

## Robber flies in Cretaceous ambers (Insecta: Diptera: Asilidae)

TORSTEN DIKOW<sup>1</sup> AND DAVID A. GRIMALDI<sup>2</sup>

### ABSTRACT

Cretaceous fossils of Asilidae are reviewed, and two new taxa from Burmese and Raritan (New Jersey) ambers are described. The first robber fly from Burmese amber, †*Burmapogon bruckschi*, new genus and species, is described based on specimens of both sexes. A scientific name is provided for the previously described but unnamed fossil assassin fly from Raritan amber, †*Cretagaster raritanensis*, new genus and species, preserved as a fragmentary specimen. The amber fossils are placed phylogenetically within Asilidae. Specifically, †*Burmapogon* is postulated to be a representative of the clade comprised of (Brachyrhopalinae + Stichopogoninae), while †*Cretagaster* is a member of the Leptogastrinae and postulated to be an extinct sister group to (Acronychini + Leptogastrini).

### INTRODUCTION

Among the plethora of insect taxa preserved in amber from deposits around the world, Diptera are the most abundant and diverse (e.g., Penney, 2010; Grimaldi and Cumming, 1999; Grimaldi et al., 2002; McKellar and Wolfe, 2010). Nematocerous Diptera in particular are well represented in amber from both the Cretaceous and Tertiary, but only certain groups of Brachycera can be considered abundant. For example, the Cretaceous Rhagionidae represent one of the most diverse and common such families; in Tertiary ambers this is usually the case for

---

<sup>1</sup> Department of Entomology, National Museum of Natural History, Smithsonian Institution, 10th Street and Constitution Avenue NW, Washington, DC 20560.

<sup>2</sup> Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024.

Dolichopodidae and Phoridae. Asilidae—assassin flies or robber flies—are uncommon to extremely rare in amber (indeed, as any type of fossil), which contrasts with their extant diversity. There are more than 7500 extant species of Asilidae known (Pape et al., 2011), but to date only two Cretaceous species have been described.

The oldest definitive Asilidae, †*Araripogon axelrodi* Grimaldi, 1990, was described from limestone of the Crato Formation (Albian, ~112 myo) in Ceará state in northeastern Brazil (Grimaldi, 1990). Since its description, several new specimens of this species and of morphologically similar specimens have become available, and it appears that there are up to three distinct species of †*Araripogon* preserved, whose detailed study is in preparation by the authors. Along with the oldest definitive Mydidae (†*Cretomydas santanensis* Willkommen and Grimaldi, 2007)—which together with Apioceridae forms the sister group to Asilidae—other diverse insect groups are known from this exceptional Cretaceous formation (e.g., Martill et al., 2007). The second Cretaceous robber fly is in amber from the Raritan Formation of central New Jersey (Turonian, ~94–90 myo) (Grimaldi and Cumming, 1999), but was never named.

Both of these Cretaceous Asilidae fossils were placed in a morphological phylogeny of Asilidae by Dikow (2009). †*Araripogon axelrodi* could be placed only at the root of a clade of Asilidae excluding Asilinae, Laphriinae, and Ommatiinae (see Dikow, 2009: fig. 121), based primarily on features of the wing venation and in particular the open wing cells found in the fossil. In contrast, the Raritan amber fossil was placed as the sister group to all remaining extant Leptogastrinae, a uniquely derived clade of assassin flies, based on a suite of characters of the proboscis, antenna, wing base, and scutal setation.

The present study increases our knowledge of the diversity of Asilidae from the Cretaceous by providing a scientific name and revised description for the Raritan amber species and describing the first known Asilidae species from Burmese amber (Albian-Cenomanian, ~100 myo), which is based on two well-preserved specimens representing both sexes.

#### MATERIAL AND METHODS

Burmese amber derives from the northern state of Kachin in Myanmar, approximately 100 km west of the town of Myitkyina (Grimaldi et al., 2002). Samples of amber from these outcrops were radiometrically dated at 99 myo using U-Pb isotopes (Shi et al., 2012). This places the age of the deposit very close to the Albian-Cenomanian boundary, which is also the boundary between the Early and Late Cretaceous. The two specimens in Burmese amber are the only Asilidae known among several tens of thousands of Burmese amber pieces that contain insects. Raritan amber is from the Raritan Formation, which outcrops in Cretaceous sections of Long Island and Staten Island, New York, and central New Jersey (Grimaldi et al., 1989, 2000). The outcrop in Sayreville, Middlesex County, New Jersey that yielded the robber fly is dated palynologically to Turonian, 90–94 myo. Of more than 2000 insect inclusions found in the amber from this outcrop there is only one asilid. Burmese amber specimens were trimmed using a water-fed trim saw with a thin (1 mm) diamond edge. The New Jersey amber specimen was embedded in EpoTek® casting epoxy prior to trimming, since this amber is highly fractile. All pieces were then ground and polished using wet emery disks

in a series of decreasing grit sizes (400, 600, 800, 1200, 2400) on a lapidary wheel (Buehler, Inc.). The holotypes of the Burmese and Raritan amber specimens are deposited in the amber collection of the Division of Invertebrate Zoology, American Museum of Natural History (AMNH). The Burmese amber paratype (female) specimen is in the private collection of James Zigras and is available for study through the AMNH. Morphological terminology and abbreviations for setae follow McAlpine (1981), Stuckenberg (1999), Cumming and Wood (2009), and Dikow (2009). Abdominal tergites are abbreviated in the descriptions with “T” and sternites are abbreviated with “S.”

Morphological features were examined using a Zeiss SteREO Discovery.V12 stereo microscope and illustrated using a drawing tube attached to a Wild M-5 stereo microscope. Wing length was measured from the tegula to the distal tip of the wing. Photomicrographs of specimens were taken using a Nikon SMZ1500 stereomicroscope with a Nikon digital camera; z-stacking was done with Nikon NIS Elements software. All specimen photomicrographs are deposited in Morphbank (<http://morphbank.net>). The permanent image numbers are included in the figure captions and the images can also be accessed in the Morphbank image collection (collection ID 832153: <http://www.morphbank.net/myCollection/index.php?collectionId=832153>). These images are automatically harvested by the Encyclopedia of Life (<http://eol.org/>) and available under the respective species page. All taxon names are registered in ZooBank (<http://zoobank.org/>; Pyle and Michel, 2008).

## SYSTEMATICS

### †*Burmapogon*, new genus

ZooBank LSID: BE54FF1B-9CD8-438B-BC61-7B3E8672D850

(<http://zoobank.org/urn:lsid:zoobank.org:act:BE54FF1B-9CD8-438B-BC61-7B3E8672D850>).

ETYMOLOGY: From *Burma*, the original name of the country where this amber is deposited, and Greek *pogon*, “beard,” a common suffix of Asilidae generic names, referring to the mystax. The generic name, to be treated as masculine, refers to the region of the amber deposit.

TYPE SPECIES: †*Burmapogon bruckschi*, new species., by monotypy.

DIAGNOSIS: Small asilid flies with antennal postpedicel parallel sided (same width throughout) and laterally compressed; antennal stylus composed of one element tapering distally and with distinct apical, setalike sensory element; frons markedly and suddenly diverging laterally; all wing cells open; tibiae with numerous macrosetae and in particular with a large, trowel-shaped metathoracic tibial spine; absence of notopleural (npl), supraalar (spa), and postalar (pal) macrosetae; female with acanthophorite plates and spines.

### †*Burmapogon bruckschi*, new species

Figures 1–6

ZooBank LSID: C3FD7954-CCD6-4512-BD36-03D3908236B3

(<http://zoobank.org/urn:lsid:zoobank.org:act:C3FD7954-CCD6-4512-BD36-03D3908236B3>).

