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ON IDENTIFICATION OF SPECIES IN THE FEATHER MITE GENUS *LAMINALLOPTES* DUBININ, 1955 (ACARI: ALLOPTIDAE)

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ABSTRACT: Based on partial sequences of two mitochondrial genes, the ribosomal 12S rRNA (12S) and ribosomal 16S rRNA (16S), we found that males and females of the two closely related feather mite species, *Laminalloptes minor* (Trouessart, 1885) and *L. simplex* (Trouessart, 1885), have been erroneously associated in the revision of the genus *Laminalloptes* (Atyeo and Peterson 1967). Careful examination of the morphological features in voucher specimens used in the molecular study and additional museum specimens revealed characters confirming this finding and allowed us to unmistakably associate males and females for each of these two species. A new identification key to *Laminalloptes* species is proposed.

KEY WORDS: Alloptidae, Laminalloptes, systematics, morphology, mitochondrial genes, Phaethontidae.

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INTRODUCTION

The feather mite genus *Laminalloptes* Dubinin, 1955 (Alloptidae: Alloptinae) includes three species associated with tropicbirds, or phaetons, (Pelecaniformes: Phaethontidae) (Dubinin, 1955; Atyeo and Peterson 1967). In the plumage of their hosts, these mites occupy the flight and covert feathers of the wings where they are located in corridors of the ventral surface of the vanes. All three species have been recorded from three extant species of phaetons, *Phaethon aethereus* Linnaeus, *P. lepturus* Daudin and *P. rubricauda* Boddaert (Trouessart 1885; Dubinin 1955; Atyeo and Peterson 1967; Miller and Miller 1986; Swift 1997; Bishop and Heath 1998; Hernandes *et al.* 2015).

In the latest revision of the genus, Atyeo and Peterson (1967) provided seemingly exhaustive redescriptions and detailed illustrations of all included species, *Laminalloptes phaetontis* (Fabricius, 1775), *L. minor* (Trouessart, 1885), and *L. simplex* (Trouessart, 1885), and it seemed that there were left no problems in the systematics of these well discernible feather mite species. In the course of the PhD project "Diversity, ecology and evolution of feather mites in seabirds", the junior author found that the pairwise genetic distances between two species, *L. minor* and *L. simplex,* are unexpectedly low. We have come up to conclusion that DNA sequence data suggest wrong sex association by previous studies. A precise morphological study of the specimens used in the molecular study and morphological analysis of additional collection samples loaned from various museums has confirmed our assumption that males and females of *L. minor* and *L. simplex* were incorrectly associated in the revision of *Laminalloptes* (Atyeo and Peterson 1967).

This error can probably be explained by the fact that the sexual dimorphism in *Laminalloptes* species is greatly pronounced and from the first glance it seems impossible to find any morphological features characterizing simultaneously both the male and female of *L. minor* and *L. simplex*. Among the three species of the genus, *L. phaetontis* is an unmistakable species because of its giant size reaching nearly 1 mm so its sexes can be easily associated. The two other species, *L. minor* and *L. simplex,* are smaller and similar in size (males about 700 μm, females 500–600 μm). In the course of our study we found differences in the structure of the two anterior pairs of legs that can unambiguously correlate males and females of each *L. minor* and *L. simplex.* In the present work we discuss genetic data supporting our conclusion and provide detailed illustrations of the leg structures of all *Laminalloptes* species and give a new key to the species. Since the original descriptions of *L. minor* and *L. simplex* by Trouessart (1885) were only from males, the determination of these two species is stated here based on this sex.

MATERIAL AND METHODS

The main part of the material used in the presents study was collected by Drs. Elena Gómez-Díaz, Raül Ramos, and Samir Martins from live

red-billed tropicbirds, *Phaethon aethereus,* on Raso Island, Cape Verde in 2006–2008. Bird capturing and handling as well as mite sampling were made in accordance with good animal practice as defined by the current European legislation and under permissions from the corresponding governmental authorities of Cape Verde. Mites were collected using the dust-ruffling method (Walther and Clayton 1997) or direct sampling with fine tweezers. Collected material was preserved in vials with absolute ethanol.

Molecular study. We individually extracted DNA from eight specimens of *Laminalloptes* using DNeasy Tissue Kit (Qiagen, Valencia, CA, USA) and the nondestructive method described by Dabert *et al*. (2008). This method allows to maintain the feather mite exoskeleton intact for subsequent morphological identification. All mites subjected to molecular analyses were mounted and kept as reference vouchers for morphological examination. Initially, based on the old morphological criteria, three of these specimens were identified as *L. minor* (all females) and five specimens as *L. simplex* (four males and one female) (Table 1).

