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## The Morphogenesis of *Kahliella franzi* (FOISSNER, 1982) nov. comb. and *Oxytricha gigantea* HORVÁTH, 1933 (Ciliophora, Hypotrichida)<sup>1)</sup>

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With 41 Figures

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### Summary

The morphogenesis of *Kahliella franzi* (FOISSNER, 1982) nov. comb. (for *Gonostomum franzi* FOISSNER, 1982) and *Oxytricha gigantea* HORVÁTH, 1933 is described. Some characters (arrangement of the fronto-ventral cirral rows, origin of the cirral rows from 5 streaks, absence of transverse and caudal cirri) suggest that *G. franzi* should be transferred to the genus *Kahliella*. It can be easily separated by the number of macronuclear segments and marginal rows from the other species of this genus. The morphogenesis of *Oxytricha gigantea* proceeds in a very similar way to that of other species of the genus, indicating that morphogenetic characters alone are not sufficient for species separation.

### Introduction

The last species that has been described in the genus *Gonostomum* is *G. franzi* FOISSNER, 1982. MAEDA and CAREY (1984) revised this genus and excluded *G. franzi* without giving any proposal where it should be classified. *Oxytricha gigantea* HORVÁTH, 1933 is the second species investigated in this paper. A resemblance with *Urosoma macrostyla* caused KAHL (1935) to transfer this species to the genus *Urosoma* KOWALEWSKI, 1882. We studied the morphogenesis of cell division to gain clearer information about the systematic position of these two species.

### Material and Methods

The population of *K. franzi* occurred in a small alpine pond near Lunz, Lower Austria. *Oxytricha gigantea* was found in the soil of a saline grassland near Lake Neusiedlersee, Burgenland, Austria. *Gonostomum affine* was isolated from the soil of an alpine pasture from the Gastein area, Salzburg (BERGER et al. 1985a). *Kahliella franzi* and *O. gigantea* were cultured in Eau de Volvie with some squashed wheat grains. The culture method of *G. affine* and the protargol staining method to reveal the infraciliature are described by FOISSNER (1982).

Drawings were made with a camera lucida. For clarity, parental cirri are shown in the Figs. 3—25 and 28—41 only by outline, whereas new ones are shaded. The designation of the fronto-ventral-transverse cirri in *O. gigantea* is according to WALLENGREN (1900). The general terminology is that of KAHL (1932), BORROR (1972), and CORLISS and LOM (1985).

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### Results

#### *Kahliella franzi* (FOISSNER, 1982) nov. comb. (Figs. 3—25)

##### Morphology of the non-dividing specimen (Figs. 3, 4)

This species is described and characterized biometrically by FOISSNER (1982) as *Gonostomum franzi*. The very short endoral membrane is not drawn, but mentioned, in the original description. Since the morphology of the pond population agrees very well with that of the soil population, we show only the ventral and dorsal infraciliature of a non-dividing specimen.

##### Morphogenesis of cell division (Figs. 5—25)

Morphogenesis commences with the formation of a long and narrow oral primordium between the left marginal row and the fronto-ventral row 4, obviously without contact to any parental cirri (Fig. 5). In the macronuclear segments the replication band is recognizable (Fig. 6). Next, a row of basal bodies from the right anterior end of the oral primordium migrates in an antieriad direction (Fig. 7). Later, 2 streaks are recognizable (Fig. 8). The right one is in a line with the cirral row 3, which appears disorganized in the posterior part, indicating that 1 or 2 cirri have been incorporated in this streak. The parental endoral membrane is somewhat stretched, which is the first sign of the beginning of its modification to a primordium (Figs. 8, 10). All cirri of the cirral row 2 — except the frontal cirrus — are disorganized. Two streaks are present at the level of the parental cytostome (Fig. 10). Few basal body pairs commence with the proliferation in the middle part of the dorsal kinety 3 (Fig. 11). The cirri of the parental cirral row 3 (except the frontal cirrus), the middle and posterior part of the cirral row 4, and some cirri posterior to the middle part of the cirral row 5 are modified to primordia in the next stage. The anlage of the undulating membranes of the opisthe is formed to the right of the oral primordium (Fig. 12). Proliferation of basal bodies occurs in all dorsal kineties at 2 sites, only indistinctly separated by 1 or 2 parental basal body pairs (Fig. 13).

