An annotated checklist of species in the family Lagenophryidae (Ciliophora, Oligohymenophorea, Peritrichia), With a brief review of their taxonomy, morphology, and biogeography

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Abstract

The genera Lagenophrys Stein, 1852, Paralagenophrys Clamp, 1987, Clistolagenophrys Clamp, 1991, and Operculigera Kane, 1969 make up the family Lagenophryidae and, together, contain more than 80 species worldwide that live mainly as ectosymbionts of crustaceans. Lagenophryids are characterized by possession of a lorica, but the lorica aperture and the associated parts of the body differ between genera. Despite their widespread distribution, relatively few papers have been published on lagenophryids in recent years, and the present paper is intended to promote research on lagenophryids by providing an annotated checklist of all known species and a brief review of the family, including data of their geographic distribution and their hosts.

Key words: Peritrichs, lagenophryids, crustacean ectosymbiont, lorica

Introduction

Peritrichs are a large subclass1 (Zhan et al. 2009) of ciliated protists (~1000 known species) in which the usually sessile trophonts live as stationary suspension feeders. Most taxa of peritrichs are highly specialized for a variety of ecological niches in terms of both their morphology and morphogenesis. Within this diverse assemblage, the family Lagenophryidae stands out as having exceptional morphological, reproductive, and developmental adaptions for living as obligate ectosymbionts of crustaceans.

More than 80 species of lagenophryids have been discovered on a diverse array of crustacean hosts, including decapods (crayfish, crabs, shrimp), amphipods, isopods, copepods, ostracods and cladocerans (Clamp 2006). Lagenophryids are relatively well-known, and many papers on their systematics, distribution, and biology have been published since their discovery by Stein (1852). However, relatively few papers have been published on lagenophryids in recent years (Clamp 2006; Mayén-Estrada & Aguilar-Aguilar 2012), and they represent an untapped potential in terms of their use as model organisms to investigate questions in the areas of phylogenetics, population genetics, morphogenesis, mechanisms of dispersal, and biogeography.

One factor that certainly prevents lagenophryids from receiving more attention is the rather demanding requirement that investigators must be equally familiar with the biology and habits of the crustacean hosts and their symbionts. The solution is either deliberate cross-training of graduate students or postdoctoral fellows to give them the ability to conceive and carry out research on symbiotic ciliates like lagenophryids or collaboration between

1. For the purposes of this paper, we have chosen to accept the proposal of Zhan et al. (2009) that mobilids are a distinct subclass separate from peritrichs; therefore, the present paper considers the Peritrichia s. str. to be those taxa formerly placed within the order Sessilida.
researchers with complementary backgrounds and skills. The present paper is intended to promote research on lagenophryids by providing an annotated checklist of all known species and a brief review of the family to researchers with diverse backgrounds.

Methodology

Geographic distribution and known hosts of each lagenophryid species were compiled from all available records in the literature. In some cases, we were able to use specific locality names and references to obtain the latitude and longitude coordinates using Google Earth™ maps. We verified the taxonomic names of crustaceans using web resources of WoRMS, the Carnegie Museum of Natural History, and the Crustacean Society.

![FIGURE 1. Gross anatomy of peritrichs. *Vorticella* sp., a typical peritrich ciliate presented for comparison with lagenophryids. Redrawn from an unpublished drawing by Eugene B. Small. Abbreviations: C, peristomial cilia (shown in outline); Hk, haplokinety; LP, peristomial lip (dark band in interior is myoneme that constricts the lip over the peristome upon contraction); Pk, peristomial polykinety; P1, infundibular polykinety 1; P2, infundibular polykinety 2; P3, infundibular polikinety 3; SM, somatic myonemes; Sc, scopula; SS, stalk spasmoneme; TB, trochal band. Scale bar, 10µm.]

Characteristics of the Family Lagenophryidae

Possession of a lorica distinguishes members of the Lagenophryidae, Usconophryidae, Vaginicolidae, and Rovinjellidae from other peritrichs. Loricae of peritrichs are composed of semirigid extracellular material secreted
around the body during attachment of the cell to a substrate (Clamp 1984). They are usually thin-walled and transparent or nearly so. Thickened parts of a lorica are relatively rigid, but thin areas are flexible to varying degrees.

Lagenophryids are distinguished from other loricate peritrichs by the following characteristics:

- **The lorica aperture and parts of the body associated with it form an elaborate closure apparatus for the lorica that is operated by a prominent band of myonemes** (Fig. 2B, PM; 2B; 3A–F; 4A–D; 5B; 9A). Usconophryids and rovinjellids have no means of closing the lorica aperture. Members of two vaginicolid genera (*Pyxicola*, *Thuricola*) form structures out of lorica material that block entrance to the lorica when the organism contracts (Trueba 1978, 1980); however, these structures are fundamentally different from the closure apparatus of lagenophryids (Clamp 1984). The anterior and posterior edges of the lorica aperture are folded to form two opposable lips in all lagenophryids except *Operculigera* (Clamp & Kane 2003), and the loricastome, a sleevelike structure, extends into the lorica from the ventral edges of these lips (Fig. 2C). The inner rim of the loricastome is thus the true lorica aperture in these genera.

- **The cell body is grossly flattened along its oral-aboral axis and laterally distorted to give it bilateral symmetry** (compare Fig. 1 to Fig. 2B–C) rather than the radial symmetrical typical of peritrichs (including vaginicolid and rovinjellid among the loricate forms). *Usconophrys* is flattened and, thus, superficially similar to lagenophryids; however, it lacks a closure apparatus for the lorica and the radically different orientation of its division plane marks its bilateral symmetry as a convergently evolved feature (Clamp 1991).

- **Attachment to the substrate is by means of the base of the lorica.** This is also a (presumably convergent) characteristic of usconophryids. By contrast, the majority of peritrichs, including rovinjellids and most vaginicolid among loricate taxa, secrete a cylindrical stalk of some sort to attach themselves to a solid substrate (Clamp & Kane 2003).

**FIGURE 2.** Characteristics of *Lagenophrys*. A. *L. aselli* on surface of pleopod of freshwater isopod. B. *Lagenophrys ampulla*, a typical representative of the genus, dorsal view. C. *Lagenophrys labiata*, lateral view. A, from Clamp 1988b; B–C, from Clamp 1991. Abbreviations: Ap, ampulla of cytostome (the cytopharynx leading into the cytoplasm is distended with a food vacuole); AL, anterior lip of lorica aperture; C, peristomial cilia (shown in outline); CT, crescentic thickening in wall of lorica anterior to lorica aperture; Cy, cytoplasm; EC, external collar of lorica aperture; ED, epistomial disk; If, infundibulum; Lo, dorsal wall of lorica; LR, rim of lorica; Ls, loricastome; LX, longitudinal axis of organism; MaN, macronucleus; MiN, micronucleus; PL, posterior lip of lorica aperture; PM, myoneme in edge of peristomial lip; TX, transverse axis of organism.

FIGURE 4. Diversity of *Lagenophrys* spp. Intraspecific variation and adaptation for attachment to setae. A, B. Two morphs in a population of *L. machaerigera* that represent the extreme range of variation in outgrowth of the anterior lip of the lorica aperture and thickening of the posterior lip. C. Dorsal view of *L. lenticula*, which attaches to setae of the amphipod *Hyalella* with a posterior prolongation of the lorica (Ps, pseudostalk). D. Dorsal view of *L. vaginicola*, which attaches to caudal setae of harpacticoid copepods. A, from Clamp 1992; B–D, from Clamp 1991. All scale bars = 10µm.
Genera of Lagenophryids

Five genera are currently recognized in the family Lagenophryidae. They are characterized by fundamental differences in the lorica aperture as well as other structural and developmental features (Table 1).

- *Lagenophrys* Stein, 1852 is the largest genus, with 62 known species. The lorica is usually hemispheroidal (Fig. 2–3) but is ovoid (Fig. 4) in a few species as an adaptation for attaching to setae of the host. The lorica aperture is an invaginated tube (loricastome) closed by drawing the outer edges (lips) together (Fig. 2B–C). Characteristics of the lorica aperture, especially the lips, are remarkably diverse among species of *Lagenophrys* (Fig. 4). Details of the lorica aperture are species-specific and, usually, show relatively little intraspecific variation (Clamp 1990); however, the lips of the lorica aperture are highly variable in a few species (Clamp 1990, 1992). Other than their distinctive lorica aperture, members of *Lagenophrys* are unique in undergoing a special sequence of asexual divisions (second-type division) to abandon the exoskeleton of the host.

- *Paralagenophrys* Clamp, 1987 (Fig. 5) has a lorica aperture that is similar to that of *Lagenophrys*, but its body and lorica aperture are twisted obliquely clockwise. The result is a lorica aperture that is displaced nearly 90° to the right and aligned almost parallel to the long axis of the body. The single species of *Paralagenophrys* is the only lagenophryid that is not restricted to a crustacean host. It also occurs on aquatic vascular plants and animals other than crustaceans (e.g., pulmonate snails) (Clamp 1987b).

- The genus *Clistolagenophrys* was created by Clamp (1991) for *Lagenophrys primitiva*, which occurs on one of the endemic species of amphipods in Lake Baikal, Russia (Swarcewsky 1930), because closure of its lorica aperture appears to be effected by a markedly different mechanism than in *Lagenophrys* (Fig. 6). *Clistolagenophrys primitiva* retracts the entire loricastome within the lorica to close the aperture with its basal edges instead of pulling the lips together.

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1. Elongate species of *Lagenophrys*, in which the posterior part of the lorica produced to form a slender ‘pseudostalk’ for attachment to setae, were formerly placed in the genus *Stylohedra*. However, Clamp (1991) determined that this single feature was not sufficient to characterize a genus and, in addition, had almost certainly evolved more than once within the genus *Lagenophrys* as well as in two other lagenophryid genera.
(Swarzewsky 1930). Jankowski (1993) maintained that the lorica aperture of *C. primitiva* was not fundamentally different from that of *Lagenophrys*; however, he offered no evidence to support this assertion.

- The diagnosis of *Setonophrys* Jankowski (1986) was emended by Clamp (1991) to include all lagenophryid species that have a lorica aperture with a rigid anterior lip and a flexible posterior lip that is pulled completely inside the lorica to press it against the anterior lip and close the aperture (Fig. 5).
- The lorica aperture of *Operculigera* Kane, 1969 is a simple opening in the lorica wall rather than an invaginated loricastome (Fig. 7), and the aperture is closed by a flexible flap of lorica material (operculum) rather than a pair of lips (Clamp 1991; Clamp & Kane 2003).

**TABLE 1.** Characteristics of lagenophryid genera.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Type of aperture</th>
<th>Orientation of lips of aperture</th>
<th>Closure apparatus</th>
<th>Mechanism of closure</th>
<th>Peristomial myoneme</th>
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<tr>
<td><em>Lagenophrys</em></td>
<td>loricastome</td>
<td>perpendicular to long axis of body</td>
<td>opposing lips; both flexible</td>
<td>edges of lips meet</td>
<td>posterior half thickened</td>
</tr>
<tr>
<td><em>Paralagenophrys</em></td>
<td>loricastome</td>
<td>at oblique angle to long axis of body</td>
<td>opposing lips; both flexible</td>
<td>edges of lips meet</td>
<td>posterior half thickened; left more than right</td>
</tr>
<tr>
<td><em>Clistolagenophrys</em></td>
<td>loricastome</td>
<td>perpendicular to long axis of body</td>
<td>opposing lips; both flexible</td>
<td>bases of lips meet</td>
<td>(not described)</td>
</tr>
<tr>
<td><em>Setonophrys</em></td>
<td>loricastome</td>
<td>perpendicular to long axis of body</td>
<td>opposing lips; only posterior flexible</td>
<td>base of posterior lip meets inner face of anterior lip</td>
<td>entire myoneme thickened</td>
</tr>
<tr>
<td><em>Operculigera</em></td>
<td>simple opening</td>
<td>(not applicable)</td>
<td>flap-like operculum</td>
<td>operculum covers aperture</td>
<td>anterior half thickened</td>
</tr>
</tbody>
</table>

**FIGURE 6.** Characteristics of *Clistolagenophrys*, from Clamp 1991. A, Lateral view of individual with lorica aperture in open position; B, Lateral view of lorica with lorica aperture retracted and closed. Scale bars = 10µm.
Cellular Anatomy and Taxonomic Characters

Lagenophryids have the same fundamental cellular anatomy as other peritrichs (Fig. 1), despite their flattened, distorted, discoid body. Owing to their superficially bilateral symmetry, a special anatomical terminology (Fig. 1B, C) has come into use for lagenophryids (Kane 1965). Like all peritrichs, lagenophryids are organized around a peristome (expanded oral area for suspension feeding) and an aboral scopula (circular field of pores interspersed with stereocilia that usually secretes a stalk) (Clamp 1984). The peristome consists of a central part, the epistomial disk, surrounded by a circular peristomial lip. In most peritrichs, the peristomial lip is a symmetrical, raised or flexible rim, enabling it to draw together on all sides like a sphincter to close over the retracted epistomial disk when the cell contracts. By contrast, the lagenophryid peristomial lip is asymmetrical, being physically bonded to the aperture of the lorica on one side to form a structural element for closure and, as a consequence, unable to contract in the typical way during extension or retraction of the epistomial disk (Clamp & Kane 2003) (Fig. 1B). Lagenophryids are able to extend only the epistomial disk out of the lorica aperture because of the association of the peristomial lip with the lorica aperture.

In Lagenophrys, approximately the dorsal one-half of the peristomial lip grasps the lower, posterior part of the loricastome (Fig. 2C). The segment of the circular myoneme (peristomial sphincter) in this portion of the peristomial lip is enlarged to form a prominent, thick band of myonemes (Fig. 1B) that spans the entire posterior half of the loricastome and curls around its lateral creases. Couch (1971, 1973) found its fine structure resembles that described for the peristomial sphincter of other peritrichs (Fauré-Fremiet et al. 1962; Bradbury 1965; Lom & Corliss 1958). Contraction of the band closes the lorica aperture, probably by drawing the posterior half of the loricastome forward and down to pull the lips of the aperture together (Couch 1971).

