SYSTEMATICS OF TRIDACTYLOIDEA (ORTHOPTERA: CAELIFERA): TAXONOMIC REVISION OF EXTINCT TAXA WITH COMMENTS ON EXTANT TAXA

BY

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DISSERTATION

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ABSTRACT

Tridactyloidea (Orthoptera: Caelifera) is a superfamily that includes three families of minute (0.5 mm) to medium-size (9 cm) crickets. Tridactylidae, pygmy mole crickets, are globally distributed, whereas mud crickets in Ripipterygidae and sandgropers in Cylindrachetidae have Neotropical and Austral distributions, respectively. The taxonomy of this superfamily was reviewed between the 1960s and 1990s. However, the monophyly of families and other taxonomical subcategories have not been resolved. My goal was to provide a stable taxonomy for this group by developing robust phylogenetic hypotheses with a total evidence approach. Specifically, I aimed to produce a taxonomic revision of fossils and to develop a phylogenetic hypothesis of relationships within Tridactyloidea.

Chapter 1 is an introduction to the superfamily Tridactyloidea. This includes general aspects of their morphology, biology, ecology, diversity, distribution, systematics, conservation, significance and applications.

Chapter 2 includes the description of two new species from Colombia and the first record of the genus *Dentridactylus* (Tridactylidae) for Colombia. This is a rare genus with only four known species, which I have now expanded to six. In the chapter, keys for the identification of the species in the Americas are provided.

Chapter 3 is a revision of the state of knowledge of immature stages in the genus *Mirhipipteryx* (Ripipterygidae). This revision highlights the gap of knowledge not only in the morphology of nymph, but also in their ecology. The chapter provides a comparison of adult and nymphal characters and additionally designates *Mirhipipteryx lobata* as a *nomen nudum*.

Chapter 4 is a revision of fossil tridactyloids from the Crato Formation of Brazil. The Crato from Brazil is a Cretaceous formation of Aptian age. Orthopterans are abundant in the fossil record from the Crato Formation. However, only two tridactyloid species are known. Here I review eleven tridactyloid-like fossils and place them in a taxonomic category of the superfamily Tridactyloidea based on morphological comparisons. From these, four new genera and species are described, expanding the known diversity of the group.

Chapter 5 is a revision of Burmese amber fossils. Orthopterans from this Cenomanian deposit are very rare, with only nine known species. I compared the morphology of five small tridactyloid-like fossils to the other known extinct and extant taxa. In this chapter descriptions of new species and a new family are provided.

Chapter 6 describes the systematics of mud crickets, pygmy mole crickets and sandgropers. Here, I provide the first phylogeny for the superfamily Tridactyloidea. This was accomplished by combining a morphological dataset with a molecular dataset. The morphological matrix was revised from an existing matrix for the family Ripipterygidae by adding new taxa (extinct and extant) and codifying new characters into it. The morphological matrix was prepared with a few samples from the Genbank and with the addition of new sequences for a fragment of COI. The findings are generally consistent with many current classifications of the group, and inconsistencies are discussed.

To My Family.

To their strength and resilience

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TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION TO TRIDACTYLOIDEA

Tridactyloidea is a small superfamily of orthopterans with ~236 species in three families. The superfamily includes the commonly known mud crickets (Ripipterygidae), sandgropers (Cylindrachetidae), and pygmy mole crickets or sand crickets (Tridactylidae) (Figures 1.1a-c). The families Tridactylidae and Ripipterygidae are easily distinguished from other orthopterans by their reduced tarsal segments (metatarsus) from the hind leg and developed apical tibial spurs that display a characteristic and unique “three fingers” look (Figure 1.2). The morphology of the family Cylindrachetidae differs substantially from the previous families and superficially resembles a mole cricket (Grylloidea: Gryllotalpidae) with a cylindrical body but significantly reduced antennae (Figure 1.1c).

Morphology. Tridactyloidea is characterized by forelegs specialized for digging, fore and middle legs with two tarsomeres, saltatorial (jumping) hind legs sometimes with swimming plates, as well as the presence of abdominal repugnatorial glands and male paraproctal lobes or brachium bearing diverse shapes (Flook & Rowell 1997, Heads 2009b) (Figure 1.3). Their general morphology consists of prognathous or hypognathous species, often with developed compound eyes and three ocelli. The antennae are filiform or moniliform. They have chewing mouthparts. The forewings or tegmina are hardened and leathery when present and the hind wings are membranous, fan-shaped with enlarged anal field; sometimes with tegminoid costal area. The fore legs are often fossorial, but also are used for walking. The middle legs are walking-type, and the hind legs are saltatorial sometimes with natatorial plates (Figure 1.3).

Biology and Ecology. These crickets inhabit riparian habitats, often tunneling and digging in the sand or mud along the margins of creeks, rivers, streams, and lakes. Others are found in crevices and small oval cells on vertical banks (Baena-Bejarano 2015). Tridactyloids are gregarious. Adults are occasionally observed on herbaceous vegetation. Nymphs are often found in the tunnels, which provide suitable environmental conditions for their development (Günther 1994a; Baena-Bejarano 2015). Historically, the family Tridactylidae (*Ellipes* and *Neotridactylus*) has been reported as algae feeders (Deyrup & Eisner 1996), and recently another genus (*Xya*) was reported as detritivores, feeding on “noncellular decomposing organic matter” with just incidental presence of algae (Kuřavová & Kočárek 2016). The records of diets in mud crickets (Ripipterygidae) have not been well-studied, but Günther (1994a) suggested this group feed on algae, fungal hyphae, lichens and mosses. Houston (2007) found that sandgropers (Cylindrachetidae) are omnivorous and feed on small invertebrates (including cannibalism), fungal material, and on fresh and decomposed plant material available mostly underground.

Diversity and distribution. The taxonomy of this group is fairly known. Extensive revision of the species from all families took place in the last decades of the 20th century. To review current classification visit Orthoptera Species File (http://Orthoptera.SpeciesFile.org) (Cigliano *et al.* 2019).The diversity of the group has grown with at least nine new extant species described in the last decade from China, Colombia, and India (Baena-Bejarano-Heads 2015, 2018; Cao *et al.* 2017; Zhang *et al.* 2018; Yin & Yin 2018; Cao *et al.* 2018). Ripipterygids seem more diverse in tropical regions (Baena-Bejarano 2015). Tridactylids are present in tropical and subtropical regions. Cylindrachetids have an austral distribution. Distribution gaps remain for countries in Africa, the Americas, Asia, and Europe. These gaps are potentially an artifact of sampling and revision of the group rather than a patchy distribution.

Systematics. Hypotheses of relationships between species were proposed by Günther (1969, 1994b), but testing the monophyly of families, subfamilies, genera, and groups of species is a task that remains to be explored in Tridactyloidea. The only exception is a phylogeny recently developed for Ripipterygidae (Baena-Bejarano 2013). Systematic approaches are important for the stability of the group's classification, and phylogenies can be applied to other fields such as to evolution, ecology, morphology, biogeography, and behavioral studies.

Conservation. Little information is available for species in Tridactyloidea. A recent assessment of the conservation status of orthopterans in Europe found that four of the six species in the family Tridactylidae had deficient data (Hochkirch *et al.* 2016). Species in this superfamily could face threats due to habitat deterioration, habitat loss, and lower species diversity (Tridactylidae and Cylindrachetidae). More research is needed to understand the impact of human activities or other pressures affecting the group. Further evaluation of species is needed and, as suggested by Hochkirch *et al.* (2016), data deficient species need further research too.

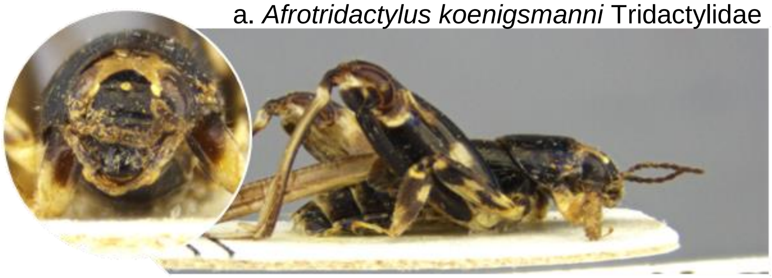
Pest species. Only species of *Cylindracheta* (sandgroper) has been reported as pests in Western Australia (Richards, 1980). Houston (2007) suggested that the attention that this group gained as a pest of legumes (lupin bean, and tagasaste) and cereals (barley, oats, and wheat) could be more an effect of taking advantage of resources left underground by other organisms, but opinions are divided (see Rentz, 1996). Sandgropers are currently classified as an insect pest with rare occurrence (Micic *et al.* 2008; DPIRD 2019).

Significance and applications. These orthopterans provide different ecosystem services. They provide supporting services as detritivores, which help with nutrient cycling. Tridactyloids could be helping with the infiltration of water to the ground by removing the soil through digging and tunneling as suggested by Steward *et al.* (2017). They also serve as a food source for other organisms such as solitary wasps of the genus *Tachytes* (Hymenoptera: Crabroninae) (Kurczewski, 1966) or mites that are presumably ectoparasites of this group (Baena-Bejarano &

Heads 2015). Tridactyloids have chemical defenses expelled through abdominal repugnatorial glands. The known repellency of this defense toward spiders and ants (Moriya & Ichinose 1988; Moriya 1989) makes tridactyloids a potential source for the discovery of new medicinal drugs (Dettner, 2015). Similar uses could be explored in aposematic species, but toxicity and compounds have yet to be discovered. Adaptations for digging and for swimming could work as a source for bioinspiration. Siddall & Kovač (2014) discarded the use of pygmy mole crickets in bioinspired research that aimed to design aerial-aquatic platforms. However, this group of organisms could be explored as models for other areas of research.

Figures

FIGURE 1.1. Head in frontal view and habitus of Tridactyloidea crickets. a) Pygmy mole cricket (Tridactylidae), body length 8.1mm. b) Mud cricket (Ripipterygidae), body length 4.6mm. c) Sandgroper (Cylindrachetidae), body length 51 mm.


a. *Afrotridactylus koenigsmanni* Tridactylidae


b. *Mirhipipteryx columbiana columbiana* Ripipterygidae


c. *Cylindroryctes spegazzinii* Cylindrachetidae

FIGURE 1.2. Characteristic “three fingers” of Tridactyloidea. This feature is useful to identifiy individuals from other orthopterans. The look is due to a reduction of the tarsal segments into a single tarsus from the hind leg and the developed apical tibial spurs that display the distinctive look in the families Tridactylidae and Ripipterygidae.

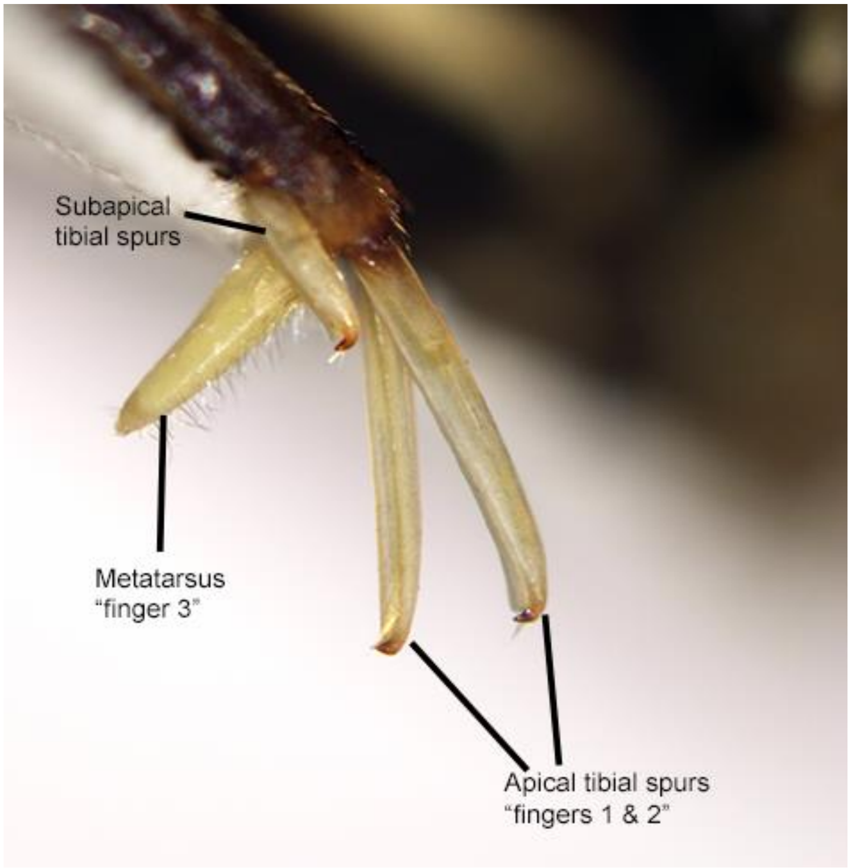
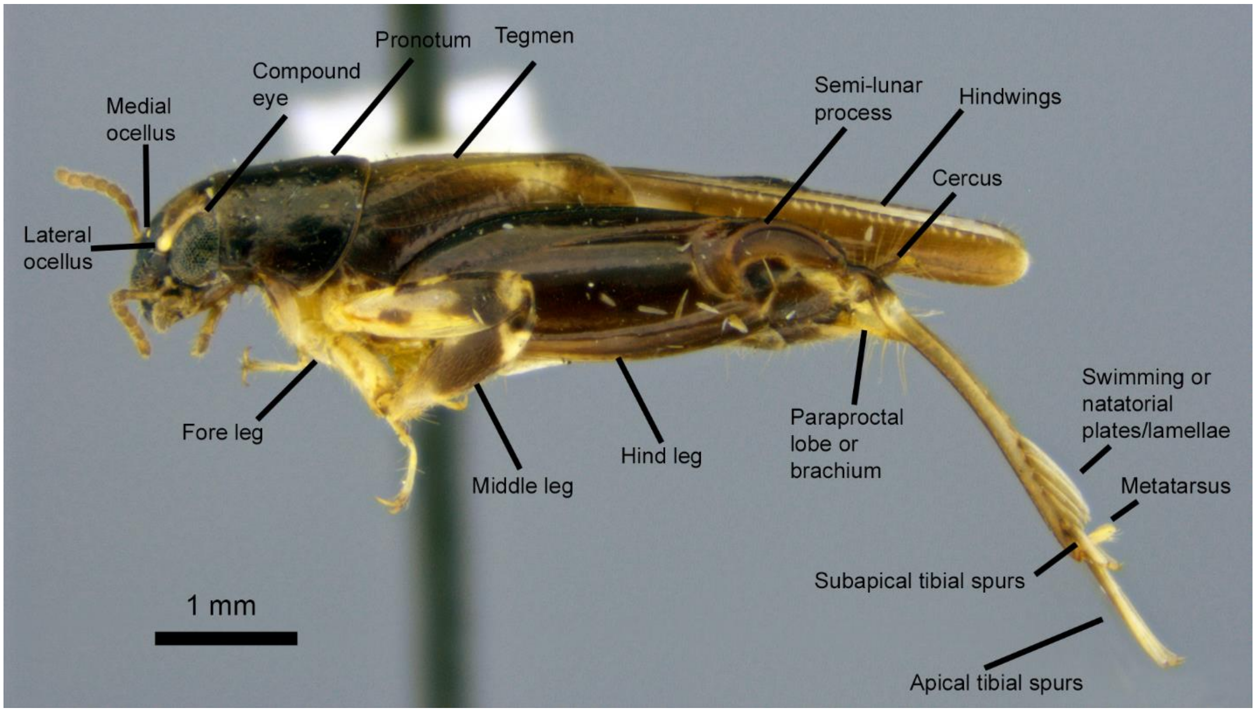


FIGURE 1.3. Habitus of *Afrotridactylus spiralatus* Günther, 1994 with terms used in morphology of Tridactyloidea.



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CHAPTER 2: FIRST RECORDS OF DENTRIDACTYLINAE (ORTHOPTERA: TRIDACTYLIDAE) FROM COLOMBIA, WITH DESCRIPTION OF TWO NEW SPECIES OF DENTRIDACTYLUS GÜNTHER[1]

Abstract

Two new species of *Dentridactylus* Günther (Orthoptera: Tridactylidae) are described and illustrated: *Dentridactylus quadratus* sp. nov. and *Dentridactylus truncatus* sp. nov. The new species represent the first record of the subfamily Dentridactylinae from Colombia and the second record for the Americas. Both come from the south of the country and are readily separated from congeners by their larger body size; *D. quadratus* sp. nov. is further delimited by the quadrate outline of the epiproct, and *D. truncatus* sp. nov. by the epiproct with lateral lobes and lateral margin of epiproct not indented. Keys for the identification of species in the Americas are provided.

Resumen

Se describen e ilustran dos nuevas especies de *Dentridactylus* Günther (Orthoptera: Tridactylidae): *Dentridactylus quadratus* sp. nov. y *Dentridactylus truncatus* sp. nov. Las nuevas especies corresponden el primer registro para la subfamilia Dentridactylinae en Colombia y el segundo en América. Ambas especies provienen del sur del país y se diferencian fácilmente de otras especies del género por ser de gran tamaño. Adicionalmente, *D. quadratus* sp. nov. se reconoce por el contorno cuadrado del epiprocto, y *D. truncatus* sp. nov. por los lóbulos laterales

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del epiprocto y la margen lateral del epiprocto sin hendidura. Se proveen claves taxonómicas para la identificación de especies en América.

Introduction

Pygmy mole crickets of the family Tridactylidae (Orthoptera: Caelifera) are small, highly specialized orthopterans restricted to moist habitats close to water sources such as lakes, ponds, rivers, and streams. They have a cosmopolitan distribution and, like many orthopteran groups, have their greatest diversity in the tropics (Cigliano *et al.* 2017). Tridactylids exhibit a number of morphological adaptations related to their fossorial and semiaquatic life histories, including modifications of the forelegs for digging (broadened protibiae, often with numerous spurs or spines), and in many species, the presence of metatibial lamellae used in swimming and jumping from the surface of water (Günther 1994; Burrows and Picker 2010). While the taxonomy and distribution of tridactylids has been studied extensively by Günther (1978, 1979, 1991, 1995), very little is known of their biology or ecology.

Dentridactylinae are a small subfamily comprising only 19 species in five genera (two of which are monotypic genera known from fossils). The subfamily is recognized by the well-developed metatarsus presenting a small but distinct subapical tooth (Günther 1979). This subfamily includes the fossil genera †*Burmadactylus* Heads, 2009 and †*Guntheridactylus* Azar & Nel, 2008, in addition to the extant genera *Bruntridactylus* Günther, 1979, *Dentridactylus* Günther, 1974, and *Paratridactylus* Ebner, 1943 (Günther 1979; Heads 2009). The distribution of dentridactylines is very unusual. *Bruntridactylus* (comprising 12 species) is the most species rich genus in the subfamily and also has the broadest distribution, occurring in Africa, the Middle East, Central and Southeast Asia, and the Indian subcontinent. In contrast *Dentridactylus* and *Paratridactylus* have much more restricted distributions, with *Dentridactylus* occurring in southernmost Africa, Australia, and South America, and *Paratridactylus* found only in tropical West Africa.

Dentridactylus is a rare genus hitherto with only four species: *D. albisignatus* Günther, 1978 and *D. keyi* Günther, 1978 from Australia; *D. raggei* Günther, 1986 from South Africa; and *D. denticulatus* (Saussure, 1874) from Brazil. The genus is readily distinguished from other dentridactyline genera by markedly shortened tegmina, the lack of hind wings, and the absence of metatibial lamellae or 'swimming plates' (Heads 2009). Here, I describe two new species representing the first records of the genus in Colombia.

Material and methods

We reviewed specimens from the entomological collection of the Instituto de Ciencias Naturales at the Universidad Nacional de Colombia. Male genitalia were dissected and preserved in vials of glycerine. Specimens were kept in 100% ethanol. Photographs and measurements were made using a Zeiss SteREO Discovery V.20 zoom stereo microscope and Zen (blue edition) software. Photographs of the phallic complex were taken using a Canon EOS 70D digital SLR attached to a Zeiss Axio Lab.A1 compound microscope. Images were stacked using Helicon Focus 6.5.1 Pro and edited in Adobe Photoshop CS5 version 12.0.4. Illustration were prepared in Adobe Illustrator CC 2015 version 19.1.0 (64-bit).

Taxonomy

Family Tridactylidae Brullé, 1835

Subfamily Dentridactylinae Günther, 1979

Genus *Dentridactylus* Günther, 1974

***Dentridactylus quadratus* sp. nov.**

Figure 2.1a-d

Holotype. Male (no. ICN 088003), COLOMBIA, Putumayo, Orito, Vda. Libano, predio UMIYAC 00°40'53.8"N, 077°02'07.2"W, 850 m, 8–14.iii.2003, Col. I. Giraldo, F. Quevedo y com. Indígenas Siona, Kofanes e Ingas. Colecta Winkle. Specimen preserved in alcohol; deposited at Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá.

Paratype. Female (no. ICN 093585) data as for holotype. Specimen preserved in alcohol; deposited at same institution as holotype.

Diagnosis. The new species can be distinguished by: [1] epiproct quadrate in outline, compact; and [2] distal margin of epiproct pointed, triangular.

Description. *Male* (holotype). Body length 7.0 mm; interocular distance 1.0 mm; pronotum length 1.5 mm, pronotum width 1.9 mm; tegmina length 1.0 mm; metatarsus 1.0 mm. (Figure 2.1a-d).

Head brown. Lateral carinae extended from the occiput towards but not reaching the compound eyes. Medial carinae on the top of the head extended along half-length of the coronal suture. Epicranial suture present. Lateral ocelli rudimentary. Medial ocellus absent, a small groove in its place. Labrum rounded. Maxillary palp with five segments; last segment bearing strong setae. Labial palp with three segments; last segment bearing strong, thick setae. Galea and lacinia elongate; lacinia heavily sclerotized and strong like a tooth; galea softer and flexible.

Antennae brown, 10-segmented. Scape wider and longer than pedicel. Flagellomere 1 longer than pedicel and flagellomere 2.

Thorax. Pronotum with patch of setae on both sides of anterior margin. Prosternum without lobe. Mesonotum (episternum) with a patch of setae. Tegmina short with subcostal vein thick. Alae absent. Prothoracic leg brown. Procoxa elongate, subquadrate, with few hairs along the inner margin. Protrochanter short. Inner margin of profemur with rows of hairs along the edges, external edge with longer setae. Protibia distally wider than basally, with three strong spines, and densely covered with two types of setae: one long and hair-like, and the other strong and spine-like. Protarsus with two tarsal segments; last segment with a pair of claws. Metathoracic leg brown, darker brown coxa, trochanter and femur, and lighter brown tibiae and tarsal segments. Metathoracic leg brown, trochanter absent; metafemur large, brown with a white vertical mark anterior to the semi-lunar process; inner carinae, ventral and dorsal edge of femur dark blackish-brown. Metatibia without lamellae, with two dorsal rows of 15 spines outer and 15 inner, a pair of short subapical spurs is present, the spurs are asymmetrical with the external spur short and the inner spur twice the size, with an inner apical group of setae. A pair of apical spurs with an inner apical group of setae are present; the spurs are twice as long as the inner subapical spurs. Metatarsus strong and as long as cerci, a terminal tooth and an outer subapical tooth are present followed by a row of minute teeth along the edge; inner dorsal edge with a row of densely clustered setae; ventral edge with one row of setae. Tip of spurs is reddish, tooth-like and the same reddish coloration is observed on the tibial rows of spines.

Abdomen brown. 10-segmented, segment 9 corresponding to the subgenital plate with rounded margin; segment 10 is merged with the terminalia. 10th tergum with medial membranous triangular groove, margin straight not extended and without lobes, a pair of setae is present near the posterior margin, each one in a corner of the membranous groove. Cerci two-segmented with setae. Brachium brown, cerci-like but shorter than cerci and covered with thicker setae. Brachium base densely covered with setae. Uncus 1-hooked. Epiproct compact, quadrate. Proximal margin almost straight, without invagination; distal margin of epiproct pointed, triangular with setae. Phallus membranous with spikes (Figure 2.2a).

Female. Body length 9.5 mm; interocular distance 1.1 mm; pronotum length 1.4 mm, pronotum width 2.0 mm; tegmina length 0.9 mm; metatarsus 1.1 mm (n=1).

Body similar to male, except for antennae brown. Scape wider than pedicel, similar length. Flagellomere 1 longer than pedicel. Flagellomere 2 shorter than flagellomere 1. Protibia distally extended with four strong spines, densely covered with thicker setae than male; two types of setae, one long and hair-like, the other strong and spine-like. Metatibia with two dorsal rows of 11 outer spines and 12 – 13 inner spines.

Abdomen brown. 10-segmented, segment 8 corresponding to the subgenital plate with rounded margin. 10th tergum with a medial membranous groove drop-shaped, margin slightly rounded; two pairs of setae are present near the posterior margin, each one in a corner of the membranous groove. Epiproct tongue-like with setae in distal margin.

Etymology. The specific epithet is from the Latin *quadratus* meaning “square” in reference to the shape of the compact, quadrate epiproct of the male.

Distribution. Known only from the type locality.

Remarks. The new species generally resembles other species in the genus. From the Australian species it is easily differentiated by the size (Table 2.1). Australian species are smaller, with males less than 5 mm (*D. quadratus* is 7 mm long). Moreover, the apex of the tegmen in *D. quadratus* is blunt (a character shared with the other new species from Colombia) whereas in the Australian species, the tegminal apex tends to be elongate and curved (especially elongated in *D. keyi*). The new species lacks white margins on the pronotum such as in *D. albisignatus* (pronotum with white marks on laterocaudal edges) and lacks a tooth or extended margin of tergite 10 such as in *D. keyi* (margin of tergite 10 with two tooth-like extensions). The female can be distinguished from *D. raggei* in the shape of the subgenital plate that does not protrude apically. From *D. denticulatus* (the Brazilian species) it is distinguished by the shape of the epiproct, the lateral margin of which is without indentation in *D. quadratus.*

***Dentridactylus truncatus* sp. nov.**

Figure 2.3a-d

Holotype. Male (no. ICN 087977), COLOMBIA, Amazonas, PNN Amacayacu, Matamata, 3°23'S, 70°06'W, 150 m, M1123. 17.xii–2.i.2000, Col. A. Parente Leg. Specimen preserved in alcohol; deposited at Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá.

Paratypes. Three specimens from same locality as holotype: (1) Male (no. ICN 093583) specimen preserved in alcohol; (2) Female (no. ICN 087911) 3°23'01"N, 70°06'01"W, 300 m, 6–12.vii.2000. A Parente Nat. specimen preserved in alcohol; (3) Female (no. ICN 093584)

3°23'01"N, 70°06'01"W, 300 m, 6–12.vii.2000. A Parente Nat. specimen preserved in alcohol. Specimens deposited at same institution as holotype.

Diagnosis. The new species can be distinguished by the following combination of characters: [1] Epiproct with lateral lobes [2] lateral margin of epiproct concave, not indented

Description. *Male* (holotype). Body length 6.2 mm; interocular distance 0.9 mm; pronotum length 1.3 mm, pronotum width 1.7 mm; tegmina length 0.9 mm; metatarsus 0.7 mm. (n=1) (Figure 2.3a-d).

Head brown. Lateral carinae extended from the occiput to the compound eyes without reaching the eyes. Medial carinae on the top of the head extended along half the length of the coronal suture. Epicranial suture present. Lateral ocelli rudimentary. Medial ocellus absent, a small groove in its place. Labrum rounded. Maxillary palp with five segments, last segment with strong setae. Labial palp with three segments, last segment with strong thick setae. Galea and lacinia elongate; lacinia heavily sclerotized and strong like a tooth; galea softer and flexible.

Antennae brown. 10-segmented. Scape wider and longer than pedicel. Flagellomere 1 longer than pedicel and flagellomere 2.

Thorax. Pronotum with patch of setae on both sides of anterior margin. Prosternum without lobe. Mesonotun (episternum) with a patch of setae. Tegmina short with subcostal vein thick. Alae absent. Forelegs brown, elongated coxa subquadrate with few hairs in the inner margin. Protrochanter short. Profemur inner margin with rows of hairs in the edges, external edge with longer setae. Protibiae distally extended with three strong spines, and densely covered with what it seems two types of setae, one long hair-like and the other strong spine-like. Protarsi with two tarsal segments; last segment with a pair of claws. Middle leg missing, brown coxa. Hind leg brown, trochanter absent; femur large, brown with a white vertical mark, anterior to the semi-lunar process; inner carinae, ventral and dorsal edge of femur dark black-brownish. Metatibia without swimming plates, with two dorsal rows of 12–13 spines outer and 12 inner, a pair of short subapical spurs is present, the spurs are asymmetrical with the external spur short and the inner spur twice the size, with an inner apical patch of setae. A pair of apical spurs with an inner apical group of setae are present; the spurs are twice longer than the inner subapical spurs. Metatarsi strong and as long as cerci, a terminal tooth and an outer subapical tooth is present followed by a row of minute teeth along the edge; inner dorsal edge with a row of setae clustered; ventral edge with one row of setae. The tip of spurs is reddish tooth-like and the same reddish coloration is observed in tibial rows of spines.

Abdomen. Brown. 10-segmented, segment 9 corresponded to the subgenital plate with rounded margin; the segment 10 is merged with the terminalia. Tergum 10th with a medial membranous groove drop-like, margin curved not extended or without lobes, a pair of setae is present near the posterior margin, each one in a corner of the membranous groove. Cerci two-segmented with setae. Brachium brown, cerci-like but shorter than cerci and covered with thicker setae. Brachium base densely covered with setae. Uncus 1-hooked. Epiproct with lateral lobes. Proximal margin with deep invagination, distal margin of epiproct triangular with setae. Phallus membranous without spikes (Figure 2.2b).

Male variation. Body length 6.2 mm; interocular distance 0.9 mm; pronotum length 1.2–1.3 mm, pronotum width 1.7 mm; tegmina length 0.8–0.9 mm; metatarsus 0.7–0.9 mm. (n=2). Metatibia with two dorsal rows of 11–13 spines outer and 10–12 inner.

Female. Body length 7.5–8.1 mm; interocular distance 0.9–1.0 mm; pronotum length 1.3–1.4 mm, pronotum width 1.8–2.0 mm; tegmina length 0.8–1.0 mm; metatarsus 0.9–1.0 mm. (n=2). Body similar to male, except for antennae brown and thinner. Foreleg tibiae distally extended with four strong spines, densely covered with thicker setae than male; two types of setae, one long hair-like and the other strong spine-like. Hind leg tibia with two dorsal rows of 11–14 spines outer and 13–14 inner. Abdomen brown. 10-segmented, segment 8 corresponded to the subgenital plate with rounded margin. Tergum 10th with a medial membranous groove drop-like, margin slightly projected rounded, 1–2 pairs of setae are present near the posterior margin, each one in a corner of the membranous groove; brown small mark at the margin of the tergum. Epiproct tongue-like with setae in distal margin, brown coloration at edges, with large triangular hyaline area.

Etymology. The specific epithet is from the Latin *truncatus* meaning “shortened” in reference to the truncate tegminal apex.

Distribution. Known from the type locality and from Leticia (also Amazonas).

Remarks. The new species is similar to other species of the genus in external morphology. However, it is distinguished from *D. albisignatus* by having a brown pronotum without white markings; from *D. keyi* by having the margin of tergite 10 entire, without tooth-like extensions. The new species differs from *D. denticulatus* by having the lateral margin of the epiproct entire, not indented. From *D. raggei* the females can be distinguished by the margin of the subgenital plate that is smoothly curved, and not produced apically. In common with *D. quadratus*, *D. truncatus* exhibits greater overall size than Australian species and the apex of the tegmen is blunt. However, *D. truncatus* differs from *D. quadratus* in the shape of the male epiproct which bears lateral lobes and is less square-shaped. In addition, male tergite 10 is straight in *D. truncatus* and curved in *D. quadratus.* Female epiproct coloration is different between Colombian species. It is lighter in *D. truncatus* (Figure 2.4b) having a triangular mid-hyaline area with brown coloration at the edges, yet is darker and more homogeneously brown in

D. quadratus (Figure 2.4a). Female antennomere 6 is longer than the scape and pedicel together in *D. truncatus* and shorter in *D. quadratus.*

Key to species of *Dentridactylus* of the Americas

1 Apex of the tegmen blunt (Figure 2.5). Male lateral margin of epiproct not indented. Larger size species. Male body length > 6 mm and female body length > 7.5 mm…...… 2

(1) Apex of the tegmen slender and rounded (Günther 1974: ABB. 31). Male lateral margin of epiproct indented. Medium to smaller size species. Male body length < 6 mm and female body length < 7 mm................…....…..……. ***D. denticulatus*** **(Saussure, 1874)**

2 Male epiproct with lateral lobes, lateral margin of epiproct concave (Figure 2.6a). Male tergite 10 is straight. Female epiproct coloration is lighter with a triangular mid-hyaline area with brown coloration at the edges (Figure 2.4b). Female antennomere 6 is longer than scape and pedicel together.…………………………………...…. ***D. truncatus*** **sp. nov.**

(2) Male epiproct compact (without lateral lobes), and quadrate in outline; lateral margin of epiproct convex (Figure 2.6b). Male tergite 10 is curved. Female epiproct coloration is darker and homogeneously brown (Figure 2.4a). Female antennomere 6 is shorter than scape and pedicel together…... ***D. quadratus*** **sp. nov.**

Discussion

Dentridactylus species are tiny and do not reach sizes greater than 10 mm. The new species described here are the largest in the genus. External morphology is very similar between species. Thus, characters for the identification of species are mostly from the terminalia. The terminalia are very important for identification of species in other families and subfamilies of

Tridactyloidea where modifications of the paraproct, epiproct and subgenital plate varies from species to species (Günther, 1969; Heads 2009). In *Dentridactylus* there is no great variation of the paraproct or male subgenital plate. Instead species identification relies on the shape of the male epiproct. In contrast to most other tridactyloid taxa, the phallic complex, being entirely membranous, is of limited use taxonomically. The shape of the phallic complex changes considerably between specimens due to dehydration, further limiting its utility. Female identification in *Dentridactylus* relies on the morphology of the subgenital plate and wings. Here, we also use the relative length of antennomeres and coloration of the female epiproct.

Acknowledgments

We are grateful for access to specimens and assistance provided by Carlos E. Sarmiento and Fernando Fernandez at the Instituto de Ciencias Naturales, Universidad Nacional de Colombia. A visit to the Muséum d'histoire naturelle de Genève to study the type specimen of *D. denticulatus* was funded by a Dissertation Travel Grant from the Graduate College of the University of Illinois at Urbana-Champaign (awarded to N.B.B.). We are grateful to Peter Schwendinger and John Hollier for their assistance during the visit.

Table and Figures

TABLE 2.1. Body length (bl) for species of *Dentridactylus* in millimeters (mm).

Species	**Author**	**Male (bl)**	**Female (bl)**	**Reference**
D. albisignatus	Günther, 1978	3.11	4.44	(Günther 1978)
D. denticulatus	(Saussure, 1874)	5.5	6.9	(Günther 1974)
D. keyi	Günther, 1978	4.88		(Günther 1978)
D. quadratus		7	9.5	
D. raggei	Günther, 1986		6.22 (6.35–7.4)	(Günther 1986)
D. truncatus		6.16–6.17	7.58–8.05	

FIGURE 2.1. *Dentridactylus quadratus*, sp. nov. holotype male. Copyright © 2018 Magnolia Press. a) Habitus in dorsal view. b) Habitus in ventral view. c) Subgenital plate in ventral view. d) Terminalia in dorsal view.

