DESCRIPTIONS OF EIGHT NEW SPECIES OF FEATHER LICE IN THE GENUS COLUMBICOLA (PHTHIRAPTERA: PHILOPTERIDAE), WITH A COMPREHENSIVE WORLD CHECKLIST

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ABSTRACT: Eight new species of lice in the genus Columbicola Ewing are described: C. harbisoni (type host: Phaps histrionica (Gould)), C. koopae (type host: Geophaps scripta (Temminck)), C. eowilsoni (type host: Geophaps smithii (Jardine and Selby), C. wombeyi (type host: Geophaps plumifera Gould), C. masoni (type host: Petrophassa rufipennis Collett), C. waiteae (type host: Columba leucomela Temminck), C. rodmani (type host: Geopelia humeralis (Temminck)), and C. smithae (type host: Turtur brehmeri (Hartlaub)). Also, we provide a comprehensive checklist for the 88 known species of Columbicola (Phthiraptera: Ischnocera) and their pigeon and dove hosts (Aves: Columbiformes).

Species of *Columbicola* Ewing have been the subject of a considerable amount of recent work on host–parasite co-evolution (Clayton et al., 1999, Clayton and Johnson, 2003, Johnson et al., 2005), host specificity (Johnson et al., 2002, Bush and Clayton, 2006), and host–parasite ecology (Clayton et al., 2005, Bush et al., 2006, Bush and Malenke, 2008, Harbison et al., 2008). These studies, which focus on central themes of evolutionary ecology, are made possible by a solid alpha-taxonomic framework and robust sampling of lice within *Columbicola*. Recent collecting efforts have yielded additional material, including 8 new species, which we describe herein, thereby bringing the total recognized *Columbicola* to 88 species. A comprehensive host–parasite checklist including all of these species and their host associations is presented (Appendix I).

MATERIALS AND METHODS

Newly collected specimens were preserved in 95% EtOH and later mounted in Canada balsam on standard microscope slides following the procedure described by Price et al. (2003). Holotypes are deposited at Oklahoma State University (OSU), Stillwater, Oklahoma, and paratypes are deposited at OSU and the Price Institute of Phthirapteran Research, University of Utah, Salt Lake City, Utah (PIPeR). All specimens were examined and measured using a Nikon DIC/phase-contrast microscope (Nikon Instruments, Melville, New York). All measurements are in mm. Abbreviations are: APW, dorsoanterior head plate width; HW, head width; HL, head length at midline; HL/HW, ratio of head length to head width; GW, male genitalia width; and TL, total length at midline. Host classification follows that of the Howard and Moore Checklist (Dickinson, 2003), with the exception that New World Columba are classified as Patagioenas Reichenbach (see Johnson et al., 2001).

REDESCRIPTION

angustus species group

(Figs. 1-20)

Diagnosis: Group includes 11 species from the following host genera: Gallicolumba Heck, Geopelia Swainson, Geophaps G. R. Gray, Macropygia Swainson, Ocyphaps G. R. Gray, Petrophassa Gould, Phapitreron Bonaparte, Phaps Selby, and Reinwardtoena Bonaparte. Species in this group have the following characteristics: body elongate; each side of metanotum with 2 long, 2 short setae; anterior marginal head carina complete (as in Fig. 3), either rounded or indented; anterior mar-

ginal head setae vary from flat, blade-like setae (as in Fig. 3) to filiform setae (as in Fig. 8). Male antenna with enlarged scape, spur on third segment (as in Fig. 3); mesosome triangular, tightly wedged between long, thin parameres, with 2–6 pores (as in Fig. 1). Female subgenital plate groove elongate (as in Fig. 2), either narrow or broad; lateral setae either lacking or, if present, quite short.

Columbicola taschenbergi Eichler

Male: Head as in Adams et al. (2005: Fig. 81); scape and third antennal segment enlarged, medioposterior setae exceeding posterior head margin, 0.09–0.14 long. Mesosome triangular with 2 pores, mesosome wedged between long, thin parameres. Dimensions include: APW, 0.14–0.16; APL, 0.07–0.08; HW, 0.32–0.35; HL, 0.59–0.63; HL/HW, 1.71–1.84; SL, 0.16–0.18; PW, 0.27–0.31; MW, 0.34–0.40; GW, 0.08–0.09; TL, 2.57–2.81.

Female: Subgenital plate groove peaked, ovoid anteriorly, constricted medially, widening posteriorly, with up to 5 setae (<0.01 long) on each side. Dimensions include: APW, 0.15–0.16; APL, 0.07–0.09; HW, 0.38–0.43; HL, 0.60–0.65; HL/HW, 1.67–1.78; SL, 0.06–0.07; PW, 0.30–0.31; MW, 0.38–0.43; TL, 3.09–3.16.

Taxonomic summary

Type host: Reinwardtoena reinwardtii (Temminck).

Material: Three males, 5 females, ex *Reinwardtoena reinwardtii*, Papua New Guinea: Gulf Province, 30 July 2002, D. H. Clayton, SEA-266 and SEA-276 (OSU, PIPeR), including specimens from the same host individual as specimen 71 from Johnson et al. (2007; Cotas.8.19.2003.9), which was not measured because it was a nymph.

Remarks

This species was originally described by Eichler (1942) based on a single male specimen. This is the first description of the female of this species. In addition, we provide measurements for 3 male specimens.

DESCRIPTIONS

Columbicola harbisoni n. sp.

(Figs. 1–2)

