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Cryptozoic copepods from Belgium: diversity and biogeographic implications[1]

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ABSTRACT. During an intensive survey of the presence and distribution of soil nematodes in Belgium, several samples were found to contain harpacticoid and cyclopoid copepods. Population characteristics could not be studied because the sampling methods were inadequate for the collection of copepods. We report here on the diversity, and discuss the habitat preferences, of those cryptozoic copepods. Four cyclopoid and 13 harpacticoid species were identified. One cyclopoid and eight harpacticoids have not been previously reported from Belgium. Species of Morariinae and Canthocamptinae were encountered in nearly every type of habitat. The presence of the hypogean cyclopoid *Graeteriella unisetigera* in leaf litter was unexpected and we discuss its distribution in Europe. Based on those observations, the concept of the importance of leaf litter in the dispersion of stygofauna and its population maintenance is advanced.

KEY WORDS: Copepoda, Cyclopoida, Harpacticoida, Cryptozoic copepods, Belgium.

INTRODUCTION

That free-living harpacticoid and cyclopoid copepods may form an important component of the cryptozoic microfauna in moist forest litter was first recognized at the end of the last century (Dendy, 1895: see Reid, 1986). In comparison, however, with the multitude of studies on aquatic systems, the number of studies on copepods in terrestrial and semi-terrestrial habitats is rather limited. Most of the reports on cryptozoic copepods are from exotic places: New Zealand beech forest litter (Harding, 1958), Australian forests (Dendy, 1895; Plowman, 1979), a sedge meadow in the Canadian tundra (Bliss *et al.*, 1973), the Paramo region in the Colombian Andes (Sturm, 1978), and a wet campo marsh in sub-tropical Brazil (Reid, 1984).

Kikuchi (1984) demonstrated that the occurrence of harpacticoids of the genus *Moraria* (Canthocamptidae) in forest litter in temperate and cool-temperate regions is not an occasional fact, but that these animals form a substantial part of the soil fauna and are widely distributed in the Japanese forests on Hokkaido and the northern part of Honshu. In addition, the same author reported on harpacticoids that were collected in mountain forests under subarctic conditions. The species richness in humid leaf litter at higher altitudes was shown by Dumont et al. (1988), who discovered five new species and a new genus in samples obtained between 1900 and 3800 m in forests of Nepal on the slopes of the Himalayas.

In Europe, with its long tradition in the study of Copepoda, the existence of this faunal component has been documented by Gurney (1932), Remy (1932), Scourfield (1939), Klie (1943), Brunberg Nielsen (1966) and Dumont (1972). Thus far, eight different species have been identified in terrestrial samples from European localities. All these studies dealt only with descriptions of the species encountered in terrestrial samples, except for the work by Brunberg Nielsen (1966), who studied several aspects of the biology of two species in Danish beech forests.

That copepods may constitute an important part of the cryptozoic assemblages in forest litter is generally known in studies of the soil fauna. While Wallwork (1976) mentioned that harpacticoid copepods were "surprisingly abundant" in moist beech litter in southern England, studies by Schaefer (1991) and Schauermann (in Schaefer, 1991) revealed that densities of 3000 to 4000 specimens per

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[1] Part of this article was presented as a poster by the same authors during the 4th Benelux Congress of Zoology (Utrecht, 14-15 November 1997) under the title: Evidence of the superficial distribution of the hypogean cyclopoid copepod: *Graeteriella unisetigera* (Graeter, 1908).
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square meter in beech forests near Goettingen and Solling (Germany) are quite normal. Diversity, however, seems rather low. SCHAUERMANN (op. cit.) assumed that the copepod populations encountered in Solling were constituted by a single (unnamed) harpacticoid copepod.

It is evident that today, at the dawn of the 21st century, our knowledge about the diversity, density and distributional range of those free-living copepods occurring in terrestrial and semi-terrestrial habitats is quite scanty.

During an intensive sampling program in Belgium (1977-1981), as part of the "European Plant Parasitic Nematodes Survey", D. DE WAELE found harpacticoid and cyclopoid copepods in 76 samples. This represents only a small fraction of the 2000 samples originally taken, but it became evident that the methodology used to quantify the nematode populations was inadequate to collect the copepods (see section on methodology). Because of these limitations, and the large differences between the number of sampled vegetation types, it is impossible to quantify the parameters of the copepod populations from these data. The aim of this paper is restricted to the presentation of the copepod diversity encountered in these terrestrial samples and some indication of their ecological preferences and distributional ranges, partly taken from the literature records.

