

Research Article

A new feather mite species of the genus *Mycterialges* Gaud & Atyeo, 1981 (Acari, Xolalgidae) from the Oriental Stork, *Ciconia boyciana* (Ciconiiformes, Ciconiidae) in Korea

Jeong Hun Shim¹⁰, Yeong-Deok Han²⁰, Sukyung Kim³⁰, Dongsoo Ha³⁰, Yongun Shin⁴⁰, Soo Hyung Eo¹⁰

3 Eco-institute for Oriental Stork, Korea National University of Education, Cheongju, Republic of Korea

4 Natural Heritage Division, Cultural Heritage Administration, Deajeon, Republic of Korea

Corresponding author: Soo Hyung Eo (eosh@kongju.ac.kr)



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Abstract

A new feather mite species, *Mycterialges boycianae* **sp. nov.** (Xolalgidae), was identified from the Oriental Stork, *Ciconia boyciana* Swinhoe, 1873, in Korea. Males of *M. boycianae* **sp. nov.** are distinguished from *Mycterialges mesomorphus* Gaud & Atyeo, 1981, in having a single triangular prodorsal shield, sinuous margins of the opisthosoma located between setae e2 and h2 on the hysteronotal shield, an oval-shaped epiandrum without posterior extensions, a shorter tibia + tarsus IV than femoragenu IV, and an absent ambulacral disc of leg IV. Females differ in having a prodorsal shield with a posterior margin that is blunt-angular, and a concave posterior margin of the hysteronotal shield with posterior extensions. This study presents the first record of the feather mite genus *Mycterialges* in birds of the genus *Ciconia* (Ciconiidae). Additionally, we determined the phylogenetic relationship among Ingrassiinae using the mitochondrial cytochrome c oxidase subunit (COI).

Key words: Analgoidea, Astigmata, COI, ectosymbionts, Ingrassiinae, systematics, taxonomy

Introduction

Feather mites (Astigmata) belong to two superfamilies (Analgoidea and Pterolichoidea), most of which are permanent ectosymbionts. These mites live on specific feathers and microsites on feathers, primarily consuming fungi and bacteria (Doña et al. 2019). They are mainly transmitted vertically from parents to offspring (Doña et al. 2017), and because of these characteristics, they exhibit high host specificity (OConnor 1982; Gaud and Atyeo 1996; Dabert and Mironov 1999; Proctor 2003). Feather mites living on endangered birds could be at risk of extinction due to their high host specificity, as a decrease in the host population could affect them (Waki et al. 2023). For example, *Compressalges nipponiae* Dubinin, 1950 (Pterolichoidea: Caudiferidae), which is associated with the Crested Ibis *Nipponia nippon* (Temminck, 1835), disappeared due to the extirpation of its native host *N. nippon* in Japan. Consequently, this mite

¹ Department of Forest Science, Kongju National University, Yesan, Republic of Korea

² Research Center for Endangered Species, National Institute of Ecology, Yeongyang, Republic of Korea

was registered as "Extinct" in the Red List of the Ministry of the Environment, Japan in 2020 (Waki and Shimano 2020; Waki et al. 2023).

The genus *Mycterialges* Gaud & Atyeo, 1981 is distinguished from other genera in the family Xolalgidae Dubinin, 1953 (Analgoidea) by the number of setae on the anterior tarsi, ambularcal disc shape, male opisthosomal lobes structure and legs IV, and the female's epigynum form (Gaud and Atyeo 1981a, 1996). This genus is associated with birds of Ciconiidae; only two species of this genus have been reported (Gaud and Atyeo 1981a, 1996; Gaud 1982). The first discovered type species was *Mycterialges mesomorphus* Gaud & Atyeo, 1981, which was recorded in the Wood Stork, *Mycteria americana* Linnaeus, 1758 in North America. Another species was found in the Saddle-billed Stork, *Ephippiorhynchus senegalensis* (Shaw, 1800) in Africa, but it has not yet been accurately described (Gaud 1982).

