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Source: Arctic, Antarctic, and Alpine Research, 38(3) : 343-356

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1523-0430(2006)38[343:PEATDO]2.0.CO;2

Arctic, Antarctic, and Alpine Research, Vol. 38, No. 3, 2006, pp. 343–356

Protozoan Epibionts and Their Distribution on the Arctic Ice-amphipod *Gammarus wilkitzkii* from Spitsbergen, Norway

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Abstract

Specimens of the Arctic sympagic amphipod *Gammarus wilkitzkii*, which were collected in the ice-covered areas near Spitsbergen, Norway, were infested with protozoan epibionts in densities of 499 to 3346 individuals per amphipod. The epibionts belong to the five ciliate genera: *Ephelota*, *Cryptacineta*, *Acineta* and *Podophrya* (suctorian ciliates), and *Epistylis* (peritrich ciliate). In this study we present the first observations of epibionts on ice-associated crustaceans and provide a detailed description of morphological and taxonomical aspects of the different ciliate genera. *Cryptacineta* has not been found earlier in the marine environment. This ciliate showed the highest density values (215–2571 individuals per amphipod), followed by *Ephelota* (2–1302 ind./amphipod). The number of individuals of *Acineta*, *Podophrya*, and *Epistylis* did not surpass 240 ind./amphipod. Epibionts colonized all appendages and the entire body surface, but were most numerous on the anterior body part of *G. wilkitzkii*. The body length of the gammarid and the number of epibionts of *Ephelota*, *Podophrya*, and *Epistylis* were positively correlated. The highest density of epibionts was found on the anterior body parts with the antennae bearing up to 613 individuals. In contrast, the posterior body showed only little burden. The number of epibionts along the caput-telson axis of the amphipod body shows a decrease towards the posterior end of the amphipod. The highest degree of infestation was found on females, followed by juveniles and eventually, males. When grouping the 37 anatomical units (including left and right appendages) to 8 body "regions," the pereiopods, as a whole, showed the highest density (39.25%), followed by the gnathopods (22.29%), and antennulae and antennae. Basibiont got infested with the sessile ciliates in the benthic and pelagic environment during the ice-free season and carried them along back to the sympagic ecosystem when colonizing the newly formed ice. Epibionts are therefore considered as indicators for bentho-sympagic coupling processes.

Introduction

Epibiosis is an association of two organisms: the epibiont and the basibiont (Wahl, 1989). 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 gives support to the epibiont (Threlkeld et al., 1993). Epibiosis between ciliated protozoa and crustacea is very common and occurs across most crustacean orders. Ciliated protozoa from the subclasses Peritrichia, Suctoria, and Chonotrichia (for taxonomical classification see Lynn and Small, 2002) are the most frequently reported epibionts on crustacea (Morado and Small, 1995; Sprague and Couch, 1971; Fernandez-Leborans and Tato-Porto, 2000a, 2000b; Fernandez-Leborans, 2001).

The central Arctic Ocean is covered by perennial (multiyear) ice in an area of 7×10^6 km^2. In the subarctic seas seasonal (first year) ice forms during winter and spring, so that the sea-ice coverage more than doubles in the course of a year (Parkinson et al., 1999). The sea ice in the Arctic Ocean is in continuous motion. The Beaufort Gyre and the Transpolar Drift Stream are the most important large-scale drift patterns (Maykut, 1985). The Transpolar Drift Stream transports sea ice from the ice formation areas along the Siberian Coast towards the Fram Strait, where it eventually melts. This drift takes 3 to 5 yr (Rigor et al., 2002). In the Canadian Basin, the sea ice can have a residence time of tens of years (Rigor et al., 2002).

Different taxonomic groups of organisms are associated with arctic sea ice. The so-called sympagic biota is separated into allochthonous and autochthonous species (Melnikov and Kulikov, 1980; Lønne and Gulliksen, 1991a, 1991b). The most conspicuous autochthonous sympagic taxa are amphipods, especially *Gammarus wilkitzkii*, *Apherusa glacialis*, and two *Onisimus* species, *O. glacialis* and *O. nanseni* (Lønne and Gulliksen, 1991a, 1991b; Melnikov, 1997; Poltermann, 1998). The amphipod abundance in arctic sea ice ranges between 0 and 490 ind. m^{-2} corresponding to biomass values of over 20 g WM m^{-2} (reviewed in Arndt and Lønne, 2002). The sympagic fauna in the Arctic is considered to play an important role both as trophic link between the sea ice and the water column, and between sea ice and semiterrestrial organisms such as marine mammals and sea birds (Bradstreet and Cross, 1982). It has been demonstrated that the biomass of the sympagic fauna is related to the age of ice (Arndt and Lønne, 2002). *Gammarus wilkitzkii* Birula, 1897 (Amphipoda: Gammaridea) is considered as a carnivorous-(detritivorous) species (Poltermann, 2001). It has a life span of about 6 yr (Beuchel and Lønne, 2002). The body length ranges from 5 to 45 mm corresponding to an adult mean dry weight of 12 to 50 mg (Gulliksen and Lønne, 1991; Sakshaug et al., 1992; Beuchel and Lønne, 2002).

The archipelago of Svalbard (Norway, with Spitsbergen being the main island) is located at the border of the perennial and seasonal arctic ice pack. Futhermore, the islands are influenced by both, warm Atlantic and cold arctic water. *Gammarus wilkitzkii* is a frequent species in both ice types, multiyear and first year ice (Lønne and Gulliksen, 1991a, 1991b; Poltermann, 1998; Arndt and Lønne, 2002). In seasonally covered seas this amphipod regularly occurs in the pelagic and benthic

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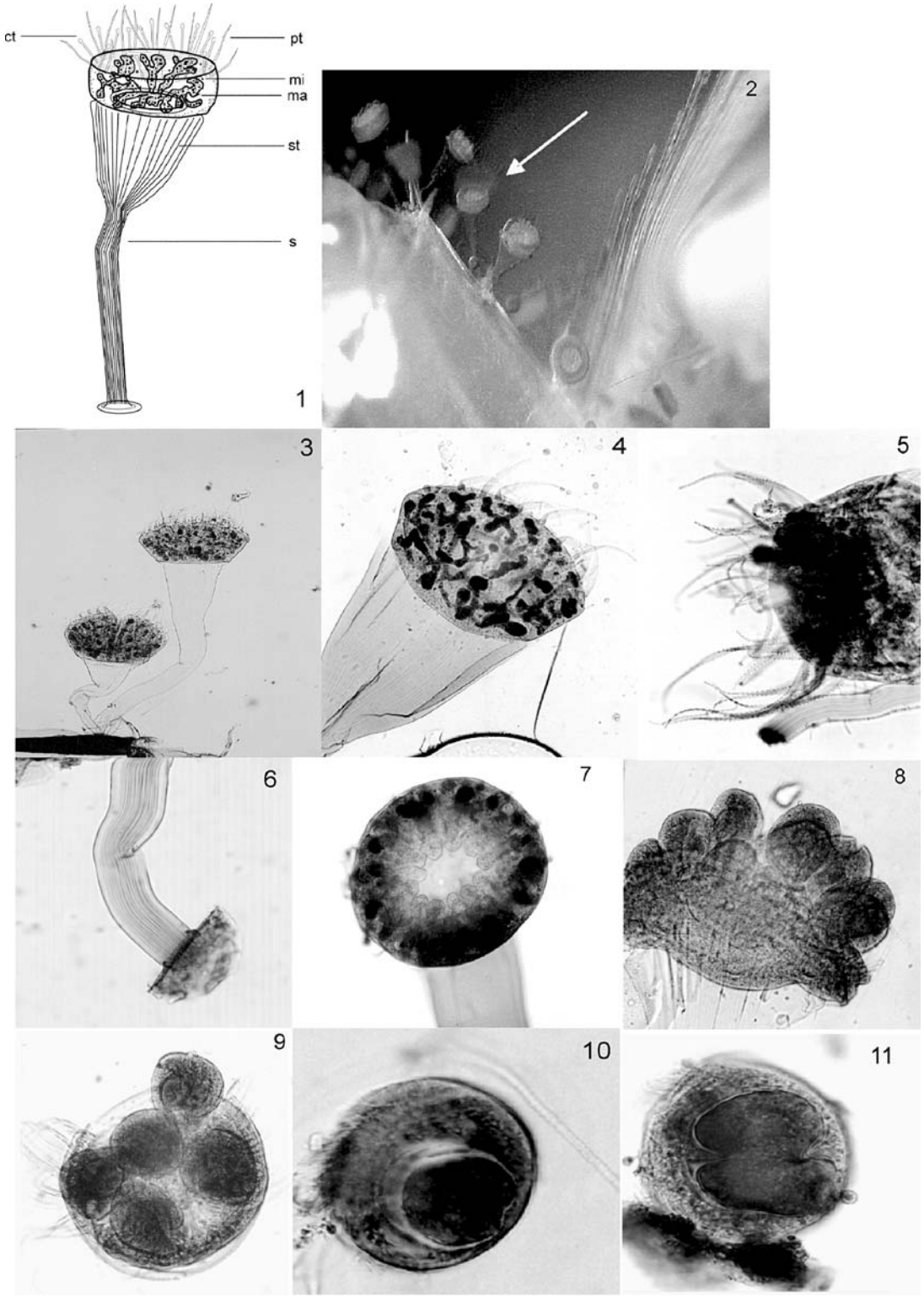

FIGURE 1. *Ephelota plana*. **1: scheme, ct: capitate tentacles, ma: macronucleus, mi: micronucleus, pt: prehensile tentacles, s: stalk, st: striations; 2: "in vivo" on a pereiopod of *Gammarus wilkitzkii* (arrow) (×35); 3: habitus (×100); 4: anterior end of the body showing suprastylar zone of stalk and macronucleus (×200); 5: apical end of the body with tentacles (×220); 6: posterior end of the stalk with striations and basal disk (×250); 7: early phase of reproductive stage with numerous buds in the center (×220); 8: lateral view of buds showing their ciliar fields (×280); 9: apical end of the body with five emerging buds (×230); 10: early stage of the swarmer with one single macronucleus (×750); 11: advanced phase of the swarmer with the macronucleus under division (×750); 12: early developmental stage of adult after settling on the basibiont, with only short capitate tentacles (×180); 13: subsequent developmental stage of adult with the macronucleus well differentiated; 14: scheme of "resistant" stage, abbreviations see 1; 15: habitus of "resistant" stage (×100); 16: apical end of "resistant" stage with folded tentacles (×250); 17: apical end of "resistant" stage showing the shape of the macronucleus (×250).** **Figure continued on next page.**

