TAXONOMIC DIVERSITY OF GROUNDWATER HARPACTICOIDA (COPEPODA, CRUSTACEA) IN SOUTHERN FRANCE A contribution to characterise hotspot diversity sites

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A contribution to characterise hotspot diversity sites

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HOTSPOT DIVERSITY SITES
TAXONOMIC DIVERSITY
CRUSTACEA, HARPACTICOIDA
ECOLOGY
EVOLUTION

ABSTRACT. – Hotspot Diversity Sites (HDS) are characterised by high taxonomic richness and high numbers of rare (generally endemic) species; for troglobitic fauna the number of stygobitic species is also an important aspect. Additional criteria for definition of HDS are proposed here, based on the taxonomic diversity of entire subterranean faunal assemblages, i.e. the use of the indices of Average Taxonomic Distinctness and the Variation in Taxonomic Distinctness as well as the number of supra-specific taxa such as genera and families. To exemplify our approach we compared assemblages of harpacticoid copepod microcrustaceans as a focal group. We analysed 44 data sets from both groundwater and surface-water sites with special emphasis on 9 sites from southern France (Moulis in Ariège). The origin and development of the taxonomic diversity of the harpacticoid assemblages from Moulis area are analysed using phenetic and cladistic methods. The colonisation process of subsurface habitats within this area is a repetitive process occurring over long periods of time. Four sites in southern France, the Baget and the Goueil di Her (karstic systems) and the Lachein and the Nert (alluvial interstitial areas) are recognised as HDS; three others are located in non-karstic areas of Central Europe (southern Germany and eastern Austria) and South America (Central Brazil).

SITES À DIVERSITÉ EXCEPTIONNELLE
DIVERSITÉ TAXONOMIQUE
CRUSTACEA, HARPACTICOIDA
ÉCOLOGIE
ÉVOLUTION

RÉSUMÉ – Les sites à diversité exceptionnelle (Hotspot Diversity Sites = HDS) sont caractérisés par une grande richesse taxonomique et un nombre élevé d'espèces rares (généralement des endémiques); pour la faune troglobie le nombre des espèces stygobies dans une communauté est utilisé comme critère important pour le choix de tels sites. On propose des critères additionnels pour la définition des HDS basés sur la diversité taxonomique des assemblages entiers de la faune souterraine, i.e. l'utilisation des indices de diversité tels l'AvTD (Average Taxonomic Distinctness = Distinction Taxonomique Moyenne) et le VarTD (Variation in Taxonomic Distinctness = Variation de la Distinction Taxonomique) ainsi que le nombre des taxa super-spécifiques tels que le nombre de genres et de familles. Pour illustrer notre approche, nous comparons des assemblages de microcrustacés appartenant au "groupe focal" des Harpacticoida. Nous analysons 44 jeux de données provenant de sites aquatiques épigés et hypogés, en portant tout spécialement l'attention sur 9 sites du sud de la France (Moulis en Ariège). L'origine et le développement de la diversité taxonomique des communautés d'Harpacticoïdes des environs de Moulis sont examinés en utilisant des méthodes phénétiques et cladistiques. On souligne que la colonisation des habitats hypogés de cette région a été un processus récurrent durant de longues périodes de temps. Quatre sites, le Baget et le Goueil di Her d'une part (systèmes karstiques), et le Lachein et le Nert (zones alluviales interstitielles) d'autre part, sont reconnus comme HDS dans le sud de la France et trois autres sont établis pour des zones non-karstiques en Europe Centrale (Sud de l'Allemagne et Est de l'Autriche), et pour l'Amérique de Sud (Brésil Central).

INTRODUCTION

Biodiversity hotspot analysis is aimed to the identification of target sites where conservation efforts can be maximised; *i.e.,* sites where more species can be supported at lower costs. Defining a Hotspot Diversity Site (HDS), however, remains a difficult task for ecologists and conservation biologists alike. Operational criteria range from the application of a single variable, such as taxonomic richness (Prendergast *et al.* 1993) or endemicity level (Baquero & Tellería 2001), to the use of a combination of variables (*e.g.,* richness + endemism + threat to extinction in Myers 1988, 1990). It has also been recognised that the degree of (evolutionary) differences among species in a community contributes to its diversity and, consequently, must be used in measuring biodiversity for conservation priorities (Williams *et al.* 1991).

Culver & Sket (2000) reviewed the HDS concept as applied to subterranean environments, systems known to merit better study and protection. For such priority needs, compare *inter alia* Marmonier *et al.* 1994, Gibert & Fournier 1997, Ward *et al.* 1998, Sket 1999a, 1999b, Culver *et al.* 1999a, 1999b, Sharratt *et al.* 2000, Pesce 2001. Considering cave and/or karstic systems, Culver & Sket (2000) restricted the HDS concept to areas harbouring at least 20 exclusively hypogean species.

We propose an approach extending that of Culver & Sket (2000), intended to be applied when only data gathered for one focal group (*sensu* Hammond 1995) are available, and which also makes use of taxonomic relatedness. Taxonomic relatedness is measured using two diversity indices recently developed by Clarke & Warwick (1998, 1999, 2001): average taxonomic distinctness (AvTD) and variation in taxonomic distinctness (VarTD). We also use data for the subterranean assemblages as a whole, i.e., the number of stygobites, the total species richness, and the number of supra-specific taxa such as families and genera. For these latter we distinguish between "species-rich genera" (with at least three species) and "species-poor genera" (with fewer than three species).

Our approach is exemplified using harpacticoid copepod crustaceans as the focal aquatic group. These minute crustaceans have been intensively sampled in several groundwater systems within the area of Moulis, southern France, for more than 75 years, thus providing reliable information for the analysis of their taxonomic diversity. Two sites included here, the Baget karstic system and the Goueil di Her cave, already appear in the list of subterranean HDSs by Culver & Sket (2000). Two other interstitial, alluvial systems (Lachein and Nert) have also been considered diversity hotspots

based on criteria other than their harpacticoid fauna (Rouch & Danielopol 1997, Danielopol *et al.* 1999). These four sites also harbour taxonomically diverse harpacticoid assemblages.

The geographic scale at which HDSs are defined is another issue of concern. The meaning of sites at a local scale, whether they might be considered 'hot-spots' or not, is dependent on relationships among sites at a regional scale (Ricklefs 1987). Relationships among harpacticoid assemblages in the area of Moulis are explored using two different approaches, phenetic and cladistic. The phenetic approach examines the degree of faunal similarity between sites, in order to identify sites with unique or disparate assemblages. The cladistic approach, on the other hand, aims to infer historical relationships among areas based on shared presence of species. It helps also to better characterise at a local scale these sites using information offered by individual taxa (species).

Finally, the information from the Moulis-area sites is compared to several data sets on harpacticoids from both surface and subsurface aquatic habitats in Europe and the Americas, to demonstrate practically how to define Hot Spot Diversity Sites using a focal group.

MATERIAL AND METHODS

The harpacticoid fauna: The harpacticoid species identified within the Moulis area (Table I, Fig. 1) belong to two groups, hypogean species, *i.e.,* crustaceans known exclusively from subterranean waters, which in many cases display morphological and/or biological adaptive traits) and epigean ones (i.e. species living in surface waters and even in semi-aquatic habitats (cryptozoic copepods, *sensu* Fiers & Ghenne 2000), which are able to colonise subterranean systems also (Table I, "Hy" and "Ep" taxa).

Two types of taxa can be defined, generalists and specialists. Generalists are species able to live in more than one type of habitat; *e.g.,* in epigean and hypogean waters, or in both karst and porous groundwaters, such as the stygobites defined by Thienemann (1925) and Humphreys (2000a). Specialist species, on the other hand, live only in one type of habitat; *e.g.,* exclusively in caves (troglobites *sensu* Racovitza 1907) or in interstitial waters (called phreatobites by Motas 1962). One should note (Table I) that *Parastenocaris fontinalis meridionalis* is here considered a valid species, *P. meridionalis,* because of its wide geographical distribution, *i.e.,* Ariège and the Upper Rhône Valley (Rouch 1990, Schminke *in litt.*).

