A NEW GENUS AND SPECIES OF PHILOPTERIDAE (PHTHIRAPTERA: ISCHNOCERA) FROM THE TRUMPETERS (AVES: GRUIFORMES: PSOPHIIDAE)

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ABSTRACT: A new chewing louse genus and species belonging to the Philopteridae, namely, *Palmaellus inexpectatus* n. gen., n. sp., is described. The new genus is distinguished from the other ischnoceran genera hitherto described by its peculiar characters of the dorsal anterior head plate with 2 postero-lateral projections, pterothorax and abdomen with scarce chaetotaxy, male genitalia with simple mesomere and paramere lacking inner digitiform projection, and the genital region of female with postero-vulvar plates bearing setae. It is a parasite of the trumpeters, an avian family endemic to South America's Amazon Basin.

Currently, only 2 species of chewing lice, Psophiicola foedus (Nitzsch, 1866) and Eulaemobothrion gracile (Giebel, 1874), are known to parasitize the species of trumpeters (Psophia Linnaeus, 1758), members of the avian Psophiidae (Gruiformes), endemic to the Amazon Basin. These 2 louse species are considered as widespread and known to parasitize many species of Psophia (Price et al., 2003). Eulaemobothrion gracile is an amblyceran louse in the Laemobothriidae, whereas Psophiicola foedus, sometimes regarded as a Rallicola Johnston & Harrison, 1911 species, is associated with the ischnoceran philopterids. The Philopteridae is the most specious family within the insect order Phthiraptera and encompasses approximately 55% of the total ischnoceran chewing louse species described. The philopterids include >140 described genera ($\sim 46\%$ of the generic diversity within Phthiraptera), with an exceptional diversity of morphological variation and habitat specialization on different regions of the host body (Price et al., 2003; Mey, 2004). Most avian host species are parasitized by several species of philopterids, and often each of these philopterids specializes on a different region of the host body (Clay, 1949; Johnson and Clayton, 2003).

Most recently described Phthiraptera genera from Philopteridae were erected from well-established generic complexes of species already characterized and described, e.g., the *Philopterus*complex (Mey, 2004). However, 2 recently described genera, *Caracaricola* (Mey and Gonzalez-Acuña, 2000) and *Corcorides* (Mey, 2004), were proposed based completely on newly discovered distinct morphotypes of lice. The new genus proposed here also is based on the discovery of a completely distinct morphotype within Philopteridae.

The new genus herein described belongs to the *Rallicola*complex due the presence of 2 long and stout tubercle-bearing setae on the ventro-lateral edge of segment IX. The *Rallicola*complex is currently composed of 2 genera, *Rallicola* Johnston & Harrison, 1911 and *Pessoaiella* Guimarães, 1940 (sensu Clay, 1953). *Rallicola* is currently divided into 3 subgenera, including the nominals *Aptericola* Harrison, 1915 and *Huiacola* Mey, 1990. However, there are 6 additional synonyms accepted by Clay (1953) and Price et al. (2003) for *Rallicola*, including *Corvicola* Carriker, 1949; *Epipicus* Carriker, 1949; *Furnaricola* Carriker, 1944; *Oncophorus* Piaget, 1880 (nec Rudow, 1870); *Parricola* Harrison, 1915; and *Psophiicola* Eichler, 1982. Here, we follow the classification of the *Rallicola*-complex proposed by Price and

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Emerson (1987). We suggest that *Osculotes* Kéler, 1939 is also a member of this complex because it has the defining feature of the *Rallicola*-complex, i.e., 2 long and stout tubercle-bearing setae on the ventro-lateral edge of segment IX and because our molecular analysis is also consistent with this hypothesis (see below). Further studies including both morphological and molecular data are needed to better resolve the generic limits within the heterogeneous *Rallicola* s.l. However, the morphological and molecular data presented herein are sufficient to distinguish the new genus from those included in this complex, as well as from other philopterid genera.

