Biodiversity in mountain groundwater: the Mercantour National Park (France) as a European hotspot

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ABSTRACT

Mercantour National Park (France) is recognized as a highly heterogeneous region with extremely varied geology, geomorphology and climatology, resulting in an exceptional biodiversity. From a hydrogeological point of view, it is also an area organized into small and discontinuous aquifers, the obligate groundwater fauna of which (stygobionts) remains absolutely unknown. This work explores the species richness of groundwaters in the Mercantour National Park, using a sampling design at the catchment (six major valleys) and aquifer (aquifers in consolidated rocks and unconsolidated sediments) scales. A major finding of this study is the discovery of 44 species restricted to groundwater, of which 43 are new to the Park and ten are new to Science. Although a relatively small number of sites were sampled (53), the area may be considered as a new hotspot of groundwater biodiversity at the European level. The particular structure of the groundwater network, the high environmental heterogeneity of the region and its Mediterranean position may explain such a high biodiversity. The species rarefaction curve showed that many species have yet to be discovered in groundwater of the Mercantour National Park. With more than 78% of species collected in the hyporheic zone, this study also highlights the importance of porous aquifers in sustaining the groundwater biodiversity of mountainous regions.

INTRODUCTION

Situated at the convergence of Alpine, Mediterranean and continental climatic influences, the Mercantour massif has long been recognized as a European hotspot of biodiversity for both fauna and flora (Ozenda & Borel 2006; Giudicelli & Derrien 2009; Deharveng et al. 2015; Villemant et al. 2015, this issue). This region is of great biogeographical interest for its role as a refuge during the Last Glacial Maximum, as a major center of endemism at the national level and as a conservation area for numerous threatened and patrimonial species (Biancheri & Claudin 2002). In this exceptional biogeographical context, considered unique in Europe, the “Parc du Mercantour” in France, and the “Parco Naturale Alpi Marittime” in Italy, have promoted the development of an exhaustive inventory of biological resources (ATBI program: All Taxa Biodiversity Inventory), also supported by the “European Distributed Institute of Taxonomy” (EDIT). The ATBI-Mercantour program aims at providing a complete inventory of biodiversity for all taxa (Leccia et al. 2009), with a special focus on least known groups (e.g., insect fauna, mosses, lichens…) and least studied ecosystems, such as groundwater.

Present knowledge of the geographical distribution of the fauna living exclusively in groundwaters (i.e., stygobionts) is extremely uneven between taxonomic groups and geographical areas (Ferreira et al. 2005, 2007; Deharveng et al. 2009). Records of stygobionts are biased towards large invertebrates (macro-fauna) relative to smaller organisms (micro- and meiofauna), mostly because they are more easily detected by cavers or non-specialists. The erosion of taxonomic expertise for some taxa (e.g., oligochaetes, water mites, nematodes, molluscs…) also explains why they are rarely reported from groundwater despite being abundant in this environment. Such a situation has led to the Wallacean and Linnean shortfalls (Lomolino et al. 2006), significantly hindering advances in groundwater biodiversity assessment (Stoch & Galassi 2010). Finally, some habitats (e.g., karst aquifers) are by far more investigated than others (e.g., porous aquifers). Sampling bias and taxonomic impediments are severely restricting our understanding of groundwater biodiversity patterns at regional to continental...
scales. Recent studies of European groundwater biodiversity patterns identified a number of regional hotspots, but they also designated regions with potentially high species richness where sampling should be given a high priority (Deharveng et al. 2009; Michel et al. 2009). The Mercantour massif is one of these promising regions, the groundwater fauna of which has yet remained virtually unexplored.

This study explores the species richness of groundwater in the Mercantour National Park, after the implementation of a sampling design comprising environmental heterogeneity at the catchment (six major valleys) and aquifer scales (aquifers in consolidated rocks vs non-consolidated sediments). Two predictions were made. First, this unexplored region would be species-rich and could be recognized, as for its surface environment, as a European hotspot of groundwater biodiversity. Second, sampling would reveal many species new to the National Park and to Science. We also assessed the importance of alluvial aquifers for sustaining groundwater biodiversity, by comparing species richness of aquifers in consolidated rocks and unconsolidated sediments. Despite the areal prevalence of consolidated-rock aquifers (Fig. 1B), we predicted that species richness would be higher in the hyporheic zone of rivers because the latter represents a zone of hydrological convergence.

STUDY AREA AND SAMPLING DESIGN

The Mercantour National Park (1465 km²) is situated at the southern end of the Alpine arc (Fig. 1A). In this region, landscapes are extremely heterogeneous, partly due to their complex and varied geology. Three major geological units can be distinguished: 1) a central crystalline massif “Argentera-Mercantour” (granite, gneiss); 2) external and intensively folded sedimentary formations of Secondary and Tertiary ages; and 3) intra-Alpine thrust sheets coming from Italy (Po) and covering the subalpine zone. The extreme diversity of landforms is also due to a rich glacial and periglacial history and to the erosive influence of the Mediterranean climate. From a geomorphological point of view, the Mercantour area is considered as a synthesis of all the structural and morphological units known in the Alps (full description in Biancheri & Claudin 2002). The resulting landscapes are highly fragmented and dominated by steep slopes (45° to 25°) in most of the park area. The strong thermal variation caused by a steep altitudinal range (more than 3100 m to less than 500 m) combines with several climatic influences (Alpine, Mediterranean, continental) and varied orientations to determine contrasting climate patches within the area. Environmental heterogeneity is extreme and results in a highly diversified mosaic of habitats in surface environments, which may also be inferred a high structural complexity of the groundwater network.

Groundwater is mainly represented by aquifers in fissured consolidated rocks (karst aquifers being practically absent), although the valley bottoms are, in some places, filled with alluvia and colluvia, which may provide important groundwater habitats for stygobionts. Local aquifers alternate with areas of non-aquiferous rocks (Fig. 1B). Most aquifers of the Mercantour massif are poorly productive (Comité de Bassin RMC 1995a, b, c) since they are characterized by moderate to low permeability (map of European groundwater habitats, Cornu et al. 2013). They do not correspond to extensive groundwater networks with important reservoirs, but form a set of small, superficial and discontinuous hydrogeological units (Comité de Bassin 1995a; b; c). This groundwater habitat fragmentation might have inflated regional species richness through allopatric speciation.

The sampling design employed derives from the PASCALIS protocols, which were specifically designed to assess biodiversity at a regional scale (Malard et al. 2002). The selection of sampling sites follows a hierarchical approach which accounts for major sources of environmental heterogeneity by integrating geographical and hydrogeological features of the landscape (Dole-Olivier et al. 2009). Basically, the stratified sampling design comprised three hierarchical levels: catchment (level 1), aquifer type (level 2) and habitat type (level 3). Six catchments were selected within the Mercantour massif (Tinée, Vésubie, Var, Roya-Bévéra, Ubaye, Verdon, Fig. 1A), each comprising two distinct types of aquifers (i.e. consolidated-rock and unconsolidated sediments aquifers). Because caves (in consolidated rocks) and wells (in unconsolidated sediments) were not available in this region, only one habitat per aquifer type was sampled, the springs in consolidated-rock aquifers and the hyporheic zone in porous aquifers (i.e. aquifers in unconsolidated sediments), reducing the scheme to two hierarchical levels. Additional sources of environmental heterogeneity were included in the design by selecting, whenever possible, sites with contrasted specific conductivity (from 43 to 2140 μS·cm⁻¹) and altitude (from 190 m to 2500 m). Sampling was carried out in spring-summer 2009 for the Tinée, Vésubie, Var and Roya-Bévéra catchments, and in summer 2010 for the Ubaye and Verdon catchments. Six sites were sampled in the Tinée, Vésubie, Var catchments, nine in the Roya-Bévéra catchment (two hyporheic sites, seven springs) and 13 in the Ubaye and Verdon catchments (Table 1).

