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.

KEY WORDS
Groundwater invertebrates,
stygobionts,
biodiversity hotspot,
Mercantour National Park,
hyporheic zone,
spring.

RÉSUMÉ

Biodiversité dans les eaux souterraines de montagne. Le Parc national du Mercantour : un « hotspot » européen.

Le Parc national du Mercantour est une région physiquement très hétérogène, avec des faciès géologiques, géomorphologiques et climatologiques extrêmement variés, à l'origine d'une biodiversité exceptionnelle. D'un point de vue hydrogéologique, son réseau souterrain est organisé en aquifères discontinus et de petite taille, dont la faune aquatique (stygobie) est aujourd'hui inconnue. Ce travail explore la richesse spécifique des eaux souterraines du Parc national du Mercantour, après la mise en œuvre d'un plan d'échantillonnage prenant en compte l'hétérogénéité environnementale à l'échelle du bassin versant (six vallées majeures) et de l'aquifère (aquifère fissuré ou poreux). Le premier fait marquant est la récolte de 44 espèces stygobies, dont 43 nouvelles pour le parc et dix nouvelles pour la Science. Sur la base d'un nombre relativement faible de sites (53), cette zone peut être considérée comme un nouveau « hotspot » de biodiversité des eaux souterraines à l'échelle européenne. La structure particulière du réseau hydrogéologique, l'hétérogénéité environnementale élevée, et la position méditerranéenne de cette région, pourraient expliquer une telle biodiversité. La courbe de raréfaction des espèces montre que nos connaissances sur le Mercantour sont néanmoins loin d'être complètes et que de nombreuses espèces restent encore à découvrir. Avec plus de 78 % des espèces récoltées dans la zone hyporhéique, ce travail souligne également le rôle des aquifères poreux, dans le maintien de la biodiversité des eaux souterraines de montagne.

MOTS CLÉS
invertébrés souterrains,
stygobies,
« hotspot » de biodiversité,
Parc national du Mercantour,
zone hyporhéique,
source.

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 km^2) 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 peri-glacial 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-Bevera 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 1936); 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 1. — List, location and physical characteristics of the 53 sites sampled in the Mercantour massif; grey areas distinguish the hyporheic zone from spring habitats. Abbreviations: **Repl.**, number of replicates; **Spec. Cond.**, specific conductance; **Temp.**, water temperature; **NA**, data not available.

