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Morphologic and Biometric Characterization of Twenty-four Soil Testate Amoebae (Protozoa, Rhizopoda)

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With 26 Figures

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Summary

24 soil dwelling testate amoebae, belonging to 34 populations, are described and biometrically characterized. An "ideal individual" for each of the investigated species is constructed by means of the biometric data. Species separation in the *Nebela tincta-parvula-bohemica-collaris* group is discussed in detail. In *Plagiopyxis declivis*, idiosomes of euglyphids occur between the xenosomes of the shell. The analysis of the coefficients of variation of all species shows the lowest variation for the length of the shell and the highest values for its aperture. In general, the Testaceafilosa and shells composed of idiosomes have wider ranges of variation as compared with the Testacealobosa and species covered with xenosomes. This indicates that the Testaceafilosa evolve faster or are evolutionary younger than the Testacealobosa. *Pseudodifflugia fascicularis*, *Euglypha strigosa* and *Difflugia lucida* have only 1 central nucleolus, which contrasts with earlier data from literature. Significant differences between populations of the same species were found and indicate the existence of several geographical races which differ only in their size.

1. Introduction

The testate amoebae hold a prominent position in the energy turnover of the soil (SCHÖNBORN 1982; MEISTERFELD 1987; FOISSNER 1988). However, ecological studies on this group are strongly hindered by taxonomic deficiencies. Characters of the shell, like size and shape, have been widely used for species identification. This appears problematical, since size and shape are subject to a high natural variability (HOOGENRAAD and DE GROOT 1937; BARTOŠ 1938; DECLOITRE 1954; ŠTĚPÁNEK and JELÍNEK 1958; SCHÖNBORN et al. 1983; OGDEN 1984a). Thus, biometric analysis is indispensable and has indeed been used by a number of authors (HOOGENRAAD and DE GROOT 1937; DECLOITRE 1954; HEAL 1963; BONNET 1980, 1984; HEDLEY and OGDEN 1973, 1974; HEDLEY et al. 1974; SCHÖNBORN et al. 1983). There exist, however, innumerable species descriptions with not or very poor biometric data.

The purpose of this study is to redescribe some common soil testate amoebae by means of modern techniques, e.g., biometric analysis, scanning electron microscopy and protargol silver staining, and to compare the results with data from literature.

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2. Materials and Methods

2.1. Site description and species investigated

Pine forest, "Ziegelwald" near Aigen (Upper Austria); 540 m NN; Litter/raw humus. Species from 0—5 cm soil depth: *Euglypha rotunda, Trinema enchelys* population (P) I, *Centropyxis aerophila* var. *sphagnicola, C. sylvatica, C. orbicularis.*

Pine forest, Oberhaag near Aigen (Upper Austria); 860 m NN; Litter/raw humus. Species from 0—5 cm soil depth: *Euglypha strigosa* (PII), *Phryganella acropodia* (PII), *Nebela tincta* (PII), *Hyalosphenia subflava* (PII). Species from 3—9 cm soil depth: *Trinema complanatum* (PII), *Corythion dubium* (PII), *Trigonopyxis arcula* (PII), *Plagiopyxis declivis* (PII).

Pine forest, "Grünwald" near Aigen (Upper Austria); 1,005 m NN; Litter/raw humus. Species from 0—5 cm soil depth: *Euglypha strigosa* (PI), *Hyalosphenia subflava* (PI), *Difflugia lucida, Assulina seminulum, Nebela tincta* (PI).

Meadow, Aigen-Schlägl (Upper Austria); 590 m NN; Brown earth. Species from 0—5 cm soil depth: *Pseudodifflugia fascicularis, Trinema lineare* (PII).

Arable soil, Niš (Serbia, Yugoslavia); 190 m NN; Loam. Species from 0—5 cm soil depth: *Trinema lineare* (PI).

Alpine pasture, Schloßalm area near Bad Hofgastein (Central Alps, Salzburg, Austria); 1,965 m NN; Podsolic brown earth. Species from 0—4 cm soil depth: *Euglypha cristata, Trinema enchelys* (PII), *Schoenbornia viscicula, Phryganella acropodia* (PI), *Cyclopyxis eurystoma.*

Pine forest, "Haitzing Alm", Schloßalm area near Bad Hofgastein (Central Alps, Salzburg, Austria); 1,750 m NN; Brown earth. Species from 0—5 cm soil depth: *Corythion dubium* (PI), *Trinema complanatum* (PI), *T. penardi, Trigonopyxis arcula* (PI), *Plagiopyxis declivis* (PI), *Nebela parvula.*

Meadow, 2.5 km south-west of Salzburg city (Austria); 430 m NN; Calcareous typical gley. Species from 0—2 cm soil depth: *Centropyxis elongata, Cryptodifflugia oviformis.*

2.2. Light microscopic investigation and biometric characterization

The testate amoebae were stained either with protargol silver or methylgreen-pyronin (1 % aqueous solution) for a study of their general shell structures and their nuclei, respectively (FOISSNER 1979, 1982, 1983). All drawings were performed at a magnification of × 1,000 (objective × 100, ocular × 10) with the help of a camera lucida.

For the biometric characterization, the shells were embedded in a saturated tylose solution (Merck). According to SCHÖNBORN et al. (1983) the following parameters were computed with an electronic calculator: arithmetic mean ($\bar{x}$), median (M; this value was used to construct the ideal individual), standard deviation (s), standard error of the mean ($s_{\bar{x}}$), coefficient of variation (V), extreme values, random numbers (n).

The comparison of two populations of certain species was done with the two sample KOLMOGOROV-SMIRNOV statistics (SACHS 1984). To compare the populations of *T. lineare* and *T. enchelys* a "pairwise multiple comparison" was applied (GAMES and HOWELL 1976). A "weighted mean" was used to calculate the mean of the coefficients of variation (SACHS 1984).

2.3. Scanning electron microscopy

The specimens were fixed with formol, then cleaned by several transfers through distilled water, placed on small glass slides which were coated with fresh egg albumen, and air-dried. The glass slides were mounted on aluminium stubs, furnished with conductive silver, and sputtered with gold (2 × 5 min). The examinations were done with a Cambridge Stereoscan 250 operating with 5 kV.

2.4. Designation of characters and identification of species

There is some confusion in literature concerning length and height of testacean shells: The parameter "length" is often used instead of "height", although the "height" of a species can be clearly defined by phylogenetic findings (SCHÖNBORN 1966a, 1983; BONNET 1975). The "length"

Table 1. Biometric characterization of the investigated testacean species. $\bar{x}$ = arithmetic mean; M = median; s = standard deviation; $s_{\bar{x}}$ = standard error of the mean; V = coefficient of variation (%); Min = Minimum; Max = Maximum; n = number of investigated individuals. All measurements in μm. ** $0.01 \geq P > 0.001$; * $0.05 \geq P > 0.01$; + $0.1 \geq P > 0.05$; ns = not significant

Character	n	$\bar{x}$	M	s	$s_{\bar{x}}$	V	Min	Max	Test
C. aerophila var. *sphagnicola*									
(1)	30	37.5	36	3.7	0.7	9.9	32	45	
(2)	31	59.9	59	6.1	1.1	10.2	49	75	
(3)	31	59.1	59	5.7	1.0	9.7	49	72	
(4)	31	28.6	28	4.9	0.9	17.1	20	44	
(5)	30	14.5	16	3.2	0.6	21.8	9	23	
(6)	18	6.6	7	0.9	0.2	13.6	5	9	
C. elongata									
(1)	30	27.2	27	1.7	0.3	6.2	23	32	
(2)	30	55.9	56	3.8	0.7	6.7	47	63	
(3)	30	33.1	33	2.2	0.4	6.6	29	36	
(4)	30	17.3	18	1.4	0.3	8.0	15	20	
(5)	19	14.1	14	1.4	0.3	9.8	12	17	
(6)	23	4.5	5	0.7	0.2	15.5	4	6	
C. orbicularis									
(1)	21	72.4	75	6.6	1.4	9.1	61	80	
(2)	21	102.8	103	5.6	1.2	5.5	93	112	
(3)	21	106.4	108	6.3	1.4	9.1	95	119	
(4)	21	44.8	45	4.9	1.1	11.0	36	55	
(5)	21	18.3	19	2.3	0.5	12.6	14	23	
(6)	21	11.8	13	1.5	0.3	12.6	10	15	
C. sylvatica									
(1)	15	59.2	59	4.5	1.2	7.6	52	65	
(2)	15	91.5	95	9.0	2.3	9.8	69	101	
(3)	15	83.4	85	8.7	2.2	10.2	67	95	
(4)	14	38.5	39	4.3	1.1	11.1	32	49	
(5)	14	25.0	25	3.2	0.8	12.7	20	32	
(6)	12	9.7	10	2.0	0.6	20.9	7	13	
(7)	6	18.5	18	2.5	1.0	13.2	17	23	
C. eurystoma									
(1)	32	38.8	38	3.3	0.6	8.6	30	45	
(2)	32	51.7	52	4.5	0.8	8.7	42	63	
(3)	32	24.8	25	2.7	0.5	10.8	19	30	
(4)	25	4.2	4	0.7	0.1	17.2	3	5	
D. lucida									
(1)	30	59.0	59	3.1	0.6	5.3	54	65	
(2)	30	29.1	30	2.1	0.4	7.1	24	32	
(3)	30	18.2	19	1.1	0.2	6.0	16	20	
(4)	30	14.6	15	1.3	0.2	8.7	12	17	
(5)	30	9.7	10	1.6	0.3	16.4	7	15	
H. subflava (PI) 1st line, (PII) 2nd line									
(1)	35	75.4	75	5.0	0.9	6.7	60	85	**
	13	67.8	68	5.0	1.4	7.4	55	72	
(2)	35	49.2	49	3.0	0.5	6.1	42	56	*
	13	45.8	45	3.3	0.9	7.1	42	53	

Table 1 (continued)

Character	n	$\bar{x}$	M	s	$s_{\bar{x}}$	V	Min	Max	Test
(3)	34	33.2	33	2.7	0.5	8.0	29	39	ns
	12	33.3	33	2.7	0.8	8.1	29	39	
(4)	35	14.8	15	2.5	0.4	17.1	13	20	
	—	—	—	—	—	—	—	—	
(5)	36	8.1	8	1.1	0.2	13.1	7	10	
	—	—	—	—	—	—	—	—	
N. parvula									
(1)	32	91.9	95	8.5	1.5	9.3	76	105	
(2)	32	68.4	69	6.8	1.2	9.9	55	82	
(3)	32	35.8	37	4.7	0.8	13.2	25	50	
(4)	32	21.7	22	2.3	0.4	10.6	17	25	
(5)	32	13.5	13	2.4	0.4	17.7	10	20	
N. tincta (PI) 1st line, (PII) 2nd line									
(1)	20	100.8	101	6.6	1.5	6.6	90	113	*
	13	90.1	91	9.4	2.6	10.4	73	104	
(2)	20	75.4	76	6.8	1.5	9.1	68	90	ns
	13	72.0	73	8.9	2.5	12.4	59	84	
(3)	20	37.6	37	3.6	0.8	9.7	32	45	ns
	8	38.9	39	3.2	1.1	8.3	33	42	
(4)	20	20.9	20	2.7	0.6	12.9	17	27	
	—	—	—	—	—	—	—	—	
(5)	20	13.8	14	2.0	0.4	14.4	10	17	
	—	—	—	—	—	—	—	—	
(6)	20	35.9	35	6.0	1.3	16.8	25	50	
	—	—	—	—	—	—	—	—	
(7)	20	4.9	5	0.6	0.1	12.4	4	6	
	—	—	—	—	—	—	—	—	
P. declivis (PI) 1st line, (PII) 2nd line									
(1)	26	44.6	45	3.4	0.7	7.7	40	50	**
	17	49.9	49	3.9	1.0	7.8	42	58	
(2)	26	71.2	70	3.5	0.7	4.9	62	80	ns
	17	73.9	74	5.2	1.3	7.1	65	86	
(3)	26	69.9	70	4.1	0.8	5.8	60	77	*
	17	74.4	72	6.1	1.5	8.2	65	91	
(4)	26	44.7	45	3.8	0.7	8.4	38	53	
	—	—	—	—	—	—	—	—	
(5)	26	19.4	20	1.5	0.3	7.6	15	22	
	—	—	—	—	—	—	—	—	
T. arcula (PI) 1st line, (PII) 2nd line									
(1)	32	63.5	62	7.0	1.2	11.0	45	75	**
	12	54.8	55	6.8	2.0	12.3	40	65	
(2)	32	108.9	110	6.9	1.2	6.4	85	120	**
	12	85.7	90	11.1	3.2	12.9	69	101	
(3) max.	32	27.3	27	3.2	0.6	11.7	20	36	
	—	—	—	—	—	—	—	—	
A. seminulum									
(1)	15	85.5	85	3.9	1.0	4.6	80	92	
(2)	15	59.2	60	2.9	0.8	4.9	55	63	
(3)	15	28.8	30	3.9	1.0	13.7	20	35	

Table 1 (continued)

Character	n	$\bar{x}$	M	s	$s_{\bar{x}}$	V	Min	Max	Test
(4)	15	16.7	17	2.2	0.6	13.0	15	21	
(5)	15	9.1	9	1.2	0.3	13.5	8	12	
Idiosomes, major axis	15	7.5	8	0.5	0.1	7.1	7	8	
Idiosomes, minor axis	15	4.9	5	0.4	0.1	7.9	4	5	
C. dubium (PI) 1st line, (PII) 2nd line									
(1)	32	44.7	44	7.3	1.3	16.4	30	60	**
	19	39.0	39	8.7	2.0	22.4	26	62	
(2)	32	29.0	28	4.1	0.7	14.3	18	35	**
	19	24.6	23	5.3	1.2	21.5	18	41	
(3)	32	17.8	18	2.8	0.5	15.7	12	23	**
	16	15.0	14	3.4	0.9	23.0	8	23	
(4)	32	12.6	13	2.3	0.4	18.6	8	18	
	—	—	—	—	—	—	—	—	
(5)	32	9.1	.8	2.4	0.4	26.0	5	15	
	—	—	—	—	—	—	—	—	
C. oviformis									
(1)	31	14.8	15	1.9	0.3	12.5	12	20	
(2)	31	11.6	11	1.5	0.3	12.9	10	15	
(3)	31	3.0	3	0.4	0.1	11.8	2	4	
E. cristata									
(1)	21	33.9	34	1.7	0.4	5.0	30	37	
(2)	21	10.6	10	1.3	0.3	12.0	8	13	
(3)	21	7.4	8	0.6	0.1	7.9	6	9	
(4)	21	8.5	9	0.6	0.1	6.7	8	10	
(5)	21	5.1	5	0.2	0.1	3.8	5	6	
(6) max.[1])	21	8.8	9	2.5	0.5	27.7	5	14	
Number of apertural plates	21	6.0	6	0.0	0.0	0.0	6	6	
E. rotunda									
(1)	30	40.5	40	7.6	1.4	18.6	28	57	
(2)	30	21.1	21	4.3	0.8	20.3	13	29	
(3)	30	16.0	16	3.2	0.6	20.0	10	23	
(4)	31	7.7	8	1.8	0.3	23.6	5	12	
Number of apertural plates	30	8.4	8	0.9	0.2	11.1	7	11	
Apertural plates, major axis	30	4.6	5	0.7	0.1	16.0	4	6	
Apertural plates, minor axis	30	3.3	3	0.6	0.1	18.9	3	5	
Idiosomes, major axis	30	4.9	5	1.4	0.3	28.5	3	8	
Idiosomes, minor axis	30	3.0	3	0.8	0.2	27.6	2	5	

Table 1 (continued)

