SOIL ORGANISMS **87** (3) · December 2015 pp. 221–228

Cave Collembola from Southwestern Germany

Michael Thomas Marx[1]* and Dieter Weber[2]

[1] Johannes Gutenberg-University Mainz, Institute for Zoology, Becherweg 13, 55128 Mainz, Germany
[2] Musée national d'histoire naturelle, 25 rue Münster, L-2160, Luxembourg
* Corresponding author, e-mail: marxm@uni-mainz.de

Received 12 March 2015 | Accepted 11 November 2015
Published online at www.soil-organisms.de 1 December 2015 | Printed version 15 December 2015

Abstract

Collembola are among the most abundant arthropod and hexapod taxa in cave ecosystems. The springtail fauna of different natural caves and artificially built underground mines and passages from southwest Germany was surveyed using pitfall traps. Altogether, 54 species were determined, of which almost 50% were classified as eutroglophile to eutroglobiont. These species are strictly bound to a hypogean habitat or, in the case of epigean species, at least able to maintain a permanent subterranean population. Two noteworthy species were found in the artificial gallery 'Bastion Drusus' in Mainz (Rhineland-Palatinate): *Lepidocyrtus violaceus* (Geoffroy, 1762) with morphological adaptations and *Disparrhopalites patrizii* (Cassagnau & Delamare Deboutevile, 1953) with a possible anthropogenically driven distribution.

Keywords springtails | subterranean habitats | troglomorphy | anthropogenic distribution

1. Introduction

Biologists and naturalists have long been fascinated by the unique morphology and adaptations of animals that live in caves. Modifications of cave vertebrates and invertebrates, such as the reduction or loss of pigmentation and eyes, the lengthening of appendages and the elaboration of nonvisual sensory systems, make them attractive models for evolutionary and developmental research (Culver & Pipan 2009). Cave animals were originally derived from surface-dwelling ancestors, which allow the developmental trajectories of troglomorphic changes to be understood. Additionally, since the cue for troglomorphic evolution is the absence of light and its consequences on primary productivity, trait changes can be attributed to such specific environmental factors (Protas & Jeffery 2012).

Collembola are among the most abundant invertebrate taxa in caves and subterranean ecosystems. Many collembolan species inhabiting caves are endemic and have evolved troglomorphic traits. Compared with southern and eastern European karst cave ecosystems, however, the above-mentioned typical troglomorphic traits of collembolan taxa are often missing in Central European cave habitats. This discrepancy has been explained by insufficient evolutionary time for troglomorphy to have evolved since the last glaciation (Christian 2002, Pipan & Culver 2012). After deglaciation, surface-dwelling species occupied subterranean habitats and were able to establish stable communities in these ecosystems.

The caves and subterranean habitats of southwestern Germany (Rhineland-Palatinate and Saarland) have been biospeleogically investigated since 1978 (Weber 1988, 1989, 1995, 2001, 2012). Through almost 40 years of sampling of about 1400 various caves and subterranean objects, different plant, vertebrate and invertebrate orders were taxonomically investigated and catalogued (Weber 2001). During this time, 54 different cave-inhabiting springtail species were also identified. The distribution pattern and classification of some abundant cave springtail species of this region are the subject of this paper, in addition to the springtail fauna of the 'Bastion Drusus', an artificial gallery in Mainz (Rhineland-Palatinate).

