MORPHOLOGY AND ONTOGENY OF HISTIOSTOMATID MITES (ACARI: ASTIGMATA) ASSOCIATED WITH CATTLE DUNG IN THE NETHERLANDS

by

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Collections of histiostomatid mites from cattle dung and/or dung inhabiting insects from various localities in the Netherlands yielded 5 species which were cultured in the laboratory to obtain all ontogenetic stages.

Descriptions are given for all stages in the life-cycles of *Histiostoma brevimanus* and *My-ianoetus simplex*, species previously known only from deutonymphs, and *Aphodanoetus teinophallus*, gen. nov., spec. nov. A neotype is designated for *H. brevimanus*. Ontogenetic character transformations are described for two other species, *Histiostoma phyllophorum* and *Rhopalanoetus fimetarius*, species in which only deutonymphs and adults were previously described.

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INTRODUCTION

Mites of the family Histiostomatidae (= Anoetidae, see OConnor, 1984, for synonymy of family names) are common inhabitants of wet microhabitats of a surprising variety. The greatest difficulty in understanding the ecology and evolution of this group of mites is the paucity of information regarding the lifecycles of the majority of species. Although revisers such as Hughes & Jackson (1958) and Scheucher (1957) attempted to provide information on the lifecycles of as many species as possible, workers since that time have concentrated on descriptions of new taxa based primarily upon the deutonymphal instar only. Some statistics reinforce this difficulty. In their contemporaneous revisions, Scheucher (1957) recognized 9 genera in the family in the European fauna, while Hughes & Jackson (1958) recognized 13 in the world fauna. The number of named genera in the family now stands at 50, with only 14 genera having at least some species described from both adult and deutonymphal instars. Thirty three genera are described from the deutonymph only, 30 of which have been described since the revisionary works of Scheucher and Hughes & Jackson. It is clear that studies on the biology and ecology of histiostomatid mites have lagged behind descriptive taxonomic studies in the past 25 years.

The present study was undertaken to investigate the histiostomatid mite fauna of cattle dung in the Netherlands. Investigations on the arthropod fauna of cattle dung, particularly in Europe where cattle are native, are important in determining the factors responsible for decomposition of the dung. Problems in the disposal of cattle dung are particularly severe in areas of the world where cattle have been introduced without the benefit of the natural community of dung-decomposing fauna and flora. In Australia, for example, in the absence of any native arthropods capable of utilizing cattle dung, the dung simply did not decompose, instead remaining on the ground surface and eventually making pastures useless. This problem has been partially solved by the introduction of particular species of dung-beetles (Scarabaeidae) which bury the dung and begin decomposition. In the New World, a potentially more serious problem has been the "filth-flies" which develop as larvae in cattle dung (Patterson, 1981). These species, some of which are native and some introduced, have few native natural enemies, and can develop enormous populations. Biological control programs have been developed which involve predators and parasites of the fly eggs, larvae and pupae in the dung. Among these predators are mites in the family Macrochelidae which eat the eggs of the flies.

We began these studies on the histiostomatid mite fauna of cattle dung with the view that some of these mites may have potential importance either as actual dung decomposers or more importantly, as predators/parasites of dung inhabiting fly larvae. Some species in the family Histiostomatidae are known to feed on fly eggs and larvae, for example *Histiostoma laboratorium* Hughes, 1950, which is associated with *Drosophila* cultures.

METHODS AND MATERIALS

Our investigations of the life-cycles of dung-inhabiting histiostomatid mites depended upon the development of pure cultures of each species. These were established in three different ways. First, cow dung was investigated in the field for the presence of dung-beetles which are the phoretic hosts of the deutonymphal instars of some of the histiostomatid mites. The beetles were returned to the laboratory where mite deutonymphs were removed and reared to the adult instar. Adult females were then isolated, and their offspring was maintained in pure culture. A second method involved collecting samples of dung in petri-dishes or plastic bags and maintaining these in the laboratory for one week. After that time, the dung was examined and adult female mites were removed for culturing. Immediate examination of dung freshly collected from the field yielded few or no mites. Finally, beetles were placed in dung samples in the laboratory. After two days, these beetles were examined for mite deutonymphs which had attached to the phoretic hosts. These were isolated, reared to adults and cultured.

Rearing of mites was accomplished at room temperature (about 25° C) in plastic petri-dishes (5 cm. diameter) during July and August, 1982. The rearing medium was cow dung, freshly collected and frozen at -20° C for at least three days to insure that no living mites were present in the original medium. After thawing, the dung was spread in the petri-dishes and brought to the right consistency. Maximum mite development was observed when the medium was wet enough to allow a thin film of water at the surface in which the mites moved and fed. After introducing the adult mites or deutonymphs, the dishes were sealed and placed in a closed container at 100% relative humidity. As a control, we prepared a petri-dish with medium but introduced no mites. After two months time, no mite development was observed in this control, indicating that the initial freezing of the dung was sufficient to kill any mites or eggs present.

Material. – The holotypes, neotypes and all figured specimens, including paratypes are deposited in the Rijksmuseum van Natuurlijke Historie, Leiden. Paratypes of the new species and voucher specimens of the other species are also deposited in the following institutions: U.S. National Museum of Natural History, Washington; Zoologische Abteilung des Ungarisches

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National Museum, Budapest; Bernice P. Bishop Museum, Honolulu; British Museum (Natural History), London; Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Hamburg; Division of Entomology, CSIRO, Canberra; Museum of Zoology, The University of Michigan, Ann Arbor; Institute of Parasitology, Czechoslovak Academy of Sciences, Prague; Department of Aquatic Ecology, Catholic University of Nijmegen, Nijmegen.

Histiostoma brevimanus (Oudemans, 1914)

(figs. 1-25)

Lipstorpia brevimanus Oudemans, 1914: 73. Anoetus brevimanus Oudemans, 1917: 392. Histiostoma brevimanus Buitendijk, 1945: 361; Hughes & Jackson, 1958: 52.

Material examined. - Neotype deutonymph and paratypes from cultures begun with female mites collected from cattle dung on the island of Terschelling, The Netherlands. The phoretic hosts of the deutonymphs were not observed.

This species was originally described from a single deutonymph collected from a hot bed [broeibak (Warmbeet)] in Sittard, The Netherlands. It has not been collected since. Oudemans' unpublished notes on this species kept in the Rijksmuseum van Natuurlijke Historie in Leiden indicate that the holotype specimen was subsequently lost. Comparisons of our deutonymphal specimens with Oudemans' original unpublished illustrations in Leiden (subsequently published by Hughes & Jackson in 1958) confirm the identity of this species. In order to fix the identity of this species, we designate a deutonymph from our rearings as neotype.

Female (figs. 1-8). – Body pear-shaped, with a tendency to fold posterioventrally when mounted. Idiosomal length 377 (309-421) μ m, width 233 (196-285) μ m.

Gnathosoma. – Chelicerae laterally flattened (fig. 3), with fixed digit having an expanded distal portion with a tiny apical tooth, a median region bearing a larger single tooth and a membranous lateral region; movable digit with up to five apical teeth. Dorsal cheliceral seta elongate. Each palp (cf. fig. 1) reflexed outward with a thin membrane along its length; apical palpal solenidion (ω) about 1.5 times as long as ventral eupathidial seta (*ul*²); two minute protuberances visible on dorso-medial portion of palp. Subcapitulum with ventral subcapitular setae (*m*) filiform.

Venter (fig. 2). – Anterior apodemes of coxal fields I (epimeres) fused medially to form a Y-shaped figure. Anterior apodemes of coxal fields I an II each extending dorsally around trochanters I-II, contiguous with posterior apodemes (epimerites) of respective coxal fields. Epimerites I fused with epimeres II ventrally. Epimerites II free medially, having a small posteriolaterally directed extension. Epimeres III connected with heavily sclerotized anterior genital papillae ("rings") anterio-laterally. Coxal apodemes III-IV





continuous dorsally around trochanters. A pair of small sejugal apodemes is present between coxal fields III-IV, lateral to ovipore. Ovipore transverse, located between coxal fields II-III. Median sclerotized region poorly-developed. One pair of vestigial genital setae posterior to genital opening. Anterior genital papillae oval, with strongly sclerotized margins; posterior papillae round, weakly sclerotized, situated in the anterio-median portion of coxal fields IV. Coxal setae I, III, and IV filiform. Anal region with two pairs of setae (the posterior pair, a_4 , often folded anteriorly in mounted specimens as indicated in fig. 2).

