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Morphological and ontogenetic comparison of two populations of *Parentocirrus hortualis* VOSS 1997 (Ciliophora, Hypotrichida)

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A b s t r a c t : *Parentocirrus hortualis* was found in a sample of activated sludge from an experimental sewage treatment plant of a paper-mill in the town of Hallein (Salzburg, Austria). Morphology and ontogenesis were compared with the type population discovered in an ephemeral birdbath in Germany. Further, physiological reorganization was investigated. The Austrian specimens match the German type population in all main features, while some morphometrics differ considerably. Part of the differences can be explained by preparation shrinkage, while others are related, via less optimal culture conditions and isometric allometry, to the smaller size of the Austrian specimens (132 × 61 µm vs. 183 × 95 µm in protargol preparations). Our stage-by-stage comparison did not reveal any significant differences in the ontogenetic patterns and processes of the two populations. However, intrapopulation variability of anlagen number and arrangement is high and causes that anlagen origin is sometimes difficult to determine. We investigated whether *Parentocirrus* transmits cirri of frontoventral rows 5 and 6 to the next generation, as suggested by VOSS (1997). No parental cirri were found in 400 morphostatic specimens, but they occurred in the 11 post-dividers and post-reorganizers observed. Physiological reorganization is remarkable in that disaggregating cirri of frontoventral rows 3 and 5 form a long primordium, while row 4 is likely inactive and generated by row 3.

Key words: Ontogenesis, activated sludge, physiological reorganization, geographic variation, Spirotrichea, resting cyst

1 Introduction

Variability is a phenomenon of life. In ciliates, there are many studies available on variability within and between populations, especially in hypotrichs, which have several distinct features easily revealed by the common silver impregnation techniques (for reviews, see BERGER 1999 and FOISSNER et al. 2002). These investigations show that ciliate variability is comparable to that found in metazoans, and that variability may strongly increase under laboratory conditions (WIRNSBERGER-AESCHT et al. 1990). In contrast, data on ontogenetic variability are limited to a few examples, though such information is very important considering that (too?) fine details are increasingly used for reconstructing evolutionary pathways (BERGER & FOISSNER 1997; EIGNER 1997, 1999).

Comparative ontogenetic data are available on populations of species of the *Stylonychia mytilus* and *Sterkiella histriomuscorum* complex (BERGER 1999; FOISSNER & BERGER 1999; PETZ & FOISSNER 1997; WIRNSBERGER et al. 1986), *Paraurostyla weissei* (JERKA-

DZIADOSZ 1965; JERKA-DZIADOSZ & FRANKEL 1969; WIRNSBERGER et al. 1985), *Engelmanniella mobilis* (WIRNSBERGER-AESCHT et al. 1990), and *Euplotes* spp. (VOSS 1989). These studies show that (i) most interpopulation differences can be explained by insufficient acquisition and/or interpretation of data, and (ii) populations of the same species and species of the same genus show the same or highly similar ontogenetic processes, frequently, however, with some variation in time and space. This is confirmed by our investigations on *Parentocirrus hortualis*, a ciliate described rather recently by VOSS (1997).

Classification of *Parentocirrus* is still controversial (for a review, see BERGER 1999). Unfortunately, our study, which largely confirms VOSS' (1997) data, does not provide new arguments for any suggestion.

2 Materials and Methods

As yet, *Parentocirrus hortualis* has been recorded only from type location, i.e., an ephemeral birdbath in the village of Bottrop, Germany (VOSS 1997). However, we discovered this species already in 1991 in activated sludge from an experimental sewage treatment plant of a paper-mill in the town of Hallein near Salzburg (13°50'E 47°40'N), but did not find time to publish the data. Very recently, we found *P. hortualis* also in a very nutrient-rich, ephemeral meadow puddle in the town of Salzburg. Obviously, this species is more common than expected from its late discovery and prefers mesosaprobic to polysaprobic habitats.

Ciliates were studied from both fresh sludge and bacterized cultures obtained by diluting small quantities of sludge with bottled spring water (Eau de Volvic, France) enriched with some crushed wheat grains to stimulate growth of bacteria and small ciliates (*Vorticella convallaria, Euplotes* sp., *Pseudochilodonopsis fluviatilis*), which served as food for *P. hortualis;* starch grains were also ingested.

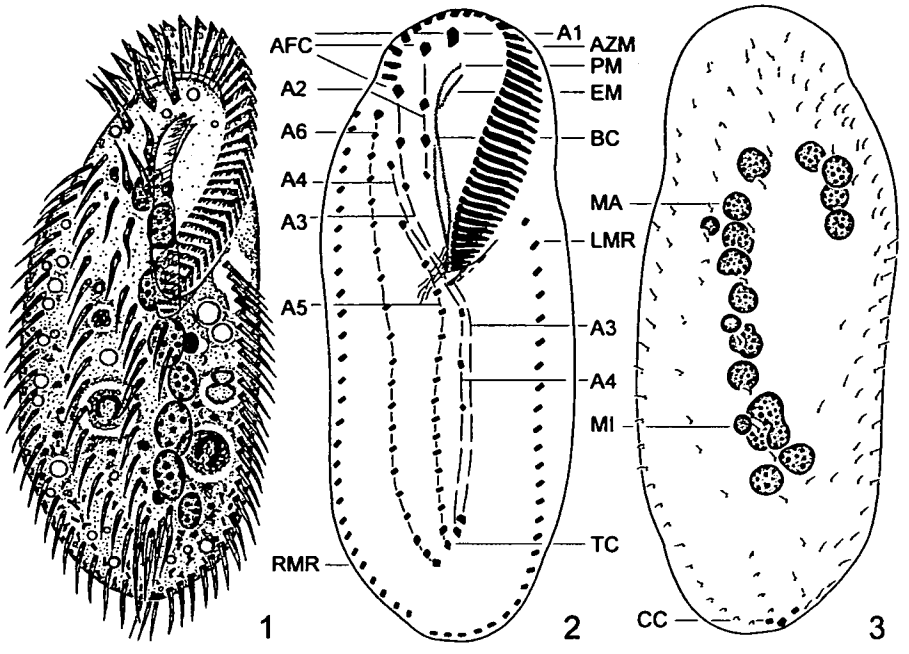
Parentocirrus hortualis was studied in vivo and with WILBERT's protargol method, as described in FOISSNER (1991). Body shape of live specimens was drawn from preparations without coverslip. All figures from impregnated cells were made with a camera lucida. To make plain the changes during ontogenesis, old (parental) structures were depicted by contour, while newly formed structures were shaded black.

Voucher slides with morphostatic and dividing, protargol-impregnated specimens have been deposited in the Biologiezentrum of the Oberösterreichische Landesmuseum in Linz (LI), Austria. Relevant cells were marked by black ink circles on the cover glass.

3 Results

3.1 Interphase morphology (Figs. 1-4, 25, 28; Table 1) and resting cysts (Figs. 26, 27)

Parentocirrus hortualis VOSS 1997 is a rather large, about 170 × 80 µm-sized, slightly ovate hypotrich ciliate with a conspicuous adoral zone of membranelles occupying almost half of body length. It has about eight macronuclear nodules in a strand left of

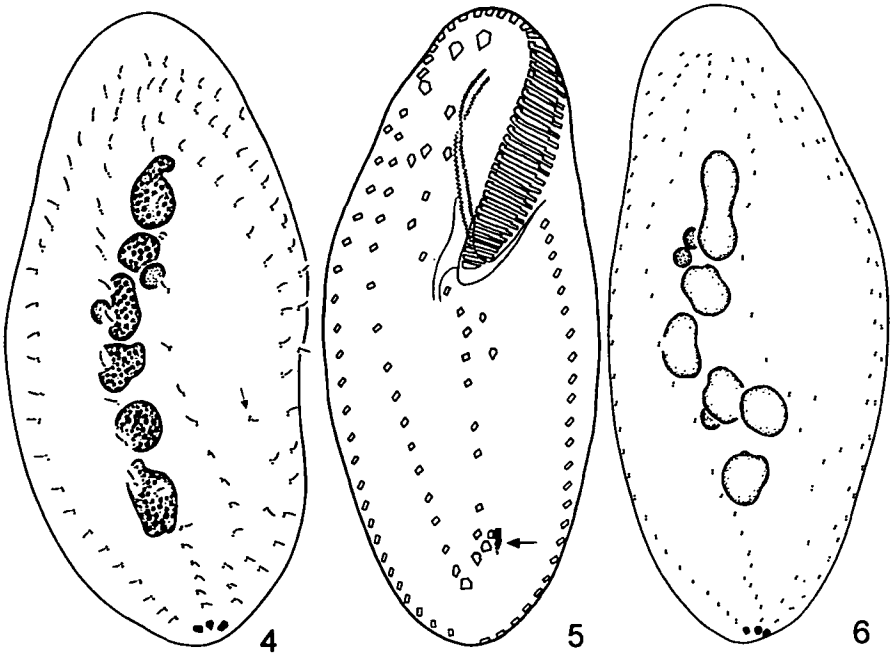


Figs. 1-3: *Parentocirrus hortualis*, interphase morphology and terminology. 1 – Ventral view of a representative specimen from life, length 165 µm. 2, 3 – Infraciliature of ventral and dorsal side and nuclear apparatus of main voucher specimen after protargol impregnation, length 155 µm. Frontoventral cirral rows originating from the same streak (anlage) during ontogenesis are numbered A1 - A6 from the left to the right. Cirri originating from the same anlage are connected by broken lines. Rarely, the posterior (transverse ?) cirri of the frontoventral rows are as distinctly enlarged as in this specimen. Similarly, dorsal kineties 4-6 are difficult to follow in this cell, either because they are longer than usual and/or some parental kinetids were maintained (cp. figure 4). A1 - A6 = frontoventral (= anlagen) rows, AFC = anterior frontal cirri, viz., distinctly enlarged anteriormost cirri of anlagen 1-3, AZM = adoral zone of membranelles, BC = buccal cirri, CC = caudal cirri, EM = endoral membrane, LMR = left marginal row, MA = macronuclear nodules, MI = micronucleus, PM = paroral membrane, RMR = right marginal row, TC = transverse cirri.

midline and two ventral and marginal cirral rows recognizable even in vivo. Transverse and caudal cirri are present, but inconspicuous (Figs. 1-4, 25, 28).

