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REVIEW

Integrative taxonomy of a new hyporheic ostracod species of the genus *Candonopsis* (Ostracoda: Candonidae) from Nouvelle-Aquitaine, France, with first evidence of *Cardinium* bacterial infection in groundwater crustaceans

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Abstract

The non-marine ostracod subfamily Candonopsinae is typically defined by the absence of a posterior seta on the caudal ramus. However, due to frequent reductions in chaetotaxy across ostracod lineages, this character must be evaluated cautiously and alongside other morphological traits, ideally supported by molecular data within an integrative taxonomic framework. *Candonopsis*, the type genus of Candonopsinae, comprises 23 extant species distributed worldwide, mostly in subtropical and tropical regions of the Southern Hemisphere. Of the six European species, two are epigean and four hypogean. Here, we describe a new hypogean species *Candonopsis danilucae* sp. nov., based on male and female specimens collected from the hyporheic zones of three rivers in the Dordogne catchment, department of Corrèze, central France. Morphologically, the new species is distinguished by a unique carapace shape and the structure of the male copulatory organ, particularly the inner lobe of the hemipenis. Molecular comparisons based on mitochondrial COI and nuclear 28S rDNA markers further support its distinctiveness and indicate that its closest genetic affinities among the taxa included in the analysis are with *Candonopsis kingsleii* (Brady & Robertson, 1870), the type species of the genus. Notably, this study, using newly designed primers, also reports the first molecular evidence of intracellular *Cardinium* infection in a groundwater crustacean, suggesting that the female-biased sex ratio observed in *C. danilucae* sp. nov. may result from sex manipulation by this endosymbiont. Our findings highlight the importance of integrative taxonomy, combining carapace morphology, limb structure, habitat preferences, and molecular data, to resolve species boundaries and understand symbiotic associations in subterranean ostracods.

Keywords Subterranean · Candonopsinae · Species delimitation · Intracellular bacteria · Molecular detection

Introduction

Over the past three decades, the diversity of groundwater organisms has gained increasing recognition (Gibert & Culver, 2009; Gibert & Deharveng, 2002; Gibert et al., 1994; Koch et al., 2024; Mammola et al., 2020; Marmonier et al., 2023; Peterson et al., 2013; Sket, 1999). Among these, metazoan stygobites, i.e., animals that live exclusively in groundwater and cannot survive in surface waters (Robertson et al., 2023), play a critical role in overall biodiversity (Boulton et al., 2008). Crustaceans, particularly Amphipoda, Copepoda and Ostracoda, represent the most diverse stygobitic invertebrates (Marmonier et al., 2023). In Europe, stygobites account for approximately 40% of all freshwater

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crustacean species, highlighting their significant contribution to crustacean diversity (Danielopol et al., 2000).

Within Ostracoda, the family Candonidae has been the most successful in colonizing groundwater environments. This family is not only the most diverse and species-rich but also one of the most taxonomically challenging groups of non-marine groundwater ostracods (e.g., Baltanás et al., 2000; Danielopol, 1978; Danielopol et al., 2011; Hotèkpo et al., 2024; Iepure et al., 2008; Karanovic, 2007; Külköylüoğlu et al., 2021). Assigning new candonid species to subfamilies or genera is often challenging due to the significant homoplasy observed in this group, necessitating an integrative approach combining morphology and molecular data (Iepure et al., 2023). The success of Candonidae in colonizing subsurface aquatic environments is attributed to their specific morphological adaptations, such as the absence of swimming setae on the second antenna, elongated carapace shapes, small body size, and well-developed chemosensory organs compensating for the lack of visual organs. Ecological traits, including oligo-stenothermy, a typically (in-)benthic lifestyle, and a preference for ecotonal environments at the interface between surface and groundwater, also play a crucial role (Danielopol, 1977, 1978, 1980b). The extensive specialization, adaptation, and high levels of endemism make groundwater Candonidae particularly significant for research in evolution, ecology, and biodiversity (Danielopol et al., 2000).

Species of the candonid subfamily Candonopsinae inhabit both surface and subterranean aquatic ecosystems worldwide, with a pronounced diversity in subtropical and tropical regions (Karanovic, 2012; Meisch et al., 2024), and are primarily defined by the absence of the posterior seta on the caudal ramus (Karanovic, 2004, 2012). However, the nearly 50 species currently assigned to nine genera within Candonopsinae (Meisch et al., 2024) likely represent multiple distinct evolutionary or genetic lineages. The primary diagnostic feature of the subfamily appears to have evolved independently several times and does not represent an apomorphic state, highlighting the urgent need for a comprehensive revision of this subfamily (Higuti & Martens, 2012) using morphological traits potentially reflecting evolutionary relationships (carapace morphology, elongation of terminal segments of mandibular palp, chaetotaxy of the cleaning leg and caudal ramus or the male clasping organs and hemipenis morphology) supplemented with molecular data in the integrative approach.

The genus *Candonopsis* was established by Vávra (1891) to accommodate *Candona kingsleii*, originally described from southeastern England by Brady and Robertson (1870). At that time, *Candonopsis* and *Candona* were the only recognized genera within what is now understood as the family Candonidae. Vávra (1891) distinguished *Candonopsis* from *Candona* based on the following diagnostic features: (1) the male second antenna with so called male bristles on a subdivided penultimate segment, (2) unusually elongated segments of mandibular palp, (3) the presence of a distinct respiratory plate on the first thoracopod (maxilliped) bearing three pinnate bristles, and (4) a slender caudal ramus lacking posterior seta.

Since its original description, the diagnosis of *Candonopsis* has been revised and expanded. Danielopol (1980a) introduced additional diagnostic characters, including the chaetotaxy of the cleaning leg, morphology of hemipenis, and the structure of Zenker's organ. Subsequently, Karanovic and Marmonier (2002) provided more detailed description of soft-part morphology, further refining the diagnostic criteria for the genus. Later, Karanovic (2004) subdivided *Candonopsis* into two subgenera: the nominotypical *Candonopsis* and the newly described *Abcandonopsis*. More recently, these subgenera were elevated to the rank of independent genera (Higuti & Martens, 2012; Meisch et al., 2024). As a result, *Candonopsis*, now comprises 23 species and remains the most species-rich and morphologically diverse genus within the subfamily Candonopsinae, which includes a total of 48 extant species across nine genera (Meisch et al., 2024). In Europe, the subfamily is represented by the genus *Candonopsis* which includes six species: two epigean (*C. kingsleii* (Brady & Robertson, 1870) and *C. scourfieldi* Brady, 1910) and four hypogean (*C. boui* Danielopol, 1978; *C. mareza* Karanovic & Petkovski, 1999; *C. thienemanni* Schäffer, 1945 and *C. trichota* Schäffer, 1945) (Danielopol, 1980a; Karanovic & Petkovski, 1999; Meisch, 2000; Schäfer, 1945).

As part of an extensive research program on the stygofauna of Nouvelle-Aquitaine Region, South-Western France (SEPANSO, 2025), specimens of the genus *Candonopsis* were collected from three hyporheic sites within the Dordogne River catchment. These specimens were confirmed to represent a new species within the genus. This paper provides its formal description using an integrative approach. We aimed to assess the genetic affinities of this new species among European representatives of the family Candonidae by employing morphological analyses alongside two-marker molecular approaches, including mitochondrial cytochrome c oxidase subunit I (*COI* mtDNA) and the more conservative nuclear 28S ribosomal DNA (*28S rDNA*).

Additionally, based on the *16S rRNA* gene sequence, we screened specimens of the new *Candonopsis* species for the presence of bacteria of the genus *Cardinium* ("*Candidatus*" Cardinium Zchori-Fein et al.). Intracellular endosymbiotic bacteria, such as *Wolbachia* Hertig (Hurst et al., 2000) and *Cardinium* (Gotoh et al., 2007), can significantly influence host biology, including reproduction and microevolutionary dynamics (Zhang et al., 2012). However, most data on endosymbiont prevalence come from studies on insects, particularly Hymenoptera, likely underestimating occurrence of these bacteria in other taxa (Ma & Schwander, 2017). To date, *Cardinium* bacteria have been recorded in freshwater ostracods across three superfamilies: Cypridoidea, Cytheroidea and Darwinuloidea (Schön et al., 2019). However, information on the presence of endosymbionts in ostracods and other aquatic crustaceans remains remarkably scarce (Mioduchowska et al., 2018). *Cardinium* has not yet been reported in stygobitic crustaceans, despite increasing interest in animals inhabiting groundwater ecosystems.

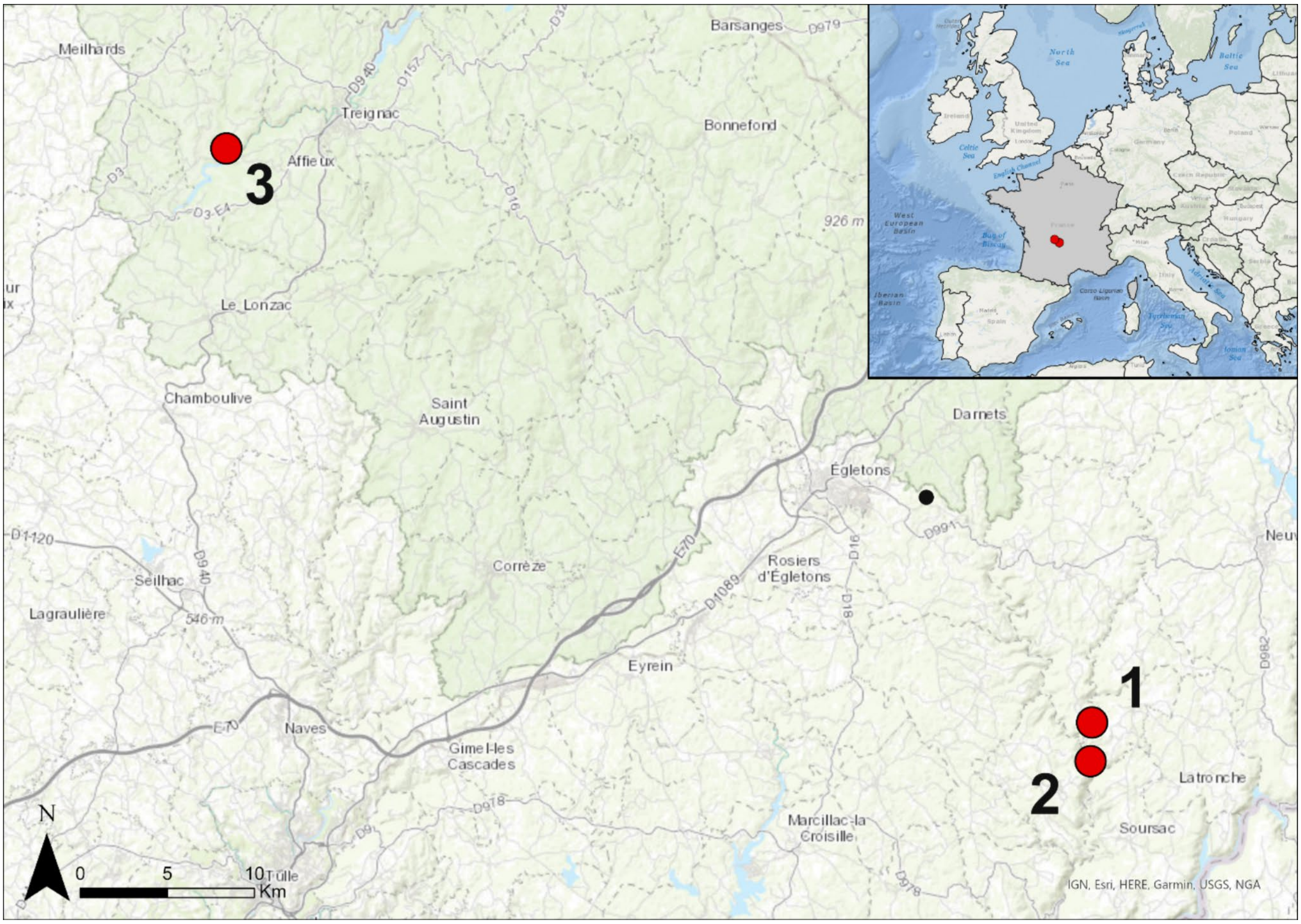
Material and methods

Study sites and sample collection

Our material of the new *Candonopsis* species was sampled from the hyporheic zone of three rivers within the Dordogne catchment in the department of Corrèze, Nouvelle-Aquitaine Region, France (Fig. 1):

1. hyporheic zone of the Vianon River (municipality of Saint-Pantaléon-de-Lapleau, departement of Corrèze; coordinates in Lambert L93 France system (L93): 636,007 m/6,469,074 m; geographical coordinates in GPS (WGS84) system in decimal degrees (DD): 45.318065° N/2.183248° E) (Online Resources 1–2)
2. hyporheic zone of the Luzège River (municipality of Saint-Pantaléon-de-Lapleau, departement of Corrèze; L93: 635,930 m/6,467,516 m; DD: 45.304019° N/2.182472° E)
3. hyporheic zone of the Vézère River (municipality of Affieux, departement of Corrèze; L93: 601,386 m/6,492,608 m; DD: 45.525851° N/1.736627° E).

The samples were taken following the protocol of the PASCALIS project (Malard et al., 2002), using the Bou-Rouch method, filtering the pumped water through a mesh size of 150 µm. At the type locality (Vianon River), 50 L of water was pumped through the hyporheic zone at depths ranging from 20 to 60 cm (mean of ca. 40 cm) below the streambed.



IGN, Esri, HERE, Garmin, USGS, NGA

Fig. 1 Geographic locations of the collection sites (red circles) where specimens of *Candonopsis danilucae* sp. nov. were sampled from hyporheic zones of the (1) Vianon River, (2) Luzège River, and (3) Vézère River within the Dordogne River catchment in the department of Corrèze, Nouvelle-Aquitaine Region, France

Animals were immediately fixed in ethanol 96%, then sorted out by taxonomic groups.

Electrical conductivity, temperature, pH, redox potential and dissolved oxygen of the hyporheic water were measured with a multi-parameter probe (Odeon, Aqualabo, France). Main ionic parameters and pollutants in the river (carbonates, sulphates, phosphates, nitrates, and ammonium) were assessed with semi-quantitative test strips (Quantofix, Macherey–Nagel, Germany).