Partial sequences of two mitochondrial genes: the ribosomal 12S rRNA (12S) and the ribosomal 16S rRNA (16S) were amplified for each feather mite using the following primers: SR-J-14199 (5'-TACTATGTTACGACTTAT-3') and SR-N-14594 (5'-AAACTAGGATTAGATACCC-3') for 12S gene (Kambhampati and Smith 1995) and 16SA2 (5'-TTTAATTGGTTACTTGTATGAATG-3') and 16C2 (5'-CGCTGTTATCCCTAGAGTAT-3') for 16S gene (Dabert*et al*. 2001). Polymerase chain reactions (PCRs) were carried out in a total volume of 25 µl containing 2.5 µl 10x reaction buffer with 15 mM $MgCl_2$ (Roche Diagnostics), 2 mM $MgCl_2$, 0.2 mM of each dNTP, 0.4 µM of each primer, 1.25 U *Taq* DNA polymerase (Roche Diagnostics) and 2 µl of DNA template. Amplification conditions for the 12S rRNA gene consisted of an initial step of 2 min at 94°C, followed by 10 cycles of denaturation at 94°C for 30 sec, annealing at 40°C for 30 sec, and extension at 68°C for 1 min, and 35 cycles of denaturation at 94°C for 30 sec, annealing at 43°C for 30 sec, and extension at 68°C for 1 min, with a final step of 5 min at 72°C. For the 16S rRNA gene, the PCR conditions followed Black and Piesman (1994). Amplification products were separated by electrophoresis on 2% agarose gel and visualized under UV light. Samples containing visible bands were sent for sequencing to Beckman Coulter Genomics (France, GenBank Accession nos KX372354–KX372371).

DNA sequences were checked and edited using Bioedit version 7.0.5.3 (Hall 1999) and all variable sites were confirmed by visual inspection of the chromatograms. Sequences were aligned for each gene independently using MAFFT version 7, with default parameters. Basic genetic statistics and standard diversity estimates (number of polymorphic sites, number of haplotypes, nucleotide diversity and haplotype diversity) were calculated for each gene and for each mite species using DNASP v.5 (Librado and Rozas 2009). Mean genetic distances between mite species and between individuals within each mite species were calculated with MEGA 4.1 software using Kimura's 2-parameter (K2P) distance model (Tamura el al. 2007).

Morphological study. For species identifications and subsequent morphological study, cuticle skeletons of samples retained after the DNA extraction as well as the intact feather mite specimens from ethanol were cleared in lactic acid for 24 h at room temperature and mounted on microscope slides in PVA medium (BioQuip Products, Rancho Dominguez, California). Slide-mounted mites were studied using a Leica DM2500 microscope (Leica Microsystems Inc.) with differential interference contrast (DIC) and a camera lucida. General morphological terms, body and leg chaetotaxy follow those in Gaud and Atyeo (1996).

Abbreviations used in collection numbers of depositories, where additional materail was loaned: NU (collection of W.T Atyeo)—University of Michigan, Ann Arbor, USA; MNHN (collection of E.L. Trouessart)—Museum National de Histoire Naturelle, Paris, France; ZISP—Zoological Institute, Russian Academy of Sciences, Saint Pe-tersburg, Russia.

RESULTS

Based on the morphological determination of *Laminalloptes simplex* and *L. minor* given in the generic revision by Atyeo and Peterson (1967), the pairwise K2P genetic distances between the two species were 4.18% (SE = 0.006) for 12S gene and 4.87% (SE=0.009) for 16S gene. When morphological determination of *Laminalloptes* species presented by our morphological study is taken into account, the sequence divergences between these two species appeared significantly higher, 20.91% (SE = 0.029) for 12S gene and 22.57% (SE = 0.044) for 16S gene. Furthermore, average genetic divergences between individuals within species also differed depending on previous or our morphological determination of the species (Table 1).

When the old determination was considered, genetic distances between individuals within *L. simplex* ranged between 8.36% for 12S gene and 9.2% for 16S gene. When the new "correct" determination of these *Laminalloptes* species was used, sequence divergences were significantly lower for both genes (0 and 0.4%, respectively). Basic genetic statistics, such as the number of polymorphic sites, haplotype diversity, nucleotide diversity, and average number of nucleotide differences, for both mitochondrial genes for *L. minor* and *L. simplex* are also shown in Table 1.

