# Two new species of *Cotingacola* Carriker, 1956 (Phthiraptera: Ischnocera: Philopteridae) from Amazonian Brazil, with comments on host-specificity

Michel P. Valim · Jason D. Weckstein

Received: 12 July 2011/Accepted: 11 September 2011 © Springer Science+Business Media B.V. 2011

Abstract This paper describes two new species of Cotingacola Carriker, 1956, C. lutzae n. sp. and C. engeli n. sp., from the cinereous mourner Laniocera hypopyrra (Vieillot) and black-necked red cotinga Phoenicircus nigricollis Swainson (Aves: Passeriformes: Cotingidae), respectively. These species are fully illustrated and compared with their morphologically closest relatives. With the addition of these two new species, this Neotropical chewing louse genus now includes ten species. We also present records from Brazil for two previously described species, C. stotzi Clayton & Price, 1998 and C. parmipapillae Carriker, 1956. The re-examination of a specimen identified as 'Cotingacola sp.' in a recent phylogenetic study confirmed that it is C. parmipapillae and that Querula purpurata (Statius Müller) regularly hosts two Cotingacola species, which means that at least three cotingid hosts carry more than one species of Cotingacola. We comment on the variability in the host-specificity of Cotingacola species.

# Introduction

*Cotingacola* Carriker, 1956 (Ischnocera: Philopteridae) is a Neotropical chewing louse genus, originally

M. P. Valim (🖂) · J. D. Weckstein

Zoology Department, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA e-mail: mpvalim@hotmail.com composed of 14 species (Carriker, 1956, 1963), which are permanent ectoparasites occurring exclusively on birds of the family Cotingidae (Aves: Passeriformes). A complete revision of Cotingacola was presented by Clayton & Price (1998), who synonymised eight previously described species and added two more. This genus is supposedly monophyletic within the Degeeriella-complex (see Johnson et al., 2002) and currently comprises eight valid species (Clayton & Price, 1998; Price et al., 2003). This paper describes two additional species of Cotingacola from two widespread Amazonian cotingids, the cinereous mourner Laniocera hypopyrra (Vieillot) and the black-necked red cotinga Phoenicircus nigricollis Swainson, which previously have no record of hosting chewing lice (Price et al., 2003). We also present new host and distributional records for other Cotingacola spp.

# Materials and methods

We collected the specimens for this study using the ethyl acetate fumigation technique as described in Bueter et al. (2009), and they were mounted on slides following the procedures of Palma (1978). Prevalence and abundance measurements presented here are based on quantitatively sampled collections made during a 2007 expedition to Japurá, Amazonas, Brazil. The somatic body parts measured and their abbreviations were: preocular width (POW), temple width (TW), head length (HL), dorsoanterior plate length (DPL), prothorax width (PW), metathorax width (MW), abdomen width at segment V (AWV), genitalia width (GW), genitalia length (GL) and total length (TL). Measurements are given in micrometres. Host names follow Dickinson (2003).

We used laboratory methods as described by Bueter et al. (2009) and modified by Valim & Weckstein (2011) to extract DNA and sequence a 379 base pair (bp) fragment of the mitochondrial cytochrome oxidase I (COI) gene from each of the new Cotingacola species to assess and document their genetic distinctiveness. DNA sequences, voucher numbers and locality data are deposed in GenBank (JN662441-JN662444). We also incorporated two sequences from GenBank, published by Johnson et al. (2002), including C. stotzi Clayton & Price, 1998 (Csto.10.12. 1999.11; GenBank Accession No. AF444854) and Cotingacola sp. (Issp.Qupur.10.12.1999.12; GenBank Accession No. AF444863) both ex Querula purpurata (Statius Müller) and used the other COI sequences published in Johnson et al. (2002) to put our Cotingacola COI sequences into a phylogenetic context (GenBank Accession Nos AF444846-AF444876).

PAUP\* (version 4.0b10; Swofford, 2003) was used to calculate uncorrected p-distances between *Cotingacola* COI sequences and to conduct a maximum parsimony (MP) heuristic search and bootstrap analysis of the combined Johnson et al. (2002) and *Cotingacola* COI dataset. For the MP heuristic search, we used TBR branch swapping, stepwise addition and 100 random addition replicates, and for the MP bootstrap analysis we performed 1,000 bootstrap replicates with ten random additions per replicate.

