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Zentralinstitut für Mikrobiologie und Experimentelle Therapie der AdW der DDR,
Abteilung Limnologie, Jena;
Zoologisches Institut der Universität Salzburg, Österreich;
Abteilung für Ökologie und Morphologie der Tiere, Universität Ulm, BRD

Observations on the Morphology and Ecology of the Soil-Inhabiting Testate Amoeba *Schoenbornia humicola* (Schönborn, 1964) Decloitre, 1964 (Protozoa, Rhizopoda)

By Wilfried Schönborn, Wolfgang Petz, Manfred Wanner, and Wilhelm Foissner[1])

With 6 Figures

Key words: *Schoenbornia humicola*; shell and cytoplasm structure; biometry; geographic races; feeding behaviour; abundance; vertical distribution; effects of liming and fertilization

Summary

Six geographically widely separated populations of *Schoenbornia humicola* were investigated. The shell, analyzed by scanning electron microscopy and silver staining, consists of shell platelets (idiosomes) of euglyphids, angular quartz, and amorphous siliceous elements. The foreign idiosomes are picked up from the soil and incorporated. They are not obtained by predation of other testaceans. A comparative biometric analysis of the shells yielded a statistically significant difference in the length of one population. This may be an indication for geographic races in *S. humicola*. The protoplasm shows a clear zonation as in euglyphids and *Nebela* species. The nucleus is spherical and has a central nucleolus. The pseudopodium is a very long endolobopodium, used to crawl (as "crawling-pseudopodium") and to feed (as "furcate-pseudopodium"). Extension of the pseudopodium is very rare. Resting stages are cysts and precysts (Kapselstadien). The more frequent resting stages are precysts. During very dry periods a bubble can form between the pseudostome plug and the retracted cytoplasm. On the basis of these observations the genus *Schoenbornia* can be classified within the family Hyalospheniidae Schulze, subfamily Nebelinae Cash & Hopkinson.

Schoenbornia humicola has certain feeding phases. During optimal periods the cell collects humus particles and stores them just outside the pseudostome as a so-called "food-bundle". Humus particles from the food-bundle are continually taken into the cytoplasm; this can take place also during suboptimal periods. This feeding strategy is interpreted as an adaptation to the often quickly changing environmental conditions in the soil. *Schoenbornia humicola* mainly inhabits the humus layers of the soil and is essentially confined to acid humus. It is an indicator species for moder and raw humus. Its percentage of the entire testacean community amounted maximally to 39.5 %. *Schoenbornia humicola* is slightly stimulated by fertilizers and depressed by lime, if liming causes an excessive increase of the *p*H of its habitat.

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Introduction

Testaceans play a substantial role in the decomposer cycle of the soil ecosystem (FOISSNER 1987; LOUSIER and PARKINSON 1984; MEISTERFELD 1986; SCHÖNBORN 1982, 1986a). Therefore it is necessary to investigate monographically the morphology and the ecology of important species of this cycle. Recently, there have been findings that *Schoenbornia humicola* (SCHÖNBORN 1964) DECLOITRE, 1964 is a dominant species in acid humus (BERGER et al. 1985; COÛTEAUX 1976; FOISSNER and ADAM 1981; FOISSNER 1985; RAUENBUSCH 1987; SCHÖNBORN 1986b). These and new data were collected simultaneously in several laboratories. Therefore it is appropriate to summarize all the results in a common study.

Materials and Methods

The study areas

The morphological investigations were performed on four populations (P1—P4) from Austria and one each from the Federal Republic of Germany (P5) and the German Democratic Republic (P6).

P1: Less used alpine pasture. Stubnerkogel near Gastein (Central Alps, Salzburg). 1,810 m NN. Vegetation is dominated by *Festuca rubra* aggr. Humus: mull-like moder. 0—5 cm: C/N = 9.9; *p*H (H_2O) = 4.8. 5—10 cm: C/N = 7.3; *p*H (H_2O) = 4.5. Investigated 1982. Detailed site description in FOISSNER and PEER (1985). Site B in Table 3.

P2: Spruce forest *(Picea abies)*. Oberhaag near Aigen [Böhmerwald (Sumava), Upper Austria]. 860 m NN. Raw humus; *p*H (H_2O) = 3.3. Investigated 1985 in 3—9 cm soil depth. Site N in Table 4.

P3: Spruce forest *(Picea abies)*. Grünwald near Aigen [Böhmerwald (Sumava), Upper Austria]. 1,005 m NN. Raw humus; *p*H (H_2O) = 3.5. Investigated 1985 in 0—5 cm soil depth.

P4: Spruce forest *(Picea abies)*. Ziegelwald near Aigen [Böhmerwald (Sumava), Upper Austria]. 540 m NN. Raw humus: *p*H (H_2O) = 3.5. Investigated 1985 in 0—5 cm soil depth.

P5: Spruce forest *(Picea abies)*. Welzheimer forest near Edelmannshof (Stuttgart). 540 m NN. Raw humus to moder; *p*H (KCl) = 2.7. Investigated 1984 in 0—5 cm soil depth.

P6: Spruce forest *(Picea abies)* near Plothen (Thuringia). 500 m NN. No ground flora. Raw humus. 5—13 cm (humus layer): C/N = 26.1; *p*H (H_2O) = 4.6. Investigated 1983—1984 in 0—5 cm (L, F horizons) and 5—13 cm (H horizon) soil depth. (Site R in Table 3). Site Q in Table 3 is near the locality of population 6. Here, the ground flora is dominated by *Deschampsia flexuosa*. C/N (humus layer) = 22.8; *p*H (H_2O) = 5.3.

In addition, some other sites were investigated to estimate vertical distribution and the relationship of *S. humicola* to various kinds of humus. These soils are characterized briefly in the headings and footnotes of Tables 3—5.

The abundance of *S. humicola* in untreated (control) and limed and fertilized plots was investigated in spruce forests of the FRG near Ulm (613 m NN) and Ochsenhausen (630 m NN) (Table 6). *U1-NF:* Spruce forest near Ulm, control plot; *p*H (KCl) = 3.1. *U1-DF:* Spruce forest near Ulm, limed with 20 kg/100 m^2 $CaCO_3$ on 1. 3. 1984 and fertilized with 5 kg/100 m^2 $Ca(NO_3)_2 \cdot NH_4NO_3$ on 15. 5. 1984. *p*H (KCl) at end of investigation = 4.5. *Ux-NF:* Spruce forest near Ochsenhausen, control plot; *p*H (KCl) = 2.9. *Ux-DF:* Spruce forest near Ochsenhausen, limed with 20 kg/100 m^2 $CaCO_3$ on 27. 12. 1983; *p*H (KCl) at end of investigation = 3.4.