ISSN 1864-6417

2. Materials and methods

The investigated caves and subterranean habitats are within the scarped ridges (Baden-Württemberg), sediments of the Upper Rhine region as well as slates and new and mottled sandstone sediments of Rhineland-Palatinate (see map in Appendix 1). For the evaluation of cave invertebrates and springtails, pitfall traps were used. For these, polystyrol-vessels (100 to 50 mm) were filled with ethylene glycol (=1,2-ethandiol) as a killing and fixation liquid. After three months the traps were replaced and the captured animals were transferred to ethanol (70 %) for storage and further processing of the samples. Altogether, about 1400 caves, galleries, deep rock covers and subterranean habitats in southwestern Germany were investigated for invertebrates. In about 80 % of these sites, springtails were found and in 204 sites springtails were determined to species level (Weber 2001). Due to different depth zones of these ecosystems, classification according to entrance area (0–5 metres inside caves), transition zone (10–30 metres) and deep zone (> 30 metres) is not possible for all investigated sites. Thus only four sites (Brohlstollen, Grube Barbarasegen, Birkenmühlstollen and Grube Bremmelsberg), in which sampling in the above-mentioned three different depth zones occur (8 traps per zone), with a length of at least 230 metres and where higher numbers of springtails could be captured, were included in this paper. Additionally, two sites (Auener Stollen and Grube Moselberg), which have a shorter length but also exhibit three different depth zones, are also included (see Tab. 1). Regarding the climatic range, the entrance area is subject of alternating daily and yearly temperature ranges and the light incidence is high (temperature: 13.3°C ± 3.7°C; relative humidity 81.7 % ± 8.8 %). The transition zone is strongly shadowed, with a lack of direct light. The daily and yearly temperature ranges show only small-to-moderate changes and the air humidity is similar to the deep zone (temperature: 10.9°C ± 2.5°C; relative humidity 88.6 % ± 7.8 %). The deep zone is characterised by constant relative air humidity and temperature, as well as a lack of light: (10.0°C ± 1.3°C; relative humidity 93.3 % ± 5.1 %).

Besides the six investigation sites mentioned above, results from the artificial gallery system 'Bastion Drusus' in Mainz (Rhineland-Palatinate) are also presented in this paper. The primary subterranean gallery and the aboveground stone wall ('Drususstein') ('Kenotaph' – an empty tomb for the Roman commander Drusus) was founded by the Romans about 1900 to 2000 years ago and was reconstructed and expanded in the 17th century as a rampart (Fig. 1). From January 2010 until January 2011, the invertebrates of this gallery were investigated using pitfall traps. The gallery has a total length of about 260 metres and 14 pitfall traps were placed in the entrance area (up to 5 metres inside the gallery), the transition zone (10–20 metres) and the accessible deep zone (30–130 metres), respectively.

The ecological classification of springtail species in cave ecosystems is quite difficult and not interchangeable between different regions of the world. For Central European caves, Eckert (1999), Eckert & Palissa (1999), Weber (2001), Sket (2008) and Zaenker et al. (2014) proposed the following classification for cave animals:

a) Eutrogloxene (trogloxene): Taxa that only erroneously or accidently occur underground. Possible reasons for an underground distribution are short-term foraging and escape behaviours, or falling through a funnel or underground chamber. Most individuals of eutrogloxene taxa reside permanently outside caves and subterranean habitats.
b) Subtroglophile: Taxa that occasionally occur underground, but without permanent residence in these habitats. Subtroglophile taxa use caves for sleeping, hibernation or aestivation, as well as for the development of larval, juvenile or adult stages.

