The evolution and host-relationships of the sucking lice of the Ferungulata.

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(With 149 figures in the text.)

CONTENTS.

I. INTRODUCTION.

This paper is a survey and analysis of the spiracle structure and main generic characters of the great majority of sucking lice infesting members of the Ferungulata, Simpson (1945). It has been shown elsewhere (Webb, 1946, 1947 and 1948) that the form of the sculpturing on the atrial wall of spiracles in Siphunculata may be used as an indication of intergeneric affinity. In those papers mentioned above, however, no attempt was made to explore the range of variation in atrial sculpturing to be found within any one genus of lice, and hence it could not be estimated to what extent this character might be used as a guide to relationships between species. From those studies of spiracle structure already published, it is clear that the evolution of the sucking lice has followed that of their hosts extraordinarily closely and, thus, determination of affinity between these parasites affords an important source of evidence of the evolution of the Eutheria themselves. Perhaps that group of lice most in need of careful study is those infesting the Ferungulata, for it is here that the relationship between spiracle structure, on the one hand, and the distribution of the parasites on the hosts, on the other, appears to be anomalous. A large number of the Ferungulata, in particular certain groups of the Artiodactyla and Perissodactyla, are infested with lice of more than one genus and, furthermore, two of these genera, namely *Linognathus* and *Haematopinus*, are found on hosts of comparatively widely separated origin. It is, therefore, only by considering the intrageneric relationships of the lice of these two groups of mammals that there lies any hope of solution to the problem of their apparently discontinuous distribution.

The writer has been fortunate in securing the loan of specimens of almost all the known species of sucking lice from Ferungulata, and for this he is indebted to Mr. G. H. E. Hopkins, lately Senior Entomologist (Medical), Uganda Protectorate; Miss Theresa Clay, British Museum (Natural History); Dr. F. L. Werneck, Instituto Oswaldo Cruz, Rio de Janeiro; Dr. C. F. W. Muesebeck, U.S. Department of Agriculture; and Mr. O. G. Babcock, Texas, U.S.A. Those few species which have not been considered here are, for the most part, typical of the genera to which they belong, and it is unlikely, therefore, that when they come to be studied, it will be found that they are at variance with the general findings given in the discussion on host relationships.

The majority of species examined in this paper belong to genera of which the spiracles of at least one species has been fully described elsewhere (Webb, 1946). In such cases the description of the spiracles is restricted to a brief comparison. Where species belong to genera of which no adequate description of spiracles has previously been published, a full account of the spiracle structure is given.

The detailed indications of the hosts of the sucking lice given below have been taken, almost without exception, from Mr. G. H. E. Hopkins' "Host-associations of the lice of mammals", and permission to quote from this unpublished work is gratefully acknowledged.

II. List of the Species of Siphunculata examined.

Linognathus pedalis (Osborn).
Linognathus stenopsis (Burmeister).
Linognathus africanus Kellogg and Paine.
Linognathus gazella Mjöberg.
Linognathus breviceps (Piaget).
Linognathus angulatus (Piaget).
Linognathus aepycerus Bedford.
Linognathus tibialis (Piaget).
Linognathus pithodes Cummings.
Linognathus lewisi Bedford.
Linognathus gnu Bedford.
Linognathus damaliscus Bedford.
Linognathus fahrenholzi Paine.
Linognathus hippotragi Ferris.
Linognathus setosus (Olfers).
Linognathus ovillus (Neumann).
Linognathus vituli (Linnaeus).
Linognathus taurotragus Bedford.
Linognathus fractus Ferris.
Linognathus limnotragi Cummings.
Linognathus brevicornis (Giebel).
Solenopotes binipilosus (Fahrenholz).
Solenopotes burmeisteri (Fahrenholz).
Solenopotes capillatus Enderlein.
Ratemia squamulata (Neumann).
Haematopinus asini asini (Linnaeus).
Haematopinus asini minor Fahrenholz.
Haematopinus asini macrocephalus (Burmeister).
Haematopinus asini burchelli Webb.
Haematopinus acuticeps Ferris.
Haematopinus eurysternus (Nitzsch).
Haematopinus bufali (de Geer).
Haematopinus tuberculatus (Burmeister).
Haematopinus taurotragi Cummings.
Haematopinus suis (Linnaeus).
Haematopinus aperis Ferris.
Haematopinus latus Neumann.
Haematopinus phacochoeri Enderlein.
Microthoracius cameli (Linnaeus).
Microthoracius mazzai Werneck.
Microthoracius praelongiceps (Neumann).
Pecaroecus javalii Babcock and Ewing.

III. Spiracle Structure in the Genus *Linognathus* Enderlein.

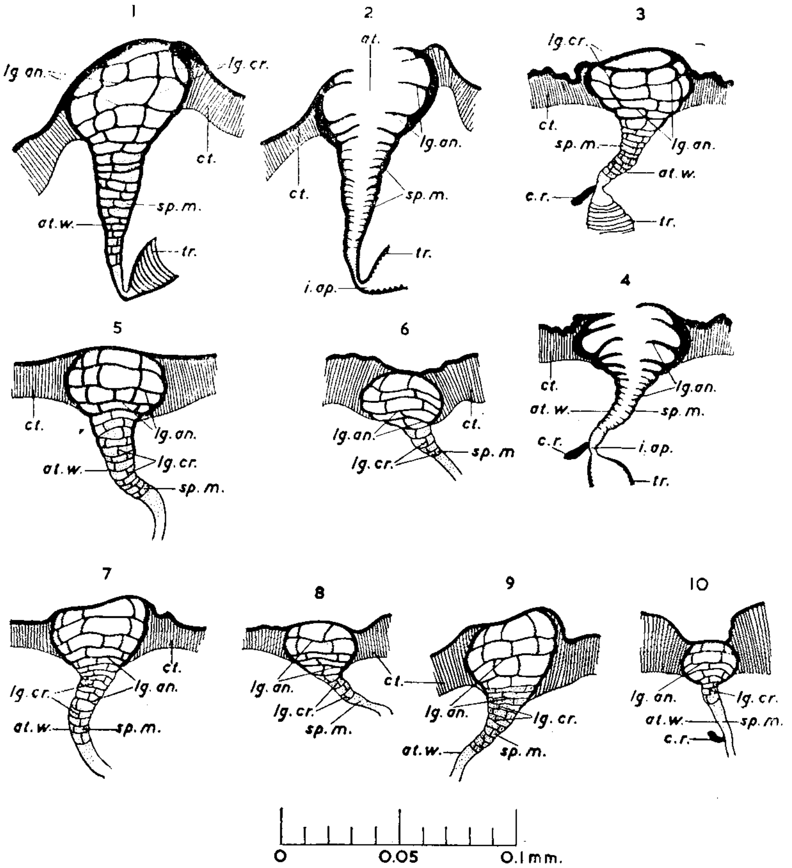
The genus *Linognathus* is one of the largest and best defined in the suborder. The species chiefly infest members of the Bovidae and Giraffidae of the Artiodactyla, though species are also found on members, both wild and domesticated, of the Canidae of the Carnivora.

Linognathus pedalis (Osborn).

Spiracles very similar to those of *Linognathus vituli* (see Webb, 1946, figs. 157–164), except that in the thoracic spiracle the ledges (figs. 1 and 2, *lg.an.* and *lg.cr.*) are more regularly arranged and the atrium (*at.*) is distinctly larger than that of the abdominal spiracle (figs. 3 and 4).

As a particularly rich supply of material containing all immature stages of this louse was available, the opportunity is taken to figure the spiracles of the nymphs (figs. 5–10). Unlike the immature stages of lice of the genus *Haematopinus* (see Webb, 1948), the spiracles of the nymphs of *L. pedalis* are similar to those of the adult in all respects except size. In *Haematopinus asini burchelli* and *H. eurysternus* it was shown that the atrial sculpturing of the spiracle developed with each instar through a series of stages recapitulating types of spiracle found in various more primitive lice. It will be noticed, too, that the arrangement of the ledges in any one spiracle of *Linognathus pedalis* remains

Figures 1–10.



The spiracles of *Linognathus pedalis* (Osborn).

Figs. 1 and 2.—Surface view and optical longitudinal section through the thoracic spiracle of the adult. Figs. 3 and 4.—Surface view and optical longitudinal section through the abdominal spiracle of the adult. Figs. 5 and 6.—Surface views of the thoracic and abdominal spiracles, respectively, of the 3rd nymph. Figs. 7 and 8.—Surface views of the thoracic and abdominal spiracles respectively, of the 2nd nymph. Figs. 9 and 10.—Surface views of the thoracic and abdominal spiracles, respectively, of the 1st nymph.

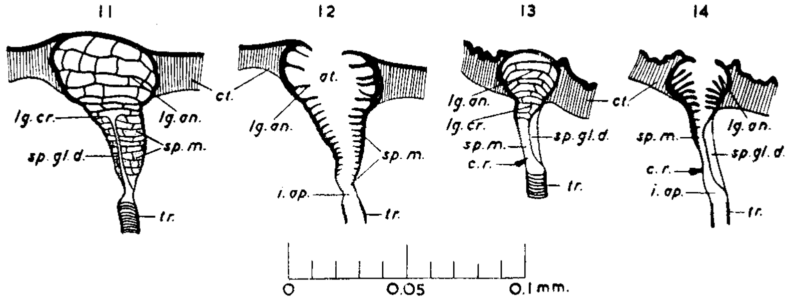
at., atrium ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.m.*, minute spines ; *tr.*, trachea.

almost unchanged from one instar to the next. The spiracles of the 2nd and 3rd nymphs (figs. 5–8) were figured from a recently moulted 3rd nymph and its exuvium.

Host.—*Ovis aries* (domestic sheep) recorded from the legs.

LINOGNATHUS STENOPSIS (Burmeister).

Figures 11–14.



The spiracles of *Linognathus stenopsis* (Burmeister).

Figs. 11 and 12.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 13 and 14.—Surface view and optical longitudinal section through the abdominal spiracle.

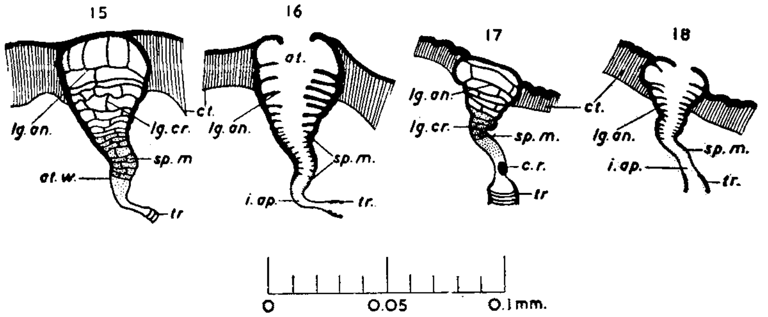
at., atrium ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.gl.d.*, duct of the spiracular gland ; *sp.m.*, minute spines ; *tr.*, trachea.

Spiracles very similar to those of *Linognathus pedalis* except that they are rather smaller, being equivalent in size to those of the 3rd nymph of that species (see figs. 5 and 11).

Host.—*Capra hircus* (domestic goat).

LINOGNATHUS AFRICANUS Kellogg and Paine.

Figures 15–18.



The spiracles of *Linognathus africanus* Kellogg and Paine.

Figs. 15 and 16.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 17 and 18.—Surface view and optical longitudinal section through the abdominal spiracle.

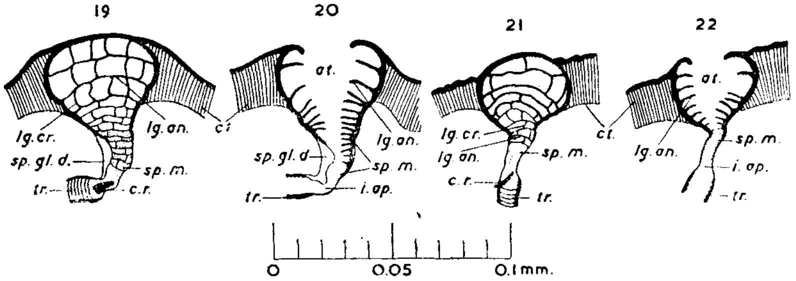
at., atrium ; *at.w.*, atrial wall ; *c.r.* chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.m.*, minute spines ; *tr.*, trachea.

Spiracles almost indistinguishable from those of *Linognathus stenopsis* except, perhaps, that the thoracic spiracle is slightly less broad in the distal region (see figs. 11 and 15).

Hosts.—*Capra hircus* (domestic goat) and *Ovis longipes* (long-legged sheep).

LINOGNATHUS GAZELLA Mjöberg.

Figures 19–22.



The spiracles of *Linognathus gazella* Mjöberg.

Figs. 19 and 20.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 21 and 22.—Surface view and optical longitudinal section through the abdominal spiracle.

at., atrium ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.gl.d.*, duct of the spiracular gland ; *sp.m.*, minute spines ; *tr.*, trachea.

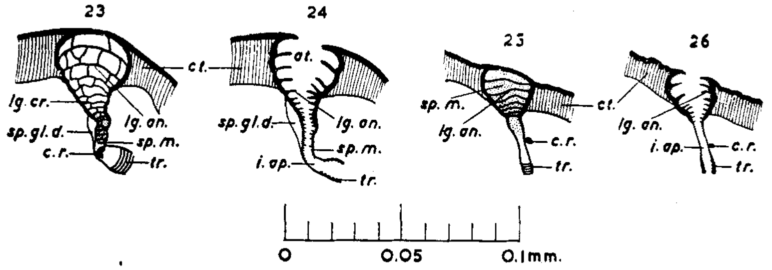
Spiracles very similar to those of *Linognathus stenopsis* except that the abdominal spiracles, in particular, are larger in size (see figs. 13 and 21).

Hosts.—*Philantomba caerulea* (blue duiker) and *Sylvicapra grimmi* (common duiker), and *Cephalophus natalensis* (South African red duiker).

LINOGNATHUS BREVICEPS (Piaget).

Thoracic spiracles (figs. 23 and 24) very similar to those of the three preceding species though rather smaller in size. The abdominal spiracles (figs. 25 and 26),

Figures 23–26.



The spiracles of *Linognathus breviceps* (Piaget).

Figs. 23 and 24.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 25 and 26.—Surface view and optical longitudinal section through the abdominal spiracle.

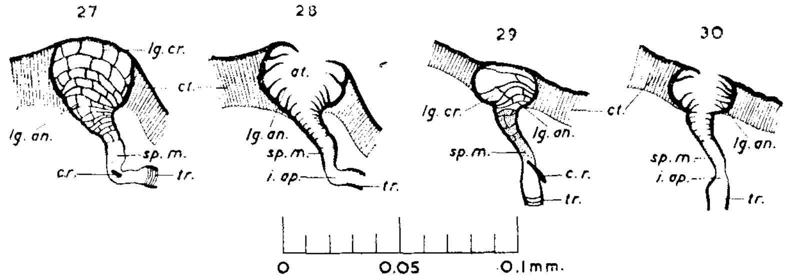
at., atrium ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.gl.d.*, duct of spiracular gland ; *sp.m.*, minute spines ; *tr.*, trachea.

on the other hand, are peculiar in so far as cross-ledges are almost entirely absent and the atrial wall between the annular ledges (*lg.an.*) is covered throughout with minute spines (*sp.m.*) such as are normally found only in the proximal region of the atrium in this genus.

Host.—Philantomba maxwelli (Maxwell's duiker).

LINOGNATHUS ANGULATUS (Piaget).

Figures 27–30.



The spiracles of *Linognathus angulatus* (Piaget).

Figs. 27 and 28.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 29 and 30.—Surface view and optical longitudinal section through the abdominal spiracle.

at., atrium ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.m.*, minute spines ; *tr.*, trachea.

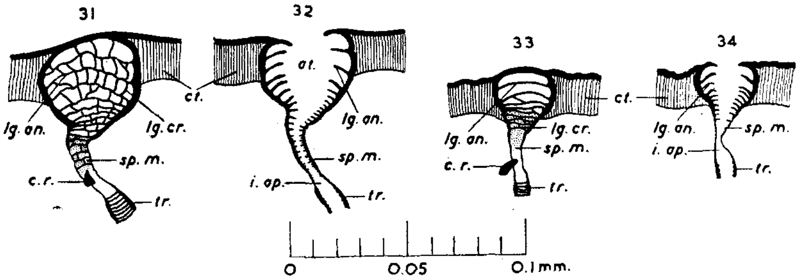
Spiracles resembling those of *Linognathus gazella* (see figs. 19–22 and 27–30) except that they are distinctly smaller in size with cross-ledges (*lg.cr.*) less numerous in the abdominal spiracle.

Host.—Cephalophus nigrifrons (black-fronted duiker).

LINOGNATHUS AEPYCERUS Bedford.

Spiracles very similar to those of *Linognathus angulatus* (see figs. 27–30 and 31–34), but with more numerous cross-ledges (*lg.cr.*) in the thoracic spiracle.

Figures 31–34.



The spiracles of *Linognathus aepycerus* Bedford

Figs. 31 and 32.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 33 and 34.—Surface view and optical longitudinal section through the abdominal spiracle.

at., atrium ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.m.*, minute spines ; *tr.*, trachea.

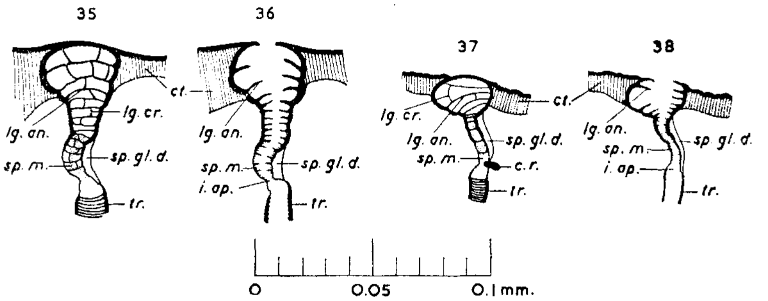
In the abdominal spiracle (see fig. 33) there are still fewer cross-ledges, some of the annular ledges (*lg.an.*) remaining unjoined.

Host.—Aepyceros melampus (the mpala).

LINOGNATHUS TIBIALIS (Piaget).

Spiracles near those of *Linognathus angulatus* (see figs. 27–30 and 35–38) except that they are slightly smaller in size and possess fewer cross-ledges (*lg.cr.*).

Figures 35–38.



The spiracles of *Linognathus tibialis* (Piaget).

Figs. 35 and 36.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 37 and 38.—Surface view and optical longitudinal section through the abdominal spiracle.

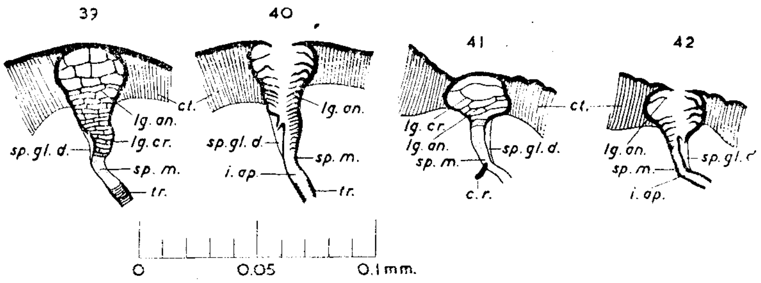
c.r., chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.m.*, minute spines ; *tr.*, trachea.

Hosts.—*Gazella subgutturosa* (Persian gazelle), *Gazella dama* (the mhorr) and possibly other *Gazella* spp., *Antidorcas marsupialis* (springbok).

LINOGNATHUS PITHODES Cummings.

Spiracles almost identical with those of *Linognathus tibialis* (see figs. 35–38 and 39–42), but with cross-ledges (*lg.cr.*) occurring rather more frequently and, in the abdominal spiracle, annular ledges (*lg.an.*) largely absent in the proximal region.

Figures 39–42.



The spiracles of *Linognathus pithodes* Cummings.

Figs. 39 and 40.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 41 and 42.—Surface view and optical longitudinal section through the abdominal spiracle.

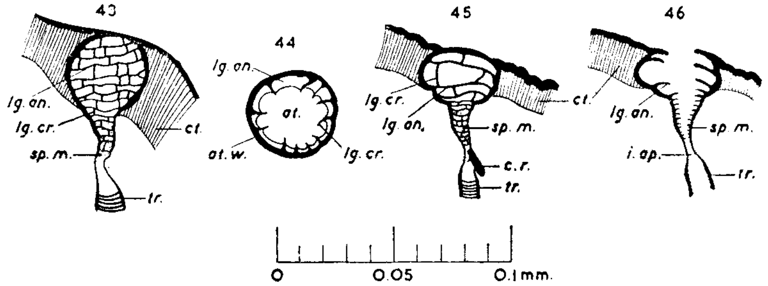
c.r., chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.gl.d.*, duct of the spiracular gland ; *sp.m.*, minute spines ; *tr.*, trachea.

Host.—*Antilope cervicapra* (blackbuck).

LINOGNATHUS LEWISI Bedford.

Spiracles close to those of *Linognathus tibialis* (see figs. 35–38 and 43–46) except that the cross-ledges (*lg.cr.*) occur more frequently, the abdominal spiracles are larger and, in the thoracic spiracle, there is a tendency for the points of junction of the annular (*lg.an.*) and cross-ledges (*lg.cr.*) to persist while the intermediate portions of the ledges are slightly reduced (see fig. 44). This results in the formation of filamentous processes projecting into the atrium (*at.*).

Figures 43–46.



The spiracles of *Linognathus lewisi* Bedford.

Figs. 43 and 44.—Surface view and optical transverse section through the distal region of the atrium of the thoracic spiracle. Figs. 45 and 46.—Surface view and optical longitudinal section through the abdominal spiracle.

at., atrium ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.m.*, minute spines ; *tr.*, trachea.

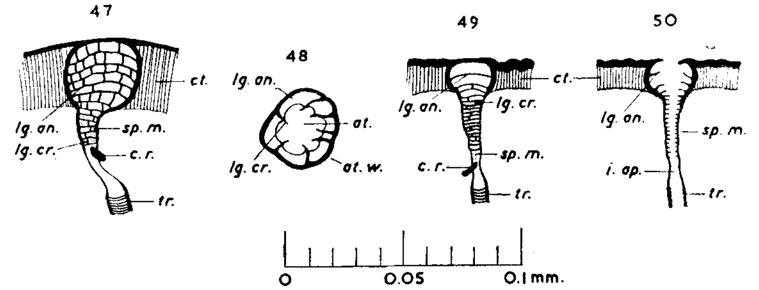
A condition approximating to this will be seen in spiracles of lice of the genera *Ratemia* (figs. 89–96), *Microthoracius* (figs. 109–116) and *Pecaroecus* (figs. 131–145).

Host.—*Gazella thomsonii* (Thomson's gazelle).

Linognathus gnu Bedford.

Spiracles similar to those of *Linognathus lewisi* (see figs. 43–46 and 47–50) except that the abdominal spiracle is considerably smaller with fewer cross-ledges (*lg.cr.*), particularly in the distal region of the atrium where some of the annular ledges (*lg.an.*) remain unjoined.

