

Redescription of Four Species of Lagenophryid Peritrichs (Ciliophora) from Australia and New Guinea, With Descriptions of Two New Species

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ABSTRACT. Four insufficiently described species of ectosymbiotic peritrich ciliates in the family Lagenophryidae that occur on crustacean hosts in Australia and New Guinea are redescribed. These include two species of *Operculigera* from phreatoicid isopods, one species of *Setonophrys* from a phreatoicid isopod, and one species of *Lagenophrys* from a palaemonid shrimp. Two undescribed species of *Operculigera*, also found on phreatoicid isopods, are described for the first time. Australian species of *Operculigera* appear to be restricted to phreatoicid hosts. This is unusual because a diverse array of other lagenophryids occur on parastacid crayfish in Australia. Furthermore, species of *Operculigera* are conspicuous symbionts of parastacids and various freshwater crabs in Chile and Madagascar. In addition to this peculiarity of distribution, the Australian species of *Operculigera* appear to comprise a morphologically distinct group within the genus.

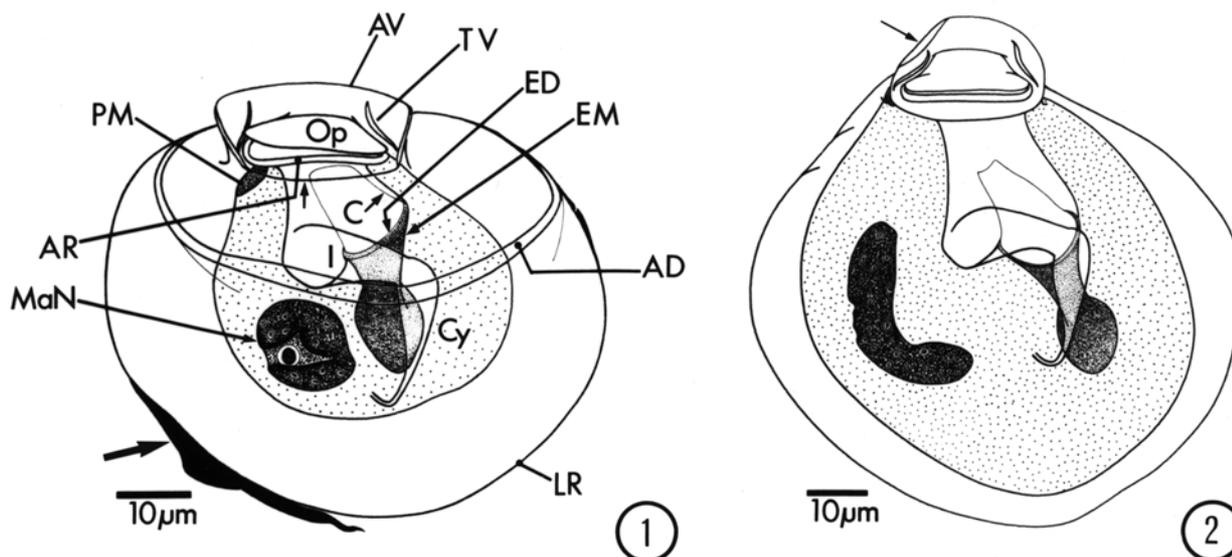
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All but one of the species of peritrich ciliates in the family Lagenophryidae Bütschli, 1889 are specialized ectocommensals of crustaceans. Lagenophryids do not have the familiar bell-, barrel-, or trumpet-shaped, radially symmetrical bodies typical of other peritrichs. Instead, they are grossly flattened and laterally distorted, with a discoid, bilaterally symmetrical shape that fits closely against the host's surface. Unlike most peritrichs, they do not secrete a cylindrical stalk for attachment but, instead, cement themselves to the host's exoskeleton with the rim of their protective lorica.

Lagenophryid loricae are usually hemispheroidal, with the flat side adherent to the host; some species, however, have a narrower, pyriform to ovoid lorica that is adapted for clinging to setae. Lagenophryids protrude only the

central, epistomial disk of the peristome (expanded oral area) from the lorica aperture during feeding. Other loricate peritrichs (e.g., all vaginicolids) project the entire oral end of the body through the lorica aperture when feeding. The aperture of a lagenophryid lorica is a complex structure that shuts tightly when the epistomial disk is retracted. Part of the peristomial margin is attached around the base of the lorica aperture in lagenophryids and closes it forcefully, using an enlarged version of the contractile, myonemal sphincter that closes the peristomial lip over the retracted epistomial disk in other peritrichs. Lagenophryids are like other peritrichs in being suspension feeders that capture particulate food such as bacteria and phytoplankton. They may associate with crustaceans because these hosts generate

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Figs. 1, 2. (1) *Operculigera montanea*, Erlich's hematoxylin preparation. Dorsal view of lectotype individual from the type locality and host, AM P62810. (AD) thickened ridge that bounds anterior depression in dorsal surface of lorica; (AR) rim of lorica aperture; (AV) anterior and lateral parts of vallum; (C) peristomial cilia originating from epistomial disk (shown in outline only); (Cy) cytoplasm (sparsely stippled areas—food vacuoles and other taxonomically irrelevant structures are omitted); (ED) epistomial disk; (EM) myonemes that retract epistomial disk (densely stippled column anchored to ED); (I) infundibulum—this is a passageway through which food particles pass to reach the cytostomal area (the bulbous ampulla leading to a tubular cytopharynx that lies beyond the constriction at the end of the infundibulum); (LR) rim of lorica—the localized areas with large accumulations of lorica material (large arrow) are not typical; (MaN) macronucleus—the micronucleus is the small, dense, darkly stained body nestled in the central area of the macronucleus; (Op) operculum (the slightly displaced left side of the closed operculum is an artefact); (PM) myoneme in edge of peristomial lip that effects closure of the operculum; (TV) thickened strip in the anterolateral wall of the vallum; small arrow, vestigial posterior part of the vallum—to see species of *Operculigera* with this part of the vallum fully developed, consult Clamp (1991). (2) *Operculigera zeehanensis*, Erlich's hematoxylin preparation. Dorsal view of lectotype individual from the type locality and host, AM P62813. The folding over of the left edge of the vallum (small arrow) is an artefact. The micronucleus was hidden underneath the macronucleus and is therefore not shown. The unfolded macronucleus indicates that this individual was probably approaching cell division when it was fixed. Most individuals in the sample examined had the ends of the macronucleus folded together.

currents of water, mainly respiratory or locomotory, which convey a steady supply of particles to their suspension-feeding symbionts (Fenchel; 1965; Clamp, 1973, 1988a).

The genera of lagenophryids with the most species are, in descending order, *Lagenophrys* Stein, 1852, *Operculigera* Kane, 1969, and *Setonophrys* Jankowski, 1986. They differ mainly with respect to the structure of the lorica aperture. In *Lagenophrys*, the aperture is closed by a pair of flexible lips that are the edges of an invaginated collar of lorica material to which the posterior edge of the peristomial lip is attached, and only the posterior half of the peristomial sphincter is enlarged (Figs. 17, 18, 22). The aperture of *Setonophrys* is superficially similar to that of *Lagenophrys*; the anterior lip of the aperture, however, is rigid in *Setonophrys*, a flexible posterior lip is folded against this rigid anterior lip to effect closure, and the entire peristomial sphincter is enlarged (Fig. 16). The lorica aperture of *Operculigera* is markedly different from that of the other two genera. Its aperture is a simple opening that is closed by a flat operculum, and only the anterior half of the peristomial sphincter is enlarged (Fig. 1). Unlike other lagenophryid genera, *Operculigera* has a thickened wall of lorica material, the vallum, which at least partially encircles the lorica aperture (Fig. 1). Some species of *Lagenophrys* have a thickened ridge of lorica material around the anterior half of the lorica aperture, but this ridge is never developed into an actual wall as it is in species of *Operculigera* (Clamp, 1991).

Lagenophryid peritrichs have been reported from all continents except Antarctica on a wide variety of crustaceans

living in many kinds of marine, brackish-water, and freshwater habitats. Kane (1969) described several lagenophryid species from hosts collected in Australia and South Africa. The descriptions, unaccompanied by figures, were published in an extended abstract in the proceedings of the 3rd International Congress of Protozoology with the intention of publishing them in more complete form soon afterward. Personal circumstances prevented Kane from doing this, however. Although brief, the descriptions in this abstract meet the minimum requirements for publication of new taxa given in Article 8 of the current, fourth edition of the International Code of Zoological Nomenclature and are not excluded under Article 9.9 because the published proceedings were widely available in book form for purchase by persons other than attendees (ICZN, 1999). Fuller accounts are desirable, however, especially since one species (*Operculigera montanea* Kane, 1969) is the type species of its genus (Clamp, 1991).

Fortunately, Kane saved permanent preparations of the species named in the 1969 publication, and additional material of two species was obtained from the Australian Museum (hereafter abbreviated AM) and the Crustacean Collection of the National Museum of Natural History, Smithsonian Institution (hereafter abbreviated NMNH-CC). This material was sufficient for redescription of four of the Australian species, adding a record from New Guinea for one of them. Two of the species that we will redescribe in this paper are species of *Operculigera* occurring on phreatoicid isopods, and a third is a species of *Setonophrys*

that also associates with phreatoicids. The fourth is a species of *Lagenophrys* found on palaemonid shrimp in northern Australia and Papua New Guinea. *Lagenophrys jacobi* (Kane, 1969), a fifth Australian species described in the 1969 abstract, apparently comprises a complex of different species (Clamp, unpublished observations), and its redescription must be deferred because it requires examination of far more material than we possess at present. The two South African species of *Lagenophrys* named by Kane (1969) will be treated in a separate paper. One new species of *Operculigera*, originally identified (Kane, 1969) as a variant of *O. montanea*, was discovered among the permanent preparations saved by Kane and another was discovered on material from the NMNH-CC. Both are described for the first time in this paper.

