Cave-dwelling oribatid mites (Acarina, Cryptostigmata) from East Austria

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Oribatid mites have largely been ignored by biospeleology. This paper presents the results of a preliminary survey of cave-dwelling oribatids of East Austria. Oribatids were recorded in nearly all sampled caves. A total of 49 species were recorded, 14 of which were restricted to the deep-cave (aphotic) zone. Oribatids turned out to be frequent and permanent members of the invertebrate communities of Austrian caves, and not merely sporadic trogloxenes. Standard sampling methods of soil zoology proved adequate for collecting cavernicolous oribatids.


Keywords: biospeleology, troglobite, soil animal, taxonomy.

Introduction

Oribatid mites are predominantly soil-dwelling animals. In addition, they are known to inhabit a great variety of biotopes, such as bark of trees, rock surface or submersed plants. The fauna of these "extraordinary" biotopes is often characterized by stenotopic species.

Oribatids have been known for more than 130 years to inhabit cave environments. In 1857, F. A. KOLENATI reported "Notaspis clavipes (HERMANN) oder Acarus coleoptratus (LINNÉ)" from a nycteribiid fly and its bat host. One mite had a "parasitic worm" between its mouthparts (in reality a fungal associate of the fly (Laboulbeniales, E. CHRISTIAN, pers. communication). KOLENATI concluded that the mites were epizoic and hunted worms on bats. They were found to represent a new species, described as "Notaspis Kolena-tii" by Julius MÜLLER two years later. According to MÜLLER (1859), the mites (on the bat) had been collected in the cave of Sloup in Moravia. His
figures clearly show a member of the oribatid family Damaeidae BERLESE, 1896.

The first record of free-living cavernicolous oribatids is PACKARD’s description of "Damaeus bulbipedata" and "Oribata alata" from Dixon’s Cave (Mammoth Cave System, Kentucky) (PACKARD 1888, p. 42 and plates X and XI). According to his figures, the first species belongs to the Damaeidae BERLESE, 1896, the latter to the Galumnidae JACOT, 1925. However, the descriptions are poor and it is not possible to assign them to valid species or genera (see VITZTHUM 1925/1926 for sarcastic comments on PACKARD’s work).

The first identifiable cave-dwelling taxon was not described until 1932. In this year, Carl WILLMANN described Belba Lengersdorfi for 2 specimens from the Iberger Tropfsteinhöhle (Harz, Germany) (WILLMANN 1932).

Are oribatid mites frequent inhabitants of caves? In regional or national biospeleological surveys, data on cave-dwelling oribatids are scarce or completely absent. For instance, STROUHAL & VORNATSCHER (1975) do not mention any findings of oribatids from Austria (for single records from Tirol and Vorarlberg see MIHELCIC 1957). From other countries, no or only very few findings are reported (BAJOMI 1977; DOBAT 1975; FRANZ et al. 1994; GUÉORGUIEV & BERON 1962; JEANNEL 1926; LENGERSDORF 1961; STRINATI 1966; WEBER 1989). Exceptions are the Belgian cave fauna by LERUTH (1939: 10 species) and the cave fauna of the Fränkische Alb by DOBAT (1978: 6 species).

Even from caves where the fauna is well known (in Austria e.g. the Drei-därrischenhöhle, Hermannshöhle [CHRISTIAN, in press], Lurgrotte [NEUHERZ 1975]) or from caves where detailed biological investigations have been carried out (e.g. Mammoth Cave system in Kentucky, BARR 1968), no or just a few specimens have been collected. PLACHTER & PLACHTER (1988) report high densities of oribatids in their extensive cave survey of South Germany, but obviously confused Oribatida and Uropodina ("Besonders die Schildkrötenmilben (Oribatei) erreichen ... mitunter sehr hohe Dichten", PLACHTER & PLACHTER 1988, p. 21).

Cooperation between (sampling) speleologists and (identifying) acarologists has until now been the only way to obtain knowledge of cave oribatids (e.g. MAHUNKA 1993, PÉREZ-ÍÑIGO 1969, WILLMANN 1954). Since these mites play no role in biospeleological research, they have generally been neglected as "accidentials". Scientific interest has been more or less restricted to taxonomic considerations and ecological classification.
In this paper, I present the results of a preliminary search for cavernicolous oribatid mites. Taking several caves in East Austria as examples, I tried to answer the following questions: (1) Is the lack of records of oribatids in Austrian caves (STROUAHL & VORNATSCHER 1975) due to a real absence or inadequate sampling in the past? (2) Are oribatids able to live permanently in the deep-cave (aphotic) zone? Do species exist that are restricted to this environment (true troglobites)?

