

Redefinition and Reassignment of the 18-cirri Genera *Hemigastrostyla*, *Oxytricha*, *Urosomoida*, and *Actinotricha* (Ciliophora, Hypotricha), and Description of One New Genus and Two New Species

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Summary. The morphology, the infraciliature, and two stages of physiological reorganization of *Hemigastrostyla elongata* spec. nov., isolated from the Yellow Sea near Qingdao (China), are described. The new species differs from the type *H. stenocephala*, *inter alia*, by the length of the dorsal bristles and the position of the pretransverse ventral cirri; from *H. enigmatica* by the number of caudal cirri; and from *H. para-enigmatica* spec. nov. – established for the *H. enigmatica* populations from the Yellow Sea – by the arrangement of the postoral ventral cirri and the cortical granulation. A key to the *Hemigastrostyla* species and some other 18-cirri hypotrichs is provided. *Hemigastrostyla szaboi* is fixed as type species of *Heterooxytricha* gen. nov. because the type population lacks the extra cirri which are characteristic for *Hemigastrostyla*. In addition, *Oxytricha geleii* is assigned to this new genus, whose species have, like many oxytrichids, 18 frontal-ventral-transverse cirri, but a *Gonostomum* dorsal kinety pattern. The old, large, and difficult genus *Oxytricha* is briefly reviewed, mainly on the basis of the dorsal kinety pattern. Very likely, only species with the *Oxytricha* pattern belong to this genus. *Oxytricha marcili* and *O. pseudofurcata*, which have the *Urosomoida* kinety pattern (i.e. kinety 3 fragmentation lacking), are transferred to *Urosomoida* which is, *inter alia*, defined by a more or less distinctly reduced number of ventral and transverse cirri. Some other *Oxytricha* species with this kinety pattern (*O. islandica*, *O. lanceolata*, *O. pseudosimilis*, *O. setigera*) are not transferred to *Urosomoida*, but preliminarily classified as *incertae sedis* in *Oxytricha*, because they have the full set of 18 cirri. The available molecular data on *O. lanceolata* indicate that this type of 18-cirri hypotrichs likely needs a genus of its own because *O. lanceolata* does not cluster with *O. granulifera*, type of this genus. The marine *Actinotricha saltans*, classified for a very long time in *Oxytricha*, seems to be a non-dorsomarginalian hypotrich according to molecular data, justifying the reactivation of the old genus *Actinotricha*. *Oxytricha shii* has a multiple dorsal kinety 3 fragmentation, three dorsomarginal rows, and the undulating membranes arranged in the *Cyrtohymena* pattern, strongly indicating that it is a member of the subgenus *Cyrtohymena* (*Cyrtohymenides*). This brief review is a further step to unravel the complicated systematics of the old, but still little-known genus *Oxytricha*. The following new combinations are made in this paper: *Cyrtohymena* (*Cyrtohymenides*) *shii* (Shi *et al.*, 1997) comb. nov.; *Heterooxytricha szaboi* (Wilbert and Song, 2005) comb. nov.; *Heterooxytricha geleii* (Wilbert, 1986) comb. nov.; *Urosomoida marcili* (Paiva and Silva-Neto, 2004) comb. nov.; *Urosomoida pseudofurcata* (Berger, 1999) comb. nov.

Key words: China, *Heterooxytricha* gen. nov., review, Spirotricha, Stichotrichia, Yellow Sea.

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INTRODUCTION

Hemigastrostyla Song and Wilbert, 1997 is a small genus unifying saltwater hypotrichs with 18–21 frontal-ventral-transverse cirri. It is characterized, *inter alia*, by the so-called extra cirri, that is, two cirri close to the rear end of the right marginal row. *Hemigastrostyla* was established with two species which were originally assigned to *Oxytricha* Bory de Saint-Vincent in Lamouroux *et al.*, 1824, namely *O. stenocephala* Borror, 1963 (type) and *O. enigmatica* Dragesco and Dragesco-Kernéis, 1986. The original classification was mainly due to the cirral pattern which is very similar (*O. stenocephala*) or almost equivalent to that of the well known *Oxytricha* species with their 18 frontal-ventral-transverse cirri “sporadically” distributed over the ventral side (for review, see Berger 1999).

Hemigastrostyla enigmatica was redescribed and ontogenetically investigated by Song and Wilbert (1997) and Song and Hu (1999), demonstrating a rather curious ontogenesis of the dorsal infraciliature, namely lack of a dorsomarginal kinety, but presence of fragmentation in two kineties. Gong *et al.* (2007) isolated *H. enigmatica* from Korean tidal flats, analyzed its morphology and 18S and 28S rRNA gene sequences, and found that it branches off rather early in the Hypotricha tree, far apart from the oxytrichids which have a dorsomarginal kinety and kinety 3 fragmentation (e.g. Foissner and Adam 1983a, Berger 1999). Gong *et al.* (2007) thus removed *Hemigastrostyla* from the oxytrichids and discussed that it belongs or is closely related to the amphisiellids because in both taxa cirri originating from two or three frontal-ventral-transverse cirri anlagen form a distinct row. However, the very different dorsal ontogenesis in *Hemigastrostyla* (with fragmentation) and the amphisiellids (without fragmentation; for review, see Berger 2008) indicates a rather distinct separation of these two taxa which is also clearly recognisable by the deep branching in the molecular tree (Gong *et al.* 2007).

Recently, we found a hypotrich in the Yellow Sea which belongs rather certainly to *Hemigastrostyla*. A detailed comparison with the known species shows that it is new to science. In addition, we separate the Yellow Sea populations of *H. enigmatica* at species level from the type population discovered in Benin since there are some significant differences (Song and Wilbert 1997, Song and Hu 1999). We also provide a brief review and a key to the species because the taxonomy

of *Hemigastrostyla* is somewhat confusing. For *H. sza-boi* Wilbert and Song, 2005, the genus *Heterooxytricha* is established because it lacks some key features of *Hemigastrostyla*.

As mentioned above, *Hemigastrostyla* has a peculiar dorsal ontogenesis (Song and Hu 1999). The dorsal kinety pattern and its formation have become important characteristics for hypotrich taxonomy. Foissner and Adam (1983a) thoroughly analyzed this cluster of characters and recognized several different patterns which were used by Berger and Foissner (1997) and Berger (1999), among other morphological and ontogenetic features, to estimate the phylogenetic relationships within the oxytrichids. Molecular analyses have agitated the classical systematics of hypotrichs and unmasked groupings which correlate with features of the dorsal infraciliature, for example, the Dorsomarginalia Berger, 2006. Of course we are far away from the final understanding of the hypotrich evolution, but the results available so far clearly demonstrate that the dorsal kinety pattern is a very important phylogenetic marker, like the ventral infraciliature. Thus, some 18-cirri species – mainly of the genus *Oxytricha*, which is certainly an artificial assemblage of flexible 18-cirri hypotrichs with caudal cirri – have to be transferred to other genera to make the characterizations of such genera less woolly (Berger 2011: 538). In the present paper we transfer some *Oxytricha* species to *Urosomoida* Hemberger in Foissner, 1982 and *Cyrtohymena* (*Cyrtohymenides*) Foissner, 2004 and reactivate the old genus *Actinotricha* Cohn, 1866 for *Oxytricha saltans* (Cohn, 1866) which was classified in *Oxytricha* for a very long time. These procedures are further steps to unravel the taxonomy of *Oxytricha*.

MATERIALS AND METHODS

Sample site and cultivation

Both *Hemigastrostyla* species described in the present paper have been found in the Yellow Sea near the city of Qingdao (36°04'N, 120°18'E), China. *Hemigastrostyla elongata* spec. nov. was discovered in the top 10 cm of the sandy littoral sediment near the Zhanqiao Pier in the Jiaozhou Bay on 6 Dec 2005. Non-clonal cultures were maintained for several weeks in the laboratory at about 20°C. Squeezed wheat grains were added to the medium (filtrated seawater from the type locality) as a food source to enrich bacteria.

The type population of *H. paraenigmatica* spec. nov. (= *H. enigmatica sensu* Song and Wilbert 1997) was discovered in water from an offshore mollusc-farm on 10 Jun 1995. A second population

from the same site was isolated on 1 Sep 1996. The observations by Song and Wilbert (1997) are based on both populations. Glass slides were used as artificial substrate to collect ciliates (Gong *et al.* 2005). Briefly, the slides were fixed to a frame and immersed in the tanks to a depth of 1 m for 7–10 d to allow colonization. The slides were transferred to Petri dishes containing seawater from the sampling site. Isolated specimens were maintained in the laboratory for 7 d as uniprotistan, non-clonal cultures at 20°C and a salinity of about 31‰. The population studied by Song and Hu (1999) is identical with the population collected by Song and Wilbert (1997) in Sep 1996. For details on culture method, see Song and Hu (1999).

Morphological methods

Living ciliates were examined using bright field and differential interference contrast microscopy. Protargol impregnation was applied to reveal the infraciliature and nuclear apparatus (Wilbert 1975). Measurements and counts on impregnated specimens were performed at a magnification of 1250 \times . Drawings of the infraciliature were made with a drawing device. In Table 1 the values for the holotype specimen of *H. elongata* (Figs 2G, H) are listed separately, but they are also included in the ordinary sample.

Table 1. Morphometric data on *Hemigastrostyla elongata* spec. nov.

Character ^a	HT	Min	Max	Mean	SD	SE	CV	n
Body, length	118	84	160	123.0	21.9	4.1	17.8	28
Body, width	55	46	102	69.0	15.1	3.0	21.8	26
Adoral zone of membranelles, length	35	30	61	43.2	7.6	1.5	17.5	27
AE of cell to frontmost postoral ventral cirrus, distance	38	34	57	43.6	6.6	1.6	15.1	18
AE of cell to rearmost postoral ventral cirrus, distance	58	50	80	64.9	9.9	2.3	15.2	18
AE of cell to right marginal row, distance	33	25	48	37.2	7.1	1.7	19.1	18
PE of cell to end of right marginal row, distance	25	8	33	22.2	6.0	1.4	27.2	18
PE of cell to rearmost transverse cirrus, distance	14	9	15	10.9	2.0	0.5	17.9	18
Anterior macronuclear nodule, length	16	10	26	18.7	4.4	0.8	23.8	29
Anterior macronuclear nodule, width	7	8	18	10.7	2.8	0.7	25.9	18
Posterior macronuclear nodule, length	16	14	25	20.0	3.3	0.8	16.4	18
Posterior macronuclear nodule, width	7	6	17	9.2	2.1	0.4	22.9	29
Macronuclear nodules, distance in between	7	3	16	9.3	3.5	0.8	37.5	19
Macronuclear nodules, number	2	2	2	2.0	0	0	0	25
Adoral membranelles, number	37	20	46	33.0	6.9	1.5	21.0	22
Buccal cirri, number	1	1	1	1.0	0	0	0	23
Frontal cirri, number	3	3	3	3.0	0	0	0	23
Frontoventral cirri, number ^b	4	3	4	3.9	0.3	0.1	7.4	23
Postoral ventral cirri, number ^b	3	3	5	3.1	0.5	0.1	14.6	23
Pretransverse ventral cirri, number	2	2	2	2.0	0	0	0	21
Transverse cirri, number	5	5	5	5.0	0	0	0	22
Left marginal cirri, number	21	18	34	22.2	4.1	0.9	18.5	21
Right marginal cirri, number	24	14	27	19.2	3.2	0.7	16.5	22
Extra cirri, number	2	2	2	2.0	0	0	0	20
Dorsal kineties, number	5	4	5	4.9	0.3	0.1	5.2	15
Dorsal kinety 1, number of bristles	18	10	24	19.7	3.8	1.1	19.2	12
Caudal cirri, number	3	3	3	3.0	0	0	0	13

^a All data are based on protargol-impregnated specimens. Measurements in μm . AE – anterior end; CV – coefficient of variation in %; HT – holotype specimen (also included in the sample n); Max – maximum; Mean – arithmetic mean; Min – minimum; n – number of specimens investigated; PE – posterior end; SD – standard deviation; SE – standard error of arithmetic mean.

^b In some specimens it is difficult to decide whether a cirrus is the rearmost frontoventral cirrus or the frontmost postoral ventral cirrus (e.g. Fig. 4C).

Terminology

General terminology is mainly according to Lynn (2008); for explanation of terms specific for hypotrichs (e.g. pseudorow, mixed row, DE-value), see Berger and Foissner (1997), Berger (1999, 2006, 2008, 2011), and Foissner and Al-Rasheid (2006). For the designation of the frontal-ventral-transverse cirri and their anlagen, the numbering system by Wallengren (1900) is used (details see Berger 1999: 16). The term 18-cirri hypotrich means a hypotrich with 18 frontal-ventral-transverse cirri (e.g. Berger 2008: 27). For definition of the new term “*Hemigastrostyla* pattern”, see chapter cell division at *Hemigastrostyla paraenigmatica* spec. nov. (Fig. 1B). The morphogenesis of *H. stenocephala*, type of the genus, is not yet known; thus, the designation of this pattern is only preliminary. Since this is a taxonomic paper, all authorities of scientific names are mentioned in the reference section.

RESULTS AND DISCUSSION

Hemigastrostyla Song and Wilbert, 1997

- 1997 *Hemigastrostyla* nov. gen. – Song and Wilbert, *Arch. Protistenk.*, 148: 421 (original description). Type species (by original designation): *Oxytricha (Urosoma) stenocephala* Borror, 1963.
- 1999 *Hemigastrostyla* Song & Wilbert, 1997 – Berger, *Monogr. Biol.*, 78: 933 (revision).
- 1999 *Hemigastrostyla* – Song and Hu, *Hydrobiologia*, 391: 251 (improved diagnosis).
- 2005 *Hemigastrostyla* Song and Wilbert, 1997 – Wilbert and Song, *J. nat. Hist.*, 39: 966 (improved diagnosis).
- 2008 *Hemigastrostyla* Song & Wilbert, 1997 – Lynn, *Ciliated Protozoa*, p. 360 (familial revision of ciliates).
- 2009 *Hemigastrostyla* Song & Wilbert, 1997 – Hu, Warren and Song, *Hypotrichs*, p. 400 (revision of hypotrichs of northern China seas).

