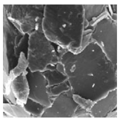
Thecamoebians from recent lake sediments from the Šumava Mts, Czech Republic

MARKÉTA LORENCOVÁ



Assemblages of thecamoebians (testate amoebae) were studied in forty-six surface samples of recent bottom sediments from five lakes in the Šumava Mts, Czech Republic. Altogether, twelve species of thecamoebians with anorganic wall were identified. The most abundant species, contained in 96% of samples, was *Difflugia globulus*. Other common species were *Difflugia oblonga* and *Centropyxis orbicularis*. Using cluster analysis it was possible to distinguish three main thecamoebian assemblages. The *Difflugia globulus* assemblage (66–100% of *D. globulus*) dominates in Plešné Lake, characterized by a higher phytoplankton content. The *Difflugia globulus* diversified cluster (4–64% of *Difflugia globulus*, 3–8 species in total) has the greatest species diversity and dominates in Laka Lake, characterized by the lowest phytoplankton biomass. The transitional *Difflugia globulus* and *Pontigulasia compressa* cluster (55–78% of *Difflugia globulus*, 12–32% of *Pontigulasia compressa*) occurs in lakes with medium values of phytoplankton biomass (Černé, Čertovo, Prášilské lakes). All the species found should be adaptable to low pH (< 6) because of the long term acidity of the investigated lakes. The species *Difflugia globulus*, *Difflugia oblonga* and *Centropyxis orbicularis* are characteristic for these lakes. The invariable morphology of *Centropyxis orbicularis* simplifies its identification and makes this species a good candidate as a palaeoenvironmental indicator. A comparison of recently evidenced taxa with the data from Černé Lake and Čertovo Lake published by Frič & Vávra (1898) was also made. Six new species have been found in these lakes (*Euglypha acanthopora, Centropyxis orbicularis, Centropyxis constricta, Difflugia viscidula, Nebela vitraea, Pontigulasia compressa*). • Key words: testate amoebae, thecamoebians, actuoecology, statistical analysis, Šumava Mts.

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Thecamoebians (testate amoebae) are a large group of freshwater amoeboid protozoans with agglutinated or autogenous tests. They are present in a wide range of habitats – soil, moss, peat, running or standing water and other moist localities. These organisms are a component of the freshwater benthos which inhabite various types of sediment (from mineral substrate with various clasts to substrate rich in sapropel). They can encyst and thus are able survive adverse conditions. Most of the species are cosmopolitan. Fossils of thecamoebians are abundant in Quaternary freshwater sediments (Medioli *et al*. 1990). Their capability for encystment, enabling them to withstand almost every unfavorable condition, keeps their evolution on a low level due to zero evolutionary pressure (Scott *et al.* 2001). An understanding of the ecology of modern thecamoebians enables palaeoecological reconstructions of freshwater environments (Scott *et al*. 2001). The use of thecamoebians as ecological and subsequently palaeoecological indicators has been the subject of many recent studies (*e.g.*, Charman 2001, Medioli *et al.* 1990).

Studies of modern thecamoebian assemblages in recent sediments from lakes in the Šumava Mts, south Czech Republic, have been undertaken to assess their use as paleoenvironmental indicators in sediments. Thecamoebians from this area were the subjects of some earlier studies. The species from mosses were analyzed by Bartoš (1949, 1951) and Balík (1992), soil thecamoebians by Rosa (1958) and lacustrine thecamoebians by Frič & Vávra (1898). Detailed variability of thecamoebian assemblages in aquatic environments were analyzed by Holcová & Lorencová (2004a). Different assemblages from stream microhabitats were studied by Holcová (2007). This paper describes lacustrine assemblages from the five lakes of glacial origin in the Šumava Mts.

Many studies dealing with lacustrine fauna have been carried out in North America, especially in Canada (Scott

Figure 1. Schematic map showing the location of studied lakes.

& Medioli 1983a, b; Patterson *et al.* 1985; Honig & Scott 1987; McCarthy *et al.* 1995; Patterson *et al.* 1996; Burbidge & Schröder-Adams 1998; Dallimore *et al.* 2000; Patterson & Kumar 2000a). Some studies were also published from European lakes (Schönborn 1962; Štěpánek 1967; Golemansky 1970, 1973; Asioli & Medioli 1992; Ellison 1995; Asioli *et al.* 1996). The assemblages in lakes from other parts of the world are less well known (Balík & Song 2000, Dalby *et al.* 2000).

The purpose of this study was to relate thecamoebian species or characteristics to limnological parameters of lakes in the Šumava Mts. Such data can be effectively used as paleoenvironmental indicators in older sediments. It is for the first time that thecamoebian fauna from recent sediments from the Šumava Mts lakes were examined on such a complex scale. Moreover, this research is closely linked to investigation of thecamoebians in other freshwater environments in the area of the Šumava Mts (Holcová & Lorencová 2004a, Holcová in press). The taxonomical concept utilised in this paper follows the typical approach used when analyzing thecamoebians in paleoecology, in contrast to the typical biological approach. This study uses the approach to thecamoebian taxonomy outlined in Medioli & Scott (1983) and Scott *et al.* (2001) which is based on fossil rather than biological assemblages. The results could also be utilized as comparative data for arcellacean fauna and variations in its assemblages depending on current limnological conditions. Last but not least, this research could be a reminder that thecameobians maybe a possible freshwater equivalent to foraminifers, and bring to the forefront the necessity for detailed study of these organisms in the paleontological record as well as in recent sediment.

The Šumava Mts and the studied lakes

The Šumava Mts are a NW-SE elongated hilly range, located along the border of the Czech Republic with Germany and Austria, with the highest hills reaching altitudes above 1400 m a.s.l. The German name of this hilly range is Böhmerwald (Bavarian Forest), the Austrian part is called Mühlviertel. The whole unit represents the largest forest complex in Central Europe, with nature protected on both sides of the border.

From the geological point of view, the Šumava Mts represent the southern part of the Moldanubicum geological unit, belonging to the Bohemian Massif. Granites, gneisses and mica-shists of Proterozoic to Lower Palaeozoic age dominate in the area. All these silicate rocks have a low ability to buffer acid precipitation and the whole area became acidified as a result of a decrease in precipitation pH during the industrial period.

The present-day geomorphology of the area was significantly affected by block movements related to Alpine orogenies in the south-located Alps during the Tertiary. Erosion and other processes have created a rolling landscape with a large upland plateau, slightly arched tops, deep valleys and glacial cirques with glacial lakes, which were formed during the glacial periods of the Quaternary (Albrecht *et al.* 2003, Veselý 1994). There are five lakes of glacial origin on the Czech side of the border, all enclosed by end moraines, and all located at approximately the same altitude of 1000–1100 m a.s.l. – Plešné Lake, Černé Lake, Čertovo Lake, Prášilské Lake and Laka Lake (Fig. 1). The moraine ramparts damming the lakes were artificialy modified and heightened in most cases.

The climate in the Šumava Mts is temperate with relatively small annual fluctuations in temperature (January average temperature –4.0 °C, July average temperature 13.1 °C, measured at the Churáňov station at an elevation of 1118 m a.s.l.), and with relatively high annual precipitation of 800–1600 mm/year. The temperature and precipitation distribution is strongly dependent on altitude. The average yearly temperature ranges between 6 °C at 750 m a.s.l., and 3 °C at about 1300 m a.s.l. (Albrecht *et al.* 2003). The water temperature of the lakes oscillates from approximately 0 to 20 °C, there is summer and winter stratification in all of the lakes except Laka Lake (Janský *et al.* 2003). The lakes are covered by ice for approximately 4 to 6 months of the year (Janský *et al.* 2003).

Studies of the lakes have been ongoing for more than 130 years. Significant changes in plankton composition and disappearance of fish resulting from lake water acidification were described (Frič & Vávra 1898, Fott *et al.* 2001, Nedbalová 2001). Long-term monitoring of the changes in limnological and hydrobiological characteristics of the lakes and reasons for their acidification are given in Kopáček *et al.* (1998), Nedbalová *et al.* (2006), Veselý (1994,

Table 1. Geographical coordinates and main characteristic of the lakes, [1] own data (GPS), [2] Janský *et al.* 2005, [3] Veselý 1996, [4] Vrba *et al.* 2002.

Parameter / Lake	Plešné Lake	Prášilské Lake	Černé Lake	Čertovo Lake	Laka Lake
N latitude [1]	48°47´	49°05´	49°11´	49°10´	49°07´
E longitude [1]	13°52´	13°24´	13°11´	13°12´	13°20´
altitude a.s.l. [m] [2]	1087	1079	1007	1027	1084
lake area [ha] [2]	7.6	4.2	18.8	10.7	2.6
max. depth [m] [2]	18.7	17.2	40.1	35.4	3.5
mean depth [m] [2]	8	8.3	15.6	17.3	1.9
pH in 1999 [4]	5.17	5.08	4.78	4.5	5.81
volume [mil. m^3] [2]	0.61	0.35	2.92	1.86	0.05
catchment area [ha] [2]	67	65	124	89	102
residence time [year] [3]	1.3	0.8	3.5	3.2	0.05
biomass of phytoplankton [μg/l C] [4]	487	118	170	167	49
geology of watersheds [3]	granite	mica-shists, quartzite	mica-shists	mica-shists, quartzite	granite, mica-shists

1996), Vrba *et al.* (2003) and Vrba *et al.* (2004). Factors affecting the chemistry of glacial lakes are examined in Kopáček *et al.* (2001). Majer *et al.* (2001) suggested a model for future evolution of lake chemistry for Plešné Lake. The recent status in geographic research is summarized in Janský *et al.* (2003, 2005). Basic descriptive parameters of the lakes are contained in Table 1.