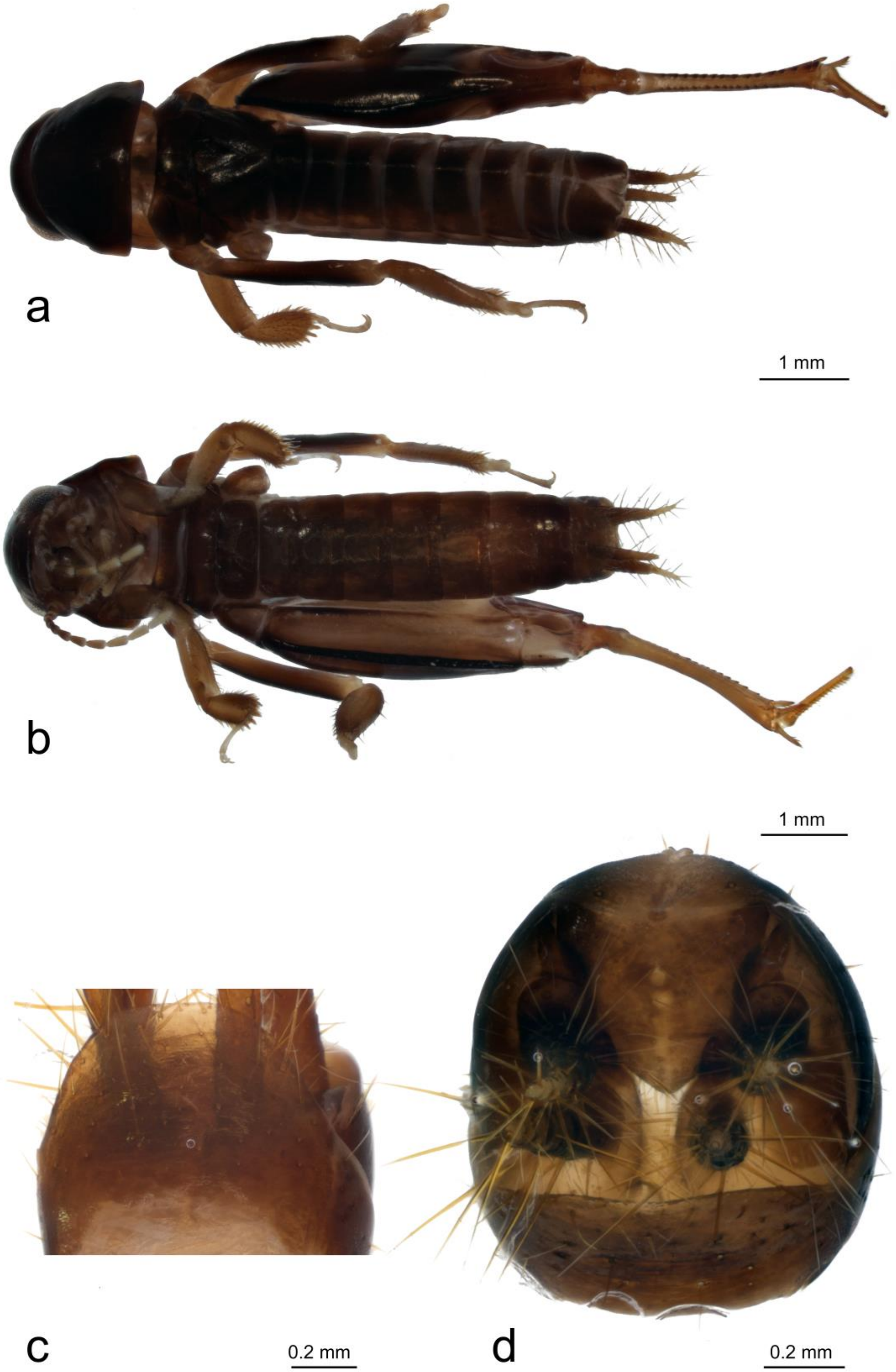


FIGURE 2.2. Phallic complex. Copyright © 2018 Magnolia Press. a) *Dentridactylus quadratus*, sp. nov. holotype. b) *Dentridactylus truncatus*, sp. nov. paratype.

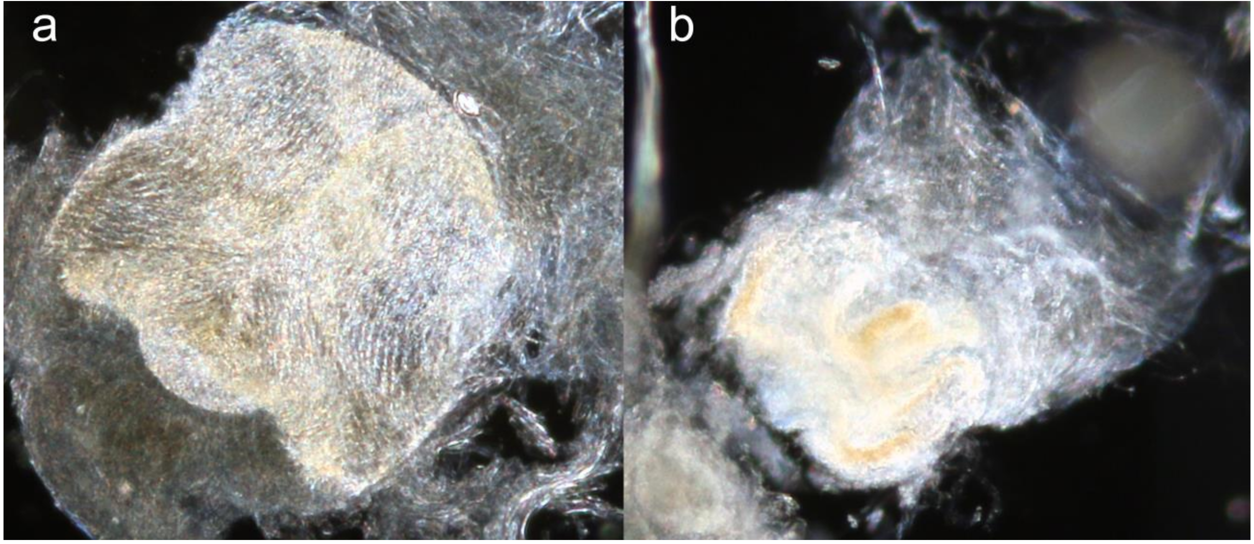


FIGURE 2.3. *Dentridactylus truncatus*, sp. nov. holotype male. Copyright © 2018 Magnolia Press. a) Habitus in dorsal view. b) Habitus in ventral view. c) Subgenital plate in ventral view. d) Terminalia of paratype male in dorsal view.

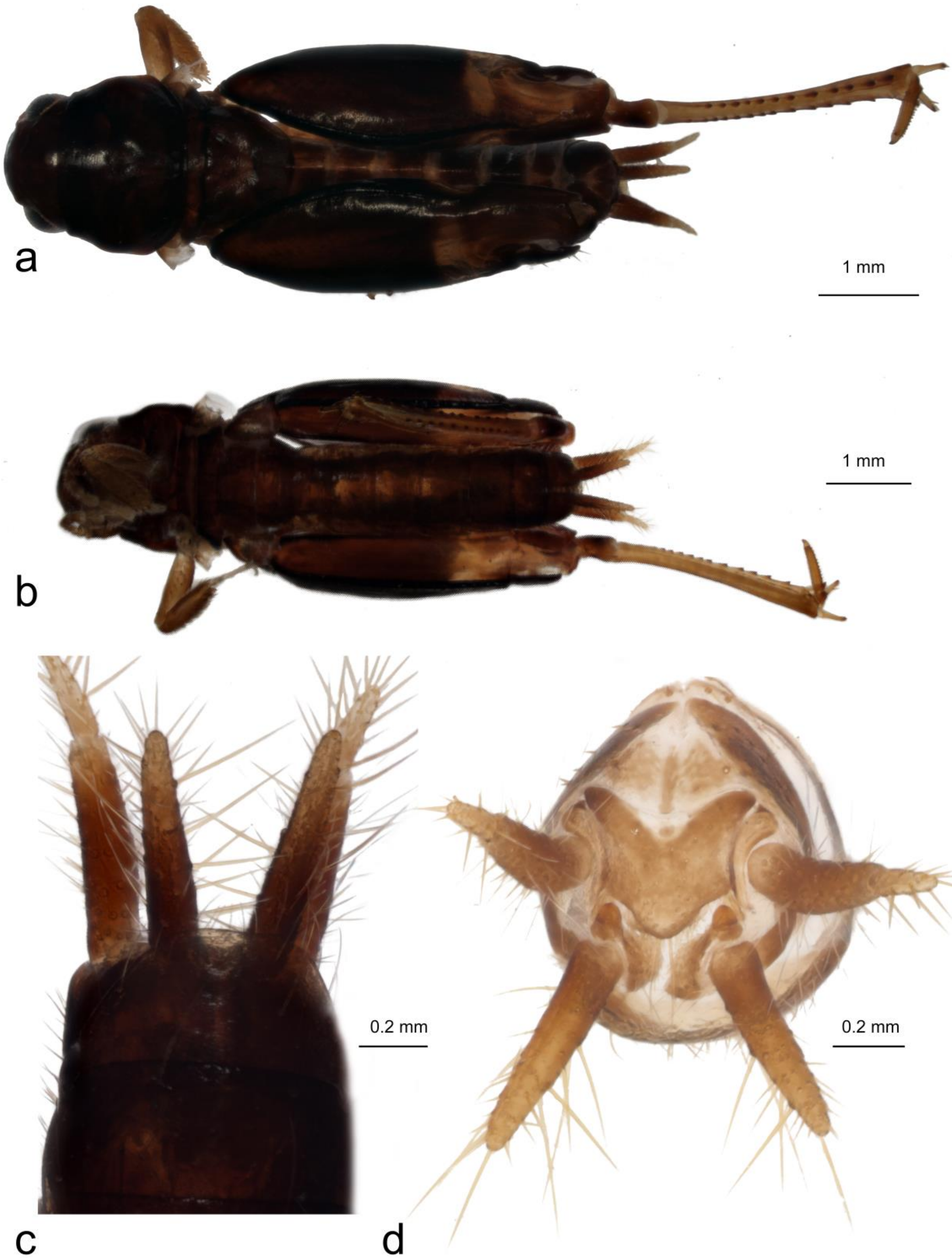


FIGURE 2.4. Dorsal view of female terminalia. Copyright © 2018 Magnolia Press. a) *Dentridactylus quadratus*, sp. n. b) *Dentridactylus truncatus*, sp. n.

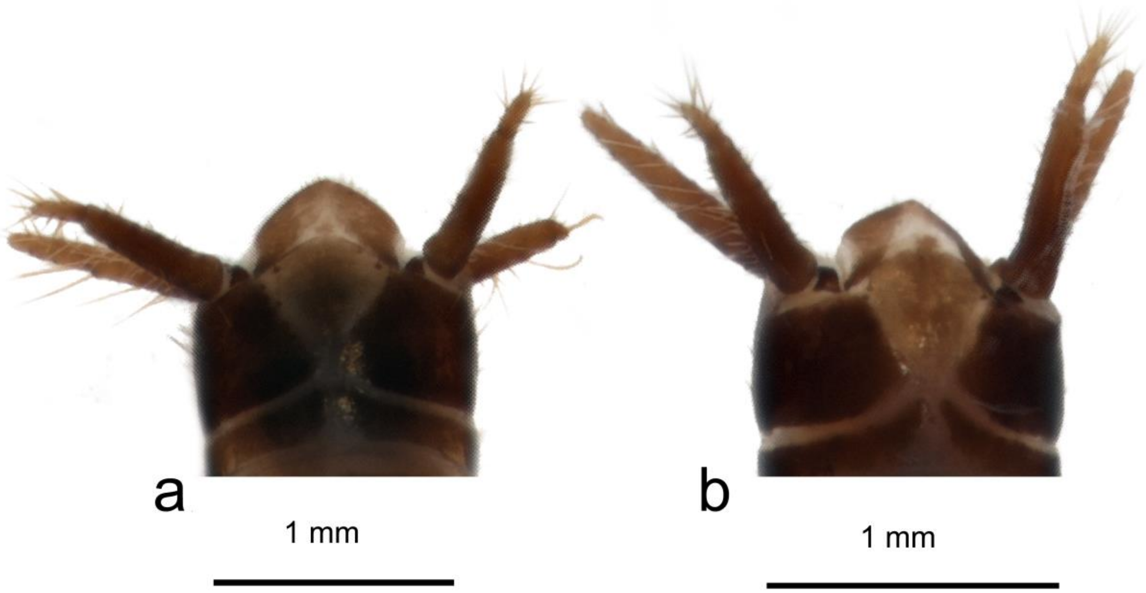


FIGURE 2.5. Dorsal view of blunt tegmina *Dentridactylus truncatus,* sp. n. Copyright © 2018 Magnolia Press.

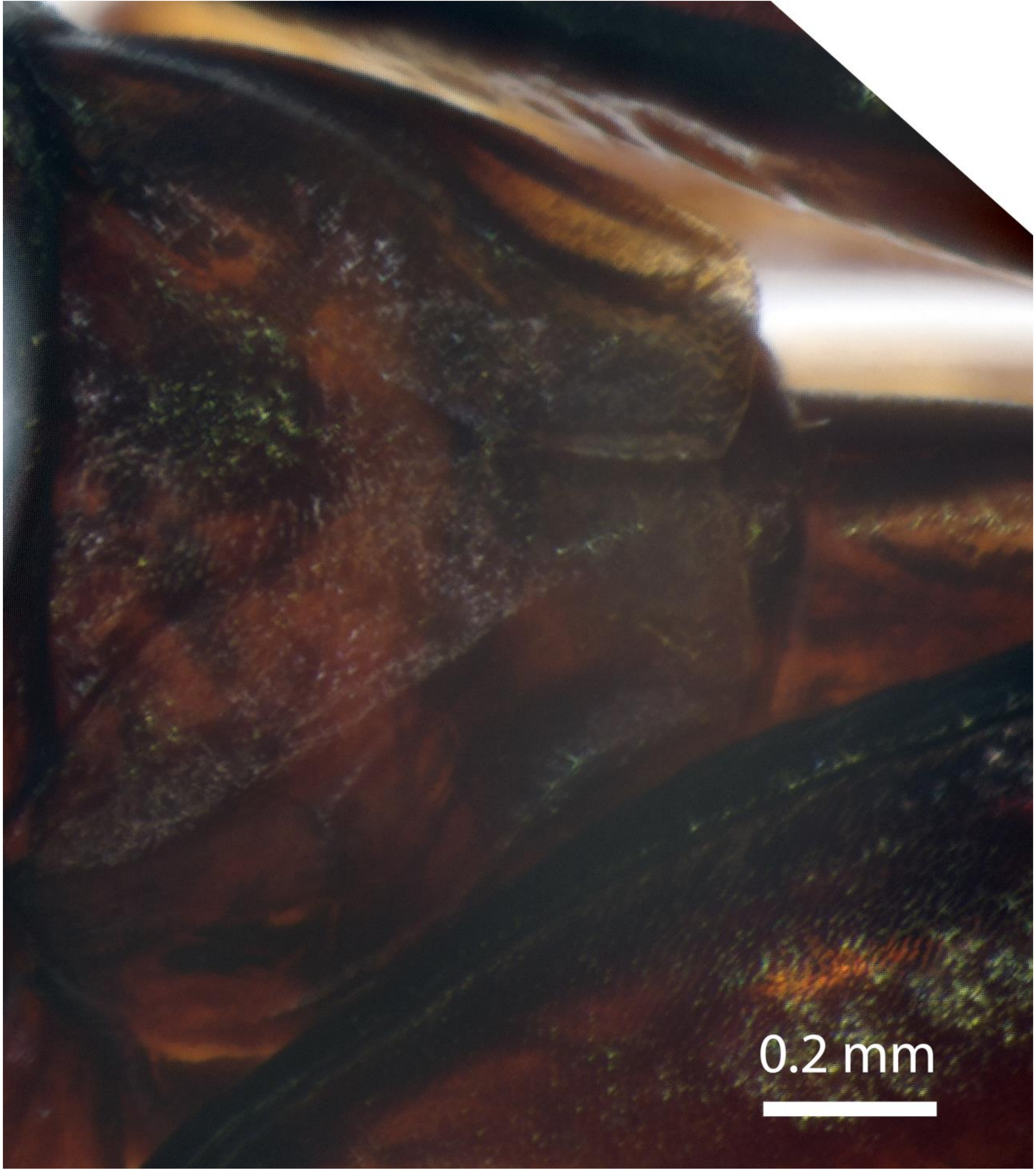
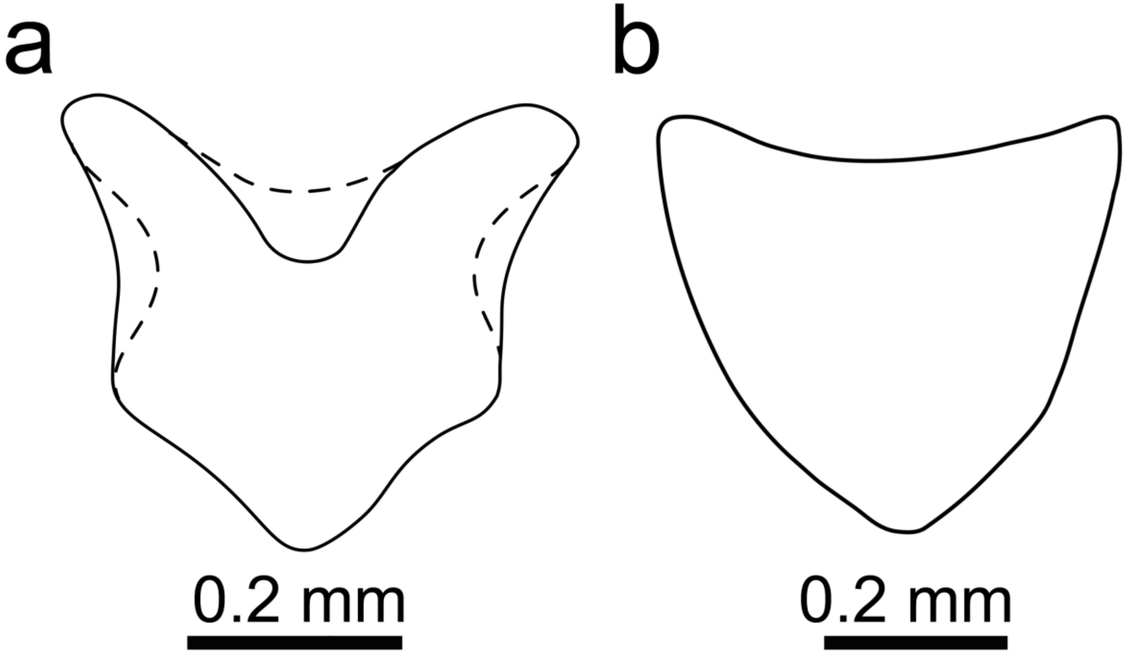


FIGURE 2.6. Illustrations of male epiproct. Copyright © 2018 Magnolia Press. a) *Dentridactylus truncatus,* sp. n. b) *Dentridactylus quadratus*, sp. n.



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CHAPTER 3: COMMENTS ON THE NEGLECTED NYMPHS OF MUD CRICKETS IN THE GENUS *MIRHIPIPTERYX* (CAELIFERA: TRIDACTYLOIDEA: RIPIPTERYGIDAE)[2]

Abstract

Mud crickets (family Ripipterygidae) comprise a small family of orthopterans distributed throughout much of the Neotropics, but knowledge of this groups' biology, ecology and distribution remains poor in comparison to most orthopteran taxa. Here we review the state of knowledge of nymphs in the genus *Mirhipipteryx* Günther 1969 and report the genus from Belize for the second time in 86 years. Because information about nymphs in this family is so scarce and nymphs are often neglected in species descriptions, we include comments on the coloration of nymphs for *Mirhipipteryx pulicaria* (Saussure 1896). Caution is suggested for the use of adult characters for the identification of immature stages in the group. Nymphs of *Mirhipipteryx pulicaria pulicaria* are similar in coloration patterns to the adults, but lighter. *Mirhipipteryx lobata* Günther 1977 is designated a *nomen nudum*.

Introduction

Mud crickets are small (<2.5 cm) insects of the family Ripipterygidae (Orthoptera: Caelifera: Tridactyloidea). The family is Neotropical (Cigliano *et al.* 2017), mostly occurring near freshwater habitats, such as streams, lakes, ponds, sandy banks, and floodplain areas (Günther 1994; Baena-Bejarano 2015). The diversity and distribution of this group in Central

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America is poorly known (Heads & Taylor 2012; Cadena-Castañeda & Monzon-Sierra 2014). In Belize, the family Ripipterygidae is represented by *Mirhipipteryx hubbelli* Günther 1969 and *Ripipteryx mopana* Heads & Taylor 2012; the first recorded by Günther (1976) from a sample that was collected in 1932 and the most recent recorded in 2012.

The earliest known mud crickets were described by Newman in 1834. He established the genus *Ripipteryx* for a single species, *Ripipteryx marginata* Newman 1834. The first significant taxonomic changes in this family took place from the 1960's to the early 1990's (Günther 1962, 1963, 1969, 1970, 1976, 1989, 1994). As a result of this body of work, mud crickets are placed in their own family, Ripipterygidae, including the genera *Ripipteryx* and *Mirhipipteryx.* Günther (1969) proposed groups of species within both genera using morphological characters, mostly based upon the last abdominal segment, genitalia and coloration. New species descriptions were subsequently added (Heads 2010a, b; Heads & Taylor 2012; Baena-Bejarano & Heads 2015) and a systematic reexamination of the classification of the Ripipterygidae is presently underway. Here, we review the knowledge of nymphs of the genus *Mirhipipteryx* and described nymphal characters for *M. pulicaria* (Saussure 1896).

Materials and Methods

We reviewed the literature on *Mirhipipteryx* looking for notes or comments on eggs and nymphs/larvae. We screened samples of orthopterans collected from cave expeditions in the Toledo District of southern Belize during the years 2011, 2012 and 2014. This material contained ten specimens of *Mirhipipteryx*, all collected in 2012 (Figure 3.1). The specimens were collected into alcohol by hand at a lighted white sheet at night or by searching shaded streamside habitats during the day. Adult male terminalia were dissected in alcohol to extract the genitalia and cleared as needed using 5–10% KOH. Terminalia and genitalia were placed in micro vials with glycerin, and are stored in association with the rest of the dissected specimen. Measurements were taken using a Zeiss Microscope with Zen ©2012 (blue edition) software. Photographs were stacked with Helicon focus 6.5.1 pro ©2015. Drawings were completed in Adobe Illustrator CS5 version 15.0.2 ©2010 and images were optimized with Adobe Photoshop CS5 version 12.0.4, ©2010. Species were compared against type specimens of *M. pulicaria pulicaria* and *M. pulicaria interposita* during visits to, and photographs from, the Academy of Natural Sciences of Drexel University (ANSP), the Insect Division, Museum of Zoology, University of Michigan (UMMZ), and the Museum of Natural History, Geneva (MHN). Comparison of color patterns of adults and nymphs is based on a dorsal view.

Material examined

Nymph 1. (INHS Insect Collection 814,924), Belize, Toledo District, Bruno's Ranch W of Dump, E of Mafredi: 25.3 km NW of Punta Gorda, Field # SWH2012-BZ 007, Notebook page 24, 29 April 2012, Col. SWHeads, SJTaylor, J.Jacoby, AEBeveridge, GBHoese, JKKrejca, KDHager, Sample# 268, BelizeProject BZ-1569. Specimen preserved in alcohol.

Nymph 2. (INHS Insect Collection 814,925), Belize, Toledo District, Rio Grande, ford near Bat Cave: 27.9 km NNW of Punta Gorda, 4 May 2012, sjt12-029, SWHBZ013, Col. SJTaylor, SWHeads, Sample# 375, BelizeProject BZ-1514. Specimen preserved in alcohol.

Adults. 8 specimens from Belize, Toledo District, Rio Grande, ford near Bat Cave: 27.9 km NNW of Punta Gorda, 4 May 2012, sjt12-029, Col. SJTaylor, SWHeads, Sample# 425, BelizeProject BZ-1524. Specimen dried and pinned; (1) ♂ (INHS Insect Collection 814,774), SWHBZ013, Sample# 375, BelizeProject BZ-1515. Specimen preserved in alcohol; (2) (INHS

Insect Collection 814,776), SWHBZ013, Sample# 375, BelizeProject BZ-1508. Specimen preserved in alcohol; (3) ♂ (INHS Insect Collection 814,777), SWHBZ013, Sample# 375, BelizeProject BZ-1509. Specimen preserved in alcohol; (4) ♂ (INHS Insect Collection 814,778), SWHBZ013, Sample# 375, BelizeProject BZ-1510. Specimen preserved in alcohol; (5) ♀ (INHS Insect Collection 814,779), SWHBZ013, Sample# 375, BelizeProject BZ-1511. Specimen dried and pinned; (6) ♀ (INHS Insect Collection 814,780), SWHBZ013, Sample# 375, BelizeProject BZ-1512. Specimen preserved in alcohol; (7) ♀ (INHS Insect Collection 814,781), SWHBZ013, Sample# 375, BelizeProject BZ-1513. (8) ♂ (INHS Insect Collection 814,775), SWHBZ014. All specimens are deposited at the Insect Collection of the Illinois Natural History Survey (INHS), Prairie Research Institute, University of Illinois, Champaign IL.

Results

Nymphs of mud crickets are poorly known in the literature (Table 3.1). The records are restricted to the number of specimens observed in entomological collections with their label data, but no details have been published regarding their morphology. The species which include nymphs as paratypes do not contain descriptions of characters specific to the nymphs. However, Günther (1994) noted that Wille's metatibial organ (Wille 1923,1924), which is present in adults, is not completely developed in nymphs. The only allusion to the ecology of nymphs was found in the same paper, suggesting that the nest built in the sand could help control environmental conditions for the development of nymphs.

Nymphs

Nymph 1 (INHS Insect Collection 814,924): Body similar to adult male and female, except: interocular distance almost half the eye width; antennae with 9 antennomeres; scape and pedicel white with ventral brown dark coloration; flagellomeres 1–5 white; flagellomere 6 white basally and brown distally, flagellomeres 7 and 8 light brown coloration; maxillar palp brown; wing pads thick with hairs along dorsal margin; hind wing pads without obvious transverse groove; abdominal sexual structures not completely developed; abdominal sternite 10 acuminate posteriorly; paraproctal lobes thick, strongly thickened at the base.

Nymph 2 (INHS Insect Collection 814,925) (Figure 3.2c): Body similar to adult male and female, except: Interocular distance almost half the eye width; antennae with 9 antennomeres; pedicel shorter than first flagellomere; flagellomeres 2 and 3 shorter than more distal flagellomeres; scape and pedicel white coloration; flagellomeres 1–6 white, flagellomere 6 darker beige, flagellomeres 7 and 8 light brown coloration; maxillary palp brown; wing pads thick with hairs along dorsal margin; hind wing pads without obvious transverse groove; abdominal sexual structures not completely developed; developing valves visible in ventral view; subgenital plate smooth, without distal notches, posterior margin concave medially.

Adults

Male. Body length including wings 4.08 mm, excluding wings 3.85 mm; pronotum length 1.00 mm, pronotum width 1.23 mm; tegmina length 1.27 mm; hind wings length 2.50 mm; mesofemur length 1.28 mm, metafemur length 2.19 mm; interocular distance 0.13 mm. (n=1) (Figure 3.2a, 3.3).

Head. Interocular distance less than half the eye width; median ocellus fully developed, smaller than lateral ocelli; white anterodorsal patch around compound eyes; internal margin of compound eyes convergent dorsally; maxillary palp black, five segmented, with second segment reduced; labial palp brown; gena below the compound eye and antennae insertion white with a brown inferior border. Antennae brown and filiform, with 10 antennomeres; scape wider than pedicel; pedicel as long as first flagellomere; flagellomeres 1 and 2 shorter than other flagellomeres; dorsodistal white spot on scape, in lateral view the white coloration covers the dorsal half and distal fourth of scape; dorsodistal white spot on pedicel; white dorsodistal spot on flagellomeres 1, 2, 3, 4; flagellomere 5 dorsally white, flagellomere 6, 7 and 8 brown coloration.

Thorax. Pronotum brown, mottled appearance with a mix of black, brown and gray; mottled black on anterior half of the pronotum; median line gray. Mesonotum gray; tegmina black with brown edge and spotted medially gray; hind wings with white, transverse groove; procoxa brown; profemora brown with a white line on inner and outer margin; protibiae brown with two distal spines and an anterior external white rounded spot close to tibiae-femora articulation; mesocoxa brown; mesotrochanter brown; mesofemora anteriorly black and distally brown; mesotibiae anteriorly black and distally brown; metafemora with a dorsal and ventral black coloration, ventral white spot in the corner before groove, brown mid area; semi-lunar process black; metatibia brown; metatarsi brown and shorter than metatibial posterior spurs.

Abdomen. Cerci unsegmented, brown; brachium brown, fusiform in lateral view; brachium spine present; epiproct rectangular, superior external pointed tip and slightly folded anteriorly; medial epiproct (distal section) anchor-like; uncus with a single hook, not embedded in base of brachium (Figure 3.3b). Male subgenital plate margin rounded; setae present in the middle of the subgenital plate, and two setae on the lateroposterior edge, one in each side; basal plate heavily sclerotized, long, basally sub-parallel and distally strongly split in two long and slender apodemes (Figure 3.3d); cingulum with apodemes elongate and well-sclerotized; sclerotized region of cingulum discontinuous with a distal membranous region in-between; virga very slender; virga extended beyond cingulum (Figure 3.3d), S-shaped.

Male variation. Body length including wings 3.81–4.45 mm, excluding wings 3.69–4.42 mm; pronotum length 0.86–1.00 mm, pronotum width 1.17–1.24 mm; tegmina length 1.22–1.49 mm; hind wings length 2.34–2.95 mm; interocular distance 0.13–0.17 mm. (n=5). Body similar to male, except for the following traits: Antennae: pedicel sometimes dorsally white coloration; flagellomere 1 sometimes dorsally white, flagellomere 3 with 1/4 basal area brown, flagellomere 4 sometimes dorsally white, flagellomere 6 dorsobasal white and distally brown coloration; setae sometimes absent in the middle of the subgenital plate.

Female. Body similar to male, except for abdominal sexual structures (Figure 3.2b). Antennae: flagellomere 5 completely white; subgenital plate smooth with two distal notches forming tips in a concave lobe in middle (Figure 3.3a).

Female variation. body length including wings 4.31–4.45 mm, excluding wings 4.15–4.45 mm; pronotum length 0.967–1.10 mm, pronotum width 1.33–1.38 mm; tegmina length 1.55–1.62 mm; hind wings length 2.84–3.03 mm; mesofemur length 0.94–1.18 mm, metafemur length 2.32–2.57 mm; interocular distance 0.17–0.18 mm. (n=3). Antenna: antenna sometimes has white coloration only on the dorsolateral side of scape; sometimes pedicel brown without white coloration; flagellomere 1 sometimes dorsally white or distal and basally white with a darker medial area, flagellomere 2 sometimes brown, flagellomere 3 with 2/4 or ¾ basal area brown, flagellomere 5 completely white, or sometimes brown ventrally, flagellomere 6 dorsobasal light brown coloration.

Discussion

The state of knowledge of nymphs in the genus *Mirhipipteryx* consists mostly of records of individuals in collections, with no research having been devoted to the biology or natural history of these life stages. Here, we link nymphs of the group with their adults, but further data is required to fill this gap. *Mirhipipteryx pulicaria pulicaria* from Belize has the same coloration patterns for adult male and females, and for nymphs (Figure 3.2). There is intraspecific variation within darker and lighter spots, but a general pattern is observed in all stages. The lighter colors of nymphs could be due to lesser sclerotization, freshly molted individuals, but color polyphenism is known in orthopterans, and highly studied species such as *Schistocerca gregaria* (Forskål 1775) have shown color variation differences due to humidity (Pener 1991), crowded conditions, and visual stimuli (Maeno & Tanaka 2007; Tanaka *et al.* 2016). Moreover, we found that nymphs have wider interocular distance than adults (Table 3.2). The interocular distance is a diagnostic character for the genera in this group; therefore, knowledge of this variation is important for taxonomic purposes. This implies that the use of interocular distance is useful in adults, but should be used with caution in nymphs. Rather, other characters should be considered, such as the length of the metatibial spurs and the metatarsus for generic assignment.

Remarks on *M. pulicaria pulicaria*

The specimens studied from Belize are in the group of species *"peruviana-pronotopunctata*" *sensu* Günther (1969) based on the uncus being strongly curved downward and with a simple hook. *Mirhipipteryx pulicaria pulicaria* from Belize is typical of this subspecies from elsewhere in the coloration pattern, and differs from *M. pulicaria interposita* in having fewer darker (black and brown) areas on the pronotum. However, *M. pulicaria pulicaria* from

Belize is darker in antennal coloration, has white coloration restricted to the scape, pedicel and flagellomeres 1–5, sometimes 6, and flagellomeres 7 and 8 completely brown. Meanwhile *M. pulicaria interposita* has completely white flagellomeres 6–7 and *M. pulicaria pulicaria* has white spots from 1–6, and sometimes 7.

In reviewing the Belizean specimens, we found that the virga of the male extends beyond the membrane, whereas the original description of the species mentions that the virga does not reach the membrane in *M. pulicaria pulicaria* and *M. pulicaria interposita*. However, after reviewing the paralectotype of *M. pulicaria pulicaria* the MHN, we found the virga extending beyond the membrane. All subspecies of *M. pulicaria* and Belizean individuals share identical phallic complex shape; the margin of the female subgenital plate is similar in shape between the two subspecies with only slight differences in length of teeth, with females from Belize. and *M. pulicaria interposita* more alike in this character. However, in terms of pronotum coloration *M. pulicaria pulicaria* types and *M. pulicaria pulicaria* from Belize are more alike. Because we did not find any other characters from the terminalia or genitalia to differentiate these subspecies, in addition to a small sample size, we elected not to erect a new subspecies for the Belize specimens, anticipating that future research should shed more light on the potential status of subspecies.

Mirhipipteryx lobata **Günther 1977 designation as a** ***nomen nudum***

Mirhipipteryx lobata Günther 1977 is considered here a *nomen nudum.* This species name was first published by Otte (1997) in the Orthoptera Species File (volume 6). The author cited Günther (1977) as the reference for the species description with the type located in “San Francisco H.” However, the paper attributed for the description (Günther 1977) does not include a description for this species. Instead the paper includes the description of *Mirhipipteryx lilo granchacensis* Günther 1977, with the type at the Instituto M. Lilo in Tucuman, Argentina. Subsequent species lists (Günther 1980, 1989) made by the same author, to whom this species was attributed, do not include any mention of *M. lobata*. Moreover, a search for the type species at the Californian Academy of Science (CAS) using online database did not reveal any specimen with this name. The search for type specimens at CAS resulted in the species *Mirhipipteryx lilo* (which is the subspecies *M. lilo lilo* Günther 1969) and *M. disparilobata* Günther 1989. Most likely, this species name came from an unintentional editing error by Otte (1997). In conclusion, this species name does not conform to Article 13 of the International Code of Zoological Nomenclature (ICZN) by not having a type or a written description.

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Tables and Figures

TABLE 3.1. Literature records for nymphs of *Mirhipipteryx*. Numbers on nymphs in comments represents the count of individual nymphs in the literature with the country record. No records of eggs where found for this genus. symbol *†* denotes fossil.

