de l'ADNr 12S), de caractères morphologiques et des patrons de coloration nuptiale. Les résultats délimitent six groupes de populations, qui sont reconnus comme espèces. *Phoxinus phoxinus* se trouve dans l'Est de la France dans les bassins de la Seine et du Rhin moyen et inférieur. *Phoxinus bigerri* est dans le bassin de l'Adour, et les populations des bassins du Léman et du Rhin supérieur sont identifiées comme *Phoxinus csikii*. *Phoxinus dragarum*, nouvelle espèce, du bassin de la Garonne, se distingue par un patron de coloration nuptiale qui lui est propre (bande verte dans la Z3 atteignant la base de la nageoire anale et la Z4 jaune-verdâtre chez le mâle ; Z4 verte-ocre et ligne noire en dessous dans la Z5 reliant les bases de nageoires pectorales à l'anale chez la femelle), et par une ligne latérale incomplète atteignant généralement la base de la nageoire anale ou juste après l'origine du dernier rayon de la nageoire anale. *Phoxinus fayollarum*, nouvelle espèce, du bassin de la Loire, se distingue par un patron de coloration nuptiale qui lui est propre (barres vertes dans les Z3 et Z4, Z4 jaune clair, et un ventre rouge chez le mâle; bande verte dans la Z3, Z4 jaune-rosée et taches rouges aux insertions des nageoires pectorales, pelviennes et anale et chez la femelle). Les vairons du bassin du Rhône sont identifiés comme *Phoxinus septimaniae*. Nous considérons *Pisciculus varius* et *Phoxynus montanus* comme *nomben oblitum, Phoxinus septimaniae* comme *nomen protectum*, et *Leuciscus obtusus* comme *incertae sedis* au sein des Leuciscidae.

INTRODUCTION

Minnows of the genus *Phoxinus* are small fishes, widespread in Eurasia from Spain to Korea (Kottelat and Freyhof, 2007). They are rheophilic and cryophilic inhabitants of streams and clear lakes (Bănărescu and Coad, 1991; Keith *et al.,* 2011). Minnows are native to all of France except Corsica, where they have been introduced to some mountain lakes (Keith *et al.,* 2011). They are generally described as fish with an olive-green coloration, a lighter longitudinal line above dark blotches on the flanks and a white-grey belly (*e.g.* Spillmann, 1961; Kottelat, 2007; Keith *et al.*, 2011). Like in most Cyprinoids, a sexual dimorphism appears during the reproductive season. It includes nuptial tubercles on the head and throat (Witkowski and Rogowska, 1992; Chen and Arratia, 1996). Moreover, during the breeding period, several chro-

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Table I. – Some descriptions of nuptial colouration in some French and Spanish catchments with English translations.

Basin	Original descriptions of nuptial colouration	Description translated in English
Ebre	"Los machos desarrollan llamativos tubérculos nupciales blancos en la cabeza durante la época de celo. Además, su coloración se realza haciéndose más llamativa; se oscurece la banda de manchas negras de los flancos, la mancha amarillenta del opérculo se aviva y se intensifica la coloración rojiza de la garganta, el vientre y la base de las aletas pares y la anal." (Leunda *et al*., 2017)	The males are marked on the head by the presence of nuptial tubercles during the spawning season. Moreover, its colouration is stronger, getting more and more striking; the band of black spots on the flanks gets darker, the yellowish spot on the operculum appears as well as a reddish colour on the throat, the belly and the base of the pectoral, pelvic and anal fins.
Geneva	"Dessus de la tête et le dos d'un brun verdâtre, plus ou moins mêlé de noir et de jaune, suivi de deux bandes longitudinales, la première dorée, et la seconde, un peu sinueuse, d'un beau noir, qui s'étendent de l'œil à l'origine de la queue. Une troisième bande, d'un beau vert d'émeraude, sablé de noir, règne immédiatement au-dessous des précédentes. Cette bande, qui est large à son origine, vers l'angle externe de l'opercule, descend plus ou moins sur les côtés du ventre, dont il suit la courbe, et se termine en pointe plus ou moins près de l'extrémité du corps ; le restant du ventre est argenté, avec des reflets dorés. Enfin, la poitrine, le milieu du ventre et le tour de la bouche sont d'un beau rouge vermillon. La joue et l'opercule sont argentés, à reflets dorés. Une tache blanche, opaline, imitant une perle fine, existe de chaque côté, à l'angle externe du bord supérieur de l'opercule ; la gorge est noire. Les nageoires sont jaunes, avec les rayons plus foncés. La dorsale est noirâtre jusqu'au premier quart environ de sa hauteur. Les ventrales et l'anale ont une partie de leur base d'un beau rouge, avec une grande tache en avant, d'un blanc éclatant." (Lunel and Lunel, 1874)	Above the head and back greenish brown, more or less mixed with black and yellow, followed by two stripes, the first golden, and the second, a little sinuous, a beautiful black, which extend from the eye to the origin of the tail. A third band, of a beautiful emerald green and dusted with black, sits immediately below the previous ones. This band, which is broad at its origin, towards the external angle of the operculum, descends more or less on the sides of the belly, of which it follows the curve, and ends in a point more or less near the extremity of the body; the rest of the belly is silver, with golden reflections. Finally, the chest, the middle of the belly and the mouth outline are of a beautiful red vermilion. The cheek and the operculum are silvery, with golden hues. A white spot, opaline, imitating a fine pearl, exists on each side, at the outer corner of the upper edge of the operculum; the throat is black. The fins are yellow, with darker rays. The dorsal fin is black until about one-quarter of its height. The ventral and anal fin bases are partly a beautiful red, with a large spot in front, bright white.
Loire	"tout le corps varié soit de couleur d'or ou d'argent, de nacre, d'azur, de rouge ou de noir…" (Millet, 1828)	The body variable, either gold or silver, mother-of-pearl, azure, red or black...
	"Il est à remarquer qu'à l'époque du frai, qui a lieu en mai et en avril, toutes les nageoires inférieures de ce poisson se colorent en rouge à leur base." (Mauduyt, 1848)	At spawning time, in May and April, it is remarkable that all the pectoral, pelvic and anal fins of this fish turn red at their base.
	"… au moment du frai c'est un mélange de vert, de bronze et d'argent, avec la base des nageoires et une partie du ventre d'un beau rouge." (Villatte des Prûgnes, 1897)	…at spawning time, it is a mix of green, bronze and silver, with the base of the fins and part of the belly a beautiful red.
	"Au moment du frai, reflets bleuâtres sur le dos, bande longitudinale de même couleur sur les flancs ; lèvres, gorge, base des nageoires et une partie du ventre rouge écarlate" (Piton, 1931)	At spawning time, bluish tinge on the back, stripe of the same colour on the flanks; lips, throat, base of fins and a part of the belly scarlet red.
	"Le mâle est alors en couleurs nuptiales très éclatantes, le ventre en rouge ou rosé, les verts de ses flancs s'avivent. Il porte sur la tête de petits tubercules cornés" (Magnan, 1982)	The male then has very bright nuptial colours, the belly red or pinkish, the green on the flanks brighter. It has on its head small callused tubercles.
Rhine	"Quelques individus ont parfois le dessous du corps et la mâchoire inférieure d'un beau rouge écarlate ; d'autres enfin présentent trois lignes longitudinales variant du bleu sombre au jaune doré" (Fournel, 1836)	A few individuals sometimes have the underside and the lower jaw a bright scarlet red; others present three stripes varying from dark blue to golden yellow.

matophores of the body skin are activated, resulting in shiny colours on mature individuals: erythrophores (red/orange pigments), xanthophores (yellow pigments), melanophores (black or brown pigments) as well as leucophores (white shine) and iridophores (iridescent shine) (*e.g*. Fuji, 2000). Spillmann (1961) pointed out the variability of the nuptial coat depending on the geographic area, and some authors described the coats in specific catchments (Tab. I).

All European minnows were previously identified as *P. phoxinus* (Linnaeus, 1758) (*e.g*. Berg, 1948; Kottelat, 1997). In 2007, based on morphological data, Kottelat (2007) described three new species, *P. bigerri* Kottelat, 2007 from the Adour drainage in southwestern France and the upper Ebro drainage in Spain, *P. septimaniae* Kottelat, 2007 from the Mediterranean coast of France, and *P. strymonicus* Kottelat, 2007 from the Strymon drainage in Greece. He also recognised *P. lumaireul* (Schinz, 1840) from Italy, *P. colchicus* Berg, 1910 from the Caucasus and *P. strandjae* Drensky, 1926 from Thrace as valid species. Also based only on morphological characters, Bianco and De Bonis (2015) described

Table I. – Continued.

Basin	Original descriptions of nuptial colouration	Description translated in English
Rhône	"Le Vairon de la Bèze a le dessous de la mâchoire inférieure noir. Au mois d'avril on voit sur la tête du mâle des petites épines coniques ; j'ai revu à la fin de mai ces mêmes caractères sur des Vairons pris dans l'Ouche, à l'aval du pont de l'hôpital. Un mâle avait sur la tête une multitude de ces petites épines coniques, si remarquables sur la majeure partie des mâles du genre Cyprin, à l'époque du frai." (Vallot, 1837)	The minnow from the Bèze River has the underside of the lower jaw black. In April one can see on the head of the male small conical spikes; I have seen at the end of May these same characters on minnows caught in the Ouche River, downriver from the bridge of the hospital. One male had on its head a multitude of these small conical spikes, so remarkable on most of the males of the Cyprin genus at the spawning season.
	"… une tache rouge à l'angle de la bouche ; dos grisâtre, maculé de brun ou d'olivâtre ; côtés à taches bleues, jaunes et verdâtres d'un bel effet, argentins en dessous de la ligne latérale ; pectorales et ventrales à base d'un jaune rougeâtre, à sommet obtus." (Ogérien, 1863)	… a red spot at the corner of the mouth; greyish back spattered with brown or olive colour; sides with beautiful blue, yellow and greenish spots, silvery below the lateral line; pectoral and ventral fins with reddish base and obtuse top.
Seine	"A l'époque du fraie, la coloration, surtout chez les mâles, est des plus brillantes ; le dos est d'un acier bleu d'acier ; le ventre est d'un jaune rougeâtre ; la base des paires, ainsi que celle de l'anale, prend une teinte d'un rouge plus ou moins vif ; la peau du mâle se recouvre d'espèces de tubercules, lors de la ponte la livrée de la femelle semble verdâtre ; les ventrales et l'anale sont légèrement teintées de rose." (Moreau, 1899)	In spawning season, the colouring, especially in males is most bright; the back is steel blue; the belly reddish yellow, the base of pectoral, pelvic fins, as well as of the anal fin, takes a more or less bright colour; the skin of the male is covered with tubercles, during spawning the livery of the female looks greenish; the ventral and anal fins slightly tinted with pink.
	"Les parures nuptiales sont brillantes ; à l'approche de la fraye (Vairons du Lunain, affluent du Loing) apparaissent au bas des flancs et sur le ventre des teintes vert émeraude. Des taches d'un blanc éclatant, soulignées d'une marge noire, sont très apparentes à la base de chacune des nageoires à l'exception de la caudale. Deux taches, blanches également, sont visibles l'une à l'angle supérieur de l'opercule, l'autre à sa partie inférieure. Le dos est de teinte foncée, bleu acier ou vert avec des reflets violacés. Une ligne de teinte claire court le long des flancs, séparant le dos de la série des taches des flancs qui sont d'un noir intense. La gorge est blanc rosé. Dans les derniers temps enfin, apparaissent des teintes d'un rouge plus ou moins vif, à la mandibule, à la base des nageoires paires et de l'anale." (Spillmann, 1961)	The nuptial coat is bright; when the spawning nears (for minnows from the Lunain, tributary of the Loing) emerald green colouring appears on the lower part of the flanks and the belly. Bright white spots with a black margin are very visible at the base of each fin except the caudal one. Two spots, also white, are visible: one at the upper angle of the operculum, the other in its lower part. The back is dark, steel blue or green with a purple tinge. A lighter coloured line runs along the flanks, separating the back from the intense black series of spots on the flanks. The throat is pink tinged with white. In the last period, more or less bright red colouring appears at the lower jaw, at the base of the pectoral, pelvic and anal fins.

four new *Phoxinus* species from Italy and the Western Balkan: *P. ketmaieri* Bianco & De Bonis, 2015 from the Krk Island, *P. karsticus* Bianco & De Bonis, 2015 from the Popovo Polje in the Trebinje endorheic drainage, *P. apollonicus* Bianco & De Bonis, 2015 from the Lake Skadar drainage, and *P. likai* Bianco & De Bonis, 2015 from the Oruca River in Croatia. Since, studies based on mitochondrial sequence data revealed the possible existence of more, yet unrecognised minnow species in Europe (Mendel *et al.,* 2012; Geiger *et al.,* 2014; Knebelsberger *et al.,* 2015; Palandačić *et al.,* 2015, 2017, 2020; Vucić *et al.,* 2018; Corral-Lou *et al.,* 2019). These molecular studies mostly support *P. bigerri*, *P. colchicus*, *P. lumaireul*, *P. septimaniae*, *P. strandjae*, and *P. strymonicus* as valid species, as already suggested by Kottelat (2007) and Kottelat and Freyhof (2007). Moreover, Palandačić *et al*. (2017) considered *P. ketmaieri* as well as potentially *P. likai* as synonyms of *P. lumaireul*, revalidated *P. csikii* Hankó, 1922 and *P. marsilii* Heckel, 1836, treated *P. apollonicus* as a synonym of *P. karsticus* and suggested *P. morella* (Leske, 1774) as potentially valid, but did not confirm *P. strymonicus* because of a lack of data. Most recently, Bogutskaya *et al*. (2019) described *P. krkae* Bogutskaya, Jelić, Vucić, Jelić, Diripasko, Stefanov & Klobučar, 2019 from the upper Krka River, a population genetically already recognised as distinct by Palandačić *et al*. (2017).

In France, four species are currently treated as valid: *P. bigerri* from the Adour drainage, *P. septimaniae* in the western Mediterranean basin (Kottelat, 2007; Kottelat and Freyhof, 2007; Keith *et al*., 2011), and *P. csikii* in the upper Rhine drainage and the Lake Geneva basin (Palandačić *et al*., 2017; Denys and Manné, 2019); all other populations are identified as *P. phoxinus* (Kottelat, 2007; Kottelat and Freyhof, 2007; Keith *et al*. 2011). However, Corral-Lou *et al*. (2019) already recognised a new molecular lineage in *Phoxinus* from the Garonne drainage, potentially corresponding to an undescribed species. Palandačić *et al*. (2017) did a synthesis of the characters used allowing the species discrimination, and morphometric or meristic discriminant characters are rare and often shared with other *Phoxinus* species. Thus, reliable diagnostic criteria are still sorely needed for minnow taxonomy despite multiple studies.

The present study reviews the French *Phoxinus* populations using mitochondrial sequence data (partial cytochrome c oxidase subunit 1 COI and complete ribosomal gene 12S), morphometric and meristic data as well as the nuptial colouration pattern, and revises the species diversity of French minnows with the description of two new species.

MATERIAL AND METHODS

Abbreviations used

AAPPMA, Association Agréée pour la Pêche et la Protection des Milieux Aquatiques, France; AFB, Agence Française pour la Biodiversité, France; BOLD, Barcoding of Life Database, Canada; FDAAPPMA, Fédération départementale des Associations Agréées pour la Pêche et la Protection des Milieux Aquatiques, France; MNHN, Muséum national d'Histoire naturelle, Paris; NGS, Next Generation Sequencing; NRM, Naturhistoriska riksmuseet, Stockholm; SL, standard length.

Sampling

Minnows were captured by angling or electrofishing with the help of the AFB field agents, the FDAAPPMA and the AAPPMA. Collections were made from May to July 2014 in order to obtain fishes with fully developed nuptial colouration. The map (Fig. 1) was created using the MapInfo Professionnal v. 7.5 software. All specimens were deposited in the MNHN collections.

Nuptial colouration

Nuptial colouration was observed on at least three populations per drainage at different times of the year to consider potential changes over the spawning cycle and to take potential local differences into account. Fish were placed for about five minutes after capture in a black bucket filled with water from the collection site, as white backgrounds affect pigmentation (Fuji, 2000). Minnows were euthanised by concussion in order not to alter the colouring and photographed with a Nikon D3000 camera with a 18-55 mm focus set at 50 mm. Sex was determined by the length and shape of the pectoral fin: the fin is long, wide, thick and rounded in male, short and less rounded in female (Frost, 1943). Colouration of the lips, operculum, belly, pectoral, pelvic and anal fins and their bases (Fig. 2A) was noted in the field.

Terminology of colour patterns

There are five pigmentation zones along the flank between the pectoral fin origin and the anal fin origin in nuptial *Phoxinus* (Fig. 2B). These pigmentation zones are usu-

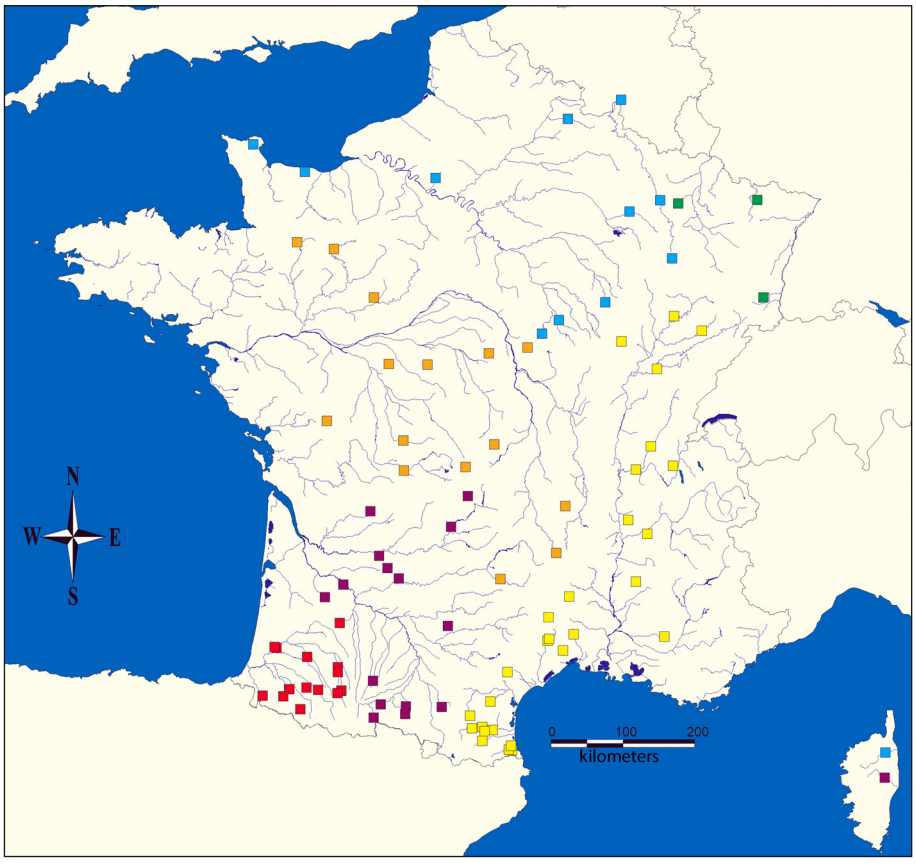

Figure 1. – Records of *Phoxinus* used in this study. Coloured squares represent the six species delineated in this study: *P. phoxinus* (blue), *P. bigerri* (red), *P. csikii* (green), *P. septimaniae* (yellow), *P. dragarum* (purple), and *P. fayollarum* (orange).

