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Epibiont protozoan communities on *Caridina lanceolata* (Crustacea, Decapoda) from the Malili lakes of Sulawesi (Indonesia)

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Abstract

The epibiont protozoan communities living on the freshwater shrimp *Caridina lanceolata* Woltereck, 1937a from the three major lakes (Towuti, Matano and Mahalona) of the Malili lake system (Sulawesi, Indonesia) were studied. The number of epibionts varied between 2 and 971 per shrimp. Seven protozoan ciliate species were found: *Acineta sulawesiensis* n. sp., *Cothurnia* sp., *Zoothamnium* sp. (in all three lakes), *Vorticella* sp. (Lake Mahalona and Lake Matano), *Opercularia* sp. (Lake Mahalona), *Epistylis* sp. (Lake Mahalona and Lake Matano), and *Podophrya* sp. (Lake Mahalona). Although these ciliates had been found previously on other crustaceans, they have not been observed as epibionts on *Caridina* H. Milne Edwards, 1837. The distribution of the different epibiont species on the anatomical units of the shrimp was analyzed in each lake. There is a statistical significant difference between the three lakes in respect to the number of epibionts on each anatomical unit of all analyzed shrimps. The total and mean densities of each epibiont species on the different analyzed shrimps showed a significant difference between the three lakes; i.e., the presence of each epibiont species on the population of *C. lanceolata* varied from one lake to another. In Lake Towuti the highest density of epibionts was found on the anterior part of the shrimp body (rostrum, antennae, antennulae and eyes) (32.41%), while in the other two lakes, the highest colonization corresponded to the maxillipeds (31.56% Lake Matano, 40.89% Lake Mahalona). In Lake Towuti the rest of epibionts colonized mainly maxillipeds and pleopods (both 45.76% of epibionts). In Lake Matano, other epibionts were distributed principally on the anterior part of the body and pleopods (in total 57.18% of epibionts). In Lake Mahalona, other epibionts were divided among the anterior part of the body, pereiopods and pleopods (in total 57.39% of the epibionts). Uropods and telson were the units less colonized in Lake Matano (3.64%) and Lake Mahalona (1.72%), while in Lake Towuti, they presented a moderate density (13.18% of the epibionts). Taking into account the distribution of epibionts along the antero-posterior axis of the shrimp, considering the different anatomical units, there was a significant correlation between the three lakes. This fact indicates that, in the three lakes, the colonization on *C. lanceolata* followed a similar distribution pattern, independently of the epibiont species present. The comparison between the distributions of the same epibiont species along the longitudinal axis of the shrimp on the diverse lakes showed that they correlated respect to their density values on the anatomical units of the shrimp. Diverse aspects of the colonization patterns are discussed.

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Morphological features, taxonomic identification, and particular distribution of the epibiont species in each lake are also included.

Keywords: Protozoan epibionts; *Caridina lanceolata*; Malili lakes; Sulawesi; Indonesia

1. Introduction

Epibiosis is an association between two organisms: the epibiont and the basibiont. The term "epibiont" includes organisms that, during the sessile phase of their life cycle, are attached to the surface of a living substratum, while the basibiont lodges and constitutes a support for the epibiont (Wahl 1989; Wahl et al. 1997).

A number of protozoan ciliate species has been described as epibiont on crustaceans. The biology and ecology of basibiont crustacean species can be explained from epibiosis (Bottom and Ropes 1988; Abelló et al. 1990; Abelló and Macpherson 1992). Crustacean groups such as cladocerans, copepods, cirripeds, isopods, amphipods and decapods, include species which have been found as basibionts for protozoan and invertebrate epibionts (Ross 1983). Protozoan epibionts are represented by members of the groups: apostomatids, chonotrichids, suctorians, peritrichs and heterotrichs (Corliss 1979; Lynn and Small 2000).

The ancient Malili lake system in the central highlands of the Indonesian island Sulawesi (Fig. 1) comprises five connected lakes that harbor, like many other ancient lakes, endemic species flocks, among these the radiation of atyid shrimps (Crustacea, *Caridina*). The basibiont *Caridina lanceolata*, which is widely distributed in the three major lakes (Zitzler, von Rintelen and Glaubrecht, unpublished data) of the system, is part of this shrimp radiation (Brooks 1950; Woltereck 1937a, b).

The protozoan epibiont communities on *C. lanceolata* from the three major lakes of the Malili lake system of Sulawesi (Indonesia) were analyzed considering the biological and taxonomical characteristics of the epibionts, and the distribution of the different epibiont species on the surface of the shrimp, in order to contribute to the description and explanation of the relationships and patterns of distribution of the protozoan epibiont communities in the *C. lanceolata* populations from the three lakes. Detailed data and results of this study are described below.

2. Material and methods

Samples of *C. lanceolata* were collected by the second author from Lake Towuti, Matano and Mahalona within the Malili lake system of Sulawesi (Indonesia) (Fig. 1). Samples were fixed in 95% ethanol and then transferred to 75% ethanol for light microscopy. In the laboratory, shrimps were dissected and each anatomical unit was observed under a stereoscopic microscope.

For scanning electron microscopy (SEM) of the epibionts shrimp specimens, fixed in 95% ethanol, were dehydrated in 100% ethanol for 30 min. Afterwards, they were critical point dried with a BAL-TEC CPD 030, mounted on aluminum specimen stubs with standard adhesive pads and coated with gold-palladium using a Polaron SC7 640 Sputter Coater. Pictures were taken on a LEO 1450VP scanning electron microscope (software: 32 V02.03) at 10 kV.

Epibionts on the surface of the shrimps' anatomical units were observed and counted under stereoscopic and light microscopes. Density of colonial species was indicated as number of zooids. In order to identify the protozoan epibionts, they were isolated and treated using the silver carbonate technique, according to the procedure described by Fernandez-Leborans and Castro de Zaldumbide (1986), and also with methyl green and neutral red. Permanent slides were obtained from the stained ciliates. Measures of the epibionts were calculated using an ocular micrometer. Light microscope images were obtained using Image Analysis (KS300 Zeiss) and the diverse morphological features from the images were used to obtain the epibiont species schemes. Statistical analyses were performed using the Statgraphics and SPSS programs.

All the examined epibionts are deposited in the Museum of Natural History, Berlin, Germany (ZMB).

3. Results

A total of seven ciliate protozoan genera were found: *Acineta*, *Cothurnia*, *Zoothamnium* (on the three lakes), *Vorticella* (Lake Mahalona and Lake Matano), *Opercularia* (Lake Mahalona), *Epistylis* (Lake Mahalona and Lake Matano), and *Podophrya* (Lake Mahalona).

3.1. Description of a new epibiont ciliate

Class Phyllopharyngea De Puytorac et al., 1974
Subclass Suctoria Claparède and Lachmann, 1858
Order Endogenida Collin, 1912
Family Acinetidae Stein, 1859
Genus *Acineta* Ehrenberg, 1833
Acineta sulawesiensis sp. nov.

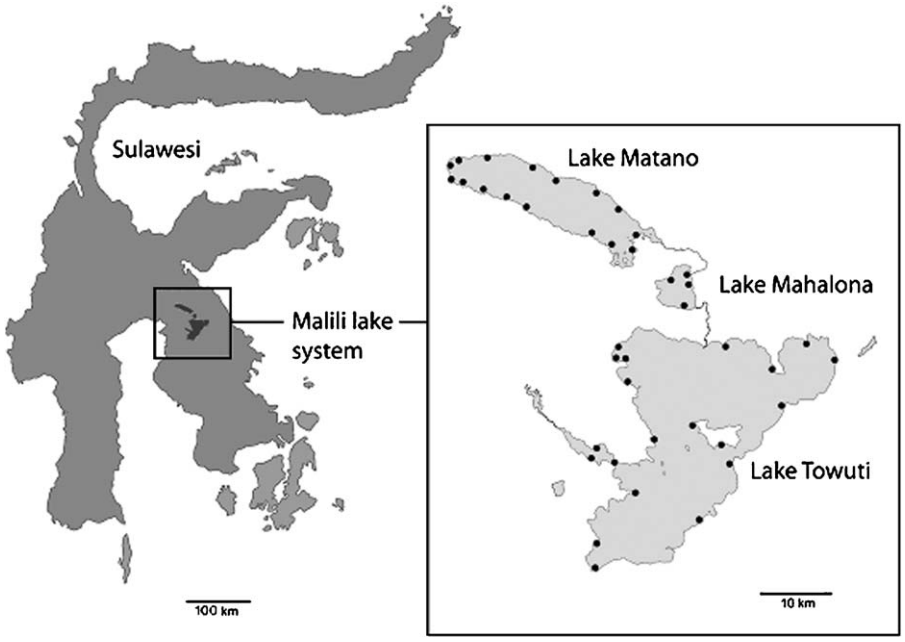


Fig. 1. The Malili lake system on the Indonesian island of Sulawesi. Distribution of *Caridina lanceolata* in the three major lakes: Lake Towuti, Lake Mahalona and Lake Matano.

3.1.1. Diagnosis

Ciliates triangular in outline or bell-shaped, loricated and pedunculate. Lorica surrounding completely the cellular body (21.1–63.4 μm long, 21.1–51.8 μm wide). Lorica with a free anterior part over the body enveloping the tentacles (12.0–12.7 μm long). Body (17.3–57.6 μm long, 11.5–46.1 μm wide), with two anterior lobular actinophores protruding on the corners, each with 27–56 capitate tentacles. Central area in the apical surface of the body depressed. Macronucleus rounded in shape, centrally located (7.7–15.4 μm long, 5.8–17.3 μm wide). A spherical micronucleus near the macronucleus. Stalk (3.8–17.3 μm long, 3.8–7.7 μm wide), joined the lorica via a cup-like expansion. Stalk with 12–18 longitudinal striations which spread out in the base of the stalk. Basal disk of stalk circular and thin (5.7–8.9 μm diameter).

3.1.2. Etymology

The name makes reference to the geographical area where they were collected (Sulawesi, Indonesia).

3.1.3. Type material

All type material was obtained from the freshwater shrimp *C. lanceolata*, collected on: (1) 28 September 2003 in Lake Towuti, Position: 2°54.13′S, 121°23.78′E. (2) 1 October 2003 in Lake Matano, Position: 2°28.5′S, 121°15.55′E. (3) 23 September 2003 in Lake Mahalona, Position: 2°34.72′S, 121°29.12′E Holotypes: Accession No. ZMB 34, mounted as permanent slide with silver carbonate impregnated individuals. Paratypes: Accession Nos. ZMB 35–36, mounted as holotypes. All material is deposited in the Museum of Natural History in Berlin, Germany (ZMB).

Code numbers: ZMB 34–36.

3.1.4. Description

The ciliates were triangular in outline or bell-shaped, loricated and pedunculated (Figs. 2a and 3–5). Cytoplasm and tentacles were confined within the lorica. The lorica surrounded completely the cellular body. The lorica had a free anterior part over the body enveloping the tentacles. The length of the body fluctuated between 17.3 and 57.6 μm, and the width was 11.5–46.1 μm. The anterior part of the body contained two lobular clearly distinguished actinophores protruding on the corners, supporting capitate tentacles. The central area of the apical surface of the body was depressed. The macronucleus was rounded. There was a spherical micronucleus near the macronucleus. The stalk joined the lorica via a cup-like expansion. The stalk showed longitudinal striations. The striations in the base of the stalk were spread out. The basal disk of the stalk was circular and thin (Table 1).

