

## Intersite epibiosis characterization on dominant mangrove crustacean species from Malaysia

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### Abstract

Epibiosis was studied in dominant mangrove crustacean species in several areas in Malaysia. The observed basibionts were the crustaceans *Mesopodopsis orientalis*, *Acetes japonicus*, *Acetes sibogae*, *Acetes indicus* and *Fenneropenaeus merguensis* and the epibionts found were the protozoan ciliates *Acineta branchicola*, *Lagenophrys eupagurus*, *Conidophrys pitelkae* and *Zoothamnium duplicatum*. Basibionts from the open sea area (*Acetes japonicus*) and from a sandy beach of Penang (*Mesopodopsis orientalis*) showed the lowest epibiont densities. Considering all the colonized anatomical units each basibiont species had a distinct epibiotic distribution and the epibiont species presented a significantly different distribution over each of the basibiont species. In the basibiont *M. orientalis* a significant difference was observed in epibiotic distribution between populations from different geographical areas. Species sampled on mangrove and offshore areas also differed in this respect. The different epibiont species varied among locations according to the structure of the community. We also report on the pattern of epibiont distribution over the anterior-posterior axis of the basibiont, on the influence of physiological characteristics of basibiont and epibiont and on the influence of environmental conditions on the epibiont communities.

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### Introduction

Epibiosis is a facultative 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 constitutes a support for the epibiont (Threlkeld *et al.*, 1993). Both concepts describe ecological functions (Wahl, 1989). Several crustacean groups such as cladocerans, copepods, cirripedes, isopods, amphipods and decapods include forms that are hosts for macroepibiont invertebrates (Porifera, Cnidaria, Platyhelminthes, Nemertea, Rotifera, Nematoda, Polychaeta, Cirripedia, Decapoda, Gastropoda, Bivalvia, Phoronida, Bryozoa, Ascidiacea and others) (Ross, 1983) and for protozoan microepibionts of the phylum Ciliophora (apostomatids, chonotrichids, suctorians, peritrichs, and heterotrichs) (Corliss, 1979; Small and Lynn, 1985).

The epibiosis involves different aspects, among which: (1) the specificity between epibionts and their crustacean basibionts; (2) the morphological and physiological adaptations of the epibionts; (3) the effects produced by the epibionts on the crustaceans; (4) the possible use of epibionts for the assessment of water quality; (5) the implications of epibionts on cultures of crustaceans and (6) the organization of the epibiont communities. A number of effects are related to epibiosis. These include advantages for the epibiont such as dispersal and geographical expansion, increase of the supply of nutrients and protection against predation

(Connell and Keough, 1985; Williams and Moyses, 1988; Abelló *et al.*, 1990; Key *et al.*, 1997). On the other hand, epibiosis can be disadvantageous to the epibiont, creating ontogenetic or behavioural changes of the basibiont. Epibiosis can provide mimetic protection for the basibiont and cleaning. Conversely, epibiosis may have the disadvantage of restricting the mobility of the basibiont, it may affect growth and moulting and the functioning of several organs (eyes, gills, appendages, reproductive systems) and it may cause an increase of the risk of predation. Epibionts and basibionts also may compete for nutrients (Wahl, 1989; Threlkeld *et al.*, 1993; Becker and Wahl, 1996).

Epibiotic associations could represent excellent models to examine diversity patterns among geographical regions on a variety of scales, including whole communities of species in different habitats. Although many crustaceans have been studied for their behaviour, few studies dealt with their associates and virtually nothing is known about the interactions between these epibionts and their basibiont hosts (Utz, 2003). The study of physical and biological factors related to the origin of symbioses, hypersymbioses and predator-prey relationships is a promising field of research (Williams and McDermott, 2004).

Many marine sessile life forms depend on the characteristics of the living substratum to which they are

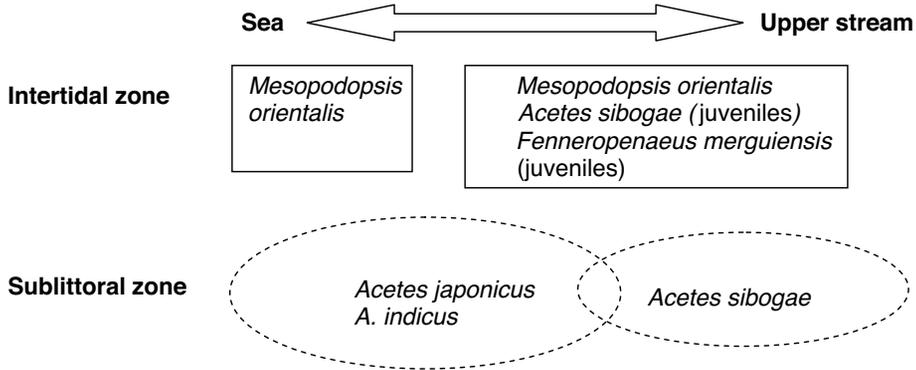


Fig. 1. Distribution of hyperbenthic crustaceans in an estuary system in Peninsular Malaysia (schematic, modified from Hanamura *et al.*, in press b)

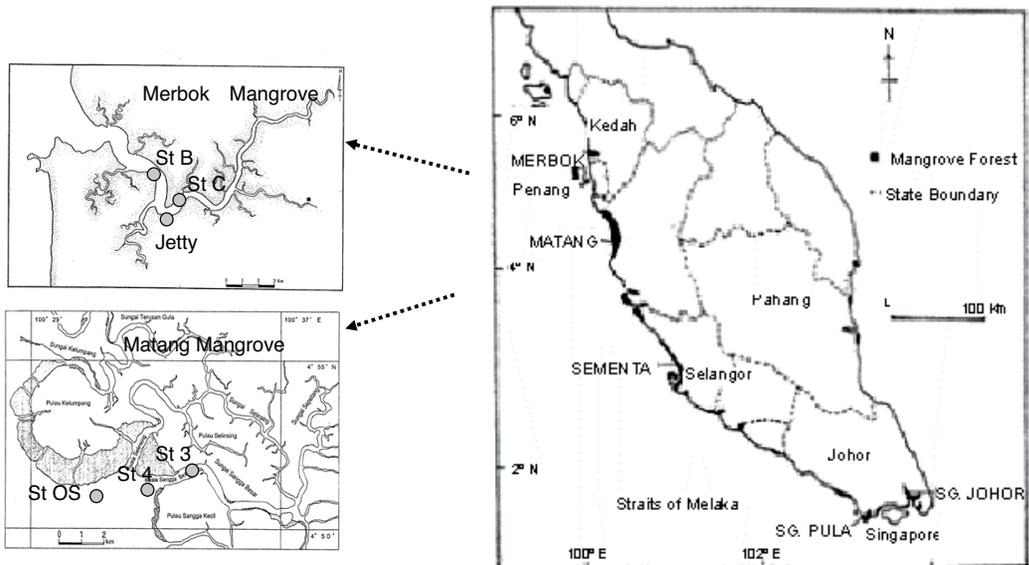


Fig. 2. Study area (right) and sampling sites (left) in north-western peninsular Malaysia. For locality names see text.

adhered (Gili *et al.*, 1993) and, consequently, structure dynamics, physiology, and ecology of the basibiont may reflect on colonisation patterns of the epibiont species, and on settlement and growth of communities of invertebrates and protists.