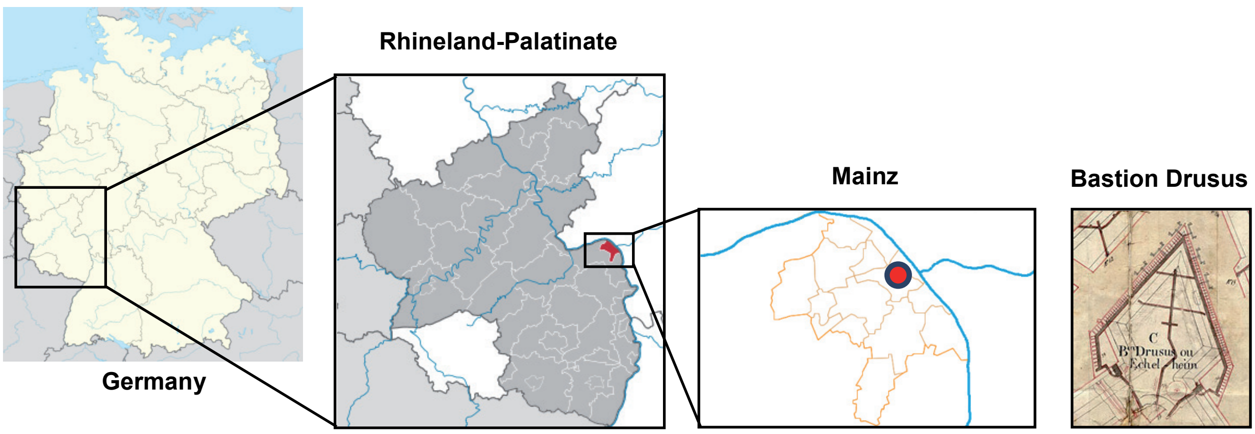

Figure 1: Location and formation of the artificial gallery 'Bastion Drusus' in Mainz.

c) Eutroglophile: Taxa that occur permanently or over several generations underground, but also survive outside caves for several generations. It does not matter if these taxa are directly (physiologically) or only indirectly (e.g. prey occurrence) connected to the subterranean habitat.
d) Eutroglobiont (troglobiont): Taxa that permanently occur underground, because they are strictly bound to subterranean habitats. Eutroglobionts are unable to survive for longer periods outside caves. These taxa often, but do not necessarily always, exhibit morphological adaptations, such as the absence of pigmentation and eyes or the occurrence of prolonged legs, antennae or sensory organs (trichobothria).

For different springtail species, a clear classification into these groups is not reasonable, due to insufficient data of the real distribution outside caves or in cases where only one or a few specimens have been registered in a single cave. These taxa are classified in an intermediate manner and are pooled together, either as eutrogloxene to subtroglophile or as eutroglophile to eutroglobiont. For the determination of springtails, the Synopses on Palearctic Collembola (Bretfeld 1999, Potapov 2001, Thibaud et al. 2004, Dunger & Schlitt 2011, Jordana 2012) and Fjellberg (1998 and 2007) were used.

3. Results

3.1. Species inventory of caves in southwestern Germany

In this survey, mainly dominant species of a few subterranean habitats are presented. From a total number of 54 sampled Collembola species [complete species list in Weber (2012)], 17 were caught in the presented subterranean habitats at the three investigated depth zones. Typical species, which occasionally or accidently live underground, include *Isotoma viridis*, *Dicyrtomina ornata* and different *Lepidocyrtus* and *Orchesella* species (Tabs 1 and 2). These species occurred mainly in the entrance area and transition zone and were often found at only one or a few investigation sites. The other species are able to live underground permanently, over several generations, or are strictly bound to underground habitats. Examples of these species are *Bonetogastrura cavicola*, *Schaefferia willemi*, *Tomocerus minor*, *Lepidocyrtus violaceus*, *Pygmarrhopalites pygmaeus* or *Disparrhopalites patrizii* (Tabs 1 and 2). In the investigated habitats, some of these species occurred in the deep zone with a higher number of individuals. Furthermore, *L. violaceus* (17x), *T. minor* (53x) and *Pogonognathellus flavescens* (63x) were frequently found in different subterranean habitats throughout the entire investigation area (Weber 2001).

3.2. The artificial gallery 'Bastion Drusus'

In the Bastion Drusus, a total of 1471 springtails from 11 species were caught during the one year of investigation. According to Zaenker et al. (2014), the majority of the determined species in this artificial gallery can be classified as eutrogloxenes to eutroglophiles, of which *Disparrhopalites patrizii* and *Lepidocyrtus violaceus* constituted more than 60 % of the individuals captured in this gallery.

Lepidocyrtus violaceus demonstrated some morphological adaptations beneficial for living in subterranean environments. It exhibits typical bluish-violet pigmentation, in addition to pale coloration, with only a few pigmented spots on the legs and the edges of some abdominal tergites (Fig. 2). The loss of pigmentation and elongation of the antennae and limbs were observed in one third of the specimens captured in the deep section of this location.