3.1.5. Taxonomic position

These ciliates belong to the genus *Acineta* Ehrenberg, 1833. As members of this genus, they had a cellular body triangular in outline or bell-shaped, tentacles in two fascicles, with lorica and stalk (Lynn and Small 2000). The most distinctive feature of these ciliates was the lorica prolonged anteriorly around the tentacles. Taking into consideration this and other morphological characteristics, the ciliates were similar to *Thecacineta*

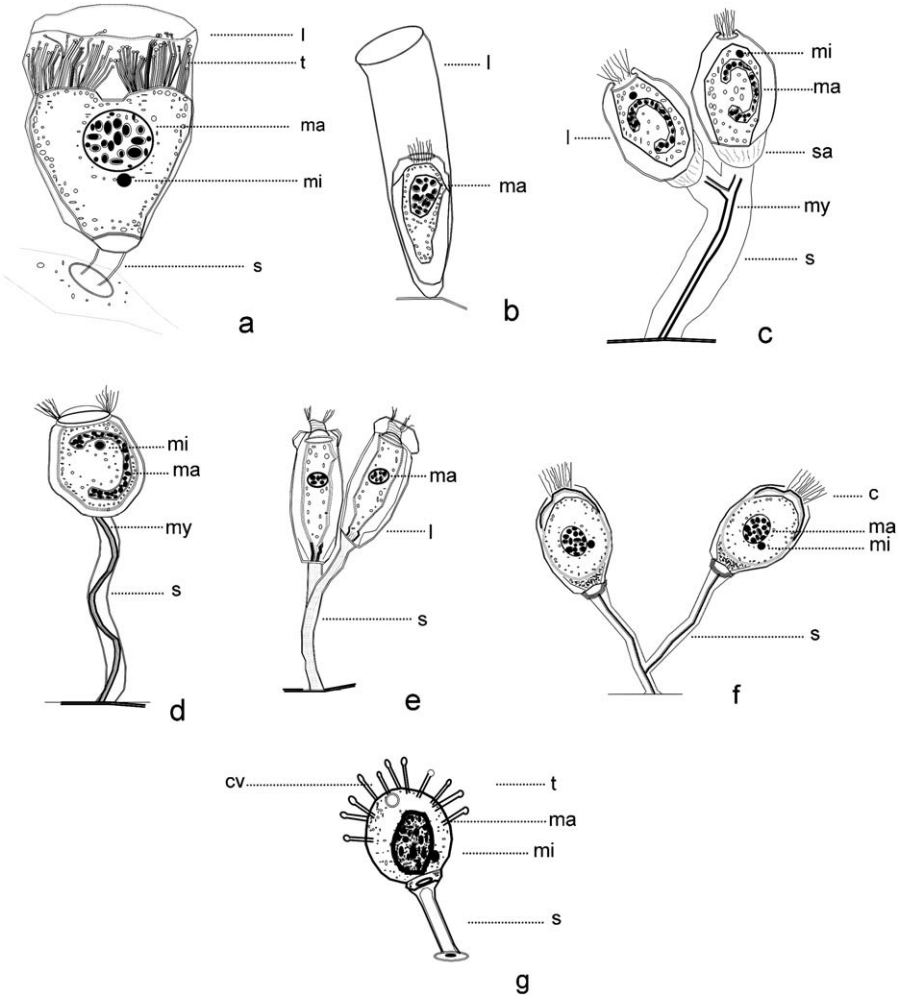


Fig. 2. (a) *Acineta sulawesiensis*. (b) *Cothurnia* sp. (c) *Zoothamnium* sp. (d) *Vorticella* sp. (e) *Opercularia* sp. (f) *Epistylis* sp. (g) *Podophrya* sp. (cv, contractile vacuole; ma, macronucleus; mi, micronucleus; my, myoneme; l, lorica; s, stalk; sa, suprastylar area; t, tentacles).

baikalica Swarczewsky, 1928 and *Thecacineta brevistyla* Swarczewsky, 1928 (cf. Swarczewsky 1928). Curds (1985) joined both species in *Acineta baikalica* Curds, 1985. They had a bell to Y-shaped body, laterally flattened, with two acinophores supporting capitate tentacles, and lorica. The apical aperture was dumb-bell shaped. The stalk, variable in length, joined the lorica without collar or other structure. The spherical macronucleus was centrally located (Curds 1985). The tentacles and the body were confined in the lorica, which project almost up to the distal end of the tentacles. The studied ciliates differed from these two species in the length of the lorica, the anterior end of the body (convex in these species, concave in the studied ciliates), and the location of the actinophores (in a depression on these species, in two lobular protrusions in the studied ciliates) (Table 2). These ciliates were included in a new species, called *A. sulawesiensis* n. sp., making reference to the geographical area where they were collected.

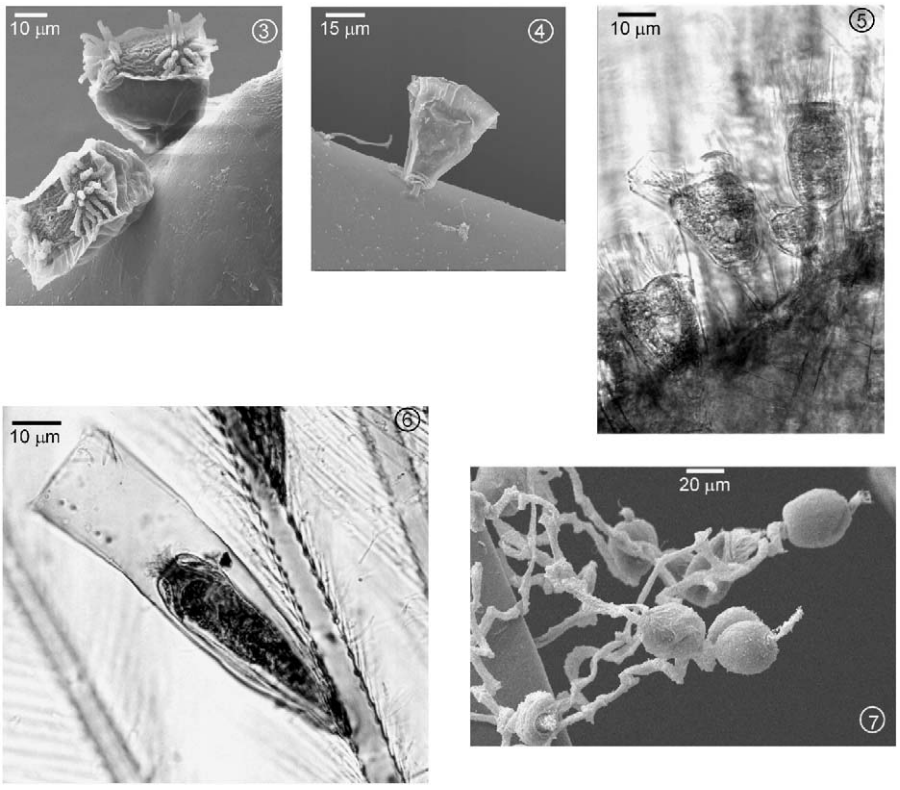
3.1.6. Geographical distribution

The basibiont *C. lanceolata*—endemic in the Malili lake system—is widely distributed in three major lakes (Fig. 1) and was found on different kinds of substrate (i.e., wood, macrophytes, rocks) or in pelagic shoals, depending on the time of day (Zitzler, von Rintelen and Glaubrecht, unpublished data).

3.2. Other recorded epibiont ciliates

3.2.1. *Cothurnia* sp.

These ciliates were loricated, and stalked (Figs. 2b and 6). The lorica was narrow and elongated, cylindrical and rounded posteriorly. The individuals were attached aborally by the stalk. In the posterior end, the lorica was connected by means of an endostyle with the cellular body. The opposite end of the lorica contained the apical aperture, which was elliptical when viewed from above, generally wider than the width in the middle



Figs. 3–7. (**3**) *Acineta sulawesiensis* n. sp. Two individuals with the tentacles and the extension of the lorica (SEM). (**4**) *Acineta sulawesiensis* n. sp. A specimen showing the stalk and the basal disk. (SEM). (**5**) *Acineta sulawesiensis* n. sp. Some ciliates with the extension of the lorica, tentacles and nuclei. (**6**) *Cothurnia* sp. Individual with the lorica and the body. (**7**) *Zoothamnium* sp. A colony (SEM).

Table 1. Biometric features of *Acineta sulawesiensis* n. sp. (measures in μm)

	Mean	SD	Minimum	Maximum
Body length	29.5	11.5	17.2	57.6
Body width	29.3	8.6	11.5	46.0
Lorica length	40.3	13.8	21.1	63.3
Lorica width	38.1	9.0	21.1	51.8
Macronucleus length	9.6	1.9	7.6	15.3
Macronucleus width	9.3	2.6	5.7	17.2
Number of tentacles per actinophore	38.0	12.0	27.0	56.0
Length of the stalk	9.1	3.5	3.8	17.2
Width of the stalk	5.6	1.5	3.8	7.6
Diameter of the basal disc	7.8	4.2	5.6	8.9
Striations of the stalk	14.3	3.4	12.0	18.0
Cyst body length	32.6	3.1	26.8	36.4
Cyst body width	19.0	3.8	13.4	28.8
Cyst lorica length	32.6	10.7	23.0	48.0
Cyst lorica width	22.5	1.8	21.1	24.9
Cyst macronucleus length	20.6	5.5	17.2	28.8
Cyst macronucleus width	6.7	1.1	5.7	7.6
Length of free anterior part of lorica	11.7	1.4	10.0	14.0

SD, standard deviation ($n = 80$).

Table 2. Comparison of biometric features of *Acineta sulawesiensis* n. sp., *A. baikalica* and *A. brevistyla* (measures in μm) (Swarczewsky, 1928; Curds, 1985)

	A. baikalica	*A. brevistyla*	*A. sulawesiensis* n. sp.
Body length	—	—	17–58
Body width	—	—	11–46
Lorica length	75–97	110	21–63
Lorica width	65	45–50	21–52
Length of free anterior part of lorica	10–16	10–12	12–14
Shape of anterior end of body	Convex	Convex	Concave
Actinophores	In two depressions	In two depressions	In two protrusions
Stalk length	45–50	16	4–17
Stalk width	2	3–5	4–8
Macronucleus length	20	13–16	8–15
Macronucleus width	11	13–16	6–17

zone. The retracted body occupied almost the half-part of the lorica. The macronucleus was ovoid, and located in the anterior half of the body. The micronucleus, was spherical and situated near the macronucleus (Table 3).

3.2.1.1. Taxonomic position. These ciliates belong to the genus *Cothurnia* Ehrenberg, 1831 (family Vaginicolidae de Fromentel, 1874; order Sessilida Kahl, 1933; subclass Peritrichia Stein, 1859; class Oligohymenophorea De Puytorac et al., 1974) (*sensu* Lynn and Small 2000). As the members of this genus, they were loricated peritrichs usually with one zooid per lorica. The lorica did not present valves or other means of closing aperture. The inner layer or septum sometimes showed an enclosed space at the posterior end of the lorica (Warren and Paynter 1991). The ciliates found were similar to those of *Cothurnia compressa* Claparede & Lachmann, 1858 in the elliptical lorica aperture, when viewed from above. The lorica aperture border presented two deep clefts. The external stalk was short, the endostyle was short and broad, and mesostyle was absent (Warren and Paynter 1991). However, there were differences in respect to the dimensions: the length and width of the lorica are higher in *C. compressa*, and the size of the contracted zooid, is also higher in *C. compressa*. In addition, *C. compressa* has been found in marine environments.

3.2.2. *Zoothamnium* sp.

These peritrich ciliates were colonial, with 1–15 zooids linked by a ramified stalk, which contained a contractile myoneme (Figs. 2c, 7 and 8). Each zooid had an external thick layer or lorica surrounding the cellular body, with a hyaline area between the zooid and the lorica. The body of the zooid was elongated. The macronucleus was C-shaped. The micronucleus was spherical and disposed next to the macronucleus. The peristomal disc was short, approximately the half of the maximum body width. The stalk was conspicuously broad in relation to the width of the body. This stalk was very diaphanous showing a rounded contour. Inside the stalk it was located the contractile myoneme (spasmoneme). The width of the stalk increased towards the base of the colony, where it was attached to the basibiont. In the colony, as a whole, the ramified stalk represented a relatively great volume. The stalk joined to the cellular body of the zooid by a cup-shaped noticeably wide structure (suprastylar area), showing a longitudinal striation (Table 3).

3.2.2.1. Taxonomic position. These epibionts belonged to the genus *Zoothamnium* Ehrenberg, 1838 (family Vorticellidae Ehrenberg, 1838; order Sessilida Kahl, 1933; subclass Peritrichia Stein, 1859; class Oligohymenophorea De Puytorac et al., 1974). As the members of this genus, they were colonial, the zooids shared continuous myonemes, and the entire colony was contractile (Lynn and Small 2000). The ciliates were similar to those of the *Zoothamnium intermedium* Precht, 1935. They coincided with the description of *Z. intermedium* in: the dichotomously branching colonies (although the number of individuals per colony was lower in the ciliates studied than in the description); the zooid dimensions; and the C-shaped macronucleus (Valbonesi and Guglielmo 1988). On the other hand, the peritrichs studied were characterized by the thick external layer or lorica around the zooid, the broad stalk and the wide suprastylar area between the stalk and the zooid.

3.2.3. *Vorticella* sp.