MATERIAL AND METHODS

SPRINGS

Three complementary sampling techniques were used to maximize the number of species collected at each spring. A drift net was used to collect organisms naturally flushed out from the massif by drift (Rouch et al. 1968); a Surber sample was taken to collect organisms at the surface of spring sediments and in the aquatic vegetation (Surber 1956); and a Bou-Rouch pump (Bou & Rouch 1967) was used to collect organisms at depth from the interstices of spring sediments (when present). The drift net (150 μm) was positioned at the spring outlet for eight to twelve hours (Rouch 1980). Once animals in the drift were collected, the Surber sample was taken by moving cobbles upstream of the Surber net (150 μm) in order to dislodge animals at the surface of springbed sediments. Finally,
<table>
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<th>Catchment / Station</th>
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<th>Habitat</th>
<th>Repl.</th>
<th>X (WGS84)</th>
<th>Y (WGS84)</th>
<th>Elevation (m)</th>
<th>Date</th>
<th>Spec. cond (μS/cm)</th>
<th>Temp.</th>
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Hotspot of groundwater biodiversity in the Mercantour National Park

FIG. 1. — A, Study area and location of sampling sites. Sites are numbered as in Table 1; B, Map of groundwater habitats (extracted from Cornu et al. 2013) with the limits of the Mercantour National Park in white.
sampling at depth into the springbed sediments was carried out whenever the sediment thickness was > 30 cm. A mobile pipe was inserted into the springbed sediments (maximum depth 50 cm below the bed surface) and 5-10 L of interstitial water and fine particles were extracted with a Bou-Rouch pump. Whatever the sampling method used, samples were elutriated, filtered (200 μm) in the field and the content net was immediately fixed with 95° alcohol.

HYPORHEIC ZONE
As recommended in the PASCALIS protocols (Malard et al. 2002), sampling optimization consisted in selecting stream reaches and bed-forms where groundwater was potentially upwelling. This is because stygobionts are known to be more diversified and abundant in groundwater upwelling zones (e.g., Dole-Olivier & Marmonier 1992; Stanley & Boulton 1993; Brunke & Gonser 1997; Malard et al. 2003; and Dole-Olivier 2011). At the reach scale, groundwater generally upwells at the stream surface in reaches located at the downstream end of bounded valley segments, at the margins of floodplains and in side-arms disconnected at their upstream end. At the bed-form scale, groundwater upwelling preferentially occurs downstream of obstacles such as dams, logjams, boulders, slope breaks and gravel bars. Once sites with potential groundwater upwelling were selected, at least three replicate samples were selected to maximize the chances of obtaining all species present at a site (Table 1). The mobile pipe was inserted to a depth of 30-50 cm into the streambed and samples were taken using a Bou-Rouch pump. At least 10 to 12 L of water and sediments were pumped, elutriated and filtered with a 200 μm mesh size net. Samples were immediately fixed with 95° alcohol.

SAMPLES AND DATA PROCESSING
All specimens (stygobionts and non-stygobionts) were sorted under a stereomicroscope and identified, whenever possible, to species level. In the present study, species identification is reported only for stygobionts. For several taxonomic groups, species names could not be attributed to damaged specimens, females and juveniles. However, in most cases, it was possible to distinguish between several morphotypes, to species level. In the present study, species identifications were based on morphological criteria, although DNA sequences (COI, 16S and 28S) were obtained for all species (Dole-Olivier et al. 2009). Species assemblages between the hyporheic zone and springs were compared using species-rank frequency ordinations.

ABBREVIATIONS LIST
Institutions in which the specimens are presently deposited
IRScNB Royal Belgian Institute of Natural Sciences, Brussels;
MNCN National Museum of Natural History, Madrid;
UCBLZ University Claude Bernard Lyon-Zoology, Lyon;
UNIVAQ University of L’Aquila, L’Aquila.

RESULTS

TAXONOMIC ACCOUNT
Phylum ANNELIDA Lamarck, 1802
Class POLYCHAETA Grube, 1850
Family NERILLIDAE Levinsen, 1883
Genus Troglochaetus Delachaux 1921

Troglochaetus beranecki Delachaux, 1921
(Fig. 2A)

Aberrantidrilus stephaniae Martin, 2015

REMARKS
Collected for the first time in the Mercantour National Park.

ABBREVIATIONS LIST

MATERIAL EXAMINED. — Site 8: 66 specimens; site 21: 2 specimens; site 22: 15 specimens; site 27: 4 specimens; site 28: 1 specimen; site 37: 1 specimen; site 46: 9 specimens. Material deposited at IRScNB, I.G. 32392.

Material examined. — Site 9: 17 specimens, mounted on slides, as well (Creuzé des Châtelliers et al. 2015).

Aberrantidrilus stephaniae Martin in Martin et al., 2015: 556.

Material examined. — Site 9: 17 specimens, mounted on slides, and many mostly immature specimens and fragments in absolute alcohol, from unsorted material. Material deposited at IRScNB, I.G. 32392 and MNHN HEL 524 (holotype) see also Martin et al. 2015, this issue.

REMARKS
To date, only known from hyporheic habitat of the Bévéra River in the Mercantour National Park. Aberrantidrilus is a thalassoid, subterranean freshwater genus, representative of the primarily marine tubificid subfamily, the Phalldriliniae, which is known to be occasionally present in ground waters as well (Creuzé des Châtelliers et al. 2009).
FIG. 2. — Some representative species collected in the Mercantour National Park: A, Troglochaetus beranecki Delachaux, 1921, length 0.6 mm; B, Parabathynella sp., length 1.5 mm; C, Nipargus foreli Humbert, 1877, length 8 mm; D, Proasellus sp., length 4 mm. Photographs: A-C, M.-J. Dole-Olivier; D, F. Malard.
Family LUMBRICULIDAE Vejdovský, 1884
Genus Stylodrilus Claparède, 1862

Stylodrilus sp. 1

MATERIAL EXAMINED. — Site 2: 1 specimen, slide 11.007.03 (first 14 segments) and vial AB31525649 (posterior part in 96% ethanol). Material deposited at IRScNB, I.G. 32392.

REMARKS
This specimen most probably represents a new species, but additional material is required to formalize its status (see Martin et al. 2015, this issue).

Genus Trichodrilus Claparède, 1862

Trichodrilus sp. 1

MATERIAL EXAMINED. — Site 14: 1 sexually mature specimen, slide 11.251.03b (first 14 segments). Material deposited at IRScNB, I.G. 32392.

REMARKS
This specimen probably belongs to a new species, as argued in Martin et al. (2015). It is characterized by tubular to quadrangular atria with short proximal ducts, and two pairs of spermathecae in XI and XII. Among Trichodrilus species with such features, T. leruthi Hrabě, 1939, T. intermedius (Fauvel, 1903) and T. tacensis Hrabě, 1963 are probably the closest species to this specimen; however, their atria are slender and do not have a duct. More material is needed to formalize the taxonomic status of the present specimen (see Martin et al. 2015).

Trichodrilus cf. tenuis Hrabě, 1960

MATERIAL EXAMINED. — Site 8: 8 specimens, site 9: 4 specimens, site 23: 2 specimens. Material deposited at IRScNB, I.G. 32392.