Epibiosis is the evolutionary result of the interaction of environmental factors with benthic life forms (Key *et al.*, 1999). It is a dynamic process, and the benefits and disadvantages to the intervening organisms vary depending on environmental conditions (Bush *et al.*, 2001). Epibiosis can appear as a temporal colonisation due to a diminution of basibiont defences (Wahl and Mark, 1999). Epibiosis may modify a number of interactions between the basibiont and biotic and abiotic components of the system. Despite its wide occurrence, epibiosis is still not very well known with respect to its consequences for both basibionts and epibionts. A number of studies of crustacean epibiosis have been performed in freshwater systems, with few focusing on marine and estuarine environments (Carman and Dobbs, 1997). Epibiosis, as one of the closest possible interspecific associations, is a common phenomenon in shallow subtidal communities. Fouling of the basibiont creates a new interface between the basibiont and its environment. Most interactions between a living organism and its biotic and abiotic environment (e.g., predation, mating, defence, mutualism, parasitism, symbiosis, drag) are linked to essential surface features of the organism (Laudien and Wahl, 2004).

Epibiont populations may have relevant functions at the ecosystem level. Epibionts showing high densities may even contribute to energy flow to higher trophic levels. The colonization of a marine hard-bottom community on newly available substrata is governed by pre-settlement (survival and distribution of colonising stages), settlement (composition of coloniser pool, competence of settling stages, substratum preferences) and post-settlement processes (competition, consumption, etc.). When, during recruitment, substratum becomes the limiting factor, dominant competitors may drive competitively inferior species to extinction (Enderlein and Wahl, 2004). Epibiosis is important with regard to biodiversity and conservation. In temperate regions diversity, or species richness, of benthos in soft substrates on the continental shelf and slope may rival that in shallow tropical seas (Brusca and Brusca, 1990).

In tropical mangrove estuaries and related coastal waters in Malaysia and Thailand several crustacean species occur in abundance, constituting a substantial portion of the hyperbenthic fauna (Hanamura *et al.*, in press a, b). These crustaceans also are major dietary resources

of mangrove fishes (e.g., Kiso and Mahyam, 2003; Chew *et al.*, 2006; Then *et al.*, 2006), which suggests that they play an important ecological role in the mangrove estuary.

These species showed a generalized distributional pattern in mangrove systems of north-western Peninsular Malaysia, as is indicated in Fig. 1, where adult and subadult *Acetes indicus* Milne Edwards 1830 and *A. japonicus* Kishinouye 1905 occur in abundance in the sublittoral zone of the river mouth, while *A. sibogae* Hansen 1919 tends to be found in increasing numbers in the middle to upper reaches. In contrast, *Mesopodopsis orientalis* (Tattersall, 1908) has a strong affinity to the littoral zone from coastal to upstream areas. Meanwhile, there is a possibility of the existence of two populations of *M. orientalis* in the studied areas, i.e., estuarine and coastal populations (Hanamura *et al.*, unpublished data). Consequently, the sampling sites of this mysid are specified for future consideration. Like *Mesopodopsis*, young juveniles of *A. sibogae* and *Fenneropenaeus merguensis* de Man 1888 occur predominantly along the littoral zone of the estuary swamp (Hanamura *et al.*, in press a, b).

Recent ecological studies on the hyperbenthos have revealed that the ciliate-crustacean association is a frequently observed phenomenon in tropical mangrove estuaries and related coastal waters (Hanamura *et al.*, unpublished data). In the present study, the epibiosis on these crustacean species was analyzed, with emphasis on the differences between basibiont species, and between the diverse sampling sites. The epibiosis was also considered in terms of preference of epibiotic species and with respect to the structure composition of the epibiont community. The purpose of this study is (1) to analyze if the epibiotic communities on the diverse basibiont species and localities present particular characteristics related to the species found, and (2) their distribution on the anatomical units of the basibiont. We will propose explanations for the different patterns of colonization. We hypothesize that dominant mangrove crustacean species present a characteristic epibiosis specific to each species and different from populations living on open sea environments.

## Material and methods

The basibiont species were sampled in areas of Malaysia and Thailand indicated in Fig. 2. The crustaceans listed below were collected as follows:

- *Mesopodopsis orientalis* or *M. orientalis* B, Merbok

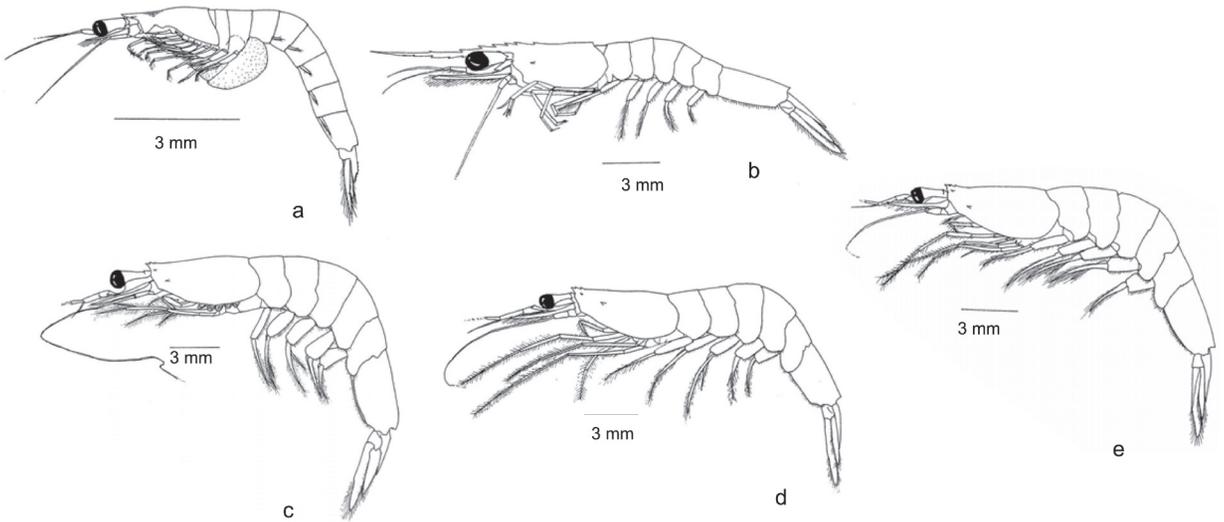


Fig. 3. Basibiont species: a, *Mesopodopsis orientalis*, adult female; b, *Fenneropenaeus merguensis*, juvenile; c, *Acetes japonicus*, adult female; d, *A. indicus*, adult female and e, *A. sibogae*, adult female.

