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Description and use of *Schellencandona rhodanensis* sp. n. (Ostracoda, Candoninae) to locate groundwater upwelling zones in rivers and wetlands

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Abstract – Hydrological exchanges between rivers and groundwater are essential for many ecosystem processes: identifying their location requires a set of physical, chemical and biological indicators. Here, we describe *Schellencandona rhodanensis* sp. n. (Ostracoda, Candoninae), a species highly sensitive to hydrologic exchanges in river sediment. The new species is close to *Schellencandona triquetra* (Klie, 1936), but mainly differs in the shapes of the female genital lobe and the male hemipenis. The species is described from the Rhône River watershed, where it occurs in at least five tributaries. It is a stygobite species (*i.e.* a groundwater specialist), occurring in both the main channel and associated wetlands, with a maximum abundance at depth of about 1 m below the sediment surface. While *S. triquetra* is collected in a wide range of groundwater habitats, *S. rhodanensis* sp. n. is mostly restricted to river interstitial habitats fed by groundwater. It can be used as a biological indicator of interstitial habitat stability and to locate groundwater upwellings in river bed sediment.

Keywords: Biological indicator / hyporheic habitat / ostracod biogeography / river sediment / river hydrology

1 Introduction

Rivers are in contact and exchange water with groundwater of underlying aquifers (Hynes, 1975; Ward *et al.*, 1999; Malard *et al.*, 2002). Inflow of groundwater to the river (hereafter called upwelling) plays an important role in several river functions (Hancock *et al.*, 2005). It often represents a crucial contribution to river discharge, mostly during low streamflow periods (Malard *et al.*, 1999; Hoehn, 2001). Strong groundwater inflow can control the thermal regime of river water (Wawrzyniak *et al.*, 2016; Marmonier *et al.*, 2020), the concentration of solutes such as calcium or potassium (Grasby *et al.*, 1999; Cook, 2013) and the availability of nutrients for organisms, including nitrate (Deutsch *et al.*, 2006) or silica (Ward *et al.*, 1999). Hence, locating upwelling zones in river channels and associated wetlands is key to managing river ecosystems (Boulton *et al.*, 2010; Graillot *et al.*, 2014; Dole-Olivier *et al.*, 2019).

Groundwater upwelling zones are frequently located using physical and chemical indicators including temperature (Wawrzyniak *et al.*, 2016; Dole-Olivier *et al.*, 2019), solute concentrations (Grasby *et al.*, 1999; Malard *et al.*, 2003), or gas content, such as ²²²Rn (Cook *et al.*, 2006; Marmonier *et al.*, 2020). In addition to these physical and chemical indicators, biological indicators have been increasingly used in the last

decades, because organisms integrate the environmental characteristics over their entire life cycle. They include diverse obligate groundwater species belonging to the Oligochaeta (Creuzé Des Châtelliers *et al.*, 2021), Copepoda (Di Lorenzo *et al.*, 2013; Stoch *et al.*, 2016), Amphipoda (Dole-Olivier *et al.*, 2022) as well as community level indicators (*e.g.* Malard *et al.*, 2003; Marmonier *et al.*, 2019).

In the Rhône River watershed, several interstitial species have been used as indicators of river-groundwater exchanges, such as the Amphipoda *Niphargus fontanus* Bate, 1859 in the Cèze River (Marmonier *et al.*, 2020a), the Coleoptera *Siettitia avenionensis* Guignot, 1925 in the Drôme River (Marmonier *et al.*, 2019) and the Oligochaeta *Rhyacodrilus balmensis* Juget, 1959 in the Ain River (Dole-Olivier *et al.*, 2022). In the Ostracoda, populations belonging to the genus *Schellencandona* closely related to *S. triquetra* (Klie, 1936) occur in several sites characterized by groundwater upwellings (Marmonier, 1988; Dole-Olivier and Marmonier, 1992). However, these populations have an unclear systematic status, as highlighted by Meisch (2000), that must be clarified.

In the present study, we first describe the morphology of these Rhône River populations and propose that they belong to a new species, *Schellencandona rhodanensis* sp. n. Second, we document the biogeographical distribution and the ecological requirements of the new species and test the hypothesis of a link with groundwater upwellings in rivers and wetlands.

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Finally, we discuss the use of *S. rhodanensis* sp. n. as an indicator for the location of river-groundwater exchanges at the scale of the river landscape.

2 Methods

In the present work, we re-analysed already published data set containing samples from several ecological research programmes carried out in the Rhône River (a large river flowing from Switzerland to the Mediterranean Sea in South-Eastern France) and five of its tributaries: the Saône River, the Ain River, the Albarine River, the Drôme River and the Cèze River (Fig. 1, Tab. 1). All species occurrence data were first included in the European Groundwater Crustacean Database under the name '*Schellencandona triquetra*' (Zagmajster *et al.*, 2014). *S. rhodanensis* sp. n. was sampled at 30 sites in the Rhône River watershed between 1979 and 2015. In wells, animals were collected with an immersed pump (PASCALIS programme, Dole-Olivier *et al.*, 2009; Creuzé des Châtelliers, personal communication for the well located close to the Saône River). In riverbed sediments, animals were collected with the Bou-Rouch pumping method (Bou and Rouch, 1967). In the present study, we used samples collected in river sediment to document several facets of the species habitat preference, as follows.

Vertical distribution: the distribution of *S. rhodanensis* sp. n. with depth inside the sediment was studied in the Valbonne gravel pit (site 6 in Gibert *et al.*, 1977; Seyed-Rehiani *et al.*, 1982), located in the Rhône River floodplain (800 m of the main channel), with 6 series of samples from March 1980 to September 1983, at -50, -100, -150 and -200 cm deep inside the sediment, with a volume pumped of 100 L of interstitial water at each depth, filtered through a 100 µm mesh net (Leg.J. Gibert, Marmonier, 1988). Differences between depths were tested with a one-way ANOVA on log-transformed abundance data.

Lateral distribution: the distribution of the species in the floodplain between the active channel and the abandoned channels was studied in two wetlands located in the Ain River floodplain (Puits Novet and Brotteaux wetlands, Tab. 1) sampled at -50 cm and -100 cm deep in 16 sites ranging from the margin of the main channel to isolated abandoned channels (160 µm mesh size; Reygrobellet, 1986). Puits Novet wetland was frequently disturbed by seasonal floods, while Brotteaux wetland was rarely impacted by flooding (Marmonier, 1988).

Altitudinal distribution: the longitudinal distribution of the species in the Albarine River, a tributary of the Ain River, documented the altitudinal preference of the new species. It was studied at 12 sites from 220 to 850 m a.s.l., at -50 cm deep inside the sediment, with 4 replicate samples of 10 L at each site (160 µm mesh size; Dole-Olivier *et al.*, 2009).