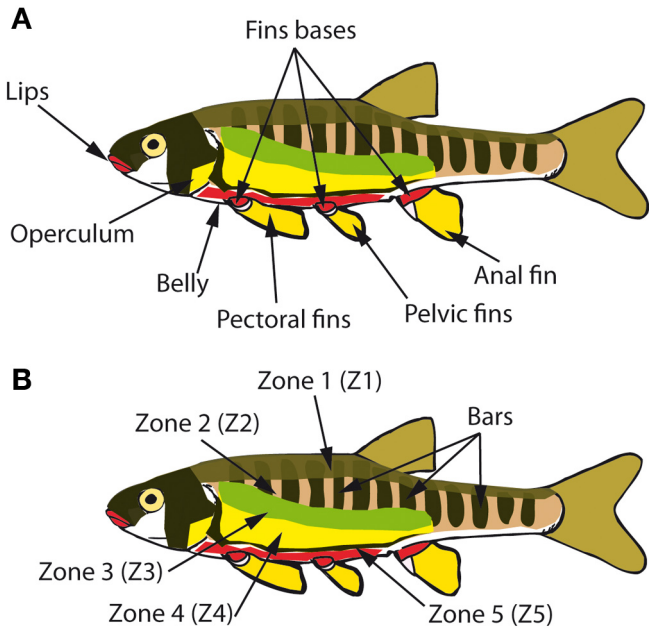

Figure 2. – Characters observed for characterising nuptial colourations patterns (**A**), to denote the body colouration with 5 zones (**B**).

ally overlaid by a black or green stripe or a series of black, dark-brown or green blotches or bars, reaching through several pigmentation zones. From the midline of the back down to the origin of the pectoral- and pelvic fins the pigmentation zones are defined as follows:

Zone 1 (Z1): dorsal pigmentation on the back, usually brown, grey or blackish, often with blackish vermiculation, blotches and spots.

Zone 2 (Z2): a stripe running between the upper edge of the operculum and the upper part of the caudal fin base, narrower than Z1 and Z3, often very narrow and bright golden, or wide and less distinct.

Zone 3 (Z3): a wide, brown or grey pigmentation field often with iridescent scales. Often, Z3 is completely or almost completely covered by a black or green midlateral stripe, or the series of blotches or bars mentioned above.

Zone 4 (Z4): a wide iridescent green or golden pigmentation zone, usually only seen in nuptial male and female. Z4 usually runs from the black bar behind the operculum to the vertical of the anal fin origin or the anal fin base, rarely beyond. Z4 might be green or golden, in some species/populations, it is golden in its upper part and greenish in its lower part or vice versa.

Zone 5 (Z5): a silvery, blackish, red or orange zone lacking iridescent scales, below Z4 and above the pigmentation on the belly, which is usually red, orange, black or silvery.

Morphological methods

Fishes were fixed and preserved in 95% EtOH as prescribed by the French legislation (substitution of formalin, article R. 4412-66), using progressive concentrations over several hours in order to reduce the body shrivelling induced by osmotic shock. Specimens with nuptial colourations were prioritised for morphomeristic studies. Measurements were made with a digital calliper and recorded to the nearest tenth of a mm. All measurements were made point-to-point, never by projection. Methods for counts and measurements follow Kottelat and Freyhof (2007). Standard length (SL) is measured from the tip of the snout to the posterior extremity of the hypural complex. Head depth is measured at the middle of the eye. The length of the caudal peduncle is measured from behind the base of the last anal fin ray to the posterior extremity of the hypural complex, at mid-height of the caudal fin base. The last two branched rays articulating on a single pterygiophore in the dorsal and anal fins are counted as "1½".

Molecular methods

A subsample of specimens was used for molecular delineation. DNA was extracted from fin clips preserved in 95% EtOH using an epMotion 5075 extraction robot (Eppendorf) with Macherey Nagel tissue extraction kits following the recommendations of the manufacturer. The cytochrome oxidase subunit 1 (COI; 592 bp) mitochondrial marker was amplified for molecular delineation. We also provide the sequences for the complete 12S rDNA (12S; 962 bp) for type specimens of each of the new described species (Gauliard *et al.*, 2019), as they are often used for environmental DNA inventories (*e.g.* Valentini *et al.*, 2016). Amplification and NGS sequencing followed Hinsinger *et al.* (2015). The reads were assembled using Geneious R11 (Kearse *et al.*, 2012) as in Hinsinger *et al.* (2015). The consensus sequences were quality-controlled and checked using BLAST similarity search on the complete NCBI nucleotide (https://blast.ncbi.nlm.nih.gov/Blast.cgi) and BOLD (http://www.boldsystems.org/; Ratnasingham and Hebert, 2007) databases. The sequences were deposited in the BOLD and NCBI nucleotide database.

Molecular data analysis

The COI sequence sampling was completed with the 385 sequences from France and other European drainages available in GenBank from Mendel *et al.* (2012), Geiger *et al.* (2014), Knebelsberger *et al.* (2015), Behrens-Chapuis *et al.* (2015), Palandačić *et al.* (2017) and Denys and Manné (2019) (Appendix). Sequences were aligned using MUSCLE (Edgar, 2004). Automatic barcode gap detection was performed with ABGD (http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html) (Puillandre *et al.*, 2012). Phylogenetic analysis by Bayesian inference with MrBayes 3.2 (Ronquist *et al.*, 2012) *via* CIPRES Science Gateway v3.3 (Miller *et al.*, 2010) used a GTR+I+G selected by JModelTest 2.1.1 (Darriba *et al.*, 2012) partitioned by codon position, in 2 independent analyses of 4 chains and 10 million generations with

sampling every 200 generations. After checking for convergence, 10% of trees were discarded. Convergences of runs were checked using TRACER v.1.6.0 (Rambaut and Drummond, 2007). Inter and intraspecific p-distances were calculated using MEGA 7 (Kumar *et al.*, 2016). Diagnostic sites for both markers were identified with the QUIDDICH package (Kühn and Hasse, 2019) for R (R Core Team, 2013).

Species delineation

We consider a species valid if the mtDNA delineation is congruent with morphological data or the nuptial colouration patterns.

RESULTS

Molecular data

Both the ABGD analysis and the phylogenetic tree for the COI marker (592 bp) inferred from 482 sequences of *Phoxinus* species discriminate 15 clades, 8 of which include French minnows (Fig. 3A). We further talk only about clades with French samples. All individuals analysed cluster by geography, except three, which are discussed below. The first clade (blue) is composed of six haplotypes from the Rhine and Meuse drainages, and one population from the Golo River in Corsica. It includes fish from the Agger River in Germany, the type locality of *P. phoxinus*. The second clade of six haplotypes includes minnows from the Seine drainage. A third clade (yellow) of 11 haplotypes included minnows from the Rhône drainage and some Mediterranean

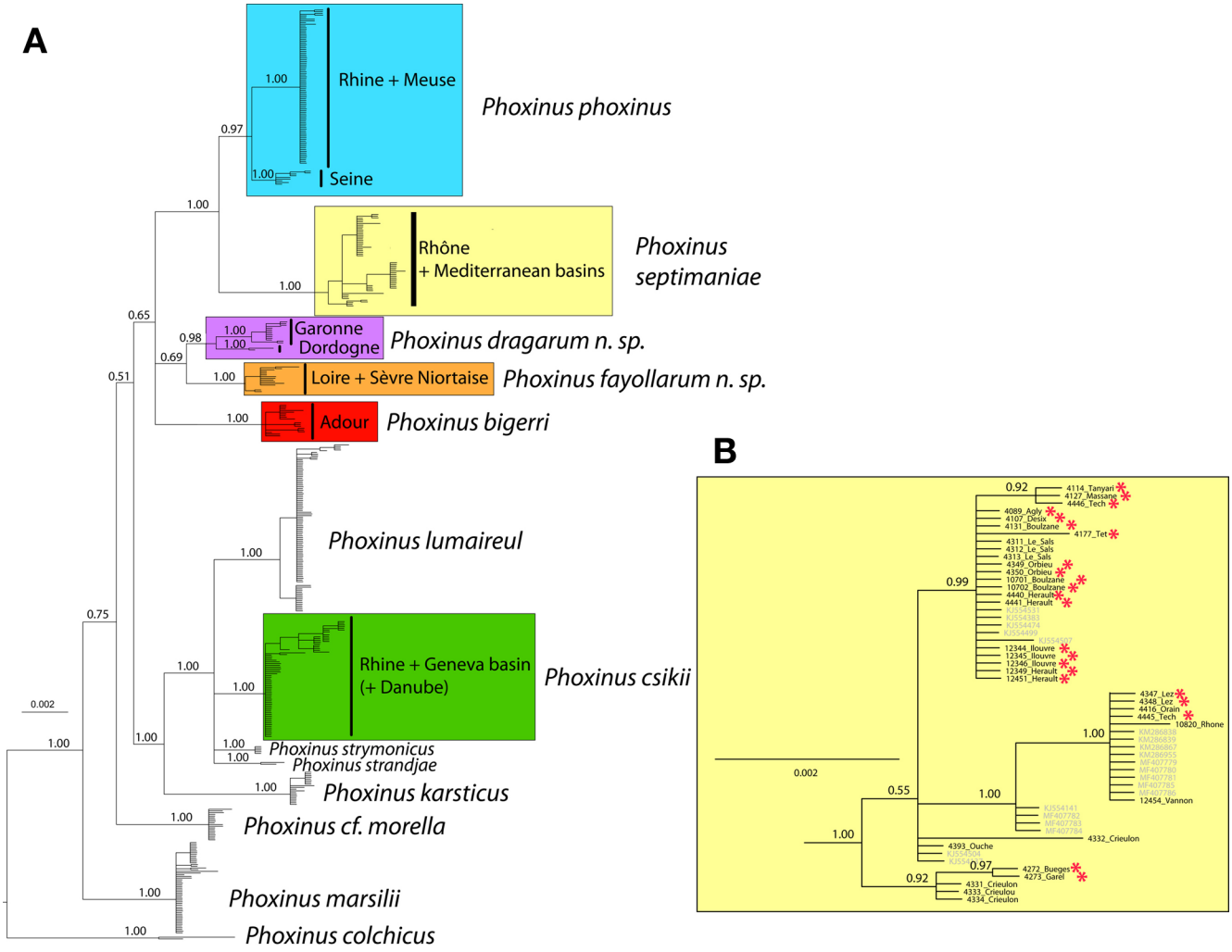

Figure 3. – Phylogenetic tree by Bayesian inference with the COI marker (592 bp) on 482 sequences of *Phoxinus* spp. (**A**) with a focus on the *P. septimaniae* clade (**B**). Coloured boxes represent evolutionary lineages containing French specimens. Bold vertical bars represent ABGD delineations. Red asterisks represent specimen with a completely scaled breast. Posterior probabilities values are indicated above the nodes.

Table II. – p-distance matrix between and within French *Phoxinus* for the cytochrome oxidase subunit 1 (COI) marker (592 bp).

		Phoxinus phoxinus		*Phoxinus septimaniae*	*Phoxinus dragarum*		*Phoxinus fayollarum*	*Phoxinus bigerri*	*Phoxinus csikii*
		Rhine + Meuse	Seine		Garonne	Dordogne			
Phoxinus phoxinus	Rhine + Meuse	< 0.1%							
	Seine	1.5%	0.3%						
Phoxinus septimaniae		4.0%	3.8%	0.6%					
Phoxinus dragarum	Garonne	3.9%	3.6%	4.4%	0.3%				
	Dordogne	3.8%	3.4%	4.3%	1.6%	0.3%			
Phoxinus fayollarum		3.7%	3.6%	3.7%	2.7%	2.7%	0.3%		
Phoxinus bigerri		4.7%	4.2%	6.1%	3.9%	4.0%	4.2%	0.5%	
Phoxinus csikii		5.5%	5.0%	6.0%	4.5%	4.6%	4.2%	4.7%	0.5%

rivers as the Vidourle and the Buège. Three other clades are new molecular lineages found during this study: one of four haplotypes from Garonne (and from the Tavignano River in Corsica), one with two haplotypes from Dordogne (both form a purple clade), and a third (orange) including 11 haplotypes from the Loire and Sèvre Niortaise drainages (and one individual from the Garonne drainage). The seventh clade (red) groups 9 haplotypes from minnows morphologically identified as *P. bigerri* from the Adour drainage. Finally, the last clade (green) is composed by 19 haplotypes of fish from the upper Rhine catchment, the Lake Geneva basin and the Danube, identified here as *P. csikii*. P-distances between and within these clades are given in table II.

Phoxinus Rafinesque, 1820

Phoxinus Rafinesque, 1820:236 (type species: *Cyprinus phoxinus* Linnaeus, 1758).

Pisciculus, Dralet, 1821: 35 (type species: *Pisciculus varius* Dralet, 1821).

Phoxinus Agassiz, 1835: 37 (type species: *Cyprinus phoxinus* Linnaeus, 1758).

Eulinneela Dybowski, 1916:101, 103 (type species: *Cyprinus phoxinus* Linnaeus, 1758).

Nomenclatural note

The genus *Acahara* Jordan & Hubbs, 1925 is currently considered as a junior synonym of *Phoxinus* Rafinesque, 1820 (Tan and Armbruster, 2018). However, the type species of this genus is *Leuciscus semotilus* Jordan & Starks, 1905 for which the valid name is *Rhynchocypris semotilus* (Jordan & Starks, 1905) (*e.g.* Lee and Sim 2017). By consequence, the genus *Acahara* Jordan & Hubbs, 1925 is a junior synonym of the genus *Rhynchocypris* Günther, 1889.

Phoxinus bigerri Kottelat, 2007
(Fig. 4)

Phoxinus bigerri Kottelat, 2007: 146, fig. 2 (type locality: Adour River in Tarbes (Séméac)).

Material examined

MNHN 2006-1703, holotype, ♀, 59.1 mm SL; France: Adour River, Tarbes, 43°13.7'N, 0°05.5'E, alt. 316 m. MNHN 2006-1704, paratypes, 2 ♂, 2 ♀, 40.9-57.2 mm SL; France: Adour River, Tarbes, 43°13.7'N, 0°05.5'E; alt. 316 m. MNHN 2014-2741, 1 ♂, 3 ♀, 52.5-63.6 mm SL; France: Louts Stream, Samadet, 43°37.5'N, 0°29.3'W, alt. 136 m. MNHN 2014-2755, 2 ♂, 4 ♀, 46.3-58.2 mm SL; France: Adour River, Estirac, 43°30.2'N, 0°01.8'E, alt. 165 m. MNHN 2014-2756, 6 ♂, 5 ♀, 42.4-57.0 mm SL; France: Lausset Stream, Cheraute, 43°14.8'N, 0°47.5'W, alt. 173 m. MNHN 2014-2749, 13, 44.0-55.4 mm SL; Bayse Stream, Aubertin, 46°15.8'N, 0°29.9'W, alt. 155 m.

Material used for molecular analysis

MNHN 2010-0487, 1, tag 4092; France: Adour River, Tarbes, 43°13.9'N, 0°05.3'E, alt. 315 m. (COI: GenBank accession number: MT975755, 12S: GenBank accession number: MT975345). MNHN 2010-0508, 1, tag 4120; France: Canal de Branc, Juillan, 43°12.1'N, 0°01.4'E, alt. 328 m. (COI: GenBank accession number: MT975761). MNHN 2010-0481, 1, tag 4096; France: Echez Stream, Larreule, 43°26.7'N, 0°01.7'E, alt. 186 m. (COI: GenBank accession number: MT975756, 12S: GenBank accession number:

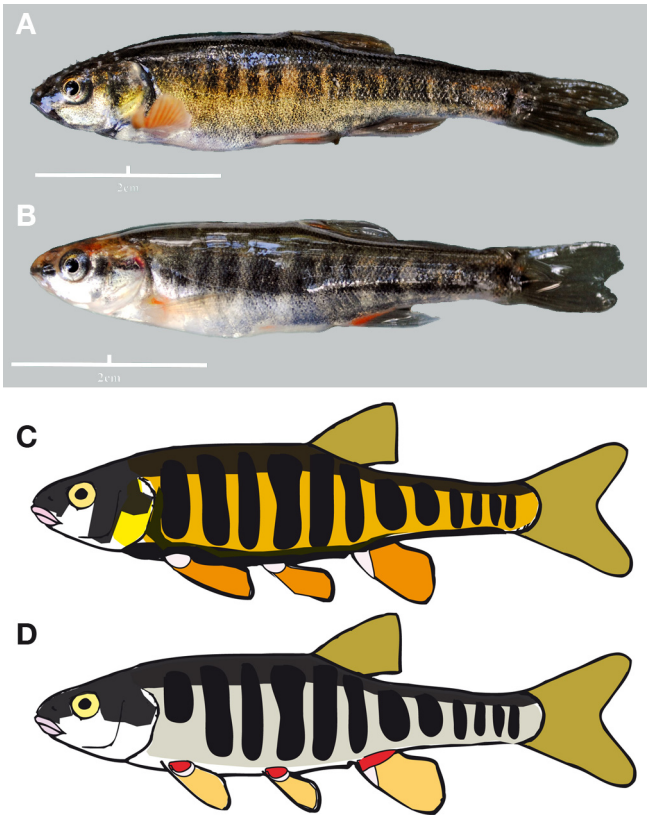

Figure 4. – *Phoxinus bigerri* in the Adour catchment: ♂ (**A**) and ♀ (**B**) from the Lausset Stream, Cheraute 43°14.8'N, 0°47.5'W, MNHN 2014-2756; nuptial colouration pattern for male (**C**) and female (**D**).

