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The biting louse genus *Werneckiella* (Phthiraptera: Trichodectidae) ectoparasitic on the horse family Equidae (Mammalia: Perissodactyla)

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Introduction

This paper deals with the species of biting lice of the family Trichodectidae parasitic principally on the mammalian family Equidae. The family Trichodectidae are the only members of the suborder Ischnocera to parasitize mammals, where they inhabit the dermecos, i.e. the microhabitat created by the host skin and its outgrowths (Smit, 1972). The only other Ischnoceran family, Philopteridae, is parasitic on birds (except *Trichophilopterus*), and contains the majority of Ischnoceran species (approximately 2610 species). The species of Trichodectidae, approximately a tenth of the Philopteridae, are distributed amongst the mammalian orders Carnivora (Canoidea and Feloidea) (with approximately 79 species), Rodentia (Geomyidae and Erethezodontidae) (*ca.* 69), Hyracoidea (*ca.* 51), and Perissodactyla and Artiodactyla (*ca.* 64). In addition, the orders Edentata and Primates (Lorisiidae and Cebidae) are parasitized by two and four Trichodectid species, respectively.

The species of Trichodectidae parasitic on each mammalian order possess characters indicating affinities within themselves rather than with Trichodectidae parasitizing the other mammalian orders, thus indicating a monophyletic origin for Trichodectidae parasitizing each host order.

The characters have often not evolved into clearly defined states, and parallel evolution has resulted in similar character states appearing in Trichodectid species infesting different mammalian orders. This renders taxonomic discrimination difficult, especially when trying to determine supraspecific boundaries. It is not surprising therefore that the last major work concerning the taxonomy of the whole family Trichodectidae was published over 25 years ago (Werneck, 1950). Werneck recognized the presence of transitional species bridging genera, and hence failed to include keys to either genera or species. Only one revision of a Trichodectid genus has been published during the intervening period—*Geomydoecus* Ewing, parasitic on the North American pocket gophers, Geomyidae (Price & Emerson, 1971 and subsequent papers).

The Trichodectidae parasitizing Perissodactyla and Artiodactyla consist of species groups recognized as genera by some taxonomists, as follows: *Damalinia* Mjoberg, *Bovicola* Ewing, *Tricholipeurus* Bedford, *Lepikentron* Keler, *Rhabdomedilon* Keler, *Cervicola* Keler, *Holakartikos* Keler and *Werneckiella* Eichler (vide Eichler, 1963). The recognition of all these species groups as genera is disputed (vide Werneck, 1950; Hopkins & Clay, 1952). With the exception of *Werneckiella*, which parasitizes principally Perissodactyla, all these genera

parasitize Artiodactyla. As the supra-specific valuation of the species infesting Artiodactyla has not been investigated, it has not been possible to include a key to the above species groups in this paper. This paper does consider, however, that the Perissodactyl-infesting Trichodectid species can be separated as a genus on good evidence, i.e. *Werneckiella*.

When Eichler (1940) erected the genus *Werneckiella*, designating *Trichodectes equi* Denny from the domestic horse as type-species, he failed to distinguish the genus adequately, with the result that the validity of *Werneckiella* remained in doubt in succeeding years. Hopkins (1949) revised its status to a subgenus of *Damalinia*, and Keler & Werneck placed their species *neglecta* (Keler, 1942), *zuluensis* (Werneck, 1950) and *aspilopyga* (Werneck, 1956) in *Bovicola*.

Other Trichodectidae, described as new taxa, have been collected from the domestic ass (*Werneckiella equi asini* Eichler, 1954), the camel (*W. trampel* Eichler, 1954) and an Asiatic ass, the kulan (*Bovicola hemioni* Blagoveshtchensky, 1967), all of which are shown to be synonyms in this paper.

Recently, biting lice were collected from Hartmann Mountain Zebra in Namibia during a programme investigating the biology of this zebra (Joubert, 1974). The lice were kindly made available for study by Dr. J. Ledger and are described below as a new species.

The opportunity is also taken to clarify the taxonomic status of *Trichodectes ocellata* Piaget, a species of uncertain validity, and to emphasize the true author of *W. equi* as Denny and not Linnaeus, as the latter's reference is a nomen nudum (see Clay & Hopkins, 1950). This error has been perpetuated for many years.

The Equidae is the only family of Perissodactyla to harbour lice, one genus of biting lice (*Werneckiella*) and two genera of sucking lice (suborder Anoplura — *Haematopinus* Leach and *Ratemia* Fahrenholz).

Materials and methods

Few *Werneckiella* specimens have been collected since Werneck (1950) and the present study is based largely on specimens used in that work, especially those from zebras.

The following dimensions of the body were measured: total body length, head length, temple length and breadth of abdominal segments II and IV which are given in the species descriptions. The chaetotaxy, both numbers and disposition, provide important taxonomic information in the Phthiraptera as a whole. For the purposes of counting the setae the body was divided into head, prothorax, pterothorax and abdomen II–VII. Each abdominal segment was further subdivided into tergite: anterior (i.e. setae anterior to the marginal setae) and margin (i.e. marginal setae), lateral plate (setae of both plates of one segment were counted as one number), and the sternite. The total setal count is the sum of these regional numbers. The numbers of setae in each region reflect the density differences between species shown by the total setal numbers. Owing to lack of space only the numbers of setae of the following regions are given in the species descriptions: total setae and the anterior tergal setae of abdominal segments III–V, as these statistics provide the most valuable taxonomic evidence.

Terminology

Two terms are introduced in this paper for structures applied for the first time as taxonomic characters in the Trichodectidae.

(*a*) Post-vulval sclerite. This term is used for the pair of obliquely directed cuticular plates situated partially on the dorsal wall of the genital chamber and partially outside the chamber underneath the gonapophyses. They are broad posteriorly where 1 to 4 min sensory structures are visible as transparent discs, and taper anteriorly (figs. 11–14). This term was first used by Dhanda (1961) for similar structures in the Philopteridae (e.g. *Aegypoecus* Clay & Meinertzhagen) and which are here considered to be homologous to the structures found in these Trichodectidae.

(*b*) Abdominal lateral flecks. These are cuticular patches on either side of the intersegmental line in the lateral-tergal regions of the abdomen (figs. 7–10). They are most developed in the mid to posterior segments.

Host names

Host classification and nomenclature follows mainly Allen (1939) and Volf (1975).

Depositaries

Specimens referred to in this paper are deposited in the following institutions: British Museum (Natural History), London, U.K. (BMNH); South African Institute for Medical Research, Johannesburg, South Africa (SAIMR); Universidad Nacional Agraria, Lima, Peru (UNA, Lima); United States National Museum, Washington, U.S.A. (USNM); Zoological Institute, Leningrad, U.S.S.R. (ZI, Leningrad).

Werneckiella Eichler

Werneckiella Eichler, 1940, 160. Type-species *Trichodectes equi* Denny, by original designation.

