Zootaxa 5723 (2): 189–208
https://www.mapress.com/zt/
Copyright © 2025 Magnolia Press

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5723.2.2
http://zoobank.org/urn:lsid:zoobank.org:pub:7E331561-4D0D-4757-A49F-E3F9F70A3BC7

On the occurrence of the genus *Schellencandona* (Ostracoda, Candonidae) in Italy, with the description of a new species

GIAMPAOLO ROSSETTI[1*], ILARIA MAZZINI[2] & MARIA CRISTINA BRUNO[3,4]
[1]*Department of Chemistry, Life Science and Environmental Sustainability, University of Parma, 43124 Parma, Italy*
[2]*CNR—IGAG, Area della Ricerca di Roma 1, 00015 Montelibretti (RM), Italy*
ilaria.mazzini@cnr.it; https://orcid.org/0000-0003-2164-7826
[3]*Research and Innovation Centre, Fondazione Edmund Mach, 38098 S. Michele all'Adige (TN), Italy*
[4]*NBFC, National Biodiversity Future Center, Palermo 90133, Italy*
cristina.bruno@fmach.it; https://orcid.org/0000-0001-7860-841X
**Corresponding author: giampaolo.rossetti@unipr.it; https://orcid.org/0000-0002-8136-6965*

Abstract

Subterranean environments harbour a diverse yet understudied ostracod fauna, particularly within the family Candonidae, which poses significant taxonomic challenges due to subtle morphological traits that require careful examination to differentiate genera and species. The genus *Schellencandona*, composed predominantly of stygobiotic species, currently includes 15 described species, many of which are endemic, while a few may have potential intercontinental distributions. This genus is characterized by considerable variability in the morphology of valve and carapace, along with homoplastic similarities to other subterranean candonid species. In contrast, the morphology of the soft parts is highly conservative across species, offering a more stable basis for taxonomic identification. This study reports the first confirmed records of living *Schellencandona* species in Italy, including one species new to science, for which a detailed morphological description of both valves and soft parts is provided. The second recorded taxon closely resembles a species previously reported from Germany and more recently from Turkey. Both species were collected from the interstitial habitats of hydrologically-dynamic river stretches and exhibit highly localized distributions. These findings suggest that *Schellencandona* may have a greater species diversity than currently recognized in Italy, where research on ostracods inhabiting groundwater and groundwater-dependent ecosystems remains limited compared to other European countries. In addition, this study provides a comprehensive review of the literature concerning the geographical distribution and habitat preferences of *Schellencandona* species. However, the potential to explore biogeographic patterns within the genus remains constrained by the general lack of illustrations accompanying existing records, which hinders the validation of their taxonomic assignments.

Key words: Interstitial ostracods, morphology, taxonomy, geographical distribution, Toncina Stream, Po River, *Schellencandona antoniae* sp. nov.

Introduction

The class Ostracoda Latreille, 1802 is an example of an evolutionarily successful group of crustaceans, notable for its temporal persistence (having appeared as early as the late Cambrian, Siveter *et al.* 2024), its ability to colonise a wide range of aquatic environments, both marine and continental (Horne 2003), and its high species diversity, as indicated by several databases (Huang *et al.* 2022). All extant non-marine ostracods belong to the order Podocopida G.O. Sars, 1866, which currently includes more than 2,400 species and approximately 300 genera (Meisch *et al.* 2024). Of these species, over 400 have been newly described between 2004 and 2023, reflecting both a vibrant interest in the taxonomic study of non-marine ostracods and the fact that our current understanding of their diversity remains significantly incomplete. This gap in knowledge is particularly pronounced for subterranean environments, where a remarkable level of ostracod diversity is anticipated, based on the results of the relatively limited research conducted to date.

Accepted by R. Smith: 18 Oct. 2025; published: 25 Nov. 2025

A substantial proportion of subterranean ostracods belong to the family Candonidae Kaufmann, 1900, within which Meisch *et al.* (2024) identified eight subfamilies and 53 genera, many of them displaying high rates of endemism and are predominantly or exclusively stygobiotic species. Despite the significant progress achieved in recent years, partly aided by molecular techniques (e.g. Hiruta *et al.* 2016, Wysocka *et al.* 2019), numerous taxonomic and systematic issues within the Candonidae remain unresolved. This is largely due to the differentiation of species being based on often subtle diagnostic morphological characters which were often overlooked in the descriptions and drawings of earlier literature. Moreover, for subterranean species, morphological traits such as limb chaetotaxy and/or valve size and shape—the latter traits that are the primary diagnostic features used for the classification of fossil ostracods—may exhibit homoplastic similarities as adaptive responses to the conditions of the subterranean environment (Iepure *et al.* 2023).

Schellencandona Meisch, 1996 is a predominantly groundwater genus of the subfamily Candoninae Kaufmann, 1900, with a Palearctic distribution. The genus was established to accommodate species previously assigned to the *schellenbergi*-species group within the genus *Pseudocandona* Kaufmann, 1900 by Danielopol (1978), due to the presence of distinctive soft part features, small carapace size, and the absence of eye pigment, all of which confirm their status as a separate phylogenetic lineage. The genus *Schellencandona* (Table 1) currently includes 15 formally described species (Meisch *et al.* 2024, Issartel & Marmonier 2025a, 2025b), although *Schellencandona mira* (Sywula, 1976) requires re-description, and its potential synonymy with other congeneric species needs to be evaluated (Meisch *et al.* 2024). The morphology of the valves in *Schellencandona* is highly variable, ranging from reniform to trapezoidal or triangular shapes, with intermediate forms. The surface of the valves can be either smooth or pitted. This variability poses significant challenges in assigning specimens to the genus when the diagnostic characteristics of the appendages are unavailable as in the fossil record.

The previous records of recent specimens of *Schellencandona* for Italy are those of Pieri *et al.* (2009) and Melis *et al.* (2012), both from Friuli Venezia Giulia Region (NE Italy). The material described by Pieri *et al.* (2009) is stored in the first author's ostracod collection at the University of Parma, Italy, consisting of two specimens (labelled as VP0602, an adult male, and VP0630, an adult female) collected from a spring in the Province of Udine; both individuals were used for SEM (Figs 5A–C in Pieri *et al.* 2009). Their soft parts (not illustrated in Pieri *et al.* 2009) are also available in the same collection. These specimens were re-examined by the first author. The valve size (approximately 0.68 mm), the presence of a well-developed umbo on the dorsal margin of the left valve, and especially the morphology of the hemipenes indicate that these specimens belong to a new species within the genus *Marmocandona* Danielopol, Namiotko & Meisch, 2012, which will be formally described elsewhere.

Melis *et al.* (2012) frequently found specimens assigned to *Schellencandona* sp. in palaeoenvironmental sequences dating back to the Roman era in the city of Trieste. The adults are approximately 0.60 mm long, with the surface of the valves finely pitted (see Figure 8 of Plate II in the aforementioned paper). However, the attribution of these specimens to *Schellencandona* cannot be confirmed with certainty. In fact, although the valve size corresponds to the upper limit of the length range for the species described in this genus, similar carapace shapes (as seen in lateral view) occur in several genera of Candoninae.

In this contribution, we report on two living species belonging to the genus *Schellencandona* collected in Italy. In the first case, we offer a detailed description of the morphology of the valve and of the soft parts and assign the specimens to a new species. In the second case, we analyse the only available specimen that exhibits notable similarities to a species previously reported in Germany in different studies and more recently also in Turkey. Additionally, we provide detailed notes on the geographical distribution of all known recent and fossil species of the genus *Schellencandona*. These notes are complemented by information on habitat preferences and a comprehensive account of published illustrations of the examined material, all based on an exhaustive review of the available literature.

Materials and methods

Site description and sampling methods

The specimens were collected from the interstitial zone of a small watercourse in the northern Apennines, the Toncina Stream, and from the piedmont section of the Po River in the western Italian Alps.

TABLE 1. Literature-based occurrences of *Schellencandona* species. The current taxonomic classification follows Meisch *et al.* (2024). [a]: reported as *Schellencandona dui* in Table 2 and as *Schellencandona* cf. *belgica* in Plate 3, g; [b]: see Issartel and Marmonier, 2025a; [c]: reported as *Shellencandona*; [d]: this record, anterior to the description of *S. rhodanensis* Issartel and Marmonier, 2025a, can most plausibly be assigned to this species.

References	Original taxonomic designation	Current taxonomic classification	Country	Habitat	Recent/fossil	Illustrated material
Pieri *et al.* 2009	*Schellencandona* sp.	*Marmocandona* sp.	Italy	Alkaline peat bog fed by resurgence springs	Recent	Valves
Petkovski *et al.* 2009	*Schellencandona* cf. *aemonae*	*Pseudocandona* cf. *aemonae*	Bosnia and Herzegovina	Cave	Recent	Valves
Issartel & Marmonier 2025b	*Schellecandona danielopoli*	*Schellecandona danielopoli*	France	Interstitial	Recent	Valves and soft parts
Marmonier & Creuzé des Châtelliers 1992	*Pseudocandona* cf. *schellenbergi*	*Schellencandona* cf. *schellenbergi*	France	Interstitial	Recent	No
Ferreira *et al.* 2003	*Schellencandona belgica*	*Schellencandona belgica*	France	Subterranean	Recent	No
Fuhrmann 2012	*Schellencandona belgica*	*Schellencandona belgica*	Germany	Cave	Late Holocene	Valves
Fuhrmann & Völker 2015	*Schellencandona belgica*	*Schellencandona belgica*	Germany	Cave sediments	Recent	No
Gerecke *et al.* 2005	*Schellencandona belgica*	*Schellencandona belgica*	Luxembourg	Interstitial	Recent	No
Hubart & Dethier 1999	*Schellencandona belgica*	*Schellencandona belgica*	Belgium	Springs	Recent	No
Klie 1937	*Candona belgica*	*Schellencandona belgica*	Belgium	Wells? Interstitial?	Recent	Valves and soft parts
Marmonier & Creuzé des Châtelliers 1992	*Pseudocandona belgica*	*Schellencandona belgica*	France	Interstitial	Recent	No
Marmonier & Creuzé des Châtelliers 1992	*Pseudocandona belgica*	*Schellencandona belgica*	Germany	Well	Recent	No
Meisch 2000	*Schellencandona belgica*	*Schellencandona belgica*	Germany	Groundwater pipes	Recent	Valves and soft parts
Szlauer-Łukaszewsk 2014	*Schellencandona belgica*	*Schellencandona belgica*	Poland	Groyne fields	Recent	No
Szlauer-Łukaszewsk *et al.* 2021	*Schellencandona belgica*	*Schellencandona belgica*	Poland	Springs	Recent	No
Issartel & Marmonier 2025b	*Schellencandona capderreyae*	*Schellencandona capderreyae*	France	Interstitial	Recent	Valves and soft parts
Chen *et al.* 2019	*Schellencandona* cf. *belgica*	*Schellencandona* cf. *belgica*	China	Lake	Recent	Valves