Improved diagnosis: More or less cephalized, non-dorsomarginalian hypotrichs with 18–21 frontal-ventral-transverse cirri. Distal portion of adoral zone extending far posteriorly. Undulating membranes roughly in *Stylonychia* pattern. Some frontoventral cirri and the postoral ventral cirri form more or less distinct row. One left and one right marginal row. Two “extra cirri” close to rear end or right marginal row. 4–6, usually five dorsal kineties. Caudal cirri present. Dorsal ontogenesis in *Hemigastrostyla* pattern. Saltwater.

Nomenclature: No derivation of the name is given in the original description or a later paper. *Hemigastrostyla* is a composite of the Greek prefix *hemi-* (partly; Werner 1972) and the genus-group name *Gastrostyla* Engelmann, 1862 (for derivation, see Berger 2008: 136). It alludes to the similarity of the cirral pattern of *Hemigastrostyla* and *Gastrostyla* species. Like *Gastrostyla* of feminine gender (Aesch 2001: 283).

Species included in *Hemigastrostyla*: (i) *Hemigastrostyla stenocephala* (Borror, 1963) Song and Wilbert, 1997 (type); (ii) *H. elongata* spec. nov.; (iii) *H. enigmatica* (Dragesco and Dragesco-Kernéis, 1986) Song and Wilbert, 1997; (iv) *H. paraenigmatica* spec. nov.

Species misplaced in *Hemigastrostyla*: *Hemigastrostyla szaboi* Wilbert and Song, 2005. Remarks: This species is now type of the new genus *Heterooxytricha* (see there).

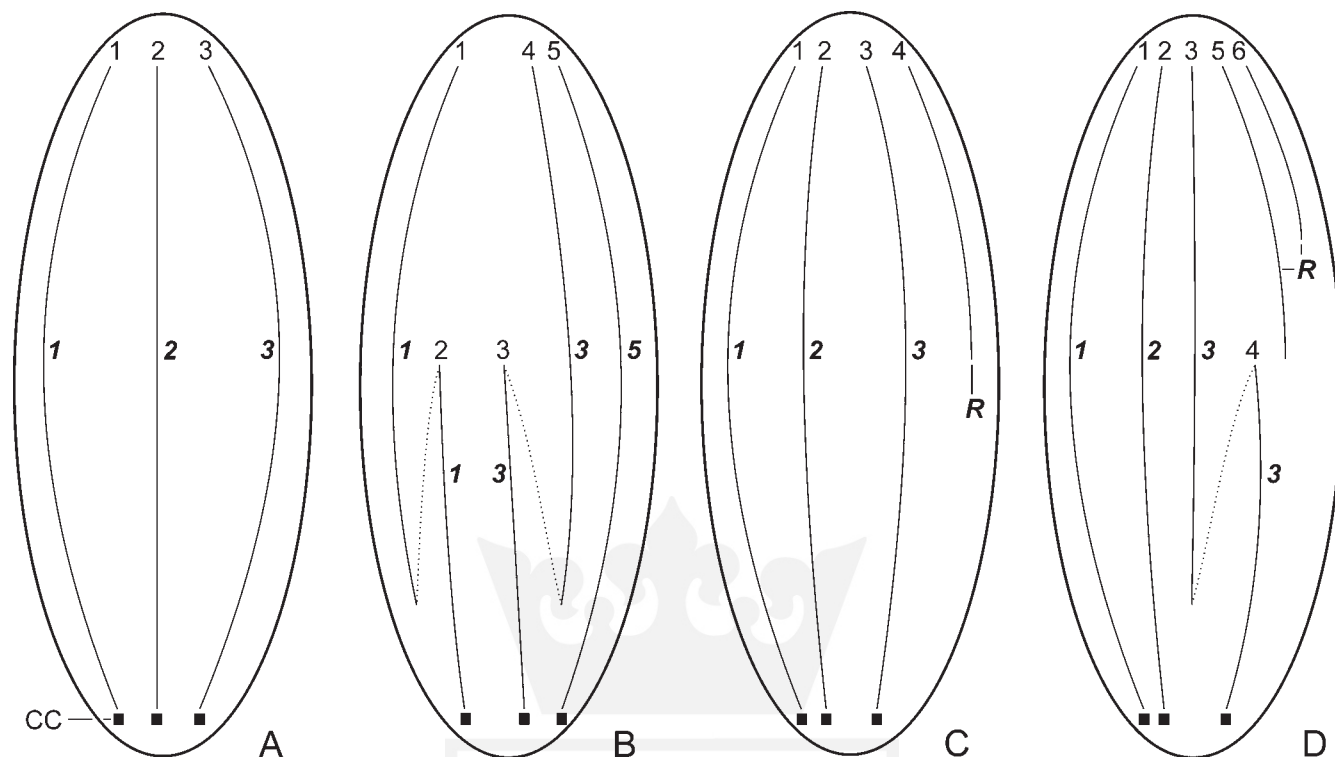
Remarks: Song and Wilbert (1997) redescribed *Oxytricha enigmatica* and simultaneously recognized that this type of 18-cirri hypotrichs needs a genus of its own because it (i) is cephalized; (ii) has few extra cirri (= lateroventral cirri in Song and Wilbert 1997) close to the rear end of the right marginal row; and (iii) very likely has seven frontal-ventral-transverse cirri anlagen (this observation is based on a single reorganizer). Thus, they established *Hemigastrostyla* and fixed *O. stenocephala* as type species, which also has a cephalized body and a very similar cirral pattern, including the extra cirri (Figs 6I–K). Berger (1999) obtained the original description of *Hemigastrostyla* rather late and therefore mentioned it only in the addenda of his review on oxytrichids.

Song and Hu (1999) studied the cell division of *H. enigmatica* and found that the extra cirri are remnants of the parental right marginal row. Furthermore, they could elucidate the formation of the curious dorsal kinety pattern, which is termed *Hemigastrostyla*-pattern in the present paper (details see *H. paraenigmatica* and Fig. 1B). These results as well as the molecular data on Korean populations of *H. enigmatica* (Gong *et al.* 2007) confirmed the clear separation of this species from the oxytrichids (e.g. *Oxytricha*, *Gastrostyla*) and therefore supported the validity of *Hemigastrostyla*.

The list of synonyms contains only key references. At present four *Hemigastrostyla* species are known. Two of them are new and described below while the other two species are briefly reviewed. In addition, we provide a key to these species and some similar taxa.

Key to *Hemigastrostyla* species and some similar taxa

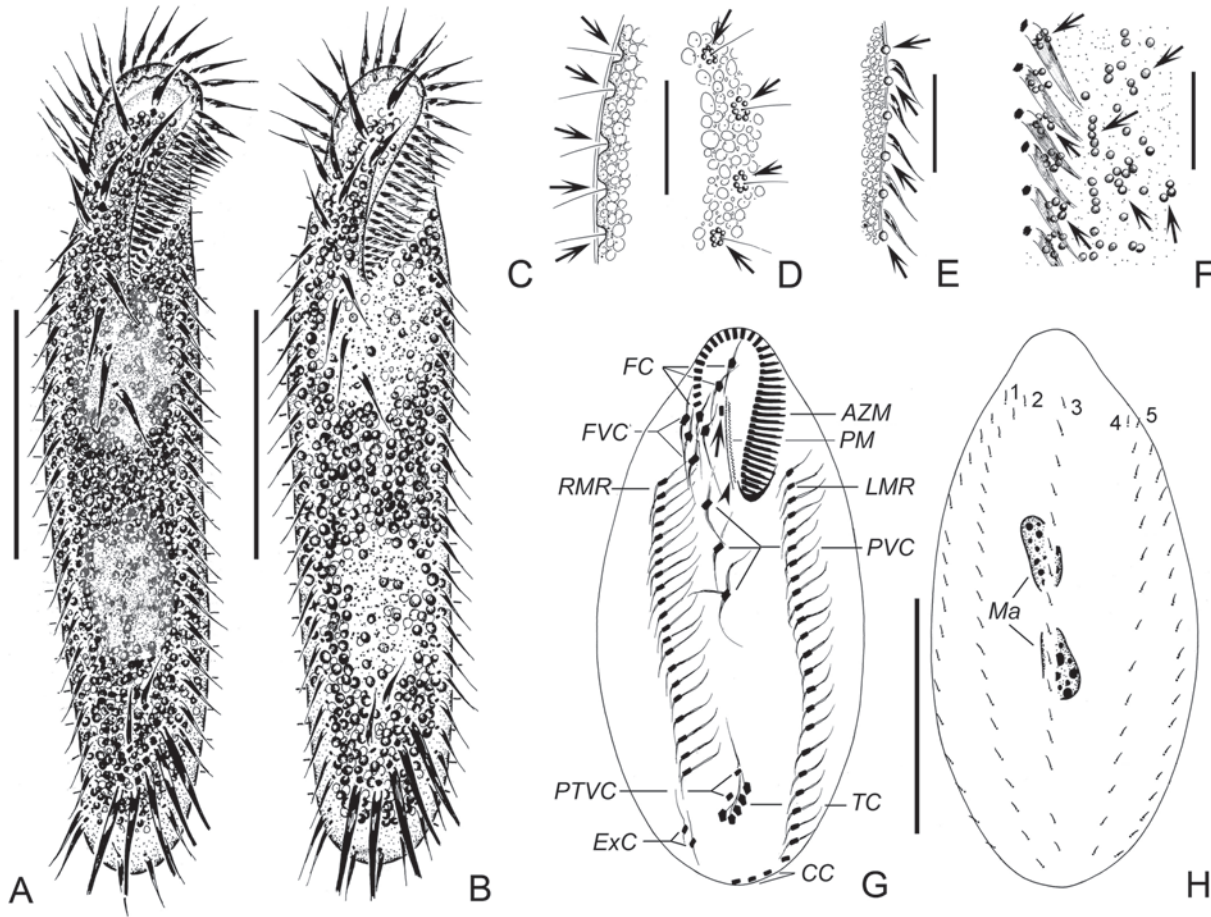
The features used in the key below can be seen in good live preparations when bright field illumination (colour of cortical granules) and differential interference microscopy (other features) are used. However, protargol impregnation is recommended to see some difficult features (number of dorsal kineties, caudal cirri) clearly.



Figs 1A–D. Scheme of various dorsal kinety patterns and origin of individual kineties (A, C, D, modified from Berger and Foissner 1997; B, reconstructed from data provided by Song and Hu 1999). **A** – *Gonostomum* pattern. Each of the three bipolar kineties divides by intrakinetal proliferation; **B** – *Hemigastrostyla* pattern. Details see text; **C** – *Urosomoida* pattern. Kineties 1–3 divide by intrakinetal proliferation while kinety 4 is a dorsomarginal kinety; **D** – *Oxytricha* pattern. Kineties 1 and 2 divide by intrakinetal proliferation; the anlage of kinety 3 fragments and forms the new kinety 3 (anterior portion) and the new kinety 4 (posterior portion). In addition, one or two dorsomarginal kineties are formed. Solid lines denote the dorsal kineties, dotted lines mark a fragmentation. CC – caudal cirri, **R** – these kineties are dorsomarginal rows, that is, originate from/near the right marginal row anlagen, 1–6 – designation of dorsal kineties in interphasic specimens (important note: not all numbers designate homologous kineties; for example, kinety 5 in (B) is not homologous with kinety 5 in (D), but with kinety 4 since both are the rightmost kinety with a caudal cirrus), **1, 2, 3, 5** – parental kineties in which the kinety anlagen originate (for example, the anlage for kinety 2 in the *Hemigastrostyla* (B) pattern is formed in the parental kinety 1).

- | | | |
|----------|--|--|
| 1 | Two extra cirri present (Fig. 2G) | 2 |
| – | Two extra cirri lacking | 6 |
| 2 | Three dorsal kineties | <i>Apogastrostyla</i> (Figs 6L–N; details see Li <i>et al.</i> 2010) |
| – | 4–6, usually five dorsal kineties | <i>Hemigastrostyla</i> 3 |
| 3 | Pretransverse ventral cirri distinctly in front of transverse cirri; dorsal bristles about 16 µm long | <i>H. stenocephala</i> (Figs 6I–K) |
| – | Pretransverse ventral cirri close to transverse cirri; dorsal bristles 2–10 µm long | 4 |
| 4 | 5–7 caudal cirri | <i>H. enigmatica</i> (Figs 6A–D) |
| – | Three caudal cirri | 5 |
| 5 | Adoral zone occupies about 50% of body length; only rearmost postoral ventral cirrus behind of level of buccal vertex; yellow cortical granules (about 1 µm across) absent | <i>H. paraenigmatica</i> spec. nov. (Figs 6E–G) |
| – | Adoral zone occupies about 35% of body length; all postoral ventral cirri at or behind of level of buccal vertex; yellow cortical granules (about 1 µm across) present | <i>H. elongata</i> spec. nov. (Figs 2A–H) |

- 6 (1) Dorsal kineties in *Gonostomum* pattern, that is, dorsomarginal kinety lacking (Fig. 1A)..... 7
- Dorsomarginal kineties present (Figs 1C, D) 8
- 7 Adoral zone in *Gonostomum* pattern *Gonostomatidae* (see Berger 2011)
- Adoral zone in *Oxytricha* pattern *Heterooxytricha* gen. nov. (see below)
- 8 (6) Dorsal kinety 3 fragmentation present (Fig. 1D) *Oxytricha* (see Berger 1999)
- Dorsal kinety 3 fragmentation lacking (Fig. 1C).....
- *Urosomoida* and species *incertae sedis* in *Oxytricha* (see below and Berger 1999)



Figs 2A–H. *Hemigastrostyla elongata* spec. nov. from life (A–F) and after protargol impregnation (G, H). **A, B** – ventral view of typical individuals; **C** – detail of dorsal surface in optical section showing the dorsal cilia within the cup-shaped depressions (arrows); **D–F** – cortical granules (arrows) around dorsal bristles, along marginal rows, and on ventral side (details see text); **G, H** – infraciliature of ventral and dorsal side and macronuclear apparatus of holotype specimen. Arrowhead marks endoral, arrow denotes buccal cirrus. AZM – adoral zone of membranelles, CC – caudal cirri, ExC – extra cirri, FC – frontal cirri, FVC – frontoventral cirri, LMR – left marginal row, Ma – macronuclear nodules, PM – paroral, PTVC – pretransverse ventral cirri, PVC – postoral ventral cirri, RMR – right marginal row, TC – transverse cirri, 1–5 – dorsal kineties. Scale bars: 40 µm (A, B), 10 µm (C–F), 50 µm (G, H).

