

The identity and occurrence of *Kerona pediculus* (Ciliophora: Hypotrichida), a well-known epizoite of *Hydra vulgaris* (Cnidaria: Hydrozoa)

A. Warren & E.A. Robson

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Alan Warren, Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK. E-mail: a.warren@nhm.ac.uk

Elaine Robson, School of Animal and Microbial Sciences, The University of Reading, P.O. Box 228, Reading RG6 6AJ, UK. E-mail: e.a.robson@reading.ac.uk

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Epizotic *Kerona pediculus* have been found on *Hydra vulgaris* and on *Cristatella mucedo* (Bryozoa) in the same habitat. On the basis of morphological characters (using Nomarski and Scanning Electron Microscopy) specimens from the two hosts are indistinguishable. Details revealed by SEM agree with previous results from silver staining, confirming the identity of *K. pediculus*. The taxonomic status of this species is briefly summarised. Host recognition, the inhibition of nematocyst discharge, and the possible role of host growth-promoting substances are not yet understood.

Introduction

*Hydra*¹ is an exemplary cnidarian: it has provoked seminal experiments in the laboratory since the eighteenth century and continues to do so (Trembley, 1744; Lenhoff, 1983; Lenhoff & Tardent, 1985). But surprisingly little is known about the biology of wild populations. This report is about the specificity of well-known epibionts associated with *Hydra* spp., and the identity of the ciliate *Kerona pediculus* (O.F. Müller, 1773). The study was prompted by finding this ciliate on the bryozoan *Cristatella mucedo* Cuvier, 1798, as well as on *Hydra* spp. from the same local habitat (Warren & Robson, 1986).

Observations on the ciliates associated with hydra are as old as the discovery of the polyp itself: they were seen by Leeuwenhoek (1703), remarked upon and illustrated by Trembley (1744), Rösel (1754) and others, and recorded with great care by Ehrenberg (1835, 1838) and Stein (1854, 1859).

The two species most commonly found as symbionts or commensals of hydra are the hypotrich *Kerona pediculus* (O.F. Müller, 1773) Blochmann, 1886, and the peritrich *Trichodina pediculus* (O.F. Müller, 1786) Ehrenberg, 1838. These often occur together on the same hydra. They appear not to damage the polyps even when present in large numbers (e.g. Cavallini, 1930; Coleman, 1966; Görtz, 1996). The eighteenth century term 'polyp louse' refers to their characteristic profiles and creeping or saccadic scurrying movements. It is noteworthy that nematocysts are not discharged. The ciliates

¹The ordinary word now used for polyps of the genus *Hydra* is hydra [see, for example, Campbell (1989)].

obtain food by filtering particles from the water (bacteria, flagellates, diatoms). *Kerona pediculus* may also pick up material from the surface of the polyp (bacteria, detritus, spent nematocysts). In contrast, the amoeba *Hydramoeba hydroxena* (Entz, 1912) Reynolds & Looper, 1928, is a detrimental parasite which consumes the tissues of *Hydra* spp. and at times causes epidemics fatal to the host (Page & Robson, 1983; Page, 1991).

Kerona pediculus and *Trichodina pediculus* have been found previously on bryozoans as well as on *Hydra* spp. (see Svec, 1897). Dr Beth Okamura advises that *K. pediculus* is commonly encountered on colonies of *Cristatella mucedo* at sites throughout the Thames Valley region. Some of these ciliates have been examined by Mr R.L. Manuel. They are especially numerous on colonies that look unhealthy and are probably suffering from myxosporidian or myxozoan parasites (Okamura & Hatton-Ellis, 1995; Okamura, 1997).

The morphology of *K. pediculus* is already well understood from light microscopical observations of live and silver-stained specimens (Pätsch, 1974; Hemberger & Wilbert, 1982). The features needed to identify this species have now been observed by Scanning Electron Microscopy (SEM) for the first time (see also Wicklow, 1979; Fleury et al., 1985). This work permits a brief review of the biology of 'polyp lice' and of their symbiosis with hydra.