Materials and methods

The majority of the material used in this study consisted of slides made by J.R. Kane in the early 1960s. These slides were made by fixing infested portions of host exoskeleton in Bouin's fluid and staining with Erlich's hematoxylin or Delafield's hematoxylin. As is typical for lagenophryids, most ciliates on the slides were still in good, well-stained condition comparable to recently collected and fixed material (Clamp, 1990a). Unlike other sessile peritrichs, taxonomically important features of lagenophryids are not affected by fixation, and it is customary to use fixed material alone when describing them (Clamp, 1989, 1990a, 1991, 1992). Four samples of infested body parts removed from phreatoicid isopods in museum collections also were included in our study. Three were from the NMNH-CC, and one was from the AM. The fixative for this material was unknown but was probably formalin since cellular features were preserved well and the vacuolate cytoplasm characteristic of alcohol fixation was not evident.

Permanent preparations of museum material were made by staining with Heidenhain's iron hematoxylin or protargol. For protargol, the quick method (Wicklow & Hill, 1992) was used with a staining time of 12–13 min at 70°C. Pieces of host exoskeleton with attached ciliates were carried through both staining processes in capsules approximately 1 cm in length made of polyethylene tubing (outside diameter 9.5 mm) sealed on one end with fine-mesh bolting silk melted into the edge of the tubing with a heated spatula. Protargol preparations were made of *Lagenophrys turneri* only. Material for protargol preparations of other species treated in this paper was either unavailable or of insufficient quantity to obtain usable views of the buccal infraciliature.

Measurements were done at 970× magnification using a filar micrometer. Height of loricae was measured by using the calibrated scale on the fine focusing knob of the microscope to determine the focal distance from the edge of the lorica base to the dorsal surface of the lorica. Phase-contrast microscopy was used for this measurement because loricae are usually too transparent for their dorsal surface to be ascertained accurately by bright-field microscopy. All individuals measured were ones oriented with the dorsal surface of the lorica uppermost and the flattened, ventral surface approximately parallel to the plane of the slide.

Drawings were made using a graticule inscribed with a grid (1 mm squares covering entire field) mounted in one objective of the microscope as a guide. A matching, printed grid was placed under a sheet of tracing paper on which the

drawing was done. The microscope used for drawings had a circular stage that could be rotated to align each ciliate with the axes of the grid. Photographs of stained ciliates were made with a Minolta X-700 camera mounted on an Olympus CH-2 microscope using Kodak T-Max film.

Full literature citations for the authorship of species of lagenophryids listed in each genus treated below are given in Kahl (1935), Jankowski (1986, 1993), or Clamp (1989, 1990a, 1991, 1992, 1993, 1994) or in the Reference section of this paper. Nicholls (1943) is a source for full literature citations for the authorship of phreatoicid species.

Results

Operculigera Clamp, 1991

Diagnosis. Solitary, loricate, with lorica aperture consisting of simple opening without either folded lips at its anterior and posterior edges or invaginated collar of lorica material (loricostome). Aperture closable by means of a flat operculum of lorica material and usually surrounded partially or completely by thickened wall of lorica material (vallum) that projects vertically from dorsal surface of lorica. Edge of peristomial lip of trophont associated with anteroventral edge of operculum. Anterior part of myonemal band within peristomial lip thickened. Macronucleus cylindroid, either long or short, often folded compactly, and varying in shape and location between species.

Type species. *Operculigera montanea* Kane, 1969 by designation (Clamp, 1991).

Generic Composition. The following species are currently assigned to *Operculigera*: *O. asymmetrica* Clamp, 1991; *O. carcini* Clamp, 1992; *O. haswelli* n.sp.; *O. inornata* n.sp.; *O. insolita* Clamp, 1991; *O. madagascarensis* Clamp, 1992; *O. montanea* Kane, 1969; *O. obstipa* Clamp, 1991; *O. parastacis* Jankowski, 1986; *O. seticola* Clamp, 1991; *O. striata* Jankowski, 1986; *O. taura* Clamp, 1991; *O. velata* Jankowski, 1986; *O. zeehanensis* Kane, 1969.

Operculigera montanea Kane, 1969

Figs. 1, 8–11; Tables 1, 6

Operculigera montanea Kane, 1969: 369.–Jankowski, 1986: 82, 83; Clamp, 1991: 365.

Redescription. Lorica hemispheroidal, suboval in dorsal view, moderately wider than long. Lorica asymmetrical in dorsal view; width of right half from midline to edge noticeably greater than width of left half from midline to edge. Rim of lorica moderately thickened. Dorsal surface of lorica with prominent, curved ridge extending across entire width of lorica and encircling concave depression in surface surrounding lorica aperture. Because of dorsal ridge, lorica with acuminate, nearly triangular profile in lateral view. Posterior part of vallum reduced to slightly thickened ridge. Anterior and lateral parts of vallum moderately tall, sloping abruptly to posterior part of vallum; posterior edges of lateral parts nearly vertical. Vallum symmetrical in height; free edge straight, even, lacking projections of any sort. Long strip near base of inner wall of each anterolateral part of vallum heavily thickened to form slightly protruding fold. Rim of lorica aperture moderately thickened. Operculum subcuneate in dorsal view. Anterior edge of operculum moderately thickened to form narrow, ventral shelf; ventral shelf smooth, lacking processes.

Macronucleus short, cylindroid; ends flexed upon centre to create compact, folded shape. Macronucleus located in left half of body. Micronucleus ovoid, located more frequently near centre of macronucleus than near either end.

Etymology. The specific name refers to the montane habitat of the type host.

Type material. LECTOTYPE, AUSTRALIA, Victoria, summit of Mt Baw Baw (1850 m elevation); 13 Oct 1963, J.R. Kane; on *Colubotelson searlei* Nicholls, 1944, pleopods. Lectotype slide with lectotype organism marked by inscribed circle (Erlich's hematoxylin), AM P62810. PARALECTOTYPE slide (Erlich's hematoxylin), International Protozoan Type Collection (hereafter abbreviated IPTC) USNM 1004287. AUSTRALIA, Victoria, Kiewa; J.R. Kane; on *Colubotelson* sp., pleopods. Paralectotype slide (Erlich's hematoxylin), AM P62811.

Other material examined. Victoria, Mt Buffalo; Feb 1926, G.E. Nicholls; on *C. joyneri* (Nicholls, 1926), pleopods (AM Z6189). Voucher slides (3 Heidenhain's hematoxylin, 2 protargol) AM P62812, P62880, P62881, P62882, P62883.

Nomenclatural note. No type species was explicitly fixed for *Operculigera* in Kane (1969); consequently, this name was not yet available because such fixation was required for genus-group names published after 1930 (ICZN, 1999). Clamp (1991) designated *O. montanea* as the type species of the genus, making the name *Operculigera* available and (inadvertently as it turned out) becoming the author of the genus. The authorship of species of *Operculigera* described in Kane (1969) and Jankowski (1986) was not affected by this action (Article 11.9.3.1 of the current Code).

Remarks. The curved ridge in the dorsal surface of the lorica (Figs. 1, 9) is a distinctive characteristic of *O. montanea* that does not occur, even in reduced form, in any other known species within the genus (Jankowski, 1986; Clamp, 1991). Indeed, this ridge has no real equivalent in any other lagenophryid species.

Operculigera montanea has a simple vallum (Fig. 1), lacking the spines or other processes so characteristic of most other species in the genus (Jankowski, 1986; Clamp,

1991). Its shape resembles that of *O. zeehanensis* Kane, 1969, *O. inornata* n.sp., and *O. obstipa* Clamp, 1991; nevertheless, its distinctive proportions make it relatively easy to recognize. The vallum of *O. montanea* is markedly shorter in relation to its width than those of either *O. zeehanensis* or *O. inornata* (Figs. 1, 2, 14, 15; Tables 1, 2, 4–6). The vallums of *O. montanea* and *O. obstipa* are both short in relation to their widths but the vallum of the former is uniform in height compared to that of the latter, which diminishes in height from left to right (Table 6; Clamp, 1991).

Approximately 50% of the ciliates in the sample of *O. montanea* from the type locality contained one or more individuals of an unknown type of spherical, unicellular parasite in their cytoplasm (Fig. 10). Neither of the other samples examined showed any evidence of infection. The mean diameter of a sample of 15 parasites was $9.5 \pm 3.2 \mu\text{m}$ (4.8–13.9 μm). Each parasite had a single, dense nucleus (Fig. 10), eliminating the possibility that they could be ciliates of any kind, such as the suctorians that parasitize some peritrich ciliates. In addition, none of the distinctive stages in the life cycle of parasitic suctorians (Lynch & Noble, 1931; Matthes, 1971) were evident.

A closely fitting, thin-walled cyst or cell wall encapsulated the cell body of the parasite. Several ruptured, empty examples of these capsules were seen (Fig. 11), and a sample of 5 of them was measured. They had a mean diameter of $14.0 \pm 0.9 \mu\text{m}$ (12.7–15.3 μm). All empty capsules were in hosts that appeared either moribund or dead and disintegrating. One such capsule had a cluster of 16 small, oval cells nearby that may have been recently escaped swimmers of some kind. Each of these small cells had a single, dense, spherical nucleus similar to that of larger, encysted cells. A sample of 5 of the small cells had a mean length of $8.2 \pm 0.5 \mu\text{m}$ (7.4–8.7 μm) and a mean width of $5.7 \pm 0.6 \mu\text{m}$ (5.0–6.3 μm). The general appearance of the parasites suggests that they are either a species of chytrid fungus or amoeboid protozoan; however, positive identification will require more material than we had and observation of living parasites to elucidate their life cycle.

Note on the lorica aperture of *Operculigera*. Until now, functioning of the lorica aperture has not been described in living individuals of any species of *Operculigera*. Clamp

Table 1. Measurements and proportions (expressed as ratios of attributes to one another) of *Operculigera montanea* from the type locality and host (n=9).