Morphological examination

Specimens were dissected and mounted following the protocol of Namiotko et al. (2011). Soft parts (limbs) were dissected under a stereoscopic reflected-light microscope and mounted in glycerin on glass slides. Carapace valves (hard parts) were stored dry in micropalaeontological slides. Illustrations of the soft parts were prepared using a camera lucida attached to a Nikon Eclipse 50i transmitted-light microscope. Carapaces and valves were gold-coated and examined using a scanning electron microscope (Prisma E, Thermo Fisher Scientific) as well as under the Nikon Eclipse 50i transmitted-light microscope. Male hemipenes were examined using a Leica Stellaris 5 confocal microscope equipped with a 405 nm laser diode with Lightning deconvolution, at Bioimaging Laboratory, Faculty of Biology, University of Gdansk.

The type specimens are deposited in the Ostracod Collection (OC-UG) of the Biological Resource Center Gdansk, University of Gdansk and in the Ostracod Collection of Pierre Marmonier at LEHNA, Claude Bernard University Lyon 1.

The model of limb chaetotaxy proposed by Broodbakker and Danielopol (1982) was followed, along with the revised version for the second antenna as proposed by Martens (1987) and Scharf et al. (2020). The length of setae and claws was related to the length of the reference segment of the respective limb and evaluated as long, medium or short following the model of Broodbakker and Danielopol (1982). Names for the limbs were used according to Meisch (2000). The higher-level taxonomy follows Meisch et al. (2024).

The shape of the carapace/valve was traditionally characterized using the bounding box method, which includes the ratio of maximum height to maximum length (H/L), and the position of the maximum height relative to the maximum length (D/L). The latter is defined as the ratio between the distance from the anterior extremity of the outline to the line of the maximum height (D) and the maximum length (L) (see Danielopol et al., 2022). Terminology for curvature of the anterior and posterior carapace/valve margins follows Lüttig (1962). The curvature of the posterior margin is further characterized and quantified by the distance from the posterior extremity of the outline to a horizontal line defined by the two convexities of the ventral valve margin, measured perpendicularly (DPE), and expressed as a ratio relative to the maximum height (DPE/H). In addition to these quantitative measures, valve shape was also described subjectively.

Abbreviations used in text and figures

Limbs: a = outer lobe of Hp; a, a’ = two setae on Pr of T1; A1 = first antenna (antennule); A2 = second antenna; alfa (α) = special seta on the 1st podomere of Md palp; b = seta on Pr of T1; b = inner lobe of Hp; beta (β) = special seta on the 2nd podomere of Md palp; CR = caudal ramus; d = seta on Pr of T1; d1, d2, dp = setae on Pr of T2 and T3; E = endopod; e = bursa copulatrix of Hp; e = setae on EI of T2 and T3; EI–EIV = 1st to 4th podomeres of E; f = setae on EII of T2 and T3; g = setae on EIII of T2 and T3 and on EIV of A2; Ga = anterior claw of CR; GM (Gm) = major (minor) claw on EIV of A2; Gp = posterior claw of CR; G1–3 = anterior and internal claws (or setae) on EIII of A2; gamma (γ) = special seta on 3rd podomere of Md palp; h1–3 = setae (or claws) on EIV of T2 and T3; Hp = hemipenis; M = chitinous internal process of hemipenis; Md = mandibula; Mdp = mandibular palp; Mx1 = maxillula; Pr = protopod; sa = anterior seta of CR; T1 = first thoracopod (maxilliped); T2 = second thoracopod (walking leg); T3 = third thoracopod (cleaning leg); t1–4 = internal setae on EII of A2; Y = aesthetasc on EI of A2; y1, y2, y3 = aesthetascs on EI, EII and EIII of A2, respectively; ya = aesthetasc on the terminal podomere of A1; z1–3 = external setae (or claws) on EII of A2.

Valves and carapace: Cp = carapace; D = distance from the anterior extremity of the outline to the line of the maximum height; DPE = distance from the position of the posterior extremity of the outline perpendicular to the horizontal line defined by the two convexities of the ventral margin; H = valve/carapace height; L = valve/carapace length; LV = left valve; RV = right valve.

DNA extraction, PCR amplification and sequencing

To assess the genetic affinities of the newly described species among closely related taxa, two molecular markers were analysed in three specimens (one female and two juveniles): mitochondrial cytochrome c oxidase subunit I (*COI* mtDNA) and the more conservative nuclear 28S ribosomal DNA (*28S rDNA*).

Each ethanol-preserved individual was rinsed in distilled water prior to DNA extraction. Total DNA was extracted from the whole body (soft parts and valves) of three individuals (two females and one juvenile) separately using the Genomic Mini Kit (A&A Biotechnology) following the manufacturer’s protocol. DNA was eluted in 100 µl of Tris–HCl pH 8.4 and stored at −20 °C until use.

The *COI* gene fragment was amplified using the LCO1490/HCO2198 primer pair (Folmer et al., 1994). PCR amplification was conducted in a total volume of 22.5 µl, containing 2 × DreamTaq Green PCR Master Mix (Thermo Fisher Scientific), 5 µM of each primer and 2 µl of lysates. The PCR protocol included an initial denaturation at 95 °C for 3 min, followed by 39 cycles of denaturation at 94 °C for 1 min, annealing at 43 °C for 1 min, extension at 72 °C for 1.3 min, and a final extension at 72 °C for 5 min.

The *28S rDNA* gene fragment was amplified using the xx/vv primer pair (Hillis & Dixon, 1991). The PCR reaction was conducted in the total of 21.5 µl, consisting of 2 × DreamTaq Green PCR Master Mix, 5 µM of each primer and 1 µl of lysates. The amplification protocol included an initial denaturation at 94 °C for 5 min, followed by 41 cycles of denaturation at 95 °C for 1 min, annealing at 50 °C for 1 min, extension at 72 °C for 1.3 min, and a final extension at 72 °C for 5 min.

The amplified fragments were visualized by electrophoresis in a 1% agarose gel and purified using exonuclease I (20 U/µl, Fermentas, Canada) and FastAP thermosensitive alkaline phosphatase (1 U/µl, Fermentas, Canada) according to the manufacturer's instructions. Sequences were obtained from both strands using Sanger's method by Macrogen Inc. (Netherlands).

Molecular comparisons

Molecular comparisons were conducted to elucidate the patterns of genetic similarity between the newly identified *Candonopsis* species and 12 representative species of the family Candonidae (Table 1). BLAST (Basic Local Alignment Search Tool) searches against the non-redundant database of the National Center for Biotechnology Information (NCBI) were performed to verify the identity of the amplified regions (Altschul et al., 1990). Sequences were quality-checked and trimmed to the same length (515 bp for *COI* fragment and 523 bp for *28S*) in Geneious Prime 2025.1.2 (Kearse et al., 2012), and consensus sequences were created for each individual. Additionally, the *COI* sequences were translated into the amino acid sequences to check for the potential presence of stop codons. All unique sequences

Table 1 Species of the family Candonidae included in the molecular comparison with *Candonopsis danilucae* sp. nov., together with information on collection year and locality, identified haplotypes (based on combined mitochondrial COI and nuclear 28S rDNA sequences and on mitochondrial COI alone), number of specimens, and corresponding GenBank accession numbers for the obtained sequences

Species	Collection locality, year	Haplotype (no. specimens) combined COI and 28S	GenBank accession numbers (28S)	Haplotype (no. specimens) COI	GenBank accession numbers (COI)
Candona candida (O.F. Müller, 1776)	Otomin, Poland, 2021	H5 (2)	PZ387124	C19 (2)	PZ388160
Candona weltneri Hartwig, 1899	Raduńskie Dolne Lake, Poland, 2013	H6 (1) H7 (1)	PZ387125; PZ387126	C17 (1) C18 (1)	MN013103; MN013104
Candonopsis danilucae sp. nov.	Saint-Pantaléon-de-Lapleau, France, 2021	H14 (3)	PZ387127	C15 (3)	PZ388161
Candonopsis kingsleii (Brady & Robertson)	Parzyńskie Lake, Poland, 2022	H15 (3)	PZ387128	C16 (3)	PZ388162
Cryptocandona vavrai Kaufmann, 1900	Dinsac, France, 2021 Saint-Bonnet-de-Bellac, France, 2021	H12 (1) H13 (1)	PZ387129; PZ387130	C13 (1) C14 (1)	PZ388163; PZ388164
Fabaeformiscandona fragilis (Hartwig, 1898)	Parzyńskie Lake, Poland, 2022	H1 (2)	PZ387131	C12 (2)	PZ388165
Fabaeformiscandona subacuta (Yang, 1982 in Hou et al., 1982)	Alcalá de Henares, Spain, 2017	H2 (2)	PZ387132	C11 (2)	PZ388166
Mixtacandona idrisi Mazzini & Rosetti, 2017	Cave near Palermo, Italy, N/A	-	-	C6 (1)	PQ586877.1
Mixtacandona thessalica Rosetti & Mazzini, 2025	Melissotrypa Cave, Greece, 2023/2024	-	-	C3 (1) C4 (2) C5 (1)	PQ586881.1; PQ586880.1 PQ586879.1; PQ586878.1
Neglecandona lindneri (Petkovski, 1969)	Prątnik, Poland, 2017	H8 (2)	PZ387133	C10 (2)	PZ388167
Neglecandona neglecta (Sars, 1887)	Brussels, Belgium, 2022	H9 (1) H10 (1)	PZ387134; PZ387135	C8 (1) C9 (1)	PZ388168; PZ388169
Pseudocandona albicans (Brady, 1864)	Oslo, Norway, 2014	H3 (2)	PZ387136	C2 (2)	MN013123
Pseudocandona hartwigi (G.W. Müller, 1900)	Otomin, Poland, 2014	H4 (2)	PZ387137	C1 (2)	MN013133

identified for individual markers were deposited in GenBank (accession numbers: PZ387124-PZ387137 for 28S and PZ388160-PZ388169 for COI).

For molecular comparisons, the best model of sequences evolution, base frequencies, and the nucleotide substitution parameters were estimated by jModelTest 2.1.7 (Darriba et al., 2012) with the Bayesian Information Criterion (BIC) for haplotypes obtained from DnaSP (Rozas et al., 2017). The Tamura-Nei (Tamura & Nei, 1993) model was used in MEGA X 10.0.3 (Kumar et al., 2018) to calculate interspecific diversity estimates for *COI* sequences.

Molecular clustering used to assess the relative genetic affinities of the analysed species was generated using Maximum-Likelihood (M-L) and Bayesian Inference (BI) approaches applied to the concatenated dataset. The M-L analyses were conducted in MEGA X (Kumar et al., 2018), while BI analyses were performed in BEAST 2 (Bouckaert et al., 2014) with the following substitution models: HKY (Hasegawa et al., 1985) with gamma-distributed rate heterogeneity (G) and a proportion of invariable sites (I) for *COI* partition; TrN with G and I for *28S*. The posterior probabilities of clades were estimated by sampling trees using Markov Chain Monte Carlo (MCMC) simulations. Four independent MCMC runs were performed to ensure convergence at the same solution. Each chain was run for 10 million generations and sampled every 1,000 generations to achieve sufficiently large effective sample sizes (ESS) of each sampled parameter (>200). Convergence of all runs and ESS were verified in Tracer 1.7.2 (Rambaut et al., 2018).

The resulting output files were combined using LogCombiner 2.7.6 (Bouckaert et al., 2014) after discarding the 15% of non-stationary burn-in phase. The maximum clade credibility tree was generated using TreeAnnotator 2.7.6 (Bouckaert et al., 2014). The final inferred tree was edited in FIGTREE v. 1.4.4 (http://tree.bio.ed.ac.uk/software/figree/). An independent M-L analysis was conducted using IQTREE 2.3.5 (Minh et al., 2020) with the same substitution models as those used for BI. Nodal support was assessed using 1,000 nonparametric bootstrap replicates. Nodes were considered strongly supported if they exhibited Bayesian posterior probability values of≥0.95 and bootstrap values of≥80.

Sequences from the ostracod *Heterocypris salina* (Brady, 1868) obtained by Kilikowska et al. (2024) were used as the outgroup for all analyses.

Genetic species delimitation

Among several approaches available for genetic species delimitation, generally based on either genetic distances or tree-based inference, in this study, we applied three statistical methods for the COI mtDNA fragment. To assess intra- and interspecific genetic divergence, we used the Automatic Barcode Gap Discovery (ABGD) method (Puillandre et al., 2012) with the Kimura two-parameter (K2P) model. We chose a minimum prior intraspecific divergence (*Pmin*) of 0.001 and a maximum distance threshold of 0.1. We also applied the Assemble Species by Automatic Partitioning (ASAP) method (Puillandre et al., 2021) using default settings and the K2P model to calculate pairwise genetic distances. As a third species delimitation approach, we used the Bayesian Poisson Tree Processes (bPTP) model (Zhang et al., 2013), which infers species boundaries based on the Poisson distribution of branch lengths in a tree of genetic relationships. The input tree was the Maximum-Likelihood COI tree, constructed in MEGA X using the HKY+I+G substitution model, and analyzed with default parameters of 500,000 MCMC generations and a 10% burn-in.

To increase taxonomic representation in the COI only dataset, we additionally included sequences of two further species belonging to the genus *Mixtacandona*, available in GenBank (see Table 1). Haplotypes obtained from the COI only dataset were labelled with the prefix “C” followed by a number (C1-C19) to distinguish them from sequences included in the concatenated dataset (Table 1).

Molecular detection of Cardinium bacteria

To detect the presence of *Cardinium* bacteria in specimens of a new *Candonopsis* species, a *16S rRNA* gene fragment from five individuals (two females and three juveniles) was amplified using our newly designed primers: CARFM (forward) 5’-GATGGGTAGGGGTTCTTAGTGGA-3’ and CARRM (reverse) 5’-GCACCTTCCGTATTACCGCG G-3’. PCR conditions for amplifying the *Cardinium 16S rRNA* region included an initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation at 95 °C for 1 min, annealing at 52 °C for 1 min, extension at 72 °C for 1 min and a final extension at 72 °C for 5 min. The total reaction volume was 20 µl and contained 2×DreamTaq Green PCR Master Mix (Thermo Fisher Scientific), 5 µM of each primer and 2 µl of DNA previously extracted from individuals of the new *Candonopsis* species.

