RESEARCH ARTICLE



One new species of the *Clubiona obesa*-group from China, with the first description of *Clubiona kropfi* male (Araneae, Clubionidae)

Pan-Long Wu¹, Feng Zhang¹

I The Key Laboratory of Invertebrate Systematics and Application, College of Life Sciences, Hebei University, Baoding, Hebei 071002, P. R. China

Corresponding author: Feng Zhang (dudu06042001@163.com)

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Abstract

The present paper describes two *Clubiona obesa-group species: Clubiona bicuspidata* **sp. n.** and the male *Clubiona kropfi* Zhang, Zhu & Song, 2003, which is described for the first time.

Keywords

Spiders, taxonomy, Clubiona obesa-group

Introduction

Clubiona Latreille, 1804, is the largest genus of the spider family Clubionidae. The genus encompasses approximately 465 species at present, is widely distributed around the world (except in South America) and has been revised both regionally and on a worldwide scale (Dondale and Redner 1976; Mikhailov 1990, 1991, 1995, 2002; Deeleman-Reinhold 2001; Platnick 2014). Because *Clubiona* is a large genus, several authors have suggested subdivisions of the genus into species groups (Simon 1932; Gertsch 1941; Lohmander 1944; Locket and Millidge 1953; Edwards 1958; Mikhailov 1995) and even subgenera (Lohmander 1944; Mikhailov 1990, 1991, 2002; Wunderlich 2011).

One of the largest species groups, *Clubiona obesa*, was first recognized by Edwards (1958) for the Nearctic species. This group is restricted to Asia and the Nearctic (Mikhailov 1995). Currently the group encompasses almost 50 species (Mikhailov 1995; Li and Wang 2014). Of these, 13 species occur in China (Li and Wang 2014): *C. corrugata* Bösenberg & Strand, 1906, *C. kurilensis* Bösenberg & Strand, 1906, *C. kurilensis* Bösenberg & Strand, 1906, *C. lena* Bösenberg & Strand, 1906, *C. aciformis* Zhang & Hu, 1988, *C. bakurovi* Mikhailov, 1990, *C. kimyongkii* Paik, 1990, *C. aciformis* Zhang & Hu, 1991, *C. irinae* Mikhailov, 1991, *C. fusoidea* Zhang, 1992, *C. fuzhouensis* Gong, 1985, *C. baishishan* Zhang, Zhu & Song, 2003, *C. kropfi* Zhang, Zhu & Song, 2003 and *C. lirata* Yang, Song and Zhu, 2003. This group is well studied in China, and only one species, *C. kropfi*, is known by female sex. However, recently collected material has permitted us to recognize the previously unknown male of *C. kropfi* Zhang et al., 2003 and to identify one species new to science. The goal of our paper is to provide a re-description of the *C. kropfi* female and a first description of its male, and, additionally, describe a new species, *Clubiona bicuspidata* sp. n.

Material and methods

All specimens were examined under a Tech XTL-II stereomicroscope. The drawings, photos and measurements were finished with a Leica M205A stereomicroscope equipped with a drawing tube and a DFC450 CCD camera. Carapace length was measured from the anterior margin to the posterior margin of the carapace medially. Eye sizes were measured as the maximum diameter of the lens in dorsal or frontal view. The measurements of legs are shown as total length (femur, patella, tibia, metatarsus, tarsus). The epigynum was cleared in a solution of potassium hydroxide (KOH) and transferred to 75% ethanol for drawing, taking photos and measuring. All measurements are in millimeters. All specimens studied are kept in 75% ethanol and deposited in the Museum of Hebei University (MHBU), Baoding, China.

The following abbreviations are used: ALE, anterior lateral eyes; AME, anterior median eyes; C, conductor; CO, copulatory openings; E, embolus; EP embolar part of bulbus; FD, fertilization ducts; MOA, median ocular area; PLE, posterior lateral eyes; PME, posterior median eyes; RTA, retrolateral tibial apophysis; S, spermathecae.

Taxonomy

Clubiona kropfi Zhang, Zhu & Song, 2003

Figs 1-12

Clubiona kropfi Zhang et al., 2003: 634, f. 2A–C (\bigcirc).

Type material. Holotype ♀, China, Hebei Province, Laiyuan County, Baishi Mountain (39°12'N, 114°42'E), 16 July 1999, Feng Zhang leg., deposited in MHBU, examined.

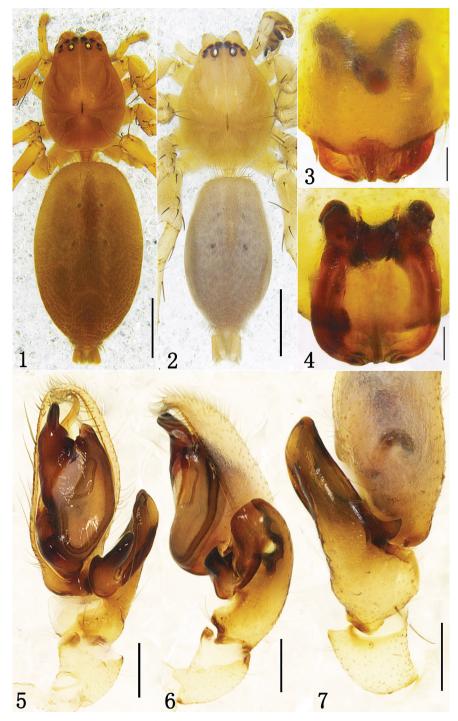
Other material examined. China: Hebei Province: Yu County, Xiaowutai Mountain (39°57'N, 114°48'E), 1 ♂ and 3 ♀, Shuigou Valley, 24 August 2012, Feng Zhang leg.; 1 ♂, Zhengjiagou Valley, 28 August 2012, Feng Zhang leg.; 1 ♂, Shuigou Valley, 5 July 2013, Panlong Wu leg.

Note. This species was described on the basis of the holotype female with the male unknown.

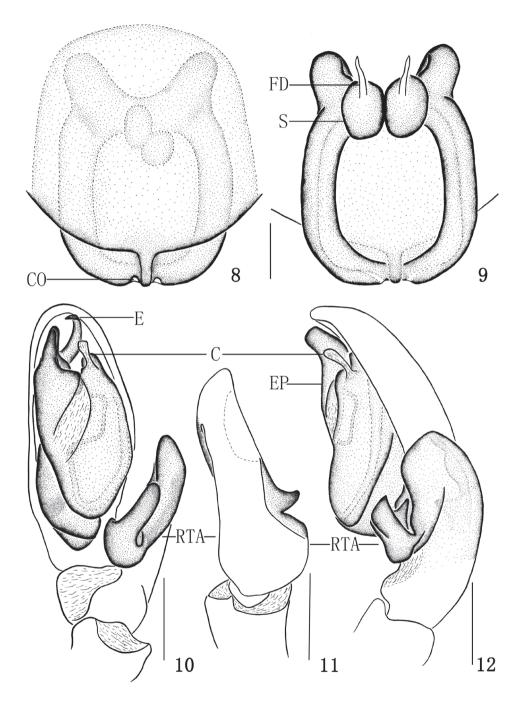
Diagnosis. This species is similar to *C. bakurovi* (Mikhailov, 1990: f. 61–65), but can be distinguished by the hilt-like ventral branch of RTA, the tip of the embolus short and anti-clockwise, the EP wedge-shaped lacking a large tooth; the absence of epigynal grooves; the copulatory openings situated on the posterior edge of epigyne, and the septum thin.

Description. Male. Total length 4.26–4.58. d from Xiaowutai Mt: body 4.26 long; carapace 1.87 long, 1.31 wide; abdomen 2.24 long, 1.26 wide. Carapace yellowish. Head region slightly elevated above thorax. In dorsal view, anterior eye row slightly recurved, posterior eye row almost stright. Eye sizes and interdistances: AME 0.08, ALE 0.10, PME 0.08, PLE 0.10; AME-AME 0.04, AME-ALE 0.04, PME-PME 0.18, PME-PLE 0.12. MOA 0.27 long, front width 0.24, back width 0.35. Clypeus height 0.02. Chelicerae yellowish, promargin with six teeth, retromargin with three teeth. Endites yellow, longer than wide. Labium yellow brown, longer than wide. Abdomen oval, brown yellow, with conspicuous anterior tufts of hairs, dorsum with yellow thin hairs, cardiac pattern yellow brown; venter brown yellow. Spinnerets and legs yellow brown. Measurements of legs: leg I 4.60 (1.32, 0.65, 1.25, 0.86, 0.52), II 4.80 (1.40, 0.68, 1.33, 0.87, 0.52), III 4.23 (1.26, 0.56, 0.92, 1.02, 0.47), IV 6.17 (1.71, 0.67, 1.44, 1.77, 0.58). Male palp as in Figs 5-7, 10-12: RTA strongly expanded, forked, with hilt-like ventral branch; embolus arching behind tegulum and directing prolaterally; EP apophysis strong, wedge-shaped, with a triangular membrane proximally; conductor small, club-like, membranous.

Female. Total length 4.73–4.98. ♀ from Xiaowutai Mt: body 4.98 long; carapace 1.82 long, 1.35 wide; abdomen 2.98 long, 1.79 wide. Eyes sizes and interdistances: AME 0.09, ALE 0.10, PME 0.08, PLE 0.10; AME–AME 0.05, AME–ALE 0.05, PME–PME 0.19, PME–PLE 0.13, ALE–PLE 0.07. MOA 0.28 long, front width



Figures 1–7. *Clubiona kropfi*, **I** female habitus, dorsal view **2** male habitus, dorsal view **3** epigyne, ventral view **4** vulva **5** left male palp, ventral view **6** same, retrolateral view **7** same, dorsal view, showing tibial apophysis. Scale bars: 1 mm (1–2); 0.1 mm (3–4); 0.2 mm (5–7).



Figures 8–12. *Clubiona kropfi*, **8** epigyne, ventral view **9** vulva **10** left male palp, ventral view **11** tibial apophysis, dorsal view **12** left male palp, retrolateral view. Scale bars: 0.125 mm (**8–9**); 0.25 mm (**10–12**).

0.25, back width 0.41. Clypeus height 0.03. Labium 0.55 long, 0.24 wide. Endite 0.31 long, 0.24 wide. Measurements of legs: leg I 3.71 (1.10, 0.61, 0.90, 0.67, 0.43), II 3.90 (1.19, 0.63, 0.97, 0.68, 0.43), III 3.58 (1.09, 0.53, 0.72, 0.85, 0.39), IV 5.56 (1.60, 0.63, 1.24, 1.56, 0.53). Coloration darker than in male. Other characters as in male. Epigyne expanding posteriorly above epigastric groove, with a strongly sclerotized hind part. Copulatory openings separated from each other by a tongue-like process in the middle of the posterior part. Copulatory ducts directed laterad, then distad, almost parallel. Spermathecae spherical (Figs 3–4, 8–9).

Distribution. China (Hebei).

Clubiona bicuspidata sp. n.

http://zoobank.org/553FF41F-8AC9-4AE0-9B22-AB22D2A3E1DE Figs 13–19

Type material. Holotype ♂, China: Xizang Autonomous Region (29°12'N, 94°12'E), Mainling County, Mingsheng Zhu leg., 18 August 2002 (collected in subadult stage, matured 29 August 2002). Paratype: 1 ♂, China: Shaanxi Province, Zhouzhi County, Taibai Mt (33°57'N, 107°45'E), 25 May 2009, Zhisheng Zhang leg.

Diagnosis. The new species resembles *C. baishishan* (Zhang et al., 2003: f. 1A–F), but differs by the shorter embolus, two pointed distal EP apophyses, and the tip of RTA without a concavity in dorsal view.

Etymology. The species name is an adjective, derived from the shape of EP apophyses.

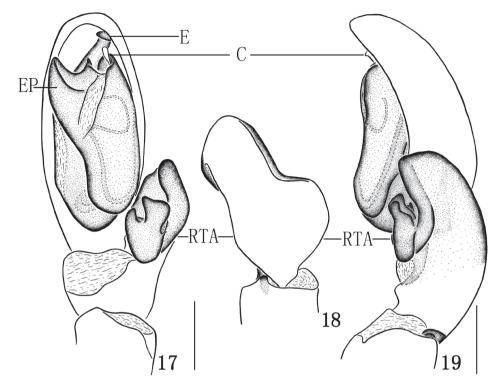
Description. Male. Total length 4.65-4.74. Holotype: body 4.65 long; carapace 2.21 long, 1.69 wide; abdomen 2.43 long, 1.26 wide. Carapace (Fig. 13) yellow. Cephalic region yellowish, slightly elevated above thorax. Median furrow longitudinal. Anterior eye row slightly recurved (in dorsal view), posterior eye row almost straight. AME black, and other eyes white. Eyes sizes and interdistances: AME 0.12, ALE 0.13, PME 0.14, PLE 0.11; AME-AME 0.07, AME-ALE 0.04, PME-PME 0.22, PME-PLE 0.12, ALE-PLE 0.07. MOA 0.31 long, front width 0.28, back width 0.45. Clypeal height 0.03. Chelicerae yellow, promargin with five teeth, retromargin with three teeth. Endites yellowish, serrula dark. Labium yellow brown, 0.51 long, 0.28 wide. Abdomen tan, with white speckles; cardiac mark yellow brown. Spinnerets and legs yellow. Measurements of legs: leg I 5.83 (2.03, 0.86, 1.18, 1.10, 0.66), II 6.48 (2.05, 0.78, 1.85, 1.15, 0.65), III 5.12 (1.54, 0.57, 1.29, 1.28, 0.44), IV 7.35 (2.15, 0.60, 1.65, 2.28, 0.67). Male palp as in Figs 14–19: RTA strongly expanded, forked, ventral branch with two processes, one incus-shaped and the other thumb-shaped. Embolus arching behind tegulum and directing prolaterally. Tegulum with two pointed EP apophyses, one small and one large. Conductor small, rod-like, membranous.

Female. Unknown.

Distribution. China (Xizang, Shaanxi).



Figures 13–16. *Clubiona bicuspidata* sp. n. **13** male habitus, dorsal view **14** left male palp, ventral view **15** same, retrolateral view **16** same, dorsal view. Scale bars: 1 mm (13); 0.2 mm (14–16).



Figures 17–19. *Clubiona bicuspidata* sp. n. **17** left male palp, ventral view **18** tibial apophysis, dorsal view **19** left male palp, retrolateral view. Scale bars: 0.25 mm (17–19).

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SHORT COMMUNICATION



Validation of Eustiromastix guianae (Caporiacco, 1954) (Araneae, Salticidae) with a first description of the female, and additions to the salticid fauna of French Guiana

Cyril Courtial¹, Lionel Picard², Frédéric Ysnel³, Julien Pétillon³

6 Avenue Pierre Donzelot 34B 35700 Rennes, France 2 13 rue Jean-Baptiste Carpeaux 56000 Vannes, France
3 Equipe Biodiversité et Gestion des Territoires URU 420, UFR SVE, Université de Rennes I, 263 Avenue du Général Leclerc 35042 Rennes Cedex, France

Corresponding author: Cyril Courtial (cyril.courtial@laposte.net)

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Abstract

In this paper, we validate the doubtful species status of *E. guianae*, with redescriptions of (supposedly lost) type and holotype males, and a first description of the female. Both sexes are measured and illustrated by pictures of habitus and copulatory organs. Seventeen new salticid species for French Guiana are also reported and a detailed catalogue of all salticid species from the Trinité National Nature Reserve is provided.

Keywords

Jumping spider, tropical forest, South America, doubtful species

Introduction

The history of arachnology in French Guiana started in 1871 with the publication of the first catalogue by Władysław Taczanowski (1871, 1872), but it remained relatively poor compared with that of adjacent countries (Brazil, Guiana, Peru, etc.). It reached its apogee in the middle of the 20th century with the work of Di Caporiacco (1954), which

clearly pleads for an urgent update on this group. The Salticidae is one of the most important spider families, with 597 genera and nearly 5700 described species worldwide (Platnick 2014) which are particularly abundant and diversified in the neotropical region (Dias et al. 2006), yet this family is poorly known in French Guiana with only 85 reported species (Vedel et al. 2013) compared to the 539 species known in Brasil (Metzner 2014). During a recent survey conducted in the Trinité National Nature Reserve (French Guiana) we collected numerous species of salticidae and among them several specimens of the genus *Eustiromastix* Simon, 1902. The spider genus *Eustiromastix* has 11 species distributed throughout South America and the southern West Indies according to Platnick (2014). Among this genus, *Eustiromastix guianae* (Caporiacco, 1954) was considered *nomen dubium* by Galiano (1979) because 1) the type was lost and not viewed 2) morphological details referring to the palp and the ambulatory formula do not fit the description of the genus.

Based on the rediscovery of the type specimen in the collection of the MNHN of Paris and on the collection of several males and females, we propose to validate the doubtful species *E. guianae* here, and provide the first description of the female. In addition we provide a detailed catalogue of all salticid species from the Trinité National Nature Reserve, with new species for French Guiana after Vedel et al. (2013).

Material and methods

Description

The following abbreviations are used:

AER anterior eye row; ALE anterior lateral eyes; AME anterior median eyes; PER posterior eye row; PLE posterior lateral eyes; PME posterior median eyes; NNR National Nature Reserve.

All the fresh specimens examined in this study were collected on leaves of several tropical trees during a survey at the Trinité NNR in December 2010. Measurements (in millimetres as in Galiano 1963) were taken on four males (the holotype and three other males) and on seven females. The leg spination was not assessed on the holotype, but on a fresh specimen. The specimens were studied using a Euromex CMEX 5000 stereomicroscope. The epigyne was macerated in 10% KOH. The specimens were preserved in 70% ethanol.

Catalogue of the National Reserve

Regional literature on salticids was consulted and the presence of valid species after Platnick (2014) was established. New data from the survey were included as well as updates. For all species, the date of first publication, locality, information about sex and dates of collection are given in Suppl. material 1 (Table 1).

Results

Description

Eustiromastix guianae (Caporiacco, 1954)

Eustiromastix guianae (Caporiacco, 1954): 176–177, figure 65, 65a; Galiano, 1979: 185.

Material. Holotype: male (MNHN): French Guiana, Charvein. 7 females, 3 males and 1 subadult male Trinité NNR, 04°36'02"N, 53°24'43"W, 09.XII.2010, Julien Pétillon and Cyril Courtial. Specimens have been deposited in the Museum National d'Histoire Naturelle, Paris (male collection number: AR 15000; female collection number: AR 15001).

Diagnosis. Among salticids, the differenciation between genera of the Plexippeae group is especially complex (Galiano 1979) and only based on genitalia. *Eustiromastix* and *Freya* are close relatives. *Freya* is distinguished by its short thick pedipalp and tibial apophyses often rectangular and wide, and the solid and robust embolus, while *Eustiromastix* presents a longer pedipalp with a very long thin embolus (Galiano 1979) and an apically curved cymbium. Females are characterised by the wide, flattened and folded copulatory ducts, which are as wide as the spermathecae (Santos and Romero 2004). *Eustiromastix guianae* differs from all species of the genus by the shape of the embolus, the presence of a long median apophysis and the small pointed tibial apophysis. The female is distinguished by the strong vertical ducts and the large openings on the epigyne.

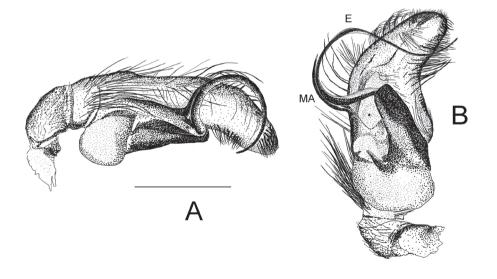


Figure 1. Drawing of the Holotype of *Eustiromastix guianae* male palp (**A** prolateral view **B** ditto ventral view) **MA**: median apophysis, **E**: embolus. Scale 1 mm.

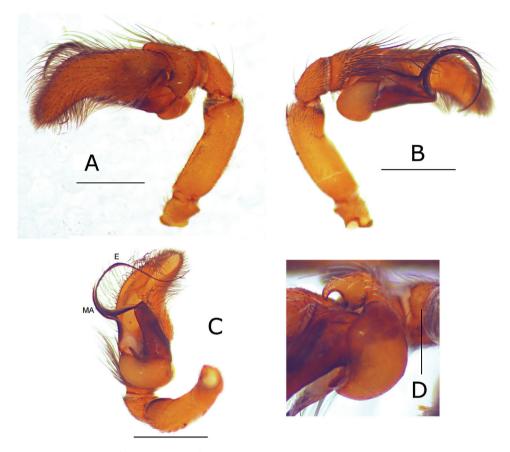


Figure 2. Pictures of the male palp of *Eustiromastix guianae*. **A–C** male palp in lateral, retrolateral and ventral views, respectively **D** detail of the tibial apophysis, ventral view. **MA** median apophysis, **E** embolus. Scales: **A–C** 1 mm, **D** 0.5 mm.

Redescription of the male (holotype from Charvein). Figs 1A, B; 2A–D; 5A. Total length 6.54. Prosoma: carapace 2.95 long, 2.35 wide and 1.83 high. Carapace: darkish brown. Cephalic region: black, and darker than thoracic region. Diameter of PME: 0.34; PLE: 0.14; AME: 0.58; ALE: 0.46. Distance PLE-PLE: 1.94; PME-PME: 2.01; PME-PLE: 0.27. Chelicerae: 1.10 long and 0.77 wide, dark brown. One promarginal and two retromarginal teeth. Legs: light brown, with dark annulations. Leg formula 3412. Length of femur: I 2.09, II 1.84, III 2.55, IV 2.27; patella: I 1.29, II 1.04, III 1.17, IV 0.87; tibia: I 1.80, II 1.32, III 1.42, IV 1.40; metatarsi: I 1.26, II 1.10, III 1.70, IV 1.83; tarse: I 0.66, II 0.62, III 0.61, IV 0.70.

Spination: femur I-III d1-1-1, r2-2 p2-2, IV d1-1-1, r1; patella I-II p1, III-IV p1, r1; tibia I-II v2-2-2, III-IV v1-2, p3, r3, d1; metatarsi I-II v2-2, III-IV v2-2, p1, r1, d2-2-2. Abdomen 3.71 long.

Dorsum: greyish with diffuse pale spots, and a median, longitudinal light brown stripe between a pair of longitudinal narrow stripes of white scales anteriorly and a

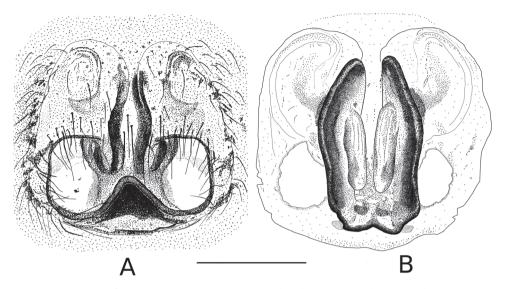


Figure 3. Drawing of *Eustiromastix guianae* epigyne (A dorsal view B ventral view). Scale 0.5 mm.

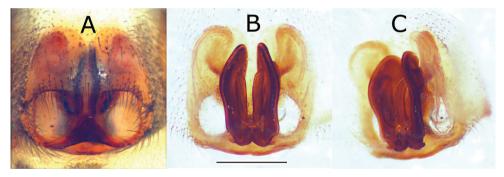


Figure 4. Pictures of the epigyne and spermathecae of *Eustiromastix guianae*. **A** dorsal view **B** vulva, ventral view after maceration **C** ditto latero dorsal view. Scale: 0.5 mm.

white chevron posteriorly in fresh specimens (see Fig. 5A). Abdominal pattern with a median dark brown band.

Male palp as in Fig. 1A, B. Cymbium flattened apically (Fig. 2A), small retrolateral tibial apophysis, pointed internally in dorsal view (Fig. 2D). Long embolus with an elongated median apophysis at about one third of the total length of the embolus (Fig. 2B, C).

Locality: Charvein.

Female. Figs 3A, B; 4A–C; 5B. Total length: 7.51. Prosoma: carapace 2.75 long, 2.19 wide, and 1.59 high. Carapace: dark brown. Cephalic region: darker than the thoracic region. Diameter of PME: 0.29; PLE: 0.10; AME: 0.62; ALE: 0.32. Distance PLE-PLE: 1.75; PME-PME: 1.83; PME-PLE: 0.30. Chelicerae: 0.83 long 0.49 wide. Legs formula 4312. Length of femur: I 1.66, II 1.52, III 1.85, IV 1.89; patella: I 0.80, II 0.69, III 0.85, IV 0.71; Tibia: I 1.29, II 1.08, III 1.13, IV 1.30; metatarsi: I 0.74,

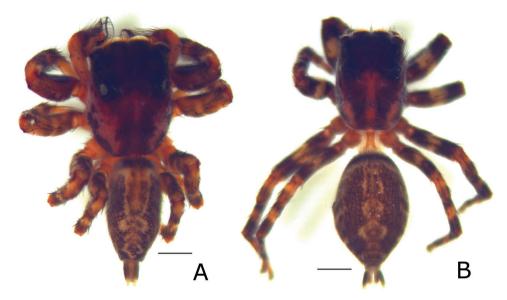


Figure 5. Habitus of Eustiromastix guianae, male, fresh specimen (A) and female (B). Scale: 1 mm.

II 0.64, III 1.16, IV 1.46; tarsi: I 0.62, II 0.58, III 0.67, IV 0.67. Spination: femur I-II d1-1-1, p2, III d1-1-1, p1, r1, IV d1-1-1, r1; patella: I-II p1, III-IV r1; tibia: I-II v2-2, p1, III-IV v1-2, r1-1-1, d1, p1-1-1; metatarsi: I-II v2-2, III d2-1-2, r1, v2-2, IV d2-2, v2-2, r1. Abdomen: 3.66 long. Dorsum: greyish to blackish (Fig. 5B) with a diffuse pale chevron in median part and a small white spot lateraly. Epigyne and spermathecae: as in Fig. 3A, B. Epigyne with two deep circular genital openings (Figs 3A, 4A). Insemination ducts: long and parallel (Figs 3B, 4B, C). Spermathecae: almost round and small at the base of the vulva (Fig. 4B, C).

Variation. Male: Total length: 6.50–7.17, carapace length: 2.40–3.38, carapace width: 2.26–2.66 (n=4). **Female:** total length: 6.32–7.51, carapace length: 2.75–3.11, carapace width: 2.19–2.31 (n=7).

