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Potentially zoonotic parasite arrives to continental France: *Clinostomum complanatum* (Trematoda: Digenea) infection in perch (*Perca fluviatilis*) from the Doubs River (Jura)

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Abstract: *Clinostomum complanatum* (Rudolphi, 1814) is known as a food-borne zoonotic parasite using freshwater fish as intermediate host, although in its native distribution area in Europe, the Danube and Po basins and the northeast of Italy, no cases have been reported. This study reports a new geographic location outside the native distribution range of this parasite. We detected high infection levels of *C. complanatum* in wild perch (*Perca fluviatilis* Linnaeus) from the Doubs River in continental France. *Clinostomum complanatum* reached a prevalence of 97% and mean intensity of 5.8 cysts per fish in 33 fish examined, with most fish already infected by the age of two years. No correlations were observed between fish traits (standard length, weight, age and sex) and the number of parasites. The distribution of *C. complanatum* cysts in the fish body was not random. The tissue surrounding the opercula and branchial cavity, and muscles along the lateral line and near the pectoral, dorsal and caudal fins were the preferred sites of infection. Morphological identification was confirmed with molecular data. The French specimens shared identical mt *cox*1 haplotypes with specimens from Italy. The distribution of this exotic parasite in freshwaters in continental France deserves further research. Under the current French law, the parasite occurrence represents an economic loss for the local freshwater aquaculture industry, and a possible zoonotic risk for consumers if undetected, especially when raw or marinated fish is consumed. We provided a list of all reported hosts for *C. complanatum* from the western Palaearctic, discussed the knowledge gap regarding the zoonotic risk of *C. complanatum* in Europe, and highlighted the lack of policy that may increase the hazards posed by food-borne emerging parasites and their broader ecological impacts as alien species in freshwaters in Europe.

Keywords: Platyhelminthes, alien species, Halzoun syndrome, food-borne disease, freshwater ecosystems, cytochrome c oxidase subunit I mitochondrial gene, 28S rRNA gene

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Alien species cause substantial negative impacts on species biodiversity and human livelihoods worldwide (Simberloff et al. 2013, Bacher et al. 2018, Brondizio et al. 2019), but their numbers keep rising (Seebens et al. 2017, 2018). Alien parasite species may be introduced inadvertently with their free-living hosts or independently (Goedknegt et al. 2016), and can lead to emerging diseases in the new ecosystems (Dunn and Hatcher 2015). Currently, the limited international policy on invasive species and parasites of wildlife hampers the capacity of managers to take action. Policy provides a framework for managers to allocate resources to assess and control the impacts related to parasite emerging diseases linked to changes in species distributions (Dunn and Hatcher 2015), for instance the hazards of emerging zoonosis.

The trematode *Clinostomum complanatum* (Rudolphi, 1814) is a freshwater parasite species with zoonotic potential (Sutili et al. 2014). This species has a complex taxonomic history (Matthews and Cribb 1998). Braun (1901) re-described *C. complanatum* (the "European type") and *Clinostomum marginatum* (Rudolphi, 1819) (the "American type") and accepted them as valid species, but their validity and priority has been disputed until recently. Their distinct status was demonstrated with convincing morphological, ecological and molecular data for the internal transcribed spacers of the ribosomal RNA (rRNA) gene and the mitochondrial cytochrome oxidase subunit 1 (*cox*1) gene (Dzikowski et al. 2004a, Caffara et al. 2011, Sereno-Uribe et al. 2013).

The European *C. complanatum* sensu lato (s.l.) was considered to have a Palearctic distribution, but later it was

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found to be genetically distinct from *Clinostomum* specimens sequenced from Asia (Locke et al. 2015 and references therein). *Clinostomum* sp. 8 of Locke et al. (2015) from China appeared as sister lineage to *C. complanatum* based on divergent sequences for the *cox*1 gene (Locke et al. 2015). However, *C. complanatum* s.l. continued to be used as a 'catch all' name for later records of *Clinostomum* in East Asia (Chen et al. 2016, Wang et al. 2017, Iwaki et al. 2018, Li et al. 2018). Only recently, the East Asian specimens of *Clinostomum complanatum* s.l. have been described as a separate species, *Clinostomum sinensis* Locke, Caffara, Barčák, Sonko, Tedesco, Fioravanti et Li, 2019 on the basis of some morphological characters of the metacercaria infecting fish, the eggs of adults from great cormorants, as well as molecular divergence in the *cox*1 and the ITS2 rDNA region, although less conspicuous in the latter (Locke et al. 2019).

Additional information from adults and a larger sampling across East Asia, as suggested by the latter authors, would help strengthen these preliminary results. Thus, the native distribution of *C. complanatum* sensu stricto (s.s.) is circumscribed to Central-East Europe along the Danube basin, the Po basin, the northeastern Italy, Turkey, Israel and Iran (e.g., Fedorčák et al. 2019, Juhásová et al. 2019, Locke et al. 2019, Menconi et al. 2020, Monnens et al. 2023). However, in the recent years *C. complanatum* s.s. has been reported outside its native distribution, infecting introduced perch in Corsica (Esposito et al. 2024), in Croatia (Gjurčević et al. 2022 and references therein) and in live bait from northern Italy used in Sicily (Gaglio et al. 2016).