A negative control (double-distilled water) was included in each PCR run to check for potential contamination. PCR products were separated by electrophoresis in a 1% agarose gel stained with to Midori Green Advance DNA Stain (ABO Ltd.) and visualized by a UV transilluminator. The PCR products were then directly sequenced in both directions by Macrogen Inc. using the CARFM/CARRM primer pair. Partial sequences were manually checked and trimmed to the same length of 211 bp in Geneious Prime 2025.1.2. The resulting sequences were compared with GenBank databases using BLAST to confirm their identity.

Results

Taxonomic account

Class: Ostracoda Latreille, 1802
Subclass: Podocopa Sars, 1866
Order: Podocopida Sars, 1866
Suborder: Cypridocopina Baird, 1845
Superfamily: Cypridoidea Baird, 1845
Family: Candonidae Kaufmann, 1900
Subfamily: Candonopsinae Karanovic, 2004
Genus: *Candonopsis* Vávra, 1891

Diagnosis A1 7-segmented. Penultimate segment of the male A2 subdivided and bearing male bristles. Terminal segment of the Md palp more than three times as long as wide, with the apical claw broadly fused to the segment. Male prehensile palps strongly asymmetrical, the right palp markedly inflated relative to the left. Each palp bearing a single sclerotized seta. L6 5-segmented, basal segment with only one seta. L7 5-segmented, with all three basal setae present. Posterior seta on the UR absent, terminal claws with or without strong spines. Hemipenis with the outer lobe approximately triangular in shape, consistently higher than the remaining two lobes.

Candonopsis danilucae Namiotko, Szwarc, Kijowska et Wysocka sp. nov. (Figs. 2, 3, 4, 5, 6, 7, 8, and 9, Online Resource 3).

Note The authors directly responsible for the new name are TN, AS, MK and AW. Accordingly, the authorship of the name, when cited, should be stated as "Namiotko, Szwarc, Kijowska et Wysocka, 2026 in Kijowska et al., 2026" in accordance with International Code of Zoological Nomenclature (ICZN, 2000: Recommendations 50 A and 51E).

Type locality (Fig. 1, Online Resources 1–2).

Hyporheic zone of the Vianon River (municipality of Saint-Pantaléon-de-Lapleau, departement of Corrèze, Nouvelle-Aquitaine, France); 45.318065° N, 2.183248° E, 380 m above sea level.

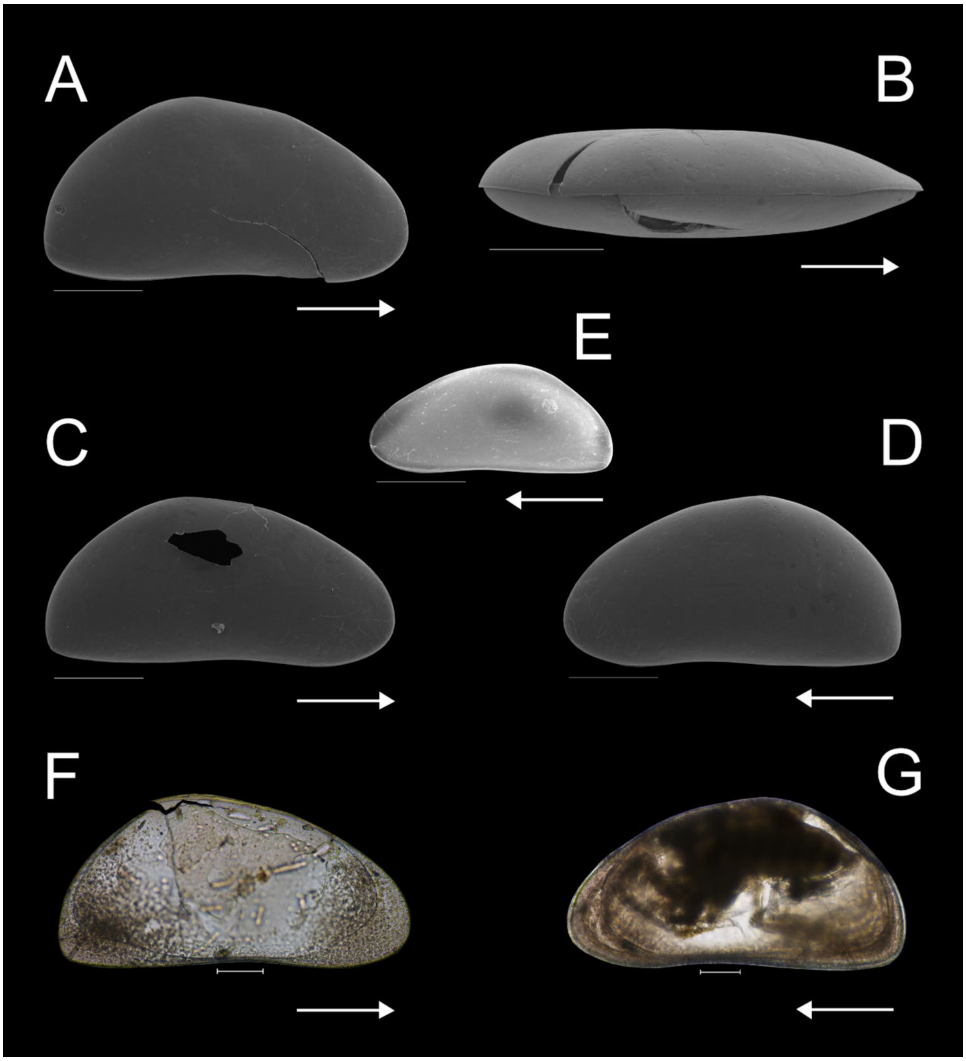
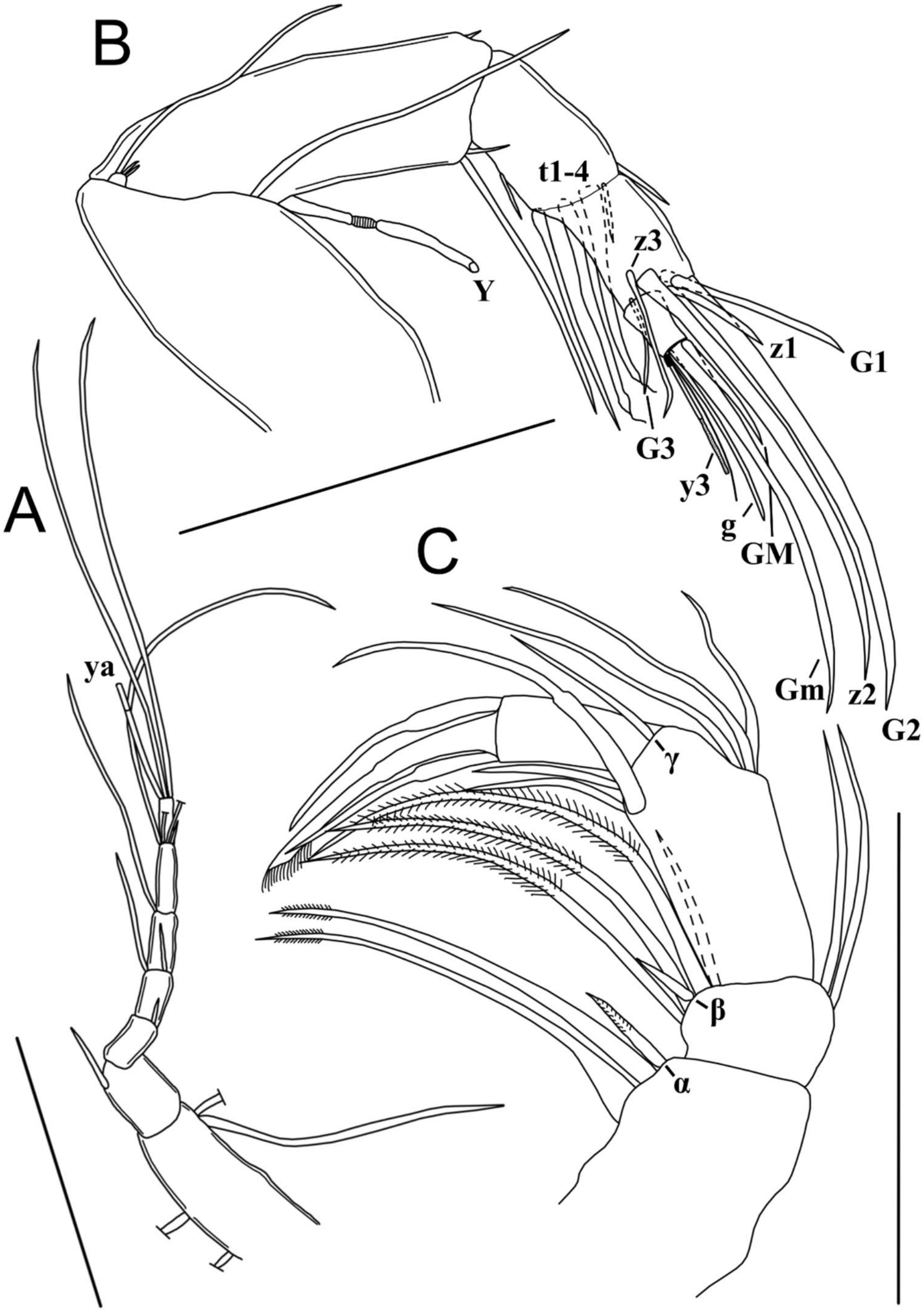


Fig. 2 Carapace and valves of *Candonopsis danilucae* sp. nov. **A.** male (OC-UG 211012–1-A1V) RV in lateral external view. **B.** female (OC-UG 211012–1-A5T) Cp in dorsal view. **C.** female (OC-UG 211012–1-A3V) RV in lateral external view. **D.** female (OC-UG 211012–1-A4V) LV in lateral external view. **E.** juvenile stage (?) A-3 (OC-UG 211012–1-A6T) Cp in left lateral view. **F.** female RV in lateral external view. **G.** male Cp in left lateral view. Scale bars: 200 µm for A–E, 100 µm for F–G. Arrow indicates anterior direction

Fig. 3 Limbs of *Candonopsis danilucae* sp. nov. male holotype (OC-UG 211012–1-A1L). **A.** A1.**B.** A2. **C.** Mdp. Scale bars: 100 µm



Type material

Holotype: one adult male with soft parts dissected and mounted on a permanent microscopic slide (OC-UG 211012–1-A1L) and RV stored dry in a micropalaeontological slide (OC-UG 211012–1-A1V), LV destroyed.

Paratypes: 1) one adult female with soft parts dissected and mounted on a permanent microscopic slide (OC-UG 211012–1-A2L) and valves destroyed; 2) one adult female with soft parts dissected and mounted on a permanent microscopic slide (OC-UG 211012–1-A3L) and RV stored dry in a micropalaeontological slide (OC-UG 211012–1-A3V), LV destroyed; 3) one adult female with soft parts dissected and mounted on a permanent microscopic slide (OC-UG 211012–1-A4L), LV stored dry in a micropalaeontological slide (OC-UG 211012–1-A4V), RV destroyed, 4) one adult female stored dry in a micropalaeontological slide (OC-UG 211012–1-A5T); 5) one juvenile stored dry in a micropalaeontological slide (OC-UG 211012–1-A6T); 6) one adult male with soft parts dissected and mounted on a

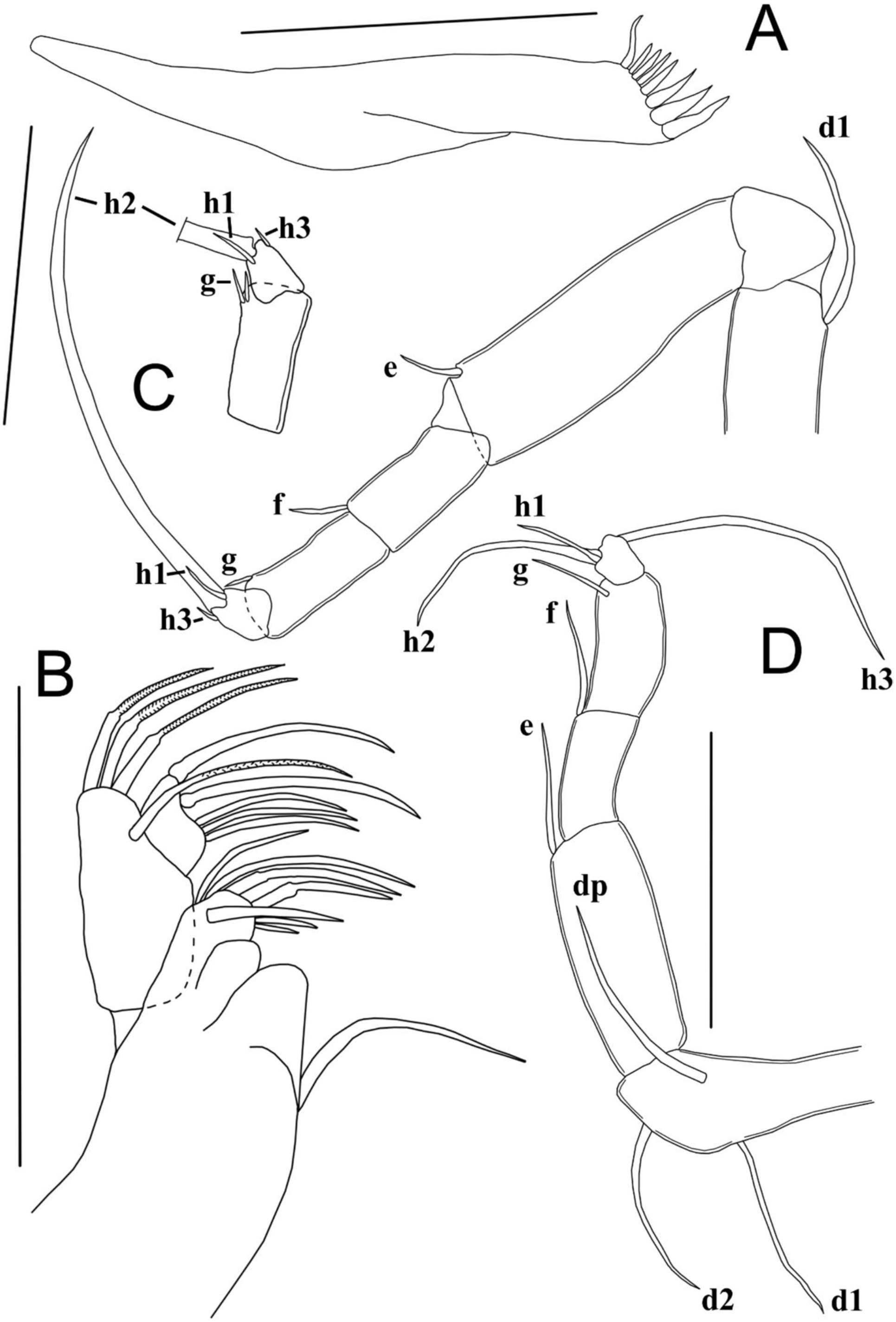


Fig. 4 Limbs of *Candonopsis danilucae* sp. nov. male holotype (OC-UG 211012–1-A1L). **A.** Md coxa. **B.** Mx1. **C.** T2 (walking leg). **D.** T3 (cleaning leg). Scale bars: 100 μm

permanent microscopic slide (OC-UG 211012–1-A7L) and valves destroyed; 7) four females, three males and six juveniles preserved in 96% ethanol (OC-UG 211012–1-AT), 8) two females and one juvenile used for DNA analysis.