Surface water-groundwater exchanges: the preference of the species for river-groundwater exchange zones was studied in four different rivers. First, in the Ain River (30 sites) where groundwater inflows were measured using thermal infrared remote sensing and interstitial water physical and chemical characteristics (temperature, electrical conductivity, dissolved oxygen and vertical hydraulic gradient, Dole-Olivier *et al.*, 2019). On the 30 sites, 13 were located in a groundwater upwelling zone and 17 in a downwelling zone. Second, in the Albarine River

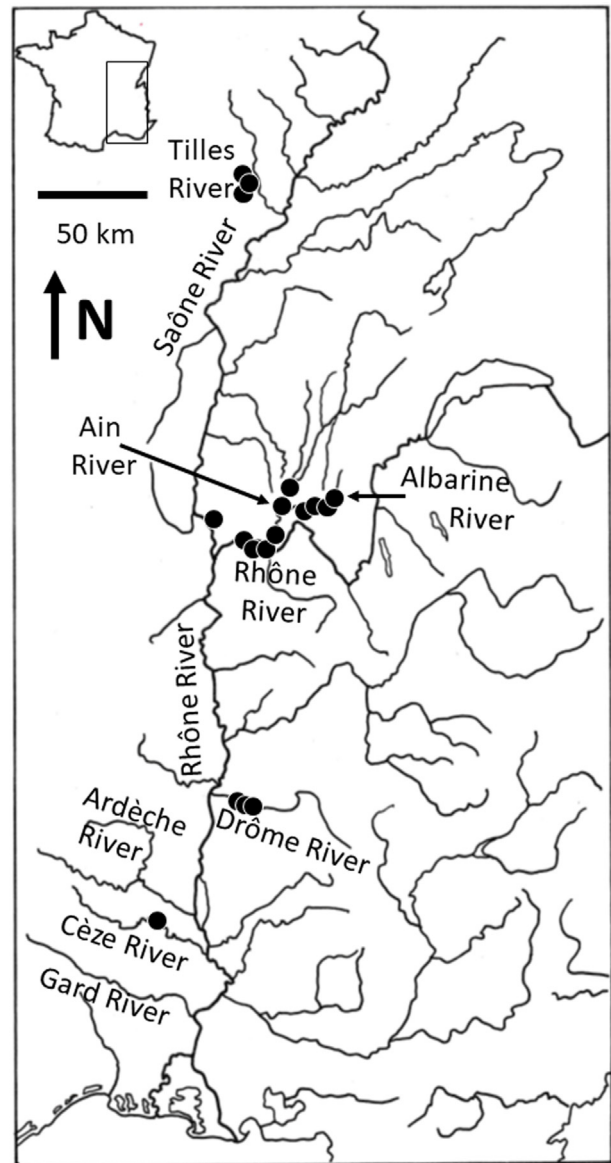


Fig. 1. Biogeography of *Schellencandona rhodanensis* sp. n. Map of the Rhône River watershed with the location of sites where the new species was collected (black dots).

(12 sites) where exchanges were estimated using dissolved oxygen retention between the surface and the interstitial water at -50 cm deep (as proposed by Dole-Olivier *et al.*, 2019). Third, in the Drôme River (27 sites) where exchanges were estimated using solute content of the interstitial water at -50 cm deep (calcium, magnesium, potassium, sodium, nitrates, dissolved oxygen and electrical conductivity, Marmonier *et al.*, 2019). Fourth, in the Cèze River (17 sites) where exchanges were estimated using surface water temperature and ^{222}Rn content (see details in Marmonier *et al.*, 2020a). In all these studies, 10 L of interstitial water were pumped and filtered through a 250 µm mesh net.

Collected specimens were fixed in the field using formaldehyde (before year 2000) or 96% ethanol (after year 2000). Dissected specimens were coloured with methyl blue and mounted in glycerine on slides and their valves stored in

Table 1. Distribution of *Schellencandona rhodanensis* sp. n. Names and location of sites (watershed, municipality, latitude and longitude in decimal degrees, WGS 84), type of water bodies and habitat. Site numbers in the Ain River is from [Dole-Olivier et al. \(2019\)](#), in the Drôme River from [Marmonier et al. \(2019\)](#) and in the Cèze River from [Marmonier et al. \(2020a\)](#).

Watershed	Name	Type	Habitat	Municipality	Latitude	Longitude
Tilles River	Fontaine St Thibaut	Spring	Sediment	Orgeux	47.3753°N	5.1813°E
	Fontaine St Martin	Spring	Sediment	Orgeux	47.3759°N	5.1718°E
	Noue Noire River	River	Sediment	Orgeux	47.3650°N	5.1709°E
	Charrière River	River	Sediment	Orgeux	47.3738°N	5.1667°E
Saône River	Pumping station	Well	Groundwater	Massieux	45.9097°N	4.8326°E
Rhône River	Canal of Miribel	River	Sediment	Nievroz	45.8107°N	5.0584°E
	Les Pêcheurs	Wetland	Sediment	Villette d'Anthon	45.8112°N	5.1121°E
	Grand Gravier	Wetland	Sediment	Balan	45.8285°N	5.1354°E
Ain River	La Valbonne	Gravel pit	Sediment	Balan	45.8331°N	5.1131°E
	Ain main channel (St. 5 and 7)	River	Sediment	Ambroay	46.0085°N	5.3058°E
	Ain main channel (St. 31)	River	Sediment	Charnoz sur Ain	45.8648°N	5.2267°E
	Brotteaux (3 sites)	Wetland	Sediment	St Maurice de Gourdans	45.8012°N	5.1913°E
	Puits Novet (2 sites)	Wetland	Sediment	St Maurice de Gourdans	45.8016°N	5.1719°E
Albarine River	Port-Galland	Wetland	Sediment	Loyettes	45.8138°N	5.2157°E
	Puits Miquet et Bettant	Well	Groundwater	Ambérieux en Bugey	45.9494°N	5.3587°E
	3rd piezometer at Balmettes	Well	Groundwater	Ambérieux en Bugey	45.9362°N	5.3783°E
	Confluence with the Ain River	River	Sediment	St Maurice de Remens	45.9651°N	5.2576°E
	Confluence with lateral channel	River	Sediment	St Maurice de Remens	45.9640°N	5.2621°E
	Cluse de Torcieux	River	Sediment	Torcieux	45.9177°N	5.3967°E
	St Rambert	River	Sediment	St Rambert	45.9495°N	5.4516°E
	Pont de la Violette	River	Sediment	Tenay	45.9340°N	5.5300°E
	Chaley	River	Sediment	Chaley	45.9515°N	5.5311°E
Drôme River	Drôme main channel (St. 1, 2, 3)	River	Sediment	Crest	44.7330°N	4.9702°E
Cèze River	Cèze main channel (St. 4)	River	Sediment	Méjannes le Clap	44.2498°N	4.3211°E

alcohol. Undissected specimens were preserved in 96% ethanol in plastic tubes. Valves and limbs were examined and figured using an Olympus BX51 microscope and Olympus DP23 camera. Complete animals and dissected valves were photographed using the Olympus camera with transmitted light or lateral light (with three diodes). The type material is deposited in the Museum National d'Histoire Naturelle (noted hereafter MNHN) in Paris and some paratypes in the zoological collection of the University Claude Bernard Lyon 1 (noted hereafter UCBLZ) in Lyon.

2.1 Abbreviations used in text and figures

The chaetotaxy of the limbs was coded according to the model of [Broodbakker and Danielopol \(1982\)](#), modified by [Martens \(1987\)](#) and [Meisch \(1996\)](#):

- General abbreviations: *H*, height; *L*, length; *W*, width; LV, left valve; RV, right valve. EI to EIV, endopodite podomeres for A2, L6 and L7.
- A1, antennule (1st antenna); α , small seta of the 7th podomere; ya aesthetasc of the 8th podomere; l, long seta; m, medium seta; s, small seta; A, anterior; P, posterior; D, distal; Pu, plumose seta.
- A2, 2nd antenna; G1, G2, G3, claws of EIII; GM, anterior claw of EIV; Gm, posterior claw of EIV; g, seta of EIV; t1-4, internal setae of EII (transformed in males); Y, y1, y2,

y3, aesthetascs of respectively EI, EII, EIII and EIV; z1-3, external setae of EIII.

- Md, mandibula (3rd limb); Mdp, mandibular palp; S1, long plumose seta of the 1st podomere; S2, short plumose seta of the 1st podomere; α , the small seta of the 1st podomere; β , small seta of the 2nd podomere; γ , long distal seta of the 3rd podomere.
- Mxu, maxillula (4th limb);
- L5, maxilliped (5th limb); a, b, d, protopodite setae.
- L6, walking leg (6th limb); d1, protopodite seta; g, seta of EIII; h1, h2, h3, setae of EIV.
- L7, cleaning leg (7th limb); d1, dp, protopodite setae; g, EII+EIII seta; h1, h2, h3, setae of EIV.
- CR, caudal ramus; sa, anterior seta; sp, posterior seta; Ga, anterior claw; Gp, posterior claw.
- Hemipenis: a, outer lobe; b, inner lobe; 'e', bursa copulatrix; M, central chitinized process; 'd1', 'd2', 'd3' and 'd4' successive sections of the labyrinth.

