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Morphology and Infraciliature of Some Haptorid Ciliates (Protista, Ciliophora, Haptoria) in Alkaline Soil Samples of Van (Turkey), with Notes on the Ontogenesis of *Enchelyodon nodosus* Berger, Foissner & Adam, 1984

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Abstract: The morphology and infraciliature of 4 haptorid ciliates obtained from alkaline soil habitats in Van, Turkey, were investigated: *Pseudoholophrya terricola* Berger, Foissner & Adam, 1984, *Paraenchelys wenzeli* Foissner, 1984, *Armatoenchelys geleii* (Foissner, 1981), and *Enchelyodon nodosus* Berger, Foissner & Adam, 1984. The descriptions were based on live observations and silver impregnated specimens and morphometry. The main morphological characteristics of these species are similar to those described in the literature. However, the dorsal brush row 3 is longer than dorsal brush rows 1 and 2 in *A. geleii*, and *E. nodosus* has a long monokinetidal tail not reported previously. This is the first record of *E. nodosus* after the original description and also the first study on its ontogenesis. Division of *E. nodosus* is homothetogenic and telokinetal; it commences with a proliferation of kinetosomes in those kineties bearing the dorsal brush. All species are new for the ciliate fauna of Turkey.

Key Words: Alkaline soil, Haptorid ciliates, *Pseudoholophrya terricola*, *Paraenchelys wenzeli*, *Armatoenchelys geleii*, *Enchelyodon nodosus*, morphology, morphometry, ontogenesis

Van (Türkiye) Alkali Topraklarında Bulunan Bazı Haptorid Siliyatların (Protista, Ciliophora, Haptoria) Morfolojisi, İnfrasiliyatürleri ve *Enchelyodon nodosus* Berger, Foissner & Adam, 1984'ün Ontogenezisi Hakkında Notlar

Özet: Bu çalışmada Van'daki alkali toprak örneklerinde bulunan 4 haptorid siliyat türü incelendi: *Pseudoholophrya terricola* Berger, Foissner & Adam, 1984, *Paraenchelys wenzeli* Foissner, 1984, *Armatoenchelys geleii* (Foissner, 1981) and *Enchelyodon nodosus* Berger, Foissner & Adam, 1984. Türlerin deskripsiyonu canlı gözlem, gümüş impregnasyon, ve morfometriye göre yapıldı. Siliyat türlerinin temel morfolojik karakterleri önceki literatür bulgularıyla benzerlik gösterir. Bununla birlikte, *A. geleii*'nin 3. dorsal fırça sil sırası 1. ve 2.'ye göre daha uzun, *E. nodosus*'ta ise 3. dorsal fırça sil sırası daha önceki çalışmalarda belirtilmemiş olan uzun monokinetal kuyruk yapısına sahiptir. Bu çalışma, *E. nodosus*'un orijinal deskripsiyonundan sonraki ilk kayıt ve aynı zamanda ontogenezisi ile ilgili ilk çalışmadır. *E. nodosus*'da bölünme homotetogenik ve telokinetaldır. Bölünme "dorsal fırça"nın bulunduğu sil sıralarında kinetozom çoğalması ile başlar. Bütün türler Türkiye siliyat faunası için yenidir.

Anahtar Sözcükler: Alkali toprak, Haptorid siliyat, *Pseudoholophrya terricola*, *Paraenchelys wenzeli*, *Armatoenchelys geleii*, *Enchelyodon nodosus*, morfoloji, morfometri, ontogenez

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Introduction

Ciliated protozoans constitute an important component of terrestrial microbial communities. Comparative studies of soil ciliate populations in different regions have provided information on the role of protozoa in terrestrial ecosystems (Schönborn, 1992a, 1992b; Ekelund et al., 2002; Foissner, 1999a): they are a link in the food chain at the level of the conversion of organic matter and are useful organisms for humus formation, and thus they increase soil fertility. It is evident from recent taxonomic studies on soil ciliates that the species composition in terrestrial habitats is rather similar. However, there is a high number of undescribed species, as claimed by Foissner et al. (2002). Detailed studies conducted in many regions revealed the existence of many new species and subspecies (Berger et al., 1983, 1984; Foissner, 1984, 1987a, 1987b, 1993, 1998, 1999b, 2000; Blatterer and Foissner, 1988; Pomp and Wilbert, 1988; Foissner et al., 2002). Although the interest in terrestrial ciliates has been increasing, information from Turkey is sparse. Only 2 new soil ciliates viz., *Colpoda orientalis* Foissner, 1993 and *Anatoliocirrus capari* Özbek & Foissner, 2002, have been found in Turkey (Foissner, 1993; Foissner et al., 2002). Therefore, our country is an excellent source for new, rare, or insufficiently known species. The present study provides descriptions and comparisons of several species, including the ontogenesis of *Enchelyodon nodosus* Berger et al., 1984.

Materials and Methods

Soil samples were obtained from the uppermost layer (0-5 cm) of an apple garden in the university campus of Van, Turkey (43° 17´ 054´E, 38° 34´ 009´N). The samples were air-dried, and then stored in plastic bags. Soils are sandy clay with the following characteristics: salinity 0.035%, lime 14.23%, organic matter 1.65%, and pH 8.3.

The air-dried soil samples were treated with the "non-flooded Petri dish method", as described by Foissner et al. (2002). All species were observed in vivo at 100-1000 magnification with Nomarski Differential Interference Contrast (DIC). Specimens were prepared by 2 silver-impregnation techniques to reveal the infraciliature and silverline pattern: Chatton-Lwoff's silver nitrate and silver carbonate, as described by Foissner (1991) and Foissner et al. (1999). Drawings of live cells were based on free-hand sketches and/or micrographs; those of impregnated cells were performed with the aid of a drawing device; illustrations of specimens are based on values near the arithmetic means. Cell measurements were made on live and silver nitrate impregnated specimens performed with a calibrated ocular micrometer at a magnification of ×400-1000. Systematic and terminology were mainly performed according to Berger et al. (1984), Foissner (1984), and Foissner et al. (2002). All figures are orientated with the anterior end of the organism directed to the top of the page.

Results and Discussion

Order Haptorida Corliss, 1974

Family Pseudoholophryidae Berger, Foissner & Adam, 1984

Pseudoholophrya terricola Berger, Foissner & Adam, 1984

Morphological and morphometrical characteristics of the Turkish population are given in Figures 1a-d, 2a-d, and Table 1. Size 40-73 × 20-45 µm in vivo; unflattened, flexible but non-contractile. Ovoidal with posterior body end more broadly rounded than anterior. Body width:length ratio 0.3-0.8 in vivo and 0.4-0.7 in silver nitrate preparations. Nuclear apparatus usually situated at or near centre of cell. Macronucleus elongate ellipsoidal to semicircular, rarely reniform. 2–3 oval to globular micronuclei adjacent to macronucleus at various positions (Figures 1a, 2a; Table 1). Contractile vacuole in posterior body end. Extrusomes form conspicuous bundle in oral opening, acicular and 4–7 0.5 µm size in vivo; also scattered in cytoplasm (Figures 1a-c; 2a,d). Cytoplasm colorless, contains slightly refractive granules. Swims rapidly by rotation about main body axis.

