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From the viewpoint of the functional morphology, this report presents scanning electron and light microscopic observations on the feeding apparatus of the adult cattle tick, *Haemaphysalis longicornis*. The digits of the chelicerae act as a cutting organ for host skin and tissues. Protrusion of the whole chelicerae may be effected by an increase in internal body pressure and regulated by the cheliceral retractor muscles. The cheliceral sheath and hypostome bear many denticles which stabilized attachment of ticks to a host. Pulsations of the hypostomal membrane appear to be associated with a flowing of host blood and tick saliva. The labrum seems to close the pharyngeal orifice so that an inflow of saliva into the pharynx is prevented. The function of the salivarium is thought to be a salivary valve, because its floor undergoes a vertical motion by antagonistic actions of the constrictor muscles of the ala. Thus, a mixture of host blood and tick saliva would be precluded by the regulation among the labrum, the salivarium and the constrictor muscles of the ala. The pharynx functions as a sucking pump for host blood by contraction and relaxation of its dilator and constrictor muscles.

INTRODUCTION

The feeding mechanism of ticks has been studied for a long time in relation to disease transmission and host immunity (Arthur, 1962, 1965; Balashov, 1972 ; Kemp *et al.,* 1982), and the structure of the feeding apparatus has been well elucidated in several species of ixodids (e. g. Gregson, 1960 for *Dermacentor andersoni* ; Kemp and Tatchell, 1971 for *Boophilus microplus*; Balashov, 1972 for *Hyalomma asiaticum)* and argasids (e. g. Sonenshine and Gregson, 1970 for *Ornithodoros kelleyi* ; Guirgis, 1971 for *Argas arboreus*). *To* our knowledge, however, there has been no morphological study on the feeding apparatus of the genus *Haemaphysalis,* except for the anatomical studies on *H. punctata* (Nuttall *et al.,* 1908) and *H. flava* (Saito, 1960). The physiology of feeding in the cattle tick, *H. longicornis* has been solved in some degree (Kitaoka, 1967, 1977), because of the economic importance of this species as a most dominant tick in pastures of Japan and as the vector for theileriosis. However, it is impossible to understand well the feeding mechanism of ticks without revealing the structure and functions of the feeding apparatus. Therefore, the aim of this study is to examine with the scanning electron and light microscopes the structure of the feeding apparatus of the adult *H. longicornis,* and to discuss its functional morphology.

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MATERIALS AND METHODS

The ticks used in this study are of the non-parasitic stage of the adults (*Haema-physalis longicornis)* which were collected by the flagging method on the pastures in the Fukuoka and Oita Prefectures.

For scanning electron microscopy, the ticks were preserved in 70 % ethanol, fixed to the specimen stubs by silver paint, and dried overnight in desiccators. The speci-mens were examined in an Hitachi SSM-2A scanning electron microscope (10 kV), following coating with gold.

On the other hand, for light microscopy, the ticks were incised on the cuticula by a lazor blade, and fixed with cold 1.5 % glutaraldehyde in Millonig's buffer (pH 7.4). After being thoroughly rinsed with the same buffer, the ticks were post-fixed with 1 % osmium tetroxide in the same buffer, dehydrated with acetone and embedded in epoxy resin. Sections ($\sim$1.5 μm) were cut on a Porter-Blum MT-l microtome, and stained with toluidine blue.

RESULTS AND DISCUSSION

Scanning electron microscopical observations on the external structure

The capitulum of **Haemaphysalis longicornis** is composed of the following four parts ; i. e. a pair of palps and chelicerae, a hypostome and a basis capitulum (Fig. la, b). Each palp consists of four segments ; a number of setae are found on segments 1–3 and palpal organ on a small segment 4 (Fig. la, b). It has been known that these palpal receptors are involved in the exploration and selection of an attachment site as well as tarsal and cheliceral receptors (Waladde and Rice, 1982). The chelicerae consist of a pair of rigid cuticular shafts, and each shaft bears a cheliceral digit at its apex, which can cut the skin and tissues of the host (Fig. la, b). The chelicerae are enclosed within the cheliceral sheaths of sclerotized cuticular tubes which protrude from the anterior part of the basis capitulum (Fig. la, b). The small denticles on the dorsal surface of the cheliceral sheath (Fig. la) are lacking in argasids and some prostriate ticks (genus *Ixodes*), both of which do not secrete cement (Kemp et al., 1982) ;