The first observation of lacustrine thecamoebians in Šumava Mts was described by Frič & Vávra (1898) in Černé Lake and Čertovo Lake. Their research was concentrated on various aspects (botanical, zoological, hydrological, geographical, bathymetric, limnological), and was not specialized on thecamoebians. Moreover, the taxonomic view and species determination has undergone many changes since that time. Nevertheless, a comparison of these historical data with recent results can be quite useful (see Results chapter).

The studied lakes of glacial origin (Plešné Lake – PL, Černé Lake – CN, Čertovo Lake – CT, Prášilské Lake – PR and Laka Lake – LA, see Fig. 1) in the Czech part of Šumava Mts, with lake areas ranging from 2.6 ha to 18.8 ha, represent unique ecosystems, with rare species and specific biological communities. The watersheds of the lakes are relatively small, with steep slopes covered predominantly by mature spruce stands. The watersheds of the studied lakes were affected by various human activities (*e.g.*, ore prospecting and mining, forest management including logging, glass production, pasturing, dam and sluice construction, fishing and fish introduction, *etc.*). These activities have occurred here since the middle of the 17th century (Veselý 1994, Vrba *et al.* 1996), but occurence was reduced after 1960 when the Šumava Mts became a protected area. Nevertheless, at the same time, the Šumava Mts were affected by acid rains resulting from atmospheric transport of anthropogenic sulphur and nitrogen oxides. The scale and rate of these changes in the lakes resulting from this atmospheric pollution are unique in the world. The processes in the Šumava Mts catchments and lakes differ from those causing acidification in the Scandinavian and Canadian lakes especially in intensity of the acidification, and in high concentration of nitrates (Veselý & Majer 1992, Veselý 2000b). The watersheds are dominated by crystalline, calcium-poor rocks with limited ability to neutralize the acid precipitation, and by naturally forested or re-forested catchment areas. The anthropogenic atmospheric acidification presumably began as early as the 1950's but certainly by the 1960's and lake acidification peaked in the 1970's. A reversal in the acidification trend began in the mid-1980's (Vrba *et al.* 2000). During the 1990s, the deposition of sulphur and nitrogen compounds decreased due to a drop in their emissions in Central Europe (Kopáček *et al.* 1998, Veselý & Majer 1992). As a result of these complex processes, all studied lakes are acidified to a different degree, even some signs of recovery from acidity have been observed during the last decade (Nedbalová *et al.* 2006). Generally PL, CN and CT are strongly acidified, PR is moderately acidified, and LA is only slightly acidified (data from the year of 2000, Vrba *et al.* 2000). Nedbalová *et al.* (2006) indicated that PR and LA were moderately acidified in 2003. A statistical comparison of seasonal data showed a significant increase in pH and a significant drop in total reactive aluminium in the period 1997–2003 (Vrba *et al.* 2004).

At the bottom of these lakes, an oxygen deficit is generally observed (Veselý *et al.* 2004), except for CN and LA. The lakes are stratified and their water is mixed twice a year (dimictic lakes), except for the shallow LA (Vrba *et al.* 2002). The sedimentation rate can vary greatly at different depths in the lakes. Sediment core studies show that the sedimentation rates are mostly between 1 and 2 mm/yr in the deep central parts of CN and CT (Veselý 1994). Hejzlar *et al.* (1998) estimated a sedimentation rate of about 1 mm/yr in PL. These sedimentation rates can be valid mostly for the central sections of the lake bottoms.

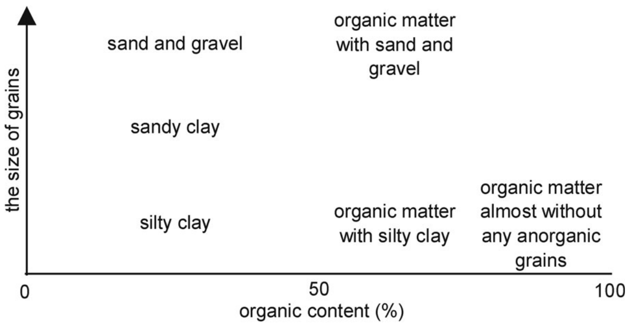

Figure 2. Types of sediment analyzed.

The sections along the lake shores show either lower (where wave action washes the sediment to a deeper section) or higher (near the small inflows) sedimention rates. All the studied lakes have catchments with a small area and only small inflow streams, which transport relatively small quantities of coarse clastic material. According to their trophic status, the lakes can be divided into two groups: oligotrophic (CN, CT) and mesotrophic (PL, PR, LA).

Material and methods

Forty-six samples were collected in June 2002 from the surface layer of the sediments from the bottom of the selected lakes. The localities were chosen in order to sample as many types of environments, substrates and water depths as possible. Substrates included silty clay, sandy clay, sand and gravel and organic matter-rich sediment, containing more than 50% organic matter of various origins (Fig. 2). Sampling was carried out from a small boat by hand or using a simple sampling device in deeper parts. The geographical location of each sample site was measured using GPS (Global Positioning System) and recorded on detailed maps. Photos of the locality, including the immediate surroundings were also taken. Water depth, distance from the actual shore line, characteristics of the bottom and the sediment present, and types of water plant vegetation in the vicinity were recorded (Table 2). An approximately 1 cm thick layer of the sediment/water interface from an area of *ca* 25 cm^2 was sampled. At most sites sampled, this thickness of the sediment layer should correspond to ten years of sedimentation (*i.e.* 1992–2002, *cf.* Veselý 1994), or less. In some cases where coarse clastic sediments were sampled, the sample could integrate longer periods of time, since the fine-grained portion of the sediment could have accumulated in the interstitial spaces of the gravel or sand.

The number of samples from the lakes was seleceted depending on the lake area, with the lowest number being 6 samples from the smallest LA, and highest number being 11 samples from both CN and CT. In three cases (PL34/02, PL35/02, CT57/02) the same sample area was sampled twice or three times at distances of 5–10 cm between replicated or triplicated samples, to detect possible local variability in the assemblages.

Twenty cm^3 of each sample was washed using 1 mm and 0.036 mm sieves. The 0.036–1 mm fractions were air dried (20–30 °C). The dried residuum of the washed sample does not contain organic tests due to their destruction during laboratory preparation, which makes the sample comparable to fossil assemblages (Scott *et al.* 2001). Staining methods for distinguishing dead and live populations were not applied because the whole study was focused on determination of total populations, integrated during the period of accumulation of the sampled sediment layer. Thecamoebians have rapid generation time so total populations provide a better estimate than living populations of the seasonal standing crop (Scott & Medioli 1980, Patterson & Kumar 2000b).

Thecamoebians were identified using an optical stereomicroscope MBC-10 (56×). Test morphology was assesed and measurements were made using a stereomicroscope Olympus SZX 12 (144×) and scanning electron microscope (SEM) JEOL JSM – 6380LV, micrographs of thecamoebians were also taken. All facilities are located in the Department of Geology and Paleontology, Charles University in Prague.

Relative abundance of thecamoebians in the samples were expressed as number of specimens in 20 cm^3 of the wet sediment. If the sample was rich in thecamoebians, the washed residual was divided into subsamples using a dry microsplitter, so that for counting purposes about 100–200 specimens were present in the subsample (Table 2).

The Shannon index of diversity was determined for each assemblage to express its diversity. It was defined as $SID = -\sum p_i * \ln(p_i)$, where p_i is the proportion of the i^{th} species in the assemblage (Patterson & Kumar 2000).

Thecamoebians assemblages were classified through cluster analysis using the STATISTICA software. (Tree Clustering using Ward's method and Euclidean distance as a type of distance measure.) The entrance data included percentual representation of species in each sample assemblage and overall abundance of assemblage (samples with no assemblage were eliminated).

Results

In three cases (samples PL34/02, PL35/02 from PL and CT57/02 from CT) the same locality was sampled twice or three times at distances of 5–10 cm from each other to determine possible variability of the assemblages (Fig. 3). Analysis of these samples supports the conclusions published in

Table 2. Water depth, distance from the actual shore line, type of sediment, abundance of thecamoebians in 20 cm^3 of wet sediment and determinated species found in each sample (as a percentage). • A – lake. • B – locality. • C – sample. • D – depth below water surface (cm). • E – distance from the shore line (cm). • F – type of sediment. • G – *Centropyxis aculeata* (Ehrenberg, 1832). • H – *Centropyxis arcula* (Leidy, 1879). • I – *Centropyxis constricta* (Ehrenberg, 1843). • J – *Centropyxis orbicularis* Deflandre, 1929. • K – *Difflugia globulus* (Ehrenberg, 1848). • L – *Difflugia oblonga* Ehrenberg, 1832. • M – *Difflugia protaeiformis* Lamarck, 1816. • N – *Difflugia viscidula* Penard, 1902. • O – *Euglypha acanthopora* (Ehrenberg, 1841). • P – *Nebela dentistoma* Penard, 1890. • Q – *Nebela vitraea* Penard, 1899. • R – *Pontigulasia compressa* (Carter, 1864). • S – number of specimens per 20 cm^3 of wet sediment. • T – Shannon index of diversity. • U – number of species.