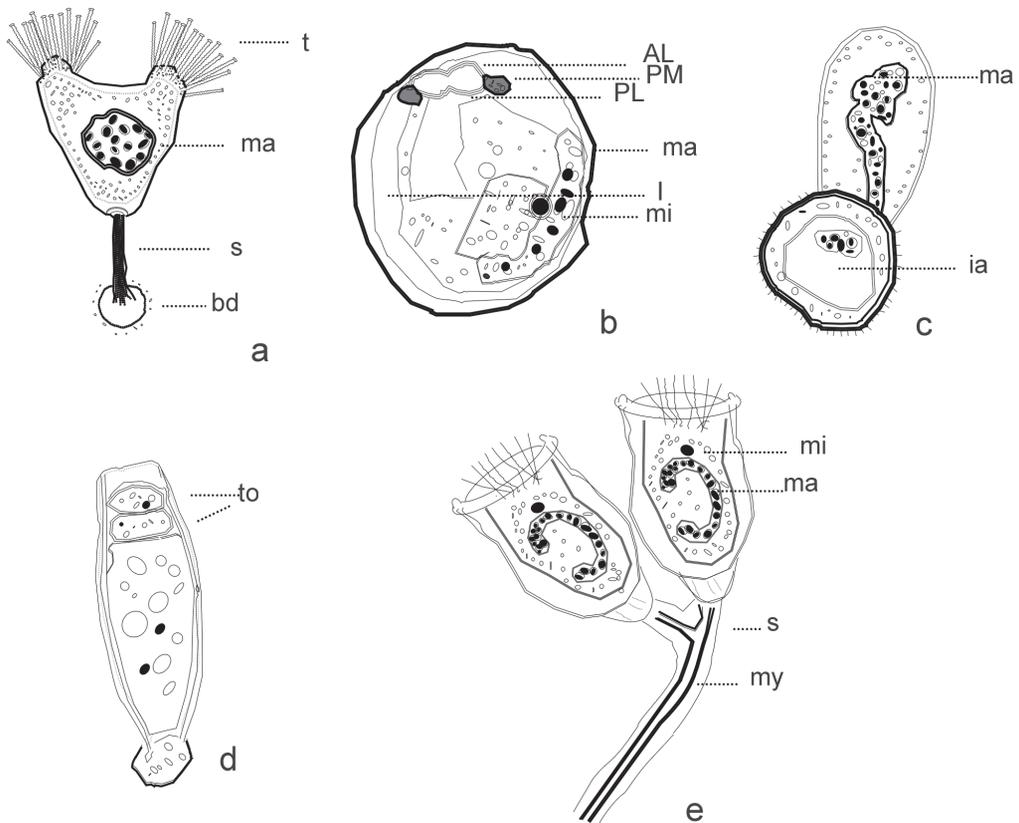


Fig. 4. Epibiont species: a, *Acineta tuberosa*; b, *Lagenophrys eupagurus*; c, *Conidophrys pitelkae*, trophont; d, *Conidophrys pitelkae*, tomont and e, *Zoothamnium duplicatum*, with ma, macronucleus; mi, micronucleus; bd, basal disc; AL, anterior lip; PL, posterior lip; PM, peristomial myoneme; I, infundibulum; ia, ingestive apparatus; to, tomite; my, myoneme; s, stalk and t, tentacles.

- mangrove, Malaysia, Station B, sandy beach, littoral, hand net, 17.05.2006 (n = 20)
- *M. orientalis* C, Merbok mangrove, Malaysia, Station C, sandy beach, littoral, hand net, 09.12.2004 (n = 20)
  - *M. orientalis* M, Merbok mangrove, Malaysia, Kampong Batu-Lintang Jetty, littoral, hand net, 16.12.2005 (n = 20)
  - *M. orientalis* OS, coastal water without mangrove, Teluk Kumbar, Penang, Malaysia, sandy beach, littoral, hand net, 16.03.05 (n = 20)
  - *M. orientalis* T, Samut Songkhram, Thailand, shrimp culture pond, sublittoral, grab, 13.07.2005 (n = 20)
  - *Acetes japonicus*, Matang Mangrove, Malaysia, Stations 3, 4, sledge, sublittoral, 15.12.2005 (n = 20)
  - *A. japonicus* OS, coastal water without mangrove, Teluk Kumbar, Penang, Malaysia, sandy beach, littoral, hand net, 18.01.2006 (n = 20)
  - *Acetes sibogae*, Matang mangrove, Malaysia, 4 km offshore of Station 4, sledge, sublittoral, 13.06.2006 (n = 20)
  - *Acetes indicus*, Matang mangrove, Malaysia, Station 4, sledge, sublittoral, 15.12.2005 (n = 20)
  - *Fenneropenaeus merguensis*, Merbok mangrove, Malaysia, Station C, sandy beach, littoral, hand net, 09.12.2004 (n = 20).

The FAO (Food and Agriculture Organization) names of the host crustaceans are *F. merguensis* (listed as *Penaeus merguensis*) - Banana prawn; *A. indicus* - Jawla paste shrimp; *A. japonicus* - Akiami paste shrimp and *A. sibogae* - Alamang shrimp (Carpenter and Niem, 1988) (Fig. 3).

Samples were fixed upon collection in 5% seawater-buffered formalin. Water temperature and salinity were measured using an electronic T-S meter (Alec ACT20 D2) (for the actual data see Hanamura *et al.*, in press a, b). Crustaceans were dissected in the laboratory and each relevant anatomical unit was observed under a stereomicroscope. Epibionts on the surface of the anatomical units were counted under stereo- and compound microscopes. The density of colonial species was measured as the number of zooids. In order to identify the protozoan epibionts, they were isolated and treated with the silver carbonate technique of Fernandez-Leborans and Castro de Zaldumbide (1986), and with methyl green and neutral red. Permanent slides were obtained from the stained ciliates. Measurements of the epibionts were taken using an ocular micrometer. Light microscope images were obtained using image analysis (KS300 Zeiss). Taxonomic classification of ciliate spe-

cies was made according to Lynn and Small (2000).

Statistical analyses were performed with Statgraphics and SPSS software and included principal component analysis, multiple comparison, multiple regression, MANOVA and hierarchical conglomerate analyses with the Manhattan metric distance.

## Results

### *Epibiont species*

Epibionts described and analyzed below were found on the following crustacean basibionts, all belonging to the class Malacostraca: *Mesopodopsis orientalis* (family Mysidae, order Mysidacea), *Acetes japonicus*, *A. sibogae* and *A. indicus* (family Sergestidae; order Decapoda) and *Fenneropenaeus merguensis* (family Penaeidae; order Decapoda).