Dorsum (fig. 1). Cuticle covered with small, thin microtrichae. Anterior propodosoma with a distinct sclerite extending posteriorly above legs I. Internal vertical setae (*vi*) filiform, positioned at anterior edge of sclerite; external vertical setae (*ve*) filiform, positioned in the anterior third of the sclerite. Coxal apodemes well developed above legs I-II, extending as surface sclerotization, especially posterio-medially from legs I. Scapular setae filiform, internal scapular setae (*sci*) short, positioned anterio-medial to longer external scapular setae (*sce*). Sejugal furrow very faint, with a pair of minute dorsal sejugal apodemes. Hysterosomal setae filiform, subequal in length. Setae d_5 and I_5 caudal (fig. 2). Four pairs of cupules present: *ia* between setae I_1 and *sh*, *im* lateral to setae I_2 , *ip* between and posterior to setae d_3 and I_3 , *ih* (fig. 2) between setae I_4 and I_5 . Opisthosomal gland opening (*gla*) between setae I_2 and I_3 . A pair of what we consider vestigial setal alveoli (*v.a.*) positioned between setae d_3 and d_4 . Copulatory opening (*c.o.*, fig. 4) dorsal, between setae d_4 (fig. 3); duct leading from bursa copulatrix short and thin (fig. 4).

Legs (figs. 5-8). Legs slender, with all five segments free. Chaetotaxy: tarsi 13-12-10-10; tibiae 2-2-1-1; genua 2-2-0-0; femora 1-1-0-1; trochanters 1-1-1-0. Solenidiotaxy: tarsi 3-1-0-0; tibiae 1-1-1-1; genua 2-1-0-0. Famulus absent. Tibia I excavated dorso-apically around common base of tarsal solenidia omega-1 and omega-2. Most leg setae spine-like with filiform apices. Dorso-apical tarsal setae d I-II elongate, filiform; setae e III-IV more elongate than f, lengths III-33, IV-38; trochanter setae pR, sR filiform. Measurements of leg characteristics in table 2.

Male (figs. 9-12). – Body box-like, well-sclerotized; idiosomal length 222 (206-241) μ m, width 111 (99-122) μ m. Gnathosoma similar to female.

Venter (fig. 12). Epimeres I fused medially to form a sternum, bearing a pair of anterior extensions in midregion. Epimerites I fused with epimeres II which are slightly fused together medially. Epimerites II fused with sejugal apodemes forming a sclerotized region along ventral sejugal furrow. Epimeres III extending to sejugal region, epimeres IV free medially. Epimerites III very









reduced, fused to epimeres IV; epimerites IV not observed. Genital papillae without sclerotized edges, situated in a trapezoid between coxal fields IV. One pair of minute genital setae (ga) anterior to genital papillae. Genito-anal region posterior to coxal fields IV; anus covered by projecting genital structures. Two pairs of anal setae (a3 and a4) present lateral and posterior of the genito-anal region. Coxal setae I, III and IV present, filiform. Hysterosomal setae I_s elongate, positioned behind anal setae.

Dorsum (fig. 11). Cuticle strongly sclerotized, with a distinct pattern of reticulations and bearing small microtrichae. Propodosoma covered by a single sclerite except directly above leg bases; propodosomal setae filiform, subequal except for *sce* which are much longer. Reticulate pattern most distinct posterior to setae *sci*. Sejugal furrow distinct. Reticulate pattern on hysterosomal sclerite distinct medially and anteriorly, becoming less distinct posteriorly and laterally. Hysterosomal setae filiform, subequal except the ventrally displaced I_5 which are much longer. Setae d_4 positioned on dorso-caudal protuberances. Four pairs of cupules present: *ia* posterior to setae I_1 , *im* lateral to setae I_2 , *ip* ventro-caudal between setae I_3 and I_4 (fig. 12), *ih* lateral of the line connecting setae d_4 and d_5 , very poorly visible. Vestigial alveoli (*v.a.*) present posterior to setae d_3 . Opisthosomal gland openings (*gla*) medial to setae I_2 .

Legs (figs. 9, 10). Legs I-II stouter than corresponding legs of female. Legs III-IV slender. Chaetotaxy and solenidiotaxy of legs as in female except solenidia phi of tibia I and omega-1 of tarsus II more elongate; omega-3 of tarsus I longer and stouter. Setae *e* of legs III-IV elongate as in female, average lengths 29 and 32 μ m respectively.

Egg. – Eggs within female body with smooth, unsculptured chorion; average length 101 μ m, width 65 μ m.

Larva (figs. 13, 14). – Length 114 (103-127) μ m, width 65 (52-80) μ m. Gnathosoma as in female.

Venter (fig. 14). Epimeres I fused medially in a V-shape. Epimeres II-III free medially, each with a short lateral extension representing epimerites I-II respectively. Claparede's organs (*Cl.o.*) in the form of small rings present laterally on coxal fields I. Coxal setae *cx I* and *III* present, short, filiform.

Dorsum (fig. 13). Cuticle with small microtrichae, bearing a number of sclerotized regions which protrude from the surface and bear all dorsal setae except h which is on unsclerotized cuticle. Propodosoma with a single large sclerite; hysterosoma with sclerites as figured. Dorsal setae all filiform; setae d_4 and l_4 missing from adult complement. Opisthosomal glands and cupules not observed.

Legs. Leg chaetotaxy similar to ancestral condition in larval Astigmata plus









loss of nG and sigma from genu III as in other Histiostomatidae. Chaetotaxy and solenidiotaxy as in female except trochanter setae I-III and solenidia omega-2 and omega-3 absent. Leg setae somewhat shorter and arranged more compactly than in female.

Protonymph (figs. 15, 16). – Idiosomal length 146 (136-163) μ m, width 86 (79-95) μ m. Gnathosoma similar to female.

Venter (fig. 16). Epimeres I fused in a broad Y-shape. Epimeres II-IV free medially. Epimerites I fused with epimeres II; epimerites II weakly developed, fused with epimeres III medially. One pair of small genital papillae in posterior region of coxal fields IV. Setae of coxal fields I and III present, filiform.

Dorsum (fig. 15). Cuticle with fine microtrichae. Propodosoma with two sclerites; anterior sclerite bearing setae vi and ve; posterior sclerite small, trapezoidal, located between setae *sce*. Hysterosoma without sclerotization; hysterosomal setae filiform, subequal in length, except I_5 (fig. 16), which is longer. Setae d_3 and d_4 on rounded protuberances. Opisthosomal glands (*gla*) present, opening medially to setae I_2 . Cupules not observed.

Legs. Legs I-III similar to larva, with same chaetotaxy except solenidion omega-2 added to tarsus I. Leg IV added in this stage, chaetotaxy similar to protonymphal chaetotaxy of other Astigmata consisting of tarsal setae w, r, d, p, q, u, and v only. Other segments glabrous. The terminal tarsal setae p are elongate.

Tritonymph (figs. 17, 18). – Idiosomal length 181 (173-210) μ m, width 112 (96-124) μ m. Gnathosoma as in female.

Venter (fig. 18). Epimeres I reduced, triangulate; epimeres II-IV free medially. Epimerites I fused to epimeres II; epimerites II-III not observed, epimerites IV present. Two pairs of round genital papillae arranged in a trapezoid between coxal fields IV. Coxal setae *cxI* and *cxIII* filiform. Setae *cxIV* and genital setae absent.

Dorsum (fig. 17). Cuticle with large sclerites and microtrichae. Propodosoma with a single large sclerite bearing both pairs of vertical and scapular setae as in larva and male. Hysterosoma with four large sclerites, an anterior median sclerite bearing setal pairs d_1 and d_2 , a central median sclerite bearing setae d_3 on a slightly elevated protuberance, and a pair of posterior sclerites, each bearing a seta d_4 on a slightly elevated protuberance. Hysterosomal setae I_4 , I_5 and d_5 ventrally displaced (fig. 18). All four pairs of cupules present; opisthosomal glands not observed.

Legs. All legs similar to female in form and chaetotaxy, except solenidion omega-3 not observed on tarsus I.

Deutonymph (figs. 19-25). – Neotype ovoid, widest in sejugal region;



Figs. 17, 18. Histiostoma brevimanus (Oudemans) tritonymph. 17. Dorsum. 18. Venter.



Figs. 19, 20. Histiostoma brevimanus (Oudemans) deutonymph. 19. Dorsum. 20. Venter.

idiosomal length of neotype 154 μ m, mean and range of 10 specimens 131 (106-158) μ m, width 112 μ m, mean and range 102 (86-124) μ m.

Gnathosoma (fig. 21). Gnathosoma reduced, chelicerae absent. Remnant of subcapitulum cylindrical, length 15 μ m, width 8 μ m (mean 14 \times 7 μ m). Palpal supracoxal setae on dorso-lateral subapical region, average length 3 μ m; palpal solenidia at apices of slightly bifurcate subcapitular remnant, average length 29 μ m.

