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A review of the louse genus *Tinamotaecola* (Insecta: Phthiraptera: Philopteridae *sensu lato*), with description of a new species

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Abstract

We studied a collection of lice from Argentina, Brazil, Paraguay and Chile containing all four known species and one new species (described herein) in the genus *Tinamotaecola*, parasites of birds of the families Cariamidae and Tinamidae. We also (1) describe previously unknown second and third nymphal instars of two *Tinamotaecola* species, (2) discuss hosts and geographical ranges for all *Tinamotaecola* species, and (3) speculate on possible macroevolutionary events that may explain the current distribution of these lice on their respective avian hosts.

Key words: *Tinamotaecola*, Philopteridae, Phthiraptera, chewing lice, new species, nymphal instars, hosts, Cariamidae, Tinamidae, *Tinamotis*, *Eudromia*, *Cariama*, *Chunga*, Argentina, Bolivia, Brazil, Paraguay, Chile

Introduction

The chewing louse genus *Tinamotaecola* was described by Carriker (1944) together with his new species *Tinamotaecola andinae* parasitic on the puna tinamou, *Tinamotis pentlandii* Vigors, 1837, from Bolivia. Subsequently, Ward (1957: 350) pointed out that, in addition to the type species of the genus, at least two other *Tinamotaecola* species parasitic on members of the Tinamidae remained undescribed, one from *Eudromia elegans* I. Geoffroy Saint-Hilaire, 1832 and *E. formosa* (Lillo, 1905), and another from *Tinamotis ingoufi* Oustalet, 1890. Cicchino & Castro (1998: 110) cited at least three additional undescribed species of *Tinamotaecola*. Finally, Hellenthal *et al*. (2002) reviewed *Tinamotaecola* and described three new species, one parasitic on *Eudromia elegans*, and two from *Cariama cristata* (Linnaeus, 1758). They also recorded *T. andinae* from *Chunga burmeisteri* (Hartlaub, 1860), but were suspicious of this host-louse association (Hellenthal *et al*. 2002: 137).

Considering that published records of *Tinamotaecola* from Argentina, Brazil, Chile and Paraguay are scarce, our aims are to present data from additional specimens collected in these countries, representing all known species of this genus, and to describe a new species from Argentina, bringing the total number of species to five. We also discuss the known geographical ranges of all *Tinamotaecola* host and louse species, and describe the hitherto unknown second and third nymphal instars of two *Tinamotaecola* species.

Material and methods

Lice were slide-mounted following conventional procedures, including staining some specimens with yellowish Eosin to enhance the colour of the sclerites (Castro & Cicchino 1978). Drawings were made using a camera lucida attached to a Wild m-20 microscope. All measurements were taken with a calibrated eyepiece, from mounted

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specimens minimally affected by curatorial procedures, and these are expressed in millimeters and identified by the following abbreviations: HL head length; POW maximum width of the forehead taken at level of the base of the coni; OW maximum width of the head; PL length of prothorax; PW maximum width of prothorax; PTL length of the pterothorax; PTW maximum width of the pterothorax; AL length of the abdomen; AW maximum width of the abdomen taken at level of segment V; TL total body length; GL maximum length of the genitalia; GW maximum width of the genitalia.

Identification of the nymphal instars: cephalic setae essentially as in the illustrations (Figs 6–7, 10–11), with inner margin of the marginal carina (*mc*) smooth. Postero-marginal pterothoracic setae distinctive, 5+5 in N III and 4+4 in N II. Abdomen without discrete sternal plates in N II or N III. First instars (N I) and eggs were not available from any of the species. According to the typology of development of the preantennal region proposed by Mey (1994), this genus should be included within the "Modus A", and from the tergal/paratergal development of the abdomen within the "Gruppe IIIa".

Descriptions were made in a comparative form, adding comments to the description of the morphologically closest species. Nomenclature of cephalic carinae and setae follows those employed by Clay (1951). The geographical distributions of the louse species (Fig. 20) were made from the material studied herein, and from specimens recorded in the literature with precise locality.

We qualify the family name Philopteridae as "*sensu lato*" because we believe it includes more than one family but, until that subject is thoroughly researched and published, we prefer to continue using that family name in its broadest sense.

Repository institutions: Specimens from Argentina, including types, in the collection of Museo de La Plata, La Plata, Provincia Buenos Aires, Argentina (MLP), and duplicates, when available, in the collection of the senior author (ACC), Mar del Plata, Provincia Buenos Aires. Brazilian specimens were deposited in the collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil. Chilean specimens were deposited in the collection of Facultad de Ciencias Veterinarias, Universidad de Concepción, Chillán, Chile (UNCC).

Systematics

Phthiraptera Haeckel, 1896

Ischnocera Kellogg, 1896

Philopteridae Burmeister, 1838 *sensu lato*

Tinamotaecola Carriker 1944

Tinamotaecola Carriker 1944: 86, figs 1d, e. Type species: *T. andinae* Carriker, 1944 (by original designation).
Tinamotaecola; Hellenthal *et al.* 2002: 136.

Diagnosis. A genus belonging to the "*Degeeriella*-complex" of Clay (1958), identifiable by the following adult features:

Head: longer than wide (Figs 2, 3), forehead rounded and circumfasciate with conspicuous marginal carina uninterrupted in the middle, and with the edge of the ventral preantennal suture thickened on each side, becoming a continuation of the ventral carina and fused distally with the complete marginal carina; dorsal preantennal suture (*dprs*) developed, reaching the bases of the very long anterior dorsal setae (*ads*); a pair of dorsal submarginal setae (*dsms*) displaced backwards and included within the dorsal preantennal suture; prenodal setae (*pns*) medium long; antennae similar in both sexes; ocular seta (*os*) very long and placed dorsally; preocular seta (*pos*) medium long and placed sub-laterally; marginal temporal setae (*ts*) 2, 4 and 5 very short, 1 and 3 very long.

Thorax: as in Fig. 1. Pronotum with single, long, lateroposterior postspiracular seta. Metanotum without anterior setae, but with 9–13 marginal posterior setae, including one small spiniform seta and one long trichoid seta each side. A median elongate and pigmented sclerite (*mes*) extending from mid-metanotum to abdominal segment II (Fig. 4). Meso and metasternal plates with 1–2 setae.

Abdomen: as in Fig. 1. Terga without anterior setae except for an antero-medial pair on tergite II; tergites

II–VIII divided at midline; IX–XI fused and with a median anterior notch. A very long postspiracular seta on each side of terga III–VIII. Without well-defined sternal plates. Male genitalia as in Figs 14–16: basal plate longer than wide and ellipsoidal, parameres long and sharply tapered, mesosomal complex with characteristic shape, genital sac elongated with small tubercles (Fig. 17), penis slender and unpigmented. Female subgenital plate roughly rounded, with two irregular rows of setae: one formed by medium fine marginal setae, another of short spiniform submarginal setae (Fig. 18).

Etymology. Not specified by Carriker (1944), but *Tinamotaecola* is formed by the prefix *Tinamotae-* (= of or from *Tinamotis*) and the Latin suffix *-cola* (= to inhabit).

Remark. Hellenthal *et al*. (2002) divided the four species of this genus into two well defined species-groups, a criterion followed here. The species groups are characterized as follows:

andinae species-group

Moderately pigmented species with the following features: a) a narrow marginal carina in both sexes; b) no more than 10 metanotal setae in males; c) female subgenital plate with less than 41 marginal plus submarginal setae. Three species are included in this group, all parasitic on hosts belonging to the *Tinamotis-Eudromia* clade of the Nothurinae (Tinamidae) (see Bertelli & Chiappe 2005). All three species have been collected in Argentina, one (*Tinamotaecola elegans*) has been recorded from Paraguay, and only one (*Tinamotaecola andinae*) is known from Chile. However, considering the that their hosts are geographically distributed in Chile (Fig. 20) and that these hosts have not been particularly well studied (Martínez & González 2004), it is likely that the remaining two *Tinamotaecola* species will be found in that country.