Somatic cilia 10–13 µm long in vivo and closely-spaced, arranged in 27–33 distinctly spiral rows. Some ciliary rows more or less shortened posteriorly. Dorsal brush with about 2 µm long bristles, inconspicuous, occupies anterior of the body (Figures 1d; 2c; Table 1).

Oral bulge only 1–1.5 µm high in vivo and hardly recognizable, but conspicuous due to the extrusomes bundle contained; circumoral kinety at base of oral bulge, hardly recognizable in squeezed specimens. Oral basket about 2/5 of cell length (Figures 1a,d; 2a).

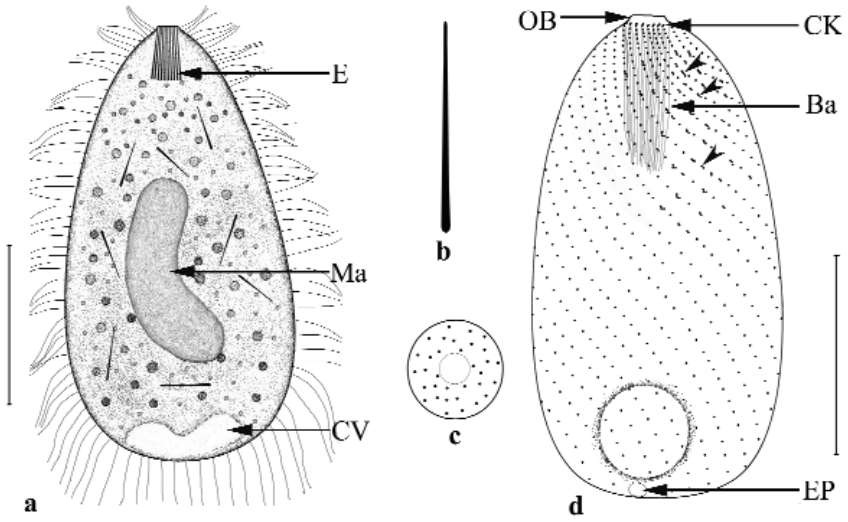

Figure 1a-d. Line diagrams of *Pseudoholophrya terricola* from life (a, b, c) and after silver impregnation (d). a: A typical specimen. Extrusomes are acicular in living specimens (b). c: Frontal view of oral bulge with extrusomes. d: Ciliary pattern of dorsal side. Arrowheads mark dorsal brush, which consists of many short kinetofragments with closely spaced kinetosomes. Ba- oral basket, CK- circumoral kinety, CV- contractile vacuole, E- extrusomes, EP- excreation pore, OB- oral bulge. Scale bars 20 µm.

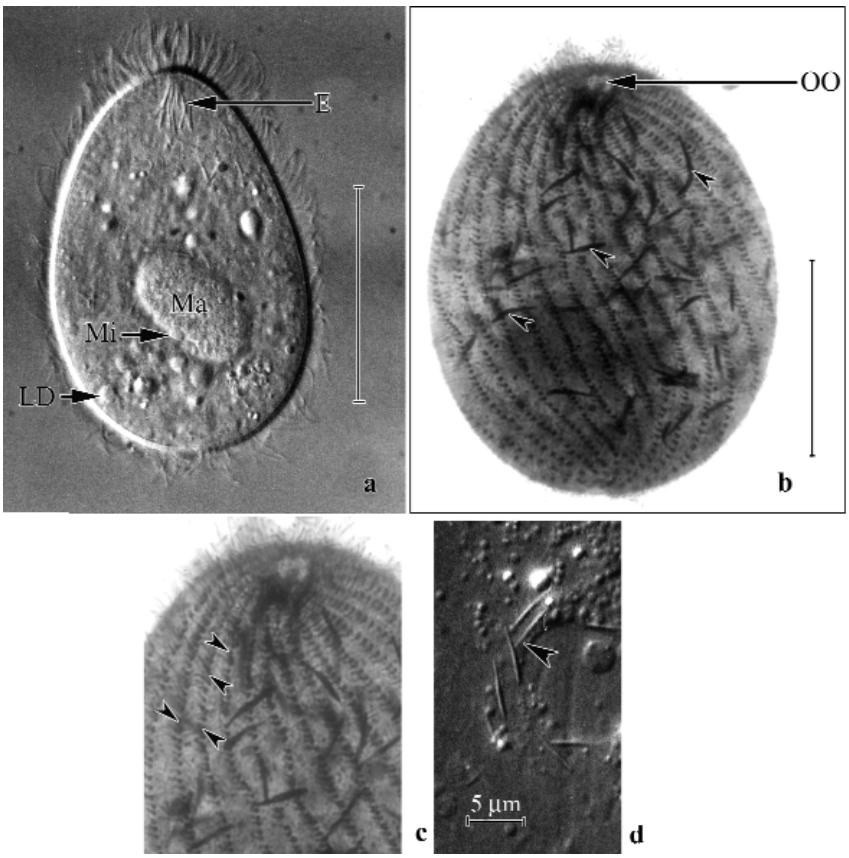

Figure 2a-d. Photomicrographs of *Pseudoholophrya terricola* from life (a, d) and after silver impregnation (b, c). a: A representative specimen. b: Infraciliature after silver carbonate impregnation, showing spiralling ciliary rows. Arrowheads mark extrusomes. c: Dorsal view of ciliary pattern. Arrowheads mark dorsal brush, consisting of small ciliary condensations. d: Acicular extrusomes (arrowhead) from life. E- extrusomes, LD- lipid droplets, Ma- macronucleus, Mi-micronucleus, OO- oral opening. Scale bars 30 µm.

Table 1. Morphometric data on *Pseudoholophrya terricola.*

Characteristics [a]	$\bar{X}$	M	SD	SE	CV	Min	Max	N
Body, length	49.1	47.0	7.9	1.2	16.1	37.0	70.0	43
Body, width	23.2	22.0	4.3	0.5	18.5	17.0	33.0	43
Body width : length, ratio	0.5	0.5	0.1	0.01	20.0	0.4	0.7	43
Oral bulge, diameter at distal end	1.9	2.0	0.3	0.05	15.8	1.5	3.0	38
Anterior body end to macronucleus, distance	21.4	20.0	6.1	1.36	28.5	12.0	35.0	20
Macronuclear figure, length	17.4	17.0	3.4	0.8	19.5	12.0	25.0	20
Macronucleus, width	8.0	7.0	2.1	0.5	26.3	6.0	12.0	20
Macronuclear figure length : body length, ratio	0.4	0.3	0.1	0.01	25.0	0.2	0.5	20
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	20
Micronuclei, diameter	2.0	2.0	0.8	0.2	40.0	1.0	3.0	11
Micronuclei, number	2.2	2.0	0.5	0.2	22.7	2.0	3.0	5
Somatic ciliary rows, number[b]	32.0	32.0	3.4	0.1	10.6	27.0	33.0	38
Kinetids in mid-body, number in 10 µm[b]	10.7	10.0	1.6	0.3	15.0	9.0	15.0	38
Oral basket, length	18.2	17.0	3.7	1.1	20.3	14.0	25.0	11
Oral basket length : body length, ratio	0.4	0.4	0.1	0.02	25.0	0.3	0.4	11

[a] Data based, if not otherwise stated, on mounted, silver-impregnated (Chatton-Lwoff), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV- coefficient of variation in %, M- median, Max- maximum, Min- minimum, N- number of individuals investigated, SD- standard deviation, SE- standard error of arithmetic mean, $\bar{X}$ - arithmetic mean.