Sampling sites: The sampling sites are located around the Moulis village (southern France), within an area of about 40 km in diameter (Fig. 2). Each site belongs either to an interstitial system (5 sites) or to a karstic one (4 sites) (Table I). Interstitial systems can be composed of alluvial or elluvial sediments, depending on whether superficial aquifers are recharged or not by nearby run-
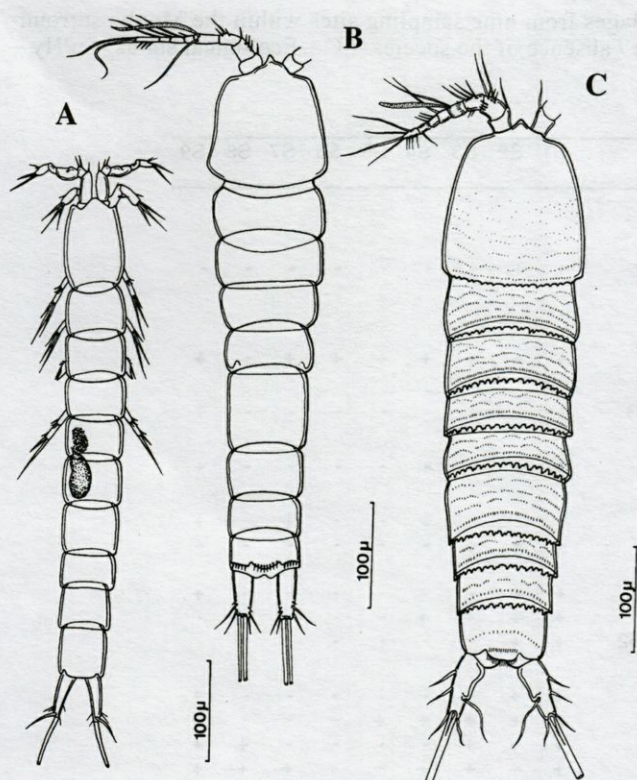
Fig. 1. – Body shapes of harpacticoid species representative from Moulis: A, *Parastenocaris dianae* Chappuis, male; B, *Parapseudoleptomesochra subterranea* (Chappuis), female; *Elaphoidella coiffaiti* Chappuis & Kiefer, female (from Rouch 1986, with kind permission from Brill Publishers).

ning waters, respectively. Phreatic habitats (*sensu* Pennak & Ward 1986 and Gibert *et al.* 1994a) are common to both types; but hyporheal or riverbed habitats (*sensu* Orghidan 1959 and Schwoerbel 1961) only occur when sediments are of alluvial origin. Within karstic systems we distinguish, following Mangin (1994), between habitats of the deep karstic zones, *i.e.*, those of the flooded (water-saturated zones) and the amphibious areas (this latter accessible to men through caves), and epikarstic aquatic habitats lying in the superficial part of the karst which forms the infiltration zone.

The Baget (S1) and the Goueil di Her (S9) are karstic systems of moderate extension (Baget, 13.25 km², Goueil di Her, 4.9 km²) belonging to two contiguous forested carbonate massifs, the Estelas and the Arbas (Fig. 2). The two subterranean karstic systems do not communicate hydrologically (Mangin 1970, 1975). Their harpacticoid fauna has been investigated over a long period of time (*cf.*, *inter alia,* Chappuis 1928, Lescher-Moutoué & Gourbault 1970), and mostly by one of the authors (*cf.*, *inter alia,* Rouch 1968, 1970, 1984, 1986a, 1986b, 1992, Rouch *et al.* 1993).

Other karstic systems here considered, Moulis-K (S7) and La Bièle (S6), are located in non-forested areas of the Sourroque massif (Fig. 2). These systems are hydrologically connected (Lescher-Moutoué 1973) and occupy a small area (Mangin pers comm). Whereas the Moulis-K site is the deep zone of the Moulis karstic system (*see* Lescher-Moutoué 1973 for an ecological description and a list of copepod species), the La Bièle site is in the subsurface epikarstic zone. In the same sampling area there is an elluvial superficial aquifer at Juan d'Arau (S5), which has also been included in this study (Fig. 2).

There are two additional interstitial systems of elluvial origin located around the Sourroque massif,
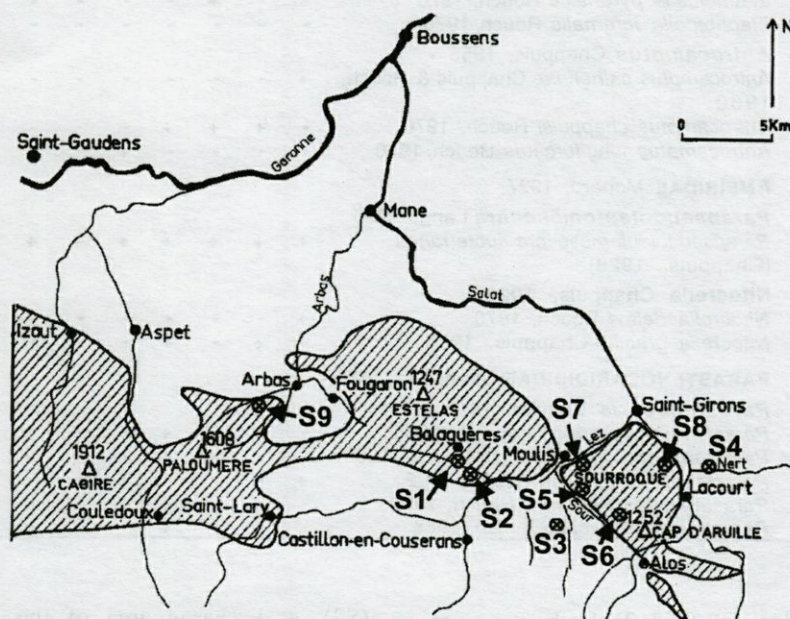
Fig. 2. – The Moulis area with the location of the nine sampling sites: 1, Baget, deep karstic system; 2, Lachein, interstitial system (hyporheal); 3, Moulis-E, interstitial elluvial system; 4, Nert interstitial system (hyporheal); 5, Juan d'Arau, interstitial elluvial system; 6, La Bièle, epikarstic system; 7, Moulis-K, deep karstic system; 8, Millas, interstitial elluvial system; 9, Goueil di Her, deep karstic system (from Lescher-Moutoué 1973, modified).

Table I. – List of species for subsurface harpacticoid assemblages from nine sampling sites within the Moulis surrounding area (Fig. 2). S1 to S9 codes as in Table II. +/ – presence / absence of the species. EC – Ecological status; Ep/Hy – Epigean/Hypogean species.