......*continued on the next page*

TABLE 1. (Continued)

References	Original taxonomic designation	Current taxonomic classification	Country	Habitat	Recent/fossil	Illustrated material
Sari & Külköylüoğlu 2010	*Schellencandona cf. belgica*	*Schellencandona cf. belgica*	Turkey	Unknown	Recent	Valves
Wang *et al.* 2022	*Schellencandona cf. belgica* [a]	*Schellencandona cf. belgica*	China	Brackish water biofaces	Late Pleistocene	Valves
Ferreira *et al.* 2003	*Schellencandona* cf. *schellenbergi* sp. 1	*Schellencandona* cf. *schellenbergi* sp. 1	France	Groundwaters	Recent	No
Ferreira *et al.* 2003	*Schellencandona* cf. *schellenbergi* sp. 2	*Schellencandona* cf. *schellenbergi* sp. 2	France	Groundwaters	Recent	No
Dole-Olivier *et al.* 2006, Prié *et al.* 2024	*Schellencandona* cf. *simililampadis*	*Schellencandona* cf. *simililampadis*	France	Springs	Recent	No
Juberthie *et al.* 2016	*Schellencandona* cf. *tea*	*Schellencandona* cf. *tea*	Russia	Groundwaters	Recent	No
Issartel & Marmonier 2025b	*Schellencandona claretae*	*Schellencandona claretae*	France	Interstitial	Recent	Valves and soft parts
Ma & Yu 2018	*Schellencandona dui*	*Schellencandona dui*	China	Ditches with mud, streams with mud and vegetation, lake with vegetation	Recent	Valves and soft parts
Fuchs *et al.* 2006, Hahn & Fuchs 2009	*Schellencandona insueta*	*Schellencandona insueta*	Germany	Boreholes	Recent	No
Klie 1938	*Candona insueta*	*Schellencandona insueta*	Germany	Well	Recent	Valves and soft parts (T3 and CR)
Löffler 1961	*Candona insueta*	*Schellencandona insueta*	Germany	Interstitial	Recent	No
Yavuzatmaca *et al.* 2015	*Schellencandona insueta*	*Schellencandona insueta*	Turkey	Spring	Recent	No
Issartel & Marmonier 2025b	*Schellencandona malardi*	*Schellencandona malardi*	France	Interstitial	Recent	Valves and soft parts
Issartel & Marmonier 2025b	*Schellencandona mercantourensis*	*Schellencandona mercantourensis*	France	Interstitial	Recent	Valves and soft parts
Sywula 1976	*Candona* (*Typhlocypris*) *mira*	*Schellencandona mira*	Poland	Wells	Recent	Valves and some soft parts

......continued on the next page

TABLE 1. (Continued)

References	Original taxonomic designation	Current taxonomic classification	Country	Habitat	Recent/fossil	Illustrated material
Dole-Olivier *et al.* 2009	*Schellencandona triquetra*	*Schellencandona rhodanensis* [b]	France	Medium and coarse alluvia	Recent	Valves
Issartel & Marmonier 2025a	*Schellencandona rhodanensis*	*Schellencandona rhodanensis*	France	Interstitial in main river channels and associated wetlands	Recent	Valves and soft parts
Marmonier & Creuzé des Châtelliers 1992	*Pseudocandona triquetra*	*Schellencandona triquetra* [b]	France	Interstitial	Recent	No
Marmonier *et al.* 2019	*Schellencandona triquetra*	*Schellencandona rhodanensis* [b]	France	Interstitial	Recent	No
Marmonier *et al.* 2020	*Schellencandona triquetra*	*Schellencandona rhodanensis* [b]	France	Interstitial and karst cavities	Recent	No
Castellarini *et al.* 2007	*Schellencandona schellenbergi*	*Schellencandona schellenbergi*	France	Streambed sediments?	Recent	No
Fuchs *et al.* 2006, Fuchs 2007, Hahn & Fuchs 2009	*Schellencandona schellenbergi*	*Schellencandona schellenbergi*	Germany	Boreholes	Recent	No
Gibert *et al.* 1981	*Candona aff. schellenbergi*	*Schellencandona schellenbergi*	France	Interstitial	Recent	No
Klie 1934	*Candona schellenbergi*	*Schellencandona schellenbergi*	Austria	Wells	Recent	Valves and soft parts
Meisch 1996	*Schellencandona schellenbergi*	*Schellencandona schellenbergi*	Germany	Interstitial	Recent	No
Vervier *et al.* 1986	*Pseudocandona schellenbergi*	*Schellencandona schellenbergi*	France	Cave, artificial substrates	Recent	No
Danielopol 1978	*Schellencandona similampadis*	*Schellencandona simililampadis*	France	Artificial tunnel in karstic system	Recent	Valves and soft parts
Ferreira *et al.* 2003	*Schellencandona simililampadis*	*Schellencandona simililampadis*	France	Subterranean	Recent	No
Kenderov & Apostolov 2008	*Schellencandona* sp.	*Schellencandona* sp.	Bulgaria	Interstitial	Recent	No
Mazzini *et al.* 2016	*Schellencandona* sp.	*Schellencandona* sp.	Albania	Lake	Late Pleistocene	No
Melis *et al.* 2012	*Schellencandona* sp.	*Schellencandona* sp.	Italy	Interstitial?	Holocene	No
Valavani *et al.* 2024	*Schellencandona* sp.	*Schellencandona* sp.	Greece	Cave	Recent	No
Yavuzatmaca *et al.* 2024	*Schellencandona* sp.	*Schellencandona* sp.	Turkey	Stream surface sediment	Recent	No
Dole-Olivier *et al.* 2009	*Schellencandona* sp. 4	*Schellencandona* sp. 4	France	Subterranean	Recent	No

......continued on the next page

TABLE 1. (Continued)

References	Original taxonomic designation	Current taxonomic classification	Country	Habitat	Recent/fossil	Illustrated material
Dole-Olivier *et al.* 2009	*Schellencandona* sp. J1 *schellenbergi*	*Schellencandona* sp. J1 *schellenbergi*	France	Limestone and coarse alluvium formations	Recent	No
Dole-Olivier *et al.* 2009	*Schellencandona* sp. J2 *insueta*	*Schellencandona* sp. J2 *insueta*	France	Subterranean	Recent	No
Dole-Olivier *et al.* 2009	*Schellencandona* sp. J3	*Schellencandona* sp. J3	France	Subterranean	Recent	No
Khand 2007	*Schellencandona* sp.?	*Schellencandona* sp.?	Mongolia	Springs and rivers	Recent	Valves and soft parts
Karanovic & Lee 2012	*Schellencandona tea*	*Schellencandona tea*	South Korea	Interstitial	Recent	Valves and soft parts
Dehédin 2012	*Schellencandona triquetra* [c]	*Schellencandona triquetra*	France	Interstitial?	Recent	No
Ferreira *et al.* 2003	*Schellencandona triquetra*	*Schellencandona triquetra*	France	Subterranean	Recent	No
Fuchs *et al.* 2006, Fuchs 2007, Hahn & Fuchs 2009	*Schellencandona triquetra*	*Schellencandona triquetra*	Germany	Boreholes	Recent	No
Fuhrman R. 2012	*Schellencandona belgica*	*Schellencandona belgica*	Germany	Boreholes	Late Holocene	Valves
Gerecke *et al.* 2005	*Schellencandona triquetra*	*Schellencandona triquetra*	Luxembourg	Interstitial	Recent	No
Hartmann & Hiller 1977	*Candona triquetra*	*Schellencandona triquetra*	Germany	Interstitial	Recent	No
Hubart & Dethier 1999	*Schellencandona triquetra*	*Schellencandona triquetra*	Belgium	Springs	Recent	No
Husmann 1956	*Candona triquetra*	*Schellencandona triquetra*	Germany	Interstitial	Recent	No
Husmann 1957	*Candona triquetra*	*Schellencandona triquetra*	Germany	Intestitial	Recent	No
Husmann 1964	*Candona triquetra*	*Schellencandona triquetra*	Germany	Interstitial	Recent	No
Klie 1936	*Candona triquetra*	*Schellencandona triquetra*	Belgium	Wells	Recent	Valves and soft parts
Leruth 1937	*Candona triquetra*	*Schellencandona triquetra*	Belgium	Cave lake	Recent	No
Muller *et al.* 2008	*Schellencandona triquetra*	*Schellencandona triquetra* [d]	France	Interstitial	Holocene	Valves
Smith & Kamiya 2006	*Schellencandona yakushimaensis*	*Schellencandona yakushimaensis*	Japan	Cracks in bedrock filled with water and sediment	Recent	Valves and soft parts
Smith & Chang 2022	*Schellencandona yakushimaensis*	*Schellencandona yakushimaensis*	Japan	Spring	Recent	Valves
Knight 2013, Knight 2017	*Mixtacandona*/*Schellencandona* sp.	Unknown	United Kingdom	Cave pool	Recent	No

The Toncina Stream rises on the slopes of Mount Pelpi and follows a course of roughly 8 km before joining the Ceno River. At Fornovo Taro, the Ceno River merges with the Taro River, which subsequently feeds into the Po River. The Toncina Stream has a torrential flow pattern, marked by reduced water levels in summer and occasional periods where surface flow ceases entirely. The sampling station is in a braided channel characterized by riffle-run-pool habitat sequences, with sediment sizes ranging from pebble-cobble gravel to boulders.

The collecting site in the upper basin of the Po River is located in a weakly braided reach affected by periodic episodes of drought, where the sediment consists mainly of cobbles and gravel (see Bruno *et al.* 2020, for further details).

Specimens were collected by filtering water pumped from the hyporheic zone. In the Toncina Stream, samples were collected with a Bou-Rouch pump, reaching about 50 cm below ground level, by filtering 20 L (July 13 and August 3, 2018) of water with a 100 µm mesh plankton net, or volumes between 10 and 60 L (May 11 and November 16, 2024) with a 50 µm mesh plankton net. In the Po River, a flexible plastic hose connected to an electric pump and generator was inserted into a piezometer, collecting 40 L of water from about 1 m below ground level; water was filtered using a 100 µm mesh plankton net. All samples were preserved in 90% ethanol in the field.

Morphological methods

In the laboratory, the samples were sorted for invertebrates under a MOTIC SMZ 168 stereomicroscope. The ostracods were dissected, with soft parts mounted in glycerine and sealed in permanent glass slides, while the valves were stored dry in micropalaeontological slides. Line drawings of the soft parts were made using a Zeiss Standard 25 light microscope with a camera lucida. Digital images of carapaces and valves were obtained using a scanning electron microscope (ZEISS EVO MA10 - SEM). The chaetotaxy of the soft parts follows Meisch (2000).

The type material of *Schellencandona antoniae* **sp. nov.** and the specimen of *Schellencandona* cf. *insueta* are deposited in the crustacean collection of the La Specola Museum of Natural History, Zoology Section, Florence, Italy; the number following the acronym MZUF indicates the collection number of the deposited specimens.