Attribute	Mean (μm)	S.D. (μm)	C.V. (%)	Range (μm)
Height of lorica	37	± 3	7.1	34–41
Length of lorica	59.4	± 2.8	4.7	54.2–62.3
Width of lorica	66.5	± 4.2	6.3	57.5–71.1
Width of dorsal concavity	56.4	± 4.2	7.5	47.4–60.8
Width of vallum	25	± 1.2	5	23.4–26.8
Width of operculum	19.6	± 0.8	4.1	18.2–21.0
Width of epistomial disk	13.1	± 1.0	7.5	11.9–14.4
Length of micronucleus	3.8	± 0.4	9.2	3.4–4.5
Width of micronucleus	3.1	± 0.2	5.8	2.8–3.4
Length/width of lorica	0.89	± 0.04	4.3	0.85–0.94
Height/width of lorica	0.56	± 0.05	9.1	0.48–0.63
Width of vallum/width of lorica	0.38	± 0.02	6	0.35–0.41
Width of operculum/width of lorica	0.3	± 0.02	5.9	0.28–0.32
Width of epistomial disk/width of lorica	0.2	± 0.02	12.2	0.18–0.25
Length/width of micronucleus	1.22	± 0.15	12.1	1.03–1.48

Table 2. Measurements and proportions (expressed as ratios of attributes to one another) of *Operculigera zeehanensis* from the type locality and host (n=11). All individuals measured were on the holotype slide.

Attribute	Mean (μm)	S.D. (μm)	C.V. (%)	Range (μm)
Height of lorica	31	± 1	4.1	29–33
Length of lorica	77.8	± 2.9	3.7	73.6–82.2
Width of lorica	84.6	± 3.2	3.7	77.6–89.4
Width of vallum	24.9	± 1.1	4.5	23.5–27.4
Width of operculum	21.2	± 0.7	3.1	20.2–22.3
Width of epistomial disk	17.2	± 0.7	4.3	15.9–18.2
Length of micronucleus	3.6	± 0.1	3	3.5–3.8
Width of micronucleus	2.9	± 0.1	4.7	2.7–3.1
Length/width of lorica	0.92	± 0.05	5.3	0.86–1.03
Height/width of lorica	0.36	± 0.02	4.3	0.35–0.40
Width of vallum/width of lorica	0.29	± 0.01	4.5	0.27–0.32
Width of operculum/width of lorica	0.25	± 0.01	4.1	0.24–0.27
Width of epistomial disk/width of lorica	0.2	± 0.01	5.4	0.19–0.22
Length/width of micronucleus	1.25	± 0.06	4.5	1.16–1.32

(1991) described the operculum as being attached to the anterior edge of the aperture, based on sections of fixed material, and as opening toward the anterior, based on a short statement in Kane (1969). In this paper, we are able to draw on Kane's personal observations of living *O. montanea* that were more fully described and illustrated in his MSc thesis (Kane, 1964) than in the 1969 publication. In *O. montanea*, the operculum opens toward the posterior to lie against the dorsal surface of the lorica posteriad of the aperture. This allows the epistomial disk to protrude from the aperture anterior of the reflected operculum instead of posteriad to it if Clamp (1991) were correct. To accomplish this, the operculum would have to be attached to the dorsum of the cell immediately posteriad of the peristomial lip instead of to the anterior edge of the aperture. The sagittal sections of two species of *Operculigera* illustrated in Clamp (1991) do not show this, but the lack of contact between the cell body and the operculum could have been a fixation artefact. Further observations of living material and sections of freshly fixed material are needed to resolve this ambiguity.

Operculigera zeehanensis Kane, 1969

Fig. 2; Tables 2, 6, 7

Operculigera zeehanensis Kane, 1969: 369.–Jankowski, 1986: 82; Clamp, 1991: 365.

Redescription. Lorica hemispheroidal, suboval in dorsal view, slightly wider than long. Lorica asymmetrical in dorsal view; width of right half from midline to edge noticeably greater than width of left half from midline to edge. Rim of lorica not thickened. Dorsal surface of lorica without curved ridge. Posterior part of vallum reduced to slightly thickened ridge. Anterior and lateral parts of vallum moderately tall; posterior edges of lateral parts sloping moderately to posterior part of vallum, giving anterior and lateral parts symmetrically rounded profile as a whole. Free edge of vallum smooth, even, lacking projections of any sort. Long strip near base of inner wall of each anterolateral part of vallum moderately thickened and projecting inward to form prominent, protruding fold. Rim of lorica aperture moderately thickened. Operculum subcuneate in dorsal

view. Anterior edge of operculum moderately thickened to form narrow, ventral shelf; ventral shelf smooth, lacking processes.

Macronucleus elongate, cylindroid, usually folded to make compact mass. Macronucleus located in left half of body. Micronucleus ovoid, located almost always near centre of macronucleus rather than near either end.

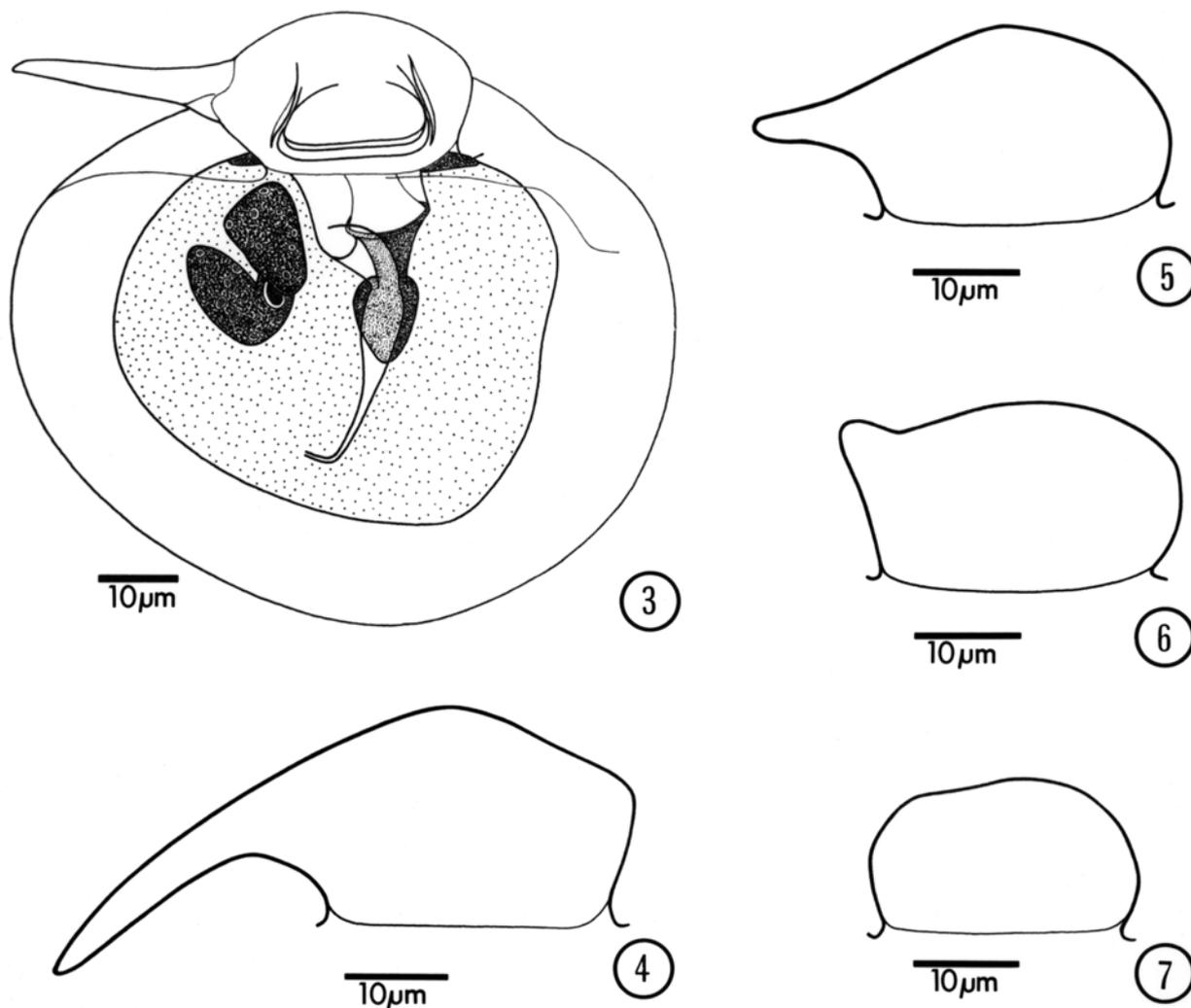
Etymology. The specific name refers to the locality from which the type host was collected.

Type material. LECTOTYPE, AUSTRALIA, Tasmania, near Zeehan; W. Drummond; on *Phreatoicoides longicollis* Nicholls, 1943, pleopods. Lectotype slide with lectotype organism marked by inscribed circle (Erlich's hematoxylin), AM P62813.

Operculigera haswelli n.sp.

Figs. 3–7, 12; Tables 3, 6

Description. Lorica hemispheroidal, suboval in dorsal view, moderately wider than long. Lorica more or less symmetrical in dorsal view; width of right half from midline to edge not noticeably greater than width of left half from midline to edge. Rim of lorica not thickened. Dorsal surface of lorica without curved ridge. Posterior part of vallum reduced to slightly thickened ridge. Anterior and lateral parts of vallum moderately tall; posterior edges of lateral parts sloping abruptly to posterior part of vallum and flaring outward. Free edge of vallum smooth, even, usually with spine on left margin. Spine varying from absent to as long as width of body of vallum. Long strip near base of inner wall of each anterolateral part of vallum moderately thickened and projecting inward to form prominent, protruding fold. Rim of lorica aperture heavily thickened. Operculum subcuneate in dorsal view. Anterior edge of operculum moderately thickened to form narrow, ventral shelf; ventral shelf smooth, lacking processes. Macronucleus elongate, cylindroid, usually folded to make compact mass. Macronucleus located in left half of body. Micronucleus ovoid, almost always located near centre of macronucleus rather than near either end.



