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Morphology and Functioning of the Mouthparts of *Dermacentor andersoni* Stiles.

By J. D. GREGSON.

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ala	ala; wing-like extension of pharynx
b.c.	basis capituli
b. can.	buccal canal
b. cav.	buccal cavity
ch.	chelicera
ch.r.	cheliceral ridge
c.g.	central ganglion (brain)
c.s.	cone sheath
d.c.	denticle cavity
di.	digit
e.	eye
g.	gut
G.o.	Gené's organ

hd.	hood of digit
h.g.	hypostome groove
hyp.	hypostome
i.c.b.	intercoxal bridge
lm.	labrum
mb.	membrane over gutter of hypostome
m.c.ph.	constrictor muscles of pharynx
m.d.c.	depressor muscles of capitulum
m.d.ph.	dilator muscles of pharynx
m.f.	membranous fold of digit
m.l.c.	levator muscles of capitulum
m.r.c.	retractor muscles of chelicera
o.c.s.	outer cheliceral sheath
oes.	oesophagus
o.m.	oval membrane-covered area of chelicera
p. I-IV	palpal segments I-IV
p.a.	porose area
p.o.	pharyngeal orifice
p.c.s.	posterior cheliceral sheath
p.	pore of internal article
ph.	pharynx
p.s.	periganglionic sinus
p.v.	pharyngeal valve
sal.	salivarium
s.ch.p.	subcheliceral plate
s.d.	salivary duct
s.g.	salivary gland
t.	tectum
t.g.	tongue-and-groove-like ridges along adjacent faces of chelicerae

Part I. The Feeding Mechanism in Relation to the Tick.

1. Introduction.

Ticks are of great importance to man and animals as parasites and as vectors of arthropod-borne diseases, as has been reviewed by NEVEU-LEMAIRE (1938), HERMS (1939), PHILIPP (1939), and others.

These relationships, by their nature, are largely brought about through the medium of the tick's mouthparts. Considering this, it is surprising that a greater knowledge does not exist on these structures. The pharyngeal apparatus, in particular, appears to be little understood in the few species that have been studied; not only is little known about the function of its various associated structures, but controversy even exists over the nature and position of the entrance to the pharynx. There is little doubt that studies along these lines have been hampered by the heavy armour encasing the mouthparts. This not only makes sectioning difficult but serves to hide further the movement of the inner structures which, in the feeding tick, are already partially obscured by the enveloping tissues of a living host. It is hoped that the present studies on *Dermacentor andersoni* Stiles will contribute to this field and explain the function of certain secretions which, possibly, play a part in the production of tick paralysis (GREGSON, 1953). Unless otherwise mentioned they refer to the female of the species.

2. Materials and Methods.

Most of the material consisted of unengorged adult *Dermacentor andersoni* Stiles females, either laboratory reared or collected from vegetation in the vicinity of Kamloops, British Columbia. A few males, early stages, and other species were studied for comparison. Dissections were made from fresh and preserved specimens, and a few preparations were cleared in caustic potash or phenol. The following procedure was adopted for serial sections. Newly moulted soft-bodied adults were dropped into hot aqueous picroformol fixative (Bouin's), decapitated, and then put into a fixative-dioxane (1-2) mixture. At 24-hour intervals, they were transferred twice to pure dioxane, infiltrated with equal parts of dioxane and Tissuemat (M.P. 52-54°C.), then passed twice through pure Tissuemat. During the first period in Tissuemat the dioxane was drawn slowly from the specimens by subjecting them to a gradually increased vacuum for about half an hour. The embedded material was cut into 10-micron sections at 15°C. using Valet razor blades in a rotary microtome. Camera lucida drawings and wax models helped in the interpretations of the sections. Sections of host tissues, containing attached and age-hardened ticks, were best sectioned by Storey's technique (ARTHUR, 1957).

Living ticks were studied while in the process of feeding, both on hosts and by artificial means. In the first instance, females that had fed on a sheep for three or four days were removed and induced to re-attach to the ear of a white mouse previously anaesthetized with either Nembutal (Abbot Laboratories Ltd., Montreal) or Dial (Ciba Drug Co., Montreal). The mouse was laid on a sheet of cork on the stage of a compound microscope with its ear stretched over a small hole in such a position that the tick's mouthparts and surrounding host tissue were illuminated by substage light. Observations were thus made in a manner similar to those of GRIFFITHS and GORDON (1952).

Other observations were made by inducing partially fed ticks to secrete or engorge by inserting their hypostomes in capillary tubes that were either empty, or contained heparinized blood (GREGSON, 1957). The tick and tube were held in place by plasticine on a large cover glass and placed over a narrow slit on a sheet of foil on a microscope slide so that only the basis of the capitulum was illuminated by transmitted light.

Motion picture records were made with a Ciné Special II Kodak camera equipped with a beam splitter that deflected only 10 per cent of the light away from the camera. Special processing of Eastman Tri-X panchromatic film permitted exposures to be made at 64 frames per second, thus enabling rapid movements of the tick's internal sucking apparatus to be studied in slow motion.

3. Anatomy of the capitulum.

a) General description.

Descriptions of the anatomy of the capitula of various species of ticks appear in the works of NUTTALL, COOPER, and SMEDLEY (1905), CHRISTOPHERS (1906), BONNET (1907), NORDENSKIÖLD (1908), SAMSON (1909), NUTTALL, Warburton, COOPER, and ROBINSON (1911), PATTON and CRAGG (1913), ROBINSON and DAVIDSON (1913a, 1913b, 1914), TRUE (1932), RUSER (1933), BERTRAM (1939), DOUGLAS (1943), ARTHUR (1946, 1951, 1957) and

SNODGRASS (1948). Particular reference is made to the work of the last three authors for a general knowledge of the capitula of the Ixodidae and only structures that have a special bearing on the topic of this paper will be discussed in detail here. Figures 1 and 2 are intended to acquaint the reader with the relationship of these structures as they appear in *Dermacentor andersoni*.

Essentially the capitulum consists of a heavily sclerotized rectangular collar, the basis capituli, bearing at its antero-lateral margins a pair of four-segmented palps and containing within it a pair of parallel protrusible shafts, the chelicerae. The ventral portion of the basis extends anteriorly beneath the chelicerae as the spoon-shaped hypostome; dorsally it is prolonged to partially ensheath them. The longitudinal space between the chelicerae and hypostome forms the buccal canal and buccal cavity. Posteriorly the large basal portion of the basis is neck-shaped and fits within an opening in the body of the tick known as the camerostome. A reflexed articulating membrane connects the two margins, permitting a limited dorsoventral movement of the capitulum and a flow of blood from the body cavity to the extremities of each of the five mouthparts. SNODGRASS (1948), in reviewing the homology of arachnid feeding organs, considers the coxae of the palps as forming the sides of the basis capituli and uniting ventrally and distally to produce the hypostome. SCHULZE (1935) even suggests that the porose areas on the antero-dorsal surface of the basis are thus derived from certain sensory organs, the cymatii, found adjoining the coxae of other arachnids and ticks. Anteriorly, and ventral to the chelicerae, these coxae are fused to a central epistome, which, as SNODGRASS (1948) shows, is invaginated in the ticks to form the subcheliceral plate.

b) *The hypostome.*

The hypostome is described by DOUGLAS (1943) and illustrated in this paper (Fig. 4, D). The coronal teeth are papilla-like (Fig. 4, E); the main denticles recurved, with their cavities continuous with the interior of the hypostome (Fig. 4, B, d. c.). When a dried hypostome is flooded with balsam each denticle appears to be served by a tracheole-like passage that branches from one of two longitudinal trunks (Fig. 4, F). In cross-section the distal portion of the hypostome (Fig. 4, C) is seen to be divided into two longitudinal chambers, the fused inner walls of which clearly depict its origin from paired structures. Proximally, where the chambers join, a core-like structure is directed ventrally from the end of the septum. Dorso-ventral muscles within these chambers, as de-

scribed by ARTHUR (1946, 1953) in *Ixodes ricinus* L. and *I. hexagonus* Leach, have not been observed. Moreover, because of the thickness of the walls of the hypostome in *D. andersoni*, it seems doubtful that any movement of this structure could originate from such muscles. Similar muscles, however, do occur further back in the region of the pharyngeal orifice, and are probably analogous to those of the hypostomal gutter mentioned by BERTRAM (1939).

A hypostomal groove, or gutter (Fig. 2, h.g.), runs the full length of the dorsal surface of the hypostome, deepening progressively towards the pharyngeal orifice. It contains a poorly staining non-cellular material of undetermined nature and is covered by a thin transparent membrane which appears to be loosely attached to the whole upper surface of the hypostome. This membrane may assume a convex or concave appearance (Fig. 4, A-C), and it would appear that its movement plays a part in the mechanism of feeding. If its shape is brought about by pressure, activation may take place at the proximal end where the contents of the groove appear to become contiguous with the body cavity of the tick (Fig. 6, K¹⁵). It is of interest to note that SEN (1935), in describing the apparently questionable stylet of *Ornithodoros (sic) papillipes* Birula, observed that pressure with a needle on the external surface of the pharynx caused a "very noticeable movement in a ridge-like structure overlying the dorsal gutter of the hypostome". RUSER (1933) mentions that the V-shaped core of a groove in the hypostome of *Argas persicus* Oken is overlain by a fine chitinous lamina that rises from the lateral walls of the hypostome.

The homology of this hypostomal membrane is not clear. ARTHUR (1957) describes the salivary channels of *Dermacentor parumapertus* Neumann as opening at the tip of the hypostome above the labrum, which structure, he states, overlies the hypostomal groove. Presumably he is referring to the membrane as a portion of the labrum. If this were to apply to *D. andersoni*, then, as will be seen later, this organ must surround the pharyngeal orifice. This would not seem likely inasmuch as according to SNODGRASS (1948) the labrum of arachnids consists of a preoral lobe which lies above the mouth only.

c) *The chelicerae.*

The chelicerae or cutting organs of the Ixodoidea are believed by some authors (ARTHUR, 1946) to be homologous with the mandibles of blood-sucking organs. SNODGRASS (1948), however, considers them to represent the corresponding second antennae of Crustacea or their homologues, the vestigial premandibular ap-

pendages of insects. In the ticks their proximal ends have become deeply inserted in the basis capituli, extending even through the capitular foramen into the body cavity (Fig. 1 and 2, ch.). The dilated basal cavity of each contains digital flexor and extensor muscles which give rise to corresponding outer and inner tendons (described in detail by RUSER, 1933). According to ROBINSON and DAVIDSON (1913a), in *A. persicus* the flexor tendon divides at the base of the internal article to supply both this and the external article. Although both tendons lie for a distance within the walls of the cheliceral shaft in *I. ricinus* (RUSER, 1933), and both are guided in grooves in the inner surface of the walls in *A. persicus* (ROBINSON and DAVIDSON, 1913a), only the extensor tendon is seated in a short groove in *D. andersoni*. A characteristic inner dorsal canal, however, is present in the cheliceral shaft. RUSER (1933) believes it to carry a trachea to serve the digit, but sections of *D. andersoni* (Figs. 5, A-H) show it to lead to the tip of the cheliceral hood. Proximally it passes within the membrane of the dorsal oval area of the chelicera (mentioned later), then shortly becomes lost in a thickened area on the inner side of the shaft.