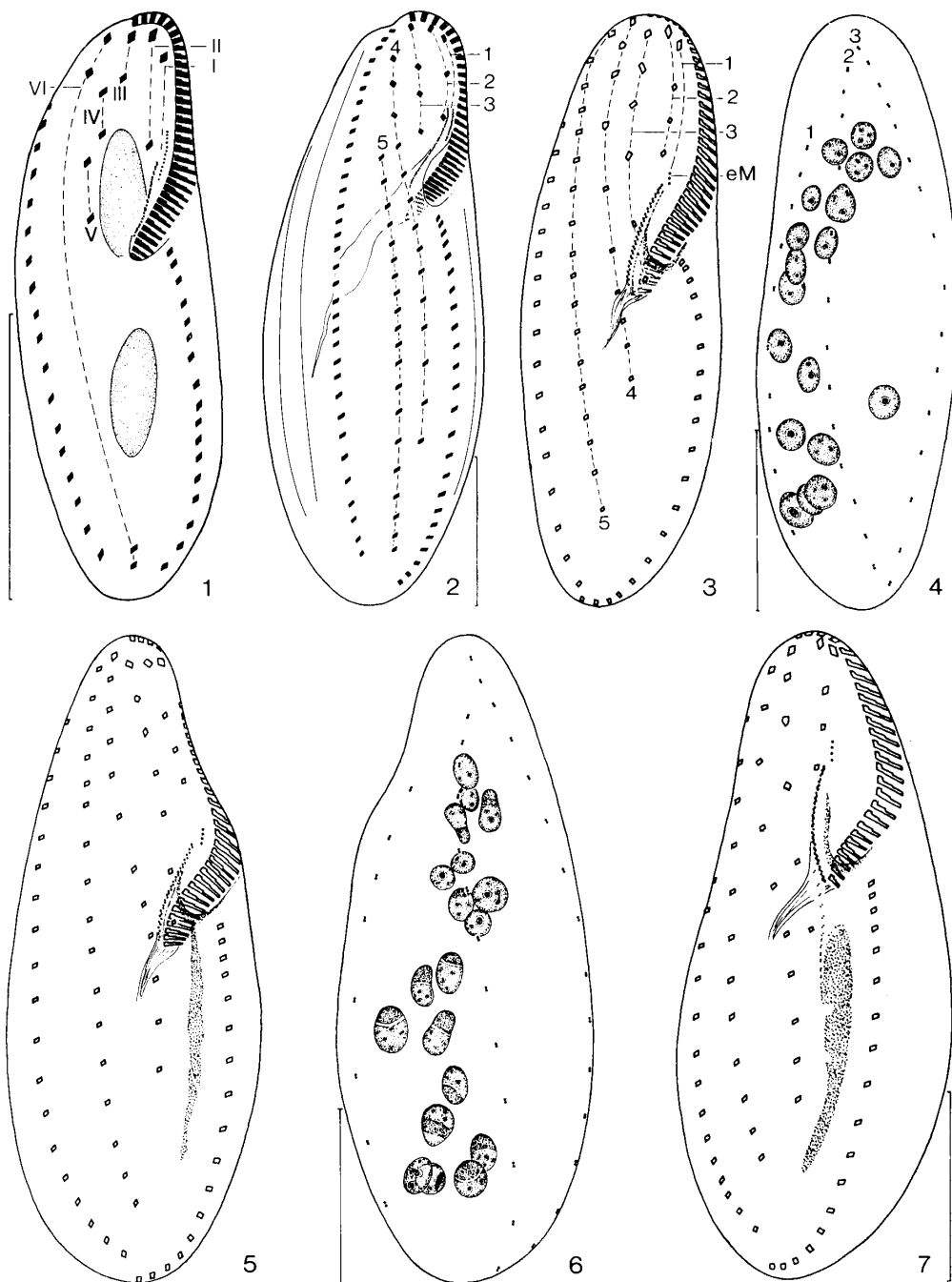
Morphogenesis continues with the formation of a second primordium in the cirral row 5 and the origin of the anterior right marginal primordium (Fig. 14). All ventral and marginal primordia are recognizable in the next stage (Fig. 16). The new frontal cirri and some cirri of the new rows 2, 3, and 4 are already segregated. The new undulating membranes of the proter (streak 1) and the parental paroral membrane are clearly separated. The primordia of the dorsal kineties are elongated and the macronuclear segments are fused (Fig. 17).

Fig. 18 shows a late division stage with the full number of adoral membranelles in the opisthe. The new endoral membranes are discernible right to the anterior end of the new paroral membranes. The primordia of the dorsal kineties of the proter and the opisthe have moved apart and are distinctly separated (Fig. 19). Cytokinesis, division of macronucleus, and displacement of the cirri are shown in the Figs. 20—25. No peculiarities are recognizable during these processes.