MATERIAL AND METHODS

Soil samples were collected using a soil corer with a diameter of 2 cm, designed to collect soil nematodes. In each locality, 2 kg of soil was removed within a circle of 20 cm diameter at various depths, and assembled in a bag. The depth of the sample depended on the vegetation type, and ranged from surface samples to a depth of 40 cm. The samples were preserved overnight at 4° C upon arrival at the laboratory.

Samples were treated as follows: after homogenizing the sample, 100 g of soil (approximatelly 5 % of the entire sample) was suspended in 300 ml distilled water; the mixture sieved on a 2 mm mesh size sieve, and the fraction smaller than 2 mm suspended in 4.5 l distilled water. This solution was sieved twice on a 38 µm mesh size sieve, after which the retained residue was fixed with a 4% formaldehyde solution (heated to 75° C). The fixed residue was twice centrifuged at 3000 rpm, once in distilled water, once in a 50 % solution of Ludox® and water.

Animals were sorted under a stereo-microscope, and stored in 75 % denatured ethyl alcohol. Copepod specimens (either preserved or dissected) were deposited in the Recent Invertebrate Collections at the Royal Belgian Institute of Natural Sciences, Brussels.

The 2015 samples collected during the survey were subdivided according to the type of primary vegetation:

Type A: 341 samples from fields under intensive cultivation;

Type D: 526 samples from deciduous forest subdivided into seven families;

Type G: 1148 samples from pastures, roadsides, riversides, and fallow land.

In only 76 samples (4.5%) were copepods found (Fig. 1). This low number could be interpreted as an indication that copepods occur only occasionally in soil samples. However, it should be noted that the sampling and sorting methods used during this study were inadequate to collect micro-arthropods such as copepods. Copepods living in leaf litter occur in the layer of decaying leaves directly on top of the forest floor (BRUNBERG NIELSEN, 1966), and in the case of grass vegetation, under the herbs directly on the soil. In contrast, nematodes penetrate much deeper into the soil, requiring a method of collecting the deeper strata of the soil where copepods do not occur. Furthermore, while at each locality about 2 kg of sediment was collected, only 100 g were effectively sorted after the entire sample was homogenized. Evidently, the possibility of finding copepods in this small subsample is rather low.

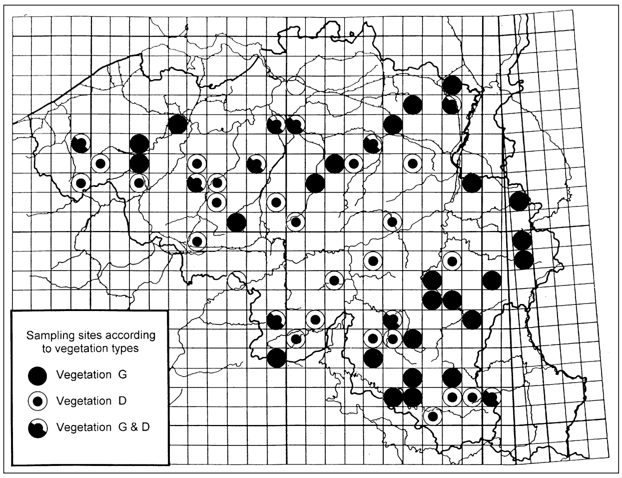

Fig. 1. – Localities where copepods were found, plotted on a UTM grid (10x10 km).

RESULTS

Species diversity (Table 1)

In the 76 samples studied, 17 different species were identified: four cyclopoids and 13 harpacticoids (Table I). Samples contained up to three different species, but in the majority (73.7%) only a single species could be detected. In 21% of the samples two different species co-occurred, and only 5.3% of the samples accommodated three different species.

Three out of the four cyclopoids were found only in a single locality. *Paracyclops fimbriatus* and *Diacyclops languidus* sensu latu were found in samples collected uphill along a riverside, while *D. crassicaudis* was detected in a sample taken in a humid *Populus* wood (Salicaceae). In both cases, the presence of a pure aquatic system nearby explains the occurrence of these three species. Of more importance, however, is the presence in 13 localities (17%) of the hypogean cyclopoid *Graeteriella unisetigera* GRAETER, 1908. This small cyclopoid, in Belgium previously only known from the southern karstic region (LERUTH, 1939), was encountered in several terrestrial samples collected far from the typical karstic area (Fig. 3). A more detailed discussion of the distribution of this species is given in a separate section below. In seven samples *G. unisetigera* was the only copepod present, but in six samples this cyclopoid co-occurred with canthocamptid harpacticoids.

