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Revision of the Genus *Askenasia* Blochmann, 1895, with Proposal of Two New Species, and Description of *Rhabdoaskenasia minima* N. G., N. Sp. (Ciliophora, Cyclotrichida)

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ABSTRACT. The planktonic ciliate genus *Askenasia* Blochmann, 1895 is reviewed and the new genus *Rhabdoaskenasia* n. gen. is established. *Askenasia* is characterized by three circumferential kinety belts and a circumoral wreath of paired argyrophilic granules without recognizable cilia and nematodesmata. A "brush" is absent. *Askenasia* apparently lacks the key characters of the Haptorida and is thus transferred to the Cyclotrichida, family Mesodiniidae. *Rhabdoaskenasia* differs from *Askenasia* in having single files of basal bodies in all kinety belts and club-shaped extrusomes. It possesses a circumoral kinety composed of dikinetids from which nematodesmata originate, forming a distinct rhabdos. Although very similar to *Askenasia* in its general appearance, *R. minima* n. sp. could belong to another order. Based on an extensive review of the literature and on silver impregnated specimens the following *Askenasia* species are recognized and described in detail: *A. volvox* (Eichwald, 1852) Kahl, 1930, *A. stellaris* (Leegaard, 1920) Kahl, 1930, *A. acrostomia* n. sp., and *A. chlorelligera* n. sp. *Askenasia faurei* Kahl, 1930 and *A. humilis* Gajewskaja, 1928 are transferred to the genus *Cyclotrichium*: *C. faurei* (Kahl, 1930) n. comb., *C. humilis* (Gajewskaja, 1928) n. comb. The systematic position of the genus *Askenasia* is discussed and keys to the genera of the Mesodiniidae and to the species of *Askenasia* are provided.

Key words. *Askenasia, Cyclotrichium,* ecology, infraciliature, revision, *Rhabdoaskenasia* n. g., systematics.

HITHERTO few species (two valid, two of uncertain affinity) of the planktonic genus *Askenasia* have been described [16, 19, 27, 37]. This is, however, not surprising because pelagic ciliates are generally poorly explored. The outstanding study of Fauré-Fremiet [19] is still the most comprehensive treatment.

So far, *Askenasia* has never been investigated with silver impregnation techniques, and the species were simply separated by body size and shape. However, the rather detailed observations of Penard [41] and Tamar [44] should be mentioned.

In this paper, the descriptions of all nominal *Askenasia* species are reviewed and three new species, including a new genus, are established using live observation and silver impregnation techniques. In addition, keys to the genera of the family Mesodiniidae Jankowski, 1980, and to the species of *Askenasia* are provided.

MATERIALS AND METHODS

Askenasia volvox, A. acrostomia, A. chlorelligera, and *Rhabdoaskenasia minima* were collected from the plankton of two excavated groundwater ponds (each about 0.08 km^2) eutrophified by drainage from agricultural areas ([17] Dr. Hans Sampl, report of Styrian provincial government; 15° 5′ 5E, 47° N). All species were examined in vivo and in protargol impregnated slides [21]. Note that this staining method generally causes shrinkage of the cells of about 20–30%. The silverline system was studied in specimens of an undetermined species impregnated by a "dry" silver nitrate technique [20]. All measurements were performed at a magnification of 1,200×. Statistical procedures follow methods described in Sokal & Rohlf [42]. The drawings of the impregnated specimens were made with the help of a camera lucida. Where possible, the type individual was used for preparing the figures; otherwise, composite drawings were made.

Prior to estimating the number of individuals, subsamples were fixed in $HgCl_2$ and subsequently stained with about 10 drops of a solution of 0.04% bromophenol blue and sedimented overnight [4]. Counts were performed on slides at a magnification of 100×. Abundance is expressed as cells per liter. The standing crop, expressed as mg per m^3, was calculated by using the estimated cell volume of protargol impregnated specimens (reducing the complicated shape to a simple geometric figure and assuming a specific-gravity of 1.0; a method widely used by hydrobiologists), multiplied by the abundance. Although this is a rough method, the values give some figure of the biomass.

Holotype and paratype slides (protargol impregnated) of the four new species have been deposited in the collection of microscope slides of the Oberösterreichischen Landesmuseums in Linz, Austria. Accession numbers: 76/1989–83/1989.

RESULTS

Nomenclature. The genus name, *Askenasia,* is a junior synonym established by Blochmann [7]. It has to be retained in accordance with the IRZN, article 23, because the senior name, *Stephanidina,* is considered as *nomen oblitum* [23].

There is much confusion concerning the synonymy and nomenclature of the type species, *A. volvox.* It was originally described by Eichwald [16] as *Trichodina volvox.* Furthermore, he proposed to establish *Stephanidina* as a new genus for this species. *Trichodina volvox* was then transferred to the genus *Halteria* [13]. At the end of the 19th century Blochmann [7] published *A. elegans* as a new genus and species, unfortunately overlooking the valid original description as well as the redescription [13]. His name is thus a synonym. Kahl [33] recognized the synonymy of *Halteria volvox* and *A. elegans* and consequently designated Blochmann's species as *A. volvox* (Claparède & Lachmann, 1859), but also disregarded the original description; hence listing the wrong author and date. Finally, Dingfelder [15] 1st mentioned the original description by Eichwald, but incorrectly stated "Blochmann, 1895" as the 1st revising author. However, Kahl is the 1st revisor and the correct citation of the taxon must be "*Askenasia volvox* (Eichwald, 1852) Kahl, 1930" [23].

General morphology and ecology of *Askenasia* (Fig. 1-4). The size ranges from 27–60 μm in length and from 22–65 μm in width, with length and width usually approximately equal. The body has an ovoid to diamond-shaped outline and can be divided into an anterior cone-shaped "rostrum" and a posterior hemispherical portion, both circular in transverse section. The cell equator represents the transition between the anterior and the posterior portion, which does not always correspond to the geometrical median plane of the cell. The shape of the rostrum varies from sharply truncated through arched to tapered. The posterior portion is broadly rounded to bluntly pointed.

A single globular to rope-like macronucleus is situated in the posterior portion or just below the cell equator. Occasionally, specimens (presumably postconjugates) were found with up to 10 globular segments. Except in *A. stellaris,* which possesses two macronuclear segments and two micronuclei, a single spherical micronucleus is attached to the macronucleus in variable position.

One, two or four contractile vacuoles discharge by conspicuous excretory pores subequatorially. The vacuole is either a simple blister or is surrounded by collecting vesicles during diastole. Multiple vacuoles are diametrically opposed and function alternately. No data are known on the cytoproct. Three species have an enigmatic crescent-shaped vacuole on the rear (we suggest the term "terminal vacuole") which is hyaline and often disappears in vivo. Protargol slides show that it adheres to the posteriormost transverse bristle row. The bristles are bent posteriad forming a basket-shaped structure which encloses the vacuole (Fig. 1; TV). Whether the vacuole contains an air-bubble or some sort of liquid is not known. Nonetheless, we suggest that it has a special function in the planktonic mode of life, possibly increasing buoyancy. *Mesodinium pulex* Claparède & Lachmann, 1858, was observed to also have such a terminal vacuole [8].

The pellicle is ribbed (seen only in optical transverse section, with the cilia extending between the ribs) and fragile. Coverslip pressure usually causes immediate lysis. Extrusomes occur in several approximately pin-like types which are packed in bundles surrounding the cytopharynx, but often a few are scattered throughout the cytoplasm. Shape and arrangement of the extrusomes represent important species characters. *Askenasia* species feed on algae and other protozoa [15, 44]. Ingestion and defecation have, however, not been observed.

Locomotion is a highly characteristic feature in the genus (Fig. 2, 3). The "pectinelles" of the pre-equatorial kinety belt (PKB) beat in a rotating ring consisting of 5–16 flame-like tufts, impressively visible during the immobile period (Fig. 3). They draw food particles toward the cytostome, while the cell rotates leisurely around the transverse axis [44]. The lightning darts and short, spiralling jumps, which alternate with abrupt stops, are caused mainly by the bell-shaped skirt, formed from the "cirri" of the equatorial kinety belt (EKB), pushing the water backwards. It is also evident that the cirral-skirt, when immobile, keeps the cell afloat. The bristles of the subequatorial kinety belt (SKB) act as stabilizers during floating but may also play a role in forward movement by contracting [41, 44].