Figs. 3–7. *Operculigera haswelli* n.sp. from the type locality and host; Heidenhain's hematoxylin preparations, AM P62814 and P62815. (3) Dorsal view of holotype individual with maximally developed spine. (4) Vallum with maximally developed spine curving posteriad. (5) Vallum with partially developed spine. (6) Vallum with minimally developed spine reduced to blunt process. (7) Vallum lacking spine.

Etymology. This species is named in honour of William A. Haswell, who published the first mention of lagenophryid peritrichs on Australian crustaceans in 1901.

Type material. HOLOTYPE, AUSTRALIA, Tasmania, Great Lake; 1914, W.M. Tattersall; on *Mesacanthotelson tasmaniae* (Thomson, 1894), pleopods (NMNH-CC USNM 60658). Holotype slide with holotype organism marked by inscribed circle (Heidenhain's hematoxylin), AM P62814. PARATYPE slides (Heidenhain's hematoxylin), AM P62815 and IPTC USNM 1004288.

Remarks. The spine on the left margin of the vallum of *O. haswelli* is unique within the genus. *Operculigera taura* Clamp, 1991 has a long, slender spine on each side of the anterior part of the vallum, but they project anteriad at a very different angle (Clamp, 1991) to the laterally projecting spine of *O. haswelli*, the tip of which curves toward the posterior in maximally developed examples (Fig. 4). *Operculigera velata* Jankowski, 1986 has a single, long, pointed process on the left margin of the vallum, but it is broad and bladelike rather than being a slender spine.

The spine on the vallum was extremely variable in its development among individual ciliates in the single sample

of *O. haswelli* that was examined. Most individuals had a spine of some sort (Figs. 3–6, 12), but the spine was completely absent in some (Fig. 7). When present, the spine varied from extremely long and acuminate (Figs. 3, 4, 12) to short, barely visible, blunt processes (Figs. 5, 6).

Operculigera inornata n.sp.

Figs. 13–15; Tables 4–7

Description. Lorica hemispheroidal, suboval to subcircular in dorsal view, slightly longer than wide. Lorica asymmetrical in dorsal view; width of right half from midline to edge noticeably greater than width of left half from midline to edge. Rim of lorica not thickened. Dorsal surface of lorica without curved ridge. Posterior part of vallum reduced to slightly thickened ridge. Anterior and lateral parts of vallum moderately tall; posterior edges of lateral parts sloping abruptly to posterior part of vallum, posterior edges nearly vertical. Free edge of vallum smooth, even, lacking projections of any sort. Long strip near base of inner wall of each anterolateral part of vallum moderately thickened and projecting inward to form prominent, protruding fold. Rim of lorica aperture moderately thickened. Operculum

Table 3. Measurements and proportions (expressed as ratios of attributes to one another) of *Operculigera haswelli* n.sp. from the type locality and host (n=20).

Attribute	Mean (µm)	S.D. (µm)	C.V. (%)	Range (µm)
Height of lorica	17	±2	12.3	14–21
Length of lorica	74.4	±3.4	4.6	69.8–83.1
Width of lorica	82.9	±4.5	5.4	73.7–89.1
Width of vallum	24.5	±1.3	5.4	22.0–27.2
Width of operculum	19.5	±1.0	5.2	16.7–21.3
Width of epistomial disk	12.7	±0.6	4.4	11.3–13.6
Length of micronucleus	5.1	±0.6	12.4	3.6–5.9
Width of micronucleus	3.3	±0.5	14.3	2.7–4.2
Length/width of lorica	0.91	±0.04	3.9	0.85–0.96
Height/width of lorica	0.22	±0.04	15.8	0.17–0.28
Width of vallum/width of lorica	0.3	±0.02	6.1	0.27–0.32
Width of operculum/width of lorica	0.24	±0.02	6.8	0.22–0.26
Width of epistomial disk/width of lorica	0.15	±0.01	7.7	0.13–0.17
Length/width of micronucleus	1.52	±0.17	11	1.23–1.79

subcuneate in dorsal view. Anterior edge of operculum moderately thickened to form narrow, ventral shelf; ventral shelf smooth, lacking processes. Macronucleus short to moderately elongate, cylindroid, usually folded to make compact mass. Macronucleus located in left half of body. Micronucleus ovoid, located more frequently near centre of macronucleus rather than near either end.

Etymology. The specific name (Latin: unadorned, simple) refers to the plain appearance of the lorica and its vallum.

Type material. HOLOTYPE, AUSTRALIA, Victoria, Otway Range; 24 Dec 1963, J.R. Kane; on *Phreatoicopsis terricola* Spencer & Hall, 1896, pleopods. Holotype slide with holotype organism marked by inscribed circle (Delafield's hematoxylin), AM P62816. PARATYPE slide (Delafield's hematoxylin), IPTC USNM 1004289. Victoria, Grampian Range, swamp near Fyan's Creek; 20 Nov 1963, J.R. Kane; on *Phreatoicopsis* sp., pleopods. Paratype slides (Delafield's hematoxylin), AMP62817 and IPTC USNM 1004290. Tasmania, Great Lake, 1914, W.M. Tattersall; on *Colubotelson chiltoni* (Sheppard, 1927), pleopods (NMNH-CC USNM 60657). PARATYPE slides (Heidenhain's hematoxylin), AM P62818 and IPTC USNM 1004291 (the latter comprises 2 slides).

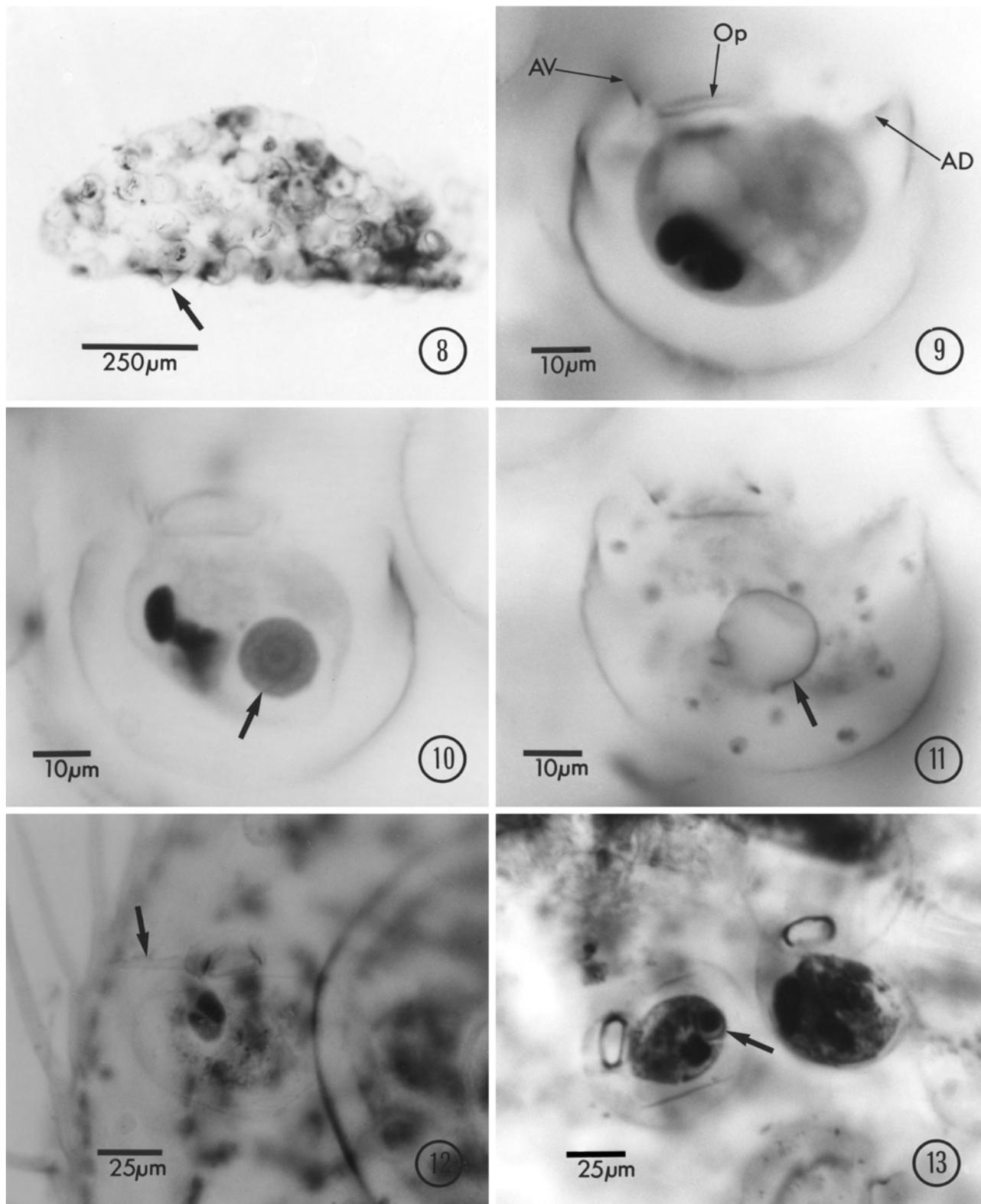
Remarks. The vallum of *O. inornata* lacks the spines or other types of processes so characteristic of some other

species of *Operculigera* (Jankowski, 1986; Clamp, 1991), but so do three other species of *Operculigera* that are hosted by various species of phreatoicid isopods (Figs. 1, 2; Table 6; Clamp, 1991). At first glance, this appears to create the potential for taxonomic confusion; however, two of these species, *O. obstipa* Clamp, 1991 and *O. montanea* (Fig. 1), are easily distinguished from *O. inornata* (Figs. 14, 15) by differences in shape and symmetry of the anterolateral part of the vallum, proportions of the lorica, and (in the case of *O. montanea*) presence of a prominent ridge in the dorsal surface of the lorica (Table 6).

