# FEATHER MITES OF THE GENUS *PROTEROTHRIX* GAUD (ASTIGMATA: PROCTOPHYLLODIDAE) FROM PARROTBILLS (PASSERIFORMES: PARADOXORNITHIDAE) IN CHINA

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ABSTRACT: Three new species of the feather mite genus *Proterothrix* Gaud, 1968 (Proctophyllodidae: Pterodectinae) are reported from parrotbills (Passeriformes: Paradoxornithidae) in China. We describe *Proterothrix paradoxornis* n. sp. from *Paradoxornis* webbianus (type host) and *Par. alphonsianus*, *P. longicaula* n. sp. from *Par. gularis*, and *P. sarahbushae* n. sp. from *Par. verreauxi* (type host) and *Par. alphonsianus*. These are the first records of mites of the Pterodectinae from the Paradoxornithidae. Within *Proterothrix*, the new species constitutes a distinct complex, characterized by the presence of a long, whip-like aedeagus and spindle-shaped setae e on tarsi I in males.

The diversity of feather mites (Acari: Astigmata: Analgoidea, Pterolichoidea) on their avian hosts has been moderately well surveyed for some non-passerine orders such as the parrots, Psittaciformes (e.g., Dabert et al., 2008); however, many lineages within the most species-rich order, the Passeriformes, remain almost unexplored. Among these are the parrotbills, an enigmatic group of 3 genera (the monospecific Conostoma and Panurus, and Paradoxornis with 19 species) that have been placed variously among the crows (Corvidae), babblers (Timaliidae), or as their own family Paradoxornithidae (Robson, 2007). Only 1 species, the geographically widespread bearded parrotbill Panurus biarmicus (Linnaeus), has been well explored for feather mites (e.g., Cerný, 1978, 1990); however, recent molecular data indicate that Panurus is unrelated to the other 2 genera of parrotbills (Alström et al., 2006; Yeung et al., 2006). The remaining species can be divided into 3 clades (Yeung et al., 2006), none of which has been surveyed for mites. A single named species of feather mite has been reported from the great parrotbill Conostoma aemodium Hodgson (Bonnet, 1924), whereas only undescribed species of Proctophyllodes (Proctophyllodidae), Trouessartia (Trouessartiidae), and Mesalges (Psoroptoididae) have been reported from 1 of the 19 species of Paradoxornis, the vinous-throated parrotbill P. webbianus (Gould) (Atyeo, 1973; Young, 1999). Here, we describe 3 new feather mite species of the genus Proterothrix from several Paradoxornis species that represent all 3 clades identified by Yeung et al. (2006).

Within the Pterodectinae (Proctophyllodidae), *Proterothrix* Gaud, 1968, plus 8 other genera constitute the *Pterodectes* generic group, which is characterized by having tarsal seta *wa* situated distinctly anterior to setae *la* and *ra* on tarsi I and II, and solenidion  $\sigma I$  on genu I shorter than solenidion  $\omega 3$  on tarsus I (Park and Atyeo, 1971). *Proterothrix* was originally established as a subgenus of *Pterodectes* Robin, 1877 and initially included 4 species (Gaud, 1968). In their generic revision of Pterodectinae, Park and Atyeo (1971) elevated *Proterothrix* to generic rank and referred a total of 15 species to this genus. Up to now, only 4 additional *Proterothrix* spp. have been described, and 1 species previously included in *Proterothrix* was transferred to *Neodectes* Park and Atyeo, 1971 (Gaud, 1979; Mironov et al., 2008).

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In general morphological appearance, Proterothrix spp. represent typical pterodectines, being characterized by a strongly elongated and narrow body, with a slightly convex and extensively sclerotized dorsal side. As for most other pterodectines, they occupy interbarb "corridors" on the ventral surface of vanes of the primary and secondary flight feathers of their host. Species of *Proterothrix* are known exclusively from the Old World and have been recorded from 2 relatively distantly related host groups, passerines (Passeriformes) and kingfishers (Coraciiformes: Alcedinidae). Proterothrix spp. living on kingfishers have been found in Africa and Madagascar (Gaud, 1979), and species occurring on passerines have been recorded on birds from various families, mostly from the infraorder Corvida, in the Indo-Malayan region and also in Madagascar (Trouessart, 1899; Sugimoto, 1941; Gaud, 1952, 1962, 1968; Mironov et al., 2008). Atyeo (1973) recorded Proterothrix from 56 species of passerine birds from 12 families in Asia, but unfortunately, no mite species from this major collecting effort have ever been described. Nevertheless, this clearly indicates that Proterothrix is a speciesrich genus widely distributed on passerines from tropical areas of the Old World.

Sixteen of the 18 previously described species of Proterothrix have been provisionally arranged into 3 species groups: wolffi (11 species), schizothyra (4 species), and megacaula (1 species) (Gaud, 1952, 1962, 1968, 1979; Park, Atyeo, 1971; Mironov et al., 2008). Representatives of the schizothyra group are restricted to kingfishers (Coraciiformes: Alcedinidae), those of the wolffi group are distributed on several families of passerines of the infraorder Corvida, and the sole species of the megacaula group (P. megacaula Mironov and Diao, 2008) is known from a host from the Muscicapidae (infraorder Passerida). The 3 new species described here from parrotbills (Passerida: Paradoxornithidae) may be formally referred to as the wolffi group, which is characterized by having closed or nearly closed coxal fields III in males and a narrow and parallel-sided terminal cleft in females. Within the wolffi group, these new species represent a distinct complex, which we name here as the "paradoxornis complex," characterized by seta e of tarsus I being lanceolate in form in males (rather than simple setiform), a feature not shown by any other species within Proterothrix. This complex may be additionally characterized by 2 other features in males, i.e., a long whiplike aedeagus and setae h3 represented by macrosetae that are longer than macrosetae h2. However, these 2 characteristics are also shown by *P. megacaula* and some representatives of the *wolffi* group.

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# MATERIALS AND METHODS

The mites examined in the present study were collected by Dr. Sarah Bush from hosts captured in Guizhou Province, People's Republic of China, in 2006 and 2007. Details of habitat and mist-netting of hosts are described in Boyd et al. (2008). Mites were removed from birds that were collected for museum specimens and were preserved in 95% ethanol prior to shipping. Mites were cleared overnight in lactic acid and then slidemounted in PVA medium (6371A, BioQuip Products Inc., Rancho Dominguez, California). Slides were cured for a minimum of 4 days on slide warmers set at 40 C. Drawings were made using a drawing tube attached to an Olympus BH-2 light microscope with DIC illumination.