The digits of the chelicerae (Figs. 1 and 2, di.) of *D. andersoni* are described briefly by DOUGLAS (1943). Each consists of an internal and external article. Both articles bear curved cusps or teeth for slashing the skin of the host; those of the internal article constitute the "dorsal process". Both articles of the digit are hollow; the cavity of the external article communicates with that of the internal article, and this in turn is continuous with the cavity of the cheliceral shaft. The dorsal side of the internal article contains a large pore which opens to the internal cavity but which appears to be protected from the exterior by the enveloping membranous fold mentioned below (Fig. 5, A, p.). NUTTALL, COOPER, and SMEDLEY (1905), NUTTALL, COOPER, and ROBINSON (1908), and ROBINSON and DAVIDSON (1913a) have referred to similar ducts or pores which they presume to open to the exterior in *Haemaphysalis punctata* Canestrini and Fanzago and *A. persicus*. ZEBROWSKI (1926), referring to *D. variabilis* (Say), speculates that a secretion from the coxal glands might pass through them. However, because of their communication with the body cavity it is difficult to accept these either as secretory channels or as passages to the exterior and it would rather seem that they permit the passage of a fluid to distend or collapse the membranous fold.

Two other structures appear at the distal end of the cheliceral shaft. One is the thin membranous fold (Figs. 1 and 2, m.f.; Fig. 5, m.f.) which arises dorsally from the base of the internal article

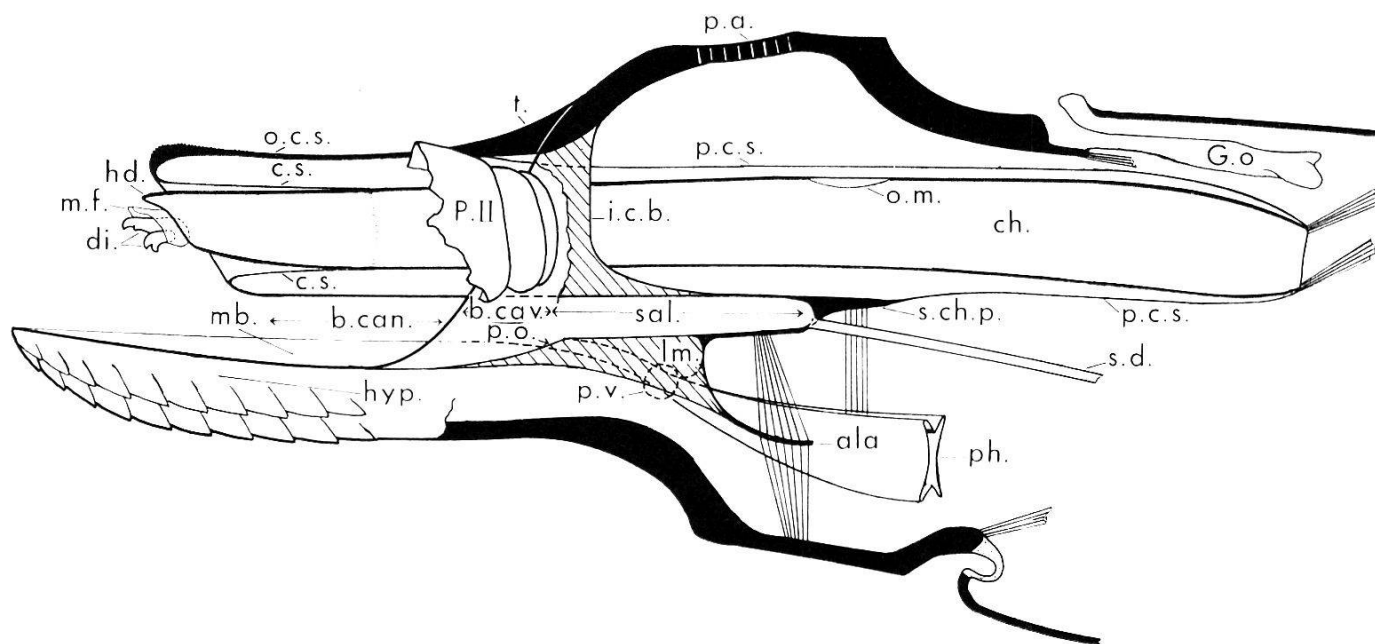


Fig. 1. Diagrammatic drawing of the capitulum of *D. andersoni* showing relationships of cheliceral sheaths and food channels.

of the digit; this is found also in *Amblyomma* (SNODGRASS, 1948). The other, the so called "hood" (Figs. 1 and 2, hd.; Fig. 5, hd.) arises from the mesal tip of the shaft. It is well described for *A. persicus* by ROBINSON and DAVIDSON (1913a) who attribute its origin to "an exuberant growth of the soft articulatory chitin of the joint between shaft and digit". In the light of the aforementioned canal in the cheliceral shaft it is possible that this flap assists in the dissemination of a secretion.

One other feature of the chelicerae referred to by NUTTALL, COOPER and ROBINSON (1908) in *A. persicus*, and present in *D. andersoni*, is an oval membrane-covered area of less sclerotized material. It is situated dorsally and about two-thirds back from the tip (Figs. 1 and 2, o.m.). ARTHUR (1957) attributes part of its covering in *D. parumapertus* to a "tertiary" cheliceral sheath. Its function is unknown.

Although retraction of the chelicerae is obviously brought about by stout muscle bundles which pass to the dorsal body wall, the mechanism of protrusion is more obscure. RUSER (1933) questions the use for this purpose of a series of small muscles described by NUTTALL as coming from the margin of the scutum and from the cervical furrow and inserted on the shafts of the chelicerae. These were not seen in *D. andersoni*. It is of interest to note here that HUGHES (1949) has observed in the Mesostigmatid mite, *Liponyssus bacoti*, a group of longitudinal muscles which pass obliquely back from the base of the epipharynx to the cheliceral sheaths and which he claims will pull the chelicerae forward. ROBINSON and DAVIDSON (1913a) and ARTHUR (1946, 1953) believe protrusion of

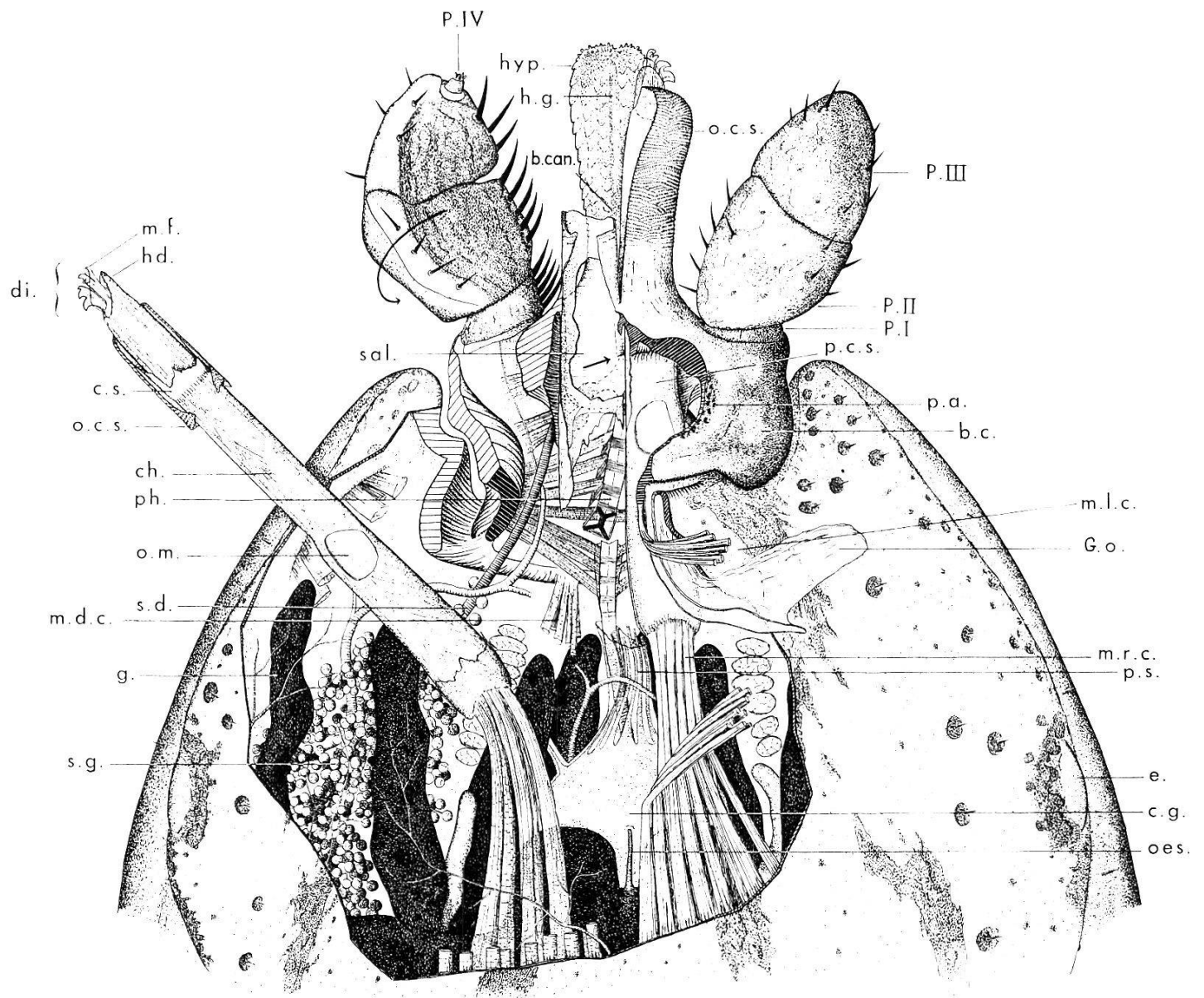


Fig. 2. Drawing of dissection of dorsal anterior portion of female *D. andersoni* with one chelicera removed from its sheath and left palp partially rotated to show ventral spines. Arrow seen through removed portion of subcheliceral plate points to the pharyngeal orifice.

the chelicerae in the tick to be effected by internal body pressure resulting from a contraction of the dorso-ventral body muscles. If this is so, it would seem that there must be a strong and delicately adjusted antagonistic action between the cheliceral retractor muscles and the body muscles during engorgement when the internal pressure of the tick and the lengths of the muscles are being continually changed by the intake of blood and the undulating movements of the integument. Only such an action would seem to explain the independent protrusion of the chelicerae. That the chelicerae still function normally, in spite of these changes, is evidenced by the fact that semi-engorged ticks, removed from a host, are still capable of reattaching and feeding.