The third species with a plain vallum, *O. zeehanensis* (Fig. 2), is much closer to *O. inornata* (Figs. 14, 15) in appearance but is separated from it by differences in the shape of the anterolateral part of the vallum and, especially, proportions of the lorica (Table 6). The lorica of *O. inornata* is subcircular to moderately longer than wide in dorsal view (Figs. 13–15; Tables 4, 5, 7). Only four individuals in the sample of *O. inornata* from Tasmania and none in the sample from Victoria had loricae that were slightly wider than they were long. By contrast, all but one individual in the sample of *O. zeehanensis* had loricae that were at least 5% wider than they were long

Table 4. Measurements and proportions (expressed as ratios of attributes to one another) of *Operculigera inornata* n.sp. from the type locality and host (n=25).

Attribute	Mean (µm)	S.D. (µm)	C.V. (%)	Range (µm)
Height of lorica	20	±2	9.6	15–23
Length of lorica	65.3	±2.0	3.1	59.5–69.1
Width of lorica	61.9	±2.9	4.8	53.5–67.1
Width of vallum	21.8	±0.8	3.7	19.0–23.3
Width of operculum	16.1	±0.7	4.6	13.7–17.1
Width of epistomial disk	12.9	±0.6	4.7	11.3–14.1
Length of micronucleus	3.1	±0.2	6.9	2.7–3.4
Width of micronucleus	2.2	±0.1	6.1	1.9–2.5
Length/width of lorica	1.06	±0.03	2.5	1.02–1.12
Height/width of lorica	0.32	±0.04	12.5	0.23–0.39
Width of vallum/width of lorica	0.35	±0.01	2.9	0.34–0.37
Width of operculum/width of lorica	0.26	±0.01	3.7	0.24–0.28
Width of epistomial disk/width of lorica	0.21	±0.01	6.1	0.19–0.24
Length/width of micronucleus	1.4	±0.11	7.9	1.25–1.59



Figs. 8–13. (8–11) *Operculigera montanea* from the type locality and host; Erlich's hematoxylin preparations, AM P62810. (8) Heavily infested pleopod of host at low magnification. Arrow, lateral view showing triangular profile of lorica. (9) Dorsal view of single individual. See Fig. 1 for explanation of symbols. (10) Dorsal view of individual with intracellular parasite (arrow). (11) Dorsal view of individual with empty, ruptured cyst of intracellular parasite (arrow). (12) Dorsal view of *Operculigera haswelli* n.sp. from the type locality and host; Heidenhain's hematoxylin preparation, AM P62814. Arrow, spine on left margin of vallum. (13) Dorsal view of two individuals of *Operculigera inornata* n.sp. from Great Lake, Tasmania; Heidenhain's hematoxylin preparation, IPTC USNM 1004291. Arrow, intracellular parasite.

Table 5. Measurements and proportions (expressed as ratios of attributes to one another) of *Operculigera inornata* n.sp. from Great Lake, Tasmania (n=19).

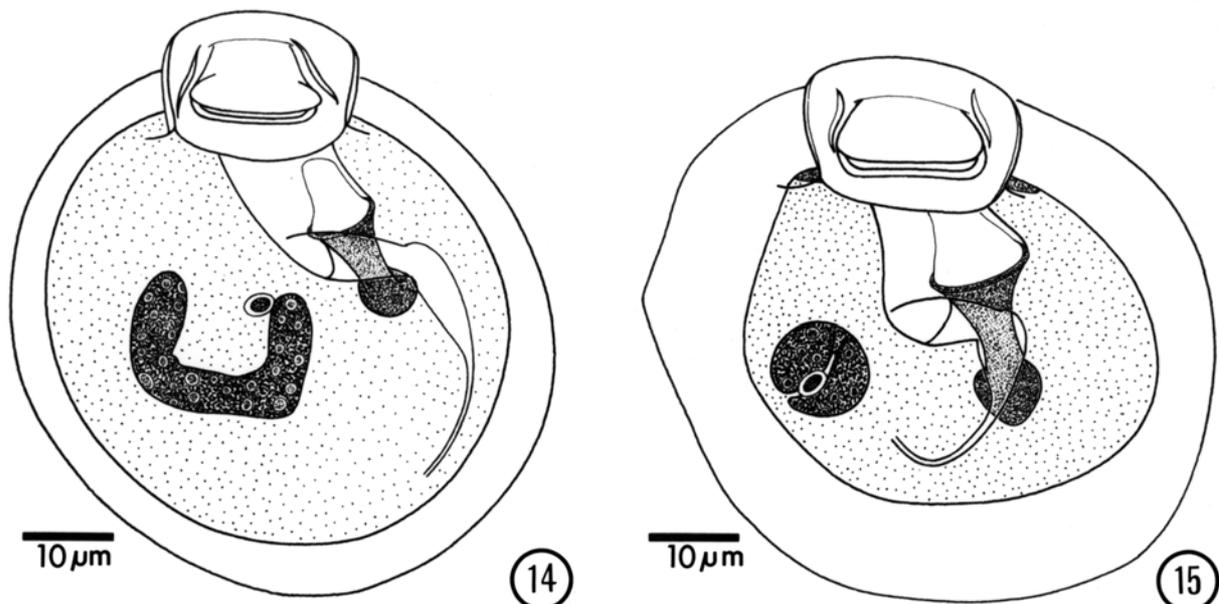
Attribute	Mean (μm)	S.D. (μm)	C.V. (%)	Range (μm)
Height of lorica	19	± 1	7.3	17–22
Length of lorica	66.3	± 4.9	7.3	58.9–76.4
Width of lorica	65.2	± 4.6	7	59.3–75.8
Width of vallum	23.4	± 1.1	4.9	21.3–25.1
Width of operculum	17.4	± 0.7	4	15.9–19.0
Width of epistomial disk	13.2	± 0.5	4	12.0–13.9
Length of micronucleus	3.9	± 0.6	16	3.2–5.7
Width of micronucleus	2.6	± 0.3	11.1	2.2–3.6
Length/width of lorica	1.02	± 0.03	3.3	0.93–1.07
Height/width of lorica	0.3	± 0.02	7.6	0.24–0.35
Width of vallum/width of lorica	0.36	± 0.02	6	0.30–0.41
Width of operculum/width of lorica	0.27	± 0.02	5.8	0.24–0.31
Width of epistomial disk/width of lorica	0.2	± 0.02	7.4	0.18–0.23
Length/width of micronucleus	1.48	± 0.15	10	1.25–1.93

(Table 7). In addition, the width of the vallum in comparison to the width of the lorica was markedly greater in both samples of *O. inornata* than in the single sample of *O. zeehanensis* (Table 7). Only one individual in the sample of *O. inornata* from Tasmania fell within the range seen in *O. zeehanensis* in regard to this proportion. Otherwise, the two species did not overlap. Finally, one characteristic of the cell body clearly differed between *O. inornata* and *O. zeehanensis*. The epistomial disk of *O. zeehanensis* was, on the average, 30% wider than the epistomial disk of *O. inornata* (Figs. 2, 14, 15; Tables 2, 4, 5).

The same type of intracellular parasite that was found in one sample of *O. montanea* was observed in the sample of *O. inornata* from Tasmania (Fig. 13); the percentage of infected individuals (approximately 8%), however, was much lower in the latter. No parasites were seen in the samples of *O. inornata* from Victoria.

Setonophrys Jankowski, 1986

Diagnosis. Solitary, loricate, with lorica aperture bounded by and closable by two opposing lips formed from folds of lorica material. Anterior lip of aperture thick-walled, rigid, usually with one or more spines on edge. Posterior lip thin-walled, flexible, pulled into lorica and pressed against anterior lip to effect closure of aperture. Vallum absent. Loricostome present, consisting of tubular passageway of lorica material that extends into interior of lorica from ventral edges of aperture lips. Edge of peristomial lip of trophont adherent to posterior surface of loricostome. Entire circumference of myonemal band within peristomial lip thickened. Macronucleus elongate, located in approximate centre of body, with same distinctive shape in all species. Medial portion of macronucleus extremely slender, straight or slightly curved, parallel to transverse axis of body or



Figs. 14, 15. *Operculigera inornata* n.sp. (14) Dorsal view of holotype individual from type locality and host; Delafield's hematoxylin preparation, AM P62816. (15) Dorsal view of individual from Great Lake, Tasmania; Heidenhain's hematoxylin preparation, AM P62818.

Table 6. Comparison of species of *Operculigera* hosted by phreatoicid isopods. Information on *O. obstipa* is derived from Clamp (1991).

<i>Operculigera</i> species	shape of lorica	proportions of lorica	presence of curved ridge in dorsal surface of lorica	symmetry of antero-lateral part of vallum	height of anterolateral part of vallum	shape of anterolateral part of vallum	processes on antero-lateral part of vallum	host(s)
<i>O. montanea</i>	asymmetrical	shorter than wide	yes	uniform in height	short	posterior edges sloping abruptly; "squared-off" shape	none	<i>Colubotelson joyneri</i> , <i>Colubotelson</i> sp.
<i>O. zeehanensis</i>	asymmetrical	shorter than wide	no	uniform in height	moderately tall	posterior edges sloping gradually; "rounded" shape	none	<i>Phreatoicoides longicollis</i>
<i>O. haswelli</i>	symmetrical	shorter than wide	no	uniform in height	moderately tall	posterior edges sloping abruptly and flared outward	laterally projecting spine on left margin	<i>Mesacanthotelson tasmaniae</i>
<i>O. inornata</i>	asymmetrical	subcircular to longer than wide	no	uniform in height	moderately tall	posterior edges sloping abruptly; "squared-off" shape	none	<i>Phreatoicopsis terricola</i> , <i>Colubotelson chiltoni</i>
<i>O. obstipa</i>	asymmetrical	shorter than wide	no	sloping from right to left	short	posterior edges sloping abruptly; "squared-off" shape	none	<i>Metaphreatoicus australis</i> (Chilton, 1891)

slanting posteriad from left to right at slight angle to transverse axis. Ends of macronucleus much thicker than medial portion, curved anteriorly away from medial portion.