These ciliates were solitary and stalked (Figs. 2d and 9). The body was globulous, and more or less ovoid when contracted. The macronucleus was C-shaped and laid transversely across the centre of the zooid widening at its extremes. A spherical micronucleus was placed

Table 3. Biometric features of *Cothurnia* sp., *Zoothamnium* sp., *Vorticella* sp., *Opercularia* sp., *Epistylis* sp. and *Podophrya* sp. (measures in μm)

	Mean	SD	Minimum	Maximum
Cothurnia sp.				
Body length	38.8	7.4	24.9	49.9
Body width	18.1	1.3	15.3	19.2
Lorica length	81.7	12.0	57.6	96.0
Lorica width	21.1	2.5	19.2	24.9
Stalk length	6.7	9.5	0.0	13.4
Stalk width	2.5	2.2	0.0	3.8
Macronucleus length	16.3	5.0	11.5	23.0
Macronucleus width	6.2	3.6	3.8	11.5
Mouth aperture	5.7	0.0	5.7	5.7
Lip diameter	11.5	2.7	9.6	13.4
Zoothamnium sp.				
Body length	30.4	3.3	24.9	38.4
Body width	24.2	4.0	15.3	30.7
Stalk length	75.4	40.4	13.4	144.0
Stalk width	9.2	2.0	5.7	13.4
Macronucleus length	9.6	4.8	5.7	23.0
Macronucleus width	17.4	5.2	9.6	28.8
Number of individuals per colony	5.2	3.9	1.0	15.0
Contractile vacuole diameter	6.7	1.0	5.7	7.6
Length of suprastylar area	4.5	0,8	3.8	5.8
Width of suprastylar area	17.2	1.1	15.9	19.2
Vorticella sp.				
Body length	28.4	9.1	13.4	46.0
Body width	22.7	5.4	13.4	32.6
Stalk length	34.9	15.2	13.4	69.1
Stalk width	5.5	1.3	3.8	7.6
Macronucleous length	12.3	8.4	3.8	32.6
Macronucleous width	11.3	4.5	5.7	21.1
Cilia length	6.1	4.3	1.9	13.4
Number of individuals per colony	1.0	0.0	1.0	1.0
Number of bends per stalk	2.9	1.1	2.0	5.0
Opercularia sp.				
Body length	28.1	1.5	26.8	30.72ç
Body width	15.5	2.6	14.8	16.9
Lorica length	34.0	0.9	32.	37.9
Lorica width	19.8	0.3	15.3	23.0
Stalk width	4.8	0.8	3.9	5.6
Length of the peristomial disc	3.4	0.2	3.0	4.7
Width of the peristomial disc	5.1	0.8	4.7	6.8
Length of the macronucleus	3.8	1.3	3.1	4.7
Width of the macronucleus	7.2	1.4	6.8	8.9
Number of zooids in a colony	3.2	3.4	1.0	8.0
Epistylis sp.				
Body length	29.7	5.0	17.2	36.4
Body width	21.9	3.4	15.3	28.8
Stalk length	30.8	12.8	5.7	61.4
Stalk width	6.6	2.1	3.8	11.5
Macronucleus length	11.1	4.9	5.7	23.0
Macronucleus width	11.5	3.4	5.7	19.2
Contractile vacuole diametre	5.4	1.8	3.8	9.6
Cilia length	9.3	1.6	7.6	11.5
Number of individuals per colony	1.5	1.3	1.0	6.0

Table 3. (*continued*)

	Mean	SD	Minimum	Maximum
Podophrya sp.				
Body length	20.3	4.2	15.3	26.8
Body width	16.5	4.4	11.5	23.0
External layer length	26.8	6.6	23.0	34.5
External layer width	19.2	1.9	17.2	21.1
Stalk length	69.7	6.1	65.2	76.8
Stalk width	5.1	1.1	3.8	5.7
Macronucleous length	10.5	1.9	7.6	11.5
Macronucleous width	7.4	1.2	5.7	8.6
Number of bends per stalk	4.3	0.5	4.0	5.0
Number of individuals per colony	3.0	1.0	2.0	4.0
Number of tentacles	12.	1.6	10.0	15.0

SD, standard deviation ($n = 80$).

next to the macronucleus. On the anterior part of the body, the peristomial lip was narrow and shorter than the width of the body. The peristomial disc was convex and elevated on the peristome. The stalk was elongated and contained a contractile myoneme along all its length and it formed between 2 and 5 bends (Table 3).

3.2.3.1. Taxonomic position. These ciliates belonged to genus *Vorticella* Linnaeus, 1767 (family Vorticellidae Ehrenberg, 1838; order Sessilida Kahl, 1933; subclass Peritrichia Stein, 1859; class Oligohymenophorea De Puytorac et al., 1974). As the members of this genus, they are sessile and solitary, with a contractile stalk. The individuals were aloricate, without somatic cilia in the adult (Lynn and Small 2000; Warren 1986). The species most similar to these ciliates was *Vorticella globosa* Ghosh, 1922. They coincide in the size and shape of the body; the C-shape and disposition of the macronucleus; the length of the stalk; the freshwater environment; and in being epibiotic (Warren 1986). It was characteristic of the ciliates observed in the widening of the extremes of the macronucleus.

3.2.4. *Opercularia* sp.

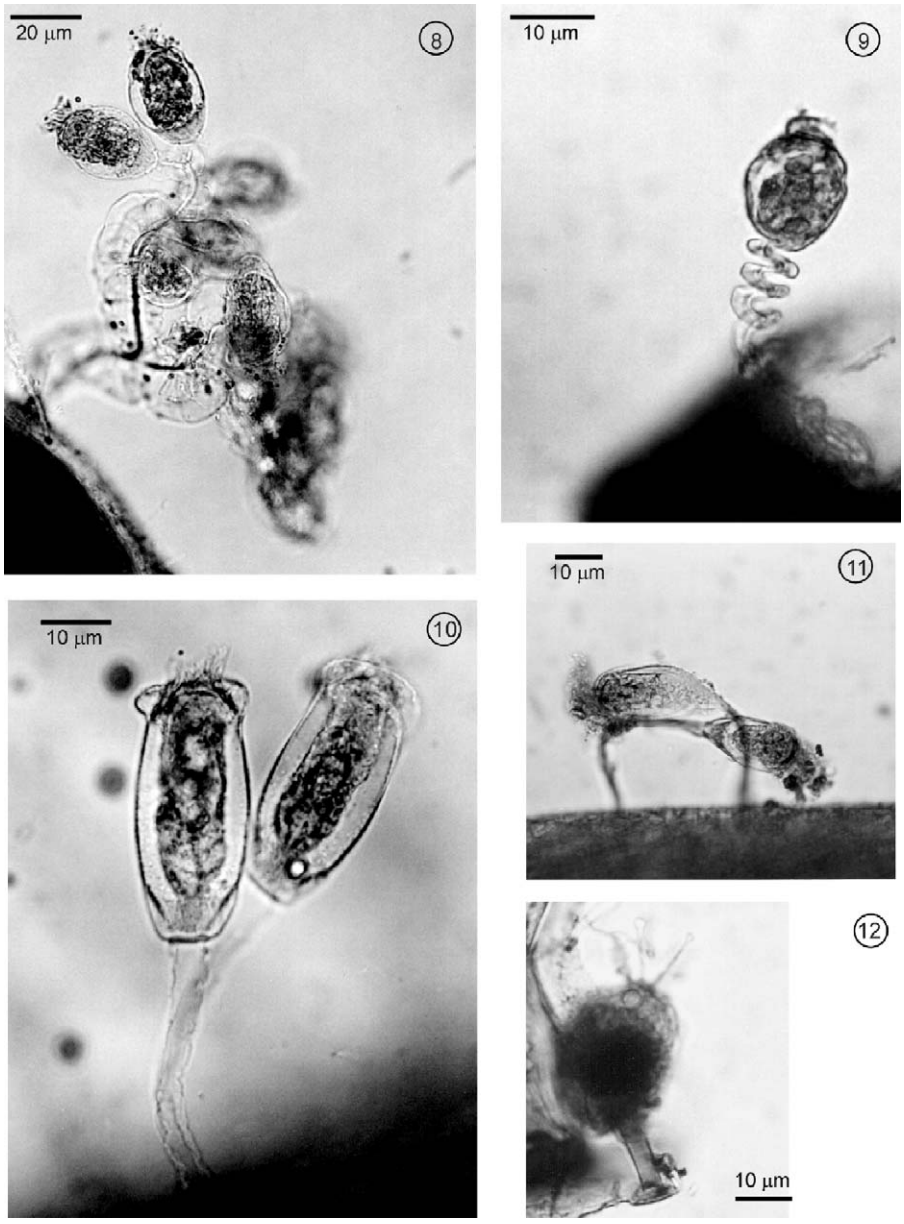
The ciliates were colonial peritrich ciliates (Figs. 2e and 10). The stalk was ramified and noncontractile. The zooids were loricate. The lorica was elongate and ovoid. The body of the zooid was elongate. The stalk was broad without myoneme. In the anterior end of the body, the peristomal disc protruded from the surface and appeared elevated from the margin of the body. The macronucleus was oval and located in the middle area of the body and a spherical micronucleus was situated near the macronucleus. The posterior end of the body connected with the basal part of the lorica by a striated narrow zone. The number of zooids in the colony varied between 1 and 8 (Table 3).

3.2.4.1. Taxonomic position. These ciliates belonged to the genus *Opercularia* Goldfuss, 1820 (family Operculariidae Fauré-Fremiet in Corliss, 1979; order Sessilida Kahl, 1933; subclass Peritrichia Stein, 1859; class Oligohymenophorea De Puytorac et al., 1974). As the members of this genus, the ciliates showed a peristomal disc on a stalk, having a furrow that separated and elevated the disc from the margin of the zooid. They were colonial, with straight peristome, with compact, rounded macronucleus. The zooids presented a lorica (Lynn and Small 2000). The ciliates were similar to those of the species *Opercularia coarctata* (Claparède and Lachmann, 1858) Roux, 1901. They coincided in the size of the body and the shape and location of the macronucleus (Foissner et al. 1992).

3.2.5. *Epistylis* sp.

These peritrich ciliates were colonial (Figs. 2f and 11). Each colony was generally composed by one to six oval zooids. The cellular body of the zooid was oval when contracted. At the apical end of the body a peristomial lip protruded outward. The macronucleus was crescent-shaped. A spherical micronucleus was located close to the macronucleus. The stalk was thin and non-contractile (Table 3).

3.2.5.1. Taxonomic position. These ciliates belong to the genus *Epistylis* Ehrenberg, 1830 (family Epistylididae Kahl, 1933; order Sessilida Kahl, 1933; subclass Peritrichia Stein, 1859; class Oligohymenophorea De Puytorac et al., 1974 subphylum Intramacronucleata Lynn, 1996) (*sensu* Lynn and Small 2000). The peritrichs were similar to those of the species *Epistylis coronata* Nusch, 1970 in: the shape and small dimensions of the zooid (although the ciliates studied had slightly smaller dimensions than those of this species); the shape and disposition of the macronucleus; the non-contractile stalk; the dichotomously branching colonies and the



Figs. 8–12. (**8**) *Zoothamnium* sp. A colony showing the broad stalk and the wide suprastylar area. (**9**) *Vorticella* sp. (**10**) *Opercularia* sp. Two individuals. (**11**) *Epistylis* sp. (**12**) *Podophrya* sp.

number of individuals per colony (Foissner et al. 1992). The peritrichs found were characterized by a thick external layer surrounding each zooid and the smaller dimensions of the zooids.

3.2.6. *Podophrya* sp.

The individuals had a characteristic spheroid body (Figs. 2g and 12). In comparison to the body the stalk can reach a considerable length. The cellular body had an external layer. The capitate tentacles were spread over the entire surface of the body. The rounded macronucleus was located eccentrically. An oval micronucleus was placed near the macronucleus (Table 3).

3.2.6.1. Taxonomic position. The suctorians belong to the genus *Podophrya* Ehrenberg 1833 (family Podophryidae Haeckel, 1866; order Exogenida Collin, 1912; subclass Suctoria Claparède and Lachmann, 1858; class Phyllopharyngea De Puytorac et al., 1974; subphylum Intramacronucleata Lynn, 1996) (*sensu* Lynn and Small 2002). The genus *Podophrya* is characterized by a spherical to ovoid body shape, capitate and ubiquitous tentacles, which are not aligned in fascicles, and the absence of actinophores (Curds 1986). The species most similar to these ciliates was *Podophrya maupasi* Butschli, 1889; they coincided in the dimensions, freshwater, spherical form of the cellular body, absence of lorica, tentacles slightly trumpet-shaped at their end, spherical

macronucleus centrally positioned and thick external layer to zooid. In the description of Curds (1986) the ciliates were free-living and attached to aquatic vegetation and inanimate objects, whereas in our study they were epibionts and attached to freshwater crustaceans.

3.3. Distribution of the epibionts

3.3.1. Lake Towuti

The number of epibionts per shrimp varied between 27 and 971 (Table 4). Taking into account the maximum and mean densities, *A. sulawesiensis* n. sp. was the most abundant species, followed by *Zoothamnium* sp. and *Cothurnia* sp. (Table 4). The epibionts distribution on the different anatomical units of *Caridina* appeared in Table 5, and the distribution of each epibiont species is shown in Table 6.