List of species	**Subspecies**	**Author, year**	**Nymph comments**
†M. antillarum		Heads 2010	No data (fossil in amber)
M. acuminata		Günther 1969	No data
M. andensis		Günther 1969	4 Bolivia (Günther 1989)
M. biloba	*M. biloba aberrans*	Günther 1989	7 nymphal paratypes Costa Rica (Günther 1989)
M. biloba	*M. biloba biloba*	(Hebard 1928)	No data
M. biloba	*M. biloba chiriquensis*	Günther 1969	21 Panama (Topotype Günther 1989)
M. biloba	*M. biloba incurvata*	Günther 1989	2 paratype nymphs, Costa Rica (Günther 1989)
M. biloba	*M. biloba riofriensis*	Günther 1969	4 Colombia (Günther 1976), 10 Colombia (Günther 1994)
M. biloba	*M. biloba sevillensis*	Günther 1969	1 female nymphal paratype Colombia (Günther 1969), 1 female nymph Colombia, 131 nymph (Günther 1994)
M. columbiana	*M. columbiana columbiana*	(Günther 1963)	No data
M. columbiana	*M. columbiana tenaensis*	Günther 1969	6 Colombia (Günther 1989)
M. disparilobata		Günther 1989	No data
M. hebardi		(Chopard 1931)	No data
M. hondurica		Günther 1969	3 Costa Rica (Günther 1976, 1989)
M. hubbelli		Günther 1969	No data
M. imperfecta		Günther 1989	No data
M. lilo	*M. lilo granchacensis*	Günther 1977	1 Argentina (Günther 1989)
M. lilo	*M. lilo lilo*	Günther 1969	2 Peru (Günther 1976)
M. lineata	*M. lineata anchicayensis*	Günther 1994	3 paratypes Colombia (Günther 1994)
M. lineata	*M. linetata lineata*	Günther 1989	No data

TABLE 3.1. (continued)

nomen nudum M. lobata		Günther 1977	No data
M. lucieni		Günther 1969	1 Colombia (Günther 1989)
M. magdalenensis		Günther 1969	1 female nymph paratype Colombia (Günther 1969), 7 nymph Colombia (Günther 1989)
M. panamica		Günther 1969	2 Panama, 1 Ecuador (Günther 1989)
M. peruviana		(Saussure, 1896)	1 Peru (Günther 1977) 5 Ecuador (Günther 1989)
M. phallica		Günther 1969	No data
M. pronotopunctata		Günther 1969	35 nymphal paratypes Mexico (Günther 1969) 1 Mexico (Günther 1976). Günther (1969, translation): "The larvae generally have the typical patterns of drawing like the imagines."
M. pulicaria	*M. pulicaria interposita*	Günther 1969	1 Costa Rica, 5 Colombia, 1 Venezuela (Günther 1976); 1 Panama, 2 Colombia (Günther 1989) 8 Colombia (Günther 1994)
M. pulicaria	*M. pulicaria pulicaria*	(Saussure 1896)	2 Mexico, 1 Honduras, 1 Nicaragua, 38 Panama (Günther 1989)
M. schuchmanni		Günther 1994	No data
M. striatipes		(Chopard 1954)	1 Bolivia (Günther 1976), 3 Peru (Günther 1989)
M. triangulata		Günther 1969	No data
M. unispinosa		Günther 1989	No data
M. variabilis		Günther 1969	1 Mexico (Günther 1969) "1 Larve, Cotypen von *Rh. Pulicaria* SAUSSURE, Mus. Genf"; 1 Nicaragua (Günther 1989)
M. venezuelensis		Günther 1976	Numerous (Günther 1976)

TABLE 3.2. Measurements (in mm) of *M. pulicaria* nymphs from Toledo District, Belize (Orthoptera: Caelifera).

Measurement	Nymph 1	Nymph 2
Body length including wing pads	3.09	3.47
Pronotum length	0.73	0.64
Pronotum width	0.93	1.20
Tegmina length	0.74	0.69
Hind wing pad length	1.27	1.31
Interocular distance	0.25	0.20
Mesofemur length	0.60	0.93
Metafemur length	1.47	1.84

FIGURE 3.1. Distribution of *Mirhipipteryx pulicaria* in Belize. a) Central America, Belize shaded gray. b) Belize, Toledo District shaded gray. c) Ecosystems / land use in the Toledo District of Belize, with major river drainage basins delineated, and localities where *Mirhipipteryx pulicaria* was collected indicated by filled circles. Copyright © 2018 Magnolia Press.

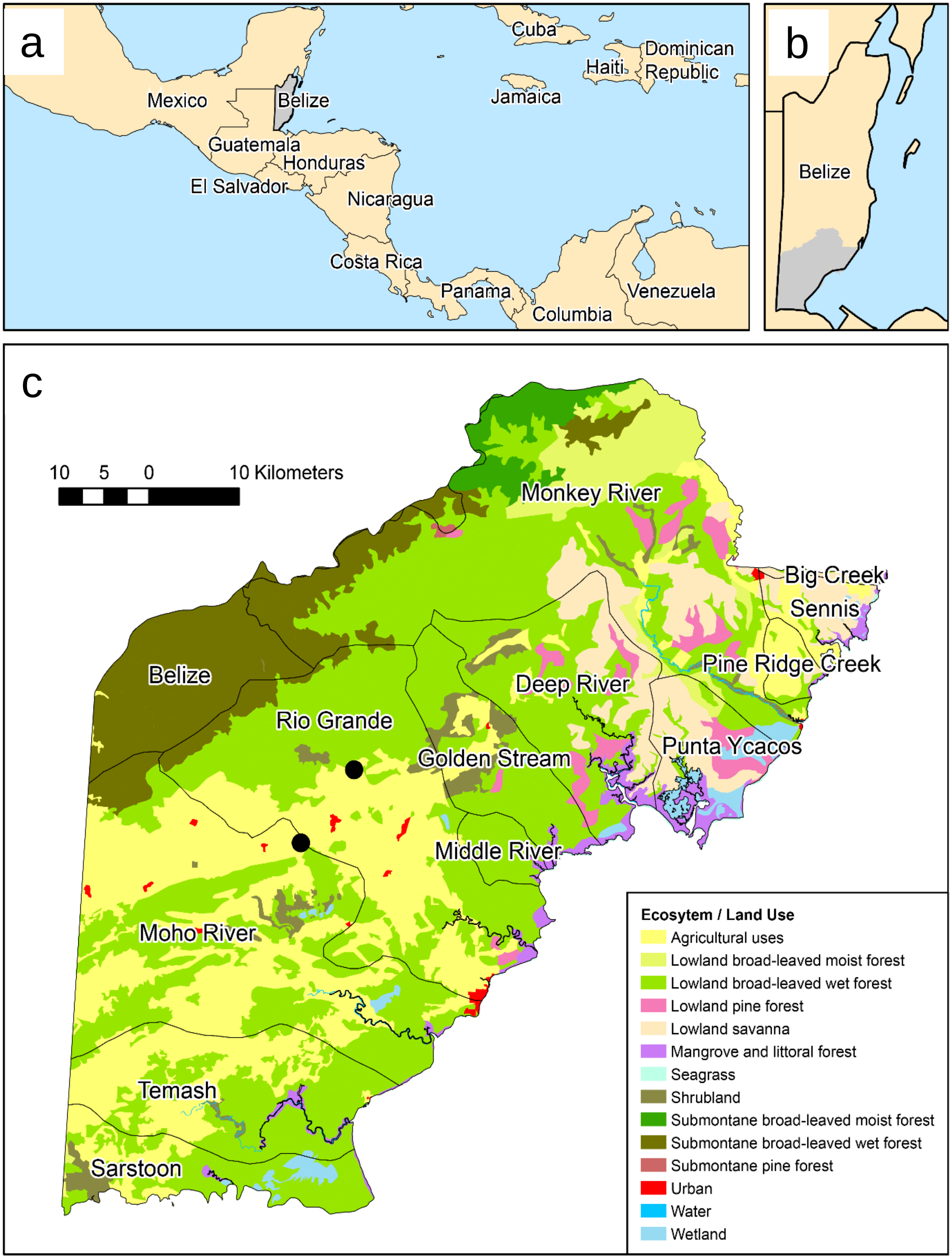


FIGURE 3.2. Dorsal view of *Mirhipipteryx pulicaria pulicaria* from Belize. a) Male (INHS Insect Collection 814,775). b) Female (INHS Insect Collection 814,781). c) Nymph (INHS Insect Collection 814,925). Copyright © 2018 Magnolia Press.

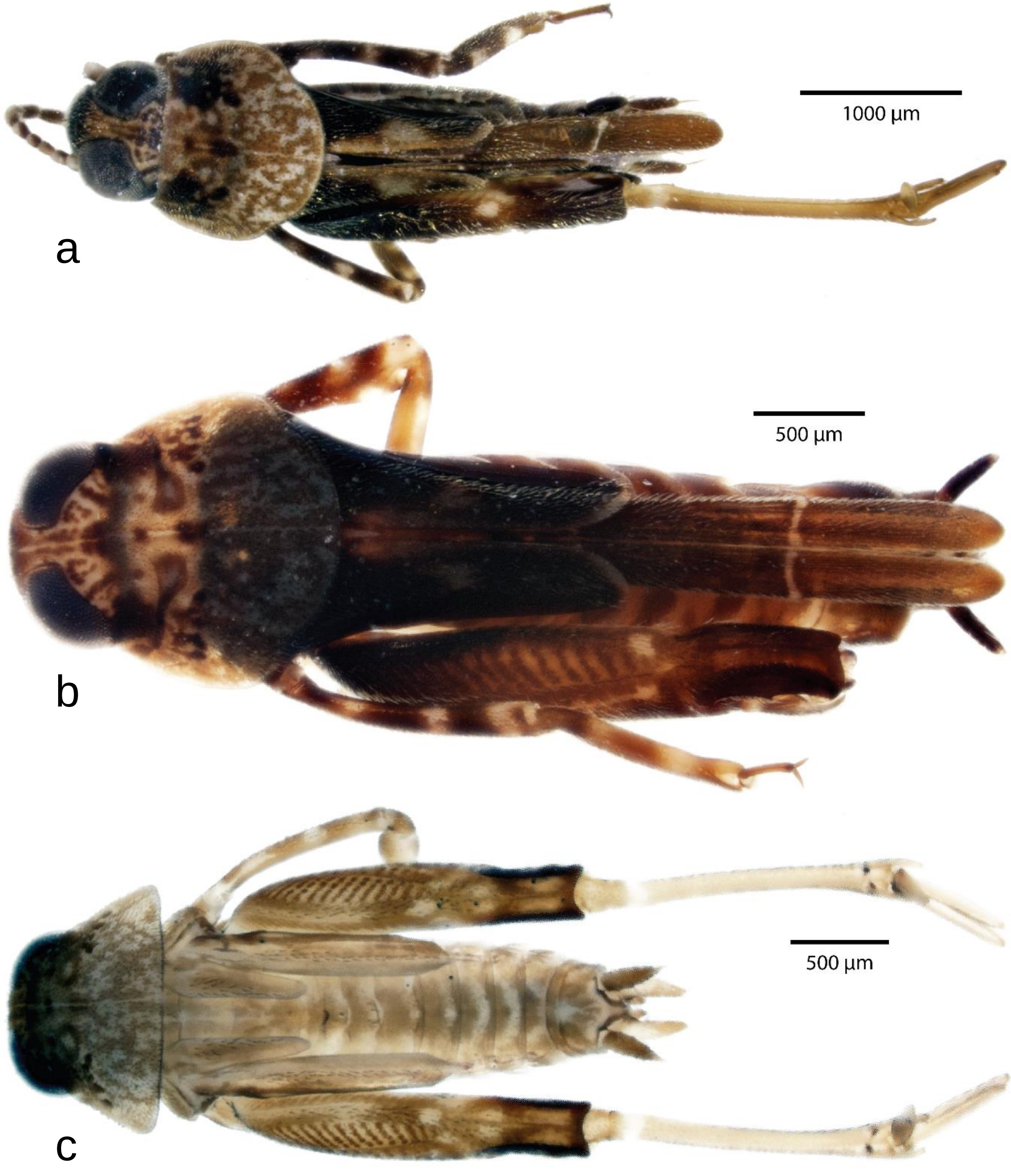
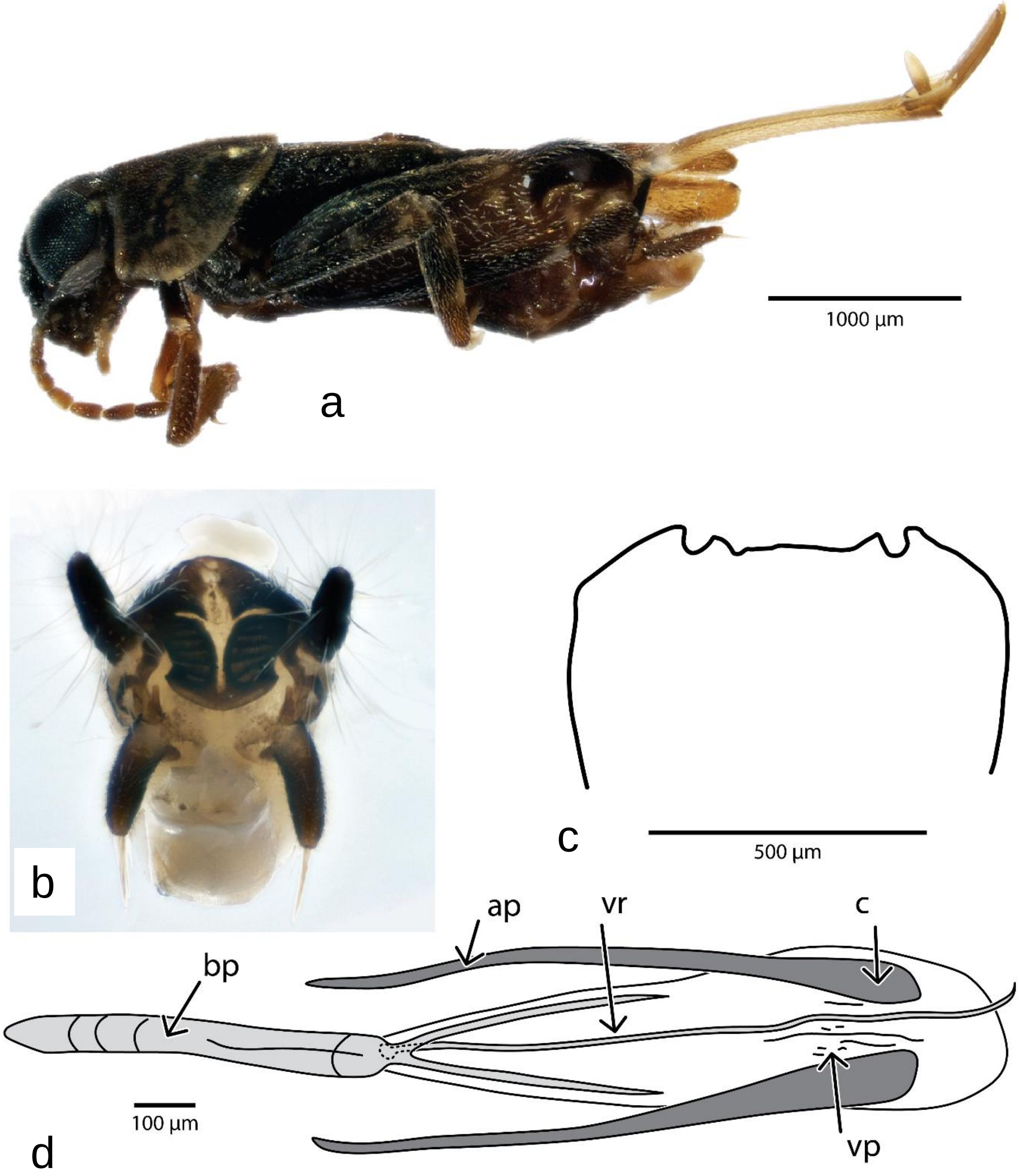


FIGURE 3.3. Adult *Mirhipipteryx pulicaria* from Belize. a) Lateral habitus (INHS no. 814,775). b) Terminalia in frontal view. c) Female subgenital plate. d) Male phallic complex. Labels on phallic complex are: ap – apodeme; bp – basal plate; c – cingulum; vp – ventral plate sclerotization; and vr – virga. Copyright © 2018 Magnolia Press.



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CHAPTER 4: NEW TRIDACTYLOIDS (ORTHOPTERA: CAELIFERA) FROM THE CRATO FORMATION OF BRAZIL

Abstract

The Crato Formation of Brazil preserves in laminated limestone an extraordinary window to Cretaceous fauna and flora. Insects and other arthropods are perhaps the most abundant and diverse animals recorded from this formation of Aptian age. Here, I reviewed tridactyloid-like fossils from the Crato Formation. Tridactyloidea is a superfamily of small orthopterans that are associated with water sources and are rare in fossil records. Eleven samples were reviewed, from which I described four new species in monotypic genera *Cratoscrofula carinata* sp. nov., *Gigantoteras brachykolos* sp. nov., *Atavidactylus fossorius* sp. nov., and *Geodactylus fortis* sp. nov. The genus *Cratodactylus* Martins-Neto is reviewed and split the two species into their own genera to improve the diagnostic features of this genus. I kept *Cratodactylus ferreirai* and erected the new *Megalopos* forming *Megalopos kellneri* comb. nov. Other specimens are placed at higher taxonomy (superfamily, family or subfamily) due to lack of diagnostic characters. The new species are placed temporarily in the subfamily Mongoloxyinae that includes species with rich venation. Finally, I provided a broader definition for this subfamily based on the fossil taxa reviewed, and morphological evidence. New morphological characters from thorax and middle legs are added. The Crato Formation from Brazil is the largest deposit of fossil tridactyloids in South America and the world and this study contributes to the evolutionary history and diversity of the superfamily Tridactyloidea.

Introduction

The most well-studied fossil insect-yielding Gondwanan Cretaceous deposit (145–66 mya) is the Crato Formation of Brazil. This formation is located in the Northeast region of Brazil (Figure 4.1a) on the north, south and southeast flanks of the Chapada do Araripe plateau. The Chapada do Araripe comprises a large area (8000 km^2) that extends over the states of Ceará, Pernambuco and Piauí (Martill & Bechly, 2007; Santos *et al.* 2011) (Figure 4.1a). The complexity of the formation has received attention for decades and recent attempts to characterize the geology lead to a better understanding of this system and its members (Figure 4.1b). The Crato Formation comprises 50–60 meters of heterolithic deposits, but fossils are abundant primarily in a layer of laminated limestone (0–13 m); this basal layer is known as Nova Olinda Member (Martill & Bechly, 2007).

Fossils from this formation are of Aptian age (approximately 113 to 125 MYA). The well-preserved paleobiota is one of the most complete and has led to greater understanding of central Gondwanan terrestrial ecosystems during the early Cretaceous. The biota includes gymnosperms (cycads, conifers and gnetophytes) and early angiosperms (flowering plants) (Selden & Nudds, 2012), vertebrates (fish, frogs, and pterosaurs) and invertebrates, mainly represented by insects (Menon & Martill 2007; Selden & Nudds, 2012). The preservation of insects in the formation includes information on not only abundance and diversity (Menon & Martill 2007; Selden and Nudds 2012), but also morphological data including microscopic features such as setae, soft tissue, and coloration (Heads *et al*. 2005; Bechly 2007; Selden and Nudds 2012). As a result, the insect assemblage of the deposit is one of the most important in the world.

Arthropods, other fauna and flora from this deposit are considered to be allochthonous. Matill *et al*. (2007) suggested that the Crato Formation occurred on a lake/lagoon with periods of hypersalinity. Only certain fish could cope with these saline waters (Selden & Nudds, 2012). Preservation of fresh water taxa such as dragonflies and mayflies are considered a consequence of drift by air or water into the lagoon (Selden & Nudds, 2012). Nevertheless, the salinity played an important role in the extraordinary preservation of organisms by delaying decomposition and allowing embedding of sediments to be placed on the samples (Matill *et al.* 2007; Selden & Nudds, 2012). A low oxygen environment suitable for anaerobic bacteria helped in the fossilization process (Matill *et al.* 2007).

Crato Formation invertebrate assemblage is dominated by insects, with the most abundant orders being Orthoptera, Blattodea, Hemiptera and Ephemeroptera (Bechly 2007; Selden & Nudds, 2012). Within these insect orders, Orthoptera is the most abundant group (Heads & Martins-Neto, 2007). Although comprehensive research has focused on orthopterans, recent discoveries warrant connections to described species and their relationships. Such work could lead to new species descriptions and/or synonymies (Heads and Martins-Neto 2007).

The Crato Formation is one of the only sources of fossil tridactyloids, yet only two species have been described to date, namely, *Cratodactylus ferreirai* Martins-Neto 1990 and *Cratodactylus kellneri* Martins-Neto 1990 (Table 4.1). A review of tridactyloid-like fossils samples will not only increase knowledge of this superfamily but could also highlight relationships between other orthopterans. The Crato Formation has yielded some of the oldest tridactyloid fossils the only ones from the Early Cretaceous of Gondwana. Expanding the knowledge of these taxa has important implications in the paleobiogeography and systematics of the group. Here, I review eleven tridactyloid-like fossils samples, from which four new monotypic genera are described. I split the genus *Cratodactylus* into two genera (*Cratodactylus* and *Megalopos* gen. nov.) with the aim of developing their diagnostic characters and providing new characters for species identification.

Materials and Methods

Tridactyloid-like samples from the Brazilian Crato Formation were requested on loan from the American Museum of Natural History (AMNH). Specimens were studied using a Zeiss SteREO Discovery V20 zoom stereomicroscope with Plan-Apochromat S 1.5x FWD 30 mm objectives. Fossils were directly examined, dried, and moistened with a thin layer of 50% ethanol under the microscope. Wing photographs were taken using an AxioCam HRc Rev. 3 attached to the stereomicroscope. Habitus photographs were taken using a camera Canon EOS 5D Mark III attached to a copy stand with a Cognisys Stackshot 3X and the software Helicon Remote 2000-2014 Version 3.4.12.W. All images were stacked using Helicon Focus 6 and edited in Adobe Photoshop CC 2015. Wing mosaics were assembled in Adobe Photoshop. All illustrations were prepared in Adobe Illustrator CC 2015.

Measurements of L1 (body length from head to wings), L2 (body length from head to abdomen), L3 (length from head to metafemur), and L4 (metafemur length) were taken following Martins-Neto (1990). Other measurements such as interocular distance, hind wing length, and pronotum length and width were also recorded when applicable. Measurements were taken with tpsDig2 Version 2.26 (Rohlf 2016).

For the taxonomic identification, I examined original descriptions, holotype, and paratype photographs of *C. ferreirai* and *Megalopos kellneri comb. nov*. Photographs of the holotypes of *C. ferreirai* (GP/1T-1649), *Megalopos kellneri comb.* nov. (GP/1T-1652), and paratypes of *C.*

ferreirai (GP/1T-1650, GP/1T-1651) were provided by the Department of Sedimentary and Environmental Geology (GSA), University of São Paulo, Brazil. Measurements were taken using tpsDig2 Version 2.26 (Rohlf 2016). Species descriptions follow Baena-Bejarano and Heads (2015, 2018). I reviewed other Tridactyloidea type specimens, descriptions, and literature (Günther 1963 – 1995; Heads 2009, 2010a, b; Baena-Bejarano and Heads 2015, 2018). Material examined includes *Archaeoellipes engeli* Heads 2009 (Holotype), *Burmadactylus grimaldii* Heads 2010 (Holotype) from American Museum of Natural History (AMNH), New York City; *Guntheridactylus grimaulti* Azar and Nel 2008 (Holotype PA 15270 and paratype 15270) from Muséum national d'Histoire naturelle MNHN -Collection de Paléontologie, Paris, France; *Tridactylus berlandi* Chopard, 1920 Muséum national d'Histoire naturelle MNHN - entomological collection, Paris, France; *Afrotridactylus madecassus* (Saussure 1896) Royal Belgium Institute of Natural Sciences, Brussels, Belgium; *Dentridactylus* spp. Instituto de Ciencias Naturales (ICN), Bogota, Colombia.

Systematic Paleontology

Order ORTHOPTERA Olivier 1789

Suborder CAELIFERA Ander, 1939

Superfamily TRIDACTYLOIDEA Brullé, 1835

Family TRIDACTYLIDAE Brullé, 1835

Subfamily MONGOLOXYINAE Gorochov, 1992

Remarks. The superfamily Tridactyloidea includes the families Cylindrachetidae, Ripipterygidae and Tridactylidae. Diagnostic characters are clearly defined for each of the previous families as of Günther (1969, 1992, 1994, 1995). Some of these diagnostic characters for each family are provided in the following paragraph. Tridactylidae or pygmy mole crickets are diagnosable by the cerci with two segments, tibial lamellae present or absent, compound eyes and female with inconspicuous ovipositor. Ripipterygidae or mud crickets are diagnosable by cerci with one segment, tibial lamellae absent, compound eyes, and female with conspicuous ovipositor. Cylindrachetidae or sandgropers have one-segmented cerci, cylindrical body, reduced compound eyes, and reduced legs modified for digging. However, the subfamily Mongoloxyinae in Tridactylidae includes a species with cerci of one segment (*Birmitoxya intermedia*), and it is represented solely from fossil taxa. Mongoloxyinae, while distinct from the recent species, is differentiated by wing venation as a potential plesiomorphic character (Azar & Nel 2008). Azar & Nel (2008) claimed this group as probably a paraphyletic assemblage that should not be included in Tridactylidae or Tridactyloidea. The position and the relationships of this assemblage require further revision. However, Mongoloxyinae is retained in Tridactylidae based on newly revised fossils (more complete specimens with full body and wing venation provide conflictive evidence against and in favor of a monophyletic Mongoloxyinae, see discussion). Here, Mongoloxyinae is defined as fossil crickets with the following characters: tegmina with more than four longitudinal veins (rich venation) (Gorochov *et al.* 2006), thorax developed (meso- and metathorax slightly shorter than mesofemur), and short middle legs (mesofemur does not reach half of the metafemur). Other subfamilies of Tridactylidae are identified by developed metatarsus with subapical tooth (Dentridactylinae) (Günther 1979) or developed metatarsus without subapical tooth and/or reduced metatarsus (Tridactylinae). The presence of this character is unknown from most fossil mongoloxyins because of missing parts such as metatarsi or body (*Cretoxya rasnitsyni*, *Mongoloxya ponomarenkoi* are known from wings). Overall, species from Tridactylidae (Tridactylinae and Dentridactylinae) and Ripipterygidae have a reduced meso-metathorax where the meso- and metacoxa are adjacent with respect to the procoxa. Wing venation is often reduced with fewer than four longitudinal veins. Cylindrachetidae are particularly modified crickets for fossorial habitat with cylindrical bodies that are not similar to species in Mongoloxyinae. However, both groups display reduction of the middle leg to some extent and developed thoracic segments.

Genus *CRATODACTYLUS* Martins-Neto, 1990

Figure 4.2

Type species. Cratodactylus ferreirai Martins-Neto 1990; from Santana do Cariri - Nova Olinda, Brazil Member

Revised diagnosis. The genus is identified by [1] compound eyes, small and rounded, [2] compound eyes on vertex [3], thorax length half of the total length of body, [4] protibiae without teeth, [5] metafemur with arrangement of tubercles.

Remarks. The genus *Cratodactylus* as defined by Martins-Neto (1990) presents difficulties for the diagnosis if compared with extant taxa. The characters provided are not only applicable to the species from the Crato Formation but also to almost any other tridactyloid (body length between 7–14 mm, moniliform antennae, reduced forewing, long hind wing, fossorial foreleg etc.), so it fails its purpose as diagnostic. However, the species *C. ferreirai* and *Megalopos kellneri comb.* nov. are indeed valid (Figure 4.2a-d). I tried to find diagnostic characters that will bring these two species together, but they exhibit differential morphology in compound eyes and fore- and hind legs. Therefore, I propose to split the two species into different genera and. The only shared characters are absence of or reduced tegmina, but this seems to be more a problem of preservation than absence of this feature (*Megalopos kellneri* comb. nov. has the tegmina partially preserved), and the straight margins of metafemur. The diagnostic characters are challenging in light of new specimens (Figure 4.3a-k). For example, the character of reduced tegmina is problematic because it is not clear if this reduction corresponds to a short forewing, or a problem of preservation. In addition, new fossils from the Crato Formation have forewings preserved, and technically this will exclude them from the genus. *Cratodactylus* is placed in Mongoloxyinae based on the thorax development that as, stated by Martins-Neto (1990), is almost half of the body length (Table 4.2).

Cratodactylus ferreirai **Martins-Neto, 1990**

Figure 4.3f-g

Material. SA45371, SA45380 from AMNH.

The fossils SA45371 (Figure 4.3f) and SA45380 (Figure 4.3g) are assigned to *C. ferreirai*. *C. ferreirai* displays organized tubercles below the dorsal margin of the metafemur (Martins-Neto 1990). The main reason to place them in *C. ferreirai* was because of a darker coloration in the metafemur of SA45371 and SA45380, which follows the pattern of distribution of tubercles (Figure 4.3f-g). Martins-Neto (1990) suggested they could be stridulatory. Moreover, hind wings are similar in shape; the proportions overlap with those of Martins-Neto (1990) and the dorsal margin of the metafemur is entire (not indented) in these samples as in the holotype (GP/1T 1649) and paratype (GP/1T-1650). For instance, the metafemur of samples SA45371 and SA45380 have a complete ventral margin; the inner corner of this margin displays a right angle (Figure 4.3f-g). This character is unknown in *C. ferreirai* types due to lack of preservation. SA45380 has a pattern of invaginations on pronotum that is not evident from the types.

***Cratodactylus aff. ferreirai* Martins-Neto, 1990**

Figure 4.3h

Material. SA 45391 from AMNH.

This specimen is placed within *Cratodactylus* based on the enlarged thorax and enlarged metafemur typical of Tridactyloidea. This specimen resembles *C. ferreirai* in the metafemur dorsal pattern of tubercles and hind wings that are straight and narrow. SA 45391 displays pronotum constriction and unique tubercles on the pronotum that are not present in other species found in the Crato Formation. However, the lack of tubercles in other fossil specimens could be due to preservation of the pronotum or position of the fossil (this cannot be observed from ventral views).

Unknown sex, adult preserved in lateral view. Measurements in Tables 4.3–4.4.

Head missing. Pronotum with multiple tubercles and constricted anteriorly (1/3 of pronotum). Small portion of tegmen remains dorsally on mesonotum, remaining longitudinal veins; no reticulate veins are evident. Hind wings longer than abdomen. Multiple longitudinal veins. No transverse veins. Mesothorax and metathorax area is twice as long as pronotum; segment division not visible due to preservation. Forelegs and middle legs missing. Hind leg poorly preserved. Metafemur robust distally rounded with semi-lunar process. Slender fragment adjacent to metafemur resembling a slender metatibia. Abdomen as long as mesothorax and metathorax area. Terminalia not visible due to preservation. Segmentation narrow.

Genus *MEGALOPOS* nov.

Derivation of name. The genus name comes from the Greek *Megalopos,* “large-eyed”. This name refers to the compound eyes that occupied half of the head in the species.

Type species. Cratodactylus kellneri (Martins-Neto 1990); from Santana do Cariri - Nova Olinda, Brazil Member

Revised Diagnosis. The genus is identified by [1] large compound eyes occupying almost half of the head, [2] pronotum longer than head in lateral view, [3] metafemur rounded basally in dorsal margin.

Material. GP/1T-1652, adult in lateral view.

Description. Head small, rounded with large compound eyes. Compound eyes occupied half of the head in lateral view and vertically elongated. Compound eyes reniform. Antenna filiform, with thick antennomere.

Pronotum short and extended over pleura. Pronotum covers procoxa and basally the profemur. Meso- and metathorax as long as pronotum. Protibia thin and distally expanded. Tarsal segment long and thin, segmentation and unguis obscure. Middle leg incomplete. Metafemur robust and enlarged, longer than abdomen. Anterodorsal margin of metafemur strongly rounded. Dorsal margin entire (not indented) without tubercles. Semi-lunar process thin. Ventral margin indented anteriorly. Ventral and dorsal sutures parallel to metafemur margin. Metatibia long and slender. A spur or metatarsus remain adjacent to metafemur. Tegmen sclerotized, only anteriorly preserved. Venation obscured. Hind wing narrow and longer than body. Dorsally sclerotized; not clear if costal area of hind wings, or if extended tegmina is covering hind wings. Longitudinal veins and cross-veins in hind wing membranous area.

Abdomen shorter than hind legs. Distally rounded.

***Megalopos kellneri* comb. nov.**

Figure 4.2a; Table 4.2

Holotype. GP/1T-1652. Adult from Santana do Cariri - Nova Olinda, Brazil Member

Revised Diagnosis. Same as in the genus.

Remarks. The genus *Cratodactylus* was created based on general characters that are typical of the family Tridactylidae and some other Tridactyloidea, but do not help to differentiate the genus from other genera in the group. The new diagnosis for the genus *Cratodactylus* is not applicable to *Megalopos kellneri* comb. nov. Therefore, this species should be placed in its own genus. A revised diagnosis for this species is provided. The Martins-Neto (1990) diagnosis was based on compound eyes, tibiae of foreleg with long spurs or teeth, and length of thorax of 1/3 and 1/4. Table 4.2 provides the measurements and the proportion L3/L2. The ratio L3/L2 includes the head length with the thorax. I obtained measurements similar to Martins-Neto (1990). However, measurements of the holotype did not match the proportions L3/L2 (Table 4.2). Measuring precision has improved in recent decades due to the availability of new techniques and technology. Differences obtained here could be due to the digital method used here. I obtained a proportion of 0.4 (1/2.5) for measurement of the thorax and 0.53 (1/1.9) for measurement of the thorax + the head. Additionally, the foreleg of holotype does not seem to display long teeth or spurs as described for the paratypes. The paratypes require further review for placement. They are kept temporarily with this species. The *Megalopos* is placed in Mongoloxyinae based on the developed thorax.

Genus *CRATOSCROFULA* nov.

Derivation of name. Cratoscrofula is the combination of the words "Crato" and "*scrofula*". "Crato" refers to the formation where this fossil was found. The Greek word *scrofula*, a diminutive of *scrofa* "swelling of the glands in the neck", is the name used in a group of species in the genus *Ripipteryx* (Scrofulosa). This group comprises species with frontal processes.

The gender is feminine.

Type species. Cratoscrofula carinata sp. nov. by monotypy.

Diagnosis. The new species is identified by [1] frontal acutely pointed keel, [2] small size, with body length of 6.48 mm.

Cratoscrofula carinata sp. nov.

Figures 4.3b, 4.4b

Derivation of name. The specific epithet Latin *carina* "keel" refers to the frontal keel of this especies.

Holotype. Male? Adult (SA45112). Preserved in dorsal view. Brazil: Ceara. Crato, Santana Formation (Early Cretaceous). American Museum of Natural History (AMNH), New York City, USA.

Diagnosis. Same as in the genus.

Description. Holotype body length 6.48 mm; pronotum length 0.34 mm, width 1.36; hind wing 5.37 mm; metafemur 2.77. Other measurements in Tables 4.3–4.4.

Head semi-globose with a medial acuminate pointed keel; head shorter than pronotum (without keel). Ocelli not visible. The left antenna has 6 antennomeres and the right has 5 antennomeres. On the left antenna, the 1–4 antennomeres are longer than wider and the 5–6 are distally as wide as the length.

Thorax. Pronotum wider than head. Posterior margin is the widest area of the pronotum. Mesonotum is the longest and widest thoracic segment. Mesothorax and metathorax tergum are partially missing. Forelegs adjacent to the sides of the head. Profemur short, with lateral margins subparallel and slightly convex; distally rounded. Middle leg femora fragment preserved in both sides of the body. Hind leg large. Metafemur longer than abdomen. Tegmina obscure. Hind wings membranous, narrow, and longer than body. Edge of wing is sclerotized; not clear if costal area of hind wings or if extended tegmina is covering hind wings. Longitudinal veins in hind wings.

Abdomen. Abdominal tergum incomplete, robust with narrow segments; distally rounded. Cerci obscured.

Remarks. *Cratoscrofula carinata* sp. nov. is placed in Mongoloxyinae based on the developed thorax found also in *Cratodactylus*. Although the presence of a frontal keel is known in the family Ripipterygidae, the frontal keel is rather pointed in this fossil species (Figure 4.4b).