***Hemigastrostyla stenocephala* (Borror, 1963) Song and Wilbert, 1997 (Figs 6I–K)**

1963 *Oxytricha (Urosoma) stenocephala* n. sp. – Borror, *Arch. Protistenk.*, 106: 512, Figs 121–124 (Figs 6I–K; original description).

1972 *Gastrostyla stenocephala* (Borror, 1963) n. comb. – Borror, *J. Protozool.*, 19: 14 (revision of hypotrichs; combination with *Gastrostyla*).

1997 *Hemigastrostyla stenocephala* (Borror, 1963) n. comb. – Song and Wilbert, *Arch. Protistenk.*, 148: 421 (fixation as type species of *Hemigastrostyla*).

1999 *Gastrostyla stenocephala* (Borror, 1963) Borror, 1972 – Berger, *Monogr. Biol.*, 78: 822, Figs 207a–f (Fig. 6I–K; detailed review).

Improved diagnosis: Body size about $190 \times 40 \mu\text{m}$ (*in vivo*?). Head rather narrow, posterior body end slightly narrowed and curved rightwards. Two macronuclear nodules. About 40 adoral membranelles. In total about 21 frontal-ventral-transverse cirri. Frontoventral row made of eight cirri. One isolated postoral ventral cirrus just behind buccal vertex. Pretransverse ventral cirri displaced far anteriorly. Dorsal bristles about $16 \mu\text{m}$ long. Two caudal cirri.

Type locality: Sandy benthal in Alligator Harbor, Franklin County, Florida, USA (Borror 1963).

Type material: According to Borror (1963: 514), type material (Chatton-Lwoff technique) is in possession of the author.

Nomenclature: The species-group name *stenocephala* is a composite of the Greek adjective *stenos* (narrow, slender) and the Greek noun *he kephale* (head; Hentschel and Wagner 1996) and refers to the narrow anterior end of the cell (Borror 1963).

Morphology: For detailed descriptions, see Borror (1963) and review by Berger (1999).

Occurrence and ecology: See Borror (1963) and review by Berger (1999).

Remarks: Borror (1963) discovered this species in sandy sediments in the Gulf of Mexico and made detailed live observations and Chatton-Lwoff preparations. Borror classified it in the subgenus *Oxytricha* (*Urosoma*) Kowalewski, 1882, likely because *Oxytricha* (*Urosoma*) *longicirrata* Kahl, 1932, which has a similar body shape according to Borror (1963), was classified in this subgenus. Later, he transferred it to *Gastrostyla* probably because the frontoventral and postoral ventral cirri form a distinct mixed row as in *G. steinii* Engelmann, 1862, type of this genus (Borror 1972).

Song and Wilbert (1997) fixed *O. stenocephala* as type of *Hemigastrostyla*. The ventral and dorsal infraciliature are basically well described and show some distinct differences to the three congeners in the following features: (i) total number of frontal-ventral-transverse cirri (21 vs. usually 18); (ii) number of cirri forming the frontoventral row (eight vs. usually six); (iii) clearly isolated postoral ventral cirrus (present vs. absent); and (iv) position of pretransverse ventral cirri (distinctly in front of transverse cirri vs. close to transverse cirri). In addition, *H. stenocephala* has only two caudal cirri (vs. three or more) and long dorsal bristles ($16 \mu\text{m}$ vs. $10 \mu\text{m}$ or less). However, other important

features agree very well, namely the far posteriorly extending distal portion of the adoral zone; the cephalisation; the saltwater habitat; the number of dorsal kineties (4–6, five in specimen illustrated); and, most important, the two extra cirri close to the rear end of the right marginal row. Unfortunately, gene sequence data are available only for the Korean populations of *H. enigmatica* (Gong *et al.* 2007) and not for the type species *H. stenocephala*, so that we do not have a molecular support or disproof for the *Hemigastrostyla* concept. At present, we hypothesize that the deviations listed above are specific features of *H. stenocephala*.

***Hemigastrostyla elongata* spec. nov. (Figs 2A–H, 3A–H, 4A–H, 5A–L; Table 1)**

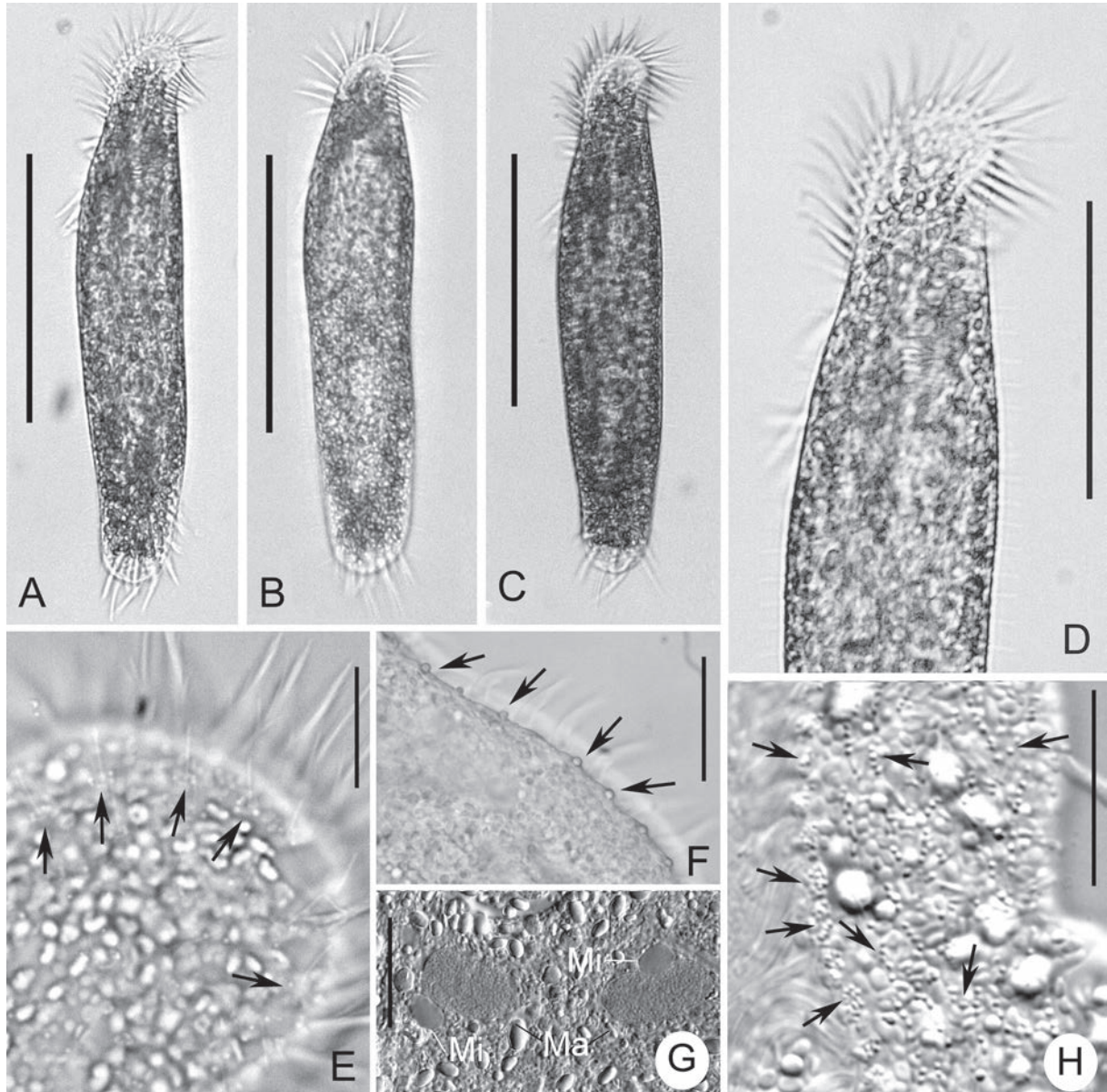
Diagnosis: Body size about $135 \times 27 \mu\text{m}$ *in vivo*. Body narrow elliptical. Two macronuclear nodules. Two types of cortical granules, namely, small ($0.5 \mu\text{m}$ across), colourless granules mainly in rosettes around marginal cirri and dorsal cilia and about $1 \mu\text{m}$ -sized yellow granules mainly along marginal rows. 43 adoral membranelles on average. Usually 18 frontal-ventral-transverse cirri with all postoral ventral cirri at and behind level of buccal vertex. Pretransverse ventral cirri close to transverse cirri. Dorsal bristles about $5 \mu\text{m}$ long. One caudal cirrus each on dorsal kineties 2, 3, and 5.

Type locality: Sandy littoral sediments in the Jiaozhou Bay, Yellow Sea, Qingdao, China (further details, see Materials and Methods).

Type material: The protargol slide (registration number SC-051206) containing the holotype specimen (Figs 2G, H; Table 1) and several paratype specimens has been deposited in the Laboratory of Protozoology, Ocean University of China (OUC), Qingdao, China.

Nomenclature: The species-group name *elongatus*, -a, -um [Latin adjective (m, f, n); prolonged, elongated, stretched; Hentschel and Wagner (1996)] refers to the oblong body shape.

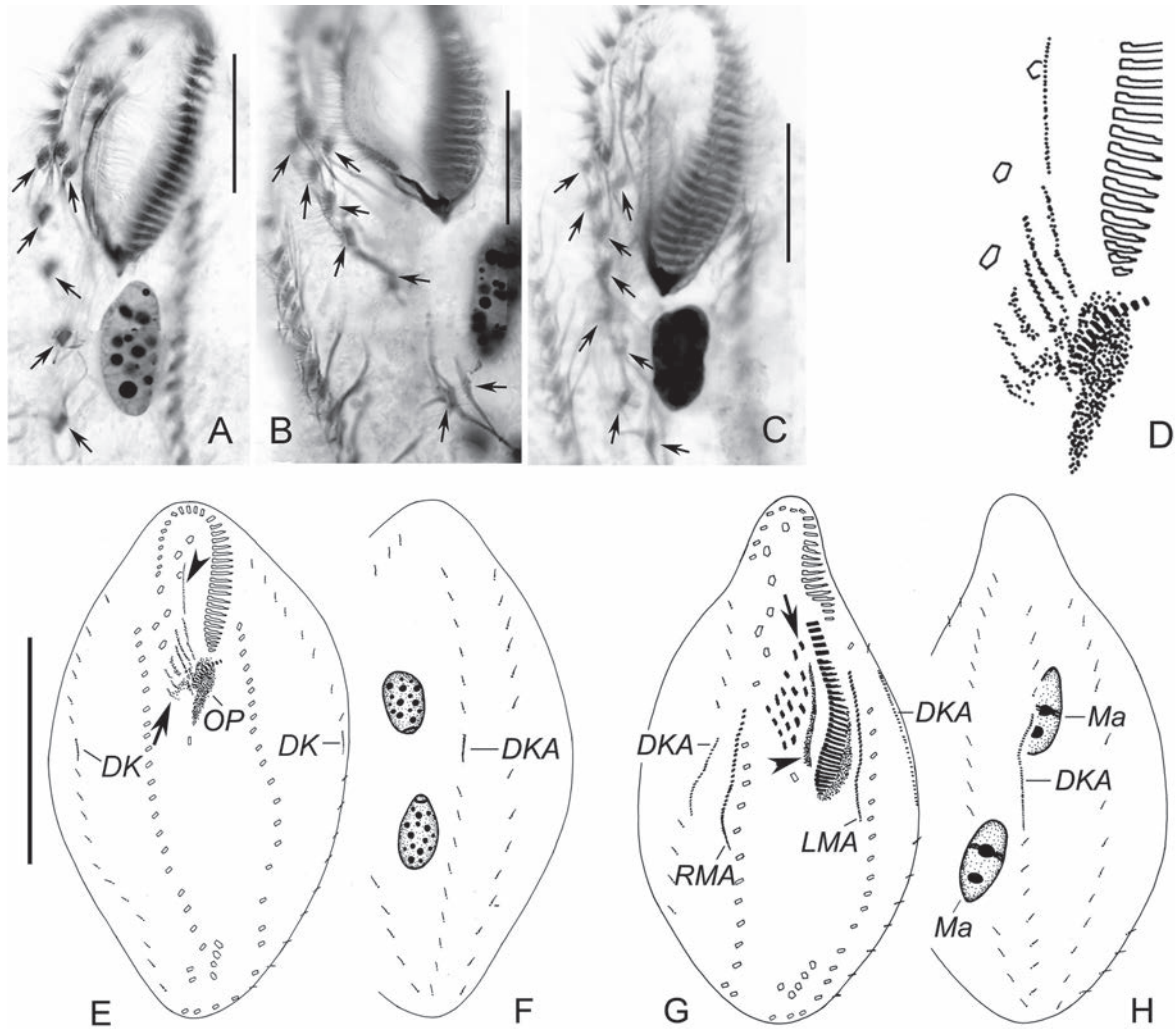
Morphology (Figs 2A–H, 3A–H, 4A–C, 5A–G; Table 1): Body size *in vivo* $95\text{--}160 \times 22\text{--}35 \mu\text{m}$, usually about $135 \times 27 \mu\text{m}$, length : width ratio thus approximately 5 : 1 *in vivo*, but only 1.8 : 1 on average in protargol preparations due to strong distension caused by the preparation method used (Figs 2A, B, G, H, 3A–C; Table 1). Body outline elongate elliptical with both ends widely rounded; frontal portion more or less narrowed causing cephalization; left cell margin roughly straight while right slightly to distinctly convex. Body usually widest in front of mid-body, about 2 : 1 flattened dorsoventrally, ventral side flat, dorsal side convex in middle