The density of epibionts on the right and left units correlated in 71% of the shrimp anatomical units (eyes, antennulae, antennae, first pereiopods, all pleopods and uropods). The canonical correlation analysis between the right and left units of the shrimp, taking into consideration the epibionts density, showed a significant correlation ($p \leqslant 0.05$). In the different analyzed individuals of *Caridina* the shrimp's length and width correlated with the mean density of *A. sulawesiensis* n. sp. and the total number of *Cothurnia* sp. and *A. sulawesiensis* n. sp. correlated to the basibiont width. With respect to the shrimps length the mean density of *Acineta* represents the factor contributing to the variance maximum (62.71%) of the total length variance. In contrast, *Zoothamnium* sp. was the species with higher variance (62.34%) respect to the shrimp width.

The Multiple Comparison Analysis performed with the mean densities of each epibiont species on each shrimp anatomical unit showed a significant difference between these epibiont species (F, 7.57; $p \leqslant 0.05$). A similar analysis made with the mean density of the epibiont species in the different shrimps indicated a significant difference between the epibiont species (F, 34.18; $p \leqslant 0.05$).

The dendrogram of the Hierarchical Cluster Analysis performed with the epibionts densities on each anatomical unit of the different shrimps, showed three clusters (Fig. 13): (1) includes the 41.94% of the units (rostrum, left first and third pereiopods and first–fourth pleopods) with a moderate epibiont density (mean 5.20 epibionts per unit); (2) 38.71% of the units (eyes and other pereiopods and pleopods) with low epibiont density (mean 1.54 epibionts per unit); (3) the units (19.35%) with the higher densities (mean 22.98 epibionts per unit), including the antennae, maxillipeds uropods and telson).

Fig. 14 shows the distribution of the different epibiont species along the antero-posterior axis of the shrimp, considering the mean values of epibiont densities and sorting the units in five groups (rostrum, antennae, antennulae and eyes; maxillipeds; pereiopods; pleopods; uropods and telson). *Zoothamnium* sp. represented the highest density on the posterior part of the body, on the pleopods, with 56.21% of the epibionts. The appendages in the anterior part of the body (rostrum, antennae, antennulae and eyes) showed the second highest density (28.28% of epibionts). Other units (maxillipeds, pereiopods, uropods and telson) had lower densities (between 0.87% and 7.91%). *A. sulawesiensis* n. sp. showed a more uniform distribution, with an important presence on the anterior part of the body (rostrum, antennae, antennulae, eyes: 32.86% of epibionts; maxillipeds: 29.72% of epibionts). Other units showed proportions fluctuating between 9.67% on pereiopods, and 15.39% of epibionts on the pleopods. *Cothurnia* sp., with lower densities of epibionts than the other species, had a greater presence on the shrimp extremes. Uropods and telson contained the highest epibionts number (55.18%), followed by anterior appendages (rostrum, antennae, antennulae, eyes, 41.36%). Other units presented 0.3–1.82% of epibionts. The Multiple Comparison Analysis indicated a significant difference between the epibiont species distribution (F, 10.04; $p \leqslant 0.05$). Fig. 15 shows detailed distributions on the different appendages. Also in this case, there was a significant difference between the species (F, 6.58; $p \leqslant 0.05$).

Table 4. Length and width of the specimens of *Caridina lanceolata* analysed and density of the epibionts on the crustacean (Lake Towuti) ($n = 40$)

	Mean	SD	Minimum	Maximum
Length of the shrimp (mm)	21.26	2.97	14.00	27.00
Width of the shrimp (mm)	2.96	0.65	2.00	4.50
Number of protozoans per shrimp	250.90	205.40	27.00	971.00
Zoothamnium sp.	40.75	59.71	0.00	357.00
Acineta sulawesiensis n. sp.	193.08	168.49	4.00	730.00
Cothurnia sp.	16.43	15.05	0.00	59.00

SD, standard deviation.

Table 5. Distribution of the ciliate protozoans on the different anatomical units of *Caridina lanceolata* in the three lakes

Anatomical unit	Mean	SD	Minimum	Maximum
Lake Towuti				
Rostrum	9.90	14.68	0	73
Left ocular orbit	0.38	1.00	0	5
Right ocular orbit	1.40	2.85	0	12
Left antennule	13.63	20.51	0	87
Right antennule	13.40	17.22	0	71
Left antenna	25.10	34.87	0	160
Right antenna	22.25	30.50	0	121
Maxillipeds	58.40	54.59	0	283
Left first pereiopod	6.50	13.60	0	76
Right first pereiopod	3.43	7.95	0	41
Left second pereiopod	1.00	2.43	0	12
Right second pereiopod	1.10	2.15	0	11
Left third pereiopod	2.65	7.17	0	42
Right third pereiopod	1.43	2.97	0	11
Left fourth pereiopod	2.13	6.50	0	39
Right fourth pereiopod	1.08	2.42	0	12
Left fifth pereiopod	0.90	1.89	0	10
Right fifth pereiopod	1.00	2.47	0	14
Left first pleopod	5.00	7.39	0	31
Right first pleopod	5.88	7.57	0	32
Left second pleopod	6.28	10.11	0	42
Right second pleopod	6.33	9.54	0	52
Left third pleopod	7.83	11.44	0	43
Right third pleopod	7.78	15.87	0	96
Left fourth pleopod	4.58	5.76	0	20
Right fourth pleopod	4.88	7.23	0	29
Left fifth pleopod	2.13	3.74	0	19
Right fifth pleopod	2.50	3.86	0	17
Telson	10.35	19.68	0	86
Left uropod	11.68	14.99	0	86
Right uropod	10.08	11.89	0	52
Lake Matano				
Rostrum	26.40	26.84	0	93
Left ocular orbit	0.65	2.03	0	9
Left antennule	1.90	2.55	0	8
Right antennule	2.70	4.21	0	13
Left antenna	2.75	4.56	0	17
Right antenna	2.60	4.59	0	17
Maxillipeds	41.65	56.41	0	189
Left first pereiopod	1.05	3.47	0	15
Right first pereiopod	1.95	4.35	0	15
Left second pereiopod	0.30	0.66	0	2
Right second pereiopod	0.55	2.04	0	9
Left third pereiopod	1.15	3.72	0	15
Right third pereiopod	2.90	7.35	0	30
Left fourth pereiopod	0.10	0.45	0	2
Right fourth pereiopod	0.05	0.22	0	1
Left fifth pereiopod	0.35	1.57	0	7
Right fifth pereiopod	0.80	3.35	0	15
Left first pleopod	8.30	12.50	0	50
Right first pleopod	7.10	15.59	0	70
Left second pleopod	3.10	6.69	0	30
Right second pleopod	3.40	6.98	0	30
Left third pleopod	6.25	15.49	0	60
Right third pleopod	4.30	9.25	0	31

Table 5. (*continued*)

Anatomical unit	Mean	SD	Minimum	Maximum
Left fourth pleopod	2.00	4.58	0	20
Right fourth pleopod	1.90	5.82	0	26
Left fifth pleopod	1.55	5.61	0	25
Right fifth pleopod	0.65	1.57	0	5
Telson	0.10	0.31	0	1
Left uropod	2.55	3.14	0	13
Right uropod	2.20	2.98	0	11
Lake Mahalona				
Rostrum	5.50	13.45	0	44
Left ocular orbit	0.90	2.79	0	12
Right ocular orbit	0.95	2.16	0	8
Left antennule	7.95	10.30	0	35
Right antennule	8.30	10.55	0	42
Left antenna	10.15	21.70	0	92
Right antenna	7.10	12.22	0	35
Maxillipeds	52.75	60.13	0	226
Left first pereiopod	4.15	10.24	0	40
Right first pereiopod	0.70	2.25	0	10
Left second pereiopod	2.00	6.68	0	30
Right second pereiopod	1.45	4.65	0	20
Left third pereiopod	2.90	6.12	0	26
Right third pereiopod	2.45	8.03	0	33
Left fourth pereiopod	2.30	7.03	0	28
Right fourth pereiopod	1.05	4.70	0	21
Left fifth pereiopod	2.60	9.54	0	42
Right fifth pereiopod	0.95	4.25	0	19
Left first pleopod	3.95	5.05	0	18
Right first pleopod	1.90	3.48	0	12
Left second pleopod	1.95	3.87	0	16
Right second pleopod	1.80	3.07	0	11
Left third pleopod	1.70	5.56	0	25
Right third pleopod	2.25	6.64	0	30
Left fourth pleopod	0.95	1.39	0	4
Right fourth pleopod	2.85	5.98	0	22
Left fifth pleopod	1.45	3.68	0	16
Right fifth pleopod	0.55	1.43	0	6
Telson	0.30	0.66	0	2
Left uropod	1.40	2.82	0	9
Right uropod	0.55	1.47	0	6

SD, standard deviation.

3.3.2. Lake Matano

The number of epibionts varied between 6 and 670 per shrimp (Table 7). Among the five epibiont species, *Epistylis* sp. and *Zoothamnium* sp. were the two showing the highest mean densities, although *Zoothamnium* sp. presented the highest maximum density (523 individuals per shrimp). The species with the lowest mean density was *Vorticella* sp. (Table 7). The distribution of the total epibiont numbers on each anatomical unit is given in Table 5. Table 6 shows the densities of each epibiont species on each anatomical unit.

There was a significant correlation between the length and width of the shrimps and the mean number of epibionts ($p \leqslant 0.05$). The total densities of *Zoothamnium* sp. in the different shrimps analyzed represents 73.77% of the total basibionts width variance respect to the other epibiont species. Likewise, *Zoothamnium* sp. represents 77.53% of the shrimp length variance, in respect to the other epibiont species. On the other hand, *Epistylis* sp. showed the highest contribution to the total epibiont variance (82.99%). Taking into account the left and right units, there was significant correlations in respect to 92.30% of the units, with the exception of the second pair of pereiopods.

The Multiple Comparison Analysis using the total densities of each epibiont species on each shrimp showed

Table 6. Number of each epibiont species on the different anatomical units of *Caridina lanceolata* (mean ± standard deviation; minimum–maximum) in the three lakes

Anatomical unit	*Zoothamnium* sp.	*Acineta sulawesiensis* n. sp.	*Cothurnia* sp.
Lake Towuti			
Rostrum	8.05 ± 14.13	0.80 ± 1.98	1.23 ± 2.12
	(0.00–71.00)	(0.00–9.00)	(0.00–10.00)
Left ocular orbit	0.08 ± 0.35	0.13 ± 0.46	0.18 ± 0.68
	(0.00–2.00)	(0.00–2.00)	(0.00–3.00)
Right ocular orbit	0.10 ± 0.44	0.98 ± 2.56	0.33 ± 0.80
	(0.00–2.00)	(0.00–11.00)	(0.00–4.00)
Left antennule	0.65 ± 2.21	12.45 ± 19.51	0.60 ± 1.28
	(0.00–13.00)	(0.00–87.00)	(0.00–6.00)
Right antennule	0.90 ± 2.56	11.90 ± 16.29	0.60 ± 1.34
	(0.00–15.00)	(0.00–69.00)	(0.00–5.00)
Left antenna	0.30 ± 0.85	22.80 ± 34.77	1.93 ± 4.05
	(0.00–4.00)	(0.00–160.00)	(0.00–23.00)
Right antenna	0.43 ± 0.90	19.88 ± 29.47	1.95 ± 2.83
	(0.00–4.00)	(0.00–121.00)	(0.00–12.00)
Maxillipeds	3.35 ± 8.26	55.13 ± 50.69	0.05 ± 0.22
	(0.00–43.00)	(0.00–239.00)	(0.00–1.00)
Left first pereiopod	1.03 ± 4.01	5.23 ± 13.19	0.05 ± 0.32
	(0.00–25.00)	(0.00–76.00)	(0.00–2.00)
Right first pereiopod	0.20 ± 0.56	3.18 ± 7.97	0.03 ± 0.16
	(0.00–2.00)	(0.00–41.00)	(0.00–1.00)
Left second pereiopod	0.05 ± 0.32	0.93 ± 2.28	0.00 ± 0.00
	(0.00–2.00)	(0.00–12.00)	(0.00–0.00)
Right second pereiopod	0.08 ± 0.35	1.13 ± 2.19	0.03 ± 0.16
	(0.00–2.00)	(0.00–11.00)	(0.00–1.00)
Left third pereiopod	0.85 ± 3.85	1.83 ± 4.02	0.00 ± 0.00
	(0.00–24.00)	(0.00–18.00)	(0.00–0.00)
Right third pereiopod	0.50 ± 1.84	0.80 ± 2.10	0.00 ± 0.00
	(0.00–9.00)	(0.00–10.00)	(0.00–0.00)
Left fourth pereiopod	0.03 ± 0.16	2.10 ± 6.50	0.03 ± 0.16
	(0.00–1.00)	(0.00–39.00)	(0.00–1.00)
Right fourth pereiopod	0.03 ± 0.16	1.03 ± 2.35	0.00 ± 0.00
	(0.00–1.00)	(0.00–12.00)	(0.00–0.00)
Left fifth pereiopod	0.08 ± 0.35	0.78 ± 1.89	0.00 ± 0.00
	(0.00–2.00)	(0.00–10.00)	(0.00–0.00)
Right fifth pereiopod	0.00 ± 0.00	0.93 ± 2.45	0.08 ± 0.47
	(0.00–0.00)	(0.00–14.00)	(0.00–3.00)
Left first pleopod	3.13 ± 6.76	1.45 ± 2.11	0.03 ± 0.16
	(0.00–28.00)	(0.00–8.00)	(0.00–1.00)
Right first pleopod	2.30 ± 5.11	3.73 ± 7.10	0.05 ± 0.32
	(0.00–21.00)	(0.00–32.00)	(0.00–2.00)
Left second pleopod	1.90 ± 5.89	3.40 ± 6.62	0.08 ± 0.47
	(0.00–34.00)	(0.00–38.00)	(0.00–3.00
Right second pleopod	2.48 ± 8.50	3.53 ± 5.36	0.00 ± 0.00
	(0.00–52.00)	(0.00–24.00)	(0.00–0.00)
Left third pleopod	5.73 ± 11.13	2.78 ± 4.52	0.03 ± 0.16
	(0.00–43.00)	(0.00–21.00)	(0.00–1.00)
Right third pleopod	3.53 ± 15.21	4.23 ± 6.95	0.05 ± 0.32
	(0.00–96.00)	(0.00–29.00)	(0.00–2.00)
Left fourth pleopod	1.68 ± 4.45	2.95 ± 4.57	0.03 ± 0.16
	(0.00–20.00)	(0.00–19.00)	(0.00–1.00)
Right fourth pleopod	2.10 ± 6.15	2.83 ± 5.08	0.00 ± 0.00
	(0.00–29.00)	(0.00–23.00)	(0.00–0.00)
Left fifth pleopod	0.48 ± 1.62	1.65 ± 3.55	0.00 ± 0.00
	(0.00–9.00)	(0.00–19.00)	(0.00–0.00)
Right fifth pleopod	0.48 ± 1.40	2.00 ± 3.78	0.03 ± 0.16