REMARKS
This species is very close to T. tenuis Hrabě, 1960, from which it can be distinguished by the absence of a so-called “pseudo-vestibule” at junction with spermathecal ducts, as mentioned by Juget & des Châtelliers (2001) in a complementary description of T. tenuis based on specimens from the eastern part of France (Lyon area). It falls in the Trichodrilus sp. group II sensu Rodriguez & Giani, 1994, a group of ill-defined species that badly needs revision. This is probably a new species, but its description should ideally be carried out within a revision of the latter group, based on additional material and genetic characterization via DNA barcoding (see Martin et al. 2015, this issue).

Trichodrilus sp.

MATERIAL EXAMINED. — Site 8: 1 immature specimen, fragments; site 9: fragments; site 21: 1 immature specimen, fragments; site 22: fragments; site 25: 1 immature specimen, fragments; site 27: 1 juvenile, fragments; site 28: fragments; site 37: fragments; site 46: fragments. Material deposited at IRScNB, I.G. 32392.

REMARKS
This Trichodrilus material is only represented by immature specimens or fragments and cannot be identified at the species level. Most Trichodrilus species occupy groundwater habitats and have localized distributions. Given the general trend in Trichodrilus for living in groundwater habitats, we consider these undetermined specimens as stygobionts.

Family ENCHYTRAEOIDEA Vejdovský, 1879
Genus Marionina Michaelsen in Pfeffer, 1890

Marionina sambugarae Schmelz, 2015

Marionina sambugarae Schmelz in Martin et al., 2015: 560.

MATERIAL EXAMINED. — Site 17: 1 adult specimen (slide 11.262.01), site 8: 1 adult specimen, site 20: 1 adult specimen, site 38: 1 adult specimen, site 39: 1 adult specimen, site 41: 1 adult specimen, site 44: 1 adult specimen.

REMARKS
This species was already mentioned in subterranean habitats of Slovenia, although it was identified as “Marionina cf. argentea” in a previous study (Giani et al. 2011). It is now reported from the Mercantour National Park, which suggests, together with its absence in surface habitats across Europe so far, that Marionina sambugarae is a true stygobiont species (see Martin et al. 2015, this issue).

Class ARACHNIDA Cuvier, 1812
Order ACARINA Leach, 1817
Family ATURIDAE Thor, 1900
Genus Ljania Thor, 1898

Ljania macilenta Koenike, 1908

Ljania macilenta Koenike, 1908: 703.

MATERIAL EXAMINED. — Site 25: 1 specimen, site 46: 1 specimen. Material deposited at MNCN.

REMARKS
Collected for the first time in the Mercantour National Park.

Family MOMONIIDAE Viets, 1926
Genus Stygomomonia Szalay, 1943

Stygomomonia latipes Szalay, 1943

Stygomomonia latipes Szalay, 1943: 59.
Material examined. — Site 27: 1 specimen; site 44: 1 specimen. Material deposited at MNCN.

Remarks
Collected for the first time in the Mercantour National Park.

Subphylum CRUSTACEA Brünnich, 1772
Class OSTRACODA Latreille, 1806
Order PODOCOPIDA Sars, 1866
Family CANDONIDAE Kaufman, 1900
Subfamily CANDONINAE Kaufman, 1900

Candoninae sp. 1

Remark
We separate here a juvenile specimen showing stygobite features that could belong to the genus Cryptocandona Kaufmann, 1900. No adult found.

Candoninae sp. 2
Material examined. — Site 1: 5 specimens; site 28: 1 specimen; site 43: 1 specimen; site 46: 1 specimen. Material deposited at UCBLZ, No. 2012-3.

Remark
We separate here stygobite specimens that are characterized by a triangular carapace and do not match species presently known in the western Palaearctic.

Candoninae sp. 3

Remark
We separate here a stygobite specimen that is characterized by a trapezoidal carapace and does not match species presently known in the western Palaearctic.

Fabaeformiscandona Krstic, 1972

Fabaeformiscandona sp. 1
Material examined. — Site 4: 19 specimens; site 10: 1 specimen; site 14: 2 specimens; site 32: 3 specimens; site 41: 5 specimens; site 44: 2 specimens. Material deposited at UCBLZ, No. 2012-3.

Remark
We separate here stygobite specimens of the genus Fabaeformiscandona that have a carapace shape similar to that of F. breuili (Paris, 1920). The species assignment requires confirmation.

Fabaeformiscandona sp. 2
Material examined. — Site 16: 6 specimens; site 17: 51 specimens; site 18: 31 specimens; site 19: 2 specimens; site 39: 7 specimens. Material deposited at UCBLZ, No. 2012-3.

Remark
We separate here stygobite specimens of the genus Fabaeformiscandona that have a carapace similar to Fabaeformiscandona individuals already sampled in other springs in the Alps (Vanoise and Bauges ranges). Species to be described.

Family CYPRIDIDAE Baird, 1845
Subfamily CYPRIDOPSINAE Kaufman, 1900

Cavernocypris subterranea
(Wolf, 1920)
Material examined. — Site 3: 1 specimen; site 16: 1 specimen; site 18: 29 specimens; site 19: 1 specimen; site 20: 26 specimens; site 29: 55 specimens; site 30: 44 specimens; site 31: 9 specimens; site 32: 2 specimens; site 37: 2 specimens; site 39: 1 specimen; site 40: 7 specimens; site 41: 1 specimen. Material deposited at UCBLZ, No. 2012-3; and at MNHN, MNHN-IU-2014-10149; MNHN-IU-2014-10150.

Remark
This stygobite species is widely distributed in Europe. These are the first records for the Mercantour National Park.

Class MAXILLOPODA Dahl, 1956
Subclass COPEPODA Milne Edwards, 1840
Order CYCLOPOIDA Burmeister, 1835
Family CYCLOPIDAE Rafinesque, 1815
Genus Diacyclops Kiefer, 1927

Diacyclops disjunctus (Thallwitz, 1927)
Cyclops languidus var. disjuncta Thallwitz, 1927: 59.
Material examined. — Site 1: 6 specimens; site 21: 5 specimens; site 22: 1 specimen. Material deposited at IRScNB (I.G. 31589).

Remarks
This species was originally described from mosses along a pond margin in Germany. Subsequently, D. disjunctus was also found in the hyporheic zone of streams and rivers, as a stygophylosous element, and in surface freshwater, as benthic element. Its distribution is relatively wide and scattered across Europe and the species is considered rare in terms of its frequency of occurrence. It has also been recorded from Japan, but this record was questioned by Stoch & Pospisil (2000). It is already known from Germany, France, Sweden, Austria, Czech Republic, Poland and Ukraine. Here recorded for the first time in the Mercantour National Park.
**Diacyclops** sp. 1

**MATERIAL EXAMINED.** — Site 28: 1 specimen; site 46: 5 specimens. Material deposited at IRScNB, I.G. 31589.

**REMARKS**
This species belongs to the *Diacyclops languidoides* species-group. The *languidoides*-group comprises *Diacyclops* species with an 11-segmented antennule and a segmental pattern of P1-P4 exopods and endopods of 2.2/3.2/3.3/3.3 (Stoch & Pospisil 2000). This group was claimed to be paraphyletic by Stoch & Pospisil (2000) in the absence of synapomorphies differentiating it from the *Diacyclops languidus*-group, which differs from the *languidoides*-group in having a 16-segmented antennule. The *D. languidoides*-group includes both stygobiotic and epigean species, most of them distinguishable on the basis of microcharacters only, which are sometimes difficult to assess clearly. The material collected from Mercantour is provisionally assigned to this group pending a revision of the genus *Diacyclops* as a whole, whose diagnosis partially overlaps that of the genus *Acanthocyclops* Kiefer, 1927 (Galassi & De Laurentiis 2004a).

