



## Ultrastructure of the lorica of species (Euglenophyta) from New Jersey, USA

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With 107 figures and 1 table

**Abstract:** A floristic and ultrastructural study on *Trachelomonas* was made in the piedmont region of central New Jersey, USA, where a large number of euglenoid taxa are contained in several freshwater bodies. Abundant and unusual loricated species were found during the observations of samples from these ponds. From the forty-seven taxa determined, eighteen are reported for the first time in the USA. Detailed ultrastructure examination with scanning electron microscopy (SEM) yielded interesting results. Among the taxa described in this work *T. compacta* var. *parvicollis* is proposed as new variety, and four are considered *affinis* to described taxa, *T. bacillifera* var. *collifera*, *T. granulosa*, *T. raciborskii* var. *incerta* and *T. verrucosa* var. *verrucosa* fo. *irregularis*, respectively. Twelve taxa are examined and documented, for the first time ever, with original SEM micrographs.

**Key words:** Euglenales, Euglenophyceae, freshwater algae, New Jersey (USA), taxonomy, *Trachelomonas*, ultrastructure

### Introduction

The genus *Trachelomonas* was described by EHRENBURG (1833), but its complete taxonomical system was published several years later by DEFLANDRE (1926). He described more than 200 species using size, shape, and envelope ornamentation for classification. Since the early days a great controversy exists about what type of characters may be used in this genus taxonomy. At first the specimens were only studied by light microscopy by researchers such as SWIRENKO (1914), PLAYFAIR (1915), BALECH (1944), CONRAD & VAN MEEL (1952), PRINGSHEIM (1953), HUBER-PESTALOZZI (1955), SAFONOVA (1965), POPOVA (1966), YACUBSON & BRAVO (1982-83), STARMACH (1983), TELL & ZALOCAR DE DOMITROVIC (1985), TELL & CONFORTI (1986), PHILLIPOSE (1988), and MENEZES (1991).

Later, great advances in the genus ultrastructure were reached with the increased use of scanning and transmission electron microscopy (LEEDALE 1975, TELL & COUTÉ 1980, COUTÉ & ILTIS 1981, COUTÉ & THÉRÉZIEN 1985, 1994, CONFORTI & TELL 1985, RINO & PEREIRA 1989-90, CONFORTI 1993, 1999, CONFORTI et al. 1994, CONFORTI & JOO 1994, CONFORTI & NUDELMAN 1994, WOŁOWSKI 1998, CONFORTI & PEREZ 2000, CONFORTI & RUIZ 2000, 2001, WOŁOWSKI & HINDÁK 2004, 2005, BROSNAN et al. 2005, WOŁOWSKI & GRABOWSKA 2007, WOŁOWSKI & WALNE 2007, DA et al. 2009).

In recent years, several biochemical, molecular and phylogenetic studies have been done which include *Trachelomonas* (BROSNAN et al. 2003, MARIN et al. 2003, NUDELMAN et al. 2003, PEREIRA & AZEITEIRO 2003, WANG et al. 2003, MILANOWSKI et al. 2006, TRIEMER et al. 2006, CIUGULEA et al. 2008, KIM & SHIN 2008).

In spite of all these studies, it is not yet clear which characters are most informative in determining the taxonomy of this genus. In most of the taxonomic studies from different places around the world, the greater utility of the lorica's features has been emphasized without taking into account their variability due to environmental conditions and developmental stage, when compared with protoplasmic structures and molecular data (SINGH 1956, CONFORTI & RUIZ 2000, BROSNAN et al. 2005).

Numerous reports of this genus from North America can be found in different limnological papers, namely in the studies by PALMER (1902, 1905), PRESCOTT (1962), and DILLARD (2000). In addition, works have been published, which include SEM data such as CONFORTI & JOO (1994) and WOŁOWSKI & WALNE (2007).

The piedmont region of central New Jersey, USA, is home to several freshwater bodies with favourable conditions for the growth of euglenoid taxa. Abundant and some unusual loricate species were found during the analysis of samples from these ponds. Forty-seven taxa of *Trachelomonas* were determined. Their ultrastructure was examined in detail with scanning electron microscopy (SEM). On the basis of these observations, one new variety is proposed: *T. compacta* var. *parvicollis*. We also examined other species with SEM for the first time. This research increases the knowledge of the ultrastructural features of the loricate euglenoids, and reveals new morphological details that can be used in delineating species.

## Materials and methods

Taxa were collected from small ponds in Piscataway, New Jersey, USA, Lake Nelson (40° 31' 97" N, 74° 34' 49" W), Paddleboat Pond (40° 51' 04" N, 74° 56' 03" W) and Duckweed Pond in the Johnson Park (40° 30' 31" N, 74° 26' 41" W), during June 1999. In table 1, they were named as LN, PP and DP, respectively. The collection sites are retention ponds which changed their environmental conditions dramatically, every time it rained. Similarly, the water temperature changed with the rainfall. Water from field samples was sieved through a 20 µm mesh

plankton net. For taxonomic identifications, unfixed samples were mounted on slides and the coverslips were sealed with melted VALAP (equal parts Vaseline, lanolin and paraffin). They were observed using an Olympus BX50 binocular microscope. The materials fixed with 4 % formaldehyde were studied under SEM. The samples were washed with bidistilled water, filtered through Millipore filters (0.20 µm pore) and air-dried. Filter pieces were attached on stubs to be subsequently coated with gold/palladium. Specimens were examined and photographed by means of a Phillips 505 SEM at the Electron Microscopy Service of CITEFA, Argentina.

Specialized literature for taxa identification was used: DEFLANDRE (1930), BALECH (1944), HUBER-PESTALOZZI (1955), POPOVA (1966), STARMACH (1983), TELL & CONFORTI (1986), DILLAR (2000), and WOLOWSKI & HINDÁK (2005). The list of recorded taxa is presented in the Table I, only those taxa which were new to science and those with unknown ultrastructure are described in detail in the text. Additional comments, on relevant morphological features, distribution characteristics and size are given for some known taxa. The characters used to delimit species and varieties were size and shape of the lorica, pore with or without collar, and type of ornamentation.

## Results

### Genus *Trachelomonas* EHRENBERG 1833

#### *T. verrucosa* STOKES var. *verrucosa* fo. *irregularis* DEFLANDRE Figs 5–7

Lorica spherical, 12–15 µm diam. Apical pore surrounded by a fine annular thickening, sometimes located in a slight depression of the lorica (see fig. 7). The young lorica showed only on the anterior area very little grains (see fig. 5). Widespread. In USA: cited as Infusoria by STOKES (1887).

#### *T. verrucosa* var. *verrucosa* fo. *irregularis* DEFLANDRE aff. Figs 8–9

The studied specimens coincided ultrastructurally with those described as the forma typo. The only difference is a crown of conical spines (0.5–0.7 µm long) disposed around the flagellar pore.

#### *T. rugulosa* STEIN var. *rugulosa* fo. *steinii* DEFLANDRE Figs 10–12

Lorica spherical to ovoid, 12.5–16 µm diam. Apical pore surrounded by a fine annular thickening. Envelope densely ornamented with slightly anastomosing ribs which radiate from the pore (fig. 12) giving the lorica a brain-like surface. Figure 10 corresponds to a young lorica. Europe, Colombia, Korea. In USA: recorded for the first time.

***T. rugulosa* var. *meandrina* CONRAD****Figs 13–14**

Lorica spherical, 15–17  $\mu\text{m}$  diam. Apical pore (2–2.5  $\mu\text{m}$  diam.) surrounded by an annular thickening (0.5  $\mu\text{m}$  wide). Wall strong, ornamented densely by robust anastomosing ribs (0.55–0.8  $\mu\text{m}$  wide) which radiate from the pore (fig. 14) giving the lorica a brain-like surface. This taxon was studied using SEM from Slovakia by WOŁOWSKI & HINDÁK (2004), but in our opinion the specimens shown represented most likely a lorica with an initial stage of mineralization. Europe. In USA: recorded for the first time.

***T. conradi* SKV.****Figs 20–21**

Lorica 18–20  $\mu\text{m}$  long, 17–18  $\mu\text{m}$  diam., broadly ellipsoid to ovoid. Envelope thick, ornamented densely by anastomosing and intricate ribs (0.8–1.2  $\mu\text{m}$  wide) with limited robust vermiform depressions giving to the lorica a particular irregular surface. Europe. In USA: recorded for the first time.

***T. intermedia* DANGEARD****Fig. 24**

Lorica 19–21  $\mu\text{m}$  long, 15–17  $\mu\text{m}$  wide, broadly ellipsoid. The observed specimens presented a thick, slightly papillate envelope among the densely distributed punctuations. Cosmopolitan. In USA: Alabama and Indiana (CONFORTI & JOO 1994), widespread (DILLARD 2000).

***T. compacta* MIDDELH. var. *compacta*****Figs 25–27**

Lorica spherical to broadly ovoid, 17–19  $\mu\text{m}$  long, 18–19  $\mu\text{m}$  diam. Apical pore 1.5–2  $\mu\text{m}$  diam., surrounded by a ring-like thickening. Envelope thick, densely scrobiculate (100–110/100  $\mu\text{m}^2$ ) with one or two punctuations in the bottom (120–135/100  $\mu\text{m}^2$ ). Uncommon. Europe. In USA: Southeast (WOŁOWSKI & WALNE 2007).

***T. compacta* MIDDELH. var. *parvicollis* nov. var.****Figs 28–32**

Diagnosis:

Varietas per collo exiguo, recto, per quam cylindro, incrassato per anulo, typi distinctia est. Lorica 20–23.5  $\mu\text{m}$  longa, 16–20  $\mu\text{m}$  lata.

Holotypus: fig. 28, leg. Richard Triemer. In Padle lacu, regionis New Jersey, USA, 26/VI/99.