Tinamotaecola andinae Carriker, 1944
(Figs 1–2, 14)

Tinamotaecola andinae Carriker, 1944: 87, figs 1d, e.
Tinamotaecola andinae; Hellenthal *et al.* 2002: 137, figs 2, 5, 9.
Tinamotaecola andinae; Price *et al.* 2003: 244.

Type host. *Tinamotis pentlandii* Vigors, 1837, the puna tinamou.

Other host. *Chunga burmeisteri* (Hartlaub, 1860), the black-legged seriema (*fide* Hellenthal *et al*. 2002: 137), but see Remarks below.

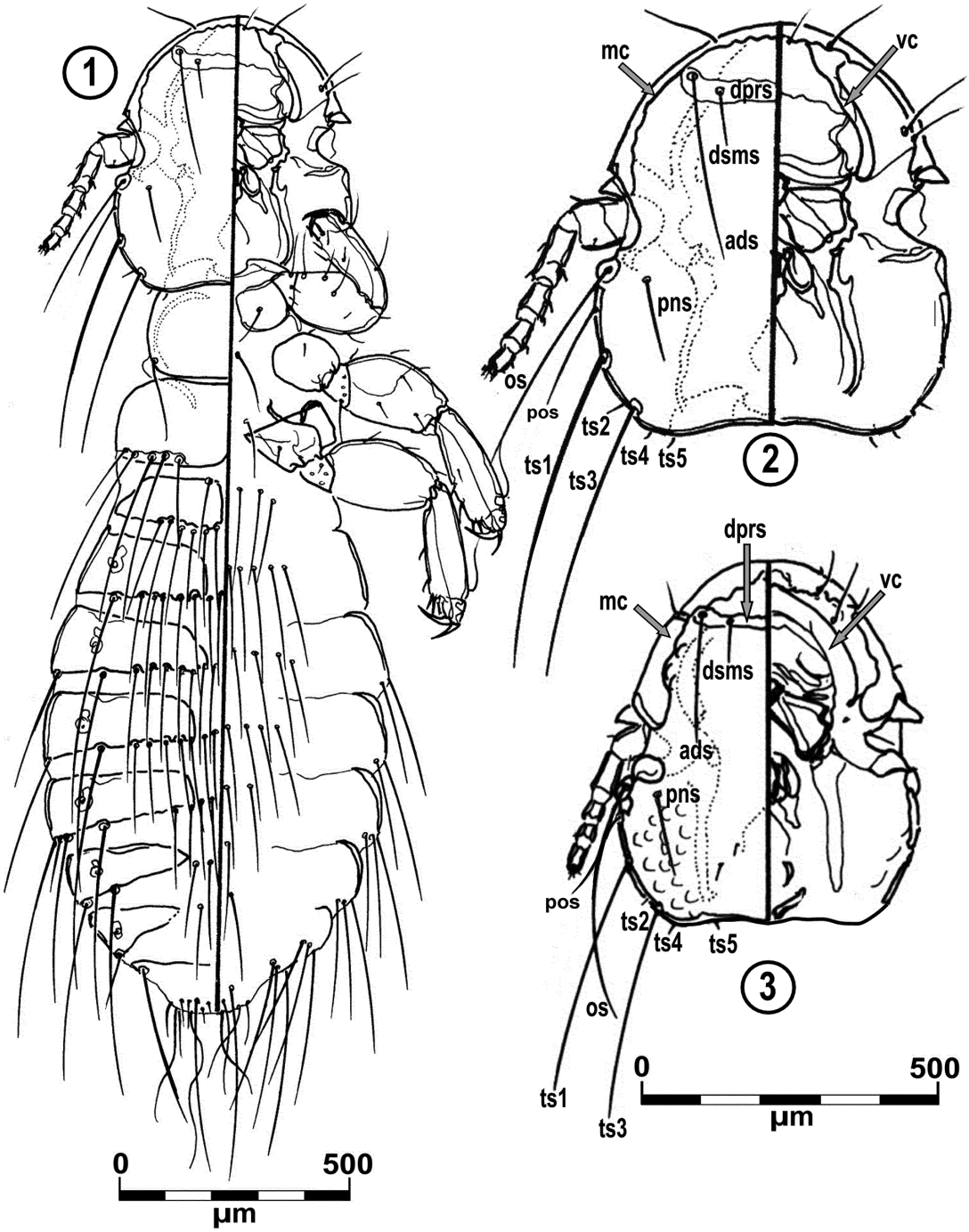
Diagnosis. Amember of the *andinae* species-group, distinguishable from the remaining two species by larger body measurements, and a tendency to have a larger number of sternal setae in both sexes. Also males have more tergal setae and larger genitalia (GL 0.430–0.460 against 0.373–0.422 in *T. elegans*) (Fig. 14).

Male: General habitus as in Fig. 1. Chaetotaxy: metanotum with 10 postero-marginal setae. Paratergal setae: segments II–III 0, IV–V 2, VI–VIII 3. Tergal setae: II 7–11, III 10–12, IV 9–13, V 8–12, VI 7, VII 4–6, VIII 2–4. Sternal setae: II 6–7, III 7–10, IV 7–9, V 6–8, VI 4–7, VII 2. Genitalia as in Fig. 14. Measurements: HL 0.565–0.610; POW 0.430–0.440; OW 0.465–0.543; PL 0.157–0.225; PW 0.301–0.381; PTL 0.211–0.270; PTW 0.362–0.505; AL 0.900–1.257; AW 0.650–0.680; GL 0.430–0.490; GW 0.125–0.146; TL 1.850–2.276.

Female: Metanotal and paratergal setae as for male. Tergal setae: II 4, III 8, IV 8 V 9, VI 9. Sternal setae: II 6, III 8, IV–V 10, VI 9, VII 6. Measurements: HL 0.630–0.670; POW 0.475–0.497; OW 0.540–0.563; PL 0.188–0.247; PW 0.338–0.350; PTL 0.227–0.285; PTW 0.457–0.490; AL 1.356–1.460; AW 0.810–0.819; TL 2.347–2.466.

Specimens examined. Ex *Tinamotis pentlandii*: 2♂, 1♀, Distrito Susques, Provincia Jujuy, Argentina, 8 Oct. 1986, J. Fernández (MLP, ACC). 1♂, Visviri, Provincia Tarapacá, Primera Región, Chile, 23 Sep. 2004, D.G. González-Acuña (UNCC). 1♂, 2♀, Potosí [19°35'S, 65°45'W, 4020m], Bolivia, 23 Jan. 1938, M.A. Carriker Jr (MZUSP #677).