MT975376). MNHN 2011-0938, 1, tag 10771; France: Gave d'Aspe, Osse-en-Aspe, 43°00.7'N, 0°36.2'W, alt. 391 m. (COI: GenBank accession number: MT975706). MNHN 2011-0940, 1, tag 10770; France: Gave de Pau, Assat, 43°14.3'N, 0°18.4'W, alt. 214 m. (COI: GenBank accession number: MT975705). MNHN 2014-2756, 2, tag 1987 and 1988; France: Lausset Stream, Cheraute, 43°14.8'N, 0°47.5'W, alt. 173 m. (COI: GenBank accession numbers: MT975743, MT975744). MNHN 2010-1024, 1, tag 4196; France: Luy Stream, Saugnac-et-Cambran, 43°43.6'N, 1°00.7'W, alt. 7 m. (COI: GenBank accession number: MT975767, 12S: GenBank accession number: MT975380). MNHN 2013-0622, 2, tag 10945 and 10946; France: Nive d'Arneguy, Uhart-cize, 43°10.1'N, 1°14.8'W, alt. 154 m. (COI: GenBank accession numbers: MT975717, MT975718). MNHN 2011-0262, 1, tag 4369; France: brook of Cabanes, 43°44.3'N, 1°02.5'W, alt. 14 m. (COI: GenBank accession number: MT975784, 12S: GenBank accession number: MT975388). MNHN 2010-1033, 1, tag 4210; France: Saison Stream, Menditte, 43°09.7'N, 0°53.8'W, alt. 177 m. (COI: GenBank accession number: MT975770). MNHN 2011-0928, 1, tag 10787; France: Rimbez Stream, Saint-Pe-Saint-Simon, 44°01.1'N, 0°03.7'E, alt. 109 m. (COI: GenBank accession number: MT975711).

Diagnosis

Phoxinus bigerri is distinguished from the other French *Phoxinus* species by its unique nuptial colour pattern. The male is diagnosed by having bold, black bars of variable widths crossing Z2 to Z4 (vs. bars only crossing Z2), no stripe on Z3 (vs. present), Z2 to Z4 golden-yellow between bars (vs. pale brownish), Z5 and belly greyish to black (vs. Z5 silvery, white or red on belly), orange pectoral, pelvic and anal fins (Fig. 4A, C) (vs. yellow). Female with long black bars on the flank (vs. a black or brown stripe along Z3), interspaces between flank-bars greyish along Z2 to Z4 (vs. silvery, greenish or yellowish), and pectoral, pelvic and anal fin bases red (Fig. 4B, D) (vs. pinkish).

Phoxinus biggeri is further distinguished from some other species as detailed below by having 68-87 scales along the lateral series (vs. 72-99), snout very stout (vs. slightly pointed), mouth terminal or slightly subterminal (vs. subterminal), anal fin margin straight to convex (vs. straight to slightly concave), and depth of caudal peduncle 2.1-3.4 times in its length (vs. 2.5-4.6).

Nuptial colouration

Male. – Snout and top of head dark greyish to black. A black bar on operculum reaching from top of head to subopercule. Cheeks white or greyish. Operculum with a white spot at uppermost, posterior corner followed by a yellow spot on lower part. Z1 black. Flank with black bars of variable widths. Z2 to Z4 golden-yellow. Z5 and belly greyish to black. Mouth pinkish. Pectoral, pelvic and anal fin orange (Fig. 4A, C).

Female. – Black flank bars reaching from Z2 to Z4, interspaces greyish, and pectoral, pelvic and anal fin bases red (Fig. 4B, D).

Molecular characterization

On the COI marker, *P. bigerri* has nine diagnostic sites, including seven synapomorphies (Tab. III). For the 12S rDNA marker, seven diagnostic sites characterise this species: G (*vs*. A) in position 25, T (*vs*. G) in position 403, C (vs. A) in position 577, G (vs. A) in position 596, T (vs. C) in position 881, T (vs. C) in position 882 and C (vs. T) in position 889.

Distribution

In France, *P. bigerri* is native to the Adour and the Leyre drainages (Fig. 1). It is introduced in the Aude catchment as well as some tributaries of the Garonne drainage adjacent to the Adour by anglers as trout bait. In Spain, it is native to the Ebro drainage and the eastern Cantabria region, and was introduced in Galicia and the Duero drainages (Corral-Lou *et al*., 2019; Garcia-Raventós *et al*., 2020).

Table III. – Diagnostic sites determined on the COI marker for the French *Phoxinus*. Unique sites are in bold. * § $ and # indicate characteristic nucleotide positions for populations from respectively Garonne, Dordogne, Meuse + Rhine and Seine drainages.

Position	6	15	18	45	51	60	66	72	78	81	102	159	168	174	184	198	204	213	219	231	234	243
Phoxinus bigerri	**G**	**A**	A	G	A	G	A/G	C	C	C	**C**	C	A	A	T	A	C/T	T	A	A	C	T
Phoxinus csikii	A	G	A/G	·	·	·	A	·	T/C	T	T	T/C	**C**	**G**	**C**	·	C	·	·	·	**T**	·
Phoxinus dragarum	A	G	·	·	·	G/C	C	·	T	·	T	·	·	·	·	**C***/A	T	C	·	A/**G**§	·	·
Phoxinus fayollarum	A	G	G	·	G	·	C	·	T/G	T/C	T	·	·	·	·	·	C	C	·	·	·	T/C
Phoxinus phoxinus	A	G	·	·	G	G/**A**$^{\#}$	G/A	T	T	·	T	·	·	·	·	·	C	·	·	·	·	·
Phoxinus septimaniae	A	G	A/G	**A**	G/A	·	G	T	T	T	T	·	·	·	·	·	T	·	G/A/T	·	·	C

Position	246	253	258	267	270	273	285	288	291	297	306	309	318	321	351	354	363	378	390	396	399	405
Phoxinus bigerri	G/A	T	C	**C**	A	T	T	G	T	C	**C**	A	C	C	T	G	T	G	A	G/A	A	T
Phoxinus csikii	A	·	·	G	·	·	·	A/G	C	·	T	·	C/T	·	·	A	**C**	A/G	·	A	·	·
Phoxinus dragarum	G	·	·	A	·	**C***/T	·	G/A	·	·	T	**G***/A	T	T	T/C	A	·	·	·	A/G	·	T/**C**§
Phoxinus fayollarum	A	·	·	A	·	·	·	·	·	·	T	·	C/T	·	**G**	A	·	·	A/G	A	·	·
Phoxinus phoxinus	A	·	·	A	**G**$^{\$}$/A	·	**C**$^{\$}$/T	·	·	·	T	·	T	**A**$^{\$}$/T	·	·	·	·	·	G	**G**$^{\$}$/A	·
Phoxinus septimaniae	**C**	T/G	T/C	A/G	·	·	·	·	C	T/C	T	·	T	T	C	A	·	·	G	A	·	·

Position	411	426	447	456	474	486	489	498	511	517	520	522	525	528	535	540	546	552	576	579	591
Phoxinus bigerri	G/C	**C**	G	T	C	G	G	C	C	C	C	**G**	C	A	T	T	A	G/C	T	T	T
Phoxinus csikii	G	T	·	C	·	**A**	·	·	·	·	C/T	A	·	A/G	**C**	·	·	A	T/C	·	**C**
Phoxinus dragarum	G	T	·	C	·	·	·	·	·	C/**T**§	C/T	A	C/T	G	·	·	·	A	·	·	·
Phoxinus fayollarum	G	T	·	C/T	·	·	·	·	**T**	·	·	A	T	G	·	·	·	A	·	C	·
Phoxinus phoxinus	G	T	A	C	·	·	G/**A**$^{\#}$	·	·	·	T	A	T	G	·	**C**	G	A/G	**A**$^{\$}$/T	·	·
Phoxinus septimaniae	A/C	T	A	C	**T**	·	·	T/C	·	·	·	A	T	G	·	·	G	A/G	·	C	·

Vernacular name

Adour minnow (English), Vairon basque (French).

Remarks

Kottelat (2007) described this species as having usually a complete lateral line. Our examination confirms that some individuals have a complete lateral line but most individuals examined by us, have an incomplete lateral line, reaching just to or slightly beyond the anal fin base.

Phoxinus csikii Hankó, 1922

(Fig. 5)

Phoxinus csikii Hankó, 1922: 1, pl. 1 (figs 1-3) (type locality: Ibar River, a tributary to the Zapadna Morava River, a tributary of the Danube, Montenegro).

Material examined

MNHN 2014-2801, 4 ♂, 6 ♀, 49.5-61.9 mm SL; France: Thur Stream, Staffefelden, 47°49.4'N, 7°15.1'E, alt. 252 m. MNHN 2011-0899, 1 ♂, 1 ♀, 50.9-57.0 mm SL; France: Rupt de Mad Stream, Essey-et-Maizerais, 48°49.2'N, 5°48.5'E, alt. 228 m. MNHN 2014-2739, 9, 55.4-71.4 SL; France: Eichel Stream, Voellerdingen, 48°57.5'N, 7°08.9'E, alt. 219 m.

Material used for molecular analysis

MNHN 2014-2801, 3, tag 1981-1983; France: Thur Stream, Staffefelden, 47°49.4'N, 7°15.1'E, alt. 252 m. (COI: GenBank accession numbers: MT975740-MT975742, 12S: GenBank accession numbers: MT975369-MT975371). MNHN 2014-2739, 1, tag 1976; France: Eichel Stream, Voellerdingen, 48°57.5'N, 7°08.9'E, alt. 219 m. (COI: GenBank accession number: MT975737).

Diagnosis

Phoxinus csikii is distinguished from the other French *Phoxinus* species by its unique nuptial colour pattern. The male has green Z3 and Z4 (vs. yellow), and a shiny red belly between the pectoral fin bases and the caudal fin origin (vs. black or white) (Fig. 5A, B, D). The female is diagnosed by a slim golden Z3 and Z4 (vs. silver, greyish or greenish) below the black stripe (Fig. 5C, E). *Phoxinus csikii* is distinguished from *P. bigerri* by having 79-94 scales

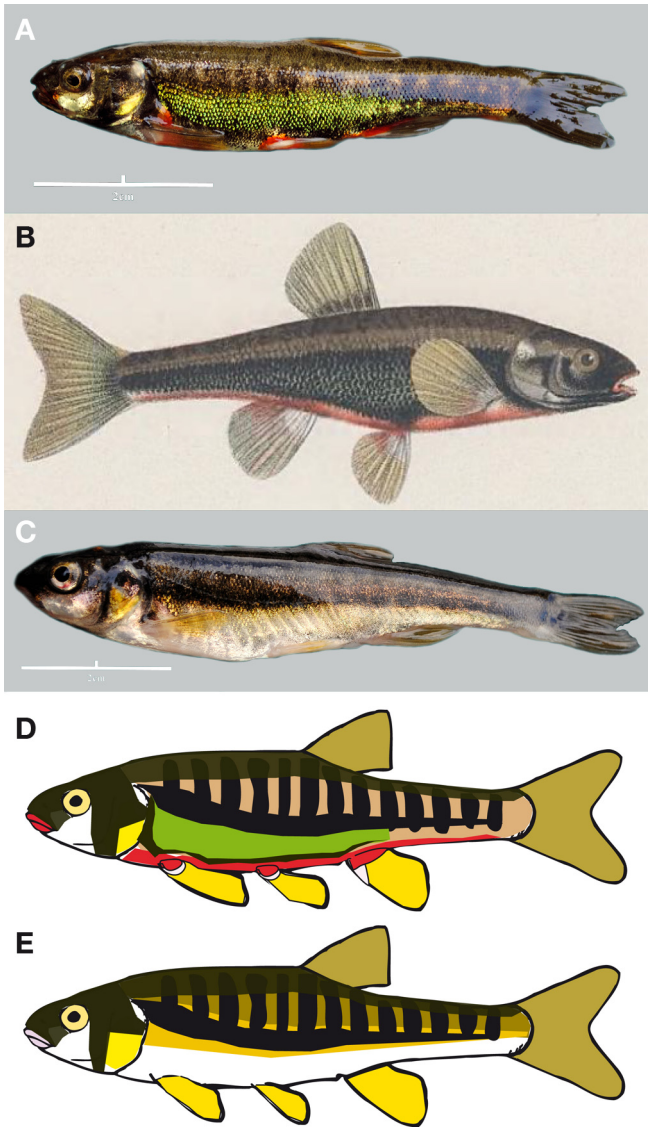

Figure 5. – *Phoxinus csikii* in the Rhine catchment: ♂ from the Thur Stream, Staffefelden 47°49.4'N, 7°15.2'E, MNHN 2014-2801 (**A**) and in the Lake Geneva basin (from Lunel and Lunel, 1874) (**B**); ♀ from the Eichel Stream, Voellerdingen 48°57.6'N, 7°08.9'E; MNHN 2014-2739 (**C**); nuptial colouration pattern for male (**D**) and female (**E**).

along the lateral series (vs. 68-87), a subterminal mouth (vs. terminal or slightly subterminal), and a narrower caudal peduncle (caudal peduncle depth 2.5-4.0 times in its length vs. 2.1-3.4).

The nuptial male *P. csikii* are distinguished from nuptial male *P. bigerri* by having a brownish Z1 (vs. black), green Z3 and Z4 (vs. yellow golden), a shiny red belly (vs. greyish to black), red lips (vs. pinkish), yellow pectoral and pelvic fins (vs. orange), and red pectoral, pelvic and anal fin origins (*vs*. pinkish). The nuptial female is distinguished by having a black stripe along Z3 (vs. no stripe), Z4 slim golden (vs. greyish), and little contrasting blackish bars reaching from from Z1 to Z2 (vs. very contrasting black bars reaching from Z2 to Z4).

Nuptial colouration

Male. – Lips and pectoral, pelvic and anal fin bases red, these fins yellow. Snout and top of head dark brown. A black bar on operculum reaching from top of head to branchiostegal rays. Cheeks white to grey. Operculum with a white spot at uppermost, posterior corner. A yellow spot on the supraoperculum. Z1 and Z2 dark brown overlaid with blackish bars. Z3 and Z4 green, reaching to caudal-peduncle origin. Blackish bars present on caudal peduncle. A slim blackish stripe sometimes fractioned in blotches along Z3 in some individuals, absent in others. Z5 black between pectoral fin and anal fin base. Belly shiny red between pectoral- and caudal fin base (Fig. 5A, B, D).

Female. – Less brightly coloured, Z1 and Z2 brownish, a black stripe along Z3, Z4 slim and golden, Z5 white or silvery and belly white (Fig. 5C, E).

Molecular characterization

On the COI marker, *P. csikii* has 12 diagnostic sites, including eight synapomorphies (Tab. II). For the 12S rDNA marker, nine diagnostic sites characterise this species: T (vs. C) in position 27, A (vs. G) in position 62, A (vs. G or C) in position 122, A (vs. G) in position 215, A (vs. G) in position 274, G (vs. A) in position 388, A (vs. G or C) in position 412, T (vs. C) in position 450 and G (vs. A) in position 522.

Distribution

P. csikii occurs in the Danube drainage from the Balkans to Germany as well as in the upper Rhine drainage (regionally introduced in the lower Rhine) (Fig. 1) west to Lake Geneva basin (Palandačić *et al*., 2017; Denys and Manné, 2019).

Vernacular name

Danubian minnow (English), Vairon du Danube (French).

***Phoxinus phoxinus* (Linnaeus, 1758)**
(Fig. 6)

Cyprinus phoxinus Linnaeus, 1758:323 (type locality: Agger River north of Lohmar, 50°50'N, 7°12'E, Nordrhein-Westfalen, Germany).

Cyprinus aphya Linnaeus, 1758:323 (type locality: Agger River north of Lohmar, 50°50'N, 7°12'E, Nordrhein-Westfalen, Germany).

Phoxinus laevis Fitzinger (ex Agassiz), 1832:337 (type locality: Agger River north of Lohmar, 50°50'N, 7°12'E, Nordrhein-Westfalen, Germany).

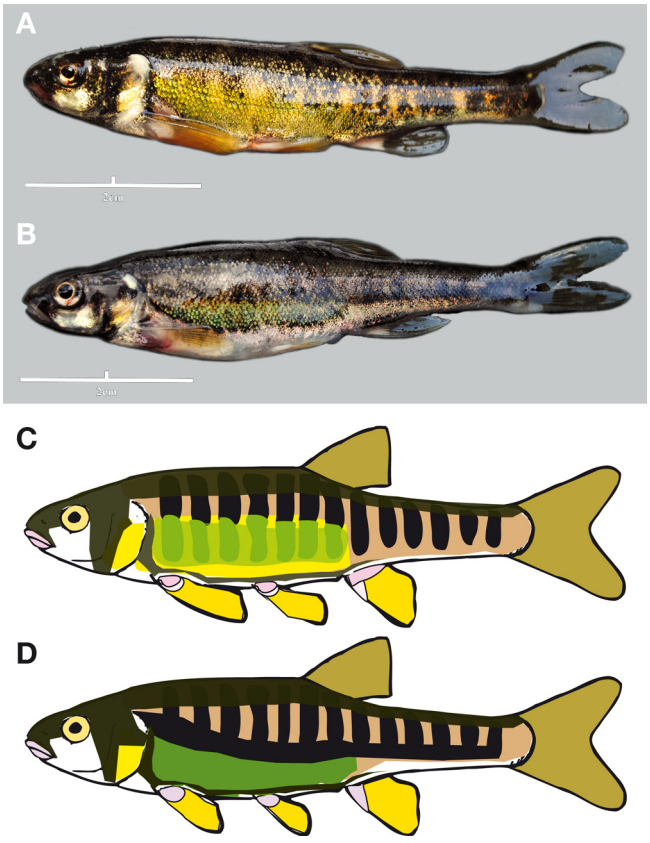

Figure 6. – *Phoxinus phoxinus* in the Seine catchment: ♂ from the Beuvron Stream, Ouagne 47°24'N, 3°29.7'E, MNHN 2014-2748 (**A**); ♀ from the Oise Stream, Gergny 49°54.6'N, 3°56.1'E, MNHN 2014-2724 (**B**), nuptial colouration pattern for male (**C**) and female (**D**).

Phoxinus varius Perty, 1832:719 (type locality: Agger River north of Lohmar, 50°50'N, 7°12'E, Nordrhein-Westfalen, Germany).