Only on two occasions were specimens of the genus *Nitocra* (Ameiridae) found. Unfortunately, they were juveniles (fifth copepodid stage), which could not be identified to species level.

In most of the samples (66 of 76, or 84.8%) one or more representatives of the family Canthocamptidae were identified. Representatives of the genera *Bryocamptus* and *Moraria* were most frequently detected, respectively, in 20 and 49 localities. Four other canthocamptids, *Attheyella crassa*, *Elaphoidella gracilis*, *Epactophanes richardi*, and the rare *Maraenobiotus vejdovskyi truncata*, were occasionally encountered (Table I).

TABLE 1

Copepod taxa encountered in terrestrial samples: Column 1: number of samples in which the species was encountered; Column 2: Vegetation types with G for grasslands, D for deciduous forest; Column 3: new records for the Belgian territory; Column 4: species previously reported from terrestrial habitats (1: including *Maraenobiotus* v. *tenuispina*).

TAXA	# of sites	vegetation type	new records	known from terrest.
ORDER CYCLOPOIDA				
Subfamily Eucyclopinae (Kiefer, 1927)				
Genus *Paracyclops* (Claus, 1893)				
Paracyclops fimbriatus (Fischer, 1853)	1	G		
Subfamily Cyclopinae (Kiefer, 1927)				
Genus *Diacyclops* (Claus, 1857)				
Diacyclops languidus sens. lat.	1	G		
Diacyclops crassicaudis (Sars, 1863)	1	D	*	
Genus Graeteriella (Brehm, 1926)				
Graeteriella G. unisetigera (Graeter, 1908)	13	D/G		
ORDER HARPACTICOIDA				
Family Ameiridae (Monard, 1927)				
Genus *Nitocra* (Boeck, 1864) *Nitocra sp.*	2	D/G		
Family Canthocamptidae (Sars, 1906)				
Subfamily Canthocamptinae (Chappuis, 1929)				
Genus *Bryocamptus* (Chappuis, 1928)				
Bryocamptus pygmaeus (Sars, 1863)	9	D/G		*
Bryocamptus typhlops (Mrázek, 1893)	6	D/G		
Bryocamptus vejdovskyi (Mrázek, 1893)	1	G	*	
Bryocamptus weberi (Kessler, 1914)	4	D/G	*	
Genus Mareanobiotus (Mrázek, 1893)				
Maraenobiotus vejdovskyi truncata (Mrazek, 1893)	1	D	*	* (1)
Genus *Attheyella* (Brady, 1880)				
Attheyella A. crassa (Sars, 1863)	5	G		
Genus *Elaphoidella* (Chappuis, 1928)				
Elaphoidella gracilis (Sars, 1863)	2	D/G	*	
Subfamily Morariinae (Borutzky, 1952)				
Genus *Moraria* (T.& A. Scott, 1863)				
Moraria brevipes (Sars, 1863)	7	D/G	*	
Moraria pectinata (Thiébaud & Pelosse, 1928)	1		*	
Moraria poppei (Mrázek, 1893)	17	D/G	*	
Moraria varica (Graeter, 1911)	26	D/G		*
Subfamily Epactophaninae (Borutzky, 1952)				
Genus *Epactophanes* (Mrázek, 1893)				
Epactophanes richardi (Mrázek, 1893)	3	D/G	*	*

Both *Bryocamptus* and *Moraria* were represented in the samples with four different species, but whereas on some occasions two species of *Moraria* co-occurred (four localities), no more than a single species of the genus *Bryocamptus* was ever observed in the same locality. In nearly half of the samples (35 localities, or 46%) species of the genus *Moraria* were the only copepods. In contrast, *Bryocamptus* was found only in six localities as the only copepod representative. In most cases, namely in 14 localities, *Bryocamptus* co-occurred either with *Moraria*, *Attheyella crassa*, *G. unisetigera*, or in combination with two of the three.

Thus far, eight harpacticoid species have been reported to occur in leaf litter and terrestrial samples in Europe (GURNEY, 1932; REMY, 1932; SCOURFIELD, 1939; KLIE, 1943; BRUNBERG NIELSEN, 1966; DUMONT, 1972). The presence of cyclopoid copepods has been reported only by DUMONT (1972), who found *Diacyclops bisetosus* (REHBERG), together with the rare harpacticoid *Attheyella (Mrazekiella) wulmeri* (DE KERHERVE), in the soil of an orchard, close to a temporary cattle pool. Besides the four species marked with an asterisk in Table 1, *Phyllognathopus viguieri* (MAUPAS), *Attheyella wulmeri* (DE KERHERVE), *Bryocamptus (B.) zschokkei* (SCHMEIL) and *Moraria frondicola* KLIE are the other four species that are known to occur in terrestrial habitats in Europe.