The family Ciconiidae consists of 20 species in six genera, which are found on all continents except Antarctica. In Korea, two species of the genus *Ciconia* occur: the Black Stork, *Ciconia nigra* (Linnaeus, 1758) and the Oriental Stork, *Ciconia boyciana* Swinhoe, 1873. Both species are observed as winter visitors and are designated as "Endangered Species Level I" by the Korea Ministry of Environment (BirdLife International 2017, 2018; Lee et al. 2020; Gill et al. 2023; NIBR 2023). Among them, *C. boyciana* has become extirpated from Korea's breeding population since the 1970s due to overfishing, habitat destruction, and food shortages (Sonobe and Izawa 1987; Chan 1991; Collar et al. 2001; Cheong 2005). In Korea, efforts have been made to restore a breeding population of *C. boyciana* since 1996 by importing Oriental Storks from Germany, Russia and Japan to increase their population. Since 2007, storks have been released into the wild to restore the breeding population (Park et al. 2011; Son et al. 2011; Eco-Institute for Oriental Stork 2023).

Research on the migration routes and nest selection of *C. boyciana* has mainly been conducted in East Asia (Shimazaki et al. 2004; Cheng et al. 2023). However, despite active research on the behavior and ecology of the Oriental Storks, research on ectosymbionts has not been actively conducted. *Pelargolichus orientalis* Waki, Mironov & Shimano, 2023 is the only known feather mite of *C. boyciana*. This mite was previously identified as *Pelargolichus didactylus* (Trouessart, 1885) (Dubinin 1956). However, Pérez and Atyeo (1992) identified mites in the Oriental Stork as a different species within the genus *Pelargolichus*, which was later described as *P. orientalis* by Waki et al. (2023). Except for this mite, little is known about other mites associated with Oriental Storks. Since 1996, ecological research has been conducted on the feeding behavior, reintroduction suitability, and habitat of Oriental Storks (Cheong 2005; Sung et al. 2008; Kim 2009; Ha 2019). Recently, we started research on ectosymbionts that can affect the host while interacting with storks.

This study reports a new species of feather mite of the genus *Mycterialges* found on captive *C. boyciana* in Korea. We provide information on the external morphology of the newly discovered feather mite species. In addition, we used the mitochondrial DNA (mtDNA) cytochrome *c* oxidase subunit I (COI) sequence information to determine the phylogenetic relationship between the new species and known closely related species.

Material and methods

Sampling and characterization

Feather mite sampling from three captive *C. boyciana* individuals was conducted in the same cage at Yesan Oriental Stork Park in Korea in October 2022, with permission from the Cultural Heritage Administration of Korea (B0030104016624). To minimize stress during the investigation, the storks were blindfolded and immobilized by the keepers; the procedure was completed within a maximum of five minutes for each individual. A new species of feather mites was identified from the wing and body feathers of the birds. The mites were carefully removed from the feathers using tweezers, and the collected mites were preserved in 95% ethanol solution. The specimens were mounted on microscope slides using a polyvinyl alcohol mounting medium (BioQuip, California, USA) after clearing with 10% lactic acid (Downs 1943; Han et al. 2016). Specimens were examined using a Dhyana 400DC camera (TUCSEN, Fuzhou, Fujian, China), Leica DM 2000 microscope (Leica, Wetzlar, Germany) with a drawing tube.

Descriptions of a new species followed the standard formats proposed for mites of the subfamily Ingrassiinae Gaud and Atyeo 1981 (Mironov and Proctor 2008; Stefan et al. 2013; Hernandes and Pedroso 2017; Han et al. 2021; Mironov and Hribar 2023). General morphological terms followed Gaud and Atyeo (1996) with minor corrections for coxal setation by Norton (1998). The classification and names of the birds followed those described by Gill et al. (2023). All measurements are in micrometres (μ m).

DNA sequencing and molecular analysis

Genomic DNA was extracted from three specimens of the new feather mite using the DNeasy Blood and Tissue Kit (QIAGEN, Hilden, Germany). The COI barcode fragment was amplified using primer set, bcdF05 (5'-TTTTCTACHAAY-CATAAAGATATTGC-3') and bcdR04 (5'-TATAAACYTCDGGATGNCCAAAAAA-3') (Dabert et al. 2008). Polymerase chain reaction (PCR) was conducted following the protocol of A-star *Taq* DNA Polymerase (BIOFACT, Daejeon, Korea). The cycle conditions were as follows: 5 min at 95 °C; 40 cycles at 95 °C for 15 sec, 50 °C for 30 sec, and 72 °C for 60 sec; and a final extension at 72 °C for 5 min (Dabert et al. 2008; Han et al. 2021).