The definitive hosts for *C. complanatum* s.s. are fish-eating birds, in particular of the Ardeidae and Phalacrocoracidae (Moszczynska et al. 2009, Caffara et al. 2011, Sereno-Uribe et al. 2013), in which the adults reside in the mouth cavity and oesophagus. The first intermediate host of *C. complanatum* s.s. are freshwater snails, such as *Radix auricularia* (Linnaeus), *R. euphratica* (Mousson), *R. ovata* (Draparnaud) and *Lymnaea stagnalis* (Linnaeus) reported from Germany or Iran (Hosseini 1987, Kalantan et al. 1987, Sharif et al. 2010, Gaglio et al. 2016), whereas the second intermediate hosts are a broad range of species of freshwater fishes and amphibians (Cojocaru 2003, Caffara et al. 2011).

The accurate identification of *Clinostomum* specimens and the taxonomic status of *Clinostomum* spp. are important because *C. complanatum* s.l. has been reported to cause a zoonotic disease known as Halzoun syndrome (Sutili et al. 2014). Most of these reports originate from Asia and thus they may correspond to *C. sinensis.* However at least one case occurred in Israel (Witenberg 1944). Humans become infected when eating raw or undercook fish flesh with encysted metacercariae (Park et al. 2009, Hara et al. 2014).

In humans, the parasite tends to locate and feed on the mucosa of the pharynx causing pharyngitis, for which no therapeutic drug can be yet applied (Park et al. 2009). Thus, mechanical removal is necessary (Sutili et al. 2014). In addition to human disease risks, infections by 'yellow grub', as this parasite is colloquially known, have a serious economic impact on fish farming (Liu 1979, Lo et al. 1981, Silva-Souza and Ludwig 2005) making the fish unappealing to the consumer and resulting in discard of carcasses during inspection (Brandão 2004; F. Pozet, personal communication).

In December 2019, a parasite infection in the flesh of European perch (*Perca fluviatilis*) was reported by a local angler, and preliminarily identified at the Departmental Analysis Laboratory of the Jura Franche-Comté as resembling to *C. complanatum*. The exotic status of this parasite in France prompted us, in collaboration with the fisheries authorities, to carry out this study. The main aims were to (i) report the infection of *C. complanatum* metacercariae in perch of different age classes from the Doubs River, (ii) assess the microhabitat distribution of the parasite in the fish, and (iii) confirm the identification of the species using molecular data. We also reviewed the records of *C. complanatum* in the western Palaearctic to evaluate the species host range and distribution. We further discussed the lack of knowledge on its zoonotic potential in Europe and the gaps in policy that increase the hazards of food-borne emerging parasites and their broader ecological impacts as alien species in European freshwaters.

MATERIALS AND METHODS

Study area and fish sampling

European perch were collected by angling from a small navigation canal between the Rhône and Rhine Rivers at Orchamps (France; 47.140225 N, 5.673275E) adjacent to the Doubs River, a transboundary river between eastern France and Switzerland in its upper part. The sampling site was 327 m long and has an area of 4750 m^2. A total of 33 perch specimens were collected in November 2020 using angling, euthanised by anoxia by Jura Departmental Federation of Approved Associations for Fishing and Protection of the Aquatic Environment (AAPPAM). Fish were brought to the Departmental Analysis Laboratory (LDA) of Jura for dissection and veterinary analysis shortly after. Measurements of fish standard and total length, weight, sex and age (by counting the number of annuli [rings] on a scale) were recorded for each specimen before parasitological examination.

Fish dissection and parasite examination

Fresh fish were dissected by removing the skin and filleting the flesh in thin layers which were first examined by naked eye and then under a stereomicroscope. All muscular tissues and particularly the tissues at the base of fins were examined for encysted parasites. Metacercariae were collected alive, removed from the cyst and fixed in 100% ethanol for molecular analyses, or in formalin for morphological identification (Cribb and Bray 2010, Justine et al. 2012).

Molecular data generation

DNA from four specimens was extracted using Chelex® in deionised water containing 0.1 mg/ml proteinase K. A partial fragment of the large ribosomal subunit (28S rRNA gene) was chosen for amplification since this marker is broadly used to distinguish species of trematode flatworms (Blasco-Costa et al. 2016). The following primers were used for amplification U178

[5'–GCA CCC GCT GAA YTT AAG– 3'] and L1642R [5' –CCA GCG CCA TCC ATT TTC A–3'] (Lockyer et al. 2003). The polymerase chain reaction (PCR) amplification protocol followed Blasco-Costa et al. (2009).

Additionally, a more variable marker, the cytochrome c oxidase subunit I mitochondrial gene (*cox*1), was also amplified using PlagDiploCO1hF [5'–ACG TTG GAT CAY AAG CG– 3'] (Blasco-Costa et al. 2014) and Plag16S-CO1dR [5'–TCG GGG TCT TTC CGT CT– 3'] (Blasco-Costa et al. 2012). The PCR amplification was run in a 20 µl reaction mixture containing 4 µl of DNA template, 10 µl of 2x MyFi™ (enzyme from Bioline, Meridian Bioscience Inc., Cincinnati, United States of America), 4.4 µl of deionised water, and 0.8 µl of each forward and reverse primers for a final concentration of 4 pmol/µl. PCR reactions ran for 35 cycles under the following conditions: denaturing at 94 °C for 50 s, annealing at 55 °C for 50 s, and extension at 72 °C for 60 s. The 35 cycles were preceded by an initial denaturation at 94 °C for 3 min, and followed by a final extension of 72 °C for 10 min.

After verification of single band PCR products via electrophoresis, amplicons were purified with a mix of exonuclease I and thermosensitive alkaline phosphatase enzymes (Werle et al. 1994). Purified amplicons were sent to Macrogen Europe (Amsterdam, Netherlands) for sequencing from both strands with the same PCR primers used for amplification (U178/L1642R and PlagDiploCOIhF/PlagCO1dR). An additional internal primer for the *cox*1 mtDNA, the reverse CO1-Trema [5'– CAA CAA ATC ATG ATG CAA AAGG –3'] (Miura et al. 2005) was also used.