Figs 3A–H. Photomicrographs of *Hemigastrostyla elongata* spec. nov. from life (A, B, bright field illumination; C–H, Normarski differential interference contrast). **A–C** – three different individuals demonstrating that the body outline is very constant; **D** – ventral view of anterior body portion showing that the distal end of the adoral zone extends far posteriorly; **E, F, H** – dorsal (E), lateral (F) and ventral (H) view showing the small (E, H) and large (F) cortical granules (arrows; arrows in E mark granules around dorsal bristles; for details see text); **G** – nuclear apparatus. Micronuclei did not stain with the protargol method used. Ma – macronuclear nodules, Mi – micronuclei. Scale bars: 60 μm (A–C), 30 μm (D), 10 μm (E, F), 20 μm (G, H).

portion; flexible but not distinctly contractile in life (Figs 2A, B, 3A–D). Invariably two macronuclear nodules usually arranged in line behind buccal vertex about in cell midline or slightly left of it; individual nodules ellipsoidal (length : width ratio about 2 : 1), with small to moderately large nucleoli. Usually one micronucleus

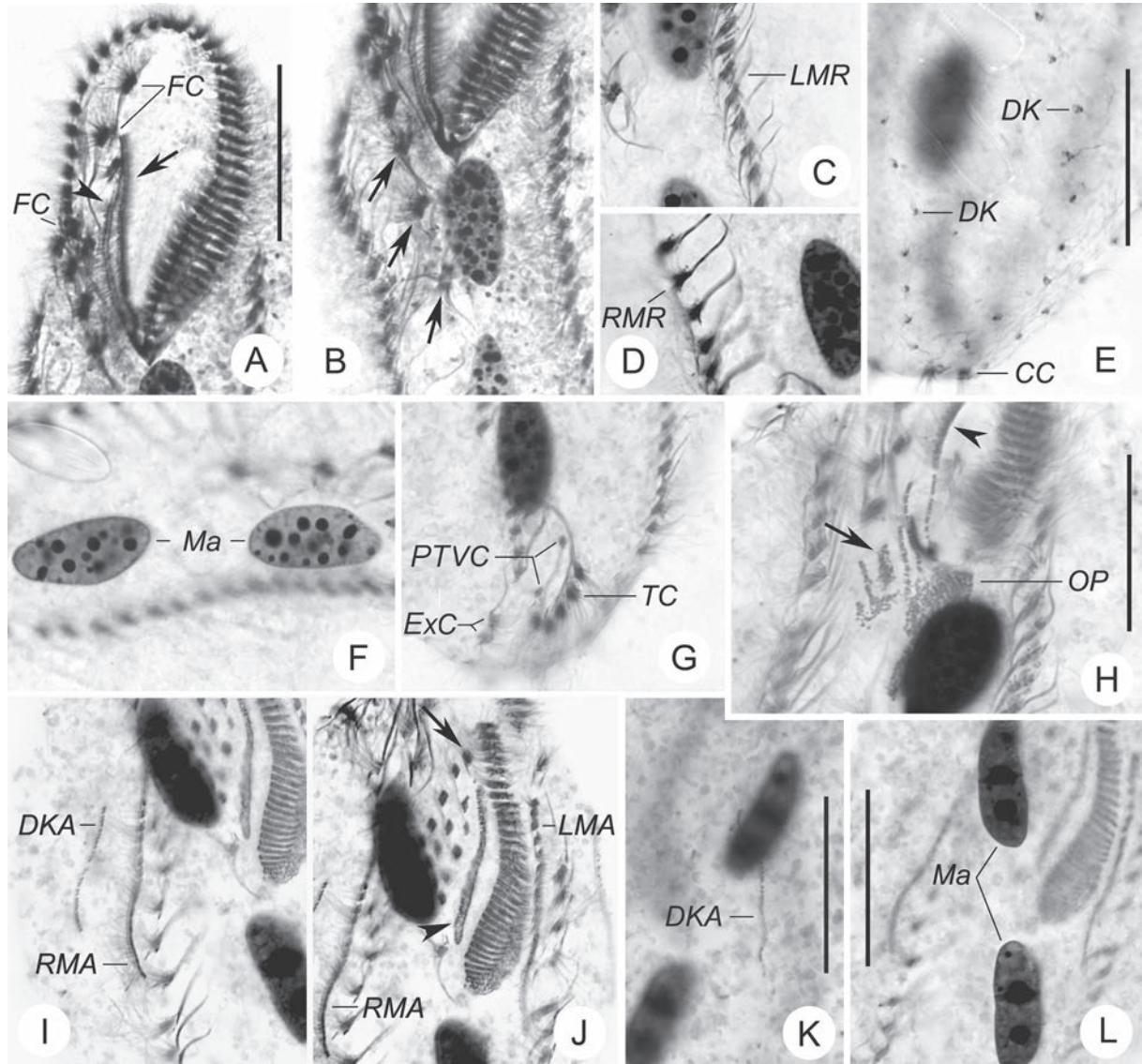
(about $6 \times 3 \mu\text{m}$ *in vivo*) attached to each macronuclear nodule (Fig. 3G); do not impregnate with the protargol method used. No contractile vacuole found, indicating absence. Two types of cortical granules: (i) small (approximately $0.5 \mu\text{m}$ in diameter), colourless granules mainly arranged in rosettes around marginal cirri and



Figs 4A–H. *Hemigastrostyla elongata* spec. nov. Protargol-impregnated specimens during interphase (A–C) and physiological reorganization (D–H). **A–C** – ventral view of specimens which do not have the ordinary number (seven) and pattern of frontoventral and postoral ventral cirri (arrows); **D–F** – infraciliature of ventral and dorsal side of early reorganizer. Arrow in (E) marks the frontal-ventral-transverse cirri anlagen, arrowhead denotes the remnants of one of the parental undulating membranes; **G, H** – infraciliature of ventral and dorsal side of a late reorganizer. Arrow marks left frontal cirrus (= cirrus I/1), arrowhead denotes undulating membrane anlage. DK – dorsal kineties, DKA – dorsal kineties anlagen in parental rows 1, 3 and 5, LMA – left marginal row anlage, Ma – macronuclear nodules, OP – oral primordium, RMA – right marginal row anlage. Scale bars: 20 μ m.

dorsal bristles, but also scattered on left and right margin of ventral side; and (ii) bright yellow, globular granules about 1 μ m across sparsely arranged along rows of marginal cirri (Figs 2D–F, 3E, F, H); do not stain with the impregnation method used. Cytoplasm hyaline and colourless, frequently containing many lipid droplets 2–3 μ m across so that cells appear opaque and dark at low magnification (Figs 2A, B, 3A–D). Movement without peculiarities, that is, glides moderately fast on sand particles and debris showing pronounced flexibility.

Adoral zone occupies 25–30% of body length *in vivo*, 35% on average in protargol preparations, composed of 20–46, on average 33 adoral membranelles of usual fine structure, that is, made of two long, one slightly shortened, and one very short row of basal bodies. Bases of largest membranelles about 7 μ m wide, cilia up to 15 μ m long. Distal portion of adoral zone extends far posteriorly onto right side of cell, that is, DE-value 0.47 in holotype specimen (Fig. 2G; for explanation of DE-value, see Berger 2006: 18). Buccal field narrow in life, but moderately wide to wide in



Figs 5A–L. Photomicrographs of protargol-impregnated *Hemigastrostyla elongata* spec. nov. during interphase (A–G) and physiological reorganization (H–L). **A–G** – details of the ventral (A–D, F, G) and dorsal (E) infraciliature, showing, *inter alia*, the frontal cirri and the paroral (arrow) and the endoral (arrowhead; A), linearly arranged postoral ventral cirri (arrows in B), left and right marginal cirri with fibres (C, D), dorsal kineties and caudal cirri (E), macronuclear nodules (F), and the pretransverse ventral cirri, the extra cirri, and the transverse cirri (G); **H** – ventral view of an early reorganizer (see Figs 4D, E). Arrow denotes a frontal-ventral-transverse cirri anlage, arrowhead marks the old undulating membranes; **I–L** – ventral (I, J, L) and dorsal (K) views of a late reorganizer (see also Figs 4G, H). The left frontal cirrus (arrow) originates, as is usual, from the undulating membrane anlage (arrowhead). CC – caudal cirri, DK – dorsal kineties, DKA – dorsal kineties anlagen, ExC – extra cirri, FC – frontal cirri, LMA – left marginal row anlage, LMR – left marginal row, Ma – macronuclear nodules, OP – oral primordium, PTVC – pretransverse ventral cirri, RMA – right marginal row anlage, RMR – right marginal row, TC – transverse cirri. Scale bars: 20 µm.

specimens impregnated with the Wilbert-method due to distension (Figs 2A, B, G, 4A–C, 5A). Buccal lip slightly curved, covering only right part of proximal portion of adoral zone (Figs 2A, B). Paroral and endoral straight to slightly curved, arranged in parallel or

slightly intersecting optically, almost of equal length, that is, undulating membranes roughly in *Stylonychia* pattern (Figs 2G, 3A–C, 5A).

All cirri relatively fine and about 8 µm long, except for frontal and transverse cirri, which are about 15 µm

long. Almost invariably 18 frontal-ventral-transverse cirri (Fig. 2G; Table 1). Frontal cirri arranged in very oblique pseudorow with right cirrus (= III/3) close to distal end of adoral zone, hardly thicker than frontoventral cirri. Buccal cirrus right of anterior end of paroral. Parabuccal cirrus (= III/2) close behind right frontal cirrus and of about same size. Remaining three frontoventral cirri, that is, two frontoterminal cirri and cirrus IV/3, form narrowly spaced row commencing right of right frontal cirrus. Postoral ventral cirri aligned, anteriormost cirrus at level of buccal vertex and rearmost at 53% of body length on average (Fig. 2G; Table 1). Pretransverse ventral cirri close to transverse cirri, which are distinctly larger. Transverse cirri in ordinary, roughly J-shaped pseudorow; rearmost cirrus (= cirrus V/1) at 91% of body length on average, that is, transverse cirri only slightly displaced anteriorly and therefore projecting beyond rear body end by one fourth to one third of their length (Figs 2A, B, G, 3A–C; Table 1). Right marginal row commences at 30% of body length, that is, slightly in front of level of buccal vertex, terminates at 82% of body length on average. Extra cirri slightly smaller and almost in line with right marginal row, but separated by a wide gap, and thus behind level of rearmost transverse cirrus in holotype specimen (Fig. 2G). Left marginal row begins left of proximal portion of adoral zone, terminates slightly in front of rear end of cell, more or less in line with caudal cirri (Figs 2A, B, G).

Dorsal bristles about 5 µm long in life, almost invariably arranged in five roughly bipolar kineties, all slightly shortened anteriorly. Individual bristles emerge from cup-shaped depressions surrounded by small cortical granules (see above; Figs 2A–D, H). Three caudal cirri at rear body margin in and slightly left of midline of cell; about 8–10 µm long and thus almost indistinguishable from marginal cirri in life (Figs 2A, B, G). For possible assignment of cirri to kineties, see next section.

Notes on physiological reorganization (Figs 4D–H, 5H–L): Only early and middle reorganizers have been found. They show the following important features: (i) the parental adoral zone is very likely completely replaced (the specimen shown in Fig. 4G formed about 32 new membranelles which corresponds incidentally the average of 33 membranelles; Table 1); (ii) the 18 frontal-ventral-transverse cirri arise in the ordinary way (1, 3, 3, 3, 4, 4) from the anlagen I–VI (Fig. 4G); (iii) the left and right marginal row originate probably *de novo*; however, we cannot exclude that one (or

two) cirri in the anterior portion of each parental row is (are) involved in anlagen formation (Figs 4G, 5I, J, L); (iv) dorsal kineties 1, 3, and 5 form a primordium each at about mid-body level (Figs 4E–G, 5I, K); since interphasic specimens have five kineties and no dorso-marginal rows are formed, we postulate that, as in *H. paraenigmatica* spec. nov. (see below), kineties 1 and 3 fragment to form kinety 2 (= posterior portion of kinety 1) and kinety 4 (= anterior portion of kinety 3); details on *Hemigastrostyla* pattern, see chapter cell division of *H. paraenigmatica* (Fig. 1B).