**Genus Acanthocyclops** Kiefer, 1927

*Acanthocyclops agamus* Kiefer, 1938

**MATERIAL EXAMINED.** — Site 3: 8 specimens; site 7: 2 specimens. Material deposited at IRScNB, I.G. 31589.

**REMARKS**
*Acanthocyclops agamus* was originally described by Kiefer (1938) from a single male specimen from Castelcivita Cave. The original description raised doubts about the generic assignment of the species (Kiefer 1938; Dussart 1969; Dussart & Defaye 1985; Einsle 1996). Subsequently, Galassi & De Laurentiis (2004a) redescribed the species from topotypic males and females, confirming the validity of the species. At present, this stygobiotic species is known from the type locality in southern Italy, from the Mazzoccolo karstic spring (Latium, central Italy) and from the Gizio karstic spring (Abruzzi Region, central Italy) (Galassi & De Laurentiis 2004a). The species shows unique features in the reduced segmental pattern of the swimming legs as result of heterochrony. The female shows an earlier arrested development than the male and consequently shows a more drastic and stable reduction in segmentation. This species is here recorded for the first time from areas outside the central-southern Apennines (Italy), significantly expanding the distributional range of the species. At present, the species should be considered rare in both terms of abundance and patchiness in its geographic distribution, and for this reason it can be considered critically endangered according to the criteria of the IUCN (2001).

**Genus Speocyclops** Kiefer, 1937

*Speocyclops racovitzai racovitzai* (Chappuis, 1923)

**MATERIAL EXAMINED.** — Site 13: 1 specimen. Material deposited at IRScNB, I.G. 31589.

**REMARKS**
This species is widely distributed in France, as stygobiotic element, mostly being recorded from karstic habitats. Its presence in the Mercantour park was expected, since *S. racovitzai* is known from the Pyrenean area with several subspecies according to Chappuis & Kiefer (1952), who pulverized the nominotypical species into eight subspecies, all recorded from western France.

*Speocyclops kieferi* Lescher-Moutoué, 1968

**Genus Graeteriella** Brehm, 1926

*Graeteriella (Graeteriella) unisetigera* (Graeter, 1908)

**MATERIAL EXAMINED.** — Site 35: 2 specimens; site 43: 1 specimen. Material deposited at IRScNB, I.G. 31589.

**REMARKS**
*Graeteriella (Graeteriella) unisetigera* has been long considered a stygobiotic species, found in both alluvial and karstic aquifers across Europe, showing a wide distribution and almost exclusively found in groundwater. The harpacticoid-like body shape allows the species to move in the interstitial environment of unconsolidated aquifers, as well as in the hyporheic zone (Galassi 2001). The species was originally described from the Grotte de Vert (Switzerland, Jura). Surprisingly, Fiers & Ghenne (2000) collected this species from 13 terrestrial samples in central and southern Belgium, lending support to their hypothesis that this species should be better allocated in the cryptozoic fauna from an ecological point of view, instead of being typical stygobiotic element. Its geographical range, extending south into the Italian peninsula and the Balkans, may be explained on the basis of its plesiotypic habitat represented by the leaf carpet of beech forests. The striking overlapping Fiers & Ghenne (2000) observed in the distribution of *G. unisetigera* and the range of *Fagus sylvatica* may support this alternative species ecology. Nevertheless, the stygomorphic traits of the species and the high frequency of occurrence in true groundwater habitats require confirmation of the still controversial ecological characterization of the species.

*Speocyclops kieferi* Lescher-Moutoué, 1968

**Genus Speocyclops** Kiefer, 1937

*Speocyclops racovitzai racovitzai* (Chappuis, 1923)

**MATERIAL EXAMINED.** — Site 28: 1 specimen; site 46: 5 specimens. Material deposited at IRScNB, I.G. 31589.

**REMARKS**
This alternative species ecology. Nevertheless, the stygomorphic traits of the species and the high frequency of occurrence in true groundwater habitats require confirmation of the still controversial ecological characterization of the species.
IRScNB, I.G. 31589.

**Remark**

This stygobiotic species is known from several localities in France. It was first collected there in 1964 at 1050 m a.s.l. at the Col de la Crouzette (Ariège) in the hypothermalorheic habitat (Mestrov 1962) and subsequently sampled in several springs of the Sourroque Massif (Ariège) and in the Malsang spring in Albi (Tarn) (Lescher-Moutoué 1968). Bou (1968) also collected this species from the Massif Central (France) in the cave Causses de Limogne and in the hyporheic zone of the Tarn basin. Morphologically, this species is close to S. racovitzai according to Lescher-Moutoué (1968).

**Genus Itocyclops** Reid & Ishida, 2000

*Itocyclops* sp. 1

**Material Examined.** — Site 13: 1 specimen, site 21: 4 specimens, site 27: 1 specimen, site 43: 1 specimen. Material deposited at IRScNB, I.G. 31589.

**Remarks**

The genus *Itocyclops* was established by Reid & Ishida (2000) to accommodate the species *Speocyclops yeozenis* (Ito, 1953), known from Japan and southeastern Alaska (USA). Subsequently, it was reported from the Great Smoky Mountains National Park, Tennessee, and in Virginia (Reid 2006), as well as from South Korea (Lee et al. 2004), but it has also been found in southern France (F. Fiers pers. obs.). The surprisingly disjunct distribution, with populations composed of few individuals, suggests that the species is very rare in both terms of abundance and frequency. At present, the genus is monotypic, and the discoveries of it in the Palaearctic region must be the result of heterochrony (Galassi & De Laurentiis 2004a, b). A new species of this genus has been discovered in the Sanguinière spring (Mercantour), with

**Canthocamptus dacicus** Chappuis, 1923

**Material Examined.** — Site 31: 2 specimens. Material deposited at UNIVAQ.

**Remarks**

This species was originally described from cave habitats in Transylvania (Romania) and subsequently recorded from several localities in the Balkan area (Slovenia, Bulgaria, eastern Italy), in both karstic environments (cave waters) and the hyporheic zone of streams and rivers. At present, the habitats from which the species has been collected suggest its stygobiotic nature. The species shows some morphological affinities with *Bryocamptus* (*E.* hoferi (Douwe, 1907) according to Borutzky (1952).

**Genus Elaphoidella** Chappuis, 1928

*Elaphoidella phreatica* (Chappuis, 1925)


**Remarks**

The stygobiotic species *Elaphoidella phreatica* is widely distributed across Europe and according to Karanovic (2001) shows a very high degree of variability. The material collected from Mercantour fits the original diagnosis of the species. *Elaphoidella phreatica* is known from several localities in France, Italy, Slovenia, Croatia, Montenegro, Romania, Hungary, Germany, Czech Republic, Slovakia and Austria. This species seems to have a wide ecological plasticity, being recorded from almost all types of groundwater habitats, from the saturated karst to the epikarst, in deep saturated unconsolidated aquifers, springs and the hyporheic zone of streams and rivers.