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U
Plešné Lake	PL34	PL34/02a	10	100	sandy clay	0	0	0	1	97	3	0	0	0	0	0	0	17550	0.2	3
	PL34	PL34/02b	10	100	sandy clay	0	0	0	2	93	4	0	0	0	0	0	0	15686	0.3	3
	PL35	PL35/02a	50	200	silty clay	0	0	0	5	95	0	1	0	0	0	0	0	2800	0.2	3
	PL35	PL35/02b	50	200	silty clay	0	0	0	4	96	0	0	0	0	0	0	0	1960	0.2	2
	PL35	PL35/02c	50	200	silty clay	0	0	0	4	96	0	0	0	0	0	0	0	2277	0.2	2
	PL36	PL36/02	1540		> 50% of organic material	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PL37	PL37/02	75	400	silty clay	0	0	0	0	83	17	0	0	0	0	0	0	4064	0.5	2
	PL38	PL38/02	1030	1500	silty clay	0	11	0	29	59	0	2	0	0	0	0	0	416	1	4
	PL39	PL39/02	10	200	sandy clay	0	2	2	12	66	13	6	0	0	0	0	0	21800	1.1	6
	PL40	PL40/02	75	300	sand and gravel	0	1	0	0	92	4	0	2	0	0	0	0	195	0.3	4
	PL41	PL41/02	40	300	sandy clay	0	0	0	0	90	10	0	0	0	0	0	0	2619	0.3	2
Prášilské Lake	PR42	PR42/02	40	100	sand and gravel	0	0	0	9	74	10	6	0	0	0	0	0	1757	0.8	4
	PR43	PR43/02	25	100	sand and gravel	0	0	0	0	97	3	0	0	0	0	0	0	6140	0.1	2
	PR44	PR44/02	1000		sand and gravel	0	5	2	13	11	59	11	0	0	0	0	0	578	1.3	6
	PR45	PR45/02	5	50	sand and gravel	0	0	5	0	88	7	0	0	0	0	0	0	252	0.4	3
	PR46	PR46/02	200	200	sandy clay	0	1	2	4	60	29	4	0	0	0	2	0	12369	1.1	7
	PR47	PR47/02	70	30	> 50% of organic material (needles), silty clay	0	27	0	14	45	9	5	0	0	0	0	0	44	1.3	5
	PR48	PR48/02	120	300	silty clay	0	3	1	2	43	51	0	0	0	0	0	0	765	0.9	5
	PR49	PR49/02	330	1500	silty clay	0	0	0	0	61	27	11	1	0	0	0	0	1480	0.9	4
Čertovo Lake	CT50	CT50/02	50	150	sand and gravel	0	1	0	0	91	8	0	0	0	0	0	0	34980	0.3	3
	CT51	CT51/02	650	400	sand and gravel	0	0	0	4	62	34	0	0	0	0	0	0	578	0.8	3
	CT52	CT52/02	160	200	sandy clay	0	0	0	2	78	14	6	0	0	0	0	0	6688	0.7	4
	CT53	CT53/02	30	150	sandy clay	0	3	3	2	81	13	0	0	0	0	0	0	2598	0.7	5
	CT54	CT54/02	140	500	silty clay	0	6	0	2	59	3	4	0	0	0	0	26	1442	1.1	6
	CT55	CT55/02	15	200	sandy clay	0	3	0	21	48	13	4	0	2	0	0	9	5554	1.5	7
	CT56	CT56/02	20	20	sand and gravel	0	0	0	0	97	0	0	0	0	0	0	3	820	0.1	2
	CT57	CT57/02a	125	800	silty clay	0	1	0	3	58	1	5	0	0	0	0	33	2260	1	6
	CT57	CT57/02b	125	800	silty clay	0	0	0	4	55	5	5	0	0	0	0	30	1520	1.1	5
	CT58	CT58/02	10	200	sand and gravel	1	5	0	20	31	3	17	0	0	0	0	22	539	1.6	7
	CT59	CT59/02	150	600	silty clay	0	0	0	0	66	5	1	0	0	0	0	28	13917	0.8	4
Černé Lake	CN60	CN60/02	20	400	sandy clay	0	5	0	22	62	9	0	0	0	0	1	1	4713	1.1	6
	CN61	CN61/02	150	1000	> 50% of organic material	0	0	0	0	100	0	0	0	0	0	0	0	116	0	1
	CN62	CN62/02	980		silty clay	0	0	0	0	67	5	0	7	0	0	0	21	9592	0.9	4
	CN63	CN63/02	70	200	sandy clay	0	2	0	24	64	7	0	0	0	0	0	3	1877	1	5
	CN64	CN64/02	30	150	> 50% of organic material (needles), sand and gravel	0	2	0	14	73	10	1	0	0	0	0	0	2128	0.8	5
	CN65	CN65/02	20	1500	> 50% of organic material	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	CN66	CN66/02	110	250	silty clay	0	3	0	34	41	22	2	0	0	0	0	0	4524	1.2	5
	CN67	CN67/02	40	100	sand and gravel	0	0	0	4	93	2	1	0	0	0	0	0	1365	0.3	4
	CN68	CN68/02	1320		silty clay	0	3	0	2	94	2	0	0	0	0	0	0	640	0.3	4
	CN69	CN69/02	50	600	> 50% of organic material (needles), silty clay	0	2	0	6	70	15	8	0	0	0	0	0	446	1	5
Laka Lake	LA70	LA70/02	40	150	silty clay	16	0	0	0	39	11	13	19	0	0	0	1	3007	1.5	6
	LA71	LA71/02	100	300	> 50% of organic material (vegetation), silty clay	7	1	0	0	48	18	9	3	0	0	0	15	404	1.5	7
	LA72	LA72/02	290		> 50% of organic material	1	0	0	0	78	5	1	3	0	0	0	12	98	0.8	6
	LA73	LA73/02	5	30	sandy clay	6	1	0	11	15	15	22	0	0	0	0	31	1802	1.7	7
	LA74	LA74/02	55	600	silty clay	1	9	0	36	4	21	2	7	0	0	0	19	229	1.7	8
	LA75	LA75/02	40	600	silty clay	0	2	0	4	29	12	9	30	0	3	0	11	2888	1.7	8

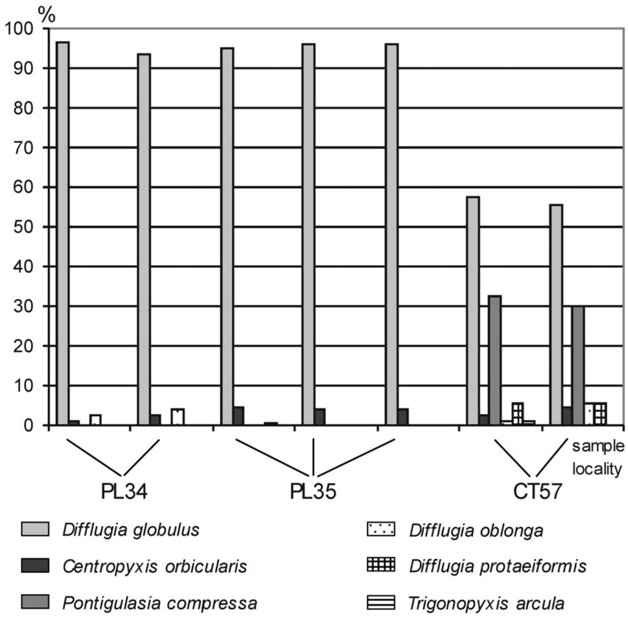

Figure 3. Similarity of species composition in samples collected within small distances (5–10 cm) in three localities (Plešné Lake – PL34, PL35, Čertovo Lake – CT57).

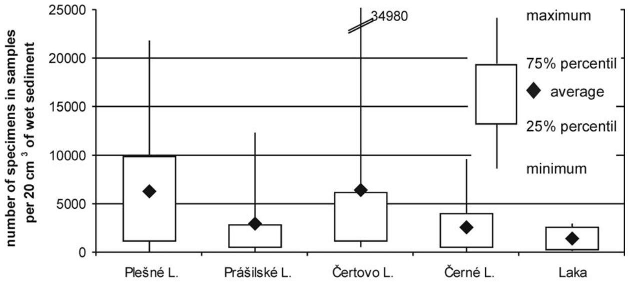

Figure 4. Abundance of thecamoebians in studied lakes.

the study by Holcová & Lorencová (2004a) that no substantial differences in assemblage composition appear within a distance of 5–10 cm. The Shannon index of diversity (SDI) for these assemblages is similar within the same localities (0.2–0.3 for two samples from PL34, 0.2 for all three samples from PL35 and 1–1.1 for two samples from CT57) (see Table 2).

Species composition and abundance in lakes

Altogether, twelve thecamoebian species were determined in the studied material (Table 2). The species *Difflugia globulus* is present in practically all assemblages (in 96% of the samples), *Difflugia oblonga* occurs in 83% and *Centropyxis orbicularis* was identified in 65% of the samples. The numbers of species per sample varied from zero to eight. The lowest number of species was observed in PL (from 0 to 6 species per sample, on average 3 species per sample), the highest number of species is typical for LA (from 6 to 8 species per sample, 7 species on average). There are 4 species on average in CN (minimum 0, maximum 6 species per sample) and 5 species in CT (minimum 2 and maximum 7 species per sample) and in PR (from 2 to 7 species per sample).

The lowest average thecamoebian abundance was found in LA with 1405 specimens on average in 20 cm^3 of wet sediment (minimum 98 specimens in a sediment with > 50% content of organic matter; maximum 3007 specimens in a silty clay sediment; the abundance of assemblages depends on the type of sediment generally, see further). A high value for average thecamoebian abundance is characteristic for PL (6306 specimens/20 cm^3 of wet sediment on average, minimum 0 in sediment with > 50% of organic matter content, and maximum of 21800 specimens in sandy clay sediment). Similarly, the assemblages from CT had 6445 specimens/20 cm^3 of wet sediment on average, with a minimum of 539 and maximum of 34980 specimens, both from sand and gravel). Here the highest number of specimens in an individual sample was found (sample CT50/02) (Fig. 4). The assemblages from other lakes are of medium abundance (average values of specimens per 20 cm^3 of wet sediment are 2923 for PR and 2540 for CN).