catchment / Station	Locality	Habitat	Repl.	X (WGS84)	Y (WGS84)	Elevation (m)	Date	Spec. cond (µS/cm)	Temp.
Roya / Bevera									
1	Tende	Spring	≥ 1	7.55752	44.11115	1027	06.VII.2009	1684	7.2
2	Tende	galerie	≥ 1	7.51230556	44.07077778	1600	22.VIII.2011	–	–
3	Breil/Roya	Spring	≥ 1	7.47518	43.97152	817	07.VII.2009	–	–
4	Tende	Spring	≥ 1	7.57981	44.04393	836	07.VII.2009	–	–
5	Tende	Spring	≥ 1	7.52055	44.07194	1452	07.VII.2009	–	–
6	Moulinet	Spring	≥ 1	7.39589	43.98073	1609	07.VII.2009	261	13
7	Sospel	Spring	1	7.43536	43.88403	363	06.VII.2009	2140	–
8	Tende	hyporheic	3	7.58884	44.09874	844	05.VIII.2009	278-287	11.1-12.5
9	Sospel	hyporheic	3	7.42103	43.8931	372	05.VIII.2009	501-1060	18.2-18.7
Tinée									
10	Roure	Spring	≥ 1	7.08986	44.11874	660	16.IV.2009	61	6.6
11	Roure	Spring	≥ 1	7.08986	44.11874	660	16.IV.2009	156	11.2
12	Roure	Spring	≥ 1	7.09027	44.12142	663	16.IV.2009	152	10.2
13	St Sauveur/Tinée	hyporheic	3	7.1051	44.08073	475	03.IV.2009	246	9.9
14	Saint-Dalmas-le-Selvage	hyporheic	3	6.887292	44.319895	1649	23.VII.2009	–	–
15	Saint-Etienne-de-Tinée	hyporheic	3	6.949298	44.234432	1082	23.VII.2009	–	–
Ubaye									
16	Uvernet-Fours	Spring	1	6.72041739	44.31144102	1825	09.VIII.2010	220	7.8
17	Uvernet-Fours	Spring	4	6.78717889	44.29824187	2440	10.VIII.2010	97	8.3
18	Jausiers	Spring	2	6.80202139	44.33113687	2500	13.VIII.2010	215	5
19	Larche	Spring	3	6.86938936	44.37332264	2350	11.VIII.2010	125	3.8
20	Uvernet-Fours	Spring	1	6.69808328	44.31569237	1825	31.VIII.2010	311	4.5
21	Uvernet-Fours	hyporheic	3	6.62104680	44.35043114	1205	15.IX.2010	280	14.1
22	Barcelonnette	hyporheic	4	6.61871795	44.38502337	1120	14.IX.2010	–	–
23	Saint-Pons	hyporheic	3	6.59095728	44.38859091	1100	14.IX.2010	607	10.6
24	Enchastrayes	hyporheic	3	6.66795729	44.38939119	1145	15.IX.2010	363	14.4
25	Faucon de Barcelonnette	hyporheic	3	6.68843161	44.39136246	1160	14.IX.2010	361	12.8
26	Meolans-Revel	hyporheic	3	6.53597527	44.39802524	1050	15.IX.2010	488	14.9
27	Meolans-Revel	hyporheic	3	6.53607138	44.39847182	1050	15.IX.2010	535	14.6
28	La Condamine Chatelard	hyporheic	5	6.74776490	44.45721556	1270	15.IX.2010	376	9.5
Var									
29	Beuil	Spring	≥ 1	6.95614692	44.07094343	1510	21.VII.2009	–	–
30	Entraunes	Spring	≥ 1	6.77111744	44.25226354	2040	21.VII.2009	–	–
31	Entraunes	Spring	2	6.77111744	44.25226354	2199	09.VIII.2010	154	3
32	Entraunes	hyporheic	3	6.74391401	44.19962647	1350	21.VII.2009	–	–
33	Guillaumes	hyporheic	3	6.83916316	44.11567488	870	21.VII.2009	–	–
34	Malaussène	hyporheic	> 3	7.15054840	43.92537804	190	22.VIII.2011	–	–
Verdon									
35	Colmars	Spring	1	6.62600258	44.18141478	1240	18.VI.2010	–	–
36	Colmars	Spring	1	6.62402287	44.18006081	1240	15.IX.2010	–	–
37	Allos	Spring	2	6.70244461	44.23925576	2199	02.VIII.2010	113	10.7
38	Allos	Spring	1	6.70677079	44.22460492	2310	02.VIII.2010	60	2.5
39	Allos	Spring	4	6.71191610	44.24948422	2273	02.VIII.2010	161	5.5
40	Allos	Spring	1	6.68825512	44.25238369	1890	03.VIII.2010	150	7.8
41	Colmars	Spring	4	6.68411376	44.22131168	1943	04.VIII.2010	–	–
42	Allos	hyporheic	3	6.63108545	44.22409666	1360	06.IX.2010	259	15.4
43	Allos	hyporheic	3	6.63175839	44.22339481	1355	06.IX.2010	269	13.9
44	Colmars	hyporheic	3	6.63549577	44.20224792	1300	06.IX.2010	320	14.5
45	Colmars	hyporheic	3	6.63164559	44.18667681	1270	15.IX.2010	289	12.5
46	Colmars	hyporheic	3	6.62373618	44.18040525	1235	15.IX.2010	347	13
47	Villars-Colmars	hyporheic	3	6.60992526	44.16208211	1200	07.IX.2010	244	12
Vésubie									
48	Belvédère	Spring	≥ 1	7.31517	44.01298	644	03.IV.2009	2033	12.4
49	St-Martin-Vésubie	Spring	≥ 1	7.261581	44.12672	1683	04.IV.2009	43	5.2
50	St-Martin-Vésubie	Spring	≥ 1	7.24444	44.08306	1211	03.IV.2009	83	7.4
51	St-Martin-Vésubie	hyporheic	3	7.25113	44.07911	1041	02.IV.2009	–	–
52	St-Martin-Vésubie	hyporheic	3	7.31401	44.08823	1511	02.IV.2009	–	–
53	St-Martin-Vésubie	hyporheic	3	7.30731365	44.08855840	1455	02.IV.2009	76	4.95

