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## Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

### Epibiontic communities on the freshwater shrimp *Caridina ensifera* (Crustacea, Decapoda, Atyidae) from Lake Poso (Sulawesi, Indonesia)

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Published online: 31 Dec 2007.

To cite this article: Gregorio Fernandez-Leborans & Kristina Von Rintelen (2007) Epibiontic communities on the freshwater shrimp *Caridina ensifera* (Crustacea, Decapoda, Atyidae) from Lake Poso (Sulawesi, Indonesia), *Journal of Natural History*, 41:45-48, 2891-2917, DOI: [10.1080/00222930701787871](https://doi.org/10.1080/00222930701787871)

To link to this article: <http://dx.doi.org/10.1080/00222930701787871>

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## Epibiontic communities on the freshwater shrimp *Caridina ensifera* (Crustacea, Decapoda, Atyidae) from Lake Poso (Sulawesi, Indonesia)

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(Accepted 5 November 2007)

### Abstract

The epibiont communities of the freshwater shrimp *Caridina ensifera*, endemic to Lake Poso (Sulawesi, Indonesia), were analysed for the first time based on their morphological and biometrical characteristics and taxonomic position. Seven ciliated protozoans and a rotifer were examined: three suctorian ciliate protozoan species (*Acineta sulawesiensis*, *Podophrya maupasi*, and *Spelaeophrya polypoides*), three peritrichs (*Zoothamnium intermedium*, *Vorticella globosa*, and *Cothurnia compressa*), a haptorid (*Amphileptus fusidens*), and the rotifer species *Embata laticeps*. A mean number of 314.6 epibionts was found per shrimp specimen. The distribution of the epibiont species on the surface of the basibiont was recorded, to allow calculation of the density on the different colonized individuals of *C. ensifera* and on each anatomical unit of the shrimp. The most abundant species, *Zoothamnium intermedium* and *Acineta sulawesiensis*, were also the ones most widely distributed. The statistical analysis showed that *Zoothamnium*, *Acineta*, *Podophrya*, and *Embata* were the epibiont genera most widely distributed on the basibiont, and the pairs of epibiont genera *Zoothamnium–Embata*, *Podophrya–Acineta*, *Spelaeophrya–Amphileptus*, and *Cothurnia–Vorticella* followed a similar pattern of distribution. There was a significant difference between the distribution patterns of the different epibiont species on the shrimp. The analysis of the densities of the epibionts throughout the longitudinal axis of the shrimp showed a gradient from the anterior to the posterior end of the body, and a significantly different distribution of each epibiont species. Their colonization follows a certain pattern of behaviour, the species occupying the available substratum, with particular requirements of each functional group, but with a trend resulting in equilibrium among species and groups, compensating for diversity and density. The possible adaptations of the epibionts, as well as the colonization patterns are discussed.

**Keywords:** *Caridina ensifera*, ciliate protozoans, epibiosis, Lake Poso, rotifer, Sulawesi

### Introduction

In recent years, a number of reports were dedicated to epibiosis in Crustacea (Dawson 1957; Eldred 1962; Maldonado and Uriz 1992; Gili et al. 1993; Morado and Small 1995; Dick et al. 1998; Key et al. 1999; Fernandez-Leborans and Tato-Porto 2000a, 2000b).

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ISSN 0022-2933 print/ISSN 1464-5262 online © 2007 Taylor & Francis

DOI: 10.1080/00222930701787871

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 hosts and constitutes a support for the epibiont (Wahl 1989; Wahl et al. 1997). The presence of epibionts, previously known as commensals, epizoics, symbionts etc., on crustaceans has been reported for a long time, although only recently has this association been considered in a new perspective. This has involved not only a noticeable increase of newly described taxa, but also the recognition that epibiotic relationships are relevant to many biological fields: physiology, ecology, evolution and those fields related to conservation and biodiversity.

A number of protozoan ciliate species have been described as epibionts on crustaceans, and the biology and ecology of their basibiont crustacean taxa can be explained by 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). The invertebrate epibionts include forms that belong to a number of different phyla (Porifera, Cnidaria, Platyhelminthes, Nemertea, Rotifera, Nematoda, Polychaeta, Cirripedia, Decapoda, Gastropoda, Bivalvia, Phoronida, Bryozoa, Ascidiacea, and others). Protozoan epibionts are representative of the following groups: apostomatids, chonotrichids, suctorians, peritrichs, and heterotrichs (Corliss 1979; Lynn and Small 2000).

The study of epibiont communities on basibionts from different lake systems, e.g. the East African lakes, the lakes of Northern Europe or the ancient lakes on Sulawesi, Indonesia, could provide comparable data from independent lakes that may increase the knowledge of evolutionary patterns, and give complementary information about the conservation and biodiversity of these special environments. This is the case for *Mysis relicta* Loven, 1862 in the lakes of Northern Europe (Fernandez-Leborans 2004), and for the shrimp genus *Caridina* Milne-Edwards, 1837 from the Malili system of Sulawesi (Fernandez-Leborans et al. 2006a). On the Indonesian island of Sulawesi (the former Celebes), two ancient lake systems, the Malili lake system and Lake Poso, are hotspots of aquatic biodiversity and harbour several endemic species flocks, for example shrimps (Schenkel 1902; Woltereck 1937a, 1937b; Chace 1997; Zitzler and Cai 2006), molluscs (Korniuschin and Glaubrecht 2003; Rintelen et al. 2004; Rintelen and Glaubrecht 2004, 2006) and fishes (Parenti and Soeroto 2004; Herder et al. 2006). The lake systems are not connected, but provide similar environmental conditions for their respective faunas. The freshwater shrimp, *Caridina ensifera* Schenkel, 1902 (Crustacea, Decapoda, Atyidae), is part of an endemic species flock of currently three lacustrine and one riverine species described from Lake Poso (Schenkel 1902; Chace 1997) (Figure 1). It is abundant in the lake and often collected by local fishermen (K. von Rintelen, personal field observation).

The epibiont communities on *C. ensifera* were analysed with respect to their biological and taxonomical characteristics as well as to their distribution on the surface of the shrimp. The aim of this work was to contribute to the description and explanation of the relationships and patterns of distribution of the protozoan epibiont communities on the endemic shrimp species from Lake Poso.

## Material and methods

Specimens of *Caridina ensifera* were collected by Matthias Glaubrecht and Thomas von Rintelen (Museum of Natural History, Berlin, Germany) from the south shore of Lake

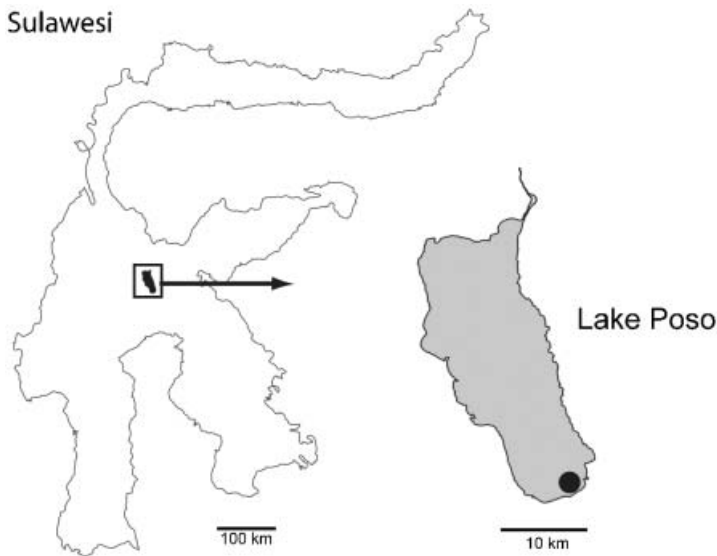


Figure 1. Geographical area of the study.

Poso, Central Sulawesi, Indonesia, in March 2004 (Figure 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. Forty colonized specimens of *C. ensifera* were analysed, of which nine were ovigerous females.

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 aluminium 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 (see Fernandez-Leborans et al. 2006a).

Epibionts on the surface of the shrimp anatomical units were observed and counted under stereoscopic and light microscopes. Numbers of colonial species were indicated as number of zooids. In order to identify the protozoan epibionts, they were isolated and treated with the silver carbonate technique 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. In order to identify the rotifers, the trophi were analysed using the procedure indicated by R. J. Shiel (University of Adelaide, Australia; personal communication), treating isolated specimens, placed in 10% glycerol/water solution with 2.5% sodium hypochlorite. Measurements 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 determine the epibiont species schemes. Statistical analyses were performed using the Statgraphics and SPSS programs. The tests used were the following: (1) multiple comparison analysis (for differences between distribution of epibiont species, and differences in colonization of right and left anatomical units); (2) principal component analysis (for groups of epibiont species with similar distribution); (3) hierarchical conglomerate analysis (to obtain clusters of anatomical units with similar colonization); (4) variance components (evaluation of

epibiont species versus variation in length and width of basibionts). Epibiosis along the anterioposterior axis of the basibiont was statistically treated in order to analyse the influence of the longitudinal activity gradient on colonization.

Results

Forty colonized specimens of *C. ensifera* were analysed, of which nine were ovigerous females. The epibionts on *Caridina ensifera* were, among the protozoan ciliates, the suctorians *Acineta* Ehrenberg, 1833, *Podophrya* Ehrenberg, 1833, and *Spelaeophrya* Stammer, 1935, the peritrichs *Zoothamnium* Ehrenberg, 1838, *Vorticella* Linnaeus, 1767, and *Cothurnia* Ehrenberg, 1831, and the haptorid *Amphileptus* Ehrenberg, 1830. In addition, there were rotifer epibionts of the genus *Embata* Bryce, 1910.

Epibionts of the genus *Acineta*

The ciliates were triangular in outline or bell-shaped, loricated, and pedunculate. The lorica completely surrounded the cellular body (28.8–78.7 µm long, 26.8–61.4 µm wide). The lorica had a free anterior part over the body enveloping the tentacles (13.2–15.5 µm long). The body (19.2–61.4 µm long, 19.2–49.9 µm wide) had two anterior lobular actinophores protruding on the corners, each with 13–31 capitate tentacles. The central area in the apical surface of the body was depressed. The macronucleus was rounded in shape and centrally located (7.6–15.3 µm long, 7.6–17.3 µm wide). There was a spherical micronucleus located near the macronucleus. The stalk (19.2–26.9 µm long, 5.8–9.6 µm wide) joined the lorica via a cup-like expansion (Table I; Figures 2a, 3, 4).

These ciliates belong to the genus *Acineta* (Lynn and Small 2000). The most distinctive feature of these ciliates was the lorica prolonged anteriorly around the tentacles. The ciliates belong to the species *Acineta sulawesiensis* Fernandez-Leborans et al., 2006. In comparison to ciliates of this species that have been observed previously in the other three lakes of the Malili system, they have a longer stalk, and a lower number of tentacles per actinophore.

Table I. Biometric features of *Acineta sulawesiensis* (measurements in µm; n=80).

