A Huge Diversity of Metopids (Ciliophora, Armophorea) in Soil from the Murray River Floodplain, Australia. II. Morphology and Morphogenesis of *Lepidometopus platycephalus* nov. gen., nov. spec.

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**Abstract.** The morphology and morphogenesis of a new Australian metopid ciliate, *Lepidometopus platycephalus* nov. gen., nov. spec., were studied using live observation, various silver impregnation methods, scanning electron microscopy, and morphometry. The new genus is outstanding in having epicortical scales (lepidosomes) and a strongly flattened and distinctly projecting preoral dome. Diagnostic features of *L. platycephalus* include a small, reniform body carrying an elongated caudal cilium, about 11 ciliary rows, and an adoral zone composed of an average of 11 polykinetids. The morphogenesis of *L. platycephalus* matches data from other metopids in that (1) the body is drastically re-shaped, (2) the parental oral structures are reorganized but do not contribute to the daughter oral ciliature, (3) the opisthe’s adoral polykinetids originate pleurotelokinetally, (4) the opisthe’s paroral membrane is formed via re-arrangement of the posterior portion of the first two perizonal rows, and (5) the opisthe’s perizonal stripe is made by three parental perizonal rows and two dorsolateral ciliary rows. The morphogenetic data corroborate phylogenetic analyses in that caenomorphids are only superficially similar to metopids; metopids and clevelandellids are closely related; and litostomateans are the best candidates for a sister group of the metopid-clevelandellid assemblage within the SAL superclade.

**Key words:** Binary fission, lepidosomes, Metopidae, morphometry, stomatogenesis

**INTRODUCTION**

The order Metopida Jankowski, 1980 unites free-living armophoreans with more or less distinct anterior body torsion and a preoral dome carrying a densely ciliated perizonal stripe (Jankowski 2007, Lynn 2008). These elegant ciliates graze bacteria in anoxic or microaerophilic environments with the aid of an obliquely extending or spiralled adoral zone of polykinetids and a tongue-like paroral membrane (Foissner et al. 1992, 2002; Esteban et al. 1995; Foissner 1998). In spite of the wide distribution and ecological significance in oxygen-depleted environments (Saccà 2012, Hu 2014, Foissner 2016a, Tirjaková et al. 2016), taxonomical and morphological research on metopids has been revived only recently (e.g., Bourland and Wendell 2014; Bourland et al. 2014, 2017; da Silva-Neto et al. 2015; Foissner 2016b, c; Omar et al. 2017; VĎačný and Foissner 2017).
Australia has a comparatively huge, undescribed diversity of metopids, several of which have a peculiar morphology (Foissner 2016b, c; Vďačný and Foissner 2017). For instance, *Heterometopus meisterfeldi* Foissner, 2016c, discovered in soil from the Fogg Dam in the Northern Territory, is outstanding in having a J-shaped adoral zone that extends slightly obliquely over the ventral side. Thus, the oral apparatus of *Heterometopus* is more similar to that of *Blepharisma* Perty, 1849 or *Pseudoblepharisma* Kahl, 1927 than to that of metopids. The floodplain of the Murray River in Southeast Australia also houses several remarkable species, such as *Metopus murrayensis* and the large *M. magnus* and *M. rex* (Vďačný and Foissner 2017). *Metopus platycephalus* nov. gen., nov. spec. was isolated from the upper 5 cm soil layer of the floodplain of the Murray River at the Landside of Ryans road near to the town of Albury, Southeast Australia (S36°06’ E146°54’). The material was collected in February 2006, air-dried for three weeks, and sealed in a plastic bag. The ciliates were reactivated from resting cysts in summer 2006, using the non-flooded Petri dish method, as described in Vďačný and Foissner (2012). A more detailed description of the sample is provided by Vďačný and Foissner (2017).

### MATERIALS AND METHODS

#### Sampling and sample processing

*Lepidometopus platycephalus* nov. gen., nov. spec. was isolated from the upper 5 cm soil layer of the floodplain of the Murray River at the Landside of Ryans road near to the town of Albury, Southeast Australia (S36°06’ E146°54’). The material was collected in February 2006, air-dried for three weeks, and sealed in a plastic bag. The ciliates were reactivated from resting cysts in summer 2006, using the non-flooded Petri dish method, as described in Vďačný and Foissner (2012). A more detailed description of the sample is provided by Vďačný and Foissner (2017).

#### Taxonomic methods

*Lepidometopus platycephalus* was studied using a combination of *in vivo* observation, silver impregnation, and scanning electron microscopy (SEM), as described by Foissner (1991, 2014). Live ciliates were studied at low and high magnifications with bright field and differential interference contrast. The ciliature was revealed with protargol and silver carbonate impregnation. The ontogenetic processes were reconstructed from protargol preparations, which show concomitantly body shape, ciliary pattern, and nuclear apparatus. *In vivo* measurements were performed at 40–1000 × while counts and measurements on protargol-impregnated specimens were conducted at a magnification of 1000 ×. Illustrations of live specimens were based on free-hand sketches and photographs while those of impregnated cells were made with a drawing device.