3 Results

3.1 Systematic description

Class OSTRACODA [Latreille, 1802](#)
 Order PODOCOPIDA [Sars, 1866](#)
 Suborder CYPRIDOCOPINA [Baird, 1845](#)
 Superfamily CYPRIDOIDEA [Baird, 1845](#)

Family CANDONIDAE Kaufmann, 1900
 Subfamily CANDONINAE Kaufmann, 1900
 Genus *Schellencandona* Meisch, 1996
Schellencandona rhodanensis sp. n.

Synonym: *Pseudocandona triquetra* in Marmonier (1988), Marmonier and Creuzé des Châtelliers (1992), Dole-Olivier et al. (1993); *Schellencandona triquetra* Dole-Olivier et al. (2009, 2022), Marmonier et al. (2019, 2020a, 2020b).

3.2 Derivatio nominis

The new species is named after the Rhône River (France) where it occurs.

3.3 Type material

Holotype: one male with body dissected and limbs mounted in glycerine, valves stored in alcohol (MNHN-IU-2024-823).

Allotype: one female with body dissected and limbs mounted in glycerine, valves stored in alcohol (MNHN-IU-2024-824).

Paratypes: three dissected males (MNHN-IU-2024-825, UCBLZ 2012-3-13-16, UCBLZ 2012-3-13-17-2) and two dissected females (MNHN-IU-2024-826, UCBLZ 2012-3-13-17-1).

Supplementary material: males, females and juveniles ($n=33$, MNHN-IU-2024-827 and $n=\text{circa } 100$ individuals, UCBLZ.2012.3.237).

Type locality: FRANCE; Ain district; Balan municipality; 45.8209°N, 5.1223°E; alt. 190 m a.s.l.; Valbonne gravel pit at La Violette, on the margin of the Valbonne military camp; Nov 1979 to Sep 1983; J. Gibert leg.

3.4 Diagnosis

Small triangular Candoninae of the genus *Schellencandona* with high-domed carapace ($H/L=0.57$). LV with hump that overlaps RV. Greatest H of LV located just mid-length. Calcified inner lamella at the anterior end of LV amounting to c. 16% of L and c. 11% for the posterior one. EII and EIII of A2 separated in males with t2 and t3 male bristles, longest claw (G2) represents 1.75x the length of EI. 2nd podomere of the mandibular palp bears $3+1+\beta$ setae. Endopodites of the maxilliped (L5) developed in males into prehensile palps, hook-shaped slightly asymmetrical. Cleaning leg (L7) 4-segmented, EII and EIII not divided, with 2 setae (d1 and dp) on the protopodite. Zenker's organs with 4 internal rings of spines and 2 end plates. The outer lobe (a) of the hemipenis slightly dorsally oriented, the inner lobe (b) with a triangular shape. Bursa copulatrix rounded. Female genital lobe with a short triangular posterior expansion.

3.5 Description of the carapace

Carapace whitish with ornamentation consisting in pits (or small fossae) in the central part that vanish progressively toward the periphery. General shape of the carapace triangular (Figs. 2 and 3). Valves strongly asymmetrical. The LV overlaps the RV with a hump-like dorsal margin without marked

cardinal angles. Highest H located at the middle of L . H slightly superior to $1/2L$: $H/L=0.57$ for the male, $H/L=0.58$ for the female. Carapace viewed dorsally (Figs. 2C and 2F) moderately compressed, with greatest W at the middle of L . Anterior end weakly beak-shaped, posterior end roundly pointed.

For both valves (Fig. 2), anterior margin moderately rounded, while posterior end more pointed. Ventral margin straight in males and slightly convex in females. Dorso-posterior margin slightly rounded in both sexes. LV is higher than RV because of the dorsal hump-shaped margin that represents 13% of H for the male and 12% for the female. RV smaller, with a straight dorsal margin with marked cardinal angles, straight dorsal margin represents 25% of L for both male and female. Calcified inner lamella wide; anteriorly it represents 16% and posteriorly 11% of L for both male and female. Fused marginal valve zone wide, representing 4% of L for both male and female, with straight and dense radial pore canals.

3.6 Dimensions

Holotype (male): LV: $L=432\text{ }\mu\text{m}$, $H=245\text{ }\mu\text{m}$ ($H/L=0.57$). RV: $L=415\text{ }\mu\text{m}$, $H=218\text{ }\mu\text{m}$ ($H/L=0.52$). $W=175\text{ }\mu\text{m}$ ($W/L=0.41$). Range for males ($n=4$): $L=423\text{--}433\text{ }\mu\text{m}$, $H=245\text{--}252\text{ }\mu\text{m}$, $W=167\text{--}175\text{ }\mu\text{m}$.

Allotype (female): LV: $L=405\text{ }\mu\text{m}$, $H=235\text{ }\mu\text{m}$ ($H/L=0.58$). RV: $L=395\text{ }\mu\text{m}$, $H=210\text{ }\mu\text{m}$ ($H/L=0.53$). $W=170\text{ }\mu\text{m}$ ($W/L=0.42$). Range for females ($n=5$): $L=405\text{--}422\text{ }\mu\text{m}$. $H=235\text{--}252\text{ }\mu\text{m}$.

3.7 Description of limbs

Antennule, A1 (Fig. 4A and 6A). I+II: A-1I(Pu), P-2I/III: A-1s/IV: A-1s/V: A-1I, P-1s/VI: A-2I, P-1m/VII: A-2I-1s (α), P-1I/VIII: D-2I-ya-1I(cs). Using IV podomere as reference, length of podomeres are 1.8–1.5–1.2–1.5–1.3 from III to VIII. ya aesthetasc very long (6 to 9 times IV podomere length).

Antenna, A2 (Fig. 4B-C-D, Fig. 6B-D-E). Protopodite: coxa with 2 plumose setae; basis with 1 long posterior seta; exopodite with 1 long and 2 short setae; EI with 1 posterior aesthetasc Y (equalling 76% of EI length) and distally 2 setae (1s and 1I).

Male A2 (Fig. 4B-C-D): EII and EIII segmented; EII with 1 short aesthetasc (y1) and 4 t setae, t1 long, t4 short, t2 and t3 transformed in male bristles with length equal to EI length; EIII with 1 short aesthetasc (y2), 3 external short setae (z1, z2, z3) slightly exceeding EIV length, G1 reduced (same EI length), G2 well developed (1.75x EI length), G3 reduced to a bristle (0.6x EI length); EIV with 2 claws, posteriorly 1 long (Gm, 1.5x EI length) and anteriorly 1 reduced (GM, 0.8x EI length), 1 aesthetasc (y3, 0.6x EI length) associated with a subequal seta and a slightly longer one (g).