[b] From silver carbonate–impregnated specimens.

Discussion: This species, type of the genus, has already been described using modern techniques (Berger et al., 1984; Foissner et al., 2002). Our observations match the original description and the redescription. According to Berger et al. (1984), *Pseudoholophrya* is characterized by the lack of a dorsal brush. However, Foissner et al. (2002) showed a dorsal brush in specimens from the type locality and the Maldives. The Turkish population matches these observations. Morphometrics also correspond to those reported by the above mentioned authors: the number of ciliary rows (on average 32 and 38 in 2 populations of Berger et al., 21 in Maldivean population, 32 in Turkish population), body size (65-75 × 35-55 µm in the populations of Berger et al., 50-80 × 20-40 µm in the Maldivean population, 40-73 × 20-45 µm in the Turkish population), extrusome length (5 µm in the populations of Berger et al., 4-9 µm in many populations investigated by Foissner et al., 4-7 µm in the Turkish population).

Paraenchelys wenzeli Foissner, 1984

Some features of the Turkish specimens of *Paraenchelys wenzeli* are given in Figures 3a-d, 4a-e, and Table 2. Size in vivo 70-113 × 43-70 µm; width:length ratio 0.4-0.8 in vivo, on average 0.7 in silver nitrate preparations. Body usually pear-like, anteriorly narrowed, posteriorly rounded; unflattened, flexible but non-contractile. One large elongate ellipsoidal to reniform macronucleus centrally located, macronucleus length:width ratio 3.1-3.9 in vivo and 1.9-3.9 in silver nitrate prepared specimens, on average 32 × 12 µm in size; micronucleus not observed (Figures 3a; Table 2). Extrusomes rather conspicuous, not numerous, 5 to 7 attached to oral bulge and some scattered in cytoplasm; look similar in vivo and silver impregnated specimens, basically drumstick-shaped, but in cytoplasm elongate drop-shaped to claviform and fusiform with filiform process; developed extrusomes about 14 µm total length in vivo, filiform process 7 µm length, thick proximal portion 7 × 1 µm in size (Figures 3a,b, 4b,e); when exploding, the filiform process extends suddenly elongating to an up to 25 µm long thread. Cytoplasm with numerous lipid droplets 1-8 µm across. Swims rapidly by rotation about main body axis.

Cilia about 9 µm long in vivo, form spiral rows, as shown in Figures 3d, 4a. On average 40 ciliary rows composed of densely arranged basal bodies, i.e., on

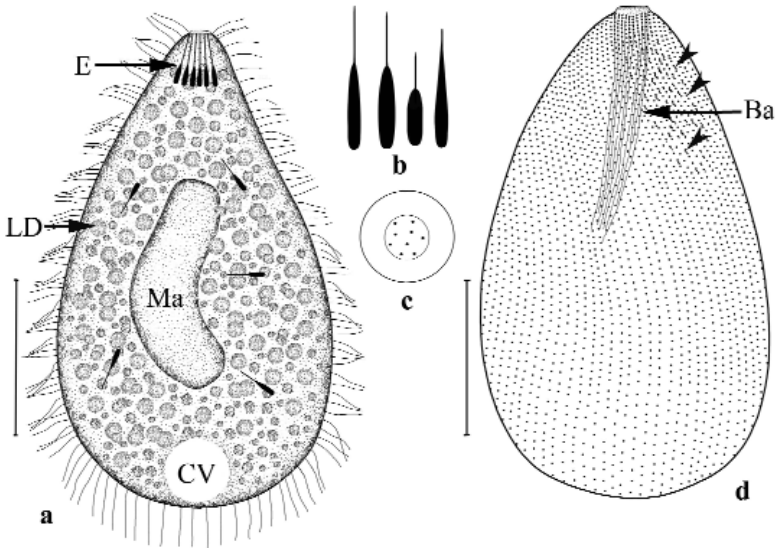

Figure 3a-d. Line diagrams of *Paraenchelys wenzeli* from life (a, c) and after silver impregnation (b, d). a: Typical specimen packed with lipid droplets. b: Variability of silver impregnated oral and cytoplasmic extrusomes (total length, about 10-15 µm). c: Frontal view of oral bulge. d: Somatic ciliary pattern, showing spiral ciliary rows and kinetofragments of the dorsal brush (arrowheads). Ba- oral basket, CV- contractile vacuole, E- drumstick-shaped extrusomes, LD- lipid droplets, Ma- macronucleus. Scale bars 30 µm.

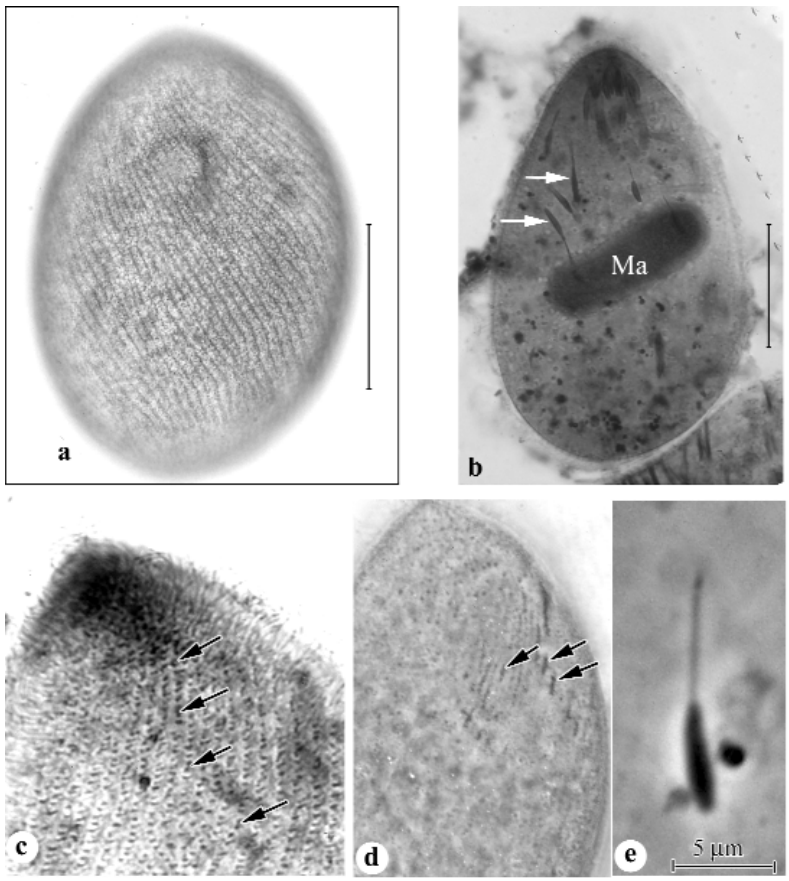

Figure 4a-e. Photomicrographs of *Paraenchelys wenzeli* after silver impregnation (a, b, c, d). and from life (e) a: Somatic infraciliature after silver nitrate impregnation. b: Extrusomes (arrows) and nuclear apparatus in a silver carbonate impregnated specimen. c, d: The dorsal brush consists of irregularly arranged kinetofragments (arrows). e: Cytoplasmic extrusome from life. Ma- macronucleus. Scale bars 30 µm.