Remarks. Dimensions and chaetotaxy of the specimens examined fall well within the ranges given by Hellenthal *et al.* (2002: 137). This species has been described from Bolivia by Carriker (1944: 87), and subsequently cited for Perú, Paraguay and Chile by Hellenthal *et al.* (2002: 137). Its probable presence in Argentina was pointed out by Cicchino & Castro (1998: 121) and is confirmed here. Hellenthal *et al.* (2002: 137)



FIGURES 1–3. *Tinamotaecola andinae*: **1**, male; **2**, details and chaetotaxy of head. *Tinamotaecola wardi*: **3**, details and chaetotaxy of head. Abbreviations: mc, marginal carina; vc, ventral carina; dprs, dorsal preantennal suture; *ads*, anterior dorsal seta; *dsms*, dorsal submarginal seta; *pns*, postnodal seta; *os*, ocular seta; *pos*, preocular seta; *ts* (1–5), marginal temporal seta.

also examined specimens from *Chunga burmeisteri* from Brazil and Paraguay, suspecting that the host-louse association was incorrect. Considering that the geographical ranges of *Tinamotis pentlandii* and *C. burmeisteri* do not overlap, i.e. these hosts are allopatric (Fig. 20), the probability of a natural host-switch by *Tinamotaecola andinae* from *T. pentlandii* onto *Chunga* is extremely low. Misidentification of the hosts or mislabelling of the samples examined by Hellenthal *et al.* (2002) are more likely explanations for that unexpected host-louse association (see also remarks under *T. wardi* below). All known locality records of *Tinamotaecola andinae* from *T. pentlandii* are shown in Fig. 20.

***Tinamotaecola elegans* Hellenthal, Price & Timm, 2002**
(Figs 4–7)

Tinamotaecola n. sp.; Cicchino & Castro 1998: 121.
Tinamotaecola elegans Hellenthal *et al.* 2002: 138, figs 6, 10.
Tinamotaecola elegans; Price *et al.* 2003: 244.

Type host. *Eudromia elegans elegans* I. Geoffroy Saint-Hilaire, 1832, the elegant crested-tinamou.

Other hosts. *Eudromia elegans albida* (Wetmore, 1921); *Eudromia elegans intermedia* (Dabbene & Lillo, 1913); *Eudromia elegans patagonica* Conover, 1950; *Eudromia formosa* (Lillo, 1905).

Diagnosis. Amember of the *andinae* species-group and very close to *T. andinae*, but both sexes of *T. elegans* can be distinguished by their smaller dimensions and fewer sternal setae, and by males with a tendency to have fewer tergal setae.

Male: General habitus as in Fig. 4. Mesosternum and metasternum with 2 setae each. Metanotum with 10 posterior setae. Paratergal setae: segments II–III 0, IV 2, V 1–2, VI 3, VII 2–3, VIII 3. Tergal setae: II 6–8, III 9–12, IV–V 8–11, VI 6–7, VII 4–6, VIII 2–5. Sternal setae: II 2, III 4–6, IV 5–7, V 5–6, VI 4–6, VII 3–4. Male genitalia much as for *T. andinae*, but somewhat smaller. Body measurements: HL 0.515–0.564, POW 0.397–0.441, OW 0.441–0.490, PL 0.156–0.235, PW 0.289–0.343, PTL 0.172–0.194, PTW 0.416–0.471, AL 1.020–1.157, AW 0.578–0.707, GL 0.373–0.422, GW 0.100–0.127, TL 1.854–2.049.

Female: General habitus as in Fig. 5. Mesosternum and metasternum with 2 setae each (less frequently 1). Metanotum with 9–11 posterior setae. Paratergal setae: segments II–III 0, IV 2–3, V 2, VI 3–4, VII–VIII 3. Tergal setae: II 7–9, III 8–13, IV 8–14, V 8–13, VI 7–12, VII 7–11, VIII 3–6. Sternal setae: II 2, III 6–8, IV 6–10, V 6–10, VI 5–9, VII 6–9. Vulva with 39–45 setae. Body measurements: HL 0.480–0.576, POW 0.430–0.470, OW 0.440–0.515, PL 0.144–0.250, PW 0.282–0.330, PTL 0.181–0.212, PTW 0.350–0.466, AL 1.220–1.350, AW 0.540–0.787, TL 1.880–2.227.

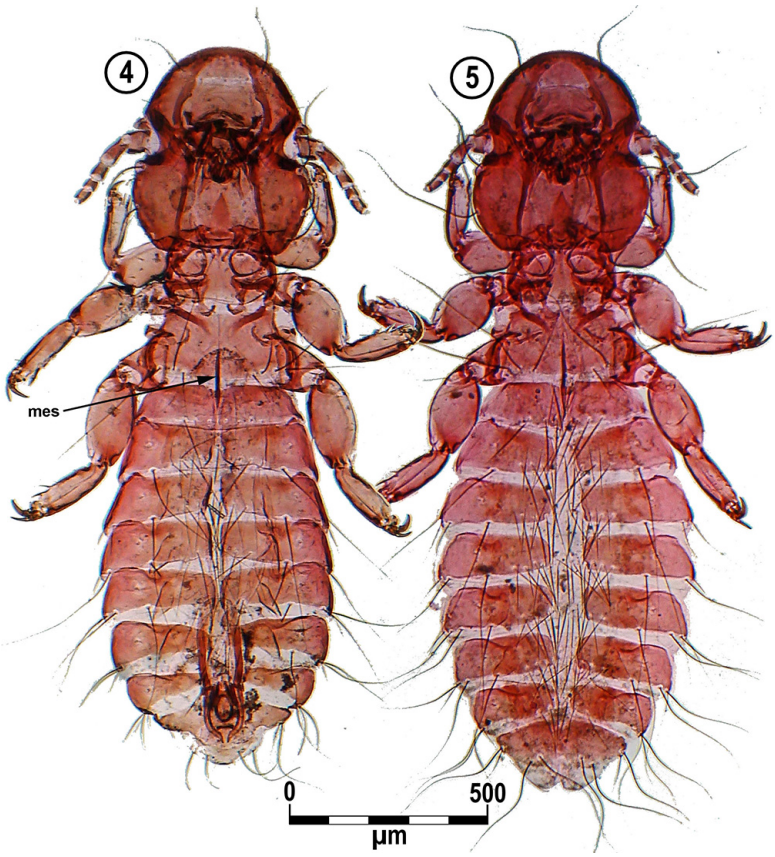
Nymph III: General habitus as in Fig. 6. Mesosternum and metasternum with 2 setae each. Metanotum with 9–10 (4–5+5) posterior setae. Paratergal setae: segment II 0, III 0–1, IV–V 2, VI–VIII 3. Tergal setae: II 6–7, III 9, IV 7–8, V 6–7, VI 5–7, VII 3–5, VIII 3–4. Sternal setae: II 2, III 4, IV 4–5, V 4–6, VI 5–6, VII–VIII 2. Body measurements: HL 0.471–0.510. POW 0.363–0.412, OW 0.417–0.461, PL 0.137–0.211, PW 0.265–0.270, PTL 0.176–0.211, PTW 0.333–0.422, AL 0.745–0.902, AW 0.460–0.608, TL 1.485–1.696.

Nymph II: General habitus as in Fig. 7. Mesosternum and metasternum with 2 setae each. Metanotum with 8 (4+4) posterior setae. Paratergal setae: segments II–III 0, IV–V 1, VI–VII 2, VIII 3. Tergal setae: II–VI 4, VII–VIII 2. Sternal setae: II–V 2, VI 4, VII–VIII 2. Body measurements: HL 0.412, POW 0.324, OW 0.363, PL 0.176, PW 0.225, PTL 0.186, PTW 0.314, AL 0.657, AW 0.392, TL 1.284.