This variety presented the same characteristics as the type, the only difference being the apical flagellar pore (2–2.5  $\mu\text{m}$  diam.) surrounded by a short straight collar (1.5–2 x 4.0–4.5  $\mu\text{m}$ ) with a ring-like thickening at the top. Lorica 20.0–23.5  $\mu\text{m}$  long, 16–20  $\mu\text{m}$  wide.

***T. sculpta* BALECH****Figs 33–34**

This species has already been analysed with SEM by CONFORTI & TELL (1986) and CONFORTI (1993, 1999), but in these samples, besides the mature loricae, we found others with an initial stage of mineralization. The crests, which divide one depression from the other, are conformed by fine granulate material. Argentina, Brazil. In USA: Southeast (WOLOWSKI & WALNE 2007).

***T. spirillifera* SCHKOR.****Figs 35–40**

Lorica 14–16  $\mu\text{m}$  long, 11–14  $\mu\text{m}$  wide, subspherical to ovoid. The studied specimens showed the same characters than those studied by CONFORTI & RUIZ (2000). Uncommon. Europe, Korea. In USA: recorded for the first time.

***T. guttata* MIDDELH.****Figs 41–43**

Lorica 20.5–24.5  $\mu\text{m}$  long, 18.5–22  $\mu\text{m}$  wide, ovoid. Flagellar pore surrounded by an annular thickening (2–2.5  $\mu\text{m}$  diam.). Envelope robust, strongly scrobiculate with one to three punctuations at the bottom. In some loricae, we could observe sparsely distributed papillae (fig. 41). Some specimens were more ornamented by a high mineralization (figs 42–43), but we concluded that they belonged to this taxon. Uncommon. Europe. In USA: recorded for the first time.

***T. granulosa* PLAYF. aff.****Figs 44–52**

Lorica 19–22  $\mu\text{m}$  long, 15–17  $\mu\text{m}$  wide, ovoid. Apical pore (2.5–3  $\mu\text{m}$  diam.) with an annular thickening, surrounded by a crown of blunt spines (2–2.5  $\mu\text{m}$  long) or a very short denticulate neck in the mature lorica (fig. 52). Envelope thick, scrobiculate with one punctuation in the bottom of the depression (130–140/100  $\mu\text{m}^2$ ), surface very irregular, granulate. In the young loricae (figs 44, 45), we could observe conical spines located on the granulation (40–50/ $\mu\text{m}^2$ ), but in the more mature ones (figs 46–52) the spines look fused with the granulations, forming conical robust elevations (55–70/100  $\mu\text{m}^2$ ), and the number of punctuations diminished (110–120/100  $\mu\text{m}^2$ ). By light microscopy, the lorica was very thick, red brown, and the cell shows chloroplasts with diplopyrenoids.

*T. granulosa* was deficiently defined by PLAYFAIR (1915), and then was described by DEFLANDRE (1926) as *species inquirenda*. We consider these specimens *affinis* to this taxon only by the type of lorica ornamentation and dimensions. This taxon always resembles *T. xenosoma* MIDDELH., but it differs from the type by chloroplast number and lorica size.

***T. oviformis* DREZ. var. *oviformis*****Figs 57–58**

Lorica 27–29  $\mu\text{m}$  long, 23–24  $\mu\text{m}$  wide, ovoid, with the anterior end narrower than the posterior. Flagellar pore 3  $\mu\text{m}$  diam., surrounded by short conical spines (0.8–1.5  $\mu\text{m}$ ). Wall densely punctuate, ornate with very short conical spines (0.1–1  $\mu\text{m}$ ), irregularly distributed on the total surface (75–90/100  $\mu\text{m}^2$ ). Uncommon. Europe, this is the first record in USA.

***T. oviformis* var. *duplex* CONF.****Fig. 59**

Lorica 27–30  $\mu\text{m}$  long, 22.5–24  $\mu\text{m}$  wide. This variety presented the same characteristics as the typical species, the only difference being the very short conical spines (0.1–1.5  $\mu\text{m}$ ), located mainly around the ends. Some are also scattered on the middle surface. The studied specimens showed the same ultrastructure as those studied by CONFORTI (1999). This taxon was originally reported from Argentina. In USA: recorded for the first time.

***T. armata* var. *setosa* DREZ.****Fig. 62**

Lorica 38–39  $\mu\text{m}$  long, 29.5–31  $\mu\text{m}$  diam., with the typical shape. Envelope densely punctuated, with short conical spines (0.5–1.5  $\mu\text{m}$  long), sparsely distributed on the surface. Posterior end ornate by a crown of longer spines (2.5–4  $\mu\text{m}$  long). The photo probably represented a young lorica. Widespread. Argentina. In USA: recorded for the first time.

***T. hispida* var. *coronata* LEMM.****Figs 68–70**

Lorica 24–30  $\mu\text{m}$  long, 18–24  $\mu\text{m}$  wide, broadly ovoid. This variety only differs from the type by the presence of a short collar (1.5–2.5 x 4.5–6  $\mu\text{m}$ ) with a crown of robust conical spines (1.5–2.5  $\mu\text{m}$  long) on the distal end. In the young loricae (fig. 68), the spines are sparsely located on the surface (15–20/100  $\mu\text{m}^2$ ), but in the more mature ones (figs 69–70), they are densely distributed (40–50/100  $\mu\text{m}^2$ ) and increase in number around the collar. Widespread. In USA: Southeast (WOŁOWSKI & WALNE 2007).

***T. sydneyensis* var. *minima* PLAYF.****Figs 71–72**

Lorica 24–25.5  $\mu\text{m}$  long, 18–19.5  $\mu\text{m}$  wide, broadly ovoid. Pore (3–3.5  $\mu\text{m}$  diam.) surrounded by a crown of divergent conical spines (1.5–2  $\mu\text{m}$  long). Widespread. It was reported as present in Southeast USA (WOŁOWSKI & WALNE 2007), but we concluded, on the basis of its size, lorica shape and type of collar, that it could be *T. sydneyensis* var. *sydneyensis*. If this is correct, it is the first record for USA.

***T. selecta* var. *megaspina* CONF.****Figs 73–74**

Lorica 22–24  $\mu\text{m}$  long, 18–20  $\mu\text{m}$  wide, broadly ellipsoid with posterior end narrower than the anterior. Flagellar pore surrounded by conical spines (1–1.5  $\mu\text{m}$  long). Wall densely punctuate, ornamented with fine conical spines irregularly distributed on the surface, longer than the type (1.8–2  $\mu\text{m}$  long) and very small papillae closely distributed (fig. 73). Brazil. In USA: recorded for the first time.

***T. raciborskii* var. *incerta* DREZ. aff.****Figs 76–83**

Lorica 22–29  $\mu\text{m}$  long, 18–19.5  $\mu\text{m}$  wide, broadly ellipsoid. Apical pore without collar. Wall strong, densely scrobiculate (65–75/100  $\mu\text{m}^2$ ), with one or two punctuations in the bottom, ornate with robust short conical spines (1–1.5  $\mu\text{m}$  long) disposed around both ends, others had a scattered distribution on the rest of the surface. Besides this, very small, irregularly distributed papillae could be observed. When the mineralization increases the spines are more robust and the depressions decrease their diameter (see figs 77–80). The specimen of the figs 81–82 probably represents a very mature lorica, because most of the punctuations and scrobiculations are totally covered. In USA: recorded for the first time.

We considered these specimens *affinis* to this variety because in the original description, the author stated “wall punctuate or smooth”. On the other hand, BALECH (1944) described *T. raciborskii* cf. var. *incerta* which coincides with our specimens.

***T. bacillifera* var. *collifera* HUB.-PEST.****Fig. 91**

Lorica 29–31  $\mu\text{m}$  long, 20–21  $\mu\text{m}$  diam., ovoid to broadly ellipsoid. This variety differs from the type by a short collar (2–2.5 x 5–5.5  $\mu\text{m}$ ) surrounding the pore, with conical spines at the free end. Envelope punctuated (60–70/100  $\mu\text{m}^2$ ), ornate with rod-like obtuse spines (0.5–1.7  $\mu\text{m}$  long), very scattered and irregularly distributed (3–20/100  $\mu\text{m}^2$ ). Uncommon. Italy, Brazil. In USA: recorded for the first time.

***T. bacillifera* var. *collifera* HUB.-PEST. aff.****Figs 92–97**

Lorica 24–28  $\mu\text{m}$  long, 17–20  $\mu\text{m}$  diam., ovoid to broadly ellipsoid. These specimens were considered *affinis* with this taxon because the loricae coincided in shape and ornamentation, but they differed by the presence of a cylindrical collar, with longer dimensions (3.5–5.5  $\mu\text{m}$ ), oblique or sometimes curved, with conical spines (1.5–2.5  $\mu\text{m}$  long), irregularly distributed at the tip. All the loricae examined by light microscopy were very dark brown, which made cell observation impossible.

***T. playfairi* DEFLANDRE****Fig. 98**

Lorica 20–25  $\mu\text{m}$  long, 18–20  $\mu\text{m}$  wide, ellipsoid to ovoid. Flagellar pore surrounded by a curved cylindrical neck (2–4 x 3–3.5  $\mu\text{m}$ ), smooth to slightly irregular at the tip. Wall finely punctuated, sparsely distributed (30–40/100  $\mu\text{m}^2$ ), not visible by light microscopy. Widespread. In USA: Kentucky and Louisiana (DILLARD 2000).

***T. lefevrei* DEFLANDRE****Fig. 99**

Lorica 23.5–25  $\mu\text{m}$  long, 20–22  $\mu\text{m}$  wide, broadly ellipsoid. Apical pore surrounded by a short collar (1–1.5  $\mu\text{m}$ ) with irregular distal end. Envelope finely punctuated (115–130/100  $\mu\text{m}^2$ ). Europa, Argentina. In USA: recorded for the first time.