All type material collected on 12 October 2021 by FM, CD, TA and FL.

Accompanying ostracod fauna: 1 juv. *Cryptocandona* cf. *reducta* (Alm, 1914).

Other material examined (Fig. 1).

1) Hyporheic zone of the Luzège River (municipality of Saint-Pantaléon-de-Lapleau, departement of Corrèze, Nouvelle-Aquitaine, France); 45.304019° N, 2.182472° E, 330 m a.s.l. Material collected on 5 October 2021 by FM, CD, TA and FL.

One adult female and one juvenile preserved in 96% and two juveniles used for DNA analysis.

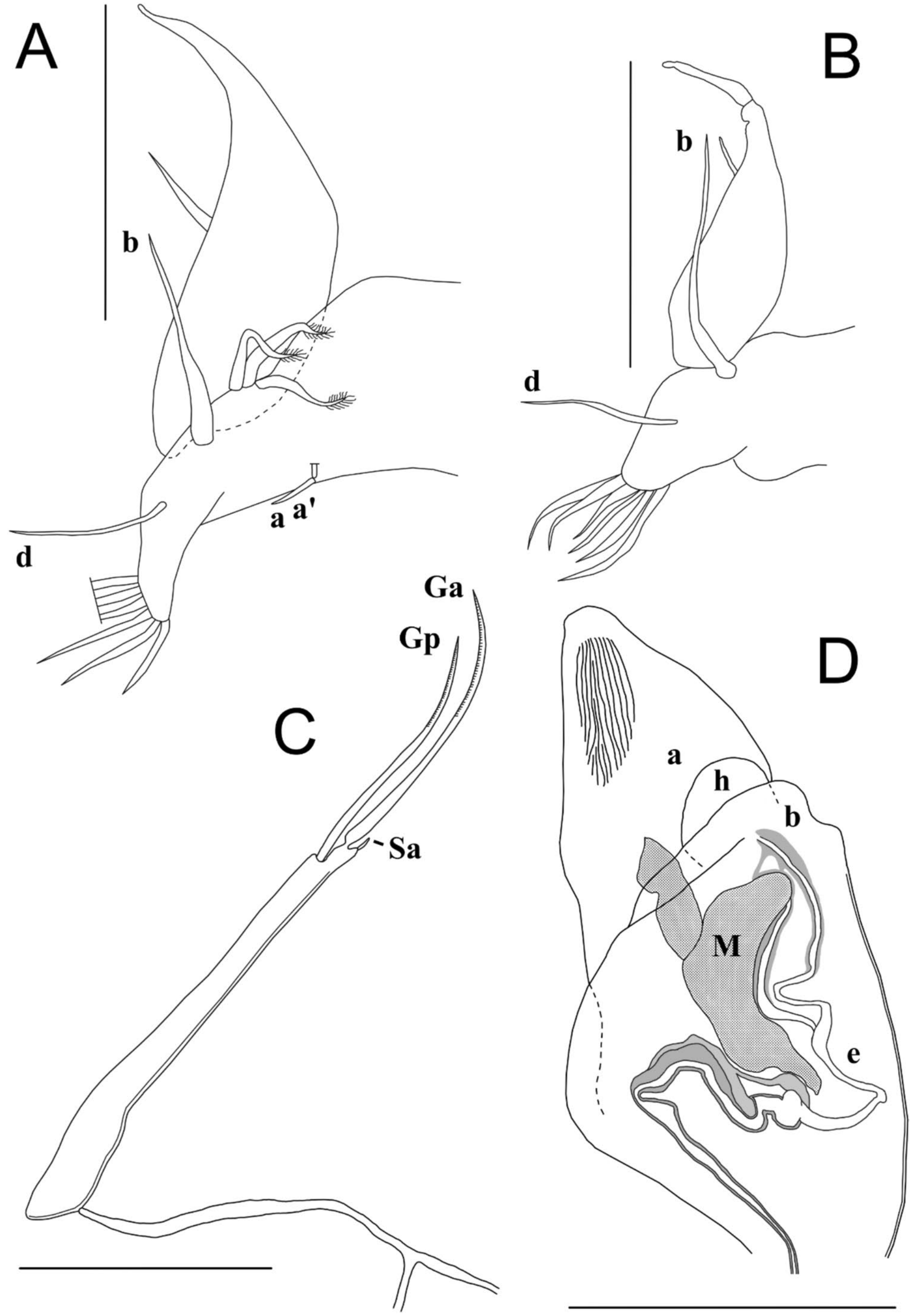


Fig. 5 Limbs of *Candonopsis danilucae* sp. nov. male holotype (OC-UG 211012–1-A1L). **A.** right T1 with prehensile palp. **B.** left T1 with prehensile palp. **C.** CR. **D.** Hp. Scale bars: 100 µm

2) Hyporheic zone of the Vézère River (municipality of Affieux, departement of Corrèze, Nouvelle-Aquitaine, France); 45.525851° N, 1.736627° E, 360 m a.s.l. Material collected on 12 October 2021 by FM, CD, TA and FL.

Etymology The species is named in honor of our esteemed colleague Dan Luca Danielopol, whose significant contributions over the years have greatly advanced the field of groundwater ecology. His work has been instrumental in deepening our understanding of stygobitic ostracods, particularly their taxonomy, evolution, and ecological adaptations.

Diagnosis Carapace in lateral view resembling a scalene triangle with maximum H situated behind mid-length (D/L in male = 0.59, D/L in female = 0.58), anterior margin broadly rounded, posterior one moderately steep and narrowly rounded towards venter, both infracurvate (DPE/H in both sexes = 0.24). In dorsal view carapace conspicuously slender with LV overlapping RV anteriorly and posteriorly.

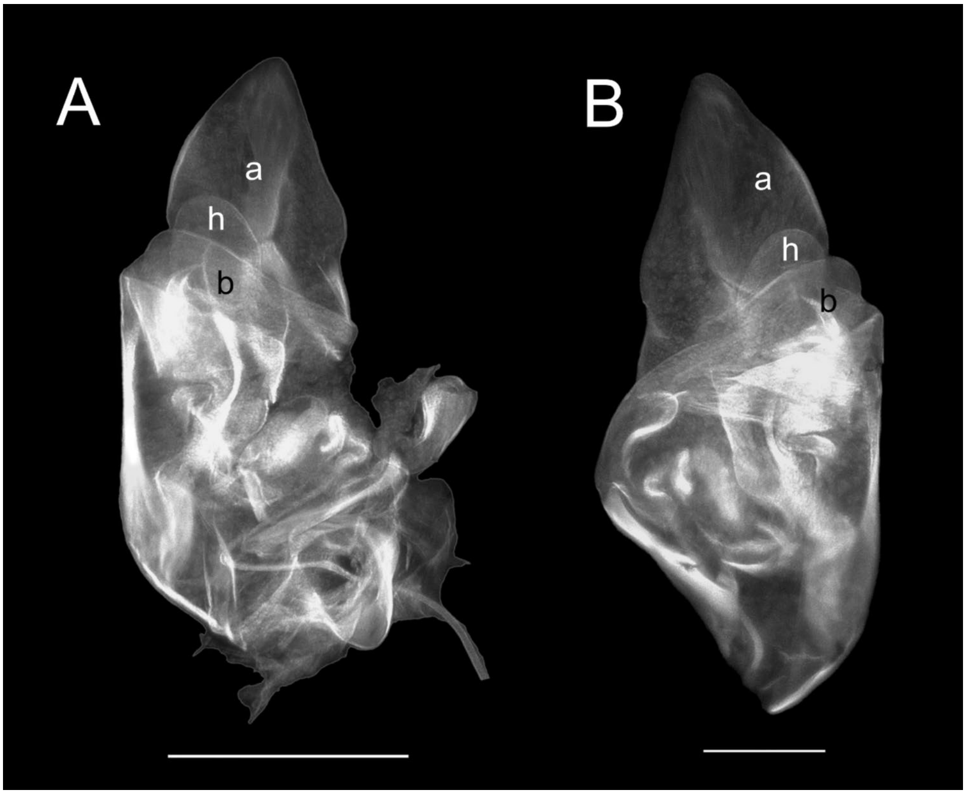


Fig. 6 Hemipenes of *Candonopsis danilucae* sp. nov. male holotype (OC-UG 211012–1-A1L). **A.** Left Hp in medial view. **B.** Right Hp in medial view. Scale bars: 40 µm

Carapace surface smooth without long setae. A1 with reduced number of setae on 3rd, 4th, 5th and 7th segments. A2 with very long sensory part of aesthetasc Y, reduction of number of t-setae in female to two (t1 and t2) and short G2 claw relative to G1 in female. Terminal segment of Mdp with three long claws. Second segment of Mx1-palp twice as wide as long with two long claws. T1 with two a-setae, b- and d- seta. T2 with two g setae. CR with claws without spines. Male left prehensile palp with elongated and slander finger, and short seta, right prehensile palp larger with curved dorsal margin, elongated finger and medium long seta. Hp with three lobes on its distal end: most elongated, triangular outer lobe (a), shortest inner lobe (b), extending toward ventral margin of Hp, and narrowly rounded intermediate medial lobe (h).

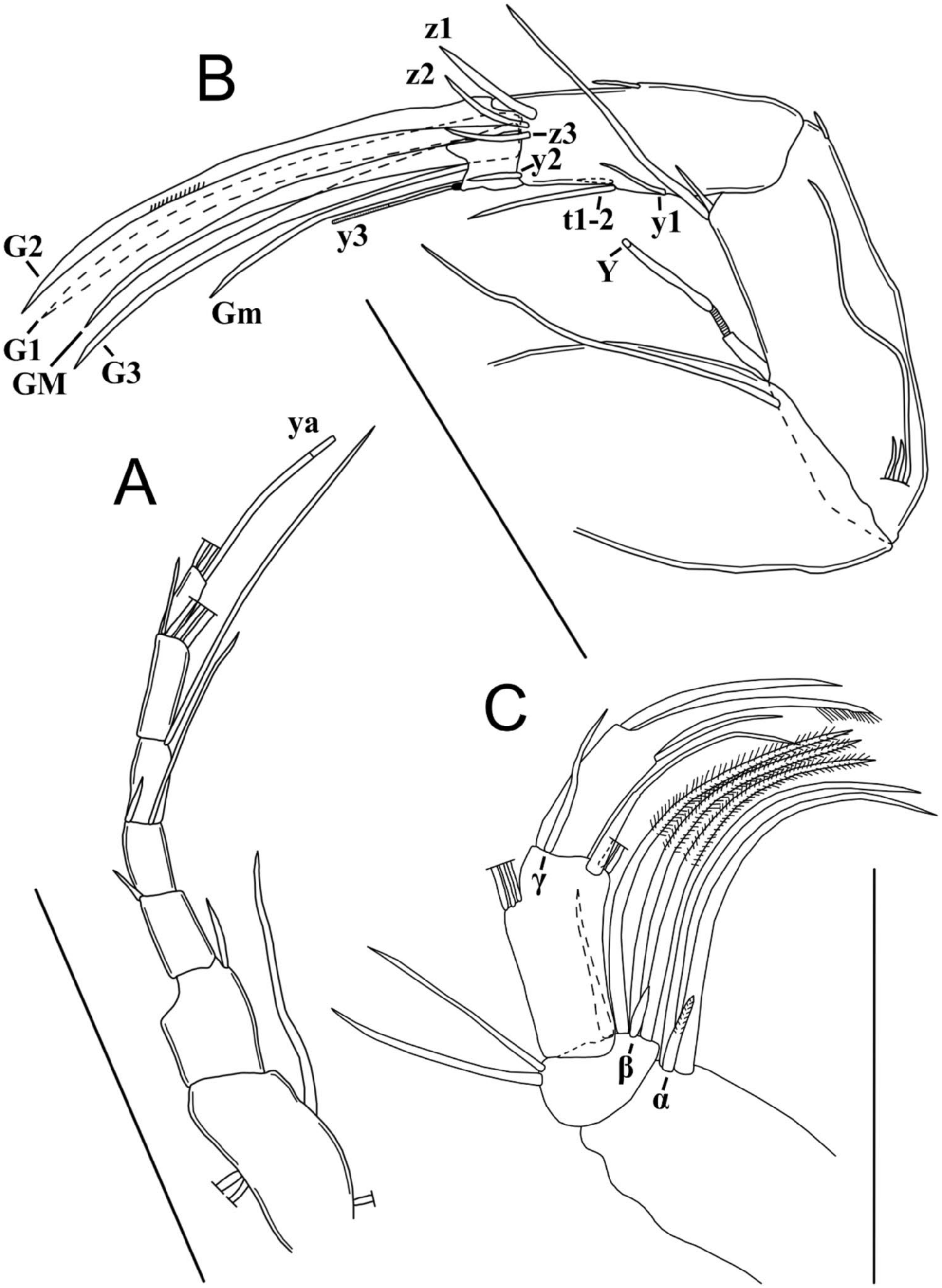
Description of male (Figs. 2A, 2G, 3, 4, 5, and 6, Online Resource 3).

Cp in right lateral view (Fig. 2A, Online Resource 3) subtriangular, resembling a scalene triangle with H/L = 0.51, an arched dorsal margin and greatest H located distinctly behind mid-length (D/L = 0.59). The anterior margin more rounded than the posterior one, which is conspicuously infracurvate, with postero-dorsal part steep and narrowly rounded towards the ventral side (DPE/H = 0.24). LV has a slightly more rounded antero-dorsal part compared to RV. The calcified part of the anterior inner lamella moderately broad (ca. 10% of L), with the inner margin rounded anteriorly but becoming straighter in the antero- and postero-ventral regions (Fig. 2G). Cp in dorsal view conspicuously narrow and elongated, with a slightly rounded posterior extremity and a more pointed or slightly beak-shaped anterior extremity. The greatest W is at mid-length. LV clearly overlaps RV along both anterior and posterior margins. Cp surface smooth.