No.	EC	HARPACTICOIDA TAXA	S1	S2	S3	S4	S5	S6	S7	S8	S9
		PHYLLOGNATHOPODIDAE Gurney, 1932									
		Phyllognathopus Mrazek, 1893									
1	Ep	*Phyllognathopus viguieri* Maupas, 1892	+	+	-	-	-	-	-	-	-
		CANTHOCAMPTIDAE Sars, 1911									
		Attheyella Brady, 1880									
2	Ep	*Attheyella crassa* (Sars, 1863)	+	+	+	+	+	+	+	-	+
		Maraenobiotus Mrázek, 1893									
3	Ep	*Maraenobiotus vejdovskyi* Mrázek, 1893	+	-	-	-	-	-	-	-	+
		Epactophanes Mrázek, 1893									
4	Ep	*Epactophanes richardi* Mrázek, 1893	+	+	-	-	-	-	-	-	+
		Moraria T. & A. Scott, 1893									
5	Ep	*Moraria brevipes* (Sars, 1863)	-	-	-	+	-	-	+	-	+
6	Ep	*Moraria pectinata* Thiébaud & Pelosse, 1928	+	+	+	-	-	-	-	-	-
7	Ep	*Moraria poppei* (Mrázek, 1893)	+	+	-	+	-	-	-	-	+
8	Ep	*Moraria varica* (Graeter, 1911)	+	+	+	+	-	-	-	-	-
9	Hy	*Moraria catalana* Chappuis & Kiefer, 1952	+	+	-	+	-	-	-	-	-
		Bryocamptus Chappuis, 1928									
10	Ep	*Bryocamptus minutus* (Claus, 1863)	+	+	-	-	-	-	-	-	+
11	Ep	*Bryocamptus pygmaeus* (Sars, 1863)	+	+	+	+	+	-	-	-	+
12	Ep	*Bryocamptus typhlops* (Mrázek, 1893)	+	+	+	-	-	-	-	+	+
13	Ep	*Bryocamptus zschokkei* Schmeil, 1893	+	+	+	+	-	+	+	+	+
14	Ep	*Bryocamptus echinatus* (Mrázek, 1893)	+	+	+	+	-	+	+	-	+
		Paracamptus Chappuis, 1929									
15	Ep	*Paracamptus schmeili* (Mrázek, 1893)	+	-	-	+	-	+	-	-	-
		Ceuthonectes Chappuis, 1923									
16	Hy	*Ceuthonectes gallicus* Chappuis, 1928	+	+	-	+	-	+	+	-	-
		Elaphoidella Chappuis, 1928									
17	Hy	*Elaphoidella bouilloni* Rouch, 1964	+	+	-	+	-	-	-	+	-
18	Hy	*Elaphoidella coiffaiti* Chappuis & Kiefer, 1952	+	+	-	-	-	-	-	-	-
19	Hy	*Elaphoidella pyrenaica* Rouch, 1970	-	-	+	-	-	-	-	-	-
20	Hy	*Elaphoidella infernalis* Rouch, 1970	-	-	-	-	-	-	-	-	+
		Antrocamptus Chappuis, 1956									
21	Hy	*Antrocamptus catherinae* Chappuis & Rouch, 1960	+	-	-	-	-	-	-	-	-
22	Hy	*Antrocamptus chappuisi* Rouch, 1970	-	+	+	-	-	-	-	+	-
23	Hy	*Antrocamptus longifurcatus* Rouch, 1970	-	-	-	-	+	-	-	-	-
		AMEIRIDAE Monard, 1927									
		Parapseudoleptomesochra Lang, 1955									
24	Hy	*Parapseudoleptomesochra subterranea* (Chappuis, 1928)	+	+	+	+	+	+	+	+	+
		Nitocrella Chappuis, 1923									
25	Hy	*Nitocrella delayi* Rouch, 1970	+	-	-	-	-	-	+	-	-
26	Hy	*Nitocrella gracilis* Chappuis, 1955	+	+	-	+	-	-	-	-	+
		PARASTENOCARIDIDAE Chappuis, 1933									
		Parastenocaris Kessler, 1913									
27	Hy	*Parastenocaris dianae* Chappuis, 1955	-	+	-	-	-	-	+	-	-
28	Hy	*Parastenocaris meridionalis* (Rouch, 1990)	-	-	-	+	-	-	-	-	-
29	Hy	*Parastenocaris mangini* Rouch, 1992	+	-	-	-	-	-	-	-	-
30	Hy	*Parastenocaris nertensis* Rouch, 1990	-	-	-	+	-	-	-	-	-
31	Hy	*Parastenocaris vandeli* Rouch, 1988	-	+	-	+	-	-	-	-	-

Moulis-E (S3) and Millas (S8) (Fig. 2). Both sites were investigated by Rouch (1968) and Lescher-Moutoué (1973).

The last two sites analysed here belong to interstitial habitats of alluvial origin. One is a small area (about 70 m²) in the riverbed of a Pyrenean brook, the Lachein (S2), a discharge area of the Baget karstic system (Rouch 1988, 1991) (Fig. 2). The second site (S4) is in the sediments of the Nert stream (about 30 m²) (Gourbault & Lescher-Moutoué 1968, Rouch, 1995) (Fig. 2).

In order to expand the geographic range of our analyses, we have gathered published information on taxonomic diversity of harpacticoid copepods in other habitats (karstic, interstitial, epigean, and water-logged soil) from Europe and the Americas. Only assemblages with at least five species have been used, because the low taxonomic diversity in very poor assemblages is meaningless for further interpretation. We also avoided discussing data on benthic harpacticoids for areas larger than those of the Moulis area, such as the Laurentian Great Lakes (Hudson *et al.* 1998). Details on the data sets used for comparative purposes are presented in Appendix 1.

Species richness, higher-taxon richness and endemicity: Besides the total number of species (species richness), taxonomic uniqueness was also used as a descriptor for defining a HDS. The taxonomic uniqueness of a genus lineage is characterised by the number of its species. We distinguished between genera with one or two species (termed $G_{1/2}$ lineages) and species-rich genera, with at least three species, termed the G_3 lineages. This way of defining taxonomic uniqueness recalls Nixon & Wheeler's (1992) ideas, *i.e.,* the value of this concept lies in its comparative approach. Viewed through an evolutionary perspective, the $G_{1/2}$ and G_3 types can be conceived as phylogenetic lineages with completely different origins. The former might represent a relict lineage of a once more-diversified group, while a species-rich genus might represent a successful subterranean lineage that underwent evolutionary radiation. Additionally, the number of exclusively subterranean species and their level of endemicity, local or regional, was also calculated for the assemblages in the area of Moulis. The term "local endemics" has been applied here to stygobite species occurring in a unique subterranean locality (e.g. a cave or a single karstic system). "regional endemics", on the other hand, refer to species known from the Pyrenean area, mainly from the surroundings of Moulis.

Taxonomic diversity (= distinctness): Taxonomic diversity (TD) can be thought of as the average taxonomic "distance" between any two organisms, chosen at random from the sample (Warwick & Clarke 1995, Clarke & Warwick 1998). This distance can be visualised simply as the length of the path connecting these two organisms, traced through a Linnean or phylogenetic classification of the full set of species involved. In special cases, Linnean classifications of super-specific taxa are able to give an idea of coarse phylogenetic relationships (Clarke & Warwick 1998, Tokeshi 1999). Hence one could use them as the surrogate of a phylogeny. For the present study we restricted our analysis to taxonomic data based on classification systems by Lang (1948) and Kiefer (1978).

Clarke & Warwick (1998) proposed as a diversity index to characterise taxonomic diversity the Average Taxonomic Distinctness (AvTD or Δ^+), which measures the average length of the taxonomic path between any two randomly chosen species *(i,j)*. This index is independent of sampling effort, thus allowing comparisons between presence/absence species lists (Clarke & Warwick 1998, 2001):

$$(\text{AvTD}) \ \Delta^+ = \left[\left(\Sigma\Sigma_{i<j}\omega_{ij} \right) / (s \cdot (s-1)/2) \right]$$

where s = number of species present and ω_{ij} = distinctness weight (taxonomic distance).

Variation in Taxonomic Distinctness (VarTD) is another diversity index which measures the evenness of taxonomic structure in the assemblage under study (Clarke & Warwick 2001, Warwick & Clarke 2001). The lower its value the more uniform is the distribution of species among higher taxonomic categories. This index is calculated by:

$$(\text{VarTD}) \ \Lambda^+ = \left[\left(\Sigma\Sigma_{i \neq j}\omega_{ij}^2 \right) / (s \cdot (s-1)) \right] - \bar{\omega}^2,$$

where $\bar{\omega} \equiv \Delta^+$, and s and ω_{ij} are as above.

These indices have been computed with the computer package PRIMER-5 (Plymouth Routines in Multivariate Ecologic Research) for Windows, version 5.2 (Clarke & Gorley 2001). Three hierarchical levels were used: species, genus, and family, the latter converging to the order Harpacticoida (see taxonomic list in Table I). The paths between these levels are standardised, so that taxonomic distance between species connected at the most distant level is set at 100 (Clarke & Warwick 1999).

Relationships among harpacticoid assemblages: The phenetic approach (cluster analysis) is aimed to produce a dendrogram that summarises faunistic similarities between sites. Resemblance in faunal composition was evaluated using the Sørensen (or Dice) coefficient of association for presence/absence of species (Sneath & Sokal 1973):

$$S_{kl} = 2a \ / \ (2a+b+c),$$

where S is the probability that a single species taken at random will occur at two sites (*k*, *l*); *a* is the actual number of species occurring at both sites; *b* and *c* are the number of species occurring at only one of the two sites.