Our observations largely agree with those from VOSS (1997). The following slightly deviating or supporting data are worth to be mentioned: (i) On average, the Austrian specimens are considerably smaller and have fewer cirri and adoral membranelles than those of the German type population (Table 1). However, values highly overlap and our largest specimens come close to VOSS' extremes (one each with 250 µm and 175 µm, several with 160 µm among 400 interphase cells investigated; 35–45 adoral membranelles and up to 38 right marginal cirri; data not included in randomized specimens of Table 1); (ii) Body shape is slightly ovate in both populations, but the Austrian specimens are rather abruptly narrowed in the right anterior quadrant, that is, at the distal end of the adoral zone of membranelles; (iii) Our specimens definitely lack specific cortical

granules. Unfortunately, VOSS' description is unclear in this respect: in the text, he states "no special cortical granules", while he mentions "conspicuous cortical granules which do not stain with methyl green-pyronin" in the explanation to figure 3; (iv) The dorsal bristle pattern is less constant than shown by VOSS (1997), especially right of midline, where frequently scattered dikinetids occur between rows 3 and 4 and in the area of the dorsomarginal kineties; possibly, some of these scattered bristles are remnants from the previous generation, as, for instance, in *Parakahliella* (BERGER & FOISSNER 1989). We checked 40 specimens of *Parentocirrus hortualis* from VOSS' type slides deposited in the Biologiezentrum of the Oberösterreichische Landesmuseum in Linz (LI). At least two cells were found with such supernumerary dikinetids between rows 3 and 4, although the dorsal kineties are difficult to recognize in most cells due to the heavily impregnated cell contents; (v) In preparations from two weeks old cultures, reorganizers and specimens with strongly decreased body size and partially reduced infraciliature are frequent; (vi) Resting cysts of the Austrian specimens are highly similar to those of the type population, both in wall structure and size (Figs. 26, 27; Table 1). Usually, the macronuclear nodules fuse to a reniform mass, rarely occur some lobate pieces. Interestingly, only one micronucleus is recognizable, indicating that the others were resorbed, as in *Coniculostomum monilata* (KAMRA & SAPRA 1993).



Figs. 4-6: *Parentocirrus hortualis*, morphology and ontogenesis after protargol impregnation. 4 – Dorsal view of a representative interphase specimen, length 130 µm. Arrow marks some dikinetids which remained from the splitting process of row 3. 5, 6 – Ventral and dorsal view of a very early divider (length 135 µm) with oral primordium (arrow) originating close to the leftmost transverse (?) cirrus. Dorsal kineties 4-6 are difficult to follow either because they are longer than usual and/or some parental kinetids were maintained.

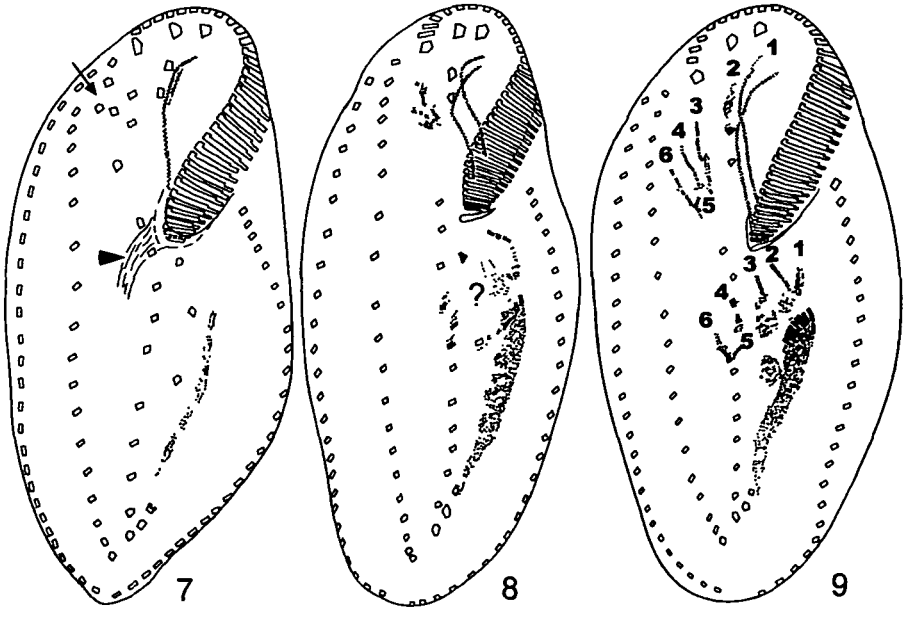
3.2 Ontogenesis (Figs. 5-15, 29-32; Tables 2, 3)

The classification of the ontogenetic stages strictly follows VOSS (1997). However, like EIGNER (1997) and BERGER (1999), we use the terms "frontoventral rows 1-6" or "anlagen 1-6" throughout, while VOSS (1997) designated the rows, respectively, anlagen 4, 5, 6, additionally, "ventral rows 1, 2, 3".

Stages 1 and 2 are very similar to those of the type population, that is, a narrow oral primordium develops and extends from the transverse cirri to mid-body (Figs. 5-7).

Stage 3: The single, appropriate divider found shows that the oral primordium develops short cirral anlagen anteriorly and some frontoventral cirri disorganize to anlagen (Fig. 8). Likely, adoral membranelles differentiate earlier in the German than Austrian specimens, while cirral anlagen in frontoventral row 5 occur slightly earlier in the Austrian than German dividers.

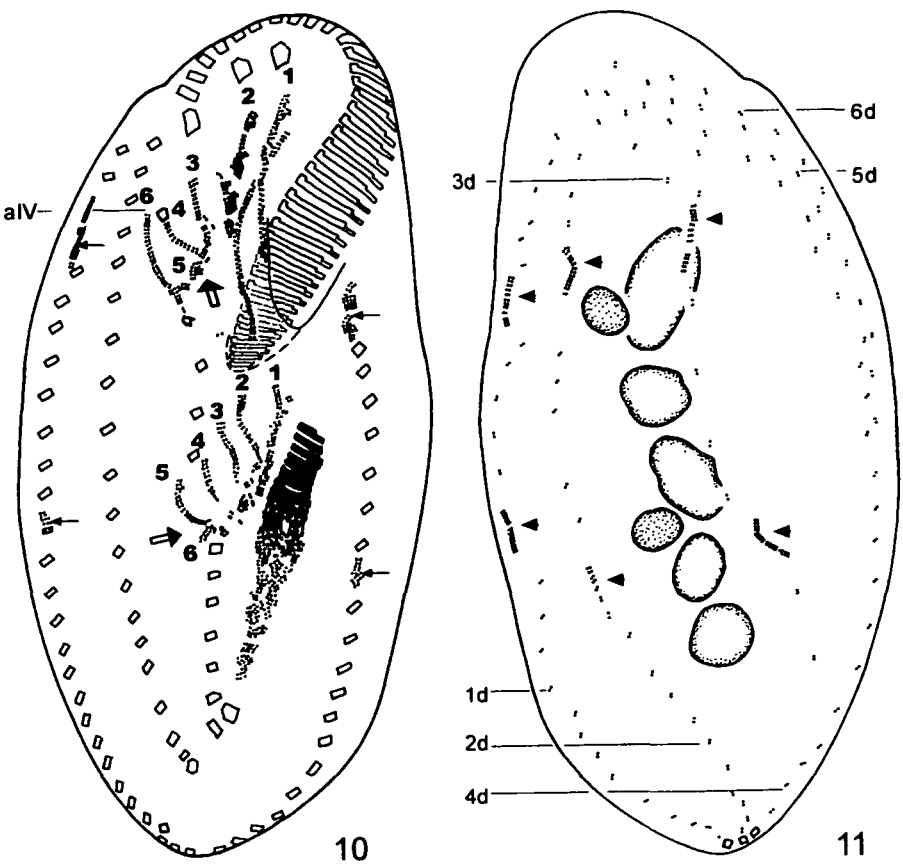
Stages 4 and 5: We did not find VOSS' stage 4 in our preparations, but early and late stage 5 dividers, which commence to disorganize the paroral's anterior end. Thus, they match well the stage 5 dividers shown by VOSS (1997) in figures 24-26, except of the marginal anlagen, which develop slightly later in the Austrian than the German specimens, when our figure 9 is compared with figure 24 in VOSS (1997). However, the