The lorica aperture of Operculigera is radically different from that of other lagenophryid genera. The aperture is a simple opening, not an invaginated loricastome, and the closure is an oval flap that is attached to the anterior part of the lorica (Clamp & Kane 2003). The anterior half of this operculum is thickened ventrally in most species of Operculigera to create a ventral shelf with a rounded projection at each end (Clamp 1991). The anterior half of the peristomial lip appears to grip this shelf to provide the attachment necessary for drawing the operculum over the aperture to close it.
The aperture is enclosed partially or completely by a wall of thickened lorica material (vallum) in most species of *Operculigera* (Clamp 1991). The vallum can be quite tall in some species and sculptured into projecting spines or blades on parts of its edge. A few species of *Operculigera* have only the anterior half of the vallum fully developed, and some species of *Lagenophrys* have a semicircular thickening around the anterior half of the lorica aperture (Fig. 2B) that almost certainly represents a vestige of this structure (Clamp 1991). Furthermore, it appears that the anterior lip of the lorica aperture of *Setonophrys*, which is rigid and often bears spines on its edge, represents another homologue of the anterior half of the vallum (Clamp 1991).

The infraciliature of the oral complex shows the pattern typical of peritrichs (Couch 1973). Variations in the three infundibular polykineties (Fig. 8) are species-specific characteristics in peritrich ciliates and are relatively well-documented in *Lagenophrys*, *Paralagenophrys*, and *Operculigera*. One or more rows of infundibular polykinety 1 (P1) are longer or shorter than the others at their adstomal ends in some species of *Lagenophrys* and *Operculigera* (Clamp, 1990a, 1991, 1992, 1994), and the first row of P1 is slightly shorter than the others in the single species of *Paralagenophrys* (Clamp 1987b). The rows of P2 are equal in length in all species of *Lagenophrys*, but the first row of P2 is significantly longer than the other two rows at its adstomal end in most species of *Operculigera* (*O. carcini* is the exception) and in *P. singularis* (Clamp 1987b). The first row of P3 is extremely short in species of *Operculigera* and some species of *Lagenophrys* (Clamp 1991) and is absent in many other species of *Lagenophrys* and in *P. singularis* (Clamp 1987a, b, 1988). Loss of a row from P3 (i.e., reduction from a trikinety to a dikinety) also has been observed in the family Vorticellidae (Sun *et al.* 2006).


The trochal band of kinetosomes is a simple dikinety in lagenophryid trophonts (Clamp 1987a), which is typical for peritrichs. In trophonts of *L. callinectes* (Couch 1967, 1971, 1973) and *L. eupagurus* (Clamp 1989), the trochal band is broken on the right side, with the two ends of the break separated by a significant gap; however,
telotrochs of both species have a normal trochal band. The trochal band surrounds a scopula that occupies a large part of the body's aboral surface in lagenophryids (Clamp 1984). Couch (1971, 1973) found no secreted bond between the scopula of *L. callinectes* and the surface of the host's exoskeleton.

Lagenophryids have one macronucleus and micronucleus (Fig. 2B). All known species of *Setonophrys* have a distinctive, elongate, cylindroid macronucleus that spans the width of the cell (Fig. 5B). By contrast, the shape, size, and location of the macronucleus vary widely among species of *Lagenophrys* and *Operculigera* (Clamp 1991). The macronucleus can be cylindroid, ovoid, or spheroid. If cylindroid, it may be slightly or sharply curved, bent at one or more points along its length, or relatively straight. More compact, ovoid or spheroid macronuclei are located on the right side of the cell in some species and on the left in others (Clamp 1987a, 1992). The variety of macronuclear shapes among species of *Lagenophrys* is unusual compared to the relative uniformity that is typical of other genera of peritrichs (e.g., *Setonophrys*). Even large genera such as *Vorticella* or *Zoothamnium* have evolved only a few different macronuclear shapes and orientations (Warren 1986; Ji *et al.* 2006). In general, macronuclear morphology is correlated with shape of the cell in ciliates, including peritrichs. One example would be vaginicolid peritrichs with elongate bodies and correspondingly long, cylindroid macronuclei (Trueba 1978, 1980). There is no apparent functional reason for the diversity of macronuclear shapes in species of *Lagenophrys* and *Operculigera*, given that all of them have essentially the same discoid cell body.

In lagenophryids, the plane of division extends diagonally across the body from a point just to the left of the lorica aperture to the center of the posterior margin of the cell (Fig. 1B). Thus, the lateral distortion of the body causes the plane of division to be oriented generally parallel to the anteroposterior axis although it is actually homologous to the oral-aboral division plane of other peritrichs (Bütschli 1889; Couch 1971). Binary fission produces a right-hand daughter that remains associated with the lorica aperture to resume feeding after a short period of quiescence and a left-hand daughter that transforms into a telotroch, which must exit the lorica by squeezing through the lorica aperture via the small gap left by the unattached ventral edge of the other daughter's peristomial lip.

Lagenophryid telotrochs possess a number of specialized structures that are not seen in other peritrichs. The body of the telotroch is flattened like that of the trophont; consequently, its trochal band is entirely on the ventral surface of the body. Protargol preparations of lagenophryid trophonts do not reveal any evidence of the radial somatic myonemes that extend from the edge of the peristome to the scopula in other peritrichs, and this absence has been confirmed by transmission electron microscopy (Couch 1973). By contrast, lagenophryid telotrochs possess partial somatic myonemes that are inserted onto the adoral edge of the trochal band and extend only halfway toward the dorsal apex of the body; thus, they are not attached to the edge of the peristome as in other peritrichs. In addition, there are 3-4 partial myonemes attached to the periphery of the scopula that also extend dorsally instead of being attached to the aboral edge of the trochal band. This unique arrangement of somatic myonemes appears to play a part in the attachment of the telotroch to the host’s exoskeleton, with the scopular myonemes raising the aboral pole of the body to create suction and hold the telotroch in place while the radial myonemes flatten the body in preparation for secretion of the lorica (Clamp 1987a). Finally, the telotroch’s peristomial lip is distorted into the shape of the lips of the lorica aperture and, presumably, plays a part in shaping them during secretion of the lorica.

**Ecology of Lagenophryids**

*Paralagenophrys singularis* Kellicott is the only member of the Lagenophryidae that shows no preference for a particular host or substrate (Clamp 1989). Other lagenophryids appear to be restricted to a single species, genus, or family of crustaceans (Clamp 1990b, 1992). Furthermore, many species are confined to one part of the host, such as its gills, locomotory appendages, maxillipeds, or antennae (Fig. 2A). Relatively few species occur on all parts of a host, and even these settle more thickly on some areas of the host’s body than others (Shomay 1955; Jakshchik 1967b; Clamp 1973). Most authors who have concerned themselves with relationships of lagenophryid species to their hosts (Abonyi 1928; Mouchet-Bennati 1931, 1932a, 1932b; Shomay 1953b, 1955; Couch 1965, 1967, 1991; Clamp 1972, 1973) agree that lagenophryids have little or no effect upon their hosts even though they may be present in great numbers (Felgenhauer & Ridgeway 1977). Abonyi (1928), however, proposed that two species of *Lagenophrys* found on semiterrestrial crustaceans are ectoparasites subsisting on the tissues of their hosts but
offered no supporting evidence. Couch (1966) reported heavy populations of \textit{L. callinectes} on gills of moribund \textit{Callinectes sapidus} held in crowded, stagnant conditions.

The forceful currents created by the host’s respiratory and locomotory movements are probably the feature of crustaceans that is of critical benefit to lagenophryids. Fenchel (1965) and Clamp (1973) demonstrated that particles of food torn up by the mouthparts of a host animal are carried by such currents to lagenophryids on other areas of its body, and the ciliates also captured particles that are swept from the surrounding water into currents created by the host.

Ectosymbionts of crustaceans face a periodic loss of habitat caused by ecdysis of their hosts and have evolved various means of dealing with it. Members of \textit{Lagenophrys} are unique among ciliates that are ectosymbiotic on crustaceans because they undergo a special type of binary fission just before their host's ecdysis. Called second-type division by Willis (1942), this process usually consists of two divisions of an adult without an intervening period of growth. The first division is identical to normal binary fission, but the second is grossly unequal (Willis 1942). The result is two telotrochs of normal size and a small, poorly developed third daughter (residual organism) that remains associated with the lorica aperture, never develops recognisable oral structures, contains only fragments of nuclear material, and dies soon after ecdysis. Willis (1942) also observed a form of second-type division in which only one unequal division took place.

**Biogeography of Lagenophryids**

The genus \textit{Lagenophrys} has a truly cosmopolitan distribution, with species having been reported from every continent except Antarctica (Fig. 9). In general, the distributions of individual species mirror those of the hosts. Species that are less specific in their choice of hosts, occurring on different members of a family or genus of crustaceans, have more extensive ranges, especially if they occur in marine or brackish-water habitats. Good examples are \textit{L. eupagurus} Kellicott (occurs on palanomids shrimp in Europe, Asia, and North America) (Clamp 1989) and \textit{L. cochinensis} Santhakumari & Gopalan (occurs on wood- and rock-boring sphaeromatid isopods in Africa, Asia, New Zealand, North America, and South America) (Clamp 2006). By contrast, the group of species found on amphipods by Swarczewsky (1930) in Lake Baikal is a notable example of endemic species with restricted distributions.

The single species of \textit{Paralagenophrys} has been reported only from scattered localities in the eastern U.S. (Clamp 1987b) (Fig. 9). Owing to its complete lack of substrate-specificity, \textit{P. singularis} might be characterized as ‘free-living’; therefore, the fact that it has not been found in Europe suggests that it might have a restricted geographic distribution. All known species of \textit{Setonophrys} appear to be endemic to Australia (Clamp & Kane 2003) (Fig. 10), and \textit{Clistolagenophrys} has been reported only from Lake Baikal (Clamp 1991). Species of \textit{Operculigera} fall into three groups, each of which is endemic to a different part of the southern hemisphere (Australia, Chile, Madagascar) (Fig. 10). This disjunct distribution suggests that \textit{Operculigera} is an extremely old genus, originating before the initial breakup of Gondwana began ~184 Ma ago (Clamp 1992).

**Taxonomic Identification of Lagenophryid Peritrichs**

Clamp (1990a) gave a summary and evaluation of morphological features used as taxonomic characters in the genus \textit{Lagenophrys}. For the most part, that information also applies to species in other genera of lagenophryids. As might be expected, accurate identification of lagenophryids to the species level is a 3-step process that begins with determination of the genus, followed by determination of the species, and ending with an evaluation of variation within the sample to confirm that the identification is consistent with information in the literature or not. The first step is relatively easy because each genus of lagenophryids is clearly unique in terms of the closure apparatus of the lorica aperture (Table 1). Within each genus, however, species identification depends on a combination of structural details of the closure apparatus (e.g., sculpturing of the lips of the aperture), shape of the macronucleus, shape and proportions of the lorica, and pattern of ciliary rows in the infundibular polykineties (Fig. 2–8).
Rather than providing a traditional dichotomous key to species, we have chosen to summarize the geographic distributions and host preferences of lagenophryid species in the form of a matrix in Table 2. Most species are associated with specific crustacean hosts that tend to have restricted geographic distributions; therefore, knowing the locality, type of habitat, and identity of the host allows the identity of lagenophryid symbionts to be narrowed to a small group of species. Using Table 2 in combination with the more detailed information about each species given in the following checklist will make this easier. This should make it possible to generate at least a tentative
identification of any known species of lagenophryid after consulting original descriptions or revisionary papers. For the future, an identification key with links to literature sources, figures, and species descriptions is planned as an on-line, electronic resource that can be updated as needed and adapted to deal with difficulties posed by species complexes, cryptic species, and highly variable species as well as molecular characters or barcoding sequences as these become available.

**TABLE 2.** Matrix showing geographic distributions, general habitat, and hosts of all known species of lagenophryid peritrichs. Species of *Lagenophrys* are categorized into species that are restricted to freshwater versus those that are marine, estuarine, or euryhaline. Members of all other genera are known only from freshwater habitats. Ostracods, copepods, and cladocerans are grouped as “Other hosts.” Lagenophryoids occurring in Lake Baikal are presented separately from other Asian species because all but one species are probably endemic to the lake.

<table>
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<tr>
<th>N. Hemisphere</th>
<th>S. Hemisphere</th>
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<td>Amphipoda</td>
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<tr>
<td>Isopoda</td>
<td>Decapoda</td>
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<td>Other hosts</td>
<td>Other hosts</td>
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</tbody>
</table>

| Lagenophrys     |  
|-----------------|-----------------|
| Freshwater      | N. Hemisphere   |
| Europe          |                 |
| Europe freshwater |                 |
| Europe freshwater |                 |
| North America   |                 |
| North America freshwater |                 |
| Asia            |                 |
| Lake Baikal     |                 |
| Africa          |                 |
| South America   |                 |

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Possible/probable geographic endemic

Annotated Checklist of Lagenophryid Species

The following checklist includes all known species in the family Lagenophryidae (Table 2). The checklist is organized by genus, within which species are sorted in descending order by habitat, broad geographic occurrence, host, and restricted geographic occurrence.

Lagenophryidae Bütschli, 1889

I. Lagenophrys Stein, 1852

A. Occurring Only In Freshwater

1. Northern Hemisphere

a. Restricted to Amphipoda

i. Europe only

L. pontocaspica Boshko, 1995


**Habitat.** Freshwater, brackish.

**Distribution.** BR: Palaeartic.

Ukraine: Danube basins; Dnieper Basin: Kakhovskoye, Kanevskoye (47°38'26.35"N, 35°5'10.30"E); Dnieper-Bug Lagoon (46°26'36.48"N, 31°59'3.74"E); Dniester (49°2'57.91"N, 24°29'37.95"E); Kiev reservoirs (50°20'30.71"N, 30°36'32.86"E); Nikolayevskaya Oblast (46°58'27.19"N, 31°59'40.12"E); Pokrovka (47°04'3.52"N, 31°31'34.43"E); Stugna River (50°24'48.63"N, 30°35'51.37"E).

**Hosts.** Ukraine: *Amathillina cristata* G. O. Sars, *Chaetogammarus ischnus* (Stebbing), *Dikerogammarus haemobaphes* (Eichwald) (cited as *Dikerogammarus haemobapes*), *D. villosus* (Sowinsky), *Obesogammarus crassus* (G. O. Sars) (cited as *Pontogammarus crassus*), *Pontogammarus abbreviatus* (Sars), *P. maeticus* (Sowinsky), *P. robustoides* (Sars) (gills and oostegites).


ii. North America only

*L. foxi* Clamp, 1987

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

USA: Illinois, Monroe Co., 3.2 km N Fountain Gap, spring (38°24'38.36"N 90°14'41.36"W); St. Clair Co., Falling Spring (38°32'10.95"N 90°10'58.43"W). Missouri, Lincoln Co., 7.2 km NNW Foley, Hurricane Cr. at MO 79 (39°6'46.45"N 90°45'23.52"W); Jefferson Co., 7.7 km NE Hillsboro, Sandy Cr. at MO 21 (38°17'41.13"N 90°31'44.08"W); Jefferson Co., 4.3 km NNE Hillsboro, creek running parallel with MO 21 at Hayden Rd. (38°16'15.34"N, 90°33'39.83"W).