Fig. **1.** Scanning electron micrographs showing dorso-lateral (a) and ventro-lateral (b) views of the capitulum of a female *Haemaphysalis longicornis.* Note the chelicerae and the cheliceral digits protruding from the cheliceral sheath by the handling depres-sion of the tick body. The following abbreviations are used in Figs. 1–5 : A, ala ; B, basis capitulum ; C, chelicera ; Ca, constrictor muscles of the ala ; Cd, cheliceral digit ; Cf, camerostomal folds ; Cn, central nerve mass ; Cs, cheliceral sheath ; Dc, dorsal constrictor muscles of the pharynx ; F, food channel ; Fe, flexor and extensor muscles of the cheliceral digit ; H, hypostome ; Hm, hypostomal membrane ; L, labrum ; Lc, lateral constrictor muscles of the pharynx ; Ld, lateral dilator muscles of the pharynx ; Lm, levator muscles of the capitulum ; M, oval membraneous window ; P, palp ; Pa, porose area ; Ph, pharynx ; Po, palpal organ ; Pl, palpal segment 1 ; P2, palpal seg-ment 2 ; P3, palpal segment 3 ; P4, palpal segment 4 ; R, cheliceral retractor muscles ; S, salivarium ; Sc, scutum ; Sd, salivary duct ; Sp, subcheliceral plate ; Va, ventral articulation between the capitulum and the idiosoma ; Vc, ventral constrictor muscles of the pharynx ; Vd, ventral dilator muscles of the pharynx.
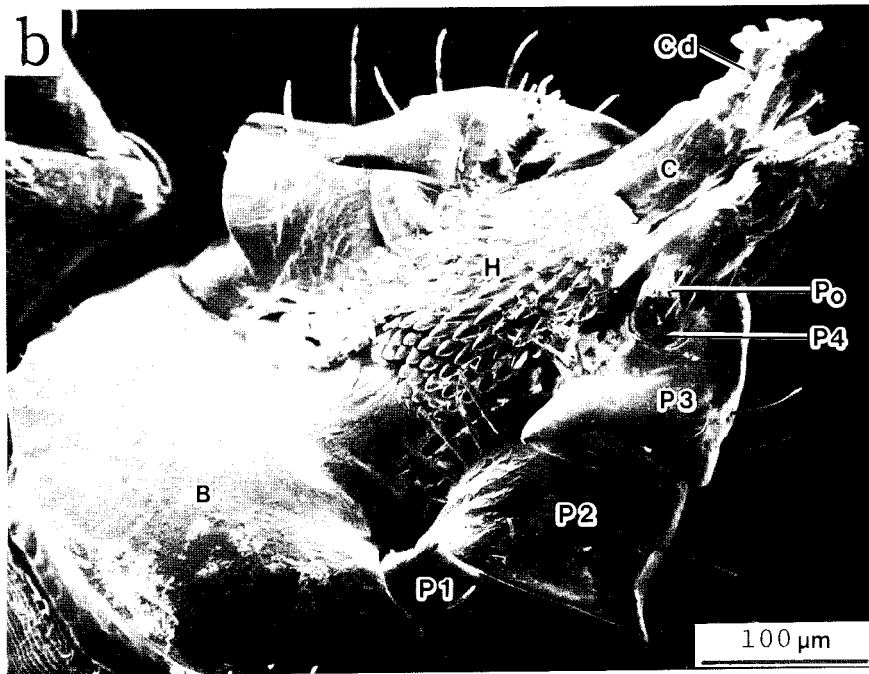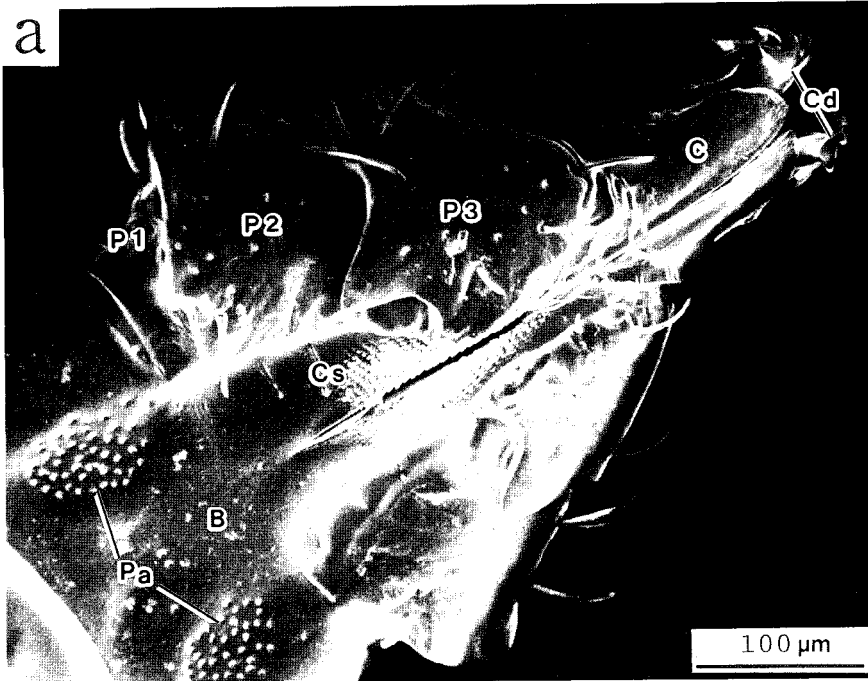
therefore, these denticles become embedded in attachment cement and may help to secure tick attachment. The ventral wall of the basis capitulum is prolonged anteriorly to form the hypostome whose external side has large recurved denticles by which attachment of ticks is still more strengthened (Fig. lb). The female has a pair of porose areas on the dorsal side of the basis capitulum (Fig. la), but the male is devoid of them.