Table 6. (*continued*)

Anatomical unit	*Zoothamnium* sp.	*Acineta sulawesiensis* n. sp.	*Cothurnia* sp.
	(0.00–8.00)	(0.00–17.00)	(0.00–1.00)
Telson	0.03 ± 0.16	10.33 ± 19.67	0.00 ± 0.00
	(0.00–1.00)	(0.00–86.00)	(0.00–0.00)
Left uropod	0.15 ± 0.66	7.08 ± 14.20	4.35 ± 4.71
	(0.00–3.00)	(0.00–86.00)	(0.00–19.00)
Right uropod	0.13 ± 0.46	5.20 ± 8.91	4.75 ± 6.83
	(0.00–2.00)	(0.00–50.00)	(0.00–33.00)

Anatomical unit	*Zoothamnium* sp.	*Cothurnia* s p.	*Acineta sulawesiensis* n. sp.	*Epistylis* sp.	*Vorticella* sp.
Lake Matano					
Rostrum	21.15 ± 27.62	0.50 ± 1.47	0.70 ± 2.90	—	0.05 ± 0.22
	(0–93)	(0–6)	(0–13)	—	(0–1)
Left ocular orbit	—	0.60 ± 2.04	0.05 ± 0.22	—	—
		(0–9)	(0–1)	—	—
Left antennule	0.65 ± 1.84	0.15 ± 0.49	1.10 ± 1.92	—	—
	(0–8)	(0–2)	(0–8)	—	—
Right antennule	0.55 ± 1.76	0.75 ± 2.67	1.35 ± 2.91		—
	(0–7)	(0–12)	(0–11)		
Left antenna		2.55 ± 4.55	0.15 ± 0.49	0.05 ± 0.22	
	—	(0–17)	(0–2)	(0–1)	
Right antenna		2.00 ± 3.32	0.55 ± 2.04		
		(0–9)	(0–9)		
Maxillipeds	13.40 ± 28.20		5.75 ± 7.93	22.40 ± 56.17	0.10 ± 0.45
	(0–81)		(0–23)	(0–186)	(0–2)
Left first pereiopod	1.00 ± 3.48	—	—	0.05 ± 0.22	
	(0–15)			(0–1)	—
Right first pereiopod	1.20 ± 3.82	—	0.10 ± 0.45	0.65 ± 2.48	—
	(0–15)		(0–2)	(0–11)	—
Left second pereiopod	0.15 ± 0.49	—	0.15 ± 0.49		
	(0–2)		(0–2)		—
Right second pereiopod	0.45 ± 2.01	—	0.10 ± 0.45	—	—
	(0–9)		(0–2)		—
Left third pereiopod	0.40 ± 1.79	—	0.05 ± 0.22	0.70 ± 3.13	
	(0–8)		(0–1)	(0–14)	
Right third pereiopod	0.25 ± 1.12	—	0.50 ± 2.24	2.15 ± 7.17	
	(0–5)		(0–10)	(0–30)	
Left fourth pereiopod	0.85 ± 3.80	—	0.10 ± 0.45	—	
	(0–17)		(0–2)		
Right fourth pereiopod	0.05 ± 0.22	—	—	—	—
	(0–1)				
Left fifth pereiopod	0.30 ± 1.34	—	0.05 ± 0.22	—	—
	(0–6)		(0–1)		
Right fifth pereiopod	0.80 ± 3.35	—	—	—	—
	(0–15)				
Left first pleopod	1.65 ± 4.31	0.50 ± 2.01	0.05 ± 0.22	6.05 ± 11.98	0.05 ± 0.22
	(0–17)	(0–9)	(0–1)	(0–50)	(0–1)
Right first pleopod	0.70 ± 2.15	1.00 ± 4.47	0.25 ± 1.12	5.15 ± 11.64	—
	(0–9)	(0–20)	(0–5)	(0–50)	
Left second pleopod	0.40 ± 0.94	—	—	2.40 ± 6.68	0.30 ± 1.34
	(0–3)			(0–30)	(0–6)
Right second pleopod	0.45 ± 1.23	0.25 ± 0.79	—	1.90 ± 6.69	0.80 ± 2.78
	(0–5)	(0–3)		(0–30)	(0–12)
Left third pleopod	0.65 ± 2.25	0.55 ± 2.24	0.10 ± 0.45	3.10 ± 11.15	1.85 ± 7.58
	(0–10)	(0–10)	(0–2)	(0–50)	(0–34)
Right third pleopod	0.60 ± 1.43	0.10 ± 0.45	—	1.60 ± 6.69	2.00 ± 7.12

Table 6. (*continued*)

Anatomical unit	*Zoothamnium* sp.	*Cothurnia* s p.	*Acineta sulawesiensis* n. sp.	*Epistylis* sp.	*Vorticella* sp.
	(0–5)	(0–2)		(0–30)	(0–31)
Left fourth pleopod	0.30±0.73 (0–3)	0.20±0.52 (0–2)	0.05±0.22 (0–1)	1.10±4.47 (0–20)	0.35±1.35 (0–6)
Right fourth pleopod	0.15±0.37 (0–1)	0.35±1.18 (0–5)	0.10±0.45 (0–2)	1.00±4.47 (0–20)	0.30±1.13 (0–5)
Left fifth pleopod	0.85±3.80 (0–17)	0.60±1.85 (0–8)	—	0.10±0.45 (0–2)	—
Right fifth pleopod	0.20±0.62 (0–2)	0.35±0.93 (0–3)	—	0.10±0.45 (0–2)	—
Telson	0.05±0.22 (0–1)	0.05±0.22 (0–1)	—	—	—
Left uropod	—	2.25±3.06 (0–13)	0.20±0.70 (0–3)	0.10±0.31 (0–1)	—
Right uropod	0.05±0.22 (0–1)	1.80±2.88 (0–10)	0.30±0.66 (0–2)	0.05±0.22 (0–1)	—

Anatomical unit	*Zoothamnium* sp.	*Opercularia* sp.	*Podophrya* sp.	*Cothurnia* sp.	*Acineta sulawesiensis* n. sp.	*Epistylis* sp.	*Vorticella* sp.
Lake Mahalona							
Rostrum	2.10±9.39 (0–42)	—	0.75±3.35 (0–15)	—	0.25±0.79 (0–3)	—	0.20±0.89 (0–4)
Left ocular orbit	—	—	—	—	0.90±2.79 (0–12)	—	—
Right ocular orbit	—	—	—	—	0.95±2.16 (0–8)	—	—
Left antennule	—	—	0.25±0.79 (0–3)	—	7.55±9.61 (0–33)	—	—
Right antennule	—	—	—	—	10.00±16.33 (0–72)	—	—
Left antenna	—	—	—	—	9.45±20.79 (0–89)	—	0.15±0.67 (0–3)
Right antenna	—	—	—	0.80±2.78 (0–12)	6.05±10.47 (0–33)	—	2.25±9.38 (0–42)
Maxillipeds	0.10±0.45 (0–2)	0.50±1.82 (0–8)	0.05±0.22 (0–1)	—	39.80±43.92 (0–176)	2.18±11.19 (0–50)	0.60±2.68 (0–12)
Left first pereiopod	—	—	—	—	1.85±5.30 (0–23)	0.70±3.13 (0–14)	0.10±0.45 (0–2)
Right first pereiopod	—	—	0.05±0.22 (0–1)	—	0.65±2.25 (0–10)	—	—
Left second pereiopod	—	—	0.05±0.22 (0–1)	—	0.90±2.79 (0–12)	0.10±0.45 (0–2)	0.90±4.02 (0–18)
Right second pereiopod	—	—	—	—	1.15±3.42 (0–14)	—	0.30±1.34 (0–6)
Left third pereiopod	—	—	—	—	2.35±6.05 (0–26)	—	0.40±1.79 (0–8)
Right third pereiopod	—	—	—	—	1.65±7.38 (0–33)	—	0.80±3.58 (0–16)
Left fourth pereiopod	—	—	0.05±0.22 (0–1)	—	0.85±3.57 (0–16)	—	1.40±6.26 (0–28)
Right fourth pereiopod	—	0.60±2.68 (0–12)	—	—	—	—	0.45±2.01 (0–9)
Left fifth pereiopod	—	0.50±2.24 (0–10)	—	—	0.20±0.89 (0–4)	—	1.90±8.50 (0–38)
Right fifth pereiopod	—	—	—	—	—	—	0.95±4.25 (0–19)

Table 6. (*continued*)

Anatomical unit	*Zoothamnium* sp.	*Opercularia* sp.	*Podophrya* sp.	*Cothurnia* sp.	*Acineta sulawesiensis* n. sp.	*Epistylis* sp.	*Vorticella* sp.
Left first pleopod	0.10±0.45 (0–2)	0.35±0.88 (0–3)	0.05±0.22 (0–1)	—	1.05±2.39 (0–9)	0.70±2.36 (0–10)	1.20±3.71 (0–15)
Right first pleopod	—	0.10±0.45 (0–2)	—	—	1.00±2.03 (0–7)	0.20±0.89 (0–4)	0.60±2.68 (0–12)
Left second pleopod	0.05±0.22 (0–1)	0.40±1.27 (0–5)	—	—	0.25±0.72 (0–3)	0.15±0.67 (0–3)	1.25±3.82 (0–16)
Right second pleopod	—	0.10±0.45 (0–2)	—	—	0.20±0.70 (0–3)	0.60±1.60 (0–6)	0.15±0.67 (0–3)
Left third pleopod	—	0.20±0.89 (0–4)	—	—	1.20±4.71 (0–21)	0.10±0.45 (0–2)	0.55±2.04 (0–9)
Right third pleopod	0.10±0.45 (0–2)	0.10±0.45 (0–2)	—	—	1.50±4.67 (0–21)	—	0.20±0.70 (0–3)
Left fourth pleopod	—	—	—	—	0.75±1.37 (0–4)	0.10±0.45 (0–2)	0.35±1.57 (0–7)
Right fourth pleopod	—	0.75±2.31 (0–8)	—	—	1.45±2.76 (0–8)	0.30±1.34 (0–6)	0.05±0.22 (0–1)
Left fifth pleopod	—	0.30±1.34 (0–6)	—	—	0.95±1.79 (0–6)	—	0.20±0.89 (0–4)
Right fifth pleopod	—	0.10±0.45 (0–2)	—	0.05±0.22 (0–1)	0.35±0.99 (0–4)	0.10±0.45 (0–2)	0.05±0.22 (0–1)
Telson	—	—	0.05±0.22 (0–1)	0.10±0.45 (0–2)	0.15±0.49 (0–2)	—	—
Left uropod	—	—	—	0.35±1.57 (0–7)	0.85±2.06 (0–7)	0.05±0.22 (0–1)	0.15±0.67 (0–3)
Right uropod	—	—	—	0.05±0.22 (0–1)	0.55±1.47 (0–6)	—	—

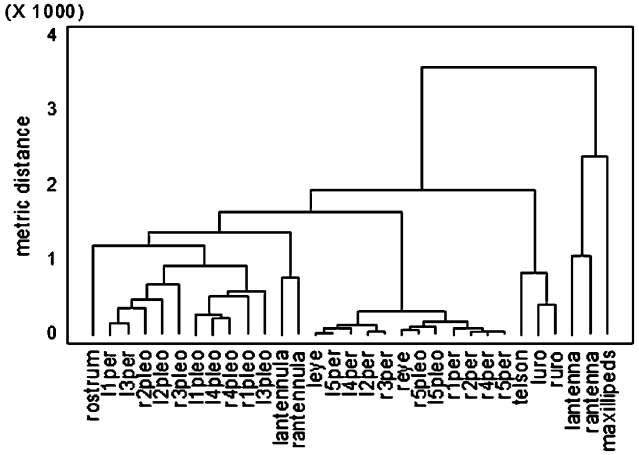


Fig. 13. Lake Towuti. Dendogram of the Hierarchical Cluster Analysis performed using the mean densities of epibionts on each anatomical unit of the shrimps (metric distance: City Block (Manhattan); method, Ward).