The following abbreviations are used throughout the text and figures: Valves. Cp: carapace; RV: right valve; LV: left valve; L: length, H: height; iv: internal view; ev: external view. Soft parts. A1: antennule; A2: antenna; Md: Mandible; Mx1: maxillule; T1: first thoracopod (maxilliped); T2: second thoracopod (walking leg); T3: third thoracopod (cleaning leg); CR: caudal ramus; exo: exopodite on A2; α: seta on A1; ya: aesthetasc on A1; t1-3 and z1-3: setae on A2; Y and y1-3: aesthetascs on A2; G1-3, GM, Gm: claws on A2; f, g and h1-3: setae and claws on T2 and T3; d1-2 and dp: setae on T3; Sa and Sp: anterior and posterior setae on CR; Ga and Gp: anterior and posterior claws on CR.

TAXONOMIC RESULTS

Taxonomic account (after Meisch *et al.* 2024)

Class Ostracoda Latreille, 1802

Subclass Podocopa G.O. Sars, 1866

Order Podocopida G.O. 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* (modified after Meisch 1996, 2000)

Carapace small, 0.4–0.6 mm long. Valves trapezoidal, subtrapezoidal, triangular or reniform, in some species LV and RV strongly asymmetrical in lateral view. Valves smooth or with shallow pits. Eye pigment absent. Male antenna dimorphic: penultimate segment subdivided and with male bristles (t2 and t3-bristles transformed). Setal group on the second segment of the mandibular palp with three setae; externo-distal seta (gamma-seta) of the penultimate segment smooth. Mx respiratory (branchial) plate with two setae. Cleaning leg: basal segment (protopod) with two setae (d1 and dp); penultimate segment with one distal seta (seta g); terminal segment with one short (h1) and two long setae (h2 and h3). Zenker organ with four+two rings of spines. M-process of the penis very flat.

Schellencandona antoniae **sp. nov.**

urn:lsid:zoobank.org:act:674BF31E-7B0A-4F89-B1C9-37F83E38CFAA

(Figures 1–3)

Type locality. Toncina Stream, approximately 600 meters upstream of its confluence with the Ceno River, near the locality of Molino dei Belli, in the municipality of Bardi, Parma, Italy. Latitude 44°35’39.9”N, longitude 9°42’15.8”E, elevation about 430 m a.s.l.

Type material. Holotype: adult ♀ (MZUF726, LV: L=575 µm, H=360 µm; RV: L=564 µm, H=311 µm) collected on July 13, 2018: soft parts dissected in glycerine in a sealed slide, valves stored dry in a micropalaeontological slide. Paratypes: adult ♀ (MZUF727, Cp: L=550 µm, H=340 µm) collected on August 3, 2018: soft parts dissected as the holotype, valves lost during dissection; adult ♀ (MZUF728, LV: L=543 µm, H=332 µm; RV: L=539, H=298 µm) collected on July 13, 2018: soft parts dissected as the holotype and valves stored dry in a micropalaeontological slide; adult ♀ (MZUF729, RV: L=533 µm, H=299 µm) collected on November 16, 2024: isolated RV stored dry in a micropalaeontological slide. The specimens were collected by Linda Faè in 2018 and by GR in 2024.

Etymology. This new species is dedicated to, and named, in honour of Antonia Cavalieri, a passionate naturalist devoted to the preservation of the environment and biodiversity, who also happens to be the beloved wife of the first author.

Description of female. Valves trapezoidal in lateral view (Fig 1A–B, G). LV larger than RV. Greatest H slightly less than ½ L and located slightly behind mid-length. Greatest L below mid-height. Anterior margin broadly rounded, posterior margin narrowly rounded. Dorsal margin straight, tapering posteriorly, gently arched on LV, posteriorly slightly sloping, more steeply than anteriorly. On RV, anterior cardinal angle slightly concave. Reticulate surface organized in strongly calcified polygonal muri and smooth fossae. Normal pore canals simple. Hinge adont (Fig 1C–D, E): LV with smooth groove; RV with smooth bar. In internal view (Fig 1C–D, E), calcified part of inner lamella wide anteriorly. Ventral margin of LV with slight but distinct convexity in the middle, complementary expansion of selvage on RV. Central muscle scar arrangement as characteristic for Candoninae (Fig 1F).

A1 seven-segmented (Figure 2A); first segment bearing a seta along ventral margin and two long, apical-dorsal setae of similar length; second and third segments with one ventral seta each, both slightly exceeding and reaching the margin of next respective segment; fourth and fifth segments with one long apical-ventral seta and one tiny apical-dorsal seta each; sixth segment with three long apical setae, one tiny apical-dorsal seta and seta α slightly exceeding the margin of next segment; seventh segment with a long aesthetasc ya and three apical setae, two of which very long and the most dorsal one as long as about the last two segments together.

A2 (Figure 2B): protopodite two-segmented, first segment (not shown) with two ventro-apical setae and one long dorsal seta, second segment with long subapical seta on ventral edge. Exo with long seta reaching 4/5 of next segment and two tiny setae, the ventral-most one with enlarged base. Endopodite three-segmented; first segment with aesthetasc Y inserted just below half of ventral margin and reaching approximately to distal edge of same segment, and two ventro-apical setae, the longest one extending slightly beyond distal margin of last endopodal segment, and about 2.5 times as long as the other; second endopodal segment with seta at mid-dorsal margin just surpassing distal end of segment, aesthetasc y1 proximally on ventral margin, three unequal t setae inserted about mid- segment, three short z setae, dorso-apical claws G1 and G2 with length ratio c. 4:1, apical-ventral claw G3 reaching to tips of claws G1 and GM, aesthetasc y2 barely exceeding distal margin of next segment; last endopodal segment distally with claw Gm and GM in a ratio of 1 to 2, and more ventrally aesthetasc y3 with thin accompanying seta; GM about twice as long as combined length of last two endopodal segments; g seta not observed.

Md (not shown): palp four-segmented; first segment with long seta, S1 seta slightly longer than former one, short alpha seta and S2 seta short and stout on distal part of ventral margin; second segment with ventrally three long, subequal setae (setal group), a short beta seta and an additional seta extending to just before distal end of last segment, and two dorsal setae of different lengths in subapical position; apical part of third segment with three dorsal setae, a ventral seta and centrally a gamma seta long and smooth; last segment with two ventral setae and two dorsal claws, the innermost one stout and with enlarged base. Coxa narrow.

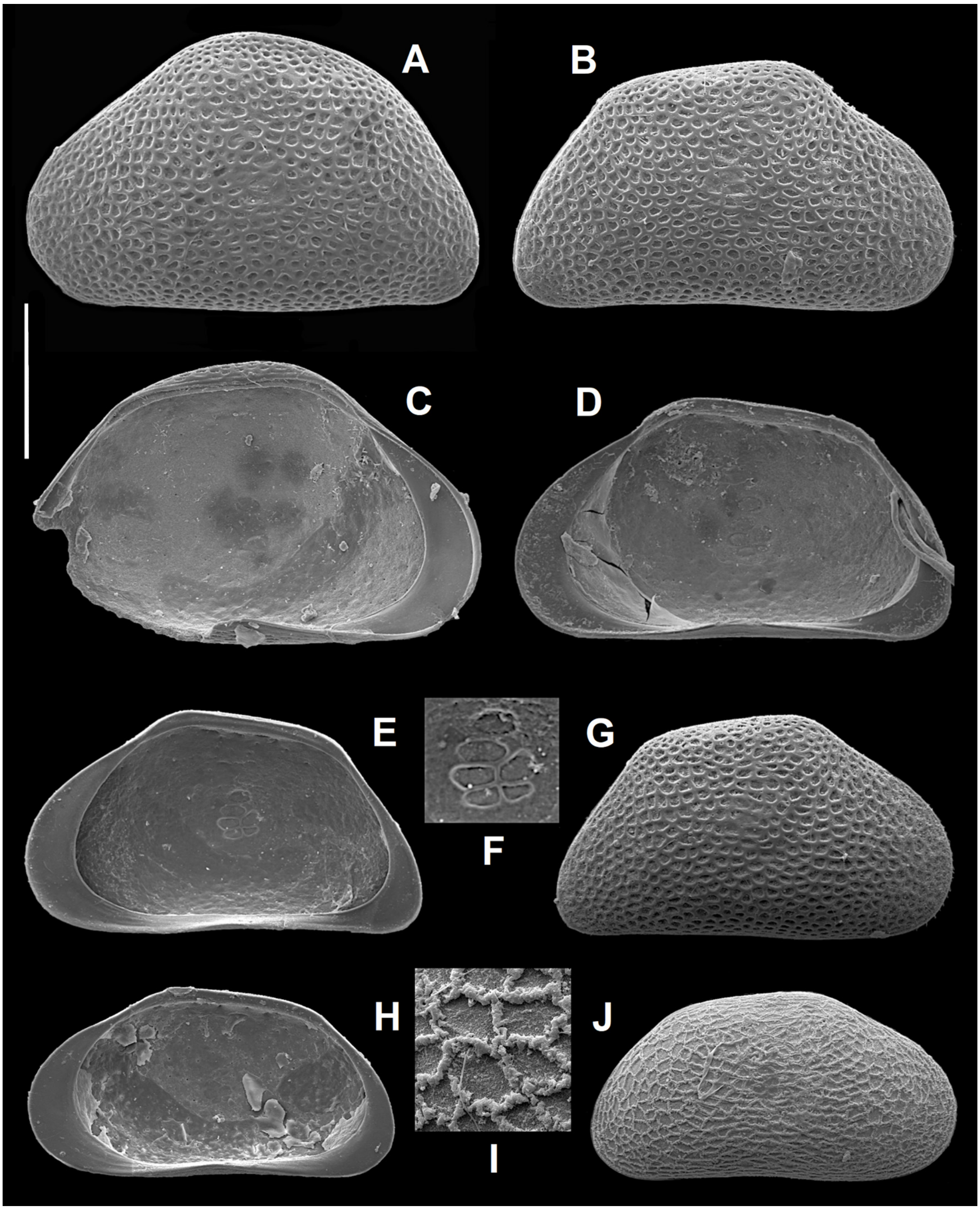

FIGURE 1. A–D: *Schellencandona antoniae* **sp. nov.** adult ♀ (MZUF726); E–G: *Schellencandona antoniae* **sp. nov.** adult ♀ (MZUF728); H–J: *Schellencandona* cf. *insueta* adult ♀ (MZUF730). A, LV ev. B, RV ev; C, LV iv. D, RV iv. E, RV, iv. F, detail RV iv, detail of the central muscle scar. G, RV ev. H, RV iv. I, RV ev, detail of the surface ornamentation. J, RV ev. Scale bar: 200 μm for A–E, G, H, J; 100 μm for F; 40 μm for I.