Light microscopical observations on the internal structure

The cheliceral sheath, hypostome, basis capitulum and scutum are formed of sclerotized cuticle which stained blue or light blue with toluidine blue. On the other hand, camerostomal folds and a ventral articulation between the capitulum (gnathosoma) and the idiosoma are made up of non-sclerotized cuticle which took a purple in toluidine blue stain (Fig. 2). The presence of these non-sclerotized cuticles may allow the capitulum to move dorso-ventrad to some extent.

The chelicera is a sclerotized cuticular tube, becoming swollen proximally. The oval membraneous window situated dorsally and about two-thirds back from the tip, may permit the chelicera to bend. The cheliceral digit is provided with the flexor and extensor muscles which arise from the distended base of the cheliceral shaft (Figs. 2 and 3a). Host skin is penetrated by cutting action of the cheliceral digit which move
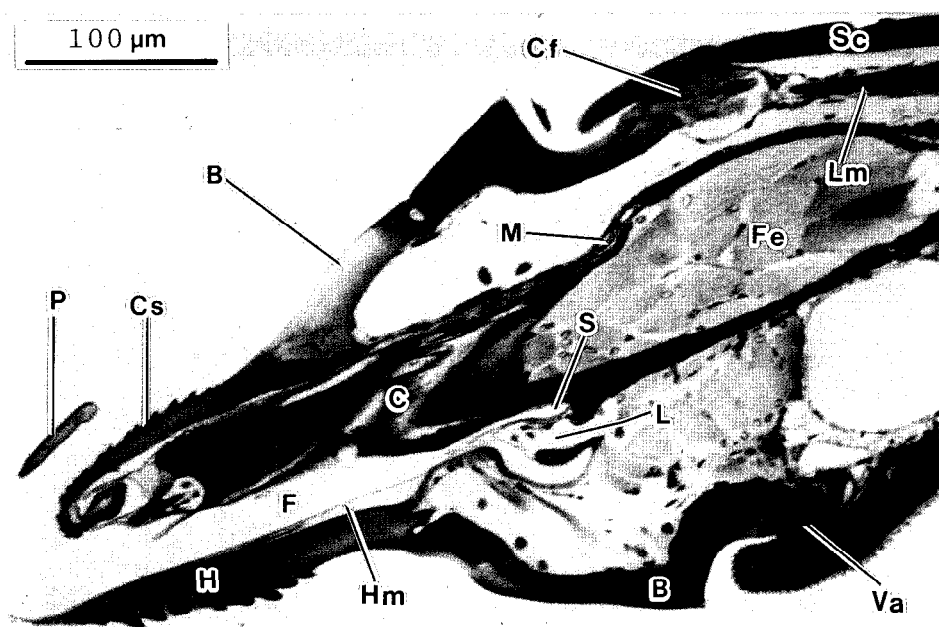