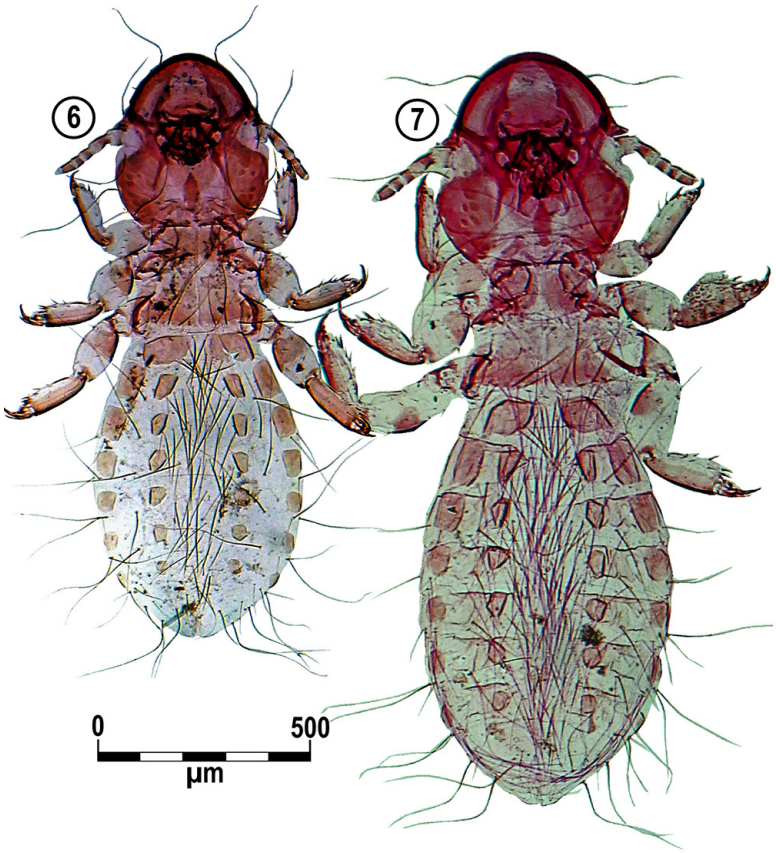
Specimens examined. Ex *Eudromia elegans elegans*: 3♂, 1♀, Distrito General Alvarado, Otamendi, Provincia Buenos Aires, Argentina, 14 Sep. 2002, A.C. Cicchino (ACC); 1♂ same data (MZUSP #2082); 1♂, 1♀, Laguna Chasicó, Partido Villarino, Provincia Buenos Aires, Argentina, Feb. 1967, A.C. Cicchino (MZUSP #2084–85).

Ex *E. elegans patagonica*: 1♂, Faro Punta Delgada, Península Valdés, Distrito Viedma, Provincia Chubut, Argentina, 18 Jan. 1972, A.C. Cicchino (ACC); 4♂, 8♀, 8 N III, 1 N II, Lago Colhué Huapi, Distrito Sarmiento, Provincia Chubut, Argentina, 10 Nov. 1989, A.C. Cicchino (ACC); 1♀, same data (MZUSP #2083); 2♂, 1♀, Península Valdés, Distrito Viedma, Provincia Chubut, Argentina, 15 Feb. 2007, D.G. González-Acuña (UNCC and ACC).

Remarks. Ranges of male chaetotaxy in specimens examined by us fall within the upper limit or slightly exceed the ranges given by Hellenthal *et al.* (2002), especially for tergites III–VI. A similar pattern applies to tergites III–VIII on females. Body measurements of both sexes are also around the upper limit of the ranges given by Hellenthal *et al.* (2002). However, in the remaining features, our material agrees with those described by Hellenthal *et al.* (2002). *Tinamotaecola elegans* was originally described from Argentinean specimens of three subspecies of *E. elegans*, and also from *Eudromia formosa* from both Argentina and Paraguay (Hellenthal *et al.* 2002: 139). Also, Cicchino & Castro (1998: 121) had previously noted the presence of this undescribed species from Argentina. To date, this *Tinamotaecola* species is confined to the two species of *Eudromia*. All known records of *T. elegans* from *E. elegans* are shown in Fig. 20.



FIGURES 4–5. *Tinamotaecola elegans*: **4**, male; **5**, female. Abbreviation: *mes*, median elongate sclerite.



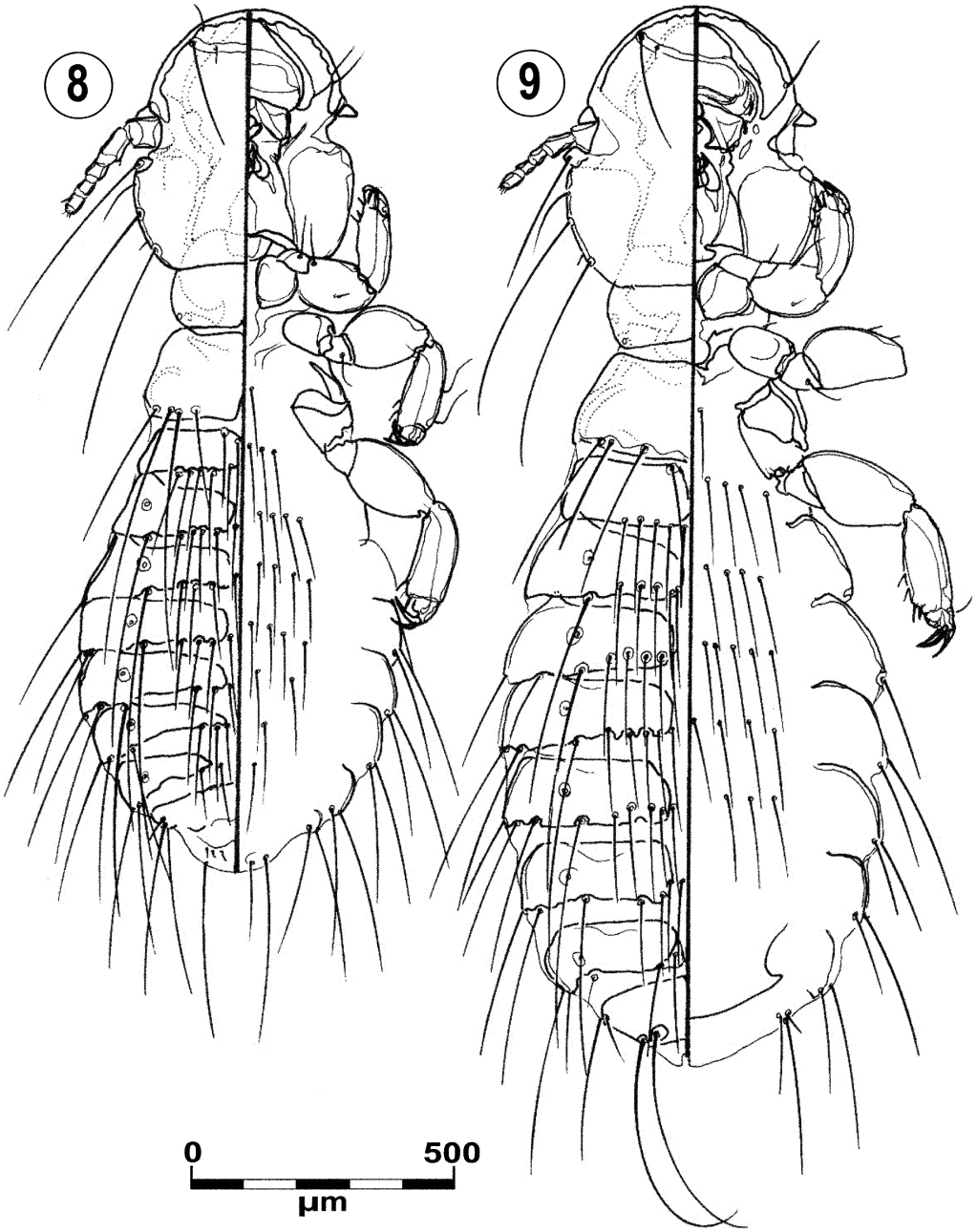
FIGURES 6–7. *Tinamotaecola elegans*: **6**, second nymphal instar (N II); **7**, third nymphal instar (N III).