The species descriptions are given in the recent standard format used for species of pterodectine mites (Mironov and Fain, 2003; Mironov, 2006; Valim and Hernandes, 2006; Mironov, 2008). General morphological terms and the leg and idiosomal chaetotaxy follow Gaud and Atyeo (1996). All measurements are in micrometers (µm). We used the following measuring techniques for particular structures: (1) length of the idiosoma was measured from the anterior margin of the prodorsum to either the lobar apices (in males) or to the lobar apices excluding the terminal appendages (in females): width of the idiosoma was measured at the level of the humeral shields; (2) the hysterosoma was measured from the level of the sejugal furrow to the lobar apices; (3) distance between different pairs of setae was taken as the shortest distance between the transverse levels formed by setae of respective pairs; (4) prodorsal shield length was measured along the midline, and width was taken at the greatest width of the posterior part; (5) hysteronotal shield length in males was the greatest length from the anterior margin to bases of setae h3; width was taken as the greatest width of anterior part at level of humeral shields; (6) anterior hysteronotal shield length in females was the greatest length from the anterior margin to the transverse furrow separating this shield from the lobar shield; width was measured in the anterior part of this shield; and (7) length of the lobar region in females was taken as the greatest length from its anterior margin to the lobar apices (the terminal appendages excluded), and width was measured at the level of the lateral extensions bearing setae h2.

Systematics and scientific names of birds mentioned in the paper follow Dickinson (2003). Type material depositories are abbreviated as follows: UASM, E.H. Strickland Entomological Museum at the University of Alberta (Edmonton, Alberta, Canada); ZISP, the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia). Depository for host material is the University of Kansas Natural History Museum (Lawrence, Kansas), accession prefix KUMNH. A set of discriminating characters for species of the *paradoxornis* complex is given in Table I.

## DESCRIPTIONS

### Proterothrix paradoxornis n. sp.

#### (Figs. 1-4)

Male (Figs. 1, 2; measurements of holotype): Length of idiosoma 392, width 135, length of hysterosoma 268, Prodorsal shield: entire, anterolateral extensions acute, posterior margin almost straight, slightly convex in median part, length of shield 122, width at posterior margin 98, surface with numerous circular lacunae (Fig. 1A). Scapular setae se separated by 49. Scapular shields narrow. Humeral shields narrow, connected by posterior ends to epimerites III; setae cp situated on ventral extension of humeral shield. Setae c2 situated on soft tegument, near antero-median angle of humeral shields. Subhumeral setae c3 lanceolate  $15 \times 7$ . Hysteronotal shield: greatest length 263, width in anterior part 78, anterior margin concave, surface except for lobar area with numerous circular lacunae (Fig. 1A). Distance between prodorsal and hysteronotal shields along midline 15. Opisthosomal lobes elongated, posterior margin of apices rounded; setae h3 situated near lobar apices. Terminal cleft Ushaped, narrow, 42 in length, 16 in width at level of setae h3; lateral margins of terminal cleft with narrow membranes in anterior half (without membranes in specimens from Paradoxornis alphonsianus). Supranal concavity circular, margins clearly outlined. Setae f2 and ps2 situated at same transverse level. Setae h1 at level of supranal concavity. Setae h3represented by macrosetae, slightly longer than macrosetae h2, 150 and 120 in length, respectively; setae ps2 setiform, slightly thickened basally, 38 long; setae ps1 minute, about 5 long, situated slightly posterior to level of setae h2, approximately equidistant from outer and inner margins of opisthosomal lobes. Distance between dorsal setae: se:c2 75, c2:d2 106,

d2:e2 73, e2:h3 70, d1:d2 53, e1:e2 27, h1:ps2 16, h2:h2 50, h3:h3 24, ps2:ps2 53.

Epimerites I fused as a long Y, posterior end of sternum (fused part) connected with middle parts of epimerites II by transverse sclerotized extension (Fig. 1B). Epimerites II long, their posterior ends extending beyond sejugal area and close to inner tips of epimerites IIa, III, and IIIa. Coxal fields I, II without wide sclerotized areas; ventral margin of scapular shields with narrow longitudinal membrane. Epimerites IIIa elongated, extending to sejugal area, their anterior tips close to posterior tips of epimerites II. Rudimentary sclerites rEpIIa absent. Coxal fields I closed, coxal fields II, III almost closed, with narrow gaps between tips of respective epimerites. Coxal fields IV with triangular sclerotized area at bases of trochanters IV. Epimerites IVa well developed, flanking genital apparatus, with setae 4a on inner tips. Genital arch of moderate size, 22 in length (from its base to bending of aedeagus backward), 26 in width at base; basal sclerite of genital apparatus large and short; aedeagus long whip-shaped, extending to apices of opisthosomal lobes, length of aedeagus from its bend to tip 155. Bases of genital papillae contiguous. Genital shields absent; adanal shields represented by small, poorly sclerotized areas around bases of setae ps3. Anal suckers 16 in diameter, corolla with 8-9 indentations. Opisthoventral shields narrow, their ventral margins smooth; setae ps3 situated anterior to anal suckers, slightly closer to each other than are centers of these suckers. Distance between ventral setae: 3b:3a 11, 3a-4a 47, 4a-g 51, g-ps3 31, ps3-ps3 24, ps3:h3 65.

Legs I slightly thicker than legs II; femur I without ventral crest, femur II with ventral crest, genu I with dorsal longitudinal crest, tibia I with dorsal and lateral longitudinal crests, tarsus with lateral longitudinal crest (Fig. 2A, B). Solenidion  $\sigma 1$  of genu I spiculiform, 5 long, situated near base of segment; seta *cGI*, *cGII*, *mGI*, *mGI* setiform, latter 2 setae with wider bases than first 2. Seta *e* of tarsus I lanceolate. Setae *d*, *f* of tarsus II subequal, seta *d* of tarsus III clearly shorter than respective setae *f*. Legs III and IV similar in form and size. Solenidion  $\sigma 1$  of genu III in proximal part of segment (Fig. 2C). Solenidion  $\varphi$  of tibia IV extending to midlevel of ambulacral disc. Tarsus IV 20 long, without apical claw, with small apico-ventral extension bearing seta *w*; setae *d*, *e* button-like, situated in basal and apical parts of segment, respectively (Fig. 2D).