#### Terminology

General terminology follows Lynn (2008). Interphase terminology is based on Kahl (1932), Jankowski (1964a), Foissner and Agatha (1999), and Foissner (2016c). The oral patterns were classified into types by Vďačný and Foissner (2017). *Lepidometopus platycephalus* represents a fourth type characterized as follows (Fig. 1): The distal portion of the preoral dome is strongly flattened and projects distinctly in lateral view, forming a right or nearly right angle with the main body axis. The dome lip is inconspicuous. The side stripe forms a moderately deep channel. The adoral zone extends vertically to strongly obliquely over the anterior half of the ventral side. This type occurs in *Lepidometopus* nov. gen. and possibly also in two insufficiently known genera, *Palmarella* Jankowski, 1975 and *Tesnospira* Jankowski, 1964b.

Ontogenetic terminology is according to Foissner (1996). Division stages are distinguished as follows: Early dividers are characterized by the proliferation of basal bodies in the dorsal, dorsolateral and postoral kinetics; the macronucleus is in the anterior body half. Mid-dividers have assembled the adoral zone of polykinetids both in proter and opisthe; the macronucleus is in the cell centre. Late dividers are constricted in the middle; the macronucleus is dumbbell-shaped.

### RESULTS

#### Lepidometopus nov. gen. Vďačný and Foissner

**Diagnosis:** More or less reniform Metopidae with epicortical scales. Five perizonal kinetics. Type 4 oral area.

**Type species:** *Lepidometopus platycephalus* nov. spec.

**Etymology:** A composite of the stem of the Latin adjective lepid-us, -a, -um [m, f, n] (charming), the thematic vowel -o-, and the genus-group name *Metopus*. Masculine gender.
Lepidometopus platycephalus nov. spec. Foissner and Vďačný

Diagnosis: Size about 45 × 20 µm in vivo. Body broadly to narrowly reniform with a somewhat rhomboidal appearance when viewed ventro- or dorsolaterally. Macronucleus between anterior and posterior end of adoral zone, globular to oblong; one globular to broadly ellipsoid micronucleus. Contractile vacuole terminal. Epicortical scales about 1.25 × 0.45 µm in SEM, flat with margin curled up. On average 11 ciliary rows; caudal cilium about 20 µm long. Perizonal stripe composed of five kineties extending approximately 46% of body length and forming about 19 false kineties. Adoral zone extends about 50% of body length, composed of an average of 11 polykinetids.

Type locality: Loamy soil and leaf litter from the floodplain of the Murray River near to the town of Albury, Australia (S36°06' E146°54').

Type material: The holotype slide and eight paratype slides with protargol-impregnated specimens have been deposited in the Museum of Natural History (Biologizezentrum) in Linz (LI), Austria. The holotype (Fig. 2K, L) and relevant paratype specimens as well as dividers have been marked by black ink circles on the coverslip.

Etymology: Derived from the Ancient Greek adjective platús (πλατύς, flat) and the Ancient Greek noun képhalos (κέφαλος [m], head), referring to the strongly flattened preoral dome. The composite name is latinized and treated as a noun in the nominative singular standing in apposition to the generic name [Art. 11.9.1.2 of the International Commission on Zoological Nomenclature (1999)].

Description: Size in vivo 35–50 × 15–30 µm, usually about 45 × 20 µm, as calculated from some in vivo measurements and the morphometric data adding 15% preparation shrinkage (Table 1). Body asymmetric and thus multi-shaped: broadly to narrowly reniform in ventro- and dorsolateral views (Figs 2A, G, K–V, 3A, B, 4C, D), broadly crescentic in lateral views (Figs 2F, H, 4B, E, 5B), and dumbbell-shaped in ventrocaudal views.

![Diagram of Lepidometopus platycephalus](image)

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**Fig. 1.** Various views of semi-schematized anterior body portion of Lepidometopus. Opposed arrowheads mark the strongly flattened distal portion of the preoral dome. AZP – adoral zone of polykinetids (black); PS – perizonal stripe (grey); SS – side stripe.
Table 1. Morphometric data on *Lepidometopus platycephalus* nov. gen., nov. spec.