***Tinamotaecola nanus* new species**
(Figs 8–11, 15)

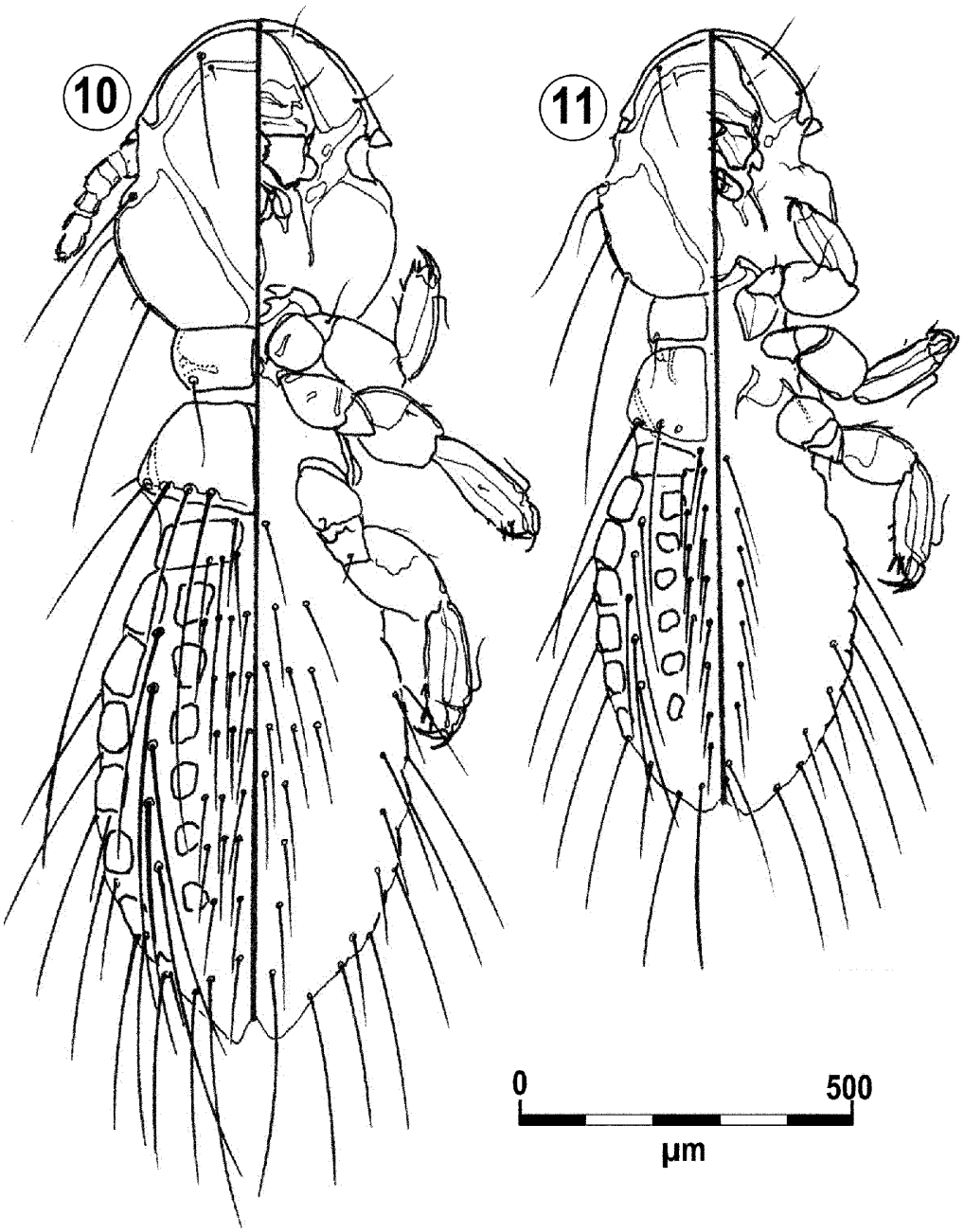
Tinamotaecola n. sp.; Ward 1957: 350.
Tinamotaecola n. sp.; Cicchino & Castro 1998: 121.

Type host. *Tinamotis ingoufi* Oustalet, 1890, the Patagonian tinamou.

Diagnosis. A member of the *andinae* species-group, distinguishable from the other two species in the group by its much smaller body measurements of the two sexes. Males are also distinguishable from *T. elegans* by having a greater number of sternal setae. Female chaetotaxy is very similar to that of *T. elegans*, but the vulvar margin has fewer setae (30 against 39–45).



FIGURES 8–9. *Tinamotaecola nanus*: **8**, male; **9**, female.



FIGURES 10–11. *Tinamotaecola nanus*: **10**, third nymphal instar (N III); **11,** second nymphal instar (N II)**.**

Male: General habitus as in Fig. 8. Metanotum with 10 setae. Paratergal setae: segments II–III 0, IV 1, V 2, VI–VIII 3. Tergal setae: II 9, III 12, IV 10, V 9, VI 6, VII 4, VIII 2. Sternal setae: II 6, III 8, IV 8, V 8, VI 4. Genitalia similar to those of *T. andinae*, but consistently much smaller (Fig. 15). Body measurements: HL 0.479, POW 0.379, OW 0.421, PL 0.189, PW 0.284, PTL 0.184, PTW 0.389, AL 0.842, AW 0.611, GL 0.374, GW 0.124, TL 1.642.

Female: General habitus as in Fig. 9. Metanotum with 10 setae. Paratergal setae: segments II–III 0, IV 1, V–VIII 2. Tergal setae: II 9, III 11, IV 12, V 10, VI 10, VIII 6, VIII 4. Sternal setae: II 6, III 8, IV 10, V–VI 8. Vulva with 11–12 long and 7 short spiniform setae on each side (total 36–38). Body measurements: HL 0.556, POW 0.433, OW 0.500, PL 0.211, PW 0.322, PTL 0.222, PTW 0.478, AL 1.211, AW 0.778, TL 2.133.

Nymph III: General habitus as in Fig. 10. Metanotum with 10 (5+5) posterior setae. Body measurements: HL 0.467, POW 0.360, OW 0.427, PL 0.173, PW 0.133, PTL 0.173, PTW 0.360, AL 0.653, AW 0.467, TL 1.533.

Nymph II: General habitus as in Fig. 11. Metanotum with 8 (4+4) posterior setae. Body measurements: HL 0.400, POW 0.307, OW 0.347, PL 0.133, PW 0.107, PTL 0.160, PTW 0.380, AL 0.547, AW 0.400, TL 1.160.

Etymology. the species epithet "*nanus*" (Latin = dwarf) refers to the small size of this species, being the smallest among all known *Tinamotaecola* species.

Specimens examined. Ex *Tinamotis ingoufi*: Holotype ♂, 1♀ paratype, 3 N II, 2 N III, Tellier, Departamento Deseado, Provincia Santa Cruz, Argentina, 20 Sep. 1962 (MLP).

Remarks. This species was mentioned by Ward (1957: 350) as a possible new species and Cicchino & Castro (1998: 121) noted the presence of this undescribed taxon in Argentina. Yet, Hellenthal *et al.* (2002) did not mention this undescribed taxon. The type locality, superimposed on the host geographical range is shown in Fig. 20.

zyskowskii species-group

Strongly pigmented species, characterized by possessing: a) head with a thick wide marginal carina, with its internal margin rugulose in both sexes; b) male metanotum with 11–13 setae; and c) female subgenital plate with more than 45 marginal and submarginal setae. Two species are included, parasitic on the two species of Cariamidae (Gruiformes or Cariamiformes, see Fain *et al*. 2007; Mayr 2002; Cracraft *et al*. 2004). One species (*T. wardi*) has been recorded from Argentina, Brazil and Paraguay, the other (*T. zyskowskii*) from Argentina and Paraguay (Fig. 20).