Disparrhopalites patrizii was exclusively found in the corridors of the 'Bastion Drusus'. *D. patrizii* is a rare, white-coloured species with a sometimes-weak dorsal pigmentation on the large abdomen (Bretfeld 1999). The eye patches (8+8 ommatidia) are dark blue and the fourth antennal segment consists of 12 subsegments. With 39 % of the total number of individuals, it was the most abundant species in this location.

4. Discussion

One paradigm of the evolution of cave animals is that the severe aphotic, food-poor environment with little environmental cyclicity imposes strong selective pressures, leading to convergent (troglomorphic) morphology of reduced pigment and eyes and elaborated extra-optic sensory structures (Pipan & Culver 2012). Many studies have shown this convergence and parallelism in morphology in different phylogenetic lines of springtails (Christiansen 1961, 1962 and 1965, Novak 2005, Lukić et al. 2010, Dányi 2011). The term troglomorphy, coined by Christiansen (1962), was to provide a morphological and evolutionary counterpoint to the ecological classifications of troglobiont, troglophile, etc., in addition to highlighting the morphological convergence of the cave fauna. This divergence between

Table 1: List of dominant collembolan species and number of individuals inhabiting different caves and subterranean habitats located in southwestern Germany (traps were removed after three months for one or two sampling periods of three months). The classification follows Zaenker et al. (2014):

Collembola species	Brohlstollen (483 m, a, su)			Grube Barbarasegen (> 250 m, a, sp, su)			Birkenmühlstollen (238 m, a, su)			Grube Bremmelsberg (715 m, na, sp, su)			Auener Stollen (113 m, na, sp)			Grube Moselberg (65 m, a, au, w)			Classification
	EA	TZ	DZ	EA	TZ	DZ	EA	TZ	DZ	EA	TZ	DZ	EA	TZ	DZ	EA	TZ	DZ	
Bonetogastrura cavicola (Börner, 1901)			4															12	etb
Hypogastrura burkilli (Bagnall, 1940)				1															etp
Hypogastrura sahlbergi (Reuter, 1895)																13			etp
Schaefferia willemi (Bonet, 1930)																		3	etp
Deuteraphorura silvaria (Gisin, 1952)			1												4		1		etp
Isotoma viridis Bourlet, 1839																12			etx
Heteromurus nitidus (Templeton, 1835)									5										etp
Lepidocyrtus curvicollis Bourlet, 1839				30				2						1					etp
Lepidocyrtus lanuginosus (Bourlet, 1839)																	1	1	etp
Lepidocyrtus lignorum (Fabricius, 1775)				6												48	1		etp
Lepidocyrtus violaceus (Geoffroy, 1762)				31								2				17	2		etp
Pseudosinella denisi Gisin, 1954															4				etp
Pogonognathellus flavescens (Tullberg, 1871)				1	14		1			1	1					9	4	1	etp
Tomocerus minor (Lubbock, 1862)			2			2						53		1	12		6		etp
Dicyrtomina minuta (Fabricius, 1783)																4			etx
Dicyrtomina ornata (Nicolet, 1842)																8			etx
Pygmarrhopalites pygmaeus (Wankel, 1860)											1	12							etp

Abbreviations: **a** – artificial gallery, **na** – natural origin of a cave but artificially expanded, **EA** – entrance area, **TZ** – transition zone, **DZ** – deep zone, **w** – sampling in winter (dec-jan-feb), **sp** – sampling in spring (mar-apr-may), **su** – sampling in summer (jun-jul-aug), au – sampling in autumn (sep-oct-nov), **etx** – eutrogloxene, **etp** – eutroglophile, **etb** – eutroglobiont.