The epibionts found belong to the following four protozoan ciliate species: *Acineta tuberosa*, *Lagenophrys eupagurus*, *Conidophrys pitelkae* and *Zoothamnium duplicatum*. Short descriptions are provided below.

phylum Ciliophora Doflein, 1901

class Phyllopharyngea De Puytorac *et al.*, 1974

subclass Suctoria Claparède and Lachmann, 1858

order Endogenida Collin, 1912

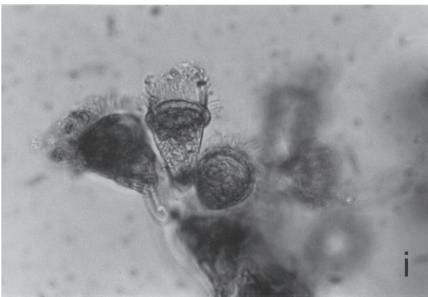
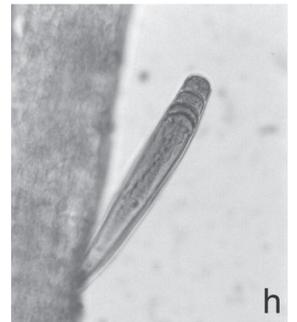
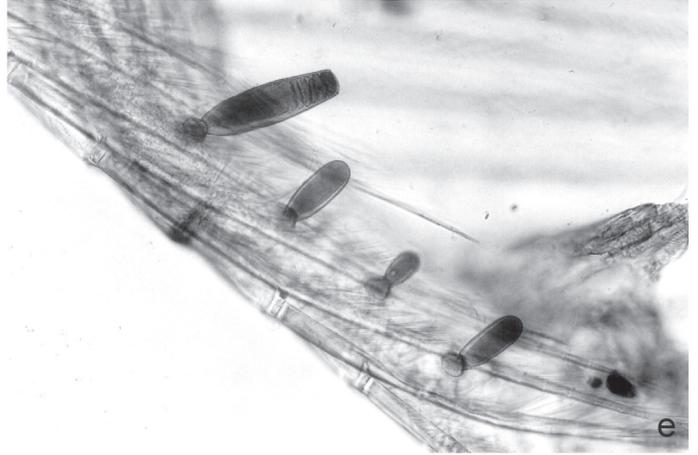
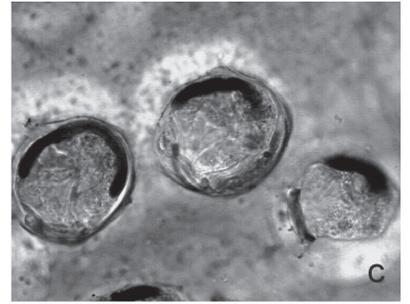
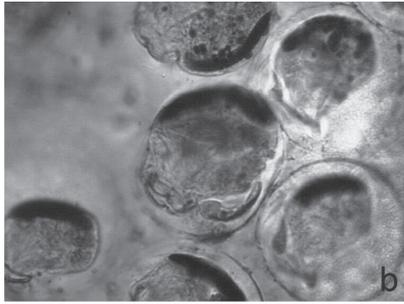
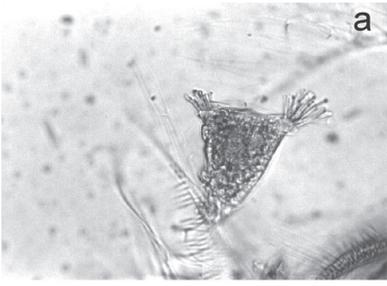
family Acinetidae Stein, 1859

genus *Acineta* Ehrenberg, 1833

*Acineta tuberosa* Ehrenberg, 1833

(Figs. 4a, 5a).

This loricate suctorian is small- to medium-sized (25-120  $\mu\text{m}$  long), bell to Y-shaped, laterally flattened. It presented two actinophores, each with a fascicle of capitate tentacles. The apical aperture is dumb-bell shaped. Cytoplasm does not always completely fill lorica. The stalk is variable in length (5-90  $\mu\text{m}$  long), joining lorica without collar or other structure, usually with basal disc. The reproduction is by endogenous budding. The spherical macronucleus is centrally located. A single contractile vacuole is situated apically. It has been found on a variety of substrata, including crustaceans: species of the shrimp *Crangon* sp., the isopods *Idothea tricuspidata* Desmarest, 1823 and *Microcerberus remyi* Chappuis, 1953 and the amphipod *Gammarus locusta* (Curds, 1985).



phylum Ciliophora Doflein, 1901  
 class Oligohymenophorea De Puytorac *et al.*, 1974  
 subclass Peritrichia Stein, 1859  
 order Sessilida Kahl, 1933  
 family Lagenophryidae Bütschli, 1889  
 genus *Lagenophrys* Stein, 1851

*Lagenophrys eupagurus* Kellicot, 1893  
 (Figs. 4b, 5b, c).

One diagnostic feature is the lips of the lorica aperture, both of which are thickened at the edge and divided into two parts by a deep cleft approximately in the middle. The point at which the anterior lip is divided is slightly off from the point at which the posterior lip is divided. The other diagnostic feature is the crescent-shaped macronucleus, which is unusual for the genus. This ciliate is common symbiont of shrimp, although it also occurs on other decapods. The host type is the hermit crab *Pagurus longicarpus* Say, 1817, and it was found also on *Upogebia affinis* Say, 1818 (Clamp, pers.comm.) The lorica is hemispheroidal, subcircular or suboval in dorsal view. The anterior margin of lorica is nearly straight. The lorica is usually tapering slightly posteriad. The lorica rim is usually heavily thickened, occasionally only slightly to moderately thickened. The lips of lorica aperture are short, located distance equal to 1/5-1/6 of length off lorica behind the anterior margin of lorica. Both lips are moderately arched. A trochal band of kinetosomes broken on right side ends of break is separated by a wide gap. Three peniculi exist. The macronucleus is cylindroid, elongate, curved, with an end thicker than the rest. The micronucleus is ovoid, usually near the center of macronucleus (Clamp, 1989).

phylum Ciliophora Doflein, 1901  
 order Apostomatida Chatton and Lwoff, 1928  
 genus *Conidophrys* Chatton and Lwoff, 1934

*Conidophrys pitelkae* Bradbury, 1975  
 (Figs. 4c, d, 5d-h).

Trophonts of 14-73  $\mu\text{m}$  long, 7-18  $\mu\text{m}$  wide (Mayén-Estrada and Aladro-Lubel, 1994). 95- 97  $\mu\text{m}$  long, 14-

18 wide (Bradbury and Tyson, 1982, from micrographs). These are ciliates with a life cycle dimorphic and related to the moult cycle of the basibiont crustacean. There is a trophont, long, cylindrical, tapering slightly at the proximal end, covered by a cyst wall. The cytostome contacted to the surface of the basibiont, the ciliate feeding on the cuticle of the basibiont (Bradbury and Tyson, 1982). The trophont becomes tropho-tomont when reproduced by tomitogenesis forming inside ciliated tomites. The tomites were finally released and may infest basibionts. When the tomite is attached to the host it becomes trophont. The tomont is 91-94  $\mu\text{m}$  long, and 14-25  $\mu\text{m}$  wide (Mayén-Estrada and Aladro-Lubel, 1994), 172-350  $\mu\text{m}$  long, 25-44  $\mu\text{m}$  wide (Bradbury and Tyson, 1982, from micrographs). It has been found as epibiont on *Crangon crangon* (Linnaeus, 1758) by Bradbury (1975) and (formerly) *Penaeus setiferus* (Linnaeus, 1767) by Mayén-Estrada and Aladro-Lubel, 1994.

phylum Ciliophora Doflein, 1901  
 class Oligohymenophorea De Puytorac *et al.*, 1974  
 subclass Peritrichia Stein, 1859  
 order Sessilida Kahl, 1933  
 family Zoothamniidae Sommer, 1951  
 genus *Zoothamnium* Bory de St. Vincent, 1826

*Zoothamnium duplicatum* Kahl, 1933  
 (Figs. 4e, 5i-k).