In males of Scrofulosa group (*Ripipteryx*), it is blunt (Günther 1969, *R. saussurei* Abb. 142). Frontal lobes are not known in females. Cerci and terminalia are often used in distinguishing the families Tridactylidae and Ripipterygidae (Günther 1994); however, none of these structures are preserved in this fossil. Similarly, hind leg parts (tarsus, spurs, and tibial lamellae) are often used in the diagnosis of genera in Tridactyloidea, but only dorsal area of femur is visible. *Cratoscrofula carinata* sp. nov. is the smallest adult tridactyloid fossil from the Crato Formation. This species differs from any other species extant or extinct by the medial pointed keel on head.

Genus *GIGANTOTERAS* nov.

Derivation of name. The genus name comes from the Greek roots *giganto* “large, gigantic” and *teras, teratos* “monster” meaning giant monster. The gender is neuter. This species is the largest fossil tridactyloid at almost 20 mm, but large in comparison to extant species in the family.

Type species. Gigantoteras brachykolos sp. nov. by monotypy.

Diagnosis. The genus is identified by [1] short mesofemur, does not overlap with metafemur [2] antennae moniliform, [3] body length higher than 15 mm including wings (19.57 mm).

***Gigantoteras brachykolos* sp. nov.**

Figures 4.3a, 4.4a

Derivation of name. Specific epithet comes from the Greek *brachykolos* meaning "with short legs" and refers to the short middle legs (mesofemur) of the fossil.

Holotype. Female? Adult (SA 45262). Fossil in ventral view.

Diagnosis. Same as in the genus.

*Description***.** Holotype body length 19.57 mm, pronotum length 1.19 mm, metafemur 9.73 mm. Other measurements in Tables 4.3–4.4.

Head semi-globose and flattened frontally. Compound eyes rounded. Interocular distance longer than the width of a compound eye. Mouthparts missing. Antennae moniliform, seven distal segments. Basal segments missing or not visible.

Thorax. Prosterno protruding ventrally, almost forming a lobe, tip of "lobe" is broken or missing. Pronotum extended laterally, embedding procoxa. Coxa insertion large. Foreleg with coxa, femur and tibia. No trochanter evident. Coxa twice longer than wider, basally rounded, and subparallel laterally. Profemur margins convex, inner margin distally extended forming a lobe. Protibiae robust with 2–3 large spines, strong setae. Right-side foreleg with a single tarsal segment. Mesonotum rectangular, mesocoxa insertion are smaller than procoxa, mesofemur distally widened, longer than mesotibia. Mesofemur margins convex. Mesotibia margins convex. Tarsal segment elongated, unguis and basitarsus missing. Mesotibia short, overlap slightly with metacoxa, but does not overlap with metafemur. Metasternum wide, twice the mesosternum. Hind leg saltatorial, large. Metafemur ventral margin rounded (convex), semi-lunar process apparently present. Tegmina obscure. Hind wings narrow, longer than abdomen. Homogeneously sclerotized, not evidently membranous. Multiple cross and longitudinal veins.

Abdomen wide, and exposed; sternum missing (not covering). Segmentation wider than longer. Cerci missing. Guts distally distinguished, genitalia missing. Paraproct two-segmented with strong setae. Apex of ovipositor visible.

Remarks. The new genus is like the extinct Crato Formation genus *Cratodactylus* in having a large thorax, in contrast with extant species. This species is placed in Mongoloxyinae. It shares the fossorial forelegs and ellipsoid middle legs with other tridactylids (Tridactylinae and Dentridactylinae). No plate is observed in prosternum as in Ripidactylidae fam. nov. (see Chapter 5). The species has a paraproctal lobe with two segments; this is known in the family Ripipterygidae and fossil species in the subfamily Dentridactylinae (Tridactylidae). However, *G. brachykolos* differs from other extant and extinct species by the reduced femur of middle leg. In extant species (Ripipterygidae and Tridactylidae), the mesofemur extends over the metafemur. Although *G. brachykolos* is a large species and the largest tridactyloid in the fossil record, it is not the largest species compared with extant species.

Genus *ATAVIDACTYLUS* nov.

Derivation of name. The genus name comes from the Latin root *Atavus* “father of a grandfather successively backward, forefather, ancestor”. *Dactylus* comes from the Greek word *daktylos,* “finger”, a character attributed to the superfamily Tridactylidae. This superfamily at the apex of the metatibiae has one tarsal segment. This metatarsus is sometimes elongated resembling a finger. Furthermore, Tridactylidae means three fingers and is derived from the metatarsus and two elongated tibial spurs resemble three “fingers” (Figure 1.2).

The gender is masculine.

Type species. Atavidactylus fossorius sp. nov. by monotypy.

Diagnosis. The genus is recognized by the following character combination: [1] cercal segments equal in length, [2] cubito-anal area of tegmina without intercalary veins, [3] area of tegmen between radial and medial veins is half of the wing, [4] rounded compound eyes.

***Atavidactylus fossorius* sp. nov.**

Figures 4.3c, 4.4c-d

Derivation of name. The specific epithet *fossorius,* adapted to digging, refers to the fossorial habits attributed to this species. The specimen shares a similar foreleg morphology with some extant tridactyloids, many of which are known to be fossorial. The forelegs of this fossil clearly show long tibial teeth and tubercles on femur with wide femora and tibia.

Holotype. Adult (holotype). Preserved in dorsal view. Brazil: Ceara. Crato, Santana Formation (Early Cretaeous). H.R. Axelrod, Coll. AMNH 44480

Diagnosis. As in the genus.

Description. *Male*. Body length 14.29 mm; interocular distance 0.66; pronotum length 2.25 mm; pronotum width 3.13 tegmina length 6.8 mm, hind wing 9.25 mm; metafemur 6.19. Other measurements in Tables 4.3–4.4.

Head prognathous, semi-globose, and almost as long as pronotum. Compound eyes circular, on top of the head. Interocular distance longer than the width of a compound eye.

Vertex near left compound eye almost inside the pronotum, vertex near right compound eye visible. Ocelli not visible. Scape under compound eyes. Antennae missing. Palps missing. Labrum glabrous.

Thorax. Pronotum shape like half-cylinder, convex; anterior margin straight, posterior margin rounded. Posterior margin is the widest area of pronotum. Sulcus along margin of pronotum, not visible on left lateral side. Mesonotum small triangular. Metanotum inflated, but missing tergum. Forelegs fossorial, on the sides of the head. Profemur robust with ventral teeth, narrow rectangular dorsal margin that extends distally in Y-shape; sulcus along margin. Protibiae robust with scattered tubercles on outer side; distally with four large teeth, strong setae ventrally. Largest tooth near the base, the size is reduced to half the size of the anterior tooth, darker coloration on tip of teeth. Last tarsal segment with one ungues, the other ungues is not visible. Middle legs slimmer than forelegs. Mesofemora longer than profemora, margins convex with sulcus on lateral margins. Mesotibiae anteriorly ellipsoid, distally not visible. Hind leg large. Metafemora dorsal margin strongly curved (convex) with sulcus, ventral margin weakly convex; semi-lunar process present, distal lobe reduced. Tegmina sclerotized, shorter than hind wings, but developed close to the tip of abdomen. Partial reduced longitudinal venation, C?, Sc, R, and M. Cubital and anal veins fusing. Cross-veins between Sc and R (5 on left, 5 on right), and between R and M (8 on left, 7 on right). Area between radial and medial veins is wide and almost half of the tegmina. Reticulate venation distally. Hind wings obscured, remnants are membranous with sclerotized costal region, narrow and longer than abdomen; longitudinal veins abundant.

Abdomen. Abdominal tergum incomplete, exposing gut and Malpighian tubules. Last abdominal tergum with a middle depression, almost the same width of the epiproct. Cerci two-segmented, long. Basal segment conical, covered on sockets missing setae. Basal segment wider than apical segment. Distal segment similar length to basal segment. Male paraproct with strong setae ventrally, inner side; outer side not visible. Epiproct rounded with strong setae apically.

Remarks. *Atavidactylus fossorius* sp. nov. is placed in Mongoloxyinae based on the developed thorax and wing venation with more than four longitudinal veins. *Atavidactylus* shares the 2-segmented cerci with Tridactylidae (Tidactylinae and Dentridactylinae). Although the tegmina venation displays more than 4 longitudinal veins as defined in the subfamily Mongoloxyinae, this fossil differs from other Mongoloxyinae species in wing venation such as lack of cross-veins in anal region (*M. ponomarenkoi*, *Cretoxya rasnitsyni*) (Gorochov, 1992, Gorochov, *et al.* 2006); reduced venation of Sc and R (shared with *C. rasnitsyni* (Gorochov *et al.* 2006), but different in *Baisoxya dolichopterus* and *Monodactyloides curtipennis* (Sharov, 1968). *Birmitoxya intermedia* (Gorochov, 2010) is a species included in Mongoloxyinae. This species lacks tegmina and exhibits cerci with one segment. The cerci segmentation is unknown in other mongoloxyin species. This sample differs from *Monodactyloides* and *Baisoxya* in having fossorial forelegs, a long pronotum (short in Sharov, 1968 species) and only two rows of intercalary veins (four in *Baisoxya*).

The *Atavidactylus* differs from *Cratoscrofula* by the absence of a keel in the frons and from *Gigantoteras* by the length of the mesotibiae that extend over the metafemora. The abdomen in this species is as long as or slightly longer than metafemur, in comparison with *C. ferreirai* and *Megalopos kellneri comb. nov* (abdomen is shorter than metafemur tip). However, this character can be difficult to use due to natural expansion or contraction of the abdomen in insects. Additionally, *A. fossorius* differs from *C. ferreirai* by having rounded eyes relatively larger and pronotum without lateral sutures. For instance, the *A. fossorius* pronotum edge has a well-marked sulcus. In dorsal view, pronotum and mesonotum are shorter than in *C. ferreirai*. Other differences are the metafemur dorsal margin smooth, not tubercles with a soft granulation. *Megalopos kellneri comb. nov* differs from *A. fossorius* in the shape of the eyes being ellipsoid-like, instead of circle-like. Both species have a short concave area on the outer margin of the eye. In addition, the pronotum has almost the same length between anterior and posterior margin in *Megalopos kellneri comb. nov*. The pronotum in *A. fossorius* is more than half the total length longer in dorsal area. The metafemur dorsal margin is strongly curved (Figure 4.3b) while in *Megalopos kellneri comb. nov* the margin is straight and anteriorly curved (Figure 4.2a).

Genus *GEODACTYLUS* nov.

Derivation of name. The genus name comes from the Greek words *Ge, gaia "*earth" and *daktylos* "finger", in reference to their life-style in the ground and the name of the family Tridactylidae. The fossil has forelegs modified for digging the ground, similar to the previous species.

Type species. Geodactylus fortis sp. nov. by monotypy.

Diagnosis. The genus is recognized by the following character combination: [1] cercal segments different length, distal is half the length of basal, spine-like, [2] pronotum robust, swollen.

Geodactylus fortis **sp. nov.**

Figures 4.3d, 4.4e; (Figure 7.34 in Grimaldi, & Engel, 2005, p.211)

Derivation of name. The specific epithet is the Latin adjective *fortis,* meaning “strong”. This species has a thickened pronotum.

Holotype. 43374 Brazil: Ceara. Crato, Santana Formation (Early Cretaceous). H.R. Axelrod, Coll. AMNH. Written in the back “5 digits on left fore tarsus (2 fell off when cleaning)”

Dorsal view.

Diagnosis. Same as in genus.

Description. Head small, smaller than pronotum. Compound eyes missing. Antennae filiform, at least 10-segmented; scape robust, larger than pedicel. Pedicel shorter than first flagellomere. First flagellomeres more filiform-like than the distal moniliform-like flagellomeres.

Thorax. Pronotum swollen, strongly convex dorsally. Anterior area of pronotum not as swollen and separated by a sulcus. Medial suture near posterior margin. Sulcus along margin of pronotum. Distal margin of pronotum curved. Forelegs fossorial, profemora robust and dorsal margin rounded. Protibiae robust with five long teeth. Basal teeth longer than distal teeth. Walking middle leg. Mesotrochanter small, triangular. Mesofemora wide, ellipsoid. Mesotibiae ellipsoid. Mesotarsi slender. Hind leg robust. Metafemora longer than abdomen. Margins complete without indentation, but dorsal margin obscure. Semi-lunar process present. Tegmina basally preserved. Sc and R curved. Anal/cubital veins thick (8 left, ~4 right). Cross-veins obscure (2 right, left not evident). Tegmina wider than hind wing. Hind wings narrow and longer than body. Costal area sclerotized, the rest of the hind wing is membranous. Longitudinal veins with few cross-veins in membranous region.

Abdomen. Cerci long, two-segmented. Basal segment cylinder-like, slightly wide basally. Distal segment thin and short, half the length of basal segment.

Remarks. *Geodactylus fortis* sp. nov. is placed in the subfamily Mongoloxyinae based on the developed thorax, short middle leg, and tegmina venation. Sc and R are strongly curved as in *A. fossorius* (Figure 4.4d) and other Mongoloxyinae. Cubital and anal veins are thick as in *A. fossorius*. No cross-veins are evident in medial-radial section; however, this area is obscure. *A. fossorius* sp. nov. and *G. fortis* sp. nov. share ventral tubercles in the profemur. Nevertheless, this species differs from *A. fossorius* in the size and shape of the second cercal segment (Figures 4.5a-b). Cerci segments are unknown in other mongoloxyins, except for *B. intermedia* with one-segmented cerci and *A. fossorius*. The pronotum of this species is completely swollen, and no other fossil species with a pronotum exhibits this feature. Extant species of *Tridactylus* such as *T. berlandi* Chopard, 1920, and *T. thoracicus* Guérin-Méneville, 1844 have a thorax similar to *G. fortis* sp. nov.

Tridactyloidea

Figure 4.3i,k

Material. SA 45291, SA 45517 from AMNH.

Remarks. SA 45291 is placed in the superfamily Tridactyloidea based on the preservation of the abdomen, and partial metamefora. However, the state of preservation of the head, legs, and view of the specimen makes it difficult to place in a lower taxonomic category.

The proportion of the thorax is not as developed as seen in other Crato Formation tridactyloid species (L3/L2 = 0.40; Table 4.3). Fore- and hind wings are not visible in this specimen, which in addition with the small size suggest this could be a nymph rather than adult. However, data on nymphs is scare in literature as reviewed by Baena-Bejarano *et al. (*2018) in a genus of Ripipterygidae.

SA 45517 is placed in Tridactyloidea based on the similarities of the legs with the group such as foreleg pubescent with strong setae, middle leg with ellipsoid mesotibia (Tridactylidae), and enlarged hind leg. The tegmina are narrow and sclerotized more alike to Ripipterygidae. However, this sample has reticulate venation and lacks any longitudinal vein. Mongoloxyinae species show a combination of longitudinal veins and distal reticulation. This sample could be in a different clade, but I opted not to erect a different clade due to the poor preservation and lack of other diagnostic characters.

Mongoloxyinae

Figure 4.3e, j

Material. SA 45290, SA 45388 from AMNH.

Remarks. SA 45290 is placed in Mongoloxyinae based on the preservation of the middle legs. The middle leg is short, and the mesofemur extends to the basal area of metafemur. Similarly to SA 45291, fore- and hind wings are not visible in the specimen, and the small size suggests this specimen could be a nymph rather than adult.

SA 45388 is placed in Mongoloxyinae based on the developed thorax and short length of mesofemur. The forewing of this specimen is completely different from any of the other species.

The shape of the forewing is different from the Crato Formation species in having an anteriorly expanded costal region; this produces two strong slopes on anterior margin. In the other fossils this feature is less pronounced. However, this shape is similar in species *C. rasnitsyni*, *B. dolichopterus*, and *M. curtipennis*. The anterior and posterior margin forms a distal tip. The SA 45388 forewing is poorly preserved. This specimen has reduced venation, but this is not conclusive. Due to the poor preservation of the wing, and lack of other characters on view, I chose not to describe it as a new species.

Discussion

Tridactyloid diversity from the Crato Formation surpasses the diversity of this group from any other fossil deposit in the world (Table 4.1). The coverage of these six species and their great preservation provides new insights on the morphology of the ancestors of extant species. The rich venation of *A. fossorius* sp. nov. and *G. fortis* sp. nov. is comparable with that of *C. rasnitsyni* and *B. dolichopterus* (Sharov, 1968; Gorochov *et al.* 2006). The importance of thorax proportions were pointed out by Martins-Neto (1990); developed thorax seem to be the case in all the Crato Formation specimens. Equally noticeable is the length of middle leg. The mesofemur of mongoloxyin species barely reaches half of the metafemur whereas in species of Ripipterygidae it exceeds half of the metafemur (as in *R. gorgonaensis, R. guacharoensis, R. gorgonaensis* Baena-Bejarano & Heads 2015) and similarly in Tridactylidae reaches half of the metafemur (*Tridactylus berlandi, A. madecassus, Dentridactylus* spp). *A. fossorius* is an extraordinarily well-preserved fossil. Not only are part of both forewings displayed, but in general head, thorax, and abdomen provide details on the morphology of this ancient group. Forewing venation on costal area resembles that of *C. rasnitsyni*; however, this fossil has a reduced venation in the cubito-anal region (lack of cross-veins). In comparison with extant species, *A. fossorius* exhibits rich venation as is expected in a fossil insect sample. *A. fossorius* is the piece that links this thoracic morphology with a rich tegminal venation and two-segmented cerci, further attesting to the great antiquity of the family Tridactylidae and their paleodistribution.

This remarkable morphology display in the specimens also provides insights into their natural history. Fossorial forelegs with strong teeth evidence a fossorial lifestyle for this group as suggested by Martins-Neto (1990). Tunnelling is known in extant Tridactylidae and *Mirhipipteryx* (Ripipterygidae). However, none of the Crato Formation fossils exhibit a morphology related to a subterranean lifestyle (Cylindrachetidae). Crato Formation fossils have hind legs that are enlarged and do not have a cylindrical body or reduced compound eyes, nor do they lack wings as in Cylindrachetidae. The morphology of the fossil specimens are more like extant Tridactylidae and Ripipterygidae species. Extant species have forelegs with long teeth for digging, but still posses long hind wings. These two families live near-water sources, such as ponds, rivers, streams (Günther, 1994b; Deyrup 2005; Baena-Bejarano 2015). Tridactyloids use their forelegs for digging and tunnelling. As suggested by Martins-Neto (1990), Crato Formation fossils probably occupied a habitat similar to current tridactyloids based on morphology. Like other fossils of the Crato Formation, tridactyloids are allochthonous fauna that were deposited into the lagoon.

Crato Formation fossils provide morphological evidence against and in favor of a monophyletic Mongoloxyinae. Morphological evidence against monophyly are the features that are probably synapomorphies of Tridactylidae and Ripipterygidae found in the species. For example, cerci segmentation has been widely used to split both families, but *Atavidactylus* and

Geodactylus display cerci with two-segments and *Birmitoxya* with one segment. Segmentation of cerci is obscured in the other fossils. Metafemora margins are convex in Tridactylidae and straight in Ripipterygidae. *Atavidactylus, Gigantoteras* (ventral view) and *Geodactylus* (dorsal view) display more alike tridactylid metafemur margins. *Cratodactylus, Megalopos, Cratoscrofula* (dorsal view), *Baisoxya,* and *Monodactyloides* (these last two species reviewed from drawings) display more alike ripipterygid metafemur margins. In fact, other features of the fossil that are similar to Ripipterygidae are the large compound eye of *M. kelleneri,* the frons process of *Cratodactylus,* the pronotum designs of *C. ferreirai*, and lack of teeth on foreleg. Other external characters are obscure, such as terminalia, ocelli, tibial spurs, tibial lamellae, and/or metatarsi. Tridactylidae and Ripipterygidae extant species co-occurred in Brazil. Song *et al.* (2015) provided a divergence time-estimate analysis for Orthoptera. This analysis places the divergence node of Tridactylidae and Ripipterygidae 153.45 million years ago with a large 95% node interval from the early Jurassic to the mid Cretaceous. In fact, Crato Formation fauna is late Aptian slightly overlapping with the end of this divergence period estimation. These fossil samples not only represent some of the oldest fossil tridactylids (Tridactylidae), but they also could represent some of the oldest fossil ripipterygids. In contrast, they all share the thorax length, the shortened forelegs (mesofemur), and the rich venation. Wing venation is considered a plesiomorphy (Azar & Nel 2008; Heads 2010a), and the other two characters (thoracic and mesofemur length) could rather be simplesiomorphies for the group, leading us to expect a common ancestor of Tridactylidae and Ripipterygidae with reduction of the thorax that is shared between these two families. This hypothesis seems more plausible than multiple lineages with reduction of the meso-metathorax. Further research should test the monophyly of this subfamily and ancient families.

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Tables and Figures

TABLE 4.1. List of fossil species in Tridactyloidea (Orthoptera: Caelifera)

Taxa	**Authority**	**Time interval (Ma)**	**Country**
Cretoxya rasnitsyni	Gorochov, Jarzembowski & Coram, 2006	Lower Cretaceous Berriasian 145.0 – 139.8	England
Cratodactylus ferreirai	Martins-Neto, 1990	Lower Cretaceous Aptian 125.0 – 113.0	Brazil
Megalopos kellneri	(Martins-Neto, 1990)	Lower Cretaceous Aptian 125.0 – 113.0	Brazil
Cratoscrofula carinata sp. nov.		Lower Cretaceous Aptian 125.0 – 113.0	Brazil
Gigantoteras brachykolos sp. nov.		Lower Cretaceous Aptian 125.0 – 113.0	Brazil
Atavidactylus fossorius sp. nov.		Lower Cretaceous Aptian 125.0 – 113.0	Brazil
Geodactylus fortis sp. nov.		Lower Cretaceous Aptian 125.0 – 113.0	Brazil
Baisoxya dolichopterus	(Sharov, 1968)	Lower Cretaceous Aptian 125.0 – 113.0	Siberia
Mongoloxya ponomarenkoi	Gorochov, 1992	Lower Cretaceous Aptian 125.0 – 113.0	Mongolia

TABLE 4.1. (continued)

Monodactyloides curtipennis	Sharov, 1968	Lower Cretaceous Aptian 125.0 – 113.0	Russia
Burmadactylus grimaldii	Heads, 2009	Upper Cretaceous Cenomanian 100.5 – 93.9	Myanmar
Cascogryllus lobiferus	Poinar, 2018	Upper Cretaceous Cenomanian 100.5 – 93.9	Myanmar
Birmitoxya intermedia	Gorochov, 2010	Upper Cretaceous Cenomanian 100.5 – 93.9	Myanmar
Guntheridactylus grimaulti	Azar & Nel, 2008	Eocene MP 7 55.8 – 48.6	France
Mirhipipteryx antillarum	Heads, 2010	Early Miocene (Burdigalian) 20.44 – 15.97	Dominican Republic
Ellipes dominicana	Poinar, 2018	Early Miocene (Burdigalian) 20.44 – 15.97	Dominican Republic
Archaeoellipes engeli	Heads, 2010	Miocene Burdigalian - Langhian 20.44 – 13.82	Dominican Republic

TABLE 4.2. Original and new measurements (in mm) of type specimens (Martins-Neto 1990). *Value recalculated and modified from original: 0.26.

		Taxa	L1	L2	L3	L4	L3/L2
GP/1T-1649	Holotype	*C. ferreirai*	10.0	7.5	3.5	5.0	0.46
GP1T_1649	New		10	7.4	3.9	3.2	0.52
GP1T_1650	Paratype		7.5	5.0	2.5	4.5	0.50
	New		7.2	6.1	2.6	3.5	0.44
GP1T_1651	Paratype		9.0	7.0	3.5	4.0	0.50
	New		8.7	6.7	3.3	3.9	0.50
AMA-I-034	Paratype		9.0	6.0	3.0	4.0	0.50
CV-2352	Paratype		7.5	6.0	3.0	3.0	0.50
CV-2353	Paratype		?	7.5	3.5	4.0	0.46
CV-2359	Paratype		7.0	5.0	2.5	3.0	0.50
CV-2436	Paratype		13.0	9.5	4.5	6.0	0.47
CV-2438	Paratype		8.5	6.5	3.5	4.0	0.54
GP/1T-1652	Holotype	*Megalopos kellneri comb. nov*	9.0	7.0	2.0	3.5	**0.28***
	New		8.6	5.4	2.9	3.4	0.53
CV-1010	Paratype		10.0	7.5	2.0	5.5	0.26
CV-2037	Paratype		11.0	8.0	2.0	6.0	0.25
CV-2039	Paratype		7.0	5.0	1.5	4.5	0.30
CV-2520	Paratype		7.5	6.0	1.8	4.5	0.30

TABLE 4.3. Measurements (in mm) of fossil samples from AMNH following Martins-Neto 1990

Taxa	Sample No.	L1	L2	L3	L4	L3/L2
Atavidactylus fossorius sp. nov.	44480	14.29	12.01	6.21	6.19	0.52
Cratoscrofula carinata sp. nov.	SA45112	6.48	4.34	2.36	2.77	0.54
C. ferreirai	SA45371	13.07	8.90	4.32	7.09	0.49
C. ferreirai	SA45380	11.47	9.75	4.04	7.52	0.42
C. aff. *ferreirai*	SA45391	N/A	N/A	N/A	3.48	0.55
Mongoloxyinae	SA45290	N/A	8.02	4.09	4.40	0.51
Mongoloxyinae	SA45388	14.35	10.54	5.52	5.56	0.52
Geodactylus fortis sp. nov.	43374	13.05	9.52	4.97	6.21	0.52
Gigantoteras brachykolos sp. nov.	SA45262	19.57	14.71	6.07	9.73	0.41
Tridactyloidea	SA45291	N/A	5.64	2.25	3.88	0.40
Tridactyloidea	SA45517	N/A	N/A	N/A	5.58	1.18

TABLE 4.4. Additional measurements (in mm) frequently used in Tridactyloidea taxonomy applied to Crato Formation fossils from the AMNH.

Sample	Pronotum length	Pronotum width	Tegmina	Hind wing	Metafemur (L4)	Interocular distance
SA45517			7.19	12.01	5.58	
SA45391	1.14			6.50	3.48	
SA45112	0.34	1.36		5.37	2.77	
SA45388	2.05	3.48	5.99	10.81	5.56	0.60
43374	2.11	3.35	5.05	9.59	6.21	0.71
44480	2.25	3.13	6.80	9.25	6.19	0.66
SA45290		1.51			4.40	
SA45371					7.09	
SA45380	1.79	3.09			7.52	
SA45262	1.19	4.38			9.73	1.76
SA45291	1.04	1.82			3.88	0.67

FIGURE 4.1. Crato Formation location and statrigraphy. a) Map showing the location of the Crato Formation (circle in purple) at the Northeast of Brazil and the states Ceará, Pernambuco and Piauí. Map created with Qgis (QGIS Development Team, 2019). b) Simplified statrigraphy of the Crato Formation. Modified from Martill & Heimhofer (2007) and Heads (2009). Laminated limestones in gray and dotted lines. Gneiss in dashed line. Thickness of Formations and Members can vary from this representation.

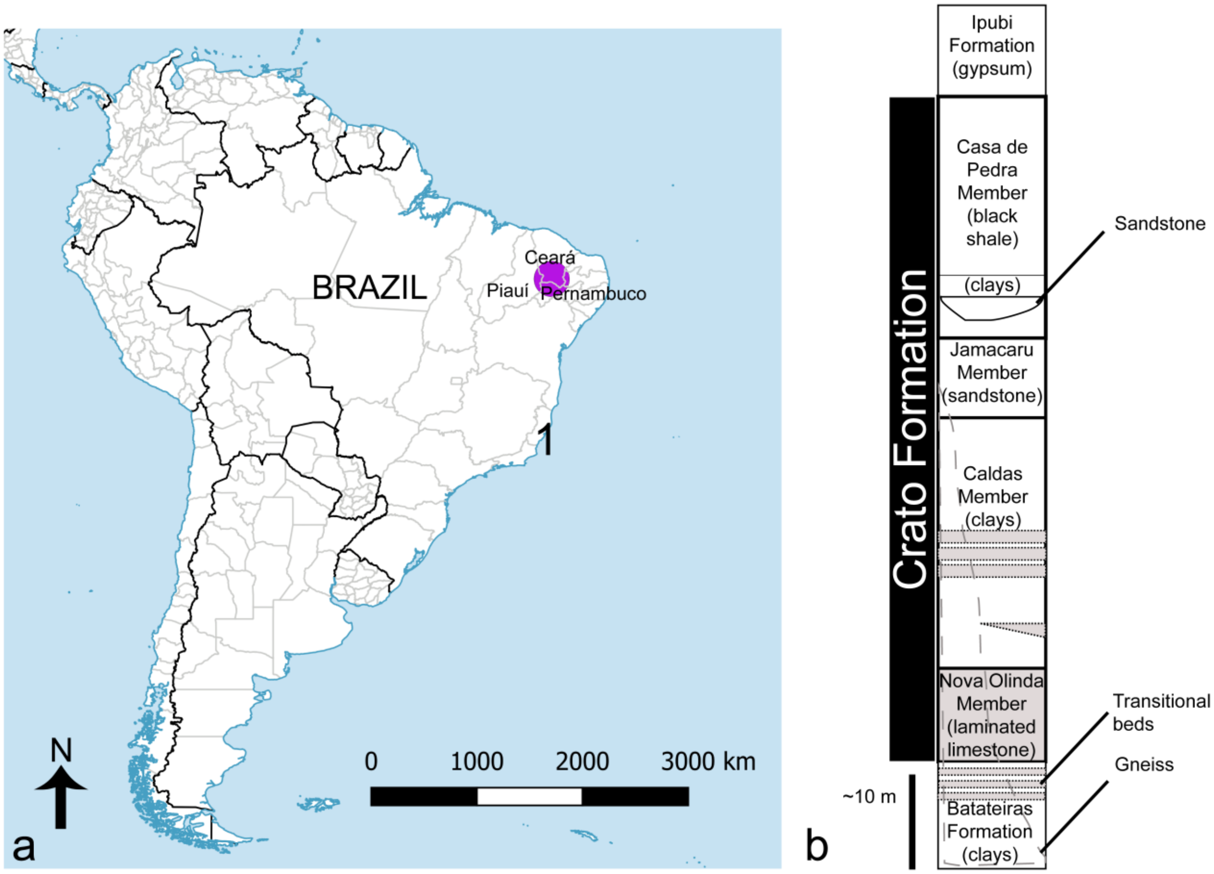


FIGURE 4.2. Holotypes and paratypes of *Cratodactylus* Martins-Neto 1990 (Orthoptera: Tridactylidae: Mongoloxyinae) from Crato Formation, Crato, Bazil. a) Photographs credit: Dr. Cibele Voltani and Dr. Juliana de Moraes Leme, Department of Sedimentary and Environmental Geology (GSA) University of São Paulo, Brazil. Scale bar 1 mm. Figure 1. *Megalopos kellneri* comb. nov. (holotype GP/1T-1652). b) *Cratodactylus ferreirai* Martins-Neto, 1990 (holotype GP/1T-1649). c) *Cratodactylus ferreirai* Martins-Neto, 1990 (paratype GP/1T-1650) from type locality. d) *Cratodactylus ferreirai* Martins-Neto, 1990 (paratype GP/1T-1651) from type locality.

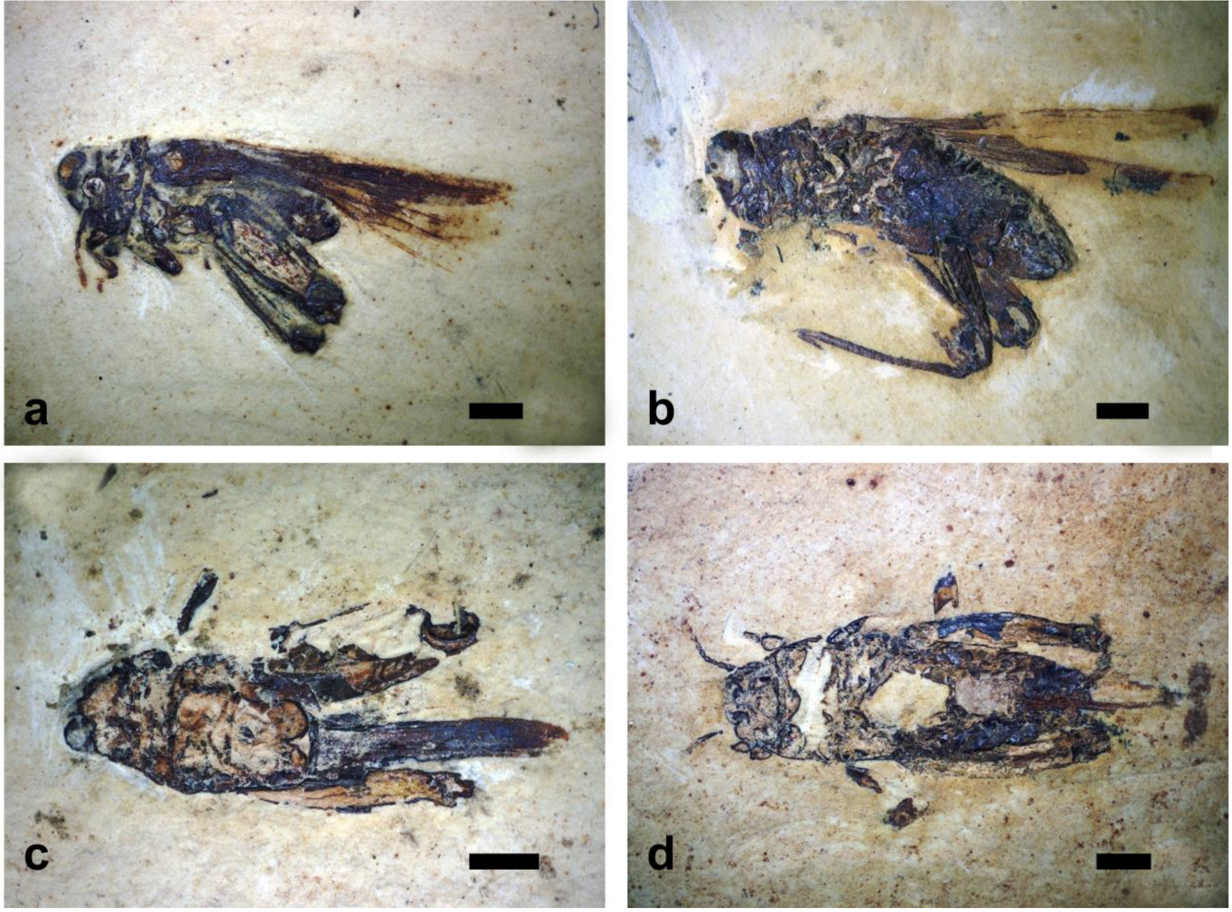


FIGURE 4.3. Specimens reviewed from Crato Formation, Crato, of Brazil. Scale bar 1 mm. Photographs credit: Valeria Estrada-Corredor. High School volunteer summer 2017. a) *Gigantoteras brachykolos* sp. nov. (holotype SA 45262). b) *Cratoscrofula carinata* sp. nov. (holotype SA45112). c) *Atavidactylus fossorius* sp. nov. (holotype 44480). d) *Geodactylus fortis* sp. nov. (holotype 43374). e) Mongoloxyinae (SA 45388). f) *Cratodactylus ferreirai* Martins-Neto, 1990 (SA45371). g) *Cratodactylus ferreirai* Martins-Neto, 1990 (SA45380). h) *Cratodactylus* aff. *ferreirai* Martins-Neto, 1990 (SA 45391). i) Tridactyloidea Nymph (SA 45291). j) Mongoloxyinae, nymph (SA 45290). k) Tridactyloidea Adult (SA 45517). Arrows with abbreviation pt: pattern of distribution of tubercles and mca: metafemur inner corner angle.

