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The epikarst habitat in Slovenia and the description of a new species

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Abstract

Paramorariopsis irenae n. sp. is the second species of the genus, which was described for the first time 15 years ago from a small cave in the southern part of Slovenia. The new species is closely related to *Paramorariopsis anae* Brancelj, 1991. The main differences are found in the ornamentation of caudal rami, abdominal somites and legs P2–P4, while P5 are very similar. It was initially assumed that the genus represented a member of the community inhabiting wet mosses near the cave's entrance. It can now be confirmed that it belongs to a specific community of Copepoda in the epikarst (i.e. part of the unsaturated karst zone). So far two genera are recognised as exclusively epikarstic: *Morariopsis* Kiefer, 1930 and *Paramorariopsis* Brancelj, 1991. Both genera were for a long time considered as monospecific with restricted distribution. Intensive sampling of the epikarst zone in Slovenia and Italy revealed that many genera, previously assumed as "rare", are in fact common, widely distributed, and show a considerable level of specific endemism. Morphological adaptations of taxa specific for the epikarst are discussed along with detailed discussion on habitat and sampling methods developed for that habitat.

Keywords: Biodiversity, caves, epikarst, Harpacticoida, Slovenia, Stygobionts

Introduction

Groundwater and karstic caves all over the world appear to be an inexhaustible source of new taxa of Copepoda, particularly Harpacticoida (Schminke and Notenboom 1990; Brancelj 1991; Galassi and Pesce 1991; Rouch 1991a, 1991b; Pesce and Galassi 1994; Reid 1995; Galassi and De Laurentiis 1997; Karanovic 1997, 1998, 1999; Stoch 1997; Karanovic and Bobic 1998; Galassi et al. 1999). The first representatives of the fauna from the unsaturated zone (including the epikarst) were described about 75 years ago when Kiefer (1930) described *Diacyclops hypogeus* (as *Cyclops hypogeus*), *Speocyclops infernus* (as *Cyclops infernus*), and *Morariopsis scotenophila* (as *Moraria scotenophila*) from the Škocjanske Jame cave (also known as Grotta di San Canzian). Nevertheless, the unsaturated zone in the karst areas attracted only limited attention for a long time. Only in the last decade has

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more intensive sampling of this habitat been started (for details see Brancelj 2000, 2002). It is a very specific habitat neglected for a long time but inhabited with a rich and specific fauna (Brancelj 2000, 2002). So far, about 40 taxa of Copepoda (Cyclopida and Harpacticoida) have been found there (Brancelj and Pipan 2004).

Some harpacticoid genera, such as *Elaphoidella*, *Moraria*, *Bryocamptus*, or *Parastenocaris*, have many representatives in subterranean environments. Some other genera are far less speciose, such as *Ceuthonectes*, *Morariopsis*, *Paramorariopsis*, and *Lessinocamptus*, all of which are stygobitic with relatively restricted distribution both in a geographical and ecological sense.

The genus *Paramorariopsis* was proposed by Brancelj (1991) for a new species, *P. anae*, collected from a small pool at the entrance to the cave Jama pod Krogom in southern Slovenia. It was assumed that the new species inhabited small crevices in rock filled with water or wet mosses at the entrances of the caves. Fifteen years later, it was accepted that members of the genus *Paramorariopsis* are typically inhabitants of the epikarst zone (Brancelj and Culver 2005). Intensive sampling of small pools in the epikarst zone in Slovenia since 2000 resulted in the discovery of several new species (Brancelj 2000, 2002), including new representatives of the genus *Paramorariopsis*. Stoch (personal communication) confirmed that several as yet undescribed species of *Paramorariopsis* have been frequently collected in samples from the unsaturated zone of caves along the southern slopes of the Alps in northern Italy. This confirms that the genus is neither rare nor endemic to Slovenia but is connected to a specific karstic habitat which has not been sufficiently sampled. The problem of adequate sampling in the unsaturated karstic zone is discussed later in this paper. The main purpose of this paper is to describe and illustrate a new species, *Paramorariopsis irenae*, collected from the Letuška Jama cave in northeastern Slovenia.