The Shannon diversity index was calculated for each sample assemblage (see Table 2 and Fig. 5). Its average value is 0.4 in PL, 0.8 in CN, 0.9 in CT and PR and 1.5 in LA.

Sediment type dependence of assemblage composition and species abundance

The number of specimens is affected by the type of sediment. Sandy clay sediment represents the environment of the diversified and relatively abundant assemblages (8478 specimens in 20 cm^3 of wet sediment on average, ranging from 1802 to 21800; 5 species on average, minimum 2, maximum 7; see Table 3 and Figs 6, 7). However, the most abundant assemblage comes from sand and gravel (CT50/02) which is the type of sediment with variable abundance of assemblages ranging from 195 to 34980 specimens in 20 cm^3 of wet sediment. The less abundant assemblages come from the organic matter-dominated sediment (with more than 50% organic matter; 405 specimens in 20 cm^3 of wet sediment on average, ranging from 0 to 2128). The relationship between the type of sediment and the number of species cannot be estimated from this quantity of data (Fig. 7). No significant relationship between abundance or presence of species and the type of sediment was observed.

Only two samples without any thecamoebians were found (see Table 2, samples PL36/02 from PL, and

CN65/02 from CN). Both samples are characterized by algal slime and coarse vegetation detritus (needles, leaves).

Cluster analysis of assemblages

Cluster analysis classified thecamoebian assemblages into three clusters (Fig. 8). They are characterized by the dominant species and their relative abundance, distribution in lakes and the depth of collected samples (Figs 9, 10).

1) ***Difflugia globulus* cluster** group assemblages with 66–100% of *Difflugia globulus*, this species is accompanied mainly by *Difflugia oblonga* (7–17%) or *Centropyxis orbicularis* (6–14 %). This cluster dominated in PL and CN (Fig. 9). It is completely absent in LA. This cluster contains the greatest number of samples (21 samples) and it is characterized by the lowest number of registered species (1–6 species, 3 on average).

2) ***Difflugia globulus* diversified cluster** includes assemblages with a lower content of *Difflugia globulus* (4–64%) followed by several other species – *Difflugia oblonga* (3–59%), *Centropyxis orbicularis* (2–35%), *Trigonopyxis arcula* (2–27%), *Pontigulasia compressa* (1–31%), *Difflugia protaeiformis* (2–21%), with 3 to 8 species in total. This cluster is found in all lakes, with the smallest abundance in PL (Fig. 9), the highest in PR and LA lakes (Fig. 9), where the majority of the assemblages are the most diversified (6–8 species, 7 species on average, altogether 9 different species). This cluster has the greatest species diversity with assemblages from samples from shallow depths (5–100 cm, average 42 cm).

3) ***Difflugia globulus* and *Pontigulasia compressa* transitional cluster** contains assemblages with a medium percentage of *Difflugia globulus* (55–78%) and a relatively higher amount of *Pontigulasia compressa* (12–32%) in comparison with the other clusters. In this cluster the percentage of *Difflugia oblonga* is less than 5%. The highest presence of this cluster is in CT (Fig. 9). These assemblages come from deeper water (water depth of 125–980 cm, on average 302 cm) and are not present at depths less than 1 m (Fig. 10). Samples of this cluster contain the highest number of specimens in 20 cm^3 of wet sediment.

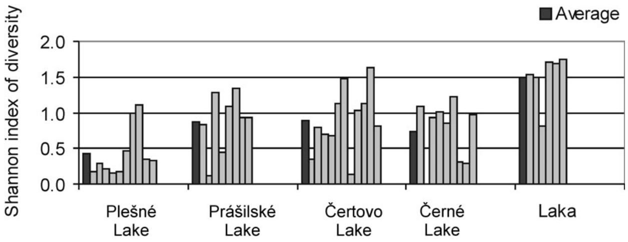

Figure 5. Shannon index of diversity for the samples from studied lakes.

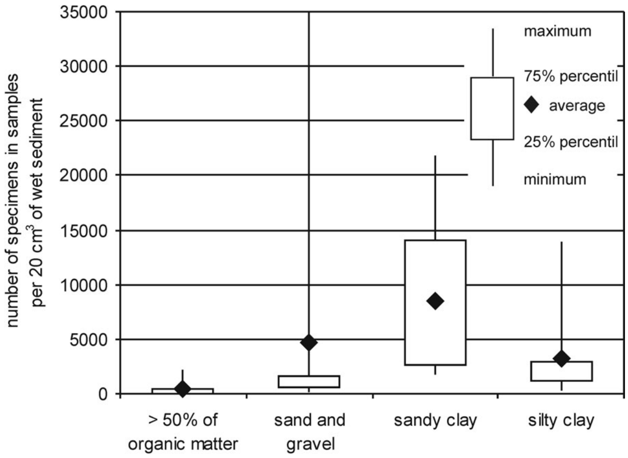

Figure 6. Abundance of thecamoebians in various types of sediment.

The SEM study showed that the species *Difflugia oblonga* was present in two distinct test size groups. The group of smaller specimens (167 × 88 μm on average) is almost three times greater in number than the group of larger ones (289 × 176 μm on average). The larger specimens are present mainly in LA, less significantly in CN. The average dimensions of the other individual species are included in the taxonomic section of this paper (see further).

Classification of the lakes based on the thecamoebians fauna

It is possible to classify the studied lakes into three categories, based on the thecamoebians fauna: 1) The strongly acidified PL with low diversificated assemblages and a do-

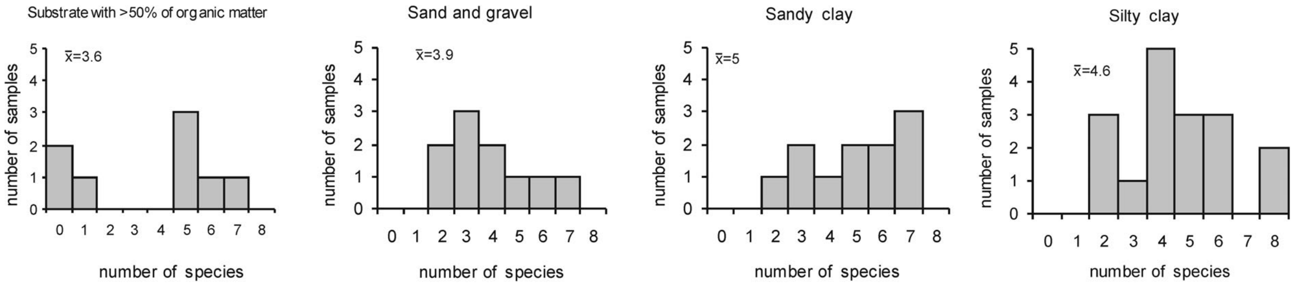

Figure 7. Number of samples from each types of sediment with various numbers of species.

Table 3. Sediment type dependence of assemblage composition and species abundance.

type of sediment	abundance [specimens in 20 cm^3 of wet sediment]			number of species		
	average	min.	max.	average	min.	max.
sand and gravel	4720	195	34980	4	2	7
sandy clay	8478	1802	21800	5	2	7
silty clay	3164	229	13917	5	2	8
substrate with > 50% of organic material	405	0	2128	4	0	7

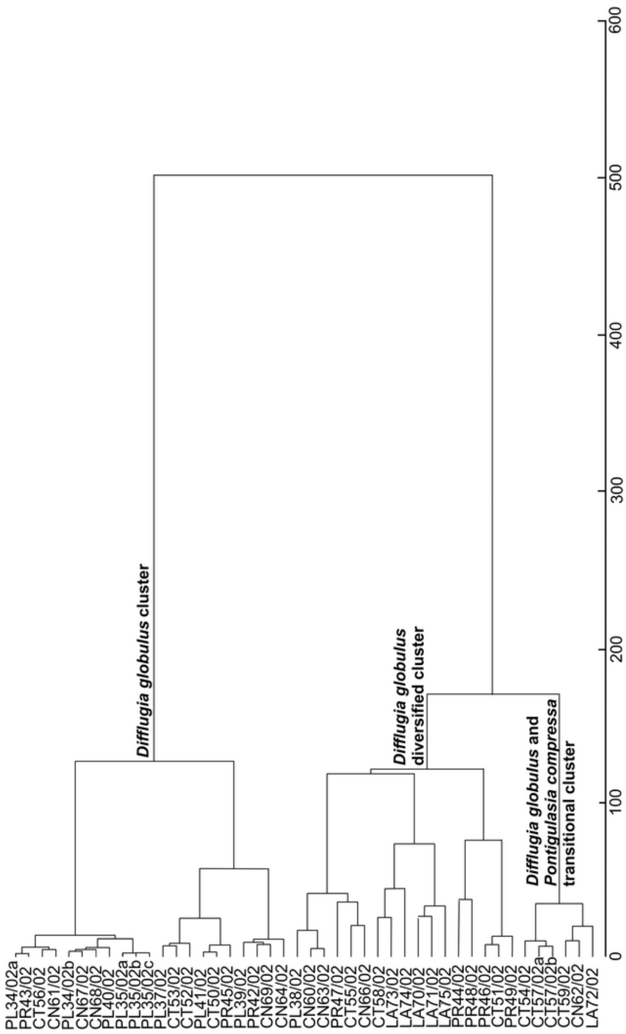

Figure 8. Results of cluster analysis (PL – Plešné Lake, CN – Černé Lake, CT – Čertovo Lake, PR – Prášilské Lake, LA – Laka Lake) (Tree Clustering using Ward's method and Euclidean distance as a type of distance measure).

minance of the species *Difflugia globulus*; 2) The shallow, partly overgrowing mesotrophic LA without water stratification hosts more diversified assemblages; 3) CN, PR and CT lakes with various types of assembleges, depending on the depth and type of sediment.