Female (Figs. 3, 4; measurements of 2 paratypes): Length of idiosoma 465-515, width 162-170, length of hysterosoma 350-370. Prodorsal shield: entire, antero-lateral extensions long and acute, posterior half slightly attenuate posteriorly, posterior angles not expressed, posterior margin straight, surface with numerous circular lacunae, length along midline 130-137, greatest width 93-102 (Fig. 3A). Setae se separated by 64-68. Scapular shields narrow. Humeral shields narrow, situated ventrally, separated from outer sclerotization of epimerites III, in length not longer than double distance between setae cp and c3; setae cp situated on soft tegument near ventral margin of humeral shields. Setae c2 situated dorsally on soft tegument. Setae c3 lanceolate,  $20-22 \times 6.5-7$ . Distance between prodorsal and hysteronotal shields 7-10. Anterior and lobar pieces of hysteronotal shield separated dorsally by narrow transverse band but remain connected ventro-laterally by narrow bands (Fig. 3B). Anterior hysteronotal part of shield roughly rectangular, anterior margin straight or slightly convex, greatest length 250-272, width at anterior margin 93-100, surface with numerous little circular lacunae as on prodorsal shield. Length of lobar region 95-98, width at level of setae h2 73-77. Terminal cleft parallel-sided, narrow; length 45-47, width at midlevel 5-8. Supranal concavity well developed, circular. Setae h1 on lobar shield, slightly anterior to supranal concavity. Setae h2 spindleshaped, without terminal filaments,  $35-42 \times 7-7.5$ . Setae *ps1* approximately equidistant from outer and inner margins of opisthosomal lobes, approximately at midlevel between setae h2 and h3. Setae h3 short, 15-20 in length, about one-fourth to one-fifth the length of terminal appendages. Distance between dorsal setae: se:c2 84-95, c2:d2 102-125, d2:e2 93-108, e2:h2 60-73, h2:h3 48-51, d1:d2 57-66, e1:e2 35-38, h1:h2 28-31, h1:h1 46-48, h2:h2 60-64, h3:h3 22-33, h2:ps1 20-22.

Epimerites I fused as a short-stemmed Y, sternum shorter than onefourth of total length of epimerites, without lateral extensions. Lateral parts of coxal fields I, II without heavily sclerotized areas, ventral margin of scapular shields with narrow longitudinal membrane (Fig. 3B). Epimerites IVa absent. Translobar apodemes of opisthosomal lobes present, poorly sclerotized, not fused to each other anterior to terminal cleft. Epigynum horseshoe-shaped, outer margins without extension, greatest width 69–75.

Proximal half of primary spermaduct narrow, uniform in width, distal half (= bursa copulatrix?) approximately 3 times wider than proximal

Character	P. paradoxornis	P. longicaula	P. sarahbushae
Males			
Aedeagus	Extending to lobar apices	Extending far beyond lobar apices	Extending to lobar apices
Pregenital sclerite	Absent	Absent	Present
Adanal shields	One poorly developed pair around bases of setae <i>ps3</i>	Absent	Two pairs of ovate form, posterior one around bases of setae <i>ps3</i>
Lateral extensions of sternum and epimerites II	Connected	Not connected	Connected
Lateral hysteronotal sclerites	Absent	Absent	Present
Length ratio of macrosetae h3:h2	1.2–1.4	1.7–1.9	1.1–1.3
Lateral crest on tibiae I, II	Present	Absent	Absent
Lateral crest on genu I	Absent	Absent	Present
Thumb-like dorsal extension on tarsus I	Absent	Absent	Present
Setae $mG$ of genua I, II	Setiform	Setiform	Spine-like
Females			
Position of setae <i>c2</i>	On soft tegument	On humeral shield	On humeral shield
Dorsal crest on tibia I	Absent	Present	Absent
Setae $mG$ of genua I, II	Setiform	Setiform	Narrowly lanceolate
Incisions in posterior margins of anterior hysteronotal shield	Not extending to level of setae e2	Not developed	Extending to level of setae e2
Position of setae <i>ps1</i> on opisthosomal lobes	Equidistant from inner and outer margins	Closer to inner margin of lobes	Closer to inner margin of lobes

TABLE I. Characters discriminating species of the Proterothrix paradoxornis complex.

half, poorly sclerotized and scarcely distinct secondary spermaducts short (Fig. 4E); copulatory opening ventral, situated at anterior terminal cleft. Distance between pseudanal setae: *ps2:ps2* 63–66, *ps3:ps3* 24–26, *ps2:ps3* 17–20; setae *ps2* situated at level of posterior half of anal opening.

Legs I slightly thicker than legs II; femur II with wide ventral crest; other segments of legs I, II without processes (Fig. 4A, B). Solenidion  $\sigma I$  of genu I thin stick-like, 4–5 long, situated slightly closer to distal margin of segment. Genual setae *cGI*, *cGII*, *mGI* setiform, latter 2 with wider bases than first 2. All setae of tarsus I setiform. Setae *d*, *f* of tarsus II subequal in length, setae *d* of tarsi III, IV 2–2.5 times shorter than respective setae *f*. Genu IV with narrow longitudinal dorsal crest, genu III not modified (Fig. 4C, D). Solenidion  $\varphi$  of tibia IV much shorter than that on tibia III.

#### **Taxonomic summary**

*Type material:* Holotype male and paratype female from the vinousthroated parrotbill *P. webbianus* (Gould, 1852) (ZISP 4423) from China, Guizhou Province, Kuankuoshui Nature Reserve, 28°13′34″N, 107°09′35″E, 1465 m, 1 May 2006, collector S. Bush (holotype host material KUMNH-97482). One paratype female (UASM80511) from *P. webbianus* from China Guizhou Province, Shuipu Village, 25°29′05″N, 107°52′54″E, 645 m, 6 April 2007, collector S. Bush (paratype host material KUMNH-99440).

*Additional material:* Four males and 3 females ex the ashy-throated parrotbill *P. alphonsianus* (Verreaux J., 1870), China, Guizhou Province, Kuankuoshui Nature Reserve, 28°13′34″N, 107°09′35″E, 1465 m, 17 April 2006, collector S. Bush (host material KUMNH-97450). One male and 2 females (ZISP 4424, 4425, 2 slides); 3 males and 1 female (UASM80512, 80513, 2 slides).

Note on host relationships: Paradoxornis webbianus is a member of the "small, brownish-feathered clade" of Yeung et al. (2006), whereas *P. alphonsianus* was not included in their phylogenetic study.