Material and methods

Ten litres of water from a pool filled exclusively by percolating water were filtered through a net with mesh size of 60 µm (for details on sampling technique see Brancelj 2003). Water samples for chemical and physical analysis were obtained before collection of biological samples to avoid effects caused by disturbance of the sediment.

Samples were stored in plastic bottles immediately after sampling and formalin was added to a final concentration of about 4%. Within one week, animals were sorted under a stereomicroscope and stored in 70% alcohol. Before dissection, specimens were placed into a mixture of glycerol and 70% alcohol (ratio ~1:1 v/v), which was replaced within 1 h by pure glycerol. The specimens were dissected at 100× magnification under an Olympus SZH2 stereomicroscope. Examination of all appendages and body ornamentation was done under a magnification of 1000×. All drawings, except for the female habitus, were made at the same magnification (1000×) with a drawing tube mounted on an Olympus microscope (BHS40). The final version of the drawings was made using the CorelDRAW®12 graphic program.

Site description

The Letuška Jama cave is situated in the Triassic limestone at an elevation of 400 m in the northeastern part of Slovenia. It is a rather horizontal cave with a 1 m wide by 0.7 m high

entrance. The whole cave consists of one chamber, 20 m long, 15 m wide and with a maximum height of about 5 m. Four small pools filled with percolating water are situated directly beneath two chimney-like structures, where roof thickness is only about 2 m. In other places, the thickness of the roof is 4–5 m. The slopes above the cave are covered with deciduous forest with beech (*Fagus sylvatica*) as the predominant species.

Water temperature on the sampling date was 5°C (for other parameters see Table I). Accompanying fauna included the stygobiont copepods *Bryocamptus pygmaeus* (Sars, 1863) and *Speocyclops infernus* (Kiefer, 1930).

Descriptive part

Paramorariopsis irenae n.sp. (Figures 1–14)

Material examined

Two females from a pool filled with percolating water in the Letuška Jama cave (type locality), near the town of Mozirje, northeast Slovenia, collected 24 March 2004.

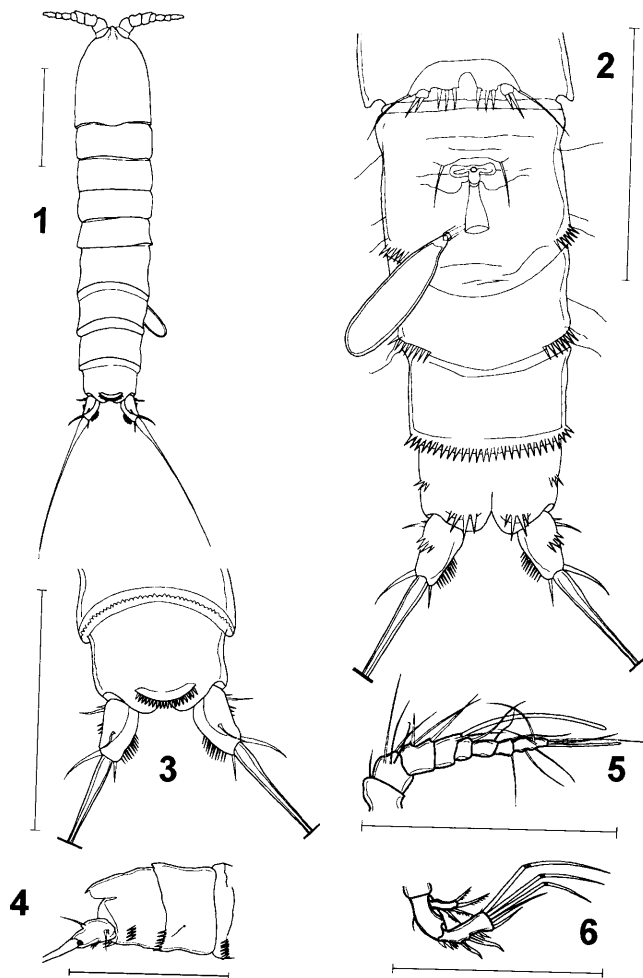
Holotype: adult female (total length of 402 µm), preserved in alcohol; deposited in the Natural History Museum (London), registration no. 2005.218. Paratype: adult female completely dissected; legs and mouth parts mounted on a slide in glycerol and sealed with nail polish; deposited in the Natural History Museum (London), registration no. 2005.219. Slide was partly broken during transport. Abdomen of the dissected female is in the author's collection.