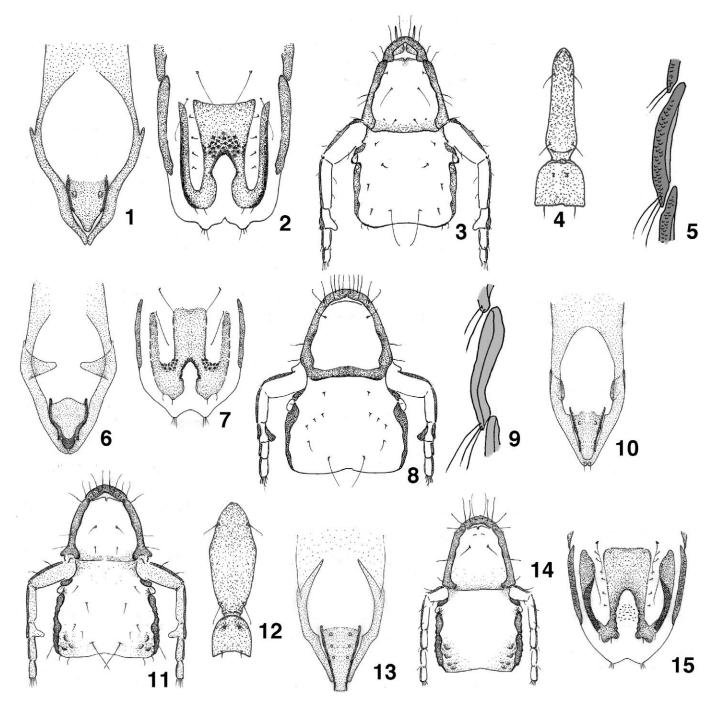
Male: Head similar to *Columbicola angustus* (Rudow) (also described in Adams et al., 2005), but with smaller HL/HW ratio; scape and third antennal segment enlarged; medioposterior setae 0.04–0.05 long. Genitalia as in Figure 1; mesosome triangular with rounded anterior indentation and 2 pores. Dimensions include: APW, 0.12–0.13; APL, 0.04–0.05; HW, 0.27–0.28; HL, 0.53–0.57; HL/HW, 1.96–2.11; SL, 0.11–0.13; PW, 0.21–0.22; MW, 0.28–0.30; GW, 0.08; TL, 2.19–2.24.

Female: Ventral terminalia as in Figure 2, with scaling anterior to subgenital plate groove. Subgenital plate groove peaked, ovoid anteriorly, constricted medially, widening posteriorly, with 3–5 short setae (0.01 long) on each side. Dimensions include: APW, 0.13–0.14; APL, 0.05–0.06; HW, 0.27–0.28; HL, 0.57–0.59; HL/HW, 2.04–2.15; SL, 0.06; PW, 0.21–0.23; MW, 0.28–0.31; TL, 2.46–2.59.

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FIGURES 1–15. Columbicola harbisoni: (1) male genitalia and (2) female genitalia. Columbicola koopae: (3) male dorsal head, (4) thoracic sternal plate, (5) lateral abdomen, (6) male genitalia, and (7) female genitalia. Columbicola wombeyi: (8) male dorsal head, (9) lateral abdomen, and (10) male genitalia. Columbicola masoni: (11) male dorsal head, (12) thoracic sternal plate, (13) male genitalia, (14) female dorsal head, and (15) female genitalia.

Taxonomic summary

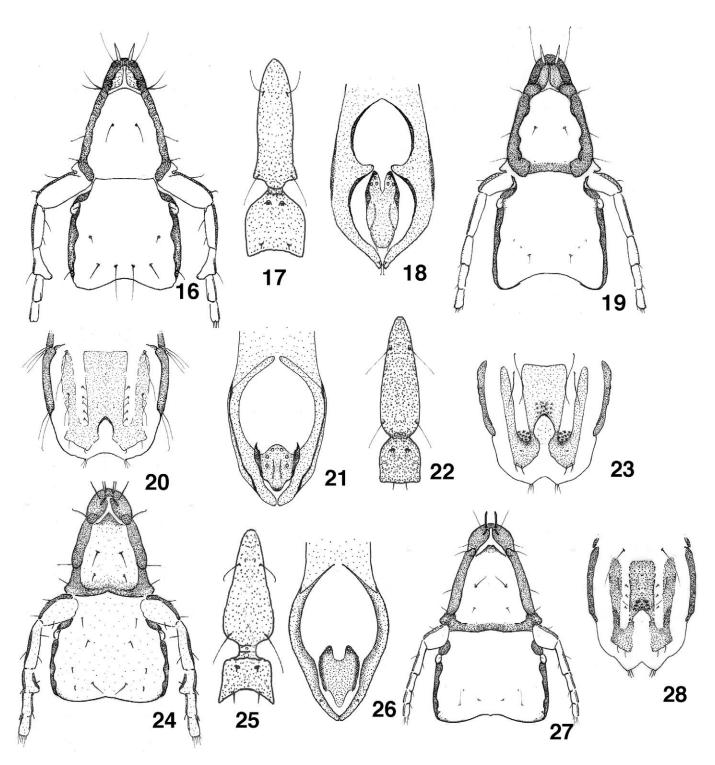
Type host: Phaps histrionica (Gould).

Type material: Holotype male, ex *P. histrionica*, Australia: Northern Territory, Borclay Taselands, 10 October 2002, D. H. Clayton, ANWC-33405 (OSU). Paratypes, all from type host species: 6 females, same data as holotype, including specimen 62 from Johnson et al. (2007; CospPhhis5.14.2003.9); 2 males, D. H. Clayton, ANWC-33407, same location and collecting date as holotype (OSU, PIPeR).

Etymology: This species is named in honor of Christopher W. Harbison, Siena College, Loudonville, New York, in recognition of his work on the transmission ecology of Columbicola spp. and other feather lice.

Remarks

This species keys to couplet 42 of Adams et al. (2005). The triangular genital mesosome of *C. harbisoni* is most similar to that of *C. angustus*. However, *C. harbisoni* differs from *C. angustus* in that the HL/HW ratio



FIGURES 16–28. Columbicola waiteae: (16) male dorsal head, (17) thoracic sternal plate, (18) male genitalia, (19) female dorsal head, and (20) female genitalia. Columbicola rodmani: (21) male genitalia, (22) thoracic sternal plate, and (23) female genitalia. Columbicola smithae: (24) male dorsal head, (25) thoracic sternal plate, (26) male genitalia, (27) female dorsal head, and (28) female genitalia.

and total length are both smaller. In addition to morphological characteristics, the placement of C. harbisoni within the angustus species group is supported molecularly. Phylogenetic reconstructions of Columbicola based on COI, 12S, and EF-1 α place C. harbisoni as a sister taxon to C. angustus ex Phaps chalcoptera (Latham) (see Johnson et al., 2007).

Columbicola koopae n. sp (Figs. 3–7)

Male: Head as in Figure 3; scape and third antennal segment enlarged; medioposterior setae exceeding posterior head margin, 0.06-

0.09 long. Anterior marginal head setae typically flattened and blade-like, but occasionally quite slender. Thoracic sternal plate shaped as in Figure 4. Pleural thickenings of lateral abdomen scaled (Fig. 5). Genitalia as in Figure 6; mesosome triangular, laterally thickened, with 2 pores, parameres with medial expansions. Dimensions include: APW, 0.13–0.14; APL, 0.03–0.04; HW, 0.27–0.28; HL, 0.50–0.52; HL/HW, 1.79–1.89; SL, 0.13–0.14; PW, 0.21–0.23; MW, 0.31–0.34; GW, 0.08–0.10; TL, 2.13–2.30.

