

On the fine structure of female *Caligus infestans* Heller, 1865 (Copepoda: Siphonostomatoida)

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Although much work has been done on the piscine parasitic genus *Caligus* Müller, 1785, morphological and especially anatomical work has been largely neglected, leading to confusion as to, for instance, the phylogenetic origin and identity of appendages. The present study provides scanning electron microscopical information on the fine structure of the female of *Caligus infestans* Heller, 1865. The study of the true ultrastructure and perhaps more important, the orientation of the appendages of these parasites, provide valuable information on the functional adaptations towards the utilization of the parasitic niche.

Alhoewel die taksonomie van die vis-parasitiese genus *Caligus* Müller, 1785, ekstensief bestudeer is, bestaan daar 'n wesentlike gebrek aan inligting aangaande die morfologie en anatomie van die genus, wat o.a. aanleiding gee tot onsekerheid aangaande die filogenetiese oorsprong en identiteit van die aanhangsels. Die huidige studie verskaf skandeerelektronmikroskopiese ultrastrukturele inligting oor die wyfie van *Caligus infestans* Heller, 1865. Die studie van die ware ultrastruktuur en miskien selfs meer belangrik, die oriëntasie van die aanhangsels, verskaf waardevolle inligting aangaande die aanpassings van die organismes ten opsigte van die benutting van die parasitiese nis.

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The family Caligidae was established in the eighteenth century by Müller (1785). Since then, much speculation has taken place concerning the validity of various taxonomic characteristics, as well as morphological features of this family (Kabata 1979). The cumulative growth of synonymy within the genus *Caligus* Müller, 1785 — some 208 species out of a total of 315 are currently recognized as valid (Margolis, Kabata & Parker 1975) — bears testimony to this observation. Additionally, the anatomy of parasitic Copepoda in general has been grossly neglected (Kabata 1981). This absence of a thorough understanding of ultrastructure and anatomical composition of the majority of species of *Caligus* has frequently given rise to heated debates on, for instance, the phylogenetic origin of morphological features such as the sternal furca (Heegaard 1947; Ferris & Henry 1949; Lang 1950; Lewis 1966) and the identity of appendages (Bouquet & Stock 1963; Nunes-Ruivo 1966; Bowman 1971).

The fine structure of *Caligus* has been selectively studied by means of scanning electron microscopy, e.g. the mouthparts (Kabata 1974), cephalothoracic appendages (Poquet 1979) and a possible chemosensory apparatus situated anterodorsally on the frontal plates of the parasite (Cressey & Cressey 1979; Kabata 1981). The present study is aimed at systematically describing the fine structure of a single species, *Caligus infestans* Heller, 1865, which, although originally described from the Indian Ocean (Heller 1865) and recorded from marine host fishes off the shore of Madagascar (Nunes-Ruivo & Formanoir 1956) and Australia (Kabata 1965), has also been found to occur at Sodwana Bay on the southern African east coast during this study.

Methods

Specimens of *C. infestans* were preserved in 50%

propanol. Preserved adult females were cleaned by brushing with a fine brush and dehydrated in a series of ethanols for scanning electron microscopy. Specimens were critical-point dried with CO₂ using amyl acetate as intermediate solvent, after which they were sputter coated with gold at 15 mA and examined in an ISI-SS60 SEM at 10kV.

Results and Discussion

The marginal membrane on the frontal plates of *C. infestans* was found to be finely striated (Figure 1b) and medially divided into two lateral halves by a central notch. This notch (Kabata 1979) is a remnant of the larval frontal filament, by which sub-adults attach to the host (Kabata 1972). As the very thin, flexible marginal membrane is commonly believed to act as a seal against the surface of the host during attachment (Kabata 1974) and this membrane has been shown to be smooth in other species (Oldewage in press), it would appear that the striated appearance is due to the particular orientation of this part of the membrane during fixation. On the dorso-median surface, a structure which was originally described as a median sucker (Wilson 1905), or 'rugose' area (Cressey & Cressey 1979) and later said to be a chemosensory apparatus (Kabata 1981), occurs. The structure of this apparatus in *C. infestans* is dorsoventrally oval with a central sulcus (Figure 1a), although it has been found to be laterally oval in *Caligus clemensi* Parker & Margolis, 1964 and rounded in *Caligus curtus* Müller, 1785 (Kabata 1981). It appears to be contractile in the present species, as the surface appeared more 'rugose' in some specimens than in others. This is borne out by the convergent, cuticular folding around this apparatus. The surface appears to be very nodular in the contracted state (Figure 1j), as opposed to the smoother, less rugose appearance when