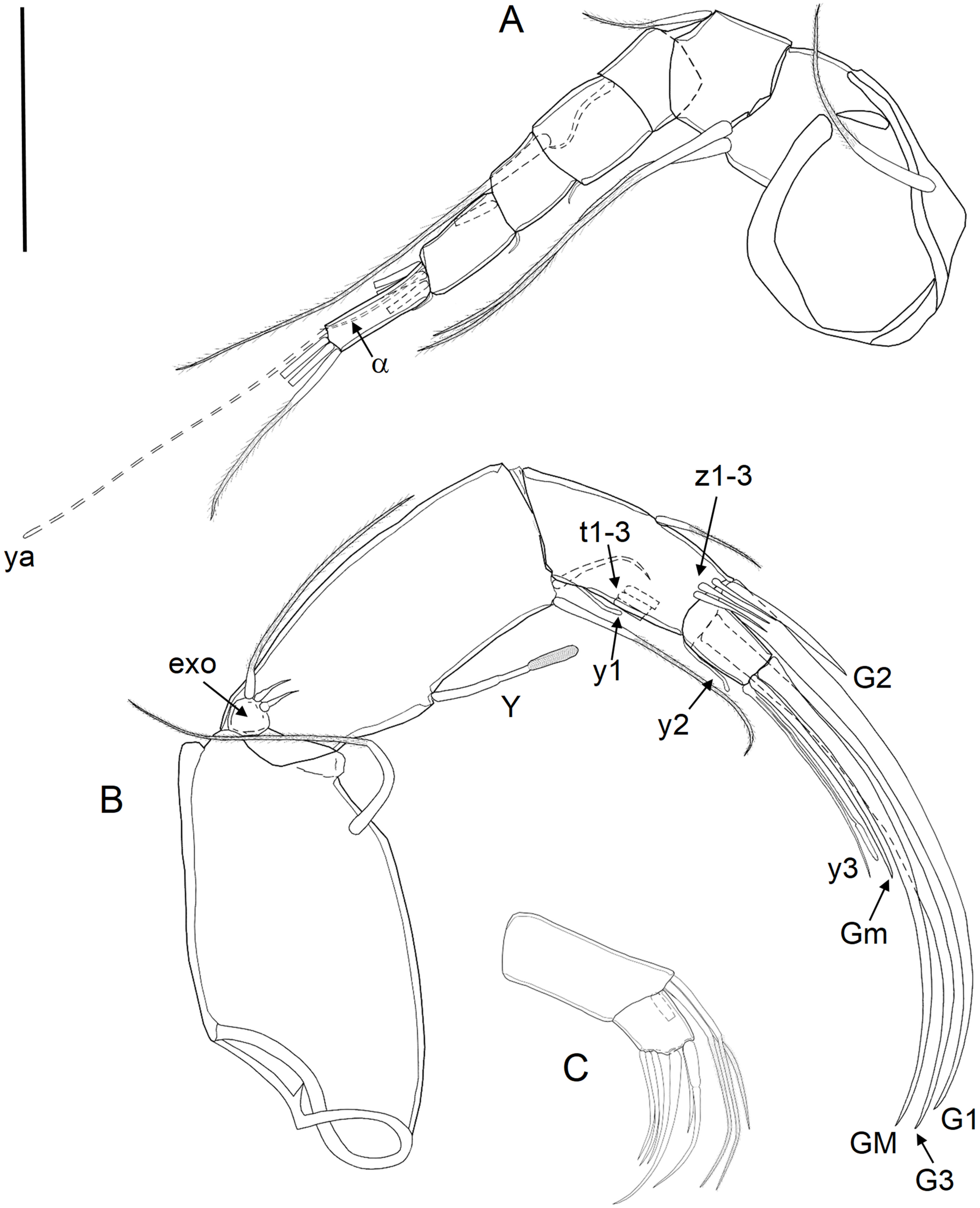

FIGURE 2. A–D: *Schellencandona antoniae* **sp. nov.** adult ♀ (MZUF728); C: *Schellencandona antoniae* **sp. nov.** adult ♀ (MZUF727). A, A1. B, A2. C, Mx. Scale bar: 50 μm.

Mx (Figure 2C): palp two-segmented; first segment bearing four setae of which three in outer position and one more central; second segment with two robust, long setae and four shorter, thinner setae.

T1: damaged in the available specimens.

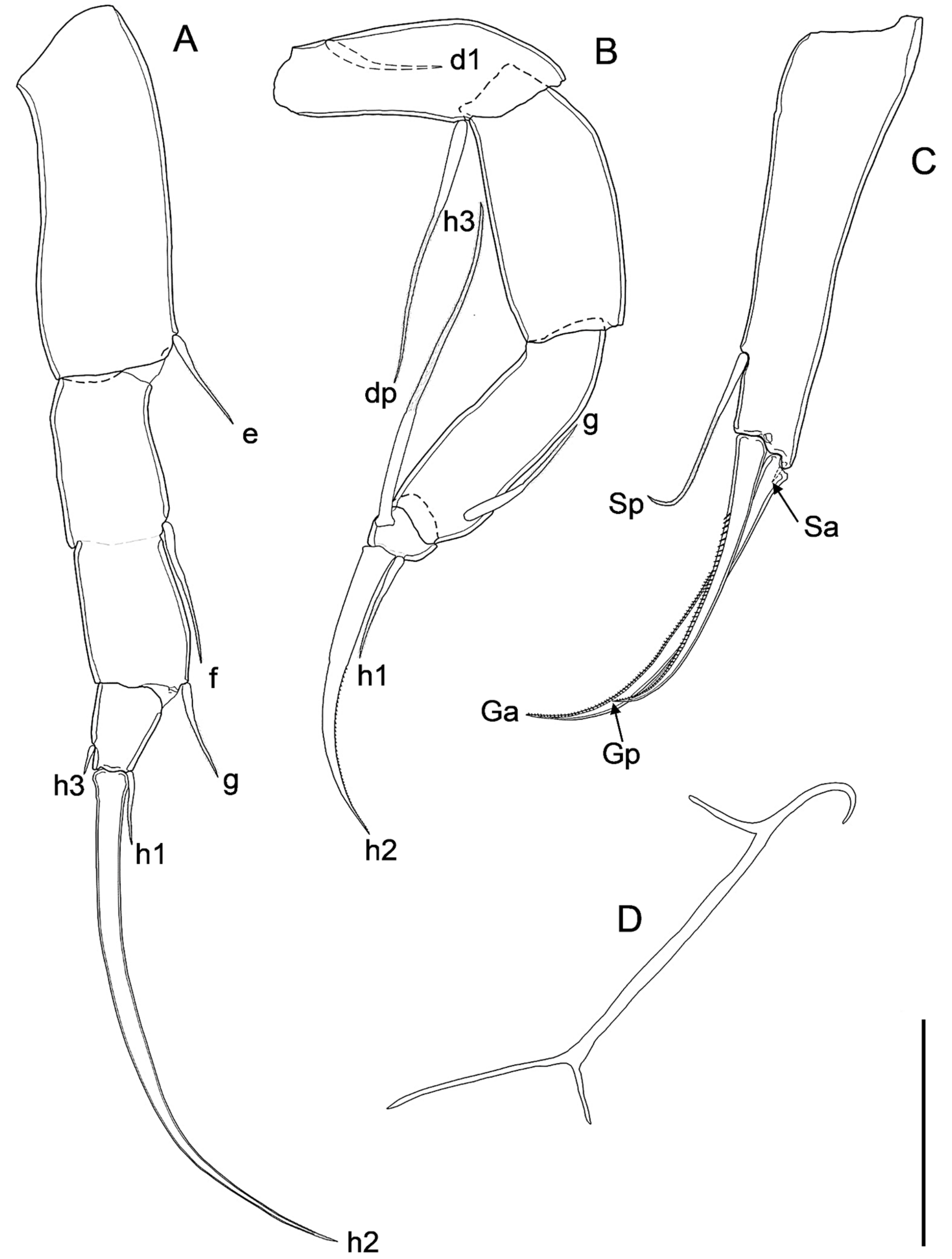

FIGURE 3. A, B, D: *Schellencandona antoniae* **sp. nov.** adult ♀ (MZUF728); C: *Schellencandona antoniae* **sp. nov.** adult ♀ (MZUF726). A, T2. B, T3. C, CR. D, CR attachment. Scale bar: 50 μm.

T2 (Figure 3A): five-segmented; basis (not shown) perhaps lacking d1 seta; second segment with antero-distal seta e; third and fourth segments weakly subdivided, with f and g setae respectively; last segment with h1 seta slightly shorter than bearing segment, stout apical h2 claw about six times longer than terminal segment and tiny h3 seta in subapical, posterior position.

T3 (Figure 3B): protopodite with short d1 seta and long dp seta, the latter exceeding distal end of next segment; endopodite with three segments; first endopodal segment without setae, second segment with subapical g seta; third segment with three setae: h1 short, h2 strong and h3 long and thin, with length ratio approximately 1:2.7:3.1.

CR (Figure 3C): rami stout, with long seta sp and strongly reduced seta sa; terminal claws robust and serrated, Ga length approx. 1.2 times Gp and 0.9 times the ramus length.

CR attachment (Figure 3D): straight, branched at both ends.

Eye pigment absent.

Description of male. Male unknown.

Accompanying ostracods. One specimen of *Cypria ophtalmica* (Jurine, 1820) and an unidentified ostracod larval stage collected on 4 July 2018.

Remarks

Schellencandona antoniae **sp. nov.** is formally described here, despite only a few female specimens being available. We have chosen to proceed with the description as both valve and soft-part characteristics are provided, enabling us to clearly distinguish the new species from its congeners, even in the absence of important diagnostic features of the male which, although not found, is presumed to exist (see Discussion). Furthermore, repeated samplings at the type locality to collect additional specimens to be studied were unsuccessful.

Schellencandona cf. *insueta*

(Figure 4)

A single adult female specimen (MZUF730) of the genus *Schellencandona* was found in a sample collected on 3 July 2018 (MCB coll.) from the interstitial zone of the Po River, near the locality of Martiniana Po (Cuneo, Italy; latitude 44°39′16” N, longitude 7°19′27” E, 351 m a.s.l.). The specimen's left valve was severely damaged prior to dissection, making it unsuitable for the taxonomic description. RV (Figures 1H–J) with straight dorsal margin slightly tapering towards posterior end. Evenly rounded anterior margin distinctly broader than posterior one, the latter gently tapering towards ventral corner. Surface covered by reticulate pattern organized in polygonal meshes, with weakly calcified muri and smooth fossae. The specimen shows notable similarity to *Schellencandona insueta* (Klie 1938) (see Figure 11, page 13 in Klie 1938a). The valves are also very similar in size (L=0.47 mm and 0.46 mm, H/L 0.51 and 0.52 in the specimen studied here and in *S. insueta*, respectively). In Klie (1938a, 1938b), the valves of *S. insueta* are described as smooth and hairy, but no mention is made of a reticulate pattern, which is instead evident in the specimen from the Po River also when observed in transmitted light.

