Acta Protozool. (2012) 51: 39–54
http://www.eko.uj.edu.pl/ap
doi: 10.4467/16890027AP.12.004.0387

ACTA
PROTOZOOLOGICA

Taxonomic Revision and Neotypification of *Zosterodasys transversus* (Kahl, 1928), with Description of a Mirror-Image Doublet (Ciliophora, Phyllopharyngea, Synhymeniida)

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Summary. The present work describes the morphology and morphometry of a freshwater ciliate, *Zosterodasys transversus*, using live observation and protargol impregnation. The population from the River Ipeľ, Slovakia is designated as a neotype because (i) no type material is available from the species described by Kahl (1928); (ii) the neotype is consistent with *Z. transversus* as described by Kahl (1928); (iii) the neotype is from the same biogeographic region as Kahl's (1928) populations; and (iv) there are several similar species (e.g., *Z. agamalievi*) whose identity is threatened by the species to be neotypified. The main features of *Z. transversus* are: (i) a body size of 120–240 × 50–115 µm *in vivo*; (ii) a broadly to narrowly obovate or elliptical body; (iii) a spherical to very narrowly ellipsoidal macronucleus with a single globular micronucleus nearby; (iv) several scattered contractile vacuoles; (v) an average of 82 ciliary rows, most of which are interrupted by a synhymenium incompletely encircling the body; and (vi) an average of 14 nematodesmal rods strengthening walls of the cyrtos. In the well-growing neotype population, a single cell of a mirror-image type was found. Most of the structures of this monster specimen are similar to those from ordinary cells, except for the double cytostome and cyrtos.

Key words: Freshwater ciliates, Ipeľ River, morphology, morphometry, Slovakia, synonymy.

INTRODUCTION

Zosterodasys transversus is an alpha- to beta-mesosaprobic ciliate that lives in the periphyton and organic mud of running and stagnant freshwaters, but rarely has been very likely erroneously reported from brackish and marine environments (for review, see Foissner *et al.* 1994). Kahl (1928) originally described this species in the genus *Chilodontopsis* Blochmann, 1895. Three years later, Kahl (1931) synonymized his species with *Chilodontopsis vorax* (Stokes, 1887). This name was used for *Z. transversus* until nearly the end of the last century (e.g. Šrámek-Hušek 1956, 1957, 1958; Dragesco 1960; Buck 1961; Webb 1961; Burkovsky 1970; Czapik 1982; Grabacka 1982 *etc.*), when Foissner *et al.* (1994) re-investigated this ciliate using detailed live observation and various silver staining techniques. These supported the validity of Kahl's species and also showed that it belongs to *Zosterodasys*. This genus was

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established by Deroux (1978) with *Z. agamalievi* as the type species. *Zosterodasys* is characterized by an ovoid to reniform body carrying (i) a conspicuous cyrtos, i.e. a tubular cytopharyngeal apparatus whose walls are strengthened by nematodesmata and lined with extensions of postciliary microtubules, and (ii) a special ciliary structure, the so-called synhymenium or hypostomial frange, a band of longer cilia transversly interrupting most of the somatic ciliary rows (Deroux 1978, Fernandez-Leborans 1990, Fernandez-Leborans and Alekperov 1996, Kivimaki *et al.* 1997, Jankowski 2007, Lynn 2008).

The genus *Zosterodasys* was revised by Fernandez-Leborans and Alekperov (1996). However, they did not include *Z. transversus* in their treatise, but recognized several nominal species that highly resemble it. Most of those species were discovered/recorded in freshwater reservoirs from the former USSR by Alekperov (1984), Aliev (1990), and Asadullayeva and Alekperov (2007). However, neither Alekperov (1984) nor Aliev (1990) compared their new taxa with *Z. transversus*. Moreover, the diagnostic characters used to discriminate those species are similar or overlapping, usually completely falling within the natural variability of *Z. transversus*. This has stimulated us to critically review all data available on *Z. transversus* and related species/populations, including new data on a Slovak population from the River Ipeľ. Our taxonomical examination has shown that it is wise to define *Z. transversus* objectively by designation of a neotype, as recommended by the International Code of Zoological Nomenclature (1999) and Foissner (2002).

In the well-growing *Z. transversus* population from the River Ipeľ, we have also found a monster cell of a mirror-image type, the so-called jumelle (e.g. Tchang and Pang 1965). The mirror-image doublet is a morph in which the two cell components are joined laterally (Frankel 1989). Doublets are mostly known in hypotrich ciliates, where they may occur spontaneously or be induced by exposure to UV light, a laser beam, an intense electric field or microsurgery (e.g. Jerka-Dziadosz 1983, Shi and Frankel 1990, Berger 1999, Dias *et al.* 2007). Monsters occur also in rapacious spathidiids, where they have been observed in both the non-flooded Petri dish (raw) cultures, though very rarely (< 1%), and in the semipure cultures, where they are comparatively frequent (~ 14%; Xu and Foissner 2005). We believe that we have reported for the first time a mirror-image doublet in a species from the order Synhymeniida. This monster morph is thus described here in detail.

MATERIAL AND METHODS

Sampling

The source of the River Ipeľ is in Central Slovakia, specifically, in the Slovenské rudohorie (Slovak Ore Mts.) from where it flows southwards to the Hungarian border. Then the Ipeľ turns southwest, west and again south along the border until it flows into the River Danube near the town of Szob in Hungary. The neotype population of *Z. transversus* was found in the Slovak part of the Ipeľ near the village of Chľaba in a littoral sample collected on November 10, 2008. The sample contained mainly fine organic mud and decaying tree leaves. The organic matter was isolated by using a sharp edged tube inserted 10 cm into the substratum. The bottom was thoroughly agitated several times and 0.5 litre of river water was taken from the water column. The collected material was transported to the Department of Zoology, Comenius University in Bratislava, Slovakia in a 1-litre thermos bottle, and was processed within a maximum of 24 hours after the sampling.

Morphological methods and terminology

Cells were studied in life using, *inter alia*, a high-power oil immersion objective and phase contrast optics. Live measurements were made at magnifications of 100–1000 ×. Although *in vivo* values are more or less rough estimates, it is worth giving such data as specimens usually contract during fixation or shrink in preparations. The ciliary pattern was revealed with the protargol method according to protocol A in Foissner (1991). Counts and measurements on prepared specimens were performed at a magnification of 1000 ×. Illustrations of live specimens are based on free-hand sketches, while those of prepared cells were based on micrographs. Terminology is according to Deroux (1978), Foissner and Xu (2007), and Lynn (2008). The higher classification of *Z. transversus* follows Gong *et al.* (2009).

RESULTS AND DISCUSSION

Zosterodasys transversus (Kahl, 1928) Foissner *et al.*, 1994

1928 ***Chilodontopsis transversa* spec. n.** Kahl, *Arch. Hydrobiol.* **19:** 78, Fig. 15b (Fig. 53; partim).

1931 ***Chilodontopsis (Chilodon) vorax* (Stokes, 1887)** – Kahl, *Tierwelt Dtl.* **21:** 225, Fig. 35, 2 (Fig. 54; erroneous synonymization of *C. transversa* with *C. vorax*).

1957 ***Chilodontopsis vorax* Stockes** – Buchar, *Čas. Národ. mus.* **126:** 138, Fig. 1G (Fig. 55; incorrect subsequent spelling of species author name; misidentification).

1957 ***Chilodontopsis vorax* (Stokes 1887)** – Šrámek-Hušek, *Věstn. Čs. zool. spol.* **21:** 12, Fig. 14 (Fig. 57; misidentification).

1960 ***Chilodontopsis (Chilodon) vorax* (Stokes) Kahl** – Dragesco, *Trav. Stn biol. Roscoff (N. S.)* **122:** 251, Fig. 129A (Figs 58–60; misidentifaction).

1961 ***Chilodontopsis (Chilodon) vorax* (Stokes)** – Buck, *Jh. Ver. vaterl. Naturk. Württ.* **116:** 202, Fig. 14 (Fig. 56; misidentification).

1968 ***Chilodontopsis vorax* (Stokes, 1887)** – Chorik, Svobodnoživuŝie infuzorii vodoemov Moldavii, p. 73 (without figure; misidentification).

1990 ***Zosterodasys azerbaijanicus* sp.n.** Aliev, *Zool. Ž.* **69:** 14, Fig. 1 (Figs 68–71; supposed synonym).

1990 ***Zosterodasys shumerica* sp.n.** Aliev, *Zool. Ž.* **69:** 16, Fig. 2, II (Figs 76–78; supposed synonym).

1990 ***Zosterodasys kurensis* sp.n.** Aliev, *Zool. Ž.* **69:** 19, Fig. 4, I (Figs 83–86; supposed synonym).

1990 ***Zosterodasys jankowskii* sp.n.** Aliev, *Zool. Ž.* **69:** 18, Fig. 4, II (Figs 72–75; supposed synonym).