Figures 47–50.



The spiracles of *Linognathus gnu* Bedford.

Figs. 47 and 48.—Surface view and optical transverse section through the distal region of the atrium of the thoracic spiracle. Figs. 49 and 50.—Surface view and optical longitudinal section through the abdominal spiracle.

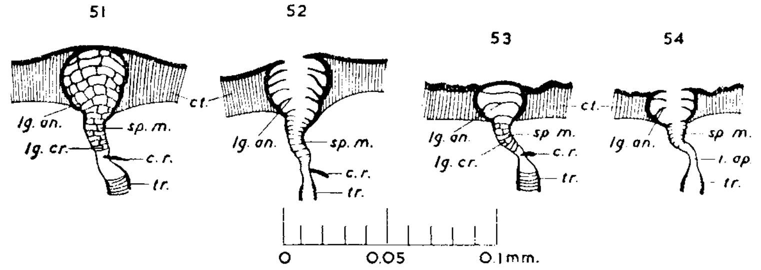
at., atrium ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.m.*, minute spines ; *tr.*, trachea.

Hosts.—*Connochaetes gnu* (white tailed gnu) and *Gorgon taurinus* (brindled gnu).

Linognathus damaliscus Bedford.

Spiracles similar to those of *Linognathus gnu* (see figs. 47–50 and 51–54) except that the intermediate portions of the annular (*lg.an.*) and cross-ledges (*lg.cr.*) are not reduced and in the abdominal spiracle cross-ledges are even fewer in number.

Figures 51–54.



The spiracles of *Linognathus damaliscus* Bedford.

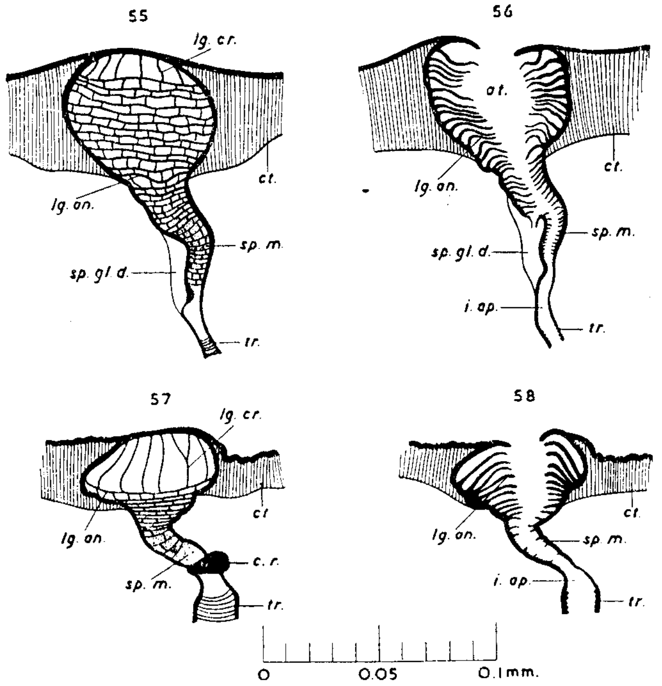
Figs. 51 and 52.—Surface view and optical longitudinal section through the thoracic spiracles. Figs. 53 and 54.—Surface view and optical longitudinal section through the abdominal spiracle.

c.r., chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.m.*, minute spines ; *tr.*, trachea.

Hosts.—Damaliscus pygargus (bontebok and blesbok) and *D. korrigum* (the korrigum).

Linognathus fahrenholzi Paine.

Figures 55–58.



The spiracles of *Linognathus fahrenholzi* Paine.

Figs. 55 and 56.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 57 and 58.—Surface view and optical longitudinal section through the abdominal spiracle.

at., atrium ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.gl.d.*, duct of the spiracular gland ; *sp.m.*, minute spines ; *tr.*, trachea.

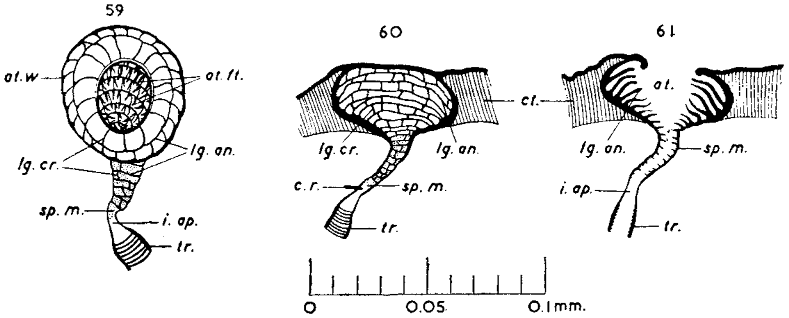
Spiracles large in size (figs. 55–58), inferior only to those of *Linognathus setosus* (see Webb, 1946, figs. 165–174) and *L. ovillus* (see figs. 62–65), and with very numerous, broad annular (*lg.an.*) and cross-ledges (*lg.cr.*). The abdominal spiracles are very broad and compressed in the distal region with annular ledges arising close together from the atrial wall. These spiracles, although conforming in general structure to those of other species of the genus, do not appear to be referable to any type previously described.

Hosts.—***Redunca arundinum*** (reedbuck), ***R. redunca*** (bohor reedbuck) and ***R. fulvorufula*** (mountain reedbuck).

LINOGNATHUS HIPPOTRAGI Ferris.

Spiracles resembling in general form those of *Linognathus fahrenholzi* (see figs. 55–58 and 59–61) though slightly smaller in size. In the thoracic spiracle (fig. 59), however, the intermediate portions of the annular (*lg.an.*) and cross-ledges (*lg.cr.*) have disappeared, leaving the points of junction of the ledges as rows of filaments projecting into the atrium (*at.ft.*). This condition is seen elsewhere in the genus in *Linognathus lewisi* (fig. 44) and *L. fractus* (fig. 70). The abdominal spiracles differ from those of *L. fahrenholzi* chiefly in the shorter distance between the external aperture of the atrium and the most distal annular ledge. Here the ledges are entire.

Figures 59–61.



The spiracles of *Linognathus hippotragi* Ferris.

Fig. 59.—Surface view of the thoracic spiracle showing the internal sculpturing of the atrial wall seen through the external aperture. Figs. 60 and 61.—Surface view and optical longitudinal section through the abdominal spiracle.

at., atrium ; *at.ft.*, filaments projecting from the atrial wall ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.m.*, minute spines ; *tr.*, trachea.

Host.—*Hippotragus niger* (sable antelope).

LINOGNATHUS SETOSUS (Olfers).

Spiracles previously described in detail elsewhere (Webb, 1946, figs. 165–174). Although conforming in general structure to those found in other species of the genus, these spiracles are aberrant in respect to their very large size, the comparatively narrow width of the ledges and the frequency with which cross-ledges occur.

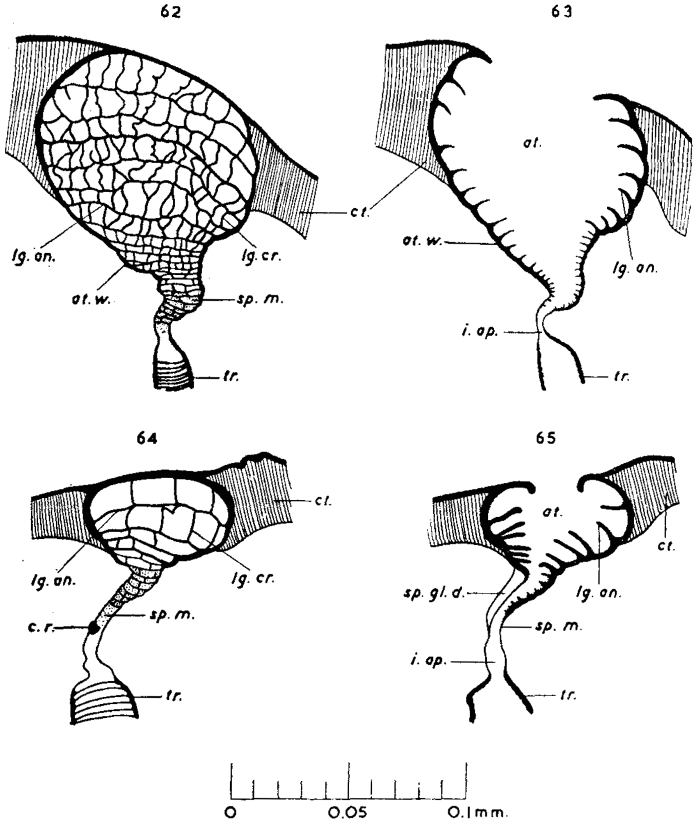
Hosts.—*Canis familiaris* (domestic dog), *C. lupus* (wolf), *C. latrans* (coyote), *C. aureus* (common jackal), *C. mesomelas* (black-backed jackal), *Alopex lagopus* (arctic fox) and *Vulpes vulpes* (common fox).

A closely-related form, *Linognathus taeniotrichus* Werneck, which has not been seen by the writer, is recorded from *Dusicyon fulvipes* and *D. thous* (brazilian dog).

Linognathus ovillus (Neumann).

Spiracles very similar to those of *Linognathus setosus* (compare figs. 62–65, and Webb, 1946, figs. 165–174). The thoracic spiracles are as large as those of *L. setosus* and the abdominal spiracles only slightly smaller than those of that species, although the ledges are, in general, broader. *L. ovillus* and *L. setosus* appear to stand apart from the remainder of the genus with regard to the form of the spiracle.

Figures 62–65.



The spiracles of *Linognathus ovillus* (Neumann).

Figs. 62 and 63.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 64 and 65.—Surface view and optical longitudinal section through the abdominal spiracle.

at., atrium ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.gl.d.*, duct of the spiracular gland ; *sp.m.*, minute spines ; *tr.*, trachea.

Host.—*Ovis aries* (domestic sheep) recorded chiefly from the face.

Linognathus vituli (Linnaeus).

Spiracles previously described in detail elsewhere (Webb, 1946, figs. 157–164). Here the spiracles are characterized by a trumpet-shaped atrium with broad ledges and comparatively little difference in size or structure between the thoracic and abdominal forms.

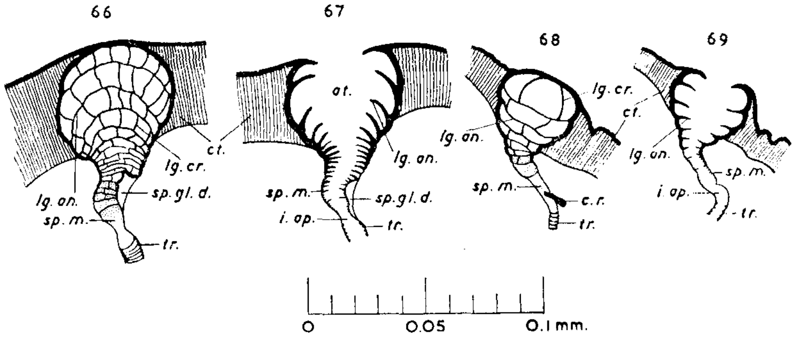
Host.—Bos taurus (domestic ox).

Linognathus taurotragus Bedford.

Spiracles very similar to those of *Linognathus vituli* (compare figs. 66–69 and Webb, 1946, figs. 157–164), except that the atrium in the thoracic spiracle is possibly slightly shorter in length and that there is a greater disparity in size between the thoracic and abdominal spiracles.

Host.—Taurotragus oryx (eland).

Figures 66-69



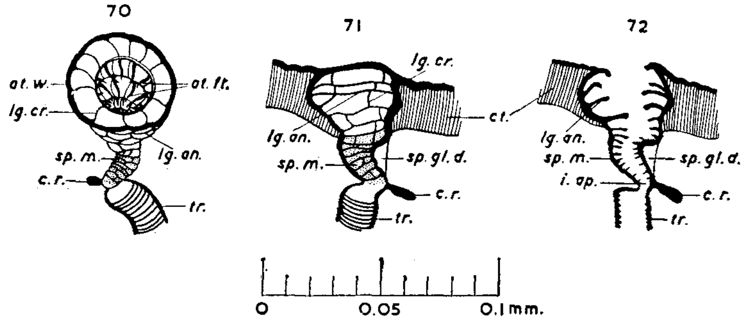
The spiracles of *Linognathus taurotragus* Bedford.

Figs. 66 and 67.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 68 and 69.—Surface view and optical longitudinal section through the abdominal spiracle.

at., atrium ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.gl.d.*, duct of the spiracular gland ; *sp.m.*, minute spines ; *tr.*, trachea.

Linognathus fractus Ferris.

Figures 70–72



The spiracles of *Linognathus fractus* Ferris.

Fig. 70.—Surface view of the thoracic spiracle showing the internal sculpturing of the atrial wall seen through the external aperture. Figs. 71 and 72.—Surface view and optical longitudinal section through the abdominal spiracle.

at.ft., filaments projecting from the atrial wall ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.gl.d.*, duct of the spiracular gland ; *sp.m.*, minute spines ; *tr.*, trachea.

Spiracles very close to those of *Linognathus taurotragus* and *L. limnotragi* (see figs. 66–69, 70–72 and 73–76), with the exception that, in the distal region of the thoracic spiracle (fig. 70), the intermediate portions of the ledges have, for the most part, disappeared, leaving the regions of junction of the annular (*lg.an.*) and cross-ledges (*lg.cr.*) projecting into the atrium as filamentous processes (*at.ft.*). A condition similar to this is found in *Linognathus lewisi* (fig. 44), *L. gnu* (fig. 48) and *L. hippotragi* (fig. 59), and also in lice of the genera *Ratemia* (figs. 89–96), *Microthoracius* (figs. 109–130) and *Pecaroecus* (figs. 131–145). The thoracic and abdominal spiracles are not greatly dissimilar in size.

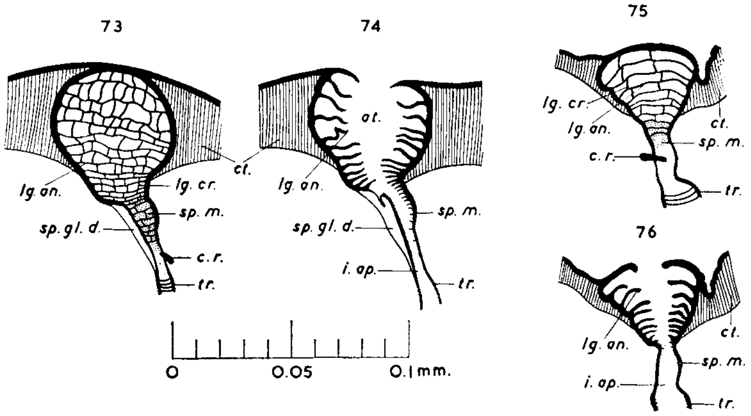
Hosts.—*Strepsiceros scriptus* (bushbuck) and *S. spekii* (situtunga).

LINOGNATHUS LIMNOTRAGI Cummings.

Spiracles near those of *Linognathus taurotragus* (see figs. 66–69 and 73–76), but more distinct from those of *L. vituli*. There is a tendency for the cross-ledges (*lg.cr.*) to be more numerous than in the previous species and for the proximal region of the abdominal spiracle to be shorter. Here again, the difference in size between the thoracic and abdominal spiracles is not great.

Hosts.—*Strepsiceros scriptus* (bushbuck) and *S. spekii* (situtunga).

Figures 73–76.



The spiracles of *Linognathus limnotragi* Cummings.

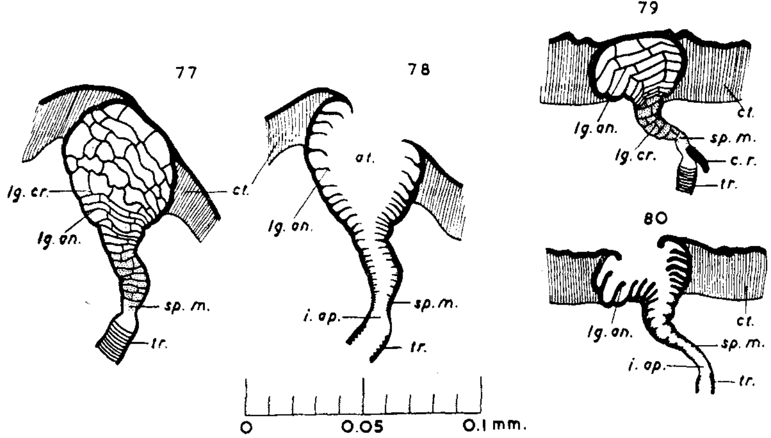
Figs. 73 and 74.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 75 and 76.—Surface and optical longitudinal section through the abdominal spiracle.

at., atrium ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.gl.d.*, duct of the spiracular gland ; *sp.m.*, minute spines ; *tr.*, trachea.

LINOGNATHUS BREVICORNIS (Giebel).

Spiracles most nearly similar to those found in *Linognathus limnotragi* (see figs. 73–76 and 77–80) and in species of the genus *Solenopotes* (see figs. 81–88). In the distal region of the thoracic spiracle (fig. 77) the annular ledges (*lg.an.*) tend to be thrown into folds so that the surface of the atrium appears to be traversed by a series of more or less sinuous lines ; the cross-ledges (*lg.cr*) are irregularly placed. In the abdominal spiracle (figs. 79 and 80) the distal region of the atrium is comparatively broad and the annular ledges (*lg.an.*) tend to be set at an angle to the atrial wall sloping backwards from the centre of the

Figures 77–80.



The spiracles of *Linognathus brevicornis* (Giebel).

Figs. 77 and 78.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 79 and 80.—Surface view and optical longitudinal section through the abdominal spiracle.

at., atrium ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.m.*, minute spines ; *tr.*, trachea.

atrium. Here the cross-ledges (*lg.cr.*) in the distal region of the atrium are more or less regularly arranged in rows one above the other.

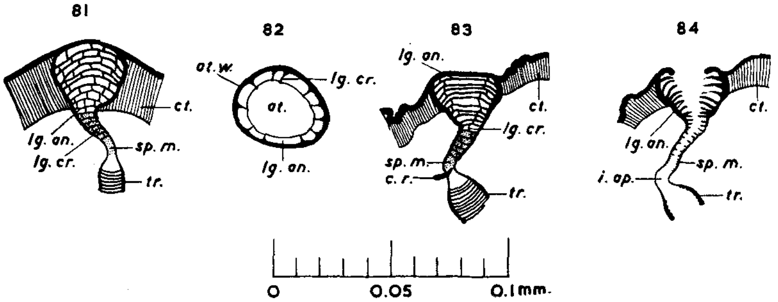
Host.—*Giraffa camelopardalis* (common giraffe).

IV. Spiracle Structure in the Genus *Solenopotes* Enderlein.

The genus *Solenopotes* comprises a small number of species and is evidently closely-related to *Linognathus*. With the exception of *Solenopotes capillatus* recorded only from *Bos taurus*, the species are exclusively parasites of members of the Cervidae (the deer). It was suggested by Ferris (1932), that the true host of *S. capillatus* was in all probability a cervid and that the infestation of domestic cattle with this parasite is secondary.

Solenopotes binipilosus (Fahrenholz).

Figures 81–84.



The spiracles of *Solenopotes binipilosus* (Fahrenholz).

Figs. 81 and 82.—Surface view and optical transverse section through the distal region of the atrium of the thoracic spiracle. Figs. 83 and 84.—Surface view and optical longitudinal section through the abdominal spiracle.

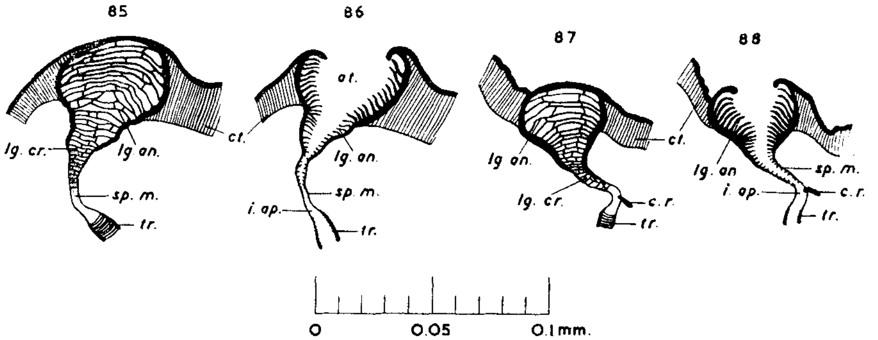
at., atrium ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.m.*, minute spines ; *tr.*, trachea.

Spiracles resembling those of *Linognathus brevicornis* (see figs. 77–80 and 81–84), except that they are considerably smaller in size and the annular ledges in the abdominal spiracle (fig. 83, *lg.an.*) are more numerous.

Hosts.—Mazama spp. (red and grey brocket).

Solenopotes burmeisteri (Fahrenholz).

Figures 85–88.



The spiracles of *Solenopotes burmeisteri* (Fahrenholz).

Figs. 85 and 86.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 87 and 88.—Surface view and optical longitudinal section through the abdominal spiracle.

at., atrium ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.m.*, minute spines ; *tr.*, trachea.

Spiracles very similar to those of *Solenopotes binipilosus* (see figs. 81–84 and 85–88) except that they are larger in size and possess more numerous annular ledges (*lg.an.*).

Host.—Cervus elephas (European red deer).

Solenopotes capillatus Enderlein.

Spiracles previously described in detail elsewhere (Webb, 1946, figs. 175–186). These spiracles are of the same type as those of *Solenopotes binipilosus* (figs. 81–84) and *S. burmeisteri* (figs. 85–88), but the abdominal spiracles in particular are of a more extreme form.

Host.—Bos taurus (domestic ox).

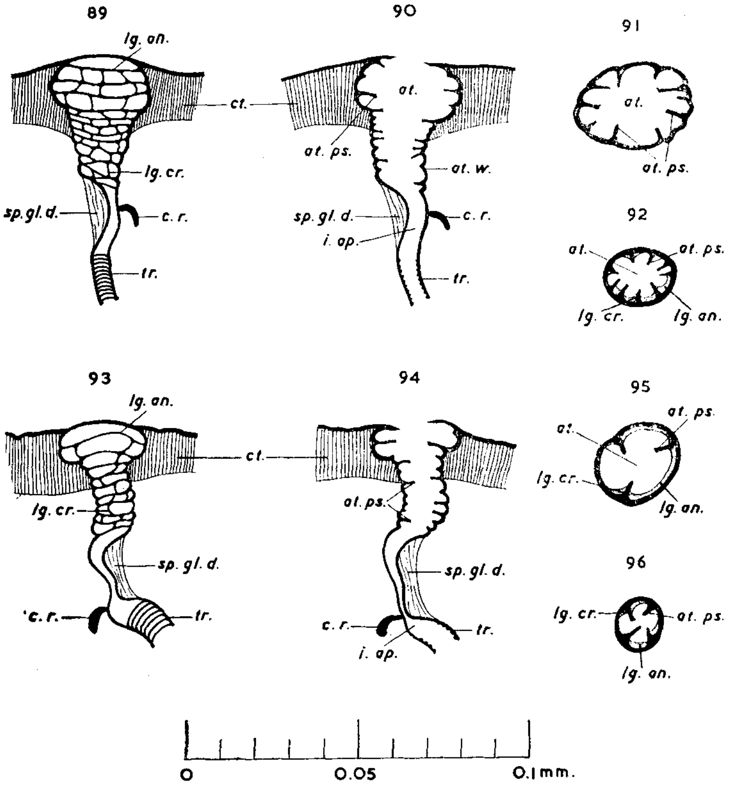
V. Spiracle Structure in the Genus *Ratemia* Fahrenholz.