	Mean	SD	Minimum	Maximum
Body length	39.55	10.61	19.20	61.44
Body width	35.95	9.72	19.20	49.92
Lorica length	49.78	14.36	28.80	78.72
Lorica width	43.61	10.03	26.88	61.44
Macronucleus length	11.20	2.40	7.68	15.36
Macronucleus width	11.92	2.61	7.68	17.28
Stalk length	21.44	3.08	19.20	26.88
Stalk width	7.13	1.45	5.76	9.60
Contractile vacuole length	6.34	1.30	3.84	7.68
Contractile vacuole width	6.53	1.62	3.84	9.60
Tentacles length	12.07	5.28	5.76	17.28
Lorica thickness	17.28	–	17.28	17.28
Body thickness	15.36	–	15.36	15.36
Length of free anterior part of lorica	14.20	0.78	13.2	15.50
Number of tentacles	26.57	6.63	13.00	31.00

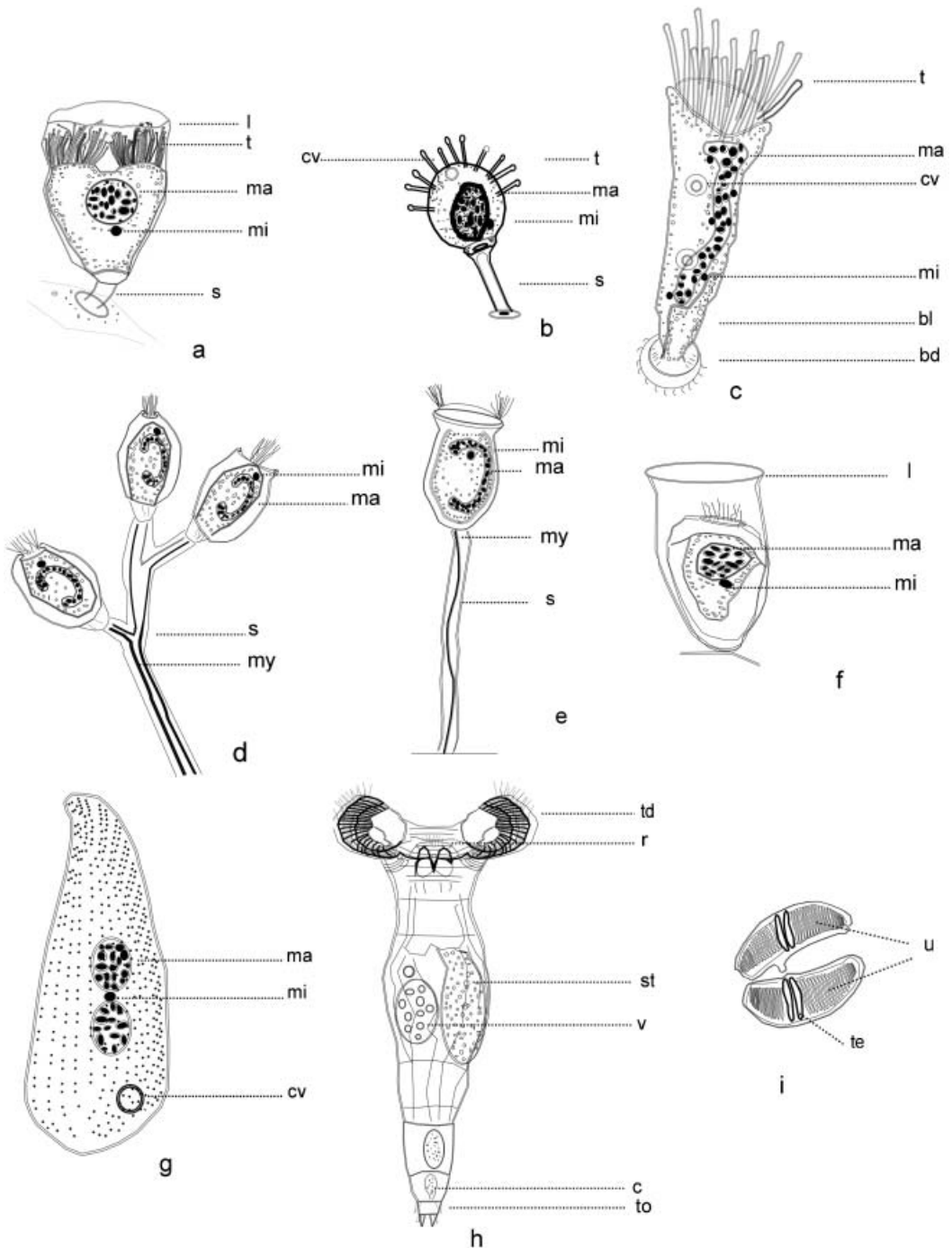
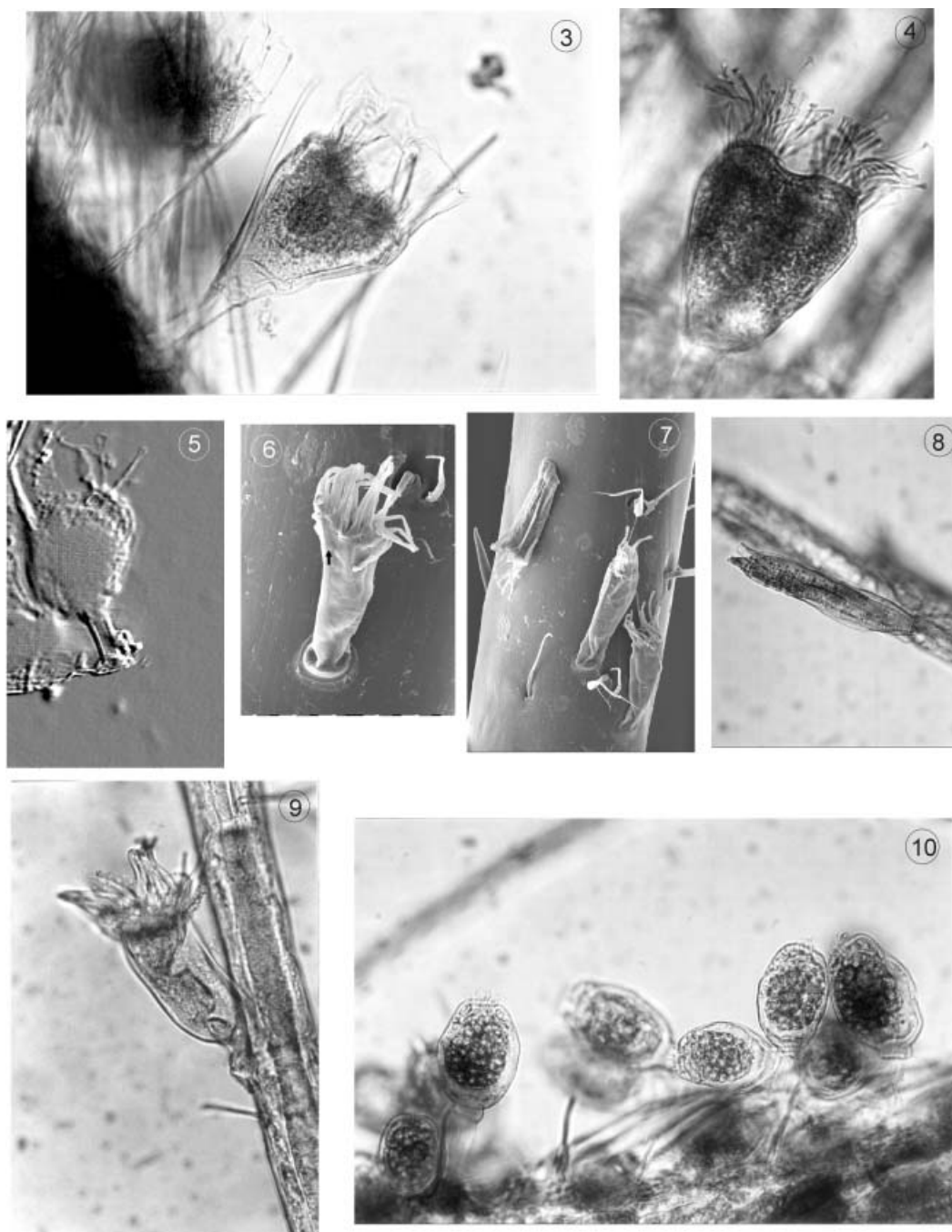


Figure 2. The epibiont species. (a) *Acineta sulawesiensis*; (b) *Podophrya maupasi*; (c) *Spelaeophrya polypoides*; (d) *Zoothamnium intermedium*; (e) *Vorticella globosa*; (f) *Cothurnia compressa*; (g) *Amphileptus fusidens*; (h) *Embata laticeps*; (i) *Embata laticeps*, the trophi. bd, basal disc; bl, basal lorica; c, cloaca; cv, contractile vacuole; l, lorica; ma, macronucleus; mi, micronucleus; my, myoneme; r, rostrum; s, stalk; st, stomach; t, tentacles; td, trochal discs; to, toes; v, vitellarium.



Figures 3–10. (3, 4) *Acineta sulawesiensis* (silver carbonate,  $\times 1070$ ): (3) the macronucleus and the anterior prolongation of the lorica; (4) the actinophores with the tentacles. (5) *Podophrya maupasi* (methyl green,  $\times 792$ ). (6–9) *Spelaeophrya polypoides*: (6) individual showing the basal disc, the tentacles and the pore of the contractile vacuole (arrow) (SEM,  $\times 280$ ); (7) several specimens in their location on the basibiont surface (SEM,  $\times 230$ ); (8) a specimen showing the elongate macronucleus (silver carbonate,  $\times 450$ ); (9) the macronucleus irregular and the inferior part articulate of the body (silver carbonate,  $\times 360$ ). (10) *Zoothamnium intermedium*, a colony showing the stalk and the shape of the zooids (silver carbonate,  $\times 420$ ).



*Epibionts of the genus Podophrya*

The individuals had a characteristic spheroid body (7.6–53.7 µm long, 7.6–32.6 µm wide). In comparison to the body, the stalk can reach a considerable length (15–192 µm long). The cellular body had an external layer. The capitate tentacles (10–15) were spread over the entire surface of the body. The rounded macronucleus (3.8–15.4 µm long) was located excentrically. An oval micronucleus was placed near the macronucleus (Table II; Figures 2b, 5).

The suctorians belong to the genus *Podophrya* (Curds 1986; Lynn and Small 2002). The species most similar to these ciliates was *Podophrya maupasi* Butschli, 1889; they have in common their dimensions, their freshwater habitat, the spherical form of the cellular body, the absence of lorica, tentacles slightly trumpet-shaped at their end, a spherical macronucleus centrally positioned and a thick external layer to the 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.