***T. planctonica* var. *planctonica* fo. *ornata* (SKV.) POPOVA****Figs 103–105**

Lorica 21.5–25  $\mu\text{m}$  long, 18–20  $\mu\text{m}$  wide, ovoid. This variety differs from the type by the conical spines irregularly and sparsely distributed on the envelope surface (12–15/100  $\mu\text{m}^2$ ). Collar (2–3 x 5–6  $\mu\text{m}$ ), with distal end slightly irregular to ornate with conical spines. Asia, Europe. In USA: recorded for the first time.

**Concluding remarks**

Among the 47 taxa described in this paper, one is considered as a new variety: *T. compacta* var. *parvicollis*, and four are considered *affinis* to already described taxa, *T. bacillifera* var. *collifera*, *T. granulosa*, *T. raciborskii* var. *incerta* and *T. verrucosa* var. *verrucosa* fo. *irregularis*, respectively. For the USA, eighteen taxa are added to previous records: *T. armata* var. *setosa*, *T. bacillifera* var. *collifera*, *T. bacillifera* var. *collifera* aff., *T. conradi*, *T. granulosa* aff., *T. guttata*, *T. lefevrei*, *T. oviformis* var. *oviformis*, *T. oviformis* var. *duplex*, *T. planctonica* var. *oblonga*, *T. planctonica* var. *planctonica* fo. *ornata*, *T. raciborskii* var. *incerta* aff., *T. rugulosa* var. *rugulosa* fo. *steinii*, *T. rugulosa* var. *meandrina*, *T. selecta* var. *megaspina*, *T. spirillifera*, *T. sydneyensis* var. *minima*, and *T. verrucosa* var. *verrucosa* fo. *irregularis* aff.

Twelve taxa were examined and photographed by SEM for the first time ever: *T. bacillifera* var. *collifera*, *T. bacillifera* var. *collifera* aff., *T. compacta* var. *compacta*, *T. compacta* var. *parvicollis*, *T. conradi*, *T. granulosa* aff., *T. guttata*, *T. oviformis* var. *oviformis*, *T. planctonica* var. *planctonica* fo. *ornata*, *T. raciborskii* var. *incerta*, *T. selecta* var. *megaspina*, and *T. verrucosa* var. *verrucosa* fo. *irregularis* aff. The remaining ones had been studied already by this method, but in some taxa some differences were observed which were specified in the respective description.

Most of the described taxa have a widespread or cosmopolitan distribution, while others were only registered in particular areas. It is important to emphasize



that in our material from the Northeast area, we found 26 taxa of the already cited ones for the Southeast (CONFORTI & JOO 1994, DILLARD 2000, WOŁOWSKI & WALNE 2007). Some species had only been recorded in Europe, e.g. *T. conradi* (Belgium and France), *T. compacta* and *T. guttata* (The Netherlands), *T. oviformis* var. *oviformis* (Poland), *T. rugulosa* var. *meandrina* (Germany and Slovakia). Others had only been described for South America, e.g. *T. oviformis* var. *duplex* (Argentina), *T. selecta* var. *megaspina* (Argentina and Brazil). *T. bacillifera* var. *minima* fo. *sparsispina*, *T. planctonica* var. *planctonica* fo. *ornata*, and *T. spirillifera*, although rarely reported, have been found only in Europe and Asia.

Of all the species registered in this study, the great majority corresponds to taxa present in temperate regions, which is consistent with the finding in WOŁOWSKI & WALNE (2007). Only two taxa, *T. oviformis* var. *duplex* and *T. selecta* var. *megaspina*, are typical of tropical and subtropical zones (CONFORTI 1993, 1999).

With regard to dominant morphotypes in the analysed samples, the lorica's shapes varied from spherical to ovoid, most of them with thick walls. Only a few taxa showed a neck around the flagellar pore, and none presented long collar or cauda. Regarding the types of ornamentation observed, most of the taxa showed punctuations, papillae, granulations, ribs, depressions, and conical or rod-like spines. Only two species presented smooth lorica, while they were better represented in other studied areas (RINO & PEREIRA, 1989–90, DA et al. 2009). We did not observe long spines like those that ornamented the typical species of tropical or subtropical areas (e.g. COUTÉ & ILTIS 1981, COUTÉ & THÉRÉZIEN 1985, CONFORTI 1993, 1999, CONFORTI & NUDELMAN 1994, DA et al. 2009).

Finally, several of the reported taxa have shown different lorica development, which made species determination very difficult. The observations of these samples allow us to suspect that many species included in the bibliography could only be morphological variables of the same taxa. This variability clearly indicates the need to study clonal cultures of the different species in order to understand their morphological plasticity. Further studies and a re-examination of the systematic of this genus are becoming essential.

## Resumen

En este estudio se describen numerosas e interesantes especies de *Trachelomonas* encontradas en muestras colectadas en cuerpos de agua dulce de la región central de New Jersey, USA. Los taxones fueron examinados en detalle con microscopía electrónica de barrido (MEB). Entre ellos *T. compacta* var. *parvicollis* se propone como una nueva variedad, y cuatro son considerados *affinis* a taxones ya descritos, *T. bacillifera* var. *collifera*, *T. granulosa*, *T. raciborskii* var. *incerta* y *T. verrucosa* var. *verrucosa* fo. *irregularis* respectivamente. De los cuarenta y siete taxones descritos, dieciocho se citan por primera vez para USA, doce se examinan y documentan por primera vez con microscopía electrónica de barrido (MEB).

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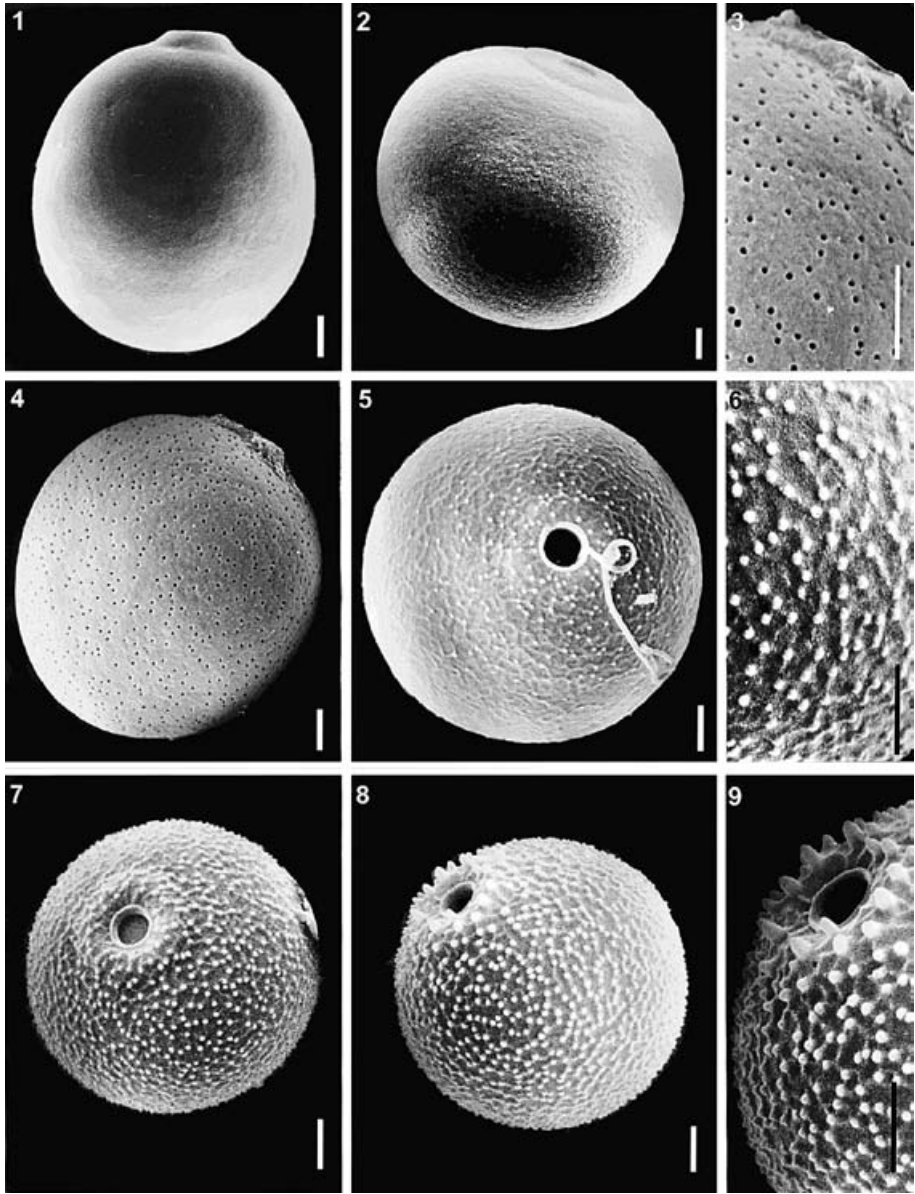
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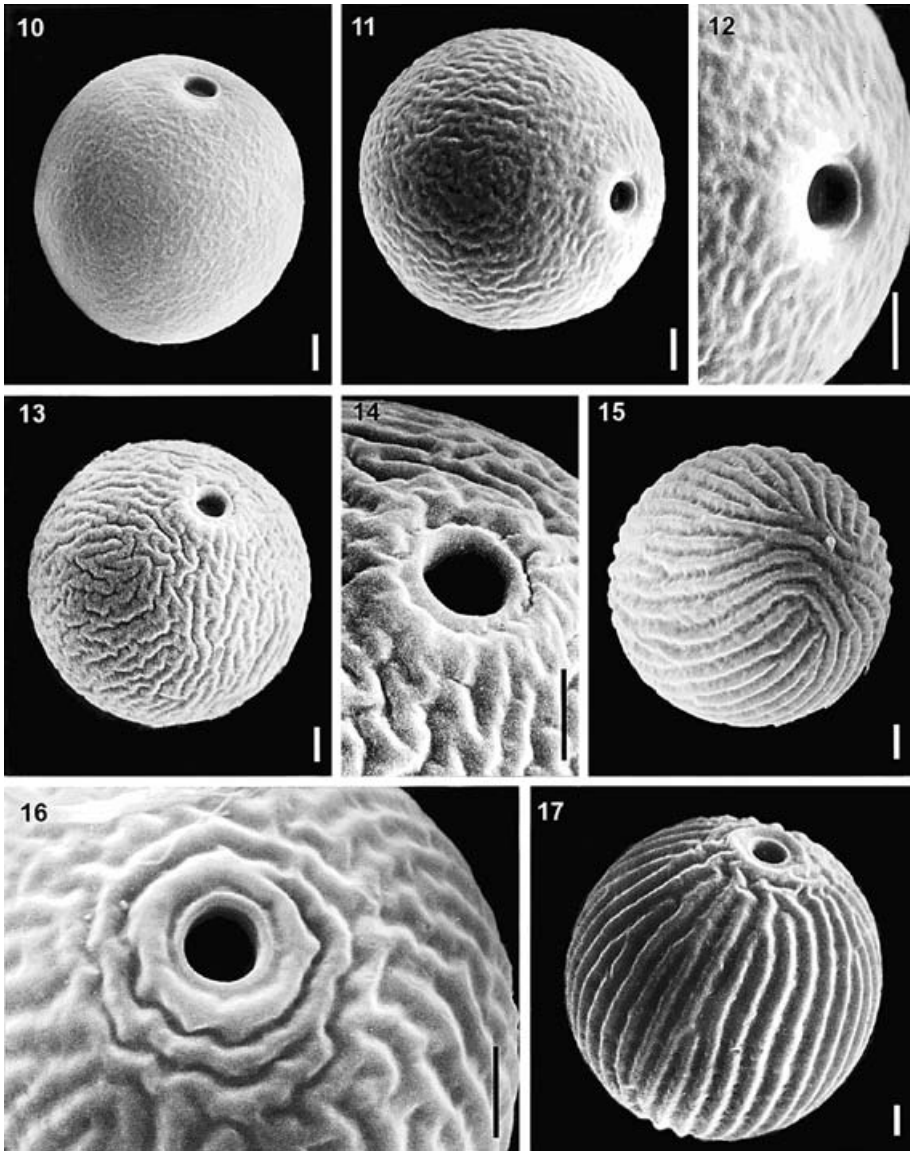
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**Table 1.** *Trachelomonas* (Euglenophyceae) from New Jersey, USA.