Discussion

Comparison with the Frič & Vávra (1898) study

A comparison of the results of this study with the results of Frič & Vávra (1898) shows (Table 4) that some new species have been found in CT (*Euglypha acanthopora, Centropyxis aculeata, Trigonopyxis arcula, Centropyxis constricta, Centropyxis orbicularis, Pontigulasia compressa*) as well as in CN (*Centropyxis orbicularis, Difflugia viscidula, Nebela vitraea, Pontigulasia compressa*). Some genera identified in this study were not reported in the 1898 study (*Arcella vulgaris* in both lakes, *Centropyxis aculeata, Corythion dubium, Cyphoderia ampula, Difflugia urceolata, Euglypha ciliata, Nebela bohemica, Nebela collaris* in CN). The results should be interpreted carefully, taking into account these facts: a) the methodology of the first study is not known; b) it seems that Frič and Vávra collected plenty of samples from the deep bottom while the present research was limited in this tendency (the majority of samples came from depths less than 150 cm, only two samples came from deeper water); c) organic walled rhizopods are not considered here, d) variability that could be observed among samples within the same lake recently suggests that more samples could contain more species. Some species recently found (*Trigonopyxis arcula, Difflugia globulus, Difflugia oblonga, Difflugia protaeiformis*) are very similar, if we look at the taxonomic changes or corrections made since that time (1898), *cf.* Medioli & Scott (1983).

Ecological indicators of thecamoebian species

Considering the most frequent occurrence of *Difflugia globulus*, *Difflugia oblonga* and *Difflugia protaeiformis* species, the conclusions of Scott *et al.* (2001), indicating the adaptability of these species to pH < 6.2 are in accordance with recent results. No similar indication of adaptability for the other common species, *Centropyxis orbicularis* and *Pontigulasia compressa,* to low pH was found in the literature.

Difflugia globulus – cold climatic indicator, relations to content of phytoplankton in water. – The frequent appearance of *Difflugia globulus* in all studied lakes could be explained by their high altitude (above 1000 m a.s.l.) and the relevant weather. It supports the hypothesis that *Difflugia globulus* is probably a good cool to cold climatic indicator (Collins *et al.* 1990).

High relative abundance of *Difflugia globulus* in PL (59–97% of the assemblage, 87% on average) and the lowest abundance in LA (4–77%, 35% on average) could be interpreted as reflecting the content of phytoplankton in these lakes. According to Scott *et al*. (2001), this species feeds on green and yellow-green algae. PL contains phytoplankton which accounts for 70% of the total biomass (Nedbalová *et al.* 2006). On the other hand, a lower number of algal taxa and low content of phytoplankton in the biomass in comparison with other lakes has been found in LA (Nedbalová *et al.* 2006, Vrba *et al.* 2002, Vrba *et al.* 2003; see also Table 1). This could be a reason for lower abundace of *Difflugia globulus*. Nedbalová *et al.* (2006) noted that they did not observe any significant general change in phytoplankton biomass in their 2003 survey in comparison with the 1999 data. According to their results, the majority of phytoplankton species are probably able to adapt to changing pH and related factors and the qualitative phytoplankton structure in the mostly frequently investigated CN has remained surprisingly stable despite drastic changes in lake water chemistry within the last seven decades. Differences in the phytoplankton content in individual lakes, and simultaneously its stability in each lake, might cause a certain heterogeneity in thecamoebian assemblages that populated these lakes. Differences in representation of *Difflugia globulus* in the lakes that have been found in this study are in accordance with the above mentioned published data.

Difflugia oblonga – related to increasing organic content in substrate. – The species *Difflugia oblonga* is present in all samples from PR (3–9%) and LA (5–21%). Scott *et al.* (2001) note that it substitutes the species *Difflugia globulus* when the amount of organic content increases. This could be expected in LA which is overgrown by rich vegetation and contains a high quantity of organic sedimentary components. The explanation for the higher presence of *Difflugia oblonga* in PR is not clear. Lower Al concentration (Kohout & Fott 2001, Vrba *et al.* 2006) and only moderate P limitation (Nedbalová *et al.* 2006) in comparison with other lakes could have some effect. According to the size of the tests it is possible to distinguish that the group of smaller specimens is almost three times greater in number than the group of larger ones. There are some suggestions found in literature (Bobrov *et al.* 1999, Scott *et al.* 2001) that the test size can be affected by nutrient conditions. The results of this study do not contradict these suggestions. Low temperature and oligotrophy of the studied lakes causing reduced availability of food could induce domination of smaller tests.

Difflugia protaeiformis – common in environments rich with organic matter. – *Difflugia protaeiformis* was found in all samples from LA (1–13 %), while in other lakes it occurs less frequently. Scott *et al.* (2001) note that it is well adapted to an environment rich in organic matter as is the environment of LA is to a great extent.

Pontigulasia compressa. – Medioli & Scott (1988) remark that *Pontigulasia compressa* can adapt to any type of water environment. The results of this research could not confirm or reject this conclusion. There is a significant number of

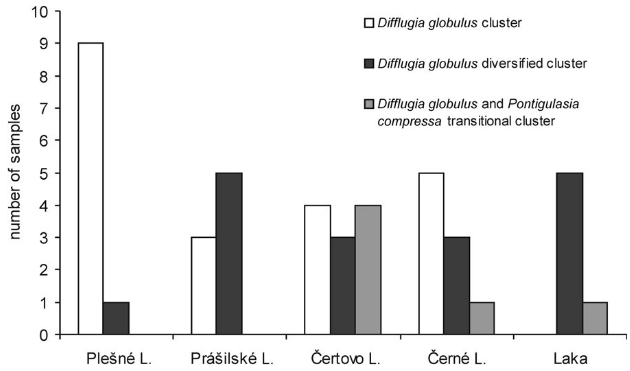

Figure 9. Representation of clusters in lakes (Tree Clustering using Ward's method and Euclidean distance as a type of distance measure).

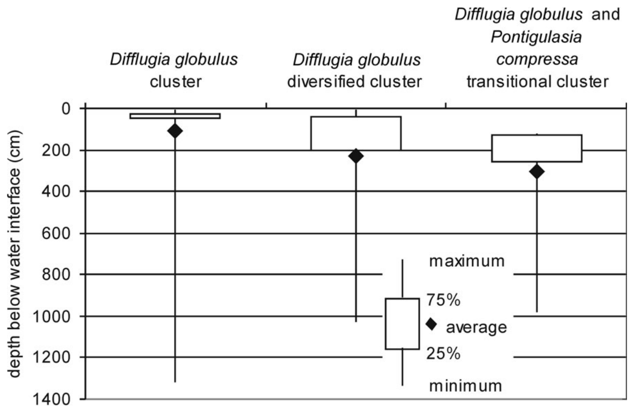

Figure 10. Depth of samples from various clusters.

this species in LA (1–31%) but it was not found in PL and PR lakes. Holcová (2007) indicated that this species is associated with flowing water. In this study, the higher number of *Pontigulasia compressa* occur in LA where the water residence time in the lake is the shortest (Veselý 1996; see also Table 1).

Centropyxis orbicularis – uniform morphotype, abundant and represented in all lakes. – No essential data concerning ecology of *Centropyxis orbicularis* were found in the literature. However it occurs in 68% of all studied samples, its abundance in the assemblages is 10%, on average. It is present in all lakes; no relationship with the type of sediment, environment, depth etc. was detected. *Centropyxis orbicularis* forms a substantial part of the diversified *Difflugia globulus* cluster where it constitutes 14–34% of the assemblages. The morphotype of this species is quite invariable and it creates such a clearly separable group that there is the possibility that it could also be easily identified in older sediments and may have some ecological effects detectable in palaeoecology.

Centropyxis constricta – opportunistic character was neither proved, nor eliminated. – Regarding the species

Table 4. Comparison of recently found thecamoebian species from Čertovo Lake and Černé Lake with data published in 1898 (Frič & Vávra 1898), species comparison according to Mediolli & Scott (1983).

Lake	Frič & Vávra (1898)	This study (2002)
Čertovo Lake	*Difflugia globulosa* Duj.	*Difflugia globulus* (Ehrenberg, 1848)
	Difflugia pyriformis Perty	*Difflugia oblonga* Ehrenberg, 1832
	Difflugia acuminata Ehbg.	*Difflugia protaeiformis* Lamarck, 1816
		Euglypha acanthopora (Ehrenb., 1841)
		Trigonopyxis arcula (Leidy, 1879)
		Centropyxis aculaeta (Ehrenb., 1832)
		Centropyxis constricta (Ehrenb., 1832)
		Centropyxis orbicularis Deflandre, 1929
		Pontigulasia compressa (Carter, 1864)
	Arcella vulgaris Ehbg.	
Černé Lake	*Difflugia pyriformis* Perty	*Difflugia oblonga* Ehrenberg, 1832
	Difflugia acuminata Ehbg.	*Difflugia protaeiformis* Lamarck, 1816
	Difflugia globulosa Duj.	*Difflugia globulus* (Ehrenberg, 1848)
	Difflugia urceolata Cor.	
		Difflugia viscidula Penard, 1902
	Difflugia arcula Leidy	*Centropyxis arcula* (Leidy, 1879)
	Centropyxis aculeata St.	
		Centropyxis orbicularis Deflandre, 1929
		Nebela vitraea Penard, 1899
	Nebela collaris Leidy	
	Nebela bohemica Tar.	
		Pontigulasia compressa (Carter, 1864)
	Euglypha ciliata Leidy	
	Corythion dubium Tar.	
	Cyphoderia ampula Leidy	
	Arcella vulgaris Ehbg.	