*Etymology:* The specific epithet derives from the generic name of the type host and is a noun in apposition.

Differential diagnosis: Among previously described species of the wolffi group, P. paradoxornis n. sp. is morphologically closest to P. coscinonota Gaud, 1968 from the Rennell Fantail Rhipidura rennelliana Mayr, 1931 (Rhipiduridae), in having a whip-like aedeagus and setae h3 in males represented by macrosetae. Proterothrix paradoxornis n. sp. is easily differentiated from P. coscinonota (and from the other 2 species of the paradoxornis complex) by the following features: in males, the aedeagus extends to lobar apices, epimerites IVa are short and setae 4a are set on their anterior tips; in females, setae h3 are no more than one-fourth the length of the terminal appendages, setae h2 are lanceolate and without a terminal filament, and the terminal cleft is slightly divergent posteriorly. In the males of *P. coscinonota*, the aedeagus extends only to the level of setae h2, and epimerites IVa are long, extending to the level of trochanters III and bear setae 4a in the central part; in the females, setae h3 are about two-thirds of terminal appendage length, setae h2 are lanceolate with long terminal filament, and the terminal cleft is slightly parallel-sided. Among the species of paradoxornis complex, P. paradoxornis is most similar to P. longicaula n. sp. (see below), but clearly differs from it by the following features: in males, the aedeagus reaches lobar apices, lateral extensions of sternum are connected to epimerites II, macrosetae h3 are slightly longer than h2 (1.1-1.3 times), and tibiae and tarsi I, II have lateral crests; in females, setae c2 are distinctly off humeral shields, and setae ps1 are situated approximately equidistant from inner and outer margins of opisthosomal lobes. In the males of P. longicaula, the aedeagus extends beyond lobar apices by almost half its length, lateral extensions of sternum are not connected to epimerites II, macrosetae h3 are almost twice as long as h2, and tibiae and tarsi I, II do not have lateral crests; in females, setae c2 are situated on the antero-mesal angles of the humeral shields, and setae ps1 sit closer to inner margins of lobes.

#### Remarks

Although male specimens of *P. paradoxornis* n. sp. from *P. alphonsianus* slightly differ from the holotype male from *P. webbianus* by the absence of a narrow membrane in the anterior part of the terminal cleft, we do not think that this difference warrants treatment of specimens from these hosts as separate species or subspecies. The compared samples are too few in number to conclude whether it is a reliable difference, part of continuous variation, or just an artifact of slide mounting; also, we did not find any clear and consistent differences between females from these 2 hosts.

# Proterothrix longicaula n. sp.

## (Figs. 5-7)

Male (Figs. 5, 6A–D; measurements of holotype, for 2 paratypes in parentheses): Length of idiosoma 470 (438–465), width 170 (160–170), length of hysterosoma 315 (290–315). Prodorsal shield: entire, antero-



FIGURE 1. Proterothrix paradoxornis, male. (A) dorsal view; (B) ventral view.

lateral extensions acute, posterior margin almost straight, length of shield along midline 142 (128–140), width at posterior margin 113 (108–115), surface with numerous small circular lacunae (Fig. 5A). Scapular setae *se* separated by 58 (53–55). Scapular shields narrow. Humeral shields well

developed, connected by posterior end to epimerites III; bases of setae cp touching ventral margin of humeral shield. Setae c2 situated dorsally on anterior end of humeral shields. Subhumeral setae c3 lanceolate, 22 (22–24) × 7 (6.5–7). Hysteronotal shield: greatest length 312 (290–305),



FIGURE 2. Proterothrix paradoxornis, legs of male. (A) leg I; (B) leg II; (C) leg III; (D) leg IV.

greatest width of anterior part 102 (88–95), anterior margin slightly concave surface, except for lobar area with numerous small circular lacunae. Distance between prodorsal and hysteronotal shields along midline 20 (15–20) (Fig. 3A). Opisthosomal lobes elongated, attenuate to apex, posterior margin of apices rounded; setae h3 situated near lobar apices. Terminal cleft narrowly V-shaped, 48 (46–53) in length, 17 (16–26) in width at level of setae h3; margins of terminal cleft without membrane. Supranal concavity drop-shaped or ovate, margins clearly outlined. Setae f2 and ps2 situated at same transverse level. Setae h1 slightly posterior to supranal concavity. Setae h3 represented by macrosetae, nearly twice as long as macrosetae h2, length 235 (215–235) and 120 (120–135) respectively; setae ps2 setiform, slightly thickened basally, 45 (40–45)

long; setae ps1 minute, about 5 long, situated slightly posterior to level of setae h2, approximately equidistant from outer and inner lobar margins. Distance between dorsal setae: se:c2 88 (77–85), c2:d2 128 (108–118), d2:e2 90 (84–95), e2:h3 82 (73–80), d1:d2 70 (65–70), e1:e2 28 (24–28), h1:ps2 22 (16–20), h2:h2 55 (54–58), h3:h3 31 (26–35), ps2:ps2 64 (64–66).

Epimerites I fused as a Y, posterior end of sternum with long and acute transverse extensions almost touching middle parts of epimerites II (Fig. 5B). Epimerites II long, posterior ends extending to sejugal area. Coxal fields I, II without wide sclerotized areas; ventral margin of scapular shield with narrow longitudinal membrane. Epimerites IIIa moderately elongated, extending to level of inner tips of epimerites III. Rudimentary sclerites rEpIIa absent. Coxal fields I almost closed, coxal fields II, III open.



FIGURE 3. Proterothrix paradoxornis, female. (A) dorsal view; (B) ventral view.