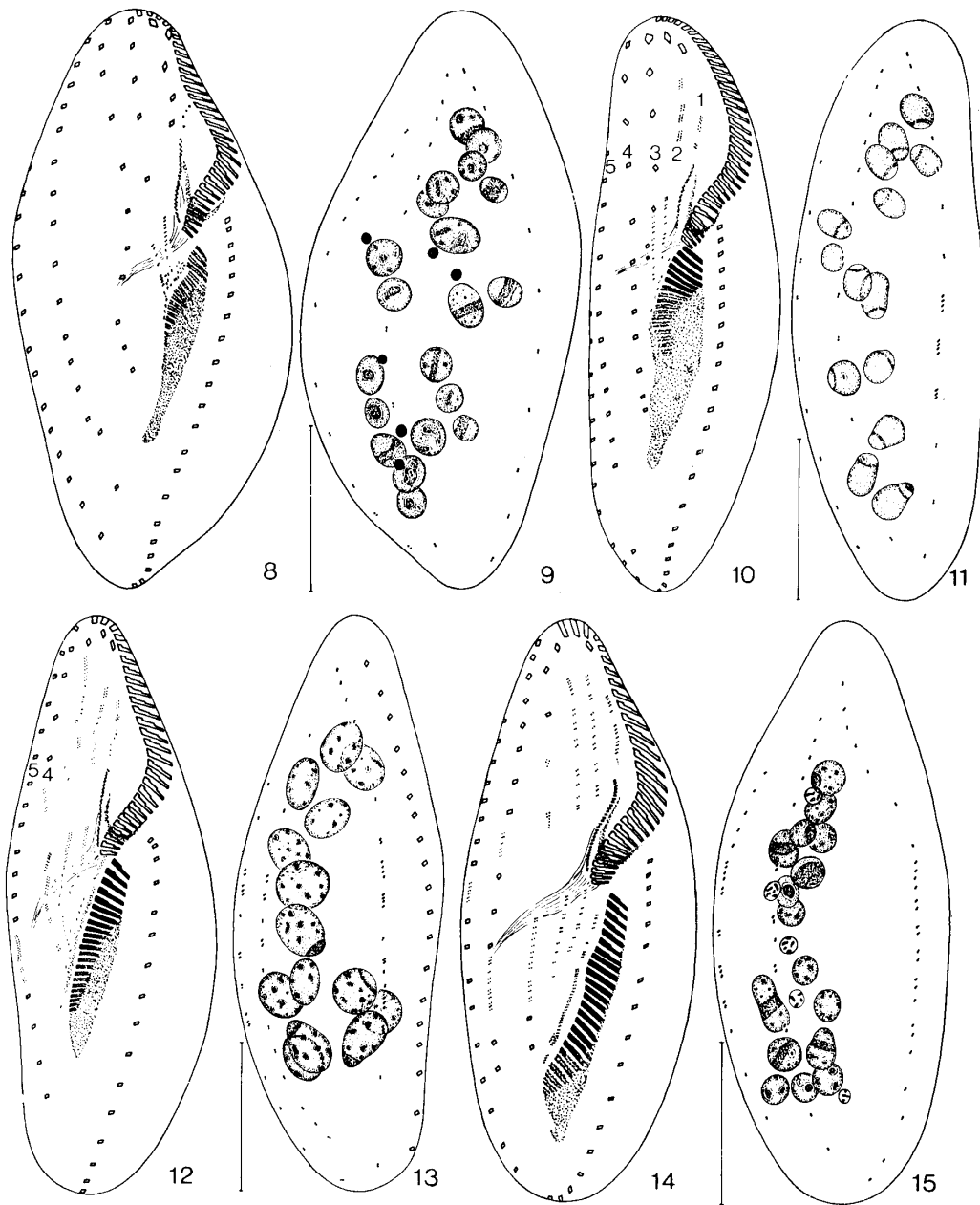
#### *Oxytricha gigantea* HORVÁTH, 1933 (Figs. 26—41)

##### Morphology of the non-dividing specimen (Figs. 26, 27)

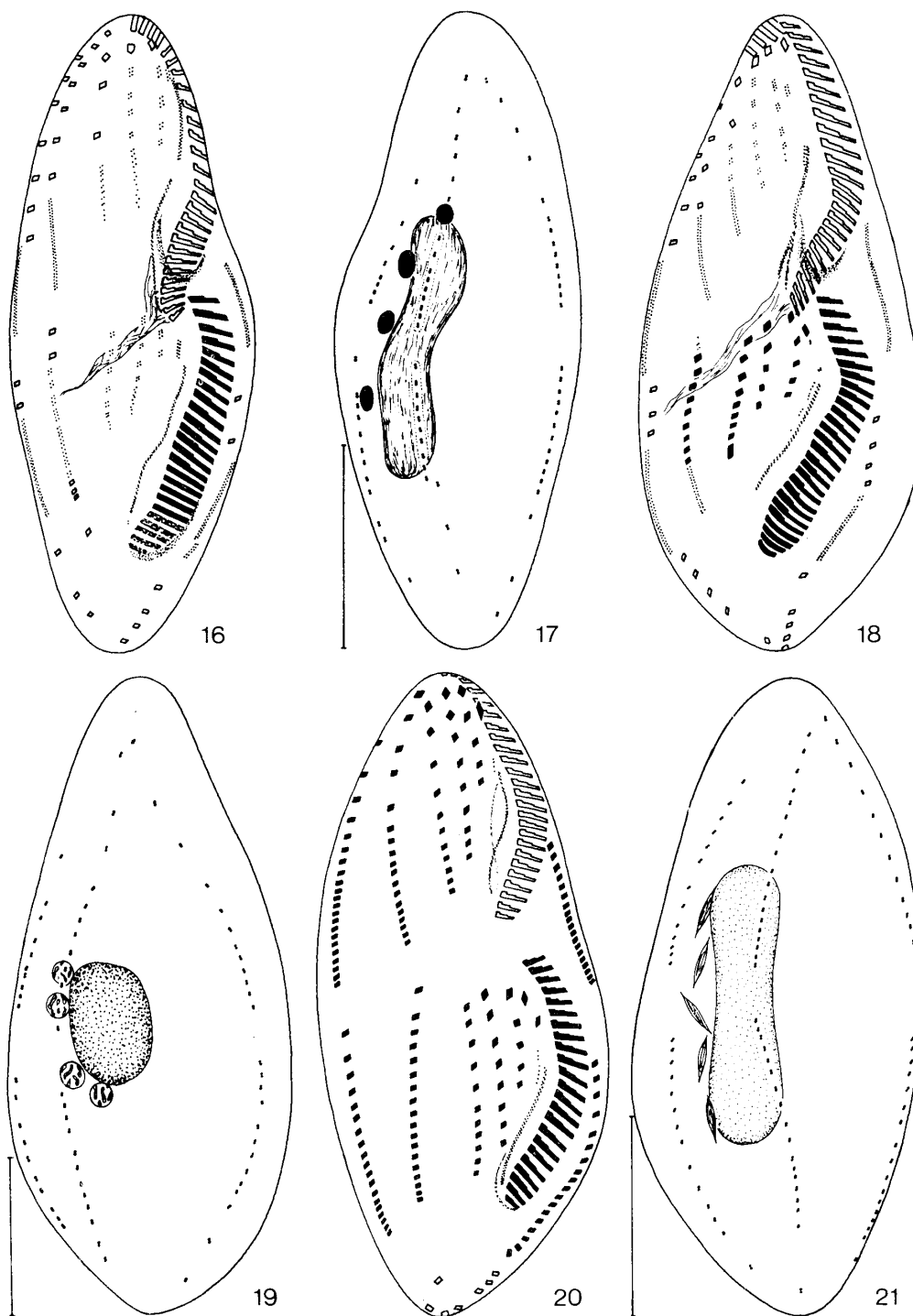
The morphology of the non-dividers of this population is described in detail by BERGER and FOISSNER (1987a) as *Urosoma gigantea* (HORVÁTH, 1933) KAHN, 1935. Thus, only the ventral and dorsal infraciliature of an interphase specimen with the designation of the fronto-ventral-transverse cirri and dorsal kineties are figured.



