



The Cretaceous Fossil *Burmaculex antiquus* Confirmed as the Earliest Known Lineage of Mosquitoes (Diptera: Culicidae)

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Abstract

A second female of mid-Cretaceous *Burmaculex antiquus* Borkent & Grimaldi, preserved in 99 myo Burmese amber, and the oldest known member of the Culicidae, is described in detail. Although generally opaque and distorted, some character states are added or refined. The discovery of well-developed scales on the legs shows that this feature must now be considered a synapomorphy of both the fossil and all extant members of the family. Previously described synapomorphies and further interpretation here confirm the phylogenetic position of this fossil as the sister group to extant and all known fossil Culicidae. It is placed in the **new subfamily Burmaculicinae**.

Key words: amber, Burmese, stem group, aquatic, Culicomorpha

Introduction

Mosquitoes are of tremendous medical and veterinary importance to humans and there is, therefore, a highly detailed description of the extant fauna, with 3,547 species (Harbach 2015). Unfortunately, there is a rather sparse fossil record with only 23 species known (Harbach 2015), leaving unanswered many questions regarding the diversification of the group over time. Only two fossil species are known from the Cretaceous, each recorded as a single specimen. *Paleoculicis minutus* Poinar, Zavortink, Pike & Johnston is based on a single male from Canadian amber, 76.5–79.5 million years old (myo) (Poinar et al. 2000); the significantly older species *Burmaculex antiquus* Borkent & Grimaldi is known as a single female from Burmese amber (Borkent & Grimaldi 2004), deposits of which have been radiometrically dated to 99 myo (Shi et al. 2012). The latter species has been somewhat controversial. Some authors have excluded it from the family because it does not bear all the features of extant mosquitoes (Poinar 2006; Poinar & Poinar 2008; Szadziewski & Gilka 2011, 2014; Zavortink & Poinar 2008). Indeed, this was the point of the cladistic analysis by Borkent & Grimaldi (2004), who showed that the species is an extinct sister group, or stem group, of all extant and other fossil species of Culicidae. It shares with all other Culicidae the following synapomorphies: an elongate probocis (only moderately so in the fossil); a stylate labrum; a long, slender lacinia; a disproportionately elongate palpal segment 3; and a further synapomorphy that is described below. All other Culicidae (extant and known fossil species except *B. antiquus*) have the following synapomorphies: fully elongate probocis, palpus of females about as long or shorter than other mouthparts, clypeus without setae, and palpus with scales (another synapomorphy is also described below). As such, *B. antiquus* is clearly a member of the lineage if phylogenetic relationships are accepted as valid. If not, the argument against it as a culicid becomes typological. Similar narrow rationale was likewise used to argue that ants preserved in Cretaceous amber were not true Formicidae since they did not possess all of the features of modern ants (Poinar et al. 1999). Such an interpretation was critiqued on the basis that it does not recognize stem-groups and transitional forms (Grimaldi & Agosti 2000), which pervade the geological record of life: early ants had short antennal scapes, early birds had teeth, early horses had toes, early snakes had limbs, and early hominids had small brains. Stem

groups are discussed in detail elsewhere (e.g., Grimaldi & Engel, 2005). Other authors, rooted in cladistic interpretation, acknowledge *Burmaculex* as a member of the Culicidae (e.g. Briggs 2013; Harbach & Greenwalt 2012; Harbach 2007, 2015; Lukasevitch 2008).

This paper describes a newly discovered second female specimen of *B. antiquus*, providing some additional insight into its morphology and phylogenetic position.

Material and methods

The specimen was prepared according to the protocol described in Grimaldi et al. (2002). It was examined, measured and drawn using a Wild M3 dissecting microscope and a Zeiss Jenaval compound microscope. Photomicrographs were taken with a Canon Rebel T34i mounted on a Jenaval microscope (Figs. 1, 2A,C and 3) or with a Nikon Eclipse compound microscope at 200-400X using a Nikon D300 DSLR camera (Fig. 2B); images were stacked using HeliconFocus or Zerene Stacker version 1.04. Terms for structures follow those in the Manual of Nearctic Diptera (McAlpine 1981) and specialized terms for Culicidae are those in Harbach & Knight (1980). The second author has extensive experience with high-resolution CT scanning of insects in amber, and has found that specimens in Burmese amber can be imaged adequately only very rarely, given extraordinary preservation. Also, most of the details required for our study (e.g., scales, fine mouthpart structures) are beyond the resolution of most commercial CT scans.

