

MATERIAL AND METHODS

The lice were collected fresh from the hosts. The mouth parts were dissected under a stereoscopic microscope. This mainly consisted of the removal of the mandibles and the labium which laid open the other mouth parts clearly. The dissected mouth parts were partly stained in haematoxylin and eosin, cleared and mounted in Canada balsam and some without staining. Some were mounted directly in Hoyer's medium and this appeared to be quite satisfactory. As mounting in the latter medium involves no processing, there was little distortion or displacement of the parts. Mountings made between two coverslips facilitated examining from the dorsal and ventral surfaces.

RESULTS AND DISCUSSION

ISCHNOCERA

The mouth parts of *L. tropicalis* are described in detail. A comparative account of the other species, only, is given with necessary drawings.

Symmons (1952) states that the clypeus extends to the ventral surface of the head, the mouth (external) being placed in the middle (Fig. 2). The labrum is in front of the external mouth or just anterior to the mandibles. The non-sclerotised pulvinus is said to represent the clypeo-labral suture. There is a chitinous bar on either side of the pulvinus (the marginal pulvinal bars, Symmons, 1952) connected by a strong band of cuticle, transversely striated. These give support to the pulvinus laterally (Symmons, 1952) (Fig. 2-B). The pulvinus takes part in deglutition. In a living specimen placed on its back in a drop of normal saline under the microscope, undulating movements of the pulvinus were clearly seen; a groove, formed in the center, held a hair and directed it towards the mouth.

Labium (Fig. 5).—This forms the posterior border of the mouth. The palpi are single-segmented, each bearing six setae. In between the palpi are two lobes constituting the ligula—short protuberances with three setae each. Between the palpi and ligula on either side is seen a small, flat, oval highly sclerotised area (Fig. 5-C), though not so prominent as in *G. gallinae*, *G. dissimilis* or *M. stramineus*. The homology of this structure has been debated by Shipley and Cummings as mentioned by Quadri (1936). It is felt unnecessary to discuss this as it is obviously a labial structure and a part of the ligula (or paraglossa). On the ventral surface of the base of the labium is a transverse band of cuticle running across and seen prominently owing to the transverse striations in contrast to the striations in the rest of this region. The lateral borders of the labium in this region are highly sclerotised forming a rim. This rim runs anteriorly, passes dorsal to the palpi and is connected with the sclerotised oval area by the side of the palpi mentioned above and then gets merged with the borders of the ligula. Near the distal ends of this rim and dorsal to them ends the stipes described below.

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Mouth Parts of Mallophaga

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ABSTRACT

The mouth parts of *Lipeurus tropicalis* are described in detail clarifying many of the structures, which earlier were not clear or misunderstood, with a comparative account of the same in four other species of Ischnocera and five species of Amblycera of domestic birds and mammals. The evolutionary trends of the mouth parts especially the anterior plate of the hypopharynx from Psocoptera through Ischnocera to Amblycera are brought out.

A DETAILED account of the mouth parts of Mallophaga, some of which are common parasites of domestic animals, is not available. The study was undertaken to clarify some of the structural features and incidentally, it showed some phylogenetic relationships, which are discussed in this paper. The lice studied are :

ISCHNOCERA.—*Lipeurus tropicalis* (Peters), *L. caponis* (Linne) *Goniocotes gallinae* (DeGeer), *Gonoides dissimilis* (Denny) of poultry ; *Damalinia bovis* (Linne) of cattle.

AMBLYCERA.—*Menopon gallinae* (Linne), *Menacanthus stramineus* (Nitzsch), of poultry ; *Heterodoxus spiniger* (Enderlein) of dogs, *Gyropus ovalis* (Nitzsch) and *Gliricola porcelli* (Linne) of Guinea pigs.

Based on the studies of the above species, some generalisations have been made.