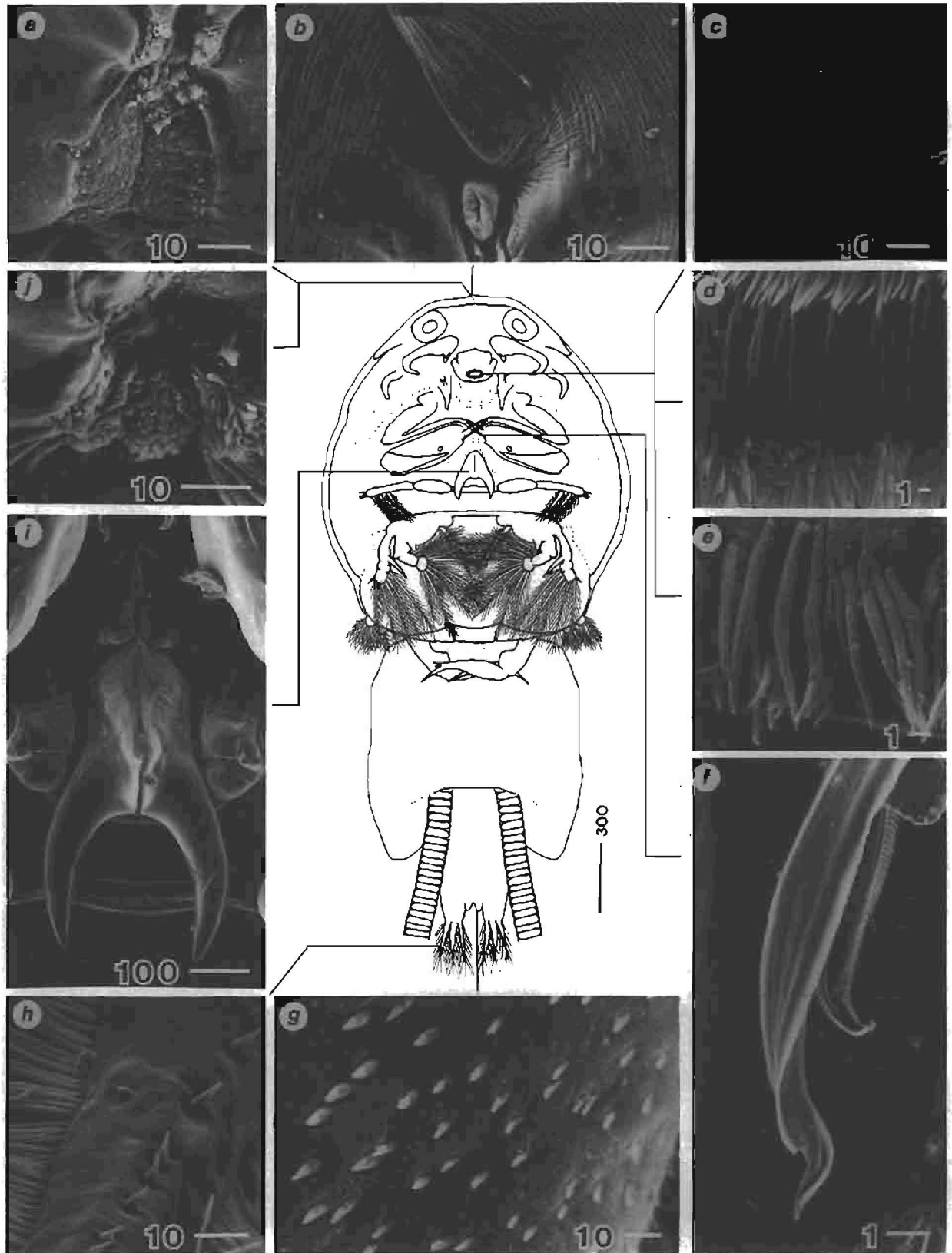


Figure 1 Scanning electron micrographs of fine structures of *Caligus infestans*: (a) the rough, rugose area on the frontal plates, (b) the central remnant of the larval attachment organ on the frontal plates, (c) view into the buccal cavity to show the strigil (arrowed), (d) the striated membrane between the two distal rows of setae on the periphery of the mouthtube, (e) a close view of the fringing row of setae of the mouthtube, (f) the serrated, bifurcated tip of the second maxilla, (g) the outwardly projecting spines on the anal labia, (h) short spines on the setae of the uropods, (i) the sternal furca, and (j) the rugose area in 1a — contracted. (Measurements in μm).