**Materials and Methods**

I searched for cavernicolous oribatids in three different ways:

1. In 1993 and 1994, I took a total of 41 samples from 9 caves in Lower Austria. Two of these caves were shaft caves, the others predominantly horizontal. Unless otherwise indicated, organic material (woody debris, rotten leaves, mammalian bones or mummies, bat faeces) together with inorganic sediment was collected from the cave floor. Each sample was sieved (50 mm). 1-3 liters were carried to the laboratory within 24 hours and extracted in a simple Berlese-Tullgren apparatus for one week. It should be noted that it was often not possible to transport the samples without disturbance. Delicate specimens may have died on the way to the lab due to hot summer temperatures, shaking and sample compaction. Within each cave, I distinguished a near-entrance and a deep-cave (aphotic) zone. The delimitation of cave zones is a point of debate in the literature (e.g. PLACHTER & PLACHTER 1988). For simplicity, I ascribed locations that appeared completely dark to the adapted eye to the aphotic zone. For data analysis, the samples of the each zone were pooled.

2. I searched the collections of a current research project on the animal ecology of the pre-alpine Schachernhöhle. In this project, G. FRITSCH and I applied two different collecting methods: 15 pitfall-traps (20 parts monoethylenglycol : 1 part formaldehyde), exposed at equal distance over the entire cave area on October 12-14, 1993. The traps were sampled on 3 dates in 1994 (April 1, July 15, November 19). Litterbags (dried leaves of hornbeam [Carpinus betulus]) were exposed at equal distance over the entire cave area on October 12, 1993 and served as colonization-traps. They were sampled on November 6, 1994. The litter was carried to the laboratory within a few hours and extracted in a simple Berlese-Tullgren apparatus for one week.
An number of vials with ethanol-preserved cave invertebrates (leg. A. GAISBERGER, collection E. CHRISTIAN) were inspected for oribatids. The animals were taken in pitfall-traps (details of trapping not known). Only positive samples are mentioned in this paper.

In the list of sampled caves below, the numbers following the cave names refer to the respective registration numbers in the "Österreichischer Höhlenkataster" (FINK et al. 1979). Speleographic data of the caves are taken from the cave register books of Lower Austria (FINK et al. 1979; HARTMANN & HARTMANN 1982, 1990).

Dreidärrischenhöhle (1914/4): Lower Austria, near Gumpoldskirchen. Entrance 520 m above sea level, length 230 m, depth 19 m. Sampled December 12, 1994.

- **DRD a**: sieved sample of woody debris and sand near entrance.
- **DRD b**: sieved sample of stony sand from the aphotic zone.

Eberbachhöhle (1868/1): Lower Austria, near Weißenbach/Triesting. Entrance 430 m a.s.l., length 55 m, depth 5 m. Sampled June 7, 1993.

- **EBB a**: sieved sample of woody debris and roots from a small chamber approximately 30 m from the entrance.
- **EBB b**: sieved sample of roots and amorphous humus from the entrance chamber.


- **GAL**: Pitfall-trap(s), position unknown.

Güntherhöhle (2921/2): Lower Austria, near Hainburg. Entrance 270 m a.s.l., length 206 m, depth 21 m. Sampled November 21, 1993.

- **GÜN a**: sieved sample of rotten wood from the entrance hall.
- **GÜN b**: sieved sample of woody detritus, clay and stones from the area between entrance hall and "Rote Halle".
- **GÜN c**: sieved sample of single blades of straw and sand from the "Sandteil".

Hermannshöhle (2871/7): Lower Austria, near Kirchberg/Wechsel. Entrance 627 m a.s.l., length 4277 m, depth 73 m. Sampled June 1 and August 25, 1993 (18 samples). For detailed description of sampling sites see BRUCKNER (in press). The samples are classed in three groups (see below).

- **HER a**: samples of algae, mosses and ferns of the lamp flora.
- **HER b**: sieved samples of woody debris and rotten wood (single splinters to board piles) from the aphotic zone.
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**HER c:** one sieved sample of woody debris, leaves, needles, and cones from the transition of aphotic and entrance zone.

**Hohlur (1869/6):** Lower Austria, near Berndorf. Entrance 600 m a.s.l., length 90 m, depth 23 m. Sampled June 7, 1993.

- **HOH a:** sieved sample of rotten wood from the end chamber of the south tunnel.
- **HOH b:** sieved sample of rotten wood from the central part of the south tunnel.

**Rohrauerhöhle (1861/24):** Lower Austria, near Ternitz. Entrance 564 m a.s.l., length 48 m, depth 6 m. Sampled September 22, 1993.

- **ROH:** sieved sample of bat bones, arthropod remains, rotten wood and underlying sand from the southwestern part of the cave.

**Rötellucke (1861/13):** Lower Austria, near Ternitz. Entrance 583 m a.s.l., length 81 m, depth 6 m. Sampled September 22, 1993.

- **RÖT:** sieved sample of a ± solid wooden branch and underlying clay, near "Forscherhalle".

**Schachernhöhle (1866/9):** Lower Austria, near Lilienfeld. Entrance 660 m a.s.l., length 1810 m, depth 158 m.

- **SCHA a:** pitfall-trap in the entrance chamber.
- **SCHA b:** litterbag from the entrance chamber.
- **SCHA c:** pitfall-traps in the aphotic zone.
- **SCHA d:** litterbags from the aphotic zone.

**Schoberbergschacht (1836/136):** Lower Austria, near Schwarzenbach/Pielach. Shaft cave. Entrance 990 m a.s.l., length 100 m, depth 46 m. Sampled August 31, 1994.