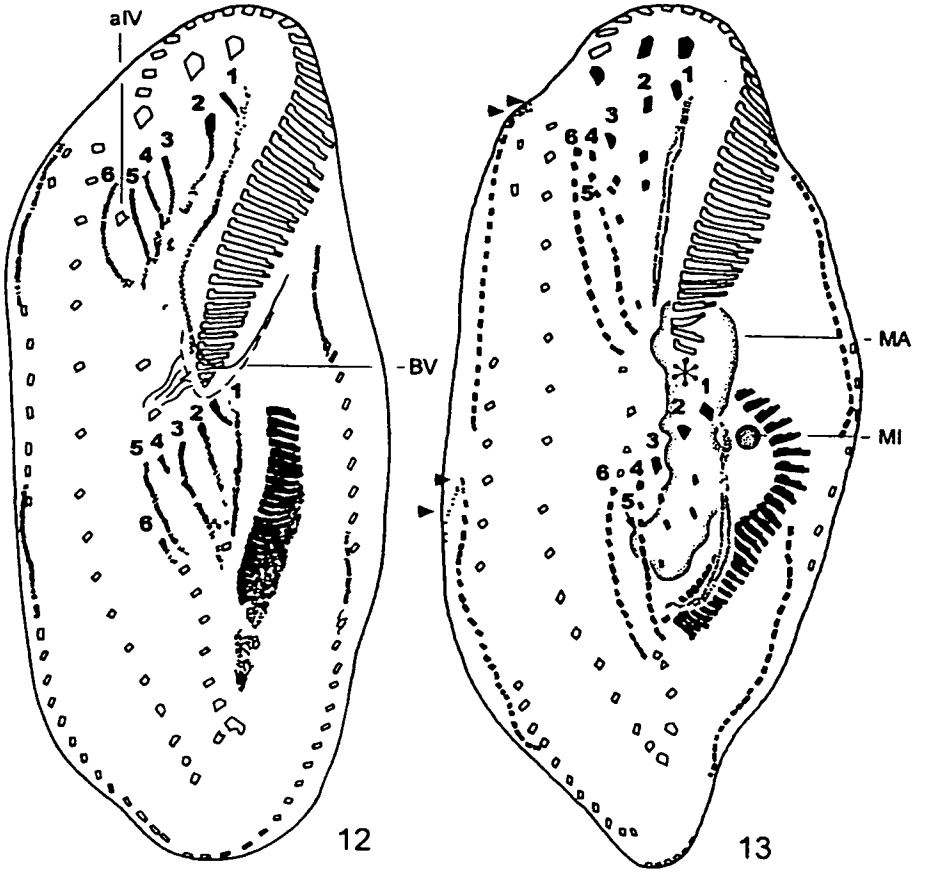
Figs. 7-9: *Parentocirrus hortualis*, ventral views of early dividers after protargol impregnation, length 120 µm, 144 µm, 130 µm. Arrow in (7) denotes a possibly distorted area, where cirri have unusual positions. Arrowhead marks pharyngeal fibres. Question mark in (8) denotes an area where the ciliary pattern could not be seen in all details due to the heavily impregnated macronuclear nodules. Furthermore, this specimen has a rather short adoral zone; short, strongly curved undulating membranes; and the proter cirral anlagen are narrower than usual. Numbers 1-6 denote the cirral anlagen; however, anlagen 4-6 are difficult to interpret (see discussion).

Austrian and German stage 5 dividers are highly similar, as evident by a comparison of our figures 10, 11 and 29 with figures 25 and 26 in VOSS (1997).

Stage 6: Our stage 6 specimen (Fig. 12) matches the respective specimen shown by VOSS (1997) in figure 33, except of the undulating membranes, which are stronger disorganized in the Austrian than the German divider.



Figs. 10, 11: *Parentocirrus hortualis*, ventral and dorsal view of an early middle divider after protargol impregnation, length 132 µm. **10** – Ventral view. Small arrows denote anlagen for the new marginal rows within the parental rows of proter and opisthe. Numbers 1-6 indicate cirral anlagen. Large arrows mark developing, V-shaped anlagen 5 and 6, but in the proter it is unclear which streak belongs to anlage 3, 4, or 5. **11** – Dorsal view. Arrowheads mark anlagen for dorsal kineties 1, 2 and 3. Parental caudal cirri are at the posterior end of kineties 1, 2 and 4. aIV = first cirrus of parental frontoventral row 4, which did not disaggregate to a cirral anlage, 1d - 4d = parental dorsal kineties, 5d, 6d = parental dorsomarginal kineties.

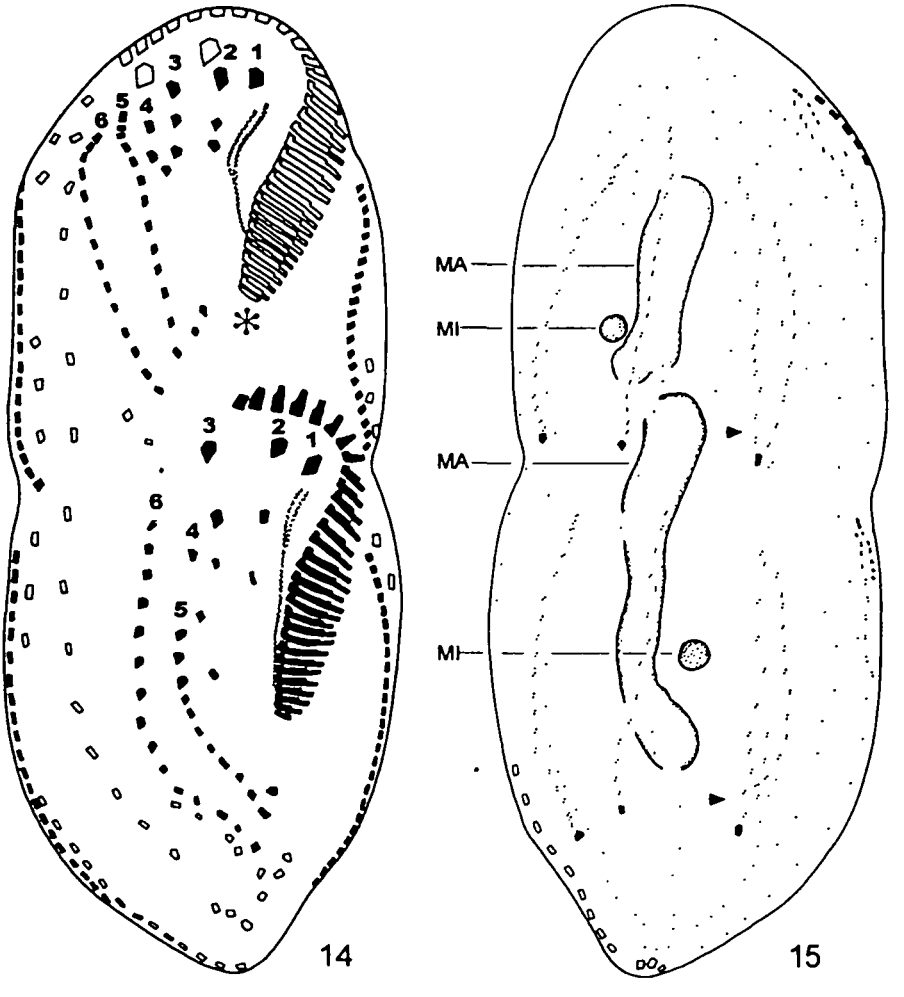


Figs. 12, 13: *Parentocirrus hortualis*, ventral views of middle dividers after protargol impregnation. 12 – Early middle divider, length 130 µm. 13 – Ventral view of a late middle divider, length 140 µm. Arrowheads mark the developing dorsomarginal kineties in proter and opisthe. Asterisk marks site of the parental buccal vertex, which disappeared (cp. figure 12). Anlage 4 develops only 3 cirri in the opisthe. Its anteriormost cirrus is, in this specimen, upon anlage 5. Numbers 1-6 denote cirral anlagen. aIV = first cirrus of parental frontoventral row 4, which did not disaggregate to a cirral anlage, BV = buccal vertex, MA = fused macronuclear nodules, MI = micronucleus.

Stage 7: Our stage 7 specimens (Figs. 13-15, 31, 32) match the respective dividers shown by VOSS (1997) in figures 42-46. Even on very detailed comparison, no differences can be found, although the overall appearance of the Austrian specimens is somewhat different due to the lower number and wider spacing of the cirri comprising anlagen 5 and 6.

Stage 8: Our stage 8 specimen (Fig. 30) matches the respective divider shown by VOSS (1997) in figure 17.