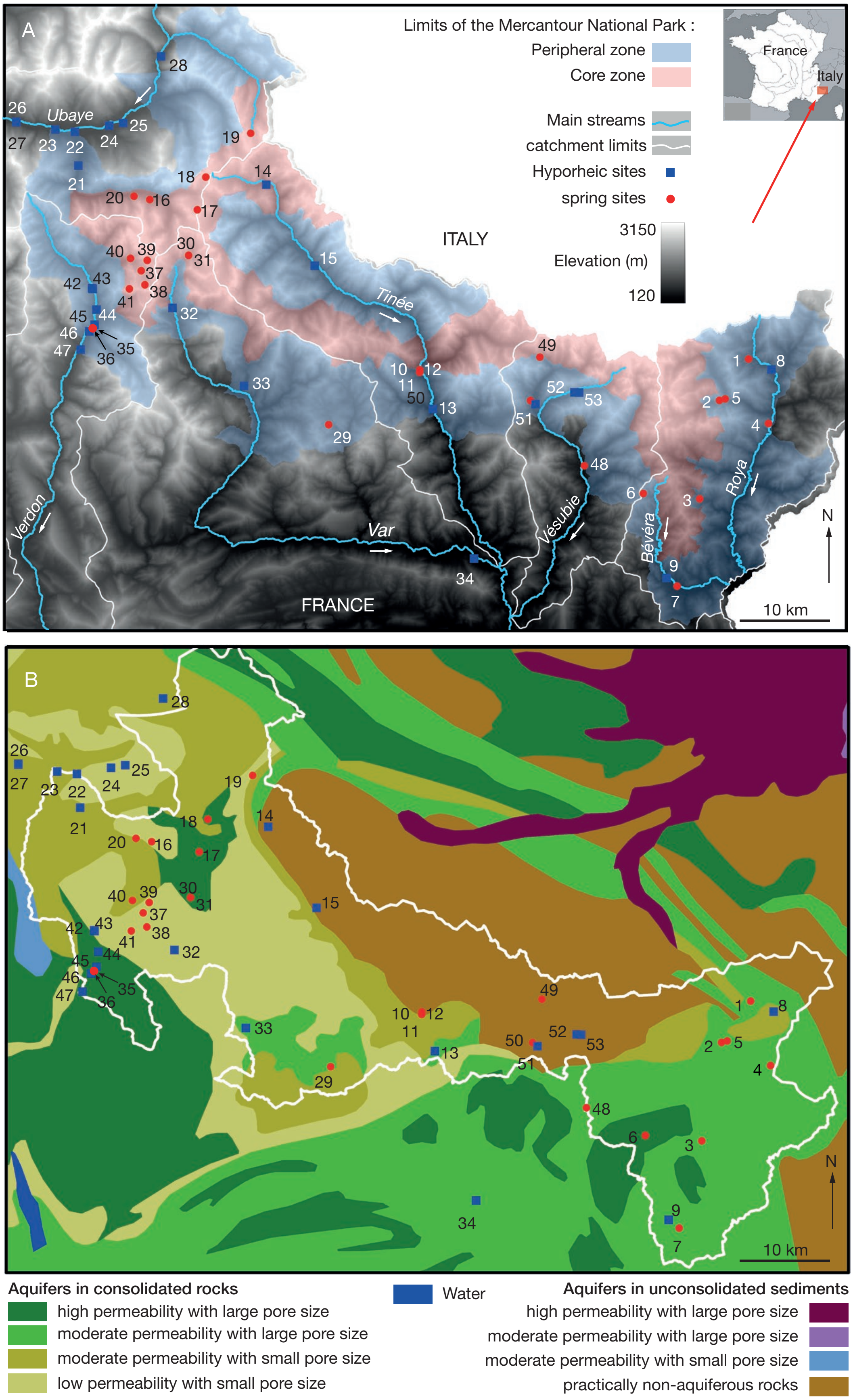


FIG. 1. — **A**, Study area and location of sampling sites. Sites are numbered as in Table 1; **B**, Map of groundwater habitats (extracted from Cornu *et al.* 2013) with the limits of the Mercantour National Park in white.

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 which we referred as sp. 1, sp. 2, and so on. Due to a lack of taxonomic expertise, the Mollusca were not identified to the species level. However, two different genera were easily distinguished based on the shape of the shell, indicating that two species at least were present. Identifications were mostly based on morphological criteria, although DNA sequences (COI, 16S and 28S) were obtained for all *Proasellus* species (Morvan *et al.* 2013).

Because different sampling methods were used, abundances could not be compared between sites. Therefore, results are presented as presence-absence data. The species rarefaction curve was calculated using EstimateS (Colwell 2009). The curve obtained for the Mercantour massif was compared with curves from six European regions, the groundwater fauna of which was sampled using a sampling protocol similar to that used in the present study (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.
MNHN	Muséum national d'Histoire naturelle, Paris.

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)

Troglochaetus beranecki Delachaux, 1921: 4.

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.

Remarks

Collected for the first time in the Mercantour National Park.

Class CLITELLATA Michaelsen, 1919
Family Naididae Ehrenberg, 1828
Subfamily Phallodrilinae Brinkhurst, 1971
Genus *Aberrantidrilus* Martin
in Martin, Schmelz & Dole-Olivier, 2015

Aberrantidrilus stephaniae
Martin, 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 Phallodrilinae, which is known to be occasionally present in ground waters as well (Creuzé des Châtelliers *et al.* 2009)