FIGURE 4.4. Illustration of new monotypic genera of Mongoloxyinae (Orthoptera: Tridactylidae) from Crato Formation, Crato, Bazil. Scale bar 1 mm. a) *Gigantoteras brachykolos* sp. nov. (holotype SA 45262). b) *Cratoscrofula carinata* sp. nov. (holotype SA45112). c) *Atavidactylus fossorius* sp. nov. (holotype 44480). d) Tegmen of *A. fossorius* sp. nov. e) *Geodactylus fortis* sp. nov. (holotype 43374).

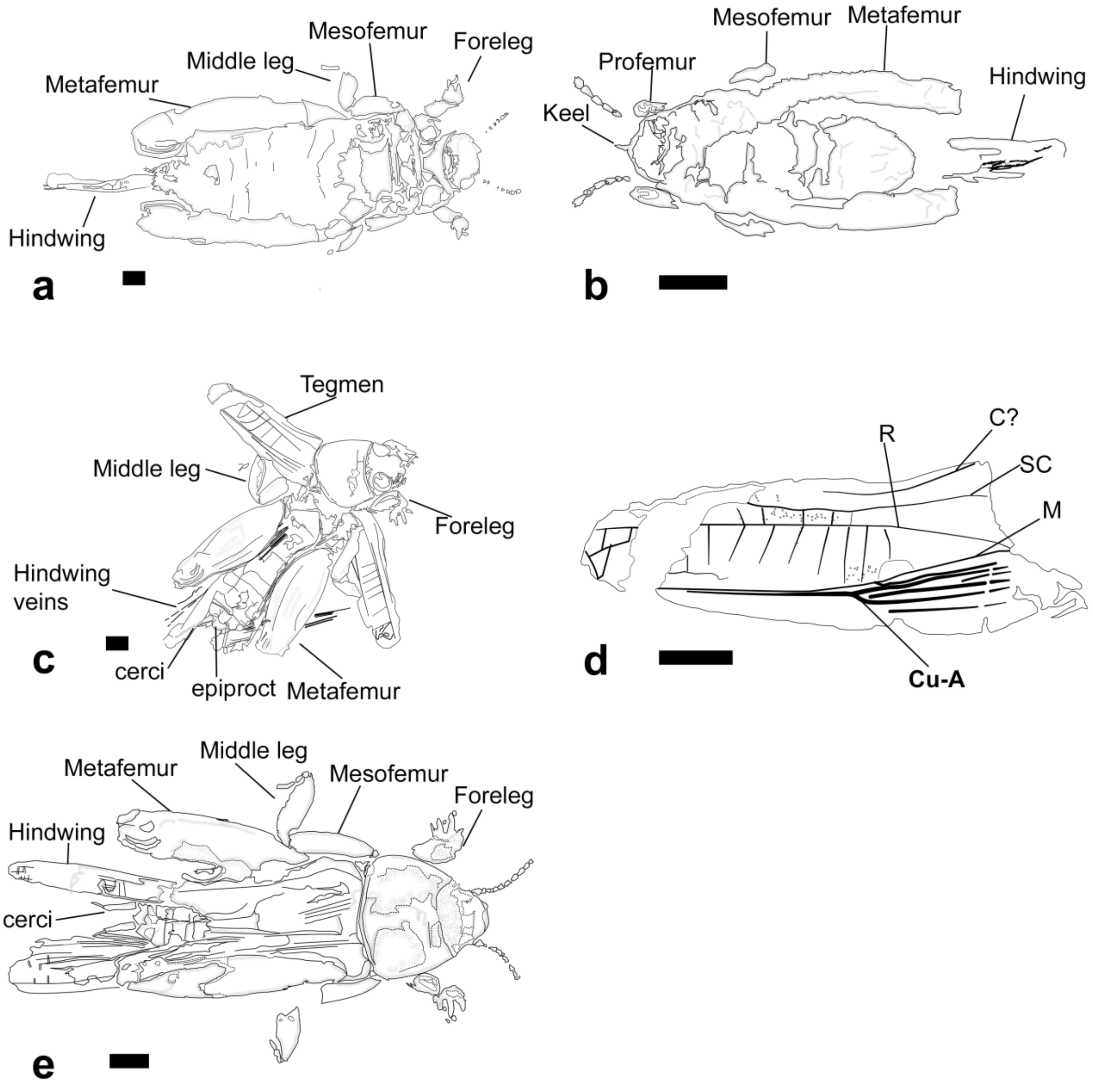
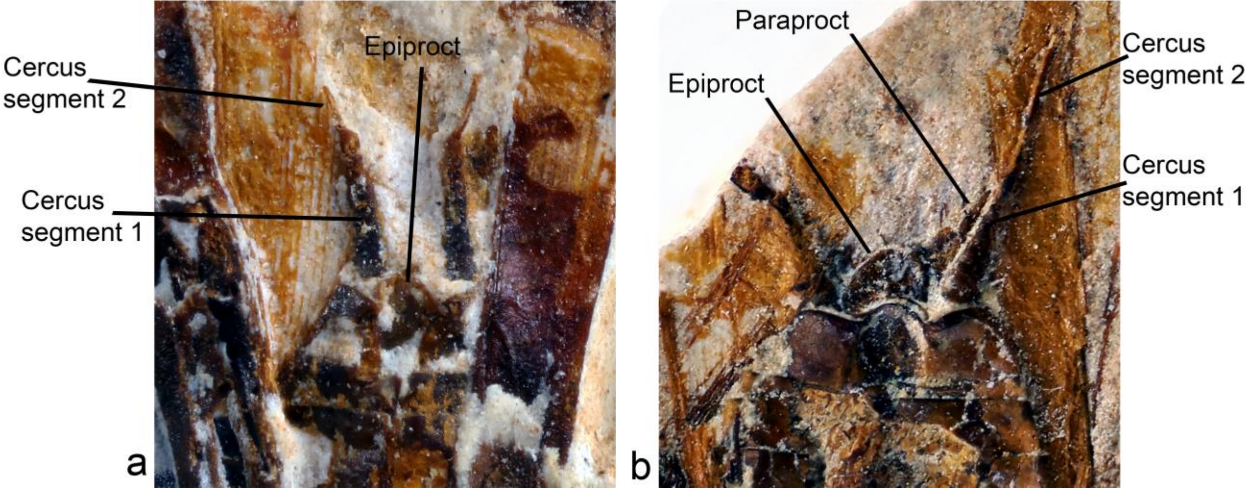


FIGURE 4.5. Terminalia with parts of species with two-segmented cerci from Crato Formation, Crato, Brazil. a) *Atavidactylus fossorius* sp. nov. (holotype 44480). b) *Geodactylus fortis* sp. nov. (holotype 43374).



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CHAPTER 5: NEW TRIDACTYLOIDEA (ORTHOPTERA: CAELIFERA) FROM BURMESE AMBER WITH COMMENTS ON PALEOCOLOGY AND FOSSIL BIAS

Abstract

Crickets and grasshopper fossils are poorly documented in Burmese amber (Burma), and the only known caeliferan fossils belong to the superfamily Tridactyloidea (Insecta: Orthoptera: Caelifera). Here, I describe a new extinct family of pygmy mole crickets Ripidactylidae nov. with two adults (*Ripidactylus chimera* gen. et sp. nov. and *Pterocalyptus ceratus* gen. et sp. nov.) and a nymph. The new family, with one-segmented cerci, is recognized by the presence of a plate-like lobe on the prosternum, absence of lateral ocelli, adults with 10 to 14 antennomeres, female with developed ovipositor valves curved and directed upward with setae. *Paraxya obscurus* sp. nov. is described and the genus *Paraxya* is assigned to the subfamily Dentridactylinae. *Paraxya* is the first genus in the subfamily with well-developed wings and the third record for this group in Burmese amber. Our placement of *P. hui* and *Paraxya obscurus* sp. nov. provides additional evidence of a wider paleobiogeographic distribution of dentridactylines. I discuss the higher abundance of tridactyloids in burmite and attribute the abundance to specimen size, taxonomic bias, and paleoecology.

Introduction

Burmese amber is one of the most important deposits for the study of mid-Cretaceous fauna (Cenomanian: 100.5–93.9 MA (Cohen *et al.* 2018)). This deposit in Burma (Myanmar) (Grimaldi & Engel 2005; Ross *et al*. 2010) is highly diverse; several species, families, and orders of arthropods and other insects have already been recorded and continue to be described (Mey *et al*. 2017). Knowledge of insect fossils has increased in recent decades, although gaps remain for many periods and groups. Orthopteran fossils are rare in Burmese amber; they represent less than 0.1% of all arthropods inclusions studied at two collections (Grimaldi *et al.* 2002). Additionally, determining the placement and relationships among fossil taxa is often difficult because: (1) fossils present a collection of derived and plesiomorphic characters that make it difficult to assign them to modern groups; (2) specimens are incomplete and/or not all the parts are visible or accessible; (3) imaging techniques may be expensive; and (4) relevant samples need to be sorted from among thousands of samples in paleontological collections (dark data). There are only eight known orthopteran species recorded in Burmese amber (Ross *et al.* 2010; Guo *et al.* 2017; Heads *et al*. 2018; Cao *et al.* 2019), or nine if an identified species of *Burmelcana,* Peñalver & Grimaldi, 2010 (Elcanidae) is included (Fang *et al.* 2015). About half of these records are of enigmatic, minute crickets in the superfamily Tridactyloidea (Heads 2009; Gorochov 2010; Poinar 2018; Cao *et al.* 2019).

Pygmy mole crickets (Tridactylidae), mud crickets (Ripipterygidae), and sandgropers (Cylindrachetidae) are minute (~0.5 cm) to medium (~7 cm) size orthopterans in the superfamily Tridactyloidea (Orthoptera: Caelifera). Their biology is similar as they inhabit their fossorial and semiaquatic habits. They are found in moist sand and/or mud at the shoreline of lakes, streams, and marshes (Hebard 1934; Deyrup 2005). However, these three families are distinct and display several differences in their internal and external morphology and geographic distributions (Günther 1992; Heads 2009; Cigliano *et al*. 2016). Tridactyloids are a small group in Caelifera in comparison with pygmy grasshoppers (Tetrigidae), and grasshoppers (Acrididae). In fact, they are the only caeliferans recorded from burmite (Table 5.1). The diversity of samples represents a great opportunity to study the evolution of this group and to make past-present comparisons between the biogeography, taphonomy (fossilization processes), and species diversity. Here, I recorded five specimens from Burmese amber in the superfamily Tridactyloidea. A new species is described for the subfamily Dentridactylinae, and a new family of pygmy mole crickets is described with two new genera and species. Nymphs are determinate to family level.

Materials and Methods

Three fossil specimens were studied from the Nanjing Institute of Geology and Paleontology Chinese Academy of Sciences and two from the paleontological collection at Illinois Natural History Survey (INHS). Fossils were prepared using standard techniques in the laboratory of Sam Heads, Illinois Natural History Survey (INHS) at the University of Illinois Urbana-Champaign. Amber samples were separately embedded in Epotek 301-2, cut, and polished. The specimens were described using a Zeiss SteREO Discovery.V20 zoom stereomicroscope with Plan-Apochromat S 0.63x FWD 81 mm and Plan-Apochromat S 1.5x FWD 30 mm objectives. Measurements were taken using the Zen 2 (blue edition) software package. Photographs were taken using an AxioCam HRc Rev. 3 attached to the microscope. Before imaging, a drop of glycerine was placed on top of the sample and then a microscope cover slip was placed on the glycerine. This procedure helped reduce the visibility of imperfections on the amber surface to make it more suitable for imaging. Images were stacked using Helicon Focus 6, and mosaics were assembled in Adobe Photoshop CC 2015. Illustrations were created in Adobe Illustrator CC 2015.

The classification follows Orthoptera Species File (Cigliano *et al.* 2016). The nomenclature follows Baena-Bejarano and Heads (2015, 2018). Wing venation follows Gorochov *et al*. (2006).

SYSTEMATIC PALEONTOLOGY

Order ORTHOPTERA Olivier 1789

Suborder CAELIFERA Ander, 1936

Superfamily TRIDACTYLOIDEA Brullé, 1835

Family TRIDACTYLIDAE Brullé, 1835

Subfamily DENTRIDACTYLINAE Günther, 1979

Genus *PARAXYA* Cao, Chen & Yin, 2019

Type species. *Paraxya hui* Cao, Chen & Yin

***Paraxya obscurus* sp. nov.**

Figure 5.1a-d

Derivation of name. The specific epithet *obscurus* refers to the dark coloration of the sample embedded in the amber. The small size and dark coloration obscured characters and details that were only visible only with illumination from multiple light sources.

Holotype. Female (No. NIGP166934), Adult = in Upper Cretaceous amber from Burma (Myanmar); Katchin, Tanai Village, on Ledo Rd. 105 km NW Myitkyna. Nanjing Institute of Geology and Paleontology Chinese Academy of Sciences, China.

Diagnosis. The new species is cryptically similar to *P. hui* in the tegmina apically widened, presence of fully developed hind wings reaching the tip of the abdomen, metatibia without swimming plates, and metafemur oblong (dorsal and ventral margins subparallel). However, it is differentiated from *P. hui* by [1] paraproctal lobe longer than cerci, [2] basal row of minute spines on metatibia, [3] apical segment of cerci longer than basal.

Description

Female (holotype). Body length 3.1 mm; pronotum length 0.6 mm; tegmina length 1.3 mm, hind wing 2.7 mm; metafemur 2.1, metatarsus 0.4 mm. (Figure 5.1a-d).

Head hypognathous, semi-globose; vertex globular. Ocelli not visible. Compound eye right eye incomplete. Left side of head below and including part of the compound eye are missing; two-segmented palpae are visible but it is indistinguishable as to labial or maxillary. No other mouth parts are distinguishable. Antennae filiform, incomplete; left antenna 8 antennomeres, right antenna 4 antennomeres. Scape and pedicel not distinguishable.

Thorax. Pronotum shape like half-cylinder; anterior margin straight, posterior margin rounded. Pronotum is wider near midline. Subapical lateral corner slightly pointed (just before reaching the apical margin) with a seta. Mesonotum with small triangular shape observable between tegmina. Metanotum covered by tegmina. Tegmina wide at the apex, anterior light, rounded spot; tegmina extends to midpoint of the abdomen; apical margin blunt. Hind wings long, slightly longer than abdomen, 6 longitudinal veins near anterior margin of the wing reaching the apex. Anal field with intercalary veins, intercalary veins not evident in costal field.

Forelegs slightly fossorial, black, or dark brown. Procoxa not visible. Profemora elongated. Protibia quadrate, covered with acuminate setae; distally covered with spine-like and acuminate setae. Two tarsal segments; basitarsus short, distal tarsus elongated with ungues. Middle legs (walking legs) longer than forelegs, slightly flattened laterally. Mesocoxal margin distally rounded. Mesotrochanter quadrate. Mesofemora elongated, distal margin slightly wider than basal margin; ventral margin with spines. Mesotarsi two-segmented, distal segment long and slender. Ungues long, curved, and with wide base. Metacoxa small. Metafemora oblong, large; it covers the abdomen, and reaches the last abdominal segment; dorsal and ventral margin subparallel. Semi-lunar process not evident; cover plate oblong with a seta on distal margin. Metatibia oblong, long and slender; ventral margin indented near the base (Figure 5.1c); dorsal margin with spines, which are small and variable in size. Interspinal distance decreases moving from base to apex. A pair of subapical and apical spurs are present near the apex of the tibiae. The spur tips are curved and tooth-like. Groups of 2–3 setae are present before the tooth, on the inner margin. The subapical spur is 0.6x smaller than the apical spur. Metatarsus is large and long, with a ventral row of hairs; the tarsal segment is split into two plates with different length. The outer plate is shorter than the inner plate, and the tip is curved and tooth-like in both. However, the shorter plate tooth looks subapical with respect to the tip of the inner plate.

Abdomen. Black or dark brown; segmentation not distinguishable. The anterior and mid-section of the abdomen is not directly observable. Cerci two-segmented, covered with long setae. Base of cerci brown, left cercus brown; right cercus hyaline with brown areas, distal area dark brown. Apical segment of cerci longer than basal (~1/3 of apical segment length). Paraproctal lobe two-segmented; basally hyaline with brown areas, distally dark brown; strong setae at the tip of the paraproctal lobe. The terminalia is homogeneously brown. The apical area is elongated and distally sclerotized. The sclerotized area resembles a couple of bi-lobed ovipositors; the structure is indeterminate due to size and limited visual (Figure 5.1d).

Remarks. *Paraxya obscurus* sp. nov. share with the holotype of *P. hui* the presence of fully developed hind wings reaching the tip of the abdomen, tegmina apically widened, and the metafemur oblong, with dorsal and ventral margins subparallel. However, *Paraxya obscurus* sp. nov. is recognized by having a basal row of minute metatibial spines and the apical segment of the cerci being longer than the basal (these characters are unknown in *P. hui*). Cao *et al.* (2019) ambiguously compared the species *P. hui* to the genus *Xya* in Tridactylinae and to the genus *Burmadactylus* in Dentridactylinae. However, the authors did not assign the species to any subfamily. The genus *Paraxya* is placed in the subfamily Dentridactylinae based on the developed metatarsi and the presence of a subapical tooth on the metatarsi. While these characters and the monophyly of the subfamily have not been tested in a systematic approach, these are characters traditionally used in the taxonomy of the group (Günther 1979; Baena-Bejarano & Heads 2018). Cao *et al.* (2019) claimed the metatarsus of *Paraxya* is absent. However, the metatarsus is evident in *P. hui* from their Figures 4 and 5. The metatarsi are developed and larger than the metatibial spurs. In fact, Cao *et al.* labelled incorrectly the metatarsi as asp (apical spur). The authors labelled the apical spurs as sasp (subapical spurs), and they failed to recognize the subapical spurs. The genus *Paraxya* differs from all the known species in Dentridactylinae by the presence of hind wings and possibly by the length of the apical segment of the cerci, which is longer than the basal. This character is unknown in *P. hui*. Furthermore, these species of *Paraxya* differ from species of *Bruntidactylus* and *Guntheridactylus* by the absence of tibial lamellae. It is distinguished from *Dentridactylus* by the long, widened tegmina that reaches almost half of the abdomen length and from *Paratridactylus* by weak dorsal metatibial spines. A character that separates *Paraxya obscurus* sp. nov. from *Burmadactylus grimaldii* is the short paraproctal lobe that in *Paraxya obscurus* sp. nov. is longer than or as long as the cerci; however, the species differ in sex. *B. grimaldii* is a male with one-segmented paraproctal lobes and *Paraxya obscurus* sp. nov. is a female with two-segmented paraproctal lobes. This difference needs to be considered with extreme caution. In fact, *P. hui* is a male sharing the short paraproctal lobes with *B. grimaldii*. *P. hui* differs by the presence of 3–4 long hairs in the paraproctal lobes; these paraproctal processes were incorrectly identified as cerci in Cao *et al.* 2019. I note in *P. hui* that hairs are present on one paraproctal lobe, but not on both lobes (Cao *et al.* 2019, Figure 5). For instance, the species *Cascogryllus lobiferus* is the only species in the subfamily that does not bear a subapical tooth. Therefore, the species in *Paraxya* differ by the presence of this character and absence of paired prosternal tubercles. One difference from the other genera in Dentridactylinae is that the second cercal segment is shorter than the apical, whereas in *C. lobiferus* they are of equal length.

Dentridactylinae

Figure 5.1e

Material. Adult (INHS 10330) in Upper Cretaceous amber from Burma (Myanmar); Katchin, Tanai Village, on Ledo Rd. 105 km NW Myitkyna. Paleontological collection at Illinois Natural History Survey (INHS)

Description. Body length 1.8 mm; interocular distance 0.2 mm; pronotum length 0.5 mm, width 0.5 mm; wingpads 0.2 mm; metafemur 1.4 mm (Figure 5.1e).

Head. Hypognathous. Vertex with epicranial suture and carinae from compound eye to vertex. Median ocelus small. Compound eyes large and rounded. Clypeus quadrate. Maxillary palps long, distal segment larger than previous segments, brown. Labial palps three-segmented, distal segment with thick setae. Antennae filiform with ~8 antennomeres. Scape thicker and larger than pedicel. Flagellomere 1 longer than pedicel and two times longer than second flagellomere. Second flagellomere quadrate and shorter than all flagellomeres. Distal flagellomere long.

Thorax. Pronotum brown and shield-like, covering mesonotum and extending laterally. Medial suture. Anterior suture at 1/3 of anterior margin. Lateral margin straight. Pronotum in dorsal view is wider near posterior margin (subposterior). Posterior margin of pronotum rounded. Wingpads small. Forelegs fossorial/walking, brown. Procoxa rectangular. Profemora rectangular densely covered in setae. Protibia ellipsoid, densely covered by setae; four long spines at apex. Tarsi two-segmented, basitarsus short and distal tarsus elongated with ungues. Middle legs brown and robust. Mesocoxa short. Mesofemora rectangular. Mesotibia shorter than mesofemora Mesotibia ellipsoid. Tarsal segments: basitarsus with adhesive structures; distal tarsus with two long slender terminal ungues. Hind leg robust, brown. Metacoxa not visible. Metafemora robust, brown with a darker brown coloration on semi-lunar process; cover plate reduced. A pair of short subapical spurs with a terminal tooth are present. Apical spurs not visible. Metatarsus robust and large, with apical and supapical tooth. Metatarsus larger than spurs.

Abdomen. Segments wider than longer. Last tergite pointed. Terminalia: cerci two-segmented elongated, longer than paraproct; long setae at apex. Basal segment robust and quadrate; apical segment coniform and slender. Paraproct cerciform with strong setae.

Remarks. The nymph (INHS 10330) is placed in the subfamily Dentridactylinae by the cerci with two segments (Tridactylidae), and the metatarsi with subapical tooth.

Order ORTHOPTERA Olivier 1789

Suborder CAELIFERA Ander, 1936

Superfamily TRIDACTYLOIDEA Brullé, 1835

Family RIPIDACTYLIDAE nov.

Derivation of name. After *Ripidactylus* by monotypy.

Type genus. *Ripidactylus* gen. nov. by monotypy.

Type species. *Ripidactylus chimera* sp. nov.

Diagnosis. The family can be distinguished by: [1] Prosternum with a square-shaped plate extending over the labium, [2] absence of lateral ocelli.

Genus *RIPIDACTYLUS* nov.

Derivation of name. The genus name *Ripidactylus* is given after combining the names of the families Ripipterygidae and Tridactylidae. The specimen displays a combination of characters that occur separately in each of the previous families.

Type species. *Ripidactylus chimera* sp. nov.

Diagnosis. Same as in the family.

***Ripidactylus chimera* sp. nov.**

Figures 5.2a, 5.3a-c

Derivation of name. The specific epithet *chimera* (Latin *chimaera*, from Greek *khímaira* = chimera) refers to the mythological monsters that display parts from different animals.

Holotype. Female (No. NIGP166935), Adult = in Upper Cretaceous amber from Burma (Myanmar); Katchin, Tanai Village, on Ledo Rd. 105 km NW Myitkyna. Nanjing Institute of Geology and Paleontology Chinese Academy of Sciences, China.

Diagnosis. The new species can be distinguished by: [1] prosternum with a square-shaped plate extending over the labium, [2] antennae with 14 antennomeres, [3] absence of lateral ocelli, [4] metatarsus shape trapezoid (almost subparallel shape, that thin at the base and apex), [5] valves upward, [6] tegmina venation, [7] tegmina widened basally.

Description. Female (holotype). Body length 7.8 mm, body length (including wings) 8.4 mm; interocular distance 0.3 mm, median ocellus diameter 0.1 mm; pronotum length 1.6 mm, pronotum width 1.5 mm; tegmina length 3.1 mm, hind wing 6.4 mm; metafemur 5.0 mm, metatarsus 0.8 mm (Figure 5.2a, 5.3a-c).

Head. Hypognathous. Vertex globular. Median ocellus large. Lateral ocelli apparently absent; the frontal view of the right eye is slightly covered, and the left eye is slightly depressed, but observation in different views did not revealed a lateral ocellus (Figure 5.3b). Patch that circumscribes the anterodorsal margin of compound eyes present. Compound eyes large and oblong. Clypeus rectangular with setae directed downward. Lateral edge of frons proximal to clypeus with a seta in each side. Labrum larger than clypeus with metallic coloration. Maxillary palps 5 segmented. Labial palps present, basal 3-segmented. Segment 2 and segments 3 elongated, interior side with setae. Antennae with 14 antennomeres. Scape longer than pedicel. Scape and pedicel wider than flagellomere 1. Flagellomere 1 (1.5x) longer than pedicel. Flagellomere 2 and 3 quadrate, (~2x) shorter than flagellomere 1. Flagellomere 3 slightly longer than 2 and 3, and distal margin wider than basal margin. Flagellomere 5 and 6 thinner and slightly longer than 3.

Thorax. Pronotum shield-like, covering mesonotum and extending laterally with posterolateral margin rounded; left side dark brown or black, right side metallic; sulcus present. Prosternum with a square-shaped plate extending over the labium; distal margin with setae pointing towards mouthparts. Metanotum forming a triangle, covered by the tegmina. Tegmina long and wide, the apex of tegmen reaches 1/3 of the abdomen. Brown, but with iridescent gleam on all areas except a dark brown band at the apex of tegmen. Longitudinal veins and a group of short cross veins present (Figure 5.3c). Hind wings longer than abdomen, hyaline with a dark brown band in the apex. Several longitudinal veins. Forelegs fossorial/walking, brown. Procoxa rectangular. Protrochanter elongated, rectangular with ventrodistal paired setae. Profemora rectangular with sparse setae. Protibia densely covered by both acuminate and spine-like setae, three large distal spines. Tarsi two-segmented, basitarsus short, distal tarsus elongated; ungues curved. Walking middle legs, brown. Mesocoxa rectangular. Mesotrochanter small. Mesofemora rectangular, elongated with a short external distal lobe, and lighter brown coloration distally covering area from lobe to the middle of mesofemur; mesofemora longer than mesotibiae. Mesotibia oblong with a ventral row of setae on inner side; cream/white band near the base. Tarsi two-segmented, basitarsus with adhesive structures, distal tarsus elongated with one long terminal unguis, a fraction of the other unguis is present. Hind leg brown with iridescent gleam. Metacoxa quadrate. Metafemora large, oblong, with dorsal margin extended; semilunar process dark brown, lobe margin rounded with a seta. Metatibia thin and long; two rows of spines on dorsal surface, 15 inner, ~15 outer (positive count confounded by optical discontinuity); a pair of short subapical spurs is present. The outer subapical spur is incomplete on right leg. Inner subapical spur with a terminal tooth, a seta is present on each side of the tooth; this spur has a thin outer fin parallel to the inner sclerotized fin, and with a minute sclerotized terminal tooth. Subapical spur shorter than apical spur. The outer apical spur is incomplete on right leg; inner apical spur with a terminal tooth; the apical tooth with 1–3 setae, right leg subapical tooth is an artefact of the lighter sclerotized fin; the apical spur of the left leg does not have a subapical tooth, and the fin is complete. Metatarsus shorter than apical spur, but longer than subapical; trapezoid, subparallel along its length, that thin at the base and apex. Metatarsus with a terminal tooth, and with an outer subapical tooth; ventral edge of outer fin with one row of setae.

Abdomen. Brown with iridescent gleam, ~10 abdominal segments; abdominal segmentation is clear only in the last three terminal segments. The abdominal pleura is distorted. Sternum with setae. Terminalia: cerci unsegmented, cone-like with wide base, setae present. Paraproct two-segmented, strongly covered with setae. Basal segment short. Second segment longer than basal segment, apically rounded (left paraproct second segment anomaly shrunken due to preservation). Valve 1 long and slender, directed upward. The tip is slender, pointed, and slightly curved. Long setae present along the entire length. There is a third tip opposite to the previous two that could belong to second valve, but the base is not visible.

Remarks. Unique characters of *Ripidactylus chimera* sp. nov. include the prosternal square-shaped plate and the antennae with 14 antennomeres. While prosternal processes are known in the family Tridactylidae, these are most commonly single tuber-like process (*Afrotridactylus*, *Neotridactylus*), or the exceptional paired tuber-like processes from *C.*

lobiferus. *R. chimera* shares characteristics with Ripipterygidae and Tridactylidae, which are two of the three families in Tridactyloidea. The third family, Cylindrachetidae, has species with cylindrical bodies and other strong fossorial adaptations (reduced compound eyes, short middle and hind legs, wings absent), but that is not the case in Ripidactylidae.

Based on the one-segmented cerci and the developed valves, *R. chimera* could have been placed in Ripipterygidae rather than in Tridactylidae where all the species have two-segmented cerci and undeveloped valves (except in the fossil record: *Paraxya obscurus* sp. nov.). Another character shared with Ripipterygidae rather than Tridactylidae is hypognathism, whereas tridactyloids tend to be prognathous. However, in *R. chimera* the metatarsal shape is different from Ripipterygidae. In Ripipterygidae, the valves and the abdominal segment are directed downward; however, in this fossil species they are directed upward. Moreover, the venation of the tegmina is moderate, and the length is short when compared with Ripipterygidae and *Monodactylus* Sharov 1968. In addition, the tegmina is basally widened. In Ripidactylidae, the hind wings are membranous without a transverse groove or slight sclerotization as observed in *Ripipteryx*. The median ocellus is almost at the same position as the antennae in Ripipterygidae, near the base of the compound eyes. However, in Tridactylidae, the ocelli can be found above the margin of the compound eyes or antennal insertion. The position of the median ocellus in this fossil is similar to Tridactylidae due to distance in between antennae insertion point and median ocellus but it is found midway between the compound eyes in Ripidactylidae.

Genus *PTEROCALYPTUS* nov.

Derivation of name. The genus name *Pterocalyptus* comes from the Greek roots *pteron* “wing” and *calypto* “covered” meaning “covered wing.” The hind wing costal field is tegminoid, covering most likely the remaining membranous wing.

Type species. *Pterocalyptus ceratus* sp. nov.

Diagnosis. The genera can be distinguished by the combination of: [1] antennae with 10 antennomeres, [2] sclerotized hind wings, [3] absence of lateral ocelli.

Pterocalyptus ceratus sp. nov.

Figure 5.2b, 5.3d

Derivation of name. The specific epithet *ceratus* (from Greek *keraia* = antenna or hornlike projection) refers to the antennae with reduced antennomeres ten as opposed to fourteen as in *Ripidactylus*.

Material. Adult (INHS 10328) in Upper Cretaceous amber from Burma (Myanmar); Katchin, Tanai Village, on Ledo Rd. 105 km NW Myitkyna. Paleontological collection at Illinois Natural History Survey (INHS).

Diagnosis. As in genus.

Description. Body length 4.1 mm; pronotum length 1.3 mm; tegmina length 2.0 mm, hind wing 3.7 mm; metafemur 2.9 mm (Figure 5.2b, 5.3d).

Head. Hypognathous. Vertex rounded. Median ocellus small. Lateral ocelli absent. Compound eyes large and oblong. Gena and antennal insertion point brown. Maxillary and labial palps present, but covered by foreleg. Antennae filiform with 10 antennomeres. Pedicel shorter than scape; flagellomere 1 longer than pedicel; flagellomere 2 shorter than flagellomere 1.

Thorax. Pronotum dark brown with edges lighter brown. Pronotum extending flat, lateral margin of pronotum do not extended laterally covering pleura with procoxa partially exposed. Lateral margin concave. Posterior margin rounded. Prosternum with a protuding structure, extending over the labium; with setae on margin. The structure does not seem like a plate, and it is covered by the procoxa. Tegmina short, posterior margin curved with three longitudinal veins. Radial vein does not reach posterior margin. Medial vein reaches posterior margin. No cross-veins in R-M area, but this is concealed by fractures. Costal area of tegmen is obscure. One short anal vein reaches half of tegmen. Hind wings slender. Costal area sclerotized "tegminoid". Forelegs fossorial/walking, brown. Procoxa elongated, rectangular; external margin distally with two setae. Protochanter short, triangle-like. Profemora rectangular. Protibia ellipsoid, densely covered by both hair-like setae and spine-like setae. Tarsal segments elongated; basitarsus shorter than distal segment. Distal segment with ungues. Middle legs, brown. Mesocoxa dark brown, quadrate. Mesofemora rectangular, with two ligther dorsal patches. Mesotibia oblong. Tarsal segments: basitarsus with adhesive structures, and one long outer seta in each side; distal tarsus with two slender terminal ungues. Hind leg brown. Metacoxa small, triangular. Metafemora robust, brown with darker brown on ventral and dorsal edges. Semilunar process black or dark brown with setae on dorsal margin. Cover plate light brown, oblong. Metatibia long, robust with two rows of spines; metatibiae missing distally. Metatarsus missing.

Abdomen 9–10 segmented. Abdominal sterna wider than longer. Subgenital plate with long setae; distal margin narrow and strongly curved, almost umbonate; with four long setae. Terminalia: cerci one segment, elongated, longer than paraproct. Paraproct short, cerciform with a long setae. Paraproct shorter than cerci; do not extend beyond subgenital plate. Structure curved and strongly pointed resembles uncus, but inconclusive due to small size.

Remarks. *Pterocalyptus ceratus* sp. nov. share the cerci one-segmented with Ripipterygidae and Ripidactylidae. However, this species differs from Ripipterygidae by having an ellipsoid mesotibiae, dorsal margin of metafemur curved, and spines on metatibia. This species is placed in Ripidactylidae by the presence of prosternal plate, absence of lateral ocelli, median ocellus midway between compound eyes, and moderate tegmina venation with expanded area between R and M. However, *P. ceratus* differs from *R. chimera* by the 10 antennomeres instead of 14, the semilunar process appears more rounded and elongated in *R. chimera* and the hind wing tegminoid instead of membranous. Although a prosternal process is distinguished in *P. ceratus*, the shape of this process resembles a pointed lobe but is not completely clear from the sample. Other characters that are missing are the metatarsi and metatibial spurs in *P. ceratus*. Only a fragment of the metatibia is preserved. Both samples differ in size with *R. chimera* (7.8 mm) almost twice the length of *P. ceratus* (4.1 mm). However, these samples differ in sex, so sex-related characters are not comparable between species and females are known to be larger than males in Tridactyloidea.

Ripidactylidae

Figure 5.2c, 5.3e

Material. Nymph (No. NIGP166936) in Upper Cretaceous amber from Burma (Myanmar); Katchin, Tanai Village, on Ledo Rd. 105 km NW Myitkyna. Nanjing Institute of Geology and Paleontology Chinese Academy of Sciences, China.

Description. Body length 4.9 mm; interocular distance 0.4 mm; pronotum length 1.3 mm; tegmina length 0.9 mm, hind wing 1.7 mm; metafemur 3.5 mm, metatarsus 0.8 mm (Figure 5.2c, 5.3e).

Head. Hypognathous. Vertex globular. Median ocelli small. Lateral ocelli apparently absent; the lateral margin of compound eyes has an emulsion slightly covering the area. Compound eyes large and oblong. Gena and antennal insertion point brown. Maxillary palps present, first segments covered in emulsion, last segment visible, brown with long setae. Labial palps not visible. Antennae filiform with ~10 antennomeres. The antennomeres are surrounded by emulsion and bubbles that reduce their visibility.

