in this group (Wurster & Benirschke 1968). In speculating about karyological evolution in the Bovidae, Wallace (1979) postulated that the common ancestral bovid had a diploid chromosome number of 60.

The poor technical quality of our G-banded specimens preclude comparison with other species. Buckland & Evans (1978a,b), using both G-banding and C-banding techniques on various bovids (including a female red hartebeest from Uganda), concluded that the conservation of banding patterns in chromosome arms strongly indicated that Robertsonian translocation type rearrangements had provided the major source of interspecies karyotype differences, with inversions and reciprocal and tandem translocations providing relatively minor contributions.

Wallace (1976) pointed out that chromosome analyses of free-ranging wild animals could be more representative of the naturally occurring situation than would analyses of the chromosomes of zoo-bred animals. Sampling errors owing to the usually small sample sizes obtainable from zoos may lead to errors in establishing karyotypes. Breeding between different subspecies or even species is not uncommon in captive animals housed together, which could be a source of mistyping. Owing to the sheltered environment and absence of natural competition in zoos, chromosome changes associated with harmful effects would not necessarily be eliminated, nor would chromosome changes attended by beneficial effects necessarily be selected for, although these factors are probably minor, compared to small sample size and possible hybridization.

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Observations on the attachment of a piscine gill parasitic ergasilid (Crustacea : Copepoda)

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The attachment of the piscine gill parasite, *Ergasilus mirabilis* Oldewage & van As, 1987 is described by means of scanning electron microscopy and light microscopy. A variety of sensory structures occur on and around the host contact surface of the parasite and proliferation of gill tissue occurs at the site of attachment. It would appear that this proliferation of host tissue results from the feeding behaviour of the parasite rather than the actual attachment thereof.

Die vashegting van die vis-kieuparasiet, *Ergasilus mirabilis* Oldewage & Van As, 1987 word beskryf aan die hand van skandeerelektronmikroskopie en ligmikroskopie. 'n Verskeidenheid sensoriese strukture kom op en in die omgewing van die gasheerkontakvlak van die parasiet voor en proliferasie van die kieuepiteel vind plaas op die plek van vashegting. Dit blyk dat die proliferasie van gasheerweefsel eerder die gevolg van die voedingsgedrag van die parasiet is as van die vashegting daarvan.

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It has been suggested, and available information supports this view, that parasitic copepods are phylogenetically derived from free-living cyclopoids (Fryer 1956; Kabata 1970a). A number of instances are reviewed by Kabata (1970b) of free-living cyclopoids displaying micropredatory behaviour, i.e. preying on fish eggs and larvae, suggesting a possible starting point

in the niche shift to a parasitic lifestyle. Although some ergasilids occur on the skin or in the nasal fossae of fish (Burris & Miller 1972; Rogers & Hawke 1978; Yamashita 1980), the majority of species frequent the gill filaments. Study of the attachment of ergasilids has been largely limited to epidemic infestations, when obvious gross pathology and host mortality occurred (Bauer 1970; Paperna 1970). Pathology is, however, linked to the mode of attachment of a particular species of *Ergasilus*, as some ergasilids simply embrace the gill filament of their host, whereas others, e.g. *Ergasilus colomeus* Thatcher & Boeger insert the entire claw and part of the third segment of the second antenna into the filament (Thatcher & Boeger 1983). In contrast to this, no pathological effects were observed in *Ictalurus punctatus* Bloch heavily parasitized by *Ergasilus arthrosis* (Gruninger, Murphy & Britton 1977). The present species, *Ergasilus mirabilis* Oldewage & van As, 1987 parasitizes a wide range of fishes of various families. This study is aimed at describing its attachment to the gill filament of its host, with a view to elucidating this particular host-parasite interaction. This was done in the light of the apparent lack of such information in existing work on ergasilid biology, as pointed out in a comprehensive review by Kabata (1981).