Female: Thoracic sternal plate shaped as in Figure 4. Pleural thickenings of lateral abdomen scaled (Fig. 5). Ventral terminalia as in Figure 7, with scaling lateral to anterior subgenital plate groove. Subgenital plate groove peaked, ovoid anteriorly, constricted medially, widening posteriorly, and up to 2 setae (<0.01 long) on each side. Dimensions include: APW, 0.13–0.16; APL, 0.04–0.05; HW, 0.25–0.29; HL, 0.52–0.55; HL/HW, 1.90–2.08; SL, 0.05–0.06; PW, 0.19–0.23; MW, 0.29–0.34; TL, 2.35–2.67.

Taxonomic summary

Type host: Geophaps scripta (Temminck).

Type material: Holotype male, ex G. scripta, Australia: Queensland, Mitchell River, 28 October 2001, T. Chesser, ANWC 29698 (OSU). Paratypes, all from type host species: 3 males, 5 females, same data as holotype, including specimen 45 from Johnson et al. (2007; CospGescr1.8.2003.10); 2 males, 2 females, Australia: 15 August 1970, I. Mason, ANWC 16123 (OSU, PIPeR).

Etymology: This species is named in honor of Jennifer Hutchens Koop, University of Utah, Salt Lake City, Utah, in recognition of her work on avian defenses against lice and other ectoparasites.

Remarks

This species keys to couplet 15 of Adams et al. (2005). It shares long, hair-like PMHS with *C. tschulyschman* Eichler and *C. mckeani* Tendeiro, but has larger dimensions than *C. tschulyschman* and *C. koopae;* it also has a smaller HW/HL ratio than *C. mckeani*. Although the genitalia most closely resemble those of *C. mckeani*, the male genitalic parameres of *C. koopae* have distinct medial expansions. In addition to morphological characteristics, the placement of *C. koopae* within the *angustus* species group is supported molecularly. Phylogenetic reconstructions of *Columbicola* based on COI, 12S, and EF-1α place *C. koopae* as a close relative of *C. mckeani* ex *Ocyphaps lophotes* (Temminck) (see Johnson et al., 2007).

Columbicola eowilsoni n. sp.

(Figs. 3, 6, 7)

Male: Head similar to *C. koopae* (Fig. 3), but with a smaller HL/HW ratio; scape and third antennal segment enlarged; medioposterior setae exceeding posterior head margin, 0.07–0.09 long. Anterior marginal head setae slender. Genitalia similar to *C. koopae* (Fig. 6); mesosome triangular, laterally thickened, with 2 pores, parameres with medial expansions. Dimensions include: APW, 0.12–0.14; APL, 0.03; HW, 0.28–0.30; HL, 0.47–0.50; HL/HW, 1.63–1.68; SL, 0.14–0.15; PW, 0.21–0.23; MW, 0.31–0.33; GW, 0.09; TL, 2.09–2.22.

Female: Anterior marginal head setae flattened. Ventral terminalia similar to *C. koopae* (Fig. 7) with 2–3 setae (<0.01 long) on each side. Dimensions include: APW, 0.13–0.15; APL, 0.04–0.05; HW, 0.28–0.31; HL, 0.51–0.56; HL/HW, 1.76–1.87; SL, 0.06; PW, 0.21–0.23; MW, 0.31–0.36; TL, 2.36–2.57.

Taxonomic summary

Type host: Geophaps smithii (Jardine and Selby).

Type material: Holotype male, ex G. smithii, Australia: Northern Territory, 25 September 2003, D. H. Clayton, ANWC 33045 (OSU). Paratypes, all from type host species: 1 male, 4 females, same data as holotype; 1 male, 1 female, Australia: Northern Territory, 25 September 2003, D. H. Clayton, ANWC 33004, which are specimens 47 and 48 from Johnson et al. (2007; Cosp.Gesmi.1.27.2004.9 and Cosp.Gesmi.1.27.2004.10); 2 males, 1 female, Australia: Northern Territory, 24 September 2003, D. H. Clayton, ANWC 22908 and 33997 (OSU, PIPeR).

Etymology: This species is named in honor of Dr. Edward O. Wilson, Harvard University, Cambridge, Massachusetts, in recognition of his

influential work on the biodiversity and conservation of all organisms, large and small.

Remarks

Similar to *C. koopae* ex *Geophaps scripta*, but *C. eowilsoni* tends to have a larger HW and smaller HL/HW ratio. In addition to morphological similarities, *C. eowilsoni* is genetically similar to *C. koopae*. Phylogenetic reconstructions of *Columbicola* based on COI, 12S, and EF- 1α indicate that *C. eowilsoni* is the sister taxon to *C. koopae* (see Johnson et al., 2007).

Columbicola wombeyi n. sp.

(Figs. 8–10)

Male: Head as in Figure 8; scape and third antennal segment enlarged; medioposterior setae exceeding posterior head margin, 0.10 long. Anterior marginal head setae filiform. Pleural thickenings of lateral abdomen without scales (Fig. 9). Genitalia as in Figure 10; mesosome triangular, laterally thickened with 2 pores, parameres with medial expansions. Dimensions include: APW, 0.14; APL, 0.03; HW, 0.32; HL, 0.47; HL/HW, 1.47; SL, 0.12; PW, 0.21; MW, 0.29; GW, 0.08; TL, 1.97.

Female: Subgenital plate groove peaked, ovoid anteriorly, constricted medially, widening posteriorly, and up to 2 setae (<0.01 long) on each side. Dimensions include: APW, 0.16–0.17; APL, 0.04; HW, 0.33; HL, 0.54–0.55; HL/HW, 1.64–1.67; SL, 0.06; PW, 0.22–0.23; MW, 0.34; TL, 2.22–2.33.

Taxonomic summary

Type host: Geophaps plumifera Gould.

Type material: Holotype male, ex *G. plumifera*, Western Australia: Strelly River, 9 May 2002, T. Chesser, ANWC-33047, which is specimen 49 from Johnson et al. (2007; CospGeplu.1.8.2003.16 (OSU). Paratypes, all from type host species: 2 females, Australia: Northern Territory, 20 October 2002, D. H. Clayton, ANWC-33467, including specimen 50 from Johnson et al. (2007; CospGeplu.7.7.2003.13; OSU and PIPeR)

Etymology: This species is named for John Wombey, Australian National Wildlife Collection, Canberra, Australia, in recognition of his contributions to Australian ornithology and his critical assistance in collecting bird lice.