Head: length approximately equal to breadth; pre-antennal marginal carina narrow to very broad anteriorly, with median interruption, anterior margin rounded or flattened; labrum high and angular or low and rounded (figs. 1 and 2); mandibles with ridges; antennae three-segmented, sexually dimorphic, distal segment with three ventral plate-like sensillae and males additionally with two subapical spinose setae on the inner dorsal margin.

Thorax: meso and metathorax fused to form the metathorax; fused pro/mesosternum of medium size, wing-shaped; coxal articulations arranged as in fig. 3.

Legs: prothoracic legs smallest, tarsi with inner opposable process bearing an apical, chitinous, spinose seta; meso and metathoracic tarsi with inner opposable process bearing an apical seta modified into a large, cylindrical, hyaline, blunt structure.

Abdomen: general shape obovate, broadest at IV; I present only as a vestigial tergite; spiracles on III–VIII; outer lateral margins of lateral plate II may be flared; intersegmental indentation shallow or deep; male with opposable

chitinous lateral flecks on posterior and anterior margins of each segment, of variable form (figs. 7–10); male with a pair of styli on posterior margin of tergite IX consisting of two chitinous areas bearing short, stout setae, of variable form (figs. 15–19); male genital plate large, consisting of two longitudinal sinuous chitinous bars laterally, connected by a broad chitinous bar anteriorly (fig. 31); female with a pair of elongated post-vulval sclerites (absent in *aspilopyga* and *zuluensis*); female gonapophyses flap-like, internal margin bearing long slender setae (fig. 4); genital chamber with compact small round chitinous maculations on dorsal and ventral walls.

Male copulatory apparatus: basic plan characteristic (figs. 33–37); basal plate long and broad, with two median sclerites posteriorly, the anterior sclerite usually long and slender and the posterior sclerite roughly square; parameres lateral, strongly curved, anterior region triangular and articulates with lateral arms of the basal plate, posterior region incurved, may be greatly expanded distally and usually with fused distal margins; endomeres central, consisting of two blade-like structures of variable form; eversible genital sac present, bearing spicules on the external surface of sac wall.

Chaetotaxy: general pattern as in figs. 31–32; setae slender, short to medium length; multiplication of the setae occurs within the genus.

Several characters distinguish *Werneckiella* from the species parasitic on Artiodactyla, notably: (1) form of female gonapophyses; (2) basic plan of male copulatory apparatus; (3) head with length approximately equal to breadth, and with characteristic rounded or flattened anterior margin; (4) form of pro/mesosternum and disposition of coxal articulations; (5) meso and metatarsi with apical setae on the inner opposable process blunt and hyaline.

The characters of most use in separating the species of *Werneckiella* are:

(*a*) chaetotaxy: *equi* (and to a lesser extent *ocellata*) show significant multiplication of setae above the basic organized pattern (fig. 38);

(*b*) structure of head: characteristic specific differences are visible in the shape of preantennal margin and carina thickness, degree of antennal fossa sclerotization, and size of male first antennal segment;

(*c*) structure of abdomen: form of male lateral flecks, female post-vulval sclerites, female tergite IX, and male copulatory apparatus.

Key to species

Males (the male of ocellata is unknown)

1 Styli long and pedunculate (fig. 19); head with very broad anterior marginal carina (fig. 24); copulatory apparatus diagnostic (fig. 37) . . . . . *neglecta*
– Styli short (figs. 15–18); head with narrower anterior marginal carina; copulatory apparatus not as in fig. 37 2
2 Temple length greater than 0·115 mm; tergites III–V with anterior setae greater than 20; antennal fossa membranous, but inner wall may show a little sclerotization (fig. 25); copulatory apparatus diagnostic (fig. 36) . . . . . *equi*
– Temple length less than 0·115 mm; tergites III–V with anterior setae usually less than 10; antennal fossa markedly sclerotized; copulatory apparatus not as in fig. 36 . . 3
3 Endomeres very broad; parameres strongly incurved, not dilated posteriorly (fig. 35) *zuluensis*
– Endomeres tapering posteriorly; parameres dilated posteriorly (figs. 33–34) . . 4
4 Copulatory apparatus diagnostic (fig. 33) . . . . . *zebrae*
– Copulatory apparatus diagnostic (fig. 34) . . . . . *aspilopyga*

Females

1 Post-vulval sclerites absent 2
– Post-vulval sclerites present 3
2 Tergite IX with circular transparent areas laterally (fig. 6) . . . . . *aspilopyga*
– Tergite IX wholly sclerotized (fig. 5) . . . . . *zuluensis*
3 Head with broad anterior marginal carina (0·034 mm); anterior margin flattened *neglecta*
– Head with narrower marginal carina (usually less than 0·030 mm); anterior margin typically rounded 4
4 Pre-antennal marginal carina smoothly rounded; antennal fossa membranous, but inner wall may show a little sclerotization (fig. 25); lateral plates without long anterior bar (fig. 7); post-vulval sclerite narrow (fig. 11); labrum high and angular (fig. 2); tergite IX wholly sclerotized . . . . . *equi*
– Without combination of characters. 5
5 Tergite IX typically with transparent circular areas; labrum low and rounded; head with anterior marginal carina breadth as *equi* . . . . . *zebrae*
– Tergite IX typically wholly sclerotized; labrum low or high; head with marginal carina broader than *equi* . . . . . *ocellata*

Werneckiella equi (Denny)

(Figs. 2–5, 7, 11, 15, 20, 25, 36)

Type host: *Equus caballus* Linnaeus

Pediculus equi Linnaeus, 1758, 612. Host: *Equus caballus* Linnaeus. Nomen nudum.
Trichodectes equi Denny, 1842, 61, 191. Host: *Equus caballus* Linnaeus.
Trichodectes pilosus Giebel, 1874, 59. Host: *Equus caballus* Linnaeus.
Trichodectes parumpilosus Piaget, 1880, 297. Host: *Equus caballus* Linnaeus.
Trichodectes parumpilosus var. *tarsata* Piaget, 1880, 399. Host: *Equus caballus* Linnaeus.
Werneckiella equi (Denny); Eichler, 1940, 160. Host: *Equus caballus* Linnaeus.
Werneckiella trampi Eichler, 1954, 330. Host: *Camelus bactrianus* Linnaeus. Syn. nov.
Boricola hemioni Blagoveshtchensky, 1967, 860. Host: *Equus hemionus kulan* Groves & Mazak. Syn. nov.

MALE. Rare, male percentage less than 1% (Hopkins, 1949). *Head:* anterior margin rounded, marginal carina narrow (fig. 20); antenna with first segment of smallest proportions in genus (fig. 20); inner wall of antennal fossa membranous, but may be partially sclerotized (fig. 25); labrum high and angular (fig. 2). *Abdomen:* lateral flecks as in fig. 7; lateral plate with hyaline anterior margin giving the appearance of a narrow plate with sharply down curved inner margin (fig. 7, cf. figs. 9 and 10); styli smallest of genus (fig. 15), lobe inconspicuous. Copulatory apparatus as in fig. 36.

FEMALE. Characters as for male. Additional characters: abdominal tergite IX wholly sclerotized; post-vulval sclerite narrower more posteriorly than in other species (fig. 11).