Live material was sampled in the field and fixed in either 10% neutral buffered formalin or 70% ethanol. Parasites were removed from the gills by micro-dissection and cleaned with sodium hypochlorite as descibed by Johnson (1969). Specimens were cleared, wax embedded and sectioned for light microscopy. Specimens for scanning electron microscopy were dehydrated in a series of ethanols, transferred to amyl acetate and critical point dried. Sputter coating was done with gold for 4 min at 20 μA and specimens were examined in an ISI-SS60 SEM at 4–10 kV.

E. mirabilis (Figure 1a) attaches to the gill filament of its host by means of the second antennae, which have been adapted to form two robust claws, with the ventral surface of the parasite resting on the surface of the gill filament. The second antenna is typical of this genus, consisting of a short, anteroventrally directed basal segment originating from the anterior periphery of the cephalothorax, a long, stout, second segment, a slender, curved, third segment and a sharp, curved, sclerotized, terminal hook (Figure 1b). The first antennae are situated directly dorsal to the second antennae (Figure 1a). A variety of apertures and fine setae occur on the body surface, especially in the area which is in direct contact with the gill filament, all of which are thought to have a sensory function. This subject has, however, not been studied in detail and needs further investigation. Three apertures occur medially in a triangular configuration between the second antennae (Figure 1d) and another four laterally on either side of two central fine setae on the anterior periphery of the cephalothorax (Figure 1e). The mouth opening is situated ventrally on the cephalothorax. Although especially the second maxilla is a cause of host damage, the mouth cavity remains closed under the labrum when the parasite is not feeding.

E. mirabilis attaches to the host's gill filament in such a way that the body, but not the egg sacs, oppose the filament, *viz.* as the parasite is orientated with the anterior end directed towards the gill arch, the caudal rami and the tip of the filament lie in line, so that the egg sacs are carried outside the gills (Figure 1f). Although the present study was not done during a hyperinfestation by *Ergasilus* — approximately seven parasites were collected per host — significant proliferation of gill tissue occurred and a definite hollow was observed in the area opposing the mouthparts (Figure 1f), which is thought to be the result of feeding. Significant distortion of the gill structure was found at the point of attachment, the gill filament being compressed to fit into the area circumscribed by the second antennae of the parasite (Figure 2a) and the terminal hooks causing a sharp indentation (Figure 1h), but not actually piercing the tissue (Figure 2b).

The normal gill structure (Figure 2c) was altered in the vicinity of the mouthparts of the parasite, a definite hollow being present in the filament in some instances and the peripheral cell layer having a frayed appearance (Figure 2d), presumably as a result of the feeding of the parasite. Damage can be seen even more clearly when comparing a section of an uninfested filament (Figure 2e) with an infested one (Figure 2f). Gross proliferation of gill epithelium occurs in the area opposing the parasite's mouthparts to such an extent that the central cartilage is set off to the extreme edge of opposite side of the filament to which the parasite is attached. There is, furthermore, a total absence of the two main blood vessels which occur centrally on either side of the central cartilage. No changes were observed in the areas opposed by thorax and abdomen.

Ergasilids exhibit significant variation in their attachment to their hosts. *Ergasilus nodosus* Wilson has, for instance, been recorded as attaching itself anywhere along the gill filament by inserting the two proximal segments of the second antennae into the gill filament (Wilson 1928), while *Ergasilus centrichidarum* Wright attaches only to the outside of the filament (Wilson 1914). An African species, *Ergasilus kandti* van Douwe, was found only on the lower parts (i.e. close to the gill arch), while *Ergasilus megachier* (Sars) occurred only on the extreme tip of the same filament (Fryer 1965), as is the case for the present species.