Sampling methods, estimation of abundance

Soil sampling for qualitative and quantitative investigations was done as described in FOISSNER (1985). The abundance of the organisms were determined in aqueous suspensions of 0.02—0.1 g wet mass of soil (FOISSNER 1985; SCHÖNBORN 1975, 1986a). For a detailed description of this direct counting method see LIFTENEGGER et al. (1988). In the needle layer of the GDR sites six needles each with a length of 7 mm [corresponding to 0.018 g (≙ 0.05 ml)] were washed off in a small dish and then the testaceans were counted in this suspension (SCHÖNBORN 1975, 1986a).

Light and scanning electron microscopy

The morphologic and biometric data of P1 are based on protargol silver impregnated individuals (FOISSNER 1982, 1983). The corresponding data of P2 were gained from specimens fixed in formalin and stained with phenolic aniline blue. The data of P3—P6 are derived from untreated shells.

The construction of the ideal individuals of P2, P5 and P6 and the preparation of shells for scanning electron microscopy follow methods described in SCHÖNBORN et al. (1983). The shell platelets (idiosomes) of P6 were analyzed by electronbeam induced X-ray microanalysis. Drawings were made with a camera lucida.

Results and Discussion

Morphology, biology, and systematics of *Schoenbornia humicola*

Shape and structure of the shell

The shell is small, colourless, transparent, elliptical or ovoid with a rounded aboral region, circular or slightly compressed laterally. The pseudostome is terminal, circular or roughly circular (Figs. 1—5). Light and scanning electron microscopy showed that a great but variable part of the shell consists of idiosomes of various euglyphids. The platelets of the following species occurring together with *S. humicola* could be identified (Figs. 1; 2D 3F, H): *Trinema* spp. (large and small round platelets), *Euglypha ciliata* (large oval body platelets and dentated apertural platelets), *Corythion dubium* (very small oval platelets). These foreign idiosomes are placed irregularly on the shells (contrary to the shell of their producers). This can also be found in *Nebela*, which likewise uses foreign platelets. Beside the foreign idiosomes the shell of *S. humicola* also contains irregular scales (Figs. 1D; 2B; 3G). In the polarizing microscope these scales appear as amorphous siliceous elements and angular quartz. The origin of these elements is unknown. It is supposed that the siliceous elements can be produced in the cell, because they can be deposited in the cytoplasm. X-ray microanalysis (n = 1) demonstrated that the amorphous siliceous platelets are characterized by a greater proportion of aluminium than the foreign platelets. The values (in counts) are: amorphous platelets 1,244 Si/628 Al, *Trinema platelets* 1,464 Si/168 Al. Quartz as a building material is very rare. There are shells composed mainly of foreign idiosomes (Figs. 1A, B; 3H) and others having many amorphous elements (Figs. 2B; 3G).

The foreign idiosomes are picked up from the soil and then incorporated. They are not obtained by predation of other testaceans. This view is supported by the following observations: *Schoenbornia humicola* incorporates great quantities of detritus (humus particles). Before incorporation the detritus is collected around the pseudostome in the form of bundles, for which we suggest the term "food-bundles". These bundles contain platelets of the above mentioned euglyphids. The maximal numbers of platelets per bundle were 18 platelets of *Trinema* and 8 platelets of *Euglypha ciliata*. Careful examination of soil samples containing euglyphids shows mostly single idiosomes. The platelets are derived from decomposition of the empty shells (SCHÖNBORN 1982).

Biometric analysis of the shell

Most characters of the six populations investigated show a high constancy and are significantly correlated with each other (Tables 1, 2). The length of P6 is significantly ($p < 0.05$) larger than that of the other populations. Likewise the shell width

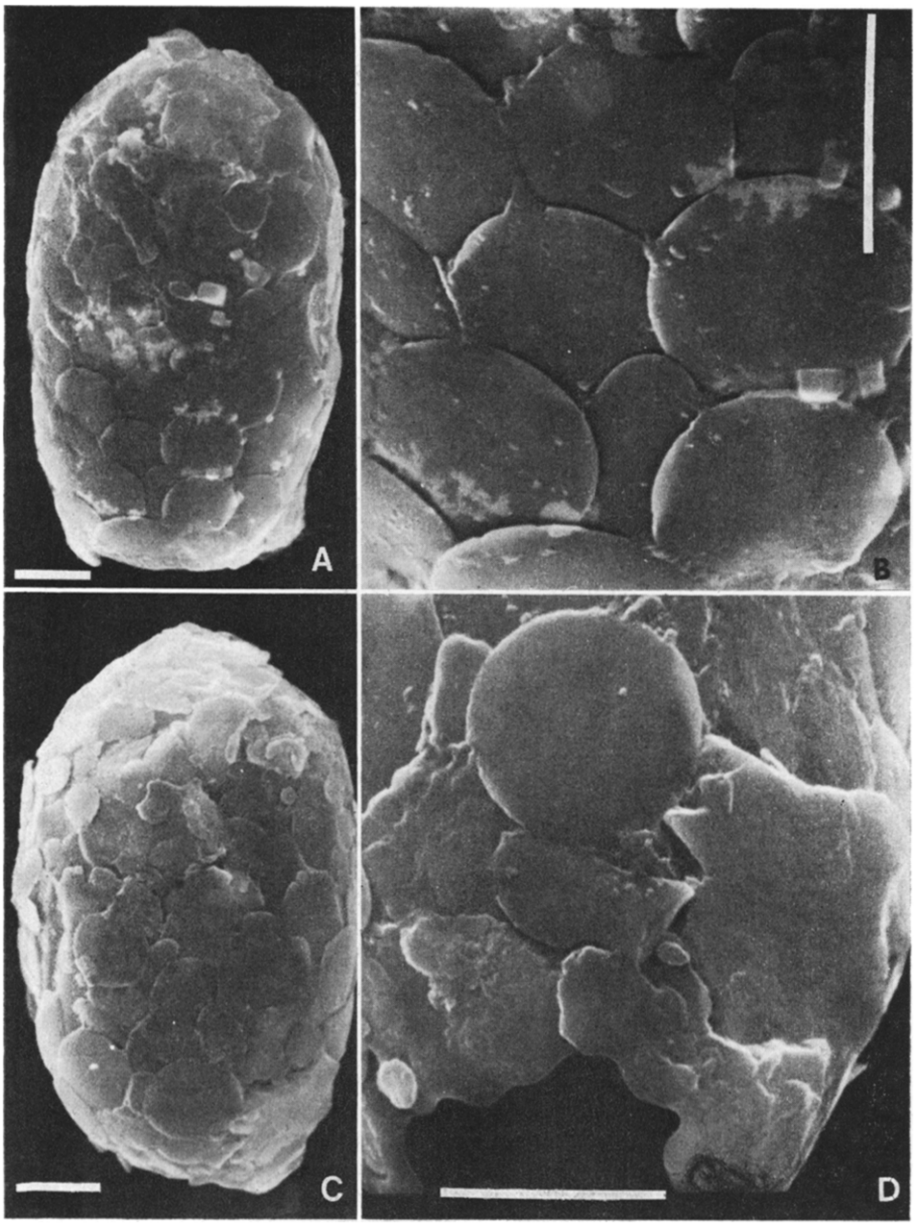


Fig. 1. SEM micrographs of shells of population 6 of *Schoenbornia humicola*. Bars = 5 µm. A: Shell mainly covered with foreign idiosomes. B: Detail of the same shell. C: Shell with foreign idiosomes and amorphous plates. D: Detail of the same shell showing the pseudostome.