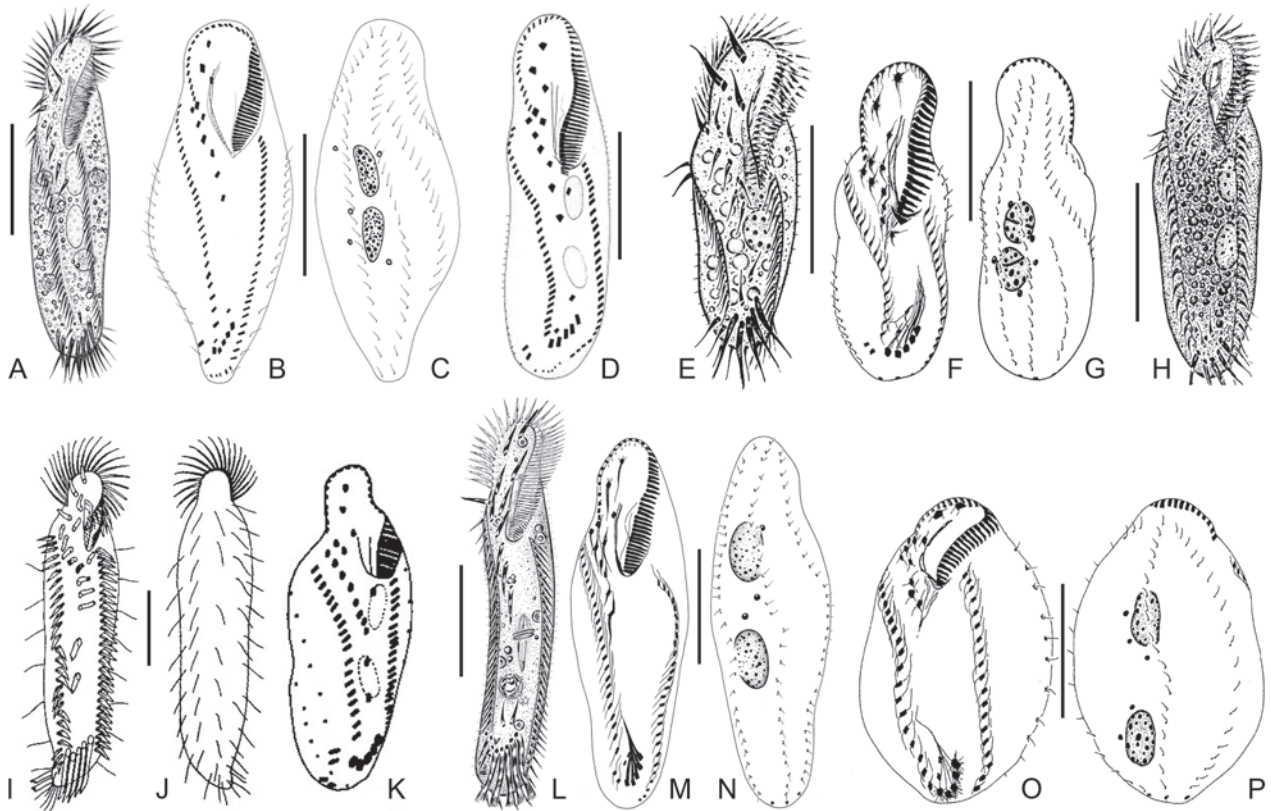
Occurrence and ecology: As yet found only at type locality.

Remarks: The most similar congener is *H. paraenigmatica* because both species have three caudal cirri. However, they can be easily separated (i) by the body length : width ratio (about 5 : 1 vs. 2.6 : 1); (ii) by the relative length of the adoral zone which is 25–30% in *H. elongata* (Figs 2A, B) against almost 50% in *H. paraenigmatica* (Fig. 6E); and (iii) by the location of the postoral ventral cirri (all of them at or behind level of buccal vertex vs. only rearmost cirrus behind level of buccal vertex). For separation from other congeners, see key above.

Hemigastrostyla enigmatica (Dragesco and Dragesco-Kernéis, 1986) Song and Wilbert, 1997 (Figs 6A–D)

- 1986 *Oxytricha enigmatica* n. sp. – Dragesco and Dragesco-Kernéis, *Faune Tropicale*, 26: 463, Planche 137F, G (Fig. 6D; original description).
- 1997 *Hemigastrostyla enigmatica* (Dragesco & Dragesco-Kernéis, 1986) n. comb. – Song and Wilbert, *Arch. Protistenk.*, 148: 421 (combination with *Hemigastrostyla*; see remarks).
- 1999 *Oxytricha enigmatica* Dragesco & Dragesco-Kernéis, 1986 – Berger, *Monogr. Biol.*, 78: 229, Fig. 82a, b, Table 15; not p. 933, Fig. 246a–h, Table 53 (Fig. 6D; detailed review).
- 2007 *Hemigastrostyla enigmatica* (Dragesco and Dragesco-Kernéis 1986) Song & Wilbert, 1997 – Gong, Kim, Kim, Min, Roberts, Warren and Choi, *J. Eukaryot. Microbiol.*, 54: 471, Figs 28–48, Table 1 (Fig. 6A–C; detailed description of two Korean populations).

Improved diagnosis (according to original description): Body size about 100 × 45 µm after protargol impregnation. Body elongate, inconspicuously cephalized. Two macronuclear nodules. 49 adoral membranelles on average. Usually 19 frontal-ventral-transverse cirri, including one isolated postoral ventral cirrus behind buccal vertex. Frontoventral row more or less linear. Pretransverse ventral cirri close to transverse cirri. Dorsal bristles about 8–10 µm long. 5–7 fine caudal cirri.



Figs 6A–P. Some 18-cirri hypotrichs. Ventral view of live specimens (A, E, H, I and J [outline], L) and infraciliature of ventral (B, D, F, I, K, M, O) and dorsal (C, G, J, N, P) side after protargol (B–D, F, G, M–P) and Chatton-Lwoff silver nitrate (I–K) impregnation. **A–D** – *Hemigastrostyla enigmatica* (A–C, from Gong *et al.* 2007; D, from Dragesco and Dragesco-Kernéis 1986); **E–G** – *Hemigastrostyla paraenigmatica* (from Song and Wilbert 1997); **H, O, P** – *Heterooxytricha szaboi* (Wilbert and Song, 2005) comb. nov. (from Wilbert and Song 2005); **I–K** – *Hemigastrostyla stenocephala* (from Borror 1963); **L–N** – *Apogastrostyla rigescens* (from Li *et al.* 2010). Scale bars: 50 µm.

Type locality: Saline pools near the shore of the brackish Lake Nokoué, Bénin (Dragesco and Dragesco-Kernéis 1986).

Type material: According Aesch (2008: 194), no type material has been designated and deposited, indicating that the slides with the type material are in the private collection of J. Dragesco.

Nomenclature: No derivation of the name is given in the original description or a later paper. For derivation of the species-group name *enigmatica*, see *H. paraenigmatica*.

Morphology: For description see Dragesco and Dragesco-Kernéis (1986), review by Berger (1999), and Gong *et al.* (2007).

Molecular data: Gong *et al.* (2007) sequenced the 18S and 28S rRNA genes of two Korean populations (GenBank accession numbers EF194084, EF194085, EF631978). Accordingly, *Hemigastrostyla enigmatica* branches off rather early in the Hypotricha tree, indicating that this type of hypotrichs belongs to the non-monophyletic assemblage “non-dorsomarginalian Hypotricha” which is “defined” by the fact that all of them do not yet have a dorsomarginal kinety (Berger 2008: 46). The vast majority of these taxa (e.g. Urostyloidea, Amphisiellidae) have only bipolar kineties (often three) with or without caudal cirri (e.g. Berger 2006, 2008; Li *et al.* 2010). By contrast, *Hemigastrostyla* and *Trachelostyla* (which also branches off rather basally)

have two specific types of dorsal kinety fragmentation, which are, however, different from the kinety 3 fragmentation of the oxytrichids (e.g. Foissner and Adam 1983a; Berger 1999, 2008; Song and Hu 1999; Shao *et al.* 2007). The convergence of another complex feature in hypotrichs – the zigzagging arrangement (= midventral pattern) of frontoventral cirri in urostyloids, uroleptids, and some oxytrichids (e.g. *Neokeronopsis*) – indicates that evolution within this large taxon is more complex than ever thought (e.g. Foissner *et al.* 2004, Berger 2006, Foissner and Stoeck 2008).

Occurrence and ecology: See Berger (1999) and Gong *et al.* (2007).

Remarks: The redescription by Gong *et al.* (2007) agrees rather well with the original description, *inter alia*, in the increased number of caudal cirri (5–7 in both descriptions) and the indistinct cephalisation. However, there are two differences which have to be briefly discussed: (i) the type population obviously has a distinctly set off postoral ventral cirrus (cirrus IV/2?) just behind the buccal vertex; this cirrus lacking in the Korean populations. Whether this is characteristic for the type population or only for the specimen illustrated is not known; and (ii) the dorsal bristles of the type population are twice as long as those of the Korean populations [8–10 μm (estimated from Planche 137G in original description) vs. 4–5 μm]. To make the diagnosis not too imprecise, the Korean data were excluded. Whether or not the Bénin population has cortical granules is not known; Gong *et al.* (2007) described very small (0.3 μm in diameter), colourless granules along the dorsal kinetids. A detailed interpretation is impossible without reinvestigation of a population from/near the type locality (Lake Nokoué, Bénin). For separation from *H. paraenigmatica* spec. nov., see remarks on this species.

Hemigastrostyla paraenigmatica spec. nov. (Figs 6E–G)

1997 *Hemigastrostyla enigmatica* (Dragesco & Dragesco-Kernéis, 1986) n. comb. – Song and Wilbert, *Arch. Protistenk.*, 148: 421, Figs 6a–j, 43–45, Table 5 (Figs 6E–G; misidentification; details see remarks).

1999 *Hemigastrostyla enigmatica* (Dragesco & Dragesco-Kernéis, 1986) Song & Wilbert, 1977 – Berger, *Monogr. Biol.*, 78: 933, Figs 246a–h, Table 53; not p. 229 and Fig. 82a, b (Figs 6E–G; incorrect year of combination; review; misclassification).

1999 *Hemigastrostyla enigmatica* (Dragesco & Dragesco-Kernéis, 1986) – Song and Hu, *Hydrobiologia*, 391: 249, Figs 1a–g, 2a–f, 3a–g, Table 1 (misidentification; ontogenesis).

Diagnosis (based on type population only): Body size about $125 \times 43 \mu\text{m}$ *in vivo*. Body roughly elliptical. Two macronuclear nodules. Cortical granules small (< 1 μm across), mainly in rosettes around dorsal cilia. 42 adoral membranelles on average. 18 frontal-ventral-transverse cirri. Only rearmost postoral ventral cirrus behind level of buccal vertex. Frontoventral row non-linear. Pretransverse ventral cirri close to transverse cirri. Anterior portion of right marginal row composed of basal body pairs. Dorsal bristles about 3 μm long. One caudal cirrus each on dorsal kineties 2, 3, and 5.

Type locality: Offshore mollusc-farming water in the Yellow Sea near Qingdao, China (further details see Materials and Methods).

Type material: We fix *H. enigmatica sensu* Song and Wilbert (1997) as type population of *H. paraenigmatica*. The protargol slide containing the holotype specimen (Fig. 1e, f in Song and Wilbert 1997; Figs 6F, G in present paper) and several paratype specimens has been deposited in the Laboratory of Protozoology, Ocean University of China (OUC), Qingdao, China, with the registration number SWB950610-01. A further slide (registration number SWB950610-02) containing five paratypes is deposited at the same locality (OUC).

Nomenclature: The species-group name *paraenigmatica* is a composite of the prefix *para-* (closely related; Werner 1972) and the Latin adjective *enigmaticus*, *-a*, *-um* (m, f, n; enigmatic, mysterious; derived and Latinised from the Greek noun *ainigma*, something obscure, inexplicable, a riddle, mystery; Brown 1954) and refers to the fact that this species is very similar to *Hemigastrostyla enigmatica*.

Morphology (Figs 6E–G): For detailed description of morphology, see Song and Wilbert (1997) and review by Berger (1999).

Cell division: This part of the life cycle has been described by Song and Hu (1999). The most interesting details are: (i) the frontal-ventral-transverse cirri as well as the dorsal kinety anlagen originate from primary primordia (Fig. 1e, f in Song and Hu 1999); (ii) the proximal half of the parental adoral is reorganized; (iii) the two extra cirri seem to be remnants of the parental right marginal row, that is, they do not originate from any of the cirral anlagen; (iv) the dorsal ontogenesis proceeds in the *Hemigastrostyla* pattern which is rather curious, namely, at first each one primordium (actually a primary primordium) occurs in the middle portion of kineties 1, 3, and 5 which subsequently divides so that both proter and opisthe have three kinety anlagen

each (Figs 2e, 3a–d in Song and Hu 1999). The anlage elongate and later the anlage originating from parental kinety 1 fragments to form the new kinety 1 (anterior portion) and new kinety 2 (posterior portion with newly formed caudal cirrus). The anlage originating from parental kinety 3 also fragments and forms the new kinety 3 (posterior portion with caudal cirrus) and new kinety 4 (anterior portion). The anlage originating from parental kinety 5 forms, as a whole, the new kinety 5 with the caudal cirrus (Fig. 1B). Thus, caudal cirri occur at the end of new kineties 2, 3, and 5.

Occurrence and ecology: So far only recorded from the Yellow Sea near the city of Qindao, China (Song and Wilbert 1997, Song and Hu 1999). For details, see Materials and Methods.