Habitat. all specimens were collected together, including males in couple with females in tropical rain forest from beating and sweeping low vegetation.

Distribution. known only from two localities in French Guiana (Charvein and Trinité NNR) Figure 1 of Suppl. material 1.

Addition to the checklist of Salticid species known from French Guiana

Twenty-eight jumping spiders have been identified at the Trinité National Nature Reserve, among them 17 are new for French Guiana (see the catalogue of saticids of the reserve: Table 1 of Suppl. material 1). A total of 102 salticid species is now recorded from French Guiana.

Acknowledgements

The authors thank Marguerite Delaval (Office National des Forêts, ONF) and ONF for funding the expedition to the Trinité National Nature Reserve; Christine Rollard and Christophe Hervé (Museum National d'Histoire Naturelle – Paris) for allowing access to the bibliography of the Arthropod laboratory and permitting the consultation of Caporiacco's collection; Christophe Hervé who found the type of *Eustiromastix guianae*; and Alain Canard and Boris Leroy for field support. Jeremy Miller, Tamás Szűts and two anonymous referees provided useful comments on an earlier draft.

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Supplementary material I

Electronic supplementary material

Cyril Courtial, Lionel Picard, Frederic Ysnel, Julien Pétillon

Data type: Specimens data

- Explanation note: Table 1. Detailed records of all salticid species in the National Nature Reserve Trinité. Figure 1. Map showing localities of NNR Trinité and Charvein.
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Link: doi: 10.3897/zookeys.420.6977.app1

RESEARCH ARTICLE



The species of *Thalerosphyrus* Eaton, 1881 (Insecta, Ephemeroptera, Heptageniidae, Ecdyonurinae) in Java and Sumatra, with some comments on the diversity of the genus in the Oriental Realm

Michel Sartori^{1,2}

I Zoologisches Museum und Biozentrum Grindel, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany
 2 Museum of Zoology, Palais de Rumine, Place Riponne 6, CH-1005 Lausanne, Switzerland

Corresponding author: *Michel Sartori* (michel.sartori@uni-hamburg.de)

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Abstract

Three species belonging to the genus *Thalerosphyrus* Eaton, 1881 are reported from Java and Sumatra. The nymphs of *Th. determinatus* (Walker, 1853) from Java, *Th. sinuosus* (Navás, 1933) from Java and Sumatra and *Th. lamuriensis* Sartori, 2014 from Sumatra are redescribed. The egg morphology of the three species is also presented for the first time. A key to the nymphs is proposed. General considerations on the composition of the genus *Thalerosphyrus* in the Oriental Realm are given. The distribution of the genus is greatly expended, and currently ranges over the Himalaya and Sumbawa in the Sunda Islands.

Keywords

Thalerosphyrus determinatus, Thalerosphyrus sinuosus, Thalerosphyrus lamuriensis, Ecdyonurus sumatranus, distribution, Bali, Sumbawa, nymph, eggs, SEM

Introduction

The genus *Thalerosphyrus* was created by Eaton (1881) to accommodate the species *Bae-tis ? determinata* Walker, 1853 described on the basis of a single male imago from Java. Later on (Eaton 1885), the same author added also *Baetis ? torrida* Walker, 1853 known

by a single female imago from the Philippines. Th. determinatus was recorded later by Ulmer (1913) also from Java, and redescribed in detail, with abdominal patterns, coloration and drawing of the genitalia. Another species was described from Java by Navás under the name Ecdyonurus ? sinuosus Navás, 1933 on the basis of a single female imago, and then transferred to the genus Thalerosphyrus by Ulmer (1939) who described the male imago and reported the species also from Sumatra. In the same work (Ulmer 1939), the author described Th. determinatus and Th. sinuosus in the nymphal stage. Dang (1967) created the genus *Ecdyonuroides* for a peculiar nymph he collected in Vietnam (E. vietnamensis) which possesses extremely well developed posterolateral expansions on the abdomen. He recognized the similarity with a nymph described by Ulmer (1939) under the name *Ecdyonurus sumatranus* and designated Ulmer's species at the type species of his new genus. Later on, Braasch and Soldán (1984) put Ecdyonuroides in synonymy with *Thalerosphyrus* on the basis of a rearing of *E. vietnamensis* nymph which gave a male imago with Thalerophyrus characters and proposed the new combination Th. vietnamensis. In the following years, two other Thalerosphyrus species were described: Th. bishopi (Braasch & Soldán, 1986b) from West Malaysia, and Th. flowersi (Venkataraman & Sivaramakrishnan, 1987) from southern India, both at the adult and nymphal stages.

Braasch and Soldán (1986a) described a new genus (*Asionurus*) from Vietnam and showed that the nymph described by Ulmer (1939) under the name *Th. sinuosus* was incorrectly associated with adults of this species and that the nymph actually belonged to this new genus and therefore proposed to call this taxon *Asionurus ulmeri*. Wang and McCafferty (2004) suggested that the nymph described by Ulmer (1939) as *Th. determinatus* was wrongly associated and should be the nymph of *Th. sinuosus* according to abdominal patterns.

The concept of the genus *Thalerosphyrus* is far from being clear, because the type material of the type species, *Th. determinatus* is in bad state, missing all legs but one as well as the abdomen (hence the genitalia) (Kimmins 1960). The uncertainties about the actual status of the genus *Thalerosphyrus* let Kluge (2004) to consider it as *incertae sedis*, referring only to the nymphs of *Th. sumatranus*, *Th. vietnamensis* and *Th. flowersi* as belonging to his non ranking taxon Ecdyonuroides/g(1) characterized by their developed posterolateral expansions of the abdomen.

When revising Ulmer's collection in the Zoologisches Museum in Hamburg, Sartori (2014d) restudied the type material of *Ecdyonurus sumatranus* Ulmer, 1939 and showed that the holotype belonged to the genus *Rhithrogena* Eaton, 1881, and thus put *Ecdyonuroides* Dang, 1967 in synonymy with *Rhithrogena* and proposed a new name for the nymph as *Th. lamuriensis*.

Within the ongoing revision of Ulmer's collection (Sartori 2014a; b; c; d), we have reinvestigated all material of *Thalerosphyrus* deposited in the Museum of Zoology in Hamburg. Despite the above mentioned uncertainties, we follow the *Thalerosphyrus* concept proposed by Ulmer (1913; 1924; 1939) because his redescription of *Th. determinatus* is in accordance with Eaton's (1885) diagnosis, especially body and wing lengths and hind leg ratios. The nymphs of the species found in Java and Sumatra are described based on this historical material as well as on specimens recently collected.

Material and methods

Original material studied here is deposited in the following institutions:

- **ZMH** Zoologisches Museum und Biozentrum Grindel, Hamburg, Germany
- MZL Musée cantonal de zoologie, Lausanne, Switzerland
- **LIPI** Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Sciences), Museum of Zoology, Bogor, Indonesia.

In the absence of adequate life stages to link nymph and adults as previously proposed by Sartori (2014a; c; d), eggs were extracted from either female imago or subimago for *Th. determinatus* and *Th. sinuosus* because no mature female nymphs were available, and from a mature female nymph for *Th. lamuriensis* as no alate stage of this species are known for sure.

Ontogenetic stage association relies thus on the following assumptions; three nymphal forms present together with three different egg morphologies, one species found only on Java, one on Java and Sumatra and the latter only on Sumatra.

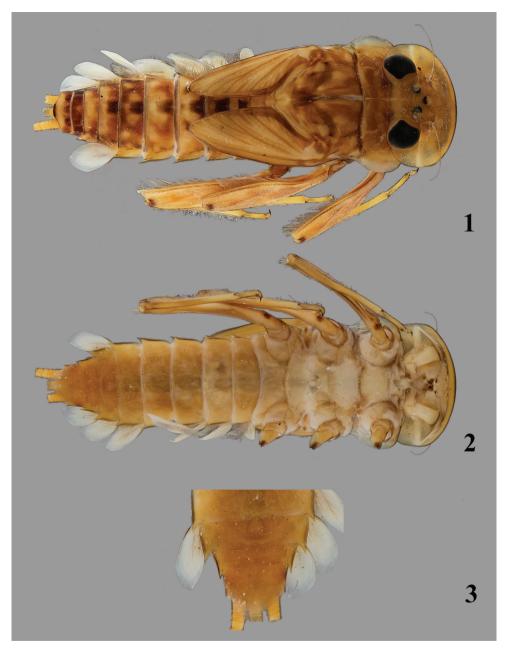
Drawings were made with the help of a camera lucida taken from stereomicroscope Leica DM 750 and pictures from microscope Zeiss Axioscop 2 or Visionary Digital Passport II. Final digital drawings were performed on Adobe Illustrator CS6. For scanning electronic microscope (SEM) pictures, the eggs were dehydrated, carbon coated, and observed under a LEO 1525 at 5.00 kV; maxillae were dehydrated, critical point dried, and then platinum coated, and observed under a FEI Quanta 250 at 5.00 kV. Final plates were assembled in Adobe Photoshop CS6.

Results

Thalerosphyrus Eaton, 1881

Nymphal diagnosis. Medium to large Heptageniidae (up to 20 mm) with contrasting color patterns.

Head broad and thickened anteriorly (Figs 2, 5, 8); labrum (Figs 16–17) small, wider than long, without conspicuous median incision; mandibles (Figs 18–19) with outer margin covered with numerous thin setae, outer and inner incisors subequal in length, outer one saw-like on both sides, inner one trifid, left mandible with tuft of setae above mola; maxillae with 3-segmented palp, ventral surface of galea-lacinia covered with numerous long setae (Fig. 25), which appear entire in optical microscope, but are slightly feathered in SEM, crown of the galea-lacinia with 20–25 comb-shape setae, median ones bearing 12–17 teeth (Fig. 26), distal dentisetae bifid and fimbriate, as the proximal one (Figs 23–24); hypopharynx with robust lingua and well developed super-linguae bend backwards (Figs 27–28); labium with rhomboid glossae (Figs 20–22), paraglossae regularly curved, apex not bend backwards and moderately expended laterally.



Figures 1–3. *Thalerosphyrus determinatus* (Walker, 1853). **I** Habitus in dorsal view **2** Habitus in ventral view **3** Detail of abdominal segments VI–IX in ventral view.

Thorax with pronotum slightly to greatly enlarged laterally; supracoxal spurs acute and well developed especially on mid- and hindlegs; femora rather similar between the three pairs of legs, row of stout and pointed bristles on inner and outer margins, no thin setae present; outer margin of fore tibia with few thin setae on proximal fourth, mid tibia with a row of thin setae on outer margin almost to tarsi, hind tibia (Figs 30, 32, 34) with two rows of thin setae, one on the outer margin, one in submarginal position, spine-like bristles absent or present.

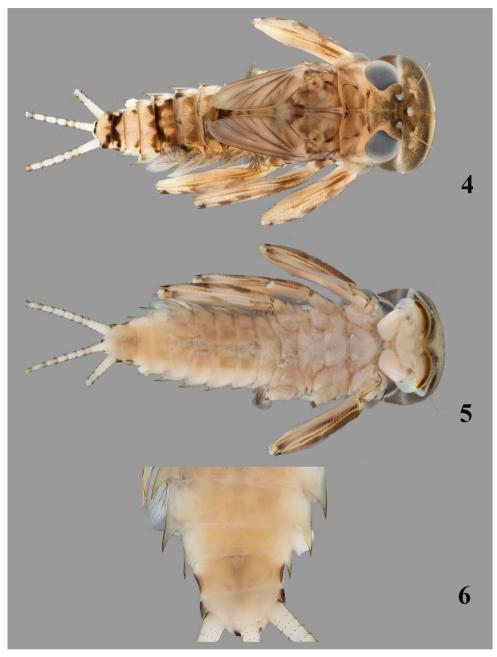
Abdomen with posterolateral projection generally greatly enlarged from segment III to VII or VIII (Figs 3, 6, 9); posterior margin of tergites (Figs 35–37) with large and pointed teeth, microdenticles present and generally numerous; all gills asymmetrical (Figs 38–49), gills I–VI with plate-like and extremely developed fibrillose parts, gill VII only plate-like; terminal filament well developed, cerci whitish with more or less enlarged brown bands; segments with whorls of stout and pointed setae.

Discussion. The scattered setae on the ventral surface of the maxilla indicate clearly that *Thalerosphyrus* belong to the subfamily Ecdyonurinae. The presence of acute supracoxal spurs, the anterior margin of the head thickened and generally well developed posterolateral projections of the abdomen are discriminating characters according to Webb and McCafferty (2008). To these we can add the shape of the gills II–V (VI) strongly asymmetrical and wider than long, with fibrillose part well developed. In the Oriental Realm, *Thalerosphyrus* could be confused with *Compsoneuriella* Ulmer, 1939 because of the acute supracoxal spurs, but is easily told by the much more developed posterolateral projections of the abdomen, the higher number of comb-like setae on the crown of the galea-lacinia, the shape of the gills which are never so wide in *Compsoneuriella*, and by the shape of the distal dentisetae, which are simple and not fimbriate in *Compsoneuriella* (Sartori 2014c).

Species included. Thalerosphyrus determinatus (Walker, 1853): Java Thalerosphyrus sinuosus (Navás, 1933): Java, Sumatra Thalerosphyrus vietnamensis (Dang, 1967): Vietnam Thalerosphyrus bishopi Braasch & Soldán, 1986: West-Malaysia Thalerosphyrus flowersi Venkataraman & Sivamarakrishnan, 1987: South India Thalerosphyrus lamuriensis Sartori, 2014: Sumatra

The species described by Ulmer (1926) as *Thalerosphyrus melli* from China has been recently assigned to another genus as *Epeorus melli* (Ulmer) by Zhou et al. (2007); the species *Th. torridus* (Walker, 1853) described based on a single female imago from the Philippines most probably belong to the genus *Afronurus* (Braasch 2011); the species *Th. separatus* Nguyen & Bae, 2004 and *Th. ethiopicus* Soldán, 1977 described from Vietnam and Sudan respectively, have been suggested to be also members of the genus *Afronurus* by Webb et al. (2006).

Distribution. The genus *Thalerosphyrus* is endemic to the Oriental Realm. It is known from India, through Southeast Asia (Thailand, Vietnam, West Malaysia), up to Sumbawa in the Sunda Islands (see below), suggesting, as for *Rhithrogena* (Sartori 2014d), that the Wallace line is not a barrier to the dispersal of some Ephemeroptera. The genus is however not currently reported from Sulawesi (Edmunds and Polhemus 1990). According to Braasch (2011), *Thalerosphyrus* is also not recorded from the Philippines, and its presence on the island of Borneo is only based on few data and no named species are known (Braasch 2011); in the MZL collections is a single nymph (Sabah, Mesilau River, 8 km north of Kundessan, 2100 m, 1.VIII.1985, J.T. & D.A. Polhemus leg) which is clearly related to *Th. lamuriensis*, but complementary material is needed before any definitive answer can be found. In the MZL collections is also



Figures 4–6. *Thalerosphyrus sinuosus* (Navás, 1933). **4** Habitus in dorsal view **5** Habitus in ventral view **6** Detail of abdominal segments VI–IX in ventral view.

deposited a single nymph from Nepal (Nawakot & Sindhu Districts, Patibhanjyang Village, elev. ca 6000', 10.IX.1968, C. Wiens leg) which expands the distribution of the genus to the Himalaya.

Thalerosphyrus determinatus (Walker, 1853)

Thalerosphyrus determinatus Ulmer, 1939, (nymph, pro parte)

Material examined. 2 nymphs, Java, Diengplateau, stream Seraju (D13), ca 1950 m a.s.l., 5.VI.1929, Prof. Thienemann leg. [ZMH] ; 1 nymph entirely mounted on microscopic slide, Java, Gedeh Panggerango, Tjisarua, 1050 m, 10.VIII.1930, Dr. Lieftinck leg [ZMH]; 1nymph, Java, Java Barat Province, rocky stream at Cibodas (CL 2186), 1300 m, 3.XI.1985, J.T. & D.A. Polhemus leg [MZL]; 1 nymph, Bali, Baturiti, Desa Antapan, 815 m, 8°19.34'S, 115°11.61'E, 9.X.2009 (BLI005), M. Balke & D. Amran leg [MZL]; 1 nymph, Sumbawa, Nusa Tenggara Barat Province, Madsewu River, 2 km above Badindi, 61 km NW of Bima (CL 2174), 750 m, 20.X.1985, J.T. & D.A. Polhemus leg [MZL].

Eggs extracted from a female imago (caught together with a male imago) and identified by Ulmer as *Th. determinatus*: West Java, Tjibodas, Tjiwalen Bridge, 1400 m, 4.IX.1932, Dr Lieftinck leg [ZMH].

Description of the nymph. Body size: up to at least 14.5 mm (not full grown nymph). Coloration pattern: see Figs 1–2.

Head. Labrum moderately expended laterally, less than 4 times larger than long, with rounded apexes (as in Fig. 16); dorsal surface and anterior margin covered with long and thin setae; ventral surface with a median arch of less than 10 strong and pointed setae. Crown of the galea-lacinia of the maxillae composed of ca. 25 comb-shape setae, the median ones bearing 12–15 teeth. Right mandible with 5–6 bifid and fimbriate setae below the inner incisor and ca. 10 long simple and thin setae below the mola; left mandible with 8–9 simple and fimbriate setae below the inner incisor and ca. 9–10 long simple and thin setae below the mola. Hypopharynx with robust lingua bearing a tuft of small setae, superlinguae densely covered with long and thin setae replaced before the apex by very small setae up to the lower part of the superlinguae (Fig. 27). Labium with glossae rhomboid, slightly concave on their outer margin near apex (Fig. 20), dorsal surface with three stout setae and numerous thin and simple setae.

Thorax. Pronotum weakly expended laterally (Fig. 1). Femora with submarginal rows of pointed bristles on the inner and outer margins, increasing in numbers from the fore to the hind leg. Bristles on the upper face of hind femora arrow-shaped, clearly pointed (Fig. 29). Hind tibia (Fig. 30) without any bristles in outer marginal or submarginal position. Tarsal claw with 2–3 teeth.

Abdomen. Posterolateral expansions not developed on segments I–II, increasing in size from segment III to VII where it may reach the middle of segment VIII, shorter on segment VIII (Fig. 3) and comparable proportionally to those of segments V–VI. Gill I (Fig. 38) with elongated and rounded plate, ca 2.5× longer than wide; gill IV strongly asymmetrical (Fig. 39), wider than long, gill VI and VII oval and asymmetrical with obtuse apex (Figs 40–41). Posterior margin of tergites with irregular pointed teeth, and numerous microdenticles (Fig. 35). Cerci rather unicolor medium brown, some segments darker in the proximal half.



Figures 7–9. *Thalerosphyrus lamuriensis* Sartori, 2014. 7 Habitus in dorsal view 8 Habitus in ventral view 9 Detail of abdominal segments VI–IX in ventral view.

Description of the eggs. Size: ca 120 μ m × 75 μ m; chorion regularly covered by small KCT'S, (1.0–1.5 μ m), a little bit larger at poles (Fig. 10), and by microgranules (< 0.3 μ m); margin of micropyle irregular and formed by microgranules (Fig. 11).

Discussion. The abdominal pattern of the nymph is the one which is the closest to the one of the male imago redescribed by Ulmer (1924). According to Wang and McCafferty (2004) and our own observations (see below), the illustration of the abdominal patterns of the nymph (Ulmer 1939, fig. 402) as *Th. determinatus* does not belong to this species, nor do any of Ulmer's, other drawings.

The species may be easily recognized from its relatives mainly by the weak posterolateral expansions of the abdomen, and the absence of bristles on the outer margin of the hind tibiae.

Th. determinatus as defined here is the less common species found in the investigated area. However it is reported from Bali and Sumbawa for the first time. The species is absent from Sumatra and seems to live in middle to high altitudes, based on the few available data.

Thalerosphyrus sinuosus (Navás, 1933)

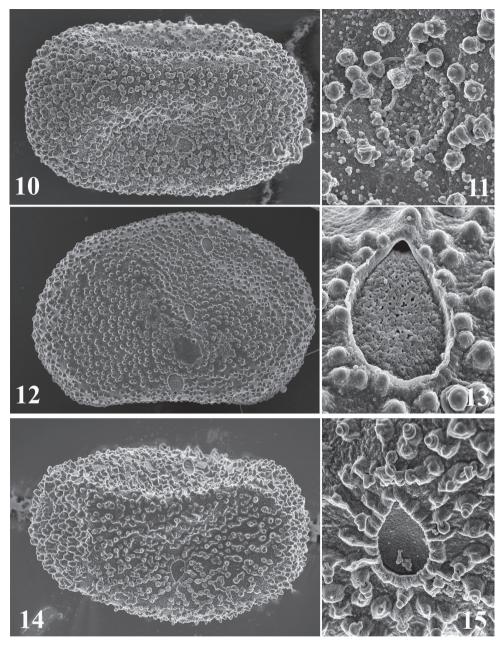
Thalerosphyrus determinatus Ulmer, 1939, (nymph, pro parte)

Material examined. 4 nymphs, two partially mounted on two microscopic slides, Sumatra, Singkarak, stream at Subanpass (F20), 1000 m, 4.III.1929, Prof. Thienemann leg [ZMH]; 1 nymph, Sumatra, Tjurup, Kali Dzernih, forested stream (M9), 7.V.1929, Prof. Thienemann leg [ZMH]; 1 nymph, Sumatra, Ranau, stream in primary forest (R25c), 29.I.1929, Prof. Thienemann leg [ZMH]; 2 nymphs, one partially mounted on a microscopic slide, Java, Gurung Ungaran, XII. 1909, Jacobson leg [ZMH]; 1 nymph, Java, Kali Tjiwalen near Tjibodas, 1350 m, in mosses and dead leaves (FY7f), 10.VII.1929, Prof. Feuerborn leg [ZMH]; 1 nymph, West Java, stream in Tjibodas, under the "mountain garden" (FY14c), 15.VII.1929, Prof. Feuerborn leg [ZMH]. [All specimens *sub. nom Thalerosphyrus determinatus* det. Ulmer].

10 nymphs, Java Tengah, Wonosobo-Kertek village road, creek, 800 m, 7°21.68'S, 109°55.67'E, 10.X.2011 (JVA011), M. Balke leg. [LIPI, MZL]; 2 nymphs, Sumatra Barat, Sijunjung / Muara area, forest, 488 m, 00°40.10'S, 101°07.26'E, 10.XI.2011 (UN7), M. Balke leg [MZL]; 7 nymphs, one entirely mounted on a microscopic slide, Sumatra Barat, Universitas Andalas campus, forest stream, 360 m, 00°54.67'S, 100°28.38'E, 8.XI.2011 (UN1), M. Balke leg [MZL]; 2 nymphs, Sumatra Barat, Lubukbargalung, Lubuk Paraku River, 50 km south Solok, 420 m, 100°32.50'E, 0°56.75'S, 25.V.2010 (SU5), J.-M. Elouard leg [MZL].

Eggs extracted from a female imago: Java, Buitenzorg, 13.II.1932, Dr Lieftinck leg [ZMH], and from a female subimago: Western Sumatra, Danau di Atas, stream near the road, 1000–1100 m (FF20e), 16.III.1929, Prof. Feuerborn leg [ZMH] and identified by Ulmer as *Th. sinuosus*.

Sequence data. One specimen from Sumatra (SU5) and one from Java (JVA011) have been used for the study by Vuataz et al. (2013) under the name "*Thalerosphyrus*" in figures and "*Thalerosphyrus* sp." in table S1, with voucher numbers "340SuTh" and



Figures 10–15. Egg structure of *Th. determinatus* (10–11), *Th. sinuosus* (12–13), *Th. lamuriensis* (14–15). 10, 12, 14 Egg in toto 11, 13, 15 Details of the micropyle and chorionic structures.

"346JaTh" respectively, with one or two mitochondrial (CO1, 16S) and two to four nuclear genes (28S, H3, wg, EF-1 α) sequenced. Access numbers in GenBank are:

Voucher #	CO1	165	285	H3	wg	EF-1a
340 SuTh	HE651394	HE651430	HE651453	HE651512	HE651485	HE651535
346JaTh	HF536601			HF536587	HF536594	

Description of the nymph. Body size: up to at least 10.5 mm (not full grown nymph). Coloration pattern: see Figs 4–5.

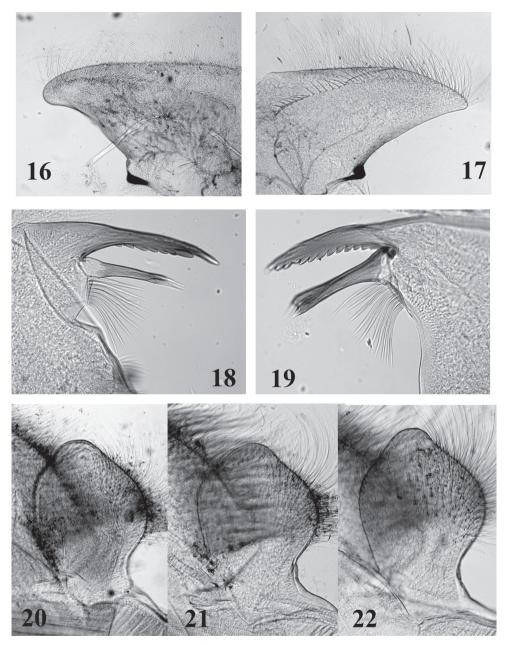
Head. Labrum slightly expended laterally, ca 3.5 times larger than long, with rounded apexes (Fig. 16); dorsal surface and anterior margin covered with long and thin setae; ventral surface with a median arch of ca 10 strong and pointed setae. Crown of the galea-lacinia of the maxillae composed of ca 25 comb-shape setae, the median ones bearing 12–15 teeth (Fig. 26). Right mandible with 7–8 fimbriate setae below the inner incisor and ca. 5–6 long simple and thin setae below the mola; left mandible with 10–11 simple and fimbriate setae below the inner incisor and ca. 8–9 long simple and thin setae below the mola: setae below the mola; left mandible with setae below the mola. Hypopharynx with robust lingua bearing a tuft of small setae, superlinguae densely covered with long and thin setae replaced before the apex by very small setae up to the lower part of the superlinguae. Labium with glossae rhomboid, slightly concave on their inner margin near apex (Fig. 21), dorsal surface with three stout setae and numerous thin and simple setae.