*Epibionts of the genus Spelaeophrya*

The ciliates were bell- or trumpet-shaped, with the body flattened and covered by a thick pellicle. The body length fluctuated between 48 and 157.4 µm (13.4–28.8 µm wide). The body joined the substrate without a developed stalk, which was sometimes replaced by a basal funnel-shaped area, as a lorica, with a length of 25.7–37.3 µm (maximum width, 19.2–25.7 µm), which in several specimens joined the rest of the body via a constriction. In some specimens this posterior zone of the body seemed to articulate with the anterior area of the body, forming an angle, as Nie and Lu (1945) have indicated. The posterior end of the body was expanded in a circular disc for attachment to the surface of the basibiont. This basal disc was 14.9–32.2 µm in diameter. In the apical area, there were 12–20 tentacles located over this surface; no actinophores were present. Each tentacle was 18–30.9 µm in length. The macronucleus was elongated and arranged alongside the longitudinal axis of the ciliate (24.9–53.7 µm long, 3.8–11.5 µm wide). In several individuals, the macronucleus was considerably flattened, and its anterior part can appear widened. The macronucleus had an anterior section forming a right angle with the rest of the macronucleus in several specimens. There were four to six spherical micronuclei near the macronucleus. In the middle of the body there were one to three contractile vacuoles, the pores of which can be distinguished in the surface of the ciliate. The SEM images did not show the division of the body with a posterior loricated area. The surface of the ciliate was continuous from the apical surface to the basal disk (Table III; Figures 2c, 6–13).

Table II. Biometric features of *Podophrya maupasi* (measurements in µm;  $n=80$ ).

	Mean	SD	Minimum	Maximum
Body length	26.50	11.05	7.68	53.76
Body width	21.60	6.35	7.68	32.64
Macronucleus length	8.45	3.75	3.84	15.36
Macronucleus width	7.68	3.62	3.84	13.44
Stalk length	122.50	95.19	15.36	192.00
Stalk width	5.76	1.36	3.84	7.68
Number of tentacles	12.00	1.6	10.0	15.0

Table III. Biometric features of *Spelaeophrya polypoides* (measurements in  $\mu\text{m}$ ;  $n=80$ ).

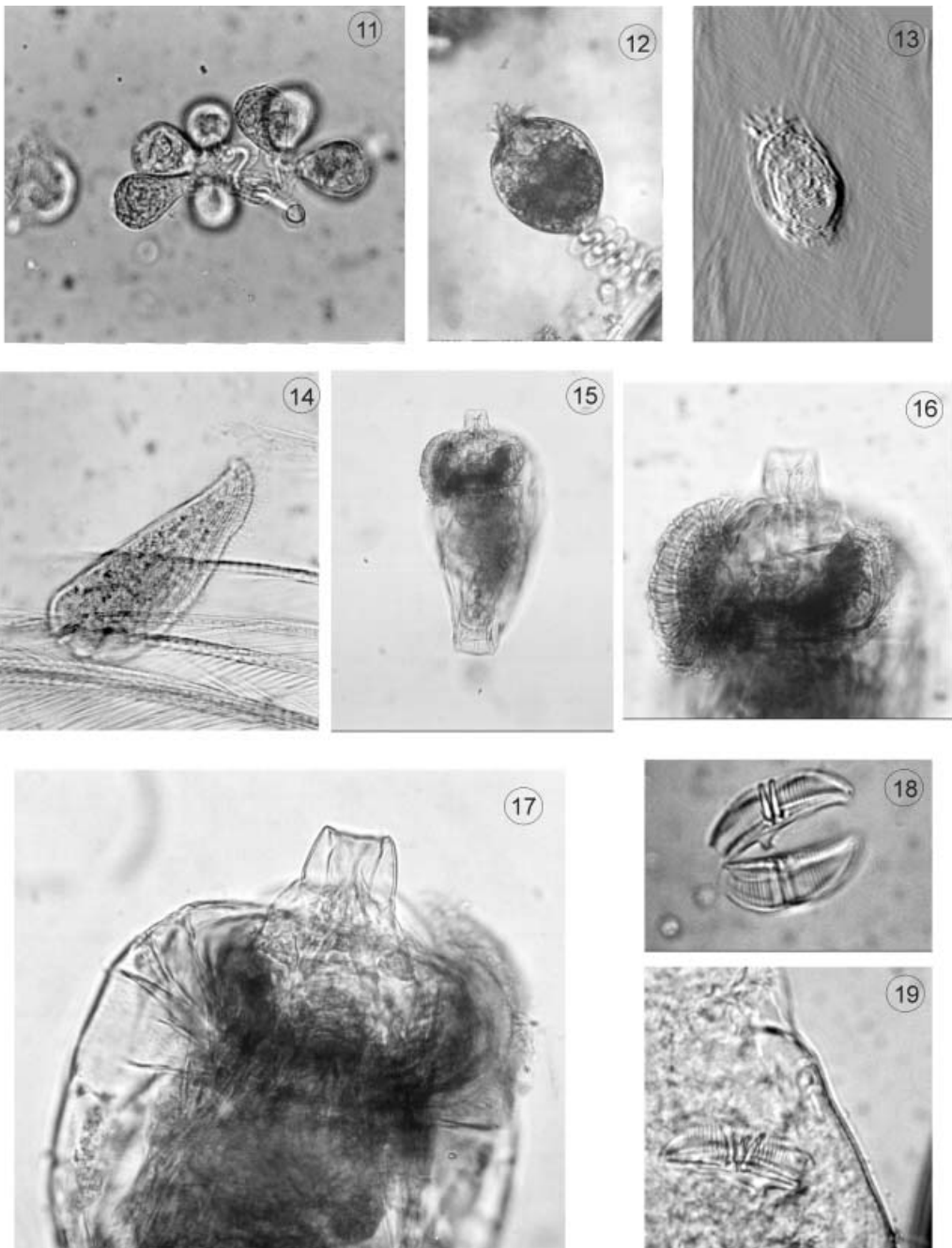
	Mean	SD	Minimum	Maximum
Body length	103.01	22.69	48.00	157.44
Apical width of the body	19.68	4.61	13.44	28.80
Macronucleus length	40.05	9.10	24.96	53.76
Macronucleus width	8.23	2.87	3.84	11.52
Basal lorica length	31.42	5.04	25.75	37.33
Maximum basal lorica width	22.74	2.81	19.22	25.75
Basal disc diameter	21.30	5.92	14.98	32.24
Tentacle length	23.90	5.89	18.02	30.9
Number of micronuclei	4.87	0.83	4.00	6.00
Number of tentacles	16.33	2.77	12	20
Number of tentacles	15.54	2.46	12	20

These ciliates belong to the genus *Spelaeophrya* (Lynn and Small 2002). The trophonts had a trumpet-shaped body with tentacles distributed over the distal end. There are two species of *Spelaeophrya*: *S. polypoides* Daday, 1910 and *S. troglocaridis* Stammer, 1935. According to Matthes et al. (1988) these two species differ in the body shape (divided into a basal hyaline part and another anterior part in *S. polypoides*, apically funnel-shaped in *S. troglocaridis* (edge of the funnel with a seam) and the macronucleus (elongated or wound, apically often bent in *S. polypoides*, band-like, apically thickens in *S. troglocaridis*). The basal zone of the body has been considered as a lorica (Nie and Lu 1945), or as a hyaline zone (Matthes et al. 1988). There are no significant differences with respect to the body size, number of tentacles, or number of micronuclei between the two species. In our specimens, there were individuals with both types of macronucleus, and the presence of a posterior pseudoloricate area seems to be a mechanism that allows the ciliate to bend and which joins the body with the basibiont surface. The external observation of the pellicle did not show any division of the ciliate body when observed by SEM (Figures 6, 7). In summary, both species could be included in the first described, *Spelaeophrya polypoides* Daday, 1910, to which the ciliates observed belong.

*Epibionts of the genus Zoothamnium*

The peritrich ciliates were colonial, with 2–18 zooids linked by a ramified stalk, which contained a contractile myoneme. The body of the zooid was oval, elongated (28.8–76.8  $\mu\text{m}$  long, 23–38.4  $\mu\text{m}$  wide). The macronucleus was C-shaped (3.8–30.7  $\mu\text{m}$  long, 3.8–23  $\mu\text{m}$  wide). The micronucleus was spherical and disposed next to the macronucleus. The peristomal disc was short, approximately half of the maximum body width. The stalk was broad (3.8–28.8  $\mu\text{m}$  wide). This stalk was very diaphanous with a rounded contour. The contractile myoneme (spasmoneme) was located inside the stalk. The width of the stalk increased towards the base of the colony, where it was attached to the basibiont. The stalk joined to the cellular body of the zooid by a cup-shaped structure (suprastylar area), with a longitudinal striation (Table IV; Figures 2d, 14, 15).

These epibionts belong to the genus *Zoothamnium* (Lynn and Small 2000). The ciliates were similar to those of *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).



Figures 11–19. (11) *Zoothamnium intermedium*, area of stalk confluence for attachment to the shrimp surface (silver carbonate,  $\times 400$ ). (12) *Vorticella globosa*, a specimen with the contracted stalk (silver carbonate,  $\times 710$ ). (13) *Cothurnia compressa*, individual showing the lorica (silver carbonate,  $\times 820$ ). (14) *Amphileptus fusidens*, the body shape and the arrangement of the kineties (silver carbonate,  $\times 770$ ). (15–19) *Embata laticeps*: (15) the entire individual showing the trochal discs, rostrum, and toes (methyl green,  $\times 200$ ); (16) the anterior area of the body with the trochal discs and the rostrum (methyl green,  $\times 410$ ); (17) detail of the rostrum (methyl green,  $\times 410$ ); (18, 19) the trophi of the mastax, showing the unci and the teeth ( $\times 520$ ).

Table IV. Biometric features of *Zoothamnium intermedium* (measurements in  $\mu\text{m}$ ;  $n=80$ ).

	Mean	SD	Minimum	Maximum
Body length	47.15	13.72	28.80	76.80
Body width	30.52	5.54	23.04	38.40
Macronucleus length	15.36	9.27	3.84	30.72
Macronucleus width	14.21	7.47	3.84	23.04
Stalk length	84.00	49.50	24.96	163.20
Stalk width	17.28	7.46	3.80	28.80
Contractile vacuole length	6.72	1.11	5.76	7.68
Contractile vacuole width	8.00	1.89	5.76	9.60
Number of individuals per colony	8.00	4.69	2.00	18.00
Number of bends per stalk	4.85	1.46	3.00	8.00

*Epibionts of the genus Vorticella*

The ciliates were solitary and stalked. The body was globulous, and more or less ovoid when contracted (23–46  $\mu\text{m}$  long, 17.3–34.6  $\mu\text{m}$  wide). The macronucleus was C-shaped (13.4–21.1  $\mu\text{m}$  long, 5.8–17.3  $\mu\text{m}$  wide) and laid transversely across the center of the zooid widening at its extremes. A spherical micronucleus was placed 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 (13.4–153.6  $\mu\text{m}$  long, 5.8–19.2  $\mu\text{m}$  wide), contained a contractile myoneme along its entire length and had between two and five bends (Table V; Figures 2e, 16).