Character	n	$\bar{x}$	M	s	$s_{\bar{x}}$	V	Min	Max	Test
E. strigosa (PI) 1st line, (PII) 2nd line									
(1)	21	75.9	75	2.2	0.5	2.9	72	80	**
	13	66.2	65	6.9	1.9	10.5	55	81	
(2)	21	44.3	45	3.0	0.7	6.7	38	51	+
	13	46.3	44	7.2	2.0	15.6	39	59	
(3)	21	21.2	22	1.3	0.3	5.9	19	23	
	—	—	—	—	—	—	—	—	
(4)	21	26.3	27	1.0	0.2	3.8	25	28	ns
	8	24.5	24	1.3	0.5	5.3	23	26	
(5)	21	14.7	15	1.0	0.2	6.6	13	17	
	—	—	—	—	—	—	—	—	
(6) max.[1])	21	7.5	8	0.8	0.2	10.8	7	10	
	—	—	—	—	—	—	—	—	
Number of apertural plates	21	10.9	11	0.7	0.2	6.4	10	12	
P. acropodia (PI) 1st line, (PII) 2nd line									
(1)	32	30.7	30	2.9	0.5	9.3	25	38	**
	10	34.0	34	2.5	0.8	7.5	29	37	
(2)	32	39.1	39	4.1	0.7	10.4	32	45	ns
	10	38.5	39	3.1	1.0	8.0	39	42	
(3)	32	18.6	19	3.2	0.6	17.2	13	25	
	—	—	—	—	—	—	—	—	
P. fascicularis									
(1)	25	33.4	34	2.3	0.5	6.9	29	38	
(2)	25	21.9	23	0.9	0.2	4.2	20	23	
(3)	25	8.1	8	0.9	0.2	11.5	8	11	
S. viscicula									
(1)	25	15.6	15	1.1	0.2	7.4	14	18	
(2)	25	11.3	11	0.9	0.2	8.0	10	13	
(3)	25	9.0	10	1.2	0.2	13.2	7	11	
(4)	25	5.0	5	0.6	0.1	11.7	4	6	
T. complanatum (PI) 1st line, (PII) 2nd line									
(1)	32	50.2	50	7.1	1.3	14.1	38	75	**
	15	31.8	26	8.5	2.2	26.6	24	48	
(2)	32	29.9	30	4.0	0.7	13.3	25	45	**
	15	19.3	16	6.5	1.7	34.0	13	29	
(3)	32	13.0	13	2.0	0.4	15.2	10	17	
	—	—	—	—	—	—	—	—	
(4)	32	10.4	10	1.8	0.3	17.1	8	16	
	—	—	—	—	—	—	—	—	
(5)	32	7.0	7	1.5	0.3	20.8	5	10	
	—	—	—	—	—	—	—	—	
Depth of shell	32	23.7	25	3.3	0.6	13.8	18	30	**
	15	15.0	13	5.3	1.4	35.4	10	33	
Idiosomes, diameter	32	6.7	7	1.4	0.2	20.2	3	9	
	—	—	—	—	—	—	—	—	

Table 1 (continued)

Character	n	$\bar{x}$	M	s	$s_{\bar{x}}$	V	Min	Max	Test
T. enchelys (PI) 1st line, (PII) 2nd line									
(1)	22	48.4	49	2.5	0.5	5.2	43	52	
	12	46.6	47	3.0	0.9	6.4	41	52	
(2)	20	19.9	20	0.5	0.1	2.3	18	20	
	12	19.6	20	2.1	0.6	10.8	16	23	
(3)	21	19.6	20	0.8	0.2	4.1	18	20	
	11	17.3	17	2.0	0.6	11.3	14	20	
(4)	21	8.8	9	1.1	0.2	12.5	7	11	
	12	9.2	9	1.3	0.4	13.8	7	11	
(5)	—	—	—	—	—	—	—	—	
	6	3.3	3	0.5	0.2	15.5	3	4	
(6)	11	3.5	4	0.2	0.1	4.3	3	4	
	10	3.4	4	0.3	0.1	10.1	3	4	
Great idiosomes, diameter	18	6.4	7	0.8	0.2	11.9	5	8	
	8	5.8	6	1.1	0.4	18.4	5	8	
Small idiosomes, diameter	18	2.5	3	0.5	0.1	20.6	2	4	
	—	—	—	—	—	—	—	—	
T. lineare (PI) 1st line, (PII) 2nd ine									
(1)	25	34.8	35	2.3	0.5	6.6	30	40	
	25	34.4	35	4.6	0.9	13.4	24	41	
(2)	25	16.9	18	1.2	0.3	7.2	15	19	
	25	14.6	15	2.2	0.4	14.9	8	17	
(3)	25	14.3	15	0.9	0.2	6.3	13	16	
	25	13.7	14	2.0	0.4	14.8	8	18	
(4)	25	8.8	9	1.0	0.2	11.0	8	10	
	25	7.2	8	1.1	0.2	15.4	5	10	
(5)	25	3.3	4	0.7	0.1	20.9	2	5	
	25	2.5	3	0.4	0.1	16.5	2	4	
(6)	25	2.8	3	0.4	0.1	14.8	2	4	
	25	2.4	3	0.4	0.1	15.3	2	4	
Great idiosomes, diameter	25	4.1	4	0.6	0.1	15.2	3	5	
	25	4.0	4	0.6	0.1	14.8	3	6	
T. penardi									
(1)	26	53.2	53	6.2	1.2	11.7	30	65	
(2)	26	30.4	30	3.8	0.7	12.4	16	35	
(3)	26	13.1	13	1.5	0.3	11.5	8	16	
(4)	26	10.2	10	1.5	0.3	14.8	5	13	
(5)	15	6.9	8	1.1	0.3	15.8	5	8	
Depth of shell	26	25.3	25	3.1	0.6	12.0	15	30	
Idiosomes, diameter	19	7.9	8	0.5	0.1	6.3	6	9	

[1]) Exclusively living individuals were measured. The values are from the longest spine of each individual.

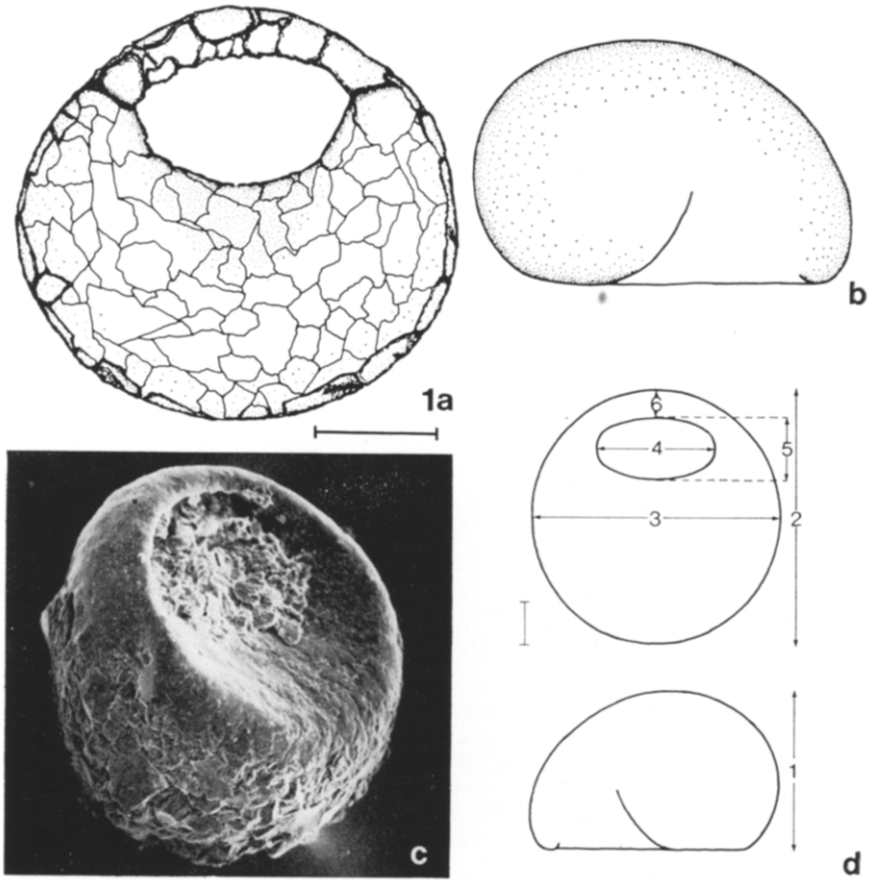


Fig. 1. *Centropyxis aerophila* var. *sphagnicola*. (a, b) Ventral and lateral view, scale bar 20 μm. (c) SEM-microphotograph, ventro-lateral view, $\times 960$. (d) Ideal individual, ventral and lateral view, scale bar 10 μm.

of *Nebela* spp. is strictly speaking their "height", and similarly the "length" of *Trinema* spp. evolutionarily considered is their height. It is important to pay attention to this, when the coefficients of variation of different species are compared, as has been done in this study.

To facilitate a comparison with the older data, the traditional designations of the shell characters have been maintained in the text. However, most parameters have been given a number, which clearly defines the character in the drawing of the ideal individual. In the tables the respective characters are in most cases named only by these numbers.

The determinations of the investigated species follow the original descriptions. Varieties etc. have in most cases not been regarded, because in our opinion most of them are so poorly defined that any identification is more arbitrary than scientific.

3. Results and Discussion

3.1. Description of species

Centropyxis aerophila var. *sphagnicola* DEFLANDRE, 1929 (Figs. 1, 25a; Table 1)

Shell approximately hemispheric, in ventral view nearly circular, some individuals of slightly elliptic shape (in transverse or longitudinal axis). Oral region slightly

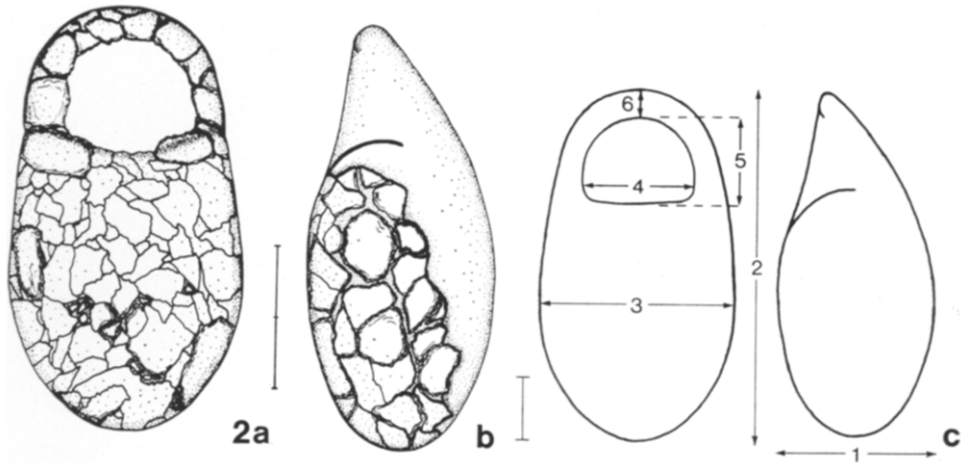


Fig. 2. *Centropyxis elongata*. (a, b) Ventral and lateral view, scale bar 20 μm. (c) Ideal individual, ventral and lateral view, scale bar 10 μm.

flattened. Aperture sub-terminal, transverse oval and invaginated. Apertural region smooth, dorsal region rough by agglutinated particles.

The coefficients of variation for characters (1)—(3) are low, whereas those for the aperture show considerable variation. Unfortunately, DEFLANDRE (1929) does not give measurements for the aperture, but the values of LAMINGER (1972) and CHARDEZ (1979) correspond well with the present data. Our characters (1) and (2) agree also with the measurements of these authors.

Centropyxis elongata (PENARD, 1890) THOMAS, 1959 (Figs. 2, 25a, 26; Table 1)

Shell in ventral view elliptic, elongated, aperture sub-terminal, oval. Apical region laterally flattened. Surface covered with irregular xenosomes. Nucleus with a central nucleolus.

Our population is quite constant in its characters and corresponds with the description of PENARD (1890) and THOMAS (1959) (56—75 × 25—40 × 18—20 μm). Merely the aperture, which is not circular but slightly oval, differs a little from the description of THOMAS (1959).

Centropyxis orbicularis DEFLANDRE, 1929 (Figs. 3, 25a; Table 1)

Shell hemispheric, brownish. Aperture in contrast to *Plagiopyxis callida* widely open, nearly semicircular. The separation between *C. orbicularis* and *P. callida* is difficult only in oblique view, in which case even *P. callida* seems to have an open aperture.

DEFLANDRE (1929) and BONNET and THOMAS (1960) give 100—140 μm for the diameter and 70 and 50—95 μm for the depth, respectively. The individuals of our population are smaller. The coefficients of variation are low with the exception of those for the aperture.

Centropyxis sylvatica (DEFLANDRE, 1929, var.) BONNET and THOMAS, 1955 (Figs. 4, 25a; Table 1)

Shell very similar to *C. aerophila* and *C. aerophila* var. *sphagnicola*. Apertural region, however, separated from the rest of the shell by a perforated diaphragm.

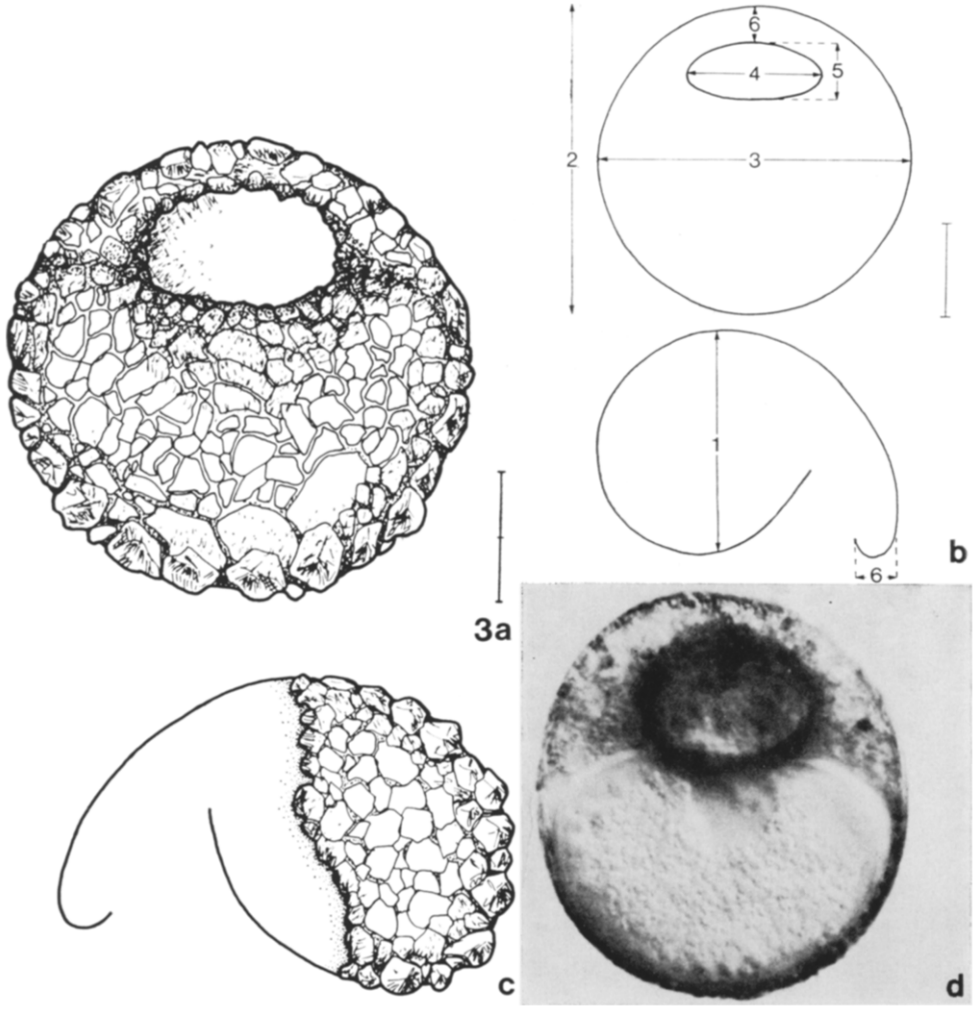


Fig. 3. *Centropyxis orbicularis*. (a, c) Ventral and lateral view, scale bar 30 μm. (b) Ideal individual, ventral and lateral view, scale bar 30 μm. (d) Living individual (temporary cyst) in phase contrast.