Fig. 2. Light micrograph showing para-sagittal section of the capitulum of a male *H. longicomis.* Sclerotized cuticle (cheliceral sheath, chelicera, hypostome, basis capitulum and scutum) and non-sclerotized cuticle (camerostomal folds and ventral articulation) stained blue and purple with toluidine blue, respectively. Abbreviations : *see* the legend to Fig. 1.
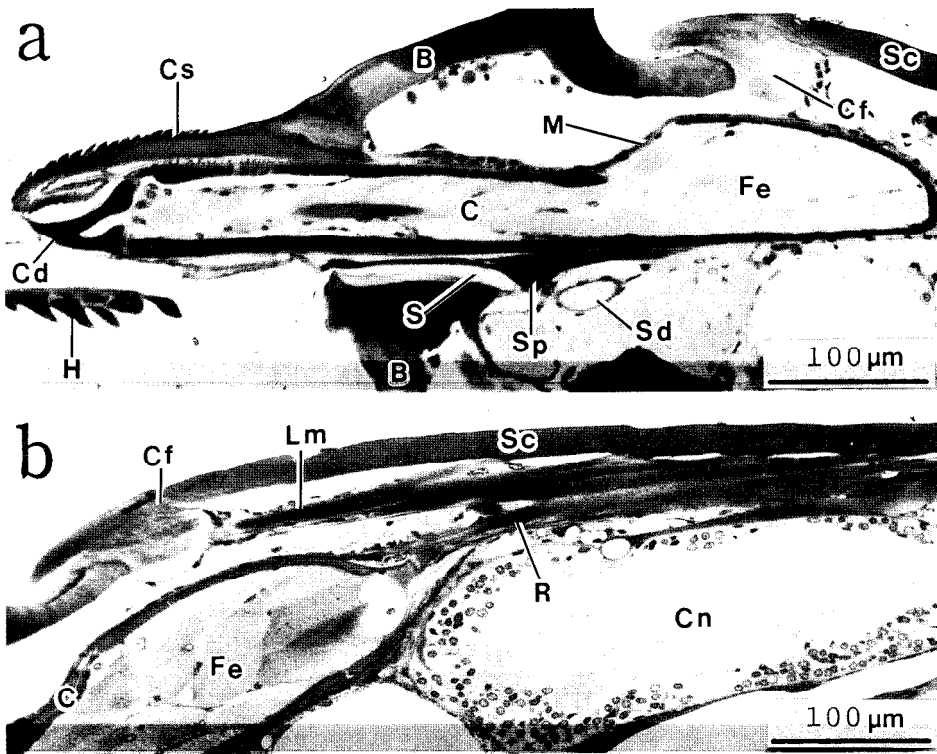
Fig. 3. Light micrographs showing para-sagittal sections of the chelicera in a male *H. longicornis*. Toluidine blue staining. a) The chelicera bears the cheliceral digit at its tip, which is provided with the flexor and extensor muscles. Oval membraneous window situates about two-thirds back from the apex. b) The cheliceral retractor muscles which seem to regulate protrusion of the chelicera insert on the base of the chelicera. Abbreviations : see the legend to Fig. 1.

by actions of these antagonistic muscles, and deeper insertion may be caused by a forward movement of the whole chelicera. Arthur (1946 for *Ixodes ricinus,* 1951 for **Ixodes** *hexagonus,* 1957 for *Dermacentor parumapertus*) has insisted that protrusion of the chelicerae is effected by contraction of the dorso-ventral somatic muscles, resulting pressure within the body cavity forcing the cheliceral shafts out through their sheaths. In **H.** *longicornis* also, protrusion of the chelicerae caused by depressing the tick body became visible (Fig. la, b). The cheliceral retractor muscles seem to regulate the protrusion degree of the chelicera inserted on the base of each chelicera (Fig. 3b).