Female A2 (Fig. 6B-D-E): EII and EIII fused with anteriorly 2 short aesthetacs (y1 and y2), 4 untransformed t setae, distally 3 short z setae (z1, z2, z3), a reduced G2 claw with a similar length to EI and 2 well developed claws G1 and G3 (1.7x EI length). EIV with anteriorly 1 long (GM, 1.5x EI length) and posteriorly 1 reduced claw (Gm, 0.5x EI length), 1

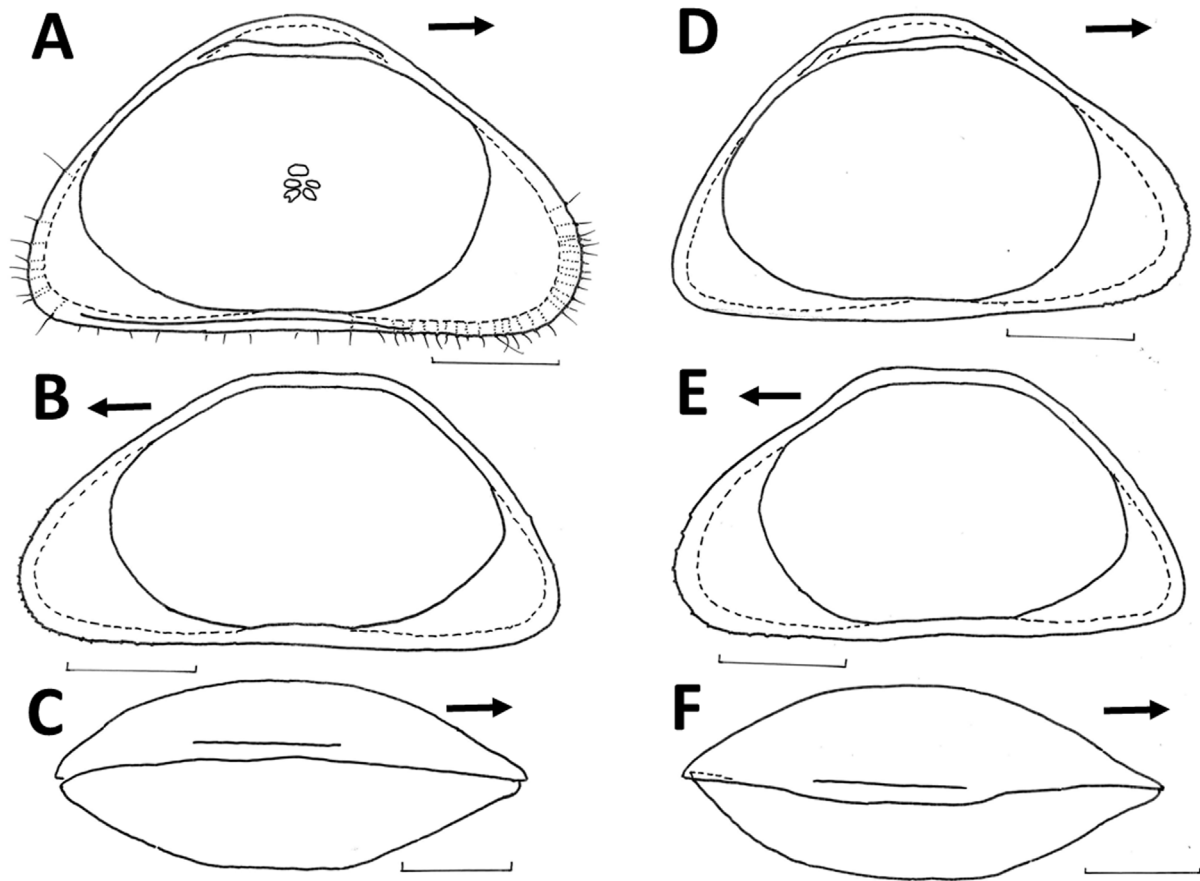


Fig. 2. *Schellen Candona rhodanensis* sp. n. A. Male left valve internal view. B. Male right valve internal view. C. Male dorsal view of the whole carapace. D. Female left valve internal view. E. Female right valve internal view. F. Female dorsal view of the whole carapace. Male MNHN-IU-2024-823. Female MNHN-IU-2024-824. Scale bars: 100 μ m for all.

aesthetasc (y3, 0.5x EI length) with a subequal seta and a slightly longer one (g).

Mandible consists of a coxal plate and a 4-segmented palp (Mdp). Coxa typically shaped, heavily chitinized with a masticatory part. 1st podomere of Mdp (Figs. 4E and 6C) with externally exopodite plate and 2 long setae, internally with 2 long setae (1 plumose S1) and 2 short setae (1 smooth, α , 1 plumose, S2). 2nd podomere with externally 2 setae and internally a group of 3 smooth setae and a second group of 2 setae (1 long and plumose, 1 short, β). 3rd podomere with externally 3 setae, distally 1 long seta (γ) and internally 3 small setae. 4th podomere with 2 serrated claws (1.5 $\times$ 3rd podomere length) and 3 small setae.

Maxillula, Mxu, with palp (Figs. 4G and 7B) two-segmented: 1st segment with 4 apical plumose setae on the outer corner. 2nd segment with 2 claw-like setae (3 $\times$ 2nd segment length) and 4 thinner setae.

Maxillipeds, L5 (Fig. 5B,C and Fig. 7D) with protopodite bearing 1 anterior seta (a) and 2 exterior setae (b and d), masticatory process (endite) apically with a group of 12 setae. Exopodite plate with 2 filaments. Male endopodites transformed in clasping hook-like organs slightly asymmetrical (left one distally inflated), tightly curved with 2 short but thick setae on the ventral side and a thin apical seta. In female, similar set of setae was observed on the protopodite and 2

filaments on the exopodite. Conical endopodite with 3 short apical setae.

Walking leg (L6, Figs. 4F and 7C) five-segmented. Protopodite with a short d1 seta. EI and EII without seta, EIII with 2 g setae, EIV with 2 short setae (h1 and h3) and a long claw (h2) serrated and equalling 1.4x EI length.

Cleaning leg (L7, Figs. 5F and 7A) four-segmented (with EII and EIII not divided). Protopodite with 1 short (d1) and 1 long (dp, 1.4x EI length) setae. EI without seta, EII+EIII with a short seta (g), EIV with 1 short (h1, 2.3x EIV length) and 2 long setae (h2, h3, 5x and 7.3x EIV length, respectively in females).

Caudal ramus (CR, Figs. 5E and 7E) robust with a long sp seta (28% to 31% of anterior margin of CR), a short sa seta (17% to 21% of anterior margin of CR) and 2 long and curved claws (Ga and Gp representing around 70% to 73% of anterior margin of CR), both claws serrated.

Female genital lobe (Fig. 7F) with a posterior short triangular expansion and an anterior rounded margin. Oocyte large (16% of valve length).

For males, Zenker's organ (Fig. 5D) with 4 internal rings of spines and 2 end plates representing 35% of total length of the carapace. Testes 3-lobed. Hemipenis (Fig. 5A) with a distal outer lobe (lobe a) narrow and slightly dorsally oriented, a triangular inner lobe (lobe b) made of 2 associated folds both

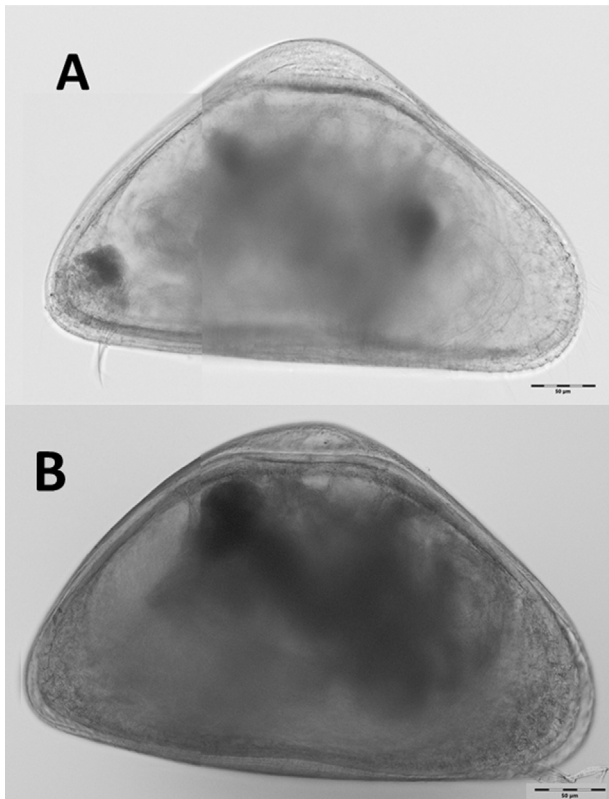


Fig. 3. *Schellencandona rhodanensis* sp. n. A. Right view of an undissected male (paratype 2, MNHN-IU-2024-825). B. Right view of an undissected female (paratype 3, MNHN-IU-2024-826). Scale bars: 50 μ m.

slightly sclerotized and a reduced plication on the ventral side. Labyrinth well sclerotized and divided into 4 sections, section d4 weakly reticulated. Copulatory tube thin, located inside a rounded and conical bursa copulatrix (e). The M-process is flat with a broad rounded distal part and a contracted thin basal part reaching the d4 section of the labyrinth.

