A REVISION OF THE SPECIES OF QUADRACEPS (MALLOPHAGA) PARASITIC ON TRINGINAE.

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With 2 Plates and 13 Text-figures.

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Introduction.

General.

The older workers on Mallophaga neither understood the value of the male genitalia as specific criteria, nor possessed a medium for preserving their specimens in such a way that the genitalia could be effectively studied. It is, therefore, hardly surprising that many of their supposed species are actually composite, and that many of their host-records are erroneous, but it is a good deal more surprising that the errors still persist even after Waterston (1914: 479; 1915: 171–176), following Mjöberg's lead, had pointed out the importance of the male genitalia and had published good figures of a number of species. Yet in a recent book on Mallophaga and other arthropod parasites, a species of Quadraceps that is almost certainly monoxenous (i.e., occurring on only one species of host) is alleged to occur on no less than 13 different species of Charadriiformes, some of which are not even at all closely related to its true host.

The fact that the Halle collection of Mallophaga, containing the type-material of all species described by Nitzsch, Burmeister and Giebel, was almost completely destroyed during the 1939–45 war means that for the interpretation of the older names we are often dependent on an inadequate description of a composite "species." In these circumstances the degree to which the species of host can be relied upon for aid in the identification of the parasites is of much

During the preparation of this paper, and another on the Quadimportance. raceps of Vanellinae which will be published by G. T., excluding specimens collected by techniques that are known to be conducive to contamination (from bird-skins in museums, for instance), and instances in which we do not know what technique was employed, we have examined batches of Quadracens from 106 individuals of a dozen species of Tringinae and Vanellinae, and in only one instance have we encountered a species of Quadraceps on a host to which it is not normal. The single exception is most instructive: a tube of parasites from Tringa glareola proved to contain a mixture of Quadraceps obscurus (Burm.) and Q. quadrisetaceus (Piaget), the former predominating; investigation of other material from the same source soon revealed a tube from Rostratula benghalensis collected at the same place on the same day, and the proof that the presence of Q. quadrisetaceus on T. glareola was due to postmortem contamination was complete when the tube from Rostratula was found to contain a mixture of the same two species of Quadraceps with Q. quadrisetaceus predominating. It may, therefore, safely be stated that straggling, at least in this section of the genus, is a rare phenomenon, and that the host-records are a good indication of parasite-species.

In the present paper we revise the Quadraceps of Tringinae, laying particular stress on the characters of the male genitalia. We also comment on the indications as to the relationships of the hosts furnished by the parasites, but in considering our remarks on this subject it is important to remember that they are based on only one species of Ischnocera from each host-species, and that therefore the possibility of secondary infestation cannot be excluded though we have no reason to assume that it has occurred.

All holotypes, allotypes and neotypes erected in this paper are in the British Museum (Natural History).

All the descriptions and figures are from specimens which have been cleared and mounted in Canada balsam, which inevitably involves some distortion, and especially some flattening of the abdomen. Unless otherwise stated, all the descriptions and figures of genitalia are taken from specimens of which the genitalia have been dissected out and mounted separately. This is a point of considerable importance, because in some instances the appearance of the genitalia when in situ is greatly affected by foreshortening.

For names of birds we have, unless otherwise stated, followed Peters (1934), regardless of whether we agree with his arrangement.

Acknowledgments.

We owe a great deal of the Uganda material to Drs. W. J. Eggeling and A. W. Williams and Messrs. T. W. Chorley, the late G. L. R. Hancock and R. G. Sangster; the collections from Tanganyika Territory were mostly made by Mr. H. F. I. Elliott. The South African material was nearly all obtained from skins preserved in the Transvaal Museum, Pretoria, by G. H. E. H., who is deeply indebted to the late Dr. Austen Roberts for permission to examine these skins. We are indebted to the Trustees of the British Museum for the opportunity to examine the Mallophaga in the Museum, particularly the Denny, Piaget and Meinertzhagen collections. Other important material has been made available by Messrs. M. A. Carriker and L. R. Guimarães.

Dr. Waterston was apparently making preparations for a revision of *Quadraceps* and related genera when he died, for a number of drawings had been prepared for him by Mr. Engel Terzi (Clay and Meinertzhagen, 1939: 450). These drawings (figs. 3, 6–8, 10 and 11) have been kindly placed at our disposal by the Trustees of the British Museum, to whom we are also indebted for all the photographs. These drawings have been supplemented by others (figs. 5, 9, 12 and 13) very kindly contributed by Mr. F. G. A. M. Smit; figs. 1 and 2 have been kindly made available by Col. R. Meinertzhagen, and fig. 4 is by G. T.

We are particularly grateful to Miss Theresa Clay for reading and criticising large portions of the manuscript and for helping us in many other ways.

QUADRACEPS CLAY AND MEINERTZHAGEN, 1939.

Quadraceps Clay and Meinertzhagen, 1939, Ann. Mag. nat. Hist. (11) 4:453. Type species: Degeeriella vanelli (Denny).

Koeniginirmus Eichler, 1940, Zool. Anz. 130:101. Type species: "Koeniginirmus punctatus (Nitzsch in Burmeister, 1838, jedoch sensu A. Koenig)."

Oedicnemiceps Eichler, 1943, Zool. Anz. 141:59. Type species: "Docophorus antennatus N.i.D. sensu Piaget, 1880, a p. 664; pl. LIV, f. 5."

Glareolites Eichler, 1944, Stettin. ent. Ztg 105:80. Type species: Nirmus ellipticus Nitzsch.

Mjöberginirmus Eichler, 1944, Stettin. ent. Ztg 105:85. Type species: Nirmus obliquus Mjöberg.

Nirmoides Eichler, 1944, Stettin. ent. Ztg 105:81. Type species: Docophorus antennatus Piaget.

Szidatiella Eichler, 1944, Stettin. ent. Ztg 105:81. Type species: Docophorus elongatus Piaget.

Haematophagus Timmermann, 1950, Fauna islandica, no. 2:1, 2. Type species: Quadraceps haematopi (Denny).

Head with broad hyaline margin arising from near anterior end of premarginal carina; premarginal and ventral carinae fused near their anterior ends but the actual tips free. Dorsal carina on each side passing inwards to form a narrow median suture. A narrow postantennal suture each side, transverse carina and temporal carinae (as in *Carduiceps*) present in some species. Pterothorax with lateral margins divergent. Abdomen with segment I small; paratergal plates with elongated re-entrant "heads" but without inwardly directed processes; tergal plates of some or all segments partly or completely divided in the median line. Apparent segment IX in male clearly demarcated from apparent segment VIII.