Generic composition. The following species are currently assigned to *Setonophrys*: *S. bispinosa* (Kane, 1965); *S. communis* (Kane, 1965); *S. lingulata* (Kane, 1965); *S. nivalis* (Kane, 1969); *S. occlusa* (Kane, 1965); *S. seticola* (Kane, 1965); *S. spinosa* (Kane, 1965); *S. tricorniculata* Clamp, 1991.

***Setonophrys nivalis* (Kane, 1969)**

Fig. 16; Table 8

Lagenophrys nivalis Kane, 1969: 369.
Circolagenophrys nivalis.—Jankowski, 1986: 87.
Setonophrys nivalis.—Clamp, 1991: 360.

Redescription. Lorica hemispheroidal, suboval in dorsal view, moderately longer than wide. Lorica symmetrical in dorsal view. Rim of lorica heavily thickened at posterior, diminishing to moderately thickened at anterior. Lips of lorica aperture tall, with vertical sides, creating almost tubular aperture. Short to moderately long spine on each side of anterior lip, originating slightly below edge of anterior lip and projecting almost directly laterad. Anterior lip thick-walled, with straight, symmetrical edge. Posterior lip thin-walled, without spines or other projections, with straight, symmetrical edge.

Macronucleus elongate, cylindroid, located in approximate centre of body. Medial portion of macronucleus slender, straight or slightly curved, usually slanting posteriad from left to right at slight angle to transverse axis of body, infrequently parallel to transverse axis of body. Ends of macronucleus thicker than medial portion; right end always

curved sharply anteriorly away from medial portion, left end usually curved sharply anteriorly away from medial portion but sometimes extending straight out from medial portion. Micronucleus ovoid, located near right end of macronucleus.

Etymology. The specific name (Latin: snowy) refers to the montane habitat of the host.

Table 7. Distributions of values for two proportions of the lorica in *Operculigera zeehanensis* and *Operculigera inornata* n.sp. OZ, *O. zeehanensis* from the type locality; OI-V, *O. inornata* from Victoria (type locality); OI-T, *O. inornata* from Tasmania. Numerals in each column are numbers of individuals with each value. Lack of individuals expressing a particular value is indicated by a dot to enhance visibility of the distributions relative to one another. L, length; W, width.

lorica L / value	lorica W			vallum W / value	lorica W		
	OZ	OI-V	OI-T		OZ	OI-V	OI-T
1.11–1.12	.	2	.	0.41–0.42	.	1	.
1.09–1.10	.	1	.	0.39–0.40	.	.	.
1.07–1.08	.	4	1	0.37–0.38	.	8	3
1.05–1.06	.	11	4	0.35–0.36	.	6	17
1.03–1.04	1	3	3	0.33–0.34	.	3	5
1.01–1.02	.	4	5	0.31–0.32	1	.	.
0.99–1.00	.	.	3	0.29–0.30	6	1	.
0.97–0.98	.	.	2	0.27–0.28	3	.	.
0.95–0.96	3	.	.				
0.93–0.94	1	.	1				
0.91–0.92	.	.	.				
0.89–0.90	3	.	.				
0.87–0.88	2	.	.				
0.85–0.86	1	.	.				

Table 8. Measurements and proportions (expressed as ratios of attributes to one another) of *Setonophrys nivalis* from the type locality and host (n=15).

Attribute	Mean (μm)	S.D. (μm)	C.V. (%)	Range (μm)
Height of lorica	26	± 3	10.8	22–30
Length of lorica	94.8	± 3.3	3.5	90.3–102.5
Width of lorica	80.8	± 3.0	3.8	74.9–86.0
Width of lorica aperture	23.1	± 1.4	6.1	20.3–25.1
Width of lorica margin	3.2	± 0.7	20.4	2.1–4.6
Width of epistomial disk	15.4	± 0.9	5.7	14.1–17.2
Length of micronucleus	5.3	± 0.6	11.6	4.5–6.3
Width of micronucleus	3.5	± 0.3	9.3	3.0–4.1
Length/width of lorica	1.17	± 0.04	3.7	1.09–1.27
Height/width of lorica	0.32	± 0.03	10.4	0.27–0.36
Width of lorica aperture/width of lorica	0.29	± 0.02	6.2	0.26–0.32
Width of epistomial disk/width of lorica	0.19	± 0.01	4.8	0.18–0.21
Length/width of micronucleus	1.54	± 0.21	13.5	1.12–1.97

Type material. LECTOTYPE, AUSTRALIA, Victoria, Mt Baw Baw (1850 m elevation); 13 Oct 1963, J.R. Kane; on *Colubotelson searlei* Nicholls, 1944, pereopods and dorsum. Lectotype slide with lectotype organism marked by inscribed circle (Erlich's hematoxylin), AM P62819. PARALLECTOTYPE slides (Erlich's hematoxylin), AM P62820, P62884, P62885, and IPTC USNM 1004292 (the latter comprises 3 slides).

Remarks. Most species of *Setonophrys* have one or more spines on the anterior lip of the lorica aperture; *S. nivalis*, however, is distinct from them in regard to the shape, position, and angle of projection of its two spines. Spines tend to be long, are always located on the anterior or anterolateral parts of the anterior lip, and project anteriorly

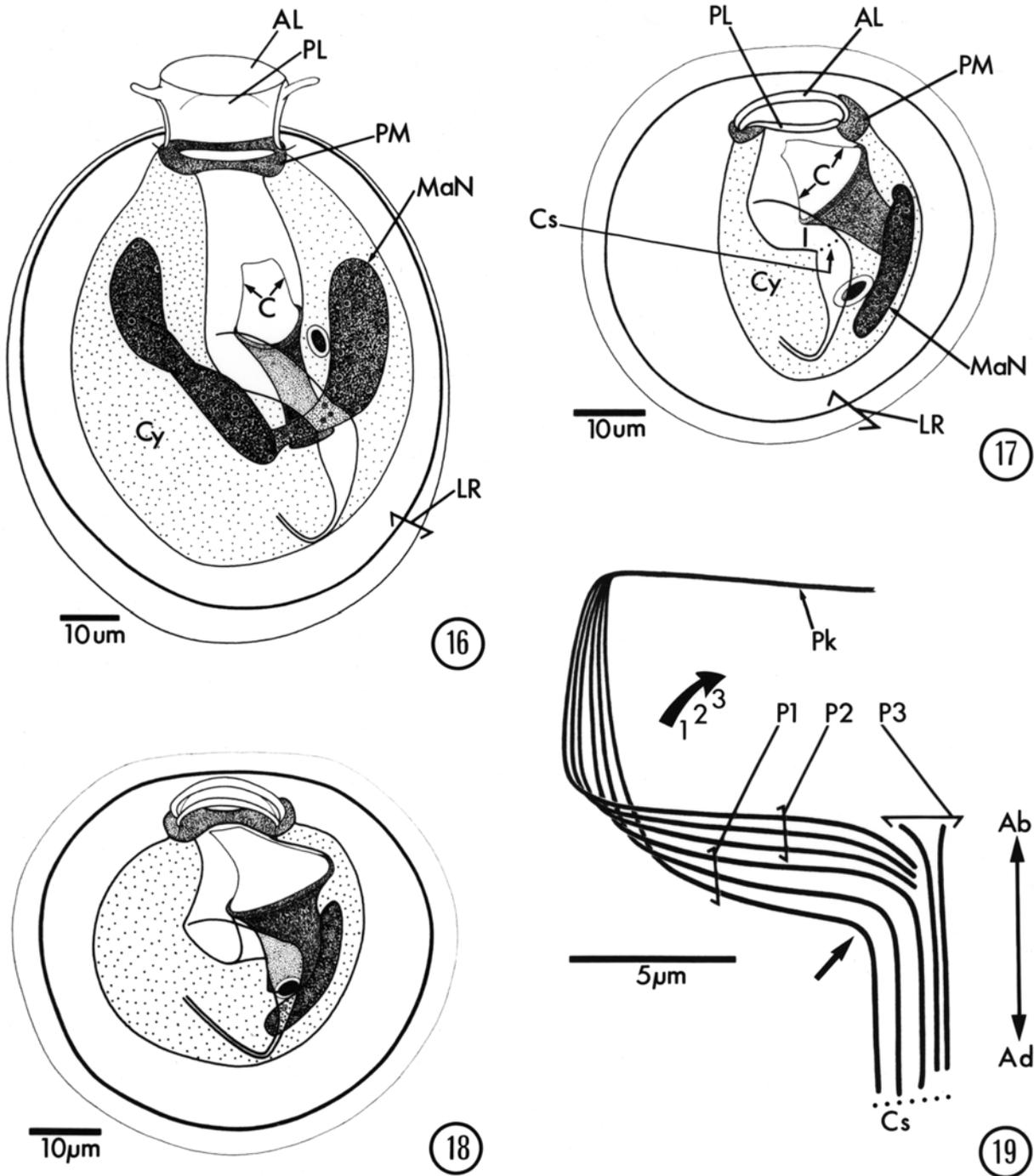
in other species of *Setonophrys* (Kane, 1965; Clamp, 1991). In addition, these spines tend to be wider at their bases, tapering gradually to a sharp tip. By contrast, the spines of *S. nivalis* are relatively short, are located on the lateral parts of the anterior lip, project directly laterad, and are quite slender from their bases to their tips (Fig. 16).

Lagenophrys Stein, 1852

Diagnosis. Solitary, loricate, with lorica aperture bounded by and closable by two opposing lips formed from folds of lorica material. Both lips of lorica aperture thin-walled, flexible, sometimes with thickened edges or processes. Spines never present on anterior lip although edges of one or both lips may be tuberculate or serrate. Lips of aperture

Table 9. Measurements and proportions (expressed as ratios of attributes to one another) of *Lagenophrys turneri* from the type locality and host (n=25). Eighteen of the individuals measured were on the holotype slide; the remainder were on one of the paratype slides.