Remarks: *Oxytricha enigmatica* was discovered by Dragesco and Dragesco-Kernéis (1986) in saline pools near the shore of the brackish Lake Nokoué, Bénin (Fig. 6D). Song and Wilbert (1997) described a Yellow Sea population and simultaneously transferred it to the newly established genus *Hemigastrostyla* with *Oxytricha stenocephala* as type species. Berger (1999: 229), who got the paper by Song and Wilbert (1997) just before he submitted the manuscript of the revision, reviewed the Bénin population and simultaneously wrote that it is rather certainly not an *Oxytricha* species. In the addendum, Berger (1999: 933) included the detailed re-description by Song and Wilbert (1997). Simultaneously, Song and Hu (1999) published the cell division from the Yellow Sea population and provided an improved diagnosis of *Hemigastrostyla*. Gong *et al.* (2007) studied the morphology and some gene sequence data of two populations from the tidal flat at Ganghwa, Korea.

A scrutiny of the descriptions demonstrates that the *H. enigmatica* population from the Yellow Sea (Song and Wilbert 1997, Song and Hu 1999) is not conspecific with the type population and the Korean populations (Dragesco and Dragesco-Kernéis 1986, Gong *et al.* 2007). They differ in the following features: (i) body length : width ratio in specimens illustrated about 2.6 : 1 (Fig. 6E) against 3.6 : 1 (Fig. 6A); (ii) cephalisation (distinct vs. relatively indistinct); (iii) number of caudal cirri (three vs. 5–7); (iv) frontoventral row formed by frontoterminal cirri, cirrus IV/3, and postoral ventral cirri (irregular vs. more or less straight); (v) anterior portion of right marginal row (formed by basal body pairs vs. normal). Likely the most important difference is the number of caudal cirri so that we have little doubt that both species – *H. paraenigmatica* and *H. enigmatica* – are valid. Interestingly, both the Afri-

can and Korean populations are from habitats where the salinity is, on average, somewhat lower than in the sea: 20–25‰ in Korean tidal flat and 0–33‰ in Lake Nokoué (Gbankoto *et al.* 2001, Gong *et al.* 2007) against rather constantly 28–32‰ in the Yellow Sea (Song and Wilbert 1997, Song and Hu 1999). For separation from other congeners, see key above.

Heterooxytricha gen. nov.

Diagnosis: Non-dorsomarginalian 18-cirri hypotrichs with slightly curved undulating membranes. Frontoventral cirri in V-shaped pattern. Postoral ventral cirri right and behind of level of buccal vertex. One left and one right marginal row. Three bipolar kineties in *Gonostomum* pattern with one caudal cirrus each. Saltwater.

Type species: *Hemigastrostyla szaboi* Wilbert and Song, 2005.

Nomenclature: The genus-group name is a composite of the Greek prefix *heteros-* (other, different; Brown 1954) and the genus-group name *Oxytricha*. *Oxytricha* itself is a composite of the Greek adjective *oxys* (sharp, acid; in present case pointed, sharp) and the Greek noun *trichos* (the hair; likely cirrus in present case; Hentschel and Wagner 1996). The name *Heterooxytricha* indicates that members of this genus are similar (but not related) to *Oxytricha*. Like *Oxytricha* of feminine gender (Aesch 2001: 291).

Species included in *Heterooxytricha*: (i) *Heterooxytricha szaboi* (Wilbert and Song, 2005) comb. nov. (type); (ii) *Heterooxytricha geleii* (Wilbert, 1986) comb. nov.

Remarks: The type species of *Heterooxytricha* was classified in *Hemigastrostyla* although it lacks two important features of this genus, namely the extra cirri near the rear end of the right marginal row and five dorsal kineties (Wilbert and Song 2005). Few years later, Wilbert and Song (2008) provided a redescription, which, however, caused some confusion because in the discussion the authors mentioned that *Hemigastrostyla szaboi* lacks extra cirri while in the figures they labelled them (Figs 12D–F in Wilbert and Song 2008). Due to these micrographs, Li *et al.* (2010) transferred *Hemigastrostyla szaboi* to *Apogastrostyla* Li *et al.*, 2010, which has – like *Hemigastrostyla* – two extra cirri, but only three bipolar dorsal kineties. Unfortunately, the whereabouts of the slides of the type population of *H. szaboi* is not known (for details, see type material at *H. szaboi*). Thus, it is not possible to recheck them, but according to the micrographs in Wilbert and Song (2005,

their Fig. 16I, J, L), it looks sure that *H. szaboi* lacks the extra cirri. By contrast, we could recheck the preparation made by Wilbert and Song (2008) showing that this population has two extra cirri. Unfortunately, the exact dorsal kinety pattern of this population is not clearly recognizable, that is, it cannot be decided whether it is of the *Gonostomum* (Fig. 1A) or the *Hemigastrostyla* (Fig. 1B) type. Thus, we remove the population described by Wilbert and Song (2008) from the synonymy of *Heterooxytricha szaboi* and adjudicate it to be indeterminable [the voucher slide of this population, sent to H. Berger by N. Wilbert on 2011.08.17, is now deposited in the Oberösterreichische Landesmuseum in Linz (LI), Upper Austria].

According to the morphological and ontogenetic data, *Heterooxytricha* is a rather basally branching hypotrich because it lacks – like some other basal groups (e.g. amphisiellids, urostyloids) – a dorsomarginal kinety. We are rather certain that this hypothesis will be supported by molecular data on reliable identified populations.

Heterooxytricha differs from *Hemigastrostyla* by the lack of the extra cirri and the number of dorsal kineties and their ontogenesis. The new genus has three bipolar kineties which are formed in the *Gonostomum* pattern (dorsomarginal kinety and kinety fragmentation lacking; Fig. 1A) while *Hemigastrostyla* has five rows which are produced by a specific type of fragmentation (Fig. 1B). In *Hemigastrostyla* the anterior body portion is distinctly narrowed (cephalized; Figs 6E–G) whereas in *Heterooxytricha szaboi* the narrowing is rather indistinct (Figs 6H, O, P).

Oxytricha oxymarina Berger, 1999, a replacement name for *Oxytricha (Oxytricha) marina* Kahl, 1932, has – according to Agamaliyev (1978) – three bipolar dorsal kineties (for review, see Berger 1999: 233). However, the redescription by Agamaliyev (1978) is based on wet silver nitrate impregnation, not very detailed, and shows a rather long adoral zone (51% of body length) while the zone is only 33% of body length in the type population (Kahl 1932). In addition, the rearmost post-oral ventral cirrus is close to the buccal vertex in Kahl (1932), but near the pretransverse ventral cirri in the population studied by Agamaliyev. Dragesco (1972) did not mention the number of dorsal kineties, and Dragesco and Dragesco-Kernéis (1986) took over the (uncertain?) number given by Agamaliyev (1978). *Oxytricha marina sensu* Kwon and Shin (2008) has, like the population studied by Agamaliyev (1978), a rather long adoral zone (about 50% of body length; from Figs

4A, B in Kwon and Shin 2008), undulating membranes in *Stylonychia* pattern, the postoral ventral cirri located posteriorly, and six dorsal kineties (likely due to dorsal kinety 3 fragmentation and two dorsomarginal rows), strongly indicating that it is not identical with the type population of *O. oxymarina* (Kahl, 1932). Very likely, the Korean and the Caspian Sea populations are stylonychines; we suppose that they belong to *Sterkiella* Foissner *et al.*, 1991 and/or *Tetmemena* Eigner, 1999. Because of these uncertainties we do not transfer *O. oxymarina* to *Heterooxytricha*.

***Heterooxytricha szaboi* (Wilbert and Song, 2005) comb. nov. (Figs 6H, O, P)**

2005 *Hemigastrostyla szaboi* nov. spec. – Wilbert and Song, *J. nat. Hist.*, 39: 966, Figs 11A–D, 16G–L, Table VIII (Figs 6H, O, P; original description).

2011 *Apogastrostyla szaboi* (Wilbert and Song, 2005) comb. nov. – Li, Huang, Song, Shin, Al-Rasheid and Berger, *Acta Protozool.*, 49: 208 (combination with *Apogastrostyla*; see remarks at genus section).

Improved diagnosis: Body size about $125 \times 40 \mu\text{m}$ *in vivo*; body outline elongate elliptical. On average 27 adoral membranelles and 23 marginal cirri per row. Two macronuclear nodules. 2–6, on average 3.7 micronuclei.

Type locality: Periphyton on rocks and tidal pools in the littoral zone of Potter Cove, King George Island, Antarctic (Wilbert and Song 2005).

Type material: According to Wilbert and Song (2005: 937), the type material has been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Upper Austria. However, so far the slides are not yet deposited there (Aescht 2008: 192; pers. comm. of E. Aescht to H. Berger from 2011.08.24), indicating that they have been lost.

Nomenclature: Dedicated to the Hungarian protozoologist Andras Szabo (Wilbert and Song 2005).

Morphology: For detailed description see Wilbert and Song (2005).

Occurrence and ecology: So far only recorded from the type locality.

Remarks: For misidentification of the population described by Wilbert and Song (2008), see remarks at genus section. *Heterooxytricha szaboi* differs from *H. geleii* in several features, namely (i) the body length (93–139 μm , on average 114 μm vs. 42–63 μm , 51 μm); (ii) the different location of the pretransverse ventral cirri (near transverse cirri vs. almost in cell centre); (iii) the micronuclei (2–6 close to the two macronuclear nodules vs. a single micronucleus between the two

macronuclear nodules); and (iv) the number of adoral membranelles (25–29, on average 27 vs. 18–21, on average 20).

***Heterooxytricha geleii* (Wilbert, 1986) comb. nov.**

1986 *Holosticha geleii* n. sp. – Wilbert, *Symposia Biologica Hungarica*, 33: 251, Figs 6a–c, 7a–d, Table 1 (original description with some details of cell division).

1999 *Oxytricha geleii* (Wilbert, 1986) comb. nov. – Berger, *Monogr. Biol.*, 78: 232, Fig. 83a–g, Tables 3, 15 (combination with *Oxytricha* and review).

Improved diagnosis: Body size about $53 \times 22 \mu\text{m}$ in protargol preparations. On average 20 adoral membranelles and 22 right and 20 left marginal cirri. A single micronucleus between the two macronuclear nodules.

Type locality: Benthic in Lake Little Manitou (salinity 9.6‰), Saskatchewan, Canada (Wilbert 1986).

Type material: According to a personnel communication by N. Wilbert to H. Berger from 2011.08.17, the type slide(s) of *H. geleii* is (are) no longer available.

Nomenclature: No derivation of the species-group name was given in the original description or the review by Berger (1999). Obviously, Wilbert dedicated this species to József Gelei (1885–1952; Maucha 1954), who published many important papers on ciliates (for bibliography, see Gellért and Müller 1954).

Morphology: For detailed descriptions, see Wilbert (1986) and Berger (1999).

Occurrence and ecology: So far only recorded from the type locality. For review, see Berger (1999).

Remarks: Besides the type species, *Holosticha geleii* – originally described by Wilbert (1986) from a saltwater habitat and later assigned to *Oxytricha* by Berger (1999: 232) – is transferred to *Heterooxytricha* because it is an 18-cirri hypotrich with only three dorsal kineties each bearing a caudal cirrus. The original misclassification in *Holosticha* is rather clearly indicated by the lack of a distinct midventral pattern and some other features characteristic for this urostyloid genus (Berger 2003, 2006). Berger (1999), who supposed a close relationship with *Oxytricha enigmatica* (now *Hemigastrostyla enigmatica*, see above), discussed that the classification in *Oxytricha* is also not definite, *inter alia*, because the number of dorsal kineties is low (three vs. six in *O. granulifera*, type of *Oxytricha*). At that time, Berger assumed that the 18-cirri pattern is an apomorphy of the oxytrichids and therefore he interpreted the evolution of the dorsal kinety pattern incorrectly. Now we are convinced that this little known species neither belongs to *Holosticha* nor to *Oxytricha* and therefore we transfer it to *Heterooxytricha* because

the ventral and dorsal infraciliature agrees with that of *Heterooxytricha szaboi*. The somewhat unusual appearance of the ventral cirral pattern is due to the distinctly anteriorly displaced pretransverse ventral cirri. For detailed comparison with the type species, see there. According to Berger (1999), the present species has 2–4 μm long dorsal bristles. However, neither the text nor the illustrations of Wilbert (1986) contain a hint about this feature. We could not reconstruct from where these values are. Neither Wilbert (1986) nor Berger (1999) provided a diagnosis. Detailed redescription, especially from life, necessary.

***Oxytricha* Bory De Saint-Vincent in Lamouroux, Bory De Saint-Vincent and Deslongchamps, 1824**

1824 *Oxitricha* – Bory De Saint-Vincent in Lamouroux, Bory De Saint-Vincent and Deslongchamps, *Encyclopédie méthodique*, p. 593 (original description). Type (by subsequent designation by Foissner 1989): *Oxytricha granulifera* Foissner and Adam, 1983a.

1932 *Oxytricha Wrzesniowski, 1877* – Kahl, *Tierwelt Dtl.*, 25: 601 (revision).

1989 *Oxytricha* – Foissner, *Sber. öst. Akad. Wiss.*, 196: 235 (fixation of type species).

1999 *Oxytricha* Bory De Saint-Vincent in Lamouroux, Bory De Saint-Vincent & Deslongchamps, 1824 – Berger, *Monogr. Biol.*, 78: 115 (detailed revision).

2007 *Oxytricha* Bory de Saint Vincent, 1824 – Jankowski, *Phylum Ciliophora*, p. 463 (generic revision of ciliates).

2008 *Oxytricha* Bory De Saint-Vincent in Lamouroux, Bory De Saint-Vincent & Deslongchamps, 1824 – Lynn, *Ciliated Protozoa*, p. 360 (familial revision of ciliates).

