J. Protozool., 28(3), 1981, pp. 291–297

A Comparative Study of the Infraciliature and Silverline System of the Fresh-Water Scuticociliates *Pseudocohnilembus putrinus* (Kahl, 1928) nov. comb., *P. pusillus* (Quennerstedt, 1869) nov. comb., and the Marine Form *P. marinus* Thompson, 1966[1]

WILHELM FOISSNER and NORBERT WILBERT

Zoologisches Institut der Universität Salzburg, Akademiestraße 26, A-5020 Salzburg, Austria and Zoologisches Institut der Universität Bonn, Poppelsdorfer Schloß, Bonn, West Germany

ABSTRACT. Three species of *Pseudocohnilembus* were examined with respect to infraciliature and the silverline system. The fresh-water species *P. putrinus* and *P. pusillus* exhibited no differences in general organization of the argyrophilic structures when compared with the marine *P. marinus*. A review of the *Pseudocohnilembus* species that have been described on the basis of silver preparations shows that at present four species have been well characterized: *P. pusillus* (Quennerstedt, 1869) nov. comb., *P. putrinus* (Kahl, 1928) nov. comb., *P. hargisi* Evans & Thompson, 1964, and *P. marinus* Thompson, 1966. *P. persalinus* Evans & Thompson, 1964 and *P. longiseta* Evans & Thompson, 1964 are regarded as identical with the older known *P. pusillus*, because with respect to morphology and argyrophilic structures they are within the range of variability of that species; and their names thus fall as synonyms of *P. pusillus*.

SCUTICOCILIATES of the genus *Pseudocohnilembus* are small organisms with a buccal cavity having two long membranes on the right side (5). Only during morphogenesis is the tetrahymenal organization of the buccal ciliature discernible (4). The only species of this genus in which the infraciliature and the silverline system have so far been studied are those of marine or salt-lake biotopes (1, 5, 23). In this paper we describe two fresh-water species, one of which, *Pseudocohnilembus pusillus* (Quennerstedt, 1869) nov. comb. (24) has been studied extensively in other regards (3, 10, 12–18). Despite its familiarity, its systematic position has remained unclear because the organization of the buccal ciliature has not been known in detail (5). The second, *Pseudocohnilembus putrinus* (Kahl, 1928) nov. comb. (14) was later treated as identical with *P. pusillus* by the same worker (see 14, 15). Our investigations, however, show that the infraciliature provides a basis for re-separating these two species.

Very little is known about the variability of the infraciliature and the silverline system of *Pseudocohnilembus*, for only one or two populations of each species have been studied. Therefore we present here a new description of *P. marinus* Thompson, 1966. In our opinion such supplementary descriptions, supported by precise drawings, are of great value; it is only by the accumulation of parallel observations that we can obtain a realistic picture of the variability within a species and thus of the number of species in a genus.

[1] The authors wish to express their thanks to the Austrian MaB-6 Program of UNESCO for financial support.

MATERIALS AND METHODS

Pseudocohnilembus putrinus was isolated from soil in the Hohe Tauern in the Austrian Central Alps (7). The ciliates were cultured by the method of Foissner (8). The species was most commonly found in the rhizosphere and was associated with many other ciliates listed elsewhere (7). It was observed extensively in vivo; for histological examination, specimens were impregnated with protargol (9), and a dry silvering method (6) was used to reveal the silverline system.

Pseudocohnilembus pusillus population I appeared in great numbers in a potato infusion to which liquid from a dungheap in Gaisbach/Wartberg (Upper Austria) had been added. The infraciliature and the silverline system were impregnated by a dry silvering method (6). Population II of this species was found in a heavily polluted tide-pool in Banyuls-sur-Mer. The infraciliature and the silverline system were impregnated by a wet silvering method (2).

Pseudocohnilembus marinus was found scattered in the upper littoral of Solar Lake (Sinai, about 20 km south of Elat), among dying blue-green algae (i.e., Cyanobacteria) and diatoms. The infraciliature and the silverline system were impregnated by a wet silvering method (2).

All statistical procedures follow methods described in either Simpson et al. (20) or Sokal & Rohlf (21).