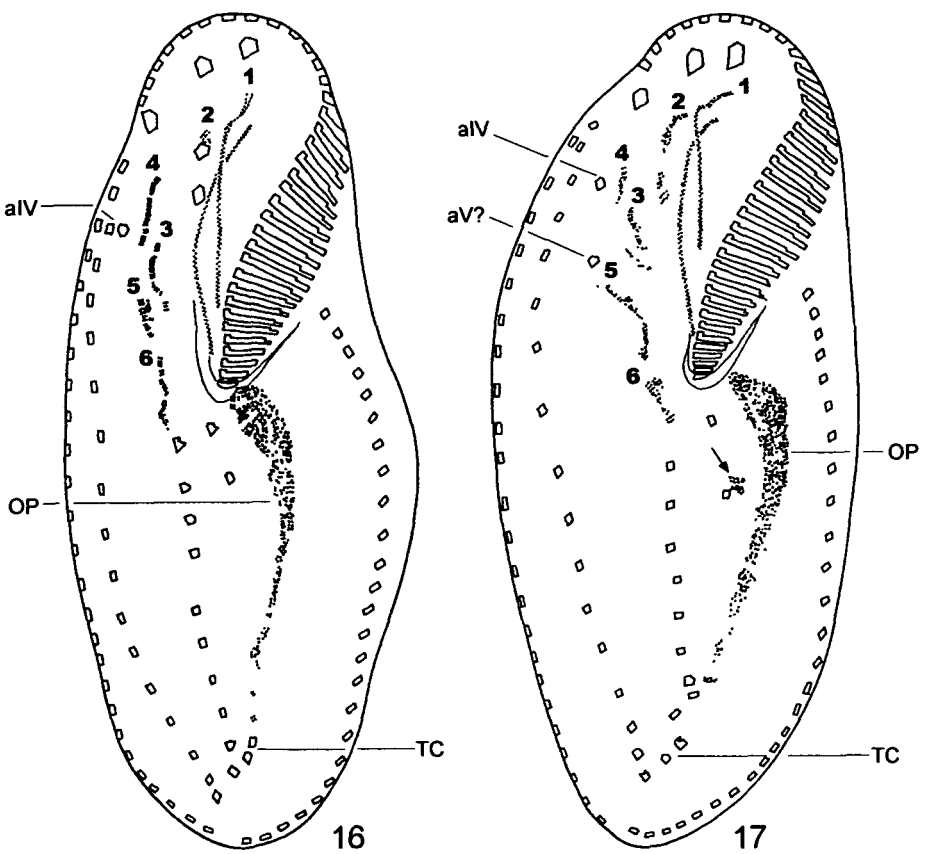
Post-dividers: Parental cirral retention is a rather important phylogenetic marker. VOSS (1997) observed parental row 6 cirri in about 2% of specimens; unfortunately, it is not clear whether the 2% include only fully developed interphase specimens or also late post-dividers and/or reorganizers. Thus, we carefully checked 400 well-impregnated interphase specimens (= those having a fully developed nuclear apparatus, buccal field, and pharyngeal fibres; no parental marginal, transverse, and caudal cirri) of our population for parental row 5 and/or row 6 cirri. Such parental cirri are lacking in our morphostatic specimens, but do occur in the 11 post-dividers and post-reorganizers observed.



Figs. 14, 15: *Parentocirrus hortualis*, ventral and dorsal view of a late divider after protargol impregnation, length 132 µm. Asterisk marks site of the parental buccal vertex, which disappeared, that is, becomes reorganized. Numbers 1-6 denote cirral anlagen. The parental dorsal kineties are still recognizable as dikinetids, but shown as monokinetids for the sake of clarity. Arrowheads mark dorsal kinety 3, which produces kinety 4 by fragmentation. MA = dividing macronuclear strand, MI = micronucleus.

3.3 Physiological reorganization (Figs. 16-24, 33, 34)

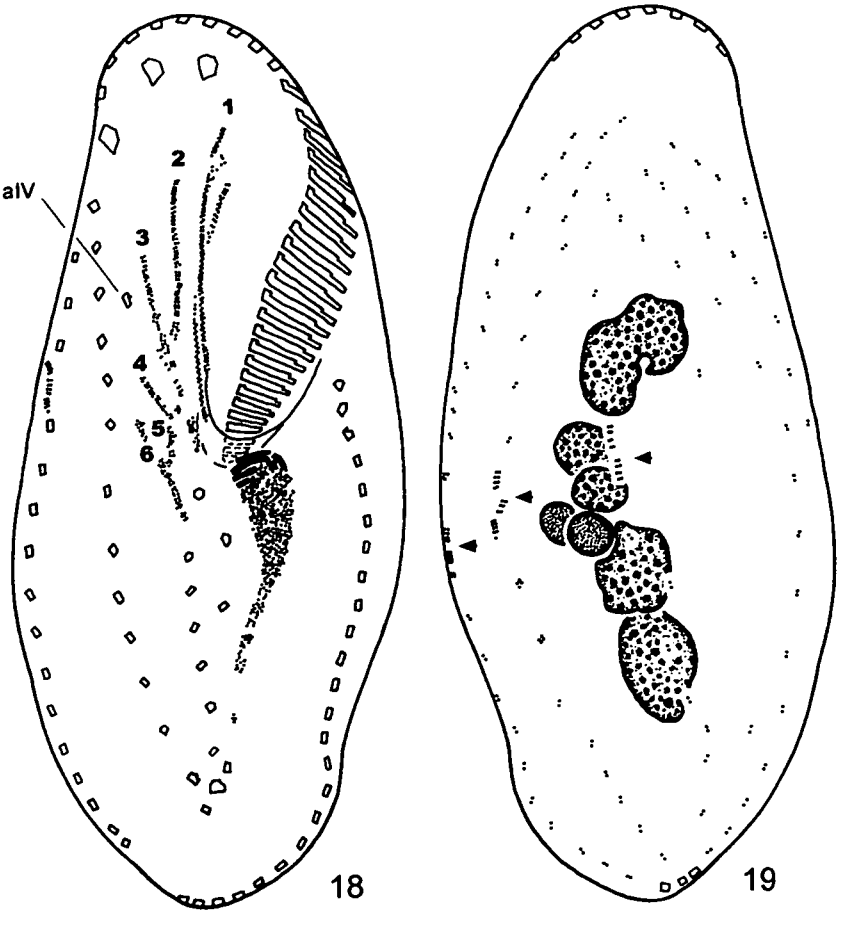
Physiological reorganization commences with the production of a large, cuneate oral primordium extending between buccal vertex and the leftmost transverse cirrus. Concomitantly, the anterior cirri of frontoventral rows 3 and 5 disaggregate forming a long primordium in the frontal area of row 5, that is, between frontoventral row 4 and the buccal cirral row (Fig. 16). The single anterior cirrus of frontoventral row 4 is inactive, that is, does not disaggregate and is thus still recognizable in most middle and late reorganizers (Figs. 16-18, 20, 21, 34); twice, a second frontoventral cirrus, likely the anteriormost cirrus of row 5, also does not disaggregate (Figs. 17, 21). Likely, the posterior



Figs. 16, 17: *Parentocirrus hortualis*, ventral views of very early reorganizers after protargol impregnation, length 138 µm, 110 µm. The specimen shown in (17) has an unusual transverse cirri pattern; possibly some parental cirri were maintained or the area was distorted by the preparation. Arrow marks proliferation of basal bodies right of the oral primordium, viz., near a cirrus of frontoventral row 4. Numbers 1-6 indicate cirral anlagen. aIV = first cirrus of parental frontoventral row 4, which did not disaggregate to a cirral anlage, aV? = supposed anteriormost cirrus of parental frontoventral row 5, OP = oral primordium, TC = transverse cirri.

portion of row 4 also does not produce cirral anlagen, but is probably involved in oral primordium formation because at least two of the three cirri have disappeared in middle and late reorganizers.

The cirral anlagen soon rearrange to six small streaks, which form a fan-like pattern right of the undulating membranes (Figs. 17, 18). Concomitantly, the anterior region of the paroral membrane disorganizes to form anlage 1, and adoral membranelles are generated in the anterior portion of the oral primordium. Furthermore, an anlage each is generated in the right and left marginal row and in dorsal kineties 1-3, the macronuclear nodules become irregular, and the micronuclei become prophasic (Figs. 17-19). As concerns the marginal rows, three to five, usually four parental cirri remain at the anterior end of the



Figs. 18, 19: *Parentocirrus hortualis*, ventral and dorsal view of an early reorganizer after protargol impregnation, length 117 µm. Arrowheads mark anlagen for dorsal kineties 1, 2 and 3. Numbers 1-6 denote cirral anlagen. Anlagen streaks 4-6 cannot be determined unequivocally. aIV = first cirrus of parental frontoventral row 4, which did not disaggregate to a cirral anlage.