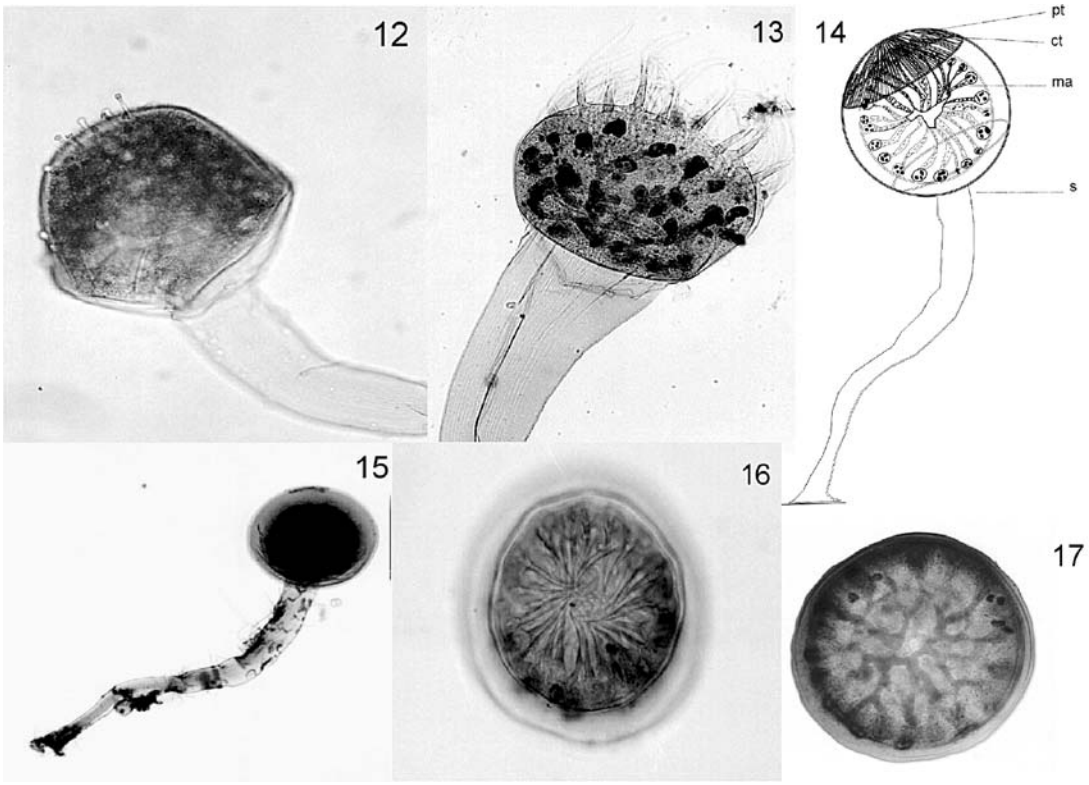

FIGURE 1. (Cont.).

habitat when the ice (their habitat) melts and eventually recolonizes sea ice during ice formation periods in shallow (coastal) areas. Specimens of *G. wilkitzkii* collected in sea ice and the underlying water column near the east coast of Spitsbergen were infested by numerous protozoan epibionts. Since this is the first recording of epibionts on a sympagic crustacea it is believed that the basibiont got infested with the sessile ciliates in the benthic and pelagic environment during the ice-free season and carried them along back to the sympagic ecosystem when colonizing the newly formed ice. Epibionts are therefore considered as indicators for bentho-sympagic coupling processes. The morphological and taxonomical characteristics of these epibiontic ciliates, as well as their distribution on the body of *G. wilkitzkii*, are presented in this study.

Materials and Methods

The specimens of *G. wilkitzkii* were sampled in September 2003 in the ice pack east of Spitsbergen, Norway. Specimens of *G. wilkitzkii* were collected in loose drift ice and open water. Thick, old drift ice of 2 to 3 m thickness prevailed at the shallow (50 m water depth) ice station. Quantitative under-ice sampling was performed using a diver-operated suction sampler (Lønne, 1988) that collected all specimens of *G. wilkitzkii* in a defined area irrespective of body length. A diver-held plankton-net sampled qualitatively. For the analysis of epibiontic infestation 30 specimens of *G. wilkitzkii* (16 females, 3 males, 11 juveniles) preserved in 10% formalin were used. Amphipod specimens were preserved in 10% formalin. They were dissected and each anatomical unit was examined under a stereoscopic microscope. The epibionts were isolated and treated using the silver carbonate technique (Fernandez-Galiano, 1976), following the procedure described by Fernandez-Leborans and Castro de Zaldumbide (1986), and were additionally treated with neutral red and methyl green. Biometric values of the epibionts were taken using an ocular micrometer. Light microscope images were obtained using image analysis (KS300 Zeiss). This study includes a detailed description of morphological features and morphometry of the different epibiont species. Statistical analysis on the distribution of epibionts on body parts and appendages ("anatomical units") of *G. wilkitzkii* was made using Statgraphics and SPSS programs.

Results

The ciliates found as epibionts on *G. wilkitzkii* belong to the following genera: *Ephelota*, *Cryptacineta*, *Acineta*, *Podophrya* (all Suctoria), and *Epistylis* (Peritrichia). The ciliates were disposed on the antennae, antenulae, pereiopods, pleopods, telson, and on the surface of the body, mainly on the abdomen of the basibiont.

CILIATES OF THE GENUS EPHELOTA

Morphological Features

The body of this suctorian ciliate was like a truncated cone, flattened and wider than long. The body size ranged between 41 and 349 μm in length and 82 and 359 μm in width (Table 1; Fig. 1: 1–7). In the apical region of the ciliate body a concave cavity was visible. Two types of tentacles were located along the edge of this cavity. The first (nonfeeding) tentacles numbered between 6 and 52 and were long, pointed, thin, and prehensile. Along their length these "prehensile tentacles" bore numerous haptocysts. The second type of tentacles was short, thick, and capitate. Between 2 and 42 "capitate tentacles," which were used for feeding, were present. The tip of each tentacle had a half-spherical structure.

The macronucleus was highly ramified and lobate, occupying a high proportion of the cellular volume, and was located in the center of the body. Numerous spherical micronuclei surrounded the macronucleus. The contractile vacuole was located laterally displaced in the apical end of the body. The stalk length was approximately four times longer than the body. Fibrillar structures and transversal striations characterized the stalk lengthwise. The apical area of the stalk

TABLE 1

Biometric features of *Ephelota plana* ($n = 60$) (in µm).

	Mean	Standard deviation	Minimum	Maximum
Body length	149.59	71.01	41.00	348.50
Body width	213.33	72.08	82.00	358.75
Length of suprastylar area	131.79	83.58	51.25	379.25
Width of suprastylar area	138.87	58.03	61.50	307.50
Length of the apical cavity	170.39	12.27	153.00	186.37
Length of stalk	439.86	204.02	174.25	871.25
Width of stalk	40.55	12.92	20.50	61.50
Number of longitudinal striations of stalk	20.32	3.14	15.00	26.00
Number of prehensile tentacles	17.38	9.89	6.00	52.00
Number of capitate tentacles	8.78	8.39	2.00	42.00
Length of prehensile tentacles	40.60	22.27	11.52	86.40
Length of capitate tentacles	14.00	6.03	3.84	26.88
Number of micronuclei	34.45	10.25	18.00	47.00
Diameter of micronucleus	5.07	1.18	3.50	7.10
Number of buds	10.00	3.11	5.00	14.00
Length of developed bud	75.90	8.20	60.35	92.30
Width of developed bud	61.33	8.38	49.70	78.10
Length of swimming phase	81.54	9.97	76.00	101.25
Width of swimming phase	53.41	14.77	41.25	89.10
Diameter of macronucleus of swimming phase	36.48	9.23	28.12	58.72
Length of left ciliar field (swimming phase)	82.64	7.01	71.25	99.18
Length of right ciliar field (swimming phase)	23.07	3.20	17.30	28.35

TABLE 2

Biometric features of *Cryptacineta* (n = 60) (in µm).

	Mean	Standard deviation	Minimum	Maximum
Body length	60.48	14.18	38.40	76.80
Body width	69.60	9.83	57.60	86.40
Length of stalk	48.32	6.59	40.32	57.60
Width of stalk	6.72	1.61	3.84	7.68
Number of tentacles per fascicle	18.00	7.83	8.00	26.00
Length of tentacles	12.96	4.54	9.60	19.20
Length of macronucleus	32.96	13.60	17.28	51.84
Width of macronucleus	27.84	16.77	9.60	51.82
Diameter of micronucleus	3.09	0.35	2.80	3.83
Width of lorica	11.76	1.17	10.70	14.20

(suprastylar area) was amplified and joined the cellular body in a conspicuous funnel-shaped widening.

Different stages of reproduction of these suctorians were observed (Fig. 1: 7–13). Some specimens showed several exogenous buds of similar size, projecting out of the apical cavity of the body. The migratory phase was pyriform with a ventral surface in which two ciliary fields can be observed: a left ciliary field, longer, prolonged surrounding the apical part of the body, and a right ciliary field, shorter than the left field. In addition, several specimens appeared to be in the initial phase of maturation. These individuals had the anterior cavity not yet differentiated and tentacles were short and all capitate. This suggests that prehensile tentacles develop during subsequent stages of the adult life.