1990 ***Zosterodasys* sp.** – Aliev, *Zool. Ž.* **69:** 23, Fig. 5, II (Figs 79–82).

1994 ***Zosterodasys transversa* (Kahl, 1928) nov. comb.** – Foissner, Berger and Kohmann, *Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft* **1/94:** 418, Figs 1–29 (Figs 61–67; taxonomic revision).

1996 ***Zosterodasys azerbaijanica* Aliev, 1990** – Fernandez-Leborans and Alekperov, *Zoosyst. Rossica* **4:** 5, Fig. 3 [taxonomic revision; incorrect emendation of species group-name to feminine gender without reasoning; figures redrawn from Aliev (1990)].

1996 ***Zosterodasys fluviatilis* sp.n.** Fernandez-Leborans and Alekperov, *Zoosyst. Rossica* **4:** 10, Fig. 10 [a new species for *Zosterodasys* sp. *sensu* Aliev (1990); figures redrawn from Aliev (1990); supposed synonym].

1996 ***Zosterodasys jankowskii* Aliev, 1990** – Fernandez-Leborans and Alekperov, *Zoosyst. Rossica* **4:** 10, Fig. 12 [taxonomic revision; figures redrawn from Aliev (1990)].

1996 ***Zosterodasys kurensis* Aliev, 1990** – Fernandez-Leborans and Alekperov, *Zoosyst. Rossica* **4:** 13, Fig. 14 [taxonomic revision; figures redrawn from Aliev (1990)].

1996 ***Zosterodasys shumerica* Aliev, 1990** – Fernandez-Leborans and Alekperov, *Zoosyst. Rossica* **4:** 16, Fig. 18 [taxonomic revision; figures redrawn from Aliev (1990)].

2007 ***Zosterodasys transversus* (Kahl, 1928)** – Jankowski, Protista II, p. 729 (emendation of species group-name to masculine gender without reasoning).

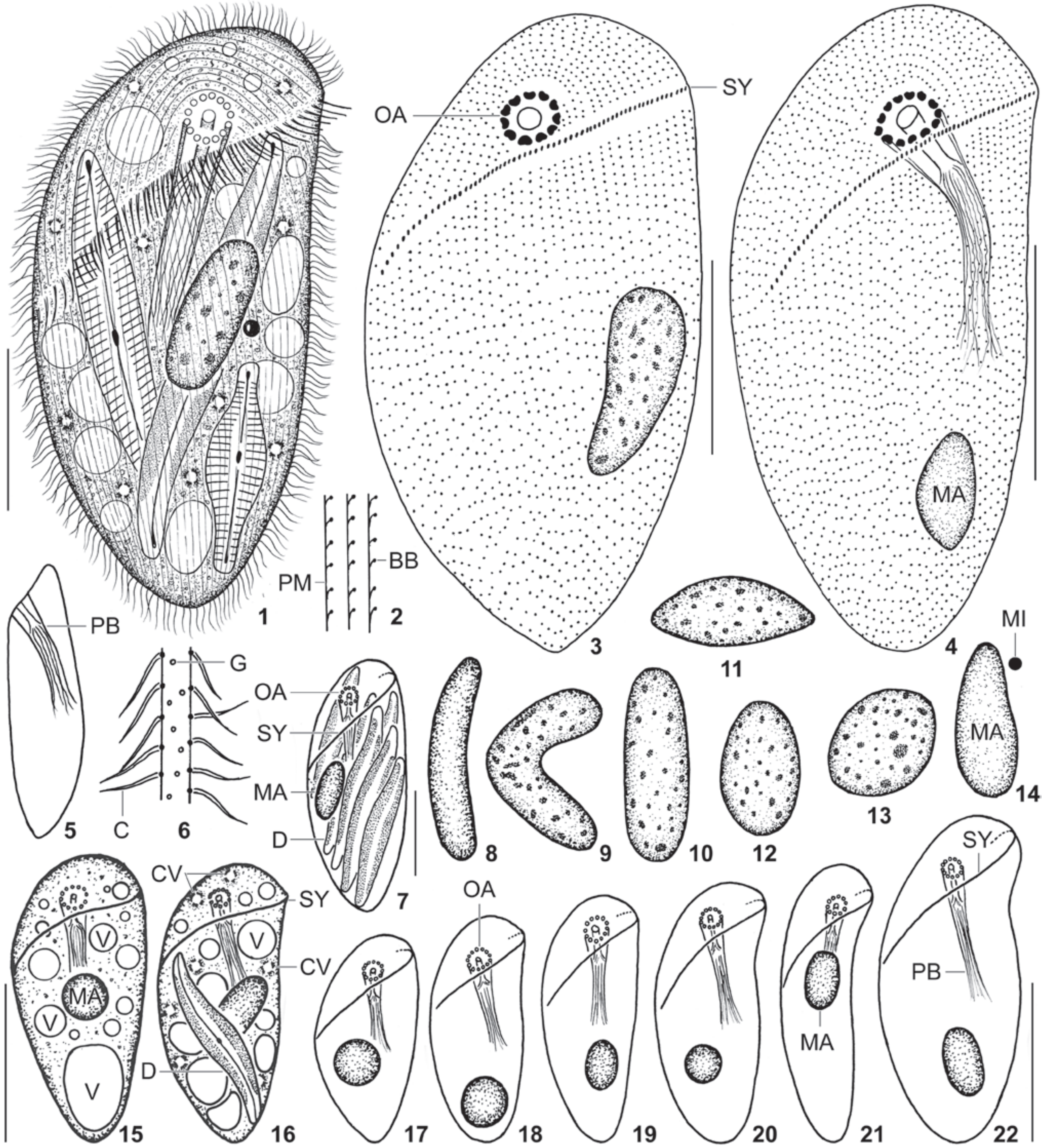
2009 ***Zosterodasys transverses*** – Gong, Stoeck, Miao, Zhang, McL. Roberts, Warren and Song, *J. Eukaryot. Microbiol.* **56:** 341 [18S rRNA gene sequence of a South Korean population (accession number EU286812); incorrect subsequent spelling and therefore unavailable according to Articles 33.3 and 33.5 of the ICZN (1999)].

non ***Chilodontopsis vorax* (Stokes) Kahl** – Agamaliev, 1967, *Cah. Biol. mar.* **8:** 20, Figs 9–10, Pl. II (marine; Agamaliev, 1983, Infusoria of the Caspian Sea, p. 71 assigned his specimens from 1967 to *Zosterodasys agamalievi* Deroux, 1978).

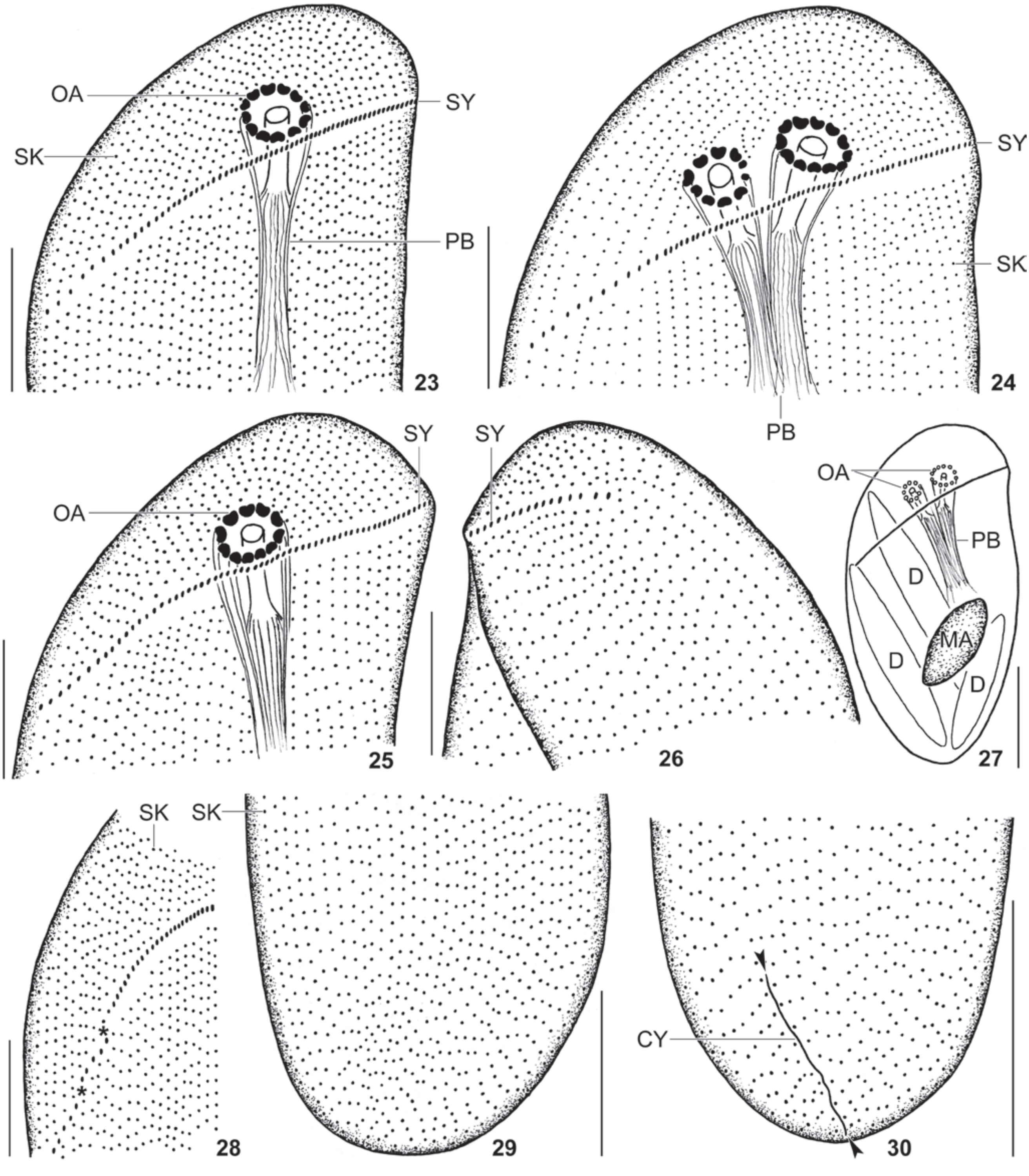
non ***Chilodontopsis vorax* (?) Stokes, 1887** – Burkovsky, 1970, *Acta Protozool.* **7:** 54, Fig. 9 (marine; ventral kineties produce a suture in meridional posterior half of cell, and thus conspecificity with *Z. transversus* can be excluded).