Results

Burmaculex antiquus Borkent & Grimaldi

Burmaculex antiquus Borkent & Grimaldi, 2008: 883. Mid-Cretaceous Burmese amber. Culicidae—Grimaldi, Engel & Nascimbene 2002: 53 (description, illustrations, photo). Culicidae-Grimaldi & Engel 2005: 506 (discussion, illustrations).

Diagnosis. The only known species of Culicidae with moderately elongate mouthparts (about 0.3–0.4x length of antenna) (Figs. 1A, C, E, 4A). Also, the only known culicid lacking scales on the wing veins (scales are present only on the costa and the posterior margin of the wing) (Figs. 2A–C), and the only culicid having R_1 with an anterior bend anterior to R_{2+3} (Fig. 2A).

The following description includes only those features that differ from or are additional to those by Borkent & Grimaldi (2004).

Description (female). Body with scales on legs (Fig. 3A), anterior and posterior wing margins (Figs. 2A–C), possibly on stem and knob of halter (Fig. 1B) (no longitudinal ridges visible on scales). Antenna with flagellomeres 2–12 each with basal whorl of sensilla chaetica arising from ring of pale cuticle (Fig. 1C). Mouthparts (Figs. 1A, C–E, 4A) moderately elongate (length of labium / length of flagellum = 0.30–0.38). Labrum slender, elongate, curved in cross-section, abruptly tapered apically. Mandible not visible. Laciniae with transverse ridges along length. Labella well-developed, divided medially, details uncertain, ligula with 7 rounded, short apical projections. Wing as in Fig. 2A–C, length = 1.6–1.9 mm, R_1 with anterior bend anterior to R_{2+3} , anal vein apex proximal to level of mcu-CuA fork, with slender setae on all veins (but not crossveins), remigium with four elongate setae, scales restricted to anterior (costa), posterior margin of wing, alula, slender microtrichia on membrane. Foreleg with femur, tibia, tarsomeres 1–4 thickly clothed with scales (Fig. 3A), Ta_1 length 0.96 X Ta_{2-5} length (Fig. 1A); mid-, hind legs with numerous setae, scales; foreleg, hind leg claws without basal tooth (Figs. 3B, 4B–C). Fore-, hind legs each with spiculate empodium (Figs. 3B, 4B–C). Abdomen with well-developed sternite 8 overlapping base of moderately elongate cerci (Fig. 3C).

Taxonomic discussion. This second specimen of *B. antiquus* is in fairly poor condition (Fig. 1A). Unlike the mostly deteriorated and partially cleared first specimen, the fossil at hand is largely opaque, collapsed and distorted. Nearly all of the body is present but there are only three attached legs, the left mid- (missing at least tarsomeres 3-5) and hind legs (one of these missing some terminal tarsomeres), and the right hind leg. A foreleg is near but detached from the body (identified as such by presence of tibial spur).