- **SCHO a:** sieved sample of rotten wood from the southernmost part of the cave.
- **SCHO b:** sieved sample of amorphous humus and stones from the southernmost part of the cave.
- **SCHO c:** sieved sample of rubble (twigs, leaves, stones) on shaft ground near entrance.

**Trichterschlund (1836/137):** Lower Austria, near Schwarzenbach/Pielach. Shaft cave. Entrance 910 m a.s.l., length 117 m, depth 63 m. Sampled August 31, 1994.

- **TRI a:** sieved sample of rubble (twigs, leaves, amorphous humus, stones) from the center (bottom) of the entrance doline.
- **TRI b:** sieved sample of amorphous humus and stones from shaft ground.
Results

Oribatologists who seek to publish species records soon experience serious difficulties because accurate identification of several taxa is still extremely problematic. More so than in other animal groups, simple species lists are of only limited value because their reliability highly depends on the scrutiny, experience and taxonomic "philosophy" ("splitter" or "lumper") of the determinator. In the list below, I therefore cite the determination literature used for each taxon and discuss problems of identification. In this way, my determinations can be verified by present and future oribatologists.

I follow the "conservative" standpoint of WOAS (1986) in the handling of the genera of the Oppiidae, but append the "modern" names of the genera in brackets (following SUBIAS & BALOGH 1989). In the Damaeoida, the definitions of some genera are still very ambiguous. I therefore mention the criteria for generic grouping of every species (genera Damaeus, Epidamaeus, Metabelba, Porobelba).

The species are listed alphabetically. The material is deposited in my collection at the Institute of Zoology, University of Agriculture, Vienna.

*Achipteria coleoptrata* (LINNÉ, 1758)

*Adoristes ovatus* (C. L. KOCH, 1840)
3 specimens in SCHA a, 2 in SCHO c.

In the genus *Adoristes*, two similar species have been described from Central Europe: *ovatus* and *poppei*. Since *ovatus* is morphologically highly variable, previous authors were sceptical about the validity of *poppei* (HAMMEN 1952, BORCARD 1992). In a great number of specimens from various localities, I have seen that the variability range of *ovatus* includes the reported character states of *poppei* (SELLNICK 1929, WILLMANN 1931). I therefore assign the cave specimens to *A. ovatus*.

*Banksinoma lanceolata* (MICHAEL, 1885)

The single specimen conforms to the nominate subspecies *lanceolata* s. str. (FUJIKAWA 1978).

*Carabodes areolatus* BERLESE, 1916
1 specimen in SCHO c. Identification: SELLNICK & FORSSLUND (1953).
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*C. femoralis* (NICOLET, 1854-1855)
1 specimen in SCHO c. Identification: SELLNICK & FORSSLUND (1953).

*C. forsslundi* SELLNICK, 1953
1 specimen in SCHO c. Identification: SELLNICK & FORSSLUND (1953).

*C. labyrinthicus* (MICHAEL, 1879)
1 specimen in SCHO c. Identification: SELLNICK & FORSSLUND (1953).

The specimen corresponds with the diagnosis and figures in NÜBEL-REIDELBACH & WOAS (1993) except that there is no sawteeth-like structure on the dorsal side of the claws ("Krallen an der Dorsalseite sägezahnartig gezackt", NÜBEL-REIDELBACH & WOAS 1993, pp. 94, 97). Other specimens of *labyrinthicus* in my collection (from other locations) exhibit the structure only faintly. A similar serration is visible in other species of *Carabodes*, e.g. *forsslundi*. Therefore, the sawteeth may be variable and not a valuable diagnostic character of *labyrinthicus*.

*C. quadridentata* (HALLER, 1882)

*C. gracilis* (MICHAEL, 1884)

*C. birulai* (KULCZYNSKI, 1902)
2 specimens in DRD a, 59 in HER c, 9 in SCHA a, 3 in SCHO c, 2 in TRI a. Identification: BECK & WOAS (1991).

*C. birulai* was described from Spitzbergen from a single specimen. Four years later, TRÄGÄRDH (1906) reported it from Lapland and gave additional descriptions. BECK & WOAS (1991) redescribed the species thoroughly and discussed its possible identity with *C. tricuspidatus* WILLMANN 1953 from the Großglockner region (Heiligenblut, Austria). Most of the cave specimens conform very well with the description and figure of BECK & WOAS (1991) and I am positive that they are conspecific with their material from Southwest Germany. However, many individuals exhibit considerable variability of diagnostic characters:

1. The shape of the sensillus ranges from ± distinctly capitate and blunt (as BECK & WOAS depicted it) to long and slender forms with a pointed tip.
2. The length of the interlamellar hairs is variable and can be shorter than shown by BECK & WOAS.
3. The cuspides are highly variable. Most individuals have the usual "Chamobates lamella form" with slender, pointed and prominent...
cuspidal tips. In contrast, 3 specimens (1 ♀ from SCH a, 2 ♂♂ from HER c) lack the cuspides completely on one lamella and only tiny ones are present on the other. Intermediate forms occur between these extremes.