Nomenclature, synonymy and taxonomy: *Zosterodasys transversus* was originally described as *Chilodontopsis transversa* by Kahl (1928). Foissner *et al.* (1994) re-investigated this species with modern morphological methods and combined it with the genus *Zosterodasys*, but without changing the species group-name to masculine gender. This was done by Jankowski (2007) but without providing any reason. According to Articles 30.2.4, 31.2 and 34.2 of the ICZN (1999) we support Jankowski's mandatory change because *Zosterodasys* is masculine gender (Aescht 2001).

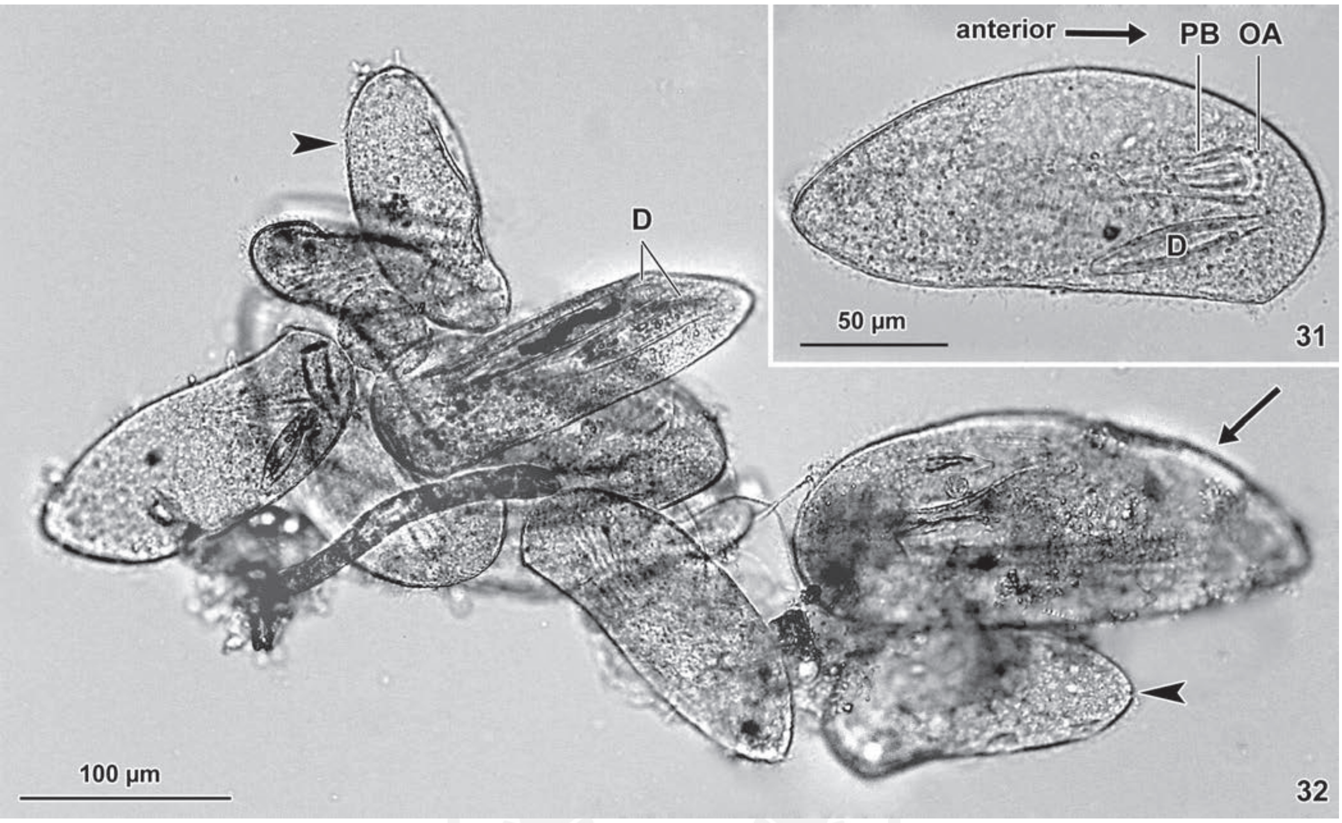
Kahl (1928) mentioned two possible older synonyms of *Z. transversus*: *Nassula oblonga* Maupas, 1883 and *N. pseudonassula* Penard, 1922. Three years later, Kahl (1931) synonymized his species with "*Chilodontopsis (Chilodon) vorax* (Stokes, 1887)." However, these synonymies were refuted by Foissner *et al.* (1994) because the synhymenium, an important feature of *Z. transversus*, was neither mentioned nor illustrated by Maupas (1883) and Penard (1922). Further, Stokes' (1887) species was recognized by Foissner *et al.* (1994) to be a poorly observed *Trithigmostoma*. As later authors followed Kahl's classification, *Z. transversus* was usually erroneously identified as *C. vorax* in faunistic studies (e.g. Šrámek-Hušek 1956, 1957, 1958; Buchar 1957; Dragesco 1960; Buck 1961; Webb 1961; Rivera



Figs 1–22. *Zosterodasys transversus*, neotype specimens from life (1, 5, 6, 15, 16) and after protargol impregnation (2–4, 7–14, 17–22). **1** – ventral view of a representative specimen; **2** – surface view of cortex showing a fibre bundle extending parallel to and right of the somatic kineties; **3**, **4** – ventral view of ciliary pattern and nuclear as well as oral apparatus of main neotype specimens; **5** – lateral view; **6** – surface view showing cortical granulation; **7** – ventrolateral view of a specimen packed with six diatoms; **8–14** – variability of macronucleus which ranges from roundish (13), broadly ellipsoidal (12), ellipsoidal (10) to very narrowly ellipsoidal (8). Rarely it is lenticular (11), curved (9) or obclavate (14); **15**, **16** – ventral view of specimens with strongly vacuolated cytoplasm. Drawn to scale; **17–22** – variability of body shape and size as well as of nuclear apparatus. Drawn to scale. BB – basal bodies, C – cilia, CV – contractile vacuoles, D – ingested diatoms, G – cortical granules, MA – macronucleus, MI – micronucleus, OA – oral apparatus, PB – pharyngeal basket, PM – postciliary microtubules, SY – synhymenium, V – vacuoles. Scale bars: 50 µm (1, 3, 4, 7) and 100 µm (15–22).



Figs 23–30. *Zosterodasys transversus*, neotype specimens after protargol impregnation. **23**, **25** – ventral view of ciliary pattern and oral apparatus of normal specimens; **24** – ventral view of ciliary pattern and oral apparatus of an abnormal specimen having a double cytostome and cyrtos; **26** – dorsal view of ciliary pattern showing synhymenium extending onto dorsal side; **27** – ventral view of the monster whose anterior body portion is shown in (24); **28** – ventrolateral view of a specimen having some breaks in synhymenium (asterisks); **29**, **30** – ventral and dorsal views of ciliary pattern in posterior body portion showing that somatic kineties extend meridionally, i.e. do not form a suture or spica. Arrowheads denote slit-like cytopyge. CY – cytopyge, D – diatoms, MA – macronucleus, OA – oral apparatus, PB – pharyngeal basket, SK – somatic kineties, SY – synhymenium. Scale bars: 20 µm (28), 30 µm (23–26, 29, 30), and 50 µm (27).