These ciliates belong to the genus *Vorticella* (Warren 1986; Lynn and Small 2000). The species most similar to these ciliates was *Vorticella globosa* Ghosh, 1922. They have in common the size and shape of the body; the C-shape and disposition of the macronucleus; the length of the stalk; the freshwater environment; and their being epibiotic (Warren 1986).

*Epibionts of the genus Cothurnia*

The ciliates were loricated, and stalked. The lorica was narrow and elongated, cylindrical and rounded posteriorly (32.6–65.3  $\mu\text{m}$  long, 17.3–28.9  $\mu\text{m}$  wide). The individuals were attached aborally by the stalk. In the posterior end, the lorica was connected through 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 zone. The retracted body (15.4–40.3  $\mu\text{m}$  long, 13.4–21.1  $\mu\text{m}$  wide) occupied almost half of the lorica. The macronucleus was ovoid and located in the anterior half of the

Table V. Biometric features of *Vorticella globosa* (measurements in  $\mu\text{m}$ ;  $n=80$ ).

	Mean	SD	Minimum	Maximum
Body length	35.67	5.52	23.04	46.08
Body width	27.69	4.06	17.28	34.56
Macronucleus length	17.66	3.15	13.44	21.12
Macronucleus width	12.67	4.42	5.76	17.28
Stalk length	43.65	35.42	13.44	153.60
Stalk width	10.88	5.11	5.76	19.20
Number of bends per stalk	5.47	1.92	2.00	10.00

Table VI. Biometric features of *Cothurnia compressa* (measurements in  $\mu\text{m}$ ;  $n=80$ ).

	Mean	SD	Minimum	Maximum
Body length	28.80	7.48	15.36	40.32
Body width	17.58	2.42	13.44	21.12
Lorica length	50.88	9.49	32.64	65.28
Lorica width	23.90	3.08	17.28	28.80
Stalk length	3.84	0.86	1.46	3.84
Stalk width	7.68	0.92	5.28	7.68
Macronucleus length	12.80	3.78	5.76	15.36
Macronucleus width	10.82	2.15	7.68	13.44

body (5.8–15.4  $\mu\text{m}$  long, 7.7–13.4  $\mu\text{m}$  wide). The micronucleus was spherical and situated near the macronucleus. The stalk was short and in several specimens considerably reduced (1.5–3.9  $\mu\text{m}$  long) (Table VI; Figures 2f, 17).

These ciliates belong to the genus *Cothurnia* (Warren and Paynter 1991; Lynn and Small 2000). The ciliates found were similar to those of *Cothurnia compressa* Claparède and Lachmann, 1858 in the elliptical lorica aperture, when viewed from above. The lorica aperture border had 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* as is the size of the contracted zooid. In addition, *C. compressa* has been found in marine environments.

#### *Epibionts of the genus Amphileptus*

The ciliates had a lanceolate-shaped body, laterally compressed (42.2–103.7  $\mu\text{m}$  long, 19.2–49.9  $\mu\text{m}$  wide). There were two oval macronuclei (each 13.4–25  $\mu\text{m}$  long, 5.8–15.4  $\mu\text{m}$  wide). There was a spherical micronucleus located between the macronuclei, 10–12 right somatic kineties and one to four left somatic kineties. A contractile vacuole was located at the posterior end of the body. There were numerous extrusomes located over the surface, each 2.9–8.1  $\mu\text{m}$  long (Table VII; Figures 2g, 18).

These ciliates belong to the genus *Amphileptus* (Lynn and Small 2000). The species most similar to these ciliates was *Amphileptus fusidens* (Kahl, 1926). They have in common the length of the body, the rounded caudal end, and the number of right and left somatic kineties (Song and Wilbert 1989; Lin et al. 2005).

Table VII. Biometric features of *Amphileptus fusidens* (measurements in  $\mu\text{m}$ ;  $n=80$ ).

	Mean	SD	Minimum	Maximum
Body length	71.42	16.52	42.24	103.68
Body width	31.49	8.34	19.20	49.92
First macronucleus length	17.28	5.20	13.44	24.96
First macronucleus width	9.12	4.54	5.76	15.36
Second macronucleus length	16.32	1.11	15.36	17.28
Second macronucleus width	8.64	2.48	5.76	11.52
Extrusome length	5.51	2.63	2.86	8.16
Number of right kineties	11.5	1.77	10.00	14.00
Number of left kineties	2.63	1.06	1.00	4.00

*Epibionts of the genus Embata*

The body of these rotifers, as in other bdelloids, had three parts: head, trunk, and foot. The individuals were 271.8–512.5 µm long and 141–215.3 µm wide. The body was elongate with a narrow stretched foot with four toes visible when they were not retracted. The head was 59.4–85.6 µm long and 115.5–148.4 µm wide. In the head, the corona was composed by two conspicuous ciliated discs, each of 39.6–79.2 µm diameter. The part of the rostrum protruding from the body was 26.4–33 µm long. The mastax had well-developed trochi, with each uncus having two teeth (each 11.2–14.4 µm long). The uncus had a length of 31.9–45.5 µm, and a width of 8–12.8 µm (Table VIII; Figures 2h, 19–23).

The rotifers belong to the genus *Embata* (Segers 2002). They are most similar to *E. laticeps* (Murray, 1905). This has straight spurs, directly posteriorly, a slender body with a transparent integument, a long foot and five segments. The teeth were 2/2 and were 508–635 µm long. It has been found on crustaceans (Koste and Shiel 1986).

*Distribution of the epibionts*

Twenty-five per cent of the infested shrimps were ovigerous females. The number of epibionts per basibiont fluctuated between 14 and 1114 (mean 314.6). Only 0.45% of these epibionts were rotifers, the ciliate protists representing the highest proportion of the mean density of epibionts (Table IX). Among the ciliate epibionts, the species with the highest density were *Zoothamnium intermedium* and *Acineta sulawesiensis*, which represented 94.2% of the mean epibiont density (*Acineta* showed the highest proportion, 59.94%). The other ciliate species accounted for 5.33% of the mean epibiont density on the shrimps (Table X).

Table XI shows the numbers of epibionts on each anatomical unit of *C. ensifera*. Antennulae, antennae, maxillipeds, and uropods were the units with the highest mean numbers of epibionts. Table XI includes the numbers of protozoan species on the anatomical units of the shrimp. The numbers of each epibiont species on the different anatomical units of *C. ensifera* can be seen in Table XII. The most abundant species, *Z. intermedium* and *A. sulawesiensis*, were also the most widely distributed on the surface of the shrimp. The rotifer, although occurring in low numbers, was widely distributed on the basibiont.

The statistical comparison between the distributions of the epibiont species on the body of *C. ensifera* indicated a significant difference between the species ( $F$ , 11.05;  $P \leq 0.05$ ). The Principal Component Analysis performed using the mean numbers of the epibiont species on the anatomical units of the shrimp showed, in the plot of the two first principal

Table VIII. Biometric features of *Embata laticeps* (measurements in µm;  $n=80$ ).

	Mean	SD	Minimum	Maximum
Body length	287.00	28.80	271.75	512.50
Body width	121.98	15.34	141.00	215.25
Diameter of ciliated disc	57.78	11.27	39.58	79.17
Head length	69.13	11.29	59.37	85.77
Head width	125.61	10.43	115.45	148.44
Length of the rostrum protruding the body	28.54	2.20	26.39	32.98
Uncus length	33.54	3.28	31.88	41.45
Uncus width	8.84	1.64	7.97	12.75
Teeth length	12.31	0.95	11.16	14.35

Table IX. Length and width of the specimens of *Caridina ensifera* analysed and distribution of the epibionts on the crustacean ( $n=40$ ).

	Mean	SD	Minimum	Maximum
Length of the shrimp (mm)	24.19	4.65	13.00	33.00
Width of the shrimp (mm)	3.90	0.78	2.00	5.00
Length of ovigerous female shrimp (mm)	25.40	3.91	19.00	29.00
Width of ovigerous female shrimp (mm)	4.60	0.55	4.00	5.00
Number of protozoans per shrimp	313.19	305.16	12.00	1110.00
Number of protozoans per ovigerous female shrimp	662.20	266.05	429.00	1110.00
Number of rotifers per shrimp	1.43	1.75	0.00	6.00
Number of rotifers per ovigerous female shrimp	3.40	2.30	1.00	6.00
Number of epibionts per shrimp	314.62	306.07	14.00	1114.00
Number of epibionts per ovigerous shrimp	665.60	266.59	430.00	1114.00

components, two clusters, one with *Amphileptus fusidens*, *Vorticella globosa*, and *Spelaeophrya polypoides*, and another including *Z. intermedium*, *A. sulawesiensis*, *Podophrya maupasi*, and *Embata laticeps*. This second cluster included the epibiont species that were most common on the basibiont; the first cluster contained species that were more scarce. The ciliate *Cothurnia compressa* was separate from both clusters. This may be explained by its presence on the end of the basibiont body in low densities (Figure 20).

The Hierarchical Conglomerate Analysis produced a dendrogram using the mean numbers of the different epibiont species on the anatomical units of the shrimp. The units appeared grouped in five clusters (Figure 21). A cluster corresponded to the antennulae, antennae, and uropods (18.75% of the anatomical units). These units had a high number of epibionts (mean 15.80 epibionts per unit). The second cluster included 46.88% of the anatomical units (rostrum, eyes, second right pereopod, third, fourth and fifth pereopods, fourth and fifth pleopods, and telson); these units showed the lowest number of epibionts (mean 2.87 epibionts per unit). The third cluster consisted of the rest of pleopods (first, second and third pleopods, 18.75% of the units) which had a moderate number of epibionts (mean 8.27 per unit). In the fourth cluster were the first and left second

Table X. Number of different epibionts on *Caridina ensifera* ( $n=40$ ).

Density	Mean	SD	Minimum	Maximum
<i>Zoothamnium intermedium</i>	107.81	154.66	0	691
<i>Z. intermedium</i> per ovigerous female shrimp	284.60	240.67	79	691
<i>Acineta sulawesiensis</i>	188.62	187.22	1	585
<i>A. sulawesiensis</i> per ovigerous female shrimp	333.80	26.49	297	362
<i>Podophrya maupasi</i>	2.48	4.61	0	18
<i>P. maupasi</i> per ovigerous female shrimp	6.40	7.57	0	18
<i>Cothurnia compressa</i>	11.14	16.40	0	49
<i>C. compressa</i> per ovigerous female shrimp	31.80	19.78	3	49
<i>Vorticella globosa</i>	1.33	4.80	0	22
<i>V. globosa</i> per ovigerous female shrimp	1.00	1.41	0	3
<i>Spelaeophrya polypoides</i>	0.67	1.20	0	4
<i>S. polypoides</i> per ovigerous female shrimp	1.40	1.52	0	3
<i>Amphileptus fusidens</i>	1.14	2.82	0	13
<i>A. fusidens</i> per ovigerous female shrimp	3.00	5.61	0	13
<i>Embata laticeps</i>	1.43	1.75	0	6
<i>E. laticeps</i> per ovigerous female shrimp	3.40	2.30	1	6

Table XI. Distribution of the epibionts on the different anatomical units of *Caridina ensifera* (the number of protozoan species is given below) ( $n=40$ ).

