

Morphology and biometry of twelve soil testate amoebae (Protozoa, Rhizopoda) from Australia, Africa, and Austria

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CONTENTS

1. Introduction	1
2. Materials and methods	1
3. Description of species	1
4. Acknowledgements	15
5. References	15

SYNOPSIS. The morphology of 12 species of testate amoebae from soils of Australia (*Bullinularia gracilis*, *Centropyxis cryptostoma*, *Heleopera sylvatica*, *Assulina muscorum*, *Corythion asperulum*, *Euglypha compressa*), Africa (*Paraquadrula irregularis*) and Austria (*Cyclopyxis kahli*, *Diffflugia stoutii*, *Nebela tubulata*, *Tracheleuglypha dentata*, *Trinema enchelys*) were investigated by light and scanning electron microscopy. All species are characterized morphometrically and an 'ideal individual' for each species is constructed by means of the morphometric data. A first record for Austria is *Diffflugia stoutii*, first records for Australia are *Bullinularia gracilis*, *Centropyxis cryptostoma*, *Corythion asperulum* and *Heleopera sylvatica*. In *P. irregularis*, numerous cells united at their apertures have been observed. Protargol silvered material convincingly shows fusion of the nuclei and nucleoli of such pairs. It is, however, uncertain whether the uniting cells are parent and daughter (autogamy) or are from 2 different specimens (conjugation).

INTRODUCTION

Many species of testate amoebae have been described and redescribed without providing reliable biometric data. The present paper is the second (Lüftenegger et al., 1988a) of a series of publications intended to improve the diagnosis of such species. This hopefully will also help ecologists with the often difficult species determinations.

MATERIALS AND METHODS

For the sources of material see Table 1. Testate amoebae were isolated with a pipette as individuals from soil suspensions (0.2 g fresh soil + 5 ml distilled water) and stained either with protargol silver or phenolic aniline blue solution (Foissner, 1983; Lüftenegger et al., 1988b). The shells of some species were made transparent overnight in a drop of albumin-glycerin (as used in histological techniques to fix sections on a slide). All drawings were produced with the help of a camera

lucida using an oil immersion objective (100 ×; eyepiece, 10 ×) and bright field illumination.

The following sample statistics were calculated according to Schönborn et al. (1983): \bar{x} , arithmetic mean; M, median (this value is used to construct the ideal individual); SD, standard deviation; SE, standard error of the arithmetic mean; CV, coefficient of variation in %; Min, Max, minimum and maximum values; n, sample size. Most shell variables were given a number which defines the corresponding character in the drawing of the ideal individual. The respective characters are identified by these numbers in the tables (Lüftenegger et al., 1988a).

For scanning electron microscopy specimens were cleaned by several transfers through distilled water before being manipulated by a single-hair brush as individuals and mounted on glass slides covered with a special adhesive (Mixture à Dorer Clariféé, Fa. Lefranc & Bourgeois). Further procedures see Lüftenegger et al. (1988a).

Determinations of species follow the original descriptions. One slide of each population has been deposited in the British Museum (Natural History) in London. Registration number is given in the species description. Several species have the same Reg. No since they are on the same slide.

Table 1. Localities of the populations.

Species Reference number	Date	Locality
<i>Bullinularia gracilis</i>	23.10.1986	Bush in the Brisbane Water National Park, 50 km north of Sydney, Australia. E 152° S 33°. Sea-level 150 m. Upper soil layer (0–2 cm soil depth) with litter and moss on sandstone. pH 5.1.
<i>Centropyxis cryptostoma</i>	23.10.1986	See <i>Bullinularia gracilis</i> .
<i>Cyclopyxis kahli</i>	10.10.1987	Aiglern near Aigen in the Ennstal, Austria, E 14° N 48°. Sea-level 650 m. Brown earth (loamy sand) of a meadow (0–5 cm). pH 6.7. (For detailed site description see Foissner et al., 1990).
<i>Diffugia stoutii</i>	10.10.1987	See <i>Cyclopyxis kahli</i> .
<i>Heleopera sylvatica</i>	18.10.1986	Coastal wood, Royal National Park, south of Sydney, Australia, E 150° S 35°. Sea-level c. 100m. Upper soil layer (0–5 cm) with litter and brown sand. pH 4.5.
<i>Nebela tubulata</i>	20.9.1988	Top of the Gaisberg, Salzburg, Austria, E 13° N 48°. Sea-level 1250 m. Rendzina of a spruce forest with <i>Luzula</i> , <i>Calamagrostis</i> , <i>Sesleria</i> (0–5 cm). pH 5.2.
<i>Paraquadrula irregularis</i>	8.5.1985	Mzima Springs, Tsavo National Park West, about 50 km east of Mt. Kilimanjaro, Kenya, E 38° S 4°. Humus layer with litter, many fungi, under acacia (0–5 cm). pH 7.0.
<i>Assulina muscorum</i>	23.10.1986	See <i>Bullinularia gracilis</i> .
<i>Corythion asperulum</i>	23.10.1986	See <i>Bullinularia gracilis</i> .
<i>Euglypha compressa</i>	23.10.1986	See <i>Bullinularia gracilis</i> .
<i>Tracheleuglypha dentata</i>	10.10.1987	See <i>Cyclopyxis kahli</i> .
<i>Trinema enchelys</i>	10.10.1987	See <i>Cyclopyxis kahli</i> .

DESCRIPTION OF SPECIES

Bullinularia gracilis Thomas, 1959

Figs 1–8, Tables 1,2

BM (NH) Reg. No. 1990. 4. 26.1.

Shell yellowish to brownish, almost hemispheric, always broader than long, ventral side smooth, structureless, covered by thin, fragile layer (Fig 7), posterior margin and dorsal side rough, covered with xenosomes (Figs 4,5). Aperture obscured by anterior lip, under which ventral side projects (Fig. 6). Approximately 30 pores, about 1–2 µm in diameter, irregularly arranged in the anterior third of shell (Fig. 8).

Characters (1)–(3) show normal variability (CV 14.0 and 12.3%), whereas characters (4) and (5) have high coefficients of variation (CV 20.0 and 30.0 %; Table 2). Thomas (1959) states 120 µm on average for the major axis of the shell. The specimen photographed by Bonnet (1961) shows a similar

Table 2. Morphometric characterization of *Bullinularia gracilis*. All measurements in µm.

Character	\bar{x}	M	SD	SE	CV	Min	Max	n
(1)	93.2	88.5	13.0	5.33	14.0	83	118	6
(2)	130.3	125.0	18.2	4.70	14.0	112	169	15
(3)	150.9	150.0	18.5	4.78	12.3	128	192	15
(4)	57.1	54.0	11.4	2.94	20.0	41	80	15
(5)	11.5	10.0	3.4	0.89	30.0	5	16	15

size, however, detailed biometric data are not provided. Regarding this character, the values of our population are about 25 % higher, which is in agreement with Golemansky (1968).

Hoogenraad & De Groot (1952b) describe two shell types for *B. indica*. The 'extraordinary' type is firm and inflexible, the 'normal' type is flexible and rather tenacious, consisting of a homogenous matrix, as stated also by Penard (1912). We suggest that the outer organic layer, which seems to be somewhat elastic (Fig. 7), is responsible for the above mentioned flexibility of shells in some *Bullinularia* populations.

Centropyxis cryptostoma Bonnet, 1959

Figs 9–13, Tables 1,3

BM (NH) Reg. No. 1990. 4. 26.2.

Shell brownish, rectangular with rounded ends in ventral view, compressed, ventral side fairly smooth, with flat xenosomes, dorsal side with rough particles. Aperture sub-apical, reniform. Posterior lip extends slightly inside shell as curved elongation of ventral side, anterior lip overhanging (Figs 10,12). Separation from *C. capucina* and *C. halophila* is mainly by smaller size and occurrence in different habitats (pH optimum for *C. halophila* 8.5–9; Bonnet & Thomas, 1960a).

Coefficients of variation of characters (1)–(4) and (7) are less than 10 %; measurements of aperture show greater variability (CV 12.5 and 14.9; Table 3). Bonnet (1959) states 45 µm for the length, 35 µm for the breadth and 27–30 µm for the depth of the shell. The individuals of our population are a little more flattened, which is in agreement with the measurements by Schönborn (1966). All other characters match well with the description by Bonnet (1959).

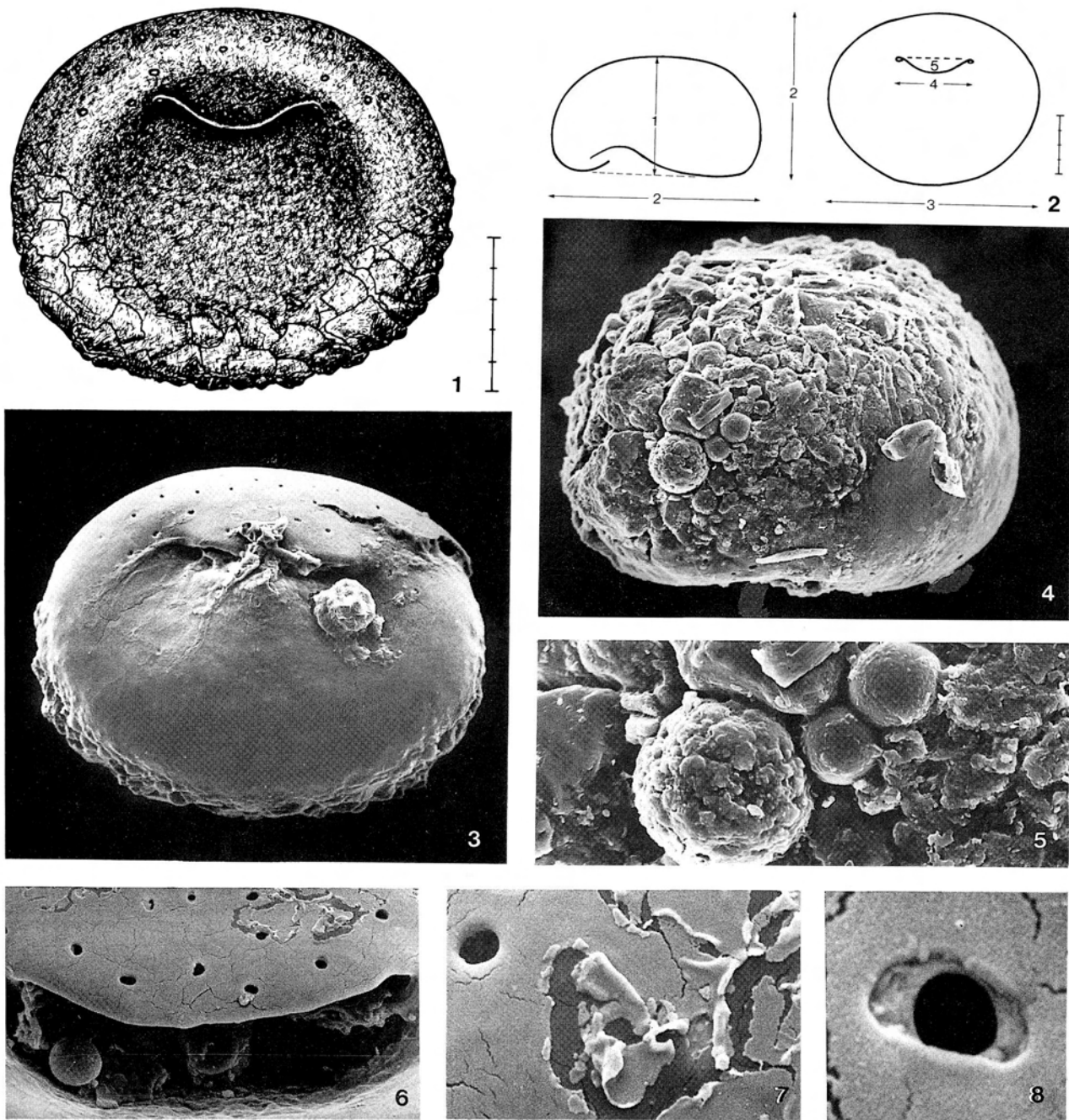
Cyclopyxis kahli (Deflandre, 1929) Deflandre, 1929