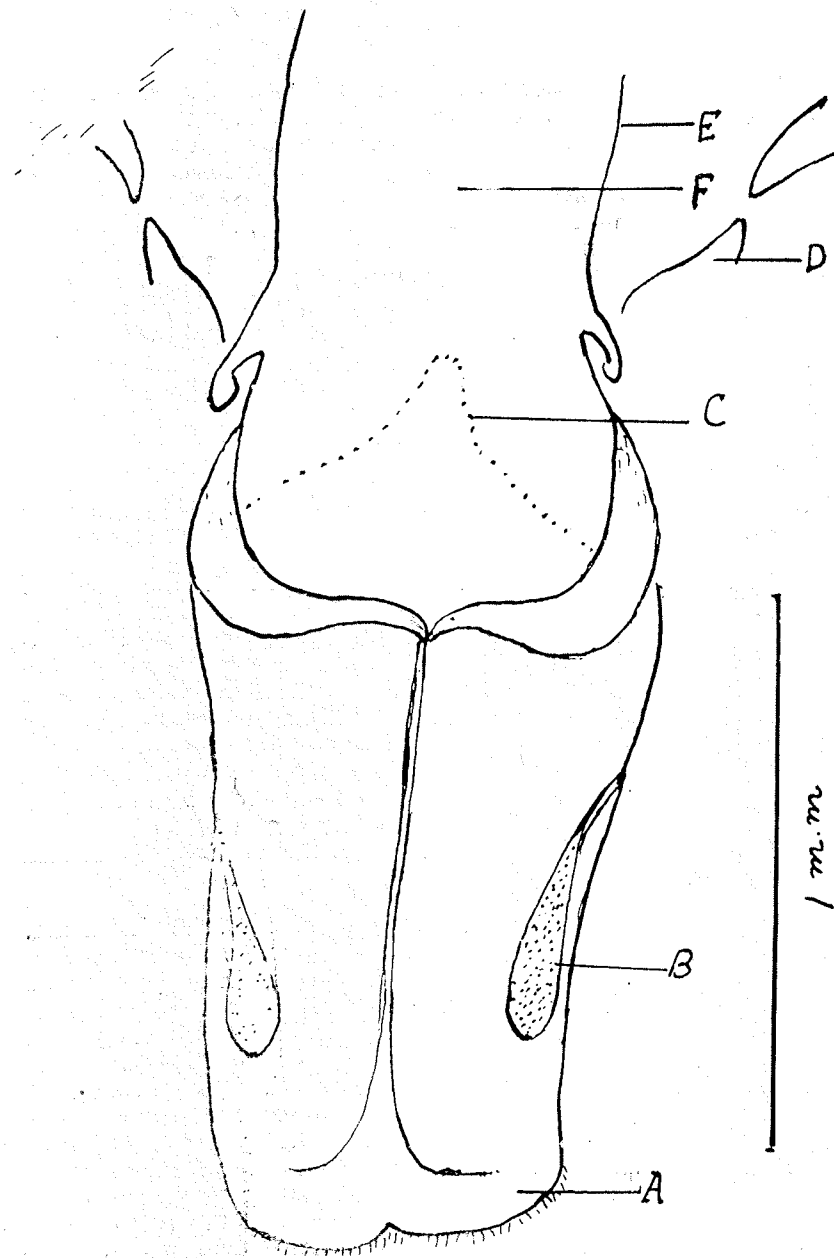


FIG. 1. Hypopharynx of *Periplaneta americana*. A—lingua; B—lingual sclerite; C—fulcrum; D—loral arm; E—oral arm; F—sitophore.

Hypopharyngeal complex (Fig. 4).—In Mallophaga, the sclerotised part of this consists of three elements, namely, (1) a pair of ovoidal sclerites, (2) anterior plate and (3) sitophore. Dorsal to the labium are the two ovoidal sclerites (formerly termed the lingual glands) and between these two and slightly dorsal is the sitophore (also termed oesophageal sclerite). As described by Cummings (1913) the ovoidal sclerites are hard oval plates in which no glandular structure is seen. Anteriorly the ovoidal sclerites are connected to what has been termed "anterior plate" (Fig. 4-C) a term retained here for want of a better one. This is three lobed; one middle and two lateral. The borders of these lobes are dentate. These are connected by sclerotised filaments and are given the following designations so that they can be followed in the species in which the ovoidal sclerites are reduced leaving only the filaments.

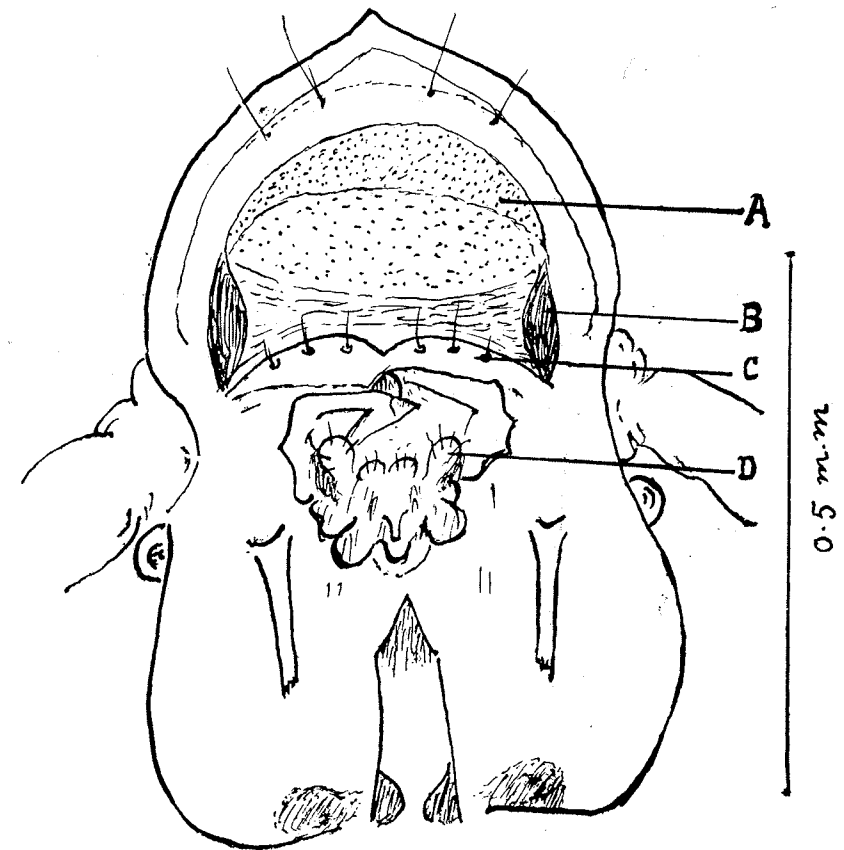


FIG. 2. *Lipeurus tropicalis*: Ventral view of the head. (A—pulvinus; B—marginal pulvinal bars; C—labrum; D—labium.)

1. The sitophore filament (Fig. 4-F). extends from the sitophore and bifurcates, a branch going to the ventral surface of each of the ovoidal sclerite. This is cross striated like a tracheal tube.

2. The lateral filament (Fig. 4-E). extends from the lateral sides of the lateral lobes of the anterior plate; each proceeds a short distance and then bifurcates one branch passing over the dorsal surface of the ovoidal sclerites diagonally and the other to the lateral border of the same, slightly dorsally and appear to be connected by a thin line to the apodemes of the ovoidal sclerites that extend posteriorly.

3. A pair of middle filaments (Fig. 4-D). seen on either side of the middle lobe of the anterior plate; each coming down approaches the lateral lobes of the anterior plate and ovoidal sclerites and stops.

Sitophore (Fig. 7). is cup-shaped with two anterior cornu and a body (the posterior cornu are reduced in this species). It is connected with the ovoidal sclerites by the sitophore filament as described above.

Homology of the hypopharyngeal elements is considered here with the hypopharynx of a generalised insect, the cockroach *Periplaneta americana*.

The hypopharynx of the cockroach (Fig. 1) has the distal part free and the proximal part embedded in the surrounding tissues. The distal part is strengthened on either side by the lingual sclerites (Fig. 1-B) which extend proximally on the ventral surface to form the fulcrum. The proximal part is supported on either side by the suspensoria (remnants of the superlingua). Midway, each suspensorium gives rise to the loral arm (Fig. 1-D) and then proceeds towards the mouth as the oral-arm (Fig. 1-E). The dorsal surface of the hypopharynx between the suspensoria is trough-like and is termed the sitophore.