Description

Female. Body length 402–410 µm ($n=2$); elongated, cylindrical, colourless (Figure 1). Naupliar eye absent. Hind margins of all abdominal somites dorsally serrated. Genital double-somite and second abdominal somite distally on both ventro-lateral parts with five to six spinules. Ventral margin of both somites smooth and without spinules. Third abdominal somite ventrally with a row of strong and robust spinules. Three pairs of sensillae (=hair-like structure; two long and one short) on the lateral side of genital double-somite and second abdominal somite (Figure 2). Anal somite with three to four spinules on ventro-lateral side, positioned at about two-thirds of the length of the segment. Four strong and robust spinules, unequal in length, at base of each caudal ramus (Figure 2). Anal

Table I. Characteristics of water from pools filled with dripping water from the Letuška Jama cave (near the town of Mozirje, northeastern Slovenia); sampled on 24 March 2004.

Nitrate (mg NO ₃ ⁻ l ⁻¹)	5.14
Total nitrogen (mg N l ⁻¹)	2.46
pH	8.17
Alkalinity (µeq l ⁻¹)	3115.00
Conductivity (µS cm ⁻¹ ; T=25°C)	412.00
Calcium (mg Ca l ⁻¹)	56.94
Magnesium (mg Mg l ⁻¹)	14.92



Figures 1-6. *Paramorariopsis irenae* n. sp. (female). (1) Habitus. (2) Abdomen, ventrally. (3) Abdomen, dorsally. (4) Abdomen, laterally (right side). (5) Antennula. (6) Antenna. Scale bars: 0.1 mm.

operculum large, rounded, with about 20 strong spinules around free margin, reaching to distal end of anal somite (Figure 3).

Receptaculum seminis (Figure 2) identical to that of *Paramorariopsis anae* and resembling condition in genus *Moraria*. Genital apertures closed off by operculum derived from fused P6, with one seta on each side. Attached spermatophore characteristic for Canthocamptidae.

Caudal rami divergent, each about 1.5 times as long as wide, tapering posteriorly (Figures 2-4). Inner margin with about 10 strong and robust spinules in distal half of ramus. Outer margin with two setae positioned close to base of caudal ramus; one of them short and spine-like, the other about four times longer, not exceeding basal width of ramus. Dorsal surface of ramus with weakly expressed hyaline ridge along its entire length. Dorsal seta inserting at about half distance from the base of ramus, as long as lateral one. Ventrolateral surface with oblique row of four small spinules positioned halfway along ramus.

Outer terminal seta spiniform, slightly curved, as long as ramus. Inner terminal seta short, spiniform. Middle terminal seta as long as abdomen, with few spinules at tip.

Rostrum small.

Antennule (Figure 5) short and moderately stout, eight-segmented. Aesthetasc on segment four cylindrical, slightly curved, with rounded tip and longer than antennule. Second aesthetasc on terminal segment slightly overreaching tip of first aesthetasc.

Antenna (Figure 6) comprising coxa, allobasis, and one-segmented exo- and endopod; short and robust. Two strong spines on the outer margin of endopod accompanied by several strong and short spinules; terminal armature consisting of one spine, one simple and three geniculate setae. Exopod with four spiniform setae, armed with coarse spinules.