MATERIAL AND METHODS

We collected the specimens for this study by using the ethyl acetate fumigation technique as described in Bueter et al. (2009); additional specimens were obtained by ruffling bird skins. All of the specimens were mounted on slides following the procedures of Palma (1978). We used the nomenclature for cephalic setae as proposed by Clay (1951) as modified by Mey (1994). The somatic body parts measured and their abbreviations are as follows: preocular length (POL), preocular width (POW), temple width (TW), head length (HL), dorso-anterior plate length at midline (DPLM), dorso-anterior plate length at lateral (DPLL), dorso-anterior plate width (DPW), prothorax length (PL), prothorax width (PW), metathorax length (ML), metathorax width (MW), abdomen width at segment V (AWV), paramera length (PAL), genitalia width at basal apodema (GW), genitalia length (GL), and total length (TL). All measurements are given in millimeters. Host names for Psophidae follow Oppenheimer and Silveira (2009) and Ribas et al. (2011).

The molecular methods used by us are the same as those described by Bueter et al. (2009) and modified by Valim and Weckstein (2011) to extract DNA and sequence a 379-base pair (bp) fragment of the mitochondrial cytochrome oxidase I (COI) gene and 347 bp of the nuclear elongation factor 1-alpha (EF1 α) gene. We sequenced these genes from samples of the new genus collected from 2 distinct host species (Psophia dextralis and Psophia napensis) to assess and document their genetic distinctiveness and the phylogenetic relationship with other genera of Philopteridae. DNA sequences, voucher numbers, and locality data for sequences that we generated for this study are deposited in GenBank (JQ717179-194) and include data from the 2 specimens of the new genus and 1 Aptericola gadowi s.l. ex Aptervx sp.; Rallicola (Parricola) irediparrae Price & Emerson, 1987 ex Irediparra gallinacean (Temminck, 1828); Pessoaiella absita (Kellogg, 1910) ex Opisthocomus hoazin (Statius Müller, 1776); Psophiicola foedus ex Psophia leucoptera Spix, 1825; Rallicola (Rallicola) advenus (Kellogg, 1896) ex Fulica americana Gmelin, 1879; and Rallicola (Rallicola) kelloggi Emerson, 1957 ex Rallus limicola Vieillot, 1819. We constructed a 102 taxon generic level Philopteridae dataset by aligning our COI and EF1a DNA sequences with Philopteridae and outgroup (3 lice from the ischnoceran trichodectids, goniodids, and heptapsogasterids) COI and $\text{EF1}\alpha$ sequences published by Cruickshank et al. (2001) (AF320353-56, AF320360-62, AF320365, AF320368, AF320371-72, AF320378-81, AF320384, AF320386-88, AF320393-95, AF320399-400, AF320407, AF320410, AF320427, AF320432, AF320435, AF320437, AF320442-43, AF320448-49, AF320451, AF320454-55, AF320457, AF320461, AF320464-66, AF320468-69, AF320476-77); Johnson, Adams, et al. (2001) (AF348658-60, AF348665, AF348854); Johnson, Moyle et al. (2001)

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(AF320445, AF348867, AF348871, AF356706, AF356708, AF356713, AF356717, AF356719-20, AF356730, AF356737, AF356744); Johnson, Weckstein et al. (2002) (AF320434, AF320459-60, AF348666, AF444846, AF444849-57, AF444859-61, AF444863, AF444866, AF444868, AF444872, AF444875, AF447184, AF447187, AF447190, AF447192, AF447194-98, AF447203, AF447207, AF447210); Johnson, Adams, et al. (2002) (AY149391, AY149400, AY149404-06, AY149430, AY149434); Johnson, Williams et al. (2002) (AF414725, AF414764); Johnson and Whiting (2002) (AF385003); Johnson et al. (2003) (AF348859, AF444876, AF497800, AF545669, AF545671-75, AF545677, AF545679, AF545681, AF545683-85, AF545690, AF545692, AF545695-97, AF545701-02, AF545704, AF545711-12, AF545719, AF545729-30, AF545734, AF545737-40, AF545743, AF545746, AF545748-50, AF545752, AF545755, AF545758-61, AF545765-70, AF545775-76, AF545778, AF545780, AF545782-84, AF545790, AF545792, AF545796, AF545799, AF545802-04); Clayton et al. 2003 (PNAS) (AF278641); and Smith et al. (2004) (AF396590, AY314808, AY314810, AY314814, AY314817-19, AY314824, AY314826, AY314828, AY314833, AY314836-38, AY314840, AY314844).