Dimensions (in millimetres). From *Equus caballus* (♂=3, ♀=19). Total body length: ♂ range 1·73–1·93, $\bar{x}$1·86; ♀ range 1·60–2·16, $\bar{x}$1·95; head length: ♂ range 0·43–0·44, $\bar{x}$0·44; ♀ range 0·44–0·50, $\bar{x}$0·48; temple length: ♂0·12; ♀ range 0·13–0·16, $\bar{x}$0·14; breadth of abdomen II: ♂ range 0·54–0·58, $\bar{x}$0·55; ♀ range 0·58–0·69, $\bar{x}$0·63; breadth of abdomen IV: ♂ range 0·68–0·70, $\bar{x}$0·69; ♀ range 0·52–0·86, $\bar{x}$0·76.

From *Equus przewalskii* (♀=3). Total body length: ♀ range 2·08–2·14, $\bar{x}$2·12; head length: ♀ range 0·48–0·52, $\bar{x}$0·50; temple length: ♀ range 0·15–0·16,

$\bar{x}$0·15; breadth of abdomen II: ♀ range 0·62–0·64, $\bar{x}$0·63; breadth of abdomen IV: ♀ range 0·80–0·84, $\bar{x}$0·82.

From *Equus hemionus kulan* (♂=1, ♀=6). Total body length: ♂ range 1·60–1·90*; ♀ range 1·80–2·10*; head length: ♂0·40; ♀ range 0·45–0·50, $\bar{x}$0·47; temple length: not recorded; breadth of abdomen II: ♂0·51; ♀ range 0·59–0·64, $\bar{x}$0·61; breadth of abdomen IV: ♂ 0·70; ♀ range 0·72–0·84, $\bar{x}$0·78. (*=taken from original description.)

Chaetotaxy. From *Equus caballus* (♂=3, ♀=19). Total setae: ♂ range 1368–1639, $\bar{x}$1507; ♀ range 1283–2026, $\bar{x}$1543; anterior tergal setae: (III) ♂ range 30–36, $\bar{x}$33; ♀ range 7–46, $\bar{x}$33; (IV) ♂ range 25–36, $\bar{x}$31; ♀ range 11–56, $\bar{x}$31; (V) ♂ range 16–32, $\bar{x}$24; ♀ range 10–55, $\bar{x}$28.

From *Equus przewalskii* (♀=3). Total setae: ♀ range 1621–1834, $\bar{x}$1771; anterior tergal setae: (III) ♀ range 42–47, $\bar{x}$45; (IV) ♀ range 41–53, $\bar{x}$46; (V) ♀ range 43–53, $\bar{x}$47.

From *Equus hemionus kulan* (♂=1, ♀=6). Total setae: ♂ 1551; ♀ range 1297–1714, $\bar{x}$1499; anterior tergal setae: (III) ♂ 37; ♀ range 34–45, $\bar{x}$40; ♂ 28; ♀ range 24–41, $\bar{x}$31; (V) ♂ 24; ♀ range 27–42, $\bar{x}$33.

Material examined

Lectotype ♀, of *Trichodectes equi* Denny, by present designation, from 'Horse', Britain, no other data, 1852–98, Denny (BMNH); paralectotypes: 2 ♀, same data as Lectotype (BMNH) [examined].

Lectotype ♀, of *Trichodectes parumpilosus* Piaget, by present designation, from 'cheval', no other data, slide No. 327, Piaget (BMNH); paralectotypes: 3 ♀, from *Equus caballus* and 'cheval', no other data, slide Nos. 326, 327, Piaget (BMNH) [examined].

Lectotype ♀, of *Trichodectes parumpilosus tarsata* Piaget, by present designation, from 'cheval de Java', no other data, slide No. 331, Piaget (BMNH); paralectotypes: 3 ♀, same data as lectotype, slide Nos. 330, 331a, Piaget (BMNH) [examined].

Paratypes 1♂, 6♀, of *Bovicola hemioni* Blagoveshtchensky, from *Equus hemionus kulan* Groves & Mazak, U.S.S.R., Kazakhstan, Aral Sea, O. Barsa Kel'mes Is., 2.iv.1964, 31.iii.1964, B. A. Pamek (ZI, Leningrad) [examined].

From *Equus caballus* L. Brazil, 30♀, Rio de Janeiro, 1941, F. L. Werneck (BMNH); England, 2♀, Kent, Orpington, i.1966, B. Hargreaves (BMNH); Scotland, 2♀, Shetland, N. Mavine (BMNH); Scotland, Shetland, N. Gluss, v.1941, J. Waterston (BMNH); Kenya, 23♀, 1937–38, Meinertzhagen (BMNH); South Africa, 1♀, Natal (BMNH); Trinidad, 2♀, Terra Nova Exped. (BMNH); Trinidad, 1♀ (from 'Frigate Bird', error), Terra Nova Exped. (BMNH); No locality, 1♀, Terra Nova Exped. (BMNH); U.S.A., 1♂ 1♀, Georgia, Waycross, 25.i.1947, A. L. Smith (BMNH); U.S.A., 1♂ 2♀, same data (USNM); U.S.A., 1♂ 2♀, Florida, Ocala, 28.ii.1948, A. L. Smith (USNM).

From *Equus przewalskii* Poliakov. England, 3♀, London Zoo, viii.1971 (BMNH).

This species is most easily distinguished by the greater density of setae, evenly rounded anterior margin of head with narrow marginal carina, membranous antennal fossa, the relatively reduced form of male first antennal segment, male abdominal flecks, male styli, and the structure of the male copulatory apparatus. The relatively undeveloped features of the species, together with its multiplication of setae, set *equi* apart from other species of the genus. The five other species all show more developed features (e.g. flattening of anterior head margin, greater sclerotization of antennal fossa, the more modified characters of the abdominal lateral region) and a density of setae significantly less than *equi*.

Denny's description of *equi* was based on specimens from both the horse and the ass. Examination of the type series, labelled as originating from a horse only, show they can be divided into horse-infesting and ass-infesting forms, the latter being *ocellata*.

Werneckiella equi, as redefined here, inhabits the flanks, sides of the neck and base of the tail of *Equus caballus* (Roberts, 1952); it prefers the finer body hairs (Murray, 1957) and feeds on the exudations and epidermal debris (Cameron, 1940). Heavy infestations may cause extreme irritation to the host and hair loss, and *equi* has been incriminated as the vector of such diseases as infectious anaemia rickettsiae.

The synonymy of *equi* has been discussed by Werneck (1936) and Keler (1938). As a result of the rarity of males and their possession of the most reliable taxonomic character, the copulatory apparatus, several names have been applied to *equi* females taken from different host individuals of *E. caballus*; these are: *equi. pilosus*, *parumpilosus* and *p. tarsata*. Type material of the latter two species was examined, and as they lie within the *equi* range of variation their conspecificity is confirmed.