Materials and methods

For the present work *Hydra vulgaris* Pallas, 1766, and *Cristatella mucedo* together with their associated *Kerona pediculus* were collected from Whiteknights Lake, The University of Reading (National Grid Reference SU737722), mainly between July and October although hydra were sampled also at other times. In the laboratory some of these *Kerona* were cultured on local *H. vulgaris* in 'M' medium (Lenhoff, 1983), and also on *H. vulgaris* (Zürich strain) provided by Professor P. Tardent. The polyps were fed twice a week with nauplii of the brine shrimp *Artemia salina* and the medium was changed after feeding (Lenhoff, 1983). Cultures were kept at 15°C (12hr light, 12hr dark).

Field and laboratory samples were prepared for examination by SEM as follows. Specimens were fixed in Parducz's solution (Parducz, 1967) comprising six parts 2% (v/v) OsO₄: one part saturated HgCl₂ at 10°C for 30 minutes. After fixation they were dehydrated rapidly through a graded series of alcohols to 100% EtOH, with 15 minutes in each solution, and taken via four steps to 100% acetone. The specimens were critical point dried from CO₂, sputter-coated with gold-palladium (3 × 30 seconds) and viewed in a Hitachi 800 Stereoscan at 5-10 kV.

Ciliate terminology is mainly according to Borror (1979) and Foissner et al. (1991).

Results

Morphological observations

By light microscopy (Nomarski) live specimens of *Kerona pediculus* isolated from *Hydra vulgaris* and *Cristatella mucedo* are indistinguishable morphologically. In all cases the body is reniform in shape, 90-180 µm long and 60-80 µm wide and dorso-

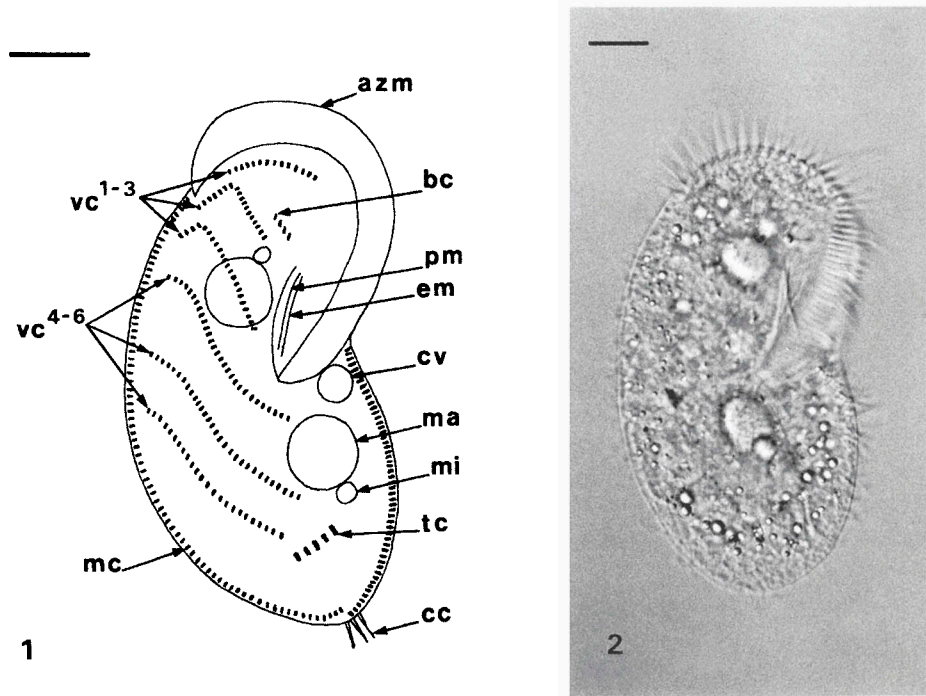


Fig. 1. *Kerona pediculus*, diagram of ventral view showing ciliature and position of nuclei and contractile vacuole. Bar = 25 μ m.