Figs 14–16, Tables 1,4

BM (NH) Reg. No. 1990. 4.26.3

Shell brownish, hemispheric, composed of xenosomes, apertural surface smooth and distinctly invaginated, aboral surface rough. Aperture surrounded by distinct rough particles (10–20 % of specimens studied), or more or less smooth (c. 80–90 %).

Shell measurements fairly variable (CV 10.6–16.0; Table 4). The data of Deflandre (1929) and Ogden (1988) agree well with ours, whereas other authors state slightly higher values (Bonnet & Thomas, 1960a; Ogden & Hedley, 1980; Ogden, 1984; Rauenbusch, 1987). The Indian population described by Guru & Dash (1983) measures only 50–65 µm in diameter (sample size not given).



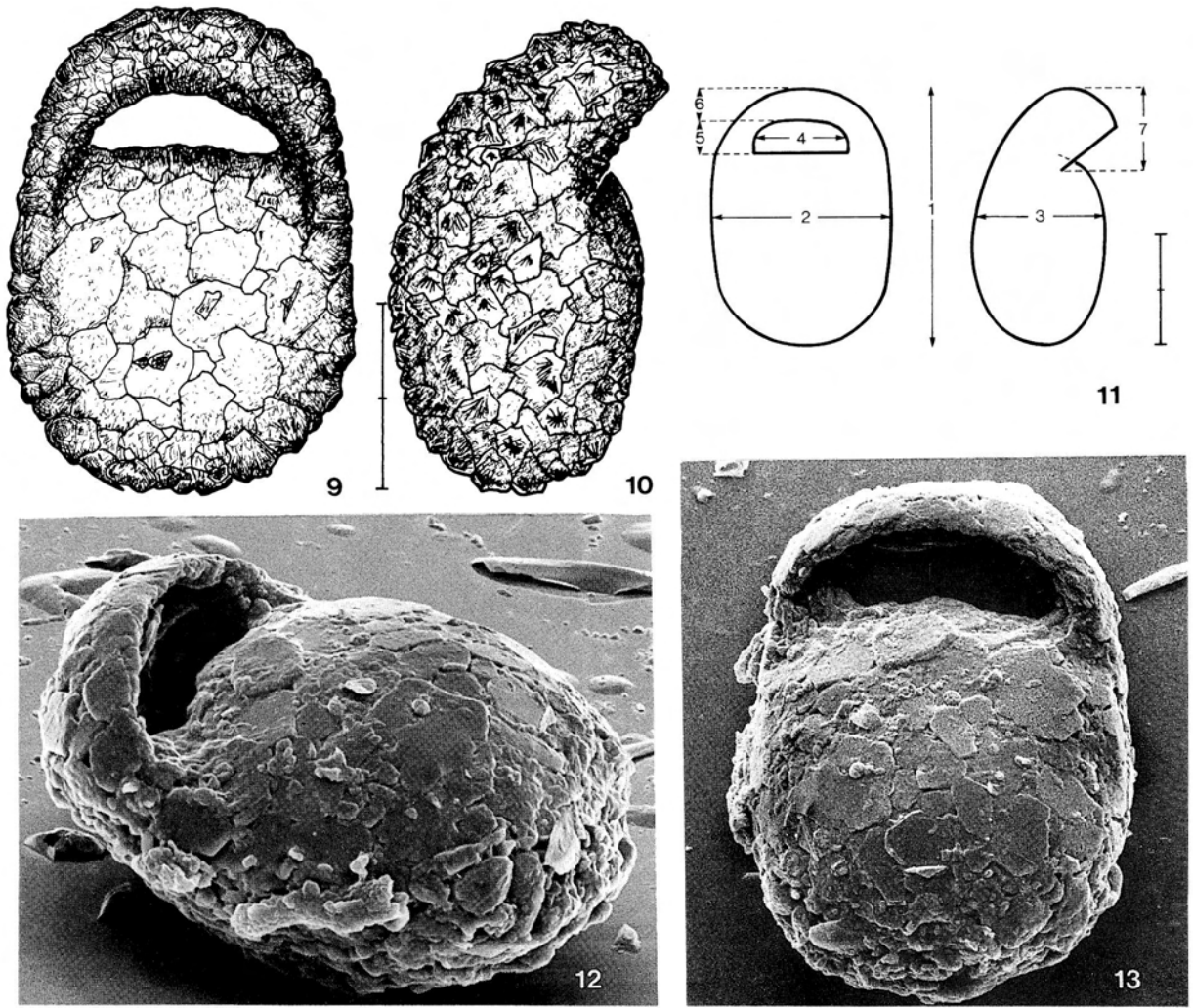
Figs 1–8 *Bullinularia gracilis*, light microscopic (Fig. 1) and SEM-aspects (Figs 3–8) and ideal individual (Fig. 2). 1 Ventral view. 2 Lateral and ventral view. 3 Ventral view, $\times 400$. 4 Lateral view, $\times 500$. 5 Detail of rough dorsal shell surface, $\times 1500$. 6 Aperture, $\times 1200$. 7 Detail of smooth ventral shell surface, $\times 3700$. 8 Pore, $\times 12000$. Scale bar divisions 10 μm .

Table 3. Morphometric characterization of *Centropyxis cryptostoma*. All measurements in μm .

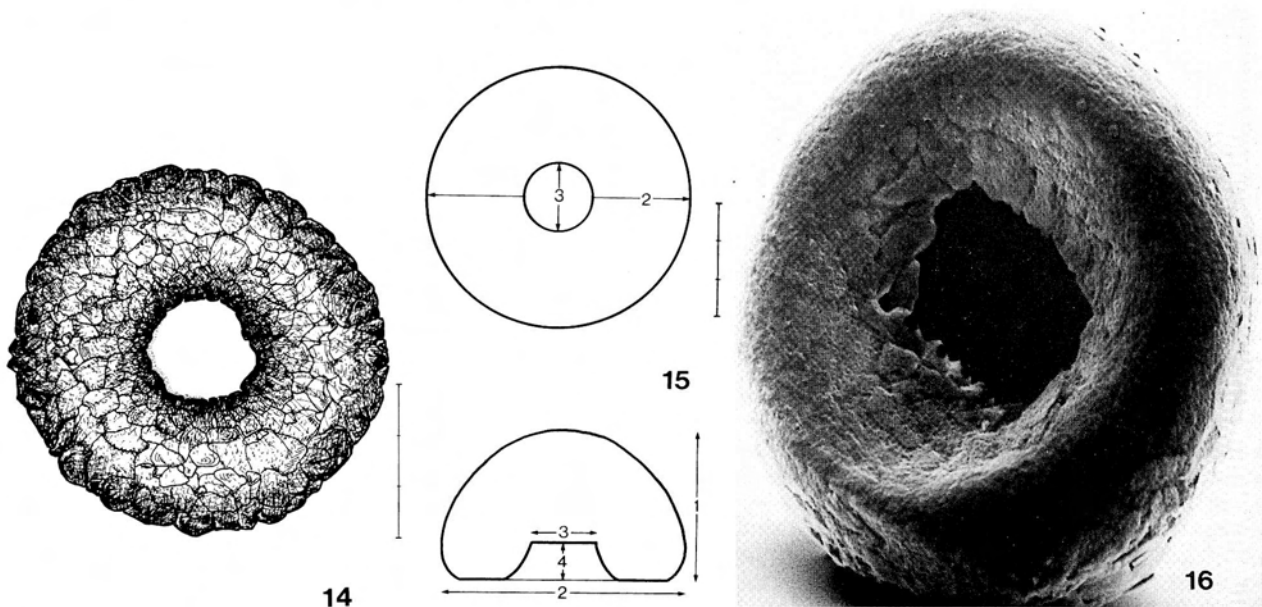
Character	\bar{x}	M	SD	SE	CV	Min	Max	n
(1)	46.1	46.0	2.0	0.64	4.4	42	48	10
(2)	32.4	32.0	2.6	0.82	8.0	28	35	10
(3)	23.2	22.5	2.0	0.65	8.8	20	27	10
(4)	15.4	16.0	1.4	0.45	9.3	13	18	10
(5)	6.4	6.3	0.9	0.30	14.9	5	8	10
(6)	5.6	6.0	0.7	0.22	12.5	4	6	10
(7)	14.7	15.0	1.4	0.45	9.7	13	17	10

Table 4. Morphometric characterization of *Cyclopyxis kahli*. All measurements in μm .