Material examined

NRM 55112, 5 ♂, 4 ♀, 45.8-57.5 mm SL; Germany: Agger River north of Lohmar, 50°50'N, 7°12'E, alt. 59 m. MNHN 2014-0021, 3 ♂, 55.9-63.1 mm SL; France: Ardennes Stream, Houille, 50°07.7'N, 4°50.4'E, alt. 107 m. MNHN 2014-2768, 5 ♀, 53.1-62.6 mm SL; France: Meuse River, Bannoncourt, 48°57.5'N, 5°30.2'E, alt. 211 m. MNHN 2014-2769, 2 ♂, 2 ♀, 51.3-55.2 mm SL; France: Anger Stream, Circourt-sur-Mouzon, 48°16.7'N, 5°42.1'E, alt. 322 m. MNHN 2014-2743, 2 ♂, 3 ♀, 47.6-56.4 mm SL; France: Ornain Stream, Revigny-sur-Ornain, 48°49.4'N, 4°58.9'E, alt. 141 m. MNHN 2014-2757, 2 ♂, 4 ♀, 50.2-63.6 mm SL; Seine River, Nod-sur-Seine, 47°45.8'N, 4°34.2'E, alt. 250 m. MNHN 2014-2724, 13 ♀, 51.5-68.6 mm SL; France: Oise Stream, Gergny, 49°54.5'N, 3°56.1'E, alt. 127 m. MNHN 2014-2748, 7 ♂, 2 ♀, 50.0-63.0 mm SL; France: Beuvron Stream, Ouagne; 47°23.9'N, 3°29.7'E, alt. 163 m.

Material used for molecular analysis

MNHN 2014-0021, 2, tag VAI2 and VAI4; France: Ardennes Stream, Houille, 50°07.7'N, 4°50.4'E, alt. 107 m. (COI: GenBank accession numbers: MT975737, MT975800). MNHN 2014-2769, 2, tag 1998 and 1999; France: Anger Stream, Circourt-sur-Mouzon, 48°16.7'N, 5°42.1'E, alt. 322 m. (COI: GenBank accession numbers: MT975750, MT975751, 12S: GenBank accession numbers: MT975374, MT975375). MNHN 2014-2748, 2, tag 1978 and 1979; France: Beuvron Stream, Ouagne, 47°23.9'N, 3°29.7'E, alt. 163 m. (COI: GenBank accession numbers: MT975738, MT975739, 12S: GenBank accession numbers: MT975367, MT975368). MNHN 2011-0403, 1, tag 4401; France: Cure Stream, Voutenay-sur-Cure, 47°33.5'N, 3°47'E, alt. 213 m. (COI: GenBank accession number: MT975790). MNHN 2011-1141, 1, tag 10871; France: Epte Stream, Guerny, 49°13.1'N, 1°41.3'E, alt. 36 m. (COI: GenBank accession number: MT975714). MNHN 2014-2743, 1, tag 1992; France: Ornain Stream, Revigny-sur-Ornain, 48°49.4'N, 4°58.9'E, alt. 141 m. (COI: GenBank accession number: MT975747, 12S: GenBank accession number: MT975372). MNHN 2014-2724, 1, tag 12460, France: Oise Stream, Gergny, 49°54.5'N, 3°56.1'E, alt. 127 m. (COI accession number: MT975729). MNHN 2011-0400, 1, tag 4413; France: Seine River, Nod-sur-Seine, 47°45.8'N, 4°34.2'E, alt. 250 m. (COI: GenBank accession number: MT975791). MNHN 2011-0266, 2, tag 4374 and 4375; France: Saires River, Brillevast, 49°36.7'N, 1°24.4'W, alt. 96 m. (COI: GenBank accession numbers: MT975785, MT975786). MNHN 2011-1136, 1, tag 10866; France: Seulles River, Tierceville, 49°17.4'N, 0°31.6'W, alt. 9 m. (COI: GenBank accession number: MT975713). MNHN 2011-0835, 1, tag 4443; France: Golo River, Campitello, 42°30.4'N, 9°19.4'E, alt. 121 m. (COI: GenBank accession number: MT975796, 12S: GenBank accession number: MT975389).

Diagnosis

Phoxinus phoxinus is distinguished from the other French *Phoxinus* species by its unique nuptial colour pattern. The nuptial male has bars of variable widths crossing Z2 to Z4 and no stripe long Z3 (vs. presence of a stripe in Z3), the bars are black in Z2 and green in Z3 and Z4 (vs. black from Z2 to Z3). Z2 is golden-yellow (vs. light brownish), Z4 green-yellowish (vs. uniform green, yellow or greyish). Lips as well as pectoral, pelvic and anal fin bases are pinkish (vs. red) (Fig. 6A, C). In the nuptal female, Z4 is green (vs. yellow or greyish), and it has a black line in Z5 between the pectoral- and anal fin bases (vs. absent) (Fig. 6B, D). *Phoxinus phoxinus* is distinguished from *P. biggeri* by having 75-99 scales in the lateral series (vs. 68-87), a slightly pointed snout (vs. very stout), a subterminal mouth (vs. terminal or slightly subterminal), a straight to slightly concave anal fin margin

(vs. straight to convex), and the caudal peduncle depth 2.8-3.9 times in its length (vs. 2.1-3.4).

Phoxinus phoxinus is distinguished from *P. csikii* by having a slightly pointed snout (*vs*. very stout and blunt), and a straight to slightly concave anal fin margin (*vs*. straight to slightly convex). The nuptial male *P. phoxinus* is further distinguished by having a pinkish or pale orange belly not extending on the caudal peduncle (vs. greyish to black not extending on the caudal peduncle in *P. bigerri*; shiny red extending on the caudal peduncle in *P. csikii*). The nuptial female is distinguished by having a black stripe along Z3 (vs. only bars in *P. bigerri*).

Nuptial colouration

Male. – Snout and top of head dark brown. A black bar on operculum reaching from top of head to branchiostegal rays. Cheeks white. Operculum with a white spot at uppermost, posterior corner. A yellow spot on lower-most posterior margin of operculum and on suboperculum. Z1 blackish. No stripe long Z3. Bars of variable widths crossing Z2 to Z4, bars black in Z2 and green in Z3 and Z4. Z4 greenish yellow, bars poorly contrasted on Z4. Bars distinct on caudal peduncle. Z5 greyish to blackish. Belly pinkish or light orange. Mouth as well as bases of pectoral, pelvic and anal fins with a pinkish tinge (Fig. 6A, C).

Female. – Z1dark brown, Z2 greyish, a black stripe on Z3 and black bars from Z1 to Z3. Z4 green and Z5 black. Female always display «male» characters: white and yellow spots on operculum and white spots at base of pectoral, pelvic and anal fins (Fig. 6B, D).

Molecular characterization

On the COI marker, *P. phoxinus* has seven diagnostic sites, including one synapomorphy. However, the Meuse + Rhine and the Seine populations are characterised respectively by five and two diagnostic sites (Tab. II). For the 12S rDNA marker, two diagnostic sites characterise this species: C (*vs*. T) in position 736 and G (*vs*. A) in position 796.

Distribution

Phoxinus phoxinus occurs in the Rhine, Meuse and Seine drainages as well as the coastal catchments of Normandy (Fig. 1). It is also found in the Thames and English Channel coastal catchments (Jörg Freyhof, pers. comm.) and these drainages were tributaries of the Channel River during the Pleistocene and Holocene (see Persat and Keith, 1997). In the Rhine drainage, it seems to form hybrid populations with *P. csikii,* which might be partly natural as both species are expected to form a contact zone, but minnows have also been introduced regionally (Palandačić *et al*., 2017). It has been introduced in the Golo River in Corsica, in the Weser drainage and in Ireland (Knebelsberger *et al*., 2015; Palandačić *et al*., 2017), and maybe elsewhere in Europe.

Vernacular name

The vernacular name of *Phoxinus phoxinus* is the Eurasian minnow (FAO-FIES, 2018) – Vairon commun in French (Keith *et al*., 2011). However, as this species is restricted to the Rhine, Meuse and Seine drainages, all ancient tributaries of the Channel River, we suggest to call it the Channel minnow (English), Vairon de la Manche (French).

Remarks

According to the COI tree (Fig. 3A), there are two distinct lineages: the first groups Rhine + Meuse and the second clade grouping Seine samples. Both clades are separated by a p-distance of 1.5% but we found no difference between both in morphology and colour pattern. We consider both as two evolutionary lineages of a same species.

Phoxinus septimaniae Kottelat, 2007
(Fig. 7)

Pisciculus varius Dralet, 1821: 35 (type locality: Luech Stream, Chamborigaud, France, see below).

Phoxynus montanus Ogérien, 1863: 362 (type locality: Ain River near Champagnole; Queue de Cheval waterfall, near Saint-Claude, France).

Phoxinus laevis var. *montanus* Blanchard, 1896: 155 (type locality: Ain River near Champagnole; Queue de Cheval waterfall, near Saint-Claude, France).

Phoxinus septimaniae Kottelat, 2007: 148, fig. 3 (type locality: River Agly, bridge downstream of Latour-de-France, 42°46'09"N, 2°39'39"E, Dépt. Pyrénées-Orientales, France).

Material examined

MNHN 2006-1701, holotype, ♂, 46.1 mm SL; France: Agly River, Latour-de-France, 42°46.1'N, 2°38.5'E, alt. 92 m. MNHN 2006-1702, paratypes, 2 ♂, 1 ♀, 41.6-46.4 mm SL; France: Agly River, Latour-de-France, 42°46.1'N, 2°38.5'E, alt. 92 m. MNHN 2014-2754, 5, 46.1-56.2 mm SL; France: Agly River, Latour-de-France, 42°46.1'N, 2°38.5'E, alt. 92 m. MNHN 2019-0264, ♂, 64.8 mm SL; France: Luech Stream, Chamborigaud, 44°19.7'N, 3°57.5'E, alt. 335 m. MNHN 2014-2804, 2 ♂, 3 ♀, 50.7-61.4 mm SL; France: Luech Stream, Chamborigaud, 44°19.7'N, 3°57.5'E, alt. 335 m. MNHN 2014-2746, 4 ♂, 3 ♀, 36.6-51.3 mm SL; France: Séran Stream, Talissieu, 45°51.3'N, 5°43.2'E, alt. 239 m. MNHN 2014-2730, 7 ♂, 11 ♀, 35.3-63.1 mm SL; France: Suran Stream, Neuville-sur-Ain, 46°04.9'N, 5°20.4'E, alt. 268 m. MNHN 2014-2742, 2 ♀, 46.8-50.1 mm SL; France: Galaure Stream, Chateauneuf-de-Galaure, 45°13.4'N, 5°57.6'E, alt. 246 m. MNHN 2014-2726, 3 ♂, 3 ♀, 53.1-61.4 mm SL; France: Bourne Stream, Saint-Thomas-en-Royan, 45°03.7'N, 5°16.8'E, alt. 173 m. MNHN 2014-

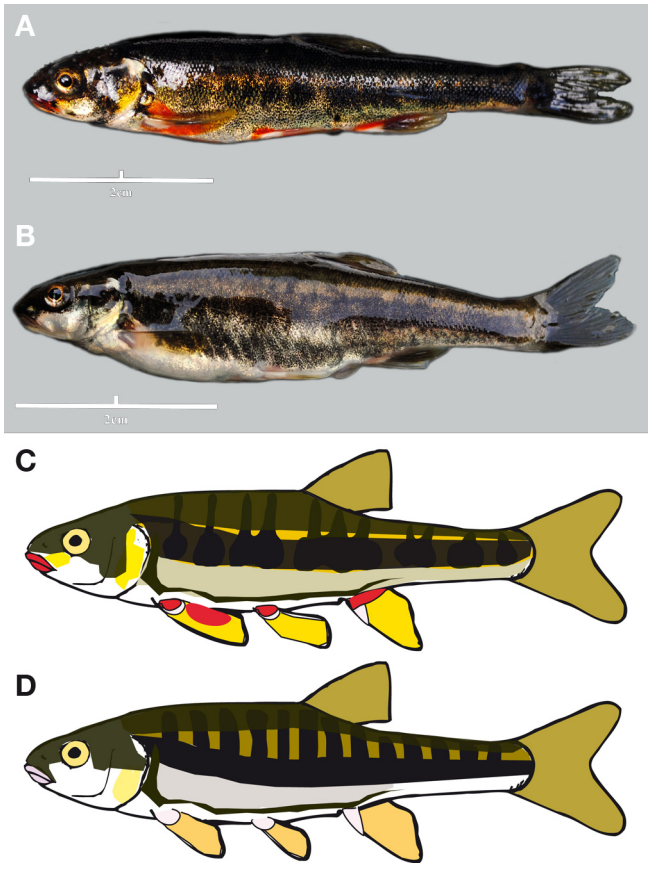

Figure 7. – *Phoxinus septimaniae* in the Rhône and Mediterranean catchments: ♂ from the Luech Stream, Chamborigaud 44°19.7'N, 3°57.5'E, MNHN 2014-2804 (**A**); ♀ from the Hérault River, Valleraugue 44°05.2'N, 3°36.3'E, MNHN 2014-2736 (**B**); nuptial colouration pattern for male (**C**) and female (**D**).

2727, 2 ♂, 3 ♀, 51.1-65.3 mm SL; France: Vannon Stream, Brotte-lès-Ray, 47°36.2'N, 5°44.1'E, alt. 204 m. MNHN 2014-2744, 1 ♂, 3 ♀, 50.6-71.2 mm SL; France: Lez Stream, Montjoux, 44°30.1'N, 5°05.2'E, alt. 444 m. MNHN 2014-2802, 1 ♀, 46.4 mm SL; France: Linotte Stream, Loulans-Verchamp, 47°26'N, 6°12.4'E, alt. 234 m. MNHN 2014-2752, 2 ♂, 3 ♀, 50.3-55.8 mm SL; France: Calavon Stream, Viens, 43°51.7'N, 5°34.3'E, alt. 342 m. MNHN 2014-2737, 4 ♂, 3 ♀, 55.4-72.3 mm SL; France: Ilouvre Stream, Babeau-Bouldoux, 43°26.8'N, 2°54.7'E, alt. 222 m. MNHN 2014-2758, 2 ♀, 54.9-57.3 mm SL; France: Orbieu Stream, Ribaute, 43°06.1'N, 2°37.3'E, alt. 107 m. MNHN 2014-2736, 4 ♂, 2 ♀, 45.1-61.9 mm SL; France: Hérault River, Valleraugue, 43°05.2'N, 3°36.2'E, alt. 430 m. MNHN 2014-2763, 2 ♂, 3 ♀, 46.1-56.2 mm SL; Lez River, Prades-le-Lez, 43°41.9'N, 3°51.3'E, alt. 61 m.

Material used for molecular analysis

MNHN 2014-2754, 1, tag 4089; France: Agly River, Latour-de-France, 42°46.1'N, 2°38.5'E, alt. 92 m. (COI: GenBank accession number: MT975754). MNHN 2019-0264, tag 1994; France: Luech Stream, Chamborigaud, 44°19.7'N, 3°57.5'E, alt. 335 m. (COI: GenBank accession number: MT975748, 12S: GenBank accession number: MT975373). MNHN 2011-0388, 1, tag 4416; France: Orain Stream, Saint-Baraing, 46°53.8'N, 5°26.8'E, alt. 496 m. (COI: GenBank accession number: MT975792). MNHN 2011-0407, 1, tag 4393; France: Ouche Stream, Fleurey-sur-Ouche, 47°18.5'N, 4°50.6'E, alt. 293 m. (COI: GenBank accession number: MT975789). MNHN 2014-2727, 1, tag 12454; France: Vannon Stream, Brotte-lès-Ray, 47°36.2'N, 5°44.1'E, alt. 204 m. (COI: GenBank accession number: MT975728, 12S: GenBank accession number: MT975360). MNHN 2011-0946, 1, tag 10820; France: Rhône River, Jons, 45°48.7'N, 5°05.5'E, alt. 180 m. (COI: GenBank accession number: MT975712). MNHN 2010-0519, 1, tag 4131; France: Boulzane Stream, Puilaurens, 42°47.3'N, 2°18.5'E, alt. 514 m. (COI: GenBank accession number: MT975764, 12S: GenBank accession number: MT975379). MNHN 2011-0838, 2, tag 10701 and 10702; France: Boulzane Stream, Saint-Paul-de-Fenouillet, 42°48.3'N, 2°29'E, alt. 252 m. (COI: GenBank accession numbers: MT975700, MT975701, 12S: GenBank accession number: MT975346). MNHN 2010-0495, 1, tag 4107; France: Desix Stream, Ansignan, 42°45.3'N, 2°31.3'E, alt. 197 m. (COI: GenBank accession number: MT975758). MNHN 2014-2737, 3, tag 12344-12346; France: Ilouvre Stream, Babeau-Bouldoux, 43°26.8'N, 2°54.7'E, alt. 222 m. (COI: GenBank accession numbers: MT975721-MT975723, 12S: GenBank accession numbers: MT975355-MT975357). MNHN 2011-0244, 2, tag 4349 and 4350; France: Orbieu Stream, Ribaute, 43°06.1'N, 2°37.3'E, alt. 107 m. (COI: GenBank accession numbers: MT975782, MT975783). MNHN 2011-0275, 3, tag 4311-4313; France: Sals Stream, Coustaussa, 42°56.3'N, 2°16.7'E, alt. 242 m. (COI: GenBank accession numbers: MT975773-MT975775, 12S: GenBank accession numbers: MT975385). MNHN 2010-1069, 1, tag 4272; France: Buèges River, Pégairolles-de-Buèges, 43°48.8'N, 3°35.5'E, alt. 176 m. (COI: GenBank accession number: MT975771, 12S: GenBank accession number: MT975384). MNHN 2010-1071, 1, tag 4273; Garel Stream, Saint-Jean-de-Buèges, 43°50'N, 3°37'E, alt. 181 m. (COI: GenBank accession number: MT975772). MNHN 2011-0834, 2, tag 4440 and 4441; France: Hérault River, Valleraugue, 43°05.2'N, 3°36.2'E, alt. 430 m. (COI: GenBank accession numbers: MT975794, MT975795). MNHN 2014-2736, 2, tag 12449 and 12451; France: Hérault River, Valleraugue, 43°05.2'N, 3°36.2'E, alt. 430 m. (COI: GenBank accession numbers: MT975726, MT975727, 12S: GenBank accession number: MT975359). MNHN 2010-1066, 1, tag 4271; France: Lez River, Prades-le-Lez, 43°41.9'N, 3°51.3'E, alt. 61 m. 12S: GenBank accession numbers: MT975383). MNHN 2011-0243, 2, tag 4347 and 4348; France: Lez River, Prades-le-Lez, 43°41.9'N, 3°51.3'E, alt. 61 m. (COI: GenBank acces-

sion numbers: MT975780, MT975781, 12S: GenBank accession number: MT975387). MNHN 2010-0511, 1, tag 4127; France: Massane River, Argelès-sur-Mer, 42°31.9'N, 2°59.3'E, alt. 68 m. (COI: GenBank accession number: MT975781, 12S: GenBank accession number: MT975387). MNHN 2010-0502, 1, tag 4114; France: Tanyari Stream, Saint-Génis-des-Fontaines, 42°32.3'N, 2°56.1'E, alt. 57 m. (COI: GenBank accession number: MT975759, 12S: GenBank accession number: MT975377). MNHN 2013-0682, 1, tag 16630; France: Maureillas Stream, Le Boulou, 42°31.1'N, 2°49.7'E, alt. 80 m. (12S: GenBank accession number: MT975364). MNHN 2010-0995, 2, tag 4445 and 4446; France: Tech River, Elne, 42°35'N, 2°58.2'E, alt. 8 m. (COI: GenBank accession numbers: MT975797, MT975798, 12S: GenBank accession number: MT975390). MNHN 2010-1000, 1, tag 4177; France: Têt River, Eus, 42°38.6'N, 2°28.9'E, alt. 275 m. (COI: GenBank accession number: MT975765). MNHN 2011-0245, 2, tag 4331 and 4332; France: Crieulon Stream, Orthoux-Serignac-Quilhan, 43°53.3'N, 4°02.1'E, alt. 59 m. (COI: GenBank accession numbers: MT975776, MT975777). MNHN 2011-0251, 2, tag 4333 and 4334; France: Crieulon Stream, Orthoux-Serignac-Quilhan, 43°53.3'N, 4°02.1'E, alt. 59 m. (COI: GenBank accession numbers: MT975386, MT975779, 12S: GenBank accession numbers: MT975386).