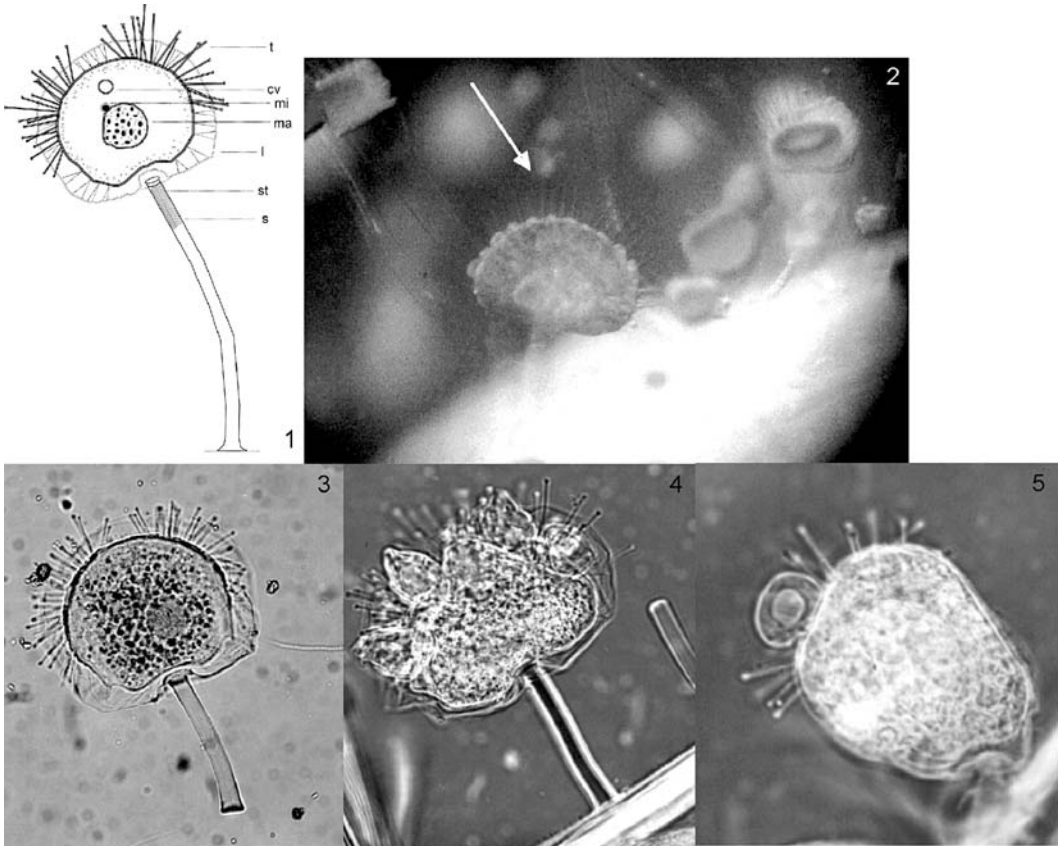

FIGURE 2. ***Cryptacineta*** **sp. 1: scheme, cv: contractile vacuole, l: lorica, ma: macronucleus, mi: micronucleus, s: stalk, st: striations, t: tentacles; 2: "in vivo" on the surface of** ***Gammarus wilkitzkii*** **(arrow), surrounded by several** ***Ephelota*** **(×260); 3: habitus showing tentacles, lorica, stalk, and macronucleus (×550); 4: apical end of the body with several buds (×650); 5: bud showing form and position of the macronucleus (×650).**

TABLE 3

Biometric features of *Acineta* (n = 60) (in μm).

	Mean	Standard deviation	Minimum	Maximum
Body length	107.62	5.92	102.50	112.75
Body width	164.00	26.46	133.25	194.75
Length of the lorica area without cellular body	38.44	15.37	20.50	51.25
Length of stalk	228.92	41.42	205.00	276.75
Width of stalk	5.12	1.11	3.84	5.76
Number of tentacles in each fascicle	16.33	3.21	14.00	20.00
Length of tentacles	18.56	7.99	9.60	24.96
Diameter of contractile vacuole	14.08	4.00	9.60	17.28
Diameter of macronucleus	35.04	8.92	23.04	44.16

Up to 10% of the ciliates of this genus presented "resistant" stages (Fig 1: 14–17). This stage was characterized by stalked individuals with spherical body. The body was encapsulated by a thick external layer. In the interior the macronucleus was present as dense and ramified nodes that extended to the external envelope. Directly beneath the external envelope and in the anterior area of the body the tentacles were closely aligned in a spiral. Unlike the vegetative forms the stalk of resting stages was constant in width longitudinally.

Taxonomic Position

These suctorians belong to the genus *Ephelota* Wright, 1858 (family Ephelotidae Kent, 1882; order Exogenida Collin, 1912; subclass Suctoria Claparède and Lachmann, 1858; class Phyllopharyngea De Puytorac et al., 1974; subphylum Intramacronucleata Lynn, 1996; phylum Ciliophora Doflein, 1901) (Lynn and Small, 2002). All ciliates of this genus are marine and characterized by the following set of traits: presence of a stalk; shape similar to a truncated cone or spherically; monoaxony. Furthermore, they are medium-sized, although this varies depending on the species. They do not have lorica. There are two types of tentacles with different functions: prehensile and capitate (feeding) tentacles. Budding is multiple and synchronic, and the buds are ellipsoidal in shape, flattened and with a horseshoe-shaped principal ciliary field (Batisse, 1994).

Body size and shape characterize the suctorian found on *G. wilkitzkii* as the species *Ephelota plana* Wailes, 1925. The lateral flattening of the body, multiple exogenic and synchronic budding and the morphometric similarities in stalk length and suprastylar extention as well as the presence of longitudinal striations are further features of this species (Grell and Benwitz, 1984a, 1984b).

CILIATES OF THE GENUS CRYPTACINETA

Morphological Features

The body of ciliates of the genus *Cryptacineta* is rounded and flattened (Table 2: Fig. 2: 1–3). With 38 to 76 μm in length and 57 to 86 μm in width, this group is much smaller than *Ephelota*. The body was covered by a thick transparent mucilaginous layer. The anterior part of the body bore two fascicles of each 8 to 26 capitate tentacles. The macronucleus was spheroid and located in the center of the body. A small spherical micronucleus was attached to it. Apically, a contractile vacuole was placed above the macronculeus. The stalk was long and had a curved spatulate end that was embedded in the posterior part of the lorica (following the types of junction between stalk and lorica described by Curds [1985]). The stalk was characterized by longitudinal striations.

Individuals of this genus were in the process of reproduction.

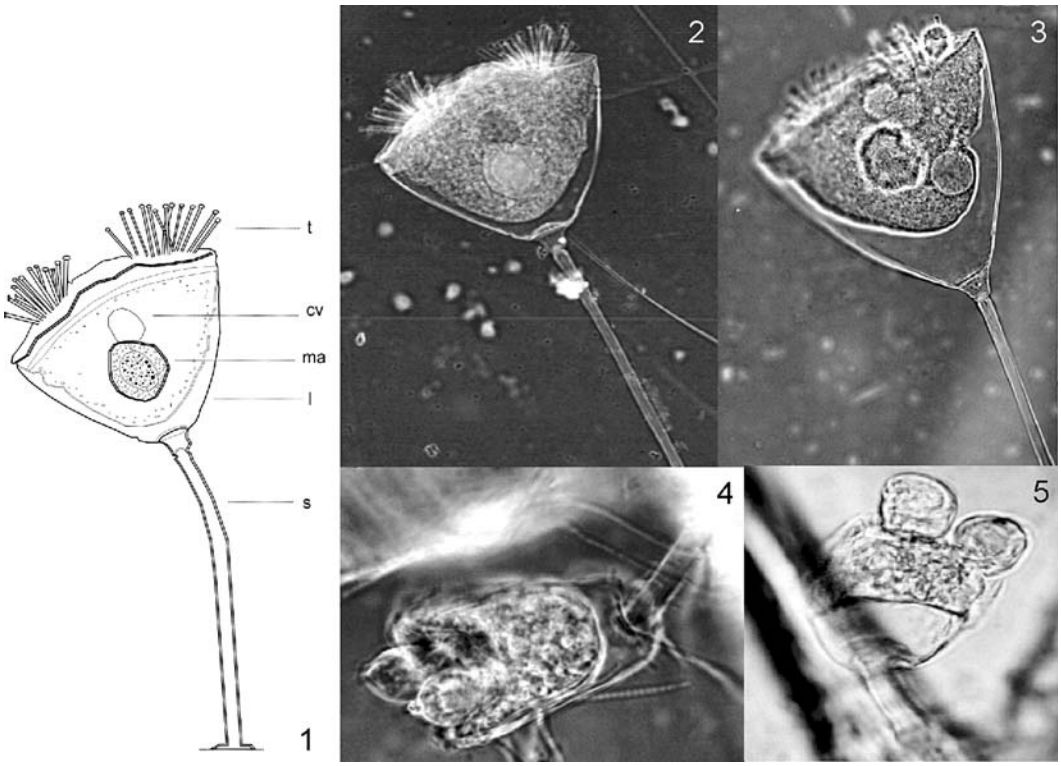

FIGURE 3. ***Acineta compressa*. 1: scheme, cv: contractile vacuole, l: lorica, ma: macronucleus, s: stalk, t: tentacles; 2: habitus showing lorica, macronucleus, contractile vacuole, stalk, and tentacles (×230); 3: early stage of budding (×230); 4: apical end of the body with two buds (×230); 5: two buds showing form and position of macronuclei (×200).**

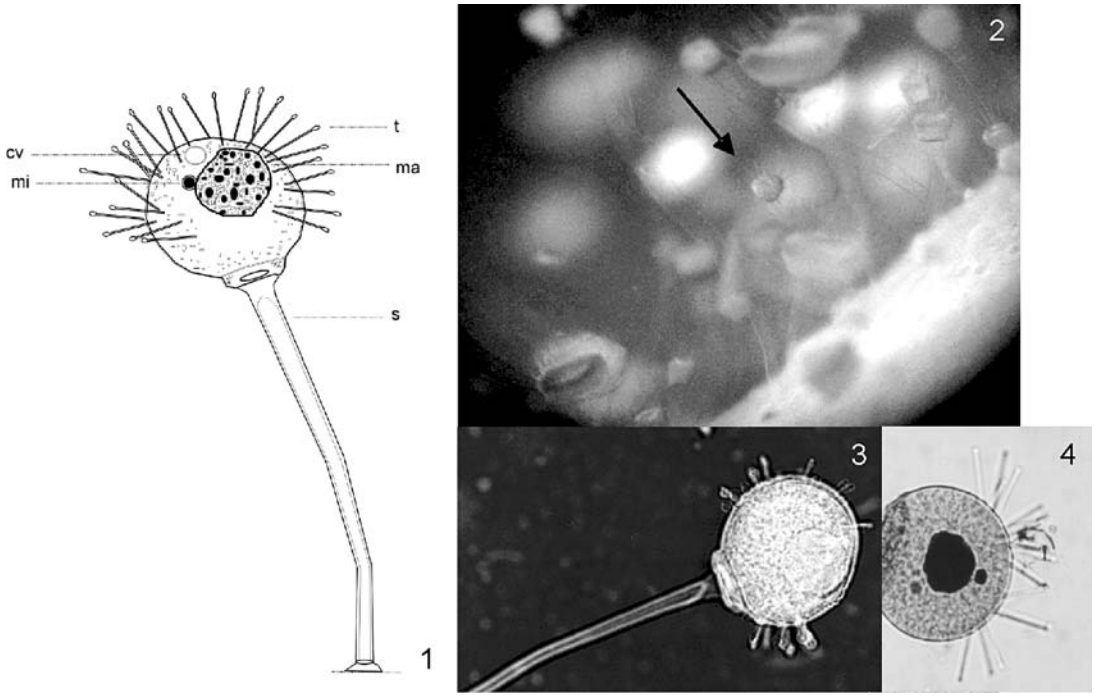

FIGURE 4. ***Podophrya fixa*. 1: scheme, cv: contractile vacuole, ma: macronucleus, mi: micronucleus, s: stalk, t: tentacles; 2: "in vivo" on the surface of *Gammarus wilkitzkii* (arrow), surrounded by *Ephelota* (×45); 3: habitus showing macronucleus, stalk, and tentacles (×650); 4: apical end of the body showing nuclei and tentacles (×650).**

Endogenous buds, pyriform in shape, were visible in the apical end of the body. Generally, no more than three buds were found per ciliate (Fig. 2: 4–5).