**References.** Clamp 1987a; Fernandez-Leborans & Tato-Porto 2000.

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**TABLE 2.** (Continued)

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¹Possible/probable geographic endemic
**L. johnsoni** Clamp, 1990

**Museum Depositions.** UNSM. 42301 Holotype; 42302, 42303, 42304, 42304 Paratypes.

**Habitat.** Brackish, freshwater.

**Distribution.** **BR:** Nearctic (Mayén-Estrada & Aguilar-Aguilar 2012).

Canada: **Ontario,** Norfolk Co., Long Point Provincial Park, Long Point Bay alongside ONT 59 (42°34'46.86"N, 80°23'4.30"W). **Quebec,** L’Islet Co., St. Jean-Port-Joli, mouth of Tortue R. at QUE 2 (47°08'56"N, 70°20'21"W).

USA: **Michigan,** Delta Co. 4 km E Isabella, Little Fishdam R. at U.S. 2 (43°35'13.81"N, 84°48'30.24"W). **New Jersey,** Monmouth Co., Brielle, Silver Fox Forge Pond (74°40'636.14"N, 74°23.85"W). **New York,** Cayuga Co., 3.2 km E Meridian, creek at NY 370 (43°9'50.44"N, 76°28'41.04"W); Oswego Co., 1.6 km S Minetto, Oswego R. alongside NY 48 (43°23'16.69"N, 76°27'46.93"W); Oswego Co., 8.5 km WSW Sandy Creek center, Sandy Pond (North Pond) at Ouderkirk Rd. (43°37'54.58"N, 76°11'17.70"W); Oswego Co., 4.5 km SSW West Monroe, Oneida Lake at Shaw's Point (43°14'42.92"N, 76°5'34.37"W).

**North Carolina,** Brunswick Co., 5.3 km S Supply, creek at Secondary Road 1115, 0.6 km from jct. Secondary Road 1125 (33°58'7.78"N, 78°15'35.41"W); Dare Co., Bodie Island, 8.8 km SSE Nag's Head, creek at NC 12, 2.6 km S jct. U.S. 64 (35°49'9.58"N, 75°33'19.33"W); Dare Co., 8 km NNW Mann's Harbor, creek near Mashoes (35°57'48.18"N, 75°49'24.53"W); Hyde Co., 7.4 km S Fairfield, Lake Mattamuskeet alongside NC 94 causeway (35°28'10.32"N, 76°12'47.43"W); Tyrrell Co., 5.9 km NW Columbia, Seuppermorg R. at River Neck (35°57'39.92"N, 76°12'33.77"W); Tyrrell Co., 4.8 km NW Travis, Bull Bay at end Secondary Road 1202 (35°55'43.07"N, 76°22'59.50"W); Tyrrell Co., Gum Neck Landing, boating access area at end Secondary Road 1316 (35°41'34.81"N, 76°6'49.78"W); Tyrrell Co., Fort Landing, Alligator Creek at end Secondary Road 1209 (35°58'44.70"N, 76°14'26.30"W); Washington Co., Albemarle Beach, Albemarle Sound at end Secondary Road 1323 (35°57'53.94"N, 76°27'42.30"W).


**L. missouriensis** Clamp, 1987

**Museum Depositions.** USNM. 40937 Holotype; 40938 Paratype.

**Habitat.** Freshwater.

**Distribution.** **BR:** Nearctic.

USA: **Missouri,** Jefferson Co., 4.3 km NNE Hillsboro, creek running parallel to MO 21 at Hayden Rd. (38°16'15.81"N, 90°33'40.88"W); Lincoln Co., 7.2 km NNW Foley, Hurricane Cr. at MO 79 (39°06'27.85"N, 90°46'14.11"W). **Wisconsin,** Bayfield Co., 3.2 km S Barksdale, stream at WIS 13 near jct. US 2 (46°35'41.82"N, 90°57'17.91"W); Bayfield Co., 6.4 km N; Washburn, Sioux Creek Slough at WIS 13 (46°43'55.85"N, 90°52'42.58"W).

**Hosts.** USA: *Gammarus pseudolimnaeus* (surfaces of peraeon and pleon).

**References.** Clamp 1987a; Fernandez-Leborans & Tato-Porto 2000.

**L. stygia** Clamp, 1990

**Lagenophrys labiata** Jakschik 1967a: 24.

**Circolagenophrys stygia** Jankowski 1993: 221.

**Museum Depositions.** USNM. 42306 Holotype; 42307, 42308 Paratypes.

**Habitat.** Subterranean.

**Distribution.** **BR:** Nearctic.

USA: **Illinois,** Champaign Co. 1 mi. S Sellers, drainage tile (40°10'14.77"N, 88°6'13.33"W); Christian Co., 4.0 mi. E Taylorville, Spring Cr. (39°33'7.43"N, 88°34'19.65"W); Vermilion Co., 1.5 mi. N Fithian, tributary of Stony Cr. (40°7'51.57"N, 87°52'22.73"W).

**Hosts.** USA: *Bactrurus mucronatus* (Forbes) (gills).


**L. hokkaidos** (Jankowski, 1993)
Circolagenophrys hokkaidos Jankowski 1993: 222.
Lagenophrys ampulla Imamura 1940: 267, 268.

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

Japan: Hokkaido, near Sapporo; Chitose, fish farm pond (42°48'11.90"N, 141°41'13.62"E).

**Hosts.** Japan: Jesogammarus (Annanogammarus) annandalei (Tattersall) (cited as Gammarus annandalei) (gills and maxillipeds).

**References.** Imamura 1940; Jankowski 1993.

### iv. Lake Baikal endemics

**L. commensalis** Swarczewsky, 1930

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

Russia: Lake Baikal, Bolschye Koty im Bezirk Biological Station (51°53'52.12"N, 105°4'22.60"E); Irkutsk (52°16'30.18"N, 104°18'12.29"E).

**Hosts.** Russia: Lake Baikal: Carinurus solsky (Dybowsky, 1874) (maxillipeds).

**References.** Swarczewsky 1930; Clamp 1984; Fernandez-Leborans & Tato-Porto 2000.

**L. inflata** Swarczewsky, 1930

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

Russia: Lake Baikal, Bolschye Koty im Bezirk Biological Station (51°53'52.12"N, 105°4'22.60"E); Bolschye Koty (51°53'52.12"N, 105°4'22.60"E); Irkutsk (52°16'30.18"N, 104°18'12.29"E).

**Hosts.** Russia: Gmelinoides fasciatus (cited as Brandtia fasciata) (pleopods).

**References.** Swarczewsky 1930; Clamp 1984; Fernandez-Leborans & Tato-Porto 2000.

**L. macrostoma** Swarczewsky, 1930

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

Russia: Lake Baikal, Irkutsk, Bolschye Koty (51°53'52.12"N, 105°4'22.60"E); Bolschye Koty (51°53'52.12"N, 105°4'22.60"E); Listwenitschnoje.

**Hosts.** Russia: Coniurus radoschkowskii (Dybowsky) (gills).

**References.** Swarczewsky 1930; Fernandez-Leborans & Tato-Porto 2000.

**L. oblonga** Swarczewsky, 1930

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

Russia: Lake Baikal, Irkutsk, Bolschye Koty (51°53'52.12"N, 105°4'22.60"E).

**Hosts.** Russia: Eulimnogammarus hyacinthus (Dybowsky) (cited as Gammarus hyacinthinus) (first pair of antennae).

**References.** Swarczewsky 1930; Clamp 1984; Fernandez-Leborans & Tato-Porto 2000.

**L. ornata** Swarczewsky, 1930

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

Russia: Lake Baikal, Irkutsk, Bolschye Koty (51°53'52.12"N, 105°4'22.60"E).

**Hosts.** Russia: Eulimnogammarus cyanoides (cited as Echinogammarus cyanoides), Carinogammarus rhodophthalmus sablotzki (cited as Carinogammarus sablotzky) (pereiopods).

**References.** Swarczewsky 1930; Fernandez-Leborans & Tato-Porto 2000.

**L. ovalis** Swarczewsky, 1930

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

Russia: Lake Baikal, Irkutsk, Bolschye Koty (51°53'52.12"N, 105°4'22.60"E).

**Hosts.** Russia: Hylelelopsis variabilis (pereiopods), Micrurus littoralis crassipes, M. talitroides (pereiopods), Macropereiopus wagneri Sowinsky (pereiopods), Eulimnogammarus cyanoides (also cited as Echinogammarus cyanoides) (pereiopods).

**References.** Swarczewsky 1930; Fernandez-Leborans & Tato-Porto 2000.
L. *parva* Swarczewsky, 1930

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

Russia: **Lake Baikal**, Irkutsk, Bolschye Koty (51°53’52.12”N, 105°422.60”E); Uschkan Islands (53°49’51.47”N, 108°37’3.15”E); Tschiwyrkui Gulf.

**Hosts.** Russia: *Crypurosp pachytus* (pereiopods), *Eulimnogammarus fuscus* (cited as *Echinogammarus fuscus*) (pereiopods).

**References.** Swarczewsky 1930; Fernandez-Leborans & Tato-Porto 2000.

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L. *similis* Swarczewsky, 1930

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

Russia: **Lake Baikal**, Irkutsk, Bolschije Koty (51°53’52.12”N, 105°422.60”E); Rayon, Biological Station.

**Hosts.** Russia: *Eulimnogammarus verrucosus* (cited as *Echinogammarus verrucosus*), *Hyalellopsis czyrnianski* (gills).

**References.** Swarczewsky 1930; Clamp 1984; Fernandez-Leborans & Tato-Porto 2000.

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L. *simplex* Swarczewsky, 1930

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

Russia: **Lake Baikal**, Irkutsk, Uschkanji Islands (53°49’51.47”N, 108°37’3.15”E); Olchonskije Worota.

**Hosts.** Russia: *Dorogammarus castaneus* (cited as *Axelboeckia castanea*), *Pallasea (Propachygammarus) bicornis* Dorogostajsky (cited as *Pallasea bicornis*) (pereiopods).

**References.** Swarczewsky 1930; Fernandez-Leborans & Tato-Porto 2000.

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L. *solida* Swarczewsky, 1930

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

Russia: **Lake Baikal**, Irkutsk (52°16’30.18”N, 104°18’12.29”E); Golf Tschiwyrkui; Smorodowaja; Bolschye Koty (51°53’52.12”N, 105°422.60”E); Tschiwyrkui Gulf; Bargusin Gulf (53°25’7.51”N, 109°1’14.76”E); mouth of Sselenga R; Kultuk (51°42’12.50”N, 103°42’11.71”E).

**Hosts.** Russia: *Plesiogammarus (Plesiogammarus) gersteckeri* (Dybowsky) (cited as *Plesiogammarus gersteckeri*) (pereiopods).

**References.** Swarczewsky 1930; Fernandez-Leborans & Tato-Porto 2000.

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L. *stokesi* Swarczewsky, 1930

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

Russia: **Lake Baikal**, Irkutsk (52°16’30.18”N, 104°18’12.29”E); Smorodowaja; Bolschye Koty (51°53’52.12”N, 105°422.60”E); Tschiwyrkui Gulf; Bargusin Gulf (53°25’7.51”N, 109°1’14.76”E); mouth of Sselenga R; Kultuk (51°42’12.50”N, 103°42’11.71”E).

**Hosts.** Russia: *Axelboeckia potanini* (gills), *Odontogammarus calcaratus*, *Ommatogammarus (Abludogammarus) flavus* (cited as *Ommatogammarus flavus*), *Ommatogammarus (Pretiositus) carneolus* (Dybowsky) (cited as *Ommatogammarus carneolus*).

**References.** Swarczewsky 1930; Fernandez-Leborans & Tato-Porto 2000.

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v. **Brood Distribution**

**L. ampulla** Stein, 1852


**Habitat.** Freshwater.

**Distribution.** BR: Nearctic, Palaeartic (Mayén-Estrada & Aguilar-Aguilar 2012).

Canada: **Alberta**, 5 mi. W Canyon Creek, creek at ALTA 2 (55°23’34.10”N, 116°1’49.34”W); 2 mi. E. Vilna, Cache L. at ALTA 28 (54°751.77”N, 111°50’59.44”W).

France: **Bretagne**, Cotes du Nord, 0.75 mi. SE Louargat, creek at D31 (48°33’26.02”N, 3°19’54.53”W); Cotes du Nord, 1.1 mi NW Louargat creek at D31 (48°34’54.59”N, 3°20’47.08”W); 2.2 mi WNW Belle-Ile-en-Terre, creek at N12 (48°32’55.04”N, 3°26’56.39”W); Finisterre Nord, 1.75 mi NWN Cleder, creek near Kersaint (48°41’37.27”N, 4°7’18.63”W).

Germany: **Bavaria**, near Erlangen; near Munich (47°8’47.74”N, 10°56’3.82”E); Bielefeld. **Saxony**, Dresden, near Tharanld, small rocky brooks (50°59’24.35”N, 13°35’6.99”E). **Wurttemberg**, near Freiburg-im-Breisgau.
Russian: Lake Baikal (53°3′10.7°, 108°17′31.3°); Anga; Barantschik Irkutzsk, Golf Smorodowaja; Bolschye Koly (51°54′12.9°, 105°4′49.9°); Golf Bargusin (53°36′58.4°, 109°8′2.6°); Golf Pestchajana; Golf Tschiwirkuj; Goloustnoje (52°1′35.2°, 105°24′15.08°); Kultuk (51°43′2.2°, 103°42′31.34°); Kleines Meer; Listwjenitschneje, Oblom (52°2′34.42°, 106°53′26.49°); Olchonskije Worota; Shilischtsche. Siberia (53°3′10.7°, 108°17′31.36°); Useckjan-Inseln.

