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Description of five new species of *Schellencandona* Meisch, 1996 (Ostracoda: Candoninae) from the southern French Alps, a highly diversified area for groundwater ostracods

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Abstract. We describe five new species of the genus *Schellencandona* Meisch, 1996 (Ostracoda, Candoninae) collected in the southern French Alps. Four of these species, *S. danielopoli* sp. nov., *S. capderreyae* sp. nov., *S. mercantourensis* sp. nov., and *S. claretae* sp. nov., are related to *S. simililampadis* (Danielopol, 1978), a species previously described from southern France. The fifth species, *S. malardi* sp. nov., is related to the species of *Schellencandona* present in the Northern Alps. These five new species were collected in the interstitial habitats of rivers, generally deep inside the bedsediment (i.e., at a depth of about 90 cm into the sediment), and show some morphological characteristics linked to a specialisation to live in groundwater (e.g., long aethetascs, large oocytes). *Schellencandona danielopoli* and *S. claretae* have a large geographic distribution and a wide altitudinal range. *Schellencandona mercantourensis* is present at high elevation in two different rivers. The last two species, *S. capderreyae* and *S. malardi*, occur at low-elevation sites in a single river. They can be considered vulnerable to future climatic changes in the Mediterranean region.

Keywords. Stygobite species, hyporheic habitat, braided river, biodiversity, mountains.

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Introduction

The genus *Schellencandona* Meisch, 1996 belongs to the subfamily Candoninae Kaufmann, 1900, and currently contains 11 species. Three species were described from Asia: *S. yakushimaensis* Smith & Kamiya, 2006 in Southern Japan, *S. tea* Karanovic & Lee, 2012 in South Korea and *S. dui* Ma & Yu, 2018 in China. Seven other species of *Schellencandona* have been described from Western Europe. *Schellencandona schellenbergi* (Klie, 1934) occurs in Austria and Germany, *S. triquetra* (Klie, 1936) in Belgium and Germany, *S. belgica* (Klie, 1937) in Belgium, Germany, and France, *S. insueta* (Klie,

1938) in Germany, and *S. mira* (Sywula, 1976) in Poland. *Schellencandona simililampadis* (Danielopol, 1978) and *S. rhodanensis* Issartel & Marmonier, 2025 occur in France: the former is endemic to the Vidourle River, whereas the latter is widely distributed from North of the Saône River to the Cèze and Drôme rivers (Fig. 1; Issartel & Marmonier 2025). Another species of *Schellencandona* was collected in Northern Italy (noted hereafter as *Schellencandona* sp.), but it has not yet been described (Rossetti & Mazzini, pers. comm.).

Very little information is available on Candoninae from the Southern Alps (between 45° latitude and the Mediterranean Sea), because most research on French ostracods has focused on species from lowland areas (Meisch *et al.* 1990; Marmonier & Creuzé des Châtelliers 1992; Issartel & Marmonier 2025). Specimens of Candoninae collected in the southern Alps have rarely been identified to the species level (Capderrey *et al.* 2013; Dole-Olivier *et al.* 2015). However, Mediterranean mountains are known to have promoted speciation events (e.g., Martin-Bravo *et al.* 2010), resulting in the occurrence of several narrowly distributed species (for example, Rabitsch *et al.* 2016; Jardim-de-Queiroz *et al.* 2022). The description of *S. simililampadis* from a single site of the Vidourle River (Danielopol 1977, 1978; Fig. 1) and the collection of *Schellencandona* sp. in Northern Italy assume the presence of the genus *Schellencandona* in other rivers of the Southern French Alps, between the left bank of the Rhône River and the Italian border (Fig. 1).

The present study focuses on the diversity of the genus *Schellencandona* in the rivers of the Southern French Alps (Fig. 1), using a large set of samples collected during five ecological surveys. During these surveys, 629 samples were collected from the bed sediments of 17 rivers. First, we describe five new species of *Schellencandona* collected from rivers draining the southern French Alps. Second, we assessed the taxonomic relationships of the five new species of *Schellencandona* with other species of the genus. Third, we discuss the ecological characteristics, geographic distribution, and conservation status of the five new species.

Material and methods

In the present study, we used multiple samples collected as part of five ecological research surveys carried out in 17 rivers of the southern French Alps, 12 of 17 rivers appeared to host the genus *Schellencandona* (Fig. 1, Table 1): the Drôme River (Marmonier *et al.* 2019), the Cèze River (Marmonier *et al.* 2020), the Lez, Eygues, Ouvèze, Buech, Jabron, and Duyes rivers (Capderrey *et al.* 2013), the Asse River (Claret, pers. comm.), the Verdon and Tinée rivers (Dole-Olivier *et al.* 2015), and a karstic system associated with the Vidourle River (Danielopol 1977).

Faunal samples were collected from the riverbed sediment using the Bou-Rouch pumping method (Bou & Rouch 1967). Specimens were recovered by filtering the pumped water through a 250 µm mesh-size net. Seventeen rivers were sampled during ecological surveys, with different numbers of sampling sites and sampling depths within the riverbed sediment across rivers (Table 2). In addition to these 17 rivers, the karstic system associated with the Vidourle River was sampled at Sauve (Table 1), in the benthic layer of a subterranean artificial gallery using a hand net (110 µm), and in a close spring by filtration, from 1970 to 1972 (samples performed by members of the Laboratoire Souterrain de Moulis, CNRS, Danielopol 1977). All species occurrence data were previously included in the European Groundwater Crustacean Database as *Schellencandona* sp. (Zagmajster *et al.* 2014).

The collected animals were fixed in the field using formaldehyde and stored in 96% ethanol (no information available for the Vidourle River). Dissected specimens were colored with methyl blue and mounted in glycerine on slides, and their valves were stored in ethanol. Undissected specimens were preserved in 96% ethanol. The valves and limbs were examined and drawn using an Olympus

BX51 microscope equipped with an Olympus DP23 camera. Complete animals and dissected valves were photographed using a camera with transmitted light or lateral light.

The type material is deposited in the Muséum national d'Histoire naturelle (MNHN) in Paris, France and some paratypes are deposited in the zoological collection of the University Claude Bernard Lyon 1 (UCBLZ) in Villeurbanne, France. The type (♂) and allotype (♀) of *Schellencandona schellenbergi* were obtained from the Klie Collection located at the University of Hamburg, Germany (440b for the holotype ♂, 440c for the allotype ♀).

Abbreviations for morphological terms used in text and figures

The chaetotaxy of the limbs was coded according to the model of Broodbakker & Danielopol (1982), modified by Martens (1987), Meisch (1996), Karanovic (2006) and Scharf *et al.* (2020) for appendages and especially the male antenna, Danielopol (1977) for the description of the hemipenis.

The abbreviations used are as follows:

α	=	small seta of the 7th podomere of Mdp
β	=	small seta of the 2nd podomere of Mdp
γ	=	long distal seta of the 3rd podomere of Mdp
A	=	anterior
A1	=	antennule (1st antenna)
A2	=	2nd antenna
a	=	outer lobe of the hemipenis
a, b, d	=	protopodite setae of L5
b	=	inner lobe of the hemipenis
C	=	hemipenis sclerotized strip linked to the M-process and the basis of e
CR	=	caudal camus
cs	=	serrated
D	=	distal
d	=	protopodite seta of L6
d1, d2, d3 and d4	=	successive sections of the labyrinth
d1, dp	=	protopodite setae of L7
EI to EIV	=	endopodite podomeres for A2, L6 and L7
e	=	bursa copulatrix
e, f, g	=	setae of L6 EI, EII and EIII, respectively
g	=	seta of EIV of the A2
g	=	EII+EIII seta of L7
G1, G2, G3	=	claws of EIII of A2
Ga	=	anterior claw of CR
GM	=	anterior claw of EIV of A2
Gm	=	posterior claw of EIV of A2
Gp	=	posterior claw of CR
H	=	height
h1, h2, h3	=	setae of EIV of L7
L	=	length
l	=	long seta
L5	=	maxilla (5th limb)
L6	=	walking leg (6th limb)
L7	=	cleaning leg (7th limb)
LV	=	left valve

M	=	central chitinized process of the hemipenis
m	=	medium seta
Md	=	mandibula (3rd limb)
Mdp	=	mandibular palp
Mx1	=	maxillula (4th limb)
P	=	posterior
pu	=	plumose seta
s	=	small seta
sa	=	anterior seta of CR
S1	=	long plumose seta of the 1st podomere of Mdp
S2	=	short plumose seta of the 1st podomere of Mdp
sp	=	posterior seta of CR
RV	=	right valve
t1–4	=	internal setae of EII of A2 (transformed in males)
W	=	width
ya	=	aesthetasc of the 8th podomere of A1
Y, y1, y2, y3	=	aesthetascs of EI, EII, EIII and EIV of A2, respectively
z1–3	=	external setae of EIII of A2

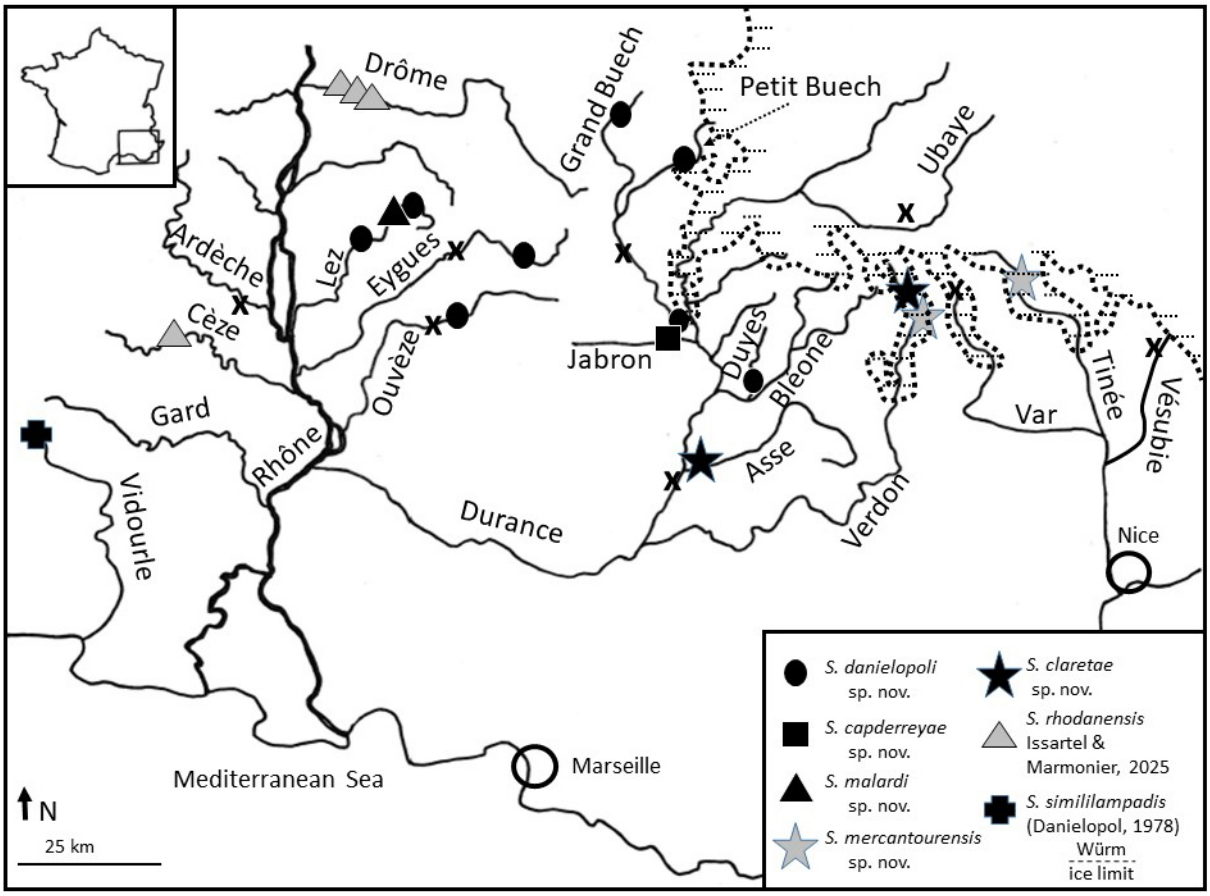

Fig. 1. Geographic distribution of the species of *Schellencandona* Meisch, 1996 in the southern French Alps. Solid lines = rivers; X = study sites without *Schellencandona*; dotted lines = western extension of Alpine glaciers during the Last Glacial Maximum (based on Julian 1997; Bosq *et al.* 2018).

Table 1. Location of sampling stations where the species of *Schellencandona* Meisch, 1996 were collected in the Southern French Alps area.

river	station names	municipalities	latitude	longitude	altitude
Drôme [1]	St 1	Crest	44.7336° N	4.9712° E	164 m a.s.l.
Drôme [1]	St 2	Crest	44.7367° N	4.9568° E	158 m a.s.l.
Drôme [1]	St 3	Crest	44.7423° N	4.9466° E	148 m a.s.l.
Cèze [2]	St 4	Rochegude	44.2516° N	4.3216° E	99 m a.s.l.
Vidourle [3]	Spring G	Sauze	43.9394° N	3.9506° E	100 m a.s.l.
Lez [4]	Montjoux	Montjoux	44.5023°N	5.0889° E	446 m a.s.l.
Lez [4]	Grignan	Grignan	44.4195° N	4.9094° E	207 m a.s.l.
Eygues [4]	Verclause	Verclause	44.3810° N	5.4255° E	534 m a.s.l.
Ouvèze [4]	Les Roches	Entrechaux	44.2322° N	5.1397° E	256 m a.s.l.
Grand Buech [4]	Col Croix haute	Luce la Crx Haute	44.6567° N	5.7112° E	1018 m a.s.l.
Petit Buech [4]	Montmaur	Montmaur	44.5608° N	5.8952° E	879 m a.s.l.
Buech [4]	Sisteron	Sisteron	44.2013° N	5.9209° E	466 m a.s.l.
Jabron [4]	Noyers	Noyers sur Jabron	44.1668° N	5.9251° E	468 m a.s.l.
Les Duyes	Le Plan Pourri	Mallemoisson	44.0412° N	6.1025° E	501 m a.s.l.
Asse [5]	Pont d'Asse	Oraison	43.8793° N	5.9051° E	335 m a.s.l.
Verdon [6]	Pont de Colmars	Colmars les Alpes	44.1789° N	6.6206° E	1225 m a.s.l.
Tinée [6]	Plan de l'Ouort	St Etienne de Tinée	44.2344° N	6.9492° E	1080 m a.s.l.

References: [1] Marmonier *et al*. (2019); [2] Marmonier *et al.* (2020); [3] Danielopol (1977–78); [4] Capderrey *et al.* (2013); [5] Claret C. pers. com.; [6] Dole-Olivier *et al.* (2015).

Table 2. Details of the ecological research programs included in this study. For each of the 17 studied rivers, the number (nb) of sites, the number (nb) of samples, the sampling strategy and the reference is given.

river	nb sites	nb samples	sampling strategy	reference
Drôme	9	81	at each site, 3 stations (centre of the river, right and left banks), 3 replicate samples of 10 l at a depth of -50 cm inside the sediment, Apr. 2014	Marmonier *et al.* 2019
Cèze	17	51	at each site, 3 replicate samples of 10 l at – a depth of 50 cm, Jul. 2013	Marmonier *et al.* 2020
Ardèche	17	17	at each site, 3 replicate samples of at least 10 l at depths of -20, -50 and -80 cm, Jun. 2024	Malard pers. com.
Lez	2	48	at each site (an alluvial plain), 2 stations, one in a losing section (upstream) and one in a gaining section (downstream of the alluvial plain); at each station, two local hydrological contexts (upwelling and downwelling zones), in each context 3 replicate samples of 10 l at -60 cm deep (in downwellings) and at depths of -30, -60, -90 cm (in upwellings), Jun. and Jul. 2010	Capderrey *et al.* 2013
Aigues	2	48		
Ouvèze	2	48		
Jabron	1	24		
Buech	3	72		
Duyes	1	24		
Asse	1	72	at each site, 4 stations (2 main channels, 1 backwater and 1 phreatic pond), 3 replicate samples of 10 l at depths of -20, -50 and -80 cm, at 2 or 4 dates from Nov. 2005 and Jan. 2008	Claret pers. com.
Durance	3	108		
Verdon	6	6	at each site, 1–3 replicate samples of 10 l at a depth of -50 cm, Jul. 2009 or Sep. 2010	Dole-Olivier *et al.* 2015
Var	2	6		
Tinée	3	7		
Ubaye	6	9		
Vésubie	3	3		
Roya	2	5		
17	80	629		

Results

Taxonomy

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

Diagnosis of the genus *Schellencandona* Meisch, 1996

Meisch (1996) gave the following characteristics to the genus *Schellencandona*: (1) Carapace small (0.4 to 0.6 mm) with six muscle scars of almost equal size and simple hinge. (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 γ 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.

List of the species: *S. schellenbergi* (Klie, 1934), *S. triquetra* (Klie, 1936), *S. belgica* (Klie, 1937), *S. insueta* (Klie, 1938), *S. mira* (Sywula, 1976), *S. simililampadis* (Danielopol 1978), *S. yakushimaensis* Smith & Kamiya, 2006, *S. tea* Karanovic & Lee, 2012, *S. dui* Ma & Yu, 2018 and *S. rhodanensis* Issartel & Marmonier (2025).

Schellencandona danielopoli sp. nov.
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Figs 2–4, 18, 20; Tables 1, 3

Diagnosis

Small candonine (L = 0.6 mm) of the genus *Schellencandona* with a triangular carapace covered with pits and small fossae. Greatest H of LV located just mid-length (H/L = 0.55). For both valves, antero-dorsal margin slightly concave. Anterior margin widely rounded and posterior margin more acute. The two valves are strongly asymmetrical: LV with a dorsal hump that overlaps the RV, RV with a dorsal margin straight and slightly inclined backwards. A1 with a reduced number of setae: absence of seta on EIII and only one anterior seta on EVI. A2 with a penultimate segment subdivided in males with male bristles. Only 3 t setae (in female) and 3 z setae, z2 transformed in a claw in male. Mdp with 2+3 setae and γ setae smooth. L5 protopodite with two a setae; exopodite with 2 plates and endopodite transformed in a pair of clasping hook-like organs highly asymmetrical, right one stocky and poorly arched, left one slender and curved. L6 without d and e setae, but with one f and one g setae. L7 protopodite with 2 setae, EII and EIII fused bearing a g seta, EIV with two long (h2–h3) and one medium-sized (h1) setae. Female genital lobe rounded with a flat central part and without dorsal expansion. Zenker's organ with 6 rings of spines. Hemipenis with outer lobe a large, rounded, dorso-distally oriented, inner lobe b sub-rectangular with a rounded ventral side. Bursa copulatrix (e) rounded with a curved sclerotized distal strip and an internal conical structure. M-process very flat. Ocular structures not visible.

Etymology

The new species is named after Dan L. Danielopol for his very important contribution to the systematics of ostracods.

Type material

Holotype

FRANCE • ♂, dissected appendages mounted in glycerine, valves stored in ethanol; Alpes-de-Haute-Provence district, Montmaur municipality; 44.5608° N, 5.8952° E; 879 m a.s.l.; Jun.–Jul. 2010; C. Capderrey leg.; interstitial habitat of the main channel of the Buech River in a large braided sector; MNHN-IU-2023-701.

Allotype

FRANCE • ♀; same data as for holotype; MNHN-IU-2023-702.

Paratypes

FRANCE • 1 ♂, dissected appendages and valves stored in ethanol; same data as for holotype; MNHN-IU-2023-703 • 1 ♂; Drôme district, Verclause municipality; 44.3810° N, 5.4255° E; 534 m a.s.l.; Jun.–Jul. 2010; C. Capderrey leg.; interstitial habitat of the main channel of the Eygues River in a braided sector; UCBLZ 2012-3-153-2 • 1 ♀; same data as for holotype; MNHN-IU-2023-704 • 1 juv.; same data as for the holotype; UCBLZ-2012-3-153-1 • 1 juv.; same locality as for holotype; undissected; UCBLZ-2012-3-207.

Other material examined

FRANCE • 23 specs of diverse stages; Lez River at Montjoux; UCBLZ-2012-3-207 • 1 juv.; Lez River at Grignan; UCBLZ-2012-3-207 • 10 specs of diverse stages; Eygues River at Verclause; UCBLZ-2012-3-207 • 2 juvs; Ouvèze River at Entrechaux; UCBLZ-2012-3-207 • 2 juvs; Grand Buech River at Luce la Croix Haute; UCBLZ-2012-3-207 • 60 specs of diverse stages; Petit Buech River at Montmaur; UCBLZ • 1 juv.; Buech River at Sisteron; UCBLZ-2012-3-207 • 5 specs of diverse stages; Les Duyes River at Mallemoisson; UCBLZ.2012.3.207.

Description

Measurements. Holotype, ♂ (MNHN-2023-701): LV: L = 600 µm, H = 330 µm (H/L = 0.55). RV = 588 µm, H = 290 µm (H/L = 0.49). W = 210 µm (W/L = 0.35). Range for males (n = 2): L = 575–600 µm, H = 570–588 µm, W = 210–225 µm. Allotype, ♀ (MNHN-2023-702): LV: L = 560 µm, H = 310 µm (H/L = 0.55). RV: L = 550 µm, H = 275 µm (H/L = 0.50). W = 205 µm (W/L = 0.36). Range for females (n = 2): L = 560–565 µm. H = 310–320 µm, W = 200205 µm.

Carapace. Whitish with ornamentation consisting of pits (or small fossae) in central part that vanish progressively toward periphery. General shape of carapace triangular (Figs 2, 18A–B). Two valves strongly asymmetrical. LV overlaps RV with hump-like dorsal margin very variable (Fig. 2A–B) and without marked cardinal angles. Highest H located at middle of L. H slightly superior to ½ L: H/L = 0.55 for both male and female. Carapace viewed dorsally (Fig. 2C, I) moderately compressed, with greatest W at middle of L. Anterior and posterior ends weakly beak-shaped. Posterior end more pointed in female.

Valves. For both valves (Fig. 2), anterior margin widely rounded, while posterior margin more acute. Dorsal margin of LV hump-like and variable in males: H/L varying from 0.55 to 0.59 (Fig. 2A–B). Dorso-posterior margin straight or slightly concave in both sexes. Dorso-anterior margin slightly concave in both sexes. Ventral margin slightly convex in both males and females. RV is smaller than LV, trapezoidal with cardinal angles well marked, dorsal margin straight and slightly inclined backward, and ventral

margin straight. Inner calcified lamella represents 11% of body length both anteriorly and posteriorly in males and slightly larger anteriorly than posteriorly in females. Fused marginal valve zone moderately large representing 2.5% of body length, with few and straight radial pore canals.