Centropyxis constricta, Scott *et al.* (2001) indicate its tolerance to extreme conditions, they are often the first pioneer forms appearing in oligotrophic periglacial lakes, immediately after deglaciation. Patterson *et al.* (1996) added that the genus *Centropyxis* is opportunistic, it can withstand low temperatures, low nutrient content and oligotrophy. The opportunistic character of this species was confirmed in the study done in Šumava Mts in streams (Holcová 2007) and in the Lipno Reservoir near the inflow of the Vltava River (Holcová & Lorencová 2004b) after the catastrophic flood events of 2002 and 2003. The appearance of this genus is not in contrary to the above mentioned data.

Centropyxis aculeata – oportune character was not proved, neither eliminated. – Information about *Centropyxis aculeata* species in the literaure is abundant and uniform. It is a typical r-strategy colonizer tolerating unfavourable environmental conditions, particularly lack of food (Collins *et al.* 1990, McCarthy *et al.* 1995) and low temperature (Charman 2001). This species is the first colonizer of coastal depressions evolving towards a freshwater status (Scott & Medioli 1983). According to Scott *et al.* (2001) it is a good indicator of oligotrophy.

Correlation of thecamoebian fauna correlates with phytoplankton content in the lakes

Classification of the lakes based on the thecamoebian fauna correlates with biomass content, which is represented here mostly by phytoplankton content of the water (Nedbalová *et al.* 2006; see also Table 5). The highest biomass with high content of phytoplankton are characteristic for the strongly acidified PL (*i.e.*, Type 1 lake, where the thecamoebian assemblages are not very diversified and *Difflugia globulus* reaches high relative abundance). Low content of phytoplankton occurs in the shallow, slowly overgrowing, mesotrophic LA (Type 2 lake, thecamoebian assemblages are more diversified, specimens of the species *Difflugia oblonga* reach greater sizes, 195–320 μm in average). There are medium values for phytoplankton content in other lakes (Type 3 lakes, with various types of assembleges, depending on the sampling water depth and the type of sediment).

Thecamoebian population in Šumava lakes compared with other lakes in the world

The species composition of thecamoebian fauna in Šumava Mts lakes is quite similar to fauna from other lakes in the world. Species *Difflugia protaeiformis, Difflugia oblonga, Pontigulasia compressa, Centropyxis aculeata, Centropyxis constricta* constitute a more or less significant part of the lacustrine fauna (Scott & Medioli 1983, Patterson *et al.* 1985, Patterson *et al.* 1996, Patterson & Kumar 2000a, Dalby *et al.* 2000). Generally these species are typical for gyttja (Medioli & Scott 1988).

A considerable difference is the dominance of *Difflugia globulus* species in the Šumava lakes and representation of

Figure 11. *Difflugia globulus* (Ehrenberg, 1848) from the south of the Czech Republic, Šumava Mts. • A, H, L, Q, Y – CT52/02 – Čertovo Lake, depth 160 cm, sandy clay. • B, C, E – CN61/02, Černé Lake, depth 150 cm, vegetable trash. • D, R, W – CN68/02, Černé Lake, depth 1320 cm, silty clay. • F, J, K, N – PL37/02, Plešné Lake, depth 75 cm, silty clay with vegetable detritus mainly algae. • G, I, S – PR43/02, Prášilské Lake, depth 25 cm, sand and gravel. • M, O, P, T, U – Pl34/02, Plešné Lake, depth 10 cm, sand to gravel, sandy sediment with needles. • V – PL41/02, Plešné Lake, depth 40 cm, sandy clay with algal slime. • X – CT55/02, Čertovo Lake, depth 15 cm, sand with vegetable detritus. • Z – CT57/02, Čertovo Lake, depth 125 cm, silty clay. • A* – PL40/02, Plešné Lake, depth 75 cm, sand and gravel with algal slime. • B* – CT53/02, Čertovo Lake, depth 30 cm, sand and gravel.

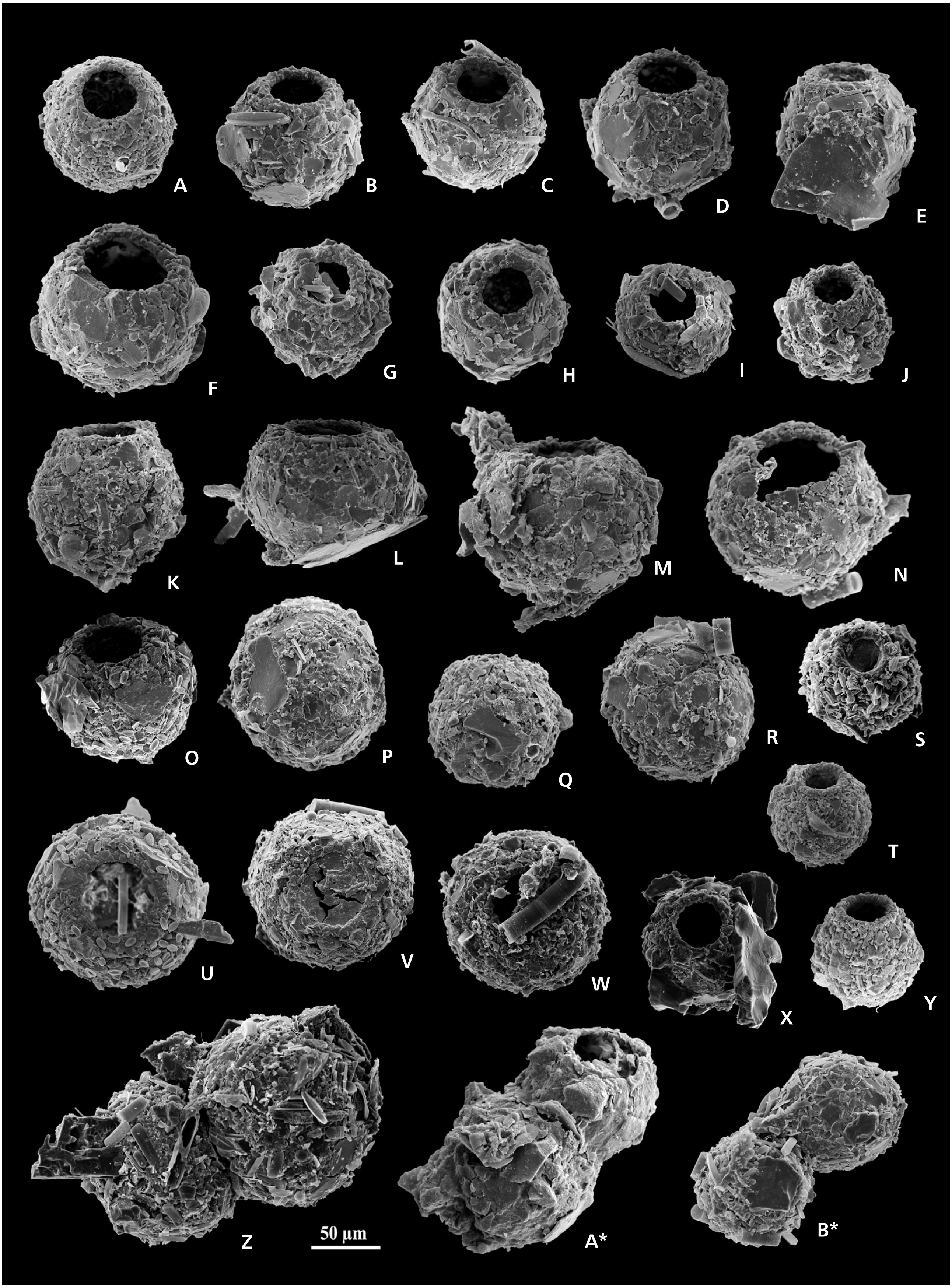
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Table 5. Three groups of lakes and their characteristics.

Type of lake	Lake	Thecamoebian assemblage
the highest biomass with high content of phytoplankton (70%)	Plešné Lake	poor diversified, high relative abundance of *Difflugia globulus*
low content of phytoplankton, shallow mesotrophic lake slowly overgrowing by vegetation, without stratification	Laka Lake	highly diversified, greater specimens of *Difflugia oblonga* (195–320 μm in average)
middle content of phytoplankton	Prášilské Lake Černé Lake Čertovo Lake	various types of assemblages

Centropyxis orbicularis and *Trigonopyxis arcula* here. According to Medioli & Scott (1988), the *Difflugia globulus* species is typical for lake sediment. Surprisingly, not many finds are recorded in the literature (*e.g.*, Scott & Medioli 1983, Patterson *et al.* 1996). The reports about two other species *Trigonopyxis arcula* and *Centropyxis orbicularis* are even more sporadic in lake environments (Gehrels *et al.* 2006).

Healthy thecamoebian faunas usually have Shannon index of diversity values higher than 2.0 (Patterson & Kumar 2002) or approaching 2.5, and an abundance of about 500 specimens/cm^3 (Patterson & Kumar 2000a). As in most stable climax communities, there is an equitable distribution of species in these healthy environments with no species overwhelmingly dominating the fauna (Patterson & Kumar 2000a). Only a few assemblages in Šumava glacial lakes meet this boundary value of abundance (PL34/02 a PL39/02 from PL, PR46/02 from PR, CT50/02 a CT59/02 from CT and CN62/02 from CN). No assemblage is so abundant in LA. The average value for thecamoebians abundance for the analyzed assemblages in the lakes are much lower. Common dominance of one or two species and low values of SDI (0.4–1.5) also indicate instability of the populations. It could be assumed that the stressing factor is the acidification of the lakes.