Once pairwise similarity measures for entire assemblages (epigean+hypogean) are available, overall similarities among the nine sites were computed using a hierarchical agglomerative approach (UPGMA) (Ludwig & Reynolds 1988), and a dendrogram reflecting such affinities was plotted. This analysis was also performed with PRIMER-5 version 5.2 (Clarke & Gorley 2001).

Inspired by procedures developed for phylogenetic systematics (Brooks & McLennan 1991, Lieberman 2000), the ecological cladistic approach aims to derive area cladograms from distributional data for species without making any phylogenetic or historical assumptions (Lambshead & Paterson 1986, Rosen 1988, Enghoff 2000). The method equates the absence of a species from a site to the "primitive" state (or character) of that site, whereas its presence is assumed to be the 'derived' state. Relationships among sites are then established based on shared "derived" character-species (synapomorphies). With regard to aquatic environments, this method was previously employed by Danielopol & Baltanás (1996) for the analysis of non-marine ostracods, and by Rundle *et al.* (2000) for limnic harpacticoids.

The cladistic analysis has been performed using the PAUP version 4.0b4 program (Swofford 1998) on a data matrix (31 character-species × 9 taxon-sites) based on Table I. The 'putative ancestor' is a theoretical site containing no species. Wagner parsimony, which allows the characters to reverse freely, was used as the optimality criterion (Wiley *et al.* 1991). All characters are equally weighted; topological constraints were not enforced, and branches collapsed (creating polytomies) if branch lengths were zero and the ACCTRAN optimisation option was in effect. When considering synapomorphies, one reversal per species was tolerated, being considered

a "local extinction", as proposed by Enghoff (2000). We used the Bootstrap method with branch-and-bound search (the number of bootstrap replicates was 1000 and 5000 respectively; initial "MaxTrees" setting = 200). A 50% majority-rule consensus tree was produced.

RESULTS

Species richness, higher-taxon richness and endemicity of the "Moulis area"

The harpacticoid fauna sampled in the area surrounding Moulis is listed in Table I. There are 31 species belonging to 13 genera and 4 families. The most species-rich genera are *Moraria*, *Bryocamptus*, *Parastenocaris* (each with 5 species), and *Elaphoidella* (4 species). The family Canthocamptidae displays the highest taxonomic diversity (8 genera and 22 species). The genus *Antrocamptus* is a regional endemic, with two species that are local endemics, each restricted to a single locality. The family Ameiridae, of marine origin, is also well represented in our study area (2 genera and 3 species).

Of 31 species, 14 are epigean, whereas 17 are exclusively hypogean species (Table I). Locally, the highest richness, between 15 and 22 species, is found in two karstic systems, Baget (S1) and Goueil di Her (S9), and two interstitial systems, Lachein (S2) and Nert (S4) (Table II). Each of the other five sites has between 5 and 10 species. Species-rich assemblages also display a high number of stygobites, from 4 to 9 species, and a high number (9-11) of $G_{1/2}$ taxa (Table II). Maximum higher-taxon richness (4 families) is reached at Baget and Lachein, whereas 3 harpacticoid families have representatives in Nert (Table II).

The karstic and elluvial systems harbour few local endemic species: the Baget, *A. catherinae* and *P. mangini;* Goueil di Her, *E. infernalis;* Moulis–E, *E. pyrenaica;* and Juan d'arau, *A. longifurcatus* (Table I). The Nert has two

parastenocaris species, *P. nertensis* and *P. meridionalis,* which do not occur at other Moulis sites but have been found elsewhere (*P. nertensis* in northern Spain, P. Martínez *in litt.* and *P. meridionalis* in the Upper Rhône valley, H.K. Schminke *in litt.*). *P. vandeli* was found only at the Lachein and Nert sites, this species may be a regional endemic of alluvial riverbed sediments.

Taxonomic distinctness

Average taxonomic distinctness and variation of taxonomic distinctness values for the Moulis sites and other localities are displayed in Tables II and III, respectively. For the Moulis area, AvTD ranges from 68.15 to 87.3 (mean = 77.2; n=9). The latter value corresponded to the assemblage at Moulis–K (S7) which, on the other hand, displays a moderate species richness (7 species). For other hypogean/ epigean assemblages, AvTD values are similar in range (54.8 to 88.4) although slightly lower on average (mean = 69.4; n=20) (Table III, Fig. 3). Those assemblages with only epigean species display the lowest values of all (mean = 61.9; range 54.5-68.5; n=15) (Table III, Fig. 3).

Variation in taxonomic distinctness is uncorrelated with species richness (*cf.* Table II, Figures 3, 4). The Moulis sites show an intermediate level in this index, compared to data sets corresponding to other epigean/hypogean assemblages or to epigean-only assemblages (Fig. 4).

Relationships among harpacticoid assemblages

Clustering localities according to their harpacticoid assemblages results in the phenogram plotted in Fig. 5. Two large clusters appear. The first cluster groups the four most species-rich assemblages (Baget, Lachein, Goueil and Nert) and two more or less isolated ones (Moulis-E and Millas). A second cluster groups localities in the Sourroque massif (Juan d'Arau, La Bièle and Moulis-K).

Table II.- Taxonomic diversity data for the Moulis surrounding area; HT – habitat type (K – karst system; K(e) – epikarstic system; I – interstitial system; A – alluvial sediments; E – elluvial sediments); $G_{1/2}$ – genus with 1 or 2 species; G_3 – genus with 3 or more species; AvTD – Average taxonomic diversity; VarTD – total taxonomic diversity.

| Code	Habitat Type	Site Name	Species Richness (No)	Hypogean Species (No)	Genus $G_{1/2}$ (No)	Genus G_3 (No)	Family (No)	AvTD	VarTD	Reference
S1	K	Baget	22	9	11	2	4	77.34	415.1	
S2	I (A)	Lachein	21	9	10	2	4	77.78	437.4	
S3	I (E)	Moulis-E	10	3	5	1	2	68.15	392.9	
S4	I (A)	Nert	17	9	7	3	3	81.86	471.7	
S5	I (E)	Juan d'Arau	5	3	5	0	2	80.00	266.7	Our data
S6	K(e)	La Bièle	5	2	4	0	2	76.67	455.6	
S7	K	Moulis-K	7	3	6	0	3	85.71	367.9	
S8	I (E)	Millas	6	3	5	0	2	75.56	365.4	
S9	K	Goueil di Her	15	4	9	1	2	71.43	368.9	
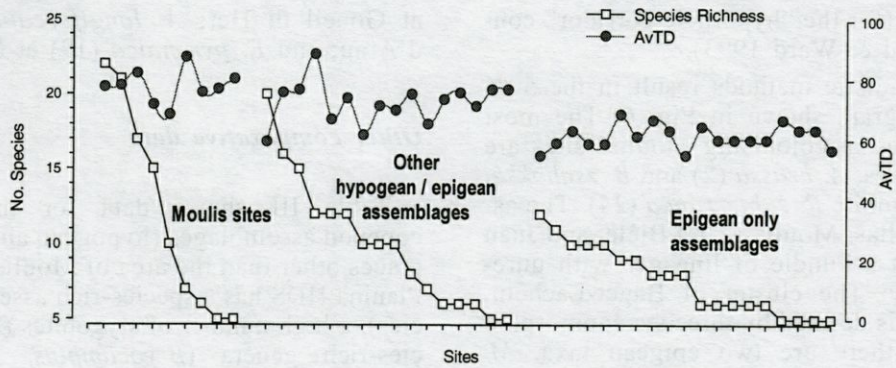
Fig. 3. – Relationship between species richness and the average taxonomic distinctness for the different sites and data sets analysed.

Within these two large clusters there are two smaller clusters within each group, the Baget-Lachein, which displays the highest similarity value, and La Bièle-Moulis-K.