The male genitalia are of a complicated type not at all unlike that found in Saemunds-sonia (see Waterston, 1915: 22, figs. A, B), which we agree with Waterston in considering to be probably primitive. The basal plate, parameres and penis are much as in Saemunds-sonia, though the penis may (as in Q. furvus) be much more developed; the endomeres are far more developed in Quadraceps and the telomeres are normally fused and may form a tube enclosing the penis; the hypomere, beneath the base of the penis, is (as Waterston notes) very difficult to distinguish.

The genus is separable from Lunaceps and Carduiceps by the fact that the hyaline margin arises anterior to the dorsal preantennal suture and by the posterior prolongation of this suture in the median line. Hopkins (1949:34) suggested that the existence of nirmoid species of Cummingsiella like C. ambigua (Burm.) made it improbable that Quadraceps could be separated from Cummingsiella, but Miss Clay kindly informs us that in the former

genus (as in Saemundssonia) the temporal carina is separated from the post-marginal carina by the postantennal suture, whereas in Cummingsiella the two carinae meet. It seems possible that Quadraceps is more closely related to Saemundssonia than to the nirmoid species of Cummingsiella which are superficially so similar, and the fact that nirmoid and docophoroid forms have evidently diverged from a common stock on at least two separate occasions

within this group of genera is of considerable interest.

Quadraceps contains a number of fairly distinct natural groups, to most of which generic rank has been given. The most distinct of the larger groups is Koeniginirmus Eichler, and the type species of this genus is admittedly superficially very different from the type species of Quadraceps (Q. hospes (Nitzsch), 1866, of which Q. vanelli (Denny), 1842, nec Q. vanelli (Schrank), 1803, is a synonym). The essential characters, however, are the same and there is an almost perfect transition from one type to the other through Q. sellatus (Burm.), Q. felix (Giebel), Q. eugrammicus (Burm.), Q. birostris (Giebel) and Q. separatus (Kellogg and Kuwana), all of which are from gulls or terms and would have to be included in Koeniginirmus if the group is recognised. We consider all of the names given by Eichler to be synonyms of Quadraceps and not even worthy of retention as subgenera.

The distribution of the genus is imperfectly known but appears to be very peculiar. It certainly occurs on all three of the groups (Charadrii, Lari and Alcae) treated by Peters as suborders of the Charadriiformes, and is present on all the larger families. But its distribution on the Scolopacidae is sporadic, since it seems not to occur on Limosa and Numenius, the Scolopacinae and the Erolinae, being replaced on at least most members of these groups by Lunaceps, Rhynonirmus and Carduiceps. There are undoubted instances of the normal occurrence of two species of the genus on the same host-species and even on

the same individual, but they appear to be decidedly rare.

The Quadraceps-species of the Tringinae.

The species of *Quadraceps* found on this group of avian hosts are of very uniform structure (figs. 1, 2). Without exception they are moderately slender forms, fulvous to dark brown in colour, and with more or less advanced division of the otherwise-continuous transverse abdominal dorsal plates or tergites, of which that of the apparent seventh segment (that bearing the last spiracular opening) in the male of all species is strongly narrowed and divided in the median line. The chaetotaxy of the body of all the species is in extensive general agreement and represents a type, as is also the case in other groups of the great "nirmoid" complex of genera.

The male genitalia, on the other hand, are extremely distinctive and fall into a number of different types; in consequence they are of the first importance

as taxonomic criteria for the separation of the individual species.

We may also emphasise that in general every member of the Tringinae is parasitised by its own characteristic *Quadraceps*, though we have found two instances in which we are unable to separate the forms found on two Tringinae regarded by ornithologists as specifically distinct, and that there is only one instance in which we think that two forms could reasonably be placed as subspecies of a polytypic species. This marked separation of the individual

forms from one another may mean that the *Quadtaceps*-species of the Tringinae (and hence their hosts) are phylogenetically ancient forms which already have a long evolution behind them.

Quadraceps obscurus (Burmeister), 1838.

(Figs. 1-4; Pl. I, figs. 1, 2.)

Type host: Tringa glareola Linn.

Nirmus obscurus Burmeister, 1838, Handbuch Ent. 2: 427 (in part).

Nirmus obscurus N. Giebel, 1866, Z. ges. NatWiss. 28: 374 (in part).

Nirmus obscurus Nitzsch; Giebel, 1874, Insecta epizoa: 163, pl. 6, figs. 2, 3 (in part).

Nirmus obscurus Giebel; Piaget, 1880, Les Pédiculines: 170 (wrongly placed as a synonym of N. furvus).

Degeeriella obscura Burmeister; Harrison, 1916, Parasitology, 9: 119.

Quadraceps obscurus (Burmeister); Hopkins, 1942, Ann. Mag. nat. Hist. (11) 9: 115.

Degeeriella obscura (Nitzsch); Blagoveshtchensky, 1948, Mag. Parasit., Leningr. 10: 283, figs. 16, 16a.

The hosts mentioned in the very brief original description are "Totan. glareola, Tot. hypol. und Limos. melanura." We accept as a principle that the first host mentioned by an author should be regarded as the type host in the absence of strong contraindications (an important restriction of the principle that is too often ignored) and in this instance material from this host agrees with the description; we therefore regard Tringa glareola as the type host. The two descriptions of the species published by Giebel both refer to the same material as was employed by Burmeister and contain the same list of hosts. Piaget considered the species inseparable from furvus, but apparently without having seen it, for the portion of his collection in the British Museum contains no specimens of obscurus. From the lists of hosts given by Denny and by Miöberg it is evident that the material they described as Nirmus obscurus was not this species. Other authors subsequent to Piaget have mostly accepted his opinion, but Harrison and Hopkins each listed obscurus as a good species with Tringa glareola as its type host, and Blagoveshtchensky's figures show clearly that the species he described is the correct one. The type-material of the species, like that of all other species in the genus Quadraceps described by Nitzsch, Burmeister and Giebel, was lost in the almost complete destruction of Nitzsch's collection during the 1939-1945 war.

A narrow species. Lateral outlines of clypeus straight.

Male (Pl. I, fig. 1).—Dark-coloured, paratergal plates nearly black, tergal and sternal plates rather dark brown and covering almost entire dorsal and ventral surfaces of abdomen. Length 1.68-1.80 mm.