RESULTS

Our observations of the morphology, the infraciliature and the silverline system of *Pseudocohnilembus* essentially agree with those of Evans & Thompson (5). Therefore in the following

TABLE I. *Morphometric light-microscopic characterization of* Pseudocohnilembus putrinus *(upper line) and* P. marinus *(lower line).*[a]

Character	$\bar{x}$	SE$\bar{x}$	CV[b]	Range	n
Size (μm)	21.4 × 9.8	0.43 × 0.26	10.8 × 14.4	17.0–27.0 × 6.6–14.6	29
	33.6 × 20.8	0.61 × 0.33	4.0 × 3.6	32.0–36.0 × 20.0–22.0	5
Number of kineties	10.0	0.0	0.0	0.0	29
	8.6	0.2	5.7	8–9	5
Number of basal bodies in a dorsal kinety[c]	15.6	0.15	5.2	14.0–17.0	29
	18.2	0.33	4.1	17.0–19.0	5
Distance from anterior to end of oral apparatus (μm)	10.5	0.15	7.8	8.0–12.0	29
	17.8	0.52	6.6	16.0–19.0	5
Size of the macronucleus (μm)	5.7 × 5.4	0.14 × 0.14	13.4 × 14.1	4.0–8.0 × 4.0–6.6	29
	10.7 × 9.2	0.08 × 0.30	1.6 × 7.2	10.5–11.0 × 9.3–10.0	5
Position of contractile vacuole pore	between 3rd and 4th kinety				29
	at 3rd ciliary meridian				5

[a] Data for *P. putrinus* based on protargol impregnated specimens. Those of *P. marinus* based on Chatton-Lwoff silvered specimens.
[b] Coefficient of variation.
[c] Basal body pairs were counted as one basal body.

descriptions only new or disparate observations will be mentioned, together with the characteristics diagnostic of the species. The biometric data presented in Tables I and II are not repeated in the textual descriptions of the species.

Pseudocohnilembus putrinus *(Kahl, 1928).* The living organisms have the form of a slender oval in ventral view and measure 25–35 × 10–16 μm. The tapered anterior end bears a conical frontal plate without cilia, set off somewhat from the remainder of the body. The posterior end of the body is usually rounded, though in some cases it is rather more pointed (Figs. 1b, 8). Viewed from the side, the ventral surface appears distinctly flattened in the region of the oral apparatus. The anterior one-fifth is bent somewhat dorsally, so that the dorsal outline has a slight sigmoid curvature (Fig. 1a). The macronucleus is spherical to slightly ellipsoid and lies at the level of the buccal entrance. The nucleoli are small, spherical, and regularly distributed. Closely apposed to the macronucleus is a spherical to slightly ellipsoidal micronucleus (Fig. 1d). The pellicle is smooth and very elastic; it is only slightly indented by the ciliary meridians. The cilia in the anterior three-quarters of the kineties are 5–6 μm long and are arranged in pairs. The cilia of the buccal membranes are about 4–5 μm long in the anterior region. A caudal cilium, about 17 μm in length, emerges from the center of the posterior pole of the body; the last third of it is bent, with its diameter reduced to a very fine projection (Figs. 1a, 1b, 8). The endoplasm is colorless, and in the anterior half of the body there are many tiny, highly refractile granules. The food vacuoles are 2–5 μm in diameter; usually they contain few bacteria, and in some cases they appear empty (Fig. 1a). Movement is very rapid and follows a broad spiral course. Sometimes the animal makes jumping movements, during which the cilia are splayed out (Fig. 1b).

The ciliary meridians are spirally arranged, especially on the dorsal surface (Figs. 1d, 1f, 4, 6). The posterior polar field, which lacks cilia, is about 5 μm in diameter (Fig. 7). Kinety 1 crosses the buccal membranes at the level of the buccal entrance; this is discernible only in protargol preparations and in vivo (Figs. 1c, 4).

The slightly depressed buccal field is bounded on the right by two membranes of equal length, both are bent to the left at the posterior end and have basal bodies that appear to be arranged in a zig-zag pattern. The membranes begin ca. 3 μm away from the anterior end of the body. The posterior one-fifth of the membranes extends into the narrow pharynx. At the posterior end of the buccal field there are always a few pairs of basal bodies in contact with the silverlines of the buccal field and with that of the cytopyge (Figs. 1a, 1b, 1c, 4, 5).