**Genus Sygepactophanes** Moeschler & Rouch, 1984

*Sygepactophanes* sp. 1

**Material Examined.** — Site 30: 2 specimens, site 31: 3 specimens. Material deposited at UNIVAQ.

**Remarks**

The genus *Sygepactophanes* was originally described by Moeschler & Rouch (1984) with the only species *Sygepactophanes jurassicus* collected from a karstic spring of the Swiss Jura. Since the formal establishment of this new canthocamptid genus, closely related to the genus *Epactophanes* Mrázek, 1893, no other species were collected or described elsewhere. The genus *Sygepactophanes* is unique in showing several reductions and character losses in its body plan, such as the total absence of the leg 5 (PS) in both males and females, the body slender and only slightly sclerotized, and the reduction trends in the segmental pattern of the swimming legs, all derived characters which may be the result of heterochrony (Galassi & De Laurentiis 2004a, b). A new species of this genus has been discovered in the Sanguinière spring (Mercantour), with
females and copepods having been found, but the male still missing. This new population shows unique features, which may place this undescribed species at the base of the evolutionary history that led to the more derived *S. jurassicus*. The new species, for instance, shows a very plesiomorphic P5, along with several other evolutionary novelties, which require an emended diagnosis of the genus (Galassi et al.). The genus is very rare, at present being known only from the type species from Switzerland and the undescribed species from Mercantour (France). The extinction risk is very high and the genus as a whole should be considered critically endangered.

**Family PARASTENOCARIIDAE** Chappuis, 1940  
**Genus Parastenocaris** Kessler, 1913  
*Parastenocaris* sp.

**MATERIAL EXAMINED.** — Site 9: 1 specimen. Material deposited at UNIVAQ.

**REMARKS**  
The systematics of the family Parastenocarididae and of the type-genus *Parastenocaris* are in state of flux and several genera were recently described, redescribed or resurrected (e.g., Jakobi 1969, 1972; Galassi & De Laurentiis 2004b; Schminke 2010 and Karanovic & Cooper 2011). Male morphological characters are crucial for the specific identification of the species. The single female collected in the Mercantour does not allow the assignment of the specimen to any species of the genus. Most members of the family are interstitial, even if some are also found in mosses, in the saturated karst and in the epikarst.

**Class MALACOSTRACA** Latreille, 1802  
**Order AMPHIPODA** Latreille, 1816  
**Family NIPHARGIDAE**, Bousfield, 1977  
**Genus Niphargus** Schiodte, 1849

*Niphargus* sp.

**MATERIAL EXAMINED.** — Site 1: 8 specimens; site 3: 1 specimen; site 4: 1 specimen; site 7: 37 specimens; site 8: 5 specimens; site 9: 11 specimens; site 10: 2 specimens; site 13: 1 specimen; site 26: 1 specimen; site 29: 5 specimens; site 34: 21 specimens; site 37: 2 specimens; site 39: 27 specimens; site 43: 7 specimens; site 48: 5 specimens; site 49: 17 specimens; site 50: 2 specimens. Material deposited at UCBLZ, No. 2014-3.

**REMARKS**  
Juveniles or strongly damaged specimens, unidentifiable at the species level. Distribution: see Table 2.

*Niphargus gineti* Bou, 1965

**Niphargus gineti** Bou, 1965: 272.

**Niphargus foreli** Humbert, 1877  
(Fig. 2C)

*Niphargus foreli* Humbert, 1877: 278.

**MATERIAL EXAMINED.** — Site 4: 19 specimens; site 7: 1 specimen; site 18: 9 specimens; site 29: 1 specimen; site 30: 14 specimens; site 31: 9 specimens; site 35: 3 specimens; site 48: 1 specimen; site 49: 1 specimen; site 50: 1 specimen. Material deposited at UCBLZ, No. 2014-3 and MNHN, MNHN-IU-2014-10147, MNHN-IU-2014-10148.

**REMARKS**  
Collected for the first time in the Mercantour National Park, which lies outside the previous distribution area of the species. However, the species assignment requires confirmation.

*Niphargus laisi* Schellenberg, 1936

*Niphargus laisi* Schellenberg, 1936: 68.

**MATERIAL EXAMINED.** — Site 9: 1 specimen; site 26: 1 specimen; site 27: 1 specimen. Material deposited at UCBLZ, No. 2014-3.

**REMARKS**  
Collected for the first time in the Mercantour National Park. Found only in spring habitats, frequently found in high altitude aquifers.

*Niphargus sp. 1*  

**REMARKS**  
Different from the three other species of *Niphargus* collected in this study.

**Family SALENTINELLIDAE**, Bousfield, 1977  
**Genus Salentinella** Ruffo, 1948

*Salentinella juberthiae* Coineau, 1968

*Salentinella juberthiae* Coineau, 1968: 186.

**MATERIAL EXAMINED.** — Site 7: 2 specimens, site 34: 17 specimens, site 52: 1 specimen. Material deposited at UCBLZ, No. 2014-3.
### Table 2. Presence-absence data for stygobiont species across the six river catchments. Names in bold indicate species new to Science. Grey and white columns correspond to hyporheic and spring sites respectively. Four additional taxa have been collected: *Trichodrilus sp.*, *Proasellus sp.*, *Niphargus sp.*, and *Bathynella sp.* These were not counted in the species number because they correspond to unidentifiable specimens (immature or damaged).

<table>
<thead>
<tr>
<th>Catchment</th>
<th>Roya / Bevera</th>
<th>Tinée</th>
<th>Ubaye</th>
<th>Var</th>
<th>Verdon</th>
<th>Vésubie</th>
</tr>
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<tbody>
<tr>
<td>Clitellata</td>
<td><em>Aberrantidrilus stephaniae</em> Martin, 2015</td>
<td>+</td>
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<td></td>
<td><em>Stylodrilus</em> sp. 1</td>
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<td><em>Trichodrilus</em> sp. 1</td>
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<tr>
<td></td>
<td><em>Trichodrilus</em> cf. <em>tenuis</em> Hrabé, 1960</td>
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<td></td>
<td><em>Marionina sambugarae</em> Schmelz, 2015</td>
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<td>Polychaeta</td>
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<tr>
<td>Mollusca</td>
<td>Probably 2 different genera (in study)</td>
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<td>+</td>
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<td>Hydracarina</td>
<td><em>Ljania macilentad</em> Koenike, 1908</td>
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<td><em>Stygomonomonia latipes</em> Szalay, 1943</td>
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<td>Cyclopoida</td>
<td><em>Acanthocyclops agamus</em> Kiefer, 1938</td>
<td>+</td>
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<tr>
<td></td>
<td><em>Diacyclops disjunctus</em> (Thallwitz, 1927)</td>
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<td><em>Diacyclops languidoideus</em> group</td>
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<td><em>Graeterella unisetigera</em> (Graeter, 1910)</td>
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<td><em>Speocyclops racovitzai</em> (Chappuis, 1923)</td>
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<td>Harpacticoida</td>
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<td><em>Bryocamptus (Echinocamptus) cf. dacus</em> (Chappuis, 1923)</td>
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<td><em>Elaphoidella phreatica</em> (Chappuis, 1925)</td>
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<td><em>Cavernocypris subterranea</em> (Wolf, 1920)</td>
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<td><em>Niphargus gineti</em> Bou, 1965</td>
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<td><em>Niphargus forei</em> Humbert, 1877</td>
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<td><em>Niphargus lais</em> Schellenberg, 1936</td>
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</tr>
<tr>
<td></td>
<td><em>Salentinella jubethiae</em> Coineau, 1968</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td>+</td>
</tr>
<tr>
<td></td>
<td><em>Bogidiella</em> sp.</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Isopoda</td>
<td><em>Proasellus</em> sp.</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Proasellus synaslloydies</em> (Henry, 1963)</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Proasellus rouchi</em> Henry, 1980</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Proasellus</em> sp. ‘<strong>Mescla</strong>’</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Proasellus</em> sp. ‘<strong>Pont Tende</strong>’</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Proasellus</em> sp. ‘<strong>Sospel</strong>’</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Proasellus</em> sp. ‘<strong>Boreon</strong>’</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td><em>Proasellus</em> sp. ‘<strong>Maglia</strong>’</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Proasellus</em> sp. ‘<strong>Sanguinierre</strong>’</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bathynellidae</td>
<td><em>Bathyrella</em> sp.</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Bathyrella</em> sp. 1</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Bathyrella</em> sp. 2</td>
<td>+</td>
<td></td>
<td>+</td>
<td></td>
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</tr>
<tr>
<td>Parabathynellidae</td>
<td><em>Parabathyrella</em> sp.</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

**Number of sites**: 7 2 3 3 5 8 3 7 6 3 3 3
**Total Number of species per habitat**: 12 11 3 7 5 18 6 7 15 4 2
**Total Number of species**: 44
REMARKS
Collected for the first time in the Mercantour National Park, mostly in the hyporheic habitat

Family BOGIDIELLIDAE Hertog, 1936
Genus Bogidiella Hertog, 1933

Bogidiella sp.