A1 (Fig. 3A) 7-segmented. First segment with two long dorsal setae (broken) and two long ventral setae (one broken). Second segment with one short dorso-apical seta (reaching tip of the next segment). Third segment with one very short ventro-apical seta (reaching the half of the next segment). Fourth segment with one medium dorso-apical seta (extending beyond the tip of the next segment) and one short ventro-apical seta (almost reaching tip of the next segment). Fifth segment with one long dorso-apical seta. Penultimate segment with three long apical setae and one very short seta. Terminal segment with two long setae and one aesthetasc ya (2.5 × length of last segment).

A2 (Fig. 3B). Second segment of Pr with one long ventro-apical seta. Exopodite with one long and two very short setae. E 4-segmented. EI with large aesthetasc Y having very long sensory part; two ventro-apical setae: one short and one long, which slightly extends beyond tip of terminal segment; and one very short dorso-apical seta. EII ventrally with one short aesthetasc y1, dorsally with one short seta reaching the half of EIII, and internally with four unequal

Fig. 7 Limbs of *Candonopsis danilucae* sp. nov. female paratype (OC-UG 211012–1-A2L). **A.** A1. **B.** A2. **C.** Mdp. Scale bars: 100 µm

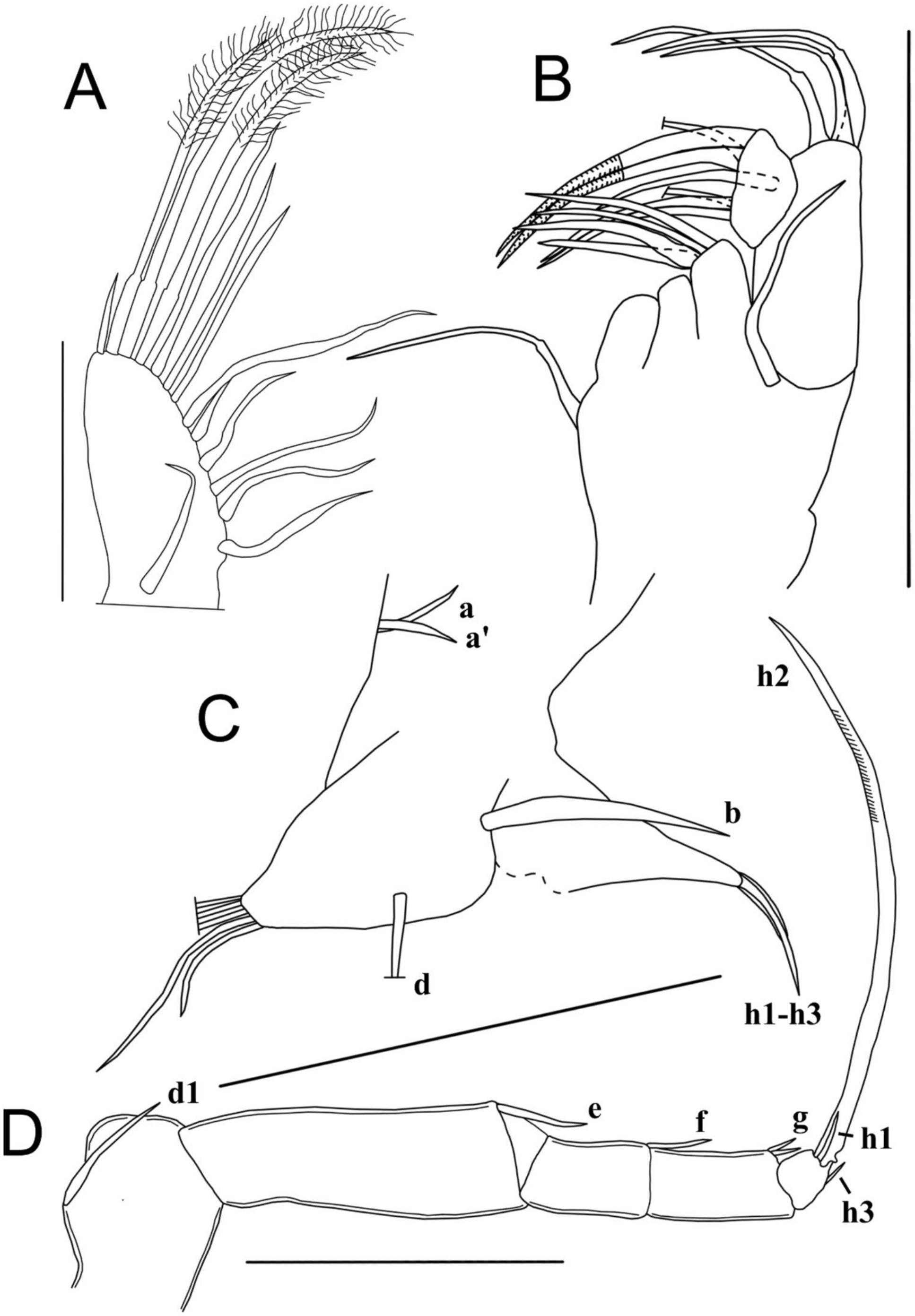


t-setae (t1-t4): seta t1 long, reaching beyond tip of terminal segment, setae t2-3 long and transformed into male bristles, and seta t4 short, reaching the half of next segment. EIII distally on external side with short claw z1, long claw z2, and medium seta z3; while on internal side EIII distally set with significantly reduced claw G1, short thin seta G3, and long claw G2. Terminal EIV with a long claw Gm, a shorter (~1/3 length of Gm) smooth claw GM, long smooth seta g (~1/2 length of Gm), and aesthetasc y3 (with very long sensory part) fused with slightly longer accompanying seta.

Mdp (Fig. 3C) 4-segmented. First segment ventro-apically with two long setae and one short α-seta. Second segment dorso-apically with two long slender setae; ventrally with three long hirsute setae, one medium smooth seta and one cone-shaped β-seta. Third segment dorso-apically with three unequally long slender setae; medio-apically with medium γ-seta and ventro-apically with two medium slender setae and one long seta. Terminal segment with three long claws, ventral-most one distally plumed.

Md-coxa (Fig. 4A) elongated, distally with rows of seven teeth and with one short smooth seta.

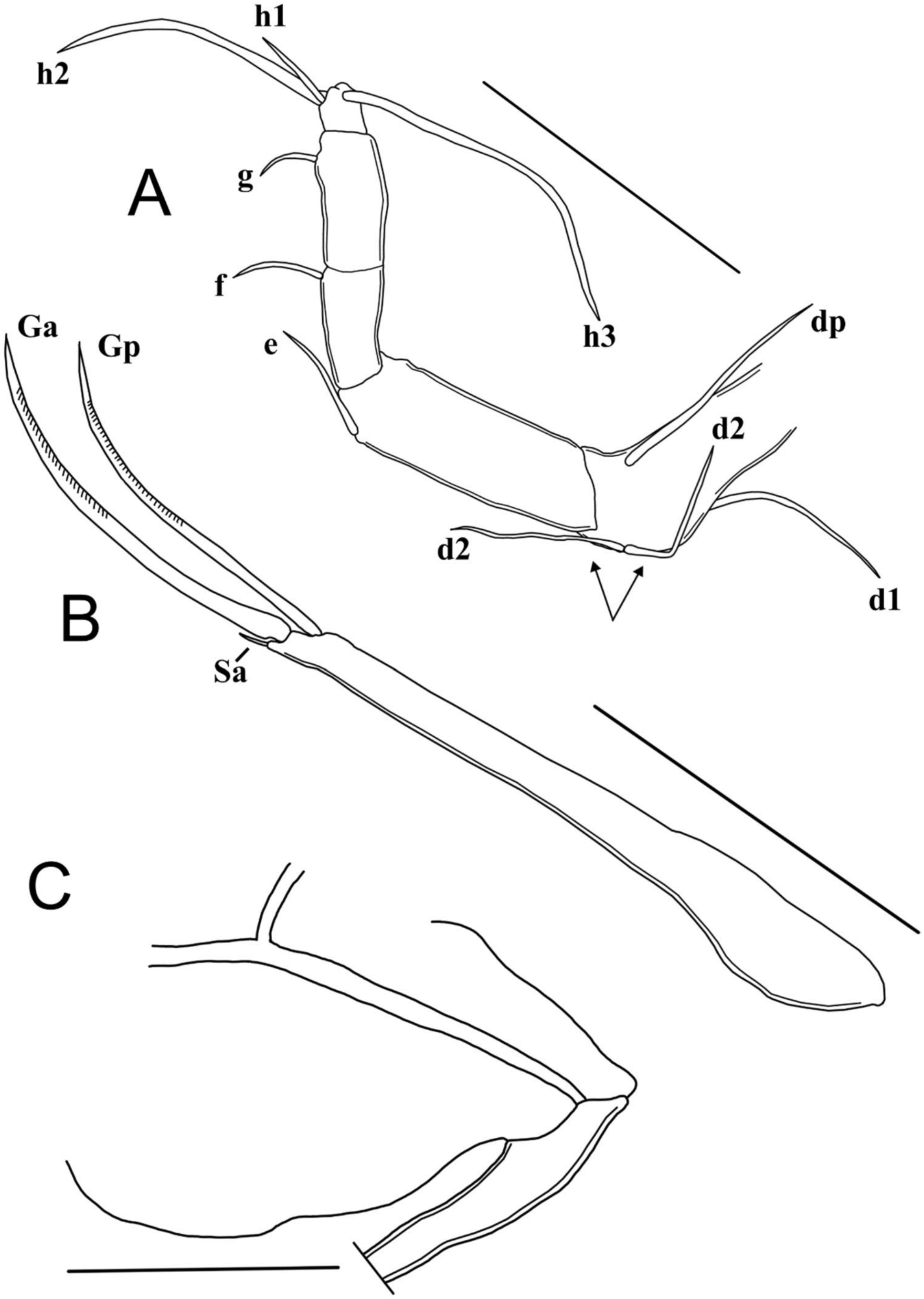
Fig. 8 Limbs of *Candonopsis danilucae* sp. nov. female paratype (OC-UG 211012–1-A2L). **A.** Mx1 respiratory plate. **B.** Mx1. **C.** T1 (maxilliped) **D.** T2 (walking leg). Scale bars: 100 µm



Mx1 (Fig. 4B) with three endites and 2-segmented palp. First endite with one long seta near its base. Third endite with two smooth teeth bristles, three long and three short smooth setae. First palp-segment with three unequal long serrated dorso-apical setae and medially with one long serrated seta. Terminal segment rectangular (~2×as wide as long), apically with two long claws (~6×as long as terminal segment) and three shorter slender setae. Respiratory plate large and elongate, with c. 25 long plumose rays.

T1 (Fig. 5A–B) forming asymmetrical prehensile palps. Pr of right T1 with two almost equal long b- and d-setae (unequal on the left T1) and short a-setae (not seen on the left one). Endite distally with c. 12 apical setae. Respiratory plate with three medium plumose rays. Right prehensile palp (Fig. 5A) with curved dorsal margin, elongated finger and medium long seta. Left prehensile palp (Fig. 5B) smaller with elongated and more slander finger and short seta.

Fig. 9 Limbs of *Candonopsis danilucae* sp. nov. female paratypes. **A.** T3 (OC-UG 211012–1-A2L). **B.** CR (OC-UG 211012–1-A2L). **C.** Genital lobe (OC-UG 211012–1-A4L). Scale bars: 100 µm. Arrows indicate two medium length setae on T2



T2 (Fig. 4C) a walking leg. Pr with one medium long seta (d1), seta d2 absent. Short (not reaching the half of next segment) antero-apical setae e and f on EI and EII, respectively. EIII with two short antero-apical setae g (~ 1/2 length of terminal segment). EIV with one short seta (h1), one long, strongly curved claw (h2) and one very short seta (h3); distal h2 claw ~ 3.5 × as long as EII.

T3 (Fig. 4D) a cleaning leg. Pr with two medium setae d1 and d2, and one longer seta dp. EI with short apical seta (e). EII and EIII subdivided, with apical short f-seta not reaching tip of EIII and subapical short g-seta reaching beyond tip of next segment. Terminal EIV as long as wide with three unequal setae, one short (h1), one medium length (h2) and one long (h3).

CR (Fig. 5C) stout. Ga and shorter Gp serrated, without spines, sa very short and sp absent. Furcal attachment branched.

Hp (Figs. 5D, 6) with three lobes. Outer lobe (a) triangular, ~ 1.5 × longer than wide, roundly pointed on the distal end and with centrally fibrous folds on its medial side. Shortest inner lobe (b) extending toward ventral margin of Hp. Intermediate medial lobe (h) with clearly rounded terminal part. The penal spermiduct with two parts, labyrinth divided into well sclerotized four compartments (d1-d4), and a tubular part running to bursa copulatrix (e), distally surrounded by sclerotized structures, including the M-process.

Zenker organ typically with 5+2 chitinous rings of spines.

Dimensions (in µm).

Holotype male RV: L=817, H=414, H/L=0.51.

Paratype males (n=2) Cp: L=813–860, H=413–436, H/L=0.51.

Description of female (Figs. 2B–D, F, 7, 8, and 9).

There is almost no sexual dimorphism in the carapace shape (Fig. 2B–D, F), with females being slightly more elongated (H/L=0.48–0.50; D/H=0.58). All female limbs as in male, except for A2, T1 and reproductive organs. E of A2 3-segmented (EII and EIII fused) (Fig. 7B) with only two internal t-setae (short t1 and t2), while t3 and t4 setae are absent. EII+III distally with three internal large claws G1, G2 and G3 of ca equal length; and external z1-z3 short setae (almost equaling to the length of EIV). Terminal EIV with long claw GM, shorter claw Gm (~2/3 length of GM) and aesthetasc y3. Seta accompanying y3 and seta g not seen. T1-endopodite (Fig. 8C) elongated, apically with three setae (h1-h3). Genital lobe (Fig. 9C) rounded, without any processes.

Note on female morphological asymmetry.

It should be noted that female has one additional medium length seta (second d2) on Pr of only one T3 (Fig. 9A).