Holotypes of the new species are deposited in the Museu de Zoologia, University of São Paulo, São Paulo, Brazil (MZUSP), and paratypes are deposited in MZUSP and the Field Museum of Natural History, Chicago, USA (FMNH). DNA voucher specimens Cost.6.9.2011.2 and Copa.6.9.2011.1 are deposited in the FMNH. DNA voucher specimens Csto.10.12. 1999.11 and Issp.Qupur.10.12.1999.12 from Johnson et al. (2002) are held in the Price Institute of Phthirapteran Research, University of Utah, Salt Lake City, USA (PIPeR). Additional specimens for further morphological comparison were borrowed from the National Museum of Natural History, Washington DC, USA (USNM). For material collected in 1999 and 2007, host specimen vouchers are deposited in the Museu Paraense Emílio Goeldi (MPEG) and the FMNH and are indicated by field numbers and where available specimen numbers.

Additional material examined. Male holotype (USNM 68666) of Cotingacola gracilis Carriker, 1956, ex Cephalopterus ornatus St-Hilaire, Rio Coroico, Santa Ana, Bolivia, 18 July 1934, col. M.A. Carriker Jr, at the USNM. Male holotype and female allotype (USNM 68667) of Cotingacola dimorpha Carriker, 1956, ex Procnias tricarniculata (Verreaux & Verreaux), Guapiles, Costa Rica, March 1903, col. M.A. Carriker Jr, at the USNM.

Phthiraptera Haeckel, 1896 Ischnocera Kellogg, 1896 Philopteridae Burmeister, 1838 *Cotingacola* Carriker, 1956

# Cotingacola lutzae n. sp.

*Type-host: Laniocera hypopyrra* (Vieillot) (Cotingidae), the cinereous mourner.

*Type-locality*: Rio Mapari Município Japurá, Amazonas, Brazil.

*Material studied*: 1 male, 3 females and 7 nymphs from 1 of 2 birds examined (prevalence 50%; abundance 5.5).

*Type-material*: Male holotype (FMNH-INS 28977), ex *Laniocera hypopyrra*, JAP307 MPEG 63184; Município Japurá, Rio Mapari (02°02'31.6"S; 67°17'16.6"W), Amazonas, Brazil, 17 July 2007, col. J.D. Weckstein, at MZUSP. Paratypes: 3 females (FMNH-INS 28906, 28978-28979; one female DNA voucher Cosp.Lahy.1.4.2011.2), same data as holotype. 1 female (DNA voucher) paratype at FMNH.

*Etymology*: Named for Holly L. Lutz (FMNH), in recognition of her interests in studying avian parasites and her extensive efforts collecting avian ectoparasites and parasitological data. Noun in the genitive case.

Description (Figs. 1–5)

*Male.* Habitus as in Fig. 1; body slender in shape. Head (Fig. 3) evenly rounded anteriorly and rounded on its posterior margin; HL/TW = 1.24; coni longer than the scape, 60 long. Pterothorax with chaetotaxy typical of genus; posterior margin with 4 very long



**Figs. 1–5** *Cotingacola lutzae* n. sp.: 1. habitus of the male; 2. habitus of the female; 3. male genitalia; 4. female head, dorsal view; 5. female terminalia, ventral view. *Scale-bars*: in micrometres

setae in 2 pairs reaching abdominal segment VII, plus 1 medium long and 1 very small seta on each corner of pterothorax. Tergites III–VII with 1 posterior and 1 sutural seta, between postspiracular setae, on each segment; tergite VIII divided medially. Sternites III-VI each with 4 setae. Paratergal chaetotaxy: II-IV, 0; V, 1; VI–VIII, 2. Abdomen with TL/AWV = 3.46. Genitalia (Fig. 4) with long and broad basal apodeme; short inwardly directed parameres distinctly squamous on distal third of paramere; short parallel-sided penial sclerite, 0.03 long, with penial arms in form of narrow inverted 'U' and distinctly fused with basal plate, bearing 2 vestigial penial setae on each side; endomeral plate broad triangular, 0.04 wide and 0.03 long. Dimensions (n=1): POW 300; TW 380; HL 407; DPL 180; PW, 240; MW 320; AWV 410; GW 80; GL 260; TL 1,420.