Venter (fig. 20). Epimeres I fused together posterior to subcapitular remnant forming a long sternum which is free posteriorly, not fused to epimeres III; epimeres II free medially, extending anterio-laterally; epimerites II broad, not fused to epimeres III posteriorly; a weakly sclerotized band connects lateral ends of epimeres and epimerites II mesal to leg trochanters; epimeres III with short lateral extensions around trochanters III and a slight anterior extension mesal to articulation points, epimeres fused together medially with a triangular enlarged area at point of fusion, continuing posteriorly as median apodeme; epimeres IV fused medially to median apodeme which extends posteriorly from the point of fusion with epimeres IV; a pair of apodemes extends posterio-medially from the point of articulation between trochanters IV and epimeres IV, fusing medially and extending anteriorly as a separate posterior median apodeme, not fusing with posterior extension of more anterior apodeme. Genital region anterior to attachment organ, opening small, oval, with two pairs of genital papillae in genital atrium (only one pair shown in fig. 20). Genital setae (ga) minute, filiform, positioned posterio-lateral to genital opening. Coxal setae cx1, cxIII and cxIV in the form of well-developed conoids; conoids of coxal fields IV surrounded by sclerotized regions, extending as subsurface apodemes anteriorly. Attachment organ large, ovoid in shape, with striate margin. Median suckers much larger than anterior suckers, each median sucker with a pair of vestigial alveoli in its center. Anterior lateral, posterior lateral and posterior median cuticular suckers with striate margins. Two pairs of conoidal setae present posterior and lateral to the median suckers. Remnant of anus positioned between anterior and median suckers. Two small vestigial alveoli visible laterally between anterior and median suckers.

Dorsum (fig. 19). Anterior propodosoma with a knoblike anterior projection from which longitudinal striations radiate posteriorly. Hysterosoma with transverse striation anteriorly, becoming longitudinal laterally and posteriorly, disappearing caudally. Hysterosomal setae mostly minute, filiform, except d_1 and l_1 which are longer (mean lengths 11 and 15 μ m respectively). Pigmented spots which we interpret as remnants of cupules *ia* and *im* between setae d_1 and l_1 and l_2 and l_3 respectively. Opisthosomal glands (gla) visible mesal to setae l_2 .





Legs (figs. 22-25). Legs generally shorter than in most *Histiostoma* species. Tarsus I relatively short in comparison with other species of Histiostoma, shorter than the combined length of the other leg segments. Trochanters I, II and IV without setae, seta sR of trochanter III filiform. Chaetotaxy of femurgenu-tibia I-IV as in female, setae spine-like except seta wF IV which is filiform. Femur-genu of legs I-II fused, non-articulating, with a thin line of membrane partially visible between the segments. Genu-tibia-tarsus III-IV fused, with a partially membranous area sometimes visibles between some segments. Tarsi III-IV subdivided medially. Tarsal chaetotaxy with the following setae present: tarsus I with wa, ra, la spinelike, in ventro-apical half of segment; f, p, and q spinelike, at tarsal apex; e elongate and foliate, with an expanded apex, at tarsal apex; d flattened, rounded apically, about half the length of e, at tarsal apex. Tarsus II similar to tarsus I except ba present, spinelike, in basal half of tarsus and e without distinct apical expansion. Tarsus III with four setae in basal portion, r elongate, w, d and s spinelike (s very short); three setae in apical half of tarsus, p and f short spines, e elongate. Tarsus IV similar to tarsus III but setae w and r are both elongate. Leg solenidiotaxy consisting of one sigma solenidion on genua I-II, one phi solenidion on tibiae I-IV, omega-1 and the famulus of leg I coupled with phi at tibial apex, omega-3 in basal half of tarsus I, and omega-1 of tarsus II in basal half of tarsus. Empodial claws present on all four pretarsi; membranous pretarsal ambulacra small, symmetrical. Measurements of leg characters in table 3.

Myianoetus simplex Mahunka, 1972 (figs. 26-50)

Myianoetus simplex Mahunka, 1972: 363; Samšiňák, 1984: 60.

Material examined. - Cultures were established from female mites which were collected from dung samples in a pasture in the vicinity of Nijmegen, The Netherlands. The phoretic hosts of the deutonymphs were not observed. Mahunka (1972) cites Hebecnema umbratica (Meigen, 1826 and Sepsis thoracica (Robineau-Desvoidy, 1830) as hosts for this species, while Samšiňák (1984) also lists Coproica lugubris (Haliday, 1836). Voucher specimes are deposited in the institutions listed in the introduction.

This species was originally described from deutonymphs collected from two species of Diptera, Hebecnema umbratica (Meigen, 1826) (Muscidae) and Sepsis thoracica (Robineau-Desvoidy, 1830) (Sepsidae) from Hungary, and from unassociated deutonymphs from France (Mahunka, 1972). Samšiňák (1984) later reported deutonymphs from Coproica lugubris (Haliday, 1836) (Sphaeroceridae) from Czechoslovakja. Our deutonymphs are in general agreement with Mahunka's (1972) description, however, two discrepancies





were noted in his table of character state distributions. Mahunka's table indicates that *M. simplex* should be characterized by a double row of punctations dorsally (his character IX, state 2) and that femoral setae vF I-II, unlike in our material, should be short, not longer than the width of the femora (his character X, state 1). We have compared our specimens with paratypes supplied by Dr. Mahunka and these agree completely with our specimens. We suspect a typographical transposition of numbers in Mahunka's table, since if the numbers 2 and 1 are exchanged in colums IX and X, the character states are in complete agreement with all examined specimes. Neither Mahunka's nor Samšiňák's figures of the deutonymph illustrate the anterior suckers of the attachment organ which, in our specimens, are always elevated away from the plane of the body and thus, difficult to see.

Female (figs. 26-33). – Body ovoid; idiosomal length 368 (331-433) μ m width 262 (167-318) μ m.

Gnathosoma. Chelicerae laterally flattened (fig. 28), with fixed digit having a membranous apex and three well-developed ventro-apical teeth, two additional teeth more proximally along membranous ventral portion; movable digit with up to four apical teeth; cheliceral seta elongate. Each palp (fig. 26) reflexed outward with a large dorsal membranous extension along its length. Each palp with three ventral membranous protuberances: a proximal median protuberance directed anterio-ventrally, bearing a small finger-like projection; a triangular median protuberance directed laterally; and an apical protuberance. Palpal solenidion (ω) elongate, with a membranous extension of the palp extending halfway along its length; ventral eupathidial seta (*ul*') less than half the length of the solenidion, also with a membranous palpal extension extending halfway along its length. A refractile spot is visible on the proximo-ventral region of the palp. Subcapitulum with ventral subcapitular seta (*m*) bifurcate, with a long posterior and shorter anterior portion.

Venter (fig. 27). Epimeres I free medially, not fused to each other, each with a posteriorly directed lateral extension mesal to the trochanters. Epimerites I fused postero-medially to epimeres II, extending dorso-laterally around trochanters I. Epimeres II extending around trochanters dorsally, slightly fused with similar dorsal extensions of epimerites II. Epimerites II bifurcate medially, almost enclosing anterior genital papillae with weakly sclerotized posterior branch. Anterior genital papillae, genital apodemes and ovipore situated between coxal fields II-III. Ovipore transverse, flanked laterally by a pair of longitudinal genital apodemes; genital valves fused medially, area of fusion sclerotized internally, extending slightly anterior of ovipore as a small point. One pair of genital setae ga well-developed, situated on fused genital valves. Epimeres III and IV relatively short, with lateral





extensions extending dorsally around trochanters. Epimerites III and IV very weakly developed. Posterior genital papillae situated directly anterior to the anus. Coxal setae I, III and IV setiform. Anus posterior ventral. Anal region with four pairs of setae, two pairs anterior to anus (a1, a2), two pairs directly lateral to anus (a3, a4).

Dorsum (fig. 26). Cuticle smooth. Propodosomal sclerite rounded posteriorly, with two posteriorly directed lateral extensions above legs I. Sejugal furrow not apparent. Propodosomal setae vi and ve setiform, situated on sclerite. Scapular and hysterosomal setae all short, setiform, except d_2 and d_3 which are stiff and brush-like apically. Setae l_5 displaced ventrally (fig. 27). Opisthosomal gland opening (gla) between setae l_2 and l_3 . Four pairs of cupules observed: *ia* between setae l_1 and *sh*; *im* lateral of opisthosomal gland opening; *ip* between setae l_3 and l_4 ; and *ih* between setae l_4 and d_5 . Vestigial alveoli (v.a.) visible posterio-lateral to the opisthosomal gland openings. Copulatory opening (co, fig. 29) dorso-caudal, between setae d_5 . Duct from bursa copulatrix small, abruptly widening at internal terminus (fig. 29).