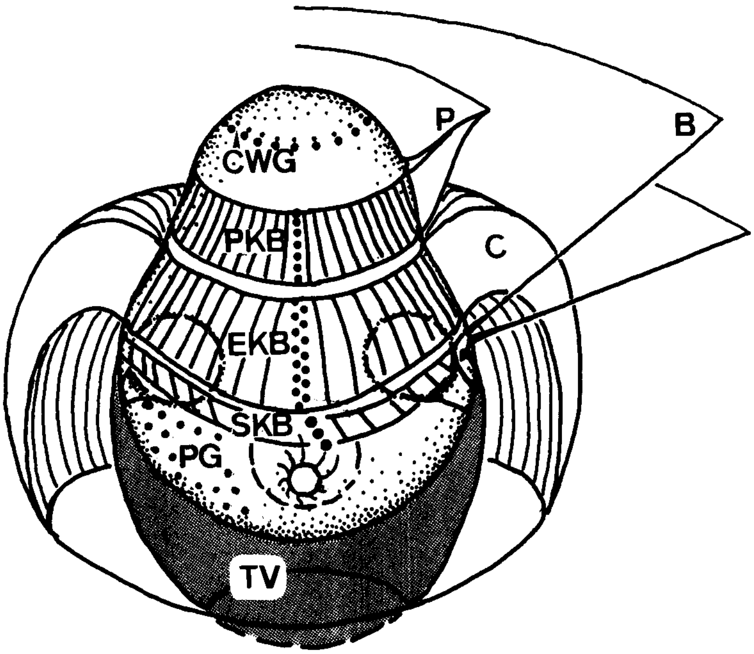
Three belts, of differently arrayed cilia, mantle the anterior portion (Fig. 1, 2). Each belt is composed of (47–)60–70 roughly longitudinal kineties and separated from its neighbor by a small gap. The 8–15 μm long pectinelles (P) originate from the pre-equatorial kinety belt (PKB), whose kineties are composed of single files of basal bodies and are interconnected by transverse fibers. The equatorial kinety belt (EKB) bears the rigid, sickle-shaped, about 20–30 μm long "cirri," which form a skirt around the posterior half of the cell. Each cirrus is composed of a double row of basal bodies arranged in zigzags and interconnected by an argyrophilic fiber. The subequatorial kinety belt (SKB) contains 20–60 μm long, flexible bristles. Each kinety is obliquely oriented to the longitudinal cell axis and comprises of three basal bodies, usually interconnected by transverse fibers. The posterior portion shows oblique single files of non-ciliated granules (PG, smaller than basal bodies) which usually lie in the center of weakly impregnated square structures, producing a more or less regular lattice. However, *A. chlorelligera* differs noticeably in the absence of these linear files and in possessing a network of polygons resembling honeycombs and enclosing single or paired granules. This network corresponds closely to the silverline system (cp. Fig. 4 with Fig. 50).

The cytostome-cytopharyngeal complex is located in the long axis of the cell and is usually equipped with conspicuous extrusomes. The cytostome, lying somewhat depressed in the center of the anterior pole (oral area), is round to slit-like [44]. The oral area is encircled by a remarkable "circumoral wreath of unciliated, paired granules" (CWG), which has a circular or more or less cloverleaf-shape. Each pair usually comprises of a larger posterior and a smaller anterior granule. Both are slightly inclined to the cell's long axis and are of equal size in *A. chlorelligera.* To date we are unable to decide whether the granules are basal bodies or mucocysts or something else, and whether the smaller satellites are parasomal sacs or not. Accordingly, we prefer the term "circumoral wreath" to "circumoral kinety." The granule pairs are usually associated with weakly impregnating fibers (longitudinal fibers, LF), which course posteriorly to the pre-equatorial kinety belt (PKB) and anteriorly to the cytostome (transverse fibers, TF; Fig. 2). The CWG is an important diagnostic feature at species level. There is now strong evidence (cp. *A. volvox*) that the apical star-like figure in *A. stellaris,* which Kahl assumes to be pharyngeal wrinkles, is also a CWG (Fig. 27, 30).

The silverline system is widely meshed, both in the posterior portion and in the oral area, whereas the middle cell area shows circumferential bands of rectangles, and, subjacently, honeycombed structures (Fig. 4).

Bipartition by transverse fission (homothetogenic fission, [44]) has not yet been studied in detail. It begins in the equatorial kinety belt with a constriction [41]. The related genus *Mesodinium* shows no constriction during bipartition [45]. The macronucleus appears dumbbell-shaped in the late fission stages (Fig. 13). The proter reorganizes the equatorial kinety belt, the opisthe the pre-equatorial kinety belt, while the reorganization of the bristles has not yet been observed. The pectinelles are active before the dividers separate. Conjugation occurs by fusion at the anterior end (Fig. 14). During conjugation the pectinelles do not cease beating (Fig. 16). The fragmented macronuclear material is present in the anterior portions of the conjugants [41, 44]. The resting cyst is known only for *A. volvox* [41]; it consists of two shell-like parts which are equipped with spines (Fig. 10).

Despite extensive biogeographic data, little information on the ecol-



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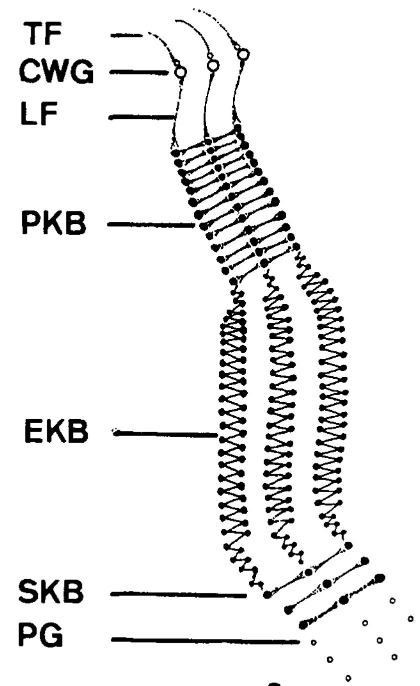

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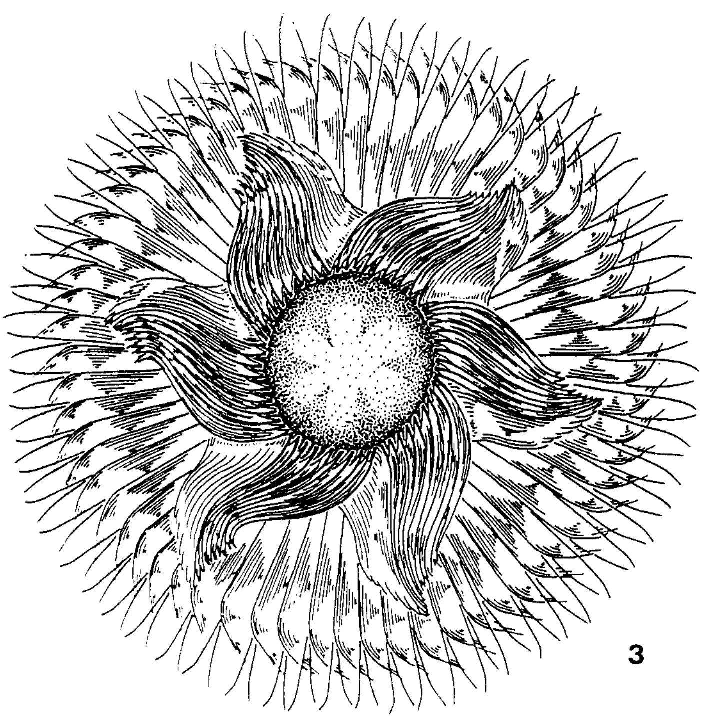

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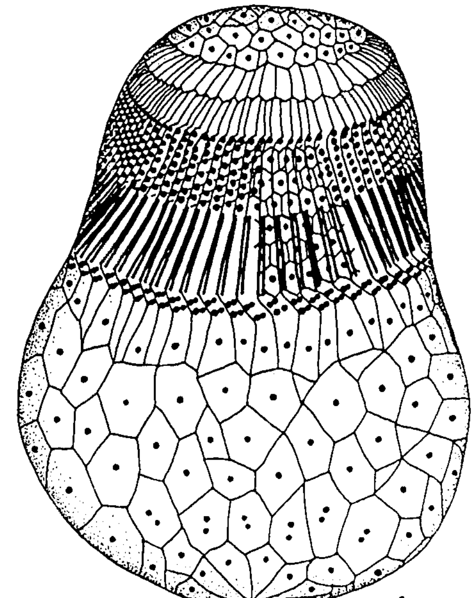

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Fig. 1-4. Schematic figures of *Askenasia* illustrating diagnostic features. **1**. Side view. **2**. Three somatic kineties showing arrangement of basal bodies and fibers usually recognizable in protargol impregnated specimens. **3**. Motion study of pectinelles as seen from anterior pole, showing characteristic flame-like tufts formed by the PKB. **4**. Silverline system of *Askenasia* sp. after dry silver nitrate impregnation. Abbreviations. B, bristles; C, "cirri"; CWG, circumoral wreath of granules; EKB, equatorial kinety belt; LF, longitudinal fibers; P, "pectinelles"; PG, posterior granules; PKB, pre-equatorial kinety belt; SKB, subequatorial kinety belt; TF, transverse fibers; TV, terminal vacuole.

ogy is available. *Askenasia* inhabits limnetic as well as marine ecosystems, preferentially the plankton. It was recorded from many localities in the holarctic region (see *A. volvox*), but is still not documented from the southern hemisphere. In freshwater ecosystems *Askenasia* is usually found in less polluted habitats, achieving highest densities in spring and fall when algae are abundant [33, 39, unpubl. observ.]. Therefore we conclude that *Askenasia* is euplanktonic and generally prefers oligo- to mesotrophic conditions. Further ecological investigations on *Askenasia* promise to be worthwhile.

Taxonomic changes. *Askenasia* comprises four valid species in our opinion. Two other nominal species, *A. faurei* and *A. humilis,* ought to be transferred to *Cyclotrichium.*

Cyclotrichium faurei (Kahl, 1930) nov. comb. was 1st described as *Askenasia elegans* [19]. Kahl [33] later classified it, in agreement with Fauré-Fremiet, as a new species, *A. faurei. Askenasia faurei,* however, lacks bristles, has a ciliated posterior portion and a single contractile vacuole with collecting canals in the rear (Fig. 21). These characters are typical for *Cyclotrichium* [19, 33, 48]. *Cyclotrichium faurei,* however, requires redescription based on silver impregnation. It is a rare species reported only twice since the original description [5, 11].