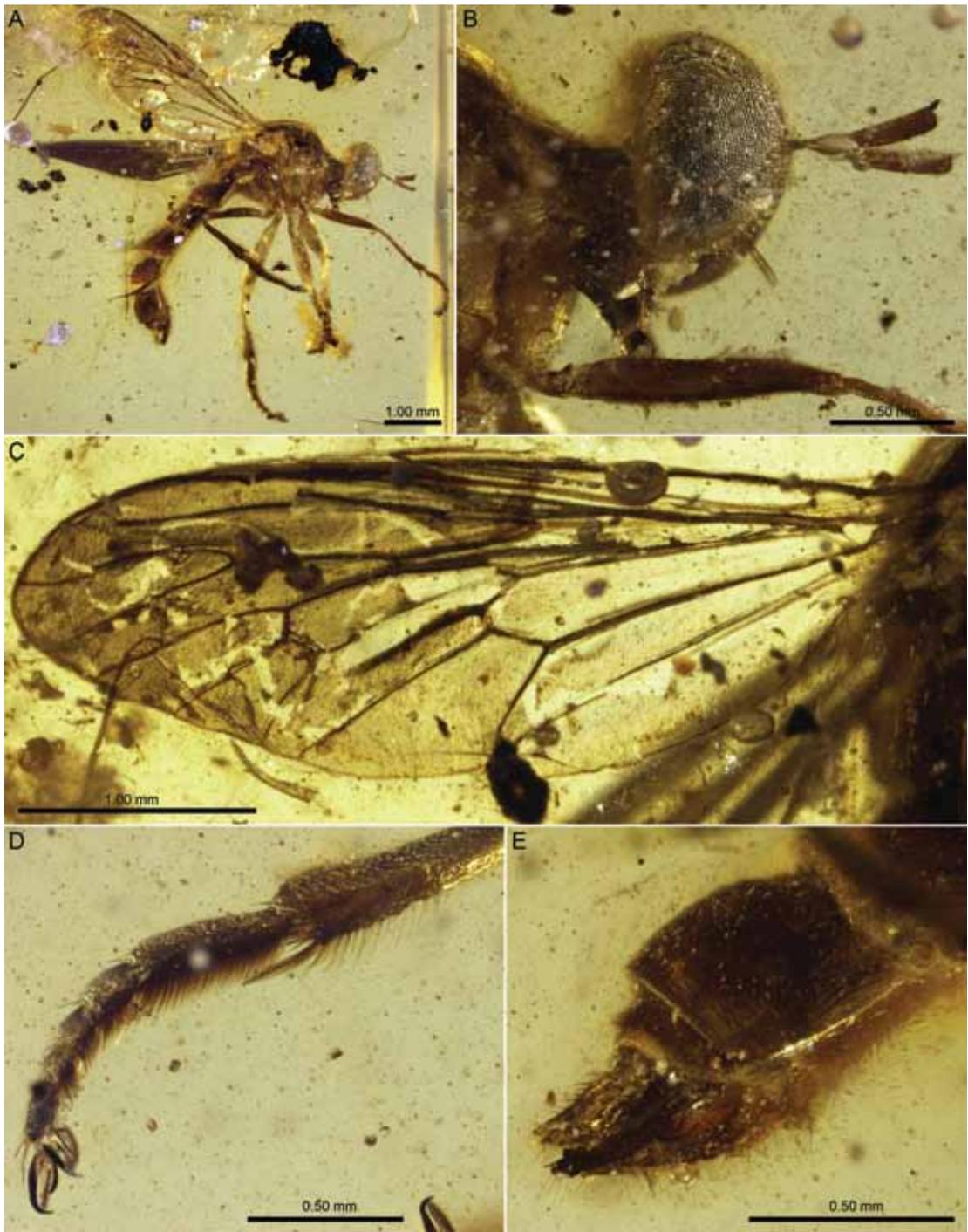


FIG. 1. Photomicrographs of †*Burmapogon bruckschi* (male holotype AMNH-Bu-KB1). A. Whole specimen lateral habitus (Morphbank: #832135). B. Head and antennae in lateral view (#832137). C. Wing (#832139). D. Left metathoracic tibia and tarsus in median view (#832141). E. Male terminalia in lateral view (#832143).

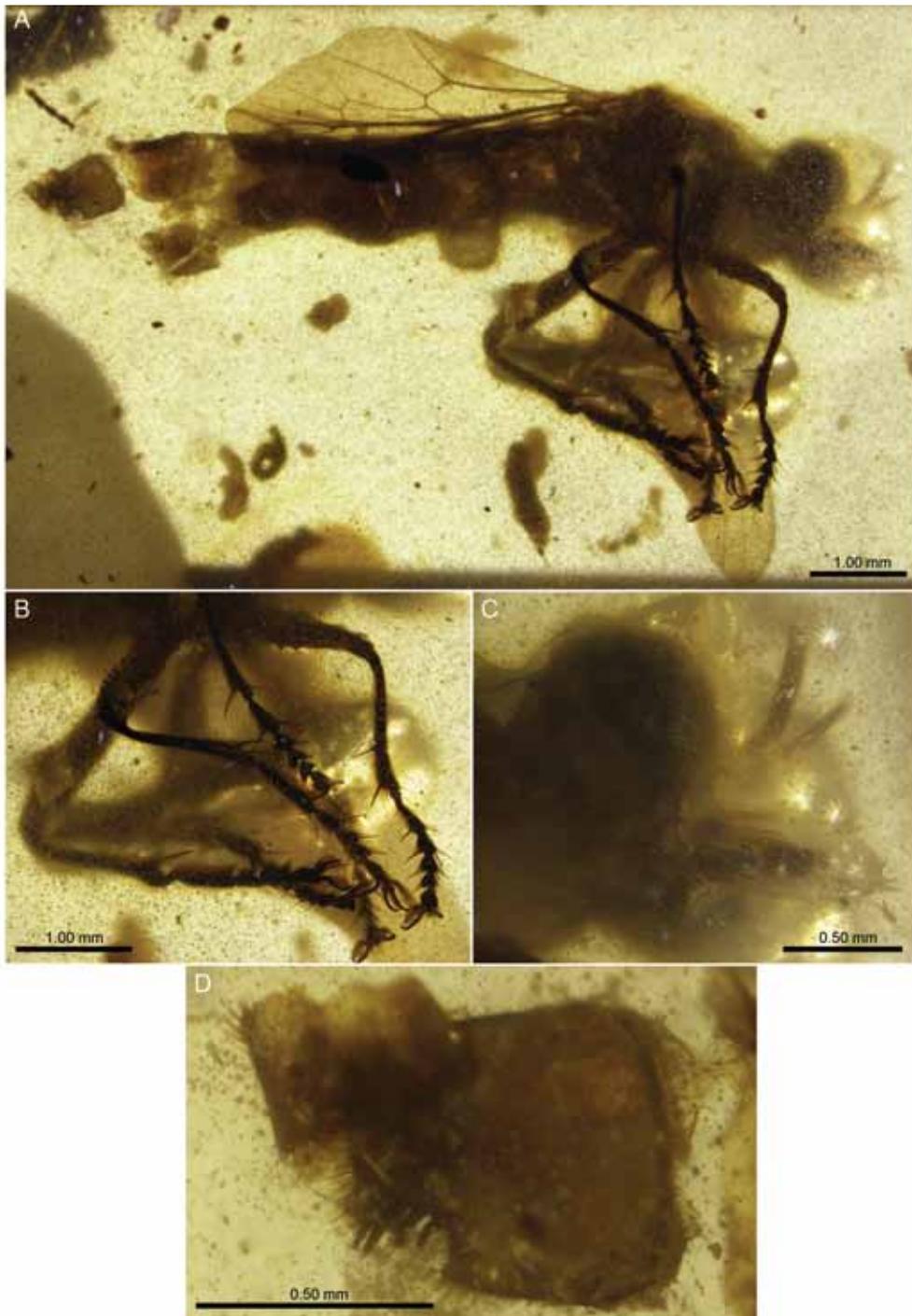


FIG. 2. Photomicrographs of †*Burmapogon bruckschi* (female paratype AMNH-JZBu-163). A. Whole specimen lateral habitus (Morphbank: #832146). B. Right legs in lateral view (#832148). C. Head and antennae in lateral view (#832150). D. Disarticulated female terminalia in dorsolateral view showing acanthophorite spines (#832152).