We used PAUP* (version 4.0b10; Swofford, 2003) to calculate uncorrected *p*-distances between the 2 new genus COI sequences from 2 different host species and to conduct a maximum parsimony (MP) heuristic search and bootstrap analysis of the combined 102 taxon matrix of COI and EF1 α data. For the MP heuristic search, we used tree bisection and reconnection branch swapping, stepwise addition, and 100 random addition replicates. For the MP bootstrap analysis, we performed 1,000 bootstrap replicates with 10 random additions per replicate. We also used PAUP* to calculate tree length (TL), consistency index (CI), and retention index (RI) for the most parsimonious trees.

For the maximum likelihood (ML) search, we determined the best fit model for the analysis by using jModelTest (Guindon and Gascuel, 2003; Posada, 2008) and conducted the ML search and bootstrap analysis by using Garli v2.0 (Zwickl, 2006; http://garli.googlecode.com), which estimates model parameters that best fit the data during the analysis. We ran 5 independent search replicates by using the model TVM+I+G, each with a different starting point, and we considered the tree with the best likelihood score the best phylogenetic hypothesis. We performed 100 bootstrap replicates with the same model to assess statistical support for nodes in the phylogeny.

Holotypes of the new species are deposited in the Museu de Zoologia, University of São Paulo, São Paulo, Brazil (MZUSP), and paratypes and additional material are deposited in MZUSP and the Field Museum of Natural History, Chicago, Illinois (FMNH). DNA voucher specimens for *P. foedus* (Rafo.1.3.2011.4), *P. inexpectatus* (Gennov.Psvi. 1.3.2011.8 and Gennov.Pscr. 1.3.2011.10), *R. (R.) advenus* (Raad.1.3.2011.11), *R. (R.) kelloggi* (Rake.1.3.2011.2), *and A. gadowi* s.l. (Rasp.Apsp.3.3.2011.4) are deposited in FMNH. For material collected in 2007, host specimen vouchers are deposited in the Museu Paraense Emílio Goeldi (MPEG); they are indicated by field numbers and, where available, specimen numbers. All of the bird skins examined for lice are deposited in the FMNH.

DESCRIPTIONS

Palmaellus Valim and Weckstein, gen. nov.

Diagnosis: Anterior dorsal head plate with 2 posterior pointed projections, 1 on each side of plate (Fig. 1). Plate unique compared with all other philopterid genera. Most philopterid genera that specialize on living on host head possess only 1 medial posterior projection, or less often, with straight posterior margin. *Ibidoecus* Cummings, 1916 (not in *Rallicola*-complex), with 2 similar posterior projections, 1 on each side of anterior dorsal head plate; anterior dorsal head plate split medially into 2, whereas plate distinctly entire in new species (Fig. 1). Furthermore, characters such as body size, body chaetotaxy, and male genitalia completely differentiate *Ibidoecus* and *Palmaellus*.

Both sexes: Very small and stout specimens. Head as long as wide (Fig. 1). Hyaline margin of forehead moderately developed and enclosing anterior dorsal head plate at anterior and lateral sides. Anterior dorsal head plate entire and square-like, without traces of striations; with straight anterior margin and with 2 conspicuous posterior projections, 1 on each side of plate. Anterior ventral head plate indistinct. Dorsal preantennal suture not dividing marginal carina, marginal carina short and reaching at most anterior ventral seta 3. Ventral carina longer than marginal carina

reaching anterior setae 2 and ventral submarginal setae 2. Anterior dorsal seta (a.d.s) long in males (~0.06) and almost indiscernible, but present in females; set on soft tegument of dorsal preantennal suture. Anterior setae 1–3 (a.s1, a.s2, a.s3) short (\sim 0.02); anterior seta 2 (a.s.2) longer (\sim 0.05– 0.10); anterior ventral setae 1 and 3 (a.v.s1, a.v.s3) sub-equal in length (~0.06–0.08). Ventral sub-marginal seta 1 (v.sm.s1) slightly longer (~0.06) than v.sm.s2 (~0.04). Conus distinct. Antennae filiform and essentially similar in both sexes. Eyes large, ocular seta (o.s) medium long (~ 0.03 -0.04); preocular (po.s) and marginal temporal-1 (m.t.s1) setae shorter (~0.01–0.02); marginal temporal 2, 4, and 5 (m.t.s2, m.t.s4, m.t.s5) setae slightly longer ($\sim 0.03-0.04$); marginal temporal setae 3 (m.t.s3) very long (~0.22–0.29). Dorsal sub-marginal seta (d.sm.s) and prenodal seta (pn.s) $3 \times$ longer (~0.03) than preconal (pc.s) and preantennal (pa.s) setae (<0.01), mandibular setae (md.s) medium long (~0.04). Postemporal (pt.s) and dorsal occipital (d.o.s) setae short (\sim 0.01). See Figure 1 for detailed chaetotaxy.