(azm) adoral zone of membranelles, (bc) buccal cirri, (cc) caudal cirri, (cv) contractile vacuole, (em) endoral membrane, (ma) macronucleus, (mc) marginal cirri, (mi) micronucleus, (pm) paroral membrane, (tc) transverse cirri, (vc) ventral cirri, rows 1-6.

Fig. 2. *Kerona pediculus*, Nomarski optics. Ventral view. Bar = 25 μ m.

ventrally flattened (figs 1,2, also 9, 10). There are two macronuclei, one situated in the anterior half of the body and the other in the posterior half, each accompanied by a single micronucleus. The contractile vacuole is situated close to the buccal cavity.

SEM also reveals no differences between specimens obtained from *Hydra* and *Cristatella*. The ciliature of the buccal, fronto-ventral-transverse (FVT) and somatic regions confirms the identification of *K. pediculus*.

The buccal ciliature (figs 3, 4) consists of the conspicuous adoral zone of membranelles (AZM) used for swimming and filter feeding, two inconspicuous undulating membranes (paroral and endoral) and the buccal cirri. The AZM is composed of 50-60 membranelles. The paroral membrane is supported by a peristomial lip with the endoral membrane situated just to the left and running parallel to it. There are 2-5 buccal cirri (table 1) which form a row anterior to, and on the right of, the buccal cavity.

The FVT ciliature (figs 1, 3) consists of the ventral and transverse cirri used in walking. There are six rows of ventral cirri. Rows 2-5 extend obliquely from anterior right towards posterior left. Rows 1-3 are confined to the anterior half of the cell and follow curved or irregular paths. Row 1 curves round the anterior margin. Rows 4-6, however, extend to the posterior part of the cell. There are 4-5 transverse cirri in a single row. This row is situated between the posterior ends of ventral rows 5 and 6.

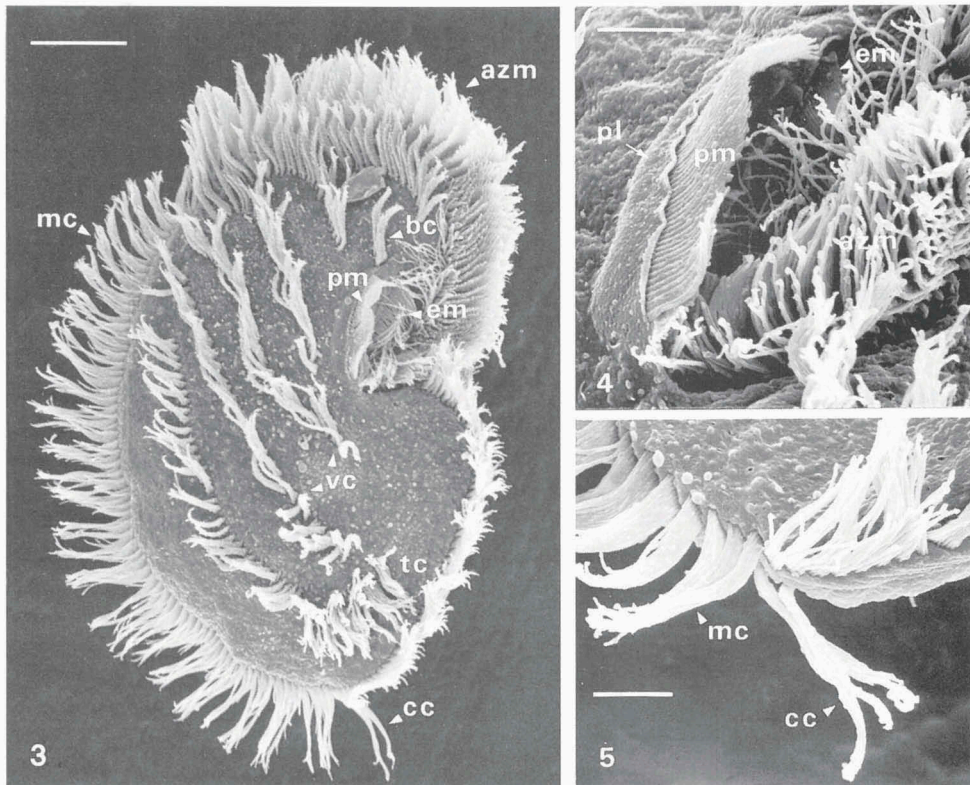


Fig. 3. *Kerona pediculus*, SEM of ventral surface. Bar = 25 μm .