Attribute	Mean (μm)	S.D. (μm)	C.V. (%)	Range (μm)
Height of lorica	16	± 2	10.2	13–18
Length of lorica	56.1	± 2.8	5	50.7–62.3
Width of lorica	61.6	± 3.6	5.8	53.7–66.6
Width of anterior lip of lorica aperture	18	± 0.5	2.7	16.9–18.8
Width of posterior lip of lorica aperture	16	± 0.5	3.2	14.9–16.6
Thickness of anterior lip of lorica aperture	3	± 0.2	7.6	2.6–3.4
Thickness of posterior lip of lorica aperture	2.1	± 0.1	6.8	1.7–2.3
Width of lorica margin	3.9	± 0.4	9	2.7–4.4
Width of epistomial disk	15	± 0.6	4.3	13.8–15.8
Length of macronucleus	29.1	± 4.9	16.9	17.3–36.1
Width of macronucleus at midpoint	5.5	± 1.0	18.1	3.6–7.3
Length of micronucleus	4.3	± 0.3	7.4	3.7–4.9
Width of micronucleus	3	± 0.2	6.9	2.7–3.5
Length/width of lorica	0.91	± 0.03	3.3	0.85–0.97
Height/width of lorica	0.26	± 0.03	11.9	0.20–0.32
Width of anterior lip of lorica aperture/ width of lorica	0.3	± 0.02	5.6	0.27–0.34
Width of anterior lip of lorica aperture/ width of posterior lip of lorica aperture	1.14	± 0.03	2.4	1.09–1.20
Thickness of anterior lip of lorica aperture/ thickness of posterior lip of lorica aperture	1.41	± 0.13	8.9	1.23–1.62
Width of epistomial disk/width of lorica	0.24	± 0.02	6.6	0.22–0.28
Length/width of macronucleus	5.29	± 1.51	28.6	2.10–9.84
Length/width of micronucleus	1.41	± 0.12	8.8	1.14–1.59



Figs. 16–19. (16) *Setonophrys nivalis*, Erlich’s hematoxylin preparation. Dorsal view of lectotype individual from the type locality and host, AM P62819. (AL) Anterior lip of lorica aperture; (PL) posterior lip of lorica aperture; see Fig. 1 for explanation of other symbols. The micronucleus is the small, ovoid, darkly stained body located near the right end of the macronucleus. (17–19) *Lagenophrys turneri*. (17) Dorsal view of lectotype individual from the type locality and host; Erlich’s hematoxylin preparation, AM P62821. The lorica aperture is partially open. (Cs) Boundary between infundibulum and cytotome (= ampulla); see Figs. 1, 16 for explanation of other symbols. The micronucleus is the small, ovoid, darkly stained body located near the posterior end of the macronucleus. (18) Dorsal view of individual from Papua New Guinea; Heidenhain’s hematoxylin preparation, AM P62822. The lorica aperture is almost closed. (19) Dorsal view of infundibular polykinetids of individual from Papua New Guinea; protargol preparation, AM P62886. The polykinetids are rows of kinetosomes and associated cilia (not shown) that are located on the wall of the infundibulum (Figs. 17, 21, 22). The rows of kinetosomes that constitute the polykinetidal infraciliature normally visible under the light microscope are shown as solid lines for the sake of convenience and clarity. (Ab) abostomal direction (= away from the cytotomal region); (Ad) adstomal direction (= toward the cytotomal region); (P1) polykinetid 1; (P2) polykinetid 2; (P3) polykinetid 3; (Pk) polykinety (the part of P1 that extends out onto the peristomal lip—only the part proximal to the infundibulum is shown); arrow with numerals shows the convention for numbering individual rows within each polykinetid; large arrow, adstomal curvature of P1.

drawn together equally to effect closure of aperture, with neither one losing its shape in doing so. Vallum absent. Loricastome present; edge of peristomial lip of trophont adherent to posterior surface of loricastome. Posterior half of myonemal band within peristomial lip thickened. Shape and location of macronucleus differs among species.

Generic Composition. The following species are currently assigned to *Lagenophrys*: *L. aegleae* Mouchet-Bennati, 1932; *L. ampulla* Stein, 1852; *L. andos* (Jankowski, 1986); *Lagenophrys anisogammari* (Jankowski, 1993) **n.comb.**; *L. antictos* Clamp, 1988c; *L. aselli* Plate, 1889; *L. awerinzewi* Abonyi, 1928; *L. bipartita* Stokes, 1890; *L. branchiarum* Nie & Ho, 1943; *L. callinectes* Couch, 1967; *L. cochinchensis* Santhakumari & Gopalan, 1980; *L. commensalis* Swarczewsky, 1930; *L. crutchfieldi* Clamp, 1993; *L. darwini* Kane, 1965; *L. dennisi* Clamp, 1987; *L. deserti* Kane, 1965; *L. diogenes* (Jankowski, 1986); *L. discoidea* Kellicott, 1887; *L. dungogi* Kane, 1965; *L. engaei* Kane, 1965; *L. eupagurus* Kellicott, 1893; *L. foxi* Clamp, 1987; *Lagenophrys hokkaidos* (Jankowski, 1993) **n.comb.**; *L. inflata* Swarczewsky, 1930; *L. jacobi* (Kane, 1969); *L. johnsoni* Clamp, 1990b; *L. labiata* Stokes, 1887; *L. leniusculus* (Jankowski, 1986); *L. lenticula* (Kellicott, 1885); *L. limnoria* Clamp, 1988a; *L. machaerigera* Clamp, 1992; *L. macrostoma* Swarczewsky, 1930; *L. matthesi* Schödel, 1983; *Lagenophrys maxillaris* (Jankowski, 1993) **n.comb.**; *L. metopauliadis* Corliss & Brough, 1965; *L. missouriensis* Clamp, 1987; *L. monolistræ* Stammer, 1935; *L. nassa* Stein, 1852; *L. novazealandae* Clamp, 1994; *L. oblonga* Swarczewsky, 1930; *L. orchestiae* Abonyi, 1928; *L. ornata* Swarczewsky, 1930; *L. ovalis* Swarczewsky, 1930; *L. parva* Swarczewsky, 1930; *L. patina* Stokes, 1887; *L. petila* Clamp, 1994; *L. platei* Wallengren, 1900; *L. pontocaspica* Boshko, 1995; *L. reflexa* Kane, 1969; *L. rugosa* Kane, 1965; *L. shiftus* (Jankowski, 1986); *L. similis* Swarczewsky, 1930; *L. simplex* Swarczewsky, 1930; *L. solida* Swarczewsky, 1930; *L. stammeri* Lust, 1950; *L. stokesi* Swarczewsky, 1930; *L. stygia* Clamp, 1990a; *L. tattersalli* Willis, 1942; *L. turneri* Kane, 1969; *L. vaginicola* Stein, 1852; *L. verecunda* Felgenhauer, 1982; *L. willisi* Kane, 1965.

Note on the nomenclature of the genus *Lagenophrys*. Jankowski (1980) created the genus *Circolagenophrys* for the many species of *Lagenophrys* that have a more or less circular outline in dorsal view and reserved the genus *Lagenophrys* for its type species, *L. vaginicola* Stein, 1852, which has a narrow lorica that is adapted for attachment to setae of its host. Clamp (1991) considered this difference in shape of the lorica insufficient to justify this generic separation, citing ample evidence to support of his position, and made *Circolagenophrys* a subjective junior synonym of *Lagenophrys*. Despite this, Jankowski (1993) has continued to use *Circolagenophrys*. We find no reason to resurrect *Circolagenophrys*, in the absence of any evidence contradicting Clamp (1991), and will, therefore, continue to include *L. turneri* in *Lagenophrys* as defined originally by Stein (1852) and redefined by Clamp (1991). Three new species of *Lagenophrys* placed in *Circolagenophrys* by Jankowski (1993) have been treated as new combinations in the listing of species given above.

Lagenophrys turneri Kane, 1969

Figs. 17–22; Tables 9, 10

Lagenophrys turneri Kane, 1969: 369.–Clamp, 1991: 358.
Circolagenophrys turneri.–Jankowski, 1986: 87.

Redescription. Lorica hemispheroidal, suboval to subcircular; if suboval, slightly to moderately wider than long. Rim of lorica very broad. Inner part of lorica rim slightly to moderately thickened; rim diminishing in thickness progressively to extremely thin edge. Lips of lorica aperture short, moderately arched; anterior lip slightly wider than posterior lip. Edges of both lips heavily thickened, smooth, without projections or indentations. Edge of anterior lip usually slightly to moderately thicker than edge of posterior lip. Anterior lip without crochets.

Trochal band of kinetosomes broken on right side in trophont; ends of break separated by wide gap. Infraciliature of infundibular polykinetids as follows: kinetosome rows of infundibular polykinetid 1 (P1) approximately equal in length, ending at cytostome; kinetosome rows of P2 equal in length, ending at abostomal curvature of P1. P2 not separated from P1 by wide gap; distance between row 3 of P1 and row 1 of P2 approximately equal to distances between rows within both polykinetids. P3 consisting of two kinetosome rows of approximately equal length. Rows of P3 slightly divergent at abostomal ends, closely parallel for remainder of length. P3 extending abostomally to point slightly beyond adstomal end of P2, ending adstomally at point slightly short of adstomal end of P1 and cytostome.

Macronucleus elongate, cylindroid, slightly curved, located along right edge of body, conforming to curve of edge of body. Micronucleus ovoid, located more often near centre of macronucleus than near either end of macronucleus.

Etymology. The species is named in honour of Mr J. Turner, who provided specimens of the host from the type locality.

Type material. LECTOTYPE, AUSTRALIA, Northern Territory, Katherine, Katherine R; 13 Sep 1963, J. Turner; on *Macrobrachium rosenbergi* (de Man), gill lamellae. Lectotype slide with lectotype organism marked by inscribed circle (Erlich's hematoxylin), AM P62821. PARALECTOTYPE slide (Erlich's hematoxylin), IPTC USNM 1004293.

Other material examined. PAPUA NEW GUINEA, Gulf District, near Malalaua, Lake Kamu R.; May 1972, L.B. Holthuis; on *M. rosenbergi*, gill lamellae (NMNH-CC USNM 141316). Voucher slides, (Heidenhain's hematoxylin, protargol) AM P62822, P62886 and (Heidenhain's hematoxylin) IPTC USNM 1004294. Additional slides of this material remain in the senior author's personal collection.