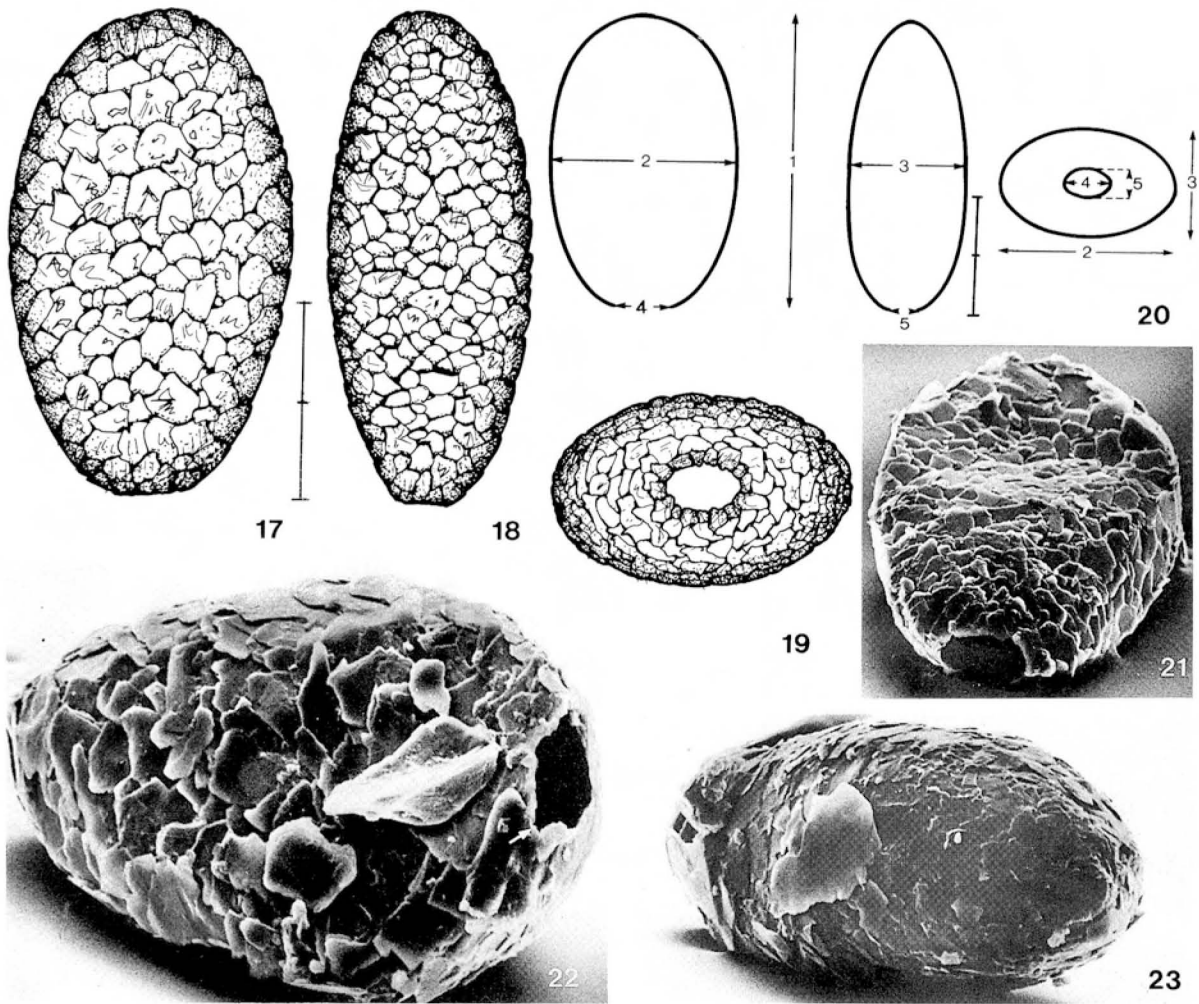
Character	\bar{x}	M	SD	SE	CV	Min	Max	n
(1)	44.3	45.0	5.6	1.16	12.6	35	54	23
(2)	70.1	70.0	7.5	1.41	10.6	58	89	28
(3)	18.0	19.0	2.5	0.51	13.8	13	22	24
(4)	11.8	11.5	1.9	0.47	16.0	10	16	16



Figs 9–13 *Cyclopyxis cryptostoma*, light microscopic (Figs 9,10) and SEM-aspects (Figs 12,13) and ideal individual (Fig. 11). 9–11 Ventral and lateral views. 12,13 Ventro-lateral and ventral view, $\times 1900$, $\times 1600$. Scale bar divisions $10\ \mu\text{m}$.



Figs 14–16 *Cyclopyxis kahli*, light microscopic (Fig. 14) and SEM-aspects (Fig. 16) and ideal individual (Fig. 15). 14 Ventral view. 15 Ventral and lateral view. 16 Ventral view, $\times 1100$. Scale bar divisions $10\ \mu\text{m}$.



Figs 17–23 *Diffflugia stoutii*, light microscopic (Figs 17–19) and SEM-aspects (Figs 21–23) and ideal individual (Fig. 20). 17–20 Broad lateral, narrow lateral and ventral views. 21 Ventral view, × 1200. 22,23 Broad and narrow lateral view, × 1600, × 1200. Arrow marks aperture. Scale bar divisions 10 µm.

Table 5. Morphometric characterization of *Diffflugia stoutii*. All measurements in µm.

Character	\bar{x}	M	SD	SE	CV	Min	Max	n
(1)	50.7	50.0	7.1	1.36	14.0	38	61	27
(2)	31.0	32.0	5.3	1.07	17.0	22	40	24
(3)	20.0	20.0	3.0	0.78	15.1	16	25	15
(4)	8.6	8.5	1.6	0.39	18.9	6	10	16
(5)	5.4	5.0	0.5	0.20	9.8	5	6	7

Table 6. Morphometric characterization of *Heleopera sylvatica*. All measurements in µm.

Character	\bar{x}	M	SD	SE	CV	Min	Max	n
(1)	65.3	65.0	3.0	0.62	4.5	59	70	23
(2)	44.0	44.0	2.2	0.46	5.0	39	48	23
(3)	28.7	29.0	2.3	0.47	7.9	25	33	23
(4)	3.4	3.0	0.9	0.19	26.9	2	5	23

Bonnet & Thomas (1960b) described a variety, *cyclostoma*, lacking the rim of rough particles around the aperture. We suggest that such elements are easily lost, since transitions in the formation or reduction of the apertural rim are common (see above and Coûteaux, 1976, Fig. 1J; Ogden & Hedley, 1980, Pl. 24; Rauenbusch, 1987 Pl. 16, Fig. a). At the present state of knowledge it seems wise to classify our population as *C. kahli*.

For detailed ecological data see Bonnet (1989a).

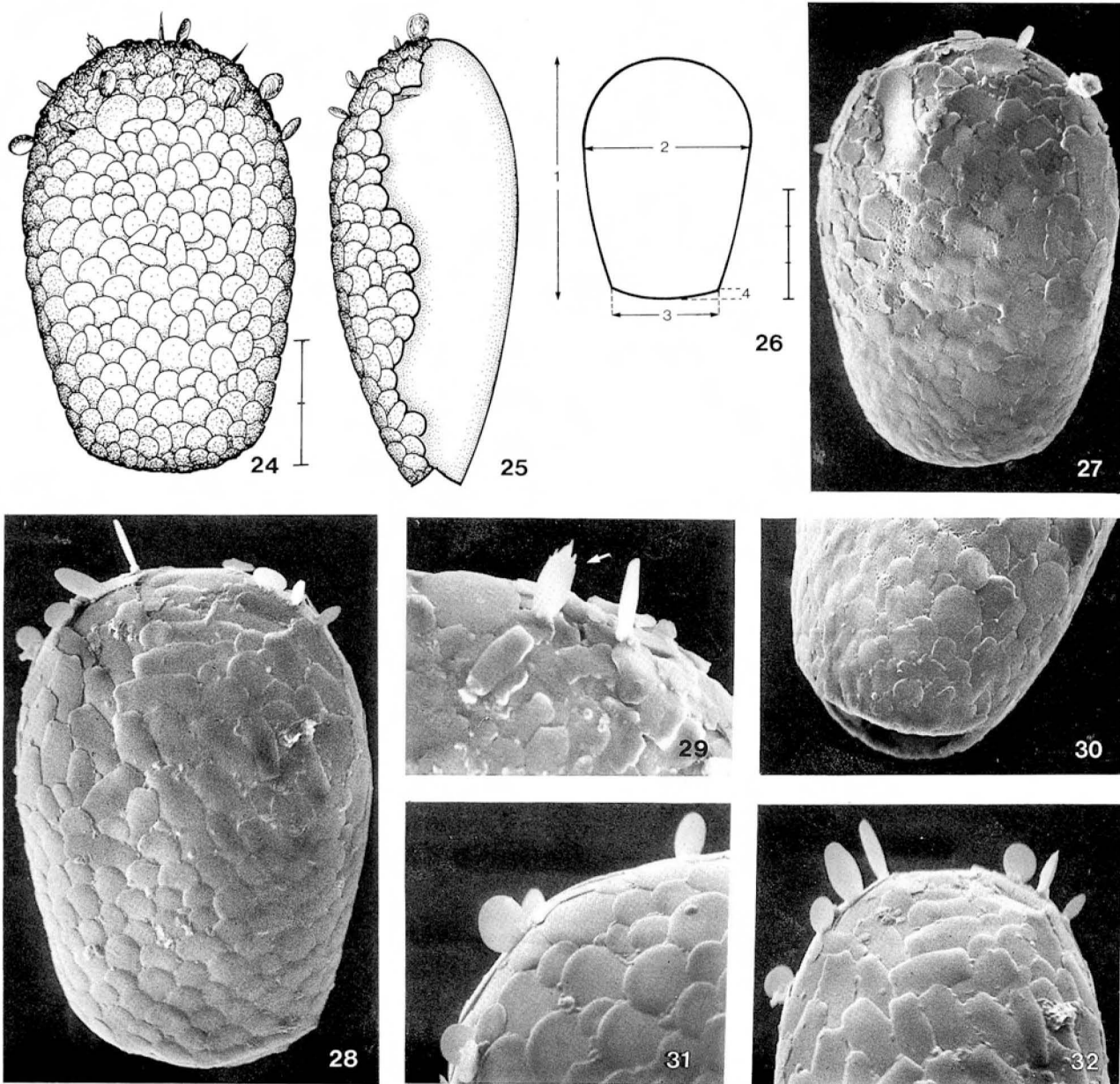
***Diffflugia stoutii* Ogden, 1983**

Figs 17–23, Tables 1,5

BM (NH) Reg. No. 1990. 4.26.4

Shell brownish, elongate ellipsoid, slightly flattened, composed of overlapping, flat xenosomes, very fragile, thus shells often collapse when air-dried (Fig. 21). Aperture elliptic.