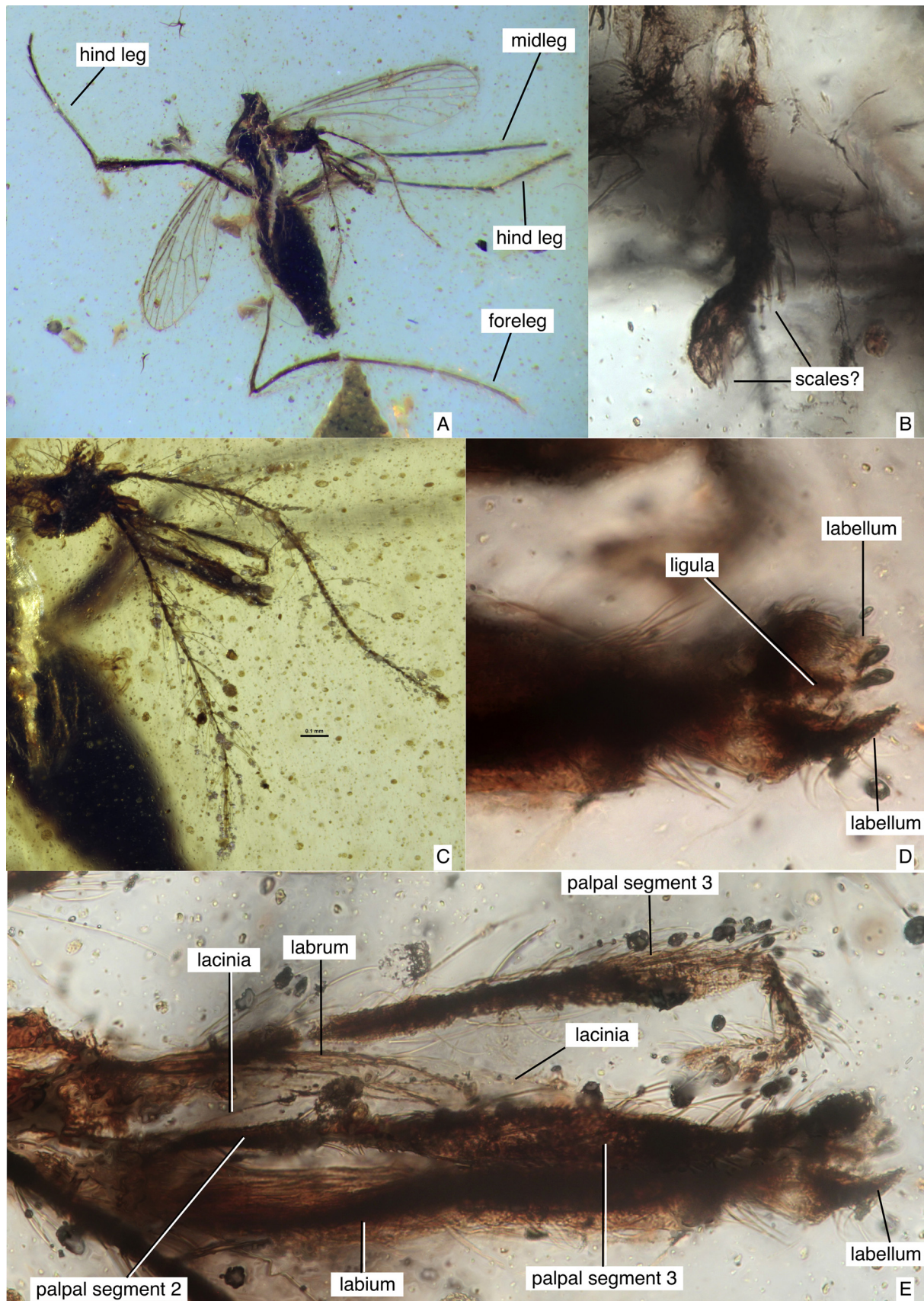


FIGURE 1. Structures of *Burmaculex antiquus*. A. Habitus, mostly in ventral view but with head bent forward, presenting oblique anterior view. B. Right halter, dorsal view. C. Head, oblique anterior view. D. Labium apex, oblique anterior view. E. Mouthparts, oblique anterior view.