The genus *Ratemia* comprises the single species *R. squamulata* first described by Neumann (1911) without an indication of the host. This louse was re-discovered by Hopkins (1946), infesting the domestic ass, *Equus* (*Asinus*) *asinus* L. and a wild Burchell's zebra, *Equus* (*Hippotigris*) *burchelli böhmi* Matschie. *R. squamulata* is of particular interest as it provides a genus characteristic of the Perissodactyla.

Ratemia squamulata (Neumann).

The spiracles in *Ratemia squamulata* (see figs. 89–96) are of moderate size with a pear-shaped atrium (*at.*) whose walls (*at.w.*) bear internally a series of annular (*lg.an.*) and cross-ledges (*lg.cr.*), similar in appearance to those found in the spiracles of species of the genera *Linognathus* and *Solenopotes*. The atrial sculpturing in *Ratemia*, however, differs from that in the majority of *Linognathus* species in so far as the ledges themselves are greatly reduced. Here the annular and cross-ledges are represented by low ridges except for their regions of junction which remain as blunt processes projecting into the atrium (*at.ps.*). Sculpturing of this type has already been described in *Linognathus lewisi* (fig. 44), *L. gnu* (fig. 48), *L. hippotragi* (fig. 59) and *L. fractus* (fig. 70). In the spiracles of *Ratemia squamulata*, as in the spiracles of all other Siphunculata yet described, there is a prominent spiracular gland, the chitinous duct (*sp.gl.d.*) of which remains in potash-cleared specimens situated at one side of the atrium, and extending from about one-third to one-half way along the length of the atrial

Figures 89–96.



The spiracles of *Ratemia squamulata* (Neumann).

Figs. 89 and 90.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 91 and 92.—Optical transverse sections, through the distal and proximal regions respectively, of the atrium of the thoracic spiracle. Figs. 93 and 94.—Surface view and optical longitudinal section through the abdominal spiracle. Figs. 95 and 96.—Optical transverse sections, through the distal and proximal regions respectively, of the atrium of the abdominal spiracle.

at., atrium; *at.ps.*, blunt process projecting into the atrium; *at.w.*, atrial wall; *c.r.*, chitinous rod of occlusor mechanism; *ct.*, cuticle; *i.ap.*, internal aperture of the atrium; *lg.an.*, annular ledge; *lg.cr.*, cross-ledge; *sp.gl.d.*, duct of the spiracular gland; *tr.*, trachea.

wall to the trachea (*tr.*). The atrium itself is divided into two regions, firstly, a distal portion in which the walls are sculptured and, secondly, a proximal, narrower portion in which the walls are devoid of sculpturing of any kind. Even the minute spines commonly found in the proximal region of the atrium in the spiracles of *Linognathus* are absent in those of *Ratemia*. It is along the wall of this proximal region of the atrium that the spiracular gland extends. There is a stout chitinous rod (*c.r.*) situated at the proximal end of the atrium which presumably serves for the attachment of the occlusor muscle. The differences between the thoracic and the abdominal spiracles of *R. squamulata* are comparatively slight, being limited to the wider diameter of the atrium in the former and the longer proximal region in the latter.

VI. SPIRACLE STRUCTURE IN THE GENUS *HAEMATOPINUS* LEACH.

The genus *Haematopinus* comprises a number of well-defined species widely distributed over members of the Artiodactyla and Perissodactyla. The spiracles of one species, *Haematopinus eurysternus*, have already been described in detail elsewhere (see Webb, 1946, figs. 189–204).

HAEMATOPINUS ASINI ASINI (Linnaeus).

Figures 97–100.

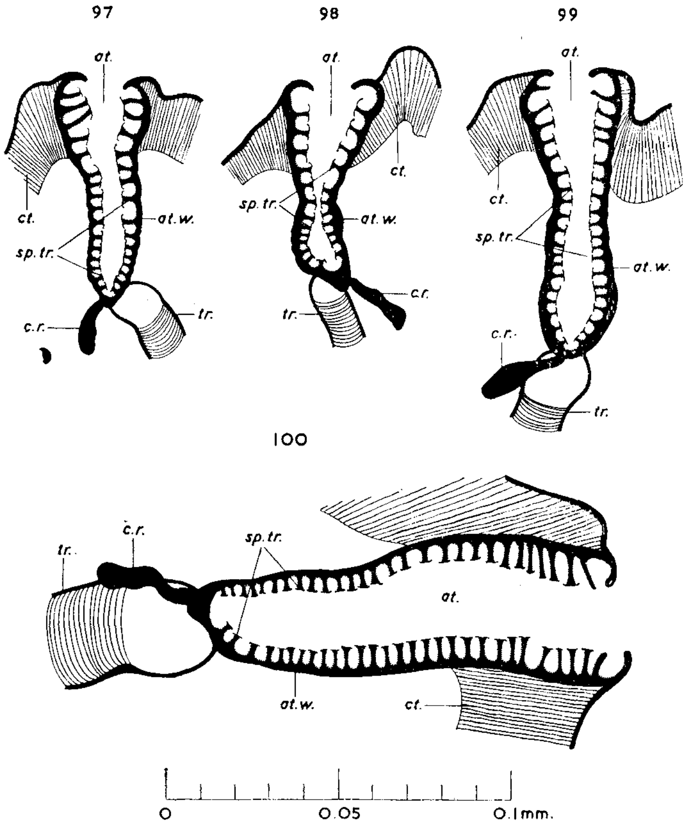


Fig. 97.—*Haematopinus asini asini* (Linnaeus)—optical longitudinal section through the last abdominal spiracle. Fig. 98.—*Haematopinus asini minor* Fahrenholz—optical longitudinal section through the last abdominal spiracle. Fig. 99.—*Haematopinus asini macrocephalus* (Burmeister)—optical longitudinal section through the last abdominal spiracle. Fig. 100.—*Haematopinus acuticeps* Ferris—optical longitudinal section through the last abdominal spiracle.

at., atrium ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *sp.tr.*, truncated atrial spines ; *tr.*, trachea.

The spiracles of *Haematopinus asini asini* (fig. 97) resemble those of *H. eurysternus* (see Webb, 1946, figs. 189–204). The length of the atrium (*at.*) of the last abdominal spiracle in both the ♂ and the ♀ is 66 μ. The atrial spines (*sp.tr.*) are large and greatly expanded at their apices to form mushroom-shaped structures. Traces of annular and cross-ledges persist as ridges on the atrial wall (*at.w.*) connecting the bases of the spines at the proximal end of the atrium in the adult (see Webb, 1948, fig. 14, *lg.an.*; *lg.cr.*).

Host.—*Equus asinus* Linnaeus (domestic ass).

HAEMATOPINUS ASINI MINOR Fahrenholz.

The spiracles of *Haematopinus asini minor* (fig. 98) closely resemble those of *H. asini asini* (see fig. 97) except that they are slightly smaller in size. The length of the atrium (*at.*) of the last abdominal spiracle in both the ♂ and the ♀ is 60 μ. Traces of annular and cross-ledges persist as ridges on the atrial wall (*at.w.*) connecting the bases of the spines at the proximal end of the atrium in the adult (see Webb, 1949, fig. 14, *lg.an.*; *lg.cr.*).

Host.—*Equus burchelli* (Gray) (common zebra).

HAEMATOPINUS ASINI MACROCEPHALUS (Burmeister).

The spiracles of *Haematopinus asini macrocephalus* (fig. 99) closely resemble those of *H. asini asini* (see fig. 97) except that they are larger in size. The length of the atrium (*at.*) of the last abdominal spiracle in the ♂ is 83 μ and, in the ♀, 85 μ. The proportions of the spines (*sp.tr.*), however, are similar to those in the previous subspecies. All traces of annular and cross-ledges have been lost in the adult (see Webb, 1948, figs. 6 and 7).

Host.—*Equus caballus* Linnaeus (horse).

HAEMATOPINUS ASINI BURCHELLI Webb, 1948 *a*.

The spiracles of *Haematopinus asini burchelli* have been described elsewhere (Webb, 1948, figs. 8–15). They resemble those of *H. asini asini* (see fig. 97) except that they are smaller in size. The length of the atrium of the last abdominal spiracle in the ♂ is 56 μ and, in the ♀, 60 μ. The atrial spines are considerably smaller than those of the previous subspecies, but possess greatly expanded apices. Traces of annular and cross-ledges persist at the proximal end of the atrium in the adult.

Host.—*Equus burchelli* (Gray) (common zebra).

HAEMATOPINUS ACUTICEPS Ferris.

The spiracles of *Haematopinus acuticeps* (fig. 100) resemble those of *H. asini asini* (see fig. 97), though they are much larger in size. The length of the atrium (*at.*) of the last abdominal spiracle in the ♀ is 125 μ (the ♂ is unknown). The atrial spines (*sp.tr.*) are of similar proportions to those in *H. asini asini*, but with the apical expansion slightly less accentuated. All traces of annular and cross-ledges have been lost in the adult (see Webb, 1948, figs. 6 and 7).

Host.—*Equus burchelli* (Gray) (common zebra).

HAEMATOPINUS EURYSTERNUS (Nitzsch).

The spiracles of *Haematopinus eurysternus* have been previously described in detail elsewhere (Webb, 1946, figs. 189–204 and 1948, figs. 1–7). The length of the atrium of the last abdominal spiracle in the ♂ is 125 μ and, in the ♀, 126 μ. All traces of annular and cross-ledges have been lost in the adult.

Hosts.—*Bos taurus* Linnaeus (domestic ox) and *B. indicus* Linnaeus (zebu).

HAEMATOPINUS BUFALI (de Geer).

The spiracles of *Haematopinus bufali* (fig. 101) are very similar to those of *H. eurysternus* (see Webb, 1946, figs. 189–204), though they are smaller in size. The length of the atrium (*at.*) of the last abdominal spiracle, both in the ♂ and in the ♀, is 112 μ. All traces of annular and cross-ledges have been lost in the adult (see Webb, 1948, figs. 6 and 7).

Figures 101–102.

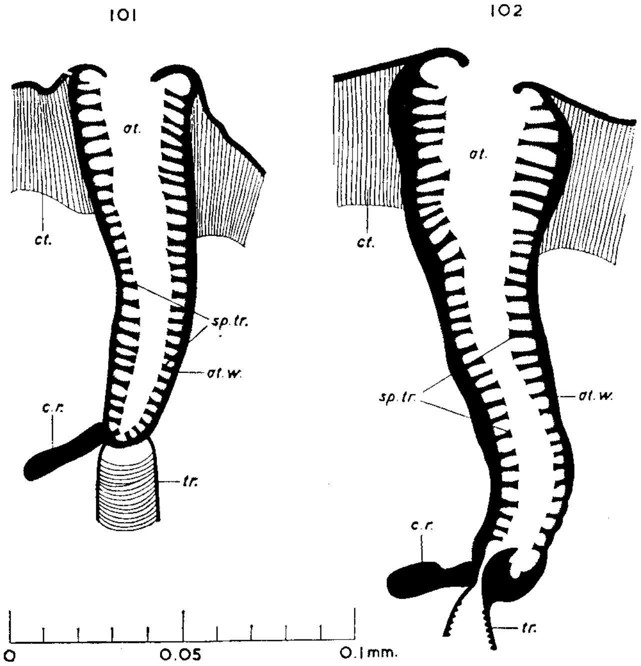


Fig. 101.—*Haematopinus bufali* (de Geer)—optical longitudinal section through the last abdominal spiracle. Fig. 102.—*Haematopinus tuberculatus* (Burmeister)—optical longitudinal section through the last abdominal spiracle.

at., atrium ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *sp.tr.*, truncated atrial spines ; *tr.*, trachea.

Host.—*Syncerus caffer* (Sparman) (African buffalo).

HAEMATOPINUS TUBERCULATUS (Burmeister).

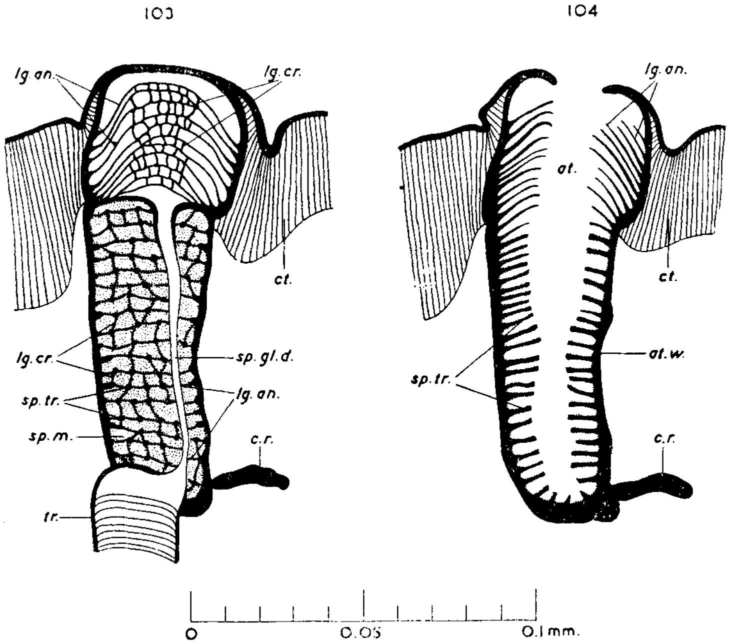
The spiracles of *Haematopinus tuberculatus* (fig. 102) are very similar to those of *H. eurysternus* (see Webb, 1946, figs. 189–204), though they are larger in size. The length of the atrium (*at.*) of the last abdominal spiracle, both in the ♂ and in the ♀, is 160 μ. All traces of annular and cross-ledges have been lost in the adult (see Webb, 1948, figs. 6 and 7.)

Host.—*Bubalus bubalis* (Linnaeus) (Indian buffalo).

HAEMATOPINUS TAUROTRAGI Cummings.

The spiracles of *Haematopinus taurotragi* (figs. 103 and 104) are clearly related to those of *H. eurysternus* (see Webb, 1946, figs. 189–204), but are significantly different in form. The atrial wall of the distal third of the abdominal spiracle bears a series of broad annular (*lg.an.*) and cross-ledges (*lg.cr.*) forming a honeycomb of forwardly directed chitinous cells (see fig. 103). Here, in this distal region, the atrial wall is devoid of the characteristic minute spines found in the spiracles of all other species of the genus. In the proximal region of the spiracle, however, both the large truncated spines (*sp.tr.*) and the armature of minute spines (*sp.m.*) are present on the atrial wall (see fig. 104). Traces of ledges are seen in the proximal region as thickenings of the atrial wall linking adjacent spines (see fig. 103, *lg.an.* ; *lg.cr.*). The length of the atrium (*at.*) of the last abdominal spiracle in the ♂ is 125 μ and, in the ♀, 127 μ.

Figures 103–104.



The spiracles of *Haematopinus taurotragi* Cummings.

Figs. 103 and 104.—Surface view and optical longitudinal section through the last abdominal spiracle.

at., atrium ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.gl.d.*, duct of the spiracular gland ; *sp.m.*, minute spines ; *sp.tr.*, truncated atrial spines ; *tr.*, trachea.

Hosts.—*Taurotragus oryx* (Pallas) (eland) and *Strepsiceros strepsiceros* (Pallas) (greater kudu).

HAEMATOPINUS SUIS (Linnaeus).

The spiracles of *Haematopinus suis* (fig. 105) are very similar to those of *H. eurysternus* (see Webb, 1946, figs. 189–204), but slightly smaller in size. The length of the atrium (*at.*) of the last abdominal spiracle in the ♂ is 110 μ and, in the ♀, 114 μ. All traces of annular and cross-ledges have been lost in the adult (see Webb, 1948, figs. 6 and 7).

Hosts.—*Sus* sp. (European domestic pig), *Sus cristata* Wagner (Indian wild boar) and *Sus vittatus* Müller and Schlegel (Malayan banded pig).

Figures 105–106.

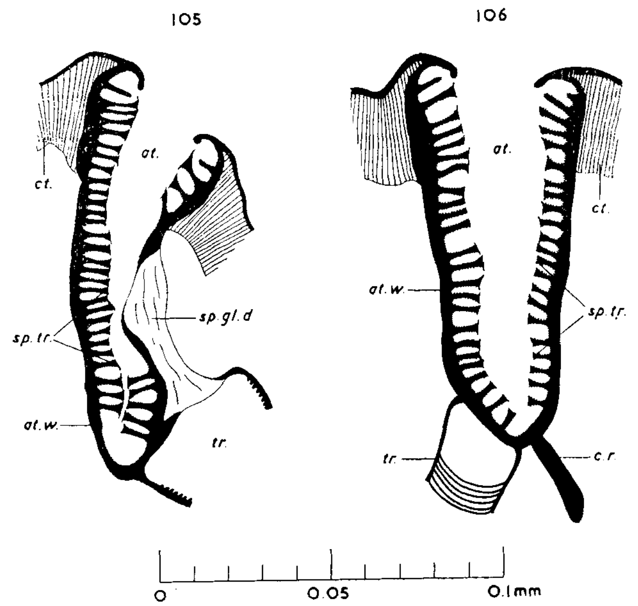


Fig. 105.—*Haematopinus suis* (Linnaeus)—optical longitudinal section through the abdominal spiracle. Fig. 106.—*Haematopinus aperis* Ferris—optical longitudinal section through the abdominal spiracle.

at., atrium; *at.w.*, atrial wall; *c.r.*, chitinous rod of occlusor mechanism; *ct.*, cuticle; *sp.gl.d.*, duct of the spiracular gland; *sp.tr.*, truncated atrial spines; *tr.*, trachea.

HAEMATOPINUS APERIS Ferris.*

The spiracles of *Haematopinus aperis* (fig. 106) are almost identical with those of *H. suis* (see fig. 105) except that they are slightly larger in size. The differences in size involved, however, are so small that they are of doubtful significance. The length of the atrium (*at.*) of the last abdominal spiracle, both in the ♂ and in the ♀, is 118 μ. All traces of annular and cross-ledges have been lost in the adult (see Webb, 1948, figs. 6 and 7).

Host.—*Sus scrofa* Linnaeus (European wild boar).

HAEMATOPINUS LATUS Neumann.

The spiracles of *Haematopinus latus* (fig. 107) are very similar to those of *H. eurysternus* (see Webb, 1946, figs. 189–204) except that they are larger in size and the apical expansions of the truncated spines (*sp.tr.*) tend to be less accentuated. The length of the atrium (*at.*) of the last abdominal spiracle in the ♂ is 139 μ and, in the ♀, 140 μ. All traces of annular and cross-ledges have been lost in the adult (see Webb, 1948, figs. 6 and 7).

Host.—*Potamochoerus porcus* (Linnaeus) (red river-hog).

HAEMATOPINUS PHACOCHOERI Enderlein.

The spiracles of *Haematopinus phacochoeri* (fig. 108) are very similar to those of *H. latus* (see fig. 107) except that the apical expansions of the truncated spines (*sp.tr.*) tend to be even less accentuated. The length of the atrium (*at.*) of the

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* Dr. F. L. Werneck has kindly informed me that the species of *Haematopinus* recorded from *Sus scrofa* should be *H. apri* Goureau, this name having priority over *H. aperis* Ferris.

Figures 107–108

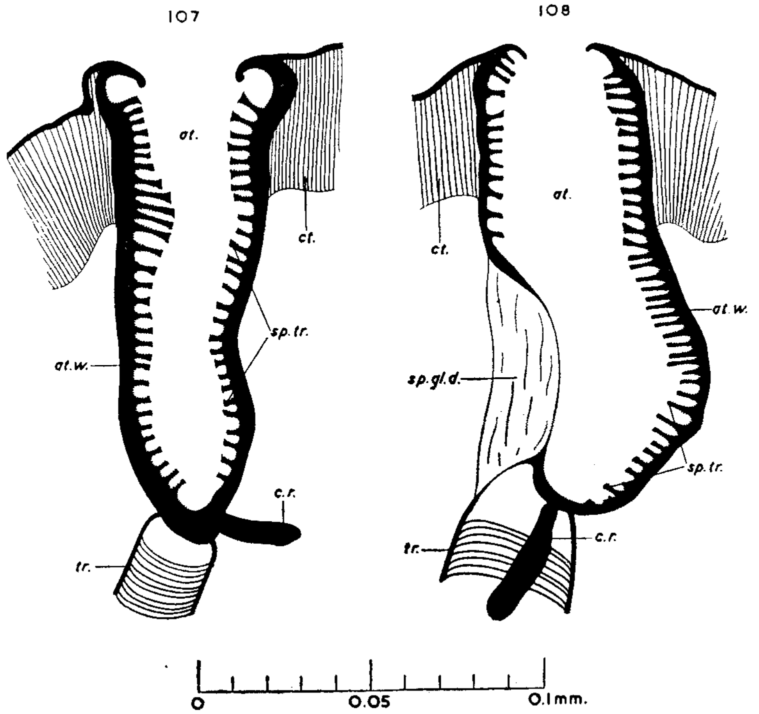


Fig. 107.—*Haematopinus latus* Neumann—optical longitudinal section through the abdominal spiracle. Fig. 108.—*Haematopinus phacochoeri* Enderlein—optical longitudinal section through the abdominal spiracle.

at., atrium ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *sp.gl.d.*, duct of the spiracular gland ; *sp.tr.*, truncated atrial spines ; *tr.*, trachea.

last abdominal spiracle in the ♀ is 140 μ (♂ not seen). All traces of annular and cross-ledges have been lost in the adult (see Webb, 1948, figs. 6 and 7).

Host.—*Phacochoerus aethiopicus* (Pallas) (wart-hog).