Antennule, A1 (Figs 3A, 4A). I+II: A-1l(Pu), P-2l(Pu)/III:0/IV: A-1s/V: A-1l, P-1s/VI: A-1l/VII: A-2l-1s (α), P-1l/VIII: D-2l-ya-1l(cs). Posterior setae of I+II plumose. Using IV podomere as reference, ratios of podomeres in male 1-1-1.1-0.9-1.2-1.2 from III to VIII. ya aesthetasc long, 5–6.5 × as long as IV podomere.

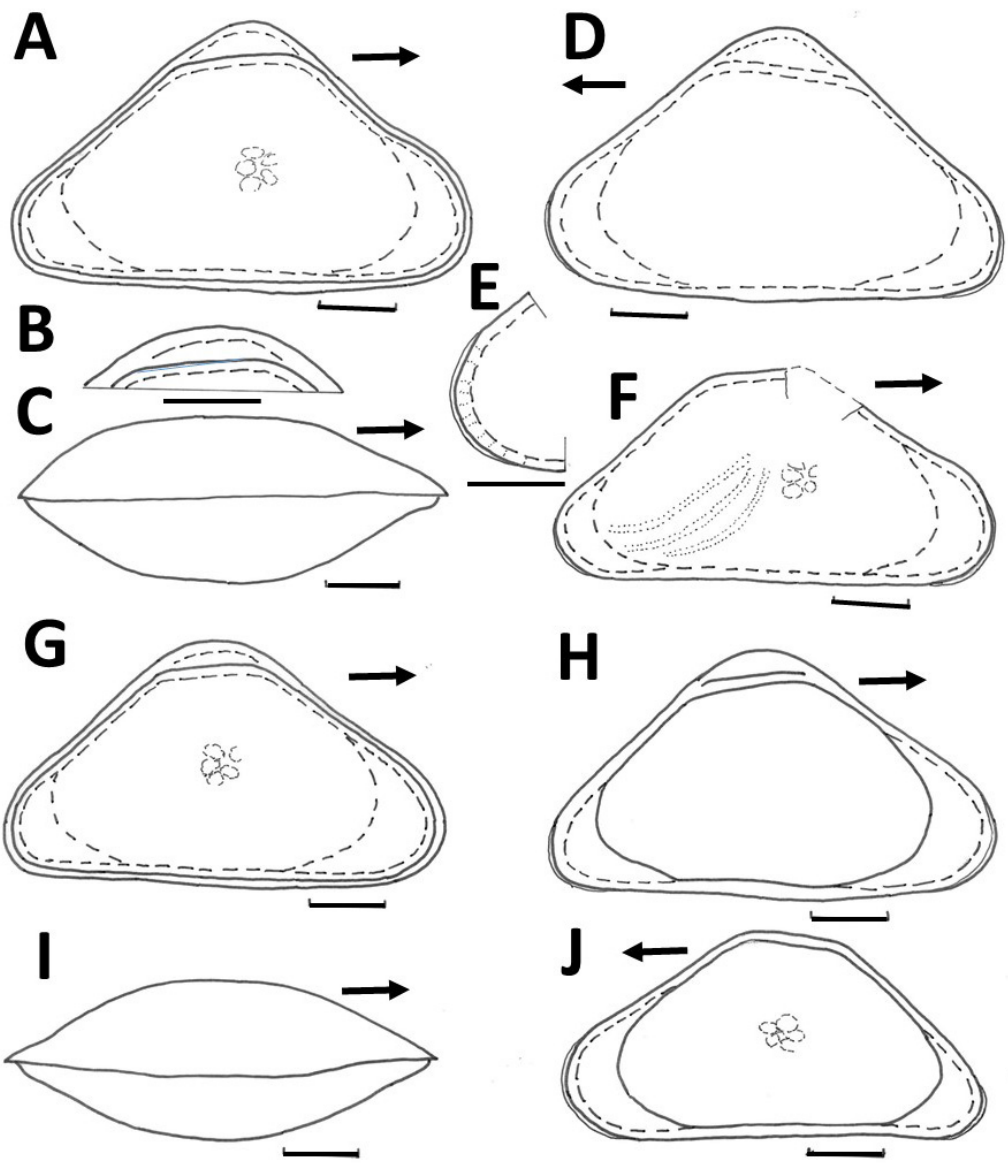

Fig. 2. *Schellencandona danielopoli* sp. nov. **A, C–D, E–F**. Holotype, ♂ (MNHN-IU-2023-701), right view of the undissected specimen. **A**. Right view of an undissected male. **B**. Paratype, ♂ (MNHN-IU-2023-703), detail of dorsal margin. **C**. Dorsal view of whole carapace. **D**. Left valve, external view. **E**. Detail of anterior margin. **F**. Right valve, external view. **G–J**. Allotype, ♀ (MNHN-IU-2023-702). **G**. Right view of undissected female. **H**. Left valve, internal view. **I**. Dorsal view of whole carapace. **J**. Right valve, internal view. Scale bars = 100 µm. Arrows point to anterior margin.

Antenna, A2 (Figs 3B–D, 4B–D). Protopodite: coxa with 3 setae, 2 long and smooth, 1 short and plumose; basis with 1 long posterior seta; exopodite with 1 long and 2 short setae; EI with 1 posterior aesthetasc Y (equalling 79% of EI length) and distally 2 setae (1s and 1l).

Male A2 (Fig. 3B–D). EII and EIII segmented as two individuated podomeres; EII with 1 short aesthetasc (y1) and 4 t setae, t1 long and plumose, t4 short, t2 and t3 transformed in male bristles with length equal to 63% of EI length. EIII with 1 short aesthetasc and 3 external z setae, z1 and z3 shorter than EIV, z2 transformed in claw (170% of EI length), G1 reduced (65% of EI length), G2 well-developed (170% of EI length), G3 reduced to bristle (47% of EI length). EIV with 2 claws, posteriorly 1 long (Gm, 160% of EI length), anteriorly 1 reduced (GM, 90% of EI length), 1 aesthetasc (y3, 50% of EI length) associated with slightly shorter seta, g seta present.

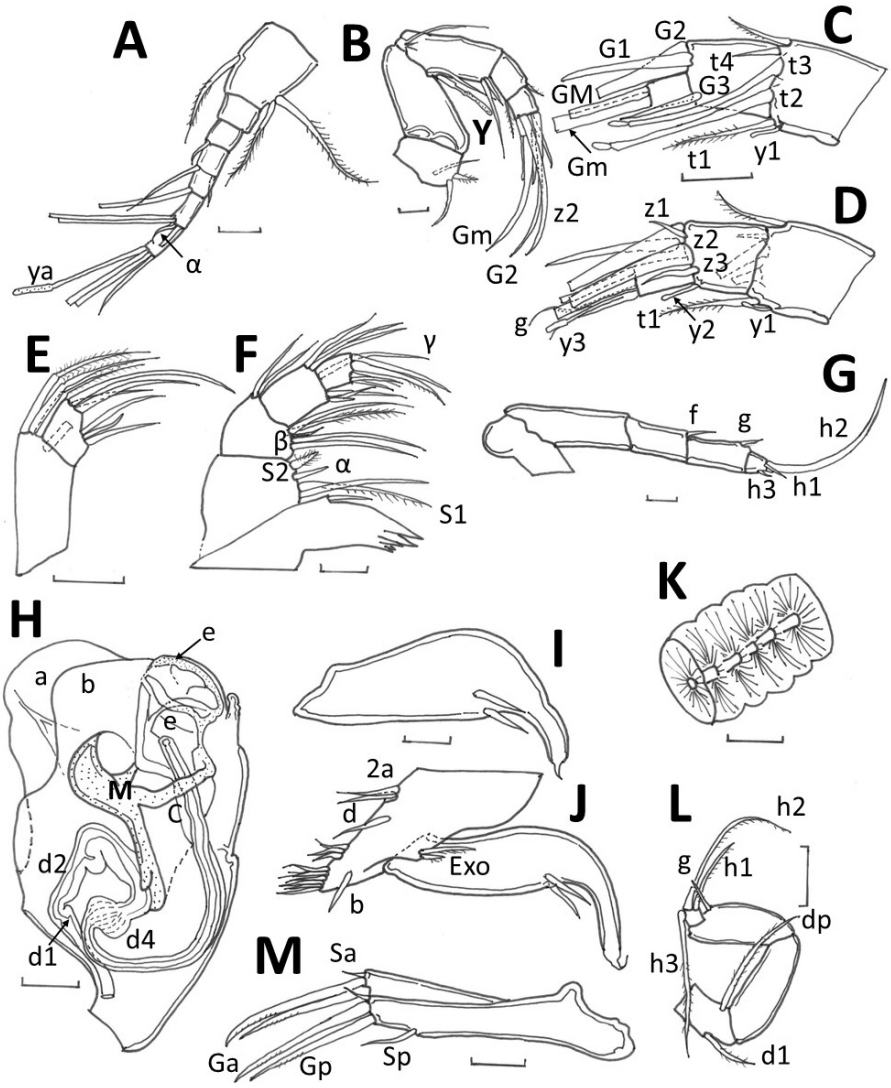

Fig. 3. *Schellencandona danielopoli* sp. nov., holotype, ♂ (MNHN-IU-2023-701). **A**. Antennule (A1). **B**. Antenna (A2). **C**. Detail of antenna, internal view. **D**. Detail of antenna, external view. **E**. Maxillula (Mx1) palp. **F**. Mandibular palp (Mdp). **G**. Walking leg (L6). **H**. Hemipenis, medial view. **I**. Right clasping organ. **J**. Left 5th limb (with clasping organ). **K**. Zenker's organ. **L**. Cleaning leg (L7). **M**. Caudal ramus. Abbreviations: see Material and methods. Scale bars = 20 µm.

Female A2 (Fig. 4B–D). EII and EIII fused with anteriorly 2 short aesthetascs (y1 and y2), 3 untransformed t setae, distally 3 z setae (z1 and z2 of medium size, z3 short), reduced G2 claw representing 60% of EI length, and 2 well-developed claws G1 and G3 (both representing 170% of EI length). EIV with anteriorly 1 long (GM, 150% of EI length) and posteriorly 1 reduced claw (Gm, 75% of EI length), 1 aesthetasc y3 (58% of EI length) associated with a subequal seta, g seta present.

Mandible. Consisting of coxal plate and 4-segmented palp (Mdp). Coxa typically shaped, heavily chitinized with a masticatory part. 1st podomere of Mdp (Fig. 3F) 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 and smooth seta (γ) and internally 3 setae (2 short setae and 1 longer). 4th podomere with 2 serrated claws (170% of 3rd podomere length) and 3 small setae.

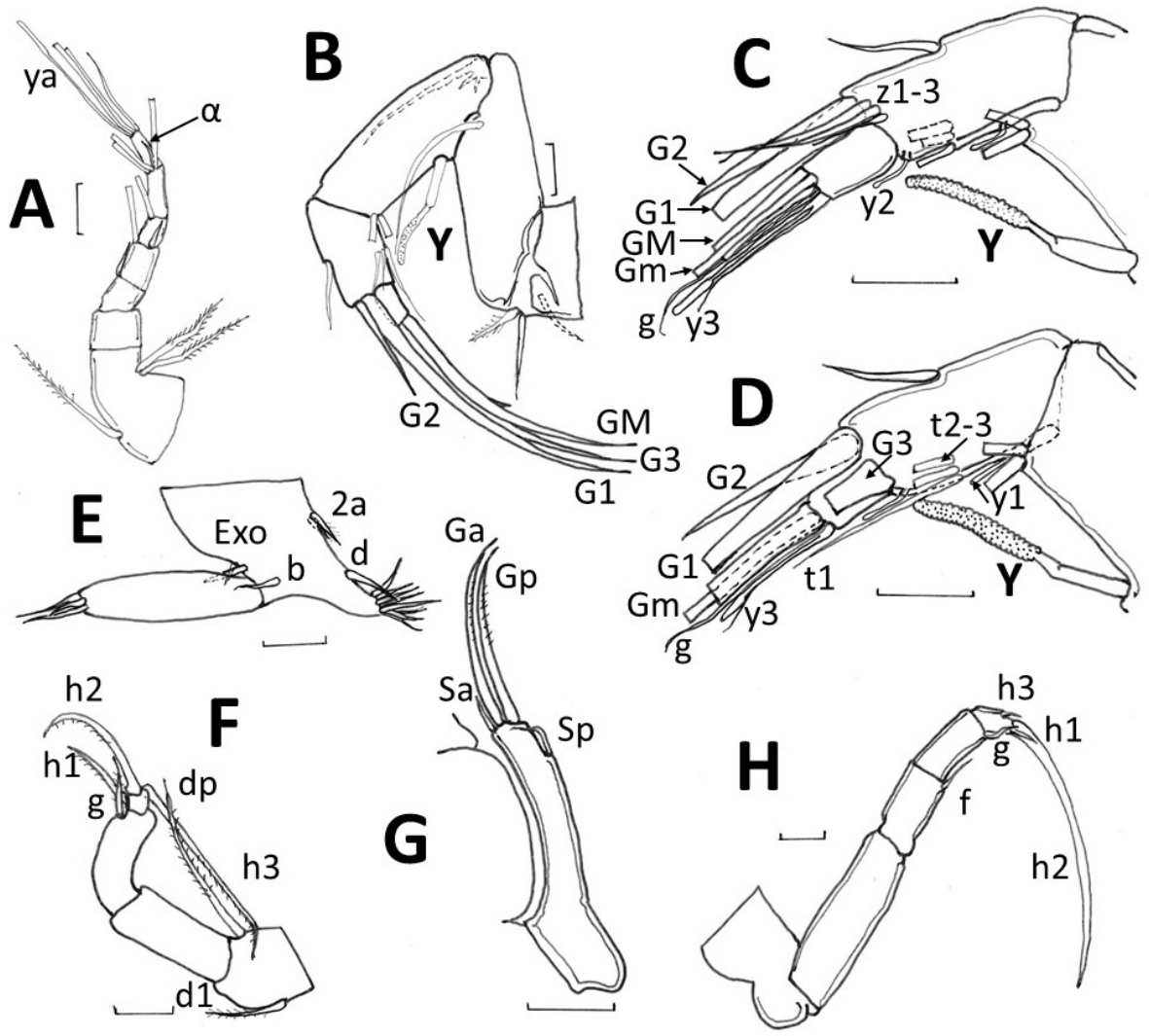

Fig. 4. *Schellencandona danielopoli* sp. nov., allotype, ♀ (MNHN-IU-2023-702). **A**. Antennule (A1). **B**. Antenna (A2). **C**. Detail of antenna, external view. **D**. Detail of antenna, internal view. **E**. Maxilla (L5). **F**. Cleaning leg (L7). **G**. Caudal ramus with genital lobe. **H**. Walking leg (L6). Abbreviations: see Material and methods. Scale bars = 20 µm.

Maxillular palp (Mx1palp, Fig. 3E). Two-segmented. 1st segment with 4 apical plumose setae on outer corner. 2nd segment with 2 claw-like setae (4 × as long as 2nd segment) and 4 thinner setae.

Maxilla (L5, Figs 3I–J, 4E). With protopodite bearing 2 anterior a setae and 2 exterior setae (b and d), masticatory process (endite) apically with group of 10 setae. Exopodite plate with 2 plumose filaments. Male endopodites transformed in clasping hook-like organs with relatively high asymmetry, right one stocky and poorly arched, left one slender and curved, with 2 short but thick setae on ventral side and thin apical seta. In female, similar set of setae was observed on protopodite and 2 filaments on exopodite. Endopodite with 3 short apical setae.

Walking leg (L6, Figs 3G, 4H). Five-segmented. Protopodite and EI without seta, EII with 1 f seta, EIII with 1 g seta, EIV with 2 short setae (h1 and h3) and long claw (h2) and equalling 160% of EI length.

Cleaning leg (L7, Figs 3L, 4F). Four-segmented (with EII and EIII fused). Protopodite with 1 short (d1) and 1 long (dp, 120% of EI length) setae. EI without seta, EII+EIII with short seta (g), EIV with 1 medium-sized seta (h1, 78% of EI length) and 2 long setae (h2, h3, 130 and 140% of EI length, respectively).

Caudal ramus (CR, Figs 3M, 4G). Robust with a medium-sized to long sp seta (30% of anterior margin of CR) exceeding the basis of posterior claw, short sa seta and 2 long and curved claws (Ga and Gp). In males, these claws are rather short, representing respectively 72% and 66% of anterior margin of CR, but very long in females (i.e., 96% and 95% respectively), both claws serrated.

Female genital lobe (Fig. 4G). rounded with flat central part and without dorsal expansion. Oocyte large (10.5% of valve length) and rounded.

Male genital organs. Zenker's organ (Fig. 3K) with 6 internal rings of spines representing 23% of total length of carapace. Hemipenis (Fig. 3H) with large rounded distal outer lobe (a) dorsally oriented, rectangular-shaped inner lobe (b) with straight distal end, rounded ventral angle and more pointed dorsal angle, with small plication on ventral side. Lobe h not observed. Labyrinth well-sclerotized and divided in 4 sections, section d4 weakly reticulated. Copulatory tube thin located inside rounded bursa copulatrix (e) with well-sclerotized distal strip and internal conical structure. M-process dorsally rounded, linked to C strip, and ventrally thin, joining d3 section of labyrinth.

Ocular structures. Not visible.

Ecology and distribution

Schellencandona danielopoli sp. nov. was collected from 8 sites of the braided river study (Capderrey et al 2013): two sites along the Lez River, one site along each of the Eygues, Ouvèze, Buech and Les Duyes rivers. The first three rivers are left-side tributaries of the Rhône River, flowing at intermediate altitudes (i.e., between 207 and 534 m a.s.l.). The last two rivers flow at higher altitudes (i.e., between 466 and 1018 m a.s.l.) in the Durance catchment, in areas close to the margin of the Würm ice sheet (Fig. 1).

In these 8 sites, the animals were mainly sampled in areas fed by groundwater upwellings (i.e., for 82% of the 102 individuals collected) with increasing abundances with depth into the river sediment (16% at -30 cm, 21% at -60 cm and 62% at -90 cm). *Schellencandona danielopoli* sp. nov. was sampled in a wide range of temperature, from 11.1°C in the Petit Buech River at Montmaur to 19.9°C in the Buech River at Sisteron (Fig. 1, Table 1). It was collected at a depth of 90 cm into the bedsediment in interstitial water with a medium electrical conductivity (329–477 $\mu S.cm^{-1}$), a pH ranging from 7.4 and 8.1 and a wide range of dissolved oxygen concentrations (3.2–7.1 $mg \cdot L^{-1}$).

Specialisation to groundwater: the length of ya of A1 and Y of A2 (i.e., more than 5 EIV podomere length of A1 and 79% of EI length of A2, respectively), the lack of eyes and the large size of the oocyte (10.5% of valve length) suggest that *Schellencandona danielopoli* sp. nov. is specialized for life in groundwater (Danielopol 1973, 1980; Issartel & Marmonier 2025) as other species of *Schellencandona*, with a wide geographical distribution in the Southern French Alps, a wide altitudinal range and a marked ecological preference for deep river sediment layers.

Taxonomic remarks

The general shape of the carapace of *Schellencandona danielopoli* sp. nov. (triangular) is rather similar to the triangular *S. triquetra* and *S. rhodanensis*, but the carapace of the new species differs by its slightly concave dorso-anterior margin, while it is straight in the two other species, and its dorsal margin slightly inclined backwards, while it is parallel to the ventral margin in the two other species (Figs 2, 18A).

In addition to the carapace shape, the soft parts of *Schellencandona danielopoli* sp. nov. differ from those of the other European species of the genus (i.e., *S. triquetra*, *S. belgica*, *S. insueta, S. mira, S. rhodanensis*), but seems closely related to *S. simililampadis and S. schellenbergi* because of (1) the stocky shape of the hemipenis, with a large a lobe dorso-distally oriented, the h lobe not visible and the curved distal sclerotized strip on the bursa copulatrix, (2) the A2 with a z2 seta transformed in a claw in males (see Fig. 19A for A2 of *S. simililampadis)* and (3) the reduced number of setae on the A1, especially the lack of seta on the podomere III in both males and females (but a seta is present in *S. schellenbergi*). In contrast, *Schellencandona danielopoli* differs from *S. simililampadis* and *S. schellenbergi* in the following four characteristics: (1) triangular shape of the carapace (trapezoid in the two other species), (2) single anterior seta on podomere VI of A1 (two setae in the others), (3) two a setae on L5 (one in the others), and (4) lack of d and e setae on L6 (present in *S. simililampadis*).

The different populations of *Schellencandona danielopoli* sp. nov. do not show any significant inter-population variability in both the carapace shape (because of a high intra-population variability of the dorsal margin, see Fig. 2A–B) and in the soft-part morphology (similar chaetotaxy in males from the Buech River (holotype, ♂ (MNHN-IU-2023-701)), and from the Eygues River (paratype, ♂ (UCBLZ 2012-3-153-2)).

Finally, the similarity of *Schellencandona danielopoli* sp. nov. with the other species described here is detailed in the Discussion.

Schellencandona capderreyae sp. nov.
urn:lsid:zoobank.org:act:C5B4806B-DBC6-4C1F-818B-7F7BC597D548
Figs 5–7, 18, 20; Tables 1, 3

Diagnosis

Small trapezoid candonine of the genus *Schellencandona* with a carapace length of about 600 µm covered by fossae. LV overlaps the RV. Greatest H of LV located at 40 and 63% of the animal length (H/L=0.50). Anterior and posterior calcified inner lamella sub-equal amounting to c. 10% of L. A1 without seta on the 3rd podomere. Male A2: EII and EIII separated with t2 and t3 male bristles, 3 z setae (z2 transformed in a claw), the longest claw (G2) represents 180% the length of EI. Female A2: EII+III with 3 t and 2 z setae. 2nd podomere of the mandibular palp bears 3+2 setae. Endopodites of the maxilla (L5) developed in males into prehensile palps slightly curved and asymmetrical. Walking leg (L6) with two g setae. Cleaning leg (L7) 4-segmented, EII and EIII fused, with 2 setae (d1 and dp) on the protopodite. Zenker's organ with 6 internal rings of spines. The outer lobe a of the hemipenis large and rounded, dorso-distally oriented, the inner lobe b sub-rectangular shaped with anterior and posterior angles rounded. Bursa

copulatrix rounded with a well-sclerotized distal strip and an internal conical structure. Female genital lobe widely rounded without any posterior expansion. Ocular structures not visible.