Thorax. Pronotum slightly expended laterally and posteriorly (Fig. 4). Femora with submarginal rows of pointed bristles on the inner and outer margins, increasing in numbers from the fore to the hind leg. Bristles on the upper face of hind femora arrow-shaped, clearly pointed (Fig. 31). Hind tibia with a row of 6–7 arrow-shaped bristles in submarginal position (Fig. 32). Tarsal claw with 2–3 teeth.

Abdomen. Posterolateral expansions not developed on segment I, weakly developed on segment II, strongly developed on segment III and increasing in size up to VII where they may be as long as segment VIII, shorter on segment VIII and smaller proportionally to those of segments III (Fig. 6). Gill I with elongated and rounded plate, less than two times longer than wide (Fig. 42); gill III–VI strongly asymmetrical, wider than long (Figs 43–44), gill VII oval and asymmetrical with inner concave margin near apex (Fig. 45). Posterior margin of tergites with irregular pointed teeth, and numerous microdenticles (Fig. 36). Cerci whitish in proximal part, with dark brown segment every two or three, distal part more uniformly medium brown.

Description of the eggs. Size: ca 130–140 μ m × 85–90 μ m; chorion regularly covered by small KCT'S, (1.5–2.0 μ m), a little bit larger at poles (Fig. 12), and by mesogranules (1.0 μ m); margin of micropyle smooth and entire (Fig. 13).

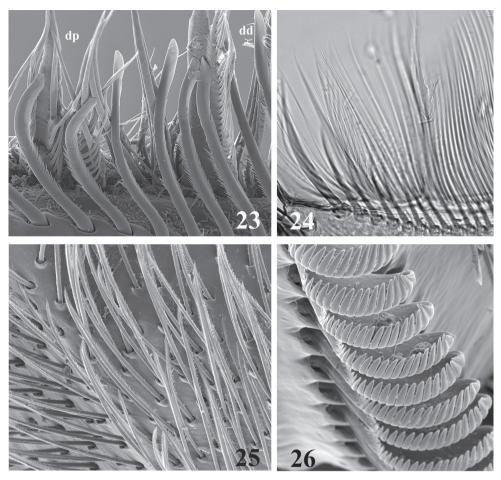
Discussion. The nymph mentioned here includes what Ulmer (1939) described as the nymph of *Th. determinatus*; the material is composed of three slides made by Ulmer himself and most of the drawings (Ulmer 1939, figs 403–418) were based on them. It appears that Ulmer confused the two species, and this is also because he made no slide preparation of the true *Th. determinatus. Th. sinuosus* as defined here is closely related to *Th. determinatus*, but can be easily separated by the shape of the posterolateral expansions of the abdomen, the shape of the glls, the shape of the gllssae, and by the presence of arrow-shaped bristles on the hind tibiae.



Figures 16–22. Mouthparts structure of *Th. determinatus* (20), *Th. sinuosus* (16, 21) and *Th. lamuriensis* (17, 18, 19, 22). 16–17 Hemi-labrum 18 Left mandible 19 Right mandible 20–22 Labial glossa.

The eggs of *Th. sinuosus* differ from those of *Th. determinatus* by the margin of the micropyle and by the presence of mesogranules on the chorion.

Th. sinuosus is present on Java and Sumatra. We cannot confirm the occurrence of the species outside these two islands, although based on egg morphology, and some



Figures 23–26. SEM (23, 25, 26) and optic (24) pictures of maxillar structure. 23–24 Dentisetae of *Th. lamuriensis* dp: proximal dentisetae, dd distal dentisetae 25 Scattered setae on the ventral face of the galea-lacinia of *Th. sinuosus* 26 Comb-shape setae on the crown of the galea-lacinia of *Th. sinuosus*.

partial details of the nymph (Boonsoong and Braasch 2013), the species could be present in Thailand, but supplementary description of the nymph is needed.

Thalerosphyrus lamuriensis Sartori, 2014

Ecdyonurus sumatranus Ulmer, 1939, (nymph, not female adult) *Thalerosphyrus determinatus* Ulmer, 1939, (nymph, pro parte) *Thalerosphyrus sumatranus* Braasch & Soldan, 1984 (nymph)

Material examined. Besides the type material mentioned in Sartori (2014d), the following specimens have been examined.

1 nymph, Sumatra, Singkarak, stream at Subanpass (F19), 1000 m, 4.III.1929, Prof. Thienemann leg [ZMH]; 3 nymph, one partially mouted on microscopic slide, Sumatra, Toba area, stream south of Balige (FT13), 8.IV.1929, Prof. Feuerborn leg [ZMH]; 2 nymphs, Sumatra, Toba area, Balige, stream at ca 1100 m (T13), 5.IV.1929, Prof. Feuerborn leg [ZMH] [All specimens *sub. nom Thalerosphyrus determinatus* det. Ulmer].

1 nymph, Sumatra Utara Province, swift stream 20 km East of Parlilitan (CL 2192), 1070 m, 10.XI.1985, J.T. & D.A. Polhemus leg [MZL]; 2 nymphs, Sumatra Barat, Tarusan, upstream Tarusan, 10 m, 100°29.84'E 1°13.61'S, 24.V.2010 (SU3), J.-M. Elouard leg [MZL]; 2 nymphs, Sumatra Barat, Kotobarapak, upstream Kototbarapack, 100 m, 100°32.08'E, 1°13.78'S, 24.V.2010 (SU4), J.-M. Elouard leg [MZL]; 4 nymphs, Sumatra Barat, Lubukbargalung, Lubuk Paraku River, 50 km south Solok, 420 m, 100°32.50'E, 0°56.75'S, 25.V.2010 (SU5), J.-M. Elouard leg [MZL].

Eggs extracted from the mature female nymph mentioned above from Polhemus collected specimens.

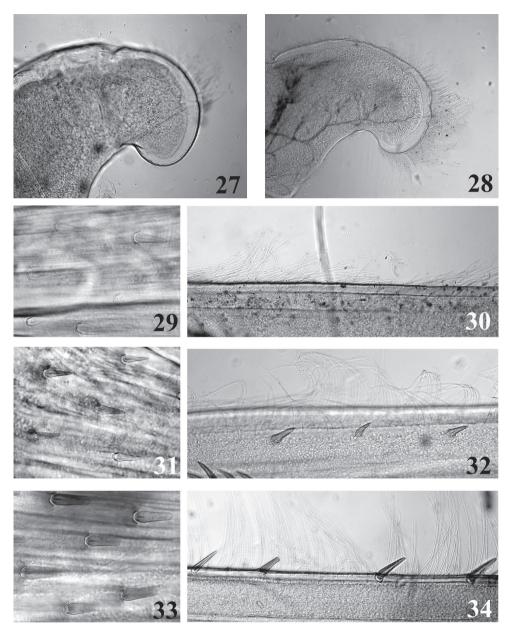
Sequence data. Three specimens (SU3, SU4, SU5) have been used for the study by Vuataz et al. (2013) under the name "*Thalerosphyrus*" in figures and "*Thalerosphyrus* sp." in table S1, with voucher numbers "319SuTh", "317SuTh" and "339SuTh" respectively, with one or two mitochondrial (CO1, 16S) and two to four nuclear genes (28S, H3, wg, EF-1 α) sequenced. Access numbers in GenBank are:

Voucher #	CO1	165	285	H3	wg	EF-1a
319 SuTh	HE651389					
317SuTh	HE651388	HE651425	HE651450	HE651508	HE651480	HE651532
339SuTh	HE651393	HE651429		HE651511	HE651484	HE651534

Description of the nymph. Body size: up to 21 mm (full grown female nymph). Coloration pattern: see Figs 7–8.

Head. Labrum greatly expended laterally, ca 4times larger than long, with narrow and somewhat acute apexes (Fig. 17); dorsal surface and anterior margin covered with long and thin setae; ventral surface with a long median arch of ca. 20 strong and pointed setae ending close to the anterior margin. Crown of the galea-lacinia of the maxillae composed of ca. 20 comb-shape setae, the median ones bearing 12–14 teeth. Right mandible (Fig. 19) with 11–12 fimbriate setae below the inner incisor and 5 long simple and thin setae below the mola; left mandible (Fig. 18) with 8–9 fimbriate setae below the inner incisor and ca. 8–9 long simple and thin setae below the mola. Hypopharynx with robust lingua bearing a tuft of small setae, superlinguae densely covered with long and thin setae up to the lower part of the superlinguae (Fig. 28). Labium with glossae rhomboid, clearly concave on their inner and outer margins near apex (Fig. 22), dorsal surface with numerous stout setae and numerous thin and simple setae.

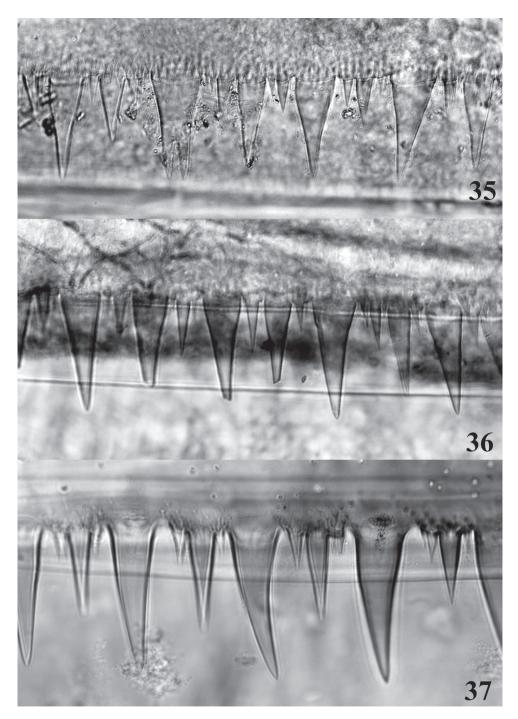
Thorax. Pronotum greatly expended laterally and posteriorly (Fig. 7). Femora with submarginal rows of pointed bristles on the inner and outer margins, only slightly increasing in numbers from the fore to the hind leg. Bristles on the upper face of



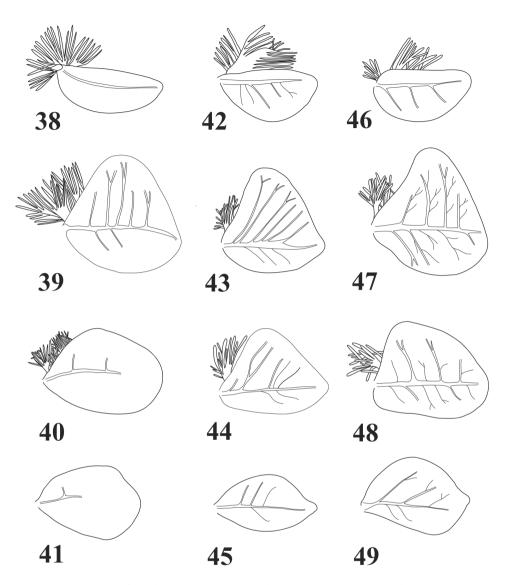
Figures 27–34. Mouthpart (27–28) and thoracic (29–34) structures of *Th. determinatus* (27, 29, 30), *Th. sinuosus* (31, 32) and *Th. lamuriensis* (28, 33, 34). 27–28 Apex of superlingua of hypopharynx 29, 31, 33 Bristles on the dorsal face of hind femur 30, 32, 34 Outer margin of hind tibia.

hind femora with subparallel or slightly convergent margins, apex rounded or truncate (Fig. 33). Outer margin of hind tibia with a row of 12–15 pointed bristles in marginal or submarginal position (Fig. 34). Tarsal claw with 3–4 teeth.

Abdomen. Posterolateral expansions not developed on segments I–II, moderately developed on segment III and strongly increasing in size up to VIII where they may



Figures 35–37. Posterior margin of abdominal tergite IV. 35 *Th. determinatus* 36 *Th. sinuosus* 37 *Th. lamuriensis.*



Figures 38–49. Gills of *Th. determinatus* (38–41), *Th. sinuosus* (42–45) and *Th. lamuriensis* (46–49). 38, 42, 46 Gill I 39, 43, 47 Gill IV 40, 44, 48 Gill VI 41, 45, 49 Gill VII.

be longer than segment IX (Fig. 9). Gill I with asymmetrical elongated and rounded plate, less than two times longer than wide (Fig. 46); gill III–VI strongly asymmetrical, wider than long (Figs 47–48), gill VII oval and asymmetrical with slightly pointed apex (Fig. 49). Posterior margin of tergites with long and pointed teeth regularly alter-

nating with two small ones, and few microdenticles (Fig. 37). Cerci whitish with 3–4 dark brown bands increasing in size towards the apex.

Description of the eggs. Size: ca 140–150 μ m × 85–90 μ m; chorion regularly covered by pedunculate KCT'S, (1.0–1.5 μ m), a little bit larger at poles (Fig. 14), no micro- or mesogranules present; margin of micropyle edged, as formed by fused peduncles (Fig. 15).

Discussion. A major surprise was to find nymphs of Th. lamuriensis among the material identified by Ulmer (1939) as Th. determinatus, because he described this nymph based on a single specimen under the name *Ecdyonurus sumatranus* (Ulmer, 1939, see Sartori 2014d for a complete development of this case). Th. lamuriensis clearly differs from the two previous species by several characters, such as the posterolateral expansions of the abdomen reaching their largest size on segment VIII (compared to segment VII in Th. determinatus and Th. sinuosus), by the setation of the hypopharynx with long setae up to the concave margin of the superlinguae, the shape of the pronotum, the shape of the bristles on the upper face of hind femora, and the ornamentation of the hind tibiae. Together with Th. vietnamensis Dang, 1967, Th. bishopi Braasch & Soldán, 1986 and Th. flowersi Venkataraman & Sivamarakrishnan, 1987, Th. lamuriensis constitutes a group called by Kluge (2004) Ecdyonuroides/g(1) and characterized by "posterolateral projections [...] on segments VI-VIII very long and pointed, exceeding segment length". The three above mentioned species are incompletely described, but Th. lamuriensis differs from them apparently by the shape of the bristles on the upper face of femora, by the shape of the first gill and by the coloration of the abdomen (Braasch and Soldán 1984).

Th. lamuriensis possesses anyway far more characters in common with *Th. determinatus* and *Th. sinuosus* than the observed (although quite obvious) differences, and there is no reason on this basis to propose other generic rearrangement for Ecdyonuroides/g(1).

Eggs of *Th. lamuriensis* are very peculiar with pedunculate KCT'S, which distinguish them from the two other species.

Th. lamuriensis is the most abundant *Thalerosphyrus* species in Sumatra, and seems widespread throughout the island. In several places, it has been found together with *Th. sinuosus*.

Key to the Thalerosphyrus nymphs occurring on Java and Sumatra

1	Posterolateral expansions on the abdomen greatly enlarged (Fig. 8), reaching
	their maximum on segment VIII; protonum greatly enlarged laterally (Fig.
	7); bristles on the dorsal face of hind femora truncate or rounded at apex (Fig.
	33); hypopharynx with outer margin of superlinguae evenly covered with
	long setae (Fig. 28)
_	Posterolateral expansions of the abdomen more or less developed, those of
	segment VIII always shorter than those of segment VII (Figs 3, 6); prono-

Notes on the male imaginal stages

2

The ZMH collections housed few male imagos of *Thalerosphyrus*, namely a single male of *Th. determinatus* and two of *Th. sinuosus*. These have been described in details by Ulmer (1913; 1924; 1939). Both species differ by the shape of the genitalia, by the coloration of the abdomen and by the tarsal composition of the hind legs. The report and description by Ulmer (1924) in Sumatra (Gunung Dempu, 1400 m, VIII.1916, Jacobson leg) of a male imago of the Philippine species "*Thalerosphyrus*" torridus (Walker, 1853) has already been considered as highly dubious by Braasch (2011). This specimen anyway displays general characteristics of the genitalia, and the tarsal composition of the hind leg. It is possible and even probable that this specimen represents the male stage of the species *Th. lamuriensis*, but only in situ rearing may bring the definitive proof.

Acknowledgments

I am indebted to the staff of the Zoologisches Museum Universität Hamburg (ZMH) for allowing me to study Ulmer's, collection, especially to Kai Schütte and Hossein Rajaei. My appreciation goes to Michael Balke (Munich) and Jean-Marc Elouard (Montpellier) for putting their collections at my disposal, and to Jeff Webb (Missoula, USA) for useful comments. Technical assistance with SEM pictures by Geneviève L'Eplattenier and Raphael Grand (MZL) and Renate Walter (ZMH) was essential and they are warmly thanked for their help.

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RESEARCH ARTICLE



A new species of *Litopeltis* Hebard, 1920 from Rio de Janeiro, Brazil (Blattodea, Blaberidae, Epilamprinae) with a key to males and geographical distribution of the remaining species of the genus

Leonardo de Oliveira Cardoso Silva¹, Sonia Maria Lopes¹

I Departamento de Entomologia, Museu Nacional, Universidade Federal do Rio de Janeiro-UFRJ

Corresponding author: Sonia Maria Lopes (sonialfraga@gmail.com)

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Abstract

This contribution describes a new species of *Litopeltis* from Brazil, *L. teresopolitensis* **sp. n.**, which shows similarities with *L. paineirensis* Lopes & Oliveira, 2010 and *L. ribeiropretano* Lopes & Oliveira, 2010. It differs in characters of morphology genitalia and configuration, with the median sclerite bearing microspines on the sclerotic apex. A map showing the geographic distribution of the Brazilian species and a key to males of the other species of the genus are also presented.

Keywords

Blaberidae, key, Litopeltis, Morphology, new species, taxonomy

Introduction

The genus *Litopeltis* was described by Hebard (1920), based on material from Colombia. Hebard's decision to include the new genus in the subfamily Perisphaerinae was supported by Rehn (1928), remarking that the male of *Litopeltis* superficially looks much like the Epilamproid genus Leurolestes, while the brachypterous females in general resemble species of Audreia of the same subfamily. However the position of Litopeltis is in the Epilamprinae, differing from Colapteroblatta in its size and poorly defined ocelli, as well as from Mioblatta in its size, absence of tomentosity, unspotted pronotum and spiked femurs (Roth 1971). The type species is *L. bispinosa* (Saussure, 1893), previously included in the genus Calolampra. Currently Litopeltis includes 11 species. Lopes and Oliveira (2010) have determined that in Brazil, members of the genus are present in Rio de Janeiro, São Paulo and Mato Grosso. Beccaloni (2013) recognized 11 species for in the genus, and confirmed its presence in Central America (Costa Rica and Panama) and South America (Ecuador); and Vélez (2008) confirmed the presence of the genus in Colombia (Fig. 1). Thus, the distribution of Litopeltis comprises three Neotropical subregions: the Caribbean subregion and the western province of Ecuador (Ecuador) and Chocó (Colombia) and Andean north (Panama), together with the eastern province of Central America and west to the Isthmus of Panama (Panama and Costa Rica); the Amazon subregion, with the province of Pantanal (Mato Grosso); and the subregion of the provinces of Floresta do Paraná (São Paulo) and the Atlantic Forest (Rio de Janeiro) (Morrone 2009). Morrone stated that in the Pre-Quaternary period, the Neotropical biota expanded northward to Central America and southward to the Andean region, which could explain the dispersal of the genus to Central America and to the Amazon and Paraná subregions.

The present contribution provides information about the genus *Litopeltis*, including a key, and a description of a new species. The habitus, head, pronotum and external and internal genitalia with of the holotypes of the Brazilian species and new species were compared, the original descriptions were studied.

Material and methods

The genital plates were removed after dissection of the posterior part of the abdomen, using traditional dissection techniques, as described by Lopes and Oliveira (2000). After analysis, the genital plates and genital pieces were stored in microtubes containing glycerin and attached to the respective exemplar, a technique developed by Gurney et al. (1964). The terminology for the genitalia and the taxonomic classification follow Roth (2003). The specimens were compared with other specimens of *Litopeltis* deposited in the Blattodea Collection of the Museu Nacional of Rio de Janeiro (MNRJ), and with descriptions in the literature. Digital images of the habitus, pronotum, head and genitalia were taken with a camera mounted on a stereoscope. The holotype is deposited in the collection of the Department of Entomology at the Museu Nacional of Rio de Janeiro (MNRJ). The text was translated by Prof. Solange Garrido and edited by Dr. Janet W. Reid. The map was taken from MAPA DA AMERICA (http://www.mapadaamerica.com/) (Fig. 1).



Figure 1. Map of geographical distribution of *Litopeltis* Hebard, 1920.

Results

Litopeltis teresopolitensis sp. n.

http://zoobank.org/6B0F173A-D1F4-439E-BBF1-90387F3DDBBC Figs 2–9

Typematerial. Holotype ♂, BRAZIL: Rio de Janeiro, Teresópolis, Parque do Ingá District, III/2013, Schilithz, A. G. col.

Etymology. The name is given for Teresópolis, the collection locality of the holotype.

Description. Dimensions (mm): Male holotype, total length: 20.7; length of pronotum: 4.0; width of pronotum: 4.5; length of tegmen: 17.5; width of tegmen: 4.4.

Male holotype. Coloration. General coloring chestnut (Fig. 2). Head with dark eyes, vertex dark with a white vertical line and interocular space in center of the forehead and center of clypeus black (Fig. 3); antennae opaque, first 26 antennomeres glossy, remainder tomentose. Central disk of pronotum with black spots (Fig. 4). Legs with bases of coxae black, spines on tibiaes, dorsal part of tarsus and claws brown, remaining segments of legs, pulvilli and arolium white. Tegmen hyaline, wings with brown veins. Abdomen with dark-brown segments and whitish-yellow lateral margins.

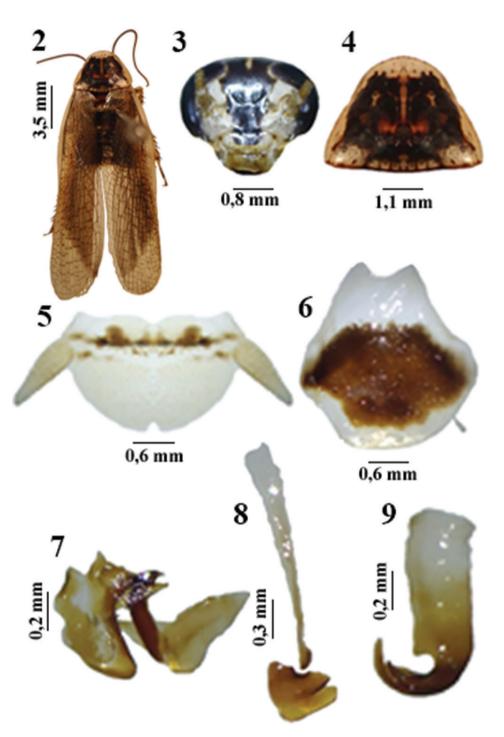
Head. Vertex hidden; interocular space ample, subequal to distance between bases of antennal insertions. Antennae tomentose distally, reaching slightly over half of length of abdomen. Ocelli developed. Maxillar palpi tomentose.

Thorax. Pronotum transverse, trapezoid, convex with rounded apex and slightly sinuous base. Legs short and robust. Femur I, anteroventral margin bearing three spines in basal half, a row of 21 spines and one longer apical spine in apical half, with a large robust spine on apex; posteroventral margin with row of seven slender spines, ending with two robust spines in apical third. Femur II, anteroventral margin bearing two robust spines, one median, the other apical; posteroventral margin with three to four robust spines. Femur III, antero- and posteroventral margin with two to three robust spines. Large pulvilli present on all tarsomeres; arolia present; claws symmetrical with slight specialization, having eight small rectangular structures.

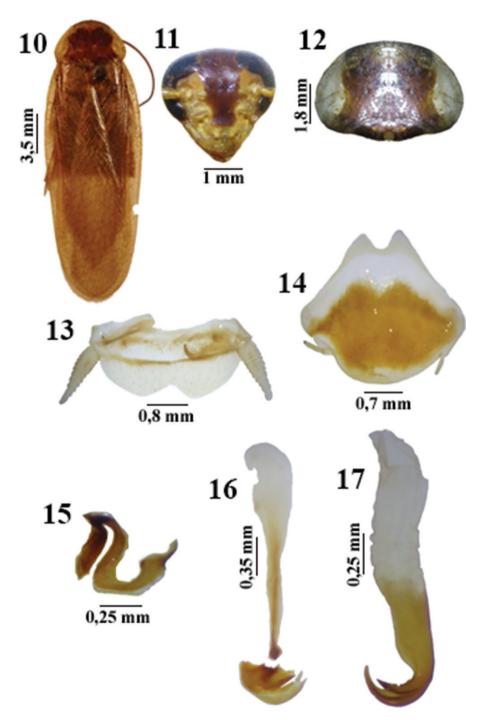
Wings. Tegmina long, overreaching apex of cerci; marginal field concave and well delineated; scapular field long and narrow with apically oblique arrangement of veins; discoidal field ample and convex, apically widened with a longitudinal arrangement of veins; anal field ample, elongated, with three axillary veins. Hind wings with costal sector having the apices of the veins dilated; apical triangle present; anal field folded fanwise.

Abdomen. Absence of tergal modifications. Supra-anal plate short and wide, with smooth median apical indentation; cerci short (Fig. 5). Subgenital plate widened and prominent medially, with acute styli in median apical region of plate (Fig. 6). Left phallomere with median sclerotic structure in shape of an inverted "V" (Fig. 7); median sclerite developed, with microspines on sclerotized apex (Fig. 8); right phallomere hook-shaped (Fig. 9).

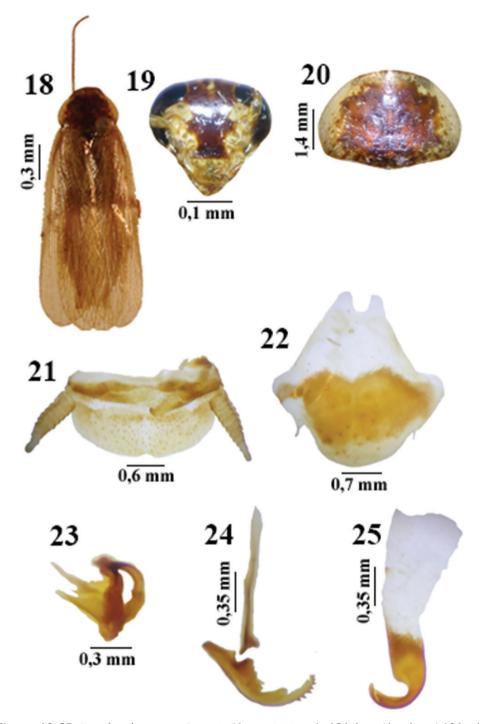
Diagnosis. This species appears to be to *L. paineirensis* Lopes & Oliveira, 2010 (Figs 10–17), which it resembles in the median sclerite (Fig. 16) and the subgenital plate (Fig. 14); and to *L. ribeiropretano* Lopes & Oliveira, 2010 (Figs 18–25), which has a similar right phallomere (Fig. 25).