Cyclotrichium humilis (Gajewskaja, 1928) nov. comb. is a bizarre-shaped species, which has, like *C. faurei,* two kinety belts and fringe-like cilia associated with the equatorial kinety belt (Fig. 22). It also requires redescription, and has not been recorded since the original description.

The type species of *Cyclotrichium* has only a single anterior kinety belt [33]. Therefore *C. faurei* and *C. humilis,* each with two kinety belts, may be transferred to a new genus in the future.

Improved diagnosis of *Askenasia.* Mesodiniidae with: (i) one circumoral wreath of argyrophilic granules; (ii) three circumferential, equatorial kinety belts (kineties of pre-equatorial belt composed of single files of basal bodies, kineties of equatorial belt composed of double rows of basal bodies arranged in a zigzag, kineties of subequatorial belt composed of three basal bodies each); and (iii) more or less needle or pin-shaped extrusomes, usually surrounding cytopharynx. Free-living, carnivorous and algivorous, freshwater and marine.

Type species. *Askenasia volvox* (Eichwald, 1852) Kahl, 1930.

Key to and Description of Species of *Askenasia*

1 Two or more contractile vacuoles 2
– Single contractile vacuole 3
2 Two contractile vacuoles with collecting vesicles, diametrically opposed. Two sausage-shaped macronuclear segments. Rostrum sharply truncated. Extrusomes rod-shaped, arranged in two whorls of six bundles each. CWG ("pharyngeal wrinkles") cloverleaf-shaped with 6–8 lobes. Marine .... *Askenasia stellaris*
– Four contractile vacuoles. Single horseshoe-shaped macronucleus. Rostrum tapered. Extrusomes needle-like with pointed ends, at least ⅔ of cell length long. CWG circular. Freshwater .... *A. acrostomia*
3 With symbiotic green algae. Macronucleus spheroidal to ellipsoid. Rostrum truncated, apically crown-like by protruding extrusome bundles. Extrusomes in two pin-shaped types. Cell shape not pyriform. CWG approximately pentagonal .... *A. chlorelligera*
– Without symbiotic green algae, but often containing ingested algae, giving cell brownish-green to dark green color. Macronucleus globular or C-shaped. Rostrum arched. Extrusomes needle- or rod-shaped. Cell shape roughly pyriform. CWG cloverleaf-shaped with 6–12 lobes. Freshwater .... *A. volvox*

Askenasia volvox (Eichwald, 1852) Kahl, 1930

Synonyms. *Trichodina volvox* Eichwald, 1852; *Halteria volvox* Claparède & Lachmann, 1858; *Askenasia elegans* Blochmann, 1895.

Surprisingly, we did not find a form which corresponds exactly to any of the available descriptions of *A. volvox.* We observed, however, a rather similar species which differs only by the more C-shaped macronucleus and the conspicuous excretory canal. Initially, we decided that it should be described as a new species; however, this view was discouraged by one of the reviewers. Thus, we withdraw our decision but separate the descriptions. Future research will decide whether this was wise or not.

Description according to data from literature (Fig. 5-20). Size in vivo 29–42(–50) × 22–27(–50) µm [7, 33, 41, 44]. Shape ovoid to pyriform. Macronucleus globular to ellipsoid (12–14.5 × 9.5–11.5 µm; [44]), contains small chromatin globules. Micronucleus 3–4 µm in diameter, very pale. Single contractile vacuole with collecting vesicles [44]. Terminal vacuole present, misinterpreted by Penard [41] as artifact of coverslip pressure (Fig. 12). Pellicle fairly fragile, flexible [44]. About 10 thin, needle-shaped, conically bundled extrusomes ("trichites"), approximately 10–12 µm in length [41, 44]. Cytoplasm hyaline to vesicular, contains globules and tiny granules (Fig. 18). In addition, spheres 2–3 µm in diameter, dark oval particles, irregular masses as well as yellow and greenish yellow inclusions (presumably *Bodo*-remnants) are recognizable [44]. Five to 12 pectinellar tufts ([33, 41, 44] Fig. 9, 15, 19, 20). Each kinety belt composed of about 60 kineties [7, 34, 41]; according to Tamar [44] only 47–48. Pre-equatorial belt kineties composed of about 10 basal bodies each, their cilia about 8–13 µm long [33, 44]. Cirri composed of two adjacent rows of 14–17 basal bodies each, cilia approximately 20 µm long. Bristles 30–40 µm in length [33, 44].

Occurrence and ecology. *Askenasia volvox* is widespread in limnetic habitats, predominantly in the plankton of lakes [1, 6, 15, 31, 36, 39, 40, 43, 46, 47], but has also been recorded from benthic habitats [2, 3, 12, 18, 28]. Data on abundances are rare. Hunt & Chein [31] found 126 cells of an undetermined *Askenasia*-species per liter of surface water in the oligotrophic Cayuga Lake (New York). In the mesotrophic Lake Erken (Sweden) highest densities were observed in June (about 2,800 cells per liter, but the number was grouped with *Halteria grandinella* [39]). *Askenasia volvox* is considered to be a beta-mesosaprobic indicator species [24]. However, it has also been recorded from ponds with beet-wastes of a sugar factory [29].

Description of an Austrian population (Fig. 35-38, 56-58; Table 1). Size in vivo 35–45 × 30–45 µm. Outline plump-pyriform. Diameter, including cirri, about 60 µm. Macronucleus C-shaped, usually with pointed ends. Chromatin bodies of various size (Fig. 35, 56). Some specimens with 2–5 spherical fragments. Single contractile vacuole with conspicuous excretory canal 4–6 µm in length, at canal base about 3 µm, at canal pore about 2 µm in diameter (Fig. 35). Extrusomes 15–22 µm long (varying length by virtue of extruded extrusomes?), thickened proximally, arranged around cytopharynx, imitating CWG-pattern (Fig. 35). Cytoplasm contains algae and cytopharyngeal baskets of ingested ciliates (presumably *Urotricha* spp.; Fig. 35).

Basal bodies of PKB-kineties ellipsoid, presumably because of impregnated bases of transverse fibers (Fig. 36, 37, 57). The EKB-kineties slightly sigmoid, about one kinety-width apart, basal bodies densely spaced (Fig. 36, 37, 57). The SKB-kineties almost rectangularly bent, each anteriormost basal body markedly smaller; no transverse fibers recognizable (Fig. 36, 37, 57). Granule pairs of CWG form 6–12 arch-shaped lobes, resembling a compounded three- or four-leaf clover (Fig. 38, 58). Transverse and longitudinal fibers form an elaborate pattern of inverted V's, their tips pointing toward cytostome (Fig. 38).

Occurrence and ecology. Although never abundant, the Austrian population is found during all seasons. The highest numbers were found in May 1986 (278 cells per liter; 4.3 mg/m^3) and in October 1986 (170 cells per liter; 2.9 mg/m^3); the lowest numbers in July 1986 and February and March 1987. High numbers were also observed in December 1986 (158 cells per liter; 2.7 mg/m^3) and in January 1987 (150 cells per liter; 2.6 mg/m^3) under a closed ice-sheet.

Askenasia stellaris (Leegaard, 1920) Kahl, 1930

Synonyms. *Lohmanniella stellaris* Leegaard, 1920.

Description (Fig. 23-34). Size in vivo 24–50 × 29–65 µm [8, 34, 37]. Lentil-shaped to somewhat flattened globular (Fig. 23, 29, 31, 32). Rostrum sharply truncated, posterior portion dish-shaped to bluntly pointed (Fig. 31, 32). Oral area shows star-like figure with 6–8 lobes encircling cytostome, very likely a CWG (Fig. 27, 30, 34). Two sausage to worm-shaped macronuclear segments, eccentrically located in cell equator (Fig. 26, 29, 33), each part enclosed in special membrane ([8] Fig. 26), size of each part approximately 17 × 7 µm [8]. Two micronuclei, about 4 µm in diameter each, closely attached to inner concave portion of macronuclear segments (Fig. 33). Two contractile vacuoles with collecting vesicles located equidistantly from macronuclei (Fig. 29, 33). Extrusomes ("trichites") rod-shaped, about 20 µm in length, arranged in two whorls of six bundles with 12–20 extrusomes each, pro-