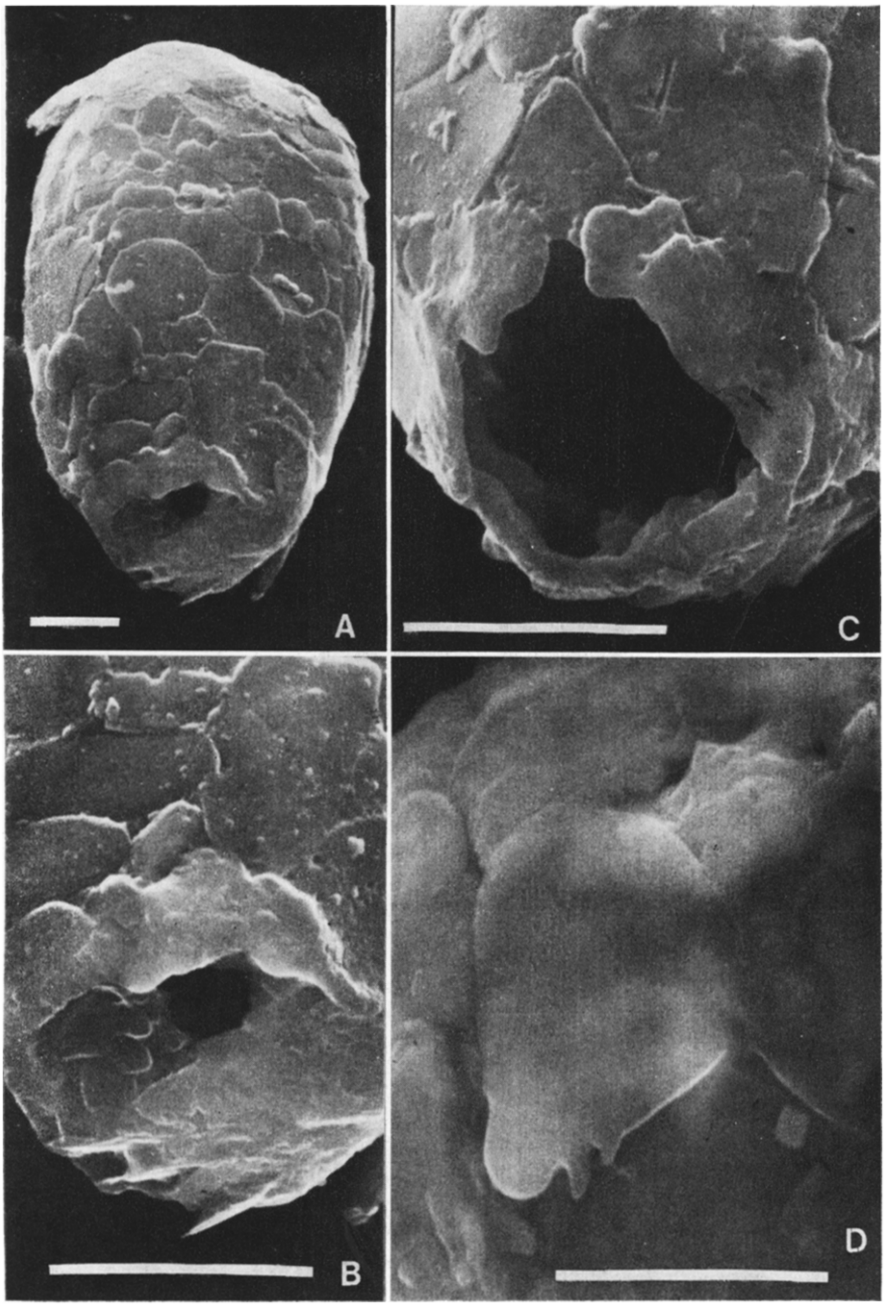
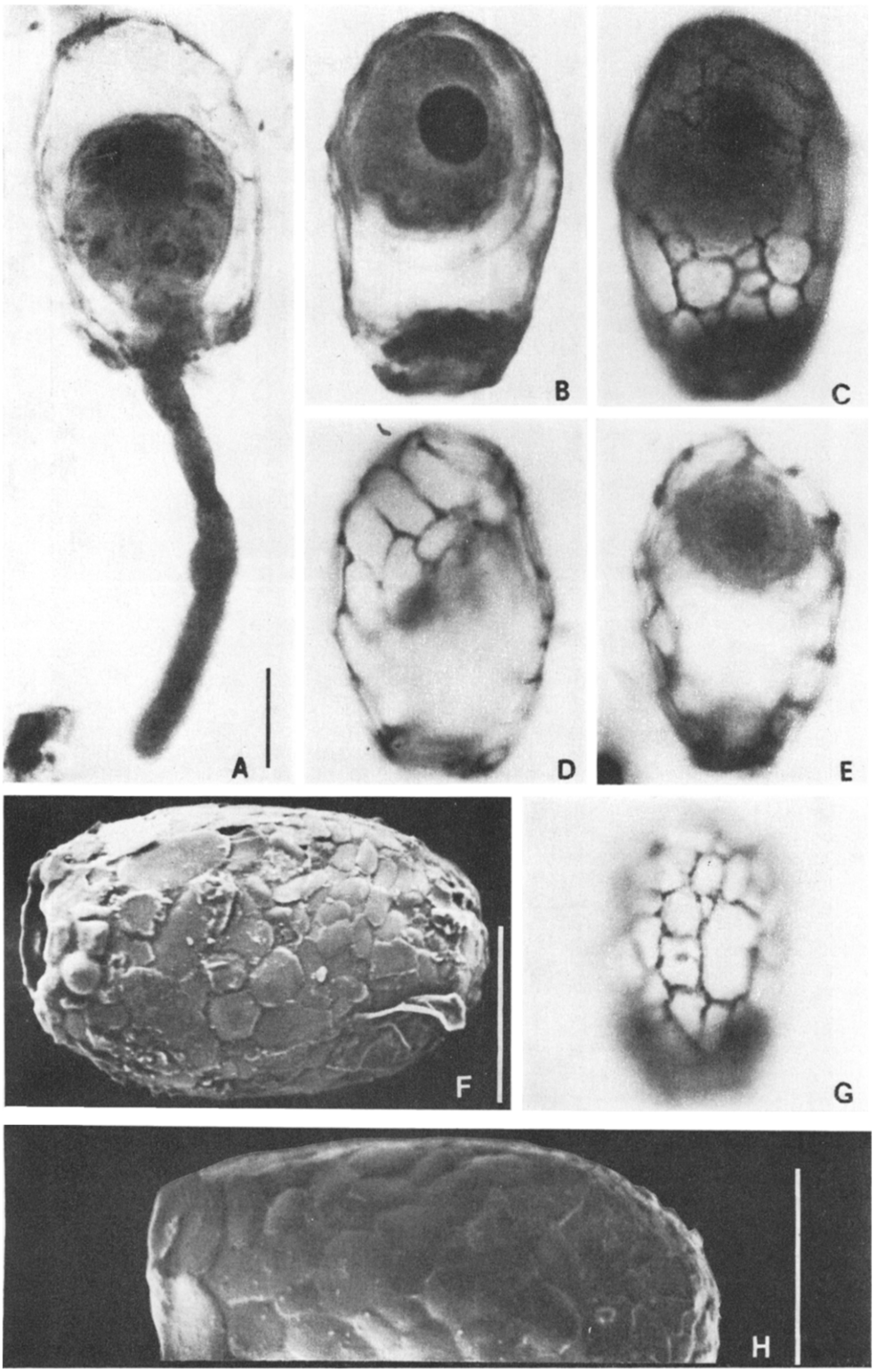