These are colonial marine peritrichs, with the stalk dichotomously branched. The zooids are bell-shaped (60-82  $\mu\text{m}$  long, 36-43  $\mu\text{m}$  wide), with double-layered oral border. The macronucleus is C-shaped, transversely oriented. There is a single vacuole apically located. The outer two kineties of peniculus 3 are well separated from the inner one, with the middle kinety conspicuously shorter than others (Ji *et al.*, 2006). It has not previously been described as epibiont.

#### *Distribution of epibionts*

The crustacean species showing the highest density of epibionts was *Acetes indicus*, with a maximum of 3,598 epibionts per basibiont, mainly due to the ciliate *Lagenophrys*. However, the basibiont with the highest mean density was *Acetes sibogae* (1,110 epibionts per crustacean). The basibionts from the open sea area (OS) (*Acetes japonicus* and *Mesopodopsis orientalis* caught on the sandy beach of Penang) showed the lowest densities of epibionts. Among the epibiont species

◀ Fig. 5. Epibiont species: a, *Acineta tuberosa*; b and c, *Lagenophrys eupagurus*; d-h, *Conidophrys pitelkae* with trophont (d), several individuals, trophonts and trophotomonts (e), and different developmental stages of trophotomonts (f-h); i-k, several colonies of *Zoothamnium duplicatum*.

Table 1. Length and width (mm) of the basibiont species (N = 20) and observed number of epibionts.

Basibiont	Length		Width		Epibionts per basibiont	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
<i>Acetes indicus</i>	15.25 ± 5.3	(14.2-17)	2.25 ± 3.2	(2-2.5)	760.0 ± 23.0	(12-3593)
<i>A. japonicus</i>	12.10 ± 2.3	(9.5-20)	2.30 ± 0.1	(1.5-7.5)	83.6 ± 3.1	(1-607)
<i>A. japonicus</i> OS	9.93 ± 3.1	(8.5-11)	1.64 ± 0.8	(1.5-2)	9.60 ± 4.3	(0-36)
<i>A. sibogae</i>	21.83 ± 4.3	(15.5-21)	3.25 ± 1.1	(3-3.5)	1110.3 ± 23.4	(501-1588)
<i>Fenneropenaeus merguensis</i>	12.17 ± 3.2	(9-16)	2.35 ± 0.7	(1.5-3)	72.1 ± 5.2	(0-271)
<i>Mesopodopsis orientalis</i> M	8.67 ± 2.2	(7-11)	1.72 ± 0.3	(1-2)	13.5 ± 4.1	(0-83)
<i>M. orientalis</i> OS	6.18 ± 2.1	(3-9)	1.31 ± 0.3	(0.5-2)	0.02 ± 0.1	(0-1)
<i>M. orientalis</i> T	7.17 ± 2.2	(4.5-10)	1.32 ± 0.3	(0.5-2)	81.8 ± 8.2	(0-277)
<i>M. orientalis</i> B	9.33 ± 3.2	(8-11)	1.66 ± 0.2	(1.5-2)	19.0 ± 2.3	(15-25)
<i>M. orientalis</i> C	3.33 ± 0.8	(3-4)	1.00 ± 0.0		12.8 ± 5.2	(1-20)

Table 2. Morphometrics (in mm) (N = 60) of the epibionts (after fixation) observed on *Mesopodopsis orientalis*, *Acetes* spp. and *Fenneropenaeus* spp.

Basibiont species Epibiont species	<i>Mesopodopsis orientalis</i>		<i>Acetes</i> spp.		<i>Fenneropenaeus</i> spp.	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
<i>Acineta tuberosa</i>						
Body length	21.75 ± 8.26	(10.30-28.10)	36.30 ± 16.23	(13.44-63.36)	38.11 ± 13.07	(19.20-61.44)
Body width	13.75 ± 5.12	(9.34-21.06)	30.19 ± 5.57	(19.20-40.32)	33.69 ± 5.44	(21.12-42.24)
Macronucleus length	6.38 ± 2.49	(4.00-9.15)	9.60 ± 1.71	(7.68-11.52)	13.08 ± 6.24	(5.76-24.96)
Macronucleus width	3.50 ± 0.57	(3.46-4.12)	9.28 ± 1.88	(7.65-11.51)	8.04 ± 1.88	(3.84-13.44)
<i>Zoothamnium duplicatum</i>						
Body length	16.71 ± 1.88	(13.70-19.40)	28.18 ± 4.42	(19.20-36.48)	28.12 ± 4.32	(21.11-40.32)
Body width	12.28 ± 0.48	(12.20-13.20)	23.57 ± 2.44	(21.12-28.80)	25.44 ± 5.42	(19.30-35.19)
Stalk length	30.40 ± 7.95	(20.40-40.37)	164.16 ± 37.64	(119.04-211.20)	237.80 ± 78.14	(96.00-316.80)
Stalk width	4.30 ± 0.67	(3.50-5.20)	6.72 ± 1.10	(5.76-7.68)	6.85 ± 2.57	(3.84-9.60)
<i>Conidophrys pitelkae</i>						
Body length	12.25 ± 0.95	(11.06-13.00)	100.87 ± 32.40	(38.40-142.08)	93.67 ± 40.45	(24.96-93.00)
Body width	5.75 ± 0.50	(5.40-6.67)	18.46 ± 5.73	(11.52-28.80)	13.64 ± 5.12	(5.76-19.20)
<i>Lagenophrys eupagurus</i>						
Body length	21.50 ± 5.89	(12.27-28.50)	38.11 ± 7.35	(19.20-49.92)	45.36 ± 9.19	(30.72-59.52)
Body width	14.16 ± 6.55	(6.20-21.70)	36.28 ± 7.72	(17.20-47.63)	37.08 ± 12.43	(13.44-63.36)

Table 3. Epibionts observed along the longitudinal axis of the basibiont over five groups of anatomical units.