Fig. 4. *Kerona pediculus*, SEM of peristomial region. Bar = 5 μm .

Fig. 5. *Kerona pediculus*, SEM of posterior end of cell, ventral view. Bar = 5 μm .

(azm) adoral zone of membranelles, (bc) buccal cirri, (cc) caudal cirri, (em) endoral membrane, (mc) marginal cirri, (pl) peristomial lip, (pm) paroral membrane, (tc) transverse cirri, (vc) ventral cirri.

These cirri are longer than the ventral ones.

The somatic ciliature (figs 1, 3, 5-8) consists of marginal and caudal cirri and dorsal bristles. The marginal cirri are arranged in two rows, forming the left and right borders respectively. Both rows terminate at the posterior end of the cell where they overlap slightly, the last cirrus of the right row lying anterior to the last cirrus of the left row. There are 2-3 caudal cirri (table 1), slightly longer than the marginal cirri, which arise at the posterior end of the cell. The dorsal bristles are arranged in 12-16 longitudinal rows (kineties) each with 16-22 bristles (fig. 6). Each bristle is 2.0-4.0 μm long and arises from a small pit.

Figs 9, 10 are included to show *Kerona pediculus* on *Hydra vulgaris*, and some of the cnidocils.

Table 1 summarises the main variations in ciliature which have been reported for *K. pediculus*, and there is no evidence for more than one species. Although figs 2-10 show specimens from *Hydra vulgaris*, as already stated those from *Cristatella mucedo* were indistinguishable by SEM.

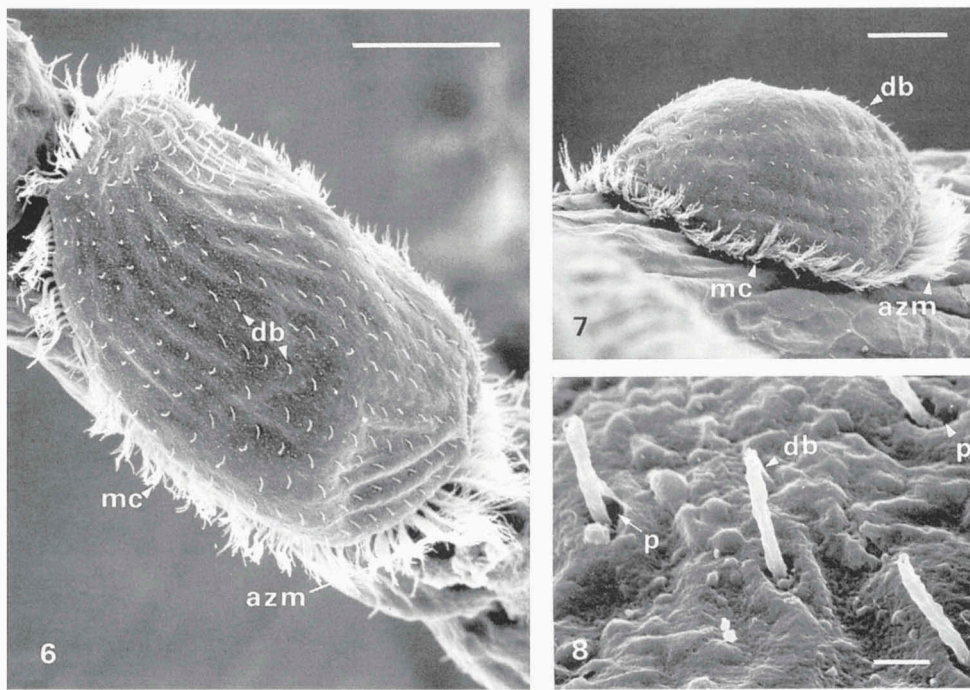


Fig. 6. SEM of *Kerona pediculus* on a tentacle of *Hydra vulgaris*, its anterior end at lower right, showing the dorsal surface. Note cnidocil towards top left corner. Bar = 25 μ m.