Table 2. Morphometric data on *Paraenchelys wenzeli.*

Characteristics [a]	$\bar{X}$	M	SD	SE	CV	Min	Max	N
Body, length	82.8	83.0	10.8	1.8	13.0	65.0	105.0	34
Body, width	54.2	54.0	9.2	1.6	17.0	34.0	78.0	34
Body width : length, ratio	0.7	0.7	0.1	0.01	10.0	0.5	0.8	34
Oral bulge, diameter at distal end	2.3	2.0	0.5	0.1	21.7	2.0	3.0	24
Anterior body end to macronucleus, distance	22.8	24.0	8.0	1.8	35.1	11.0	39.0	19
Macronuclear figure, length	31.9	32.0	6.4	1.5	20.1	24.0	46.0	19
Macronuclear figure length : body length, ratio	0.4	0.4	0.1	0.1	25.0	1.9	3.7	19
Macronucleus, width	12.1	12.0	1.4	0.3	11.6	10.0	14.0	19
Macronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Somatic ciliary rows, number[b]	39.2	40.0	3.1	0.7	6.5	34.0	45.0	20
Kinetids in a ventral kinety, number[b]	94.5	94.0	4.2	2.1	4.4	90.0	100.0	8

[a] Data based, if not otherwise stated, on mounted, silver-impregnated (Chatton-Lwoff), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV- coefficient of variation in %, M- median, Max- maximum, Min- minimum, N- number of individuals investigated, SD- standard deviation, SE- standard error of arithmetic mean, $\bar{X}$ - arithmetic mean.

[b] From silver carbonate–impregnated specimens.

average 94 kinetids in a kinety (Table 2). Eight to twelve rows with dorsal brush fragments irregularly arranged in anterior portion of the cell, bearing 3-4 µm long bristles in vivo irregularly interspaced among ordinary cilia (Figures 3d, 4c,d). Oral area at anterior body end, minute, about 3 µm across in vivo. Circumoral kinety not observed, even in good silver nitrate and silver carbonate preparations. Oral basket, extends about 1/2 of cell length.

Discussion: The genus *Paraenchelys* is characterized by "the drumstick shaped extrusomes" attached to the oral bulge and scattered in cytoplasm as described originally (Foissner, 1983). Since then, 5 species (*P. wenzeli, P. terricola, P. pulchra, P. brachyarmata, P. brachyoplites*) have been assigned to this genus (Foissner, 1983, 1984; Foissner et al., 2002).

Paraenchelys wenzeli was described from wall moss by Foissner (1984), based on living and protargol-impregnated specimens; no further studies have been conducted. The type population of *Paraenchelys wenzeli* is very similar to that found in Turkey in terms of general morphology (including the infraciliature, macronuclear apparatus, dorsal brush) and extrusome size and shape. As usual, there are some inconspicuous morphometric differences (e.g., oral basket nearly 1/2 of body length vs. nearly body length), some likely caused by different preparation methods.

The population studied here is similar to *Paraenchelys pulchra* Foissner et al., 2002 in general appearance and the oral basket length, differing in the shape of the oral extrusomes, which are an important diagnostic feature in gymnostomatid haptorids as remarked by Foissner (1983, 1984, 2000) and Foissner et al. (2002).

Family Enchelyidae Ehrenberg, 1983

Armatoenchelys geleii (Foissner, 1981) Vd'ačný, 2007

Basionym: *Lagynophrya geleii* Foissner, 1981, combination: *Enchelys geleii* (Foissner, 1981) Foissner, 2000, combination: *Armatoenchelys geleii* (Foissner, 1981) Vd'ačný, 2007.

The main features of the Turkish *Armatoenchelys geleii* are presented in Figures 5a-g, 6a-e, and Table 3. Cell size about 80-113 × 25-53 µm in vivo, width:length ratio 0.2-0.5, on average 0.4. Body shape strongly variable, slenderly to broadly oblong, elongate ovoidal or ovoidal with anterior region usually narrower than posterior; convex in dorsal brush area; sometimes slightly curved, not flattened, non-contractile (Figures 5a-d). Macronucleus vermiform and tortuous, uncoiled macronucleus about 160 µm long in vivo, many spherical micronuclei scattered in cytoplasm, difficult to recognize in vivo due to many similarly sized cell inclusions. Contractile vacuole in posterior end, with about 4-5

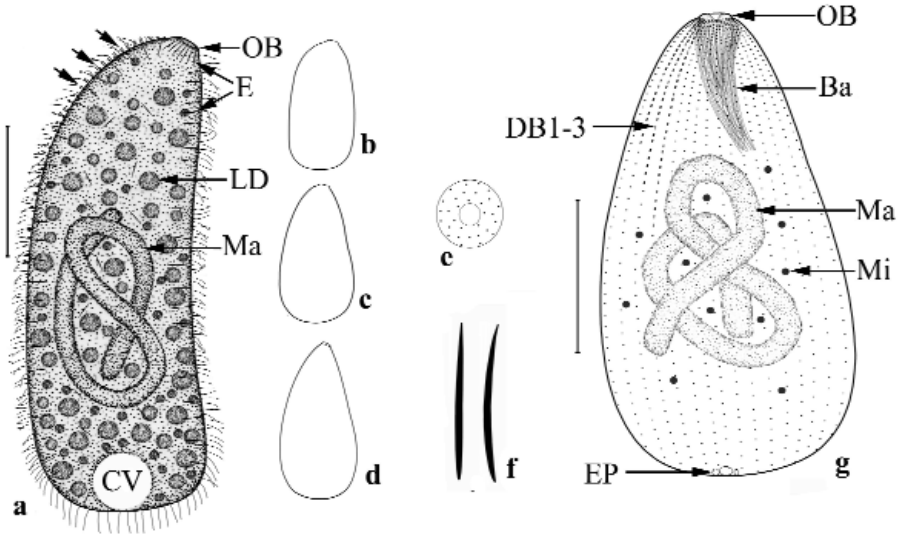

Figure 5a-g. Line diagrams of *Armatoenchelys geleii* from life (a-f) and after silver impregnation (g). a: General view showing the tortuous macronucleus, dorsal brush (arrows). b, c, d: Variability of body shape. e: Upper view of the oral bulge. f: Oral and somatic extrusomes are fusiform. g: Infraciliature. Ba- oral basket, CV- contractile vacuole, DB1-3- dorsal brush rows, E- extrusomes, EP- excreation pores, LD– lipid dropletes, Ma- macronucleus, Mi- micronuclei, OB- oral bulge. Scale bars 30 µm.