The variability of characters (1)-(3) is of interest because they have been used to distinguish the two European species of Chamobates with a tripartite rostrum, birulai and tricuspidatus. Especially the form of lamellae without cuspides was considered highly characteristic of tricuspidatus. However, in the cave material, a small proportion of two birulai-populations also exhibited this character state. In other birulai-populations, the proportion of individuals without cuspides may be greater or even predominant. I therefore believe that the tricuspidatus-specimens described by WILLMANN (1953) from Heiligenblut are variants of birulai.

The body size of the cave material is considerably variable (length: 514 μm, standard deviation: 20, range: 495-564 μm; breadth: 384 μm, standard deviation: 19, range: 327-465 μm; length/breadth ratio = 1.34, range: 1.17-1.70, n = 75). The values comprise those given for tricuspidatus by WILLMANN (1953: 510 × 390 μm) and SCHWEIZER (1956: 450 × 360 μm). However, they do not comprise the values given for birulai by BECK & WOAS (1991, length: 420-465 μm) and TRÄGÅRDH (1906, length: 420 μm).

Sex ratio: ♀/♂ = 0.98 (n = 75).

I have also found this species in great abundance in wind tubes under permafrost soil (Ötscher region, Lower Austria, CHRISTIAN 1993).

Chamobates borealis (TRÄGÅRDH, 1902)
3 specimens in SCH a, 2 in TRI a.

Using the key of SELNNICK (1960), the specimens key out at C. incisus HAMMEN, 1952, a junior synonym of C. borealis (TRÄGÅRDH, 1902) (FORSSLUND 1956). They correspond with the diagnosis and figure of C. borealis in BECK & WOAS (1991), but do not exhibit the great variability of the rostral notch mentioned by the authors.

Chamobates voigtsi (OUDEMANS, 1902)
1 specimen in SCH a, 27 in TRI a.

The collected specimens are very similar to two insufficiently described species, C. voigtsi and C. spinosus. The former was poorly described without illustrations by OUDEMANS in a footnote in a paper by VOIGTS (1902). The only potentially useful character OUDEMANS gave for voigtsi was the existence of a fine translamella ("Translamella nur eine Linie"). The translamella has never been mentioned by later authors. C. spinosus was de-
scribed and sketched in the key of SELLNICK (1929) who did not mention voigtsi. According to this description, spinosus can be recognized by large, rod-like and barbed setae on the ventral side (aggenital neotrichy, TRAVE 1978) and by the existence of a sharp angle at the edge of the pteromorpha. Behind this angle may be one or two sharp points ("... eine sehr scharfe Ecke, hinter der bisweilen ... noch eine oder zwei kleine Zacken zu sehen sind"). However, in his key of 1960, SELLNICK attributes two sharp angles at the edge of the pteromorphae to spinosus ("Hinter der Vorderecke der Ptm. eine kleine Bucht, so daß eine zweite Ecke entsteht") in contrast to one edge in voigtsi ("Ptm. hat nur eine Ecke"), and two distal tutorial teeth in spinosus in contrast to one tooth in voigtsi.

All characters: the shape of the edge of the pteromorphae, the dentation of the tutoria, and ventral neotrichy exhibit considerable variation in the related species, C. dactyloscopicus (BERNINI & MAHUNKA 1982). Thus, it is questionable if they are of great taxonomic value in this group.

WILLMANN (1931) sketched a lateral view of a pteromorpha of spinosus that exhibited a conspicuous striate surface structure (similar to C. dactyloscopicus BERNINI & MAHUNKA, 1982). No pteromorphal surface structure was shown in the sketch of voigtsi immediately below.

The cave specimens exhibit one sharp point at the edge of the pteromorpha, a striate surface of the pteromorphae, no translamella, rod-like and barbed ventral setae (but no neotrichia). The number of tutorial teeth is quite variable: 17 (of 28) specimens have one, 9 have two and 2 have three tutorial teeth. In 8 cases, the number of teeth is asymmetric, i.e. different between right and left tutorium.

Body dimensions are in agreement with the descriptions of both species (length: 387 µm [356-426 µm], breadth: 294 µm [277-327 µm], n = 28).

I therefore assign the specimens to C. voigtsi (in agreement with key and figures of a recent paper by PAVLITSHENKO [1994], as Xiphobates voigtsi). However, without having studied the variability of the diagnostic characters mentioned above, I cannot exclude that the two species are conspecific. If so, spinosus would be a junior synonym of voigtsi.

Cultroribula bicultrata (BERLESE, 1904)

Damaeus lengersdorfi (WILLMANN, 1932)
1 specimen in SCHAc. Identification: WILLMANN (1932).

The specimen matches the original description with the exception of a longer apophysis P between legs I and II (it does not project over the body
contour as in the description) and longer interlamellar setae. The specimen belongs to *Damaeus* because all tibial solenidia are free (Norton 1979).

*Damaeus nidicolus* (Willmann, 1936)  
1 specimen in RÖT, 1 in SCHA a, 1 in SCHA b. Identification: Willmann (1936).  
The specimens match the original description of *nidicola* with the exception of a rounded (not pointed) apophysis P between legs I and II. The two specimens belong to *Damaeus* because all tibial solenidia are free (Norton 1979). I collected this species around the entrance of the Schachernhöhle where it occurred in great abundance.