The chelicerae are invested in membranous sheaths, the origin and arrangement of which have caused considerable confusion among acarologists. The relationship of these structures as they appear to exist in *D. andersoni* are shown diagrammatically in Fig. 1. The outer cheliceral sheaths (Figs. 1 and 2, o.c.s.), according to ROBINSON and DAVIDSON (1913a) and BERTRAM (1939), are derived from the dorsal conical prolongation of the basis capituli and, as NUTTALL *et al.* (1905) aptly state, resemble the legs of a pair of trousers. There is considerable controversy over the situation and form of an inner sheath. ROBINSON and DAVIDSON (1913a) state that in *A. persicus* "This inner sheath is formed by the inflected distal margin of the outer cheliceral sheath which is invaginated between the outer sheath and the shaft, and passes backwards as far as the base of the latter, where it is again reflected forward and continues directly into the margin of the expanded base of the cheliceral shaft". This suggestion is adopted by SNODGRASS (1948) and DOUGLAS (1943) for *D. andersoni* and offers a reasonable explanation for its origin.

ZEBROWSKY (1926), however, states that in *D. variabilis* the distal margins of the "mandibular" (outer cheliceral) sheaths are fused directly with the "digital sheaths" (sheaths "attached to the basal portions of the digits"). NUTTALL *et al.* (1905) and NUTTALL *et al.* (1908) similarly refer to an invagination of the outer sheaths of *H. punctata*, each to form a thin membranous portion (ZEBROWSKY's "digital sheath"?) that becomes attached to the cheliceral shaft some little distance posterior to the digit. BERTRAM (1939) calls similar inflections from the outer sheaths to the cheliceral shafts of *O. moubata* "cone sheaths", stating that they possibly serve to protect the inner recesses of the shafts from foreign matter. THON (1906) (see SNODGRASS, 1948), in describing the capitulum of *Holothyrs braueri* (Oribatoidea), likewise shows the outer cheliceral sheath to invaginate into itself and shortly become attached to the cheliceral shaft. BERTRAM's description appears to apply to *D. andersoni* and the term "cone sheath" is adopted for the anterior invagination of the outer cheliceral sheath (Fig. 1 and 2, c.s.).

There exists also in *D. andersoni* a pair of posterior cheliceral sheaths (Fig. 1 and 2, p.c.s.). As shown by BERTRAM (1939) in *O. moubata* ("inner sheath") and by ARTHUR (1957) in *D. parum-apertus* ("internal cheliceral sheath") these membranes originate dorsally from the inner part of the tectum (the dorsal portion of the basis capituli overlying the chelicerae) and ventro-laterally from the epistome or subcheliceral plate. THON (see above) describes similar posterior cheliceral sheaths; SNODGRASS comments

that a posterior ensheathment of this kind is difficult to understand morphologically.

Distally the outer cheliceral sheaths are cushionlike, dorsally blunt, rounded anterio-laterally, with their inner faces flattened and opposed. The lateral and dorsal surfaces bear numerous small reflexed denticles regularly arranged in oblique rows and giving a shagreened appearance. The apices, composed of outer and cone sheaths, closely envelop the hooded digits and are fringed on the inner surface with papilla-like outgrowths (Fig. 5, A-D). This portion of the sheath is also illustrated by ARTHUR (1953) for *I. hexagonus*.

d) *The buccal canal, buccal cavity, and salivarium.*

The food channel, anterior to the pharyngeal orifice, is formed by the close apposition of the hypostome, ventrally, and the two chelicerae, dorsally, and lies in the central axis of the three structures. Considerable confusion has arisen over the proper definitions for this space and the adjoining cavity which lies posterior to the pharyngeal orifice. BERTRAM (1939) writes: "CHRISTOPHERS (1906) employs the term 'mouth' to denote the entire space enclosed by the mouth-parts, and PATTON and CRAGG (1913) refer to the buccal canal and buccal cavity together as the buccal cavity. A reconsideration of the limits of the true buccal cavity in ticks would appear to warrant attention, but provisionally the definition of ROBINSON and DAVIDSON (1913a) is accepted." The latter writers regard the site of the fusion of the hypostome and palps with the ventro-lateral margin of the dorsal conical prolongation of the basis capituli as marking the end of the buccal canal and the beginning of the buccal cavity. This definition is also accepted for *D. andersoni*.

The buccal canal (Fig. 1, b. can.) of *D. andersoni* thus extends from the apices of the chelicerae to the position where the cheliceral sheaths become fused to the hypostome by means of the supporting basis capituli. A fine longitudinal tongue-and-groove between the inner surfaces of the sheaths and cushion-like flanges where their ventro-lateral margins are adpressed to the hypostome (Figs. 4, A and 5, F) serve to render a tight seal for the passage of blood or saliva.

The buccal cavity (Fig. 1, b. cav.) likewise extends from the buccal canal to the pharyngeal orifice. It is significant to note that in *D. andersoni* the pharyngeal orifice opens into the buccal cavity, whereas in *O. moubata* (see BERTRAM, 1939) it opens into the

buccal canal. According to the present writer's terms, BERTRAM's "buccal cavity" would be called the salivarium.

The salivarium (Fig. 1, sal.) is the term accepted here for the cavity posterior to the pharyngeal orifice. It continues from the buccal cavity in the form of a blind pouch into whose postero-lateral corners the two salivary ducts enter. The anterior portion of the floor of the salivarium consists of the labrum (Figs. 1, lm., and 6, C-E). If, as SNODGRASS (1948) states, the subcheliceral plate is to be homologized with the epistome because of its support of the labrum and the dorsal pharyngeal muscles, then it would appear that the remaining portion of the floor of the salivarium is made up of the anterior part of this plate; BERTRAM (1939) describes muscles running from the floor of the salivarium to the pharynx in *O. moubata*, and a similar condition has been observed in *D. andersoni* (Fig. 6, F). ARTHUR (1957), however, describes the salivarium of *D. parumapertus* as existing "between the subcheliceral plate and the upper surface of the hypostome", posteriorly becoming "embedded within the subcheliceral plate". He confirms the above observations that the floor of the salivarium receives muscles from portions of the pharynx. There thus seems to be doubt as to whether the roof of the salivarium is made up of a portion of the epistome or consists, as BERTRAM (1939) says, of "the posterior limit of the ventral surface of the dorsal conical prolongation of the basis capituli".

The space containing the buccal cavity and salivarium is sinuous in transverse outline, arched medially and flattened along the margins (Fig. 6, A-F (sal.)). Anterior to the entrance of each salivary duct a longitudinal protuberance (Figs. 3 and 6, F¹), arising from the roof of the salivarium, appears to either seal off the salivary passage from the salivarium proper for some distance and to allow the fluid to pass into it only when the floor is lowered. Possibly this movement is aided by a pair of non-sclerotized areas in the floor of the salivarium (Figs. 3 and 6, G²). These same areas may also serve to regulate a longitudinal valve-like structure (Fig. 6, C-G³) in the floor of each salivary channel. ARTHUR (1957) has observed similar structures in *D. parumapertus*. Paired longitudinal spaces (Fig. 6, C-H¹⁴) which lie below the salivary channel may also take part in this process.

e) *The salivary glands.*

The paired salivary glands (Fig. 2, s.g.) are large and usually extend as far back as the spiracles. They are in close contact with the caecal lobes of the stomach, portions of the malpighian tubules,

and a ramifying mass of trachae. The grape-like clusters of alveoli are of two kinds and are described in detail for *A. persicus* by ROBINSON and DAVIDSON (1913b). In *D. andersoni* the more numerous type of alveolus is made up of some fifteen large nucleated cells grouped around a central lumen. These cells appear to be of two kinds. A relatively large type with small centrally placed nucleus surrounds the opening of the alveolus. They are about five in number and stain a deep red with Mallory's triple stain. The second type makes up the greater portion of the structure and is arranged in a ring of five and a distal cap of five. These cells have larger, lighter staining nuclei and a more granular cytoplasm, and stain blue.

ROBINSON and DAVIDSON (1913b), and CHRISTOPHERS (1906) attribute the difference in staining to the progression of secretory processes. However, since in *D. andersoni* this difference was observed in both unfed and fed specimens, this explanation does not seem satisfactory. BONNET (1907) found that the alveoli of *I. hexagonus* similarly contain two types of cells, although he notes that the differences disappear as the glands secrete. As *D. andersoni* engorges the alveoli become greatly distended, their diameters increasing by about three times, and the outer cells assume a flattened appearance. These alveoli are arranged around and drain into short secondary lobular ducts which in turn empty into the two main salivary ducts.

A second type of alveolus, mentioned by BONNET (1907), SAMSON (1909), KUNSSBERG (1911), ROBINSON and DAVIDSON (1913b), and TRUE (1932), in *I. hexagonus*, *I. ricinus*, *A. persicus*, *O. coriaceus* Koch, *O. moubata*, is also present in *D. andersoni*. This type is, with the exception of *I. ricinus* (SAMSON, 1909), confined to the anterior half of each gland on the median side of the main duct. It appears to be slightly larger than the first type in the unfed tick, but remains unchanged in size as the others increase during secretion. Its cellular structure is indistinct and stains poorly. BONNET (1907) compares its structure with that of the secreting cells in the glands of certain snakes and concludes that it may produce a venom. Anticoagulants and digestive ferments have also been attributed to these or other cells in the salivary glands (ROBINSON and DAVIDSON, 1913b).

Considerable attention has been paid to the spiral thickenings and longitudinal cuticular folds of the salivary ducts (NORDENSKIÖLD, 1908; ROBINSON and DAVIDSON, 1913b; ZEBROWSKI, 1926; and TRUE, 1932). BERTRAM, having noticed both circular and comma shaped cross-sections of ducts, suggests that their structure may aid a possible dilation and collapse due to pharyngeal

movements, and in turn assist the flow of saliva. The outer wall of the ducts is made up of poorly defined cells with granular protoplasm and central nuclei. Considering the variety of secretions that presumably flow from the salivary gland system reference is made to DAY's (1951) suggestion that in the cockroach even the ducts themselves may contribute to the production of saliva.