Dorsal anterior plate of head ("signature") shield-shaped, its posterior angle fairly well marked. Median posterior angle of pterothorax very obtuse and not well marked, latero-posterior angles with one very small and one long seta followed by a group of 3 rather long setae. Posterior margin of pterothorax (from outer end to middle) with 1 very long, 1 shorter and 1 still smaller seta on each side. Abdomen 3-0-3-1 times as long as wide, widest at fourth or fifth segment, its sides very weakly convex. First abdominal

¹ Many of the Mallophaga in the Hopkins collection were cleared by boiling in a solution of caustic potash and are consequently partly decolourised. Our notes on colour have usually been taken from material preserved in alcohol.

tergite completely divided in the median line,² second and third with incision extending almost to posterior margin, fourth sometimes very deeply and more frequently quite shallowly incised, fifth and sixth at most shallowly notched, seventh divided, eighth not divided but with a posterior median incision reaching about to the middle, terminal tergite well-separated, crescentic with rounded apices, its concave anterior margin not lobed. First tergite with on each side a single tergocentral seta,³ second to fifth with 2, sixth with

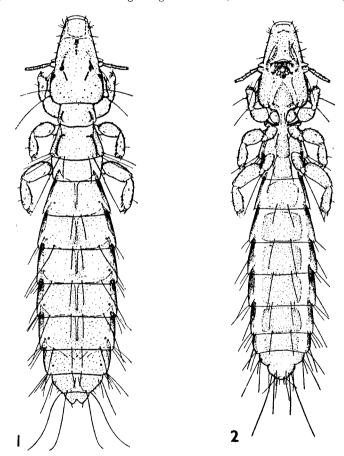


Fig. 1-2.—Q. obscurus (Burmeister). (1) Dorsal surface of female. (2) Ventral surface of male.

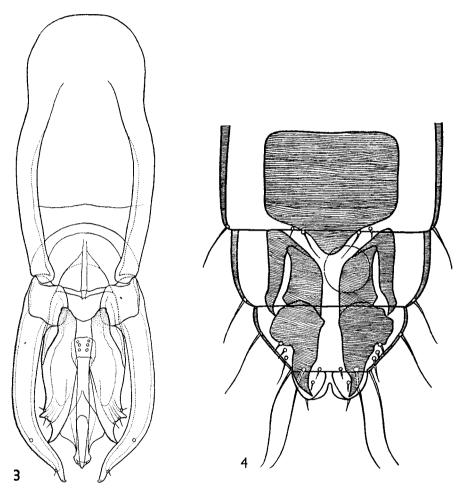
1, all these setae slender or very slender and much shorter than the segments from which they arise; a single stout and very long tergolateral seta on segments 3–6 and a much smaller one on segment 7. Paratergites only slightly oblique to long axis of abdomen, narrow; pleural setae slender and of moderate length. Gular and pterothoracic sternal plates well developed, former with its anterior portion an equilateral triangle with almost straight sides and its posterior portion roughly quadrangular, slightly broader than long, and containing a quadrangular pale area which is longer than broad, pterothoracic plate

² Our numbering of segments applies solely to the apparent segments, and the word "apparent" should be understood before the number in every instance.

³ For the nomenclature of setae see Kéler, 1938, Nova Acta Leopoldina (N.F.) 5:419.

elongate oval with a single small anterior lateral seta and a similar posterior lateral seta. Sternite of first abdominal segment roughly bell-shaped and bearing on each side a single sternocentral seta slightly longer than the plate itself, sternites of remaining segments quadrangular.

Genitalia (fig. 3): basal plate moderately long, with a conspicuous median basal splint. Parameres rather long and slender, tapering slightly and gradually, regularly curved in-



Figs. 3-4.—Q. obscurus (Burmeister). (3) Genitalia of male from *Tringa stagnatilis* near Le Havre, France. (4) Ventral surface of terminal segments of abdomen of of female from *Tringa glareola*.

wards from base to about three-quarters, then more strongly curved, extreme tips curved outwards; endomeres very stout and rather long (five-eighths length of parameres), outer aspect with a large and prominent triangular tooth with serrated tip at about eleventhirteenths, apex curved outwards in the shape of a rose-thorn with moderately sharp tip; penis straight, projecting very little beyond the hypomere.

Female (Pl. I, fig. 2).—Only slightly paler than male. Length 1.9-2.0 mm. Abdomen 3.1-3.3 times as long as wide, very narrow at first segment, widest at fourth and fifth, its

sides only slightly convex. First tergal plate completely divided, second to sixth incised almost to posterior margin (sixth rarely hardly beyond half), seventh and eighth usually shallowly notched. Terminal segment bilobed, the lobes with smoothly rounded apices and divided by a shallow sulcus. Ventral surface of terminal segments as in fig. 4.

Neotype a male (Pl. I, fig. 1) and neallotype a female (Pl. I, fig. 2) from Tringa glareola Linn., Kenya: Nanyuki, -.iii.1949, Meinertzhagen coll. no. 18830.

Other material examined.—67 male and 72 female neoparatypes from Tringa glareola, Kenya, Uganda, Sudan, South Africa, Germany, Czechoslovakia, Estonia and England. Specimens from Tringa stagnatilis (Bechstein), of which we have examined 47 males and 30 females from Kenya, Uganda, Sudan, India, Iran and France, appear to be inseparable from those from the type host. Blagoveshtchensky gives drawings of the genitalia of a male from Tringa glareola and one from Tringa stagnatilis as his figs. 16 and 16a respectively, but the slight differences he depicts seem to be within the range of individual variation.

Quadraceps falcigerus (Peters), 1951. (Fig. 5; Pl. I, figs. 3, 4.)

Type host: Tringa flavipes Gmelin.

Degeeriella falcigera; Peters, 1931, Ann. ent. Soc. Amer. 24: 583, fig. 1.

Quadraceps falcigerus (Peters); Hopkins and Clay, 1952, Check List of Genera and Species of Mallophaga: 310.

Described from a very long series collected from *Totanus flavipes* (Gmelin) (now known as *Tringa flavipes*) from Sandusky, Ohio (type locality) and other localities in the United States and the Bahama Islands.

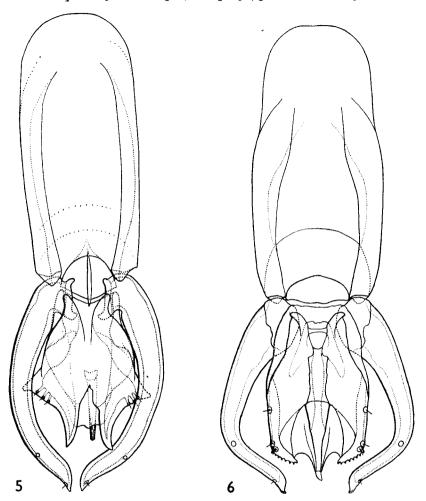
Darker than Q. obscurus, in particular the paratergites blacker and more extensive. The principal difference, however, is in the structure of the male genitalia (fig. 5), which resemble those of Q. obscurus in general (in the shape of the parameres, for instance) but differ in many details: basal plate narrower and with straighter margins; tips of parameres slightly more curved outwards; endomeres with lateral tooth much larger, placed nearer base (its centre at about two-thirds), and forming an equilateral triangle decidedly reminiscent of the lateral fin of a skate, or ray, apex of endomere also longer than in obscurus; penis and telomere subequal in length, not nearly reaching level of apex of endomere; telomere narrower and without the pronounced preapical outward bulge found in obscurus.