Figures 2–9. *Litopeltis teresopolitensis* sp. n., male 2 habitus (dorsal view) 3 head (ventral view) 4 pronotum (dorsal view) 5 supra-anal plate (dorsal view) 6 subgenital plate (ventral view) 7 left phallomere (dorsal view) 8 median sclerite (dorsal view) 9 right phallomere (dorsal view).



Figures 10–17. *Litopeltis paineirensis* Lopes & Oliveira, 2010, male. **10** habitus (dorsal view) **11** head (ventral view) **12** Pronotum (dorsal view) **13** supra-anal plate (dorsal view) **14** subgenital plate (ventral view) **15** left phallomere (dorsal view) **16** median sclerite (dorsal view) 17 right phallomere (dorsal view)



Figures 18–25. *Litopeltis ribeiropretano* Lopes & Oliveira, 2010, male. **18** habitus (dorsal view) **19** head (ventral view) **20** pronotum (dorsal view) **21** supra-anal plate (dorsal view) **22** subgenital plate (ventral view) **23** left phallomere (dorsal view) **24** median sclerite (dorsal view) **25** right phallomere (dorsal view)

Key to adult males of the genus Litopeltis

The species *L. brevitarsis* (Saussure, 1893), *L. compleptera* Roth & Gutierrez, 1998 and *L. musarum* Rehn, 1928 were not included in the key because they were described from females.

1	Neotropical species endemic to Brazil
_	Neotropical species, however occurring outside of Brazil4
2	Central disk with nonuniforme spots on pronotum; apex of median sclerite
	without spike like protuberances (Figs 4, 8, 12 and 16)
_	Central disk with uniforme spots on pronotum; apex of median sclerite with
	spike-like protuberances (Figs 20 and 24)
3	Right phallomere abruptly tapering pre-apically (Fig. 9) <i>L. teresopolitensis</i> sp. n.
_	Right phallomere only slightly tapering pre-apically (Fig. 17) L. paineirensis
4	Total length larger than 15,6 mm
_	Total length less than or equal to 15,6 mm
5	Dorsal sclerite from median sclerite rounded in the apex and developed, al-
	most reaching the prepuce extension
_	Dorsal sclerite from median sclerite, reduced and thin in the apex, not reach-
	ing all prepuce extension
	<i>L. biolleyi</i> (Saussure, 1895) (Figs 42–44 in Roth 1971)
6	Dorsal sclerite from median sclerite foliaceous, not reaching the middle of
	prepuce <i>L. oreas</i> Rehn, 1928 (Figs 45–47 in Roth 1971)
_	Dorsal sclerite from median sclerite not foliaceous
7	Length of pronotum less than or equal to 4,8 mm L. votos Rehn, 1928
_	Length of pronotum longer than 4,8 mm
8	Width of tegmen less than or equal to 6,2 mmL. deianira Rehn, 1928
_	Width of tegmen longer than 6,2 mm <i>L. calverti</i> Rehn, 1938

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RESEARCH ARTICLE



Description of Ortheziolamameti tranfagliai new species (Hemiptera, Coccoidea, Ortheziidae) from India

Éva Szita¹, Mehmet Bora Kaydan^{1,2}, Zsuzsanna Konczné Benedicty¹

Plant Protection Institute, Centre for Agricultural Research, Hungarian Academy of Sciences, Herman Ottó
 u. 15, H-1022 Budapest, Hungary 2 Çukurova Üniversity, Imamoglu Vocational School, Adana, Turkey

Corresponding author: Éva Szita (szita.eva@agrar.mta.hu)

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Abstract

This paper describes a new *Ortheziolamameti* species from the Oriental region (India), namely *Ortheziola-mameti tranfagliai* Konczné Benedicty, **sp. n.** The examined material was extracted from forest litter from India, using Berlese funnels. With this new species the genus *Ortheziolamameti* now includes six species. An identification key and distribution map are provided.

Keywords

Ensign scale, taxonomy, distribution, identification key, Oriental region

Introduction

The family Ortheziidae (Hemiptera: Coccoidea), or ensign scale insects, have been considered to be one of the oldest families among the scale insects (Koteja 1996, Kozár and Miller 2000, Vea and Grimaldi 2012). According to Kozár (2004), the Ortheziidae family consists of four subfamilies: Ortheziinae Kozár, Newsteadiinae Kozár, Ortheziolinae Kozár and Nipponortheziinae Kozár. The subfamily Ortheziolinae is characterized by having: (i) the dorsum of the adult female entirely covered by

wax plates, and a narrow band in midline of the dorsum, (ii) 3-segmented antennae (the size, shape, number, and type of setae highly variable), (iii) eye stalks protruding, thumb-like, fused with sclerotized area at base of antennae, sometimes called pseudobasal antennal segment, (iv) tarsi without digitules and (v) abdominal spiracles ventral on anterior segments, with at least one present on each side of abdominal segments I, II, or III; if present, posterior abdominal spiracles located on dorsum near anal ring surrounded by a cluster of multilocular disc pores. Ortheziolinae species are mainly found in the soil and distributed in the Palaearctic, Oriental and Ethiopian regions, and their host plant relationships are not well-known. In the subfamily there are four tribes, namely Ortheziolamametini Kozár, Ortheziolini Kozár, Matileortheziolini Kozár and Ortheziolacoccini Kozár.

Ortheziolamametini is characterized by having: (i) dorsum covered by wax plates, those in the middorsum being triangular, (ii) midthorax of venter without wax plates, and (iii) two spine bands inside the ovisac band. Species of Ortheziolamametini are distributed in the Ethiopian, Oriental and Palaearctic Regions. Although the genus is a typical member of the subfamily Ortheziolinae, it somewhat resembles *Arctorthezia* of subfamily Ortheziinae, known mainly in the northern part of the Holarctic region, in having the triangular wax plates on the middorsum. The genus includes 5 species, namely *O. guineensis* (Morrison, 1954), *O. loebli* (Richard, 1990), *O. kosztarabi* (Kozár & Miller, 2000), *O. maeharai* Tanaka & Amano, 2007, and *O. taipensiana* Shia & Kozár, 2004; two of them are distributed in West Africa (*O. guineensis* and *O. kosztarabi*), two are in the Oriental Region (*O. taipensiana* and *O. loebli*), and one (*O. maeharai*) is in the Far-East (Palaearctic).

In the present paper one new *Ortheziolamameti* species is described from the Oriental region (India). An identification key, distribution map and new additional locality records for the currently known *Ortheziolamameti* species are provided.

Material and methods

The specimens described and recorded in this study were all collected using soil and litter sampling devices, and extracted by Berlese funnel. The samples are preserved in the Muséum d'Histoire Naturelle de Genève (MHNG) collection.

Specimens were prepared for light microscopy using the slide-mounting method discussed by Kosztarab and Kozár (1988). The morphological terminology used follows Kozár (2004), while the key was adopted from Kozár (2004) and Tanaka and Amano (2007).

The digital images of unmounted females were made with a Canon Eos400D camera and an MBC-10 stereomicroscope, and focus-stacking was processed by CombineZP software (Hadley 2010). All type material of the new species are deposited in the Muséum d'Histoire Naturelle de Genève (MHNG).

All measurements and counts were taken from all the material available and the values are given as a range for each character.

Results and discussion

Genus Ortheziolamameti Kozár, 2004: 483.

Type species. Ortheziolamameti guineensis Kozár, 2004, 484.

Diagnosis of genus. Dorsum of intact adult female covered with irregular and triangular shell-like wax plates; ventral thoracic wax plates around the appendages and on margin, thorax medially lacking wax plates; wax cover corresponding to wax plates on slide-mounted specimens on both sides (Kozár 2004) (Fig. 1).

Slide-mounted adult female with 3-segmented antenna; third antennal segment with slender apical seta, flagellate sensory seta and small subapical seta; second segment with 1 sensory pore. Eye stalk protruding, thumb-like, fused with base of antenna. Legs well developed; leg setae robust, spine-like; trochanter and femur fused, tibia and tarsus fused; tibia with 1 sensory pore and at least 1 fleshy sensory seta; tarsus without tarsal digitules; claw digitules hair-like, claw without a denticle. Labium 1 segmented, with many setae; with 3 long setae near apex of labium, setae very close together, all situated in a single setal socket. Anal ring situated in a fold of derm on dorsal surface, ring bearing 6 setae. Sclerotized plate present on dorsum anterior to anal ring, wider than long. Thumb-like pores forming a cluster on each side of anal ring. Abdominal spiracles in centre of multilocular disc pore cluster present laterad to anal ring (Kozár 2004).

Distribution. The six *Ortheziolamameti* species are distributed in the Ethiopian, Oriental and Palaearctic regions (Fig. 3). For detailed distribution data of previously known five species, see ScaleNet (Ben-Dov et al. 2013). New locality records for several *Ortheziolamameti* species were discovered during the study of the MHNG collection, which are listed below.

Key to species of Ortheziolamameti

1	Setae on antennae hair-like	2
_	Setae on antennae spine-like	5
2	Multilocular disc pores absent around vulva	3
_	Multilocular disc pores present around vulva	4
3	Plates 13, 17 and 18 resembling very small groups of spines, without cluster of spines between hind legs, second spine band in ovisac area in a sparse row	
	O. tranfagliai sp. 1	1.
_	Plates 13, 17 and 18 in complete groups of spines, large cluster of spines be tween hind legs with a second spine band in ovisac area forming a complete	
	row	li
4	Wax plate 9 narrow anteriorly, so that wax plate 9 is shaped like an elongate	d
	isosceles triangle; wax plate 10 similar in shape to wax plate 9, not so wid	le
	anteriorly	ır

-	Wax plate 9 wide anteriorly, so that wax plate 9 almost forms an equilatertal
	triangle; wax plate 10 not similar to wax plate 9, but norrow posteriorly and
	widening anteriorlyO. maeharai Tanaka & Amano
5	Multilocular disc pores present in a band anterior of each spine band within
	ovisac
_	Multilocular disc pores present in a row only in anterior spine band within
	ovisac

Ortheziolamameti tranfagliai Konczné Benedicty, sp. n.

http://zoobank.org/309E49AD-10F9-4EF6-B764-04985114D053 Figure 1

Material examined. *Holotype.* Adult female. Slide with two specimens, holotype clearly marked, signed red. India, Kerala, Cardamon Hills, 26.12.1972, Leg. Bes/Löbl [MHNG code: Bes/Löbl (50), PPI code: 9807].

Paratypes. 3 adult females, 1 specimen on same slide as holotype, 2 specimens on a separate slide, same data as holotype.

Description. Unmounted female. Not seen.

Mounted female (Figure 2).

Adult female. 1.554–1.709 mm long; 1.114–1.295 mm wide. Length of antennal segments: 1^{st} 72–101 µm, 2^{nd} 60–76 µm; 3^{rd} 290–372 µm; 3^{rd} segment nearly parallel sided; apical seta of antenna 146–180 µm long; subapical setae 55–61 µm long; flagellate sensory setae near apical seta 24–30 µm long; microsetae absent from apex of antenna; without unusual hair-like setae near subapical setae; with several small setae near posterior edge of antennae; all segments of antennae covered with many hair-like, curved, pointed setae, longest seta 25 µm long; first antennal segment with 2 capitate sensory setae on each side; third segment with 27–37 setae.

Venter. Labium 151–168 μ m long. Stylet loop slightly longer than labium. Leg segment lengths: front coxa 101–144 μ m, middle 120–156 μ m, hind 144–178 μ m; front trochanterfemur 312–382 μ m, middle 331–398 μ m, hind 357–434 μ m; front tibia-tarsus 323–382 μ m long, middle 357–408 μ m, hind 434–525 μ m; front claw 45–60 μ m, middle 48–55 μ m, hind 53–60 μ m; claw digitules 17–21 μ m long, legs with longitudinal rows of robust setae, longest seta on trochanter-femur 16 μ m; with 1 or 2 flagellate sensory seta on tibia-tarsus each 22 μ m long; trochanter with 3 or 4 sensory pores on each surface. Wax plates present on marginal areas of head and thorax, with wide marginal wax band laterad of each thoracic spiracle (plates 15 and 16); plates 13, 17 and 18 resembling very small groups of spines; without a cluster of spines between hind legs; with 2 bands of spines within ovisac band, second one with an incomplete row of spines. Thoracic spiracles usually associated with 3 or 4 multilocular disc pores, each pore with 8 loculi, 6 μ m in diameter; diameter of anterior thoracic spiracles 20–26 μ m. Flagellate setae few, with several setae near

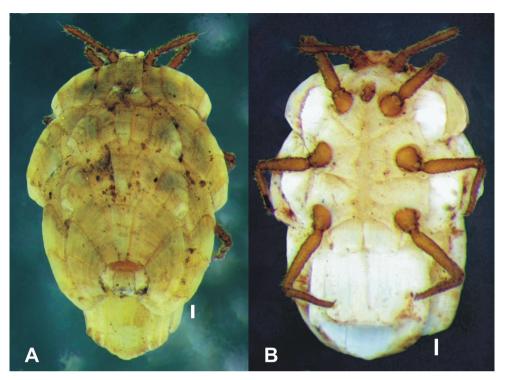


Figure I. *Ortheziolamameti taipensiana* Shiau & Kozár, 2004, unmounted adult female **A** dorsal view **B** ventral view. Scale = 0.1 mm. Photo: É. Szita.

anterior edge of ovisac band, with several setae associated with anterior and posterior multilocular disc pore rows.

Quadrilocular pores 3 µm in diameter, scattered in the ovisac band. Multilocular disc pores with 8–12 loculi around perimeter, one loculus in central hub; 7–8 µm in diameter; present near anterior edges of spine bands, scattered along lateral edge of each ovisac band. Abdominal spiracles present anterior of ovisac band; without sclerotized vestibule.

Dorsum. Wax plates covering the whole surface; mediolateral thoracic plates large (plates 3, 5 and 6), covering most of mediolateral thoracic areas; medial area without wax plates, this area with 3 triangular wax plates (plates 8, 9 and 10). Spines at margin of wax plate 4, each $12-14 \mu m$ long, in middle of wax plates $18-21 \mu m$ long; spines apically capitate. Setae present in marginal clusters near posterior edges of marginal wax plates (plates 2 and 4), with 3 or 4 setae laterad of each thoracic spiracle, $27-30 \mu m$ long; also present in very small numbers on other wax plates. Quadrilocular pores 3 μm in diameter, scattered, mainly along margins of wax plates. Multilocular disc pores present in a cluster near anal ring, near the sclerotized plate, and on the margin at the level of ventral thoracic spiracles. Sclerotized plate $80-120 \mu m$ long, $265-330 \mu m$ wide. Anal ring with two complete rows of round pores ($4-5 \mu m$ in diameter); three pairs of anal

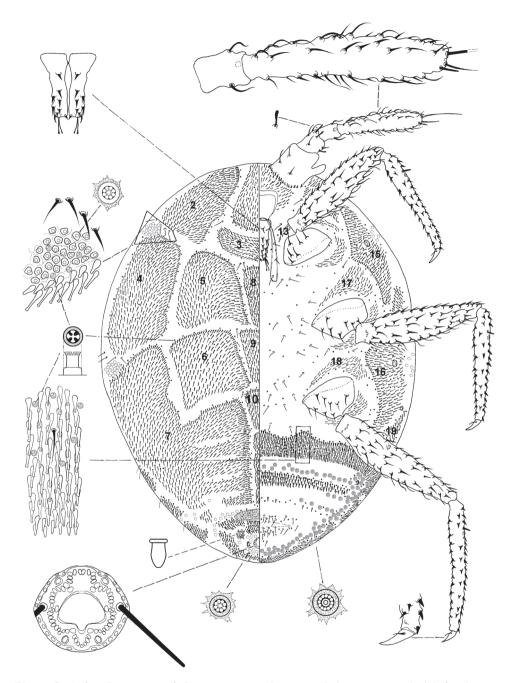


Figure 2. Ortheziolamameti tranfagliai Konczné Benedicty sp. n., holotype, mounted adult female.

ring setae each 45–21 μ m long; anal ring 43–53 μ m wide, 43–53 μ m long. Thumb-like pores forming a cluster on each side of anal ring, each 5–8 μ m long. Modified pores (quadrilocular pores) 3–4 μ m long, scattered on surface. The abdominal spiracle is located in centre of the multilocular disc pore clusters laterad to anal ring.

Ecology. Host plants. Unknown. Collected from forest litter.

Distribution. India.

Etymology. This species is named after the Italian coccidologist Dr. Antonio Tranfaglia.

Comments. Ortheziolamameti tranfagliai sp. n. can be recognized by the following combination of characters: (i) having hair-like setae on antennal segments, (ii) having two spine bands in the ovisac area and (iii) lacking multilocular disc pores around vulva. O. tranfagliai is similar to O. loebli in having hair-like setae on antennae and lacking multilocular disc pores around vulva, but differs from O. loebli in the following characters (those of O. loebli in brackets), (i) plates 13, 17 and 18 resembling very small groups of spines (plates 13, 17 and 18 complete); (ii) without cluster of spines between hind legs (with large cluster of spines between hind legs) and (iii) second spine band in ovisac area in a sparse row (in a complete row).

Distribution of Ortheziolamameti species in the world

Ortheziolamameti guineensis (Morrison, 1954)

Distribution. Guinea. Distribution note of Ghana (Ben Dov et al. 2013, Kozár 2004) might be a mistranslation of French Guinea mentioned by Morrison (1954). The

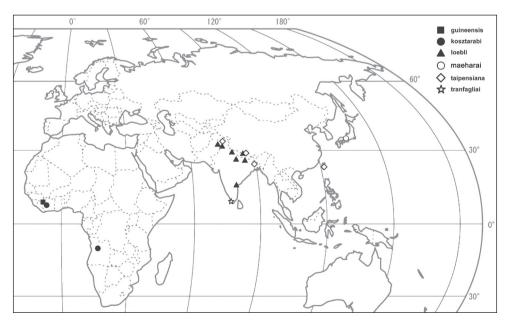


Figure 3. Distribution map of Ortheziolamameti species in the world.

Nimba Mountains where the type species originates from, currently a national park in Guinea. New records: Ivory Coast, Man, Cascades, 7.10.1980, leg. V. Mahnert, L. Perret [MHNG code: 80/12 Cote d'Ivorie, PPI code: 9624].

Ortheziolamameti kosztarabi (Kozár & Miller, 2000)

Distribution. Angola (Kozár and Miller 2000).

Ortheziolamameti maeharai Tanaka & Amano, 2007

Distribution. Japan (Tanaka and Amano 2007).

Ortheziolamameti loebli (Richard, 1990)

Distribution. Nepal (Richard 1990; Ben-Dov et al. 2013). New records: India, Khajjiar, East of Dalhousia, 21.10.1988, leg. S. Vit [MHNG code: 30.INDE, PPI code: 9646]; India, Uttar Pradesh, Garhwal, 27.10.1979, leg. I. Löbl [MHNG code: Löbl (26), PPI code: 9803]; India, Uttar Pradesh, Kumaon, Rangarh, 9.10.1979, leg. I. Löbl [MHNG code: Löbl (6, 7), PPI code: 9789, 9816]; India, Uttar Pradesh, Kumaon, Chambattiva prés Ranikhet, 12–13.10.1978, leg. I. Löbl [MHNG code: Löbl (10), PPI code: 9811]; India, Madras, Anai matai Hills, 18.11.1972, leg. Besuchet, Löbl [MHNG code: Bes/Löbl (35), PPI code: 9815]; India, Madras, Nilgiri, 22.11.1972, leg. I. Löbl [MHNG code: Löbl (22), PPI code: 9809]; Nepal, Bagmati, Bahrabise, North-East of Dobate Ridge, 2700 m a.s.l., 2.05.1981, leg. Löbl, A. Smetana [MHNG code: Löbl, A. Smetana [MHNG code: 12. INDE, PPI code: 9649]; Pakistan, Punjab, Murree, 1950 m a.s.l., 23.04.1984, leg. S. Vit [MHNG code: Pak-84/22, PPI code: 8948].

Ortheziolamameti taipensiana Shiau & Kozár, 2004

Distribution. Taiwan, Thailand (Kozár 2004). New records: India, Tigerhill, 25002600 m a.s.l., 18.10.1978, leg. Besuchet, Löbl [MHNG code: Besuchet/Löbl (19), PPI code: 9631]; India, Meghalaya, Khasi Hills, 1850 m a.s.l., 28.10.1978, leg. Besuchet, Löbl [MHNG code: Besuchet/Löbl (27), PPI code: 9638]; Nepal, Bagmati, Malemchi, 2900 m a.s.l., 14.04.1981, leg. Löbl, Smetana [MHNG code: Löbl/ Smetana (23), PPI code: 9648].

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RESEARCH ARTICLE



Identity of the leafhopper Kolla albescens, with new synonymy (Hemiptera, Cicadellidae)

Ze-hong Meng^{1,2}, Mao-fa Yang¹, Mick Webb³

1 Institute of Entomology, Guizhou University; Guizhou Provincial Key Laboratory for Agricultural Pest Management of the Mountainous Region, Guiyang Guizhou, 550025, P. R. China 2 Guizhou Tea Research Institute, Guiyang Guizhou, 550006, P. R. China 3 The Natural History Museum, London, UK.

Corresponding author: Mao-fa Yang (yangmaofa@sohu.com)

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Abstract

Newly collected male and female specimens of the leafhopper *Kolla albescens* Jacobi, 1943 from the typelocality (Northeast China), are identified as *Pagaronia albescens* (Jacobi), **comb. n.** (Evacanthinae: Pagaroniini). A redescription of the species is provided together with habitus photographs of the male and female and illustrations of the male and female genitalia. *P. continentalis* Anufriev, 1970 is placed as a junior synonym of *P. albescens* **syn. n.**

Keywords

Auchenorrhyncha, China, new combination, Pagaroniini, taxonomy

Introduction

The leafhopper *Kolla albescens* was described by Jacobi (1943) based on a female specimen from Northeast China. In Young's (1986) Cicadellinae revision he did not examine the type specimen of *K. albescens* so placed it in *Kolla* following Metcalf (1965). Although Wilson et al. (2009a, b) provided body images of the type specimen, the lack of a male specimen has prevented the species being formally redescribed or revised. Fortunately, we have been able to collect several specimens from the type locality in Northeast China of *K. albescens*. Based on colour, external features and the male genitalia, this species should be included in the leafhopper genus *Pagaronia* Ball (Evacanthinae: Pagaroniini). Subsequent comparison with figures of *Pagaronia* in Kwon (1981) indicated that it was a senior synonym of *Pagaronia continentalis* Anufriev (1970), the only species of *Pagaronia* from China (Kwon and Huh 2001). Habitus photographs of the male and female and illustrations of the male and female genitalia of *P. albescens* are provided.

Material and methods

The male and female genital structures were prepared according to the techniques described by Oman (1949) and Mejdalani (1998), respectively. The dissected parts are stored in small vials with glycerin and attached below the specimens. The morphological terminology adopted herein follows mainly Young (1986), except for the facial areas of the head (Hamilton 1981; Mejdalani 1998), the leg chaetotaxy (Rakitov 1998) and that of the female genitalia (Nielson 1965; Davis 1975; Mejdalani 1998). All specimens studied are housed in the Institute of Entomology, Guizhou University, Guiyang, China (GUGC).

Taxonomy

Pagaronia albescens (Jacobi, 1943), comb. n. Figs 1–21

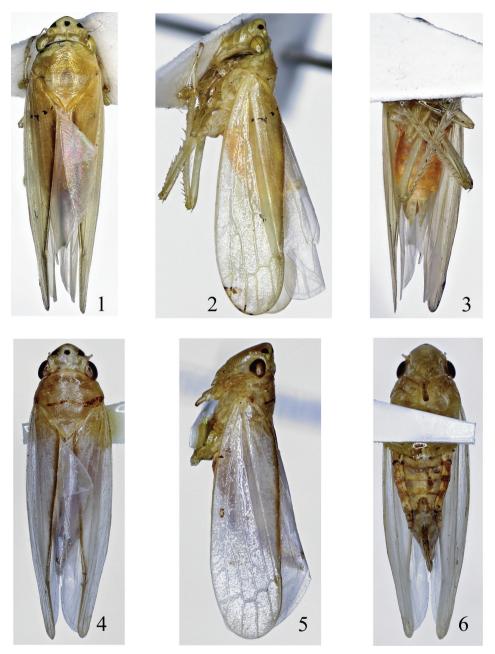
Kolla albescens Jacobi, 1943: 28; Wilson et al. (2009a, b) Pagaronia continentalis Anufriev, 1970, 18: 555; Kwon 1983: 18 (in key). syn. n.

Type-locality. "Gaolinzsy" (NE China).

Description. Length of males 8.5–9.0 mm, females 8.7–9.8 mm.

Coloration. Male: Head, thorax and pygofer yellowish-white; apical 1/3 of crown with three transverse black spots, one at median portion and one at each lateral margin; forewing with brown costal margin; abdomen orange-yellow in ventral view, pygofer yellow-white. Female: Head, thorax and abdominal sternites yellowish-brown; forewing pale lacteous; other coloration similar to male.