As already noted, the two main ducts are received by the salivarium. No longitudinal movement of these ducts during cheliceral motion, as mentioned by ZEBROWSKI (1926) in *D. variabilis*, has been observed in *D. andersoni*.

f) *The pharyngeal orifice.*

The pharyngeal orifice of ticks has attracted a considerable amount of attention and controversy. Its nature and operation forms an important part of this paper.

CHRISTOPHERS (1906) describes it in *O. savignyi* (Audouin) as a small crescent-shaped opening protected by a projecting tongue. NUTTALL, COOPER, and SMEDLEY (1905) and NUTTALL, COOPER, and ROBINSON (1908) refer to the aperture only as "leading downward and backward" and figure it in *H. punctata* as a slanting channel on the floor of the "buccal cavity". SAMSON (1909) describes the orifice in *I. ricinus* as being covered by a short flap which she terms the "elastische Platte". ROBINSON and DAVIDSON (1913b) state (and illustrate) that the pharyngeal orifice of *A. persicus* "is situated in the middle of the floor of the buccal cavity... and is guarded above by a tongue-like cuticular flap formed from a forward continuation of the floor of the buccal cavity". They (1913a) regard the function of this process as being to close the pharyngeal opening so that the salivary secretion is forced into the wound made by the hypostome. ZEBROWSKI (1926) describes the pharyngeal opening as a slit-like aperture in *D. variabilis*. TRUE (1932) again refers to a flap or tongue projecting over the orifice in *O. coriaceus*. RUSER (1933) mentions a tongue-shaped extension that is capable of closing off the pharynx in *A. persicus*. SEN (1934, 1935, 1937) describes in *O. papillipes* a hollow refractile, open-ended, stylet, overlying the gutter of the hypostome and which he believes to be a tubular continuation of the pharynx. DOUGLAS (1943) accepts Sen's stylet, stating that in *D. andersoni* it is tripartite and quite short, extending only about one-third of the length of the hypostome. BERTRAM (1939) questions the presence of such a structure in *O. papillipes* (which he considers a synonym of *O. tholozani* (L. and M.)) and *O. moubata*, but describes and illustrates a "tongue-like process", in the form of a

hollow flap arising from a broad base on the dorsal surface of the hypostome. The hind part of this flap is thickened laterally, leaving only a thin mesial membrane. These chitinous thickenings then fuse in the mid-line, ventral to the membrane, to form a stout transverse bar which passes back to contribute to the formation of the floor of the buccal cavity and the roof of the pharynx. Excepting for the anterior flap-like extension, this description will be seen to apply to the pharyngeal apparatus of *D. andersoni* (Fig. 6, D, E, and K).

However, his description of a further development of the tongue-like process to form both a dorsal thin-walled posterior pouch on the floor of the buccal cavity and a ventral thin-walled closed chamber on the dorsal region of the pharynx cannot be interpreted in the present studies of *D. andersoni*. ARTHUR (1946) describes and figures for *I. ricinus* essentially the same apparatus as described by BERTRAM (1939), including also the stylet-like process of SEN. His (1951) descriptions of a sclerotized wedge in *I. hexagonus*, which fits into the pharynx and spreads dorsally into a crescentic plate, agree closely with the similar structure in *D. andersoni*. However, the nature of the pharyngeal opening is not clear, and his statement and illustrations that the food channel is a backward continuation of the hypostomal groove and is roofed by a membranous portion of the labrum imply that the pharyngeal orifice is covered by an extensive labral membrane. This is also suggested in Fig. 3 of his subsequent paper (ARTHUR, 1953). SNODGRASS (1948) states: "In *Ixodes*, *Dermacentor*, and *Amblyomma* the so-called 'stylet' is long and slender; when pulled away from the hypostome there is usually to be seen attached to each side of it a narrow, very delicate membrane with an irregular and apparently broken margin." He accepts the filamentous axial "stylet" as being the mid-rib of a long, thin blade that covers at least the proximal two-thirds of the hypostomal gutter, admitting that the edges become torn by removal from the hypostome. It appears to the writer that this structure might easily have been confused with the thin covering of the hypostomal groove which is both transparent and easily torn; in fact the very contour of the base of the "stylet" in Snodgrass' illustration of the labrum of *D. variabilis* agrees closely with the shape of the pharyngeal orifice of *D. andersoni*. The present writer has found no evidence of any such stylet or protruding labral membrane in *D. andersoni*. The flap above the hypostomal gutter, shown by BERTRAM (1939) (Figs. 7 and 8), is absent in Fig. 6B of the present work. In short, the pharyngeal orifice appears merely as a furrowing in the membrane overlying the hypostomal groove

and is not guarded by any form of a loose flap or stylet. Its position is shown by an arrow in Fig. 2; it appears in transverse section B in Figs. 3 and 6. Immediately posterior to this it becomes covered by the truncate thickening structure of the labrum (Fig. 1, lm.).

g) *The pharynx.*

The anterior portion of the pharynx of *D. andersoni* has been reconstructed in Fig. 3, and a series of sections, at levels corresponding to the lettering on this figure, are shown in Fig. 6. The superscripts following the letters denote corresponding structures in the two figures. Reference is also made to Figs. 1 and 2 for the relationship to the surrounding capitulum. The pharynx commences where the trough of the hypostomal membrane becomes covered by the thin labral membrane (Fig. 6, C⁴). As it continues back its roof separates from the dorsal labral layer, becomes V-shaped, sclerotized, and finally forms a heavy tooth (Figs. 3 and 6, F⁵) that is supported by lateral arms continuous with the dorsal surface of the pharyngeal alae (Figs. 3, ala, and 6, G). This tooth continues posteriorly, to shape the sclerotized dorsal surface of the pharynx for the remainder of its length (Fig. 6, H-J).

The ventral wall of the pharyngeal orifice is V-shaped and soon becomes sclerotized and fused to the pharyngeal supports beneath it (Figs. 3 and 6, D¹²). At this point there occurs a ventral globular, non-sclerotized structure (Figs. 1, p.v., 3 and 6, E⁶) which, because of its slit-like passage and inner tongue-and-groove-like surface, appears to function as a primary valve. Behind the valve and just before the dorsal Y-shaped portion of the passage receives the above mentioned tooth-like structure there appears on each side of the passage an oblique row of minute pharyngeal teeth (Fig. 6, F and K¹³). Similar teeth have been noted by NUTTALL *et al.* (1905), in *H. punctata*, by SEN (1935), in *Amblyomma haebrium*, *A. gemma*, and *Rhipicephalus evertsi*, and by ARTHUR (1951), in *I. hexagonus*, *ricinus*, *cookei*, *wellingtoni*, *baergi*, and *pacificus*. The succeeding main tooth appears to rest against a pair of sclerotized rods (Fig. 6, G⁷) and may function as a secondary valve. Both valve-like structures are apparently activated by muscles extending dorso-mesially from the capitular walls, first to the outer pharyngeal supports (Figs. 3 and 6, D⁸), then to apophysial processes thereon (Fig. 6, E⁹). DOUGLAS (1943) refers to a pharyngeal valve of the second type in *D. andersoni* and illustrates a row of small teeth on each side of the central tooth. TRUE (1932) and ROBINSON and DAVIDSON (1913b) were unable to locate any valve-like structures in *O. papillipes* and *A. persicus*. Posteriorly, as it approaches the pharynx

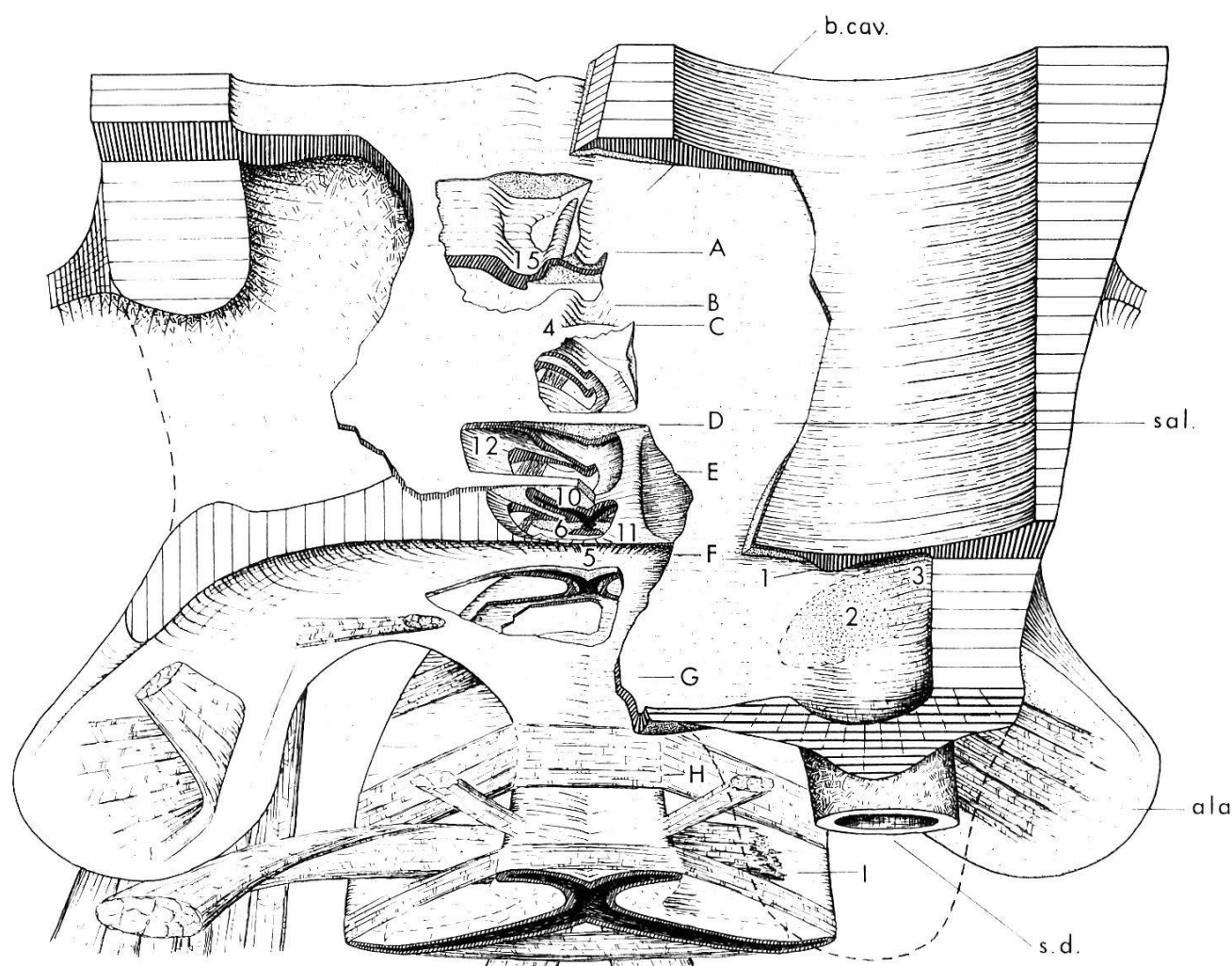


Fig. 3. Schematic drawing of portion of dissection shown in Fig. 2 showing pharyngeal orifice, prepharynx and associated supporting structure. Numerals are referred to by superscripts in text. Letters refer to position of sections shown in Fig. 6.

proper, the ventral portion of the food channel assumes Λ like extensions (Fig. 6, F-H).