Alignments and phylogenetic analyses

Sequences were assembled and inspected for errors in Geneious 8.1.9. Available sequences for representative taxa belonging to *Clinostomum* species were extracted from GenBank and aligned together with our sequences using MAFFT (Katoh et al. 2005) implemented in Geneious to confirm the species identity of our specimens. As outgroup, sequences of a sister taxon outside the genus (*Diplostomum* spp. for the 28S analysis [KR269765 and KR269766], and *Euclinostomum* spp. for the *cox* [KC894795 and KP721404] were included in each alignment based on previous studies (Locke et al. 2019). The newly generated sequences were submitted to GenBank (accession numbers PQ365666–PQ365669 and OP580488). Additionally, the genetic divergence (p-distance) between *Clinostomum* spp. was assessed using Geneious.

The phylogenetic relationships were investigated using maximum likelihood (ML) and Bayesian inference (BI) criteria and the analyses carried out in the public computational resource CIPRES (Miller et al. 2010). The best nucleotide substitution model for ML analysis was selected using JModelTest (GTR + GAMMA for 28S rDNA dataset and GTR + CAT for the *cox*1).

Maximum likelihood analyses were conducted using the programme RAxML ver. 8 (Stamatakis 2006) with all model parameters and bootstrap nodal support values (1000 repetitions) estimated from the programme. BI phylogenies were constructed using MrBayes 3.2.6 (Ronquist et al. 2012), running two independent Markov Chain Monte Carlo runs of four chains for ten million generations and sampling tree topologies every 1000th generations. Burn-in periods were automatically set to 25% of generations. The tree generated using maximum likelihood criteria was used for the representation in our figure with the Bootstrap support values and Bayesian posterior probabilities.

Haplotype network analysis

The frequency and relationship of each unique haplotype of *Clinostomum complanatum* and *C. sinensis* in the *cox*1 alignment (362 bp long), including all the sequences available in GenBank and three newly generated sequences, were assessed using integer Neighbour-Joining network in PopART v1.7 (Leigh and Bryant 2015). The geographic origin of each sequence was used as grouping variable.

Infection data and statistical analysis

Basic infection descriptors, such as prevalence (%), mean abundance (MA) and the range of the intensity of infection, were calculated as described by Bush et al. (1997) for the parasite infrapopulations in 33 European perch. The correlation between cyst abundance and fish standard length, weight, age and sex was run using the correlation function cor() in R (R 3.6.2 version, Development Core Team, 2016) using the Pearson correlation coefficient. Cyst localisation schemes for each individual fish were loaded in Image J v1.8.0 v (NIH, USA, available at https://wsr.imagej.net/distros/win/ij153-win-java8.zip) and the XY coordinates of each cyst were recorded. In order to visualise the areas of preferential localisation of cysts in the fish the XY coordinates were projected onto a 2D density heatmap using the ggplot2 R package (Wickham 2009), in the R statistical environment.

RESULT

Host range and distribution of *Clinostomum complanatum* in Europe and Middle East

The compilation of all records of *Clinostomum complanatum* from the literature in Europe and Middle East resulted in a total of 43 reported host species (Table 1). The list of hosts includes four molluscs from three genera (*Ampullaceana* Servain, *Lymnaea* Lamarck and *Radix* Montfort) as first intermediate hosts, 30 fishes from six families (Cobitidae, Centrarchidae, Cyprinidae, Cyprinodontidae, Percidae and Odontobutidae) and two amphibians (*Lissotriton vulgaris* [Linnaeus] and *Triturus carnifex* [Laurenti]) as second intermediate hosts, six birds from three genera (*Ardea*, *Egretta* and *Nycticorax*) and one mammal (*Homo sapiens* Linnaeus in Middle East) as definitive hosts. Overall, the first intermediate and the definitive hosts of *C. complanatum* are rarely reported in the literature, whereas mentions of infection in its second intermediate hosts are much more frequent (see Table 1).

Clinostomum complanatum s.s. parasitising perch in France

The morphological examination of trematode larvae encysted in perch pointed to *Clinostomum* spp. (Fig. 1), with the worm having a large body, concave dorsally, oral sucker surrounded by collar-like fold, ventral sucker muscular and well developed. Caeca long, with sinuous wall. Testes irregular located in posterior half of body, cirrus sac and genital pore opening lateral to anterior testis (Fig. 1B,C). Ovary intertesticular and uterus intercaecal.

Table 1. Host records for *Clinostomum complanatum* (Rudolphi, 1814) in Europe and Middle East.