Again, the dimension of the aperture varies most; the other parameters vary 7—10 % round about the mean. The measurements correspond with the data of DEFLANDRE (1929) and BONNET and THOMAS (1960).

Cyclopyxis eurystoma (DEFLANDRE, 1929) DEFLANDRE, 1929 (Fig. 5; Table 1)

Shell yellowish — brownish, hemispheric with a circular, slightly invaginated aperture (distinction between *C. eurystoma* and *Phryganella acropodia*!). As a rule, aperture in relation to the diameter of the shell greater than in *P. acropodia*.

The diameter of our population corresponds with the data given by DEFLANDRE (1929) and BONNET and THOMAS (1960) (45—66 μm). The values of OGDEN and HEDLEY (1980) are higher than ours (69—80 μm). The coefficients of variation of the investigated parameters are moderately high (8.6—10.8 %).

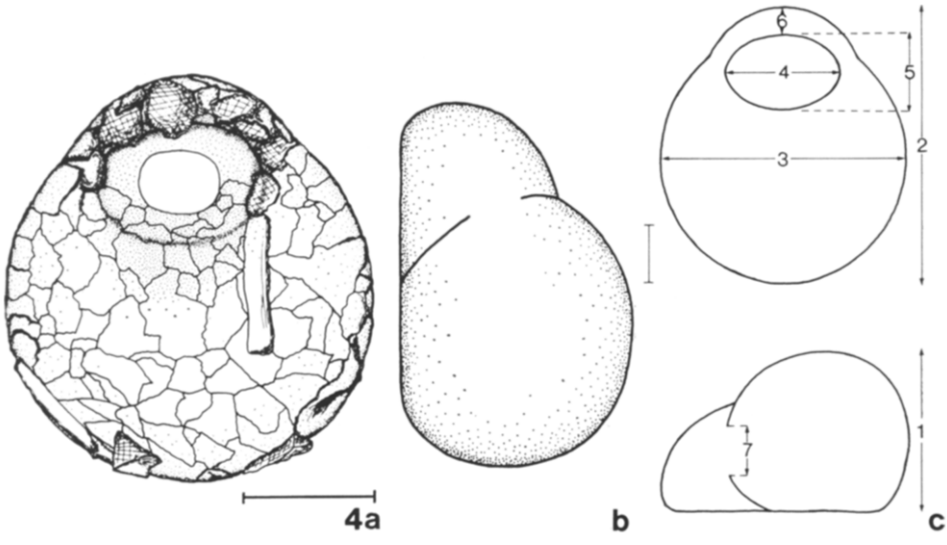


Fig. 4. *Centropyxis sylvatica*. (a, b) Ventral and lateral view, scale bar 30 μm. (c) Ideal individual, ventral and lateral view, scale bar 20 μm.

Difflugia lucida PENARD, 1890 (Figs. 6, 26; Table 1)

Shell slightly compressed, covered with flat quartz particles. Living individuals accumulate mainly inorganic material round the elliptic aperture (Figs. 6a, f, g). This aggregation of particles is probably drawn into the shell when the amoebae encysts and is lost when the cell dies. SCHÖNBORN (1966a) believes that they represent stored reserve xenosomes. Recently, SCHÖNBORN et al. (1987) described food-bundles in *Schoenbornia humicola* which look rather similar to the particle aggregation observed by us in *D. lucida* and *P. fascicularis*. We suggest that it is a peculiar kind of apertural "plug" to avoid desiccation of the cytoplasma during short periods of dryness. Nucleus with a central nucleolus.

The coefficients of variation of characters (1)—(4) are rather low. OGDEN (1983) also mentions a remarkable uniformity regarding character (1): only 7 of 36 individuals were not within the range of 70—80 μm. Our values correspond with those of PENARD (1890, 1902) and CASH and HOPKINSON (1909). GAUTHIER-LIÈVRE and THOMAS (1958) distinguish 3 groups concerning character (1): (a) 44—50 μm; (b) 55—70 μm; and (c) 83—90 μm. Our population belongs to group (b).

Hyalosphenia subflava CASH and HOPKINSON, 1909 (Fig. 7; Table 1)

Shell ovoid, smooth, yellowish, compressed. Aperture elliptic with a thickened border. The apical porus which is described by CASH and HOPKINSON (1909) and GROSPIETSCH (1965) could not be found by us and WANNER (1987). Likewise, OGDEN and HEDLEY (1980) do not mention such a structure.

Our biometric data correspond in the main with those of CASH and HOPKINSON (1909), GROSPIETSCH (1965), BONNET and THOMAS (1960), OGDEN and HEDLEY (1980) and WANNER (1987). Merely character (3) deviates. However, most of the above mentioned authors have obviously measured only a few individuals. In WANNER's (1987) population the difference between minimum and maximum in character (3)

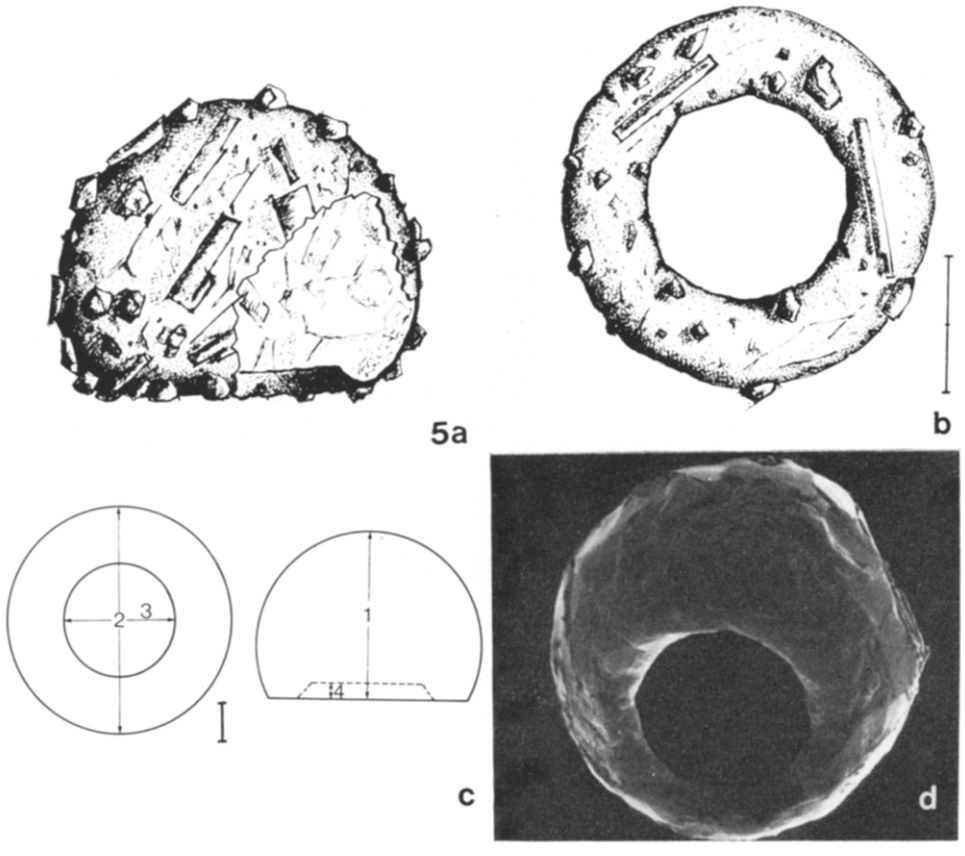
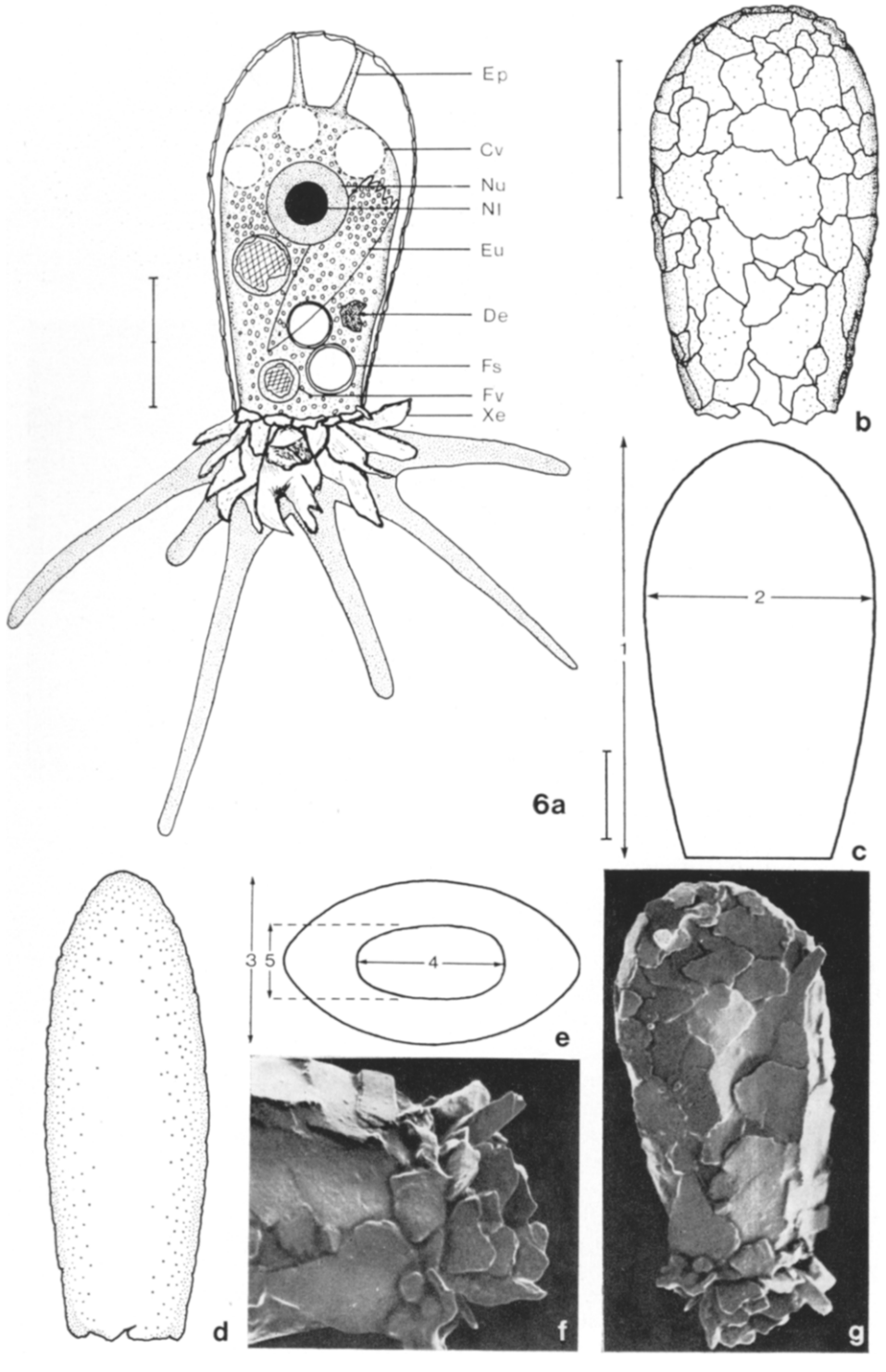


Fig. 5. *Cyclopyxis eurystoma*. (a, b) Lateral view, shell opened, and ventral view, scale bar 20 μm. (c) Ideal individual, ventral and lateral view, scale bar 10 μm. (d) SEM-microphotograph, ventral view, $\times$ 1,610.

is more pronounced (V = 23.6) than in ours. The dimensions of the aperture vary most, the other parameters are relatively constant (Table 1). There is a significant difference between (PI) and (PII) in the tested parameters (1) and (2). No significant difference exists in character (3). Previously CASH and HOPKINSON (1909) noted similar variations between populations from different habitats.

Fig. 6. *Difflugia lucida*. (a) Living aspect, broad lateral view, scale bar 20 μm. Ep = Epipods; Cv = Contractile vacuoles; Nu = Nucleus; Nl = Nucleolus; Eu = Ingested *Euglypha* sp.; De = Detritus; Fs = Ingested fungal spores; Fv = Food vacuoles; Xe = Xenosomes. (b) Broad lateral view, scale bar 20 μm. (c) Ideal individual, broad lateral view, scale bar 10 μm. (d) Narrow lateral view. (e) Ideal individual, ventral view. (f) SEM-microphotograph of the accumulation of xenosomes around the aperture, $\times$ 2,538. (g) SEM-microphotograph of the shell in broad lateral view, $\times$ 1,184.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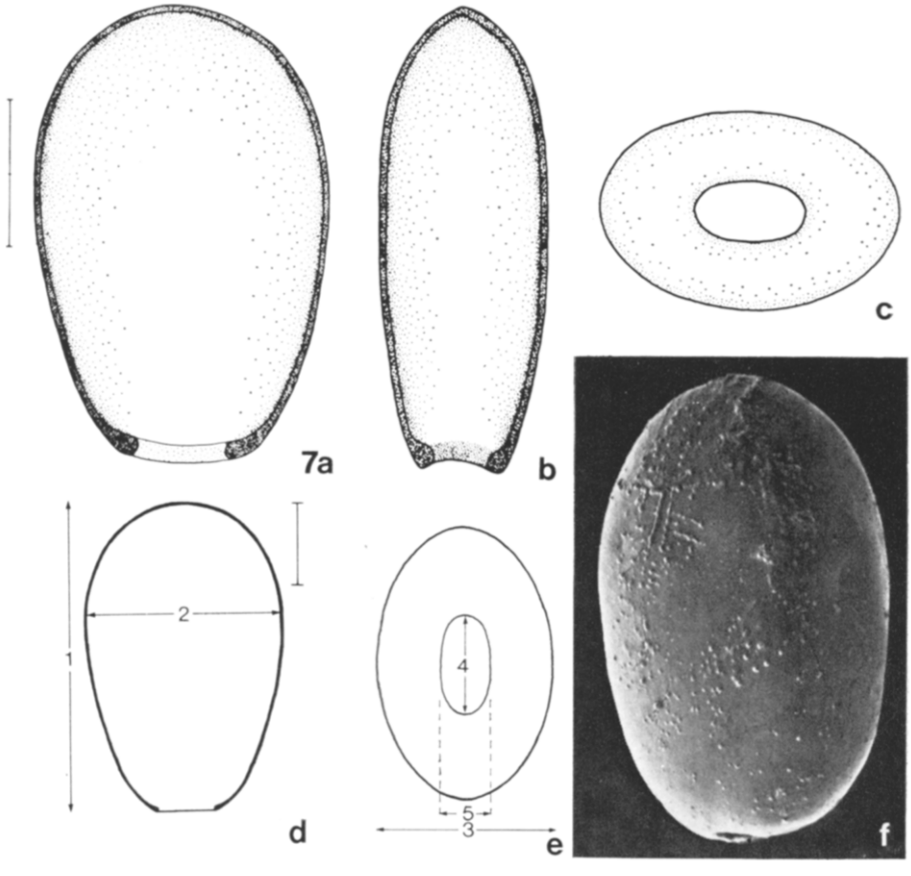


Fig. 7. *Hyalosphenia subflava*. (a, b, c) Broad lateral, narrow lateral and ventral view, scale bar 25 μm. (d) Ideal individual of the (PI), broad lateral view, scale bar 20 μm. (e) Ideal individual, ventral view. (f) SEM-microphotograph in broad lateral view, $\times$ 1,070.