Taxonomic Position

These ciliates belong to the genus *Cryptacineta* Jankowski, 1978 (order Endogenida Collin, 1912; subclass Suctoria Claparède and Lachmann, 1858; class Phyllopharyngea De Puytorac et al., 1974; subphylum Intramacronucleata Lynn, 1996; phylum Ciliophora Doflein, 1901) (Lynn and Small 2002). This suctorian genus is characterized by a thick mucoid lorica, which completely envelops the stalked tulip-shaped body. Anteriorly two fascicles of tentacles project through the lorica, and posteriorly the stalk also penetrates the surrounding lorica (Curds, 1985). Jankowski (1978) described the species *Cryptacineta operta* (Swarczewsky, 1928), which lives attached to two gammarid amphipod species, *Carinogammarus seidlizi* and *C. wagneri*, in the Lake Baikal. According to Curds (1985), reproduction and type of buds remain undescribed. We considered the group of ciliates found in this study as *Cryptacineta* sp.

TABLE 4

Biometric features of *Podophrya* (n = 60) (in μm).

	Mean	Standard deviation	Minimum	Maximum
Body length	43.68	6.53	38.40	51.84
Body width	43.20	1.92	42.24	46.08
Length of stalk	151.68	49.60	96.00	201.60
Width of stalk	4.80	1.11	3.84	5.76
Number of tentacles	23.66	4.09	20.00	28.00
Length of tentacles	16.00	5.54	9.60	19.20
Length of macronucleus	19.84	4.00	15.36	23.04
Width of macronucleus	23.04	5.76	17.28	28.80
Diameter of micronucleus	4.93	0.20	4.53	5.21

CILIATES OF THE GENUS ACINETA

Morphological Features

The ciliates of the suctorian *Acineta* were covered by a lorica, triangular or bell-shaped and laterally flattened (Table 3; Fig. 3). Body size ranged between that of *Ephelota* and *Cryptacineta* (122–163 μm in length; 133–194 μm in width). Since some parts of the body were occasionally uncovered by the lorica, the body size varied significantly. Two fascicles of 14 to 20 capitate tentacles were located at the anterior end of the body. The spherical macronucleus was located centrally along with a contractile vacuole placed above. The long stalk joined the lorica in a definite collar-like region (Curds, 1985). Some specimens showed endogenous buds of variable size.

Taxonomic Position

These ciliates belong to the genus *Acineta* Ehrenberg, 1833 (family Acinetidae Stein, 1859; order Endogenida Collin, 1912; subclass Suctoria Claparède and Lachmann, 1858; class Phyllopharyngea De Puytorac et al., 1974; subphylum Intramacronucleata Lynn, 1996; phylum Ciliophora Doflein, 1901) (Lynn and Small, 2002). The set of traits for this genus is: the presence of lorica; a laterally compressed body, borne upon a stalk; anteriorly, two fascicles of tentacles, arranged in discrete clumps but not rows, that project through an apical aperture with their dumb-bell shape. Two lobe-like actino-

TABLE 5

Biometric features of *Epistylis* (n = 60) (in μm).

	Mean	Standard deviation	Minimum	Maximum
Body length	59.84	9.04	46.08	71.04
Body width	44.80	5.10	38.40	49.92
Length of stalk	61.44	11.08	51.84	71.04
Width of stalk	15.74	3.15	13.44	21.12

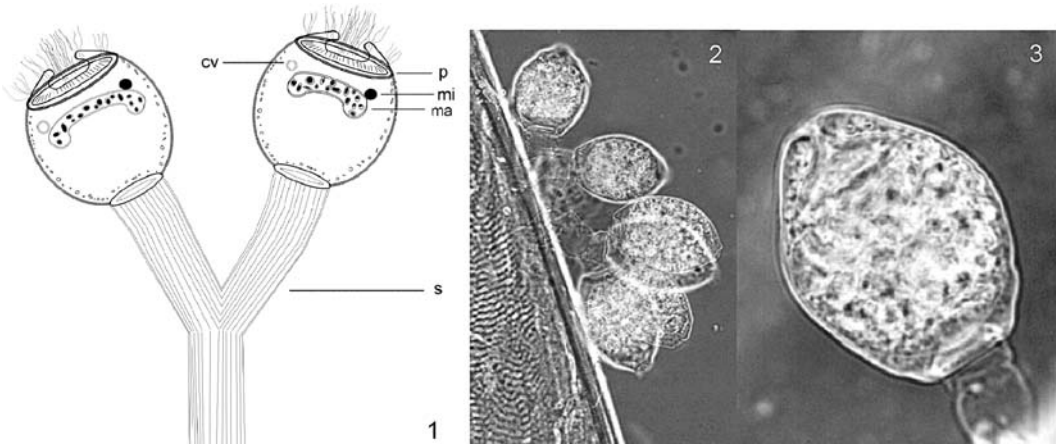

FIGURE 5. ***Epistylis*** **sp. 1: scheme, cv: contractile vacuole, ma: macronucleus, mi: micronucleus, p: peristomial disk, s: stalk; 2: habitus of a colony on the surface of *Gammarus wilkitzkii* (×320); 3: zooid showing stalk and peristomial lip (×830).**

phores usually bear each a fascicle of suctorial, capitate tentacles (Curds, 1985). The individuals of *Acineta* examined on *G. wilkitzkii* belong to the species *Acineta compressa* Claparède and Lachmann, 1859. This species is regularly found as epibiont in the marine environment and shows similar morphometric values (length of body and stalk), the collar-like joint between stalk and lorica, a spherical macronucleus and the presence of only a single contractile vacuole as described above.

CILIATES OF THE GENUS PODOPHRYA

Morphological Features

The individuals of the genus *Podophrya* were miniature in size (38–51 μm in length; 42–46 μm in width) and had a characteristic spheroid body (Table 4; Fig. 4). In comparison to the body the stalk can reach a considerable length. The capitate tentacles were spread over the entire surface of the body. The rounded macronucleus was located excentrically. A spherical micronucleus was disposed close to the macronucleus. A contractile vacuole was placed above the macronucleus near the apical end of the body. Several individuals appeared with buds at the apical end of the body.

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; phylum Ciliophora Doflein, 1901) (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). Dimensions of the body, shape of the tentacles, and the presence of only one contractile vacuole and a micronucleus make the *Podophrya*-types found in this study most like *Podophrya fixa* (Müller 1786) Ehrenberg 1833. Although Curds (1986) indicates that the stalk length usually equals the body diameter, Matthes et al. (1988) showed that morphometric values allow for plasticity.

CILIATES OF THE GENUS EPISTYLIS

Morphological Features

These peritrich ciliates were colonial with colonies generally composed of two oval zooids (Table 5; Fig. 5). The zooid was 46 to 71 μm in length and 38 to 49 μm in width. At the apical end of the body a peristomial lip protruded outward. The macronucleus was crescent-shaped. The micronucleus was spherical and located close to the macronucleus. A contractile vacuole was placed above the macronucleus. The stalk was robust and noncontractile and characterized by numerous longitudinal striations. The stalk of the two zooids was short.

Taxonomic Position

These peritrich 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; phylum Ciliophora Doflein, 1901) (Lynn and Small, 2002). The genus *Epistylis* is characterized by the following set of traits: formation of colonies; the peristomial disc lacks a stalk; the stalk of the body is noncontractile. This genus comprises a large number of species, but species determination is difficult. We therefore consider this species as *Epistylis* sp.

DISTRIBUTION OF THE PROTOZOAN EPIBIONTS ON G. WILKITZKII

The number of epibionts per amphipod ranged between 499 and 3346 individuals. Taking into account the genera, *Cryptacineta* showed the highest densities (215–2571 individuals per amphipod), followed by *Ephelota* (2–1302 ind./amphipod), and in lesser proportion the other three genera, *Acineta*, *Podophrya*, and *Epistylis*, which did not surpassed 240 ind./amphipod (Table 6).

TABLE 6

Biometric data of the basibionts and densities of each genera of epibiont.

	Mean	Standard deviation	Minimum	Maximum
Length (cm)	2.90	0.88	1.30	4.00
Width (cm)	0.48	0.11	0.30	0.60
Total number of epibionts	1723.27	855.81	499.00	3346.00
Ephelota	399.82	408.04	2.00	1302.00
Cryptacineta	1209.36	725.97	215.00	2571.00
Acineta	26.64	71.98	0.00	240.00
Podophrya	36.18	31.97	2.00	112.00
Epistylis	51.27	51.02	0.00	158.00

TABLE 7

Density of epibionts [mean ± standard deviation] (minimum-maximum) on each anatomical unit for juveniles, males, and females of *G. wilkitzkii*.