Family	Host species	Country	References
Mollusca: Gastropoda			
Lymnaeidae	*Lymnaea stagnalis* (Linnaeus)	Iran, Italy	Kalantan et al. (1987), Gaglio et al. (2016)
	Radix auricularia (Linnaeus)	Iran	Hosseini (1987)
	Radix euphratica (Mousson)	Iran	Sharif et al. (2010)
	Ampullaceana balthica (= *Radix ovata*) (Draparnaud)	Italy	Gaglio et al. (2016)
Fish: Actinopterygii			
Cobitidae	*Cobitis bilineata* Canestrini	Italy	Gaglio et al. (2016)
	Cobitis elongatoides Băcescu et Mayer	Ukraine, Slovakia	Žitňan (1979), Fedorčák et al. (2019)
	Cobitis taenia Linnaeus	Czech Republic, Iran, Slovakia	Vojtek (1959), Ergens and Lom (1970), Žitňan (1979), Vojtek (1981), Shamsi et al. (1997), Aghlmandi et al. (2018)
	Misgurnus fossilis (Linnaeus)	Ukraine, Slovakia	Movchan and Smirnov (1988), Oros and Hanzelová (2009)
Centrarchidae	*Lepomis gibbosus* (Linnaeus)	Italy	Caffara et al. (2011), Locke et al. (2015)
Cyprinoidei	*Alburnoides bipunctatus* (Bloch)	Iran	Shamsi et al. (1997), Aghlmandi et al. (2018)
	Alburnus mossulensis Heckel	Iran	Maleki et al. (2018)
	Barbus barbus (Linnaeus)	Italy	Caffara et al. (2011), Locke et al. (2015)
	Barbus meridionalis Risso	Italy	Caffara et al. (2011), Locke et al. (2015)
	Barbus sp.	Iran	Hosseini (1987)
	Capoeta capoeta (Güldenstädt)	Iran	Shamsi et al. (1997), Malek and Mobedi (2001), Monnens et al. (2023)
	Capoeta damascina (Valenciennes)	Iran	Maleki et al. (2018)
	Capoeta gracilis (Keyserling)	Iran	Aghlmandi et al. (2018)
	Carasobarbus canis (Valenciennes)	Israel	Dzikowski et al. (2004a)
	Carassius auratus (Linnaeus)	Iran	Hosseini (1987)
	Cyprinus carpio Linnaeus	Croatia, Iran, Russia	Dubinina (1949), Hosseini (1987), Gjurčević et al. (2022)
	Garra rufa (Heckel)	Iran	Aghlmandi et al. (2018)
	Gobio gobio (Linnaeus)	Romania	Cojocaru (2003)
	Gobio sp.	Romania	Cojocaru (2009)
	Pseudorasbora parva (Temminck et Schlegel)	Iran, Romania	Malek and Mobedi (2001), Cojocaru (2003)
	Rhodeus amarus (Bloch)	Czech Republic	Gelnar et al. (1994), Kadlec et al. (2003), Dávidová et al. (2008), Francová and Ondračková (2013)
	Rutilus rutilus (Linnaeus)	Poland, Romania	Grabda-Kazubska (1974), Cojocaru (2003)
	Rutilus sp.	Romania	Cojocaru (2009)
	Scardinius erythrophthalmus (Linnaeus)	Romania, Slovakia	Ergens and Lom (1970), Ergens et al. (1975), Vojtek (1981), Cojocaru (2003), Locke et al. (2019)
	Squalius cephalus (Linnaeus)	Croatia, Iran, Italy, Romania	Shamsi et al. (1997), Cojocaru (2003), Cojocaru (2009), Caffara et al. (2011), Locke et al. (2015), Aghlmandi et al. (2018), Maleki et al. (2018), Gjurčević et al. (2022)
Cyprinodontidae	*Aphanius dispar* (Rüppell)	Iran, Saudi Arabia	Kalantan et al. (1986, 1987), Hosseini (1987)
Percidae	*Gymnocephalus cernua* (Linnaeus)	Hungary	Molnár (1966)
	Perca fluviatilis Linnaeus	Bulgaria, Corsica, France, Italy, Poland, Romania, Serbia	Ergens and Lom (1970), Grabda-Kazubska (1974), Vojtek (1981), Cojocaru (2003), Goga and Codreanu–Bălcescu (2011), Djikanovic et al. (2012), Juhásová et al. (2019), Locke et al. (2019), Menconi et al. (2020), Esposito et al. (2024) and this study
Odontobutidae	*Perccottus glenii* Dybowski	Hungary	Antal et al. (2015)
	"many freshwater fishes"	Romania, Ukraine	Yamaguti (1958, 1971), Davydov et al. (2011)
Amphibians: Amphibnia			
Salamandridae	*Lissotriton vulgaris* (Linnaeus)	Italy	Caffara et al. (2014), Locke et al. (2015)
	Triturus carnifex (Laurenti)	Italy	Caffara et al. (2014), Locke et al. (2015)
Birds: Aves			
Ardeidae	*Ardea alba* Linnaeus	Iran	Shamsi et al. (2013)
	Ardea cinerea Linnaeus	Germany, Iran, Slovakia	Rudolphi (1819), Yamaguti (1958, 1971), Hosseini (1987)
	Ardea purpurea Linnaeus	Iran	Macko (1960), Shamsi et al. (2013)
	Ardea spp.	Poland, Russia	Shigin (1957), Grabda-Kazubska (1974)
	Egretta garzetta (Linnaeus)	Iran	Dzikowski et al. (2004a,b), Shamsi et al. (2013)
	Nycticorax nycticorax (Linnaeus)	Iran	Shamsi et al. (2013), Monnens et al. (2023)
Mammal: Mammalia			
Hominidae	*Homo sapiens* Linnaeus	Israel	Witenberg (1944)

The molecular analyses confirmed the species level identification as *C. complanatum* based on the mt *cox*1 fragment. Both, the haplotype network analysis and phylogeny based on the *cox*1 mtDNA gene showed that our specimens of *C. complanatum* are more closely related to the Italian population of *C. complanatum* s.s. (Fig. 2B,C). *cox*1 sequence divergence amongst the French specimens was 0% to 0.2% whereas the divergence from the Italian, Turkish, Romanian and Iranian sequences was 0–0.6%, 0.2–0.6%, 0.6–1.0% and 0.4–1.0%, respectively. In contrast, the French specimens differed 2.8–3.2% from those of *Clinostomum sinensis* (previously *C. complanatum* s.l.) from China and Taiwan.