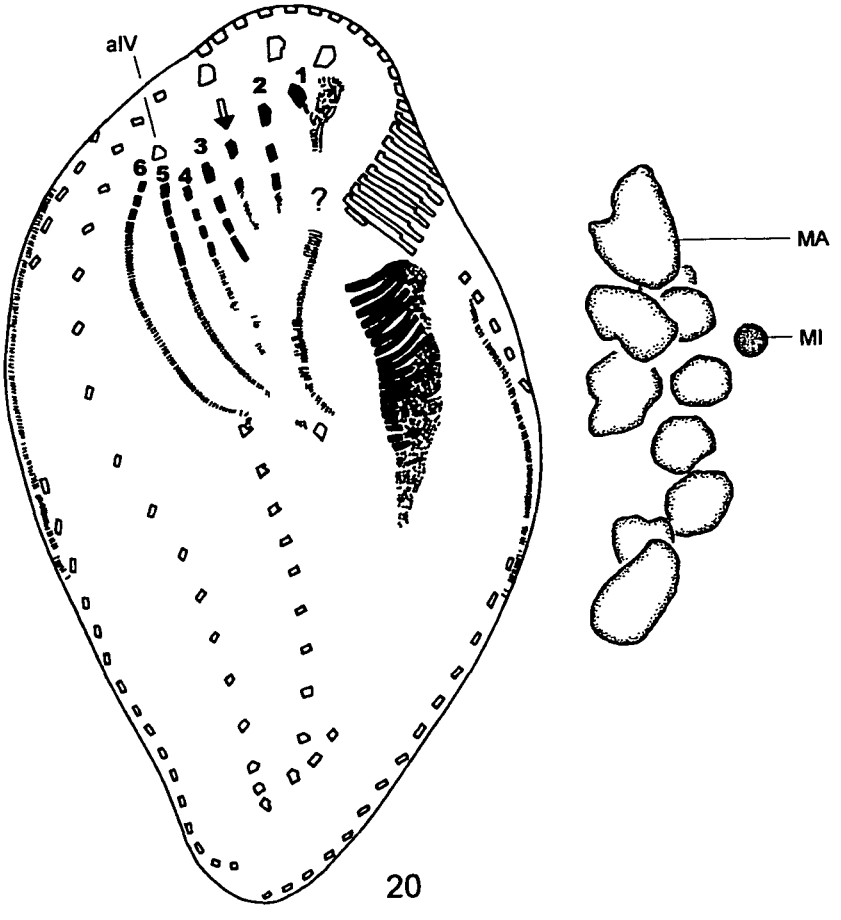


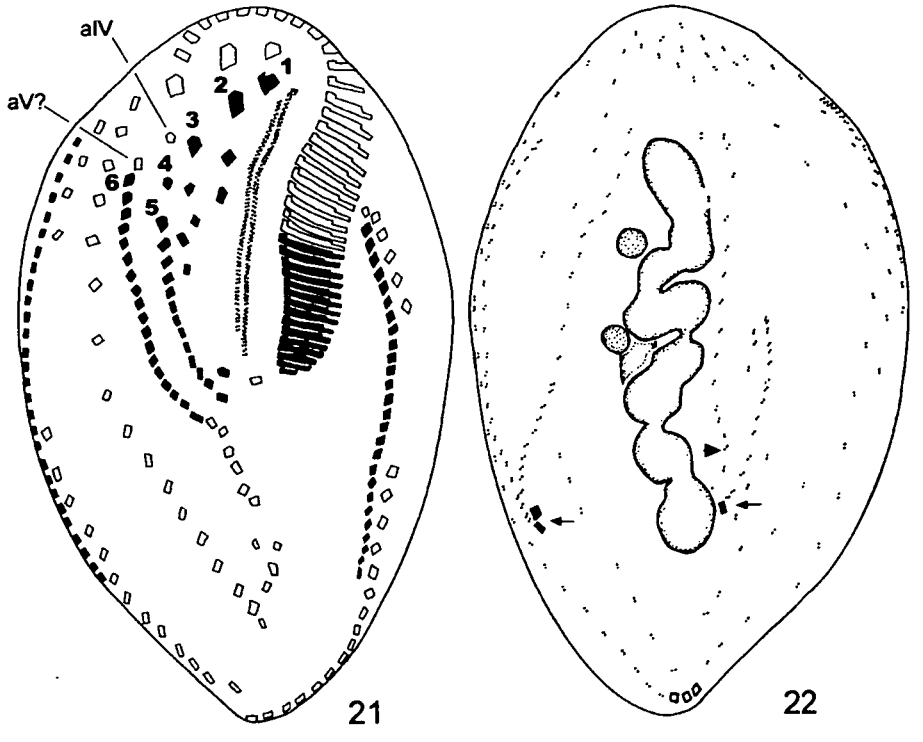
Fig. 20: *Parentocirrus hortualis*, ventral view of a middle reorganizer after protargol impregnation, length 122 µm. In this specimen occurs an additional, seventh anlage (arrow). Question mark denotes an area where the ciliary pattern could not be seen due to the heavily impregnated macronuclear nodules. Numbers 1-6 denote cirral anlagen. aIV = first cirrus of parental frontoventral row 4, which did not disaggregate to a cirral anlage, MA = macronuclear nodule, MI = micronucleus.

right row and three to six, usually five at the anterior end of the left row. In dividers, only one to three cirri remain at right and none at left (Figs. 10, 12-14, 29, 31).

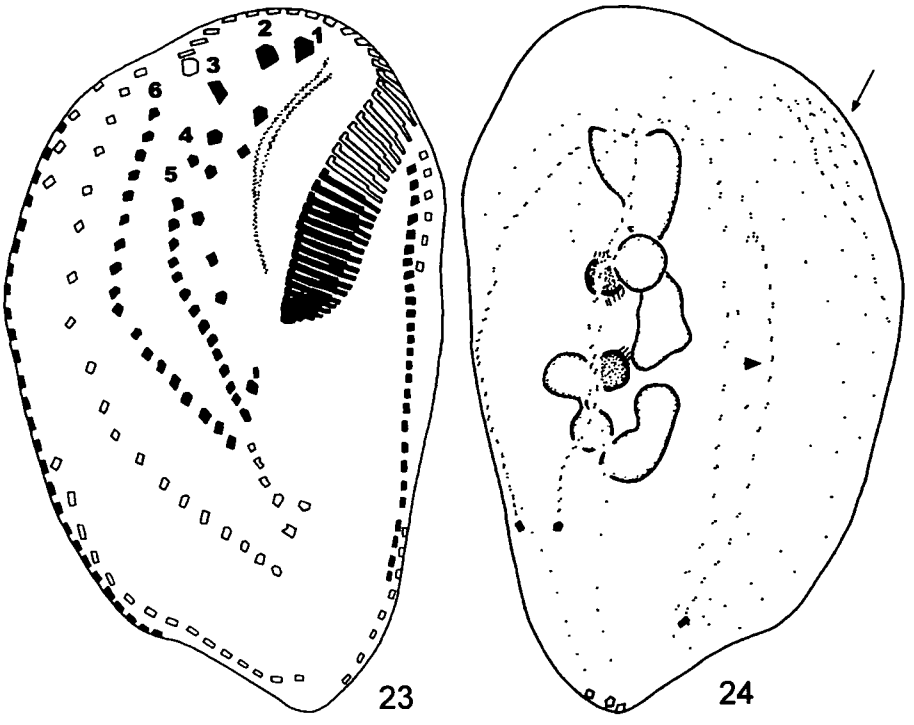
In early-middle and middle reorganizers, the macronuclear nodules fuse to a sausage-shaped mass; the buccal cavity flattens; the buccal vertex disappears; and the proximal 40% of the adoral zone of membranelles are replaced by the new membranelles produced in the oral primordium. The cirral anlagen streaks are now fully developed and segregate cirri from anterior to posterior (Figs. 20, 21, 33, 34). Of 12 middle reorganizers found, 10 have six cirral anlagen streaks and two have a small seventh anlage, which either produces one or two additional cirri or is resorbed in late reorganizers. Dorsally, row 3 fragmentizes and produces row 4, as in dividers; frequently, some extra dikinetids

remain between rows 3 and 4. Two to three dorsomarginal kineties develop near the anterior end of the right marginal primordium and close to the parental marginal cirri not involved in primordium formation (Figs. 22, 24).

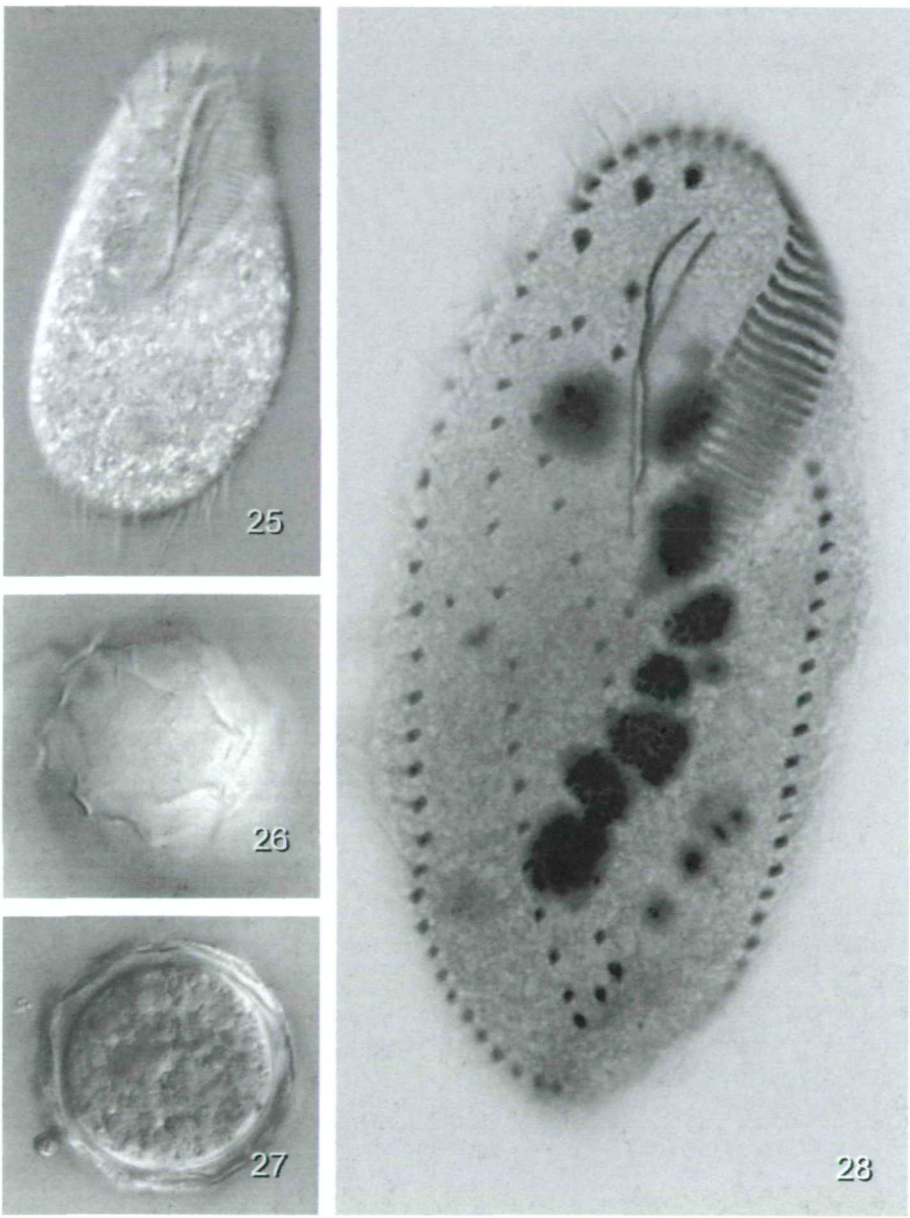
Late reorganizers develop like late dividers, that is, the undulating membranes form two parallel rows which later, when the new buccal cavity deepens, optically cross each other; a new buccal vertex develops; the newly formed cirri migrate to their specific sites; and the cirri and dorsal bristles, which were not involved in anlagen formation, are resorbed (Figs. 21-24).