Fig. 2. SEM micrographs of shells of population 6 of *Schoenbornia humicola*. Bars = 5 μm. A: Amorphous siliceous plates close the pseudostome. B: Detail of the same shell. C: Pseudostome region with amorphous siliceous plates and quartz. D: Detail of a shell showing an apertural plate of *Euglypha ciliata*.


A
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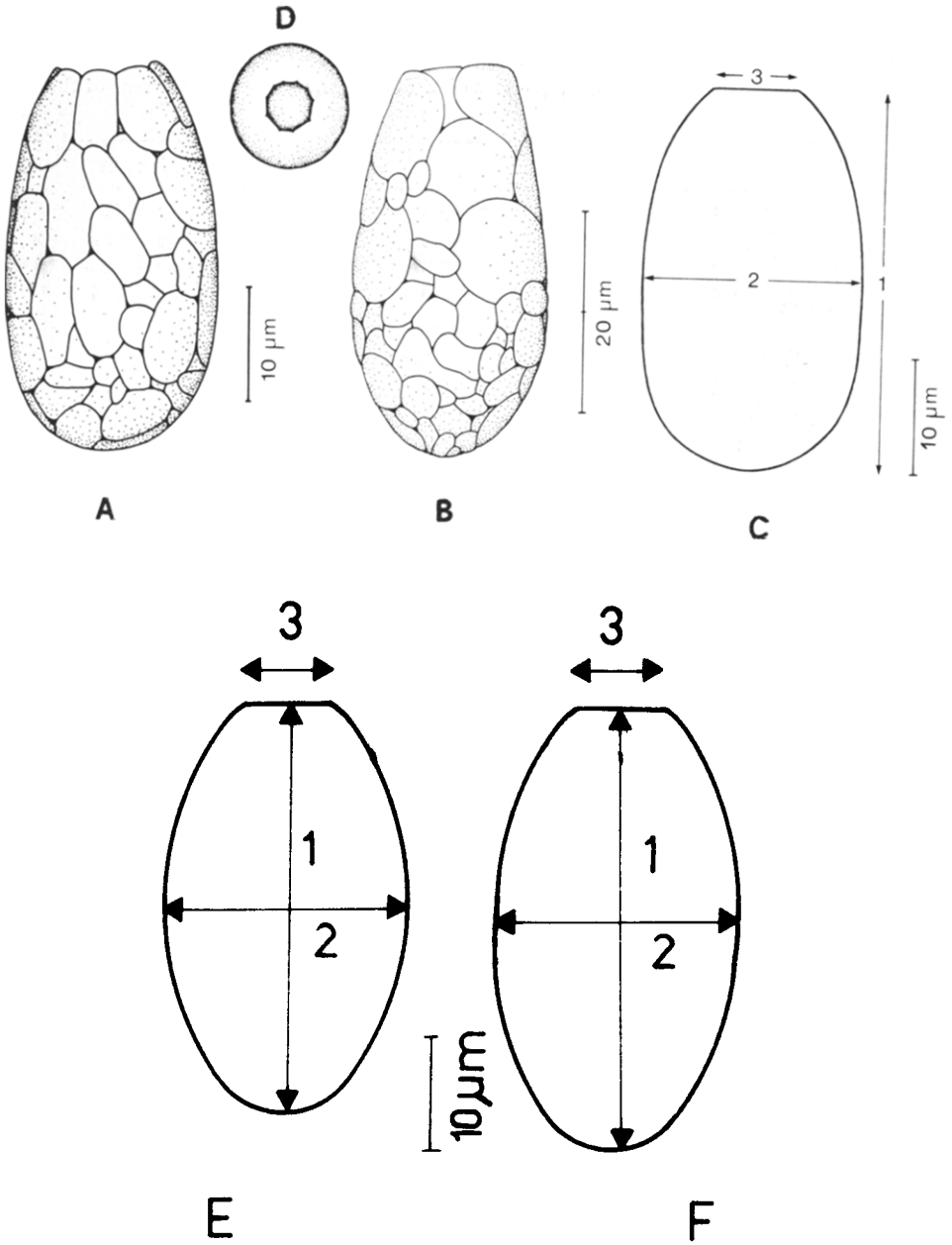

Fig. 4. *Schoenbornia humicola*. A, B: Lateral view of population 2 after protargol impregnation. C: Ideal individual of population 2. D: Frontal view of population 2 showing the pseudostome. E, F: Ideal individuals of populations 5 and 6, respectively.