Coxal fields IV with triangular sclerotized area at bases of trochanters IV. Epimerites IVa well developed, flanking genital apparatus laterally, with setae *4a* on inner ends. Genital arch of moderate size, 31 (26–33) long, 33 (32–38) wide; basal sclerite of genital apparatus large and short; aedeagus

long and whip-shaped, extending beyond lobar apices by almost half its length, length of aedeagus from anterior bend to tip 375 (350–380). Bases of genital papillae contiguous. Genital and adanal shields absent. Anal suckers 17 (15–18) in diameter, corolla with 8–9 indentations. Opisthoventral



FIGURE 4. Proterothrix paradoxornis, details of female. (A) leg I; (B) leg II; (C) leg III; (D) leg IV; (E) spermatheca and spermaducts. co, copulatory opening; hs, head of spermatheca; pd, primary spermaduct; sd, secondary spermaduct.

shields narrow, with smooth inner margin; setae *ps3* situated anterior to anal suckers, slightly closer to each other than are centers of suckers. Distance between ventral setae:  $3b:3a \ 9 \ (12-17), \ 3-4a \ 45 \ (42-45), \ 4a-g \ 60 \ (55-60), \ g-ps3 \ 44 \ (40-42), \ ps3-ps3 \ 24 \ (22-24), \ ps3:h3 \ 75 \ (70-77).$ 

Legs I slightly thicker than legs II; femur II with ventral crest, other segments of legs I, II without any processes. Solenidion  $\sigma I$  of genu I stick-like, 8 (7–8) long, situated in basal part of segment; setae *cGI*, *cGII*, *mGI*, *mGI* setiform, the last of these with wider base than first 3. Seta *e* of tarsus I lanceolate, 18 (15–17) long. Setae *d*, *f* of tarsus II subequal in length, seta *d* of tarsus III approximately half the length of respective seta *f*. Legs III and IV similar in form and size. Solenidion  $\sigma I$  of genu III in proximal part of segment. Solenidion  $\varphi$  of tibia IV extending to base of ambulacral stalk. Tarsus IV 25 (24–26) long, without apical claw, with small apico-ventral extension bearing seta *w*; setae *d*, *e* button-like, situated in basal and apical parts of segment, respectively (Figs. 6A–C).

*Female (Figs. 6F–H, 7; measurements of 3 paratypes):* Length of idiosoma 552–580, width 185–192, length of hysterosoma 380–410. Prodorsal shield:

entire, antero-lateral extensions long and acute, posterior half with convex lateral margins, posterior angles not expressed, posterior margin straight, surface with numerous circular lacunae, length 150-162, greatest width of posterior half 115-122 (Fig. 7A). Setae se separated by 70-75. Scapular shields narrow. Humeral shields narrow, situated ventro-laterally, separated from outer sclerotization of epimerites III; setae cp situated on ventral margin of humeral shields. Setae c2 situated in antero-mesal angles of humeral shields. Setae c3 lanceolate,  $21-24 \times 6.5-7$ . Distance between prodorsal and hysteronotal shields 5-10. Anterior and lobar pieces of hysteronotal shield separated dorsally by narrow transverse band but remain connected ventrolaterally by narrow bands. Anterior hysteronotal part of shield roughly rectangular, anterior margin slightly concave, greatest length 290-305, width at anterior margin 105-115, surface with numerous small circular lacunae. Length of lobar region 105–110, width at level of setae h2 85–93. Terminal cleft U-shaped, narrow, with slightly divergent posterior margins, length 55-57, width at midlevel 10-12. Supranal concavity well developed, circular. Setae h1 on lobar shield, slightly anterior to level of supranal concavity. Setae



FIGURE 5. Proterothrix longicaula, male. (A) dorsal view; (B) ventral view.

h2 spindle-shaped, without terminal filaments,  $44-48 \times 6.5$ -7.5. Setae *ps1* closer to inner margin of opisthosomal lobes, approximately at midlevel between setae h2 and h3. Setae h3 26–34 in length, about one-third of terminal appendages. Distance between dorsal setae: *se*:*c2* 95–102, *c2:d2* 125–130,

*d2:e2* 130–138, *e2:h2* 72–80, *h2:h3* 50–54, *d1:d2* 66–74, *e1:e2* 52–60, *h1:h2* 38–42, *h1:h1* 52–55, *h2:h2* 70–77, *h3:h3* 34–38, *h2:ps1* 20–22.

Epimerites I fused as a short-stemmed Y, sternum short, about onesixth of total length of epimerites, without lateral extensions. Lateral parts

![](_page_8_Figure_1.jpeg)

FIGURE 6. *Proterothrix longicaula*, details. (A) leg I of male; (B) leg II of male; (C) tibia and tarsus III of male; (D) tibia and tarsus IV of male; (E) femur, genu, and tibia II of female; (F) femur and genu III of female; (G) femur and genu IV of female; (H) spermatheca and spermaducts.

of coxal fields I, II without heavily sclerotized areas, ventral margin of scapular shields with narrow longitudinal membrane (Fig. 7B). Epimerites IVa absent. Translobar apodemes of opisthosomal lobes wide, fused to each other anterior to terminal cleft. Epigynum horseshoe-shaped, lateral margins with a small ledge, greatest width 68–78.

Proximal half of primary spermaduct narrow, with striated enlargement near head of spermatheca; distal half (= bursa copulatrix?) 3–4 times wider than proximal half (Fig. 6H); secondary spermaducts short; copulatory opening ventral, situated slightly anterior to margin of translobar apodeme. Distance between pseudanal setae: *ps2:ps2* 57–62,

![](_page_9_Picture_1.jpeg)

FIGURE 7. Proterothrix longicaula, female. (A) dorsal view; (B) ventral view.

*ps3:ps3* 24–26, *ps2:ps3* 20–22; setae *ps2* situated at level of posterior half of anal opening.

Legs I noticeably larger than legs II; femur II with narrow ventral crest, genu I with smooth longitudinal dorsal crest, tibia I with finely indented

longitudinal dorsal crest (Fig. 6E); other segments of legs I, II without processes. Solenidion  $\sigma I$  of genu I thin, stick-like, 8–9 long, situated approximately at midlevel of segment. Seta *cGI*, *cGII*, *mGI*, *mGI* setiform. Seta *e* of tarsus I setiform. Seta *e* of tarsus I setiform. Seta *e* of tarsus I setiform.

tarsi III, IV approximately one-half the length of respective setae *f*. Genu IV with narrow longitudinal dorsal crest, genu III not modified (Fig. 6F, G). Solenidion  $\varphi$  of tibia IV much shorter than that on tibia III.

#### Taxonomic summary

*Type material:* Male holotype (ZISP 4426), 2 male and 3 female paratypes ex the grey-headed parrotbill *P. gularis* Gray 1845, China, Guizhou Province, Kuankuoshui Nature Reserve, 28°13'34"N, 107°09'35"E, 1465 m, 14 April 2006, collector S. Bush (host material KUMNH-97451). Holotype, 1 male and 2 female paratypes (ZISP 4426, 4427, 2 slides), 1 male and 1 female paratype (UASM80514, 1 slide).

Note on host relationships: Paradoxornis gularis is a member of the "large parrotbill" clade of Yeung et al. (2006).

*Etymology:* The specific epithet derives from *kaulos* (stem, stalk, Gr.) to refer to the extraordinarily long aedeagus in the male.