Legs (figs. 30-33). Legs slender, with all five segments free. Chaetotaxy: tarsi 13-12-10-10; tibiae 2-2-1-1; genua 2-2-0-0; femora 1-1-0-1; trochanters 1-1-1-0. Famulus absent. Solenidion omega-2 clearly more basal than omega-1 on tarsus I, omega-3 elongate, tapering, at tarsal apex. Most leg setae spine-like except dorso-apical seta *d* of tarsi I-II. Setae *e* III-IV spine-like, but longer than *f*. Empodial claws well-developed; membranous pretarsal ambulacra asymmetrical, with processes extending around empodial claws; lobes of pretarsus I blunt to slightly bilobed, those of pretarsi II-IV bifurcate, with one rounded and one tapering lobe. Measurements of leg characteristics in table 2.

Male (figs. 34-37). – Body form similar to female, ovoid to pear-shaped; idiosomal length 282 (264-350) μ m, width 188 (162-251) μ m. Gnathosoma as in female.

Venter (fig. 37). Epimeres I fused medially, forming a short sternum, with triangular extensions around trochanters. Epimeres II-IV free medially. Epimerites I fused medially with epimeres II, extending dorsally around trochanters as in female. Epimerites II and epimeres III contacting ventral sejugal apodemes (*s.a.*). Epimeres III with anterior and posterior extensions around trochanters. Epimerites III fused with epimeres IV. Epimerites IV not observed. Ventral margins of coxal fields I-II slightly sclerotized around trochanters. A small opening between the bases of legs II and III leads via a sclerotized duct to an internal gland. Genito-anal region between and slightly posterior to coxal fields IV. Genital papillae arranged in a trapezoid anterior to genital opening, anterior pair in contact medially. Genital setae anterior to genital papillae. Aedeagus directed ventrally, perpendicular to ventral body surface



Figs. 36, 37. Myianoetus simplex (Mahunka) male. 36. Dorsum. 37. Venter.



Figs. 38, 39. Myianoetus simplex (Mahunka) larva. 38. Dorsum. 39. Venter.

in life, opening at the end of a conical tubercle. In mounted specimens, aedeagus sometimes directed anteriorly, sometimes posteriorly. Anus immediately posterior to genital region, covered in mounted specimens when genital tubercle bends posteriorly (visible as double curved line left of center in fig. 37). Two pairs of anal setae present, a4 at tip of genital tubercle, a3 at base of genital tubercle. Hysterosomal setae l_5 lateral to anus. Setiform setae present on coxal fields I, III, and IV.

Dorsum (fig. 36). Cuticle smooth, without microtrichae. Propodosomal sclerite longer than in female, concave posteriorly, bearing setae vi and ve. Dorsal continuations of epimerites I visible around trochanters I. Sejugal furrow very faint, with a pair of very weak dorsal sejugal apodemes. All hysterosomal setae setiform, including d_2 and d_3 , none barbed apically. Setae l_4 , l_5 , and d_5 displaced ventrally (cf. fig. 37). Openings of opisthosomal glands (gla) and cupules with positions similar to female; vestigial alveoli (v.a.) posterio-lateral to opisthosomal gland openings.

Legs (figs. 34, 35). All legs slender; form, chaetotaxy and solenidiotaxy as in female with the following exceptions: solenidion omega-3 of tarsus I shorter than in female, with a blunt apex; solenidion omega-1 of tarsus II and phi of tibia I much longer than in female. Measurements of leg characteristics in table 2.

Egg. – Eggs within female body with smooth, unsculptured chorion, average length 93 μ m, average width 71 μ m.

Larva (figs. 38, 39). – Idiosomal length 124 (85-148) μ m, width 82 (54-102) μ m. Gnathosoma as in female but membrane along palpal solenidion distinctly widened distally.

Venter (fig. 39). Epimers I free medially. Epimeres II-III free medially, with median and lateral extensions. Claparede's organs (*Cl.o.*) in the form of circular rings lateral on coxal fields I. Filiform setae present on coxal fields I and III.

Dorsum (fig. 38). Cuticle smooth, with lightly sclerotized shields. Propodosoma with a single large sclerite bearing setiform vertical and scapular setae. Hysterosomal sclerites as figured, all hysterosomal setae setiform. Hysterosoma with 10 pairs of setae, d_4 and l_4 absent, l_5 ventrally positioned (cf. fig. 39). Opisthosomal glands and cupules not observed.

Legs. Leg chaetotaxy and solenidiotaxy as in female except trochanter setae I-III and solenidia omega-2 and omega-3 absent. Legs relatively shorter than in adults, especially the tarsi, with concomitant shifts in positions of some setae and solenidia. Pretarsal ambulacra blunt to slightly bilobed on legs I-II, distinctly bilobed with one rounded and one tapering lobe on leg III.

Protonymph (figs. 40, 41). – Idiosomal length 192 (147-236) μ m, width 114



(95-143) μ m. Gnathosoma similar to female except membrane along palpal solenidion distinctly widened apically as in larva.

Venter (fig. 41). Epimeres I fused in a V-shape, with triangular extensions around trochanters. Epimeres II-IV free medially. Epimerites I fused with epimeres II; epimerites II free medially; epimerites III-IV not observed. One pair of genital papillae between legs IV, immediately lateral to the anterior end of the anus. One pair of genital setae (ga) present anterior to genital papillae. Two pairs of anal setae added (a3, a4). Two pairs of very short dorsal opisthosomal setae, d_5 , and l_5 ventrally displaced to a position lateral to anus. Setae of coxal fields I and III present, filiform.

Dorsum (fig. 40). Cuticle smooth. Propodosoma with faintly sculptured sclerite bearing setae vi and ve. Scapular setae situated on protuberances. Sejugal furrow weakly developed. All dorsal setae filiform except d_4 which are brush-like, thickened and apically barbed. Dorsal hysterosomal setae (excepts h and d_3) situated on protuberances. Opisthosomal gland opening (gla) between setae l_3 and l_3 . One pair of cupules (*ip*) visible between setae d_3 and d_4 .

Legs. Legs I-III similar to larva, with same chaetotaxy except solenidion omega-2 added on tarsus I. Leg IV added in this stage, chaetotaxy similar to protonymphal chaetotaxy of other Astigmata. Pretarsi I-II with a single ambulacral lobe; pretarsi III-IV biolobed. Empodial claws similar to other homeomorphic stages.

Tritonymph (figs. 42, 43). – Idiosomal length 203 (169-249) μ m, width 150 (117-180) μ m. Gnathosoma as in female.

Venter (fig. 43). Epimeres I reduced and triangulate. Epimeres II-IV free medially. Epimerites I fused to epimeres II, anterior part of epimerites I extending dorso-laterally around trochanters I; epimerites II fused with epimeres III, not extending laterally to trochanters II; epimerites III not observed; epimerites IV weakly developed. Two pairs of genital papillae arranged in a rectangle between coxal fields IV. Genital setae (ga) anterior to genital papillae. Two pairs of anal setae present, anterior pair (a3) lateral to posterior genital papillae, posterior pair (a4) lateral to anus. Coxal setae cxI and cxIII setiform, cxIV minute, setiform.

Dorsum (fig. 42). Cuticle smooth. Propodosoma with a smooth anterior sclerite bearing setae vi and ve; remaining dorsal cuticle unsclerotized. Sejugal furrow not observed. Paired subsurface sclerotizations present in dorsal sejugal region (not always visible). All dorsal setae setiform, including d_4 . Setae l_5 ventrally positioned (fig. 43). Four pairs of cupules observed, positioned as in female. Opisthosomal glands not observed.

Legs. All legs similar to female in form and chaetotaxy, except ambulacrum of pretarsus II which is not bilobed in this stage.











Deutonymph (figs. 44-50). – Body subcircular, idiosomal length 139 (122-152) μ m, width 120 (98-132) μ m.

Gnathosoma (fig. 50). Subcapitular remnant cylindrical, average length 14 μ m, width 6 μ m. Palpal solenidia arising directly from subcapitular apex, length 37 μ m; palpal supracoxal setae dorso-apical, length 6 μ m.