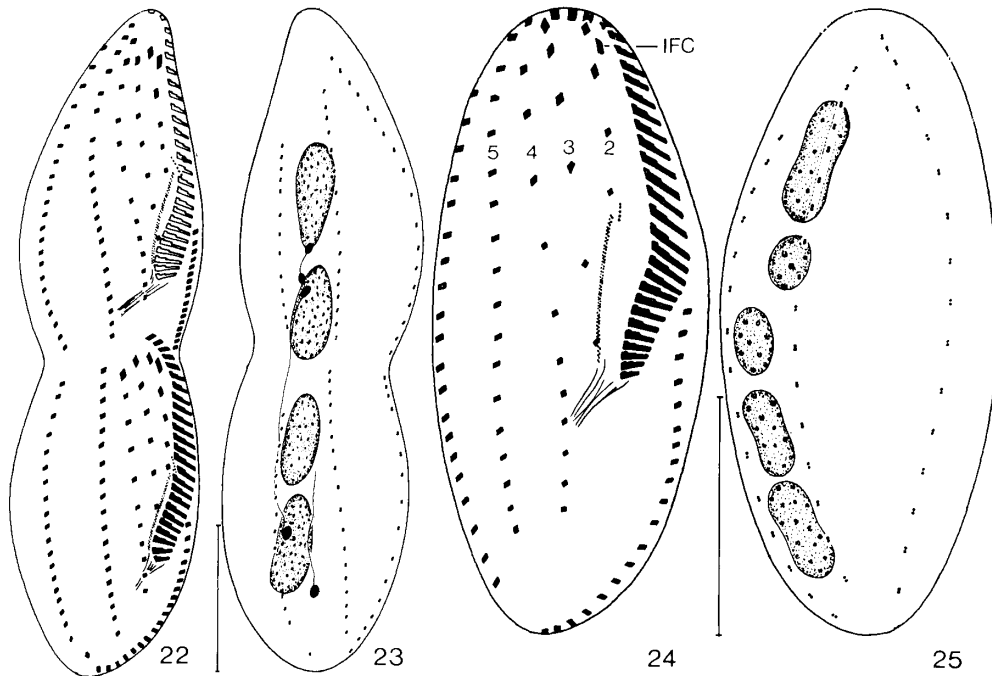
Figs. 1—7. *Gonostomum affine* (1), *Kahliella simplex* (2), and *K. franzi* (3—7). Infraciliature after protargol impregnation. 1—3: ventral view. The cirri of a primordium are connected by a dashed line. The additional marginal rows of *K. simplex* are symbolized by solid lines. 4: dorsal view. 5—7: very early morphogenetic stages in ventral and dorsal view. eM = endoral membrane, I—VI = cirral rows in *G. affine*; 1—5 = fronto-ventral rows and dorsal kineties in *K. simplex* and *K. franzi*. Scale marks: 30  $\mu$ m.



Figs. 8—15. Infraciliature of *Kahliella franzi* after protargol impregnation. Early and middle morphogenetic stages in ventral and dorsal view. 1—5 = fronto-ventral rows and primordia. Scale marks: 30  $\mu$ m.



Figs. 16—21. Infraciliature of *Kahliella franzi* after protargol impregnation. Middle and late stages in ventral and dorsal view. Scale marks: 30 μm.