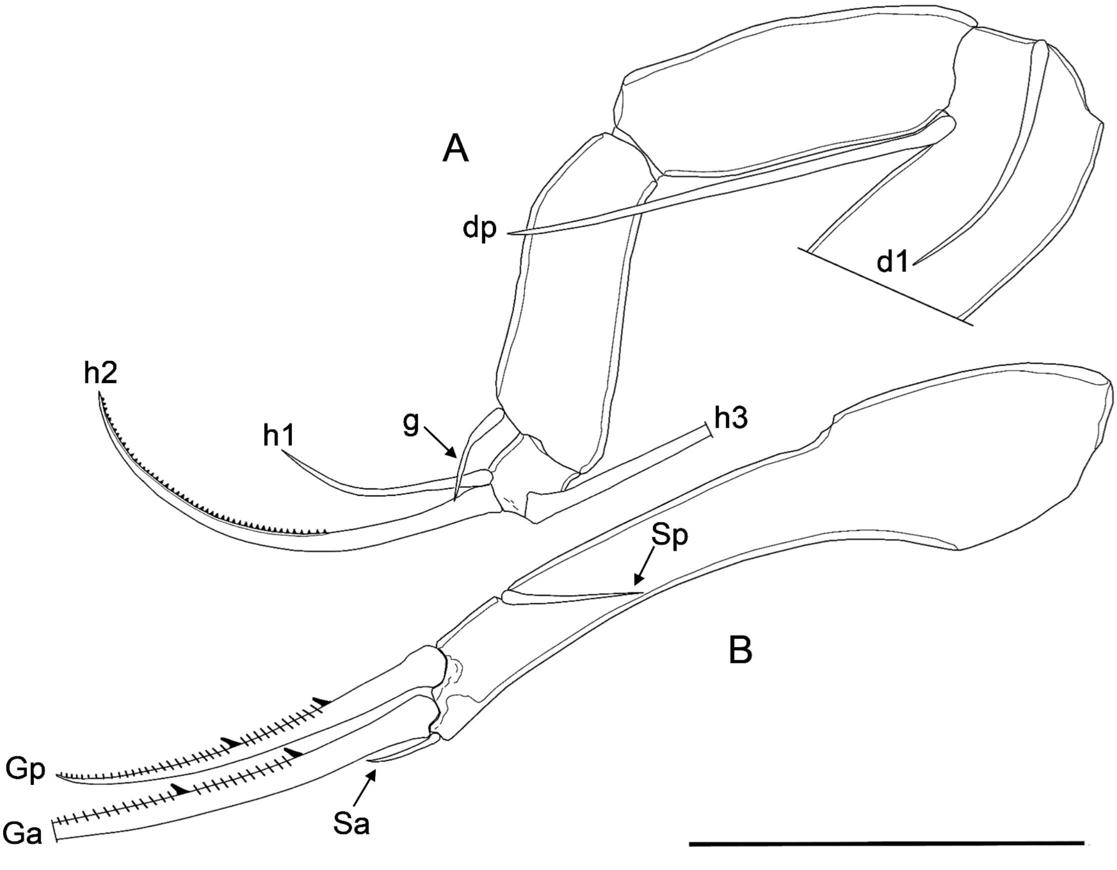

FIGURE 4. *Schellencandona* cf. *insueta* adult ♀ (MZUF730). A, T3; B, CR. Scale bar: 50 µm.

Regarding the soft parts of the female of *S. insueta*, Klie (1938a) only published drawings of the cleaning leg and the furcal ramus. In the specimen examined here, the ratio between seta h1 and seta g of the cleaning leg is approximately 2:1 (Figure 4A), whereas in *S. insueta* the two setae are of similar lengths (Klie 1938a; Figure 15, page 14). Particularly interesting is the presence in the Po River specimen of two denticles and two rows of setulae on each of the two terminal claws of the furcal ramus (Figure 4B), similar to what is illustrated by Klie (1938a; Figure 16, page 14) for *S. insueta*. Notably, this feature is not detectable in any other known species of the genus *Schellencandona*.

The studied specimen contained bundles of sperm inside the carapace, indicating the presence of males at the sampling site.

Since only one specimen from the Po River was available and its preservation was insufficient, along with the lack of highly diagnostic male sexual characteristics, it seems advisable to refrain from fully confirming its specific status at this stage, despite the observed similarities to *S. insueta*. A more definitive verification will require the potential acquisition of additional material.

Discussion

Studies on subterranean ecosystems continue to reveal the existence of highly diverse communities, which hold significant value for exploring evolutionary processes and adaptation mechanisms (Boulton *et al.* 2023). Meanwhile, various shortfalls and impediments (Ficetola *et al.* 2019, Mammola *et al.* 2019) still severely restrict our knowledge of these faunas.

Research conducted in recent years has significantly increased both the number of species and the geographical distribution of the genus *Schellencandona* (Smith & Kamiya 2006, Karanovic & Lee 2012, Yavuzatmaca *et al.* 2015, Ma & Yu 2018, Juberthie *et al.* 2016, Issartel & Marmonier 2025a, 2025b), to which the records reported in the present article should be added. *Schellencandona antoniae* **sp. nov.** can be readily distinguished from all congeneric species by its valve morphology. Among species with pitted, triangular–trapezoidal valves, the most similar are *Schellencandona triquetra* Klie, 1936 and *Schellencandona rhodanensis* Issartel & Marmonier, 2025a; however, the new species differs from both by its considerably larger size (length 0.53–0.58 mm versus approximately 0.40 mm in adult females) and by the shape of the dorsal, anterior and posterior margins of the valves. *Schellencandona danielopoli* Issartel & Marmonier, 2025 also exhibits small pits and a size comparable to *S. antoniae* **sp. nov.**, but its carapace is distinctly triangular.

Despite these advancements, several critical aspects of this genus remain unresolved. One of the most persistent challenges lies in understanding the mechanisms and timeline associated with the colonisation of subterranean habitats. While neontological data provide important insights, the transition from surface to subterranean environments is complex and likely involved a combination of ecological, physiological and evolutionary factors that are still poorly understood. Compounding this issue is the difficulty in developing robust taxonomic tools that bridge the gap between living (neontological) and extinct (paleontological) species. Currently, taxonomic approaches tend to focus on extant representatives, relying on soft-part morphology and molecular data. However, these methods are inapplicable to fossil ostracod species, which are typically known only from calcified carapaces. As a result, there is a pressing need for integrative taxonomic frameworks that incorporate morphological characters observable in both fossil and living specimens. Without such tools, the accurate identification and classification of fossil *Schellencandona* species remain problematic, hampering our understanding of their evolutionary history and biogeographic patterns. Furthermore, the phylogenetic relationships among both extant and extinct species of *Schellencandona* are still not resolved. Fossil records have the potential to illuminate lineage divergence and historical distributions, but this potential remains underutilized due to taxonomic uncertainty, since in numerous scholarly contributions species identifications remain uncertain. To further complicate the situation, the valves—and, for living species, the soft parts as well—have been illustrated and described in a limited number of studies (Table 1).

The oldest fossil records identified as *Schellencandona* date back to the Late Pleistocene (Table 1); however, the scarcity (and possibly even the reliability) of the available information does not allow to draw robust hypotheses regarding the origin of the genus and the timing of its invasion of subterranean waters. While the morphology of the soft parts remains consistent across different species, the high variability in the shape of the valves and carapaces, as well as the homoplastic similarities with subterranean species of other candonid genera, greatly complicates the attribution of fossil taxa to *Schellencandona*. At present, no diagnostic valve characteristics derived from the analysis of living forms have been proposed that would permit the unambiguous assignment of fossil specimens to the genus.

As it commonly occurs in various ostracod lineages with representatives in subterranean waters, many species are endemic. This can certainly be explained by the fact that groundwater habitats act as sites of speciation and that dispersal in such habitat can be more limited compared to epigean environments (Malard *et al.* 2023). All species within the genus are assumed to reproduce sexually, with the probable exception of the Asian species (*Schellencandona tea*, *Schellencandona dui* Ma & Yu, 2018, *Schellencandona yakushimaensis* Smith & Kamiya, 2006) and consequently have a lower colonization potential than parthenogenetic species.

Issartel & Marmonier (2025b) demonstrated that even at relatively small geographical scales and within the same hydrographic system, different *Schellencandona* species can be found as a result of hydrological and longitudinal gradients along river ecosystems, which foster speciation events. However, at least in part, the high incidence of endemic species in *Schellencandona* may be attributed to the limited availability of distributional data across vast regions, a pattern also observed in other groundwater crustaceans (Cottarelli & Bruno 2025). Conversely, certain species within the genus have been widely reported in several Central European and Mediterranean countries (i.e., *S. triquetra* and *S. insueta*), and possibly even in the eastern Palearctic (*Schellencandona belgica* (Klie, 1937)). The identification of *Mixtacandona/Schellencandona* sp., reported by Knight (2013, 2017) from the United Kingdom, remains highly uncertain due to the absence of both morphological description and illustrations, and is therefore excluded from further consideration (Table 1).

Although information on the ecology of species within the genus *Schellencandona* is extremely scarce, differences in their distribution ranges can plausibly be attributed to varying degrees of tolerance and adaptation to environmental conditions. For instance, Issartel & Marmonier (2025a, 2025b) have linked the presence of certain interstitial species within this genus to factors such as water temperature, oxygen content, and habitat characteristics, noting distinct preferences for specific depths within the riverbed and for upwelling or downwelling zones. Indeed, the two species recorded in this study were collected in river stretches characterized by hydrological intermittence (Burgazzi *et al.* 2017, 2018; Bruno *et al.*, 2020). The specimens of *Schellencandona antoniae* **sp. nov.** were collected from the Toncina Stream in 2018, a high precipitation year, but with a reduction in rainfall in June–July; water was upwelling from the hyporheic zone to the surface in July, and downwelling in August (MCB, unpublished data). Intermediate flow rates were observed during the 2024 surveys; however, no data are available on flow conditions preceding these sampling periods. *Schellencandona* cf. *insueta* was collected in the Po River during a low flow period when the aquifer was receding; this low flow period occurred after a five-month long supraseasonal drought followed by six months of flow (Bruno *et al.* 2020).

Historical factors also play a crucial role in shaping the current distribution of species, particularly those linked to specific geological events such as glaciation and deglaciation phases. For instance, Stein *et al.* (2012) proposed a classification of groundwater based on stygofauna composition in Germany. Of the four *Schellencandona* species identified in the country, three (*S. belgica*, *S. insueta*, *S. triquetra*) are confined to a single stygoregion unaffected by glaciation periods, while *Schellencandona schellenbergi* (Klie, 1934) occurs both in that stygoregion and in a second one that was once covered by the Last Glacial Maximum (LGM) ice shield. Similarly, Issartel & Marmonier (2025b) attributed differences in the dispersal history of various *Schellencandona* species found in France to LGM glacial expansions and subsequent post-glacial recolonization.