The cavity formed between the dorsal labral layer and the lateral walls of the pharynx is filled with a homogenous substance (Figs. 3 and 6, E¹⁰) that stains blue with Mallory's. Anteriorly, this material is indistinctly enclosed by what are presumably the confines of the labrum, but otherwise appears to be contiguous with the similar substance beneath the hypostome membrane. Posteriorly it is separated from the ensuing body cavity by a membrane (Fig. 3¹¹) which arises from the opposing pharyngeal supports and alae.

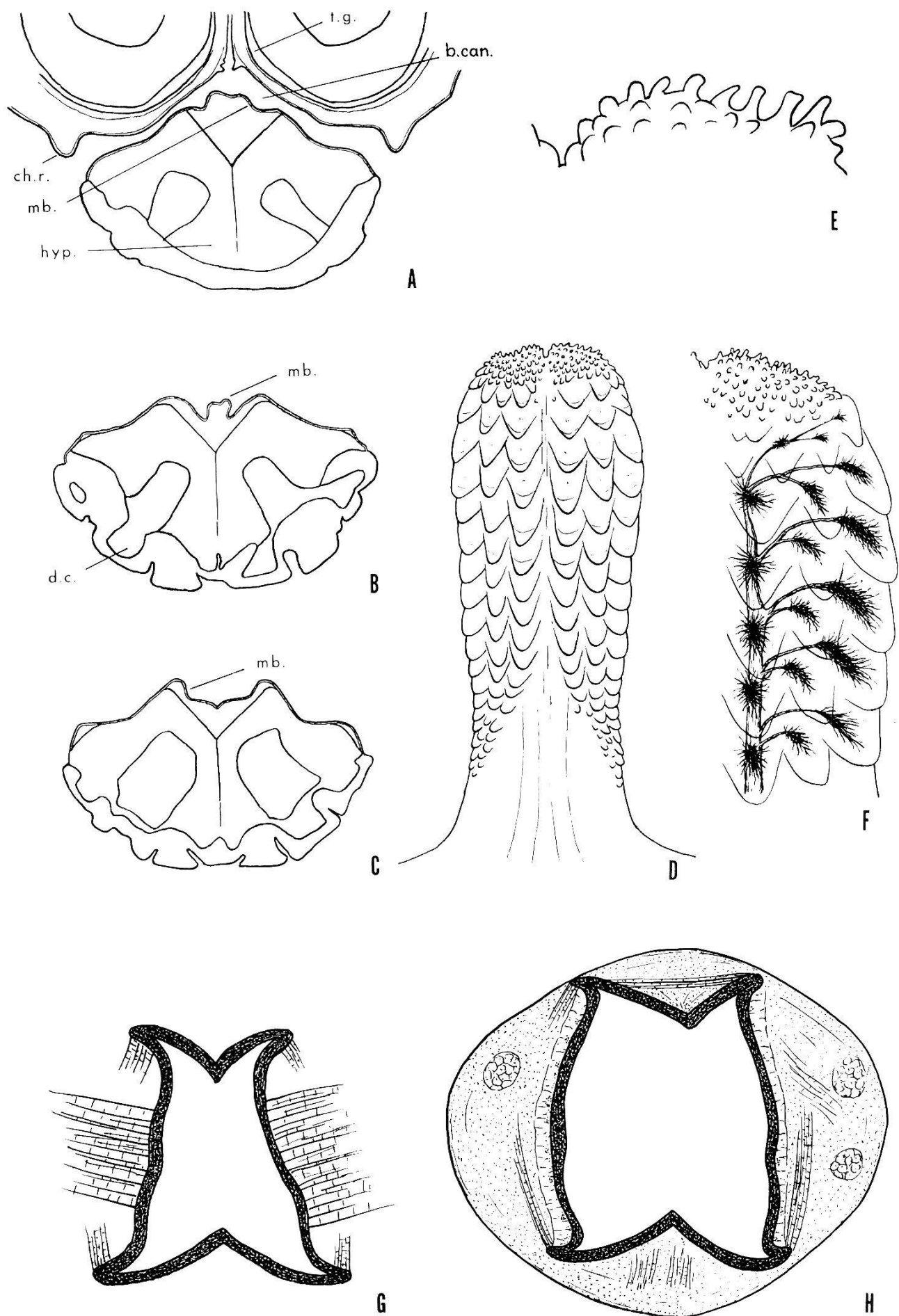
The pharyngeal supporting structure and alae (Figs. 3 and 6, F-H) form functionally, if not morphologically, an integral part of the pharyngeal apparatus. Dorsally, the supporting structure is fused to the floor of the salivarium (Fig. 6, F and G), which in turn is suspended between the supporting intercoxal bridge (Fig. 1,

i.c.b.; see also ARTHUR, 1951). Posteriorly it appears as a transverse vertical bar terminating at each side in a scapula-like blade or ala. Medially this bar thins dorsally into the membrane backing the labral cavity (Fig. 3, F¹¹); ventrally it spreads to form the toothed roof of the pharynx. Anteriorly and laterally the dorsal margin of this bar spreads horizontally towards the margins of the salivarium and hypostome but drops mesially to form a supporting trough for the pharyngeal valve, where, as mentioned, it acts as a source of attachment for anterior sub-pharyngeal muscles (Figs. 3 and 6, D¹²). Anteriorly, where this trough continues beyond the pharyngeal orifice its mesial-distal end rises and separates from the continuing hypostomal groove in the manner illustrated (Fig. 3, A¹⁵).

The musculature of the alae appears to be relatively simple. Strong bands pass backwards from the ventral surfaces of the alae to the base of the capitulum (Fig. 3). They are opposed by a corresponding pair between the dorsal surfaces and the floor of the salivarium (and not, as DOUGLAS [1943] states, to the dorsal wall of the pharyngeal valve). ARTHUR (1957) refers to these muscles as the depressor and elevator muscles of the alae. Smaller muscles appear to pass from the alae to an area within the subcheliceral non-sclerotized area (Figs. 3 and 6, G²). SNODGRASS (1948) considers the muscles of the alae to be the anteriormost fibers of the constrictors of the pharynx. RUSER (1933) believes that they serve to close the pharynx from saliva. It would seem that the function of these muscles and the alae is to create a rocking movement that would assist in the operation of one or both of the pharyngeal valves.

The pharynx proper is long and fusiform. In cross-section it takes the form of the two Y's with their bases end to end, the lower arms being the longer. Seven pairs of lateral dilator muscles (Fig. 6, I, m.d.ph.), converging from each side of the mid-line of the pharynx to lateral protuberances within the basis, and a similar number of ventral dilators, diverging from the outer surfaces of the ventral arms to the bottom of the basis, serve to dilate this pumping organ. About three pairs of small dorsal dilator muscles also extend from the anterior portion of its dorsal arms

Fig. 4. Female *D. andersoni*. A: Cross section of hypostome, cheliceral ridges, and mesial interlocking tongue- and -grooves. Membrane of hypostome gutter is expanded. B: Cross section of hypostome with membrane folded. C: Cross section of hypostome with membrane collapsed. D: Ventral view of hypostome. E: Corona of hypostome. F: Tracheole-like passages of hypostome. G: Cross section of pharynx in dilated position. H: Cross section of oesophagus in dilated position, within surrounding periganglionic sinus.



to the posterior forks of the subcheliceral plate. Contraction is achieved by muscles extending in a circular fashion from the distal ridges of each arm (Fig. 6, H, m.c.ph.). These constrictor muscles alternate with the dilators. Where muscle attachments are absent the pharyngeal walls appear to be surrounded by areas of parenchymous tissue. RUSER (1933) suggests that wave-like contractions and dilations of the pharynx force blood towards the oesophagus. One serial section of *D. andersoni* (Fig. 4, G and H) showed the pharynx dilated for its entire length. Unless this represents an unnatural occurrence, it would appear that the action is not peristaltic. The rigid longitudinal nature of the organ would moreover substantiate this theory.