SYSTEMATICS

Family Alloptidae Gaud, 1957
Subfamily Alloptinae Gaud, 1957
Genus *Laminalloptes* Dubinin, 1955

Laminalloptes phaetontis (Fabricius, 1775)

(Figs. 1, 4A)

Acarus phaetontis Fabricius 1775: 815, No. 25.

Gamasus phaetontis, Fabricius 1805, Syst. Antliat., p. 363, no 16 (cited after: Atyeo and Peterson 1967).

Dermaleichus phaetonis, Buchholz 1869: 52, figs. 39–45.

Alloptes phaetontis, Trouessart 1885: 67; Oudemans 1929: 694.

Laminalloptes phaetontis, Dubinin 1955: 270, figs. 8 (1, 2), 10; Atyeo and Peterson 1967: 449, figs. 1–8; Hernandes *et. al*. 2015: 82.

Type host: *Phaethon lepturus fulvus* von Brandt.

Material examined. From *Phaethon lepturus* Daudin: BERMUDA ISLANDS (British Overseas Territory)—3 males, 2 female (ZISP 19882; 19883), 5 May 1881, V.B. Dubinin. From *Phaethon lepturus dorotheae* Mathews: FEDERAL STATES OF MICRONESIA**,** Caroline Islands, Kusaie Island (now Korsae Island)—1 male, 1 female (NU 21300), April, 1931, N. Wilson.

From *Phaethon rubricauda* Boddaert: no location data—1 male, 3 females (ZISP 19884), 1843, V.B. Dubinin. From *Phaethon aethereus* Linnaeus: CAPE VERDE, Raso Island (16°36′N, 24°35′W) —1 male (ZISP 6900), (bird ring: 7500202), 4 April 2008, col. S. Martins; 1 female ZISP 6905 (bird ring: 7500201), 1 April 2008, col. R. Ramos; 1 female—(ZISP 6906) (bird ring: 7500203), 6 April 2008, col. R. Ramos; 1 female (ZISP 6907) (bird ring: 7500194), 24 March 2008, col. S. Martins.

Laminalloptes phaetontis is an unmistakable species among all feather mites mostly because of its really giant size reaching nearly 1 mm long. Among *Laminalloptes* species it is probably the most derived species because of the greatly modified tarsi I and II in males and females (Figs. 1A, E). Interestingly because of extremely large size of this species it is possible to distinguish minute rudiments of the proral setae *p* and *q* on all tarsi (Figs 1A–F). These setae are considered to be lost in all other Analgoidea.

Laminalloptes simplex (Trouessart, 1885)

(Figs. 2, 4B)

Alloptes phaetontis var. *simplex* Trouessart 1885: 67. (Syntypes, slides 40C7, 40C12 in MNHN, not studied.)

Laminalloptes microphaeton Dubinin 1955: 271 (part), figs. 8 (3, 5), 9 (2) (female of *L. minor*), 11.

Laminalloptes simplex, Atyeo and Peterson 1967: 457 (part), figs. 17 (male), 19 (female, not 18), 9, 10 (male tarsi), 15, 16 (female tarsi, not 11, 12); Hernandes *et. al*. 2015: 83.

Type host: *Phaethon aethereus* Linnaeus.

Material examined. From *Phaethon rubricauda melanorhynchus* Mathew: USA, Central Pacific, Midway Atoll, Eastern Island—2 males (NU 4006, 4812), 20 July 1962, col. H.I. Fisher.

From *Phaethon* sp.: USA, Central Pacific, Midway Island—1 female (NU 4002), 4 December 1959, col. J.C. Downey. From *Phaethon aethereus* from CAPE VERDE, Raso Island (16°36'N 24°35'W): 1 male (ZISP 6891*), (bird ring: 14.s.a), 13 January 2006, col. E. Gómez-Díaz; 2 males (ZISP 6900, ZISP 6895*) (bird ring: 7500202), 4 April 2008, col. S. Martins; 1 male (ZISP 6892*) and 1 female (ZISP 6896*) (bird ring: 7500201), 1 April 2008, col. R. Ramos; 1 male (ZISP 6893*) and 1 female (ZISP 6897*) (bird ring: 7500197), 30 March 2008, col. S. Martins; 1 male (ZISP 6894*) and 1 female (ZISP 6898*) (bird ring: 7500210), 8 April 2008, col. S. Martins.

Asterisk (*) indicates specimens used for extracting sequences.