Sequence editing including assembly, alignment, and trimming, was performed using the GENEIOUS v.10.2.5 software (Kearse et al. 2012). We obtained a 635–683 bp fragment sequence of the COI gene from three individuals per mite species. Subsequently, the sequences of these three specimens were used for phylogenetic analysis, together with 17 COI regions of the subfamily Ingrassiinae obtained from the National Center for Biotechnology Information (NCBI). In addition, we collected data from the NCBI on one individual of the subfamily Xolalginae Dubinin, 1953 (Gaud and Atyeo 1981a, b, 1996). The samples were aligned using GENEIOUS and the COI fragment was trimmed to 548 bp. A phylogenetic tree was constructed using COI fragments of the 21 feather mites (Table 1) and generated using the maximum-likelihood (ML) algorithm in PhyML v.3.0 (Guindon et al. 2010). To calculate nucleotide substitution, we used the Hasegawa-Kishino-Yano-1985 (HKY85) + gamma distribution and

Mite subfamily	Mite species	Host species	Sample source	GenBank accession No.	Reference
Xolalginae (outgroup)	Xolalgoides sp.	Vireo hypochryseus	Mexico	KU203107	Klimov et al. 2017
Ingrassiinae	Analloptes sp.	Xiporhynchus flavigaster		KU203108	
	Glaucalges sp.	Tyto alba	Germany	EU271955	Dabert et al. 2008
				EU271956	
	Glaucalges attenuatus	Asio otus		EU271957	
				EU271958	
	<i>Ingrassia</i> sp.	_	-	EU271954	Unpublishied
		-	_	GQ864347	Dabert et al. 2010
	Ingrassia chionis	Chionis albus	Antarctica	MZ489649	Han et al. 2021
				MZ489650	
	Ingrassia oceanodromae	-	_	OL685164	Unpublishied
	Ingrassia philomachi	Calidris pugnax	Kazakhstan	KU203104	Klimov et al. 2017
	Ingrassia veligera	Tringa glareola	Korea	MK031706	Han and Min 2019
	Ingrassiella sp.	Catharus fuscater	Peru	KU203102	Klimov et al. 2017
	Metingrassia pelecani	-	_	MG407963	Unpublishied
		_	-	MG408765	
		_	-	MG410544	
	<i>Mycterialges boycianae</i> sp. nov.	Ciconia boyciana	Korea	OR802170	This study
				OR802171	
				OR802172	
	Vingrassia velata	Anas crecca	Russia	KU203105	Klimov et al. 2017

Table 1. Feather mites used for the phylogenetic analysis in this study (COI barcode fragment).

invariant site (G+I) model, which was selected as the best model based on Smart Model Selection (SMS) (Lefort et al. 2017). The reliability of the tree was tested using 1000 bootstrap replicates (Felsenstein 1985).

Results

Systematics

Superfamily Analgoidea Trouessart & Mégnin, 1884 Family Xolalgidae Dubinin, 1953 Subfamily Ingrassiinae Gaud & Atyeo, 1981

Genus Mycterialges Gaud & Atyeo, 1981

Type species. *Mycterialges mesomorphus* Gaud & Atyeo, 1981, by original designation.

Remarks. To date, the genus *Mycterialges* has included only one described species, *M. mesomorphus*, found on the Wood Stork, *Mycteria americana* (Ciconiiformes: Ciconiidae), in Florida, USA (Gaud and Atyeo 1981a). In the review of feather mites associated with ciconiiforms in Africa, Gaud (1982) recognized one more *Mycterialges* species from the Saddle-billed Stork, *Ephippiorhynchus senegalensis* in Uganda. This unnamed species known only from a single male was illustrated but has never been formally described.

Mycterialges boycianae Shim, Han & Eo, sp. nov. https://zoobank.org/FAEA2BCB-5781-4E20-B15B-5B46F77DCC34

Type material. Male *holotype* (Prof. Eo lab, Kongju National University no. ESH_Em00001), and two male and three female *paratypes* (Prof. Eo lab no. ESH_Em00002-ESH_Em00006) from wing coverts and plumages of *Ciconia boyciana* (Ciconiiformes: Ciconiidae), Korea, Chungcheongnam-do, Yesan-gun, Yesan Oriental Stork Park, 36°32'32"N, 126°48'08"E, 17 October 2022, coll. by Shim JH and Han Y.-D.