Prothorax entire, with slightly divergent sides and 1 postero-lateral seta (~0.10 long) on each side, plus 3 short anterior dorsal setae on each side (not pronotal marginal anterior setae, sensu Mey, 1994). Pterothorax not divided, each side with 1 short lateral seta, 1 long lateral trichobothrium (~0.12), 1 medium long sublateral (~0.04–0.07), 2 very long (~0.22–0.27), 1 sublateral and other posterior, and 1 medium long seta at posterior margin, on each side. Sternal plates very indistinct, more discernible in some specimens on mesosternum. One pair of long meso- and metasternal setae very long and 1 claw much longer than other claw.

Abdomen oval, with tergites II–VIII medially divided. Tergal plates as long and narrow triangles in shape, lacking posterior projection on postero-lateral margins. One row of medium long ($\sim 0.05-0.06$) setae on each tergite II–VIII, tergite II without anterior pair of setae. Post-spiracular setae very short (~ 0.02) and present only on segment VII, without tracks of associated sensillus. Sternites without central plates, except on VI in males; II–VI with row of medium long setae. Terminal segment rounded.

Male: Genital opening set termino-dorsal. Genitalia distinctive, with long and slender paramera almost straight to slightly curved inward, with 1 submarginal sensillus and 1 terminal with seta barely discernible; long and simple mesosoma occupying 2/3 of paramera length, with superficial rugosity in its posterior end represented by vestigial sensillae and 2 submarginal sensillae with distinct setae.

Female: Vulva convex, slightly concave medially. Vulvar margin with medium long setae and subterminal spiniform setae, with tubercle on ventro-lateral edge of segment IX bearing 2 long (rarely 3 on 1 side), stout setae. Below vulvar margin, postero-vulvar plates bearing long setae on each side.

Nymphs: Unknown.

Taxonomic summary

Site of infection: Based on the body shape, probably the head and neck feathers.

Location and hosts: South America, trumpeters (Gruiformes: Psophii-dae).

Etymology: Named in honor to Ricardo L. Palma who is currently one of the leading authorities on the bird lice of the world and has made important contributions to our knowledge of both the taxonomy and evolutionary biology of this group. His efforts, friendship, and support have helped to motivate and encourage M.P.V. to endure in his studies of this group of insects. The suffix *-ellus* (L.), masculine, means small, and is used here in an affective way and because of the small body dimensions of this new genus. Gender masculine.

Palmaellus inexpectatus Valim and Weckstein, gen. nov., sp. nov. (Figs. 1–7)

Male: Habitus as in Figure 2. Features and chaetotaxy of head and thorax as indicated under generic description. Abdominal tergal central setae for holotype: II–VIII, 2, but V, 3. Variation on males examined: II–III, 4 and IV–V, 3 setae (2 specimens); and II–IV, 4; V, 3. Postspiracular setae short and present only on VII (Fig. 3). Pleural setae: II, 0; III–V, 2 (both medium long, 1 ventral and another lateral); VI–VII, 3, (1 medium long ventral and 2 very long lateral); VIII, 2 (both very long). Inner most pleural setae on segment VIII distinctly modified as a trichobothrium and set on plate (Fig. 3), not included in pleural setal account. Tergal setae on



FIGURES 1-4. *Palmaellus inexpectatus* gen. nov. et sp. nov. male. (1) Head, dorso-ventral views. (2) Habitus, dorso-ventral views. (3) Terminalia, dorso-ventral views. (4) Genitalia, dorsal view.



FIGURES 5-7. Palmaellus inexpectatus gen. nov. et sp. nov. female. (5) Habitus, dorso-ventral views. (6) Terminalia, dorso-ventral views. (7) Genital region, ventral view.