Switzerland: Basel, near Basel, Allschwil (47°3′24.0.97°, 7°3′21.26°); near Basel, Schusterinsel. Geneve, near Geneva (46°11′38.00°, 6°8′20.95°); Aire, Rhone R. (46°9′7.17°, 6°4′33.70°). Coppet, Lac Leman (littoral zone) (46°18′58.58°, 6°11′36.82°). Vaud, near Ste. Croix (south of the city), Tourbieres de la Sange (peat bog) (46°4′32.78°, 6°30′20.16°).

UK: Leicester, stream near Leicester University (52°3′21.52°, 1°8′36.34°).

USA: Minnesota, Clearwater Co. Lake Itasca State Park, L. Itasca (47°12′52.16°, 95°12′25.51°); Kandiyohi Co. 2 mi. E. Spicer, Woodcock L. (45°14′15.75°, 94°57′0.04°).

Hosts. Canada: Gammarus lacustris lacustris Sars (gills), Crangonyx sp. (gills). France: Echinogammarus berilloni (Catta) (gills), Gammarus duebeni Liljeborg (gills), G. pulex var. pulex (Linnaeus) (cited as Gammarus pulex pulex) (gills). Germany: Gammarus pulex Linnaeus (gills), Gammarus sp. (gills). Netherlands: Gammarus pulex var. pulex (cited as Gammarus pulex pulex) (gills). Russia: (in all cases found on the gills): Acanthogammarus (Ancyracanthus) victorii Dybowski, Acanthogammarus (Acanthogammarus) albus (Garjajeff) (cited as Acanthogammarus albus), Acanthogammarus (Acanthogammarus) godlewskii (Dybowski) (cited as Acanthogammarus godlewskii), Axelboeckia carpenteri (Dybowski), A. potanini (Dorogostaiky), Branditia latissima (Gerstfeldt), B. latissima lata (Dybowski) (cited as Branditia lata), Carinogammarus cinamnomeus (Dybowski), C. rhodophilus rhodophilus (Dybowski). C. rhodophilus salbottziki (Sowinsky), Crypturopus inflatus (Dybowski), C. pachytus (Dybowski), C. rugosus (Dybowski) (cited as Crypturopus rugosus), C. tuberculatus (Dybowski), Diplectronus brevispinus (Dorogostaiky) (cited as Acanthogammarus brevispinus), Dorogammarus castaneus (Dorogostaiky) (cited as Axelboeckia castanea), Echiuropus macronychus Sowinsky, E. morawitzi (Dybowski), Eucarinogammarus wagi (Dybowski) (cited as Eucarinogammarus wagi), Eulimnogammarus aheneus (Dybowski) (cited as Echinogammarus aheneus), E. capreolus (Dybowski). E. cruentus (Dorogostaiky) (cited as Echinogammarus cruentus), E. cyaneus (Dybowski) (cited as Echinogammarus cyaneus), E. cyanoideus (Sowinsky) (cited as Echinogammarus cyanoideus), E. fuscus (Dybowski) (cited as Echinogammarus fuscus), E. lividus (Dybowski) (cited as Echinogammarus lividus), E. maackii (Gerstfeldt) (cited as Echinogammarus lividus maacki), E. olivaceus (Dybowski) (cited as Echinogammarus olivaceus), E. sophianus (Dybowski), E. verrucosus (Gerstfeldt) (cited as Echinogammarus verrucosus), E. viridis (Dybowski) (cited as Eulimnogammarus viridis viridis), Garrajewia cabaniisii (Dybowski) (cited as Garrajewia cabaniisii), Gmelinoides fasciatus Stebbing (cited as Branditia fasciata), Heterogammarus sophianosii (Dybowski) (cited as Heterogammarus sophianosii), Hyalellopsis cyprianci (Dybowski) (cited as Hyalellopsis cyprianci), H. variabilis (Dorogostaiky), Micruropus fixsenii (Dybowski) (cited as Micruropus fixseni), M. glaber (Dybowski), M. kluki (Dybowski) (cited as Micruropus kluki), M. littoralis crassipes Sowinsky, M. rugosus, M. talitroides (Dybowski), M. vahlii (Dybowski) (cited as M. vahlii), Micruropus (Microgammamus) vortex (Dybowski) (cited as Micruropus vortex), Odontogammarus calcaratus (Dybowski), O. margaritaceus demianowiczii Dorogostaiky (cited as O. demianowiczii), Omnomuogammarus (Abludogammarus) flavus (Dybowski) (cited as Omnomuogammarus flavus), Pallasea cancellus (Pallas), P. cancelloides (Gerst.), P. grubei (Dybowski), P. kessleri (Dybowski), Parapallasea puzylli (Dybowski). Switzerland: Gammarus pulex, Gammarus sp. (gills). UK: Gammarus pulex (gills). USA: Gammarus lacustris lacustris (gills).


L. labiata Stokes, 1887

Lagenophrys labiata Stokes 1887: 40; Stokes 1888: 262-263; von Ubisch 1913: 43; Keiser 1921: 286; Abonyi 1928: 9, 18; Swarczewsky 1930: 458; Kahl 1935: 796.

Museum Depositions. USNM. 42316, 42317 Neotypes; 42318, 42319, 42320.

Habitat. Freshwater, brackish.


Netherlands: Gelderland, 1.1 mi SW Uddel, Hierdensche R. (52°14′48.56°N, 5°45′46.15°E).
USA: Michigan, Ottawa Co., 8.0 km S Grandhaven, slough at Lakeshore Drive (42°59'30.04"N, 86°13'11.53"W); Ottawa Co., 3.8 km W West Olive, mouth of Pigeon R. (42°54'3.64"N, 86°11'4.43"W). New Jersey, Mercer Co., near Trenton (40°12'17.84"N, 74°46'1.66"W); Monmouth Co., Brielle, Silver Fox Forge Pond (40°6'15.34"N, 74°3'4.31"W). New York, Cayuga Co., Fair Haven Beach State Park, The Pond (43°20'2.55"N, 76°41'31.16"W); Oswego Co., 8.5 km WSW Sandy Creek center, Sandy Pond (North Pond) at Ouderkirk Rd. (43°37'54.58"N, 76°11'17.70"W); Oswego Co., 4.5 km SWW West Monroe, Oneida Lake at Shaw's Point (43°14'42.92"N, 76°53'4.37"W). North Carolina, Tyrrell Co., 5.9 km NW Columbia, Scuppernong R. at River Neck (35°57'10.74"N, 76°17'27.75"W); Tyrrell Co., Alligator Cr. at Fort Landing (35°54'52.06"N, 76°12'28.32"W); Washington Co., Albemarle Beach, Albemarle Sound at end SR 1323 (35°56'10.74"N, 76°38'27.99"W).


**L. lenticula (Kellicott, 1885)**

Stylohedra lenticula Kellicott 1885: 122; Stokes 1888: 262.


**Museum Depositions.** USNM. 42123 Neotype; 42124.

**Habitat.** Freshwater.

**Distribution.** BR: Neartic, Neotropical (Mayén-Estrada & Aguilar-Aguilar 2012).

Canada: Alberta, 16 km S Little Smoky, creek at ALTA 43 (54°8'24.70"N, 117°4'36.25"W); 3.2 km W Village, Cache Lake at ALTA 28 (54°16'29.75"N, 116°51'50.69"W). Newfoundland, near Norris Point, pond alongside NFLD 73, 4.8 km N jct. NFLD 44 (49°31'41.53"N, 57°52'54.88"W). Ontario, Carleton Co., Rideau River, S Ottawa (45°3'12.10"N, 75°39'17.78"W); Middlesex Co., Thamesford, creek at ONT 19 just S town limit (43°3'19.52"N, 80°59'27.78"W); Norfolk Co., 2.6 mi. S Port Rowan, Long Point, marsh alongside ONT 59 (42°35'12.54"N, 80°26'32.39"W); Norfolk Co., Long Point Provincial Park, Long Point Bay at ONT 17 (46°21'58.52"N, 81°24'7.2"W); Sudbury Co., 4.8 km W Naughton, small lake alongside ONT 17 (46°23'34.56"N, 81°15'30.39"W); Welland Co., Wainfleet, canal at ONT 3 (42°55'28.6"N, 79°22'35.08"W). Quebec, Gatineau Co., Gatineau National Park, Taylor Lake (45°36'12.58"N, 76°02'57.38"W).

Mexico: Michoacán, Cuitzeo lake, San Cristóbal (19°57´41"N, 101°18´55"W)* present work; Pátzcuaro lake (19°32´ to 19°41´N, 101°12´ to 101°43´W)* present work; Tecocomulco lake (19°42´13.7" to 19°59´30"N, 98°11´46.2" to 98°27´30"W). Uruguay: near Montevideo, pond at Sayago (34°47´37.52"N, 56°11´12.7"W); Near Montevideo, small temporary ponds (34°55´35.91"N, 56°09´17.27"W).

USA: Indiana, Whitley Co., 4.8 km WNW Churubusco, Blue Lake (41°14´26.45´N, 85°22´19.29´W), Michigan, Barry Co., 8.0 km SW Hastings, Leach Lake (42°40´52.07´N, 85°17´22.77´W); Muskegon Co., Whitehall, White River (43°15´46.07´N, 86°6´6.91´W); Oakland Co., 7.2 km SW Pontiac, ditch running into Pine Lake at N shore of lake (42°35´21.1´N, 83°21´10.61´W); Ottawa Co., 8.0 km S Grandhaven, slough at Lakeshore Dr. (42°59´24.47´N, 86°13´12.38´W); Ottawa Co., 3.8 km W West Olive, mouth of Pigeon River; Shiawassee Co., Corunna, Shiawassee River, above dam (43°19´16.92´N, 84°05´21.96´W); near Owosso, Mud Lake (42°48´14.41´N, 83°54´13.94´W). Minnesota, Clearwater Co., Lake Itasca State Park, Lake Itasca (47°12´52.16´N, 95°12´25.51´W); Kandyohi Co., 3.2 km E Spicer, Woodcock Lake (45°13´15.75´N, 94°57´0.04´W); Pine Co., 2 mi. E Hinckley, Grindstone River at MN 48 (46°00´39.4´N, 92°53´14.34´W); Stearns Co., 1.6 km W Richmond, stream at MInn 23 near jct. Co. Rd. 43 (45°26´55.02´N, 94°32´14.95´W).

**Hosts.** Canada: Hyalella azteca (Saussure) (setae pereiopods). Mexico: Hyalella azteca (setae pereiopods, antennae, pleopods, uropods and telson), Hyalella sp. (corporal surface). Uruguay: Hyalella curvispina Shoemaker


**L. matthesi** Schödel, 1983

**Habitat.** Freshwater.


**Hosts.** France: *Gammarus zaddachi* Sexton (cited as *Gammarus zadacchi*) (maxillipeds). Germany: *Gammarus pulex*, *G. roeselii* Gervais (cited as *Carinogammarus roeselii*) (maxillipeds and gnathopods).

**References.** Schödel 1983; Rustige 1991; Clamp 2005.

**L. nassa** Stein, 1852

**Habitat.** Freshwater.


**References.** Clamp 1984; Rustige 1991; Rustige & Mannesmann 1991.

**L. patina** Stokes, 1887


**Museum Depositions.** USNM. 42701 Neotype; 42321, 42322, 42323, 42324, 42325, 42326, 42327.

**Habitat.** Freshwater.

**Distribution.** BR: Neartic, Neotropical (Mayén-Estrada & Aguilar-Aguilar 2012). Canada: *Alberta*, 10 Mi. S Little Smoky, creek at ALTA 43 (54°35'42.73''N, 117°2’48.91’’W); 20 mi. W High Prairie, creek at ALTA 2 (55°38'14.10''N, 116°51'4.17''W); 5 mi. W Canyon Creek, creek at ALTA 2 (55°20'43.76''N 115°11'47.28''W); 2 mi. E Vilna, Cache L. at ALTA 28 (54°8'27.85''N, 111°46'51.82''W); Faust, shallows of Lesser Slave L. (55°19'22.62''N, 115°38'16.67''W). *Newfoundland*, near Porris Point, pond alongside NFLD 73, 3 mi. N jct. NFLD 44. *Ontario*, Carleton Co. Rideau R. S. Ottawa (45°25'32.48''N, 75°40'13.65''W); Middlesex Co., Thamesford, creek at ONT 19, just S town limit (43°3'20.23''N, 80°59'25.92''W); Norfolk Co., 2.6 mi. S Port Rowan, marsh alongside ONT 59 at head of long Point (42°35'8.78''N, 80°26'58.79''W); Norfolk Co., Long Point Provincial Park, Long Point Bay alongside ONT 59 (42°34'40.34''N, 80°26'19.32''W); Sudbury Co., 4 mi. W Whitefish, ditch alongside ONT 17 (46°22'1.29''N, 81°23'56.15''W); Sudbury Co., 3 mi. W Naughton, lake alongside ONT 17 (46°23'35.36''N, 81°15'21.96''W); Welland Co., Wainfleet, canal at ONT 3 (42°55'21.97''N,
Quebec, Gatineau Co., Gatineau National Park, Taylor L. (45°30'22.15"N, 75°48'46.42"W).

Mexico: Michoacán, Cuitzeo lake, San Cristóbal (19°57'41"N, 101°18'55"W)**present work; Pátzcuaro lake (19°32' to 19°41'N, 101°32' to 101°43"W). Puebla, creek near city of Puebla; Alchichica lake (19°24'13"N, 97°24'00"W)**present work; Atexcac lake (19°13'21"N, 97°27'19"W)**present work; La Preciosa lake (19°13' to 19°24'N, 97°17' to 97°29"W)**present work.

Uruguay: Near Montevideo, pond at Sayoga and temporary ponds (34°51'0.70"S, 56°15'0.36"W).