*Epidamaeus clavigerus* (Willmann, 1954)  
The material from the Hermannshöhle differs from the original description in several respects. The specimens are larger (body length: 710 μm, range: 683-723 μm; breadth: 406 μm, range: 396-415 μm; n = 4 [1 ♂, 3 ♀♀]), tubercles Sa, Sp (between legs II and III) and discidium are present and pointed (neither drawn nor mentioned by Willmann 1954), and the secretion on the sensilli is situated in the central parts of the sensilli, not distally. The sensillus of fig. 19a by Willmann (1954) is obviously not intact. Despite these differences to the original description, I do not doubt the identity of my specimens since *E. clavigerus* has a unique appearance. The attribution of *clavigerus* to the genus *Epidamaeus* is based on the lack of tibial seta d on legs II-IV of the adult and the absence of propodolateral apophysis P (Norton 1979). One ♀ had three nymphal scalps on its back.

*Eueremaeus cf. oblongus* (C. L. Koch, 1836)  
2 specimens in SCHO c.  
The cave specimens correspond very well with the illustration of *E. hepaticus* C. L. Koch 1836 in Beck & Woas (1991), but are larger (length and breadth respectively: ♀: 663 / 375 μm, ♂: 594 / 327 μm). Beck & Woas suspected *hepaticus* and *oblongus* (and several other species) to be synonyms of one polymorphic species since they found the diagnostic characters of the two species to be highly variable. They even doubted the only presumably "good" distinguishing character reported in literature, i.e. the presence of 10 (*oblongus*) vs. 11 (*hepaticus*) notogastral setae.  
However, in her review of the Eremaeidae of North America, Behan-Pelletier (1993) stated that the notogastral setation is very stable in all eremaeid species. She concluded that the specimens of Beck & Woas
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(10 setae) would not belong to *hepaticus*, but to *oblongus*. Additionally, the specimens of BECK & WOAS exhibited a U-shaped postanal process that is characteristic of the genus *Eueremaeus* MIHELCIC, 1963, of which *oblongus* is the type species.

If the specimens of BECK & WOAS and of the present study actually belong to *oblongus*, the species would vary considerably in body length (BECK & WOAS: 520 μm; present study: 663 μm).

*Euphthiracarus monodactylus* (WILLMANN, 1919)

*Gemmazetes alpestris* (WILLMANN, 1929) sensu lato
- *alpestris* (sensu stricto): 5 specimens in EBB a, 24 in HER b,
- *cavaticus* (sensu stricto): 13 specimens in GAL, 7 in HOH a, and 23 in HOH b,
- *G. alpestris* s.s. from HER b is quoted as *G. cavaticus* in BRUCKNER (in press).

The specimens from GAL, HOL a and HOL b resemble the original description of *G. cavaticus* by KUNST (1962) in most respects. However, both the form of the notogaster and the excision of the notogastral plate behind the anal plates are variable in my material. In addition to specimens with a posteriorly angled notogaster (as illustrated in KUNST), some have a posteriorly rounded notogaster. Even circular forms occur (length/breadth ratio = 1.00), thus resembling *G. forsslundi* (KUNST, 1965). The notogastral excision is distinctly present in 7 of 12 specimens from GAL and only very shallow in the HOH material.

The specimens from EBB a and HER b also resemble *cavaticus* very closely but are characterized by the presence of three tarsal claws (instead of one in *cavaticus*). The only tridactyl species of *Gemmazetes* known from Central Europe is *G. alpestris* (FUJIKAWA 1978). Unfortunately, the figure and original description of *alpestris* by WILLMANN (1929) are inadequate and tridactyly is the only valuable diagnostic character that allows its separation from congeners. Another possibly unique character described for *alpestris*, the existence of a membranous triangle posterior to the anal plate ("... Hinterende des Hysterosoma zwischen Ventral- und Dorsalplatte ein Dreieck, das nur von der dünnen Verbindungshaut zwischen den beiden Platten bedeckt ist", WILLMANN 1929) appears similar to the notogastral excision of *cavaticus*.