Venter (fig. 45). Epimeres I fused medially to form a long sternum which fuses posteriorly with fused epimeres III. Epimeres II fused posterio-medially to epimeres III. Epimerites I short, fused to epimeres II. Epimerites II weakly developed, with a small internal portion posterior to trochanters II, continuing as surface sclerotization to area around trochanter III. Epimeres III fused together medially, connecting with median apodeme. Epimeres IV also fused together medially and to median apodeme. Genital opening surrounded by a circular apodeme with an anterior median extension which approaches posterior end of median apodeme. Two pairs of genital papillae within genital atrium. Genital setae (ga) setiform, positioned directly laterally of opening. Setae of coxal fields I, III, and IV vestigial; alveoli prominent as sclerotized rings. Attachment organ pentagonal, with smooth margin. Anterior suckers small, stalked; median suckers large, with an internal ring surrounding two vestigial alveoli. Anterior lateral, posterior median and posterior lateral cuticular suckers absent. Two pairs of spine-like conoidal setae in a transverse row posterior to median suckers. A pair of thin spots positioned between and lateral to anterior and median suckers. An internal apodeme arched anterior to and beneath anterior suckers. Remnant of anus situated between anterior suckers.

Dorsum (fig. 44). Propodosoma very reduced, setae *sce* about twice as long as *sci*. Hysterosoma smooth, evenly sclerotized, with small, subequal setae. Homologues of cupules *ia* and *ip* represented by enlarged, elongated depressions; cupules *im* normally formed, positioned near setae l_2 . Remnants of opisthosomal gland (*gla*) openings visible as spots between setae l_3 and d_4 .

Legs (figs. 46-49). Legs generally similar in form to other *Myianoetus* species. Trochanters I, II and IV without setae; seta of trochanter III filiform. Chaetotaxy of femur-genu-tibia I-IV as in female, setae generally spine-like or setiform except vF I-II which are filiform. Femur-genu of legs I-II fused, non-articulating, with a thin line of membrane partially visible between the segments. Genu-tibia-tarsus III-IV fused, with a partially membranous area sometimes visible between some segments. Tarsus III subdivided medially, tarsus IV undivided. Tarsal chaetotaxy 5-6-6-7 with the following setae present: tarsus I with wa and ra spinelike, in basal half of segment; la and d spinelike, in apical half of segment; e thickened basally, enlarged and foliate apically. Tarsus II similar to I except seta ba present, spinelike, in basal half of

segment, and wa more apically positioned. Tarsus III with four setae in basal portion, r elongate, w, d and s spinelike, two setae in apical portion of tarsus, e elongate and filiform, f shorter and spinelike. Tarsus IV with r much longer than homolog on tarsus III, w, s and d spinelike, f and p spinelike, apical, and e very elongate, longer than leg, arising from tarsal apex. Solenidiotaxy consisting of sigma-1 on genu I, tapering, about as long as tibia-tarsus; sigma of genu II short, rounded apically; tibia I with phi elongate, tapering, about as long as genu-tibia-tarsus, omega-1 of tarsus I displaced onto tibial apex, base not contiguous with that of solenidion phi, famulus very short; tibia II with phi elongate, tapering, about as long as tibia-tarsus; phi of tibiae III-IV tapering; tarsus I with omega-3 tapering, in middle of segment, somewhat longer than tarsus I. Pretarsi I-III with bifurcate empodial claws; pretarsus IV absent. Measurements of leg characteristics in table 3.

Aphodanoetus gen. nov.

Type-species: Aphodanoetus teinophallus spec. nov.

Female. – Body rounded, unsclerotized except for small prodorsal sclerite. Coxal apodemes I fused to form a sternum. Ovipore region small, lateral genital apodemes fairly closely spaced; median sclerotized area well-developed. Genital papillae small, rounded, anterior pair at posterio-lateral corners of genital region, posterior pair slightly anterior to anus. All body setae simple except *vi* which are T-shaped. One pair of anal setae present. Legs long; pretarsal ambulacra not enlarged.

Male. – Dorsum somewhat sclerotized, bearing a pattern of rounded tubercles. Coxal apodemes I fused to form a long sternum which is very weakly fused with the median ends of coxal apodemes II. Genito-anal region flanked by a pair of para-anal suckers and three pairs of anal setae. Aedeagus very long, projecting beyond the posterior edge of the body. Tarsus II with soleni-dion omega only slightly longer than homolog in female; other body and leg chaetotoxy as in female.

Deutonymph. – Gnathosomal remnant elongate. Dorsum without ornamentation. Coxal apodemes generally as in *Histiostoma*. Coxal setae I, III and IV in the form of conoids. Attachment organ with all suckers and conoids welldeveloped. Leg chaetotaxy normal for family except tarsi III-IV with only six setae each. Pretarsus IV reduced to a pointed ambulacrum; empodial claw absent.

Etymology. – The generic name is a combination of the Greek Aphodos (= cattle dung) and Anoetus (the first genus described in the family), and is masculine. The specific name is a combination of the Greek teino (= to







Figs. 55-60. Aphodanoetus teinophallus spec. nov. adult legs. 55. Female, leg I, dorsal, apex ventral. 56. Female, leg II, dorsal, apex ventral. 57. Female, leg III, dorsal, apex ventral. 58. Female, leg IV, lateral. 59. Male, leg I, dorsal, apex ventral. 60. Male, leg II, dorsal, apex ventral.

stretch) and *phallos* (= penis), referring to the elongate male aedeagus, and is a noun in aposition.

Aphodanoetus teinophallus spec. nov.

(figs. 51-75)

Material examined. – Cultures were begun with deutonymphs which were collected from *Aphodius frater* Mulsant (Coleoptera: Scarabacidae) collected from cattle dung in the vicinity of Nijmegen, The Netherlands. Other stages reared in the laboratory.

Female (fig. 51-58). – Body ovoid; idiosomal length of holotype 413 μ m, average in 10 specimens 332 (248-432) μ m, width 305 μ m, average 237 (177-305) μ m.

Gnathosoma. Chelicerae laterally flattened (fig. 53), with fixed digit having a flattened, edentate apex; more proximally with a ventrally directed process bearing three minute teeth; and basally with a membranous ventral expansion; movable digit with up to five apical teeth; cheliceral seta elongate. Each palp (cf. fig. 51) reflexed outward, with a membranous extension along its length. Each palp with two ventral protuberances, one distal and one proximal. Palpal solenidion (ω) about twice the length of the ventral eupathidial seta (ul^{r}). Subcapitulum with ventral subcapitular seta (m) setiform.

Venter (fig. 52). Epimeres I fused, forming a very short sternum, each with a posteriorly directed lateral extension mesal to the trochanters. Epimerites I fused postero-medially to epimeres II, extending dorso-laterally around the trochanters. Epimeres II posterio-medially directed, with a posteriorly directed lateral extension mesal to the trochanters. Epimerites II fused posteriomedially with epimeres III, without extensions around genital opening. Epimeres III-IV distinctly curved. Epimeres IV with anteriorly directed extensions laterally. Epimerites III and IV not observed, although a cuticular fold is present posterior to leg III. Ovipore transverse, flanked laterally by a pair of longitudinal genital apodemes; genital valves fused medially, area of fusion sclerotized internally. Anterior genital papillae oval, situated posterior to the genital opening and the genital sclerites between the median ends of epimeres III. One pair of genital setae (ga) well-developed, situated between anterior part of genital papillae and the middle of the fused genital valves. Posterior genital papillae oval, situated anterior of the anus. Filiform coxal setae present on fields I, III and IV. Coxal setae IV medially displaced. Anus posteriorly ventral. Anal region with one pair of setae (a4) lateral to the anus.

Dorsum (fig. 51). Cuticle smooth. Propodosomal sclerite rounded posteriorly, bearing a faint honeycomb-like pattern. Internal vertical setae (vi) and external vertical setae (ve) situated on sclerite; vi T-shaped, with bifid ends, ve





spine-like. Scapular setae and other dorsal setae filiform with expanded bases, generally all similar in length. Setae l_2 and d_3 on a large hysterosomal protuberance. Openings of the lateral opisthosomal glands (gla) between setae l_2 and l_3 . Four pairs of cupules observed: *ia* between setae l_1 and *sh*, *im* lateral of l_2 , *ip* between l_3 and l_4 , *ih* (fig. 51) lateral of the line connecting setae d_5 and l_5 . Copulatory opening (*co*, fig. 54) dorso-caudal, between setae d_5 (fig. 51), surrounded by a small sclerotized ring; duct to bursa copulatrix small (fig. 54).

Legs (figs. 55-58). Legs slender, with all five segments free. Chaetotaxy: tarsi 13-12-10-10; tibiae 2-2-1-1; genua 2-2-0-0; femora 1-1-0-1; trochanters 1-1-1-0. Famulus absent. Solenidiotaxy: tarsi 3-1-0-0; tibiae 1-1-1-1; genua 2-1-0-0. Solenidion omega-2 of tarsus I closely associated with omega-1. Omega-3 of tarsus I relatively short, blunt. Most leg setae spine-like, except seta d of tarsi I-II. Pretarsi with empodial claws well-developed; membranous ambulacra relatively small, unmodified. Measurements of leg characteristics in table 2.