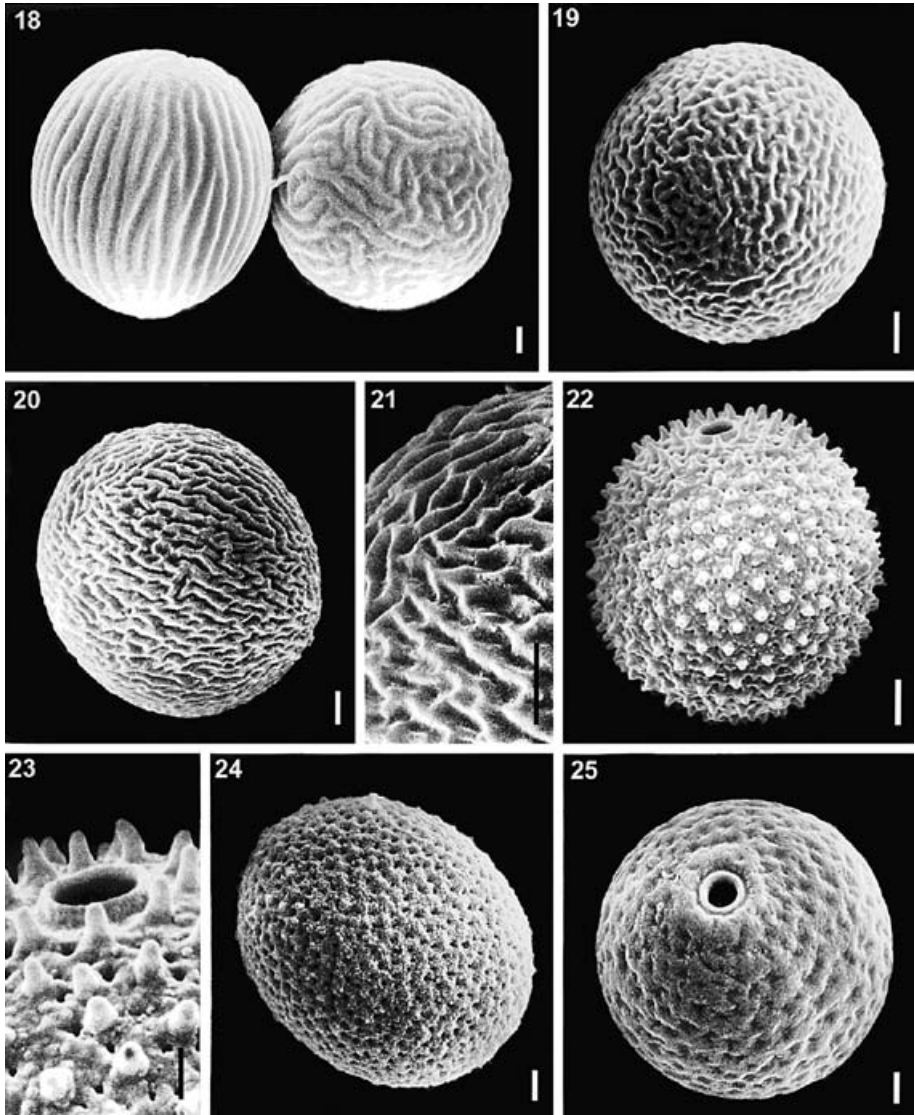
	Taxa	PONDS			FIGS
		DUCK	NELSON	PADLE	
1	<i>T. armata</i> (EHR.) STEIN var. <i>armata</i>			x	60
2	<i>T. armata</i> var. <i>setosa</i> DREZ.			x	62
3	<i>T. armata</i> var. <i>steinii</i> LEMM. emend. DEFL.			x	61
4	<i>T. bacillifera</i> var. <i>collifera</i> HUB.-PEST.			x	91
5	<i>T. bacillifera</i> var. <i>collifera</i> HUB.-PEST. aff.			x	92-97
6	<i>T. bacillifera</i> PLAYF. var. <i>minima</i> fo. <i>minima</i>		x		86-89
7	<i>T. bacillifera</i> var. <i>minima</i> fo. <i>sparsispina</i> DEFL.			x	90
8	<i>T. compacta</i> MIDDELH. var. <i>compacta</i>			x	25-27
9	<i>T. compacta</i> MIDDELH. var. <i>parvicollis</i> nov. var.			x	28-32
10	<i>T. conradi</i> SKV.			x	20-21
11	<i>T. curta</i> DA CUNHA			x	2
12	<i>T. granulosa</i> PLAYF. aff.			x	44-52
13	<i>T. guttata</i> MIDDEL.			x	41-43
14	<i>T. hispida</i> var. <i>coronata</i> LEMM.			x	68-70
15	<i>T. hispida</i> var. <i>crenulatocollis</i> (MASK.) LEMM.			x	66-67
16	<i>T. hispida</i> (PERTY) STEIN emend. DEFL. var. <i>hispida</i>			x	63
17	<i>T. hispida</i> var. <i>minor</i> BOURR.	x	x	x	64-65
18	<i>T. intermedia</i> DANG.			x	24
19	<i>T. kellogii</i> SKV. emend. DEFL. var. <i>kellogii</i>			x	84
20	<i>T. kellogii</i> var. <i>nana</i> BALECH			x	85
21	<i>T. lacustris</i> DREZ. var. <i>lacustris</i>			x	53-54
22	<i>T. lacustris</i> var. <i>ovalis</i> DREZ. emend. DEFL.		x	x	55-56
23	<i>T. lefevrei</i> DEFL.			x	99
24	<i>T. nexilis</i> PALMER			x	19
25	<i>T. oviformis</i> DREZ. var. <i>oviformis</i>	x		x	57-58
26	<i>T. oviformis</i> var. <i>duplex</i> CONF.		x		59
27	<i>T. planctonica</i> var. <i>oblonga</i> DREZ.	x			102
28	<i>T. planctonica</i> SWIR. var. <i>planctonica</i> fo. <i>planctonica</i>			x	100, 101
29	<i>T. planctonica</i> var. <i>planctonica</i> fo. <i>ornata</i> (SKV.) POPOVA			x	103-105
30	<i>T. playfairi</i> DEFL.			x	98
31	<i>T. pusilla</i> var. <i>punctata</i> PLAYF.	x			3-4
32	<i>T. raciborskii</i> WOL. var. <i>raciborskii</i>			x	75
33	<i>T. raciborskii</i> DREZ. var. <i>incerta</i> aff.				76-83
34	<i>T. rugulosa</i> var. <i>meandrina</i> CONR.			x	13-14
35	<i>T. rugulosa</i> var. <i>paralella</i> TELL. et ZALOC.			x	15-18 left
36	<i>T. rugulosa</i> STEIN var. <i>rugulosa</i> fo. <i>rugulosa</i>			x	18 right
37	<i>T. rugulosa</i> var. <i>rugulosa</i> fo. <i>steinii</i> DEFL.	x			10-12
38	<i>T. sculpta</i> BALECH			x	33-34
39	<i>T. selecta</i> var. <i>megaspina</i> CONF.			x	73-74
40	<i>T. similis</i> STOKES var. <i>similis</i>		x		106
41	<i>T. similis</i> var. <i>spinosa</i> HUB.-PEST.			x	107
42	<i>T. spirillifera</i> SCHKOR.			x	35-40
43	<i>T. sydneyensis</i> var. <i>minima</i> PLAYF.			x	71-72
44	<i>T. verrucosa</i> var. <i>verrucosa</i> fo. <i>irregularis</i> DEFL.	x			5-7
45	<i>T. verrucosa</i> var. <i>verrucosa</i> fo. <i>irregularis</i> DEFL. aff.	x			8-9
46	<i>T. volvocina</i> var. <i>derephora</i> CONR.	x			1
47	<i>T. woycickii</i> fo. <i>pusilla</i> (DREZ.) POPOVA	x			22-23



**Fig. 1.** *T. volvocina* var. *derephora*, 2. *T. curta*, 3, 4. *T. pusilla* var. *punctata*, 3- detail of the lorica surface, 4- general view, 5-7. *T. verrucosa* var. *verrucosa* fo. *irregularis*, 5, 7- loricae differently developed, 6- detail of the mature lorica surface, 8, 9. *T. verrucosa* var. *verrucosa* fo. *irregularis* aff., 8- general view, 9- detail of the pore ornamentation. Scale bars = 2  $\mu$ m.