0.2 substitutions/site

FIGURE 8. Maximum likelihood phylogram of the *Rallicola*-complex clade taken from the larger 102 taxon philopterid DNA dataset. Numbers above nodes (in bold) are maximum likelihood boostrap support, whereas those below the lines (in regular type) are maximum parsimony bootstrap support. Only support values >50 are shown on the trees. Arrow indicates the *Rallicola*-complex clade.

tergite IX+X (Fig. 3): 1 long and 1 short on dorsal surface, with tergal plate surrounding their bases; 1 long and 2 short setae on lateral of segment IX+X, 1 of latter set latero-dorsally. Abdominal sterno-central setae: II–V, 2; VI, 3–4. Genitalia as illustrated in Figure 4. Measurements (n = 4): POL, 0.10–0.11; POW, 0.22–0.25; TW, 0.34–0.37; HL, 0.32–0.36; DPLM, 0.06–0.08; DPLL, 0.09–0.11; DPW, 0.10–0.11; PL, 0.13–0.14; PW, 0.23–0.26; ML, 0.09–0.10; MW, 0.29–0.33; AWV, 0.33–0.35; PAL, 0.08–0.09; GW, 0.03–0.04; GL, 0.18–0.20; and TL, 0.84–0.90.

Female: Habitus as in Figure 5. General aspects similar to male, but larger and with some dimorphic characters. Abdominal tergal central setae: II-VI, 4 (rarely 2 or 3 in 1 of segments); VII-VIII, 2. Rarely II-III, 4; IV, VIII, 2. Tergal setae on tergite IX+X (Fig. 6): 1 long and 1 short on dorsal surface, with tergal plate surrounding their bases; 1 short setae and 2 long on lateral of segment IX+X, 1 of latter set latero-dorsally, on each side. Post-spiracular as in males (Fig. 6), in 1 specimen present also on VI only on one side. Pleural setae: II, 0; III-IV, 3 (2 of them medium long ventral and 1 small lateral; rarely only lateral present); V-VIII, 3-4, (1-2 medium long ventral and 2 very long lateral). Ventral medium long setae of pleural region set in distinct tubercules (Figs. 5, 6). Inner most pleural setae on segment VIII also modified to trichobothrium as in males (Fig. 6). Abdominal sterno-central setae: II, 2; III-VI, 4. Very indistinct rounded lateral plates present ventrally on segments III-VII. Vulvar region as illustrated in Figure 7. Genital region with 2 small setae on subgenital plate and 2 longer ones off plate (Figs. 6, 7), with 2-3 small setae postero-lateral on each side. Vulvar margin with 29-40 medium long (~0.03) setae in 2 indistinct rows, plus 3-4 (rarely 2 in one side) subterminal spiniform setae on each side. Postero-vulvar plates with 9-12 longer ($\sim 0.05-0.06$) setae on each side. Presence of 2 (rarely 3) tubercle bearing setae (~0.06) on ventro-lateral edge of segment IX, between vulvar margin and postero-vulvar plates, on each side. Measurements (n = 8): POL, 0.11-0.13; POW, 0.24-0.26; TW, 0.37-0.40; HL, 0.35-0.36; DPLM, 0.07; DPLL, 0.10-0.11; DPW, 0.11-0.12; PL, 0.13-0.15; PW, 0.26-0.28; ML, 0.10-0.12; MW, 0.35-0.37; AWV, 0.44-0.49; and TL, 0.99 - 1.10.

Taxonomic summary

Type host: Psophia dextralis Conover, 1934 (Psophiidae), brown-winged trumpeter.

Other hosts: Psophia crepitans Linnaeus, 1758; gray-winged trumpeter; Psophia napensis P. L. Sclater & Salvin; and 1873, gray-winged trumpeter napensis.

Site of infection: Probably the feathers of head and neck.

Type locality: Plot of the Brazilian Program for Biodiversity Research (PPBIO) (01°57′S, 51°36′W), Floresta Nacional (FLONA) do Caxiuanã, Portel, Pará, Brazil.

Prevalence and mean intensity: Prevalence 50% and intensity 3.0 on *P. dextralis*; and prevalence 100% and intensity 6.0 on *P. napensis.*

Other localities: Colombia and Surinam.