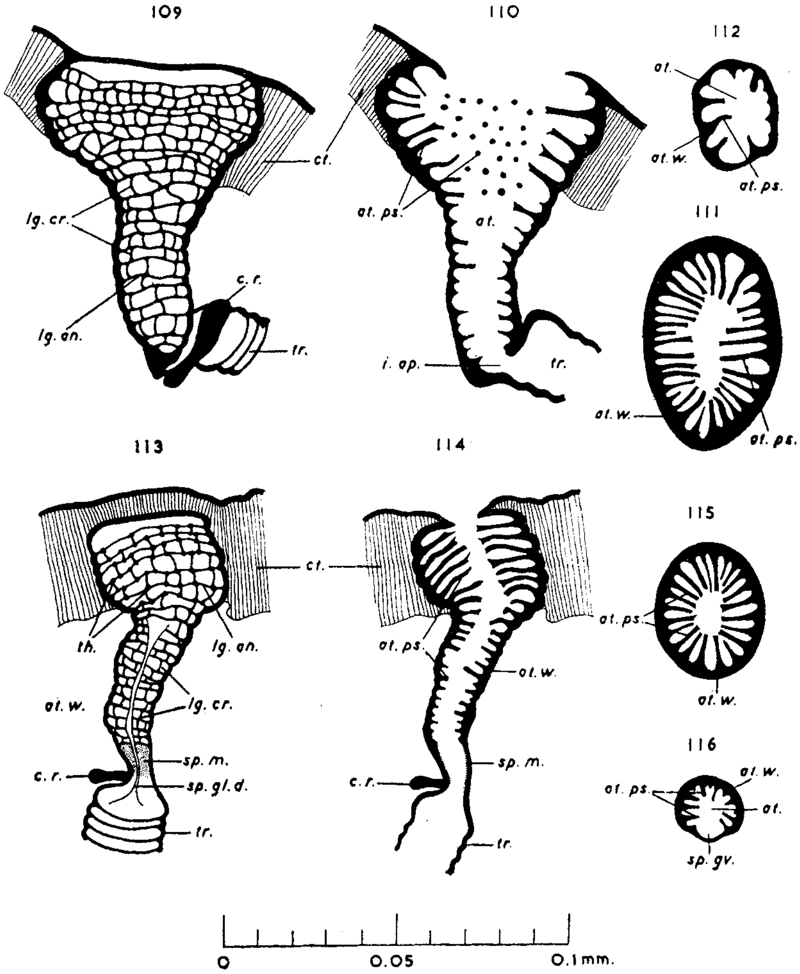
VII. Spiracle Structure in the Genus *Microthoracius* Fahrenholz

The genus *Microthoracius* comprises only four species of which the spiracle structure of three is here described. The genus is quite distinct and is entirely restricted to members of the Camelidae (camels and llamas).

Microthoracius cameli (Linnaeus).

The spiracles of *Microthoracius cameli* (figs. 109–116) are very large. They resemble those of *Linognathus vituli* (see Webb, 1946, figs. 157–164) in the external appearance of the atrium but, internally, they approximate in atrial structure to the abdominal spiracle of the 3rd nymph of *Haematopinus asini burchelli* (see Webb, 1948, figs. 12 and 13). In the thoracic spiracle (figs. 109 and 110) the atrium (*at.*) is pear-shaped and the atrial wall (*at.w.*) is covered with a close reticulum of annular (*lg.an.*) and cross-ledges (*lg.cr.*). These ledges, however, have partially disappeared, except at their points of junction, so that the internal sculpturing on the atrium consists of a number of large finger-like processes (*at.ps.*) projecting inwards and joined at their bases by the vestigial portions of the ledges (see Webb, 1948, fig. 16 *E.*). The finger-like processes

Figures 109–116.



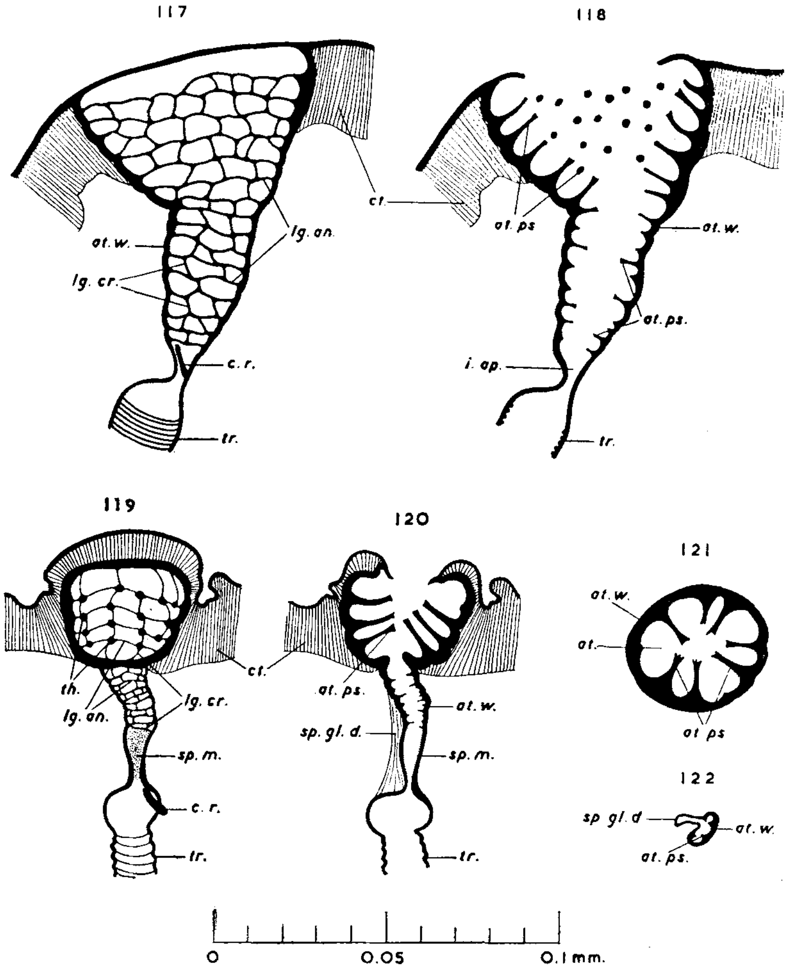
The spiracles of *Microthoracius cameli* (Linnaeus).

Figs. 109 and 110.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 111 and 112.—Optical transverse sections, through the distal and proximal regions respectively, of the atrium of the thoracic spiracle. Figs. 113 and 114.—Surface view and optical longitudinal section through the abdominal spiracle. Figs. 115 and 116.—Optical transverse sections, through the distal and proximal regions respectively, of the atrium of the abdominal spiracle.

at., atrium; *at.ps.*, blunt process projecting into the atrium; *at.w.*, atrial wall; *c.r.*, chitinous rod of occlusor mechanism; *ct.*, cuticle; *i.ap.*, internal aperture of the atrium; *lg.an.*, annular ledge; *lg.cr.*, cross-ledge; *sp.gl.d.*, duct of the spiracular gland; *sp.gv.*, spiracular groove leading to the duct of the spiracular gland; *sp.m.*, minute spines; *th.*, thickening at the point of junction of annular and cross-ledges; *tr.*, trachea.

resemble, and are evidently homologous with, the truncated spines (figs. 97–108, *sp.tr.*) characteristic of the spiracles in species of the genus *Haematopinus*. These processes are longest at the distal end of the spiracle (fig. 111) and decrease in length towards the proximal end (fig. 112). There is a large chitinous rod (fig. 109, *cr.*) arising from the point of junction of the atrium of the spiracle and the tracheal trunk (*tr.*). To this rod is evidently attached an occlusor muscle passing to the body wall.

Figures 117–122.



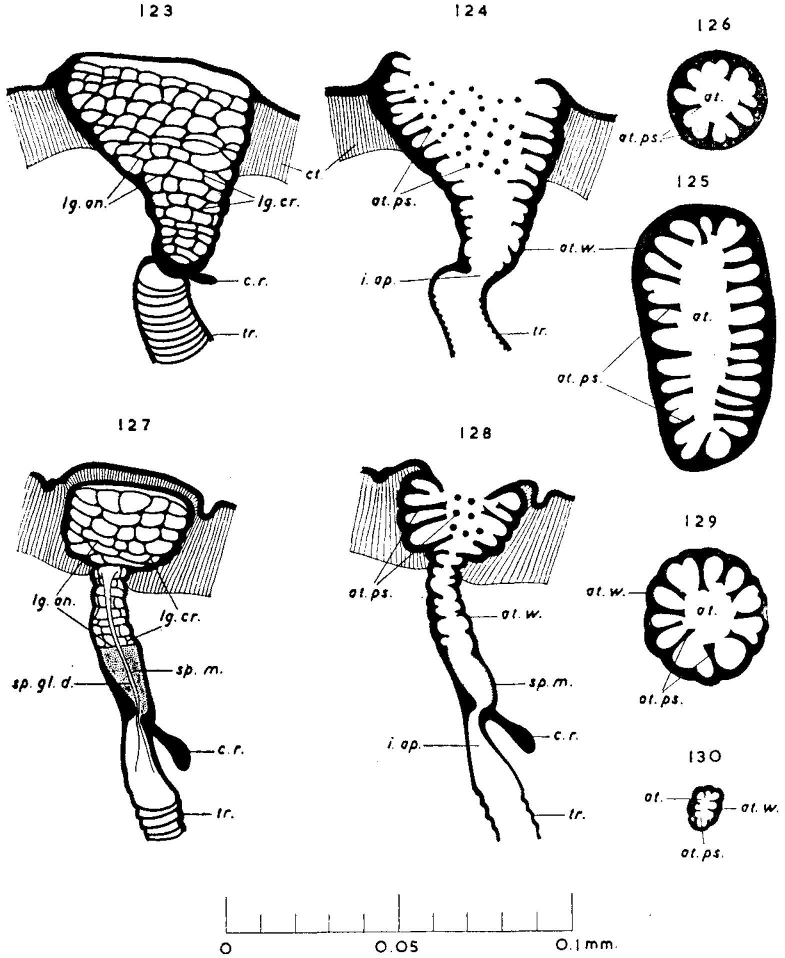
The spiracles of *Microthoracius mazzai* Werneck.

Figs. 117 and 118.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 119 and 120.—Surface view and optical longitudinal section through the abdominal spiracle. Figs. 121 and 122.—Optical transverse sections, through the distal and proximal regions respectively, of the atrium of the abdominal spiracle.

at., atrium; *at.ps.*, blunt process projecting into the atrium; *at.w.*, atrial wall; *c.r.*, chitinous rod of occlusor mechanism; *ct.*, cuticle; *i.ap.*, internal aperture of the atrium; *lg.an.*, annular ledge; *lg.cr.*, cross-ledge; *sp.gl.d.*, duct of the spiracular gland; *sp.m.*, minute spines; *th.*, thickening at the point of junction of annular and cross-ledges; *tr.*, trachea.

The abdominal spiracle (figs. 113 and 114) is very similar in form to the thoracic spiracle except that the atrium is narrower in diameter and, at its proximal end, lacks the annular (*lg.an.*) and cross-ledges (*lg.cr.*). Here the internal surface of the atrium is covered with minute spines (figs. 113 and 114, *sp.m.*) of the type present at the proximal end of the atrium of the spiracles in *Linognathus vituli*, and also on and in between the truncated spines in the *Haematopinus* spiracle (see Webb, 1946, figs. 157–164 and 189–204). The atrium itself is divided more or less clearly into two regions, a distal region in which the finger-like processes are large (fig. 115, *at.ps.*) and the chitin is heavily sclerotized, and a proximal region in which these processes are considerably smaller (fig. 116, *at.ps.*) and the chitin is far less heavily sclerotized. Throughout

Figures 123–130.



The spiracles of *Microthoracius praelongiceps* (Neumann).

Figs. 123 and 124.—Surface view and optical longitudinal section through the thoracic spiracle. Figs. 125 and 126.—Optical transverse sections, through the distal and proximal regions respectively, of the atrium of the thoracic spiracle. Figs. 127 and 128.—Surface view and optical longitudinal section through the abdominal spiracle. Figs. 129 and 130.—Optical transverse sections, through the distal and proximal regions respectively, of the atrium of the abdominal spiracle.

at., atrium ; *at.ps.*, blunt process projecting into the atrium ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.gl.d.*, duct of the spiracular gland ; *sp.m.*, minute spines ; *tr.*, trachea.

the atrium the network of vestigial ledges is clearly seen so that, in surface view, the spiracle closely resembles that of *Linognathus vituli*. There is a prominent spiracular gland, the duct (fig. 113, *sp.gl.d.*) of which is visible in potash-cleared specimens and, commencing as a shallow groove (fig. 116, *sp.gv.*), extends from the outer limit of the proximal portion of the atrium, along one side of the atrial wall, to join the tracheal trunk (*tr.*). The detailed structure of a gland of this type is given elsewhere (see Webb, 1946). A stout chitinous rod (figs. 113 and 114, *c.r.*) arises from the point of junction of the atrium and the tracheal trunk, and is presumably for the attachment of an occlusor muscle.

Host.—*Camelus dromedarius* Linnaeus (one-humped camel).

MICROTHORACIUS MAZZAI Werneck.

The spiracles in *Microthoracius mazzai* (figs. 117–122) are essentially similar in form to those of *M. cameli* (see figs. 109–116). The most obvious differences between the spiracles of the two species are the comparatively large spaces between the ledges (figs. 117 and 119, *lg.an.* and *lg.cr.*) and hence between the finger-like processes (figs. 118, 120 and 121, *at.ps.*) in *M. mazzai*, and the small size of the chitinous rod (figs. 117 and 119, *c.r.*) of the closing mechanism. Here, too, the differentiation between the proximal and distal portions of the atrium, particularly in the abdominal spiracle (figs. 119 and 120), is greatly accentuated. In all other respects the spiracles of this species and those of the last are very closely related.

Host.—*Lama huanaca* (Linnaeus) (guanaco, llama and alpaca).

MICROTHORACIUS PRAELONGICEPS (Neumann).

In *Microthoracius praelongiceps* the structure of the spiracles (figs. 123–130) approaches that found in *M. cameli* (see figs. 109–116), even more closely than those of *M. mazzai* (see figs. 117–122). The only differences worthy of note are the relatively short and compressed atrium of the thoracic spiracle (figs. 123 and 125) with a weak chitinous rod (*c.r.*), and the accentuated differentiation of the proximal and distal portions of the atrium of the abdominal spiracle (figs. 127–130). The spiracles in *M. praelongiceps*, therefore, are somewhat intermediate in structure between those of *M. cameli* and those of *M. mazzai* with obvious relationships to both.

Host.—*Lama huanaca* (Linnaeus) (guanaco, llama and alpaca).

VIII. SPIRACLE STRUCTURE IN THE GENUS *PECAROECUS* BABCOCK AND EWING.

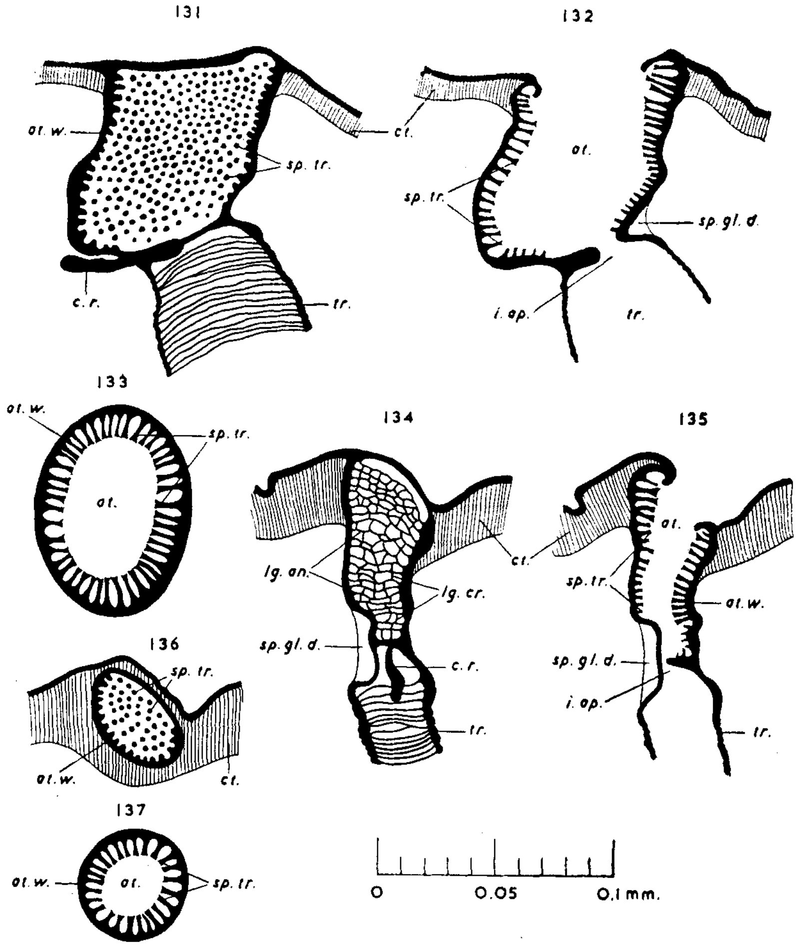
The genus *Pecaroecus* was erected in 1938 to receive a single species of Siphunculata from the collared peccary, *Tayassu tajacu*. This louse is of particular interest not only because of its great size, but also because it exhibits a number of generalized characters and provides a genus of lice characteristic of the Suina.

PECAROECUS JAVALII Babcock and Ewing.

The spiracles of *Pecaroecus javalii* (figs. 131–137) are very similar to those characteristic of species of the genus *Haematopinus* (see figs. 97–108) except for the complete absence in the adult of any trace of the minute spines on the atrial walls and the sides of the truncated spines. In the thoracic spiracle (figs. 131–133) the atrium (*at.*) is almost as broad as it is long with a wide external aperture. The atrial walls (*at.w.*) are covered with truncated spines (*sp.tr.*) with expanded apices. Traces of ledges connecting the bases of these spines one with another remain. There is a very stout chitinous rod (*c.r.*) to which an occlusor muscle passing to the body wall is presumably attached. The duct of a spiracular gland (fig. 132, *sp.gl.d.*) was present in the cleared specimens examined. This duct is very short and is situated on the side of the atrial wall opposite to the chitinous rod.

The abdominal spiracle (figs. 134–137) differs from the thoracic spiracle not only in size and shape but also in the greater retention on the atrial wall (*at.w.*) of a net-work of ridges (*lg.an.*, *lg.cr.*) joining the bases of the truncated spines (*sp.tr.*) one to another. The atrium, although as long as that of the thoracic spiracle, is considerably smaller in diameter (figs. 134 and 135, *at.*). Atrial

Figures 131–137.



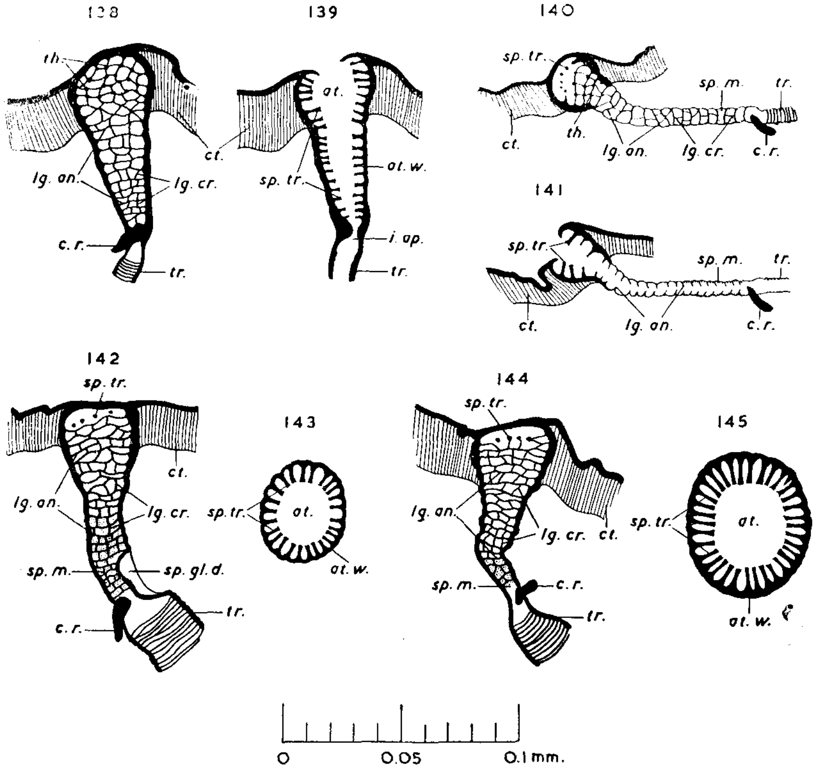
The spiracles of *Pecaroecus javalii* Babcock and Ewing.

Fig. 131.—Surface view of the thoracic spiracle of the adult. Figs. 132 and 133.—Optical longitudinal and transverse sections respectively, through the atrium of the thoracic spiracle of the adult. Figs. 134 and 135.—Surface view and optical longitudinal section through the abdominal spiracle of the adult. Figs. 136 and 137.—Optical tangential and transverse sections, respectively, through the atrium of the abdominal spiracle of the adult.

at., atrium ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.gl.d.*, duct of the spiracular gland ; *sp.tr.*, truncated atrial spines ; *tr.*, trachea.

sculpturing of the type seen here is similar to that found in species of the genus *Microthoracius* (see figs. 109–130), and also in the spiracles of the immature stages of *Haematopinus eurysternus* and *H. asini burchelli* (see Webb, 1948). There is a well-formed duct of the spiracular gland (*sp.gl.d.*) and a large chitinous rod (*c.r.*) for attachment of the occlusor muscle. There are no minute spines on the atrial wall between the ledges.

Figures 138–145.



The spiracles of *Pecaroecus javalii* Babcock and Ewing.

Figs. 138 and 139.—Surface view and optical longitudinal section through the thoracic spiracle of the 1st nymph. Figs. 140 and 141.—Surface view and optical longitudinal section through the abdominal spiracle of the 1st nymph. Figs. 142 and 143.—Surface view of the abdominal spiracle and transverse optical section through the atrium of the thoracic spiracle, respectively, of the 2nd nymph. Figs. 144 and 145.—Surface view of the abdominal spiracle and transverse optical section through the atrium of the thoracic spiracle, respectively, of the 3rd nymph.

at., atrium ; *at.w.*, atrial wall ; *c.r.*, chitinous rod of occlusor mechanism ; *ct.*, cuticle ; *i.ap.*, internal aperture of the atrium ; *lg.an.*, annular ledge ; *lg.cr.*, cross-ledge ; *sp.gl.d.*, duct of the spiracular gland ; *sp.m.*, minute spines ; *sp.tr.*, truncated atrial spines ; *th.*, thickening at point of junction of annular and cross-ledges ; *tr.*, trachea.

In the 1st nymph of *Pecaroecus javalii* the thoracic spiracle (figs. 138 and 139) is very similar to the spiracles of the 1st nymph of *Haematopinus eurysternus* and the 3rd nymph of *H. asini burchelli* (see Webb, 1948, figs. 1, 2, 12 and 13). The atrial wall is covered by a network formed from annular and cross-ledges (fig. 138, *lg.an* and *lg.cr.*) and, in the distal region particularly, the points of junction between these ledges are thickened (*th.*) as in the early stages of formation of the truncated atrial spines in *Haematopinus eurysternus.* The thoracic spiracle of the 1st nymph differs in shape from that of the adult in so far as it is long and narrow, and, in the 2nd and 3rd nymphs (figs. 143 and 145), there is a gradual progression from the form found in the 1st nymph to that of the adult. The annular and cross-ledges are reduced with each instar leaving its points of junction projecting into the atrium as a truncated spine (*sp.tr.*), while the diameter of the atrium, but not its length, is correspondingly increased.