Nebela parvula CASH and HOPKINSON, 1909 (Fig. 8; Table 1) and *Nebela tincta* (LEIDY, 1879) AWERINTZEW, 1906 (Figs. 9, 26; Table 1)

Shell pear-shaped, slightly brownish, compressed, with a small neck and an oval aperture. Shell wall composed of platelets from *Euglypha* spp., *Trinema* spp. and *Corythion* spp. (Fig. 9g), according to the accompanying testacean fauna (GNEKOW 1981). *N. tincta* can at present be distinguished from *N. parvula* only by having two lateral pores. Nucleus of *N. tincta* with several spherical or ovoid nucleoli.

Most parameters in *N. parvula* vary ca. 10% round about the mean. The parameters of *N. tincta* show variations from 6.6 to 16.7%. The range of variation of different characters within the 2 investigated populations is variable, too. Only parameter (1) of the (PI) is pretty constant. Concerning this population, character (6) shows the highest variation. In the (PII), character (2) varies most. Both populations differ significantly in the tested parameter (1). We compared characters (1) and (2) of our populations with the corresponding characters of the so-called "typical population" of HOOGENRAAD and DE GROOT (1937). Since this population is very

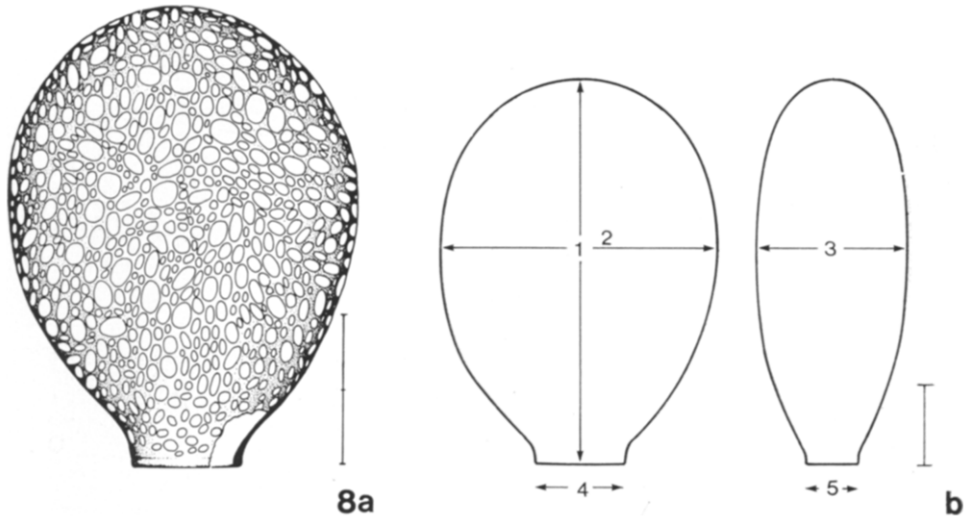
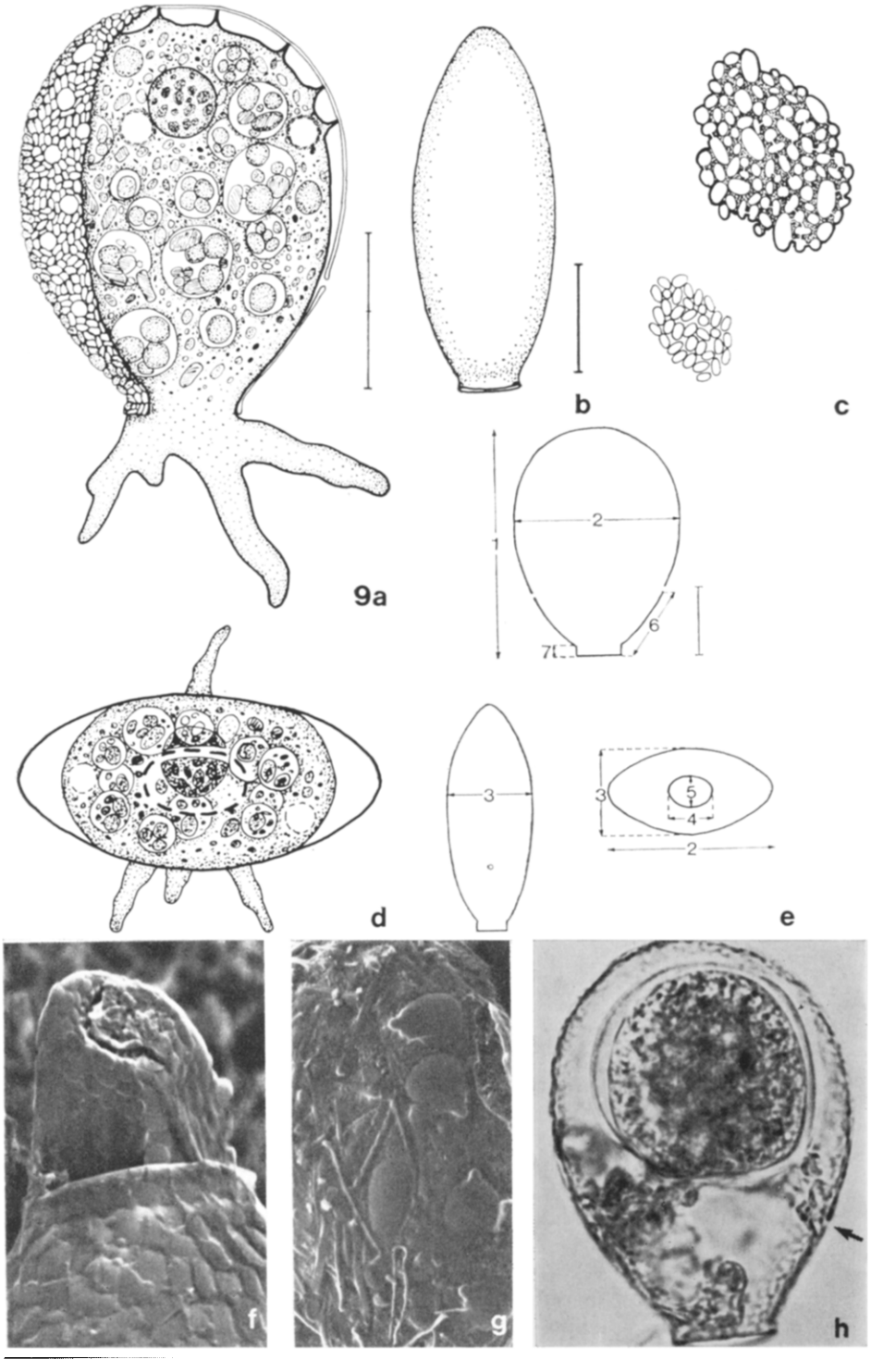


Fig. 8. *Nebela parvula.* (a) Broad lateral view, scale bar 30 μm. (b) Ideal individual, broad and narrow lateral view, scale bar 20 μm.

similar to ours, we could find a significant difference only in parameter (1) between our (PI) and HOOGENRAAD and DE GROOT's (1937) population ($0.01 \geq P > 0.001$).

The determination within the *N. tincta-parvula-bohemica-collaris* group is exceedingly difficult. A criterion which is often used to discriminate these species is the presence or absence of lateral pores. Referring to this, a lot of contradictory or insufficient descriptions exist (LEIDY 1879; TARÁNEK 1881; CASH and HOPKINSON 1909; KLITZKE 1913; DEFLANDRE 1936; JUNG 1942). However, HEAL (1963) and MEISTERFELD (pers. comm.) consider the presence or absence of pores as an ambiguous character, since they can be hidden by the shell platelets. With our population, the pores always could be seen, despite thick shell covering. CASH and HOPKINSON (1909) do not pay attention to this criterion, as is evident from their genus and species description. We regard DEFLANDRE (1936), who investigated *N. parvula* by himself, as the valid revisor, and therefore *N. parvula* as strictly without pores.

The species of the *N. tincta-parvula-bohemica-collaris* group show great variations in size (HOOGENRAAD and DE GROOT 1937; HEAL 1963). But in general *N. parvula* and *N. tincta* are smaller than *N. bohemica* and *N. collaris*. For *N. parvula* CASH and HOPKINSON (1909) give a length of 80 μm, DEFLANDRE (1936) measures 78—80 μm. For *N. tincta* LEIDY (1879) states 79—82 μm, CASH and HOPKINSON (1909) 85 to 90 μm (sometimes 110 μm and more) OGDEN and HEDLDY (1980) 76—94 μm and GNEKOW (1981) 85—106 μm (GNEKOW also mentions a smaller form). HOOGENRAAD and DE GROOT (1937) restrict *N. tincta* to the range of 78—97 μm. HEAL (1963) decides from the measurement of 1,060 individuals that all shells with lateral pores in the range of 75—95 μm belong to *N. tincta*. He cannot determine individuals with similar appearance but larger size. DEFLANDRE (1936), however, describes a variety *major* with a length of 90—120 μm. For *N. bohemica* TARÁNEK (1882) gives a length of 85—125 μm, KLITZKE (1913) 110 μm, DEFLANDRE (1936) 100—120 μm. For *N. collaris* one can find measurements from 101—231 μm (TARÁNEK 1882), 107 to 184 μm (PENARD 1902), 115—130 μm (DEFLANDRE 1936), about 130 μm (LEIDY 1879) and 98—153 μm (OGDEN and HEDLEY 1980).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These observations suggest that the species complex can be rather well separated on the basis of size into *N. tincta*/*N. parvula* (about 80—110 µm) and *N. bohemica*/*N. collaris* (about 100—200 µm; there are only two findings out of this range). However, intermediate forms exist and will always be problematic. HEAL (1963) notes that *N. collaris sensu stricto* can easily be distinguished from the other species by the curved apertural lips, and that *N. collaris sensu lato* also includes *N. bohemica*. This was already realized by HOOGENRAAD and DE GROOT (1937). *N. tincta* and *N. parvula* are very similar in shape and size. For their separation we use — as long as no better criterions are known — the presence or absence of lateral pores. The possibility to confuse *N. tincta* with *N. flabellulum*, which is indicated by HEAL (1963), is not given with our populations.

Plagiopyxis declivis BONNET and THOMAS, 1955 (Figs. 10, 26; Table 1)

Shell hemispheric, ventral side covered with flat xenosomes, smooth, dorsal side covered with rough xenosomes. Anterior lip of the shell with a sharp, irregular margin, overhanging; posterior lip projects inside the shell as an elongation of the ventral side, therefore difficult to recognize. Scanning electron micrographs show that platelets of other testate amoebae (*Trinema* spp., *Corythion* spp., *Euglypha* spp.?) are incorporated on the anterior lip and the ventral side (Fig. 10g). Nucleus with several nucleoli. Separation between *P. declivis* and *P. minuta* mainly by means of the size.

The two investigated populations are fairly constant in their characters. Parameter (4) shows the highest variation in (PI) (V = 8.4). There is a significant difference between (PI) and (PII) in the tested characters (2) and (3). The values of BONNET and THOMAS (1955) and THOMAS (1958) go well together with our measurements, those of SCHÖNBORN (1964a) are slightly lower. The observation of foreign idiosomes between the xenosomes is of special interest and can be also seen in a scanning electron micrograph of BONNET (1975; Fig. 55). It is unknown, whether they are gained by predation of euglyphids or by collecting of platelets from the soil, as has been suggested for *Schoenbornia humicola* (SCHÖNBORN et al. 1987). The second possibility is more likely since one can hardly imagine that euglyphids are incorporated through the narrow aperture of *Plagiopyxis*.

Trigonopyxis arcula (LEIDY, 1879) PENARD, 1912 (Figs. 11, 26; Table 1)

Shell brownish, hemispheric. Aperture central, clearly invaginated, in ideal case triangular, but often more or less irregular, surrounded by a small ring of organic cement. CASH and HOPKINSON (1909) also describe great differences in the shape of the aperture (PL. XXII, Figs. 8—10). Nucleus with some spheric nucleoli.

Diameter of (PI) is fairly constant, whereas characters (1) and (3) are more variable. The shell measurements of our populations are rather low as compared with the findings of other authors (LEIDY 1879; BONNET and THOMAS 1960; OGDEN and HEDLEY 1980), but correspond with the values of CASH and HOPKINSON (1909), PENARD (1902) and HOOGENRAAD and DE GROOT (1937), who found a size range of 58—132 µm

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Fig. 9. *Nebela tincta*. (a, d) Living aspect in broad lateral and dorsal view, shell opened, scale bar 40 µm. (b) Narrow lateral view, scale bar 30 µm. (c) Shell structure, details. (e) Ideal individual of the (PI), broad lateral, narrow lateral and ventral view, scale bar 30 µm. (f) SEM-microphotograph of an individual feeding on a *Trinema* sp., ×1,974. (g) Detail of the shell structure with platelets and probably spines of *Euglypha* sp., ×2,256. (h) Light microscopic photograph of an encysted individual. The arrow marks a pore.

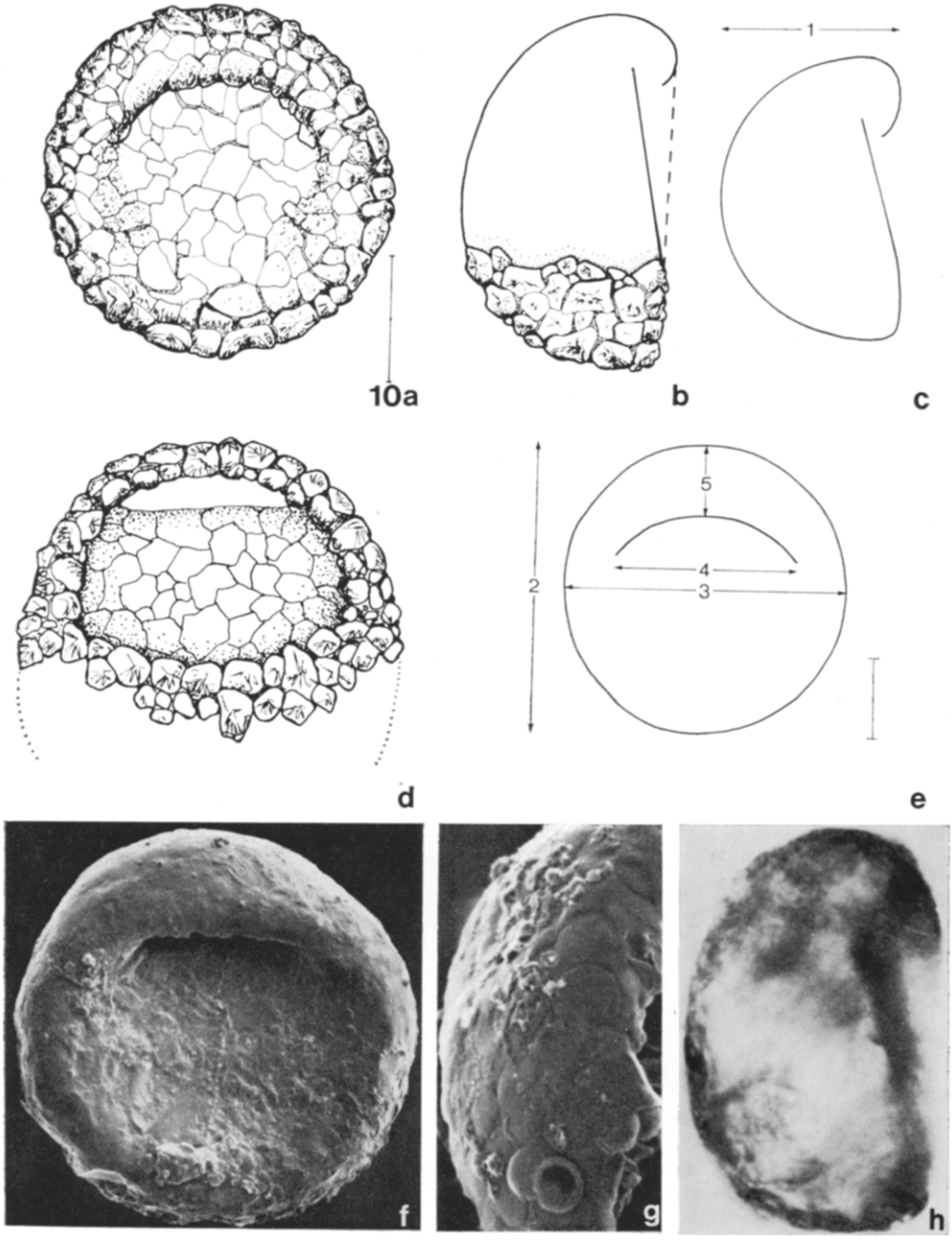

Fig. 10. *Plagiopyxis declivis.* (a, b, d) Ventral view, lateral view and aperture of a tilted shell, scale bar 25 μm. (c, e) Ideal individual of the (PI), lateral and ventral view, scale bar 20 μm. (f) SEM-microphotograph, ventral view, $\times$ 787. (g) Detail of the apertural lip. Note the circular platelets! $\times$ 2,304. (h) Light microscopic photograph of the shell in lateral view.