No eye observed.

3.8 Biogeographic distribution

Schellencandona rhodanensis sp. n. occurred in many localities in the Rhône River watershed, from the Tilles River (Saône River watershed) in the north ($X=47.3753^{\circ}\text{N}$) to the Cèze River in the south ($X=44.2498^{\circ}\text{N}$; Fig. 1, Tab. 1). In the Tilles river watershed, the species occurred in the interstitial habitat of two springs (Fontaine St Martin, Fontaine St Thibault) and two small rivers (the Noue Noire and the Charrière River, Tab. 1). About 166 km downstream of the Tilles River, the species was sampled in a well located at Massieux on the floodplain of the Saône River, very close to the main channel.

In the Rhône River, *S. rhodanensis* sp. n. was sampled in the interstitial habitat of the main channel (Canal de Miribel), in two wetlands associated with the Rhône River (Pêcheurs and Grand Gravier, Tab. 1), and in the Valbonne gravel pit (Military camp of La Valbonne, type locality) located at 1 km from the Rhône River. Along the Ain River, the species was sampled in

both the main channel of the river (near Ambronay and Charnoz-sur-Ain) and in associated wetlands (e.g. Puits Novets, Brotteaux, Tab. 1). In the Albarine River, a tributary of the Ain River (Fig. 1), the species was sampled in the interstitial habitat of the main channel (at 6 sites) and in two wells situated in the Albarine floodplain (Tab. 1). In the southern part of the Rhône River watershed, the species was sampled in the sediment of the main channel of the Drôme River and the Cèze River (Fig. 1, Tab. 1).

3.9 Habitat preferences

The species was rarely collected in wells reaching groundwater (only 3 wells, thus 10% of the sites); groundwater wells in which the species was collected were located very close to a river (i.e. one along the Saône River and two wells along the Albarine River, Tab. 1). In all other cases (i.e. 27 sites), *S. rhodanensis* sp. n. was sampled in the interstitial habitat of rivers or very close to rivers: in springs (6.7%), in floodplain wetlands (30%) and in the bottom sediment of the river channel itself (53.3%, Tab. 1). As part of the European PASCALIS programme, Dole-Olivier *et al.* (2009) sampled 19 springs, 24 wells and 13 karstic systems in the watershed of the Albarine River. The species was present in only 2 wells, but never occurred in springs or in karstic systems. Similarly, in the Cèze River programme (Marmonier *et al.*, 2020b), 4 springs and 6 karstic systems were sampled along the river, but *S. rhodanensis* sp. n. was never collected outside of the river main channel.

The vertical distribution of *S. rhodanensis* sp. n. inside the sediment of the Valbonne gravel pit (Fig. 8A) was characterized by maximum abundances at depth of 1 m below the water-sediment interface (abundances ranging from 6 to 86 individuals for 100 L of pumped water, significantly higher than at other depths, $F_{(2,15)}=3.86$, $P < 0.05$). Abundances measured at a depth of 50 cm were generally low (ranging from 0 to 26 individuals for 100 L) and the species was never collected in the benthic layer of this gravel pit nor in that of any other wetland of the area.

The lateral distribution of the species in the wetlands of the Ain River showed preference of the species for groundwater-fed wetlands located far from the main channel. In the Puits Novet wetland (which is frequently inundated during floods), the species was only present in the most isolated sites of the floodplain (black squares on the external paleo channel of the wetland, Fig. 8B). In the Brotteaux wetland (which was rarely inundated during floods), the species was sampled at most sites along the wetland-main channel transect (black squares on the three paleo channels of the wetland, Fig. 8B). Finally, the species was absent in the sediment of the small stagnant pools located close to the main channel and in the main channel itself.

The altitudinal distribution of the species in the Albarine River (Fig. 8C) showed that the species did not occur in the two stations above 430 m a.s.l., but without clear monotonic decline along the altitudinal gradient. The other sites where the species occurred in the Rhône River watershed were low elevation sites (175 m a.s.l. along the Rhône River itself, 200 m along the Ain River, 160 m along the Drôme River, and 100 m along the Cèze River).

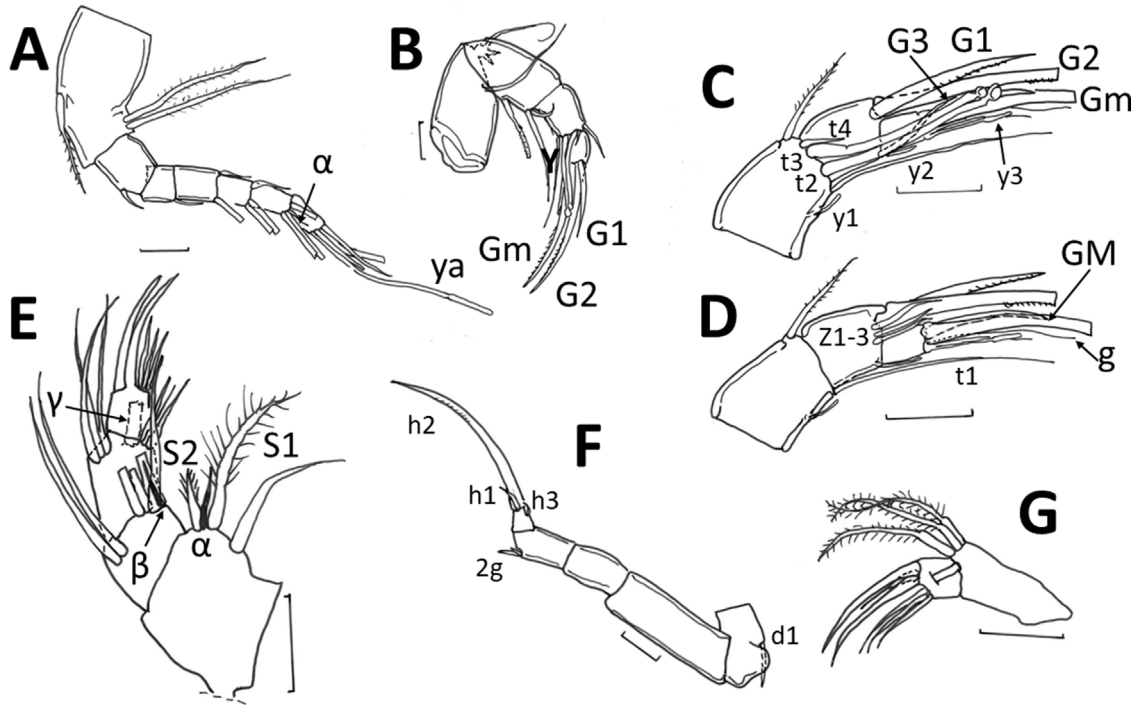


Fig. 4. *Schellencandona rhodanensis* sp. n. Male (MNHN-IU-2024-823). A. Antennule (A1). B. Antenna (A2). C. Detail of antenna in internal view. D. Detail of antenna external view. E. Mandibular palp (Mdp). F. Walking leg (L6). G. Maxillula (Mxu) palp. Scale bars: 20 μ m.