Etymology

The new species is named after Cécile Capderrey who collected this species during her PhD.

Type material

Holotype

FRANCE • ♂, dissected appendages mounted in glycerine, valves stored in ethanol; Alpes de Haute Provence district, Noyer-sur-Jabron municipality; 44.1668° N, 5.9251° E; 468 m a.s.l.; Jun.–Jul. 2010; C. Capderrey leg.; interstitial habitat of the Jabron River before its confluence with the Buech River; MNHN-IU-2023-705.

Allotype

FRANCE • ♀; same data as for holotype; MNHN-IU-2023-706.

Paratypes

FRANCE • 1 ♂; same data as for holotype; MNHN-IU-2023-707 • 2 ♂♂; same locality as for holotype; undissected; UCBLZ 2012-3-208 • 2 juvs; same data as for holotype; UCBLZ 2012-3-153-3 to UCBLZ 2012-3-153-4.

Other material examined

FRANCE • 8 juvs, undissected; UCBLZ.2012-3-208.

Description

Measurements. Holotype, ♂ (MNHN-2023-705): LV: L = 600 µm, H = 300 µm (H/L = 0.50). RV = 585 µm, H = 285 µm (H/L = 0.48). W = 205 µm (W/L = 0.34). Range for males (n = 2): L = 595–600 µm, H = 300 µm, W=195–205 µm. Allotype, ♀ (MNHN-2023-706): LV: L=537 µm, H=260 µm (H/L=0.48). RV: L=530 µm, H=232 µm (H/L=0.43). W=180 µm (W/L=0.33).

Carapace. Whitish with ornamentation consisting of fossae on its entire surface. General shape of carapace trapezoid (Figs 5, 18C–D). LV overlaping RV with marked cardinal angles. Highest H located at 40 and 63% of animal length. H/L = 0.50 for male and H/L=0.48 for female. Carapace slightly compressed centrally in dorsal view (Fig. 5C, G), with greatest W at ⅓ and ⅔ L, representing 33% of L. Anterior and posterior ends weakly beak-shaped.

Valves. For both valves (Fig. 5), anterior margin widely rounded, while posterior margin more pointed, dorso-posterior margin straight and dorso-anterior margin slightly concave. RV smaller than LV (3% of L difference). LV with ventral margin slightly concave in male and straight in female (Fig. 5D, H). RV with a dorsal margin slightly concave (Fig. 5B, F), while LV is straight (Fig. 5D) or poorly curved (Fig. 5H). Dorsal margin representing 33% of L in both male and female. Anterior and posterior calcified inner lamellas sub-equal, representing 10% of L. Fused marginal valve zone narrow, representing 2.5% of L for both male and female, with straight and dense radial pore canals, more numerous anteriorly.

Antennule, A1 (Figs 6A, 7A). I+II: A-1l(pu), P-2l(pu)/III: 0/IV: A-1s/V: A-1l, P-1m/VI: A-1l/VII: A-2l-1s(α), P-1l/VIII: D-2l-ya-1l(cs). Using IV podomere as reference, the ratios of podomeres are 1.4-1-1.3-1-1.6-1.6 from III to VIII. The ya aesthetasc very long, 7–11 × as long as IV podomere.

Antenna, A2 (Figs 6B–D, 7B–D). Protopodite: coxa with 3 setae, 2 long and smooth, 1 short and plumose; basis with 1 long posterior seta; exopodite with 1 long and 2 short setae; EI with 1 posterior aesthetasc Y (equalling to 60% of the length of EI) and distally 2 setae (1s and 1m).

Male A2 (Fig. 6B–D). EII and EIII segmented as 2 individuated podomeres. EII with 1 short aesthetasc (y1) and 4 t setae, t1 medium, t4 short, t2 and t3 transformed in male bristles with length equal to 80% of EI length. EIII with 1 short aesthetasc (y2), 3 external z setae, z1 and z3 equal or slightly longer than EIV length, z2 transformed in long claw (160% of EI length). G1 reduced (56% of EI length), G2 well-developed (180% of EI length), G3 reduced to long bristle (84% of EI length). EIV with

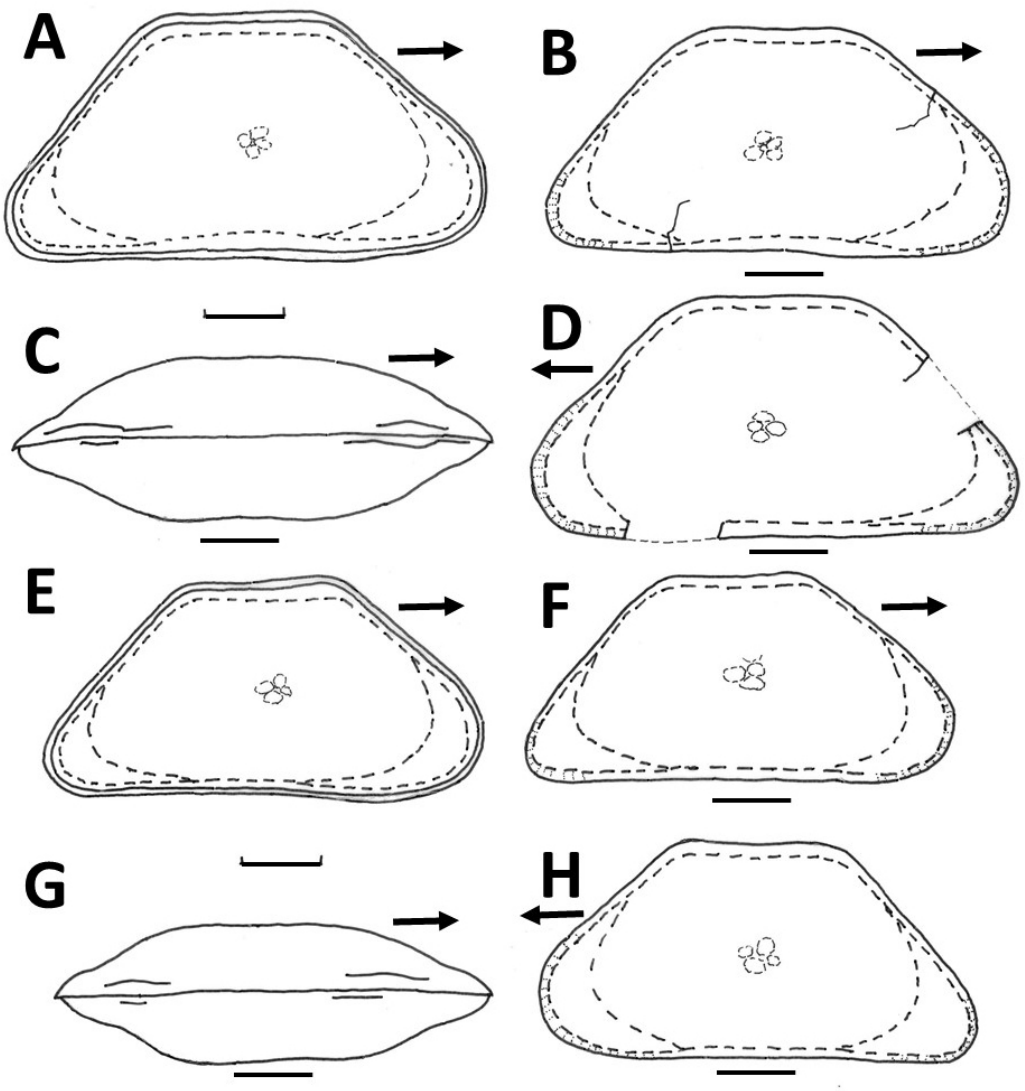

Fig. 5. *Schellencandona capderreyae* sp. nov. **A**–**D**. Holotype, ♂ (MNHN-IU-2023-705) **A**. Right view of the undissected specimen. **B**. Right valve, external view. **C**. Dorsal view of whole carapace. **D**. Left valve, external view. **E**–**H**. Allotype, ♀ (MNHN-IU-2023-706). **E**. Right view of the undissected specimen. **F**. Right valve, external view. **G**. Dorsal view of whole carapace. **H**. Left valve, external view. Scale bars = 100 μm. Arrows point to anterior margin

2 claws, posteriorly 1 long (Gm, 170% of EI length) and anteriorly 1 reduced (GM, 52% of EI length), 1 aesthetasc (y3, 60% of EI length) associated with subequal seta, g seta present.

Female A2 (Fig. 7B–D). EII and EIII fused, with anteriorly 2 short aesthetacs (y1 and y2), 3 t setae, distally 2 z setae (z1 twice the length of EIV and z2 short). G2 claw reduced (55% of EI length). G1 and G3 claws well-developed and sub-equal (170% EI length). EIV with anteriorly 1 long (GM, 140% of EI length) and posteriorly 1 reduced claw (Gm, 66% of EI length), 1 aesthetasc (y3, 45% of EI length) with subequal seta, g seta present.

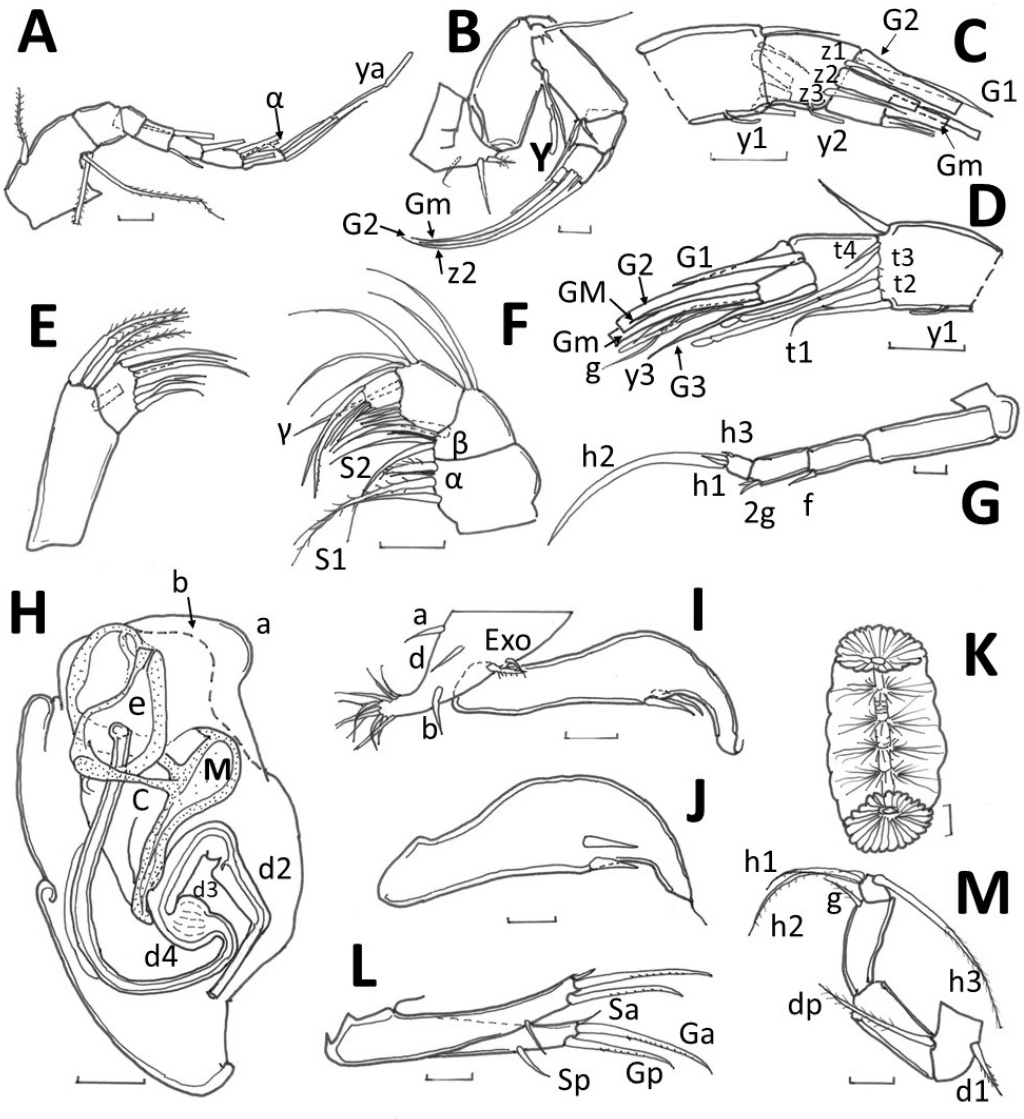

Fig. 6. *Schellencandona capderreyae* sp. nov., holotype, ♂ (MNHN-IU-2023-705). **A**. Antennule (A1). **B**. Antenna (A2). **C**. Detail of antenna, external view. **D**. Detail of antenna, internal view. **E**. Maxillula (Mx1) palp. **F**. Mandibular palp (Mdp). **G**. Walking leg (L6). **H**. Hemipenis, outer view. **I**. Left 5th limb (with clasping organ). **J**. Right clasping organ. **K**. Zenker's organ. **L**. Caudal ramus. **M**. Cleaning leg (L7). Abbreviations: see Material and methods. Scale bars = 20 µm.

Mandible. Consists of coxal plate and 4-segmented palp (Mdp). Coxa typically shaped, heavily chitinized with masticatory part. 1st podomere of Mdp (Figs 6F, 7F) 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 group of 3 smooth setae and second group of 2 setae (1 long and 1 short, β). 3rd podomere with externally 3 setae, distally 1 long and smooth seta (γ) and internally 3 small setae. 4th podomere with 2 serrated and long claws (190% of 3rd podomere length) and 3 small setae.

Maxillular palp (Mx1palp, Figs 6E, 7E). Two-segmented: 1st segment with 4 apical plumose setae on outer corner. 2nd segment with 2 claw-like setae (4 time as long as 2nd segment) and 4 thinner setae.

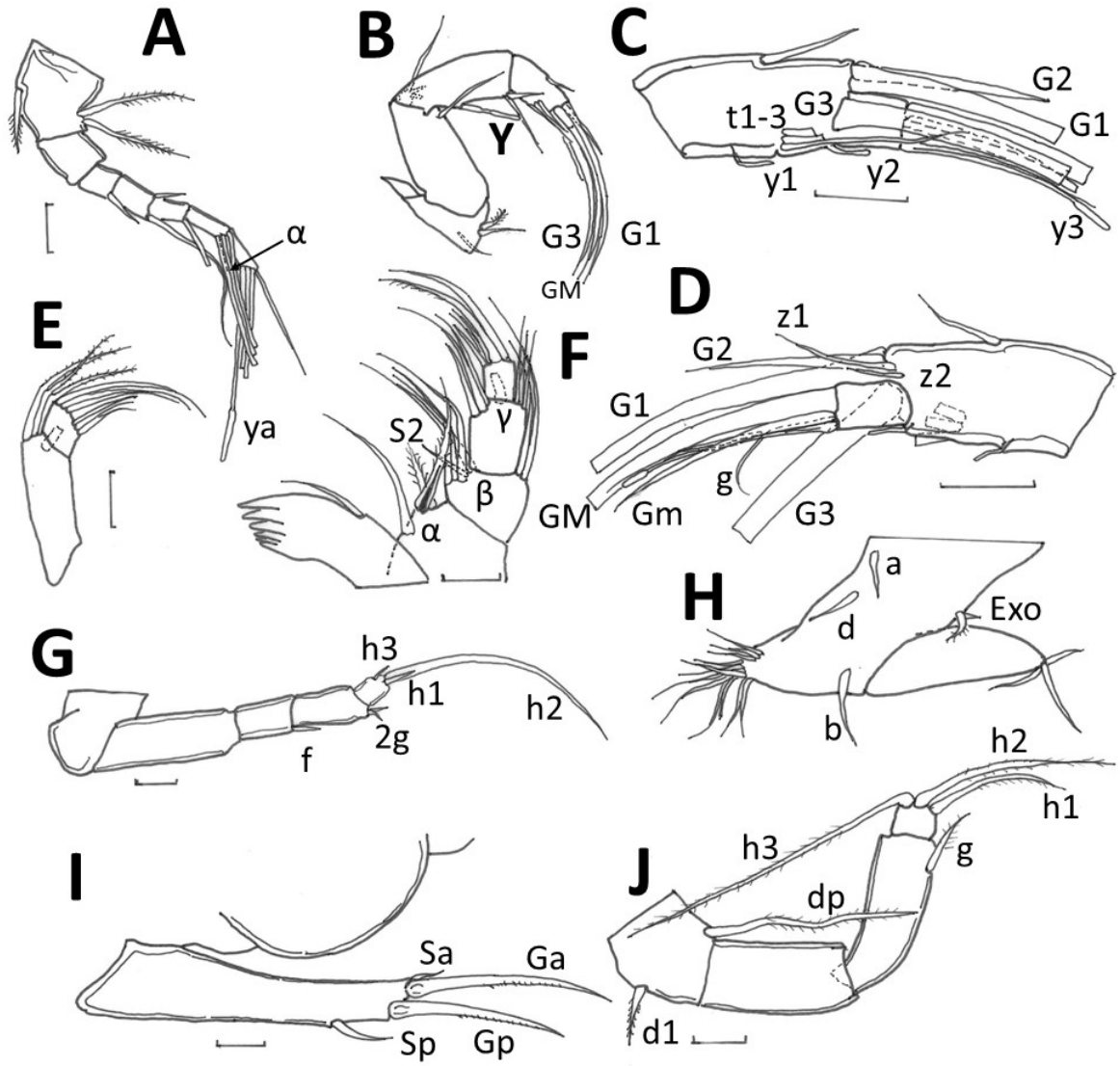

Fig. 7. *Schellencandona capderreyae* sp. nov., allotype, ♀ (MNHN-IU-2023-706). **A**. Antennule (A1). **B**. Antenna (A2). **C**. Detail of antenna, internal view. **D**. Detail of antenna, external view. **E**. Maxillula (Mx1) palp. **F**. Mandibular palp (Mdp). **G**. Walking leg (L6). **H**. Maxilla (L5). **I**. Caudal ramus with genital lobe. **J**. Cleaning leg (L7). Abbreviations: see Material and methods. Scale bars = 20 μm.

Maxilla (L5, Figs 6I–J, 7H). With protopodite bearing 1 anterior seta (a) and 2 exterior setae (b and d), masticatory process (endite) apically with group of 11 setae. Exopodite plate with 2 filaments. Male endopodites transformed in asymmetrical clasping organs (right one more developed, left one slender), slightly curved with 2 short but thick setae on ventral side and thin apical seta. In female, similar set of setae observed on protopodite and 2 filaments on exopodite. Endopodite with 3 short apical setae.

Walking leg (L6, Figs 6G, 7G). Five-segmented. Protopodite and EI without seta. EII with f seta and EIII with 2 g setae. EIV with 2 short setae (h1 and h3) and long claw (h2) equalling 160% of EI length.

Cleaning leg (L7, Figs 6M, 7J). Four-segmented (with EII and EIII fused). Protopodite with 1 short (d1) and 1 long setae (dp, 130% of EI length). EI without seta, EII+EIII with short seta (g). EIV with 3 long setae: h1 (sub-equal to EI length), h2 and h3 (130% and 200% of EI length, respectively).

Caudal ramus (CR, Figs 6L, 7I). Robust with medium-sized sp seta (22%–27% of anterior margin of CR, just reaching basis of Gp), short sa seta and 2 long and curved claws (Ga and Gp representing around 80–84% to 64–67% of anterior margin of CR, respectively), both claws serrated.

Female genital lobe (Fig. 7I). Widely rounded without posterior expansion. Oocyte large (12% of valve length).

Male genital organs. Zenker's organ (Fig. 6K) with 6 internal rings of spines representing 20% of total length of carapace. Hemipenis (Fig. 6H) with distal outer lobe (a) large and rounded, dorso-distally oriented, inner lobe (b) sub-rectangular shaped with anterior and posterior angles rounded and small plication on ventral side. Lobe h not observed. Labyrinth well-sclerotized and divided in 4 sections, section d4 weakly reticulated. Copulatory tube thin located inside rounded bursa copulatrix (e) with well-sclerotized curved distal strip and internal conical structure. M-process flat with broad rounded dorso-distal part, linked to C strip, and thin basal part reaching d4 section of labyrinth.

Ocular structures. Not visible.

Ecology and distribution

Schellencandona capderreyae sp. nov. was collected from the interstitial habitat of a single river, the Jabron River, a tributary of the Durance River (Fig. 1), in a single sample at an elevation of 468 m a. s.l. It was sampled at the downstream end of a gravel bar (groundwater upwelling zone) at a depth of 90 cm into the riverbed sediment. Water had a temperature of 18.7°C, an electrical conductivity of 382 $\mu S.cm^{-1}$, a pH of 7.9 and a rather high dissolved oxygen concentration (i.e., 6.3 $mg \cdot L^{-1}$).

Specialisation to groundwater: its very long aethetascs (ya on A1, Y and y3 on A2), the lack of visible eyes and the large size of the oocyte (12% of the body length) suggest a specialisation of the species to groundwater life. *Schellencandona capderreyae* sp. nov. can be considered, for the moment, as an endemic stygobiotic species.

Taxonomic remarks

The general shape of the carapace of the new species (trapezoid) is very similar to those of *S. schellenbergi* and *S. simililampadis*, but differs by the dorsal margin, which is parallel to the ventral margin in the new species (Figs 5, 18C), while it is inclined backwards in the two other species.

The new species differs from the other European species. It is very close to *S. simililampadis* and *S. schellenbergi*, but differs in the three following characteristics: (1) A2 with a z2 seta transformed in a claw in males (see Fig. 19A for A2 of *S. simililampadis)*; (2) stocky shape of the hemipenis, with the dorso-distal location of the outer a lobe, the small size of the h lobe (not visible) and the curved distal

sclerotized strip on the bursa copulatrix. In addition, S*chellencandona capderreyae* sp. nov. differs from the above-mentioned two species by (1) the A1 with a reduced number of setae, especially the lack of seta on podomere III in both males and females (seta present in *S. schellenbergi*), (2) the single anterior seta on podomere IV of A1 (two setae in the two other species), and (3) the lack of d and e setae on L6 (both present in *S. simililampadis*).

The relationships between S*chellencandona capderreyae* sp. nov. and the four other species described in this work are detailed in the Discussion.