USA: Arkansas, Lee Co., 2.9 mi. NE Brickey’s tributary to Frenchman’s Bayou at US 79 (34°54'17.78"N, 90°31'48.09"W); Montgomery Co., 4.0 mi. E Mt. Ida, Shady creek at US 270 (34°33'59.11"N, 93°38'58.52"W). Delaware, Kent Co., Milford, Haven L. (38°54'47.88"N, 75°26'52.41"W); Kent Co., 1.7 mi. N Cheswold, Garrison’s L. (39°14'39.94"N, 75°35'39.04"W); Kent Co., Smyrna, L. Como (39°17'27.75"N, 75°36'16.02"W). Florida, Bay Co., Mexico Beach, creek at US 98, 0.4 mi. SE jct. FLA 386A (29°55'6.95"N, 85°22'47.60"W); Leon, Co., near Tallahassee, L. Jackson (30°30'22.18"N, 84°18'33.02"W). Georgia, McIntosh Co., Sapelo Island, ornamental pond on grounds of University of Georgia Marine Institute (31°23'49.37"N, 81°16'51.22"W). Illinois, Coles Co., 2.5 mi. SE Charleston, L. Charleston (39°28'13.40"N, 88°7'58.07"W); Vermilion Co., just E Muncie, pond south of US 150 (40°6'47.64"N, 87°50'19.31"W). Indiana, Whitley Co., 3.0 mi. WNW Churubusco, Blue L. (41°14'39.03"N, 85°22'29.48"W). Louisiana, Orleans Pa., 1.8 mi. SSW Green’s Ditch, oxbow of Bayou LeSaire alongside US 90 (30°5'23.69"N, 89°46'38.22"W); Vermilion Pa., 12.5 mi. SW Abbeville, ditch alongside LA 334, 4.0 mi. jct. LA 82 (29°47'12.72"N, 92°29'20.20"W). Michigan, Barry Co., 5.0 mi. SW Hastings (42°35'31.60"N, 85°21'24.23"W); Leach L. at boating access (42°41'1.79"N, 85°17'21.90"W); Muskegon Co., Whitehall, White R. at city park (43°24'24.65"N, 86°19'59.96"W); Ottawa Co., 5.0 mi. S Grandhaven slough at Lakeshore Dr. (42°59'26.13"N, 86°13'35.60"W); Ottawa Co., 2.4 mi. W West Olive, mouth of Pigeon R. (42°54'13.30"N, 86°10'56.36"W); Oakland Co., 4.5 mi. SW Pontiac, ditch at N shore Pine L. (42°35'32.0"N, 83°20'36.38"W); Shiawassee Co., Corunna Shiawassee R. above dam (42°55'45.79"N, 84°4'20.21"W). Minnesota, Clearwater Co., Lake Itasca State Park, L. Itasca (47°13'3.33"N, 95°12'6.54"W); Clearwater Co., L. Itasca State Park, L. Itasca, headwaters of Mississippi R. (47°13'3.33"N, 95°12'6.54"W); Clearwater Co., Red Lake Indian Reservation, Lower Red L., 1 mi. N Red Lake R. (47°52'53.02"N, 95°0'0.89"W); Clearwater Co., Red Lake Indian Reservation, mouth of Sandy R. (47°52'29.16"N, 95°12'35.04"W); Kandiyohi Co., 2 mi. E Spicer, Woodchuck L. (45°13'56.00"N, 94°53'56.98"W); Pennington Co., 1 mi. E S. Hilaire, Thief R. at Co. Rd. 31 (43°53'28.81"N, 103°28'53.87"W); Pine Co., 2 mi. E Hinckley, Grindstone R. at MN 48 (45°20'14.32"N, 92°53'13.82"W); Stearns Co., 1.0 mi. W Richmond stream at MN 23, near jct Co. Rd. 43 (45°26'37.55"N, 94°33'22.02"W). Nebraska, Dawes Co., 26 mi. S Chadron, Niobrara R. below dam at Box Butte Reservoir (42°27'7.90"N, 102°58'12.67"W); Morrill Co., 3mi. N Bridgeport, stream at US 385 (41°13'40.81"N, 73°11'50.98"W). New Jersey, Atlantic Co., Hammonton, Hammonton L. (39°37'47.23"N, 74°46'41.10"W); Mercer Co., near Trenton (40°12'17.84"N, 74°46'1.66"W). New York, Cayuga Co., Fair Haven Beach State Park, The Pond (43°19'46.23"N, 76°41'49.95"W); Genesee Co., 3.5 mi. NW Alabama, marsh alongside Meadeville Rd. on Tonawanda Game Area 0.5 mi. S jct. Co. Rd. 12 (43°7'9.44"N, 78°27'23.79"W); Oswego Co., 5.3 mi. WSW Sandy Creek center, Sand Pond (North Pond) at Ouderkirk Rd. (43°37'57.55"N, 76°11'24.59"W); Oswego Co., 1.7 mi. N New Haven, Catfish Cr. at Co. Rd. (43°30'7.52"N, 76°18'58.67"W). North Carolina, Bertie Co., 1.9 mi. N Windsor, Hoggard Mill Cr. at SR 1301 (36°13'38.20"N, 76°57'6.25"W); Carteret Co., Portsmouth Island, Portsmouth village, freshwater pond in sand dunes (35°41'14.24"N, 76°35'1.66"W); Columbus Co., Lake Waccamaw, canal near NW shore of L. Waccamaw (34°17'26.41"N, 78°28'26.13"W); Wake Co., 5.0 mi. SW Raleigh center, Yates Mill Pond (35°43'14.12"N, 78°21'40.68"W). North Dakota, McLean Co., 5.0 mi. N Turtle Lake, pond alongside ND 41 (47°35'43.04"N, 100°54'17.12"W). Ohio, Ashland Co., Ashland, creek at OH 58 (40°53'20.46"N, 82°18'2.14"W); Huron Co., 4.5 mi. E North Fairfield, creek at OH 162, 1.0 mi. W jct. US 520 (41°6'4.09"N, 82°31'26.16"W). Wisconsin, Sawyer Co., 4 mi. NE Winter, creek at WIS 70 (45°52'7.43"N, 90°58'0.58"W).

References. Felgenhauer 1979; Clamp 1984, 1990a; Mayén-Estrada & Aladro-Lubel 2006; **present work.

b. Restricted to Isopoda

i. Europe only

*L. platei* Wallengren, 1900

Habitat. Freshwater.

Distribution. BR: Palearctic (Mayén-Estrada & Aguilar-Aguilar 2012).

Germany: Bavaria, Erlangen, Botanical Garden; near Erlangen, upper Dechsendorfer-Weiher (49°35′56.67″N, 11°0′23.97″E). North Rhine-Westphalia, Bonn, Bonn Botanical Garden, Poppelsdorfer Weiher (50°43′25.36″N, 7°53′6.83″E). Wurttemberg, Freiburg-im-Breisgau, tanks of the zoological and biological institutes of the University of Freiburg (47°59′50.66″N, 7°51′52.88″E); Near Freiburg-im-Breisgau, Hugstetten (48°3′42.70″N, 7°47′3.30″E); "Hanflochern" ("hemp pits").

Poland: Szczecin (53°25′23.86″N, 14°33′42.62″E).

Sweden: Malmöhus, near Lund (55°36′27.12″N, 12°58′15.56″E).


*L. monolistrae* Stammer, 1935

Habitat. Freshwater.

Distribution. BR: Palearctic (Mayén-Estrada & Aguilar-Aguilar 2012).

Italy: Vicenza, Monti Berici (group of hills south of city of Vicenza), near Monticello, Covolo delle Tette (cave) (45°28′17.46″N, 11°31′22.83″E); Vicenza, Monti Berici, near Lumingnano, Covolo delle Guerra (cave) (45°27′18.27″N, 11°35′4.13″E).

Republic of Croatia: Istra, near Pinguente, Pecina Glavici (cave) (45°24′25.91″N, 13°58′2.04″E).


ii. Broad Distribution

*L. aselli* Plate, 1889

Museum Depositions. USNM. 40923, 40924, 40925, 40926, 40927.

Habitat. Freshwater.

Distribution. BR: Nearctic, Palearctic (Mayén-Estrada & Aguilar-Aguilar 2012).

Canada: Ontario, Carleton R. below Ottawa (45°23′22.30″N, 75°40′40.17″W); Lanark Co., 8 km E Perth, Cockburn Cr. at ONT 43 (44°53′43.32″N, 76°10′50.69″W); Norfolk Co., 4.2 km S Port Rowan, marsh along side ONT 59 at head of Long Point (42°35′8.66″N, 80°23′4.30″W). Quebec, L'Islet Co., St. Jean-Port-Joli, mouth of Riviere Tortue at QUE 2 (47°08′56″N, 70°20′21″W).

Denmark: South Jutland, near Ribe, brook at Vedsted (57°8′57.30″N, 9°41′55.45″E).

France: Bretagne, Finistere Nord. 1 km SSE Plougarneau, creek at highway D32 (48°36′1.49″N, 4°29′54.81″W); Pont-Menou, Douren R. at highway N78 (48°38′40.63″N, 3°39′43.27″W).

Germany: Bavaria, near Erlanger: pond near Oberndorf (50°41′56.64″N, 8°27′19.69″E); Bade-Weiher, Regnitzquerzone. Hamburg, near Hamburg (53°33′2.37″N, 9°59′36.21″E). Hessen, Marburg (50°45′44.07″N, 8°44′30.59″E). North Rhine-Westphalia, Bonn, Bonn Botanical Garden (50°43′22.72″N, 7°5′27.39″E); Poppelsdorfer Weiher. Wurttemberg, Freiburg im Breisgau, University of Freiburg (47°59′50.66″N, 7°51′52.88″E).

UK: Liverpool (no locality given).

USA: Alabama, Mobile Co. Mobile, Mobile Bay at mouth of Mobile R. (30°39′60.00″N, 88°1′35.82″W), Delaware, Kent Co., Milford, Haven L. (38°54′43.57″N, 75°27′1.61′′W); Kent Co., 2.7 km N Cheswold, Garrison's L. (39°14′36.47″N, 75°35′37.72′′W). Louisiana, Vermilion Parish, Pecan Island, canal
alongside Louisiana 82, 1.3 km S Schooner Bayou Canal (29°44′1.26″N, 92°19′56.23″ W). **Michigan**, Ottawa Co., 8 km S Grandhaven, slough at Lakeshore Dr. (42°59′30.04″N, 86°13′11.53″W). **New York**, Oswego Co., 3 km S Southwest Oswego, Eightmile Cr. at New York 104 (43°22′52.48″N, 76°34′27.57″W); Oswego Co., 2.7 km N New Haven, Catfish Cr. at Co. Rd. 1 (43°30′47.58″N, 76°11′17.70″W); Oswego Co., 4.5 km SSW West Monroe, Oneida Lake at Shaw’s Point (43°14′42.92″N, 76° 5′34.37″W). **North Carolina**, Tyrrell Co., Gum Neck Landing, state boating access area at end SR 1316 (35°41′50.15″N, 76°34′27.58″W); Tyrrell Co., 2.1 km NW Columbia, ditch alongside SR 1209 (35°56′10.04″N, 121°45′48.01″W). **Oregon**, Klamath Co., 19 km N Klamath Falls, Barkley Springs (42°23′53.78″N, 120°54′48.01″W). **South Carolina**, Florence Co., Lynches River State Park, Lynches R. (34°2′13.90″N, 79°47′4.48″W). **Wisconsin**, Bayfield Co., 3.2 km S Barksdale, creek at Wisconsin 13 near jct. U.S. 2 (46°43′56.18″N, 90°52′40.43″W); Sawyer Co., 6.4 km NE Winter, creek at Wisconsin 70 (45°2′7.33″ N, 90°58′0.46″W); Sawyer Co., 8 km N Loretta, creek at Co. Rd. GG (45°57′24.54″N, 90°50′39.36″W).

**Hosts.** Canada: *Caecidotea communis* (Say) (cited as *Asellus communis*), *C. racovitzai racovitzai* (Williams) (cited as *Asellus racovitzai racovitzai*). Denmark: *Asellus aquaticus*. France: *Asellus aquaticus*. Germany: *Asellus aquaticus* (underside of gills). UK: *Asellus aquaticus*. USA: *Asellus* sp. (pleopods and pereiopods), *Caecidotea attenuata* (Richardson) (cited as *Asellus attenuatus*), *C. communis* (Say) (cited as *Asellus communis*), *C. forbesi* (Williams) (cited as *Asellus forbesi*), *C. laticaudata* (Williams) (cited as *Asellus laticaudatus*), *C. occidentalis* (Williams) (cited as *Asellus occidentalis*), *C. racovitzai racovitzai* (Williams) (cited as *Asellus racovitzai racovitzai*), *Lirceus lineatus* (Say) (pleopods), and suspended glass slide.


c. **Decapoda**

1. **North America only**

**L. dennisi** Clamp, 1987

**Museum Depositions.** USNM. 40928 Holotype; 40929 Paratype.

**Habitat.** Freshwater.


**Hosts.** Mexico: *Cambarellus patzcuarensis* Villalobos (exposed body surface). USA: *Cambarus (Cambarus) bartonii bartonii* (Fabricius, 1798), *C. chasmodactylus* James, *Orconectes illinoiensis* Brown (exposed body surface).


**L. diogenes** (Jankowski, 1986)

* Circolagenophrys diogenes* Jankowski 1986: 81-82.

**Lagenophrys incompta** Clamp 1987: 385-386.

**Museum Depositions.** USNM. 40930 Holotype; 40931 Paratype.

**Habitat.** Freshwater.

**Distribution.** BR: Nearctic.

USA: **Pennsylvania** (41°11′58.50″N, 77°11′47.26″W). **Missouri**, Jefferson Co. 4.3 km NNE Hillsboro, creek running parallel to MO 21 at Hayden Rd. (38°16′14.36″N, 90°33′21.04″W).

**Hosts.** USA: *Cambarus diogenes* Girard (gills), *Orconectes illinoiensis* (gills and branchial chamber).

Lagenophrys oregonensis Clamp 1987: 386-387.


Habitat. Freshwater.

Distribution. BR: Nearctic, Palaeartic (Mayén-Estrada & Aguilar-Aguilar 2012).

USA: Nevada Storey Co. Reno, Truckee (39°36'23.04''N, 119°18'12.21''W). Oregon, Lincoln Co. 3.2 km NW Eddyville, Marys R. alongside US 20 (44°39'17''N, 123°48'37.03''W); Harney Co. near Drewsey, Malheur R. (43°48'42''N, 118°22'32.8''W). Washington, Wahkiakum Co. Deep R. at Peter McKinnon log dump (46°19'47.65''N, 123°41'52.30''W).

Hosts. USA: Pacifastacus connectens (Faxon), P. leniusculus leniusculus (Dana), P. leniusculus trowbridgii (Stimpson) (gills and other corporal surfaces).


L. metopauliadis Corliss and Brough, 1965

Museum Depositions. USNM. 24241 Holotype; 24242 Paratype.

Habitat. Freshwater (tank epiphytic bromeliads).

Distribution. BR: Neotropical.

Jamaica: West Indies (18°5'24.50"N, 77°17'35.26"W).