Valve morphology serves as a primary diagnostic tool in the taxonomic and phylogenetic analysis of recent ostracods and, in the case of fossil specimens, constitutes the only available means of identification. The species of the genus *Schellencandona* can be classified into five distinct types based on the valve shape. They may have elongated valves—either with an arched dorsal margin and maximum height at the middle, or with an almost straight dorsal margin inclined forward, with maximum height in the posterior third—or less-elongated valves. The compressed forms can be trapezoidal, with parallel dorsal and ventral margins, or the dorsal margin sloping downwards, or they can be triangular. Further distinctions among species exist in valve ornamentation, which may be absent, reticulated, or pitted, as well as in the degree of symmetry between the right and left valves, the convexity of the anterior and posterior margins, and sexual dimorphism. Valve length ranges from 0.4 to 0.6 mm, while the height to length ratio varies from 0.44 to 0.62. There are no distinct patterns linking the geographical distribution of species to valve morphology, as restricted areas and even the same hydrographic basin can host species with highly diverse shapes. However, *Schellencandona* species with elongate valves and a height to length ratio ≤0.46 (*S. tea*, *S. dui*, *S. yakushimaensis*, all characterised by an arched dorsal margin and maximum height at the middle) are exclusively found in East Asia. In addition, *S. belgica* (including forms identified as *S.* cf. *belgica*), the only species in the genus with an almost straight dorsal margin inclined forward, maximum height in the posterior third, height to length ratio ~0.48, surface smooth with shallow rounded pits occurring only in the central area (Fuhrmann 2012, Plate 43), may have a potential intercontinental distribution (Table 1).

These differences in carapace morphology—and only in some cases in geographical distribution—are unlikely to represent distinct evolutionary lineages, as the morphology of soft body parts remains mostly consistent. Rather, they may reflect different periods of adaptation to specific habitat types, particularly subterranean environments, or may have other ecological significance (Iepure *et al.* 2023).

As suggested by Danielopol (1980), the degree of morphological and biological specialisation for subterranean life may provide clues about the antiquity of a hypogean animal group. Observations from other Candoninae genera, which either include or are entirely composed of subterranean species (e.g., *Pseudocandona* Kaufmann, 1900, *Marmocandona* Danielopol *et al.*, 2012, *Mixtacandona* Klie, 1938b, *Typhlocypris* Vejdovský, 1882), indicate that traits such a reduced size and the dominance of triangular or trapezoidal valve shapes are common traits among stygobiotic species. The presence of similar morphological features in *Schellencandona* species may thus indicate a prolonged evolutionary history in subterranean habitats. It is noteworthy that the only known records of *Schellencandona* species from surface water environments involve forms with an elongate carapace: *S.* cf. *belgica* has been found in lakes (Chen *et al.* 2019), while *S. dui* has been recorded in both lentic and lotic habitats (Ma & Yu 2018). This pattern suggests that the elongate carapace morphology may be more typical of epigean forms, while the shorter, more angular valve shapes are potentially linked to life in subterranean or interstitial habitats. These morphological trends underscore the adaptive significance of valve shape in response to environmental pressures and support the hypothesis that carapace variation in *Schellencandona* is more likely ecophenotypic or adaptive rather than phylogenetic in origin.

Nevertheless, alternative explanations can be proposed. For instance, Karanovic & Sitnikova (2017) suggest that ancient lakes, beyond serving as refuges, might have functioned as "biodiversity pumps", facilitating the transition of species already preadapted to deep and dark benthic environments into subterranean habitats, taking as an example the morphological similarities between some *Schellencandona* species and *Baicalocandona* Mazepova, 1976, the latter genus characterised by lacustrine species with a trapezoidal valve shape.

Soft-part characteristics can also indicate varying degrees of adaptation to subterranean life, especially sensory structures that compensate for permanent darkness. Enhanced non-visual sensing is often accompanied by reduction or loss of photoreceptive systems and by behavioral shifts, such as increased reliance on chemotaxis and mechanoreception, altered foraging strategies, and mating behaviours that no longer depend on vision (Lunghi *et al*. 2024). For example, Danielopol (1980) linked increased length of the A2 aesthetasc Y, interpreted as a putative chemoreceptor, with prolonged subterranean adaptation in Candoninae. In *S. antoniae* **sp. nov.** this aesthetasc is moderately developed relative to other candonids, and its ratio to the first endopodal segment of the A2 falls within the relatively narrow range reported for congeners. The same applies to aesthetasc y3 of A2 and ya of A1, for which no extreme reduction or elongation is evident among species of the genus. Overall, variation in aesthetasc length, both absolute and relative to segment length, does not display a consistent pattern across the genus; potential intraspecific variability must also be considered when making comparisons. Detailed, fine-scale morphological analyses are required to test and validate these preliminary observations.

An approach based solely on morphological characters undoubtedly limits the analysis of adaptive processes and evolutionary reconstructions. The study of phylogenetic relationships between and within other Candoninae genera has greatly benefited from an integrated taxonomic approach (e.g. Hiruta *et al.* 2016, Karanovic & Sitnikova 2017, Wysocka *et al.* 2019, Rossetti *et al.* 2025), but for *Schellencandona*, no genetic sequences appear to have been published to date.

Conclusions

This study presents the first confirmed records of living species of the genus *Schellencandona* in Italy. Both sampling sites were not covered by ice during the Last Glacial Maximum (Hughes *et al.* 2006, Baroni *et al.* 2018).

Schellencandona antoniae **sp. nov.** and *S. cf. insueta* appear to have an extremely localised distribution and possibly very low population densities. Further sampling conducted in May 2024 by GR in the hyporheic zone of left and right tributaries in the middle course of the Ceno River, within a 20 km radius from the sampling site at the Toncina Stream, did not yield additional specimens of *Schellencandona*. Similarly, no individuals of this genus were found at a station of the Po river with a perennial flow and located a few kilometres upstream from the site where *S.* cf. *insueta* was collected (Bruno *et al.* 2020).

If new findings confirm the presence of *S. insueta* in Italy, this will offer a significant opportunity to further explore the species' zoogeography, which remains somewhat enigmatic. To date, *S. insueta* has been recorded in southwestern Germany at its type locality (Klie 1938b) and at another site by Löffler (1961), and in the province of Adiyaman in south-central Turkey (Yavuzatmaca *et al.* 2015) (Table 1). However, the publications following the species' original description lack illustrations of the valves and carapace, limiting the potential for further morphological comparisons and the validation of existing records.

It is likely that the genus *Schellencandona* has a wider distribution and greater species diversity in Italy, where research on ostracods inhabiting groundwater and groundwater-dependent ecosystems remains considerably limited compared to other European countries (Mori *et al.* 2025).

Acknowledgements

The authors are indebted to Pierre Marmonier and to an anonymous reviewer for their scrupulous and insightful revisions of the manuscript, which have significantly contributed to enhancing its quality and clarity. We gratefully acknowledge the PRIN NOACQUA Project *"Risposte di comuNità e processi ecOsistemici in corsi d'ACQUA soggetti a intermittenza idrologica"* (code 2O1572HW8F_003), funded by the Italian Ministry of Education, University and Research, and all its team members for providing several of the specimens included in this study. We thank Linda Faè and Sebastian-Daniel Stoenescu for their assistance in the field and in sorting invertebrates and Matteo Paciucci (CNR-IGAG) for patiently taking all the SEM images.

References

Baroni, C., Guidobaldi, G., Salvatore, M.C., Christl, M. & Ivy-Ochs, S. (2018) Last glacial maximum glaciers in the Northern Apennines reflect primarily the influence of southerly storm-tracks in the western Mediterranean. *Quaternary Science Reviews*, 197, 352–367.
https://doi.org/10.1016/j.quascirev.2018.07.003

Boulton, A.J., Bichuette, M.E., Korbel, K., Stoch, F., Niemiller, M.L., Hose, G.C. & Linke, S. (2023) Chapter 23. Recent concepts and approaches for conserving groundwater biodiversity. *In*: Malard, F., Griebler, C. & Rétaux, S. (Eds.), *Groundwater Ecology and Evolution. 2nd Eiditon.* Academic Press, Cambridge, Massachusetts, pp. 525–550.
https://doi.org/10.1016/B978-0-12-819119-4.00001-9

Bruno, M.C., Doretto, A., Boano, F., Ridolfi, L. & Fenoglio, S. (2020) Role of the hyporheic zone in increasing the resilience of mountain streams facing intermittency. *Water*, 12, 2034.
https://doi.org/10.3390/w12072034

Burgazzi, G., Laini, A., Raccheti, E. & Viaroli, P. (2017) Mesohabitat mosaic in lowland braided rivers: Short-term variability of macroinvertebrate metacommunities. *Journal of Limnology*, 76, 29–36.
https://doi.org/10.4081/jlimnol.2017.1650

Burgazzi, G. (2018) *Macroinvertebrates in riverine systems with different degree of intermittence: influence of community dynamics and environmental variables at different spatial scales.* Doctoral dissertation, University of Parma, Parma. Available from: https://www.repository.unipr.it/bitstream/1889/3545/7/PhD_Thesis_Burgazzi_Gemma.pdf (accessed 20 October 2025)

Castellarini, F., Malard, F., Dole-Olivier, M.J. & Gibert, J. (2007) Modelling the distribution of stygobionts in the Jura Mountains (eastern France). Implications for the protection of ground waters. *Diversity and Distributions*, 13 (2), 213–224.
https://doi.org/10.1111/j.1472-4642.2006.00317.x

Chen, L., Liu, J., Tang, Z.P., Liu, S., Huang, W., Han, S.L., Wang, Z.Q. & Xie, Y.S. (2019) Characteristics of distribution and ecology of Recent ostracods from Dongting Lake. *Acta Sedimentologica Sinica*, 37 (1), 143–154.

Cottarelli, V. & Bruno, M.C. (2025) First record and a new taxon of *Stammericaris* Jakobi, 1972 (Copepoda, Harpacticoida) from the Philippines; with an amendment to the generic diagnosis and reassignment of three Palearctic species. *Zootaxa*, 5609 (2), 215–235.

https://doi.org/10.11646/zootaxa.5609.2.4

Danielopol, D.L. (1978) Ostracodes du sud de la France 2. *Pseudocandona simililampadis* sp. nov. *International Journal of Speleology*, 10 (1), 57–71.
https://doi.org/10.5038/1827-806X.10.1.4

Danielopol, D.L. (1980) An essay to assess the age of the freshwater interstitial ostracods of Europe. *Bijdragen tot de Dierkunde*, 50 (2), 243–291.
https://doi.org/10.1163/26660644-05002001

Danielopol, D.L., Namiotko, T. & Meisch, C. (2012) *Marmocandona* nov. gen.(Ostracoda, Candoninae), with comments on the contribution of stygobitic organisms to micropalaeontological studies. *Kölner Forum für Geologie und Paläontologie*, 21, 13–16.