Diagnosis

Phoxinus septimaniae is distinguished from the other French *Phoxinus* species by its unique nuptial colour pattern. The male has a blackish stripe along Z3 sometimes fractioned in blotches (vs. green stripe or black / green bars), Z4 greyish (vs. greenish or yellowish), pectoral fin bases yellow-orange with a red disc on the inner side (vs. yellow or orange without disc), a yellow spot between the eye and the mouth (vs. absence) (Fig. 7A, C). In the nuptial female, the Z4 is white (vs. greyish, yellowish or greenish) (Fig. 7B, D).

Phoxinus septimaniae is further distinguished from *P. bigerri* by having 75-94 scales along the lateral series (vs. 68-87), a slightly pointed snout (vs. very stout), a subterminal mouth (vs. terminal or slightly subterminal), a straight to slightly concave anal fin margin (vs. straight to convex), a deep caudal peduncle (caudal peduncle depth 2.7-4.6 times in its length vs. 2.1-3.4), and some populations have continuous breast scale patches across the breast (vs. separated or rarely connected anteriorly by 1-2 rows of scales).

Phoxinus septimaniae is further distinguished from *P. csikii* by having a slightly pointed snout (vs. very stout and blunt), a straight to slightly concave anal fin margin (vs. straight to slightly convex), and in some populations the breast is fully covered by scales (vs. two scale patches separated by an unscaled area).

The nuptial male *P. septimaniae* is further distinguished by having, black bars crossing Z2-Z3 (vs. Z1-Z5 in *P. bigerri*), Z4 greyish (vs. golden-yellow in *P. bigerri*; green in *P. csikii*; green-yellowish in *P. phoxinus*), belly white (vs. greyish to black in *P. bigerri*; shiny red in *P. csikii*), lips red (vs. pinkish in *P. bigerri* and *P. phoxinus*), pectoral, pelvic and anal fin bases red (*vs*. pinkish in *P. bigerri* and *P. phoxinus*). The nuptial female is further distinguished by having a black lateral stripe along Z3 (vs. no stripe), and no bars (vs. bold black bars crossing Z2 to Z4 in *P. bigerri*).

Nuptial colouration

Male. – Snout and top of head dark brown. A black bar on operculum reaching from top of head to branchiostegal rays. Cheeks white. Yellow spot between eye and mouth, a second one covering suboperculum and posterior part of operculum. Lips red. Z1 brown to black, Z2 pale-brown to golden. A blackish stripe along Z3 fractioned in blotches in some individuals and at some places. Z4 greyish, without green colouration, except rarely around pectoral fin. Z5 blackish. Pectoral fin bases usually yellowish-orange or red with a red disc at inners side (Fig. 7A, C).

Female. – No or an indistinct yellow spot on operculum. Z1 brownish. Z2 pale-brown. Stripe black along Z3. Z4 silvery white and Z5 black. (Fig. 7B, D).

Molecular characterization

On the COI marker, *P. septimaniae* has 10 diagnostic sites, including three synapomorphies (Tab. II). For the 12S rDNA marker, three diagnostic sites characterise this species: A (vs. G) in position 304, T (vs. A or G) in position 390 and T (vs. C) in position 394.

Distribution

Phoxinus septimaniae occurs in all the Rhône drainage as well as the French coastal Mediterranean catchments (Fig. 1) until northeastern Spain (Palandačić *et al*., 2017; Corral-Lou *et al*., 2019). It was introduced in the Roya, the Rhine catchments as well as in the Geneva (France/Switzerland) and the Ceresole (Italy) Lakes (Kottelat, 2007; Palandačić *et al*., 2017).

Vernacular name

Languedoc minnow (English), Vairon du Languedoc (French).

Remarks

Phoxinus septimaniae was originally diagnosed having a continuous patch of breast scales (Kottelat, 2007). The specimens examined by Kottelat (2007) originate from the Tech River, the stream Lez, the Gardon (Rhône drainage), the River Hérault and the stream Vidourle. We examined materials from all these populations and identified these morpho-

logically as *P. septimaniae* according to Kottelat (2007). However in our analysis, these "scaled breast" minnows form a paraphyletic group within the Mediterranean clade which includes also fish having two separated scaled patches on the breast from the Rhône drainage and some Mediterranean rivers as the Vidourle and the Buège (Fig. 3B). While the "scaled breast" minnows have very different haplotypes, each of these haplotypes is present in other minnows from Mediterranean catchments (stream Lez, Aude catchment) and in the Rhône drainage without the connection between the patches of breast scales. Kottelat (2007) had observed that some specimens from the Vidourle and the Aude catchment had two separate patches of breast scales and hypothesized the existence of introgressions with *P. phoxinus*. This hypothesis is plausible as there were many stocking operations of minnows in Europe (Palandačić *et al*., 2020). However, an alternative explanation would be that the continuous patches of breast scales are a variable character state in *P. septimaniae*. Then, *P. septimaniae* should include populations from the Rhône drainage, which have separated breast scaled patches in order to be a monophyletic group. Therefore, we identify the fish from the Rhone as *P. septimaniae*.

Nomenclatural notes

The name *Pisciculus varius*, first introduced by Rondelet (1555: 205), is made available by Dralet (1821: 35). No type specimens are known and no type locality is mentioned, as this was not the standard at these times. Dralet (1821) diagnosed *P. varius* by having a gold shining back, a silver belly and crimson at its sides ("l'or brille sur son dos, l'argent sur son ventre et le pourpre à ses côtés" in the original French description). This is the translation of Rondelet's description: "*Dorsum aurei splendoris est, venter argentei, latera purpurascut*" (Rondelet, 1555). The minnow drawn by Rondelet (1555: 205) is one of the syntypes mentioned by Dralet. Moreover, Dralet describes the taste and the flesh texture of the species. These minnows, which were eaten, also belong to the syntype series, but as Dralet lived in southwestern France, they might have come from another drainage (Garonne or Adour) and in fact might belong to another species (*P. dragarum* or *P. bigerri*). Thus, we designate the specimen illustrated by Rondelet as lectotype of *Pisciculus varius* Dralet, 1821. The type locality of *Pisciculus varius* is restricted to the locality of the lectotype. Rondelet (1555) gave no information on the origin locality of the specimen drawn. Rondelet was born and lived in Montpellier, however he also travelled to Paris, Maringues, Florence, the Netherlands and Belgium. So, while the lectotype could have come from the French Mediterranean, it could also have originated from the Seine, Loire, Meuse or Rhine catchments and could be attributed to *P. septimaniae*, *P. phoxinus* or *P. fayollarum*. Furthermore, the illustration of the lectotype does not allow us to identify a minnow (Cuvier and Valenciennes, 1844), much less the *Phoxinus* species to which it may correspond. Rondelet's collection, if it has ever existed, has disappeared. The lectotype is thus not extant. On the different colouration patterns described in these areas (*e.g*. Fournel, 1836; Selys-Longchamps, 1842; Villatte des Prûgnes, 1897; Moreau, 1899; Piton, 1931), only the description from Crespon (1844: 296-297) is concordant. Crespon lived in Nîmes (about 50 km to the Northeast of Montpellier) and described the minnows living in the Fountain basins as having "…a golden line on each side of the body, crimson and purplish glints with gold-coloured stripes on the sides; silver belly…" ("… une lignée dorée sur chaque côté du corps, des reflets pourprés et violâtres avec des lames couleur d'or sur les côtés; ventre argentin…" in the original French description). Both descriptions given by Rondelet (1555) and Crespon (1844) are very similar, so we consider that the lectotype of *Pisciculus varius* came from the French Mediterranean catchments where Rondelet worked extensively. We need to stabilise the type locality (art. 75.3.1) choosing a population adjacent to Montpellier and Nîmes for which we already have molecular and morphological data allowing the identification among all other French *Phoxinus* species (art. 75.3.2; see above). We designate as neotype the specimen MNHN 2019-0264 (art. 75.3.3) (64.8 mm SL), as the lectotype is not extant (art. 75.3.4) and corresponds to what we know of the former types (art. 75.3.5). The neotype came from a locality close to the original type locality (art. 75.3.6) in the lower Rhône drainage close to Montpellier and Nîmes (France: Luech stream, Chamborigaud, 44°19.7'N, 3°57.5'E), which now becomes the type locality of *Pisciculus varius*. This specimen is now deposited in the MNHN collections (art. 75.3.7). Consequently, we consider *Pisciculus varius* Dralet, 1821 and *Phoxinus septimaniae* Kottelat, 2007 as the same species. However, *Pisciculus varius* was used as a valid name only in 1821 to our knowledge, so before 1899 (art. 23.9.1.1). Moreover, since its description in 2007, *P. septimaniae* was used as a presumed valid name in at least 31 works by 28 different authors (Kottelat and Freyhof, 2007; Hanel *et al*., 2009; de Sostoa *et al*., 2010; Collin and Fumagalli, 2011; Keith *et al*., 2011; Agence Gaïadomo, 2012; Almeida *et al*., 2013; Maceda-Veiga, 2013; Witté *et al*., 2013; Geiger *et al*., 2014; Behrens-Chapuis *et al*., 2015; Denys, 2015; Fernández Cortés, 2015; Ibrahim, 2015; Knebelsberger *et al*., 2015; Miró and Ventura, 2015; Palandačić *et al*., 2015, 2017, 2020; Aparicio *et al*., 2016; Civade, 2016; Leunda *et al*., 2017; Maire *et al*., 2017; Aparicio, 2018; Arsento *et al*., 2018; Schönhuth *et al*., 2018; Vucić *et al*., 2018; Bogutskaya *et al*., 2019; Corral-Lou *et al*., 2019; Gauliard *et al*., 2019; Vinyoles *et al*., 2019) (art. 23.9.1.2). Consequently, we state that, to our knowledge, the condition in Article 23.9.1 applies. From the date of publication of that act *P. septimaniae* Kottelat, 2007 has precedence over *Pisciculus varius* Dralet, 1821. *Phoxinus septimaniae* is a *nomen protectum* and *Pisciculus varius* a *nomen oblitum*.

Then, *Pisciculus varius* Dralet, 1821 is a senior synonym of *Phoxinus septimaniae* Kottelat, 2007.

Ogérien (1863) described *Phoxynus montanus* from the Ain River near Champagnole and the Queue de Cheval waterfall near Saint-Claude (Eastern France, Rhône drainage). This species is characterised by having 10 pectoral fin rays (confirmed by Blanchard (1896)) (vs. 13-16 in *P. septimaniae*) and a nuptial colouration greyish black spattered with brown or olive colour and the flank with blue, yellow and greenish spots (vs. without blue or greenish spots in *P. septimaniae*). Lunel and Lunel (1874) stated the population at the type locality is distinguished from the minnows observed in the Lake Geneva basin where characteristic haplotypes of both *P. csikii* and *P. septimaniae* were found suggesting that these minnows are hybrids (Palandačić *et al*., 2017). With the absence of a syntype series and waiting for further investigations, we consider *Phoxynus montanus* Ogérien, 1863 and *P. septimaniae* Kottelat, 2007 as the same species. However, *Phoxynus montanus* was not used as a valid name after 1899 (art. 23.9.1.1). As discussed for *P. varius*, the article 23.9.1.2 is also applied for *P. septimaniae*. By consequence, we state that, to our knowledge, the condition in Article 23.9.1 applies here too. This makes *P. montanus* a *nomen oblitum*. Therefore, *Phoxynus montanus* Ogérien, 1863 becomes a senior synonym of *P. septimaniae* Kottelat, 2007.

Phoxinus laevis var. *montanus* Blanchard, 1896 is already an objective synonym of *Phoxynus montanus* Ogérien, 1863. *Phoxinus laevis* var. *montanus* Blanchard, 1896 is a senior synonym of *P. septimaniae* Kottelat, 2007.

***Phoxinus dragarum*, new species**
(Fig. 8)

Holotype

MNHN 2019-0262, ♂, 49.5 mm SL; France: Arrat-Devant Stream, Manent-Montané, 43°20.7'N, 0°37.5'E, alt. 275 m.

Paratypes

MNHN 2014-2725, 5 ♂, 18 ♀, 44.9-61.2 mm SL; France: Arrat-Devant Stream, Manent-Montané, 43°20.7'N, 0°37.5'E. MNHN 2014-2813, 2 ♂, 4 ♀, 49.3-57.5 mm SL; France: Ciron Stream, Escaudes, 44°19.2'N, 0°11.4'W, alt. 76 m. MNHN 2014-2807, 1 ♀, 62.7 mm SL; France: Couze Stream, Bayac, 44°48.3'N, 0°43.8'E, alt. 64 m. MNHN 2014-2735, 1 ♂, 6 ♀, 43.6-60.8 mm SL; France: Thèze Stream, Montcabrier, 44°32.4'N, 1°03.9'E, alt. 123 m. MNHN 2014-2738, 3 ♂, 45.5-51.9 mm SL; France: Vère Stream, Cahuzac-sur-Vère, 43°59.2'N, 1°53.7'E, alt. 189 m.

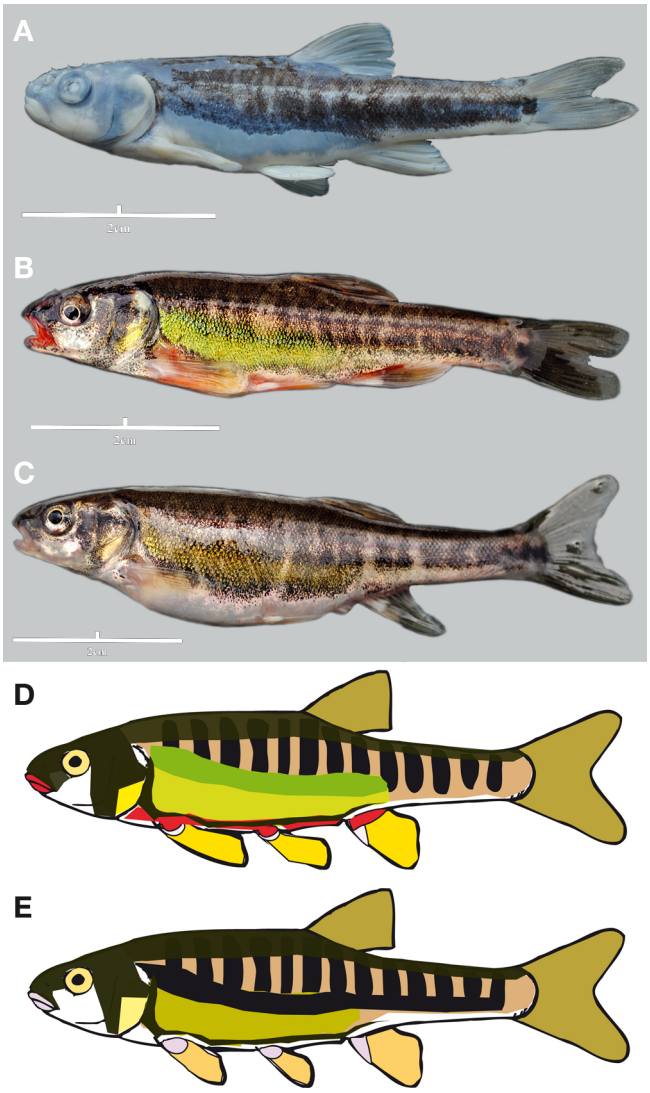

Figure 8. – *Phoxinus dragarum* Holotype ♂ (**A**), 49.52 mm SL from the Arrat-Devant Stream, Manent-Montané 43°20.7'N, 0°37.5'E, MNHN 2019-0262; paratypes ♂ (**B**) and ♀ (**C**), same location as holotype, MNHN 2014-2725; nuptial colouration pattern for male (**D**) and female (**E**).

Additional material

MNHN 2014-2761, 3 ♀, 44.7-53.7 mm SL; France: Dronne Stream, Bourdeilles, 45°19.4'N, 0°35.1'E, alt. 94 m. MNHN 2014-2759, 4 ♀, 57.6-66.5 mm SL; France: Dropt Stream, Gaugeac, 44°39.7'N, 0°52.5'E, alt. 134 m. MNHN 2014-2731, 4 ♀, 51.0-57.6 mm SL; France: Volp Stream, Montesquieu-Avantès, 43°02.7'N, 1°11.2'E, alt. 451 m.