Shell measurements, especially characters (2) and (4), show considerable variability (Table 5). Ogden (1983), who



Figs 24–32 *Helopera sylvatica*, light microscopic (Figs 24,25) and SEM-aspects (Figs 27–32) and ideal individual (Fig. 26). **24, 25** Broad and narrow lateral view. **26** Broad lateral view. **27,28** Broad lateral views, $\times 1000$, $\times 1200$. **29** Detail of surface, $\times 2100$. Note euglyphid apertural platelet (arrow). **30** Aperture, $\times 1200$. **31,32** Details of surfaces, $\times 1800$, $\times 1200$. Scale bar divisions $10\ \mu\text{m}$.

discovered this species in a *Sphagnum* sample from North Wales (England), states the following values ($n = 4$): $47\text{--}59\ \mu\text{m}$ length, $33\text{--}36\ \mu\text{m}$ breadth, $9\text{--}12\ \mu\text{m}$ diameter of aperture. Our measurements agree well with those data (Table 5). However, our population is slightly compressed and has an elliptic aperture, possibly caused by living in the soil.

As far as we know, this is the first record since the original description.

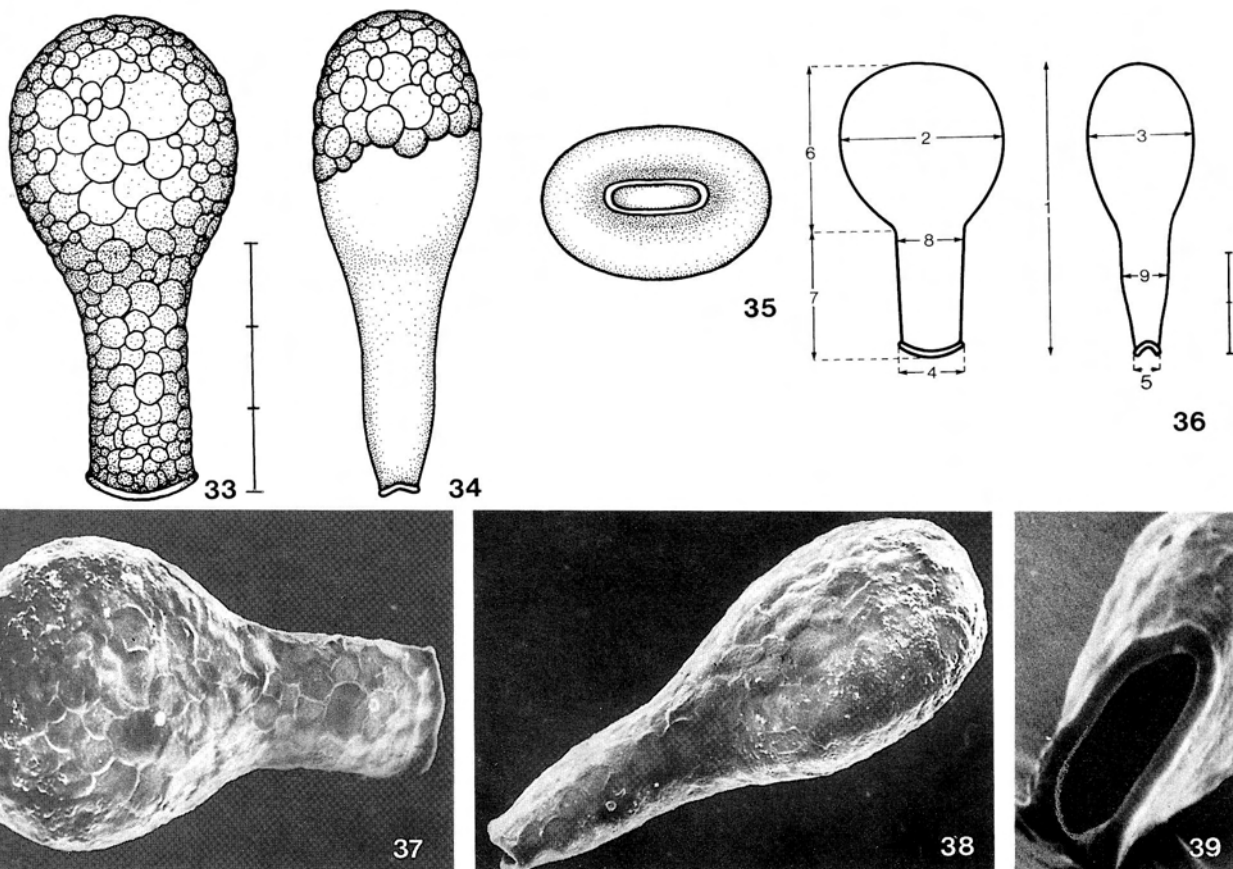
Helopera sylvatica Penard, 1890

Figs 24–32, Tables 1,6

BM (NH) Reg. No. 1990.4.26.5

Shell slightly yellowish, transparent, obovoid, flattened about 2:1, composed of siliceous shell platelets from other testaceans and sometimes rough xenosomes, found mainly in aboral region. Some individuals are completely covered with such acquired idiosomes (Fig. 28). The aboral region often has euglyphid platelets (*Euglypha*, *Trinema*) extending at right-angles like spines (Figs 28,29,31,32). Aperture terminal, slightly convex in broad view, slit-like to elliptic with small border of organic cement (Fig. 30). Nucleus with several nucleoli (protargol impregnation).

Shell measurements with exception of character (4) are fairly constant (Table 6) and agree well with the data of Penard (1890). Cash & Hopkinson (1909) state a smaller shell breadth ($25\text{--}30\ \mu\text{m}$).



Figs 33–39 *Nebela tubulata*, light microscopic (Figs 33–35) and SEM-aspects (Figs 37–39) and ideal individual (Fig. 36). 33–35 Broad lateral, narrow lateral and ventral view. 36 Broad and narrow lateral view. 37,38 Broad and narrow lateral view, $\times 1100$, $\times 1200$. 39 Aperture, $\times 2500$. Scale bar divisions 10 μm .

The drawings in Penard (1890, Pl. VIII, Figs 79,80,84,86,87) clearly show individuals having peculiar spine-like structures in the aboral region and are even mentioned in his description. Hoogenraad & De Groot (1940) also state 'eigentümliche dornartige Fortsätze' for *H. petricola*, and Penard (1890) assumes very narrow idiosomes erected on the shell surface for *H. picta*. This suggestion is now confirmed by means of scanning electron microscopy. No other study describing such platelets is known to us. The paper by Coûteaux & Munsch (1978, Pl. III, Fig. 3), however, includes a scanning electron micrograph of a specimen designated as *Placocista lens*. We suggest that it is a *Heleopera* with spine-like siliceous platelets. (Unlike to *Heleopera*, the genus *Placocista* is an euglyphid taxon, having filose pseudopodia and shells with regularly arranged, self-made platelets). Presumably, all species of the genus *Heleopera* have the ability to erect platelets.

For detailed ecological data see Bonnet (1989b).

Nebela tubulata Brown, 1910

Figs 33–39, Tables 1,7

BM (NH) Reg. No. 1990.4.26.6

Shell colourless, flask-like with distinctly separated, parallel-sided neck, slightly compressed, fragile, composed of different sized circular and elliptic platelets from other

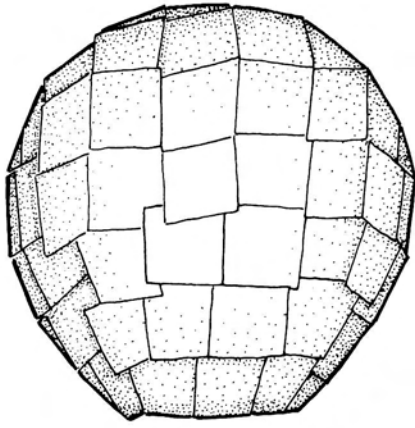
Table 7. Morphometric characterization of *Nebela tubulata*. All measurements in μm .

Character	\bar{x}	M	SD	SE	CV	Min	Max	n
(1)	60.6	61.0	2.1	0.58	3.5	57	64	13
(2)	31.4	32.0	2.5	0.69	8.0	28	38	13
(3)	22.2	22.0	2.5	1.11	11.2	20	26	5
(4)	14.3	14.0	0.9	0.24	6.2	13	16	13
(5)	5.1	5.0	0.8	0.23	15.1	4.5	6	11
(6)	33.9	34.0	2.4	0.65	7.0	29	37	13
(7)	26.5	26.0	2.0	0.55	7.5	22	29	13
(8)	14.5	14.0	1.6	0.43	10.7	12	17	13
(9)	9.6	10.0	1.5	0.57	15.8	9	12	7

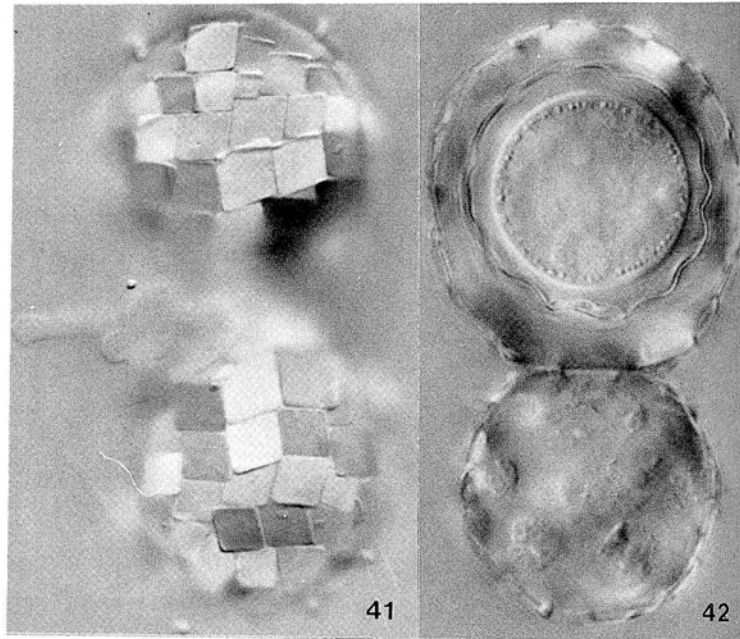
testaceans (Fig. 33). Aperture terminal, elongate elliptic, concave in lateral view, surrounded by organic collar (Fig. 39).