Thorax. Pronotum brown, like half-cylinder, convex; covering mesonotum and extending laterally; anterior and posterior margin are fractured near midline, posterior margin rounded. Pronotum in dorsal view is wider near midline. Prosternum with a square-shaped plate extending over the labium; no distinguishable setae on margin. Wings reverted, and thick. Tegmina short, posterior margin slightly curved. Hind wings slender. Forelegs fossorial/walking, brown. Procoxa elongated, rectangular. Profemora rectangular densely covered in setae. Protibia ellipsoid, densely covered by both stronger acuminate setae and thinner spine-like setae. Tarsi covered by emulsion. Middle legs, hyaline with some dark brown patches. Mesocoxa not visible due to bubbles and optical discontinuity. Mesofemora rectangular, with a darker ventrodistal brown coloration than the forelegs. Mesotibia oblong; ventrally darker brown. Tarsal segments: basitarsus with adhesive structures, and one long inner seta; distal tarsus with two long slender terminal ungues. Hind leg brown. Metacoxa quadrate. Metafemora robust, brown with a lighter cream coloration on semilunar process and area just before apex; cover plate distally brown. Metatibia long, robust, but covered with bubbles that makes it look wider. A pair of short subapical spurs with a terminal tooth is present. A pair of apical spurs with a terminal tooth are present. Apical spurs are larger than subapical spurs. Metatarsus robust and large, ventral edge with one row of setae. Metatarsus larger than apical spurs.

Abdomen. Abdominal terga covered by a white emulsion with bubbles hiding segmentation. Terminalia: cerci elongated, longer than paraproct; long setae at apex; segmentation unclear. Paraproct cerciform with a strong seta on apex.

Remarks. The specimen is not assigned to any species due to the fact that it is an immature individual. This specimen is assigned to Ripidactylidae based on the presence of a square-shaped plate on the prosternum and the absence of lateral ocelli. This nymph is assigned to *Pterocalyptus* gen. nov. based on the lower number of antennomeres. *Pterocalyptus* differs from *Ripidactylus* gen. nov. by the 10 antennomeres instead of 14. A lower number of antennomeres is expected in immature specimens. This nymph also differs from *R. chimera* in having thicker antennae, although the apparent thickness could be due to the emulsion. The semilunar process is more rounded in this specimen (similar to *P. ceratus*), while it is elongated in *R. chimera*. The metatarsus is larger and thicker in comparison to the slender and trapezoidal metatarsus of *R. chimera*. Moreover, the metatarsus is longer than the apical spurs in *Ripidactylus*, a trait unknown in *Pterocalyptus.* Coloration appears to differ among all specimens; no iridescence gleam is evident in the nymph. However, the metafemur possesses a pattern with a lighter coloration near the semi-lunar process that resembles that of *R. chimera* rather than *P. ceratus*.

Discussion and Conclusions

The known number of Burmese amber tridactyloids is increasing considerably in comparison to other caeliferans due to recent finds. The addition of these three species to the fossil record makes Tridactyloidea the most abundantly represented superfamily of Orthoptera and still the only caeliferan group recorded from Burmese amber (Guo *et al.* 2017). Orthopterans are rare from Burmese amber when compare to other insects. Guo *et al.* (2017) recorded 587 arthropods from which 421 were insect species. The representation of tridactyloids could be explained in different ways. The group may have gone through a high diversification period before or during the Cretaceous. In support of a highly diverse period are the records of tridactyloids from other deposits in the world; they are represented in different geographic areas and periods (mostly from the Cretaceous, but also from the Eocene and Miocene) (Gorochov *et al.* 2006; Azar & Nel 2008; Heads 2010) (Table 5.1). Moreover, the records of *P. hui* and *Paraxya obscurus* sp. nov. in Burmese amber add evidence in support of a wider paleobiogeographic distribution of dentridactyline. Although the fossil record initially indicated placement of the subfamily Dentridactylinae in Gondwana, we now have evidence of multiple fossils in Burmese amber, placing the subfamily in Laurasia (Heads 2009, Poinar 2018). Therefore, as suggested by Heads (2009), the subfamily Dentridactylinae most likely had a more widespread distribution that was subsequently affected by extinction events.

However, the presence of tridactyloids in the fossil record could be explained by an ecological bias. The paleoenvironment of Burmese amber is considered tropical (Grimaldi *et al.* 2002; Ross *et al.* 2010), a perception that could create a bias towards species from this environment. Tridactyloids, at least from the family Ripipterygidae, have higher diversity and endemicity near the equator (Baena-Bejarano & Heads 2015). In fact, Grimaldi *et al.* (2002)

mentioned how regions from Southeast Asia and Colombia had developed “Cenomanian-aged” rainforests. Pygmy mole crickets (Tridactylidae) are terrestrial insects that inhabit riparian habitats. They are found in moist sand and/or mud at the shoreline of lakes, rivers, streams, and marshes (Hebard 1934; Deyrup 2005; Baena-Bejarano 2015). Tridactylids feed on algae and organic detritus; *Neotridactylus archboldi,* Deyrup & Eisner 1996 gut content recorded algal material (Deyrup & Eisner 1996) and recently *Xya pfaendleri,* Harz 1970 and *X. variegata* (Latreille 1809) were reported as detritivores (KuřAvová & KočáRek 2016). Therefore, Burmese amber could be revealing inhabitants of riparian habitats, albeit not exclusively, aquatic or semiaquatic specimens have been found in this deposit. In fact, the most diverse arthropods in Burmese amber were Diptera and Coleoptera that exhibit considerably diverse life histories (Grimaldi 2002).

These scenarios are not necessarily mutually exclusive. Moreover, another explanatory factor may be observing biases due to size and preservation of the specimens may be a concern. The fossils described here are small and belong to a group of tiny to medium-sized crickets. Sample preservation is of the highest quality, with just some minor missing structures such as antennal segments or damage. In fact, key characters for the identification of the group were visible. Grimaldi *et al.* (2002) found bias based on the size of the pieces between two collections and the number of orders represented. Moreover, amber is known for the presence of small individuals when compared with other preservation types (Grimaldi & Engel 2005). Furthermore, sorting out taxonomic bias can require a specialist with knowledge of the extant fauna.The samples offer an odd combination of plesiomorphic and apomorphic characters that increase the difficulty of identification and taxonomic placement. The stage of organismal development can lead to a misidentification of a species. For extant taxa, Baena-Bejarano *et al.*

(2018) recommended caution with traditional morphological characters used for the identification of genera in *Mirhipipteryx* (Ripipterygidae) when dealing with nymphs. Skejo *et al.* (2018) provided characters to differentiate nymphs and adults of pygmy grasshoppers (Tetrigidae), after nymphs of *Euscelimena harpago*, (Serville 1838) were repeatedly described as new species. Therefore, I have kept the nymph in the genus *Pterocalyptus* without linking the nymph with any of the species here proposed for the family. There are considerable differences between the samples that lead me to consider it as a different species; however, I elected not to create a new species until more research is done with fossils or extant nymphs that will increase understanding of the morphology in the group.

Ripidactylidae placement is intriguing, as new taxa exhibit a combination of derived and plesiomorphic characters based on terminalia characteristics that are more closely related to Ripipterygidae; however, characters such as unsegmented cerci and developed female valves seem to be plesiomorphic. The metatarsi resemble those of the Tridactylidae, which similarly seems to be plesiomorphic. Whether as a sister family of Tridactylidae-Ripipterygidae or sister to Ripipterygidae, Ripidactylidae is an exceptional finding for the superfamily Tridactyloidea. This extinct family not only sheds light on the past diversity of the group, it also has features such as the iridescence observed in the adult provide the first record of this characteristic in fossil tridactyloids. Iridescence is most often found in species of the genus *Ripipteryx* (Ripipterygidae), but species of the genus *Xya* (Tridactylidae) can be shiny or matte (NBB, pers. obs.). Iridescence in insects has been linked with aposematism (Fabricant *et al.* 2014). However, the coloration here could be due to optical discontinuity and/or the type of preservation in amber specimens. For instance, the nymphs of Ripidactylidae and *Pterocalyptus* do not exhibit iridescence, showing a different pattern of coloration. Another morphological finding in *Paraxya obscurus* sp. nov. and *P. hui* is the presence of fully developed wings. These are the first species in the subfamily Dentridactylinae with fully developed wings within fossil and modern taxa. In fact, the tegmina is present in the taxa, but this is the first time to report a well-developed hind wing.

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Table and Figures

TABLE 5.1. Fossil record of the family Tridactylidae modified from data extracted from Paleobiology Database and Orthoptera Species File.

Subfamily	Taxa	Authority	Time interval (Ma)	Country or state
	Tridactylidae indet. (77192)		Late/Upper Aptian 122.46 – 112.03	Australia
Dentridactylinae Günther, 1979				
	Burmadactylus grimaldii	Heads 2009	Early/Lower Cenomanian 99.6 – 93.5	Myanmar
	Cascogryllus lobiferus	Poinar 2018		Myanmar
	Guntheridactylus grimaulti	Azar & Nel 2008	MP 7 55.8 – 48.6	France
	Paraxya hui	Cao, Chen & Yin		Myanmar
Mongoloxyinae Gorochov, 1992				
	Baisoxya dolichopterus	(Sharov, 1968)	Aptian 125.0 – 113.0	Siberia
	Birmitoxya intermedia	Gorochov, 2010	Early/Lower Cenomanian 99.6 – 93.5	Myanmar
	Cretoxya rasnitsyni	Gorochov, Jarzembowski & Coram, 2006	Early/Lower Berriasian 145.0 – 140.2	United Kingdom (England)
	Mongoloxya ponomarenkoi	Gorochov, 1992	Aptian 125.0 – 113.0	Mongolia

TABLE 5.1. (continued)

Monodactyloides curtipennis	Sharov, 1968	Aptian 125.0 – 113.0	Russia
Tridactylinae Brullé, 1835			
Archaeoellipes engeli	Heads, 2010	Burdigalian - Langhian 20.44 – 13.82	Dominican Republic
Cratodactylus ferreirai	Martins-Neto, 1990	Late/Upper Aptian 122.46 – 112.03	Brazil
Cratodactylus kellneri	Martins-Neto, 1990	Late/Upper Aptian 122.46 – 112.03	Brazil
Ellipes dominicana	Poinar 2018		Dominican Republic
Tridactylus sp.		Chattian 28.1 – 23.03	France

FIGURE 5.1. Family Dentridactylinae from Upper Cretaceous amber from Burma (Myanmar); Katchin, Tanai. a-d *Paraxya obscurus* sp. nov. No. NIGP166934 (Holotype); Adult. a) Photograph habitus. b) Illustration habitus. c) Metatibia ventral margin showing indentation near the base. d) Terminalia. e) Dentridactylinae (INHS 10330); nymph = in Upper Cretaceous amber from Burma (Myanmar); Katchin, Tanai. All scale bars represent 1 mm, except 3 – 4, which is 0.1 mm.

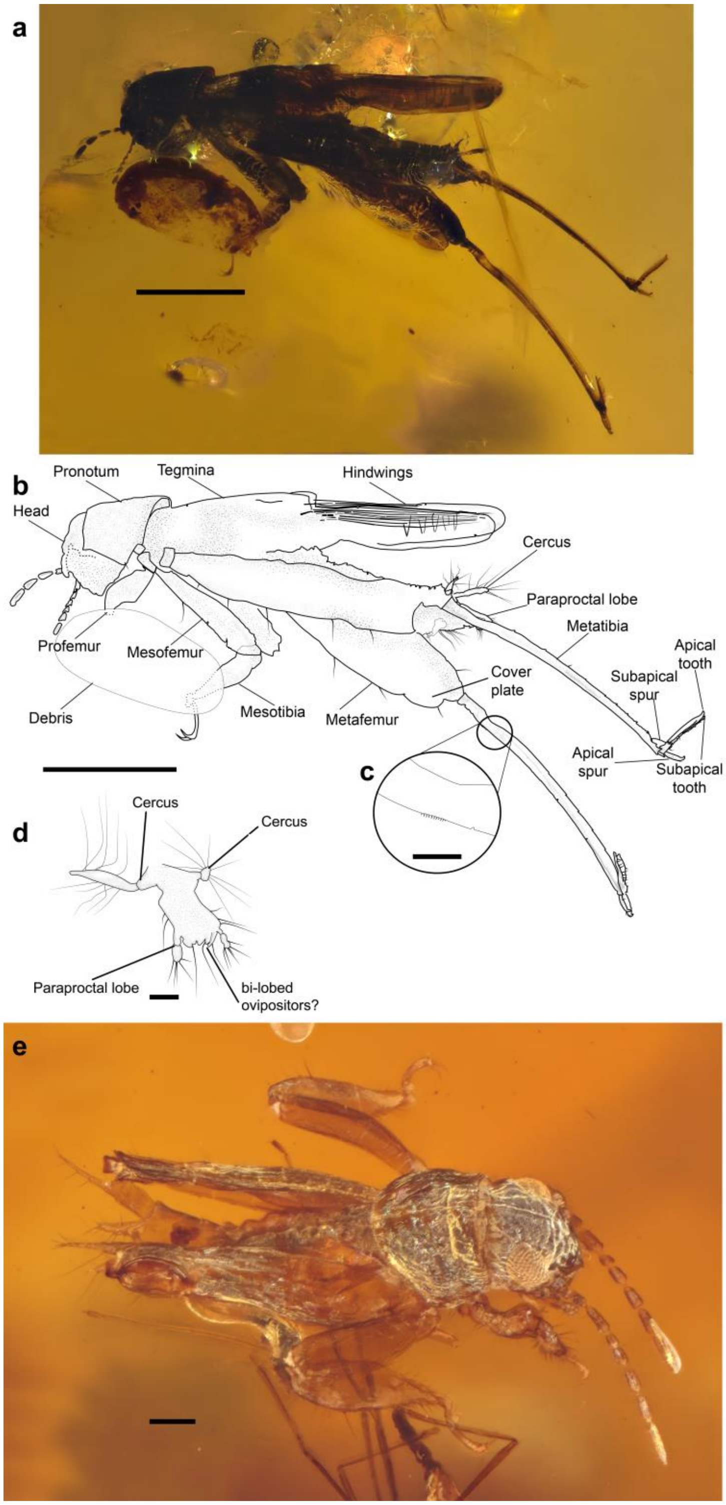


FIGURE 5.2. Photographs of Ripidactylidae fam. nov. in Upper Cretaceous amber from Burma (Myanmar); Katchin, Tanai. a) *Ripidactylus chimera* gen. et sp. nov. No. NIGP166935 (Holotype); adult habitus. b) *Pterocalyptus ceratus* gen. et sp. nov. No. INHS 10328 (Holotype); adult habitus. c) Ripidactylidae indet. No. NIGP166936; nymph habitus. Scale bars represent 1 mm.

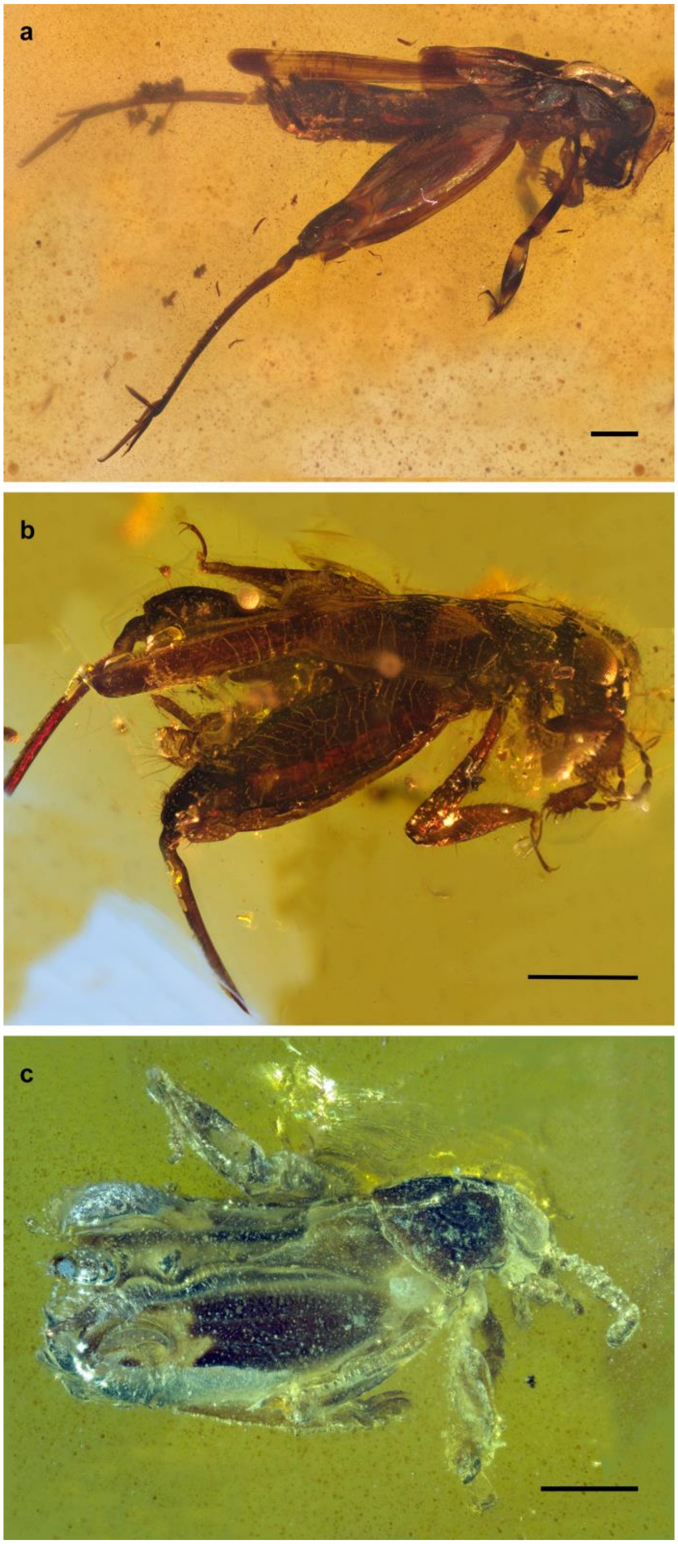
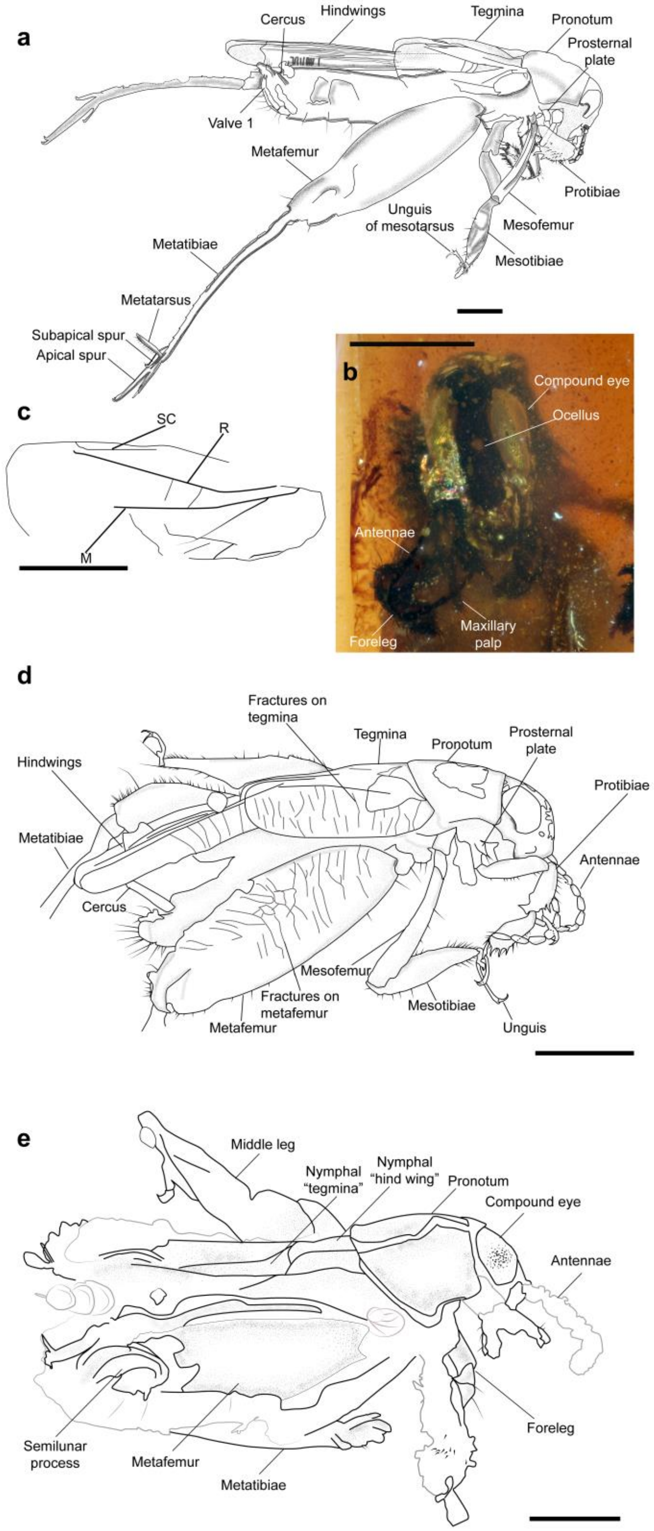


FIGURE 5.3. Ripidactylidae fam. nov. in Upper Cretaceous amber from Burma (Myanmar); Katchin, Tanai. a) *Ripidactylus chimera* gen. et sp. nov. No. NIGP166935 (Holotype); adult habitus. b) Head in frontal view. c) Tegmen with venation. d) *Pterocalyptus ceratus* gen. et sp. nov. No. INHS 10328 (Holotype); adult habitus. e) *Pterocalyptus* nymph No. NIGP166936. Scale bars represent 1 mm.



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CHAPTER 6: PHYLOGENY OF MUD CRICKETS, PYGMY MOLE CRICKETS AND SANDGROPERS (ORTHOPTERA: CAELIFERA: TRIDACTYLOIDEA)

Abstract

Pygmy mole crickets (Tridactylidae), mud crickets (Ripipterygidae), and sandgropers (Cylindrachetidae) together comprise the superfamily Tridactyloidea. This superfamily is globally distributed, but each family exhibits distinct biogeographic distributions and diverse life histories. The current classification of these families—particularly their subfamilies, genera, subgeneric groups, and extant and fossil taxa— is based entirely on morphological data analyzed within a phyletic framework. No morphological or molecular analyses has ever been published for this group. I provide a phylogenetic analysis of the cricket superfamily Tridactyloidea utilizing extant and fossil taxa and a combination of morphological and molecular characters (COI). I included samples from all families and subfamilies to test their monophyly. This was accomplished by preparing a total evidence matrix with a morphological matrix available for Ripipterygidae expanded to include other extant tridactyloid species and fossils. I also sequenced a COI fragment for 19 tridactyloids and included other sequences from Genbank. I analyzed the matrix under Parsimony Analysis (PA), Maximum Likelihood (ML), and Bayesian Analysis (BA). The findings are consistent with most of the current classification of Tridactyloidea. However, the family Tridactylidae was not monophyletic due to the placement of some fossils in a polytomy with Cylindrachetidae and outgroups; however, the extant tridactylids grouped together. The subfamily Dentridactylinae was not found to be monophyletic, but Tridactylinae formed a clade. Fossil placement of Mongoloxyinae was recovered within extant Tridactylidae with low support. The family Ripipterygidae was recovered as monophyletic, but the genus

Ripipteryx was paraphyletic with respect to *Mirhipipteryx*. Overall, resolution is inconsistent across the phylogeny. This study successfully elucidates relationships at different levels in Tridactyloidea and direct subsequent research on taxon and character sampling.

Introduction

Robust phylogenies are important for taxonomic classifications and the importance of including multiple sources of data to obtain robust phylogenies has being long known as total evidence (Friedrich *et al*. 2014; Giribet, 2015). Historically, the exclusive use of morphology to construct phylogenies was displaced to an extent by DNA sequencing due to benefits including reduction of time to generate and increased volume of data obtainable from a single sample in comparison to the analysis of morphological characters. However, the reintegration of morphological data into phylogenetics with inclusion of fossils and/or stratigraphic data has proceeded in the last decade (Pyron 2017).

The insect order Orthoptera includes the familiar grasshoppers, crickets, and katydids. While the biology of these insects is relatively well-known, we lack phylogenetic hypotheses for most groups, and fossils are rarely included. Previous approaches primarily use morphological characters for constructing phylogenies, but recently more emphasis has been placed on molecular phylogenetics. Fossil calibrations of these phylogenies have depicted evolutionary history of Orthoptera reaching back ca. 300 million years, with the suborders Caelifera and Ensifera diverging in the Permian (Song *et al.* 2015). Fossil Caelifera provide hints on distribution patterns. Acridoids and tetrigoids are the largest superfamilies in the infraorder Acrididea (Caelifera). Acridoid distributions seem to be better explained by dispersal after the continents drifted (Song *et al.* 2015). Tetrigoids with nine known fossils lack further discussion on the general distribution patterns for the superfamily, but Heads (2009a) suggested a fast diversification for a subfamily in the Caribbean. For example, in the infraorder Tridactylidea (Table 6.1), tridactyloids exhibit other distinctive distribution patterns. The family Cylindrachetidae is a classic example of a disjunct austral distribution, with taxa present in Australia (Australia and New Guinea) and South America (Grimaldi & Engel, 2005). While the tridactylid subfamily Dentridactylinae at first glance appeared to have an austral distribution, fossil records now suggest a historically more widespread distribution that was subsequently affected by extinctions (Heads 2009b). Although fossils initially placed the subfamily in Gondwana, there is evidence of a fossil from Burmese amber placing the subfamily in Laurasia (Heads 2009b). Our understanding of distribution as well as estimation of divergence rate for specific groups are both affected by fossil studies. This is particularly true of the mud crickets, pygmy mole crickets, and sandgropers of the superfamily Tridactyloidea, which have not been well studied and for which a modern phylogenetic analysis is needed. Tridactyloids are the most basal clade in the suborder Caelifera and represent a key taxon to study the evolution of these ecologically and economically important caeliferans. This group contains about 239 described species, 14 of which are fossils (Cigliano *et al.* 2019).

Background on Tridactyloidea

Tridactylidae. Pygmy mole crickets or sand grasshoppers are in the family Tridactylidae. This is probably the best known family of tridactyloids due to their worldwide distribution and larger number (~150) of extant and fossil species (Cigliano *et al.* 2019). However, no phylogenetic analyses are available for the family, and the relationships between species, genera, and subfamilies remain unknown. Following Orthoptera Species File classification (Table 6.1) (Cigliano *et al.* 2019), Tridactylidae is the family that holds the majority of known fossils, with thirteen species. Günther (1979) proposed to split the family into the subfamilies Tridactylinae and Dentridactylinae based on metatarsal morphology. Dentridactylinae has three fossil species in their own genera and Tridactylinae with four fossil species in two genera. Gorochov (1992) included a third subfamily known only from fossil records and based this group on wing venation characters: Mongoloxyinae is the third subfamily with five species, each one in its own genus. The placement of this subfamily is controversial due to known convergences in wing venation within orthopterans. The subfamily is differentiated from the extant subfamilies by the higher number of longitudinal veins in the tegmen. Tridactylinae and Dentridactylinae only have 2 to 4 weak longitudinal veins (Gorochov *et al.* 2006). Azar & Nel (2008) considered this group to be paraphyletic and argued for an exclusion of this group from tridactyloids. One more fossil species recently described was not assigned to any subfamily (Cao, Chen & Yin, 2019).

Ripipterygidae. Mud crickets in the family Ripipterygidae are exclusively Neotropical. Although these small, cryptic orthopterans are morphologically similar to the more diverse and globally distributed Tridactylidae, they are readily distinguished by their unsegmented cerci, the prominent dorsolateral lobes of the epiproct with a transverse comb-like array of teeth, ovipositor valves extending beyond the subgenital plate in females, and unique genitalia in males (Günther 1994; Heads 2010a, 2010b). Günther (1969) proposed a hypothesis of relationships for all of the species in the family and subdivided them into a number of species groups. He proposed six species groups for the genus *Ripipteryx* and three for *Mirhipipteryx;* the only known fossil in this group is in the genus *Mirhipipteryx* (Heads 2010b). Günther's (1969) analysis was entirely phyletic, although he considered all groups as monophyletic except for the "Marginipennis-

Bruneri” group. The latter group was composed of morphologically heterogeneous species that could not be readily placed elsewhere in his scheme (Günther 1969). Later, Heads (2010a) proposed names for the *Ripipteryx* species groups and reduced the number to five. Heads (2010a) highlighted that the monophyly of the groups has yet to be tested and advocated a cladistic analysis to resolve their relationships. The same is also true for both genera in the family. A preliminary morphological phylogeny for the family found *Ripipteryx* paraphyletic with respect to *Mirhipipteryx* and did not support the monophyly of the species groups *sensu* Günther (1969) and Heads (2010a), but further analysis with a higher set of characters (DNA) was recommended because it could reveal more conclusive results (Baena-Bejarano 2013).

Cylindrachetidae. Sandgropers in the family Cylindrachetidae present a classically disjunct austral distribution, recorded in southernmost South America and Oceania. Most of the species are known from Australia (14 species), with the exception of two species: one in New Guinea and one in Argentina. From a biogeographic perspective, their distribution suggests that this group was affected by continental drift (Grimaldi & Engel, 2005). This family contains the largest species of the superfamily (30–90 mm body length). They appear superficially similar to mole crickets in the suborder Ensifera. Compared to tridactylids and ripipterygids, sandgropers seem less dependent on water sources and are extremely specialized for digging and fossorial life as evidenced by their completely cylindrical bodies. The anterior legs are strongly modified for digging and the middle and posterior legs are substantially reduced. The compound eyes are reduced and wings have been lost in this family, in addition to reductions in the antennae and cerci. The family is composed of three genera: *Cylindracheta*, *Cylindraustralia* and *Cylindroryctes* (Günther, 1992). The main taxonomic review is that of Günther (1992) but, as in the Tridactylidae, the relationships between genera and species have yet to be explored phylogenetically. No fossil cylindrachetids are known.

The small number of species in Tridactyloidea facilitates a higher coverage of the taxa in a phylogenetic analysis. Here I provide the most comprehensive phylogenetic analysis of Tridactyloidea with extant and fossil taxa inferred from morphology and a 700 bp fragment of the mitochondrial Cytochrome Oxidase subunit I (COI).

Methods

Taxa for analyses. The classification scheme follows the Orthoptera Species File (Cigliano *et al.* 2019). At least two species from each taxonomic rank are required to test the monophyly of a group. Therefore, our ingroup includes extant and fossil species when possible with at least two species from each family and their subdivisions (species group, genera, and subfamilies).

Molecular dataset. A DNA matrix was prepared with the protein-coding mitochondrial DNA gene cytochrome c oxidase subunit I (COI). COI is a staple for DNA barcoding in insects and other organisms that could provide insights for the relationship of closely related species. Additionally, this gene is widely available for different taxa. For the outgroup, complete COI sequences (~1500 bp) were downloaded from Genbank. The outgroup selection follows Song *et al.* (2015) and includes species in Caelifera (Tetrigidae), Ensifera (Tettigoniidae and Gryllidae), and the polyneopteran orders Grylloblattodea, Mantodea, Mantophasmatodea and Phasmatodea (Table 6.2). However, only four Tridactyloidea COI sequences were available in Genbank. To increase ingroup taxa, DNA was obtained from specimens preserved dry or wet in ethanol from entomological collections (Table 6.2) in addition to samples collected in Illinois that were preserved in 100% ethanol. More than one specimen per species was added if samples were from different localities. At Collaborative Ecological Genetics Lab (CEGL) (INHS), standard protocols were followed for extraction from hind legs with DNeasy kit (Qiagen, Germany). COI fragments (~700 bp) were amplified by PCR with Bullseye Taq Plus Master Mix (Midwest Scientific, Inc, MO). I initially used the primers OR-COX1J-3 and OR-COX1N-1 for *B. tartarus* and *R. rivularia* (Sheffield *et al.* 2010). Due to amplification failure of some samples, I tested and subsequently used the universal COI primers jgLCO1490 and jgHCO2198 (Geller *et al.* 2013). PCR was completed using the following conditions: 1 μL of template DNA, 12.5 μL of master mix, 10.8 μL of molecular grade water and 7 μL of 10 μM forward and reversed primers, respectively. PCR conditions: 1 cycle of 94°C 5 min; 50 cycles of 94°C 45 sec, 49°C 1 min, 72 °C 1 min 30 sec with 1 cycle extension of 72°C 5 min. Annealing temperature was optimized via gradient PCR. This was repeated for samples that failed to amplify at 49°C. I prepared 1% agarose gels with 1 μL GelRed (Biotium Inc., CA). Gels were loaded with PCR products and 100 bp and 1 kb ladders, then run with TAE buffer 1% at 90 V, for 75 min. Gels were examined for single bands in a range close to ~700 bp. Raw PCR products were sent to Eurofins Genomics LLC, KY for Sanger sequencing. I failed to extract DNA from the species *Dentridactylus truncatus* and to amplify DNA fragments for *Ripipteryx boliviana* from ICN, *Xya variegata* from Zoological Museum Split Croatia, *Xya* sp. and *Dentridactylus* n.sp. from Western Australian Museum Entomology. The forward and reverse sequences were assembled and aligned in Sequencher 5.4 2015. Sequences were imported to Mesquite version 3.3 (build 854) (Maddison & Maddison 2017) and aligned using Muscle 3.8.3. The final dataset was 34 terminals x 1548 bp.

Genetic distances (uncorrected pairwise distance p) for Tridactyloidea sequences were calculated. Distance comparisons are provided between species (*Ellipes*, *Mirhipipteryx* and *Ripipteryx*) and within species (*Ellipes*, *Neotridactylus*, *Mirhipipteryx*) in genera with more than one sequence.

Morphological dataset. I coded a matrix using a morphological matrix developed for Ripipterygidae (49 taxa x 79 morphological characters) (Baena-Bejarano 2013). The matrix from Baena-Bejarano (2013) was imported to Mesquite. I added 25 terminals (20 extant and 5 fossil) achieving coverage of all families and subfamilies in Tridactyloidea (Table 6.3; Appendix A, B) as well as expanding the samples for species groups in *Ripipteryx*. Char 41 was removed because it was not applicable for the new outgroup samples (Baena-Bejarano 2013). Ninety-six additional characters were added from descriptions or keys (diagnostic characters) or from direct observation of samples and edited as needed. Non-informative characters were removed from the morphological dataset, except for characters that were informative in then total evidence matrix. The final dataset was 74 taxa x 151 chars.

Total evidence matrix. A total evidence matrix (97 Terminals and 1699 characters) was built combining the molecular (1548 chars, 91.12%) and the morphological dataset (151 chars, 8.88%) (Appendix B). Few family level diagnostic characters were added for outgroup species that did not have a match in the morphological matrix. Data were obtained from photographs of holotypes of these species. No morphology was added to the sequence of *Tridactylus* sp. because of the missing species identification. Preliminary analyses of the molecular dataset with the total 1548 nucleotides (coding as missing data the fragment ~700–1548 bp) and with a matrix using the initial fragment 1~700 bp were run. I continued using the larger dataset rather than the shorter version, due to the resolution and congruence of the larger dataset at the higher-level relationships with the phylogeny of Orthoptera (Song *et al.* 2015).

Phylogenetic analyses. Total evidence analysis was performed under maximum parsimony (PA), maximum likelihood (ML), and Bayesian inference (BA). PA was run in the program TNT version 1.5 2019 sponsored by the Willi Hennig Society (Goloboff & Catalano, 2016). The general RAM was set to 1000 MB, and the maximum trees were increased to 30000. The taxa *Grylloblatta sculleni* was selected as outgroup. A New Technology search was set using sectorial search, ratchet, drift, and tree fusing with driven search set to find minimum length 20 times and random seed 0. Bremer support was calculated in TNT. Bootstrap support was calculated in PAUP* 4.0 3.99.165.0 (Swofford, D. L. 2003. Sinauer Associates, Sunderland, Massachusetts). Support values are display on strict consensus tree. PartitionFinder2 (Lanfear *et al.* 2016) on XSEDE in the portal CIPRES (Miller *et al.* 2010) was used to estimate the best partition and models of evolution for nucleotides; PartitionFinder settings were applied to ML and BA (Appendix C). The ML tree was obtained in RAxML-HPC v.8 on XSEDE (in CIPRES) with settings adjusted for outgroup that was set for *Grylloblatta sculleni*, GTRGAMMA + I for all partitions, GTR model for DNA subsets, MULTICAT model, MK model for morphology. Bootstrap support of 1000 iterations was obtained for the majority rule consensus tree. BA was performed in MrBayes on XSEDE (3.2.6) (in CIPRES) with unlinked parameters across partitions and applying the model Nst=6 Rates=invgamma for DNA subsets and rates=gamma for morphology with variable partition rates. The search was set to 20000000 generations with sample frequency 1000, print frequency 1000, nruns=4, nchains=4, default temperature, and burn-in of 25%. Outputs were assessed base on convergence to 1 of potential scale reduction factore (Gelman and Rubin, 1992) and effective sample sizes >200. Posterior probability support is provided. Consensus trees were edited using FigTree, Tree Figure Drawing Tool Version 1.4.3 (Rambaut, 2016).