Differential diagnosis: Proterothrix longicaula n. sp. is most similar to P. paradoxornis based on the general shape of the opisthosoma in males (Figs. 1A, 5A) and differs from the latter species by the following features: in males, the aedeagus is extremely long and extends beyond the lobar apices by almost half its length, lateral extensions of sternum are well developed but not connected to epimerites II, macrosetae h3 are nearly twice (1.7-1.9) as long as h2, tibiae and tarsi I and II are without lateral crests; in females, tibia I has a longitudinal dorsal crest with fine indentations, setae c2 are situated on antero-mesal angles of humeral shields, and setae ps1 are situated closer to the inner margins of lobes than to the outer one (Table I). In the males of *P. paradoxornis*, the aedeagus reaches the lobar apices only, lateral extensions of sternum are connected to epimerites II, macrosetae h3 are 1.1-1.3 times longer than h2, tibiae and tarsi I and II have lateral longitudinal crests; in females, setae c2 are situated off the humeral shields, setae ps1 are approximately equidistant from the inner and outer margins of opisthosomal lobes.

#### Proterothrix sarahbushae n. sp.

#### (Figs. 8–10)

Male (Figs. 8, 9A-E; measurements of holotype, for 2 paratypes in parentheses): Length of idiosoma 445 (435-446), width 160 (152-165), length of hysterosoma 305 (303-310). Prodorsal shield: entire, anterolateral extensions acute, posterior angles well expressed, posterior margin straight, length of shield along midline 122 (118-122), width at posterior margin 128 (122-126); surface with numerous small circular lacunae, in anterior part of shield lacunae noticeably larger and arranged in transverse rows (Fig. 8A). Scapular setae se separated by 62 (60-62). Scapular shields narrow, with hook-like antero-mesal extensions. Humeral shields well developed, posterior ends connected to epimerites III; setae cp situated on ventral extensions of humeral shields. Setae c2 situated dorsally, on antero-mesal angles of humeral shields. Subhumeral setae c3 lanceolate, 22  $(20-22) \times 9$  (7.5-9). Hysteronotal shield: greatest length 305 (305-312), greatest width of anterior part 104 (95-100), anterior margin slightly concave, surface except for lobar area with numerous small circular lacunae. Distance between prodorsal and hysteronotal shields along midline 13 (13-20). Lateral hysteronotal sclerites present, situated slightly anterior to level of trochanters IV. Opisthosomal lobes elongated, attenuate to apex, posterior margin of apices rounded; lateral margins of lobes with rounded ledges bearing setae  $h_2$ ; setae  $h_3$  situated near lobar apices. Terminal cleft narrow V-shaped, 66 (60-66) in length, 20 (12-18) in width at level of setae h3. Supranal concavity elongate, roughly ovate, margins clearly outlined. Setae f2 and ps2 situated at same transverse level. Setae h1 at level of supranal concavity. Setae h3 represented by macrosetae, slightly longer than macrosetae h2, length 195 (205-215) and 185 (170-180), respectively; setae ps2 setiform, 40 (40-45) long; setae ps1 setiform 15 (15-22) long, situated at midlevel between setae h2 and h3, approximately equidistant from outer and inner lobar margins. Distance between dorsal setae: se:c2 70 (75-80), c2:d2 120 (110-115), d2:e2 73 (70-82), e2:h3 93 (88-90), d1:d2 62 (58-60), e1:e2 44 (42-51), h1:ps2 20 (17-22), h2:h2 55 (50-53), h3:h3 37 (28-32), ps2:ps2 70 (62-68).

Epimerites I fused as a Y, posterior end of sternum connected with middle parts of epimerites II by transverse sclerotized extensions. Epimerites II long, posterior ends fused with inner tips of epimerites IIa and anterior tips of elongated epimerites IIIa forming hexagonal structure in median part of propodosoma (Fig. 8B). Coxal fields I, II without wide sclerotized areas; epimerites IIa with narrow longitudinal membrane on inner margin. Epimerites IIIa elongated, extending to sejugal area. Rudimentary sclerites rEpIIa absent. Coxal fields I, II closed, coxal fields III almost closed, with narrow gaps between tips of epimerites III and IIIa. Epimerites IVa well developed, laterally flanking genital apparatus, with setae 4a on inner margin, approximately at level of genital arch apex. Pregenital sclerite present, stick-shaped, posterior end connected with inner tips of epimerites IVa. Coxal fields IV with large sclerotized area connecting bases of epimerites IV and IVa. Genital arch of moderate size, 27 (26-28) long, 28 (28-32) wide; basal sclerite of genital apparatus short and wide; aedeagus long whip-shaped, extending to apices of opisthosomal lobes, length of aedeagus from its anterior bend to tip 205 (188-195). Genital papillae anterior to genital arch, their bases contiguous. Genital shield absent; 2 pairs of adanal shields present, both pairs represented by small ovate plates, posterior pair bearing bases of setae ps3. Anal suckers 20 (16-20) in diameter, corolla indented, with 5-6 small teeth. Opisthoventral shields narrow, with smooth inner margin; setae ps3 antero-mesal to anal suckers, noticeably closer to each other than are centers of suckers. Distance between ventral setae: 3b:3a 8 (6-8), 3a-4a 55 (50-55), 4a-g 55 (51-55), g-ps3 27 (28-32), ps-ps3 20 (20-22), ps3:h3 86 (84-90).

Legs I longer and thicker than legs II; femur II with wide ventral crest, genu I with dorsal and lateral longitudinal crests, tarsus I with thumb-like dorsal process, genu II with dorsal crest in anterior part of segment and with narrow lateral crest, tarsus II with narrow lateral crest (Fig. 9A, B); other segments of legs I, II without processes. Lateral margin of tarsus and tibia I wedge-shaped and strongly sclerotized. Solenidion  $\sigma I$  of genu I spiculiform, 4 (4-6) long, situated at base of segment; setae cGI, cGII setiform; setae mGI, mGII spiniform, 13 (13-15) and 13 (11-13) long, respectively. Seta e of tarsus I narrowly lanceolate, 15 (14–16) long. Seta d of tarsus II slightly longer than corresponding seta f; seta d of tarsus III approximately half the length of corresponding seta f. Legs IV slightly thicker than legs III. Solenidion  $\sigma 1$  of genu III at base of segment. Solenidion  $\varphi$  of tibia IV slightly extending beyond tarsal apex. Tarsus IV 24 (24-26) long, without apical claw, with a small apico-ventral extension bearing seta w; setae d, e button-like, situated in basal and apical parts of segment, respectively (Fig. 9C, D).