Shell measurements with exception of characters (5) and (9) are fairly constant (Table 7). Character (1) has lowest variability (CV 3.5). Our values agree well with those of Brown (1910), Wailes & Penard (1911), Deflandre (1936), Hoogenraad & De Groot (1940, 1952a), Gauthier-Lièvre (1957) and Ogden & Hedley (1980).

Nebela tubulata is separated from *N. lageniformis* by its smaller size (*N. lageniformis* always larger than 90 μm), and from *N. militaris* by the abrupt narrowing of the shell

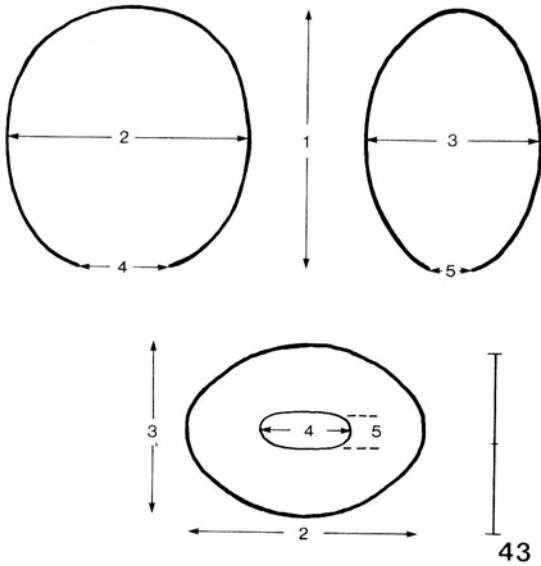


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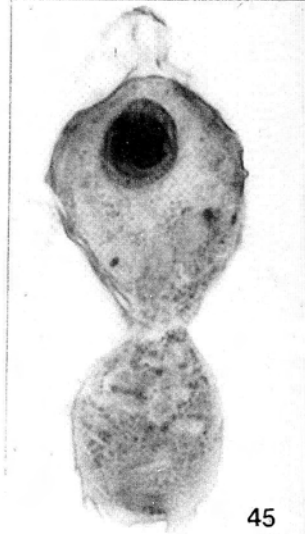
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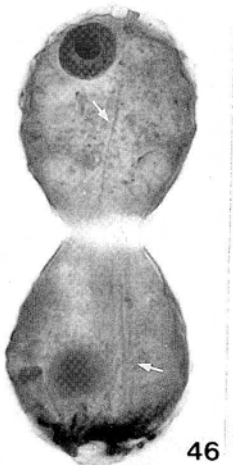
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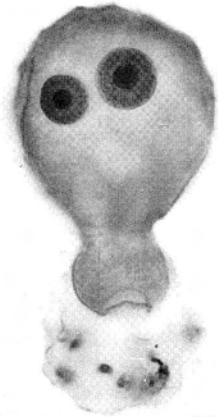
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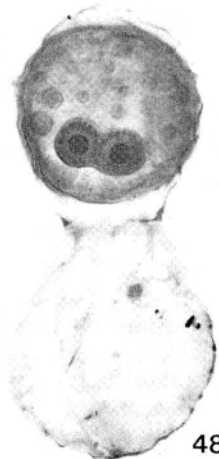
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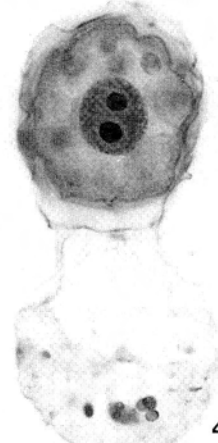
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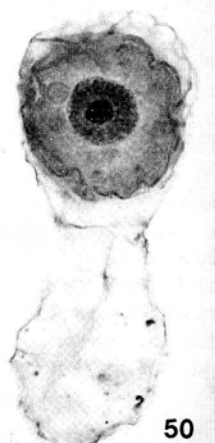
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Figs 40–50 *Paraquadrula irregularis*, light microscopic aspects of living (Figs 40–42) and protargol silver impregnated specimens (Figs 44–50), and ideal individual (Fig. 43). **40** Broad lateral view. **41,42** Light microscopic photographs of specimens united at their apertures, both $\times 1500$. Note cyst in Fig. 42. **43** Broad lateral, narrow lateral and ventral view. **44** Specimen showing 1 pseudopodium. Note nucleus with central nucleolus (arrow). **45** Dividing cell. **46** Parent and daughter cell. Note microfilaments stretching between cells (arrows). **47** Fusion of 2 cells. **48** Nuclear fusion. **49** Early stage of encystation; nucleus contains 2 nucleoli. **50** Resting cyst; nucleus contains 1 nucleolus. Figs 44–50 $\times 1000$. Scale bar divisions 10 μm .

Table 8. Morphometric characterization of *Paraquadrula irregularis*. All measurements in μm .

Character	\bar{x}	M	SD	SE	CV	Min	Max	n
(1)	29.3	29.0	2.2	0.47	7.4	26	32	21
(2)	26.6	26.0	1.9	0.41	7.0	24	30	21
(3)	19.3	19.0	1.2	0.30	6.2	16	21	16
(4)	10.3	10.0	1.5	0.36	14.8	8	13	18
(5)	3.9	4.0	1.0	0.27	24.9	3	6	13
Platelets, length	5.9	6.0	0.9	0.19	15.1	4.5	8	21

Table 9. Morphometric characterization of *Assulina muscorum*. All measurements in μm .

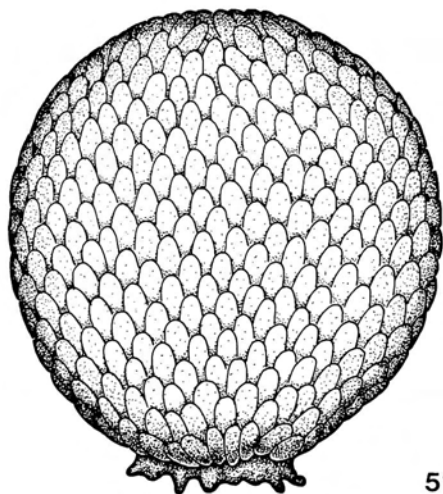
Character	\bar{x}	M	SD	SE	CV	Min	Max	n
(1)	43.0	42.0	5.0	1.12	11.6	38	53	20
(2)	32.3	31.0	5.1	1.13	15.6	26	45	20
(3)	18.3	19.0	1.7	0.44	9.5	16	22	16
(4)	8.5	8.0	2.0	0.44	23.2	6	13	20
(5)	4.8	5.0	0.8	0.21	17.3	4	6	16
(6)	3.1	3.0	0.9	0.22	29.0	2	5	16

towards the parallel-sided neck. Lateral pores as found by Hoogenraad & De Groot (1940) in some individuals did not occur in our population.

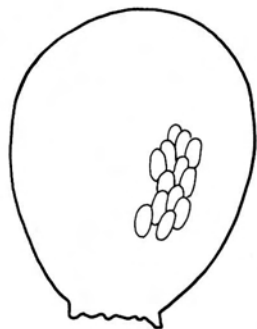
Paraquadrula irregularis (Archer, 1877) Deflandre, 1932
 Figs 40–50, Tables 1,8
 BM (NH) Reg. No. 1990.4.26.7

shell colourless, transparent, circular in broad view, slightly flattened laterally, composed of more or less quadratic calcareous platelets, sometimes irregularly arranged (Figs 40,42). Aperture elliptic. Nucleus with central nucleolus. Separation from the very similar *P. discoides* by lesser flattening in *P. irregularis*.

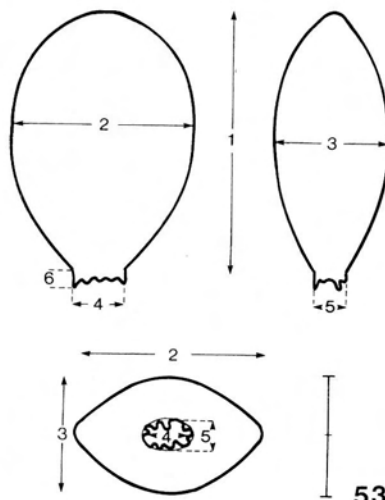
Characters (1)–(3) fairly constant, while measurements of



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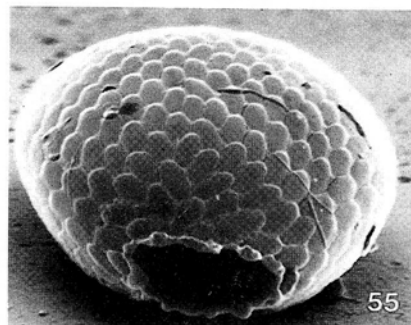
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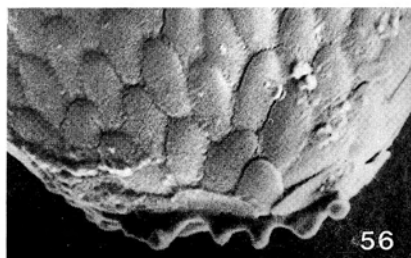
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Figs 51–56 *Assulina muscorum*, light microscopic (Figs 51,52) and SEM-aspects (Figs 54–56) and ideal individual (Fig. 53). **51** Broad lateral view of atypically broad specimen. **52** Broad lateral view of typical specimen. **53** Broad lateral, narrow lateral and ventral view. **54,55** Broad lateral and ventral view, $\times 2100$, $\times 1700$. **56** Aperture showing organic cement, $\times 3400$. Scale bar divisions 10 μm .

aperture and platelets show greater variability (Table 8). Cash & Hopkinson (1909) describe a maximum shell length of 30–38 μm , Grospietsch (1954) about 45 μm , Bonnet & Thomas (1960a) 30–35 μm and Decloitre (1961) 30–40 μm . The shell measurements of our population deviate slightly, being smaller (Table 8).

Strikingly often 2 differently sized individuals can be found united at their apertures. In most cases the larger of the two specimens contains a cyst (Fig. 43) which has, especially when older, a jagged cyst wall. This phenomenon, which is frequent among all members of the genus *Paraquadrula*, has been reported by many authors (Penard, 1902; Deflandre, 1932; Gauthier-Lièvre, 1953; Schönborn, 1965) and might be interpreted as a form of sexuality (see Figs 45–50). Although sexual processes have been described for some testacean species, they are poorly documented. Some authors reported conjugation, followed by encystation, but did not observe nuclear fusion (Penard, 1902; Awerintzew, 1907; Cash & Hopkinson, 1909; Pateff, 1926; Deflandre, 1932; Chardez, 1960), e.g. the cysts contained 2 nuclei.