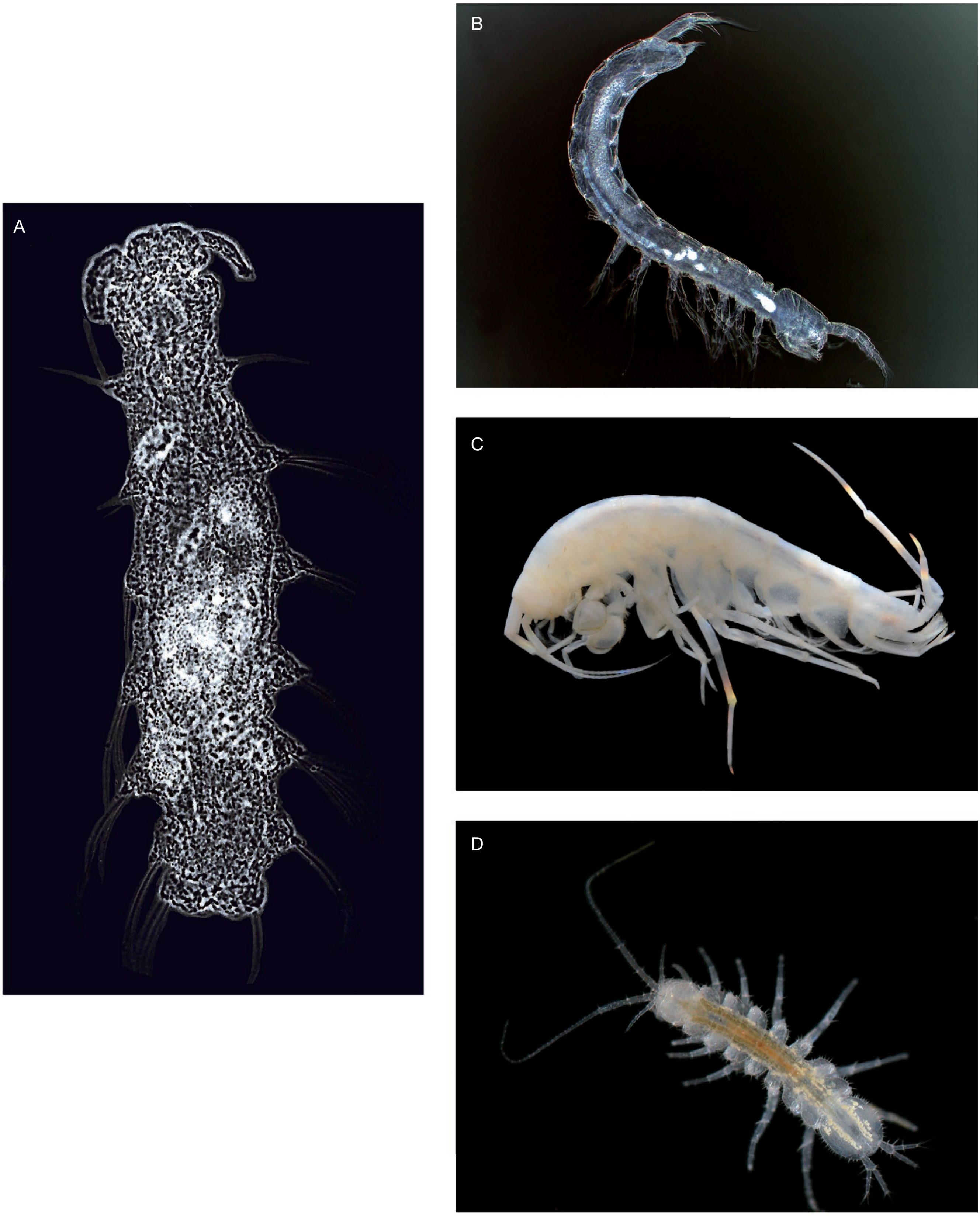


Fig. 2. — Some representative species collected in the Mercantour National Park: **A**, *Troglochaetus beranecki* Delachaux, 1921, length 0.6 mm; **B**, *Parabathynella* sp., length 1.5 mm; **C**, *Nipargus foreli* Humbert, 1877, length 8 mm; **D**, *Proasellus* sp., length 4 mm. Photographs: A-C, M.-J. 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 ENCHYTRAEIDAE 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

Material examined. — Site 9: 1 specimen. Material deposited at UCBLZ, No. 2012-3.

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

Material examined. — Site 15: 1 specimen. Material deposited at UCBLZ, No. 2012-3.

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)

Cypridopsis subterranea Wolf, 1920: 3.

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 stygophylous 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 stygobite 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

Acanthocyclops agamus Kiefer, 1938: 4.

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 *Graeteriella* Brehm, 1926

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

Cyclops unisetiger Graeter, 1908: 49.

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.

Genus *Speocyclops* Kiefer, 1937

Speocyclops racovitzai racovitzai (Chappuis, 1923)

Cyclops racovitzai Chappuis, 1923: 587.

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

Speocyclops kieferi Lescher-Moutoué, 1968: 170.

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.

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 hypothelminorheic 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 7: 1 specimen. Material deposited at IRScNB, I.G. 31589.

Remarks

The genus *Itocyclops* was established by Reid & Ishida (2000) to accommodate the species *Speocyclops yezoensis* (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 may represent the "missing link" bridging the gap between the records from the Nearctic and Oriental regions. Only one specimen has been collected from the Mercantour park in the Torraca spring (Sospel), but its generic assignment requires confirmation, as does its specific status. *Itocyclops yezoensis* has mostly been collected from semi-terrestrial habitats (like *Graeteriella unisetigera*, see above), as well as in springs and wells (Reid & Ishida 2000; Lee *et al.* 2004).