The contribution of the epigean and hypogean fraction to this overall resemblance among sites was explored through similarity measurements on each component. The similarity between Baget and Lachein is mainly due to the epigean component (*cf.* Table I). Both localities are hydrologically connected (the Baget karst discharges into the Lachein) and share 12 epigean species but only 6 hypogean ones. Similarly, La Bièle epikarst represents the zone of infiltration for the deep karstic zone of the Moulis-K system, which explains their faunal similarity. A remarkable relationship is that between Baget and Goueil di Her. Both are karstic systems unconnected in depth but contiguous at the surface (see Material and Methods), a feature which results in a high number of common epigean species (10) but a low number of shared hypogean species (2). Another example of "connected" sites is La Bièle and Juan d'Arau, which share 1 hypogean species and 2 hypogean ones. Both sites belong to the Sourroque massif, where the elluvial aquifer (Juan d'Arau) lies very superficially and is likely connected to the epikarst (La Bièle). Lachein

and Nert, whose assemblages have 14 species in common (7 epigean and 7 hypogean), seem to be connected also but in a different way. These two sites are located far from each other (about 15 Km) but are related through the hyporheic corridor of
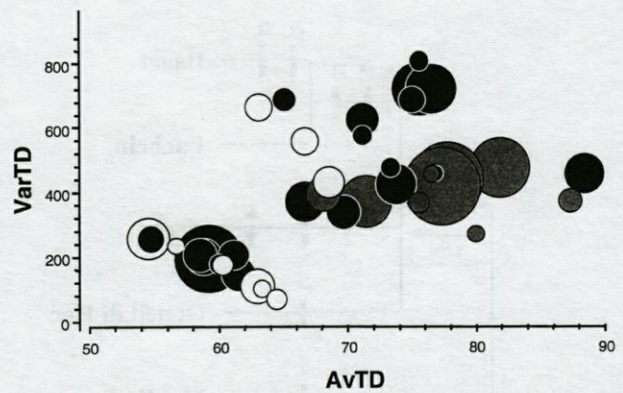

Fig. 4. – Plot of average taxonomic distinctness (AvTD), variation of taxonomic distinctness (VarTD) and species richness (proportional to circle size) for all harpacticoid copepod assemblages (white circles – epigean-only assemblages; grey circles – sites in the area of Moulis; black circles – other epigean/hypogean assemblages).
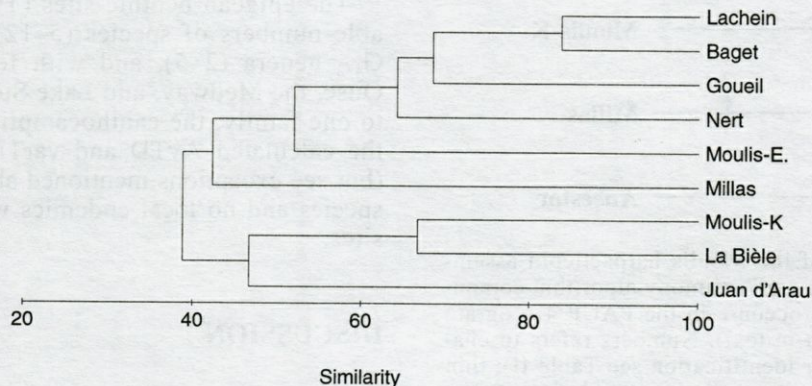

Fig. 5. – Phenogram of the Moulis harpacticoid assemblages (Table II), expressed as Sørensen coefficients of species similarity computed with an UPGMA algorithm.

the Salat stream (for the "hyporheic corridor" concept see Stanford & Ward 1993).

Ecological cladistic methods result in the 50% consensus cladogram shown in Fig. 6. The most successful species in colonising Moulis' sites are the epigean species, *A. crassa* (2) and *B. zschokkei* (12) and the stygobite *P. subterranea* (24). The assemblages of Millas, Moulis-K, La Bièle, and Juan d'Arau represent a bundle of lineages with unresolved polytomy. The cluster of Baget-Lachein, Nert and Goueil is defined by three synapomorphic species. Again there are two epigean taxa, *M. poppei* (7) and *B. minutus* (10), and a hypogean taxa, *N. gracilis* (26). Note that Nert and Goueil di Her form an unresolved polytomy. Finally Baget and Lachein form a cluster defined by two hypogean taxa, *M. catalana* (9) and *E. coiffaiti* (18), and an epigean taxa, *P. viguieri* (1). There are several species occurring at unique sites, equivalent to autapomorphic characters: *A. catherinae* (21) and, *P. mangini* (29) at Baget; *P. meridionalis* (28) and *P. nertensis* (30) at Nert; *E. infernalis* (20)

at Goueil di Her; *A. longifurcatus* (23) at Juan d'Arau; and *E. pyrenaica* (19) at Moulis-E.

Other comparative data

Table III shows data for the harpacticoid copepod assemblages (hypogean and epigean) from places other than the area of Moulis. The Postojna-Planina HDS has a species-rich assemblage (20 species), a high number of stygobites (8), and two species-rich genera (*Bryocamptus*, 8 species and *Elaphoidella*, 5 species). The number of $G_{1/2}$ genera is moderate (6 genera), with all taxa belonging to one family, the Canthocamptidae. This situation contributed to low values of both the AvTD (59.21) and VarTD (193).

Harpacticoid assemblages from interstitial alluvial habitats display a wide range of values (Table III). The Lobau, on the Danube in Austria, is remarkable for its high number of stygobites (5 of a total of 12 species), belonging to two families, Ameiridae (1 species) and Parastenocarididae (4 species), the other species being canthocamptids and a phyllognathopodid. The AvTD and the VarTD values are high (88.38 and 454, respectively), due mainly to the numerous $G_{1/2}$ lineages and the number of families (4). The assemblages collected exclusively from riverbed sediment sites (*i.e.*, hyporheic habitats), the Seebach (Lunz) and Wappinger Creek (North America), displayed a relatively high number of species (12) belonging to a rather high number of $G_{1/2}$ genera (6–7) and to 2 or 3 families (Table III). These assemblages have AvTD values (66.7 and 73.7) in the lower range of the sites in Moulis, but very similar VarTD values (370 and 421). The assemblages of the Brenta and the Adige rivers in Italy, the Singine River in Switzerland, and Coxing Kill in North America (Table III) have variable numbers of species (5–10) and low numbers of stygobites (1–3); AvTD values range between 54.76 and 76.67, with a wide range of VarTD values (178-685).

The epigean benthic sites (Table III) have variable numbers of species (5–12) belonging to few $G_{1/2}$ genera (2–5), and with few exceptions (the Ouse, the Medway, and Lake Stechlin) they belong to one family, the canthocamptidae. Consequently, the calculated AvTD and varTD values were low (but see exceptions mentioned above). No stygobite species and no local endemics were found at these sites.
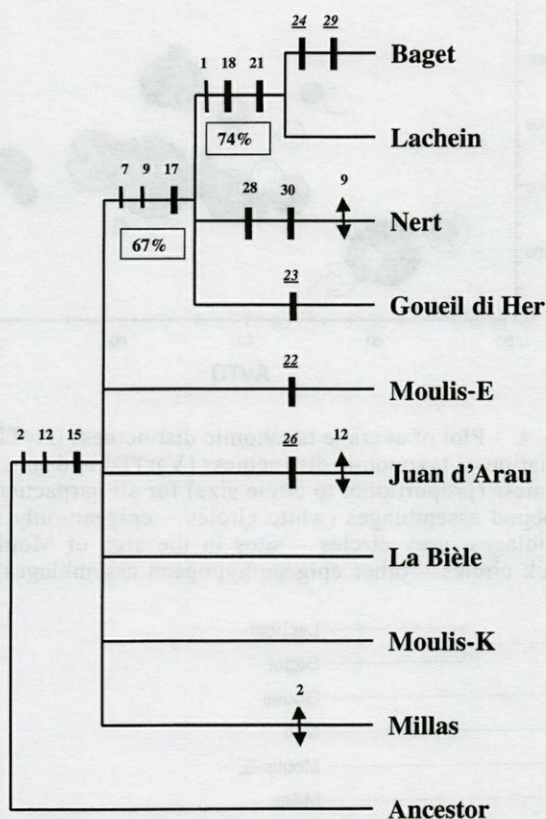

Fig. 6. – Cladogram of the Moulis harpacticoid assemblages using the Maximum Parsimony algorithm computed by the Bootstrap procedure in the PAUP 4 program (additional information in text). Numbers refers to character-species (for their identification see Table II); thin lines – epigean species; thick line – stygobitic species; underlined number – "autapomorphic" species; double arrow – "reversal" character. Percentages refer to the retention degree of congruent solutions.