The importance of the gill structure and the arrangement of filaments on the various gill arches of a species of fish to the attachment of ergasilids has been pointed out by Shotter (1977), who found an equal distribution of parasites on a host with an even number of filaments on all gill arches, as opposed to an unequal distribution in fish with an uneven number of filaments on each pair of gill arches. This observation suggests an opportunistic trend in the attachment strategy of at least some ergasilids. As *E. mirabilis* was not found to show any recognizable pattern of distribution on the gills of the nine hosts which it parasitizes, this species shows little host specificity, in accordance with the suggestion by Cressey & Collette (1971), that ergasilids are generally not host specific. In fact, up to three species,

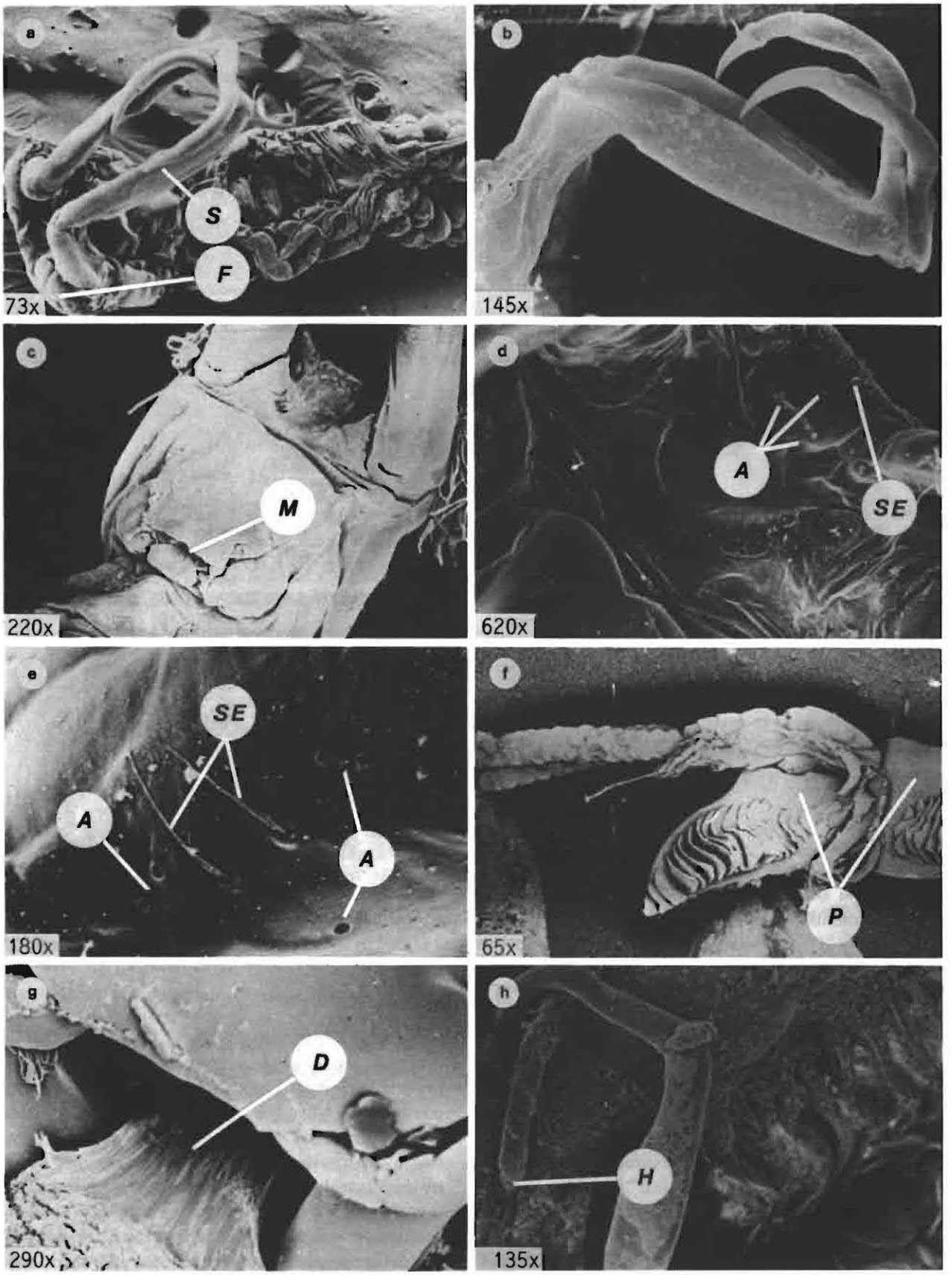

Figure 1 Scanning electron micrographs of the attachment and attachment structures of *E. mirabilis*: a. ventral view of the whole organism to show the orientation of the first (F) and second (S) antennae; b. second antennae, lateral; c. ventral view of cephalothorax showing the mouth opening (M); d.& e. presumed sensory apertures (A) and setae (SE) on the host contact surface ventrally between the first antennae; f. lateral view of the attached organism on a gill filament, showing cellular proliferation (P) of host tissue; g. dorsal view of attachment to illustrate deformation of the filament (D); h. the overlapping subterminal segments of the second antennae, with the sclerotized , terminal hook (H) embedded in the gill tissue.