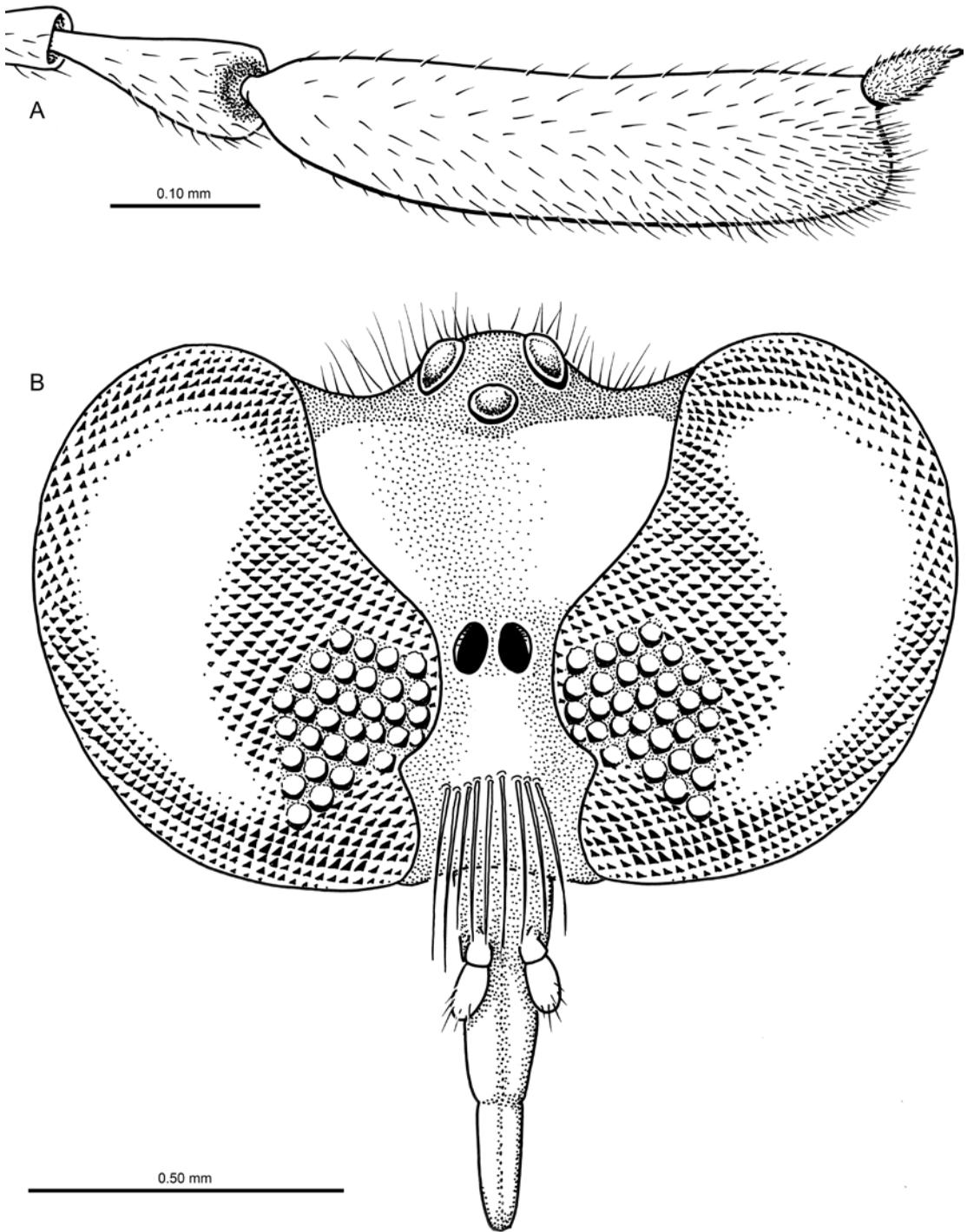


FIG. 3. †*Burmapogon bruckschi* (male holotype AMNH-Bu-KB1). **A.** Antennal postpedicel and stylus in lateral view. **B.** Head in anterior view (antennae omitted; note: left side of head deformed by expanded air bubble and here reconstructed from right side).

**ETYMOLOGY:** This species is named after Klaus-Peter Brucksch of Kuranda, Queensland, Australia, who acquired the amber piece containing the male holotype in the Hukawng Valley in Myanmar.

**DESCRIPTION:** Approximate specimen length 6.5 mm (male holotype AMNH-BuKB1) and 8.0 mm (female AMNH-JZC Bu163 paratype). **Head** (fig. 3B): wider than high in anterior view; face wide, three times as wide as adjacent ommatidia, anterior ommatidia distinctly larger than lateral ones; mystax comprised of nine light-colored, stiff setae (male holotype AMNH-Bu-KB1), arranged in a single, transverse row on clypeal-facial margin; facial swelling not developed; frons markedly and abruptly diverging dorsolaterally; vertex sharply depressed; ocellar triangle prominent with a few, short ocellar (oc) setae; postocular (pocl) setae long, lightly angled anteriorly in distal half; median occipital sclerite without macrosetae; proboscis straight; maxillary palpus two-segmented, about 1/4 length of proboscis. **Antenna** (fig. 3A): scape and pedicel cylindrical, about equal in length, pedicel dorsally and ventrally microsetose; postpedicel parallel sided throughout, laterally compressed, microsetose throughout (particularly evident distally on anteroventral margin), about 1.5 times as long as combined length of scape and pedicel; stylus short, about 1/8 length of postpedicel, comprised of one element, stylus tapering distally, aetose, but densely covered by microtrichia, and positioned at dorso-distal tip of postpedicel, tipped with distinct apical, setalike sensory element.

**THORAX:** Pronotum divided into ante- and postpronotum, postpronotum much wider than anteppronotum, anteppronotal (aprn) and lateral postpronotal (lat pprn) setae present; postpronotal lobes only slightly extending medially, short setose; scutum covered with short posteroclinate setae, longer laterally and posteriorly, acrostichal (acr) and dorsocentral (dc) setae not distinguishable from scutal setation; no evidence of notopleural (npl), supraalar (spa), or postalar (pal) macrosetae; scutellum large, discal scutellar (ds sctl) and apical scutellar (ap sctl) setae present, all of same length; superoposterior anepisternum setose (but not macrosetose), anatergite aetose, katatergite setose; metakatepisternum small and not visible between mesothoracic and metathoracic coxae; postmetacoxal bridge absent, postmetacoxal area entirely membraneous.

**WING:** (figs 1C, 4): Length 4.0–4.1 mm; densely covered by microtrichia, veins brown; cells  $r_1$ ,  $r_4$ ,  $r_5$ ,  $m_3$ , and cup open; anterior margin of wing straight (C not bulging anteriorly), C circumambient; apex of  $R_{2+3}$  arching sharply anteriorly to meet C;  $R_4$  and  $R_5$  diverging from each other,  $R_4$  terminating very slightly anterior to and  $R_5$  posterior to wing apex,  $R_4$  relatively straight (not sinuate); supernumerary stump vein ( $R_3$ ) at base of  $R_4$  absent; r-m distinct, positioned at the midline of cell d; distal end of cell d formed by base of  $M_2$  and m-m in nearly a straight line;  $M_1$ ,  $M_2$ , and  $M_3$  all reaching wing margin,  $CuA_1$  and  $CuA_2$  distinct, reaching wing margin,  $CuA_2$  approximating  $A_1$ , but not closing cell cup; alula reduced in size to small lobe; microtrichia on posterior margin developed in a single plane; halter light brown.