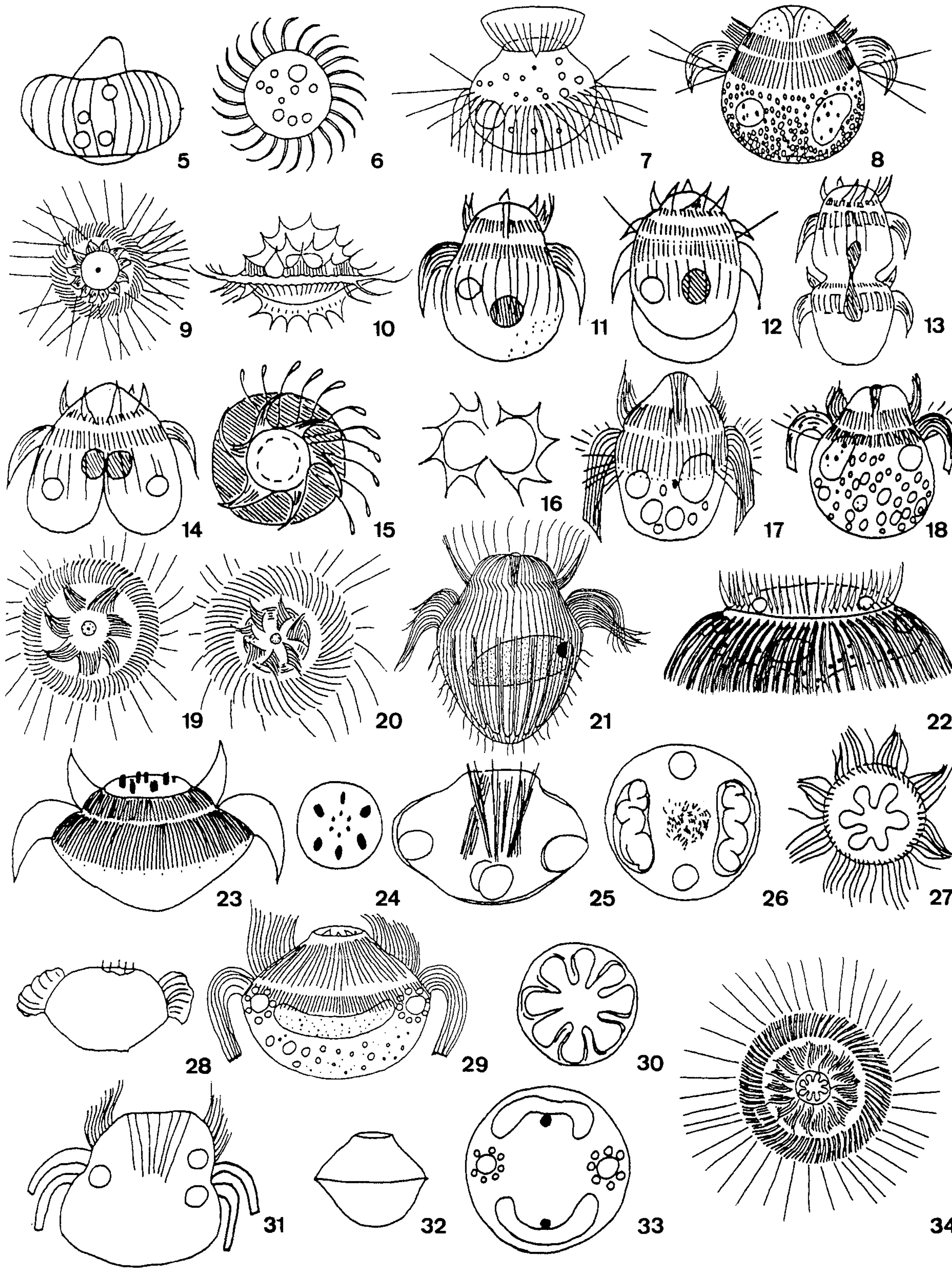

Fig. 5-34. 5–20, *A. volvox,* 21, *A. faurei,* 22, *A. humilis,* 23–34, *A. stellaris.* **5, 6.** Lateral and anterior view after Eichwald [16]. 7. After Claparède & Lachmann [13]. **8, 9.** Lateral and anterior view after Blochmann [7]. 10–16, after Penard [41]. **10.** Resting cyst. **11.** Side view. Note spherical macronucleus. **12.** Side view, showing terminal vacuole. **13.** Bipartition. Note constriction and dumbbell-shaped macronucleus. **14.** Conjugation. **15.** Anterior view, showing flame-like tufts of pectinelles. **16.** Anterior view, showing pectinelles of conjugants. **17-20.** Side and anterior views after Kahl [33, 34], showing tufts of pectinelles, skirt of equatorial belt of cirri and bristles. **21.** *A. faurei* from Kahl [33] after Fauré-Fremiet [19]. **22.** *A. humilis* after Gajewskaja [27]. **23–34.** *A. stellaris.* 23–26, after Borror [8]. **23.** Side view. Note protruded tips of

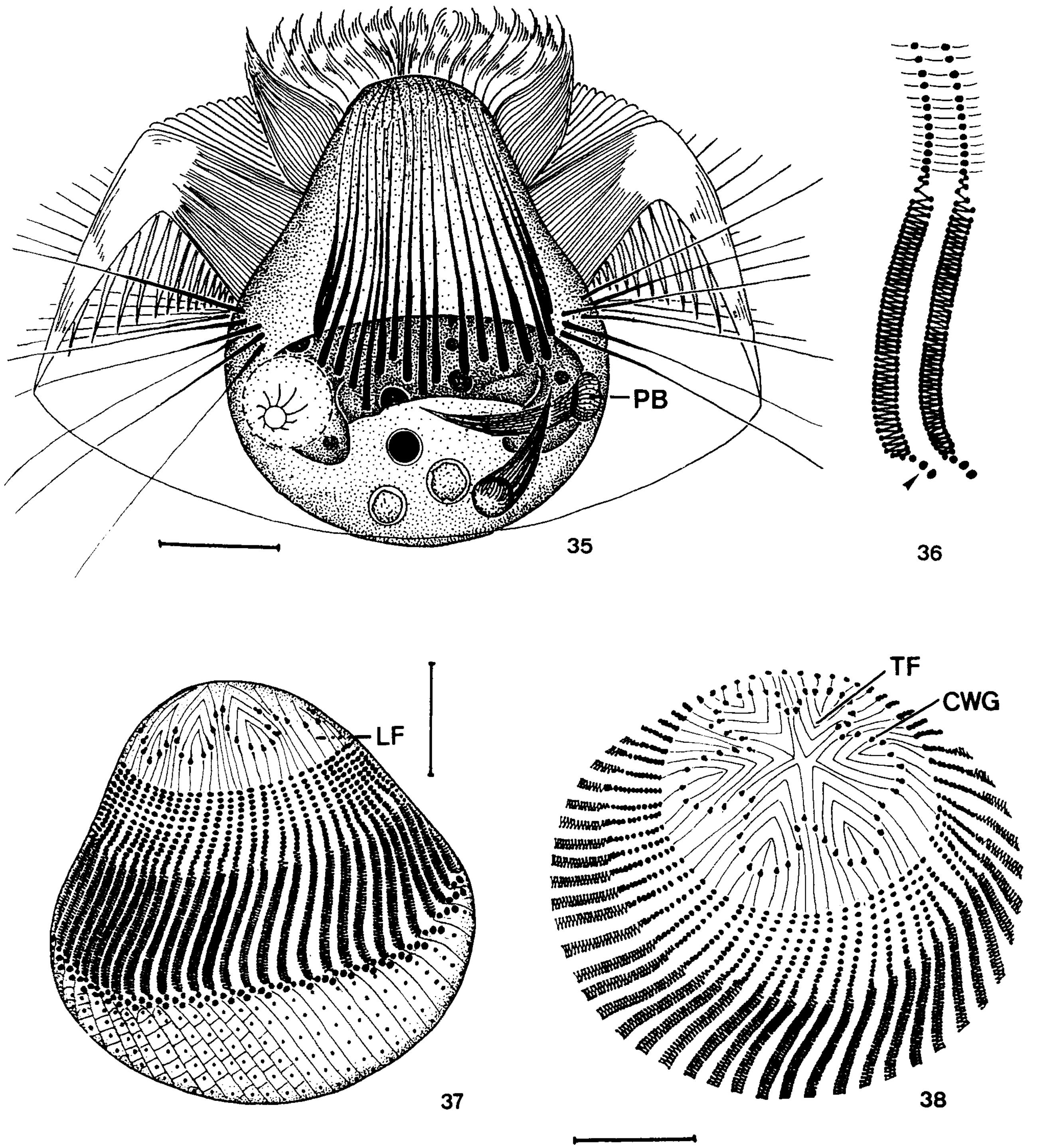

Fig. 35–38. *A. volvox* (Austrian population), from life (Fig. 35) and protargol-impregnated specimens (Fig. 36–38). **35**. Side view, showing nuclear apparatus, contractile vacuole, extrusomes, and pharyngeal baskets of ingested ciliates (PB). **36**. Details of somatic kineties. Note the three basal bodies of a SKB-kinety (arrow), the anteriormost basal body of which is distinctly smaller. **37, 38**. Infraciliature in side view and in oblique anterior view, showing cloverleaf-shaped circumoral wreath of granules (CWG) and longitudinal fibers (LF) producing V-shaped pattern in oral region together with transverse fibers (TF). Note lattice pattern in posterior portion. Bars = 10 μm.

←

extrusomes on oral area. **24**. Apical view of oral area, showing whorls of extrusomes. **25**. Longitudinal section, showing extrusome ("trichite") bundles and contractile vacuoles. **26**. Cross-section, showing worm-like macronuclear segments, tips of extrusome bundles and two contractile vacuoles. 27, 28, after Leegaard [37]. **27**. Anterior view, showing hexagram-like ("hexaster") figure. **28**. Side view, showing extrusome tips. 29–34, after Kahl [33, 34]. **29**. Side view, showing truncated oral area and doubled contractile vacuole with collecting vesicles. **30**. Apical aspect of oral area, showing eight arch-shaped lobes encircling cytostome. **31**. Side view of early fission stage. **32**. Starved specimen. **33**. Cross-section showing macronuclear segments, micronuclei and contractile vacuoles. **34**. Anterior view, showing pectinelles, cirri and bristles.