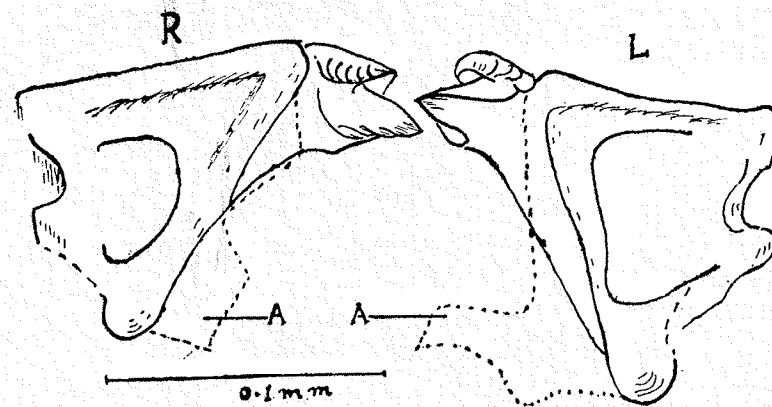


FIG. 3. *L. tropicalis*: Mandibles. (L—Left; R—Right; A—prostheca.)

Snodgrass (1944) homologises the lingual sclerites with the ovoidal sclerites of Psocoptera and Mallophaga as the same muscle (No. 78) is attached to the lingual sclerites and the apodeme of the ovoidal sclerites. The sitophore of Psocoptera and Mallophaga is homologised with the sitophore of the cockroach. The clypeo-labral region in Mallophaga, as already stated, extends to the ventral surface. In this

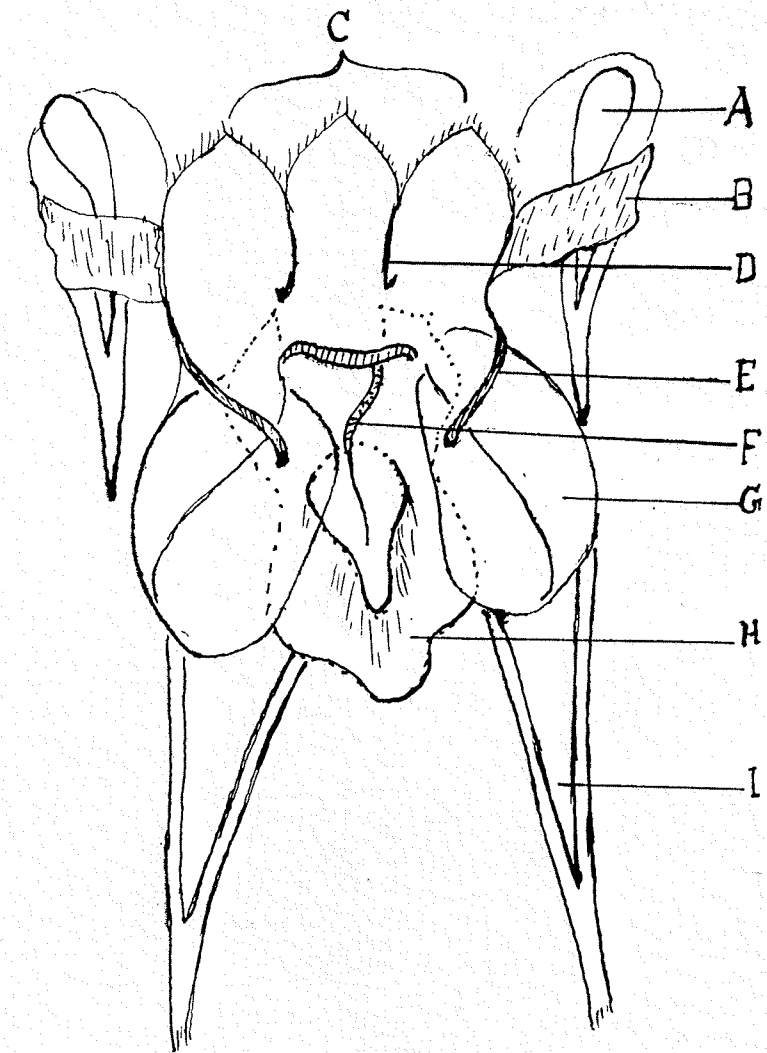


FIG. 4. *L. tropicalis*: Hypopharyngeal complex. (A—lacinia; B—galea; C—anterior plate; D—middle filament; E—lateral filament; F—sitophore filament; G—ovoidal sclerite; H—sitophore; I—apodeme.)

process of shifting, it can be imagined that the lingual sclerites were retracted posteriorly along with the ventral surface of the proximal part of the hypopharynx and thus the ovoidal sclerites (lingual sclerites) come to lie on the ventral surface of the sitophore. The free distal part of the hypopharynx (lingua, Fig. 1-A) of the cockroach, now devoid of the sclerites, has probably become the anterior plate in Mallophaga. This agrees with our observation that in Mallophaga the anterior plate

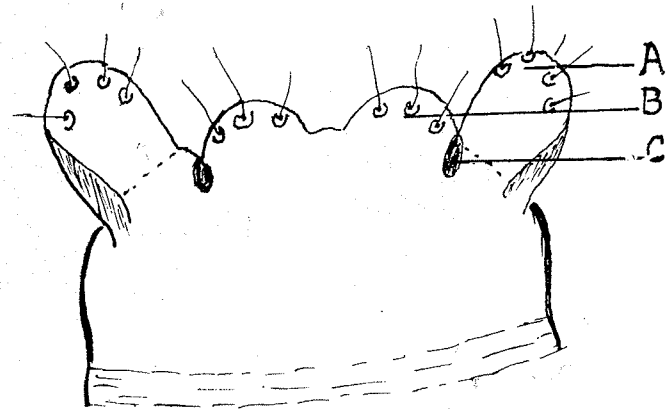


FIG. 5. *L. tropicalis*: Labium. (A—labial palp; B—ligula; C—oval sclerotised structure.)