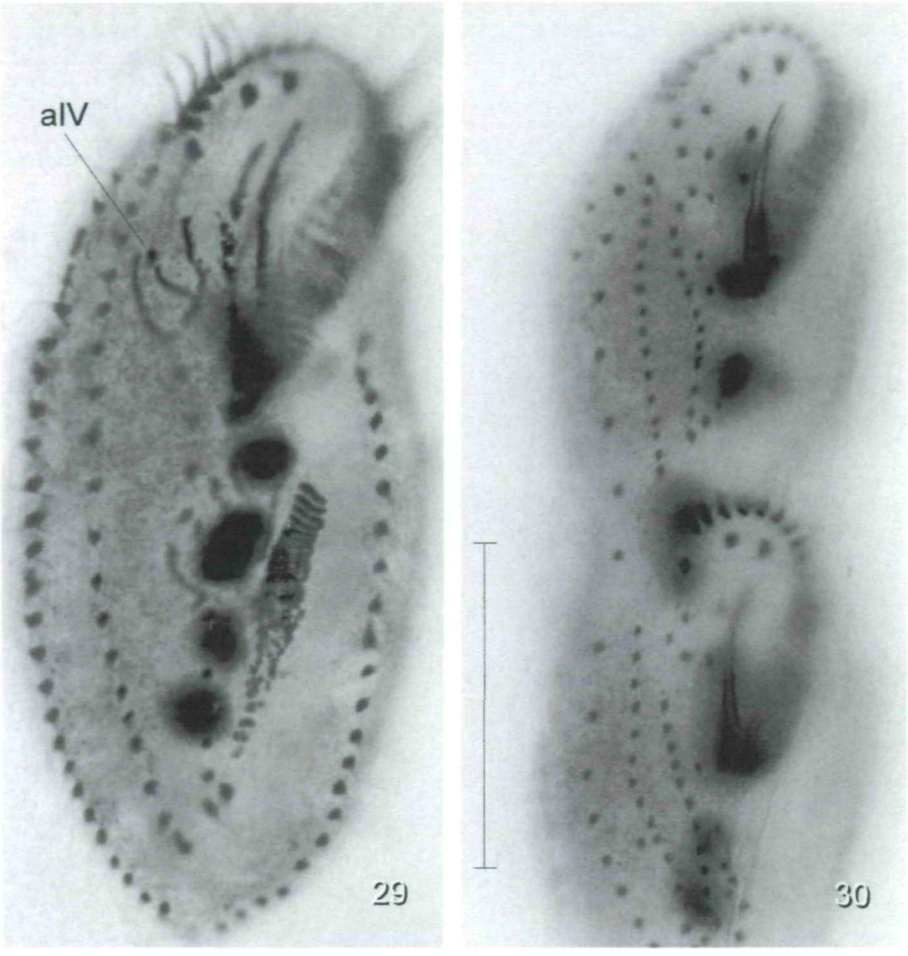
Figs. 21, 22: *Parentocirrus hortualis*, ventral and dorsal view of a late reorganizer after protargol impregnation, length 107 µm. The parental dorsal kineties are still visible and composed of dikinetids. Dorsal kinety 3 shows fragmentation (arrowhead), that is, generates kinety 4. Note newly formed caudal cirri (arrows). Numbers 1-6 denote cirral anlagen. aIV = first cirrus of parental frontoventral row 4, which did not disaggregate to a cirral anlage, aV? = supposed anteriormost cirrus of parental frontoventral row 5.



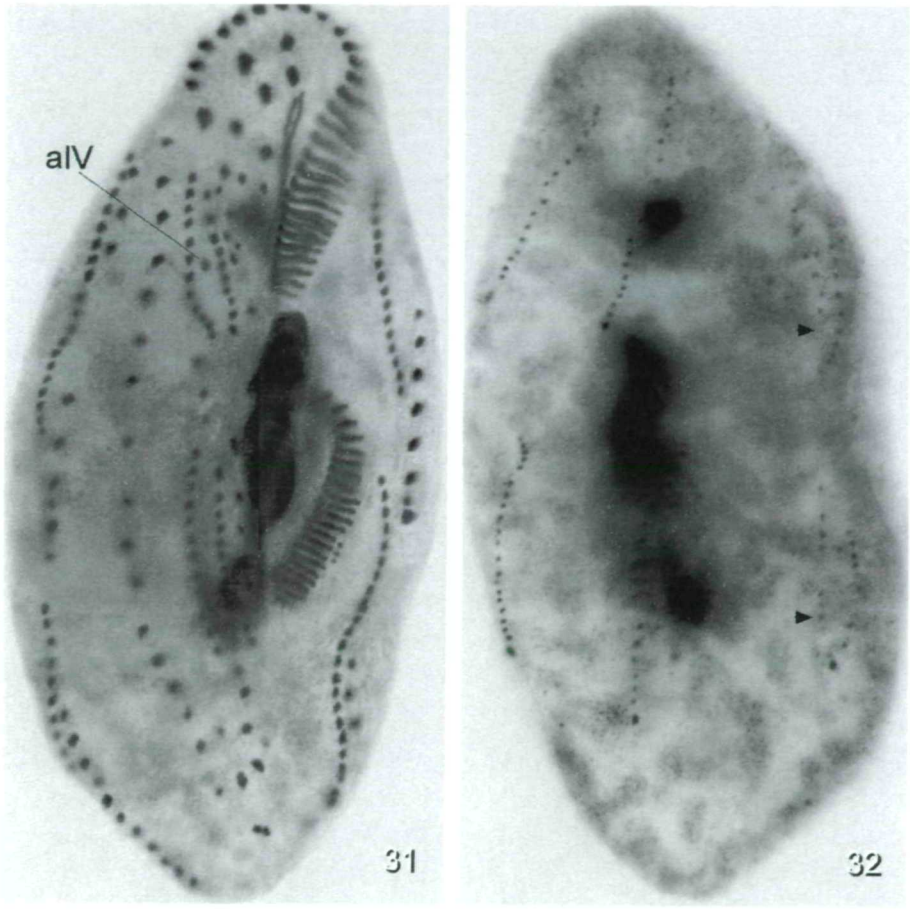
Figs. 23, 24: *Parentocirrus hortualis*, ventral and dorsal view of a late reorganizer after protargol impregnation, length 115 µm. Most parental dorsal kineties are still visible as dikinetids, but are depicted as monokinetids for the sake of clarity. Dorsal kinety 3 fragmented, viz., produced kinety 4 (arrowhead). In this specimen, three dorsomarginal kineties developed (arrow). Numbers 1-6 denote cirral anlagen.



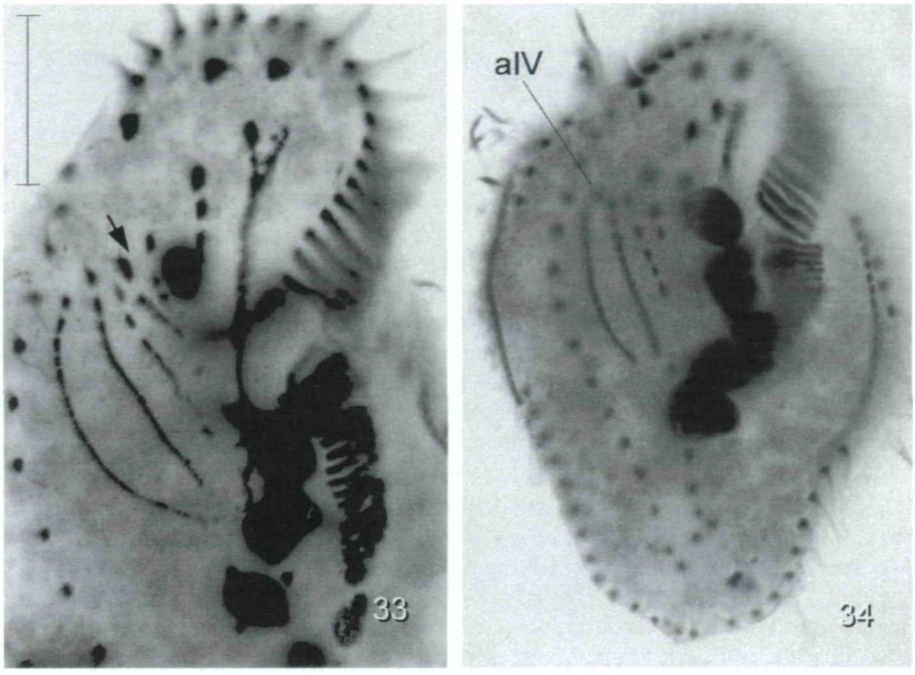
Figs. 25-28: Morphology of *Parentocirrus hortualis*. **25** – Ventral view from life, length about 160 µm. **26, 27** – Surface view and optical section of a resting cyst from life, diameter about 50 µm. **28** – Ventral view of a morphostatic specimen after protargol impregnation.



Figs. 29, 30: *Parentocirrus hortualis*, ventral views of a middle and a late divider after protargol impregnation, length 132 µm, scale bar 50 µm. aIV = first cirrus of parental frontoventral row 4, which did not disaggregate to a cirral anlage.



Figs. 31, 32: *Parentocirrus hortualis*, ventral and dorsal view of a middle divider after protargol impregnation, length 140 µm. Dorsal kinety 3 (arrowheads) fragmentizes and produces kinety 4. aIV = first cirrus of parental frontoventral row 4, which did not disaggregate to a cirral anlage.