| Characteristics                        | Mean  | M    | SD   | SE   | CV   | Min  | Max  | n  |
|----------------------------------------|-------|------|------|------|------|------|------|----|
| Body, length                           | 37.2  | 38.0 | 3.7  | 0.8  | 10.0 | 31.0 | 44.0 | 21 |
| Body, maximum width of preoral dome    | 19.7  | 20.0 | 2.6  | 0.6  | 13.2 | 14.0 | 24.0 | 21 |
| Body, width at cytostome               | 17.3  | 17.0 | 2.0  | 0.4  | 11.6 | 14.0 | 21.0 | 21 |
| Body, maximum postoral width           | 22.0  | 22.0 | 3.5  | 0.8  | 16.0 | 15.0 | 28.0 | 21 |
| Body, length:width ratio               | 1.8   | 1.7  | 0.3  | 0.1  | 1.77 | 1.4  | 2.8  | 29 |
| Anterior body end to proximal end of PS, distance | 17.1  | 17.0 | 2.5  | 0.5  | 14.4 | 12.0 | 21.0 | 21 |
| Perizonal stripe, percentage of body length | 46.1  | 47.4 | 5.9  | 1.3  | 12.7 | 34.1 | 58.3 | 21 |
| Anterior body end to distal end of AZP, distance | 6.3   | 6.0  | 1.0  | 0.2  | 5.15 | 5.0  | 8.0  | 21 |
| Anterior body end to proximal end of AZP, distance | 18.7  | 19.0 | 1.7  | 0.4  | 9.0  | 15.0 | 21.0 | 21 |
| Adoral zone of polykinetids, percentage of body length | 50.3  | 50.0 | 3.4  | 0.7  | 6.8  | 45.7 | 58.8 | 21 |
| Anterior body end to distal end of PM, distance | 9.9   | 10.0 | 1.6  | 0.4  | 5.15 | 7.0  | 13.0 | 19 |
| Anterior body end to macronucleus, distance | 6.5   | 5.5  | 2.8  | 0.6  | 42.6 | 3.0  | 15.0 | 21 |
| Macronucleus, length                   | 12.4  | 12.0 | 2.6  | 0.6  | 21.4 | 8.5  | 20.0 | 21 |
| Macronucleus, width                    | 7.1   | 7.0  | 1.4  | 0.3  | 20.1 | 4.0  | 9.0  | 21 |
| Macronucleus, length:width ratio       | 1.9   | 1.6  | 0.9  | 0.2  | 48.1 | 1.0  | 5.0  | 21 |
| Macronucleus, number                   | 1.0   | 1.0  | 0.0  | 0.0  | 0.0  | 1.0  | 1.0  | 21 |
| Micronucleus, largest diameter         | 2.5   | 2.5  | 0.0  | 0.0  | 0.0  | 2.0  | 3.0  | 21 |
| Micronucleus, number                   | 1.0   | 1.0  | 0.0  | 0.0  | 0.0  | 1.0  | 1.0  | 21 |
| Somatic ciliary rows, total number     | 11.1  | 11.0 | 1.1  | 0.2  | 10.1 | 9.0  | 13.0 | 23 |
| Perizonal ciliary rows, number         | 5.0   | 5.0  | 0.0  | 0.0  | 0.0  | 5.0  | 5.0  | 21 |
| False kineties in perizonal stripe, number | 18.7  | 19.0 | 2.5  | 0.5  | 13.1 | 15.0 | 23.0 | 21 |
| Adoral polykinetids, number            | 11.0  | 11.0 | 0.9  | 0.2  | 7.8  | 10.0 | 12.0 | 23 |
| Paroral membrane, length               | 10.3  | 10.0 | 1.1  | 0.2  | 10.2 | 9.0  | 13.0 | 19 |

*Data based on mounted, protargol-impregnated, and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. AZP – adoral zone of polykinetids; CV – coefficient of variation (%); M – median; Max – maximum; Mean – arithmetic mean; Min – minimum; PM – paroral membrane; PS – perizonal stripe; n – number of individuals investigated; SD – standard deviation; SE – standard error of arithmetic mean.*

(Figs 2I, 5C); body ends somewhat angular providing cells with a rhomboid or triangular appearance, depending on observation perspective; distal portion of preoral dome strongly flattened and thus hyaline, only 2–3 µm thick *in vivo* (Fig. 3A–C, asterisks), projects distinctly in lateral views, forming a right or nearly right angle with main body axis (Fig. 4B, E, opposed arrowheads); postoral body portion unflattened and usually distinctly vaulted (Figs 4A–E, 5B, C). Localization of nuclear apparatus very stable, i.e., between anterior and posterior end of adoral zone and left of cell’s midline. Macronucleus broadly ellipsoid (52.4%), ellipsoid (23.8%), narrowly ellipsoid (9.5%) or globular (14.3%), i.e., length:width ratio 1.0–5.0:1, size about 8–20 × 4–9 µm, usually 12 × 7 µm in protargol preparations; nucleoli 0.5–1 µm across. Micronucleus usually attached to anterior portion of right margin of macronucleus; shape and size rather stable, i.e., globular to broadly ellipsoid and 2–3 µm in diameter after protargol impregnation (Figs 2A, K, J, M, O–V, 3C, E–H; Table 1). Contractile vacuole in posterior body end, globular to ellipsoid during diastole (Figs 2A, K, O–Q, S–V, 3A, B, D). Cortex flexible, covered by epicortical scales (lepidosomes) usually forming a 1–2 µm, rarely an up to 4 µm thick layer with slimy or fibro-granular appearance *in vivo* (Fig. 3A, C, D, opposed arrowheads) and flake-like appearance in SEM (Figs 4H, 5A), not recognizable in protargol or silver carbonate preparations. Individual lepidosomes with irregular shape, flat with margin curled up, rather variable in size, viz., 0.5–1.65 × 0.20–0.80 µm, on average 1.25 × 0.45 µm in SEM (Figs 2E, 4H, 5A). No cortical granules recognizable. Cytoplasm colourless, contains many 3–6 µm-sized food vacuoles with bacterial spores; symbiotic bacteria neither
Description of *Lepidometopus platycephalus*