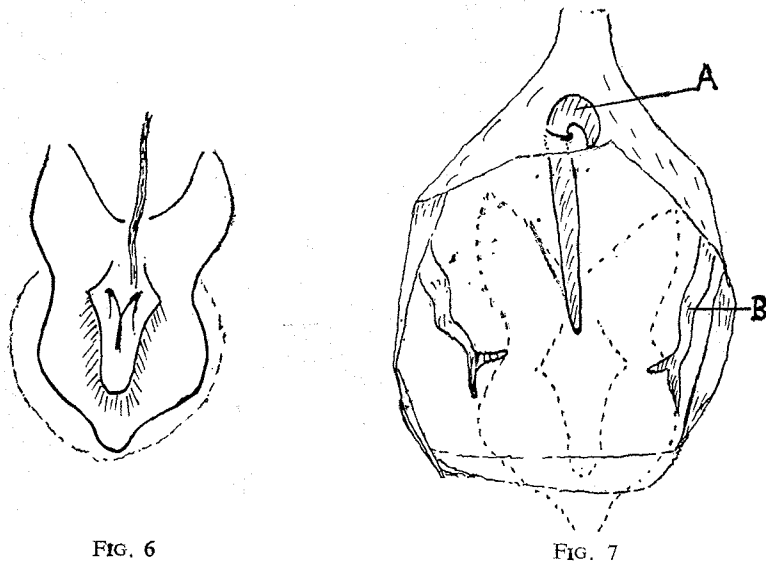


FIG. 6. *L. tropicalis*: Sitophore enlarged.

FIG. 7. *L. tropicalis*: Epipharyngeal apparatus. (A—pestle; B—side sclerotised structure.)

is slightly dorsal to the ovoidal sclerites and anterior to the sitophore. In the cockroach, the dorsal wall of the salivary duct is formed by the hypopharynx and in Mallophaga the ovoidal sclerites form the dorsal wall, because of their posterior shifting.

Epipharyngeal apparatus (Fig. 7).—Directly above the sitophore on the dorsal wall of the cibarium (epipharynx) a sclerotised oval rim is seen. From its anterior end hangs down a rod (pestle, Fig. 7-A) by a well formed hook, towards the sitophore. On either side of this rim is seen a sclerotised structure (Fig. 7-B) going down to the sitophore. This gives the impression that this may fix the sitophore during the movement of the pestle. The pestle from epipharynx and the sitophore as mortar are well developed in Psocoptera and are believed to function as pestle and mortar apparatus in the breakdown of the food particles. Risler (1951) thinks that in *Bovicola (Damalinia)*, this is not possible, as the muscle attached to the pestle is very small. How far in other species of Mallophaga, this helps in crushing the food particles

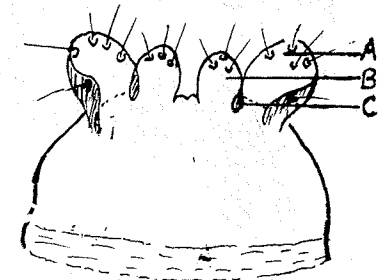


FIG. 9

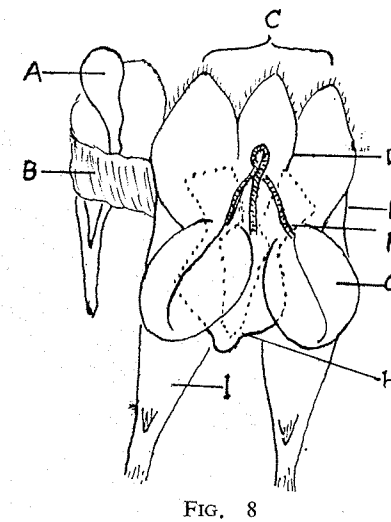


FIG. 8

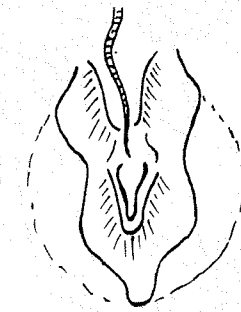


FIG. 10

FIGS. 8-10. *Lipeurus caponis*: 8. Hypopharyngeal complex, 9. Labium, 10. Sitophore enlarged. (same lettering as in Figs. 4 and 5.)

is not clear, as the apparatus appears rather feeble to do this function. A greater possibility is that the pestle may act as a valve for allowing easy passage of the food particles towards the stomodaeum or prevent its regurgitation. A groove extending posteriorly from the sclerotised rim indicates the oesophagus. Slight variations in the appearance of the epipharyngeal apparatuses than what have been figured, may be seen. This was found to be due to the degree of sclerotisation it has undergone and the position of the pestle in the mounted specimens—whether it is at its place of origin or come down towards the sitophore.

Mandibles (Fig. 3).—They are roughly quadrilateral but appear triangular from the ventral surface owing to three heavy lines of sclerotisation—anterior, diagonal and lateral. The apex (antero-medial angle) is bifid, the smaller anterior tooth being annulated and the larger, posterior tooth being concave on its posterior surface to which is apposed the galea. The antero-lateral angle forms a socket to which fits in a