*Female*. Habitus as in Fig. 2. Head and body shape and both tergal and sternal chaetotaxy much as for males, but differing in larger dimensions and terminalia. HL/ TW = 1.22-1.23 and TL/AWV = 3.24-3.42. Tergite VIII divided medially; vulval margin slightly concave and with 14–17 medium long (*c*.40) marginal setae, plus 4 very short (<10) medial setae (Fig. 5). Dimensions (n=3): POW 310–340; TW 400–410; HL 490–500; DPL 180; PW 260–270; MW 330–340; AWV 490–500; TL 1,590–1,710.

# Remarks

This new species is morphologically close to C. dimorpha Carriker, 1956. Both sexes can be readily distinguished by head shape and head width ( $<350 \,\mu m$ in C. dimorpha). In males, tergite VIII is not medially fused (fused in C. dimorpha) and the genitalia are completely different from those of C. dimorpha. In females, tergite VIII possesses an anterior notch, which is lacking in C. dimorpha. The male genitalia of C. lutzae n. sp. are morphologically similar to those of C. gracilis Carriker, 1956, but both species can be easily separated by head shape (not anteriorly rounded in C. gracilis) and many somatic measurements: head length (540–560 µm in C. gracilis; female unknown); width of the abdomen (360–370  $\mu$ m and TL/AWV = 4.57-5.00 in C. gracilis); and total length body (1,690–1,800 µm in C. gracilis).

# Cotingacola engeli n. sp.

*Type-host: Phoenicircus nigricollis* Swainson (Cotingidae), the black-necked red cotinga.

*Type-locality*: Rio Mapari Município Japurá, Amazonas, Brazil.

*Material studied*: 43 males, 47 females and 72 nymphs from 3 of 5 birds examined (prevalence 60%; abundance 32.4)

*Type-material*: Male holotype (FMNH-INS 28980), ex *Phoenicircus nigricollis*, JAP158 MPEG 63160; Município Japurá, Rio Mapari (02°02'59.6"S; 67°15'47. 1"W), Amazonas, Brazil, 14 July 2007, col. J.D. Weckstein, at MZUSP. Paratypes: 2 males and 3 females (FMNH-INS 28905, 28981-28984; one female DNA voucher Cosp.Phni.1.4.2011.1), same data as holotype. 1 male and 1 female (DNA voucher) paratypes at FMNH.

*Etymology*: Named for Joshua I. Engel (FMNH), in recognition of his past and ongoing efforts to collect avian parasites in the field. Noun in the genitive case.

Description (Figs. 6–10)

Male. Habitus as in Fig. 6; body slender in shape. Head (Fig. 8) with distinct medioanterior protuberance and rounded on its posterior margin; HL/TW = 1.35–1.37; coni longer than scape, 60–70 long. Pterothorax with chaeotaxy typical of genus. Tergites III-VII with 1 posterior and 1 sutural seta, between postspiracular setae, on each segment; tergite VIII narrowed medially but not divided and lacking medioanterior indentation. Sternites III-VI each with 4 setae. Paratergal chaetotaxy: II–IV, 0; V, 1; VI–VIII, 2. Abdomen with TL/AWV = 3.47-3.74. Genitalia (Fig. 9) with long, broad basal apodeme; short inwardly directed parameres distinctly squamous on distal third of paramere; very long parallel-sided penial sclerite, 70 long, with penial arms roughly straight and perpendicular to penial sclerite, bearing 2 penial setae on each side; endomeral plate triangular, 60 wide and 30 long. Dimensions (n = 3): POW 280-290; TW 370-380; HL 500-520; DPL 210; PW 230-240; MW 290-310; AWV 380-430; GW 100; GL 350-380; TL 1,420-1,490.