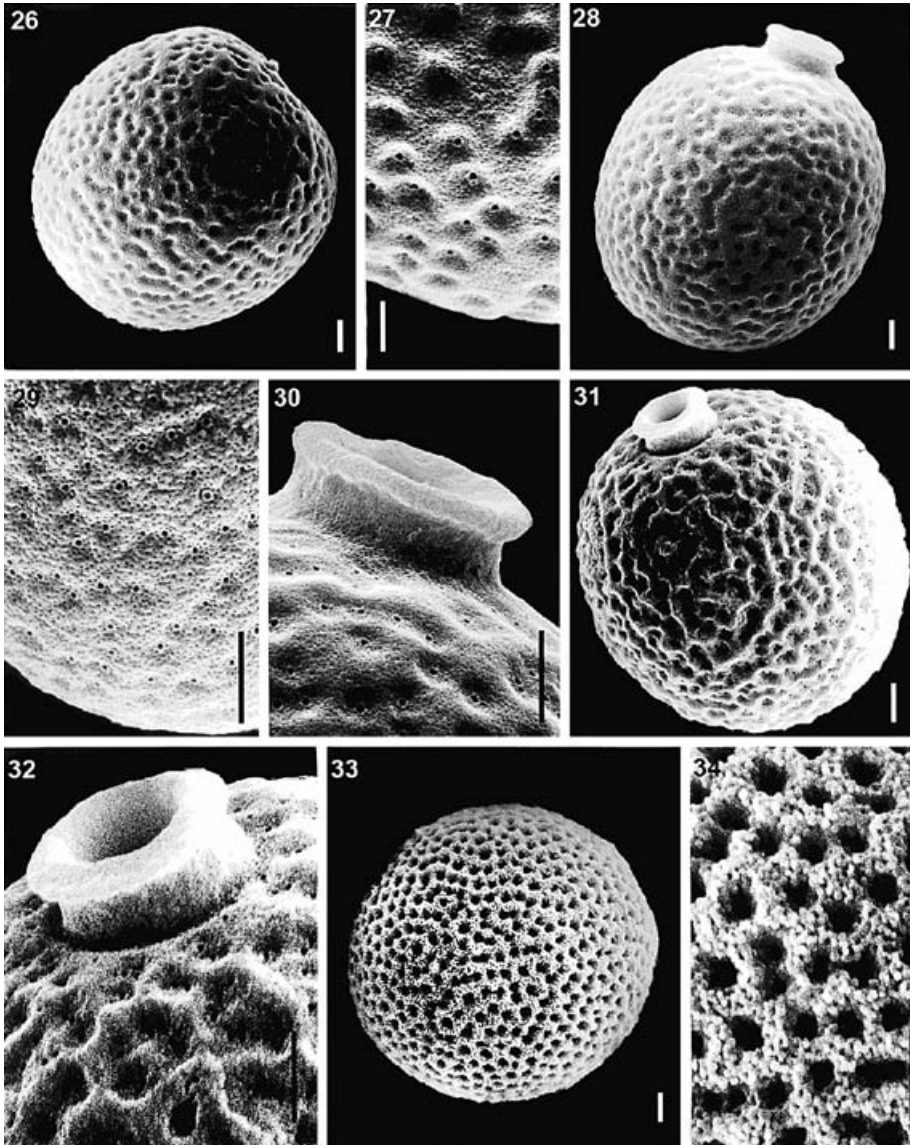


**Figs 10–12.** *T. rugulosa* var. *rugulosa* fo. *steinii*, 10, 11- general views of loricae differently developed, 12- detail of the pore and lorica ridges, **13, 14.** *T. rugulosa* var. *meandrina*, 13- general view, 14- detail of the pore and lorica ridges, **15–17.** *T. rugulosa* var. *parallelata*, 15- general posterior view, 16- detail of the pore and lorica ridges, 17- general view. Scale bars = 2  $\mu$ m.

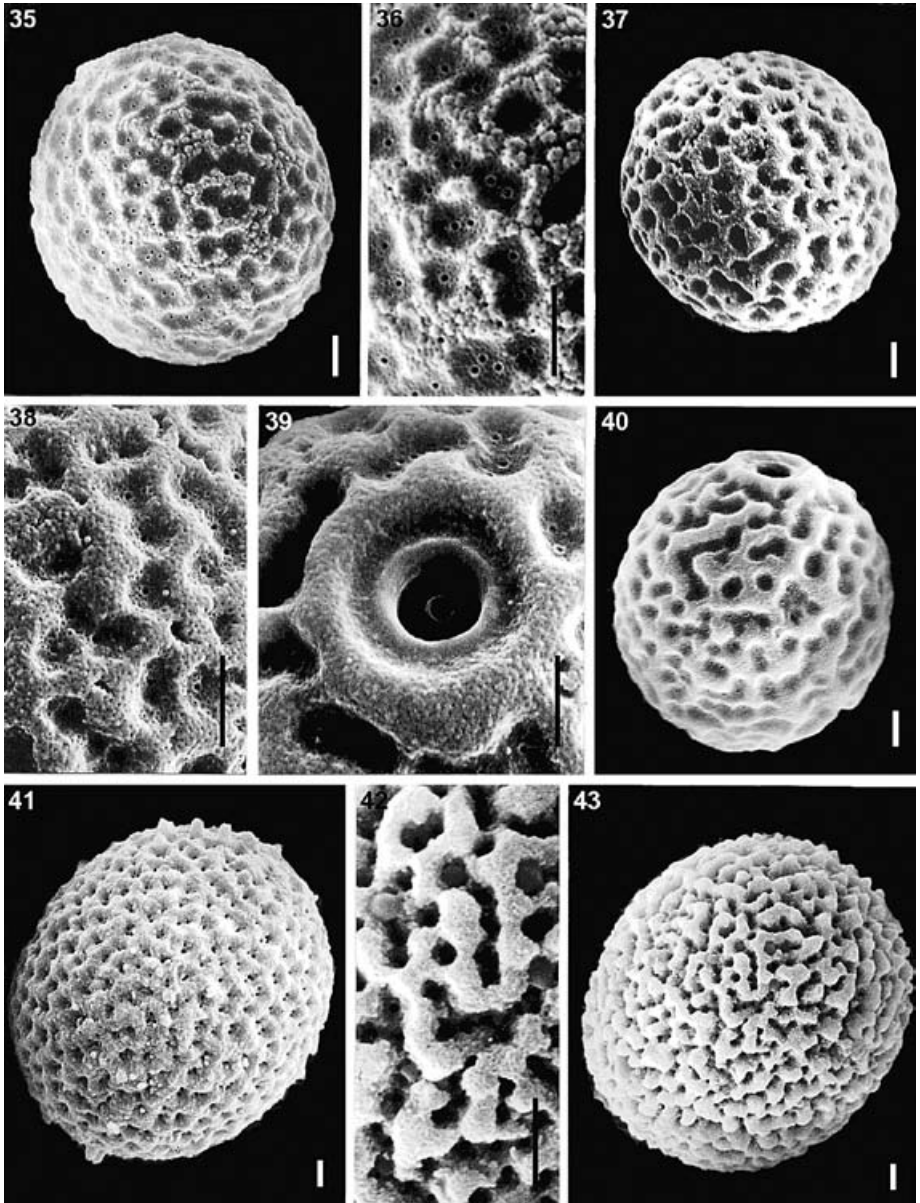


**Fig. 18.** *T. rugulosa* var. *parallela* (left) and *T. rugulosa* var. *rugulosa* (right), **19.** *T. nexilis*, **20, 21.** *T. conradi*, **20-** general view, **21-** detail of lorica ridges, **22, 23.** *T. woycikii* var. *pusilla*, **22-** general view, **23-** detail of the pore and lorica surface, **24.** *T. intermedia*, **25.** *T. compacta* var. *compacta*, general apical view. Scale bars = 2  $\mu$ m.