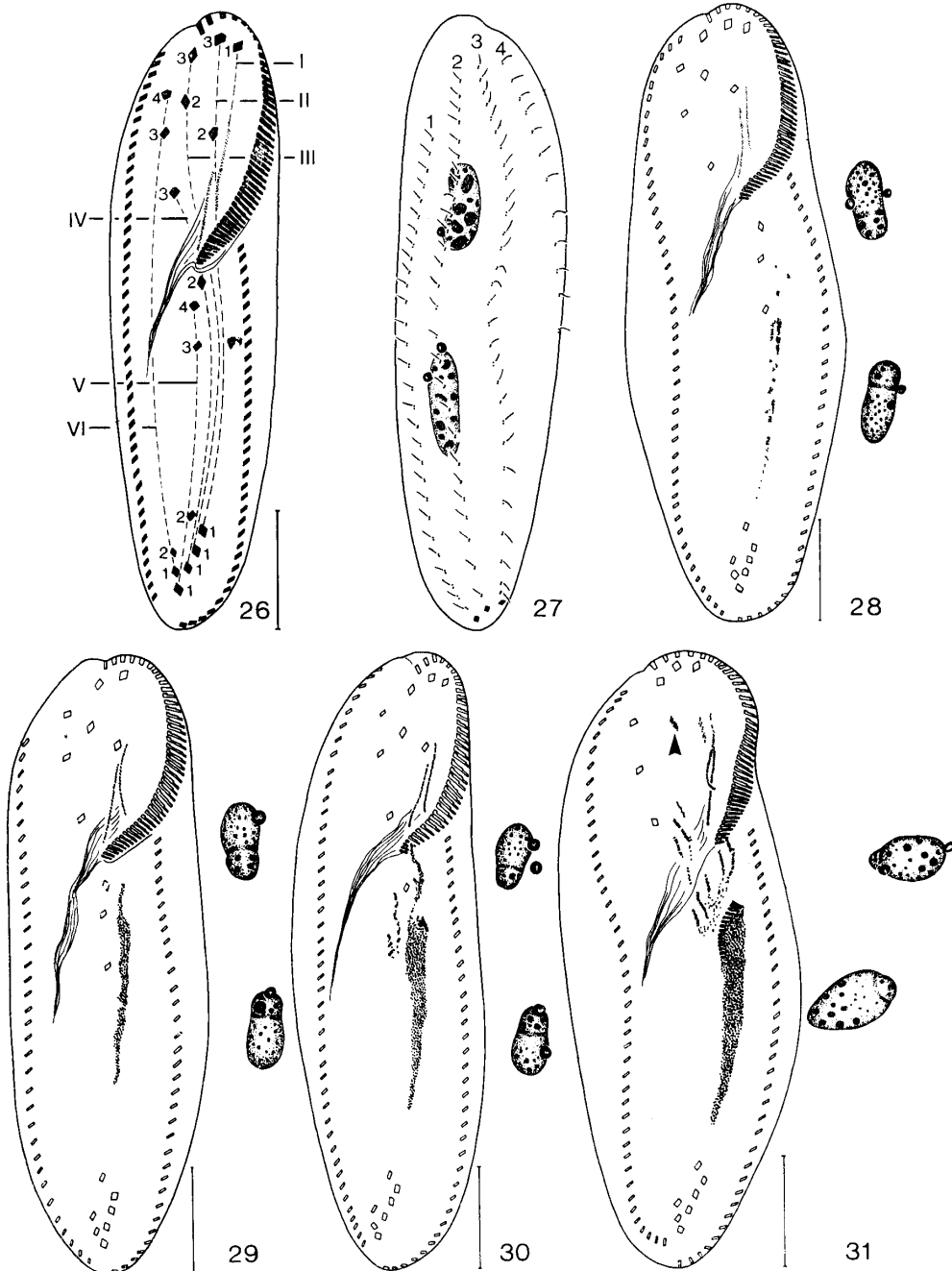


Figs. 22—25. Infraciliature of *Kahlia franzi* after protargol impregnation. Very late morphogenetic stage and postdivider in ventral and dorsal view. IFC = frontal cirrus of cirral row 1, 2 to 5 = cirral rows 2—5. Scale marks: 30  $\mu\text{m}$  (Figs. 22, 23) and 20  $\mu\text{m}$  (Figs. 24, 25).

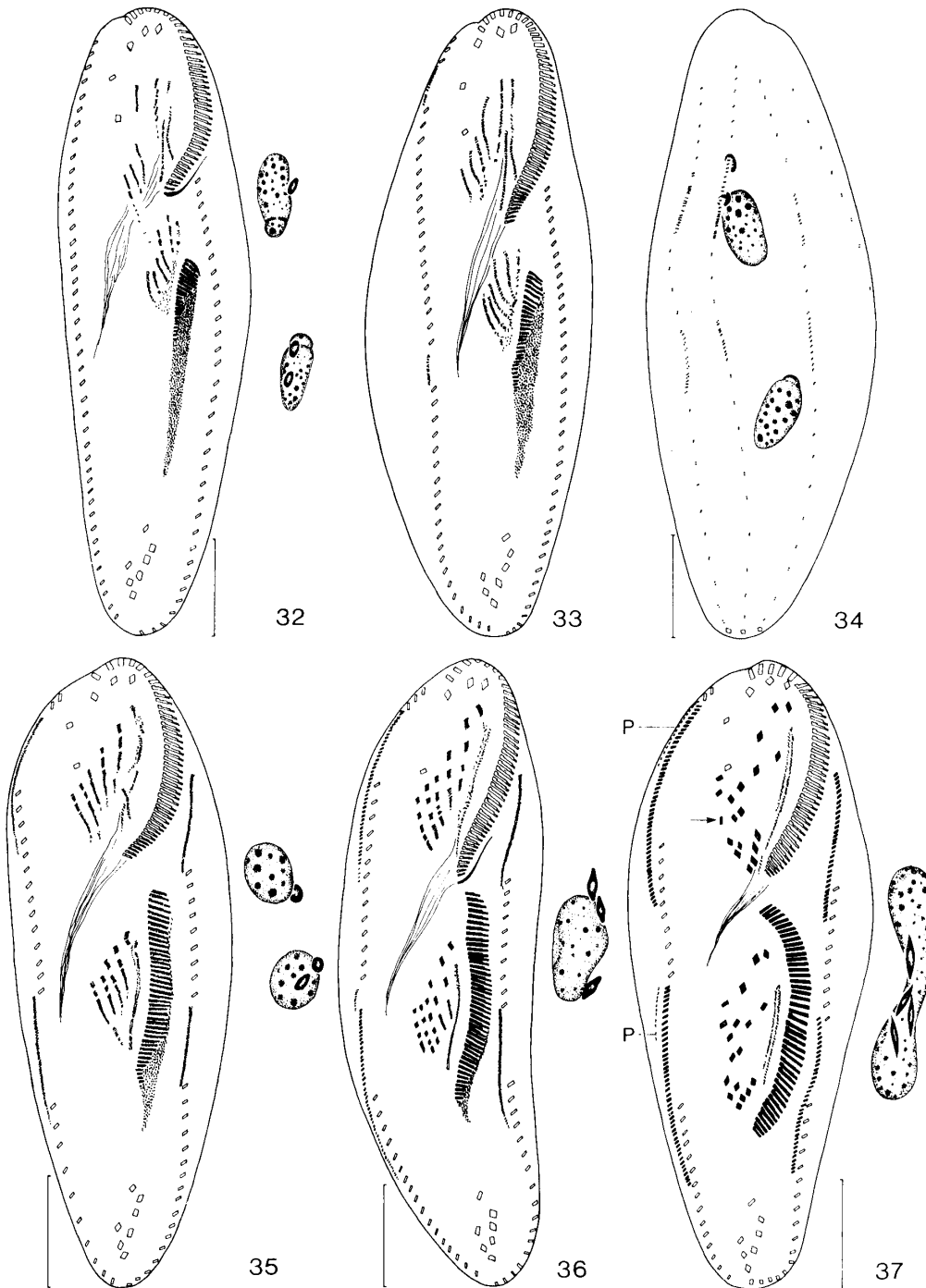
#### Morphogenesis of cell division (Figs. 28—41)