There are no clear differences in body measurements among the cave populations (Fig. 1, Tab. 1). The ranges of total length as well as total breadth...
Fig. 1: Body lengths (left graph) and breadths (right graph) of the cave populations of *Gemmazetes alpestris* s.s. (Eberbach- and Hermannshöhle) and *G. cavaticus* s.s. (Galmeihöhle and Hohlur). Arithmetic means (columns) ± 1 standard deviation (error bars) and maximum and minimum values (open circles). — Körperlänge (linke Graphik) und -breite (rechte Graphik) der Höhlenpopulationen von *Gemmazetes alpestris* s.s. (Eberbach- und Hermannshöhle) und *G. cavaticus* s.s. (Galmeihöhle und Hohlur); Arithmetic means (Columns) ± 1 standard deviation (Error bars) and maximum and minimum values (open circles).
Tab. 1: Arithmetic mean (mean), standard deviation (std) and minimal-maximal value (range) of body measurements of cave populations of *Gemmazetes alpestris* s.s. (alp) and *G. cavaticus* s.s. (cav). All values in μm. Own data from Galmeihöhle (GAL), Hohlur (HOH), Eberbachhöhle (EBB) and Hermannshöhle (HER), own data pooled in TOTAL. Literature data from KUNST (1962) (= KUN), SCHWEIZER (1956) (= SCHW) and WILLMANN 1929 (= WILL). The ratios total length/breadth and length notogaster/breadth of KUN are calculated from fig. 1 in KUNST (1962). — Arithmeticische Mittelwerte (mean), Standardabweichung (std) und Spannweiten (range) der Körpermaße der Höhlenpopulationen von *Gemmazetes alpestris* s.s. (alp) und *G. cavaticus* s.s. (cav). Alle Werte in μm. Angaben für die Galmeihöhle (GAL), Hohlur (HOH), Eberbachhöhle (EBB) und Hermannshöhle (HER) sind Originaldaten, summiert in TOTAL. Übrige Angaben aus der Literatur: KUNST (1962) (= KUN), SCHWEIZER (1956) (= SCHW) and WILLMANN 1929 (= WILL). Die Verhältnisse Länge/Breite (total length/breadth) und Notogasterlänge/Breite (length notogaster/breadth) sind aus fig. 1 in KUNST (1962) berechnet.
overlap and include the values reported for *alpestris* and *cavatica* (Tab. 1). The four populations differ slightly from each other in form and setation of the sensillus (ranging from slightly clavate and densely barbed to slenderly spindle-shaped with terminating hair), in the spacing of the lamellae and the form of the rostrum. I have not been able to quantify these differences but I observed that the variability of the two characters was greater between the populations than within the populations.

I therefore cannot exclude that each of my cave forms of *Gemmazetes* represent one of several sibling or incipient species that may be defined by subtle, but stable characters. A comparable situation exists in (free-living) members of the Scheloribatidae (WUNDERLE et al. 1990, WEIGMANN & WUNDERLE 1990).

However, I suspect that *cavaticus* is not a good species, but a monodactyl variant of *alpestris* s.s. Maybe this *alpestris* s.l. is more variable than previously thought and includes such dissimilar forms as *Oribella alpestris* of SCHWEIZER (1956, p. 290) or *O. clavigera* MIHELCIC, 1958.

If this is true, then tridactyly is probably a stable character on the level of populations (since I did not find any monodactyl specimens in tridactyl populations and vice versa) but not on the level of species. A comparable tendency to reduce the number of claws within species was stated for *Nothrus anauniensis* and *N. silvestris* (GRANDJEAN 1965).

Sex ratio ($$ : cσf$):


*Hemileius initialis* (BERLESE, 1908)


*Hermanniella punctulata* BERLESE, 1908


*Liacarus xylariae* (SCHRANK, 1803)


*Liebstadia humerata* SELLMICK, 1928

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**Metabelba cf. romandiolae** (SELLNICK, 1943)
1 specimen in SCHA a.

This specimen belongs to a group of very similar species in the vicinity of *M. italic* (SELLNICK, 1931). The description of *romandiolae* by SELLNICK (1943) is the only one that fits consistently. Especially the form of leg IV, the lengths of its segments, the peculiar form of most leg setae ("Die meisten Borsten ... sind ... über ihren Ansatzstellen recht verdickt, spitzen ... gleichmäßig und sehr scharf zu", SELLNICK 1943) and the body size (length: 644 μm / breadth: 405 μm) correspond with this species.

However, the description of *romandiolae* is short and without drawings. The identity of the cave specimen is therefore doubtful.

This species belongs to *Metabelba* in the sense of GRANDJEAN (1936).

**Metabelba** sp. A
2 specimens in SCHA c.

**Metabelba** sp. B
1 specimen in DRD b.

**Neoribates** sp.
1 specimen in TRI a.

**Oppiella (Neotrichoppia) confinis** (PAOLI, 1908)

BECK & WOAS (1991) refer to the number of bristles on the sensilli since this character complicates the differentiation between *confinis* and the closely related *fallax* PAOLI 1908. The number of bristles in my specimens ranges from 7 to 10 (terminal bristle not included) and is symmetrical (n = 5).

Body length: 349 μm (standard deviation: 12, range: 337-366 μm), body breadth: 202 μm (standard deviation: 5, range: 198-208 μm), length/breadth ratio = 1.73 (range: 1.67-1.80); n = 5.

**Oppiella (Lauroppia) falcata** (PAOLI, 1908)
7 specimens in SCHA d, 10 in SCHO a, 2 in SCHO b, 5 in SCHO c, 1 in HOH b. Identification: WOAS (1986).

**Oppiella (Lauroppia) cf. fallax** (PAOLI, 1908)
1 specimen in HER b, 1 in EBB a, 1 in SCHA d, 10 in SCHO a, two in SCHO b.