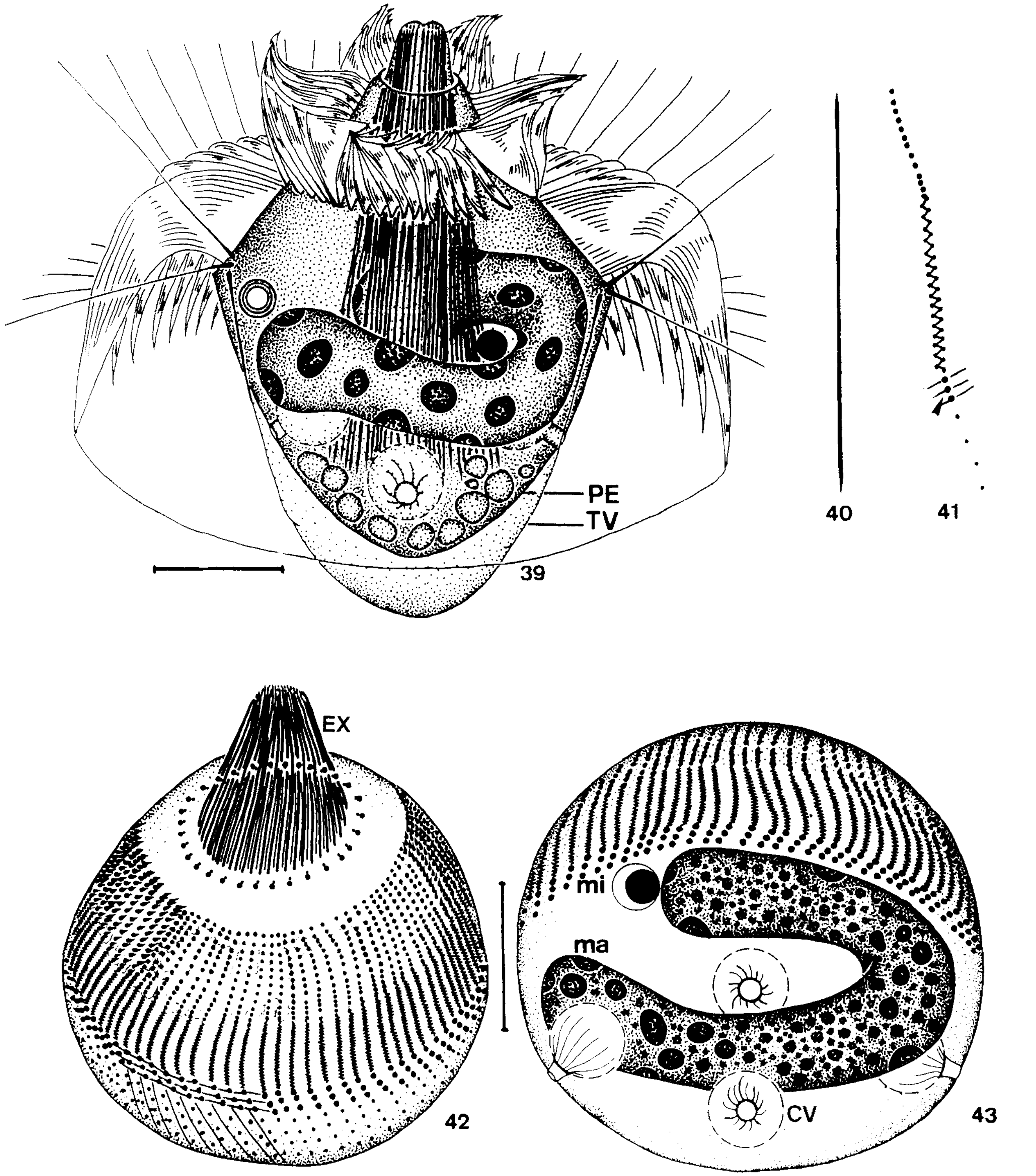

Fig. **39–43**. *Askenasia acrostomia* n. sp., from life (Fig. 39, 40) and protargol-impregnated specimens (Fig. 41–43). **39**. Side view, showing pellicle (PE) and terminal vacuole (TV). **40**. Extrusome. **41**. Detail of a somatic kinety. The SKB-kinety (arrow) consists of three basal bodies. **42**. Infraciliature in side view. Note protruding tip of conical extrusome bundle (EX). **43**. Infraciliature in oblique posterior view, showing macronucleus (ma), micronucleus (mi) and contractile vacuoles (CV). Bars = 10 μm.

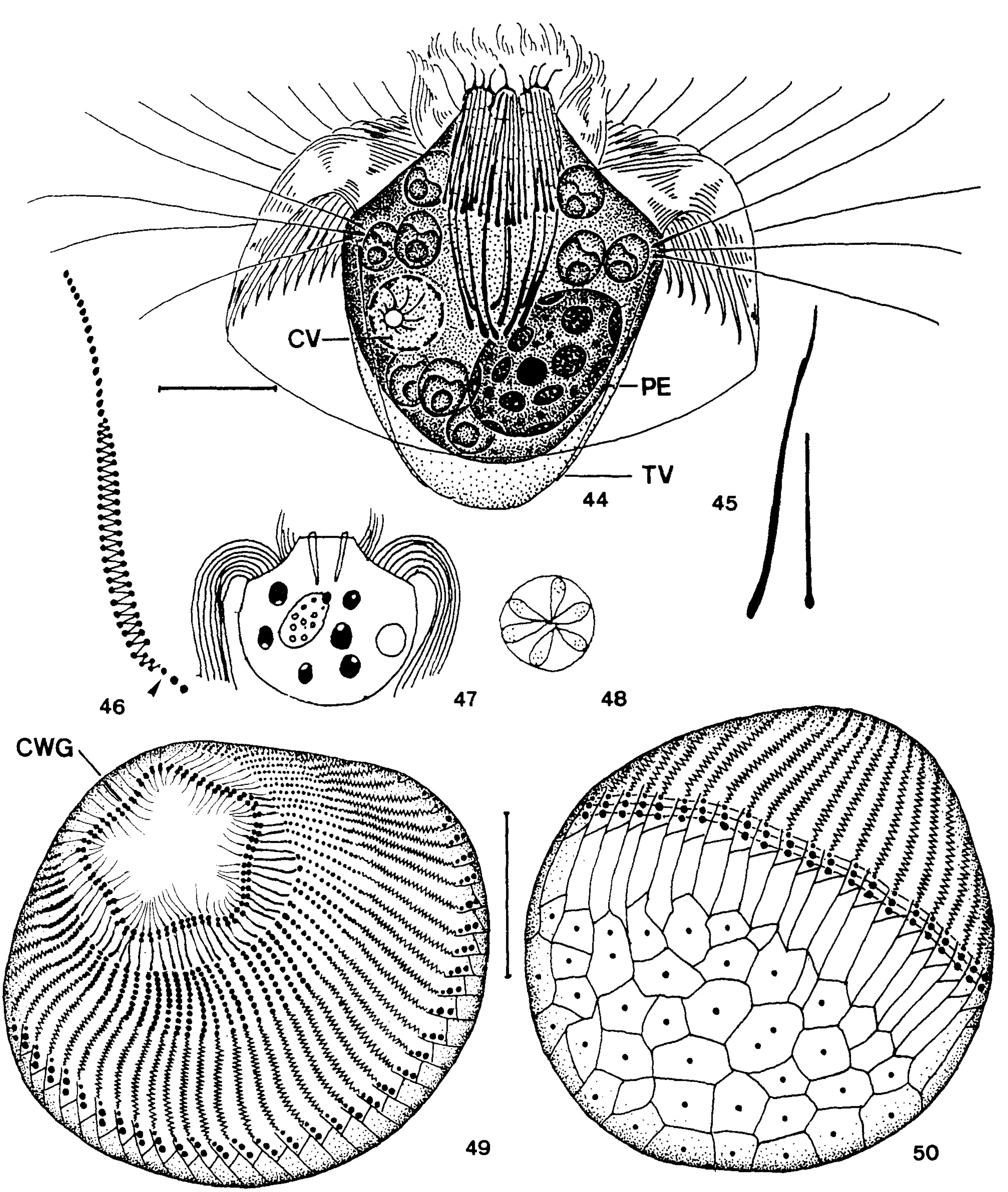

Fig. 44-50. *A. chlorelligera* n. sp. Fig. 47, 48 after Kahl [35], other originals from life (Fig. 44) and protargol-impregnated specimens (Fig. 45, 46, 49, 50). **44**. Side view, showing the two extrusome types, nuclear apparatus, contractile vacuole (CV), pellicle (PE), terminal vacuole (TV) and symbiotic green algae. **45**. Extrusome types. **46**. Detail of a somatic kinety. SKB-kinety (arrow) consists of three basal bodies and EKB-kinety has a short "tail" at posterior end. **47**. Side view, showing truncated oral area, extrusome bundles, symbiotic green algae. **48**. Apical aspect showing radially arranged bumps of extrusome bundles, resembling cross-section of apple-core. **49**. Infraciliature in oblique anterior view, showing pentagonal circumoral wreath of granules (CWG). **50**. Infraciliature in oblique posterior view. Bars = 10 μm.