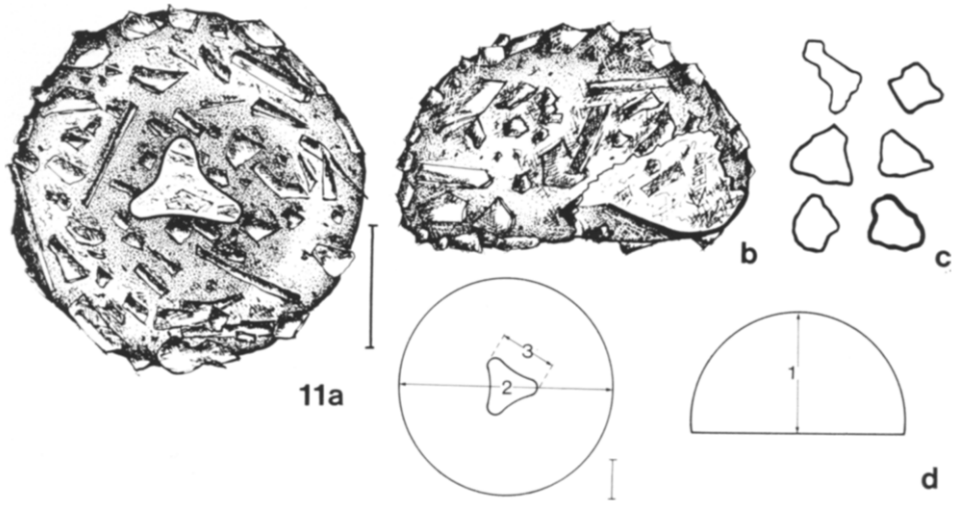

Fig. 11. *Trigonopyxis arcula*. (a, b) Ventral and lateral view, shell opened, scale bar 40 μm. (c) Different forms of the aperture. (d) Ideal individual of the (PI), ventral and lateral view, scale bar 20 μm.

(Median = 105) when measuring about 1,700 individuals. There are significant differences between (PI) and (PII) in the tested parameters (1) and (2).

Assulina seminulum (EHRENBERG, 1848) LEIDY, 1879 (Fig. 12; Table 1)

Young shells yellowish, older ones light to dark brown, composed of oval platelets. Aperture surrounded by overlapping shell platelets with a thin border of organic cement, which holds the platelets together (OGDEN and HEDLEY 1980). Separation between *A. seminulum* and *A. muscorum* only by their size, which is in *A. seminulum* about 1,5 × greater than in *A. muscorum* (HOOGENRAAD and DE GROOT 1937).

Shell length and width fairly constant, greatest range of variation in parameters (3) and (4). The measurements correspond with those of CASH et al. (1915) and OGDEN and HEDLEY (1980). LEIDY (1879) gives a shell length of 50—83 μm, EHRENBERG (1848) 100—208 (!) μm, indicating that he worked with mixed material. Our mean values are about 6 μm higher than those of the "Wissel"-population of HOOGENRAAD and DE GROOT (1937), so their population is significantly different ($0.01 \geq P > 0.001$) from our material in characters (1) and (2).

Corythion dubium TARÁNEK, 1881 (Fig. 13; Table 1)

Shell ovoid, flattened. Idiosomes oval, irregularly arranged. Aperture sub-terminal, circular to oval, invaginated. Apertural plates with a median tooth.

Our measurements correspond in the main with those of other authors (TARÁNEK 1881, 1882; PENARD 1902; BONNET and THOMAS 1960; COWLING 1986; OGDEN and HEDLEY 1980). CASH et al. (1915) already mentioned the great variability of this species, which is confirmed by the high coefficients of variation of our populations. The (PII) shows no $V < 20$. Both populations differ significantly from each other in the tested parameters (1), (2) and (3).

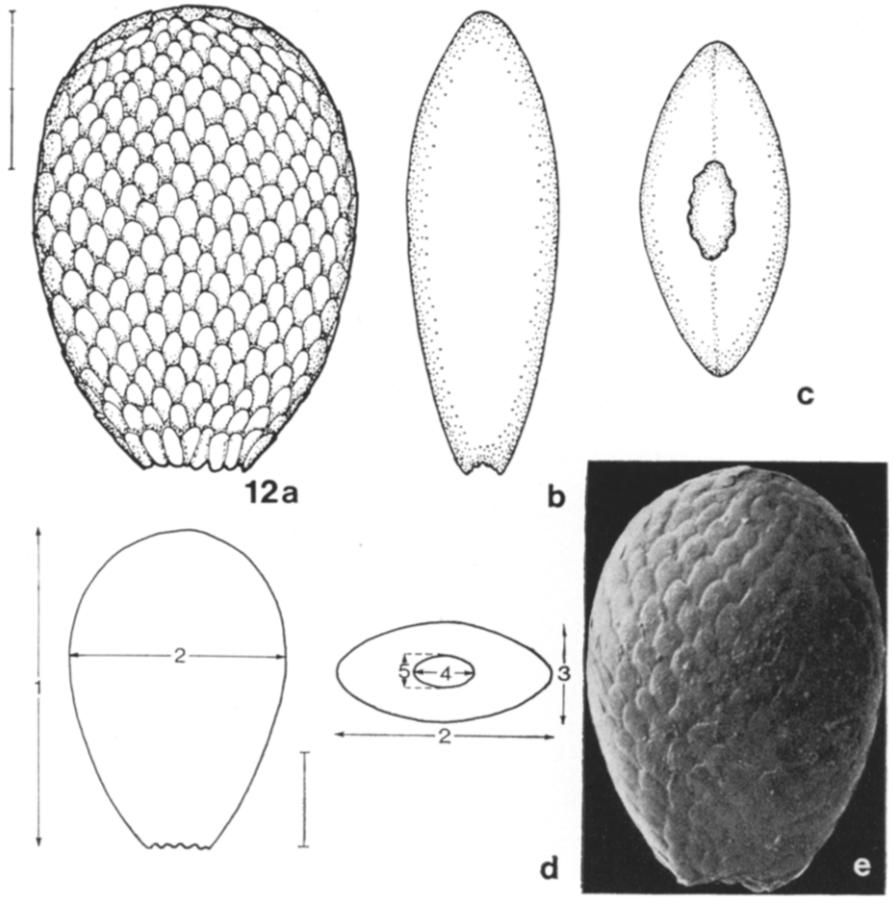

Fig. 12. *Assulina seminulum*. (a, b, c) Broad lateral, narrow lateral and ventral view, scale bar 30 μm. (d) Ideal individual, broad lateral and ventral view, scale bar 25 μm. (e) SEM-microphotograph, broad lateral view, $\times$ 800.

Cryptodifflugia oviformis PENARD, 1890 (Fig. 14; Table 1)

Shell ovoid, colorless, with a smooth surface and a rigid shell wall. Aperture circular, central, slightly thickened. Shell circular in transverse section.

Our measurements are in accordance with the findings of PENARD (1890), THOMAS (1959), GROSPIETSCH (1964) and SCHÖNBORN (1965). All parameters are moderately variable.

There is some confusion about the genera *Difflugiella* and *Cryptodifflugia* (DEFLANDRE 1953; THOMAS 1959; GROSPIETSCH 1964; SCHÖNBORN 1964b, 1965; PAGE 1966; HEDLEY et al. 1977). We follow the clear argumentation of PAGE (1966), who includes in *Cryptodifflugia* those species with a rigid shell wall.

Euglypha cristata LEIDY, 1874 (Figs. 15, 26; Table 1)

Shell elongated, colorless, sligthly compressed. Aboral region with a bunch of several 5 to 14 μm long, curved spines. Aperture circular, constantly 6 elongated

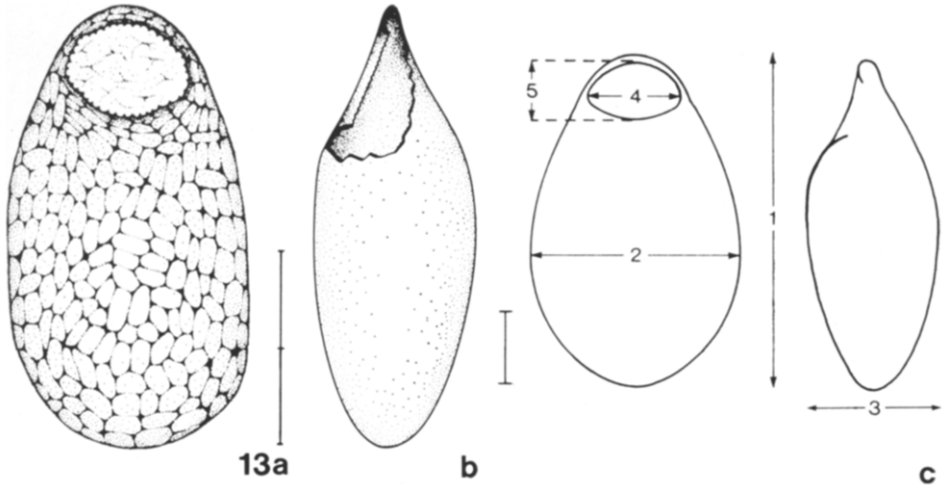

Fig. 13. *Corythion dubium.* (a, b) Ventral and lateral view, shell opened, scale bar 20 μm. (c) Ideal individual of the (PI), ventral and lateral view, scale bar 10 μm.

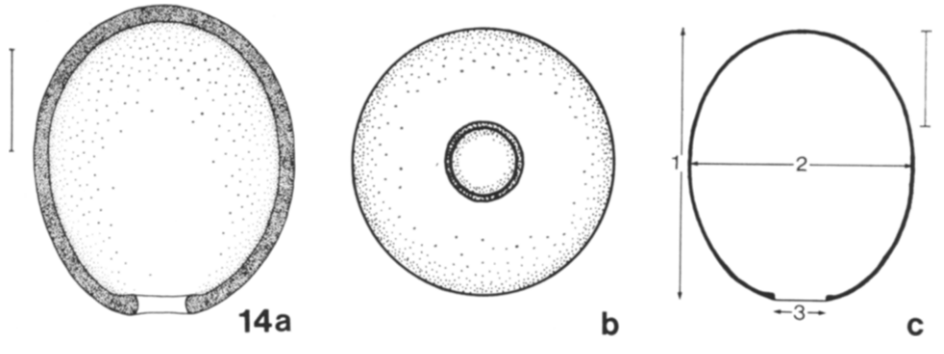

Fig. 14. *Cryptodifflugia oviformis.* (a, b) Lateral and ventral view, scale bar 5 μm. (c) Ideal individual, lateral view, scale bar 5 μm.

apertural plates, each having one median tooth which is bent inwards, and 3 pairs of smaller lateral teeth. Nucleus with a small central nucleolus.

LEIDY (1879) gives a shell size of 40—72 × 10—22 μm, the values of CASH et al. (1915), OGDEN and HEDLEY (1980) and OGDEN (1984b) are also in this range. Our individuals are smaller (30—37 μm), like those of PENARD (1902) and COÛTEAUX et al. (1979). However, the latter authors have measured 2 individuals only. The length of the spines shows a great variability, though it cannot be excluded that broken off spines were also measured. Concerning the number and structure of the apertural plates, our observations agree with those of COÛTEAUX et al. (1979). LEIDY (1879) mentions 4—6, OGDEN and HEDLEY (1980) 5—7 plates. The slight lateral compression of the shell, which was found with living individuals, contrasts with the description of LEIDY (1879), but likewise is shown in the scanning electron micrographs of GROSPIETSCH (1982).

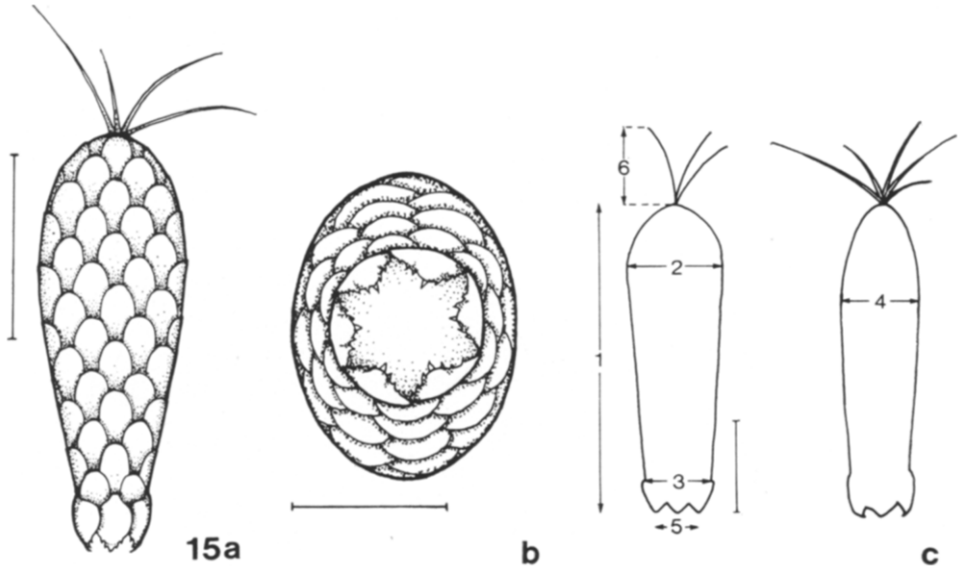

Fig. 15. *Euglypha cristata*. (a) Lateral view, scale bar 15 μm. (b) Ventral view, scale bar 20 μm. (c) Ideal individual, broad and narrow lateral view, scale bar 10 μm.

Euglypha rotunda WAILES and PENARD, 1911 (Figs. 16, 26; Table 1)

Shell ovoid, colorless, compressed. Aperture circular (= distinction between *E. rotunda* and *E. laevis*!), plates nearly circular with two narrow rounded ends, one median tooth which is bent towards the interior of the mouth, and 2 pairs of fairly strong lateral teeth. 2 contractile vacuoles, nucleus with a central nucleolus.

All parameters show a rather great variability, especially the size of the idiosomes and the diameter of the aperture. However, our data correspond in the main with those of other authors (WAILES and PENARD 1911; CASH et al. 1915; HEDLEY and OGDEN 1973; COWLING 1986). The structure of the apertural plates agrees with the scanning electron micrographs of NETZEL (1972) and the drawings of COÛTEAUX et al. (1979) for *E. rotunda* var. *minor*, indicating that our population which corresponds with the original description, cannot be separated from the variety by means of this character.