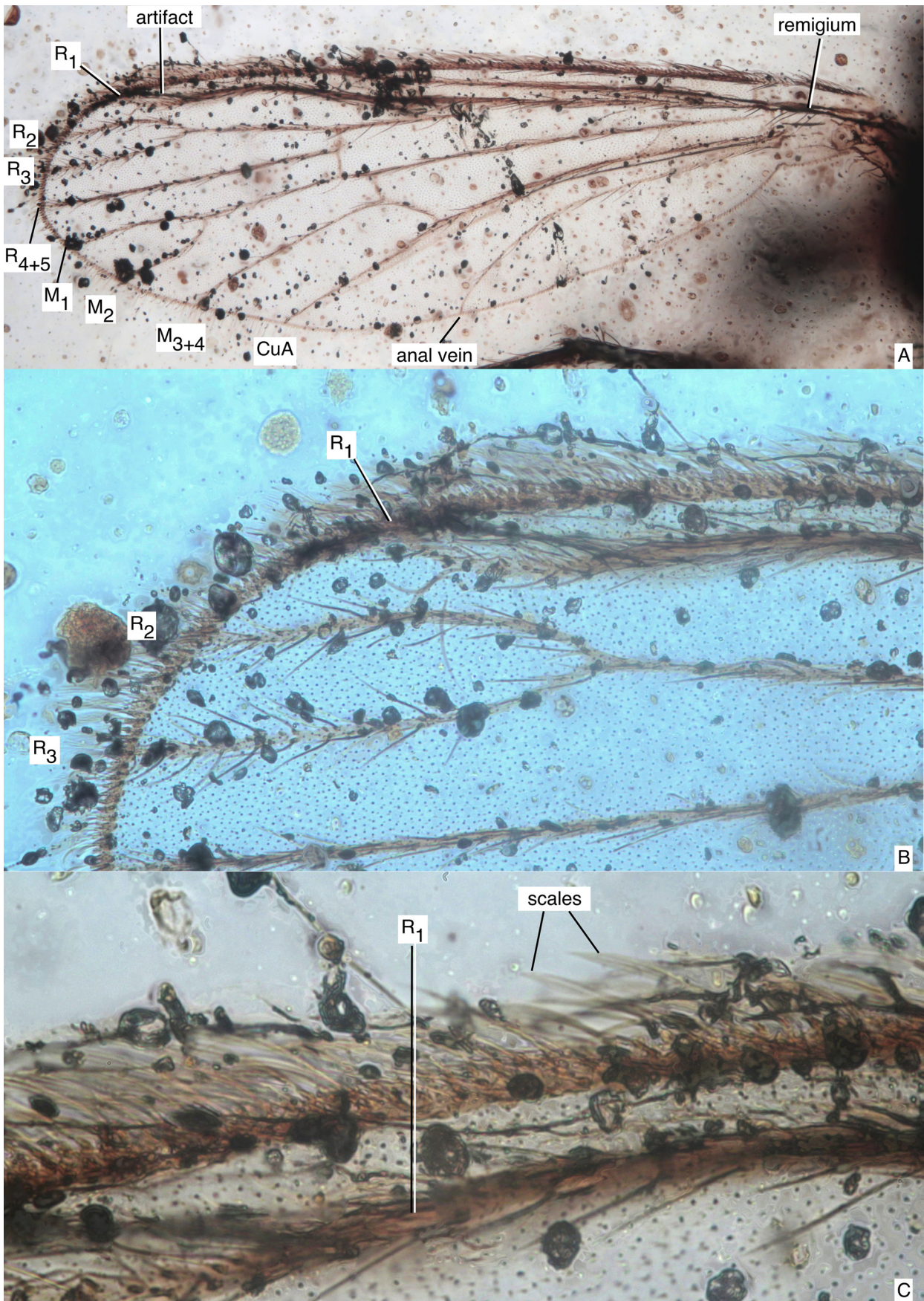


FIGURE 2. Structures of *Burmaculex antiquus*. A. Left wing, dorsal view. B. Anterodistal portion of left wing, dorsal view. C. Portion of anterior of left wing with, in part, anterior bulge of R₁, dorsal view.