L. verecunda Felgenhauer, 1982

Habitat. Freshwater.

Distribution. BR: Nearctic.

USA: Arkansas, Monroe Co., 6.3 mi. E Holly, Big Cypress Cr. at ARK 86 (34°36'7.09"N, 91°5'19.85"W), Florida, Lake Jackson, Leon Co. (30°31'21.58"N, 84°19'19.93"W); near Tallahassee (30°30'22.18"N, 84°18'33.02"W); Levy Co., 4 mi. NW Bronson, Little Waccasassa R. at FL 339 (29°29'26.51"N, 82°42'23.03"W).

Hosts. USA: Palaemonetes kadiakensis, P. paludosus (gills).


iii. Asia only

L. branchiarum Nie and Ho, 1943

Habitat. Freshwater.

Distribution. BR: Nearctic.

China: Sichuan (Szechwan) (30°33'18.53"N, 103°55'51.45"E); Beibei (Pehpei), pond near National Institute of Zoology and Botany, Academia Sinica (29°48'11.07"N, 106°23'44.05"E).


d. Restricted to Other Hosts (Copepoda, Cladocera, Ostracoda)

L. bipartita Stokes, 1890

Habitat. Freshwater.

Distribution. BR: Nearctic.

USA: no locality given.

Hosts. USA: Daphnia sp. (surface of body).


L. discoidea Kellicott, 1887

Lagenophrys discoidea Kellicott 1887: 232; Kane 1965: 121.


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**Museum Depositions.** USNM. 42309 Neotype; 42310, 42311, 42312, 42313, 42314, 42315.

**Habitat.** Freshwater.

**Distribution.** BR: Neartic, Neotropical, Palaeartic (Mayén-Estrada & Aguilar-Aguilar 2012).

Argentina: **Buenos Aires.** San Miguel del Monte lagoon.

Canada: **Ontario.** 3.2 km WSW Crystal Beach, Point Abino, swamp at jct. Pt. Abino Rd./Erie Rd. (42°51'32.60"N, 79°52'16.2"W).

China: **Jiangsu** (Kiangsu) (32°25'10.1"N, 118°45'12.5"E); **Najing** (Nanking) (32°3'49.84"N, 118°47'52.24"E).

Sweden: **Malmöhus,** near Landskrona, small pond at the base of the Ronnebergagard (55°52'31.71"N, 12°50'32.15"E).

Switzerland: **Solothurn,** Seewen lake (47°25'43.26"N, 7°39'41.50"E), **Basel,** near Basel, Schusterinsel (47°33'21.07"N, 7°35'38.05"E). French portion of Switzerland, near Behringersmuhl, Stempfermuhl spring.

Ukraine: **Dnieper Basin** (47°38'26.35"N, 35°51'30.30"E).

USA: **Florida,** Franklin Co., 10.7 km N Carrabelle, flooded pit alongside state secondary road 67 (29°56'42.60"N, 84°37'52.98"W). **Georgia,** McIntosh Co., Sapelo Island, ponds near ocean beach at S end of island (31°23'36.38"N, 81°16'37.34"W). **Illinois,** Lake Charleston, Coles Co. (39°28'10.99"N, 88°9'2.08"W). **Louisiana,** Orleans Pa., 2.9 km S Green's Ditch, oxbow of Bayou LeSaire alongside U.S. 90 (30°7'0.81"N, 89°45'48.45"W).

**Virginia,** Great Exuma Rd., Great Exuma Island, oxbow pond alongside Great Exuma Rd., N of Snag Point (32°11'35.36"N, 76°52'44.58"W).

**New York,** Oswego Co., 4.5 km SSW West Monroe, swamp near Oneida Lake alongside Shaw Dr. (43°14'45.40"N, 76°6'4.01"W); Oswego Co., 8.6 km WSW Sandy Creek center, Sandy Pond (North Pond) at Ouderkerk Rd. (43°37'54.58"N, 76°11'17.70"W). **North Carolina,** Alleghany Co., 3.0 km NW Twin Oaks, New R. at state secondary road 1345 (36°33'4.15"N, 81°10'54.11"W); Franklin Co., 10.4 km E Youngsville, Crooked Cr. at U.S. 401 (36°0'44.25"N, 78°21'40.00"W); Onslow Co., Topsail Island, West Onslow Beach, pond just S jct. NC 210 with state secondary road 2224 (35°55'42.2"N, 78°23'45.83"W). **Oregon** (45°36'41.35"N, 122°31'25.24"W). **Virginia,** Grayson Co., 5.1 km S Independence, New R. at U.S. 21-221 (36°34'3.63"N, 81°9'27.31"W).


**L. stammeri** Lust, 1950

**Habitat.** Freshwater.

**Distribution.** BR: Palaeartic.

Germany: **Bavaria,** near Hersbruck, Hersbrucker Quelle (spring) (49°30'17.09"N, 11°27'45.46"E).

**Hosts.** Germany: *Cypria ophtalmica* (Jurine) (external surface of carapace).


**L. vaginicola** Stein, 1852

**Lagenophrys obovata** Stokes 1887: 147; Stokes 1888: 59; von Ubisch 1913: 43; Swarczewsky 1930: 458; Kane 1965: 120, 121.

**Lagenophrys vagenicola** Wallengren 1900: 358, 360, 362; von Ubisch 1913: 42, 43, 44, 52, 75.

**Habitat.** Freshwater.

**Distribution.** BR: Neartic, Palaeartic (Mayén-Estrada & Aguilar-Aguilar 2012).

Austria: **Voralberg,** 7 mi. SSW Bludenz, Lunersee (47°32'22.96"N, 9°45'48.29"E).
Canada: Ontario, 2.0 mi. WSW Crystal Beach, Point Abino, swamp at jct. Pt. Abino Rd./Erie Rd. (42°51'32.60"N, 79°5'42.16"W).

China: Jiangsu (Kiangsu), Nanjing (Nanking) (32°2'55.10"N, 118°45'12.50"E).


Germany: Bavaria, near Erlangen (49°35'35.32"N, 10°59'42.16"E). Potsdam, Niemegk (52°4'58.44"N, 12°42'0.17"E). Wurttemberg, Freiburg-im-Breisgau, Hochdorf (47°59'50.66"N, 7°5'1.82"E).

Slovakia: High Tatra Mountains near Kezmarck, lakes Kezsmarker Gruner-See, Kezsmarker Schwarzer-See, Kezsmarker Weiesser-See (49°9'6.17"N, 12°42'0.17"E).

Switzerland: Basel, Dornach, meadow ponds (47°28'57.41"N, 7°36'30.90"E). Geneve, near Geneva, Pinchat (46°10'22.17"N, 6°49.81"E); near Geneva, Rouelbeau, marsh (46°14'30.78"N, 6°13'5.68"E); near Geneva, Florissant, small pond (46°11'37.11"N, 6°9'34.29"E); near Geneva, Valavaran, bog; Lac Leman, littoral region (46°12'34.31"N, 6°9'46.48"E); near Geneva, Chatelaine Lake; near Geneva, Vieuxbois, lake; near Geneva, Feuillas, marsh.

USA: Delaware, 1.7 mi. N Cheswold, Garrison’s L. (39°14'39.94"N, 75°35'39.04"W). New Jersey, Mercer Co., near Trenton (40°12'17.84"N, 74°46'1.66"W). New York, Erie Co., near Buffalo, early spring (42°53'28.02"N, 78°52'53.41"W). North Carolina, Tyrrell Co., 2.5 mi. NW Columbia, swamp at jct. SR 1209/SR 1211 (35°56'50.53"N, 76°16'52.58"W); Tyrrell Co., 1.5 mi. NW Columbia, swamp alongside SR 1209 (35°56'61.61"N, 76°16'11.05"W); Washington Co., 1.8 mi. SW Creswell, swampy margin of Scuppernong (35°51'14.00"N, 76°25'02.52"W).

Canada: harpacticoid copepod (caudal bristles). China: Canthocamptus sp. (caudal bristles). Germany: Canthocamptus staphylinus (Jurine) (swimming legs and caudal bristles), Cyclops sp. Switzerland: Canthocamptus staphylinus (caudal bristles), Canthocamptus sp., Metacyclops minutus (Claus) (cited as Cyclops minutus), Cyclops sp. USA: harpacticoid copepod (caudal bristles), Bryocamptus minutus (Claus) (setae of swimming legs, caudal bristles), Canthocamptus sp.


2. Southern Hemisphere (Restricted to Decapoda)

a. South America only

L. aegleae Mouchet-Bennati, 1932

Museum Deposition. USNM: 40919, Neotype.

Habitat. Freshwater.

Distribution. BR: Neotropical (Mayén-Estrada & Aguilar-Aguilar 2012).


Uruguay: Montevideo, Arroyo Miguelete (34°51'25.92"S, 56°12'08.65"W).


L. andos (Jankowski, 1986)

Circolagenophrys andos Jankowski 1986: 82.

Habitat. Freshwater.

Distribution. BR: Neotropical.

Chile: Valparaiso (33°2'34.35"S 71°36'58.27"W).


L. anticthos Clamp, 1988

USNM. 40920 Holotype ; 40921, 40922 Paratypes.

Habitat. Freshwater.

Distribution. BR: Neotropical (Mayén-Estrada & Aguilar-Aguilar 2012).


Uruguay: Montevideo (34°54'57.80"S, 56°11'12.22"W).


*L. shiftus* (Jankowski, 1986)

Circolagenophrys *shiftus* Jankowski 1986: 82.

Habitat. Freshwater.

Distribution. BR: Neotropical.

Chile: *Valparaíso* (33°2'34.52"S, 71°37'10.21"W).

Hosts. Chile: *Parastacus pugnax* (cited as *Parastacus chilensis*) (gills).


b. Australia and New Guinea only

*L. darwini* Kane, 1965

Habitat. Freshwater.

Distribution. BR: Australian.

Australia: *Northern Territory*, stream near Darwin (12°27'58.96"S, 130°50'26.26"E).


*L. deserti* Kane, 1965

Habitat. Freshwater.

Distribution. BR: Australian.

Australia: *Western Australia*, rivers in southwestern part of state (30°45'56.57"S, 119°29'0.06"E).


*L. dungogi* Kane, 1965

Habitat. Freshwater.

Distribution. BR: Australian.

Australia: *New South Wales*, stream near Dungog (32°24'5.93"S 151°45'37.73"E). Near Hornsby, Galston Gorge, Berowra Cr. (33°34'37.26"S, 151°7'40.82"E).


*L. engaei* Kane, 1965

Habitat. Freshwater.

Distribution. BR: Australian (Mayén-Estrada & Aguilar-Aguilar 2012).


Hosts. Australia: *Engaeus fultoni* Smith and Schuster (setae), *E. hemicirratulus* Smith and Schuster (gills, pleopods and exposed surface), *E. victoriensis* Smith and Schuster (gills), *Engaeus* sp. (gills, pleopods and exposed surface).


*L. jacobi* (Kane, 1969)

Stylohedra *jacobi* Kane 1969:368-369.

Habitat. Freshwater.

Distribution. BR: Australian.


References. Kane 1969.

*L. petila* Clamp, 1994

Museum Depositions. USNM. 47734 Holotype; 47735 Paratype.

Habitat. Freshwater.

Distribution. BR: Australian (Mayén-Estrada & Aguilar-Aguilar 2012).

Australia: *Tasmania*: Derwent Bridge (42°8’6.97"S, 146°13’52.68"E).

Hosts. Australia: *Parastacoides tasmanicus* (Erichson) (setae of gills and pleopods).

*L. rugosa* Kane, 1965

**Habitat.** Freshwater.

**Distribution.** BR: Australian.


**Hosts.** Australia: *Engaeus marmoratus* Clark (gills), *Geocharax falcata* Clark (gills).


*L. turneri* Kane, 1969


**Museum Depositions.** AM P62821 Lectotype. USNM. 1004293 Paralectotype; 1004294.

**Habitat.** Freshwater.

**Distribution.** BR: Australian (Mayén-Estrada & Aguilar-Aguilar 2012).

Australia: *Northern territory*, Katherine, Katherine R. (14°30'22.21"S, 132°13'0.10"E).

Papua New Guinea: Gulf District near Malalaua, Lake Kamu R. (146° 8'48.29"E, 146° 8'48.29"E).


*L. willisi* Kane, 1965

**Habitat.** Freshwater.

**Distribution.** BR: Australian.


**Hosts.** Australia: *Cherax albidus* Clark, *C. destructor* Clark, *C. rotundus, C. rotundus setosus* (gills).


c. *New Zealand only*

*L. novazealandae* Clamp, 1994

**Museum Depositions.** USNM. 47731 Holotype; 47732, 47733 Paratypes.

**Habitat.** Freshwater.

**Distribution.** BR: Australian.


**Hosts.** New Zealand: *Paraneophrops setosus* Hutton, *P. zealandicus* (White) (bases and filaments of gills).


d. *South Africa only*

*L. reflexa* Kane, 1969

*Stylohedra reflexa* Kane 1969: 369.

**Habitat.** Freshwater.

**Distribution.** BR: Ethiopian.

South Africa (no locality given).

**Hosts.** South Africa: *Mesamphisopus capensis* (Barnard) (setae).

**References.** Kane 1969.

e. *Madagascar only*

*L. machaerigera* Clamp, 1992

**Museum Depositions.** USNM. 43090 Holotype; 43091, 43092, 43093 Paratypes.

**Circolagenophrys machaerigera** Jankowski 1993: 221.

**Habitat.** Freshwater.

**Distribution.** BR: Ethiopian.

Madagascar, central portion (19°13'28.96"S, 46°41'32.86"E).

**Hosts.** Madagascar: *Foza goudoti* (H. Milnes Edwards) (cited as *Gecarcinuates goudoti*) (gills).
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3. Broad Distribution

L. awerinzewi Abonyi, 1928

Habitat. Freshwater.

Distribution. BR: Australian, Ethiopian, Oriental (Mayén-Estrada & Aguilar-Aguilar 2012).

Burma: Upper Tenasserim (12°27'52.85"N, 99°0'36.72"E).

China: Guangdong (Kwangtung) Hainan Dao (Hainan) near Kachek, Mt. Betcholia (22°34'40.30"N, 114°53'52.48"E). Shandong (Shantung) (36°39'51.00"N, 117°1'11.16"E); Jinan (Tsinan) (36°38'58.42"N, 117°7'12.47"E); Taminghu. Sichuan (Szechwan) (30°33'18.53"N, 103°55'51.45"E); Yibin (Ipin) (28°46'11.66"N, 104°38'30.66"E); Suifui.