DISCUSSION

From the information presented here (44 data sets), it appears that the species richness of entire assemblages is the most readily available

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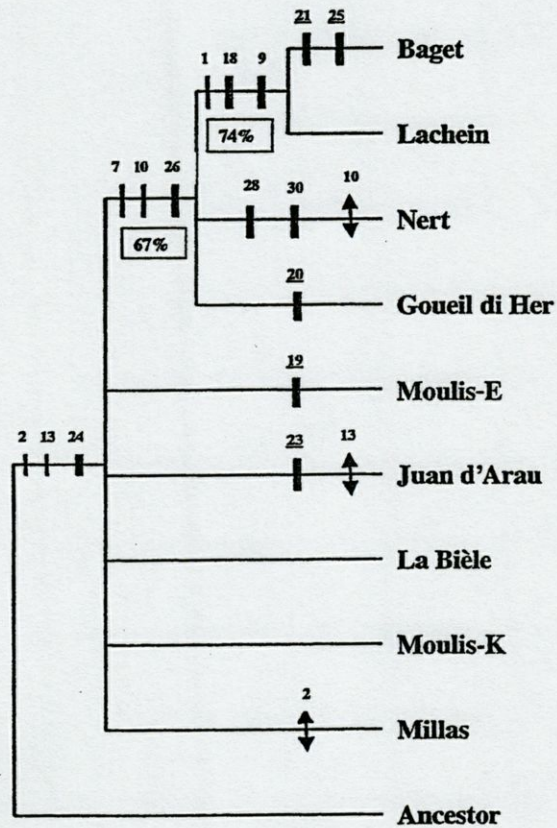
This is the correct Fig 6 which considers the numbers of the species mentioned in the Table I.

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Table III. – Taxonomic diversity data for harpacticoid assemblages from the literature (codes as in Table II).

Habitat Type	Site Name	Species Richness (No)	Hypogean Species (No)	Genus $G_{1/2}$ (No)	Genus G_3 (No)	Family (No)	AvTD	VarTD	Reference
Karstic Systems	Postojna-Planina (Slovenia)	20	8	6	2	1	59.21	193	Brancelj, 1986
	Dorvan-Cleyzieu (France)	10	2	5	1	1	61.48	146	Gibert, 1986
Elluvial Interstitial Waters	Langenwald Q. Todtmoos (Germany)	16	5	2	3	3	75.56	717.3	Steenken, 1998
	Kleislewald Q. Kirchzarten (Germany)	7	1	2	1	2	65.08	685.3	Steenken, 1998
	Kleislewald 4 Q. (Germany)	6	1	4	0	2	73.33	474.1	Steenken, 1998
	Brunnmaettle Q. Herrischried (Germany)	6	1	2	1	2	75.56	805.9	Steenken, 1998
	Saegenbuck 1 Q. Waldshut (Germany)	5	1	4	0	2	76.67	454.3	Steenken, 1998
	Saegenbuck Q. (Germany)	10	2	2	2	2	71.11	455.6	Steenken, 1998
Alluvial Interstitial Waters	Lobau at Vienna (Austria)	12	5	8	1	4	88.38	572.8	Pospisil, 1994; Danielopol et al., 2000; Danielopol & Pospisil, 2001
	Seebach-Lunz (Austria)	12	1	6	1	2	66.67	684.5	Schmid-Araya & Schmid, 1995
	Adige River – A51 (Italy)	5	1	4	0	2	76.67	336.9	Ferrarese & Sambugar, 1976
	Adige River – A22 (Italy)	6	1	3	1	2	71.11	622.2	Ferrarese & Sambugar, 1976
	Brenta River – B4 (Italy)	8	3	4	1	3	75	718	Braioni et al., 1980
	Singine River – 5 (Switzerland)	8	0	2	2	1	54.76	233.3	Kowarc, 1993
	Singine River – CS (Switzerland)	9	0	2	2	1	61.11	555.6	Kowarc, 1993
	Singine River – 3 (Switzerland)	10	0	4	1	1	58.52	661.8	Kowarc, 1993
	Singine River – 4 (Switzerland)	11	0	3	2	1	58.79		Kowarc, 1993
	Coxing Kill (USA)	10	2	5	1	2	69.63		Strayer, 1988
	Wappinger Creek (USA)	12	2	7	2	3	73.74	455.6	Strayer, 1988
Interstitial Habitat (seasonally water logged soil)	Água Limpa – site C (Brazil)	15	10?	2	3	3	76.51	177.8	Reid, 1984
Epigean Benthic Habitats	Danube River at Vienna (Austria)	5	0	2	1	1	56.67	69.14	Schönbauer, 1999
	Singine River – HS (Switzerland)	6	0	3	1	1	60	100	Kowarc, 1993
	Medway River (UK)	8	0	3	1	2	66.67	177.8	Rundle & Hildrew, 1990
	Ouse River (UK)	8	0	3	1	2	63.1	205.2	Rundle & Hildrew, 1990
	Twyi and Camddwr streams (UK)	12	0	2	1	2	54.55	109.7	Rundle, 1993
	Gooseberry Creek (USA)	5	0	4	0	1	63.33	428.7	Shiozawa, 1991
	Buckboard Creek (USA)	5	0	5	0	1	66.67	370.4	Shiozawa, 1991
	Valley Creek (USA)	6	0	3	1	1	60	205.2	Shiozawa, 1991
	Elbow Lake Creek (USA)	6	0	3	1	1	60	200.6	Shiozawa, 1991
	Lake Geneva – 5 (Switzerland)	6	0	5	0	1	64.44	255.1	Dussart, 1966
	Lake Geneva – 11 (Switzerland)	5	0	4	0	1	63.33	205.2	Dussart, 1966
	Lake Geneva – 13 (Switzerland)	6	0	3	1	1	60	177.8	Dussart, 1966
	Lake Geneva – T (Switzerland)	10	0	4	1	1	58.52	257.1	Dussart, 1966
	Lake Pääjärvi (Finland)	10	0	5	1	1	62.96	177.8	Sarvala, 1986
	Lake Stechlin (Germany)	9	0	3	2	2	68.52	421.4	Flössner et al., 1985

descriptor and the first to be applied for defining HDS. Those assemblages having 15 or more species are good candidates (Tables II, III). An additional twist is provided by taxonomic diversity. Degree of relatedness and the taxonomic structure of the assemblage are also of value. A group of n species belonging to many high-rank taxa is more diverse than the same number of congeneric species. Statistics related to those features can be easily estimated even if only presence/absence data are at hand. Of course, estimations can be significantly enhanced when quantitative data on the relative abundances of the species in the assemblage are available and there is a phylogenetic hypothesis concerning the focal group.

The average taxonomic distinctness (AvTD) gives us an idea of the taxonomic diversity within the assemblage, irrespective of its species richness. As seen from our data, even assemblages with a low number of species could display high AvTD values (e.g. Moulis-K, Table II, Fig. 3 & 4). Taxonomically diverse subterranean assemblages generally display values higher than 70 points, an arbitrary threshold that can be used for the quantitative selection of candidates for HDS. The high taxonomic diversity of some interstitial systems is very similar to those of caves or karstic systems. Therefore we consider that the concept of HDS can be used for both karstic and non-karstic subterranean

sites within the framework of a unified research programme of groundwater ecology, as discussed by Gibert et al. (1994a).

Variation of taxonomic distinctness (VarTD) also provides some hints for the selection of HDS. Because it measures the variability in taxonomic structure within an assemblage, lower values indicate the coexistence of species evenly distributed among higher-rank taxa (e.g., classes, families or genera, cf. Tables I-III). When combined with AvTD, VarTD can be fruitfully used for understanding the structure of the taxanomic assemblage. For instance, Postojna-Planina has already been designed as a HDS because of the high number of stygobiont species that harbours (Culver & Sket 2000). Although it also has a large number of harpacticoid species (Table III), both AvTD and VarTD values were low. This reflects that, taxonomically, the species in the assemblage are relatively closely related and that the structure is fairly uniform (only 2 speciose genera out of 8 i.e. genera represented by 3 or more species in the site).