The validity of this and related species is a point of debate in the literature (WILLMANN 1931, BECK & WOAS 1991, WOAS 1986) and determination in
The validity of this and related species is a point of debate in the literature (Willmann 1931, Beck & Woas 1991, Woas 1986) and determination in this group is a most dubious matter. My specimens do not coincide well with the descriptions of fallax by Paoli (1908) and Pérez-Iñigo (1964). I suppose that this is due to considerable variability of the prodorsal costulae and sensilli. Several individuals even resemble Oppia falcata marginidentata Strenzke 1951 but have a rounded rostrum and are much larger.

Body length: 386 μm (standard deviation: 19.96, range: 359-415 μm), breadth: 189 μm (standard deviation: 8.37, range: 182-212 μm); n = 11.

Oppiella (Moritzoppia) keilbachi (MORITZ, 1969)

The cave specimens match the original description perfectly. It should be noted, however, that I cannot find convincing differences between keilbachi and unicarinata Paoli 1908 (using the descriptions of the latter by Bernini 1973). A possible distinction between the two species is the form of the notogaster: drop-shaped in keilbachi and elongated-ovoid in unicarinata (cf. fig. 19 in Paoli 1908). This character is variable: several individuals with unicarinata-like notogaster occur in both populations (length/breadth ratio of notogaster: ≈ 1.25 in keilbachi and ≥ 1.50 in unicarinata). A slight difference may exist in body size since keilbachi is reported to be 30-40 μm smaller than unicarinata (MORITZ 1969). Although the cave specimens increase the size range of the typical individuals, they are still smaller than unicarinata (280/130 μm, according to the original description of unicarinata by Paoli 1908).

Length: 231 μm (standard deviation: 12.92, range: 207-258 μm), breadth: 121 μm (standard deviation: 9.90, range: 98-139 μm); n = 100 (34 from HOHa, 66 randomly selected from HERb).

Oppiella (Dissorhina) ornata (Oudemans, 1900)
2 specimens in HERc, 2 in TRIa. Identification: WOAS (1986).

Oppiella sp.
1 specimen in SCHA d.

Oribatella calcarata (C. L. Koch, 1836)

Oribatella brevipila Bernini, 1977

Oribatula tibialis (Nicolet, 1854-1855)
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Oribella pectinata (MICHAEL, 1885)

Pantelozetes paolii (OUDEMANS, 1913)

Phthiracarus sp.
1 specimen in RÖT, 2 in TRI a.
Due to the great morphological variability of the species of this genus (BERG et al. 1990) and to the mostly poor descriptions I am not able to properly identify any of the specimens of Phthiracarus I found.

Pilogalumna tenuiclava (BERLESE, 1908)

Platynothrus peltifer (C. L. KOCH, 1839)

Porobelba spinosa (SELLNICK, 1920)
1 specimen in SCHA a. Identification: SELNNICK (1920), WILLMANN (1931).
This species belongs to Porobelba in the sense of GRANDJEAN (1936).

Poroliodes farinosus (C. L. KOCH, 1840)

Sphaerozetes cf. piriformis (NICOLET, 1854-1855)
3 specimens in SCHO c. Identification: NICOLET (1854-1855).
The specimens resemble both S. piriformis (NICOLET, 1854-1855) and orbicularis (C. L. KOCH, 1836). According to WILLMANN (1931) and SELNNICK (1960), the lamellar cuspides are rounded in orbicularis and pointed in piriformis on the antiauxial side. In the material of SCHO c, the cuspides are pointed in one specimen, but blunt in another. The third specimen exhibits a slightly pointed cuspis on the right lamella, but a blunt one on the left. The size of my specimens (length: 693-752 μm, breadth: 485-545 μm) exceeds the size WILLMANN (1931) and SELNNICK (1960) reported for orbicularis (575/420 μm) and piriformis (660/440 μm). However, they are much smaller than (and morphologically different from) S. maiör IRK 1939 (930 μm) and S. maximus WILLMANN 1953 (960 μm). Figures 679 and 680 of GHILAROY & KRIVOLUTSKIJ (1975) show that two pairs of posterior Areae porosae are elongated in orbicularis, but round in piriformis. In my specimens, the areae are ovoid and hardly visible.
The specimens do not concur with the drawings of NICOLET (1854-1855) due to differences in form of the lamellae (not distally tapering as in orbicularis or bended inwards as in piriformis of NICOLET). However, the interlamellar setae are short (but do not cross each other) and the body sides are ± parallel. These characters point more to piriformis. However, it should be noted that a definition of these two species that comprises the apparent variability is still lacking and any identification is therefore speculative.

_Steganacarus herculeanus_ WILLMANN, 1953  
7 specimens in SCHO c, 12 in TRI a, 1 in TRI b. Identification: NIEDBALA (1992), WILLMANN (1953).

_Suctobelba trigona_ (MICHAEL, 1888)  
1 specimen in HER c. Identification: WOAS (1986).

_Xenillus_ sp.  
1 specimen in EBB b.

_Zygoribatula frisiae_ (OUDEMANS, 1900)  

My specimen conforms with the descriptions of frisiae in the keys of WILLMANN (1931) and SELNICK (1929) and with fig. 609 in GHIAROY & KRIVOLUTSKII (1975). However, it is smaller than the reported size of frisiae (measurements of my specimen: length: 386 µm, breadth: 257 µm). An interesting detail that seems to be unique in Zygoribatula is a thin chitinous line that runs from each shoulder to the region of the Area porosa adalaris (cf. fig. 609 in GHIAROY & KRIVOLUTSKII 1975).