Dimensions (in µm).

Female Cp (n=1): L=777, W=189.

Female Cp (n=6): L=757–810, H=371–398, H/L=0.48–0.50; LV (n=1): L=757, H=380, H/L=0.50; RV (n=1): L=783, H=379, H/L=0.48.

Description of the (?) 6th stage (A-3) juvenile carapace (Fig. 2E).

Cp in left lateral view almost triangular, with an arched dorsal margin and the greatest H positioned behind mid-length. Anterior margin is slightly more narrowly rounded than posterior one, while ventral margin is nearly straight. Cp surface smooth.

Dimensions (in µm).

Juveniles of A-3 stage (n=3) Cp: L=521–539, H=247–259, H/L=0.47–0.49.

Juvenile of A-4 stage (n=1) Cp: L=414, H=180, H/L=0.43.

Distribution and ecology

The species is only known from the hyporheic zone of three rivers within the Dordogne catchment in the department of Corrèze, Nouvelle-Aquitaine Region, France (Fig. 1). It is mid-mountain region on crystalline rocks, in the foothills of the Massif Central, an ancient volcanic mountain, in the center of France. In situ water parameters at the type locality were as follows: temperature 9.04 °C, dissolved oxygen 7.76 mg/l, pH 6.1, electrical conductivity 32.07 µS/cm, redox potential 245.8 mV, and concentrations of nitrates, sulphates, phosphates, and ammonium below the detection limit.

Keys to the identification of European species of the genus Candonopsis

Two keys were prepared for the identification of seven European species of the genus *Candonopsis*, one based on both soft parts and valves, and the second one based solely on carapace characters.

Key to European *Candonopsis* species based on both limbs and carapace characters (partly based on Karanovic & Marmonier, 2002).

1. Anterior and posterior Cp ends covered with long, stiff, spine-like setae *C. trichota* Schäffer, 1945

- Cp surface without long setae…………………….. 2

2. Gp on CR transformed to thin long seta *C. thienemanni* Schäffer, 1945

- Gp on CR a well-developed claw…………………..3

3. Cp maximum H at around mid-length *C. mareza* Karanovic & Petkovski, 1999

- Cp maximum H behind mid-length……… 4

4. G2 claw on female A2 shorter than neighboring terminal claws G1 and G3……………………………….…….5

- G2 claw on female A2 about as long as claws G1 and G3…………………………….………………………….6

5. Male left prehensile palp almost straight, slightly inflated in the middle; outer lobe (a) of Hp oblong *C. scourfieldi* Brady, 1910

- Male left prehensile palp almost straight, not inflated in the middle; outer lobe (a) of Hp triangular *C. boui* Danielopol, 1978

6. Valves sub-reniform in lateral view, with a wide, almost straight anterior inner lamella *C. kingsleii* (Brady & Robertson, 1870)

- Valves sub-triangular in lateral view, with mostly rounded anterior inner lamella *C. danilucae* sp. nov.

Key to European *Candonopsis* species (based solely on carapace characters).

1. Strongly infracurvate posterior margin (DPE/H<0.25) ……………………….…………………………………..2

- Less infracurvate posterior margin (DPE/H>0.30)… …………………………….………………………………..4

2. Cp L<0.65 mm *C. thienemanni* Schäffer, 1945

- Cp L>0.65 mm……………………………….……..3

3. Maximum H approx. at mid-L (D/L = 0.51–0.52) *C. mareza* Karanovic & Petkovski, 1999

- Maximum H posterior to mid-L (D/L = 0.58–0.59) *C. danilucae* sp. nov.

4. Cp covered with long, stiff, spine-like setae *C. trichota* Schäffer, 1945

- Cp without long setae……………………………….....5

5. Anterior inner lamella wide (14–15% of Cp L) and nearly straight ………………………………………… ………………......*C. kingsleii* (Brady & Robertson, 1870)

- Anterior inner lamella narrow (about 10% of Cp L) ……………………..…………………….......................6

6. Dorsal margin slightly arched …………………… ……………..…….. *C. boui* Danielopol, 1978

7. Dorsal margin mostly rounded ………………..……… ……………………....................... *C. scourfieldi* Brady, 1910

Molecular analyses

A concatenated alignment of 24 sequences (1038 bp) was used for further analyses. The alignment of *COI* sequences was unambiguous, and the inferred amino acid sequences contained no stop codons. Analysis with DnaSP identified 14 haplotypes among the sequences examined (a fifteenth haplotype, corresponding to the outgroup, was included for comparison), including those belonging to the new species. Genetic distance estimates, calculated under the TrN substitution model, indicated an overall mean genetic distance of 0.73, while pairwise distances between the identified haplotypes ranged from 0.00 to 1.41 (Fig. 10).

Molecular trees obtained using M-L and BI methods showed identical topologies. Consequently, we present the BI tree, with posterior probabilities and bootstrap values marked over the branches (Fig. 11). Using molecular markers with different mutation rates allowed for the resolution of both shallow and deep groupings in the inferred tree. The resulting tree, which includes representatives of six genera, highlights the distinct genetic placement of *Candonopsis danilucae* sp. nov. Our results suggest that *Candonopsis danilucae* sp. nov. is most closely related to *Candonopsis kingsleii*, the type species of the genus. Both species formed a well-supported, distinct group, with a genetic distance of 0.21.

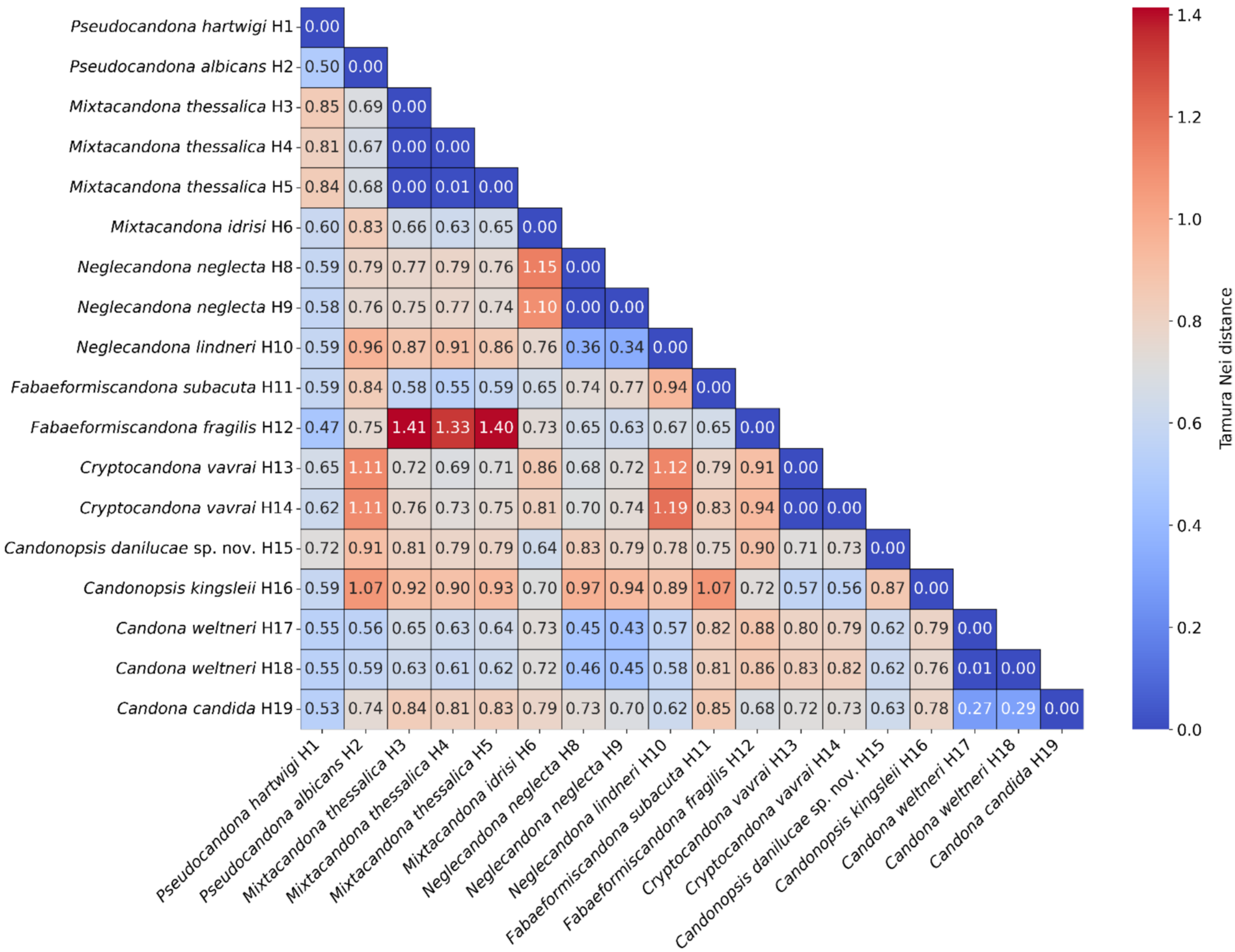
While the analyzed species number is limited, the finding of a closegenetic affinity between the *Candonopsis* lineage and one species of the genus *Cryptocandona* (*C. vavrai* Kaufmann, 1900) is remarkable. These two genera, which belong to separate subfamilies, Candonopsinae and Cryptocandoninae, respectively, together form a distinct group that is clearly separated from the representatives of the subfamily Candoninae. The latter group comprises species belonging to the genera: *Candona* Baird, *Fabaeformiscandona* Krstić, *Neglecandona* Krstić and *Pseudocandona* Kaufmann included in the analyses (Fig. 11).

Species delimitation

A total of 29 sequences, each 515 bp in length, were included in the analyses. From these, 19 distinct haplotypes were identified using DnaSP, reflecting the genetic variation within the studied dataset, while a 20th haplotype represented the outgroup, consistent with the concatenated dataset analyses. All three species delimitation methods: ABGD, ASAP and bPTP produced broadly consistent results, recovering between 12 and 14 molecular operational taxonomic units (MOTUs), depending on the method. Most species were consistently recovered as distinct MOTUs across all methods, including the newly described *Candonopsis danilucae* (C15), which formed a well-supported, separate group from the closely related *C. kingsleii* (C16). Some MOTUs, however, combined haplotypes corresponding to more than one morphologically recognized species. For example, haplotypes of *Candona candida* (C19) and *Candona weltneri* (C17–C18) were grouped together in some analyses, reflecting close genetic similarity and limited divergence within this lineage, although in the ASAP method these two species were recovered as separate MOTUs. Despite these minor discrepancies, the high degree of concordance among the three delimitation approaches, underscores the overall robustness and reliability of the identified MOTU structure within the dataset. The inferred relationships among haplotypes and their corresponding MOTUs are summarized in Fig. 12, with haplotypes systematically labeled C1–C19 to correspond to the COI only dataset (see Table 1).

Cardinium detection

Amplification of the *16S rRNA* gene fragment confirmed the presence of endosymbiotic bacteria of the genus *Cardinium* in three out of five screened individuals of *Candonopsis danilucae* sp. nov. (one female and two juveniles). The length of the amplified gene fragment (211 bp) was insufficient for comprehensive comparative analyses with *Cardinium* sequences previously identified in ostracods and deposited in GenBank. Nevertheless, BLAST analysis revealed that the amplified bacterial DNA fragment showed the highest similarity with the sequence deposited under accession number MH908935, which was previously obtained from an ostracod specimen by Schön et al. (2019).



	Pseudocandona hartwigi H1	*Pseudocandona albicans* H2	*Mixtacandona thessalica* H3	*Mixtacandona thessalica* H4	*Mixtacandona thessalica* H5	*Mixtacandona idrisi* H6	*Neglecandona neglecta* H8	*Neglecandona neglecta* H9	*Neglecandona lindneri* H10	*Fabaeformiscandona subacuta* H11	*Fabaeformiscandona fragilis* H12	*Cryptocandona vavrai* H13	*Cryptocandona vavrai* H14	*Candonopsis danilucae* sp. nov. H15	*Candonopsis kingsleii* H16	*Candona weltneri* H17	*Candona weltneri* H18	*Candona candida* H19
Pseudocandona hartwigi H1	0.00																	
Pseudocandona albicans H2	0.50	0.00																
Mixtacandona thessalica H3	0.85	0.69	0.00															
Mixtacandona thessalica H4	0.81	0.67	0.00	0.00														
Mixtacandona thessalica H5	0.84	0.68	0.00	0.01	0.00													
Mixtacandona idrisi H6	0.60	0.83	0.66	0.63	0.65	0.00												
Neglecandona neglecta H8	0.59	0.79	0.77	0.79	0.76	1.15	0.00											
Neglecandona neglecta H9	0.58	0.76	0.75	0.77	0.74	1.10	0.00	0.00										
Neglecandona lindneri H10	0.59	0.96	0.87	0.91	0.86	0.76	0.36	0.34	0.00									
Fabaeformiscandona subacuta H11	0.59	0.84	0.58	0.55	0.59	0.65	0.74	0.77	0.94	0.00								
Fabaeformiscandona fragilis H12	0.47	0.75	1.41	1.33	1.40	0.73	0.65	0.63	0.67	0.65	0.00							
Cryptocandona vavrai H13	0.65	1.11	0.72	0.69	0.71	0.86	0.68	0.72	1.12	0.79	0.91	0.00						
Cryptocandona vavrai H14	0.62	1.11	0.76	0.73	0.75	0.81	0.70	0.74	1.19	0.83	0.94	0.00	0.00					
Candonopsis danilucae sp. nov. H15	0.72	0.91	0.81	0.79	0.79	0.64	0.83	0.79	0.78	0.75	0.90	0.71	0.73	0.00				
Candonopsis kingsleii H16	0.59	1.07	0.92	0.90	0.93	0.70	0.97	0.94	0.89	1.07	0.72	0.57	0.56	0.87	0.00			
Candona weltneri H17	0.55	0.56	0.65	0.63	0.64	0.73	0.45	0.43	0.57	0.82	0.88	0.80	0.79	0.62	0.79	0.00		
Candona weltneri H18	0.55	0.59	0.63	0.61	0.62	0.72	0.46	0.45	0.58	0.81	0.86	0.83	0.82	0.62	0.76	0.01	0.00	
Candona candida H19	0.53	0.74	0.84	0.81	0.83	0.79	0.73	0.70	0.62	0.85	0.68	0.72	0.73	0.63	0.78	0.27	0.29	0.00

Fig. 10 Heatmap depicting the number of base substitutions per site among analyzed Candonidae species and their haplotypes C1–C19 (see Table 1 for information on haplotype numbers) based on *COI* sequences and estimated using the Tamura–Nei substitution model

Discussion

Zoogeography and diagnostically important traits within the genus Candonopsis

Claw armament and reductions in caudal ramus morphology

The first attempt to divide the genus *Candonopsis* into species groups was made by Klie (1932) based on the presence or absence of spines on CR claws: a) species with spines on both anterior (Ga) and posterior (Gp) claws, b) species with a spine on only Gp, and c) species without spines on either claw. Although later studies revealed intraspecific variation in the number of spines on CR claws, e.g., Martens (1984) found *C. africana* Klie, 1944 specimens from the type locality with spines on one or both claws, and Karanovic and Marmonier (2002) documented variation in spine morphology and presence in three Australian species (*C. dani* Karanovic & Marmonier, 2002, *C. kimberleyi* Karanovic & Marmonier, 2002 and *C. murchinsoni* Karanovic & Marmonier, 2002), the presence of a spine on at least one claw appears to characterise a relatively coherent group, both morphologically and biogeographically (Table 2). It has even been suggested that this feature may represent a valid synapomorphy defining a distinct lineage within *Candonopsis* (Karanovic, 2005).