Male (figs. 59-62). – Body form generally like female but somewhat more box-like; idiosomal length 191 (174-223) μ m, width 128 (114-150) μ m. Gnathosoma as in female.

Venter (fig. 62). Epimeres I fused medially, forming a long sternum which is weakly fused with the fused epimeres II posteriorly; with small triangular extensions around trochanters ventrally. Epimerites I fused with epimeres II ventrally, extending dorsally around trochanters. Epimeres II weakly fused together medially. Epimerites II fused ventrally with epimeres III, with dorsal extensions around trochanters. Epimeres III-IV curved anterio-medially, ending freely. Epimerites III-IV not observed. Genito-anal region between coxal fields IV. Genital papillae arranged in a trapezoid anterior to genital opening. Genital setae (ga) anterior to genital papillae. Genito-anal region situated on a conical elevation. Aedeagus large, extending posteriorly beyond the edge of the body. A pair of large para-anal suckers situated immediately laterally of the base of the aedeagus. Anus positioned on posterior side of genito-anal protuberance. Three pair of anal setae situated on the genito-anal protuberance: setae al anterior-lateral to para-anal suckers and setae a3 and a4 posterior-lateral. Hysterosomal setae l_5 , d_5 , and l_4 and cupules *ih* ventrally positioned behind genito-anal region. Setiform coxal setae present on coxal fields I, III and IV.

Dorsum (fig. 61). Cuticle sculptured. A distinctly sculptured propodosomal shield anteriorly with a distinct posterior border; shield bearing T-shaped internal vertical setae and spine-like external vertical setae. Scapular setae filfiorm apically, with expanded bases, positioned on sculptured pro-tuberances. Dorsal continuations of epimerites I an II are visible around

trochanters I and II. Sejugal furrow well marked by the anterior edge of a large hysterosomal sclerite. Hysterosomal sclerite with well defined lateral and posterior edges. Hysterosomal setae filiform with expanded bases, subequal in length. Setae l_4 , l_5 , and d_5 displaced ventrally (cf. fig. 62). Setae d_2 , l_2 , l_3 and d_4 situated on protuberances. Openings of lateral opisthosomal glands (gla) between setae l_2 and d_3 . Four pairs of cupules present: *ia* between setae l_1 and *sh*, *im* posterior-lateral of setae l_2 at the margin of the elevation, *ip* posterolateral of setae l_3 , *ih* ventral (cf. fig. 62), laterad of the line connecting setae d_5 and l_5 .

Legs (fig. 59, 60). Legs slender, with five free segments, relative long compared to the female. Chaetotaxy and solenidiotaxy as in the female with the following exceptions: solenidion omega-1 of tarsus II and phi of tibia I more elongate, omega-3 of tarsus I wider.

Egg. – Eggs within the female with smooth, unsculptured chorion, average length 115 μ m, average width 80 μ m.

Larva (fig. 63, 64). – Idiosomal length 135 (115-157) μ m, width 90 (75-107) μ m. Gnathosoma as in the female.

Venter (fig. 64). Epimeres I fused together medially. Epimerites I represented by small, laterally directed extensions fused with epimeres II. Epimeres II-III free medially. Claparede's organs (Cl.o.) in the form of circular rings in the centers of coxal fields I. Setae of coxal fields I vestigial, not visible in all specimens, situated anterio-medially from Claparede's organs. Setae of coxal fields III not observed.

Dorsum (fig. 63). Dorsal cuticle smooth, without apparent sclerotized shields. Internal vertical setae T-shaped as in other stages. Other dorsal setae filiform with expanded bases. Hysterosoma with 10 pairs of setae, d_4 and l_4 absent, l_5 ventrally positioned (cf. fig. 64). Most hysterosomal setae situated on protuberances.

Legs. Leg chaetotaxy and solenidiotaxy as in the female except trochanter setae I-III and solenidia omega-2 and omega-3 of tarsus I absent. Legs relatively shorter and stouter than in adults, with setal positions slightly altered.

Protonymph (figs. 65, 66). – Idiosomal length 170 (143-201) μ m, width 120 (83-142) μ m. Gnathosoma similar to female.

Venter (fig. 66). Epimeres I fused in a V-shape, with triangular extensions around trochanters. Epimers II-IV free medially, with lateral extensions around trochanters. Epimerites I very small, fused with epimeres II medially. One pair of relative large genital papillae between coxal fields IV. One pair of genital setae (ga) lateral to genital papillae. Anus relative large, without associated anal setae. Setae of coxal fields I and III present, filiform.

Dorsum (fig. 65). Cuticle smooth. Propodosoma with weakly sculptured



Figs. 63, 64. Aphodanoetus teinophallus spec. nov. larva. 63. Dorsum. 64. Venter.



Figs. 65, 66. Aphodanoetus teinophallus spec. nov. protonymph. 65. Dorsum. 66. Venter.



Figs. 67, 68. Aphodanoetus teinophallus spec. nov. tritonymph. 67. Dorsum. 68. Venter.

sclerite bearing setae vi and ve; form of these and other dorsal setae as in larva. Two pairs of opisthosomal setae added at this stage (d_5 and l_5 ; cf. fig. 66). Openings of opisthosomal glands (gla) between setae l_2 and d_3 . Cupules not observed.

Legs. Legs I-III longer and relatively thinner than in larva. Chaetotaxy as in larva but solenidion omega-2 added on tarsus I. Leg IV added in this stage, chaetotaxy similar to protonymphal chaetotaxy of other Astigmata. Pretarsi as in other stages.

Tritonymph (figs. 67, 68). – Idiosomal length 179 (142-221) μ m, width 128 (98-163) μ m. Gnathosoma as in female.

Venter (fig. 68). Epimerae I reduced, triangular. Epimerae II-IV free medially. Epimerites not observed. Two pairs of genital papillae arranged in a rectangle between coxal fields coxal fields IV. Genital setae (ga) anterior to genital papillae. One pair of anal setae (a4) present laterally of anus. Opisthosomal setae l_5 ventrally displaced, positioned posterior to the anus. Setae of coxal fields I vestigial, only the base is visible. Setae of coxal fields III filiform. Setae of coxal fields IV short, displaced medially to a position posterior and lateral to the posterior genital papillae.

Dorsum (fig. 67). Cuticle smooth. Propodosomal sclerite with a faint honeycomb-like pattern, bearing both pairs of vertical setae. Internal vertical setae T-shaped as in other stages; external vertical setae and scapular setae filiform with expanded bases. Hysterosomal setae similar in form except setae l_1 , d_2 , d_3 , and d_4 which are spine-like. All setae situated on individual protuberances except d_2 , both of which are on a single protuberance. Setae l_5 displaced ventrally (cf. fig. 68). Lateral opisthosomal glands and cupules not observed.

Legs. All legs similar to female in form and chaetotaxy.

Deutonymph (figs. 69-75). – Body ovoid, idiosomal length 173 (152-193) μ m, width 127 (109-140) μ m.

Gnathosoma (fig. 71). Remnant of the subcapitulum cylindrical, average length 24 μ m, width 7 μ m. Palpal solenidia arising directly from subcapitular apex, length 50 μ m; palpal supracoxal setae setiform, dorso-apical, length 8 μ m.

Venter (fig. 70). Epimeres I fused anterio-medially to form a long sternum which ends freely. Epimeres II fused posterio-medially to epimeres III. Epimerites I short, fused to epimeres II. Epimerites II very weakly developed. Epimeres III fused together medially, with a very short posterior median apodemal extension extending from point of fusion. Epimeres III with weakly delimited surface sclerotization extending laterally from internal apodemes and posterio-medially directed processes extending to coxal conoids III. Epi-







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meres IV well-developed, fused medially to posterior median apodeme and each with a well-developed element extending posterio-medially from trochanters to genital region. Epimerites III-IV absent. Genital opening and coxal conoids IV surrounded by a large circular apodeme with a bifurcate, anterior median extension which approaches posterior end of median apodeme. Two pairs of genital papillae within genital atrium. Genital setae (ga)setiform, positioned posterio-laterally of opening. Coxal setae I, III, and IV in the form of conoids. Surface of coxal fields sclerotized from bases of legs I to posterior portion of coxal fields III, with sclerotization most pronounced around bases of trochanters I-II. Attachment organ slightly trapezoidal, widest anteriorly, rounded posteriorly, with striated margins. Anterior suckers stalked (slightly displaced posteriorly in fig. 70), with striate margins. Median suckers slightly larger than anterior suckers, with well-sclerotized margins; small internal refractile spots surrounding central pair of vestigal alveoli. Anterior lateral, posterior lateral and posterior median cuticular suckers present, with striated margins. Two pairs of conoidal setae present, lateral and posterior to the median suckers. Remnant of anus situated between anterior suckers.