Several other harpacticoid species have been collected from semi-aquatic habitats such as mosses, liverworts, *Spagnum*, and tree-holes (OLOFSSON, 1918; LANG, 1931; GURNEY, 1932; SCOURFIELD, 1939; see REID, 1986 for review), but the present collection clearly demonstrates that quite a few other species that are generally known as typical aquatic animals have the capacity to maintain populations in moist leaf litter and moist soil under herbs.

To date, 71 copepod species have been reported from the territory of Belgium (DUMONT, 1989): 42 Cyclopoida, 22 Harpacticoida, and seven Calanoida. DUMONT (1989) estimated that 80% of the Belgian copepod fauna was reported. With the present collection we add nine species (one cyclopoid, eight harpacticoids) new for the Belgian fauna to this list (see Table 1). Most are widely distributed throughout central Europe (*Moraria brevipes, M. poppei, Epactophanes richardi, Bryocamptus weberi, B. vejdovskyi* and *Elaphoidella gracilis*) and were to be expected in Belgium. However, two harpacticoid species are rather rare, and show a strikingly disjunct distribution pattern within Europe.

Maraenobiotus vejdovskyi truncatus GURNEY, 1932 was originally described from woodland moss in Great Britain (North Wales, Norfolk, and Oxford) where it was detected in large numbers in early spring. Since then, this animal has been found only a few times: from leaf litter in Haute-Saône (France, KLIE 1943), the Carpathian Mountains in Slovakia (STERBA, 1964), from an undefined locality in Germany (JANETZKY et al., 1996), and more recently in the interstitia from a temporary riverflow and cave near L'Aquila (PESCE et al., 1994). Based on these few reports, it is evident that this animal is much more common and has a much wider distribution than previously known, but its cryptic life in mosses and among leaf litter has generally impeded detection.

Upon the discovery of three adults and one juvenile specimen in interstitia from a temporary riverflow and cave near L'Aquila (Italy), PESCE et al. (1994) advanced some doubts about the validity of the subspecific status of *B. v. truncatus*. However, based on such a limited number of specimens, it seems too speculative to synonymize the subspecies *truncatus* with *B. v. vejdovskyi* (MRÁZEK), which displays a much wider distribution. After all, GURNEY (1932) observed hundreds of specimens from different localities in Great Britain and pointed out the specific habitat preferences of the three known subspecies.

Moraria pectinata (THIÉBAUD & PELOSSE, 1928) was long known only from its type-locality in the Ardèche (southern France). Only with the extensive studies of the stygobiotic realm in the French Pyrenees and Alps was this animal found again (ROUCH, 1968). Evidently, the presence of this animal in a much more northern locality indicates that this species has been largely overlooked because of its cryptic habit.

Habitat preferences

Comparisons between vegetation types **(Table 2).** Copepods were only found in samples taken in vegetation types D and G, and none was encountered in samples where agricultural activities are performed (type A). Half the samples yielding copepods (38) were collected in deciduous forest litter, and half in vegetation of type G. Roughly twice as many samples were originally gathered in type G than in type D, which seems to indicate that the probability of finding copepods in the former is somewhat less than half the probability of encountering them in forest litter.

Both vegetation types harboured a nearly equal number of species: 12 different species in type D, against 15 species in type G vegetation. Ten species were found to occur in both vegetation types (Table 1).

The faunal composition seemed fairly equal in both types on a family level. In 38 samples from type D vegetation, Canthocamptidae were encountered in 36 samples and Cyclopoida in eight samples. Only at one station was a juvenile ameirid encountered. Type G vegetation harboured Canthocamptidae in 32 samples, Cyclopoida in seven samples, and Ameiridae in one sample.

More striking were the differences in faunal composition on the sub-family level. On this level, type G vegetation had a more pronounced diversity than type D. In the latter the Morariinae occurred in the largest number of the samples (28 of 36), followed by the Cyclopinae and Canthocamptinae occurring in nine and eight stations, respectively. Only in one station were Epactophanidae and Ameiridae detected. A quite different picture was encountered in the G vegetation. In this type, the number