The group of species bearing spines on at least one CR claw comprises 14 species largely restricted to subtropical and tropical regions (Karanovic, 2004, 2012; Karanovic & Marmonier, 2002; Meisch et al., 2024). The Afrotropical region is the most species-rich with six endemic surface-water species (Table 2). Another seven species with spines on CR claws occur in Asia, Australia and Oceania (Table 2). In addition, *Candonopsis hummelincki* Broodbakker, 1983 characterized by spines on both CR claws, has been reported from wells in the Caribbean and Venezuela (Broodbakker, 1983, 1984).

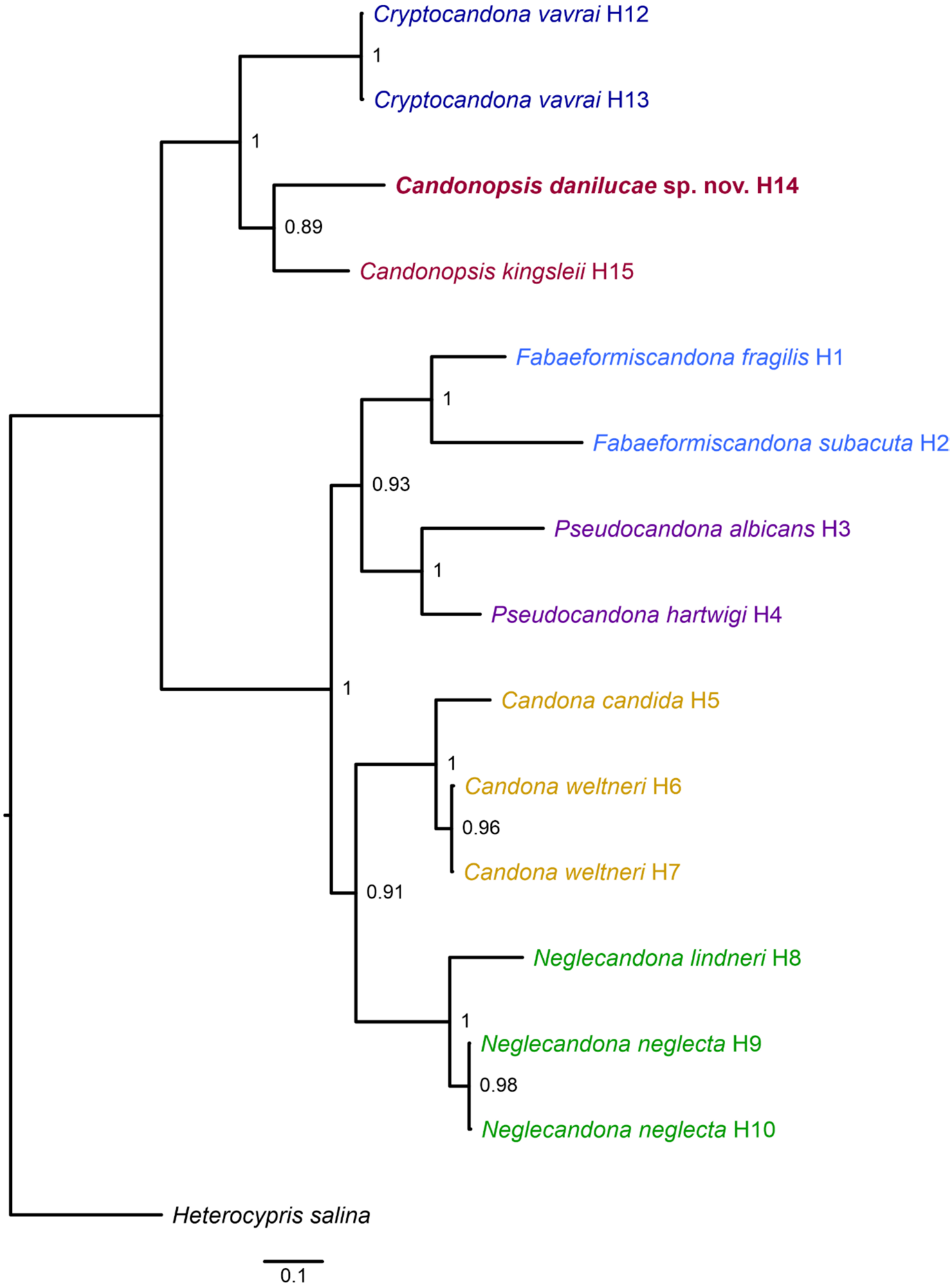
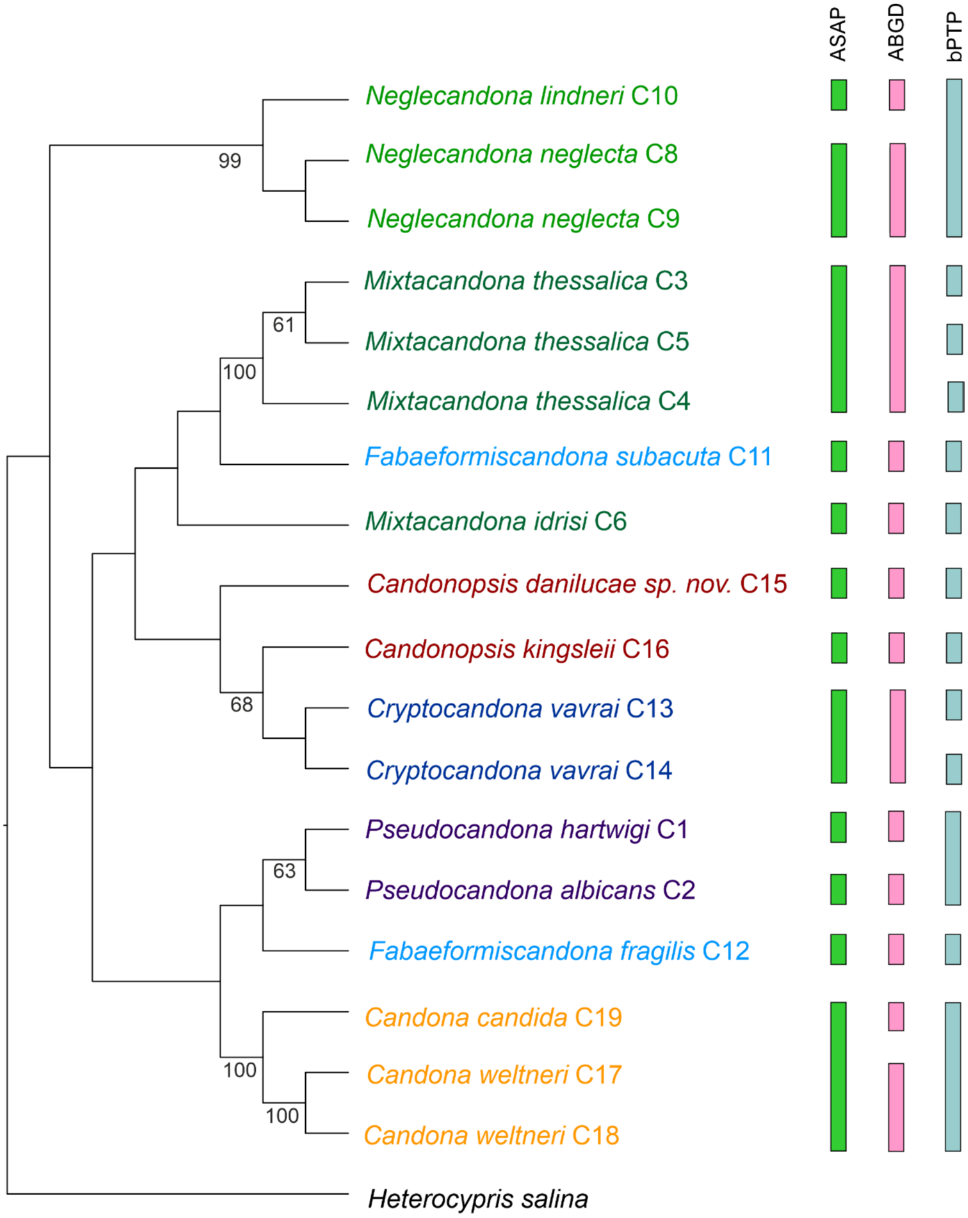


Fig. 11 Tree depicting the relationships among selected species of the family Candonidae, inferred from the combined mitochondrial *COI* gene and nuclear *28S rDNA* gene.. Analyses of mtDNA polymorphism and relative haplotype frequencies revealed 14 haplotypes (H1–H14) among 24 individuals (see Table 1 for information on haplotype numbers). Numbers at the nodes indicate Bayesian posterior probabilities and bootstrap support values, respectively

Candonopsis danilucae sp. nov. belongs to the species group lacking spines on the CR claws. This group includes an Afrotropical *C. anteroacuta* Rome, 1962, an Oriental *C. urmilae* Gupta, 1988, an Australian *C. westaustraliensis* Karanovic & Marmonier, 2002, and six European species (Table 2). Among the latter is *C. kingsleii*, the most widespread species of the genus, reported not only from Europe but also from Asia, North Africa and North and Central America, although some American records may require verification (Table 2).

Beyond spine presence on the CR claws, most of the other characters used in species identification within *Candonopsis* appear to be homoplastic, as confirmed in the cladistic analysis by Karanovic (2005). Various reductions in CR morphology are particularly common and may be linked to a subterranean lifestyle of some species (Karanovic, 2004), such as the transformation of Gp into a seta in *C. westaustraliensis*, a seta-like reduction of Gp in European *C. thienemanni* (Schäfer, 1945), or shortening the CR relative to its claws in Indian *C. urmilae* (Gupta, 1988). Reductions are also seen in the anterior seta (sa) on CR, which is completely absent in African surface water *C. navicula* (Daday, 1910), and very short in females or absent in males in groundwater Indonesian *C. putealis* (Klie, 1932).

Fig. 12 Tree based on a fragment of the *COI* mtDNA gene showing the relationships among selected representatives of Candonidae and the results of different species delimitation methods (ABGD, ASAP, bPTP). The numbers next to nodes indicate ML bootstrap values (>60%)



Chaetotaxy of the first and second antenna

Similarly, reductions in A1 chaetotaxy (see Karanovic, 2005 and in our new species) do not appear to represent synapomorphies, further complicating phylogenetic reconstruction within the genus. One potentially informative character may be the relative length of the G2 claw on the female A2: a short G2 (noticeably shorter than G1) is shared by three European species (*C. boui*, *C. mareza* and *C. scourfieldi*) and the Indian *C. urmilae* (see Karanovic, 2005).

Morphology of hemipenis

In our opinion a promising but underutilized character for phylogenetic analysis may be the morphology of the hemipenis (Hp), particularly the presence of the middle lobe h. In *C. danilucae* sp. nov., we clearly demonstrated the presence of this middle lobe in addition to the outer lobe a and inner lobe b. This feature is explicitly described in the most recent species (re-)descriptions (*C. dani*, *C. murchinsoni*, *C. westaustraliensis* and *C. tenuis* (Brady, 1886)) and diagnoses of the genus (Karanovic, 2004, 2012; Karanovic & Marmonier, 2002), which characterize the Hp as having a triangular middle lobe that is distinctly higher than the other two.