From the paleontological point of view, the important limnological parameters are mainly trophy, pH value of the water, abundance of phytoplankton and type of sediment. These variables may have some affect on thecamoebian assemblages as it is shown above.

Conclusions

Thirteen species of thecamoebians with anorganic tests were determined in 46 samples of recent sediments collected in 2002 from the bottoms of lakes in the Czech part of the Šumava Mts (Plešné, Černé, Čertovo, Prášilské and Laka lakes). The most common species are *Difflugia globulus* (present in 96% of samples), *Difflugia oblonga* (in 83% of samples) and *Centropyxis orbicularis* (in 65% of samples). Number of species per sample varies from zero to eight.

Cluster analysis classified thecamoebian assemblages into three clusters. Their distribution according to the thecamoebian assemblages enables us to distinguish three groups within the five investigated lakes. This division corresponds to classification of the lakes according to biomass content which is represented here mostly by the phytoplankton content of the water:

– Plešné Lake, with low species richness and high relative abundance of *Difflugia globulus*; the lake contains the greatest biomass with a high content of phytoplankton (70% of biomass) and is strongly acidified;

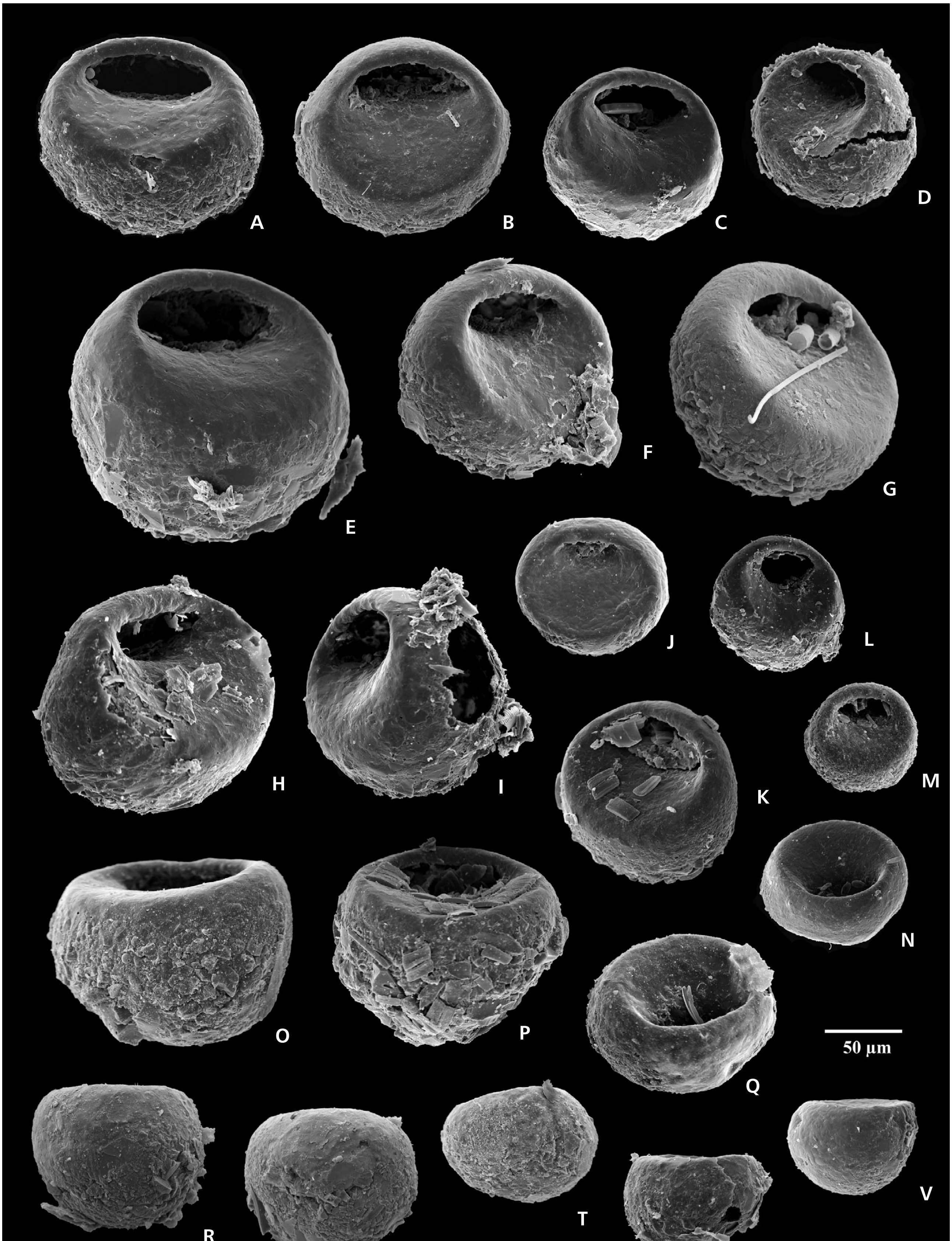
– Laka Lake, with high species richness and the lowest relative abundance of *Difflugia globulus*, specimens of *Difflugia oblonga* reach greater sizes (345 μm × 169 μm on average); it is a shallow mesotrophic lake with the lowest phytoplankton biomass, slowly becoming overgrown by vegetation, without stratification, moderately acidified;

– Prášilské, Čertovo and Černé lakes, with various types of assemblage depending on the type of sediment and depth; phytoplankton content in these lakes attaining medium values;

The studied lakes are acidified to different degrees, all have pH values < 6 yet. Therefore, all species of thecamoebians found should be adaptable to low pH.

From the point of ecological demands on the observed species, *Difflugia globulus* seems to be a cold climate indicator with a positive relationship to the content of phytoplankton in lake water, *Difflugia oblonga presence* is related to increasing organic content in the substrate, represented mainly in LA and PR, and *Difflugia protaeiformis* is common in environments rich in organic matter. The possible opportunistic character of

Figure 12. *Centropyxis orbicularis* Deflandre, 1929 from the south of the Czech Republic, Šumava Mts. • A, B, P – CT58/02, Čertovo Lake, depth 10 cm, sand and gravel. • C – PL39/02, Plešné Lake, depth 10 cm, clayey sand with fine vegetable detritus. • D, L, R, S, U – PL38/02, Plešné Lake, depth 1030 cm, silty clay with algal slime. • E, I, N – CT55/02, Čertovo Lake, depth 15 cm, sand, vegetable detritus. • F, G, J, V – CT66/02, Černé Lake, depth 110 cm, sandy clay, woody detritus. • H – LK74/02, Laka Lake, depth 55 cm, silty clay with moss. • K – PL55/02, Plešné Lake, depth 10 cm, sandy clay with needles. • T – CN60/02, Černé Lake, depth 20 cm, sandy clay with leaves.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Centropyxis aculeata and *Centropyxis constricta* was neither proved, nor eliminated.

Centropyxis orbicularis occurs in 68% of the samples. It is present in all studied lakes, no dependance on the type of sediment, environment, depth *etc*. was detected. The morphotype of this species is quite invariable and creates a clearly separable group. This species could possibly be used in paleoecological considerations during studies of older sediments.

A comparison of the results of this study with the study done in 1898 shows that some new species have been found in CT (*Euglypha acanthopora, Centropyxis aculeata, Trigonopyxis arcula, Centropyxis constricta, Centropyxis orbicularis, Pontigulasia compressa*), as well as in CN (*Centropyxis orbicularis, Difflugia viscidula, Nebela vitraea, Pontigulasia compressa*). Some genera identified in this study were not reported in the 1898 study (*Arcella vulgaris* in CT and CN, *Centropyxis aculeata, Corythion dubium, Cyphoderia ampula, Difflugia urceolata, Euglypha ciliata, Nebela bohemica, Nebela collaris* in CN). Finds of other species (*Trigonopyxis arcula, Difflugia globulus, Difflugia oblonga, Difflugia protaeiformis*) are very similar, if we take into account the taxonomic changes or corrections made since that time (1898) according to Medioli & Scott (1983).

From the paleontological point of view, the important limnological parameters discussed are mainly the lake trophy, pH value of the water, abundance of phytoplankton, and type of sediment. These variables may have some affect on thecamoebian assemblages as it is shown above.

Taxonomic remarks

The taxonomic approach described in the paper by Scott & Medioli (1983) was followed in principle. They define several "natural-assemblages species" after a large study of their morphology and intragradational variants described in literature and observed in the field or in laboratory. Medioli & Scott (1983) assumed that fossil assemblages are even more variable than living or subrecent assemblages collected at one particular point in time. In these taxonomical remarks, morphological variability of the species in the investigated material are described.

Genus *Difflugia* Leclerc *in* Lamarck, 1816

Difflugia globulus (Ehrenberg, 1848)
Figure 11

The test is most often spherical, the size of measured specimens varies from 71 μm to 138 μm and the aperture width reaches 34–53% of test width. The test is covered by xenosomes of various sizes, sometimes by frustules of diatoms or enormous sand grains (Fig. 11X). Finer grains often border the aperture. Some specimens have the aperture closed by some epiphragm or some sort of plug that could be considered a cyst (see Fig. 11S, V). Some "conjoined twins" have been found (see Fig. 11Z–B*) that could be some part of the reproductive cycle, possibly parental and daughter tests.