HAMMEN (1952) stated that OUDEMANS erroneously described and figured coarse (instead of smooth) prodorsal setae. Contrary to this, these hairs are distinctly and finely ciliate in my specimen.

_Zygoribatula interrupta_ WILLMANN, 1939  

The specimen fully coincides with the description and figure in WILLMANN (1939). The only exception is the form of the anterior border of the notogaster which is straighter than in interrupta. In this character, my specimen resembles _Z. saxicola_ KUNST 1959 which is very similar to interrupta. I am uncertain if saxicola represents a good species since in 1963, MIHELCIC described the subspecies _Z. interrupta major_ which would be an intermediate form between interrupta and saxicola.
In total, I collected 49 species. Eight of these are new for the fauna of Austria and two are of dubious taxonomic status: *Chamobates birulai, Damaeus lengersdorfi, Epidamaeus clavigerus, ? Gemmazetes cavaticus s.s., Hermanniella punctulata, ? Metabelba cf. romandiola, Oppiella confinis, O. keilbachi.*

The record of *D. lengersdorfi* by JAHN (mentioned in SCHATZ 1983, p. 25) is dubious since the paper cited (in: Mitt. Forstl. Bundesvers.-anstalt Wien) has not yet been published.

Oribatids were detected in every sampled cave except for Güntherhöhle. As expected (PECK 1976), most of the species (71 %) were restricted to the caves’ entrances. 14 species (or species-groups) occurred in the deep cave zone: *Damaeus lengersdorfi, D. nidicolus, Epidamaeus clavigerus, Gemmazetes alpestris s.l., Metabelba sp. A, M. sp. B, Oppiella confinis, O. cf. fallax, O. falcata, O. keilbachi, O. sp., Phthiracarus sp., Platynothrus peltifer, Steganacarus herculeanus.*

**Discussion**

The present investigation demonstrates that cave-dwelling oribatids can be collected easily by standard methods of soil zoology (cf. SELLNICK 1932) that yield many more specimens and species than the usual "browsing" sampling techniques of biospeleologists (cf. BERNINI 1980; MORITZ et al. 1971). The comparatively great number of new records for the Austrian fauna is simply the result of inadequate sampling (and lack of interest) in the past.

As a central result of this survey, oribatid mites turn out to be frequent and permanent members of the invertebrate communities of Austrian caves and not only sporadic trogloxenes. This holds for the entrance as well as for the deep-cave zone.

Several of the species collected in the aphotic zone usually live above ground. They probably entered the caves by means of dripping or running water or (in the case of *Platynothrus peltifer* and *Steganacarus herculeanus* in one shaft cave) falling litter.

Other species of the deep-cave region are also known to have surface populations (*Oppiella confinis (?), O. falcata, O. cf. fallax*). In contrast to the former group, they were collected in greater numbers or in more than...
one cave. This provides evidence for their ability to exploit organic cave deposits, to reproduce and to build up viable cave populations (PÉREZ-INIGO 1969, SELNICK 1932, TARMAN 1969). Probably single individuals of these species entered the caves from the surface, reached favourable habitats (organic debris), and persisted. It is interesting in this respect that all the species of this group are oppiid mites that are believed to be obligatory parthenogenetic. This way of reproduction facilitates the colonization of island biotopes.

It remains questionable if there are true troglobitic species in the present material (and if such oribatids exist at all). This uncertainty is partly due to difficulties with the identification of supposed subterranean species (Gemmazetes cavaticus, Oppiella keilbachi). Another problem is the assessment of the status of species that have been recorded only once (Epidamaeus clavigerus).

The classification of a troglobite can, on the one hand, be deduced from the lack of surface records (CHAPMAN 1986). This criterion can be misleading in oribatid mites, since the inventory of taxa and the biogeographical knowledge of this group is far from complete. On the other hand, "trogломorphic characters" or "trogломorphies" like hypertrophy of appendages or tactile sensory apparatus can indicate a strictly subterranean life (CHAPMAN 1986). Epidamaeus clavigerus and Damaeus lengersdorfi exhibit unusually long and slender legs. Accordingly, D. lengersdorfi has been repeatedly regarded as a troglobite (MORITZ et al. 1971, VANDEL 1965, WILLMANN 1954).

As mites of the Damaeoida are often large, long-legged and epigeic, they appear to be predisposed to cave life. The apparent lack of troglomorphic characters in the cavernicolous, non-damaeid species is surprising at first glance. It should be considered, however, that the majority of the smaller edaphic species inhabit microcaverns (≤ 1 mm, HOWARTH 1983) in soil or detritus. They experience the cave environment on a different spatial scale than the Damaeoida, and most likely they have different foraging and life-history strategies. For these tiny animals, the subterranean environment may spatially resemble ordinary soils, so that there would be no need for further morphological adaptation. In such cases however, the absence of troglomorphicies does not exclude troglobiosis.

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