morphological and habitat specialisation was considered very useful (Pipan & Culver 2012). In the case of Central European caves, habitat specialisation, in particular, can thus far be considered negligible in Collembola, due to the lack of endemic and morphologically high-adapted species. Our results particularly confirm this viewpoint. During the entire investigation period, no endemic springtail species were detected in the caves and subterranean habitats of southwestern Germany. The registered collembolan species of almost all investigated caves and subterranean habitats (with the exception of the 'Bastion Drusus') did not show typical troglomorphic features. This number is negligible compared with the high numbers of endemic and troglomorphic species in the subterranean karst ecosystems of Eastern Europe (Novak 2005, Lukić et al. 2010). One hypothesis to explain this gap is the (lack of) influence since the last glaciation period in Central Europe (Pipan & Culver 2012). Cave-inhabiting species were strongly disturbed and disappeared during the glaciation period and, after the ice retreated, the newly formed niches were occupied by aboveground and soil-dwelling species from outside the caves. The short timespan after the last glaciation was thus not sufficient for major troglomorphic features to develop, which could explain the lack of these features and endemic species in Central European caves.

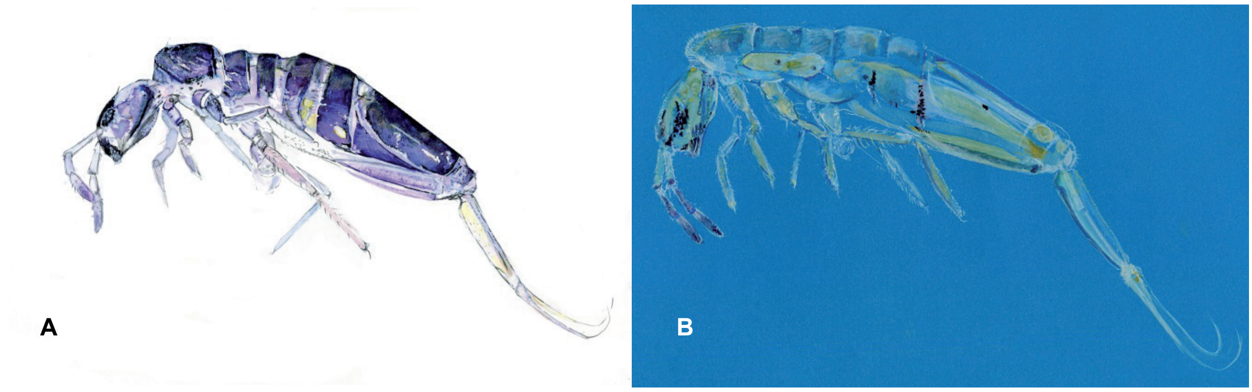

Figure 2: Morphological variations of *Lepidocyrtus violaceus* between (**A**) the entrance area with typical bluish violet coloration of individuals and (**B**) the deep zone with bright or pale coloration of individuals with further prolonged antennae and limbs (Drawings by ©Anne Kuprat, Mainz). Both morphological variations were found in the artificial gallery 'Bastion Drusus'.

Table 2: List of collembolan species and number of individuals inhabiting the artificial gallery 'Bastion Drusus' (traps were replaced after three months at four sampling dates in the year 2010). The classification follows Zaenker et al. (2014):

Collembola species	Bastion Drusus (~130m; a)				Classification
	EA	TZ	DZ		
Hypogastrura sp.	3		245		
Lepidocyrtus curvicollis Bourlet, 1839	67	31	160		etp
Lepidocyrtus cyaneus Tullberg, 1871		9	11		etp
Lepidocyrtus lignorum (Fabricius, 1775)	4		3		etp
Lepidocyrtus violaceus (Geoffroy, 1762) (violet coloration)	7	120	121		etp
Lepidocyrtus violaceus (Geoffroy, 1762) (pale coloration)			71		etp
Pseudosinella alba (Packard, 1873)	1				etp
Pseudosinella immaculata (Lie-Pettersen, 1896)		1	1		etp
Pseudosinella sp.		1	34		
Orchesella cincta (Linnaeus, 1758)	1				etx
Orchesella villosa (Geoffroy, 1762)	4				etx
Disparrhopalites patrizii (Cassagnau & Delamare Deboutteville, 1953)	48	199	329		etp
Total	**135**	**361**	**975:**	**1471**	

Abbreviations: **a** – artificial gallery, **EA** – entrance area, **TZ** – transition zone, **DZ** – deep zone, **etx** – eutrogloxene, **etp** – eutroglophile.