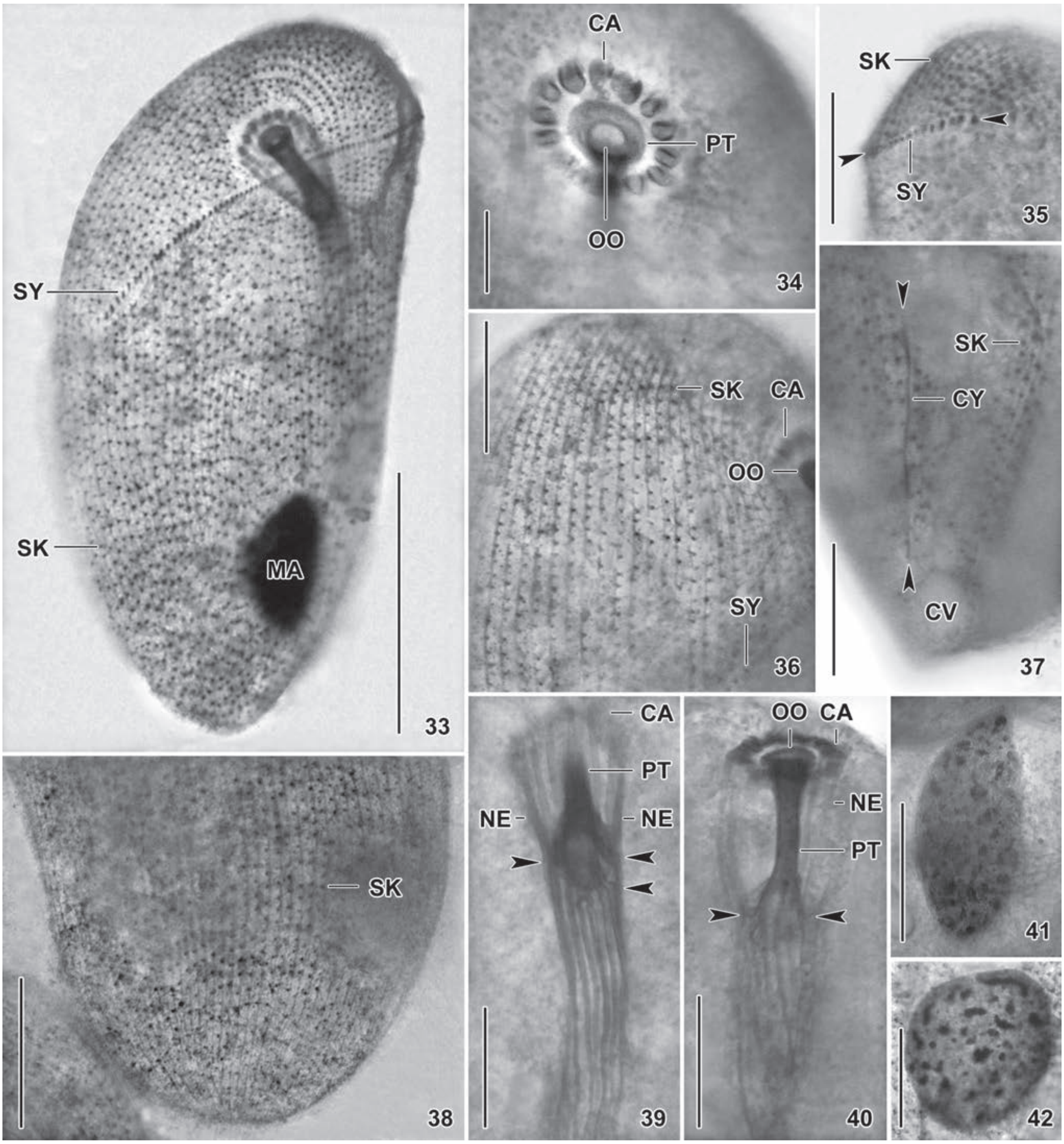


Figs 31–32. *Zosterodasys transversus*, neotype specimens from life. All specimens are from a field sample processed within 24 hours of collection. **31** – ventral view of a representative neotype cell with an ingested diatom; **32** – variability of body shape and size. Note that the largest specimen (arrow) is almost twice the size of the smaller ones (arrowheads). D – diatoms, OA – oral apparatus, PB – pharyngeal basket. Scale bars: 50 µm (31) and 100 µm (32).

et al. 1979; Czapik 1982; Grabacka 1982; Detcheva 1986; Pettigrosso and Cazzaniga 1987).

Agamaliev (1983) considered *Chilodontopsis vorax* (i.e. *Z. transversus*) as a synonym of *Z. agamalievi*. Indeed, both species are highly similar, but can be distinguished by the body size (120–250 µm in *Z. transversus* vs. 80–150 µm in *Z. agamalievi*) and, especially, habitat (freshwater vs. saltwater). Considering that few ciliates live in both, limnetic and saline environments, we keep *Z. transversus* and *Z. agamalievi* separate, assigning limnetic records to the former and saline ones to the latter. This is also supported by the 18S rRNA gene data, according to which *Z. transversus* differs from *Z. agamalievi* by approximately 2% (Gong *et al.* 2009, Kivimaki *et al.* 2009). Thus, Kahl (1928) very likely mixed *Z. transversus* with *Z. agamalievi*. We consider Kahl's specimens from a duck puddle near Gasthof Saselbek as *Z. transversus*, while those from Oldesloer saltwaters as *Z. agamalievi*.

Proposed new synonyms: Aliev (1990) and Fernandez-Leborans and Alekperov (1996) described five nominal freshwater *Zosterodasys* species, viz., *Z. azerbaijanicus*, *Z. fluviatilis*, *Z. kurensis*, *Z. jankowskii*, and *Z. shemerica*, which strongly resemble *Z. transversus*. Specifically, they have a similar body shape and size as well as the number of the nematodesmal rods as *Z. transversus* (Table 1). As concerns the contractile vacuole pattern, neither Aliev (1990) nor Fernandez-Leborans and Alekperov (1996) mentioned it in live specimens and figured only fixed cells, in which contractile vacuoles are very difficult to discern. There is only one feature, i.e. the number of the ciliary rows, that can be seemingly used for separating those species from *Z. transversus* (50–70 vs. 74–95). However, data of Aliev (1990) and Fernandez-Leborans and Alekperov (1996) came from limited material (n = 4–6), giving a poor reflection of intraspecific variability. Moreover, Aliev (1990) and Fernandez-Leborans and Alekperov (1996)



Figs 33–42. *Zosterodasys transversus*, neotype specimens after protargol impregnation. **33** – ventral view of ciliary pattern, nuclear and oral apparatus of a main neotype specimen; **34**, **39**, **40** – frontal (34) and lateral (39, 40) views of oral apparatus which consists of a central deeply impregnated pharyngeal tube and nematodesmal rods arranged in a ring. The nematodesmata are straight for most of their length but curve toward the oral opening at their distal end, where they are capped by a capitulum. Arrowheads (39, 40) note the site where the cytopharyngeal tube radiates fibres towards the nematodesmata; **35** – dorsal view of ciliary pattern showing synhymenium extending onto dorsal side (opposed arrowheads); **36** – surface view showing a fibre bundle extending in parallel and right of the somatic kineties; **37**, **38** – dorsal and ventral views of ciliary pattern in posterior body portion. The somatic kineties extend meridionally, i.e. do not form a suture. Arrowheads in (37) denote the slit-like cytopyge. **41**, **42** – lenticular and globular macronucleus. CA – capitulum, CV – contractile vacuole, CY – cytopyge, MA – macronucleus, OO – oral opening, NE – nematodesmal rods, PT – pharyngeal tube, SK – somatic kineties, SY – synhymenium. Scale bars: 10 µm (34), 20 µm (39–42), 30 µm (35–38), and 50 µm (33).

Table 1. Comparison of *Zosterodasys transversus* populations and supposed synonyms of that species.

Species/Population	Body size	Number of nematodesmal rods	Number of ciliary rows[a]	Reference
Chilodontopsis transversa Kahl, 1928[b]	90–120 µm long *in vivo*	12–16	?	Kahl (1928)
Chilodontopsis (Chilodon) vorax (Stokes, 1887)	120–160 µm long *in vivo*, 180 µm according to figure legend	16	?	Kahl (1931)
Zosterodasys azerbaijanicus Aliev, 1990	140–150 µm long after fixation, up to 200 × 50–55 µm *in vivo*	10–12	50–55 in mid-body	Aliev (1990)
Zosterodasys fluviatilis Fernandez-Leborans and Alekperov, 1996[c]	135–145 × 60 µm after fixation	15	about 70	Aliev (1990)
Zosterodasys jankowskii Aliev, 1990	170–180 µm long after fixation, 210–230 × 40–45 µm *in vivo* (n = 6)	15	55–60 in mid-body	Aliev (1990)
Zosterodasys kurensis Aliev, 1990	220 × 90 µm after fixation	14–15	60–65 in mid-body	Aliev (1990)
Zosterodasys shumerica Aliev, 1990	150–160 µm long after fixation, 160–180 × 50–55 µm *in vivo* (n = 4)	13	60–65 in mid-body	Aliev (1990)
Zosterodasys transversa (Kahl, 1928), Austrian population	130–250 × 65–90 µm *in vivo*	12–18	79–120 in total	Foissner *et al.* (1994)
Zosterodasys transversus (Kahl, 1928), Slovak neotype population	120–240 × 50–115 µm *in vivo*	12–16	74–95 in total	Present study

[a] Aliev (1990) slightly underestimated the total number of the ciliary rows, because he counted them in mid-body and not posterior to the level of the synhymenium, where their number is higher by about 5–10 as several marginal ciliary rows do not reach mid-body.