Female (Figs. 9F-G, 10; measurements of 3 paratypes): Length of idiosoma 422-482, width 155-175, length of hysterosoma 335-345. Prodorsal shield: entire, antero-lateral extensions acute, posterior half with convex lateral margins, posterior angles not expressed, posterior margin straight, surface with numerous small circular lacunae, length 124-126, greatest width of posterior part 112-122 (Fig. 10A). Setae se separated by 77-84. Scapular shields narrow, with hook-like antero-mesal extensions. Humeral shields narrow, separated from sclerotization of epimerites III; bases of setae cp situated on soft tegument or touching ventral margin of humeral shields. Setae c2 situated dorsally in anteromesal angles of humeral shield. Setae c3 lanceolate, 20-22  $\times$  6.5-7. Distance between prodorsal and hysteronotal shields 6-10. Anterior and lobar pieces of hysteronotal shield separated dorsally by narrow transverse band but remain connected ventro-laterally by narrow bands. Anterior hysteronotal part of shield roughly rectangular, anterior margin straight, greatest length 245-260, width at anterior margin 105-115, surface with numerous small circular lacunae. Length of lobar region 95-106, width at level of setae h2 75-85. Terminal cleft U-shaped, narrow, slightly divergent posteriorly, length 48-52, width at midlevel 4-6. Supranal concavity well developed, circular. Setae h1 on lobar shield, anterior to supranal concavity. Setae h2 spindle-shaped, without terminal filaments, 42–44  $\times$ 7-9. Setae ps1 closer to inner margins of opisthosomal lobes, approximately at midlevel between setae h2 and h3. Setae h3 short, 12-15 long, about one-sixth the length of terminal appendages. Distance between dorsal setae: se: c2 72-86, c2:d2 115-128, d2:e2 95-110, e2:h2 56-66, h2:h3 46-51, d1:d2 66-73, e1:e2 37-48, h1:h2 35-40, h1:h1 44-53, h2:h2 57-68, h3:h3 25-33, h2:ps1 20-22.

Epimerites I fused as a short-stemmed Y, sternum about one-sixth of total length of epimerites, without lateral extensions. Lateral parts of coxal fields I, II without heavily sclerotized areas, ventral margin of scapular shields with narrow longitudinal membrane (Fig. 10B). Epimerites IVa absent. Translobar apodemes of opisthosomal lobes present, fused to each other anterior to terminal cleft. Epigynum horseshoe-shaped, outer margins with blunt-angular extensions, greatest width 56–73. Proximal half of primary spermaduct narrow, slightly enlarged near entrance to spermatheca, distal half (= bursa copulatrix?) approximately 3 times wider than proximal half; secondary spermaducts short (Fig. 9G); copulatory opening ventral, situated at anterior margin of translobar apodeme. Distance

![](_page_11_Figure_1.jpeg)

FIGURE 8. Proterothrix sarahbushae, male. (A) dorsal view; (B) ventral view.

between pseudanal setae: *ps2:ps2* 55–68, *ps3:ps3* 22–24, *ps2:ps3* 20–26; setae *ps2* situated at level of posterior half of anal opening.

Legs I slightly thicker than legs II; femur II with wide ventral crest; genu I with narrow longitudinal dorsal crest; other segments of legs I, II without

processes. Solenidion  $\sigma I$  of genu I thin stick-like, 5–7 long, situated approximately at midlevel of segment. Setae *cGI*, *cGII* setiform; setae *mGI*, *mGII* narrowly lanceolate, 12–15 and 16–20 long, respectively. Setae *e* of tarsus I setiform. Setae *d*, *f* of tarsus II subequal in length, setae *d* of tarsi III,

![](_page_12_Figure_1.jpeg)

FIGURE 9. *Proterothrix sarahbushae*, details. (A) leg I of male; (B) leg II of male, I–IV; (C) tibia and tarsus III of male; (D) tibia and tarsus IV of male; (E) femur and genu III of female; (F) femur and genu IV of female; (G) spermatheca and spermaducts.

IV 2–2.5 times shorter than corresponding setae *f*. Genu IV with narrow longitudinal crest, genu III not modified (Fig. 9E, F). Solenidion  $\varphi$  of tibia IV much shorter than that on tibia III.

Bush (host material left in China and not incorporated into a collection). One male and 1 female (ZISP 4430, 1 slide); 1 male and 2 females (UASM80516–18, 3 slides).

#### **Taxonomic summary**

*Type material:* Male holotype (ZISP 4428), 2 male and 3 female paratypes ex the golden parrotbill *Paradoxornis verreauxi* (Sharpe, 1883), China, Guizhou Province, Kuankuoshui Nature Reserve, 28°13'34"N, 107°09'35"E, 1465 m, 14 April 2006, collector S. Bush (host material KUMNH-97447). Holotype, 1 male and 2 female paratypes (ZISP 4428, 4429, 2 slides); 1 male and 1 female paratype (UASM80515, 1 slide).

Additional material: Two males, 3 females ex the ashy-throated parrotbill *P. alphonsianus* China, Guizhou Province, Kuankuoshui Nature Reserve, 28°13'34"N, 107°09'35"E, 1465 m, 19 April 2006, collector S.

Note on host relationships: Paradoxornis verreauxi is a member of the "small, yellowish-feathered clade" of Yeung et al. (2006), whereas *P. alphonsianus* was not included in their phylogenetic study.

*Etymology:* The species is dedicated with gratitude to Dr. Sarah Bush, collector of the 3 new species of *Proterothrix* described in this paper.