Remarks. The infundibular infraciliature of *L. turneri* (Figs. 19, 22) is essentially identical to that of *L. eupagurus* Kellicott, 1893 and *L. callinectes* Couch, 1967 (Couch, 1973; Clamp, 1989). All three species also share the unusual characteristic of having the trochal band of kinetosomes broken on the right side in the trophont, leaving a wide gap (Couch, 1967, 1973; Clamp, 1989). The trochal band is a continuous ring of kinetosomes in trophonts of other species of *Lagenophrys* that have been stained with protargol (Clamp, 1987, 1988a,b, 1990a,b, 1992, 1994), as is typical in peritrichs. In addition, the shape and position of the macronucleus (Figs. 17, 18, 21) in *L. turneri* is the same as in *L. eupagurus* and *L. callinectes*.

Table 10. Measurements and proportions (expressed as ratios of attributes to one another) of *Lagenophrys turneri* from Papua New Guinea (n=25).

Attribute	Mean (μm)	S.D. (μm)	C.V. (%)	Range (μm)
Height of lorica	17	± 2	12.1	13–21
Length of lorica	58.6	± 1.7	2.9	55.5–62.3
Width of lorica	61.9	± 2.2	3.6	56.6–66.3
Width of anterior lip of lorica aperture	16.1	± 0.4	2.8	15.2–17.0
Width of posterior lip of lorica aperture	14.9	± 0.5	3.4	13.6–15.6
Thickness of anterior lip of lorica aperture	1.6	± 0.1	9.1	1.4–1.9
Thickness of posterior lip of lorica aperture	1.3	± 0.1	11.1	1.1–1.6
Width of lorica margin	3.5	± 0.5	14.3	2.4–4.7
Width of epistomial disk	15.5	± 0.8	5.5	13.8–17.0
Length of macronucleus	24.8	± 3.6	14.4	19.4–32.8
Width of macronucleus at midpoint	4	± 0.5	12.6	3.2–4.9
Length of micronucleus	3.8	± 0.4	9.7	3.1–4.5
Width of micronucleus	2.2	± 0.1	6	2.0–2.5
Length/width of lorica	0.95	± 0.02	1.9	0.92–0.98
Height/width of lorica	0.28	± 0.03	12.3	0.21–0.34
Width of anterior lip of lorica aperture/width of lorica	0.26	± 0.01	3.1	0.25–0.28
Width of anterior lip of lorica aperture/width of posterior lip of lorica aperture	1.09	± 0.02	2.2	1.04–1.14
Thickness of anterior lip of lorica aperture/thickness of posterior lip of lorica aperture	1.23	± 0.13	10.5	0.94–1.46
Width of epistomial disk/width of lorica	0.25	± 0.02	6.5	0.22–0.30
Length/width of macronucleus	6.14	± 0.94	15.3	3.09–7.73
Length/width of micronucleus	1.69	± 0.21	112.3	1.32–2.05

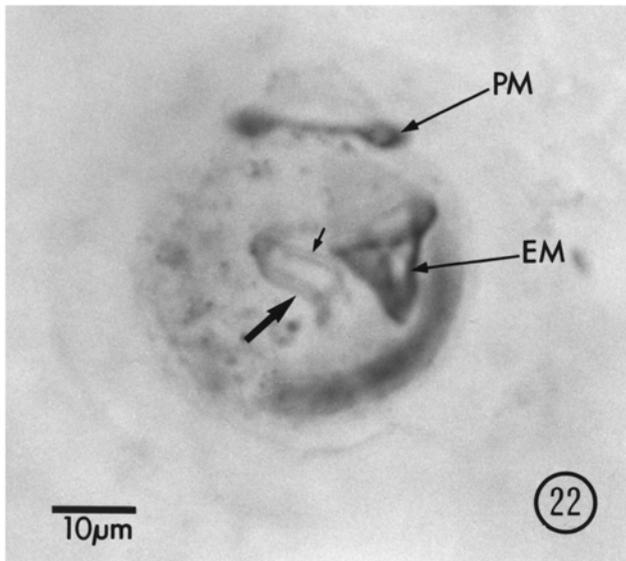
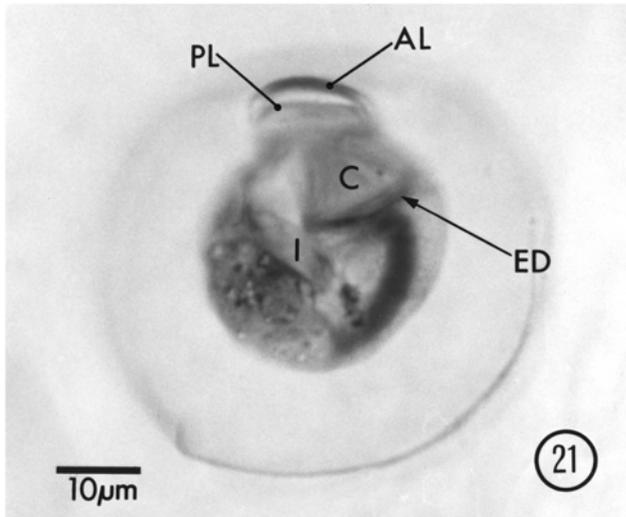
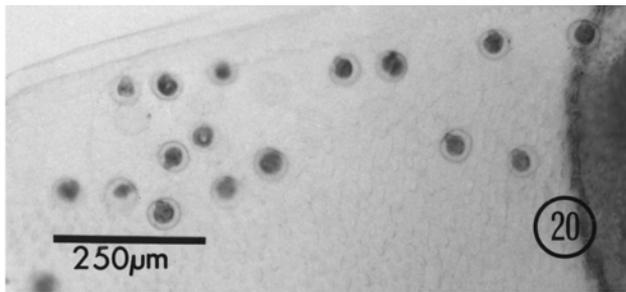
The edges of both lips of the lorica aperture are heavily thickened in *L. turneri*, *L. eupagurus*, and *L. callinectes*, but the latter two species have deep clefts in each lip that are lacking in *L. turneri* (Figs. 17, 18, 21; Couch, 1967; Clamp, 1989). The lips of the lorica aperture of *L. turneri* resemble those of *L. callinectes* more than those of *L. eupagurus* in having the anterior lip significantly thicker than the posterior lip (Fig. 18; Tables 9, 10; Clamp, 1989). The differences in the morphology of the lorica aperture confirm the distinctness of *L. turneri* as a species while the several apparent synapomorphies that it shares with *L. eupagurus* and *L. callinectes* suggest that the three species may share a close phylogenetic relationship within the genus. Their restriction to decapod crustaceans as hosts reinforces this hypothesis.

Discussion

Operculigera has a far-flung distribution in the Southern Hemisphere, occurring exclusively on freshwater hosts in Australia, Chile, and Madagascar (Kane, 1969; Jankowski, 1986; Clamp, 1991, 1992). The Australian species of *Operculigera* constitute a group that is ecologically distinct from those in other areas. In Chile, all of the several known species of *Operculigera* occur on parastacid crayfishes and aeglid crabs (Jankowski, 1986; Clamp, 1991). The two species of *Operculigera* described from Madagascar also live on decapods, one on a parastacid crayfish and another on a potamoid crab (Clamp, 1992). In striking contrast to this, all species of *Operculigera* discovered in Australia so far have been found on phreatoicid isopods, with the single exception of an undescribed species on the amphipod *Austrochiltonia* (Kane, 1969; Clamp, 1991; Clamp, unpublished observations).

Observer bias cannot be the source of this disparity since, between them, the authors have examined many species of Australian parastacids and other freshwater decapods, such as shrimps and crabs, without finding a single species of *Operculigera* on any of them. Australian parastacids host a rich, diverse fauna of lagenophryid peritrichs, including many species of *Lagenophrys* and *Setonophrys* (Kane, 1964, 1965; Clamp, 1991), but *Operculigera* seems to be genuinely absent from them. By contrast, five species of *Operculigera* have been discovered on a mere handful of the many species of Australian phreatoicids, suggesting that a significant number of undescribed species of *Operculigera* may remain to be found on others.

Aside from their unusual lack of distribution on decapods, Australian species of *Operculigera* appear to form a group that is morphologically distinct from other members of the genus. Species of *Operculigera* reported from Madagascar and Chile fall into two general groups: (1) those with no vallum (*O. carcini*) or a greatly reduced vallum (*O. striata*) and (2) those with a well-developed vallum (*O. asymmetrica*, *O. insolita*, *O. madagascarensis*, *O. parastacis*, *O. seticola*, *O. taura*, *O. velata*) that usually has one or more spines or other kinds of prominent processes on the anterior part (Jankowski, 1986; Clamp, 1991, 1992). Most species in the latter group also show at least partial development of the posterior part of the vallum (see *O. parastacis* in Jankowski, 1986 and *O. insolita* in Clamp, 1991). Species of *Operculigera* on Australian phreatoicids differ from those in both of these groups by having the anterior part of their vallum well developed but, excepting the spinose morphs of *O. haswelli*, with no spines or other processes. Unlike species in the second group, all of the Australian species of *Operculigera* have the posterior half of the vallum reduced to a slight ridge of lorica material at most.



Figs. 20–22. *Lagenophrys turneri* from Papua New Guinea. (20) Infested gill lamella of host at low magnification; Heidenhain's hematoxylin preparation. (21) Dorsal view of single individual; Heidenhain's hematoxylin preparation. See Figs. 1, 16 for explanation of symbols. (22) Dorsal view of single individual; protargol preparation. Large arrow, infundibular polykinetids; small arrow, haplokinety—the haplokinety is a band of dikinetids that extends into the infundibulum from the peristome, where it is the outer band of kinetosomes. It does not vary among sessiline peritrichs and is routinely omitted from views such as Fig. 19 for that reason. See Fig. 1 for explanation of symbols.

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