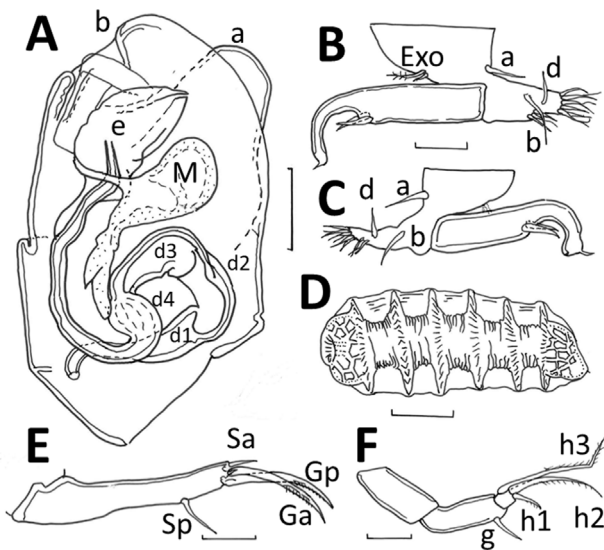


Fig. 5. *Schellencandona rhodanensis* sp. n. Male (MNHN-IU-2024-823). A. Hemipenis. B. Male right 5th limb (with clasping organ). C. Male left 5th limb (with clasping organ). D. Zenker's organ. E. Cauda ramus. F. Cleaning leg (L7). Scale bars: 20 μ m.

The relation of the species with surface water-groundwater exchanges was documented in four rivers. In the main channel of the Ain River, *S. rhodanensis* sp. n. was rare and collected at only three of 30 sampling sites. Two sites (5 and 7 in Dole-Olivier *et al.*, 2019) were located in a groundwater upwelling zone, on a total of 13 sites where inflows of groundwater were clearly documented from infrared

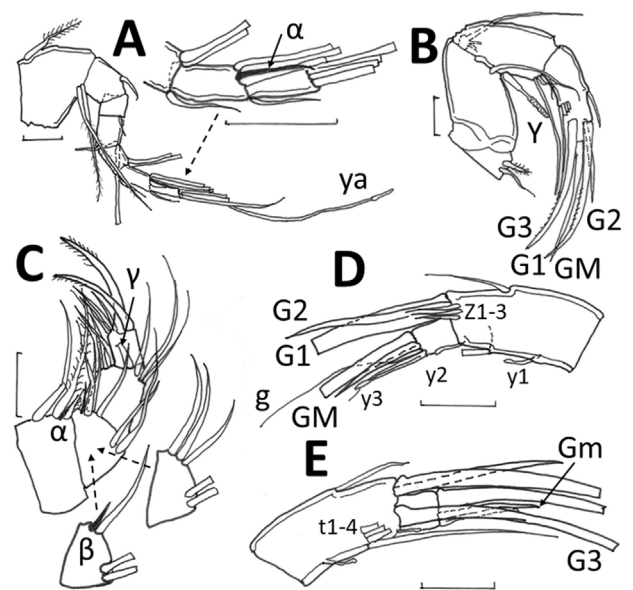


Fig. 6. *Schellencandona rhodanensis* sp. n. Female (MNHN-IU-2024-824). A. Antennule (A1) with detail of the 7th and 8th podomere. B. Antenna (A2). C. Mandibular palp (Mdp) with details of the second podomere. D. Detail of the antenna in external view. E. Detail of the antenna in internal view. Scale bars: 20 μ m.

photography (Dole-Olivier *et al.*, 2019) and measurements of the interstitial water chemistry (Dole-Olivier *et al.*, 2022). At these two sites, interstitial water temperature was lower than 18 °C (against 24 °C in surface water), electrical conductivity higher than 490 μ S cm⁻¹ (against 350 μ S cm⁻¹

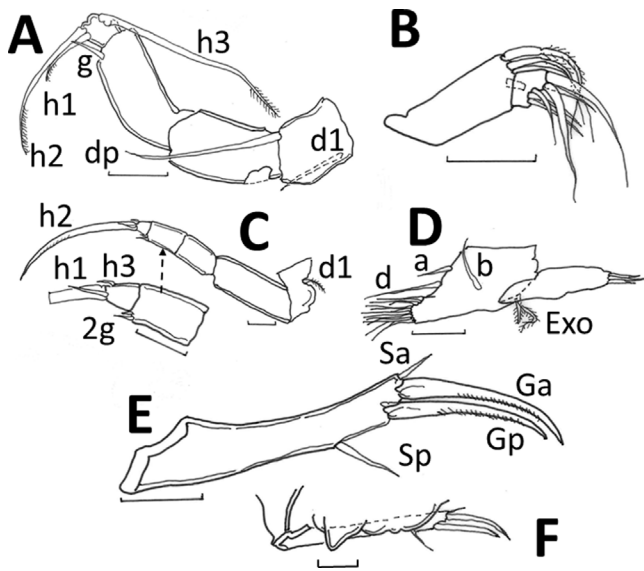


Fig. 7. *Schellencandona rhodanensis* sp. n. Female (MNHN-IU-2024-824). A. Cleaning leg (L7). B. Maxillula (Mxu) palp. C. Walking leg (L6) with detail of the 3rd and 4th podomere. D. Maxilliped (L5). E. Caudal ramus. F. Genital lobe. Scale bars: 20 µm.

in surface) and the percentage of the saturation in dissolved oxygen was lower than 30% (against more than 100% in surface water). The third one, site 31, was located in a downwelling zone (on a total of 17 sites), but 350 m downstream of a strong upwelling zone (interstitial water temperature 15 °C and electrical conductivity 530 µS cm⁻¹, in [Dole-Olivier et al., 2019](#)).

In the sediment of the Albarine River (below 450 m a.s.l., [Fig. 8C](#)), *S. rhodanensis* sp. n. occurred in sites characterized by low hydrological exchanges with surface water as indicated by the dissolved oxygen retention ([Dole-Olivier et al., 2019](#)). In the sites where the species occurred, interstitial dissolved oxygen was reduced by 13–44% compared to surface water. In contrast, in station where the species was absent, dissolved oxygen concentration was similar in surface water and inside the sediment (2–8% decrease).

In the Cèze River, the species occurred in only one of 17 sites (site 4 in [Marmonier et al., 2020a](#)). This site was one of the 7 sites located in a stretch of river fed by groundwater as indicated by low surface water temperature and high ²²²Rn content ([Marmonier et al., 2020a](#)).

In sediment of the Drôme River, *S. rhodanensis* sp. n. was sampled from three of 27 sites (sites 1, 2 and 3 in [Marmonier et al., 2019](#)). Two of these sites were fed by groundwater (on a total of 6 sites located in an upwelling zone): positive hydraulic gradients, interstitial water temperature 3 °C lower than in surface water, and higher electrical conductivity and calcium concentration inside the sediment than in surface water ([Marmonier et al., 2019](#)).

4 Discussion

The Rhône River populations (previously assigned to *S. triquetra*) show significant morphological, biogeographical and ecological differences compared with other *Schellencandona*

species, which justify the creation of a new species, *S. rhodanensis* sp. n.

4.1 Systematic position of *S. rhodanensis* sp. n.

The new species fits with most of the morphological characteristics given by [Meisch \(1996\)](#) in his description of the genus *Schellencandona*. (1) Carapace small (0.4 to 0.6 mm). (2) Surface of the carapace smooth or with shallow pits. (3) Eye absent. (4) A2 with a penultimate segment subdivided in males with male bristles. (5) Mdp with 2+3 setae and gamma setae smooth. (6) L5 exopodite with 2 plates. (7) L7 protopodite with 2 setae. (8) EII of L7 fused with EIII bearing a g seta. (9) EIV of L7 with two long (h2-h3) and one short (h1) setae. (10) Zenker's organ with 4+2 rings of spines. (11) Hemipenis with a very flat M-process. The only character that differs is the ornamentation of the carapace, the new species is covered by fossae in its central part.