Schellencandona mercantourensis sp. nov.
urn:lsid:zoobank.org:act:EE6DF96A-2A5F-4345-9FA7-1D76CFB3FBD4
Figs 8–10, 18, 20; Tables 1, 3

Synonymy

Candoninae sp. 3 – Dole-Olivier *et al.* 2015: 537, table 2.

Diagnosis

Small trapezoid candonine of the genus *Schellencandona* (L = 545 µm). Carapace thin without ornamentation. Anterior margin widely rounded, while posterior margin more pointed, dorsal margin straight in LV and slightly concave in RV, dorso-posterior margin slightly convex. Greatest H of LV located in the anterior third (H/L=0.50) in male. Strong asymmetry between the two valves: LV overlaps the RV, RV 4% shorter in length than LV, resulting in a posterior gap between the two valves. Anterior and posterior calcified inner lamellas amounting to c. 14% and 9% of L, respectively. A1 without seta on the 3rd podomere and 2 setae on the 6th podomere. Male A2: EII and EIII separated with t2 and t3 transformed in male bristles, 3 z setae (z2 longer than z1 and z3), the longest claw (G2) represents 175% of EI length. Female A2: EII+III with 3 t and 2 z setae (z1 longer than z2). 2nd podomere of the Mdp bears 3+2 setae. Endopodites of the maxilla (L5) developed in males into prehensile palps strongly asymmetrical, the right one hook-shaped with a ventro-distal angle marked by a sclerotized hump. Walking leg (L6) with d, e, f setae and one g seta. Cleaning leg (L7) 4-segmented, EII and EIII fused, with 2 setae (d1 and dp) on the protopodite. Zenker's organ with 6 internal rings of spines. The outer lobe (a) of the hemipenis large and rectangular shaped, dorso-distally oriented. The inner lobe (b) is dorsally widely rounded. Lobe h short and ventrally rounded. Bursa copulatrix (e) rounded with a conical internal structure and a well-sclerotized dorsal strip. Female genital lobe anteriorly slightly rounded with a small posterior triangular expansion. Ocular structures not visible.

Etymology

The new species is named after the Mercantour National Park where the species was collected during a groundwater biodiversity survey.

Type material

Holotype

FRANCE • ♂, dissected appendages mounted in glycerine, valves stored in ethanol; Alpes de Haute Provence district, Colmars les Alpes municipality; 44.1789° N, 6.6206° E; 1225 m a.s.l.; Sep. 2010; M.-J. Dole-Olivier leg.; interstitial habitat of the Verdon River; MNHN-IU-2023-708.

Allotype

FRANCE • ♀; same data as for holotype; MNHN-IU-2023-709.

Paratype

FRANCE • 1 ♀, dissected appendages mounted in glycerine, valves stored in ethanol; Alpes Maritimes district, Saint Etienne de Tinée; 44.2344° N, 6.9492° E; 1080 m a.s.l.; Apr. 2009; M.-J. Dole-Olivier leg.; interstitial habitat of the Tinée River; MNHN-IU-2023-710.

Other material examined

FRANCE • 3 juvs, undissected; collected in the Verdon River; UCBLZ.2012-3-217.

Description

Measurements. Holotype, ♂ (MNHN-2023-708): LV: L = 545 µm, H = 275 µm (H/L = 0.50). RV: L = 520 µm, H = 245 µm (H/L = 0.47). W = 190 µm (W/L = 0.34). Allotype, ♀ (MNHN-2023-709): LV: L = 510 µm, H = 275 µm (H/L = 0.54). RV: L = 485 µm, H = 250 µm (H/L = 0.52). W = 185 µm (W/L = 0.36). Paratype, ♀ (MNHN-2023-710): LV: L = 520 µm, H = 260 µm (H/L = 0.50). RV: L = 495 µm, H = 235 µm (H/L = 0.47). W = 170 µm (W/L = 0.33).

Carapace. Whitish and thin, without ornamentation. Carapace trapezoid with marked cardinal angles (Figs 8, 18E–F). Highest H found at anterior third of animal (i.e., 42% of L). H/L = 0.50 for male and 0.50–0.54 for females. Carapace (Fig. 8C, G) moderately compressed in dorsal view, with greatest W at 50% of L, representing 0.33–0.36 of L. Anterior end weakly pointed. Posterior end moderately rounded.

Valves. For both valves (Fig. 8), anterior margin widely rounded, posterior margin more pointed, dorso-posterior margin slightly convex. Both valves are strongly asymmetrical: LV overlaps RV, RV 4% shorter in length than LV, causing posterior gap between two valves (Fig. 8A, E). Dorsal margin straight in LV and slightly concave in RV, representing 28% of L. Ventral margin straight in LV and slightly concave in RV for both male and female (Fig. 8D, H). Anterior calcified inner lamella larger (14% and 11% of L for male and female respectively) than posterior one (9% of L for both sex). Fused marginal valve zone narrow, representing 2.5% of L in both male and female, with straight and dense radial pore canals, more numerous anteriorly.

Antennule, A1 (Figs 9A, 10A). I+II: A-1l(pu), P-2l(pu)/III: 0/IV: A-1s/V: A-1l, P-1s/VI: A-2l/VII: A-2l-1s(α), P-1l/VIII: D-2l-ya-1l(cs). Using IV podomere as reference, lengths of podomeres are in the ratios of 1.2-1-1.1-1-1-1.1 from III to VIII in male. ya aesthetasc very long, equal to 6× as long as IV podomere.

Antenna, A2 (Figs 9B–D, 10B–D). Protopodite: coxa with 3 setae, 2 long and smooth, 1 short and plumose; basis with 1 long posterior seta; exopodite with 1 long and 2 short setae; EI with 1 posterior aesthetasc Y (equalling 69% of EI length) and distally 2 setae (1s and 1m).

Male A2 (Fig. 9B–D). EII and EIII segmented forming 2 distinct podomeres. EII with 1 short aesthetasc (y1) and 4 t setae, t1 medium, t4 short, t2 and t3 transformed in male bristles with length equal to 94% of EI length. EIII with 1 short aesthetasc (y2), 3 external z setae, z1 and z3 slightly longer than EIV length, z2 of medium size (40% of EI length). G1 reduced (72% of EI length), G2 well-developed (175% of EI length), G3 reduced to long bristle (45% of EI length). EIV with 2 claws, posteriorly 1 long (Gm, 150% of EI length) and anteriorly 1 reduced (GM, 55% of EI length), 1 aesthetasc (y3, 58% of EI length) associated with subequal seta, g seta present.

Female A2 (Fig. 10B–D). EII and EIII fused, with anteriorly 2 short aesthetacs (y1 and y2), 3 t setae, distally 2 z setae (z1 150% of EIV length and z2 short). G2 claw reduced (45% of EI length). G1 and G3 claws well-developed and sub-equal (185 and 160% of EI length, respectively). EIV with anteriorly 1

long (GM, 147% of EI length) and posteriorly 1 reduced claw (Gm, 50% of EI length), 1 long aesthetasc (y3, 70% of EI length) with sub equal seta, g seta present.

MANDIBLE. Consisting of coxal plate and 4-segmented palp (Mdp). Coxa typically shaped, heavily chitinized with masticatory part. 1st podomere of Mdp (Figs 9F, 10F) with externally exopodite plate and 2 long setae, internally with 2 long setae (1 smooth and 1 plumose S1) and 2 short setae (1 smooth, α, and 1 plumose, S2). 2nd podomere with externally 2 setae and internally group of 3 smooth setae and second group of 2 setae (1 long and 1 short, β). 3rd podomere with externally 3 setae, distally 1 long smooth seta (γ) and internally 3 small setae. 4th podomere with 2 serrated and long claws (2.2 × as long as 3rd podomere) and 3 small setae.

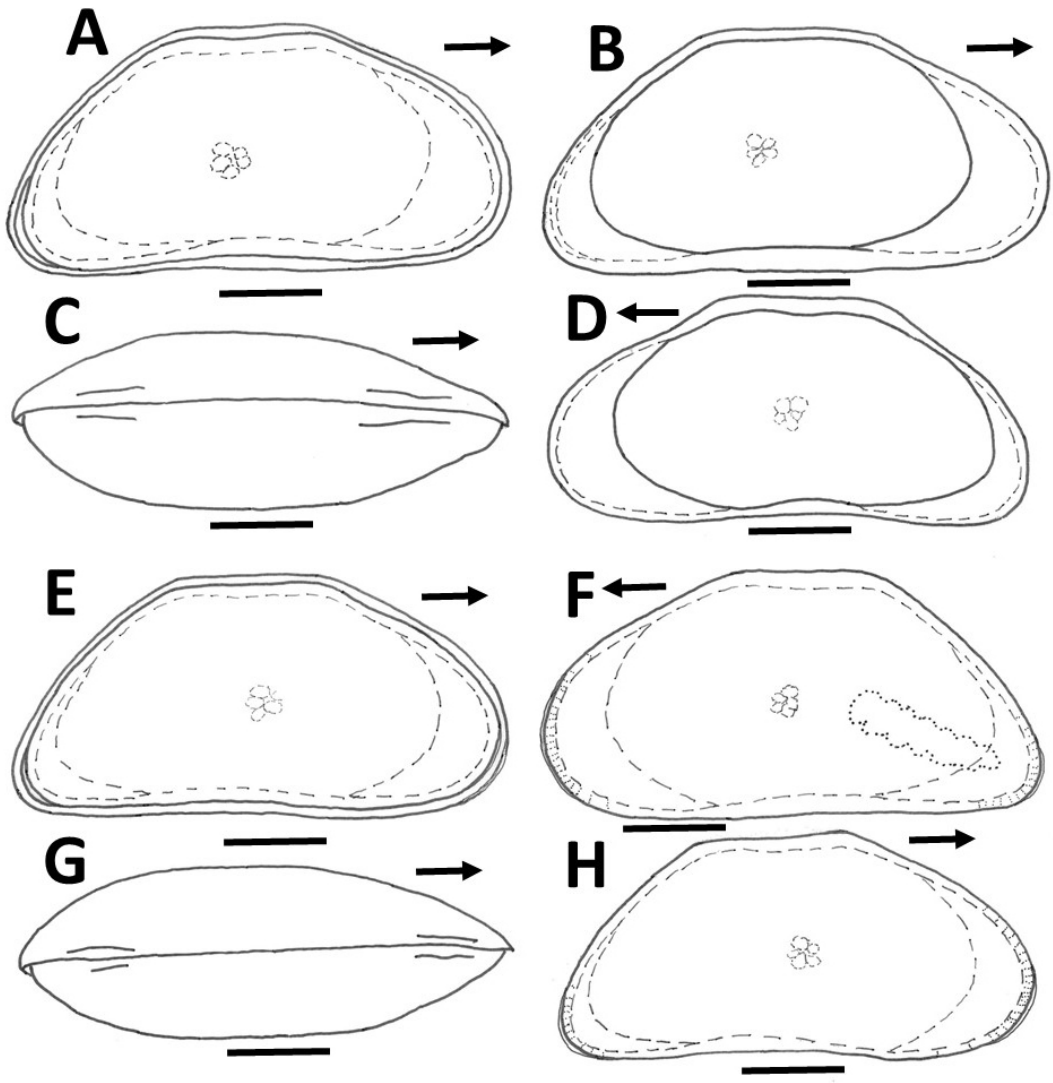

Fig. 8. *Schellencandona mercantourensis* sp. nov. **A–D**. Holotype, ♂ (MNHN-IU-2023-708) **A**. Right view of the undissected specimen. **B**. Left valve, internal view. **C**. Dorsal view of whole carapace. **D**. Right valve internal view. **E–H**. Allotype, ♀ (MNHN-IU-2023-709). **E**. Right view of the undissected specimen. **F**. Left valve, external view. **G**. Dorsal view of whole carapace. **H**. Right valve, external view. Scale bars = 100 μm. Arrows point to anterior margin.

Maxillular palp (Mx1palp, Figs 9E, 10E). Two-segmented: 1st segment with 4 apical plumose setae on outer corner. 2nd segment with 2 claw-like setae (4.7 × as long as 2nd segment) and 4 thinner setae.

Maxilla (L5, Figs 9I–J, 10I). With protopodite bearing 1 anterior seta (a) and 2 exterior setae (b and d), masticatory process (endite) apically with group of 10 setae. Exopodite plate with 2 filaments. Male endopodites transformed in clasping organs strongly asymmetrical. Right one strongly sclerotized, distal end hook-shaped, ventro-distal angle marked by sclerotized hump. Left one stocky and slightly curved. Two endopodites bear 2 short but thick setae on ventral side and thin apical seta. In female, similar set of setae observed on protopodite and 2 filaments on exopodite. Endopodite with 3 short apical setae.

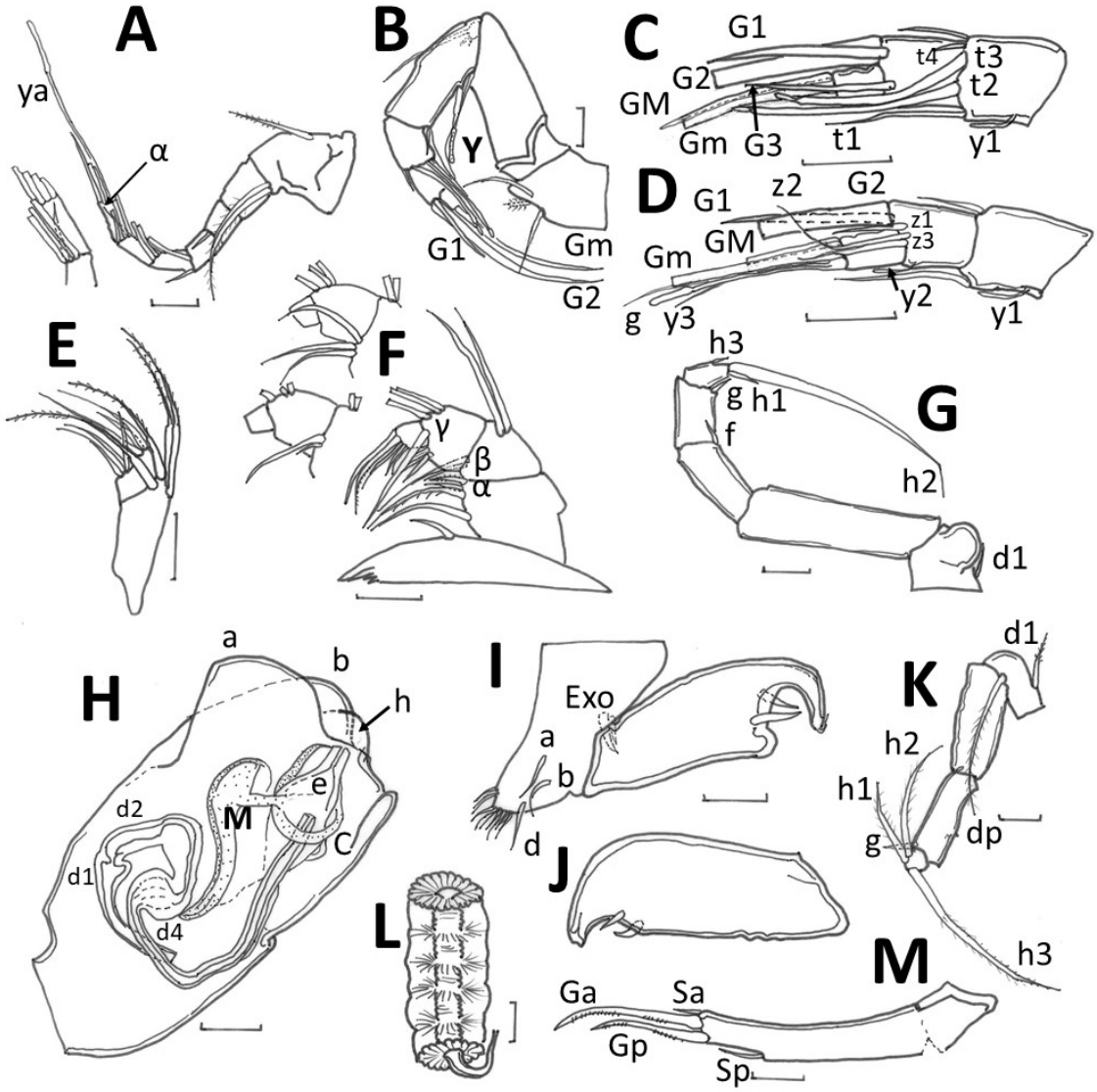

Fig. 9. *Schellencandona mercantourensis* sp. nov., holotype, ♂ (MNHN-IU-2023-708). **A**. Antennule (A1) with a detail of the 7th and 8th podomeres. **B**. Antenna (A2). **C**. Detail of antenna, internal view. **D**. Detail of antenna, external view. **E**. Maxillula (Mx1) palp. **F**. Mandibular palp (Mdp) with details of the 2nd podomere. **G**. Walking leg (L6). **H**. Hemipenis, outer view. **I**. Right 5th limb (with clasping organ) **J**. Left clasping organ. **K**. Cleaning leg (L7). **L**. Zenker's organ. **M**. Caudal ramus. Abbreviations: see Material and methods. Scale bars = 20 µm.

Walking leg (L6, Figs 9G, 10J). Five-segmented. Protopodite with one d seta, EI with one e seta (not observed in male holotype), EII with f seta and EIII with one g seta. EIV with 2 short setae (h1 and h3) and long claw (h2) serrated and equalling 145% the EI length.

Cleaning leg (L7, Figs 9K, 10G). Four-segmented (with EII and EIII fused). Protopodite with 1 short (d1) and 1 long setae (dp, 125% of EI length). EI without seta, EII+EIII with short seta (g). EIV with 3 long setae: h1, h2 and h3 (80%, 110% and 175% of EI length, respectively).

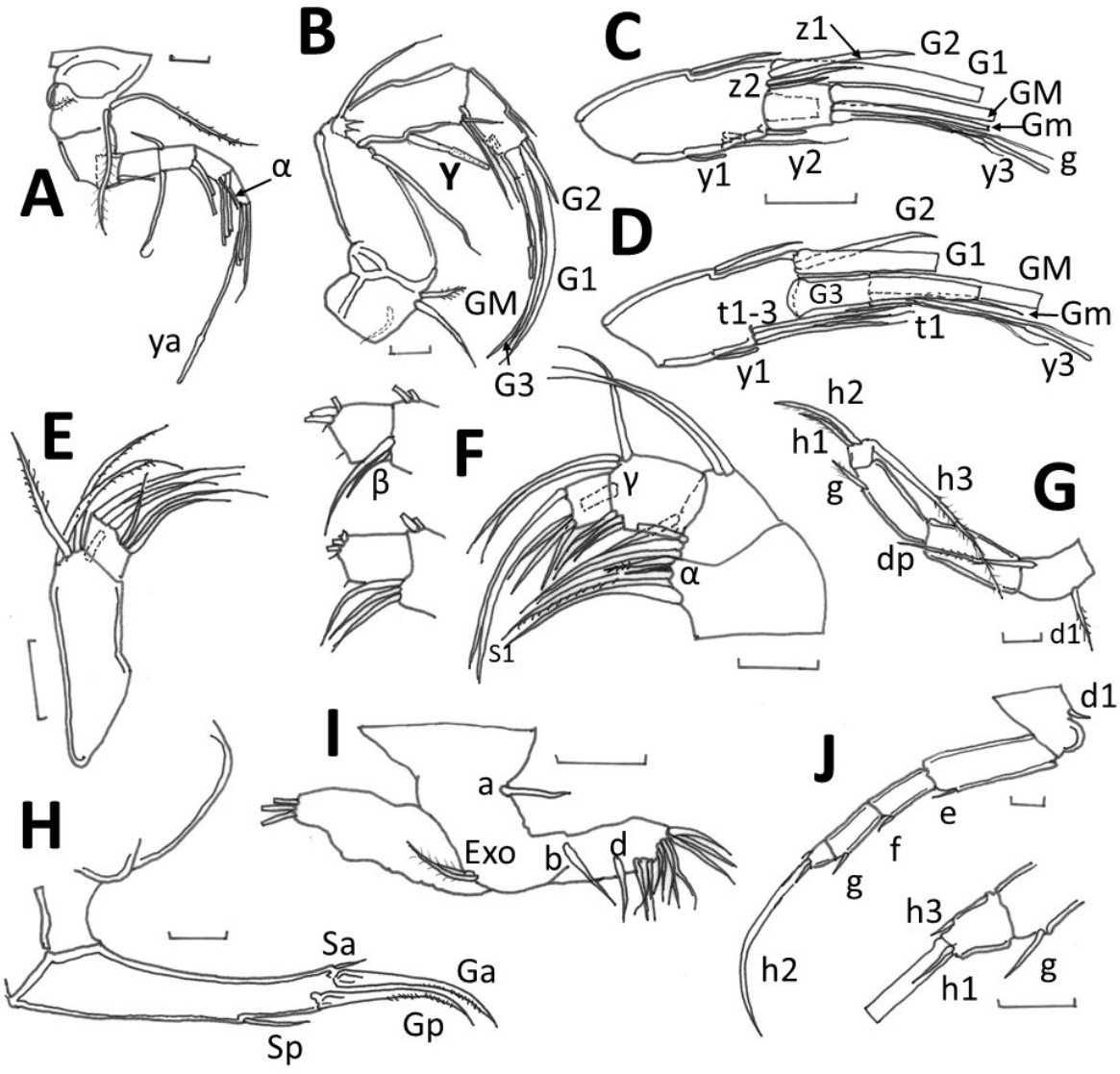

Fig. 10. *Schellencandona mercantourensis* sp. nov., allotype, ♀ (MNHN-IU-2023-709). **A**. Antennule (A1). **B**. Antenna (A2). **C**. Detail of antenna, external view. **D**. Detail of antenna, internal view. **E**. Maxillula (Mx1) palp. **F**. Mandibular palp (Mdp) with details of the 2nd podomere. **G**. Cleaning leg (L7). **H**. Caudal ramus with genital lobe. **I**. Maxilla (L5). **J**. Walking leg (L6) with a detail of EIII and EIV. Abbreviations: see Material and methods. Scale bars = 20 µm.

Caudal ramus (CR, Figs 9M, 10H). Robust with medium-sized sp seta (22%–29% of anterior margin of CR, not reaching basis of Gp), short sa seta and 2 long and curved claws (Ga and Gp representing around 69–71% and 54–65% of the anterior margin of CR, respectively), both claws serrated.

Female genital lobe (Fig. 10H). Anteriorly slightly rounded, with small posterior triangular expansion. Oocyte medium to large (9% of valve length).