Order HARPACTICOIDA Sars, 1903
Family Canthocamptidae Brady, 1880
Genus *Bryocamptus* Chappuis, 1928

Bryocamptus* (*Echinocamptus*) *dacicus (Chappuis, 1923)

Canthocamptus dacicus Chappuis, 1923: 25.

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)

Canthocamptus phreaticus Chappuis, 1925: 69.

Material examined. — Site 48: 5 specimens. Material deposited at UNIVAQ and at MNHN: MNHN-IU-2013-11999 (1 ♀), MNHN-IU-2013-12000 (1 ♂).

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 *Stygepactophanes* Moeschler & Rouch, 1984

Stygepactophanes sp.1

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

Remarks

The genus *Stygepactophanes* was originally described by Moeschler & Rouch (1984) with the only species *Stygepactophanes 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 *Stygepactophanes* is unique in showing several reductions and character losses in its body plan, such as the total absence of the leg 5 (P5) 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 copepodids 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 Parastenocarididae 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* Schiödte, 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.

Material examined. — Site 1: 1 specimen; site 2: 2 specimens; Vievola spring; Valaura mine. Material deposited at UCBLZ, No. 2014-3.

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 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. Found only in spring habitats, frequently found in high altitude aquifers.

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, in the hyporheic habitat.

Niphargus sp. 1

Material examined. — Site 26: 1 specimen, site 28: 11 specimens. Material deposited at UCBLZ, No. 2014-3.

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).

	Catchment →	**Roya / Bevera**		**Tinée**		**Ubaye**		**Var**		**Verdon**		**Vésubie**	
Clitellata	***Aberrantidrilus stephaniae*** Martin, 2015		+										
	Stylodrilus sp. 1		+										
	Trichodrilus sp.		+				+			+	+		
	Trichodrilus sp. 1						+						
	Trichodrilus cf. *tenuis* Hrabě, 1960		+				+						
	Marionina sambugarae Schmelz, 2015		+		+	+				+	+		
Polychaeta	*Troglochaetus* cf. *beranecki* Delachaux, 1921		+				+			+	+		
Mollusca	Probably 2 different genera (in study)	+	+	+		+	+	+	+			+	
Hydracarina	*Ljania macilenta* Koenike, 1908						+				+		
	Stygomomonia latipes Szalay, 1943						+				+		
Cyclopoida	*Acanthocyclops agamus* Kiefer, 1938	+											
	Diacyclops disjunctus (Thallwitz, 1927)	+					+						
	Diacyclops languidoides group						+				+		
	Graeteriella unisetigera (Graeter, 1910)									+	+		
	Itocyclops sp. 1	+											
	Speocyclops kieferi Lescher-Moutoué, 1968				+		+				+		
	Speocyclops racovitzai (Chappuis, 1923)				+								
Harpacticoida	*Parastenocaris* sp.		+										
	Bryocamptus (*Echinocamptus*) cf. *dacicus* (Chappuis, 1923)							+					
	Elaphoidella phreatica (Chappuis, 1925)											+	
	Stygepactophanes sp.1							+					
Ostracoda	*Fabaeformiscandona* sp. 1	+		+	+				+	+	+		
	Fabaeformiscandona sp. 2					+				+			
	Candoninae sp. 1		+										
	Candoninae sp. 2	+					+				+		
	Candoninae sp. 3				+								
	Cavernocypris subterranea (Wolf, 1920)	+				+		+	+	+			
Amphipoda	*Niphargus* sp.	+	+	+	+		+	+	+	+	+	+	
	Niphargus gineti Bou, 1965	+											
	Niphargus foreli Humbert, 1877	+				+		+		+		+	
	Niphargus laisi Schellenberg, 1936		+				+						
	Niphargus sp.1						+						
	Salentinella juberthiae Coineau, 1968	+							+				+
	Bogidiella sp.				+		+						
Isopoda	*Proasellus* sp.										+		
	Proasellus synaselloides (Henry, 1963)						+						
	Proasellus rouchi Henry, 1980								+				
	Proasellus sp. '***Mescla***'								+				
	Proasellus sp. '***Pont Tende***'	+	+										
	Proasellus sp. '***Sospel***'		+										
	Proasellus sp. '***Boreon***'				+							+	+
	Proasellus sp. '***Maglia***'	+											
	Proasellus sp. '***Sanguiniere***'							+					
Bathynellidae	*Bathynella* sp.						+		+				
	Bathynella sp. 1						+				+		
	Bathynella sp. 2						+				+		
Parabathynellidae	*Parabathynella* sp.						+				+		
Number of sites		7	2	3	3	5	8	3	3	7	6	3	3
Total number of species per habitat		12	11	3	7	5	18	6	7	7	15	4	2
Total Number of sites		9		6		13		6		13		6	
Number of empty sites		2		2		1		1		5		1	
Total number of species		20		8		21		11		17		5	
Species per site (average)		2.2		1.3		1.6		1.8		1.3		0.8	
Number of exclusive species		10		2		4		5		1		1	
Total number of species: 44													

REMARKS
Collected for the first time in the Mercantour National Park, mostly in the hyporheic habitat

Family BOGIDIELLIDAE Hertzog, 1936
Genus *Bogidiella* Hertzog, 1933

Bogidiella **sp.**

MATERIAL EXAMINED. — Site 15: 7 specimens, site 27: 7 specimens. Material deposited at UCBLZ, No. 2014-3.