The resemblance to Q. obscurus is sufficient to suggest that the two species are more closely related to one another than are any other pair of species found on the Tringinae. But the differences in the male genitalia seem too great to allow of Q. falcigerus and Q. obscurus being considered to be conspecific⁴

Holotype male and allotype female, United States National Museum cat. no. 43514 (not seen).

Material examined.—The 17 males and 11 females of Q. falcigerus that we have examined are all from Tringa flavipes Gmelin, and include a pair of paratypes. They are from U.S.A., Canada and Brazil.

4 G. T. does not agree and would prefer to consider falcigerus a subspecies of obscurus.



Figs. 5-6.-(5) Q. falcigerus (Peters). Genitalia of a male paratype. (6) Q. similis (Giebel). Genitalia of male from Tringa nebularia, Avret Hissar, Greece.

Quadraceps similis (Giebel), 1866. (Fig. 6; Pl. I, figs. 5, 6.)

Type host: Tringa nebularia (Gunnerus).

Nirmus similis; Giebel, 1866, Z. ges. NatWiss. 28: 374. Nirmus similis Giebel; Giebel, 1874, Insecta epizoa: 164.

Nirmus similis Giebel; Piaget, 1880, Les Pédiculines: 170 (wrongly considered a synonym of furvus).

Nirmus interruptus; Piaget, 1880, l.c.: 173, pl. 14, fig. 6.

Nirmus interruptus [Piaget]; Piaget, 1885, Pédiculines Supplément: 21. Nirmus interruptus Piaget; Waterston, 1913, Ent. mon. Mag. 49: 18.

Nirmus clypeatus; Kellogg and Paine, 1914, Rec. Indian Mus. 10: 237, pl. 14, fig. 3.

Degeeriella clypeata Kellogg and Paine; Harrison, 1916, Parasitology 9:110.

Degeeriella interrupta Piaget; Harrison, 1916, l.c.: 115.

Degeeriella similis Giebel; Harrison, 1916, l.c.: 123.

Mallophaga: 309.

Degeeriella austini; Peters, 1931, Ann. ent. Soc. Amer. 24: 585, fig. 2. Quadraceps similis (Giebel); Hopkins, 1942, Ann. Mag. nat. Hist. (11) 9:115. Degeeriella dissimilis; Blagoveshtchensky, 1948, Mag. Parasit., Leningr. 10: 283, figs. 15. 15a.

15, 15a.

Quadraceps austini (Peters); Hopkins and Clay, 1952, Check List of Genera and Species of

Quadraceps clypeatus (Kellogg and Paine); Hopkins and Clay, l.c.: 309.

Quadraceps similis (Giebel); Hopkins and Clay, 1952, l.c.: 316 (interruptus and dissimilis placed as synonyms).

Described from a single female obtained from Totanus glottis, now known as Tringa nebularia (Gunnerus). Piaget (1880: 170) seems to have sunk similis to furvus without having seen specimens, for, though he mentions Totanus glottis as a host, there are no specimens labelled furvus from this host in the portion of his collection which is in the British Museum. Piaget found on a skin of a cormorant, however, a Quadraceps which he described as Nirmus interruptus and which he subsequently recorded (1885:21) from Totanus glottis; Waterston (1913) suggested that the true host of interruptus is Tringa nebularia, but apparently did not suspect its identity with similis. We have examined the male holotype of interruptus and one of the specimens that Piaget recorded as this species in 1885, and both are undoubtedly similis. Subsequent authors mostly accepted Piaget's erroneous belief that similis is indistinguishable from furvus. Nirmus clupeatus was described from a single male collected from a skin of Corvus cornix, Kashgar, E. Turkestan; we have been fortunate enough to have the opportunity to see the holotype (which belongs to the Indian Museum) and to confirm that it is similis; in view of the locality the true host must have been Tringa nebularia. Degeeriella austini Peters was described from specimens obtained from Totanus melanoleucus (now Tringa melanoleuca) from Windy Tickle, Labrador, while D. dissimilis Blagoveshtchensky is from Tringa nebularia.

Extremely similar to Q. obscurus but larger and darker. Lateral margins of elypeus straight.

Male (Pl. I, fig. 5).—Length 1·75–2·14 mm. First abdominal tergite not always wholly divided but very frequently only with a wedge-shaped incision reaching to the level of the alveoli of the median bristles, incisions of tergites 4–6 deeper, seventh and eighth tergites divided. Abdomen 2·9–3·0 times as long as broad.

Genitalia (fig. 6): Parameres long and slender, little tapered, very strongly bent at about two-thirds. Endomeres very broad, almost as long as penis and bound up with it, their apices obliquely truncate, finely but very distinctly serrate.

Female (Pl. I, fig. 6).—Similar to the same sex of Q. obscurus but larger (2·09-2·21 mm.). Abdomen 2·8-3·0 times as long as wide.

We are unable to separate specimens from *Tringa melanoleuca* from those from *T. nebularia*, though there is a small average difference in the male genitalia, the penis and telomeres usually (but not always) being shorter in the former, rarely extending beyond the endomeres. In view of the overlap, we think this average difference too small to permit of the recognition of *Q. austini* as a subspecies of *Q. similis*.

Neotype male and neallotype female from Tringa nebularia (Gunnerus), UGANDA: Bunyoro, Kibero, 31.xii.1933 (W. J. Eggeling).

Other material examined.—34 male and 42 female neoparatypes from Tringa nebularia, Uganda, South Africa, Aden, Britain and Greece. The male lecto-

type of Nirmus interruptus Piaget and the male holotype of N. clypeatus Kellogg and Paine. 15 males and 8 females from Tringa melanoleuca (Gmelin), U.S.A. and Brazil.

Quadraceps furvus (Burmeister), 1838. (Fig. 7; Pl. I, figs. 7, 8.)

Type host: Tringa erythropus (Pallas).

Nirmus furvus; Burmeister, 1838, Handb. Ent. 2: 427 (in part).

Nirmus furvus; Giebel, 1861, Z. ges. NatWiss. 18: 312 (in part).

Nirmus furvus N.; Giebel, 1866, Z. ges. NatWiss. 28: 374 (in part).

Nirmus furvus Nitzsch; Giebel, 1874, Insecta epizoa: 163, pl. 5, figs. 2, 3 (in part).

Nirmus furvus N.; Piaget, 1880, Pédiculines: 169, pl. 14, fig. 3 (in part).

Degeeriella furva Nitzsch; Harrison, 1916, Parasitology 9: 113 (in part).

Quadraceps furvus (Burmeister); Hopkins, 1942, Ann. Mag. nat. Hist. (11) 9: 115.

Degeeriella furva (Nitzsch); Blagoveshtchensky, 1948, Mag. Parasit. Leningr. & Moscow, 10: 281, figs. 14, 14a.