Male genital organs. Zenker's organ (Fig. 9L) with 6 internal rings of spines representing 15% of total length of carapace. Hemipenis (Fig. 9H) with medium-sized distal outer lobe (a) and rectangular shaped, dorso-distally oriented. Inner lobe (b) dorsally widely rounded and small plication on ventral side. Lobe h short and ventrally rounded. Labyrinth well-sclerotized and divided in 4 sections, section d4 weakly reticulated. Copulatory tube thin located inside rounded bursa copulatrix (e) with marked dorsal sclerotized strip and conical internal structure. M-process flat with narrow rounded dorsal part, linked to C strip that joins base of e, and thin basal part reaching d4 section of labyrinth.

Ocular structures. Not visible.

Ecology and distribution

Schellencandona mercantourensis sp. nov. was sampled in the Mercantour National Park. It was collected in the interstitial habitat of two alpine rivers (i.e., the Verdon and Tinée rivers, Fig 1) at a depth of 50 cm into the riverbed sediment of two high-elevation sites (i.e., 1225 and 1080 m a.s.l., respectively). The species was not collected from the springs sampled in the same valleys and seems restricted to the interstitial habitat of the two rivers.

Specialisation to groundwater: the very long aesthetascs (ya on A1, Y and y3 on A2), the medium to large oocyte size (close to 9% of the body length) and the lack of a visible eye suggest a specialisation of the new species to groundwater. *Schellencandona mercantourensis* sp. nov. may be, for the moment, considered as a species specialized in riverbed sediment, with a narrow distribution area at high elevation in the Mercantour Mountains of the southern French Alps.

Taxonomic remarks

The general shape of *Schellencandona mercantourensis* sp. nov. is rather similar to the trapezoid *S. schellenbergi* and *S. simililampadis*, but the new species differs by its dorsal margin parallel to the ventral one (inclined backwards in the two other species), its convex dorso-posterior margin (straight in *S. schellenbergi*), and the asymmetry of the two valves (see below).

The new species differs from the other European and Asiatic species by the following four characteristics: (1) the strong asymmetry between the two valves (RV 4% shorter in length than LV inducing a posterior gap between the two valves), (2) by the shape of the L5 clasping organs (especially the strongly sclerotized hook-shaped right one) and (3) the shape of the hemipenis, rather thin, with a distally oriented a lobe and a very small but visible distal rounded h lobe. These three characteristics have never been observed in the genus *Schellencandona* before.

Despite these differences, *Schellencandona mercantourensis* sp. nov. may be related to *S. simililampadis* because of two light similarities: (1) a rather similar A1 chaetotaxy, without seta on podomere III and the two setae on podomere VI, and (2) the A2 with a z2 seta very long compared to z1, but not transformed in a claw like in *S. simililampadis* and *S. schellenbergi*.

The comparison between *Schellencandona mercantourensis* sp. nov. and the other species described here is detailed in the Discussion.

Schellencandona claretae sp. nov.
urn:lsid:zoobank.org:act:8EE9955F-D3A9-4AAF-A5E9-943602D30B46
Figs 11–14, 18, 20; Tables 1, 3

Diagnosis

Small trapezoid candonine of the genus *Schellencandona* (L = ~545 µm for the female and ~480 µm for the male). Carapace thin with poor ornamentation consisting of pits and a few fossae in the centre of the valves. Anterior margin widely rounded, posterior margin more pointed, dorsal margin slightly concave in both valves, dorso-posterior margin straight. Greatest H of LV located in the anterior third (H/L = 0.48). Strong asymmetry between the two valves: LV overlaps the RV, RV 5% shorter in length than LV inducing a posterior gap between the two valves. Calcified inner lamella amounting to ca 13% and 12% of L for the anterior and the posterior ones, respectively. A1 without seta on the 3rd podomere. Male A2: EII and EIII separated with t2 and t3 transformed in male bristles, 2 z setae (z2 medium to long), the longest claw (G2) represents 180% of EI length. Female A2: EII+III with 3 t and 2 z setae. 2nd podomere of the Mdp bears 3+2 setae. Endopodites of the maxilla (L5) developed in males into prehensile palps strongly asymmetrical, the right one hook-shaped with a ventro-distal angle marked by a sclerotized hump. Walking leg (L6) with e, f and 2 g setae. Cleaning leg (L7) 4-segmented, EII and EIII fused, with 2 setae (d1 and dp) on the protopodite. Zenker's organ with 6 internal rings of spines. The outer lobe (a) of the hemipenis large and rectangular shaped, dorso-distally oriented. The inner lobe (b) widely rounded posteriorly and the lobe h with a sub-triangular distal expansion. Bursa copulatrix (e) conical with a ventral well-sclerotized strip. Female genital lobe rounded without posterior expansion. Ocular structures not visible.

Etymology

The new species is named after Cécile Claret who collected the species during an ecological study of the Asse River.

Type material

The only available male has an unusual shape and length of its carapace. A female is therefore chosen as the holotype.

Holotype

FRANCE • ♀, dissected appendages mounted in glycerine, valves stored in ethanol; Hautes-Alpes district, Oraison municipality; 43.8793° N, 5.9051° E; 335 m a.s.l.; Jun. 2007; C. Claret leg.; interstitial habitat of the Asse River; MNHN-IU-2023-711.

Allotype

FRANCE • ♂; same data as for holotype; MNHN-IU-2023-712.

Paratype

FRANCE • 1 ♀, dissected appendages mounted in glycerine, valves stored in ethanol; Alpes de Hautes Provence district, Colmars les Alpes municipality; 44.1789° N, 6.6206° E; 1225 m a.s.l.; Sep. 2010; M.-J. Dole-Olivier leg.; interstitial habitat of the Verdon River; MNHN-IU-2023-713.

Other material examined

FRANCE • 5 juvs, undissected; collected in the Asse River; UCBLZ.2012-3-168; UCBLZ • 1 juv., undissected; collected in the Verdon River; UCBLZ.2012-3-217.

Description

Measurements. Holotype, ♀ (MNHN-2023-711): LV: L = 545 µm. H = 265 µm (H/L = 0.48). RV L = 515 µm, H = 250 µm (H/L = 0.48). W = 210 µm (W/L = 0.38). Paratype, ♀ (MNHN-2022-713): LV: L = 545 µm, H = 270 µm (H/L = 0.49). RV: L = 525 µm, H = 235 µm (H/L = 0.45). W = 180 µm (W/L = 0.33). Allotype, ♂ (MNHN-2023-712): LV: L = 480 µm, H = 230 µm (H/L = 0.48). RV L = 450 µm, H = 215 µm (H/L = 0.47). W = 185 µm (W/L = 0.38).

Carapace. Whitish and thin, with poor ornamentation of rare pits and small fossae in centre of valves. General shape of carapace trapezoid with marked cardinal angles (Figs 11A, E, G, 18G–H). Highest H located at third anterior part of animal (i.e., at 39% of L) with H/L = 0.48 for both male and female. Carapace viewed dorsally (Fig. 11D, F, H) moderately compressed, with greatest W at 50% of L in female, representing 38% of L. Carapace of male with greatest W at last third, representing 38% of L. Anterior end weakly beak-shaped in both sexes. Posterior end moderately rounded in female (Fig 11D) and more pointed in male (Fig. 11H). In female collected in Verdon River, similar general shape of carapace in lateral view (Fig. 11E; H/L = 0.49), but slenderer than holotype in dorsal view (Fig. 11F), with W representing 33% of L.

Valves. Two valves strongly asymmetrical: LV overlaps RV, RV 5% shorter in length than LV inducing posterior gap between two valves (Fig. 11A, E, G). For both valves, anterior margin widely rounded, while posterior margin more pointed, dorso-posterior margin straight. Dorsal margin slightly concave, representing 34% of L. Ventral margin slightly convex in LV (Fig. 11C, J) and slightly concave in RV for both male and female (Fig. 11B, I). Anterior calcified inner lamella larger (13% and 14% of L for female and male respectively) than posterior one (12% of L for female and 10% for male). Fused marginal valve zone narrow, representing 2% of L for both male and female, with straight and dense radial pore canals, more numerous anteriorly. Strong difference between male and female, in size (12% difference, see below) and in shape of the carapace, especially in dorsal view. Greatest width at 50% of length in female and at last third in male. Posterior end gently rounded in female, pointed and triangular-shaped in male.

Antennule, A1 (Figs 12A, 13A, 14A). I+II: A-1l(pu), P-2l(pu)/III: 0/IV: A-1s/V: A-1l, P-1s/VI: A-2l/VII: A-2l-1s(α), P-1l/VIII: D-2l-ya-1l(cs). Using IV podomere as reference, ratios of podomeres are 1.4-1-1.3-1.4-1.4-1.2 from III to VIII. ya aesthetasc very long, equalling 7.1 × as long as IV podomere. Female of Verdon River with similar set of setae on A1 and similarly long ya (Fig. 14A). Using IV podomere as reference, ratios of podomeres are 1.6-1-1.3-1.2-1.5-1.6 from III to VIII.

Antenna, A2 (Figs 12B–D, 13B–D, 14B–D). Protopodite: coxa with 2 setae, only 1 long and smooth seta observed, and 1 short and plumose; basis with 1 long posterior seta; exopodite with 1 long and 2 short setae; EI with 1 posterior aesthetasc Y (equalling 68% of EI length) and distally 2 setae (1s and 1m).

Male A2 (Fig. 12B–D). EII and EIII forming 2 distinct podomeres. EII with 1 short aesthetasc (y1) and 4 t setae, t1 and t4 short, t2 and t3 transformed in male bristles with length equal to 70% of EI length. EIII with 1 short aesthetasc (y2), 2 external z setae, z1 slightly shorter than EIV length, z2 of medium size (45% of EI length). G1 reduced (60% of EI length), G2 well-developed (180% of EI length), G3 reduced to short bristle (20% of EI length). EIV with 2 claws, 1 long posteriorly (Gm, 150% of EI length) and 1 reduced anteriorly (GM, 57% of EI length), 1 medium-sized aesthetasc (y3, 42% of EI length) associated with subequal seta, g seta not observed.

Female A2 (Fig. 13B–D). EII and EIII fused, with anteriorly 2 short aesthetascs (y1 and y2), 3 t setae, distally 2 z setae (both short). G2 claw reduced (63% of EI length). G1 and G3 claws well-developed (205% and 180% of EI length, respectively). EIV with anteriorly 1 long (GM, 170% of EI length) and posteriorly 1 reduced claw (Gm, 80% of EI length), 1 long aesthetasc (y3, 83% of EI length) with

subequal seta, g seta present. Female paratype of Verdon River (Figs 14B–D) with similar number of t and z setae on A2. Claws generally shorter than in the holotype: G2 reduced to 45% of EI length, G1 and G3 representing 190 and 175% of EI length. EIV with anteriorly 1 long claw (GM, 160% of EI length), posteriorly 1 reduced one (Gm, 50% of EI length) and y3 representing 57% of EI length, g seta present.

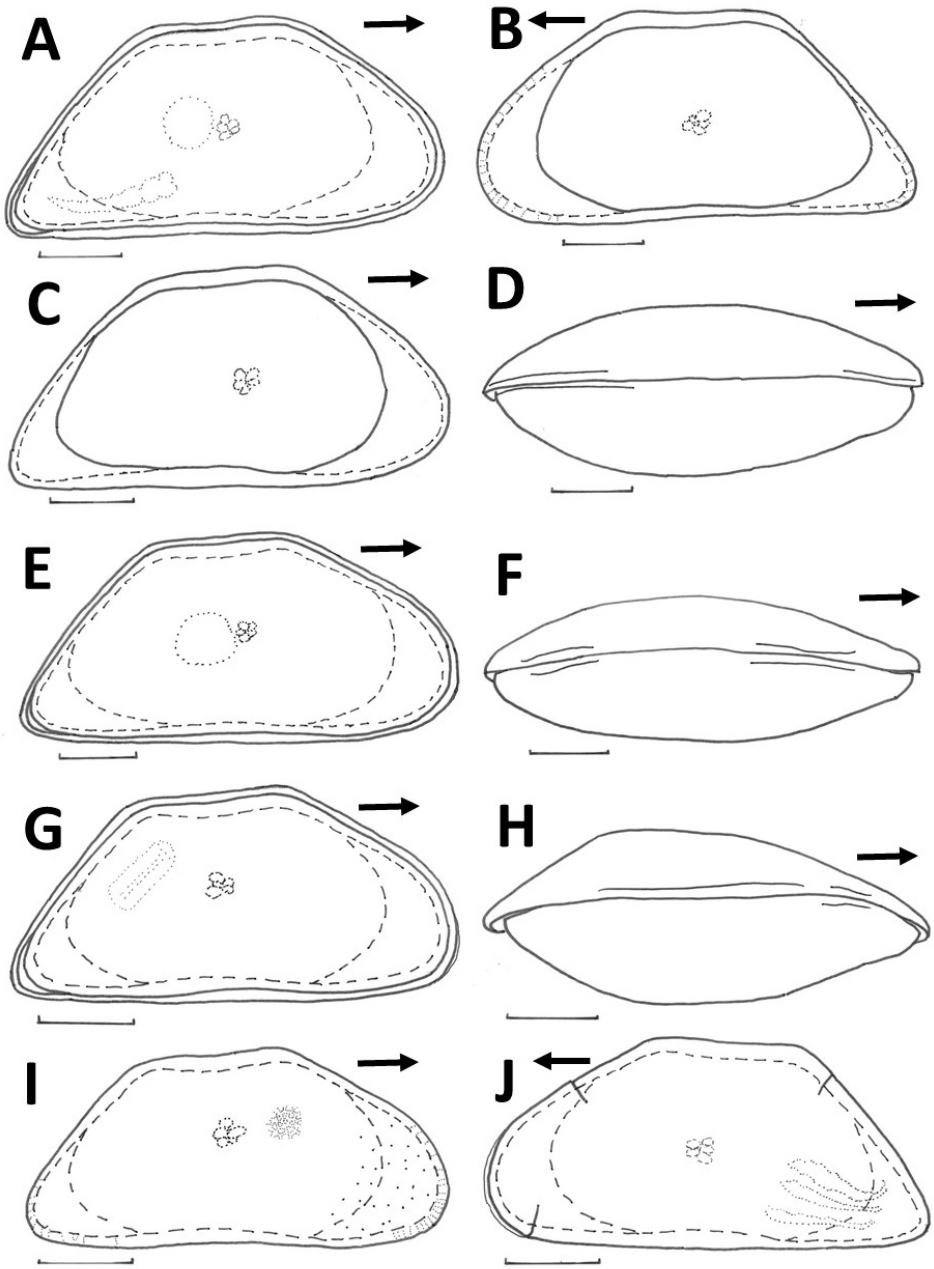

Fig. 11. *Schellencandona claretae* sp. nov. **A**–**D**. Holotype, ♀ (MNHN-IU-2023-711). **A**. Right view of the undissected specimen. **B**. Right valve, internal view. **C**. Left valve, internal view. **D**. Dorsal view of whole carapace. **E**–**F**. Paratype, ♀ (MNHN-IU-2023-713). **E**. Right view of the undissected specimen. **F**. Dorsal view of whole carapace. **G**–**J**. Allotype, ♂ (MNHN-IU-2023-712). **G**. Right view of the undissected specimen. **H**. Dorsal view of whole carapace. **I**. Right valve, external view with details of pits and small fossae. **J**. Left valve, internal view. Scale bars = 100 µm. Arrows point to the anterior margin.

MANDIBLE. Consisting of coxal plate and 4-segmented palp (Mdp). Coxa typically shaped, heavily chitinized with masticatory part. 1st podomere of Mdp (Figs 13E, 14F) with externally exopodite plate, internally with 2 long setae (1 smooth and 1 plumose S1) and 2 short setae (1 smooth α, 1 plumose, S2). 2nd podomere with externally 2 setae and internally group of 3 smooth setae and second group of 2 setae (1 long and 1 short, β). 3rd podomere with externally 3 setae, distally 1 long smooth seta (γ) and internally

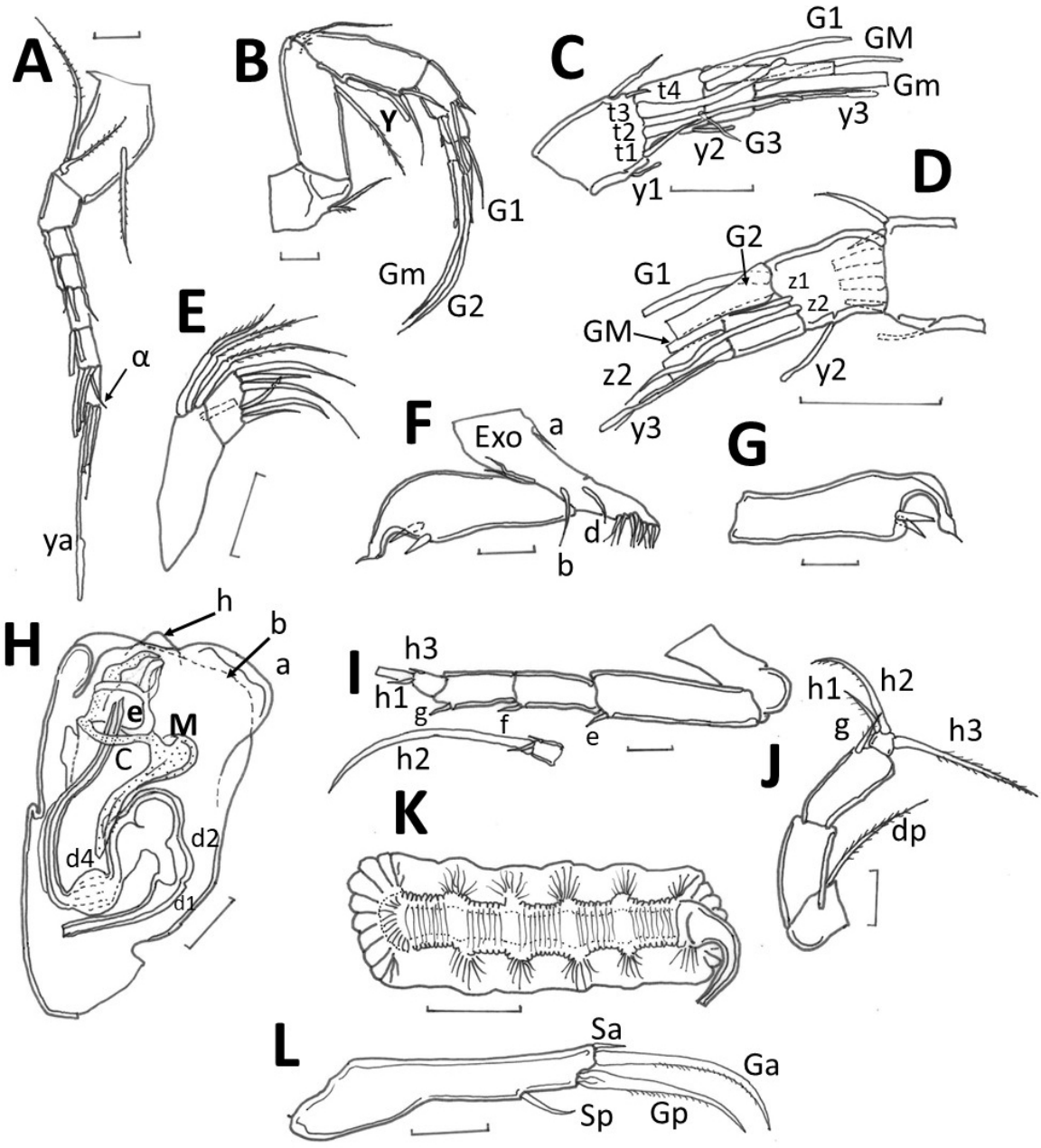

Fig. 12. *Schellencandona claretae* sp. nov., allotype, ♂, (MNHN-IU-2023-712), Asse River. **A**. Antennule (A1). **B**. Antenna (A2). **C**. Detail of antenna, internal view. **D**. Detail of antenna, external view. **E**. Maxillula (Mx1) palp. **F**. Left 5th limb (with clasping organ). **G**. Right clasping organ. **H**. Hemipenis, outer view. **I**. Walking leg (L6) with details of EIV. **J**. Cleaning leg, left clasping organ. **K**. Zenker's organ. **L**. Caudal ramus. Abbreviations: see Material and methods. Scale bars = 20 μm.

3 small setae. 4th podomere with 2 serrated and long claws (166% of the 3rd podomere length in holotype and 160% of 3rd podomere in paratype from Verdon River) and 3 small setae.

Maxillular palp (Mx1palp, Figs 12E, 13F, 14E). Two-segmented: 1st segment with 4 apical plumose setae on outer corner. 2nd segment with 2 claw-like setae (370% of 2nd segment length) and 4 thinner setae.