[b] Some of the data might refer to *Z. agamalievi* because Kahl (1928) very likely mixed this species with *Z. transversus*.

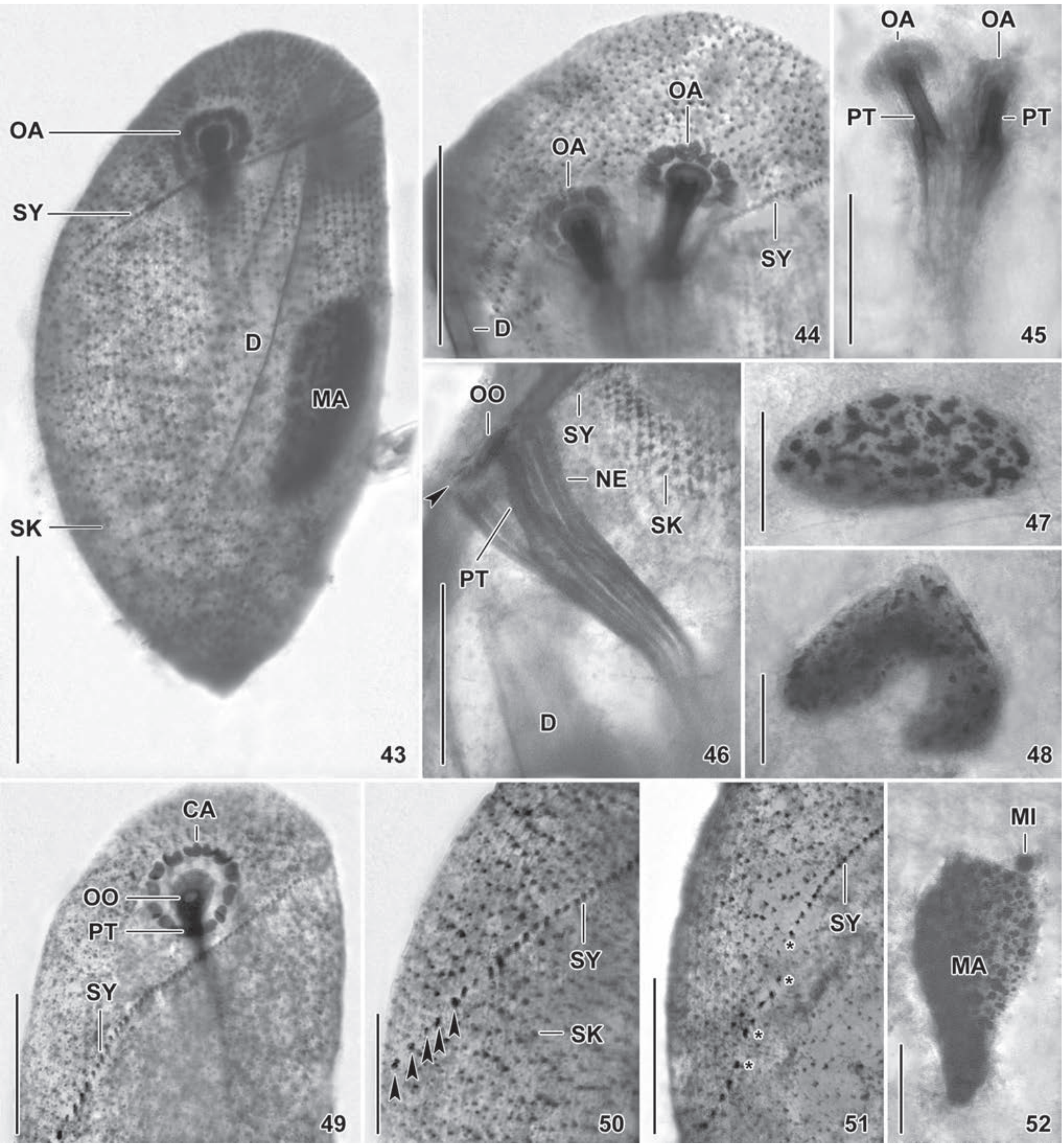
[c] Fernandez-Leborans and Alekperov (1996) established this species for *Zosterodasys* sp. *sensu* Aliev (1990).

slightly underestimated the total number of the ciliary rows, because they counted them in mid-body and not posterior to the level of the synhymenium, where their number is higher by about 5–10 as several marginal ciliary rows do not reach mid-body (Figs 68, 72, 75, 76, 78, 81, 85). When this value is added, the total number of the ciliary rows is close or matching the lower limit of the neotype specimens (Table 1). Therefore, we suggest *Z. azerbaijanicus*, *Z. fluviatilis*, *Z. kurensis*, *Z. jankowskii*, and *Z. shemerica* as subjective junior synonyms of *Z. transversus* at the present state of knowledge. However, if further research shows that this morphometric difference is stable and statistically significant, these species can be resurrected as subspecies of *Z. transversus* according to the species/subspecies concept of Foissner *et al.* (2002) and Foissner and Xu (2007).

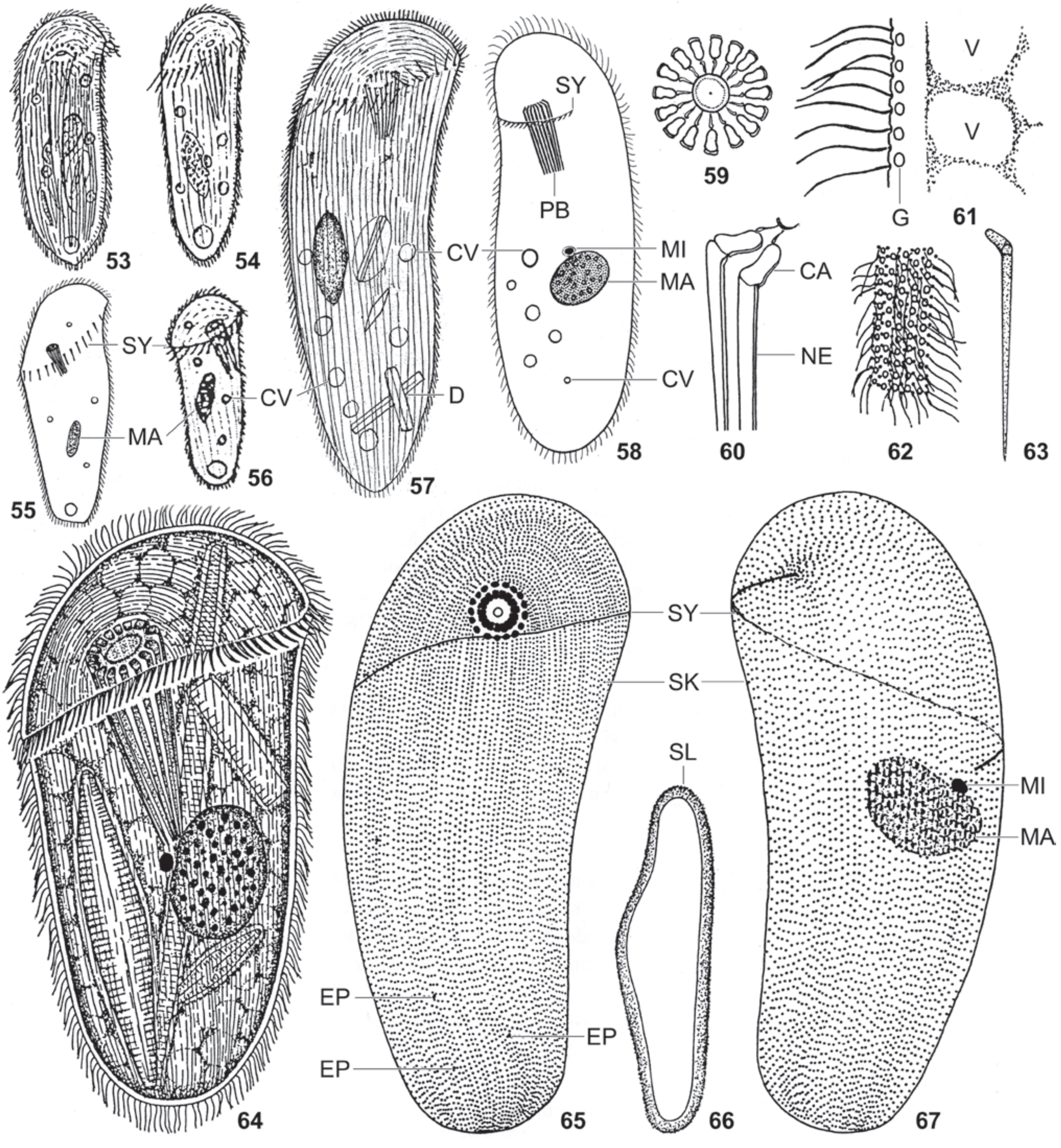
Neotypification: We neotypify *Z. transversus* with a Slovak population from the River Ipeľ for the following objections: (i) it is generally known that no type material is available from species described by Kahl (1928); (ii) there is strong evidence that the neotype is consistent with *Z. transversus* as originally described by Kahl (1928) and revised by Kahl (1931) although synonymized with *Chilodontopsis vorax*; (iii) the neotype is from the same biogeographic region; (iv) the existing descriptions are decisively incomplete, e.g. they lack detail morphometric data; (v) there are several similar species (e.g. *Z. agamalievi*) whose identity is threatened by the species to be neotypified; and (vi) neotype slides are of a good quality allowing the specific features to be clearly recognized.