The abdominal spiracle of the 1st nymph (figs. 140 and 141) is almost identical with that of the 1st nymph of *Haematopinus eurysternus* and the 3rd nymph of *H. asini burchelli* (see Webb, 1948, figs. 1, 2, 12 and 13). The atrium is long and narrow and the atrial wall is covered with annular and cross-ledges (*lg.an.* and *lg.cr.*). At the extreme distal end of the atrium, however, the intermediate portions of the ledges have disappeared leaving their points of junction projecting into the atrium as truncated spines (fig. 140, *sp.tr.*). Proximal to this region the ledges are present first with their points of junction thickened (fig. 140, *th.*) and then with their junctions unthickened (fig. 140, *lg.an.* and *lg.cr.*). The proximal region of the spiracle, therefore, possesses atrial sculpturing of a type characteristic of lice of the genus *Linognathus* (see Webb, 1946, figs. 157–164). The proximal third of the atrial wall only is studded with minute spines (fig. 140, *sp.m.*). Here again, therefore, in a single spiracle the stages in formation of truncated atrial spines from a series of annular and cross-ledges are successively represented, leaving no doubt that the atrial spines in *Pecaroecus* are homologous with those of *Haematopinus.*

In the 2nd and 3rd nymphs (figs. 142 and 144) the spiracle is of the same length but wider in diameter. The annular and cross-ledges become reduced to mere ridges on the atrial wall except for their points of junction, which project into the atrium as truncated spines. The minute spines on the atrial wall between the ledges in the proximal region of the spiracle occupy a smaller and smaller area with each successive instar until, in the adult, they are entirely absent.

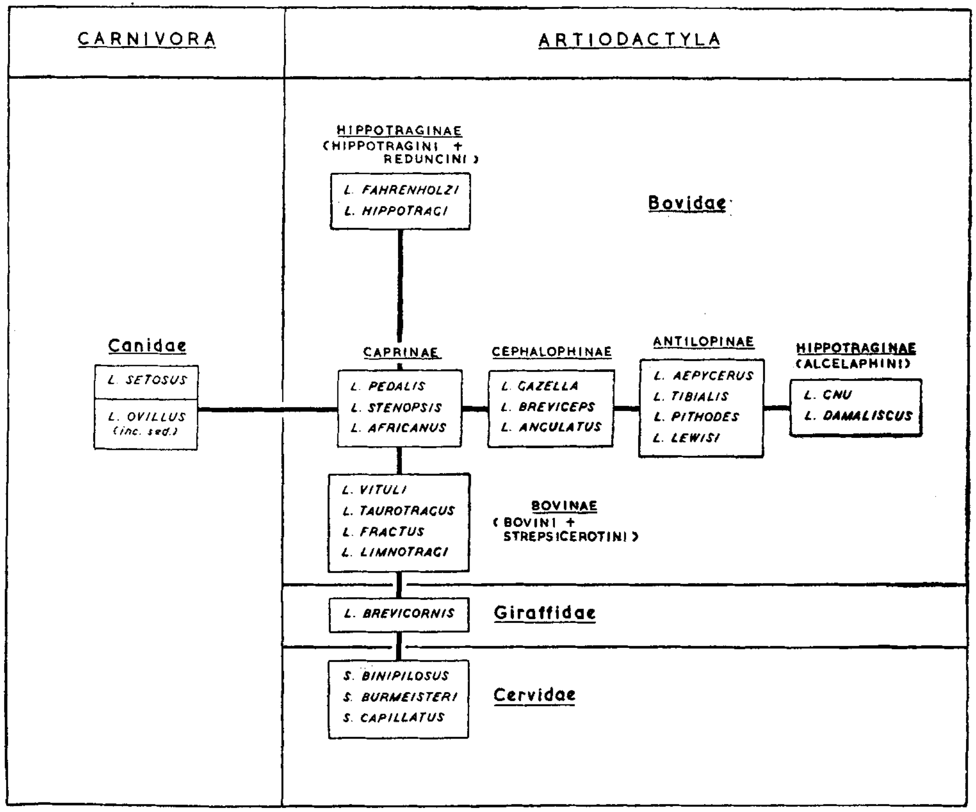
IX. HOST-RELATIONSHIPS OF THE GENERA *LINOGNATHUS* AND *SOLENOPOTES.*

The spiracles of lice of the genera *Linognathus* and *Solenopotes* form a more or less continuous series with those of forms such as *L. brevicornis* (figs. 77–80) being far more akin to the less extreme type of *Solenopotes* spiracle (figs. 81–84) than to those of other species of *Linognathus* such as *L. ovillus*, *L. fahrenholzi* or *L. damaliscus* (figs. 62–65, 55–58, and 51–54 respectively). In a discussion of their host-relationships, therefore, these two genera cannot be considered apart. With the exception of *L. setosus* and *L. taeniotrichus* which infest a variety of members of the family Canidae, the lice of these genera are restricted to Artiodactyla of the infra-order Pecora.

The spiracles in the *Linognathus-Solenopotes* series are so similar in their general structure that it is a difficult matter to arrange them in sequence of form. They may, however, be divided broadly into three or possibly four main groups. Taking the spiracles of *L. pedalis* (figs. 1–10) as a central type, a continuous series of modifications exists extending in the one direction to *L. damaliscus* (figs. 51–54) and, in the other, to *Solenopotes capillatus* (see Webb, 1946, figs. 175–186). This group, possibly divisible into two halves at the point of *L. pedalis*, includes the great majority of species. Standing apart, both from the remaining species and from each other, are *L. fahrenholzi* and *L. hippotragi* (figs. 55–61) on the one hand, and *L. setosus* (see Webb, 1946, figs. 165–174) and *L. ovillus* (figs. 62–65) on the other. This arrangement of the species together with their host distribution is illustrated diagrammatically in fig. 146.

Considering the *pedalis* group as a whole, with the spiracles of *L. pedalis* (figs. 1–10) as perhaps the most generalized type within that group, it is possible to indicate certain associations of forms which appear to show affinity, although the entire series is without an obvious break. The species with spiracles nearest to those of *L. pedalis* from the sheep are *L. stenopsis* (figs. 11–14) and *L. africanus* (figs. 15–18) from the goat, both hosts being members of the Caprini. The next association includes *L. gazella* (figs. 19–22), *L. breviceps* (figs. 23–26) and *L. angulatus* (figs. 27–30), all from various duikers, members of the *Cephalophinae*, and is followed by *L. aepycerus* (figs. 31–34), *L. tibialis* (figs. 35–38), *L. pithodes* (figs. 39–42) and *L. lewisi* (figs. 43–46) from various members of the *Antilopinae*. Finally, the most extreme forms in this series are *L. gnu* (figs. 47–50) and *L. damaliscus* (figs. 51–54) from members of the Alcelaphini of the *Hippotraginae*. Thus, it will be seen that, although there is a considerable difference between the spiracles of *L. pedalis*, on the one hand, and *L. gnu* and *L. damaliscus*, on the other, they are connected by a complete series of intermediate forms.

Figure 146.



The affinities and host-relationships of sucking lice of the genera *Linognathus* and *Solenopotes*. (Note that the association of *L. ovillus* with *L. setosus* is almost certainly unnatural.)

Radiating from *L. pedalis* in another direction is a series commencing with *L. vituli* (see Webb, 1946, figs. 157–164), *L. taurotragus* (figs. 66–69), *L. fractus* (figs. 70–72) and *L. limnotragi* (figs. 73–76) from the domestic ox, the eland and the bushbuck, all members of the *Bovinae*, and ending with *Solenopotes binipilosus* (figs. 81–84), *S. burmeisteri* (figs. 85–88) and *S. capillatus* (see Webb, 1946, figs. 175-186) from a group of lice characteristic of the Cervidæ (deer). Intermediate in spiracle structure between lice infesting members of the *Bovinae* and those from Cervid hosts is *Linognathus brevicornis* from the giraffe. Here again, there is considerable difference in form between the spiracles of *L. pedalis*, on the one hand, and those of *S. capillatus*, on the other, but the gap between them is bridged by intermediate forms.

The *L. fahrenholzi*-*L. hippotragi* group, however, is distinct from *L. pedalis* and associated forms and is not connected with that association by any known intermediate types. *L. fahrenholzi* and *L. hippotragi* infest members of the Reduncini and Hippotragini of the *Hippotraginae*. A further separate group is formed by *L. ovillus*, the face louse of sheep, and *L. setosus*, a rather extreme form found on a variety of Canidae both domestic and wild. Undoubtedly, *L. taeniotrichus*, a species not seen by the writer, should also belong to this group as it appears to be allied to *L. setosus* in structure and is also from a canid host.

The inter-relationships of the lice of the genera *Linognathus* and *Solenopotes* according to their spiracle structure, when viewed in the light of their distribution on pecoran and carnivoran hosts, permit tentative suggestions to be made on the possible affinities of those hosts. The *Caprinae*, *Bovinae* and *Cephalophinae* form a more or less closely-related central group of the Bovidae with the *Antilopinae* and the Alcelaphini of the *Hippotraginae* respectively, of rather more distant origin and more closely-related one to another than either is to the *Caprinae*. The position of *L. fahrenholzi* and *L. hippotragi* is, however, more difficult to explain. The hosts of these two species are members of the tribes Reduncini (reedbuck, etc.) and Hippotragini (sable antelope, etc.), and together with the Alcelaphini (gnus) comprise, in Simpson's (1945) classification, the subfamily *Hippotraginae*. Now the spiracles of *L. gnu* and *L. damaliscus* from members of the Alcelaphini are near those of lice infesting members of the *Antilopinae* and are as widely different from those of *L. fahrenholzi* and *L. hippotragi* as this rather compact series allows. A further species, *L. peleus* Bedford, 1936, from *Pelea capreolus* (vaal rhebok), another member of the Reduncini, has not been seen by the writer, but is clearly of the same type as *L. fahrenholzi* with large spiracles and should no doubt be grouped with that species and *L. hippotragi*. Here, then, is a case in which the distribution of the parasites does not show reasonable agreement with the accepted classification of the hosts. According to the evidence derived from louse affinities, it would appear that the *Hippotraginae*, as defined by Simpson, is probably an unnatural assemblage, since the Alcelaphini lice show affinities with those from the *Antilopinae*, while lice from the Hippotragini and Reduncini fall together as a group showing no close affinity either with those from the Alcelaphini or, for that matter, with any Siphunculata here examined, from any Bovidae. Furthermore, the *Hippotraginae* is a group as to the validity of which Simpson himself suggests reasonable doubt may be inferred. Simpson states that "The *Hippotraginae*, as I define the subfamily, form a tentative group, one not so surely natural as the others here recognized and one not quite like any in previous classifications. Yet each student has provided bits of evidence that tend not only to separate these three tribes from others, but also to unite them with one another. Schlosser showed that in the teeth and in some other respects all three have definite, and in part similar, bovine tendencies. Schwarz (relying heavily on Pocock) showed that all three likewise have a series of very gazelle-like characters, to such an extent that he placed the gnus in the *Antilopinae* (Antilopini of my arrangement). Pilgrim protested against this union and left the three groups separate and without recognized affinities. It is possible that these three groups of what could be called 'boödont antelopes,' did develop independently, but even if so, they are morphologically definable as a single group and there is real, however inconclusive, evidence of their possible common origin . . . ." The evidence given here, therefore, based on the structure of the spiracles of their parasites, suggests that the *Hippotraginae* may not be a natural group in so far as the Alcelaphini should possibly be placed with the Antilopini.

The position of lice of the genus *Solenopotes*, from cervid hosts, near those from members of the *Bovinae* is of great interest, as it suggests some relationship between the Cervidae, on the one hand, and a central group of the Bovidae on the other. Furthermore, the intermediate position of *L. brevicornis* between cervid and bovid lice upholds the view that the Giraffidae arose, either as an early offshoot from the Cervidae or from a position somewhere between the Bovidae and Cervidae at a time shortly after this bifurcation took place. It seems virtually certain that the genus *Solenopotes* evolved from *Linognathus* on the cervid stock. The presence of *S. capillatus* on the domestic ox, as pointed out by Ferris (1932) and later by Hopkins (1949), is evidently a case of secondary infestation either from *Alces alces*, the only living European deer from which no species of louse of that genus is recorded, or from *Megaloceros giganteus*, the extinct Irish elk. In any case the fact that *S. capillatus* has been able to establish itself successfully on an alien host, argues a possible close affinity between the domestic ox and the true host in view of the extreme specificity usually exhibited by Siphunculata.

Linognathus setosus and *L. ovillus* possess spiracles which differ from those of other species of the genus chiefly with regard to their great size. Now, as there is no question that the apparent similarity of the spiracles in these two species can mean that hosts of the parasites, members of the Canidae and the domestic sheep respectively, are more nearly related to each other than either is to the remainder of the Pecora, four possible interpretations of the facts remain. Firstly, it is possible that both *L. setosus* and *L. ovillus* are normal or primary parasites, that is, they have not been secondarily acquired from another host at some time in the past, and that the form of their spiracles has been independently acquired through a process of parallel evolution. If this is the case, then no further discussion on their relationship is necessary. Secondly, neither *L. setosus* nor *L. ovillus* may be a normal parasite, in which case, again, no further comment on their relationship is needed. Thirdly, it is possible that *L. setosus* is closely related to *L. ovillus* and has transferred to a canid host from the sheep or, fourthly, the reverse may be true and *L. ovillus* may be a derivative of *L. setosus* transferred to a sheep from some member of the Canidae. As far as the third and fourth possibilities are concerned, the extreme form of *L. setosus*, not only with regard to spiracles but also in the remainder of its external features, together with its wide distribution on wild Canidae and in particular the arctic fox, *Alopex lagopus*, suggests that, if *L. setosus* has been secondarily acquired by Canidae, then the transference must be of very ancient origin. Furthermore, the presence of an allied species *L. taeniotrichus* with even larger spiracles on the South American dog *Dusicyon*, supports this view and increases the probability that these species of *Linognathus* are normal to Canidae. With regard to *L. ovillus*, on the other hand, the existence of two distinct species of the same genus on one host is an unusual, but not at all, unknown phenomenon, and there are no valid grounds here for assuming that either *L. ovillus* or *L. pedalis* must have been secondarily acquired by the sheep. Furthermore, on characters other than the spiracles, it is *L. pedalis* and not *L. ovillus* which more nearly resembles *L. setosus*. In fact, Ferris (1932) was led to advance the suggestion that the dog had acquired *L. setosus* by transference and subsequent modification of *L. pedalis* from the sheep. The view held here, therefore, is that, in all probability, *L. setosus* and *L. taeniotrichus* are normal to Canidae or at least were acquired at a very early date, possibly long before the sheep had been evolved, and that both *L. ovillus* and *L. pedalis* are normal to the sheep, the similarity of spiracles in *L. setosus* and *L. ovillus* being fortuitous and no indication of particularly near affinity.

X. HOST-RELATIONSHIPS OF THE GENUS *RATEMIA*.

Ratemia squamulata, the only known species of the genus, is a louse with undeniable affinities with the genus *Linognathus*. The spiracles of *R. squamulata* (figs. 89–96) are of the linognathoid type both with regard to the shape of the atrium and the form and distribution of the atrial sculpturing. Admittedly the annular and cross-ledges have partially disappeared, leaving their points of junction projecting into the atrium as a series of blunt-ended processes, but this is a condition arrived at independently by several species of *Linognathus*, namely *L. lewisi* (fig. 44), *L. gnu* (fig. 48), *L. hippotragi* (fig. 59) and *L. fractus* (fig. 70), and is not necessarily an indication of close relationship with *Haematopinus*, *Microthoracius* or *Pecaroecus*, genera in which similar atrial spines or processes are normally present and are formed in the same way. In addition, the proximal end of the atrium, particularly in the abdominal spiracle, forms a narrow, somewhat sinuous, smooth-walled tube, a character in keeping with most linognathoid spiracles and also those of *Microthoracius*, but absent in the spiracles of *Haematopinus* and *Pecaroecus*. The presence of the pleural or paratergal plates on abdominal segments 4–6 is, perhaps, a character more to be associated with *Haematopinus* and *Pecaroecus* than *Linognathus* or *Microthoracius*. It is doubtful, however, what importance may be attached to the presence of pleural plates in this instance, for a similar arrangement of plates on abdominal segments 4–6 in *Pedicinus* from Old World monkeys, has evidently been achieved independently. Finally, the absence of prominent post-antennal angles and the weak first pair of legs are characters shared by *Linognathus* and *Ratemia*, and separating the latter from *Haematopinus*.

Ratemia is known only from members of the Perissodactyla and is the only genus of sucking louse peculiar to that order. As *Ratemia* can be considered a close relative, if not a derivative, of *Linognathus*, then the existence of lice of the linognathoid type on the Artiodactyla, Carnivora and Perissodactyla suggests a probable common origin for these three eutherian orders.

XI. Host-Relationships of the Genus *Haematopinus*.

The survey given here of spiracle structure in the genus *Haematopinus* (figs. 97–108) shows that, with the exception of *H. taurotragi* (figs. 103 and 104), the degree of variation between spiracles of different species is very small. The chief differences to be noted are length of the atrium relative to body length, degree of apical expansion of the truncated atrial spines and persistence or absence of vestiges of the primitive ledge-system connecting the bases of the spines. Constancy of spiracle structure within the genus may be taken to indicate the homogeneity of the group, while differences in structure may indicate intrageneric relationships. In *H. taurotragi* the spiracles, although related to those of other species, stand apart because, at the distal end of the atrium there is a honeycomb of ledges directed inwards and, in the proximal region, all the truncated spines are joined at their bases by low ridges representing the vestiges of a similar ledge-system. In this unusual retention of ledges, these spiracles may, perhaps, be considered primitive. It is difficult to understand why the spiracles of *H. taurotragi* should depart so far from the normal form in the genus for, in other respects, *H. taurotragi* appears to be close to *H. eurysternus* in which the spiracles are typical (see Webb, 1946, figs. 189–204).

The genus may be divided into three main groups according to the length of the atrium of the spiracle relative to the length of the body and the persistence of vestiges of the annular and cross-ledges. In Table I the length of the last abdominal spiracle, together with the total body length of both the male and the female are given, and the ratio between the length of the spiracle and length of the body in the male is calculated. It was noticed that the length of the atrium in the abdominal spiracle in any one individual varied according to the position on the body, but that a spiracle in any given position, such as the last abdominal spiracle, was extraordinarily constant in length both between individuals of the same and of opposite sexes. Thus, in spite of the normal disparity in size between the male and the female, their spiracles were of almost equal dimensions. For comparison of spiracle length with body length, the length of the body of

TABLE I.

Haematopinus sp.	Atrial length of last abdominal spiracle in ♀.	Atrial length of last abdominal spiracle in ♂.	Total length of ♀.	Total length of ♂.	$\frac{\text{♂ spir. length}}{\text{♂ body length}}$.	Host.	Host Group.
H. asini asini	66 μ	66 μ	2·7 mm.	2·3 mm.	29	*Equus asinus.*	Perissodactyla Equidae.
H. asini macrocephalus	85 μ	83 μ	3·2 mm.	2·8 mm.	30	*Equus caballus.*	
H. asini minor	60 μ	60 μ	2·5 mm.	2·1 mm.	29	*Equus burchelli.*	
H. asini burchelli	60 μ	56 μ	2·8 mm.	2·5 mm.	22	*Equus burchelli.*	
H. acuticeps	125 μ	♂ unknown	5·3 mm.	♂ unknown	29†	*Equus burchelli.*	
H. eurysternus	126 μ	125 μ	3·1 mm.	2·6 mm.	48	*Bos taurus.*	Artiodactyla *Bovinae.*
H. bufali	112 μ	112 μ	3·9 mm.	2·7 mm.	40	*Syncerus caffer.*	
H. taurotragi.........	127 μ	125 μ	4·3 mm.	3·5 mm.	36	*Taurotragus oryx.*	
H. tuberculatus	160 μ	160 μ	5·1 mm.	3·6 mm.	44	*Bubalus bubalis.*	
H. suis	114 μ	110 μ	4·6 mm.	3·8 mm.	29	*Sus* sp.	Artiodactyla *Suinae.*
H. aperis	118 μ	118 μ	5·0 mm.	4·3 mm.	27	*Sus scrofa.*	
H. phacochoeri	140 μ	not seen	6·1 mm.	5·0 mm.*	28	*Phacochoerus aethiopicus*	
H. latus	140 μ	139 μ	5·3 mm.	4·5 mm.	30	*Potamochoerus porcus.*	

Table showing (*a*) the constancy of spiracular size in both the ♂ and the ♀ of any given species of *Haematopinus*, and, (*b*) the relationship between the ratio " ♂ spiracular length/♂ body length," and the host group of the parasite.

* Figure taken from Ferris. † Figure calculated from ♀ spiracle length/expected ♂ body length.

the male was taken, as it showed less variation in the size of the abdomen. Dividing the length of the spiracle in μ by the body length of the male in millimetres, it was found that the figures obtained for those species infesting members of the *Bovinae* were significantly higher than those for species infesting Equidae or Suina, indicating that the spiracles were exceptionally large in relation to body size. Moreover, the ratio obtained for the remaining species examined fell within the very close range of 27–30, with one exception, in spite of the fact that the body length of the male in different species varied from 2·1 mm. to 5·0 mm. The exception was *H. asini burchelli* from the zebra with a spiracle/body length ratio of 22. Clearly, then, on this factor alone the species may be divided into two groups: firstly, those infesting the *Bovinae* with large spiracles relative to body size and, secondly, those from Equidae and Suina with small spiracles relative to body size.

TABLE II.

Haematopinus sp.	Stage in development of atrial structure.							
	1st Nymph.		2nd Nymph.		3rd Nymph.		Adult.	
	abd.	thor.	abd.	thor.	abd.	thor.	abd.	thor.
H. asini asini	—	—	—	—	—	—	E–F	E–F
H. asini macrocephalus	—	—	—	—	—	—	F	F
H. asini minor	D	D	E	E	E	E	E–F	E–F
H. asini burchelli	A	D–E	B–C	E	D–E	E	E–F	E–F
H. acuticeps	—	—	—	—	—	—	F	F
H. eurysternus	D–F	D–F	E–F	E–F	F	F	F	F
H. bufali	D–F	D–F	E–F	E–F	F	F	F	F
H. taurotragi	D	D	D	D	—	—	D–E	D–E
H. tuberculatus	—	—	—	—	—	—	F	F
H. suis	—	—	—	—	—	—	F	F
H. aperis	—	—	—	—	—	—	F	F
H. phacochoeri	—	—	F	F	—	—	F	F
H. latus	—	—	—	—	—	—	F	F

Table showing the stages A–F (Webb, 1948, fig. 16) in development of atrial structure of the spiracles of adults and nymphs of species of the genus *Haematopinus*.