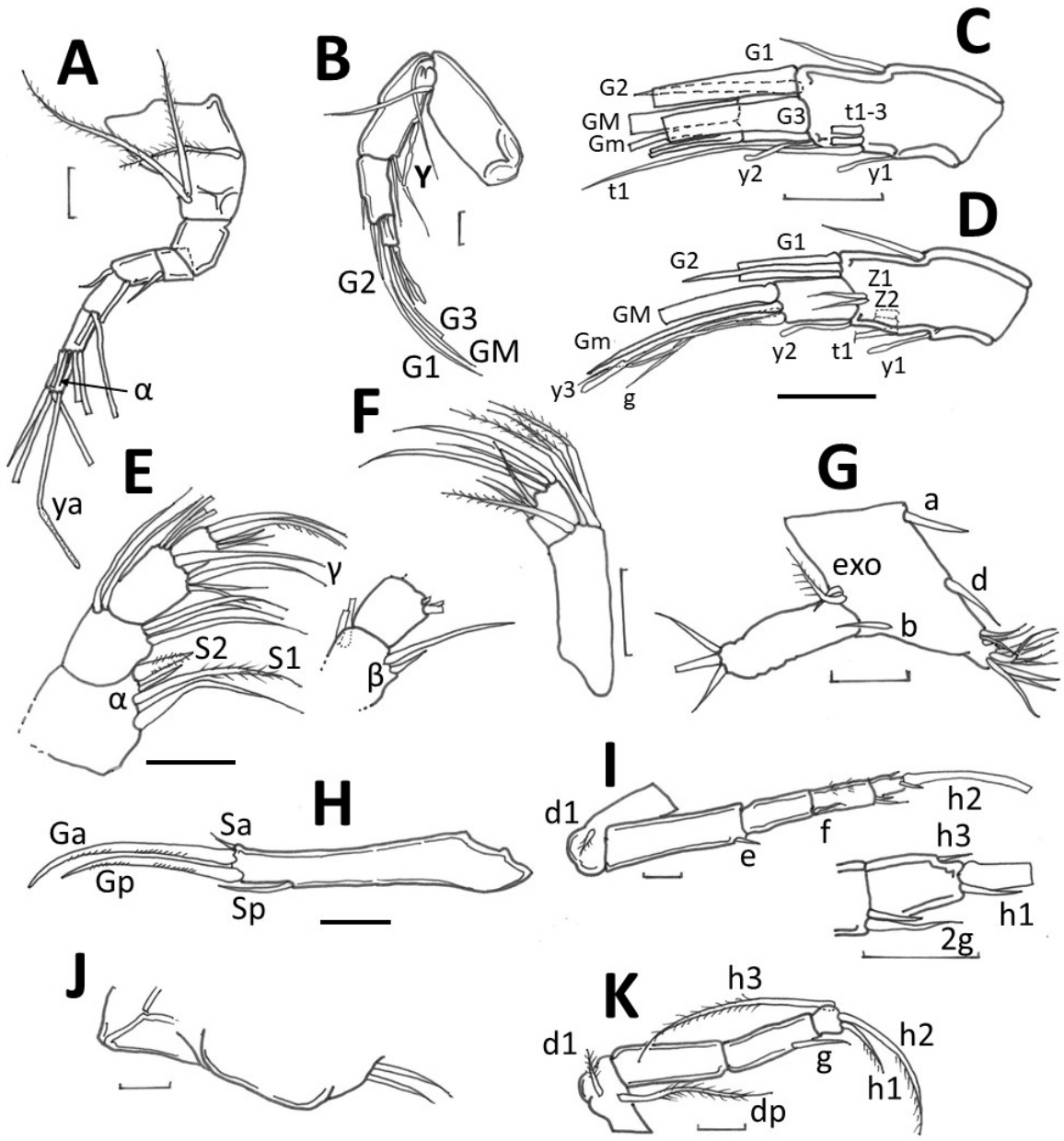

Fig. 13. *Schellencandona claretae* sp. nov., holotype, ♀ (MNHN-IU-2023-711), Asse River. **A**. Antennule (A1). **B**. Antenna (A2). **C**. Detail of antenna, internal view. **D**. Detail of antenna, external view. **E**. Mandibular palp (Mdp) with details of the 2nd podomere. **F**. Maxillula (Mx1) palp. **G**. Maxilla (L5). **H**. Caudal ramus. **I**. Walking leg (L6) with details of EIII and EIV. **J**. Caudal ramus with genital lobe. **K**. Cleaning leg (L7). Abbreviations: see Material and methods. Scale bars: = 20 µm.

Maxilla (L5, Figs 12F, 13G). With protopodite bearing 1 anterior seta (a) and 2 exterior setae (b and d), masticatory process (endite) apically with group of 11 setae. Exopodite plate with 2 filaments. Male endopodites (Fig. 12F–G) transformed in clasping organs markedly asymmetrical. Right one strongly sclerotized, distal end hook-shaped, ventro-distal angle marked by a sclerotized hump. Left one more rounded and slightly curved. Two endopodites bear 2 short but thick setae on ventral side and thin apical seta. In female (Fig 13G), similar set of setae observed on protopodite (a, b, d). Exopodite with 2 filaments and endopodite with 3 terminal setae.

Walking leg (L6, Figs 12I, 13I, 14G). Five-segmented. Protopodite with d seta (not observed in the male), EI with e seta, EII with f seta and EIII with 2 g setae (only one observed in male). EIV with 2 short

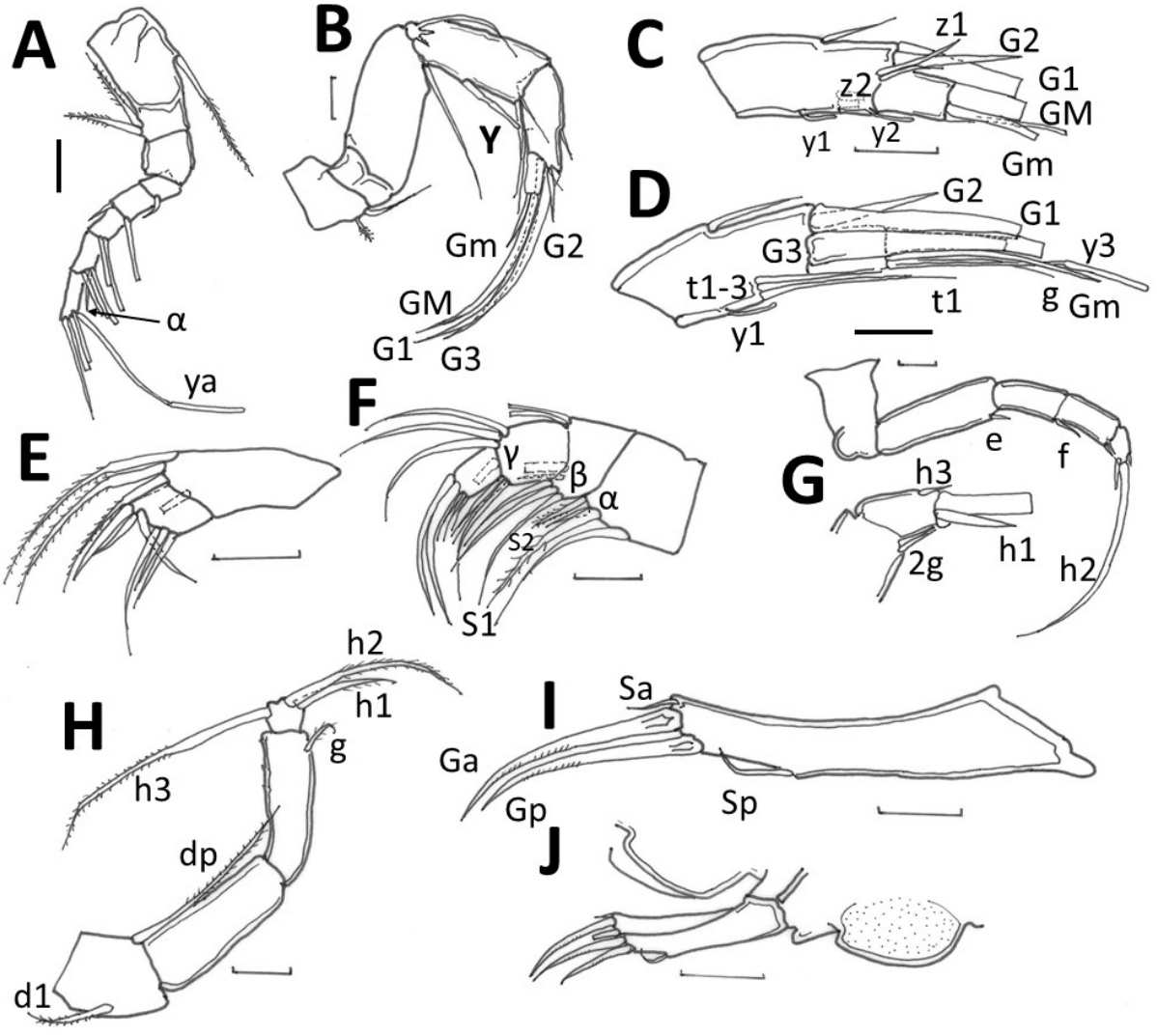

Fig. 14. *Schellencandona claretae* sp. nov., paratype, ♀ (MNHN-IU-2023-713), Verdon River. **A**. Antennule (A1). **B**. Antenna (A2). **C**. Detail of antenna, external view. **D**. Detail of antenna, internal view. **E**. Maxillula (Mx1) palp. **F**. Mandibular palp (Mdp) **G**. Walking leg (L6) with details of EIII and EIV. **H**. Cleaning leg (L7). **I**. Caudal ramus. **J**. Caudal ramus with genital lobe. Abbreviations: see Material and methods. Scale bars = 20 µm.

setae (h1 and h3) and long claw (h2) equalling 270% EII length. In paratype from Verdon River, similar setal arrangement observed (d, e, f and 2 g) with claw h2 representing 300% EII length.

Cleaning leg (L7, Figs 12J, 13K, 14H). Four-segmented (with EII and EIII fused). Protopodite with 1 short (d1) and 1 long seta (dp, 130–154% of EI length). EI without seta, EII+EIII with a short seta (g). EIV with 1 medium seta h1 (60–65% of EI length) and two long setae, h2 and h3 (130%–190% of EI length, respectively). In paratype from Verdon River, similar set of setae observed, with similar length for dp and h1, but slightly shorter h2 (120%) and h3 setae (160% of EI length).

Caudal ramus (CR, Figs 12L, 13H, 14I). Robust, with long sp seta (33% of anterior margin of CR) exceeding basis of posterior claw, short sa seta, 2 long and curved claws (Ga and Gp representing around 90% and 79% of anterior margin of CR, respectively), both claws serrated. In paratype from Verdon River, sp shorter (representing 26% of CR, not reaching basis of Gp), and Ga and Gp also shorter compared to holotype from Asse River (representing 79% and 73% of CR, respectively).

Female genital lobe. Simple (Figs 13J, 14J) simply rounded for both the holotype (Fig. 13J) and paratype (Fig. 14J), without posterior expansion. Oocytes large (14% of valve length).

Male genital organs. Zenker's organ (Fig. 12K) with 6 internal rings of spines representing 15% of total length of carapace. Hemipenis (Fig. 12H) with distal outer lobe (a) large and subrectangular, dorso-distally oriented. Inner lobe (b) widely rounded dorsally and with small plication on ventral side. Lobe h short with sub-triangular distal expansion. Labyrinth well-sclerotized and divided in 4 sections, section d4 weakly reticulated. Thin copulatory tube located inside conical bursa copulatrix (e) with well-sclerotized ventral strip C. The M-process flat with narrow rounded dorsal part, linked to C strip joining base of e and thin basal part reaching d4 section of labyrinth.

Ocular structures. Not visible.

Ecology and distribution

Schellencandona claretae sp. nov. was sampled in the interstitial habitat of two rivers located in the Southern Alps, both tributaries of the Durance River (the Verdon River and the Asse River, Fig 1). In the Verdon River, the species occurs at high elevation (i.e., 1225 m a.s.l.), at a depth of 50 cm into the riverbed sediment, but it has never been sampled in the springs of the same valley (Dole-Olivier *et al.* 2015). In the Asse River, the species occurs close to the confluence with the Durance River (Fig. 1), at low elevation (335 m a.s.l.). In the Asse River, the species always occurred deeper than 20 cm in the riverbed sediment: at a depth of -80 cm in the main channel and at depths of -50 and -80 cm in the 'backwaters' and the 'phreatic ponds' (partially or totally isolated secondary channels fed by groundwater, Table 2), respectively.

Specialisation to groundwater: the very long aesthetascs (ya on A1, Y, and y3 on A2), the large oocyte size (close to 10% of the body length), and the lack of eyes suggest specialisation of the new species to groundwater. *Schellencandona claretae* sp. nov. may be considered as a species living deep in river sediment, more frequently in marginal pools than in the main active channel, with a wide elevation range. The species is known only from two tributaries of the Durance River.

Morphological remarks

Variability between male and female

We observed strong differences between the male and the two females. The only male available for this species (allotype (MNHN-IU-2023-712)) is a mature adult with complete development of the A2 (with male bristles), of the Zenker's organ, the testes and the hemipenis, but with a surprisingly reduced

size compared to the females of both the Asse and the Verdon rivers (12% shorter than the female). In addition, this male has a rather different shape in dorsal view, with a posterior end that is more pointed and triangular. It is not possible, for the moment, to be certain whether these differences between males and females are attributable to a sexual dimorphism characteristic of the species or are linked to a teratological development of the only available male (e.g., Rossetti & Martens 1996).

Variability between populations

We observed some differences between the female collected in the Asse River (type locality; holotype (MNHN-IU-2023-711)) and the female collected in the Verdon River (paratype (MNHN-IU-2023-713)). This latter appears slenderer in dorsal view (W/L = 0.33 vs 0.38) than the Asse River individual. It also has slightly smaller claws on A2 (i.e., G2 representing 45% vs 63%, Gm representing 50% vs 80% and ya representing 57% vs 83% of EI length, respectively) and shorter terminal setae on L7 (i.e., h2 representing 120% vs 130% and h3 representing 160% vs 190% of EI length, respectively) than the Asse River individual. Similarly, the caudal ramus of the female collected in the Verdon River is shorter and stockier than in the Asse River: Ga representing around 79% vs 90% of the anterior margin length, Gp 73% vs 79%, and Sp representing 26% vs 33%, respectively.

Taxonomic remarks

The general shape of *Schellencandona claretae* sp. nov. is rather similar to the trapezoid *S. schellenbergi* and *S. simililampadis*, but the new species differs by the strong asymmetry between the two valves (see below), its dorsal margin parallel to the ventral one (inclined backwards in the two other species), by its rounded anterior end in dorsal view (beak-shaped in *S. schellenbergi*), and its pointed posterior margin (rounded in *S. simililampadis*).

The new species differs from the other European and Asiatic species by the following characteristics: (1) strong asymmetry between the two valves (length of RV 5% shorter than LV with a posterior gap between the two valves), (2) the shape of the L5 clasping organs (especially the strongly sclerotized hook-shaped right one with a distal hump) and (3) the shape of the hemipenis, rather thin, with a distally oriented a lobe and a small triangular distal h lobe.

Despite these three differences, *Schellencandona claretae* sp. nov. may be related to *S. simililampadis* because of the following two characteristics: (1) a similar chaetotaxy of the A1, without seta on the podomere III in both male and female and two setae on the podomere VI and (2) the z2 seta of the A2 being very long compared to z1 (but not transformed in a claw like in *S. simililampadis* and *S. schellenbergi*).

The similarity between *Schellencandona claretae* sp. nov. and the other species described here is detailed in the Discussion section.

Schellencandona malardi sp. nov.
urn:lsid:zoobank.org:act:C6E7925B-8EEA-4C2A-A919-23576D70C9BB
Figs 15–18, 20; Tables 1, 3

Diagnosis

Small trapezoid candonine of the genus *Schellencandona* (L = 485 µm). Carapace thick with strong ornamentation consisting of fossae on the entire valve surface. In lateral view, anterior margin widely rounded, while posterior margin poorly curved, dorsal margin straight or slightly concave in both valves, inclined backwards (decrease of 5.5% of H between the anterior and the posterior cardinal angle), postero-dorsal and ventral margins straight. Greatest H of LV located at the third anterior part (H/L =

0.49). In dorsal view, carapace swallen (W represents 50%–55% of L), pyriform and triangular shaped both anteriorly and posteriorly, with slightly beak-shaped ends. Calcified inner lamella amounting to c. 10% and 7% of L for the anterior and the posterior parts, respectively. A1 with a seta on the anterior side of the 3rd podomere. Male A2: EII and EIII separated with t2 and t3 transformed in male bristles, 2 short z setae (z1 longer than z2), the longest claw (G2) represents 170% of EI length. Female A2: EII+III with 3 t and 2 z setae. 2nd podomere of the Mdp bears 3+2 setae. Endopodites of the maxilla (L5) developed in males into prehensile palps, poorly asymmetrical, both elongated and slightly curved. Walking leg (L6) with f and 2 g setae. Cleaning leg (L7) 4-segmented, EII and EIII fused, with 2 setae (d1 and dp) on the protopodite. Zenker's organ with 6 internal rings of spines. Hemipenis with an outer lobe (a) large and sub-rectangular, dorso-distally oriented. The inner lobe (b) dorsally pointed (close to a 90° angle). Bursa copulatrix (e) rounded with a curved distal strip and an internal sub-conical structure. Female genital lobe rounded anteriorly without posterior expansion. Ocular structures not visible.

Etymology

The new species is named after Florian Malard who collected the species during an ecological study of the braided rivers of the southern French Alps.

Type material

Holotype

FRANCE • ♂, dissected appendages mounted in glycerine, valves stored in ethanol; Drôme district, Monjoux municipality; 44.5023° N, 5.0889° E; 446 m a.s.l.; Jun.–Jul. 2010; C. Capderrey leg.; interstitial habitat of the Lez River; MNHN-IU-2023-714.

Allotype

FRANCE • ♀; same data as for holotype; MNHN-IU-2023-715.

Paratypes

FRANCE • 1 ♂; same data as for holotype; MNHN-IU-2023-716; MNHN • 1 ♂; same data as for holotype; UCBLZ.2012-3-153-5; UCBLZ • 1 ♀; same data as for holotype; MNHN-IU-2023-717; MNHN • 1 juv.; same data as for holotype; UCBLZ.2012-3-153-6.

Other material examined

FRANCE • several juvs, undissected; same data as for holotype; UCBLZ.2012-3-210.

Description

Measurements. Holotype, ♂ (MNHN-2023-714): LV: L = 485 µm, H = 240 µm (H/L = 0.49). RV=470 µm, H=230 µm (H/L=0.49). W=245 µm (W/L=0.50). Range for males (n=2): L=485 to 500 µm, H=240 to 245 µm, W=245 to 250 µm. Allotype, ♀ (MNHN-2023-715): LV: L=465 µm, H=240 µm (H/L=0.51). RV: L= 455 µm, H=230 µm (H/L=0.50). W=255 µm (W/L=0.55). Range for females (n=2): L=465 to 490 µm, H=230 to 240 µm, W=255 to 260 µm.

Carapace. Whitish, with strong ornamentation (fossae) on entire carapace surface. General shape of carapace trapezoid with marked cardinal angles (Figs 15, 18I–J). Highest H located at anterior third with H/L = 0.49 and 0.51 for male and female, respectively. Carapace viewed laterally with anterior margin widely rounded, posterior margin and ventral margin straight and dorsal margin inclined backwards (5.5% decrease of H between anterior and posterior cardinal angle). Carapace viewed dorsally (Fig. 15C, F) very enlarged, pyriform and triangular-shaped both anteriorly and posteriorly, with greatest W located at last third of animal (at 60% of L in both male and female), representing 50% and 55% of L for male and female, respectively. Anterior and posterior ends slightly beak-shaped.

Valves. LV overlaps the RV on all sides (Fig. 15A, G). Dorsal margin of LV and RV slightly concave in the male. Dorsal margin representing 37% of LV length and 33% of RV length. Dorso-posterior margin straight on both valves. Ventral margin straight in LV and RV, slightly convex near oral area (Fig. 15B, E). Anterior calcified inner lamella larger (around 10% of L) than posterior one (7% of L for both sexes). Fused marginal valve zone narrow, representing 2.5% of L for both male and female, with straight and dense radial pore canals, more numerous anteriorly (Fig. 15D).

Antennule, A1 (Figs 16A, 17A). I+II: A-1l(pu), P-2l(pu)/III: A-1s/IV: A-1s/V: A-1l, P-1s/VI: A-2l/VII: A-2l-1s(α), P-1l/VIII: D-2l-ya-1l(cs). Using IV podomere as reference, podomeres are in ratios of 1.8-1-1.5-1-1.5-1.6 from III to VIII. ya aesthetasc very long, 10.7× as long as IV podomere.

Antenna, A2 (Figs 16B–D, 17B–D). Protopodite: coxa with 3 setae, 2 long and smooth, 1 short and plumose; basis with 1 long posterior seta; exopodite with 1 long and 2 short setae; EI with 1 posterior aesthetasc Y (equalling 55% to 73% of EI length in male and female, respectively) and distally 2 setae (1s and 1m).

Male A2 (Fig. 16B–D). EII and EIII segmented, forming 2 distinct podomeres. EII with 1 short aesthetasc (y1) and 4 t setae, t1 and t4 short, t2 and t3 transformed in male bristles having length equal

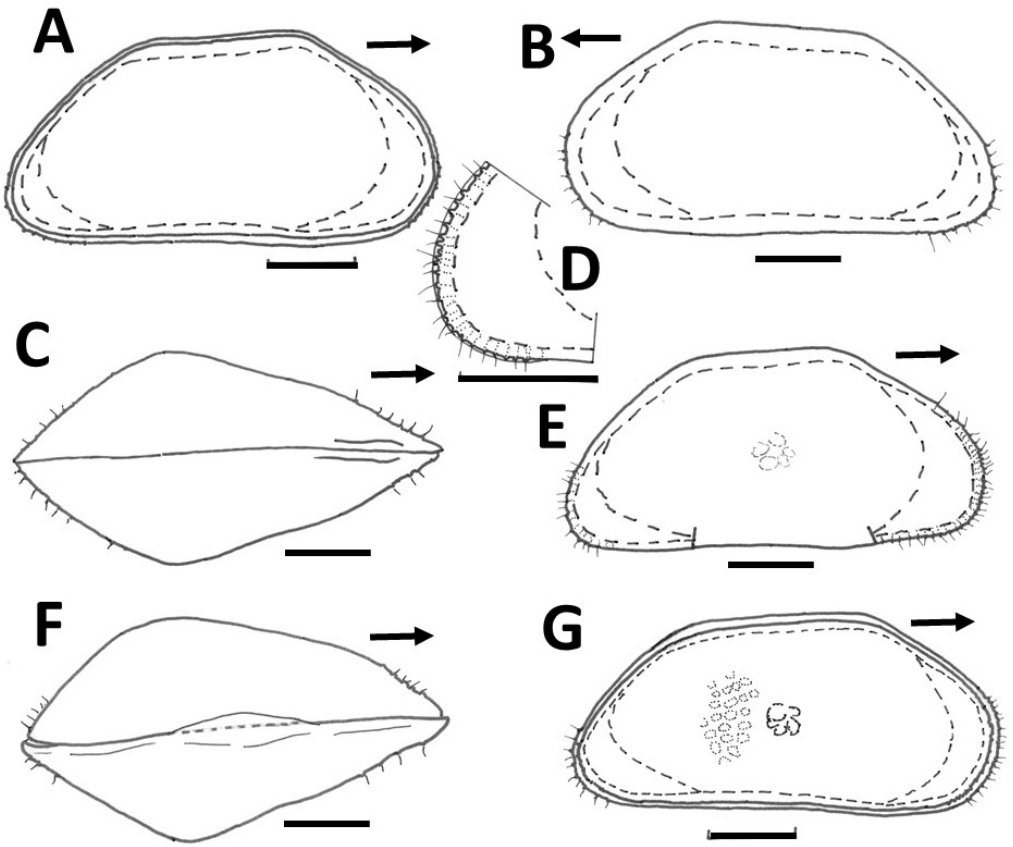

Fig. 15. *Schellencandona malardi* sp. nov. **A–E**. Holotype, ♂ (MNHN-IU-2023-714). **A**. Right view of the undissected specimen. **B**. Left valve, external view. **C**. Dorsal view of whole carapace. **D**. Detail of anterior margin. **E**. Right valve, external view. **F–G**. Allotype, ♀ (MNHN-IU-2023-715). **F**. Ventral view of whole carapace. **G**. Right view of the undissected specimen. Scale bars = 100 µm. Arrows point to anterior margin.

to 90% of that of EI. EIII with 1 short aesthetasc (y2), 2 external z setae, z1 slightly longer than EIV length, z2 short (15% of EI length). G1 reduced (96% of EI length), G2 well-developed (170% of EI length), G3 reduced to short bristle (45% of EI length). EIV with 2 claws, posteriorly 1 long (Gm, 165% of EI length) and anteriorly 1 reduced (GM, 69% of EI length), 1 small aesthetasc (y3, 39% of EI length) associated with subequal seta, g seta present.