h) *The oesophagus.*

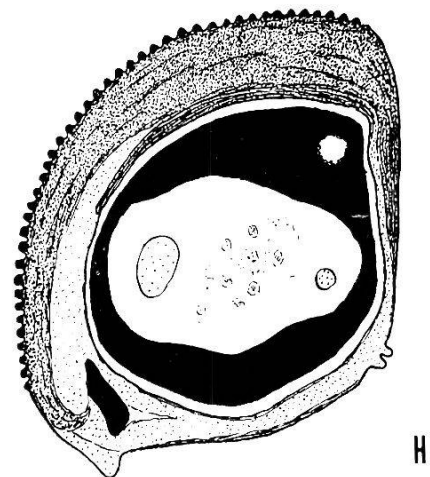
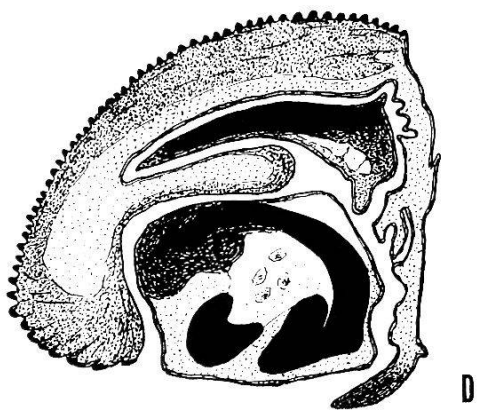
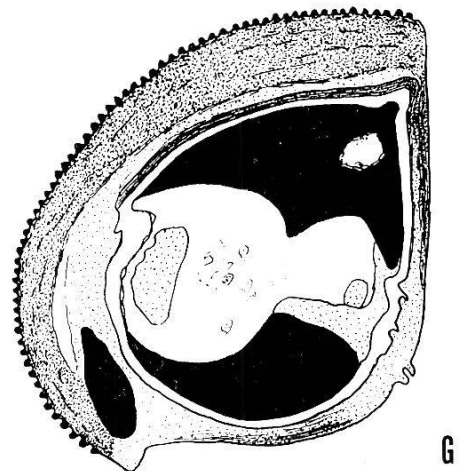
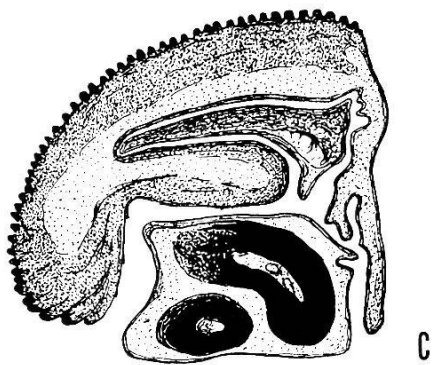
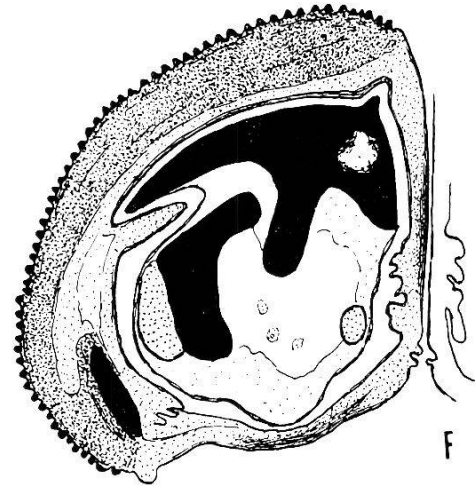
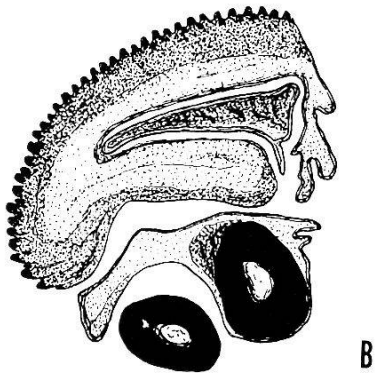
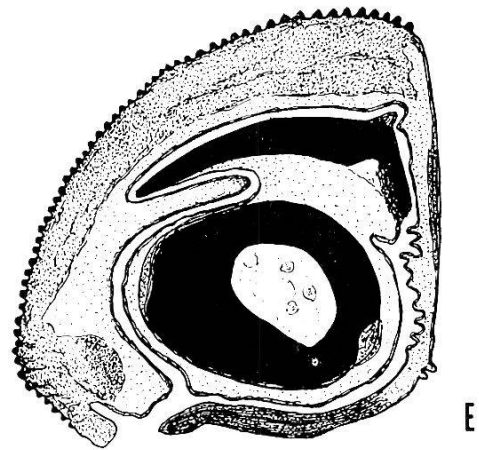
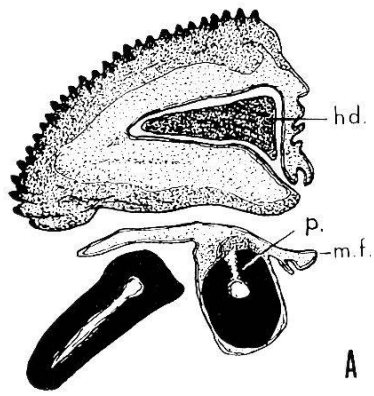
The oesophagus connects the pharynx to the stomach as a simple constricted channel. It is surrounded by vestiges of the pharyngeal constrictor muscles and enclosed in the circular peripharyngeal sinus. It passes postero-dorsally through the brain and enters the mid-gut at the site of a weak proventricular valve.

4. *Mechanism of the buccal apparatus.*

It seems that no attempts have previously been made to observe the internal feeding mechanism of ticks in action. The difficulties involved were partly overcome by the methods described earlier in this paper.

When a tick is offered blood by means of a capillary tube placed over its hypostome, two actions appear to occur within the capitulum. One of these accompanies the ejection of saliva into the tube and is seen as rapid postero-laterally directed fluttering movements (about 10 per second) within the basal portion of the hypostome. It seems to be caused by the action of the anterior subpharyngeal muscles (Fig. 6, D⁸) which, as BERTRAM (1939) states for *O. moubata*, probably bring about a change in the elevation of the "hypostomal furrow". The movements are thus accompanied by a simultaneous pulsation of the membrane covering the entire length of the hypostome gutter. The transverse contours of elevated and depressed membranes in the hypostome of three different specimens of *D. andersoni* are illustrated in Fig. 4, A, B, and C. Studies of the salivaria of these ticks suggest that

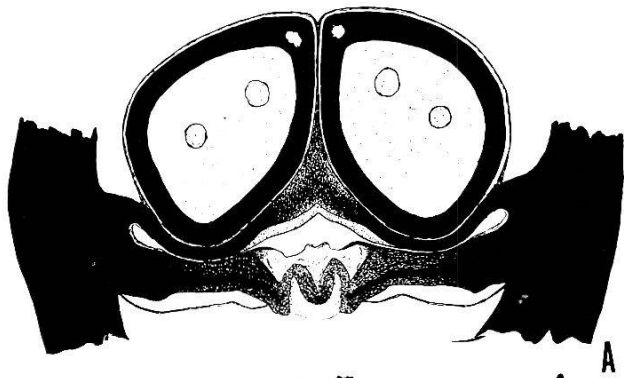
Fig. 5. Camera lucida drawings of alternate 10μ cross sections of tip of chelicera of female *D. andersoni*.



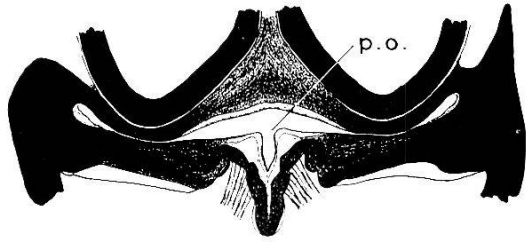
the positive pressure applied to raise the membrane also serves to compress the salivarium dorso-ventrally. This action, with the aid of the valve-like structures in the salivary channels (Fig. 6, C-G³), would appear to block the salivary secretion and may represent a resting position. When the membrane on the hypostome is depressed, the peripheral channels of the salivarium open freely to the center. This lowering of the floor of the salivarium also appears to be associated with the opening of the pharyngeal valve (Fig. 6, E⁶), either by the levering action of the two supporting pharyngeal arms, or by a direct pull from the afore-mentioned subpharyngeal muscles. Because these supports are also directly connected to the adjacent alae, it would seem that a movement of these wings also occurs during the above mentioned action. Indeed, it can be assumed that, in rising, the pull of some of their dorsal muscles on the posterior floor of the salivarium (Fig. 6, G) would serve to pull it down at the same time that the forward cantilever action of the adjoining prepharyngeal supporting trough dropped, thus, as mentioned, depressing the hypostomal membrane. The opposite action would correspondingly raise the floor of the entire food channel. Unfortunately, it has not been possible to discern any change in the position of the alae in either living or dead ticks. BERTRAM (1939) acknowledges the possibility of such a hydraulic action but attributes it to the movements of the pharynx. This seems improbable in *D. andersoni* inasmuch as it is known that the ejection of saliva can occur independently between periods of pharyngeal constriction or dilation.

The second movement within the capitulum of the feeding tick is that of the pharynx and occurs when the tick is sucking. It is rapid but spasmodic, and pulsations may occur singly or repeatedly at a rate of up to about one per second, each action occupying about one twenty-fifth of a second. During these movements the blood, and occasionally air also, is forced rapidly backwards. The parts played by the valves (Fig. 6, E⁶ and F⁵) are not clearly understood. Presumably one or both serve to prevent a regurgita-

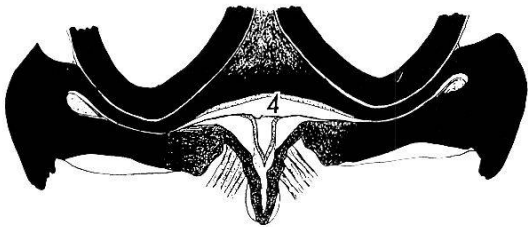
Fig. 6. Camera lucida drawings of 10 μ sections of food channel of female *D. andersoni*. Numerals are referred to by superscripts in text. Positions of sections are shown by corresponding letters in Fig. 3. A: Cross section 1, at posterior region of hypostomal groove. B: Cross section 5, at entrance to pharynx. C: Cross section 6, showing pharyngeal orifice. D: Cross section 9, in sublabial region. E: Cross section 12, at pharyngeal valve. F: Cross section 15, at pharyngeal teeth. G: Cross section 17, posterior to labial cavity. H: Cross section 20, at posterior margin of subcheliceral plate. I: Cross section 23, at posterior tips of alae. J: Cross section 66, at oesophagus, within periganglionic sinus. K: Sagittal section through pharynx showing pharyngeal orifice, and pharyngeal teeth.