The silverline system has two components: the directly connecting silverline system, very similar in form to that of *P. persalinus* (see 5; and Figs. 1e, 1f, 5, 6), and the indirectly connecting silverline system, which is discernible only after dry silver impregnation and has not previously been described. Its nature is unknown. As in many other Scuticociliatida (26), it consists of approximately orthogonal meshes whose longitudi-

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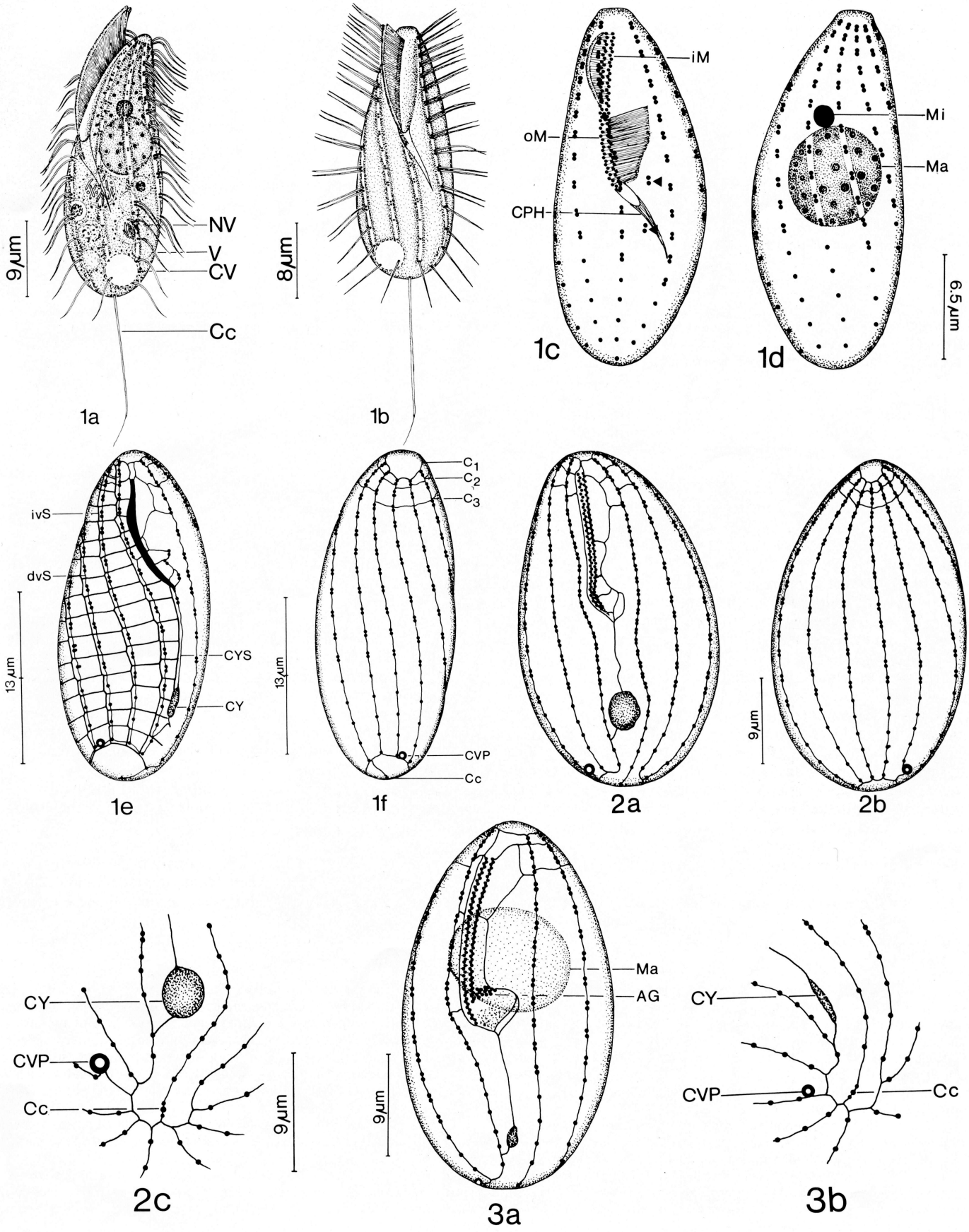
Fig. **1a–f.** Slightly schematized drawings of *Pseudocohnilembus putrinus*. **1a.** Left lateral view, from life. Cc, caudal cilium; CV, contractile vacuole; NV, food vacuole; V, vacuole without particulate content. **1b.** Ventral view, from life. **1c.** Infraciliature of the ventral side after protargol impregnation. The arrows indicate basal body pairs in the region of the buccal field. CPH, cytopharynx; iM, inner membrane of the oral apparatus; oM, outer membrane of the oral apparatus. **1d.** Infraciliature of the dorsal side after protargol impregnation. Ma, macronucleus; Mi, micronucleus. **1e.** Slightly right lateral view of a dry silvered individual. The indirectly connecting silverline system (ivS) is drawn in only on the side to the right of the oral apparatus. CY, cytopyge; CYS, cytopyge silverline; dvS, directly connecting silverline system. **1f.** Infraciliature and silverline system of the dorsal side after dry silver impregnation. C_1, C_2, C_3, intermeridional silverlines; Cc, basal body complex of the caudal cilium; CVP, contractile vacuole pore.