A comparison of the statistical data shows that lice from *E. przewalskii* Poliakov and *E. hemionus kulan* Groves & Mazak are also inseparable from *equi* infesting *E. caballus*. This can be explained either because of negligible character divergence of the louse populations while their hosts evolved, or because the lice on these hosts are the result of a recent host-change from *E. caballus*. The latter seems the more likely explanation, as the lice from *E. przewalskii* were collected from a zoo host individual and the lice from *E. hemionus kulan* were collected from captive kulans in a reserve on O. Barsa-Kel'mes Island in the Aral Sea, north of their natural range. Both host individuals may have come into contact with domestic horses, allowing an opportunity for *equi* individuals to cross over and start new populations.

The louse population sample from the kulan requires further discussion, as it was ranked a distinct species, *Bovicola hemioni*, by Blagoveshtchensky (1967). Examination of paratypes showed that the alleged diagnostic characters of *hemioni*, i.e. "structural details of the head and the male copulatory apparatus", lie within the range of variation of *equi*. However, a greater proportion of males on *Equus hemionus kulan* (18·75%) indicates that lice populations on *E. caballus* and *E. hemionus kulan* are genetically distinct to some extent. Their true biological relationship should therefore be investigated further by means of studies on host-parasite relations of Asiatic asses.

Eichler (1954) named a series of females from a circus camel (*Camelus bactrianus* L.) as *Werneckiella trampel*. He cited the form of head and tarsi, and the chaetotaxy as diagnostic characters. His description was accompanied by a good figure of the whole animal which clearly shows all the diagnostic features of *equi*. There can be little doubt that the captive camel acquired these lice from a horse.

Werneckiella ocellata (Piaget)

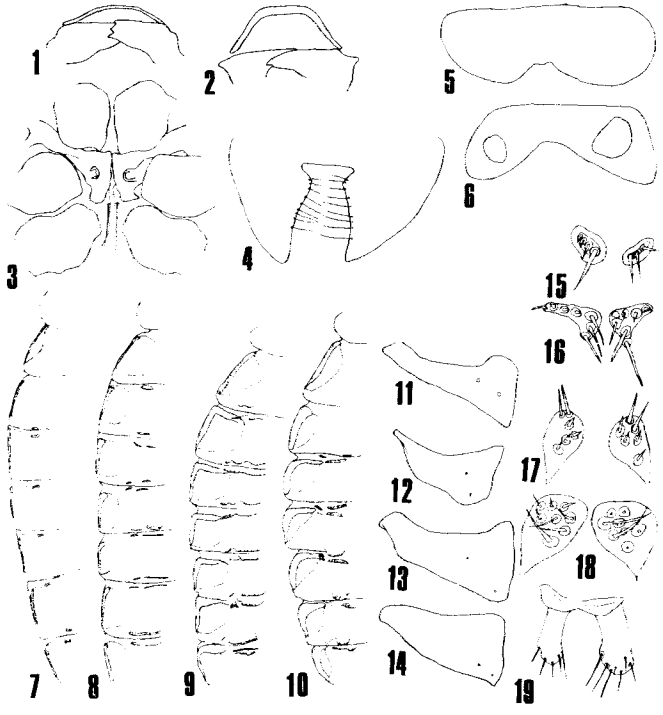
(Figs. 1, 12, 26)

Type host: *Equus burchellii* (Gray), ? error. (probably *Equus a. asinus* Linnaeus.)

Trichodectes parumpilosus var. *ocellata* Piaget, 1880, 398. Host: *Equus burchellii* (Gray).
Werneckiella ocellata (Piaget); Eichler, 1940, 161. Host: *Equus burchellii* (Gray).
Werneckiella equi asini Eichler, 1953, 445. Host: *Equus asinus* Linnaeus. Syn. nov.

MALE. Unknown.

FEMALE. *Head:* anterior margin flattened and marginal carina broader than *equi*; antennal fossa entirely sclerotized (fig. 26); labrum typically low and rounded (fig. 1). *Abdomen:* post-vulval sclerites typically broader more anteriorly than *equi* (fig. 12); tergite IX entirely sclerotized; lateral plates with anterior margin typically as a long sclerotized bar.



FIGS. 1–19. *Werneckiella* spp. (1 and 2) Labrum: (1) *W. ocellata*; (2) *W. equi*. Venter of thorax: (3) *W. equi*. Female gonapophyses: (4) *W. equi*. (5 and 6) Female tergite IX: (5) *W. equi*; (6) *W. aspilopyga*. (7–10) Male lateral regions of abdomen: (7) *W. equi*; (8) *W. zebrae*; (9) *W. aspilopyga*; (10) *W. neglecta*. (11–14) Female post-vulval sclerites: (11) *W. equi*; (12) *W. ocellata*; (13) *W. zebrae*; (14) *W. neglecta*. (15–19) Male styli: (15) *W. equi*; (16 *W. zebrae*; (17) *W. aspilopyga*; (18) *W. zuluensis*; (19) *W. neglecta*.

Dimensions (in millimetres). From *Equus burchellii* (♀=6). Total body length: ♀ range 1·94–2·18, $\bar{x}$2·12; head length: ♀ range 0·48–0·54, $\bar{x}$0·51; temple length: ♀ range 0·13–0·16, $\bar{x}$0·15; breadth of abdomen II: ♀ range 0·63–0·70, $\bar{x}$0·67; breadth of abdomen IV: ♀ range 0·80–0·93, $\bar{x}$0·88.

From *Equus asinus* (♀=13). Total body length: ♀ range 1·77–2·05, $\bar{x}$2·12; head length: ♀ range 0·42–0·54, $\bar{x}$0·46; temple length: ♀ range 0·12–0·15, $\bar{x}$0·14; breadth of abdomen II: ♀ range 0·54–0·66, $\bar{x}$0·61; breadth of abdomen IV: ♀ range 0·68–0·87, $\bar{x}$0·79.

Chaetotaxy. From *Equus burchellii* (♀=6). Total setae: ♀ range 1278–1572, $\bar{x}$1393; anterior tergal setae: (III) ♀ range 11–15, $\bar{x}$14; (IV) ♀ range 13–23, $\bar{x}$18; (V) ♀ range 14–20, $\bar{x}$18.

From *Equus asinus* (♀=13). Total body setae: ♀ range 682–1414, $\bar{x}$1074; anterior tergal setae: (III) ♀ range 6–15, $\bar{x}$10; (IV) ♀ range 2–20, $\bar{x}$10; (V) ♀ range 7–17, $\bar{x}$10.

Material examined

Lectotype ♀, of *Trichodectes parumpilosus ocellata* Piaget, by present designation, from *Equus burchellii*, no other data, slide No. 328a, Piaget (BMNH); paralectotypes: 5♀, same data as lectotype (BMNH) [examined].