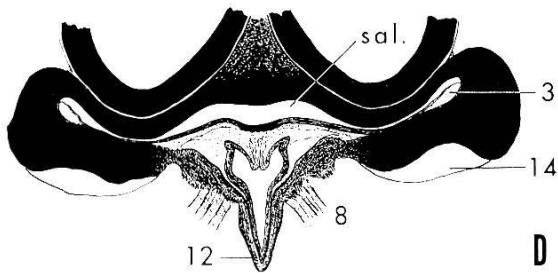
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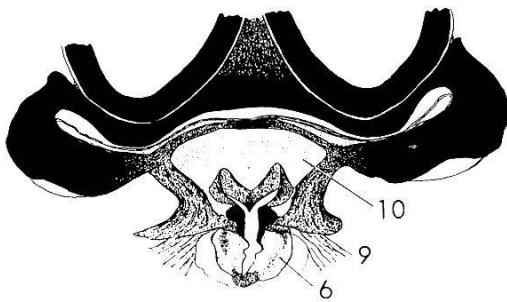
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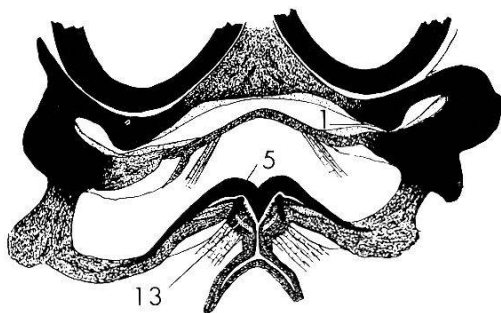
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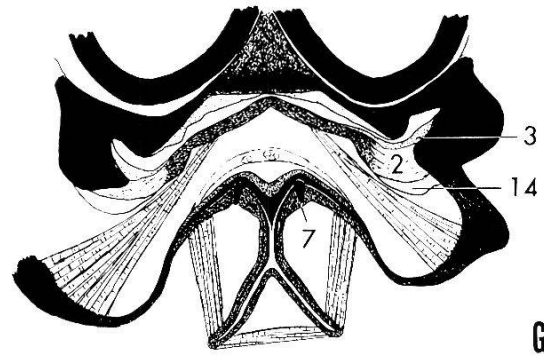
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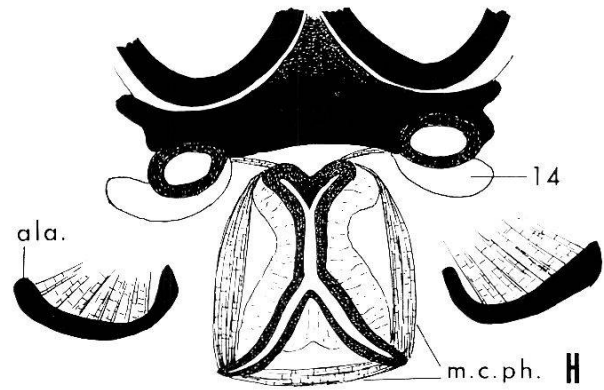
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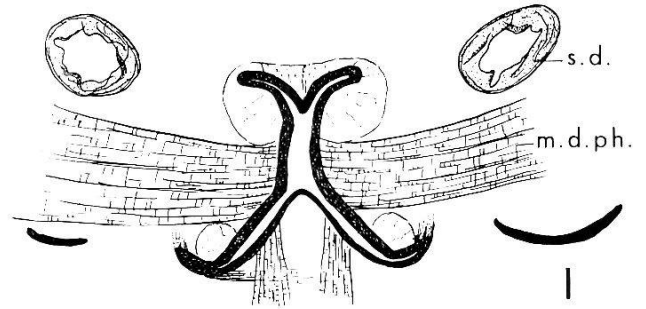
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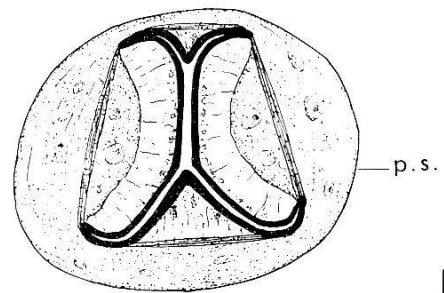
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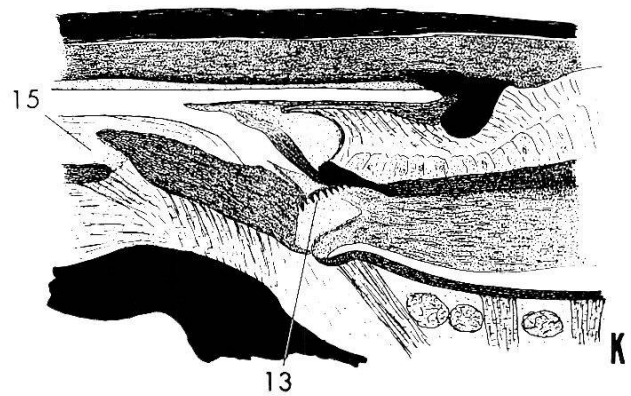
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K

tion of blood when the dilated pharynx constricts. However, since BERTRAM's (1939) "posterior closed chamber" overlying the pharynx could not be observed in *D. andersoni*, it is felt that any action by the pharynx on the pharyngeal valve (Fig. 6, E⁶) would have to be exerted through the labial chamber (Fig. 6, E¹⁰). This action may of course also affect the hypostomal membrane. Because the movement of the pharynx does not appear to be peristaltic, it is difficult to conceive that valve F⁵ is closed before the pharynx commences to constrict. Possibly valve E⁶ prevents regurgitation during swallowing, and F⁵ serves more to prevent a backward leakage while the pharynx is constricted, particularly if valve E⁶ is open during salivary secretion.

As far as can be ascertained, the two actions of ejecting and swallowing are distinct; they may alternate with each other with varying frequency or be separated by periods of inactivity. It is not known whether the flow of saliva into the salivarium is controlled during these resting periods, nor whether some is released and swallowed with blood during sucking. The appearance of the salivary channels at the margins of the salivarium, in sections made from a tick that was apparently in the act of sucking (Fig. 4, G), suggest that during pharyngeal dilation the floor of the salivarium is not depressed to allow a direct flow of saliva to the pharyngeal aperture.

In any event, the salivarium cannot be considered to act as a reservoir for saliva; its walls are not capable of any marked distension, nor can it possibly contain the amount of secretion that may be continuously liberated into a glass tube (up to 30 mg. for a 400 mg. tick!) (GREGSON, 1957). Rather it would seem that either the glands act as the reservoirs, or that the secretion is manufactured at will—perhaps both.

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Part II. The Feeding Mechanism in Relation to the Host.

1. Introduction.

While making studies on the feeding mechanism of *Dermacentor andersoni* Stiles (GREGSON, 1959) it became apparent that observations should also be made during the tick's normal attachment and feeding on a host. A review of literature showed that references to this approach were even more scanty than to the morphological aspect.

NUTTALL (1908), in describing the mechanism of the bite of ticks, mentions that the chelicerae penetrate into the skin, dragging with them the hypostome, the teeth of which serve to anchor the parasite to the host. BERTRAM (1939) states that *Ornithodoros moubata* (Murray) may insert the chelicerae and hypostome into the host's skin up to the level of the apex of the "dorsal conical prolongation" of the basis capituli. ARTHUR (1951) and SNODGRASS (1948) describe a "sleeve-like papilla" around the site of attachment of *Dermacentor*, *Amblyomma*, and *Boophilus* which they interpret as an outgrowth of the host's skin.

HOEPPLI and FENG (1931) described this papilla as a "homogenous eosinophilic area" which surrounded the mouthparts of attached specimens of *Dermacentor sinicus* Schulze, and which extended for a short distance under the keratinised layer of the epidermis. They believed it to be of a double nature, representing both secretion discharged by the tick and destroyed host tissue and were puzzled when they could not obtain a similar destruction of tissue by an artificial injection of tick glands.

COWDRY and DANKS (1933), in dealing with *Rhipicephalus appendiculatus* Latr. refer to the material as a cement-like substance and observe that it is laid down in definite layers. They assume that the fraction formed from degenerating epithelial cells is a small one, and that the main portion of the cement originates from the tick.

ARTHUR (1953) notes the presence of a cement which ensheathed the hypostome and chelicerae of *Ixodes hexagonus* Leach and appears to have flowed along lines of least resistance between the fibres of the dermis to a distance of 1.0 mm. from the point of mouthpart insertion. The nature of deposition leads him to believe that the cement was deposited locally and at an early stage during penetration by the mouthparts, and that it was fluid in life.

LAVOPIERRE and RIEK (1955), using the technique described by GRIFFITHS and GORDON (1952), appear to be the first workers to have made direct observations on the feeding of ticks. However, their studies were on argasid ticks only, and no mention is made of any cement-like material.

2. *Materials and Methods.*

The ticks used consisted entirely of spring-collected *Dermacentor andersoni* females from the vicinity of Kamloops. Laboratory reared adults were not used because of irregularities which were apparent during feeding; although they would readily attach to a host, engorgement would not necessarily follow.

Other techniques, particularly the use of the ears of anaesthetized mice, and the recording of results by means of cinemicrophotography are referred to in part I of this study (p. 50).

3. *The Process of Attaching.*

The succession of actions leading to normal attachment to a host by a tick may be said to commence when the tick comes into a questing state. Questing in *D. andersoni* commences only with the arrival of early spring weather, even although adults of both sexes have been present since the preceding summer (GREGSON, 1951). At this time the sexes crawl up low vegetation to wait for passing hosts, almost always a large animal in nature. Upon contact with a host their normal response is to crawl upwards until they reach a region in the vicinity of the neck and head. Thus it is seen that attachment does not take place immediately a host is reached, but rather that a brief period of wandering is customary before the tick settles down. It has similarly been noticed that unfed ticks, placed under a capsule on a host, often tend to roam for a few hours before attaching. On the other hand, females¹ which have been feeding for several days on a host will usually reattach immediately if removed and applied to the skin of the same, or another suitable animal. Combining the latter fact with the knowledge that adult *D. andersoni* are capable of engorging on mice (GREGSON, 1956, p. 49) it was found that females that had first fed for several days on a sheep could frequently be induced to reattach to the ears of anaesthetized mice. Some individuals commence to attach in a matter of seconds; others showed no inclination to do so over periods of several hours.

Observations from these studies revealed that attachment commences by the application of the tip of the hypostome and chelicerae to the skin of the host. This action is immediately followed by alternate outward lacerating movements of the digits for about ten seconds. This initial cutting is shallow and does not appear to extend beyond the outer squamous epithelial layer. A milky-

¹ The habits of the males are ignored from here on. They attach for a period of only a few days before seeking females and mating and do not engorge appreciably, nor, so it is believed, are they capable of causing paralysis. An unmated female, on the other hand, remains attached and slowly engorging for a period of about two weeks. Mated females engorge in about seven days.

white free-flowing fluid then appears from between the hypostome and chelicerae (Fig. 1). This is slowly exuded over a period of up to ten minutes, during which time it is seen to gradually climb around the above mouthparts and under the closely applied palps. It also flows into the puncture and beneath the outer epithelial layer of the host's skin, forming a white area about one millimeter in diameter.

Almost as soon as the fluid is secreted it hardens into a latex-like material, moulding itself around the denticles and crenulations of the hypostome and chelicerae and firmly cementing these structures to the host. It is resistant to teasing with a sharp needle and is so superficially applied to the host tissue that such manipulations, in tearing it away, give the effect of adherence entirely to the outside of the skin. Histologically, the cement is strongly eosinophilic and is seen to penetrate under only a very thin layer of the squamous epithelium (Fig. 2).

The papule so formed by the cement is cone-shaped, and is without doubt the structure mentioned by SNODGRASS (1948) and other authors who have taken it to be an outgrowth of host tissue. The origin of the fluid has not been demonstrated, but it is presumed that it arises in the salivary glands. Because ticks can re-attach at various stages of engorgement it is apparent that the secretion can be produced at will. Once attachment is completed, its production is presumed to cease. Studies have not yet shown what is responsible for its rapid solidification.