Improved diagnosis (neotype population): Size about 120–240 × 50–115 µm *in vivo*. Body shape broadly to narrowly obovate or elliptical. Macronucleus roundish to very narrowly ellipsoidal with a single globular micronucleus nearby. Several scattered contractile vacuoles. On average 82 narrowly spaced ciliary rows: 44 ventral and 37 dorsal. Synhymenium composed of about 72 dikinetids ventrally and 17 dikinetids dorsally, occupies 48% of body length, and incompletely encircles cell. On average 14 (12–16) nematodesmal rods. Freshwater.

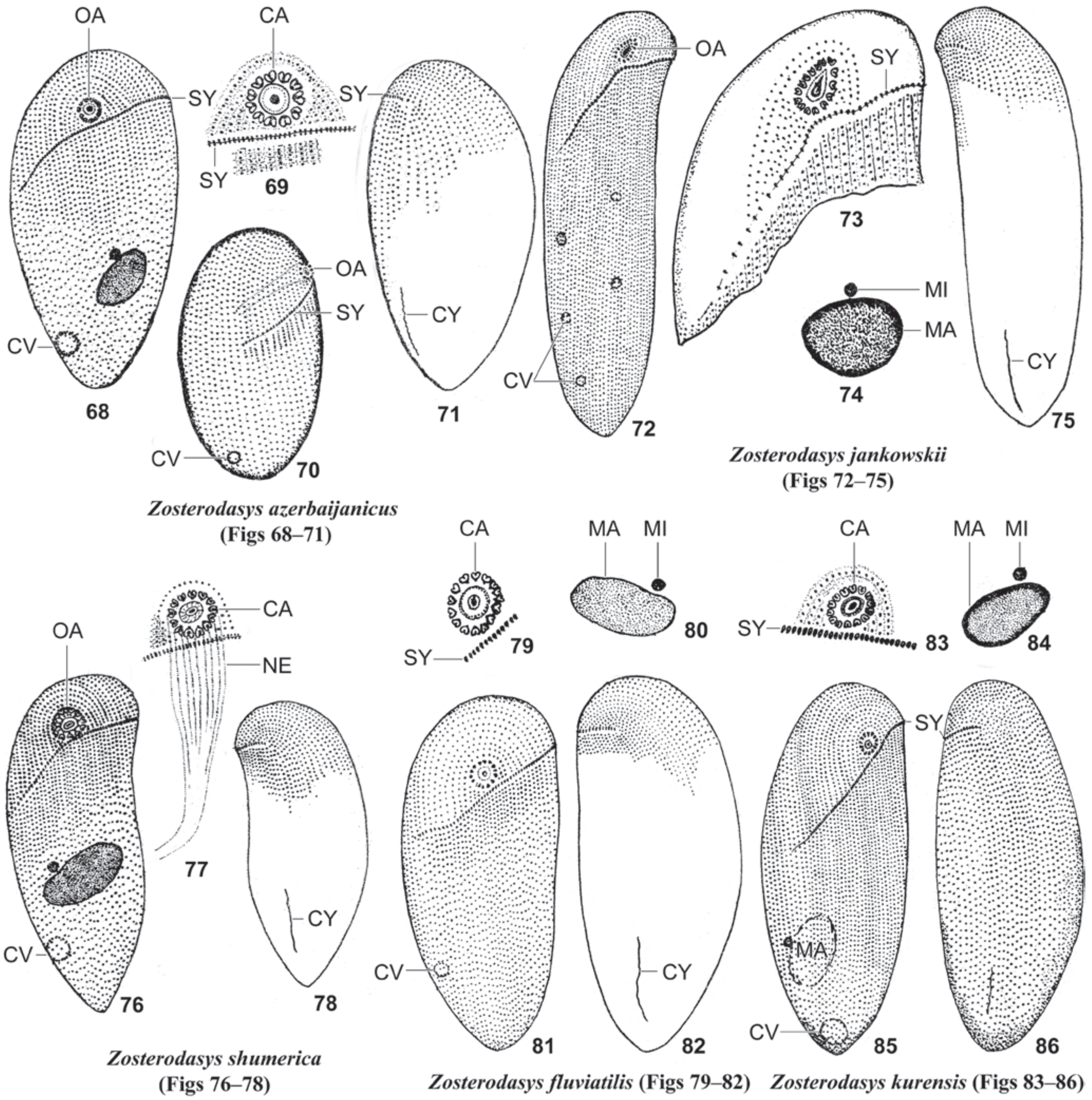
Type locality: Kahl (1928) mentioned two sites, i.e. duck puddle near Gasthof Saselbek and Oldesloer saltwaters, but did not fix any as the type locality. The neotype is from fine organic mud and decaying tree leaves from the River Ipeľ near the village of Chľaba,



Figs 43–52. *Zosterodasys transversus*, neotype specimens after protargol impregnation. **43** – ventral view of ciliary pattern, nuclear and oral apparatus of a neotype specimen; **44** – ventral view of ciliary pattern and oral apparatus of a mirror-image cell; **45** – dorsal view of double pharyngeal tube of the monster shown in (44); **46** – lateral view of oral apparatus. The nematodesmal rods are straight for most of their length, but curve toward the oral opening at distal end (arrowhead); **47**, **48**, **52** – shape variability of macronucleus. Most specimens have an ellipsoidal macronucleus (47), while some display a curved (48) or a clavate (52) macronucleus; **49** – ventral view of anterior body portion showing oral apparatus and synhymenium; **50** – synhymenium extends obliquely interrupting most of the ciliary rows. It is composed of narrowly spaced dikinetids, except for the posterior tail, where they are spaced comparatively loosely (arrowheads); **51** – ventrolateral view of a specimen having some breaks in synhymenium (asterisks). CA – capitulum, D – ingested diatom, MA – macronucleus, MI – micronucleus, OA – oral apparatus, OO – oral opening, NE – nematodesmal rods, PT – pharyngeal tube, SK – somatic kineties, SY – synhymenium. Scale bars: 20 µm (47, 48, 50–52), 30 µm (44–46, 49), and 50 µm (43).



Figs 53–67. *Zosterodasys transversus* and its supposed synonyms from life (53–64), after protargol impregnation (65, 67), and after methyl green-pyronin stain (66). After Kahl 1928 (53), 1931 (54); Buchar 1957 (55); Buck 1961 (56); Šrámek-Hušek 1957 (57); Drageso 1960 (58–60); and Foissner *et al.* 1994 (61–67). **53** – *C. transversa*, length 90–120 µm; **54** – *C. vorax*, length 180 µm; **55** – *C. vorax*, length 200 µm; **56** – *C. vorax*, length 175 µm; **57** – *C. vorax*, length not given; **58–60** – *C. vorax*, total dorsal view, length 185 µm (58); frontal view of oral apparatus (59); and lateral view of nematodesmal rods (60); **61–67** – *Z. transversa*, optical section (61) and surface view (62), showing cortical granulation and vacuolated cytoplasm; the nematodesmal rods are anteriorly curved (63); total ventral view, length 160 µm (64); ventral (65) and dorsal (67) views of ciliary pattern and nuclear apparatus, length 185 µm; with methyl green-pyronin staining the cells are first covered by a red substance of small plates which later becomes blue and structureless (66). CA – capitulum, CV – contractile vacuoles, D – ingested diatoms, EP – excretory pores, G – cortical granules, MA – macronucleus, MI – micronucleus, NE – nematodesmata, PB – pharyngeal basket, SL – slime layer, SK – somatic kineties, SY – synhymenium, V – vacuoles.