From *Equus a. asinus* L. BRITAIN, 4♀ (labelled 'Horse'. Error. See discussion under *equi*), no other data, Denny (BMNH): KENYA, 1♀, 1938, Hopkins (BMNH); MALAGASY REPUBLIC, 2♀, 3.viii.1948, G. Uilenberg (BMNH); NAMIBIA, 26♀, 80 m west of Windhoek, 14.ix.1971, E. Joubert (SAIMR); PERU, 2♀, Cajamarca, Cajamarca Prov., 10.x.1974, W. Dale, UA77–74 (UNA, Lima); UGANDA, 1♀, Tsavo District, iii.1942, T. R. Cox (BMNH); no locality, 5♀, Piaget, slide Nos. 334, 335 (BMNH).

From *Equus caballus* L. (result of host-change). PERU, 3♀, Cajamarca, Cajamarca Prov., 11.x.1974, W. Dale, UA 78–74 (UNA, Lima).

Owing to the lack of males, distinguishing characters of *ocellata* are difficult to formulate, since none of the female characters of this species differs absolutely from the other species of *Werneckiella*. Females of *ocellata* may be most easily distinguished from *equi* by the flattened anterior margin of the head, sclerotized antennal fossa, the generally greater sclerotization of the abdominal lateral region and the broader post-vulval sclerites. They differ from *aspilopyga* and *zuluensis* by the presence of post-vulval sclerites; from *neglecta* by the narrower anterior marginal carina of the head; and from *zebrae* by the apparent absence of transparent circular areas in tergite IX, and the generally greater sclerotization of the lateral regions of the abdomen.

After its original description in 1880 *ocellata* was accepted as a valid species for many years, but only because no one examined Piaget's type-specimens. Keler (1938) was the first person to synonymize *ocellata* with *equi*, but there is no evidence that he examined Piaget's type-specimens. However, Eichler (1940) maintained its validity. Werneck (1950) misidentified a series of zebra lice as *ocellata* without examining the type-specimens of *ocellata*, but later, on examination of these types, he renamed the zebra lice as *aspilopyga*, and synonymized *ocellata* with *equi* (Werneck, 1956).

It is well known that Piaget worked with specimens collected almost entirely from zoo hosts and museum skins (Keler, 1938; Clay, 1949). Werneck (1956) felt that Piaget's specimens from *Equus burchellii* had resulted from

contamination from a horse. However, flattening of the anterior margin of the head, sclerotized antennal fossa, abdominal lateral thickening and reduced density of setae (although lying just within the range for *equi*) are sufficient to place it apart from *equi* and nearer to the species infesting zebras. The absence of males prevents a more definite demonstration of the discreteness of this taxon.

Examination of *Werneckiella* from the domestic ass revealed the same character states as those of *ocellata*. Lice from a domestic ass were named *asini* by Eichler (1953). It has not been possible to examine the type-specimens of *asini* despite an attempt to borrow them from Eichler's collection. However, the figure in the original description, although poor, clearly shows the *ocellata* characters of flattened anterior head margin and sclerotized antennal fossa. There can be little doubt that *asini* is conspecific with *ocellata*.

The true host identity of *ocellata* is problematical because of the numerous records from *E. asini* and yet only the one record from *E. burchellii*, i.e. Piaget, 1880. The following explanations are possible. The most probable explanation is that the *ocellata* type-specimens found on a Burchell's zebra may have been contaminants from a domestic ass. This would imply that *E. burchellii* is not the natural host of *ocellata*. Alternatively, it is not impossible that the *ocellata* type-specimens may actually have originated from *Equus burchellii* as Piaget stated. Records at Rotterdam Zoo for the period Piaget worked in the Netherlands were destroyed during the Second World War, but enquiries at Leiden Museum revealed that two skins of *Equus b. burchellii* were recorded in a catalogue of mammals by F. A. Jentink published in 1892. It is likely that the Leiden Museum received these specimens some years before (Husson, pers. comm.). Thus it is conceivable that Piaget examined the skins and collected the *ocellata* type-specimens from them. If this actually happened the possible taxonomic distinction between lice from *E. b. burchellii* and *E. asinus* can only be endorsed by the discovery of males, which is no longer possible in the case of *E. b. burchellii* because of its extinction (Volf, 1975).

Neither of these explanations can be dismissed completely, and very likely the true type host of *ocellata* will remain unknown.

Werneckiella zebrae sp. nov.

(Figs. 8, 13, 16, 21, 27, 31–33)

Type host: *Equus zebra hartmannae* Matschie.

Male (fig. 31). *Head:* roughly equal proportions; anterior margin typically flattened, marginal carina with same thickness as *equi* (fig. 21); first antennal segment enlarged (fig. 21); antennal fossa sclerotized (fig. 27); temple similar to *equi*; labrum high or low. *Abdomen:* lateral flecks as in fig. 8, much smaller on anterior segments; lateral plates typically as *ocellata*, but may show the form of *equi* in some species; styli as in fig. 16. Copulatory apparatus: as in fig. 33.

Female (fig. 32). Characters as for male. Additional characters: abdominal tergite IX with transparent circular areas laterally; form of postvulval sclerite similar to *ocellata* (fig. 13).

Dimensions (in millimetres). (♂=2, ♀=4.) Total body length: ♂ range 2·18–2·20, $\bar{x}$2·19; ♀ range 2·21–2·40, $\bar{x}$2·29; head length: ♂0·46; ♀ range 0·48–0·50, $\bar{x}$0·49; temple length: ♂ 0·11; ♀ range 0·13–0·14, $\bar{x}$0·14; breadth of abdomen II: ♂ range 0·62–0·64, $\bar{x}$0·63; ♀ range 0·66–0·72, $\bar{x}$0·70; breadth of abdomen IV: ♂ range 0·74–0·75, $\bar{x}$0·75; ♀ range 0·83–0·93, $\bar{x}$0·88.

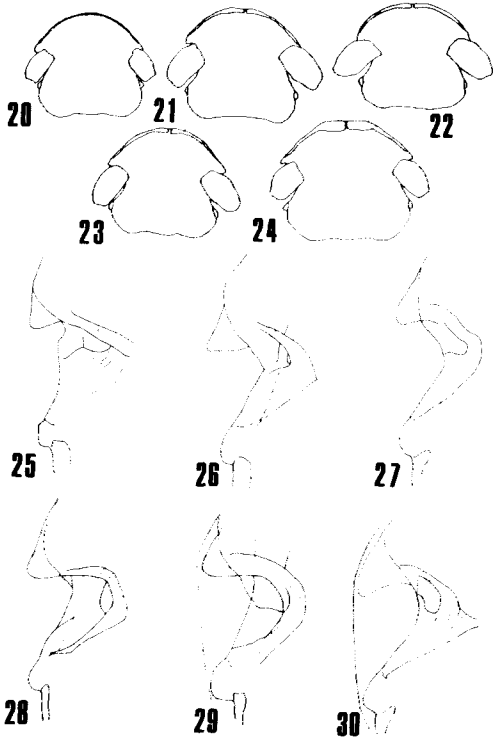
Chaetotaxy. (♂=2, ♀=4.) Total setae: ♂ range 886–1052, $\bar{x}$966; ♀ range 617–1214, $\bar{x}$970; anterior tergal setae: (III) ♂ range 5–10, $\bar{x}$8; ♀ range 5–21, $\bar{x}$13; (IV) ♂ range 6–9, $\bar{x}$8; ♀ range 3–17, $\bar{x}$10; (V) ♂ range 5–8, $\bar{x}$7; ♀ range 1–12, $\bar{x}$7.