Fig. 7. *Kerona pediculus* on body of *Hydra vulgaris*, SEM, antero-lateral view. Bar = 25 μ m.

Fig. 8. *Kerona pediculus*, SEM of dorsal bristles. Bar = 1 μ m.

(azm) adoral zone of membranelles, (db) dorsal bristles, (mc) marginal cirri, (p) pit.

Ecological observations

The continuity of symbiotic associations with *Hydra* spp. is not well understood, but relevant observations are summarised below.

Hydra spp. have been collected from Whiteknights Lake since 1981, by taking submerged littoral vegetation and litter from three or four regular collecting sites and placing this in bowls with lake water until next day. In this way four species have been found: *H. vulgaris* Pallas, 1776; *H. oligactis* Pallas, 1776; *H. viridissima* Pallas, 1776 (uncommon); and *H. circumcincta* Schulze, 1914 (unusual: identified by Dr R.D. Campbell, personal communication). Until 1985 the species usually found was *H. vulgaris*. From 1984 *H. oligactis* was noted, and since 1986 it has replaced *H. vulgaris* in routine collections. In 1984, at the end of a warm summer, the bryozoan *Cristatella mucedo* was found on the same vegetation as hydra (August to October). The numbers of hydra always increase during summer and autumn, but even in January and February specimens with buds may be found. [See Bryden (1952) for a population study of *H. oligactis*, and Okamura (1997) in respect of *C. mucedo*. Note that polyps of *Hydra* spp. may overwinter whereas in autumn, *Cristatella* colonies produce statoblasts and may not themselves survive until spring.]

Most collections of hydra have been examined for epizoites. From summer

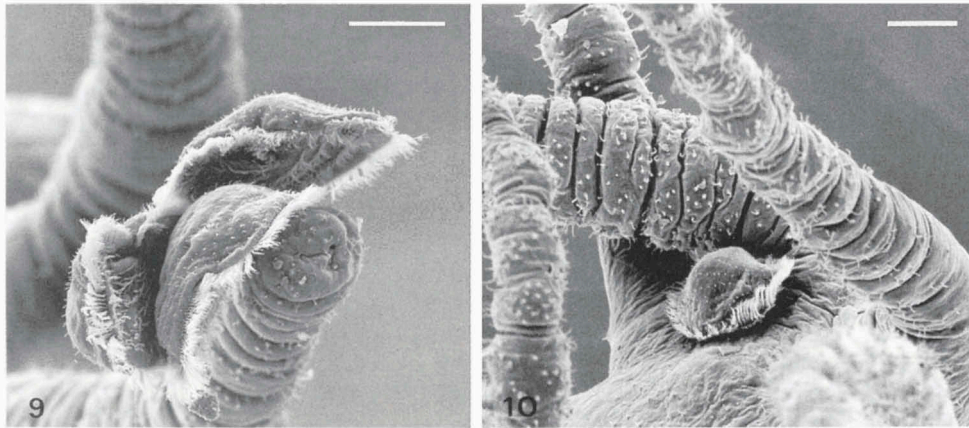


Fig. 9. Contracted tentacle of *Hydra vulgaris* with three individuals of *Kerona pediculus* (two probably displaced after fixation). Bar = 50 μ m.

Fig. 10. *Kerona pediculus* on the hypostome of *Hydra vulgaris* (between tentacles and mouth). Note cnidocils on tentacles and hypostome. Bar = 100 μ m.

onwards *Kerona pediculus* is almost universally present, becoming scarce or absent only in the depths of winter (January, February). In summer and autumn, when field samples are kept in the laboratory the number of *K. pediculus* per hydra quickly increases (e.g., from present or common to numerous within a few days). *Trichodina pediculus* has been noted only three times (November 1983, June 1984, January 1990), but in samples brought into the laboratory it too multiplies rapidly. *Hydramoeba hydroxena* is seldom obvious but it may be seen on polyps collected in late autumn (October, November).