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)

Asellus synaselloides Henry, 1963: 99.

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

Proasellus rouchi Henry, 1980: 183.

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"

MATERIAL EXAMINED. — Site 9: 27 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: 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 (43'95633°N, 7'50075°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"

MATERIAL EXAMINED. — Site 30: 12 specimens; site 31: 4 specimens. Material deposited at UCBLZ, No. 2012-11.

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.

		Permeability					
		High	**Moderate**		**Low**		
Catchment/ Station	**Locality**	**Large pore**	**Large pore**	**Small pore**	**Small pore**	**Non aquiferous**	**Species Richness**
Roya / Bevera							
1	Tende		×				4
2	Tende		×				1
3	Breil/Roya		×				4
4	Tende		×				4
5	Tende		×				0
6	Moulinet	×					0
7	Sospel		×				5
8	Tende						5
9	Sospel		×				9
Tinée							
10	Roure					×	2
11	Roure					×	0
12	Roure					×	0
13	St Sauveur/Tinée		×				4
14	Saint-Dalmas-le-Selvage					×	1
15	Saint-Etienne-de-Tinée					×	2
Ubaye							
16	Uvernet-Fours				×		2
17	Uvernet-Fours	×					2
18	Jausiers	×					3
19	Larche			×			2
20	Uvernet-Fours			×			1
21	Uvernet-Fours			×			6
22	Barcelonnette			×			7
23	Saint-Pons			×			2
24	Enchastrayes				×		0
25	Faucon de Barcelonnette				×		3
26	Meolans-Revel			×			5
27	Meolans-Revel			×			8
28	La Condamine Chatelard			×			6
Var							
29	Beuil		×				3
30	Entraunes	×					4
31	Entraunes	×					5
32	Entraunes				×		2
33	Guillaumes		×				1
34	Malaussène		×				4
Verdon							
35	Colmars	×					2
36	Colmars	×					0
37	Allos				×		4
38	Allos				×		0
39	Allos				×		3
40	Allos			×			1
41	Colmars				×		2
42	Allos				×		0
43	Allos				×		8
44	Colmars	×					3
45	Colmars	×					0
46	Colmars	×					7
47	Villars-Colmars	×					0
Vésubie							
48	Belvédère		×				3
49	St-Martin-Vésubie					×	2
50	St-Martin-Vésubie					×	3
51	St-Martin-Vésubie					×	1
52	St-Martin-Vésubie					×	1
53	St-Martin-Vésubie					×	0

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 Noodt, 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 is here 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 Mercantour 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 *Proasellus* was highly diversified, with eight species. A relatively high richness was also found among annelids (five or perhaps six clitellate species, see Martin *et al.* this issue; one polychaete species) with a high abundance of the rare freshwater polychaete *Troglochaetus* 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 *Proasellus rouchi* Henry, 1980, were not only new to the Mercantour National Park but also to the whole Mercantour massif. *Proasellus 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 *Proasellus*, one harpacticoid copepod of the genus *Stygepactophanes*, one cyclopid copepod of the genus *Itocyclops*, and two species of Clitellata, described as *Aberrantidrilus stephaniae* and *Marionina* sambugarae (Martin *et al.* 2015 this issue). The six most frequent taxa (frequency > 10 %) were, in decreasing order of occurrence, *Niphargus* sp., *Cavernocypris subterranean* (Wolf, 1920), *Niphargus foreli* Humbert, 1877, *Trichodrilus* sp., *Marionina sambugarae*, *Troglochaetus* cf. *beranecki* and *Fabaeformicandona* 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 species, 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 km^2. 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 km^2 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 (Cornu *et al.* 2013; Fig. 1B), although they potentially represent species-rich groundwater habitats.