Figs. 33, 34: *Parentocirrus hortualis*, ventral views of middle reorganizers after protargol impregnation. **33** – Anterior portion of a specimen with an additional, seventh anlage (arrow). Scale bar 20 µm. **34** – A specimen with 6 cirral anlagen, length 90 µm. aIV = first cirrus of parental frontoventral row 4, which did not disaggregate to a cirral anlage.

4 Discussion

4.1 Interphase morphology

When comparing the German and Austrian populations of *Parentocirrus hortualis*, it must be taken into account that culture and preparation conditions are rather unspecified in both. This can influence results considerably, especially metric features connected by more or less pronounced isometric allometry, such as body size and the numbers of cirri and adoral membranelles. Likely, this happened in the present investigation, where many averages differ considerably, while individual values highly overlap (Table 1). Although the main diagnostic features and the size of the cells from raw cultures match well the cultivated German specimens, the cultivated Austrian cells are smaller by 28% and have distinctly fewer cirri and adoral membranelles, suggesting that differences are real, that is, are not caused by different shrinking rates during preparation, but by less optimal culture conditions.

Thus, we propose conspecificity of the German and Austrian populations because they agree in the main diagnostic features (gross body shape and size, nuclear apparatus, cirral and dorsal kinety pattern, resting cyst structure, ontogenesis) and most morphometric differences can be related to the smaller size of the cultivated Austrian cells.

4.2 Ontogenesis

Our stage-by-stage comparison shows a high similarity in the ontogenetic processes and patterns of the German and Austrian *P. hortualis*. Most differences observed are obviously related to the lower number of cirri in the Austrian specimens (Table 2), while others might be caused by preparation artifacts and some natural variability. The most conspicuous differences will be discussed now in some detail. (i) The German dividers have more ontogenetically inactive cirri between the proter and opisthe anlagen streaks than the Austrian specimens (4-8 according to VOSS' figures vs. 2-6, median 3). Likely, this is simply an effect of the higher number of frontoventral cirri the German specimens have (Table 1); (ii) The developing anlagen streaks are usually shorter and less conspicuous in the Austrian than the German dividers. Likely, this is caused by the lower number of cirri and a stronger preparation shrinkage in the Austrian specimens.

A problem not mentioned in our and VOSS' descriptions, is the high intrapopulation variability in anlagen number and arrangement. As concerns number, which varies from 5-7, see Table 3. The pattern variability is considerable, and the stages depicted are, hopefully, representative examples matching VOSS' stages not only by chance. We will not discuss all the minor variations observed, but concentrate on two examples that show how difficult, and even arbitrary, streak recognition and allocation may be (see also example above). The V-shaped figure formed by the anlagen 5 and 6 is much less distinct in the Austrian than the German specimens, partially due to the stronger shrinkage of the former, but also due to their larger size in the latter. Thus, anlage 6 is a risky interpretation in both proter and opisthe of the specimen shown in figure 10. Further, figure 10 does not exclude that opisthe anlage 4 is generated by frontoventral row 5. The second example concerns proter anlagen 4-6 which may be separate or more or less distinctly connected posteriorly. Thus, the origin of the individual anlagen is difficult to follow, for instance, we cannot exclude that anlage 4 develops de novo in figures 9 and 12 or by splitting of anlage 3 in figure 10.

4.3 Physiological reorganization

Physiological reorganization is still insufficiently studied in oxytrichid hypotrichs, though the basic processes are known and match our observations in *P. hortualis*, for instance, that only the proximal half of the parental adoral zone of membranelles is replaced, while the entire somatic infraciliature is renewed (JERKA-DZIADOSZ & FRANKEL 1969; WIRNSBERGER et al. 1985; PETZ & FOISSNER 1996; BERGER 1999). Our study adds two, likely genus-specific main features to the existing knowledge: (i) Physiological reorganization differs from divisional ontogenesis in that disaggregating cirri of frontoventral row 3 and 5 form a long primordium, while row 4 is likely inactive and generated by row 3; (ii) Early reorganizers and dividers can be distinguished by two features, viz., the oral primordium (abutting vs. distinctly separate from parental buccal vertex; Figs. 8, 9, 16, 17) and the location of cirral anlagen streaks 1-3 (right of undulating membranes,

that is, at anterior end of frontoventral row 5, where a long primordium is generated vs. at anterior end of oral primordium with which the three anlagen form a candle-like pattern; Figs. 8, 9, 16-18 and VOSS 1997). Further, adoral membranelles are slightly earlier produced in dividers than reorganizers, viz., when the buccal cirri commence to disaggregate vs. have disaggregated.

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6 References

BERGER H. (1999): Monograph of the Oxytrichidae (Ciliophora, Hypotrichia). — Monographiae biol. **78**: 1-1079.

BERGER H. & W. FOISSNER (1989): Morphology and morphogenesis of *Parakahliella haideri* nov. spec. (Ciliophora, Hypotrichida). — Bull. Br. Mus. nat. Hist (Zool.) **55**: 11-17.

BERGER H. & W. FOISSNER (1997): Cladistic relationships and generic characterization of oxytrichid hypotrichs (Prototozoa, Ciliophora). — Arch. Protistenk. **148**: 125-155.

EIGNER P. (1997): Evolution of morphogenetic processes in the Orthoamphisiellidae n. fam., Oxytrichidae, and Parakahliellidae n. fam., and their depiction using a computer method (Ciliophora, Hypotrichida). — J. Euk. Microbiol. **44**: 553-573.

EIGNER P. (1999): Comparison of divisional morphogenesis in four morphologically different clones of the genus *Gonostomum* and update of the natural hypotrich system (Ciliophora, Hypotrichida). — Europ. J. Protistol. **35**: 34-48.

FOISSNER W. (1991): Basic light and scanning electron microscopic methods for taxonomic studies of ciliated protozoa. — Europ. J. Protistol. **27**: 313-330.

FOISSNER W. & H. BERGER (1999): Identification and ontogenesis of the nomen nudum hypotrichs (Protozoa: Ciliophora) *Oxytricha nova* (= *Sterkiella nova* sp. n.) and *O. trifallax* (= *S. histriomuscorum*). — Acta Protozool. **38**: 215-248.

FOISSNER W., AGATHA S. & H. BERGER (2002): Soil ciliates (Protozoa, Ciliophora) from Namibia (Southwest Africa), with emphasis on two contrasting environments, the Etosha region and the Namib Desert. — Denisia **5**: 1-1459.

JERKA-DZIADOSZ M. (1965): Morphogenesis of ciliature in division of *Urostyla weissei* (STEIN). — Acta Protozool. **3**: 345-353.

JERKA-DZIADOSZ M. & J. FRANKEL (1969): An analysis of the formation of ciliary primordia in the hypotrich ciliate *Urostyla weissei*. — J. Protozool. **16**: 612-637.

KAMRA K. & G.R. SAPRA (1993): Morphological and ultrastructural changes during encystment in *Coniculostomum monilata* (Ciliophora, Hypotrichida, Oxytrichidae). — J. Pure and Applied Zoology (New Delhi) **3**: 273-302.

PETZ W. & W. FOISSNER (1996): Morphology and morphogenesis of *Lamtostyla edaphoni* BERGER and FOISSNER and *Onychodromopsis flexilis* STOKES, two hypotrichs (Protozoa: Ciliophora) from Antarctic soils. — Acta Protozool. **35**: 257-280.

PETZ W. & W. FOISSNER (1997): Morphology and infraciliature of some soil ciliates (Protozoa, Ciliophora) from continental Antarctica, with notes on the morphogenesis of *Sterkiella histriomuscorum*. — Polar Record **33**: 307-326.

VOSS H.-J. (1989): Vergleichende morphologische Untersuchung von 13 Arten der Gattung *Euplotes* (Ciliophora, Hypotrichida). — Arch. Protistenk. **137**: 331-344.

VOSS H.-J. (1997): Morphology and morphogenesis of *Parentocirrus hortualis* nov. gen., nov. spec.: a new genus within the redefined family Kahliellidae sensu EIGNER 1995 (Ciliophora, Hypotrichida). — Europ. J. Protistol. **33**: 30-47.

WIRNSBERGER E., FOISSNER W. & H. ADAM (1985): Cortical pattern in non-dividers, dividers and reorganizers of an Austrian population of *Paraurostyla weissei* (Ciliophora, Hypotrichida): a comparative morphological and biometrical study. — Zool. Scr. **14**: 1-10.

WIRNSBERGER E., FOISSNER W. & H. ADAM (1986): Biometric and morphogenetic comparison of the sibling species *Stylonychia mytilus* and *S. lemnae*, including a phylogenetic system for the oxytrichids (Ciliophora, Hypotrichida). — Arch. Protistenk. **132**: 167-185.

WIRNSBERGER-AESCHT E., FOISSNER W. & I. FOISSNER (1990): Natural and cultured variability of *Engelmanniella mobilis* (Ciliophora, Hypotrichida); with notes on the ultrastructure of its resting cyst. — Arch. Protistenk. **138**: 29-49.

Table 1: Morphometric data on *Parentocirrus hortualis* from Austria (upper line) and Germany (lower line; from VOSS 1997).