Fig. 3. Population 1 of *Schoenbornia humicola* after protargol impregnation (A—E, G) and scanning electron microscopy (F, H). Bars = 10 µm. A: Endolobopodium. B: Cyst. C: Shell with idiosomes and amorphous plates, lateral view (B, C, the same individual, different levels of focus). D: Shell with only oval plates, lateral view. E: Nucleus with large central nucleolus. F: Shell with many idiosomes, lateral view. G: Shell with amorphous plates, lateral view. H: Shell with differently shaped idiosomes.

Table 1. Biometric characterization of the shells of 6 populations of *Schoenbornia humicola*. For characters see Fig. 4C. All measurements in μm. M = Median, Max = maximum, Min = minimum, n = number of investigated individuals, s = standard deviation, $s_{\bar{x}}$ = standard error of the mean, V = coefficient of variation, $\bar{x}$ = arithmetic mean

Character	Population	$\bar{x}$	M	s	$s_{\bar{x}}$	V	Min	Max	n
1	1	34.5	35.0	2.5	0.6	7.3	29	38	15
	2	33.3	33.0	2.3	0.4	6.9	29	38	30
	3	33.5	34.0	2.8	0.6	8.5	26	39	25
	4	33.9	33.0	4.0	1.5	11.9	29	39	7
	5	33.7	35.0	2.9	0.6	8.6	27	36	21
	6	37.4	37.5	2.3	0.5	6.2	31	44	24
2	1	22.0	23.0	2.7	0.7	12.4	17	25	15
	2	20.8	20.0	2.4	0.5	11.8	16	26	30
	3	22.0	22.0	2.0	0.4	9.2	18	25	25
	4	18.8	19.0	1.8	0.7	9.7	17	21	7
	5	21.4	21.8	2.3	0.5	10.6	17	26	21
	6	20.5	21.2	1.6	0.3	10.6	18	24	24
3	1	7.4	7.0	1.1	0.3	15.1	5	9	15
	2	7.7	7.5	1.3	0.2	16.7	6	11	30
	3	8.2	8.0	1.2	0.2	14.0	6	10	25
	4	7.3	7.0	0.7	0.3	9.6	6	8	7
	5	9.0	9.0	1.1	0.2	12.7	6	10	21
	6	8.6	9.3	1.4	0.3	16.2	6	10	20

Table 2. Correlation between characters of population 5 of *Schoenbornia humicola*. For characters see Table 1 and Fig. 4C. Number of investigated individuals = 21

Character-pair	Coefficient of correlation	Error probability (%)
2/1	0.5997	1
3/1	0.5479	5
3/2	0.8865	1

of P1 differs significantly ($p < 0.05$) from that of P4. But this is probably caused by the preparation. Only P6 may be a real geographic race. It is known, that such differences could be caused by structural peculiarities of the habitat. For example, most small-shelled varieties of larger species occur in lake sediments or soils with reduced pore space (SCHÖNBORN 1968; BERGER et al. 1985). No such differences could be observed in the investigated spruce forests. Thus, the reason for the higher length of P6 remains obscure.

There is already biometric evidence for geographic races in testate amoebae (SCHÖNBORN et al. 1983). The Testacea are very probably an asexual group. Therefore it is not possible to transfer the known mechanisms of the origin of geographic races to the testate amoebae. The races in Testacea urgently need a genetic elucidation, because the origin of species in asexual groups is generally nearly unknown.

For three of the investigated populations an "ideal individual" is constructed (Fig. 4). These ideal individuals already demonstrate the least habitual differences.

Protoplasm

The protoplasm shows the same zonation as that of the Hyalospheniidae and Euglyphidae (Fig. 5A). The aboral region, which contains the nucleus, is clear and is followed by a zone which contains small inclusions, probably excreta. The lower region is occupied by food vacuoles. The spherical nucleus has a central nucleolus (Figs. 3B, E; 5A; 6). Three contractile vacuoles are located at the periphery of the cytoplasm (Fig. 5A).

Intensive ingestion of food results in destruction of this zonation. Then, coarse food inclusions occupy the entire cytoplasm (Figs. 5B, C).

Individuals are rarely seen with extended pseudopodia. *Schoenbornia humicola* produces only one very long endolobopodium used to crawl ("crawling-pseudopodium") (Figs. 3A; 5B, D; 6). The pseudopodium contracts and pulls the shell along; at this point a new pseudopodium develops at the aperture. The crawling-pseudopodium can be about 2.7 times as long as the shell (Figs. 3A; 5B). When it encounters detritus or other particles, the pseudopodium forks off ("furcate-pseudopodium") and encloses the particles (Fig. 5D).

Ingestion of food

In periods of increased population growth, most cells suddenly enter the feeding phase. Detritus particles, caught by the furcate-pseudopodium, reach the pseudostome as the pseudopodium contracts, pulling the shell along as described above. The detritus particles accumulate just outside the pseudostome. This is achieved by small cytoplasmic protusions which bind the particles together at the apertural edge (Figs. 5C; 6). Humus particles constantly pass from these food-bundles into the cytoplasm. The apertural zone becomes rich in inclusions, and cytoplasmic movements efface the zonation (Figs. 5C; 6). The incorporation of the humus material does not indicate how much detritus or how many of the attached bacteria are in fact digested.

Feeding phases and food-bundles have also been observed in other soil testate amoebae, e. g. *Assulina* and *Corythion,* but they are most frequent in *S. humicola,* which showed periods where up to 70% of the cells have such bundles. In P6 nine peaks of abundance could be registered during a year. In those periods only five intensive feeding phases occurred. Food-bundles could be found seldom during non-feeding phases and during periods when the population density was low.

What is the ecological and physiological advantage of the food-bundles? Certainly, they can store a great quantity of food during optimal periods which are favourable for the extension of the pseudopodia. The incorporation of the particles from the bundles into the cytoplasm can take place also at suboptimal periods, e. g. decreasing moisture content. Thus, we conclude, that both, the rare extension of the pseudopodia and the formation of food-bundles in soil testaceans, are meaningful adaptations to the often rapidly changing conditions in the soil.

Schoenbornia humicola shows that foreign idiosomes are not necessarily connected with a predatory foraging strategy. Many species of *Nebela* also incorporate humus particles and *Sphagnum* detritus. Presumably not all *Nebela* species are predaceous macrophages, which is supported by recent investigations of Rauenbusch (1987). It is highly probable that *Nebela* also collects loose platelets of euglyphids and uses them for shell building. Thus, the Nebelinae to which *Schoenbornia* belongs, are the scrap-collectors of the testacean thanatocoenosis and therefore they contribute to a recycling of the residues from shells.