REMARKS
Not identifiable to the species level (damaged specimens); first record of the genus in the Mercantour National Park, in hyporheic habitat.

Order ISOPODA Latreille, 1817
Family ASELLIDAE Rafinesque, 1815
Genus Proasellus Dudich, 1925

Proasellus synaselloides (Henry, 1963)


MATERIAL EXAMINED. — Site 26: 2 specimens; site 27: 3 specimens. Material deposited at UCBLZ, No. 2012-11.

REMARKS
First record of the species in the Mercantour National Park.

Proasellus rouchi Henry, 1980


MATERIAL EXAMINED. — Site 34: 2 specimens. Material deposited at UCBLZ, No. 2012-11.

REMARKS
Type locality of the species, species known only from the type locality.
DNA sequences accession numbers: JQ921383 (COI) JQ921805 (16S) JQ921985 (28S), from Morvan et al. (2013).

Proasellus sp. 1 “Mescla” (Fig. 2D)

MATERIAL EXAMINED. — Site 34: 1 specimen. Material deposited UCBLZ, No. 2012-11.

REMARKS
This specimen belongs to a new species, the description of which is in progress.
DNA Sequences accession numbers: JQ921353 (COI) JQ921793 (16S) JQ921973 (28S), from Morvan et al. (2013).

Proasellus sp. 2 “Pont Tende”

MATERIAL EXAMINED. — Site 4: 1 specimen; site 8: 12 specimens. Material deposited at UCBLZ, No. 2012-11.

REMARKS
A description of this species, which is new to science, is in progress.

Proasellus sp. 3 “Sospel”


REMARKS
A description of this species, which is new to science, is in progress.
DNA sequence accession numbers: JQ921357 (COI) JQ921795 (16S) JQ921975 (28S), from Morvan et al. (2013).

Proasellus sp. 4 “Boreon”

MATERIAL EXAMINED. — Site 13: 4 specimens; site 50: 3 specimens; site 51: 3 specimens. Material deposited at UCBLZ, No. 2012-11.

REMARKS
A description of this species, which is new to science, is in progress.
DNA sequence accession numbers: JQ921342 and JQ921345 (COI), JQ921787 and JQ921788 (16S), and JQ921969 (28S) from Morvan et al. (2013).

Proasellus sp. 5 “Maglia”

MATERIAL EXAMINED. — Site 3: 1 specimen. Material deposited at UCBLZ, No. 2012-11. Some specimens were also collected at the Brugia Pousse spring (43°59′53″N, 7°50′07″E).

REMARKS
A description of this species, which is new to science, is in progress.
DNA sequence accession numbers: JQ921349 (COI) JQ921791 (16S) JQ921971 (28S), from Morvan et al. (2013).

Proasellus sp. 6 “Sanguiniere”


REMARKS
A description of this species, which is new to science, is in progress. Sequence accession numbers: JQ921355 (COI) JQ921794 (16S) JQ921974 (28S), from Morvan et al. 2013.
TABLE 3. — Habitat designation and species richness of the 53 sites. Permeability classes are detailed in Fig. 1B.

<table>
<thead>
<tr>
<th>Catchment/Station</th>
<th>Locality</th>
<th>Permeability</th>
<th>Species Richness</th>
</tr>
</thead>
<tbody>
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<td>Roya / Bevera</td>
<td></td>
<td>High</td>
<td>Moderate</td>
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<td>1</td>
<td>Tende</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Tende</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Breil/Roya</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Tende</td>
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<td>5</td>
<td>Tende</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Moulinet</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Sospel</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Tende</td>
<td></td>
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</tr>
<tr>
<td>9</td>
<td>Sospel</td>
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</tr>
<tr>
<td>Tinee</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>Roure</td>
<td></td>
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</tr>
<tr>
<td>11</td>
<td>Roure</td>
<td></td>
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</tr>
<tr>
<td>12</td>
<td>Roure</td>
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<td></td>
</tr>
<tr>
<td>13</td>
<td>St Sauveur/Tinee</td>
<td></td>
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<td>Saint-Dalmas-le-Selvage</td>
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<td>Saint-Etienne-de-Tinee</td>
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<tr>
<td>16</td>
<td>Uvernet-Fours</td>
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<tr>
<td>17</td>
<td>Uvernet-Fours</td>
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</tr>
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</tr>
<tr>
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<td>Larche</td>
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<tr>
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<td>Uvernet-Fours</td>
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<td>21</td>
<td>Uvernet-Fours</td>
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<tr>
<td>22</td>
<td>Barcelonnette</td>
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<tr>
<td>23</td>
<td>Saint-Pons</td>
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<tr>
<td>24</td>
<td>Enchastrayes</td>
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<tr>
<td>25</td>
<td>Faucon de Barcelonnette</td>
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</tr>
<tr>
<td>26</td>
<td>Meolans-Revel</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>27</td>
<td>Meolans-Revel</td>
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<tr>
<td>28</td>
<td>La Condamine Chatelard</td>
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<tr>
<td>Var</td>
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<tr>
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<td>Beuil</td>
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<td>Entreaunes</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>31</td>
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<tr>
<td>32</td>
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</tr>
<tr>
<td>33</td>
<td>Guillaumes</td>
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<td>Malaussène</td>
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<tr>
<td>35</td>
<td>Colmars</td>
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<td>Colmars</td>
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<td></td>
</tr>
<tr>
<td>37</td>
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<td>Allos</td>
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<td>41</td>
<td>Colmars</td>
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<tr>
<td>42</td>
<td>Allos</td>
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</tr>
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<td>43</td>
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<td>x</td>
<td></td>
</tr>
<tr>
<td>46</td>
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<td>x</td>
<td></td>
</tr>
<tr>
<td>47</td>
<td>Villars-Colmars</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vésubie</td>
<td></td>
<td></td>
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<tr>
<td>48</td>
<td>Belvédère</td>
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</tr>
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<td>49</td>
<td>St-Martin-Vésubie</td>
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<td></td>
</tr>
<tr>
<td>50</td>
<td>St-Martin-Vésubie</td>
<td></td>
<td></td>
</tr>
<tr>
<td>51</td>
<td>St-Martin-Vésubie</td>
<td></td>
<td></td>
</tr>
<tr>
<td>52</td>
<td>St-Martin-Vésubie</td>
<td></td>
<td></td>
</tr>
<tr>
<td>53</td>
<td>St-Martin-Vésubie</td>
<td></td>
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</tr>
</tbody>
</table>
Superorder SYNCARIDA Packard, 1885  
Order BATHYNELLACEA Chappuis, 1915  
Family BATHYNELLIDAE Grobben, 1905

Bathynellidae gen. sp.  
MATERIAL EXAMINED. — Site 21: 6 specimens; site 22: 2 specimens;  
site 25: 1 specimen; site 27: 3 specimens; site 33: 1 specimen.  
Currently with J.-L. Cho, National Institute of Biological Resources,  
Gyoungseo-dong, Incheon, South Korea, for study.