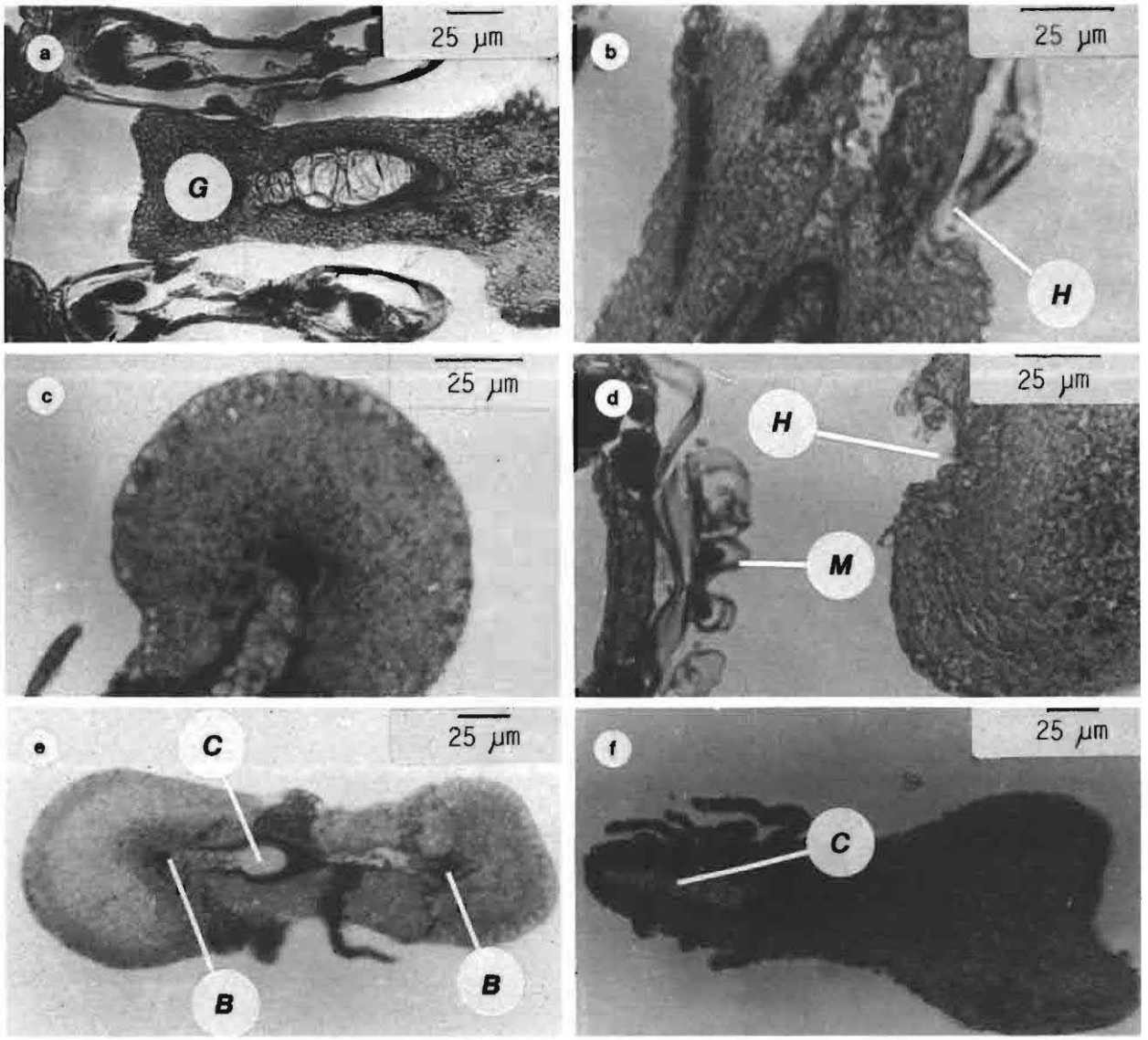

Figure 2 Light microscopical sections of: a. a gill filament (G) in the vicinity of the second antennae of *E. mirabilis*; b. the terminal, scleritonized hook (H) embedded in the gill tissue; c. the inner edge of a normal filament; d. a filament opposing the mouthparts (M) of the parasite, showing the hollow (H) presumably caused by the feeding of the parasite; e. a whole gill filament with blood vessels (B) and central cartilage (C); f. a whole, infested filament showing the absence of blood vessels, proliferation of gill tissue and the altered location of the central cartilage (C).

i.e. *E. kandti, Ergasilus flaccidus* Fryer and *E. megachier* have been reported from a single gill filament (Fryer 1965). This suggestion might well hold true, as the area circumscribed by the second antennae of *E. mirabilis* is variable because of the significant overlap of the subterminal segments and the variable angular orientation of the connection between the third and fourth segments, which provides significant lengthwise extention of the circumscribed area. This facilitates attachment to gill filaments of varying circumference, depending on the host species involved. Furthermore, the peripheral deformability of the gill filament suggests that once a grip has been secured, gradual compression of the gill tissue occurs in order to assure firm attachment. It is generally accepted that ergasilids feed on the gill tissue of their hosts. Some doubt exists, however, as to what component is mainly utilized and reports vary from blood , mucus or gill epithelium to a combination of the three mentioned components (Einszporn 1965). Scanning electron microscopy during this study has shown that the mouth opening is covered by the ventrally projecting labrum in such a way that the mouthparts are not in contact with the host tissue during periods of non-feeding. Feeding must, however, occur regularly in order to sustain the parasite and thus significant proliferation of gill tissue occurs in the vicinity of the mouthparts and damage as a result of feeding shown by sectioned material, suggests that *E. mirabilis* feeds indiscriminately on gill tissue, as suggested for *Ergasilus seiboldi* von Nordmann by Einszporn (1965), who reported the presence of blood, mucus and gill epithelium in the gut of this parasite.