The morphogenesis begins apokinetally with the proliferation of basal bodies in the area between the postoral ventral cirri and transverse cirri. The replication bands have moved about  $\frac{2}{3}$  of the length of the macronuclear segments in this stage (Fig. 28). A long oral primordium is formed (Fig. 29). Its narrowed anterior part elongates to the level of the cytostome and splits up in the middle region to form streaks I and II. The postoral ventral cirri V/3 and V/4 are modified to primordia (Fig. 30). Next, the postoral ventral cirrus IV/2 is disorganized. Five streaks of the opisthe are recognizable at this stage (Fig. 31). At the same time, the buccal cirrus (II/2) and the cirrus III/2 organize primordia for the proter. Three other primordia are present at the level of the cytostome. At least the middle and the right primordia are derived from a streak of the opisthe. Six fronto-ventral-transverse primordia are discernible in the next stage in both the proter and the opisthe. Cirrus IV/3 has been resorbed (Fig. 32). Some loosely arranged basal bodies are present between the right streak (primordium VI) of the proter and the primordium IV of the opisthe.

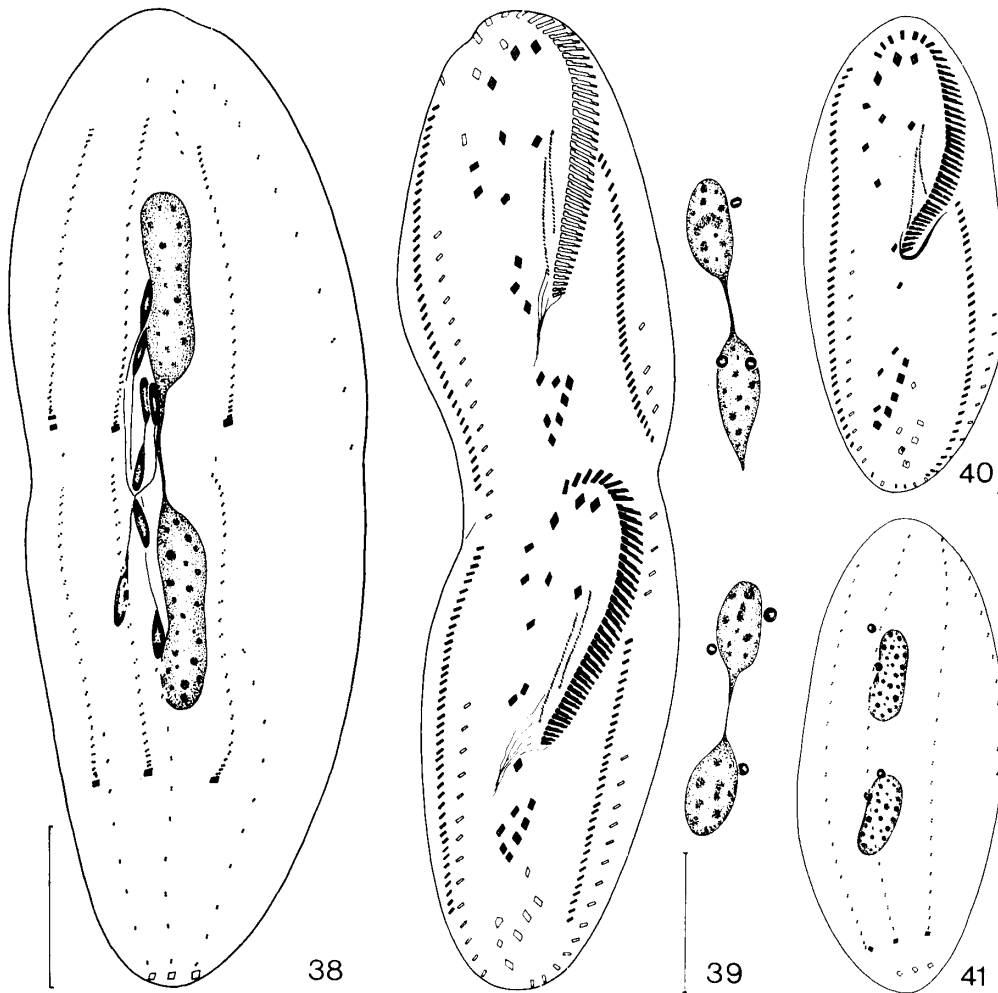
Morphogenesis continues with the elongation of the fronto-ventral-transverse streaks and the formation of marginal primordia in the anterior and middle part of the right marginal row (Fig. 33). The proliferation of new basal body pairs occurs at 2 levels in the dorsal kineties 1, 2, and 3 (Fig. 34). The parental membranes commence with reorganization when the undulating membranes of the opisthe are formed. The anterior cirri are already segregated from the fronto-ventral-transverse streaks. Both the right and left marginal primordia are elongated (Fig. 35). The primordia of the