Poulson & White (1969) advanced the idea of caves and subterranean habitats as being identical or highly similar habitats, in which replicated evolutionary and ecological processes occur. However, it is more useful to think of subterranean habitats as occurring along a continuum of several selective factors (Pipan & Culver 2012), such as the absence of light, the strength of environmental cues (e.g. temperature, light or relative humidity), the amount and flux of organic carbon and nutrients and, finally, the intensity of competition (for reviews, see Pipan & Culver 2012 and Protas & Jeffery 2012). The idea of a continuum of several selective factors is very interesting concerning the two noteworthy and most abundant species found in the artificial gallery 'Bastion Drusus'. The migration of surface-dwelling springtail species into this subterranean habitat should be extraordinarily high, due to the short length and small period of time since the reconstruction of this artificial gallery was completed. The morphological variations between *Lepidocyrtus violaceus* individuals of the entrance area and the deep zone of the artificial gallery 'Bastion Drusus' are, therefore, quite remarkable. The investigated corridors were constructed about 350 years ago. Therefore, the time frame for the development of the troglomorphic variations in this species was very short. Due to the lack of nearby subterranean habitats, a colonisation or migration from such locations seems unlikely. Eckert & Palissa (1999) also detected morphological variations of *L. violaceus*, finding individuals of this species with reduced pigmentation in deep cave zones of southeastern Germany. *L. violaceus* was the most abundant springtail species found in the cave habitats investigated by these authors (Eckert et al. 1998). This reduction was interpreted as a typical example for the transition of a subtroglobiont to eutroglobiont modes of life. However, in surface-dwelling populations of *Lepidocyrtus cyaneus* from the Podolsky district (Moscow region), a loss of pigmentation was also observed (N. A. Kuznetsova and M. Potapov; personal communication). These results indicate a possible high phenotypic plasticity in this species.

Disparrhopalites patrizii has been classified as hygrophile (Dallai & Malatesta, 1982) and is often found in caves of different European countries (Delamare Deboutteville & Bassot 1957, Gough 1972, Gama 1988). Christian (1998) collected this species in the catacombs of St. Stephans Cathedral in Vienna. It was also found in the city fortifications of Luxembourg City (Marx & Weber 2013). In addition, specimens were also found in open habitats in south Italy and Germany (Dallai 1970 and 1973, Schleuter 1985), but the specimen collected by Schleuter (1985) in Kottenforst-Ville (also founded by the Romans) near Cologne showed a dark-brownish coloration with two pale lateral spots on the large abdomen. Its classification as *Disparrhopalites patrizii* should be re-evaluated. The species can therefore be classified as an eutroglophilic cave species of southern Europe. The northern distribution of this species could have been anthropogenically driven over the past 2000 years due to the almost exclusive sampling points in gallery or catacomb locations founded by the Romans.

5. Conclusions and perspectives

The investigation of cave Collembola in southwestern Germany is mainly based on pitfall trapping. Using other methods, such as hand collecting and photoeclector extraction of organic material present in caves may provide a broader spectrum of collembolan taxa, e.g. small forms restricted to particular cave microhabitats. Nevertheless the current knowledge about cave Collembola in southwestern Germany can be considered sufficient to good. In these subterranean habitats, a lack of occurrence of endemic cave Collembola species could be observed. The majority of species also occur outside the caves. Nevertheless, many cave habitats have not yet been investigated due to safety problems or blocked entrance areas. Over the next years, some of these investigation gaps will be closed. Furthermore, different cave collembolan species will be categorised as part of the German barcoding project (GBOL: 'Subterranean fauna').