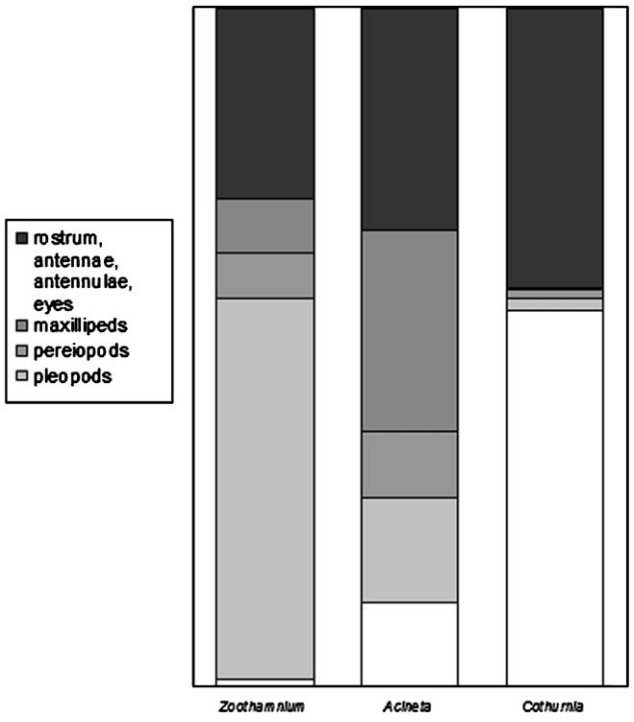


Fig. 14. Lake Towuti. Distribution of the each epibiont species (mean densities) along the anterioposterior axis of *Caridina lanceolata*. Anatomical units are considered in five groups.

significant differences between the different epibiont species (F, 2.57; $p \leqslant 0.05$). There were significant differences between the distributions of *Zoothamnium* sp. and *A. sulawesiensis* n. sp., *Zoothamnium* sp. and *Vorticella* sp., and *Epistylis* sp. and *Vorticella* sp.

The Principal Component Analysis performed with the mean densities of each epibiont species on each anatomical unit showed three species together (*Zoothamnium* sp., *A. sulawesiensis* n. sp. and *Epistylis* sp.), while *Vorticella* sp. and *Cothurnia* sp. appeared separated in the two first principal components graphic (Fig. 16).

The dendrogram of the Hierarchical Cluster Analysis made using the epibiont density per anatomical unit on the different shrimps (Fig. 17), showed two units clearly that separated from the rest: the rostrum and the maxillipeds, which had a mean density of 34.03 epibionts. Other units were grouped into three clusters: (1) units with the highest epibiont densities (mean 6.49 epibionts per unit); these units (8% of the total units) were the first and third pleopods. (2) The major cluster (50% of the units), with a moderate epibionts density (mean 2.14 epibionts per unit); this cluster included the right antennula, antennae, left eye, right first and third pereiopods, second, fourth and fifth pleopods and uropods). (3) The 30% of units with lowest densities (mean 0.58 epibionts per unit); they were the left antennula, right first, second, fourth and fifth pereiopods and telson.

Fig. 18 shows the epibiont species distribution along the antero-posterior axis of the shrimp. *A. sulawesiensis* n. sp. dominated on the anterior part of the body (rostrum, antennae, antennulae, eyes, and maxillipeds) where it represented 82.13% of the epibionts. *Cothurnia* sp. was located mainly on pleopods (42.9% of epibionts), anterior part of the body (rostrum, antennae, antennulae, eyes, 35.12%), and uropods (21.98% of the epibionts). *Epistylis* sp. was more abundant on the maxillipeds and pleopods, where it was almost equally distributed, representing both 92.29% of the epibionts. *Vorticella* sp. was located principally on the pleopods (97.41% of the epibionts). In Fig. 19 appeared the epibiont species distribution on each anatomical unit along the shrimp. There was a significant correlation between the distribution of *Acineta* sp. and *Epistylis* sp. (0.75; $p \leqslant 0.05$).

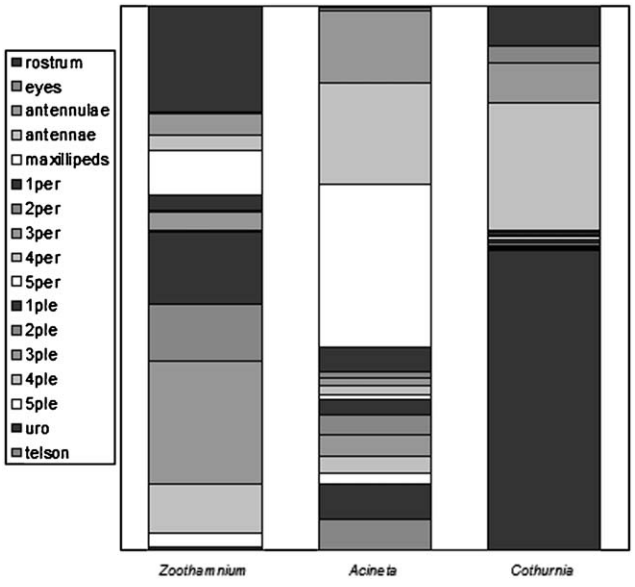


Fig. 15. Lake Towuti. Distribution of the each epibiont species (mean densities) along the anterioposterior axis of *Caridina lanceolata*. Anatomical units are considered individually.

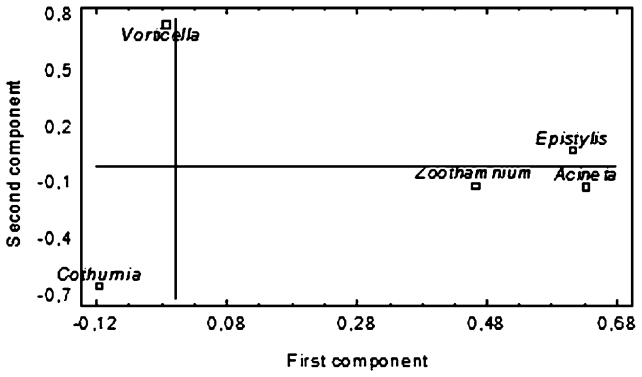


Fig. 16. Lake Matano. Two first principal components of the Principal Component Analysis performed using the mean densities of epibionts on each anatomical unit of the different shrimps analyzed.

Table 7. Length and width of the specimens of *Caridina lanceolata* analysed and density of the epibionts on the crustaceans (Lake Matano) ($n = 40$)

	Mean	SD	Minimum	Maximum
Length of the shrimp (mm)	16.10	3.06	11	21
Width of the shrimp (mm)	2.65	0.61	2	4
Number of ciliate protozoans per shrimp	131.25	143.56	6	670
Zoothamnium sp.	51.25	51.49	0	177
Cothurnia sp.	14.55	23.35	0	98
Acineta sulawesiensis n. sp.	11.75	12.04	0	31
Epistylis sp.	48.65	120.73	0	523
Vorticella sp.	5.80	21.38	0	96

SD, standard deviation.

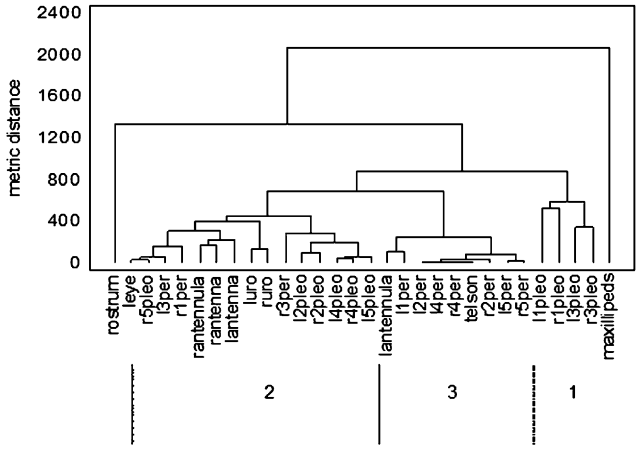


Fig. 17. Lake Matano. Dendogram of the Hierarchical Cluster Analysis performed using the mean densities of epibionts on each anatomical unit of the shrimps (metric distance: City Block or Manhattan distance; method, Ward).

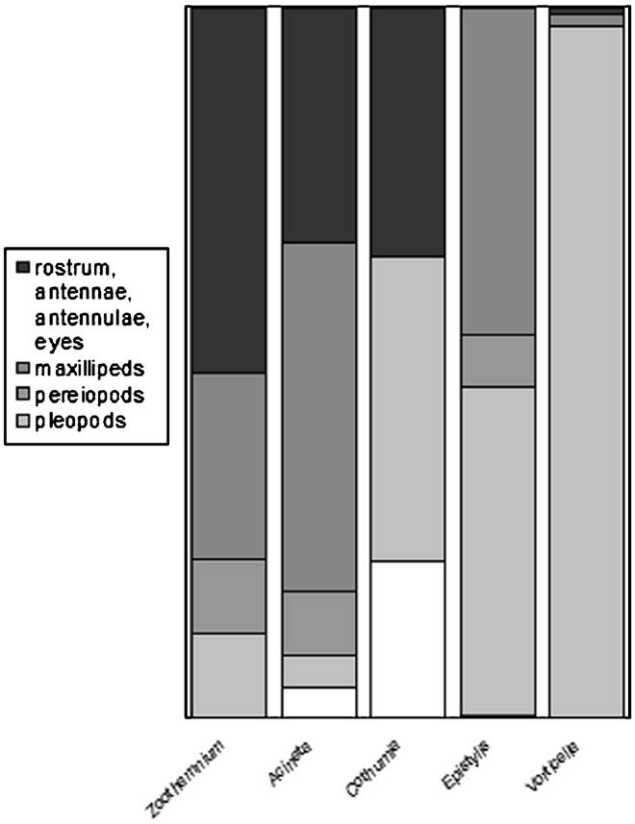


Fig. 18. Lake Matano. Distribution of the each epibiont species (mean densities) along the anterioposterior axis of *Caridina lanceolata*. Anatomical units are considered in five groups.

3.3.3. Lake Mahalona

The number of epibionts per shrimp varied between 2 and 523 (mean 135.75) (Table 8). Seven epibiont species were found, among them *A. sulawesiensis* n. sp. was the most abundant, followed by *Vorticella* sp. The lowest frequent species were *Podophrya* sp. and *Cothurnia* sp. (Table 8). The total epibiont distribution on each anatomical unit of the shrimp is shown in Table 5, and the numerical data of each epibiont species presence on the basibiont anatomical units are included in Table 6.

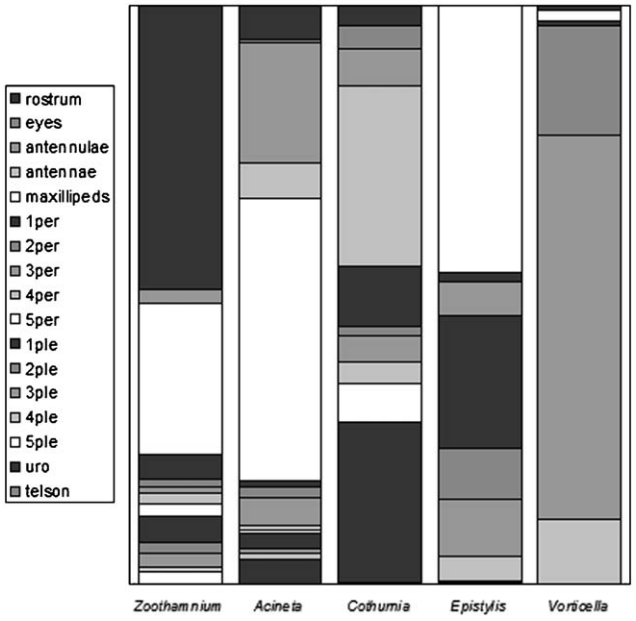


Fig. 19. Lake Matano. Distribution of the each epibiont species (mean densities) along the anterioposterior axis of *Caridina lanceolata*. Anatomical units are considered independently.