Description. Male (holotype, range for 2 paratypes in parentheses) (Figs 1, 2, 5A-E). Length of idiosoma from anterior end to bases of setae h3 460 (465-470), greatest width 200 (210-220), length of hysterosoma 290 (285-300). Lateral margins of subcapitulum lateral margins with small tooth-like extensions. Prodorsal shield: narrow triangular plate occupying median part of prodorsum, posterior margin slightly convex and almost extending to level of scapular setae se, 81 (78–79) in length along midline, 45 (43–45) in width in posterior part (Fig. 1). Setae se separated by 75 (74–76), setae si situated slightly posterior to level of setae se. Scapular shields wide, with inner margin almost straight. Setae c2 represented by macrosetae, 370 (280-290) long, situated on soft tegument. Humeral shields well developed, fused ventrally with epimerites III. Humeral setae cp 390 (290-310) long, situated on posterior margins; setae c3 filiform, 93 (62–71) long, situated ventrally on anterior margin of humeral shields. Hyteronotal shield: anterior margin straight, anterior angles represented by narrow finger-like extensions anterior to setae d1, lateral margins with rounded convexities posterior to level of setae cp, length of shield from tips of anterior extensions to bases of setae h3 280 (270-275) (Fig. 1). Setae d2 represented by macrosetae, 350 (270-345) in length. Opisthosoma nearly as wide as one-third of anterior part of hysterosoma, lateral margins of opisthosoma between levels of setae e2 and h2 shallowly concave, width at level of setae h2 53 (45-52). Supranal concavity circular, separated from the terminal cleft. Terminal cleft small angular, 12 (12-13) long. Opisthosomal lobes fused to each other in basal part and separated by median sclerotized septum, free parts of lobes represented by short and rounded convexities on posterior margin of opisthosoma. Setae ps1 situated at level of setae h2. Distance between dorsal setae: c2:e1 140 (130-140), e1:d2 48 (43-49), d2:h3 100 (95-100), h3:h3 27 (26-29), ps1:ps1 14 (15).

Epimerites I fused into a Y with stem about 2/3 the length of epimerites. Coxal fields I–II open; coxal fields III almost closed, with small gap in anterior end. Coxal fields IV completely sclerotized, with posterolateral angles fused with lateral margins of hysteronotal shields. Setae 4a and 4b situated on inner margins of sclerotized coxal fields IV. Coxal setae 4b posterior to level of setae 3a. Genital apparatus 21 (20–21) long and 19 (18–20) wide, with base situated at level of anterior margin of trochanters IV. Paragenital apodemes fused into large teardrop-shaped sclerite 72 (72–78) long and 30 (27–32) wide, encircling genital apparatus and setae g. Genital papillae situated on anterior part of fused paragenital apodemes. Opisthoventral shields fused to each other at midline forming entire shield flanking anal field posterolaterally. Diameter of adanal suckers 7 (7–8). Distance between ventral setae: 4b:4b 30 (38–43), 4b:3a 21 (17–18), 4b:g 95 (81–86), g:ps3 37 (40–41), ps3:h3 70 (62–72).



Figure 1. Mycterialges boycianae sp. nov., male dorsal view.

Tarsi I, II without apico-dorsal extension. Ventral setae *la*, *s* of tarsi I and setae *la*, *wa* and *s* of tarsi II absent. Tibia I, II with spine-like ventral processes. Leg IV short and thickened, with tibia and tarsus extending beyond lobar apices.



Figure 2. Mycterialges boycianae sp. nov., male ventral view.

Length of tibia IV along external margin 19 (18–22). Tarsus IV conical, 25 (24–26) long, ambulacral disc absent, ambulacral stalk acute apically, setae d and e of tarsus IV filiform and spine, respectively. Length of solenidia: σ I 90

(64–77), σII 47 (43–46), σIII 68 (63–64), φI 100 (93–94), φII 105 (77–90), φIII 87 (83–88), φIV 33 (32–32).

Female. (Range for 3 paratypes) (Figs 3, 4, 5F, G). Length of idiosoma from anterior end to bases of setae h3 425–440, greatest width 190–200, length of hysterosoma 270–275. Subcapitulum shaped as in male. Prodorsal shield: shaped almost as in male, except posterior margin blunt-angular and extending beyond level of setae *si*, 85–92 long, 58–62 wide (Fig. 3). Setae *se* separated by 85–88. Scapular shields more narrow than in male. Humeral shields not developed. Setae c2 short filiform, situated on soft tegument. Setae *cp* situated ventrally on soft tegument, 135–150 long. Hysteronotal shield: large longitudinal plate occupying median part of hysterosoma; anterior margins almost straight, extending to or beyond level of setae *cp*; lateral margins slightly concave; posterior margin deeply concave, posterior angles encompassing bases of setae e2; greatest length 185–190, greatest width 74–83. Setae *d1, e1* and *e2* situated on hysteronotal shield, setae *d2* situated on striated tegument. Distance between dorsal setae: *c2:d2* 92–95, *d2:e2* 112–118, *e2:h3* 50–55, *d2:d2* 91–93, *e2:e2* 71–75, *h2:h2* 59–65, *h3:h3* 49–50.