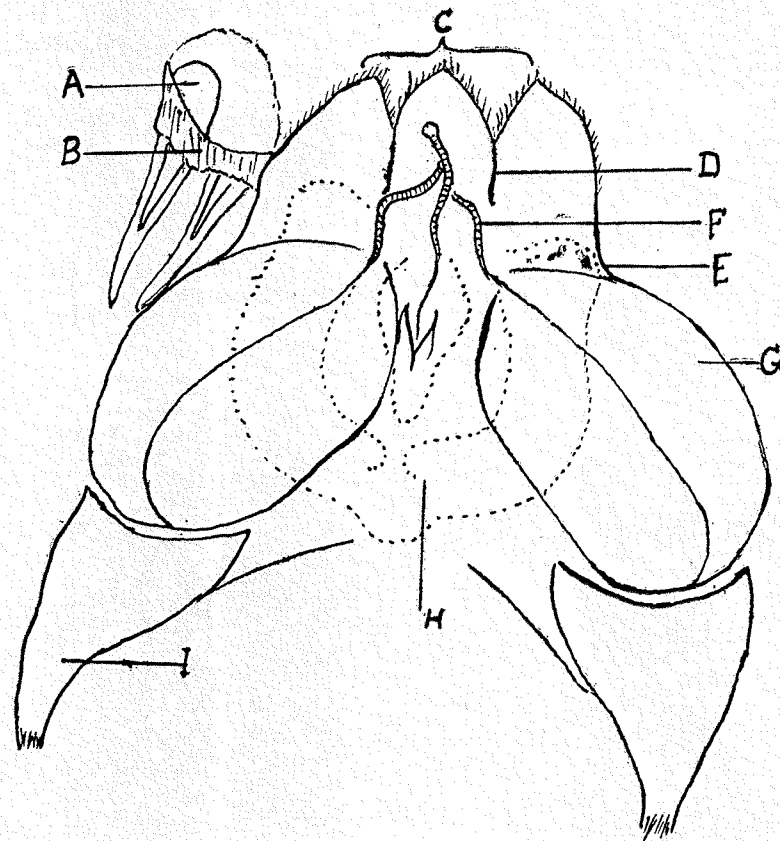


FIG. 11. *Gonoides dissimilis*: Hypopharyngeal complex (same lettering as in Fig. 4).

condyle formed by the subgena, constituting the anterior articulation or ginglymus. The postero-lateral angle forms a condyle which fits into a socket formed by the gena constituting the posterior articulation. Projecting mesally from each mandible is a broad flexible plate like prostheca (Fig. 3-A). The right prostheca has the mesal projection bluntly rounded whereas that of the left side has an angular projection. Quadri (1936) has termed this process of the right mandible as the quadrangular process and that of the left as the basal process.

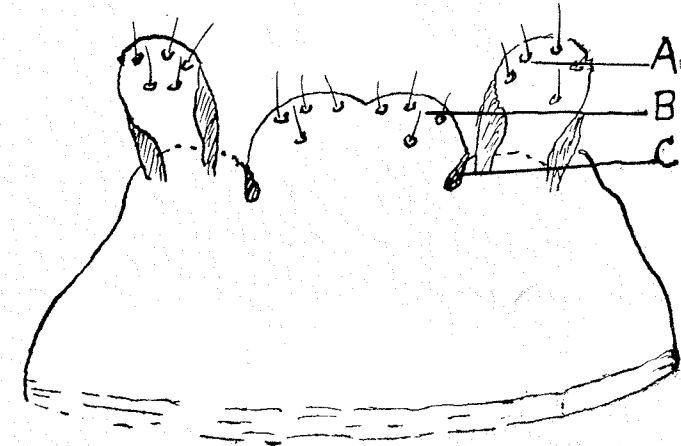


FIG. 12

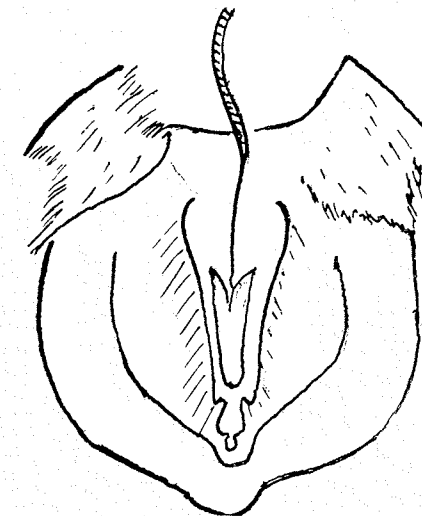


FIG. 13

FIGS. 12 and 13. *Gonoides dissimilis*: 12. Labium, 13. Sitophore (lettering as in Fig. 5).

I maxillae (Fig. 4-A and B).—The presence of the 1st maxillae in Ischnocera has been much debated. Quadri (1936) observed that in any Ischnocera, there was a lobe, slightly dorsal on each side of the labium which appeared to be the maxillae in which the maxillary lobes and palpi are highly reduced. Matsuda (1965) states that in *Bovicola* the maxilla is represented by the galea and lacinia. In *L. tropicalis* and in the other ischnocerans studied, the maxilla could easily be demonstrated on the removal of the mandibles and the dorsal wall of the head to give a good contrast. This consists of a semi-cylindrical galea and a thin lacinia dorsally. The latter is rather delicate, liable to distortion and is seen in good preparations. The galea arises from a stalk, presumably the stipes. Posteriorly, this bends medially and ends dorsal to the posterior terminations of the rim of the labium described above. Anteriorly, the galea and lacinia are in close apposition with concave posterior surface of the posterior tooth of the mandible overlapped dorsally by the prostheca.

Of the mouth parts, namely, labium, ovoidal sclerites, sitophore, epipharyngeal complex, mandibles and 1st maxillae, the same pattern is seen in the other ischnocerans and a comparative account of them is given below. Minor modifications of the mandibles in the different species are not discussed.

1. *L. caponis* (Figs. 8–10).—The mouth parts are practically similar to those of *L. tropicalis*. The shape of the sitophore is slightly different and is shown in the figure.

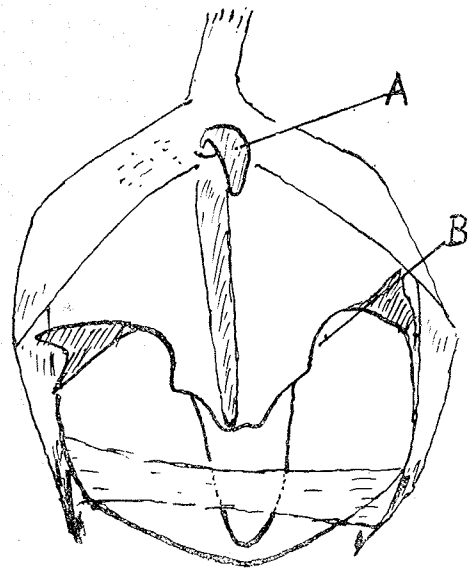


FIG. 14. *Gonoides dissimilis*: Epipharyngeal apparatus (same lettering as in Fig. 7).