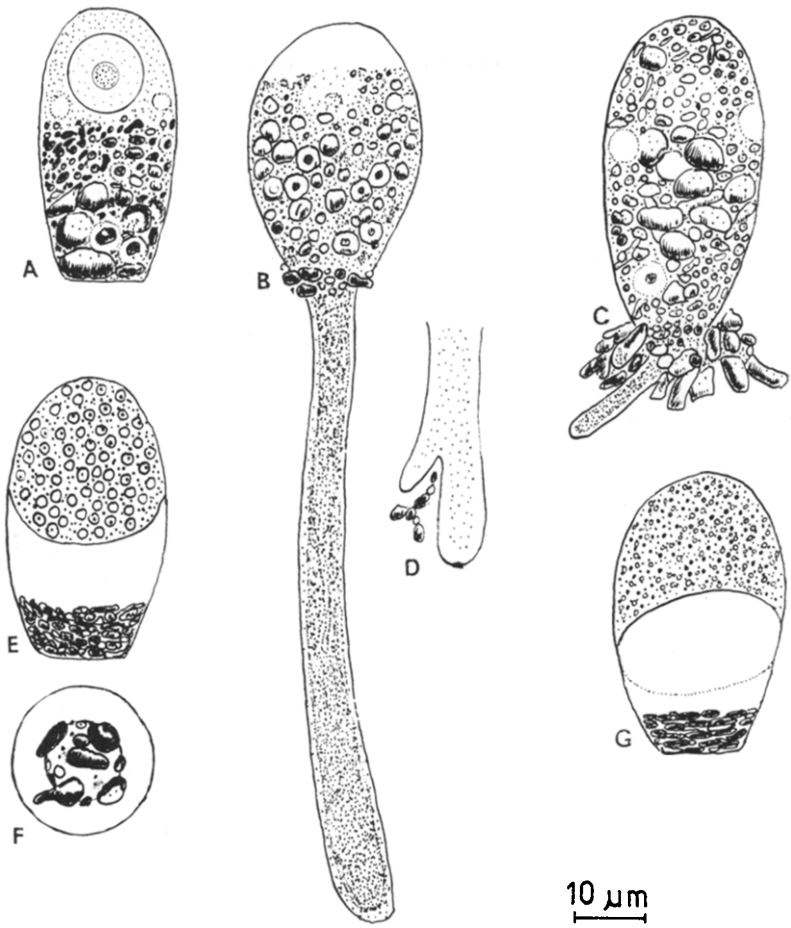

Fig. 5. Population 6 of *Schoenbornia humicola*. Different aspects of living cells. A: Inactive stage with clear zonation of the cytoplasm. B: Active phase with endolobopodium, completely expanded. C: Active, feeding phase. Food-bundles around the pseudostome. The zonation of the cytoplasm is nearly effaced. D: Furcate-pseudopodium with detritus particles. E: Precyst (= Kapselstadium). F: Precyst in front view. The pseudostome is closed by a diaphragm with adherent detritus particles. G: Precyst with a bubble between the pseudostome plug and the interior membrane.

Resting stages

Resting stages occur as cysts and precysts (Kapselstadien). Cysts are spherical and enclosed in a thick membrane (Fig. 3 B). They are distinctly separated from the shell wall. Precysts are very similar to those of the euglyphids as described by VOLZ (1929). They have a retracted cytoplasm, which closely adjoins the shell wall, and is surrounded by a thin membrane. A bubble between the pseudostome plug and the retracted cytoplasm could be observed in precysts during long lasting periods of low moisture content of the soil (Fig. 5G). These shells stand upright with the pseudostome downward in soil suspensions. The same has been described for *Nebela tincta* (GNEKOW 1981).

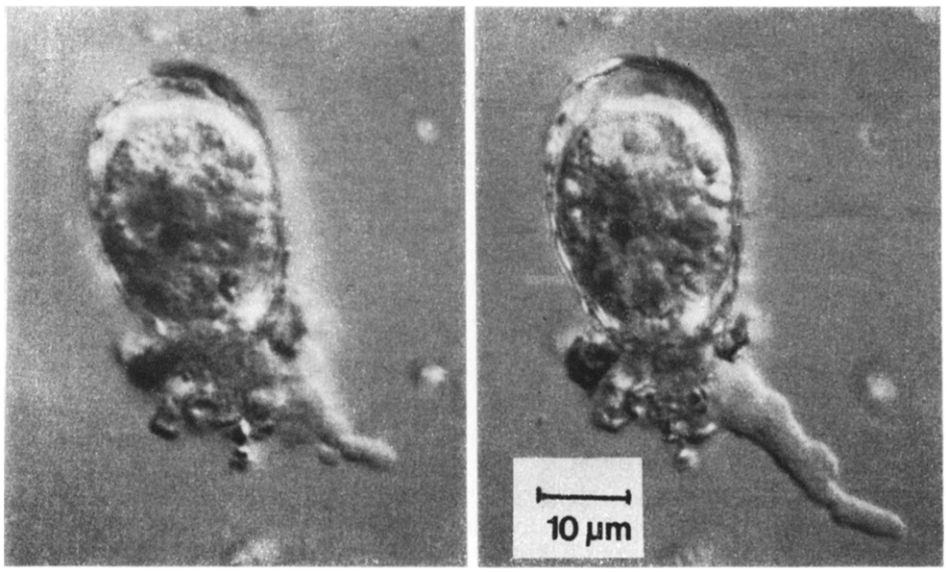

Fig. 6. Two interference contrast micrographs of population 5 of *Schoenbornia humicola* showing endolobopodia collecting food-bundles. As a consequence of the incorporation of humus particles, the zonation of the cytoplasm is indistinct. In the upper third of the cell, the nucleus with a large nucleolus is visible.

Shells with cysts as well as precysts have their pseudostome sealed by a thin membrane (diaphragm), often covered with detritus. The detritus can be very dense and appearing as a plug. In such cases the diaphragm is not visible (Figs. 5E, F). In addition to detritus, amorphous siliceous platelets can be found in the sealed pseudostome. Attempts to demonstrate these elements succeeded only seldom (Fig. 2A, B). GNEKOW (1981) always found siliceous platelets in the detritus plugs of encysted *Nebela tincta*.

An analysis of all living individuals found in P6 yielded the following results: active 48%; precysts 43%; cysts 9%. The more frequent resting stages are precysts which were unknown in Nebelinae for a long time. Recently COÛTEAUX (1976) found them in soil-inhabiting species of *Nebela*. Most *Nebela* species populate *Sphagnum*, mosses or lakes and do not occur frequently in soils. The frequent formation of precysts in the terricolous genus *Schoenbornia* can be interpreted as an (genetic) adaptation to the life in the soil.