Access numbers of molecular sequences (fragments 12S and 16S, respectively): ZISP 6891 (KX372358, KX372367), ZISP 6892 (KX372362, KX372371), ZISP 6893 (KX372359, KX372368), ZISP 6894 (KX372360, KX372369), ZISP 6895 (KX372361, KX372370), ZISP 6896 (KX372355, KX372364), ZISP 6897 (KX372356, KX372365), ZISP 6898 (KX372357, KX372366).

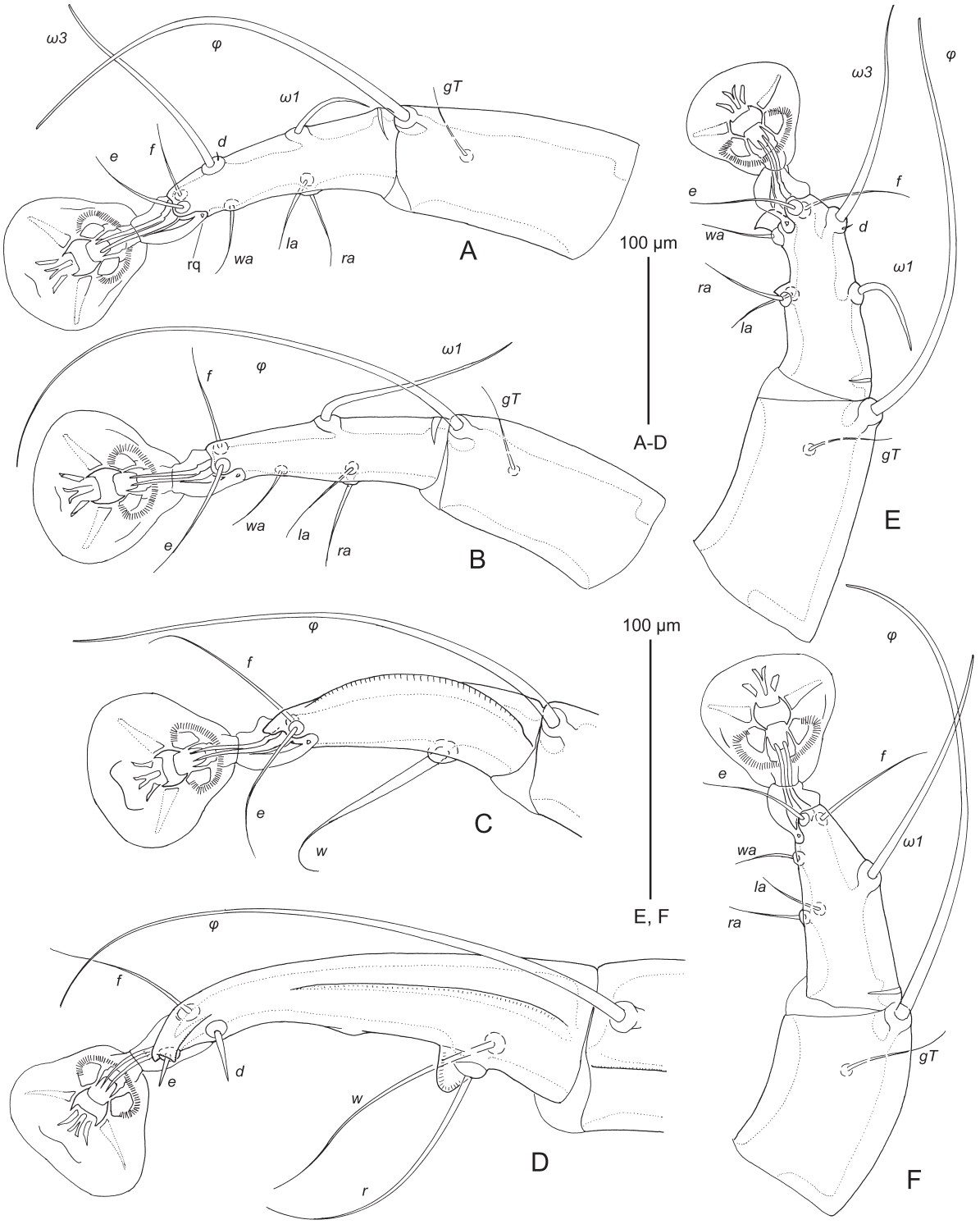

Fig. 1. *Laminalloptes phaetontis*, distal segments of legs. A—tarsus and tibia I of male, B—tarsus and tibia II of male, C—tarsus III of male, D—tarsus IV of male, E—tibia and tarsus I of female, F—tibia and tarsus II of female. rq—rudimentary proral seta *q*.