Remarks

This species can be distinguished from *C. koopae* and *C. eowilsoni* by the shape of the male genitalia and its unique anterior head shape. Although blade-like anterior marginal head setae (AMHS) are typical of most species of *Columbicola*, the AMHS of *C. wombeyi* are filiform. These filiform AMHS are similar to those of *C. masoni* (described below). In addition to morphological characteristics, the placement of *C. wombeyi* within the *angustus* species group is supported molecularly. Phylogenetic reconstructions of *Columbicola* based on COI, 12S, and EF-1a place *C. wombeyi* within a clade of lice that includes *C. koopae* and *C. eowilsoni*, which are lice in the *angustus* species group found on other species of *Geophaps* (see Johnson et al., 2007).

Columbicola masoni n. sp.

(Figs. 11-15)

Male: Head as in Figure 11; scape and third antennal segment enlarged; medioposterior setae exceeding posterior head margin, 0.07–0.10 long. Anterior marginal head setae filiform. Thoracic sternal plate shaped as in Figure 12. Genitalia as in Figure 13; parameres mesosome triangular, laterally thickened with 6 pores. Dimensions include: APW, 0.14–0.15; APL, 0.03–0.04; HW, 0.31–0.32; HL, 0.49–0.53; HL/HW, 1.58–1.71; SL, 0.14–0.15; PW, 0.26–0.29; MW, 0.37–0.40; GW, 0.08–0.09; TL, 2.43–2.53.

Female: Head as in Figure 14. Anterior marginal head setae filiform. Thoracic sternal plate shaped as in Figure 12. Ventral terminalia as in Figure 15, with scaling in subgenital plate groove. Subgenital plate groove peaked, ovoid anteriorly, slight constriction posteriorly, and 4–7 setae (<0.01 long) on each side. Dimensions include: APW, 0.13–

0.16; APL, 0.03–0.04; HW, 0.30–0.35; HL, 0.51–0.58; HL/HW, 1.59–1.76; SL, 0.06; PW, 0.27–0.30; MW, 0.37–0.41; TL, 2.58–2.80.

Taxonomic summary

Type host: Petrophassa rufipennis Collett.

Type material: Holotype male, ex *P. rufipennis*, Australia: Northern Territory, 28 October 2003, D. H. Clayton. Paratypes, all from type host species: 5 males, 6 females, same data as holotype, including specimens 54 and 55 from Johnson et al. (2007; Cosp.Peruf.1.27.2004.12 and Cosp.Peruf.1.27.2004.13); 2 males, 4 females, Australia: I. Mason, collected from a barrel of 56 *P. rufipennis* preserved in alcohol.

Additional material: Five males, 6 females, ex Petrophassa albipennis Gould, Australia; Northern Territory, 20 October 2002, D. H. Clayton, ANWC-33493 and ANWC-33469, including specimens 51 and 52 from Johnson et al. (2007; Cosp.Pealb.5.14.2003.13 and Cosp.Pealb.5. 14.2003.14); 1 female, Australia: 7 June 1982, ANWC-41241 (OSU, PIPeR).

Etymology: This species is named for Ian Mason, Australian National Wildlife Collection, Canberra, Australia, in recognition of his contributions to Australian ornithology and his critical assistance in collecting bird lice.

Remarks

Columbicola masoni shares filiform anterior marginal head setae with C. wombeyi; however, the former can be distinguished from the latter by differences in head shape and genitalia. The head of C. masoni is textured with small indentations along lateral posterior margins (Figs. 11, 14). The male genitalia have a triangular mesosome, as do the other members of this species group, but C. masoni is the only species in the group to have 6 pores. In addition to the morphological characteristics, the placement of C. masoni within the angustus species group is supported molecularly. Phylogenetic reconstructions of Columbicola, based on COI, 12S, and EF-1α place C. masoni in a clade with other lice in the angustus species group (Johnson et al., 2007). Morphologically, the lice from P. rufipennis and P. albipennis are inseparable; however, molecular data indicate that lice from these 2 hosts are quite divergent. Although these lice may represent cryptic species, we are conservatively recognizing them both as C. masoni on the basis of morphology.

Columbicola guimaraesi species group Columbicola waiteae n. sp.

(Figs. 16-20)

Adult: Body elongate; each side of metanotum with 2 long, 2 short setae.

Male: Head as in Figure 16; scape and third antennal segment enlarged; medioposterior setae exceeding posterior head margin, 0.07–0.09 long. Thoracic sternal plate shaped as in Figure 17. Genitalia as in Figure 18; mesosome ovoid, laterally thickened, with 6 pores, and parameres with medial expansions. Dimensions include: APW, 0.12–0.13; APL, 0.07–0.08; HW, 0.29–0.31; HL, 0.54–0.56; HL/HW, 1.86–1.93; SL, 0.14–0.15; PW, 0.23–0.24; MW, 0.29–0.33; GW, 0.10–0.11; TL, 2.33–2.58.

Female: Head as in Figure 19. Ventral terminalia as in Figure 20. Subgenital plate groove ovoid, thickened anteriorly, constricted medially, widening posteriorly, with 3–6 setae (0.02–0.035 long) on each side. Dimensions include: APW, 0.13–0.14; APL, 0.08; HW, 0.31–0.34; HL, 0.58–0.61; HL/HW, 1.87–1.97; SL, 0.06; PW, 0.23–0.26; MW, 0.31–0.34; TL, 2.68–2.90.

Taxonomic summary

Type host: Columba leucomela Temminck.

Type material: Holotype male, ex *C. leucomela*, Australia: New South Wales, 9 September 2003, I. Mason and J. Wombey, ANWC-33890 (OSU). Paratypes, all from type host species: 3 males, 4 females, same data as holotype, including specimen 103 from Johnson et al. (2007; Cosp.Coleu.1.27.2004.7; OSU, PIPeR).

Etymology: This species is named in honor of Jessica L. Waite, University of Utah, Salt Lake City, Utah, in recognition of her work on the ecology of parasite interactions.