Taking into account the density of each epibiont species on each anatomical unit of the shrimp, there were significant correlations between right and left units in 78.57% of the units, excepting eyes, fourth pereiopods, and second pleopods. The Multiple Comparison Analysis performed using the total and mean number of each epibiont species on each analyzed shrimp, showed a significant difference between the epibiont species (F, 12.64; $p \leqslant 0.05$). The most contributing factor to the maximum variance of the shrimps length and width was the densities sum of *A. sulawesiensis* n. sp.

The Principal Component Analysis made with the mean densities of each epibiont species on the shrimps units showed two clusters, one including *Zoothamnium* sp., *Podophrya* sp. and *Vorticella* sp., and another with the other species (*A. sulawesiensis* n. sp., *Epistylis* sp., *Cothurnia* sp. and *Opercularia* sp.) (Fig. 20). The Hierarchical Cluster Analysis made using the epibiont densities on each shrimp anatomical unit showed a dendrogram in which the densities cluster in four groups (Fig. 21). One corresponds to the maxillipeds, with the highest epibiont density (mean 52.75). Another cluster includes 12.90% of the units (antennulae and antennae)

Table 8. Length and width of the specimens of *Caridina lanceolata* analysed and density of the epibionts on the crustacean (Lake Mahalona) ($n = 40$)

	Mean	SD	Minimum	Maximum
Length of the shrimp (mm)	15.90	2.62	11.00	19.70
Width of the shrimp (mm)	3.12	0.81	2.00	4.60
Number of protozoans per shrimp	135.75	137.78	2	523
Zoothamnium sp.	2.45	9.35	0	42
Opercularia sp.	4.00	8.09	0	30
Podophrya sp.	1.30	4.90	0	22
Cothurnia sp.	1.35	5.17	0	23
Acineta sulawesiensis n. sp.	94.80	87.94	0	318
Epistylis sp.	5.90	16.10	0	68
Vorticella sp.	15.15	37.08	0	141

SD, standard deviation.

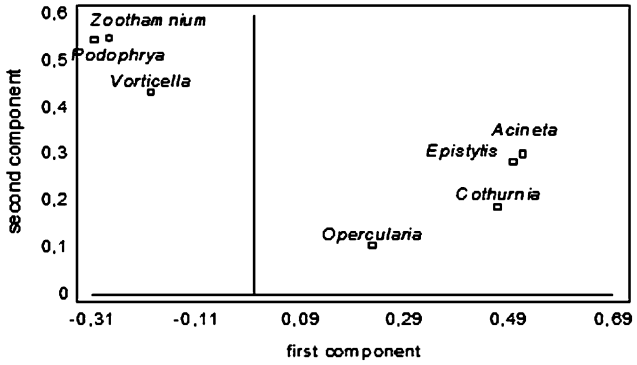


Fig. 20. Lake Mahalona. Two first principal components of the Principal Component Analysis performed using the mean densities of epibionts on each anatomical unit of the different shrimps analyzed.

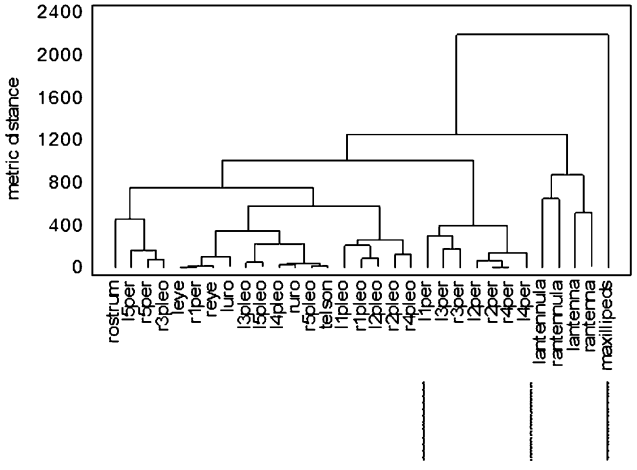


Fig. 21. Lake Mahalona. Dendogram of the Hierarchical Cluster Analysis performed using the mean densities of epibionts on each anatomical unit of the shrimps (metric distance: City Block or Manhattan distance; method, Ward).

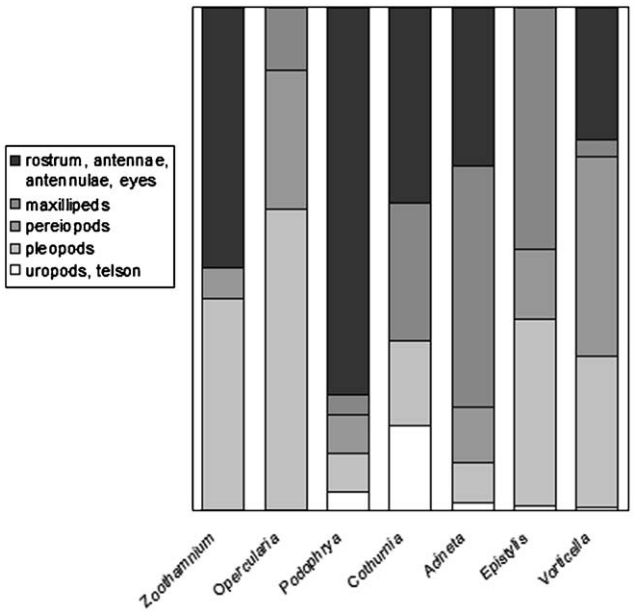


Fig. 22. Lake Mahalona. Distribution of the each epibiont species (mean densities) along the anterioposterior axis of *Caridina lanceolata*. Anatomical units are considered in five groups.

presenting high epibiont densities (mean 8.39 epibionts per unit). The third cluster was formed by 22.58% of the units, with a moderate epibiont density (mean 2.33 epibionts per unit), and includes the left first, second, third and fourth pereiopods. The fourth cluster was the most numerous, representing 61.29% of units, with the lowest epibionts density (mean 1.75 epibionts per unit); these units were rostrum, eyes, right first and fifth pereipods, pleopods, uropods and telson.

Fig. 22 shows the epibiont distribution along the longitudinal axis of the shrimp. *Zoothamnium* sp. was distributed mainly on the anterior part of the body (rostrum, antennae, antennulae, eyes, and maxillipeds),

with 51.85% of the epibionts, and also on the pleopods (41.98%). *Opercularia* sp. presented an increase of densities towards the posterior end of the shrimp, with the highest proportion on the pleopods (60% of the epibionts). *Podophrya* sp. predominated on the anterior part of the shrimp (rostrum, antennae, antennulae, eyes, and maxillipeds), where it represented 76.92% of the epibionts. *Cothurnia* sp. was also more abundant on the anterior part of the body, but this time including the maxillipeds. The epibionts mean on the two anterior groups of the shrimp represented 66.10% of this species' total number. The same occurred with *A. sulawesiensis* n. sp., which, although it was present on pereiopods, pleopods, uropods and telson, it had the highest abundance on the anterior part of the body (79.28% of the epibionts). *Epistylis* sp. colonized mainly the maxillipeds and pleopods of the shrimp, zones where it had 85.34% of the epibionts. *Vorticella* sp. was distributed along the anterior part of the body (rostrum, antennae, antennulae, eyes, and maxillipeds), pereiopods and pleopods (95.87%). The most densely colonized units were the pereiopods (39.63% of their epibionts). The Multiple Comparison Analysis indicated a significant difference between the longitudinal distribution of the epibiont species (F, 4.77; $p \leqslant 0.05$). Fig. 23 shows the species distribution along the longitudinal axis of the shrimp on the different units. There was also a significant difference between the species distributions (F, 3.85; $p \leqslant 0.05$).

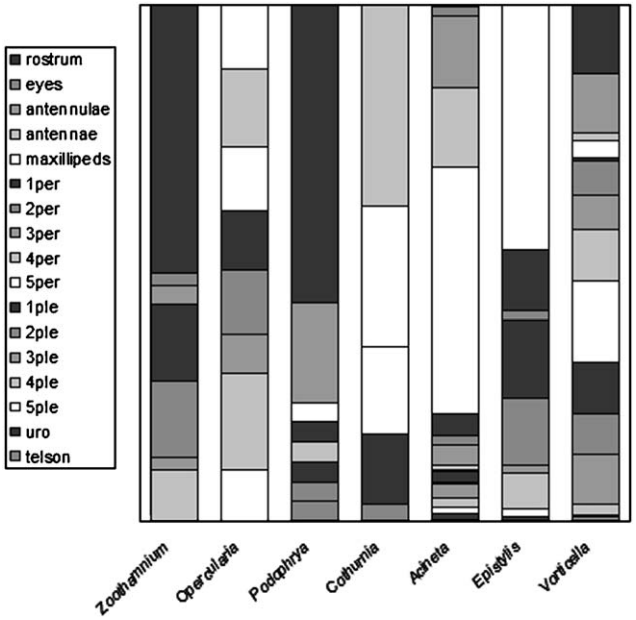


Fig. 23. Lake Mahalona. Distribution of the each epibiont species (mean densities) along the anterioposterior axis of *Caridina lanceolata*. Anatomical units are considered separately.

3.4. Distributions in the three lakes

Taking into consideration the epibiont mean number in the different anatomical units of the shrimp, there was a significant difference between the three lakes (F, 6.23; $p \leqslant 0.05$).

The Canonical Population Analysis performed using the number of epibionts in each anatomical unit of all the analyzed shrimps, showed a significant difference between the three lakes (F, 3.34; $p \leqslant 0.05$). The same analysis was made with two lakes and it indicated also significant differences. Taking into account the total density on the different analyzed shrimps, there were significant differences between the three lakes in respect to each epibiont species.

Fig. 24 shows the epibiont's total number distribution along the antero-posterior axis of *C. lanceolata*, considering the anatomical units in five groups (rostrum, antennae, antennulae and eyes; maxillipeds; pereiopods; pleopods; uropods and telson). In Lake Towuti, the highest epibionts density was found on the anterior part of the body (rostrum, antennae, antennulae and eyes) (32.41%), while in the other two lakes, the highest colonization corresponded to the maxillipeds (31.56% Lake Matano, 40.89% Lake Mahalona). In Lake Towuti the rest of the epibionts colonized mainly maxillipeds and pleopods (both 45.76% of epibionts). In Lake Matano, other epibionts were distributed principally on the anterior part of the body and pleopods (in total 57.18% of epibionts). In Lake Mahalona, other epibionts were divided among the anterior part of the body, pereiopods and pleopods (in total 57.39% of the epibionts). Uropods and telson were the units less colonized in Lake Matano (3.64%) and Lake Mahalona (1.72%), while in Lake Towuti, they presented a moderate density (13.18% of the epibionts). There is not a significant correlation between the three lakes.

Fig. 25 illustrates the distribution of epibionts along the antero-posterior axis of the shrimp, making an allowance for the mean densities of epibionts on the different anatomical units. In this case, there was a significant correlation between the three lakes (0.66–0.89; $p \leqslant 0.05$). This fact point out that considering the densities along the longitudinal axis together, independently of the epibiont species present, the epibiosis distribution in the three lakes are similar.

On the other hand, the comparison between the distributions of the same epibiont species along the longitudinal axis of the shrimp between the diverse lakes, indicated that they correlated with respect to their density values on the anatomical units of the shrimp.

4. Discussion

The correlation between the three lakes in respect to the distribution of epibionts along the antero-posterior

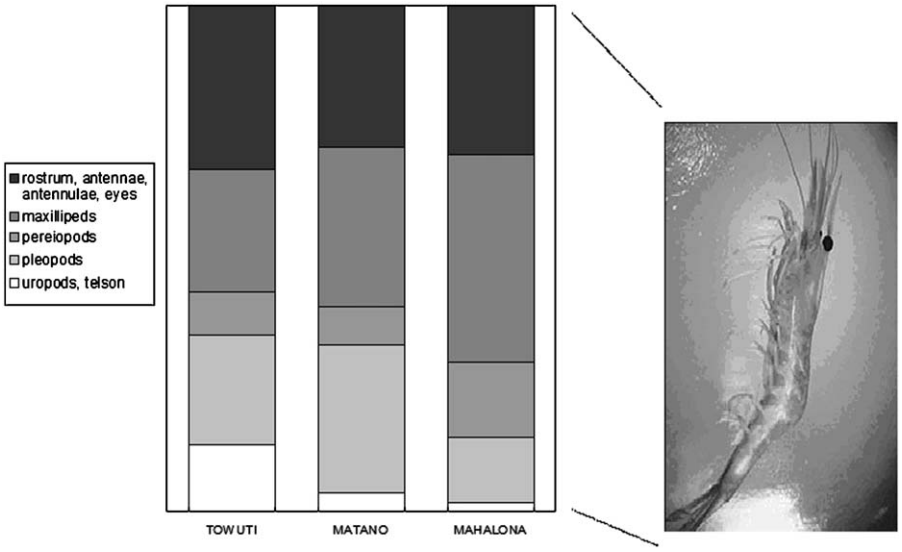


Fig. 24. Distribution of the epibionts (total mean densities) along the longitudinal axis of *C. lanceolata* in the three lakes. Anatomical units are considered in five groups.