*Female*. Habitus as in Fig. 6. Head and body shape and both tergal and sternal chaetotaxy much as for males,



**Figs. 6–10** *Cotingacola engeli* n. sp.: 6. habitus of the male; 7. habitus of the female; 8. male genitalia; 9. female head, dorsal view; 10. female terminalia, ventral view. *Scale-bars*: in micrometres

but differing in larger dimensions and terminalia. HL/ TW = 1.30-1.31 and TL/AWV = 3.69-3.85. Tergite VIII entire, with shallow concavity medially; vulval margin deeply concave and with 16 medium length (*c*.40) marginal setae, plus 4 short (*c*.20), medial setae (Fig. 10). Dimensions (n=3): POW 310–330; TW 420–430; HL 550–560; DPL 220–240; PW 260; MW 330–350; AWV 460–490; TL 1,770–1,810.

## Remarks

Cotingacola engeli n. sp. is also morphologically close to C. dimorpha. Both sexes are distinguishable by the shape of the anterior head margin and tergites VIII (in males of C. dimorpha these have the same breadth throughout their length and in females lack the shallow medial concavity). Furthermore, this new species is significantly smaller than C. dimorpha (1,560–1,570 μm in males; 1,840–1,890 μm in females). The male genitalia of both species are quite distinct with regard to the shape of the penial arms (a long inverted 'U'-shape in C. dimorpha) and by the gap between the parameres and the penial sclerite (the penial sclerite occupying two-thirds of the length of the space between the basal plate and the tip of parameres in C. dimorpha). Cotingacola engeli n. sp. can be readily separated from C. lutzae n. sp. by the head shape of both sexes, the male genitalia and the size of the vulval medial setae in the female.

### Cotingacola stotzi Clayton & Price, 1998

*Type-host and locality: Querula purpurata* (Statius Müller), Cerro de Pantiacolla, Madre de Dios, Peru (Clayton & Price, 1998).

*Material studied*: 3 males, 4 females and 5 nymphs from 3 of 6 birds examined (prevalence 50%; abundance 2) ex *Querula purpurata*, Brazil (details below). *Material examined*: Male holotype (FMNH-INS 28614) and 1 female paratype (FMNH-INS 28619), ex *Querula purpurata*, Cerro de Pantiacolla, *c*.600m, Madre de Dios, Peru, 17 December 1985, col. D.H. Clayton, at FMNH. 3 females and 5 nymphs (FMNH-INS 28908; 1 female DNA voucher Cost.6.9.2011.2), ex *Q. purpurata*, JAP429 MPEG 63170, Município Japurá, Rio Acanauí (02°01'38.4"S; 66°40'28.3"W), Amazonas, Brazil, 21 July 2007, col. J.D. Weckstein, at FMNH and MZUSP. 1 male and 1 female (FMNH- INS 28907); same data as previous, except JAP595 FMNH 457267, 26 July 2007. 2 males; same data as previous, except JAP512 MPEG 63169, (02°00'53.3"S; 66°39'55.5"W), 24 July 2007. 1 female (no number, Csto.10.12.1999.11; GenBank Accession No. AF444854), ex *Q. purpurata*, MO-005 (MPEG), Fazenda Morelândia, 8 km N de Santa Barbara do Pará (1°12'40"S; 48°14'47"W), Pará, Brazil, 14 August 1999, col. J.D. Weckstein, at PIPeR.

# Cotingacola parmipapillae Carriker, 1956

*Type-host and locality: Pyroderus scutatus scutatus* (Shaw), Nova Teutônia, Mato Grosso [sic] (= Santa Catarina), Brazil (Carriker, 1956; Clayton & Price, 1998).

*Material studied*: 4 males, 2 females and 1 nymph from 1 of 6 birds examined (prevalence 16.7%; abundance 1.17) ex *Querula purpurata*, Brazil (details below).

*Material examined*: 4 males, 2 females and 1 nymph (FMNH-INS 28909–28910; 1 male DNA voucher, Copa.6.9.2011.1), ex *Querula purpurata*, JAP250 MPEG 63173, Município Japurá, Rio Mapari (02°02'31. 6"S; 67°17'16.6"W), Amazonas, Brazil, 16 July 2007, col. J.D. Weckstein. 1 female (no number, Issp. Qupur.10.12.1999.12; GenBank Accession No. AF444 863), ex *Q. purpurata*, MO-005 (MPEG), Fazenda Morelândia, 8 km N de Santa Barbara do Pará (1°12'40"S 48°14'47"W), Pará, Brazil, 14 August 1999, col. J.D. Weckstein, at PIPeR. 1 female (FMNH-INS 28935), ex *Cephalopterus ornatus* St-Hilaire, 20 km NW Pillcopata, Cuzco, Peru, 1 December 1985, col. D.H. Clayton, at FMNH.