The food channel which extends from the buccal opening to the pharyngeal orifice, is a common duct for the intake of host blood and for the output of tick saliva. The floor of the food channel forms a V-shaped groove of the hypostome, the roof of the groove being covered by a thin hypostomal membrane (Figs. 2 and 4a). This membrane of other ixodids has been thought to have the following functions in feeding: i. e. in *Dermacentor* **andersoni,** pulsations of membrane may assist a flowing of host blood and
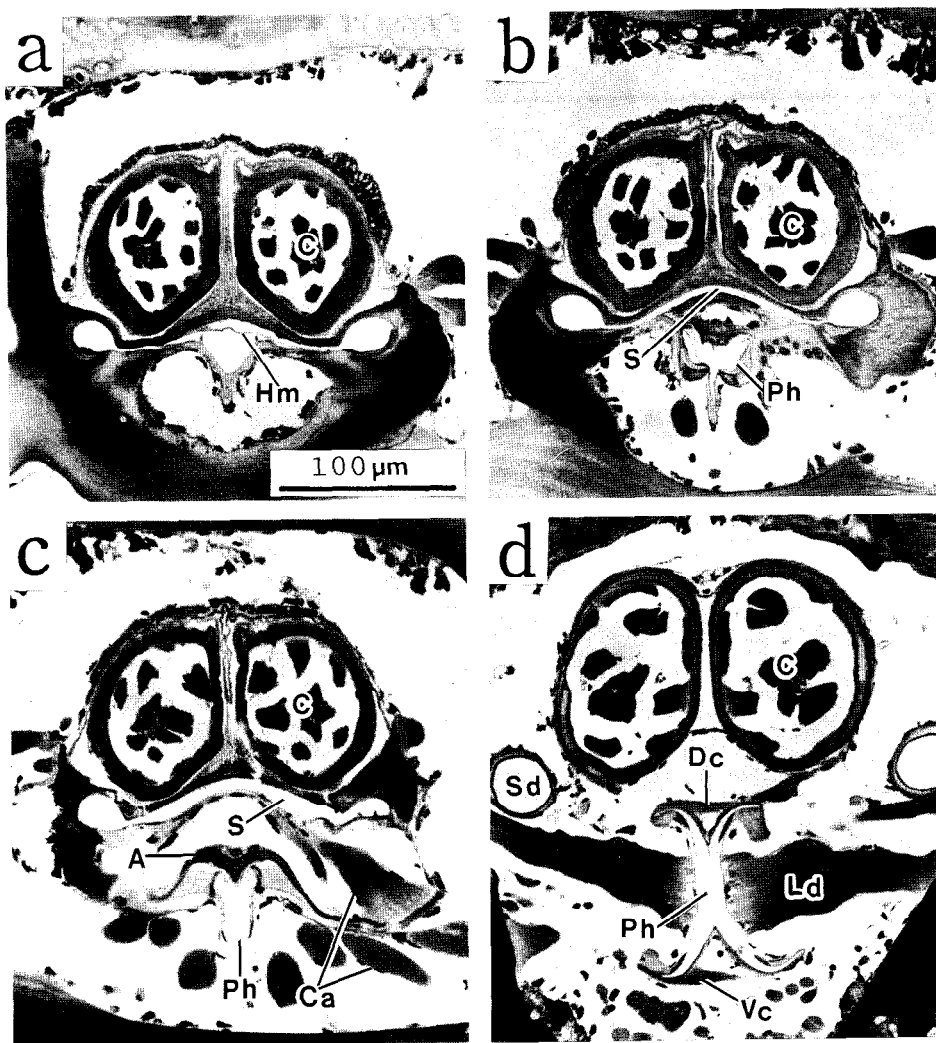
Fig. 4. Light micrographs showing cross sections of the capitulum of a female *H. longicornis* at successive levels from anterior to posterior (a-d). The cutting levels (a-d) are shown in Fig. 6. Toluidine blue staining. The scale as in (a). Abbreviations : *see* the legend to Fig. 1.

tick saliva, and the rising and depressing action of the membrane also appears associated with regulation of salivation (Gregson, 1960) ; on the other hand, m *Boophilus microplus,* in the resting position the hypostomal (gutter) membrane may be raised to block the food channel, and in the feeding position this membrane may be lowered to open the food channel at the same time as the pharyngeal valve opens (Kemp and Tatchell, 1971).