Dorsum (figs. 69, 70). Propodosoma very reduced, with subequal, filiform scapular setae. Cuticle smooth, anterior margin of hysterosoma with transverse striations. All setae very short. Cupules *ia* between setae d_1 and *sh*, *im* ventrally positioned between and lateral to legs III and IV, *ip* between setae l_3 and l_4 , ih ventral, posterio-lateral to posterior lateral cuticular suckers. Opisthosomal gland openings between setae *sh* and l_3 .

Legs (figs. 72-75). Trochanters I, II and IV without setae; seta of trochanter III spine-like. Chaetotaxy of femur-genu-tibia I-IV as in female, setae generally spine-like or setiform. Femur-genu of legs I-II fused, non-articulating, with a thin line of membrane partially visible between the segments. Genutibia-tarsus III-IV fused, with a partially membranous area sometimes visible between some segments. Tarsi III-IV subdivided medially. Tarsal chaetotaxy 8-9-6-6 with the following setae present: tarsus I with setae la spine-like, in basal half of segment; wa spine-like, slightly anterior to middle of segment; ra, f, p and q spine-like, near apex of tarsus; d flattened, apical; and e thickened basally, expanded and spoon-like apically, at tarsal apex. Tarsus II shorter than tarsus I, setae generally similar except seta ba present, spinelike, in basal half of segment, and seta e not spoon-like. Tarsus III with four setae in basal portion, r more elongate, d and w spinelike, and s a very short spine; two setae in apical portion of tarsus, f an apical spine, e slightly elongate and flattened. Tarsus IV with w longer and filiform, r shorter than rIII; setae d, s, and f similar in form and position to homologues on tarsus III; seta e an elongate apical spine. Solenidiotaxy consisting of sigma-1 on genu I, tapering, about as long as genu; sigma of genu II with a rounded apex; tibia I with phi elongate, tapering, omega-1 of tarsus I displaced onto tibial apex, base contiguous with that of solenidion phi, famulus elongate, about twice the length of omega-1; tibiae II-III with phi tapering, phi IV much shorter. Solenidion omega-3 of tarsus I positioned proximally near the base of the tarsus. Pretarsi I-II similar in form, consisting of a blade-like empodial claw and a short, unmodified ambulacrum. Pretarsus III similar, but claw smaller. Pretarsus IV without empodial claw, ambulacrum present, with rounded base and tapering extension. Measurements of leg characteristics in table 3.

Systematic position. - On the basis of the presence of para-anal suckers in the male, *Alphodanoetus* would be assigned to the subfamily Spinanoetinae as defined by Scheucher (1957). However, because para-anal suckers occur in males of many other families of astigmatid mites, we believe that their presence in some Histiostomatidae represents a plesiomorphic condition not useful in defining natural taxa (OConnor, 1981). The loss of setae p and q from tarsi III-IV in the deutonymph is a synapomorphy shared by Aphodanoetus and Copronomoia Mahunka, 1976, a monotypic genus known only from deutonymphs associated with sphaerocerid flies whose natural habitat may be assumed to be dung. This synapomorphy is also shared with Bonomoia Oudemans, 1911, known from both adults and deutonymphs associated with subcortical habitats. However, Bonomoia exhibits additional setal reductions on the anterior tarsi, notably the loss of setae p and q from tarsi I-II, and more importantly, retains a more plesiomorphic ontogeny of the anterior trochanter setae. For the present, we regard Aphodanoetus to be possibly related to Copronomoia, a hypothesis which can be tested when the post-deutonymphal stages of Copronomoia are discovered.

Histiostoma phyllophorum (Oudemans, 1905)

Anoetus phyllophorus Oudemans, 1905: 238; 1912: 236; Mahunka, 1970: 26. Histiostoma phyllophorus Buitendijk, 1945: 362; Hughes & Jackson, 1958: 97. Histiostoma phyllophorum Scheucher, 1957: 318.

Material examined. – Cultures were begun with deutonymphs collected from *Aphodius fimetarius* Linné (Coleoptera: Scarabaeidae) and female mites, both collected from dung samples in a pasture in the vicinity of Nijmegen, The Netherlands. Other stages reared in the laboratory.

This species was originally described from a deutonymph collected from *Oniscus asellus* Linnaeus, 1758 (Isopoda) in Leiden, The Netherlands (Oudemans, 1905). Oudemans (1912) later reported additional deutonymphs from

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Oxythyrea funesta Poda, 1761 (Coleoptera: Scarabaeidae) and an unidentified passalid beetle from what is now Tanzania. Later workers have questioned the identification of the latter record. Scheucher (1957) described the adults of this species from material collected from cattle dung in Erlangen, Germany. Hughes & Jackson (1958) also described the adults; from specimens reared from "near compost pile, . . . in duck pen, . . . and in damp woods" in Virginia, USA. Hughes & Jackson synonymized the species *Histiostoma nichollsi* Womersley, 1941, with *H. phyllophorum. Histiostoma nichollsi* was described from "a small beetle" from Queensland, Australia. Womersley's description and figures of this species are not adequate to determine if this synonymy is justified.

Because both adults and deutonymphs of this species have been adequately described, we offer here only some observations regarding the ontogeny of certain characters. The pattern of sclerotized plates in the larva, protonymph and tritonymph and the position of dorsal setae on these plates is similar to the patterns seen in *H. brevimanus*. The setae of coxal fields I and III are larval, while the setae of coxal fields IV appear first in the deutonymph, then disappear in the tritonymph to reappear again in the adults. This pattern is identical with that of *H. brevimanus*. The genital setae appear in the deutonymph and are retained in the tritonymph and adult, contrasting with the pattern seen in *H. brevimanus* in which these setae appear in the deutonymph but disappear in the tritonymph, to reappear in the adult male but not in the female. One pair of anal setae is added in the protonymphal instar, with two additional pairs appearing in the adults (possible homology of the deutonymphal suckers with anal setae is not considered here). The epimeres I of the tritonymph are very reduced as in the other species described here.

Rhopalanoetus fimetarius (Canestrini & Berlese, 1882)

Histiostoma fimetarium Canestrini & Berlese, 1882: 150 (not Histiostoma fimetarius sensu Hughes & Jackson, 1958).
Rhopalanoetus fimetarius Samšiňák, 1962: 96; Mahunka, 1970: 66.
Anoetus lanceocrinus Oudemans, 1914: 72.
Histiostoma lanceocrinus Buitendijk, 1945: 362; Hughes & Jackson, 1958: 82.
Rhopalanoetus lanceocrinus Scheucher, 1957: 362; Mahunka, 1962: 117.
Anoetus tienhoveni Oudemans, 1926: 123.

Andeus nennoveni Oudemans, 1920: 125.

Material examined. – Cultures were begun with deutonymphs collected from *Aphodius fimetarius* Linné and *Teuchestes fossor* Linné (Coleoptera: Scarabaeidae) which were collected from cattle dung in the vicinity of Nijmegen, The Netherlands. Other stages reared in the laboratory.

This species is widespread and commonly associated with cattle dung and similar habitats in Europe and has been recorded in phoretic association with a

variety of scarabaeid beetles (*Aphodius, Geotrupes, Oniticellus*) (Mahunka, 1970). *Rhopalanoetus fimetarius* is also present in North America; one of us (B.M.OC.) has collected all stages of this species from cattle dung and deutonymphs from *Aphodius* species (Scarabaeidae) in New York and Michigan, USA.

This species was first described on the basis of adults and immatures from dung in Italy (Canestrini & Berlese, 1882). Deutonymphs were first described by Oudemans (1914) as *Anoetus lanceocrinus*. Both adults and deutonymphs of this species have been most recently described by Scheucher (1957), who proposed the genus *Rhopalanoetus* with *Anoetus lanceocrinus* Oudemans as type-species. On the basis of the rearings of Scheucher, Samšiňák (1962) synonymized *Anoetus lanceocrinus* Oudemans, 1914 with *Histiostoma fimetarium* Canestrini & Berlese, 1882; the latter name having priority. Hughes & Jackson (1958) described a deutonymph and adults which they referred to *Histiostoma fimetarium*. Mahunka (1967) noted that this was a misidentification, the material of Hughes & Jackson in fact representing a new species, which he named *Anoetus jacksoni*. This species should be properly referred to the genus *Histiostoma*.

We provide the following information regarding the timing of ontogenetic changes in this species. The dorsum of the larva bears eight discrete sclerites: a pair of anterio-lateral sclerites bearing setae l_1 and h, a pair of medio-lateral sclerites bearing setae l_2 , a pair of posterio-lateral sclerites bearing setae d_5 , an unpaired anteriomedian sclerite bearing setae d_2 , and an unpaired median sclerite bearing setae d_3 . In the protonymph, the median sclerite of the larva bearing setae d_3 is divided into two separate sclerites which are more laterally positioned, and setae d_4 are positioned on the posterior lateral sclerites with d_5 on membranous integument. This pattern of sclerotization is repeated in the tritonymph.