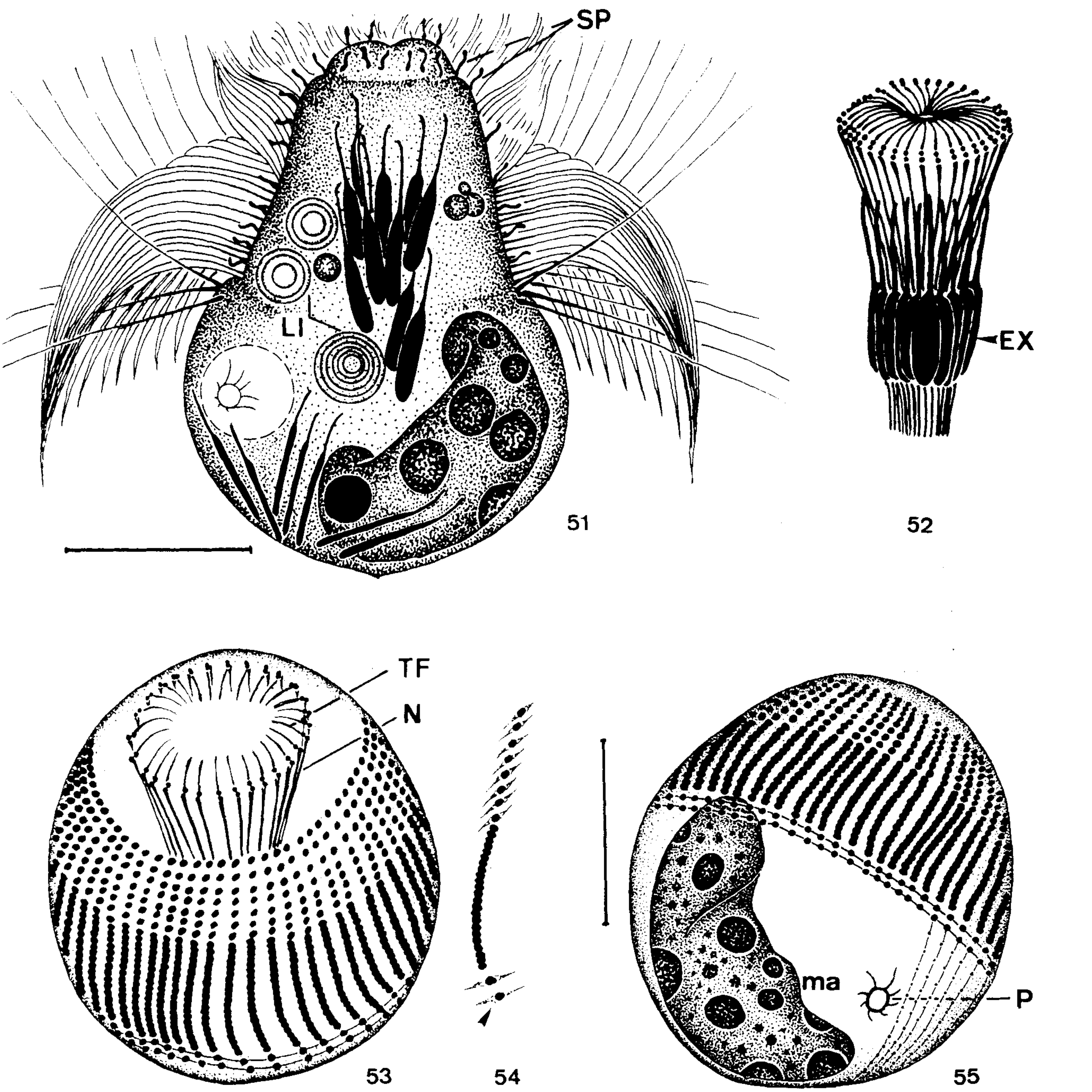

Fig. 51-55. *Rhabdoaskenasia minima* n. sp., from life (Fig. 51) and protargol-impregnated specimens (Fig. 52–55). **51**. Side view, showing nuclear apparatus, contractile vacuole, extrusomes and lithosome-like inclusions (LI). Note spirills (SP) on surface of rostrum. **52**. Rhabdos, "armed" with extrusomes, slightly schematized. **53**. Infraciliature in oblique anterior view, showing nematodesmata (N) and transverse fibers (TF). **54**. Detail of a somatic kinety. SKB-kinety consists of only two basal bodies (arrow). **55**. Infraciliature in oblique posterior view, showing macronucleus (ma) and pore of contractile vacuole (P). Bars = 10 μm.

truding from rostrum (Fig. 23–25). Feeds on cocci and algae. Kinety belts comprise approximately 70 kineties. Pectinelles beat in 6–16 tufts [8, 34]. Bristles from 20–60 μm in length [8, 34].

Occurrence and ecology. This species was discovered in the plankton of coastal waters of the Finnish Gulf (eastern Baltic Sea), numbering 1,540 cells per liter at a depth of 20 m [37]. It has also been recorded from coastal waters of the North Sea near Hamburg, FRG [34], from diatom detritus of Alligator Harbor, Florida [8], and from littoral sands of the Kandalaksha Gulf, White Sea, USSR [10].

Remarks. This marine species was originally described under the name *Lohmanniella stellaris*. It was transferred by Kahl [33] to the genus *Askenasia*. *Askenasia stellaris* is the sole marine species described. It is well characterized by its nuclear and excretory apparatus. However, redescription with silver impregnation techniques is required.

Askenasia acrostomia n. sp.

Diagnosis. Size in vivo 40–50 × 30–40 μm. Circumoral wreath of granules circular. Macronucleus horseshoe-shaped to rope-like. Extrusomes needle-like with pointed ends. Four contractile vacuoles.

Type location. Excavated groundwater ponds near Graz (Styria, Austria).

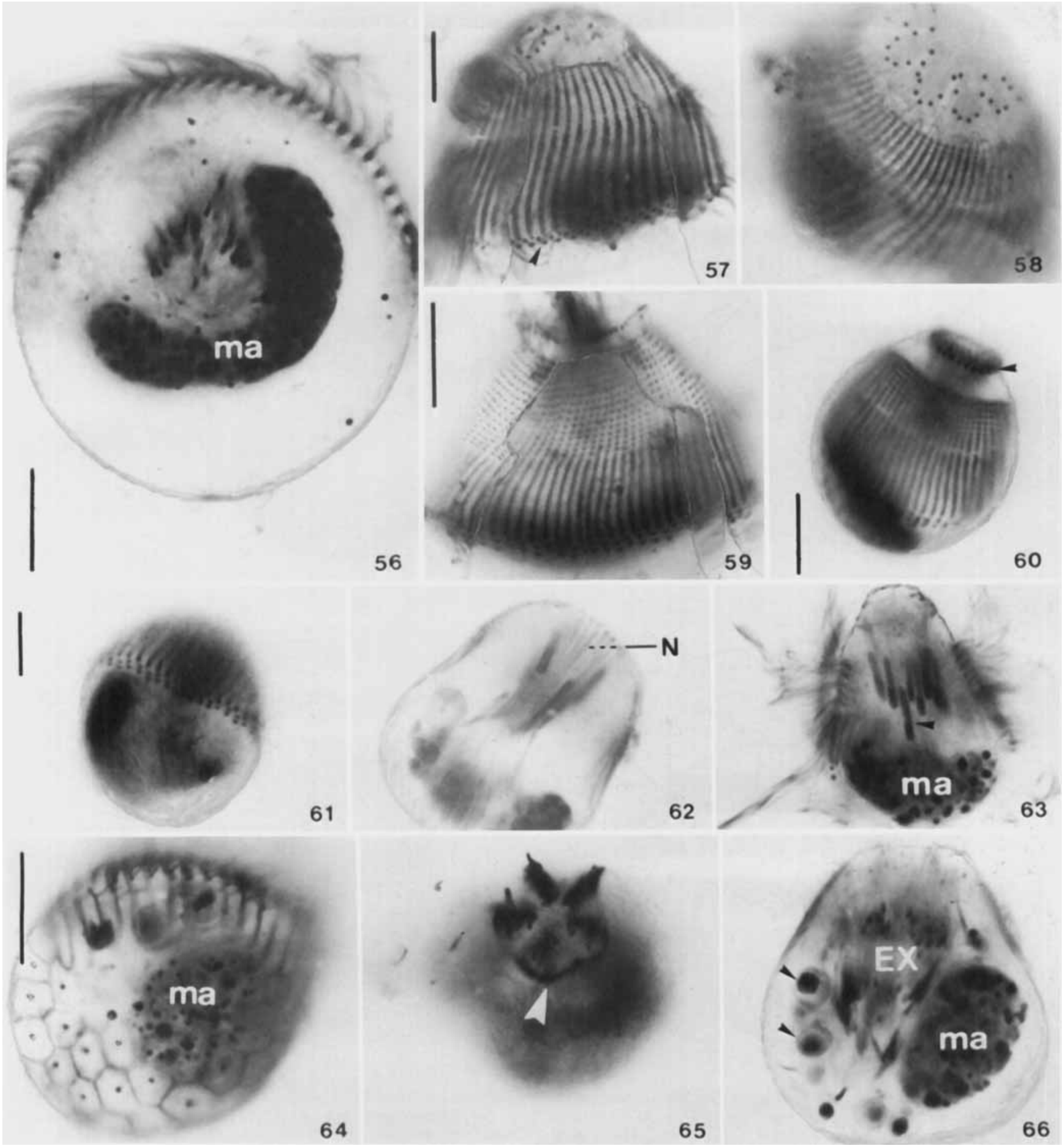

Fig. **56-66**. *Askenasia* spp. Infraciliature after protargol impregnation. All bars indicate 10 μm. *A. volvox*, Austrian population (Fig. 56–58). Fig. 57 and 59 are composites formed by superimposing images of different focal planes to provide a clear view of the total surface of this large ciliate. **56**. C-shaped macronucleus (ma) in optical cross-section. **57**. Side view. Note subequatorial kinety belt (arrowhead). **58**. Oblique anterior view showing cloverleaf-shaped circumoral wreath of granules. **59**. Side view of *A. acrostomia* n. sp. *Rhabdoaskenasia minima* n. sp. (Fig. 60–63). **60**. Side view. Note circumoral kinety (arrowhead). **61**. Oblique posterior view. **62**. Optical longitudinal section showing nematodesmata (N). **63**. Optical longitudinal section showing extrusomes (arrowhead) and macronucleus (ma). *A. chlorelligera* n. sp. (Fig. 64–66). **64**. Oblique posterior view showing honeycomb-like polygons and macronucleus (ma). **65**. Apical aspect of oral area showing five bumps of protruding extrusome tips, enclosed by the roughly pentagonal circumoral wreath of granules (arrowhead). **66**. Optical section, showing symbiotic green algae (arrowheads), extrusomes (EX) and macronucleus (ma).