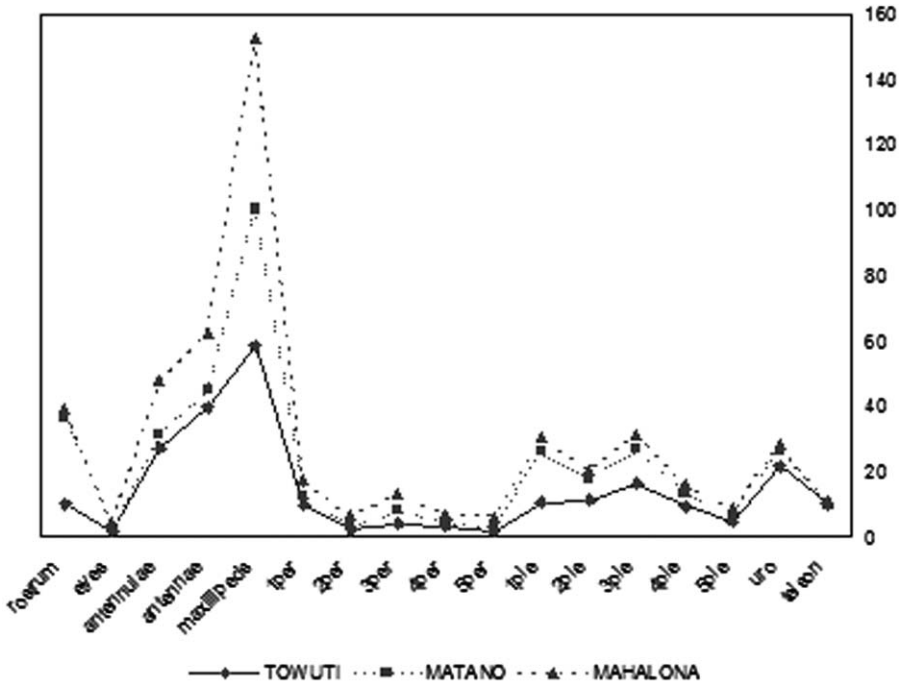


Fig. 25. Distribution of the epibionts (total mean densities) along the longitudinal axis of *C. lanceolata* in the three lakes. Anatomical units are considered individually.

axis of the shrimp indicates that, in terms of epibiont mean densities, in the three lakes the colonization of *C. lanceolata* follows a similar distribution, independently of the epibiont species present. The epibionts in the three lakes show a similar colonization pattern respect to the longitudinal axis of the shrimp. They presented high densities on the anterior areas of the body, especially on the maxillipeds, antennae and antennulae. The pleopods and uropods are the second group of most colonized appendages, in comparison with the pereiopods, which showed a lower density of epibionts.

C. lanceolata represents a highly mobile host compared to other invertebrates in the Malili lake system, for example pachychilid snails (Rintelen and Glaubrecht

2005), on which epibionts have never been observed. Unlike other *Caridina* species from the lakes, among these *Caridina spongicola* (Zitzler and Cai, 2006), *C. lanceolata* does not show preferences for a certain habitat, but seems to be a generalistic feeder on different kinds of substrates, i.e., wood, rocks or macrophytes (Zitzler, von Rintelen & Glaubrecht, unpublished data). The high colonization on the anterior part of the shrimp may be due to the characteristic feeding mechanism of *Caridina* as described in Fryer (1960): instead of filtering like other atyid shrimps, small food particles are swept from the underground by the setae of the very mobile chelipeds and are passed with extreme rapidity to the mouthparts. This behavior, which could also be observed in *C. lanceolata* in the lakes (Zitzler, pers. obs.), brings the mouthparts and feeding appendages into close and permanent contact with the substrate (for example, macrophytes) and thus determines an increase of the nutrient material in the frontal and anterior ventral areas of the body. The high epibiont densities on the pleopods and uropods of the posterior ventral areas, may depend on the morphology of these appendages, that are more flattened and ramified than pereiopods and possibly more adequate for the attachment of the epibionts. Also this location could be advantageous for the epibiont, which can find available the nutrients from the movement of the posterior appendages with respect to the bottom, since this movement disturbs the sediment removing organic particles and microorganisms, which can feed by the epibiont.

The lack of correlation between the three lakes in respect to the epibiont distribution on five groups of anatomical units along the longitudinal axis of the shrimp may be due to the differences in the size of the basibiont. Shrimps of Lake Towuti presented a colonization on the uropods and telson that was higher than in the other lakes, and these shrimps showed the highest length of the three lakes, which results in a greater surface for colonization. On the other hand, the higher comparative densities on the pereiopods of the shrimps of Lake Mahalona, possibly represent an alternative for the scarce surface of other appendages in shrimps that have the lowest mean length of the three lakes.

In contrast, if the epibiont density on each anatomical unit of the shrimp and also each analyzed shrimp are considered, there is a significant difference between the three lakes, as it is showed by the Canonical Correlation Analysis. This fact might indicate that in the shrimp population of a lake the colonization depends on the particular characteristics of the present shrimps. This is corroborated by the fact that the total density of each species on the different analyzed shrimps showed a significant difference between the three lakes, which indicates that the presence of each epibiont species on the population of *C. lanceolata* varied from one lake to another.

The significant correlation between the same epibiont species, in respect to their mean density values along the longitudinal axis of the shrimp on the diverse lakes, indicates that, independently of the present species, each epibiont species tends to colonize the shrimp following the same distribution pattern. *A. sulawesiensis* n. sp. (the most abundant in two of the three lakes) in the three lakes tends to colonize the anterior appendages (rostrum, antennae, antennulae and eyes) and the maxillipeds. *Zoothamnium* sp. was also frequent on the pleopods. *Cothurnia* sp. was also present with high densities on the group of uropods and telson. *Epistylis* sp., which appeared in Lake Matano and Lake Mahalona was shared principally on maxillipeds and pleopods. *Vorticella* sp. was most abundant in Lake Matano on pleopods, and in Lake Mahalona also on pereiopods and maxillipeds. *Podophrya* sp. only present on Lake Mahalona with low densities predominates on pereiopods and pleopods.

The epibiont species found belong to the genera *Vorticella*, *Acineta*, *Cothurnia*, *Epistylis*, *Opercularia*, *Zoothmanium* and *Podophrya*. Although these species had been found previously on other crustaceans, they have not been recorded formerly as epibionts on *Caridina* (Morado and Small 1995; Fernandez-Leborans and Tato-Porto 2000a, b; Fernandez-Leborans 2001), in which the sole described protozoan as epibiont was *Spelaeophrya* (Nie and Lu 1945). Besides the presence of these protozoan ciliate genera, the recorded epibionts showed particular morphological characteristics, which might represent diverse strategies for adaptation to the epibiosis life. It is the case of *A. sulawesiensis* n. sp. with the anterior extension of the lorica forming collar-like protecting tentacles against the fouling activities of the basibiont or the abrasion arising from the movement of the shrimp. The species similar to *A. sulawesiensisi* n. sp., *Acineta balkalica* and *Acineta brevistyla*, also showed this extension of the lorica, and they were found in the Lake Baikal, as epibionts of gammarids (Swarczewsky 1928). Another possible adaptation was referred to the individuals of *Zoothamnium* sp., which presented the body covered by a thick layer similar to a lorica, a wide suprastylar area, and a stalk very bulked; and all they could prevent the ciliate from the basibiont activities or the substrata peculiarities, which can snatch away or hinder the epibionts. In general, other free-living species of the same genera do not display these particular morphological features. Together with these species, *Cothurnia* sp. also showed the lack of a stalk, and a strong direct attachment of the lorica, which allows it to settle on almost all smooth surfaces of the host. The individuals of *Podophrya* sp. were characterized by a short stalk. Similar ciliates were found previously on *Gammarus wilkitzkii* in the Arctic region (Arndt et al. 2005), but showing a long stalk. This ciliate was located mainly on the pereipods on *G. wilkitzkii*,

while in *C. lanceolata* it was most frequent on the rostrum and antennulae, where a long stalk is probably not adequate for obtaining nutrients, while the thicker and shorter stalk and less and broader tentacles, in comparison to the ciliates of *G. wilkitzkii*, may provide advantages for survival in epibiotic life. Other ciliates involved in the epibiont community, such as *Cothurnia* with its lorica, and *Epistylis* and *Opercularia* with a conspicuous external layer, presented morphological adaptations to protect the epibiont body. These adaptations, clearly evident in the epibiont species of these lakes, could indicate an independent evolution in these singular environments.

The protozoan community is the most important and, in general, the sole epibiont component associated to *C. lanceolata*. Among all the observed specimens, only one appeared colonized by an alga, located on the middle ventral surface of the shrimp. The presence of the alga, in this case displaces the protozoan epibiont species, but apparently the low infestation of the alga, in comparison with the protozoa, seems to indicate the biological success of the latter in the colonization of the shrimp. The short generation time, the dispersion, and the adaptations to the epibiotic life, confer ciliate protozoans numerous advantages in colonization. An indication of this fact is the numerous protozoan communities described as epibionts in many crustacean species (Morado and Small 1995; Fernandez-Leborans and Tato-Porto 2000a, b).

The protozoan ciliate epibionts probably did not harm the basibiont. Within the epibiont community there are diverse trophic links and, therefore, as it occurs in free environments, there is a sort of energy feed-back (microbial loop or other relations), and e.g., several species can feed on other present protozoan in the epibiotic community, or on other organisms belonging to the community associated to the host (that have free movement around the basibiont), as suctorians feeding on other ciliates. Peritrich ciliates could depend on the nutrients arising from the activities of the shrimp. Protozoa of lake environments are considered as a major link in the limnetic food web and they have key functions in energy flow and cycling in freshwater ecosystems. Protozoa are a very important link in the transfer of energy to the higher trophic levels and they are a common nutrient for crustaceans and fish larvae (Porter et al., 1985). The changes in the community structure of protozoa may significantly affect other components of the aquatic food web, and thus may influence the distribution and abundance of both lower and higher organisms (Beaver and Crisman 1989; Cairns and McCormick 1993; Carrick and Fahnenstiel 1992). Ciliates have important ecological significance in free environments, especially in benthic areas, where they show high growth rates and an important trophic diversity (Fenchel 1990; Patterson et al. 1989; Fernandez-Leborans and Fernandez-Fernandez 2002). Although in a small scale, these conditions could be transferred to an epibiotic community, which could reflect the biodiversity in the environment (Fernandez-Leborans and Gabilondo 2006).

The basibiont represents a dynamic environment in which the epibiont community species acquire a colonization pattern. The species were located following a particular strategy, and this is proved by the results: the species followed a tendency correlated to the different lakes. Independently of the present species and in all cases, each species was established fitting the same general way of distribution.

5. Conclusions

(1) The protozoan ciliate epibionts observed in *C. lanceolata* from three lakes of Sulawesi (Indonesia), were found by first time in this basibiont species. Morphological and taxonomical aspects of these ciliates were described.
(2) Among these epibiont species, one was described as a new species called *A. sulawesiensis*.
(3) Some morphological features of the epibiont species may represent an adaptation to the epibiotic life, which have possibly evolved in an independent way in these particular environments like the lakes of the Malili system.
(4) The statistical analysis of the distribution of the ciliate epibionts on the surface of *C. lanceolata*, considering the epibiont density in the different anatomical units of each shrimp examined, showed that there was a significant difference between the three lakes considered.
(5) In Lake Towuti the highest density of epibionts was present on the anterior part of the shrimp (rostrum, antennae, antennulae and eyes), followed by the maxillipeds and pleopods.
(6) In Lake Matano epibionts were located mainly on the maxillipeds, followed by the anterior part of the body and pleopods.
(7) In Lake Mahalona epibionts were more abundant on the maxillipeds, followed by the anterior part of the body, pereiopods and pleopods.
(8) In each lake there was an epibiont community on *C. lanceolata* characterized by the present epibiont species, their distribution and density on the anatomical units of the basibiont, and the variation of the distribution on the different colonized shrimps.
(9) The colonization on *C. lanceolata* offered a similar pattern in the three lakes, with a gradient along the antero-posterior axis of the basibiont body.

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