### Discussion

MP bootstrap analysis of the partial mitochondrial COI sequences does not provide strong support for the monophyly of *Cotingacola*. However, *Cotingacola* is monophyletic in all four of the MP trees (TL = 1964, CI = 0.303, RI = 0.395). Most likely, the lack of statistical support for the monophyly of the genus is due to a short stretch (379 bp) of relatively saturated DNA sequence data. Uncorrected p-distances indicate that the morphologically diagnosable *Cotingacola* species, *C. parmipapillae*, *C. stotzi*, *C. engeli* n. sp.

and C. lutzi n. sp. are genetically differentiated as well. Uncorrected p-distances between these four species averaged 21.3% and ranged from 18.2-23.8%, whereas uncorrected p-distances within C. stotzi (1.9%) and C. parmipapillae (1.3%) were much lower. P-distances within C. stotzi and C. parmipapillae were calculated from sequences of lice collected from the south bank of the Rio Japurá in the Napo area of endemism (NW Amazonia) generated for the present study and from sequences of lice from the Belém area of endemism in SW Amazonia, previously published by Johnson et al. (2002). Therefore, intraspecific comparisons are based on specimens separated geographically by the Solimões/Amazon River. Mitochondrial variation across the basin for these two Cotingacola taxa is relatively low and thus consistent with intraspecific level mtDNA variation in these louse morphospecies (e.g. Price & Weckstein, 2005, 2006; Weckstein, 2004; Valim & Weckstein, 2011).

The host-specificity of species of Cotingacola appears to be quite variable (Table 1). For example, so far C. lutzae n. sp., C. engeli n. sp, C. gracilis, C. fitzpatricki Clayton & Price, 1998 and C. stotzi are each known from only a single host taxon, whereas C. parmipapillae, C. tergalis Carriker, 1956, C. rupicolae Carriker, 1956, C. meridae Carriker, 1963 and C. dimorpha are all known from multiple host taxa. Cotingacola parmipapillae was known from two host species, Pyroderus scutatus and Cephalopterus ornatus (see Clayton & Price, 1998), but the morphological and DNA analyses of voucher specimens (Issp.Qupur.10.12.1999.12 and Copa.6.9. 2011.1) in this study confirm that it is also parasitises Querula purpurata. We now know that several host taxa [Q. purpurata, Pipreola arcuata (Lafresnaye) and Cephalopterus ornatus] harbour two species of Cotingacola. For example, one Q. purpurata (MO-005) host specimen sampled by one of us (JDW) in 1999

 Table 1 Host and geographical distribution of the species of Cotingacola

Species of Cotingacola	Species of hosts	Locality(-ies)	Reference(s)
C. dimorpha	Procnias tricarunculata (Verreaux & Verreaux)	Costa Rica, Colombia*	Carriker (1956)
	Procnias nudicollis (Vieillot)	Brazil	Valim et al. (2005)
C. engeli n. sp.	Phoenicircus nigricollis (Swainson)	Brazil	Present study
C. fitzpatricki	Snowornis subalaris (Sclater)	Peru	Clayton & Price (1998)
C. gracilis	Cephalopterus ornatus St-Hilaire	Bolivia	Carriker (1956)
C. lutzae n. sp.	Laniocera hypopyrra (Vieillot)	Brazil	Present study
C. meridae	Pipreola arcuata (Lafresnaye)	Venezuela	Carriker (1963)
	Pipreola riefferii melanolaema (Sclater)	Venezuela	Carriker (1963)
C. parmipapillae	Cephalopterus ornatus	Bolivia, Peru	Carriker (1956); Present study
	Pyroderus s. scutatus (Shaw)	Brazil	Carriker (1956)
	Querula purpurata (Statius Müller)	Brazil	Johnson et al. (2002)**; Present study
C. rupicolae	Cotinga nattererii (Boissonneau)	Colombia	Carriker (1956)
	Pipreola r. riefferii (Boissonneau)	Colombia	Carriker (1956)
	Rupicola peruviana (Latham)	Ecuador, Peru	Carriker (1956)
	Rupicola p. saturata Cabanis & Heine	Bolivia, Peru	Carriker (1956)
	Rupicola p. aequatorialis Taczanowski	Colombia	Carriker (1956)
C. stotzi	Querula purpurata	Peru, Brazil	Clayton & Price (1998); Johnson et al. (2002); <b>Present study</b>
C. tergalis	Pipreola arcuata	Venezuela	Carriker (1956)
	Pipreola a. aureopectus (Lafresnaye)	Colombia	Carriker (1956)
	Pipreola intermedia signata (Hellmayr)	Bolivia	Carriker (1956)