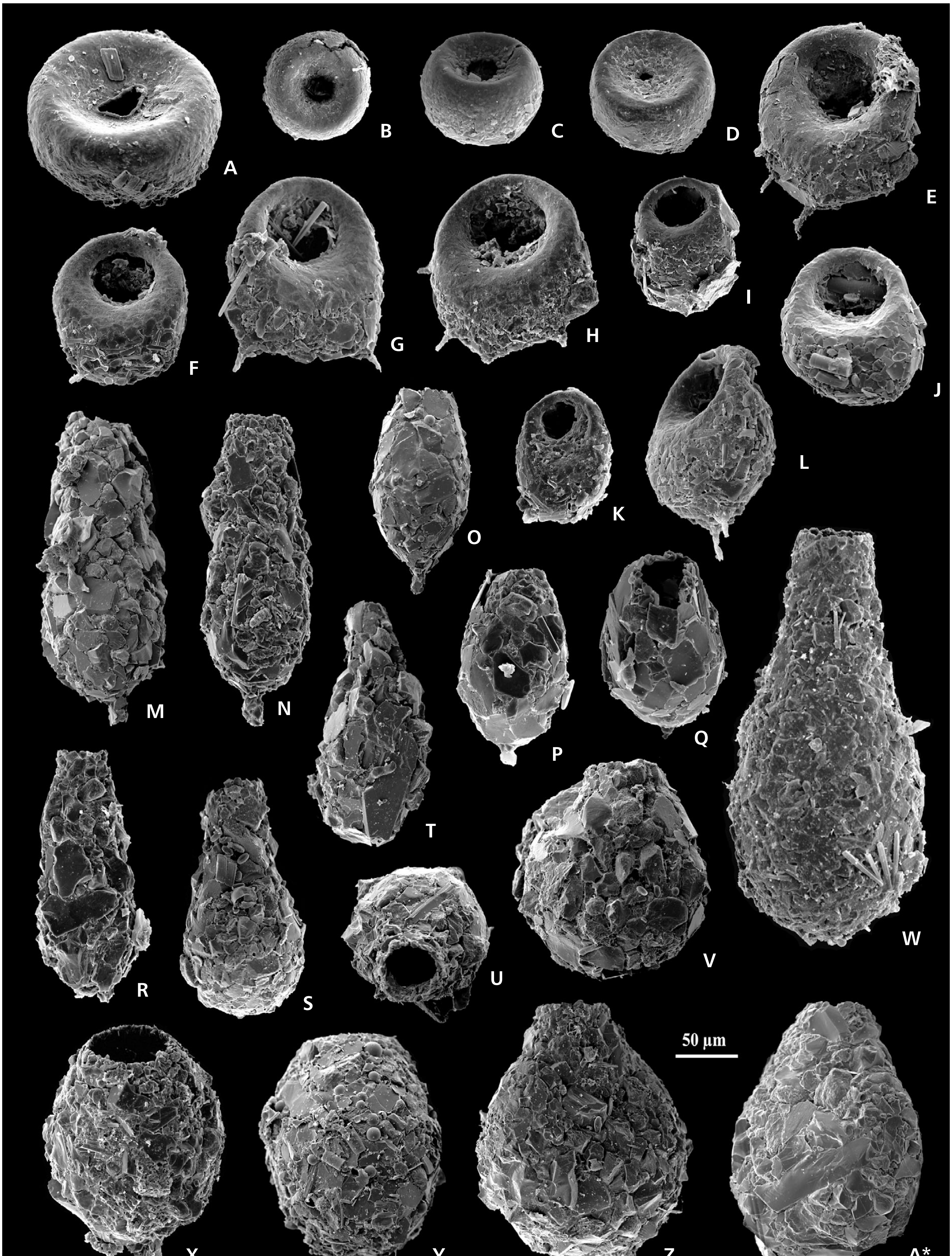
Difflugia oblonga Ehrenberg, 1832
Figure 13S–W

The test is oval and laterally compressed or pyriform mostly with a rounded fundus. Pyriform forms have mostly a clearly defined neck that could taper to the aperture. The aperture is oval or circular and surrounded by small particles. Sand grains cover the surface of the test. We could distinguish two groups of pyriform forms differing in size. Smaller specimens with a size of 167 × 88 μm on average and the larger ones that reached values 289 × 176 μm on average.

Difflugia protaeiformis Lamarck, 1816
Figure 13M–R

The shape of the test is an elongate oval, pyriform or ovoid mostly with a fundus ending in a terminal conical protube-

Figure 13. Thecamoebians from the south of the Czech Republic, Šumava Mts. • A–D – *Trigonopyxis arcula* (Leidy, 1879). A – CT54/02, Čertovo Lake, depth 140 cm, silty clay. B – Lipno Reservoir Nová Pec, depth 60 cm, silty clay. C – Lipno Reservoir, silty clay. D – Lipno Reservoir, sand. • E–H – *Centropyxis aculeata* (Ehrenberg, 1832). E – LA71/02, Laka Lake, depth 100 cm, silty clay with > 50% of organic matter. F, G – LA70/02, Laka Lake, depth 40 cm, silty clay. H – LA73/02, Laka Lake, depth 5 cm, sandy clay. • I–L – *Centropyxis constricta* (Ehrenberg, 1843). I – PR44/02, Prášilské Lake, depth 1000 cm, sand and gravel. J – PL39/02, Plešné Lake, depth 10 cm, sandy clay. K – CT55/02, Čertovo Lake, depth 15 cm, sandy clay. L – PR45/02, Prášilské Lake, depth 5 cm, sand and gravel. • M–R – *Difflugia protaeiformis* Lamarck, 1816. M, N – LA73/02, Laka Lake, depth 5 cm, sandy clay. O – PR44/02, Prášilské Lake, depth 1000 cm, sand and gravel. P – CT55/02, Čertovo Lake, depth 15 cm, sandy clay. Q – CT57/02, Čertovo Lake, depth 125 cm, silty clay. R – CN69/02, Černé Lake, depth 50 cm, silty clay sediment with > 50% organic matter (needles). • S–W – *Difflugia oblonga* Ehrenberg, 1832. S – PL34/02, Plešné Lake, depth 10 cm, sandy clay. T – PR44/02, Prášilské Lake, depth 1000 cm, sand and gravel. U – LA71/0, Laka Lake, depth 100 cm, silty clay with > 50% organic matter. V – PL34/02, Plešné Lake, depth 10 cm, sandy clay. W – LA72/02, Laka Lake, depth 290 cm, algae, needles. • X, Y – *Difflugia viscidula* Penard, 1902. X – LA71/02, Laka Lake, depth 100 cm, silty clay with > 50% organic matter. Y – LA75/02, Laka Lake, depth 40 cm, silty clay. • Z, A* – *Pontigulasia compressa* (Carter, 1864). Z – LA71/02, Laka Lake, depth 100 cm, silty clay with > 50% organic matter. A* – LA73/02, Laka Lake, depth 5 cm, sandy clay.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rance or horn. A neck could be present. The aperture is circular and surrounded by a rim of small grains. The test is created by sand particles. The size varies between 100 and 235 μm.

Difflugia viscidula **Penard, 1902**
Figure 13X, Y

The test morphology is relatively uniform in its ovoid shape. The aperture is circular and surrounded by small grains. The rest of the test is covered with sand grains of various sizes.

Genus *Centropyxis* Stein, 1859

Centropyxis aculeata **(Ehrenberg, 1832)**
Figure 13E–H

The test is circular or ovoid and bilaterally symmetric from a dorsal view, in lateral view it is depressed and tapers anteriorly towards the aperture. The apertural side is large with a subcentral oval or circular invaginated aperture. The anterior angle (according to Medioli & Scott 1983) is small. Several spines could be developed along the fundus or lateral margins. The rough dorsal side of the test is composed of sand grains, the ventral side is smoother and covered by organic matrix. The size mostly ranges from 90–155 μm.

Centropyxis constricta **(Ehrenberg, 1843)**
Figure 13I–L

The test is elliptical from a dorsal view, slightly compressed and tapering anteriorly from a lateral view. The anterior angle is larger than in *Centropyxis aculeata*, the ventral side is small. The ratio of height : length is high (around 0.7 in several measured specimens). The aperture is usually large, invaginated, oval or circular in shape and is situated anteriorly. The test is created by sand particles of various sizes, the ventral side is smooth and covered by organic matrix. The size of the test is intermediate (85–115 μm).

Centropyxis orbicularis **Deflandre, 1929**
Figure 12A–V

The test is irregularly hemispherical; height of the fundus is the highest of species considered in this study. The test is circular in dorsal view. The large apertural side bears a slightly invaginated oval aperture in its anterior part; it is not rare to find arch-shape or crescent apertures. The dorsal side is curved along its whole length. The test is covered by xenosomes, rough ones on the dorsal side, on the apertural side the xenosomes are often likely to be overlapped by an autogenous product in order to produce a smoother surface. The size of measured specimens varies from 71 to 167 μm. The ratio between height and width of the aperture is 0.35–0.64. It is not possible to measure the anterior angle because of the curved dorsal side. Height : length ratio is high (0.5–0.9).

Genus *Trigonopyxis* Penard, 1912

Trigonopyxis arcula **(Leidy, 1879)**
Figure 13A–D

From a dorsal view the test is circular, laterally it is hemispherical and symmetrical. The apertural side is slightly invaginated and smoothly covered with organic matrix; the dorsal side is rough and created by sand grains. The aperture is central or subcentral, circular, triangular or irregular and usually surrounded by a small collar. Test diameter varies from 85 to 155 μm.

Genus *Pontigulasia* Rhumbler, 1895

Pontigulasia compressa **(Carter, 1864)**
Figure 13Z, A*

Morphology of the large test (mostly above 200 μm) is relatively uniform, ovoid or pyriform and laterally compressed. A short neck tapers to the aperture and joins the body by a characteristic V-shaped constriction. The aperture is oval or circular. The rough surface of the test is produced by sand grains, the neck is usually smoother and produced by smaller particles.

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