Quadraceps furvus (Burmeister); Hopkins and Clay, 1952, Check List of Genera and Species of Mallophaga: 311.

The very brief original description gives "Tot. maculat., T. glottis und Strepsil. interpres" as hosts, but agrees best with material from the first-named now known as Tringa erythropus. Giebel's main description, the figures and the Latin diagnosis quoted from Nitzsch's manuscript (Giebel, 1874:163) also seem to refer to material from this host. Piaget's redescription is partly from material from Totanus fuscus (= Tringa erythropus), but it is certain that he confused other species with furvus, for the material labelled by him with this name in the part of his collection that is in the British Museum comprises a single female of furvus and a series of 2 males and 6 females from Vanellus cristatus (now V. vanellus); the latter specimens, including one pair labelled both furvus and obscurus, are all Quadraceps junceus (Scopoli). Subsequent authors have described or recorded species of Quadraceps under the name furvus, but only Blagoveshtchensky appears to have had the species to which we restrict the name.

A somewhat compact species with straight lateral outlines of the clypeus. The specimens we have seen are yellowish brown, but all are mounted and may be somewhat decolorised.

Male (Pl. I, fig. 7).—Length 1·54–1·73 mm. First abdominal tergite divided, second to fifth deeply incised, sixth with shallow incision, seventh and eighth divided. Abdomen about 2·4 times as long as broad.

Genitalia (fig. 7): Basal plate straight-sided, about twice as long as wide. Parameres long and slender, with a slight sigmoid curve, their outer margin notched just before the apex and there bearing a minute seta. Endomeres hardly more than half length of parameres, shaped like a very broad sabre-blade. Telomeres usually extending well beyond apex of endomeres, terminating in a blunt tip with two distinct laterally-directed teeth. Penis extremely characteristic, far longer than in any other species known to us, in mounted specimens extremely strongly curved into an S-shape and then bearing a marked resemblance to the trunk of an elephant with the bulbous base of the penis representing the forehead, but doubtless in unmounted specimens not bent over to one side but lying with the middle portion of its length vertical and directed towards the dorsum of the insect, when it would appear straight; Blagoveschtchensky's fig. 14a seems to represent such a specimen.

Female (Pl. I, fig. 8).—First tergite completely divided, second to sixth deeply incised. Length 1.87-1.92 mm., abdomen 2.6 times as long as wide.

Type-material.—The original type-series was destroyed in the 1939–1945 war. We select as neotype a male (Pl. I, fig. 7) and as neallotype a female (Pl. I, fig. 8) from Tringa erythropus (Pallas), INDIA: Rajputana, -.i.1952, Meinertzhagen coll. no. 19617. We have also seen 24 male and 12 female neoparatypes from the same host-species, India, Japan, England and Lapland.

Quadraceps ochropi (Denny), 1842.

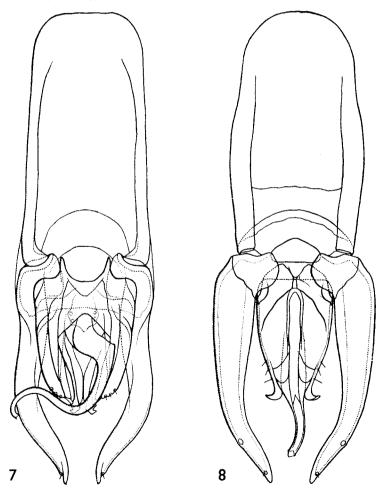
(Fig. 8; Pl. I, figs. 9, 10.)

Type host: Tringa ochropus Linn.

Nirmus ochropi; Denny, 1842, Mon. Anopl. Brit.: 52, 134, pl. 11, fig. 12.

Nirmus ochropi Denny; Piaget, 1880, Pédiculines: 170.

Degeeriella ochropi Denny; Harrison, 1916, Parasitology, 9:119.



Figs. 7-8.—(7) Q. furvus (Burmeister). Genitalia of male from Tringa erythropus, Yarmouth, England. (8) Q. ochropi (Denny). Genitalia of male from Tringa ochropus, Fair Isle, Shetland.

Quadraceps ochropi (Denny); Hopkins, 1942, Ann. Mag. nat. Hist. (11) 9:115.

Degeeriella ochropi (Denny); Blagoveshtchensky, 1948, Mag. Parasit., Leningr. & Moscow, 10: 284, fig. 17.

Quadraceps ochropi (Denny); Hopkins and Clay, 1952, Check List of Genera and Species of Mallophaga: 314.

Described from material of both sexes obtained from *Totanus ochropus* (now *Tringa ochropus*) in Britain; only one female of the type-series survives and this is not in good condition, having apparently been subjected to too much potash while being mounted. Piaget, evidently without having seen specimens, considered *ochropi* to be the same as *furvus*, but Harrison listed it as a good species.

A moderately narrow, rather dark brown species. Lateral margins of clypeus weakly concave.

Male (Pl. I, fig. 9).—Length 1·53–1·63 mm. Tergal plate of first abdominal segment medially divided or deeply incised, that of second deeply incised and that of third incised to beyond middle, plates of following segments slightly notched, that of seventh segment divided, that of eighth sometimes divided and sometimes merely with deep median anterior or posterior incision. Abdomen $2\cdot7$ – $2\cdot9$ times as long as wide.

Genitalia (fig. 8): Basal plate short, with well-developed transverse sclerotic bar but the median splint poorly developed. Parameres long, moderately stout and regularly tapered, basal half practically straight, remainder first curving fairly strongly inwards and then feebly outwards. Endomeral complex more or less pyriform, the endomeres terminating at about two-thirds length of parameres in strongly hooked outwardly-directed points. Penis stout, strongly curved (in dissections), extending far beyond tips of endomeres.

Female (Pl. I, fig. 10).—Length 1-82-1-97 mm. First tergite medially divided or deeply incised, second and third deeply incised, fourth incised to beyond middle, fifth to middle, sixth and seventh slightly incised. Abdomen 2-9-3-1 times as long as broad.

Type-material.—The only surviving syntype is a female in the Denny collection in the British Museum (Natural History). This is in poor condition, but we can see no characters that show it not to be the species redescribed above.

Other material examined.—45 males and 52 females from Tringa ochropus Linn., British Isles, Uganda, Tanganyka Territory and Afghanistan.

Quadraceps waterstoni sp. n.

(Fig. 9; Pl. II, figs. 11, 12.)

Type host: Tringa solitaria Wilson.

A moderately narrow, very dark, species. Lateral outlines of clypeus straight.

Male (Pl. II, fig. 11).—Length 1.40 mm. First abdominal tergite completely divided, that of second segment incised to well beyond middle, that of third nearly or quite to middle, those of fourth to sixth segments slightly incised, tergites of seventh and eighth segments divided. Abdomen 2.4–2.8 times as long as wide.