Mandible (Figure 7) short and robust, with three strongly chitinised teeth on gnathobase. Mandibular palp relatively long, two-segmented, with one seta on proximal segment (basis) and four setae, sub-equal in length, on distal segment (endopod).

Maxillule with five strong and robust spines on praecoxal arthrite and additional strong seta, originating from the dorsal side of the segment. Basis with two strong, beak-like outgrowths, with several short bristles on distal part and four setae at the base.

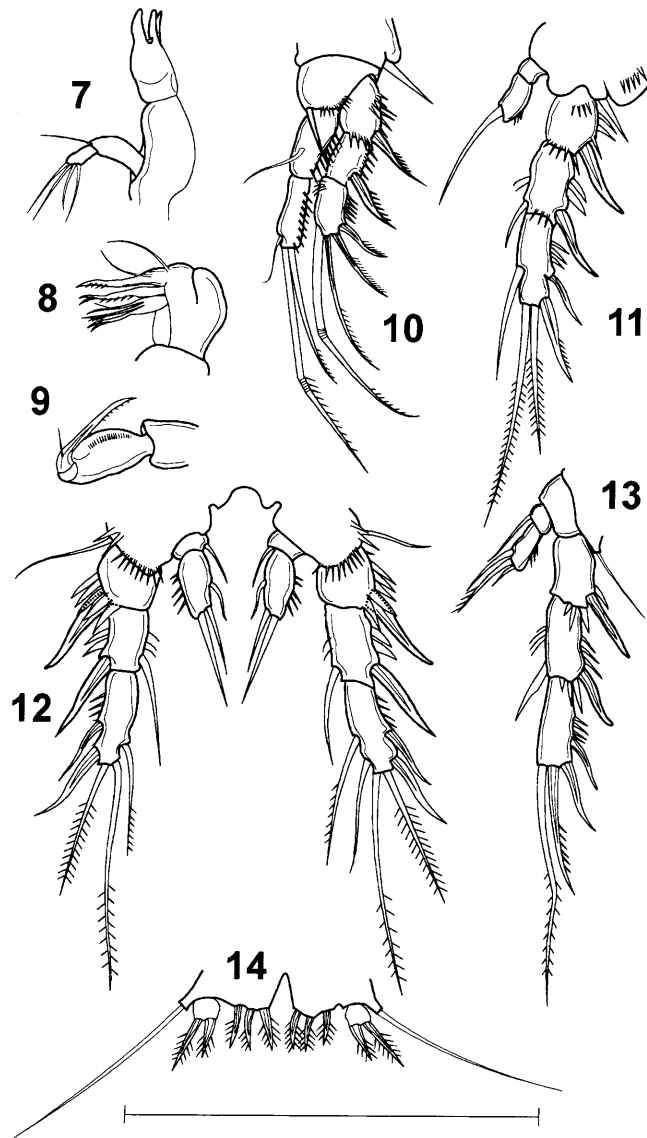
Maxilla two-segmented (Figure 8); proximal one wide and robust. Distal segment with three lobes. Outer one with beak-like outgrowth with two setae, middle one with two strong spines, the inner one with four strong spines.

Maxilliped comprising syncoxa, basis, and one-segmented endopod (Figure 9). Syncoxa slightly longer than wide, with no spinules or setae. Basis with about 20 spinules positioned near palmar margin. Endopod drawn out into strong, acutely curved claw; slightly longer than basis and armed with spinules in distal half; accessory armature represented by short seta.

P1 (Figure 10) with three-segmented exopod and two-segmented endopod. Endopod as long as exopod. Basis with a strong inner and outer basal spine. Exopod with one strong outer spine and several small spinules on proximal and median segments. Distal segment with one strong spine laterally, two long setae terminally and one long, geniculate, inner seta subdistally. Outer terminal seta as long as exopod and spine-like, with several small spinules unilaterally in distal half. Proximal segment of endopod with a row of about eight strong spinules along outer margin; long seta at two-thirds length of inner margin. Distal segment with three setae; innermost small, median seta very long and geniculate, outer one spiniform with strong spinules unilaterally at tip. Outer margin with a row of about 10 spinules.