\* Locality registered but with an incorrect host-record association

\*\* Identified as 'Cotingacola sp.', re-examined in the present study

was infested with both C. stotzi and C. parmipapillae (syn. 'Cotingacola sp.' of Johnson et al., 2002). We found only simple infestations (one louse species per host) for both of these species of Cotingacola (see above for the material examined) from Q. purpurata collected during a 2007 expedition to Japurá, Amazonas, Brazil. Thus it is unclear how often these two louse taxa co-infest the same host individuals. One of these louse taxa, C. stotzi, is a host specialist, whereas the other, C. parmipapillae, is a host generalist. One possibility is that host specialisation may be driven by the coexistence of congeners on the same hosts. For example, Johnson et al. (2009) found that for dove wing lice (species of Columbicola Ewing, 1929), host generalists evolved from host specialists, and that in the presence of a congener (a potential competitor) there are many cases where one of a pair of coexisting species of these chewing lice evolved host generalisation. Johnson et al. (2011) found a similar pattern for dove body lice (family Goniodidae) in which host generalists evolved from host specialists, but they did not find a correlation between generalisation and the presence of potential competitors. Several morphological features of C. stotzi and C. parmipapillae suggest that competition may be driving both niche partitioning and variability in host-specificity. Firstly, C. parmipapillae has a stout body and a small posterior projection on the anterior dorsal head plate, which is relatively common in most head inhabiting lice (MPV, personal observation), whereas C. stotzi has a relatively larger and more slender body with a rounded posterior margin of the anterior dorsal head plate. Secondly, C. stotzi and C. parmipapillae differ in their colouration, with C. parmipapillae being more lightly pigmented and C. stotzi darkly pigmented. The plumage of the host, Q. purpurata, is black and thus the dark pigmentation of C. stotzi might be cryptic colouration to avoid host preening, whereas the lack of dark cryptic pigmentation in C. parmipapillae is consistent with this taxon inhabiting the head, one of the few regions of the body that the host cannot see.

Another example of the co-distributed *Cotingacola* spp. is from the host *P. arcuata*, which harbours one slender-bodied (*C. tergalis*) and one stout-bodied (*C. meridae*) species of this louse genus. The coexistence of host generalist and host specialist species of *Contingacola* with a potentially different host niche specialisation may be consistent with this hypothesis, i.e. that competition drives patterns of host-specificity

and coexistence in the group. Further studies of *Cotingacola* species are needed to confirm a relationship between these features, body morphology and colouration patterns, and host-specificity. Phylogenetic reconstructions and morphological analysis of additional *Cotingacola* taxa would enable further tests of this hypothesis.

Acknowledgements We thank Alexandre Aleixo (Museu Paraense Emílio Goeldi, Belém, Brazil), Shannon Hackett and John Bates (Field Museum of Natural History, Chicago, USA) for their support and assistance during fieldwork and/or the collection of the data presented herein. We also thank the Field Museum Insect Division, including Margaret Thayer, Daniel Summers and James Boone, for their advice and access to the Field Museum of Natural History collection, Floyd Shockley for access to and loan of type-specimens in the National Museum of Natural History collection, Dale Clayton and Sarah Bush for access to Cotingacola DNA voucher specimens held in the Price Institute of Phthirapteran Research, University of Utah and Petra Sierwald, who made her National Science Foundation -Partnerships for Enhancing Expertise in Taxonomy funded microscope available for our use. This work was supported in part by the Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil, with a postdoctoral fellowship 200453/ 2010-6 to MPV, the National Science Foundation DEB-0515672 and DEB-1120054 to JDW, and the Field Museum's Emerging Pathogens Project, funded by the Davee Foundation and the Dr Ralph and Marian Falk Medical Research Trust. DNA sequencing was carried out at the Field Museum's Pritzker Laboratory for Molecular Systematics and Evolution, which is operated with the support of the Pritzker Foundation.