Fig. 2. A–V. *Lepidometopus platycephalus* from life (A, D, F–I), after silver carbonate (B, C) and protargol (J–V) impregnation, and in the SEM (E). A. Ventrolateral view of a representative specimen, length 45 µm. Arrows denote left side cilia; arrowhead marks the distally tapered caudal cilium. B. The perizonal stripe is composed of five rows: the first three rows are arranged more closely than the two last rows whose dikinetids are slightly shifted, providing the stripe with a staggered appearance. C. The oral ciliature consists of an average of 11 adoral polykinetids and a paroral membrane optically intersecting the adoral zone. D. Optical section showing the epicortical layer. E. Epicortical scales have various shapes and are about 1.25 × 0.45 µm in size. F–I. Body perspectives. J, O–V. Variability of body shape and size as well as of nuclear apparatus. Dashed line delimits the strongly flattened anterior body portion. Drawn to scale. K–N. Dorso- and ventrolateral views of ciliary pattern and nuclear apparatus of the holotype (K, L) and of a paratype (M, N) specimen. AZP – adoral zone of polykinetids; CP – cytopharynx; CV – contractile vacuole; LE – lepidosomes; MA – macronucleus; MI – micronucleus; PD – preoral dome; PM – paroral membrane; PS (1–5) – perizonal stripe (rows); SC – somatic cilium; SK – somatic kineties. Scale bars: 20 µm.
Fig. 3. A–H. *Lepidometopus platycephalus* from life (A–D) and after silver carbonate impregnation (E–H). Asterisks mark the strongly flattened preoral dome (A–C, E). Opposed arrowheads denote cortex and epicortical scale layer (A, C, D). A, B, E. Vento- (A, B) and dorsolateral (E) overviews, showing general body organization. C. Detail of anterior body portion. D. Detail of posterior body end, showing the single elongated caudal cilium. F. Lateral view, showing somatic ciliary pattern and nuclear apparatus. G, H. Dorsolateral views of anterior body portion, showing the oral ciliary pattern, the perizonal stripe, and the nuclear apparatus. AZP – adoral zone of polykinetids; CC – caudal cilium; CV – contractile vacuole; MA – macronucleus; MI – micronucleus; PM – paroral membrane; PS – perizonal stripe; SK – somatic kineties; SC – somatic cilia. Scale bars: 10 µm (C, G, H) and 20 µm (A, B, D–F).
Fig. 4. A–J. *Lepidometopus platycephalus* in the SEM. A–E. Ventral (A), right side (B), dorsolateral (C, D), and left side (E) overview, showing general body organization. Opposed arrowheads mark the strongly flattened distal portion of the preoral dome (B, E); arrows denote left side cilia (B–D). F. Ventrolateral view, showing the paroral membrane and the perizonal stripe. G. Dorsolateral view, showing five perizonal rows. H. Epicortical scales. I, J. Only a single basal body is ciliated in the postoral dikinetids (I) except for the left side kineties where both basal bodies are ciliated (J). (1–5) – perizonal rows; AZP – adoral zone of polykinetids; PD – preoral dome; PM – paroral membrane; PS – perizonal stripe; SC – somatic cilia. Scale bars: 1 μm (H), 2 μm (G), 3 μm (F), 5 μm (I, J), and 20 μm (A–E).
Fig. 5. A–E. *Lepidometopus platycephalus* in the SEM. A. Epicortical scales (lepidosomes). B. Left side overview, showing the strongly flattened preoral dome (asterisk). C. Oblique posterior polar view, showing the globular postoral portion roofed by the cap-shaped preoral dome. D. Detail of oral area, showing the tongue-like paroral membrane and the adoral zone of polykinetids whose cilia spread backwards. The dome lip is very narrow while the side stripe forms a rather deep channel covered with epicortical scales. E. Ventrolateral view of oral body portion. The arrowhead marks entrance to buccal cavity. This cell lost lepidosomes during the preparation process. AC – adoral cilia; DL – dome lip; PD – preoral dome; PM – paroral membrane; PS – perizonal stripe; SC – somatic cilia; SS – side stripe. Scale bars: 1 µm (A), 5 µm (D, E), and 20 µm (B, C).
detected in vivo nor in protargol preparations (Fig. 3A). Creeps slowly and ungainly on microscope slides, rotates slowly about main body axis when swimming.