Material used for molecular analysis

MNHN 2019-0262, holotype, tag 12470; France: Arrat-Devant Stream, Manent-Montané, 43°20.7'N, 0°37.5'E, alt. 275 m. (COI: GenBank accession number: MT975386, 12S: GenBank accession number: MT975361). MNHN 2014-

2813, paratypes, 2, tag 1989 and 1990; France: Ciron Stream, Escaudes, 44°19.2'N, 0°11.4'W, alt. 76 m. (COI: GenBank accession numbers: MT975361, MT975746). MNHN 2014-2738, paratype, 2, tag 12342 and 12343; France: Vère Stream, Cahuzac-sur-Vère, 43°59.2'N, 1°53.7'E, alt. 189 m. (COI: GenBank accession number: MT975720, 12S: GenBank accession numbers: MT975353, MT975354). MNHN 2011-0933, 1, tag 10781; France: Avance Stream, Montpouillan, 44°28.1'N, 0°07.6'E, alt. 25 m. (COI: GenBank accession number: MT975709, 12S: GenBank accession number: MT975350). MNHN 2011-0937, 1, tag 10778; France: Boralde de Flaujac Stream, Espalion, 44°32'N, 2°47.5'E, alt. 386 m. (COI: GenBank accession number: MT975708). MNHN 2010-0491, 1, tag 4103; France: Douctouyre Stream, Dun, 43°02.3'N, 1°47.6'E, alt. 321 m. (COI: GenBank accession number: MT975757). MNHN 2011-0416, 1, tag 4427; France: Doustre Stream, Saint-Bazile-de-la-Roche, 45°08.5'N, 1°57.6'E, alt. 525 m. (COI: GenBank accession number: MT975793). MNHN 2010-0513, 1, tag 4124; France: Job Stream, Lespiteau, 43°04.1'N, 0°45.5'E, alt. 367 m. (COI: GenBank accession number: MT975762). MNHN 2011-0278, 2, tag 4390 and 4391; France: Pique Stream, Cierp-Gaud, 42°54.7'N, 0°03.8'E, alt. 493 m. (COI: GenBank accession numbers: MT975787, MT975788). MNHN 2011-0928, 1, tag 10786 and 10787; France: Rimbez Stream, Saint-Pe-Saint-Simon, 44°01.1'N, 0°03.7'E, alt. 109 m. (COI: GenBank accession number: MT975710, 12S: GenBank accession numbers: MT975351, MT975352). MNHN 2010-0504, 1, tag 4116; France: Salat Stream, Rivèrenert, 42°57.4'N, 1°10.6'E, alt. 412 m. (COI: GenBank accession number: MT975760, 12S: GenBank accession number: MT975378). MNHN 2010-0476, 1, tag 4031; France: Triouzoune Stream, Saint-Angel, 45°30.2'N, 2°14.1'E, alt. 637 m. (COI: GenBank accession number: MT975753). MNHN 2011-1570, 2, tag 10931 and 10932; France: Tavignano River, Piedicorte-di-Gaccio, 42°12.8'N, 9°18.8'E, alt. 153 m. (COI: GenBank accession numbers: MT975715, MT975716).

Diagnosis

Phoxinus dragarum is distinguished from the other French *Phoxinus* species by its unique nuptial colour pattern. The male has a green stripe in Z3 reaching anal fin base (vs. stripe black or absent), and greenish yellow Z4 (Fig. 8B, D) (vs. green or golden yellow). The female has a green-ochre colouration in Z4 (vs. yellow, green, greyish or white), and a black line in Z5 from pectoral fin bases to anal fin base (Fig. 8C, E) (vs. absence of black line).

Phoxinus dragarum is further distinguished from *P. bigerri* by having 50-74 pored scales (vs. 68-87), a slightly stout snout (vs. very stout), and a straight to slightly concave anal fin margin (vs. straight to convex). It is further distinguished from *P. csikii* by having a snout slightly stout (vs. very stout and blunt), and a straight to slightly concave anal fin margin (vs. straight to slightly convex). The new species is further distinguished from *P. phoxinus* by having an incomplete lateral line usually reaching anal fin base or just after the last ray (vs. reaching to caudal peduncle), and a slightly stout snout (vs. slightly pointed).

Phoxinus dragarum is further distinguished from *P. septimaniae* by having an incomplete lateral line usually reaching anal fin base or just after the last ray (vs. reaching caudal peduncle or almost complete), 50-74 pored scales (vs. 73-86), a slightly stout snout (vs. slightly pointed), and 2 scaled patches at the pectoral fin bases separated by an unscaled area (vs. scaled breath between the pectoral fin bases in some populations).

The nuptial male *P. dragarum* is further distinguished by having a red belly, the red colour ending before the caudal peduncle (vs. belly greyish to black in *P. bigerri*; red belly extending to the caudal peduncle in *P. csikii*; belly pinkish to light orange in *P. phoxinus*; white in *P. septimaniae*), lacking a yellow dot between the mouth and the eye (vs. presence in *P. septimaniae*), having red lips (vs. pinkish in *P. bigerri* and *P. phoxinus*), yellow pectoral, pelvic and anal fins (vs. orange in *P. bigerri*; yellow-orange pectoral fin with a red disc at the interior side in *P. septimaniae*), and red pectoral, pelvic and anal fins bases (*vs*. pinkish in *P. bigerri* and *P. phoxinus*). The nuptial female is further distinguished by having a black stripe along Z3 (vs. no stripe in *P. bigerri*), a black Z5 (vs. white in *P. bigerri* and *P. csikii*), a pale yellow spot on the operculum (vs. absence in *P. bigerri*; marked yellow in *P. phoxinus*), and pale yellow pectoral fin (vs. marked yellow in *P. phoxinus*).

Description

Morphometric data is shown in table IV. Largest examined specimen 66.5 mm SL. Body moderately elongate, dorsal and ventral profile about symmetric or ventral profile slightly more convex. Dorsal profile of head markedly more convex than ventral one. Caudal peduncle length 2.3-3.5 times in depth of caudal peduncle. Snout slightly stout. Mouth terminal or slightly subterminal, upper lip and snout not projecting beyond tip of lower jaw. Tip of upper lip at level or above level of lowest point of eye. In lateral view, eye not or almost flushed with dorsal profile. No supraorbital ridge.

Dorsal fin with 3 simple and 6½-8½ branched rays. Distal dorsal fin margin markedly convex, second branched ray longest, dorsal fin origin behind vertical of pelvic fin origin. Pectoral fin with 1 simple and 13-18 branched rays (10 for one specimen; usually 14-15), reaching to pelvic fin origin in male, not reaching it in female. Pelvic fin with 1 simple and 5-8 branched rays (usually 7-8), reaching slightly beyond anal fin origin in male, not reaching in female. Anal fin with 3 simple and 6½-8½ branched rays. Anal fin origin

Table IV. – Morphometric data of *Phoxinus dragarum* (holotype: MNHN 2019-0262; paratypes: MNHN 2014-2725, MNHN 2014-2813, MNHN 2014-2807, MNHN 2014-2735, MNHN 2014-2738; and additional materials (MNHN 2014-2761, MNHN 2014-2759, MNHN 2014-2731; n = 52). The calculations include the holotype.

	Holotype	Holotype & other individuals			
		Mean	Min	Max	SD
SL (mm)	49.5	52.8	43.6	66.5	5.6
In percent of standard length					
Head length	26.5	26.7	24.0	29.7	1.1
Predorsal length	52.7	56.3	52.7	59.6	1.5
Post dorsal length	36.9	36.2	33.7	39.9	1.4
Prepectoral length	27.5	26.1	23.7	28.2	1.1
Prepelvic length	46.8	48.6	44.3	52.2	1.8
Preanal length	65.2	64.9	57.2	68.4	2.0
Body depth	21.0	23.2	19.5	26.4	1.7
Distance dorsal anal	20.6	23.3	19.9	26.4	1.4
Distance pectoral pelvic	18.9	20.8	16.4	25.7	2.4
Pectoral fin length	20.2	18.2	16.0	21.1	1.3
Pelvic fin length	16.4	14.7	12.5	18.9	1.5
Dorsal fin length	22.3	20.3	18.1	24.2	1.4
Anal fin length	22.3	20.0	18.1	22.8	1.1
Caudal peduncle length	28.0	25.9	23.5	28.1	1.2
Caudal peduncle depth	9.1	9.3	7.7	14.1	0.9
In percent of head length					
Head depth	51.3	51.1	46.9	54.3	1.9
Eye diameter	25.5	25.8	21.5	30.6	2.0
Snout length	29.8	29.2	23.7	35.6	2.5
Inter-orbital width	27.1	33.3	25.8	40.4	3.0

slightly in front of vertical through insertion of dorsal fin or behind. Anal fin margin straight to slightly concave, second branched ray longest.

Lateral line incomplete usually reaching to vertical of dorsal-fin base or to vertical of base of last anal fin ray. 70-97 lateral scales, including 50-74 pored scales. Two scaled patches at pectoral fin insertions separated by an unscaled area. No scales between pectoral fin bases. Nuptial tubercles observed in both sexes.

Nuptial colouration

Male. – Snout and top of head dark-brown. A black bar on operculum reaching from top of head to branchiostegal rays. Cheeks white. Operculum with a white spot at uppermost, posterior corner. A yellow spot on suboperculum. Lips red. Z1 brown to black. Z2 pale brown. Black vermiculations in Z1 to Z2. Z3 green. Z4 yellow or yellowish-green. A black line along Z5 from pectoral fin origin to caudal peduncle. Belly red, red couloration not extending to caudal peduncle. Fins yellow-orange. (Fig. 8B, D).

Female. – Z3 with a black stripe. Z4 green-ochre until anal fin. A black line along Z5 from pectoral fin origin to caudal peduncle. Pinkish tinge visible at base of pectoral, pelvic and anal fins and on mouth. Belly white. White and yellow spots on operculum and white spots at origin of pectoral, pelvic and anal fins (Fig. 8C, E).

Colouration in preservation

Dark bars remain after preservation in ethanol. Green colouration turns to dark grey, yellow and red colourations faded and usually absent (Fig. 8A).

Molecular characterization

On the COI marker, *P. dragarum* has six diagnostic sites, including two synapomorphies. However, the Garonne and Dordogne populations are characterised both by three diagnostic sites (Tab. II). For the 12S rDNA marker, five diagnostic sites characterise this species: G (*vs*. A) in position 179, A (vs. G) in position 307, T (vs. A or G) in position 310, C (vs. A or G) in position 412 and A (vs. G) in position 478.

Distribution

This species is endemic to the Garonne drainage (Fig. 1). It has been introduced to Spain, in the Ebro drainage along the Pyrenean side (Corral-Lou *et al*., 2019) and also in the Guadalquivir drainage (Sáez-Gómez and Prenda, 2019: fig. 2).

Ecology

Phoxinus dragarum is abundant in the barbel zone (Ibarra *et al*., 2005). It is usually found in headwater streams (Ibarra *et al*., 2005; Santoul *et al*., 2005) with a low slope in altitude and a high fish species richness (Céréghino *et al*., 2005). It is often found in sympatry with *Gobio occitaniae* Kottelat & Persat, 2005 (Céréghino *et al*., 2005). Studies made on populations from the stream Ariège and the Garonne River demonstrated that *P. dragarum* prefers shallow water located along the bank, with no or low velocity and a mixed substrate (pebbles, gravel, sand and sludge) (Mastrorillo *et al*., 1996, 1997; Reyjol *et al*., 2001). Intraspecific variations of functional traits (such as body mass, metabolic rate, excretion rate and boldness) were observed within several populations due to local adaptations to water temperature or predation pressure, or co-variations driven by genetic drift (Raffard *et al*., 2019). The spawning season occurs from April to May, June in higher altitude (Denys, pers. obs., 2014).

Etymology

The species name dragarum is the genitive of a latinized name “dragas” which are fairies from of the Occitan folklore. Dragas are the companions of the Drac, a kind of dragon living in the streams of the Ariège department (Garonne drainage). In the land of Foix, these melusian serpentiform fairies attack intruders crossing their territory. The sound of bells alone can stop them. They come out only to wash their clothes with a gold beater, not without having closely

watched the area with their only eye in the middle of the forehead (Ely and Tsaag Valren, 2013).

Vernacular name

Garonne minnow (English), Vairon de la Garonne (French).

Remarks

The Garonne and Dordogne clades are separated by a divergence of 1.6%. As we find no other character states distinguishing both population groups, we consider them as two evolutionary lineages of a same species.

***Phoxinus fayollarum*, new species**
(Fig. 9)

Holotype

MNHN 2019-0263, ♂, 58.1 mm SL; France: Boron Stream, Pionsat, 46°06.4'N 2°41.1'E; 522 m.

Paratypes

MNHN 2014-2729, 5 ♂, 3 ♀, 57.5-68.1 mm SL; France: Boron Stream, Pionsat 46°06.4'N 2°41.1'E; alt. 522 m. MNHN 2014-2732, 2 ♂, 2 ♀, 50.2-58.9 mm SL; France: stream Nièvre, Dompierre-sur-Nièvre, 47°14.1'N 3°15.0'E; alt. 231 m.

Additional material

MNHN 2010-0992, 2 ♂, 1 ♀, 50.2-56.1 mm SL; France: Ance du Nord Stream, Sauvessanges, 45°23.1'N 3°53.6'E; alt. 800 m. MNHN 2010-1055, 2 ♂, 1 ♀, 48.9-54.8 mm SL; France: Aurence Stream, Aixe-sur-Vienne, 45°47.9'N 1°09.1'E; alt. 205 m. MNHN 2011-0819, 2 ♂, 4 ♀, 41.0-60.5 mm SL; France: Allier Stream, Saint-Haon, 44°50.4'N 3°44.2'E; alt. 734 m. MNHN 2011-0910, 5 ♀, 41.0-47.0 mm SL; France: Varenne Stream, Soucé, 48°28.1'N 0°39.5'W; alt. 114 m. MNHN 2014-2733, 4 ♂, 11 ♀, 48.1-67.0 mm SL; France: Esves Stream, Ciran, 47°02.6'N 0°53.6'E; alt. 88 m. MNHN 2014-2740, 1 ♂, 4 ♀, 59.1-73.6 mm SL; France: Ouatier Stream, Rians, 47°10.2'N 2°35.6'E; alt. 158 m. MNHN 2014-2745, 2 ♂, 8 ♀, 43.4-70.1 mm SL; France: Tusson Stream, Vancé, 47°49.4'N 0°38.6'E; alt. 83 m. MNHN 2014-2767, 4 ♂, 4 ♀, 41.2-51.9 mm SL; France: Céphons Stream, Moulins-sur-Céphons, 47°02.2'N 1°33.1'E; alt. 121 m.

Material used for molecular analysis

MNHN 2019-0263, holotype, tag 12474; France: Boron Stream, Pionsat, 46°06.4'N 2°41.1'E; alt. 522 m. (COI: GenBank accession number: MT975733, 12S: GenBank accession number: MT975362). MNHN 2014-2729, paratype, 1, tag 12475; France: Boron Stream, Pionsat, 46°06.4'N 2°41.1'E; alt. 522 m. (COI: GenBank accession number: MT975734, 12S: GenBank accession number: MT975363). MNHN 2010-0992, 1, tag 4209; France: Ance du Nord Stream, Sauvessanges, 45°23.1'N 3°53.6'E; alt. 800 m. (COI: GenBank accession number: MT975768, 12S: GenBank accession number: MT975381). MNHN 2010-1055, 1, tag 4237; France: Aurence Stream, Aixe-sur-Vienne, 45°47.9'N 1°09.1'E; alt. 205 m. (COI: GenBank accession number: MT975769, 12S: GenBank accession number: MT975382). MNHN 2011-0819, 1, tag 10741; France: Allier Stream, Saint-Haon, 44°50.4'N 3°44.2'E; alt. 734 m. (COI: GenBank accession number: MT975702, 12S: GenBank accession number: MT975347). MNHN 2011-0910, 1, tag 10752; France: Varenne Stream, Soucé, 48°28.1'N 0°39.5'W; alt. 114 m. (COI: GenBank accession number:

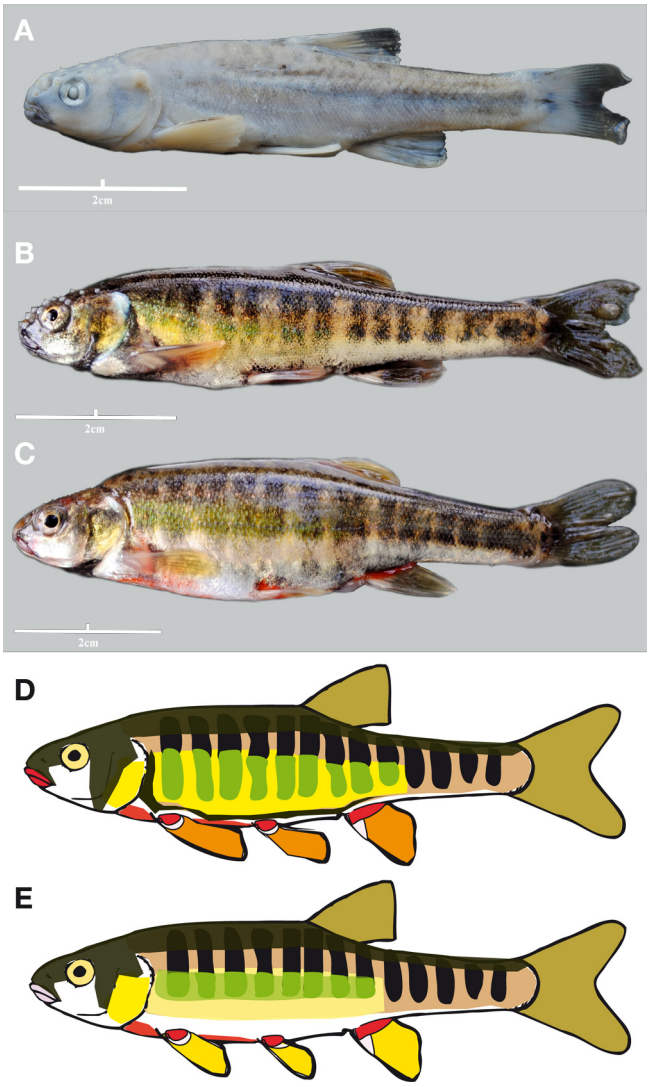

Figure 9. – *Phoxinus fayollarum* Holotype ♂ (**A**), 58.13 mm SL from the Boron Stream, Pionsat 46°06.4'N, 2°41.1'E, MNHN 2019-0263; paratypes ♂ (**B**) and ♀ (**C**), same location as holotype, MNHN 2014-2729; nuptial colouration pattern for male (**D**) and female (**E**).