TABLE 2

Presence of copepod species according to vegetation type

	VEGETATION OF TYPE D								VEGETATION OF TYPE G (Grasses)				
	Acera.	Betu.	Capri.	Faga.	Rosa.	Salica.	Ulma.	Mix.	Fallow. wood	Hedge	Pasture	Road	River
P. fimbriatus											•		
D. languidus													•
D. crassicaudis						•							
G. unisetigera		•		•		•			•			•	•
Nitocra sp.		•											•
B. pygmaeus						•			•	•	•	•	•
B. typhlops			•	•							•	•	•
B. vejdovskyi													•
B. weberi		•				•							•
M. v. truncata				•									
At. A. crassa											•	•	•
El. gracilis		•											•
M. brevipes		•			•				•		•		•
M. pectinata													•
M. poppei	•		•	•		•			•	•	•		•
M. varica	•	•		•		•	•	•	•			•	•
Ep. richardi				•								•	

of stations containing Morariinae was nearly equal to the number of stations with Canthocamptinae (18 and 17 stations, respectively). Cyclopinae were found in six stations, and Epactophaninae in two. Eucyclopinae and Ameirinae occurred only in a single locality.

***Comparison between vegetation sub-types* (Fig. 2).** Vegetation type G was subdivided into five categories (with total number of sample sites in parentheses): fallow (44), hedges (54), pasture (503), roadsides (485) and riversides (62). Riverside samples far outnumbered all other types,

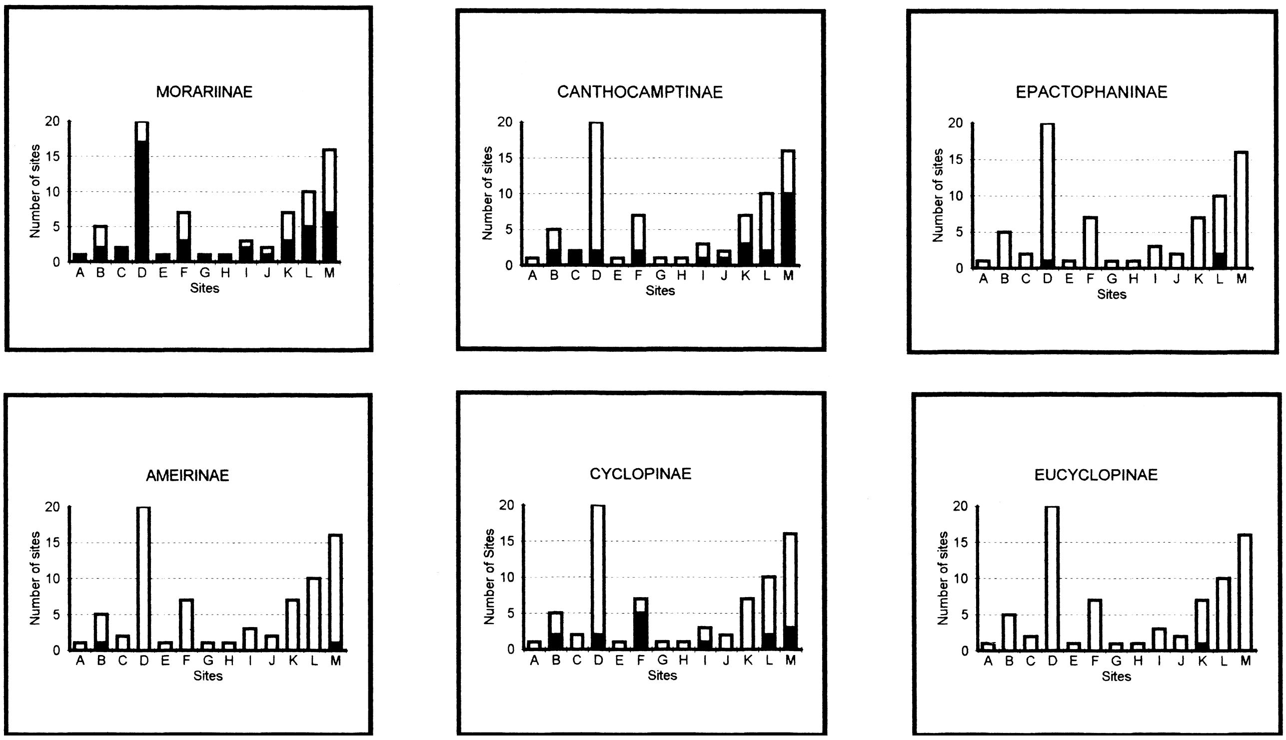

Fig. 2. – Presence of copepods of each subfamily in each habitat type. – A: Aceraceae; B: Betulaceae; C: Caprifoliaceae; D: Fagaceae; E: Rosaceae; F: Salicaceae; G: Ulmaceae; H: mixed foliage; I: Fallow; J: Hedges; K: Pasture; L: Roadsides; M: Riversides (A-H vegetation type D, I-M vegetation type G).

with copepods in 26% of the samples. Clearly, the particular environment of waterlogged supralittoral sediments favours the presence of copepod populations.