**LEGS:** (figs. 1D, 5): Coxae directed ventrally, setose (not macrosetose), anterior metathoracic coxa without any protuberance; metathoracic trochanter simple, setose medially; femora of equal size (metathoracic femur slightly more expanded), setose (not macrosetose); prothoracic tibia straight, 3 posteroventral macrosetae (fig. 5C–D): 1 weak macroseta at slightly less

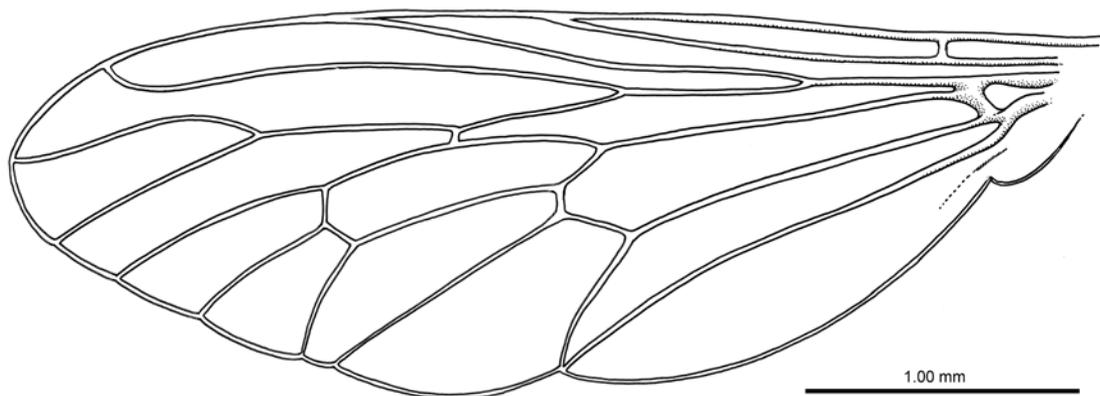


FIG. 4. Wing of †*Burmapogon bruckschi* (male holotype AMNH-Bu-KB1).

than 1/2 length, 1 strong macroseta at 2/3 length, 1 strong macroseta at 4/5 length; 3–4 short anterodorsal macrosetae in distal 1/2, several short macrosetae at distal tip; mesothoracic tibia straight, 1 posteroventral macroseta at 2/3 length, several short antero- and posteroventral macrosetae in distal 1/2, several long macrosetae at distal tip; no evidence of prothoracic tibial projections (neither a small posteroventral S-shaped spur nor a large anteroventral spine); metathoracic tibia straight, expanded distally with a marked ventral indentation in distal 9/10 (fig. 5A–B); primarily macrosetose, shorter proximally, longer and stronger distally (particularly ventrally), long macrosetae at distal tip; ventral tip with distinct, long, trowel-shaped, partly laterally compressed macroseta (longer than adjacent “regular” macrosetae), with median surface hollow and facing tibia and tarsus; prothoracic and mesothoracic tarsomere 1 longer than tarsomeres 2–3 combined, metathoracic tarsomere 1 longer than tarsomeres 2–4 combined, each tarsomere short, macrosetose, and distally with 1 long anterior and 1 long posterior macroseta; empodium 2/3 length of claw, slightly curved dorsally; claws abruptly angled distally, pointed; pulvilli present, as long as claws, with two dorsal ridges.

**ABDOMEN** (fig. 1A): Somewhat dorsoventrally flattened; tergites entirely sclerotized dorsally and smooth; tergites short, densely setose, marginal and medial macrosetae absent; T2 wider than long, T2–3 rectangular (not forming a distinct “waist”), T6 similar to T5 and not concealing distal tergites and terminalia.

**MALE TERMINALIA** (figs 1E, 6B): T1–T7 well developed (T8 cannot be examined in detail), T7 and following tergites and terminalia partly retracted under T6; hypopygium not rotated and pointing posteriorly; epandrium separated medially and joining proximally, surstylus absent; epandrium and hypandrium not approximating (separated by gonocoxites); gonocoxites long setose distoventrally and protruding beyond tip of epandrium.

**FEMALE TERMINALIA** (figs. 2D, 6A): T7 normally developed; T8 and following segments comprising ovipositor, T8 with erect setae, T8 with anterior rectangular apodeme (entirely fused to tergite); S8 platelike, slightly emarginate mediodistally, macrosetose posteriorly especially posterolaterally; T9 small and triangular, T10 divided into two heavily sclerotized acanthophorite plates with five acanthophorite spines on each plate, T9–10 entirely fused.

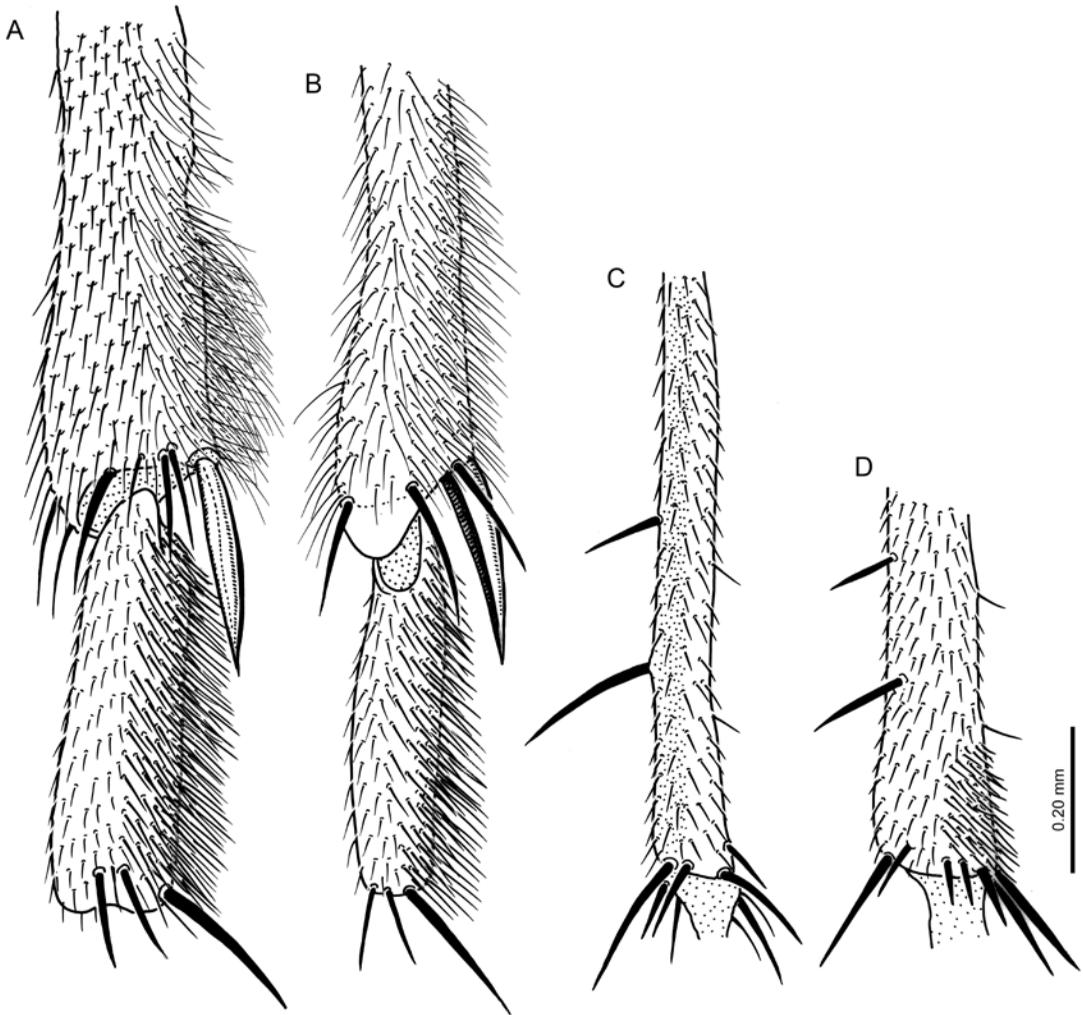


FIG. 5. †*Burmapogon bruckschi* (male holotype AMNH-Bu-KB1). A. Tip of left metathoracic tibia and tarsomere 1 in median view. B. Tip of right metathoracic tibia and tarsomere 1 in dorsolateral view. C. Distal half of right prothoracic tibia in dorsal view. D. Tip of left prothoracic tibia in median view.