Fig. **2a–c.** Slightly schematized drawings of *Pseudocohnilembus pusillus*, from dry silvered individuals. **2a.** Infraciliature and silverline system of the ventral side. **2b.** Infraciliature and silverline system of the dorsal side. **2c.** Infraciliature and silverline system in the region of the posterior pole. Cc, basal body complex of the caudal cilium; CVP, contractile vacuole pore; CY, cytopyge.

Fig. **3a–b.** Slightly schematized drawings of *Pseudocohnilembus marinus*, from wet silvered individuals. **3a.** Infraciliature and silverline system of the ventral side. AG, argyrophilic granules at the posterior end of the inner membrane of the oral apparatus; Ma, macronucleus. **3b.** Infraciliature and silverline system in the region of the posterior pole. Drawn to same scale as 3a. Cc, basal body complex of the caudal cilium; CVP, contractile vacuole pore; CY, cytopyge.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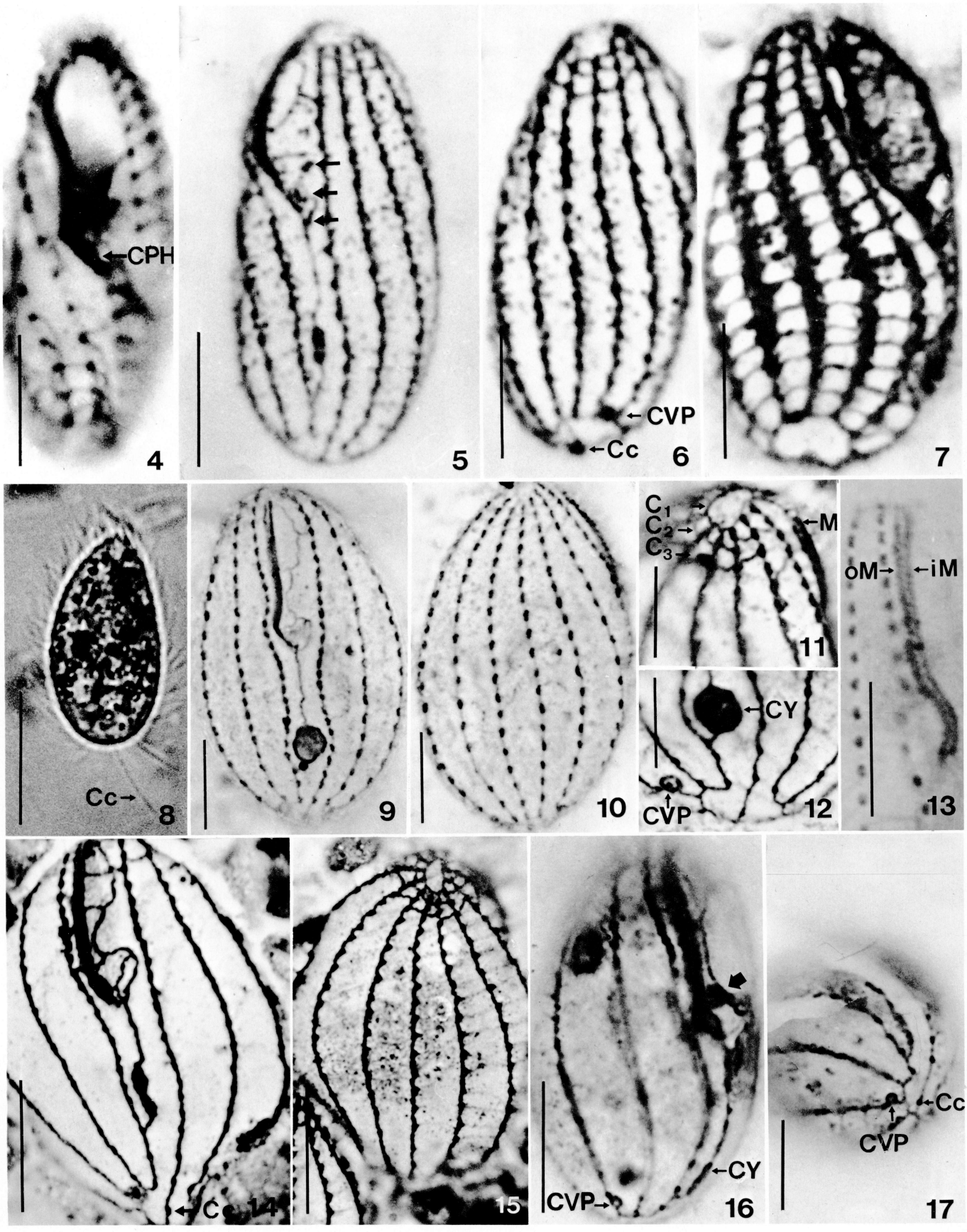
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TABLE II. *Morphometric light-microscopic characterization of* Pseudocohnilembus pusillus *population I (upper line) and* P. pusillus *population II (lower line).*[a]