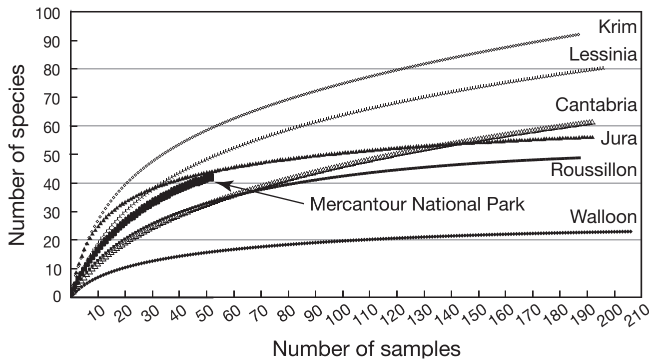
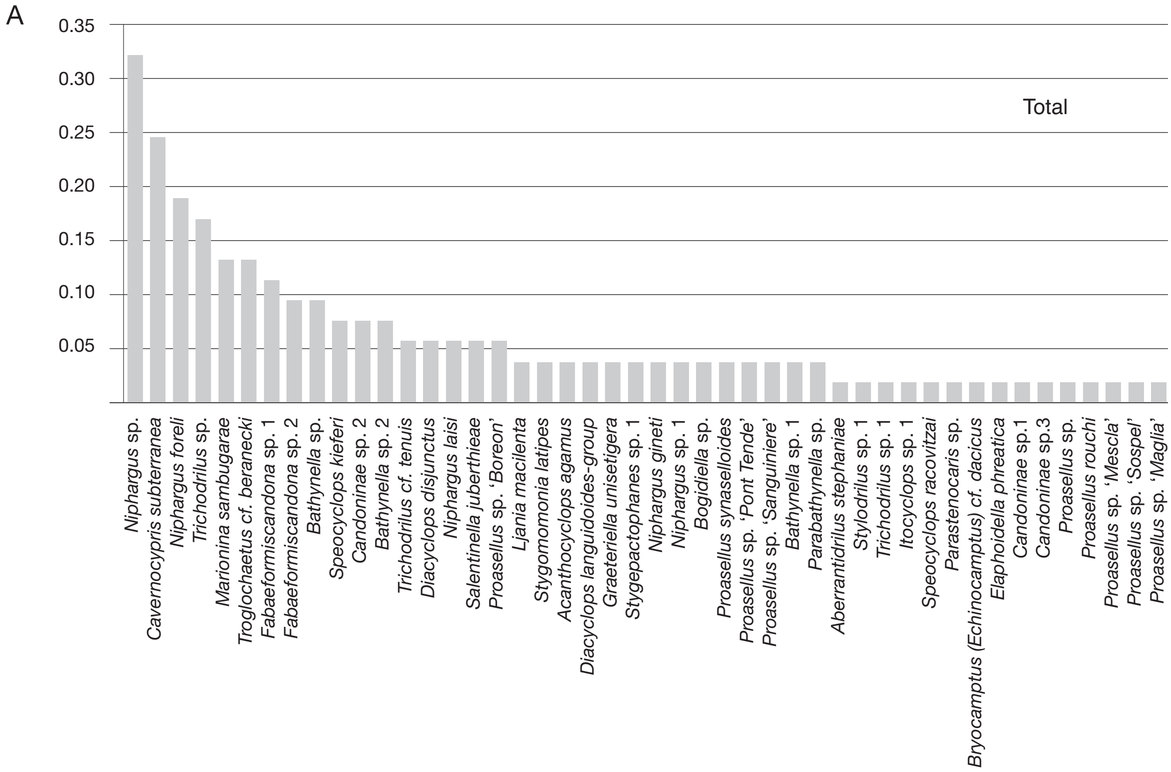


Fig. 3. — Species rarefaction curves for the Mercantour National Park and six other regions in Europe (Krim Massif in Slovenia, Lessinian Mountains in Italy, Cordillera Cantabria in Spain, Southern Jura Mountains and Roussillon region in France, and Walloon karst in Belgium) from Dole-Olivier *et al.* (2009) (with permission).

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 (*Bythiospeum articense* Bernasconi, 1985; *Fissuria boui* Boeters, 1981; *Moitessiera locardi* Coutagne, 1883; *Graziana cezairensis* Boeters, 2000; *Graziana provincialis* Boeters, 2000,