Material examined

Holotype ♂, from *Equus zebra hartmannae* Matschie, Namibia, 80 m west of Windhoek, 18.i.1970, F. Zumpt (SAIMR).

Paratypes, 1♂ 4♀, same data as Holotype (SAIMR).

This species is most easily distinguished by the characters of the male copulatory apparatus. Other characters mentioned in the description distinguish *zebrae* only in their combination.



Figs. 20–30. *Werneckiella* spp. (20–24) Male heads: (20) *W. equi*; (21) *W. zebrae*; (22) *W. aspilopyga*; (23) *W. zuluensis*; (24) *W. neglecta*. (25–30) Antennal fossa: (25) *W. equi*; (26) *W. ocellata*; (27) *W. zebrae*; (28) *W. zuluensis*; (29) *W. aspilopyga*; (30) *W. neglecta*.

Werneckiella aspilopyga (Werneck) comb. nov.

(Figs. 6, 9, 17, 22, 29, 34)

Type host: *Equus burchellii boehmi* Matschie.

[*Bovicola ocellata* (Piaget): Werneck, 1950, 84.]
Bovicola aspilopyga Werneck, 1956, 28. Host: *Equus burchellii boehmi* Matschie.

MALE. *Head:* anterior margin rounded or flattened, marginal carina broader than *equi* (fig. 22); antennae with medium or greatly enlarged first antennal segment; antennal fossa sclerotized (fig. 29); temple length greatly reduced; labrum high and angular or rounded. *Abdomen:* lateral plates as *ocellata*; lateral flecks as in fig. 9; styli as in fig. 17. Copulatory apparatus: as in fig. 34.

FEMALE. Characters as for male. Additional characters: tergite IX with two distinct transparent circular areas laterally (fig. 6); post-vulval sclerites absent.

Dimensions (in millimetres). (♂ = 6, ♀ = 5.) Total body length: ♂ range 1·62–1·80, $\bar{x}$1·72; ♀ range 1·61–1·90, $\bar{x}$1·83; head length: ♂ range 0·41–0·45, $\bar{x}$0·43; ♀ range 0·40–0·47, $\bar{x}$0·45; temple length: ♂ range 0·089–0·110, $\bar{x}$0·090; ♀ range 0·110–0·150, $\bar{x}$0·12; breadth of abdomen II: ♂ range 0·58–0·64, $\bar{x}$0·60; ♀ range 0·59–0·69, $\bar{x}$0·66; breadth of abdomen IV: ♂ range 0·67–0·77, $\bar{x}$0·70; ♀ range 0·70–0·86, $\bar{x}$0·82.

Chaetotaxy (♂ = 6, ♀ = 5). Total setae: ♂ range 660–1028, $\bar{x}$859; ♀ range 651–971, $\bar{x}$805; anterior tergal setae: (III) ♂ range 0–12, $\bar{x}$5; ♀ range 0–4, $\bar{x}$2; (IV) ♂ range 0–9, $\bar{x}$4; ♀ range 0–6, $\bar{x}$2; (V) ♂ range 0–7, $\bar{x}$2; ♀ range 0–5, $\bar{x}$2.

Material examined

Lectotype ♂, of *Bovicola aspilopyga* Werneck, by present designation, from *Equus burchellii boehmi* Matschie, UGANDA, Jie County, Karamoja, ix.1941, T. W. Chorley (BMNH).

Paralectotypes: 1♀, same data as lectotype (BMNH); 1♂, TANZANIA, Shinyanga, iv.1946, Hopkins (BMNH) [examined].

TANZANIA, 4♀, Shinyanga, x.1946, Hopkins (BMNH).

For a discussion of *aspilopyga*, see after *zuluensis*.

Werneckiella zuluensis (Werneck) comb nov.

(Figs. 18, 23, 28, 35)

Type host: *Equus burchellii antiquorum* (Hamilton Smith).

Bovicola zuluensis Werneck, 1950, 88. Host: *Equus burchellii antiquorum* (Hamilton Smith).

MALE. *Head:* anterior margin typically flattened, but may be broadly rounded, breadth of marginal carina as *aspilopyga* (fig. 23); antenna first segment greatly enlarged; antennal fossa (fig. 28); temple as *aspilopyga*: labrum rounded, high or low. *Abdomen:* as described for *aspilopyga*. Copulatory apparatus: as in fig. 35.

FEMALE. Characters as for male. Additional characters: tergite IX entirely sclerotized; post-vulval sclerites absent.

Dimensions (in millimetres). (♂ = 6, ♀ = 6). Total body length: ♂ range 1·76–1·90, $\bar{x}$1·85; ♀ range 1·78–2·00, $\bar{x}$1·91; head length: ♂ range 0·44–0·46, $\bar{x}$0·45; ♀ range 0·46–0·50, $\bar{x}$0·48; temple length: ♂ range 0·09–0·11, $\bar{x}$0·10; ♀ range 0·10–0·14, $\bar{x}$0·12; breadth of abdomen II: ♂ range 0·59–0·66, $\bar{x}$0·64; ♀ range 0·66–0·72, $\bar{x}$0·69; breadth of abdomen IV: ♂ range 0·72–0·81, $\bar{x}$0·78; ♀ range 0·86–0·94, $\bar{x}$0·90.

Chaetotaxy (♂ = 6, ♀ = 6). Total setae: ♂ range 858–1190, $\bar{x}$1015; ♀ range 875–1234, $\bar{x}$1040; anterior tergal setae: (III) ♂ range 4–12, $\bar{x}$7; ♀ range 4–12, $\bar{x}$8; (IV) ♂ range 2–11, $\bar{x}$6; ♀ range 0–9, $\bar{x}$5; (V) ♂ range 1–8, $\bar{x}$4; ♀ range 4–9, $\bar{x}$5.

Material examined

Holotype ♂, of *Bovicola zuluensis* Werneck, from *Equus burchellii antiquorum* (Hamilton Smith), SOUTH AFRICA, Zululand, F. L. Werneck 2723 (BMNH).

Paratypes: 13♂ 15♀, same data as Holotype (BMNH).

The preceding species, *aspilopyga*, is discussed here as it is very close to *zuluensis*, differing only in the form of male copulatory apparatus and the sclerotization of female tergite IX. The copulatory apparatus of the two species differ chiefly in *aspilopyga* possessing needle-shaped endomeres and relatively less broad and incurved posterior parameres, whereas *zuluensis* possesses broad endomeres and broader, more incurved posterior parameres. Female *aspilopyga* also has tergite IX with distinct circular transparent areas laterally, this tergite being entirely sclerotized in *zuluensis*.

Both these species are most easily distinguished from the other *Werneckiella* species by the major features of the male copulatory apparatus, the absence of female post-vulval sclerites, and the more pronounced development of the following characters: size of the male first antennal segment, antennal fossa sclerotization, size of male abdominal flecks and reduction of temple length. In both *aspilopyga* and *zuluensis* the male styli are larger than in *equi* and *zebrae*, but have no visible pedunculate lobe as in *neglecta*.