REMARKS  
Not identifiable to genus or species level (damaged specimens).  
The family is here reported for the first time in the Mercantour National Park.

_Bathynella_ Vejdovsky, 1882

_Bathynella_ Vejdovsky, 1882: 48.
The collected material could not be attributable to known species  
(immatures, females or damaged specimens). However on the basis  
of morphology it was possible to distinguish two different species,  
referred to here as _Bathynella_ sp. 1 and _Bathynella_ sp. 2.

REMARKS  
This genus is found for the first time in the Mercantour National Park.

_Bathynella_ sp. 1

MATERIAL EXAMINED. — Site 22: 4 specimens; site 43: 2 specimens.  
Currently with J.-L. Cho, National Institute of Biological Resources,  
Gyoungseo-dong, Incheon, South Korea, for study.

_Bathynella_ sp. 2

MATERIAL EXAMINED. — Site 22: 2 specimens; site 28: 4 specimens;  
site 43: 1 specimen; site 46: 1 specimen. Currently with J.-L. Cho,  
National Institute of Biological Resources, Gyoungseo-dong, Incheon,  
South Korea, for study.

Family PARABATHYNELLIDAE Nooit, 1965
Genus _Parabathynella_ Chappuis, 1926

*Parabathynella* sp.  
(Fig. 2B)

MATERIAL EXAMINED. — Site 21: 1 female; site 43: 1 juvenile.  
Currently with J.-L. Cho, National Institute of Biological Resources,  
Gyoungseo-dong, Incheon, South Korea, for study.

REMARKS  
Not identifiable (female and/or young specimen). This genus  
here is recorded for the first time in the Mercantour National Park.

**Biodiversity Assessment**

In total, 53 sites were explored during the two sampling periods (27 sites in 2009 and 26 in 2010), with a sampling  
effort slightly higher in consolidated-rock aquifers (28 sites)  
than in porous aquifers (25 sites). More than 146 species,  
mixing surface and obligate groundwater species, have been  
identified, of which 44 are exclusively groundwater species  
(stygobionts) (Table 2). Of the 53 sites, 12 contained  
no stygobionts, including five sites located in the Verdon  
catchment. The species rarefaction curve did not level off  
at 53 sites, indicating that sampling more sites in the Mer-  
cantour massif would provide additional species (Fig. 3).  
The most appropriate way to compare species rarefaction curves  
between European regions is to use a point of equal number  
of sampled sites. Using the number of species collected in  
c. 50 sites, the Mercantour massif ranks among the four most  
species-rich regions in Europe.

As generally observed in groundwater, most of the species  
belongs to the Crustacea (more than 75% of the species,  
Table 2). Among them, the genus _Prosellus_ was highly  
diversified, with eight species. A relatively high richness was  
also found among annelids (five or perhaps six citellate  
species, see Martin _et al._ this issue; one polychaete species)  
with a high abundance of the rare freshwater polychaete  
_Trighochaetus cf. beranecki_ Delachaux, 1921 at some of the  
sites (i.e. 66, 19, 11 specimens at sites 8, 22, 27). All species  
collected during the study, except _Prosellus rouchi_ Henry,  
1980, were not only new to the Mercantour National Park  
but also to the whole Mercantour massif. _Prosellus rouchi_  
had previously been collected in hyporheic habitats at the  
confluence between the Var and Tinée Rivers (type locality  
of the species). The amphipod _Niphargus rhenorhodanensis_  
Schellenberg, 1937 had been previously reported for the  
Massif, but it was not collected during the present study.  
This first exploration also led to the discovery of ten species  
new to Science, including six isopods of the genus _Prosellus_,  
one harpacticoid copepod of the genus _Stypegactophantes_,  
one cyclopoid copepod of the genus _Ictocyclops_, and two species  
of Clitellata, described as _Aberrantidrilus stephaniae_ and _Mar-  
nonina sambugarae_ —(Martin _et al._ 2015 this issue). The six  
most frequent taxa (_frequency > 10 %_), were in decreasing  
order of occurrence, _Niphargus sp._, _Cavernocypris subterraneae_  
(Wolf, 1920), _Niphargus foreli_ Humbert, 1877, _Trichodri-  
lus sp., Marionina sambugarae, Troglochaetus cf. beranecki_  
and _Fabaformicandona cf. breuili_ (Paris, 1920) (Fig. 4A).  
Springs had far less species than hyporheic habitats (Fig. 4B,  
C). The springs harbour less than half of the collected spe-  
cies, whereas the hyporheic zone contains more than 78%  
of the species (only ten species not collected). Among the  
ten species exclusive to consolidated-rock aquifers, four are  
new to Science.

It was not possible to test for differences in species richness  
between catchments and aquifers and their interaction because  
the sampling design was unbalanced. Yet, catchments with a  
low species richness (eight and five species in the Tinée and  
Vésubie catchments, respectively) had much of their surface  
...
area occupied by practically non-aquiferous rocks (sites 10-11-12 and 14-15 in the Tinée valley and sites 49 to 53 in the Vésubie valley, Fig. 1, Tables 2, 3).

DISCUSSION

HIGH SPECIES RICHNESS

Until the present study, groundwater ecosystems of the Mercantour National Park were poorly investigated. This resulted in a gap in the distribution pattern of stygobionts in France (see Atlas in Ferreira 2005). This study is the first regional-scale sampling survey of the obligate groundwater fauna in consolidated and unconsolidated aquifers of the Mercantour massif. A major finding of this study is the collection of 44 species strictly restricted to groundwaters. This number of species would be considered low for surface freshwater environments, but it is actually high for groundwater systems, which are characterized by poor trophic resources (Gibert et al. 1994). For comparison, at a local scale Malard et al. (1997) emphasized the exceptional richness of groundwater fauna in the Lez aquifer (France), which contains a total of 37 species. Species richness for the 20 richest aquifers in the world ranges from 12 to 60 species (Culver & Sket 2000). In the Danube Floodplain National Park, Danielopol & Pospisil (2001) mentioned a remarkable level of biodiversity, with 35 species in an area of approximately 0.8 km². At broader spatial scales, 64 species are known from the Rhône river aquifers (excluding tributary aquifers) (Olivier et al. 2009), more than 35 species in the alluvia of the Rhine River, and 60 species along the Danube River (Dole-Olivier et al. 1994). Highest numbers are reported from the Pilbara region (Western Australia) with more than 78 species (Eberhard et al. 2005a-b). Nevertheless, comparisons among regions are not entirely informative because of large differences in region size and sampling effort (e.g., an area of 178 000 km² for the Pilbara region, and over 800 samples for the study in the Danube floodplain National Park: Eberhard et al., 2005a; Danielopol & Pospisil 2001). The area effect is supposedly strong in groundwater because of the high proportion of species with a narrow geographic range. As area increases by aggregation of local units, overall species richness rises much more rapidly than in the surface environment (Gibert & Deharveng 2002). Accurate comparisons between groundwater systems are only possible when data are acquired at similar grain size and spatial extent, and the sampling design captures the same amount of spatial heterogeneity. The present sampling design was in many respects comparable to that used as part of the European project PASCALIS for assessing species richness in six European regions (Dole-Olivier et al. 2009) previously recognized as hotspots of groundwater biodiversity (except the Walloon karst, Deharveng et al. 2009). Comparison of species rarefaction curves based on an equal number of sites per region (i.e. 53 sites) shows that the Mercantour massif is among the richest regions in Europe (Fig. 3). Moreover, the shape of the rarefaction curve suggests that many more species remain to be discovered. Thus, this first (yet incomplete) assessment of species richness in the Mercantour National Park raises this area to the rank of a European hotspot of groundwater biodiversity, comparable to the seven major biodiversity centers recognized by Deharveng et al. (2009), i.e. Slovenia and Northeastern Italy, Northern Italian Alps, Ariège region of the Pyrénées, Southern Jura and Rhône valley near Lyon, Rhine alluvial plain (23 species) and Cévennes in Southern France, and Cordillera Cantabrica in northwestern Spain (22 species). However, the Mercantour massif exhibits a striking difference to other European hotspots, because it harbours a set of small aquifers. European centers of biodiversity generally correspond to large karst systems (e.g., Lez aquifer [Malard et al. 1997a]), and regions with extensive carbonated formations (e.g., the Southern Jura [Dole-Olivier et al. 2009], or alluvial deposits [e.g., Rhône, Rhine, Danube], which generally contain great volumes of groundwater and concomitantly high numbers of species). High species richness has often been associated with the large size of studied aquifers (e.g., Culver & Sket 2000). In contrast, the Mercantour aquifers are very small in size, shallow and spatially discontinuous. The hyporheic zone of streams does not expand longitudinally and laterally to form extensive and productive alluvial aquifers. Rather, it consists of small isolated patches of sediments that are often separated by bedrock outcrops. These small alluvial aquifers of poor water productivity are not shown on large-scale hydrogeological maps (Corno et al. 2013; Fig. 1B), although they potentially represent species-rich groundwater habitats.