Genitalia (fig. 9) very reminiscent of those of *cchropi*, but parameres shorter, broader and more strongly curved, and endomeral complex with much more convex sides. Basal plate short, broadest at base and the lateral bars exceptionally broad basally.

Female (Pl. II, fig. 12).—Length 1·68–1·85 mm. First abdominal tergite divided, second and third deeply incised, fourth and fifth divided to middle, fifth and sixth slightly incised. Abdomen 2·8–2·9 times as long as broad.

Holotype male and allotype female from Tringa solitaria Wilson, Colombia: Bolivar, 5.ix.1913.

Other material examined.—Two male and 3 female paratypes from Tringa solitaria, Colombia, Paraguay and Massachusetts.

Quadraceps conformis (Blagoveshtchensky), 1940.

(Fig. 10; Pl. II, figs. 13, 14.)

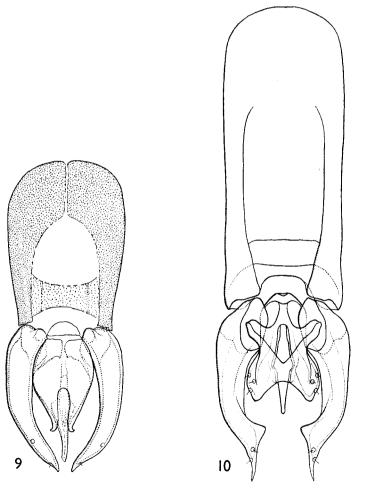
Type host: Tringa totanus totanus (Linn.).

Degeeriella "furva Nitzsch"; Fresca, 1925 (nec Burmeister, 1838), Eos, Madr. 1:286, fig. 7 (male genitalia).

Degeeriella conformis; Blagoveshtchensky, 1940, Mag. Parasit., Leningr. & Moscow, 8:56, 84, fig. 14.

Degeeriella conformis Blagoveshtchensky; Blagoveshtchensky, 1948, Mag. Parasit., Leningr. & Moscow, 10: 285, fig. 19 (male genitalia).

Quadraceps conformis (Blagoveshtchensky); Hopkins and Clay, 1952, Check List of Genera and Species of Mallophaga: 310.



Figs. 9-10.—(9) Q. waterstoni sp. n. Genitalia of male paratype, from Tringa solitaria, Riacho, Paraguay. (10) Q. conformis (Blagoveschtchensky). Genitalia of male from Tringa totanus, Shetland Isles.

Originally described, from the female only, from material collected from *Totanus totanus* (now *Tringa totanus totanus*), from Kumbashi, Talysh Lowlands, Azerbaijan. Blagoveshtchensky's later description of the male is from material from the same host-species.

A rather pale brown, moderately stout, species with lateral margins of the clypeus straight.

Male (Pl. II, fig. 13).—Length $1\cdot40-1\cdot50$ mm. Tergal plate of first segment divided, those of second and third segments deeply incised, that of the fourth incised to half, that of the fifth slightly notched, those of the sixth to eighth segments divided. Sixth segment without tergocentral setae. Abdomen $1\cdot8-1\cdot9$ times as long as wide.

Genitalia (fig. 10).—Basal plate moderately long, straight-sided, with a sclerotic transverse bar near its distal end. Parameres unlike those of any other species, rather short, their inner side extended into a triangular lobe beyond which the paramere bends outwards and tapers to a sharp point. Endomeres forming two short wing-like lobes between which the fairly long spindle-shaped penis projects.

Female (Pl. II, fig. 14).—Length 1·65–1·82 mm. Tergite of first segment of abdomen divided, those of the second to fifth segments deeply, that of the sixth feebly, and that of the seventh hardly at all incised. Abdomen 2·3–2·5 times as long as wide.

Material examined.—150 males and 123 females from Tringa totanus totanus (Linn.), T. totanus britannica Mathews, T. totanus robusta (Schiøler) and T. totanus terrignotae Meinertzhagen and Meinertzhagen, British Isles, Finland, Czechoslovakia, Morocco, Sudan, Nepal and India.

Quadraceps ravus (Kellogg), 1899.

(Fig. 11; Pl. II, figs. 15, 16.)

Type host: Actitis macularia (Linn.).

Nirmus furvus var. ravus Kellogg, 1899, Occ. Pap. Calif. Acad. Sci. 6:14, pl. 2, fig. 1. Degeeriella rava Kellogg; Harrison, 1916, Parasitology, 9:122.

Degeeriella subfusca Blagoveshtchensky, 1948, Mag. Parasit. Leningr. & Moscow, 10: 286, figs. 20, 20a.

Quadraceps ravus (Kellogg); Hopkins and Clay, 1952, Check List of the Genera and Species of Mallophaga: 316.

Quadraceps subfuscus (Blagoveshtchensky); Hopkins and Clay, 1952, l.c.: 317.

Kellogg's original description was of a female from Actitis macularia from Panama. Blagoveshtchensky had six males and fifteen females from Actitis hypoleucus.

A moderately stout dark brown species. Margins of clypeus not straight but compressed in a concave manner and thus becoming reminiscent of the shape of head in *Saemundssonia*.

Male (Pl. II, fig. 15).—Length 1·27–1·34 mm. Tergal plate of first segment divided, that of the second deeply and those of the third to fifth more shallowly incised, those of sixth to eighth segments divided in the middle line. Abdomen 1·6–1·8 times as long as wide.

⁵ Peters calls the British subspecies *T. totanus bewickii* (Rennie), but according to Witherby, Jourdain, Ticehurst and Tucker (1948, *Handbook of British Birds*, 4: 324) Rennie's name does not refer to the redshank but to the ruff. Peters places *T. totanus terrignotae* as a synonym of *T. t. eurhinus* (Oberholzer) but notes an unresolved controversy about this synonymy.

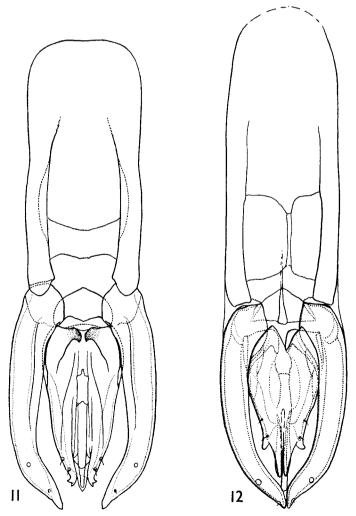
Genitalia (fig. 11): Basal plate with a sclerotic transverse bar joining the two lateral bars. Parameres slender, nearly straight to about three-quarters where they bend slightly inwards. Endomeres closely bound together with penis and other structures to form an elongate, roughly pyriform, complex extending nearly to the tips of the parameres, tips of endomeres bidentate and extending to almost the same point as the apex of the penis.