Basibiont species, locality	Anatomical units				
	Rostrum, eyes, antennae, antennulae	Maxillae, maxillipeds	Pereiopods	Pleopods	Uropods, telson
<i>Acetes indicus</i>	1075	150	496	390	142
<i>Acetes japonicus</i>	388	43	5	311	89
<i>Acetes japonicus</i> , OS	15	0	0	78	3
<i>Acetes sibogae</i>	1228	164	384	1039	498
<i>Fenneropenaeus merquiensis</i>	1112	19	16	200	95
<i>Mesopodopsis orientalis</i>	29	0	36	169	28
<i>Mesopodopsis orientalis</i> , T	323	0	564	653	196
<i>Mesopodopsis orientalis</i> , B	1	0	13	3	40
<i>Mesopodopsis orientalis</i> , C	0	0	1	9	28
<i>Mesopodopsis orientalis</i> , OS	0	0	1	0	0

<i>Acineta</i> sp.		<i>Lagenophrys</i> sp.		<i>Conidophrys</i> sp.		<i>Zoothamnium</i> sp.	
Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
1.00 ± 0.3	(0-4)	535.3 ± 22.7	(0-1685)	4.00 ± 0.7	(0-8)	30.3 ± 14.0	(0-106)
0.10 ± 0.5	(0-1)	69.0 ± 4.2	(0-607)	10.5 ± 1.3	(0-36)	4.00 ± 2.2	(0-17)
0.30 ± 0.2	(0-3)			9.30 ± 3.2	(0-36)		
202.7 ± 12.2	(0-577)	650.3 ± 12.3	(451-1028)	36.7 ± 4.6	(8-79)	211.3 ± 13.4	(42-432)
15.2 ± 3.4	(0-72)	4.75 ± 1.2	(0-21)	12.2 ± 4.6	(0-67)	39.9 ± 5.2	(0-164)
10.9 ± 2.2	(0-82)	0.30 ± 0.1	(0-6)	0.23 ± 0.1	(0-3)	1.38 ± 0.7	(0-26)
0.02 ± 0.1	(0-1)						
72.8 ± 6.1	(0-252)					3.60 ± 1.1	(0-31)
2.33 ± 0.7	(1-4)			2.33 ± 0.3	(0-6)	14.3 ± 4.1	(9-21)
12.7 ± 4.2	(1-20)						

presented, *Acineta* appeared on all basibiont species. Among the basibionts *Mesopodopsis orientalis* OS showed the lowest proportion of epibiont species (Table 1).

The general biometrical characteristics of the epibiont species (Table 2) were compared between the three genera of basibionts. *Acineta*, *Zoothamnium* and *Conidophrys* did not show significant differences, but *Lagenophrys* showed a statistically significant difference ( $F = 14.92$ ;  $p < 0.05$ , df 3). The body size of individual epibionts was largest in *Fenneropennaeus* and smallest in *Mesopodopsis* and in *Acetes* they showed intermediate values. This epibiont was also present in high densities in *Acetes*, while in *Fenneropennaeus* and *Mesopodopsis*, it was found in lower abundance. The mean densities of epibionts on the different anatomical units of the basibionts were calculated considering the longitudinal axis of the crustacean. There were species showing a high level of colonization on the anterior areas of the body, such as *A. indicus*, *A. japonicus*, *A. sibogae* and *F. merguensis*, while *A. japonicus* OS and various populations of *M. orientalis* tended to be heavier colonized towards the posterior part of the body. Multiple comparison analysis indicated a significant difference between the species ( $F = 9.53$ ;  $p < 0.05$ , df 9). There were significant differences between *A. japonicus* and *A. japonicus* OS, and also between *M. orientalis* and *M. orientalis* OS.

The anatomical units were subdivided into five groups through the anterioposterior axis of the basibiont (1, rostrum, eyes, antennulae, antennae; 2, maxillae, maxillipeds; 3, pereopods; 4, pleopods, 5, uropods and telson). Group 1 dominated in *A. indicus* and *F. merguensis*, where it accounted for 47.7% and 77.1% of the epibionts respectively. In contrast, *A. japonicus* and *A. sibogae* presented similar higher proportions on

pleopods (37.2 and 31.4%) and the most anterior part of the body (rostrum, eyes, antennulae and antennae) (46.4 and 37.1%). Pleopods were the most colonized units on *A. japonicus* OS, *M. orientalis* and *M. orientalis* T (Table 3). Multiple comparison analysis on these data showed a significant difference between the species ( $F = 3.92$ ;  $p < 0.05$ , df 6).

In each basibiont species, epibiont species generally presented a different distribution. This was corroborated by multiple comparison analysis. In *A. indicus*, *A. japonicus*, *A. sibogae*, *M. orientalis* M, *M. orientalis* T, and *A. japonicus* OS there was a significant difference between the distributions of epibiont species. However, in the case of *F. merguensis* and *M. orientalis* B, a statistically significant difference was not found.

On the other hand, taking into account the mean densities of epibionts on each anatomical unit of the *Mesopodopsis orientalis*, multiple comparison analysis showed a significant difference between the epibiosis in the diverse geographical areas sampled ( $F = 48.43$ ;  $p < 0.05$ , df 4). As in the analysis of data with respect to the longitudinal axis of the basibiont, *M. orientalis* and *M. orientalis* OS, as well as *A. japonicus* and *A. japonicus* OS, presented a statistically significant difference ( $t = 4.91$  and  $t = 3.39$  respectively;  $p < 0.05$ ).

A principal component analysis was performed using the mean densities of epibionts in each anatomical unit of the different basibiont species. The two first principal components showed three clusters: (1) a group including all species of *Mesopodopsis* except *M. orientalis* OS; (2) a group consisting of the species of *Acetes* and *F. merguensis* and (3) *M. orientalis* OS (Figure 6).

This analysis indicated the peculiar epibiosis in *Acetes* and *Mesopodopsis*, and also the difference with

Fig. 6. Principal component classification of basibiont species, based upon epibiont density. Clusters are (1) a group including all species of *Mesopodopsis* except *M. orientalis* OS; (2) a group consisting of the species of *Acetes* and *F. merquiensis* and (3) *M. orientalis* OS.

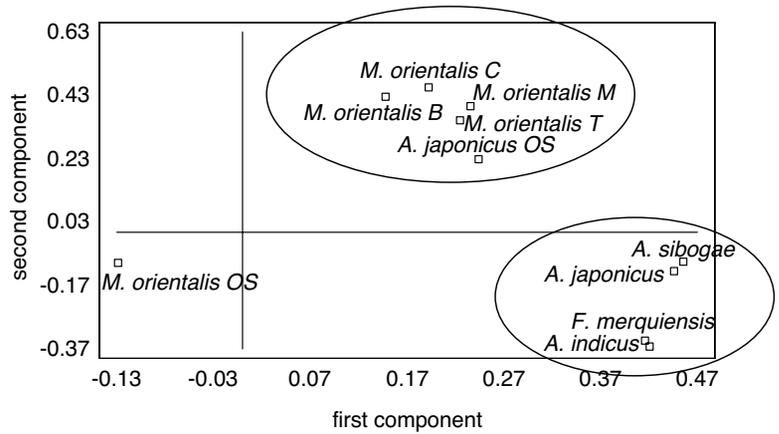


Fig. 7. Dendrogram of the hierarchical conglomerate analysis performed using the mean density of epibionts on the anatomical units of the basibiont species (Lant, Rant, left and right antennae; Lantl, Rantl, left and right antennulae; Leye, Reye, left and right eyes; Lmax, Rmax, left and right maxillae; Lmxp, Rmxp, left and right maxillipeds; L1-5per, left 1-5 pereopods; R1-5per, right 1-5 pereopods; L1-5ple, left 1-5 pleopods; R1-5ple, right 1-5 pleopods. Luro, Ruro, left and right uropods; tel, telson).