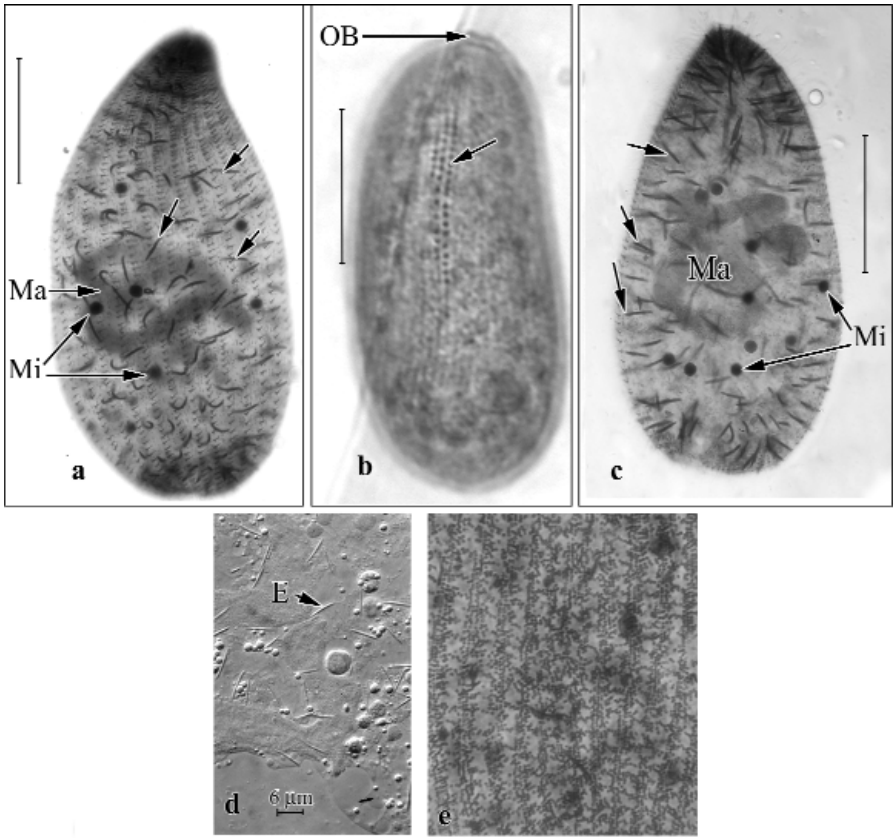

Figure 6a-e. Photomicrographs of *Armatoenchelys geleii* after silver impregnation (a, b, c, e) and from life (d). a, c: Infraciliature, nuclear apparatus and extrusomes after silver carbonate impregnation. Arrows mark extrusomes. b: Dorsal view of a silver nitrate impregnated specimen showing the dorsal brush (arrow). d: Extrusomes in squeezed specimen. e: Cortical granules after silver carbonate impregnation. E- extrusomes, Ma- macronucleus, Mi- micronuclei, OB- oral bulge. Scale bars 30 µm.

Table 3. Morphometric data on *Armatoenchelys geleii*.

Characteristics [a]	$\bar{X}$	M	SD	SE	CV	Min	Max	N
Body, length	86.5	88.0	12.7	1.4	14.7	61.0	115.0	79
Body, width	43.7	44.0	8.2	0.9	18.8	23.0	69.0	79
Body width:length, ratio	0.5	0.5	0.1	0.01	20.0	0.4	0.7	79
Oral bulge, width	6.1	6.0	1.2	0.1	19.8	4.0	9.0	72
Oral bulge, height	1.3	1.0	0.4	0.1	30.8	1.0	2.0	72
Macronucleus, length (spread)	113.1	115.0	29.4	6.4	26.0	72.0	185.0	21
Macronucleus, width	5.0	5.0	1.0	0.2	20.0	4.0	8.0	21
Macronucleus length : body length, ratio	1.3	1.2	0.3	0.1	23.1	0.9	2.2	21
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Micronuclei, diameter	2.7	3.0	0.5	0.1	18.5	2.0	3.0	23
Micronuclei, number	15.7	15.0	3.8	0.8	24.2	10.0	22.0	21
Somatic ciliary rows, number[b]	31.7	31.0	2.0	0.5	6.3	28.0	35.0	16
Kinetids in a ventral kinety, number[b]	83.1	80.5	16.7	4.2	20.1	60.0	114.0	16
Brush row 1, length	30.1	32.0	5.5	1.5	18.3	25.0	45.0	13
Brush row 2, length	40.5	40.0	6.2	1.7	15.3	31.0	52.0	13
Brush row 3, length	47.8	45.0	5.2	1.4	10.9	40.0	56.0	13
Dikinetids in brush row 1, number[b]	19.8	19.5	1.0	0.5	5.1	19.0	21.0	4
Dikinetids in brush row 2, number[b]	31.8	32.0	1.3	0.6	4.1	30.0	33.0	4
Dikinetids in brush row 3, number[b]	35.3	35.0	2.1	1.03	5.9	33.0	38.0	4
Oral basket, length	26.2	25.0	2.0	0.8	7.6	25.0	30.0	6
Oral basket length : body length, ratio	0.3	0.3	0.03	0.01	10.0	0.25	0.31	6

[a] Data based, if not otherwise stated, on mounted, silver-impregnated (Chatton-Lwoff), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV- coefficient of variation in %, M- median, Max- maximum, Min- minimum, N- number of individuals investigated, SD- standard deviation, SE- standard error of arithmetic mean, $\bar{X}$ - arithmetic mean.

[b] From silver carbonate–impregnated specimens.

excretion pores (Figures 5a,g). Extrusomes in oral bulge and, especially, in anterior body region, perpendicularly attached to pellicle, some scattered in cytoplasm. Individual extrusomes 5-7 µm long in vivo, fusiform, straight or slightly curved, moderately thick (Figures 5a,e,f, 6a,c,d). Cortex flexible, contains numerous minute granules impregnating with silver carbonate (Figure 6e). Cytoplasm usually opaque due to many fat globules up to 5 µm across, especially in ovoidal specimens.

Cilia about 6-7 µm long in vivo, arranged in 28-35 bipolar rows, 3 anteriorly differentiated to dorsal brush, anterior bristles shorter than posterior ones, decrease in length from 2-2.5 µm posteriorly to 1 µm anteriorly. Brush row 1 shorter than row 2 and row 3, composed of an average of 20 dikinetids; row 2 composed of an average of 32 dikinetids; brush row 3 slightly longer row 2, composed of an average of 35 dikinetids (Figures 5g, 6b; Table 3).

Discussion: This species was originally described in the genus *Lagynophrya* by Foissner in 1981. *Lagynophrya* has a dikinetidal circumoral kinety and lacks oralised somatic kinetids. Therefore, Foissner (2000) transferred *Lagynophrya geleii* Foissner, 1981 to the genus *Enchelys* Müller, 1773. Then the species is referred to a new genus, *Armatoenchelys*, which differs from the other genera of the family Enchelyidae in having both oral bulge and body extrusomes attached to the somatic cortex (Vd'ačný, 2007).