Are low (or high) VarTD values operationally valid attributes for defining a HDS? The answer depends on the values of the AvTD. A highly taxonomically diverse assemblage (high AvTD) with low VarTD reflects the existence of many or few, depending on species richness, distantly-related

species. The same AvTD value accompanied by a high VarTD implies that there are sub-groups of closely related species in the assemblage coexisting with many unrelated lineages. Because of the risk of extinction, the presence of isolated lineages (without close relatives in the area) within an assemblage can be used as an argument for site protection, and hence to define an HDS, an argument also advocated by Warwick & Clarke (2001) and documented for subterranean harpacticoids by Pesce (2001). Additionally, the origin of high taxonomic distinctness in an assemblage can be further explored by examining the number of $G_{1/2}$ and G_3 genera and the number of local endemic species. For instance, species-rich assemblages in Lake Baikal (Boxshall & Evstigneeva 1994) or those of the Postojna–Planina karstic system are dominated by species-flocks belonging to a few G_3 genera.

Not all the quantitative parameters to evaluate Taxonomic Diversity in order to delineate a HDS are always congruent. This is the case, for instance, with the Goueil di Her. This site is considered a HDS (Culver & Sket 2000) because of the high number of stygobitic species, but the hypogean harpacticoid fraction is smaller than those occurring at the Baget and Lachein sites (Table II). Therefore it is useful, beside quantitative estimators when one intends to define and/or to protect a HDS, to consider also non-quantitative criteria based on the intrinsic value of the subterranean fauna. The presence of interesting local endemics and/or highly adapted stygobitic animals can provide useful criteria. Goueil di Her, for instance, harbours such an endemic species, *Elaphoidella infernalis*. Other sites are remarkable for speciose G_3 genera, *e.g.* the Nert site has a rich fauna of the genus *Parastenocaris*, represented by four species occurring within 30 m² (Table I).

Spatial scale also plays a role in the process of HDS selection because different results can be achieved depending on whether a meso- (metre), macro- (Kilometre) or giga- (over 100 Kilometres) scale is used. Similarity analysis helps to reveal faunistic resemblances among local sites and to identify the presence of "unique" sites.

The utility of the HDS concept using a focal organismal group increases with the addition of supplementary information on the origin and development of the animal assemblage at various sites. The comparative data among the four assemblages of the HDS around Moulis and the assemblage of the Postojna-Planina karstic system, a HDS listed by Culver & Sket (2000), showed differences in taxonomic diversity. These differences are apparently due to the different evolutionary histories of the faunas in the two geographic areas (for the Slovenian area, see Sket 1999). While, within the Moulis area, hypogean representatives of the families Ameiridae and Parastenocarididae as well as species of the regional endemic canthocamptid genus *Antrocamptus* commonly occur, the Planina-Postojna system is dominated by a high number of canthocamptid species belonging to only two genera, *Bryocamptus* and *Elaphoidella*. This also explains the low AvTD value of the Slovenian karstic system compared to those of the four Moulis sites.

The harpacticoid groups from which stygobitic taxa originated have miniaturised and elongated body shapes, with short setae on the antennal appendages (Fig. 1); these general characters allow them to live within the benthic zone of the aquatic environment and predispose them to colonise subsurface habitats. The harpacticoid assemblages that we described from the area surrounding Moulis include an important fraction of epigean generalist species (Table I) known to colonise a large variety of surface-water habitats in Europe (Kiefer 1978). Notorious examples are *Attheyella crassa, Moraria poppei, Epactophanes richardi, Paracamptus schmeili,* and *Bryocamptus minutus*. Most of the epigean species listed in Table I also live in cryptozoic (semi-terrestrial) habitats, *i.e.,* within the film of water accumulated between the soil and organic debris (decaying plant remains), as documented by Dussart (1967) and Fiers & Ghenne (2000) among others. Epigean *Elaphoidella* species colonise cryptozoic habitats in tropical forests (Defaye & Heymer 1996).

Harpacticoids also have a high propensity to colonise new habitats. For instance *A. crassa* colonised a new benthic habitat in a man-made channel in Austria within 1–2 years (Gaviria 1998). Members of the genus *Phyllognathopus* also easily colonise subsurface habitats (Rouch 1972), and *Ph. viguieri*, a generalist cosmopolite species (Lehman & Reid 1992), is known to colonise interstitial habitats as well (Dussart 1966).

The cladistic analysis (Fig. 6) offered information from individual taxa about the history of the various sites of the Moulis area. For instance, Baget and Lachein and the Goueil di Her and the Nert apparently developed an ecological environment more favourable for the persistence of more similar and/or unique rare species than the sites located in the Sourroque carbonate massif. Turning to the hypogean fraction of the assemblages colonising the 9 sites of the Moulis area, one notices (Fig. 6) that generalist species such as *Parapseudoleptomesochra subterranea, Ceuthonectes gallicus,* and *Nitocrella gracilis* occur in addition to specialised species such as *Elaphoidella infernalis, Antrocamptus longifurcatus,* and *N. delayi*.

Ameirid species (*i.e.,* representatives of the genera *Parapseudoleptomesochra* and *Nitocrella*) belong to an essentially marine group. Their representatives may have colonised the subterranean limnic inland waters during past geological epochs, possibly during the Tertiary (Rouch 1986b).

The higher taxonomic diversity of the Moulis assemblages is due also to the strong tendency to speciate of some harpacticoid lineages. These induce the speciose genera *Bryocamptus, Moraria, Elaphoidella* and *Parastenocaris* (Kiefer 1978, Rouch 1986a, 1986b). Especially interesting is the case of *Elaphoidella sensu lato* which has 186 species of which 109 live in subterranean waters of temperate and subtropical zones (Rouch 1984, 1994, Dussart & Defaye 1990, Reid 1993, Bruno *et al.* 2000). All this information suggests that the colonisation of subterranean habitats is a permanent historical process.

An additional factor which induced the high diversity of several harpacticoid assemblages of this area is the hydrologic connectivity between various ecological systems. The important fraction of epigean species within the Baget and Goueil di Her assemblages is due, in our opinion, to the contribution of cryptozoic species, which develop at the surface of karstic systems in the forested areas. Those species penetrate with the infiltration of surface water into the subsurface karstic systems where they can establish perennial populations (Rouch 1977, 1984, 1986a). The high number of epigean species, as well as some hypogean species, occurring at the Lachein site is also due to its hydrological connection to the Baget karstic system. The outlet of the latter discharges into the Lachein close to the interstitial site discussed here (Rouch 1970, 1991). There is also a possible exchange of fauna through hyporheic corridors between the assemblages of the Lachein and the fauna inhabiting other sites within the Salat drainage system, *e.g.* the Nert. This could explain the presence of the hypogean *Parastenocaris vandeli* at both sites. A similar hydrological connection could explain the similarities between the species composition (especially the epigean fraction) of La Bièle and Moulis-K, *i.e.*, a part of the epigean fauna of the epikarstic area around La Bièle is transmitted to the deeper karstic habitat Moulis-K. The lower diversity of the epigean fraction of the Moulis karstic systems seems to be due to the lack of a diversified epigean harpacticoid fauna at the surface of this area.

The size and number of microhabitats available to the harpacticoid fauna within one macrohabitat also explains the differences between the Moulis assemblages. Compared to the Moulis system, the Baget karstic system is larger and has a better-developed annex system; its hypogean harpacticoid fauna is much richer (Tables I, II). The richness of the Nert sampling site is less than the half that of Lachein, and the harpacticoid diversity of the former is markedly lower than of the latter (Tables I, II).

The presence of hypogean taxa belonging to taxonomic groups such as *Parapseudoleptomesochra* and *Nitocrella,* or groups known to have a high an-

cestry such as *Parastenocaris* and *Elaphoidella* (Chappuis 1927, Thienemann 1950) suggests that the extinction rate of taxa within the subterranean assemblages of the Moulis area is lower than that of the epigean fauna of surface aquatic sites in Europe (Kiefer 1978).

Finally, the time factor also plays a role in increasing the diversity of harpacticoid assemblages. Hypogean species are able to extend their distribution through the connectivity of different subsurface habitats, *e.g.,* the taxa occurring at both the Lachein and Nert sites or at Juan d'Arau and La Bièle (Tables I, II).