Female A2 (Fig. 17B–D). EII and EIII fused, with anteriorly 2 short aesthetacs (y1 and y2), 3 t setae, distally 2 z setae (both short). G2 claw reduced (85% of EI length). G1 and G3 claws well-developed and sub-equal (196% EI length). EIV with anteriorly 1 long (GM, 163% of EI length) and posteriorly 1 medium-sized claw (Gm, 129% of EI length), 1 medium-sized aesthetasc (y3, 79% of EI length) with subequal seta, g seta present.

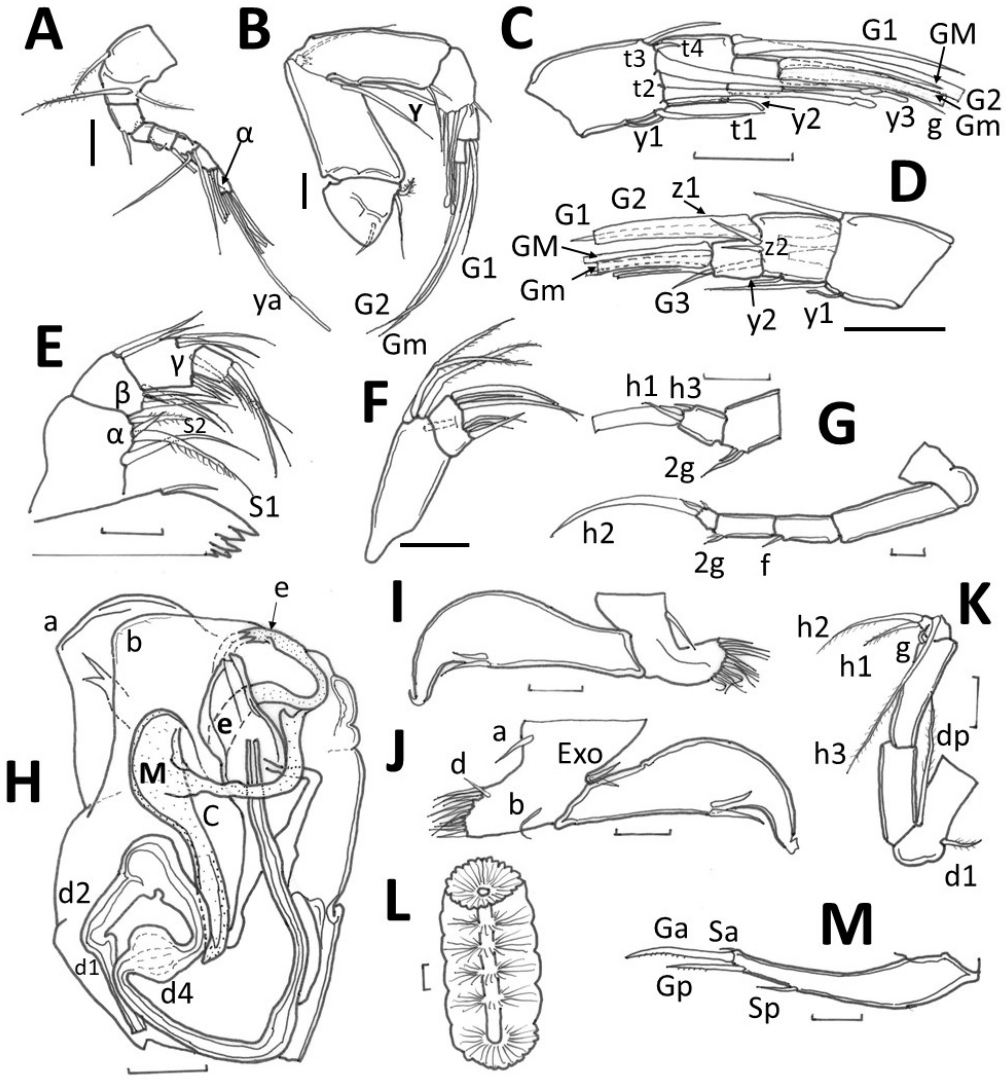

Fig. 16. *Schellencandona malardi* sp. nov., holotype, ♂ (MNHN-IU-2023-714). **A**. Antennule (A1). **B**. Antenna (A2). **C**. Detail of antenna, internal view. **D**. Detail of antenna, external view. **E**. Mandibular palp (Mdp). **F**. Maxillula (Mx1) palp. **G**. Walking leg (L6) with details of EIII and EIV. **H**. Hemipenis, inner view. **I**. Left 5th limb (with clasping organ). **J**. Right 5th limb (with clasping organ). **K**. Cleaning leg (L7). **L**. Zenker's organ. **M**. Caudal ramus. Abbreviations: see Material and methods. Scale bars = 20 µm.

Mandible. Consisting of coxal plate and 4-segmented palp (Mdp). Coxa typically shaped, heavily chitinized with masticatory part. 1st podomere of Mdp (Figs 16E, 17F) with externally exopodite plate, internally with 2 long setae (1 smooth and 1 plumose S1) and 2 short setae (1 smooth (α), 1 plumose, S2). 2nd podomere with externally 2 setae and internally group of 3 smooth setae and second group of 2 setae (1 long and 1 short, β, see detail in Fig. 16E). 3rd podomere with externally 3 setae, distally 1 long seta (γ) and internally 3 small setae. 4th podomere with 2 serrated and long claws (160% of the 3rd podomere length) and 3 small setae.

Maxillular palp (Mx1palp, Figs 16F, 17E). Two-segmented: 1st segment with 4 apical plumose setae on outer corner. 2nd segment with 2 claw-like setae (4.7× as long as 2nd segment) and 4 thinner setae.

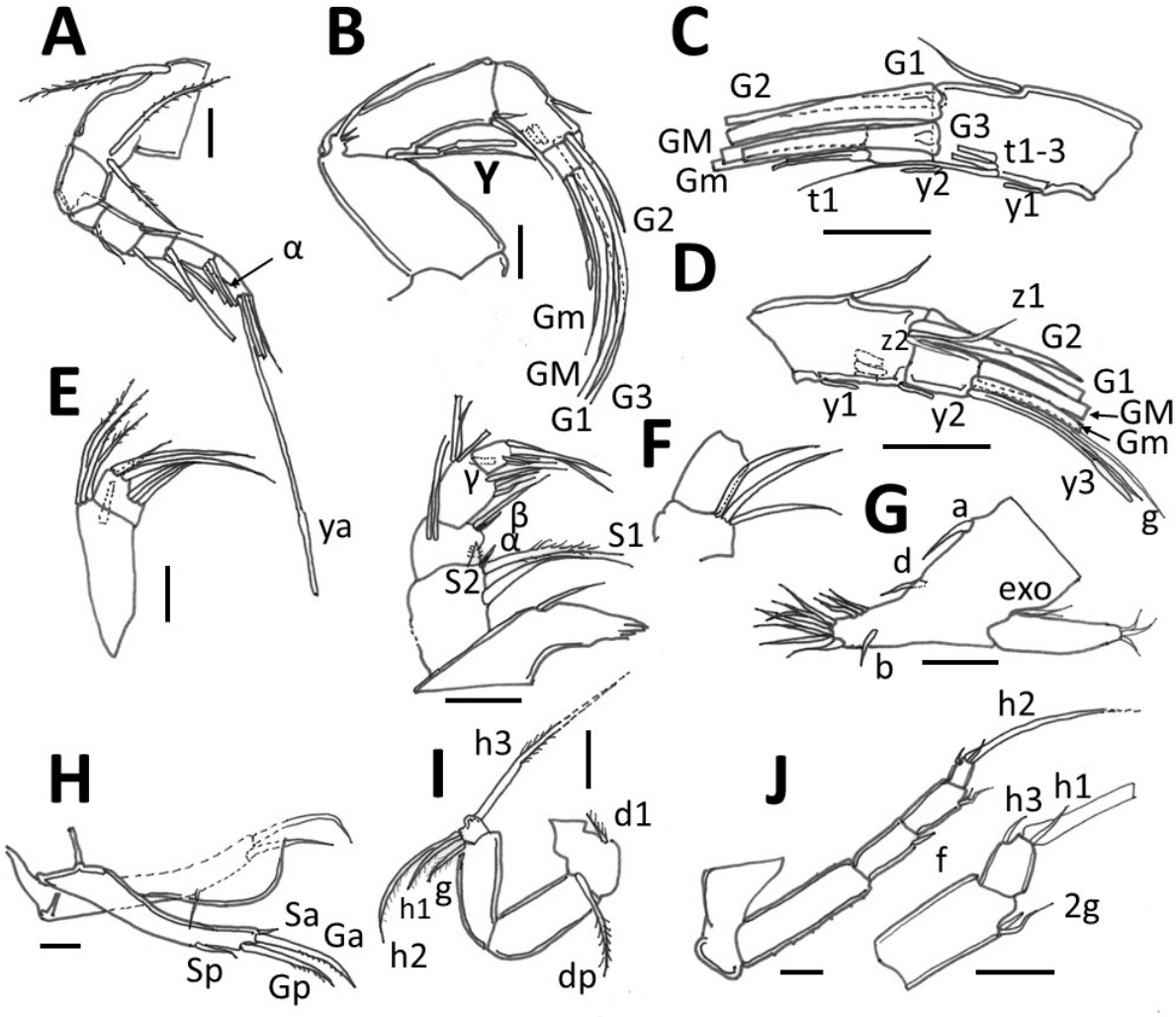

Fig. 17. *Schellencandona malardi* sp. nov., allotype, ♀ (MNHN-IU-2023-715). **A**. Antennule (A1). **B**. Antenna (A2). **C**. Detail of antenna internal view. **D**. Detail of antenna external view. **E**. Maxillula (Mx1) palp. **F**. Mandibular palp (Mdp) with details of the 2nd podomere. **G**. Maxilla (L5). **H**. Caudal ramus with genital lobe. **I**. Cleaning leg (L7). **J**. Walking leg (L6) with a detail of EIII and EIV. Abbreviations: see Material and methods. Scale bars = 20 µm.

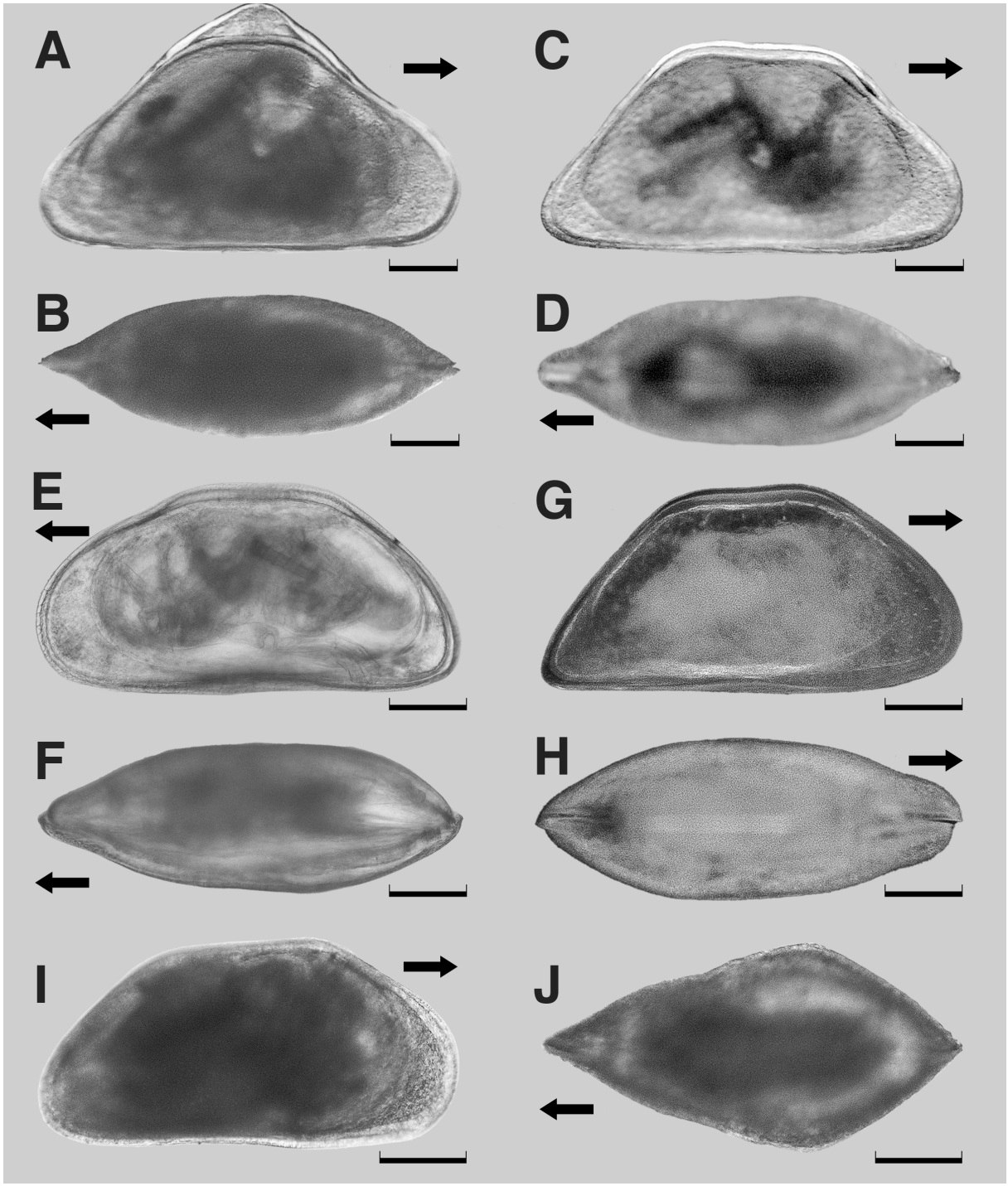

Fig. 18. A–**B**. *Schellencandona danielopoli* sp. nov., holotype, ♂ (MNHN-IU-2023-701). **A**. Entire animal, right view. **B**. Dorsal view. **C**–**D**. *Schellencandona capderreyae* sp. nov., holotype, ♂ (MNHN-IU-2023-705). **C**. Entire animal, right view. **D**. Dorsal view. **E**–**F**. *Schellencandona mercantourensis* sp. nov., holotype, ♂ (MNHN-IU-2023-708). **E**. Entire animal, left view. **F**. Dorsal view. **G**–**H**. *Schellencandona claretae* sp. nov., holotype, ♀ (MNHN-IU-2023-711). **G**. Entire animal, right view. **H**. Dorsal view. **I**–**J**. *Schellencandona malardi* sp. nov. male (MNHN-IU-2023-714). **I**. Entire animal, right view. **J**. Dorsal view. Scale bars = 100 µm. Arrows point to anterior margin.

Maxilla (L5, Figs 16I–J, 17G). With protopodite bearing 1 anterior seta (a) and 2 exterior setae (b and d), masticatory process (endite) apically with group of 10 setae. Exopodite plate with 2 filaments. Male endopodites transformed in clasping organs weakly asymmetrical, both elongated and slightly curved; right one thicker than left one. Two endopodites bear 2 short but thick setae on ventral side and thin apical seta. In female, similar set of setae observed on protopodite (a, b, d). Exopodite plate with two filaments. Endopodite ending with three short setae.

Walking leg (L6, Figs 16G, 17J). Five-segmented. Protopodite without d seta, EI without e seta, EII with f seta and EIII with 2 g setae. EIV with 2 short setae (h1 and h3) and long claw (h2) serrated and equal to 250% of length of EII.

Cleaning leg (L7, Figs 16K, 17I). Four-segmented (with EII and EIII fused). Protopodite with 1 short (d1) and 1 long setae (dp, 140% of EI length). EI without seta, EII+EIII with g seta (short in male and longer in female, 45% of EI length). EIV with 1 medium seta h1 (62 to 69% of EI length) and two long setae, h2 and h3 (118% and 195% of EI length, respectively).

Caudal ramus (CR, Figs 16M, 17H). Slender, with relatively short sp seta (22%–25% of anterior margin of CR, not reaching basis of Gp), short sa seta and 2 relatively short and curved claws (Ga and Gp representing around 64–66% and 47–60% of anterior margin of CR, respectively), both claws serrated.

Female genital lobe. Simple (Fig. 17H) widely rounded anteriorly without posterior expansion. Oocytes large (10% of valve length).

Male genital organs. Zenker's organ (male, Fig. 16L) ith 6 internal rings of spines representing 23% of total length of carapace. Hemipenis (Fig. 16H) with distal outer lobe (a) dorso-distally oriented, large and sub-rectangular (with dorsal angle well marked in most individuals, but not all). Inner lobe (b) dorsally pointed, close to 90° angle, and small plication on ventral side. Lobe h not visible. Labyrinth well-sclerotized and divided in 4 sections, section d4 weakly reticulated. Copulatory tube thin located inside rounded bursa copulatrix (e) with well-sclerotized and curved distal strip and internal sub-conical structure. M-process flat with narrow and widely rounded dorsal part, linked to C strip joining base of e and thin basal part reaching d4 section of labyrinth.

Ocular structures. Not visible.

Ecology and distribution

Schellencandona malardi sp. nov. was sampled in the interstitial habitat of a single river, the Lez River, an east-side tributary of the Rhône River (Fig. 1, Table 1), at low elevation (i.e., 446 m a.s.l.). The species was exclusively sampled in groundwater upwelling zones (at the downstream end of gravel bars), never at a depth of 30 cm, rarely at a depth of 60 cm (10%) and mostly at a depth of 90 cm into the riverbed sediment (90% of the individuals). The water collected at a depth of 90 cm had a temperature ranging from 15.5 to 17.2°C, an electrical conductivity ranging from 407 to 452 $\mu S.cm^{-1}$, a near-neutrality pH (7.4–7.7) and a wide range of dissolved oxygen concentration (2.15–7.3 $mg \cdot L^{-1}$).

Specialisation to groundwater: the well-developed aesthetascs (especially ya on A1 and Y on A2), the large size of the oocytes (10% of carapace length) and the lack of developed eyes suggest that *Schellencandona malardi* sp. nov. is specialized to groundwater life. *Schellencandona malardi* may thus be considered as a stygobiotic species endemic to the Lez River, living deep in the river bottom sediment and in a wide range of dissolved oxygen concentrations.

Taxonomic remarks

The new species fits with all the characteristics listed by Meisch (1996) for *Schellencandona* (see above) except for the surface of the carapace that is strongly ornamented with fossae on its entire surface. In the genus *Schellencandona*, the new species differs from all the species described in Europe and in Asia by the pyriform shape of the carapace in dorsal view. This shape is, for the moment, unique in the genus *Schellencandona*.

Schellencandona malardi sp. nov. has a hemipenis very similar to those of *S. simililampadis* and *S. schellenbergi* (stocky shape, with a large a lobe dorso-distally oriented, the h lobe not visible and a curved distal sclerotized strip on the bursa copulatrix), but differs from those of the above-mentioned species in (1) the presence of one seta in the 3rd podomere of A1 (absent in the two other species) and (2) the size of the z2 seta on A2 not transformed in a claw and smaller than z1 (claw-like in the two other species).

To our knowledge, the most closely related species are two unpublished species of *Schellencandona* collected in the Jura Mountains (Northern French Alps, noted *Schellencandona* sp. J1 and sp. J3 in Dole-Olivier *et al.* 2009). These two undescribed species exhibit markedly different carapace shapes compared to those of *Schellencandona malardi* sp. nov., yet share a striking similarity in hemipenis shape as well as A1 and A2 chaetotaxy (for example, see A2 of *Schellencandona* sp. J1 in Fig 19B). At present, *Schellencandona malardi* can be regarded as related to this group of Jura Mountain species; however, this classification requires a thorough evaluation following the complete description of the group.

The similarity of *Schellencandona malardi* sp. nov. with the other species described here is detailed in the Discussion.

Discussion

Morphological variabilities within the five new species

Differences in chaetotaxy between males and females

Some differences in the chaetotaxy of males and females of the same species are observed in limbs not directly associated with reproduction (e.g., the caudal ramus in *Schellencandona danielopoli* sp. nov.), but these weak differences between males and females are frequent in the Candoninae (e.g., Namiotko *et al.* 2004). Other observed differences consist of the lack of some setae: the e seta on the L6 of the male of *Schellencandona mercantourensis* sp. nov., and the g seta on the EIV of A2, one of the two g setae and the d seta on L6 of the male of *Schellencandona claretae* sp. nov. In both species, only one male was available, that may limit the quality of the observations.

Another surprising difference is observed in the only available male of *Schellencandona mercantourensis* sp. nov. that is consistently smaller than the adult females (12% smaller) and that shows a rather different posterior carapace shape (i.e., pointed and triangular in the male versus rounded in the females). It is, for the moment, not possible to be certain that these differences in size and carapace shape between the male and the females are a characteristic of the species or may be due to a teratologic development of this male.

Differences among populations of the same species

In many cases, species with a large distributional area and limited dispersal efficiency show a high morphological variability justifying splitting the species into different sub-species (e.g., *Cryptocandona kieferi* was divided in three subspecies by Namiotko *et al*. 2005) or different species (e.g., *Schellencandona triquetra* and *S. rhodanensis*, see Issartel & Marmonier 2025). In this study, three

species showed medium to large distribution areas at the scale of the Southern French Alps, but when comparing distant populations for each of these species, we found a weak inter-population variability.