Dehédin, A. (2012) *Changements globaux et assèchement des zones humides fluviales: conséquences sur les processus biogéochimiques et les communautés d'invertébrés*. Doctoral dissertation, University Claude Bernard-Lyon I, Lyon. Available from: https://theses.hal.science/tel-00976026 (accessed 20 October 2025)

Dole-Olivier, M.J., Martin, D., Bou, C. & Prié, V. (2006) *Interprétation du suivi hydrobiologique de la faune stygobie, réalisé sur le système karstique des Cent Fonts lors du pompage d'essai*. Conseil Général de L'Hérault, Montpellier, 40 pp.

Dole-Olivier, M.J., Malard, F., Martin, D., Lefébure, T. & Gibert, J. (2009) Relationships between environmental variables and groundwater biodiversity at the regional scale. *Freshwater Biology*, 54 (4), 797–813.
https://doi.org/10.1111/j.1365-2427.2009.02184.x

Ferreira, D., Dole Olivier, M.J., Malard, F., Deharveng, L. & Gibert, J. (2003) Faune aquatique souterraine de France: base de données et éléments de biogéographie. *Karstologia*, 42 (1), 15–22.
https://doi.org/10.3406/karst.2003.2528

Ficetola, G.F., Canedoli, C. & Stoch, F. (2019) The Racovitzan impediment and the hidden biodiversity of unexplored environments. *Conservation Biology*, 33 (1), 214–216.
https://doi.org/10.1111/cobi.13179

Fuchs, A. (2007) *Erhebung und Beschreibung der Grundwasserfauna in Baden-Württemberg*. Doctoral dissertation, University of Koblenz-Landau, Koblenz and Landau in der Pfalz. Available from: https://d-nb.info/987249320/34 (accessed 20 October 2025)

Fuchs, A., Hahn, H.J. & Barufke, K.P. (2006) *Grundwasser-Überwachungsprogramm-Erhebung und Beschreibung der Grundwasserfauna in Baden-Württemberg*. Landesanstalt für Umwelt, Messungen und Naturschutz Baden-Württemberg, Karlsruhe, 70 pp.

Fuhrmann, R. (2012) Atlas quartärer und rezenter Ostrakoden Mitteldeutschlands. *Altenburger Naturwissenschaftlichen Forschungen*, 15, 1–320.

Fuhrmann, R. & Völker, R. (2015) Die Ostrakoden-und Molluskenfauna der Höhlensedimente im Glatten Gewölbe der Höhle Heimkehle (Uftrungen, Südharz). *Beiträge zur Geologie von Thüringen*, 8, 5–26.

Gerecke, R., Stoch, F., Meisch, C. & Schrankel, I. (2005) Die Fauna der Quellen und des hyporheischen Interstitials in Luxemburg, unter besonderer Berücksichtigung der Acari, Ostracoda und Copepoda. *Ferrantia*, 41, 1–134.

Gibert, J., Ginet, R., Mathieu, J. & Reygrobellet, J.L. (1981) Structure et fonctionnement des écosystèmes du Haut-Rhône Français; IX: Analyse des peuplements de deux stations phréatiques alimentant des bras morts. *International Journal of Speleology*, 11 (1), 141–158.
https://doi.org/10.5038/1827-806X.11.1.14

Hahn, H.J. & Fuchs, A. (2009) Distribution patterns of groundwater communities across aquifer types in south-western Germany. *Freshwater Biology*, 54 (4), 848–860.
https://doi.org/10.1111/j.1365-2427.2008.02132.x

Hartmann, G. & Hiller, D. (1977) Beitrag zur Kenntnis der Ostracodenfauna des Harzes und seines nördlichen Vorlandes (unter besonderer Berücksichtigung des Männchens von *Candona candida*). *Naturwissenschaftlicher Verein Goslar*, 125, 99–116.

Hiruta, S.F., Kobayashi, N., Katoh, T. & Kajihara, H. (2016) Molecular phylogeny of cypridoid freshwater Ostracods (Crustacea: Ostracoda), inferred from 18S and 28S rDNA sequences. *Zoological Science*, 33 (2), 179–185.
https://doi.org/10.2108/zs150103

Horne, D.J. (2003) Key events in the ecological radiation of the Ostracoda. *The Paleontological Society Papers*, 9, 181–202.
https://doi.org/10.1017/S1089332600002205

Huang, H.H.M., Yasuhara, M., Horne, D.J., Perrier, V., Smith, A.J. & Brandão, S.N. (2022) Ostracods in databases: State of the art, mobilization and future applications. *Marine Micropaleontology*, 174, 102094.
https://doi.org/10.1016/j.marmicro.2022.102094

Hubart, J.M. & Dethier, M. (1999) La faune troglobie de Belgique: état actuel des connaissances et perspectives. *Bulletin de la Société royale belge d'Entomologie*, 135, 164–178.

Hughes, P.D., Woodward, J.C. & Gibbard, P.L. (2006) Quaternary glacial history of the Mediterranean mountains. *Progress in Physical Geography*, 30 (3), 334–364.
https://doi.org/10.1191/0309133306pp481ra

Husmann, S. (1956) Untersuchungen über die Grundwasserfauna zwischen Harz und Weser. *Archiv für Hydrobiologie*, 52 (1/2), 1–185.

Husmann, S. (1957) Die Besiedlung des Grundwassers im südlichen Niedersachsen. *Beiträge zur Naturkunde Niedersachsens*, 10, 87–96.

Husmann, S. (1964) Studien zur Ökologie und Verbreitung der Gattung *Chappuisius* Kieffer, 1938 (Copepoda, Harpacticoida); Mitteilung über Neufunde aus den Grundwasserströmen von Lahn, Niederrhein, Ruhr, Leine und Unterweser. *Crustaceana*, 6 (3), 179–194.
https://doi.org/10.1163/156854064X00588

Iepure, S., Wysocka, A., Sarbu, S.M., Kijowska, M. & Namiotko, T. (2023) A new extremophile ostracod crustacean from the Movile Cave sulfidic chemoautotrophic ecosystem in Romania. *Scientific Reports*, 13 (1), 6112.
https://doi.org/10.1038/s41598-023-32573-w

Issartel, C. & Marmonier, P. (2025a) Description and use of *Schellencandona rhodanensis* sp. n. (Ostracoda, Candoninae) to locate groundwater upwelling zones in rivers and wetlands. *International Journal of Limnology*, 61, 2.
https://doi.org/10.1051/limn/2025001

Issartel, C. & Marmonier, P. (2025b) Description of five new *Schellencandona* species (Ostracoda, Candoninae) from the southern French Alps, a highly diversified area for groundwater ostracods. *European Journal of Taxonomy*, 1022, 85–133.
https://doi.org/10.5852/ejt.2025.1022.3083

Juberthie, C., Sidorov, D., Decu, V., Mikhaljova, E. & Semenchenko, K. (2016) Subterranean fauna from Siberia and Russian Far East. *Ecologica Montenegrina*, 7, 507–529.
https://doi.org/10.37828/em.2016.7.21

Jurine, L. (1820) *Histoire des Monocles, qui se trouvent aux environs de Genève*. J.J. Paschoud, Genève, XVI + 260 pp.
https://doi.org/10.5962/bhl.title.10137

Karanovic, I. & Lee, W. (2012) A review of candonid ostracods (Crustacea: Ostracoda: Podocopida) from East Asia, with descriptions of five new species from South Korea. *Zootaxa*, 3368 (1), 7–49.
https://doi.org/10.11646/zootaxa.3368.1.3

Karanovic, I., Sidorov, D.A. & Marmonier, P. (2015) Zoogeography of the ostracod genus *Nannocandona* (Podocopa) with description of two new species from Europe and East Asia. *Annales de Limnologie-International Journal of Limnology*, 51 (4), 297–313.
https://doi.org/10.1051/limn/2015028

Karanovic, I. & Sitnikova, T.Y. (2017) Phylogenetic position and age of Lake Baikal candonids (Crustacea, Ostracoda) inferred from multigene sequence analyzes and molecular dating. *Ecology and Evolution*, 7 (17), 7091–7103.
https://doi.org/10.1002/ece3.3159

Kaufmann, A. (1900) Cypriden und Darwinuliden der Schweiz. *Revue suisse de Zoologie*, 8, 209–423.
https://doi.org/10.5962/bhl.part.10584

Kenderov, L. & Apostolov, A. (2008) Composition and structure of hyporheal crustacean complex of Iskar River Valley in different environmental conditions. *Natura Montenegrina*, 7 (2), 145–167.

Khand, Y. (2007) Quaternary Ostracods of Mongolia and their environments. *The Korean Journal of Quaternary Research*, 21 (2), 59–61.

Klie, W. (1934) Zwei neue subterrane Ostracoden der Gattung *Candona*. *Zoologischer Anzeiger*, 106, 193–199.

Klie, W. (1936) Neue Candoninae (Ostr.) aus dem Grundwasser von Belgien. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 12 (13), 1–13.

Klie, W. (1937) Weitere Ostracoden aus dem Grundwasser von Belgien. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 13 (4), 1–6.

Klie, W. (1938a) Ostracoda, Muschelkrebse. *Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen une nach ihrer Lebensweise*, 34, 1–230.

Klie, W. (1938b) Ostracoden aus dem Grundwasser der oberrheinischen Tiefebene. *Archiv für Naturgeschichte*, 7, 1–28.

Knight, L.R.F.D. (2013) Pen Park Hole Invertebrate Survey 2013. 23 pp. Available from: https://www.penparkhole.org.uk/resources/Pen_Park_Hole_Biological_Report_2013.pdf (accessed 2 April 2025)

Knight, L.R.F.D. (2017) The invertebrate community of the Pen Park Hole SSSI, Bristol, UK. *Cave and Karst Science*, 44 (1), 19–30.

Leruth, R. (1937) Exploration biologique des cavernes de la Belgique et du Limbourg Hollandais XXIe Contribution: Deuxième liste des grottes visitées (Suite). *Natuurhistorisch Maandblad*, 26 (4), 43–47.

Löffler, H. (1961) Grundwasser-und Brunnenostracoden aus Südwestdeutschland und den Vogesen. *Beiträge zur naturkundlichen Forschung in Südwestdeutschland*, 20, 31–42.