Euglypha strigosa (EHRENBERG, 1872) LEIDY, 1878 (Figs. 17, 26; Table 1)

Shell ovoid, elliptic in transverse section. Several fairly stout spines, which project singly or pairwise from the junctions of the shell platelets. Aperture circular, 10 to 12 apertural plates. Plates thickened, on the anterior end usually broadly rounded, with one median tooth bent sharply towards the interior of the mouth, and 2—3 pairs

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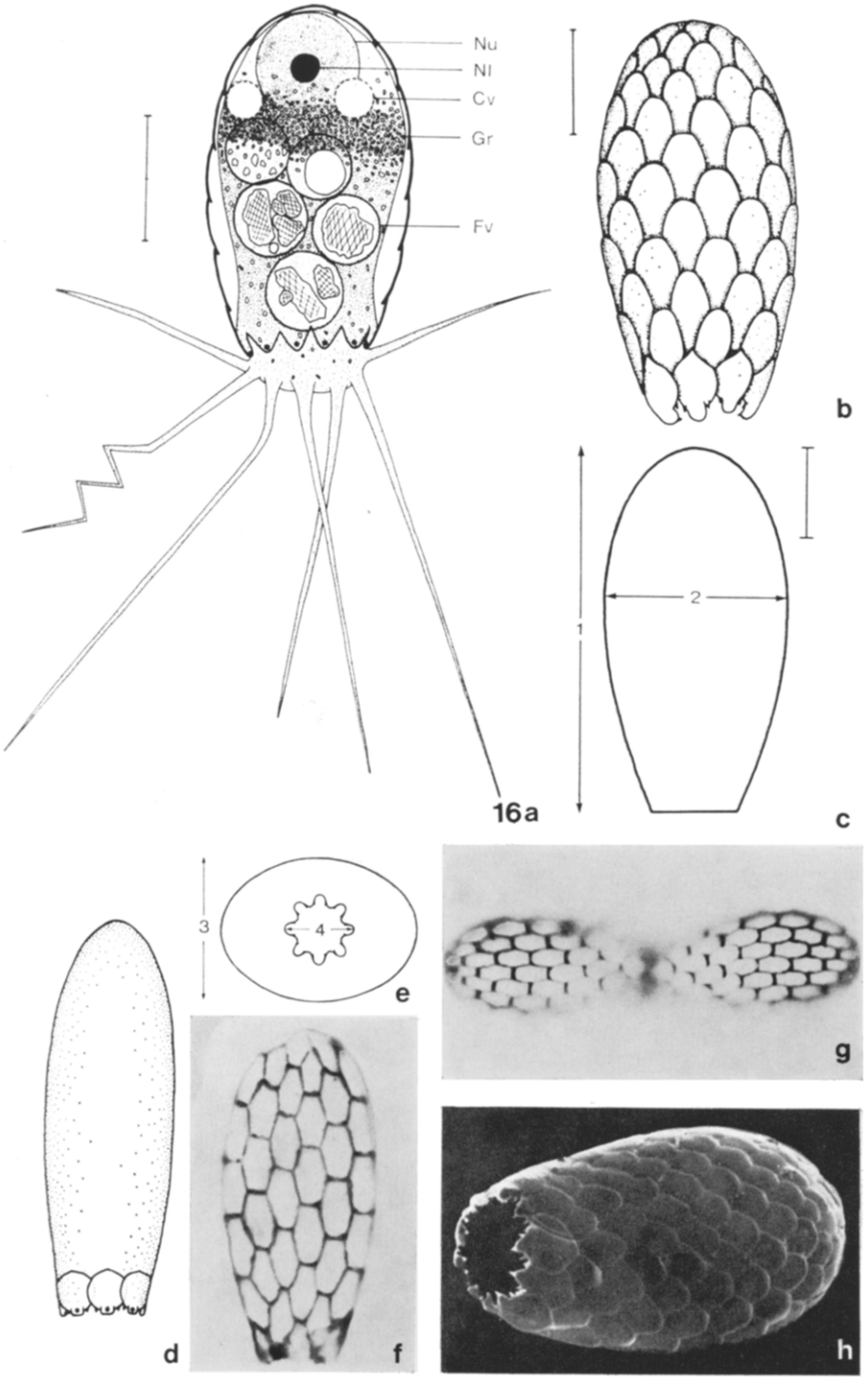
Fig. 16. *Euglypha rotunda*. (a) Living aspect, broad lateral view, scale bar 15 μm. Nu = Nucleus; Nl = Nucleolus; Cv = Contractile vacuoles; Gr = Granules; Fv = Food vacuoles. (b, d) Broad and narrow lateral view, scale bar 10 μm. (c, e) Ideal individual, broad lateral and ventral view, scale bar 10 μm. (f, g) Interphase individual and dividing cell, protargol silver impregnation. (h) SEM-microphotograph, ventro-lateral view, $\times$ 2,400.


Nu
Nl
Cv
Gr
Fv
16a
b
c
1
2
3
4
d
e
f
g
h

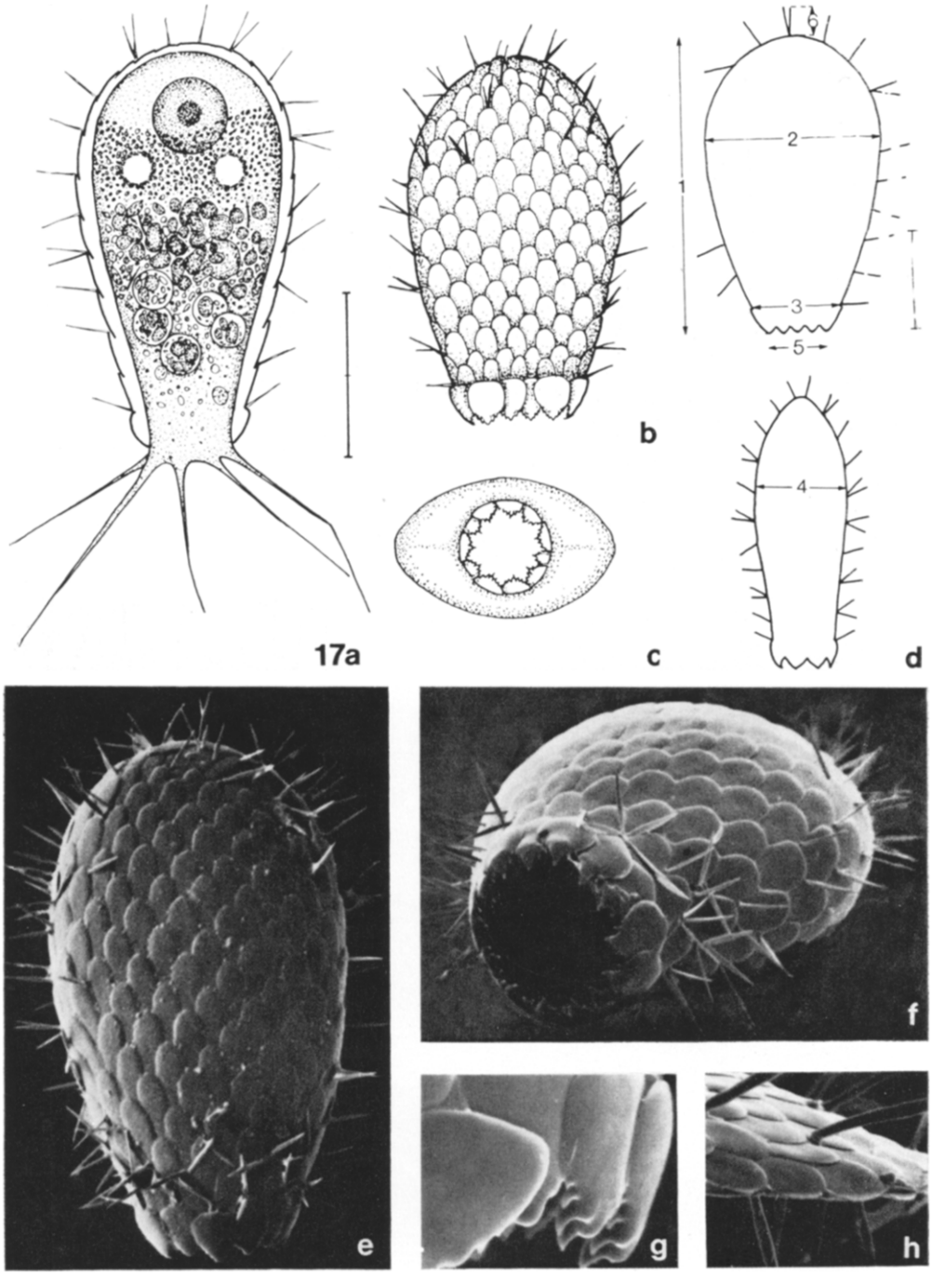


Fig. 17. *Euglypha strigosa*. (a, b, c) Living aspect, broad lateral view, shell morphology, broad lateral and ventral view, scale bar 30 μm. (d) Ideal individual of the (PI), broad and narrow lateral view, scale bar 35 μm. (e, f) SEM-microphotographs, broad lateral and ventral view, $\times$ 1,029 and 1,485, respectively. (g) Apertural plates, detail, $\times$ 6,633. (h) Spines, detail, $\times$ 3,069.

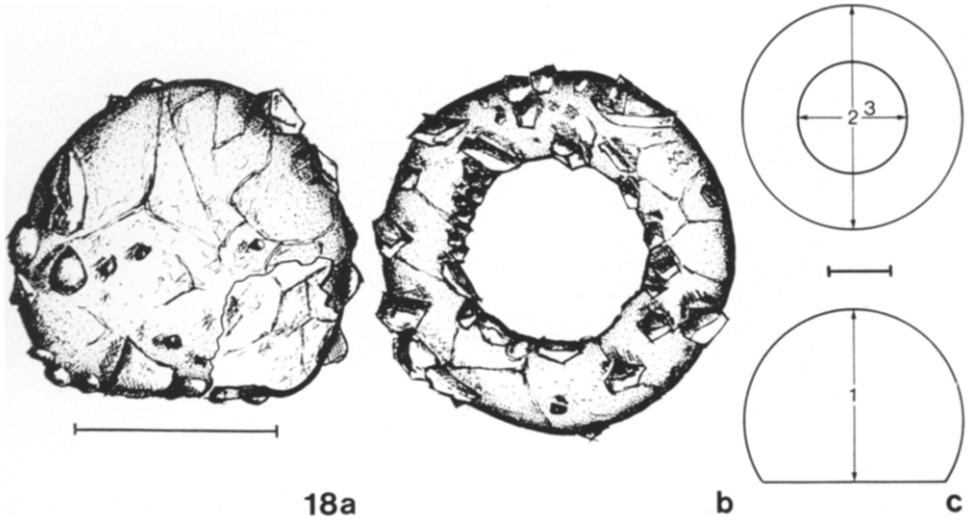


Fig. 18. *Phryganella acropodia.* (a, b) Lateral view, shell opened, and ventral view, scale bar 20 μm. (c) Ideal individual of the (PI), ventral and lateral view, scale bar 10 μm.

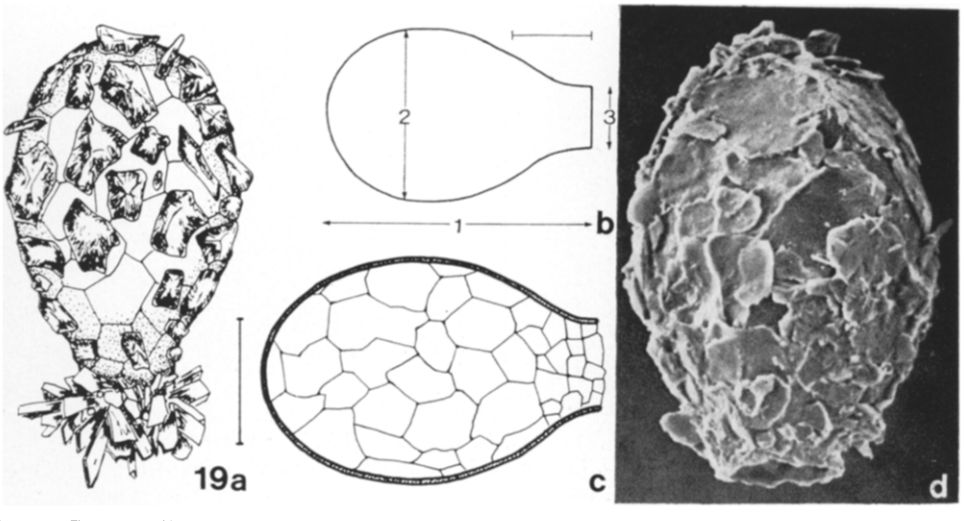


Fig. 19. *Pseudodifflugia fascicularis.* (a, c) Living cell and structure of the shell after protargol silver impregnation, lateral view, scale bar 10 μm. (b) Ideal individual, lateral view, scale bar 10 μm. (d) SEM-microphotograph, lateral view, $\times$2,100.

of lateral teeth, whose size decreases from the center to the edge (Fig. 17g). Nucleus with a central nucleolus.

The (PI) is rather constant in its characters, whereas parameters (1) and (2) of the (PII) vary fairly strongly, although both populations originate from similar habitats. CHARDEZ and LECLERCQ (1963) also describe interesting size and shape variation in *E. strigosa*, depending on the habitat. There is a significant difference between (PI) and (PII) in the tested parameters (1) and (2). No significant difference results

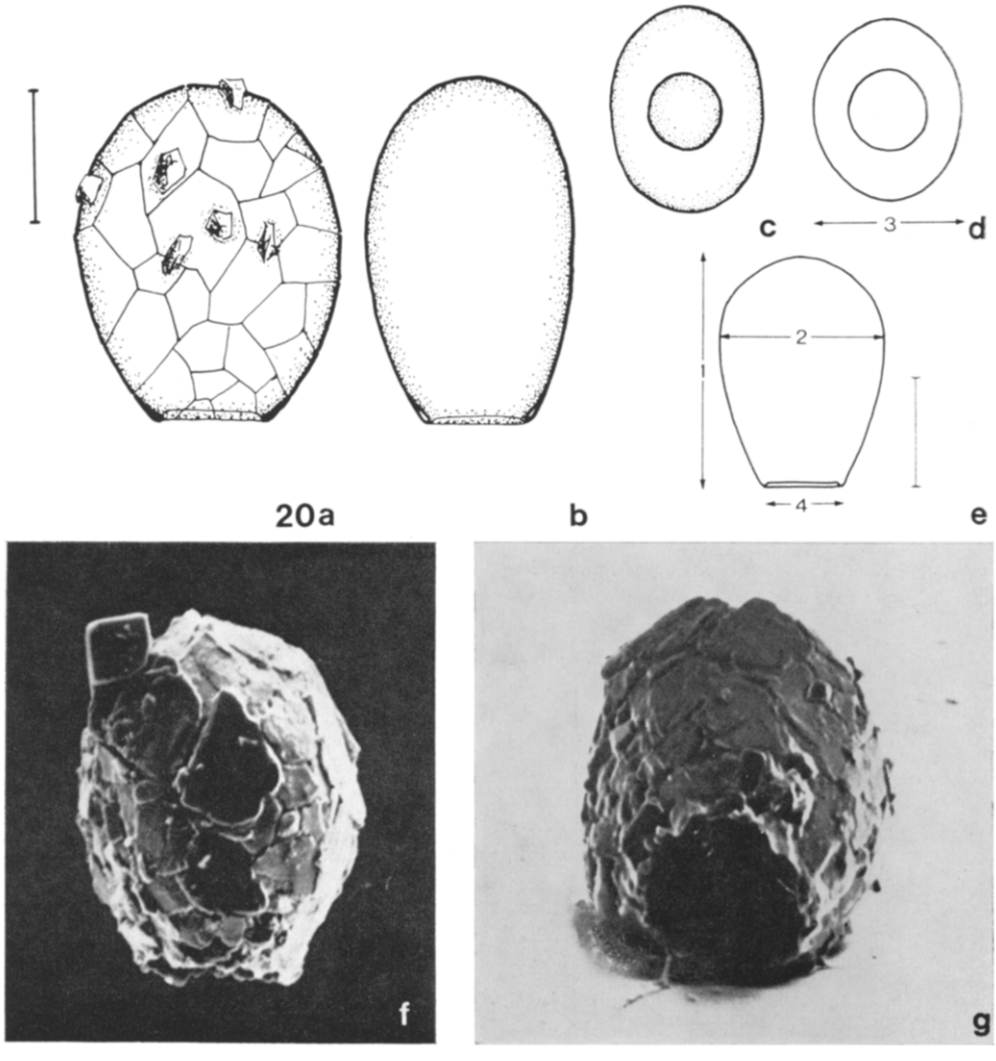


Fig. 20. *Schoenbornia viscicula*. (a, b, c) Structure of the shell in broad lateral view, partly after protargol silver staining, shell shape in narrow lateral and ventral view, scale bar 5 μm. (d, e) Ideal individual, ventral and broad lateral view, scale bar 7 μm. (f, g) SEM-microphotographs, broad lateral and ventral view, $\times$ 2,058 and 1,764, respectively. The pictured individuals originate from a population from the Stubnerkogel (Central Alps, Austria).

from the analysis of character (4). The values of HEDLEY et al. (1974), who investigated a clone (n = 100), and the variability ascertained by them, correspond with our findings. They state, however, a spine length from 2—23 μm, which is higher than in our (PI). The values of SCHÖNBORN (1964b) agree with ours, those of COÛTEAUX et al. (1979) deviate downwards, the length of spines was not measured. Regarding the apertural plates, there is a great conformity in the structure of the individuals investigated by us, CASH et al. (1915), COÛTEAUX et al. (1979) and HEDLEY et al. (1974).