Head anterior margin almost angulate; median length of crown 5/7 of interocular width; coronal suture distinct at posterior half of crown; crown concave between ocellus and coronal suture, with fovea between ocellus and eye; ocelli located in front of imaginary line between anterior eye angles, each closer to eye than to median line of crown; lateral frontal sutures extending onto crown, attaining ocelli; frons flattened medially, muscle impressions distinct in female and obscure in male; epistomal suture



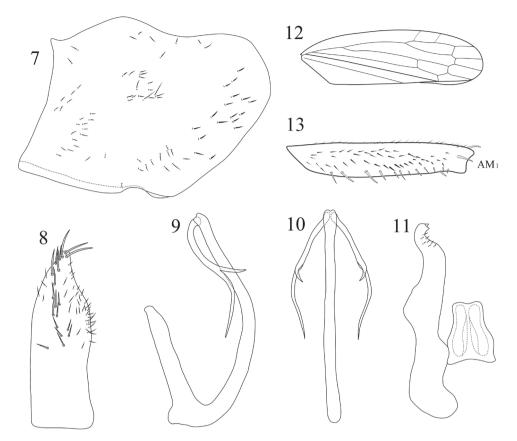
Figures 1–6. *Pagaronia albescens* (Jacobi, 1943), comb. n. 1–3 body of male (9.0 mm): 1 dorsal view 2 lateral view 3 ventral view 4–6 body of female (9.8 mm) 4 dorsal view 5 lateral view 6 ventral view.

complete. Pronotum broader than head; anterior margin broadly rounded; posterior margin concave medially; disk transversely rugulose medially; dorsopleural carinae distinct; scutellum flattened behind transverse depression; transverse depression straight,

located in middle of disk, attaining lateral margins of scutellum; forewing (Fig. 12) with base of second apical cell more proximal than base of third; medial inner subapical cell open. Fore legs with femur (Fig. 13), in anterior view, with intercalary row comprising about 10 widely spaced stout setae on distal half, first anteromedial seta (AM1) located near base of ventroapical femoral lobe, anteroventral row with about four stout setae. Hindleg with apical femoral setal formula 2:1:1. Male abdominal apodemes small, reaching near mid length of third segment.

Male genitalia with pygofer (Fig. 7), in lateral view, broad and strongly produced posteriorly, dorsal margin with anterior half convex and posterior half slightly concave; posterior margin broadly rounded; ventral margin with fold, fold concave near apex; disk apicoventral portion with sparse short macrosetae; microsetae also present. Subgenital plate (Fig. 8) small, distinctly shorter than pygofer; posterior area abruptly narrowed, apex nearly acute and slightly curved outwards; apical half with sparse microsetae and irregularly triseriate macrosetae medially. Aedeagus (Figs 9, 10) with long basal apodeme, as long as half of shaft; aedeagal shaft slender, curved posterodorsally, with apical aedeagal processes branched, longer branch extending beyond mid-length of shaft with short sub-branch medially. Connective shield-shaped (Fig. 11), with basal half broader. Style (Fig. 11) strong and extending posteriorly beyond connective apex, preapical portion with several microsetae; apical portion curved, S-shaped, and apex with two denticles.

Female genitalia. Sternite VII (Fig. 14), in ventral view, slightly longer than broad; posterior margin convex and with shallow concavity medially; surface with few small setae mostly on anterior half. Pygofer (Fig. 15), in lateral view, moderately produced posteriorly; posterior margin with subacute apex, dorsoposterior margin obliquely truncate; surface with macrosetae mostly on ventral margin, arranged almost in a row. Valvifers I (Fig. 16), in lateral view, longer than tall; posteroventral margin angulate. Valvifers II (Fig. 17), in lateral view, nearly fusiform, with small group of clustered setae near articulation point, articulation point located on 2/3 of dorsal margin. Valvulae relatively narrow in lateral view. Valvulae I (Fig. 16) with base subtriangular in ventral view; with convex lateral outer margin; in lateral view (Figs 16, 18, 19) with dorsal and ventral margins nearly parallel over basal two thirds behind basal curvature, thereafter slightly convex and narrowed to acute apex; dorsal sculptured area restricted to posterior 2/3 of shaft, formed mostly by subrectangular sculpture arranged in oblique lines, except basally were it is arranged horizontally; ventral sculptured area formed by dense imbricate sculpture restricted to apical portion of shaft; length of ventral interlocking device corresponding to approximately 2/3 of blade length beyond basal curvature. Valvulae II (Figs 20, 21), in lateral view, with anterior fused basal section nearly 2/3 length of blade; only slightly expanded beyond basal curvature and dorsal hyaline region; dorsal and ventral margins approximately parallel; apex narrowly rounded; preapical prominence absent; shaft bearing approximately 25 teeth (Fig. 21: to) over posterior 1/3 of blade; each tooth subtriangular; apicoventral margin without distinct teeth; teeth and dorsal margin of shaft without secondary denticles; ducts sparse, extending toward teeth and toward apical



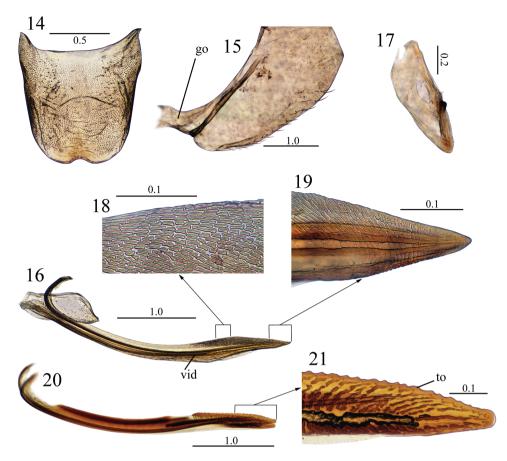
Figures 7–13. *Pagaronia albescens* (Jacobi, 1943), comb. n., male genitalia **7** pygofer, lateral view **8** subgenital plate, ventral view **9** aedeagus, lateral view **10** aedeagus, caudoventral view **11** connective and style, dorsal view **12** forewing **13** fore femur, anterior view. AM₁ = first anteromedial seta.

blade portion. Gonoplacs, in lateral view, expanded at apical half; apex obtuse; surface with macrosetae mostly distributed on apical portion and extending anteriorly along ventral margin of apical half.

Known distribution. Russia, Korea, China.

Material examined. 3 males and 5 females, China, Liaoning Province, Henren County, Benxi Laotuding Preserve, 19 to 21 July 2011, coll. Fan Zhi-hua and Yu Xi-ao-fei; 1 female, China, Jilin Province, Mt. Changbai, 24 July 2011, coll. Yu Xiao-fei.

Remarks. This species was described from a single female specimen (holotype) from "Gaolinzsy" (NE China). The type specimen, deposited in Deutsches Entomologisches Institut im ZALF, Müncheburg, Germany, has not been examined but our material has been compared with an image of the type (see introduction). The identity and reference for the *Pagaronia* species recorded from China in Hayashi et al. (2010) and Kamitani et al. (2012) was established as *P. continentalis* recorded by Kwon and Huh (2001) (M. Hayashi, pers. com.).



Figures 14–21. *Pagaronia albescens* (Jacobi, 1943), comb. n., female genitalia: **14** sternite VII, ventral view **15** pygofer, lateral view **16** valvifer I and valvula I, lateral view **17** valvifer II, lateral view **18** dorsal sculptured area of valvula I, lateral view **19** apical portion of valvula I, lateral view **20** valvulae II, lateral view **21** apex and apical portion of valvulae II, lateral view. go = gonangulum, to = tooth, vid = ventral interlocking device. Scale bars in millimeters.

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RESEARCH ARTICLE



Morphological identification of Lucilia sericata, Lucilia cuprina and their hybrids (Diptera, Calliphoridae)

Kirstin A. Williams¹, Martin H. Villet²

I Entomology Department, Durban Natural Science Museum, Durban, South Africa 2 Southern African Forensic Entomology Research Laboratory, Department of Zoology and Entomology, Rhodes University, Grahamstown, 6140 South Africa

Corresponding author: Kirstin A. Williams (Kirstin.Williams@durban.gov.za)

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Abstract

Hybrids of *Lucilia sericata* and *Lucilia cuprina* have been shown to exist in previous studies using molecular methods, but no study has shown explicitly that these hybrids can be identified morphologically. Published morphological characters used to identify *L. sericata* and *L. cuprina* were reviewed, and then scored and tested using specimens of both species and known hybrids. Ordination by multi-dimensional scaling indicated that the species were separable, and that hybrids resembled *L. cuprina*, whatever their origin. Discriminant function analysis of the characters successfully separated the specimens into three unambiguous groups – *L. sericata*, *L. cuprina* and hybrids. The hybrids were morphologically similar irrespective of whether they were from an ancient introgressed lineage or more modern. This is the first evidence that hybrids of these two species can be identified from their morphology. The usefulness of the morphological characters is also discussed and photographs of several characters are included to facilitate their assessment.

Keywords

Greenbottle blowflies, keys, morphology, discriminant analysis

Introduction

The use of maggot debridement therapy (MDT) in South Africa has gained interest in the past decade (Williams et al. 2008, Du Plessis and Pretorius 2011). The identification of the maggots used for this therapy remains an issue, as most medical doctors are not adequately trained in entomology to correctly identify the flies (Williams et al. 2008, Tantawi et al. 2010). *Lucilia sericata* is the most commonly used species (Sherman et al. 2000) but it is often misidentified as *L. cuprina*. These two species are also used in forensic entomology (Louw and van der Linde 1993, Smith and Wall 1997, Anderson 2000, Oliva 2001, Clark et al. 2006, Day and Wallman 2006) and *L. cuprina* is the species most often responsible for sheep strike – myiasis of sheep by the maggots of this fly (Hepburn 1943, Ullyett 1945, Vogt and Woodburn 1979, Heath and Bishop 2006), but *L. sericata* is responsible for sheep strike in northern Europe where *L. cuprina* is absent (Rose and Wall 2011). Correct identification of these flies is thus vitally important for these three fields.

Several identification keys have been produced either specifically for *L. sericata* and *L. cuprina*, or for larger suites of Luciliinae or Calliphoridae that included these two species (Waterhouse and Paramonov 1950, Rognes 1980, 1994, Dear 1986, Holloway 1991, Wallman 2001, Whitworth 2006, 2010), but several of the diagnostic characters are sometimes omitted while others are included that are less reliable or difficult to observe. Although both species occur worldwide, some of the differences between the character suites in these studies may arise from considering samples from relatively limited geographical regions. The first aim of this study was to consider the value of the published characters based on a sample of specimens from across the world.

A complicating factor is the known and widespread existence of natural hybrids of these species (Stevens et al. 2002, Wallman et al. 2005, Tourle et al. 2009, DeBry et al. 2010, Williams and Villet 2013), which has been established by molecular methods. Tourle et al. (2009) developed a semi-quantitative morphological index for discriminating *L. sericata* and *L. cuprina*, and it provides some evidence that their hybrids might also be morphologically distinguishable. Specifically, genetically identified hybrid specimens tended to show more extreme index values than either parent species. The index incorporated six characters: femur colour; the numbers of paravertical setulae, scutellar hairs and humeral hairs; the pattern of the postoccular microtrichial pile; the length of the sternal hairs of males; and the position of the inner vertical seta of females. The second aim of this study was to determine if hybrid specimens can in fact be determined from their morphology.

Materials and methods

Twenty-four specimens of *L. sericata*, *L. cuprina* and their hybrids (Table 1) were chosen from specimens that had been sequenced for 28S, COI and Per genes (Williams and Villet 2013). These specimens were chosen to include geographically diverse locations

Species	Specimen	Country of origin
Lucilia cuprina	C_EGT_01	Egypt - Alexandria
Lucilia cuprina	C_SA_BFN_01	South Africa – Bloemfontein
Lucilia cuprina	C_SA_BFN_02	South Africa – Bloemfontein
Lucilia cuprina	C_SA_BRT_01	South Africa – Britstown
Lucilia cuprina	C_SA_BRT_02	South Africa – Britstown
Lucilia cuprina	C_SA_DBN_12	South Africa – Durban
*Lucilia cuprina	C_SA_DBN_01	South Africa – Durban
*Lucilia cuprina	C_SA_DBN_06	South Africa – Durban
*Lucilia cuprina	C_SA_NEL_01	South Africa – Nelspruit
*Lucilia cuprina	C_SA_NEL_02	South Africa – Nelspruit
*Lucilia cuprina	C_THA_03	Thailand – Chiang Mai
*Lucilia cuprina	C_ZIM_02	Zimbabwe – Matobos
Lucilia sericata	S_FRC_02	France – Montferrier-Sur-Lez
Lucilia sericata	S_GER_01	Germany – Kempen
Lucilia sericata	S_JPN_04	Japan – Iwate
Lucilia sericata	S_NAM_01	Namibia – Possession Island
Lucilia sericata	S_NAM_02	Namibia – Possession Island
Lucilia sericata	S_SA_CT_01	South Africa – Cape Town
Lucilia sericata	S_SA_CT_05	South Africa – Cape Town
Lucilia sericata	S_SA_GHT_01	South Africa – Grahamstown
Lucilia sericata	S_SA_GHT_02	South Africa – Grahamstown
Lucilia sericata	S_SA_PTA_02	South Africa – Pretoria
Lucilia sericata	S_SA_WTB_02	South Africa – Witbank
Lucilia sericata	S_USA_01	United States of America – Michiga

Table 1. Specimens previously identified by molecular markers (Williams and Villet 2013) used in the morphological analyses. (*hybrids).

including Egypt, France, Germany, Japan, Namibia, South Africa, Thailand, the United States of America and Zimbabwe.

A total of 18 distinguishing morphological characteristics of adults of *L. sericata* and *L. cuprina* (Table 2) were obtained by reviewing several published sources (Waterhouse and Paramonov 1950, Rognes 1980, 1994, Dear 1986, Holloway 1991, Wallman 2001, Tourle et al. 2009, Whitworth 2006, 2010). Three characters referred to the male genitalia and three characters were specific to females. The males' characters could not be viewed without dissecting the specimens and because the majority of the genetically-identified specimens were female (Williams and Villet 2013), it was decided to include only females in the analysis. This reduced the number of characters to 15. Photographs of the specimens were taken using a Nikon D800 camera with a 105 mm lens and 124 mm extension to show several of the characters.

Each specimen was scored against the 15 characters (Table 2). Each character was then evaluated for its effectiveness in discriminating between the species and its practical value for identification, first univariately and qualitatively, and then multivariately and quantitatively using non-metric multi-dimensional scaling (MDS) in PAST3

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Table

hara orbat	Turilia samirata	Tucilia cunrina	Analysis	sis
UIAIAUEI	LUCILIA SCIICALA	тисны сирпна	MDS DFA	DFA
General				
Number of paravertical setulae or occipital bristles (Waterhouse and Paramonov 1950, Dear 1986, Holloway 1991, Rognes 1994, Whitworth 2006, 2010)	Usually 2+2 but up to 8+8 (not always equal numbers i.e. can be 1+2 etc.)	1+1	yes	ou
Shape of postocular microtrichial pile on vertex (viewed obliquely from behind) (Holloway 1991)	Boundary between pale and dark areas not straight or sharply defined	Boundary straight and sharply defined	ou	ou
Width of the frontal stripe (frontal vitta) (Waterhouse and Paramonov 1950, Rognes 1980, 1994)	Twice as wide as a parafrontal (fronto-orbital) plate	As wide as a parafrontal (fronto-orbital) plate	yes	yes
Colour of the frontoclypeal membrane (Waterhouse and Paramonov 1950, Wallman 2001)	Light brown	Dark brown to black	yes	yes
Second pair of presutural acrostichals (Waterhouse and Paramonov 1950)	Extend at least as far as insertions of the first pair of postsutural acrostichals	Do not extend to first pair of postsutural acrostichals	yes	ou
Number of setulae on 'quadrat' between discal setae and anterior margin of scutellum (Holloway 1991)	35–55	15–25	yes	yes
Bristles on the scutellum (Waterhouse and Paramonov 1950)	Dorsal bristles distinctly smaller than lateral hairs	Dorsal bristles slightly smaller than or equal to lateral hairs	ou	ou
Number of hairs on the posterior slope of the humeral callus behind the basal setae (Waterhouse and Paramonov 1950, Rognes 1994, Whitworth 2006)	6–8	0-4	yes	yes
Number of hairs on the edge of the notopleuron behind the posterior notopleural seta (Waterhouse and Paramonov 1950, Rognes 1994, Whitworth 2006)	8–16	2 - 5	yes	yes
Metasternal area – sclerite midventrally between middle and hind coxae (Rognes 1994, Wallman 2001, Whitworth 2006)	Hairy	Bare	ou	ou
Colour of the fore femora (Waterhouse and Paramonov 1950, Dear 1986, Wallman 2001)	Dark metallic blue to black or dark brown	Metallic green	yes	yes
Contour of the last abdominal tergite (Waterhouse and Paramonov 1950)	Irregular depressions	Generally smooth	no	no
Females				
Distance between the outer and inner vertical setae of females (Holloway 1991)	Equal to 0.5–0.7 distance between prevertical and inner vertical setae	Equal to the distance between prevertical and inner vertical setae	yes	оп

Character Size of the angle formed by the inner vertical seta relative to the prevertical and Obtuse outer vertical sense of females (Hollowyr 1901)	Tuella sociate	I wills mine	Analysis	IS
		rucina cuprina	MDS DFA	DFA
ouch vertical sciae of terrianes (1 10100 as 1)		Right angle	yes 1	ou
Extent of metallic sheen on parafrontal sclerites of females (Holloway 1991) and not en	From vertex barely to base of upper orbital seta and not enclosing bases of any frontal setae bases of 1 or 2 frontal setae	From vertex almost to base of lower orbital seta and enclosing bases of 1 or 2 frontal setae		yes
Males				
Shape of apical halves of cerci (Waterhouse and Paramonov 1950, Holloway 1991) Broad and tapering		Slender and parallel	no	ou
Shape of apical halves of surstyli (Waterhouse and Paramonov 1950, Rognes 1980, Curved and broad Holloway 1991)		Straight and slender	uo I	ou
Form of apical setae of cerci (Holloway 1991) Long and wavy		Minute and straight	no	no

(Hammer et al. 2001) using a Manhattan distance metric because of the mixed data forms in the character state matrix.

To explore the diagnosibility of the hybrids, a discriminant function analysis (DFA) was performed using PAST3 (Hammer et al. 2001) on the scored character matrix to determine which characters were most influential in identifying the species. Four of the 15 characters (shape of postocular microtrichial pile, hairiness of metasternal area, contour of the last abdominal tergite, bristles on the scutellum; Table 2) were either not easily visible or the hairs were broken or missing in at least half of the specimens and were therefore excluded from the DFA. Another four of the characters showed no variation within species and therefore had to be excluded from the DFA, which therefore included only seven characters (Table 2). The hybrid specimens were not separated.

Results

Univariate assessment of characters

The number of paravertical setulae or occipital bristles (Table 2; Figure 1). This character was relatively consistent and reliable, but it is not easily viewed and scored if the specimens have been kept in ethanol. The hybrid specimens all keyed out as *L. cuprina*. This character was left out of the DFA analysis due to lack of variation within *L. cuprina*.

The shape of the postocular microtrichial pile on the vertex (Table 2) (Holloway 1991) is a difficult character to see when the specimens have been stored in ethanol because the microtrichia are not visible unless the specimen is dry, and even then the microtrichia sometimes appear to be absent. Due to the difficulty in viewing and scoring this character, it was eventually left out of all further analyses.

The relative positions of the three vertical setae (Table 2; Figure 1) that form a triangle on either side of the ocellar triangle in females (Holloway 1991) is a reliable character that consistently separated the two species. This character was excluded from the DFA because it did not show variation within taxa but was included in the MDS analysis. The hybrid specimens consistently keyed out as *L. cuprina*.

The angle formed by the three vertical setae (Table 2; Figure 1). This character is consistent and easily seen even if the setae have fallen out as they have sockets, which are easily visible. Due to lack of variation within species and the hybrids being identified as *L. cuprina*, this character was also excluded from the discriminant function analysis but it was included in the MDS analysis.

The extent of the metallic sheen on the parafrontal sclerites of females (Table 2 and Suppl. material 1; Figure 1). This character is easier to observe in dried specimens than ethanol-preserved specimens and there is some variation. The division between the two species is not absolute – there is some overlap within this character but it was not specific to the hybrids. It was included in both the DFA and MDS analyses.

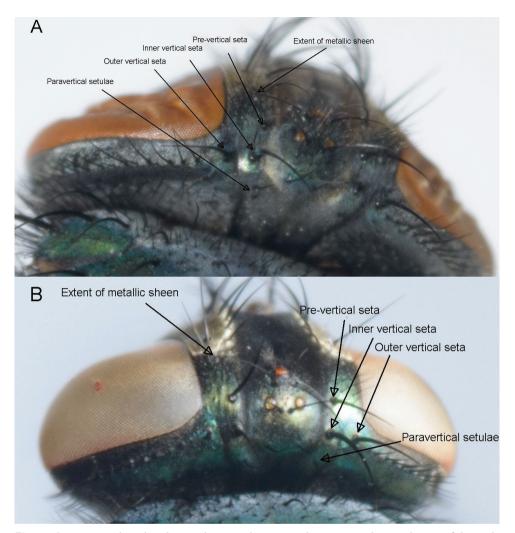


Figure 1. Paravertical setulae, distance between the outer and inner vertical setae, the size of the angle at the inner vertical triangle and extent of metallic sheen on parafrontal sclerites. *L. sericata* (A) and *L. cuprina* (B).

The relative width of the frontal stripe (frontal vitta) (Table 2 and Suppl. material 1; Figure 2). Waterhouse and Paramonov (1950) suggested that this character was more reliable in males than females. We found that the width varied from being equal to the parafrontal to being more than twice the width in both species. The hybrids were not distinguishable from *L. cuprina*. This character was included in the MDS and the DFA analyses.

The colour of the frontoclypeal membrane (Table 2 and Suppl. material 1; Figure 3). It was not always easily visible if the proboscis was not extended but it could usually be viewed by either manipulating the proboscis or viewing the specimen from

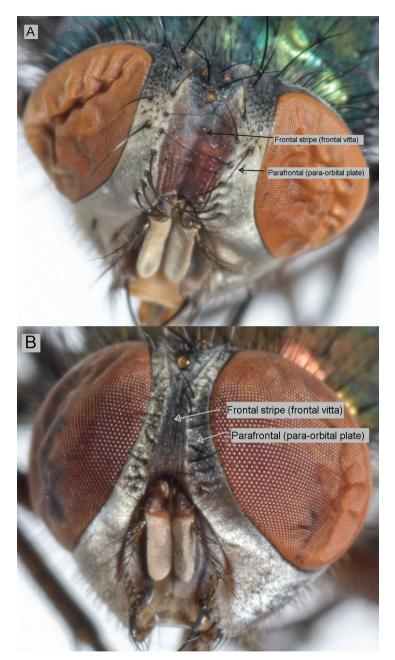


Figure 2. Frontal stripe – L. sericata (A) and L. cuprina (B).

a lateral angle (Waterhouse and Paramonov 1950). The hybrid specimens were not distinct from *L. sericata* or *L. cuprina*.

The length of the second pair of presutural acrostichals (Table 2) is a character that is easier to see in well-preserved specimens (Waterhouse and Paramonov 1950).

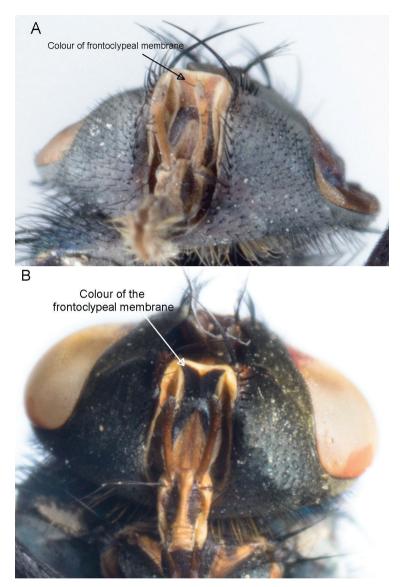


Figure 3. Colour of the frontoclypeal membrane. L. sericata (A) and L. cuprina (B).

This character is not scorable if the bristles are broken or have fallen out. It was left out of the analyses because it does not show any intraspecies variation.

The number of setae on the scutellum (Table 2 and Suppl. material 1; Figure 4) in the 'quadrat' demarcated by the discal setae and the anterior margin of the scutellum represents the axis in the discriminant analysis that separated *L. sericata* and *L. cuprina* (Holloway 1991). This character can be used even when the setae have fallen out because they have sockets that are visible and can be counted. There was overlap in the number of setae between the two species, but generally *L. cuprina* had obviously fewer

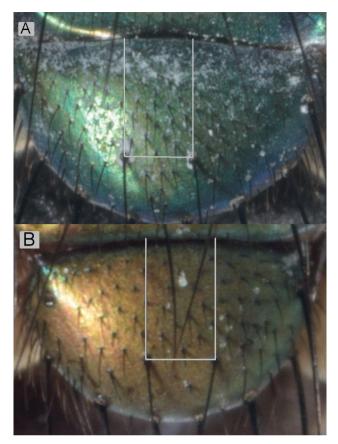


Figure 4. Number of setae on 'quadrat' between the anterior margin and discal setae on the scutellum. *L. sericata* (**A**) and *L. cuprina* (**B**).

setae. The number of setae in the hybrids was not obviously different from either of the pure species. This overlap may be as a result of the challenge of counting the setae as they are not in straight rows.

The length of the bristles on the scutellum (Table 2 and Suppl. material 1) describes the length of the hairs between the two anterior bristles on the lateral margin of the scutellum in relation to the length of the hairs on the dorsal surface of the scutellum (Waterhouse and Paramonov 1950). This character was not easy to use as the hairs were broken or had fallen out in half of the specimens and therefore it was left out of the analyses.

The hairiness of the posterior slope of the humeral callus (Table 2 and Suppl. material 1; Figure 5) behind the basal setae is a reliable character in separating *L. sericata* and *L. cuprina* even though there is variation within species in the number of hairs. The hybrids tended to have more hairs than the pure *L. cuprina* specimens, but there was still overlap in the numbers of hairs between the hybrids and pure *L. cuprina*.

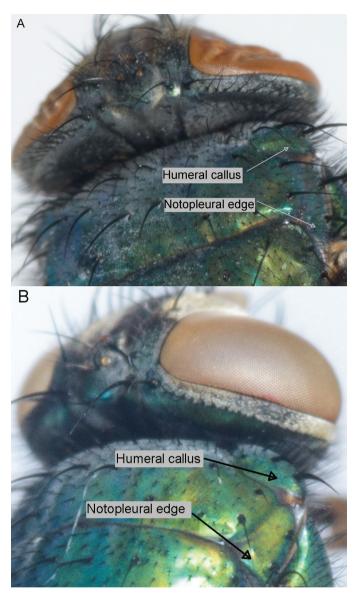


Figure 5. Posterior slope of the humeral callus behind the basal setae and the posterior edge of notopleuron behind the posterior notopleural seta. *L. sericata* (**A**) and *L. cuprina* (**B**).