Tinamotaecola zyskowskii Hellenthal, Price & Timm, 2002
(Figs 12, 16–17)

Tinamotaecola n. sp.; Cicchino & Castro 1998: 122.
Tinamotaecola zyskowskii Hellenthal *et al.* 2002: 139, figs 1, 3, 7.
Tinamotaecola zyskowskii; Price *et al.* 2003: 244.

Type host. *Cariama cristata* (Linnaeus, 1758), the red-legged seriema.

Male: General habitus as in Fig. 12. Metanotum with 11–12 posterior setae. Tergal setae: segment II 6, III–V 10, VI 7, VII 8, VIII 4. Paratergal setae: II–III 0, IV 1, V–VI 2, VII–VIII 3. Genitalia as in Fig. 16, with small but conspicuous tubercles on the internal sac (Fig. 17). Body measurements: HL 0.673, POW 0.481, OW 0.558, PL 0.240, PW 0.365, PTL 0.260, PTW 0.519, AL 1.250, AW 0.750, GL 0.510, GW 0.140, TL 2.308.

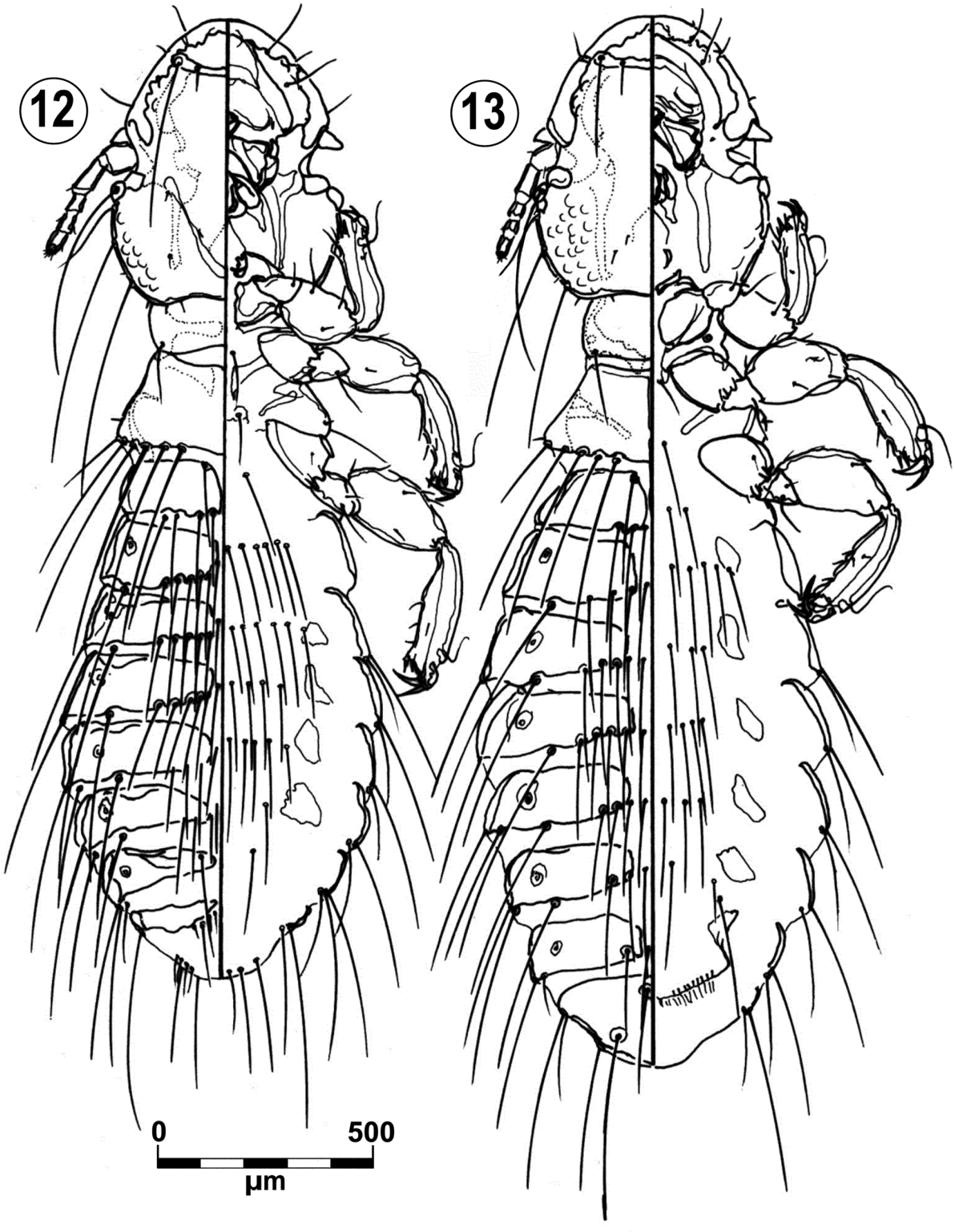
Female: no female specimen was available for this study.

Remarks. The original description was based on specimens from Paraguay. Cicchino & Castro (1998: 122) noted that this species was found in Argentina, but at the time it was undescribed. All known records of *T. zyskowskii* on *Cariama cristata* are shown in Fig. 20.

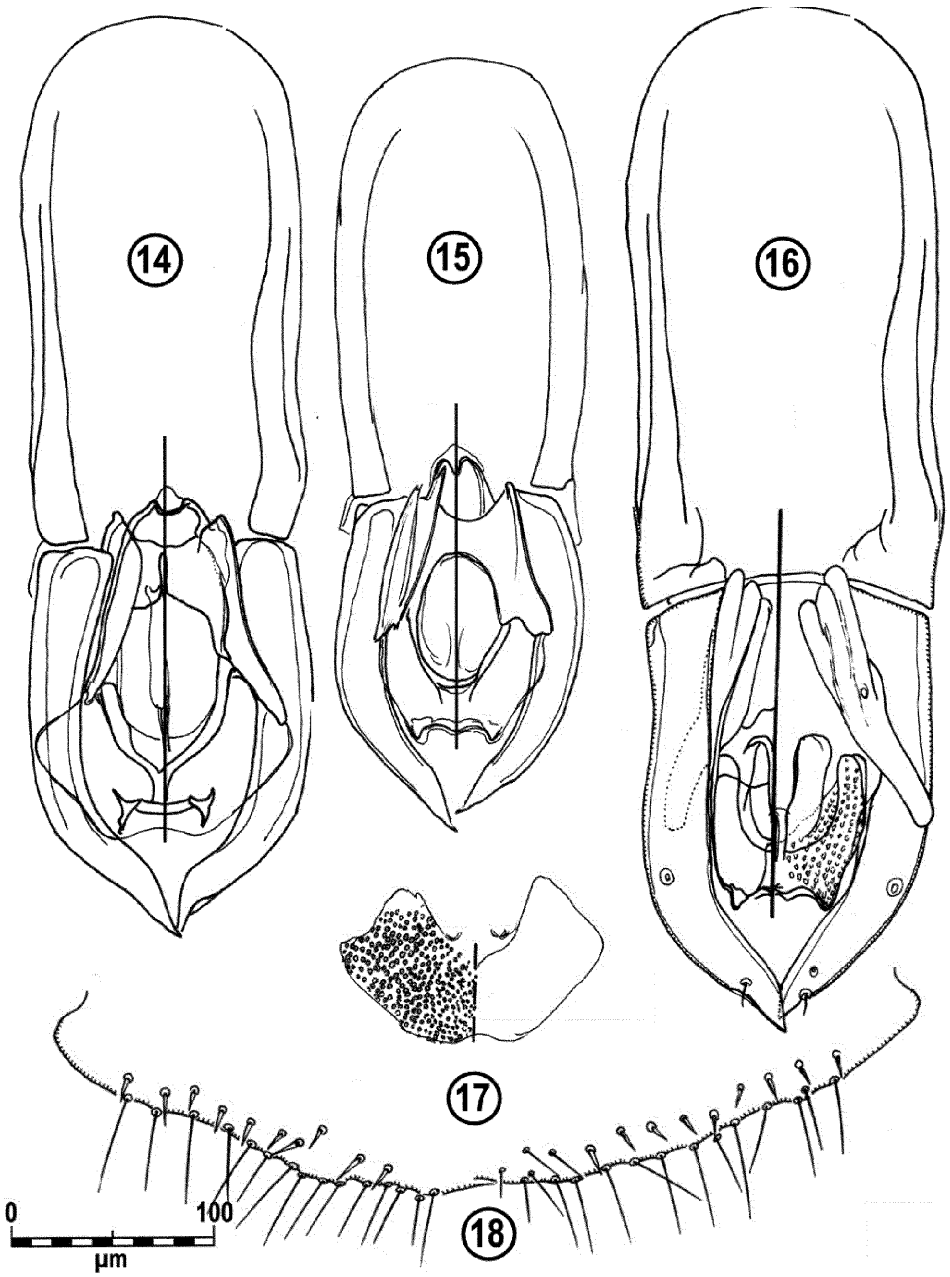
Specimens examined. Ex *Cariama cristata*: 2♂, Departamento Trancas, Provincia Tucumán, Argentina, 28 Mar. 1959 (MLP, ACC).