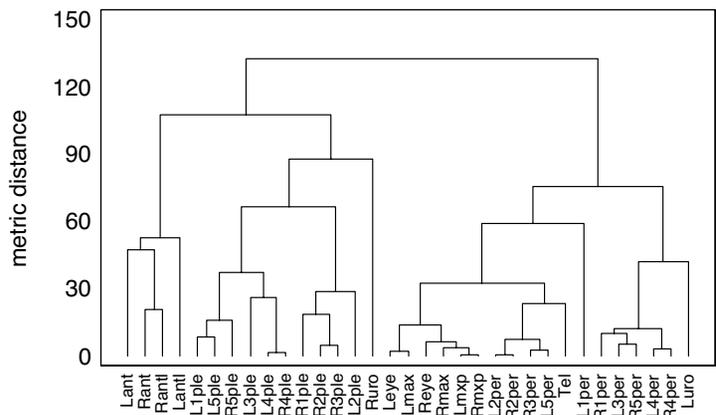
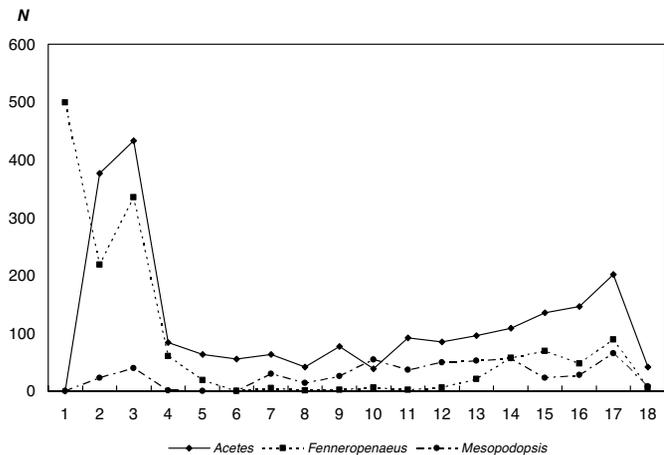


Fig. 8. Mean density of epibionts observed over the anterioposterior axis of the basibiont genera *Acetes* (diamond symbols), *Fenneropenaeus* (square symbols) and *Mesopodopsis* (round symbols). (1, rostrum; 2, antennulae; 3, antennae; 4, eyes; 5, maxillae, 6, maxillipeds; 7, first pereopods; 8, second pereopods; 9, third pereopods; 10, fourth pereopods; 11, fifth pereopods; 12, first pleopods; 13, second pleopods; 14, third pleopods; 15, fourth pleopods; 16, fifth pleopods; 17, uropods; 18, telson).



regard to open sea species. This result coincided with the result obtained in hierarchical conglomerate analysis, in which also three similar clusters appeared in the dendrogram (Fig. 7). In this analysis, the different anatomical units of the basibionts were also considered. The dendrogram indicated that the units were grouped into four clusters: (1) the first cluster represented 12.1%

of the units with the highest density of epibionts (mean 91.33 epibionts per anatomical unit), and included the antennae and antennulae; (2) the second cluster comprised 33.3% of the anatomical units (pleopods and right uropod) with high density of epibionts (mean 39.05 epibionts per unit); (3) the third cluster included units (36.4% of the total units) with the lowest density

of epibionts (1373 epibionts per unit), eyes, maxillae, maxillipeds, left first pereopod, second pereopods, right third pereopod, left fifth pereopod and telson and (4) the fourth cluster represented 18.2% of the units, with a moderate density of epibionts (mean 22.27 epibionts per unit), and included the right first, left third, right fifth and fourth pereopods, and the left uropod.

A multiple regression analysis was made involving total mean density of epibionts in the different areas sampled and temperature, salinity, mean length and mean width of the basibionts. At the 90% confidence level there is a statistically significant relationship between variables, length and width being the variables with lower p-values and high significance. In contrast, temperature was the variable with the lowest significance. Correlation analysis showed a significant relationship between the total mean number of epibionts and the length and width of the basibionts (0.87 and 0.76 respectively,  $p < 0.05$ ). MANOVA performed with total mean densities of epibionts showed a significant relationship with the different basibiont species and with the length and width of the basibionts. The analysis of variance indicated that length was the variable most strongly contributing to the variance of the total number of epibionts.

In order to compare the different basibiont genera, overall mean values of density of epibionts on the different anatomical units were calculated for *Fenneropenaeus*, *Acetes* and *Mesopodopsis* from the mangrove areas. The multiple comparison analysis indicated that the three genera showed significant differences with respect to the distribution of epibionts ( $F = 5.13$ ;  $p < 0.05$ ). The highest difference was observed between *Mesopodopsis* and *Acetes* ( $t = 4.95$ ;  $p < 0.05$ , df 2). In general, *Acetes specimens* tend to have the anterior appendages (antennulae and antennae) heavily colonized and also, secondarily, on the posterior pleopods and uropods. In contrast, *Mesopodopsis specimens* showed the highest colonization on the posterior pereopods, pleopods and uropods, while anterior areas of the body had lower densities of epibionts. *Fenneropenaeus specimens* exhibited a clear colonization on the most anterior areas (rostrum, antennulae and antennae) (Figure 8).

## Discussion

The crustacean basibionts of this study are rather common and familiar to carcinologists because of their commercial importance, although their etiology in the tropical mangroves is poorly studied. The epibiont

species found constituted the first record of their presence on the crustacean species of this study. These epibionts have previously been found on other crustacean species (Morado and Small, 1995). The genus *Acineta* has been described on gammarids, decapods, cladocerans, ostracods, copepods and isopods, with a higher diversity of species on gammarid amphipods (Fernandez-Leborans and Tato-Porto, 2000a; Morado and Small, 1995). Species in the genus *Zoothamnium* are also very common epibionts and have been recorded previously on gammarids, isopods, decapods and copepods, also with a higher diversity on gammarid amphipods. This is probably due to the fact that epibiosis on freshwater gammarids have been more profusely studied (Fernandez-Leborans and Tato-Porto, 2000b; Morado and Small, 1995). Although these ciliates may be found attached to other substrata, *Lagenophrys peritrichs* are typically found as epibiont on crustaceans, having been recorded on decapods, gammarids, isopods, cladocerans, ostracods and copepods, with a higher diversity on decapods and gammarid amphipods (Fernandez-Leborans and Tato-Porto, 2000b; Morado and Small, 1995). The pilisuctorian genus *Conidophrys* has been observed only on crustaceans. *Conidophrys pilisuctor* has been observed on marine amphipods and isopods from the coasts regions in the northern hemisphere (Chatton and Lwoff, 1934, 1936; Mohr and Leveque, 1948; Fenchel, 1965; Jones and Khan, 1970; Boshko and Dovgal, 2000). Subsequently, Mayén-Estrada and Aladro-Lubel (2004) have described this species on the freshwater amphipod *Hyalella azteca* from Mexico. *Conidophrys pitelkae* was found on the sand shrimp *Crangon crangon* from the Atlantic coast of France (Bradbury, 1975), and later on several decapod species from the Atlantic coast of Mexico (Mayén-Estrada and Aladro-Lubel, 1994).