Character	$\bar{x}$	SE$\bar{x}$	CV[b]	Range	n
Size (μm)	34.5 × 20.8	0.60 × 0.48	9.4 × 12.6	29.0–42.0 × 15.0–26.0	29
	31.3 × 15.4	0.57 × 0.42	9.8 × 14.7	25.0–39.0 × 12.0–20.0	29
Number of kineties	11.0	0.0	0.0	0.0	29
	10.0	0.0	0.0	0.0	29
Number of basal bodies in a dorsal kinety[c]	19.1	0.28	8.0	16.0–22.0	29
	17.8	0.38	11.5	15.0–23.0	29
Distance from anterior to end of oral apparatus (μm)	17.2	0.31	9.6	15.0–22.0	29
	15.7	0.24	8.3	13.0–18.0	29
Size of the macronucleus (μm)[d]	6.5 × 6.1	0.14 × 0.13	11.2 × 8.0	5.0–7.8 × 5.1–8.1	29
	6.9 × 6.3	0.13 × 0.12	10.0 × 9.8	5.4–8.0 × 5.0–8.0	29
Position of contractile vacuole pore	at 3rd ciliary meridian				29
	at 4th ciliary meridian				29

[a] Data for population I based on dry silvered specimens. Those of population II based on Chatton-Lwoff silvered specimens.
[b] Coefficient of variation.
[c] Basal body pairs were counted as one basal body.
[d] Based in population I on haematoxylin stained specimens.

nal strands run closely by the directly connecting silverlines of the ciliary meridians (Figs. 1e, 7). It is absent from the nonciliated polar fields and from the buccal cavity.

Pseudocohnilembus pusillus *(Quennerstedt, 1869).* The two populations we studied were very similar. In its appearance in vivo, this species corresponded to the descriptions of Quennerstedt (24), Hoare (12), and Kahl (15). The infraciliature and especially the pattern of the silverline system departed only very slightly from those of *P. persalinus* as described by Evans & Thompson (5); it is highly likely that the latter species is but a local modification of *P. pusillus* (see Discussion). Thus we refer the reader to the extensive treatment of the argyrophilic structures of *P. pusillus* given by Evans & Thompson (5) and to Figs. 2a–c and 9–15. The few discrepancies are noted in the Discussion.

Pseudocohnilembus marinus *Thompson, 1966.* The population we studied corresponded in the essential characteristics to that described by Thompson (23). A characteristic of the species is the small, horizontally oriented group of argyrophilic granules (basal bodies?) at the posterior end of the abbreviated inner membrane, which appears L-shaped as a result (Figs. 3a, 16). According to Thompson, *P. marinus* has 10 ciliary meridians that run in a slight spiral. The contractile vacuole pore is near the posterior end of kinety 4; the silverline that passes dorsally from the caudal cilium joins the posterior silverline ring between kineties 5 and 6. By contrast, our population has only 8–9 kineties, and the contractile vacuole pore is near the posterior end of kinety 3.[2] The silverline running dorsally from the caudal cilium joins the posterior silverline ring between kineties 4 and 5 (Figs. 3b, 17). Such differences between the two populations are evidently brought about by the larger number of ciliary meridians in the population first described (23). Additional deviant characteristics are the size of the macronucleus, which is about twice as large in our strain, and the size of the body (Table I). The shape of our animals is a broad oval: that of Thompson's, a slender oval. The caudal cilium is ca. 18 μm long.