4. The Process of Feeding.

Attachment is followed by an intermittent probing and cutting of the underlying tissues by the digits. As blood becomes freed from ruptured capillaries a small amount of now clear salivary fluid is released to prevent clotting². The pool which is formed is then sucked up and swallowed. As more blood becomes available, the actions become more prominent.

By subjecting a mouse's ear, with tick attached, to a beam of transmitted light, this alternate process of salivation and sucking can be observed and photographed with relative ease. The two actions appear to vary in time and intensity, depending, no doubt, on both the tick's rate of feeding, which increases as the tick nears

² It has been found that crushed salivary glands of *D. andersoni* contain a mild anticoagulant and delay the clotting time of blood by two or three times the normal period. As irritation by the tick and injections of secretion continue during the several days of normal feeding on sheep, the blood is seen to form haemorrhagic pools which extend into the substrata of the skin. In this respect, it is apparent that the tick is a pool feeder.



Fig. 1. Enlargement from motion picture film strip of tick attaching to ear of mouse, showing the cement, as a white fluid, creeping up under the palps and extending in front of them under the squamous epithelium. Reflected light.

Fig. 2. Histological section of mouse ear cut through site of tick attachment. Cement area has been inked in black. Imprints of hypostome and cheliceral denticles appear on inner right and left margins, respectively.

Fig. 3. Enlargement from motion picture film strip showing mouthparts of tick applied to margin of mouse ear. The ear tissue is dark with the blood that is being sucked toward the tick. Transmitted light.

Fig. 4. Same as Fig. 3, except that the blood has retracted and saliva is now being expelled into the tissue.

Fig. 5. Enlargement from motion picture film strip showing the mouthparts of a detaching tick leaving the capsule which cemented it to its host. Transmitted light.

Fig. 6. Continuation of Fig. 5, after the capsule has been discarded (mouthparts on extreme left).

repletion, particularly if it has mated, and upon the availability of blood.

A limited number of observations on mouse ears, when the ticks were about half engorged, suggest that the two actions alternate about every 5-30 seconds. The periods of sucking were usually longer than those of salivation. One tick which had previously fed four days on a sheep alternately secreted (figures underlined) and sucked during the following intervals (in seconds): . . . 7, 15, 5, 15, 7, 30, 30, 15, 5, 15, 4, 12, 5, 18, 15, 30, 35, 25, 4, 10, 5, 15, 4, 30, 30, 25, 5, 20, 4, 35, 35, 20, 10, 20, 10, 25, 35, 30, 15, 25 . . . The sucking of blood (Fig. 3) is characterized by a jerking motion of blood cells towards the tick's mouthparts, caused by spasmodic movements of the pharynx. Towards the end of this period the blood appears to slip back slightly after each gulp, suggesting the formation of a negative pressure within the host tissue. The ensuing output of saliva (Fig. 4) seems to corroborate this opinion since it appears to gush into the area anterior to the mouthparts with a considerable velocity as if under suction. It is, of course, possible that a pressure build-up within the salivary glands aids this expulsion. The blood then gradually diffuses back towards the mouthparts, and the process is repeated. The periods of sucking and secreting may also be interrupted by periods of inactivity, during which there is no apparent movement of blood or saliva. A similar process of sucking, secreting, and inactivity has been observed by LAVOPIERRE and RIEK (1955) in *Argas boueti*.

The salivation into host tissue at frequent intervals substantiates the theory that tick paralysis is caused by some action of the tick's saliva on the host (GREGSON, 1953). This disease is dependent on the continued attachment of the tick, and because the symptoms may lessen within half an hour after its removal, it is presumed that the causative toxin must be replenished at frequent intervals between feeding. It has, however, been observed (GREGSON, 1957) that when empty capillary tubes are placed over the hypostomes of ticks that have recently been removed from a host, the ticks may secrete into the tubes continuously for periods up to 20 minutes. Furthermore, when offered similar tubes of heparinized blood (or even water, either acid or alkaline) such ticks will suck the fluid for similar periods, with no or only very small expulsions of saliva. In the light of the above observations it is believed that these artificial stimulations do not produce normal feeding responses. Further experiments along these lines showed that salivary secretion appeared to be induced by tactile stimulation of the tips of the chelicerae. A tube that fitted too loosely over the chelicerae and hypostome, or one that fitted over the palps as well,

elicited no fluid. Considering all of the above observations, it is possible that the normal feeding action is somewhat automatic, the presence of blood around the chelicerae stimulating a sucking movement which ceases when the blood becomes no longer available. Its absence may then stimulate the liberation of a limited amount of secretion, which then remains in the adjacent tissue pending the diffusion of blood back to the chelicerae.

5. *The Process of Detaching.*

The final response to attachment occurs either when the tick reaches repletion or when it is accidentally detached from its host. Prior to this time the tick is so firmly attached to the skin by its cement-like secretion that only a strong pull will dislodge it. Even then, the cone-shaped papilla is usually pulled away with the mouthparts, and manual separation of the two is so difficult that the capitulum can be torn off by the pull. Yet, when the tick is ready to leave its host, or within a minute or two after its artificial removal, it merely backs away from the papilla (Figs. 5 and 6).

Such an apparently effortless release is puzzling. Although a small drop of saliva may be released during the process, it does not appear that any substance is liberated that dissolves the cement. It seems rather that the tick is normally held to the capsule by a close molding of the cement around the mouthparts, and that its release is effected by retraction of the chelicerae, with consequent invagination and withdrawal of the soft outer chelical sheaths. The resulting effect would be like withdrawing two of three fingers from a tightly fitting pocket, thus loosening the remaining one (the hypostome). If these two fingers were tightly gloved, so that the fabric was invaginated by their withdrawal, the analogy is even closer.

6. *Discussion.*

The fact that *D. andersoni* secretes a substance that cements it to the skin of its hosts arouses some interesting thoughts. It would appear without doubt that a similar cement has been observed in *Amblyomma*, *Boophilus*, *Rhipicephalus*, and *Ixodes* species and one might correctly assume that it is present in all the slow-feeding ixodid ticks. Whether this is true for the argasid ticks is open to conjecture; with the exception of the early stages of *Otobius* species and the larvae of certain other species most of this group are rapid feeders and seldom remain attached for longer than a few hours. On the other hand, such a secretion may not be con-

finied to the ticks. An interesting parallel is perhaps to be seen in the stylosome or feeding tubes of the trombiculid mites. These tubes appear to be formed in the dermal and epidermal layers of the host by the saliva of feeding chiggers. According to ALLRED (1954), the canals may extend to twice the length of the parasite.

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Résumé.

On décrit la morphologie du capitulum de *Dermacentor andersoni*, en se référant à des publications antérieures concernant les pièces buccales de tiques. Une fine membrane transparente couvre la partie dorsale de l'hypostome, ainsi que le contenu non cellularisé de la gouttière hypostomale. Les chélicères sont entourés de gaines extérieures, postérieures et coniformes. On discute les différents éléments de l'appareil pharyngien ; l'orifice pharyngien s'ouvre dans la cavité buccale où il fait suite à un sillon de la membrane hypostomale ; il n'est

muni ni d'un stylet, ni d'un clapet labral. Aux entrées des conduits salivaires, ainsi que dans la portion antérieure du pharynx, on note la présence de structures flexibles ressemblant à des valves; toutes ces parties, y compris la membrane hypostomale, semblent être activées par les mouvements des ailes pharyngiennes, apparemment en connexion avec le flux de la salive. Des mouvements autonomes et non péristaltiques du pharynx accompagnent l'ingestion du sang.

Lorsqu'on observe des femelles de *Dermacentor andersoni* en train de se gorgier sur des oreilles de souris anesthésiées, on remarque qu'elles sécrètent une substance qui se durcit rapidement et soude ainsi les chélicères et l'hypostome intimement sur la peau de l'hôte. Bien que la capsule coniforme ainsi formée, de même que des couches interstitielles, entourant l'hypostome comme une espèce de ciment, aient déjà été observées par des auteurs précédents, leur origine n'a cependant jamais pu être interprétée d'une façon satisfaisante jusqu'à présent. Lorsqu'une tique se gorge, il y a alternance entre l'injection de salive sous la peau de l'hôte et l'ingestion de sang, et cela environ toutes les 5 à 30 secondes. Bien que la tique, grâce à la capsule coniforme, soit fermement soudée à la peau de l'hôte pendant l'acte hématophage, elle peut cependant se libérer spontanément assez rapidement. Ce procédé est facilité par l'invagination des gaines extérieures, provoquée par la rétraction répétée des chélicères.

Zusammenfassung.

Es wird die Morphologie des Capitulum von *Dermacentor andersoni* beschrieben unter Bezug auf frühere Publikationen über die Mundteile von Zecken. Eine dünne, durchsichtige Membran bedeckt die Dorsalseite des Hypostoms und den nicht cellulären Inhalt der Hypostomalrinne. An den Cheliceren werden äußere, hintere und kegelförmige Scheiden beschrieben. Die verschiedenen Bestandteile des Schlundapparates werden diskutiert; die Pharynxpforte mündet in die Mundhöhle und bildet die Fortsetzung einer Furche der Hypostomalmembran; am Eingang zum Pharynx ist weder eine Stechborste noch eine Labralklappe vorhanden. An den Eingängen zu den Speichelgängen und im vorderen Abschnitt des Pharynx bemerkt man elastische, ventilartige Strukturen; sie alle scheinen gemeinsam mit der Hypostomalmembran durch die Bewegungen der Pharynxflügel mitaktiviert zu werden, offenbar in Verbindung mit dem Speichelfluß. Autonome, nichtperistaltische Bewegungen des Pharynx begleiten die Blutaufnahme.

Beobachtet man Weibchen von *Dermacentor andersoni* beim Blutsaugen auf den Ohren anästhesierter Mäuse, so bemerkt man, daß sie eine rasch erhärtende Substanz ausscheiden, welche die Cheliceren und das Hypostom der Zecke mit der Haut des Wirtes fest verbindet. Obschon die so entstandene kegelförmige Kapsel, gleichzeitig mit interstitiellen, cementartigen Ablagerungen um das Hypostom herum, schon von früheren Autoren beobachtet worden ist, so konnte doch ihre Entstehung bisher nie in befriedigender Weise gedeutet werden. Beim Füttern der Zecke wechseln das Injizieren von Speichel unter die Wirtshaut und das Aufsaugen von Blut etwa alle 5 bis 30 Sekunden miteinander ab. Obschon die Zecke dank der Kittkapsel während des Saugaktes fest auf der Wirtshaut fixiert ist, so kann sie sich doch rasch spontan ablösen, wobei ihr offenbar anfänglich ein Einstülpen der äußeren Chelicerenscheiden zustatten kommt, hervorgebracht durch wiederholtes Zurückziehen der Cheliceren.