In *H. longicornis,* the labrum of a flexible tongue-like structure is shorter (Fig. 2)

than that of argasids. Argasids possess the extensive labrum : in *Argas persicus* (Robinson and Davidson, 1913a) and in *Ornithodoros papillipes* (Sen, 1935), the function of the labrum seems to close the pharyngeal orifice so that saliva is forced into the feeding lesion ; moreover, in *Ornithodoros kelleyi* and *Ornithodoros denmarki* (Sonenshine and Gregson, 1970) and *Argas arboreus* (Guirgis, 1971), the labrum act as a prepharyngeal valve which is activated by hydrostatic pressure. On the contrary, because the labrum of ixodids is short, it is unlikely that it could exclude saliva from the food channel or act as a valve (Kemp *et al.,* 1982).

The salivarium, which lies above the labrum, (Fig. 2) is roofed by the subcheliceral plate (Fig. 3a), into whose postero-lateral angles the two salivary ducts open. In terms of the function, the salivarium has been regarded as a salivary valve, a reservoir or a pump (Kemp *et al.,* 1982) : in *D. andersoni* (Gregson, 1960) and *A. arboreus* (Guirgis, 1971), the salivarium cannot be considered a reservoir for saliva, because strong sclerotization of its wall incapacitates the salivarium from remarkable expansion ; however, the salivarium is described as a salivary reservoir in *Hyalomma asiaticum* (Balashov, 1972) and thought to function as a salivary valve or as a small reservoir in *B. microplus* (Kemp and Tatchell, 1971).

The pharynx whose wall is composed of an inner cuticular layer and an outer thin epithelial layer, shows a Y-shape in cross sections just behind the pharyngeal orifice (Fig. 4b). In subsequent sections, the ala or a wing-like cuticular extension is observed at the dorsal side of the pharynx ; in *H. longicornis,* the constrictor muscles pass dorsally from the ala to the floor of the salivarium and connect ventrally to the ala and the basis capitulum (Fig. 4c). The similar muscles are present in *D. parumapertus* (Arthur, 1957), *D. andersoni* (Gregson, 1960) and *H. asiaticum* (Balashov, 1972), but absent in *B. microplus* (Kemp and Tatchell, 1971) ; Arthur (1957) suggests that these muscles function antagonistically and are associated with closing and opening of the pharynx. At the middle and the posterior parts, cross sections of the pharynx show an X-shaped (or a double Y-shaped) appearance (Fig. 4d) which is seen also in other metastriate ticks, e. g. the genus *Hyalomma* (Balashov, 1972), *Boophilus* (Kemp and Tatchell, 1971), *Rhipicephalus* (Till, 1961) and *Dermacentor* (Arthur, 1957 ; Gregson, 1960) ; while in prostriate ticks, the genus *Ixodes* (Arthur, 1946, 1951) and argasid ticks, e.g. the genus *Ornithodoros* (Sen, 1935 ; Sonenshine and Gregson, 1970) and *Argas* (Robinson and Davidson, 1913b ; Guirgis, 1971), the pharynx has a triple Y-shaped cross-section. At this level, the constrictor muscles attach to the dorsal, ventral and lateral walls of the pharynx, and the dilator muscles pass from the lateral and ventral walls of the pharynx to the basis capitulum (Figs. 4d and 5a-c). The pharynx changes the capacity of the inner cavity by contraction or relaxation of these muscles (Fig. 5a, b), and functions as a sucking pump for host blood.

Based on the above results, the feeding apparatus of *H. Zongicornis* is reconstructed in Fig. 6, being morphologically similar to that of other metastriate ticks. As mentioned above, however, information on the function of the feeding apparatus varies with tick species and/or investigators, and consequently confusion arises in the mechanism of feeding and salivation.