2, 3. *G. gallinae* and *G. dissimilis* (Figs. 11–17).—The sclerotised oval structure between the labial palp and ligula is prominent. The lateral filament of the ovoidal sclerite does not branch. It extends from the lateral lobe of the anterior plate to the dorsal surface of the ovoidal sclerite and its thin connection with the apodeme is seen. The epipharyngeal apparatus is more heavily sclerotised.

4. *D. bovis* (Figs. 18–21).—The ligula of the labium is almost flat. The epipharyngeal apparatus is more heavily sclerotised. The anterior cornu of the sitophore are prolonged.

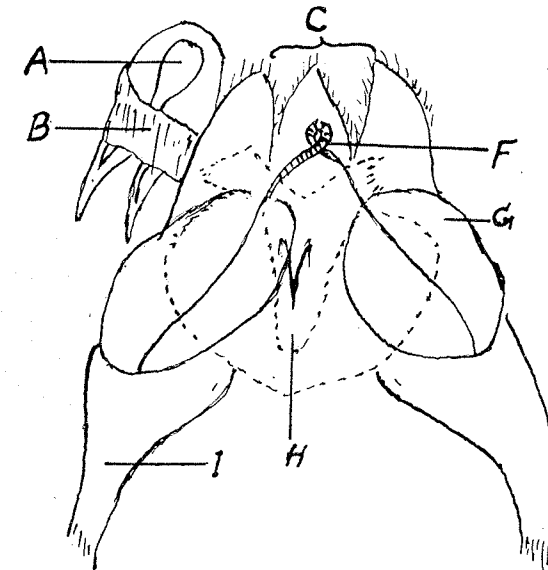


FIG. 15

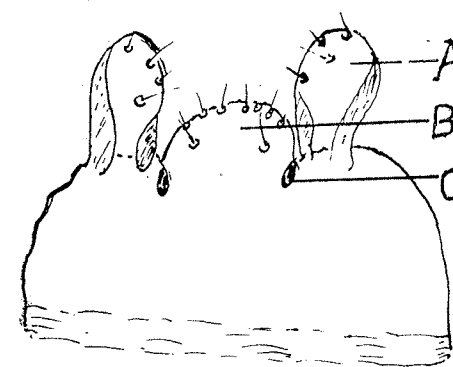


FIG. 16

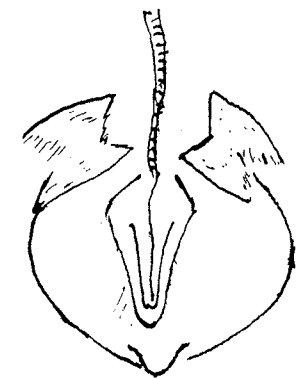


FIG. 17

Figs. 15–17. *Goniocotes gallinae*: 15. Hypopharyngeal complex, 16. Labium, 17. Sitophore (same lettering as in Figs. 4 and 5).

AMBLYCERA

1. *Menopon gallinae* (Figs. 22-24).—The mouth parts show many interesting features which have both ischnoceran and amblyceran characters and one is tempted to view it as a connecting link between the two suborders. The ovoidal sclerite (absent in the other amblycerans*) are advanced anteriorly, almost quadrilateral in shape, the lateral borders being thin. The sitophore is globular at its base as in Ischnocera (not plate-like in the other amblycerans*). The pestle (absent in the other amblycerans*) is well developed, though comparatively short. The epipharyngeal apparatus (absent in the other amblycerans*) is more heavily sclerotised.

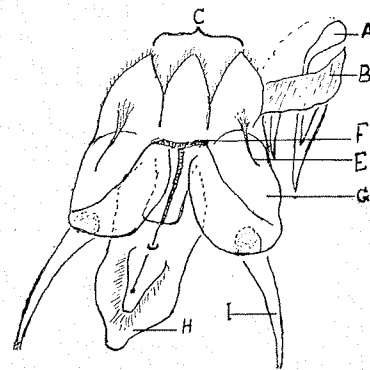


FIG. 18

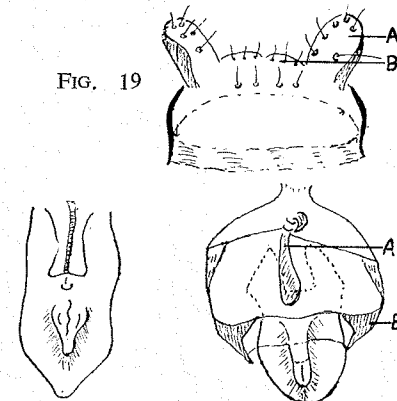


FIG. 20

FIG. 21

Figs. 18-21. *Damalina bovis*: 18. Hypopharyngeal complex, 19. Labium, 20. Sitophore, 21. Epipharyngeal apparatus (same lettering as in Figs. 4, 5 and 7).

Amblyceran characters.—The anterior plate is modified as in the other amblycerans (*). The lateral filament is short, not branched and starts quite away from the lateral borders of the ovoidal sclerites, just by the side where the sitophore filament ends. It extends to the dorsal surface of the ovoidal sclerite and a thin line connecting it with the apodeme can be seen. The mesal border of the lateral lobes are dentated, which are more filamentous in structure. Between the lateral lobes are two strands delicately dentated. These probably represent the pair of middle filaments which have come together with the reduction of the median lobe. The labium is advanced anteriorly and the palpi project beyond the mandibles. The galea of the maxilla is serrated and strongly developed as well as the four segmented maxillary palpi as in the other members of this sub-order. The dentated borders of the two galea are in apposition and are seen prominently between the mandibles.

* Amblycerans included in this paper.

In short, the essential ischnoceran characters of the mouth parts in this amblyceran are (1) Clear cut ovoidal sclerites, (2) cup-shaped sitophore (3) presence of the pestle.

2. *Menacanthus stramineus* (Figs. 25-27).—The ovoidal sclerites are completely reduced and their outlines cannot be made out. Only their apodemes are seen which extend up to the lateral lobes of the anterior plate. The latter is similarly modified as in *M. gallinae*. The lateral filament is short and extends from the lateral lobe to the apodeme. The pair of middle filaments are dentated as in *M. gallinae*. The sitophore filament bifurcates as in the other species, and the common stem extending from the sitophore is long. The sitophore is reduced to a plate-like structure and not cup-shaped as in Ischnocera or *M. gallinae*. Correlated with this modification, the pestle is completely reduced and not seen as in the other amblycerans discussed below.