Coxal setae I and III appear first in the deutonymph, then disappear in the tritonymph, appearing again in the adult male only. The setae of coxal fields IV appear in the deutonymph, disappear in the tritonymph and reappear in both adult male and female. The genital setae appear first in the protonymph and are retained in all subsequent stages. One pair of anal setae appears in the protonymph, with an additional three pairs appearing in the adult male. The tritonymph and adult female retain only the single protonymphal pair of anal setae. As in the other taxa examined, the tritonymph exhibits a reduction of epimeres I.

DISCUSSION

Ontogenetic character transformations have great potential use as characters in phylogeny reconstruction. However, because few taxa in the Histiostomatidae have been described from all ontogenetic stages, only very preliminary conclusions can be drawn from the information derived from this study. Within the Histiostomatidae, ontogenetic transformations in characters such as sclerotization patterns and setal additions have been previously described only for taxa assignable to the subfamily Histiostomatinae (*Histiostoma julorum* Koch, 1881 by Hughes & Jackson, 1958; *Hormosianoetus mallotae* by Fashing, 1973). In this study, the first ontogenetic series are described for the subfamilies Myianoetinae (*Myianoetus simplex* Mahunka, 1972) and Spinanoetinae (*Rhopalanoetus fimetarius* (Canestrini & Berlese, 1882)), as well as for *Aphodanoetus teinophallus* spec. nov.

For the present, it is worth noting that certain ontogenetic transformations occur in all histiostomatid mites so far examined. Two such transformations are unique to this family when compared with other astigmatid mites. These character state transformations are the reduction of epimeres I in the tritonymph and the loss of the opisthosomal glands in the tritonymph. The latter character exhibits an ontogeny unique to this family, with the gland being absent in the larva, appearing in the protonymph and deutonymph, disappearing in the tritonymph, and reappearing in the adult. Outgroup comparison with other astigmatid mites suggests that in the ancestral condition the gland is present in all ontogenetic stages. When additional information becomes available for other histiostomatid taxa, the utility of these and other ontogenetic transformations in ascertaining either character state polarities (the ontogenetic criterion of Hennig) or phylogenetic relationships may be established.

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	Histiostoma		Myianoetus		Aphodanoetus	
	brevin	ıanus	simplex		teinophallus	
	Ŷ	ď	ę	ď	Ŷ	്
Idiosoma length	377	222	368	282	332	191
Idiosoma width	233	111	231	188	237	128
vi	11	9	13	12	14	9
ve	9	8	9	9	14	7
sci	16	11	9	9	23	12
sce	35	30	11	10	28	16
d_1	25	18	11	9	26	14
d_2	26	16	25	10	29	15
d_3	27	14	27	11	33	15
d_4	31	15	17	12	36	15
d_5	35	18	14	10	25	12
l_1	31	20	13	10	30	16
l_2	30	15	12	10	26	13
l_3	36	22	14	10	27	14
l_4	36	24	16	11	29	13
l_5	44	60	16	13	23	12
h	38	23	13	11	24	15
sh	35	19	12	10	27	14
ga	*	4	15	8	9	7
al	-	—	12		-	8
a2	-	-	16	_	_	_
аЗ	37	8	15	5	-	10
a4	42	10	15	5	7	9
CX I	15	10	16	15	10	10
CX III	17	11	17	14	12	10
CX IV	12	7	16	19	7	10
Palp solenidion	64	31	54	44	49	37
ul'	23	20	21	18	20	13
<i>m</i>	39	20	21	14	18	12

Table 1. Measurements in μm of idiosomal and gnathosomal characters of adults; * indicates structure not measurable; - indicates structure absent.

	Histiostoma		Myianoetus		Aphodanoetus	
	brevim	anus	simple	x ~1	ieinop	nauus
Log Llogoth	¥ 120	0	¥	0	¥	125
Leg I length	120	8/	198	185	10/	135
Leg II length	120	91	157	148	140	115
Leg III length	104	78	158	146	141	116
Leg IV length Solenidia	131	91	183	171	165	136
Omega-1 I	12	12	16	15	13	11
Omega-2 I	13	12	12	14	6	5
Omega-3 I	9	17	55	35	16	10
Omega-1 II	15	28	16	38	13	20
Phi I	15	30	19	25	26	28
Phi II	15	13	18	17	11	9
Phi III	14	10	19	18	11	9
Phi IV	11	8	22	17	10	7
Sigma-1 I	12	12	9	11	8	7
Sigma-2 I	12	10	15	16	10	12
Sigma II	6	5	12	13	10	10
Setae						
aa l	6	5	6	4	8	6
ba I	9	6	7	8	8	5
ba II	13	9	8	8	10	6
la I	24	14	11	6	12	7
la II	21	15	11	10	12	9
ra I	19	11	9	7	10	6
ra II	20	15	9	7	11	9
r III	19	10	7	5	9	8
r IV	22	14	6	6	9	8
wa I	15	6	6	4	9	5

Table 2. Measurements in μm of some characters of the legs of the adults; * = structure not measurable.

	Histic	Histiostoma brevimanus		Myianoetus simplex		Aphodanoetus teinophallus	
	brevi						
	ę	ď	Ŷ	ď	ę	ď	
wa 11	15	7	6	6	11	8	
w III	12	8	9	9	11	9	
w IV	14	10	8	7	11	9	
d I	38	30	78	60	74	54	
d II	40	34	48	39	41	29	
d III	6	4	7	7	9	6	
d IV	7	4	6	6	9	7	
s I	12	6	10	6	9	5	
s II	10	7	8	7	10	7	
s III	15	8	10	8	12	9	
s IV	16	7	10	9	12	9	
hT I	8	5	6	6	9	7	
hT II	7	5	5	6	8	6	
gT I	15	10	7	6	10	7	
gT II	18	14	7	6	10	8	
kT III	6	5	6	6	8	6	
kT IV	5	5	5	5	9	6	
mG I	5	3	10	9	7	5	
mG II	5	4	10	10	6	5	
cG I	10	7	7	6	8	5	
cG II	11	7	6	6	7	5	
vFI	7	6	10	9	8	6	
vF II	7	6	9	8	9	7	
wF IV	24	17	10	9	9	7	
pR I	23	12	*	*	6	6	
pR II	27	18	8	9	7	5	
sR III	28	19	8	9	10	8	

Table 2. (continued).

Histiostoma brevimanus	Myianoetus simplex	Aphodanoetus teinophallus
53	82	101
49	72	82
42	57	78
46	33	73
12	14	20
13	30	10
10	10	15
19	4	31
5	16	5
5	3	5
6	4	8
5	7	5
4	3	7
6	4	6
16	*	17
7	6	4
7	5	5
16	16	14
14	22	6
8	4	10
8	3	10
6	5	9
6	4	6
19	11	18
16	14	16
25	14	10
	$\begin{array}{c} Histiostoma \\ brevimanus \\ 53 \\ 49 \\ 42 \\ 46 \\ 12 \\ 13 \\ 10 \\ 19 \\ 5 \\ 5 \\ 6 \\ 5 \\ 4 \\ 6 \\ 16 \\ 7 \\ 7 \\ 16 \\ 14 \\ 8 \\ 8 \\ 6 \\ 6 \\ 19 \\ 16 \\ 25 \\ \end{array}$	HistiostomaMyianoetusbrevimanussimplex 53 82 49 72 42 57 46 33 12 14 13 30 10 10 19 4 5 16 5 3 6 4 5 7 4 3 6 4 16 $*$ 7 6 7 5 16 16 14 22 8 4 8 3 6 5 6 4 19 11 16 14 25 14

Table 3. Measurements in μm of some characters of the legs of the deutonymphs.

	Histiostoma	Myianoetus	Aphodanoetus
e IV	25	simplex 65	28
fI	5		4
f II	5		4
fIII	3	3	3
f IV	3	3	3
s III	2	3	2
s IV	6	2	5
рI	4	_	3
p II	4		3
p III	3		
p IV	3	3	_
q I	3	-	3
q II	3		3
hT I	10	7	7
hT II	8	5	7
gT I	7	23	7
gT II	5	15	6
kT III	6	7	9
kT IV	6	5	8
mG I	9	22	9
mG II	8	11	10
cG I	6	25	9
cG II	6	18	8
vFI	9	19	8
vF II	10	23	12
wF IV	14	12	12
sR III	12	16	17

Table 3. (continued).