As revealed in previous work (Foissner, 2000), this species is highly variable in size and body shape, and thus shows rather different appearances in vivo, but after impregnation, all have the same ciliary pattern. The form studied in the present paper is similar to *Armatoenchelys geleii* as redescribed by Foissner (2000), except for the length of the brush row 3, which is longer than the other rows. However, there is an important diagnostic feature

which is highly similar in 2 populations, namely the shape and size of the extrusomes. However, the dorsal brush structure in different populations should be checked by various impregnation techniques.

A. geleii highly resembles 2 soil species, *Enchelys vermiformis* and *Enchelys longitricha*, originally described by Foissner (1987b) and Foissner et al. (2002), and then transferred to the genus *Armatoenchelys* by Vd'ačný (2007). The former has rod-shaped extrusomes and 17 ciliary rows, the latter is characterized by the long bristles of the dorsal brush.

Family: Enchelyodontidae Foissner, Agatha & Berger, 2002

Enchelyodon nodosus Berger, Foissner & Adam, 1984

Some morphological and ontogenetical features of the Turkish population are given in Figures 7a-e, 8a-c, 9a-h, 10a-f, and Table 4. Size in vivo 140-250 × 53-88 µm, width:length ratio 0.3-0.5, both in vivo and in silver-nitrate preparations (Table 4). Shape somewhat variable, basically bursiform and slightly curved, rarely cylindroidal. Posterior end broadly rounded, anterior end with

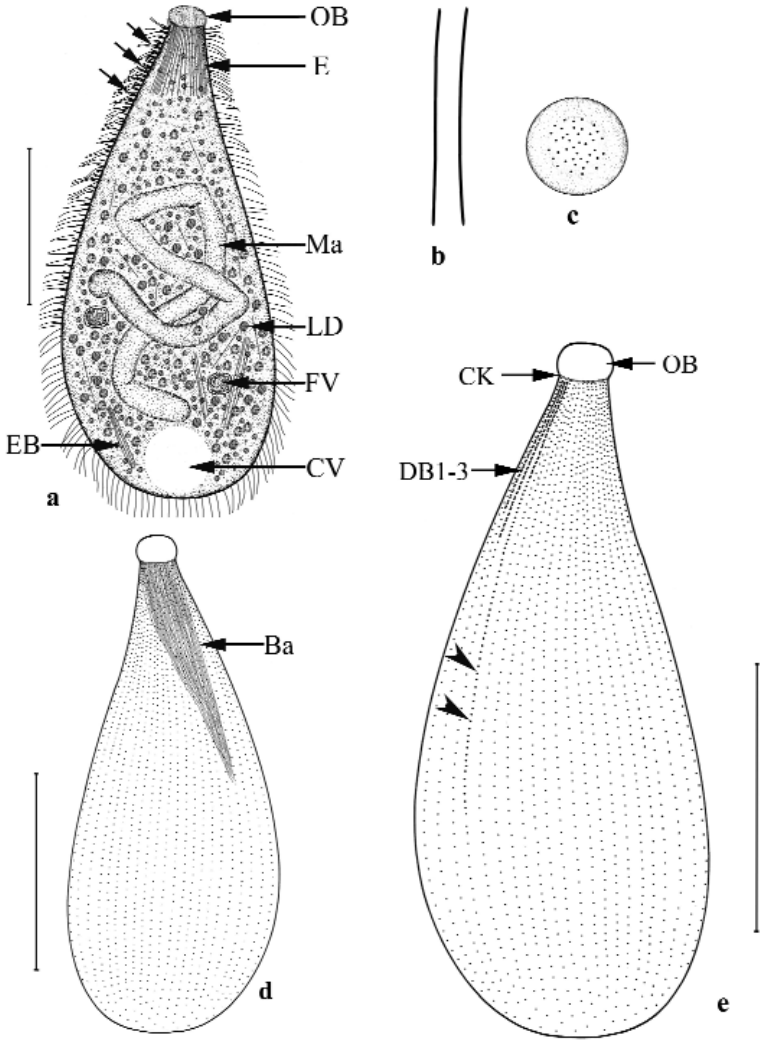

Figure 7a-e. Line diagrams of *Enchelyodon nodosus* from life (a, b, c) and after silver impregnation (d, e). a: Right lateral view of a typical specimen. Arrows indicate dorsal brush brisles. b: Extrusomes are rod-shaped. c: Frontal view of oral bulge, which is filled with extrusomes. d, e: Ciliary pattern of ventral and dorsal side of representative specimen. Arrowheads indicate brush 3 with monokinetidal tail. Ba- oral basket, CK- circumoral kinety, CV- contractile vacuol, DB1-3- dorsal brush rows, E- extrusomes, EB- extrusomes bundle, LD- lipid dropletes, FV- food vacuole, Ma- macronucleus, OB-oral bulge. Scale bars 50 µm.

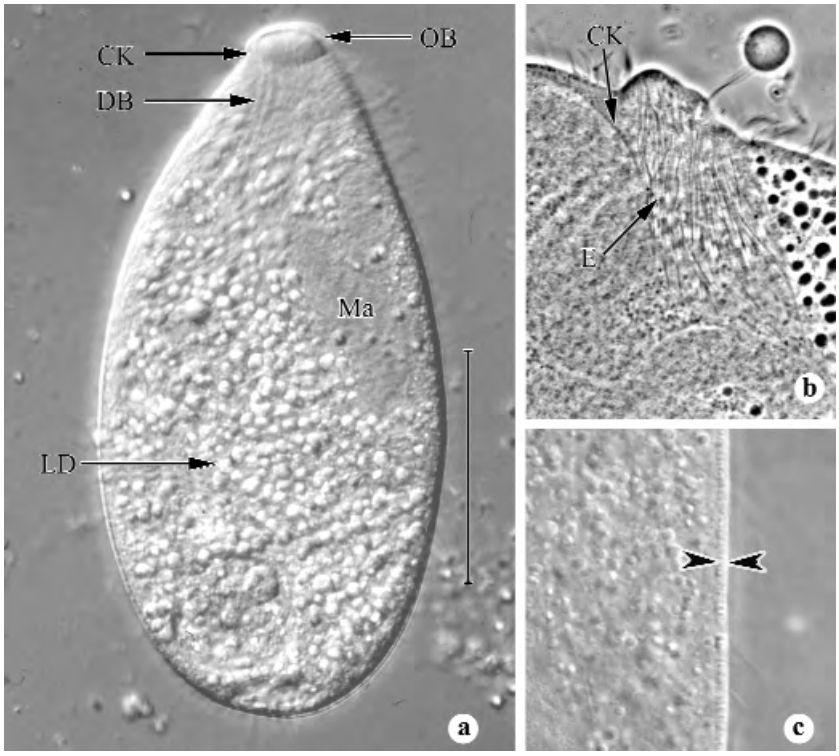

Figure 8a-c. Photomicrographs from life of *Enchelyodon nodosus*. a: Total view of slightly flattened (by cover glass) of the cell. b: Squeezed specimen showing the extrusomes in the oral bulge. c: Cortex with mucocysts (indicated by opposed arrowheads). CK- circumoral kinety, DB- dorsal brush, E- extrusomes, LD- lipid droplets, Ma- macronucleus, OB- oral bulge. Scale bars 50µm.