In three (6.8 %) of the samples taken from untreated or abandoned ground (fallow) copepods were found. The presence of copepods in the other vegetation types was far less significant. Copepods were found in only two samples under hedges (3.7%), in seven samples from pastures (1.4%), and in ten samples taken along roadsides (2%).

Vegetation type D was subdivided into 12 categories according to tree families, but only in the following eight categories were copepods found (with total number of sampled localities in parentheses): Aceraceae (19), Betulaceae (56), Caprifoliaceae (7), Fagaceae (266), Rosaceae (64), Salicaceae (101), Ulmaceae (4), and mixed wood (1).

Of the 19 samples taken under foliage of Aceraceae, only one yielded copepods. Six of 56 stations taken under Betulaceae contained copepods. All were found under *Alnus* sp. foliage. Soil of *Betula* or *Caprinus* did not harbour any copepods.

Two of seven stations under *Sambucus* (Caprifoliaceae), one of four stations under *Ulmus* (Ulmaceae), and a single sample taken under *Sorbus* (Rosaceae) yielded copepods.

Samples were collected under two tree species of the family Salicaceae: 87 samples under *Populus* and 14 under *Salix*. Copepods were found in 11 and two stations, respectively. Both tree species are in many cases encountered in rather humid terrestrial environments, with *Salix* often bordering small streams and rivulets. *Populus*, however, is often cultivated in groups on water logged soils. Whereas the foliage of *Salix* is rapidly dispersed, *Populus* foliage is often encountered in large quantities, creating a thick moist carpet at the base of the trees.

Among the Fagaceae, three samples were taken under *Castanea*, 104 under *Fagus*, and 159 under *Quercus*. Copepods were found in ten stations under *Fagus* and in 12 stations under *Quercus*. Thus, we found copepods in roughly 10% of the sites having a foliage carpet of these trees. Both deciduous tree species accumulate at their feet a thick continous carpet of dead leaves. Decomposition of these leaves is apparently slow, as several layers in different stages of decomposition can be found in a cross-section of the leaf carpet. The moist environment within the leaf layer favours the presence of a multitude of terrestrial animals (Schaeffer, 1991) and even seems to form a suitable microhabitat for small aquatic animals such as copepods. Taking into account that the sampling technique used here proved to be largely inadequate to collect copepods, we may assume that a more specific sampling strategy would reveal that the presence of copepods in such foliage carpets is much more common than previously supposed.

A particular case: the cyclopoid *Graeteriella unisetigera*

The small, almost harpacticoid-shaped, cyclopoid *Graeteriella unisetiger* was described by the late Swiss copepod researcher, Eduard Graeter in 1908 who discovered this animal in Grotte de Vert (Switzerland, Jura). In the years following, the species was detected in several caves and in affluents in karstic regions throughout Europe. The species is generally considered to be a strict stygobiont, highly specialized to explore interstitia and caves (Pesce, 1985).

In Belgium, Leruth (1939) collected this animal in six caves and one well in the provinces Namur and Liège, both located in the southern part of Belgium (Fig. 3). The material was identified by the late German copepodologist Friedrich Kiefer, and still forms part of his collection in Karlsruhe (Germany, Franke, 1989). To our knowledge, *G. unisetigera* was never reported again from the Belgium territory, until now, when we encountered this species in 13 terrestrial samples located in central and southern Belgium (Fig. 3).

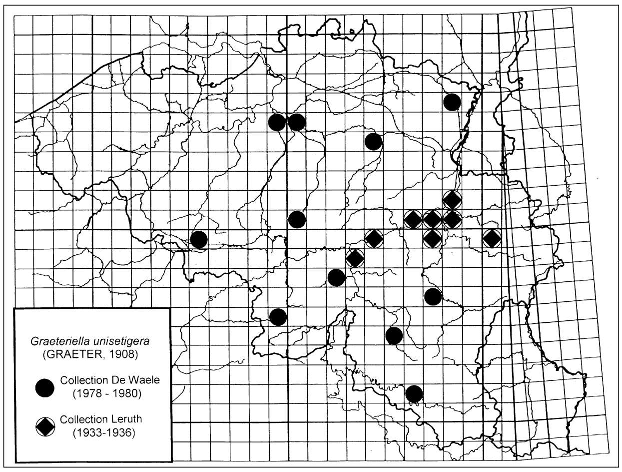

Fig. 3. – *Graeteriella unisetigera* (Graeter, 1908). – Distribution in Belgium. Map with UTM grid (10x10 km).