First, *Schellencandona danielopoli* sp. nov. had the widest distribution area, with eight sites in five different rivers. It was collected from Les Duyes River, at the eastern end of its distribution area to the Lez River, at the western end of its distribution (Fig. 1). These two most distant rivers were separated by a straight distance of 100 km, but by a hydrological distance of 220 km along the river course. Despite this distance, no significant difference was observed in the carapace shape, soft-part morphology, or hemipenis shape of the two males collected from the Eygues and Buech rivers (Fig. 1). However, the different populations of this species are all located in the Rhône River watershed and may have recently exchanged individuals through dispersal along hyporheic corridors or direct groundwater pathways between the left tributaries of the Rhône River. Several stygobiotic species, including the asellid isopods *Proasellus walteri* (Chappuis, 1948) and *P. synaselloides* (Henry, 1963), were found to have a wide geographic distribution across several tributaries of the Rhône River (Eme *et al.* 2013; Malard *et al.* 2017).

Second, *Schellencandona mercantourensis* sp. nov. was collected in the upstream part of the Verdon and the Tinée rivers (i.e., 25 km away from each other in a direct way, Fig. 1), two rivers that do not show any downstream connection (the Verdon River flowing towards the Rhône River and the Tinée River flowing directly towards the Mediterranean Sea; Fig. 1). Very few adults were collected at the two stations, but the two dissected females did not show any consistent morphological differences, suggesting the existence of hydrological connections between the upstream reaches of these two alpine rivers (e.g., either via surface or groundwater pathways; Agence de l'Eau Rhône-Méditerranée 2021), or recent and rapid colonisation of subterranean habitats.

Finally, *Schellencandona claretae* sp. nov. was sampled downstream of the Asse River and upstream of the Verdon River (i.e., 70 km between the two stations; Fig. 1). These rivers are hydrologically connected downstream of the Durance River (Fig. 1) and may exchange organisms through hyporheic corridors. In addition, groundwater systems belonging to two rivers are hydrologically connected (Agence de l'Eau Rhône-Méditerranée 2014), potentially allowing faunal exchanges across catchment boundaries. At each station, one adult female was collected and dissected (Figs 11, 13–14). It is not clear for the moment if the differences in the shape of the carapace and the chaetotaxy of the limbs between the two females may represent a difference between two individuals or between the two populations. Future research must include more mature individuals to examine the morphological variability inside each population, together with molecular affinities between the two populations.

Taxonomic relationships with the other species of *Schellencandona*

In Asia, three species of *Schellencandona* have been described from South Korea (*S. tea*), Japan (*S. yakushimaensis*), and China (*S. dui*). Their carapace shapes are similar (i.e., elongated, with anterior and posterior margins rather similarly rounded, dorsal margin convex, and ventral margin concave), and thus very different from the five new species described here (i.e., triangular or trapezoid shapes, asymmetrical anterior and posterior margins). Similarly, the claws of A2 (especially G1, G3, GM) are rather short in the Asiatic species compared to the long claws of the five new species described here. The males of the three Asiatic species are unknown; thus, no comparison with the hemipenis morphology is currently possible.

In Europe, seven species have been described in the genus *Schellencandona* (*S. triquetra*, *S. belgica*, *S. insueta*, *S. mira*, *S. rhodanensis*, *S. schellenbergi* and *S. simililampadis*; Meisch 2000; Meisch *et al.* 2024; Issartel & Marmonier 2025) and an additional one has been communicated from Italy (Rossetti pers. com.). Despite some convergence in the carapace shape (like for the triangular shapes

of *Schellencandona danielopoli* sp. nov., *S. triquetra* and *S. rhodanensis*), the five new species have carapace shapes that differ from those of *S. belgica* and *S. mira* (both dorsally rounded) and *S. insueta* (widely rounded posterior margin), but seem related to a group formed by the trapezoidal *S. schellenbergi* and *S. simililampadis*, as highlighted by Danielopol (1978). However, several differences, especially in the hemipenis shape, the A1 and A2 chaetotaxy, and the L5 clasping organs, allowed us to separate the five new species into three morphological groups (Table 3, Fig. 20).

First group: *Schellencandona mercantourensis* sp. nov. and *Schellencandona claretae* sp. nov. This first morphological group is based on five original morphological characteristics (Table 3, Fig. 20). (1) A strong asymmetry between the left and right valves (RV is 5% shorter in length than LV, inducing a posterior gap between the two valves). (2) A rather thin and elongated hemipenis (see Fig. 20), with a distally oriented outer lobe (a), a small but visible lobe h, and a simple bursa copulatrix without distal curved strip as in the three other species. (3) The lack of setae on the A1 3rd podomere and two setae on the A1 6th podomere. (4) A long z2 seta on male A2, longer than z1, but not transformed into a claw. (5) Unusually shaped L5 clasping organs (strongly asymmetrical, with a well-sclerotized right one, hook-

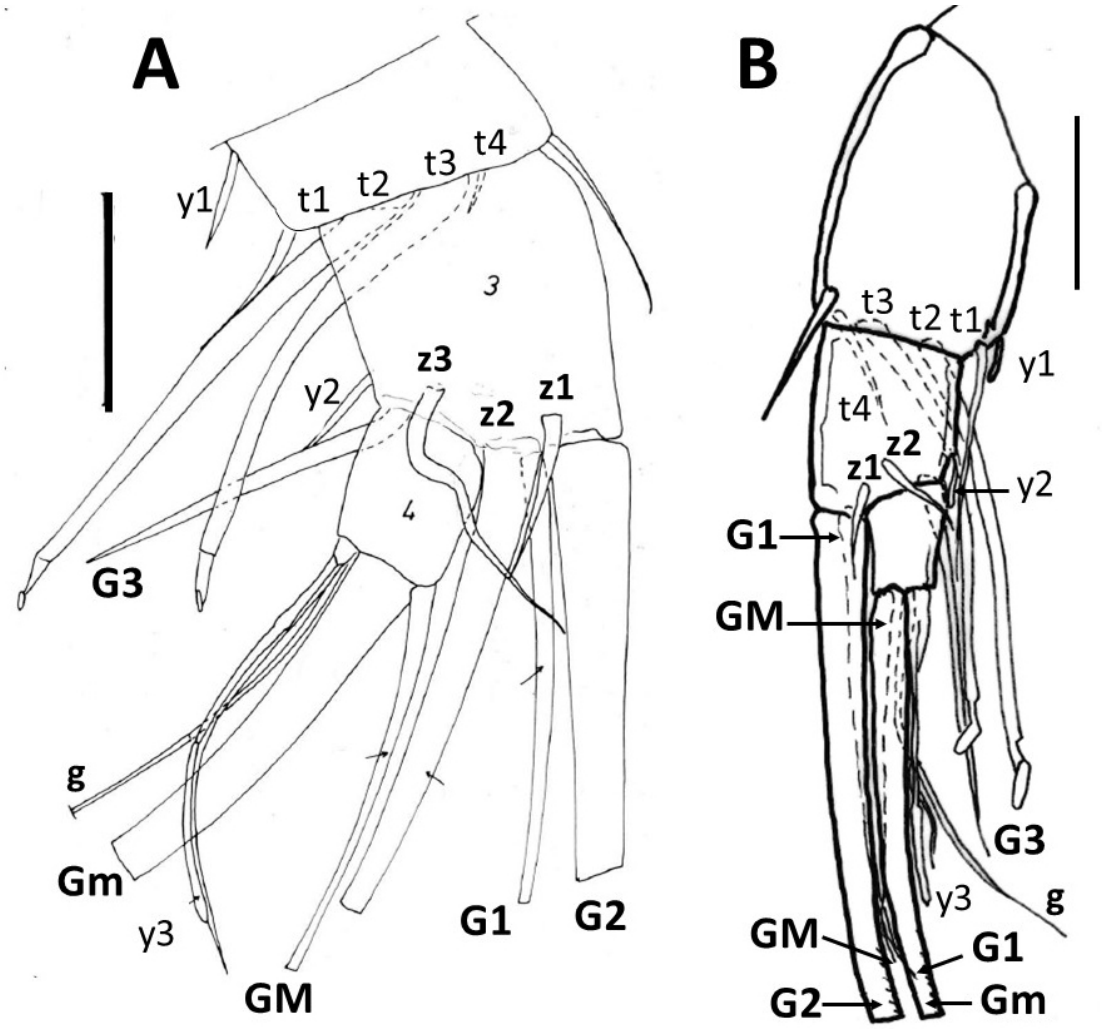

Fig. 19. A. *Schellencandona simililampadis* (Danielopol, 1978), detail of male A2, external view (redrawn after Danielopol 1978). **B**. *Schellencandona* sp. J1 (UCBLZ 2012-3-14-36), detail of male A2, external view. Abbreviations: see Material and methods. Scale bars = 20 µm.

shaped, and with a sclerotized ventro-distal angle). This group may be related to *S. simililampadis* and *S. schellenbergi*, even if the first and last characteristics were not observed in these two species.

In this first group, the two species differ in several characteristics (Table 3, Figs 18, 20): (1) the shape of the carapace, especially the postero-dorsal margin, which is slightly convex in *Schellencandona mercantourensis* sp. nov., but straight in *Schellencandona claretae* sp. nov., resulting in a pointed posterior end. (2) The lack of ornamentation on the carapace of the first species and reduced ornamentation of pits and small fossae in *Schellencandona claretae*. (3) Three z setae in *Schellencandona mercantourensis*, but two in *Schellencandona claretae*. (4) The medium size of Sp seta that does not reach the basis of Gp in *Schellencandona mercantourensis*, whereas it is long in *Schellencandona claretae*. (5) The h lobe of the hemipenis rounded in *Schellencandona mercantourensis*, whereas it is triangular in *Schellencandona claretae*. (6) The shape of the bursa copulatrix which is conical with a thin dorsal sclerotized fold in *Schellencandona mercantourensis*, whereas it is ventrally well-sclerotized in *Schellencandona claretae*. Finally, (7) the female genital lobe, which is anteriorly rounded with a small posterior triangular expansion in *Schellencandona mercantourensis*, while it is without posterior expansion in *Schellencandona claretae*.

Second group: *Schellencandona danielopoli* sp. nov. and *Schellencandona capderreyae* sp. nov. The second morphological group is based on four distinctive morphological characteristics (Table 3, Fig. 20). (1) A rather stocky hemipenis, with a dorso-distally oriented outer lobe (a), without a visible h lobe, a curved distal sclerotized strip on the bursa copulatrix. (2) Lack of seta on the A1 3rd podomere and only one seta on the 6th one. (3) The z2 seta transformed in a claw. (4) The L5 clasping organs nearly similar and regularly curved. These four characteristics make these two species close to *S. simililampadis* (see A2 in Fig. 19A) and, to a lesser extent, to *S. schellenbergi* (except point 2). The transformation of the seta z2 in a claw, while z1 remains a seta, was observed, for example, in the genus *Latinopsis* (Karanovic & Datry 2009) or the African genus *Benincandona* (Hotèkpo *et al.* 2024), while it is generally the z1 seta that is transformed into a claw in European species (e.g., in *Typhlocypris*, Namiotko & Danielopol 2004, or in *Pseudocandona*, Smith & Kamiya 2015).

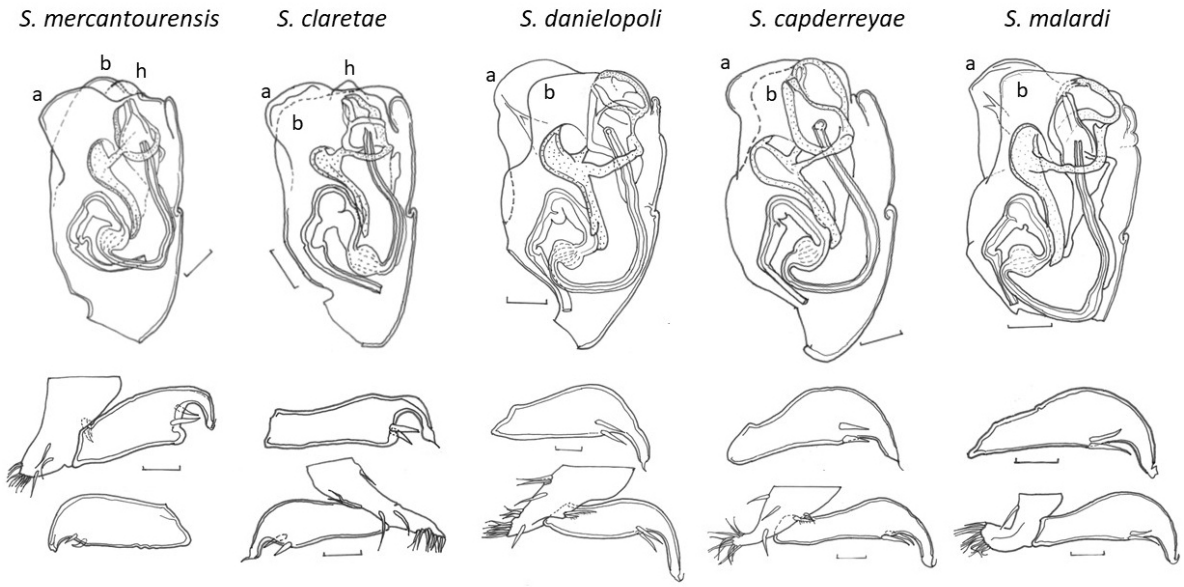

Fig. 20. Hemipenis (top) and L5 clasping organs (bottom) of the five new species of *Schellencandona* Meisch, 1996. Scale bars = 20 µm.

Table 3. Comparison of the five new species based on their morphological differences. Carapace sizes in µm. Abbreviations: L = length; H = height; nb = number; for A1, III = 3rd podomere; VI = 6th podomere; for A2, EI = 1st endopodial article.

characteristics	***S.danielopoli*** sp. nov.	***S. capderreyae*** sp. nov.	***S. mercantour*** sp. nov.	***S. claretae*** sp. nov.	***S. malardi*** sp. nov.
carapace shape					
lateral view	triangular	trapezoid	trapezoid	trapezoid	trapezoid
dorsal view	compressed	compressed	compressed	compressed	pyriform
carapace size					
male L	600	600	545	480	485
H	330	300	275	230	240
H/L	0.55	0.50	0.50	0.48	0.49
female L	560	537	510	545	465
H	310	260	275	265	240
H/L	0.55	0.48	0.54	0.48	0.51
A1 -III nb seta	0	0	0	0	1
A1 -VI nb seta	1	1	2	2	2
A2 male (%EI)					
G1	65%	56%	72%	60%	96%
G2	170%	180%	175%	180%	170%
G3	47% (seta)	84% (seta)	45% (seta)	20% (seta)	45% (seta)
z2	170% (claw)	160% (claw)	40% (seta)	45% (seta)	15% (seta)
Gm	160%	170%	150%	150%	165%
nb z setae	3	3	3	2	2
L5 a seta	2	1	1	1	1
L6 d seta	0	0	1	1	0
L6 g seta	1	2	1	2	2

The two new species of this second morphological group differ by four characteristics (Table 3, Figs 18, 20). (1) The shape of the carapace (trapezoidal in *Schellencandona capderreyae* sp. nov. and triangular in *Schellencandona danielopoli* sp. nov.). (2) Two a setae on *Schellencandona danielopoli*. L5 protopodite, whereas there is only one in *Schellencandona capderreyae*. (3) The presence of 2 g setae on L6 of *S. caperreae* and only one in *Schellencandona danielopoli*. (4) The small size of Sp seta of CR in *Schellencandona capderreyae*, whereas Sp is long in *Schellencandona danielopoli*.

Third group: *Schellencandona malardi* sp. nov.

Schellencandona malardi sp. nov. differs from the other four species described in this work by three major characteristics (Table 3, Fig 20). (1) The presence of a seta on the 3rd podomere of A1, which is absent in the other four species. (2) The z2 seta of male A2 is short (even shorter than z1), whereas it is long or transformed in a claw in the other four species. (3) The pyriform shape of the carapace, a characteristic never observed before in the genus *Schellencandona*.

When considering the male organs, *Schellencandona malardi* sp. nov. seems to be related to the second group of species, *S. schellenbergi* and *S. simililampadis*, with symmetrical and gently curved L5 clasping organs and a rather stocky hemipenis, with a dorso-distally oriented outer lobe (a), a reduced not visible h lobe, a curved distal sclerotized strip on the bursa copulatrix (Fig. 20). Despite these similarities, this species seems closely related to the *Schellencandona* species of the Northern French Alps, which have a very similar hemipenis shape and the same set of setae on A1 and A2 (see Figs 16D, 19B for A2), except for the carapace pyriform shape.

The three groups of species proposed here are based on morphological characteristics, but must be validated in the future using molecular analyses. Four of the five new species (i.e., *Schellencandona danielopoli* sp. nov., *Schellencandona capderreyae* sp. nov., *Schellencandona mercantourensis* sp. nov. and *Schellencandona claretae* sp. nov.) seem closely related to *S. simililampadis*, a species collected in the karstic system of Sauve along the Vidourle River located at only 50 km of the Rhône River and the studied sector (Fig. 1). None of these five species appeared to be related to *S. rhodanensis* (especially in the shape of L5 clasping organs and the hemipenis, Issartel & Marmonier 2025) despite it being present in the Rhône, Drôme, and Cèze rivers, all sites being rather close to the studied sector (Fig. 1). In addition, *S. rhodanensis* never co-occurs with any of the new species described here, despite the surface hydrological connections between these rivers (Fig. 1). Differences in the dispersal history of *S. rhodanensis* and the five new species, especially during the successive Pleistocene glacial expansions and subsequent post-glacial recolonisations (see below), may explain this disjunction in their distributional area. Here again, molecular analyses of several populations of species of *Schellencandona* may help clarify their dispersal history (see, for example, Eme *et al.* 2013 for a molecular assessment of the dispersal history of species of *Proasellus* Dudich, 1925, Isopoda, in the Rhône River watershed).

Geographical distribution and protection status

The ostracods of the southern French Alps have long been understudied. Distribution records were essentially available for the Vanoise sector (Claret *et al.* 1997) and for the Chartreuse sector (Claret & Marmonier 2019), two sectors located in the northern French Alps outside of Mediterranean influence. In addition, candonine specimens, when collected in the southern French Alps, were generally not identified to the species level (Capderrey *et al.,* 2013, Dole-Olivier *et al.,* 2015).

The high species richness of the genus *Schellencandona* in the southern French Alps may be associated with two major features of this mountainous area. First, the area has long offered a high diversity of climatic and hydrological conditions because of the gradients in latitude (from 45°N to 43°N for the area considered here) and elevation (from sea level to more than 3000 m a.s.l.). Glacial and Mediterranean rivers occur over relatively short distances (Ward 2009; Piegay *et al.* 2009). Steep environmental gradients along the slopes of the southern French Alps may have promoted ecological speciation events (Martin-Bravo *et al.* 2010), resulting in a high number of endemic species (Rabitsch *et al.* 2016; Jardim de Queiroz *et al.* 2022).

Second, the climatic history of the area may also explain the local diversity of *Schellencandona*. During Pleistocene glaciations, the central part of the Alps was covered with ice (see Fig. 1), whereas the foothill rivers provided refugia for many aquatic species, including groundwater crustaceans (e.g., the amphipod *Niphargus* Schiødte, 1847, Foulquier *et al.* 2007). Refugial areas (and their associated interstitial habitats) may have been isolated from each other (e.g., for lakes, Georgopoulou *et al.* 2016, or for rivers, Pauls *et al.* 2006). This past habitat insularity may also have promoted non-ecological speciation events by reducing gene flow among isolated populations (Wallis *et al.* 2016; Hotaling *et al.* 2017).

The five new species described in this study appear to be specialized to groundwater life (aethetasc length, oocyte size, lack of visible ocular structures, see above), representing stygobiotic species with

contrasting distributions: two species occur at a single station (*Schellencandona capderreyae* sp. nov. and *Schellencandona malardi* sp. nov.), two others in two different river systems (*Schellencandona mercantourensis* sp. nov. and *Schellencandona claretae* sp. nov.) and the last one (*Schellencandona danielopoli* sp. nov.) is widely distributed across the studied area. The distribution of *Schellencandona danielopoli* in eight different rivers may be explained by its ecological characteristics: a significant number of individuals were sampled at shallow depths inside the river bed sediment (37% were collected above -60 cm deep). Its colonisation success may be explained by its ability to occupy shallow sediment layers where environmental conditions are variable in temperature (from 11.1 to 19.9°C) and oxygen concentrations (3.2–7.1 $mg \cdot L^{-1}$), as already highlighted for *Fabaeformicandona wegelini* (Petkovski, 1962) (Danielopol *et al.* 1994).

Stygobiotic species are frequently considered to be particularly sensitive to environmental disturbances (Di Marzio *et al.* 2018), but differences in the geographic distributions observed for the five species of *Schellencandona* suggest different protection statuses in response to future environmental changes. The International Union for Conservation of Nature (IUCN) has provided guidelines for the definition of the protection status of species (Mace *et al.* 2008; IUCN 2012). Three levels of protection were proposed (i.e., critically endangered, endangered and vulnerable species) using three criteria: (1) high decline rate, (2) reduced geographic range and (3) small population size and decline. Assessing the population size of interstitial micro-crustaceans remains challenging. In contrast, the extent of their distribution range has been increasingly documented (Danielopol *et al.* 1994). Among the five species of *Schellencandona* described herein, *Schellencandona capderreyae* sp. nov. and *Schellencandona malardi* sp. nov. have the smallest area of occupancy, reduced to a single station (i.e., in the Jabron and Lez rivers, Fig. 1). A local pollution event (Mace *et al.* 2008) or a future decrease in summer river discharge (Zierl & Bugmann 2005) may induce a destruction of the entire habitat of these two species, potentially leading to their extinction. Although their exact area of occupancy is yet to be determined, current knowledge indicates that both species may be classified as endangered (area of occupancy < 500 km^2), or at least vulnerable (< 2000 km^2).

The case of *Schellencandona mercantourensis* sp. nov. is rather different; it occurs in only two alpine rivers, the Verdon and Tinée rivers (Fig. 1). However, its relatively small area of occupancy is likely due to the reduced number of available samples, primarily from the upstream reaches of these two rivers (Table 1). The two stations where the species was collected were covered by ice during the Würm period (Fig. 1), suggesting that the species recolonised the upper reaches of the Verdon and Tinée rivers from downstream reaches. Thus, its area of occupancy is supposedly larger. Nevertheless, the two sites where the species was collected are both located at high elevation (i.e., 1225 and 1080 m a.s.l.): they are predicted to experience drastic environmental changes in the face of climate change (Rangwala & Miller 2012). *Schellencandona mercantourensis* may thus be considered a vulnerable species. Finally, *Schellencandona claretae* sp. nov. and *Schellencandona danielopoli* sp. nov., present in two or more stations at high and low elevations, may be considered as least concerning species.

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