The suctorian genus *Acineta* is a predator that feeds principally on other ciliates, although it may also eat algae. *Zoothamnium spp* are peritrich ciliates that consume particulate organic material suspended in the water, especially bacteria. Some species can also feed on algae. The peritrich genus *Lagenophrys* feed on detritus, diatoms and dinoflagellate from the surface of the bottom substratum, and when the basibiont moves the sediment re-suspends the nutrient due to its feeding activity. This ciliate can be found in large densities on the basibiont. As its body is conspicuously flattened, the individuals may completely cover the surface of the anatomical units colonized. The pilisuctorian genus *Conidophrys* can be considered as a parasite organism, since the individuals possesses a feeding apparatus or

citostome that can connect to the exoskeleton of the basibiont, liquefy it by means of an enzymatic action, and incorporate the fluids from the cuticle into food vacuoles. The ingestion structure is composed of a microtubular and fibrillar subcellular bag-shaped device similar to the rosette of other apostomatids (Bradbury and Tyson, 1982).

*Lagenophrys* was abundant in *Acetes*, but not in *Mesopodopsis* and *Fenneropenaeus*. There are two possible reasons for this: *Lagenophrys* prefers large-sized, more powerful swimming basibionts; or this epibiont prefers the sublittoral zone rather than the littoral zone for its mode of feeding as it is a detritus feeder.

There is a significant correlation in epibiosis in general where larger-sized basibionts carry a large number of epibionts. *Mesopodopsis* reach 7-8 mm BL at most. Adult *Acetes* reach 30-40 mm BL or slightly more. Juveniles of *Fenneropenaeus* examined in this study were intermediated between them (ca 20 mm). Usually, smaller crustaceans (or juveniles) are assumed to have a shorter inter-moult period than larger and adult crustaceans; this may affect the formation of epibiont assemblages.

The epibiosis in each crustacean species and in each sampling locality showed a particular pattern which was revealed by the statistical analysis. Taking into consideration the same basibiont species, e.g., *Mesopodopsis*, the pattern of epibiosis was statistically different among the different sampling sites, and this could be due to the different ecological conditions. In general, the colonization was predominantly observed on the anterior part of the body in *Acetes* and *Fenneropenaeus*, and it tends to be more abundant on the mid and posterior areas in *Mesopodopsis*. However, the different epibiont species varied their location according to the structure of the community and the basibiont species. In *Mesopodopsis*, when all the epibiont species were present, *Acineta* and *Zoothamnium* were located mainly on the middle and posterior areas of the body, whereas *Conidophrys* and *Lagenophrys* were attached anteriorly. In contrast, in *Acetes*, where *Lagenophrys* was noticeably abundant, this ciliate species and *Acineta* colonized mainly on the anterior areas, while *Zoothamnium* and *Conidophrys* were found posteriorly. *Fenneropenaeus* clearly showed a higher colonization on the anterior areas of the body, possibly because in this zone the appendages provide wide areas for the settlement of the epibionts, together with the presence of nutrients from the feeding activity by the buccal appendages of the crustacean basibiont.

The distribution of the epibiont species is related to

specific basibiont species, and the pattern of colonization of the epibiont community. In this study, their distribution showed a trend similar to that observed in other areas, e.g., the epibiosis on *Caridina lanceolata* from the Malili lakes of Sulawesi (Fernandez-Leborans et al., 2006): the epibiont species were located following a particular pattern, which the results show: the species tended to be correlated to the different lakes. Independently of the present species and in all cases, each species was established fitting the same general way of distribution. In each basibiont species, each epibiont species followed a distribution pattern related to that of other epibiont species present. The epibionts tend to occupy the sites available fitting the whole surface with adequate environment for colonization (nutrient input, protection against predators, abrasion or other antifouling mechanisms, hydrodynamic effects, etc.). When an epibiont would have a relation with a different basibiont species, the pattern of colonization may be modified. The basibiont represents a dynamic environment in which the epibiont community species acquire a colonization pattern. The short generation time, the dispersion, and the adaptations to the epibiotic life, confer to ciliate protozoans numerous advantages in colonization. An indication of this fact is the numerous protozoan communities described as epibionts in many crustacean species (Morado and Small, 1995; Fernandez-Leborans and Tato-Porto, 2000a, b).

The changes in the community structure of protozoans may significantly affect other components of the aquatic food web, and may thus influence the distribution and abundance of both lower and higher organisms (Beaver and Crisman, 1989; Carrick and Fahnenstiel, 1992). Ciliates have an important ecological significance in free environments, especially in benthic areas, where they show high growth rates and important trophic diversity (Patterson et al. 1989; Fenchel, 1990; Fernandez-Leborans and Fernandez-Fernandez, 2002). Although in a small scale, these conditions could be transferred to an epibiotic community, which could reflect the biodiversity in the environment (Fernandez-Leborans and Gabilondo, 2006).

A slightly harsher condition in the littoral zone of the open sandy beach could attribute to a lower incidence of epibionts as compared with the estuarine counterparts which inhabit a calm environment. Another possibility is that high productivity in the mangrove estuary could contribute to a higher incidence of epibionts. Chong et al. (2003) suggested that the zooplankton biomass in the Matang mangrove swamp is noticeably higher than that in its offshore waters. The

biomass of littoral hyperbenthos is also appreciably higher in the mangrove estuaries than in the coastal area without mangrove (Hanamura *et al.*, unpublished data). This may reflect higher primary productivity in the mangrove swamp (see also Tanaka and Choo, 2000), and it would also provide rich foods for epibiont ciliates.

Otherwise, the marked difference in the incidence of epibiosis gives an indication of ecological separation between the estuarine and coastal populations. They usually stay in their own habitats for a considerable time and consequently the interactions between the two populations do not occur frequently. In the studied mangrove estuaries, the water temperature was rather stable throughout the year. In contrast, the salinity showed a wide range of variations according to the rainfalls. The hyperbenthic crustaceans in the mangrove estuary evidently showed considerably wide euryhalinity (Hanamura *et al.*, in press a, b): hence, the crustacean epibionts found in this study may also have a broad range of salinity tolerance corresponding with their basibionts.

Large-sized basibionts provide a wider substratum to be attached for epibionts. In this respect, the appendages of *Acetes* are markedly wider than those of *Mesopodopsis* (Fig. 3). In addition, the inter-moult period of basibionts may quantitatively and qualitatively contribute to the epibiont assemblage. For example, juveniles of *Fenneropenaeus* may have a shorter inter-moult duration than that of adult *Acetes*. *Mesopodopsis* are also assumed to have comparatively shorter instar stages when compared with *Acetes*. The incidence of epibiosis is much lower in the coastal area. Environmental conditions in the mangrove swamp is assumed to have a higher primary productivity than in off shore areas. As mentioned before, the physical condition also differs between the two, but the former factor is believed to be more important. Taking into account the special characteristics of the epibiotic association, in many cases it is not easy to find colonized basibiont individuals. This is the reason for the relatively low number of infested specimens analyzed in each species and locality. In addition, the time required for the detailed observation of the anatomical units of the basibiont and the count of the epibionts of diverse species on these units must be taken into account, since different basibiont species and sites were considered. The principal aim of the work was to obtain a general view of the epibiosis on mangrove dominant crustacean species in Malaysia and their special characteristics on basibiont species and sites.

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