Epimerites I fused into a Y, stem about half as long as epimerites. Epigynum shaped as thick bow-shaped transverse bulk with a pair of acute posterior branches, 29–34 long, 56–63 wide. Apodemes of oviporus long, posterior ends extending to midlevel of trochanters III (Fig. 4). Seta *4a* situated on epigynum. Setae *4b*, *g*, *3a*, and *4a* short filiform, not exceeding length of femorogenua III, IV. Setae *h3* slightly shorter than setae *h2*.

Legs I, II as in the male. Leg IV with distal half of tarsus extending beyond posterior end of opisthosoma. Tarsi III, IV without apical spines. Length of tarsi III and IV 73–75 and 81–84, respectively. Lengths of solienidia: σ I 67–71, σ II 24–33, σ III 49–52, φ III 57–67, φ IV 91–100 (Fig. 5F, G).

Differential diagnosis. The genus *Mycterialges* has included only the type species, Mycterialges mesomorphus, and one additional undescribed species (Gaud and Atyeo 1981a; Gaud 1982). The new species Mycterialges boycianae sp. nov. differs from M. mesomorphus by a number of characters: in males of *M. boycianae*, the prodorsal shield consists of a single triangular plate, the anterior part of the hysteronotal shield is widened and has a pair of narrow extensions, the paragenital apodemes are fused into a large teardrop sclerite encompassing genital apparatus, the legs IV are much shorter than legs III, and tibia + tarsus IV are shorter than femoragenu IV, tarsus IV is conical and ambulacral disc of tarsus IV is absent; in females, the posterior margin of prodorsal shield is blunt-angular and extends slightly beyond the level of setae si, the hysteronotal shield is as wide as the prodorsal shield and its posterior margin is deeply concave, setae e2 are situated on the posterior corners of the hysteroronotal shield, and setae g and 3a are situated on the same transverse level. In males of M. mesomorphus, the prodorsal shield consists of two plates (triangular anterior parts and trapezoidal posterior part), the anterior part of the hysteronotal shield is narrowed and without extensions, the paragenital apodemes are fused into ovate sclerites around genital apparatus and with a pair of posterior projections, the legs IV are almost as long as legs III, and tibia + tarsus IV are much longer than femoragenu IV, tarsus IV has a claw-like apical process, and ambulacral disc of tarsus IV is narrowly lanceolate; in females, the posterior margin of prodorsal shield is straight and does not extend to the level









Figure 5. *Mycterialges boycianae* sp. nov., details, ventral view **A** opisthoma of male, dorsal view **B** leg I of male **C** leg II of male **D** leg III of male **E** leg IV of male **F** tibia and tarsus III of female **G** tibia and tarsus IV of female.

of setae *si*, the hysteronotal shield is narrow, approximately half as wide as the prodorsal shield and its posterior margin is straight, setae e2 are situated on the soft tegument at the level of the posterior margin of the hysteronotal shield, and setae g are anterior to level of setae 3a. Actually, M. mycterialges sp. nov. is much more similar to the unnamed Mycterialges species, known only from male and illustrated but not described (Gaud 1982: fig. 6a, b), in sharing the following features: the prodorsal shield is triangular, the anterior end of the hysteronotal shield has a pair of narrow extensions, legs IV are much shorter that legs III, and tibia+tarsus IV are shorter than femoragenu IV, tarsus IV is conical, and ambulacral disc of pretarsus IV is absent. Males of M. boycianae differs from those of the unnamed Mycterialges species in the following features: setae d2 are represented by macrosetae extending beyond the posterior margin of opisthosoma, setae cp are situated on the humeral shields, and the paragenital apodemes fused into the teardrop-shaped sclerite free from epimerites IV. In the male of the unnamed *Mycterialges* species, setae d2 extend to midlevel between setae e2 and h2, setae cp are situated on striated tegument, and the paragenital apodemes fused into the teardrop-shaped sclerite are fused with the inner tips of epimerites IV.

Etymology. The specific name is taken from the species epithet of the type host and is a noun in the genitive case.