Schellencandona rhodanensis sp. n. differs from other *Schellencandona* species by six morphological characteristics: (1) the triangular shape of the left valve of the carapace, while it is trapezoidal with a straight dorsal margin in *S. schellenbergi* ([Klie, 1934](#)), *S. insueta* ([Klie, 1938](#)) and *S. simililampadis* ([Danielopol, 1978](#)) or more dorsally rounded in *S. belgica* ([Klie, 1937](#)), *S. mira* ([Sywula, 1976](#)), *S. yakushimaensis* [Smith and Kamiya, 2006](#), *S. tea* [Karanovic and Lee, 2012](#), and *S. dui* [Ma and Yu, 2018](#), that have a more or less reniform carapace shape. (2) The shape of the L5 male clasping organs, which are both long with a hook-like shape rather similar to some *Mixtacandona* species (e.g. *M. juberthiae*, [Danielopol, 1978](#)). In other *Schellencandona* species the clasping organs are short (e.g. *S. simililampadis*, [Danielopol, 1978](#)). (3) The lack of e and f setae on L6 in *S. rhodanensis* sp. n. compared to *S. simililampadis*, *S. belgica*, *S. yakushimaensis*, *S. tea* and *S. dui*. (4) The shape of the hemipenis with a narrow outer a-lobe compared to *S. schellenbergi* ([Klie, 1934](#)), which has a rather large a-lobe ([Danielopol, 1978](#); [Meisch, 2000](#)). (5) The triangular shape of the b-lobe of the hemipenis, which is more rounded in *S. schellenbergi*, *S. simililampadis* or *S. insueta*. (6) Finally, the h-lobe not visible compared to the bilobate h-lobe of *S. belgica* (see [Meisch, 2000](#)).

Populations of *S. rhodanensis* sp. n. were attributed to *Schellencandona triquetra* ([Klie, 1936](#)) in previous publications (see synonymy list). The characteristics of this species is a triangular carapace shape and a small size (400 and 420 µm for females and males, respectively). The female genital lobe is widely rounded with a long posterior process that protrudes ventrally. L5 male clasping organs are moderately curved. The hemipenis outer a-lobe is straight and distally oriented, the b-lobe distally flat with a well visible ventral plication almost as long as the b-lobe itself ([Klie, 1936](#); [Meisch, 2000](#)).

S. rhodanensis sp. n. shows six major differences with *S. triquetra*. (1) The size of *S. triquetra* is similar to *S. rhodanensis* sp. n. but the LV is slightly higher in *S. triquetra* ($H/L=0.62$) than in *S. rhodanensis* sp. n. ($H/L=0.57$), with a more angular shape in male LV dorsal margin. (2) The female genital lobes of the new species have a small triangular posterior expansion instead of a long posterior process. (3) In males, while the left endopodite of L5 is similar in the two species, the right one is more curved in the new species than in

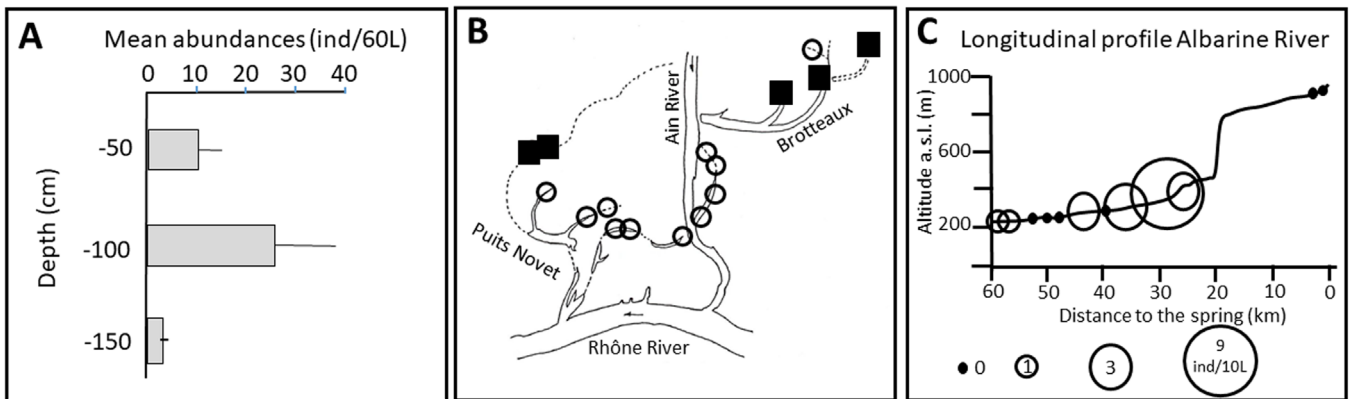


Fig. 8. Distribution of *Schellencandona rhodanensis* sp. n. A. Vertical distribution in the sediment of the Valbonne gravel pit from March 1980 to September 1983 (mean abundance and standard error; $n=6$ sampling dates per depth). B. Lateral distribution in the wetlands of the Ain River (Puits Novet and Brotteaux) located close to the confluence with the Rhône River, at 16 sites, at -50 cm and -100 cm deep inside sediments, from March 1985 to September 1986 ($n=6-9$ samples). Black square: species present in at least one sample. White circle: species absent. C. Altitudinal distribution in the bed sediment of the Albarine River, at 12 sites ranging from 939 to 220 m a.s.l. The size of the circle is proportional to the abundances (number of individuals per 10 L of pumped water).

S. triquetra. (4) The hemipenis a-lobe is dorso-distally oriented in the new species, while it is straight and distally oriented in *S. triquetra*. (5) The b-lobe is triangular shaped in the new species, while it is flat on its distal end in *S. triquetra*. (6) Finally, the ventral plication of the b-lobe is smaller in the new species than in *S. triquetra*.

These six differences justify the assignment of the population of the Rhône River watershed to a new species: *S. rhodanensis* sp. n. However, molecular analyses of several populations of the Rhône River and of *S. triquetra* collected in the Meuse and Rhine River watersheds may reinforce this specific status and reveal possible cryptic species (Eme *et al.*, 2018).

4.2 Biogeographic distribution

All sites where *S. rhodanensis* sp. n. was sampled are located in the Rhône River watershed (*i.e.* from the Tilles River in the North to the Cèze River in the South). In the northeastern part of the Rhône River watershed (known as the upper Rhône River) the species was never sampled upstream of the confluence with the Ain River. It was not sampled in the Brégnier-Cordon or in the Chautagne sectors (Marmonier and Creuze des Chatelliers, 1992; Claret *et al.*, 1999) despite their low altitude (*i.e.* 200 and 240 m a.s.l. respectively). These two sectors, which were located under the Rhône Glacier during the last glacial period, exhibit a low diversity of groundwater taxa (Dole-Olivier *et al.*, 2009; Eme *et al.*, 2015). The recolonisation process after the end of glaciation observed in Europe (*e.g.* Eme *et al.*, 2013) seems strongly limited in this upstream part of the Rhône River watershed, even if other environmental constraints may influence the present distribution.

The new species was not sampled in left tributaries of the Rhône River located downstream of the Drôme River (*i.e.* the Lez, the Eygues or the Buech rivers, Capderrey, 2013; Capderrey *et al.*, 2013). In these tributaries other *Schellencandona* species are present (descriptions in prep.). At the same latitude, *S. rhodanensis* sp. n. occurs in only one of the

right tributaries of the Rhône River (*i.e.* in the Cèze River). Future sampling survey should focus on the southern right tributaries of the Rhône River, including the Ardèche and the Gard rivers (Fig. 1), to determine the southern limit of the distribution of the new species.