Figs 68–71. *Zosterodasys azerbaijanicus* after protargol impregnation (from Aliev 1990). **68**, **70**, **71** – ventral, lateral and dorsal views of ciliary pattern and nuclear as well as contractile vacuole apparatus, length 150 µm, 125 µm and 150 µm; **69** – ciliary pattern in oral region.
Figs 72–75. *Zosterodasys jankowskii* after protargol impregnation (from Aliev 1990). **72**, **75** – ventral and dorsal views of ciliary pattern and arrangement of contractile vacuoles, length 190 µm; **73** – detail of ciliary pattern in anterior body portion; **74** – nuclear apparatus.
Figs 76–78. *Zosterodasys shumerica* after protargol impregnation (from Aliev 1990). **76**, **78** – ventral and dorsal views of ciliary pattern and nuclear as well as contractile vacuole apparatus, length 225 µm and 190 µm; **77** – oral apparatus.
Figs 79–82. *Zosterodasys fluviatilis* after protargol impregnation (from Aliev 1990). This species was designated as *Zosterodasys* sp. in Aliev (1990). **79** – oral apparatus and short portion of synhymenium; **80** – nuclear apparatus; **81**, **82** – ventral and dorsal views of ciliary pattern and contractile vacuole apparatus, length 145 µm and 150 µm.
Figs 83–86. *Zosterodasys kurensis* after protargol impregnation (from Aliev 1990). **83** – oral apparatus; **84** – nuclear apparatus; **85**, **86** – ventral and dorsal views of ciliary pattern and nuclear as well as contractile vacuole apparatus, length 215 µm. CA – capitulum, CV – contractile vacuoles, CY – cytopyge, MA – macronucleus, MI – micronucleus, NE – nematodesmal rods, OA – oral apparatus, SY – synhymenium.

Slovakia (47°49′N18°49′E). According to Article 76.3 of the ICZN (1999), the place of origin of the neotype becomes the type locality of the nominal species-group taxon, despite any previously published statement of the type locality.

Type material: No type material is available from Kahl's specimens. We deposit four neotype slides with hundreds of protargol-impregnated specimens from the neotype locality in the Biology Center of the Museum of Natural History of Upper Austria, Linz (LI). Relevant specimens are marked by black ink circles on the coverslip.

Etymology: Not given in the original description. The Latin adjective *transvers·us*, *-a*, *-um* ([m, f, n]; transverse, oblique) obviously refers to the course of the synhymenium that transversely extends over the ventral side of the cell.

Description of neotype population: Size *in vivo* variable, usually about 120–240 × 50–115 µm (Figs 31 and 32). Body slightly flexible and acontractile. Shape broadly to narrowly obovate or sometimes elliptical, i.e. length:width ratio 1.8–2.7:1, averaging 2.3:1 after protargol impregnation (Table 2); may be strongly deformed in over- or under-nourished cells. Anterior end arched, while posterior one tapering, narrowly rounded or rarely broadly rounded; body margins more or less convex depending on nutritional state; inconspicuous snout-like projection on left side margin where synhymenium extends onto dorsal side (Figs 1, 3–5, 15–22). Ventral side flat, dorsal one more or less vaulted; dorsoventrally flattened about 3–4:1 (Fig. 5).

Nuclear apparatus usually in mid-body, but sometimes localized only slightly posterior to level of oral opening or displaced to rear body end in protargol im-

Table 2. Morphometric data on the neotype population of *Zosterodasys transversus* from the River Ipeľ, Slovakia. Data based on mounted, protargol-impregnated (Foissner's method), and randomly selected specimens from a field sample. Measurements in µm. CV – coefficient of variation in %, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of specimens investigated, SD – standard deviation, SE – standard error of arithmetic mean.

Characteristics	Mean	M	SD	SE	CV	Min	Max	n
Body, length	148.2	144.0	25.6	0.9	17.3	109.0	206.0	27
Body, width	66.2	67.0	12.9	0.5	19.5	43.0	98.0	27
Body length:width, ratio	2.3	2.3	0.3	0.0	11.2	1.8	2.7	27
Anterior body end to cytostome, distance	16.1	15.0	2.5	0.1	15.6	13.0	20.0	21
Cytostome, largest diameter	15.3	15.0	1.9	0.1	12.5	12.0	19.0	21
Nematodesmal rods, number	14.0	14.0	1.0	0.0	7.0	12.0	16.0	21
Cyrtos, maximum length	72.0	70.5	8.9	0.4	12.4	59.0	87.0	21
Anterior body end to macronucleus, distance	63.1	60.0	19.3	0.9	30.6	32.0	122.0	21
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	27
Macronucleus, length[a]	36.0	34.0	6.9	0.3	19.1	27.0	50.0	21
Macronucleus, width[a]	25.1	26.0	6.8	0.3	26.9	14.0	37.0	21
Macronucleus, length:width ratio[a]	1.5	1.3	0.4	0.0	28.2	1.0	2.4	21
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	3
Micronucleus, largest diameter	3.7	4.0	–	–	–	3.0	4.0	3
Ventral somatic kineties, number[b]	43.7	43.0	4.4	0.2	10.0	36.0	52.0	23
Dorsal somatic kineties, number[b]	36.5	36.0	3.6	0.2	9.9	30.0	43.0	17
Somatic kineties, total number	82.4	81.0	6.2	0.5	7.6	74.0	95.0	13
Somatic basal bodies in mid-body in 10 µm, number	3.6	4.0	–	–	–	3.0	4.0	21
Anterior body end to posterior end of synhymenium, distance	66.0	66.0	8.9	0.4	13.4	49.0	83.0	21
Synhymenium, % of body length	47.6	46.9	8.4	0.4	17.7	35.4	69.0	21
Dikinetids in ventral portion of synhymenium, number	71.8	72.0	8.5	0.4	11.8	53.0	94.0	21

[a] Specimens with a narrowly to very narrowly ellipsoidal macronucleus were not included in this morphometric analysis.

[b] Counted at level slightly posterior to synhymenium, i.e. not in mid-body.

pregnated specimens (Figs 1, 3, 4, 7, 15–22, 33, 43; Table 2). Invariably a single macronucleus, rather variable in shape and size, ranging from spherical to very narrowly elliptical, or rarely lenticular, curved and clavate (Figs 8–14, 41, 42, 47, 48, 52; Table 2). Nucleoli evenly distributed, globular to lobate, 1.5–3 µm in diameter after protargol impregnation (Figs 3, 9–13, 41, 42, 47, 48, 52). Invariably a single globular to broadly ellipsoidal micronucleus usually positioned close to mid-portion of macronucleus; approximately 4 µm across in protargol preparations where sometimes surrounded by a thin hyaline capsule; usually not impregnated with the protargol method used (Figs 14, 52; Table 2).

Several to many irregularly distributed contractile vacuoles, posterior one sometimes distinctly enlarged; difficult to recognize in specimens with strongly vacuolated cytoplasm (Figs 1, 15, 16). Cytopyge slit-like, located on dorsal posterior portion of cell, sometimes impregnates deeply with the protargol method used (Figs 30 and 37, arrowheads). Cortical granules (very likely mucocysts) loosely spaced, colourless, only about 0.8–1 µm across and thus inconspicuous, impregnate faintly with protargol (Fig. 6). Cytoplasm colourless, usually strongly vacuolated, packed with granules and food vacuoles containing pennate, rarely centric, diatoms (Figs 1, 7, 15, 16, 31, 32). Movement unresting, swims by rotation about main body axis, also jerks to and fro, or glides and roots between particles of organic mud.

Somatic cilia about 10 µm long *in vivo*; ordinarily to widely spaced, i.e. intrakinetidal distance usually about 2.5–3.5 µm after protargol impregnation; somatic basal bodies associated with (postciliary?) fibres extending backwards on right side of kineties (Figs 2, 36, 38). Ciliary rows equidistantly and narrowly spaced, that is, intrakinetal distance on average 1.5 µm ventrally and 1.8 µm dorsally. On average 82 (74–95) ciliary rows: 36–52 ventrally and 30–43 dorsally. Preoral kineties start on anterior side of synhymenium arching over cytostome, while postoral kineties commence slightly posterior (2–3 µm) to synhymenium extending meridionally to rear body end, i.e. not forming a suture or spica (Figs 3, 4, 23, 25, 29, 30, 33, 38, 43). Left dorsal kineties begin on posterior side of synhymenium, while right dorsal kineties curve up toward anterior pole and then bend down to abut on anterior side of synhymenium (Figs 26, 35). Synhymenium an oblique row of paired cilia incompletely encircling body, i.e. extending from left dorsal surface through ventral side to reach right dorsal surface; on average occupies 47% of body length; composed of densely spaced dikinetids, except for posterior tail where arranged comparatively widely (Figs 3, 4, 23, 25, 26, 33, 43, 49, 50); very rarely with some breaks (Figs 28 and 51, asterisks). Number of synhymenial dikinetids: 53–94 ventrally and about 15–20 dorsally (Table 2).