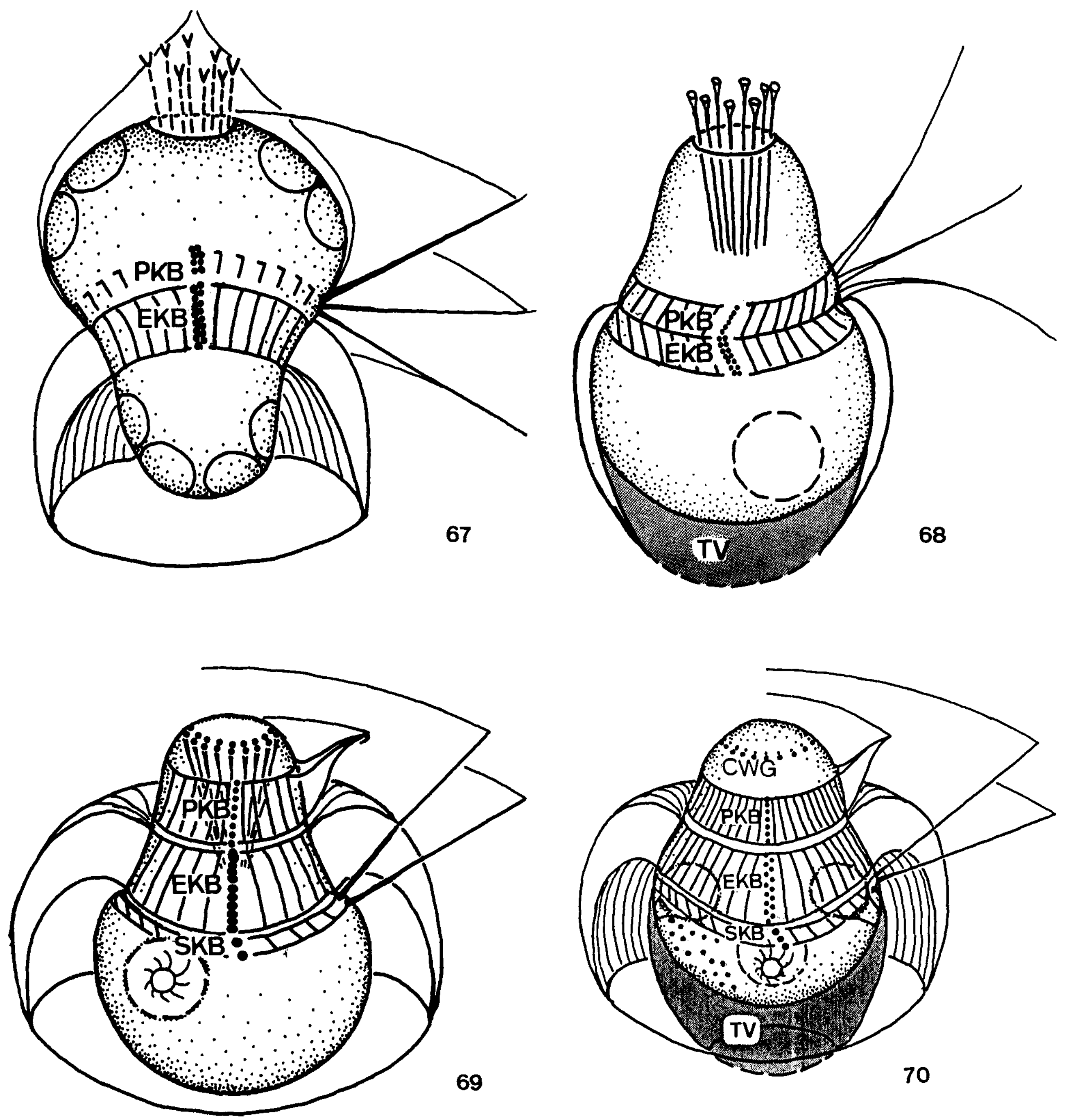

Fig. 67–70. Schematic figures of the genera of the Mesodiniidae (from several sources). **67**. *Myrionecta* Jankowski, 1976. **68**. *Mesodinium* Stein, 1867. **69**. *Rhabdoaskenasia* n. gen. **70**. *Askenasia* Blochmann, 1895. CWG, circumoral wreath of paired granules; EKB, equatorial kinety belt; PKB, pre-equatorial kinety belt; SKB, subequatorial kinety belt; TV, terminal vacuole.

Derivatio nominis. "acrostomia" refers to the tapered rostrum.

Description (Fig. 39–43, 59; Table 1). Outline approximately rhomboid with distinct cell equator (Fig. 39). Anterior portion tapering, constricted at level of oral area, where a single extrusome bundle protrudes (Fig. 39, 42). Well-fed specimens with globular posterior portion. Macronucleus with chromatin bodies of various shapes and sizes (Fig. 43). Several specimens observed with two sausage-like fragments (resembling *A. stellaris*). Micronucleus usually located at end of a macronuclear arm (Fig. 43). Four contractile vacuoles diametrically arranged in posterior 3rd of cell, discharging by short excretory canals about 1 μm in length. Bases of excretory canals framed by argyrophilic fibers (Fig. 43). Extrusomes about 23 μm long, extending at least $2/3$ of cell length posteriorly from apex (Fig. 39, 40). They usually discharge on fixation, forming tangles of threads; in protargol slides having knobbed posterior ends not discernible in vivo. Furthermore, impregnations suggest presence of a 2nd, shorter type. We have not, however, ascertained it in vivo. Cytoplasm of starved specimens, colorless in posterior portion some greasily shining inclusions. Feeds on algae and ciliates. Terminal vacuole discernible in vivo (Fig. 39).

The EKB-kineties are approximately two kinety widths apart with

Table 1. Biometric characterization of *Askenasia volvox* (Av), *A. acrostomia* (Aa), *A. chlorelligera* (Ac) and *Rhabdoaskenasia minima* (Rm).[a]

Character	Species	$\bar{x}$	SD	CV	Min	Max	n
Body, length	Av	37.8	4.0	10.6	30	42	14
	Aa	32.2	5.2	16.1	22	37	17
	Ac	27.2	2.9	10.7	24	32	11
	Rm	23.3	3.8	16.3	18	30	15
Body, width	Av	34.6	4.4	12.8	25	42	21
	Aa	28.6	4.2	14.7	24	37	23
	Ac	26.5	5.1	19.2	22	38	11
	Rm	19.9	3.8	19.1	16	26	19
Macronucleus, longer axis	Av	24.9	4.1	16.5	17	31	12
	Aa	22.8	0.8	3.5	22	24	5
	Ac	12.5	2.4	19.2	10	18	12
	Rm	14.5	2.7	18.6	11	22	17
Macronucleus, width	Av	7.1	1.5	21.1	5	12	16
	Aa	5.2	1.4	26.9	2	8	23
	Ac	8.3	1.9	22.9	6	12	12
	Rm	6.1	1.7	27.9	5	10	17
Micronucleus, diameter	Av	2.3	0.2	8.7	1.4	2.4	10
	Aa	1.9	0.5	26.3	1	2	14
	Ac	1.8	0.7	38.9	1	2	10
	Rm	2.2	0.5	22.7	1	3	10
No. granule pairs of CWG	Av	58.9	3.4	5.8	53	63	8
	Aa	32.5	2.9	8.9	30	39	8
	Ac	54.4	4.4	8.1	48	60	13
No. dikinetids of circumoral kinety	Rm	28.6	2.3	8.0	22	32	14
Distance CWG to PKB	Av	2.4	0.6	25.0	1	4	16
	Aa	2.0	0.8	40.0	1	4	10
	Ac	2.1	0.6	28.6	2	2.4	10
No. basal bodies per PKB-kinety	Av	13.1	2.9	22.1	9	18	9
	Aa	11.9	2.6	21.8	9	18	23
	Ac	10.2	1.8	17.6	8	12	6
	Rm	6.7	1.6	23.9	4	9	22
PKB-kinety, length	Av	5.9	1.0	16.9	5	7	17
	Aa	7.4	1.2	16.2	6	10	11
	Ac	4.4	1.0	22.7	4	6	10
	Rm	4.3	0.9	20.9	4	7	17
No. EKB-kineties	Av	60.2	0.7	1.2	59	61	12
	Aa	73.2	3.6	4.9	70	78	6
	Ac	57.4	2.5	4.3	54	64	12
	Rm	62.2	2.7	4.3	57	66	9
EKB-kinety, length	Av	10.0	1.5	15.0	8	12	16
	Aa	5.9	0.9	15.2	5	8	28
	Ac	5.6	1.4	25.0	5	10	10
	Rm	4.7	1.0	21.3	4	7	16
No. basal bodies per SKB-kinety	Av	3.0	0.0	0.0	3	3	10
	Aa	3.0	0.0	0.0	3	3	19
	Ac	3.0	0.0	0.0	3	3	7
	Rm	2.0	0.0	0.0	2	2	17

[a] All data are based on the investigations of selected protargol-impregnated specimens. All measurements in micrometers. CV, coefficient of variation in %; CWG, circumoral wreath of granules; EKB, equatorial kinety belt; Max, maximum; Min, minimum; No., number; PKB, pre-equatorial kinety belt; SD, standard deviation; $\bar{x}$, arithmetic mean.

basal bodies loosely spaced (Fig. 41, 42, 59). The SKB-kineties are interconnected by transverse fibers (Fig. 41, 42, 59). Granule pairs of CWG do not show fibers under impregnation method (Fig. 42).