MT975703, 12S: GenBank accession number: MT975348). MNHN 2014-2740, 2, tag 12347 and 12348; France: Ouatier Stream, Rians, 47°10.2'N 2°35.6'E; alt. 158 m. (COI: GenBank accession numbers: MT975724, MT975725, 12S: GenBank accession number: MT975358). MNHN 2010-0474, 1, tag 4029; France: Dejoune Stream, Felletin, 45°50.5'N 2°12.1'E; alt. 578 m. (COI: GenBank accession number: MT975752). MNHN 2010-1008, 1, tag 4189; France: Semme Stream, Droux, 46°09.1'N 1°08.7'E; alt. 198 m. (COI: GenBank accession number: MT975766). MNHN 2011-0920, 1, tag 10755; France: Sarthe Stream, Moulin-le-Carbonel, 48°23.1'N 0°02.1'W; alt. 133 m. (COI: GenBank accession number: MT975704, COI: GenBank accession number: MT975349). MNHN 2014-0015, 2, tag 18978 and 18979; France: Sèvre niortaise River, Sainte-Eanne, 46°22.9'N 0°09.4'W; alt. 64 m. (COI: GenBank accession numbers: MT975735, MT975736, 12S: GenBank accession numbers: MT975365, MT975366). MNHN 2011-0937, 1, tag 10777; France: Boralde de Flaujac Stream, Espalion, 44°32'N 2°47.5'E, alt. 386 m. (COI: GenBank accession number: MT975707).

Diagnosis

Phoxinus fayollarum is distinguished from the other French *Phoxinus* species by its unique nuptial colour pattern. The male has black bars in Z1 to Z2 and green in Z3 to Z4 (vs. black in Z2 to Z3). Z4 is bright yellow (vs. greyish of green) and the belly is red (vs. white, pinkish to light orange or greyish to black) (Fig. 9B, D). The female has a green stripe along Z3 (vs. black if present), the Z4 is yellow-pinkish (vs. greyish or green), the belly red (vs. white), and the female has red spots at the pectoral, pelvic and anal fins bases (vs. pinkish) (Fig 9C, E).

Phoxinus fayollarum is further distinguished from *P. bigerri* and *P. csikii* by a straight to slightly concave anal fin margin (vs. straight to convex), from *P. phoxinus* and *P. septimaniae* by a stout and blunt snout (vs. slightly pointed, and two scaled patches at the pectoral fin bases separated by a nonscaled area (vs. scaled breath between the pectoral fin insertions in some populations of *P. septimaniae*), and from *P. dragarum* by an incomplete lateral line usually reaching to the caudal peduncle (vs. usually reaching to the anal fin base or just slightly behind the last anal fin ray), and 56-84 pored scales (vs. 50-74).

The nuptial male *P. fayollarum* is further distinguished by its clearly distinct green bars crossing Z3 and Z4 (vs. indistinct in *P. phoxinus*), the red belly not extending to the caudal peduncle (vs. extending in *P. csikii*), having red pectoral, pelvic and anal fins bases (*vs*. pinkish in *P. bigerri* and *P. phoxinus*), orange pectoral, pelvic and anal fins (vs. yellow in *P. csikii* and *P. dragarum*), no red disc on the inner side of the pectoral fin (presence in *P. septimaniae*), and the absence of a yellow dot between the mouth and the eye (vs. the presence in *P. septimaniae*). The nuptial female is distinguished by a white Z5 (vs. black in *P. phoxinus*, *P. septimaniae* and *P. dragarum*).

Description

Morphometric data is shown in table V. Largest examined specimen 73.6 mm SL. Body moderately elongated, dorsal and ventral profile about symmetric or ventral profile slightly more convex. Dorsal head profile markedly more convex than ventral one. Caudal peduncle length 2.2-3.5 times in its depth. Snout stout and blunt. Mouth slightly subterminal, upper lip and snout projecting beyond tip of lower jaw. Tip of upper lip at level or above level of lowest point of eye. In lateral view, eye not or almost flushed with dorsal profile. No supraorbital ridge.

Dorsal fin with 3 simple and 6½-8½ branched rays. Distal dorsal-fin margin markedly convex, second branched ray longest, dorsal-fin origin behind pelvicfin insertion. Pectoral fin with 1 simple and 11-16 branched rays (usually 14-15), reaching to pelvicfin origin in male, not reaching in female. Pelvicfin with 1 simple and 6-9 branched rays (mainly 7-8), reaching slightly beyond anal fin origin in male, not reaching

Table V. – Morphometric data of *Phoxinus fayollarum* (holotype: MNHN 2019-0263; paratypes: MNHN 2014-2729, MNHN 2014-2732; and additional materials (MNHN 2010-0992, MNHN 2010-1055, MNHN 2011-0819, MNHN 2011-0910, MNHN 2014-2733, MNHN 2014-02740, MNHN 2014-2745, MNHN 2014-2767; n = 69). The calculations include the holotype.

	Holotype	Holotype & other individuals			
		Mean	Min	Max	SD
SL (mm)	58.1	53.5	41.0	73.6	8.0
In percent of standard length					
Head length	27.6	26.0	23.6	28.2	1.0
Predorsal length	51.9	55.5	51.9	59.1	1.6
Post dorsal length	36.2	35.9	28.0	40.0	2.0
Prepectoral length	24.6	26.0	22.8	30.3	1.3
Prepelvic length	45.1	48.3	42.7	53.4	1.9
Preanal length	63.5	65.3	61.2	69.5	1.9
Body depth	21.5	21.3	15.2	28.3	2.3
Distance dorsal anal	23.7	22.2	16.8	27.0	2.0
Distance pectoral pelvic	17.1	20.8	16.2	25.0	2.2
Pectoral fin length	18.5	18.1	14.2	21.4	1.6
Pelvic fin length	15.7	14.8	12.1	18.3	1.4
Dorsal fin length	21.8	20.3	16.4	22.9	1.3
Anal fin length	19.3	19.9	16.6	23.5	1.4
Caudal peduncle length	25.9	25.5	20.9	28.9	1.6
Caudal peduncle depth	9.4	9.1	6.9	11.2	0.8
In percent of head length					
Head depth	50.0	52.0	45.6	57.7	2.9
Eye diameter	22.3	26.4	21.5	32.3	2.6
Snout length	30.9	29.0	18.8	36.8	2.9
Inter-orbital width	32.1	32.5	26.1	38.3	2.7

in female. Anal fin with 3 simple and 6½-8½ branched rays. Anal fin origin slightly in front of vertical through dorsal-fin origin. Anal fin margin straight to slightly concave, second branched ray longest.

Lateral line incomplete reaching caudal peduncle. 72-91 lateral scales, including 56-84 pored scales. Two scaled patches at pectoral fin origin separated by an unscaled area. No scale between pectoral fin bases. Nuptial tubercles present in both sexes, smaller in female.

Nuptial colouration

Male. – Snout and top of head dark brown. A black bar on operculum reaching from top of head to branchiostegal rays. Cheeks white. Lips dark pink or red. Large yellow spot on operculum almost covering whole opercular and a white spot above at upper corner. Z1 brown to black. Z2 pale brown. Flank bars crossing Z1 to Z4, flank bars black from Z1 to Z2 and green from Z3 to Z4. Z4 bright yellow. A black line along Z5 between pectoral fin base and caudal peduncle, from pelvic fin base to caudal peduncle in some individuals. Pectoral, pelvic and anal fins yellow-orange. Pectoral, pelvic and anal fin bases red. (Fig. 9B, D). Female: Nuptial colouration pattern similar to male but paler with black bars in Z1 to Z2, a green stripe along Z3, Z4 yellow-pinkish, and Z5 white. Lips pinkish and belly red. Presence of "male" characters in the female: white and yellow spots on operculum and red spots at pectoral, pelvic and anal fin bases (Fig 9C, E).

Colouration in preservation

Dark green, brown and black bars and dots remain after preservation in ethanol. Green colouration turns to dark brown, whereas yellow and red colourations are faded (Fig. 9A).

Molecular characterisation

On the COI marker, *P. fayollarum* has six diagnostic sites including two synapomorphies (Tab. II). For the 12S rDNA marker, 6 diagnostic sites characterise this species: C (vs. A or G) in position 122, C (*vs*. T) in position 357, T (vs. C) in position 454, C (vs. T) in position 649, G (vs. A) in position 675 and A (vs. G) in position 874.

Distribution

This species is endemic to the Loire drainage as well as the Sèvre Niortaise catchment (Fig. 1). It has been introduced in Garonne and Rhône drainages adjacent to the Loire catchment, for example in the stream Boralde de Flaujac and in the Chassezac River, Grevieres (Geiger *et al*. (2014). This lineage was named *Phoxinus sp*. 16 by Palandačić *et al*. (2017).

Ecology

This species is common in the whole Loire drainage, and is especially abundant in the greyling zone (Lasne *et al*., 2007). It inhabits mostly clear and shallow streams with a slow discharge and a sandy or gravely ground. The spawing period is from April to May (Mauduyt, 1848) and in June-July in higher altitudes (Denys, pers. obs., 2014).

Etymology

The species name *fayollarum* is the genitive of a latinized name "fayolles", fairies from of the Auvergne region folklore, in the headwater of Loire drainage. Fayolles are fairies who create spring waters. And we owe to one of them, called "Grande Fayolle", the thermal waters of Vichy (Ely and Tsaag Valren, 2013).

Vernacular name

Loire minnow (English), Vairon ligérien (French).

Nomenclatural note

De la Pylaie (1835: 533) described *Leuciscus obtusus* as a little leuciscid or small minnow without spots ("Able ou petit Verdon sans taches" in French) in the Vendée department (so possibly in the Loire drainage). This name is a *nomen nudum* and potentially synonym of *P. phoxinus* (Kottelat, 1997). However, a minnow is characterised by the presence of spots on the snout, the flanks and the tail. According to the original description (the absence of spots), this taxon could correspond to another leuciscid species but not to a *Phoxinus*, even if the ancient French word "verdon" means minnow. Moreover, no type specimen is known. Thus, we consider this taxon as an *incertae sedis* in Leuciscidae.

CONCLUSION

The nuptial colouration patterns allow the diagnosis minnow species, as in some other Leuciscids, Percids or Cichlids (*e.g*. Pauers, 2010; Kraczkowski and Chernoff, 2014; Stepien and Haponski, 2015). This character is useful to identify live fish during the spawning period in the field, whereas morphomeristic data cannot well discriminate species.

Most of our descriptions of nuptial colourations patterns of *P. csikii*, *P. bigerri*, *P. fayollarum*, *P. phoxinus* and *P. septimaniae* correspond to the description of minnows by Lunel and Lunel (1874) from the Lake Geneva basin, Leunda *et al*. (2017) (Ebro drainage), Villates des Prûgnes (1987) and Magnan (1982) (Loire drainage), Spillmann (1961) (Seine drainage), and Vallot (1837) (Rhône drainage) (see Tab. V).

Our molecular results are congruent with the nuptial colouration patterns and support six minnow species in France. However, a very recent study pointed out a seventh French evolutionary lineage of *Phoxinus* in the Charente catchment

(Garcia-Raventós *et al*., 2020), which proves that the taxonomy of *Phoxinus* is far from resolved.

Key to French species of *Phoxinus* (male)

1a. – Z4 green; belly continuously red between pectoral and caudal fin bases. . . . . ***Phoxinus csikii***
1b. – Z4 yellow or greyish; belly white, grey, black or red, if red, then red colour not extended to caudal fin base **2**

2a. – Flank bars reaching from Z2 to Z3, forming a stripe along Z3 . . . . . **3**
2b. – Flank bars reaching from Z2 to Z4 or Z5, not forming a stripe along Z3. . . . . **4**

3a. – A green stripe along Z3; Z4 yellow-green; pectoral fin yellow; no yellow dot between mouth and eye; lateral line incomplete, usually reaching to a point anterior of anal fin origin or slightly beyond base of last anal fin ray; 50-74 pored scales along lateral line; snout slightly stout; two scaled patches at pectoral fin bases separated by an unscaled area . . . . . ***Phoxinus dragarum***
3b. – A black stripe along Z3; Z4 greyish; pectoral fin yellow-orange with a red blotch behind inner fin base; a yellow dot between mouth and eye; lateral line complete or incomplete, reaching beyond anal fin base to caudal fin base in some individuals; 73-86 pored scales along lateral line; snout slightly pointed; breast completely covered by scales between pectoral fin bases in some populations (two scaled patches at pectoral fin bases separated by an unscaled area in others) . . . . . ***Phoxinus septimaniae***

4a. – Bars crossing Z1 and Z5 black; belly greyish to black; anal fin margin straight to convex . . . . . ***Phoxinus bigerii***
4b. – Bars crossing Z3 and Z4 green; belly red, pinkish or pale orange; anal fin margin straight to slightly concave **5**

5a. – Z4 bright yellow; flank bars green with sharp margins; lips, pectoral, pelvic and anal fin bases and belly red; pectoral fin orange; snout stout and blunt . . . . . ***Phoxinus fayollarum***
5b. – Z4 greenish yellow; flank bars green with diffuse margin; lips, pectoral, pelvic and anal fin bases pinkish, belly pinkish or pale orange; pectoral-fin yellow; snout slightly pointed. . . . . ***Phoxinus phoxinus***

Key to French species of *Phoxinus* (female)

1a. – Flank bars reaching from Z2 to Z4, not forming a stripe along Z3; Z4 greyish . . . . . ***Phoxinus bigerri***
1b. – Flank bars reaching from Z2 to Z3, forming a stripe along Z3; Z4 yellow, green or white.. . . . . **2**

2a. – Stripe along Z3 green, Z4 bright yellow; belly below pectoral fin origin red; pectoral, pelvic and anal fin bases red. . . . . ***Phoxinus fayollarum***
2b. – Stripe along Z3 black, Z4 golden, white or greenish; belly completely white; pectoral, pelvic and anal fin bases pinkish. **3**

3a. – Z4 golden; Z5 white; anal fin margin straight to slightly convex. . . . . ***Phoxinus csikii***
3b. – Z4 white or greenish; Z5 black; anal fin margin straight to slightly concave. **4**

4a. – Z4 white; breast between pectoral fin origins completely covered by scales in some populations (two scaled patches at pectoral fin bases separated by an unscaled area in others). . . . . ***Phoxinus septimaniae***
4b. – Z4 greenish; breast between pectoral fin origins with scale patches separated by unscaled area or connected by 1-2 rows of scales.. . . . . **5**

5a. – Z4 green; lateral line incomplete, reaching to beyond anal fin base, to caudal peduncle; snout slightly pointed. . . . . ***Phoxinus phoxinus***
5b. – Z4 green-ochre; lateral line incomplete, usually reaching to a point anterior of anal fin origin or slightly beyond base of last anal fin ray; snout slightly stout.. . . . . ***Phoxinus dragarum***

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Appendix – List of COI sequences retrieved from NCBI GenBank with information on drainage and country of origin.

Species	Drainage	Country	GenBank	Reference
Phoxinus bigerri	Ugarana	Spain	KJ554128	Geiger *et al*., 2014
Phoxinus bigerri	Ugarana	Spain	KJ554275	Geiger *et al*., 2014
Phoxinus bigerri	Ugarana	Spain	KJ554288	Geiger *et al*., 2014
Phoxinus bigerri	Adour	France	KU729252	Behrens-Chapuis *et al*., 2015
Phoxinus bigerri	Adour	France	KU729253	Behrens-Chapuis *et al*., 2015
Phoxinus cf. *morella*	Danube	Czech Republic	HQ960469	Mendel *et al*., 2012
Phoxinus cf. *morella*	Danube	Czech Republic	HQ960470	Mendel *et al*., 2012
Phoxinus cf. *morella*	Danube	Czech Republic	HQ960471	Mendel *et al*., 2012
Phoxinus cf. *morella*	Elbe	Czech Republic	HQ960477	Mendel *et al*., 2012
Phoxinus cf. *morella*	Elbe	Czech Republic	HQ960538	Mendel *et al*., 2012
Phoxinus cf. *morella*	Danube	Czech Republic	HQ960606	Mendel *et al*., 2012
Phoxinus cf. *morella*	Elbe	Czech Republic	HQ960697	Mendel *et al*., 2012
Phoxinus cf. *morella*	Elbe	Czech Republic	HQ960698	Mendel *et al*., 2012
Phoxinus cf. *morella*	Elbe	Czech Republic	HQ960699	Mendel *et al*., 2012
Phoxinus cf. *morella*	Elbe	Czech Republic	HQ960700	Mendel *et al*., 2012
Phoxinus cf. *morella*	Elbe	Czech Republic	HQ960952	Mendel *et al*., 2012
Phoxinus cf. *morella*	Elbe	Czech Republic	HQ960953	Mendel *et al*., 2012
Phoxinus cf. *morella*	Elbe	Czech Republic	HQ960970	Mendel *et al*., 2012
Phoxinus cf. *morella*	Elbe	Czech Republic	HQ961030	Mendel *et al*., 2012
Phoxinus cf. *morella*	Elbe	Czech Republic	HQ961031	Mendel *et al*., 2012
Phoxinus cf. *morella*	Weser	Germany	KM286877	Knebelsberger *et al*., 2015
Phoxinus cf. *morella*	Weser	Germany	KM286879	Knebelsberger *et al*., 2015
Phoxinus cf. *morella*	Weser	Germany	KM286880	Knebelsberger *et al*., 2015
Phoxinus cf. *morella*	Weser	Germany	KM286881	Knebelsberger *et al*., 2015
Phoxinus colchicus	Mchishta	Georgia	KU729254	Behrens-Chapuis *et al*., 2015
Phoxinus colchicus	Natanebi	Georgia	KU729255	Behrens-Chapuis *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286805	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286809	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286824	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286836	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286847	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286848	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286849	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286850	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286853	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286854	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286855	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286856	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286857	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286861	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286862	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286873	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286916	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286918	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286921	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286935	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286951	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286964	Knebelsberger *et al*., 2015