Although most historical species descriptions recognize only two Hp lobes, our examination of original illustrations suggests that as many as seven species (*C. boui*, *C. kingsleii*, *C. mareza*, *C. putealis*, *C. sumatrana*, *C. thienemanni*, and *C. urmilae*) may also possess a third, medial lobe. Thus, in

Table 2 Checklist of Candonopsis species categorized by the presence or absence of spines on the caudal ramus claws, along with their recorded countries of occurence

Species	Geographical distribution and references
Species bearing spines on at least one claw of caudal ramus	
C. africana Klie, 1944[e]	Democratic Republic of Kongo: Klie, 1944; Rome, 1962; Sudan: Martens, 1984
C. bujukuensis Löffler, 1968[e]	Uganda: Löffler, 1968
C. dani Karanovic & Marmonier, 2002 [h]	Australia: Karanovic & Marmonier, 2002
C. fessleri Löffler, 1968[e]	Tanzania: nominotypical subspecies: Löffler, 1968; Kenya: subspecies *C. fessleri daburui*: Löffler, 1968
C. hummelincki Broodbakker, 1983 [h]	Haiti, Puerto Rico, British Virgin Islands, Saint Martin, Venezuela: Broodbakker, 1983, 1984
C. kimberleyi Karanovic & Marmonier, 2002 [h]	Australia: Karanovic & Marmonier, 2002
C. murchisoni Karanovic & Marmonier, 2002 [h]	Australia: Karanovic & Marmonier, 2002
C. nama Daday, 1913[e]	Namibia: Daday, 1913; Botswana: Szwarc & Namiotko, 2022
C. navicula Daday, 1910[e]	Kenya and Tanzania: Daday, 1910; Burkina Faso: Klie, 1935; Tanzania: Rome, 1962 as *C. depressa* and *C. dorsoerecta* (see Karanovic, 2002 for synonymy); Botswana: Szwarc & Namiotko, 2022
C. putealis Klie, 1932 [h]	Indonesia: Klie, 1932; India Victor & Fernando, 1979 – this record is likely erroneous (see Karanovic, 2004)
C. solitaria Vávra, 1895[e]	Tanzania: Vávra, 1895; Cameroon: Klie, 1936
C. sumatrana Klie, 1932[e]	Indonesia: Klie, 1932; Salomon Islands: Harding, 1962 as *C. calva*; Samoa and Tonga: Victor & Fernando, 1978 misidentified as *C. tenuis* (see Karanovic, 2004); Taiwan Republic of China: Yu et al., 2009
C. tenuis (Brady, 1886)[e,h]	Australia: Brady, 1886; Sars, 1896; Karanovic & Marmonier, 2002; Indonesia: Klie, 1932; Japan: Smith & Janz, 2008; South America: Müller, 1912 – this record is likely erroneous
C. transgrediens Brehm, 1923[e]	China: Brehm, 1923; South Korea: Karanovic & Lee, 2012
Species lacking spines on caudal ramus claws	
C. anteroacuta Rome, 1962[e]	Tanzania: Rome, 1962
C. boui Danielopol, 1978 [h]	France: Danielopol, 1978
C. danilucae sp. nov[h]	France: this paper
C. kingsleii (Brady & Robertson, 1870)[e]	common in Europe: Meisch, 2000; Russia: Semenova, 2005; Turkey: Özuluğ et al., 2018; Japan: Okubo, 2004; India: Bhatia & Singh, 1970; Algeria: Ghaouaci et al., 2017 (as *C.* cf. *kingsleii*); North and Central America: Meisch, 2000; Acosta-Mercado et al., 2012 (as *C.* cf. *kingsleii*); Smith & Horne, 2016; Meisch et al., 2024
C. mareza Karanovic & Petkovski, 1999 [h]	Montenegro: Karanovic & Petkovski, 1999
C. scourfieldi Brady, 1910[e]	several countries in Europe: Meisch, 2000; Turkey: Özuluğ et al., 2018
C. thienemanni Schäfer, 1945 [h]	Greece: Schäfer, 1945
C. trichota Schäfer, 1945 [h]	Greece: Schäfer, 1945
C. urmilae Gupta, 1988 [h]	India: Gupta, 1988
C. westaustraliensis Karanovic & Marmonier, 2002 [h]	Australia: Karanovic & Marmonier, 2002

Abbreviations: *e* epigean species, *h* hypogean species

total, five species explicitly show three Hp lobes (including *C. danilucae* sp. nov.), and another seven are likely to have this feature. This suggests that the presence of three Hp lobes may be a shared trait across *Candonopsis*, with interspecific variation in the degree of development of lobe h. If, however, future studies confirm that some species lack this lobe, it would represent a significant morphological divergence, potentially justifying a division of the genus into distinct phylogenetic lineages.

We therefore recommend the re-examination of type specimens to verify the number of Hp lobes. Given the scarcity of clear morphological synapomorphies, a robust understanding of relationships and diversity within *Candonopsis* requires molecular evidence based on genetic markers. An integrative approach, combining molecular data with geometric morphometric analysis of carapace shape, is essential for resolving the taxonomy and systematics of this morphologically diverse genus with a long geological history.

Comparative diagnosis

The newly described species belongs to the group of *Candonopsis* species with the spineless CR claws. The three extra-European species from this group can be easily distinguished from the new one. *Candonopsis westaustraliensis* can be easily distinguished from *C. danilucae* sp. nov. and other species by the unique morphology of its Gp claw on CR, which is transformed into short, swollen, pappose seta (Karanovic & Marmonier, 2002). *Candonopsis urmilae* occupies an isolated position within the genus due to its very short CR, strongly asymmetrical valves, and pitted carapace surface (Gupta, 1988). *Candonopsis anteroacuta* is unique in having an extremely narrow and elongated terminal segment of Mdp (width 1/9 of the length) and a uniformly curved dorsal carapace margin (Rome, 1962).

When considering six *Candonopsis* species known from Europe, *C. danilucae* sp. nov. can be distinguished primarily by the shape of the carapace and the male copulatory organs.

In lateral view, the carapace of *Candonopsis danilucae* sp. nov. most closely resembles that of two stygobitic species: *C. mareza*, from the Mareza spring near Podgorica, Montenegro (Karanovic & Petkovski, 1999), and *C. thienemanni*, from wells in Armenio and Stefanovikeio, Thessaly, Greece (Schäfer, 1945). All three species share a carapace shape characterized by a weakly arched to nearly straight antero-dorsal margin, a steep postero-dorsal margin, and a narrowly rounded postero-ventral junction, which gives this region a distinctly infracurvate appearance (i.e., narrowly rounded ventrally), with $DPE/H<0.25$. However, *C. mareza* differs in having a carapace shaped as a near-isosceles triangle, with the greatest height (H) located approximately at mid-L ($D/L=0.51$–0.52), whereas *C. danilucae* sp. nov. exhibits a scalene triangular form with $D/L=0.58$–0.59. Additionally, *C. mareza* has a very narrow anterior inner lamella, less than 8% of the carapace L (see Karanovic & Petkovski, 1999), compared to 10–12% in *C. danilucae* sp. nov. In contrast, *C. thienemanni* has its maximum H positioned posterior to mid-length ($D/L=0.52$–0.55), and a notably wide anterior inner lamella comprising approximately 17% of the carapace L. It is also the smallest European species of the genus, with a carapace L of only 0.64 mm (Schäfer, 1945). The remaining four European *Candonopsis* species have laterally viewed carapaces that do not exhibit a triangular shape and possess a more broadly rounded and less infracurvate posterior margin ($DPE/H>0.30$). These species are: 1) *C. boui*, from wells in Albi (Chemin du Go) and fluvial sediments in Avalats, Occitania, France (Danielopol, 1978, 1980a, 1980b); 2) *C. trichota*, from a well in Armenion, Thessaly, Greece (Schäfer, 1945); 3) *C. scourfieldi*, from various surface water bodies and interstitial habitats across Europe (Meisch, 2000), reported also from Turkey (Özuluğ et al., 2018) and Canary Islands (Castillo-Escrivà et al., 2023); and 4) the widespread Holarctic surface-water species *C. kingsleii* (Meisch, 2000; Meisch et al., 2024). *Candonopsis trichota* further differs from *C. danilucae* sp. nov. in its small size ($L=0.71$ mm), a carapace resembling a trapezoid in lateral view, a wide anterior inner lamella (~17% of L), and the presence of long, stout setae at both the anterior and posterior ends of the carapace (Schäfer, 1945). *Candonopsis boui* and *C. scourfieldi* are relatively more elongate, with H/L ratios below 0.5, in contrast to the higher, more triangular carapace of *C. danilucae* sp. nov. ($H/L=0.49$–0.51). *Candonopsis kingsleii* is distinctly larger (female $L\geq0.85$ mm; male $L\geq0.96$ mm) than *C. danilucae* sp. nov. (female $L\leq0.81$ mm; male $L\leq0.86$ mm), and also features a wide, nearly straight anterior inner lamella occupying approximately 14–15% of carapace L (see Meisch, 2000).

The hemipenis (Hp) of *C. danilucae* sp. nov. is further diagnostic, characterized by a large, triangular outer lobe (a), a clearly rounded medial lobe (h), and a distinctly, broadly rounded inner lobe (b) with a wrinkled dorsal margin. This combination of features distinguishes it from its congeners, particularly *C. mareza* and *C. thienemanni*, both of which possess more rounded outer lobes (see Schäfer, 1945; Karanovic & Petkovski, 1999, respectively). *Candonopsis kingsleii* has a more pointed outer lobe (Brady & Robertson, 1870; Meisch, 2000), while *C. scourfieldi* has a shorter outer lobe (Brady, 1910; Meisch, 2000) than *C. danilucae* sp. nov. The Hp of *C. boui* is most similar in shape but differs in having a more rectangular inner lobe (Danielopol, 1978, 1980a). Since male of *C. trichota* remains undescribed (Schäffer, 1945), comparisons of copulatory organs are not possible.

Molecular aspects of species delimitation

The extent of interspecific molecular divergence in mitochondrial *COI* sequences varies considerably across taxonomic groups and even families. In crustaceans, Léfebure et al. (2006) identified a 0.16 p-distance between *COI* sequences as a threshold for species delimitation, whereas Jeffery et al. (2011) applied a more conservative 0.03 threshold in brachiopods–a value also reported for various crustaceans by Costa et al. (2007). In ostracods, interspecific *COI* divergence within a single genus typically ranges from 0.06 to 0.14 (Martens et al., 2013). Notably, within the subfamily Candoninae, TrN genetic distance values ranging from 0.28 to 0.30 have been reported between certain species of the genus *Typhlocypris*, along with a high average genetic distance of 0.33 observed within the genus *Fabaeformiscandona* (Wysocka et al., 2019). In our analyses, the highest TrN distance reached 1.41, considerably exceeding previously reported values for European representatives of this subfamily, highlighting the pronounced genetic divergence among the studied lineages.

Although the broader evolutionary relationships of species within the family Candonidae remain unresolved (Wysocka et al., 2019), our results reaffirm the close relationship between the genera *Cryptocandona* and *Candonopsis*. Analyses integrating both nuclear and mitochondrial gene fragments provided stronger support for the connection between these taxa than previous studies based solely on mitochondrial markers. A wider coverage, however, is needed to improve accuracy, generalize our findings, and resolve complex evolutionary relationships of Candonidae. This can be achieved by including more taxa, more genetic loci, or by using whole-genome sequencing.

Finally, the high congruence observed among the three genetic species delimitation methods (ABGD, ASAP, bPTP) provides robust support for the identified molecular operational taxonomic units (MOTUs) within the studied Candonidae dataset. In particular, *Candonopsis danilucae* sp. nov. was consistently recovered as a distinct single-MOTU lineage across all analyses, further confirming its genetic distinctiveness and corroborating the morphological data. The clear separation of this MOTU, together with its genetic divergence relative to other lineages, serves as the ultimate molecular confirmation of its taxonomic validity.

Distribution and ecology of Candonopsis danilucae sp. nov.

Despite extensive sampling within the Nouvelle-Aquitaine Region (more than 350 investigated sites, see the SEPANSO website, 2025), *Candonopsis danilucae* sp. nov. was found at only three locations, all within the Dordogne River catchment in the department of Corrèze, suggesting a potential micro endemism. At the type locality (River Vianon, Saint-Pantaléon-de-Lapleau), as well as at the other sampling sites, hyporheic water was well oxygenated, moderately acidic, and exhibited low electrical conductivity. None of the major ionic compounds and parameters measured in the river (sulphates, phosphates, nitrates, ammonium) indicated abnormal values, suggesting an absence of pollution and a well-preserved, pristine environment. The associated taxa: niphargids, syncarids, copepods, and oligochaetes, most of which were stygobitic, indicate a diverse hyporheic fauna and a well-functioning biocenosis. Furthermore, macro-invertebrates indicative of good water quality, such as plecopteran and ephemeropteran larvae, were relatively abundant in the riverbed.

Cardinium detection

One of the earliest reports of endosymbiotic bacteria in non-marine ostracods was the detection of unidentified Gram-negative bacteria via electron microscopy in laboratory-cultured specimens of *Heterocypris incongruens* (Ramdohr, 1808) (Vandekerckhove, 1998). More recent studies using 16S rDNA amplification have revealed a relatively high incidence, compared to other arthropods (Nakamura et al., 2009; Weeks et al., 2003), of *Cardinium* bacterial infections in natural populations of several non-marine ostracod species. These infections have been detected in specimens collected from a wide range of biotopes, including surface/groundwater ecotones, however, to date, *Cardinium* has not been reported in ostracods inhabiting true groundwater environments (Çelen et al., 2019; Mioduchowska et al., 2018; Munakata et al., 2021, 2022, 2024; Schön & Martens, 2020; Schön et al., 2019, 2025).

Our investigation of *Candonopsis danilucae* sp. nov. provides the first evidence of intracellular *Cardinium* symbiosis within a groundwater ostracod host. To the best of our knowledge this also constitutes the first record of *Cardinium* infection in any groundwater-dwelling crustacean. While *Cardinium* infections have been documented in other subterranean arthropods, for instance in terrestrial cave-dwelling harvestmen (Opiliones) (Zhao et al., 2024), and a few cases of groundwater crustaceans hosting other intracellular bacterial symbionts are known (e.g., an anchialine atyid shrimp harboring chemosynthetic endosymbionts: Pakes et al., 2014), we are not aware of any confirmed instance of *Cardinium* infecting crustacean species from groundwater habitats.

In this study, molecular analyses were conducted on five specimens of *C. danilucae* sp. nov. (two females and three juveniles), and *Cardinium* was detected in three of them (one female and two juveniles), suggesting a preliminary infection rate of 60%. While this sample size is limited, the finding is intriguing, especially given the female-biased sex ratio observed in the new species (2: 1 in the type locality). It is possible that this skewed ratio is influenced by the presence of the endosymbiont, which is known to manipulate host reproduction in various ways, including feminization, male killing, and maintenance of reproductive polymorphisms. In ostracods, such manipulation may result in the coexistence of sexual (non-infected) and asexual (infected) strains within the same population (Schön & Martens, 2020).

The discovery of *Cardinium*, a known reproduction-manipulating endosymbiont, in ostracods from a specialized groundwater environment opens new avenues for research into host-symbiont interactions. It presents an opportunity to explore how endosymbiotic relationships evolve and function under the unique selective pressures of subterranean ecosystems.

Conclusion

Our findings underscore the value of integrative taxonomy, combining carapace morphology, limb structure, and molecular data, for resolving species boundaries and elucidating symbiotic associations in subterranean ostracods, as exemplified by the newly described *Candonopsis danilucae* sp. nov.

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Author contributions Conceptualization: MK, AS, AW, TN; Material collection: FL, TA, XC, FM, CD; Methodology: MK, AS, MM, AW, TN; Formal analysis and investigation: MK, AS, MM; Writing–original draft preparation: MK, AS, TN, FL; Writing–review and editing: MK, AS, TN, FL, AW, TA; Funding acquisition: MK, TN, FL, TA, XC; Data curation: MK, AS, TN, FL. All authors read and approved the final manuscript.

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Data availability All data generated and analysed during this study are provided in this manuscript. Sequence data were submitted to GenBank under accession numbers provided in Table 1.

Declarations

Competing interests The authors declare no competing interests.

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