The second character used to group the species of *Haematopinus* was the presence or absence of vestiges of the annular and cross-ledges both in the adult and in the immature stages. The results of this survey are given in Table II and are based on the spiracle structure in the adult and on a limited amount of immature material of certain species. The stages A–F in the development of atrial sculpture mentioned in Table II are those illustrated diagrammatically in an earlier paper (Webb, 1948, fig. 16). Briefly, stage A represents the absence of sculpturing on the atrial wall except for the internal covering of minute spines; stage B is the formation of annular constrictions at points along the length of the atrium; stage C is the further development of the annular constrictions to form a series of annular ledges subdividing the atrium into a number of inter-communicating chambers; stage D is the formation of cross-ledges joining adjacent annular ledges and resulting in a honeycomb of rectangular cells on the internal surface of the atrium; stage E represents the partial disappearance of intermediate portions of the ledge-system leaving the points of junction between the annular and cross-ledges projecting from the atrial wall and connected at their bases by low ridges; stage F is the final disappearance of ledges except for the thickened points of junction which remain as the truncated atrial spines. Vestiges of the primitive ledge system were found either in the spiracles of the adult or in those of the immature stages of all those species from Equidae and *Bovinae* except *H. asini macrocephalus*, *H. acuticeps* and *H. tuberculatus*. In these three species no nymphs were available for study. Nevertheless, there is no doubt that *H. asini macrocephalus* and *H. acuticeps* belong to the group from Equidae and *H. tuberculatus* to those from *Bovinae*, and it is to be expected that vestigial ledges will be found in the spiracles of the nymphs of these species when they come to be examined. The group of species from Suina, on the other hand, not only show no trace of vestigial ledges in the adult but also, in the one instance, *H. phacochoeri*, in which an immature stage was available for examination, the spiracles were as advanced in structure as those of the adult and differed only in size. It would appear, therefore, that on this character the species from Suina can be separated as a group distinct from those from Equidae. Thus, by combining both the character of relative spiracle size and that of retention of ledges, three groups of species may be distinguished. These are firstly, *H. asini* s.spp. and *H. acuticeps*, in which the spiracles are relatively small and traces of ledges are retained; secondly, *H. eurysternus*, *H. bufali*, *H. tuberculatus* and *H. taurotragi*, in which the spiracles are relatively large and traces of ledges are also retained; and, thirdly, *H. suis*, *H. aperis*, *H. phacochoeri* and *H. latus*, in which the spiracles are relatively small, but no traces of ledges remain even in the nymph. Furthermore, these three groups correspond with the distribution of the genus on members of the Equidae of the Perissodactyla and on members of the *Bovinae* and Suina of the Artiodactyla, respectively. It may be significant, too, that *H. taurotragi*, in which the spiracles are distinct from those of other species, infests a member of the tribe Strepsicerotini, whereas other species with which it is here grouped are from members of the tribe Bovini of the same subfamily, the *Bovinae*. The difference in spiracle structure between *H. taurotragi* and other species from *Bovinae* is, perhaps, greater than might be expected in view of the comparatively close relationship between their hosts. These differences are, in fact, far greater than the differences in spiracle structure involved between all other species of *Haematopinus*, even though their hosts are far more widely separated, as in the case of species from Equidae and Suina. It can only be supposed that, in this instance, if the peculiar structure of the spiracles of *H. taurotragi* has any significance from the point of view of phylogeny, then it is largely qualitative, suggesting that the hosts are separate, but in no way representing the degree of that separation or the length of time for which the two host lines have been distinct.

The host relationships of the genus *Haematopinus* are difficult to understand for, unlike most Siphunculata, the genus is not characteristic of a single family nor yet of one order of the Eutheria. In addition to those groups of species already mentioned infesting Equidae, *Bovinae* and Suina, a single species, *H. longus* (not seen by the writer), is recorded from a cervid host. A distribution of this type may have arisen in one of two ways. The genus may have been represented on Eutheria ancestral to both the Perissodactyla and the Artiodactyla and thus, with the evolution of those orders, have come to be widely distributed throughout the host families, later dying out or giving rise to new genera on some families while remaining relatively unchanged on others. On the other hand, the genus *Haematopinus* may have achieved its present apparently discontinuous distribution by straggling from its normal host, whatever that may be, and becoming established at some period more or less remote on hosts of different groups. It is remarkable, however, that almost all the eutherian families on which *Haematopinus* is represented also harbour other, characteristic, genera of Siphunculata. The fact that the species of *Haematopinus* fall into three groups coincident with the grouping of the hosts, suggests that none of these infestations is of particularly recent date and supports the view that *Haematopinus* was either present on a common ancestor of the Equidae, *Bovinae* and Suina or else, if straggling did take place, it occurred comparatively early in the evolution of the hosts. If, however, straggling is postulated as the cause of the discontinuous distribution of *Haematopinus*, then it is surprising that it should have been so extensive when the great majority of the sucking lice appear to be so host specific. It is probable that we do not yet know the full extent of the host range of *Haematopinus*. Doubtless new species will be discovered, and these may show that the distribution of the genus is far less discontinuous than it appears at the moment.

XII. Host-Relationships of the Genus *Microthoracius*.

The very distinct genus *Microthoracius* is characteristic of Artiodactyla of the suborder Tylopoda, family Camelidae. Both *M. praelongiceps* and *M. mazzai* have been taken many times from each of the three forms of *Lama huanaca*, the guanaco, the llama and the alpaca; while another species, *M. minor*, which has not been seen by the writer, is also recorded from the alpaca and the llama. *Microthoracius cameli*, on the other hand, is a parasite of *Camelus dromedarius* and, therefore, unlike the previous species, is an Old World form. The spiracles of the three species studied here are clearly related in structure. Those of *M. praelongiceps* (figs. 123–130) and *M. mazzai* (figs. 117–122) are, perhaps, closer to one another than to those of *M. cameli* (figs. 109–116). This might be expected, since the species from the New World hosts must have been separated from that from the Old World host for a considerable period of time, certainly since the Pliocene and possibly earlier. In spite of the isolation of the Old and New World species of *Microthoracius*, there is a very close similarity between the spiracles indicating a high degree of stability and supporting the view that the spiracle is a structure of considerable taxonomic value.

The spiracles of *Microthoracius* fall within the developmental series of atrial sculpturing recapitulated by the nymphs of *Haematopinus eurysternus* and *H. asini burchelli* (see Webb, 1948, figs. 1, 12 and 16 *E*), in so far as the sculpturing is a network of annular and cross-ledges with intermediate regions of the ledges reduced and their points of junction remaining as atrial processes. This does not necessarily mean, however, that *Microthoracius* is particularly closely related to *Haematopinus*, as a similar condition is found in the spiracles of some species of *Linognathus* (see figs. 44, 48, 59 and 70) and also in *Ratemia squamulata*, which seems to be a linognathoid rather than a haematopinoid type. Furthermore, the general shape of the spiracles, together with the proximal region free from ledges but bearing minute spines, and the absence of those spines in the distal region of the spiracle, are all characters far more reminiscent of the spiracles of *Linognathus* than those of *Haematopinus*. On the other hand, the atrial processes with their expanded tips are very like the truncated spines of the *Haematopinus* spiracle, and the form of the abdominal spiracle with its prominent distal end resembles in some ways the abdominal spiracle of *H. taurotragi*.

From spiracle structure alone it is not possible to state with certainty that *Microthoracius* is derived directly from either *Linognathus* or *Haematopinus*, although it may unquestionably be grouped with them. The safest assumption that can be made is that *Microthoracius* is nearer to *Linognathus* than to *Haematopinus*, and probably arose from a linognathoid type of more generalized structure than either *Linognathus* or *Haematopinus*. The close association of *Microthoracius* with other genera of lice infesting Ferungulata, in spite of its specialized body form, is in keeping with the phylogeny of the hosts although it casts no fresh light on the origin of the Tylopoda.

XIII. HOST-RELATIONSHIPS OF THE GENUS *PECAROECUS*.

In *Pecaroecus javalii* from the collared peccary, a member of the Tayassuidae, we have a louse possessing many generalized characters and yet with spiracles whose form is almost as specialized as those from any genus infesting Ferungulata. The spiracles of *P. javalii* (figs. 131–145) are very similar, indeed, to those characteristic of the genus *Haematopinus* and are, in fact, more typical of that genus than those of a form such as *H. taurotragi*. The retention of a ledge-system as a series of low ridges connecting the bases of the truncated spines is more complete in the spiracles of *P. javalii* than is usually found in the spiracles of *Haematopinus*, although this condition is approached in the spiracles of some of the species infesting Equidae and *Bovinae* such as *H. asini burchelli*. A more striking difference between the spiracles of the two genera appears to be the complete absence of the covering of minute spines in the adult of *P. javalii*, although these are found in a restricted area at the proximal end of the abdominal spiracle in the nymphs. Minute spines are of general occurrence throughout the atria of the spiracles of *Haematopinus*.

As far as spiracles are concerned, *P. javalii*, like *Microthoracius*, belongs to the *Linognathus-Haematopinus* group though, unlike that genus, its affinities lie rather with *Haematopinus* than with *Linognathus*. As with *Microthoracius*, however, it is not possible to suggest that *Pecaroecus* is a direct derivative of any known genus of Siphunculata, although it is highly probable that both *Haematopinus* and *Pecaroecus* are evolved from a common stock represented by some more generalized ancestor, though whether that ancestor also gave rise to *Linognathus* and *Microthoracius* is a matter for conjecture. Here, again, the affinities of the host are not particularly clarified by the relationships of *Pecaroecus*. It is quite certain that the Tayassiudae are related to the pigs, which also harbour species of *Haematopinus*, but then so do the Equidae and *Bovinae* with which the peccaries cannot be nearly related.

XIV. THE INTERGENERIC AFFINITIES OF SIPHUNCULATA FROM FERUNGULATA.

In reaching conclusions with regard to the affinities between the different genera of sucking lice from Ferungulata, it is not sufficient to consider only the structure of the spiracles. Although it is believed here that the spiracles are probably the most important single character on which affinities may be based, it would be unwise to neglect such evidence as may be available from other morphological features either in support or in contradiction of evolutionary trends in the spiracles. As will be shown later, it is highly probable that a number of characters in lice, in particular the spiracles, have undergone parallel evolution, so that similarity of structure does not necessarily mean particularly close affinity. In such cases evidence derived from any one character alone may be definitely misleading and give rise to a false picture of relationships which may, perhaps, be corrected when a number of characters are considered together as a group. To aid in the analysis of the morphology of these lice, a table has been prepared showing the main characteristics of each genus infesting members of the Ferungulata (see Table III). An examination of this table shows that the 12 genera considered appear to fall broadly into two groups, firstly, those whose structure approximates to that of *Linognathus* and, secondly, those approximating to *Haematopinus*. It should be realized, however, that neither *Linognathus* nor *Haematopinus* are themselves sufficiently generalized to be ancestral to the group in question. Furthermore, some of the genera, for instance, *Microthoracius* and *Ratemia*, undoubtedly show affinities with both the linognathoid and the haematopinoid types. The grouping of the genera is shown in Table IV.

In reaching these conclusions it has been considered that, apart from spiracles, certain of the generic characters listed in Table III are of greater phylogenetic importance than others. These are, firstly, the post-antennal

TABLE IV.

Linognathoid Group.	Haematopinoid Group.
Linognathus. *Solenopotes.* *Ratemia.* *Microthoracius.* *Prolinognathus.*	*Haematopinus.* *Pecaroecus.* *Hybophthirus.* *Echinophthirius.* *Proechinophthirus.* *Antarctophthirus.* *Lepidophthirus.*

angles in the haematopinoid group and their absence in the linognathoid group; secondly, the occipital apophyses from the post-dorsal margin of the head present in the haematopinoid group and also in *Microthoracius* and *Prolinognathus*; thirdly, the presence of a spermatheca in females of the linognathoid group though, here again, a structure which may be a spermatheca is present in *Lepidophthirus*. These three characters, together with the rather definite differences in the form of the spiracles in all but the pinnipede lice, *Echinophthirius*, *Proechinophthirus*, *Antarctophthirus* and *Lepidophthirus*, serve to separate the linognathoid and haematopinoid groups with a fair degree of certainty. As to the remaining characters, they are a mixture of generalized and specialized features which require critical examination. This can, perhaps, best be done by listing what appear to the writer to be generalized characters, and then comparing each genus with a hypothetical generalized ancestral form. The generalized characters are as follows :—

(1) Head with post-antennal angles.
(2) Occipital apophyses on post-dorsal margin of head.
(3) Legs equal in size.
(4) Tibia and tarsus separate.
(5) Tibial pads absent.
(6) Notum of thorax well developed.
(7) Broad sternal plate present on thorax.
(8) Postero-lateral thoracic lobe present.
(9) Paratergal plates present on abdominal segments.
(10) Tergal and sternal plates present on abdominal segments.
(11) Probably long marginal setae present on abdominal segments 7 and 8.
(12) Genital plate of the male entire, *i.e.*, not lyriform.
(13) Spermatheca probably absent.
(14) Gonapophyses present.
(15) Eyes well developed.
(16) Spiracles of type C or D (see Webb, 1948, fig. 16).

In comparing the characters of each genus with the above list, it is clear that *Pecaroecus* and *Haematopinus* possess by far the greatest number of generalized features. *Pecaroecus* is specialized only in the reduction of the thoracic notum, the absence of long marginal setae on the abdomen (if, indeed, this is a specialized character), the presence of a tibial pad apposing the claw on the first pair of legs only and the advanced stage of development of the atrial sculpturing of the spiracles. *Haematopinus*, on the other hand, is only more specialized than *Pecaroecus* in the possession of tibial pads on all the legs and the greater degree of reduction of the eyes (see Webb, 1948 *b*). Thus, although it is improbable that *Haematopinus* developed directly from *Pecaroecus*, since the greater reduction of the thoracic sternal plate and the absence of minute spines on the atrial walls of the spiracles of the latter are characters more specialized than those to be found in *Haematopinus*, yet the two genera are evidently very close together and *Pecaroecus* may well be very near the ancestral form.

Another genus showing a number of haematopinoid characters is *Hybophthirus,* although this louse from the Tubulidentata (aard-vark) is also specialized in other respects. The disparity in the size of the legs and the fusion of the tibia with the tarsus in the 2nd and 3rd pairs, is an advance over the structure of the legs in *Haematopinus.* Further specializations in *Hybophthirus* are the loss of the thoracic sternal plate and the tergal, sternal and genital plates in the abdomen, though here the transverse furrows in the abdominal cuticle are reminiscent of both *Haematopinus* and *Pecaroecus.* It seems possible, therefore, in this instance that *Hybophthirus* may be a direct derivative of *Haematopinus.*

It is reasonable to assume that all the pinnipede-infesting genera, *Echinophthirius, Proechinophthirus, Antarctophthirus* and *Lepidophthirus,* are derived from a common ancestral genus and, therefore, may be considered together from the point of view of their origin. Here, again, the post-antennal angles, the presence of occipital apophyses, the equal legs in *Echinophthirius* and the possible absence of a spermatheca, point to an ancestral form similar to, if not identical with, *Haematopinus.* Naturally, in lice living under the extreme conditions obtaining in the fur of a pinnipede, it would be expected that their structure would become highly modified. These modifications are seen in the development of the spiracles into a type not readily referable to any others known in the Siphunculata and the development of a formidable armature of spines. In addition, the 1st pair of legs becomes reduced, the tibia and tarsus fuse and the sclerotized tergal and sternal plates of both the thorax and the abdomen almost entirely disappear. The presence of a lyriform type of genital plate in the male of *Echinophthirius* is not held to suggest relationship with other lice in which a similar plate is found, for the lyriform plate could well be formed independently in different genera merely by the disappearance of the central portion of an entire genital plate such as is seen in *Haematopinus.* Equally, the absence of gonapophyses is a character peculiar to this group of genera. Among these genera specialization appears to have proceeded to an increasing degree in the order *Echinophthirius, Proechinophthirus, Antarctophthirus* and *Lepidophthirus.*

Among the genera here included in the linognathoid group none appears to retain so many characters of a generalized nature as are to be found in *Pecaroecus* or *Haematopinus.* The greatest number of primitive characters are, perhaps, retained by *Linognathus.* These include the retention of at least part of the notum and sternum of the thorax, the long marginal setae on the abdominal segments 7 and 8 and the entire genital plate in the male. Moreover, unlike the haematopinoid group, *Linognathus* possesses a spiracle with atrial sculpturing of a definitely more primitive type. *Linognathus* is more specialized than *Haematopinus,* however, in the absence of post-antennal angles and occipital apophyses in the head, the reduction of the first pair of legs and the fusion of the tibia and tarsus in the second and third pairs, the absence of tergal, sternal and paratergal plates in the abdomen, and in the greater reduction of the eyes. The presence of a spermatheca, too, may well be a specialized character. Clearly, from the structure of the spiracles, *Linognathus* and *Haematopinus* are related forms, but it is equally evident that neither of these forms could have been derived directly from the other, since the mixture of special and general characters in each are not complementary. Nor, for the same reason, could *Pecaroecus* itself have been ancestral to *Linognathus.* We are forced to the conclusion, therefore, that it is probable that both *Linognathus,* on the one hand, and *Pecaroecus* and *Haematopinus,* on the other, represent two branches of a bifurcation arising from a still more primitive ancestral form. This bifurcation is probably reflected in the division here of the ferungulate genera of lice into two groups, the linognathoid group and the haematopinoid group.

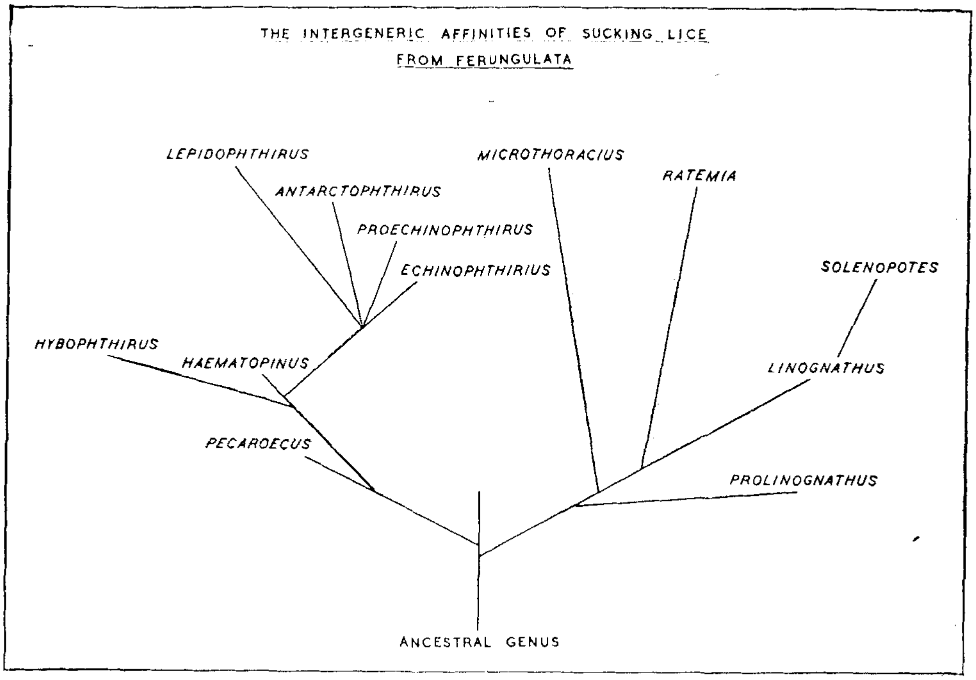
The genus *Prolinognathus* is related to *Linognathus* and, although more specialized in some respects, it retains some important primitive features not found in the latter. The spiracles, particularly of the abdomen (see Webb, 1947), are the most primitive known from lice of the Ferungulata and, in the head, vestiges of the occipital apophyses remain. Furthermore, the first pair of legs are not so greatly reduced as in *Linognathus*. On the other hand, the absence of notal and sternal plates in the thorax and the reduction of the genital plate in the male to the lyriform type are characters showing a greater degree of specialization than those of *Linognathus*. Here, again, neither *Linognathus* nor *Prolinognathus* could have been ancestral to one another as such. The most probable interpretation of the facts is that *Prolinognathus* is an early offshoot from a stock later giving rise to *Linognathus*.

Also related to *Linognathus* is the genus *Ratemia*. *Ratemia* is, however, more primitive than *Linognathus*, in the retention of paratergal plates on abdominal segments 4–6 and in a possible absence of a spermatheca, though this is not certain from the specimens to hand. The sternal plate of the thorax is also broader in *Ratemia*, but this is, perhaps, of little importance. On the other hand, *Ratemia* is more specialized than *Linognathus* in the reduction of the genital plate in the male to the lyriform type and possibly in the short marginal setae on the abdomen. The spiracles are of a type found in a few species of *Linognathus*, but are more advanced than those of the majority of species of that genus. The only character which suggests that *Ratemia* could not have been derived directly from *Linognathus* is the retention of paratergal plates; nevertheless, it is reasonable to suppose that the two genera are comparatively close and that *Ratemia* may well have arisen from the same stock as *Linognathus*, possibly at a later date than *Prolinognathus*.

The position of the genus *Microthoracius* is somewhat more difficult to assign. The primitive features it possesses are the well-formed occipital apophyses, the slight reduction only of the first pair of legs, the separate tibia and tarsus in all three pairs of legs, and the well-developed eyes. None of these characters are found in *Linognathus* though they are present in *Pecaroecus*. The form of the spiracles, the absence of prominent post-antennal angles on the head, the absence of paratergal plates and the possession of a spermatheca, on the other hand, are linognathoid characters, although it is probable that only spiracle form and the spermatheca are important. It is possible that absence of post-antennal angles, paratergal plates, reductions in thoracic and abdominal plates and setae are all features which may have evolved independently and therefore may have little phylogenetic value. The generalized character of the legs, the occipital apophyses and the well-developed eyes, although evidently primitive, do not preclude evolution from the base of the linognathoid rather than the haematopinoid stock. The spiracle form and the spermatheca, on the other hand, are positive linognathoid characters, and therefore it is tentatively concluded that *Microthoracius* is an early offshoot from somewhere near the base of the linognathoid stock, possibly a little later than *Prolinognathus*, in view of the structure of the spiracles. With *Pecaroecus* arising from the base of the haematopinoid stock and *Microthoracius* from the base of the linognathoid stock, it is not surprising that they should possess many characters in common in spite of later specializations.

As far as the remaining genus *Solenopotes* is concerned, it appears to be almost certainly a direct derivative of *Linognathus*. The only characters listed above that are not shared by the two genera are the form of the thoracic sternal plate and the form of the genital plate in the male. The differences in shape in the sternal plate are more in the nature of a specific, rather than a generic, distinction, and the lyriform genital plate, as explained above, is easily derived from the more primitive entire genital plate by loss of the central portion and, indeed, appears to have been so formed on a number of separate occasions, notably in *Microthoracius* and *Echinophthirius*. There is, therefore, no reason to suppose otherwise than that the form of *Solenopotes* could be derived from one as advanced as *Linognathus*. The arrangement of the genera of sucking lice from

Figure 147.



Ferungulata postulated in this discussion of their affinities has been illustrated diagrammatically in fig. 147. It should be stressed, however, that the length of the lines connecting the different genera on the diagram are not necessarily indicative of their degree of separation.