Anatomical unit	Mean	SD	Minimum	Maximum
Rostrum	4.62	12.14	0	46
	4.57	12.16	0	46
Left ocular orbit	0.76	1.22	0	5
	0.71	1.23	0	5
Right ocular orbit	2.24	5.27	0	22
	2.24	5.27	0	22
Left antennule	17.29	20.82	0	68
	17.29	20.82	0	68
Right antennule	15.19	18.73	0	56
	15.19	18.73	0	56
Left antenna	16.29	21.09	0	79
	16.19	21.02	0	79
Right antenna	15.76	20.27	0	84
	15.62	20.19	0	84
Left maxilliped	50.24	55.67	0	211
	50.14	55.57	0	211
Right maxilliped	49.14	57.83	1	204
	49.05	57.83	1	204
Left first pereopod	12.57	19.61	0	70
	12.48	19.52	0	70
Right first pereopod	8.67	12.46	0	48
	8.67	12.46	0	48
Left second pereopod	6.67	8.11	0	32
	6.62	7.95	0	31
Right second pereopod	4.81	9.12	0	35
	4.81	9.12	0	35
Left third pereopod	2.62	3.72	0	14
	2.52	3.76	0	14
Right third pereopod	4.05	7.74	0	26
	4.00	7.76	0	26
Left fourth pereopod	2.86	8.01	0	36
	2.86	8.01	0	36
Right fourth pereopod	2.19	4.19	0	15
	2.19	4.19	0	15
Left fifth pereopod	2.05	4.61	0	16
	2.05	4.61	0	16
Right fifth pereopod	0.38	1.53	0	7
	0.38	1.53	0	7
Left first pleopod	6.81	14.29	0	55
	6.71	13.95	0	53
Right first pleopod	9.19	13.48	0	47
	9.19	13.48	0	47
Left second pleopod	8.33	25.07	0	116
	8.33	25.07	0	116
Right second pleopod	10.71	25.76	0	116
	10.62	25.79	0	116
Left third pleopod	6.95	13.56	0	58
	6.90	13.55	0	58
Right third pleopod	7.90	15.80	0	60
	7.86	15.68	0	60
Left fourth pleopod	4.19	7.84	0	29
	4.19	7.84	0	29



Table XI. Continued.

Anatomical unit	Mean	SD	Minimum	Maximum
Right fourth pleopod	3.90	8.80	0	39
	3.86	8.82	0	39
Left fifth pleopod	2.10	3.97	0	17
	2.10	3.97	0	17
Right fifth pleopod	2.81	5.12	0	18
	2.71	5.00	0	17
Telson	3.90	4.24	0	13
	3.90	4.24	0	13
Left uropod	16.76	17.51	0	52
	16.67	17.36	0	52
Right uropod	13.90	19.29	0	61
	13.86	19.17	0	60

pereiopods (9.38% of the units), with a mean of 9.26 epibionts per unit. The fifth cluster corresponds to the maxillipeds (6.25%), the units with the highest infestation (mean 49.6 epibionts per unit).

The dendrogram obtained with the mean numbers of the epibiont species on the anatomical units of the shrimp showed four clusters, each corresponding to two species, which followed a similar pattern of distribution: *Z. intermedium*–*E. laticeps*, *P. maupasi*–*A. sulawesiensis*, *S. polypoides*–*A. fusidens*, and *C. maupasi*–*V. globosa* (Figure 22).

With respect to the sum of numbers on the anatomical units of *C. ensifera*, the species contributing most to the total variance of the length and width of the shrimp was *A. sulawesiensis*. The sum of epibionts on each anatomical unit of the different shrimps showed that, in relation to the epibiosis, the unit most contributing with the maximum variance was the right antennula. Its contribution represented 75% of the total variation in length of shrimps. With respect to the width, the maximum variance corresponded to the left antennula. Its contribution represented 60.53% of the total variation in width of shrimps.

The Comparison Analysis of the epibiosis on left and right units indicated that there was no significant difference between these units when considered as pairs. On the other hand, the distribution is similar in antennulae, antennae, maxillipeds, first, second, third and fifth pereiopods, first, second, third and fourth pleopods, and uropods, and these showed a significant correlation between left and right appendages. The Multiple Comparison Analysis between the units of the left side of the shrimp indicated a significant difference among them ( $F$ , 8.14;  $P \leq 0.05$ ). Also, there was a significant difference with respect to the right side ( $F$ , 7.40;  $P \leq 0.05$ ).

#### *Distribution throughout the longitudinal axis of Caridina ensifera*

Figure 23 shows the mean proportion of different epibiont species and the total epibiont mean proportion along the anteroposterior axis of the shrimp. Anatomical units were considered in five groups (rostrum, antennae, antennulae, and eyes; maxillipeds; pereiopods; pleopods; uropods and telson). *Z. intermedium* was distributed mainly on the posterior half of the body, especially on the pleopods where it represented 50.48% of the epibionts. Also, it was found attached to the pereiopods (18.3%) and the maxillipeds (15.4%). In contrast, *A. sulawesiensis* was more abundant on the anterior part of the shrimp, and 73.90% of the epibionts were located on the maxillipeds (43.2%), rostrum, antennae,

Table XII. Number of each epibiont species on the different anatomical units of *Caridina ensifera* (mean  $\pm$  SD; minimum–maximum) ( $n=40$ ).

Anatomical unit	<i>Acineta sulawesiensis</i>	<i>Vorticella globosa</i>	<i>Podophrya maupasi</i>	<i>Cothurnia compressa</i>	<i>Zoothamnium intermedium</i>	<i>Spealophrya polypoides</i>	<i>Amphileptus fusidens</i>	<i>Emabata laticeps</i>
Rostrum	3.05 $\pm$ 8.43 (0–35)	0.10 $\pm$ 0.44 (0–2)	–	0.05 $\pm$ 0.22 (0–1)	1.29 $\pm$ 5.89 (0–27)	–	0.10 $\pm$ 0.30 (0–1)	0.05 $\pm$ 0.22 (0–1)
Left ocular orbit	0.10 $\pm$ 0.44 (0–2)	0.05 $\pm$ 0.22 (0–1)	0.05 $\pm$ 0.22 (0–1)	–	0.52 $\pm$ 1.21 (0–5)	–	–	0.05 $\pm$ 0.22 (0–1)
Right ocular orbit	0.29 $\pm$ 0.78 (0–3)	–	–	–	1.95 $\pm$ 5.06 (0–22)	–	–	–
Left antennule	15.19 $\pm$ 19.78 (0–68)	0.10 $\pm$ 0.44 (0–2)	–	0.14 $\pm$ 0.48 (0–2)	1.43 $\pm$ 2.94 (0–11)	0.29 $\pm$ 0.90 (0–4)	0.14 $\pm$ 0.36 (0–1)	–
Right antennule	13.86 $\pm$ 16.72 (0–47)	0.05 $\pm$ 0.22 (0–1)	–	0.29 $\pm$ 0.96 (0–4)	0.10 $\pm$ 0.44 (0–2)	–	–	–
Left antenna	13.05 $\pm$ 18.80 (0–74)	–	–	0.76 $\pm$ 1.41 (0–5)	2.14 $\pm$ 4.62 (0–18)	0.10 $\pm$ 0.30 (0–1)	0.05 $\pm$ 0.22 (0–1)	0.10 $\pm$ 0.30 (0–1)
Right antenna	12.48 $\pm$ 17.07 (0–72)	–	–	0.76 $\pm$ 2.30 (0–9)	2.10 $\pm$ 3.62 (0–11)	0.14 $\pm$ 0.65 (0–3)	0.14 $\pm$ 0.48 (0–2)	0.14 $\pm$ 0.48 (0–2)
Left maxilliped	40.10 $\pm$ 44.51 (0–144)	–	0.86 $\pm$ 3.93 (0–18)	–	9.10 $\pm$ 16.86 (0–67)	–	–	0.10 $\pm$ 0.44 (0–2)
Right maxilliped	41.29 $\pm$ 54.08 (0–204)	–	0.33 $\pm$ 1.06 (0–4)	–	7.33 $\pm$ 13.19 (0–45)	–	0.10 $\pm$ 0.30 (0–1)	0.10 $\pm$ 0.44 (0–2)
Left first pereopod	6.57 $\pm$ 12.43 (0–53)	–	–	–	5.81 $\pm$ 12.50 (0–48)	0.05 $\pm$ 0.22 (0–1)	0.05 $\pm$ 0.22 (0–1)	0.14 $\pm$ 0.36 (0–1)
Right first pereopod	5.38 $\pm$ 11.01 (0–39)	–	0.24 $\pm$ 0.89 (0–4)	–	3.05 $\pm$ 5.30 (0–19)	–	–	–
Left second pereopod	4.10 $\pm$ 5.74 (0–21)	–	–	–	2.52 $\pm$ 4.47 (0–15)	–	–	0.05 $\pm$ 0.22 (0–1)
Right second pereopod	2.14 $\pm$ 4.53 (0–19)	–	0.10 $\pm$ 0.44 (0–2)	–	2.57 $\pm$ 5.74 (0–20)	–	–	–
Left third pereopod	1.95 $\pm$ 3.34 (0–13)	–	–	–	0.57 $\pm$ 1.36 (0–6)	–	–	0.10 $\pm$ 0.44 (0–2)
Right third pereopod	0.86 $\pm$ 2.41 (0–11)	–	0.05 $\pm$ 0.22 (0–1)	–	3.05 $\pm$ 7.33 (0–26)	–	–	0.05 $\pm$ 0.22 (0–1)
Left fourth pereopod	1.62 $\pm$ 4.25 (0–18)	0.43 $\pm$ 1.96 (0–9)	–	–	0.76 $\pm$ 1.95 (0–8)	–	–	–
Right fourth pereopod	1.52 $\pm$ 2.80 (0–10)	0.05 $\pm$ 0.22 (0–1)	–	–	0.62 $\pm$ 2.40 (0–11)	–	–	–

Table XII. Continued.