The only clear character of *Laminalloptes simplex* allowing to associate univocally its males and females and distinguish them from those of *L. minor* is the position of three ventral setae on tarsi I and II. In this species, bases of the setae *la, ra*, and *wa* are distinctly closer to each other (Fig. 2A, B, E, F), while in *L. minor*, the seta *wa* is situated distinctly anterior from the setae *la* and *ra* (Figs. 3A, B, E, F).

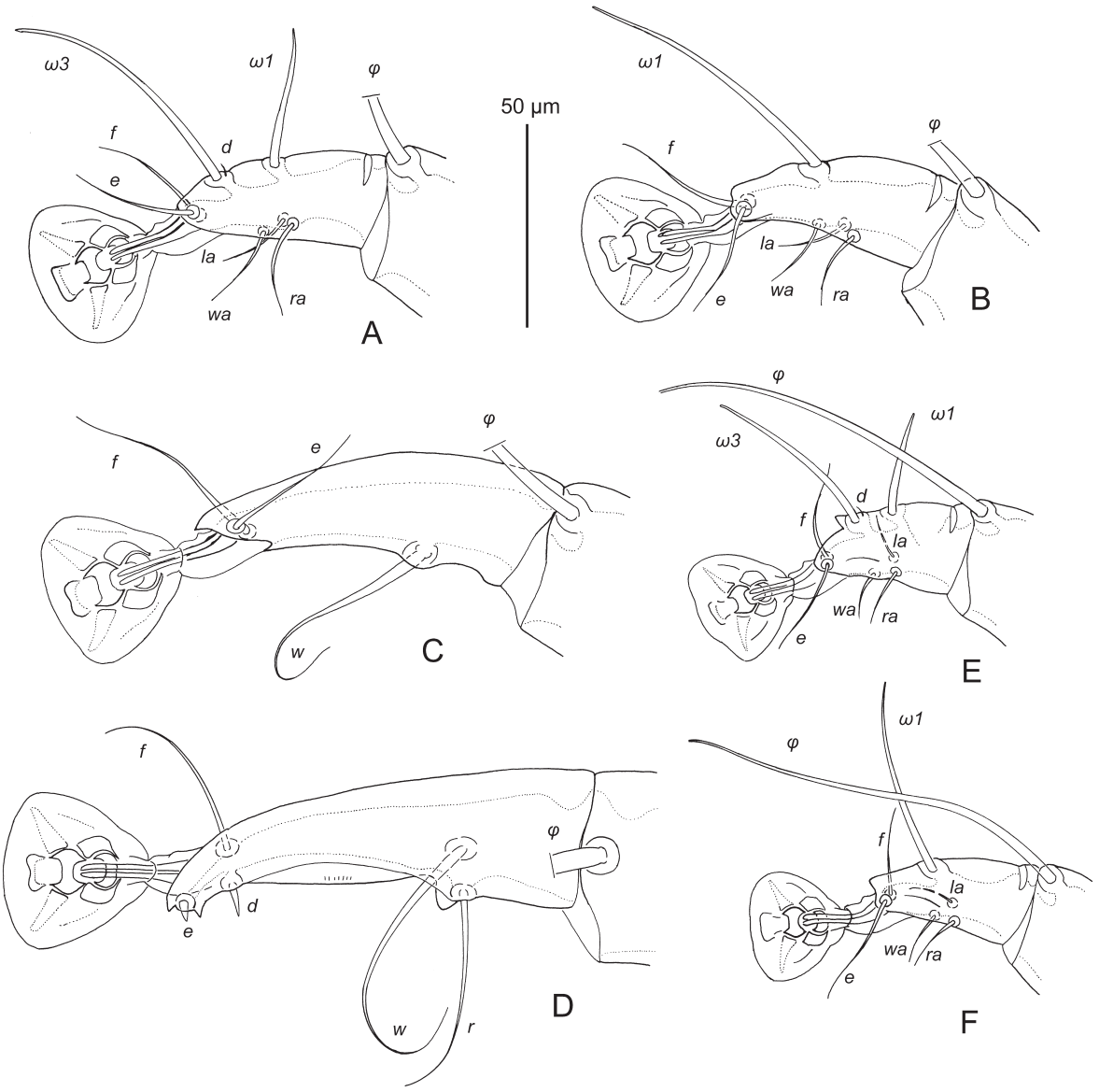

Fig. 2. *Laminalloptes simplex*, tarsi I–IV. A—tarsus I of male, B—tarsus II of male, C—tarsus III of male, D—tarsus IV of male, E—tarsus I of female, F—tarsus II of female.