This animal has been frequently encountered in central Europe. Its distribution pattern apparently is closely related to the extent of the great river systems (Rhine, Meuse, Wezel, Rhone and Danube) (Fig. 4). Its absence from central and western France seems to be an anomaly, as this animal is known from the eastern part of the country, and from the adjacent countries (Great Britain (Gurney, 1932) and central Belgium, present contribution). Apparently the virtual absence from western France results from inadequate sampling within this region.

Whereas the distribution of the species in central and northern Europe can be easily understood as a function of the extended south-north drainages of the major river basins, its presence south of the Pyrenees (northern Spain, Kiefer, 1937), south of the Alps (northern and central Italy, Pesce, 1985), and in the Balkans (Pandourski, 1997) is more difficult to account for.

With the discovery of this animal in the leaf carpet of beech forests, a possible explanation for its southern distribution may be inferred from the European distribution of the beech forests. The striking coincidence between the distribution of *G. unisetigera* and the range of *Fagus sylvaticus* is depicted in Fig. 4.

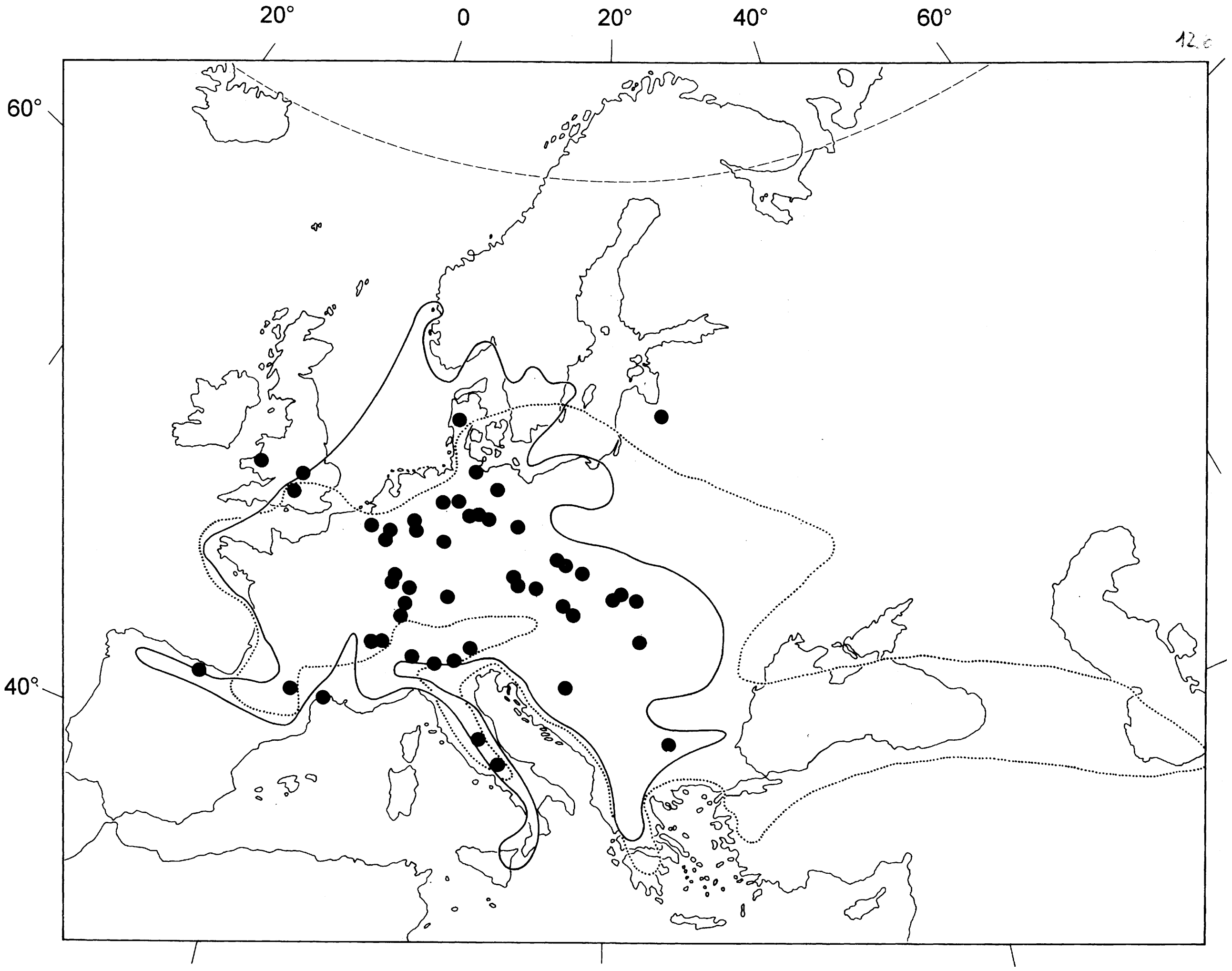

Fig. 4. – *Graeteriella unisetigera* (Graeter, 1908). – Distribution in Europe. Dots may indicate more than one locality. Solid contour line indicates range of beech (*Fagus sylvaticus*), dotted contour line indicates range of hornbeam (*Carpinus betulus*). Contours of trees after JAHN, 1991.

Fagus sylvatica formed local populations in submontane and montane regions in southern Europe about 10,000 year BP (Preboreal), from where it extended its range southwards and northwards. The vast forests formed by this tree – with the thick leaf carpet on the ground – seem to have facilitated the distribution of *G. unisetiger* on both sides of the great mountain ranges.

CONCLUSIONS

In recent years the study of biodiversity in all its aspects has received tremendous attention. However, basic estimations of diversity can only be of value if all possible habitats are sampled and adequate sample and extraction techniques are deployed. Copepod research in Belgium is now roughly 130 years old, and 71 copepod species were known to occur in Belgium (DUMONT, 1989). The results here presented demonstrate that this list is far from complete, as we succeeded in adding several species. Further research on commonly overlooked habitats may reveal the presence of quite a few more species, which are presently known only from central and southern Europe.

In the last decades, there has been much debate on aspects of colonization of the subterranean realm and dispersion of stygobionts (see BOTOSANEANU et al. 1991; NOTENBOOM, 1991; HOLSINGER, 1994). With the development of the concepts of marine transgression relicts and stranding models, stygobionts are ordered according to their origin as thalassostygobionts, sharing a marine ancestor, and limnostygobionts, which are descendants from a freshwater ancestor. All the species encountered in the terrestrial samples studied herein (with the possible exception of the ameirids) are descendants from freshwater ancestors (limnostygobionts). Several became adapted for living within caves and in the phreatic realm.