Systematics of *Schoenbornia*

The endolobopodium shows that *Schoenbornia* belongs to the order Testacealobosa DE SAEDELEER, suborder Eulobosa DEFLANDRE. In the original description *Schoenbornia* was provisionally classified within the Reticulobosa DEFLANDRE, because only incompletely extended pseudopodia had been observed (SCHÖNBORN 1964a). The use of foreign idiosomes to build the shells is characteristic of the genus *Nebela*. Likewise, the combination of foreign idiosomes with amorphous siliceous elements and quartz is widespread among the Hyalospheniidae, to which *Nebela* belongs. On the basis of these features *Schoenbornia* can be classified within the family Hylospheniidae SCHULZE, subfamily Nebelinae CASH & HOPKINSON. Most species of *Nebela* are large and compressed.

Schoenbornia with its strikingly small and circular to slightly compressed shell as well as its restriction to soil demonstrates a specialized evolutionary line within the Nebelinae.

Full shells and actively feeding individuals of *S. humicola* can be mistaken for *Pseudodifflugia gracilis* var. *terricola* BONNET. But this species has filopodia and its shell consists mainly of xenosomes. Another similar species is *Euglyphidion enigmaticum* BONNET. This species, however, possesses two kinds of idiosomes: large and small platelets, which do not touch. No clear separation is possible from *Nebela podzolica* KORGANOVA, 1981, which is thus best synonymized with *S. humicola*.

The genus contains two reliable species, *S. humicola* (SCHÖNBORN, 1964) DECLOITRE, 1964 and *S. viscicula* SCHÖNBORN, 1964.

Ecology of *Schoenbornia humicola*

Relationship to the kind of humus

Schoenbornia humicola and *S. viscicula* are found essentially in moder and raw humus (BERGER et al. 1985; COÛTEAUX 1976, 1978; FOISSNER 1985; FOISSNER and ADAM 1981; FOISSNER and PEER 1985; RAUENBUSCH 1987; SCHÖNBORN 1964a, b, 1986a). This is strengthened by the data shown in Tables 3—6 which prove the low abundance of *S. humicola* in mull (approximately neutral) soils. Therefore this species is a valuable indicator for acid humus.

Abundance and vertical distribution

Peak values up to 7,000 individuals · g^{-1} dry mass of soil were observed at site R. The average annual density at this site, however, amounted to 700 individuals · g^{-1} dry mass of soil (Table 3). Most abundances do not exceed 2,000 individuals · g^{-1} dry mass of soil (Tables 3—6).

The proportion of *S. humicola* in the entire testacean community reaches 39.5 % and 25.9 % in sites B and R, respectively (Table 3). In acid humus this value is scarcely lower than 10 % (Tables 3—6), indicating that *S. humicola* is in fact an important species in this type of humus.

The ratio of full to empty shells (as an expression of the decomposition speed of empty shells) in most cases is less than 1 : 5 (Tables 3—6). These values correspond to the magnitude generally known for decomposition of testacean shells in moder. Ratios $>$ 1 : 10 which are characteristic for raw humus have not been observed, indicating that the empty shells of *S. humicola* are not very stable.

In spruce forest soils, which are clearly separated into needle and humus layer, *S. humicola* is nearly confined to the humus layer (RAUENBUSCH 1987; SCHÖNBORN 1986a, b; Tables 3, 4). In other soils (meadow, deciduous forest) this typic vertical distribution is less defined; most individuals occur in the upper 5 cm of the soil. However, the percentage of *S. humicola* in the entire testacean community is nearly always higher in the lower layers than in the upper ones, even in these soils, indicating that this species prefers the lower (humus) layer of the soil (Tables 3—5). This is supported by the circular cross-section of the shell which is a characteristic life-type in the humus layer (FOISSNER 1987).

Effects of liming and fertilization

Liming causes a significant ($p < 0.05$) increase in the abundance of *S. humicola*, but its percentage in the total number of living testaceans significantly ($p < 0.1$)

Table 3. Abundance (Individuals/g dry mass of soil) and vertical distribution of *Schoenbornia humicola* in soils from Austria (A—M) and the German Democratic Republic (Q, R)

Site[1])	Living individuals (absolute numbers and percentage (%) of total numbers of testaceans)		Empty shells		Kind of humus
	Soil depth (cm)				
	0—5	5—10	0—5	5—10	
A	10/0.8	0/0	21/0.8	10/0.5	mull-like moder
B	394/13.1	720/39.5	890/13.5	1,441/42.0	mull-like moder
C	745/9.6	529/10.0	1,421/7.6	1,251/11.2	moder
D	1,803/16.5	976/34.2	3,529/9.4	2,519/29.3	raw humus/moder
E	288/4.7	402/14.4	606/3.9	624/10.3	mull-like moder
F	0/0	0/0	0/0	5/1.4	mull-like moder
G	4/0.3	3/0.3	14/1.0	0/0	mull
H	1/0.2	0/0	6/0.6	0/0	mull-like moder
I	0/0	0/0	0/0	0/0	mull
K	0/0	0/0	0/0	0/0	mull
L	0/0	0/0	0/0	0/0	mull
M	12/1.6	5/1.6	11/0.7	3/0.7	moder-like mull
Q	0/0	200/14.3	0/0	1,000/3.3	raw humus
R	30/0.1	700/25.9	90/0.0	1,750/8.6	raw humus

[1]) A—E: Stubnerkogel near Gastein, Austria. Detailed site description in FOISSNER and PEER (1985). A = alpine pasture on alpine pseudogley. B = less used alpine pasture on alpine pseudogley. C, D = alder stands on alpine pseudogley. E = heavily eutrophic, marshy alpine pasture *(Rumicetum alpini)* on alpine pseudogley. All values are the means of 3 sampling occasions during the vegetation period of year 1982. *p*H (H_2O) 3.0—4.6.
F—M: Tullnerfeld in Lower Austria. Detailed site description in FOISSNER *et al.* (1985). F, H = xerothermic sites without trees (Shallow brown alluvial soils). G, I = bottomlands (Gleyic grey alluvial soils). K, L = dryland fields (Tschernozem and grey alluvial soil). M = beech forest on decalcified brown earth. All values are the means of 10 sampling occasions within 27 months (Aug. 1980—Okt. 1982). *p*H (H_2O) 6.9—7.5.
Q, R: Sites in the GDR (see "Materials and Methods"). The values are the means of 10 sampling occasions during years 1983 and 1984.