Somatic ciliature composed of dikinetids, anterior cillum lacking in postoral kinetids (Fig. 4I) except for those extending along left body margin, an unusual feature observed in vivo, after protargol impregnation, and confirmed in SEM (Figs 2A, 3C, 4B–D, arrows, J). Somatic cilia comparatively widely spaced, rather rigid, in vivo 10–12 µm long in mid-body, up to 13 µm on rear body end; a single elongated caudal cillum with filiform fibres originate from proximal end of adoral zone and paroral membrane, extend backwards forming a funnel about 15 µm long in protargol preparations (Fig. 2L, N). Dome lip inconspicuous because only 0.25–0.50 µm wide in SEM. Side stripe a comparatively deep, 2.3–3.3 µm wide channel in the scanning electron microscope, covered by epicortical scales (Fig. 5D, E).

Morphogenesis of Lepidometopus platycephalus

Division mode: Binary fission is homothetogenic and occurs in freely motile (non-encysted) condition. Body shape changes drastically. Stomatogenesis is pleurotelokinetal. The parental oral structures are reorganized but are not involved in the formation of the daughter oral ciliature.

Body changes: Early dividers are 48–55 × 23–25 µm in size, i.e., they are slightly larger than morphostatic specimens and gradually loose the reniform and rhomboid appearance, becoming Metopus-shaped (Fig. 6A–H). The cell portion carrying the prospective adoral polykinetids transforms into a small bulge recognizable in lateral view (Fig. 6E, F). On the other hand, the parental oral area is still unchanged, i.e., the preoral dome is strongly flattened and distinctly projects from body proper (Fig. 6C).

In mid-dividers, the body slightly shortens and conspicuously broadens to 45–50 × 30–38 µm. These cells are thus the stoutest and shortest dividers. Body shape drastically changes: (1) the outline becomes broadly elliptic, (2) the ventral side becomes strongly inflated, and (3) the preoral dome turns into a small, rounded protuberance projecting from the left anterior body margin (Fig. 7A–F).

Just before separation, the daughter cells are broadly ellipsoid without any sign of a preoral dome (Fig. 8A, B). However, fundamental changes in cell shape and size take place after division: (1) the body intensively grows from about 33 × 23 µm to about 55 × 22 µm, (2) the anterior portion of the cell flattens, and (3) the preoral dome pulls out of the cell to roof the adoral zone by twisting leftwards taking along the perizonal stripe which thus obtains the typical Γ-shaped pattern (Fig. 8C–H). Nevertheless, late post-dividers are still very dissimilar from morphostatic cells. They are oblong, not or only slightly twisted anteriorly (Fig. 8G, H), and longer than morphostatic specimens (on average 55 × 22 µm vs. 38 × 20 µm in protargol preparations). This indicates that their further development must be associated with body shortening, possibly as a consequence of massive remodelling to a reniform/rhomboid shape.
Fig. 6. A–J. Lepidometopus platycephalus, ciliary pattern and nuclear apparatus of early dividers (A–H) and of an early mid-divider (I, J) after protargol impregnation. Arrowheads mark the prospective adoral polykinetids formed at the posterior end of dorsal and dorsolateral kineties. Asterisks denote the prospective adoral polykinetids developing at the anterior end of the postoral kineties. Arrow in (I) points to two dorsolateral kineties which migrate towards the growing perizonal stripe to become perizonal rows 4' and 5' in the opisthe. BU – bulge; CV – contractile vacuole; MA – macronucleus; MI – dividing micronucleus; OAZP – opisthe’s adoral zone of polykinetids; PAZP – proter’s adoral zone of polykinetids; PM – paroral membrane; PPS – proter’s perizonal stripe. Scale bars: 20 µm.
Description of *Lepidometopus platycephalus*

Fig. 7. A–F. *Lepidometopus platycephalus*, ciliary pattern and nuclear apparatus of mid-dividers after protargol impregnation. Asterisks denote scattered dikinetids of perizonal rows 1 and 2 that migrate along the new adoral zone to assemble the opisthe’s paroral membrane. Arrows point to two dorsolateral kineties which migrate towards the opisthe’s perizonal stripe to become rows 4' and 5'. Arrowheads mark newly formed ciliary rows left of opisthe’s adoral zone. CH – chromosomes; F – fibres; MA – macronucleus; MI – micronucleus; OAZP – opisthe’s adoral zone; OPM – opisthe’s paroral membrane; PAZP – proter’s adoral zone; PD – preoral dome; PPM – proter’s paroral membrane; PS – perizonal stripe rows. Scale bars: 20 µm.
Development of adoral zone: The formation of the opisthe’s adoral zone is associated with two concomitantly proceeding events taking place in early dividers: (1) proliferation of dikinetids (protopolykinetids) in the posterior portion of about six dorsal and dorsolateral kineties (Fig. 6A–G, arrowheads) and (2) the production of dikinetids in the anterior portion of about three postoral kineties, i.e., slightly posterior to the proximal end of the perizonal stripe (Fig. 6A, C, E, G, asterisks). In early mid-dividers, the newly formed dikinetids detach...
Description of *Lepidometopus platycephalus*  