Figs. 26—31. Infraciliature of *Oxytricha gigantea* after protargol impregnation. 26, 27: non-dividing specimen in ventral and dorsal view after BERGER and FOISSNER (1987 a). The cirri of a primordium are connected by a dashed line. Designation according to WALLENGREN (1900). 28—31: Early morphogenetic stages in ventral view. I—VI = cirri rows, 1—4 = cirri within a cirral row and dorsal kineties, arrow head = cirrus III/2. Scale marks: 30  $\mu$ m.



Figs. 32—37. Infraciliature of *Oxytricha gigantea* after protargol impregnation. Middle and late morphogenetic stages in ventral and dorsal view. P = primordium of the new dorsal kinety 4, arrow = supernumerary cirrus within the primordium VI. Scale marks: 30  $\mu$ m.



Figs. 38—41. Infraciliature of *Oxytricha gigantea* after protargol impregnation. Very late morphogenetic stages and opisthe in ventral and dorsal view. Scale marks: 30  $\mu$ m.

dorsal kineties 4 originate at the anterior end of the right marginal primordia at about the time when the macronuclear segments are fusing (Fig. 36).

The rest of the morphogenetic events is very similar to that known of other oxytrichids with 18 frontal, ventral, and transverse cirri, e.g., *Oxytricha granulifera* and *Stylonychia* spp. (FOISSNER and ADAM 1983a; WIRNSBERGER et al. 1985). Thus, the reader is referred to the Figs. 37—41 where the important stages are shown. The constant number of 18 cirri is formed within the fronto-ventral-transverse primordia I—VI as follows: 1, 3, 3, 3, 4, and 4 cirri (Fig. 39).

### Discussion

*Kahliella franzi* (FOISSNER, 1982) nov. comb. (pro *Gonostomum franzi* FOISSNER, 1982)

FOISSNER (1982) has already mentioned that his species probably does not belong to *Gonostomum* STERKI, 1878. Indeed, MAEDA and CAREY (1984) excluded it from this genus, because of the deviating cirral pattern. They did not, however, suggest a new combination. The following characters argue for an inclusion of this species in the genus *Kahliella* CORLISS, 1960:

a) the morphogenetic analysis proves the absence of transverse and caudal cirri in *K. franzi*, as in *K. acrobates* and *K. simplex*, and their presence in *G. affine*, the type of the genus (Figs. 1—4, 23; HORVÁTH 1932; 1934; BUITKAMP 1977; TUFFRAU 1979; FLEURY and FRYD-VERSAVEL 1982; FLEURY et al. 1985; FOISSNER 1982; HEMBERGER 1982; BERGER and FOISSNER 1987a). The absence or presence of caudal and transverse cirri is used as a character to separate genera of hypotrichs (KAHL 1932; BORROR 1972);

b) the arrangement of the fronto-ventral cirral rows in *K. franzi* is very similar to that of other species of *Kahliella*, e.g., *K. acrobates* or *K. simplex* (compare Figs. 2 and 3; FLEURY and FRYD-VERSAVEL 1982). In *G. affine* the cirri are grouped as in other oxytrichids. The postoral ventral cirri, however, are situated in the frontal area, simulating a cirral pattern which is rather different from the general pattern of the typical oxytrichids (Fig. 1; BUITKAMP 1977; FOISSNER 1982; HEMBERGER 1982; WIRNSBERGER et al. 1986);

c) the morphogenesis of the fronto-ventral infraciliature of *K. franzi* proceeds in a similar way to that of *K. acrobates* and other members of the family Kahliellidae, e.g., *Parakahliella macrostoma* and *P. haideri* (FLEURY and FRYD-VERSAVEL 1982; BERGER et al. 1985b; BERGER and FOISSNER 1987b). Usually 5 fronto-ventral streaks are developed which produce a distinctly larger number of cirri than the 6 primordia of the Oxytrichidae, such as in *O. gigantea* and *G. affine* (Figs. 1—3, 26; HEMBERGER 1982).