Occurrence and ecology. The highest numbers were found in May 1986 (836 cells per liter; 8.3 mg/m^3), in August 1986 (560 cells per liter; 5.6 mg/m^3), and in October 1986 (445 cells per liter; 4.4 mg/m^3). During cold isothermal conditions, the numbers did not exceed 200 cells per liter. The lowest numbers were found in February and March 1987. In the littoral zone 380 cells per liter and 3.8 mg/m^3 were observed in May 1987.

Askenasia chlorelligera n. sp.

Diagnosis. Size in vivo 30–40 × 25–45 µm. Circumoral wreath of granules roughly pentagonal. Macronucleus spheroidal to ellipsoid (3: 2). Two types of pin-shaped extrusomes. Single contractile vacuole.

Type location. Excavated groundwater ponds near Graz (Styria, Austria).

Derivatio nominis. "chlorelligera" refers to the symbiotic green algae.

Description (Fig. 44–50, 64–66; Table 1). Rostrum truncated, crown-like structure comprised of 5–6 bumps apically, produced by protruding bundles of shorter extrusome type. "Crown" resembles cross-section of apple-core (Fig. 44, 48). Macronucleus with spherical chromatin bodies of various sizes (Fig. 44, 64). Several specimens with two spheroidal fragments. Excretory canal of contractile vacuole about 2 µm long (Fig. 44). Short extrusomes about 10 µm, knobbed proximally, packed in posteriorly slightly diverging, in cross-section elliptical bundles (Fig. 44, 45, 66). Long extrusomes about 18 µm, slightly curved, extending half-cell length posteriorly from crown, forming a basket in the center of the cell (Fig. 44, 66). Extrusome tips impregnated conspicuously with protargol (Fig. 65). Cytoplasm contains about 20–30 *Chlorella*-algae and several green algae seemingly in terms of several characters, belonging to *Siderocelis* (Fig. 44, 66). Algae give the cell a grass-green color. Terminal vacuole discernible in vivo (Fig. 44). The EKB-kineties are about one kinety width apart, basal bodies comparatively loosely spaced

(Fig. 46, 49). The EKB-kineties have short trunks of 5–8 basal bodies at the posterior end. The SKB-kineties interconnect by transverse fibers (Fig. 50). The posterior hemisphere shows polygonal, argyrophilic pattern (Fig. 50, 64). At the cell's equator there is a circumferential belt of rectangular structures linking polygons with EKB-kineties (Fig. 50, 64). The CWG comprises of paired granules of equal size, resembling a haptorid oral dikinetid, encircling extrusome bumps (Fig. 49, 65).

Occurrence and ecology. Very abundant in spring, reaching peak in May 1986 (1,904 cells per liter; 14.1 mg/m³). In late fall relatively abundant, smaller peak of 245 cells per liter and 1.8 mg/m³ occurred in October 1986. Abundances correspond to O_2-values of 10–14 mg per liter and temperatures between 8° C and 22° C.

Remarks. This is obviously the green, pelagic *A. volvox* which Kahl [35] found in the plankton of several freshwater ponds near Hamburg, although already assuming it to be a new species (Fig. 47, 48).

Rhabdoaskenasia n. gen.

Diagnosis. Mesodiniidae with circumoral kinety composed of dikinetids giving rise to nematodesmata which form a distinct basket (rhabdos). Kineties of equatorial and pre-equatorial belt composed of single files of basal bodies, those of subequatorial belt composed of two basal bodies each.

Type species. *Rhabdoaskenasia minima* n. sp.

Derivatio nominis. The name refers to the distinct rhabdos and to the similarity to *Askenasia.* Feminine gender.

Rhabdoaskenasia minima n. sp.

Diagnosis. Size in vivo 20–35 × 18–30 μm. Conical. Macronucleus reniform. Two types of club-shaped extrusomes. Single contractile vacuole.

Type location. Excavated groundwater ponds near Graz (Styria, Austria).

Derivatio nominis. "minima" (lat. small) refers to the small size.

Description (Fig. 51–55, 60–63; Table 1). Cell constricted at cell equator and subapically at oral area, which has distinct centrally depressed bulge. Postequatorial portion globular, posterior pole with very short knob. Single macronucleus in rear end of cell. Chromatin bodies large, globular. Single, spherical micronucleus (Fig. 51). Contractile vacuole subequatorial, excretory canal about 2 μm in diameter. Anterior extrusomes 8–9 μm long, arrayed around rhabdos, comprising club-shaped posterior part about 5 × 1 μm in size and needle-like, distally curved anterior part about 3.5 μm in length (Fig. 51, 52, 63). Posterior extrusomes 7–8 μm long, scattered in rear end, comprising slender bat-shaped posterior part about 5 × 0.5 μm in size and curved needle-like anterior part about 3 μm in length. Both types strongly reminiscent of the extrusomes of *Paraenchelys wenzeli,* a haptorid genus [22]. Pellicle firm resulting in fairly constant cell form, withstanding extended coverslip pressure. Cytoplasm pale green, sparsely filled with lithosome-like inclusions. Bacteria (spirills) attached to anterior portion (Fig. 51). No terminal vacuole observed.

The PKB-kineties with oblong basal bodies are associated with obliquely oriented fibers (Fig. 54, 60). The SKB-kineties are interconnected by transverse fibers (Fig. 55, 61). Circumoral kinety composed of paired, barren basal bodies of equal size. Curved transverse fibers originate from inner basal bodies, extending radially toward cytostome (Fig. 52, 53, 60). Nematodesmata originate from outer basal bodies, forming distinct rhabdos extending to the cell's center (Fig. 52, 53, 62).

Occurrence and ecology. Relatively abundant in all seasons (100–250 cells per liter) but culminating on October 21, 1986, with 2,670 cells per liter and 9.3 mg/m³ at a depth of 1 m and 1,720 cells per liter and 6.0 mg/m³ at a depth of 3 m. Lowest numbers observed in December 1986 and January 1987.

DISCUSSION

Classification of *Askenasia.* According to Corliss [14], *Askenasia* belongs to the class Kinetofragminophora, subclass Gymnostomata, order Haptorida, family Didiniidae. Our investigations show that *Askenasia* lacks important haptorian characteristics: the distinct rhabdos, the dorsal brush, and the tightly meshed silverline system [14, 26]. Thus, we transfer *Askenasia* to the order Cyclotrichida Jankowski, 1980, family Mesodiniidae Jankowski, 1980, whose key features readily match those of *Askenasia* [26]. However, the Cyclotrichida themselves are in urgent need of investigation and revision under silver impregnation techniques. The Cyclotrichida may possibly belong not to the subclass Haptoria but to another [26].

Systematic position of *Rhabdoaskenasia.* The general plan of *Rhabdoaskenasia* is very similar to that of *Askenasia.* However, the distinct rhabdos and the single filed kineties of the equatorial kinety belt indicate that this similarity might be only superficial, resulting from convergent evolution. The rhabdos of *Rhabdoaskenasia* is in fact highly similar to that of many haptorids [22, 25, 26]. However, *Rhabdoaskenasia* lacks the dorsal brush, which is the main character defining the members of the order Haptorida [26]. *Rhabdoaskenasia* should therefore not be included in this order. It probably belongs to the order *Pseudoholophryidae,* as indicated by its extrusomes. However, the general organization is too close to that of *Askenasia* to justify such a major shift without electron microscopic evidence.

Illustrated key to the genera of the family Mesodiniidae (subclass Haptoria, order Cyclotrichida). The following key (Fig. 67–70) is based on the present results and on investigations by other authors [9, 19, 30, 32, 38, 45].

1 Two equatorial kinety belts, equatorial belt (EKB) bearing "cirri," pre-equatorial belt (PKB) bearing bristles 2
– Three equatorial kinety belts, equatorial belt (EKB) bearing sickle-shaped "cirri," pre-equatorial belt (PKB) bearing "pectinelles," subequatorial belt (SKB) bearing bristles 3
2 Anterior portion larger than posterior. The EKB-kineties are composed of double rows of basal bodies arranged in zigzag. The PKB-kineties comprise of groups of square-packed basal bodies. On apex distally forked tentacles, retractable. No contractile vacuole observed. Cytoplasm with permanent obligatory symbionts. Marine (Fig. 67) .... Single species *Myrionecta rubra* (Lohmann, 1908) Jankowski, 1976
– Anterior portion smaller than posterior. The EKB-kineties with double rows of basal bodies. The PKB-kineties with single files of basal bodies. Apically retractable stylets, distally with suckers. Contractile vacuole in rear end. Crescent-shaped terminal vacuole. Several freshwater and marine species (Fig. 68) ... . *Mesodinium* Stein, 1862
3 Distinct rhabdos comprising nematodesmata originating from circumoral kinety composed of dikinetids. The EKB-kineties are composed of single files of basal bodies. The SKB-kineties are composed of two basal bodies. Freshwater (Fig. 69) .... Single species *Rhabdoaskenasia minima* n. sp.
– Oral area encircled by circumoral wreath of paired granules (CWG). Nematodesmata not recognizable. The EKB-kineties are composed of double rows of basal bodies arranged in zigzag. The SKB-kineties are composed of three basal bodies each. Several freshwater and marine species (Fig. 70) .... *Askenasia* Blochmann, 1895

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