# References

- Bueter, C., Weckstein, J. D., Johnson, K. P., Bates, J. M., & Gordon, C. E. (2009). Comparative phylogenetic histories of two louse genera found on *Catharus* thrushes and other birds. *Journal of Parasitology*, 95, 295–307.
- Carriker, M. A., Jr. (1956). Estudios sobre Mallophaga Neotropicales (XIV) (Piojos de las Cotingidae). *Revista* Academia Colombiana de Ciencias Exactas, Fisicas y Naturales, 9, 365–380.
- Carriker, M. A., Jr. (1963). New and little known Mallophaga from Venezuelan birds (Part II). *Memoria Sociedad de Ciencias Naturales La Salle*, 23, 5–42.
- Clayton, D. H., & Price, R. D. (1998). Taxonomic review of *Cotingacola* (Phthiraptera: Philopteridae) from the cotingas (Passeriformes: Tyrannidae), with descriptions of two new species. *Journal of Medical Entomology*, 35, 732–739.
- Dickinson, E. C. (2003). The Howard & Moore complete checklist of the birds of the world. (3rd Ed.) Princeton, NJ: Princeton University Press, 1056 pp.
- Johnson, K. P., Malenke, J. R., & Clayton, D. H. (2009). Competition promotes the evolution of host generalists in obligate parasites. *Proceedings of the Royal Society of London B*, 276, 3921–3926.

- Johnson, K. P., Weckstein, J. D., Bush, S. E., & Clayton, D. H. (2011). The evolution of host specificity in dove body lice. *Parasitology*, in press.
- Johnson, K. P., Weckstein, J. D., Witt, C. C., Faucett, R. C., & Moyle, R. G. (2002). The perils of using host relationships in parasite taxonomy: Phylogeny of the *Degeeriella* complex. *Molecular Phylogenetics and Evolution*, 23, 150–157.
- Palma, R. L. (1978). Slide mounting of lice: a detailed description of the Canada balsam technique. *New Zealand Entomologist*, 6, 432–436.
- Price, R. D., Hellenthal, R. A., & Palma, R. L. (2003). World checklist of chewing lice with host associations and keys to families and genera. In: Price, R. D., Hellenthal, R. A., Palma, R. L., Johnson, K. P., & Clayton, D. H. (Eds.) *The chewing lice: world checklist and biological overview*. Champaign, IL: Illinois Natural History Survey Special Publication, pp. 1–448.
- Price, R. D., & Weckstein, J. D. (2005). The genus Austrophilopterus Ewing (Phthiraptera: Philopteridae) from toucans, toucanets, and araçaris (Piciformes: Ramphastidae). Zootaxa, 918, 1–18.

- Price, R. D., & Weckstein, J. D. (2006). *Picicola* Clay and Meinertzhagen (Phthiraptera: Philopteridae) from jacamars and puffbirds (Piciformes: Galbulidae, Bucconidae), with descriptions of five new species. *Zootaxa*, 1367, 37–50.
- Swofford, D. L. (2003). PAUP\*: Phylogenetic analysis using parsimony (\*and other methods), version 4.0b10. Sunderland, MA: Sinauer.
- Valim, M. P., Teixeira, R. H. F., Amorim, M., & Serra-Freire, N. M. (2005). Malófagos (Phthiraptera) recolhidos de aves silvestres no Zoológico de São Paulo, SP, Brasil. *Revista Brasileira de Entomologia*, 49, 584–587.
- Valim, M. P., & Weckstein, J. D. (2011). Two new species of *Brueelia* Kéler, 1936 (Ischnocera, Philopteridae) parasitic on Neotropical trogons (Aves, Trogoniformes). *Zookeys*, 128, 1–13.
- Weckstein, J. D. (2004). Biogeography explains cophylogenetic patterns in toucan chewing lice. *Systematic Biology*, 53, 154–164.