Lunghi, E., Mammola, S., Martínez, A. & Hesselberg, T. (2024) Behavioural adjustments enable the colonization of subterranean environments. *Zoological Journal of the Linnean Society*, 201 (2), 549–559.
https://doi.org/10.1093/zoolinnean/zlad133

Ma, S. & Yu, N. (2018) Freshwater ostracods (Crustacea) from Tiantong National Forest Park and Dongqian Lake, eastern China, with descriptions of two new species. *Journal of Natural History*, 52 (27–28), 1825–1868.
https://doi.org/10.1080/00222933.2018.1489085

Malard, F., Garcia Machado, E., Casane, D., Cooper, S., Fišer, C. & Eme, D. (2023) Chapter 8 - Dispersal and geographic range size in groundwater. *In*: Malard, F., Griebler, C. & Rétaux, S. (Eds.), *Groundwater Ecology and Evolution (Second Edition)*. Academic Press, Cambridge, Massachusetts, pp. 185–207.

https://doi.org/10.1016/B978-0-12-819119-4.15003-6

Mammola, S., Cardoso, P., Culver, D.C., Deharveng, L., Ferreira, R.L., Fišer, C., Galassi, D.M.P., Griebler, C., Halse, H., Humphreys, W.F., Isaia, M., Malard, F., Martinez, A., Moldovan, O.T., Niemiller, M.L., Pavlek, M., Reboleira, A.S.P.S., Souza-Silva, M., Teeling, E.C., Wynne, J.J. & Zagmajster, M. (2019) Scientists' warning on the conservation of subterranean ecosystems. *BioScience*, 69 (8), 641–650. https://doi.org/10.1093/biosci/biz064

Marmonier, P. & Creuzé des Châtelliers, M.C. (1992) Biogeography of the benthic and interstitial living ostracods (Crustacea) of the Rhône River (France). *Journal of Biogeography*, 19 (6), 693–704. https://doi.org/10.2307/2845710

Marmonier, P., Dole-Olivier, M.J., Creuzé des Châtelliers, M.C., Paran, F., Graillot, D., Winiarski, T., Lara Konecny-Dupré, L., Navel, S. & Cadilhac, L. (2019) Does spatial heterogeneity of hyporheic fauna vary similarly with natural and artificial changes in braided river width? *Science of the Total Environment*, 689, 57–69. https://doi.org/10.1016/j.scitotenv.2019.06.352

Marmonier, P., Creuzé des Châtelliers, M., Dole Olivier, M.J., Johannet, A., Ré-Bahuaud, J., Chapuis, H., Graillot, D. & Cadilhac, L. (2020) Les invertébrés aquatiques indicateurs des relations entre le karst et la rivière. Exemple de la Cèze. *Karstologia*, 75 (1), 51–58. https://doi.org/10.3406/karst.2020.3329

Mazepova, G.F. (1976) Novoe o fauna Baikala. *Transactions of the Limnological Institute*, 18, 53–73.

Mazzini, I., Gliozzi, E., Galaty, M., Bejko, L., Sadori, L., Soulie-Maersche, I., Koçi, R., Van Welden, A. & Bushati, S. (2016) Holocene evolution of Lake Shkodra: Multidisciplinary evidence for diachronic landscape change in northern Albania. *Quaternary Science Reviews*, 136, 85–95. https://doi.org/10.1016/j.quascirev.2016.01.006

Meisch, C. (1996) Contribution to the taxonomy of *Pseudocandona* and four related genera, with the description of *Schellencandona* nov. gen. a list of the Candoninae genera, and a key to the European genera of the subfamily (Crustacea, Ostracoda). *Bulletin de la Société des Naturalistes Luxembourgeois*, 97, 211–238.

Meisch, C. (2000) Freshwater Ostracoda of Western and Central Europe. *In*: Schwoerbel, J. & Zwick, P. (Eds.), *Süßwasserfauna von Mitteleuropa 8/3*. Spektrum Akademischer Verlag, Heidelberg, Berlin, pp. 1–522.

Meisch, C., Smith, R.J. & Martens, K. (2024) An updated subjective global checklist of the extant non-marine Ostracoda (Crustacea). *European Journal of Taxonomy*, 974, 1–144. https://doi.org/10.5852/ejt.2024.974.2767

Melis, R., Furlani, S., Antonioli, F., Biolchi, S., Degrassi, V. & Mezgec, K. (2012) Sea level and paleoenvironment during roman times inferred from coastal archaeological sites in Trieste (northern Italy). *Alpine and Mediterranean Quaternary*, 25 (1), 41–55. [original URL provided was: https://amq.aiqua.it/index.php/amq/article/view/44]

Mori, N., Vehovar, Ž., Brad, T., Balázs, G., Englisch, C., Fišer, C., Gaviria, S., Gottstein, S., Griebler, C., Kenesz, M., Knight, L.R.F.D., Malard, F., Mammola, S., Marmonier, P., Martínez, A. & Zagmajster, M. (2025) A comprehensive occurrence dataset for European Ostracoda inhabiting groundwater and groundwater-dependent ecosystems. *Global Ecology and Biogeography*, 34 (6), e70065. https://doi.org/10.1111/geb.70065

Muller, S.D., Bruneton, H., Soulié-Märsche, I., Rey, T., Thiéry, A., Waterkeyn, A., Brendonck, L., Schevin, P., Yavercovski, N. & Grillas, P. (2008) Long-term dynamics of a Mediterranean alkaline vernal pool (Rhone delta, southern France). *Wetlands*, 28, 951–966. https://doi.org/10.1672/07-112.1

Petkovski, T., Scharf, B.W. & Keyser, D. (2009) Freshwater Ostracoda (Crustacea) collected from caves and the interstitial habitat in Herzegovina, NW Balkan, with the description of two new species. *Bulletin de la Société des naturalistes luxembourgeois*, 110, 173–182.

Pieri, V., Martens, K., Stoch, F. & Rossetti, G. (2009) Distribution and ecology of non-marine ostracods (Crustacea, Ostracoda) from Friuli Venezia Giulia (NE Italy). *Journal of Limnology*, 68 (1), 1–15. https://doi.org/10.4081/jlimnol.2009.1

Prié, V., Alonso, C., Bou, C., Galassi, D.M.P., Marmonier, P. & Dole-Olivier, M.J. (2024) The Cent Fonts aquifer: An overlooked subterranean biodiversity hotspot in a stygobiont-rich region. *Diversity*, 16 (1), 50. https://doi.org/10.3390/d16010050

Rossetti, G., Sarbu S.M., Ștefan, A. Motoc, R. & Mazzini, I. (2025) *Mixtacandona thessalica*, a new species of ostracod (Crustacea, Ostracoda) from a sulfidic cave in central Greece. *Subterranean Biology*, 52, 111–133. https://doi.org/10.3897/subtbiol.52.142113

Sari, N. & Külköylüoğlu, O. (2010) Ostracods (Crustacea) and habitat similarities in the Bolu region (Turkey). *Turkish Journal of Zoology*, 34 (2), 225–230. https://doi.org/10.3906/zoo-0902-25

Siveter, D.J., Briggs, D.E., Siveter, D.J. & Sutton, M.D. (2024) Preserved appendages in a Silurian binodicope: implications for the evolutionary history of ostracod crustaceans. *Biology Letters*, 20 (5), 20240097. https://doi.org/10.1098/rsbl.2024.0097

Smith, R.J. & Chang, C.Y. (2022) Two new species of non-marine Ostracoda (Crustacea) of the genera *Vestalenula* Rossetti

& Martens, 1998 (Darwinuloidea) and *Microloxoconcha* Hartmann, 1954 (Cytheroidea) from Tsushima, Japan, and a summary of the non-marine ostracod fauna of the island. *Zootaxa*, 5150 (4), 529–555.
https://doi.org/10.11646/zootaxa.5150.4.4

Smith, R.J. & Kamiya, T. (2006) Six new species of fresh and brackish water ostracods (Crustacea) from Yakushima, Southern Japan. *Hydrobiologia*, 559, 331–355.
https://doi.org/10.1007/s10750-005-0946-2

Stein, H., Griebler, C., Berkhoff, S., Matzke, D., Fuchs, A. & Hahn, H.J. (2012) Stygoregions–a promising approach to a bioregional classification of groundwater systems. *Scientific Reports*, 2 (1), 673.
https://doi.org/10.1038/srep00673

Sywula, T. (1976) Notes on Ostracoda 16. New species of Ostracoda (Crustacea) from subterranean waters of Poland. *Bulletin de l'Académie polonaise des Sciences, classe 2, série des sciences biologiques*, 24 (5), 271–278.

Szlauer-Łukaszewska, A. (2014) The dynamics of seasonal ostracod density in groyne fields of the Oder River (Poland). *Journal of Limnology*, 73 (2), 298–311.
https://doi.org/10.4081/jlimnol.2014.865

Szlauer-Łukaszewska, A., Pešić, V. & Zawal, A. (2021) Environmental factors shaping assemblages of ostracods (Crustacea: Ostracoda) in springs situated in the River Krąpiel valley (NW Poland). *Knowledge & Management of Aquatic Ecosystems*, 422, 14.
https://doi.org/10.1051/kmae/2021010

Valavani, D., Papadopoulou, P., Frenzel, P., Alivernini, M., Tsoni, M., Groumpou, M., Tsourou, T., Kolomaznik, S., Kreuzheck, M. & Iliopoulos, G. (2024) Palaeoenvironmental insights from cave ostracods in Greece: the Cave of the Lakes, Kastria, Greece. *Il Naturalista Siciliano*, 48, 119–120.
https://doi.org/10.5281/zenodo.13762368

Vejdovský, F. (1882) *Tierische Organismender Brunnengeswässer von Prague*. Selbstverlag, Prague, 70 pp.

Vervier, P., Gibert, J., Laurent, R. & Couturaud, A. (1986) Plongée souterraine et hydrobiologie dans la Source Bleue, Montperreux, Doubs. Utilisation de substances artificiels pour étudier la faune des réseaux noyés. *Spelunca*, 22, 37–42.

Wang, H., Xu, H., Aye, K.K., Hong, Y., Cao, M. & Yasuhara, M. (2022) Ostracods reveal the palaeoenvironmental changes in Laizhou Bay, Bohai Sea (eastern China) since the Late Pleistocene. *Marine Micropaleontology*, 175, 102150.
https://doi.org/10.1016/j.marmicro.2022.102150

Wysocka, A., Kilikowska, A., Mori, N., Iepure, S., Kijowska, M. & Namiotko, T. (2019) Monophyletic status of European morphogenera of the subfamily Candoninae Kaufmann, 1900 (Ostracoda: Candonidae) in relation to their mtDNA phylogenies. *The Journal of Crustacean Biology*, 39 (5), 567–573.
https://doi.org/10.1093/jcbiol/ruz041

Yavuzatmaca, M., Çelekli, A., Dügel, M. & Lekesiz, Ö. (2024) Distribution of non-marine ostracods in the streams of the Ceyhan River Basin (Turkey) and assessment of their indicator properties for water quality. *Animal Taxonomy and Ecology*, 70 (1), 2–21.
https://doi.org/10.1556/1777.2024.09741

Yavuzatmaca, M., Külköylüoğlu, O. & Yılmaz, O. (2015) Distributional patterns of non-marine Ostracoda (Crustacea) in Adiyaman province (Turkey). *Annales de Limnologie-International Journal of Limnology*, 51 (2), 101–113.
https://doi.org/10.1051/limn/2015005