Differential diagnosis: Among the species of the paradoxornis complex, Proterothrix sarahbushae n. sp. appears closest to *P. paradoxornis* n. sp. based on the aedeagus extending only to the lobar apices and by the structure of the propodosomal epimerites in males (Figs. 1B, 8B). *Proterothrix sarahbushae* differs from the latter species as follows. In both sexes, genual setae *mG*I, *mG*II are spine-like. In males, a pregenital sclerite is present and is connected to anterior tips of epimerites IVa; a pair

![](_page_13_Figure_1.jpeg)

FIGURE 10. Proterothrix sarahbushae, female. (A) dorsal view; (B) ventral view.

of lateral hysteronotal sclerites and 2 pairs of adanal shields are present; lateral extensions of sternum, distal parts of epimerites II, IIa, and IIIa form a hexagonal structure in the center of the propodosoma. In females, setae *c2* are situated in the antero-mesal angles of humeral shields, and the posterior margin of the anterior hysteronotal shield has a pair of incisions extending beyond the level of setae *e2*. In both sexes of *P. paradoxornis* genual setae *mG*I, *mG*II are setiform; in the males, the pregenital sclerite and lateral hysteronotal sclerites are absent, the adanal shields are represented by one pair of poorly developed sclerotized areas around bases of setae ps3, the distal tips of epimerites II, IIa, and IIIa are close to each other but do not form a closed hexagonal structure; in females, setae *c2* are situated on soft tegument, and the posterior margin of the anterior hysteronotal shield has a pair of short incisions that do not extend to the level of setae e2.

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# LITERATURE CITED

- ALSTRÖM, P., P. G. P. ERICSON, U. OLSSON, AND P. SUNDBERG. 2006. Phylogeny and classification of the avian superfamily Sylvioidea. Molecular Phylogenetics and Evolution 38: 381–397.
- ATYEO, W. T. 1973. Feather mites. *In* Some ectoparasites of the birds of Asia, H. E. McClure and N. Ratanaworabhan (eds.). Jintana Printing Ltd., Bangkok, Thailand, p. 54–78.
- BONNET, A. 1924. Révision des genres *Megninia*, *Mesalges* et genres voisins de la sous-famille des sarcoptides plumicoles (Première Partie). Bulletin de la Société Zoologique de France **49:** 146–188.
- BOYD, R. L., A. S. NYÁRI, B. W. BENZ, AND G. CHEN. 2008. Aves, province of Guizhou, China. Check List 4: 107–114.
- ČERNÝ, V. 1978. *Proctophyllodes balati* sp. n., a new species of feather mites (Analgoidea, Proctophyllodidae) from the bearded titmouse. Folia Parasitologica **25**: 222.

—. 1990. Faunistic records from Czechoslovakia. Acta entomologica Bohemoslovaca **87:** 159–160.

- DABERT, J., S. V. MIRONOV, AND R. EHRNSBERGER. 2008. Systematic revision of the feather mite genera *Apexolichus* Gaud et Atyeo and *Titanolichus* Gaud et Atyeo (Astigmata, Pterolichidae), parasites of parrots of the Old World (Psittaciformes, Psittacidae). Acta Parasitologica 53: 46–80.
- DICKINSON, E. C. 2003. The Howard and Moore complete checklist of the birds of the world, 3rd ed. Princeton University Press, Princeton, New Jersey, 1056 p.
- GAUD, J. 1952. Sarcoptides plumicoles des oiseaux de Madagascar. Mémoires de l'Institut Scientifique de Madagascar, Séries A 7: 81–107.
  — 1962. Sarcoptiformes plumicoles (Analgesoidea) parasites d'oiseaux de l'Ile Rennell. The Natural History of Rennell Island, British Solomon Islands 4: 31–51.

—. 1968. Sarcoptiformes plumicoles (Analgoidea) parasites d'oiseaux de l'Ile Rennell. The Natural History of Rennell Island, British Solomon Islands 5: 121–151.

- —. 1979. Sarcoptiformes plumicoles des oiseaux Coraciiformes d'Afrique. II. Parasites des Alcedinidae. Revue de Zoologie Africaines 93: 245–266.
- —, AND W. T. ATYEO. 1996. Feather mites of the world (Acarina, Astigmata): The supraspecific taxa. Musée Royal de l'Afrique

Centrale, Annales, Sciences Zoologiques 277: Pt. 1, 1–193; Pt. 2. 1–436.

- MIRONOV, S. V. 2006. Feather mites of the genus *Montesauria* Oudemans (Astigmata: Proctophyllodidae) associated with starlings (Passeriformes: Sturnidae) in the Indo-Malayan region, with notes on systematics of the genus. Acarina 14: 21–40.
- 2008. New feather mites of the subfamily Pterodectinae (Astigmata: Proctophyllodidae) from passerines (Aves: Passeriformes) in Africa. Annales Zoologici 58: 403–418.
- —, W. DIAO, Y. ZHANG, C. ZHANG, AND Z. H. YAN. 2008. A new feather mite species of the genus *Proterothrix* Gaud (Astigmata, Proctophyllodidae) from *Ficedula zanthopygia* (Hay) (Passeriformes: Muscicapidae) in China. Acarina **16:** 31–38.

—, AND A. FAIN. 2003. New species of the feather mite subfamily Pterodectinae (Astigmata: Proctophyllodidae) from African passerines (Aves: Passeriformes). Bulletin de la Société Royale Belge d'Entomologie 139: 75–91.

- PARK, C. K., AND W. T. ATYEO. 1971. A generic revision of the Pterodectinae, a new subfamily of feather mites (Sarcoptiformes: Analgoidea). Bulletin of the University of Nebraska State Museum 9: 39–88.
- ROBSON, C. 2007. Family Paradoxornithdae (Parrotbills). In Handbook of the birds of the world. Vol. 12. Picathartes to tits and chickadees, J. del Hoyo, A. Elliott, and D. A. Christie (eds.). Lynx Edicions, Barcelona, Spain, p. 292–320.
- SUGIMOTO, M. 1941. Studies on the Formosan mites (fourth report) (on the feather mites, Analgesidae Canestrini, 1892, Part II.). Sylvia (Journal of the Taihoku Society of Agriculture and Forestry) 5: 129–149.
- TROUESSART, E. L. (1898) 1899. Diagnoses préliminaires d'espèces nouvelles d'Acariens plumicoles. Additions et corrections à la sousfamille des Analgésinés. Bulletin de la Société d'Etudes Scientifiques d'Angers 28: 1–62.
- VALIM, M. P., AND F. A. HERNANDES. 2006. Redescription of four species of the feather mite genus *Pterodectes* Robin, 1877 (Acari: Proctophyllodidae: Pterodectinae) described by Herbert F. Berla. Acarina 14: 41–55.
- YEUNG, C., F.-M. LAI, X.-J. YANG, L.-X. HAN, M.-C. LIN, AND S.-H. LI. 2006. Molecular phylogeny of the parrotbills (Paradoxornithidae). Journal of Ornithology 147 (Suppl. 1): 87–88.
- YOUNG, S.-M. 1999. Feather mites in Taiwan and their parasitical relationship. Chinese Journal of Entomology, Special Publication 12: 71–82.