In conclusion, the feeding mechanism of the cattle tick *H. longicornis,* seems to be as follows. Host blood flows through the food channel by pulsations of the hypostomal membrane, and reachs the oesophagus which links the pharynx and the midgut, by

pumping up of the pharynx. Opening and closing of the pharynx (pharyngeal valve) are effected by the constrictor muscles of the ala. These constrictor muscles also cause the floor of the salivarium to move vertically by contraction or relaxation, thus the salivarium in *H. longicornis* appears to act as a salivary valve, but unlikely to function as a reservoir for the bulk of saliva because its sclerotized wall precludes the ability of conspicuous expansion. The labrum in *H. longicornis* seems not to have such a
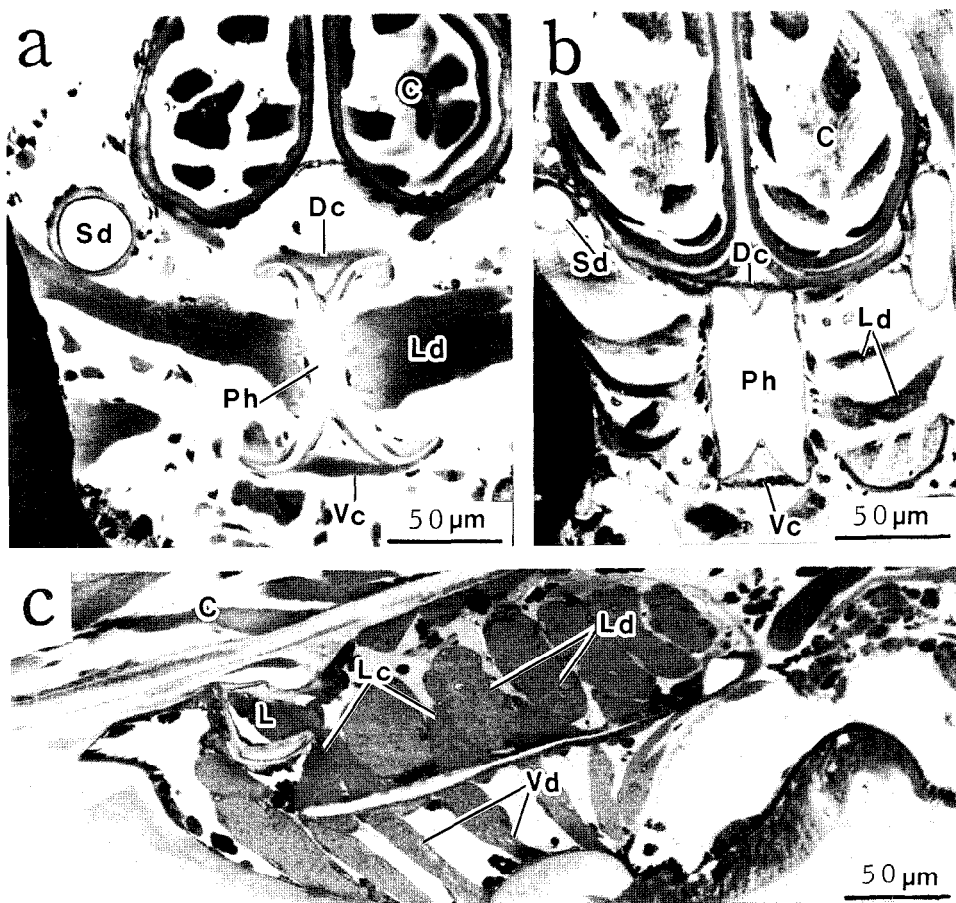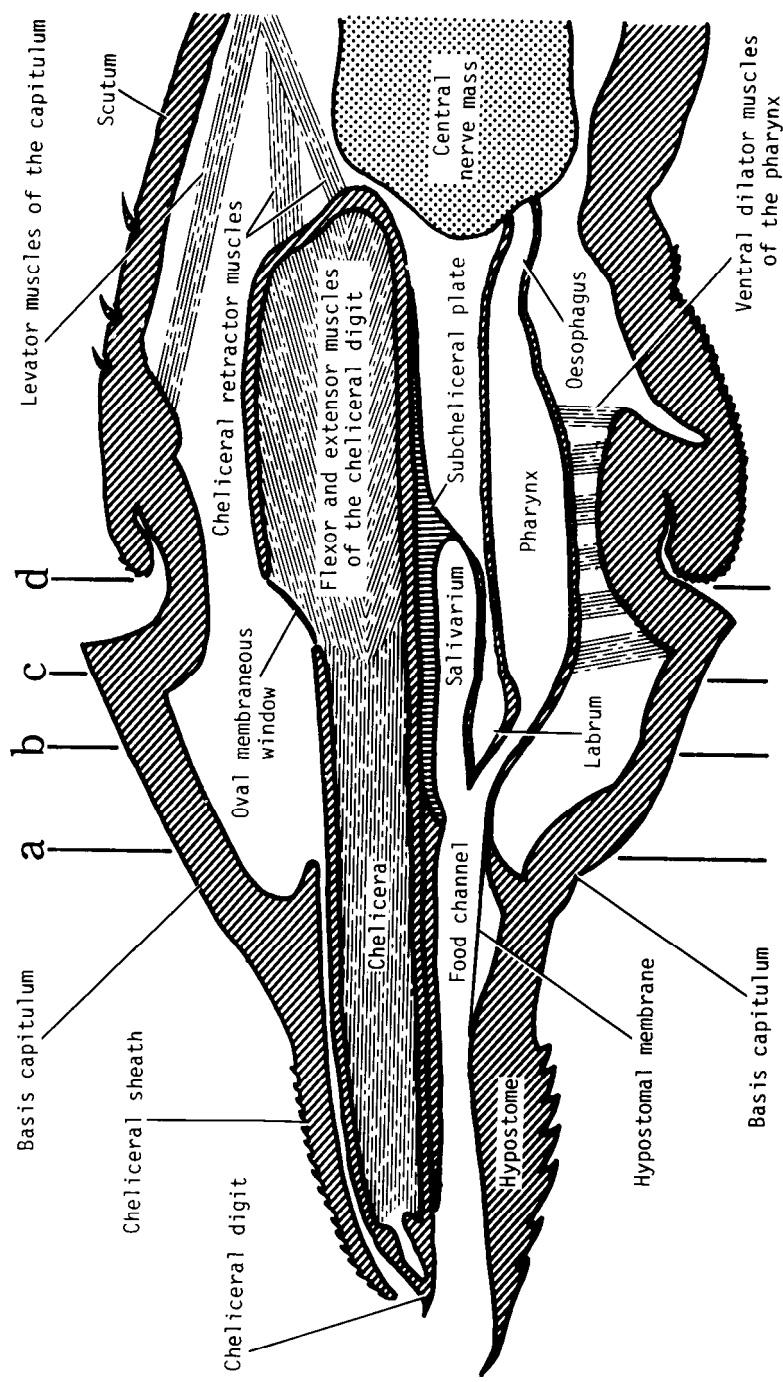