The silverline pattern in the region of the apical pole, not shown by Thompson (23), is typical of the genus (Fig. 3a). In the region of the buccal field the silverline system departs from the pattern drawn by Thompson in a few small details which are shown in Fig. 3a. There is a silverline running close to the left side of the outer membrane of the oral apparatus that is connected by short silverlines with ciliary meridian 1 and the anterior silverline ring. And the second (posterior) horizontally

[2] In the population studied by Borror (1), the contractile vacuole pore lies on meridians 1–2.

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Figs. **4–8**. *Pseudocohnilembus putrinus*. **4**. Infraciliature of the ventral side after protargol impregnation. CPH, cytopharynx. Scale bar, 7.5 μm. **5**. Infraciliature and silverline system of the ventral side after dry silver impregnation. The arrows indicate basal body pairs in the region of the buccal field. Scale, 8 μm. **6**. Infraciliature and silverline system of the dorsal side after dry silver impregnation. Cc, basal body complex of the caudal cilium; CVP, contractile vacuole pore. Scale, 8 μm. **7**. Right lateral aspect of an individual in which the indirectly connecting silverline system is impregnated. Dry silver impregnation. Scale, 8 μm. **8**. Photograph of a living, slightly compressed individual. Cc, caudal cilium. Scale, 18 μm.

Figs. **9–15**. *Pseudocohnilembus pusillus*, infraciliature and silverline system after dry and wet (Fig. 13) silver impregnation. **9**. Ventral view. Scale, 9 μm. **10**. Dorsal view. Scale, 9 μm. **11**. Right lateral view of the anterior region of the body. C_1, C_2, C_3, intermeridional silverlines; M, inner and outer membrane of the oral apparatus. Scale, 4.5 μm. **12**. Ventral view of the posterior pole. CVP, contractile vacuole pore; CY, cytopyge. Scale, 4.5 μm. **13**. Right lateral view of the oral apparatus from a specimen of population II. iM, inner membrane of the oral apparatus; oM, outer membrane of the oral apparatus. Scale, 8 μm. **14**. Ventral view. Cc, basal body complex of the caudal cilium. Scale, 13 μm. **15**. Dorsal view. Scale, 12 μm.

Figs. **16–17**. *Pseudocohnilembus marinus*, infraciliature and silverline system after wet silver impregnation. **16**. Right lateral view. The arrow indicates the aggregation of argyrophilic granules at the posterior end of the inner membrane of the oral apparatus. CVP, contractile vacuole pore; CY, cytopyge. Scale, 12 μm. **17**. View of the posterior pole. Cc, basal body complex of the caudal cilium; CVP, contractile vacuole pore. Scale, 5.5 μm.

oriented silverline of the buccal field is nearer to the anterior end of the animal.

DISCUSSION

Pseudocohnilembus putrinus was described very superficially by Kahl (14). According to him, characteristics of this species, which he found in a plant infusion with fresh water, include a pointed posterior end of the body and a distinctly spiral arrangement of the ciliary meridians. Our identification was based on the spiral arrangement of the kineties and the biotope. The posterior end of the body was rarely as sharply pointed as Kahl (14) drew it. The ciliary meridians of *P. hargisi* Evans & Thompson, 1964 are also spirally arranged. Moreover, this species resembles *P. putrinus* in that the posterior, ciliafree polar field is notably large in comparison with the size of the body and the silverlines in the posterior part of the buccal field are not as curved as in *P. pusillus* (Figs. 1e, 2a). But it is very probable that these two species are not identical, for *P. hargisi* has 14 ciliary meridians and 1–3 (usually 2) contractile vacuole pores (1, 5).