Curiously Atyeo and Peterson (1967: Figs. 9–16) had actually illustrated these diagnostic features of the legs, but did not recognize them and associated males and females incorrectly. Thus, in their figures, it is clearly illustrated that three ventral setae of tarsi I and II in males of *L. simplex* are grouped near the center of the segment, while on tarsi of females of "*L. simplex*", the seta *wa* is situated distinctly anterior from the two others situated in the center.

***Laminalloptes minor* (Trouessart, 1885)**

(Fig. 3, 4C)

Alloptes phaetontis var. *minor* Trouessart 1885: 67. (Syntypes, slide 40C8 in MNHN, not studied.)

Alloptes longipes Ewing 1911, Psyche, 18:41–42, PI. 7, fig. 3.

Laminalloptes pseudophaetontis Dubinin 1955: 273, figs. 8 (4, 6), 9 (1).

Laminalloptes simplex, Atyeo and Peterson 1967: 457 (part), figs. 11, 12 (female tarsi, not 15, 16), 13, 14 (male tarsi), 18 (female, not 19), 20–22 (male); Hernandes *et al*. 2015: 83.

Type host: *Phaethon aethereus* Linnaeus.

Material examined. From *Phaethon rubricauda melanorhynchus* Mathew: USA, Central Pacific, Midway Atoll, Eastern Island—1 female (NU 4809), 20 July 1962, col. H.I. Fisher. From *Phaethon* sp.: USA, Central Pacific, Midway Island—2 males (NU 4002), 4 December 1959, col.