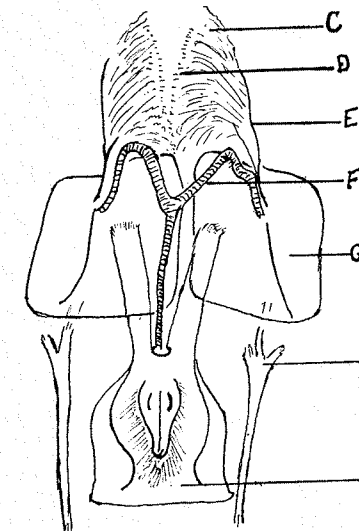


FIG. 22

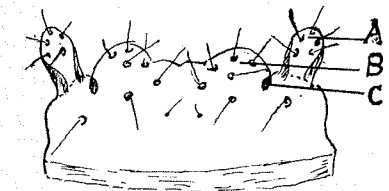


FIG. 23

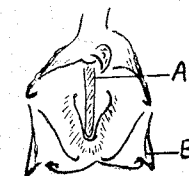


FIG. 24

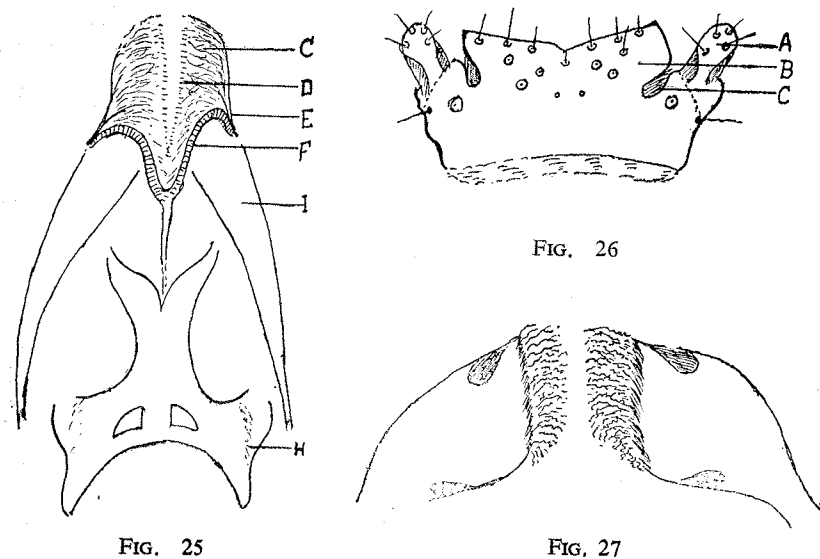
Figs. 22-24. *Menopon gallinae*: 22. Hypopharyngeal complex, 23. Labium, 24. Epipharyngeal apparatus (same lettering as in Figs. 4, 5 and 7).

3. *Heterodoxus spiniger* (Figs. 28-29).—The ovoidal sclerites are absent. The sitophore is plate like and the pestle is absent. The sitophore filament is broad and cross striations are not observed. The common stem is very short. The lateral filament is split into two proximally, the two joining together a little posteriorly. This then curves medially and ends at the centre near the similar ending of its fellow of the opposite side. The apodemes are lightly sclerotised and are in apposition with the posterior curvature of the lateral filament.

This curved nature of the lateral filament, almost semi-circular, with the bifurcated sitophore filament in the centre may simulate the appearance of the ovoidal sclerites. Cummings (1913) says that in *Heterodoxus macropus*, which possesses a similar structure, as per the figure given by him, says that there is no trace of the gland (ovoidal sclerite). The pair of middle filaments with minute denticles are seen. The teeth or filamentous structures of the lateral lobes are more numerous and well developed. The labium is at the level of the mandibles and not so far advanced as in the previous species.

4. *Gyropus ovalis* (Figs. 31-32).—The labium is shifted forward and anterior to the mandibles. The latter are small and just meet at the center. The ovoidal sclerites are absent. The apodemes extend up to the lateral lobes of the anterior plate and the lateral filament is almost merged with it. The sitophore filament is very feebly striated and its common stem is almost absent. The lateral lobes of the anterior plate have filamentous teeth and the two strands of the middle filament have minute denticles as in the other Amblycera.

5. *Gliricola porcelli* (Figs. 33-34).—The labium is well advanced anteriorly and almost to the anterior border of the head. The mandibles are small and the two just meet at the center. The lateral lobes of the

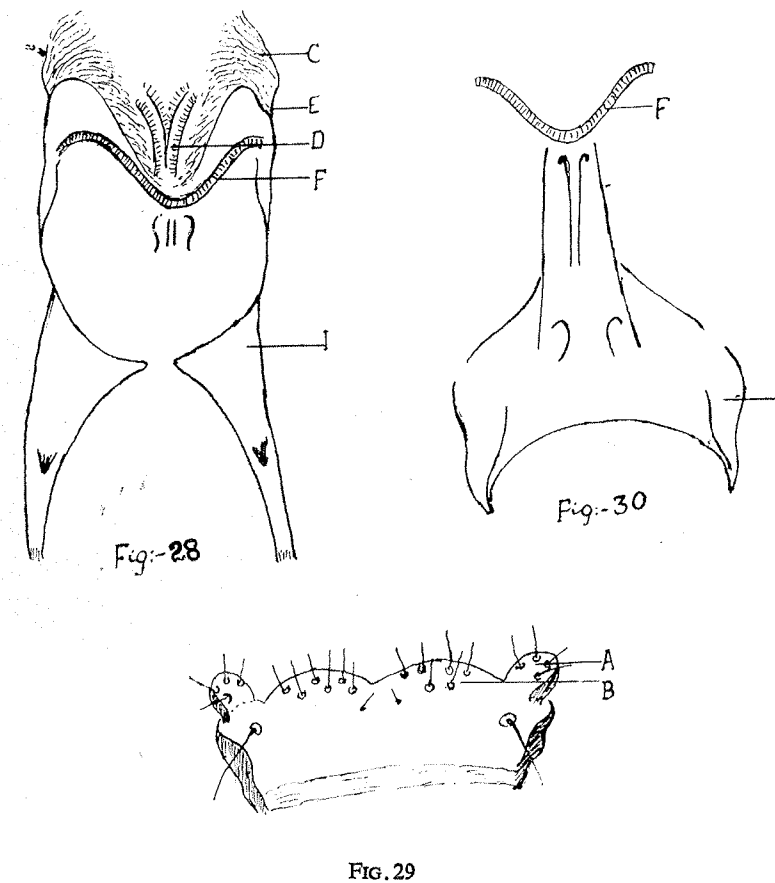


Figs. 25-27. *Menacanthus stramineus*: 25. Hypopharyngeal complex, 26. Labium, 27. Galeae (same lettering as in Figs. 4 and 5).