**MATERIAL EXAMINED:** Holotype male (fig. 1): Complete specimen (AMNH-Bu-KB1, ex Klaus-Peter Brucksch), in excellent condition, clearly visible with very little obfuscation by other inclusions. Proboscis partly obscured by right prothoracic leg and air bubble, left side of head deformed by expanded air bubble, left scutum and thorax partly covered by air bubble, and right mesothoracic tibia broken off. Paratype female (fig. 2): Complete specimen (AMNH-JZBu-163, in James Zigras Collection) in good condition, but in a rather turbid piece of amber in which not all morphological features are clearly visible. Portions of head and thorax obscured by air bubbles and abdomen damaged and disarticulated from T6 onward, but all structures remain embedded in the amber close to the main portions of the body. Both specimens agree in external morphology and can therefore be regarded to represent the same species without any apparent sexual dimorphism.

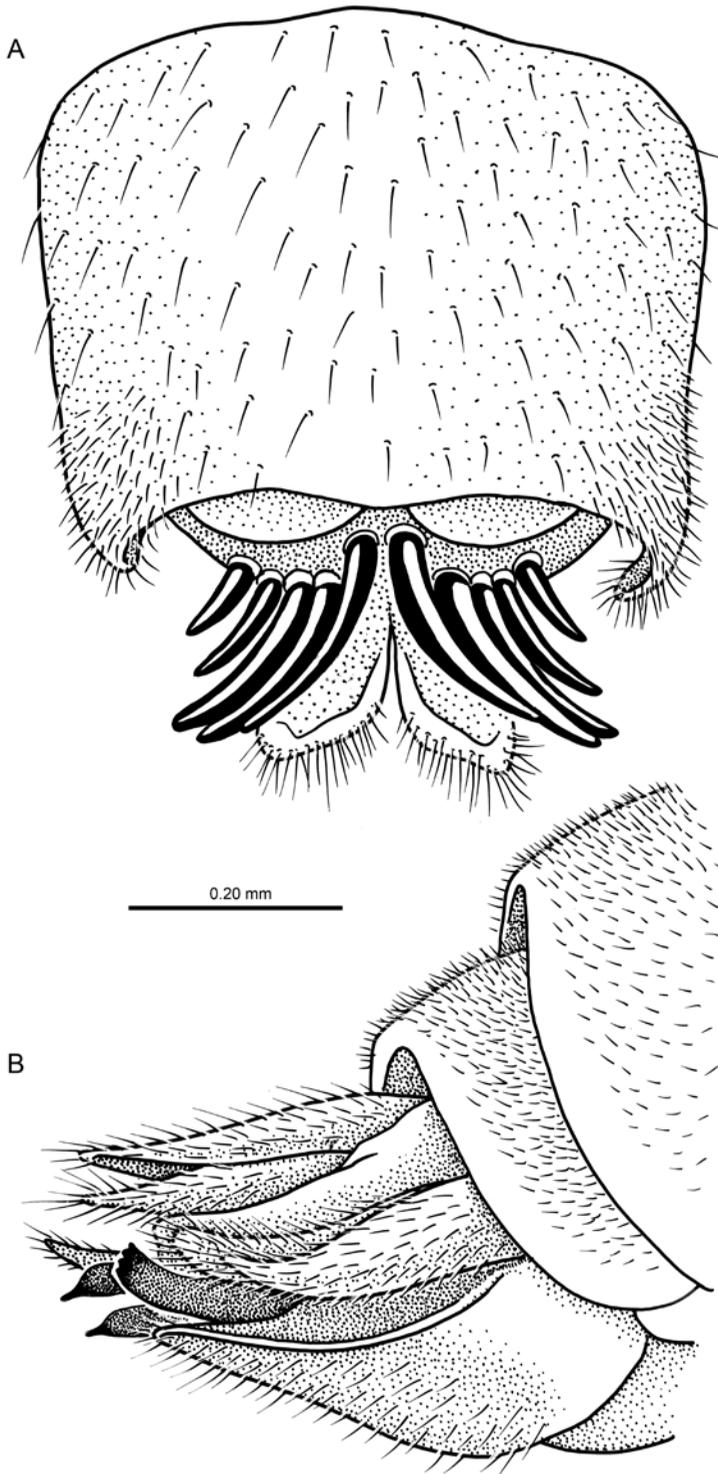


FIG. 6. Terminalia of †*Burmapogon bruckschi*. **A.** Female terminalia in dorsal view (female paratype AMNH-JZBu-163). **B.** Male terminalia in lateral view (male holotype AMNH-Bu-KB1).

†*Cretagaster*, new genus

ZooBank LSID: 6840A2DA-5FC9-4C47-8FE7-33FD213862E0

(<http://zoobank.org/urn:lsid:zoobank.org:act:6840A2DA-5FC9-4C47-8FE7-33FD213862E0>).

ETYMOLOGY: From the Latin *creta*, “chalk” (root of the word *Cretaceous*), and Greek *gaster*, “stomach, belly,” the latter a common suffix of generic names for slender Leptogastrinae. The generic name, to be treated as masculine, refers to the Cretaceous age of this currently oldest known Leptogastrinae.

TYPE SPECIES: †*Cretagaster raritanensis*, new species, by monotypy.

DIAGNOSIS: Small asilid flies with sparsely developed mystax (arranged in a single row); facial swelling not developed; hypopharynx with setalike spicules spaced far apart on dorsolateral surface; antennal base elevated above eye margin in lateral view; antennal stylus composed of two elements (short proximal element and longer distal element with apical setalike sensory element); supraalar (spa) and postalar (pal) setae present; alula of wing reduced in size to small lobe.

†*Cretagaster raritanensis*, new species

Figure 7

ZooBank LSID: 91E3654F-24EC-4432-8865-02C5F6DC63F2

(<http://zoobank.org/urn:lsid:zoobank.org:act:91E3654F-24EC-4432-8865-02C5F6DC63F2>).

ETYMOLOGY: The specific name refers to the Raritan Formation of the northeastern United States, from which this species has been recovered.

DESCRIPTION Grimaldi and Cumming (1999): Thorax length = 2.63 mm. **Head** (fig. 7B): large; compound eyes with fairly large, flat, frontal surface, but no differentiation of frontal and lateral ommatidia, bare; vertex not excavated, probably bare; ocellar triangle raised only slightly; compound eyes widely separated frontally, distance between inner margin 0.28 width of head; inner margins with slight emargination just below antennal bases; face with very simple mystax, composed of only 2 stouter, light-colored setae, plus several finer, slightly shorter setae; proboscis of moderate length; hypopharynx with 3 sharp spicules on dorsal surface that are set far apart; maxillary palpus short and bare, two-segmented. **Antenna** (fig. 7A): pedicel cup shaped, postpedicel drop shaped, stylus two-segmented, short proximal segment (presence difficult to discern) and longer distal segment, tipped with apical “setalike” sensory element.

**THORAX** (fig. 7A): Pronotum fairly large; 2 fine, stiff supraalar (spa) setae; row of 3 fine, stiff postalar (pal) setae; scutum and scutellum largely bare.

**WING** (fig. 7A): Alula small, but base of wing folded, obscuring bases of veins M and Cu.

**LEGS** (fig. 7C): Prothoracic tibia with approximately six stiff, long macrosetae and numerous finer, shorter setae (legs very difficult to observe).