It is evident from protargol silver impregnated specimens of *P. irregularis* that nuclear fusion takes place. Figures 45–50 document the following steps: A cell divides into 2 daughter cells (Fig. 45; this stage occurred in 5.5% of 200 investigated specimens = 100%), each having a nucleus with central nucleolus (Fig. 46; 11%); the plasma of 2 cells fuse (Fig. 47; 12%); the 2 nuclei fuse (Figs 48,49; 14.5%), followed by the fusion of their nucleoli (Fig. 50; 17%); a cyst is formed (Figs 42,50). Without doubt, the processes photographed in Figs 47–50 show fusions of 2 cells and not binary fissions, since the shells of the united specimens are complete, and even food residues of the former cells are easily to be seen in the abandoned shells (cp. Fig. 45, representing binary fission).

Unfortunately, we could not follow these processes in living specimens; thus it is unclear, whether the uniting cells are parent and daughter or are from 2 different specimens, which would be a true conjugation. The former suggestion is confirmed by Schönborn (1965), who documented a reunion of parent and daughter cells without nuclear fusion, speculating that this phenomenon is caused by formation of an undersized daughter test. However, we also found cysts in smaller or equal sized shells. Such cases have been attributed to plasmogamy by Schönborn (1965). On the other hand, Pateff (1926) and Deflandre (1932) described copulation of strikingly different sized specimens in *Diffflugia mammillaris* and in *P. irregularis* (without nuclear fusion), and Penard (1902) reported for *Cryptodiffflugia oviformis* that cysts are always formed in the smaller of the two tests.

Valkanov (1962b) has observed copulation of equal sized specimens in *P. madarica*, followed by nuclear fusion. He also provided photographic evidence of a syncaryon in *Euglyphella delicatula* (Valkanov 1962a, Abb. 1). Our figures 45–50 are, with exception of Valkanov's picture, the first photographic document of nuclear fusion in testate amoebae. Further investigations are needed to determine, whether autogamy takes place or not, and to follow the fate of the syncaryotic cysts.

For detailed ecological data of this species see Bonnet (1989b).

Assulina muscorum Greeff, 1888

Figs 51–56, Tables 1,9

BM (NH) Reg. No. 1990.4.26.8

Young shells yellowish, older ones light to dark brown, compressed, composed of elliptic, sometimes irregularly arranged platelets. Aperture terminal, elliptic, with more or less pronounced collar of organic cement (Fig. 56; cp. Ogden & Hedley, 1980; Ogden, 1981, 1984). Collar distinctly lobed, contrary to *A. collaris*, Kufferath, 1932, which is, in our opinion, a doubtful species—but see Schönborn & Peschke (1988).

Parameters (1) and (3) fairly constant (CV 8.3 and 8.5) variability of characters (4) and (5) relatively high (CV 17.5 and 23.3; Table 9). The data of Cash et al. (1915) correspond with ours, while those of Ogden & Hedley (1980) and Ogden (1984) are moderately higher. Hoogenraad & De Groot (1937) studied different populations of *A. muscorum*, of which the so-called 'Middel'-population (Fig. 4 of Hoogenraad & De Groot, 1937) matches our population well. This is also true for the Thuringian population analyzed biometrically by Schönborn & Peschke (1988), despite the great geographic distance! Even the coefficient of variation of each single character coincides strikingly well.

Corythion asperulum Schönborn, 1988 in Schönborn & Peschke, 1988

Figs 57–62, Tables 1,10

BM (NH) Reg. No. 1990.4.26.2.

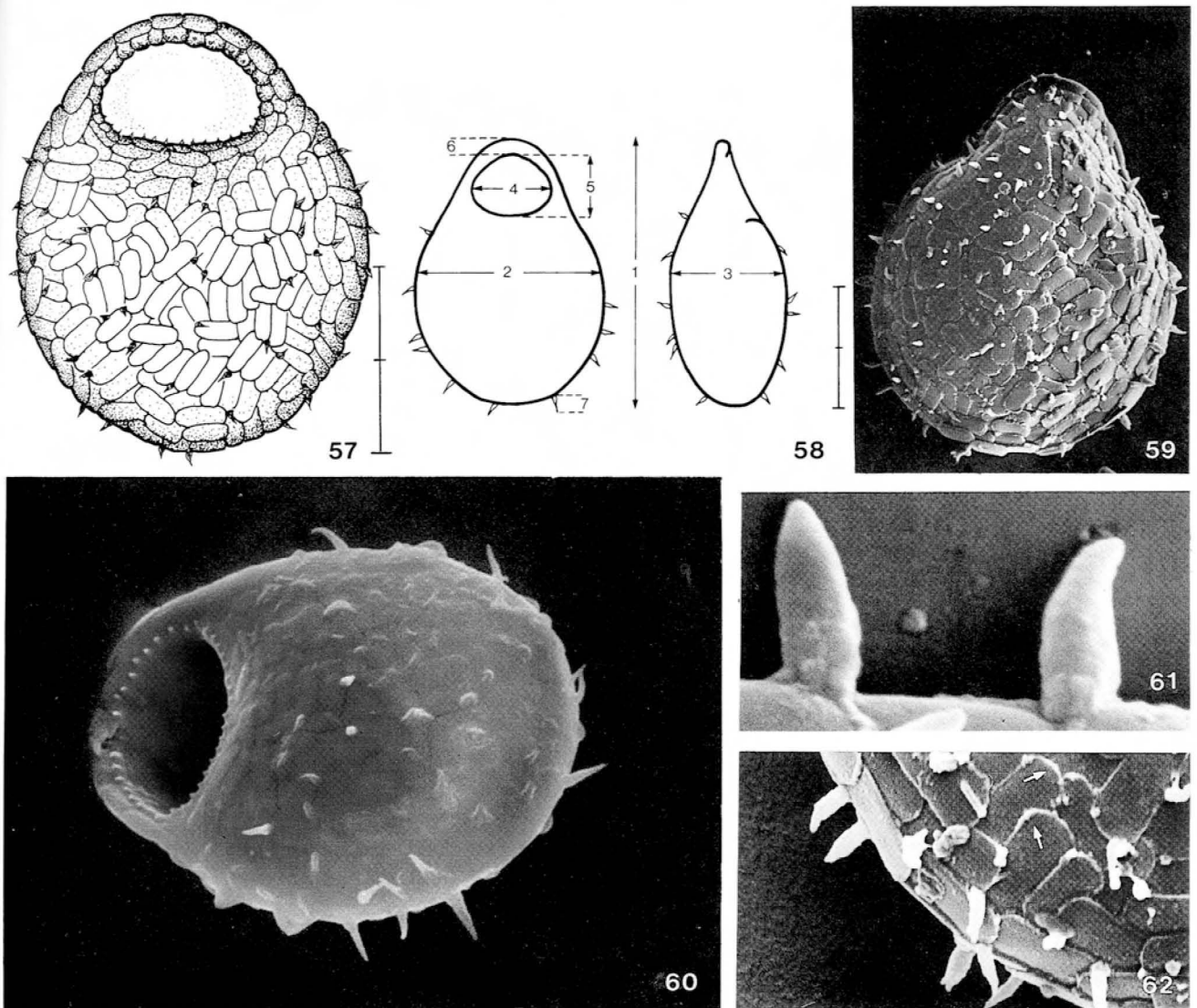
Shell colourless, ovoid, flattened, composed of irregularly arranged elliptic shell platelets (Fig. 57). Numerous about 3 μm long, siliceous, 'flame-like' spines projecting from junctions of idiosomes over entire shell except in apertural region (Figs 60,61). Organic cement plentiful, can be seen as small border surrounding each platelet (Fig. 62). Separation from the very similar *C. dubium* var. *spicatum* by means of the spines, which are longer, in 1 single row and consist of chitin in *C. dubium* var. *spicatum*.

Table 10. Morphometric characterization of *Corythion asperulum*. All measurements in μm .

Character	\bar{x}	M	SD	SE	CV	Min	Max	n
(1)	44.7	45.0	3.9	1.03	8.7	32	48	14
(2)	32.7	32.0	3.3	0.92	10.1	23	36	13
(3)	18.9	19.0	3.0	0.87	16.0	13	22	12
(4)	14.0	14.0	2.3	0.63	16.2	8	16	13
(5)	10.6	10.0	1.9	0.51	17.4	6	13	13
(6)	3.2	3.0	0.9	0.24	27.3	2	5	13
(7)	3.0	3.0	0.7	0.19	22.7	2	4	13

Table 11. Morphometric characterization of *Euglyphella compressa*. All measurements in μm .

Character	\bar{x}	M	SD	SE	CV	Min	Max	n
(1)	87.4	88.5	10.8	2.42	12.4	65	115	20
(2)	61.2	61.0	7.0	1.56	11.4	50	76	20
(3)	32.4	33.0	2.6	0.97	7.9	29	35	7
(4)	24.2	24.0	3.4	0.76	14.1	18	32	20
(5)	14.6	14.0	2.8	1.07	19.4	10	19	7
(6)	8.0	8.0	0.9	0.23	11.8	6.5	10	16
(7)	22.1	22.0	3.3	0.78	15.0	16	29	18
(8)	8.1	8.0	1.5	0.36	18.3	6	11	17
(9)	4.6	4.0	1.2	0.29	25.6	3	7	17



Figs 57–62 *Corythion asperulum*, light microscopic (Fig. 57) and SEM-aspects (Figs 59–62) and ideal individual (Fig. 58). 57 Ventral view. 58 Ventral and lateral view. 59,60 Dorsal and ventral view, $\times 1200$, $\times 1700$. 61 Spines, $\times 12300$. 62 Detail of surface, $\times 3200$. Note organic cement surrounding platelets (arrows). Scale bar divisions 10 μm .

Shell measurements show rather high variability; only parameter (1) has a CV less than 10% (Table 10). The biometric data of Schönborn & Peschke (1988) correspond almost perfectly to our own, despite the extreme geographic distance. Only character (3) shows a slightly higher variability in our population. Schönborn & Peschke (1988) did not mention the organic cement surrounding the platelets (Fig. 62).