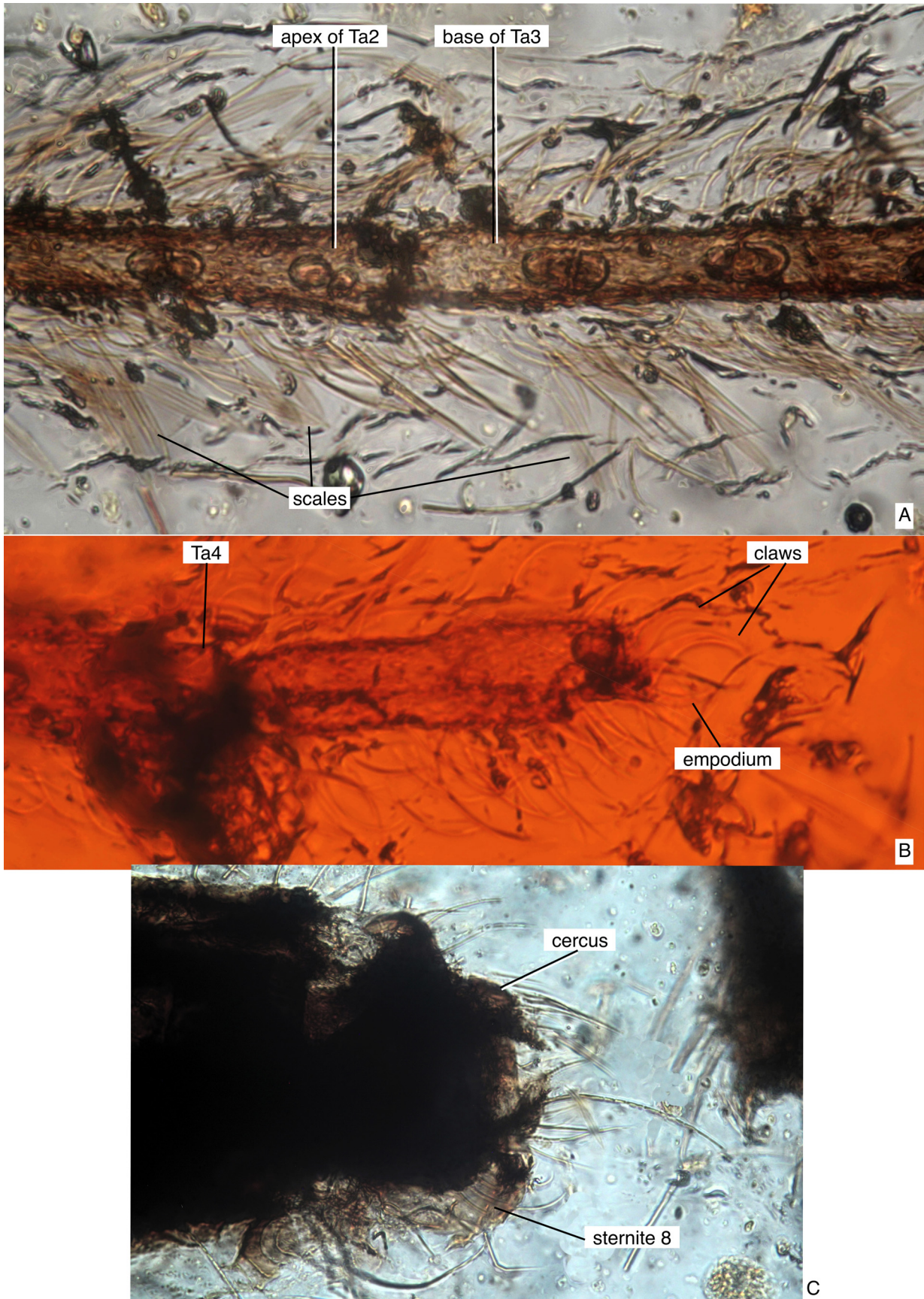


FIGURE 3. Structures of *Burmaculex antiquus*. A. Fore leg apex of tarsomere 2, base of tarsomere 3, lateral view. B. Foreleg tarsomere 4–5, lateral view. C. Apex of abdomen, dorsal view.