Fig. 5. Light micrographs of the muscle attachment to the pharynx. Toluidine blue staining. a) and b) Cross sections of a female *H. longicornis* showing the situations of the pharynx when the lateral dilator muscles relaxed and contracted, respectively, and attachment of the dorsal and ventral constrictor muscles which seem to grasp expansion of the pharynx. c) Para-sagittal section of a male tick showing the running direction of the lateral and ventral dilator muscles, and the lateral constrictor muscles of the pharynx. Abbreviations: see the legend to Fig. 1.

Fig. 6. Diagramatic reconstruction in a para-sagittal section of the capitulum of *H. longicornis*. The symbols indicated on the vertical lines show the cutting levels in Fig. 4a-d. (opposite page)

Levator muscles of the capitulum

Scutum

Central nerve mass

Ventral dilator muscles of the pharynx

Cheliceral retractor muscles

Flexor and extensor muscles of the cheliceral digit

Subcheliceral plate

Oesophagus

Basis capitulum

Oval membraneous window

Salivarium

Pharynx

Labrum

Cheliceral sheath

Chelicera

Food channel

Basis capitulum

Cheliceral digit

Hypostome

Hypostomal membrane

a   b   c   d

function of saliva exclusion as in argasids, but is long enough to close the pharyngeal orifice so saliva does not flow into the pharynx. Therefore, a mixture of host blood and tick saliva would be prevented by the complexly and delicately adjusted balance among the labrum, the salivarium and the ala whose constrictor muscles attach to the floor of the salivarium.

ACKNOWLEDGEMENTS

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