Improved diagnosis: Flexible 18-cirri Oxytrichidae with undulating membranes in *Oxytricha* pattern and adoral zone formed like a question mark. Frontoventral cirri in V-shaped pattern. One left and one right marginal row. Five or six dorsal kineties in *Oxytricha* pattern, that is, one or two dorsomarginal kineties and simple kinety 3 fragmentation present. Caudal cirri present on dorsal kineties 1, 2, and 4.

Nomenclature: For derivation of genus-group name, see *Heterooxytricha*. The type species problem has been discussed by Foissner (1989) and Berger (1999).

Remarks: The list of synonyms includes only some key references. For a more detailed listing, see Berger (1999).

Oxytricha is one of the oldest and most difficult hypotrich genera and was and is a melting pot (*inter alia* because no seriously defined type species was fixed) for flexible 18-cirri hypotrichs with caudal cirri (e.g. Kahl 1932, Borror 1972; for brief discussion of history, see Berger 1999). Only Foissner (1989) proposed *O.*

granulifera as type, a morphologically and morphogenetically very well studied species which represents a typical *Oxytricha* (Foissner and Adam 1983a). In this species the dorsal kineties are formed according to the so-called *Oxytricha* pattern (Berger and Foissner 1997). This pattern, which includes formation of one or two dorsomarginal kineties and (simple) fragmentation of kiny 3, is very likely characteristic for a large group, the Oxytrichidae (Berger 2006), which were previously defined mainly via the 18-cirri pattern (Berger and Foissner 1997, Berger 1999). However, molecular data indicate that only the subgroup with a rigid body – the Stylonychinae Berger and Foissner, 1997 – forms a monophylum, at least when the small subunit rRNA gene is analyzed (e.g. Foissner *et al.* 2004; Schmidt *et al.* 2007, 2008; Paiva *et al.* 2009; Hu *et al.* 2011). In contrast, the Oxytrichinae Ehrenberg, 1838, reactivated by Berger and Foissner (1997) for the 18-cirri hypotrichs with a flexible body, proved to be a non-monophyletic assemblage according to different molecular markers (e.g. Foissner *et al.* 2004, Schmidt *et al.* 2007, Paiva *et al.* 2009, Hu *et al.* 2011). Thus, the oxytrichines have been deactivated by Berger (2008: 47). The non-monophyly of this group is very likely due to the use of the 18-cirri pattern as main apomorphy for the Oxytrichidae. However, the distribution of this pattern throughout the whole molecular Hypotricha tree caused Berger (2006, 2008) to hypothesize its first occurrence in the stemline of this group.

In the revision by Berger (1999), 54 species are classified in *Oxytricha*. According to the knowledge about their dorsal infraciliature they can be divided into four groups, namely (i) those species which have the *Oxytricha* pattern like the type species *O. granulifera*; (ii) those for which the pattern is not or only insufficiently known; (iii) those which have the so-called *Urosomoida* pattern, that is, three bipolar kineties (dorsal kiny fragmentation lacking) and one (or two) dorsomarginal rows; and (iv) those which have another pattern (*Oxytricha saltans* and *O. shii*; see below). There is little doubt that species of the third group are misplaced in *Oxytricha*, as already stated by Berger (2011: 538). This is not only indicated by the different dorsal kiny pattern, but also by molecular data. *Oxytricha lanceolata* and *O. longa*, both having the *Urosomoida*-pattern, do not cluster with the type species *O. granulifera* or other species with the *Oxytricha* kiny pattern, as *O. longigranulosa* and *O. elegans* (e.g. Schmidt *et al.* 2007, Sonntag *et al.* 2008, Paiva *et al.* 2009, Hu *et al.* 2011). Unfortunately, not even the *Oxytricha* species

of group (i) and, more serious, not even various populations identified as *O. granulifera* by morphological features form a monophyletic group (e.g. Schmidt *et al.* 2007, Paiva *et al.* 2009).

These problems, which can have various reasons (e.g. morphological misidentification; mistakes in the molecular analyses, see also remarks at *Actinotricha saltans*), clearly demonstrate that we are very far away from a final understanding of the evolution of the hypotrichs. Nevertheless, we transfer two *Oxytricha* species (*O. marcili*, *O. pseudofurcata*), which have the *Urosomoida* dorsal kiny pattern and a slightly reduced number (< 18) of frontal-ventral-transverse cirri, to *Urosomoida* (see there for explanation). *Oxytricha lanceolata*, which also has the *Urosomoida* dorsal kiny pattern, is clearly separated from the *O. granulifera* cluster in molecular trees (e.g. Schmidt *et al.* 2007, Paiva *et al.* 2009). However, since it has 18 frontal-ventral-transverse cirri it is classified, like three other species with the same morphological features, as *incertae sedis* in *Oxytricha*. In addition, we reactivate *Actinotricha*, whose type species (*A. saltans*) was classified in *Oxytricha* for a long time (see below).

Oxytricha shii Shi, Wei and Wang, 1997, a species overlooked by Berger (1999), has eight or nine dorsal kineties, including three dorsomarginal rows. Kiny 3 does not make a simple, but a double fragmentation, that is, the anterior portion of anlage 3 becomes kiny 3, the middle portion becomes kiny 4, and the posterior portion becomes kiny 5 (Shi *et al.* 1998). Thus, caudal cirri are attached to kineties 1, 2, and 5. This dorsal kiny pattern as well as the *Cyrtohymena*-like undulating membranes indicate that this species is closely related to *Cyrtohymena* (*Cyrtohymenides*) *aspoecki* Foissner, 2004. We therefore transfer *O. shii* to *Cyrtohymena* (*Cyrtohymenides*) Foissner, 2004: *Cyrtohymena* (*Cyrtohymenides*) *shii* (Shi, Wei and Wang, 1997) comb. nov.

The procedures discussed above are a further step to unravel the complicated taxonomy of the old, but still little-known genus *Oxytricha*.

Species included in *Oxytricha*: The species now included are divided into three (non-taxonomical) groups, namely those for which the dorsal kiny pattern is known, those for which the pattern is not yet known, and four species which are classified as *incertae sedis*. The type species is listed first; within the groups, the species are arranged alphabetically. Taxonomy follows Berger (1999), respectively, the original descriptions for species which were described later.

Oxytricha granulifera Foissner and Adam, 1983a (type species of *Oxytricha*). Remarks: See Berger (1999: 197).

***Oxytricha* species for which the dorsal kinety pattern is known:**

Oxytricha africana Foissner, 1999.

Oxytricha arabica Foissner, Quintela-Alonso and Al-Rasheid, 2008.

Oxytricha auripunctata Blatterer and Foissner, 1988. Remarks: Five dorsal kineties present, but pattern difficult to recognise because cortical granules stain with protargol. Details see Berger (1999: 196).

Oxytricha balladyna Song and Wilbert, 1989. Remarks: See Berger (1999: 126) for comment on dorsal kinety pattern.

Oxytricha elegans Foissner, 1999. Remarks: This species has, according to the original description, four dorsal kineties with distinct breaks in kineties 1 and 4. The number of kineties (four) and the pattern indicate a classification in *Urosomoida*. However, according to the gene sequence analyses by Schmidt *et al.* (2007), *O. elegans* clusters together with several *O. granulifera* populations, indicating that it is a true *Oxytricha*. Thus, the break in kinety 4 is obviously a misinterpretation (Fig. 15c, f in Foissner 1999). We suppose that this species has a break in kinety 1; a more or less bipolar kinety 2; a kinety 3 which terminates slightly behind mid-body; a short kinety 4 composed of three bristles only (this is actually the rear portion of kinety 3 after the ordinary kinety 3 fragmentation, Fig. 1D); and one dorsomarginal kinety (= kinety 5). Caudal cirri are attached, as is usual for the *Oxytricha* pattern, to kineties 1, 2, and 4 according to our interpretation of the pattern.

Oxytricha fallax Stein, 1859. Remarks: See Berger (1999: 137). A difficult species which needs detailed redescription.

Oxytricha granulosa Schmitz, 1986. Remarks: See Berger (1999: 148). Dorsal kinety pattern described, but difficult to interpret.

Oxytricha hymenostoma Stokes, 1887. Remarks: See Berger (1999: 150).

Oxytricha longigranulosa Berger and Foissner, 1989. Remarks: See Berger (1999: 213).

Oxytricha longissima Dragesco and Njine, 1971. Remarks: See Berger (1999: 164). Five kineties present, but pattern neither described nor illustrated.

Oxytricha minor (Maskell, 1887) Kahl, 1932. Remarks: This species has, according to a redescription, only three dorsal kineties. However, it cannot be excluded that this is a misobservation and therefore the

generic assignment is not changed. Details see Berger (1999: 166).

Oxytricha monspessula (Chatton and Séguéla, 1940) Borror, 1972. Remarks: Perhaps a *Sterkiella histriomuscorum*, according to Berger (1999: 168).

Oxytricha nauplia Berger and Foissner, 1987. Remarks: Five kineties present, but pattern difficult to interpret. Details see Berger (1999: 215).

Oxytricha opisthomuscorum Foissner, Blatterer, Berger and Kohmann, 1991. Remarks: Kinety 4 only inconspicuously separated from kinety 3. Details see Berger (1999: 217, 925).

Oxytricha ottowi Foissner, 1996a. Remarks: See Berger (1999: 218).

Oxytricha quadricirrata Blatterer and Foissner, 1988. Remarks: See Berger (1999: 223).

Oxytricha rubripuncta Berger and Foissner, 1987. Remarks: See Berger (1999: 224).

Oxytricha siseris Vuxanovici, 1963. Remarks: Dorsal kinety pattern known (usually five, rarely six kineties), but difficult to interpret. Likely not an *Oxytricha* because of the deviating undulating membrane pattern. Details see Berger (1999: 187).

Oxytricha tenella Song and Wilbert, 1989. Remarks: Dorsal kinety pattern difficult to interpret; details see Berger (1999: 191).

Oxytricha variabilis Grolière, 1975. Remarks: Five dorsal kineties present, but pattern neither described nor illustrated. Details see Berger (1999: 193).

***Oxytricha* species for which the dorsal kinety pattern is not known:**

Oxytricha aeruginosa Wrzesniowski, 1866. Remarks: See Berger (1999: 122).

Oxytricha alfredi Berger, 1999. Remarks: See Berger (1999: 125).

Oxytricha alfredkahli Foissner, 1987. Remarks: See Berger (1999: 227).

Oxytricha chlorelligera Kahl, 1932. Remarks: See Berger (1999: 129).

Oxytricha crassistilata Kahl, 1932. Remarks: See Berger (1999: 135).

Oxytricha discifera Kahl, 1932. Remarks: Very likely not an *Oxytricha* species because distinctly cephalized. Details see Berger (1999: 227).

Oxytricha durhamiensis Berger, 1999. Remarks: Very likely not an *Oxytricha*. Details see Berger (1999: 228).

Oxytricha elongata (Smith, 1897) Kahl, 1932. Remarks: See Berger (1999: 136).

Oxytricha faurei Tucolesco, 1962. Remarks: See Berger (1999: 146).

Oxytricha halophila Kahl, 1932. Remarks: See Berger (1999: 232).

Oxytricha kahlovata Berger, 1999. Remarks: See Berger (1999: 157).

Oxytricha longicirrata Kahl, 1932. Remarks: See Berger (1999: 163).

Oxytricha matritensis Ramirez-Montesinos and Perez-Silva, 1966. Remarks: See Berger (1999: 165).

Oxytricha multiseta Dragesco, 1966. Remarks: See Berger (1999: 169).

Oxytricha oxymarina Berger, 1999. Remarks: See remarks at new genus *Heterooxytricha*. For review, see Berger (1999: 233).

Oxytricha parahalophila (Wang and Nie, 1935) Berger, 1999. Remarks: See Berger (1999: 170).

Oxytricha parallela Engelmann, 1862. Remarks: See Berger (1999: 171).

Oxytricha procera Kahl, 1932. Remarks: See Berger (1999: 220).

Oxytricha proximata Shibuya, 1930. Remarks: See Berger (1999: 221).

Oxytricha pseudofusiformis Dragesco and Dragesco-Kernéis, 1986. Remarks: See Berger (1999: 222).

Oxytricha saprobia Kahl, 1932. Remarks: See Berger (1999: 174).

Oxytricha similis Engelmann, 1862. Remarks: See Berger (1999: 183).

Oxytricha sphagni Kahl, 1932. Remarks: See Berger (1999: 190).

Species incertae sedis in *Oxytricha*: The four *Oxytricha* species listed below have four dorsal kineties arranged in the *Urosomoida* pattern, but they invariably have 18 frontal-ventral-transverse cirri. Thus, it seems not wise to transfer them to the genus *Urosomoida*, which is characterised, *inter alia*, by a reduced number of ventral and/or transverse cirri (Foissner 1982, Berger and Foissner 1997, Berger 1999). In *O. pseudosimilis* the anlagen V and VI of the proter are very likely formed as in *Oxytricha*, that is, together with the anlagen for the opisthe (Hemberger 1982, Foissner and Adam 1983a, Berger 1999). By contrast, in *Urosomoida agilis* (type of *Urosomoida*) and *U. agiliformis*, the anlagen V and VI of the proter originate *de novo* (Buitkamp 1975, Foissner and Adam 1983b). This indicates that “*Oxytricha*” species with the full set of 18 cirri and four dorsal kineties neither belong to *Oxytricha* nor to *Urosomoida*. A more or less distinct separation of *O. lanceolata* from *O. granulifera* is also indicated by gene sequence analyses (e.g. Schmidt *et al.* 2007, Paiva *et al.* 2009, Hu *et al.* 2011). Actually this would justify

the establishment of a new genus. However, *Oxytricha longa* (= *Urosomoida longa* in present paper, see below), which is very similar to *O. pseudosimilis* [sole(?) difference four vs. five transverse cirri], never clusters with *O. lanceolata* indicating that flexible 18-cirri hypotrichs with four dorsal kineties are morphologically rather similar, but not closely related, likely because both features (18-cirri pattern, *Urosomoida* pattern) are relatively old. Because of these uncertainties we preliminary refrain from the establishment of one or more new genera until more morphogenetic and molecular data are available.