The number of hairs on the edge of the notopleuron (Table 2 and Suppl. material 1; Figure 5). Both the hairs on the notopleuron and the humeral callus are relatively easy to observe although ethanol-preserved specimens need to be dried so that the small hairs are visible. It is another reliable character in separating *L. sericata* from *L. cuprina* despite variation in the number of hairs within species. The hybrids showed no discernable difference in numbers of hairs from *L. cuprina*.

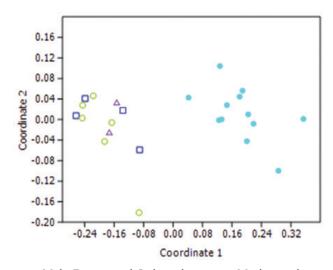


Figure 6. Non-metric Multi-Dimensional Scaling plot using a Manhattan distance metric using 11 characters. Light blue solid circles = *L. sericata*, Green open circles = *L. cuprina*, dark blue squares = introgressed hybrids, purple triangles = modern hybrids.

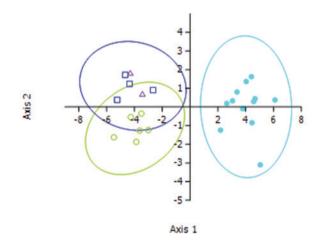


Figure 7. Ordination plot of the first two roots of the discriminant function analysis using seven characters. Ellipses represent 95% confidence regions. Light blue solid circles = *L. sericata*, Green open circles = *L. cuprina*, dark blue squares = introgressed hybrids, purple triangles = modern hybrids.

The hairs on the metasternal area (Table 2), which is the sclerite mid-ventrally between the middle and hind coxae, are exceedingly difficult to view if the legs are not set appropriately to facilitate this. All of the specimens that we examined were preserved in ethanol and it was not easy to view the metasternal area and this character was therefore not analysed.

The colour of the fore femora (Table 2 and Suppl. material 1) has long been used as a character to identify *L. sericata* and *L. cuprina* (Ullyett 1945). It is a controversial

Character	Root 1	Root 2
Number of setulae on 'quadrat' demarcated by discal setae and anterior margin of scutellum	1.5822	0.0324
Number of hairs on edge of notopleuron behind posterior notopleural seta	0.5576	0.3300
Number of hairs on posterior slope of humeral callus behind basal setae	0.4216	0.9066
Colour of fore femora	0.2591	-0.2023
Relative width of frontal stripe (frontal vitta)	0.1551	0.0104
Extent of metallic sheen on parafrontal sclerites of females	0.0519	-0.0697
Colour of frontoclypeal membrane	-0.1551	-0.0104
Eigenvalue	18.5560	0.7406

Table 3. Eigen vectors and values for the first two roots of the discriminant function analysis.

character as it varies according to when the flies were killed, if the adults were fully matured and if the specimens were fouled or not during collection and thus is subject to personal interpretation. The hybrids keyed out as *L. cuprina*. Due to the variation in this character it was included in the DFA.

The contour of the last abdominal tergite (Table 2) is applicable only to dried specimens (Waterhouse and Paramonov 1950) as it relies on the hardness of the tergite. It was therefore not a character that could be used in our analyses as all our specimens were ethanol-preserved. It was excluded from the analyses and is probably unreliable even in dried specimens because it relies on the preservation of the specimen and how it is pinned, which affects the contour of the last abdominal tergite.

Multivariate assessments of characters

Superficially, the hybrid specimens were identified as *L. cuprina* when keyed out using any of the published keys. There were no obvious differences in the morphology of the hybrids. When the characters were analysed using MDS, the hybrid specimens were not separated from the *L. cuprina* specimens (Figure 6).

However, the ordination plot of the DFA (Figure 7) clearly shows three groups – *L. sericata*, *L. cuprina* and hybrids. The most influential characters were the number of setae on the scutellum (Root 1) and the number of hairs on the humeral callus (Root 2) (Table 3). It is not obvious in the morphology that there is a difference between the pure and hybrid strains, but statistically one can separate the hybrids from the pure *L. cuprina* specimens.

Discussion

Assessment of characters

Due to the greater number of female flies in the molecular study from which we chose our specimens, we did not include any males. Therefore the male genitalia characters are not discussed in detail. It is not possible to properly view the male genitalia without dissecting them and this is not ideal for non-entomologists such as medical doctors who are using these flies for MDT as one needs experience to dissect out the genitalia. It is possible to correctly identify these flies without using the male genitalia by using the other characters described in Table 2.

Geographical variation

Holloway (1991) suggested that the characters that she described were specifically for *L. sericata* and *L. cuprina* from New Zealand and that they might not apply to specimens from other parts of the world. This does not seem to be the case, as the flies examined in this study are from several different countries around the world (Table 1) and the characters described (excluding the male genitalia) were useful in identifying these two species and their hybrids.

Identifying hybrids

The DFA unambiguously separated the *L. cuprina* specimens from the hybrids and it was statistically significant. This was not noted in previous studies where hybrids were identified only through molecular techniques (Stevens et al. 2002, Wallman et al. 2005, Tourle et al. 2009, DeBry et al. 2010, Williams and Villet 2013). Examination of the number of hairs on the scutellum, humeral callus and notopleuron show a consistent difference that separates these groups. The first two characters were included in the morphological index designed by Tourle et al (2009), which explains the trend found in their results.

The introgressed and modern hybrids were not separated in the DFA ordination plot (Fig. 6).

Conclusion

Introgressed and modern hybrids of *L. sericata* and *L. cuprina* can be statistically recognized using the characters described in this paper.

Four of the characters were consistently successful at separating *L. sericata* and *L. cuprina* (number of paravertical setulae or occipital bristles, distance between the outer and inner vertical setae of females, size of the angle at the inner vertical in triangle joining pre-, outer and inner vertical setae of females, second pair of presutural acrostichals) with little variation within the characters. The number of setae on the scutellum and the number of hairs on the humeral callus and notopleuron are also useful characters although they did show variation within species. It is advisable to use a combination of several characters to identify these two species as no single character was sufficient to separate *L. sericata* and *L. cuprina*.

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Supplementary material I

Character-taxon matrix

Kirstin A. Williams, Martin H. Villet

Data type: Species data

Explanation note: Character-taxon matrix used in the MDS and DFA analyses

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DATA PAPER



CracidMex1: a comprehensive database of global occurrences of cracids (Aves, Galliformes) with distribution in Mexico

Gonzalo Pinilla-Buitrago^{1,7}, Miguel Angel Martínez-Morales¹, Fernando González-García², Paula L. Enríquez³, José Luis Rangel-Salazar³, Carlos Alberto Guichard Romero⁴, Adolfo G. Navarro-Sigüenza⁵, Tiberio César Monterrubio-Rico⁶, Griselda Escalona-Segura¹

I El Colegio de la Frontera Sur, unidad Campeche. Avenida Rancho Polígono 2-A, Ciudad Industrial, Lerma, Campeche, Campeche, 24500, Mexico 2 Red de Biología y Conservación de Vertebrados, Instituto de Ecología, AC. Carretera antigua a Coatepec No. 351, El Haya, Xalapa, Veracruz, 91070, Mexico 3 El Colegio de la Frontera Sur, unidad San Cristóbal. Carretera Panamericana y Periférico Sur s/n, Barrio María Auxiliadora, San Cristóbal de Las Casas, Chiapas, 29290, Mexico 4 Zoológico Miguel Álvarez del Toro. Calzada Cerro Hueco s/n, Colonia Zapotal, Apartado Postal 6, Tuxtla Gutiérrez, Chiapas, 29094, Mexico 5 Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México. Apartado Postal 70-399, México DF, 04510, Mexico 6 Facultad de Biología, Universidad Michoacana de San Nicolas de Hidalgo. Edificio R, Ciudad Universitaria, Morelia, Michoacán, 58000, Mexico 7 Present address: Instituto de Ciencias Naturales, Universidad Nacional de Colombia. Ciudad Universitaria, Av. Carrera 30 No. 45, Bogotá DC, 111321, Colombia

Corresponding author: Miguel Angel Martínez-Morales (mmartinez@ecosur.mx)

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Abstract

Cracids are among the most vulnerable groups of Neotropical birds. Almost half of the species of this family are included in a conservation risk category. Twelve taxa occur in Mexico, six of which are considered at risk at national level and two are globally endangered. Therefore, it is imperative that high quality, comprehensive, and high-resolution spatial data on the occurrence of these taxa are made available as a valuable tool in the process of defining appropriate management strategies for conservation at a local and global level. We constructed the CracidMex1 database by collating global records of all cracid taxa that occur in Mexico from available electronic databases, museum specimens, publications, "grey literature", and unpublished records. We generated a database with 23,896 clean, validated, and standardized geographic records. Database quality control was an iterative process that commenced with the consolidation and elimination of duplicate records, followed by the geo-referencing of records when necessary, and their taxonomic and geographic validation using GIS tools and expert knowledge. We followed the georeferencing protocol proposed by the Mexican National Commission for the Use and Conservation of Biodiversity. We could not estimate the geographic coordinates of 981 records due to inconsistencies or lack of sufficient information in the description of the locality.

Given that current records for most of the taxa have some degree of distributional bias, with redundancies at different spatial scales, the CracidMex1 database has allowed us to detect areas where more sampling effort is required to have a better representation of the global spatial occurrence of these cracids. We also found that particular attention needs to be given to taxa identification in those areas where congeners or conspecifics co-occur in order to avoid taxonomic uncertainty. The construction of the CracidMex1 database represents the first comprehensive research effort to compile current, available global geographic records for a group of cracids. The database can now be improved by continuous revision and addition of new records. The CracidMex1 database will provide high quality input data that could be used to generate species distribution models, to assess temporal changes in species distributions, to identify priority areas for research and conservation, and in the definition of management strategies for this bird group. This compilation exercise could be replicated for other cracid groups or regions to attain a better knowledge of the global occurrences of the species in this vulnerable bird family.

Keywords

Ortalis, Penelope, Penelopina, Oreophasis, Crax, Cracidae, Aves, chachalacas, guans, curassows, Mexico, Neotropic, geographic record, Darwin Core

Introduction

Cracids are a primitive family of Neotropical Galliformes. They are mainly frugivorous birds that inhabit primary forests, and may play an important role in regenerating and structuring forests through the dispersion and predation of seeds (Peres and Roosmalen 1996; Sedaghatkish 1996; Muñoz and Kattan 2007). Based on this and on their sensitivity to disturbance, the presence of viable populations of cracids in an area is considered indicative of forest quality.

Cracids are one of the most vulnerable groups of Neotropical birds because almost half of the 54 recognized species (AOU 2014) are at risk, and some of them are almost extinct (Brooks and Strahl 2000). This vulnerability is a consequence of their strong dependence on primary forests, and their susceptibility to habitat destruction and degradation, in addition to the intensity of hunting faced by cracids (Silva and Strahl 1991, 1997; Brooks and Strahl 2000; del Hoyo and Motis 2004). These factors together with life history traits of delayed age of first reproduction, low chick survival, and low reproduction rates, act in synergy to exacerbate the vulnerability of cracids to human pressures. In Mexico there are 12 cracid taxa of which six are included in the national list of threatened species (SEMARNAT 2010) and two (*Oreophasis derbianus* and *Crax rubra griscomi*) are globally endangered (Brooks and Strahl 2000; Martínez-Morales et al. 2009; IUCN 2013).

The lack of up to date, high quality data on the presence and abundance of cracids in many regions of their distribution prevents the definition and implementation of appropriate management strategies for their conservation (Brooks and Strahl 2000; González-García et al. 2001). Although their distribution has already been depicted in maps (Delacour and Amadon 2004; Ridgley et al. 2012), and even analysed in the context of global climate change (Peterson et al. 2001), we still do not know the present species distribution with a high level of certainty as a result of continual changes in forest cover. Not to mention that for several species or regions there are still significant gaps in knowledge of species distribution. In this regard, the former Cracid Specialist Group recommended an urgent revision of cracid distribution (Brooks and Strahl 2000; Brooks 2006).

To tackle this imperative need for information, we constructed the CracidMex1 database that embodies an exhaustive, high quality, and updated compilation of the global geographic records of the eight cracid species with distribution in Mexico. The collation of records from numerous sources required a thorough process of quality control in terms of consolidation and elimination of record redundancies, completion of missing data, verification of record localities and their spatial precision, and validation of taxa identity. This involved an iterative process of automatized tasks and the use of expert knowledge in terms of species and regions.

The CracidMex1 database will provide high quality, input data that could be used to identify areas where more research is needed, generate species distribution models, assess temporal changes in species distribution, identify priority areas for cracid conservation, and even in the definition of management strategies for this avian group. This compilation exercise could be replicated for other groups of cracids or regions to achieve a more complete knowledge of the global occurrences of the species of this vulnerable bird family.

This open access database will be continuously reviewed and supplemented with additional records, and all contributions to the database are very welcome.

Data published through

http://ipt.pensoft.net/ipt/resource.do?r=cracidmex1

Taxonomic ranks

Kingdom: Animalia
Phylum: Chordata
Class: Aves
Order: Galliformes
Family: Cracidae
Genera: Ortalis, Penelope, Penelopina, Oreophasis, Crax
Species: Ortalis vetula (Wagler, 1830), Ortalis wagleri Gray, 1867, Ortalis poliocephala (Wagler, 1830), Ortalis leucogastra (Gould, 1843), Penelope purpurascens Wagler, 1830, Penelopina nigra (Fraser, 1852), Oreophasis derbianus Gray, 1844, Crax rubra Linnaeus, 1758 (Table 1).

Common names: Chachalacas, Guans, and Curassows

Species/Subspecies	Common name	CITES ¹	IUCN ²	NOM-059 ³	Endemicity
Ortalis vetula	Plain Chachalaca	III^4	Least Concern		Not endemic
O. v. vetula					• E Mexico to Costa Rica
O. v. mccalli					• SE USA, E Mexico
O. v. pallidiventris					• Yucatan Peninsula (Mexico)
O. v. deschauenseei					• Utila Island (Honduras)
O. v. intermedia					• S Mexico, Guatemala, Belize
Ortalis wagleri	Rufous-bellied Chachalaca		Least Concern		North western Mexico
Ortalis poliocephala	West Mexican Chachalaca		Least Concern		Central western Mexico
Ortalis leucogastra	White-bellied Chachalaca		Least Concern	Special protection	Northern Central America (Pacific slope)
Penelope purpurascens	Crested Guan	III ⁵	Least Concern	Threatened	Not endemic
P. p. purpurascens				• Threatened	Not endemic
P. p. aequatorialis					Not endemic
P. p brunnescens					• N Colombia, N Venezuela
Penelopina nigra	Highland Guan	III ⁶	Vulnerable	Endangered	Northern Central America
Oreophasis derbianus	Horned Guan	Ι	Endangered	Endangered	S Mexico, Guatemala
Crax rubra	Great Curassow	III ⁷	Vulnerable	Threatened	Not endemic
C. r. rubra				• Threatened	• Not endemic
C. r. griscomi				• Endangered	• Cozumel Island (Mexico)

Table 1. Conservation and endemic features of the cracid taxa included in the CracidMex1 database.

¹Convention on International Trade in Endangered Species of Wild Fauna and Flora http://www.cites.org/eng/app/appendices.php.

²The IUCN Red List of Threatened Species <http://www.iucnredlist.org>.

³Mexican environmental legislation (SEMARNAT 2010).

⁴Guatemala and Honduras.

⁵Honduras.

⁶Guatemala.

⁷Guatemala, Honduras, Costa Rica, and Colombia.

Taxonomic coverage

The CracidMex1 database comprises 23,896 global records of 12 taxa of cracid species and subspecies with distribution in Mexico. This includes eight cracid species distributed in Mexico, out of the 54 recognized species in the Neotropical region (AOU 2014). The database also includes records of *O. v. deschauenseei* from the Utila Island, Honduras, and of two other subspecies of *P. purpurascens (aequatorialis* and *brunnescens)* which are not distributed in Mexico (Table 2). The genus *Ortalis* accounted for most of the records, followed by *Penelope, Crax, Penelopina*, and *Oreophasis*. This bias in records at a genus level is also mirrored at species level (Figure 1). However, at subspecies level this bias is not evident because only 19.9% of the records assignable to subspecies level are given to this taxonomic level (4.6% in *O. vetula*, 43.5% in *P. purpurascens*, and 100% in *C. rubra*).

Spatial coverage

General spatial coverage

Valid distributional records (22,731), based on the native distribution of taxa, cover distributions from southern Texas, USA, in the north, to Loja, Ecuador, in the south, including Mexico, Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica,

Genus/Species/Subspecies	Records	Proportion (%)
Ortalis	17,663	73.9
O. vetula	14,366	60.1
O. v. vetula	193	0.8
O. v. mccalli	291	1.2
O. v. pallidiventris	119	0.5
O. v. deschauenseei	4	0.0
O. v. intermedia	58	0.2
Ortalis wagleri	1,151	4.8
Ortalis poliocephala	1,754	7.3
Ortalis leucogastra	392	1.6
Penelope	3,100	13.0
P. purpurascens	3,100	13.0
P. p. purpurascens	1,152	4.8
P. p. aequatorialis	164	0.7
P. p brunnescens	29	0.1
Penelopina nigra	907	3.8
Oreophasis derbianus	401	1.7
Crax	1,825	7.6
C. rubra	1,825	7.6
C. r. rubra	1,797	7.5
C. r. griscomi	28	0.1

Table 2. Number of records in the CracidMex1 database by genus, species, and subspecies.

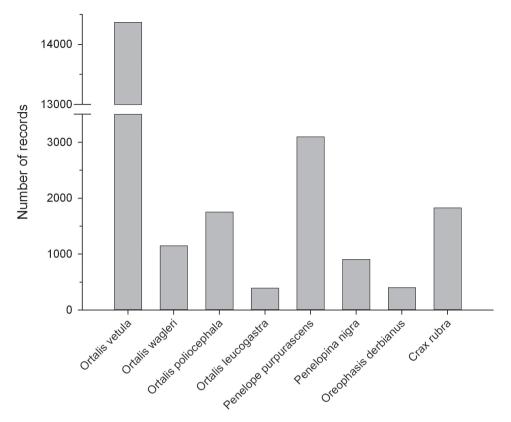


Figure 1. Distribution of the 23,896 records by species in the CracidMex1 database.

Panama, Colombia, Venezuela, and Peru (Table 3, Figures 2 and 3). These records are labelled as *presente* (present) in the "occurrenceStatus" field of the database. Other records corresponded to zoo specimens (49), records with spatial inconsistencies or ambiguities (143), and records for which coordinates could not be calculated due to insufficient information in the description of the locality (981). These records are labelled as *ausente* (absent) or *dudoso* (doubtful) in the "occurrenceStatus" field. In this case a label of "absent" (186 records) means that the record is out of the distributional range of the species (e.g., zoo records), and "doubtful" (979) means that the species could be present in the area, but the ambiguity in the description of the locality prevents an unequivocal assertion of the spatial validity of the record (e.g., Locality: Mexico).

Coordinates

-4.3327 to 31.1707 Latitude; -109.4433 to -61.1382 Longitude. This range includes the location of only the 22,731 valid distributional records (Figure 2).

Country	O.vetula	0.wagleri	O.poliocephala	O.leucogastra	P.purpurascens	P.nigra	O.derbianus	C.rubra	Total
USA	9,904	0	0	0	0	0	0	0	9,904
Mexico	2,938	1,113	1,675	124	642	533	145	430	7,600
Belize	533	0	0	0	175	0	0	112	820
Guatemala	408	0	0	87	176	145	210	115	1,141
Honduras	134	0	0	0	33	42	0	16	225
El Salvador	1	0	0	78	10	29	0	10	128
Nicaragua	17	0	0	33	21	73	0	17	161
Costa Rica	57	0	0	0	1,410	0	0	769	2,236
Panama	0	0	0	0	141	0	0	59	200
Colombia	0	0	0	0	128	0	0	43	171
Venezuela	0	0	0	0	41	0	0	0	41
Ecuador	0	0	0	0	90	0	0	13	103
Peru	0	0	0	0	1	0	0	0	1
Total	13,992	1,113	1,675	322	2,868	822	355	1,584	22,731

Table 3. Number of valid distributional records of cracid species by country in the CracidMex1 database.

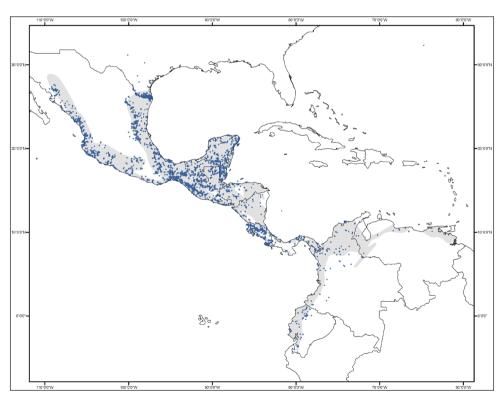


Figure 2. Geographic distribution of the 22,731 valid distributional records of cracids in the Cracid-Mex1 database. Grey shadeing represents the area where the species occurrence is expected based on Ridgley et al. (2012).

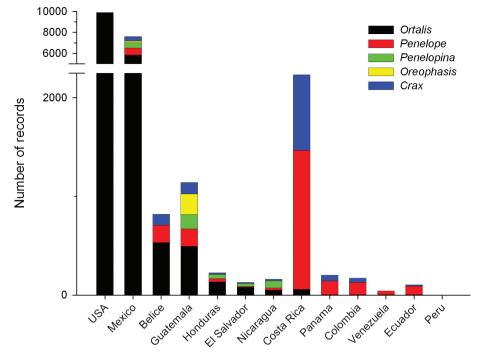


Figure 3. Distribution of cracid genera by country for the 22,731 valid distributional records in the CracidMex1 database.

Temporal coverage

The date of occurrence records (year-month-day) encompasses from 1700-01-01 to 2013-10-25. However, of the 22,731 valid distributional records, 854 lack information on recording date. Although temporal coverage spans more than 300 years, most of the records were generated in the last decades (Figure 4). A boom in reporting or generating species records started at the end of the last century, most probably due to the emergence of the Internet and technological advancement in field survey equipment. Additionally, this observed pattern might be due to an increased interest in studying this bird group. Information gathered through years of research and observation of the species' natural history led to the publication in 1973 of the first edition of the inspiring book "Curassows and related birds" by Delacour and Amadon. Added to which the First International Symposium on the Family Cracidae was organized in 1981, which may also have triggered an exponential increase in the interest for studying this avian group, and thus, an increase in reporting species occurrences.

Project description

Title: Present and future distribution models of cracids occurring in Mexico.

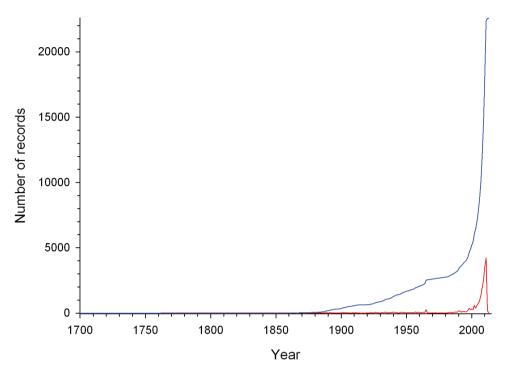


Figure 4. Number of cracid records gathered per year (red line) and the cumulative number of cracid records gathered from 1700 to 2013 (blue line).

Personnel: Miguel Angel Martínez-Morales (Project Coordinator, Resource Contact, Resource Creator), Gonzalo Enrique Pinilla-Buitrago (Database Manager, Metadata Provider), Fernando González-García, Paula L. Enríquez, José Luis Rangel-Salazar, Carlos Alberto Guichard Romero, Adolfo G. Navarro-Sigüenza, Tiberio César Monterrubio-Rico, Griselda Escalona-Segura (Data Contributors).

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Study area descriptions/descriptor: Valid distribution records are located in the northern portion of the Neotropical region, including the transitional zone with the Nearctic region (Figure 5). Native vegetation in this area ranges from tropical dry to humid forests, and from lowlands to montane forests. However, a large proportion of the native vegetation has been converted to pasture and agricultural areas. The expansion of human settlements, infrastructure, and mining have also contributed to forest degradation and deforestation in the region. Tropical forests have the largest net loss of forested area compared to other forest types in the world (FAO and JRC 2012), and the Neotropical region is not the exception. The study area includes the Mesoamerica biodiversity hotspot, the Chocó/Darién/Western Ecuador hotspot, and marginally the Tropical Andes hotspot (Myers et al. 2000), but these hotspots harbour only 20 to 25% of the original extent of primary vegetation.

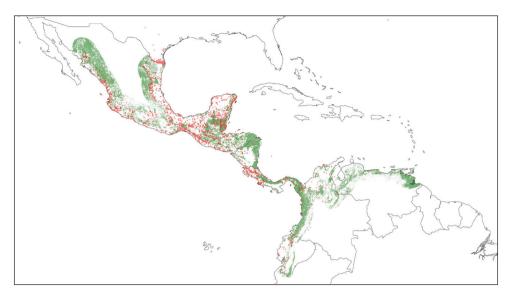


Figure 5. Geographic distribution of the 22,731 valid distributional records of cracids in the Cracid-Mex1 database. Present pattern of forest cover is depicted in green shading. Forest cover was obtained from INEGI (2012) for Mexico, the World Bank and CCAD (2000) for Central America, and the European Commission Joint Research Centre (http://www-gem.jrc.it/glc2000) for South America.

Given the current pattern of forest cover in the region, and the temporal coverage of records in the CracidMex1 database, many records, particularly older records, are now located outside of currently forested areas (Figure 5). This suggests a substantial reduction in the distribution of cracid species, particularly for those species restricted to primary forests (*P. purpurascens, P. nigra, O. derbianus*, and *C. rubra*). Habitat loss and hunting pressure are the main drivers of cracid population declines and distribution contractions, the synergy of which has caused the endangerment of these species (Silva and Strahl 1991, 1997; Brooks and Strahl 2000; del Hoyo and Motis 2004).