P2 (Figure 11) outer basal seta spiniform; with three-segmented exopod and two-segmented endopod. Endopod slightly longer than proximal segment of exopod. Proximal segment of exopod as long as wide; with one strong outer spine, with slightly rounded tip; with three short spinules on outer margin and one group with four to five spines on proximal anterior surface and one group around distal margin. Middle segment with one strong outer spine and one short, inner, spiniform seta; with two short spinules along outer margin. Distal segment with two outer spines, two terminal setae (outer seta shorter than inner one; inner one as long as exopod) and spiniform inner seta. Proximal segment of endopod as long as wide, unarmed. Distal segment twice longer than wide, with one basal seta, positioned sub-terminally and about 1.5 times longer than endopod. Inner margin of endopod with three to four small spinules around distal outer margin.

P3 (Figure 12) outer basal seta setiform; exopod similar to P2 but additional seta on inner margin of terminal segment can be present. Endopod two-segmented; proximal segment very short, with short inner seta. Terminal segment with two terminal setae of



Figures 7–14. *Paramorariopsis irenae* n. sp. (female). (7) Mandible. (8) Maxilla. (9) Maxilliped. (10) P1. (11) P2. (12) P3. (13) P4. (14) P5. Scale bar: 0.1 mm.

unequal length (inner seta shorter; as long as terminal segment); inner margin with one short spine-like seta at half length of the segment.

P4 (Figure 13) outer basal seta setiform; with three-segmented exopod and two-segmented endopod. Proximal and middle segments of exopod similar to those in P2 and P3. Terminal segment with two outer and two distal setae (inner one about twice as long as outer one; outer one distally with row of small but strong spinules along outer margin); no seta or spine on inner margin. Proximal segment of endopod with one inner seta, reaching tip of the distal segment. Distal endopod segment with three setae positioned laterally on inner margin of endopod; proximal two approximately as long as endopod; third one shorter than terminal segment of endopod.

P5 (Figure 14) with separate exopod and baseoendopod; endopodal lobe small, with three short, strong spines of equal length, bearing five to six strong spinules on each side. Exopod small, as long as wide, with two strong and robust setae, slightly longer but similar in shape to those on endopodal lobe. Outer lateral seta on baseoendopod very long.

Male. Not known.

Etymology

The new species is dedicated to my wife Irena.

Discussion

Relations within genus Paramorariopsis

Paramorariopsis anae Brancelj, 1991 and *P. irenae* n. sp. are two closely related species, with several distinctive characters. Both are exclusive inhabitants of the unsaturated karstic zone, specifically the epikarst (for details see below). The most obvious common characteristic is the structure and form of P5 which is identical in both species. A common character for both taxa is also the shape of the spines on the proximal and middle exopodal segments of P2 and P3 which have rounded tips. In *P. irenae* the tips are slightly less rounded than in *P. anae*. Both species have a similar shape of the female genital field which resembles the condition in the genera *Morariopsis* and *Moraria*, indicating a close relationship with *Paramorariopsis*.

The main differences between both species of the genus *Paramorariopsis* are:

- *Paramorariopsis irenae* has a longer and more slender antennule than *P. anae*.
- Endopods of P2 and P3 two-segmented in *P. irenae*, but only one-segmented in *P. anae*.
- No spine on inner margin of terminal exopod segment of P4 in *P. irenae*.
- Free margin of anal operculum with about 20 spinules in *P. irenae*, but smooth in *P. anae*.
- Caudal ramus in *P. irenae* about 1.5 times as long as wide, but as long as wide in *P. anae*.
- Inner margin of caudal ramus in *P. irenae* with about 10 strong and relatively robust spinules in distal half of ramus, while in *P. anae* the inner margin has no spinules.
- Syncoxa of maxilliped in *P. anae* with seta, which is absent in *P. irenae*.