		Juvenile	Male	Female	Total
Ant 1	L	33.25 ± 14.91 (14–46)	9.20 ± 12.99 (0–32)	81.67 ± 25.29 (49–122)	60.82 ± 31.20 (14–122)
Ant 1	R	31.50 ± 25.80 (14–69)	8.20 ± 9.01 (0–23)	73.83 ± 35.57 (43–137)	55.45 ± 35.85 (14–137)
Ant 2	L	56.25 ± 24.35 (24–81)	13.20 ± 18.86 (0–42)	148.17 ± 61.03 (94–262)	107.27 ± 65.23 (24–262)
Ant 2	R	88.50 ± 52.42 (25–142)	10.60 ± 10.41 (0–24)	170.33 ± 118.61 (0–351)	129.91 ± 100.58 (0–351)
Max 1	L	12.75 ± 9.67 (5–25)	0.00 ± 0.00 (0–0)	20.67 ± 5.09 (13–27)	15.91 ± 9.16 (0–27)
Max 1	R	8.75 ± 2.06 (7–11)	1.00 ± 1.41 (0–3)	14.50 ± 13.03 (3–35)	11.55 ± 9.94 (3–35)
Mxp	L	35.00 ± 67.34 (0–136)	1.20 ± 1.64 (0–4)	18.83 ± 20.22 (3–59)	23.55 ± 40.76 (0–136)
Mxp	R	35.50 ± 68.34 (0–138)	1.80 ± 2.49 (0–6)	19.50 ± 11.79 (4–34)	24.36 ± 39.47 (0–138)
Gna 1	L	62.00 ± 59.03 (17–146)	7.80 ± 4.97 (1–13)	104.83 ± 57.95 (46–208)	83.27 ± 58.14 (17–208)
Gna 1	R	41.00 ± 34.93 (0–84)	9.40 ± 8.20 (0–17)	172.33 ± 78.11 (75–293)	113.18 ± 89.65 (0–293)
Gna 2	L	46.25 ± 23.39 (19–74)	6.00 ± 8.94 (0–20)	114.83 ± 54.23 (41–189)	82.18 ± 55.34 (19–189)
Gna 2	R	57.50 ± 36.16 (20–102)	2.60 ± 4.34 (0–10)	123.50 ± 64.76 (54–223)	89.45 ± 64.63 (13–223)
Per 1	L	41.00 ± 24.37 (15–66)	5.60 ± 7.64 (0–19)	81.83 ± 36.43 (39–130)	62.09 ± 37.01 (15–130)
Per 1	R	36.00 ± 27.80 (12–74)	11.60 ± 10.16 (1–24)	66.83 ± 33.84 (25–115)	54.82 ± 32.15 (12–115)
Per 2	L	42.50 ± 33.77 (7–84)	11.40 ± 5.77 (3–19)	65.33 ± 32.12 (32–124)	56.27 ± 31.36 (7–124)
Per 2	R	51.25 ± 36.31 (22–99)	6.20 ± 9.42 (1–23)	75.00 ± 40.14 (40–146)	62.36 ± 38.01 (22–146)
Per 3	L	45.25 ± 52.62 (14–124)	11.00 ± 16.31 (1–40)	76.50 ± 30.26 (41–110)	63.18 ± 39.12 (14–124)
Per 3	R	55.75 ± 49.95 (24–130)	13.80 ± 23.12 (1–55)	76.33 ± 23.29 (48–106)	68.18 ± 33.49 (24–130)
Per 4	L	45.00 ± 41.42 (22–107)	22.60 ± 28.12 (0–70)	103.33 ± 68.90 (54–233)	83.00 ± 61.67 (22–233)
Per 4	R	56.75 ± 43.55 (21–120)	0.00 ± 0.00 (0–0)	81.67 ± 31.40 (33–124)	65.18 ± 40.97 (0–124)
Per 5	L	23.00 ± 15.56 (0–33)	0.00 ± 0.00 (0–0)	105.00 ± 53.55 (30–176)	65.64 ± 59.95 (0–176)
Per 5	R	23.75 ± 22.60 (0–53)	0.00 ± 0.00 (0–0)	107.67 ± 30.34 (62–148)	67.36 ± 52.94 (0–148)
Ple 1	L	22.50 ± 25.33 (1–54)	2.60 ± 3.44 (0–8)	8.67 ± 0.82 (8–10)	14.09 ± 15.46 (1–54)
Ple 1	R	31.75 ± 35.64 (7–83)	0.60 ± 0.55 (0–1)	8.00 ± 9.03 (1–25)	16.18 ± 24.01 (1–83)
Ple 2	L	18.25 ± 12.42 (5–35)	0.60 ± 0.89 (0–2)	12.17 ± 6.24 (6–24)	13.55 ± 9.32 (3–35)
Ple 2	R	16.25 ± 21.27 (3–48)	0.60 ± 0.89 (0–2)	15.33 ± 5.16 (9–21)	14.55 ± 12.80 (3–48)
Ple 3	L	15.00 ± 7.44 (10–26)	11.80 ± 14.91 (0–30)	21.50 ± 11.22 (9–40)	22.55 ± 15.36 (9–59)
Ple 3	R	25.25 ± 21.93 (6–56)	8.00 ± 8.69 (0–21)	22.00 ± 11.68 (12–39)	24.82 ± 15.50 (6–56)
Uro 1	L	29.50 ± 37.55 (6–85)	4.20 ± 4.32 (1–11)	17.83 ± 15.79 (2–46)	22.36 ± 24.09 (2–85)
Uro 1	R	19.25 ± 25.93 (1–56)	1.60 ± 3.05 (0–7)	8.83 ± 4.79 (2–15)	12.55 ± 15.54 (1–56)
Uro 2	L	9.25 ± 13.28 (1–29)	3.40 ± 5.27 (0–12)	8.17 ± 6.74 (2–19)	9.36 ± 9.07 (1–29)
Uro 2	R	8.50 ± 8.74 (2–21)	0.80 ± 1.10 (0–2)	8.00 ± 4.24 (3–13)	7.82 ± 5.79 (2–21)
Uro 3	L	23.75 ± 40.35 (0–84)	3.60 ± 5.90 (0–14)	46.00 ± 8.94 (33–57)	35.36 ± 26.09 (0–84)
Uro 3	R	28.75 ± 40.53 (3–89)	5.80 ± 10.31 (0–24)	43.00 ± 13.54 (23–60)	36.55 ± 25.29 (3–89)
Tel	L	2.50 ± 3.32 (0–7)	1.00 ± 1.41 (0–3)	4.50 ± 2.59 (2–8)	3.82 ± 2.79 (0–8)
Tel	R	3.00 ± 2.16 (0–5)	1.40 ± 2.61 (0–6)	7.00 ± 1.41 (5–9)	5.55 ± 2.54 (0–9)
Abd		20.00 ± 14.72 (5–40)	23.40 ± 47.45 (0–108)	39.00 ± 10.37 (23–50)	39.18 ± 29.52 (5–117)
Total		1202.00	222.60	2172.50	1723.27

Epibionts colonized 37 anatomical units of *G. wilkitzkii* (including left and right appendages): antennulae, antennae, maxillae, maxillipeds, gnathopods, pereiopods, pleopods, uropods, telson, and abdomen (Table 7). With regard to the means of epibionts per anatomical unit, females showed the highest value (2172.5 ind./amphipod, $N = 16$), followed by the juveniles (1202.00 ind./amphipod, $N = 11$), and the males (222.80 ind./amphipod, $N = 3$).

With regard to the presence-absence of the different genera of protozoan epibionts on the anatomical units of *G. wilkitzkii* (Table 8), only *Ephelota* and *Cryptacineta* were present on all these anatomical units. *Acineta* was more confined to the posterior parts of the amphipod body, while *Podophrya* and *Epistylis* were restricted to the anterior body parts. A positive relationship was found between epibiont burden and host size for *Ephelota* (0.73; $P \leq 0.05$), *Podophrya* (0.65; $P \leq 0.05$), and *Epistylis* (0.68; $P \leq 0.05$).

The dendrogram in Figure 6 shows the results of a cluster analysis of the epibiont-assemblage on each of the specified anatomical units based on all 30 examined specimens of *G. wilkitzkii* combined. In general, separation of body parts by degree of infestation is not well distinguishable by clusters. However, the majority of posterior units are grouped in cluster I and II whereas most anterior appendages are aligned in cluster V. Cluster I is separated from the remaining body parts on the highest dissimilarity level (32.4%). This group comprises the posterior body parts and appendages (uropods 1–2, most pleopods) but also the paired maxillipeds. The mean density per unit was ~24 individuals. The abdomen, which hosts highest number of epibionts on the posterior body end (mean: ~40 ind./unit), is part of cluster II. The appendages with the highest degree of infestation (~91 ind./unit) are both pairs of gnathopods (between ~82 and 113 ind./unit) and pereiopod 1 and 5; they are combined in cluster III. The anterior appendages such as antennulae, antennae, maxillae 1 but also some pereiopods are grouped in cluster V and have an average density of ~61 ind./unit. Highest densities of epibionts were found on the antennae (107–130 ind./unit). As in some other appendages the infestations of left and right antennulae and antennae are grouped in "nearest neighbor" clusters. The cluster with the lowest mean densities (cluster IV: 9.64 ind./unit) comprises the majority of the pereiopods, uropod 3, and parts of telson.

The number of epibionts decreased towards the posterior end of the amphipod. The antennae were the most infested units. The Multiple Comparison Analysis between the epibiont distribution on males, females, and juveniles showed that there was a significant difference between them ($F = 13.56$; $P \leq 0.05$). The cluster analysis performed with the mean density of epibionts on each anatomical unit of the males, females, and juveniles (Fig. 7) showed two major clusters: (a) a group composed of 47.37% of the total units with highest densities

(mean 152.17 epibionts per unit) (antennae, antennulae, gnathopods, and pereiopods); (b) a second group (52.63 %) including units with low densities (mean 35.36 epibionts per unit) (maxillae, maxillipeds, pleopods, uropods, telson, and abdomen). In Figure 8 the different units were grouped in eight major body regions: (1) antennulae and antennae, (2) maxillae and maxillipeds, (3) gnathopods, (4) pereiopods, (5) pleopods, (6) uropods, (7) telson, and (8) abdomen. All pereiopods combined showed the highest degree of infestation (39.25%), followed by the gnathopods (22.29%), and antennulae and antennae (21.40%). Telson, abdomen, and uropods were the areas with lowest epibiontic burden (0.5, 2.37, and 3.15%, respectively). The Multiple Comparison Analysis showed no significant differences in densities per body region between males, females, and juveniles but between males and juveniles ($P = 0.028$; $P \leq 0.05$).

Distribution with Respect to the Epibiontic Genera

In comparison, *Cryptacineta* showed the highest mean densities on the most colonized areas, followed by *Ephelota* and *Acineta*. In contrast, *Podophrya* and *Epistylis* appeared with lower values (Table 9).

Discussion

In general, an epibiota has not been described for any of the sympagic organisms and in particular, it has not been observed for sympagic crustaceans even though ice ecologists have focused on this group since the early 1980s (B. Gulliksen and O. J. Lønne, pers. com.). We have presented herein the first description of epibiontic ciliates on the ice-amphipod *Gammarus wilkitzkii* (Morado and Small, 1995; Fernandez-Leborans and Tato-Porto, 2000a, 2000b; Fernandez-Leborans, 2001).