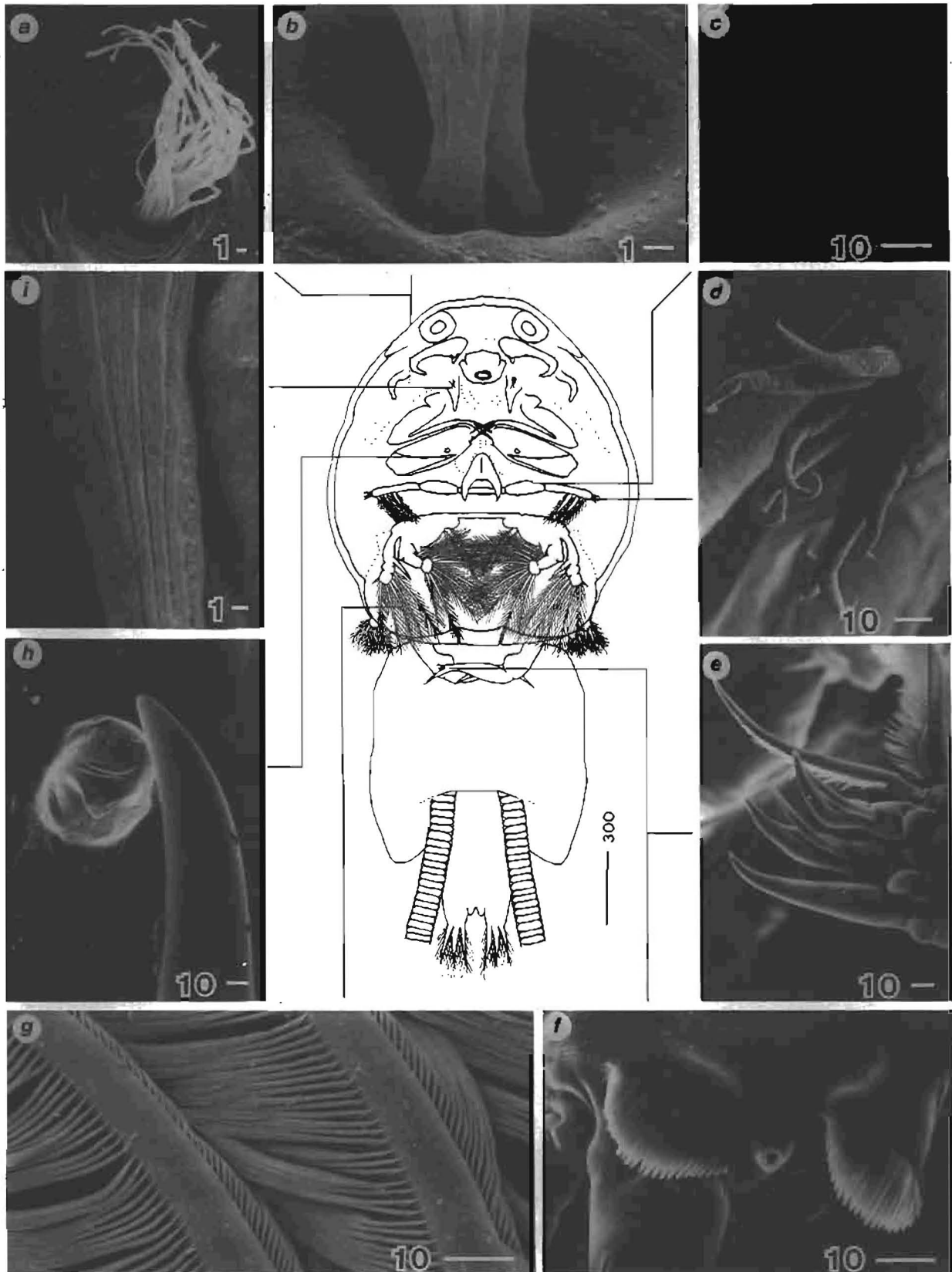


Figure 2 Scanning electron micrographs of fine structures of *Caligus infestans*: (a) sensory setae on the dorsal surface of the cephalothorax. (b) same, close-up to show biramous origin of setae, (c) spines on basal segment of first leg, (d) terminal spines on second segment of first leg, (e) setated tip of fourth leg, (f) densely packed spines on terminal segment of fourth leg, (g) densely packed setules on setae of swimming legs, (h) the hooked segment of maxilliped opposed by pod on basal segment, (i) the creased appearance of the setae of the maxillulary papilla of the first maxilla, indicating the presence of a covering membrane. (Measurements in μm).

relaxed. We agree with Kabata (1981) in provisionally assigning it a chemosensory function.

The mouthtube is of the typical tubular, caligoid form. The strigil is situated ventrally in the buccal cavity and is ventrally denticulated (Figure 1c), as has also been shown to be the case in *Caligus curtus* and *Caligus clemensi* (Kabata 1974). The frayed proximal orifice (Figure 1c & 1d) bears two rows of setae. A simple, single row of setae is present on the inner, subproximal surface (Figure 1d). From this point a continuous, striated, marginal membrane extends to a terminal row of setae, which varies in length (Figure 1e). This membrane is believed to assist in sealing off the mouthtube from the environment during feeding (Kabata 1974). Thus it appears that the 'striated' nature of this part of the mouthtube in the present study may once again be the result of the fact that the mouthtube was relaxed upon fixation. As the parasites feed by means of a sucking action (Kabata 1974), the greater area created by the 'striations' above suggests that this part of the tube is in fact laid down flat on the host surface and that the second, shorter row of bristles forms the final seal between the parasite and the host.