Using this approach and the data presented above, we designated the following areas within the Moulis surrounding area as HDS: the Baget, the Goueil di Her, the Lachein, and the Nert. In this way we corroborate earlier conclusions based on different criteria (Introduction). We also corroborate the decision of Culver & Sket (2000), who elected the Postojna–Planina karstic system as a HDS, and that of Danielopol & Pospisil (2001) in the case of the restricted Lobau area around sites A, B and C (Table III). Two other areas could also be nominated as HDS, the spring Langenwald–Todtmoos (the outlet of an elluvial aquifer) in southern Germany, and the Agua Limpa site C in Brazil (Table III).

Hotspot Diversity Sites with faunal assemblages having a high number of hypogean species, and a high number of genera, each with few species, some of these species being local or regional endemics, can be metaphorically compared with an art museum containing many valuable items (Danielopol 1998). Implementation of coherent measures for environmental protection of subterranean Hotspot Diversity Sites requires the protection of entire ecosystems, giving equal chances for protection to as many species as possible, considering that they are irreplaceable resources to humanity. We employ here the arguments of Wilson (1992), but see also the arguments developed by Rouch & Danielopol (1997), Gould (1998), Sket (1999a, 1999b), Culver *et al.* (1999a, 1999b), Ghilarov (2000), Humphreys (2000b), Danielopol & Pospsil (2001) and Boulton (2001), to quote only a few scientists who argue for efficient protection of our natural environs.

(Martinsville, Virginia), S Rundle (Plymouth), B Sambugar (Verona), HK Schminke (Oldenburg), D Strayer (Millbrook, New York) and two reviewers. DLD is much indebted for financial support to the Austrian "Fonds der wissenschaftlichen Forschung" Project N° 11149).

APPENDIX I – *Additional information concerning localities and harpacticoid data sets*

Postojna-Planina Cave System (Slovenia), karstic system. A complex of galleries about 20–30 km long and with numerous aquatic habitats (Brancelj 1986). This area harbours the world's most diverse subterranean fauna (Culver & Sket 2000). 48 taxa belong to the aquatic hypogean fauna.

Dorvan-Cleyzieu (French Alps), karstic system (10.5 Km^2) (Gibert 1986, Gibert *et al.* 1994b, 2000). Harpacticoid fauna identified by J Gibert and R Rouch (data in Gibert 1986) and by D Galassi (unpubl data pers comm J Gibert).

Langenwaldquelle Todtmoos, Kleislewaldquelle Kirchzarten, Kleislewaldquelle Nr 4, Brunnmaettlequelle Herrischried, Saegenbuckquelle and Saegenbuckquelle Nr 1–Waldshut (Southern Baden-Württemberg, Germany). All are springs flowing out of an elluvial granitic aquifer. Groundwater fauna was filtered from the springs for 24 hours at seven different times of the year and described by Steenken (1998).

Site C in Fazenda Agua Limpa, Distrito Federal, Brazil. A savannah area with seasonally water-logged terrestrial habitats harbouring species-rich harpacticoid and cyclopoid assemblages (Reid 1984). Because of the large number of new species of Parastenocarididae from this Brazilian site left in open nomenclature (Reid 1984), the total number of stygobites was only approximately evaluated here (Table III).

Lobau A, B and C in the "Untere Lobau" wetlands at Vienna, Austria. An alluvial aquifer along the Danube sampled intensively in an area of about 0.8 Km^2 (Danielopol 1983, Pospisil 1994, Pospisil & Danielopol 2000, Danielopol *et al.* 2000, Danielopol & Pospisil 2001). With regard to the number of stygobites (35 species), this area ranks fourth in the list of the world's most species-rich areas (Danielopol & Pospisil 2001). According to criteria developed by Culver & Sket (2000), this is a Hot Spot Diversity Site.

The Ritrodat site on the Seebach at Lunz am See, Austria. Hyporheic habitat (70 m^2 riverbed area) monitored since 1976 by G. Bretschko and his students. Schmid-Araya & Schmid (1995) catalogued 12 harpacticoid species.

Site A22 on the Adige River at Ceraino and Site B4 on the Brenta River, both in northern Italy. Hyporheic habitats (Ferarese & Sambugar 1976, Braioni *et al.* 1980).

Singine HS (Fribourg, Switzerland), riverbed sediments in an alpine stream. Surface-dwelling benthic fauna sampled with a Surber sampler. Sediment samples (20 cm deep) with interstitial harpacticoids obtained with a freezing-core at four sites, Singine River 3, 4, 5 and CS (Kowarc 1993).

Wappinger Creek (near Millbrook) and Coxing Kill (near New Paltz) (southern New York State, U.S.A.). Hyporheic habitats with interstitial harpacticoid fauna sampled during one year on a monthly basis (Strayer 1988).

Danube River, main channel, Vienna area, Austria. Meiobenthic fauna, including harpacticoids, sampled during one year at six sites along the Danube channel from Km 1942 to Km 1925 (Schönbauer 1999).

Medway and Ouse rivers (south east England). Benthic fauna sampled with a Surber sampler at 13 sites within an area with a radius of about 7 Km (Rundle & Hildrew 1990). Similarly, Rundle (1993) investigated 3 sites located within an area with a radius of about 5 Km on the Twyi and Camddwr streams in mid-Wales.

Buckboard Creek, Elbow Lake Creek, Gooseberry River and Valley Creek (Minnesota, U.S.A.). Benthic stream fauna sampled with mini-box cores which penetrated into the sandy gravel sediments down to 2.5 cm (Shiozawa 1991).

Thonon-les-Bains (between Yvoire and Pointe Ripaille, Lake Geneva). Surface benthic harpacticoid fauna from 14 samples (Dussart 1966). The samples discussed here (we use for the sites the numbers given in Dussart's publication) are: Lake Geneva–5 (off Vion, 6–8 m deep), Lake Geneva–11 (Pointe de Ripaile, 50–60 m deep), Lake Geneva–13 (Yvoire, 50–60 m deep). For comparative purposes we also calculated the taxonomic diversity of the total benthic fauna of this area (Lake Geneva–T, in Table III).

Lake Pääjärvi (Finland), benthic harpacticoid data from 60 sampling sites (littoral and sub-littoral areas down to 10 m deep) around the lake (13 Km^2 surface, and 85 m maximum depth) (Sarvala 1986, 1998).

Lake Stechlin (Rheinsberg, Germany), harpacticoid fauna mainly from the littoral and sub-littoral zones (Flössner *et al.* 1985) of this mid-size lake (4.3 Km^2, Krey 1985).

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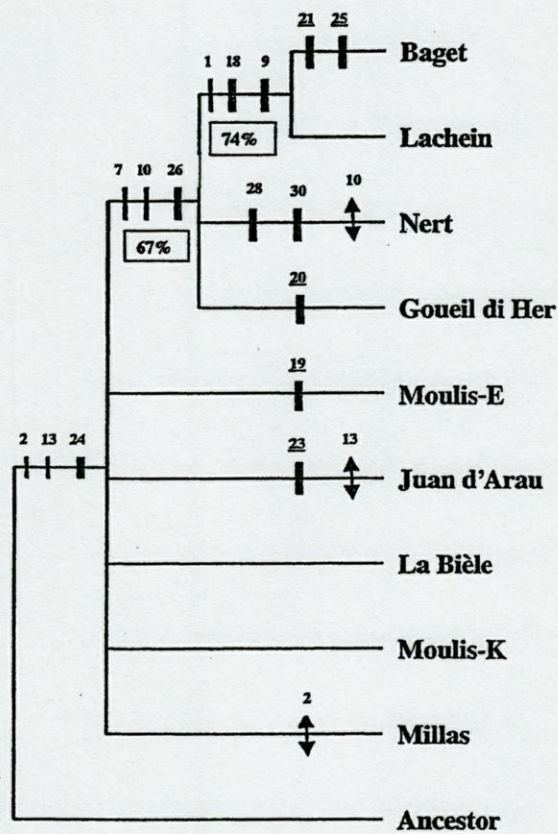
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ERRATUM

This is the correct Fig 6 which considers the numbers of the species mentioned in the Table I.

Cette figure est à insérer page 8 à la place de la figure 6.

Substitute this figure for figure 6, page 8