Female (Pl. II, fig. 16).—Length 1·49-1·63 mm. Tergal plate of first segment divided, those of second and third segments deeply incised and that of the fourth incised to a half.

Abdomen 1.9-2.2 times as long as wide.

We are unable to distinguish specimens from Actitis macularia from those from Actitis hypoleucos.

Material examined.—Redescribed from 8 males and 7 females from Actitis macularia (Linn.) from U.S.A. and Costa Rica. We have also examined



Figs. 11-12.—(11) Q. ravus (Kellogg). Genitalia of male from Actitis hypoleucos, Fochabers, Moray, Scotland. (12) Q. impar sp. n. Genitalia of male holotype.

39 males and 48 females from Actitis hypoleucos (Linn.), from British Isles, Liberia, Sudan, Uganda, Nepal and Philippine Isles.

Quadraceps impar sp. n.

(Fig. 12,; Pl. II, figs. 17, 18.)

Type host: Heteroscelus brevipes (Vieillot).

This species is noteworthy for its marked sexual dimorphism, the male being relatively very much smaller and broader-headed than the female (cephalic index of male 0.85, of female 0.71). The lateral margins of the clypeus are straight.

Male (Pl. II, fig. 17).—Length 1.35 mm. In the sole specimen available the divisions of the tergites cannot be distinguished satisfactorily. Abdomen 1.7 times as long as broad.

Genitalia (fig. 12): Basal plate parallel-sided, the lateral sclerotic rods joined by a weakly sclerotised transverse bar. Parameres rather slender, uniformly and rather weakly curved to just before the tips, which are curved outwards. Endomeral complex elongate oval, the endomere of each side terminating in a blunt projection at the level of about five-eighths of the length of the parameres. Penis straight, extending nearly to apex of parameres, surrounded by telomere to shortly before its apex but the latter free.

Female (Pl. II, fig. 18).—Length 1·62-1·81 mm. First tergite divided, second to fifth deeply notched and sixth incised nearly to middle; at apex of each incision a markedly darker patch of pigment. Abdomen 1·8-1·9 times as long as broad.

Holotype male and allotype female from Heteroscelus brevipes (Vieillot), Saghalin, Meinertzhagen collection, slide no. 11013a.

Other material examined.—Two female paratypes from Heteroscelus brevipes (Vieillot), Saghalin, and one female from Heteroscelus incanus (Gmelin) from California. H. brevipes is regarded by some ornithologists as a subspecies of H. incanus, but Peters treats them as specifically distinct.

Quadraceps carrikeri sp. n.

(Fig. 13; Pl. II, figs. 19, 20.)

Type host: Catoptrophorus semipalmatus inornatus (Brewster).

As in the preceding species, the difference in size between the sexes is somewhat considerable. Lateral margins of clypeus straight.

Male (Pl. II, fig. 19).—Length 1·52-1·67 mm. First abdominal tergite apparently divided, second and third tergites incised to beyond middle, fourth to sixth only slightly notched, seventh and eighth divided. Abdomen 2·1 times as long as broad.

Genitalia (fig. 13).—Basal plate with margins markedly sinuate, convex basally and distally but concave in the middle, with a transverse sclerotic bar joining the two lateral rods. Parameres short, exceptionally broad and strongly curved. Endomeral complex regularly oval, the endomeres without lateral projection. Penis short and straight, extending little beyond apex of endomeral complex.

Female (Pl. II, fig. 20).—Length 1.91–2.06 mm. First tergite probably completely divided, second to fifth deeply incised, sixth either incised to middle or only slightly notched. Abdomen 2.6 times as long as broad.

Holotype male and allotype female from Catoptrophorus semipalmatus inornatus (Brewster), California: San Diego, March 1939, Meinertzhagen collection, slide no. 12898.

Other material examined.—21 male and 18 female paratypes from C. semipalmatus inornatus, from California and Texas.

 \hat{Q} . impar and Q. carrikeri show no indications of particularly close relationships either with the other species or with one another; the latter species, in particular, stands wholly apart.

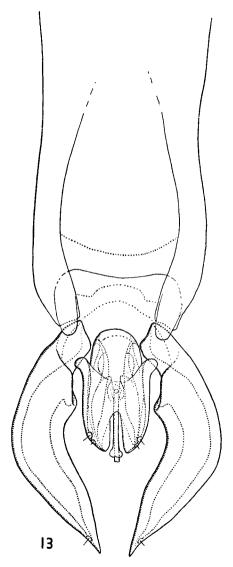


Fig. 13.—Q. carrikeri sp. n. Genitalia of male paratype from Catoptrophorus semipalmatus inornatus, San Diego, California.

Species incertae sedis.

Quadraceps naumanni (Giebel), 1874.

Nirmus naumanni; Giebel, 1874, Insecta epizoa: 163. Quadraceps naumanni (Giebel); Hopkins and Clay, 1952, Check List of Genera and Species of Mallophaga: 313.

The host of this species is given as "Totanus gilvipes," which is apparently not the name of any bird. The description is utterly inadequate, and there seems to be no possibility of identifying the species now that the syntypes are lost. It has been suggested to us that the host-name may have been a slip for T. flavipes, but the description does not fit the Quadraceps found on the latter and the name naumanni must be regarded as inapplicable.

Quadraceps major (Kellogg).

Nirmus fissus var. major; Kellogg, 1899, Occ. Pap. Calif. Acad. Sci. 6: 15, pl. 2, fig. 2. Quadraceps major (Kellogg); Hopkins and Clay, 1952, Check List of . . . Mallophaga: 313.

We have not been able to identify this species owing to the inadequacy and probable incorrectness of the host-record. The species was described from "Several specimens, including male, female and immature specimens, from Tringa sp. (Baja California)." The facies of the insect is, however, that of the group of Quadraceps found on the Charadriinae, and we think the host-record is almost certainly incorrect. Professor Ferris has kindly searched in the Kellogg collection for the syntypes but is unable to find them.

AVIPARASITOLOGICAL CONTRIBUTIONS TO THE SYSTEMATICS OF THE TRINGINAE.

Some ornithologists use the genus *Tringa* in a very wide sense, while others split it up into a number of genera. Peters rejects many of the subdivisions but recognises *Pseudototanus*, *Xenus*, *Actitis*, *Catoptrophorus* and *Heteroscelus*. From an aviparasitological point of view there is no objection to the inclusion of all the species in one genus, *Tringa*, but in that case *Actitis*, *Catoptrophorus* and *Heteroscelus* ought also to be suppressed because, parasitologically speaking, there are no characters which would justify our placing the species referred to these groups apart from all the others. We cannot decide how far this applies also to the genera *Pseudototanus* and *Xenus* because we have not been able to examine any *Quadraceps*-material from birds of these two genera, but the presence on *Xenus* of a species of the genus *Carduiceps*, whose occurrence on a given host seems to be at least usually incompatible with the occurrence of *Quadraceps*, suggests the probability that *Xenus* is more distinct than the other groups concerned.