As far as we know, this is the the first record since the original description, and especially remarkable, being from Australia!

***Euglypha compressa* Carter, 1864**

Figs 63–68, Tables 1,11

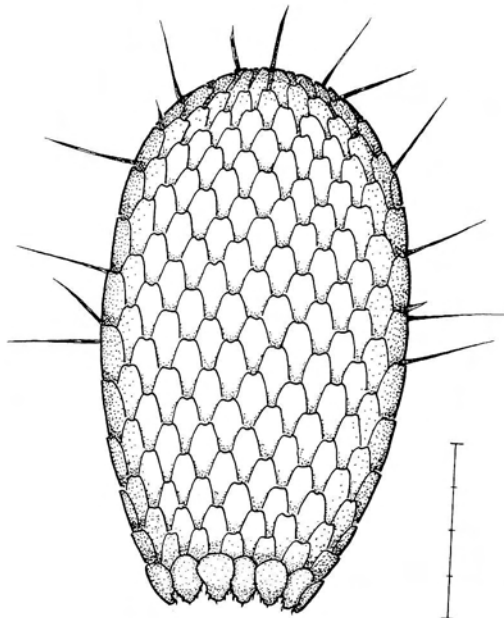
BM (NH) Reg. No. 1990.4.26.1

Shell colourless, obovoid, compressed 2:1, composed of about 300 platelets (often with notched narrow side; Fig. 68).

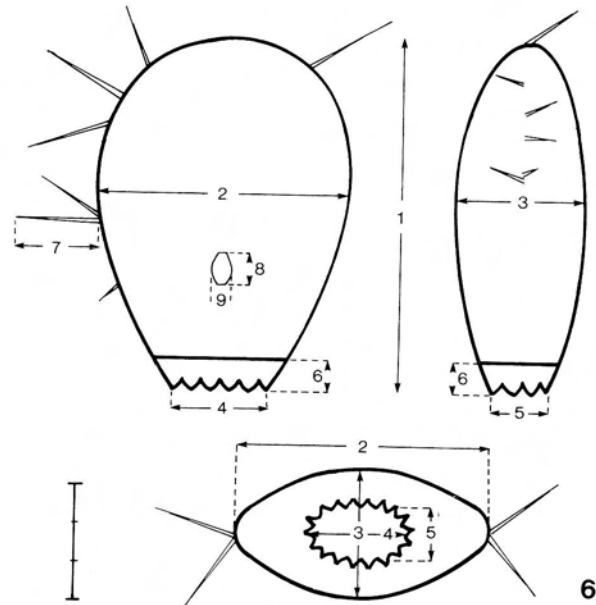
Several 16–19 μm long spines projecting singly from junctions of shell platelets close to lateral margins (Fig. 66). Aperture elliptic, about 15 apertural platelets. Platelets thickened at denticulate margins, carrying 1 large median tooth. Presumably always 3 pairs of lateral teeth, of which only 2 are easy to see; third is bent inward at right-angles to apertural opening, very small and thus difficult to recognize (Fig. 67).

Shell measurements moderately varying (Table 11), corresponding well with those of Wailes & Penard (1911), Cash et al. (1915) and Ogden & Hedley (1980). The values of Carter (1864) are slightly higher, those of Ogden (1981) lower (61–75 μm length; $n = 31$).

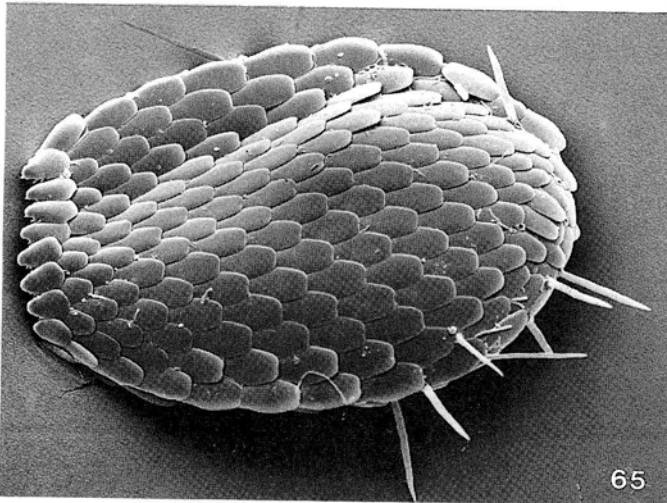
The peculiar notching of the idiosomes, which give the platelets a hexagonal appearance (Penard, 1902; Cash et al., 1915) is also evident in the scanning electron micrographs of Ogden & Hedley (1980), Ogden (1981) and Rauenbusch (1987, for *E. compressa* var. *glabra*). The drawings in Cash et al. (1915) show 5 different types of spines. Ogden (1981) also emphasizes that 2 types exist within this species. The spines of



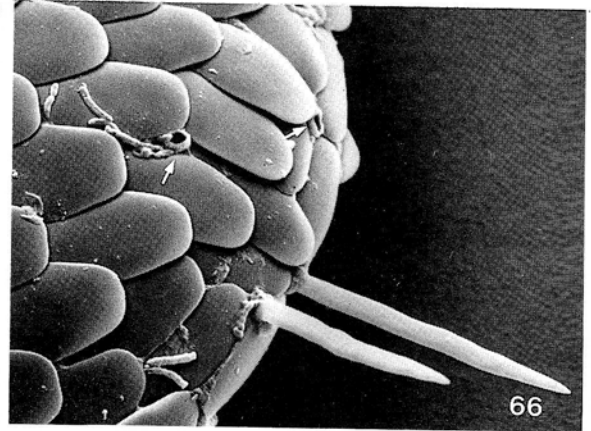
63



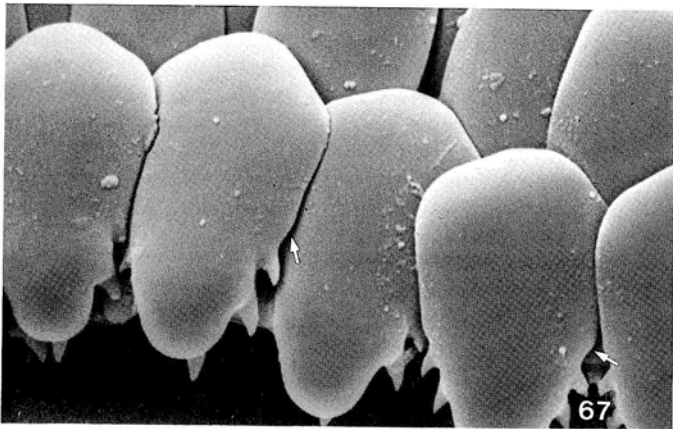
64



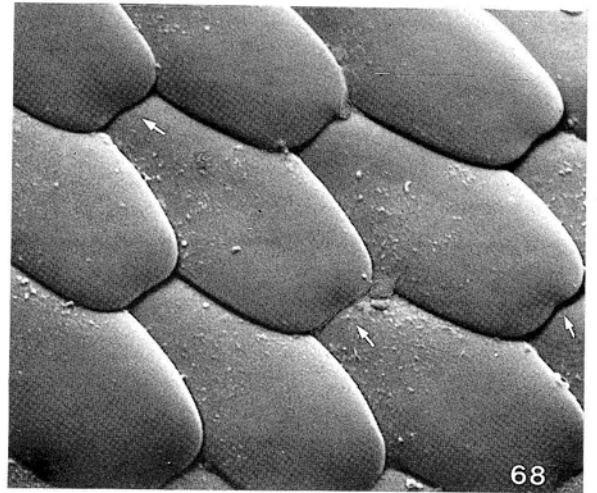
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66

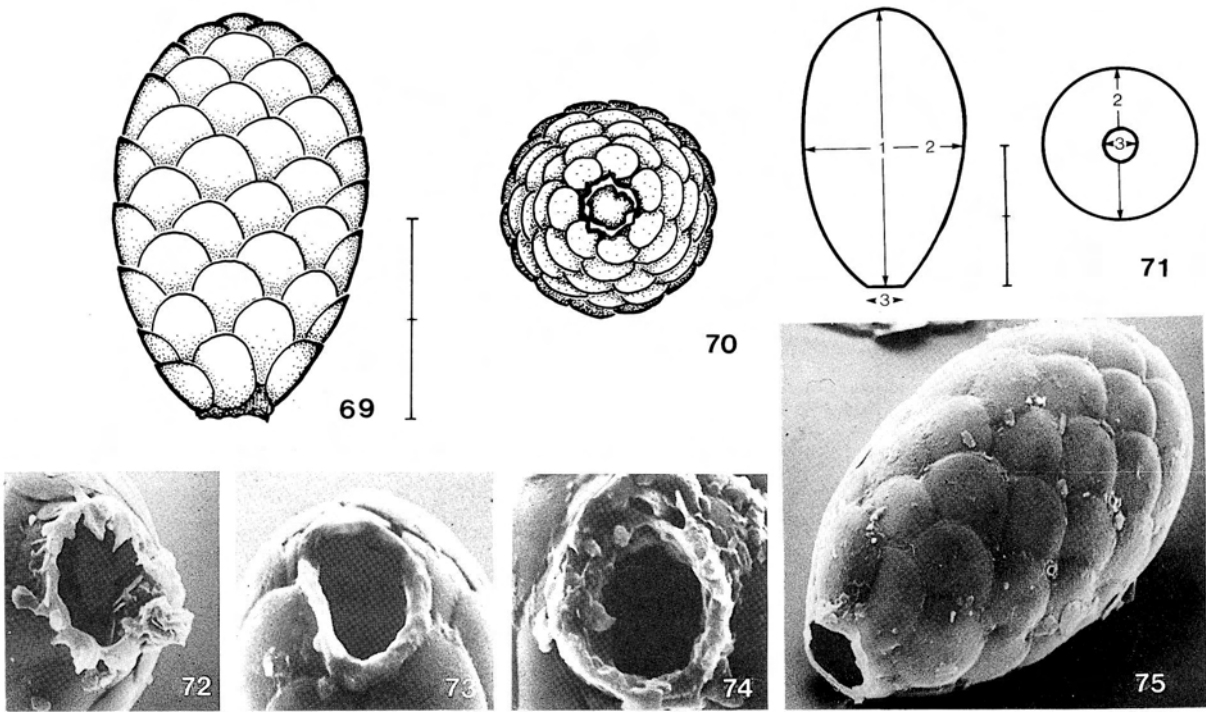


67



68

Figs 63–68 *Euglypha compressa*, light microscopic (Fig. 63) and SEM-aspects (Figs 65–68) and ideal individual (Fig. 64). **63** Broad lateral view. **64** Broad lateral, narrow lateral and ventral view. **65** Broad lateral view, $\times 800$. **66** Detail of surface showing spines projecting from junctions of platelets, $\times 2500$. Note points where spines are lost (arrows). **67** Apertural plates, $\times 5800$. Third pair of teeth are hardly recognizable (arrows). **68** Shell plates, $\times 4000$. Note notching of platelets (arrows). Scale bar divisions 10 μm .