India: Assam (26°11'25.88"N, 92°56'11.41"E); Ganjam (12°58'53.64"N, 77°37'0.60"E); North Cachar (24°46'11.42"N, 92°51'24.28"E). Maharashtra (19°40'18.68"N, 75°43'52.54"E); Khandala (18°45'26.30"N, 73°22'20.23"E); Bombay (19°4'31.02"N, 72°52'53.55"E); Kolaba (18°18'39.15"N, 72°57'35.55"E). Tamil Nadu (11°7'14.16"N, 78°39'31.33"E); Madras (11°43'19.44"N, 78°35'6.86"E); Shevaroy Hills (11°50'37.30"N, 78°13'28.24"E).

Liberia: Gbarnga District, stream tributary to St. John’s R. (6°59'52.89"N, 9°29'15.84"W).

Malaysia: North Borneo, Mt. Kinabalu (6°3'48.09"N, 116°32'47.58"E).

New Guinea (no locality given).

Taiwan: Hsinchu (24°7'57.40"N, 120°57'23.01"E); Hsien (22°36'57.05"N, 120°17'31.61"E); Kungse.


Uganda: Entebbe (0°3'3.39"N, 32°27'53.46"E).


B. Marine, Estuarine, Euryhaline

1. Restricted to Amphipoda

L. anisogammani (Jankowski, 1993)

Circolagenophrys anisogammani Jankowski 1993: 220-221.

Habitat. Marine.

Distribution. BR: Palaeartic.

Russia: Southern Sakhalin on the boundary of the Sea of Japan and the Sea of Okhotsk, Busse lagoon (45°53’30.59"N, 142°4’52.32"E).


L. crutchfieldi Clamp, 1993

Circolagenophrys crutchfieldi Clamp, 1993: 221.

Museum Depositions. USNM. 43086 Holotype; 43087, 43088, 43089 Paratypes.

Habitat. Marine, estuarine.

Distribution. BR: mainly Neotropical (Mayén-Estrada & Aguilar-Aguilar 2012).

Brazil: Santa Catarina, Ilha de Santa Catarina (27°36'7.31"S, 48°30'4.70"W); Santa Catarina, Ilha de Sao Francisco (26°19'25.69"S, 48°38'22.79"W).

Dominican Republic: Boca de Infiero, small beach on southern shore of Bahia de Samana (19°10'50.15"N, 69°16'22.33"W).

Mexico: Baja California, La Paz (24°8'44.26"N, 110°20'23.26"W).
USA: Florida, Monroe Co., West Summerland Key at Spanish Harbor Channel (24°40'N, 81°20'W); Monroe Co., 7.5 mi. NNE Key Largo, Barnes Sound alongside U.S. 1 (25°11'N, 80°17'W).

Virgin Islands: St. Croix, mangrove island, Salt River lagoon (17°41'10.78"N, 64°53'2.80"W).


**References.** Clamp 1993.

*L. maxillaris* (Jankowski, 1993)

*Lagenophrys* sp. Fenchel 1965: 290, 301.

*Circolagenophrys maxillaris* Jankowski 1993: 221.


**Habitat.** Brackish, marine.

**Distribution.** BR: Palaeartic (Mayén-Estrada & Aguilar-Aguilar 2012).

Denmark: near Helsingborg, northern part of the Øresund, shore to below 5-6 m in depth (56°02'26.42"N, 12°37'18.53"E).

England: *Cornwall*, Looe Bay (50°21'05.02"N, 4°27'6.92"E).

France: *Bretagne*, Finistere-Nord, Isle de Siec (48°42'26.11"N, 4°03'58.56"E).

Norway: *Raunefjorden* (60°16'32.01"N, 5°12'32.66"E).


*L. orchestiae* Abonyi, 1928

**Habitat.** Freshwater, estuarine (semiterrestrial).

**Distribution.** BR: Neartic, Palaeartic (Mayén-Estrada & Aguilar-Aguilar 2012).

Hungary: *Transdanubia*, Revfulop, northern shore of Lake Balaton in the vicinity of the Biological Station (46°49'54.54"N, 17°38'48.34"E); *Transdanubia*, Abrahamhegy (village on northern shore of Lake Balaton) (46°48'48.66"N, 17°34'28.85"E).


Russia. (no locality given).

USA: Georgia, McIntosh Co., Sapelo Island, salt marsh on grounds of University of Georgia Marine Institute (31°23'49.37"N, 81°16'51.22"W). *North Carolina*, Beaufort Co., 5.5 mi. ENE Bath, Banjo Cr. at SR 1718 (35°29'38.51"N, 76°42'52.22"W); Dare Co., Bodie Island, 5.5 mi. SSE Nags Head, creek at NC 12, 1.6 mi S jct. US 64/US 264 (35°53'2.95"N, 75°35'24.49"W).


USA: *Orchestia uhleri* Shoemaker (gills).


*L. tattersalli* Willis, 1942

**Habitat.** Marine.

**Distribution.** BR: Palaeartic (Mayén-Estrada & Aguilar-Aguilar 2012).


**Hosts.** France: *Echinogammarus marinus* (Leach) (cited as *Gammarus marinus*) (gill plates). UK: *E. marinus* (cited as *Gammarus marinus*) (gill plates).

**References.** Willis 1942; Clamp 1984.

2. **Restricted to Isopoda**

*L. cochinensis* Santhakumari & Gopalan, 1980

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Museum Depositions. USNM. 1075882, 1075907, 1075917, 1075919, 1075922, 1075930, 1075931, 1075932, 1075933.

Habitat. Marine, estuarine.

Distribution. BR: Australian, Ethiopian, Nearctic, Neotropical (Mayén-Estrada & Aguilar-Aguilar 2012).

Cameroon: no locality given.

Cuba: Bahia de Nuevitas, mouth of Saramaguacan River.

India: Kerala, Cochin, Ramanthuruth area (9°58’54.80”N, 76°15’34.25”E); Kerala, Cochin, Cochin Backwater (9°58’52.78”N, 76°15’34.05”E); Southwest coast; Tamil Nadu, Pamban (9°16’11.58”N, 79°13’14.71”E) and Rameswaram (9°17’8.65”N, 79°18’58.22”E); Cochin Backwater, Kayamkulam Lake, Ayiramthengu; Cochin Backwater, Karunagappally (southern region of Kayamkulam Lake); Cochin Backwater, 0.3 km from barmouth, at Neendakara (8°56’23.09”N, 76°32’56.70”E); Cochin, Cochin Backwater, Aroor station (9°53’19.77”N, 76°17’53.83”E); Kerala, north shore of Cochin Harbor, pier in brackish water and from wooden craft; Tamil Nadu (11°7’14.16”N, 78°39’31.33”E); Madras (11°43’19.44”N, 78°3’56.68”E).


Malaysia: Kedah, Putani, Sungei.

New Zealand: North Island, near Wellington, Pauatahunui, Inlet (41°6’14.68”S, 174°52’4.81”E); South Island, Kenepuru Sound (41°11’54.90”S, 173°57’33.13”E); North Island, Wairoa R. at Hawke’s Bay (39°46’10.97”S, 176°44’3.82”E).

Philippines: Aklan, New Washington, fish pond (11°39’0.24”N, 122°25’40.05”E).

Thailand: Nong Pang, Bangpakong R.

USA: California, Humboldt Co., Humboldt Bay (40°43’10.25”N, 124°14’33.36”W); Alameda Co., Berkeley, Berkeley Marina (37°51’11.25”N, 122°18’28.86”W). Florida, Brevard Co., Grant, Indian River.

Venezuela: Maracaibo Bay (10°33’48.40”N, 71°35’59.40”W).


L. limnoriae Clamp, 1988


Circolagenophrys circularis Jankowski 1986: 79.

Museum Depositions. USNM. 39508 Holotype; 39509 Paratype.

Habitat. Marine.


Canada: British Columbia, Sechelt, tidal creek at Porpoise Bay (49°29’20.14”N, 123°45’54.14”W).

Norway. (no locality given).

USA: North Carolina, Brunswick Co. Sunset Harbor, mouth of Lockwood Folly R. (33°55’16.13”N, 78°13’59.65”W); Cartaret Co., Beaufort, shore of Newport R. at SR 1208 bridge to Piver’s Island (34°43’11.25”N, 76°40’23.67”W); Pender Co. (Topsail Beach, Topsail Sound) (34°21’48.06”N, 77°37’46.23”W).

White Sea. (no locality given).


3. Restricted to Decapoda

L. callinectes Couch, 1967


**Museum Depositions.** USNM. 42344, 42345, 42346, 42347, 42348, 24239 Holotypes; 24240 Paratype.

**Habitat.** Marine, estuarine.

**Distribution.** BR: Nearctic, Neotropical (Mayén-Estrada & Aguilar-Aguilar 2012).

USA: **Florida,** Indian River Co., Vero Beach, W bank of Indian R. N of FLA 60 (27°38’16.43”N, 80°22’32.68”W); Near Pensacola, Gulf of Mexico. **Georgia,** estuaries. **Louisiana,** Gulf of Mexico, near New Orleans; S of Terrebonne Parish, Shipshoal lease area (Gulf of Mexico) (29°1’59.58”N, 90°44’52.3”W). **Maryland,** Chesapeake Bay. **North Carolina,** Cartaret Co., 26 km N Beaufort, Adams Cr.; Beaufort (34°57’7.34”N, 76°39’20.06”W). **South Carolina,** Charleston Co., Charleston, Wando R.; Trenchard’s Inlet (32°45’2.45”N, 79°52’49.09”W). **Virginia,** Chincoteague Bay.

Venezuela: **L. Maracaibo,** Río de los Pojaros 1 km upstream from L. Maracaibo.


*Lagenophrys eupagurus* Kellicott, 1893


**Museum Depositions.** USNM. 42331, 42332, 42333, 42334, 42335, 42336, 42337, 42338, 42339, 42340, 42341, 42342, 42343.

**Habitat.** Marine, estuarine, freshwater.

**Distribution.** BR: Neartic, Neotropical, Oriental, Palaeartic (Mayén-Estrada & Aguilar-Aguilar 2012). Belgium: **Antwerpen,** Lillo (Anvers), ditches flooded by tides from Escaut R. (51°14’9.16”N, 4°23’0.23”E). China: **Sichuan** (Szechwan) (30°33’18.53”N, 103°55’51.45”E); Beibei (Pehpei) (29°48’11.07”N, 106°23’44.05”E); pond near National Institute of Zoology and Botany, Academia Sinica (25°3’3.94”N, 121°37’18.02”E). Japan: **Hokkaido,** Sapporo (no locality given).

Mexico: **Yucatán,** Dzilam (21°26’N, 88°56’W); Sisal (21°10’N, 90°02’W).


*Lagenophrys eupagurus* Kellicott, 1893


**Museum Depositions.** USNM. 42331, 42332, 42333, 42334, 42335, 42336, 42337, 42338, 42339, 42340, 42341, 42342, 42343.

**Habitat.** Marine, estuarine, freshwater.

Fort Bragg Military Reservation, Texas L.; Dare, Co. Stumpy Point, Stumpy Point Bay at end SR 1100 (35°42'32.12"N, 75°43'11.39"W); Dare Co. Bodie Island, 1.6 mi S jct. US 64 with US 264, creek at NC 12 (35°53'2.95"N, 75°32'24.49"W); Dare Co., Hatteras Island, 0.5 mi. N Waves, creek at NC 12 (35°34'39.89"N 75°28'25.00"W); Dare Co., Hatteras Island just S Salvo Town limit, creek at NC 12 (35°32'7.63"N, 75°28'24.44"W); Dare Co., Hatteras Island, 1.5 mi. NNE Buxton Center (35°16'51.86"N, 75°31'2.08"W); Pamlico Sound (35°14'42.97"N, 75°59'30.03"W); Hyde Co. 1.0 mi S Fairfield Lake Mattamuskeet at NC 94 causeway (35°31'38.80"N, 76°13'9.07"W); Hyde Co., Ocracoke Island, 4.3 mi. ENE Ocracoke, Quork’s Point Cr. at NC 12 (35°8'2.59"N, 75°43'0.84"W); Hyde Co., Ocracoke Island, 5.5 mi NE Ocracoke, Molasses Cr. at NC 12 (35°2'3.83"N, 75°53'6.00"W); New Hanover Co., Wrightsville Beach, Wrightsville Sound (34°12'30.49"N, 77°47'47.31"W); Onslow Co., West Onslow Beach, brackish ponds at N end of Topsail Island (34°28'45.18"N, 77°27'14.07"W); Pender Co., New Topsail Beach, public boating access area at end SR 1316 (35°41'34.81"N, 76°6'49.78"W); Wake Co., 5.0 mi. SW Raleigh center, Yates Mill Pond (35°43'14.12"N, 78°41'20.68"W).

Texas, aquaculture ponds; Brazoria Co., ponds of Texas A & M University shrimp culture project (30°36'44.63"N, 96°21'11.12"W).

Virginia, Accomack Co., 2.3 mi. Chincoteague, Queen Sound at VA 175; Accomack Co., Chincoteague Bay.

Hosts. Belgium: Palaemonetes varians (Leach) (all surfaces of body except gills). China: Macrobrachium nipponense (cited as Macrobrachium nipponiensis) (antennae and pleopods). Japan: Palaemon paucidens de Haan (uropods, carapace, terga, maxillipeds, pleopods, basal parts of antennae, and eyestalks) (also cited as Leander paucidens and Palaemonetes paucidens). Mexico: Farfantepenaeus brasiliensis (Lateille) (gills), Palaemonetes pugio Holthuis (gills). Thailand: Macrobrachium rosenbergii de Man (gill lamellae). USA: Apocorophium acutum (Chevreux) (cited as Corophium acutum) (gills), Pagurus longicarpus Say (gill lamellae), Palaemonetes sp. (all surfaces of body), Macrobrachium ohione (Smith) (medial surfaces of pleura), Litopenaeus setiferus (Linnaeus) (cited as Penaeus setiferus), Litopenaeus vannamei (Boone) (cited as Peneaus vannamei), Upogebia affinis (Say) (all surfaces of body).


II. Paralagenophrys Clamp, 1987

P. singularis (Kellicott, 1887)


Museum Deposit. USNM. 39507.

Habitat. Freshwater.

Distribution. BR: Nearctic.