The first maxilla is simple, bearing the usual papilla. The setae on the papilla have a folded, creased appearance (Figure 2e), which indicates that a membranous covering is present on this appendage. The terminal segment of the second maxilla is bifurcated; each part is bilaterally flattened and bears a denticulated sharp edge (Figure 1f), very similar to that of *Caligus crummae* (Castro Romero & Kuroki 1982). This detail was not recorded for *C. infestans* by Pillai (1969), who simply described the second maxilla as having setae of unequal length. Although some confusion has existed as to the true identity of the first maxillae (Lewis 1969), the fact that this appendage (described above) was found to be enervated from the suboesophageal ganglion (Scott 1901), resulted in, amongst others, Heegaard (1945), Heegaard (1948), and Ferris & Henry (1949), assigning it the name of first maxilla. Heegaard (1945) subdivided the structure further and called the maxillary papilla a maxillule. This division has, however, since been discarded by general consent.

The scleritized, terminally hooked segment of the maxilliped folds back on the first segment and rests on a short pod (Figure 2h). This pod differs somewhat from that found recently for a different species of *Caligus*, which has a U-shaped structure into which the terminal hook is placed, presumably during attachment (Oldewage, in press). Although this has not been shown for the majority of species, it is likely that it is a common feature of all caligids. Thus Oakley (1926) indicated the existence of such a protrudence in *Caligus zeii* Norman & Scott, 1906. As the maxillipeds are used to attach to the gills of the host, this structure possibly enlarges the circumference of the area to which the parasite can attach securely.

The sternal furca is sharply pointed and bears a central ridge ventrally (Figure 1j). This structure is believed to be a remnant of the intercoxal plates of a vestigial pair of

swimming legs (Lewis 1969), although it has been argued to be an outgrowth of the sternal plate of the second maxillary segment (Heegaard 1945) or a remnant of an appendage of a primordial ninth body segment (Ferris & Henry 1949). The function of the sternal furca has not been previously discussed *a priori*, but as the attachment of caligids comes about in such a way that the ventral cephalothorax is sealed off from the environment by means of the thin marginal membrane under suction and the sternal furca has been observed to be ventrally movable (Kabata & Hewitt 1971) it appears probable that the sternal furca may be functional in acting as a supporting strut during attachment, thus enlarging the area under the cephalothorax and consequently the suction, which is necessary for attachment, as suggested by Wilson (1905). The presence of very fine, inwardly projecting spines on the marginal membrane on, for instance, *C. curtus* (Parker, Kabata, Margolis & Dean 1968) and other species (Oldewage in press), would thus enhance the attachment by counteracting the upward and inward forces on the cephalothorax as a result of the erection of the sternal furca in the vertical position to counteract the downward pressure on the cephalothorax as a result of said suction.

The first pair of swimming legs bear a number of short spines on the basal segment (Figure 2c) and seven stout setae on the terminal segment (Figure 2e). These spines are probably functional in offering positional support to the organism during movement; especially as the first and second legs are the main locomotory appendages (Kabata & Hewitt 1971). The feathered setae on the first, second, and third swimming legs bear bilateral rows of long setules originating from the setae (Figure 2g), thus creating a dense, uniform surface on especially the second leg which can effectively be used in locomotion. The fourth leg bears five terminal setae, of which two are bifurcated. All setae have denticulated edges, except two longer ones, which are feathered (Figure 2e). In addition to this, two neat rows of densely packed spines occur on the basis of the terminal segment (Figure 2f).

The anus is slitlike and opens between two anal labia between the uropods. Each of the labia bears a number of outwardly directed, short spines (Figure 1g). The uropods each have three feathered setae, but, as opposed to other setae on, for instance, the swimming legs, these setae have an additional row of short spines extending along the setae perpendicular to the densely packed setules (Figure 1h).

Finally, a number of complex sensory setae occur dorsally on the cephalothorax (Figure 2a) which may, in some instances, originate basally as two setae (Figure 2b), and as the name suggests, have a mechanosensory function (Parker *et al.* 1968).

As stated by Kabata (1981), the study of the piscine parasitic Copepoda has not outgrown its descriptive stage as yet. In order to understand the natural history of these parasites it is, however, essential to accurately describe not only the true structure of its appendages, but also their spatial orientation. This was shown for a single species during the present study, but further

research on the spectrum of caligids is necessary in order to understand the true adaptation in the morphology, as well as the life history of these organisms to the parasitic niche.

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