The absence of additional marginal rows, a character which all other species of *Kahliella* (BORROR 1972) possess, reminds one more of *Gonostomum* than of *Kahliella*. However, the establishment of a new genus, based on only this character was avoided, since the characters mentioned above sufficiently suggest an inclusion in the genus *Kahliella*. The same decision was recently done for *Parakahliella haideri* (BERGER et al. 1985b; BERGER and FOISSNER 1987b).

The shape of the adoral zone of membranelles and the undulating membranes is very similar in *Gonostomum* and *Kahliella* (compare Figs. 1 and 2). Obviously, the typical „*Gonostomum*-like“ shape of the buccal apparatus has evolved independently in genera which are classified in different families, indicating a low taxonomic value of this character.

Species comparison: *Kahliella franzi* can be separated from the other members of the genus by the number of macronuclear segments and the possession of only 1 left and 1 right marginal row (HORVÁTH 1932, 1934; KAHL 1932; GELEI 1954; DRAGESCO 1970; BORROR 1972; DRAGESCO and DRAGESCO-KERNEIS 1986; BERGER and FOISSNER 1987a).

The systematic position of *Oxytricha gigantea* HORVÁTH, 1933

KAHL (1935) transferred *O. gigantea* to the genus *Urosoma* KOWALEWSKI, 1882, because of its elongated and posteriorly converging body shape. The confused history

of the genus *Urosoma* is explained by FOISSNER (1983). When *O. gigantea* was redescribed by BERGER and FOISSNER (1987a) as *U. gigantea* (HORVÁTH, 1933) KAHL, 1935, the morphogenesis was still unstudied. Likewise, the morphogenesis of the type-species of *Urosoma*, *U. cienkowski*, is unknown, so that the decision to which genus HORVÁTH's species belongs cannot be clarified unequivocally. FOISSNER (1983), however, investigated the division of the closely related species *U. macrostyla*. A comparison of the morphogenesis of these species argues for the retention of *O. gigantea* in the genus *Oxytricha*. The main difference between the morphogenetic patterns exists in the origin and formation of the fronto-ventral-transverse streaks. "Primary streaks" are formed in *U. macrostyla*. They divide in the middle stages of the morphogenesis and form the "secondary primordia" that are the primordia for the infraciliature of the proter and the opisthe. This type of morphogenesis occurs also in *G. affine* and *Tachysoma pellionella* (HEMBERGER 1982; FOISSNER 1983). In contrast, in *O. gigantea* only streaks IV (?), V, and VI of the proter arise from streak IV of the opisthe (Figs. 31, 32). This type of fronto-ventral-transverse streak formation appears also in, e.g., *O. granulifera* and *Urosomoida agiliiformis* (FOISSNER and ADAM 1983a, b; GANNER et al. 1987).

The second character that supports the inclusion in the genus *Oxytricha* is the position of the cirrus III/2, that is the cirrus behind the right frontal cirrus (Fig. 26). Already FOISSNER (1982) recognized that in typical members of the genus *Urosoma* this cirrus is always situated anteriorly to the cirrus VI/4. Thus, the cirri III/2, VI/4, VI/3, and IV/3 form nearly a line (KOWALEWSKI 1882; STOKES 1887; KAHL 1932; WANG and NIE 1935; FOISSNER 1982, 1983, 1984; DRAGESCO and DRAGESCO-KERNEIS 1986; BERGER and FOISSNER 1987a). On the other hand, in *O. gigantea* and other *Oxytricha*-species, e.g., *O. granulifera* and *O. lanceolata* the cirrus III/2 is situated left of the area between the cirri VI/4 and VI/3. Thus, these cirri form a V-like figure (Fig. 26; SHIBUYA 1930; HORVÁTH 1933; FOISSNER and ADAM 1983a; BERGER and FOISSNER 1987a). Very probably, the position of the cirrus III/2 is the most appropriate character with which to separate *Oxytricha* and *Urosoma*, since *Urosoma*-species which do not have the tail-like posterior end of the type-species, *U. cienkowski* are known to exist (KOWALEWSKI 1882; KAHL 1932; FOISSNER 1987).

BORROR (1972) and HEMBERGER (1982) synonymized *O. gigantea* HORVÁTH, 1933 with *Urosomoida agilis* (ENGELMANN, 1862) HEMBERGER, 1985 and *O. parallela* ENGELMANN, 1862, respectively. However, it is clear from the original description and the redescription of BERGER and FOISSNER (1987a) that it can be separated from these and other related species by the characters body size, morphogenetic pattern, subpellicular granules, and the habitat.

### Zusammenfassung

Es werden die Morphogenesen von *Kahliella franzi* (FOISSNER, 1982) nov. comb. (für *Gonostomum franzi* FOISSNER, 1982) und *Oxytricha gigantea* HORVÁTH, 1933 beschrieben. Einige Merkmale (Anordnung der Fronto-Ventral-Cirrenreihen, Entwicklung der Cirrenreihen aus 5 Anlagen, Fehlen von Transversal- und Caudalcirren) weisen darauf hin, daß *G. franzi* in die Gattung *Kahliella* gestellt werden sollte. *Kahliella franzi* kann durch die Anzahl der Makronukleus-Teile und Marginalreihen eindeutig von den anderen Arten der Gattung unterschieden werden. Die Morphogenese von *O. gigantea* verläuft ähnlich wie bei anderen Arten der Gattung. Dies zeigt, daß Merkmale der Morphogenese allein nicht für die Trennung von Arten ausreichen.

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