Table 1. Numerical variation in the ciliature of *Kerona pediculus* from *Hydra* spp.

Sources: (1) Uhlemeyer, 1922; (2) Pättsch, 1974; (3) Wicklow, 1979; (4) Hemberger & Wilbert, 1982.

Ciliary structures	Previous authors	Present work
Membranelles in AZM	30-35 (2)	55-60
	37-45 (2)	
	60-64 (4)	
Buccal cirri	4 (2, 4)	¹ 2-5
Transverse cirri	4 (2)	4-5
	5 (4)	
Caudal cirri	2 (2)	¹ 2-3
	3 (4)	
Dorsal kineties	12-15 (3)	14-16
	16-18 (2)	
	² dorsal field (4)	

Note to table 1

¹ In the case of buccal and caudal cirri, the lowest numbers observed here cannot be definitive.

² i.e., dorsal bristles not aligned.

Kerona pediculus remains on the host and is seldom observed to swim off despite its ability to do so. If the polyps are fed, the ciliates are easily maintained with them (i.e., their microbial food supply increases). But if *H. vulgaris* is starved until the polyps are moribund, *K. pediculus* eventually leaves them and swims or creeps away (C. Amer, personal communication). The behaviour of *Kerona pediculus* while finding new hosts has not yet been observed. In the field, *K. pediculus* does not appear to distinguish between *H. vulgaris* and *H. oligactis* as hosts and when found on *Cristatella mucedo*, it moves about over the centre of the colony in a normal manner.

Discussion

Nomenclature of *Kerona pediculus*

The first description of *Kerona pediculus* was that of O.F. Müller (1773) who called it *Cyclidium pediculus*. Ehrenberg (1835) then described the same organism under the name *Kerona polyporum*. Subsequent redescriptions were made by Kent (1882) and Uhlemeyer (1922) who also reviewed the taxonomy of the genus *Kerona* [for further discussion see Borror (1979) and Jankowski (1979)]. Confusion over the nomenclature of this species continued with either one of two names, *K. pediculus* or *K. polyporum*, being used. The situation was resolved when Foissner (1987) formally transferred *Cyclidium pediculus* O.F. Müller, 1773, to the genus *Kerona* as *Kerona pediculus* (O.F. Müller, 1773) comb. nov., with *K. polyporum* Ehrenberg, 1835, becoming a junior synonym. Subsequently, however, Foissner et al. (1991) reattributed the authority as *K. pediculus* (O.F. Müller, 1773) Blochmann, 1886.

Kerona pediculus is still the only established species of *Kerona*, as data presented for other species [e.g., Gourret & Roeser (1888); Dumas (1929)] do not allow contemporary criteria for identifying *Kerona* to be applied.

The 'polyp lice' of hydra

Symbiosis is defined most broadly as different animals living together (Görtz, 1996). It may be supposed that, as no free-living *Kerona* spp. have yet been found, the symbiosis of *K. pediculus* and *Hydra* spp. offers mutual advantages. A hydra has few predators thanks to its armature of nematocysts [e.g., Trembley (1744) fed polyps to fish, which spat them out] and symbionts too are protected. On bryozoans (Svec, 1897) *Kerona pediculus* is sheltered by being in the lee of zooid feeding currents (see Okamura & Hatton-Ellis, 1995). When on a hydra, *K. pediculus* feeds by filtration, alternatively scavenging materials from the host's surface; it may also venture into the coelenteron (Victor-Jones, 1915; Professor P. Tardent, personal communication). Coleman (1966) thought that *K. pediculus* had a food requirement for a non-cellular material produced by hydras. The possibility that secretions or activators from *Hydra* spp. might influence growth or division in *K. pediculus* is realistic (Christensen et al., 1998). Other experiments, which would be worth repeating, suggested that the growth rate of hydra polyps was sometimes enhanced by the presence of *K. pediculus* (Coleman, 1966: 708).