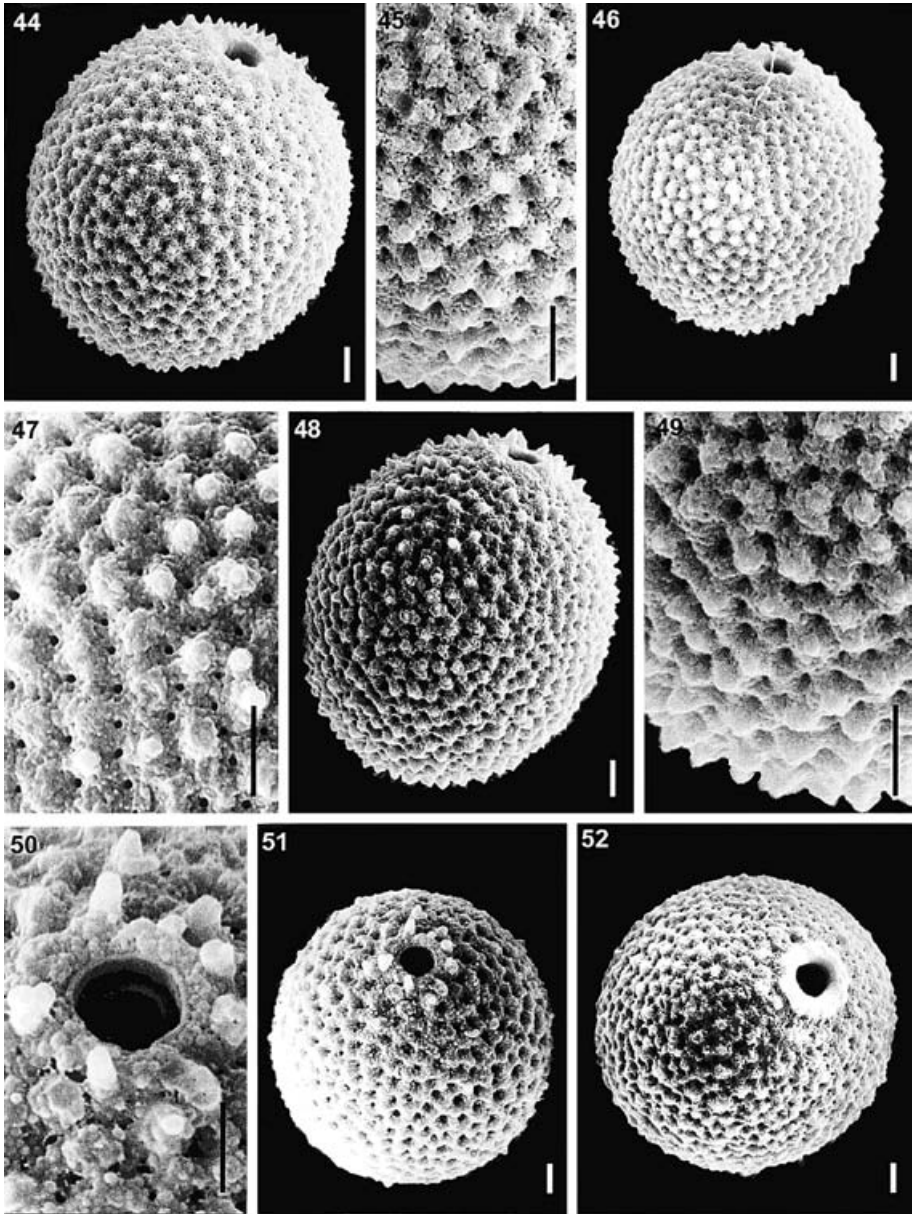




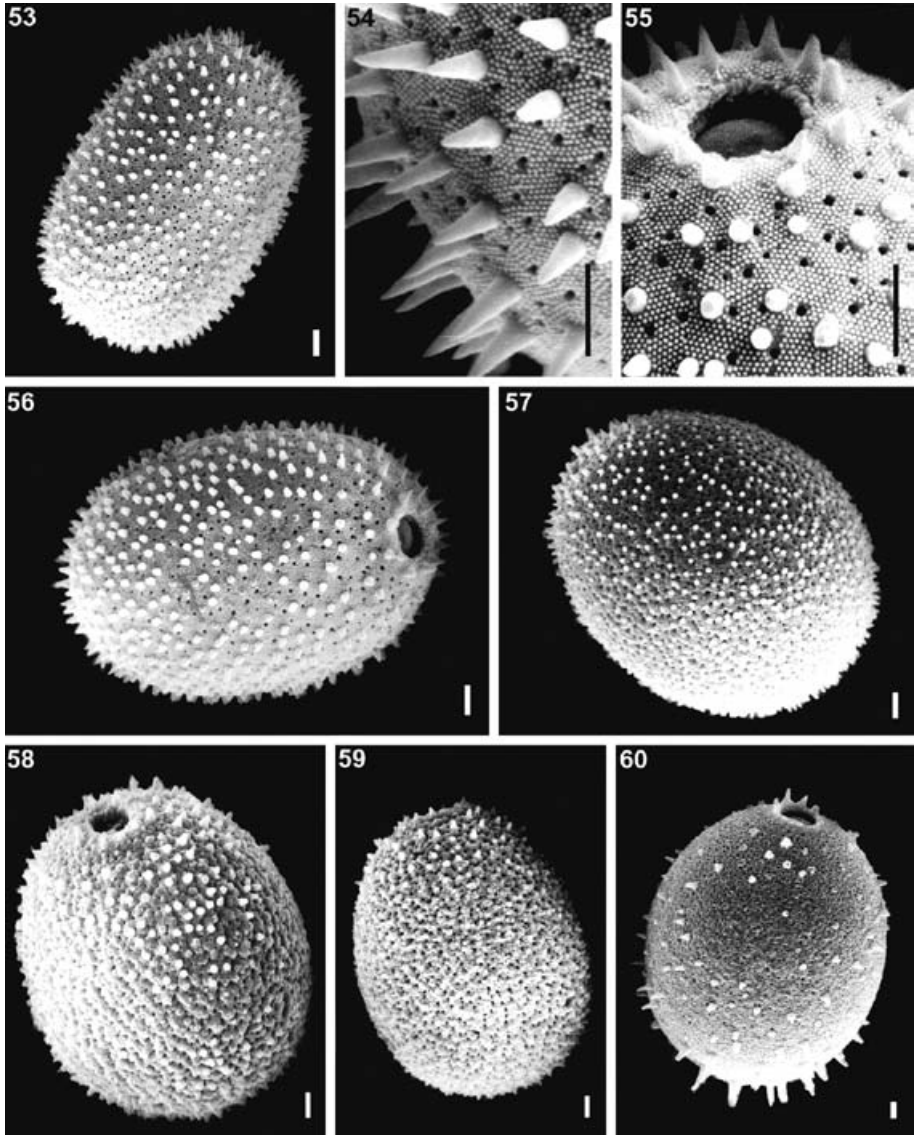
**Figs 26, 27.** *T. compacta* var. *compacta*, 26- general view, 27- detail of the lorica surface, **28-32.** *T. compacta* var. *parvicollis*, 28, 31- general views, 29- detail of the lorica surface, 30, 32- detail of the collar, **33-34.** *T. sculpta*, 33- general view, 34- detail of a young lorica surface. Scale bars = 2  $\mu$ m.



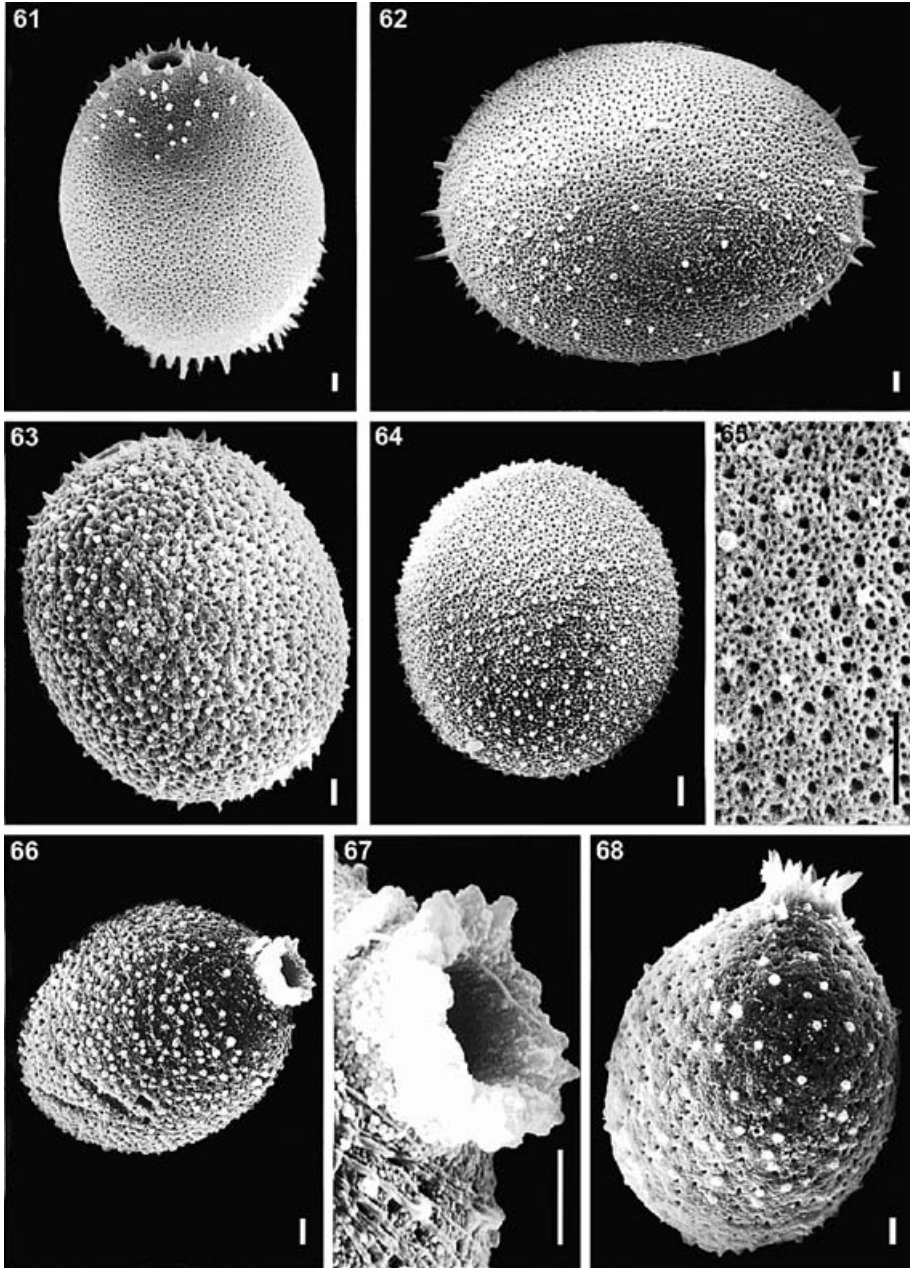
**Figs 35–40.** *T. spirillifera*, 35, 37, 40- general views, 36, 38- details of the loricae surface, 39- detail of the pore, **41–43.** *T. guttata*, 41, 43- general views of differently developed loricae, 42- detail of the lorica surface. Scale bars = 2  $\mu$ m.