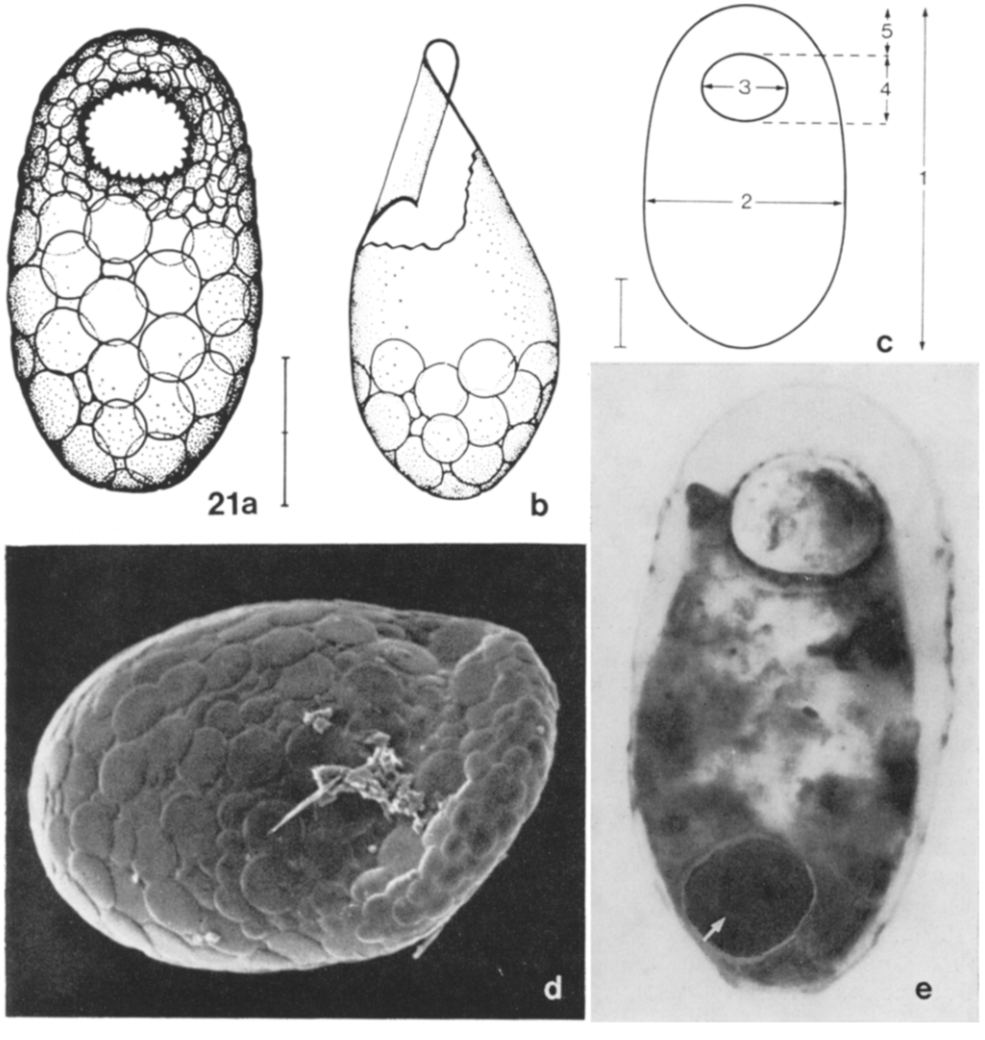


Fig. 21. *Trinema complanatum*. (a, b) Ventral and lateral view, shell opened, scale bar 20 μm. (c) Ideal individual of the (PI), ventral view, scale bar 10 μm. (d) SEM-microphotograph, dorsal view, $\times$ 2,030. (e) Light microscopic photograph of the shell in ventral view after protargol silver impregnation. Note the large central nucleolus (arrow) of the nucleus.

Phryganella acropodia (Hertwig and Lesser, 1874) Hopkinson, 1909 in Cash and Hopkinson, 1909, p. 74 (Fig. 18; Table 1)

Shell hemispheric, yellowish-brown, composed of xenosomes. Separation from the very similar *Cyclopyxis eurystoma* by means of the non invaginated aperture.

The diameter of our population corresponds quite well with the data of Hertwig and Lesser (1874), Cash and Hopkinson (1909), Bonnet and Thomas (1960) and Ogden (1984a). The variability of the parameters (1) and (2) is not very great, whereas character (3) varies considerably (V = 17.2). Both investigated populations differ significantly only in the tested parameter (1).

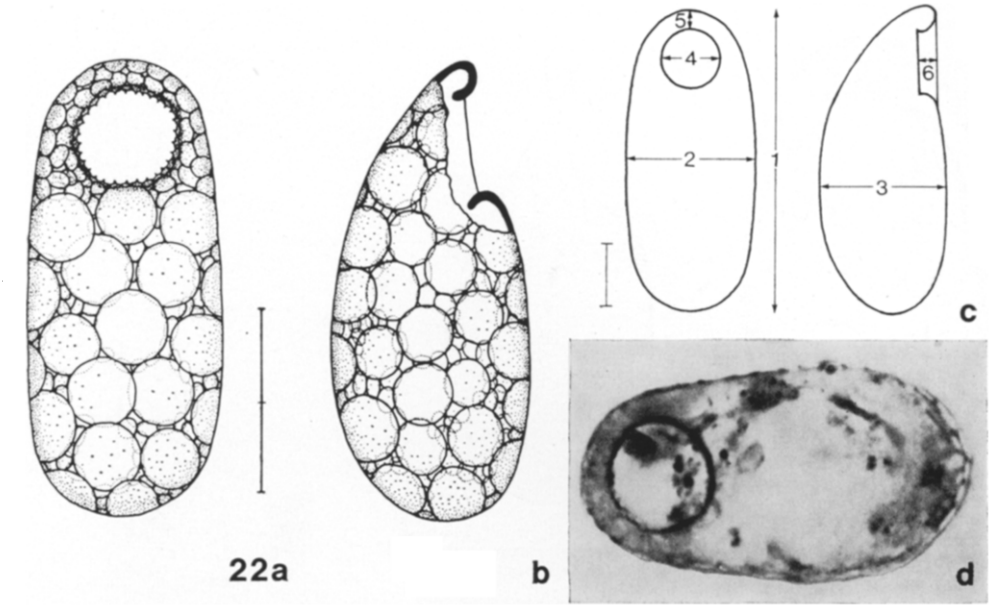


Fig. 22. *Trinema enchelys*. (a, b) Ventral and lateral view, shell opened, scale bar 20 μm. (c) Ideal individual of the (PII), ventral and lateral view, scale bar 10 μm. (d) Light microscopic photograph of the shell of an alpine population, ventral view.

Pseudodifflugia fascicularis PENARD, 1902 (Figs. 19, 26; Table 1)

Shell pear-shaped, with an inner layer of flattened xenosomes, which are covered with more or less rough particles. Aperture circular, with an accumulation of mainly inorganic material, which is lost when the cell dies. These particles probably serve the same purpose as those of *D. lucida*. Nucleus with a small central nucleolus.

The measurements of the length of different authors are in the range of 15—71 μm (PENARD 1902; DE SAEDELEER 1934; BARTOŠ 1954). The corresponding character of our population shows relatively little variability between 29—38 μm.

Schoenbornia viscicula SCHÖNBORN, 1964 (Figs. 20, 26; Table 1)

Shell slightly compressed, composed of irregular flat platelets with agglutinated rough xenosomes. Aperture circular, nucleus with a central nucleolus.

The measurements of characters (1) and (2) correspond with the data of SCHÖNBORN (1964b), whereas the slight lateral compression of the shells, which is also mentioned by WANNER (1987), contrasts with the original description. SCHÖNBORN (1964b) states a mean value of 8.6 μm for the diameter of the aperture, the corresponding value of our population is 5 μm. WANNER (1987) describes an oval aperture, which shows the greatest variability of the investigated parameters. Character (3) and (4) of our population vary most.

Trinema complanatum PENARD, 1890 (Figs. 21, 25b, 26; Table 1)

Shell ovoid in ventral view, slightly compressed, composed of circular idiosomes of different size. Aperture oval, slightly invaginated. Nucleus with a central nucleolus.

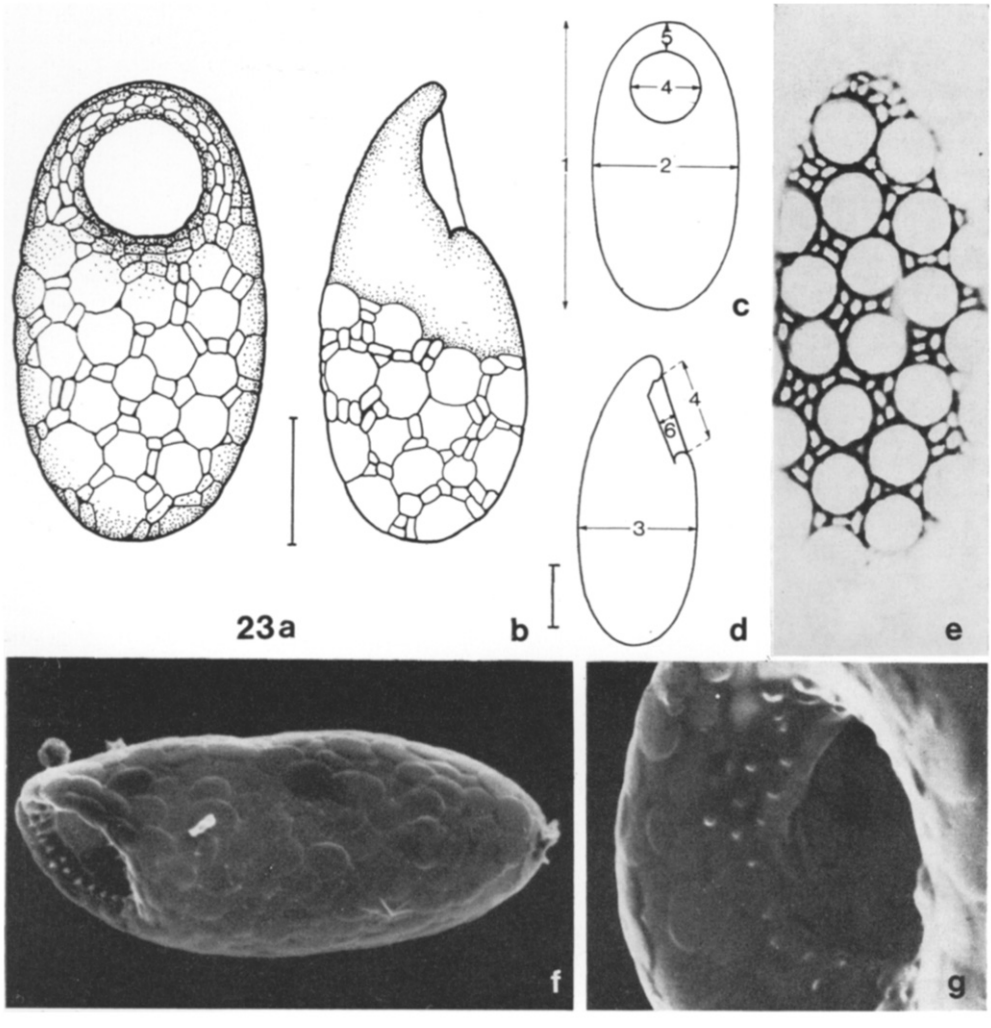


Fig. 23. *Trinema lineare*. (a, b) Ventral and lateral view, shell opened, scale bar 10 μm. (c, d) Ideal individual of the (PI), ventral and lateral view, scale bar 10 μm. (e) Shell structure after protargol silver impregnation. (f) SEM-microphotograph, lateral view, $\times$2,722. (g) Aperture, $\times$4,356.

The character "depth of the shell" of the (PII) generally shows the highest coefficient of variation of the characters of all investigated species and populations (V = 35.4). Both populations differ significantly in the tested main characters (1)—(3). The measurements, however, correspond with data from literature (PENARD 1890; CASH et al. 1915; BONNET and THOMAS 1960), which reinforces the great variability of this species.

Trinema enchelys (EHRENBERG, 1838) LEIDY, 1878 (Figs. 22, 25c; Table 1)

Shell elliptic, oval in transverse section. Aperture circular, invaginated, toothed. Distinction between *T. enchelys* and the very similar *T. lineare* only by their size (see chapter 3.2.).

Table 2. Pairwise multiple comparison of 2 populations of *Trinema enchelys* (P1, P2) and 2 populations of *T. lineare* (P3, P4). 1st line = shell length; 2nd line = shell width; 3rd line = shell depth; 4th line = diameter of aperture. ** $0.01 \geq P > 0.001$; * $0.05 \geq P > 0.01$; + $0.1 \geq P > 0.05$; ns = not significant

	P1	P2	P3
P2	ns		
	ns		
	+		
	ns		
P3	**	**	
	+	**	
	*	**	
	ns	ns	
P4	**	**	ns
	**	**	**
	**	**	ns
	*	*	*

The (PI) is fairly constant in characters (1)—(3). Only character (4) shows a higher coefficient of variation. The parameters of the (PII) are more variable. Both populations are significantly different in character (3). LEIDY (1879), AWERINTZEW (1906a) and CHARDEZ (1956) stress the high variability of this species. Their data as well as those of EHRENBERG (1838), PENARD (1902), CASH et al. (1915), OGDEN and HEDLEY (1980) and OGDEN (1984b) agree rather well with ours. The population of DECLOITRE (1954) is significantly different from our (PI) and (PII) in character (1) ($0.01 \geq P > 0.001$) and (2) ($0.05 \geq P > 0.01$).