Specimens deposited: \circ holotype, ex Psophia dextralis, PPBIO 107 MPEG 61659, BRAZIL: Pará, Portel, FLONA do Caxiuanã, Plot PPBIO (01°57'S, 51°36'W), 17.I.2007, J. D. Weckstein col. Paratypes: 2 φ (1 female DNA voucher, Gennov.Psvi.1.3.2011.8), same data as holotype. Non-type material. 6 φ (1 female DNA voucher, Gennov.Pscr.1.3.2011.10), ex *P. napensis*, JAP 553 MPEG 62396, BRAZIL: Amazonas, Município Japurá, Rio Acanauí, 25.VII.2007, J. D. Weckstein col. 1 \circ , ex *P. crepitans*, FMNH422924, SURINAM: Nickerie, Kayser Gebergte Airstrip, Zuid River, 23.VI.2011, M. P. Valim col. (skin collected in 10.XI.1960, H. A. Beatty col.). 2σ , ex. *P. napensis*, FMNH419487, COLOMBIA: Meta, Serrania de la Macarena, Rio Guapaya (330 m), 23.VI.2011, J. D. Weckstein col. (skin collected in 7.III.1957, K. von Sneidern col.).

Repository: Male holotype and 1 female paratype taken off *P. dextralis* are deposited in MZUSP, 1 female paratype (DNA voucher) off *P. dextralis* in FMNH; 1 male and 3 females off *P. napensis* in MZUSP, 1 male off *P. crepitans*, and 1 male and 3 females (one DNA voucher) off *P. napensis* in FMNH.

Etymology: The species name (an adjective in masculine form) refers to the unexpected nature of the discovery of a new species of chewing lice on the well-studied trumpeter hosts.

DISCUSSION

Morphological data indicate that *Palmaellus* gen. nov. is a novel morphotype, different from all other described philopterid genera. For example, the uniquely shaped anterior dorsal head plate with 2 posterior pointed projections (Fig. 1) is not shared by any other described philopterid genera. Genetic data are also consistent with this unique morphology (Fig. 8). Uncorrected pairwise *p*-distances calculated from the COI and EF1 α sequences between the *Palmaellus* gen. nov. specimens and all other philopterid genera in our molecular data set show substantial differences, averaging 29.9% (range, 16.9–35.7%) for COI and 12.6% (7.2–18.2%) for EF1 α .

Palmaellus gen. nov. is provisionally monotypic. However, DNA sequences between the Palmaellus inexpectatus gen. nov. et sp. nov. collected from the different host taxa (P. dextralis: DNA voucher Gennov.Psvi.1.3.2011.8 and P. napensis: DNA voucher Gennov.Pscr.1.3.2011.10) and different geographic regions, differ at both COI and EF1a by 15.3 and 1.4% uncorrected p-distance, respectively. Although these are moderate genetic differences, and sometimes enough for specific differentiation (e.g., Valim and Weckstein, 2011), there are no obvious morphological features that differ between these specimens and thus we are not certain whether the populations of Palmaellus gen. nov. found on these hosts are evolving on their own separate evolutionary trajectories. One possibility is that the small series of specimens available to us is not sufficient for discerning either discrete or quantitative morphological differences. In the future, a larger series of specimens for a deep morphological comparison and additional population level genetic data may clarify the species limits in this group. Thus, it is possible that more than 1 species level taxon is involved within this new genus.

The new genus proposed exhibits several morphological characters that are consistent with it belonging to the Rallicolacomplex. Phylogenetic analysis of COI and EF1 a DNA sequences also support this hypothesis (Fig. 8). In all 5 MP trees (TL = 7629, CI = 0.107, RI = 0.390), the 2 Palmaellus inexpectatus gen. nov. et sp. nov. specimens are placed within a clade of Rallicolacomplex members that all share the presence of 2 long and stout tubercle bearing setae on ventro-lateral edge of segment IX. These include Aptericola, Furnaricola, Rallicola (Rallicola), Rallicola (Parricola), Pessoaiella, Psophiicola, and Osculotes. The ML tree topology is similar and contains the same clade with slightly different internal relationships. Both MP and ML bootstrapping indicate strong statistical support for the node uniting the 2 P. inexpectatus specimens. Neither analysis indicates strong statistical support for the monophyly of the Rallicola-complex including P. inexpectatus gen. nov. et sp. nov. However, if this topology is correct, then the Rallicola-complex contains 4 Amazonian endemic lice, Osculotes and Pessoaiella, and Psophiicola and Palmaellus gen. nov., which are found on Hoatzin (O. hoazin) and trumpeters (Psophia spp.), which are both Amazonian endemic bird lineages.

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