**MATERIAL EXAMINED**: Unique holotype of unknown sex (AMNH NJ-558) collected by Debra Abernathy at the White Oaks (Old Crossman’s) Clay Pits, Sayreville, New Jersey. The specimen is in a milky amber and only most of the head, thorax, portions of some legs, and the proximal quarter of the wings are preserved.

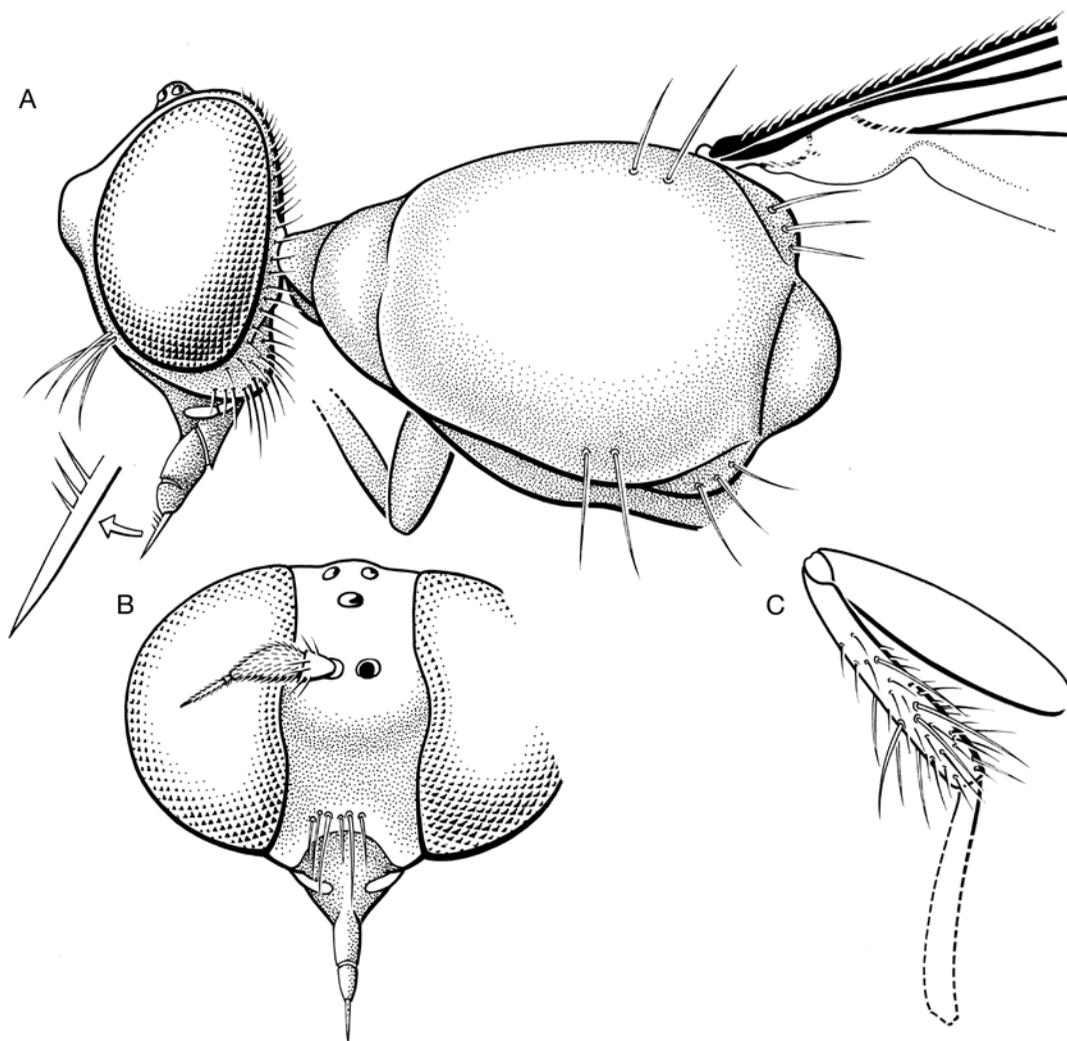


FIG. 7. †*Cretagaster raritanensis* (holotype AMNH-NJ-558). **A.** Incomplete specimen in dorsolateral view (with enlarged structure of hypopharynx). **B.** Head in anterior view. **C.** Left prothoracic leg in lateral view (reproduced from Grimaldi and Cumming, 1999).

## DISCUSSION

This review of the two Cretaceous amber fossils of robber flies provides an important contribution for future studies aiming to date the ages of divergences within Asilidae. We attempt to place both fossils phylogenetically in an apomorphy-based hierarchy, as suggested by Gandolfo et al. (2008) and Parham et al. (2012), using the morphological phylogeny of Asilidae by Dikow (2009: fig. 120).

An attempt was made to include both †*Burmapogon* and †*Cretagaster* in the phylogenetic character matrix published by Dikow (2009). Although 68% and 25% of the 220 characters in the matrix could be coded for the two Cretaceous amber fossils, respectively, the cladistic analysis



resulted in relationships not found previously and both fossil taxa were part of a large polytomy at the base of the Asilidae (results not shown). These unresolved relationships are likely caused by the limited taxon sampling employed. Even though the study by Dikow (2009) is the most comprehensive cladistic hypothesis of Asilidae relationships, only about 2% of the extant, described Asilidae species are included. It is quite likely that the increased sampling of extant taxa, as well as additional fossils currently being studied (e.g., from Baltic and Dominican amber), will enhance the resolution and that all fossil taxa be explicitly placed based in cladistic analyses.

Here we provide a detailed discussion of the possible placement based on external features observable in the Cretaceous amber fossils, although two problems were encountered that make this task challenging. On the one hand, †*Burmapogon bruckschi*, preserved well for both sexes, is unique in its morphology, with character combinations not found in extant robber flies. On the other hand, the limited data available for †*Cretagaster raritanensis* provide very limited evidence for phylogenetic placement. However, by summarizing our observations based on a selected set of characters observable in both Cretaceous fossils and extant taxa (based on the taxon sampling and character polarization employed in Dikow, 2009) we hope to provide enough background to justify our conclusions (fig. 8).

#### PLACEMENT OF †BURMAPOGON

Features that cannot be adequately studied in †*Burmapogon bruckschi*, but that might clarify its placement, are: development of the prosternum, the maxillary stipites, shape of the hypandrium, the extent of fusion of the hypandrium and gonocoxite, and the position of the gonostyli in the male terminalia.

The presence of acanthoporphorite spines in the female paratype of †*Burmapogon bruckschi* provides evidence that excludes this fossil from several subfamily taxa, which either never developed such spines or secondarily lost them (see discussion of the apomorphy/plesiomorphy polarization of this character state within Asilidae in Dikow, 2009: 120). While it is certainly possible that †*Burmapogon* belongs to a taxon that lost the acanthoporphorite spines after the divergence of †*Burmapogon* and its sister group, this hypothesis is not testable with the current morphological data. Such a hypothesis could potentially be postulated for every single apomorphic character state that is not found in extant species but that occurs in fossil species. What is needed to answer this scenario is a time-calibrated hypothesis of relationships based on morphological and molecular data and additional fossil species.

The open wing cells  $r_1$ ,  $m_3$ , and *cup* as found in †*Burmapogon*, which represent the apomorphic condition, are evidence that exclude this fossil from several subfamily taxa. Because these two character systems are easy to observe and compare, the discussion below is organized based on the presence/absence of acanthoporphorite spines and open/closed wing cell  $r_1$ .

ACANTHOPHORITE SPINES ABSENT, WING CELL  $r_1$  CLOSED: **Asilinae**, **Laphriinae**, **Ommatiinae**: †*Burmapogon bruckschi* does not represent a taxon of the stem or crown clade of the earliest divergences within Asilidae, i.e., Laphriinae and (Asilinae + Ommatiinae) (fig. 8), because wing cells  $r_1$ ,  $m_3$ , and *cup* are closed in these three subfamilies (a plesiomorphic condition), and they lack acanthoporphorite spines.