XV. Parallel Evolution in the Anoplura.

In this study of the Siphunculata it has become more and more evident that many of the structures used in the classification of these insects have developed independently. This seems to be due to parallel evolution brought about not so much by similar environmental stimuli causing similar mutations to be selected because of their survival value, but rather as a result of inherent tendencies in lice of related groups to develop certain structures in a definite direction, independently of one another. It is suggested that evolution of this type may arise through genes, possibly under suitable stimulation, tending to mutate in a certain way thus producing a series of structures in what may be termed a predetermined sequence.

After examining a number of sucking and biting lice, it is the opinion of the writer that a number of their characters have developed in this manner. One of the best examples is seen in the development of the spiracles in the Trichodectidae and the Siphunculata. Whereas the spiracles of the Siphunculata have been worked out in considerable detail, those of the Trichodectidae have received only a limited treatment, nevertheless, sufficient is known of the latter group to enable a comparison to be made. In a series represented by sucking lice from certain rodents and from Ferungulata, it has been shown (Webb, 1946 and 1948) that, as the spiracle evolves, the size of the atrium increases and the atrial wall undergoes a number of convolutions resulting in a definite pattern of sculpturing. First, the atrial wall becomes annularly constricted to form ledges, next these become joined by cross-ledges to form a honeycomb of cells, and finally the ledges disappear to a varying degree, leaving their points of junction projecting into the atrium as chitinous processes. Now in the Trichodectidae, the spiracles, apart from being almost exactly similar in construction, develop atrial sculpturing in exactly the same manner. The spiracles develop annular ledges (Webb, 1946, fig. 50), which become joined by cross-ledges (Webb, 1946, figs. 43 and 46), and finally the intermediate portions of the ledges begin to break down, leaving chitinous filaments projecting into the atrium, where the ledges joined one another (Webb, 1946, figs. 30–32). So similar is the development of the spiracles that, if the spiracle of say, *Trichodectes canis*, is compared with one from *Linognathus vituli* (Webb, 1946, figs. 30–32 and 157–159), they would be accepted as spiracles of species of the same genus. Now any connection between the Trichodectidae and the Siphunculata can only be very distant, the groups having been distinct from at least the Cretaceous period and possibly earlier, at which time the spiracles of the Siphunculata, at least, and almost certainly those of the Trichodectidae, too, were not only very small, but were also devoid of atrial sculpturing. We must conclude, therefore, that the evolution of the spiracles in *Trichodectes canis* and *Linognathus vituli* has been entirely separate and that the development of almost identical structure has been achieved independently from simple beginnings.

It may be argued that the agreement between the structure of the spiracles in Siphunculata and Trichodectidae may have arisen as a result of their sharing the same environment. This is true to the extent that both biting and sucking lice are found together on the same host animal. Such an argument would be valid if the structures involved were purely adaptive. Here, although the development of the spiracles is in a sense adaptive, the most efficient form of spiracle evolved in the series has been arrived at by a circuitous route when it could have been developed directly from the basic structures already in existence. Furthermore, as has already been stated, it appears that the method of development adopted was identical in both Trichodectidae and Siphunculata. Now the atrium of the spiracle appears to serve only one function, that of the removal of dust from the inspiratory air-stream. This filtering mechanism is achieved in a spiracle of the type under discussion mainly by the passage of air into a comparatively large chamber through a small aperture leading from the exterior. Thus, while passing through the atrium, the velocity of the air-stream falls considerably and, possibly at the same time, swirling movements occur and dust previously held in suspension by air movement, is deposited on the walls of the atrium (see Webb, 1945). One of the evolutionary trends seen in these spiracles is the increase in the size of the atrium. This fulfils the double purpose of increasing the efficiency of the atrium as a deposition chamber and providing a greater volume in which larger and larger quantities of dust may accumulate without seriously impairing the efficiency of the atrium or, indeed, blocking it entirely. In addition, some mechanism is required to hold the dust as it accumulates on the atrial wall. If the atrial wall were entirely smooth, then dust collected there might be expected to find its way eventually into the trachea merely by the action of the insect's body movements. This need is fulfilled in both the Siphunculata and the Trichodectidae by the coating of the atrial wall with a sticky fluid secreted by a spiracular gland (see Webb, 1946), and by the provision of irregularities on the internal surface of the atrium in between which dust can collect. It is the form of these irregularities which is of interest at the moment. In the simplest, smallest and presumably most primitive spiracles in the Siphunculata the atrial wall is covered with minute projections for holding dust accumulations. Now, theoretically, it would be expected that one of the most efficient forms of dust trap would be a series of long spines projecting from the atrial wall and coated with a sticky fluid. Spines of this type would not subdivide the atrium and therefore reduce its effective volume as a deposition chamber for air could pass freely between them. At the same time, however, the spines would serve not only to filter larger particles from the air-stream, but also to anchor the dust accumulations to the atrial wall as the deposit became thicker and thicker, right up to the point when the entire space between the spines is filled with dust and the volume of the atrium so reduced that it can no longer serve either as a direct filter or as a deposition chamber. The form of atrial sculpturing in which the atrium is either subdivided by annular ledges or covered with box-like cells when the annular ledges are joined by cross-ledges, should be less efficient than a series of spines simply because the ledge-system reduces the effective volume of the atrium and forces air to pass in a comparatively swiftly flowing stream down the ledge-free central channel. If this disadvantage is overcome by a still greater increase in atrial volume, thus forming a large open central channel, the atrium remains less efficient than one using spines to hold the dust as, in the absence of spines, there is no direct filtering of air. The filtering effect of spiracles with either ledges or spines is well seen in the far greater quantities of dust which are almost always found in the latter in comparison with the amounts in spiracles even with the most highly developed ledge system. It is significant, too, that the most advanced spiracles in the Siphunculata possess atrial spines, but only after first developing a series of ledges. The efficiency of the atrial spines as a filtering mechanism is demonstrated elsewhere (Webb, 1946, figs. 189 and 190). The method of developing these spines is most unusual for, after a series of box-like cells is formed on the atrial wall from annular and cross-ledges, these are then broken down leaving only the points of junction of the ledges projecting into the atrium. As the small primitive spiracle in Siphunculata starts with a covering of minute spines, it would surely have been more direct to have developed these as the atrium increased in size rather than to have evolved an entirely new type of sculpturing, and later to modify that to reach the same end.

The point of importance here, then, is that, in both the Siphunculata and the Trichodectidae, the evolution of the spiracle is not necessarily adaptive as what would appear to be an easier, more direct method of reaching the most efficient type of atrial sculpture from a basal form already laid down in the small spines of primitive spiracles, is discarded in favour of the same more devious route in both groups. It is suggested, therefore, that the development of a sequence of types of atrial sculpture in both groups of lice is due to the selection by environmental conditions of favourable novelties not from a variety of chance mutations, but from a series of mutations tending to occur in a more or less definite direction. There is evidence, too, to suggest that this is not an isolated instance for, to a more limited extent, the same process seems to have occurred in the development of spiracle structure within the Siphunculata themselves. The genera *Haematopinus*, *Microthoracius*, *Ratemia* and a few species of *Linognathus* such as, *L. fractus* and *L. hippotragi*, possess spiracles of a similar advanced type with atrial processes formed from the breakdown of a ledge system, and yet it has been shown above that these lice probably diverged at an early date from an ancestral form whose spiracles must have had a more or less complete ledge system. It is clear, then, that the break-down of ledges to form spines in these genera and species has occurred independently at least four and probably more times, as each species of *Linognathus* with atrial spines or processes has almost certainly acquired them separately.

The development of cross-ledges joining the annular ledges in the atrium appears to be connected in some way with the size of the spiracle in the adult. The sucking lice from rodents almost all possess small spiracles, that is up to about 20 μ diameter at the widest part of the atrium, with a characteristic type of sculpturing in the form of a series of annular ledges only. In *Prolinognathus* from hyrax, the thoracic spiracle is rather larger than those commonly found in lice from rodents while the abdominal spiracle is of the same order of size as those from that group (Webb, 1947). In the thoracic spiracle of that species cross-ledges are present in the distal region only, while, in the abdominal spiracle, they are absent. It seems, then, that the thoracic spiracle is just over the threshhold of size at which cross-ledges are formed. In *Linognathus* the spiracles of almost all species are considerably larger than 20 μ diameter and possess both annular and cross-ledges throughout. The series of species of *Linognathus* from Bovidae and Giraffidae, with the exception of *L. fahrenholzi*, *L. hippotragi* and *L. ovillus*, have spiracles of much the same type, but covering a considerable range in size. Now the abdominal spiracles of some of the species in this series, notably *L. brĕviceps*, *L. gnu* and *L. damaliscus*, are very small, not greatly exceeding 20 μ diameter and here the cross-ledges are noticeably few in number or are absent entirely. Although we cannot be certain that the small abdominal spiracles in these species of *Linognathus* are not primitive, it seems more probable that they are derived from a more normal type of linognathoid spiracle with a comparatively large number of cross-ledges by means of a process of reduction. Thus, it would seem that, when the size of the atrium reaches a low limit of about 20 μ diameter, the cross-ledges disappear and the spiracle reverts to the type common in some rodent lice. To illustrate this point, the diameter of the distal region of the abdominal spiracle of each species was measured and the number of cross-ledges on the atrial wall in that region counted (see Table V). A graph was drawn showing the relationship between atrial diameter and number of cross-ledges (see fig. 148), and it was found that the points plotted fell more or less into a straight line with the number of cross-ledges increasing regularly as the diameter increased above 20 μ. Thus annular ledges may be present in spiracles of under 20 μ diameter, but not cross-ledges. As soon as the atrium reaches a size above 20 μ diameter, cross-ledges begin to appear and increase in number with spiracle size. Similarly, should the size of the spiracle decrease for any reason, then the cross-ledges become fewer in number and finally disappear at a diameter of about 20 μ. This relationship, however, seems only to apply to adults of different species within a related series. In the spiracles of the nymphs of *L. pedalis* there is very little variation in the number of cross-ledges in the distal bulb of the atrium from one instar to the next, although there is a considerable increase in diameter (see fig. 148). There are as many cross-ledges in the abdominal spiracle of the first nymph, which is 25 μ diameter, as would be expected to be found in an adult spiracle of 38 μ diameter in the *Linognathus*

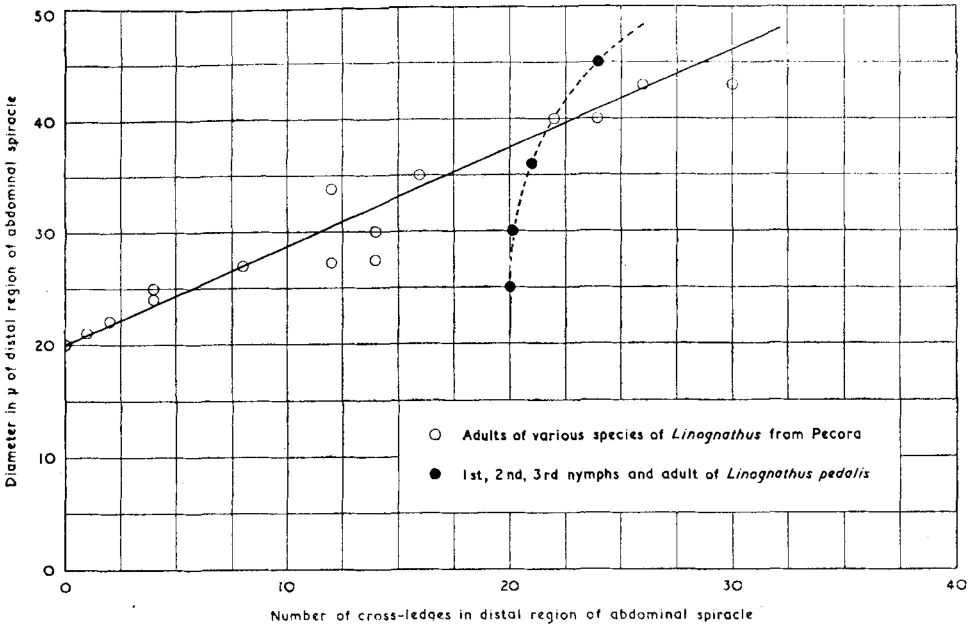
TABLE V.

Species of *Linognathus*.	Diameter in μ of distal region of abdominal spiracle.	No. of cross-ledges in distal region of abdominal spiracle.
pedalis (adult)	45	24
pedalis (3rd nymph)	36	21
pedalis (2nd nymph)	31	20
pedalis (1st nymph)	25	20
stenopsis	27	14
africanus	30	14
gazella	40	24
breviceps	20	0
angulatus	27	12
aepycerus	25	4
tibialis	25	4
pithodes	27	8
lewisi	34	12
gnu	22	2
damaliscus	21	1
taurotragus	35	16
fractus	40	22
limnotragi	43	26
brevicornis	43	30

The relationship between the size of the abdominal spiracle and the number of cross-ledges in certain species of *Linognathus*.

series under discussion. Clearly, then, the formation of cross-ledges only when a spiracle exceeds 20 μ diameter is not due to any mechanical impossibility of forming cross-ledges in a spiracle at that size, for the spatial arrangement of ledges in the first nymph spiracle is so close that there is ample room in a spiracle of less than 20 μ diameter to develop some cross-ledges equally closely-spaced. Nor would it seem that the appearance and increase in number of cross-ledges is a straightforward case of allometry, for their number does not increase exponentially with increase in atrial size. Furthermore, if we turn to the species *L. fahrenholzi*, *L. hippotragi* and *L. ovillus*, which were excepted from the *Linognathus* series tabulated above, the number of ledges present in their abdominal spiracles in relation to size agrees neither with those of other species of *Linognathus* nor with each other. Thus it may be concluded that the spacing of cross-ledges in the *Linognathus* spiracle is not fixed, and that the ratio between the number of ledges and atrial size is not necessarily the same in all species, although it may be so in related species. It should be added that the lower limit of 20 μ atrial diameter for the development of cross-ledges appears to apply equally to spiracles of both Siphunculata and Trichodectidae. In the Trichodectidae, although only a few species have been studied, those spiracles without cross-ledges, such as the abdominal spiracles of *Bovicola ovis*, *Cervicola longicornis* and *Eutrichophilus setosus*, are all about 20 μ or a little less in diameter at the widest part of the atrium. The thoracic spiracle in each of these species is considerably larger and bears both annular and cross-ledges.

Figure 148.



The relationship between the number of cross-ledges in the abdominal spiracle and its size in the species of *Linognathus* given in Table V.

It has been suggested earlier that parallel evolution in the Siphunculata is not confined to the spiracles. In sucking lice from Ferungulata, for instance, there appears to be a tendency for the first pair of legs to become reduced and the second and third pairs enlarged. This has occurred, independently, certainly twice in the lice from Pinnipedia and in *Linognathus* and probably five or six times, if other genera, such as *Ratemia* and *Hybophthirus* are separately derived, as they almost certainly are, from lice with equal legs. Other characters acquired independently by more than one group are the fusion of the tibia and tarsus in some or all of the legs, the reduction of thoracic notal and sternal plates, the disappearance of tergal, sternal and paratergal plates in the abdomen, the disappearance of the central portion of an entire genital plate in the male to form a lyriform plate, and also the almost complete loss of eyes. It is quite evident, therefore, that great care is needed in analysing the complex mixture of generalized and specialized characters to be found in all forms of lice existing to-day before an assessment of their affinities is made.

XVI. The Development of a Louse Fauna in the Ferungulata.

The foregoing sections of this paper have been concerned chiefly with providing a body of data on the morphology, particularly of the spiracles, of the various genera of sucking lice from Ferungulata and, by analysis, determining their probable intergeneric affinities. Attention has been paid to host relationships only in so far as the distribution of species within any one genus provides evidence as to the possible affinities of the hosts, and no attempt has yet been made to relate the affinities of the louse genera to their distribution on the eutherian orders comprising the Ferungulata. It has been stressed often before, that the validity of any assumptions of eutherian affinities based on those of their louse fauna is subject to the provision that any particular louse is normal to its host, that is, the infestation is of a primary and not a secondary nature due to straggling, however ancient, from a host of one species to one of another, even of the same genus. It is assumed that normal infestations of lice are always, and always have been, acquired by the host from a member of the same species, either from male to female or, more probably, from parent to offspring. It is to this fact that the virtual absence of obligate ectoparasites in any group other than the birds and mammals, which show parental care, may perhaps be attributed. Now, the sucking lice are more specific in their hosts than any other ectoparasite with the possible exception of some of the Acarina. Hopkins (1949) considers the straggling of lice from one host species to another to be an occurrence of great rarity. Instances of straggling are known, however, as in the case of *Pediculus mjöbergi* infesting South American monkeys probably from man, and *Solenopotes capillatus* from a deer infesting domestic cattle, but both these transferences are of comparatively recent date. Nevertheless, it is rare for lice transferred from one host species to another to become thoroughly established even though they may live for a time. Such cases of recent straggling are usually easily detectable. Although instances of recent straggling may be obvious, those of long standing in which the parasite has had time to become adapted to its new host, and may even have evolved along a line differing from that of the parent stock, may be almost impossible to determine. This may be particularly true of any secondary infestations dating from a time very early in the evolution of both the Siphunculata and the Eutheria. It is probable that, as the different orders of Eutheria were at the point of inception, they were much closer to one another in both morphology and physiological constitution. Thus any host specificity shown by the parasites at that time would be less highly developed than it is to-day and would not, therefore, provide so effective a barrier against the establishment of secondary infestations. The problem of the interrelationships of the Siphunculata and their hosts should be approached with this in mind, and, consequently, it is impossible to be dogmatic about any of the conclusions tenatively reached below.

The most striking feature of the distribution of Siphunculata on Ferungulata is the way in which the majority of the host groups harbour lice characteristic of themselves. As far as is known at present, *Ratemia* is found on Equidae and nowhere else, the genus *Linognathus* and its relative *Solenopotes* are almost confined to the Pecora, *Microthoracius* is characteristic of the Camelidae, *Pecaroecus* is recorded only from Tayassuidae, and the genera *Echinophthirius*, *Proechinophthirus*, *Antarctophthirus* and *Lepidophthirus*, which may here be treated as one group, are characteristic of Pinnipedia. In addition, *Prolinognathus* is found only on Procaviidae and *Hybophthirus* on Tubulidentata. Unlike these genera, however, *Haematopinus* is far more widely distributed and is found on Equidae, Suidae, Bovidae and Cervidae. A species of *Haematopinus*, *H. tuberculatus*, is also recorded from camels in domestication but, as this is almost certainly a case of secondary infestation, it is here disregarded. Now, however these genera of lice may be related to one another, it is clear from evidence of spiracle structure and other characters, that they form a natural group with reference to the remainder of the Siphunculata and, as they are all found on Ferungulata, which presumably is also a natural group, we may assume that the presence of these lice, as a whole, on Ferungulata is a result of one or more primary infestations dating back to the inception of the host group. Similarly, each genus of lice characteristic of a single ferungulate group is probably also derived from a later primary infestation. The wide, somewhat discontinuous distribution of the genus *Haematopinus* has been discussed at some length earlier in this paper, when the view was expressed that the genus probably achieved its present distribution through the presence on the common ancestral group of those hosts on which it is found to-day. At the same time, the possibility of straggling from a primary host to a variety of secondary hosts was not excluded. Another point of importance in this discussion is the presence of species of *Linognathus* on Carnivora of the family Canidae, when the remaining species of the genus infest pecoran hosts. This question, too, has been considered above, and the view adopted is that *L. setosus* and *L. taeniotrichus* are normal to Canidae although, here again, there is a possibility of ancient straggling from an early artiodactyl on to a carnivore. If this is correct, then the genera *Haematopinus* and *Linognathus* are far more ancient than has hitherto been supposed. The only other sucking lice found on Carnivora are the related genera from Pinnipedia which, although highly specialized, appear to be derived either from *Haematopinus* or a close relative. The existence of primary infestations of either *Haematopinus* or a derivative on Carnivora, Perissodactyla and Artiodactyla means that *Haematopinus* must have been present on the common ancestor of these three eutherian orders. The genus *Linognathus*, too, is also present on Carnivora and Artiodactyla and, therefore, was presumably present on a common ancestor of these two orders. These two important conclusions mean that the genera *Linognathus* and *Haematopinus* have been in existence since, at the earliest, the end of the Cretaceous or possibly the beginning of the Palaeocene period and that, by that time, lice on the Ferungulata had run through the entire range of evolution of atrial sculpturing of their spiracles, later evolution involving only minor modifications of existing atrial types. Thus phylogenies of both parasite and host, based on the relationship between these main types of atrial structure and other characters, are referable to the period commencing with the origin of the Siphunculata on Eutheria, possibly near the origin of the Eutheria themselves, and say, the beginning of the Palaeocene, a period during which the great majority of eutherian orders became differentiated, and one in which the fossil history of the Eutheria is least well known and partly conjectural.

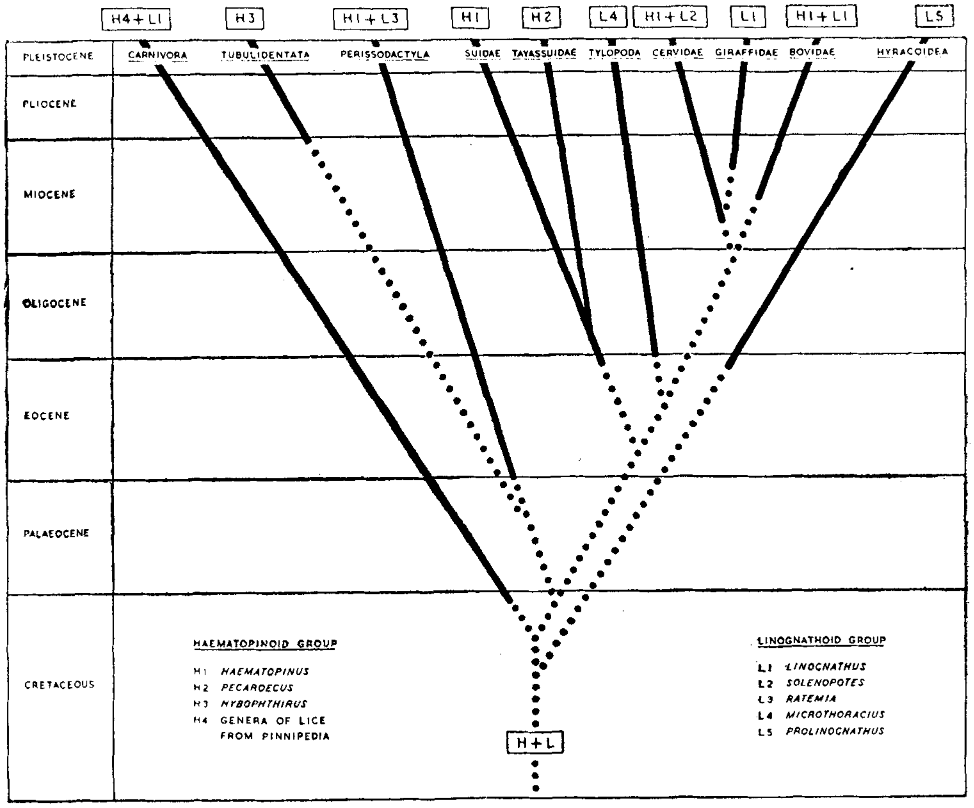
Following these arguments to a logical conclusion, it is evident that the ancestral stock of the Ferungulata must have been infested with at least three, and probably more, genera of sucking lice, namely, *Haematopinus*, *Linognathus* and, probably, the ancestors of *Pecaroecus*, *Microthoracius*, *Ratemia* and *Prolinognathus*. Some indication of the richness of the louse fauna of early Eutheria is probably given by the number of different lice on the Procaviidae, in which two species of sucking louse and at least eight species of four genera of Trichodectidae (Hopkins, 1949) have been recorded. The lice of Ferungulata, as seen to-day, are probably the remnants of a much more extensive fauna which, like their hosts, reached a peak in diversification and have since largely become extinct. The existence of a large number of different genera and species of lice on single host individuals would result from increasing specialization along different lines from generalized ancestors, and the tendency for these lines to evolve further would gradually diminish as each form of louse became more and more closely adapted to its host. Once adaptation had been achieved, however, competition between different genera or even species of lice would tend to result in the extinction of all but one or two forms. That such competition between ectoparasites does occur is well known, for in almost all cases of multiple infestation, both of Siphunculata and Mallophaga, it is rare to find different species occurring in more or less equal numbers, almost always one species greatly predominates.