Werneckiella neglecta (Keler) comb nov.

(Figs. 10, 14, 19, 24, 30, 37)

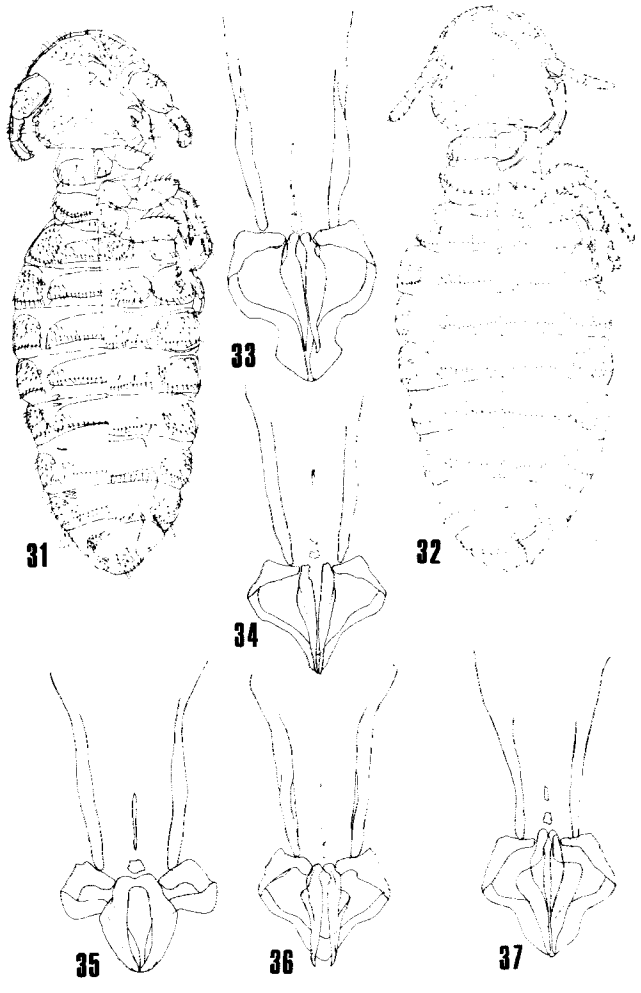
Type host: *Ammotragus lervia* Pallas.

Bovicola neglecta Keler, 1942, 77. Host: *Ammotragus lervia* Pallas.

MALE. *Head:* anterior margin markedly flattened and with very broad marginal carina (fig. 24); first antennal segment similar to *zebrae* (fig. 24); antennal fossa sclerotized (fig. 30); temple long; labrum of variable form. *Abdomen:* lateral plates as *ocellata* and lateral flecks large (fig. 10); styli well developed, with pedunculate lobes (fig. 19). Copulatory apparatus: as in fig. 37.

FEMALE. Characters as for male. Additional characters: degree of antennal fossa sclerotization similar to *ocellata*; tergite IX entirely sclerotized; post-vulval sclerite as *ocellata* (fig. 14).

Dimensions (in millimetres). (♂ = 2, ♀ = 2.) Total body length: ♂ 1·88; ♀ range 2·04–2·16, $\bar{x}$2·10; head length: ♂ 0·49; ♀ range 0·52–0·53, $\bar{x}$0·53; temple length: ♂ 0·13; ♀ range 0·17–0·18, $\bar{x}$0·18; breadth of abdomen II: ♂ 0·54; ♀ range 0·64–0·66, $\bar{x}$0·65; breadth of abdomen IV: ♂ 0·70; ♀ range 0·84–0·92, $\bar{x}$0·88.



FIGS. 31–37. *Werneckiella* spp. (31 and 32) *W. zebrae* sp. nov.: (31) male; (32) female. (33–37) Male copulatory apparatus: (33) *W. zebrae*; (34) *W. aspilopyga*; (35) *W. zuluensis*; (36) *W. equi*; (37) *W neglecta*.

Chaetotaxy (♂=2, ♀=2). Total setae: ♂ range 706–769, $\bar{x}$740; ♀ range 636–935, $\bar{x}$792; anterior tergal setae: (III) ♂ 3; ♀ range 2–11, $\bar{x}$7; (IV) ♂ 3; ♀ range 5–6, $\bar{x}$6; (V) ♂ range 0–8, $\bar{x}$4; ♀ range 3–4, $\bar{x}$4.

Material examined

1♂ 1♀, from 'Ovis ornatus Audouin' (=*Ammotragus lervia* Pallas), no locality, Piaget (BMNH); ENGLAND, 1♂ 1♀, London Zoo, 1969 (BMNH); SUDAN, 1♀, Khartoum Zoo, v.1946, T. Chorley (BMNH).

This species is the most distinctive of the genus. Characters which provide its easy recognition are the broad, flattened marginal carina of the head, the pedunculate male styli and the form of the male copulatory apparatus. The structure of the latter resembles most closely that of *zuluensis* in possessing deeply incurved posterior parameres which are, however, broader; also the endomeres are needle-like.

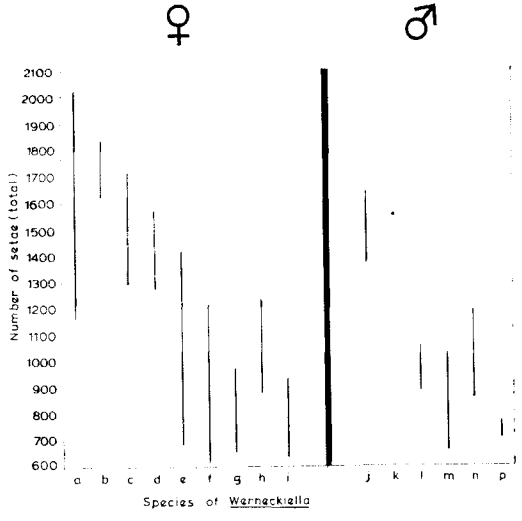


FIG. 38. Ranges of total numbers of setae (head, thorax, and abdominal segments II–VII) of *Werneckiella*. (*a*), (*j*): *equi* on *E. caballus* (32♀, 3♂): (*b*): *equi* on *E. przewalskii* (3♀): (*c*), (*k*): *equi* on *E. hemionus kulan* (6♀, 1♂); (*d*): *ocellata* on *E. burchellii* (6♀); (*e*): *ocellata* on *E. asinus* (13♀); (*f*), (*l*): *zebrae* (4♀, 2♂); (*g*), (*m*): *aspilopyga* (5♀, 6♂); (*h*), (*n*): *zuluensis* (6♀, 6♂); (*i*), (*p*): neglecta (2♀ 2♂).

The known occurrence of *neglecta* on captive *A. lervia* leaves some doubt as to the authenticity of this host. However, its discovery on this host on at least four separate occasions supports the argument that *A. lervia* is the natural host of *neglecta*.