The alternative to placing all the birds closely related to *Tringa* in one large single group, as was done by Hartert, is to attempt to split them into numerous smaller groups, as was done by Lowe (1931), on the basis of anatomical investigations and (following him) by Peters (1934). Aviparasitology supports the view that this second solution accords better with natural relationships than the first, although on the basis of parasitology we would make use of a somewhat

different grouping from that of Lowe. The latter refers three species (ochropus, solitaria and glareola) to the genus Tringa, but states at the same time that he is strongly inclined to separate T. glareola from the other two species and place it in a separate genus, Rhyacophilus. This suggestion is entirely supported by aviparasitology, for the Quadraceps-species from Tringa ochropus and T. solitaria have male genitalia of the same type and undoubtedly belong together, whereas the species parasitic on T. glareola belongs to a quite different type. Hartert was unquestionably right when he emphasised that T. solitaria reminded him very forcibly of T. ochropus, a suggestion also accepted by Lowe (1931: 723) and by Witherby et al. (1948).

Tringa stagnatilis shows aviparasitologically an extremely close relationship with T. glareola and a somewhat more remote one with the North American T. flavipes. Tringa totanus, T. erythropus, Catoptrophorus semipalmatus and Heteroscelus brevipes all stand quite alone (except that entirely inadequate evidence places H. brevipes with H. incanus), while on the other hand T. melanoleuca and T. nebularia seem to constitute a natural group. Here, also, Hartert seems to show the soundness of his feeling for phylogenetic relationships when he remarks that, judging by its size and general appearance, T. melanoleuca must be very close to T. nebularia. On the other hand, parasitology does not suggest any justification for the recognition as natural entities of the genera Totanus and Glottis (both sensu Lowe, the former comprising the species totanus, flavipes, melanoleuca and erythropus, the latter nebularia, stagnatilis and guttifer). The linking together of Actitis macularia and A. hypoleucos is entirely supported by the evidence derived from their parasites.

SUMMARY.

The species of the genus Quadraceps occurring on Tringinae have been much confused but are easily separable by means of differences in the male genitalia. The known species are redescribed in this paper and three new species are described; in all instances photographs of both sexes and line-drawings of the male genitalia are given. The possible bearing of the distribution of these Mallophaga on the relationships of their hosts is briefly discussed.

References.

CLAY, T., 1951, An introduction to a classification of the Avian Ischnocera (Mallophaga). Part 1. Trans. R. ent. Soc. Lond. 102:171-194.

Hartert, E., 1921, Vögel der paläarktischen Fauna 2:1606–1625.

HOPKINS, G. H. E., 1949, Stray notes on Mallophaga . . . IX. Ann. Mag. nat. Hist. (12) 2: 29-54.

Lowe, P. R., 1931, An anatomical review of the "Waders" (Telmatomorpha) with special reference to the families, sub-families and genera within the suborders Limicolae, Grui-Limicolae and Lari-Limicolae. *Ibis* (13) 1: 712-771.

Peters, J. L., 1934, Check List of Birds of the World. 2.

WATERSTON, J., 1915, An account of the bird-lice of the genus *Docophorus* (Mallophaga) found on British auks. Part 2: Morphological. *Proc. roy. phys. Soc. Edinb.* 19:171-176.

WITHERBY, H. F., et al., 1940, Handbook of British Birds. 4.

PLATE I.

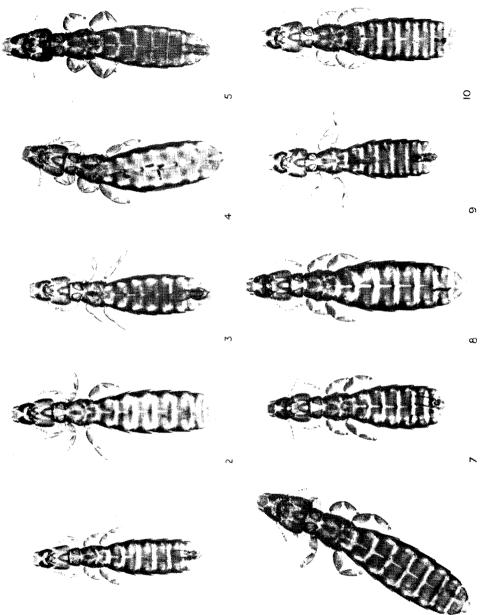
FIG. 1.—Quadraceps obscurus (Burmeister). Male neotype.
FIG. 2.—The same. Female neallotype.
FIG. 3.—Q. falcigerus (Peters) Male, from Tringa flavipes, California.
FIG. 4.—The same. Female, from Tringa flavipes, California.
FIG. 5.—Q. similis (Giebel). Male neotype.
FIG. 6.—The same. Female neallotype.

Fig. 7.—Q. furvus (Burmeister). Male neotype.

Fig. 8.—The same. Female neallotype.

Fig. 9.—Q. ochropi (Denny). Male, from Tringa ochropus, Namanve, near Kampala Uganda.

Fig. 10.—The same. Female, data as for male.



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PLATE II.

Fig. 11.—Quadraceps waterstoni sp. n. Male holotype.

Fig. 12.—The same. Female allotype.

Fig. 13.—Q. conformis (Blagovestchensky). Male, from Tringa totanus britanniae, Orkney Isles.

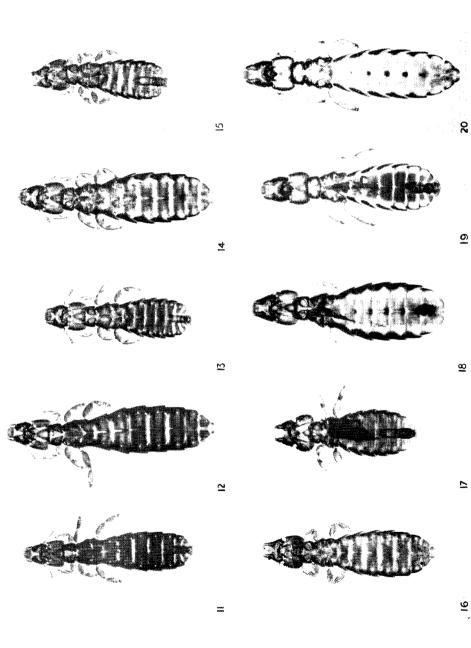
Fig. 14.—The same. Female, data as for male.

Fig. 15.—Q. ravus (Kellogg). Male, from Actitis macularia, Costa Rica. Fig. 16.—The same. Female, data as for male.

Fig. 17.—Q. impar sp. n. Male holotype. Fig. 18.—The same. Female allotype.

Fig. 19.—Q. carrikeri sp. n. Male holotype. Fig. 20.—The same. Female allotype.

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