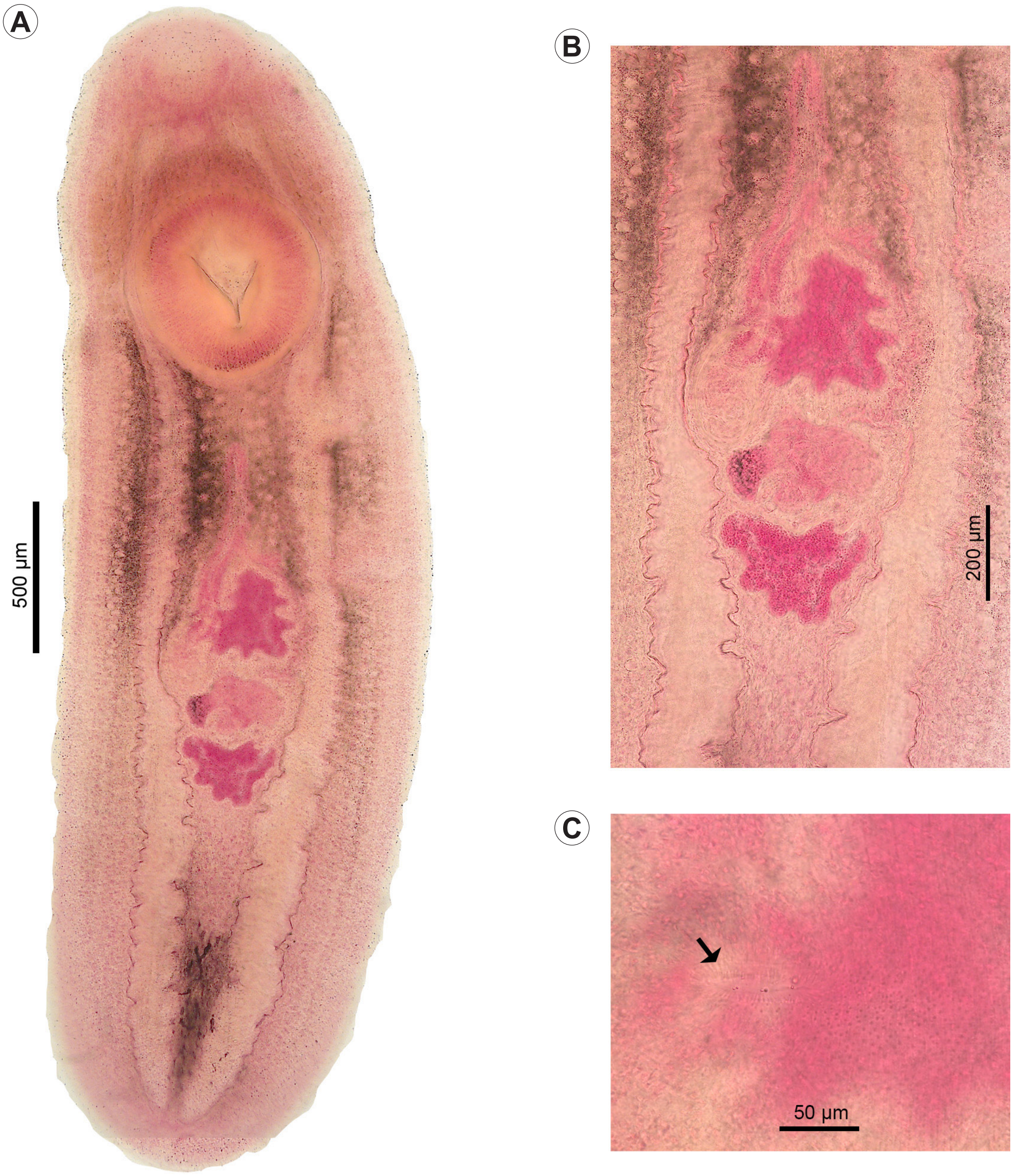


Fig. 1. Microphotographs of *Clinostomum complanatum* (Rudolphi, 1814) s.s. **A** – whole-mounted specimen from *Perca fluviatilis* Linnaeus, Doubs River at Orchamps (France), stained with iron-acetic carmine; **B** – close up microphotograph of the genitalia; **C** – view of the genital pore opening lateral to anterior testis.

Infection prevalence in perch was very high, up to 97% of the individuals were infected with metacercariae of *C. complanatum*, and only one out of 33 perch was free of cysts (Fig. 3). The examination of the infection abundance as a function of fish age showed that most infections occurred in the first two years. Thereafter, the number of infections remained relatively stable between years 2 and 3 (Fig. 3B). No correlations were observed between fish standard length, weight, age or sex and parasite abundance. However, the spatial distribution of *C. complanatum* cysts in the fish body was not random. We observed an aggregation of cysts at the level of the opercula, in the muscles located near the caudal and dorsal fins, and of the lateral line (Fig. 3A–C).

DISCUSSION

Our study provides the first record of *Clinostomum complanatum* infecting the muscle of perch from a watercourse in continental France, the Doubs River. The high prevalence of the parasite and the abundance of cysts in perch of different age classes suggest that this introduced species is already established in the area, with transmission among the hosts occurring locally. The establishment of this alien zoonotic parasite has potential implications for aquaculture and human health, especially because there exist a freshwater fishery industry and a strong culture of recreational fishing in the region.