Suctorian ciliates of the genus *Ephelota* have been found as epibionts on different groups of crustacea: copepods, decapods, euphausids, and on the caprellid amphipod *Caprella acutifrons* (Fernandez-Leborans and Tato-Porto, 2000b). However, this genus has not been described previously as epibiont on gammarids. The genus *Cryptacineta* and its only species *Cryptacineta operta* have been found on two gammarid amphipods of Lake Baikal, *Carinogammarus seidlizi* and *C. wagneri* (Swarczewsky, 1928; Jankowski, 1978) and, therefore, ours is the first sighting of this ciliate in the marine environment. In addition, reproduction phases of *Cryptacineta* have not been described previously (Curds, 1985). We therefore present the first observation of budding in *Cryptacineta* in this study.

Ciliates of the genus *Acineta* have been found as epibionts on decapods, cladocerans, copepods, ostracods, isopods, and in numerous amphipod species (Fernandez-Leborans and Tato-Porto, 2000b). From these species of amphipods, the majority are freshwater gammarids from the Lake Baikal. *Acineta gammari* was found on *Gammarus pulex* (Matthes, 1954). In addition, other species found on gammarids are *A. corophii* on the marine amphipod *Corophium volutator* from Roscoff (France); *A. talitrus* on the marine amphipod *Talorchestia*; *A. tuberosa* on *Gammarus locusta* and *G. pulex;* and *Acineta* sp., on *Gammarus tigrinus* (see references in Fernandez-Leborans and Tato-Porto, 2000b). The species found in our study, *A. compressa*, has been described as epibiont on the freshwater cladoceran *Daphnia* (Fernandez-Leborans and Tato-Porto, 2000b).

Members of the *Podophrya*-group generally infest decapods (*P. sandi* on *Cambarellus patzcuarensis*), copepods (*P. flexilis* on *Cyclops*) (Curds, 1986), and gammarid amphipods (*P. niphargi* on *Niphargus strouhali*) (Fernandez-Leborans and Tato-Porto, 2000a). The species found on *Gammarus wilkitzkii*, *P. fixa*, has not yet been found as an epibiont.

TABLE 8

Presence (+) and absence (–) of the different epibiont genera on the anatomical units of G. wilkitzkii (m, males; f, females; j, juveniles).

	Ephelota	*Cryptacineta*	*Acineta*	*Podophrya*	*Epistylis*
Ant 1					
L	+ (m, f, j)	+ (m, f, j)	+ (m)	+ (m,f)	+ (j)
R	+ (m, f, j)	+ (m, f, j)	+ (m)	+ (m, f)	–
Ant 2					
L	+ (m, f, j)	+ (m, f, j)	+ (m, f)	+ (f, j)	+ (f, j)
R	+ (m, f, j)	+ (m, f, j)	+ (m)	+ (m, f)	+ (f)
Max 1					
L	+ (f)	+ (f, j)	–	–	+ (f)
R	+ (m, f)	+ (m, f, j)	–	+ (f)	+ (f)
Mxp					
L	+ (m)	+ (m, f, j)	–	+ (m, f)	+ (j)
R	+ (m, f)	+ (m, f, j)	–	+ (f)	+ (m, f)
Gna 1					
L	+ (m, f, j)	+ (m, f, j)	+ (m)	+ (m, f, j)	+ (m, f, j)
R	+ (m, f)	+ (m, f, j)	–	+ (m, f)	+ (m, f)
Gna 2					
L	+ (m, f, j)	+ (m, f, j)	–	+ (f)	+ (f, j)
R	+ (m, f, j)	+ (m, f, j)	–	+ (f, j)	+ (f)
Per 1					
L	+ (m, f, j)	+ (m, f, j)	–	+ (m, f, j)	+ (m, f)
R	+ (m, f, j)	+ (m, f, j)	+ (m)	+ (m, f, j)	+ (m, f)
Per 2					
L	+ (m, f, j)	+ (m, f, j)	+ (m)	+ (m, f, j)	+ (m)
R	+ (m, f, j)	+ (m, f, j)	+ (m)	+ (m, f, j)	+ (m, f, j)
Per 3					
L	+ (m, f, j)	+ (m, f, j)	+ (m, f)	+ (m, f, j)	+ (m)
R	+ (m, f, j)	+ (m, f, j)	+ (m, f, j)	+ (m, f, j)	+ (m)
Per 4					
L	+ (m, f, j)	+ (f, j)	+ (m)	+ (m, f, j)	+ (m, f, j)
R	+ (f, j)	+ (f, j)	+ (j)	+ (f, j)	+ (f)
Per 5					
L	+ (f, j)	+ (f, j)	+ (f, j)	+ (f, j)	+ (f)
R	+ (f, j)	+ (f, j)	–	+ (f, j)	+ (f, j)
Ple 1					
L	+ (m, f, j)	+ (f, j)	+ (m)	+ (f, j)	+ (m)
R	+ (m, f, j)	+ (m, f, j)	+ (j)	+ (m, j)	+ (j)
Ple 2					
L	+ (m, f, j)	+ (f, j)	+ (f)	+ (m, f)	–
R	+ (f, j)	+ (f, j)	–	+ (m, f)	+ (m, j)
Ple 3					
L	+ (m, f, j)	+ (f, j)	+ (m)	+ (m, f, j)	+ (m, j)
R	+ (m, f, j)	+ (f, j)	+ (m)	+ (f)	+ (m, j)
Uro 1					
L	+ (m, f, j)	+ (m, f, j)	+ (m)	+ (m, f, j)	+ (m)
R	+ (m, f, j)	+ (f, j)	+ (m)	–	–
Uro 2					
L	+ (m, f, j)	+ (m, f, j)	–	+ (f)	–
R	+ (m, f, j)	+ (f, j)	+ (m)	–	–
Uro 3					
L	+ (m, f, j)	+ (m, f, j)	+ (f)	+ (m, f)	+ (f)
R	+ (m, f, j)	+ (f, j)	+ (f)	+ (m, f, j)	+ (m)
Tel					
L	+ (m, f)	+ (m, f, j)	–	–	–
R	+ (m, f)	+ (f, j)	–	+ (f)	+ (m, f)
Abd	+ (m, f, j)	+ (f, j)	+ (m, j)	–	–

TABLE 9

Density of the different epibiontic genera on each anatomical unit of *G. wilkitzkii* [mean ± standard deviation] (minimum-maximum).