It is generally known that dispersion of stygobionts is strongly limited, and largely results from interaction between physical characteristics of the aquifer, availability of food resources, and quality of interstitial water (NOTENBOOM et al., 1996). The physical limitations of the environment are particularly evident for large macrofaunal elements (thermosbaenaceans, decapod natantids, isopods and amphipods) which consequently show a considerable level of endemism in karstic regions.

In contrast, however, typical hypogean harpacticoids and cyclopoids seem to occupy a much larger distribution area, as has been demonstrated herein for *Graeteriella unisetigera, Maraenobiotus vejdovskyi truncatus* and *Moraria pectinata*, and which is known for several other copepods (i.e. *Speocyclops*, many subterranean *Diacyclops* species, etc.). Evidently, the dispersion limitations (e.g. porosity) for these small animals (0.5 mm long adults) differ from those for macrofaunal elements, but this does not explain the wide distribution of these taxa.

As pointed out by BOTOSANEANU et al., 1991, stream capture has been largely overlooked in stygobiology as a phenomenon to transfer hyporheic associations from one river aluvium to another. Detailed geological research has demonstrated that such events have happened frequently. When a river starts to erode its interfluvium, it will break through the interfluvium limits, and will become a tributary from the other aquifer. For example, the river Moezel served for a long time (from the Late Miocene on) as an important tributary of the river Meuse until it changed its course and made contact with the River Rhine, some 300,000 years ago (GOOSSENS, 1984). Comparable scenarios for other riverine systems have been documented, but it should be clear that such drastic events evolved over long periods of time. Although this phenomenon can explain the introduction of a specialized hyporheic fauna within a riverine interfluvium, it inevitably raises two problems: (1) colonization towards the upper course of the newly acquired basin implies an active dispersion policy of the faunal components, and (2) the abrupt separation of the populations drastically reduces the gene-flow from the ancestral population, which should result in greater endemism.

Based on the observation that a considerable diversity of copepods lives in the particular microhabitat formed by decomposing tree leaves, the hypothesis is advanced here that the particular circumstances present in the moist leaf carpet (dixit SCOURFIELD, 1939) represent (1) a means of dispersion into uncolonized aquifers, and (2) a means of preventing genetic separation between the populations.

Although we are aware of the limitations of this study that result from the sample techniques used, we are confident that a more rigorous coordinated study of specific microhabitats could add valuable information to our understanding of the ecology, population characteristics and dispersion of this faunal element.

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