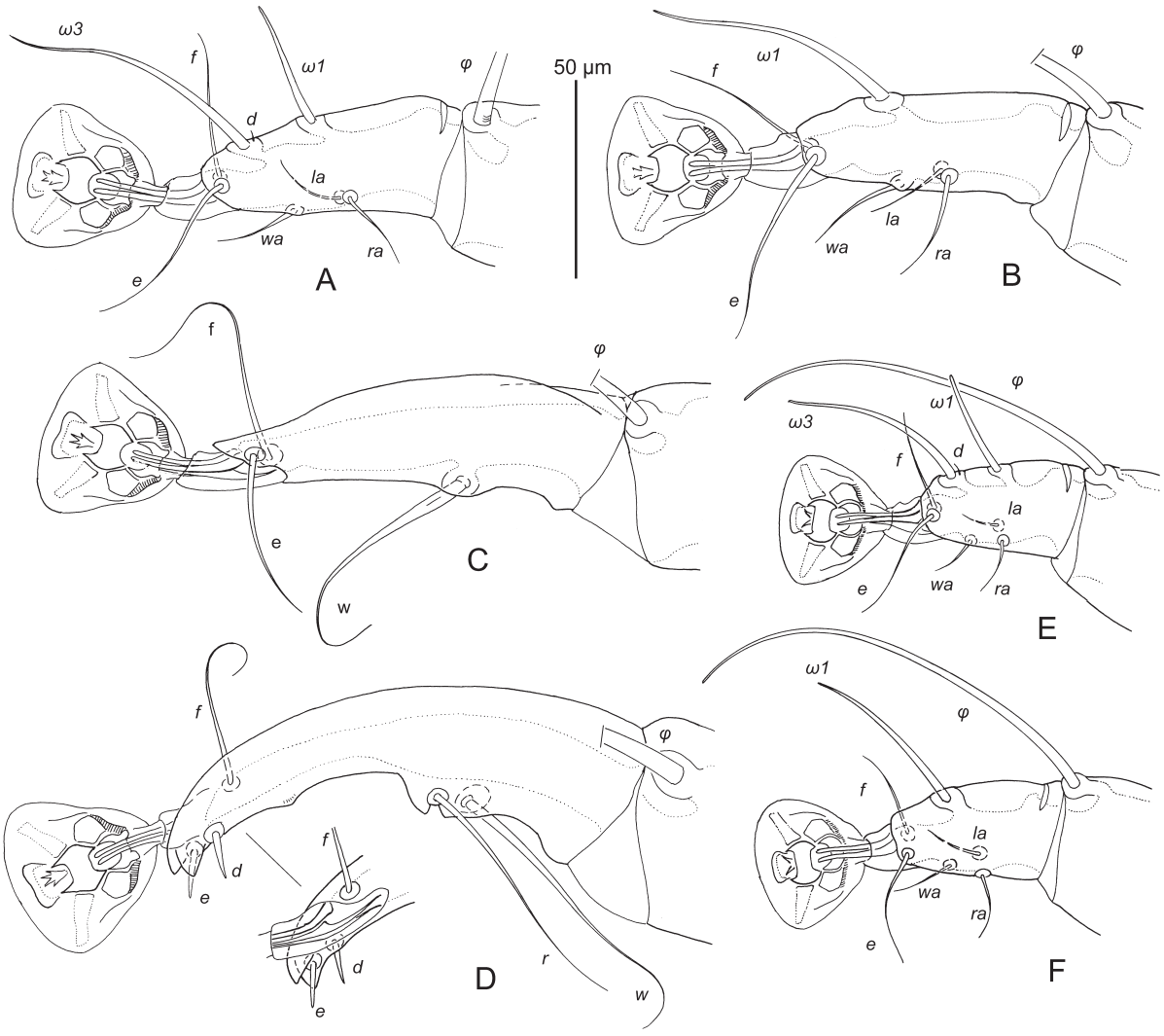

Fig. 3. *Laminalloptes minor*, tarsi I–IV. A—tarsus I of male, B—tarsus II of male, C—tarsus III of male, D—tarsus IV of male, E—tarsus I of female, F—tarsus II of female.

J.C. Downey. From *P. aethereus*: CAPE VERDE, Raso Island (16°36'N 24°35'W)—1 male (ZISP 6895), 2 females (ZISP 6889*, 6890), (bird ring: 7500202), 4 April 2008, col. S. Martins

Access numbers of molecular sequences (fragments 12S and 16S, respectively): ZISP 6889 (KX372354, KX372363).

The only character of *Laminalloptes minor* providing correct association of its males and females is the position of three ventral setae of tarsi I and II. In *L. minor*, the seta *wa* is situated distinctly anterior from the setae *la* and *ra*, i.e. almost at the midlength between these setae and the base of the ambulacral stalk (Figs 3A, B, E, F).

Key to *Laminalloptes* species

(Males and females)

1. In both sexes, sclerotized areas flanking bases of coxae I, II wide, with flame-shaped posterior margin, seta *wa* of tarsi I, II closer to base of ambulacral stalk than to seta *ra* (Figs. 1A, B, E, F). In males, length of idiosoma 900–1000 µm; tarsi I, II nearly 3 times longer than wide at base; femora III, IV each with long and acute paraxial spine directed backward, seta *d* on tarsus IV more distant from tarsal apex than seta *f* (Fig. 1D). In female, length of idiosoma 700–800 µm, tarsus I with apicoventral claw-like extension (Fig. 1E), tibia I nearly 2 times longer than wide at base .... *L. phaetontis* (Fabricius, 1775)
— In both sexes, sclerotized bands flanking bases of coxae I, II narrow, with smooth posterior margin;