anterior plate have filamentous teeth and in addition, their anterior border is arched laterally into almost a circular process with strong teeth (Fig. 33-C). The lateral filament has merged with the apodeme of the ovoidal sclerites which have disappeared. The sitophore is plate like and the pestle is absent. The sitophore filament is advanced anteriorly and appears merged with the mesal borders of the lateral lobes. The common stem of the bifurcated sitophore filament is reduced and not seen.

General discussion—phylogenetic relationships.

The Mallophaga is regarded to have close affinity to Psocoptera and Cummings (1913) states that a plausible theory has been suggested that the former are Psocidae which have taken to a parasitic existence.



Figs. 28-30. *Heterodoxus spiniger*: 28. Hypopharyngeal complex without sitophore, 29. Labium, 30. Sitophore, (same lettering as in Figs. 4 and 5).

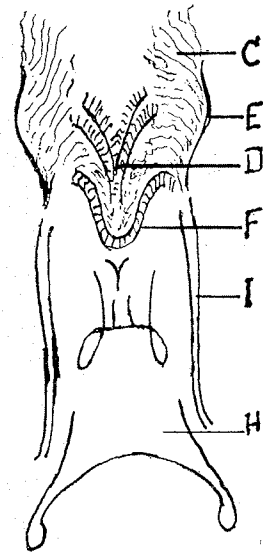


FIG. 31

FIGS. 31-32. *Gyropus ovalis*: 31. Hypopharyngeal complex, 32. Labium.
(Lettering as in Figs. 4 and 5).

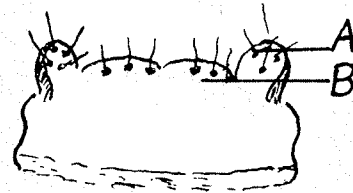


FIG. 32

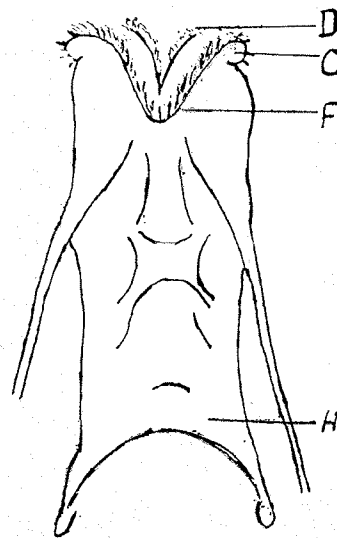


FIG. 33

FIGS. 33-34. *Glicicola porcelli*: 33. Hypopharyngeal complex (C—lateral process of the lateral lobe of anterior plate strongly dentated. D—middle filament. F—sitophore filament, H—sitophore. 34. Labium (Same lettering as in Fig. 5).

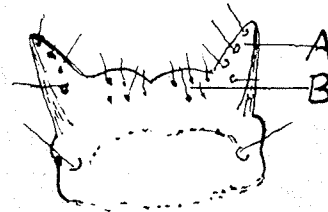


FIG. 34

In Psocoptera, the ovoidal sclerites are quite away from the sitophore. In Ischnocera, they have come forward and in *M. gallinae* much more forward. In the other amblycerans studied the ovoidal sclerites are reduced, leaving only their filaments and apodemes. The sitophore is cup-shaped in Psocoptera, Ischnocera and *M. gallinae* of Amblycera and plate like in the other amblycerans. The pestle is well developed and functioning in Psocoptera and this structure has been retained in Ischnocera and *M. gallinae* though whether it serves the same purpose is doubtful. In the other amblycerans, it has disappeared correlated to the reduction of the sitophore to a plate like structure. This leads one to the view that Ischnocera is more related to Psocoptera than Amblycera and hence more primitive as against the common belief that Amblycera is more primitive mainly based on their possession of jointed maxillary palps and the mouth parts not having shifted backwards as in Ischnocera, considering these as generalised characters. *M. gallinae* (and probably some other species of Amblycera) has ischnoceran and amblyceran characters in the mouth parts and may be regarded as intermediary form between the two sub-orders. The mouth parts of Ischnocera and their gradual evolution in Amblycera is clear in the studies made here. The anterior plate (part of the hypopharynx) shows a gradual development of filamentous teeth and denticles, more suitable for piercing than biting. The species studied are arranged serially to demonstrate this—the extreme being *Glicicola porcelli* in which strong teeth are seen on the lateral process of the lateral lobe. Probably this leads on to a modification to a piercing type of mouth parts. Clay (1948) states that *Trochiloectes* (Amblycera—Ricinidae) has a piercing type of mouth parts and this consists of “three closely associated stylet like structures almost certainly of hypopharyngeal origin, which are joined by a common membrane, only their distal tips being free”. This leads support to the above hypothesis.

The labium has practically generalised features in Ischnocera and Amblycera. The galea and lacinia are present in all the species of Ischnocera studied. The homology of the anterior plate of Ischnocera with the dentated modified structure in a corresponding position in Amblycera, is also clear from a topographical and anatomical point of view.

Our thanks are due to Dr. R. D. Nanjiah, the then Director of Instruction (Vety.) and to Dr. P. N. Kamalapur, Professor of Medicine, University of Agricultural Sciences, Bangalore, for kind facilities afforded for this work.

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