Results

Total evidence

In the PA (Figure 6.1) 78 trees of length 4149 (CI = 0.36, RI = 0.55) were obtained. Tridactyloidea was recovered as monophyletic, as were the families Cylindrachetidae and Ripipterygidae. The PA failed to recover the monophyly of Tridactylidae (extinct and extant taxa). Two groups of extinct taxa (*A. fossorius* sp. nov. with *G. fortis* sp. nov. and *Paraxya obscurus* sp. nov. with *B. grimaldii*) were found in a polytomy with a group of Cylindrachetidae samples. The fossil *R. chimera* was found in a clade with all of the extant Tridactylidae. The subfamily Tridactylinae was recovered in a monophyly, but Dentridactylinae was not recovered. The genera *Afrotridactylus, Ellipes, Tridactylus* and *Xya* made a group with low support. The PA failed to recover any monophyly of genera in Ripipterygidae. However, the PA recovered the groups of species Limbata-Marginata (*lawrencei-boliviana sensu* Günther 1969 and *hydrodroma-marginata sensu* Günther 1969), Marginipennis (*marginipennis-bruneri sensu* Günther 1969), Scrofulosa (*scrofulosa-biolleyi*), but not Forceps (*procesata-carbonaria sensu* Günther 1969) or Crassicornis (*atra-crassicornis sensu* Günther 1969). Low support of nodes was found across the consensus tree.

The ML tree (Figure 6.2) did not recover the superfamily Tridactyloidea and the families Cylindrachetidae and Tridactylidae as monophyletic, although a group of the species of Cylindrachetidae was found with the family Tetrigidae with low support. No subfamilies of Tridactylidae were recovered as monophyletic. In Tridactylinae, *Afrotridactylus, Ellipes* and *Xya* formed a clade with moderate bootstrap support. Only the family Ripipterygidae was recovered in a clade. Genera and groups of species were not monophyletic in Ripipterygidae; except for the group of species Marginipennis (*marginipennis-bruneri*) and Scrofulosa (*scrofulosa-biolleyi*), but with very low support. Node supports were low across the consensus tree.

The BA (Figure 6.3) consensus tree did not recover Tridactyloidea. *C. spegazzinii* was found in a clade with Mantophasmatodea and Phasmatodea. *Cylindraustralia* sp. was found in a polytomy of the families Ripipterygidae and Tetrigidae, other tridatylids, and the fossils *Paraxya* n. sp, *R. chimera* sp. nov., *B. grimaldii*. The subfamily Dentridactylinae was not monophyletic, but the subfamily Tridactylinae relationships were not clear. There is a polytomy between tridactylins, a clade of the fossils *A. fossorius* sp. nov. and *G. fortis* sp. nov., and *Bruntridactylus.* A cluster of the genera *Afrotridactylus, Ellipes* and *Xya* was recovered with regular support. The family Ripipterygidae was monophyletic. The genus *Ripipteryx* was paraphyletic with respect to *Mirhipipteryx.* Three clades were recovered. The first clade included the groups Forceps + Crassicornis. The species from Forceps were found in a group, and Crassicornis was not monophyletic. A second clade recovered a monophyly of the genus *Mirhipipteryx*, and the third clade includes species of Limbata-Marginata + Marginipennis + Scrofulosa. The BA recovered clusters with regular support that included all the species of Scrofulosa, and a group of species of Marginipennis.

Genetic distances

The range of genetic distance with COI for all of the samples was 0 to 0.31 (Figure 6.4). The uncorrected pairwise distance within species in Tridactyloidea was from 0.000 to 0.026 while the distance between species was 0.094 to 0.244 (Table 6.4).

Discussion

Methods of phylogenetic inference

Selecting a method of inference is not an easy task in phylogenetic studies. My selection is based on previous publications on performance and simulations under certain assumptions that match this data. The total evidence matrix has a large amount of missing data per taxa. The matrix was limited by the number of samples obtained for DNA extraction that worked with the primers. This led to an average of 75% missing data (Appendix D), with fossils representing samples with the most missing characters.

Missing data is a critical problem in phylogenetic analyses (Wiens & Morrill, 2011). Some authors have addressed the effects on missing data by removing these taxa or characters with missing data whereas other authors will retain the taxa. Simulations have shown that phylogenetic relationships can still be recovered when large amounts of missing data are included (Wiens and Moen 2008; Thomson and Shaffer 2010). Missing data effects on PA and ML were approached by Padial *et al. (*2014). They found that PA collapsed unsupported nodes by the ambiguity of missing data. For instance, ML has provided unsupported nodes despite the lack of evidence. Guillerme & Cooper (2015), in a series of simulations comparing missing data from different datasets in total evidence analysis, found BA to outperform ML. Therefore, the ML tree obtained will not be discussed further. Additionally, Guillerme & Cooper (2015) found that better tree topologies were recovered and placement of fossils was achieved in matrixes with missing data if morphology of at least 50% of the living taxa was included. This study included morphology for more than 50% of the extant taxa as suggested. Tree topology differed between PA and BA in our results. I am focusing primarily on the BA tree to discuss the systematics of Tridactyloidea because this approach includes models that fit our molecular data. Wiens (2015) simulations showed in some instances higher accuracy of Bayesian analyses on combined matrixes (DNA and fossils) than PA.

Phylogeny of mud crickets, pygmy mole crickets and sandgropers Tridactyloidea

Tridactyloidea was not recovered as monophyletic. The species *C.* S*pegazzinii* (Cylindrachetidae) was in a clade with outgroup species, and low resolution prevented the elucidation of the relationships between a clade of the family Tetrigidae (outgroup), the other cylindrachetid, Burmese Amber fossil tridactyloids, and a major clade of tridactylid species near the base of the tree. The major clade of extant Tridactylidae with low support was recovered with the placement of the Crato Formation fossils *A. fossorius* and *G. fortis* (Mongoloxyinae); in addition to the subfamily Dentridactylinae failing the test of monophyly. Relationships between subfamilies Tridactylinae and Mongoloxyinae remain obscured due to lack of resolution, although a closer relationship was found between the genera *Afrotridactylus, Ellipes,* and *Xya* in Tridactylinae. The placement of the Crato Formation fossils from Brazil in this phylogeny corroborates the controversial inclusion of the subfamily Mongoloxyinae in Tridactyloidea in a clade with low support. I tested only two of the most complete specimens assigned to this group. Inclusion of the other less complete representatives, especially fossils known only from wings or from different geographic areas, is necessary to test the monophyly of this presumable paraphyletic assemblage (Azar & Nel, 2008).

For instance, the monophyly of Dentridactylinae has traditionally been recognized without controversies but needs further revision based on my findings. Dentridactylinae species are recognize by the presence of a subapical tooth in the metatarsi (Günther 1991; Baena-Bejarano & Heads 2018). However, this character did not behave as a synapomorphy for the group. Priority should be given to other characters that could accentuate the relationships of a species with other groups rather than the small subapical tooth of the developed metatarsi. Implications of the polyphyly of Dentridactylinae significantly affect the understanding of patterns of past and present distribution in the group. A Gondwanan origin and an ancestral broader range of distribution have been proposed for dentridactlines and explained by extinctions (Heads 2009b); however, a more restricted understanding of extant groups could lead to a Gondwanan or southern hemisphere group (*Dentridactylus* and *Paratridactylus*) vs a northern hemisphere group (*Bruntridactylus*) (Cigliano *et al.* 2019; Baena-Bejarano & Heads 2018). This does not clarify the placement of fossil dentridactylins.

Although Ripipterygidae is monophyletic, the genus *Ripipteryx* was found to be paraphyletic with respect to *Mirhipipteryx.* BA recovered three major clades (Posterior probability support >80). (1) species cluster of Forceps *sensu* Heads 2010 and Crassicornis *sensu* Heads 2010. Only Forceps was monophyletic; (2) a monophyletic *Mirhipipteryx;* (3) species cluster of all remaining *Ripipteryx* including species from the groups Limbata-Marginata *sensu* Heads 2010, Marginipennis *sensu* Heads 2010 and Scrofulosa *sensu* Heads 2010. Marginipennis and Scrofulosa were monophyletic with low support. These results are similar to the findings of Baena-Bejarano (2013), although the topology of the trees is substantially different from her pectinated tree. The major difference with our current tree is in the recovery and relationships of clade 3.

Baena-Bejarano (2013) found Forceps-Crassicornis (clade 1) as a natural group supported by spots restricted to head and legs. The species in this group are characterized by body almost entirely black, phallic complex with basal plate, cingulum with long apodemes, and with or without antennomere modifications. BA recovered Crassicornis in a paraphyly with species of

Forceps, with Forceps monophyletic and closely related to *R. gorgonaensis*. Baena-Bejarano & Heads (2015) pointed out the problematic placement of *R. gorgonaensis* that shares features from both groups. Therefore, I suggest recognizing the group Forceps-Crassicornis as one. Moreover, the strong split from the other two clades hints that this group is a separate genus. Clade 2 recovered *Mirhipipteryx* with the highest support. This genus is distinctive by the closeness of the compound eyes in comparison to the other species in Tridactyloidea, in addition to other morphological characters traditionally used for the identification of the group in the family, such as the length of the metatarsi. A revision of the genus is needed to understand the relationships within the group and to help clarify the position of this genus with respect the other *Ripipteryx.* This genus appeared to be more closely related to clade 3 but in Baena-Bejarano (2013) the genus was more closely related to clade 1.

Clade 3 recovered all of the species with predominance of other colors (colors in addition to black) with combination of black/yellow, black/orange, black/white, including that could be considered aposematic and/or disruptive. Aposematism or disruption cannot be excluded from clade 1 (species are predominantly black with very restricted white spots). There is no known research on coloration patterns in the family Ripipterygidae. Any potential toxins produced by these species have yet to be identified. Clade 3 has other less supported divisions (clades) where I recovered the group Scrofulosa and Marginipennis as monophyletic. Scrofulosa is a group that includes small Central American species that exhibit aposematic colorations (black and yellow, black and orange) and males with a process in the frons. The Marginipennis is a group that includes very heterogeneous species. Marginipennis clade consisted of a group characterized by the predominance of black coloration with small white margins on the pronotum, legs and antennae (except for *R. amazonica* and *R. insignis* that exhibits black and yellow coloration).

Günther (1969) proposed the assemblage of species *marginipennis-bruneri* doubting this was a natural assemblage. However, finding the group is not completely controversial. Characters from terminalia and genitalia have been useful for the placement of species in this group. *R. guacharoensis*, a species that was recently described and assigned to this group (Baena-Bejarano 2015), was recovered in the clade, suggesting that the initial assignation to the group was accurate. The group of species Limbata-Marginata was not recovered, nor was the previous organization *lawrencei-boliviana sensu* Günther 1969 and *hydrodroma-marginata sensu* Günther 1969. Relationships in this group/groups remain obscured due to low support and lack of resolution (a polytomy of *hydrodroma-marginata* species with the clade of Marginipennis + *lawrencei-boliviana*).

Low resolution was an issue in the BA consensus tree (Figure 6.3). If it is a consequence of limited data, then could be improved upon by increasing morphological and/or molecular data. However, if resolution is a consequence of incongruence in the data, an exploration of the characters and taxa in the matrix should take place. This procedure could help to dectect other problems such as long-branch attraction or repulsion. The lack of resolution was not consistent across the tree, so future research should consider character and taxon sampling in the matrix to evaluate incongruence. A thorough understanding of phylogenetic relationships and a stable taxonomic system are essential to understand the biology of any group of organisms. This study is a major accomplishment in understanding the relationships of mud crickets, pygmy mole crickets and Sandgropers, the most basal extant group in Caelifera. Even though resolution was not consistent in the tree, the data from morphology and COI helped elucidating relationships at all levels.

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Tables and Figures

TABLE 6.1. Classification of the superfamily Tridactyloidea (Orthoptera: Caelifera). † denotes fossil taxa

Family	**Subfamily**	**Genus**	**Author**	**Species group**
Cylindrachetidae		*Cylindracheta*	Kirby, 1906	
		Cylindraustralia	Günther, 1992	
		Cylindroryctes	Tindale, 1928	
Ripipterygidae	Ripipteryginae	*Mirhipipteryx*	Günther, 1969	"*peruviana-pronotopunctata*", "*variabilis-hebardi*", "*biloba-phallica*" *sensu* Günther (1969)
		Ripipteryx	Newman, 1834	Limbata-Marginata, crassicornis, forceps, marginipennis, scrofulosa *sensu* Heads (2010a)
Tridactylidae		*†Paraxya*	Cao, Chen & Yin, 2019	
	Dentridactylinae	*Bruntridactylus*	Günther, 1979	
		†Burmadactylus	Heads, 2009	
		†Cascogryllus	Poinar, 2018	
		Dentridactylus	Günther, 1974	
		†Guntheridactylus	Azar & Nel, 2008	
		Paratridactylus	Ebner, 1943	
	†Mongoloxyinae	*†Baisoxya*	Gorochov & Maehr, 2008	
		†Birmitoxya	Gorochov, 2010	
		†Cretoxya	Gorochov, Jarzembowski & Coram, 2006	

TABLE 6.1. (continued)

	†Mongoloxya	Gorochov, 1992
	†Monodactyloides	Sharov, 1968
Tridactylinae	*Afrotridactylus*	Günther, 1994
	†Archaeoellipes	Heads, 2010
	Asiotridactylus	Günther, 1995
	†Cratodactylus	Martins-Neto, 1990
	Ellipes	Scudder, 1902
	Neotridactylus	Günther, 1972
	Tridactylus	Olivier, 1789
	Xya	Latreille, 1809

TABLE 6.2. List of taxa used in the molecular dataset.

Order/suborder	Family	Species	Accession number	Source	ID
OUTGROUP					
Grylloblattodea	Grylloblattidae	*Grylloblatta sculleni*	DQ241796.1	Genbank	
Mantodea	Mantidae	*Tamolanica tamolana*	DQ241797.1	Genbank	
Mantophasmatodea	Mantophasmatidae	*Sclerophasma paresisense*	NC_007701.1	Genbank	
Phasmatodea	Timematidae	*Timema californicum*	DQ241799.1	Genbank	
Orthoptera					
ENSIFERA	Gryllidae	*Acheta domesticus*	MG458975.1	Genbank	
	Gryllidae	*Xenogryllus marmoratus*	JQ301448.1	Genbank	
	Tettigoniidae	*Xizicus maculatus*	NC_040974.1	Genbank	
CAELIFERA	Tetrigidae	*Tetrix japonica*	NC_018543.1	Genbank	
	Tetrigidae	*Tetrix subulata*	MG378361.1	Genbank	
	Tetrigidae	*Alulatettix yunnanensis*	NC_018542.1	Genbank	
INGROUP		*Euparatettix nigritibis*	EU414825	Genbank	
	Cylindrachetidae	*Cylindraustralia* sp.	KM657344	Genbank	
	Ripipterygidae	*Mirhipipteryx* sp.		ICN	Maffpul22
	Ripipterygidae	*Mirhipipteryx* sp.		ICN	Mirh16
	Ripipterygidae	*Mirhipipteryx* sp.		ICN	Mirh47

TABLE 6.2. (continued)

Ripipterygidae	*Mirhipipteryx* sp.		ICN	Mirh48
Ripipterygidae	*Mirhipipteryx andensis*	NC028065Mt	Genbank	
Ripipterygidae	*Mirhipipteryx* sp.		ICN	Mpint7
Ripipterygidae	*Ripipteryx aff. saopauliensis*		ICN	Raffsao2
Ripipterygidae	*Ripipteryx capotensis*		ICN	Rcap18
Ripipterygidae	*Ripipteryx crassicornis*		INHS	Rcra59
Ripipterygidae	*Ripipteryx forceps*		ICN	Rfor8
Ripipterygidae	*Ripipteryx rivularia*		ICN	Rriv4
Tridactylidae	*Bruntridactylus tartarus*		INHS	B27tartarus253
Tridactylidae	*Ellipes minuta*	GU945502	Genbank	
Tridactylidae	*Ellipes minuta minuta*		INHS	EmminDam162
Tridactylidae	*Ellipes minuta minuta*		INHS	EmminDix76
Tridactylidae	*Ellipes minuta minuta*		INHS	EmminJohnD60
Tridactylidae	*Ellipes minuta minuta*		INHS	EmminPhilt34
Tridactylidae	*Ellipes minuta minuta*		INHS	EmminPW66
Tridactylidae	*Neotridactylus aff. apicialis*		INHS	Neo43mal362
Tridactylidae	*Neotridactylus aff. apicialis*		INHS	NeoHav74
Tridactylidae	*Neotridactylus aff. apicialis*		INHS	NeoWO87
Tridactylidae	*Tridactylus* sp.	NS2016Mt	Genbank	

TABLE 6.3. List of taxa used in the morphological dataset.

Family/Subfamily	**Genera**	**Species**	**Data source**	**ID**
Cylindrachetidae	*Cylindroryctes*	*C. spegazzinii*	Museo Civico di Storia Naturale Giacomo Doria MSNG, Genoa holotype	Cspe
Ripidactylidae fam. nov.		*Ripidactylus chimera* sp. nov.	Nanjing Institute of Geology and Paleontology Chinese Academy of Sciences, China. holotype No. NIGP166935	Fam1
Ripipterygidae				
	Mirhipipteryx	*M. acuminata*	ANSP, Philadelphia holotype. (Günther 1969)	Macu
		M. andensis	UMMZ, Ann Arbor holotype. Samples determined by Günther 1974 (ANSP). (Günther 1969)	Mand
		M. columbiana tenaensis	UMMZ, Ann Arbor holotype. Samples determined by Günther 1988 (ANSP). (Günther 1962, 1969).	Mirhitenaensis1
		M. phallica	ANSP, Philadelphia holotype. (Günther 1969)	Mpha
		Mirhipipteryx pulicaria pulicaria	(Günther 1969)	Mpul
		M. triangulata	ANSP, Philadelphia holotype (Günther 1969)	Mtri
		Mirhipipteryx sp*1*	AvH-E113893	Mirhisp1
		Mirhipipteryx sp*2*	IAvH-E113866	Mirhisp2
		Mirhipipteryx sp*3*	IAvH-E 113892	Mirhisp3
		Mirhipipteryx sp*4*	NB0203	Mirhisp4
		Mirhipipteryx sp*8*	ICN, Bogotá NBUV028 Cambia	Mcambia
		Mirhipipteryx sp.	ICN088019, Bogotá	MirhiI88
	Ripipteryx	*R. antennata*	ANSP, Philadelphia holotype No. 968	Rant
		R. capotensis	ICN 086984 and ICN 088010, Bogotá; Rcap18	Rcap
		R. crassicornis	INHS	Rcra
		R. laticornis	MfN, Berlin holotype (Günther, 1963); IAvHE113900	Rlat
		R. nodicornis	ANSP, Philadelphia holotype; IAvH-E 113802, 113805, 113808, 1138886	Rnod
		R. gorgonaensis	IAvH-E 113896; MUSENUV No. GOR 3728-1; (Baena-Bejarano & Heads 2015)	Rgor

TABLE 6.3. (continued)

R. aff. nigra	NB0118	Raffnig
R. carbonaria	IAvHE IAvHE 113820, 113827, 113828, 113829; (Günther 1969)	Rcar
R. diegoi	IAvH-E 142877, IAvH-E 137238, IAvH-E 137239	Rdie
R. ecuadoriensis	MfN, Berlin holotype; IAvH-E 113838 - 113837; (Günther 1962, 1969)	Recu
R. forceps	MHNG, Geneva Museum, holotype; ICN 086981-086982, Bogotá. INHS Rfor8; (Günther 1969)	Rfor
R. paraprocessata	ICN 086986, Bogotá	Rpar
R. aff. boliviana	ICN 086987-086988, 087997, 087975, 088012, Bogotá	Raffbol
R. aff. cyanipennis	IAvH-E 113813 113814	Raffcya
R. aff. saopauliensis	NB0201	Raffsao
R. aff. trilobata	IAvH-E 113809, 113810, 113888	Rafftri
R. boliviana	ANSP, Philadelphia lectotype; (Günther 1969)	Rbol
R. cruciata	ANSP, Philadelphia holotype	Rcru
R. cyanipennis	MHNG, Geneva Museum lectotype. (Günther 1969); determined by Günther 1974 (ANSP)	Rcya
R. furcata	ANSP, Philadelphia holotype	Rfur
R. hydrodroma	(Günther 1969); NB0202	Rhyd
R. lawrencei	ANSP, Philadelphia holotype	Rlaw
R. limbata	MfN, Berlin holotype. Samples determined by Hebard 1924 Tukeit BG: British Guiana (ANSP)	Rlim
R. notata	(Günther 1969)	Rnot
R. ornata	MNHN, Paris syntypes. (Günther 1969); Samples determined by Chopard. (ANSP)	Rorn
R. rivularia	MHNG, Geneva Museum, ICH. (Günther 1969); IAvHE113887; ICN 086991, Bogotá	Rriv4
R. trilobata	(Günther 1969)	Rtri
R. aff. amazonica	IAvH-E 113885 and male M.3387 Vaupés	Raffama
R. difformipes	SI NMNH, Washington holotype No. 62095	Rdif
R. femorata	SI NMNH, Washington holotype. (SI_NMNH No. 62097)	Rfem

TABLE 6.3. (continued)

		R. guacharoensis	IAvH-E 113834, IAvH-E 137237	Rgua
		R. insignis	DEI, DEI Müncheberg holotype. (Günther 1969); samples determined by Günther 1975 (ANSP)	Rins
		R. marginipennis	ANSP, Philadelphia holotype	Rmar
		R. sturmi	(Günther 1963)	Rstu
		R. vicina	SI NMNH, Washington holotype No. 62096	Rvic
		R. biolleyi	ANSP, Philadelphia neotype. (Günther 1969); samples determined by Günther 1965	Rbio
		R. mediolineata	UMMZ, Ann Arbor holotype. (Günther 1969); samples determined by A.B. Gurney 1974 (SI_NMNH)	Rmed
		R. mexicana	MHNG, Geneva Museum. (Günther 1969); Samples determined by Hebard as *R. fraterna*. Synonimy of *R. mexicana* (ANSP)	Rmex
		R. mopana	INHS 0338 holotype	Rmop
		R. saltator	(Günther 1969); samples determined by Günther 1965 (ANSP)	Rsal
Tridactylidae				
Dentridactylinae	*Bruntridactylus*	*B. tartarus*	INHS	Btar
	†Burmadactylus	*†B. grimaldii*	American Museum of Natural History, New York (AMNH)	Bgr
	Dentridactylus	*D. quadratus*	ICN 088003, ICN 093585, Bogotá	Dqua
	Dentridactylus	*D. truncatus*	ICN 087977, ICN 093583, ICN 087911, ICN 093584, Bogotá	Dtru
	†Paraxya	*†Paraxya obscurus* sp. nov.	Nanjing Institute of Geology and Paleontology Chinese Academy of Sciences, China	Paraxyasp
Tridactylinae	*Afrotridactylus*	*A. madecassus*	Royal Belgium Museum of Natural History IRSNB	Amad
	Ellipes	*Ellipes* sp. *1*	IAvH-E113860	Ellsp1
	Ellipes	*E. minuta minuta*	INHS EmminPhilt34	Emmin
	Neotridactylus	*Neotridactylus* sp. *1*	Specimen from Universidad Distrital Francisco José de Caldas, Laboratorio de Sanidad Forestal sample: 961225	Neosp1
	Neotridactylus	*Neotridactylus* sp. *2*	INHS	Neosp2
	Neotridactylus	*N. aff. apicialis*	Museum d'Histoire Naturelle Geneva MHNG, sample NICA, Jicaral. Leg. B. Landry	NaffapiNIC
	Neotridactylus	*N. aff. apicialis*	INHS	Neo43

TABLE 6.3. (continued)

	Tridactylus	*Tridactylus* sp.	Royal Belgium Institute of Natural Sciences, Brussels, Belgium	Trid2
	Xya	*X. variegata*	ZMSC, Zoological Museum Split Croatia	Xvar
†Mongoloxyinae		*Atavidactylus fossorius* n. sp.	American Museum of Natural History, New York (AMNH) 44480	Fossilsp3
		Geodactylus fortis n. sp.	American Museum of Natural History, New York (AMNH) 43374	Fossilsp4
Tetrigidae			NB0112, ICN Bogotá, Universidad Nacional de Colombia	Tetrsp1
Tetrigidae			INHS	Tetrsp2
Tettigoniidae			INHS	Tett
Gryllidae	*Acheta*	*A. domesticus*	http://www.linnean-online.org/26239/	Adom

TABLE 6.4. Uncorrected pairwise distance p of COI in Tridactyloidea. Distance within species and between species in the same genus.

Genus	**Intraspecific distance (min-max)**	**Interspecific distance (min-max)**
Mirhipipteryx	0-0.006	0.094-0.236
Ripipteryx		0.118-0.243
Ellipes	0-0.015	0.186-0.244
Neotridactylus	0.005-0.026	0.155-0.231

FIGURE 6.1. Total evidence of Tridactyloidea with parsimony analysis (PA). Strict consensus of 78 trees of length 4149 (CI = 0.36, RI = 0.55). Node values are Bremer and Bootstrap support (Bremer/Bootrstrap). Outgroup in red, fossil taxa in gray (includes subfamily Mongoloxyinae), subfamily Dentridactylinae (Tridactylidae) maroon, subfamily Tridactylinae (Tridactylidae) in pink, Group of species of *Ripipteryx* (Ripipterygidae) Forceps in black, Crassicornis in blue, Limbata-Marginata in yellow, Scrofulosa in purple, Marginipennis in green, genus *Mirhipipteryx* in aquamarine.

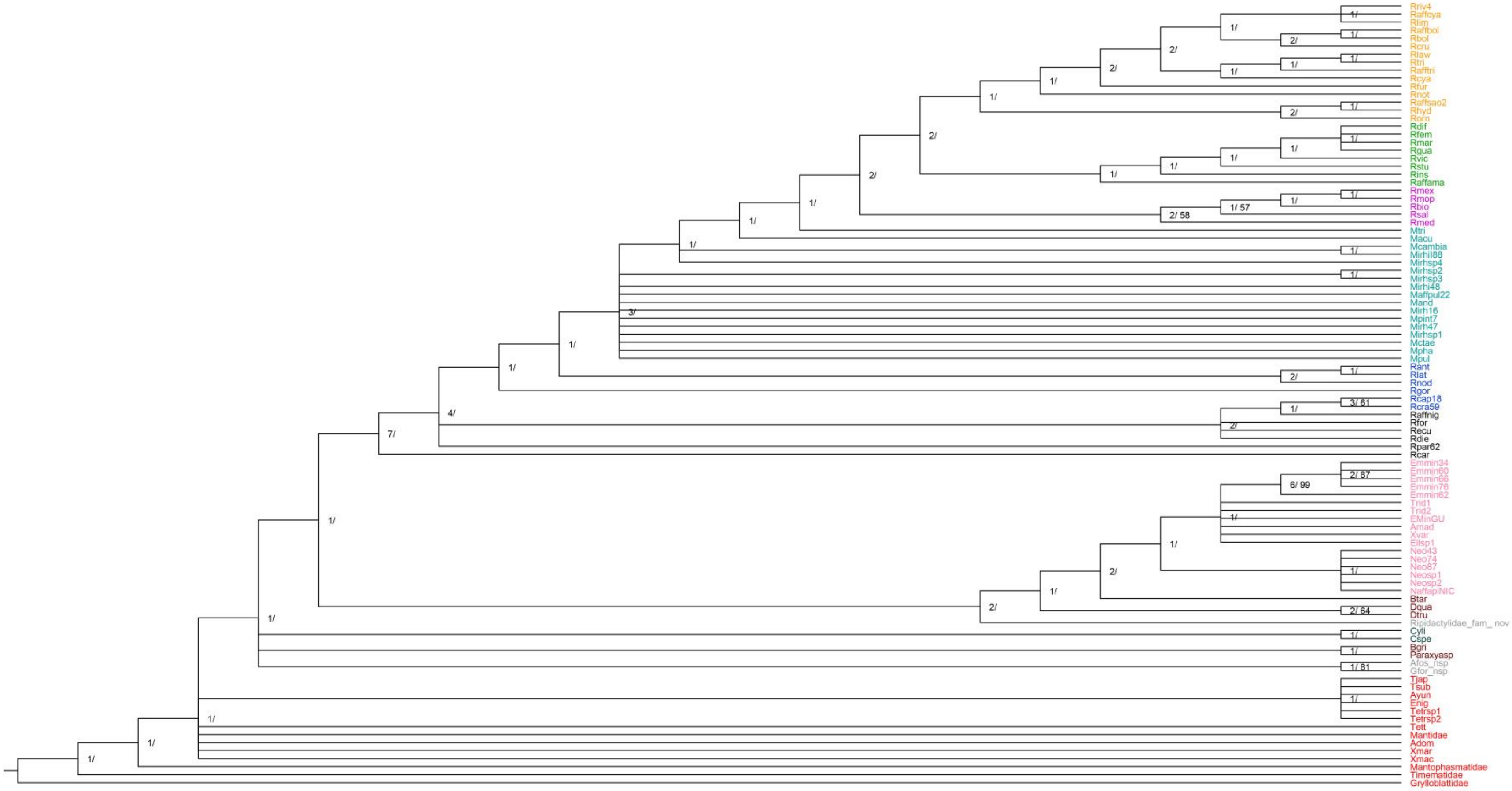


FIGURE 6.2. Total evidence of Tridactyloidea with Maximun Likelihood (ML). Majority rule consensus tree. Node values are Bootstrap support; only values higher than 50 are shown. Outgroup in red, fossil taxa in gray (includes subfamily Mongoloxyinae), subfamily Dentridactylinae (Tridactylidae) maroon, subfamily Tridactylinae (Tridactylidae) in pink, Group of species of *Ripipteryx* (Ripipterygidae) Forceps in black, Crassicornis in blue, Limbata-Marginata in yellow, Scrofulosa in purple, Marginipennis in green, genus *Mirhipipteryx* in aquamarine.

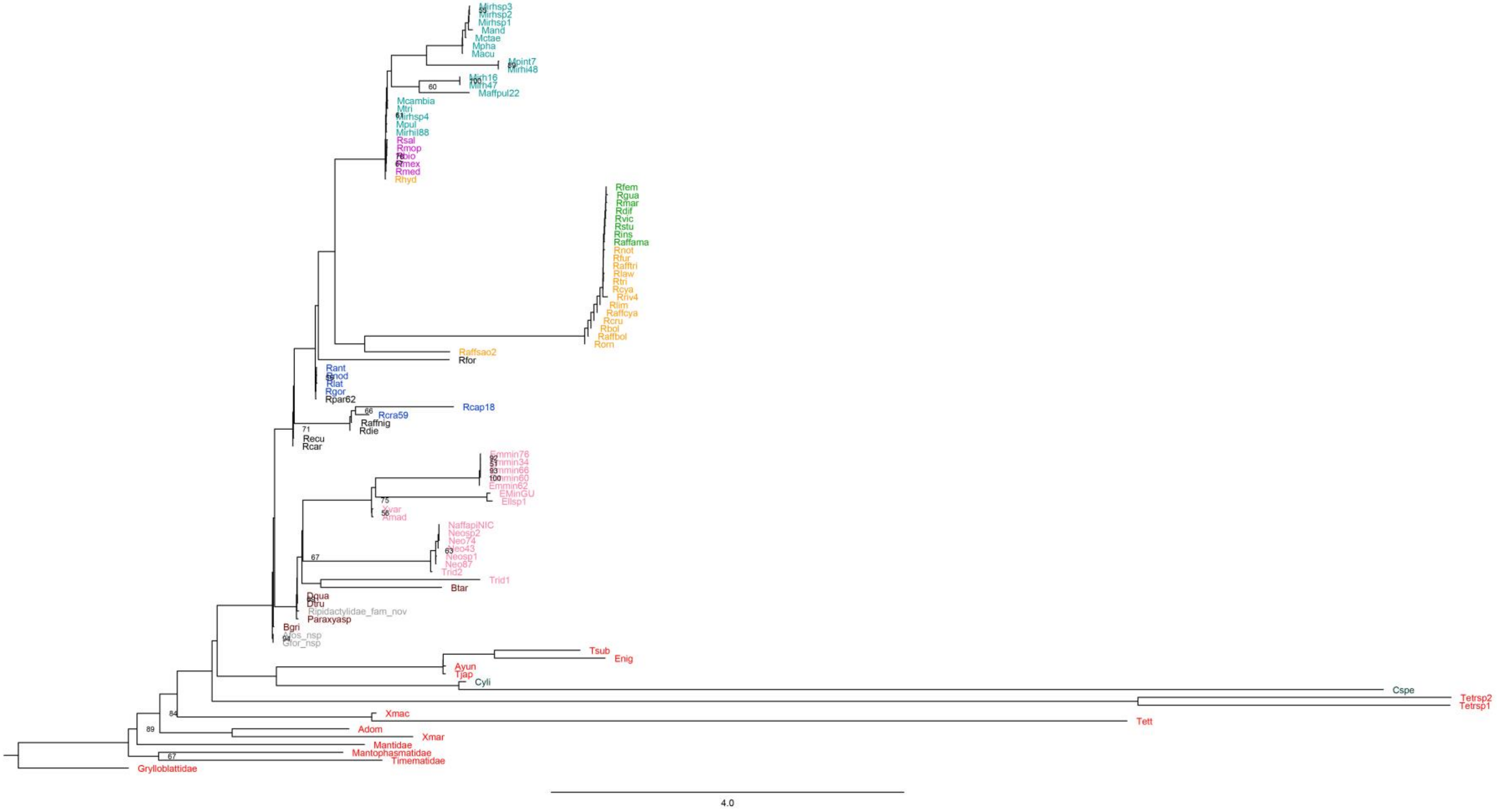


FIGURE 6.3. Total evidence of Tridactyloidea with Bayesian inference (BA). Majority rule consensus tree. Node values are posterior probability support in percentage; only values higher than 50 are shown. Outgroup in red, fossil taxa in gray (includes subfamily Mongoloxyinae), subfamily Dentridactylinae (Tridactylidae) maroon, subfamily Tridactylinae (Tridactylidae) in pink, Group of species of *Ripipteryx* (Ripipterygidae) Forceps in black, Crassicornis in blue, Limbata-Marginata in yellow, Scrofulosa in purple, Marginipennis in green, genus *Mirhipipteryx* in aquamarine.