Cytostome usually in anterior 1/10 of body length on mid-ventral surface, approximately 15 µm in diameter after protargol impregnation (Table 2). Cyrtos a prominent obconical structure anteriorly associated with cytostome and penetrating deep into cytoplasm, composed of (i) nematodesmal rods arranged around cytostome in a ring and (ii) a central cytopharyngeal tube lined by postciliary microtubules (Figs 3, 4, 23, 25, 33, 34, 39, 40, 46, 49). On average 14 nematodesmal rods per cyrtos; individual nematodesmata about 59–87 µm long after protargol impregnation, straight for most of their length but curving toward oral opening at their distal end, where capped by a capitulum about 3 µm across (Figs 34, 46, 49; Table 2). Cytopharyngeal tube 15–20 µm long, deeply impregnated with protargol, its proximal portion radiates fibres contacting nematodesmata and then extending to their posterior end (Figs 39 and 40, arrowheads).

Description of mirror-image doublet (Figs 24, 27, 44, 45): A single monster cell of a mirror-image type was found in a field sample, containing more than 300 cells from the neotype population of *Z. transversus*. Most of the structures of the doublet are similar to those from singlets, except for the oral apparatus.

The doublet measures 164 µm long and 81 µm wide after protargol impregnation, and is obovate in shape, i.e. has a length:width ratio of about 2:1. The macronucleus is situated in the third body quarter and has a size of approximately 50 × 25 µm. The small to medium-sized globular nucleoli are evenly distributed over the macronucleus. The micronucleus is not recognizable. There are about 47 postoral ventral ciliary rows which are interrupted by an obliquely extending synhymenium composed of about 72 narrowly spaced dikentids. The distal preoral kineties curve over the double cytostome, while some of the proximal preoral kineties bend only over the left, slightly larger component. The left cytostome is approximately 15 µm in diameter and it is supported by 12 nematodesmata, while the right cytostome is 12 µm across and is associated with 10 nematodesmata. The left cytopharyngeal tube is 19 µm long, while the right one is shorter measuring 12 µm. At least one of the cytostomes can participate in food acquisition, as shown by three ingested pennate diatoms having a length of 25–120 µm.

Comparison with related species: There are several freshwater *Zosterodasys* species that resemble *Z. transversus*. *Zosterodasys kasymovi* Aliev, 1990 and *Z. mirabilis* Alekperov, 1984 are distinguished from *Z. transversus* by the much larger body (300–350 µm vs. 120–250 µm), while *Z. alizadei* Aliev, 1990 and *Z. debilis* Alekperov, 1984, on the contrary, by the much smaller one (50–70 µm, rarely up to 90 µm). *Zosterodasys raikovi* Aliev, 1990 and *Z. derouxi* Aliev, 1990 differ from *Z. transversus* by the higher number of the micronuclei (1–3, usually 2 vs. invariably 1) and, especially, by the course of the ventral postoral ciliary rows (forming a suture vs. extending meridionally). In contrast to *Z. transversus*, *Z. henarensis* Fernandez-Leborans and Alekperov, 1996 displays a much longer synhymenium which completely (vs. incompletely) encircles the body. On the other hand, *Z. serrani* Fernandez-Leborans, 1990 has a synhymenium restricted to the ventral side (vs. extending onto the dorsal side in *Z. transversus*) and a much higher number of nematodesmal rods (20–24 vs. usually 12–16, rarely up to 18).

Occurrence and ecology: These were reviewed by Foissner *et al.* (1994). In the studies published before 1994, *Z. transversus* is called *Chilodontopsis vorax* because the determination followed Kahl (1931).

Zosterodasys transversus has been as yet recorded only from two main biogeographic regions, viz., the Holarctic (e.g. Kahl 1928, 1931; Buck 1961; Czapik 1982; Foissner *et al.* 1992, 1994 *etc.*) and the Neotropics (e.g. Pettigrosso and Cazzaniga 1987), indicating a restricted distribution. It occurs in the periphyton and organic mud of running and stagnant waters with peak abundances in spring (Kahl 1928, Foissner *et al.* 1994), or during fall according to Detcheva (1986) and our experience from the River Ipeľ. Rivera *et al.* (1979) observed *Z. transversus* also in tap water from Mexico City. Feeds exclusively on small to large diatoms, preferring pennate ones (Kahl 1928, 1931; Czapik 1982; Foissner *et al.* 1994). Biomass of 10^6 middle-sized specimens is approximately 300 mg according to Foissner *et al.* (1994).

Locus classicus of *Z. transversus* is fine organic mud and decaying tree leaves from the River Ipeľ near the village of Chľaba, Slovakia. We consider the locus classicus of *Chilodontopsis transversa* to be a duck puddle near Gasthof Saselbek, Germany (Kahl 1928). Locus classicus of *Z. azerbaijanicus* is benthos of temporary pools of the Ohčularčaj [Okhchularchay] River, Šamhor [Shamkhor] Region, Azerbaijan, where Aliev (1990) found it at 18–22°C, pH 7.5 and 8.9 mg/l O_2. *Zosterodasys fluviatilis* [= *Zosterodasys* sp. *sensu* Aliev (1990)] was recorded at the same place as *Z. azerbaijanicus* but, additionally, also in the Rivers Dzegamčaj [Dzegamchay] and Dašbulag [Dashbulag], Šamhor [Shamkhor] Region, Azerbaijan in sands of varied grain size at 18–20°C, pH 7.5 and 10.2 mg/l O_2 (Aliev 1990, Fernandez-Leborans and Alekperov 1996). *Zosterodasys jankowskii* was discovered between water plants in the middle region of the Džandar [Dzhandar] Lake, Kazah [Kazakh] Region, Azerbaijan at 18–20°C, pH 7.0 and 10.1 mg/l O_2 (Aliev 1990). Locus classicus of *Z. kurensis* is benthos of temporary pools of the Rivers Dzegamčaj [Dzegamchay] and Ohčularčaj [Okhchularchay] by the village of Dašbulag [Dashbulag], Šamhor [Shamkhor] Region, Azerbaijan, where Aliev (1990) reported numerous specimens at 17–25°C, pH 8.9 and 8.5–10.5 mg/l O_2. Locus classicus of *Z. shumerica* is benthos of the Fatmai Lake, Apšeron [Apsheron] Peninsula, Azerbaijan, where Aliev (1990) found very high numbers of cells at 25–28°C, pH 6.5, 8.5–10.5 mg/l O_2, and 4.5‰ salinity.

Records from running waters: frequently and numerous in various beta-mesosaprobic running waters in Nordwürttemberg, Germany (Buck 1961); common in beta-mesosaprobic rivers in Bayern, Germany and Austria (Foissner *et al.* 1992, 1994); widespread but achieving low abundances in beta-mesosaprobic (rate in alpha-mesosaprobic) streams and rivers in Poland (Czapik 1982, Grabacka 1982) and the Czech Republic (Šrámek-Hušek 1956, 1957, 1958; Buchar 1957); in various spring areas and rivers from Slovakia (Tirjaková 1997a, b, 2003; Tirjaková and Stloukal 2004); in the alpha-mesosaprobic Sava River, Croatia (Primc 1988); in various slightly to strongly polluted Italian rivers (Madoni and Bassanini 1999, Madoni 2005, Madoni and Braghiroli 2007); in the strongly polluted Tisza River, Hungary (Jósa 1974); in the Dniester and Byk Rivers, Moldavia (Chorik 1968); in a beta-mesosaprobic Argentinean river (Pettigrosso and Cazzaniga 1987).

Records from stagnant waters: rarely in the aerobic freshwater organic mud of the Elbe estuary, Germany (Pfannkuche *et al.* 1975); in the aerobic sediment of a eutrophic lake in England (Webb 1961); fine sand from the Excenevex beach, Lake Léman, France (Dragesco 1960); up to 500,000 ind./m^2 in Dubossarsk water reservoir, Moldavia (Chorik 1968); in a littoral rocky pond near Incheon, South Korea (Gong *et al.* 2009); in a pond from Michigan, USA at 24°C and pH 7 (Cairns and Yongue 1966); in a shallow puddle at 15–17°C (Gittleson and Ferguson 1971).

Records from brackish or sea waters are very likely misidentifications (e.g. Bock 1960, Agamaliev 1967, Burkovsky 1970, Küsters 1974, Knüpling 1979, Gong *et al* 2009). Most of them possibly refer to *Z. agamalievi*, while the population of Burkovsky (1970), whose ventral kineties produce a suture in meridional and posterior half of cell, could be a distinct species.

Saprobic classification: Foissner *et al.* (1994) classified *Z. transversus* as a beta-mesosaprobic ciliate with the following valencies: o = 1, b = 7, a = 2, I = 3, SI = 2.1. For further details, see Foissner *et al.* (1994).

Acknowledgements. We are grateful to Prof. Dr. Wilhelm Foissner and Dr. William A. Bourland for their help with obtaining the literature. Financial support was provided by the Slovak Scientific Grant Agency (VEGA projects 1/0600/11 and 1/0124/09).

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Received on 21st November, 2011; Revised on 20th December, 2011; Accepted on 30th December, 2011