The present study has also shown that pressure on the gill filament caused by attachment of the parasite, perhaps in conjunction with the gross proliferation of gill tissue in the vicinity of the mouthparts, causes the two main blood vessels in the filament to be occluded. This restricts the functional capability of the filament, which could lead to hypoxia. During hyperinfections this can result in death, as recorded by Hoffmann (1977).

The role of sensory or chemosensory structures in finding a suitable host was first suggested by Fryer (1966). According to this author spatial distribution and host diversity should also be linked to the behaviour of the fish host. Parasites were, however, found on a wide variety of hosts during this study and no common ethological characteristic has as yet been found among the recorded hosts. The answer lies, perhaps, in the fact that some *Ergasilus* larvae exhibit a diurnal, vertical migration pattern (Bauer 1970), which would facilitate the infestation of benthic, as well as pelagic hosts. Although sensory apertures and setae have been shown to occur over the entire soma of *E. mirabilis* (Oldewage & van As 1987), it is significant that a number of these occur directly between the second antennae, suggesting a chemosensory role for the apertures and a mechanosensory role for the fine setae. This, together with the sensory function ascribed to the first antennae (Hoffmann 1977) and the fact that live specimens have been observed to respond to mechanical stimulation in the antennal region by executing a grabbing action with the second antennae, suggests that this variety of sensory structures is functional in the location of a gill filament once the parasite finds itself in the gill cavity of a potential host, as well as in the final orientation of the parasite on the gill filament.

Finally, the evidence presented supports the view mentioned before, that ergasilids are widely adaptable to different hosts and environments, which in turn suggests that they are relatively unspecialized parasites.

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