		Ephelota	*Cryptacineta*	*Acineta*	*Podophrya*	*Epistylis*
Ant 1	L	5.55 ± 5.22 (0–15)	54.00 ± 29.20 (13–113)	0.27 ± 0.90 (0–3)	0.82 ± 1.47 (0–4)	0.18 ± 0.60 (0–2)
Ant 1	R	3.82 ± 4.67 (0–12)	50.09 ± 36.75 (13–133)	0.73 ± 2.41 (0–8)	0.82 ± 0.98 (0–2)	0.00 ± 0.00 (0–0)
Ant 2	L	20.73 ± 27.78 (0–81)	81.73 ± 42.56 (16–179)	0.18 ± 0.40 (0–1)	1.36 ± 2.16 (0–6)	3.27 ± 5.61 (0–16)
Ant 2	R	17.64 ± 25.27 (0–83)	107.18 ± 86.84 (0–306)	0.64 ± 2.11 (0–7)	1.18 ± 2.48 (0–8)	3.27 ± 8.55 (0–28)
Max 1	L	0.09 ± 0.30 (0–1)	14.82 ± 8.42 (0–25)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	1.00 ± 3.32 (0–11)
Max 1	R	0.45 ± 0.93 (0–3)	10.82 ± 9.35 (2–32)	0.00 ± 0.00 (0–0)	0.09 ± 0.30 (0–1)	0.18 ± 0.60 (0–2)
Mxp	L	0.09 ± 0.30 (0–1)	23.18 ± 40.93 (0–136)	0.00 ± 0.00 (0–0)	0.18 ± 0.40 (0–1)	0.09 ± 0.30 (0–1)
Mxp	R	1.18 ± 3.31 (0–11)	20.91 ± 40.00 (0–138)	0.00 ± 0.00 (0–0)	0.18 ± 0.60 (0–2)	2.09 ± 6.61 (0–22)
Gna 1	L	5.27 ± 7.06 (0–21)	74.82 ± 59.43 (5–206)	0.73 ± 2.41 (0–8)	0.73 ± 0.90 (0–3)	1.73 ± 3.85 (0–12)
Gna 1	R	7.09 ± 14.12 (0–47)	104.0 ± 86.6 (0–282)	0.00 ± 0.00 (0–0)	0.64 ± 1.03 (0–3)	1.45 ± 4.20 (0–14)
Gna 2	L	11.09 ± 14.27 (0–41)	69.27 ± 50.89 (10–181)	0.00 ± 0.00 (0–0)	1.09 ± 1.92 (0–6)	0.73 ± 1.62 (0–4)
Gna 2	R	13.55 ± 21.36 (0–65)	67.55 ± 41.21 (10–131)	0.00 ± 0.00 (0–0)	1.09 ± 1.64 (0–5)	7.27 ± 13.89 (0–46)
Per 1	L	16.27 ± 19.04 (0–59)	44.18 ± 29.26 (4–111)	0.00 ± 0.00 (0–0)	1.18 ± 1.60 (0–5)	0.45 ± 1.04 (0–3)
Per 1	R	18.00 ± 22.25 (0–60)	32.27 ± 22.80 (1–74)	2.18 ± 7.24 (0–24)	0.91 ± 1.45 (0–4)	1.45 ± 3.70 (0–12)
Per 2	L	16.27 ± 16.24 (0–44)	33.36 ± 28.65 (2–94)	1.73 ± 5.73 (0–19)	3.82 ± 9.21 (0–31)	1.09 ± 3.62 (0–12)
Per 2	R	12.64 ± 16.72 (0–47)	43.27 ± 34.60 (3–114)	2.09 ± 6.93 (0–23)	1.18 ± 0.98 (0–3)	3.18 ± 7.78 (0–26)
Per 3	L	21.00 ± 25.29 (0–78)	40.00 ± 41.83 (0–123)	0.18 ± 0.40 (0–1)	1.45 ± 1.37 (0–4)	0.55 ± 1.81 (0–6)
Per 3	R	23.2723.39 (0–58)	40.82 ± 40.60 (2–130)	0.73 ± 1.56 (0–5)	2.82 ± 3.63 (0–10)	0.55 ± 1.81 (0–6)
Per 4	L	34.64 ± 32.48 (0–94)	39.00 ± 51.81 (0–168)	1.36 ± 4.52 (0–15)	2.09 ± 3.56 (0–12)	5.91 ± 7.96 (0–24)
Per 4	R	24.18 ± 28.92 (0–77)	35.27 ± 31.89 (0–120)	0.09 ± 0.30 (0–1)	2.73 ± 4.56 (0–16)	2.91 ± 6.02 (0–20)
Per 5	L	30.45 ± 38.09 (0–111)	29.55 ± 29.24 (0–91)	0.18 ± 0.40 (0–1)	2.55 ± 4.70 (0–16)	2.91 ± 5.68 (0–16)
Per 5	R	23.45 ± 29.39 (0–95)	37.91 ± 30.60 (0–91)	0.00 ± 0.00 (0–0)	2.45 ± 4.70 (0–16)	3.55 ± 6.02 (0–16)
Ple 1	L	3.00 ± 3.26 (0–9)	9.82 ± 14.66 (0–45)	0.09 ± 0.30 (0–1)	0.45 ± 0.82 (0–2)	0.73 ± 2.41 (0–8)
Ple 1	R	2.09 ± 3.51 (0–12)	13.36 ± 20.79 (0–69)	0.09 ± 0.30 (0–1)	0.27 ± 0.65 (0–2)	0.36 ± 1.21 (0–4)
Ple 2	L	3.36 ± 3.14 (0–9)	9.64 ± 10.77 (0–35)	0.09 ± 0.30 (0–1)	0.45 ± 1.04 (0–3)	0.00 ± 0.00 (0–0)
Ple 2	R	4.18 ± 5.06 (0–15)	9.73 ± 13.14 (0–48)	0.00 ± 0.00 (0–0)	0.36 ± 0.50 (0–1)	0.27 ± 0.65 (0–2)
Ple 3	L	7.82 ± 8.64 (0–26)	11 ± 7.09 (0–26)	0.27 ± 0.90 (0–3)	0.55 ± 0.82 (0–2)	2.91 ± 9.01 (0–30)
Ple 3	R	10.91 ± 11.24 (0–36)	11.64 ± 16.75 (0–56)	0.82 ± 2.71 (0–9)	0.36 ± 0.67 (0–2)	1.09 ± 3.02 (0–10)
Uro 1	L	6.73 ± 6.08 (0–19)	13.55 ± 25.00 (1–85)	0.18 ± 0.60 (0–2)	1.36 ± 1.86 (0–5)	0.55 ± 1.81 (0–6)
Uro 1	R	4.09 ± 3.81 (0–13)	8.36 ± 16.51 (0–56)	0.09 ± 0.30 (0–1)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
Uro 2	L	2.27 ± 3.17 (0–10)	6.73 ± 8.66 (0–29)	0.00 ± 0.00 (0–0)	0.36 ± 1.21 (0–4)	0.00 ± 0.00 (0–0)
Uro 2	R	3.09 ± 3.78 (0–13)	4.55 ± 6.42 (0–21)	0.18 ± 0.60 (0–2)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
Uro 3	L	12.36 ± 14.89 (0–44)	21.55 ± 24.40 (0–84)	0.18 ± 0.60 (0–2)	1.18 ± 2.99 (0–10)	0.09 ± 0.30 (0–1)
Uro 3	R	12.36 ± 13.37 (0–35)	22.45 ± 24.50 (0–89)	0.09 ± 0.30 (0–1)	1.27 ± 2.37 (0–8)	0.36 ± 1.21 (0–4)
Tel	L	1.27 ± 1.90 (0–6)	2.55 ± 2.46 (0–7)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)
Tel	R	1.36 ± 1.63 (0–4)	2.91 ± 2.21 (0–7)	0.00 ± 0.00 (0–0)	0.18 ± 0.40 (0–1)	1.09 ± 2.43 (0–6)
Abd		18.18 ± 17.18 (0–48)	7.55 ± 8.74 (0–22)	13.45 ± 33.57 (0–108)	0.00 ± 0.00 (0–0)	0.00 ± 0.00 (0–0)

The peritrich ciliate *Epistylis* has been observed as epibiont on various groups of crustacea (copepods, decapods, cladocerans, branchiopods, and amphipods). Among the amphipods, *Gammarus tigrinus* showed the highest diversity of *Epistylis*-species: *E. gammari*, *E. nitocrae*, *E. ovalis*, *E. thienemanni*, *E. zschokkei*, and *Epistylis* sp. (Fernandez-Leborans and Tato-Porto, 2000a). Species of *Epistylis* have also been described on *G. oceanicus*, *G. salinus*, *G. pulex*, and *Gammarus* indet. (see references in Fernandez-Leborans and Tato-Porto, 2000a) and *G. duebeni* (Dunn and Dick, 1998).

In the present study, several observations of the epibiont morphology seem to indicate a particular adaptation to the arctic environment. In the case of *Ephelota*, the "resistant stages" of this ciliate have not been observed previously. We have analyzed *Ephelota* epibionts on parasite copepods of salmon from Scotland (Fernandez-Leborans et al., 2005), and on diverse free-living decapod crustacea also from Scotland (Fernandez-Leborans and Gabilondo, 2005), but such resistant stages were not found. Another striking observation is the relative high proportion of reproductive phases of *Ephelota* found in comparison to nonreproductive forms. Also the relatively high number of buds per specimen is a peculiarity of *Ephelota* epibionts never observed in other environments. The described phenomena probably represent an adaptation of the epibiont to the physical constraints of the polar environment or the sympagic life style of its host, *G. wilkitzkii*.

It is difficult to make a comparison with other crustaceans with respect to the degree of infestation due to the morphological differences in the herein presented epibiontic species and the lack of observations. On some species of *Gammarus* (*G. duebeni* and *G. tigrinus*) from freshwater habitats in Ireland, the burden of ciliate epibionts fluctuated between 2.67 and 29.36 per individual (Dunn and Dick, 1998), which were notably lower than the densities found in the present study. Epibiontic ciliates have been described for *Euphasia superba* from the Antarctic south of Australia (Rakusa-Suszczewski and Nemoto, 1989). The degree of infestation was highest for juvenile krill (72%), followed by male (35–62%) and female specimens (43%); the densities of the ciliate genera *Ephelota* fluctuated between 110 and 308 per individual (Rakusa-Suszczewski and Nemoto, 1989) and were therefore up to four-fold lower than found for *G. wilkitzkii*. We assume that a molt cycle with long intermolt phases such as suggested for polar crustaceans (Clarke, 1982) allow for the establishment of a rich epibiont community on the body surface.

Similar to our observations, the abundance of protozoan epibionts is positively correlated with the size of the basibiont in benthic crustacea (Key and Barnes, 1999) and zooplankton (Threlkeld et al., 1993). Principally, this may be due to the ontogenic decrease in molting frequency of the basibiont (Moyano, 1989). The presence of

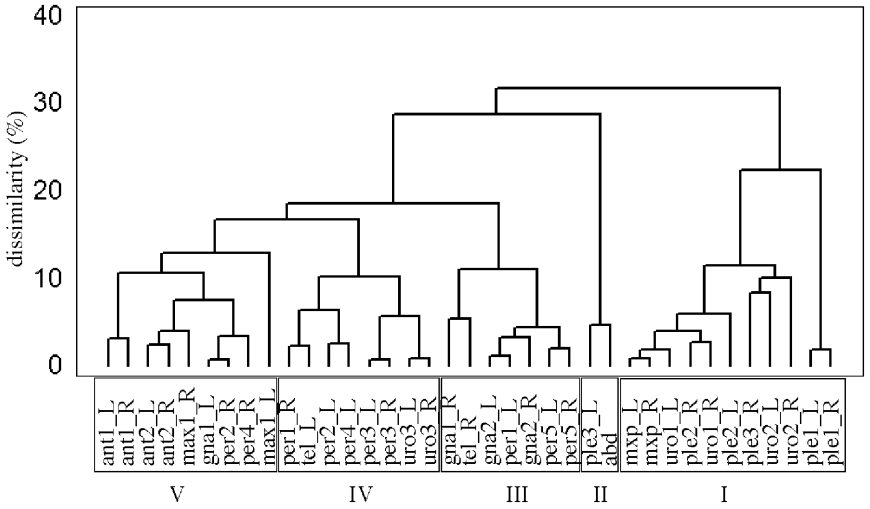

FIGURE 6. Dendrogram showing the results of a cluster analysis of the epibiont-assemblage on each of the specified anatomical units of *G. wilkitzkii* (the vertical axis displays the percentage of dissimilarity). Abbreviations: ant (antenna), max (maxilla), gna (gnatopod), per (pereiopod), tel (telson), ur (uropod), ple (pleopod), abd (abdomen), mxp (maxilliped).

high numbers of epibionts on *G. wilkitzkii* may be called disadvantageous for the amphipod. The epibionts represent a supplementary weight for the basibiont and they can reduce mobility by modifying the hydrodynamics of the body and hindering the movement of the appendages (Threlkeld et al., 1993). The epibiontic burden possibly increases the vulnerability of the amphipod to potential predators (Overstreet, 1983). In sea ice predator pressure is probably more reduced as compared to a pelagic life style.

Gammarus wilkitzkii is an omnivore that preys on conspecifics and other crustaceans and sympagic meiofauna, and grazes on ice algae and other plant material (Poltermann, 2001). The strong body setation of *G. wilkitzkii* entraps suspended particles that have been interpreted as supplementary food supply (Poltermann, 2001). The intense grooming and cleansing behavior of *G. wilkitzkii* possibly determine the degree of infestation on the different body parts of the amphipod, with the anterior (grooming) appendages being the most infested due to their combing activity of the entire body setation. *Gammarus wilkitzkii* can survive starvation periods of up to 8 to 10 mo (Poltermann, 1997). Synchronization between the life cycles of the basibiont and the epibiont has been described for crustaceans (Fenchel, 1965; Eggleston, 1971): the epibiont couples its reproduction to the molt cycle of the crustacean. Encystment and the production of "resistant" stages in *Ephelota* may indicate that *G. wilkitzkii* is in the state of molting. In some marine ciliates the production of cysts is an adaptation to changes in environmental conditions. For example, in oligotrich ciliates from intertidal pools encystment is synchronized with the tidal cycle to ensure their dispersion during high tide (Fauré-Fremiet, 1948; Santamaría and Montagnes, 2000).