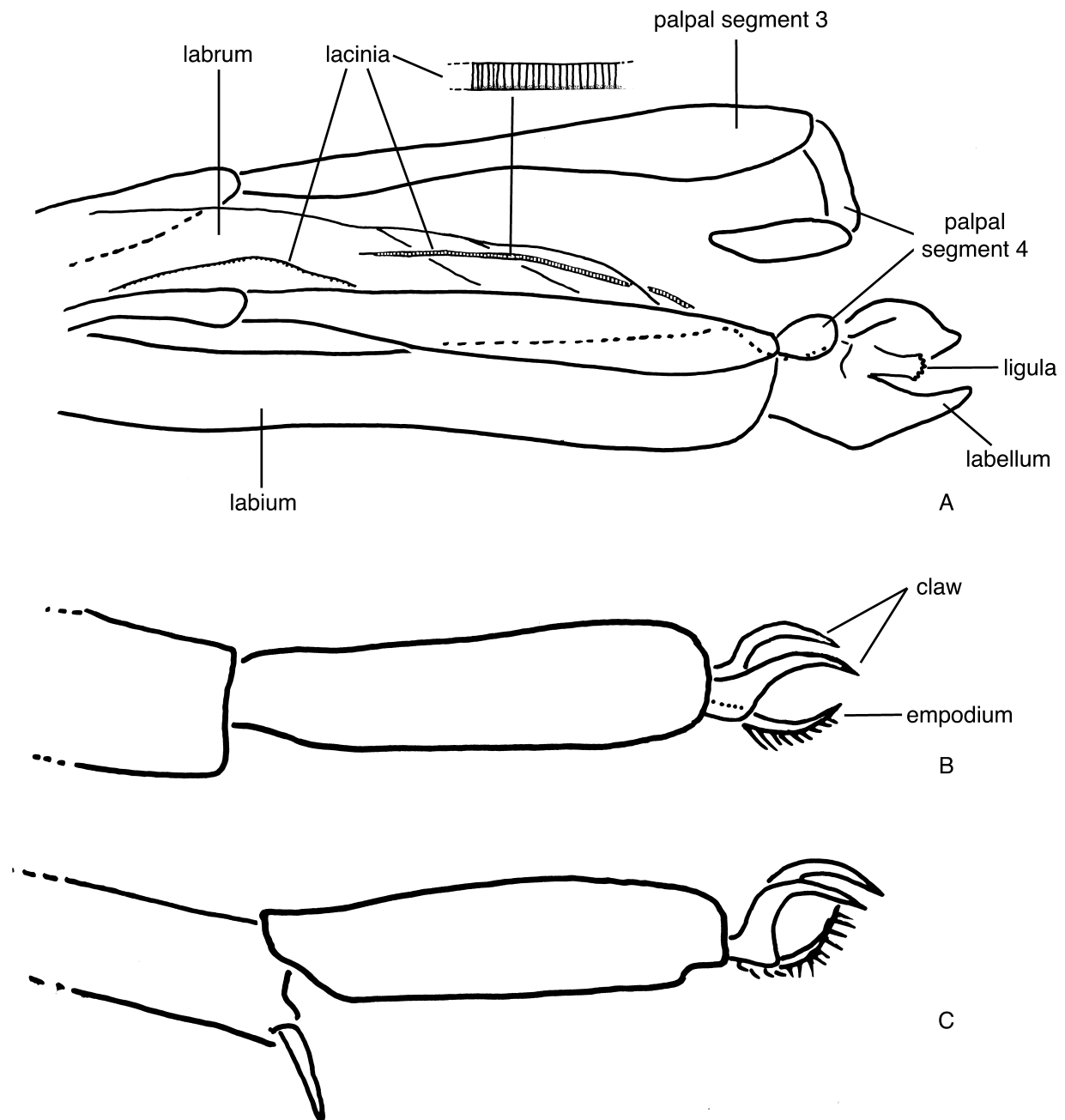


FIGURE 4. Structures of *Burmaculex antiquus*. A. Mouthparts, in oblique anterior view. B. Foreleg tarsomere 5, lateral view. C. Hind leg tarsomere 5, lateral view.

Some of the mouthparts were visible in the fossil, confirming that the laciniae (both visible) have transverse ridges (Fig. 4A) and are slightly thickened mesially, features which are unique among the stylets of extant Culicidae (mandibles lack these features) (Lee & Craig 1983). The apices of the laciniae and labrum are obscured by the palpi and perhaps are within the apex of the labium. The mandibles are not visible (probably because they are either too close to the laciniae or are yet enclosed by the labium; in extant species they are extremely slender, with apical teeth at most, and are often difficult to locate in slide-mounted specimens).

Borkent & Grimaldi (2004) reported the possibility of a gap between palpal segments 2 and 3 but this is not present in this second specimen, indicating that this is likely an artifact of preservation in the holotype. There is, however, a lightening of the cuticle between segments 2 and 3 of at least the left palpus in this second specimen (Fig. 1E). Similarly, a possible gap at the very base of R_{4+5} in the holotype, but not in this second specimen, is also likely an artifact.

The amber piece holding the fossil has been cut into four pieces, with a small flat slab now bearing the specimen. The slab bearing the fossil also includes a trichome and a very small poorly preserved arthropod. The three separated pieces of amber cut away from the fossil include the anterior portion of a myriapod, several trichomes, various distorted parts of arthropods, as well as debris.

The fossil was collected from the same locality as the first *B. antiquus*, is housed in a small plastic box at the American Museum of Natural History, and is labeled with "BURMESE AMBER (Cretaceous E. Cenomanian), Myanmar: Kachin, James Zigras Collection, JZC-Bu213, PIP: ♀, Culicidae Burmaculex", "Kachin: Tanai Village (on Ledo Rd.), 105 km NW Myitkyna, Burma" and "*Burmaculex antiquus*, female, det. Borkent and Grimaldi".

Phylogenetic position of *Burmaculex antiquus*. Borkent & Grimaldi (2004) provided a phylogenetic analysis of the features of *B. antiquus* and other Culicidae, with four synapomorphies defining the monophyly of the family including *B. antiquus* and four synapomorphies defining Culicidae exclusive of *B. antiquus*. Here we report additional synapomorphies and an autapomorphy of *B. antiquus*.