Tinamotaecola wardi Hellenthal, Price & Timm, 2002
(Figs 3, 13, 18)

Tinamotaecola wardi Hellenthal *et al.* 2002: 140, figs 4, 8.
Tinamotaecola wardi; Price *et al.* 2003: 244.
Tinamotaecola wardi; Marietto-Gonçalves *et al.* 2012: 208.



FIGURES 12–13. *Tinamotaecola zyskowskii*: **12**, male. *Tinamotaecola wardi*: **13**, female.



FIGURES 14–18. Male genitalia: **14**, *Tinamotaecola andinae*; **15**, *T. nanus*; **16**, *T. zyskowskii*. Male internal genital sac: **17**, *Tinamotaecola zyskowskii*. Female vulva: **18**, *Tinamotaecola wardi*.

Type host. *Cariama cristata* (Linnaeus, 1758), the red-legged seriema

Other host. *Chunga burmeisteri* (Hartlaub, 1860), the black-legged seriema (see Remarks below).

Male: No specimen of this sex was available from Argentina or Chile for this study. However, we examined two males from *Chunga burmeisteri* from Paraguay and two males from *Cariama cristata* from Brazil, which agree well with measurements given by Hellenthal *et al*. (2002: 140). Body measurements: HL 0.618–0.636, POW 0.474–0.492, OW 0.559–0.561, PL 0.158–0.214, PW 0.364–0.370, PTL 0.246–0.258, PTW 0.536–0.545, AL 1.311–1.349, AW 0.765–0.794, GL 0.493–0.547, GW 0.141–0.151, TL 2.281–2.390.

Female: General habitus as in Fig. 13. Head as in Fig. 3. Metanotum with 10 posterior setae. Tergocentral setae: segment II 6, VII–V 10, VI 7, VII 8, VIII 4. Sternal setae: II 4, III 10, IV–VI 8, VII 4. Vulva with 15–17 long and 9–10 spiniform setae on each side (total 48–54) (Fig. 18). Body measurements: HL 0.654–0.696, POW 0.495–0.526, OW 0.538–0.609, PL 0.183–0.229, PW 0.337–0.401, PTL 0.221–0.268, PTW 0.462–0.621, AL 1.413–1.581, AW 0.808–0.929, TL 2.471–2.695

Specimens examined. Ex *Chunga burmeisteri*: 1♀, Rosario de la Frontera, Provincia Salta, Argentina, 20

Nov. 1904 (MLP); 2♂, Benjamín Aceval, Departamento Presidente Hayes, Paraguay, no date, F. Schade coll. (ACC).

Ex *Cariama cristata*: 2♂, 2♀ (topotypes from the type series, not originally designated), Franco da Rocha (23°20'S, 46°43'W), 723m, State of São Paulo, Brazil, Jul. 1949, M. Peña coll. (MZUSP #1629–30); 1♂, 2♀, Botucatu, State of São Paulo, Brazil, 17 Aug. 2005, G.A. Marietto-Gonçalves coll. (MZUSP #2407–08); 3♂, 2♀, Blumenau, State of Santa Catarina, Brazil, 2001, J.C. Souza Jr. coll. (MZUSP #2888–89).

Remarks. *Tinamotaecola wardi* was originally described from specimens collected on *Cariama cristata* in Brazil. However, other louse samples from *C. cristata* collected in Argentina and Paraguay are *T. zyskowskii*. Based on the material available of *Tinamotaecola wardi* from *Chunga burmeisteri*, we believe that this bird is probably its regular host in northern Argentina and Paraguay. This scenario is similar to that of *Bothriometopus macrocnemis* (Burmeister, 1838) (Ischnocera, Philopteridae *sensu lato*), a louse species that regularly parasitizes *Anhima cornuta* (Linnaeus, 1766) (Anseriformes, Anhimidae), but which has also been recorded on *Chauna torquata* (Oken, 1816) in some Brazilian localities. However, *Chauna torquata* is the regular host for *B. simillimus* (Giebel, 1874) (see Cicchino & Mey 2007: 53). We speculate that dispersal or recent host-switching of *T. wardi* from *Chunga burmeisteri* to *Cariama cristata*, or vice-versa, may have occurred, primarily in regions where both species of Cariamidae are or were sympatric, with a later spread of these hosts over other areas bearing the newly acquired louse species (see Johnson *et al.* 2003; Paterson *et al.* 1999; Brooks & Ferrao 2005; Hoberg & Brooks 2008). All known records of *T. wardi* from its two host species are shown in Fig. 20.

Host distribution of *Tinamotaecola* species

Considering that only the phylogenies of seriemas (Cariamiformes) (e.g. Fain & Houde 2004; Fain *et al.* 2007, Ericson *et al.* 2007) and tinamous (Tinamiformes) (e.g. Bertelli *et al.* 2002; Bertelli & Porzecansky 2004; Bertelli & Chiappe 2005) are reasonably resolved, but not the phylogeny of *Tinamotaecola*, we adopt the "narrative approach" of Brooks (1981) in an attempt to explain the distribution of species of this genus on hosts belonging to two exclusively Neotropical bird orders (Fig. 19). The two extant seriemas carry two related *Tinamotaecola* species belonging to the *zyskowskii* species-group, and the other three louse species – the *andinae* species-group – are parasitic solely on species of the *Tinamotis-Eudromia* clade of the Nothurinae (see Bertelli & Chiappe 2005). This unexpected and apparently anomalous distribution of lice on hosts of two phylogenetically unrelated bird orders that have undergone most of their cladogenetic events in arid and dry areas, may be explained by three macroevolutionary events: 1) "host switching" at an early stage in their cladogenesis; 2) subsequent cospeciation within the *Cariama-Chunga* and *Tinamotis-Eudromia* clades; and 3) "inertia" (Paterson *et al.* 2003) or "failure to speciate" (Clayton *et al.* 2003; Johnson *et al.* 2003) within the *Eudromia* clade, resulting in the host-louse associations (Fig. 19) and geographical distributions (Fig. 20) known today.