Pseudocohnilembus pusillus differs from *P. putrinus* in the meridional course of the ciliary meridians, the position of the contractile vacuole pore, and the absence of scattered basal bodies in the region of the buccal field. On the other hand, it exhibits no significant differences from *P. persalinus* Evans & Thompson, 1964; the slight differences in size, body shape and infraciliature are not, in our opinion, sufficient to establish the two as separate species. The size and body shape of *P. pusillus* are strongly variable (12, 13, 17). In comparing our drawings with those of Evans & Thompson (5) it should be noted that our animals were prepared by a dry silvering method in which the shape of the body is not as well preserved as in the wet method used by Evans & Thompson. In particular, the anterior taper expanded considerably during dehydration. The body shape of the Chatton-Lwoff stained specimens of *P. pusillus* population II was very similar to that described and figured by Evans & Thompson for *P. persalinus*. When the salinity of the medium in which *P. persalinus* is cultured is reduced, individuals with 11–12 ciliary meridians appear (5)—a number that agrees well with our count in *P. pusillus* (Table II).

Further points of agreement are the position of the contractile vacuole pore and the arrangement of the silverlines in the buccal field. Note, however, that in the rather highly diagrammatic drawing of Evans & Thompson (5), the representation of the silverline pattern in the buccal field is only approximately correct if one takes the published photograph (Fig. 3 in Ref. 5) as a reference. The inner membrane of the oral apparatus of *P. persalinus* is somewhat shorter than the outer membrane (5), a feature that we did not observe in our dry-silvered specimens (Figs. 9, 13). This detail is discernible only in protargol preparations (5). In *P. persalinus* the silverline originating at the caudal cilium encounters ciliary meridian 4 (5); in *P. pusillus* it joins the posterior silverline ring between the ciliary meridians 6 and 7. This difference is presumably due to the difference in the total number of meridians. Evans & Thompson (5), unfortunately, made no explicit comparison of species-distinguishing characteristics of *P. persalinus* and *P. pusillus*.

On the basis of our findings, and in view of the current state of knowledge of the genus *Pseudocohnilembus*, *P. persalinus* must be regarded as identical with *P. pusillus*, with names thus synonymous. The slight differences listed above do not justify separation of the two. If one were to take these differences as diagnostic features at the species level, then the forms of *P. marinus* Thompson, 1966 and *P. hargisi* Evans & Thompson, 1964, redescribed by Borror (1), as well as our *P. marinus*, would have to be ranked as new species, because these also differ somewhat from the original descriptions (Table I). In these cases, however, it is evident that they are only local variants. We also believe that the form described by Evans & Thompson (5) and redescribed by Thompson (22) as *P. longisetus* is only a local variant of *P. pusillus*. *Cyclidium sapropellicum* Vuxanovici, 1962 is also very likely identical with *P. pusillus*. This view is supported by the size, the body shape, and the triangular membrane of the mouth of this species, which are very similar to those known in *P. pusillus*.

On the basis of our findings and the list of synonyms given by Kahl (15), with which we agree, the following names of species must be regarded as junior synonyms of *P. pusillus* (Quennerstedt, 1869) (24): *Uronema marina* Möbius, 1888 (18), *Lembadion ovale* Gourret & Roeser, 1886 (10), *Lembus moebii* Kahl, 1926 (13), *Cyclidium sapropellicum* Vuxanovici, 1962 (25), *Pseudocohnilembus persalinus* Evans & Thompson, 1964 (5), and *Pseudocohnilembus longisetus* Evans & Thompson, 1964 (5). Thus the genus currently contains four clearly distinguishable species: *P. pusillus* (Quennerstedt, 1869) nov. comb., *P. putrinus* (Kahl, 1928) nov. comb., *P. hargisi* Evans & Thompson, 1964, and *P. marinus* Thompson, 1966. The type species is *P. pusillus*, as designated by Evans & Thompson under the name *P. persalinus* (5).

Borror (1) proposed withdrawing Evans & Thompson's (5) name *Pseudocohnilembus* in favor of Kahl's (15) earlier *Paralembus*. This suggestion was evidently based on a misinterpretation of Kahl's (15) report, which expressly pointed out that the second membrane, present in *Lembus* (=*Pseudocohnilembus*), is lacking in *Paralembus*. Moreover, the buccal infraciliature of the two genera is very different (11, 19); and *Paralembus* has strongly developed adoral membranelles that are lacking in *Pseudocohnilembus* (11).

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Received 2 X 80; accepted 27 II 81