Remarks

This species keys to couplet 24 of Adams et al. (2005), which distinguishes Columbicola grandiusculus Tendeiro from C. vitiensis Ten-

deiro. Columbicola waiteae differs from both of these species in the shape of the male mesosome, which is more elongate than either C. grandiusculus or C. vitiensi, and is indented anteriorly. The shape of the female subgenital plate groove also distinguishes C. waiteae from the other 2 species: it is shorter and is thickened anteriorly. In addition to morphological characteristics, the placement of C. waiteae within the guimaraesi species group is supported molecularly. Phylogenetic reconstructions of Columbicola based on COI, 12S, and EF-1 α place C. waiteae as a sister taxa to C. guimaraesi Tendeiro ex Chalcophaps spp. (see Johnson et al., 2007).

Columbicola mjoebergi species group

Columbicola mjoebergi Eichler

Taxonomic summary

Type host: Geopelia striata (Linnaeus).

Material: Ex *G. placida* Gould and *G. cuneata* (Latham). From *G. placida* we examined 5 males and 3 females, Australia: Northern Territory, 24–25 October 2002, D. H. Clayton (PIPeR) ANWC 33671–33673, 33996, including specimen 65 of Johnson et al. (2007; Cosp. Gepla.5.14.2003.17). From *G. cuneata* we examined 2 males, Australia: Northern Territory, 24 October 2003, D. H. Clayton (PIPeR).

Remarks

Geopelia striata has been the only recognized host of *C. mjoebergi*, based on morphological examination of specimens (Eichler, 1943). Although *C. mjoebergi* was recorded from *Streptopelia chinensis* by Tendeiro (1973, *C. fradeorum* = *C. mjoebergi*), this record was considered a case of "straggling" by Adams et al. (2005) because it was collected in Thailand, where *G. striata* and *S. chinensis* are commonly held together in captivity.

Johnson et al. (2007) published a molecular phylogeny of *Columbicola* in which they refer to *Columbicola* from both *G. cuneata* and *G. humeralis* (Temminck) as *C. mjoebergi*. Morphological examination of the specimens sequenced by Johnson et al. (2007), and other specimens from these hosts, confirms that *Columbicola* from *G. cuneata* is morphologically inseparable from *C. mjoebergi* ex *G. striata*. However, the *Columbicola* from *G. humeralis* is quite distinct and merits specieslevel designation (see *C. rodmani* below). This is not surprising, as Johnson et al. (2007) acknowledged that the *Columbicola* from *G. humeralis* is genetically distinct from *C. mjoebergi* ex *G. cuneata*. In addition, we examined specimens from *G. placida* and found that they were morphologically indistinguishable from *C. mjoebergi*, thus representing a new host record.

Columbicola rodmani n. sp.

(Figs. 21-23)

Adult: Body elongate; each side of metanotum with 2 long, 2 short setae.

Male: Head similar in shape to *C. mjoebergi* (see, Adams et al., 2005, Fig. 108); scape and third antennal segment enlarged; medioposterior setae short, not reaching posterior head margin, 0.04–0.05 long. Thoracic sternal plate shaped as in Figure 22. Genitalia as in Figure 21; mesosome with small posterior extension, short but distinct anterior projections on lateral margins, with 6 genital pores. Dimensions include: APW, 0.13–0.14; APL, 0.07–0.08; HW, 0.27–0.29; HL, 0.52–0.55; HL/HW, 1.89–1.93; SL, 0.13–0.14; PW, 0.21–0.23; MW, 0.26–0.30; GW, 0.09–0.10; TL, 2.38–2.54.

Female: Ventral terminalia as in Figure 23, with scaling anterior to and lateral to medial subgenital plate groove. Subgenital plate groove ovoid anteriorly, constricted medially, widening posteriorly with irregular margins, with up to 3 short setae (<0.01 long) on each side. Dimensions include: APW, 0.14–0.15; APL, 0.08; HW, 0.29–0.30; HL, 0.56–0.59; HL/HW, 1.90–1.97; SL, 0.05–0.06; PW, 0.21–0.24; MW, 0.27–0.32; TL, 2.70–2.90.

Taxonomic summary

Type host: Geopelia humeralis (Temminck).

Type material: Holotype male, ex *G. humeralis*, Australia: Northern Territory, 24 October 2002, D. H. Clayton, ANWC-33615 (OSU). Paratypes, all from type host species: 3 males, 5 females, same data as

holotype; 1 male, 1 female, Australia: Northern Territory, Darwin, 16 October, 2002, D. H. Clayton, ANWC-33408 (OSU, PIPeR), including specimens 69 and 70 from Johnson et al. (2007; Cosp.Gehum.5.14. 2003.11 and Cosp.Gehum.5.14.2003.12).

Etymology: This species is named in honor of Dr. James E. Rodman, former Program Director, National Science Foundation, Bethesda, Maryland, in recognition of the fundamental role he has played in garnering support for the systematics community.

Remarks

This species keys to *C. mjoebergi* in couplet 40 of Adams et al. (2005); however, *C. rodmani* is consistently larger than *C. mjoebergi*, has a smaller HL/HW ratio, and the shape of the male genitalia is distinctly different. The mesosome of *C. rodmani* is longer and has thickened lateral anterior projections that are absent on *C. mjoebergi*; furthermore, the parameres of *C. rodmani* are continuous structures whereas the parameres of *C. mjoebergi* are divided into several distinct parts.

Johnson et al. (2007) provide the first record of *Columbicola* from *G. humeralis*. In their study, the authors refer to these lice as "*C. mjoebergi* 2" based on molecular data from 2 specimens, i.e., specimens 69 and 70. Morphological examination of these specimens, as well as other specimens from the same host species, indicates that these lice are, in fact, a species distinct from *C. mjoebergi*.

Additional species Columbicola smithae n. sp.

(Figs. 24-28)

Adult: Body elongate; each side of metanotum with 2 long, 2 short setae.

Male: Head as in Figure 24; scape and third antennal segment enlarged, medioposterior setae short, not reaching posterior head margin, 0.04–0.05 long. Thoracic sternal plate shaped as in Figure 25. Genitalia as in Figure 26; mesosome ovoid with anterior indentation and posterior projection and thick lateral margins, and 5–7 genital pores. Dimensions include: APW, 0.13–0.14; APL, 0.07–0.08; HW, 0.31–0.32; HL, 0.49–0.51; HL/HW, 1.58–1.63; SL, 0.11–0.12; PW, 0.21–0.22; MW, 0.28–0.30; GW, 0.09–0.10; TL, 1.95–2.07.