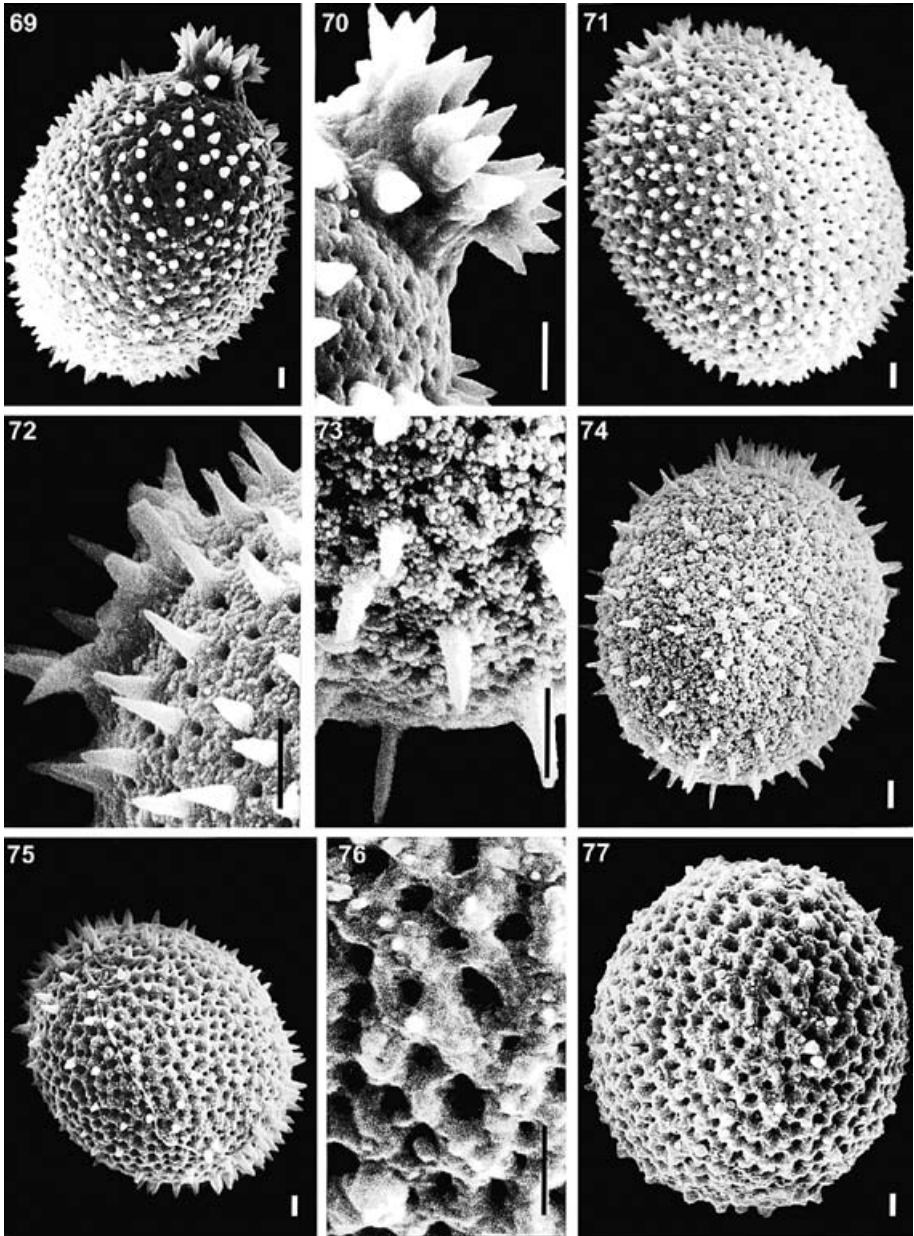
**Figs 44–52.** *T. granulosa* aff., 44, 46, 48- general views of differently developed loricae, 45, 47, 49- details of the loricae surface, 50, 51- details of the pore surrounded by conical spines, 52- details of the pore surrounded by a short collar. Scale bars = 2  $\mu$ m.



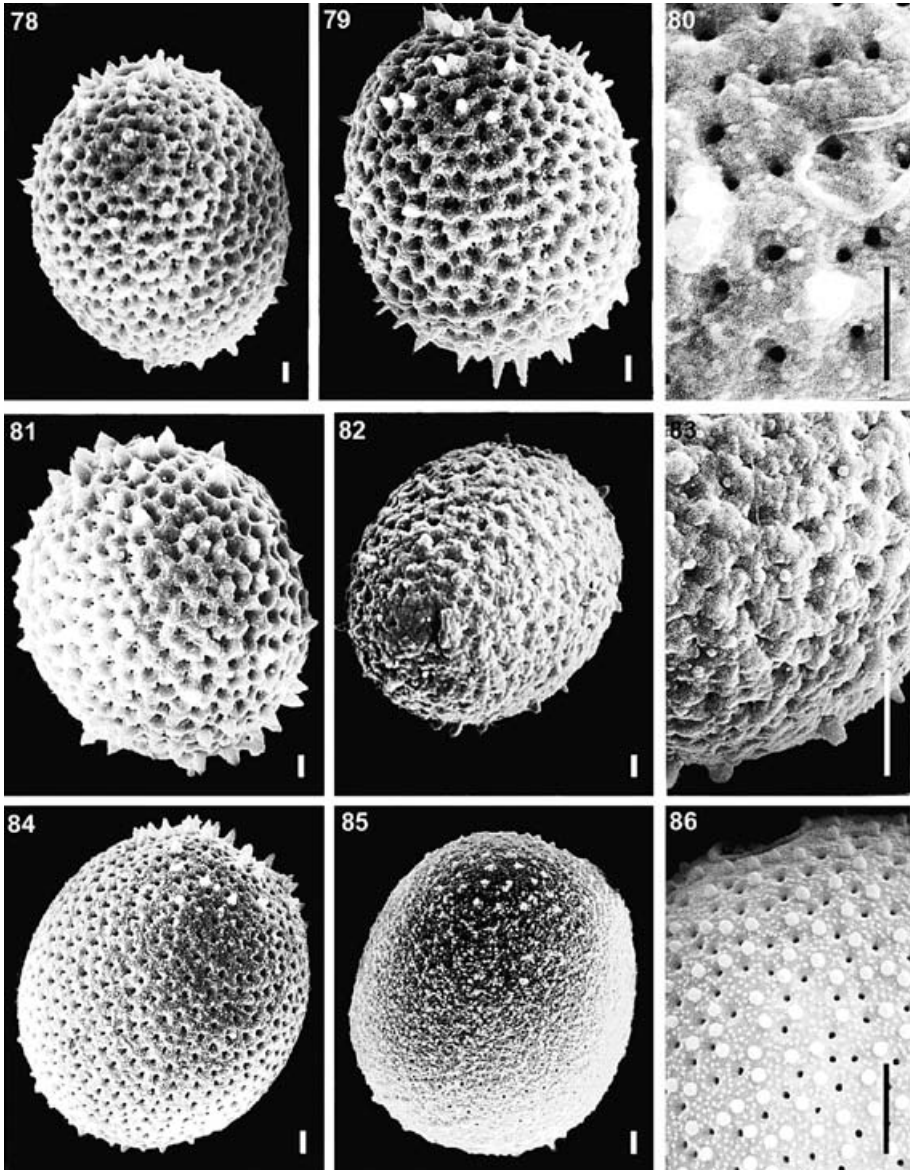
**Figs 53, 54.** *T. lacustris* var. *lacustris*, 53- general view, 54- detail of the lorica surface, **55, 56.** *T. lacustris* var. *ovalis*, 55- detail of the pore and lorica surface, 56- general view, **57, 58.** *T. oviformis* var. *oviformis*, **59.** *T. oviformis* var. *duplex*, **60.** *T. armata* var. *armata*. Scale bars = 2  $\mu$ m.