Anatomical unit	<i>Acineta sulawesiensis</i>	<i>Vorticella globosa</i>	<i>Podophrya maupasi</i>	<i>Cothurnia compressa</i>	<i>Zoothamnium intermedium</i>	<i>Spealophrya polypoides</i>	<i>Amphileptus fusidens</i>	<i>Emabata laticeps</i>
Left fifth pereopod	$0.38 \pm 1.53$ (0–7)	–	–	–	$1.67 \pm 3.90$ (0–15)	–	–	–
Right fifth pereopod	$0.38 \pm 1.53$ (0–7)	–	–	–	–	–	–	–
Left first pleopod	$0.57 \pm 1.40$ (0–6)	–	–	–	$6.10 \pm 13.92$ (0–53)	$0.05 \pm 0.22$ (0–1)	–	$0.10 \pm 0.44$ (0–2)
Right first pleopod	$1.43 \pm 2.60$ (0–11)	–	–	$0.10 \pm 0.44$ (0–2)	$7.62 \pm 13.08$ (0–44)	–	$0.05 \pm 0.22$ (0–1)	–
Left second pleopod	$0.57 \pm 1.36$ (0–5)	–	–	$0.14 \pm 0.48$ (0–2)	$7.48 \pm 24.84$ (0–114)	–	$0.05 \pm 0.22$ (0–1)	–
Right second pleopod	$0.52 \pm 1.63$ (0–7)	–	$0.33 \pm 1.53$ (0–7)	$0.14 \pm 0.48$ (0–2)	$9.62 \pm 24.57$ (0–109)	–	–	$0.10 \pm 0.44$ (0–2)
Left third pleopod	$0.86 \pm 1.90$ (0–8)	–	–	$0.14 \pm 0.48$ (0–2)	$5.90 \pm 13.46$ (0–58)	–	–	$0.05 \pm 0.22$ (0–1)
Right third pleopod	$0.33 \pm 0.91$ (0–3)	$0.05 \pm 0.22$ (0–1)	–	–	$7.52 \pm 15.74$ (0–60)	–	–	$0.05 \pm 0.22$ (0–1)
Left fourth pleopod	$0.71 \pm 0.71$ (0–7)	–	–	–	$3.48 \pm 7.98$ (0–29)	–	–	–
Right fourth pleopod	$0.48 \pm 1.54$ (0–7)	–	–	$0.19 \pm 0.51$ (0–2)	$3.19 \pm 8.63$ (0–38)	–	–	$0.05 \pm 0.22$ (0–1)
Left fifth pleopod	$0.62 \pm 1.83$ (0–8)	–	–	$0.76 \pm 2.30$ (0–9)	$0.67 \pm 1.56$ (0–6)	$0.05 \pm 0.22$ (0–1)	–	–
Right fifth pleopod	$0.10 \pm 0.30$ (0–1)	–	$0.14 \pm 0.65$ (0–3)	–	$2.33 \pm 4.85$ (0–17)	–	$0.10 \pm 0.30$ (0–1)	$0.10 \pm 0.30$ (0–1)
Telson	$0.33 \pm 1.11$ (0–5)	$0.29 \pm 1.31$ (0–6)	$0.29 \pm 1.31$ (0–6)	–	$2.62 \pm 3.83$ (0–12)	–	$0.38 \pm 1.75$ (0–8)	–
Left uropod	$8.14 \pm 11.78$ (0–44)	–	–	$5.33 \pm 10.91$ (0–33)	$3.19 \pm 5.14$ (0–16)	–	–	$0.10 \pm 0.30$ (0–1)
Right uropod	$9.67 \pm 16.37$ (0–60)	$0.24 \pm 1.09$ (0–5)	$0.10 \pm 0.44$ (0–2)	$2.33 \pm 5.15$ (0–21)	$1.52 \pm 5.02$ (0–23)	–	–	$0.05 \pm 0.22$ (0–1)

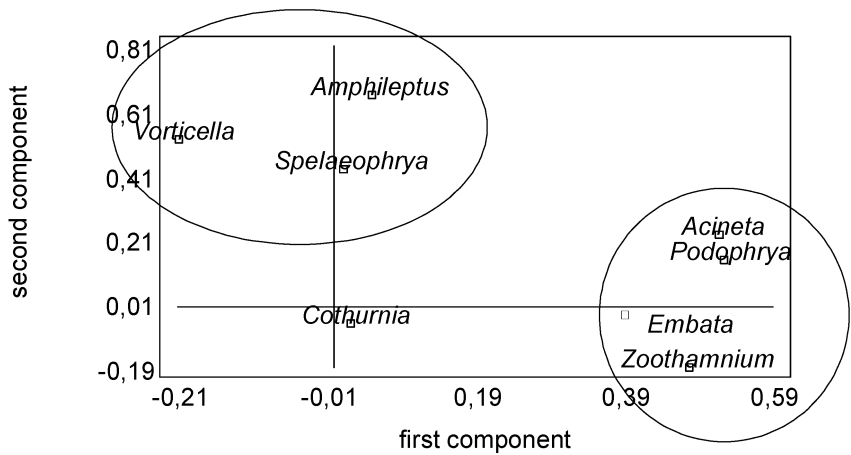


Figure 20. Two first principal components of the Principal Component Analysis performed using the mean density of epibionts on each anatomical unit of the different shrimps analysed.

antennulae, and eyes. *C. compressa* and *V. globosa* were more numerous towards the posterior end of the body, where they accounted for 68.8 and 39% of epibionts, respectively, although *V. globosa* was remarkably numerous on the pereipods (35.3% of the epibionts). *S. polypoides* was more abundant on the anterior part of the body (rostrum, antennae, antennulae, and eyes) (77.9%). *P. maupasi* mainly colonized the maxillipeds, and *A. fusidens* the ends of the body, while *E. laticeps* was distributed on the anterior end, pereipods, and pleopods. The epibiont community was distributed following a pattern in which the species occupied the places with behaviour of ensemble, with each species showing a distinctive distribution along the basibiont body. There was no significant correlation among the epibiont species, but a significant difference among them ( $F, 5.98$ ;  $P \leq 0.05$ ). The total count data indicated that no zone on the anteroposterior axis of the shrimp showed a remarkable difference in colonization; the areas fluctuated between

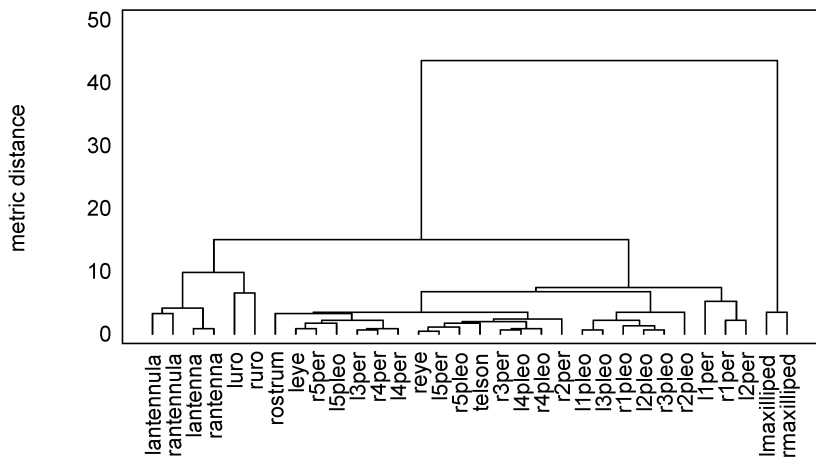


Figure 21. Dendrogram of the Hierarchical Cluster Analysis (anatomical units) performed using the mean densities of epibionts on the different anatomical units of the shrimps analysed (metric distance: City Block (Manhattan); method: Ward).

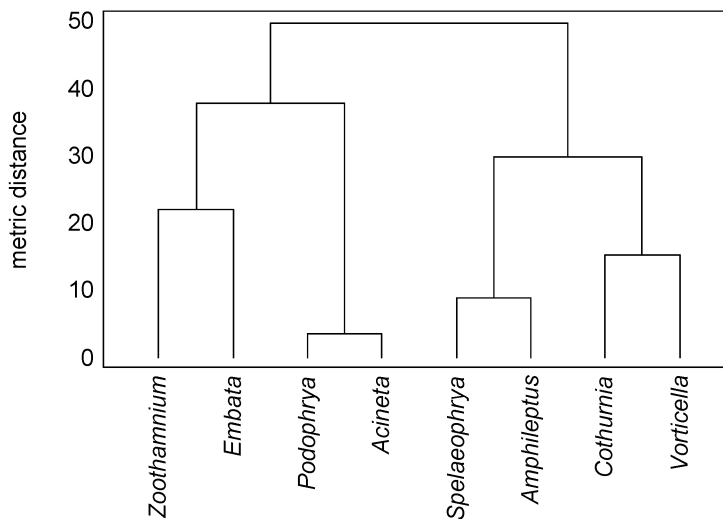


Figure 22. Dendrogram of the Hierarchical Cluster Analysis (epibiont species) performed using the mean densities of epibionts on the different anatomical units of the shrimps analysed (metric distance: City Block (Manhattan); method: Ward).

11.02% on the posterior end and 31.67% on the maxillipeds. The anterior region (rostrum, antennae, antennulae, eyes, and maxillipeds) of the basibiont accounted for 54.37% of the colonization. Pereiopods, pleopods, uropods, and telson accounted for 45.63% of the colonization.

The distribution of the epibiont species on the different body areas along the longitudinal axis of *C. ensifera* is shown in Figure 24. As in the distribution throughout the longitudinal axis in five groups of anatomical units of the shrimp, here there was a significant difference between the distribution of the different epibiont species ( $F$ , 5.07;  $P \leq 0.05$ ).

## Discussion

Forty colonized specimens of *C. ensifera* were analysed, of which nine were ovigerous females. The protozoan epibiont species found (*Acineta sulawesiensis*, *Podophrya maupasi*, *Spelaeophrya polypoides*, *Zoothamnium intermedium*, *Vorticella globosa*, *Cothurnia compressa*, and *Amphileptus fusidens*) have not been recorded formerly as epibionts on *Caridina ensifera*, although species of the genera *Acineta*, *Podophrya*, *Zoothamnium*, *Vorticella*, and *Cothurnia* had previously been observed as epibionts on crustaceans (Morado and Small 1995; Fernandez-Leborans and Tato-Porto 2000a, 2000b; Fernandez-Leborans 2004). The ciliate species found belong to the genera *Acineta*, *Cothurnia*, *Zoothamnium*, *Vorticella*, and *Podophrya* and have only recently been observed as epibionts on *Caridina lanceolata* (Fernandez-Leborans et al. 2006a). *Acineta tuberosa* Ehrenberg, 1833, *Thuricola elegans* Biernacka, 1963, *Cothurnia compressa*, *Vorticella campanulata* (Kahl, 1933), *Opercularia coarctata* (Claparède and Lachmann, 1858), and *Zoothamnium* sp. have been found on several *Caridina* species from Sulawesi (Fernandez-Leborans et al. 2006b). Table XIII lists the epibiont species found in the species of *Caridina* from Sulawesi. The suctorian species *Spelaeophrya polypoides* has been found previously on *Caridina* sp. in Chungking (China) (Nie and Lu 1945), on *Palaemonetes antennarius* (Milne Edwards, 1837) and *Atyaephyra desmaresti* (Millet, 1831) (Europe), and on *Xiphocaridina* Bouvier, 1909 (Africa and Asia)