Female: Head as in Figure 27. Ventral terminalia as in Figure 28, with scaling anterior to subgenital plate groove. Subgenital plate groove elongate, peaked anteriorly, with irregular lateral margins, and 2–3 setae (<0.01 long) on each side. Dimensions include: APW, 0.14–0.15; APL, 0.07–0.08; HW, 0.32–0.34; HL, 0.51–0.56; HL/HW, 1.56–1.65; SL, 0.05–0.06; PW, 0.22–0.24; MW, 0.30–0.36; TL, 2.39–2.57.

Taxonomic summary

Type host: Turtur brehmeri (Hartlaub).

Type material: Holotype male, ex T. brehmeri, Ghana: Goaso, 28 March 2003, K. P. Johnson, KPJ-144 (OSU). Paratypes, all from type host species: 1 male, 2 females, same data as holotype; 2 males, 3 females, same date and location as holotype, J. Weckstein, JDW-604, including specimen 139 from Johnson et al. (2007; Cosp.Tubre.7.27. 2004.2).

Etymology: This species is named in honor of Wendy A. Smith, University of Utah, Salt Lake City, Utah, in recognition of her work on the endosymbiotic bacteria of Columbicola and other feather lice.

Remarks

It is unclear to which species group *C. smithae* belongs, as it keys to couplets 40–42 of Adams et al. (2005), but the male genitalia of *C. smithae* are very different from all other species in these couplets (*C. mjoebergi, C. fradei* Tendeiro, *C. tashenbergi*, and *C. angustus*). Molecular evidence in Johnson et al. (2007) suggests that the closest relatives of *C. smithae* are *C. streptopeliae* (Clay and Meinertzhagen) and *C. meinertzhageni* Tendeiro. However, *C. smithae* does not resemble either of these species morphologically. Unlike *C. smithae*, *C. streptopelia* has an ovoid body shape and an interrupted anterior marginal head carina. Although *C. meinertzhageni* is known to infest doves in the genus *Turtur*, the male genitalia of *C. smithae* is a simple-shaped structure unlike the complex mesosomal structure of *C. meinertzhageni* (see Adams et al., 2005; Fig. 37).

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APPENDIX I. Host associations for the 88 described Columbicola species.

Columbiform host genera and species* in alphabetical order	Columbicola species & species groups†
Alectroenas	
madagascariensis (Linnaeus)‡ sganzini (Bonaparte)	brygooi Tendeiro ^S brygooi Tendeiro ^S
Caloenas	
nicobarica (Linnaeus)‡	effeminatus Tendeiro ^G
Chalcophaps	
indica (Linnaeus)‡ stephani Pucheran	guimaraesi Tendeiro ^B guimaraesi Tendeiro ^B
Claravis	
mondetoura (Bonaparte) pretiosa (Ferrari-Pérez)	passerinae (Wilson) ^v passerinae (Wilson) ^v
Columba	
arquatrix Temminck‡	browni Adams, Price & Clayton ^C
bollii Godman‡	stresemanni Eichler ^A
eversmanni Bonaparte	columbae (Linnaeus) ^A
guinea Linnaeus	columbae (Linnaeus) ^A
hodgsonii Vigors‡	keleri Tendeiro ^A
larvata Temminck‡	fradei Tendeiro ^L
larvata Temminck‡	obliteratus Tendeiro ^Z
leucomela Temminck‡	waiteae n. sp. ^{B,1}
leuconota Vigors	tschulyschman Eichler ^A
livia J. F. Gmelin‡	columbae (Linnaeus) ^A
livia J. F. Gmelin	tschulyschman Eichler ^A
malherbii J. & E. Verreaux‡	insularis Tendeiro ^R
oenas Linnaeus	columbae (Linnaeus) ^A
palumbus Linnaeus‡	claviformis (Denny) ^A
punicea Blythe	vitiensis Tendeiro ^B
rupestris Pallas‡	tschulyschman Eichler ^A
vitiensis Quoy & Gaimard‡	vitiensis Tendeiro ^B
Columbina	
buckleyi (Sclater & Salvin)	passerinae (Wilson) ^V
cruziana Prévost	passerinae (Wilson) ^V

^{*} Host names are from Dickinson (2003), with the exception of New World Columba, which are now called Patagioenas (see Johnson et al., 2001).

APPENDIX I. Continued.

Columbiform host genera and	Columbicola species
species* in alphabetical order	& species groups†
inca (Lesson)	passerinae (Wilson) ^V
minuta (Linnaeus)	passerinae (Wilson) ^v
passerina (Linnaeus)‡	passerinae (Wilson) ^V
picui (Temminck) ²	baculoides (Paine) ^T
picui (Temminck)	passerinae (Wilson) ^V
talpacoti (Temminck)	passerinae (Wilson) ^V
Cryptophaps	
poecilorrhoa (Brüggemann)‡	grandiusculus Tendeiro ^B
Ducula	
aenea (Linnaeus)‡	cavifrons (Taschenberg)Y
badia (Raffles)‡	cavifrons (Taschenberg) ^Y
badia (Raffles)‡	sikoraae Eichler ^Y
bicolor (Scopoli)	wolffhuegeli EichlerQ
chalconota (Salvadori)	claytoni Bush & PriceQ
cineracea (Temminck)	longiceps (Rudow)Q
concinna (Wallace)‡	emersoni Tendeiros
concinna (Wallace)‡	mendesi Adams, Price & Clayton ^Q
forsteni (Bonaparte)	cavifrons (Taschenberg) ^Y
goliath (G. R. Gray)‡	becheti Tendeiro ^H
lacernulata (Temminck)	cavifrons (Taschenberg)Y
latrans (Peale)	longiceps (Rudow)Q
melanochroa (P. L. Sclater)	cavifrons (Taschenberg)Y
oceanica (Lesson & Garnot)	cavifrons (Taschenberg) ^Y
pacifica (J. F. Gmelin)‡	malenkeae Bush & PriceQ
perspicillata (Temminck)‡	longiceps (Rudow)Q
pickeringii (Cassin)	cavifrons (Taschenberg) ^Y
pinon (Quoy & Gaimard)‡	harrisoni Tendeiro ^Y
pistrinaria (P. L. Sclater)	malenkeae Bush & PriceQ
rosacea (Temminck)	mendesi Adams, Price & Clayton ^Q
rufigaster (Quoy & Gaimard)‡	claytoni Bush & PriceQ
Ectopistes	
migratorius (Linnaeus)‡	extinctus Malcomson ^U
Gallicolumba	
beccarii (Salvadori)‡	beccarii (Tendeiro)F
jobiensis (A. B. Meyer)	exilicornis (Piaget)F

¹ This is n. sp. 2 in Johnson et al. (2007).