Design description: The construction of the CracidMex1 database aimed to gather most of the globally available records of cracids which are distributed in Mexico, in order to generate global species distribution models. We initiated the construction of the database by collating records from six electronic databases available through the Internet: GBIF <http://data.gbif.org>, ORNIS <http://www.ornisnet.org>, REMIB <http://www.conabio.gob.mx/remib/doctos/remib_esp.html>, UNIBIO <http://unibio.unam.mx>, SpeciesLink <http://splink.cria.org.br>, and IBC <http://ibc.lynxeds.com>. Additionally, we obtained records from the National System of Information on Biodiversity (SNIB) database at CONABIO and from museum specimen records contained in the Bird Atlas of Mexico. We also obtained records from published papers through searches in BioOne <http://www.bioone.org>, EBSCO <http://search.ebscohost.com>, JSTOR <http://www.jstor.org>, ScienceDirect <http://www.

sciencedirect.com>, Springer Link <http://www.springerlink.com>, Web of Science <http://apps.webofknowledge.com>, Wiley Online Library <http://onlinelibrary. wiley.com>, Zoological Record <http://thomsonreuters.com/zoological-record/>, Redalyc <http://www.redalyc.org>, SciELO <http://www.scielo.org>, and Google Scholar <scholar.google.com>. We also reviewed the bulletins of the Cracid Group of the Galliformes Specialists Group <http://www.cracids.org>. Added to which, we gathered records from "grey literature" through searches in technical reports and theses. These searches included the electronic portal of CONABIO and the repositories OpenDOAR <http://opendoar.org> and the Registry of Open Access Repositories <http://roar.eprints.org>. Finally, we gathered records from our own and unpublished databases of colleagues through personal contacts. After the GBIF, these personal unpublished databases were the second most important source of records, followed by records gathered from the SNIB and published papers (Table 4).

Database quality control, based on the standards described in CONABIO (2012), was an iterative process that commenced with the detection, consolidation and elimination of duplicate records (the same record reported in more than one source). For detection of duplicate records within and among sources we first gave priority to the fields "institutionCode", "catalogNumber", "country", "state", "locality", "decimalLatitude", and "decimalLongitude". The consolidation process consisted of the creation of a single record with more complete data from duplicate records. In the case of inconsistencies in duplicate records, we referred to the original source of the record. We avoided and corrected errors (omission, typographic,

Source	0.vetula	O.wagleri	O.poliocephala	O.leucogastra	P.purpurascens	P.nigra	O.derbianus	C.rubra	Total
GBIF	13,479	982	896	279	2,751	734	233	1,524	20,878
ORNIS	180	19	11	64	2	1	0	2	279
REMIB	86	0	0	0	0	0	0	12	98
UNIBIO	0	0	0	0	0	0	0	0	0
SpeciesLink	1	0	0	0	5	0	0	1	7
IBC	0	0	0	0	1	0	0	1	2
SNIB	209	1	435	8	17	26	9	12	717
Bird Atlas Mex	120	95	31	1	57	34	2	51	391
Published papers	235	47	77	37	131	56	40	90	713
"Grey literature"	37	3	6	3	20	4	2	16	91
Unpublished DB	19	4	298	0	116	52	115	116	720
Total	14,366	1,151	1,754	392	3,100	907	401	1,825	23,896

Table 4. Relative contribution of records of cracid species by the different sources used in the construction of the CracidMex1 database. Numbers represent non-duplicate records. GBIF was the main source of records, but its relative contribution is magnified in this table because in the consolidation process we considered this source as the reference database.

contextual, redundancy, convention, and congruence) through automatized tasks and case by case revision of the database. We then calculated geographic coordinates and their uncertainties for those records lacking these data, based on the standards described in CONABIO (2008). All coordinates refer to the datum WGS84. We used a variety of resources for geo-referencing, namely Google Earth 7 <http://www. google.com/earth/index.html>, Google Maps and the tools of Map Labs <http:// maps.google.com>, glosk <http://www.glosk.com/>, CONABIO <http://www.conabio.gob.mx/informacion/metadata/gis/loc2000gw.xml? httpcache=yes& xsl=/db/ metadata/xsl/fgdc_html.xsl&_indent=no>, GEOSiB <http://www.humboldt.org. co/geoinformacion/geosib>, and Georeferencing Calculator <http://manisnet.org/ gci2.html>. We also consulted regional experts for advice during the geo-referencing process. Once we were sufficiently certain of the correct location of the record, we checked that each location was consistent with taxa identification by displaying the records in a GIS. This taxonomic and geographic validation through the use of GIS tools and expert knowledge allowed us to detect inconsistencies. Where possible, we corrected inconsistencies through an iterative process, otherwise we labelled the record as "doubtful" (979 records) or "absent" (186) in the "occurrenceStatus" field as described above (Figure 6).

The CracidMex1 database has 41 fields based on the standard Darwin Core version 1.4 (Table 5).

Field	Definition
institutionCode	The name (or acronym) in use by the institution having custody of the object(s) or information referred to in the record. In the case of personal records, we used the value "NA" <i>No aplica</i> (Not applicable).
collectionCode	The name, acronym, code, or initials identifying the collection or data set from which the record was derived. If the record was not held in a collection, we used the value "NA" <i>No aplica</i> (Not applicable). If the collection name was not known, we used the value "ND" <i>No determinado</i> (Not determined).
datasetName	The name identifying the data set from which the record was derived. If the data set name was not known, we used the value "ND" <i>No determinado</i> (Not determined).
basisOfRecord	 The specific nature of the data record. <i>Ejemplar preservado</i> (Preserved specimen). Denoting a preserved specimen in a collection. <i>Observación</i> (Human observation). Denoting an observation made by one or more people. <i>Observación con aparato</i> (Machine observation). Denoting an observation made by a machine. <i>Ocurrencia</i> (Occurrence). Denoting a case where no information is available on how the record was obtained.

Table 5. Definition of fields included in the CracidMex1 database based on the standard Darwin Core version 1.4.

occurrenceID	A uniform resource name as a unique identifier for the record. In the absence of a persistent global unique identifier, this was constructed in the form: "[institutionCode]: [collectionCode]: [catalogNumber]". If the record lacked a value in one of these fields (NA or ND) a sequential number was assigned
	at the end.
catalogNumber	An identifier for the record within the data set or collection. If the record did not have a catalogue number, we used the value "NA" <i>No aplica</i> (Not applicable). If we did not know the catalogue number, we used the value "ND" <i>No determinado</i> (Not determined).
recordNumber	An identifier given to the occurrence at the time it was recorded. This often serves as a link between field notes and an occurrence record, such as a specimen collector's number. If the record did not have a record number, we used the value "NA" <i>No aplica</i> (Not applicable). If we did not know the record number, we used the value "ND" <i>No determinado</i> (Not determined).
recordedBy	A list (concatenated and separated) of names of people, groups, or organizations responsible for recording the original occurrence. The primary collector or observer, especially one who applies a personal identifier (recordNumber), is listed first. If we did not know the name of the collector, we used the value "ND" <i>No determinado</i> (Not determined).
individualCount	The number of individuals recorded at the time of the occurrence. We left the value empty if individualCount was unknown.
occurrenceStatus	 A statement about the presence or absence of a taxon at a location. <i>Presente</i> (Present). There is at least one well documented record of the taxon's presence in the area. <i>Ausente</i> (Absent). There is evidence to document the absence of a taxon in the area. <i>Dudoso</i> (Doubtful). The taxon is presumed present in the area, but there is doubt over the evidence, including taxonomic or geographic imprecision in the records.
associatedReferences	A list (concatenated and separated) of identifiers (publication, bibliographic reference, global unique identifier) of literature associated with the occurrence. If no reference was associated, we used the value "NA" <i>No aplica</i> (Not applicable).
year	The four-digit year in which the event occurred, according to the Common Era Calendar. If we did not know the year, we used "9999".
month	The ordinal month in which the event occurred. If we did not know the month, we used "99".
day	The integer day of the month on which the event occurred. If we did not know the day, we used "99".
country	The name of the country or major administrative unit in which the location occurs. If we did not know the name, we used the value "ND" <i>No determinado</i> (Not determined).
stateProvince	The name of the next smaller administrative region below country (state, province, canton, department, region, etc.) in which the location occurs. If we did not know the name, we used the value "ND" <i>No determinado</i> (Not determined).
county	The full, unabbreviated name of the next smaller administrative region below stateProvince (county, shire, department, municipality) in which the location occurs. If this administrative region does not apply, we used the value "NA" <i>No aplica</i> (Not applicable). If we did not know the name, we used the value "ND" <i>No determinado</i> (Not determined).

locality	The specific description of the place. This term may contain information modified from the original to correct perceived errors or standardize the
	description. If we did not know the description, we used the value "ND" <i>No determinado</i> (Not determined).
decimalLatitude	The geographic latitude (in decimal degrees, using the spatial reference system given in geodeticDatum) of the geographic centre of a location. Positive values are north and negative values are south of the Equator. We left the value empty if decimalLatitude was unknown.
decimalLongitude	The geographic longitude (in decimal degrees, using the spatial reference system given in geodeticDatum) of the geographic centre of a location. Positive values are east and negative values are west of the Greenwich Meridian. We left the value empty if decimalLongitud was unknown.
geodeticDatum	The ellipsoid, geodetic datum, or spatial reference system upon which the geographic coordinates given in decimalLatitude and decimalLongitude are based. We used the value "ND" <i>No determinado</i> (Not determined) when no data was available in decimalLatitude and decimalLongitude.
coordinateUncertaintyInMeters	The horizontal distance (in meters) from the given decimalLatitude and decimalLongitude describing the smallest circle containing the entire location. We left the value empty if the uncertainty was unknown, could not be estimated, or was not applicable (because there are no coordinates).
georeferencedBy	A list (concatenated and separated) of names of people, groups, or organizations who determined the geo-reference for the location.
georeferenceProtocol	A description or reference for the methods used to determine the spatial footprint, coordinates, and uncertainties.
georeferenceSources	A list (concatenated and separated) of maps, gazetteers, or other resources used to geo-reference the location.
identifiedBy	A list (concatenated and separated) of names of people, groups, or organizations who assigned the taxon to the subject. If we did not know the name, we used the value "ND" <i>No determinado</i> (Not determined).
dateIdentified	The date on which the subject was identified as representing the taxon. Format yyyy-mm-dd. If we did not know the date, we used "9999".
typeStatus	A list (concatenated and separated) of nomenclatural types applied to the subject. If the nomenclatural type did not apply, we used the value "NA" <i>No aplica</i> (Not applicable).
scientificName	The full scientific name of the lowest taxonomic rank determined.
originalNameUsage	The taxon name, as it originally appeared when first determined.
kingdom	The full scientific name of the kingdom in which the taxon is classified.
phylum	The full scientific name of the phylum in which the taxon is classified.
class	The full scientific name of the class in which the taxon is classified.
order	The full scientific name of the order in which the taxon is classified.
family	The full scientific name of the family in which the taxon is classified.
genus	The full scientific name of the genus in which the taxon is classified.
specificEpithet	The name of the species epithet of the scientificName.
infraspecificEpithet	The name of the lowest or terminal infraspecific epithet of the scientificName. If the infraspecific epithet did not apply, we used the value "NA" <i>No aplica</i> (Not applicable).
taxonRank	The taxonomic rank of the most specific name in the scientificName.
scientificNameAuthorship	The authorship information for the scientificName formatted according to the conventions.
taxonomicStatus	The status of the use of the scientificName as a label for a taxon.

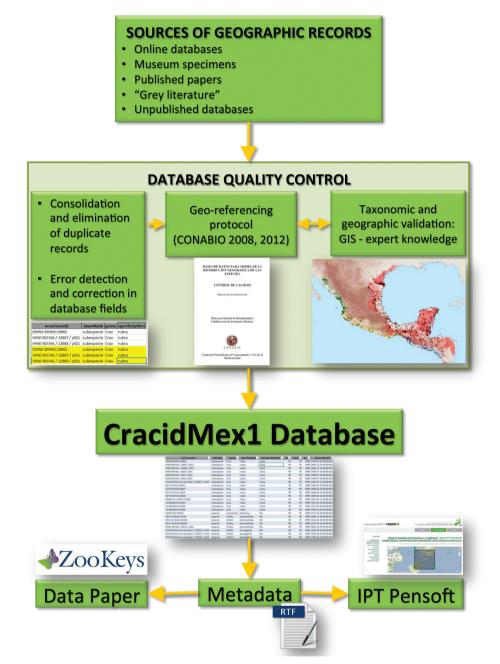


Figure 6. Flowchart depicting the iterative process for the construction of the CracidMex1 database up to publication.

Dataset description

Object name: Darwin Core Archive CracidMex1: a comprehensive database of global occurrences of cracids (Aves, Galliformes) with distribution in Mexico Character encoding: UTF-8 Format and storage mode: xlsx; ASCII csv, tab-delimited; decimal separator: '.' Distribution: http://ipt.pensoft.net/ipt/resource.do?r=cracidmex1 Publication date of data: 2014-03-10 Language: Spanish. Metadata language: English. Date of metadata creation: 2014-01-08 Hierarchy level: Dataset

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RESEARCH ARTICLE



Avibase – a database system for managing and organizing taxonomic concepts

Denis Lepage¹, Gaurav Vaidya², Robert Guralnick²

1 Bird Studies Canada, P.O. Box 160, 115 Front St., Port Rowan, ON Canada NOE 1MO **2** Department of Ecology and Evolutionary Biology, and CU Museum of Natural History, University of Colorado Boulder, Campus Box 265, Boulder, CO, United States of America 80309-0265

Corresponding author: Denis Lepage (dlepage@bsc-eoc.org)

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Abstract

Scientific names of biological entities offer an imperfect resolution of the concepts that they are intended to represent. Often they are labels applied to entities ranging from entire populations to individual specimens representing those populations, even though such names only unambiguously identify the type specimen to which they were originally attached. Thus the real-life referents of names are constantly changing as biological circumscriptions are redefined and thereby alter the sets of individuals bearing those names. This problem is compounded by other characteristics of names that make them ambiguous identifiers of biological concepts, including emendations, homonymy and synonymy. Taxonomic concepts have been proposed as a way to address issues related to scientific names, but they have yet to receive broad recognition or implementation. Some efforts have been made towards building systems that address these issues by cataloguing and organizing taxonomic concepts, but most are still in conceptual or proof-of-concept stage. We present the on-line database Avibase as one possible approach to organizing taxonomic concepts. Avibase has been successfully used to describe and organize 844,000 species-level and 705,000 subspecies-level taxonomic concepts across every major bird taxonomic checklist of the last 125 years. The use of taxonomic concepts in place of scientific names, coupled with efficient resolution services, is a major step toward addressing some of the main deficiencies in the current practices of scientific name dissemination and use.

Keywords

Biodiversity informatics, scientific names, taxon circumscription, taxonomic concepts, taxonomic database

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Introduction

The ability to unambiguously describe a concept through nomenclature is fundamental to science. This is particularly true for organizing information about global biodiversity (Patterson et al. 2010); yet, scientific names of biological organisms often poorly resolve the concepts they are intended to describe (Kennedy et al. 2006, Franz and Thau 2010, Franz and Cardona-Duque 2013). In a review of 12 successive classifications of German mosses published over 73 years, Geoffroy and Berendsohn (2003) found that a mere 13% of 1548 taxonomic entities remained consistent in both name and circumscription. In a comparison of North American vascular plant taxonomies published between 1927 and 2006, Franz et al. (2008) found that only 55% of taxa remained unchanged. As the use of database systems for managing vast amounts of biodiversity data becomes increasingly prevalent, there is a strong need for a system designed to organize the millions of taxonomic entities with which the diversity of life is catalogued, and for resolving the meanings behind their names.

A fundamental problem with taxonomic names is that they only refer unambiguously to type specimens, instead of the biological circumscriptions that underlie most name usages. Because our views of these circumscriptions are constantly being challenged and redefined, the circumscriptions attached to a valid name may change dramatically without any change in the name itself. This issue is of great practical importance to people building large-scale biodiversity repositories. Key biological features, such as geographic ranges or overall genetic variability, are shared properties of taxon circumscriptions, not names. As more aggregate trait and phylogenetic databases are published, it is essential to ensure that producers and consumers have clear ways to understand the circumscriptions being used. For managers of biological collections databases, the fluid definitions of names are furthermore compounded by issues such as homotypic and heterotypic synonymy, homonymy and emendations of names based on the rules of the codes of nomenclature. There are millions of valid species and subspecies names and probably an even greater number of proposed names that have later been placed in synonymy, in addition to the many orthographic variants because of a change in genus, changes in gender agreement or other emendations (e.g. David and Gosselin 2002).

Carefully constructed nomenclatural databases with resolution services for homonyms and synonyms, such as the one proposed by the Global Names Architecture (Patterson et al. 2010), can go a long way to addressing these issues. Equally important will be efforts to semantically model the processes and results of taxonomic effort, leading to ontologies for taxonomic names (Franz and Peet 2009, Franz and Thau 2010) and tools such as the Euler/ASP toolkit (Chen et al. 2014, Franz et al. 2014). Such ontologies help ensure interoperability across individual implementations, a much-needed step given the scope of the problem of aggregating taxon names. Fundamental to the development of these projects is the notion of taxonomic concepts (Berendsohn 1995, Kennedy et al. 2006), which have been proposed as a solution to the issue of the everchanging usage of names. They refer to a scientific name's underlying circumscription by providing a reference to an author and publication where this circumscription is defined, or from which it can be inferred. For instance, the name *Parus major* Linnaeus, 1758 *sec*. Clements 2000 refers to the circumscription of the Great Tit as inferred from the Clements Checklist of the Birds of the World, 5th edition (Clements 2000). This taxonomic concept can be said to be congruent with *Parus major* Linnaeus, 1758 *sec*. Dickinson 2003 as both refer to congruent sets of individuals, but only partly overlapping with *Parus major* Linnaeus, 1758 *sec*. Gill and Donsker 2013, which has a much more restricted range and is entirely included in the former.

The limitations of taxonomic concepts

Although taxonomic concepts address some of the limitations of names, they have limitations and issues of their own. While taxonomic concepts have the theoretical advantage of removing the ambiguity associated with scientific names, they are most useful when the relationships between overlapping concepts are well understood. A significant challenge is that there are potentially many more taxonomic concepts than there are taxonomic names, requiring descriptions of relationships between overlapping concepts. Most development regarding taxonomic concepts has focused on establishing relationships between pairs of concepts, whether within a particular publication (vertical relationships) or among different taxonomic publications (horizontal relationships). The relationships between concepts can be expressed with predicates that describe the degree of congruency (Franz and Peet 2009). While this provides an invaluable framework and is a necessary step to developing more detailed formal ontologies, it can be very difficult to scale up given that the number of pairwise comparisons grows at an exponential rate and there are potentially hundreds of sources of taxonomic concepts and thousands of concepts to compare.

Birds provide an excellent example of the challenges inherent in managing taxonomic concepts. There are at least eight major global and widely used taxonomic authorities that have published checklists of taxonomic names (and thus concepts) encompassing all known bird species, several regional authorities that have focused exclusively on a particular geographic area (e.g. Christidis and Boles 2008), and countless more specialized publications that have focused on specific taxonomic groups or individual species. Most sources have published several major versions of the same checklist over the course of several decades, as well as many other minor revisions. The American Ornithologists' Union's Checklist of North American Birds, for example, has published seven full checklist editions and 54 partial revisions between 1886 and 2013.

Birds stand out from many other taxonomic groups because they are well studied, and multiple taxonomies curated by multiple sources are available. This also creates a large number of concepts to organize for any given name. Concept management for such a well-studied taxonomic group is particularly challenging because a simple solution, such as documenting only taxonomic changes instead of recording every concept in every checklist, is not feasible for several reasons. First, such a solution assumes that there is a strictly linear temporal sequence in publications, something that only applies within a given authority, such as Clements or the American Ornithologists' Union, and does not help resolve relationships between independent authorities or even pairs of non-consecutive publications within the same authority. Secondly, because concepts from taxonomic publications may be used as proxies to refer to original concepts, all taxonomic concepts from a publication at a particular point in time need to be resolvable, not only those that are representing changes from earlier publications. While this information is rarely provided in published taxonomic data, data custodians will generally be able to identify which authority and version they were using to describe names at the time their data were curated.

Avibase, the World Bird Database

Avibase (Lepage 2014) is a large taxonomic database system that attempts to organize all authoritative avian taxonomic concepts, particularly those published in the form of comprehensive global or regional checklists (relational concepts, *sensu* Franz and Peet 2009). Avibase contains taxonomic concepts from 151 taxonomic checklists published in the last 125 years by 17 different authorities (Table 1), as well as taxonomic concepts from other sources. These cover both global checklists (e.g. Howard and Moore, Clements, and the International Ornithological Committee checklists) and regional checklists (e.g. the British Ornithologists' Union and the American Ornithologists' Union's North and

Table I. Source of taxonomic concepts included in Avibase, with the number of versions published
(including major editions as well as minor revisions). * indicates regional checklists only covering species
for a specific part of the world.

Checklist source	Publ. Years	N of versions (incl. revisions)
African Bird Club *	2004-2010	6
American Ornithologists' Union *	1886-2013	61
Birdlife	2007-2012	6
British Ornithologists' Union *	2006-2009	2
Christidis and Boles (Australia) *	2008	1
Commission internationale pour les noms français des oiseaux	1993-2009	2
Clements Checklist of Birds of the World	1974–2013	18
eBird Checklist	2010-2013	4
Howard and Moore	1980-2008	11
Handbook of the Birds of the World	1992-2011	1
International Ornithological Committee	2006-2012	22
Morony, Bock and Farrand	1975	1
Oriental Bird Club *	2001	1
James Lee Peters	1931–1987	1
Sibley and Monroe	1993-1998	3
South American Classification Committee *	2003-2013	11
Zoonomen – Zoological Nomenclature Resource	2007	1

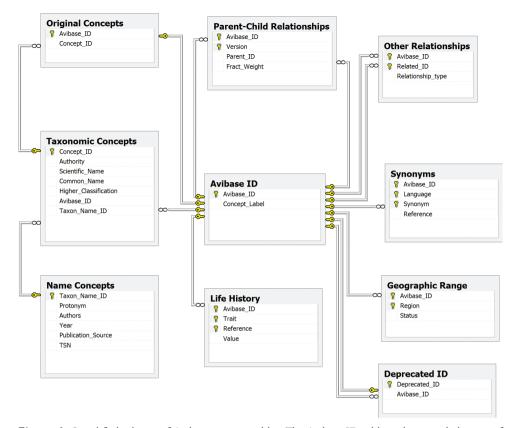


Figure 1. Simplified schema of Avibase primary tables, The Avibase ID table is the central element of Avibase, to which all other concepts are related, and which aims to represent all distinct taxonomic concepts ever published for birds. Published **taxonomic concepts** (species and subspecies, as well as subspecies groups in some cases), along with their scientific and common names as recognized in the publication, are each mapped to a single Avibase ID. A table of **parent-child relationships** is used to describe relationships between different Avibase IDs. Because all taxonomic concepts are congruent with Avibase IDs, relationships among taxonomic concepts themselves are not needed. Biological properties (geographic range, life-history, etc.) are linked directly to Avibase ID, as are **synonyms**, a table that partly overlaps with the names used by taxonomic concepts, but that can also extend to vernacular names in multiple languages. **Name concepts**, which relate to names attached to original type specimens, are a property of taxonomic concepts, and can themselves be linked to ITIS Taxonomic Serial Number (TSN) identifiers.

South American Classification Committees) of all birds known and currently recognized, including both the original publication of these checklists and all subsequent revisions. These currently represent over 844,000 taxonomic concepts for species and 705,000 concepts for subspecies (there are typically about twice as many recognized subspecies of birds as there are species, but not all authorities include subspecies in their treatment).

At the heart of Avibase is the notion of transparent and consistent representation of distinct taxonomic concepts. While there are vast numbers of taxonomic concepts in the "shallow" sense of unique name/source combinations (concept labels), there **Table 2.** A breakdown of distinct taxonomic concepts in Avibase. 38,755 distinct concepts were obtained from the 151 bird checklists listed in Table 1; the remaining 11,941 were described elsewhere (e.g. hybrids) or represent unique taxon assemblages (e.g. groups of species) and were added to the database separately. Note that although a distinct Avibase ID denotes a congruent circumscription cluster, it need not indicate the same rank: for example, 1,634 concepts were described by some authorities as species and by others as subspecies, while still denoting congruent sets of individuals. Other taxonomic treatments within checklists refer primarily to subspecies and species groups, as well as to distinct phenotypic forms.

Treatment in checklists	Number of concepts
Species only	10,964
Subspecies only	22,477
Other only	1,474
Species or subspecies	1,634
Species or other	468
Subspecies or other	961
Species, subspecies or other	777
Only Avibase IDs	
New taxa, formally described	3
New taxa, not yet formally described	33
Doubtful or invalid taxon	93
Genera (including extinct and synonyms)	3,934
Species groups (e.g. superspecies)	252
Subspecies groups	265
Species hybrids	3,231
Subspecies intergrades	55
Subspecies (junior synonyms)	3,014
Fossil species or subspecies	1,027
Phenotypic forms	34
Subtotal (only Avibase IDs)	11,941
Total	50,696

are far fewer "deeper", taxonomically unique (non-congruent) concept clusters that represent unique circumscriptions. Avibase assigns a unique database identifier to each of these distinct concept clusters (called an Avibase ID), composed of a random hexadecimal key (e.g. 2624054ED644AABB). The table of Avibase IDs, the central component around which the entire database is constructed (Fig. 1), attempts to capture all distinct taxonomic concepts ever published in those major authoritative sources. If one includes all taxonomic concepts that have been originally published as species and subspecies, as well as superspecies, subspecies groups, hybrid forms and phenotypic forms (sometimes originally described as valid species), there are 50,696 unique taxonomic concepts that have so far received an Avibase ID. Of these, 38,755 are from the 151 bird checklists in Avibase; the remaining 11,941 concepts are from other publications or represent unique taxon assemblages and were added separately (Table 2).