Figs 69–75 *Tracheleuglypha dentata*, light microscopic (Figs 69, 70) and SEM-aspects (Figs 72–75) and ideal individual (Fig. 71). 69–71 Lateral and ventral views. 72–74 Apertures with differently shaped collars, $\times 3800$, $\times 3900$, $\times 4200$. 75 Ventro-lateral view of specimen without distinct collar, $\times 1500$. Scale bar divisions $10\mu\text{m}$.

our population represent the type photographed in Pl. 78 of Ogden & Hedley (1980). Presumably such populations should be separated at species level.

Tracheleuglypha dentata (Penard, 1890) Deflandre, 1928

Figs 69–75, Tables 1, 12

BM (NH) Reg. No. 1990.4.26.3

Shell colourless, obovoid, circular in transverse section, composed of about 100 circular, regularly overlapping platelets, usually about $7\mu\text{m}$ in diameter (often smaller in apertural region). Circular aperture terminal, usually, but not always, surrounded by chitinous collar (Figs 72–75).

Coefficients of variation are between 11.3 and 17.5%. Character (3) and diameter of shell platelets show the greatest variability (Table 12). Our measurements correlate well with those of Penard (1890, 1902), Cash et al. (1915), Thomas & Gauthier-Lièvre (1959) and Rauenbusch (1987), whereas the population of Ogden & Hedley (1980) is slightly larger. A comparison of our values with the average values (1 free-living and 3 cultivated populations combined) of Ogden & Coûteaux (1987) shows a high conformity, even in standard deviations. The measurements for *T. acolla*, given by Bonnet & Thomas (1955), also agree with ours.

As already mentioned, specimens of our population may or may not have a collar. Traditionally, individuals without collar are considered as a separate species, *T. acolla* (Bonnet & Thomas, 1955). The transitions between individuals with and without collar are manifold and have indeed been documented by numerous authors using scanning electron microscopy. Thus, Fig. 6 in Ogden & Coûteaux (1987), Pl. 34 Fig. 4

in Rauenbusch (1987) or Pl. 90 Fig. B in Ogden & Hedley (1980), which are described as *T. dentata*, correspond with the scanning electron micrographs of *T. acolla* in Bonnet (1975), Grospletsch (1982) and Chardez & Rassel (1985). Ogden & Coûteaux (1987, 1988), however, suggest that the collar serves in holding parent and daughter cells together during division, and may be absent, especially in empty shells taken from field samples (presumably by natural causes such as predation or influence of bacteria).

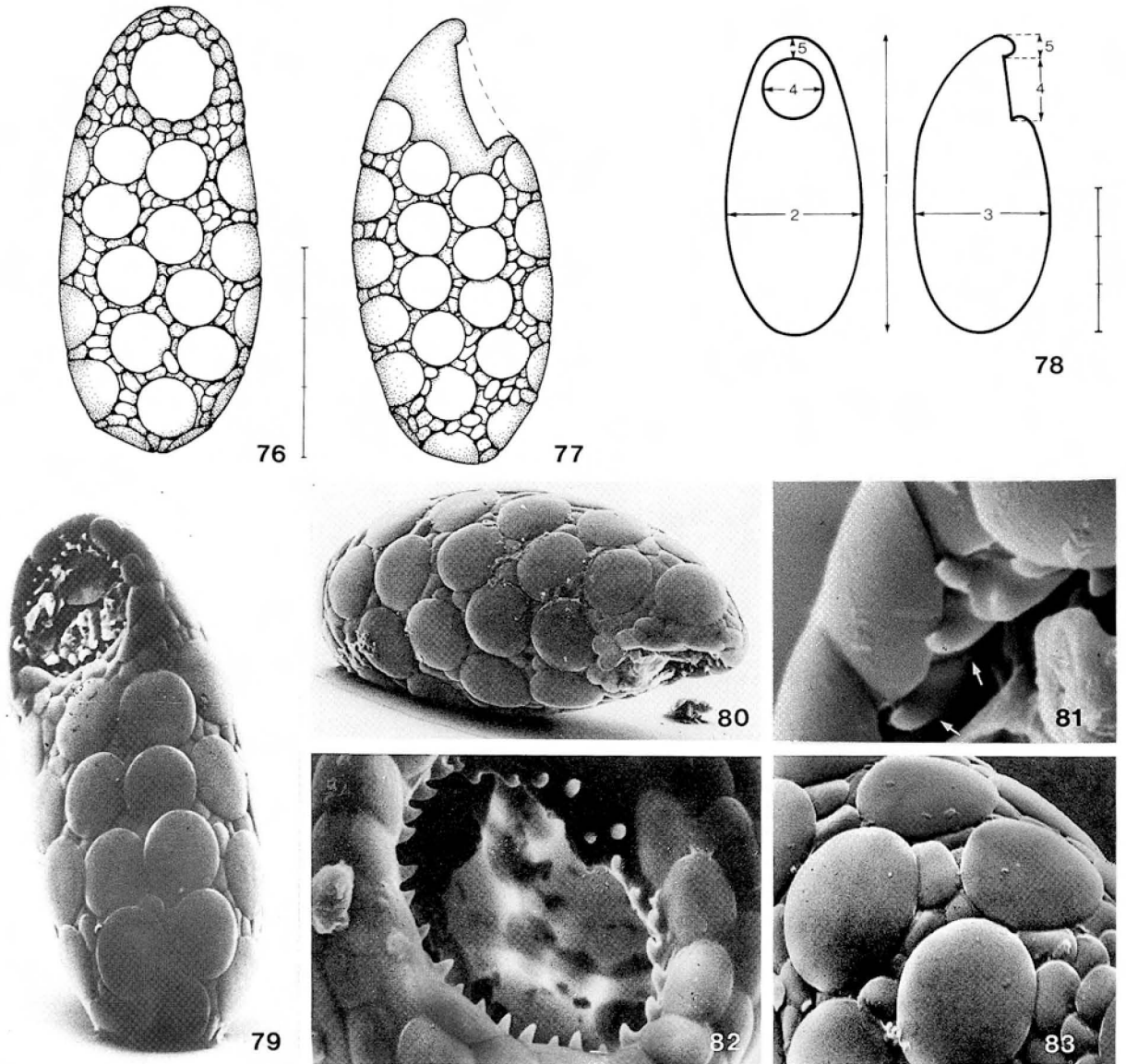
The larger shell platelets of *T. acolla* are considered an additional criterium in separating it from *T. dentata* (Bonnet & Thomas, 1955). However, Chardez (1960) found 4 different types of platelets in various populations of *T. acolla*. Our population matches the type with large (about $9\mu\text{m}$) circular platelets (Fig. 75). Regarding the drawings of Bonnet & Thomas (1960a), which unfortunately do not give measurements for the diameters of platelets, it is evident that the platelets of their species designated as *T. acolla* have a maximum diameter of $5\mu\text{m}$. This is even smaller than in our population. These data strongly suggest synonymy of *T. dentata* and *T. acolla* as already indicated by Ogden & Coûteaux (1987).

Trinema enchelys (Ehrenberg, 1838) Leidy, 1878

Figs 76–83, Tables 1, 13

BM (NH) Reg. No. 1990.4.26.4

Shell colourless, elliptic, almost circular in transverse section, composed of about 60 circular, scarcely overlapping large platelets. Many smaller, different sized platelets fill space between large ones (Fig. 83). Aperture circular, invaginated, surrounded by 2 rows of small idiosomes and about 30



Figs 76–83 *Trinema enchelys*, light microscopic (Figs 76,77) and SEM-aspects (Figs 79–83) and ideal individual (Fig. 78). **76–78** Ventral and lateral views. **79,80** Ventral and lateral view, $\times 1400$, $\times 1000$. **81** Apertural platelets (arrows), $\times 6500$. **82** Aperture, $\times 3500$. **83** Detail of surface, $\times 2500$. Scale bar divisions 10 μm .

Table 12. Morphometric characterization of *Tracheleuglypha dentata*. All measurements in μm .

Character	\bar{x}	M	SD	SE	CV	Min	Max	n
(1)	41.1	40.0	4.7	0.92	11.3	35	51	26
(2)	23.2	22.0	2.8	0.55	12.0	19	29	26
(3)	6.2	6.0	1.0	0.21	16.5	5	8	26
Platelets, diameter	6.7	8.0	1.2	0.23	17.5	5	9	25

apertural platelets, each having 1 median tooth (Figs 81,82).

Coefficients of variation of characters (1)–(3) are less than

Table 13. Morphometric characterization of *Trinema enchelys*. All measurements in μm .

Character	\bar{x}	M	SD	SE	CV	Min	Max	n
(1)	64.3	63.0	5.7	1.51	8.8	58	74	14
(2)	27.9	28.5	2.8	0.74	9.9	23	32	14
(3)	28.5	28.0	2.6	0.71	9.0	25	32	13
(4)	12.3	13.0	1.4	0.37	11.3	10	15	14
(5)	4.9	5.0	0.8	0.21	15.9	4	6	14
Great platelets, diameter	8.6	8.5	1.3	0.36	15.7	7	11	14

10%, others have greater variability (Table 13). The populations investigated by Lüftenegger et al. (1988a) are considerably smaller (< 50 µm), but the coefficients of variation—especially those of the (PII)—agree quite well with the new data (Table 13). The high interpopulation variability of *T. enchelys* (Chardez, 1956) is evident from data in the literature, ranging all the way from 40 µm to 140 µm (Hoogenraad & De Groot, 1940; Rauenbusch, 1987). However, its usual size is 50–60 µm, which agrees well with our own data and with those of Ogden & Hedley (1980).

Shell shape and shape and arrangement of platelets are very similar in all populations investigated with the scanning electron microscope (Ogden & Hedley, 1980; Rauenbusch, 1987; Figs 79–83).

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