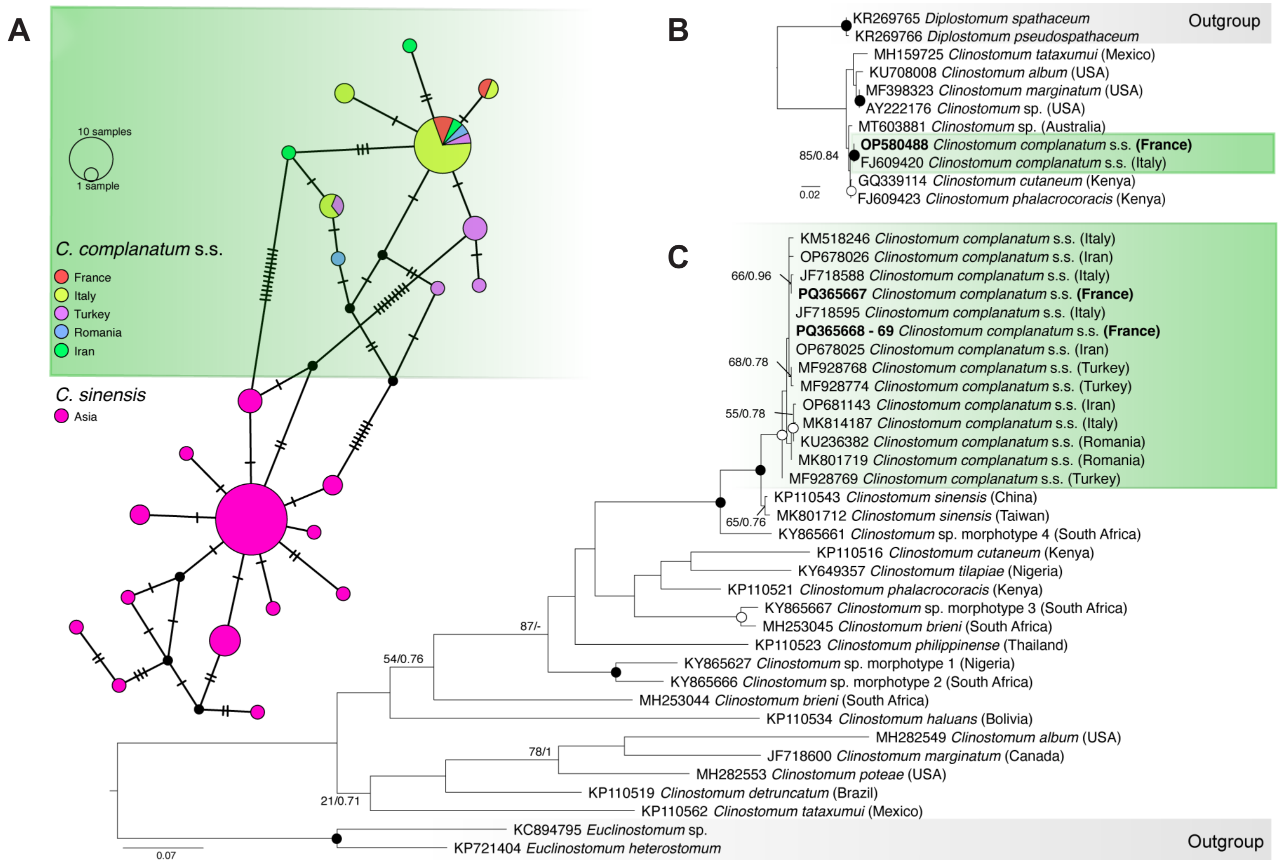


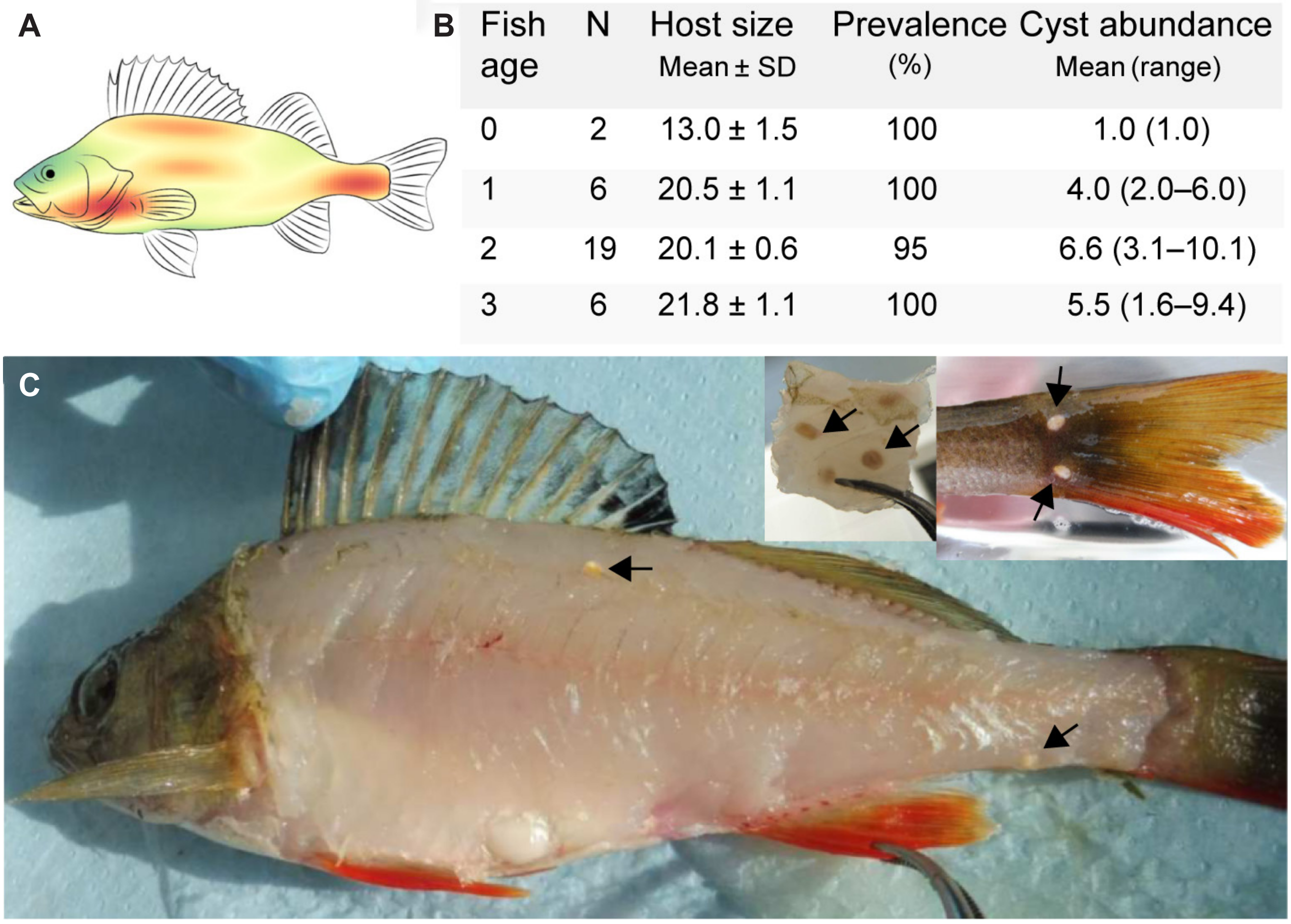
Fig. 2. Haplotype network and phylogenetic trees showing the position of the new sequences obtained for specimens of *Clinostomum complanatum* (Rudolphi, 1814) from France. **A** – neighbour-joining network of the *cox*1 haplotypes from *C. complanatum* s.s. and *C. sinensis* Locke, Caffara, Barčák, Sonko, Tedesco, Fioravanti et Li, 2019 (formerly *C. complanatum* s. l.). Haplotypes are colour-coded by geographic origin, with circle-size proportional to the number of individuals sampled with such haplotype. Each hatch mark or black dots between the haplotypes corresponds to a nucleotide substitution representing intermediate hypothetical haplotypes not observed in the data; **B** – maximum likelihood (ML) phylogram based on 28S rDNA sequences of *C. complanatum*, as well as selected sequences of *Clinostomum* spp. from GenBank, and two sequences of *Diplostomum* spp. as outgroup; **C** – ML phylogram based on *cox*1 mtDNA gene sequences of *C. complanatum*, selected sequences of *Clinostomum* spp. from GenBank, and two sequences of *Euclinostomum* spp. as outgroup. Values indicated above the branches of the phylogenetic trees are bootstrap support (BS) values followed by Bayesian posterior probabilities (PP). Newly obtained sequences have GenBank accession numbers highlighted in bold. Full circles in the trees illustrate high support values (BS > 90, PP = 1) and empty circles illustrate moderate support (BS = 70–90, PP = 0.90–0.99). Scale bar indicates the number of substitutions per site.

The precise identification of *Clinostomum* spp. is important from a One Health perspective of food-borne trematodosis (Jenkins et al. 2015). The analysis of *cox*1 molecular sequences showed a close relationship between the French specimens of *C. complanatum* and specimens from Italy, Romania and Turkey, and confirmed that our specimens belong to *C. complanatum* s.s., rather than the sister species *Clinostomum sinensis* (formerly *C. complanatum* s. l.) from Asia.

On the one hand, *C. sinensis* (referred to as *C. complanatum* in the literature) is considered a zoonotic agent of the Halzoun syndrome (Chen et al. 2016, Wang et al. 2017, Fedorčák et al. 2019, Juhásová et al. 2019, Locke et al. 2019, Menconi et al. 2020), given the occurrence of cases in Asia where this species occurs. However, no molecular data have been obtained from specimens retrieved from human cases, nor they were deposited in collections to confirm or re-examine the identification of the parasite.