Some distinct taxonomic concepts share the same scientific name across all checklists: for example, the name *Nycticorax nycticorax* refers to a congruent circumscription cluster and maps to the same Avibase ID in all 151 checklists within Avibase. However, such concordance among authorities is far from the norm: only 11 of the 19,260 unique combinations of circumscriptions and scientific names for species (bearing both the same exact name and the same Avibase ID) have been used by all 151 authorities. Many circumscriptions can therefore bear several distinct names (concept synonyms), and the same names can often be used to describe different circumscriptions (concept homonyms). For instance, the names *Francolinus gariepensis*, *F. levaillantoides*, *F. levalliantoides*, *Scleroptila gutturalis* and *S. levaillantoides* can all refer to a congruent circumscription cluster (Avibase ID 8E833C63E70A547C), whereas the name *Puffinus lherminieri* can refer to up to 12 distinct circumscriptions. When restricting this analysis to the 70 global authorities, we found 18,278 unique combinations of scientific species names and distinct taxonomic concepts, with 4,451 being used in all 70 cases, less than half of the 10,000 currently recognized species.

For managers of biological data collections, the benefits of having a permanent identifier for a stable biological unit that is not subject to the changing nature of names or circumscriptions are apparent. Databases which only track names and their synonyms, such as the Integrated Taxonomic Information System (ITIS), cannot address the ambiguities of circumscriptions. In Avibase, a unique Avibase ID always denotes a distinct, unique circumscription cluster. Congruent taxonomic concepts by definition share all their biological properties because they refer to taxonomically congruent sets of individuals. Ecological and biological traits such as geographic distribution, life-history characteristics, genotypes, behavior, and ecological preferences are all properties of the biological circumscription, linked together in Avibase by the Avibase ID, instead of being attached to names that may change in either orthography or definition (Fig. 1).

Concept trees

Because each Avibase ID identifies a distinct taxonomic concept, and many published taxonomic concepts are congruent to each other, it is sufficient to build entity relationships among Avibase IDs rather than among all taxonomic concepts individually. This greatly reduces the number of relationships to describe. The primary type of relationship that has been implemented in Avibase is the direct one-to-many parent-child relationship between Avibase IDs, corresponding to the "Includes" (>) predicate *sensu* Franz and Peet (2009), with the main exception of hybrids. When built in hierarchical trees, which we refer to as "concept trees", direct parent-child relationships allow programmatic derivation of many of the other types of relationships, such as indirect descendants, partial overlap between concepts, congruency, and exclusion. We discuss this in more detail below.

As an example of a concept tree, we consider the Solitary Vireo complex. The 6th edition of the AOU North American Checklist (American Ornithologists' Union 1983) recognized a single species in this complex, *Vireo solitarius*. In the Forty-first Supplement (Banks et al. 1997), two groups of subspecies within this species were

Vireo solitarius (sensu lato) 048F1F046E31AC96

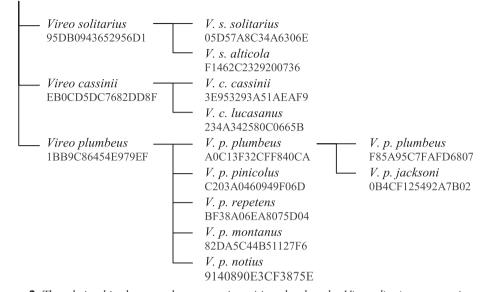


Figure 2. The relationships between the taxonomic entities related to the *Vireo solitarius* superspecies. Numbers under each name refer to Avibase IDs. Subspecies *jacksoni* Oberholser, 1974 has been now subsumed into the nominal *plumbeus* subspecies. The concept for the nominal *plumbeus sec.* Oberholser, 1974 is therefore distinct from the concept for the nominal subspecies *plumbeus* when *jacksoni* is subsumed. It is worth noting however that the recognition or not of *jacksoni* does not affect the higher related concepts, such as the *plumbeus* species, any of its other subspecies, or the rest of the *Vireo solitarius* complex because they are either orthogonal to those alternative arrangements or they completely include both. In the database model (Fig. 1), these trees are maintained with the parent-child relationship table in which each Avibase ID only needs to identify its immediate parent, while other relationships can be calculated programmatically.

raised to full species: *Vireo plumbeus* (including subspecies *plumbeus, pinicolus, repetens, montanus* and *notius*) and *Vireo cassinii* (including subspecies *cassinii* and *lucasanus*). There are therefore two separate taxonomic concepts in Avibase, with separate Avibase IDs but the same name *Vireo solitarius*: one represents *Vireo solitarius sensu lato*, which includes *plumbeus* and *cassinii*, and the other represents *Vireo solitarius sensu stricto*, which does not overlap with *plumbeus* and *cassinii* and *V. solitarius s.s.*) are children of *Vireo solitarius s.l.* (Fig. 2). Each of these three forms can in turn have their own subspecies. This type of relatively simple model with a single tree represents a majority of relationships among related taxonomic concepts.

Avibase IDs are only needed for the smallest operational unit used by concept publishers, which in the case of birds is usually the species or the subspecies, and relationship trees will generally only need to capture relationships among taxa within a superspecies group or among species that have been historically considered as conspecific. Avibase IDs can also be created for other taxonomic levels, such as genera, or even for arbitrary taxonomic arrangements such as subspecies groups or pairs of species that might be confused in the field but are not necessarily genetically close, as is used extensively in the eBird taxonomy (Clements et al. 2013). A disadvantage of creating Avibase IDs for higher taxonomic levels that comprise many children (e.g. family) is that they tend to be challenging to manage, because of the higher number of possible combinations of children at those levels, with each combination representing a possible circumscription requiring an Avibase ID. Fortunately, some of the tasks that one may want to perform with those higher taxonomic levels can also be achieved more simply without creating Avibase IDs. For example, for evaluating whether genus or family concepts are congruent between distinct authorities, one could programmatically look at whether they are comprised of the same trees or portions of trees in each authority.

Alternate concept trees

Alternate concept trees are required in those relatively rare cases (5.7% of all Avibase IDs) where several mutually contradictory arrangements have been proposed. For instance, the superspecies Pterodroma arminjoniana is now considered three distinct species (P. arminjoniana, P. heraldica and P. atrata), but several arrangements of those have been proposed which involve at least two different relationship trees (Fig. 3): one in which atrata is included in heraldica s.l. and one in which it is not. From these two alternative taxonomic trees, four different valid combinations of taxonomic concepts are possible and have been published within the same checklist: 1) the superspecies P. arminjoniana (abc) alone, 2) P. arminjoniana (ab, including heraldica) and P. atrata (c), 3) P. heraldica (ac, including atrata) and P. arminjoniana (b) and 4) P. heraldica (a), P. arminjoniana (b) and P. atrata (c) as distinct species. The use of those concepts by various checklists can be visualized in a grid (http://avibase.bsc-eoc.org/species.jsp?aviba seid=A26C9D6B5C859E5E&sec=taxontable). Note that in all four combinations of concepts, the three letters representing the finer levels (a, b and c) are always included, and included only once. This property of the relationship trees can be used to validate the arrangements and map the taxonomic concepts to Avibase IDs (see section "Validating parent-child relationships across checklists using fractional weights"). One should also note that taxon concept combinations 1 and 4 are present in both taxonomic trees A and B. In checklists that use those combinations, it is not possible to determine which alternate tree applies, nor is it necessary because both trees lead to the same solution for mapping taxonomic concepts and Avibase IDs.

Alternate concept trees are not necessary in all cases of taxonomic revision. For instance, if two populations previously treated as part of the same subspecies are split into two subspecies, it suffices to extend the terminal branch of the tree for that species with new child nodes, without affecting any of the higher levels or the rest of the tree structure, as all previously existing nodes continue to refer to congruent concept sets. Likewise, independent trees that do not share nodes can be merged together to form a larger tree (e.g. if two species were found to have close affinity and lumped together).

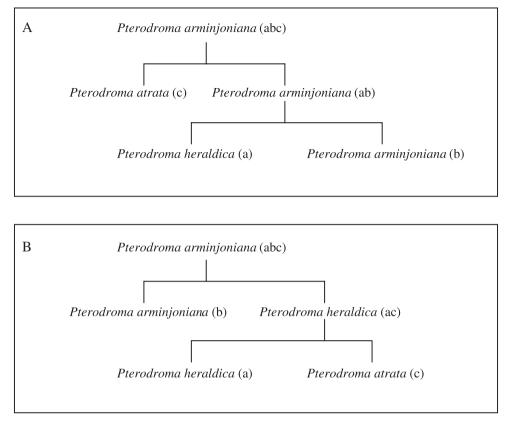


Figure 3. The relationships between *Pterodroma arminjoniana*, *P. heraldica* and *P. atrata*, with two alternative arrangements (**A** and **B**) of biological concepts found in taxonomic authorities. Concepts with the same lowercase letters in brackets in the two diagrams represent congruent circumscriptions.

It is also possible to create new nodes within the tree by grouping existing branches together (such as by lumping *Vireo cassinii* and *V. plumbeus* together, but without *V. solitarius* in Fig. 2). However, any taxonomic changes that require moving nodes to different branches, such as reassigning a subspecies to a different species, will require a new tree, and most likely will also require new nodes to represent these new combinations. Generally speaking, a model that minimizes the number of alternate trees is greatly preferable, whenever this can be achieved.

In Avibase, alternate trees sharing some of the same branches or nodes are constructed in such a way that they also share the same root taxon node. That is, each taxon should have the same highest-level root parent concept in all alternate trees. In some cases, this could mean building trees representing large species complexes that are frequently lumped together in various arrangements – in birds, the species complexes for *Larus argentatus s.l.*, *Puffinus lherminieri s.l.*, and *Otus magicus s.l.* are some of the most elaborate examples with up to a dozen possible candidate species, many subspecies, nine node levels and up to five possible alternate relationship trees. This may require creating Avibase IDs for concepts that have never been suggested historically as representing a distinct taxon on their own, and for which a new labeling system may be required (Franz et al. 2014). For instance, one can imagine two genetically related species A and B (e.g., part of the same genus) that have never been considered as part of a superspecies or lumped under the same species, and therefore being top nodes of unrelated trees each containing several subspecies. If, following a scientific study, a checklist suggests moving some of the subspecies of species B under species A, new species-level concepts A' (containing the original subspecies of A plus the ones moved from B) and B' (containing the original subspecies of B minus those moved to A) will need to be created, each with a new combination of subspecies. Rather than maintaining 4 distinct trees (with top nodes A, B, A' and B'), a more useful approach is to create a new parent concept that encompasses the entire group (A+B), and that can serve as the top node for a tree that includes both A and B, and another tree that includes concepts A' and B', as well as their respective subspecies. Doing so allows easy identification of related concepts because they share the same top root node, which can be invaluable when trying to define the types of relationships described in Franz and Peet (2009), such as partial overlaps, additions, and subtractions. This approach is also required for the use of fractional weights as a mean of validating and facilitating concept mapping and relationships, which is described in more detail below.

Mapping taxonomic concepts in Avibase

As new taxonomic checklists are published, each taxonomic concept they contain must either be mapped to an existing Avibase ID or have a new Avibase ID assigned to it. Avibase treats each partial revision of a checklist as if it was published in full again but with the changes implemented. For instance, when the AOU publishes a limited list of annual revisions, it implicitly leaves all other concepts unchanged. While it may seem redundant to repeat all taxonomic concepts at each revision, including the ones that did not change, this process greatly simplifies identifying concepts in use at a given point in time. For authorities that do not have a versioning approach and where corrections are gradually implemented as they are acted upon throughout the year, such as the South American Classification Committee, Avibase periodically freezes a version arbitrarily (in this case, about once a year). We strongly encourage publishers of taxonomic concepts to apply a consistent versioning approach and to maintain and make available archived versions.

In all cases, the process of mapping concepts is most easily done by comparing a new checklist with another one already mapped in Avibase, preferably one that uses similar taxonomic treatments. If the new checklist is a relatively minor revision of an existing checklist already mapped in Avibase, most of its taxonomic concepts will have the same scientific or common name, a congruent biological meaning and will map to the same Avibase IDs, thereby greatly simplifying the work.

The database manager handling the addition would initially attempt to match all scientific names of all concepts (species and subspecies) shared by the two checklists, and look for differences. Changes in scientific name alone, such as reassignment to a new genus or a change in the spelling of the epithet to reflect gender agreement, do not warrant a change in Avibase ID but do complicate the initial matching of the two checklists. This issue can be addressed by manual inspection or by relying on common names, other identifiers provided by the publisher, or a table of scientific name synonyms. Creating a new Avibase ID is required only where the biological underpinning of a name has changed, such as following additions to the checklist (e.g. new species) or taxonomic splits, lumps, and partly overlapping relationships, which can often be easily detected by looking for any additions or deletions of concepts or reassignments of subspecies. In many cases where a new Avibase ID is required, a congruent taxonomic concept will already have been defined by another authority and mapped to an existing Avibase ID: for example, in the 2013 version of the Clements checklist (Clements et al. 2013), there were 10,324 species listed, including 176 (1.7%) that were not in the previous edition (Clements et al. 2012). Since other checklists already contained these concepts, only 41 (23.3%) represented concepts entirely new to Avibase for which new Avibase IDs were needed.

Concept publishers, in their justification for taxonomic changes, often provide the information necessary to identify the circumscription intended by a taxonomic concept. For instance, they may explicitly say that they are splitting or lumping concepts to create new ones. Other information, such as phenotypic descriptions (plumage, song, behavior, etc.) and geographic range, can also be used to assess whether taxonomic concepts are congruent with those of other authorities. The examination of other concepts within the same checklist can also reveal implicit circumscriptions: for example, *Parus major s.l.* sometimes contains *Parus major s.s.* and *Parus cinereus*. A checklist that contains *P. major* but not *P. cinereus* is probably referring to *P. major s.l.* and not *P. major s.s.* The list of subspecies assigned to a species may be useful in identifying its circumscription. Ultimately, this process in Avibase requires some level of manual processing on the part of a database manager with some knowledge of the taxonomic group. While properties of concepts and concept trees can help identify and validate candidate concepts for mapping, expert knowledge is necessary for proper curation.

Validating parent-child relationships across checklists using fractional weights

Parent-child relationships and concept trees may be used both to identify relationships in new publications and to validate existing relationships. The algorithm used by Avibase assigns and stores fractional weights for each node of a concept tree, starting with a weight of 1.0 for the top concept in a tree. Child nodes recursively receive an equal fraction of the weight of their parent. *Vireo solitarius, cassinii* and *plumbeus,* for instance, would each receive a weight of 0.333 (Fig. 4). The two subspecies of *solitarius* and *cassinii* would each receive a weight of 0.167 (half of their parent node), and the *Vireo solitarius (sensu lato)* w = 1.000

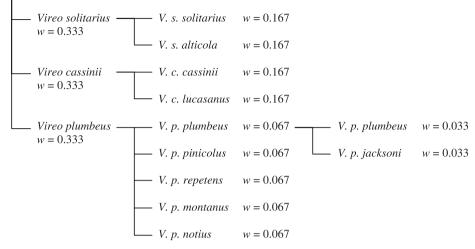


Figure 4. Fractional weights (w) can be used to validate the taxonomic arrangements within a particular authority. In this example, in any valid listing of the concepts within an authority, the sum of all taxonomic concepts related to the superspecies *Vireo solitarius* should add up to 1.0 at both the species and the subspecies levels.

five recognized subspecies of *plumbeus* would each receive (0.067) (one-fifth of their parent node). Finally, the subsumed subspecies *jacksoni* and the nominal *plumbeus* that excludes *jacksoni* would each receive a weight of 0.033. Within any authority with global coverage, such as a global bird checklist, there should always be at least one alternate tree for which the sum of weights yields a total of 1.0 for a suite of related species concepts. In the *Vireo* example, the two valid options at the species level are listing *Vireo solitarius s.l.* alone (total weight = 1.0), or the three forms individually (total weight = 0.333 + 0.333 + 0.333 = 1.0). For authorities that are restricted in coverage or incomplete in scope, such as a checklist of North American birds, the same approach can be used but with weights recalculated to exclude portions of the trees that are not covered by the scope of the authority. It is possible for a set of incorrect arrangements to add up to 1.0 by chance; Avibase uses a series of rules (listed in Table 3) to detect such cases.

It is possible to automate mapping of the taxonomic concepts from an authority to an Avibase ID using fractional weights and the properties of indirect dependencies. This requires examining all possible combinations of Avibase IDs that match the names present in a given authority in order to find which valid combination will provide a total fractional weight sum of 1.0 without breaking the descendant rules. For example, Avibase contains two distinct taxonomic concepts that bear the name *Vireo solitarius* (Fig. 4): *Vireo solitarius s.l.* (w=1.0), and *Vireo solitarius s.s.* (w=0.333). Taking a hypothetical example, if a comprehensive checklist from a new authority is incorporated into Avibase that only contains *Vireo solitarius*, and not the other two possible species names

Table 3. To be valid, an assemblage of related taxonomic concepts within an authority should follow at least the following set of rules, which emerge as logical constructs from the database design. While these rules are not strictly enforced in Avibase, any deviations would suggest either a problem with the mapping of taxonomic concepts to Avibase IDs, or a problem in the concept trees of Avibase IDs.

1.	The sum of fractional weights for species-level taxonomic concepts mapping to Avibase IDs within the same tree should be equal to 1.0 in at least one particular complete taxonomic arrangement and should never exceed 1.0, even in alternative trees. This rule should also hold above the species level, but as higher taxa can generally be completely specified by listing the species within them, such an approach is probably unnecessary.
2.	In cases where there are alternative trees, only a single mapping of taxonomic concepts to Avibase IDs should provide a sum of 1.0 on one or more of the alternate trees. In the example of <i>Pterodroma</i> (Fig. 3), concepts a, b and c are present and validly arranged in both trees, and both will offer the same solution in term of mapping taxonomic concepts to Avibase IDs when all three species are present.
3.	The sum of weights for subspecies concepts in a given checklist should equal the weight of the species in which they are included. In other words, if a checklist includes a concept for <i>Vireo plumbeus</i> that maps to an Avibase ID with a weight of 0.33 in a given tree, the sum of the Avibase ID weights for the subspecies of <i>V. plumbeus</i> in the same checklist should also equal 0.33 in the same tree.
4.	Only one taxonomic concept per checklist should map to a particular Avibase ID across all taxonomic levels. One exception is that of monotypic species and their nominal subspecies, which both refer to the same Avibase ID because they have exactly identical circumscriptions. The latter are typically not included in taxonomic checklists for that very reason. While the same exception also applies to other monotypic taxonomic levels (e.g. genera with a single species), these higher groups are generally not mapped in Avibase.
5.	Taxonomic concepts at a given taxonomic level within a checklist (e.g. species) should not map to Avibase IDs that are found along the same branch of the tree in any given arrangement. If concept A is a child of concept B, and concept B is in turn a child of concept C, only one of A, B or C should be present at the same time at the same taxonomic level.
6.	The parent-child relationships within a checklist (e.g. species and subspecies relationships) must exhibit the same parent-descendant relationships as the Avibase IDs they are mapped to. For instance, if an authority publishes the species concept <i>Vireo solitarius</i> that includes <i>V. s. alticola</i> as one of its subspecies, the Avibase ID for <i>V. s. alticola</i> also needs to be a descendant of the Avibase ID for <i>V. solitarius</i> .
7.	Alternate trees should share all the same terminal nodes, as well as the same top parent node, but they can have a different suite of intermediate nodes. Intermediate nodes that are shared among alternate trees should also have the same terminal children nodes in all those trees (i.e. the nodes must represent the same population of individuals in all trees).

(*V. cassinii* and *V. plumbeus*), then this authority's concept of *V. solitarius* is determined as identical to the *Vireo solitarius s.l.* (w=1.0) concept. If a later revision of that checklist includes all three taxa (*V. solitarius, V. cassinii* and *V. plumbeus*), Avibase could recognize that this authority's concept matches the *Vireo solitarius s.s.* concept (w=0.333). If a further revision were to elevate a subspecies of *V. solitarius* (say, *V. s. alticola*) to a species, there would now be three separate taxonomic concepts with weights of 1.0, 0.333 and 0.167 for *V. solitarius* (the last matching the concept for the former nominal subspecies, which would now be treated as a full species). This process can be extended to more complicated arrangements, and as long as the relationships are properly constructed, there should always only be a single valid combination possible. A recent attempt to use such an automated approach to mapping taxonomic concepts showed promising results. For this, we used species concepts from Peters' *Check-List of Birds of the World*, a landmark series of books published between 1931 and 1987 and recently converted into a database (Peters et al. 1931–1987, Lepage and Warnier 2014). As with the manual mapping process, the first step was to assign scientific names to name concepts using Avibase's extensive synonymy database. The process then looked for unique combinations of Avibase IDs that, when mapped to these particular name concepts, provided a sum of fractional weights of 1.0, and for which only one solution existed. Out of the nearly 8,900 species concepts included in Peters, the vast majority of them (97%) were successfully mapped to a unique Avibase ID on a first attempt. Upon examination, the ~300 species that could not be mapped represented either new concepts for Avibase or revealed problems with incorrectly constructed taxon trees breaking one or more of the rules listed in Table 3. With manual adjustments of the concept trees, all concepts were eventually successfully mapped to Avibase IDs.

Dealing with uncertainty

Whether or not automation is used, there will be instances where circumscriptions cannot be established with full confidence, particularly when checklist authorities provide incomplete information. An example is the African parrot subspecies suahelicus, found from Tanzania to Angola and northeastern South Africa, which has been alternatively included as part of *Poicephalus robustus* or *P. fuscicollis* by various authors, thus creating two possible distinct species concepts for each name, each with very different definitions. In one case, the nominate P. r. robustus endemic to South Africa is combined with P. r. suahelicus, and the monotypic species P. fuscicollis is restricted to western Africa from Gambia to Angola. In the alternative treatment, the monotypic species P. robustus is restricted to South Africa, and the subspecies suahelicus is combined with P. fuscicollis, covering most of sub-Saharan Africa. In a checklist or publication that contains only the two species names P. robustus and P. fuscicollis, without a list of subspecies or phenotypic characteristics (such as range or plumage) which might disambiguate the possible circumscriptions, there will be uncertainty in mapping those concepts to the correct Avibase IDs. In such cases, Avibase relies on circumstantial evidence to help with the mapping process. If, for instance, one of the two arrangements had not been recognized as valid for quite some time, it may be safe to assume that the authors intended to refer to the contemporary concepts. A more refined approach would be to categorize the criteria used to establish each mapping and the degree of uncertainty attached to it, something that Avibase has not yet dealt with.

Another approach to dealing with those uncertain cases could be to create new Avibase IDs for each of those poorly defined nominal concepts, with their own partially constructed relationship tree (e.g. without subspecies nodes). Because the taxonomic tree of relationships in those cases is incomplete, there will be uncertainty in establishing the relationship of those poorly defined taxonomic concepts to other concepts in alternate arrangements. The framework proposed by Franz and Peet (2009) allows describing these types of relationships that involve poorly defined concepts by combining expressions with the symbol OR. For instance, if two taxonomic concepts share the same name, they can be assumed to at least partly overlap and may possibly also be entirely congruent, something that can be captured in the table of Other Relationships in the Avibase database model (Fig. 1). While this is a problem that Avibase has not yet attempted to address, this issue will be mainly limited to nominal concepts, published without sufficient information to allow proper mapping, which does not usually apply to authoritative checklists mapped into Avibase.

Mapping biodiversity data to taxonomic databases

The system of automated mapping may also be used to disambiguate taxonomic concepts in biodiversity databases. Unlike names in checklists, those attached to biodiversity data often do not contain information that reveals their circumscription, unless they were published as taxonomic concepts. Avibase has yet-untapped potential as a taxonomic concept resolution service. Users would pass a list of names to the service and Avibase would find those names across concept trees, helping to resolve any ambiguity. If these names serve as labels to other information, such as specimen records, Avibase could thus disambiguate the intended circumscription of such records. This is especially valuable for older records, which may use names and concepts long out of date.

For biodiversity databases that rely primarily on scientific names and not taxonomic concepts to index records, other properties of the records could be used to determine the intended circumscription. For instance, one could evaluate a historical record originally described as *Vireo solitarius* in Vancouver, B.C. as almost certainly referring to the current species concept *Vireo cassinii*, because the probability of observing *V. solitarius s.s.* at that location and date is minimal. A request to such a service could include some or all of the following properties for each record that needs to be assessed, represented in standard formats described in the Darwin Core standard (Wieczorek et al. 2012): scientific name, scientific name author, taxonomic concept source (authority name and publication year), vernacular names (in English or other languages), record collection site (country, state or province, county, geographic coordinates, etc.), record collection date and so on.

Such services have not yet been implemented in Avibase, providing a compelling rationale for further development, which is ongoing. Each property could be assigned a relative weight so that scores are assigned to prospective matches. Each taxonomic concept could be classified as regular, rare, or absent from a geographic area, and different scores assigned to each of these categories. This information is already available in Avibase for several thousand geographic regions (e.g. continents, countries, state/ provinces, islands), and a more elaborate version could make use of increasingly available distribution data available from sources such as eBird (http://ebird.org) and Map

of Life (http://mappinglife.org; Jetz et al. 2012) to assign probability scores that a particular bird taxon would be observed at a specific location and date. Different types of uses could be more tolerant to uncertainty than others, something that would be left to the discretion of the user. Fuzzy taxonomic name matching algorithms such as TaxaMatch (Rees 2009, 2011), which are particularly suited to identifying common errors in writing and transcribing taxonomic names, could also be implemented to account for variants and errors in spelling. While these methods may become increasingly refined over time, their probabilistic nature means that they will probably never fully replace the need for expert opinion. Experts and users should be able to decide how much weight is given to various considerations in the scores, and what degree of certainty is required for their specific need.

Conclusion

Avibase provides a clear demonstration that taxonomic concepts can be successfully organized on a large scale, and perhaps more importantly, that it can be done by relying on the taxonomic "currency" already used by most practitioners, i.e. the names published in the form of authoritative checklists. We hope and expect that other researchers will continue to further develop the ontological framework and the database models that are needed to organize concepts, populate databases and build relationships, as well as develop services that will allow interacting with these systems. As global biodiversity databases aggregated from various sources continue to grow in size and in scope, and as taxonomic advances continue, the deficiencies of relying solely on scientific names should become increasingly apparent. The use of taxonomic concepts in place of scientific names, together with the development of taxonomic concept databases and easily available resolution services, would be a major step forward in addressing some of these issues, and in facilitating the paradigm shift needed to transition from taxonomic names to taxonomic concepts.

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