Comparing both species of the genus, *P. anae* shows more morphological reductions; i.e. in the size of antennule and in the number of endopod segments in P2 and P3. The reductions may suggest that *P. anae* is a more specialised inhabitant of the epikarst. *Paramorariopsis irenae* displays variability in the number of inner setae on the P2 exopod (Figure 12). Having examined only two specimens thus far, it is at present impossible to decide whether this reflects genuine intraspecific variability or whether this character has not yet attained evolutionary stasis.

Epikarst—the specific habitat inhabited by Paramorariopsis (and Morariopsis)

“The epikarst, or subcutaneous zone, is the upper-most part of karstified rock. It has been variously defined but in general it is the boundary between soil and rock in karst,

honeycombed with small fractures and solution pockets" (Brancelj and Culver 2005). In nature it is a relatively thin layer, 1 m to several metres in depth, where most water can be found as capillary water and where connection between voids in a horizontal direction is limited. The epikarst is always positioned on the plateaus or slopes where no surface water is found. Exceptionally in some depressions small temporary pools can persist for short periods (usually hours or days).

So far in Slovenia about 40 taxa of Copepoda (Cyclopoida and Harpacticoida) have been found in the epikarst, which represents about 90% of all fauna found there (Brancelj and Pipan 2004). Most of the stygobitic genera of Copepoda from the epikarst can be found in other types of subterranean environment, including the phreatic zone and karstic springs. So far, only two genera (*Paramorariopsis* and *Morariopsis*) are recognised as strictly epikarstic inhabitants and they have some specific adaptations (see Morphological adaptations).

Inhabitants of the epikarst belong to a unique community. Their habitat is from time to time only partly filled with water (equivalent to amphibious zone in epigeal aquatic habitats) but it is never completely dry. The amount of water in the fractures is related to precipitation.

Epikarst communities cannot be studied *in situ* because no adequate sampling technique is known for such an environment (Brancelj and Culver 2005). So far they have been studied only in the form of drift from the epikarst zone which can be sampled from the pools on the floor of cave galleries or directly from the drips from the ceiling. Members of such "washed-out" communities are considered as "sink populations" which are exposed to severe competition/predation in the pools from the moment they arrive there and their community structure changes with time (Brancelj 2002). This is why some taxa were considered as "rare" (like *Morariopsis* and *Paramorariopsis*). In fact members of both taxa are expected to be quite abundant in the original epikarstic environment where they are not (presumably) exposed to severe competition. But they become vulnerable, and consequently out-competed, in other types of habitats, such as the pools on the floor of cave galleries. In Slovenia, the site of most systematic studies of the epikarstic Copepoda fauna, it appears that *Speocyclops infernus* is probably the most competitive species which determines the secondary structure of Copepoda populations in the pools after being washed out from the epikarst. Among the most vulnerable taxa there are representatives of the genera *Parastenocaris*, *Morariopsis*, and *Paramorariopsis*, while representatives of other taxa seem to be more resistant to interspecific competition. After heavy rains representatives of most genera (including those three already mentioned) are represented in the pools with relatively high numbers of specimens. After prolonged periods of drought, when percolation completely stops, most of the taxa are still present there. Some of them are in low and some in high abundance (especially *S. infernus*) but there are no representatives of *Parastenocaris*, *Morariopsis*, and *Paramorariopsis*. This indicates that it is important to sample the epikarst fauna immediately after a rainy period.

Due to geological activities (orogenesis) and erosion, the unsaturated karstic zone is fragmented in geological units (blocks) of different sizes, characterised by a complete absence of surface water bodies. Geological blocks can be measured on a scale of several hundreds of metres to several kilometres. In the unsaturated zone (including the epikarst) there is a characteristic predominance of vertical water movement along small cracks and fissures and with relatively limited horizontal connections. Each geological block thus functions as an isolated hydrological unit (an equivalent to epigeal watershed). Actually it can be compared to an "island with its own fauna, where distribution/migration of

individuals, including genetic material, is limited" (Brancelj and Culver 2005). The restricted possibility for exchange of genetic material among the populations is the key factor for speciation. The result of this isolation of populations in the geological past is a high degree of endemism (Brancelj 2001).