On the other hand, *C. complanatum* has not been previously reported to cause any disease in Europe. The only reported case of *C. complanatum* s.l. infecting humans outside Asia is from the Middle East, in Israel (Witenberg 1944). Given that *C. complanatum* is broadly distributed along the fly way of its definitive hosts (Monnens et al. 2023), the reported cases in Israel must correspond to *C. complanatum* s.s. Thus, further research is needed to confirm the zoonotic potential of *C. complanatum* s.s. If zoonotic cases occur in the future, it will be crucial to accurately characterise the retrieved *Clinostomum* specimens with a molecular marker sufficiently variable at the population level, such as the mt *cox*1 gene, to confirm the species identification.

Cultural differences in culinary traditions could explain the lack of zoonotic cases of *C. complanatum* in its native distribution range in Europe. Although Europeans consume less raw fish than the Asiatic population, this tendency starts to equalise with the internationalisation of Asiatic dishes with raw fish (e.g., sushi or sashimi) and the evolution of the culinary trends. Furthermore, perch is important in many gastronomic dishes and more recently,



Fish age	N	Host size Mean ± SD	Prevalence (%)	Cyst abundance Mean (range)
0	2	13.0 ± 1.5	100	1.0 (1.0)
1	6	20.5 ± 1.1	100	4.0 (2.0–6.0)
2	19	20.1 ± 0.6	95	6.6 (3.1–10.1)
3	6	21.8 ± 1.1	100	5.5 (1.6–9.4)

Fig. 3. Distribution of cysts of *Clinostomum complanatum* (Rudolphi, 1814) on the fish body and infection parameters. **A** – two dimensional density heatmap of the localisation of *C. complanatum* cysts, with reddish colour indicating the most frequent localisation of the cysts in perch (n = 33, *Perca fluviatilis* Linnaeus) and yellow-greenish colour the least contaminated areas of the fish; **B** – infection parametres according to age class based on 33 perch specimens examined (N – sample size; S.D. – standard deviation); **C** – cysts (black arrows) under the skin and in the muscle of perch as observed during dissections.

it is often prepared marinated rather than cooked (Kestemont et al. 2015). The presence of this putatively zoonotic parasite represents an additional pressure on human health in western Europe, at least locally. *Perca fluviatilis* from France and Switzerland is known to be the host of two other zoonotic parasites.