Phylogenetic relationships based on mtDNA COI

The ML phylogenetic tree of the COI barcode fragment showed *Mycterialges boycianae* sp. nov. to be grouped within the subfamily Ingrassiinae clade with three individuals of *M. boycianae*, exhibiting 93.7% bootstrap support for this grouping. Among the COI sequences collected from NCBI, the genus *Glaucalges* formed the clade closest to *M. boycianae* (Fig. 6). The genetic distance between *M. boycianae* and *Glaucalges* species was estimated to be ~16.1–16.2%.



Figure 6. Maximum-likelihood phylogenetic tree of COI barcode fragment for members of the subfamily Ingrassiinae. Bootstrap percentages of more than 50% are shown. Scale bars indicate the number of substitutions per nucleotide site. The subfamily Xolalginae is the outgroup taxon.

Discussion

This study describes a new feather mite species, Mycterialges boycianae sp. nov. found on the wings and body of captive Ciconia boyciana at the Yesan Oriental Stork Park in Korea. The genus Mycterialges has the following features: in both sexes, tarsi I, II only have two and one ventral setae, respectively, and the ambulacral disc is inverted triangle-shaped with a concave middle; in males, the opisthosomal lobes are fused and bluntly rounded, leg IV is hypertrophied; in females, the epigynum is short and straight (Gaud and Atyeo 1981a, 1996). Mycterialges boycianae has all these main characteristics (Figs 1-5), but exhibits significant variation from the type species in the legs IV. In the case of the type species M. mesomorphus, the male legs IV are hypertrophied, but not to the terminal width, and there is an ambulacrum (Gaud and Atyeo 1981a). In contrast, legs IV of M. boycianae and M. sp. (Gaud and Atyeo 1981a, 1996), are hypertrophied to the extent of the terminal width, have a femorogenu that combines the femur and genu, and have a claw instead of an ambulacrum (Figs 1-2, 5) (Gaud and Atyeo 1996). Despite these significant differences, no other species have been identified in Mycterialges apart from the type species so far. Therefore, we have included the newly discovered feather mite in Mycterialges based on the form of M. sp., despite the lack of precise identification by Gaud and Atyeo (1981a, 1996). We observed that the mites discovered in the genus Mycterialges exhibit significant differences in legs IV, thus suggesting that there is a need to redefine this genus.

We showed the phylogenetic relationship of Ingrassiinae using the COI barcode fragment (Fig. 6). However, despite gathering all available Ingrassiinae data from the NCBI, our tree could only provide minimal information. This is due to the fact that, while the Ingrassiinae consists of 16 genera and 106 species (Gaud and Atyeo 1981a; Mironov and Galloway 2002; Mironov et al. 2005; Dabert et al. 2008; Constantinescu et al. 2013; Stefan et al. 2013; Hernandes 2014; Li and Zhang 2016; Mironov et al. 2017; Hernandes and Pedroso 2017; Han et al. 2021; Hernandes and Brito 2022), our tree data includes only seven genera and 12 species, some of which have not been accurately described. Therefore, it is necessary to collect more data on mites to obtain more accurate results (Maddison and Knowles 2006; Knowles and Klimov 2011).

Finally, we discuss the situations faced by *M. boycianae*. This mite's host, *C. boyciana*, is not only an endangered species in Korea, but is also listed as an 'Endangered' (EN) species on the International Union for Conservation Nature (IUCN) Red List (BirdLife International 2018). Moreover, the nesting sites of the Oriental Stork are extremely limited and confined to parts of Russia and China (Zhou et al. 2013; BirdLife International 2018). Given its high host specificity, this situation could be extinction-threatening for *M. boycianae*, a permanent ectosymbiont (OConnor 1982; Doña et al. 2019). Therefore, we believe that it is necessary to investigate the distribution, biology, ecology, and conservation status of feather mites, including *M. boycianae*, to confirm whether ectosymbionts are at risk of extinction.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Funding acquisition: YS. Investigation: YDH, JHS. Methodology: JHS, YDH. Project administration: SK, SHE, DH. Supervision: SHE. Writing – original draft: JHS. Writing – review and editing: SHE, YDH.

Author ORCIDs

Jeong Hun Shim [©] https://orcid.org/0009-0000-1858-7725 Yeong-Deok Han [©] https://orcid.org/0000-0002-6625-8966 Sukyung Kim [©] https://orcid.org/0000-0003-3545-0282 Dongsoo Ha [©] https://orcid.org/0000-0002-1943-9190 Yongun Shin [®] https://orcid.org/0000-0001-7491-994X Soo Hyung Eo [©] https://orcid.org/0000-0001-6719-1612

Data availability

All of the data that support the findings of this study are available in the main text.

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