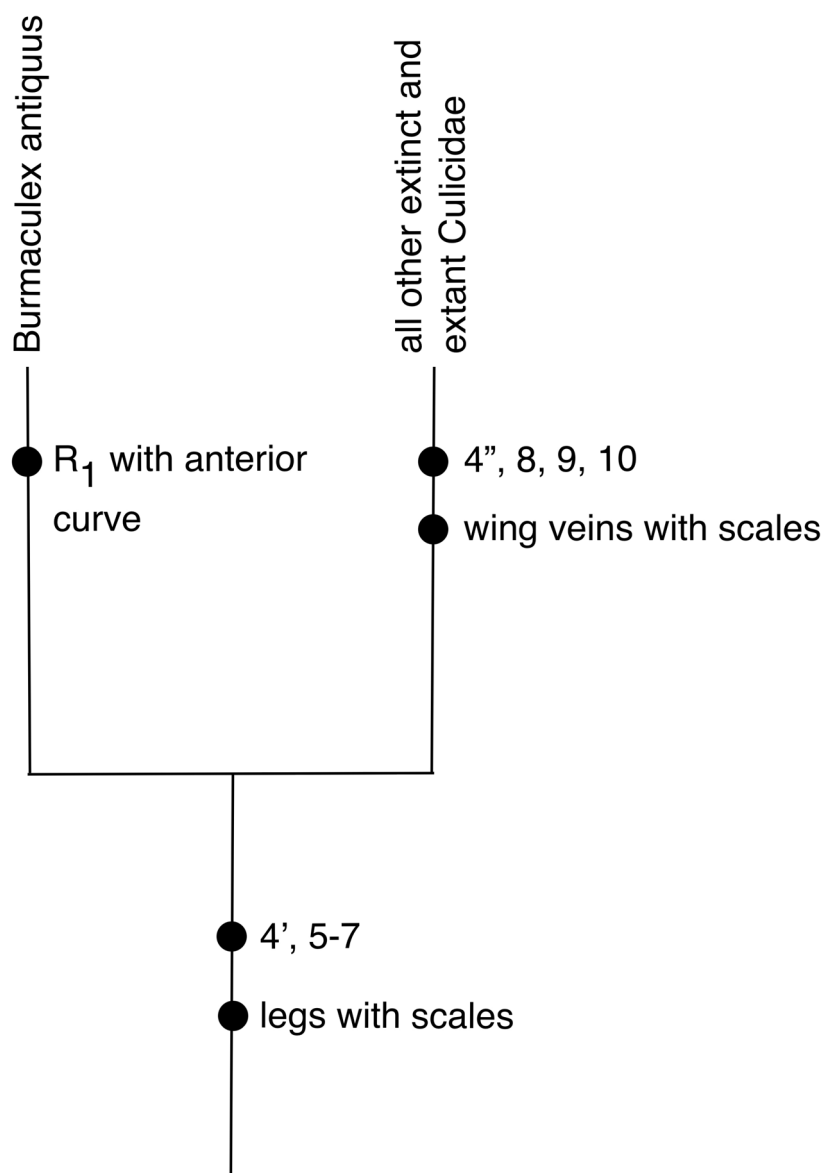


FIGURE 5. Cladogram indicating the relationship of *Burmaculex antiquus* to other Culicidae. Circles refer to synapomorphies discussed in the text and numbered states are those discussed more fully by Borkent & Grimaldi (2004).

The new *Burmaculex* fossil has abundant scales on the legs, from the base of the femur to at least tarsomere 4 of each leg, and these were particularly evident on the well-preserved foreleg (Fig. 3A). This apomorphic state is shared with all other extant and fossil Culicidae (Fig. 5) and is unique within at least the Culicomorpha. Among

other nematoceros Diptera, leg scales are also present in some Cecidomyiidae and Psychodidae where they are clearly independently derived.

The presence of scales on the palpus of all Culicidae other than *B. antiquus* remains a valid synapomorphy (synapomorphy 10 of Borkent & Grimaldi 2004) (Fig. 5). *Burmaculex antiquus* also lacks scales on the head capsule, thorax and abdomen. Although the latter may be through loss by rubbing and from flowing resin, we consider this unlikely since these surfaces on the insect show no traces of scales while they are abundantly present on the legs. Scales appear to be present on the head capsule and thorax of at least all extant Culicidae (their presence or absence uncertain in some fossils). Most species of Anophelinae lack scales on the abdomen (tergites and sternites usually without scales, sternites always largely devoid of scales) and may have only narrow thoracic scales restricted to the scutellum of the thorax. As such, scales on the head capsule and at least the scutellum may be another synapomorphy of Culicidae other than *B. antiquus*, but perhaps directly related to the presence of scales on the palpus and wing veins (i.e. they may all be one character—"more broadly distributed scales"). The halter may have scales (Fig. 1B) but visibility was limited and this is uncertain. There is likely more phylogenetic information in the specific distribution of body scales in Culicidae but that is beyond the scope of the present paper.

Borkent & Grimaldi (2004) pointed out that the presence or absence of wing vein scales (other than on the wing margin) was difficult to interpret cladistically because scales are present on the wing veins of Chaoboridae and Corethrellidae (Chaoboridae is the sister group of Culicidae and Corethrellidae of Chaoboridae + Culicidae (Borkent 2012)). Dixidae lack wing scales. Further information is now available regarding this character. The worldwide revision of Corethrellidae by Borkent (2008) showed that all the early lineages of Corethrellidae have only quite slender scales on their wing veins. Unfortunately, the single specimen of the oldest fossil, from Lebanese amber, *Corethrella cretacea* Szadziewski, is missing its wings. The earliest extant lineage of Chaoboridae, *Eucorethra underwoodi* Underwood, has only slender scales on its wing veins. Species of *Mochlonyx* Loew and *Chaoborus* Lichtenstein have very narrow scales that could also be called somewhat widened setae. As such, the broad wing scales of all extant and fossil Culicidae other than *B. antiquus*, is unique and therefore considered a synapomorphy of that lineage. The simple setae on the wing veins of *B. antiquus* might be considered derived but the simple setae of Dixidae and the rather small difference between the condition in *B. antiquus*, *Mochlonyx*, *Chaoborus*, and early lineages of Corethrellidae suggest this is at best a weak indicator of relationship.