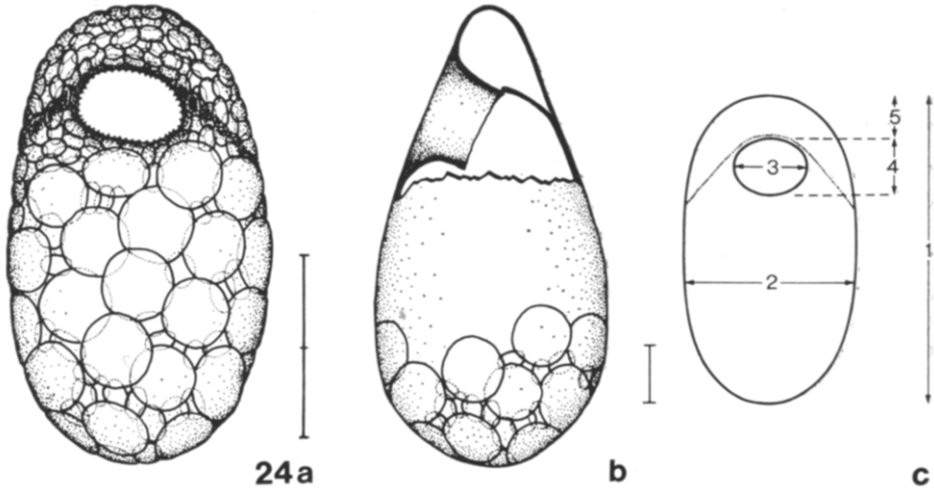


Fig. 24. *Trinema penardi*. (a, b) Ventral and lateral view, shell opened, scale bar 20 µm. (c) Ideal individual, ventral view, scale bar 10 µm.

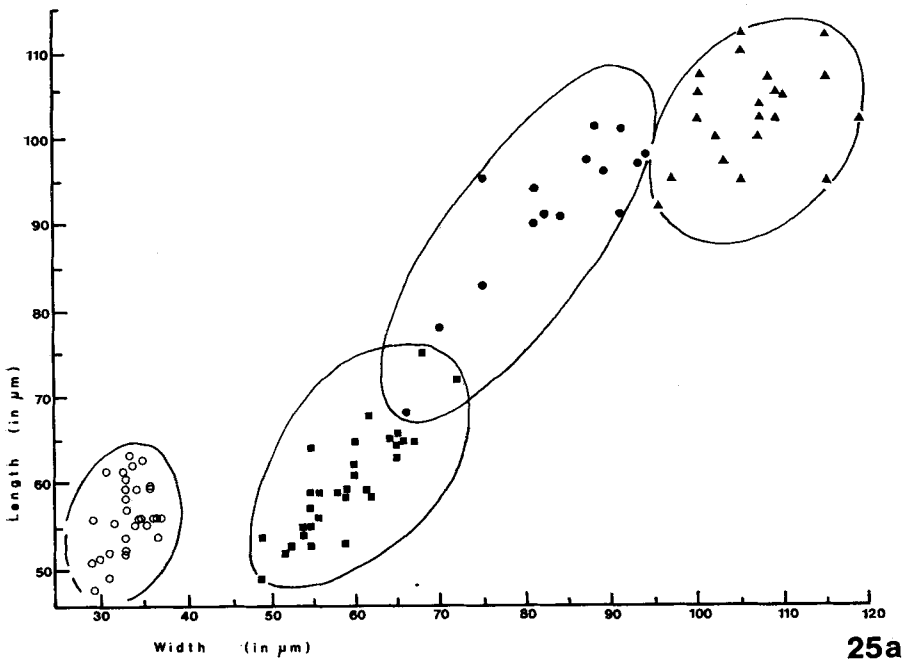
Table 3. Analysis of the coefficients of variation of different testacean groups. 1st line = Testacealobosa; 2nd line = Testaceafilosa; 3rd line = shells composed of xenosomes; 4th line = shells composed of idiosomes. The evaluation also includes some data of HOOGENRAAD and DE GROOT (1937), DECLOITRE (1954) and SCHÖNBORN (1965). Only phylogenetically homologous characters are pooled and evaluated

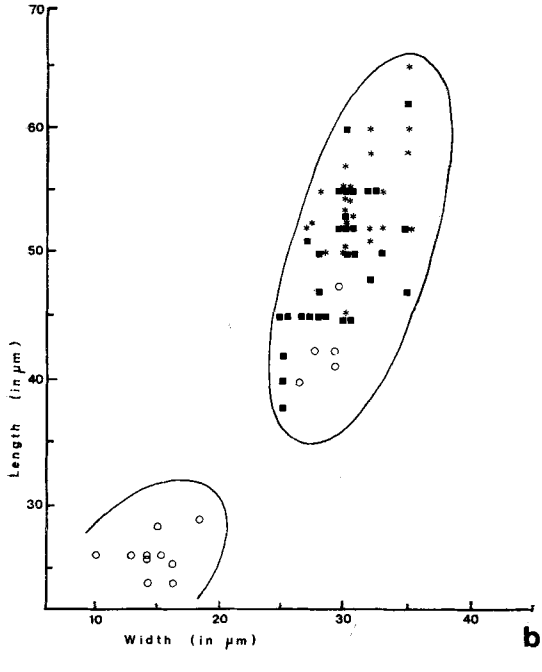
Character (see Figures)	Weighted $\bar{x}$ of V	Min of V	Max of V	Number of species	Number of populations	Number of individuals
(1) Length	7.1	4.2	12.3	11	16	491
	11.5	2.9	26.6	11	19	443
	8.3	5.3	12.8	11	14	337
	12.1	2.9	26.6	9	17	393
(2) Width	4.5	4.9	13.1	11	16	492
	13.4	2.3	45.2	11	19	441
	7.7	4.2	13.0	11	14	338
	14.3	2.3	45.2	9	17	391
(3) Depth	8.3	5.8	13.2	11	15	352
	12.6	3.8	35.4	11	16	348
	8.1	4.2	13.2	11	14	338
	13.3	3.8	35.4	9	14	298
(4) Aperture, major axis	11.7	8.0	17.1	11	11	303
	13.5	3.8	18.6	11	13	311
	11.7	8.0	17.2	9	11	298
	13.8	3.8	18.6	9	11	261
(5) Aperture minor axis	14.9	9.8	21.8	9	9	234
	14.7	3.8	26.0	11	13	311
	14.4	9.8	21.8	9	9	228
	15.3	3.8	26.0	9	11	261

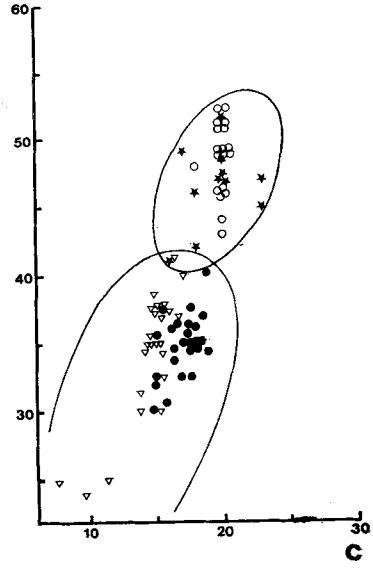
Trinema lineare PENARD, 1890 (Figs. 23, 25c, 26; Table 1)

Shell elliptic, oval in transverse section. Shell platelets hardly seen in vivo, but distinct after silver-staining (Fig. 23e). Aperture circular, invaginated, toothed. Individuals with an evaginated aperture, as described by MEISTERFELD (1979), have never been observed. Nucleus with a central nucleolus.

All characters of the (PII), with the exception of parameter (6) and the size of the idiosomes, vary more than those of the (PI). Our measurements correspond with those of CASH et al. (1915), DECLOITRE (1954) and HEDLEY and OGDEN (1974). However, PENARD (1890, 1902), MEISTERFELD (1979) and WANNER (1987) give a maximum length of 30 μm, whereas we measured 40 μm, which complicates in some cases a reliable differentiation from *T. enchelys* (Fig. 22; and see chapter 3.2.). *T. lineare* shows a high variability in shape (CASH et al. 1915; HEDLEY and OGDEN 1974; MEISTERFELD 1979; WANNER 1987). Therefore the widely used criterion of the more slender shape of this species is often not quite correct, as is also evidenced by the plump shape of the individuals of our (PI). This explains the significant differences between the (PI) and DECLOITRE's (1954) population in character (2) ($0.01 \geq P > 0.001$). No significant difference could be proved in character (1), and no significant difference exists between our (PII) and DECLOITRE's (1954) population. The number of rows of toothed apertural plates is also variable (WANNER 1987). Our (PII) has double or threefold rows, whereas the populations of MEISTERFELD (1979), HEDLEY and OGDEN (1974) and OGDEN and HEDLEY (1980) have only single rows.


Length (in µm)
Width (in µm)
25a


Length (in µm)
Width (in µm)
b


c

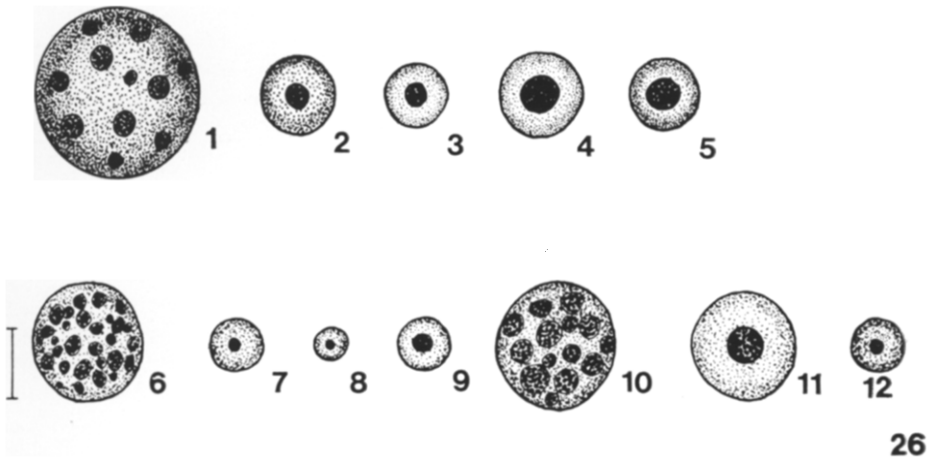


Fig. 26. Nuclei with nucleoli of some testacean species. (1) *Trigonopyxis arcula;* (2) *Trinema complanatum;* (3) *Euglypha rotunda;* (4) *Difflugia lucida;* (5) *Centropyxis elongata;* (6) *Nebela tincta;* (7) *Pseudodifflugia fascicularis;* (8) *Schoenbornia viscicula;* (9) *Trinema lineare;* (10) *Plagiopyxis declivis;* (11) *Euglypha strigosa;* (12) *Euglypha cristata.* Scale bar 8 μm.

A pairwise multiple comparison of 2 populations of *T. enchelys* and *T. lineare* each shows that both populations of *T. enchelys* are significantly different from both populations of *T. lineare* in characters (1), (2) and (3) (Table 2). Regarding character (4) there is a significant difference only between one population of *T. lineare* and the 3 other populations. Further significant differences exist between the 2 populations of *T. enchelys* in character (3), and also between the 2 populations of *T. lineare* in characters (2) and (4).

Trinema penardi THOMAS and CHARDEZ, 1958 (Figs. 24, 25b; Table 1)

Shell composed of two independent parts. Outer component carries the circular shell platelets, inner part forms the oval aperture. In contrast to the very similar *T. galeata*, the inner shell does not form an anterior apertural rim.

THOMAS and CHARDEZ (1958) give a size of 42—55 × 20—30 × 14—20 μm, and a major axis of the aperture of 10—15 μm. The measurements of our population vary in a wider range (for example length 30—65 μm), and only the character "diameter of idiosomes" has a $V < 10$.

3.2. Analysis of characters

The analysis of the coefficients of variation of all investigated species and populations proves the lowest variability for parameter (1), followed by (2) and (3) (Table 3). The measurements of the aperture vary most (characters 4, 5). In general, the Testa-

Fig. 25. Biometric comparison of certain closely related species. (a) Biometric comparison of *Centropyxis elongata* (○), *C. aerophila* var. *sphagnicola* (■), *C. sylvatica* (●) and *C. orbicularis* (▼). (b) Biometric comparison of *Trinema complanatum* (PI) (■) and (PII) (○), and *T. penardi* (✳). (c) Biometric comparison of *T. enchelys* (PI) (○) and (PII) (✲), and *T. lineare* (PI) (●) and (PII) (▽).

ceafilosa and tests composed of idiosomes have wider ranges of variation as compared with the Testacealobosa and species covered with xenosomes. This indicates that the Testaceafilosa evolve faster or are evolutionary younger than the Testacealobosa. Further reasons might be the different phylogenetic origins of both groups, as is suggested in some new systematic approaches (MÖHN 1984; BOVEE 1985a, b).

The biometric comparison of the 4 investigated species of *Centropyxis* shows that they can be separated by their size (Fig. 25a). Nevertheless, intermediate sizes exist between *C. sylvatica* and *C. aerophila* var. *sphagnicola*. The biometric comparison of *T. penardi* and *T. complanatum* (Fig. 25b) proves that both species have a similar length, with the exception of the small individuals of *T. complanatum* (PII). The possibility of confusing these smaller forms with *T. lineare* is rather negligible, due to their different shapes. The comparison of *T. enchelys* and *T. lineare* shows 2 accumulations of shell length in the range of 30—38 μm and 45—52 μm, indicating that these species can be rather well separated by their size (Fig. 25c). An overlapping exists only in the range of about 40 μm.

There exist significant differences between populations of the same species (Table 1). Similar results have been reported by HOOGENRAAD and DE GROOT (1937), CHARDEZ and LECLERCQ (1963), SCHÖNBORN (1966b, 1983) and SCHÖNBORN et al. (1983), and explained as eco-races or geographic variations.

On the other hand, the shape of the apertural plates seems to be rather constant. *T. lineare*, for instance, has apertural plates which differ in their number, but are constant in shape. Our results, which agree with earlier investigations of COÛTEAUX et al. (1979) indicate that the structure of these plates, especially within the Euglyphidae, are a reliable criterion for species discrimination (but probably not for varieties; see *E. rotunda*).

The structure of the nucleus has sometimes been used for species separation (GROSPIETSCH 1965; SCHÖNBORN 1966a).

Difflugia lobostoma and *D. limnetica*, for example, are separated by the number and location of the nucleoli. The structure of the nuclei of 9 of our 12 investigated species corresponds with the data of PENARD (1902).

D. lucida, *P. fascicularis* and *E. strigosa* have only one nucleolus, which contrasts with the descriptions of PENARD (1902). Recently, we found a population of *D. lucida* in an Austrian saline soil, which shows nuclei with numerous small nucleoli. Some variability has also been reported for *A. seminulum* and *T. complanatum* (PENARD 1902; CASH et al. 1915). These data suggest that nuclear structures sometimes vary with populations, but unfortunately the data are still too fragmentary to rate the taxonomic value of this character.

Zusammenfassung

Es werden 24 bodenbewohnende Testaceen-Arten, die zu 34 Populationen gehören, beschrieben und biometrisch charakterisiert. Die Konstruktion des „Ideal-Individuums" jeder Art erfolgte an Hand der biometrischen Daten. Die Artentrennung innerhalb der *Nebela tincta-parvula-bohemica-collaris* Gruppe wird detailliert diskutiert. *Plagiopyxis declivis* baut die Idiosomen euglyphider Testaceen zwischen ihre Xenosomen ein. Die Analyse der Variabilitätskoeffizienten aller Arten zeigt die niedrigste Variabilität für die Schalenlänge und den höchsten Wert für die Schalenöffnung. Generell weisen die Testaceafilosa und Schalen, welche aus Idiosomen zusammengesetzt sind, im Vergleich mit den Testacealobosa und Arten mit Xenosomen-Gehäusen einen weiteren Variationsbereich auf. Dies deutet darauf hin, daß die Testaceafilosa schneller evolvieren oder entwicklungsgeschichtlich jünger sind als die Testacealobosa. *Pseudodifflugia fascicularis*, *Euglypha strigosa* und *Difflugia lucida* haben im Gegensatz zu früheren Literaturangaben nur einen ein-

zigen zentralen Nucleolus. Es wurden signifikante Unterschiede zwischen Populationen der gleichen Art gefunden, was die Existenz geographischer Rassen nahelegt, die sich in ihrer Größe unterscheiden.

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