USA: Arkansas, Arkansas Co., 6.6 mi S Gillett, Moore Bayou at ARK 1 (34°1'52.39"N, 91°22'29.40"W), Maryland, Wicomico Co., Powellville, Adkin’s Mill Pond (38°19'56.33"N 75°22'28.08"W). North Carolina, Avery Co., 1.2 mi S Crossnore, Linville R. at SR 1536 (36°0'15.79"N, 81°56'0.78"W); Brunswick Co., 2.3 mi. SW Belville, Jackey’s Cr. At NC 133 (34°13'58.04"N 77°58'51.61"W); Columbus Co., Tabor City, Spivey’s Pond (34°8'24.83"N, 78°49'21.16"W); Columbus Co., Lake Waccamaw, canal near northwest shore of L. Waccamaw (34°17'26.58"N 78°28'27.09"W); Cumberland Co., 6.7 mi NW Hope Mills, pond at Lake Rim State Fish Hatchery (35°1'53.78"N, 79°2'25.05"W); Duplin Co., near Kenansville, Tea Swamp at NC 50 (34°57'12.30"N 77°57'10.27"W); Johnston Co., 1.5 mi W Princeton, Holt’s Pond (35°27'56.78"N, 78°11'12.80"W); Johnston Co., 3.0 mi NE Four Oaks, Holt’s L. at NC 96 (35°28'9.76"N, 78°23'4.89"W); Moore Co., near Vass, farm pond (35°15'30.27"N, 79°17'20.56"W); Tyrrell Co., 0.6 mi S Columbia, ditch alongside NC 94 (35°54'33.19"N, 76°14'50.81"W).

Hosts. USA: Cambarus (Cambarus) bartonii bartonii (cited as Cambarus bartonii) (carapace), Lepina sp. (underside of leaves), on leaves of moss attached to bases of cypressess, Ludwigia sp. (underside of leaves), Amnicola sp. (external surface of shell), unidentified aquatic vascular plant (underside of leaves), Myriophyllum sp. (rotting plant debris), Utricularia sp. (rotting plant debris).

References. Clamp 1987b.

III. Clistolagenophrys Clamp, 1991

A. Occurring Only In Freshwater
1. Northern Hemisphere
   a. Restricted to Amphipoda
      i. Lake Baikal endemics

   *C. primitiva* (Swarczewsky, 1930)


   **Habitat.** Freshwater.

   **Distribution.** BR: Palaearctic.

   Russia: Lake Baikal, Irkutsk (52°16'30.18"N, 104°18'12.29"E).

   **Hosts.** Russia: *Pallasea cancellus* (pereiopods, pleopods).


   IV. *Setonophrys* Jankowski, 1986

   1. Australia only, Freshwater, Restricted to Decapoda.

   *S. bispinosa* (Kane, 1965)

   *Lagenophrys bispinosa* Kane 1965: 109, 117, 120, 121.

   **Habitat.** Freshwater.

   **Distribution.** BR: Australian.


   **Hosts.** Australia: *Cherax rotundus setosus* (swimmerets).


   *S. communis* (Kane, 1965)


   **Lagenophrys latispinosa** Kane 1965: 109, 118, 120, 121; Sprague & Couch 1971: 533.

   **Lagenophrys lawrii** Kane 1965: 109, 118, 120; Sprague & Couch 1971: 533.

   **Museum Depositions.** USNM. 42125, 42676, 42677, 42678, 42679.

   **Habitat.** Freshwater.

   **Distribution.** BR: Australian.

   Australia: New South Wales, Euston, Murray river (34°34'40.56"S, 142°44'47.49"E); near Newcastle, waterhole (32°56'19.32"S, 151°46'25.63"E); Wentworth, Murray river at Lock 10 (34°26'12.12"S, 142°10'48.87"E).

   **Northern territory**, Groote Eylandt (Island in Gulf of Carpentaria, NE end of island on side of Little Lagoon (13°56'17.09"S, 136°44'40.81"E); near Darwin, stream (12°26'26.92"S, 130°52'3.73"E). Victoria, Apollo Bay; 9 mi. ESE Healesville (37°44'2.89"S, 145°38'54.87"E); Brabham Ferry (34°47'15.19"S, 138°32'38.95"E); Craigburn, Merri Creek (37°42'33.29"S, 144°58'52.11"E); dams around Melbourne, Panton Hill (37°38'43.19"S, 145°14'32.49"E); Heathcote, Hamilton (36°55'0.23"S, 144°22'29.64"E); Maryborough (37°24'00.00"S, 143°44'13.28"E); 15 mi. N Orbost (37°30'46.11"S, 148°27'10.29"E); Panton Hill (20 mi. northeast of Melbourne) (37°39'39.10"S, 145°17'29.68"E).


   *S. lingulata* (Kane, 1965)

   *Lagenophrys lingulata* Kane 1965: 109, 118, 120, 121.

   **Museum Depositions.** USNM. 42680 Neotype; 42681 42682.

   **Habitat.** Freshwater.

   **Distribution.** BR: Australian.

   Australia: New South Wales, Wentworth, Murray river at Lock 10 (34°26'2.12"S, 142°10'48.87"E); Queensland (20°55'58.47"S, 142°42'3.27"E). Victoria, Brahmah Ferry (34°47'15.19"S, 138°32'38.95"E); Craigieburn, Merri Creek (27 km north of Melbourne) (37°34'17.95"S, 144°57'39.34"E); Heathcote (36°55'0.23"S, 144°22'29.64"E); Maryborough (37°24'00.00"S, 143°44'13.28"E); Merri Creek (Merri Merri Creek) is a tributary of the Yarra River (37°34'17.95"S, 144°57'39.34"E); near Melbourne (37°37'32.24"S, 144°54'28.31"E).


**S. nivalis** (Kane, 1969)


* Circulagenophrys nivalis* Jankowski 1986: 87.

*Setonophrys nivalis* Clamp 1991: 360.

**Museum Depositions.** AM P62819 Lectotype; P62820, P62884, P62885 Paralectotypes. USNM. 1004292 Paralectotype.

**Habitat.** Freshwater.

**Distribution.** BR: Australian. Australia: *Victoria*, Mt. Baw (37°51′22.95″S, 146°16′10.16″E).

**Hosts.** Australia: *Colubotelson searlei* Nicholls (pereiopods and dorsum).

**References.** Clamp & Kane 2003.

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**S. occlusa** (Kane, 1965)

*Lagenophrys occlusa* Kane 1965: 118-119, 120, 121.

**Museum Deposition.** USNM. 42683.

**Habitat.** Freshwater.

**Distribution.** BR: Australian. Australia: New South Wales (31°15′27.30″S, 146°55′15.61″E). *Victoria*, Craigieburn, Merri Cr. (37°34′17.95″S, 144°57′39.34″E); Grampian Mountains, Wannon R. (37°31′35.60″S, 142°11′29.73″E); Heathcote (36°55′0.23″S, 144°42′29.64″E); Maryborough (37°2′49.00″S, 143°44′13.28″E); Victoria Central (37°29′11.16″S, 144°48′31.00″E); West Victoria (37°48′29.38″S, 144°11′12.38″E).


**References.** Kane 1965; Clamp 1984; Fernandez-Leborans & Tato-Porto 2000.

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**S. seticola** (Kane, 1965)

*Lagenophrys seticola* Kane 1965: 109, 119-120, 121.

**Museum Deposition.** USNM. 42684 Neotype.

**Habitat.** Freshwater.

**Distribution.** BR: Australian. Australia: New South Wales, Newcastle (32°56′30.47″S, 151°46′17.52″E). *Victoria*, Grampian Mountains, Wannon River (37°31′35.60″S, 142°11′29.73″E); Melbourne, Templestowe, bank of Yarra River (37°45′12.16″S, 145°13′19.17″E); Warburton.


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**S. spinosa** (Kane, 1965)

*Lagenophrys spinosa* Kane 1965: 109, 117, 120, 121.

**Habitat.** Freshwater.

**Distribution.** BR: Australian. Australia: Melbourne, Heathcote, 50 miles north of Melbourne (37°4′52.26″S, 144°52′22.02″E).

**Hosts.** Australia: *Cherax destructor* (exposed parts).

**References.** Kane 1965; Clamp 1984; Fernandez-Leborans & Tato-Porto 2000.

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**S. tricorniculata** Clamp, 1991

**Museum Deposition.** USNM. 42685 Holotype.

**Habitat.** Freshwater.

**Distribution.** BR: Australian. Australia: *Victoria*, Grampian Mountains, Wannon River (37°34′30.84″S, 142°15′26.08″E).

**Hosts.** Australia: *Geocharax falcata* (pleopods).


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V. *Operculigera* Kane, 1969

A. Australia only (Restricted to Isopoda)

**O. haswelli** Clamp and Kane, 2003

**Museum Depositions.** AM P62814 Holotype; P62815 Paratype. USNM. 1004288 Paratype.
Habitat. Freshwater.

Distribution. BR: Australian.
Australia: Tasmania, Great Lake (41°54'4.67"S, 146°45'52.48"E).

Hosts. Australia: Mesacanthotelson tasmaniae (Thomsom) (pleopods).

References. Clamp & Kane 2003.

**O. inornata** Clamp and Kane, 2003

Museum Depositions. AM P62816 Holotype; P62817, P62818 Paratypes. USNM. 1004289, 1004290, 1004291 Paratypes.

Habitat. Freshwater.

Distribution. BR: Australian.
Australia: Victoria, Otway Range (38°47'36.74"S, 143°32'31.24"E); Grampian Range, swamp near Fyan’s creek (37°5'17.77"S, 142°33'43.84"E); Tasmania, Great Lake (41°54'4.67"S, 146°45'52.48"E).

Hosts. Australia: Phreaticopsis terricola Spencer and Hall, Phreaticopsis sp. (pleopods), Colubotelson chiltoni (Sheppard) (pleopods).

References. Clamp & Kane 2003.

**O. montanea** Kane, 1969


Museum Depositions. AM P62810 Lectotype; P62811 Paralectotype. USNM. 1004287 Paralectotype.

Habitat. Freshwater.

Distribution. BR: Australian.
Australia: Victoria, summit of Mt Baw (37°51'22.95"S, 146°16'10.16"E); Mt. Buffalo (36°43'39.52"S, 146°49'22.15"E); Kiewa (36°15'40.86"S, 147°0'30.09"E).

Hosts. Australia: Colubotelson joyneri (Nicholls) (pleopods), C. searlei (pleopods), Colubotelson sp.


**O. obstipa** Clamp, 1991

Museum Depositions. USNM. 42694 Holotype; 42695 Paratype.

Habitat. Freshwater.

Distribution. BR: Australian.

Hosts. Australia: Metaphreatoicus australis (Chilton) (pleopods).


**O. zeehanensis** Kane, 1969

Museum Depositions. AM P62813 Lectotype.

Habitat. Freshwater.

Distribution. BR: Australian.

Hosts. Australia: Phreaticoides longicollis Nicholls (pleopods).

References: Kane 1969; Clamp & Kane 2003.

B. South America only (Restricted to Decapoda)

**O. asymmetrica** Clamp, 1991

Museum Depositions. USNM. 42687 Holotype; 42689, 42691 Paratypes.

Habitat. Freshwater.

Distribution. BR: Neotropical.
Chile: Concepción, Concepción (36°49'37.73"S, 73°3'4.23"W); Talcahuano (36°43'27.98"S, 73°6'45.63"W).

Hosts. Chile: Parastacus pugnax (Poeppig), Samastacus spinifrons (Philippi) (gills).


**O. insolita** Clamp, 1991

Museum Depositions. USNM. 42692 Holotype; 42693 Paratype.

Habitat. Freshwater.

Distribution. BR: Neotropical.
Chile: Concepción, Talcahuano (36°43'27.98"S, 73°6'45.63"W). Malleco, Puren (38°2'33.95"S, 73°5'11.39"W).

Hosts. Chile: Parastacus pugnax (gills).

**O. parastacis** Jankowski, 1986

**Museum Deposition.** USNM. 42686.

**Habitat.** Freshwater.

**Distribution.** BR: Neotropical.

Chile: **Valparaíso** (33°234.52"S, 71°37'10.21"W).

**Hosts.** Chile: *Parastacus pugnax* (cited as *Parastacus chilensis*) (gills).

**References.** Jankowski 1986.

**O. seticola** Clamp, 1991

**Museum Depositions.** USNM. 42688 Holotype; 42690 Paratype.

**Habitat.** Freshwater.

**Distribution.** BR: Neotropical.

Chile: **Concepción,** Concepción (36°49'37.73"S, 73°3'4.23"W).

**Hosts.** Chile: *Parastacus pugnax* (setae on bases of gills).


**O. striata** Jankowski, 1986

**Museum Depositions.** USNM. 42696 Holotype; 42697 Paratype.

**Habitat.** Freshwater.

**Distribution.** BR: Neotropical.

Chile: **Concepción,** Concepción (36°49'37.73"S, 73°3'4.23"W). Malleco, Puren (38°2'33.95"S, 73°5'11.39"W).

**Hosts.** Chile: *Parastacus pugnax* (gills).


**O. taura** Clamp, 1991

**Museum Depositions.** USNM. 43099 Holotype; 43100, 43101 Paratypes.

**Habitat.** Freshwater.

**Distribution.** BR: Ethiopian.


**Hosts.** Madagascar: *Foza goudoti* (cited as *Gecarcinuates goudoti*) (gills).


**O. velata** Jankowski, 1986

**C. Madagascar only (Restricted to Decapoda)**

**O. carcini** Clamp, 1992

**Museum Depositions.** USNM. 43099 Holotype; 43100, 43101 Paratypes.

**Habitat.** Freshwater.

**Distribution.** BR: Ethiopian.


**Hosts.** Madagascar: *Foza goudoti* (cited as *Gecarcinuates goudoti*) (gills).


**O. madagascarensis** Clamp, 1992

**Museum Depositions.** USNM. 43094 Holotype; 43095, 43096, 43097, 43098 Paratypes.

**Habitat.** Freshwater.

**Distribution.** BR: Ethiopian.

Madagascar: Antananarivo (18°55'41.60"S, 47°32'23.26"E) (bought in marketplace).

**Hosts.** Madagascar: *Astacoides granulimanus* Monod and Petit (gills) (cited as *Astacoides madagascarensis granulimanus*).

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AN ANNOTATED CHECKLIST OF SPECIES IN THE FAMILY LAGENOPHYRIIDAE


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