Dibothriocephalus latus (Linnaeus, 1758) is a tapeworm encysted in fish muscles that causes bothriocephalosis (Golay and Mariaux 1995, Dupouy-Camet and Yera 2015, Radačovská et al. 2020), whilst the protist *Cryptosporidium parvum* (Tyzzer, 1912) is known to cause severe diarrhoea (Certad et al. 2015). Zoonotic cases of bothriocephalosis in the neighbouring region of Switzerland were often related to the consumption of traditional preparations of marinated or undercooked perch (Dupouy-Camet and Peduzzi 2004, Scholz et al. 2009 and citations therein).

The introduction and establishment of *C. complanatum* s.s. in the French Jura poses also economic risks. The local freshwater fishery and aquaculture industries, focused mostly on the production of perch, and recreational anglers are directly impacted by the presence of this parasite. The French legislation requires the disposal of all commercialised fish with visible signs of parasite infections that are intended for human consumption (Ministère de l'agriculture et de l'alimentation Instruction technique DGAL/SDSSA/2022-307 15/04/2022), whereas European regulations only apply to marine fisheries (The European Parliament and the council of the European Union Regulation (EC) No. 853/2004). Nevertheless, other widely used practices in fishery management, aquatic conservation and restoration are exempted of these regulations. In particular, the commercialisation of fish for sustaining wild or cultured populations through stocking practices via translocation or reintroduction of fish individuals is exempted of regulations.

These common practices are poorly policed and lack control from the authorities, even though they entail numerous risks, like the spreading of parasites and diseases to the receiving ecosystems (e.g., Epifanio and Waples 2016). Mapping cyst location on the fish allowed us to identify the preferential microhabitat of infection of *C. complanatum*, including the tissue surrounding the gill operculum and gills, the muscle near the pectoral, dorsal and caudal fins, and at the lateral line. This infection sites are close to typical entry points for cercariae, via the water current through the oral cavity, gills or operculum and by attaching to the soft tissues around the base of fins and to the lateral line. Our results coincide with those reported in other fish species (e.g., *Cobitis elongatoides* Băcescu et Mayer; Fedorčák et al. 2019), and can serve to orient visual inspections conducted by veterinarian practitioners, professionals and recreational anglers to prevent further spreading of this parasite.

Parasitic alien species can be inadvertently introduced to new areas through the natural dispersion of their hosts (e.g., Poulin and De Angeli Dutra 2021), and quite often, through anthropogenic activities (Dunn 2009). For instance, the use of commercial live bait of *Cobitis bilineata* Canestrini from northern Italy was reported as a hazard for the introduction of *C. complanatum* in Sicily (Gaglio et al. 2016). Illegal introduction of perch in Corsica has resulted in the cointroduction of *C. complanatum*, both species becoming self-sustained established populations now (Esposito et al. 2024).

It is highly unlikely that the parasite was already present in France and had never been reported in the literature. The parasite cysts are easily visible to the naked eye, and perch is a frequently caught and studied fish species (it comprises more locality records for *C. complanatum* than any other intermediate host – see Table 1).

Although it is difficult to clarify the origin and mode of introduction of alien species, three scenarios seem plausible in our case study: (i) fish reintroductions for management, (ii) the use of infected live bait for fishing, and (iii) natural dispersal of bird hosts. Regardless, the arrival of this new parasite has also ecological implications for the ecosystem. A high number of cysts in fish muscle can increase fish mortality (Lo et al. 1985, Sutili et al. 2014, Wang et al. 2017). Once *C. complanatum* is established in a locality, infected definitive hosts of the Ardeidae present in the area could easily spread the parasite geographically. Furthermore, a broad fish-host range of *C. complanatum* favours survival in alien locations. Indeed, since the parasite was first recorded in 2019–2020, several other infection foci have been detected (e.g., in common rudd, *Scardinius erythrophthalmus* [Linnaeus], from a pond in the Indre department, F. Pozet – Departmental Analysis Laboratory of Jura, France, personal communication). Thus, it will be relevant to assess the extent of the distribution of *C. complanatum* in the French territory and nearby regions to prevent the emergence of food-borne zoonoses and anticipate the ecological implications of its presence.

To conclude, this first record and confirmed molecular identification of *C. complanatum* s.s. infecting perch from the French Jura adds another parasite to the list of alien species in France. Given the impact of this potentially zoonotic species for the aquaculture industry, the environment and human health in the region, broader knowledge about the extent of its distribution in France should be gathered to anticipate its consequences.

Furthermore, we highlight the lack of appropriate policy regarding the aquatic conservation management and fisheries. Due to the knowledge gap regarding the zoonotic risk of this parasite in Europe any future human cases should conduct a molecular confirmation of the infection using the mt *cox*1 marker. A better understanding of the spatial distribution, host-range and impacts as well as potential mitigation approaches of *C. complanatum* in western European waterbodies will be essential to meet the challenges of this expanding food-borne zoonosis hazard.

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