Environmental conditions and the behavior of the basibiont determine the distribution of epibionts. In several freshwater and marine cold-water environments, the ciliate epibionts of several species of *Gammarus* (*G. oceanicus*, *G. zaddachi*, *G. duebeni*, *G. salinus*, and *G. locusta*) have been studied (Fenchel, 1965). Twenty-five species of ciliate protozoans were reported (among these *Epistylis* and *Acineta*). Some species appear host-specific only to these amphipods, although the lack of comparative analysis with similar species does not confirm their taxonomical position. Despite the fact that Fenchel (1965) does not provide data on the statistical distribution and densities of epibionts on the different body parts of the amphipods, his work may allow comparison with the present study. Although the total number of genera was lower in the present study, the number of suctorian genera was higher. *Acineta* was observed only on *G. duebeni*, while *Epistylis* is documented for *G. oceanicus*, *G. salinus*, and *G. zaddachi* (Fenchel, 1965). *Epistylis* infested only the antennae, while *Acineta* was restricted to the pleopods. The higher number of epibiont species appears to coincide with a higher degree of site specification on the host, while in the present study the low number of epibiontic species was accompanied by a more unspecific distribution. In Fenchel (1965)

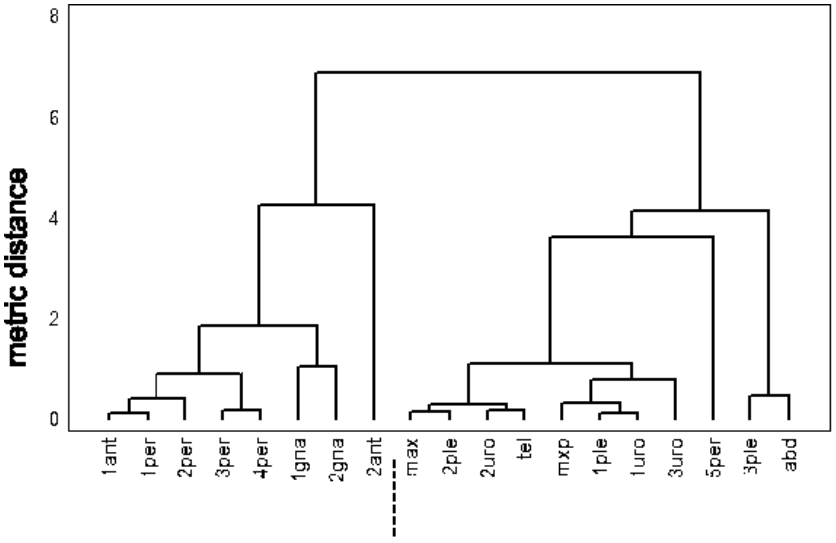

FIGURE 7. The cluster analysis performed with the mean density of epibionts on each anatomical unit of the males, females, and juveniles, from the anterior to the posterior end of the basibiont (the vertical axis shows the metric [Manhattan] distance). Same abbreviations as in Figure 6.

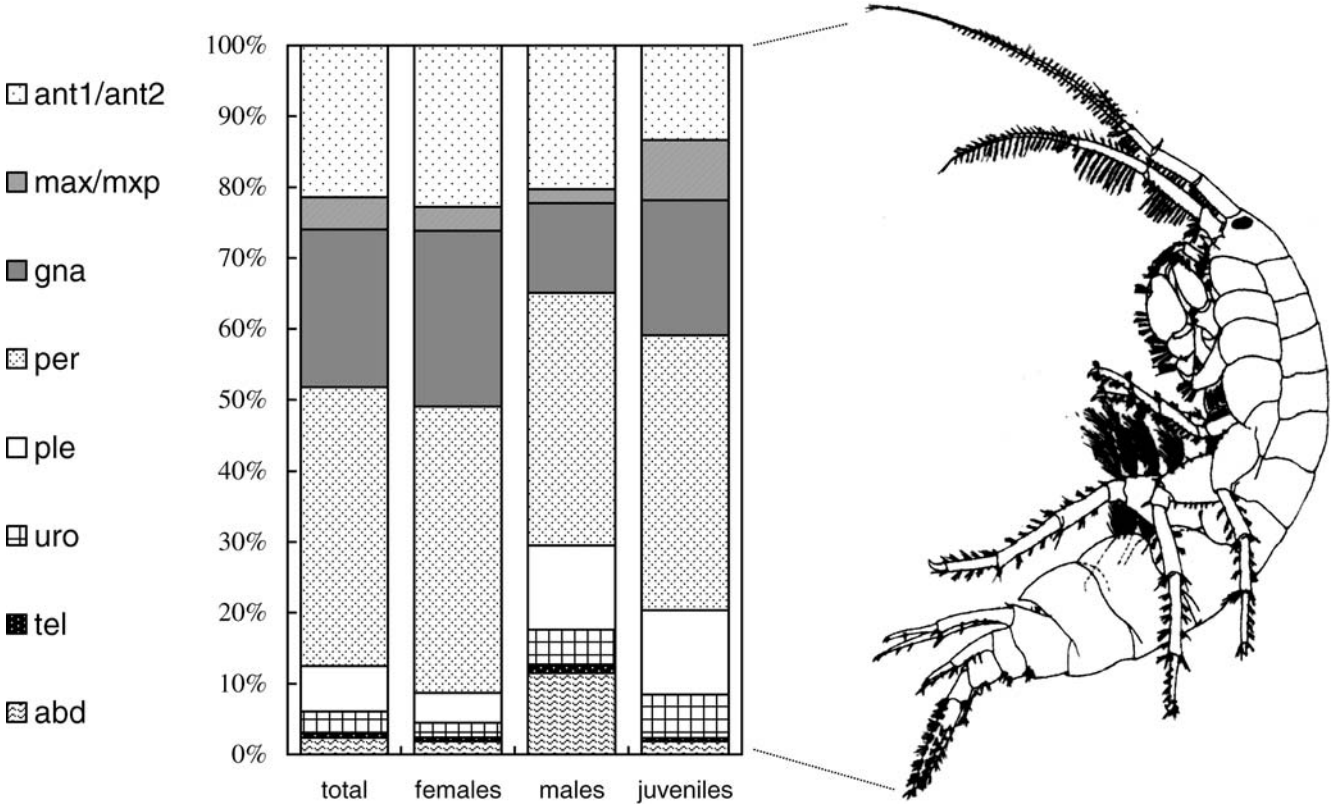

FIGURE 8. Percentages of epibionts on all, males, females, and juveniles, from the anterior to the posterior end of the basibiont. The different units were grouped in eight major body regions: antennulae and antennae, maxillae and maxillipeds, gnathopods, pereiopods, pleopods, uropods, telson, and abdomen (the vertical axis is the relative frequency). Same abbreviations as in Figure 6.

also the molt cycle of gammarids was synchronized with the production of reproductive forms in ciliates (telotrochs in peritrichs, buds in suctorians).

The high burden of epibionts on the anterior regions of the body of *G. wilkitzkii* can be related to the feeding mode of the basibiont. Since epibionts filter organic particles from the media they live in, they usually settle in areas that are characterized by relatively high water movements such as caused by the respiratory current (Arndt, 2002). Gnathopods and head appendages are therefore the most infested body units. As mentioned earlier, these appendages are also involved in grooming and are therefore the most susceptible body units for epibionts. Moreover, the hosts' grooming pattern may determine the size spectrum of epibionts on different body parts of the basibiont. *Ephelota* was the largest epibiont found in this study and was most abundant on antennae and pereiopods but scarce on the buccal appendages and gnathopods. On the contrary, the small *Cryptacineta*-species was very frequent on the mouthparts. These ciliates bear the lorica as a protective shield against eventual abrasion by the amphipod. *Acineta* was more abundant on the posterior part of the body of *G. wilkitzkii*, which could be related to the enhanced nutrient supply in the cloaca area (Threlkeld et al., 1993). In general, the dorsal body part may be considered the most unsuitable for settling of epibionts because of the high potential of abrasion when moving in narrow channels such as in the ice interior (Cook et al., 1998). In addition, water motion is greatly reduced on the dorsal side of the amphipod body as compared to the ventral side. Biotic and abiotic conditions probably vary significantly along the body surface of the basibiont, creating various microhabitats which are favorable for different epibiontic species. Due to their small body size and low densities on the surface of the basibiont, *Podophrya* and *Epistylis* contribute little to the overall epibiont biomass. *Podophrya* was found even attached to the stalk or to the basal disc of *Ephelota*, and could use nutrients that are not ingested by this ciliate. Like *Podophrya*, *Epistylis* was more abundant on anterior regions of the amphipod. This has been observed earlier for *Gammarus* species (Fenchel, 1965). *Epistylis* is a peritrich ciliate, which is a very effective purificator of waste water (Foissner et al., 1992).

In summary:

(1) Epibiontic ciliates have not been described previously for a sympagic crustacean.
(2) *Ephelota* has not yet been documented as an epibiont on gammarid amphipods. We present the first observation of the genera *Cryptacineta* in the marine environment.
(3) The number of epibionts per amphipod was extraordinary high for *G. wilkitzkii* reaching up to 3346 individuals. *Cryptacineta* showed the highest density values, followed by *Ephelota*. *Acineta*, *Podophrya*, and *Epistylis* whose species contributed only little to the overall epibiontic burden.
(4) The epibionts were present on all 37 anatomical units examined on *G. wilkitzkii*. Females showed the highest density per anatomical unit, followed by the juveniles and the males.
(5) *Ephelota* and *Cryptacineta* were equally distributed on all amphipodal body parts. In contrast, *Acineta* was more confined to the posterior parts of the crustacean body, while *Podophrya* and *Epistylis* were restricted to the anterior body parts.
(6) The length of the gammarid was positively correlated with the number of epibionts for *Ephelota* (0.73; $P \leq 0.05$), *Podophrya* (0.65; $P \leq 0.05$) and *Epistylis* (0.68; $P \leq 0.05$). The right and the left sides of the gammarid were equally infested.
(7) Considering the distribution of the epibionts along the axis of the amphipod body, there was a decrease in the number of

epibionts towards the posterior end of the body. The highest degree of infestation was observed on the antennae.

Acknowledgments

We would like to thank Bjørn Gulliksen, the crew on RV *Jan Mayen*, UNIS, and Total E&P for logistical and financial support. We also express to Dr. Corliss (a very distinguished protistologist) many thanks for his constructive comments on the manuscript and his help in the improvement of the final version, and for the kindly attention that he has paid to our works.

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Ms accepted November 2005