Characteristics[1)]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length (in vivo)	163,3	160,0	-	-	-	150	180	3
	186,6	178,2	22,2	7,0	11,8	163,4	222,8	10
Body, width (in vivo)	76,7	80,0	-	-	-	70	80	3
	86,9	89,1	11,1	3,5	12,8	74	104	10
Body length : width, ratio	2,14	2,25	-	-	-	1,88	2,29	3
(in vivo)	2,15+	-	-	-	-	-	-	10
Body, length	131,7	133,0	14,9	3,2	11,3	106	155	22
	183,1	183,5	37,2	7,6	20,6	128,5	300,9	25
Body, width	60,7	60,5	6,4	1,4	10,5	49	77	22
	94,7	91,6	22,5	4,5	23,8	62	165,7	25
Body length : width, ratio	2,18	2,17	0,2	0,0	10,6	1,68	2,54	22
	1,93+	-	-	-	-	-	-	25
Macronuclear nodules, number	8,1	7,0	2,7	0,6	33,3	5	16	22
	7,8	8,0	1,5	0,3	19,2	6	12	25
Macronuclear nodules, length [2)]	11,3	11,0	2,7	0,6	24,2	7,5	17	22
	13,4	11,0	3,6	0,7	26,1	9,2	25,7	25
Macronuclear nodules, width	7,8	7,8	1,4	0,3	18,2	5	11	22
	-	-	-	-	-	-	-	-
Micronuclei, number	3,0	3,0	1,2	0,3	39,7	1	6	22
	3,5	3,0	1,0	0,2	28,6	2	6	25
Micronuclei, length [2)]	4,2	4,0	-	-	-	3,8	5	22
	3,9	3,9	-	-	-	3	5	25
Micronuclei, width	4,0	4,0	-	-	-	3,5	4,5	22
	-	-	-	-	-	-	-	-
Posterior end to posteriormost cirrus of frontoventral rows (usually A6 in Fig. 2), distance	13,0	13,0	3,4	0,7	26,3	7,5	19	22
	-	-	-	-	-	-	-	-

(continued)

Characteristics[1)]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Anterior body end to proximal end of adoral zone, distance	59,6	61,5	6,1	1,3	10,2	46	66	22
	85,0	86,2	22,3	4,5	26,2	55,5	157,8	25
Body length : length of adoral zone, ratio	2,21	2,2	0,2	0,0	6,8	1,81	2,46	22
	2,15+	-	-	-	-	-	-	-
Adoral membranelles, number	36,9	37,0	2,8	0,6	7,5	33	42	22
	45,0	44,0	4,6	0,9	10,2	38	57	25
Left marginal cirri, number	26,3	26,5	2,2	0,5	8,4	23	30	22
	32,0	32,0	4,4	0,9	13,8	23	43	25
Right marginal cirri, number	25,3	24,5	2,6	0,6	10,4	19	30	22
	32,2	33,0	4,0	0,8	12,4	23	42	25
Anterior frontal cirri, number [3)]	3,0	3,0	0,0	0,0	0,0	3	3	22
	3,0	3,0	0,0	0,0	0,0	3	3	25
Posterior frontal cirri, number [4)]	2,0	2,0	0,0	0,0	0,0	2	2	22
	2,0	2,0	0,0	0,0	0,0	2	2	25
Buccal cirri, number [5)]	2,5	2,0	-	-	-	2	3	22
	2,8	3,0	0,5	0,1	17,9	2	4	25
Frontoventral row 4, number of cirri [6)]	3,4	3,0	1,0	0,2	31,2	2	6	22
	4,2	4,0	1,3	0,3	31,0	3*	9*	25
Frontoventral row 5, number of cirri [6)]	13,7	13,0	2,0	0,4	14,4	10	20	22
	19,1	19,0	2,4	0,5	12,6	16	24	25
Frontoventral row 6, number of cirri [6)]	16,8	17,0	2,4	0,5	14,2	12	21	22
	24,3	24,0	2,2	0,4	9,1	19	30	25
Transverse cirri, number [7)]	3,6	4,0	0,6	0,1	16,4	2	4	22
	4,1	4,0	0,3	0,1	6,8**	4**	5**	25
Ventral cirri, total number (all cirri, except of marginal and caudal)	45,0	44,5	4,0	0,8	8,8	36	53	22
	59,3+	-	-	-	-	-	-	25
Caudal cirri, number	3,0	3,0	0,2	0,0	7,2	2	3	22
	3,1	3,0	0,3	0,1	9,7	3	4	25
Dorsal kineties, number 8)	6,1	6,0	0,4	0,1	5,8	6	7	21
	6,1	6,0	0,3	0,1	4,9	6	7	25
Dikinetids in dorsal kinety 1, number	28,6	28,0	3,9	0,9	13,5	24	36	18
	-	-	-	-	-	-	-	-
Dikinetids in dorsal kinety 2, number	24,8	25,0	3,9	0,9	15,6	19	34	19
	-	-	-	-	-	-	-	-
Dikinetids in dorsal kinety 3, number	16,8	16,0	3,1	0,7	18,7	13	26	19
	-	-	-	-	-	-	-	-
Dikinetids in dorsal kinety 4, number	18,6	18,0	3,3	0,8	17,9	12	24	19
	-	-	-	-	-	-	-	-
Dikinetids in dorsal kinety 5, number	14,6	14,0	3,5	0,8	23,9	8	23	19
	-	-	-	-	-	-	-	-
Dikinetids in dorsal kinety 6, number	7,4	7,0	1,4	0,3	18,8	6	12	19
	-	-	-	-	-	-	-	-

(continued)

Characteristics[1)]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Scattered dikinetids between dorsal kineties 3 and 4, number	1,9 -	1,0 -	2,4 -	0,6 -	126,7 -	0 -	7 -	19 -
Resting cysts of Austrian population (in vivo)								
Cyst diameter (in 7 days old activated sludge)	52,6	55,0	9,1	3,0	17,3	40	65	9
Cyst diameter (cultivated specimens)	49,7	50,0	4,4	1,0	8,9	45	59	19
Cyst wall, thickness (cultivated specimens)	3,7	3,8	0,6	0,1	16,1	3	5	19

1) Data of both populations based, if not stated otherwise, on protargol-impregnated (WILLERT's method), mounted, and randomly selected specimens from bacterized, exponentially growing cultures, except of the in vivo measurements of the Austrian specimens, which are from cells of the fresh activated sludge sample. Measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum. Min = minimum, n = number of individuals investigated, SD = standard deviation of mean, SE = standard error of arithmetic mean, $\bar{x}$ = arithmetic mean.

2) VOSS provided only "diameter" (longest axis?).

3) The anterior, distinctly enlarged cirri of frontoventral rows 1-3.

4) Second and third cirrus of frontoventral row 3.

5) Cirri of frontoventral row 2, except of first, enlarged (frontal) cirrus.

6 Designation according to BERGER (1999). Values without transverse cirri (= posteriormost cirrus of each row – see text).

7) Posteriormost cirrus of frontoventral rows 6 and 5, and nearby positioned posteriormost cirrus of frontoventral rows 4 and often 3. In one of more than 2000 specimens (not included in the counts), there is an extraordinary fifth transverse cirrus of unknown origin. Whether or not this species possesses transverse cirri at all, and how many, depends on their definition, which is beyond the scope of the paper.

8) Usually four long kineties and two or three shorter dorsomarginal kineties.

* different values in VOSS' tables 1 and 3.

** values corrected according to personal information from VOSS.

\+ calculated from VOSS' table 1.

Table 2: Origin of fronto-ventral-transverse cirral anlagen and number of cirri produced in the anlagen of *Parentocirrus hortualis* (calculated from interphase specimens, see Table 1; VOSS' values taken from his table 3). Upper line – Austrian population, lower line – German population from VOSS (1997).

Anlage	Proter	Opisthe	Number of cirri produced in the anlagen [1,2)]							
			$\bar{x}$	M	SD	SE	CV	Min	Max	n
1	undulating	oral	1	1	0,0	0,0	0,0	1	1	22
	membranes	primordium	1	1	0,0	0,0	0,0	1	1	?
2	buccal cirri	oral	3,5	3	0,5	0,1	14,8	3	4	22
		primordium	-	-	-	-	-	3	5	?
3	posterior	oral	3,6	4	0,5	0,1	13,5	3	4	22
	frontal cirri [3,4)]	primordium [4)]	-	-	-	-	-	4	5	?
4	frontoventral	frontoventral	4,3	4	1,1	0,2	25,2	3	7	22
	row 4 [4)]	row 4 [4)]	-	-	-	-	-	5*	7*	?
5	frontoventral	frontoventral	14,7	14	2,0	0,4	13,4	11	21	22
	row 5 [5)]	row 5	-	-	-	-	-	17	25	?
6	frontoventral	frontoventral	17,8	18	2,4	0,5	13,4	13	22	22
	row 5	row 5	-	-	-	-	-	20	31	?

1) Data based on protargol-impregnated specimens as described in table 1. CV = coefficient of variation in %, M = median, Max = maximum. Min = minimum, n = number of individuals investigated, SD = standard deviation of mean, SE = standard error of arithmetic mean, $\bar{x}$ = arithmetic mean. For designation of anlagen and frontoventral rows, see text and figure 2.

2) Designation according to BERGER (1999).

3) Second and third cirrus of frontoventral row 3.

4) Values rough because there is sometimes a supernumerary anlage between the anlagen 2 and 5, causing that one anlage must be arbitrarily excluded.

5) After VOSS, proter anlage 5 is also generated by frontoventral row 4. In our population this is difficult to interpret.

* uncertain because values different in VOSS' tables 1 and 3.

Table 3: Number of cirral anlagen in 21 stage 5 to stage 7 dividers of the Austrian population of *Parentocirrus hortualis*.

Number of anlagen	Number of specimens
Proter	
5	1
6	18
7	2
Ophiste*	
6	16
7	3

* in three specimens one anlage (probably anlage 4) consists of only one cirrus.

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