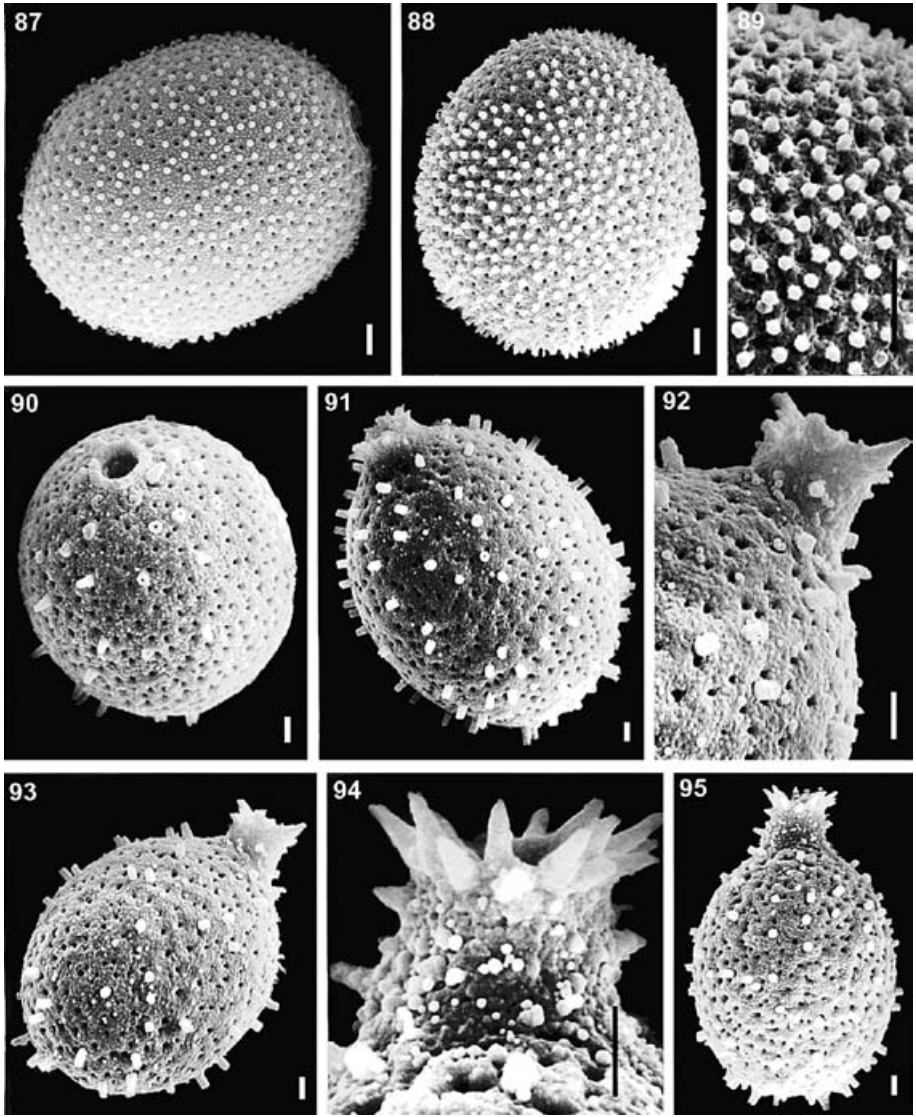
**Fig. 61.** *T. armata* var. *steinii*, **62.** *T. armata* var. *setosa*, general view, **63.** *T. hispida* var. *hispida* fo. *hispida*, **64.** **65.** *T. hispida* var. *hispida* fo. *minor*; 64- general view, 65- detail of the lorica surface, **66.** **67.** *T. hispida* var. *crenulato-collis*, 66- general view, 67- detail of the pore surrounded by a short collar, **68.** *T. hispida* var. *coronata*, young lorica general view. Scale bars: 2  $\mu\text{m}$ .



**Figs 69, 70.** *T. hispida* var. *coronata*, 69- mature lorica general view, 70- detail of the collar, **71, 72.** *T. sydneyensis* var. *minima*, 71- general view, 72- detail of the pore and lorica surface, **73, 74.** *T. selecta* var. *megaspina*, 73- detail of the lorica surface, 74- general view, **75.** *T. raciborskii* var. *raciborskii*, **76, 77.** *T. raciborskii* cf. var. *incerta*, 76- detail of a young lorica surface, 77- general view. Scale bars: 2  $\mu$ m.

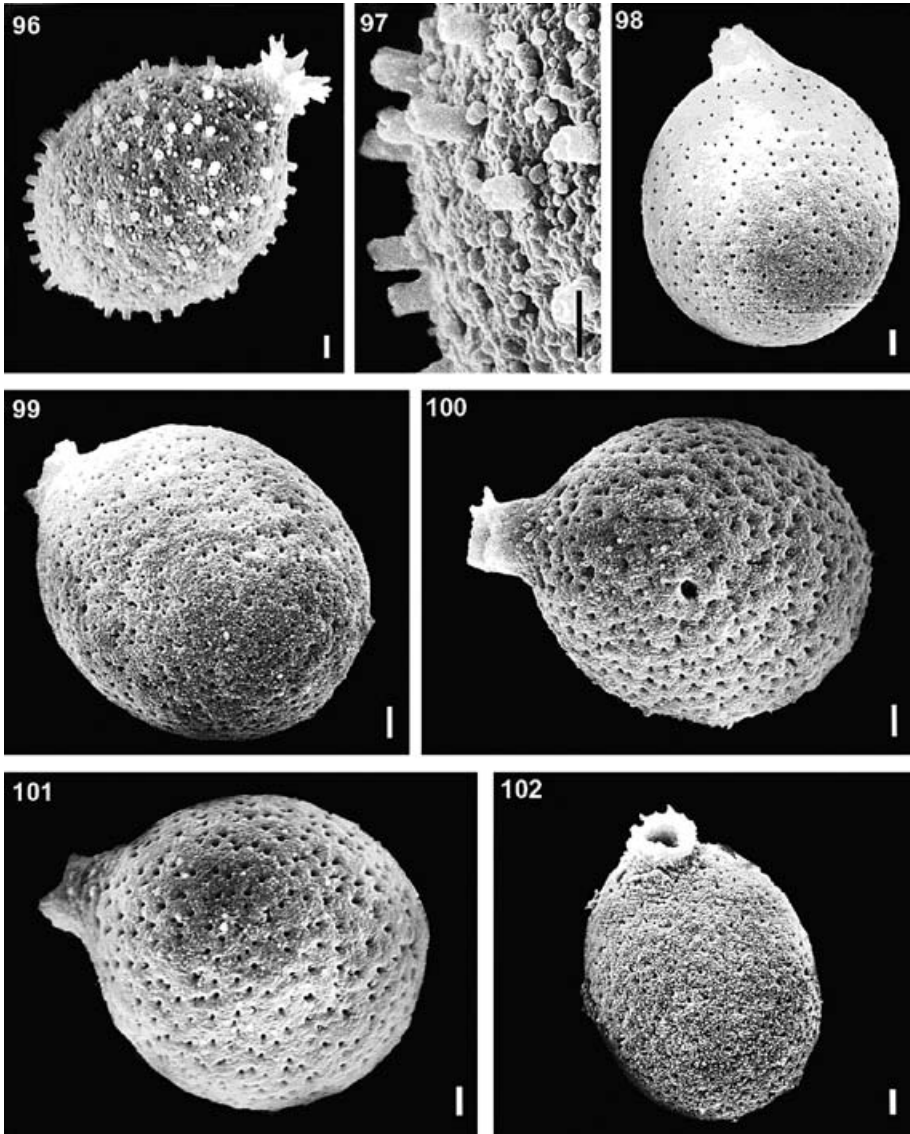


**Figs 78–83.** *T. raciborskii* var. *incerta* aff., 78, 79, 81, 82- general views of differently developed loricae, 80, 83- details of the loricae surface, **84.** *T. kellogii* var. *kellogii*, general view, **85.** *T. kellogii* var. *nana*, general view, **86.** *T. bacillifera* var. *minima* fo. *minima*, detail of a young lorica surface. Scale bars: 2  $\mu$ m.

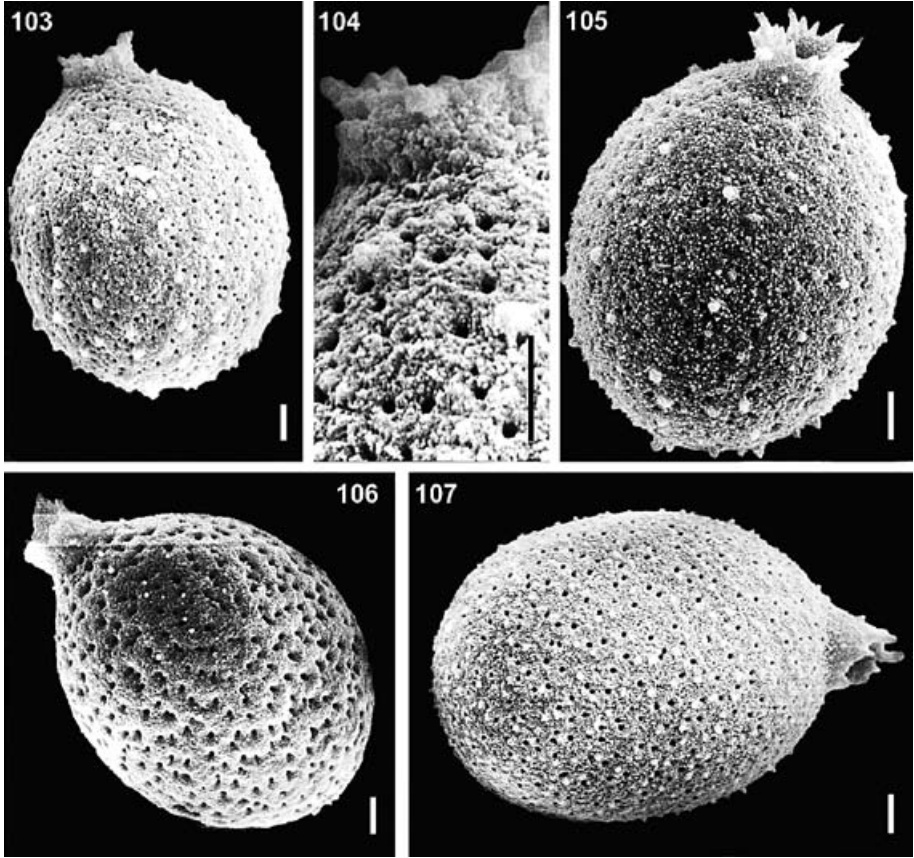


**Figs 87–89.** *T. bacillifera* var. *minima* fo. *minima*, 87, 88- general views of differently developed loricae, 89- detail of a mature lorica surface, **90.** *T. bacillifera* var. *minima* fo. *sparsispina*, **91.** *T. bacillifera* var. *collifera*, **92–95.** *T. bacillifera* var. *collifera* aff. 93, 93, 95- general views, 92, 94- details of the collar and lorica surface. Scale bars: 2  $\mu$ m.





**Figs 96, 97.** *T. bacillifera* var. *collifera* aff., 96- general view of a mature lorica, 97- detail of the mature lorica surface, **98.** *T. playfairi*, **99.** *T. lefevrei*, **100, 101.** *T. planctonica* var. *planctonica* fo. *planctonica*, **102.** *T. planctonica* var. *oblonga*. Scale bars: 2  $\mu$ m.



**Figs 103–105.** *T. planctonica* var. *planctonica* fo. *ornata*, 103, 105- general views of differently developed loricae, 104- detail of the young lorica surface, **106.** *T. similis* var. *similis*, **107.** *T. similis* var. *spinosa*. Scale bars: 2  $\mu$ m.