Finally, we observed a potential segregation between *S. rhodanensis* sp. n. and *S. triquetra* at a European scale. *S. rhodanensis* was never collected north of the Tilles River and seems for the moment limited to the Rhône River watershed. In contrast, *S. triquetra* was never collected in the Rhône watershed whereas it is widely distributed in north-western Europe. It was described by Klie (1936) in Belgium, in the Meuse River watershed (Leruth, 1939; Martin *et al.*, 2009). In Germany, it was collected in the Rhine River watershed, at Bonn and in the Baden Wurttemberg (Hahn and Fuchs, 2009), in the Weser River, the Oker River and the Leine River watersheds (Danielopol and Hartmann, 1986; Meisch, 2000). It is not clear for the moment if all *S. triquetra* of Northern Europe belong to a single species or may include some undescribed cryptic species. This problem is out of the topic of the present article, but the northern distributional limit of *S. rhodanensis* sp. n. and the southern limit of *S. triquetra* are not clearly defined for the moment and need further investigations.

4.3 Habitat preference and ecological characteristics

S. rhodanensis sp. n. was never sampled in surface water and the eye never observed, suggesting a specialization of the new species to groundwater. Other morphological characteristics support this possible specialization. The aesthetascs are long compared to surface water species: the aesthetasc ya of A1 represents 6–9 times the IV podomere length and the aesthetasc Y of A2 represents 76% of EI length. In addition, the oocyte is large, representing 16% of the valves' length. All these characteristics suggest that *S. rhodanensis* sp. n. is a stygobite species (see discussion in Danielopol, 1980), similarly to the five other *Schellencandona* species present in Europe (Meisch, 2000).

Table 2. The use of four Ostracoda species as biological indicators of interstitial habitat hydrology. Downwelling zones: area fed by surface water infiltrations inside the river sediment. Upwelling zones: area fed by groundwater outflow inside the river. Mixed zones: area fed by a mix of surface water and groundwater. ++: frequently sampled. +: rarely sampled.

	Downwelling zones	Mixed zones	Upwelling zones
<i>Fabaeformiscandona wegelini</i> (Petkovski, 1962)	++		
<i>Marmocandona zschokkei</i> (Wolf, 1920)	++	+	
<i>Cryptocandona kieferi</i> (Klie, 1938)		++	++
<i>Schellencandona rhodanensis</i> sp. n.			++

S. rhodanensis sp. n. and *S. triquetra* seem both specialized to groundwater, but with rather different habitat use. The new species is mostly found in the interstitial habitat of rivers and wetlands (i.e. 83% of the occurrences), while *S. triquetra* colonises a wide range of subterranean habitats. In Belgium, it was sampled by Leruth (1939) in a well at Hermalle-sous-Argenteau, in two caves (Grotte de Han at Hans sur Lesse, and Grotte de Lyell at Ramouille) and two springs (at Marche en Famenne). More recent collections of *S. triquetra* in Belgium by Martin *et al.* (2009) were from a well (at Profondville), three karst systems (Drainage de la Prairie de Tridaine at Rochefort, Grotte de Warre at Durby, Galerie de Senenne at Senenne) and a single sample in the bed sediment of a stream at Presseux. In Germany, all occurrences of *S. triquetra* are from wells located in Westphalia (Danielopol and Hartmann, 1986), Baden-Württemberg (Hahn and Fuchs, 2009) and Lower Saxony (Meisch, 2000). In contrast, *S. rhodanensis* sp. n. mostly occurs in riverbed sediments (83% of the occurrences). When collected in springs (6% of the occurrences) or in wells (10% of the occurrences) they are all closely related to a river. *S. rhodanensis* sp. n. seems a good candidate for an efficient indicator of interstitial habitat quality.

4.4 Use of *S. rhodanensis* sp. n. as an ecological indicator

The new species preferentially colonize habitats showing a high hydrological and chemical stability. In the Brotteaux and Puits Novet wetlands, *S. rhodanensis* sp. n. occurs at sites that are rarely flooded by the main river. The influence of the stability of the sedimentary habitats on the composition of the interstitial invertebrate assemblages has been well studied in river channels (e.g. Williams and Hynes, 1974; Dole-Olivier and Marmonier, 1992; Olsen and Townsend, 2005), but more rarely documented in floodplain wetlands (Dole and Chessel, 1986; Dehedin *et al.*, 2013). In the Rhône floodplain, Dole-Olivier *et al.* (1993) showed that several groundwater specialist species, such as *Microcharon reginae* Dole and Coineau, 1987, *Troglochaetus beranecki* Delachaux, 1921 and *Schellencandona rhodanensis* sp. n. (as ‘*Schellencandona triquetra*’) were restricted to the lateral margins of the floodplain where floods were scarce and the habitat stability high. Our finding that *S. rhodanensis* sp. n. preferentially occurred at a depth of 1 m into the sediment of a stagnant waterbody such as the Valbonne gravel pit suggests that it is

particularly sensitive to surface water variability. This sensitivity to disturbance makes *S. rhodanensis* sp. n. an efficient indicator of the stability of interstitial habitats (*sensus* Dole and Chessel, 1986).

In addition, *S. rhodanensis* sp. n. is most often associated with groundwater upwellings in rivers and wetlands. The new species do not occur in all upwelling sites sampled in the four ecological surveys included in this study (i.e. in 14% of the upwelling sites in the Cèze River, 15% in the Ain River, 33% in the Drôme River and in all sites with poor exchanges with the surface in the Albarine River), but when the species is collected, it is mostly inside or very close to an upwelling zone (i.e. 85% of the cases). The presence of the new species indicates groundwater inflows, but it is a rare species and its absence do not indicate an absence of exchange with groundwater. This relationship makes this species a consistent biological indicator to locate groundwater inflows in rivers and wetlands (Graillet *et al.*, 2014). Together with *S. rhodanensis* sp. n., three other Ostracoda species constitute a set of biological indicators that may help to understand river-groundwater exchanges (Tab. 2). *Fabaeformiscandona wegelini* (Petkovski, 1962) is associated with downwelling of surface waters inside river sediments (Dole-Olivier and Marmonier, 1992). This species is mostly restricted to the main channel of rivers where it occurs at shallow depth (around –50 cm deep; Rogulj *et al.*, 1994). *Marmocandona zschokkei* (Wolf, 1920) is also associated to downwelling zones, but develop abundant population in deep sediment layer (around –100 cm deep, Dole-Olivier and Marmonier, 1992). In contrast, *Cryptocandona kieferi* (Klie, 1938) is mostly sampled in areas fed by groundwater or a mix of surface and groundwater, in sediment with a high porosity and low organic matter content (Dole-Olivier and Marmonier, 1992; Namiotko *et al.*, 2005). It is generally sampled in deep sediment layers (until –2 m deep in the Miribel canal; Dole-Olivier and Marmonier, 1992). These two species occur in the main channel of rivers and more rarely in associated wetlands (Dole-Olivier *et al.*, 1993).

5 Conclusions

S. rhodanensis sp. n. represents a consistent biological indicator for both the stability and the hydrology (i.e. direction of surface water-groundwater exchanges) of river interstitial habitats. Together with three other Ostracoda species, it may

help both scientists and river managers to generate river-groundwater interaction maps (e.g. [Graillet et al., 2014](#)). These maps, that summarize the location of downwelling and upwelling zones, are essential to evaluate the ecological characteristics of river bed sediments. Downwelling zones are characterized by high amounts of dissolved oxygen and fresh organic matter and represent an attractive habitat for benthic fauna ([Dole-Olivier et al., 2022](#)). These areas must be protected for their contribution to the river invertebrate total biomass. In contrast, upwelling zones are characterized by a high hydrological and thermic stability and constitute a habitat where stygobite species can develop abundant populations at shallow depth inside the river sediments ([Dole-Olivier and Marmonier, 1992](#)). They must be protected for their contribution to river and wetland biodiversity. The location of both downwelling and upwelling zones is thus key to manage river ecosystems and their biodiversity ([Boulton et al., 2010](#)).

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Conflicts of interest

The authors have no competing interests to declare that are relevant to the content of this article.

Data availability statement

The datasets analysed in the present study are available from the authors on request.

Author contribution statement

Sampling and fieldwork by Pierre Marmonier. Dissection and photography of specimens were performed by Colin Issartel. Both authors contributed to the interpretation and the redaction of the manuscript.

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