[†] Host associations from Price et al. (2003), Adams et al. (2005), Bush and Price (2006), Johnson et al. (2007), and current paper.

[‡] Indicates type host.

[§] Indicates new host record.

A columbae group.

^B guimaraesi group.

^C meinertzhageni group. $^{\rm D}\,streptopeliae$ group.

E theresae group.

F angustus group.

^G effeminatus group.

^н becheti group.

I fortis group.

J tasmaniensis group.

K mjoebergi group.

^L fradei group.

^M galei group.

^N fulmeki group.

^o veigasimoni group.

P palmai group.

Q longiceps group.

R clayae group.

s emersoni group.

T baculoides group.

U extinctus group.

v passerinae group.

gracilicapitis group.

x tendeiroi group.

Y cavifrons group.

z species group unknown.

² These records from Price et al. (2003) were inadvertantly left off the checklist published by Adams et al. (2005).

³ Johnson et al. (2007) referred to specimens of this species as C. mjoebergi; however, these specimens represent a new species described herein as C.

⁴ Johnson et al. (2007) referred to the sequenced specimens as n. sp. 3; however, these specimens represent a new host record of C. mjoebergi, not a new species.

⁵ Johnson et al. (2007) referred to the sequenced specimens as n. sp. 3; however, this specimen is C. mjoebergi.

⁶ This is n. sp. 9 in Johnson et al. (2007).

⁷ This is n. sp. 7 in Johnson et al. (2007).

⁸ This is n. sp. 8 in Johnson et al. (2007).

⁹ Johnson et al. (2007) erroneousely reported that C. drowni occurs on Metriopelia aymara. Specimen 154 (Coalt.1.8.2003.4) was, in fact, collected from the type host species, M. melanoptera, from Bolivia: Lago Poopo, 2 November 2001, K. McCracken, KGM-511.

 $^{^{\}rm 10}$ This is n. sp. 6a in Johnson et al. (2007).

¹¹ This is n. sp. 6b in Johnson et al. (2007).

 $^{^{12}}$ This is n. sp. 5 in Johnson et al. (2007).

¹³ Johnson et al. (2007) referred to a new host-Columbicola association for Streptopelia decipiens. However, the poor quality of the specimens makes it impossible to confirm this assumption, or to assign the specimens to one of the three species of Columbicola known to infest S. decipiens. Thus, we have conservatively chosen not to include the n. sp. from Johnson et al. (2007) in the checklist at this time.

¹⁴ This is n. sp. 4 in Johnson et al. (2007).

APPENDIX I. Continued.

APPENDIX I. Continued.

capensis (Linnaeus)

theresae Ansari^E

Columbiform host genera and Columbicola species Columbiform host genera and Columbicola species species* in alphabetical order species* in alphabetical order & species groups† & species groups† Geopelia Otidiphaps mjoebergi Eichler^K nobilis Gould‡ fortis (Taschenberg)^I cuneata (Latham) humeralis (Temminck) rodmani n.sp.K,3 Patagioenas maugei (Temminck) timorensis Tendeiro^K cavennensis (Bonnaterre) adamsi Clayton & Price^U maugei (Temminck)‡ fulmeki Eichler^N fasciata (Say) extinctus Malcomson^U mjoebergi Eichler^{K,4} placida Gould§ macrourae (Wilson)^U leucocephala (Linnaeus)2 striata (Linnaeus) exilicornis (Piaget)F waggermani Clayton & Price^U leucocephala (Linnaeus) mjoebergi EichlerK,5 striata (Linnaeus)‡ maculosa (Temminck) adamsi Clayton & Price^U Geophaps triangularis Eichler^T maculosa (Temminck) plumifera Gould‡ wombeyi n.sp.F,6 nigrirostris (P. L. Sclater) adamsi Clayton & Price^U scripta (Temminck)‡ koopae n sp.F,7 picazuro (Temminck) adamsi Clayton & Price^U wilsoni n.sp.^{F,8} smithii (Jardine & Selby)‡ picazuro (Temminck)2 baculoides (Paine)T picazuro (Temminck)‡ triangularis Eichler^T Geotrygon plumbea (Vieillot) adamsi Clayton & Price^U frenata (Tschudi) waltheri Clayton & PriceW plumbea (Vieillot) macrourae (Wilson)^U macrourae (Wilson)^U linearis (Prévost) speciosa (J. F. Gmelin)‡ adamsi Clayton & Price^U waltheri Clayton & PriceW linearis (Prévost) waggermani Clayton & Price^U squamosa (Bonnaterre)‡ macrourae (Wilson)^U montana (Linnaeus) subvinacea (Lawrence) macrourae (Wilson)^U mystacea (Temminck) macrourae (Wilson)^U Petrophassa violacea (Temminck) macrourae (Wilson)^U masoni n.sp F,10 rufipennis Collett‡ Goura masoni n.sp E11 albipennis Gould cristata (Pallas)‡ gourae TendeiroQ Phapitreron Gymnophaps exilicornis (Piaget)F amethystinus Bonaparte galei Adams, Price & Clayton^M albertisii Salvadori‡ amethystinus Bonaparte‡ veigasimoni Tendeiro^o Leptotila leucotis (Temminck)‡ deboomi Tendeiro^E timmermanni TendeiroW cassini (Lawrence) leucotis (Temminck) veigasimoni Tendeiro^o gracilicapitis CarrikerW iamaicensis (Linnaeus) Phaps plumbeiceps (Sclater & Salvin) gracilicapitis Carriker^W chalcoptera (Latham)‡ angustus (Rudow)F plumbeiceps (Sclater & Salvin) macrourae (Wilson)^U chalcoptera (Latham)‡ tasmaniensis Tendeiro^J rufaxilla (Richard & Bernard)‡ timmermanni Tendeiro^W tasmaniensis Tendeiro^J elegans (Temminck) verreauxi (Bonaparte) baculoides (Paine)T histrionica (Gould)‡ harbisoni n.sp.F,12 gracilicapitis CarrikerW verreauxi (Bonaparte)‡ Ptilinopus macrourae (Wilson)^U verreauxi (Bonaparte) greyii Bonaparte emersoni Tendeiros verreauxi (Bonaparte) timmermanni Tendeiro^W jambu (J. F. Gmelin) elbeli Tendeiro^R Leucosarcia magnificus (Temminck)‡ reedi Adams, Price & Clayton^Z melanoleuca (Latham)‡ palmai Adams, Price & melanospilus (Salvadori) emersoni Tendeiros Clayton^P occipitalis (Gray & Mitchell)‡ xavieri Tendeiro^z Lopholaimus pulchellus (Temminck) emersoni Tendeiros antarcticus (Shaw) paradoxus TendeiroQ purpuratus (J. F. Gmelin)‡ curtus Tendeiros regina Swainson§ emersoni Tendeiro^S Macropygia richardsii (E. P. Ramsay)‡ emersoni Tendeiro^S amboinensis (Linnaeus) exilicornis (Piaget)F rivoli (Prévost)‡ wecksteini Adams, Price & mackinlayi E. P. Ramsay exilicornis (Piaget)F Claytons nigrirostris Salvadori‡ arnoldi Adams, Price & superbus (Temminck) emersoni Tendeiro^S Clayton^F tannensis (Latham) emersoni Tendeiro^S ruficeps (Temminck) exilicornis (Piaget)F emersoni Tendeiro^S wallacii (G. R. Gray) unchall (Wagler) exilicornis (Piaget)F Reinwardtoena Metriopelia reinwardtii (Temminck)‡ taschenbergi Eichler^F aymara (Prévost)‡9 altamimiae Clayton & PriceV Starnoenas ceciliae Lesson‡ gymnopeliae Eichler^V melanoptera (Molina) altamimiae Clayton & Price^V cyanocephala (Linnaeus)‡ tendeiroi MeyX melanoptera (Molina)‡9 drowni Clayton & Price^v Streptopelia **Ocyphaps** bitorquata (Temminck)‡ cicchinoi Tendeiro^E lophotes (Temminck)‡ mckeani TendeiroF capicola (Sundevall)‡ capicolae (Clay & Meinertzhagen)D capicola (Sundevall)‡ meridionalis Tendeiro^C capensis (Linnaeus)‡ oenae (Hopkins)D capicola (Sundevall) theresae Ansari^E