ACANTHOPHORITE SPINES ABSENT, WING CELL  $r_1$  OPEN: **Dioctriinae, Leptogastrinae, Trigonimiminae:** †*Burmapogon* shares the open wing cells  $r_1$  and  $m_3$  (but not *cup*) and the reduced alula lobe in the wing with the clade (Dioctriinae + (Leptogastrinae + Trigonimiminae)) (fig. 8). While open wing cells are a symplesiomorphy for this clade, a variably reduced alula is an apomorphy for a larger clade comprising Brachyrhopalinae, Dioctriinae, Leptogastrinae, Stichopogoninae, and Trigonimiminae (fig. 8). While no extant Dioctriinae, Leptogastrinae, and Trigonimiminae exhibit acanthophorite spines on the female ovipositor, these spines are present in Brachyrhopalinae and Stichopogoninae (see discussion below). The general morphology of the abdomen of †*Burmapogon*, with a shiny cuticle and T2 with a proximal protuberance, remind one of extant Dioctriinae. However, the development of the antennae and male terminalia in extant Dioctriinae is unique and different from that found in †*Burmapogon*.

ACANTHOPHORITE SPINES PRESENT, WING CELL  $r_1$  OPEN: **Stichopogoninae:** The diverging frons, an autapomorphy of Stichopogoninae, suggests a possible placement of †*Burmapogon bruckschi* in this taxon (fig. 3B). However, Stichopogoninae exhibit a second autapomorphy (compound eyes distinctly sinuate in ventral half), which is not found in †*Burmapogon* (see fig. 1B). Stichopogoninae share the open wing cells  $r_1$  and  $m_3$  (but not *cup*) and a slightly reduced alula with †*Burmapogon*. In †*Burmapogon*, the maxillary palpus is two-segmented and the male epandrium is comprised of two sclerites; both of these character states are found in some, but not all, extant species of Stichopogoninae.

**Willistoninae:** In contrast to Stichopogoninae, the two genera *Trichoura* and *Willistonina* (Willistoninae) possess a diverging frons and the compound eyes are sinuate in the ventral quarter only, an apomorphic feature also found in †*Burmapogon* (see fig. 1B). While wing cell  $r_1$  is open in both *Trichoura* and *Willistonina*, cells  $m_3$  and *cup* are only open in *Willistonina*. Willistoninae is a clade with interesting biogeography, as representatives occur in western North America, southern Africa, and one genus, *Sisyrynodytes*, also occurs in northern Africa and the Middle East. A unique feature of this clade is the dorsoventrally flattened setae on the legs, which are absent in †*Burmapogon*, and the absence of discal and apical scutellar setae, which are absent in the Burmese amber fossil.

**Bathypogoninae and Phellinae:** These two species-poor taxa are endemic to the Southern Hemisphere; they share an open wing cell  $r_1$  with †*Burmapogon*, but cells  $m_3$  and *cup* are closed. Bathypogoninae also shares the anteriorly arched vein  $R_{2+3}$  (fig. 4) with †*Burmapogon*. However, Bathypogoninae are larger flies with numerous macrosetae and well-developed fascial swelling and mystax not found in †*Burmapogon*. Phellinae is unique, among other characters, in the elongated female abdominal segments 7–8 that form the ovipositor, which is not found in †*Burmapogon*.

**Tillobromatinae:** All extant representatives form a species-poor clade of Southern Hemisphere endemic taxa (Argentina, Chile, and southern Africa) that have open wing cells, a two-segmented maxillary palpus, and a divided male epandrium, like †*Burmapogon*. However, extant Tillobromatinae are very stout flies with macrosetae on the thorax and legs, a well-developed facial swelling with an extensive mystax, as well as other characteristics of the antennae and male terminalia, which are not present in †*Burmapogon*.

**Stenopogoninae:** This clade, as redefined by Dikow (2009: 105), comprises stout robber flies with the facial swelling and mystax extending over at least the lower facial half, and all ommatidia are of the same size. Both of these character states are not present in †*Burmapogon* (fig. 3B).

**Dasyopogoninae:** The absence of any prothoracic tibial protuberances in †*Burmapogon* (see fig. 5C–D), which are present in Dasyopogoninae (autapomorphically), exclude †*Burmapogon* from this taxon. Although the large prothoracic tibial spine is absent in the dasyopogonine *Archilestris*, it is postulated to be a loss. †*Burmapogon* appears not to be closely related to this taxon since it does not exhibit two or more macrosetae on the median occipital sclerite on the head, which is another autapomorphy of Dasyopogoninae.

**Brachyrhopalinae:** Several clades possess one of the two types of prothoracic tibial protuberances (Australian Brachyrhopalini and Chrysopogonini and several Northern Hemisphere genera; see Dikow, 2009: 120), which are absent in †*Burmapogon* (see fig. 5C–D). The presence of acanthophorite spines is a symplesiomorphy of this clade, but these spines have been lost at least once in the Australian Chrysopogonini. Wing cells  $r_1$  and  $m_3$  are always open in Brachyrhopalinae, while cell *cup* is usually closed, in contrast to †*Burmapogon* (fig. 4). This clade, newly established as a subfamily taxon by Dikow (2009: 109), is a remnant of the Dasyopogoninae and Stenopogoninae *sensu* previous authors (Hull, 1962a; Papavero, 1973; Geller-Grimm, 2004) and is a diverse clade that is not delimited by many unique apomorphic character states. Additional phylogenetic research needs to be conducted to assign possible additional genera to this clade.

Based on the above overview and the information provided in figure 8, we propose to place †*Burmapogon* in a clade comprised of (Brachyrhopalinae + Stichopogoninae), a grouping that was originally proposed by Dikow (2009). Although Brachyrhopalinae is a diverse clade both in species numbers and in morphology, it is a clade of small to medium-sized assassin flies to which †*Burmapogon* appears to be closely related. The phylogenetic relationships within the Brachyrhopalinae are still not well resolved and additional genera will most likely be assigned to this taxon when explicit cladistic studies include better taxon sampling. Thus, at this point, a more precise placement of †*Burmapogon* is not possible.

#### MORPHOLOGICAL UNIQUENESS OF †BURMAPOGON

Features that are unique to †*Burmapogon* include the structure of the antennal postpedicel and stylus and the presence of an unusual metathoracic tibial spine. There are many robber-fly species that possess a cylindrical postpedicel. The postpedicel in †*Burmapogon* is unique in that it is parallel sided throughout and laterally compressed (figs. 1B, 3A). In addition, the one-segmented stylus is positioned at the dorsodistal end of the postpedicel (fig. 3A) and is tipped with an apical setalike sensory element. Robber flies with a cylindrical postpedicel exhibit either a two-segmented stylus or the apical setalike sensory element is positioned in a subapical cavity of the stylus (or when the stylus is further reduced in a subapical cavity of the postpedicel itself) (see diversity of antennal shapes in Hull, 1962b: figs. 1–396, and discussion in Dikow, 2009: 33, for comparison).

The unusual metathoracic tibial spine (fig. 5A–B), which is trowel shaped, partly laterally compressed and with the median surface (facing tibia and tarsus) hollow, is to our knowledge unknown in any extant Asilidae species.