Oxytricha islandica Berger and Foissner, 1989. Remarks: See Berger (1999: 207).

Oxytricha lanceolata Shibuya, 1930. Remarks: See Berger (1999: 209).

Oxytricha pseudosimilis Hemberger, 1985. Remarks: See Berger (1999: 222).

Oxytricha setigera Stokes, 1891. Remarks: See Berger (1999: 175).

Species misplaced in *Oxytricha*: Very many species have been incorrectly assigned to *Oxytricha*, either originally or subsequently. It is not possible to list all of them in the present paper. For almost complete lists, including many species indeterminate, see Berger (1999, 2001).

***Urosomoida* Hemberger in Foissner, 1982**

1982 *Urosomoida* Hemberger, 1981 – Foissner, *Arch. Protistenk.*, 126: 345 (original description). Type species (by original designation): *Uroleptus agilis* Engelmann, 1862.

1999 *Urosomoida* Hemberger in Foissner, 1982 – Berger, *Monogr. Biol.*, 78: 345 (revision).

2007 *Urosomoida* Hemberger in Foissner, 1982 – Jankowski, *Phylum Ciliophora*, p. 463 (generic revision of ciliates).

2008 *Urosomoida* Hemberger in Foissner, 1982 – Lynn, *Ciliated Protozoa*, p. 360 (familial revision of ciliates).

Improved diagnosis: Flexible non-oxytrichid “18-cirri” Dorsomarginalia with undulating membranes in *Oxytricha* pattern and adoral zone formed like a question mark. Number of postoral ventral cirri, and/or pretransverse ventral cirri, and/or transverse cirri reduced, that is, usually less than 18 frontal-ventral-transverse cirri. One left and one right marginal row. Four dorsal kineties in *Urosomoida* pattern, that is, three bipolar kineties and one dorsomarginal row. Caudal cirri present on kineties 1–3.

Nomenclature: For derivation of name, see Berger (2008: 514).

Remarks: The list of synonyms contains only some key references. For some further pre-1999 entries, see Berger (1999).

Urosomoida was established for caudally more or less distinctly tapered “18-cirri” hypotrichs with a reduced number of pretransverse ventral and/or transverse cirri (Foissner 1982, Hemberger 1985). *Urosomoida agilis*, originally classified in the difficult genus *Uroleptus* Ehrenberg, 1831 (see He *et al.* 2011 for brief review) and later transferred to *Oxytricha* by Borror (1972), was fixed as type species. To date, the small subunit rRNA of *U. agilis* is not yet analysed, that is, we do not have molecular evidence for the phylogenetic position of this genus. Foissner (1982), Berger and Foissner (1997), Berger (1999), Jankowski (2007), and Lynn (2008) classified it in the Oxytrichidae while Eigner (1997) assigned *U. agilis* to the Parakahliellidae Eigner, 1997, an inhomogeneous assemblage of stylonychines, flexible oxytrichids, and some other species.

The classification of *Urosomoida* in the oxytrichids was mainly due to the 18-cirri pattern which was hypothesized as apomorphy for this group previously (Berger and Foissner 1997, Berger 1999). Species which have a dorsomarginal kinety but lack dorsal kinety 3 fragmentation belong to the non-monophyletic assemblage “non-oxytrichid Dorsomarginalia” according to Berger (2006, 2008), regardless of whether or not the taxon has 18 frontal-ventral-transverse cirri because the 18-cirri pattern has evolved in the stem line of the Hypotricha according to this hypothesis. *Kahliella* Corliss, 1960 and *Parakahliella* Berger *et al.*, 1985, two kahliellid genera according to Berger (2011), have basically the same dorsal kinety pattern as *Urosomoida*. Thus, it is likely that all of them appear in the non-oxytrichid Dorsomarginalia area in molecular trees.

Berger and Foissner (1997) and Berger (1999) included the ontogenetic feature “primordia of V and VI of proter originate *de novo*” in the characterisation of *Urosomoida*, an attribute also occurring in *Notohymena* Blatterer and Foissner, 1988 and *Cyrtohymena* Foissner, 1989. Since ontogenetic data are sparse in *Urosomoida* [Buitkamp 1975, *U. agilis*; Foissner and Adam 1983b, *U. agilisformis*; Ganner *et al.* 1987, *U. longa* (this species shows a different type of this feature)], we preliminarily remove this feature from the diagnosis until more of the 14 species now included are analysed in this respect.

Four *Oxytricha* species which have the typical *Urosomoida* dorsal kinety pattern are not included in *Urosomoida* because they invariably have the full set of 18 frontal-ventral-transverse cirri. They are, preliminarily, classified as *incertae sedis* in *Oxytricha* (details see there).

Species included in *Urosomoida*:

Urosomoida agilis (Engelmann, 1862) Hemberger in Foissner, 1982 (type species). Remarks: See Berger (1999: 347).

Urosomoida agilisformis Foissner, 1982. Remarks: See Berger (1999: 356).

Urosomoida antarctica Foissner, 1996b. Remarks: See Berger (1999: 365).

Urosomoida deserticola Foissner, Agatha and Berger, 2002.

Urosomoida dorsincurisura Foissner, 1982. Remarks: See Berger (1999: 362).

Urosomoida granulifera Foissner, 1996b. Remarks: See Berger (1999: 352).

Urosomoida longa (Gelei and Szabados, 1950) Foissner, Blatterer, Berger and Kohmann, 1991 (basionym *Oxytricha longa*). Remarks: For this species the SSU rRNA gene has been analysed (GenBank accession number AF508763), based on a population isolated from the Ten Mile Creek in Colorado (USA) and identified by W. Foissner (Hewitt *et al.* 2003). Its phylogenetic position is rather variable, but generally it occurs close to the stylonychines (Schmidt *et al.* 2007, Sonntag *et al.* 2008, Paiva *et al.* 2009, Hu *et al.* 2011). Supposed that this position within the oxytrichids is correct, we have to postulate that *O. longa* has lost kinety 3 fragmentation. Only recently, Küppers *et al.* (2011) described the same phenomenon in *Parasterkiella thompsoni* (Foissner, 1996b). However, according to Küppers *et al.* (2011), *Oxytricha longa* (AF164125) clusters outside the oxytrichids making a final decision about its real position difficult at the present state of knowledge. We remove it from *Oxytricha* because of the different dorsal kinety pattern and the reduced number of pretransverse ventral and transverse cirri and classify it in *Urosomoida*, as already proposed by Foissner *et al.* (1991: 300, 301). However, we would like to stress that this assignment is very likely only preliminary until molecular data of *Urosomoida agilis*, type of *Urosomoida*, are available. Probably a new genus has to be established for *O. longa*. For review, see Berger (1999: 158).

Urosomoida marcili (Paiva and Silva-Neto, 2004) comb. nov. (basionym *Oxytricha marcili*). Remarks: This species has, in addition to the *Urosomoida* dorsal kinety pattern, invariably ($n = 20$) only one pretransverse ventral cirrus (Paiva and Silva-Neto 2004). Because of this combination of features, it is assigned to *Urosomoida*.

Urosomoida minima Hemberger, 1985. Remarks: See Berger (1999: 366).

Urosomoida monostyla Foissner, Agatha and Berger, 2002.

Urosomoida namibiensis Foissner, Agatha and Berger, 2002.

Urosomoida perthensis Foissner and O'Donoghue, 1990. Remarks: See Berger (1999: 362).

Urosomoida pseudofurcata (Berger, 1999) comb. nov. (basonym *Oxytricha pseudofurcata*). Remarks: This species has very likely the *Urosomoida* dorsal kinety pattern and obviously only four transverse cirri. Thus, it is preliminary classified in *Urosomoida*. For review, see Berger (1999: 173).

Urosomoida reticulata Foissner, Agatha and Berger, 2002.

Actinotricha Cohn, 1866

1866 *Actinotricha* nov. gen. – Cohn, *Z. wiss. Zool.*, 16: 299 (original description). Type (by monotypy): *Actinotricha saltans* Cohn, 1866.

1882 *Actinotricha*, Cohn – Kent, *Manual infusoria* II, p. 790 (revision).

Improved diagnosis: Basal branching (non-dorsomarginalian?) Hypotricha with bipartite adoral zone; distal adoral membranelles widely spaced and radially arranged. Undulating membranes short and in parallel. Buccal lip with distinct spine. One left and one right marginal row. More than three dorsal kineties. Caudal cirri present. Saltwater.

Nomenclature: *Actinotricha* is a composite of the word *actino-* (from the Greek noun *aktinos*; ray, beam; Brown 1954) and the Greek noun *trichos* (the hair; adoral membranelles in present case; Hentschel and Wagner 1996) and refers to the radially arranged anterior-most adoral membranelles.

Species included in *Actinotricha*: (i) *Actinotricha saltans* Cohn, 1866.

Remarks: See single species.

Actinotricha saltans Cohn, 1866

1866 *Actinotricha saltans* nov. gen. et spec. – Cohn, *Z. wiss. Zool.*, 16: 283, Tafel XIV, Fig. 24–26 (original description).

1932 *Actinotricha saltans* Cohn, 1866 – Kahl, *Tierwelt Dtl.*, 25: 604, Fig. 113₂₅ (revision).

1997 *Oxytricha saltans* (Cohn, 1866) – Song and Wilbert, *Arch. Protistenk.*, 148: 420, Fig. 5a–e, 19, 20, Table 5 (redescription and neotypification).

1999 *Oxytricha saltans* (Cohn, 1866) Rees, 1881 – Berger, *Monogr. Biol.*, 78: 236, 931, Fig. 86a–k, 87a–l, 88a–g, 89e, 245a–e, Table 15 (detailed review).

Improved diagnosis: Body size about 60 × 22 μm *in vivo*. Two macronuclear nodules and two or more micronuclei. Constantly seven frontal, buccal, and fron-

toventral cirri, three far posteriorly located postoral ventral cirri, two pretransverse ventral cirri, and five distinctly enlarged transverse cirri. 8–10 left marginal cirri. Right marginal row commences at or behind mid-body, composed of 5–7 cirri only. Usually five dorsal kineties and constantly three caudal cirri (ontogenesis not known).

Type locality: Due to the neotypification by Song and Wilbert (1997: 420), the type locality of *A. saltans* is an area with fish- and mollusc-farming waters off the coast of the city of Qingdao (China), Yellow Sea. The original type locality is not known because Cohn (1866) found *A. saltans* in an aquarium containing material from both near the island of Heligoland (Germany; North Sea) and Dorsetshire (UK; Atlantic Ocean).

Type material: The slide with the neotype population (accession number SWB931027) has been deposited in the College of Fisheries (Protozoological Laboratory), Ocean University of Qingdao, Qingdao, China (Song and Wilbert 1997).

Nomenclature: The species-group name *saltans* (Latin adjective; dancing, jumping; Hentschel and Wagner 1996) refers to the jumping movement.

Remarks: The lists of synonyms contain only some key references. For more detailed chronological synonymies, see Berger (1999).

Cohn (1866) discovered this rather small, but very conspicuous marine species in an aquarium, also containing, *inter alia*, *Trachelostyla pediculiformis* (Cohn, 1866) Borror, 1972. It was redescribed several times and has one subjective synonym, namely *Actinotricha hyalina* Pereyaslavzewa, 1886 (for details, see Berger 1999). In 1881, Rees transferred *A. saltans* to *Oxytricha* and therefore synonymized the genus *Actinotricha* with *Oxytricha*. Kahl (1932) classified, although somewhat cryptic, *Actinotricha* as subgenus of *Oxytricha*, but simultaneously listed *A. saltans* in the subgenus *Oxytricha* (*Tachysoma*) Stokes, 1887. In 1972, Borror transferred it to *Tachysoma*, a classification which is very likely incorrect because caudal cirri are present in *A. saltans*. Only Lepsi (1926, 1965), Wang (1934), and Esteban and Finlay (2007), an ecological paper, accepted *Actinotricha* as discrete genus. More recent morphological analyses (Song *et al.* 1991, Song and Wilbert 1997) and the basal branching in molecular Hypotricha trees (e.g. Schmidt *et al.* 2007, Guo *et al.* 2008, Paiva *et al.* 2009, Hu *et al.* 2011) based on a population isolated by Z. Chen and W. Song (GenBank accession number AF370028) support the decision by Cohn (1866) to es-

establish a distinct genus. *Actinotricha saltans* has five (rarely six) dorsal kineties and three caudal cirri (Song *et al.* 1991, Song and Wilbert 1997). Unfortunately, we do not know the ontogenesis, but the basal branching in the molecular trees strongly indicates that the dorsal kineties are not formed according to the *Oxytricha* pattern. Very likely a special type evolved, perhaps similar to those described for *Hemigastrostyla* or *Trachelostyla* (Song and Hu 1999, Shao *et al.* 2007). The molecular classifications of *A. saltans* are rather different. According to Schmidt *et al.* (2007), it is closely related to *Gonostomum*, according to Paiva *et al.* (2009) it is related with *Holosticha*, and Hu *et al.* (2011) estimated *Hemigastrostyla enigmatica* as next relative, proving that trees based on gene sequences have to be interpreted with due skill, care and diligence. In spite of these discrepancies, we follow Paiva *et al.* (2008) and Berger (2011: 538) and reactivate *Actinotricha* with *A. saltans* as single species (at the present state of knowledge) because of strong morphological (and likely also ontogenetic) evidence and a clear separation from *Oxytricha granulifera* (type of *Oxytricha*) in molecular trees.

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