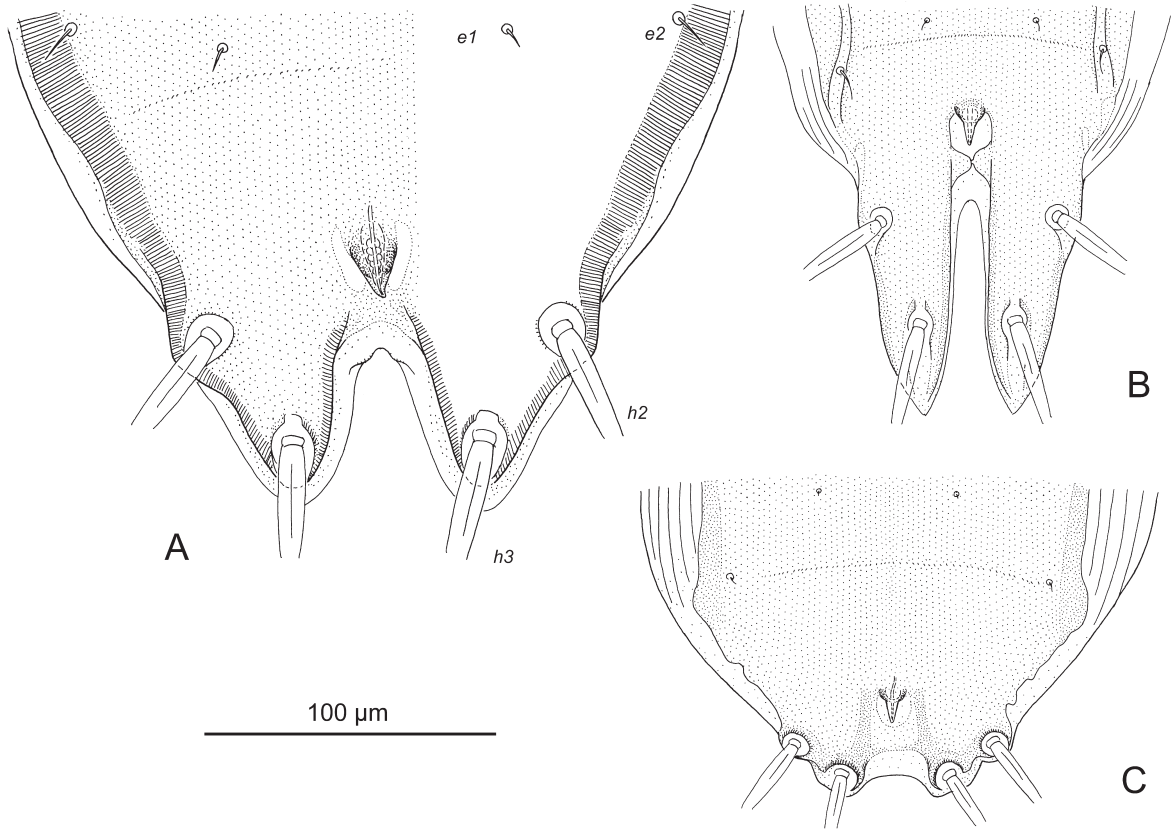

Fig. 4. Females of *Laminalloptes* species, posterior end opisthosoma. A—*Laminalloptes phaetontis*, B—*L. simplex*, C—*L. minor*.

seta *wa* of tarsi I, II situated approximately at mid-length between ambulacral stalk and seta *ra* or closer to the latter (Figs. 2E, 3E). In males, length of idiosoma about 700 µm; femora III, IV without acute paraxial spine, or small spine can present on femora IV, seta *d* on tarsus IV more distant from tarsal apex than seta *f* (Fig. 1D). In female, length of idiosoma 500–600 µm, tarsus I without apicoventral claw-like extension, tibia I less than 1.5 times longer than wide at base.....2

2. In both sexes, bases of ventral setae *ra, wa* and *la* of tarsi I, II grouped close to each other (Figs. 2E, F). In male, setae *h2* simple whip-like, coxal fields III without oblique sclerite running along central part of these fields; tarsus IV with one small blunt spine at level of setae *r* and *w*, seta *d* of tarsus IV twice longer than seta *e* and distinctly moved from tarsal apex (Fig. 2D). In females, idiosoma noticeably elongate, about 2.5 times longer than wide, opisthosomal lobes long and narrow, two times longer than wide at base, terminal cleft narrow U-shaped, tarsus I with small spine anterior to base of solenidion *ω3* (Figs. 3E, 4B).....
.....*L. simplex* (Trouessart, 1885)

— In both sexes, base of ventral seta *wa* of tarsi I, II not close to bases of setae *ra* and *la* (Figs. 3E, F). In male, setae *h2* with ovate-shaped enlargement in medial part; coxal fields III with narrow sclerite running obliquely along central part of these fields; tarsus IV with two blunt spines near bases of setae r and w (Fig. 3D); setae *d* and *e* of tarsus IV spiculiform, similar in length and both situated near its apex. In females, idiosoma robust, less than 2 times longer than wide; opisthosomal lobes short, scarcely expressed, terminal cleft shallow, tarsus I without spine near base of solenidion *ω3* (Figs. 3E, 4C).....*L. minor* (Trouessart, 1885)

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Table 1.

Basic genetic statistics based on two mitochondrial genes (12S and 16S) of the two mite species inhabiting *Phaeton aethereus*, considering the old morphological determination (A) and the new determination (B). Number of individuals sequenced (N), number of polymorphic sites (Np), number of haplotypes (Nh), haplotype diversity (h), nucleotide diversity (π), average number of nucleotide differences (k), and average genetic divergence between individuals within species (d) are shown.

Mite species	N	Np		Nh		h		π		k		d	
		12S	16S	12S	16S	12S	16S	12S	16S	12S	16S	12S	16S
(A) *L. simplex* (4M, 1F)	5	56/310	28/165	2	3	0.4	0.7	0.073	0.079	22.4	11.4	0.084 (SE=0.011)	0.092 (SE=0.018)
L. minor (3F)	3	0/308	1/143	1	2	0	0.667	0	0.005	0	0.667	0	0.005 (SE=0.004)
(B) *L. simplex* (4M, 3F)	7	0/308	2/143	1	3	0	0.524	0	0.004	0	0.571	0	0.004 (SE=0.003)
L. minor (1F)	1	-	-	-	-	-	-	-	-	-	-	-	-

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