The new genus *Lepidometopus* differs from all described metopids in having the body coated by epicortical scales (lepidosomes). Such peculiar structures are present also in...
trachelophyllids where their morphologies have been used to define particular genera (Nicholls and Lynn 1984; Foissner et al. 2002; Foissner 2005a, 2016b). Lepidosomes have been detected also on resting cysts of some oligotrichs, hypotrichs, and even colpodids, for instance, in Meseres corlissi (Foissner 2005b), Halteria grandinella, Oxytricha granulifera, Colpoda inflata, and C. lucida (Foissner et al. 2007). The scales of Lepidometopus are simple, flat structures without ornamentation. On the other hand, the epicortical scales of trachelophyllids are complex and ornamented while they are conical or tubular in resting cysts of oligotrichs, some hypotrichs, and colpodids. This indicates an independent origin of lepidosomes in various ciliate lineages, as already suggested by Foissner (2005b).

Lepidometopus is further outstanding within the family Metopidae Kahl, 1927 in that it has lost the typical metopid shape. Its body is reniform with somewhat angular margins that provide the ciliate with a remarkable, rhomboid appearance in ventrolateral and dorsolateral views. Moreover, the strongly flattened distal portion of the preoral dome distinctly projects laterally forming a right angle with the main body axis (Fig. 1). In this respect Lepidometopus resembles two insufficiently known genera, Palmarella Jankowski, 1975 [substitute name of the preoccupied Palmarium Gaievskaia, 1925; for details see Aescht (2001)] and Tesnospira Jankowski, 1964b.

Identity and taxonomic affiliation of Palmarella are problematic and require re-description of the type species “Palmarium salinum Gaievskaia, 1925”. Gaievskaia (1925) considered Palmarella as a hypotrich while Kahl (1932) classified it as a heterotrich with affinities either to Condylostoma or small Metopus species. Jankowski (1964a, b) speculated that it could be between Metopus Claparède and Lachmann, 1858 and Tropidoatractus Levander, 1894. He also transferred three further species to Palmarella: Metopus angustus Kahl, 1927; M. latus Kahl, 1927; and M. mucicola Kahl, 1927. Gaievskaia’s and Jankowski’s illustrations of Palmarella resemble some body shapes observed in Lepidometopus. Indeed, both genera can be reliably separated only by the presence/absence of a mucilaginous body cover at the present state of knowledge. We argue that lepidosomes were not overlooked in the aforementioned Palmarella/Metopus species because Kahl (1930, 1932) recognized a mucous coat in trachelophyllids and mucilaginous houses in P. mucicola (= M. mucicola). Although P. mucicola cells are not covered by a mucilaginous layer after leaving their houses, we cannot exclude that this species represents a transition between Palmarella and Lepidometopus or that it belongs to Lepidometopus. As concerns P. lata (= M. latus), Jankowski (1964a, b) did not mention any mucilaginous layer in his redescriptions and no epicortical layer is recognizable in a photograph of that species in Bourland et al. (2014), who used a high-power oil immersion objective.

Tesnospira can be clearly separated from Lepidometopus by the very short and inconspicuous perizonal stripe as well as by the suture formed by the ciliary rows in the anterior pole area. Moreover, Tesnospira lacks a side stripe, i.e., there is no cilia-free area between adoral zone and perizonal stripe (Jankowski 1964a, b). On the other hand, Lepidometopus has a well-developed perizonal and side stripe but does not exhibit a suture in the anterior body area.

The new species Lepidometopus platycephalus

The most prominent features of L. platycephalus include the reniform and somewhat rhomboid body, the macronucleus situated in the anterior body half, the strongly flattened preoral dome, and the type 4 oral area. There are several insufficiently described species with strongly flattened anterior body portion and possibly also with a type 4 oral area: Palmarella salina (Gaievskaia, 1925) Jankowski, 1975; P. lata (Kahl, 1927) Jankowski, 1975; P. mucicola (Kahl, 1927) Jankowski, 1975; P. angusta (Kahl, 1927) Jankowski, 1975; and Tesnospira alba Jankowski, 1964b.