Appendix. Continued

Species	Drainage	Country	GenBank	Reference
Phoxinus csikii	Rhine	Germany	KM286967	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286973	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286974	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286975	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286977	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286978	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286981	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286983	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286988	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM286995	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM287000	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM287003	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM287005	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM287006	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM287008	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM287013	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM287017	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM287019	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM287020	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM287022	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM287025	Knebelsberger *et al*., 2015
Phoxinus csikii	Danube	Germany	KM373651	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM373657	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM373662	Knebelsberger *et al*., 2015
Phoxinus csikii	Rhine	Germany	KM373664	Knebelsberger *et al*., 2015
Phoxinus csikii	Danube	Montenegro	MF407712	Palandačić *et al*., 2017
Phoxinus csikii	Danube	Montenegro	MF407713	Palandačić *et al*., 2017
Phoxinus csikii	Danube	Montenegro	MF407714	Palandačić *et al*., 2017
Phoxinus csikii	Danube	Montenegro	MF407715	Palandačić *et al*., 2017
Phoxinus csikii	Danube	Montenegro	MF407716	Palandačić *et al*., 2017
Phoxinus csikii	Danube	Montenegro	MF407717	Palandačić *et al*., 2017
Phoxinus csikii	Brestovacka	Serbia	MF407718	Palandačić *et al*., 2017
Phoxinus csikii	Brestovacka	Serbia	MF407719	Palandačić *et al*., 2017
Phoxinus csikii	Brestovacka	Serbia	MF407720	Palandačić *et al*., 2017
Phoxinus csikii	Brestovacka	Serbia	MF407721	Palandačić *et al*., 2017
Phoxinus csikii	Brestovacka	Serbia	MF407722	Palandačić *et al*., 2017
Phoxinus csikii	Krupacko Barje	Serbia	MF407724	Palandačić *et al*., 2017
Phoxinus csikii	Krupacko Barje	Serbia	MF407725	Palandačić *et al*., 2017
Phoxinus csikii	Krupacko Barje	Serbia	MF407726	Palandačić *et al*., 2017
Phoxinus csikii	Krupacko Barje	Serbia	MF407727	Palandačić *et al*., 2017
Phoxinus csikii	Krupacko Barje	Serbia	MF407728	Palandačić *et al*., 2017
Phoxinus csikii	Danube	Serbia	MF407731	Palandačić *et al*., 2017
Phoxinus csikii	Danube	Serbia	MF407732	Palandačić *et al*., 2017
Phoxinus csikii	Danube	Serbia	MF407733	Palandačić *et al*., 2017
Phoxinus csikii	Danube	Serbia	MF407734	Palandačić *et al*., 2017
Phoxinus csikii	Danube	Serbia	MF407735	Palandačić *et al*., 2017
Phoxinus csikii	Danube	Serbia	MF407736	Palandačić *et al*., 2017
Phoxinus csikii	Danube	Serbia	MF407737	Palandačić *et al*., 2017

Appendix. Continued

Species	Drainage	Country	GenBank	Reference
Phoxinus csikii	Danube	Serbia	MF407738	Palandačić *et al*., 2017
Phoxinus csikii	Rhine	France	MK310229	Denys & Manné 2019
Phoxinus karsticus	Moraca	Montenegro	MF407745	Palandačić *et al*., 2017
Phoxinus karsticus	Moraca	Montenegro	MF407746	Palandačić *et al*., 2017
Phoxinus karsticus	Moraca	Montenegro	MF407747	Palandačić *et al*., 2017
Phoxinus karsticus	Musnica	Bosnia and Herzegovina	MF407748	Palandačić *et al*., 2017
Phoxinus karsticus	Musnica	Bosnia and Herzegovina	MF407749	Palandačić *et al*., 2017
Phoxinus karsticus	Musnica	Bosnia and Herzegovina	MF407750	Palandačić *et al*., 2017
Phoxinus karsticus	Musnica	Bosnia and Herzegovina	MF407751	Palandačić *et al*., 2017
Phoxinus karsticus	Trebisnjica	Bosnia and Herzegovina	MF407752	Palandačić *et al*., 2017
Phoxinus karsticus	Trebisnjica	Bosnia and Herzegovina	MF407753	Palandačić *et al*., 2017
Phoxinus karsticus	Trebisnjica	Bosnia and Herzegovina	MF407754	Palandačić *et al*., 2017
Phoxinus karsticus	Trebisnjica	Bosnia and Herzegovina	MF407755	Palandačić *et al*., 2017
Phoxinus karsticus	Trebisnjica	Bosnia and Herzegovina	MF407756	Palandačić *et al*., 2017
Phoxinus karsticus	Orahovstica	Montenegro	MF407757	Palandačić *et al*., 2017
Phoxinus karsticus	Zalomka	Bosnia and Herzegovina	MF407758	Palandačić *et al*., 2017
Phoxinus karsticus	Zalomka	Bosnia and Herzegovina	MF407759	Palandačić *et al*., 2017
Phoxinus karsticus	Zalomka	Bosnia and Herzegovina	MF407760	Palandačić *et al*., 2017
Phoxinus karsticus	Moraca	Montenegro	MF407761	Palandačić *et al*., 2017
Phoxinus karsticus	Moraca	Montenegro	MF407762	Palandačić *et al*., 2017
Phoxinus karsticus	Moraca	Montenegro	MF407763	Palandačić *et al*., 2017
Phoxinus karsticus	Moraca	Montenegro	MF407764	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	KJ554125	Geiger *et al*., 2014
Phoxinus lumaireul	Po	Italy	KJ554282	Geiger *et al*., 2014
Phoxinus lumaireul	Po	Italy	KJ554304	Geiger *et al*., 2014
Phoxinus lumaireul	Isonzo	Slovenia	MF407787	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407788	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407789	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407790	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407791	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407792	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407793	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407794	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407795	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407796	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407797	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407798	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407799	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407800	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407801	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407802	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407803	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407804	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407805	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407806	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407807	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407808	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407809	Palandačić *et al*., 2017

Appendix. Continued

Species	Drainage	Country	GenBank	Reference
Phoxinus lumaireul	Po	Italy	MF407810	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407811	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407812	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407813	Palandačić *et al*., 2017
Phoxinus lumaireul	Baska	Croatia	MF407814	Palandačić *et al*., 2017
Phoxinus lumaireul	Baska	Croatia	MF407815	Palandačić *et al*., 2017
Phoxinus lumaireul	Baska	Croatia	MF407816	Palandačić *et al*., 2017
Phoxinus lumaireul	Baska	Croatia	MF407817	Palandačić *et al*., 2017
Phoxinus lumaireul	Lake Krn	Slovenia	MF407818	Palandačić *et al*., 2017
Phoxinus lumaireul	Lake Krn	Slovenia	MF407819	Palandačić *et al*., 2017
Phoxinus lumaireul	Lake Krn	Slovenia	MF407820	Palandačić *et al*., 2017
Phoxinus lumaireul	Lake Krn	Slovenia	MF407821	Palandačić *et al*., 2017
Phoxinus lumaireul	Lake Krn	Slovenia	MF407822	Palandačić *et al*., 2017
Phoxinus lumaireul	Malinska	Slovenia	MF407824	Palandačić *et al*., 2017
Phoxinus lumaireul	Malinska	Slovenia	MF407825	Palandačić *et al*., 2017
Phoxinus lumaireul	Malinska	Slovenia	MF407826	Palandačić *et al*., 2017
Phoxinus lumaireul	Malinska	Slovenia	MF407827	Palandačić *et al*., 2017
Phoxinus lumaireul	Malinska	Slovenia	MF407828	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407829	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407830	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407831	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407832	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407833	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407834	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407835	Palandačić *et al*., 2017
Phoxinus lumaireul	Nanoscica	Slovenia	MF407836	Palandačić *et al*., 2017
Phoxinus lumaireul	Nanoscica	Slovenia	MF407837	Palandačić *et al*., 2017
Phoxinus lumaireul	Nanoscica	Slovenia	MF407838	Palandačić *et al*., 2017
Phoxinus lumaireul	Nanoscica	Slovenia	MF407839	Palandačić *et al*., 2017
Phoxinus lumaireul	Nanoscica	Slovenia	MF407840	Palandačić *et al*., 2017
Phoxinus lumaireul	Nanoscica	Slovenia	MF407842	Palandačić *et al*., 2017
Phoxinus lumaireul	Notranjska Reka	Croatia	MF407843	Palandačić *et al*., 2017
Phoxinus lumaireul	Osapska	Slovenia	MF407844	Palandačić *et al*., 2017
Phoxinus lumaireul	Osapska	Slovenia	MF407845	Palandačić *et al*., 2017
Phoxinus lumaireul	Podgora by Loz	Slovenia	MF407846	Palandačić *et al*., 2017
Phoxinus lumaireul	Podgora by Loz	Slovenia	MF407847	Palandačić *et al*., 2017
Phoxinus lumaireul	Podgora by Loz	Slovenia	MF407848	Palandačić *et al*., 2017
Phoxinus lumaireul	Podgora by Loz	Slovenia	MF407849	Palandačić *et al*., 2017
Phoxinus lumaireul	Podgora by Loz	Slovenia	MF407850	Palandačić *et al*., 2017
Phoxinus lumaireul	Podgora by Loz	Slovenia	MF407851	Palandačić *et al*., 2017
Phoxinus lumaireul	Predjama	Slovenia	MF407852	Palandačić *et al*., 2017
Phoxinus lumaireul	Predjama	Slovenia	MF407853	Palandačić *et al*., 2017
Phoxinus lumaireul	Predjama	Slovenia	MF407854	Palandačić *et al*., 2017
Phoxinus lumaireul	Predjama	Slovenia	MF407855	Palandačić *et al*., 2017
Phoxinus lumaireul	Predjama	Slovenia	MF407856	Palandačić *et al*., 2017
Phoxinus lumaireul	Predjama	Slovenia	MF407857	Palandačić *et al*., 2017
Phoxinus lumaireul	Rizana	Slovenia	MF407858	Palandačić *et al*., 2017
Phoxinus lumaireul	Rizana	Slovenia	MF407859	Palandačić *et al*., 2017

Appendix. Continued

Species	Drainage	Country	GenBank	Reference
Phoxinus lumaireul	Rizana	Slovenia	MF407860	Palandačić *et al*., 2017
Phoxinus lumaireul	Rizana	Slovenia	MF407861	Palandačić *et al*., 2017
Phoxinus lumaireul	Rizana	Slovenia	MF407862	Palandačić *et al*., 2017
Phoxinus lumaireul	Rizana	Slovenia	MF407863	Palandačić *et al*., 2017
Phoxinus lumaireul	Rizana	Slovenia	MF407864	Palandačić *et al*., 2017
Phoxinus lumaireul	Rizana	Slovenia	MF407865	Palandačić *et al*., 2017
Phoxinus lumaireul	Rizana	Slovenia	MF407866	Palandačić *et al*., 2017
Phoxinus lumaireul	Rizana	Slovenia	MF407867	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407868	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407869	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407870	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407871	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407872	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407873	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407874	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407875	Palandačić *et al*., 2017
Phoxinus lumaireul	Po	Italy	MF407876	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407877	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407878	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407879	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407880	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407881	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407882	Palandačić *et al*., 2017
Phoxinus lumaireul	Isonzo	Slovenia	MF407883	Palandačić *et al*., 2017
Phoxinus lumaireul	Zrmanja	Croatia	MF407884	Palandačić *et al*., 2017
Phoxinus marsilii	Oder	Czech Republic	HQ960812	Mendel *et al*., 2012
Phoxinus marsilii	Oder	Czech Republic	HQ960813	Mendel *et al*., 2012
Phoxinus marsilii	Oder	Czech Republic	HQ960814	Mendel *et al*., 2012
Phoxinus marsilii	Oder	Czech Republic	HQ960815	Mendel *et al*., 2012
Phoxinus marsilii	Elbe	Czech Republic	HQ960816	Mendel *et al*., 2012
Phoxinus marsilii	Danube	Czech Republic	HQ960893	Mendel *et al*., 2012
Phoxinus marsilii	Danube	Czech Republic	HQ960910	Mendel *et al*., 2012
Phoxinus marsilii	Danube	Czech Republic	HQ960931	Mendel *et al*., 2012
Phoxinus marsilii	Danube	Czech Republic	HQ960937	Mendel *et al*., 2012
Phoxinus marsilii	Danube	Czech Republic	HQ960939	Mendel *et al*., 2012
Phoxinus marsilii	Danube	Austria	MF407956	Palandačić *et al*., 2017
Phoxinus marsilii	Vistula	Poland	MF407957	Palandačić *et al*., 2017
Phoxinus marsilii	Vistula	Poland	MF407958	Palandačić *et al*., 2017
Phoxinus marsilii	Vistula	Poland	MF407959	Palandačić *et al*., 2017
Phoxinus marsilii	Vistula	Poland	MF407960	Palandačić *et al*., 2017
Phoxinus marsilii	Vistula	Poland	MF407961	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Hungary	MF407962	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Hungary	MF407963	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Hungary	MF407964	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Hungary	MF407965	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Hungary	MF407966	Palandačić *et al*., 2017
Phoxinus marsilii	Oder	Poland	MF407967	Palandačić *et al*., 2017
Phoxinus marsilii	Oder	Poland	MF407968	Palandačić *et al*., 2017

Appendix. Continued

Species	Drainage	Country	GenBank	Reference
Phoxinus marsilii	Oder	Poland	MF407969	Palandačić *et al*., 2017
Phoxinus marsilii	Oder	Poland	MF407970	Palandačić *et al*., 2017
Phoxinus marsilii	Oder	Poland	MF407971	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Poland	MF407972	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Poland	MF407973	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Poland	MF407974	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Poland	MF407975	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Poland	MF407976	Palandačić *et al*., 2017
Phoxinus marsilii	Vistula	Poland	MF407977	Palandačić *et al*., 2017
Phoxinus marsilii	Vistula	Poland	MF407978	Palandačić *et al*., 2017
Phoxinus marsilii	Vistula	Poland	MF407979	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Hungary	MF407980	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Hungary	MF407981	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Hungary	MF407982	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Hungary	MF407983	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Hungary	MF407984	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407985	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407986	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407987	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407988	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407989	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407990	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407991	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407992	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407993	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407994	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407995	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407996	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407997	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407998	Palandačić *et al*., 2017
Phoxinus marsilii	Danube	Austria	MF407999	Palandačić *et al*., 2017
Phoxinus phoxinus	Rhine	Germany	KM286804	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286811	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286812	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286813	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286814	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286815	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286816	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286817	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286818	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286819	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286820	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286821	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286822	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286823	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286825	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286826	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286827	Knebelsberger *et al*., 2015

Appendix. Continued

Species	Drainage	Country	GenBank	Reference
Phoxinus phoxinus	Rhine	Germany	KM286828	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286829	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286830	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286831	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286832	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286834	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286835	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286837	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286840	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286841	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286842	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286843	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286844	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286845	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286846	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286851	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286852	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286858	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286863	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286864	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286865	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286866	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286868	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286874	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286882	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286883	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286884	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286886	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286887	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286888	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286889	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286900	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286901	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286902	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286903	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286906	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286908	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286909	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286911	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286912	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286914	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286922	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286926	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286930	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286936	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286938	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286940	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286941	Knebelsberger *et al*., 2015

Appendix. Continued

Species	Drainage	Country	GenBank	Reference
Phoxinus phoxinus	Rhine	Germany	KM286942	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286943	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286946	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286949	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286962	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286969	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM286992	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KM287014	Knebelsberger *et al*., 2015
Phoxinus phoxinus	Boyne	Ireland	KU729256	Behrens-Chapuis *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KU729257	Behrens-Chapuis *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	KU729258	Behrens-Chapuis *et al*., 2015
Phoxinus phoxinus	Rhine	Germany	MF407768	Palandačić *et al*., 2017
Phoxinus phoxinus	Rhine	Germany	MF407769	Palandačić *et al*., 2017
Phoxinus phoxinus	Rhine	Germany	MF407770	Palandačić *et al*., 2017
Phoxinus phoxinus	Rhine	Germany	MF407771	Palandačić *et al*., 2017
Phoxinus phoxinus	Rhine	Germany	MF407772	Palandačić *et al*., 2017
Phoxinus phoxinus	Rhine	Germany	MF407773	Palandačić *et al*., 2017
Phoxinus phoxinus	Rhine	Germany	MF407774	Palandačić *et al*., 2017
Phoxinus phoxinus	Rhine	Germany	MF407775	Palandačić *et al*., 2017
Phoxinus phoxinus	Rhine	Germany	MF407776	Palandačić *et al*., 2017
Phoxinus phoxinus	Rhine	Germany	MF407777	Palandačić *et al*., 2017
Phoxinus phoxinus	Rhine	Germany	MF407778	Palandačić *et al*., 2017
Phoxinus strandjae	Sakarya	Turkey	KJ554187	Geiger *et al*., 2014
Phoxinus strandjae	Rezovska	Bulgaria	KU729264	Behrens-Chapuis *et al*., 2015
Phoxinus strymonicus	Struma	Greece	KJ554101	Geiger *et al*., 2014
Phoxinus strymonicus	Struma	Greece	KJ554135	Geiger *et al*., 2014
Phoxinus strymonicus	Struma	Greece	KJ554301	Geiger *et al*., 2014
Phoxinus strymonicus	Struma	Greece	KJ554359	Geiger *et al*., 2014
Phoxinus strymonicus	Struma	Greece	KJ554386	Geiger *et al*., 2014
Phoxinus septimaniae	Roya	France	KJ554137	Geiger *et al*., 2014
Phoxinus septimaniae	Rhone	France	KJ554141	Geiger *et al*., 2014
Phoxinus septimaniae	Herault	France	KJ554383	Geiger *et al*., 2014
Phoxinus septimaniae	Herault	France	KJ554474	Geiger *et al*., 2014
Phoxinus septimaniae	Aude	France	KJ554499	Geiger *et al*., 2014
Phoxinus septimaniae	Var	France	KJ554504	Geiger *et al*., 2014
Phoxinus septimaniae	Agly	France	KJ554507	Geiger *et al*., 2014
Phoxinus septimaniae	Aude	France	KJ554531	Geiger *et al*., 2014
Phoxinus septimaniae	Rhine	Germany	KM286838	Knebelsberger *et al*., 2015
Phoxinus septimaniae	Rhine	Germany	KM286839	Knebelsberger *et al*., 2015
Phoxinus septimaniae	Rhine	Germany	KM286867	Knebelsberger *et al*., 2015
Phoxinus septimaniae	Rhine	Germany	KM286955	Knebelsberger *et al*., 2015
Phoxinus septimaniae	Rhine	Germany	MF407779	Palandačić *et al*., 2017
Phoxinus septimaniae	Rhone	Switzerland	MF407780	Palandačić *et al*., 2017
Phoxinus septimaniae	Rhone	Switzerland	MF407781	Palandačić *et al*., 2017
Phoxinus septimaniae	Po	Italy	MF407782	Palandačić *et al*., 2017
Phoxinus septimaniae	Po	Italy	MF407783	Palandačić *et al*., 2017
Phoxinus septimaniae	Po	Italy	MF407784	Palandačić *et al*., 2017
Phoxinus septimaniae	Rhone	France	MF407785	Palandačić *et al*., 2017
Phoxinus septimaniae	Rhone	France	MF407786	Palandačić *et al*., 2017