#### PLACEMENT OF †CRETAGASTER

Features that cannot be studied in †*Cretagaster raritanensis*, but that would be helpful for the placement of this species, are the remainder of the wing, the female abdomen including the ovipositor, and structures of the general thorax and legs. Dikow (2009) placed †*Cretagaster* as the sister group to all remaining Leptogastrinae and this hypothesis is corroborated here. Of the apomorphic character states delimiting Leptogastrinae, as defined by Dikow (2009: 107) (including the genus *Acronyches*), the following are present in †*Cretagaster*: seta-like spicules on hypopharynx spaced far apart (fig. 7A); ocellar setae absent; and presutural dorsocentral setae absent. Additional characters supporting the placement in Leptogastrinae are the reduced alula, the few mystacal setae, the undeveloped facial swelling, and the shape of the postpedicel. An autapomorphy of the more inclusive Leptogastrini, i.e., anteriorly and medially extended postpronotal lobes that nearly touch medially, is not present in †*Cretagaster* nor in *Acronyches* (Acronychini), which instead exhibit the plesiomorphic state found in all other Asilidae (postpronotal lobes extending medially, but not anteriorly). The antennal stylus in †*Cretagaster* is two-segmented whereas it is one-segmented in both Acronychini and Leptogastrini. †*Cretagaster* possesses a parallel-sided frons (fig. 7B) as is also found in Leptogastrini and other Asilidae (plesiomorphic condition), whereas in *Acronyches* the frons is markedly approximating at its dorsal margin (apomorphic condition). These character states support the placement of †*Cretagaster* as the sister group to (Acronychini + Leptogastrini) and not the placement within one or the other taxon. The elevated antenna on the head is a feature found in the majority of extant Dioctriinae (fig. 8), which have a unique antennal morphology that is not present in †*Cretagaster*.

#### CONCLUSION

The two Burmese amber fossils described here provide a glimpse into the early morphological evolution of Asilidae. While they do not represent the oldest, definitive robber flies, their morphology does possess features shared in many extant taxa as well as a unique combination of features not found in extant species. The two Cretaceous amber fossils described here, along with the other Cretaceous taxon †*Araripogon*, will be of great importance to estimate divergence times of Asilidae in future studies. †*Araripogon* provides a minimum age of a large clade of assassin flies excluding (Laphriinae + (Asilinae + Ommatiinae)) at ~112 myo; †*Burmapogon* a minimum age for the clade (Brachyrhopalinae + Stichopogoninae) at ~100 myo; and †*Cretagaster* a minimum age of ~94–90 myo for Leptogastrinae. While a more precise placement of †*Burmapogon* is not possible at this time, future cladistic studies including more species in general and in particular the 140 genera not included by Dikow (2009), may be able to place this fossil as it is so well preserved.

Asilidae has been estimated to be 135 myo based on a chronogram of divergences by the AToL Diptera project (Wiegmann et al., 2011: fig. S3). The oldest Cretaceous assassin-fly species indicate that the morphological evolution and the main diversifications into larger clades had taken place already 40 million years later.

#### ACKNOWLEDGMENTS

We thank Dan Bickel (Australian Museum, Sydney) for making us aware of the male Burmese amber specimen, and Klaus-Peter Brucksch for making it available to our study through purchase by the AMNH. James Zigras kindly loaned the sole asilid in his extensive Burmese amber collection for study. We thank the two anonymous reviewers and the editor for their suggestions that improved the manuscript. The Burmese amber specimens were purchased by the AMNH with generous funds provided by Robert Goelet, Chairman Emeritus of the AMNH. This project is funded by a U.S. National Science Foundation REVSYS Grant (DEB 0919333; PI Torsten Dikow, Co-PI David Yeates). Any opinions, findings, and conclusions or recommendations expressed in this manuscript are those of the authors and do not necessarily reflect the views of the National Science Foundation. Partial funding is also provided by the John D. and Catherine T. MacArthur Foundation funding of the Biodiversity Synthesis Group of the Encyclopedia of Life.

#### REFERENCES

- Cumming, J.M., and D.M. Wood. 2009. Adult morphology and terminology. *In* B.V. Brown et al. (editors), *Manual of Central American Diptera*, vol. 1: 9–50. Ottawa: NRC Press.
- Dikow, T. 2009. Phylogeny of Asilidae inferred from morphological characters of imagines (Insecta: Diptera: Brachycera: Asiloidea). *Bulletin of the American Museum of Natural History* 319: 1–175.
- Gandolfo, M.A., N.C. Nixon, and W.L. Crepet. 2008. Selection of fossils for calibration of molecular dating models. *Annals of the Missouri Botanical Garden* 95 (1): 34–42.
- Geller-Grimm, F. 2004. World catalogue of the genera of the family Asilidae (Diptera). *Studia Dipterologica* 10 (2): 473–526.
- Grimaldi, D.A. 1990. Insects from the Santana Formation, lower Cretaceous, of Brazil. *Bulletin of the American Museum of Natural History* 195: 1–191.
- Grimaldi, D.A., and J.M. Cumming. 1999. Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. *Bulletin of the American Museum of Natural History* 239: 1–124.
- Grimaldi, D., C.W. Beck, and J.J. Boon. 1989. Occurrence, chemical characteristics, and paleontology of the fossil resins from New Jersey. *American Museum Novitates* 2948: 1–28.
- Grimaldi, D., A. Shedrinsky, and T.P. Wampler. 2000. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. *In* D. Grimaldi (editor), *Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey*: 1–76. Leiden: Backhuys.
- Grimaldi, D.A., M.S. Engel, and P.C. Nascimbene. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates* 3361: 1–71.

- Hull, F.M. 1962a. Robber flies of the world—the genera of the family Asilidae. *Bulletin of the United States National Museum* 224 (1): 1–430.
- Hull, F.M. 1962b. Robber flies of the world—the genera of the family Asilidae. *Bulletin of the United States National Museum* 224 (2): 431–907.
- Martill, D.M., G. Bechly, and R.F. Loveridge (editors). 2007. *The Crato fossil beds of Brazil: window into an ancient world*. Cambridge: Cambridge University Press.
- McAlpine, J.F. 1981. Morphology and terminology—adults. *In* J.F. McAlpine et al. (editors), *Manual of Nearctic Diptera*, vol. 1: 9–63. Hull: Research Branch Agriculture Canada.
- McKellar, R.C., and A.P. Wolfe. 2010. Chapter 9. Canadian amber. *In* D. Penney (editor), *Biodiversity of fossils in amber from the major world deposits*: 149–166. Manchester: Siri Scientific Press.
- Papavero, N. 1973. Studies of Asilidae (Diptera) systematics and evolution. I. A preliminary classification in subfamilies. *Arquivos de Zoologia* 23 (3): 217–274.
- Pape, T., V. Blagoderov, and M.B. Mostovski. 2011. Order Diptera Linnaeus, 1758. *Zootaxa* 3148: 222–229.
- Parham, J.E., et al. 2012. Best practices for justifying fossil calibrations. *Systematic Biology* 61 (2): 346–359.
- Penney, D. (editor). 2010. *Biodiversity of fossils in amber from the major world deposits*. Manchester: Siri Scientific Press.
- Pyle, R.L., and E. Michel. 2008. Zoobank: developing a nomenclatural tool for unifying 250 years of biological information. *Zootaxa* 1950: 39–50.
- Shi, G., et al. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37: 155–163.
- Stuckenberg, B.R. 1999. Antennal evolution in the Brachycera (Diptera), with a reassessment of terminology relating to the flagellum. *Studia Dipterologica* 6 (1): 33–48.
- Wiegmann, B.M., et al. 2011. Episodic radiations in the fly tree of life. *Proceedings of the National Academy of Sciences of the United States of America* 108 (14): 5690–5695.
- Willkommen, J., and D.A. Grimaldi. 2007. Diptera: true flies, gnats and crane flies. *In* D.M. Martill, G. Bechly, and R.F. Loveridge (editors), *The Crato fossil beds of Brazil: window into an ancient world*: 369–386. Cambridge: Cambridge University Press.

All issues of *Novitates* and *Bulletin* are available on the web (<http://digitallibrary.amnh.org/dspace>). Order printed copies on the web from:

<http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html>

or via standard mail from:

American Museum of Natural History—Scientific Publications  
Central Park West at 79th Street  
New York, NY 10024

♻️ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).