The peritrich *Trichodina pediculus* similarly occurs on several species of *Hydra* and

also on the bryozoans *Cristatella mucedo* and *Plumatella repens* (see Svec, 1897), but its range of hosts is wider and includes the freshwater medusa *Craspedacusta sowerbii* Lankester, 1880, amphibia (larvae and adults) and a number of fish (young and adult), and it is also reported from plankton (Svec, 1897; Matthes et al., 1988). The original hosts of *T. pediculus* may prove to be *Hydra* spp., the others being alternate or supplementary (Professor Jiri Lom, personal communication). Other species of *Trichodina* are associated mainly with fish (gills, bladder) and these include some damaging ectoparasites, with amphibians, and with certain invertebrates [e.g. *T. ctenophorii* Estes, Reynolds & Moss, 1997 on the comb-plates of ctenophores (Estes et al., 1997)].

The parasitic amoeba *H. hydroxena* is widely distributed among species of *Hydra* and it too occurs on *Craspedacusta sowerbii* (see Page, 1991).

For *Kerona pediculus* and *Trichodina pediculus*, life on the shifting, somewhat irregular surface of a hydra alternates between adhesion and locomotion. The low, humped profile of *K. pediculus* allows it to stay on the hydra at low Reynolds numbers, stationary or creeping along by means of its cirri. It uses the AZM to filter feed, or occasionally to swim away. *Trichodina pediculus* has a characteristic adhesive disc, a flexible and complex structure by which it attaches; in crowded circumstances it may even settle on *K. pediculus* [James-Clark, 1865, in Kent (1882)]. On hydras it readily swims off or hover-glides along. Food particles are always collected by filtration, and the buccal apparatus is apical as in other peritrichs. The formation of food vacuoles was traced by Ehrenberg (1838).

Although not immune to nematocyst toxins, the epizoites of *Hydra* spp. do not cause nematocysts to discharge. The reasons for this are not understood. Other ciliates such as *Paramecium* cause discharge on contact (Zick, 1929; 1932). *Kerona pediculus* and *Trichodina pediculus* appear to displace cnidocils and sensory cilia at close range but without visible effect, suggesting that inhibition rather than excitation may be provoked (e.g., see Westfall & Townsend, 1976; Westfall & Sims, 1978; Tardent, 1995; Holstein, 1995; Thurm et al., 1998). The discharge of a single nematocyst into *T. pediculus*, however, kills it at once (personal observation; Hausmann, 1979). Probably as a result of its scavenging behaviour *Kerona pediculus* may show food vacuoles containing discharged and sometimes undischarged nematocysts (Stein, 1859; Uhlemeyer, 1922). In principle, the epizoites do not prevent their hosts from catching prey.

Symbioses are maintained through a combination of long-standing characteristics such as behaviour, habit and life-history. In which respects the behaviour of 'polyp lice' may be host-specific is not known. Ciliates are very sensitive to mechanical and chemical stimuli, and much of their behaviour is governed via changes in membrane potential (Mechemer & Teunis, 1996). Swimming speeds for different species are usually in the range 0.5-1 mm/sec (i.e. 2-3 m/hr), suggesting that *K. pediculus* and *T. pediculus* would have a good capacity for dispersal and for finding new hosts. These ciliates multiply rapidly and division has been studied in some detail in *Kerona pediculus* (Cavallini, 1930; Hemberger & Wilbert, 1982). The life history of *K. pediculus* is otherwise unknown, but in taking a broad perspective one might search for evidence that significant sources of genetic variation exist.

The calm, lacustrine conditions in which *Hydra* spp. and freshwater Bryozoa flourish are nowhere found in the sea (Trembley, 1744; Bushnell & Rao, 1979; Okamu-

ra & Hatton-Ellis, 1995): fish ponds and ditches, or grand unfiltered water systems seem to have no marine equivalent. In consequence, records of ciliates associated with marine hydroids or bryozoans are rather few (e.g., Bouillon, 1994) and cannot be compared. The authors regret this, and conclude that *K. pediculus*, like hydra polyps, may unexpectedly be unique.

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