Table 4. Abundance (Individuals/g dry mass of soil) and vertical distribution of *Schoenbornia humicola* in a spruce forest and a meadow of Austria

Site[1])	Living individuals (absolute numbers and percentage (%) of total numbers of testaceans)			Empty shells			Kind of humus
	Soil depth (cm)						
	0—1	1—3	3—9	0—1	1—3	3—9	
N	0/0	673/2.1	6,692/38.5	119/0.1	2,007/0.6	3,8078/19.5	raw humus
O	45/1.2	22/1.5	8/1.4	78/1.7	148/3.6	152/4.3	mull

[1]) N: Spruce forest in Oberhaag (see "Materials and Methods, P 2"). The values are the arithmetic means of four samplings in October 1985.
O: Meadow near the Zoological Institute of the University of Salzburg. 430 m NN. *p*H (H_2O) 7.2. The values are the arithmetic means of three parallel samples collected on 19. 12. 1985.

Table 5. Abundance (Individuals/g dry mass of soil in a single collection on 22. 12. 1985) and vertical distribution of *Schoenbornia humicola* in a beech forest (Bergheim near Salzburg city; 450 m NN) of Austria

Site	Living individuals (absolute numbers and percentage (%) of total numbers of testaceans)		Empty shells		Kind of humus
	Soil depth (cm)				
	0—2	2—4	0—2	2—4	
P	126/0.7	35/1.3	753/1.3	70/0.9	mull

Table 6. Abundance (Living individuals/g dry mass of soil in the O_{F+H} horizon) of *Schoenbornia humicola* in two treated (U 1—DF, Ux—DF) and untreated (U 1—NF, Ux—NF) spruce forests near Ulm (FRG)

Month/Year	Absolute numbers and percentage (%) of total numbers of living testaceans			
	Sites and treatment[1])			
	U 1—NF	U 1—DF	Ux—NF	Ux—DF
4/1984	—	—	328/41.9	1,290/65.1
6/1984	572/8.2	630/21.0	783/46.2	1,911/34.6
8/1984	833/11.1	670/8.7	161/11.1	411/8.0
10/1984	456/7.0	365/10.3	1,814/32.3	2,757/24.4
12/1984	255/4.5	252/4.0	1,265/19.3	1,337/13.6
4/1985	716/5.0	605/8.2	2,506/26.4	2,422/12.4
Means ($\bar{x}$)	566/7	504/10	1,143/30	1,688/26

[1]) Site description and treatments see "Materials and Methods".

decreases (Table 6; sites Ux-NF, Ux-DF). Similar results have been reported by BERGER et al. (1986). This strongly suggests that *S. humicola* is less stimulated by liming than the rest of the testacean community and supports the above mentioned conclusion that this species prefers an acid environment.

Liming *and* fertilization decreases ($p < 0.1$) the abundance of *S. humicola*, but its percentage in the total number of living testaceans increases (Table 6; sites U1-NF, U1-DF). This difference, however, is statistically insignificant ($p > 0.1$). But the trend is obvious and confirms results of BERGER et al. (1986) who observed a statistically significant higher number of *S. humicola* in plots fertilized with thomasphosphate. This fertilizer changed the *p*H only by 0.2 units, whereas liming and fertilization altered the *p*H by 2.0 units in the present experiment. This may explain why the fertilizer in our experiment was not as effective as in that one of BERGER et al. (1986).

These results suggest that *S. humicola* is stimulated by fertilizers and depressed by lime, if liming causes an excessive increase of the *p*H of its habitat. Soil compaction influences *S. humicola* lesser than many other species, probably due to the small size of its shell (BERGER et al. 1985).

Zusammenfassung

Es wurden 6 geographisch weit voneinander entfernte Populationen von *Schoenbornia humicola* untersucht. Das Gehäuse besteht nach rasterlektronenmikroskopischen Analysen und Protargolsilberimprägnationen aus Schalenplättchen (Idiosomen) von Euglyphiden und aus eckigen Quarz- und amorphen Silizium-Teilchen. Die Fremd-Idiosomen werden nicht durch Predation anderer Testaceen-Arten gewonnen, sondern vom Boden aufgelesen und in die Schale inkorporiert. Die statistische Analyse verschiedener Schalenmerkmale zeigt bei einer Population einen signifikanten Unterschied in der Schalenlänge. Dies wird als Hinweis auf geographische Rassen bei *S. humicola* interpretiert. Das Protoplasma zeigt die gleiche klare Zonierung wie bei den Euglyphiden und Hyalospheniiden. Der Zellkern ist kugelförmig und hat einen zentralen Nucleolus. Das Pseudopodium wird sehr selten ausgestreckt und ist ein sehr langes Endolobopodium, das als Kriech-Pseudopodium zur Fortbewegung und als Gabel-Pseudopodium zur Nahrungsaufnahme verwendet wird. Als Ruhestadien treten Cysten und häufiger Kapselstadien auf. Während sehr trockener Perioden kann sich ein Gasbläschen zwischen dem Pseudostom-Pfropf und dem zurückgezogenen Cytoplasma bilden. Auf Grund dieser Beobachtungen wird die Gattung *Schoenbornia* in die Familie der Hyalospheniidae Schulze, Unterfamilie Nebelinae Cash und Hopkinson gestellt.

Die Nahrungsaufnahme erfolgt bei *S. humicola* diskontinuierlich. In Perioden optimaler Umweltbedingungen sammelt sie Humuspartikel und speichert diese in der Nähe des Pseudostoms als sogenanntes Freßbündel.

Die Humuspartikel werden vom Freßbündel in das Cytoplasma transportiert, was auch während suboptimaler Perioden erfolgen kann. Diese Ernährungsweise wird als Anpassung an die oft sehr rasch wechselnden Umweltbedingungen im Boden interpretiert. *Schoenbornia humicola* besiedelt hauptsächlich den Humushorizont und ist im wesentlichen auf sauren Humus beschränkt. Sie ist eine Indikator-Art für Moder und Rohhumus. Ihr Anteil an der gesamten Testaceenzönose betrug maximal 39,5 %. Dünger führen zu einer leichten Erhöhung der Abundanz von *S. humicola*, Kalk vermindert sie dagegen, wenn die Kalkung einen zu starken Anstieg des *p*H-Wertes ihres Habitats verursacht.

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Authors' addresses: Dr. habil. WILFRIED SCHÖNBORN, Akademie der Wissenschaften der DDR, Zentralinstitut für Mikrobiologie und experimentelle Therapie Jena, Abteilung Limnologie, Beutenbergstraße 11, Jena, DDR - 6900; Dr. WOLFGANG PETZ und Univ.-Prof. Dr. WILHELM FOISSNER, Universität Salzburg, Institut für Zoologie, Hellbrunnerstraße 34, A - 5020 Salzburg (Austria); Dipl.-Biol. MANFRED WANNER, Universität Ulm, Abteilung für Ökologie und Morphologie der Tiere, Oberer Eselsberg M 25, D - 7900 Ulm.