A SET OF NEW SPECIES

Records prior to this study reported a single stygobiont in the Mercantour National Park (Ferreira 2005), the mollusc Graziana trinitatis (Caziot, 1910) (Boeters 1970). Two other species had been collected in the Mercantour massif outside of the National Park, Proasellus rouchi in the Var River valley (Henry 1980) and Niphargus rhenorhodanensis (Ginet: PASCALIS database) in the Vésubie River valley. Six mollusc species (Bathyopeum articense Bernasconi, 1985; Fissuria boui Boeters, 1981; Moitessiera locardi Coutagne, 1883; Graziana cezairensis Boeters, 2000; Graziana provincialis Boeters, 2000,
<table>
<thead>
<tr>
<th>Species</th>
<th>Groundwater (A)</th>
<th>Hyporheic (B)</th>
<th>Springs (C)</th>
</tr>
</thead>
<tbody>
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<td></td>
<td></td>
</tr>
<tr>
<td>Troglochaetes cf. beranecki</td>
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<tr>
<td>Niphargus sp.</td>
<td></td>
<td></td>
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<tr>
<td>Bathynella sp.</td>
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<td></td>
<td></td>
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<tr>
<td>Speocyclops kieferi</td>
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<td>Bathynella sp. 2</td>
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<td>Trichodrilus cf. tenuis</td>
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<td>Marionina sambugarensis</td>
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<td>Fabaeformiscandona sp. 1</td>
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<tr>
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<tr>
<td>Niphargus laisi</td>
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<td>Ljania macilenta</td>
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<td>Proasellus sp. 'Pont Tende'</td>
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<td>Proasellus sp. 'Sospel'</td>
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<td>Acanthocyclops agamus</td>
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<td>Bryocamptus (Echinocamptus) cf. dacoicus</td>
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and Graziana trinitatis), four species of amphipods (Niphargopsis casparyi (Prat, 1866), Niphargus ciliatus Chevreux, 1906, Niphargus gallicus Schellenberg, 1935, and Niphargus nicaensis Isnard, 1916) and one cyclopoid copepod (Graeteriella unisetigera (Graeter, 1908)) were known from the nearby massifs (Ubaye, Pelat, Prealps of Nice, Trois Évêchés) (Bertrand et al. 1999, Boeters 2000). Of these 14 species, potentially present in the Mercantour massif, only two (P. rouchi and G. unisetigera) were collected in the present study. This may either reflect the extremely narrow range of some species, such as Graziana cezairensis and Niphargus nicaensis, or an insufficient sampling effort. Several species with large geographic ranges, such as Niphargopsis casparyi and Niphargus ciliatus, were not collected in the Mercantour massif.

On the other hand, this study resulted in many species new for the Mercantour massif (43 species) and provided a high rate (10/44) of species new to Science. Discovery of many new species may have several non-exclusive explanations. First, groundwater ecosystems of the Mercantour massif had never been extensively sampled, even though the region is known to be characterized by a high rate of endemism among flora and fauna. Second, environmental heterogeneity is extremely high, due to variations in geology, geomorphology, climate and altitude. Heterogeneous environments with a complex mosaic of habitats may favor niche specialization, which eventually leads to speciation. Third, habitat fragmentation, as reflected by discontinuous aquifers, may have promoted allopatric speciation, leading to numerous closely-related species. For example, Morvan et al. (2013) found that Proasellus species of the Mercantour massif were closely-related evolutionary units belonging to two distinct clades.

**IMPORTANCE OF THE HYPORHEIC ZONE**

For historical reasons, research on groundwaters has long focused on the fauna of consolidated-rock aquifers, more particularly karst aquifers. Despite the recognition and development of Phreatobiology (Danielopol 1982) and the implementation of sampling techniques for the investigation of shallow and deep habitats in porous aquifers (Malard et al. 1997b; Malard et al. 2002), biodiversity in unconsolidated-sediment aquifers, especially in the hyporheic zone, has largely been neglected. However, comparisons of species richness between karst and porous aquifers have shown that species richness may be higher in porous aquifers (Malard et al. 2009; Dole-Olivier et al. 2009). With a comparable number of sites in the hyporheic zone (25) and in the consolidated-rock aquifers (28), the hyporheic zone yielded 78% of the total species richness, i.e. 15 species more than springs fed by consolidated-rock aquifers. This difference represents a large proportion of the total richness (34%) and highlights the role of the hyporheic zone for sustaining groundwater biodiversity. This result underlines the biological importance of even small habitat patches of alluvia and colluvia in the valley bottoms of this mountainous region. The hyporheic zone probably receives groundwater from nearby consolidated-rock aquifers, thereby acting as a zone of hydrological and biological convergence.
CONCLUSION

The species inventory of the Mercantour National Park contributes to our knowledge of European groundwater biodiversity. This southern mountainous region is of great scientific and conservation interest, not only for surface flora and fauna, but also for the groundwater fauna. With a total of 44 species, of which 43 are new to the Park and ten are new to Science, the Mercantour massif can be considered as a new hotspot of groundwater biodiversity at the European level. High species richness can be attributed to one or several striking features of this mountainous region, including a high climatic and topographic heterogeneity and the occurrence of many small and discontinuous aquifers. Our findings suggest that regions with small-sized aquifers of moderate water productivity may be as rich as regions with extensive productive aquifers. The shape of the species rarefaction curve indicates that our knowledge of groundwater fauna in the Mercantour massif is far from being complete and that many more species remain to be discovered. We recommend that a stronger sampling effort be applied to hyporheic habitats of headwater streams (e.g., Ubayette, Boréon, Ardon, Lance, and Tuebi), which may also warrant increased conservation attention due to their small size (Kløve et al. 2013).

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REFERENCES


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