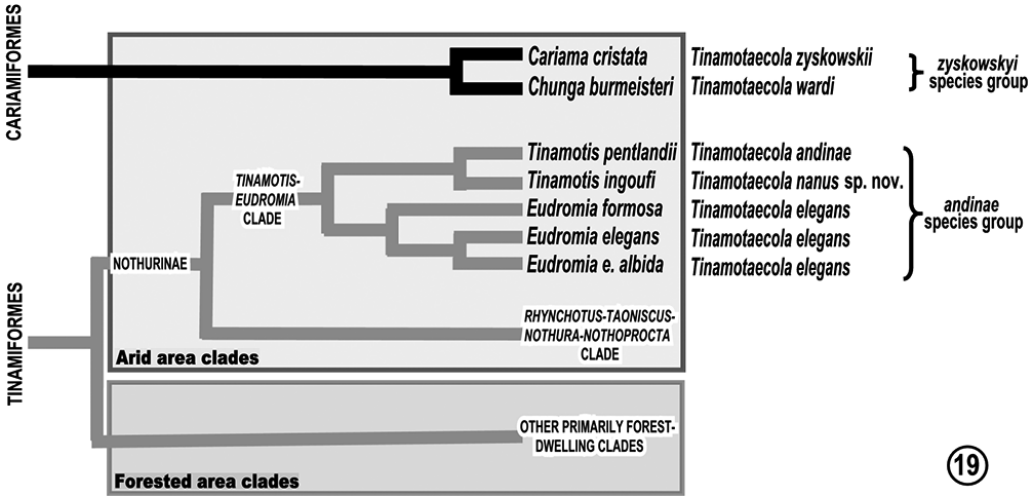


FIGURE 19. Pictorial representation to explain our hypothesis for the present day distribution of all *Tinamotaecola* species on Cariamidae and Tinamidae. The simplified cladogram for Tinamidae has been modified from Bertelli & Porzecansky (2004). See additional explanations in the text.

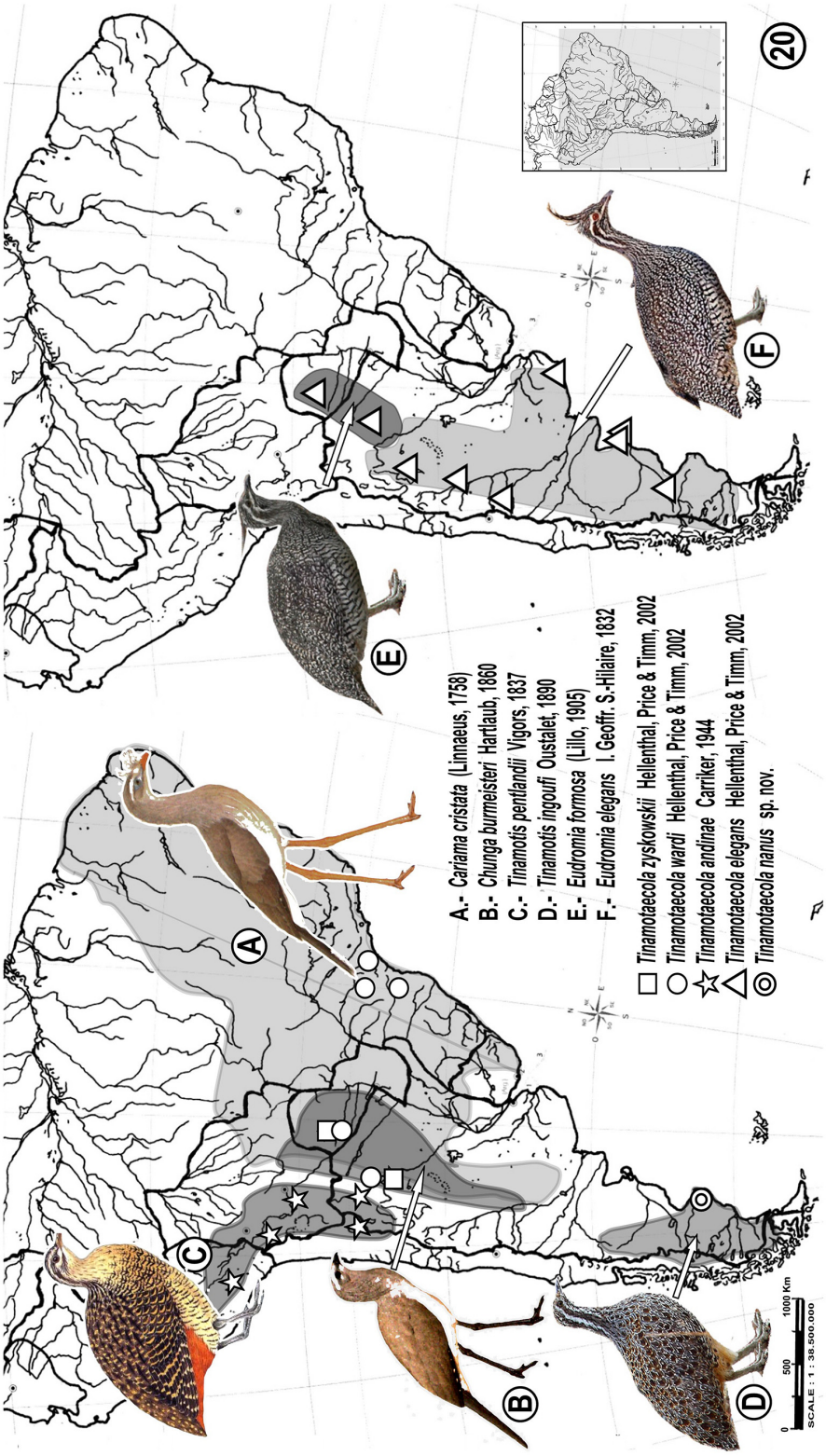


FIGURE 20. Geographical ranges of *Cariama cristata*, *Chunga burmeisteri* (Cariamidae), *Tinamotis* spp. and *Eudromia* spp. (Tinamiformes), showing sites where species of *Tinamotaecola* were collected from them.

The relationships between hosts and their parasites are primarily of ecological nature (Hennig 1950). The fossil evidence as well as the present-day distribution of Cariamiformes (Fain *et al*. 2007, Noriega *et al*. 2009) and the *Tinamotis-Eudromia* clade of the Tinamiformes (Bertelli *et al.* 2002, Bertelli & Chiappe 2005) were and still are

largely sympatric in large areas of open arid or semi-arid regions of southern South America. Members of the Tinamiformes as a whole are hosts to all but two species of the Heptapsogasteridae (193 spp.) and three out of five *Tinamotaecola* species, clustered in the morphological well-defined *andinae* species-group. The two extant species of seriemas are hosts to the two species of *Heinrothiella* Eichler, 1942 (Heptapsogasteridae), and the two species of *Tinamotaecola* included in the clearly defined *zyskowskii* species-group. Thus, we hypothesize that within this ecological scenario a primary host-switch of two louse clades (*Tinamotaecola* and *Heinrothiella*) occurred, probably from the *Tinamotis-Eudromia* clade onto the cariamiform clade. Subsequent cospeciation may have occurred within both clades, resulting in two species of *Tinamotaecola* (the *zyskowskii* species-group), and two species of *Heinrothiella* on the Cariamidae. Also, cospeciation may have been the process which gave rise to the three species of *Tinamotaecola* (the *andinae* species-group), plus three species in two undescribed genera of Heptapsogasteridae (cited as *Heptapsogaster* by Ward 1957: 350) from the *Tinamotis-Eudromia* clade of the Tinamidae. Once these ecological macroevolutionary events – together with other microevolutionary events (see Paterson *et al.* 2003)—are better known, the unusual present-day distribution of these unique seriema-tinamou louse genera may be better understood.

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