The view taken here, then, is that, on the ancestral stock of the Ferungulata, primitive more or less generalized sucking lice had given rise to two groups of genera represented by the haematopinoid and linognathoid groups outlined above. These groups contained the genera *Haematopinus* and *Linognathus* as they are known to-day and probably a number of other forms which may either have been generically identical with the other genera found at present on Ferungulata, or have been ancestral to them. As the orders and families comprising the Ferungulata became differentiated, these lice became distributed over an increasing number of host groups and, in some cases, proceeded to evolve along lines of their own. Gradually, competition, both interspecific and intergeneric, brought one group of lice after another to extinction until, in most host groups, only one or two forms remained, different genera surviving in each case, each now characteristic of its own host group. More recently, with the formation of new species in the host groups, new species of lice evolved, bearing much the same relation one to another as their hosts. Such speciation is still proceeding. Later, the extinction of a great many of the ferungulate groups occurred and left a residue of forms infested with a few widely differing lice whose affinities now are difficult to trace. Such, then, may well be the origin of the different genera of lice characteristic of each group in the Ferungulata.

Now the affinities between lice can only be of value in indicating host relationships, if the lice in question had been evolved on the host stock after that stock had become differentiated, and this is evidently true in only a limited number of cases. Firstly, the ferungulate lice as a whole are clearly related, and therefore indicate that the Ferungulata themselves are a related group. After this, however, apart from the relationship between the genera *Linognathus* and *Solenopotes* indicating bovid and cervid affinity, and the relationship between the pinnipede lice, a corresponding affinity between the pinnipede groups, only interspecific louse relationships are of importance in determining ferungulate affinities. The existence of a form like *Pecaroecus* on Tayassiudae and *Microthoracius* on Camelidae, does not mean that the peccaries and the camels are of exceptionally ancient origin because their lice are particularly generalized. It is quite evident that *Pecaroecus* and *Microthoracius* date back to a time long before either of the host groups had become separated off from their ancestral stock. The peccaries and the camels have, in fact, received their lice as a legacy from that ancestral stock, although these lice may have evolved further on their present host groups. The same findings apply to the genus *Haematopinus*. The existence of species of that genus on both Perissodactyla and Artiodactyla is no indication of particularly close affinity in the hosts, although it presupposes their common origin. The interspecific relationships, on the other hand, within each of the main groups of *Haematopinus* on Equidae, Suidae and Bovidae, are undoubtedly of significance (see Webb, 1948 *a*). In the same way, the presence of species of *Linognathus* on both Carnivora and Artiodactyla means nothing more than that the two orders arose from a common stock infested with *Linognathus*. The affinities between the species on pecoran hosts, however, may, as has already been shown, be taken as evidence towards the relationships of the groups, one with another within the Pecora. Both *Haematopinus* and *Linognathus* are evidently relatively stable genera and have existed as such over a period of time during which enormous progress has been made in the evolution of the hosts. Thus it is only their recent speciation which is of importance in determining host affinities.

It should be mentioned here that the evolutionary scheme outlined in this paper for Siphunculata from Ferungulata is in complete conformity with the arrangement of the host groups put forward by Simpson (1945) except, possibly, for the indication that the *Hippotraginae* of the Bovidae is not a natural group. That there should be so high a measure of agreement is strong indication, both of the correctness of the interpretation of ferungulate phylogenies and of the primary nature of at least the main infestations of Siphunculata on these hosts. As has already been stated, the importance of determinations of parasite affinities to mammalogists lies not so much in the confirmation of already well-proved mammalian relationships, though such confirmation gives confidence to proceed further, but in the indications of affinity between the larger groupings such as orders, super-orders and cohorts, whose origins lie far back in time and are not so surely known from the fossil record. An example of this is the

Figure 149.



THE DISTRIBUTION OF SUCKING LICE ON FERUNGULATA

A diagram showing the probable evolution of the Ferungulata and the distribution of Siphunculata on the Ferungulate groups.

probable connection between the Ferungulata and the Glires, as shown by the intermediate form of the spiracles of *Prolinognathus* between those characteristic of lice from Ferungulata and certain of the lice from Rodentia. How far this contention may be supported in the future may depend largely on the pattern of evolution emerging from the rodent lice as a whole which yet require to be worked out in detail. Confirmation of this relationship, however, is available from another source. In a paper on the helminth-fauna of South Africa, Baer (1925), writes : " Fuhrmann (1908) has shown that it is possible to establish the relationship between two groups of birds by their Cestode parasites. This has, to our knowledge, never been known to occur for Mammalian Cestodes, and in most cases does probably not exist. However, the genus *Inermicapsifer* may one day be shown to establish a certain relationship between the hyrax and rodents . . . ."

" We find the genus *Inermicapsifer* in the hyrax and in rodents, and we find, on the other hand, the genus *Anoplocephala* in the hyrax and in ungulates. Time and further study will show if this is a coincidence or if this is a true case where the relationship of the mammalian hosts is established by their Cestode parasites." This agreement in mammalian affinities postulated from two entirely separate parasite sources adds greatly to their probability, and suggests that profitable results may well emerge from an extended study of other parasitic groups, in particular the Cestoda and Trematoda.

XVII. SUMMARY.

(1) An account is given of the structure of the spiracles of the majority of the species of the genera *Linognathus*, *Solenopotes*, *Ratemia*, *Haematopinus*, *Microthoracius* and *Pecaroecus*, including the nymphal spiracles of *Linognathus pedalis* and *Pecaroecus javalii*. A list of the species is given on page 134.

(2) The host-relationships of the genera *Linognathus* and *Solenopotes* are discussed. The spiracles of lice of these two genera form a more or less continuous series and are therefore treated together. This series can be divided into three main groups the largest of which, with the spiracles of *L. pedalis* as a more or less central type, comprises species from members of the Alcelaphini of the *Hippotraginae*, the *Antilopinae*, the *Cephalophinae*, the *Caprinae*, the *Bovinae*, the Giraffidae and the Cervidae. The spiracles in this group form a continuous series of modifications. The second group comprises two species, *L. fahrenholzi* and *L. hippotragi* from members of the Hippotragini and Reduncini of the *Hippotraginae*. The third group includes *L. setosus* and probably *L. taeniotrichus* from Canidae and also *L. ovillus* from the domestic sheep. This last group is almost certainly unnatural, the similarity in the spiracles of *L. setosus* and *L. ovillus* in all probability being due to convergence and not indicative of close affinity.

(3) It is concluded from a study of their sucking lice that the *Caprinae*, *Bovinae* and *Cephalophinae* form a more or less closely related central group of the Bovidae with the *Antilopinae* and the Alcelaphini of the *Hippotraginae* respectively, of rather more distant origin and more closely related, one to another, than either is to the *Caprinae*.

(4) The spiracles of *Linognathus gnu* and *L. damaliscus* from members of the Alcelaphini of the *Hippotraginae* are near those of lice infesting members of the *Antilopinae*. The spiracles of *L. fahrenholzi* and *L. hippotragi* from members of the Reduncini and Hippotragini, also of the *Hippotraginae*, on the other hand, are as widely different from those of *L. gnu* and *L. damaliscus* as this rather compact group allows. Thus, according to the evidence derived from louse affinities, it would appear that the *Hippotraginae* is probably an unnatural assemblage, since the lice from Alcelaphini show affinities with those from the *Antilopinae*, while lice from the Hippotragini and Reduncini fall together as a group, showing no close affinity either with those from the Alcelaphini or, for

that matter, with any Siphunculata here examined from any Bovidae. Simpson (1945), who has defined the *Hippotraginae*, has expressed doubts as to its validity.

(5) The position of lice of the genus *Solenopotes* from Cervidae, near those from members of the *Bovinae*, suggests some relationship between the Cervidae, on the one hand, and a central group of the Bovidae on the other. Furthermore, the intermediate position of *Linognathus brevicornis* from the giraffe between cervid and bovid lice upholds the view that the Giraffidae arose, either as an early offshoot from the Cervidae, or from a position somewhere between the Bovidae and Cervidae at a time shortly after this bifurcation took place.

(6) The possibility of Canidae acquiring lice from sheep or *vice versa* to account for the similarity in spiracle structure in *Linognathus setosus* and *L. ovillus* is discussed. The view adopted is that, in all probability, *L. setosus* is normal to Canidae, or at least was acquired at a very early date, possibly long before the sheep had been evolved, and that *L. ovillus* is normal to the sheep, the similarity of spiracles in *L. setosus* and *L. ovillus* being fortuitous.

(7) The host-relationships of the genus *Ratemia* are discussed. *R. squamulata* is claimed to possess undeniable affinities with the genus *Linognathus* because of its spiracle structure, but, at the same time, presents characters more in keeping with *Microthoracius*, *Pecaroecus* and *Haematopinus*. *Ratemia* is known only from Perissodactyla and, as it may be considered a relative of *Linognathus*, then the existence of lice of the linognathoid type on the Artiodactyla, Carnivora and Perissodactyla suggests a probable common origin for these three eutherian orders.

(8) The host-relationships of the genus *Haematopinus* are discussed. With the exception of the spiracles of *H. taurotragi*, the degree of variation between spiracles of different species is very small. The species fall into three groups: firstly, those in which the spiracles are small relative to body length and bear traces of a ledge system on the atrial walls—these species infest Equidae; secondly, those in which the spiracles are large relative to body length and also retain traces of a ledge system—these species infest Bovidae; thirdly, those in which the spiracles are small relative to body length, but retain no traces of ledges even in the nymph—these species infest Suidae. The fact that the species of *Haematopinus* fall into three groups coincident with the grouping of the hosts, suggests that none of these infestations is of particularly recent date and that *Haematopinus* was either present on a common ancestor of the Equidae, Bovidae and Suidae or else, if straggling did take place, that the parasites were acquired comparatively early in the evolution of their hosts. The possible causes of the discontinuous distribution of *Haematopinus* are discussed, and it is thought more probable that lice of this genus are normal to their hosts and were present on the common ancestor of the Artiodactyla and Perissodactyla than that they achieved their present distribution by extensive straggling, though some degree of straggling is not excluded as a possible contributory cause.

(9) The difference in spiracle structure between *Haematopinus taurotragi* and other species of that genus infesting *Bovinae* is greater than might be expected, in view of the comparatively close relationship between their hosts. This distinction, however, may reflect their host affinities, for *H. taurotragi* infests a member of the tribe Strepsicerotini, whereas other species with which it is here grouped are from members of the tribe Bovini of the same subfamily, the *Bovinae*. It should be noted, however, that the differences in spiracle structure involved are greater than those between all other species of *Haematopinus*, even though their hosts are far more widely separated, as in the case of species from Equidae and Suina.

(10) The host-relationships of the genus *Microthoracius* are discussed. It is noted that the spiracles of species from the Old and New World Camelidae show a close similarity indicating a high degree of stability in this structure, in view

of the fact that the hosts must have been separated since the Pliocene period and possibly earlier. Species of *Microthoracius* from llamas possess spiracles which are closer to one another than they are to those of species from the camel. It is considered that the spiracles in *Microthoracius* are nearer to those of *Linognathus* than to those of *Haematopinus*, though probably not derived directly from either. The close association of *Microthoracius* with other genera of lice infesting Ferungulata, in spite of its specialized body form, is in keeping with the phylogeny of the hosts, although it casts no fresh light on the origin of the Tylopoda.

(11) The host-relationships of the genus *Pecaroecus* are discussed. *P. javalii*, from the collared peccary, is a louse possessing more generalized characters than any other from Ferungulata and yet has spiracles almost identical with those of *Haematopinus*, and as specialized as any found within the group. The affinities of this louse lie rather with *Haematopinus* than with *Linognathus*, although, like *Microthoracius*, it is clearly not derived directly from either. The affinities of the Tayassuidae are not particularly clarified by the relationships of *Pecaroecus*.

(12) An analysis of the main characters of each genus of sucking lice infesting members of the Ferungulata is made. It is evident from this study that the twelve genera considered fall broadly into two groups, the first called the linognathoid group comprises the genera *Linognathus*, *Solenopotes*, *Ratemia*, *Microthoracius* and *Prolinognathus*; the second, the haematopinoid group, comprises the genera *Haematopinus*, *Pecaroecus*, *Hybophthirus*, *Echinophthirius*, *Proechinophthirus*, *Antarctophthirus* and *Lepidophthirus*.

(13) On a basis of comparison of 16 generic characters, it is concluded that *Pecaroecus* is the most generalized genus of sucking louse from Ferungulata and that *Haematopinus* is only slightly less primitive. It is held to be improbable that *Haematopinus* was derived directly from *Pecaroecus*, although the two genera evidently originated from the same stock.

(14) The genus *Hybophthirus* from Tubulidentata, although more specialized, has a number of characters in common with *Haematopinus* and could be a direct derivative from that form.

(15) The pinnipede-infesting genera, *Echinophthirius*, *Proechinophthirus*, *Antarctophthirus* and *Lepidophthirus* are evidently derived from a common ancestral genus, and therefore are considered together. In spite of their extreme specialization, sufficient remains of their fundamental body plan to indicate that they have either arisen from *Haematopinus* or from a form very near that genus.

(16) Among the genera included in the linognathoid group the greatest number of primitive characters are to be found in *Linognathus*, although this form is not nearly so generalized as *Pecaroecus* or *Haematopinus*. It is concluded that, although *Linognathus* and *Haematopinus* are related, neither could have been derived directly from the other, nor could *Pecaroecus* itself have been ancestral to *Linognathus*. It is thought probable that both *Linognathus*, on the one hand, and *Pecaroecus* and *Haematopinus*, on the other, represent two branches of a bifurcation arising from a still more primitive ancestral form.

(17) The genus *Prolinognathus* is related to *Linognathus* and, although more specialized in some respects, it retains some important primitive features not found in the latter. Here, again, neither *Linognathus* nor *Prolinognathus* could have been ancestral to one another as such. The most probable interpretation of the facts is that *Prolinognathus* is an early offshoot from a stock later giving rise to *Linognathus*.

(18) Another genus related to *Linognathus* is *Ratemia*. *Ratemia* is, however, more primitive than *Linognathus* in some respects, and more specialized in others. *Ratemia*, too, could not have been derived directly from *Linognathus*, although it may well have arisen from the same stock, possibly at a later date or at about the same time as *Prolinognathus*.

(19) A genus less surely to be assigned to the linognathoid group is *Microthoracius*. In spite of its possession of a number of primitive characters in common with *Pecaroecus*, in the form of the spiracles and in other respects it is definitely linognathoid in character. It is tentatively concluded, therefore, that *Microthoracius* is an early offshoot from somewhere near the base of the linognathoid stock, possibly a little later than *Prolinognathus* in view of the structure of its spiracles.

(20) The genus *Solenopotes* appears to be almost certainly a direct derivative of *Linognathus*.

(21) It is suggested that some of the characters used in the classification of the Siphunculata have arisen independently, on a number of separate occasions and therefore are not necessarily indicative of particularly close affinity. An example cited here is the parallel development of atrial sculpture in the spiracles of Siphunculata and Trichodectidae from simple beginnings in a manner which is thought to be non-adaptive. The close resemblance of spiracles from *Trichodectes canis* and *Linognathus vituli* is such as might be expected from species of the same genus, rather than from members of two distinct suborders.

(22) It is considered that the most efficient type of spiracle serving as a dust trap in the Siphunculata is one in which processes project into the atrium from the atrial wall. The most primitive spiracles in that suborder are very small and have the beginnings of such an arrangement in the minute spines which cover the internal atrial wall. This sculpturing, however, is not elaborated as the spiracle increases in size, the minute spines being replaced as the functional mechanism for retaining dust within the atrium by a less efficient system of annular and cross-ledges. It is only in the most advanced spiracles that the ledge system is broken down, leaving the points of junction of the ledges projecting into the atrium as atrial processes of one type or another. The same indirect method of forming atrial processes is adopted in both Siphunculata and Trichodectidae. There is evidence, too, to suggest that such atrial processes have been formed independently, in the same manner, in a number of genera and species within the Siphunculata themselves.

(23) It is noted that cross-ledges joining annular ledges are not formed in spiracles of diameter less than about $20\,\mu$. In spiracles above $20\,\mu$ diameter cross-ledges appear to be formed almost invariably, and in a series of species of *Linognathus*, in which both annular and cross-ledges are characteristically present in the spiracles, a presumed secondary reduction in spiracle size results in the almost complete disappearance of cross-ledges at about an atrial diameter of $20\,\mu$. Furthermore, in a related series of species of *Linognathus*, the number of cross-ledges present on the atrial wall increases approximately directly as the atrial diameter increases above $20\,\mu$. Not all species of *Linognathus*, however, fall within this series, as in some the ratio between number of cross-ledges and atrial diameter is significantly different. The appearance or disappearance of cross-ledges in a spiracle of diameter greater or less than $20\,\mu$ is evidently not due to the mechanical impossibility of forming cross-ledges at less than a certain distance apart, for the spatial arrangement of ledges in the spiracle of the first nymph of *Linognathus pedalis* is so close that there is ample room in a spiracle of less than $20\,\mu$ diameter, to develop some cross-ledges equally closely spaced. The lower limit of $20\,\mu$ atrial diameter for the development of cross-ledges appears to apply equally to spiracles of both Siphunculata and Trichodectidae.

(24) It is suggested that, in sucking lice from Ferungulata, a number of characters other than atrial sculpture have been developed independently by different genera. Among these are included the reduction of the anterior pair of legs and enlargement of the posterior pairs, the fusion of tibia and tarsus, the reduction of eyes and the partial or complete reduction of some or all of the sclerotic plates of the thorax and the abdomen. It is stressed that, in view of widespread parallel evolution, great care is needed in analysing the complex

mixture of generalized and specialized characters to be found in all forms of lice existing to-day, before an assessment of their affinities is attempted.

(25) It is stressed that the validity of any assumptions of eutherian affinities based on those of their louse fauna is subject to the provision that any particular louse is normal to its host, that is, the infestation is of a primary and not a secondary nature due to straggling, however ancient, from a host of one species to one of another, even of the same genus. A permissible exception to this rule occurs when host affinities are inferred from parasites which, although they may have originated on the ancestral host stock by straggling, have infested the same line of hosts for the entire period during which the evolutionary developments of the hosts took place.

(26) It is suggested that transference of lice takes place either from parent to offspring or between members of opposite sexes. The virtual absence of obligate ectoparasites in any group other than the birds and mammals, is attributed to the fact that only in the higher vertebrates is parental care sufficiently well developed to ensure comparatively certain transference of parasites.

(27) The low incidence of straggling in view of the high degree of host specificity shown by Siphunculata is noted. It is thought possible, however, that the establishment of louse species on alien hosts might have been easier at a time early in the evolution of the Eutheria, when the various orders must have been nearer to one another physiologically than they are to-day and host specificity on the part of the parasite less highly developed. Straggling occurring at such a time might now be difficult, if not impossible, to detect.

(28) It is concluded that, as the Siphunculata from Ferungulata evidently form a natural group and as the Ferungulata, too, is presumably a natural group, the presence of these lice, as a whole, on the Ferungulata is the result of one or more primary infestations dating back to the inception of the host group. Similarly, as most of the groups within the Ferungulata harbour lice characteristic of themselves, these, too, are probably also derived from later primary infestations.

(29) The existence of primary infestations of *Haematopinus* and *Linognathus* on Carnivora and Artiodactyla and of *Haematopinus* on Perissodactyla, suggest that lice of those genera infested the common ancestors of these eutherian orders. It is concluded, therefore, that the genera *Linognathus* and *Haematopinus* must have been in existence since, at the earliest, the end of the Cretaceous and possibly the beginning of the Palaeocene period and that, by that time, lice on the Ferungulata had run through the entire range of evolution of atrial sculpturing of their spiracles, later evolution involving only minor modifications of existing atrial types. Thus, phylogenies of parasite and host based on the main types of atrial sculpture, and other characters are referable to the period during which the great majority of the eutherian orders became differentiated.

(30) It is thought that the ancestral stock of the Ferungulata must have been infested with at least three, and probably more, genera of sucking lice, namely, *Haematopinus*, *Linognathus* and the ancestor or ancestors of *Pecaroecus*, *Microthoracius*, *Ratemia* and *Prolinognathus*. The lice of Ferungulata as seen to-day are probably the remnants of a much more extensive fauna which, like their hosts, reached a peak of diversification and have since largely become extinct through interspecific and intergeneric competition among the lice themselves and through the extinction of their hosts. Thus, through different genera of lice surviving on each host group and later undergoing speciation, the present position of a number of genera of lice, each characteristic of a single ferungulate group, would arise.

(31) As the affinities between lice can only be of value in determinations of host relationships if the lice in question had been evolved on the host stock after that stock had become differentiated, it is evident that some louse affinities will

bear little relationship to those of their hosts. Forms such as *Pecaroecus* and *Microthoracius* evidently date back to a time long before either of the host groups had become separated off from their ancestral stock, and their existence on peccaries and camels does not mean that those mammals are of exceptionally ancient origin. Thus, the use of louse affinities as a guide to eutherian phylogeny is limited to the following cases: firstly, the relationships between large groupings of lice where these occur on equally circumscribed groups of mammals, such as the probable relationship between ferungulate lice and those characteristic of many rodents as indicating a probable origin of the Ferungulata themselves from the base of the rodent stock ; secondly, the indication of common origin of some eutherian orders, though not necessarily of close affinity, provided by the wide distribution of a genus and its derivatives, such as the distribution of *Haematopinus*, and derivatives on Artiodactyla, Perissodactyla, Carnivora and Tubulidentata; thirdly, the comparatively recent interspecific or occasionally intergeneric relationships, where the genera are close, of lice infesting definite restricted host groups, such as *Linognathus* and *Solenopotes* on Pecora and *Haematopinus* on Equidae.

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