Host-parasite relations

Delineation of *Werneckiella* from the other species parasitic on the Artiodactyla reflects the separation of the Equidae, in the Perissodactyla, from

the Artiodactyla. In discussing the higher classification of the recent Equidae Groves & Mazak (1967) note that the number of genera is in dispute, but there seems to be little doubt that recent Equidae have evolved into five main groups, i.e. *Equus* Linnaeus, *Hemionus* Stehlin & Graziosi, *Asinus* Gray, *Dolichohippus* Heller, and *Hippotigris* Hamilton Smith (Volf, 1975).

The five species of biting-lice parasitic on the Equidae can be divided essentially into two main groups: (*a*) *equi* and (*b*) *ocellata*, *zebrae*, *aspilopyga* and *zuluensis*, by several characters, especially: density of setae, structure of the pre-antennal region of the head and the degree of sclerotization of antennal fossae. This arrangement parallels the interpretation that the caballine equids (*Equus* s. str.) diverged from the line giving rise to the zebrine equids.

The only reliable *equi* material currently available is from the domestic horse, *E. caballus*. Doubts about the authenticity of specimens from *E. przewalskii* and *E. hemionus kulan* (see discussion under *equi*) render these records unreliable for the purposes of this discussion. Further material from wild host populations must be studied before the host-parasite relations of these taxa can be analysed. However, if the *equi* population found on the O. Barsa Kel'mes *hemionus kulan* proves to be natural then this Phthirapteran evidence would support the contention of Liu & You (1974, fig. 4) that *Hemionus* diverged nearer to the caballine stem than to the *Asinus*/zebra stem. The increased percentage of *equi* males on *hemionus kulan* suggests that incipient speciation might now be in progress on this new host. Arguments against *equi* occurring naturally on *hemionus kulan* from O. Barsa Kel'mes gains support from Groves & Mazak (1967) who considered that the subgenus *Hemionus* is more closely related to the subgenus *Asinus* than to the subgenus *Equus* s. str.. If this opinion is correct, one would surmise that lice occurring on wild *Hemionus* should most resemble *ocellata*.

The subgenus *Hippotigris* contains two species, each divided into subspecies. One of the host species, *burchellii*, harbours two louse species (*aspilopyga* and *zuluensis*), on two of its subspecies. The other *Hippotigris* species, *zebra*, harbours one Trichodectidae species, *zebrae*, which infests *zebra hartmannae*. *Werneckiella zebrae* is distinct from the other *Werneckiella* species on the *burchellii* subspecies and therefore supports the accepted classification of *Hippotigris*.

The natural occurrence of *W. ocellata* on the type host *E. burchellii* remains to be proved, but very likely it is endemic to domestic *Asinus*.

The equid-inhabiting groups of *Werneckiella* are distinct from *neglecta*, the very distinctive characters suggesting an early host-change, possibly from a host of the subgenus *Asinus*. Both *Ammotragus* and *Asinus* originated in Central Asia (Newbigin, 1936), and were sympatric in North-west Africa before the extinction of the latter host in that region. It is therefore possible that the ancestors of *neglecta* migrated from *Asinus* to *Ammotragus* where strong selection pressures have differentiated the taxa.

There is increasing danger that wild populations of Equidae and *Ammotragus* may soon die out. This is especially likely for Asiatic and African asses, *Ammotragus* and Grevy's zebra (*Equus* (*Dolichohippus*) *grevyi* Oustalet). If the taxonomic decisions taken in this paper are to be confirmed adequately, it is imperative that more samples of lice are collected as soon as possible from these rarer hosts.

Summary

The genus *Werneckiella*, parasitic on horses, asses and zebras (Perissodactyla : Equidae) and the barbary sheep (Artiodactyla : Caprinae) is described fully for the first time. Six species are described, including one new species, *zebrae* from Hartmann Mountain Zebra, and *ocellata*, a species of hitherto uncertain validity; three new synonyms and three new combinations are recognized. A species key is provided and there is a host-parasite discussion.

Acknowledgments

I am grateful to Drs. Theresa Clay, G. B. White and Mr. K. G. V. Smith for making helpful suggestions during the preparation of this manuscript; to Dr. A. W. Gentry of the Mammal Section, Zoology Department, British Museum (Natural History) for allowing me to examine Equidae skins; to Dr. A. M. Husson of the Rijksmuseum Van Natuurlijke Historie, Leiden, Netherlands and to the Director of Rotterdam Zoo, Netherlands for information concerning hosts from which Piaget collected; and to Dr. D. I. Blagoveshtchensky, Zoological Institute, Leningrad, U.S.S.R.; Dr. W. E. Dale, Universidad Nacional Agraria, Lima, Peru; Dr. K. C. Emerson, U.S.A.; and Dr. J. Ledger, The South African Institute for Medical Research, Johannesburg, Republic of South Africa for the loan of material.

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Studies on spirostreptoid millipeds XIV. A new species of *Gonoplectus* from Thailand, with notes on the status and distribution of the genus (*Spirostreptida : Harpagophoridae*)

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Introduction

Gonoplectus is an interesting harpagophorid genus because of its somewhat disjunct gonopod structure; moreover the distribution of the presently known species appears to be important with respect to the interface between the Indochinese and Indian divisions of the Oriental Region. To some extent the area of *Gonoplectus* corresponds to that of certain sphaeropoeid taxa in the eastern Himalayan orogenic belt, these two examples having pronounced taxonomic contrast with other members of their respective families occurring in peninsular India.

So far 18 species and subspecies have been accounted in *Gonoplectus*. Since no fewer than five of these are known from the vicinity of Darjeeling alone, one may predict that if a similar local proliferation occurs elsewhere in the range of the genus, certainly more than a hundred species may be expected. It may be reminded that so far virtually nothing is known of the milliped faunas of Burma, south-west China and Assam.

Material of an undescribed *Gonoplectus* from northern Thailand, loaned for study by the California Academy of Sciences, permits the recording of the genus from that country for the first time, and in taking this opportunity to provide a name for the species we give also a brief account of the general distributional pattern of its relatives collectively.

Taxonomy

Gonoplectus was originally proposed in 1921 for a single new species collected in 'Northern India'. Although the gonopods were described in some detail, nowhere was the generic 'diagnosis' comparative, and it was therefore impossible to deduce why *Gonoplectus carletoni* was thought to warrant separate generic status. Both names promptly dropped into well-deserved obscurity.

In 1936, in his "Diplopoda of India", Graf Attems proposed two new genera, *Thyroglutus* and *Gongylorrhus*, for species in which the prostatic groove ran out on a branch separate from that which he referred to as 'spine-branch'. Although this situation is of considerable systematic importance, Attems subverted it at once in separating the two 'genera' by an utterly insignificant character: whether the ultimate segment was produced into a projecting process (*Thyroglutus*) or not (*Gongylorrhus*). As distinguished on this basis, *Thyroglutus* was proposed with four species previously named by J. Carl, and four new species; *Gongylorrhus* contained three new species. All of the novelties in both groups came from north India, Assam, or western China.