conspicuous oral bulge; unflattened and non-contractile, but flexible. Cytoplasm often studded with tiny, refractive granules and large food vacuoles probably containing small ciliates making cells opaque and dark at low magnification (Figures 7a, 8a). Macronucleus in central body portion, about 152 µm long, filiform and tortuous, on average longer than cell length (Figure 7a). Usually more than 8 micronuclei scattered throughout cell, about 2-3 µm across, difficult to discern because of very similar size as cytoplasmic inclusions. Contractile vacuole in posterior end, 3-9 excretory pores. Extrusomes attached to oral bulge and scattered in cytoplasm, fine, rod-shaped, in vivo 28-38 µm long (Figures 7a-c, 8b). In silver carbonate preparations, extrusomes become black and irregularly curved; form bundles in posterior body part in some specimens and produce a corona over the oral bulge in some specimens. Additionally, in the cytoplasm there appear extrusomes enlarged in their midregion (developing extrusomes) (Figures 9b,h). Cortex flexible; contains mucocysts about 2 µm in vivo, forming a dense layer (Figure 8c). Movement moderately rapidly by rotation about main body axis.

Cilia 10-11 µm long in vivo, arranged in 37-47 meridional ciliary rows, which abut to the circumoral kinety (Figures 7d,e, 9a). Dorsal brush 3-rowed. Brush row 1 slightly shorter than row 2, each composed of 22-36 pairs of about 3 µm long bristles, row 3 consists of 13-18 dikinetids followed by a monokinetidal tail with about 2.5 µm long bristles; tail extends about 70% of the body length (Figures 7d, 8a, 9b-d, g).

Oral bulge occupies anterior body end, conspicuous because comparatively large, appearing button-like in vivo and contains the anterior portion of the extrusomes; on average 10 µm wide and 14 µm high in vivo, in silver nitrate slides slightly widened (Figures 7a,d, 8a, 9a,e; Table 4). Circumoral kinety at base of oral bulge, composed of about 75 dikinetids with about 8 µm long cilia, exceeding the number of somatic kineties (Figures 7d, 8b, 9a,g). Oral basket about 2/5 of body length (Figures 7e, 9f).

Notes on Ontogenesis: Division of *E. nodosus* is homothetogenic and telokinetal, i.e., the mouth ciliature of the opisthe originates from the somatic ciliary rows.

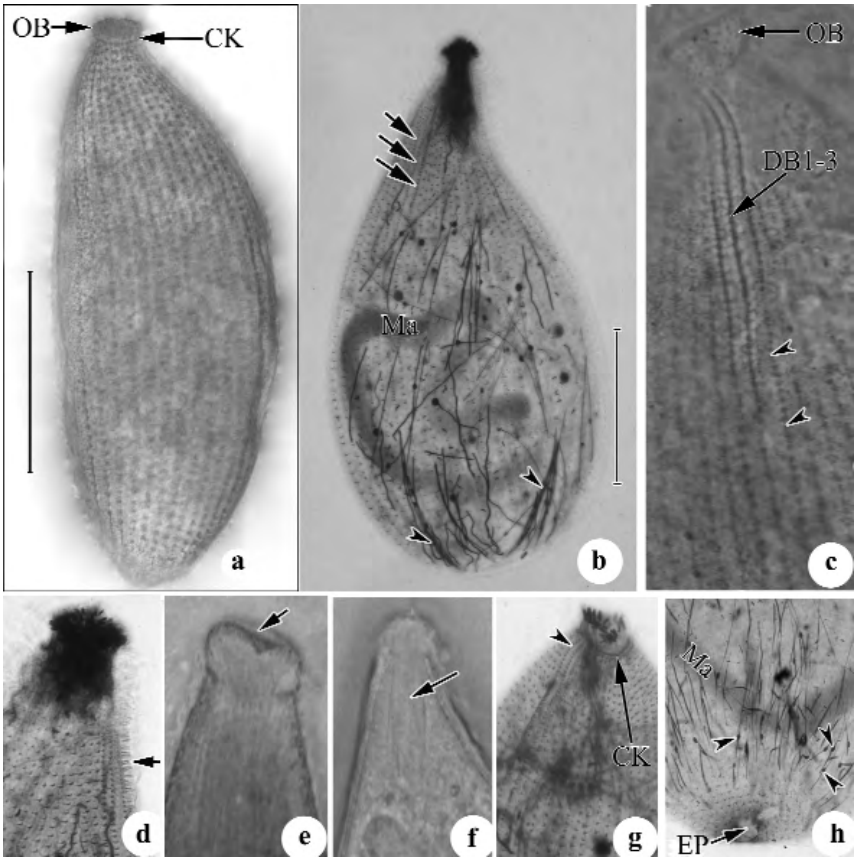

Figure 9a-h. Photomicrographs of silver nitrate (a, c, e, f) and silver carbonate (b, d, g, h) impregnated cells of *Enchelyodon nodosus*, showing somatic and oral infraciliature, nuclear apparatus, and extrusomes. a: Ciliary pattern of ventral side. b: Ciliary pattern of right dorsolateral side. Dorsal brush (arrows) and extrusomes bundles (arrowheads). c: Dorsal brush and silverline system with much broader meshes in the field of the dorsal brush. Arrowheads mark brush row 3 with monokinetidal tail. d: Paired (dikinetids) bristles (arrow) in the brush area. e: Oral bulge. f: The nematodesmata originating from circumoral dikinetids. Arrow indicates oral basket. g: The circumoral kinety at the base of the oral bulge and dorsal brush rows (arrowhead). h: Posterior body portion showing excreation pores and extrusomes. Extrusomes with a globular part (arrowheads). CK- circumoral kinety, DB1-3- dorsal brush rows, EP- excreation pores, Ma- macronucleus, OB- oral bulge. Scale bars 50 µm.

When ontogenesis begins, the cells are on average slightly longer and stouter than interphase specimens. The oral infraciliature and dorsal brush of the proter do not show any changes during division. The opisthe obtains the parental contractile vacuole, while a new contractile vacuole and excretory pores are generated in the proter, just above the prospective fission area. However, we could not observe when the new contractile vacuole is generated. Likewise, we could not follow the origin of the oral basket and micronuclear division, because they are difficult to distinguish from cytoplasmic inclusions.

Ontogenesis commences with the intrakinetal proliferation of basal bodies in the dorsal brush area underneath the prospective division furrow. The brush primordium is recognizable by the narrow and irregular spacing of the basal bodies. At this time, a slight indentation develops in the prospective fission area. When the proliferation of basal bodies begins in the dorsal brush area, the tortuous macronuclear strand begins to extent in main body axis (Figure 10a).

Intermediate stages of fission are shown in Figures 10b,c. Body indentation becomes more distinct in the prospective fission area. The division furrow is transverse and almost equatorial. The newly formed basal bodies in the brush area become dikinetidal to form the dorsal brush rows. The opisthe's dorsal brush develops within the same rows as in the parent. At this stage, all somatic ciliary rows are separated in the division furrow. The macronucleus appears smoothed and less tortuous.