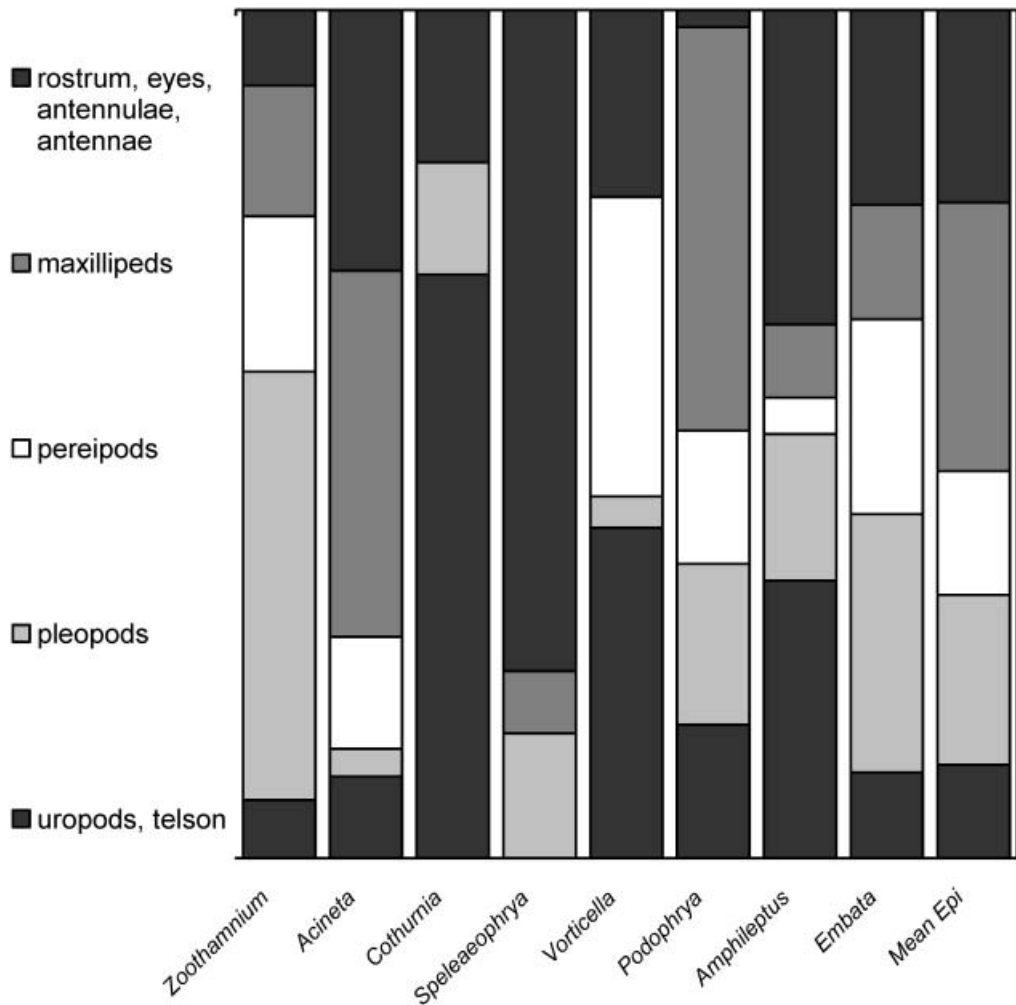


Figure 23. Distribution of each epibiont species (mean densities) and total mean density of epibionts, along the anteroposterior axis of *Caridina ensifera*. Anatomical units are considered in five groups.

(Daday 1910; Nozawa 1938; Hadži 1940). Species similar to *S. polypoides* and *S. troglocaridis* have been described from the cave shrimp *Troglocaris schmidtii* Dormitzer, 1853 (Stammer 1935; Matjašič 1956; Matthes et al. 1988). The species of the genus *Amphileptus* have never been previously found as epibionts on crustaceans, although they are not typical sessile ciliates and therefore, they should be considered as ciliates of the fauna associated with *C. ensifera*. Rotifers are well-known as epibionts or as living in close association with other organisms, but little is known of the types of relationships involved (May 1989). Seisonidae, Monogononta, and Bdelloidea include epizoic and parasitic species associated with Protozoa, Porifera, Rotifera, Annelida, Mollusca, Bryozoa, Echinodermata, Mollusca, Crustacea, and Vertebrata. The rotifer species found in this study, *Embata laticeps*, has been found previously on *Asellus aquaticus* (Linnaeus, 1758) and *Gammarus pulex* (Linnaeus, 1758). Other rotifers are epizoic on diverse freshwater crustacea, as *Daphnia* Muller, 1785, *Asellus* Geoffroy, 1762, *Gammarus* Fabricius, 1775 (May 1989), or decapods

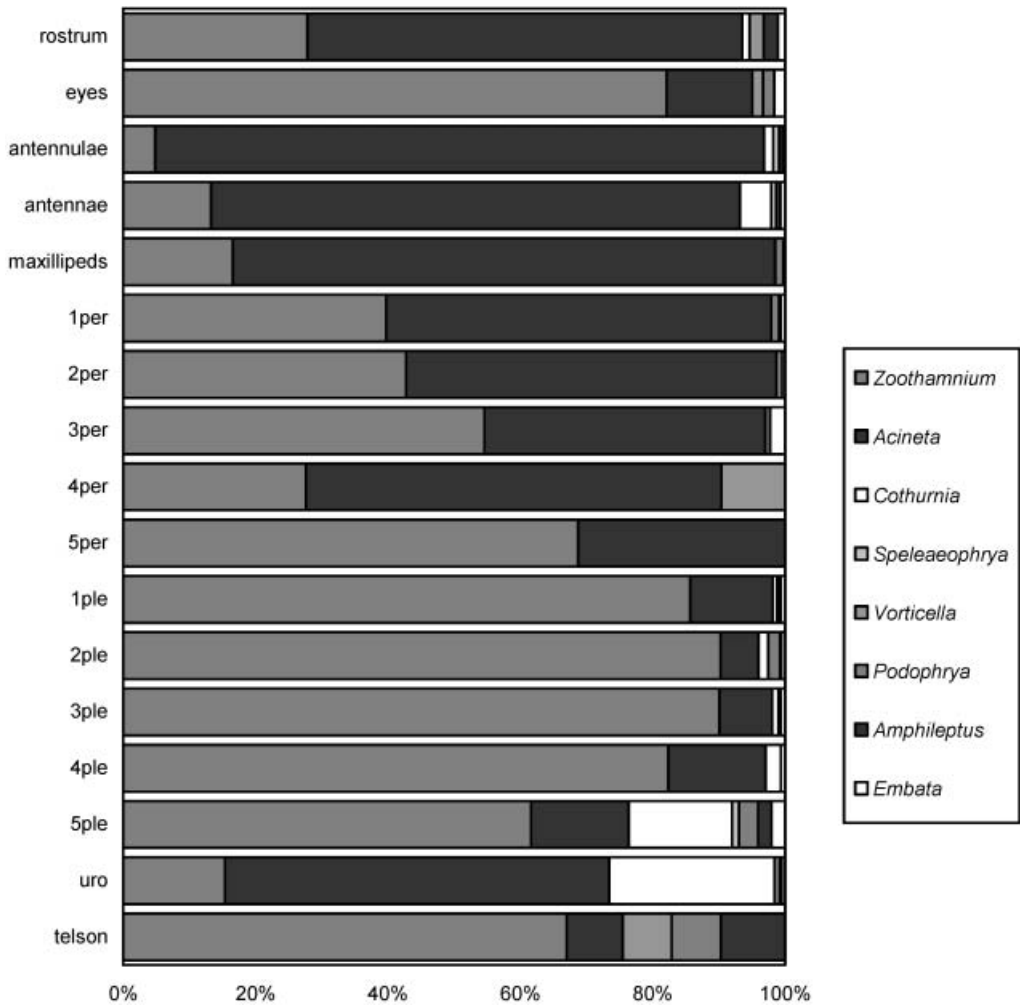


Figure 24. Distribution of each epibiont species (mean densities) along the anterioposterior axis of *Caridina ensifera*. Anatomical units are considered individually. per, pereopod; ple, pleopod; uro, uropod.

(*Austropotamobius* Skorikow, 1908, *Astacus* Fabricius, 1775, *Potamon* Savigny, 1816, *Chasmagnathus* De Haan, 1835) (Hauer 1926, 1959; Carlin 1939; Wulfert 1957; Mañé-Garzón and Montero 1973; Fontaneto et al. 2004). Table XIV summarizes the recorded presence of rotifer species on crustacea. Excepting *Spelaeophrya polypoides*, *E. laticeps* was the epibiont species with the lowest maximum abundance, perhaps due to its relative higher biomass in comparison to other epibionts. It was scarcely present along the shrimp from the antennae to the uropods. As in the case of *Gammarus pulex* and *Asellus aquaticus*, the rotifers do not appear to cause any harm to their basibiont and are generally considered as epizoans, obtaining transport from the association (May 1989). Also, they could feed on the organic matter treated by the host, especially on locations such as the maxillipeds and uropods.

The epibiont species observed are similar to others found as epibionts or as free-living ciliates. However, in several cases, they exhibit peculiar characteristics, which may

Table XIII. List of epibionts found on *Caridina* from Sulawesi (Fernandez-Leborans et al. 2006a, 2006b, and data from this study; some species names have been revised from Fernandez-Leborans et al. 2006a, 2006b).