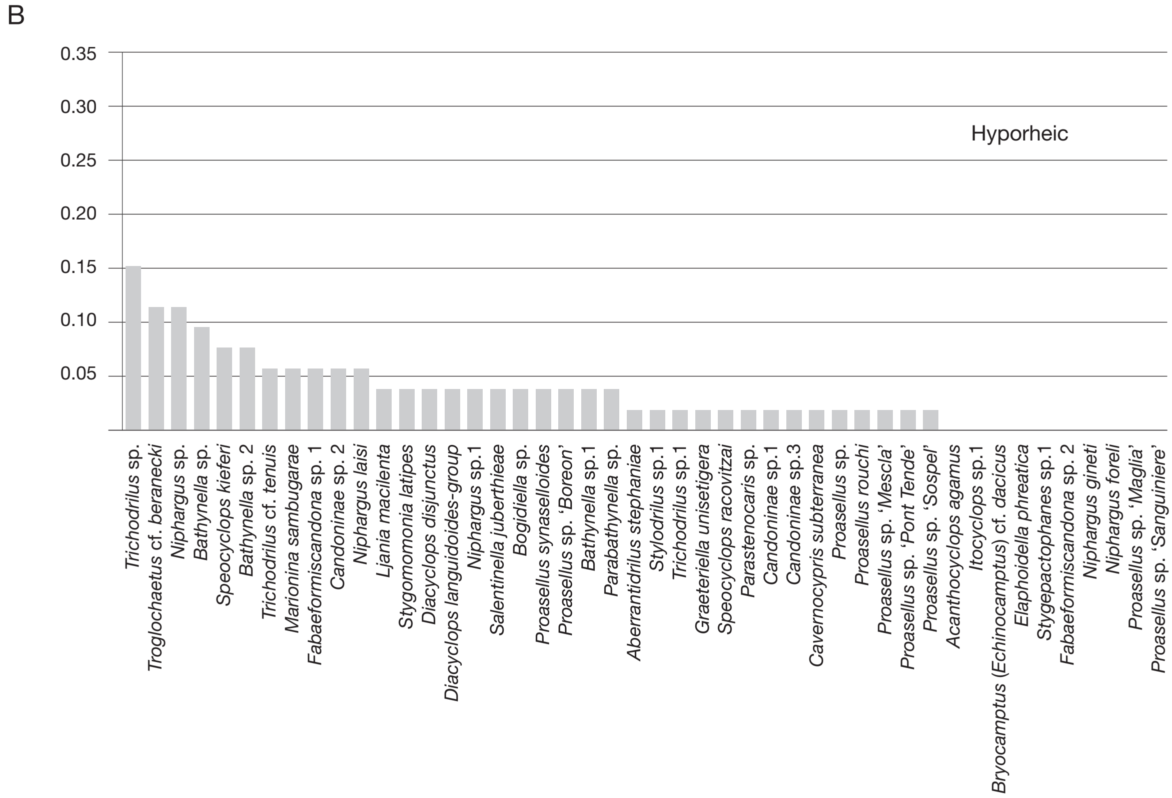


FIG. 4. — Species-rank frequency ordination (%) of species collected in groundwater (total) (**A**), unconsolidated-sediment aquifers (hyporheic) (**B**), and consolidated-rock aquifers (springs) of the Mercantour massif (**C**).

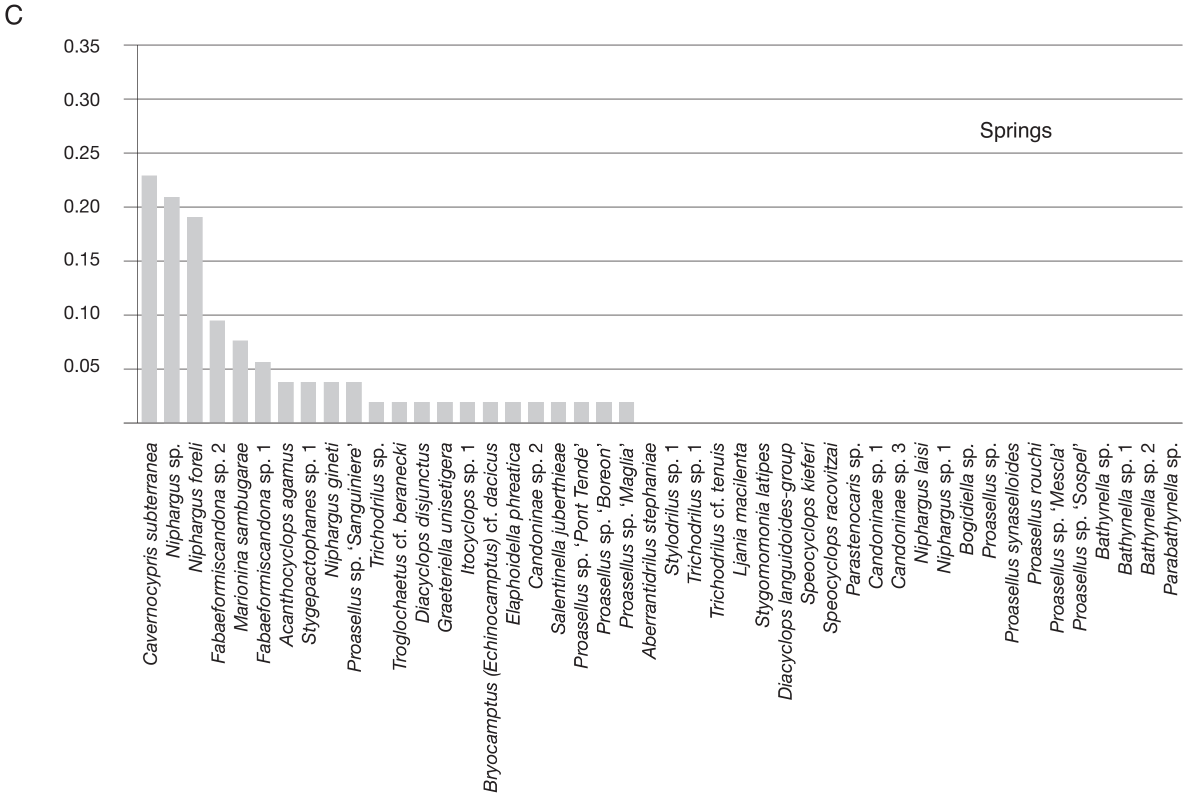


Fig. 4. — Continuation.

and *Graziana trinitatis*), four species of amphipods (*Niphargopsis casparyi* (Pratz, 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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