APPENDIX I. Continued.

Columbiform host genera and	Columbicola species
species* in alphabetical order	& species groups†
1	
chinensis (Scopoli)	theresae Ansari ^E
chinensis (Scopoli)‡	fulmeki Eichler ^N
decaocto (Frivaldszky)	bacillus (Giebel) ^A
decipiens (Hartlaub &	bacillus (Giebel) ^A
Finsch) ¹³	(Class 6
decipiens (Hartlaub & Finsch)	streptopeliae (Clay & Meinertzhagen) ^D
decipiens (Hartlaub & Finsch)	theresae Ansari ^E
lugens (Rüppell)	orientalis Tendeiro ^E
orientalis (Latham)	fulmeki Eichler ^N
orientalis (Latham)	theresae Ansari ^E
orientalis (Latham)‡	orientalis Tendeiro ^E
orientalis (Latham)‡	turturis (Uchida) ^A
picturata (Temminck)‡	hoogstraali Tendeiro ^E
roseogrisea (Sundevall)	bacillus (Giebel) ^A
semitorquata (Rüppell)	bacillus (Giebel) ^A
semitorquata (Rüppell)‡	meinertzhageni Tendeiro ^C
senegalensis (Linnaeus)‡	senegalensis Tendeiro ^D
senegalensis (Linnaeus)‡	theresae Ansari ^E
tranquebarica (Hermann)	bacillus (Giebel) ^A
tranquebarica (Hermann)	theresae Ansari ^E
turtur (Linnaeus)‡	bacillus (Giebel) ^A
vinacea (J. F. Gmelin)	theresae Ansari ^E
vinacea (J. F. Gmelin)‡	streptopeliae (Clay &
	Meinertzhagen) ^D
Treron	
apicauda Blyth‡	wardi Tendeiro ^R
bicinctus (Jerdon)	elbeli Tendeiro ^R
calvus (Temminck)‡	clayae Tendeiro ^R
calvus (Temminck)‡	meinertzhageni Tendeiro ^C
curvirostra (J. F. Gmelin)‡	davisae Adams, Price & Clayton ^R
formosae Swinhoe	sphenurus Tendeiro ^R
formosae Swinhoe	elbeli Tendeiro ^R
fulvicollis (Wagler)	elbeli Tendeiro ^R
griseicauda Bonaparte	elbeli Tendeiro ^R
olax (Temminck)	elbeli Tendeiro ^R
oxyurus (Temminck)	wardi Tendeiro ^R
phoenicopterus (Latham)‡	phoenicopterae Tendeiro ^R
phoenicopterus (Latham)‡	elbeli Tendeiro ^R
pompadora (J. F. Gmelin)‡	elbeli Tendeiro R
pompadora (J. F. Gmelin)	phoenicopterae Tendeiro ^R
sanctithomae (J. F. Gmelin)‡	longantennatus Tendeiro ^C
sieboldii (Temminck)	elbeli Tendeiro ^R
sphenurus (Vigors)‡	sphenurus Tendeiro ^R
vernans (Linnaeus)	elbeli Tendeiro ^R
waalia (F. A. A. Meyer) Turacoena	clayae Tendeiro ^R
manadensis (Quoy & Gaimard)‡	<i>juliusriemeri</i> Eichler & Mrosek ^Z
Turtur	
abyssinicus (Sharpe)	carrikeri Tendeiro ^E
brehmeri (Hartlaub)‡	smithae n.sp. ^{Z,14}
chalcospilos (Wagler)	meinertzhageni Tendeiro ^C
chalcospilos (Wagler)‡	carrikeri Tendeiro ^E
Uropelia	canerr rendent
campestris (Spix)	passerinae (Wilson) ^V
-mapesia (Spin)	rsee (Tillson)

APPENDIX I. Continued.

Columbiform host genera and species* in alphabetical order	Columbicola species & species groups†
Zenaida	
asiatica (Linnaeus)	macrourae (Wilson) ^U
auriculata (Des Murs)	baculoides (Paine)T
auriculata (Des Murs)	macrourae (Wilson) ^U
auriculata (Des Murs)	triangularis Eichler ^T
aurita (Temminck)	macrourae (Wilson) ^U
galapagoensis Gould	macrourae (Wilson) ^U
macroura (Linnaeus)‡	baculoides (Paine)T
macroura (Linnaeus)‡	macrourae (Wilson) ^U