6. Acknowledgements

The authors are highly appreciated to the editor and two reviewers for improving the manuscript

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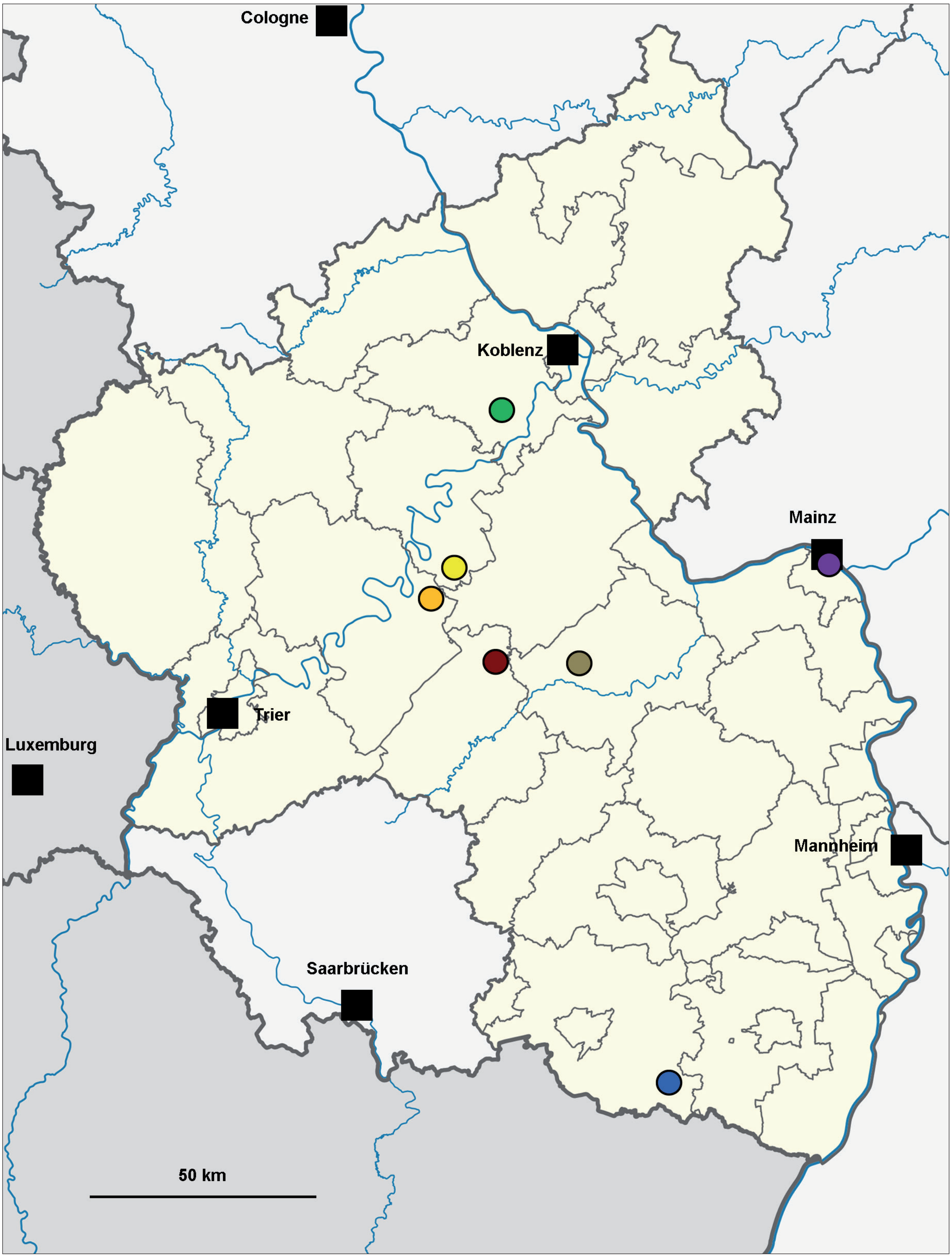
Appendix 1: Locations of the different caves and subterranean habitats in southwestern Germany:



Bastion Drusus
Grube Moselberg
Grube Bremmelsberg
Brohlstollen
Grube Barbarasegen
Birkenmühlstollen
Auener Stollen