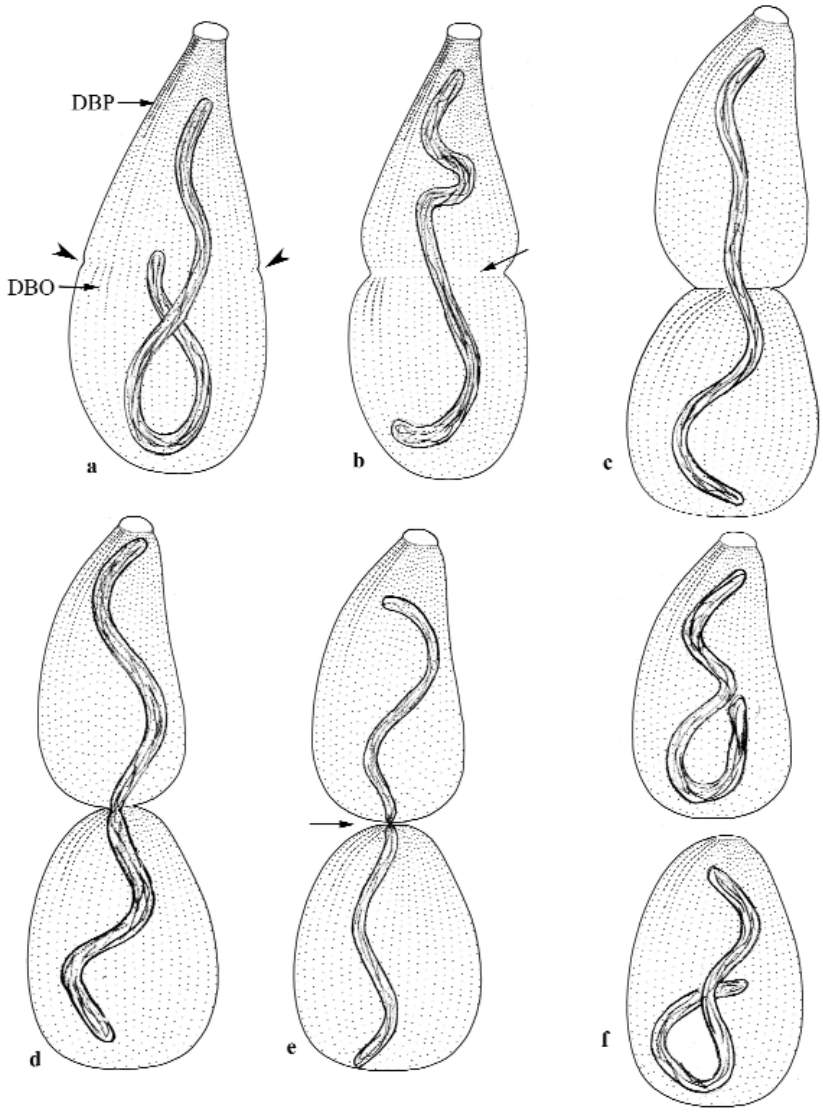

Figure 10a-f. Line diagrams belonging to ontogenesis of *Enchelyodon nodosus* after silver impregnation to show infraciliature and nuclear apparatus. a: Early ontogenetic stage. Arrowheads mark indentation in the prospective fission area. b, c: Intermediate ontogenetic stage. Developing division furrow (arrow) and extending macronucleus. d, e: Late ontogenetic stage. Arrow indicates to macronuclear connection by a fiber in very late divider. f: post-dividers.

Figures 10d,e show very late ontogenetic stages. The division furrow quickly constricts the cell until only a narrow neck occurs. The dorsal brush of the opisthe is almost completed. The macronucleus is still a single strand. The oral apparatus can be completed only after division because the daughters are connected in oral region until separation. Finally, the daughters separate, and the macronucleus breaks into 2 parts in slightly different length, which are still connected by a fibre in the division furrow (Figure 10e, arrow).

In the early post-dividers, macronuclei become sligtly tortuous that is commence to contract and acquire the typical shape of a non-dividing specimen. Proter post–dividers have an ovate shape and are slightly curved, i.e., similar to small interphase specimens, while opisthe post–dividers are stouter, slowly developing the species-specific shape of body and oral bulge (Figure 10f). Most probably the circumoral kinety is formed during post-divisional shaping of the oral bulge.

Table 4. Morphometric data on *Enchelyodon nodosus.*

Characteristics [a]	$\bar{X}$	M	SD	SE	CV	Min	Max	N
Body, length	128.7	123.0	23.7	3.6	18.5	80.0	178.0	43
Body, width	50.9	52.0	8.6	1.3	16.9	30.0	68.0	43
Body width : length, ratio	0.4	0.4	0.1	0.01	25.0	0.3	0.6	43
Oral bulge, width	11.9	12.0	1.8	0.3	15.1	8.0	16.0	43
Oral bulge, height	6.4	6.0	1.1	0.2	17.2	4.0	9.0	43
Macronucleus, length (spread)	151.8	157.5	37.4	8.4	24.6	75.0	200.0	20
Macronucleus, width	6.7	6.5	1.3	0.3	19.4	5.0	10.0	20
Macronucleus length : body length, ratio	1.2	1.1	0.3	0.1	25.0	0.6	1.5	20
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	20
Micronuclei, diameter	2.4	2.0	0.5	0.1	20.8	2.0	3.0	20
Micronuclei, number	12.7	12.5	4.4	1.3	34.6	8.0	20.0	12
Somatic ciliary rows, number[b]	43.2	44.0	2.3	0.6	5.3	37.0	47.0	20
Kinetids in a ventral kinety, number[b]	75.6	72.5	11.7	2.6	15.5	62.0	108.0	20
Dorsal brush 1, length	30.0	30.0	7.1	1.6	23.7	12.0	45.0	20
Dorsal brush 2, length	37.6	37.5	5.0	1.1	13.3	29.0	50.0	20
Dorsal brush 3, length	19.1	20.0	6.4	1.4	33.5	10.0	35.0	20

[a] Data based, if not otherwise stated, on mounted, silver-impregnated (Chatton-Lwoff), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV- coefficient of variation in %, M- median, Max- maximum, Min- minimum, N- number of individuals investigated, SD- standard deviation, SE- standard error of arithmetic mean, $\bar{X}$ - arithmetic mean.

[b] From silver carbonate–impregnated specimens.

Discussion: Berger et al. (1984) originally described 2 populations of this species from terrestrial habitats. Although there were statistically important differences in all studied features the populations had great overall similarity. Thus, they did not separate the populations at species or subspecies level. The Turkish population agrees well with the original description of population 2 both in general morphology and main morphometrics, and is thus likely conspecific with the Turkish specimens. The dorsal brush is similar to that described by Berger et al. (1984). However, Berger et al. (1984) obviously overlooked the monokinetidal bristle tail of row 3.

As yet, no exact description of the ontogenesis of a species of the family Enchelyodontidae exists. Thus, we cannot compare our results with earlier data. However, the division pattern of *E. nodosusus* appears very similar to that found in other haptorids (Berger et al., 1983; Foissner et al., 2002; Xu and Foissner, 2005).

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