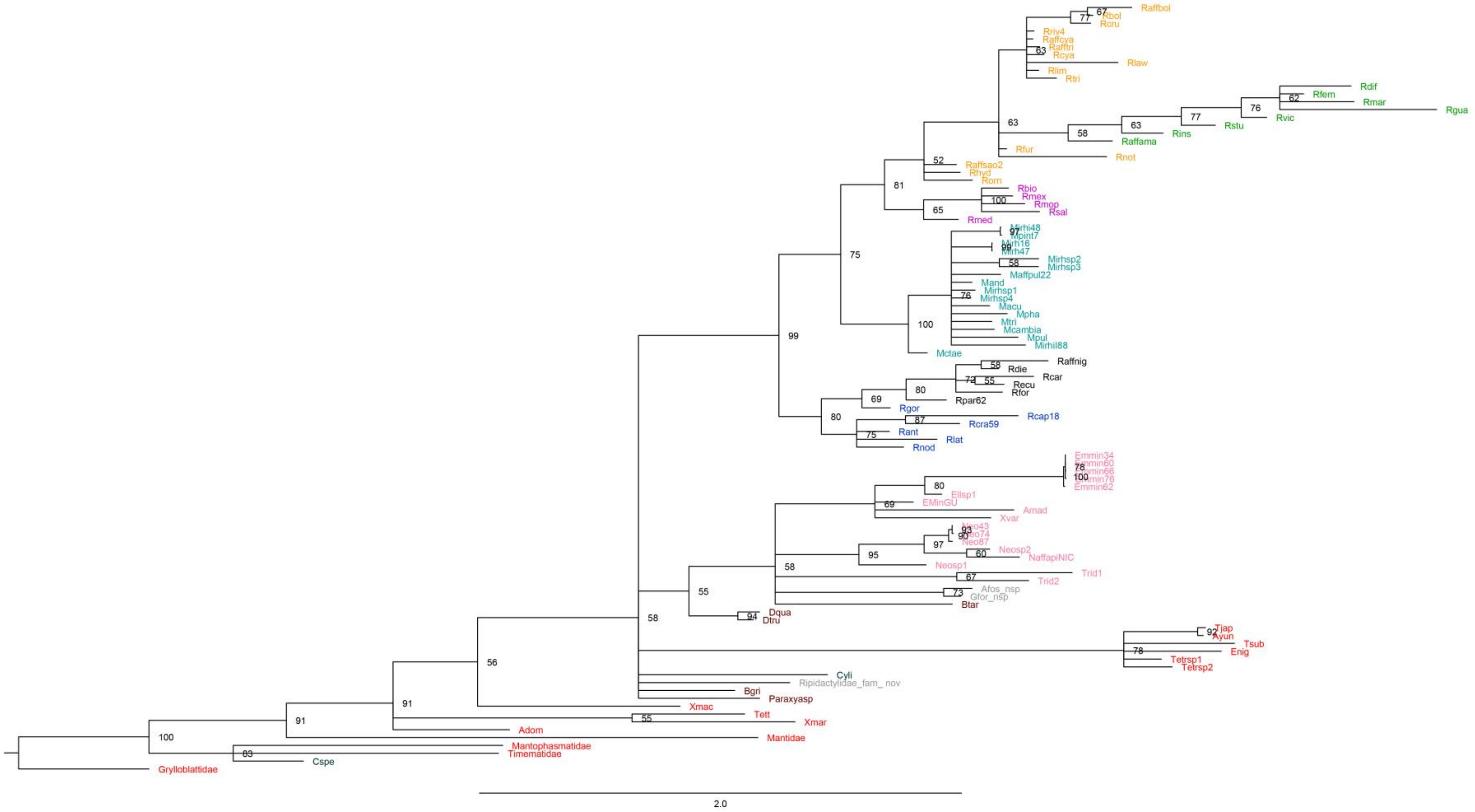
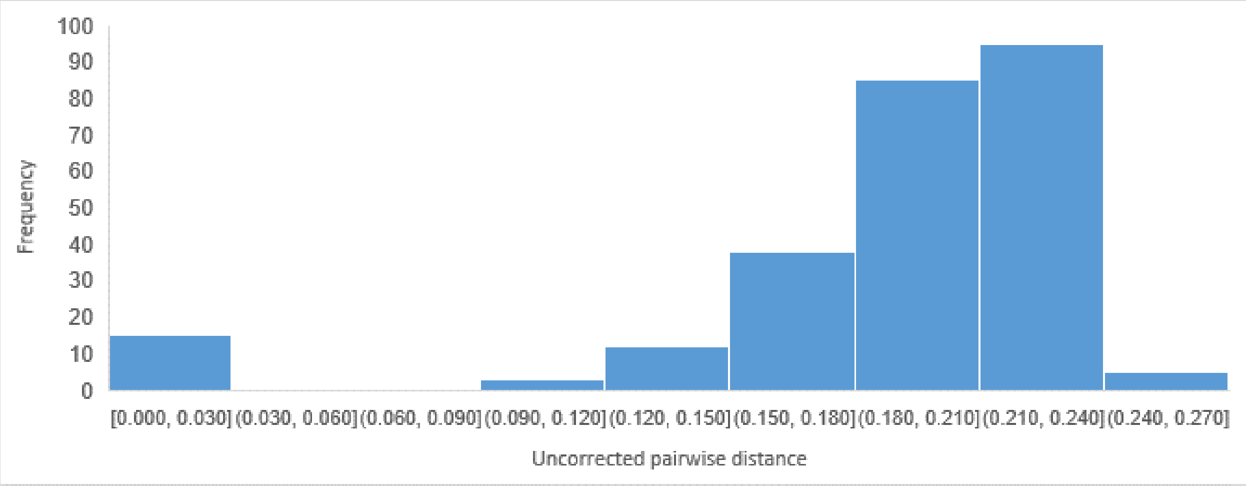


FIGURE 6.4. Uncorrected pairwise distance p of COI across molecular dataset. Notice gap for distance within species and between species.



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APPENDIX A: LIST OF MORPHOLOGICAL CHARACTERS

1–78 characters as stated in Baena-Bejarano (2013)

Characters developed in this document:

79. Vertex: 0 flat; 1 rounded. In lateral view.

80. Antenna length: 0 longer than head; 1 shorter than head.

81. Antennae length: 0 longer than body. 1 shorter than body. This is a character traditionally used in Orthoptera for the diagnosis between suborders.

82. Antennomeres: 0 seven segments; 1 9–10 segments; 2 fourteen segments; 3 11–12; 4 more than 20.

83. Compound eyes: 0 large; 1 small. Size of compound eyes is relative to the head. If the compound eye was extended vertically on the head occupying at least 50% of the area between vertex and gena was codified as large. Otherwise, the compound eye was small.

84. Medial ocellus: 0 absent; 1 present. The character state present is understood as any trace of developed or underdeveloped ocellus. Any noticeable shape, coloration or state of ocellus was codified as present.

85. Medial ocellus: 0 Aligned; 1 Triangle; 2 Inverted Triangle (Figure A1). This character refers to the position of the medial ocellus with respect to the lateral ocelli. Here the state aligned corresponded to all ocelli almost on a straight line. The state triangle refers to the lateral ocelli in a lower position with respect to the medial ocelli or base of compound eyes (lateral ocelli are missing in *R. chimera*). The state inverted triangle refers to the upper position of the lateral ocelli with respect to the medial ocelli.

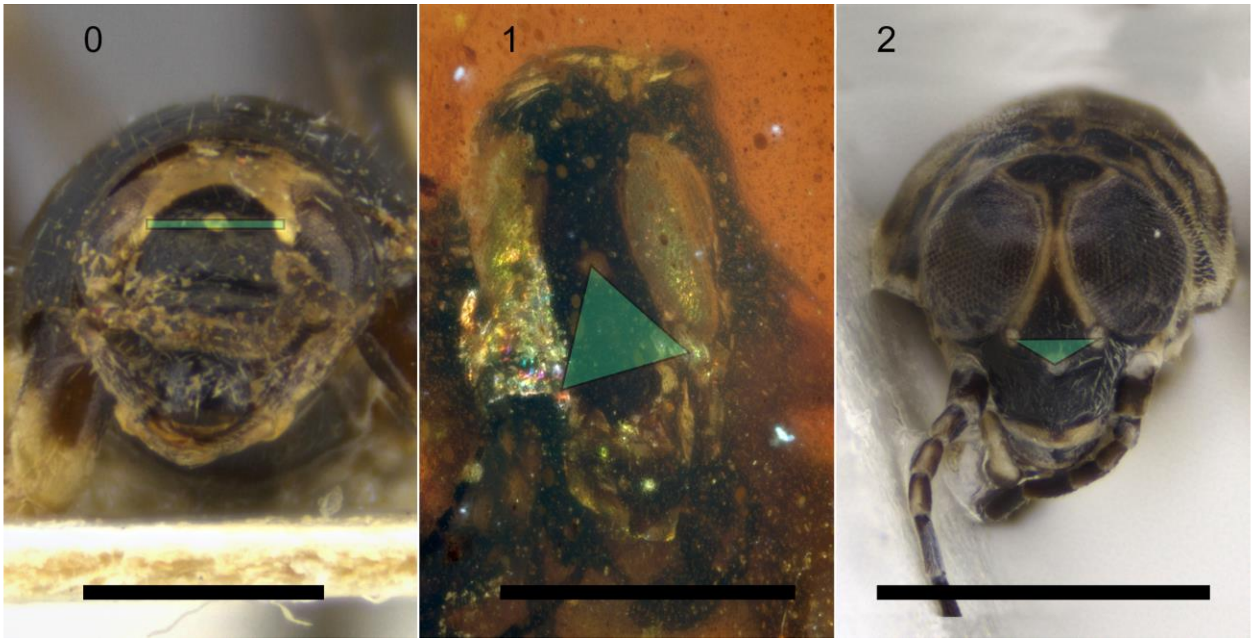

FIGURE A.1. Frontal view showing medial ocellus position in Tridactyloidea. Character states: 0 Aligned; 1 Triangle; 2 Inverted Triangle (Figure 6.5). Scale 1 mm.

86. Lateral ocelli: 0 absent; 1 present. The absence of ocelli seems to be known only from fossil taxa. This is a diagnostic character for the identification of Burmese amber fossil Tridactyloidea (Baena-Bejarano *et al.et al.* in prep; see Chapter 5). Heads (2009b) recorded also from a fossil apparently lacking this feature.

87. Mesothoracic-metathoracic segments (Figure A2): 0 developed; 1 reduced. Martins-Neto (1990) registered in Crato Formation fossils a more elongated thoracic segments form than what was known in extant taxa. This developed segments were reported to be half the length of the body. See Chapter 4 for more details.

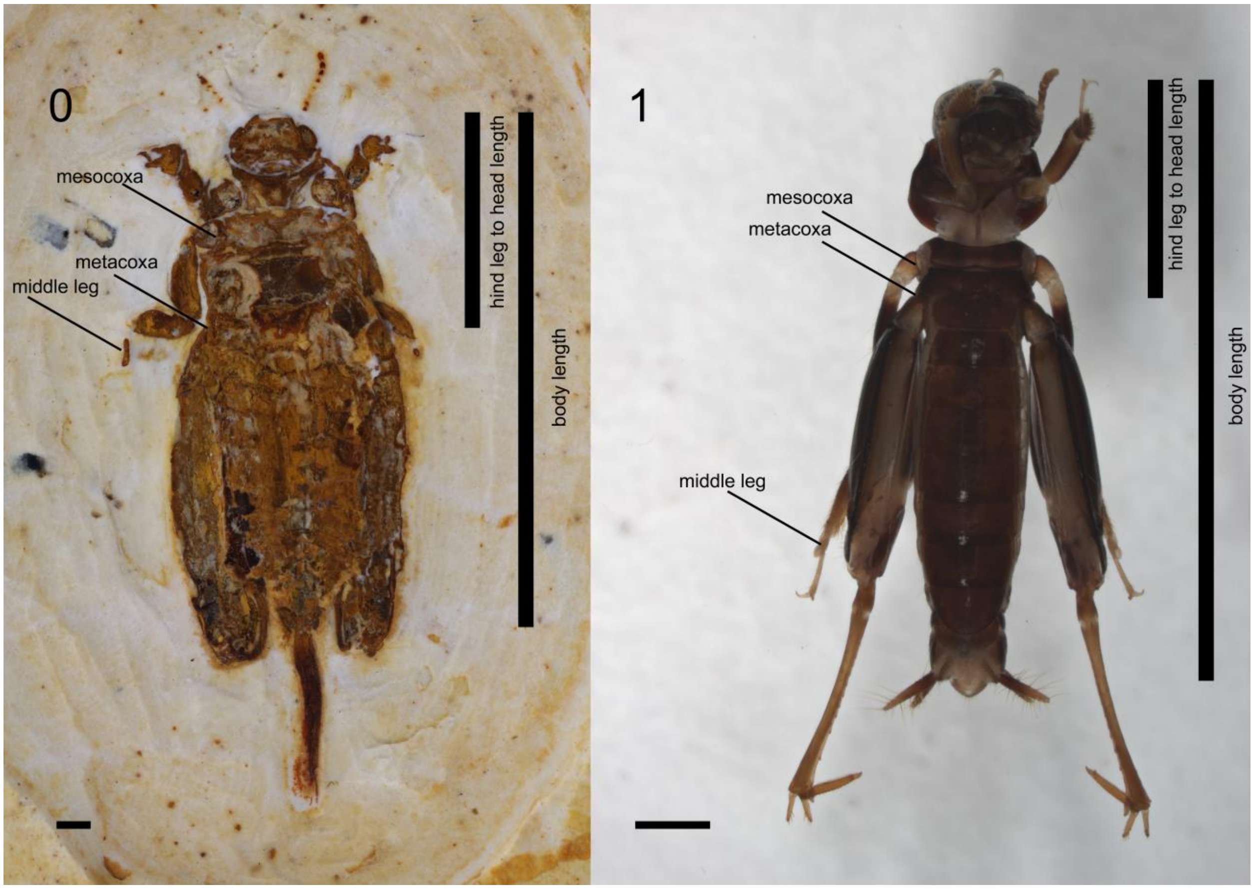

FIGURE A.2. Ventral view of Tridactyloidea showing mesothoracic-metathoracic segments (character states: 0 developed; 1 reduced), distance between mesocoxa and metacoxa, and middle leg length. Bottom left scale 1mm.

88. Pronotum: 0 not extended on abdomen; 1 extended on abdomen. This is a traditional character used for the identification of the family Tetrigidae. Here, this family is used as an outgroup.

89. Prosternal process: 0 absent; 1 present. Günther (1972, Figure/Abb. 2; 1995) used this character for identification keys of genera and species. A prosternal process is known to occur in the genus *Neotridactylus*. More recently modification of prosternal processes are being recorded from fossils (Poinar 2018; also see Chapter 5 for square-like prosternal process).

90. Prosternal process: 0 single tubercle (As in Günther (1972, Figure/Abb. 2); 1 paired tubercles (Poinar 2018); 2 square-shaped plate (see Chapter 5).

91. Forewing longitudinal veins: 0 More than 4; 1 fewer than 4. Character proposed for Gorochov *et al. (*2006) to identify the extinct subfamily Mongoloxyinae known only from fossil records. Species of this subfamily present more than 4 longitudinal veins and species in the subfamily Dentridactylinae and Tridactylinae are known to have 2–4 weak longitudinal veins.

92. Reticulate venation: 0 absent; 1 present.

93. Hind wings: 0 absent; 1 present.

94. Forelegs: 0 not modified for digging; 1 modified for digging. A modified leg for digging was treated here as an enlarged shape near extremities with spines and concave. Spines of any sizes.

95. Profemur shape (lateral view): 0 basally widened; 1 distally widened; 2 quadrate or subparallel.

96. Profemur outer process (Figure A3): 0 absent; 1 present.

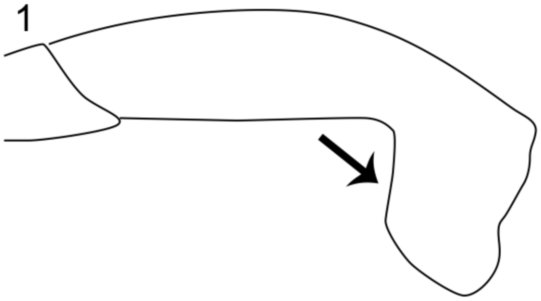

FIGURE A.3. Lateral view of Tridactyloidea profemur. Arrow showing presence of outer process (character states: 1).

97. Profemur outer process developed/lobed: 0 sliglty curved; 1 lobed.

98. Margin profemora lobe: 0 entire; 1 serrated.

99. Protrochanter: 0 reduced; 1 enlarged.

100. Protrochanter spines: 0 absent; 1 present.

101. Protibiae shape/ margins (figure A4): 1 distally widened; 2 quadrate or subparallel; 5 C-shaped; 6 V-shaped (State 6 was modified from Günther 1975: Abb. 6).

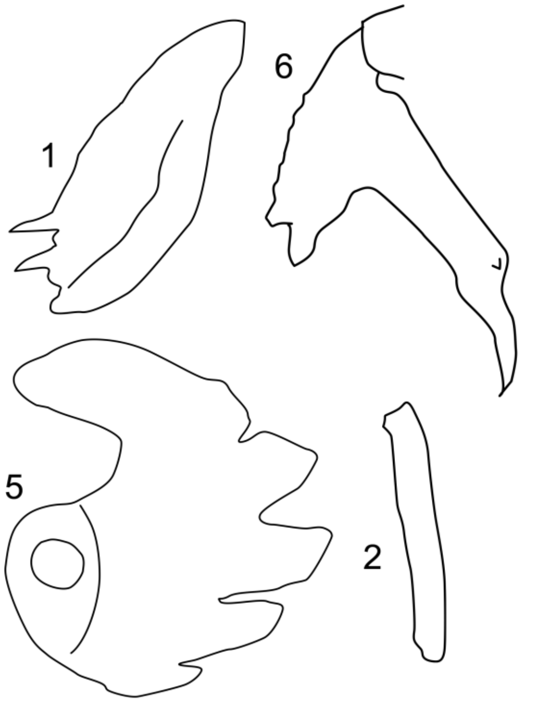

FIGURE A.4. Tridactyloidea protibiae shapes. Character states: 1 distally widened; 2 quadrate or subparallel; 5 C-shaped; 6 V-shaped (State 6 was modified from Günther 1975: Abb. 6).

102. Tarsomeres forelegs: 0 four; 1 three; 2 two.

103. Length of middle leg: 0 mesofemur as long as mesotibiae; 1 mesofemur longer than mesotibiae; 2 mesofemur shorter than mesotibiae.

104. Length of mesofemur: 0 reach base of metafemur; 1 does not reach the metafemur; 2 reach half of the metafemur; 3 surpasses half of metafemur.

105. Mesofemur process: 0 absent; 1 present.

106. Mesofemur shape: 0 basally widened; 1 distally widened; 2 quadrate or subparallel; 3 rounded/convex; 4 ellipsoid.

107. Mesotibiae shape: 0 quadrate or subparallel; 1 ellipsoid.

108. Mesotibiae process: 0 absent; 1 present.

109. Hind leg: 0 saltatorial; 1 not saltatorial/reduced.

110. Metafemur shape (Figure A5): 0 apically slender “chicken leg”; 1 not slender apically.

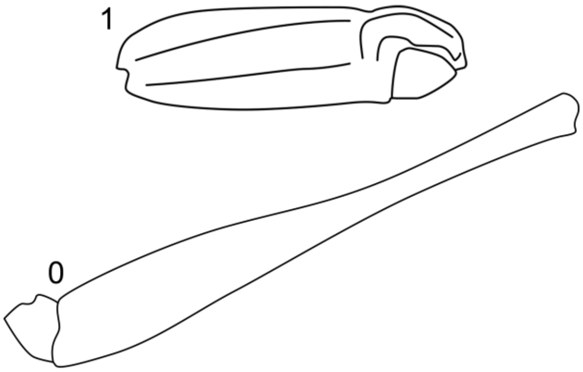

FIGURE A.5. Metafemur shapes codified in matrix. Character states: 0 apically slender “chicken leg”; 1 not slender apically.

111. Metafemur dorsal margin shape (Figure A6): 0 anteriorly rounded; 1 medially rounded.

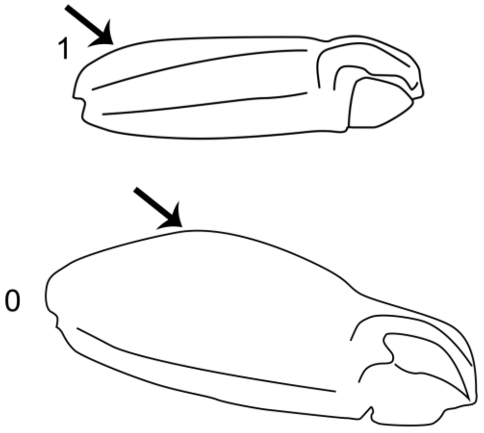

FIGURE A.6. Metafemur dorsal margin shape. Arrow is pointing dorsal margin character states: 0 anteriorly rounded; 1 medially rounded.

112. Metafemur margins (Figure A7): 0 subparallel; 1 convex; 2 asymmetric (notice arrow pointing concave margin).

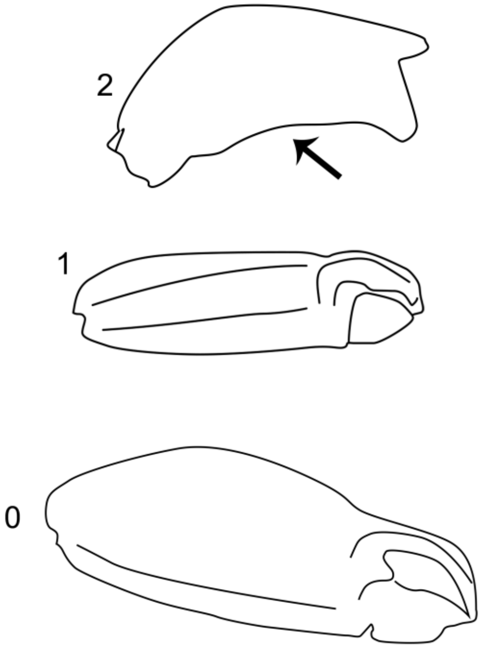

FIGURE A.7. Metafemur margins showing character states: 0 subparallel; 1 convex; 2 asymmetric. Arrow is pointing concave margin.

113. Semi-lunar process: 0 absent; 1 present.

114. Metatibiae spines: 0 absent; 1 present.

115. Metatibiae spines (area): 0 arranged across all tibiae; 1 only distally.

116. Tibial lamellae or swimming plates: 0 absent; 1 present.

117. Male tibial lamellae of inner margin: 0 zero; 1 one; 2 two; 3 three; 4 four.

118. Female Tibial lamellae of inner margin: 0 zero; 1 one; 2 two; 3 three; 4 four.

119. Male tibial lamellae of outer margin: 0 zero; 1 one; 2 two; 3 three; 4 four.

120. Female Tibial lamellae of outer margin: 0 zero; 1 one; 2 two; 3 three; 4 four.

121. Subapical tibial spurs: 0 absent; 1 present.

122. Tarsomeres hind leg: 0 five; 1 three; 2 two; 3 one.

123. Metatarsus: 0 more than one articulated segments; 1 one articulated segment.

124. Metatarsus: 0 developed; 1 reduced/vestigial.

125. Subapical tooth metatarsus (Figure A8): 0 absent; 1 present.

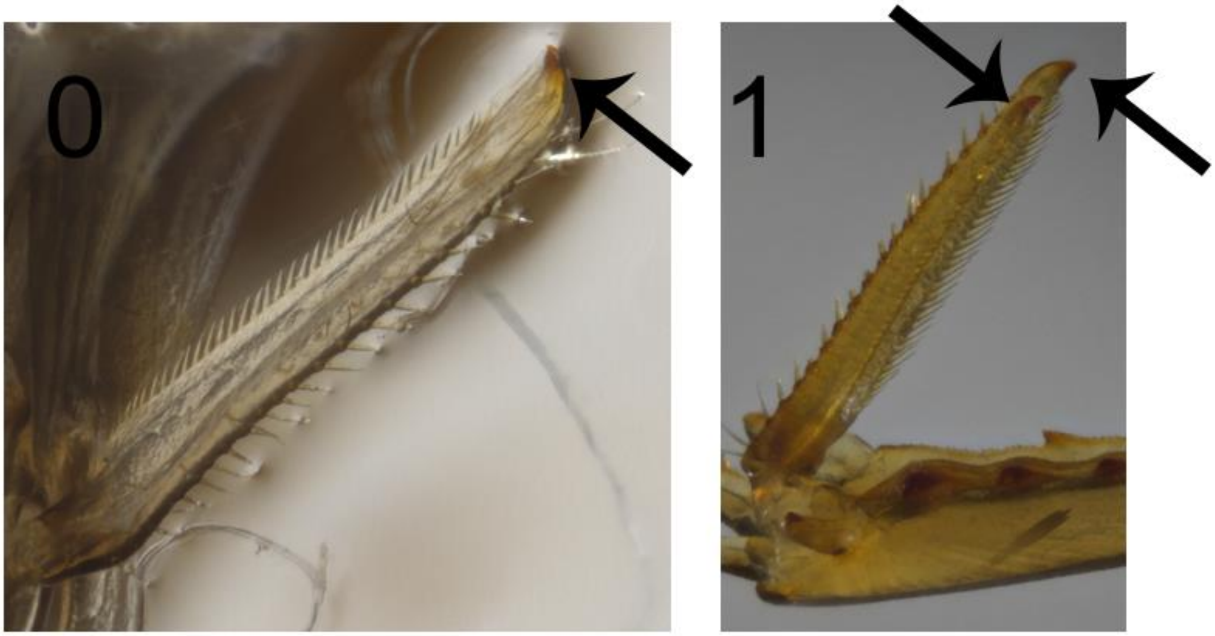

FIGURE A.8. Metatarsus of Tridactyloidea showing presence of apical tooth and subapical tooth with arrows. Character states: 0 subapical tooth absent and apical tooth present; 1 apical tooth and subapical tooth are present.

126. Apical tooth metatarsus: 0 absent; 1 present.

127. Cerci length (in lateral view): 0 shorter than paraproctal lobes; 1 longer than paraproctal lobes.

128. Cerci segment length: 0 apical segment shorter that basal; 1 apical segment longer that basal; 2 apical segment equal to basal.

129. Female paraproctal segments: 0 one; 1 two.

130. Female ovipositor: 0 absent; 1 present/developed.

131. Male subgenital plate: 0 without a process; 1 with a process.

132. Female subgenital plate margin: 0 entire; 1 with notches.

133. Female subgenital plate margin: 0 not lobed; 1 lobed or narrowed apically.

134. Metatarsus (Figure A9): 0 compact, continuous fins; 1 with two fins; 2 compact, without two fins.

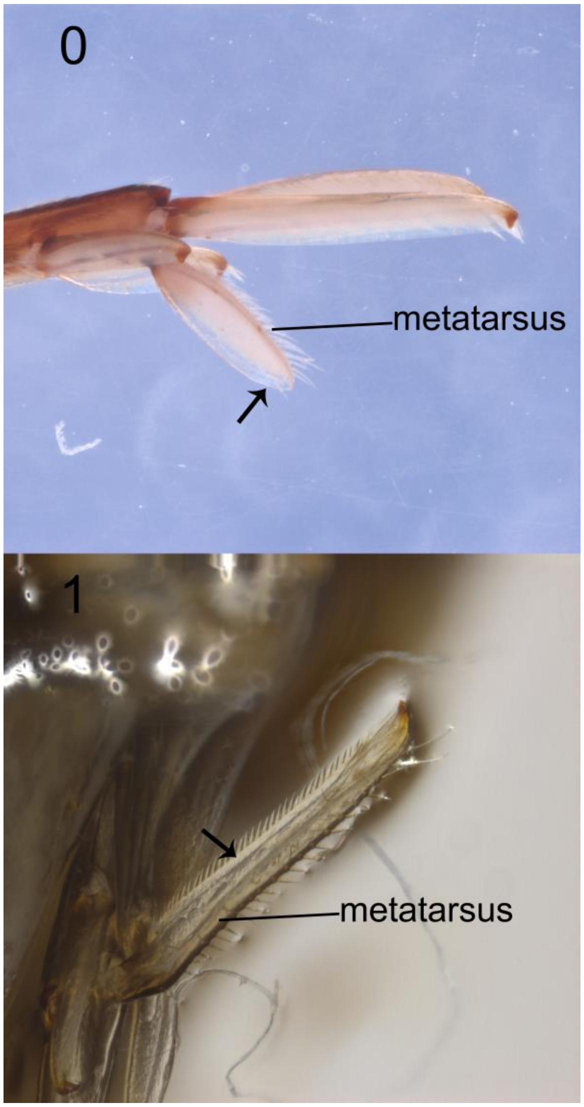

FIGURE A.9. Metatarsus of Tridactyloidea. Character states: 0 compact, continuous fins; 1 with two fins.

135. Pronotum widest: 0 anterior; 1 medial; 2 posterior; 3 subposterior

136. Hind wings costal field: 0 sclerotized; 1 membranous

137. sclerotized hind wing: 0 brigth; 1 mate

138. Profemur ventral margin male: 0 without inner row of spines; 1 with inner row of setae; 2 with inner row of scarce setae (5)

139. Profemur ventral margin male: 0 without outer row of long setae; 1 with outer row of long setae; 2 with outer row of scarce long and small setae; 3 with outer row of spines

140. profemur shape: 0 flat; 1 globose; 2 globose with a second layer

141. protibiae shape: 0 flat; 1 globose

142. mesofemur shape: 0 flat; 1 globose

143. mesotibiae shape: 0 flat; 1 globose

144. mesotibiae: 0 thicker than mesofemur; 1 thinner than mesofemur; 2 alike

145. Uncus: 0 absent; 1 present

146. Phallic complex composition: 0 only virga or spikes sclerotized; 1 More structures are sclerotized such as Cingulum, basal plate.

147. Basal plate: 0 absent; 1 present

148. Virga: 0 absent; 1 present

149. Pulvilli in basitarsus foreleg: 0 absent; 1 one; 2 two; 3 three

150. Pulvilli in basitarsus middle leg: 0 absent; 1 one; 2 two; 3 three

151. Body lenght withouth hind wings: 0 Larger than 6 mm; 1 smaller than 6 mm

APPENDIX B: TOTAL EVIDENCE MATRIX

Total evidence matrix of 98 taxa x 1699 characters.

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DIMENSIONS NTAX=98 NCHAR=1699;
 GAP = - MISSING = ? SYMBOLS = " 0 1 2 3 4 5 6 7 A B C G K M R S T W Y ";
MATRIX
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Mantophasmatidae

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Timematidae

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Adom

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Xmar

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Tjap

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Tsub

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TAATAATTACA??
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Ayun

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Enig

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Cyli

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Trid1

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Trid2

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Neo43

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Neo87

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Emmin34

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Emmin60

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Emmin62

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Emmin66

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Emmin76

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Mirhi48

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Rcra59

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Raffsao2

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Rriv4

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Maffpul22

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Mirh16

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Mpint7

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APPENDIX C: PARTITION FOR MAXIMUN LIKELIHOOD (ML) AND BAYESIAN ANALYSIS (BA)

a) Partition as best scheme suggested by PartitionFinder. b) Partition used in BA analysis with linked branch length. Analyses performed without linking branch lengths did not converge to 1 (potential scale reduction factor and the effective sample sizes were not larger than 100. Trials increasing the number of generations from 20 to 100 million did not pass the assessment. By linking branches less parameters were estimated for the data.

RaxML partition

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DNA, Subset1 = 1-1548\3, 2-1548\3
DNA, Subset2 = 3-1548\3
MULTI, Morph = 1549-1699
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MrBayes partition

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a) begin mrbayes;


        charset Subset1 = 1-1548\3 2-1548\3;
        charset Subset2 = 3-1548\3;


        partition PartitionFinder = 2:Subset1, Subset2;
        set partition=PartitionFinder;


        lset applyto=(1) nst=6 rates=invgamma;
        lset applyto=(2) nst=6 rates=invgamma;
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        prset applyto=(all) ratepr=variable;

        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) tratio=(all);

        unlink brlens=(all);


end;


b) begin mrbayes;


        charset Subset1 = 1-1548\3 2-1548\3;

        charset Subset2 = 3-1548\3;


        partition PartitionFinder = 2:Subset1, Subset2;

        set partition=PartitionFinder;


        lset applyto=(1) nst=6 rates=invgamma;

        lset applyto=(2) nst=6 rates=invgamma;


        prset applyto=(all) ratepr=variable;

        unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) tratio=(all);


end;
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APPENDIX D: PERCENTAGE OF MISSING DATA IN TOTAL EVIDENCE MATRIX

Columns DNA and Morphology (Morpho) indicates the source of data available for each taxa.

Taxa	**%**	**DNA**	**Morphology**
Adom	63.27	DNA	Morpho
Btar	53.80	DNA	Morpho
Emmin34	53.62	DNA	Morpho
Emmin60	53.62	DNA	Morpho
Emmin62	53.62	DNA	Morpho
Emmin66	53.62	DNA	Morpho
Emmin76	53.74	DNA	Morpho
Mand	2.41	DNA	Morpho
Neo43	53.56	DNA	Morpho
Raffsao2	53.86	DNA	Morpho
Rcap18	55.50	DNA	Morpho
Rcra59	52.97	DNA	Morpho
Rfor	54.33	DNA	Morpho
Rriv4	53.50	DNA	Morpho
Ayun	9.30	DNA	
Cyli	9.30	DNA	
EMinGU	9.65	DNA	
Enig	61.62	DNA	
Grylloblattidae	9.89	DNA	

Maffpul22	60.15	DNA	
Mirh16	60.15	DNA	
Mirh47	60.15	DNA	
Mpint7	60.15	DNA	
Neo74	60.62	DNA	
Neo87	60.62	DNA	
Ripi48	60.68	DNA	
Mantophasmatidae	9.59	DNA	
Timematidae	9.12	DNA	
Tjap	9.24	DNA	
Trid1	9.95	DNA	
Tsub	68.98	DNA	
Mantidae	9.30	DNA	
Xmac	9.12	DNA	
Xmar	8.65	DNA	
Amad	93.11		Morpho
Bgri	95.29		Morpho
Cspe	95.17		Morpho
Dqua	94.53		Morpho
Dtru	94.82		Morpho
Ellsp1	94.35		Morpho
Atavidactylus fossorius n. sp.	97.53		Morpho
Geodactylus fortis n. sp.	97.12		Morpho

Macu	92.70	Morpho
Mcambia	92.00	Morpho
Mctae	95.00	Morpho
MirhiI88	92.05	Morpho
Mirhsp1	93.11	Morpho
Mirhsp2	93.11	Morpho
Mirhsp3	93.11	Morpho
Mirhsp4	93.64	Morpho
Mpha	93.41	Morpho
Mpul	94.59	Morpho
Mtri	93.23	Morpho
NaffapiNIC	92.88	Morpho
Neosp1	93.47	Morpho
Neosp2	98.23	Morpho
Pobs	95.76	Morpho
Raffama	93.17	Morpho
Raffbol	91.58	Morpho
Raffcya	93.29	Morpho
Raffnig	92.64	Morpho
Rafftri	92.88	Morpho
Rant	92.70	Morpho
Rbio	93.00	Morpho
Rbol	92.94	Morpho

Rcar	91.64	Morpho
Rchi	94.41	Morpho
Rcru	92.58	Morpho
Rcya	92.70	Morpho
Rdie	92.82	Morpho
Rdif	93.23	Morpho
Recu	92.41	Morpho
Rfem	92.82	Morpho
Rfur	92.58	Morpho
Rgor	92.53	Morpho
Rgua	92.29	Morpho
Rhyd	92.76	Morpho
Rins	92.76	Morpho
Rlat	92.41	Morpho
Rlaw	93.64	Morpho
Rlim	93.64	Morpho
Rmar	93.41	Morpho
Rmed	93.88	Morpho
Rmex	92.94	Morpho
Rmop	93.64	Morpho
Rnod	92.53	Morpho
Rnot	92.70	Morpho
Rorn	93.23	Morpho

Rpar	93.11	Morpho
Rsal	94.06	Morpho
Rstu	93.88	Morpho
Rtri	93.76	Morpho
Rvic	92.53	Morpho
Tetrsp1	96.65	Morpho
Tetrsp2	94.41	Morpho
Tett	95.06	Morpho
Trid2	93.41	Morpho
Xvar	92.58	Morpho
Average	75.05	
min	2.41	
max	98.23	