Taxon	Locality	<i>Caridina</i> basibiont
Ciliate epibionts		
<i>Acineta sulawesiensis</i> Fernandez-Leborans, Zitzler, and Gabilondo, 2006	Malili lakes, Lake Towuti, SW shore	<i>C. lanceolata</i>
	Malili lakes, Lake Matano, S shore	<i>C. lanceolata</i>
	Malili lakes, Lake Mahalona, NW shore	<i>C. lanceolata</i>
	Lake Poso, S shore	<i>C. ensifera</i>
<i>Acineta tuberosa</i> Ehrenberg, 1833	Malili lakes, Lake Towuti, N shore	<i>C. sp. 1</i>
	Malili lakes, Lake Towuti, Loeha Island, S shore	<i>C. lanceolata</i>
	Malili lakes, Lake Towuti, E shore	<i>C. lanceolata</i>
	Malili lakes, Lake Towuti, W shore	<i>C. lingkonae</i>
	Malili lakes, Petea River	<i>C. loehae</i>
	Malili lake system, Lake Masapi	<i>C. masapi</i>
	South Sulawesi, Tarrak River	<i>C. sp. 2</i>
	South Sulawesi, Maros karst, Bantimurung	<i>C. typus</i>
	Lake Poso, S shore	<i>C. ensifera</i>
<i>Amphileptus fusidens</i> (Kahl, 1926)	Lake Poso, S shore	<i>C. ensifera</i>
<i>Cothurnia compressa</i> Claparède and Lachmann, 1858	Malili lakes, Lake Towuti, Loeha Island, S shore	<i>C. lanceolata</i>
	Malili lakes, Lake Towuti, E shore	<i>C. lanceolata</i>
	Malili lakes, Lake Towuti, W shore	<i>C. lingkonae</i>
	Malili lakes, Petea River	<i>C. loehae</i>
	Malili lakes, Lake Masapi	<i>C. masapi</i>
	South Sulawesi, Maros karst, Bantimurung	<i>C. typus</i>
	Malili lakes, Lake Towuti, SW shore	<i>C. lanceolata</i>
	Malili lakes, Lake Matano, S shore	<i>C. lanceolata</i>
	Malili lakes, Lake Mahalona, NW shore	<i>C. lanceolata</i>
	Malili lakes, Lake Matano, S shore	<i>C. lanceolata</i>
<i>Epistylis coronata</i> Nusch, 1970	Malili lakes, Lake Mahalona, NW shore	<i>C. lanceolata</i>
	Malili lakes, Petea River	<i>C. loehae</i>
	South Sulawesi, Maros karst, Bantimurung	<i>C. typus</i>
<i>Opercularia coarctata</i> (Claparède and Lachmann, 1858)	Malili lakes, Lake Mahalona, NW shore	<i>C. lanceolata</i>
	Lake Poso, S shore	<i>C. ensifera</i>
<i>Podophrya maupasi</i> Butschli, 1889	Malili lakes, Lake Mahalona, NW shore	<i>C. lanceolata</i>
<i>Thuricola elegans</i> Biernacka, 1963	Malili lakes, Petea River	<i>C. loehae</i>
	Lake Poso, S shore	<i>C. ensifera</i>
<i>Spelaeophrya polypoides</i> Daday, 1910	Lake Poso, S shore	<i>C. ensifera</i>
<i>Vorticella globosa</i> Ghosh, 1922	Lake Poso, S shore	<i>C. ensifera</i>
<i>Vorticella campanulata</i> (Kahl, 1933)	Malili lakes, Lake Matano, S shore	<i>C. lanceolata</i>
	Malili lakes, Lake Mahalona, NW shore	<i>C. lanceolata</i>
	Malili lakes, Lake Towuti, Loeha Island, S shore	<i>C. lanceolata</i>
	Malili lakes, Petea River	<i>C. loehae</i>
	South Sulawesi, Tarrak River	<i>C. sp. 2</i>
<i>Zoothamnium intermedium</i> Precht, 1935	Lake Poso, S shore	<i>C. ensifera</i>
<i>Zoothamnium</i> sp.	Malili lakes, Lake Towuti, N shore	<i>C. sp. 1</i>
	Malili lakes, Lake Towuti, Loeha Island, S shore	<i>C. lanceolata</i>
	Malili lakes, Lake Towuti, E shore	<i>C. lanceolata</i>
	Malili lakes, Lake Towuti, W shore	<i>C. lingkonae</i>
	Malili lakes, Petea River	<i>C. loehae</i>
	Malili lakes, Lake Masapi	<i>C. masapi</i>
	South Sulawesi, Tarrak River	<i>C. sp. 2</i>
	Malili lakes, Lake Towuti, SW shore	<i>C. lanceolata</i>
	Malili lakes, Lake Matano, S shore	<i>C. lanceolata</i>
	Malili lakes, Lake Mahalona, NW shore	<i>C. lanceolata</i>
Rotifer epibiont		
<i>Embata laticeps</i> (Murray, 1905)	Lake Poso, S shore	<i>C. ensifera</i>



Table XIV. List of rotifer species epibiont on crustacea (data from Koste and Shiel 1986; May 1989; Settele and Thalhofer 2003; present study).

Epibiont	Basibiont
<i>Brachionus sessilis</i>	<i>Diaphanosoma excisum</i> , <i>D. sarsii</i> , <i>D. brachyurum</i>
<i>Brachionus rubens</i>	<i>Daphnia magna</i> , <i>D. pulex</i> , <i>D. longispina</i> , <i>Moina rectirostris</i> , <i>M. brachiata</i> , <i>Polyphemus pediculus</i>
<i>Proales daphnicola</i>	<i>Daphnia</i>
<i>Testudinella epicopta</i>	<i>Acantholeberis curvirostri</i>
<i>Brachionus variabilis</i>	<i>Daphnia longispina</i> , <i>Ceriodaphnia longispina</i>
<i>Collotheca volutata</i> var. <i>sessilis</i>	<i>Monospilus dispar</i>
<i>Brachionus novaezealandiae</i>	<i>Pseudomonias lemnae</i> , <i>Daphnia carinata</i> , <i>Ceriodaphnia</i> sp.
<i>Seison annulatus</i>	<i>Nebalia</i> sp.
<i>Paraseison nudus</i> , <i>P. proboscideus</i> , <i>P. ciliatus</i>	<i>Nebalia</i> sp.
<i>Rotaria sociales</i> , <i>R. magna-calcarata</i> , <i>Testudinella elliptica</i> , <i>T. truncata</i> , <i>T. caeca</i> , <i>Embata parasitica</i> , <i>E. laticeps</i> , <i>E. commensalis</i>	<i>Asellus aquaticus</i>
<i>Embata parasitica</i> , <i>E. laticeps</i> , <i>E. hamaca</i> , <i>Proales daphnicola</i> , <i>Philodina convergens</i> , <i>Dicranophorus hauerianus</i> var. <i>siedleckii</i> , <i>Enicentrum grande</i>	<i>Gammarus pulex</i>
<i>Lepadella astacicola</i> , <i>L. branchiola</i> , <i>L. parasitica</i> , <i>L. boreales</i> , <i>Cephalodella crassipes</i> , <i>Dicranophorus hauerianus</i>	<i>Astacus</i> sp.
<i>Lepadella borealis</i> , <i>L. astacicola</i> , <i>L. lata</i> , <i>D. hauerianus</i>	<i>Cambarus affinis</i>
<i>Macrotrachela cancrøphila</i> , <i>Anomopus telphusae</i>	<i>Telphusa fluviatilis</i>
<i>Anomopus chasmagnathi</i>	<i>Chasmagnathus granulatus</i>
<i>Proales paguri</i>	<i>Pagurus bernhardus</i>
<i>Rotaria tardigrada</i>	Crustacea (branchial chambers)
<i>Rotaria rotatoria rotatoria</i>	Crustaceans
<i>Embata laticeps</i>	<i>Caridina ensifera</i>

constitute adaptations to the epibiont life. For example, *Acineta sulawesiensis* has the lorica as a free anterior part over the body enveloping the tentacles, possibly protecting them from possible damage caused by the movement of the basibiont. Other ciliates, such as *Cothurnia*, are protected by a lorica completely surrounding the body, and with a noticeably short stalk, which allows the ciliate to settle close to the surface of the basibiont. Something similar occurs in *Podophrya* which, in contrast to the free-living species, has a very short stalk. *Zoothamnium* has a broad stalk, which is noticeably wider on *Caridina lanceolata*. This not only protects the stalk, but also the colony (Fernandez-Leborans et al. 2006a). The genus showing the most obvious adaptation to the epibiont life is *Spelaeophrya*. Although it is lacking a conspicuous lorica, the body is flattened, and in the posterior area the body can be folded, resting next to the surface of the antennae, where these suctorians are most abundant. In several individuals, the macronucleus was considerably flattened, and its anterior part can appear widened, probably due to the adoption of the ciliate of a squash-shape reducing the friction by the linkage with the surface of the appendages of the shrimp. These ciliates have only been found as epibionts on crustaceans.

The distribution of epibiont species on *C. ensifera* followed a gradient from the anterior to the posterior end of the body, and the maximum colonization corresponded to the anterior areas of the body, without significant differences between the left and right appendages. This phenomenon was also observed in the epibiont communities of *C. lanceolata* and could be correlated to the behaviour of the shrimp (Fernandez-Leborans et al. 2006a). Like *C. lanceolata* in the Malili lake system, *C. ensifera* is abundant and widely distributed in Lake Poso and often found in pelagic swarms (K. von Rintelen, personal field observation).

Its rapid and characteristic feeding behaviour, as described for *Caridina* in general (Fryer 1960), along with its high mobility mainly brings the anterior part (i.e. the feeding appendages) of the shrimp into contact with different kinds of soft and hard substrates (rocks, wood, sand, macrophytes). This was similarly observed in *C. lanceolata* from the Malili lakes (Fernandez-Leborans et al. 2006a).

In addition, the physical characteristics of the basibiont surfaces and their morphology were important for colonization. In the anterior part of the body, the surface of the antennulae and antennae provide substrata for the settlement of epibionts and the movement of these appendages facilitates the colonization. Other units with high densities of epibionts, for example the maxillipeds, showed three characteristics which possibly explain the remarkable epibiosis: the wide available surface, the protected location of these appendages, and the frequent presence of nutrient particles due to their function. Other morphological sites with high epibiosis were the uropods, possibly due to their wide exposed surface, and their position in the body with an important passage of organic material from the digestion and movement of the shrimp.

Many sessile organisms depend upon the characteristics of the living substratum to which they adhere (Gili et al. 1993) and, therefore, the structure, dynamics, physiology, and ecology of the basibiont reflect the colonization pattern of the epibiont species, and the development of the protozoan and invertebrate communities. Epibiosis may contribute to the discernment of important aspects of the biology of the basibiont. The density and distribution of epibionts on the different anatomical units of the basibiont can indicate terminal moult, seasonal differences of moult pattern between the two sexes, the asynchronic moult between populations of different geographical areas, burying and feeding behaviours, etc. (Bottom and Ropes 1988; Abelló et al. 1990; Abelló and Macpherson 1992; Gili et al. 1993; Fernandez-Leborans et al. 1997).

Lake Poso showed a high density and diversity of epibiont species, mainly ciliate protozoans, while the density of other epibionts was less than 1%. The statistical data showed that the different epibiont species had a distinctive distribution on the basibiont, involving the differential presence of epibiont species on the anatomical units of the shrimp, and the pattern of distribution along the longitudinal axis of the basibiont which varied significantly between species. However, the community seems to show a certain pattern of behaviour by ensemble, which can be verified by their colonization pattern. The species tend to occupy the available substratum, with particular requirements of each functional group, but with a general trend towards equilibrium among species and groups, compensating for diversity and density.

The protozoan ciliate epibionts probably do not harm the basibiont. Within the epibiont community there are diverse trophic links and, therefore, as happens in free environments, there is a sort of energy feed-back (microbial loop or other relations), and several species can feed on other protozoans that are present in the epibiotic community, or on other organisms belonging to the community associated to the host (that have free movement around the basibiont), as, for example, suctorians feed 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 limnic 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 (Patterson et al. 1989; Fenchel 1990; Fernandez-Leborans and Fernandez-Fernandez 2002). On a small scale, these conditions could be transferred to an epibiotic community, which could reflect the biodiversity of 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. Independently of the present species and in all cases, each species has established a similar pattern of distribution.

## Acknowledgements

We thank Matthias Glaubrecht and Thomas von Rintelen (Museum of Natural History, Berlin, Germany) for collecting the material from Lake Poso. We are further grateful to Daisy Wowor and Ristiyanti Marwoto (Museum Zoologicum Bogoriense, Bogor, Indonesia) for their logistic support in Indonesia and to P. T. Inco in Soroako. LIPI (Indonesian Institute of Sciences) provided research permits.

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