Geographical distribution

So far, the genus *Paramorariopsis* is known from three locations in Slovenia. The first location of *P. anae* is the small Jama pod Krogom cave (Slovenian Cadastral no. SCN 1793) in the southwestern part of Slovenia. The second location of *P. anae* (personal observation) is a pool in a small cave called Divja Jama nad Plavmi (SCN 828) about 60 km north of the type locality. Both locations are in the area where the westernmost part of the Dinaric Alps meets the southeastern part of the Alps. The dominant climate in the area is the Mediterranean with some influence of the Alps.

The new species, *P. irenae*, was found in a small cave in the easternmost part of the Alps, where the Alpine climate prevails. The type locality of *P. irenae* is 50–60 km from both known localities of *P. anae*. From the geological–tectonic point of view, both species are well separated by the Dinaric Alps which penetrate the Alpine region from the southeast to the western part of Slovenia. Tectonic activities probably separated the common ancestor of both species. In Italy (west of Slovenia), several specimens of the genus *Paramorariopsis* have been recorded (F. Stoch, personal communication), but no information exists on the actual number of species and their relation to the Slovenian congeners.

Morphological adaptations

The genera *Morariopsis* and *Paramorariopsis* have several adaptations which distinguish them as highly specialised inhabitants of small crevices in the unsaturated zone of karst—more specifically the epikarst zone. One of the most important problems faced by epikarstic organisms is the risk of being washed away from the unsaturated zone (phenomenon of vertical drift). Animals living in such an environment must have some morphological adaptations to prevent their spontaneous transport downward. Adaptations are different and multiple. The most obvious are some reductions, which could be attributed to the environment, where food is scarce and rational use of energy is obligate (Hüppop 2005). Both genera show a characteristic reduction in endopodal segmentation to two or even a single segment. Parallel with segmental reduction there is also a reduction in the number of spines and setae on the terminal segments of both endopods and exopods. In addition to reduction of spines and setae on the swimming legs (including P5), there is a similar reduction of spines and setae on the caudal rami. Both genera, *Morariopsis* and *Paramorariopsis*, have only one long terminal seta, while the inner and outer setae are frequently spiniform (e.g. *P. irenae*, *M. scotenophila*, and *M. dumonti*). The tips of the terminal setae of the caudal rami are far apart which can be regarded as a potential adaptation to avoid being washed out from small crevices. Short and robust setae on the endopodal lobe of P5 as well as the very strong spinules at the base of the caudal rami are also an adaptation to prevent downward drift from crevices.

The short and robust mandible, with three strongly chitinised teeth on the gnathobase, is indicative of a detritivorous feeding mode, possibly combined with predation. A predatory feeding mode is supported by the relatively long beak-like spine on the maxilliped, armed with strong teeth along the inner margin. In addition, the basis is equipped with a row of

sharp and long spinules along the palmar margin, possibly involved in efficient gripping of prey items. Shape and structure of the mandible is similar to that in *Morariopsis dumonti*, another inhabitant of the unsaturated zone in the karst (Brancelj 2000).

Sampling techniques

Collecting fauna from the unsaturated zone, including the epikarst, requires special techniques. The most frustrating factor in working on fauna from the unsaturated zone in the karst is the amount of water that can be collected. Water in the unsaturated zone in the karst (including the epikarst) appears in the form of drips, fine film on the speleothems, small pools on speleothems, or on the clay floor. To collect the small amount of water there, special sampling methods must be used, such as filtering dripping water, collecting water by means of pipettes from small pools, etc. (for details see Brancelj 2003; Brancelj and Culver 2005). Apart from using appropriate sampling techniques and devices, most important is the mesh size used, which should be between 60 and 100 μm . Specimens of taxa living in small crevices in the limestone are usually smaller than their epigeal relatives, thus nets with finer mesh size are recommended.

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