Palmarella salina and P. lata resemble L. platycephalus in the small body size, the loose ciliature, and the elongated caudal cilium. However, they have a different body shape and the macronucleus is located centrally. Moreover, P. salina lives in hyper-saline environments. Palmarella mucicola forms mucilaginous houses, lacks elongated caudal cilia, and the macronucleus is in mid-body. Palmarella angusta differs from L. platycephalus by the broadly fusiform and densely ciliated body, the multiple caudal cilia, and the centrally situated macronucleus. Tesnospira alba can be distinguished from L. platycephalus by the slightly larger body (70 µm vs. 35–50 µm), the localization of the macronucleus (in mid-body vs. in anterior body half), the higher number of ciliary rows (24 vs. 11), and the much shorter adoral zone extending about one fifth vs. one half of body length.

Morphogenesis

Although the interphase morphology of L. platycephalus is rather different from that of typical me-
topids, its morphogenesis follows the metopid mode as described by Foissner and Agatha (1999): (1) the body undergoes fundamental re-shaping, (2) the parental oral structures are reorganized but do not contribute to the daughter oral ciliature, (3) the opisthe’s adoral polykinetids originate pleurotelokinetally as migrating kinetosomes that detach from the posterior end of dorsal and dorsolateral kineties as well as from the anterior end of postoral kineties, (4) the opisthe’s paroral membrane is formed from the dissociated posterior portion of two perizonal rows, and (5) the opisthe’s perizonal stripe has a hybrid origin, i.e., it is formed by three parental perizonal rows and two dorsolateral ciliary rows.

The morphogenetic processes of metopids show only minor differences that concern (1) the number of postoral and dorsal kineties involved in the production of adoral polykinetids, (2) the extent of reorganization of the parental adoral zone and paroral membrane, (3) the timing of disappearance of the preoral dome, (4) modifications of the posterior body end, and (5) changes in the position of the macronucleus (Table 2).

Phylogeny

The armophoreans are a “riboclass”, i.e., a molecular class for which morphological synapomorphies are not known (Lynn 2004). Lynn (2008) subdivided the Armophorea Lynn, 2004 into two orders: Armophorida Jankowski, 1964b and Clevelandellida Puytorac and Grain, 1976. The armophorids are considered as free-living anaerobes carrying a perizonal stripe of four or five rows, an adoral zone composed of paramembranelles, and a paroral membrane made of a single file of dikinetids. The clevelandellids are endocommensals in the digestive tract of various invertebrates and vertebrates; they lack a perizonal stripe, the adoral zone is composed of heteromembranelles, and the paroral membrane is made of two files of oral kinetosomes separated by a ridge (for a review, see Lynn 2008). However, the phylogenetic relationships among and within these orders conflict with the morphology-based classification. The armophorid family Metopidae Kahl, 1927 is consistently depicted as paraphyletic since it includes the monophyletic order Clevelandellida. The “Metopidae + Clevelandellida” assemblage is very likely related to the class Litostomatea (Vďačný et al. 2010; Lynn and Wright 2013; Paiva et al. 2013; Bourland et al. 2014, 2017; da Silva-Neto et al. 2015; Li et al. 2016, 2017). On the other hand, the armophorid family Caenomorphidae Poche, 1913 could be a sister group of the “Metopidae + Clevelandellida” cluster or, more likely, could have diverged at the base of the Spirotrichea or the Intramacronucleata (Paiva et al. 2013). Thus, the class Armophorea is very likely non-monophyletic with caenomorphids not being closely related to metopids + clevelandellids within the “SAL” (Spirotrichea + Armophorea + Litostomatea) supercluster recognized from extensive molecular datasets (Gentekaki et al. 2014, 2017; Gao et al. 2016).

Our morphogenetic data corroborate the phylogenetic analyses very well. Thus, the ontogenesis of caenomorphids and metopids is only superficially similar and does not corroborate a monophyly of the Armophorida. Originally, this order contained only the caenomorphids (Jankowski 1964b, 1980), later the metopids were added by Small and Lynn (1985) and Puytorac (1994), who very likely assumed homology of the caenomorphid and metopid perizonal stripe. However, not only the fine structure but also the ontogenetic function and origin of the perizonal stripe are so different in caenomorphids and metopids that homology is unlikely. The caenomorphid stripe generates adoral polykinetids, the paroral membrane and the perizonal stripe for the opisthe. Specifically, the new adoral polykinetids and the new paroral membrane are derived from the posterior end of numerous “false kineties” of the parental perizonal stripe, and the new perizonal stripe originates by proliferation at the anterior end of all parental perizonal rows (Martin-Gonzáles et al. 1987; Table 2). In contrast, the metopid stripe does not generate adoral polykinetids, the new paroral membrane is formed from the dissociated posterior portion of only two perizonal rows, and the new perizonal stripe has a hybrid origin, i.e., it is formed by three parental perizonal rows and two dorsolateral ciliary rows (Foissner and Agatha 1999, present study). Moreover, caenomorphids undergo a complex binary fission reminiscent of the enantiotropic division of oligotrich spirotricheans (Martin-Gonzáles et al. 1987). On the other hand, the metopid division is clearly homothetogenic (Foissner and Agatha 1999, present study). Therefore, we support the ordinal rank proposed for metopids by Foissner and Agatha (1999).

Although the data on morphogenesis of clevelandellids are rather incomplete, they support the metopid kinship rather well. Like in metopids, the clevelandellid stomatogenesis is pleurotelokinetial, i.e., the new adoral polykinetids originate from some somatic kineties in the posterior cell region (Santos et al. 1986; Table 2). Since clevelandellids do not possess a perizonal stripe, their paroral membrane originates from ordinary somatic
### Table 2. Comparison of ontogenetic features of *Lepidometopus platycephalus* nov. gen., nov. spec. with other armophoreans.

| Characteristics | *Lepidometopus platycephalus* | *Metopus hasei* Sondheim, 1929 | *Metopus inversus* (Jankowski, 1964) | *Nyctotherus ovalis* Leidy, 1850 | *Caenomorpha medusula* Perty, 1852 |
|-----------------|-------------------------------|---------------------------------|-----------------------------------|---------------------------------|-----------------------------------|
| Binary fission  | Homothetogenic                | Homothetogenic                  | Homothetogenic                    | Homothetogenic                  | Enantiotropic                     |
| Posterior body end of mid-dividers | Broadly rounded | Furrowed | Broadly rounded and slightly projecting | Broadly rounded | Broadly rounded, caudal spine completely disappears |
| Disappearance of peroral dome | In mid-dividers | In early dividers | In mid-dividers | Not applicable | In early dividers |
| Position of nuclear apparatus | Changes | Changes | Does not change | Slightly changes | Does not change |
| Origin of opisthe’s adoral polykinetids | From three postoral and six dorsal kineties | From three postoral and four dorsal kineties | From five postoral and eight dorsal kineties | From all right side kinetics and 8–10 ventral kinetics | From the posterior end of numerous “false kinetics” of the parental perizonal stripe |
| Reorganization of parental adoral polykinetids | Yes, resorption of some rows in most polykinetids | Yes but only proximal polykinetids disorder | Yes, proximal polykinetids disorder | Possibly partially reorganized | No |
| Origin of opisthe’s paroral membrane | From perizonal stripe rows 1 and 2 | From perizonal stripe rows 1 and 2 | From perizonal stripe rows 1 and 2 | From right side somatic kinetics | From the posterior end of numerous “false kinetics” of the parental perizonal stripe |
| Reorganization of parental paroral membrane | Yes | Yes but only proximal portion | Yes | Possibly partially reorganized | Yes |
| Origin of opisthe’s perizonal stripe ciliary rows | From parental stripe rows 3–5 and two dorsolateral ciliary rows | From parental stripe rows 3–5 and two dorsolateral ciliary rows | From parental stripe rows 3–5 and two dorsolateral ciliary rows | Not applicable | From the anterior end of the parental perizonal stripe |
| References | Present study | Foissner and Agatha (1999) | Foissner and Agatha (1999) | Santos *et al.* (1986) | Martín-González *et al.* (1987) |
ciliary rows. Interestingly, the paroral dikinetids arrange into two parallel files during clevelandellid stomatogenesis, which might be a reminiscence of the formation of the metopid paroral membrane from two perizonal rows. In this light, clevelandellids can be considered as a metopid lineage that lost the perizonal stripe very likely in connection with the endobiotic lifestyle.

Although metopids and litostomateans are morphologically very dissimilar, Vďačný et al. (2010) assembled morphogenetic evidence that they could have a common ancestry. Specifically, (1) the stomatogenesis is purely somatic and telokinetal, (2) the proliferation of basal bodies commences in the dorsal and dorsolateral kineties, (3) the paroral membrane of metopids and the circumoral kinety of litostomateans originate from kinetofragments detaching from somatic origin (Foissner and Xu 2007, Vďačný and Foissner 2012). In contrast, spirotricheans, the other group belonging to the SAL supercluster or synapomorphies supporting our Lamellicorticata hypothesis (Vďačný et al. 2010) requires further investigations.

Acknowledgements. We are grateful to Dr. Barbara Harl and Robert Schörghofer for technical assistance. Financial support was provided by the Austrian Science Fund (FWF Project P26325_B16) and the Wilhelm and Ilse Foissner Stiftung. This work was supported also by the Slovak Research and Development Agency under the contract No. APVV-15-0147 and by the Grant Agency of the Ministry of Education, Science, Research and Sport of the Slovak Republic and Slovak Academy of Sciences under the Grant VEGA 1/0041/17.

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Received on 3rd April, 2017; revised on 19th May, 2017; accepted on 26th May, 2017