The anterior curve of R_1 in the portion anterior to R_{2+3} of the wing of *B. antiquus* (Fig. 2A) is unique within Culicomorpha (including all fossils) and is therefore considered an autapomorphy of the species. One of the two wings of the Middle to Late Jurassic Chaoboridae fossil *Hypsocorethra toficolae* Kalugina illustrated by Kalugina & Kovalev (1985: fig. 34b) shows an anteriorly curved R_1 , but the other wing (their fig. 34a) is shown with this vein straight. The adult mouthparts of this species are relatively short and if the immatures are correctly associated, *H. toficolae* is clearly a member of the Chaoboridae (having larval synapomorphies with other members of the family). As such we consider any potential similarity between the R_1 of *H. toficolae* and *B. antiquus* to be, at best, due to homoplasy.

These hypotheses of character polarity are summarized in figure 5, with character states 4–10 referring to those discussed by Borkent & Grimaldi (2004) and listed as follows:

4. Short proboscis (plesiomorphic); moderately long proboscis (Figs. 1A, C, E, 4A) (apomorphic'); very elongate proboscis (apomorphic"). 5. Female labrum relatively short, broad, and dorsal to remaining mouthparts (plesiomorphic); labrum stylate, partially enclosed by the labium (Figs. 1E, 4A) (apomorphic). 6. Female lacinia either reduced or as a flattened blade with retrorse hooks (plesiomorphic); lacinia a long, slender stylet bearing fine, flattened, transverse ridges (Fig. 4A) (apomorphic). 7. Palpal segment 3 short or of moderate length (plesiomorphic); palpal segment 3 disproportionately elongate (Figs. 1C, E, 4A) (apomorphic). 8. Female palpus longer than other mouthpart elements (Figs. 1C, E, 4A) (plesiomorphic); palpus equal in length or shorter than other mouthpart elements (apomorphic). 9. Clypeus with setae (plesiomorphic); clypeus without setae (apomorphic). 10. Palpus without scales (plesiomorphic); with scales (apomorphic).

Discussion

Chaoboridae are the sister group of the Culicidae and have a fossil record going back into the Jurassic. Borkent & Grimaldi (2004) discussed the problematic lack of adult synapomorphies for the Chaoboridae, making it impossible to distinguish some fossil Chaoboridae from early lineages of Culicidae. There are larval

synapomorphies grouping all Chaoboridae, but there are no Mesozoic larval Culicidae. This indicates the need to search for possible adult synapomorphies of extant Chaoboridae, which might help clarify the position of abundant adult Cretaceous fossils presently placed in the Chaoboridae.

Burmaculex antiquus is clearly the sister group to all remaining extant and fossil Culicidae. All evidence indicates that its phylogenetic position is secure, and therefore we propose the **new subfamily Burmaculicinae** to reflect this, with its diagnosis being that of its only included species, *Burmaculex antiquus*. The presence of an autapomorphic character state for the species (and therefore of the subfamily) indicates that this species does indeed represent a sister group to other Culicidae, rather than the possibility of representing an ancestral lineage.

Here we have considered this second fossil as conspecific with the holotype of *B. antiquus*. However, there is a possibility that the differences in the presence or absence of leg scales in the two fossils are not due to preservation but are authentic. We consider this highly unlikely, considering that scales are so easily rubbed from extant specimens and that the holotype of *B. antiquus* was quite deteriorated and almost certainly had lost its leg scales (as well as many setae). If the holotype of *B. antiquus* really had no scales, this would be evidence that the second specimen described here represents a closer lineage to other Culicidae than the first (i.e. *Burmaculex* would therefore be paraphyletic). This is contradicted by the uniquely derived anteriorly curved R_1 shared by both specimens, indicating their monophyly and supporting their conspecificity.

Hartkopf-Fröder et al. (2011) reported loose scales on mid-Cretaceous (Late Albian–Early Cenomanian) charred fossil flowers of Chloranthaceae that they attributed to a species of Culicidae through comparisons to extant taxa bearing scales. At the time, *B. antiquus* was thought to be without scales but this second fossil has abundant scales on at least the legs and therefore might be a candidate as the source of the scales. However, we were unable to see with compound microscopy the thin cross-ribs lying between the longitudinal ridges of individual scales, indicated by Hartkopf-Fröder et al. (2011) to be restricted to the Culicidae. Identification of the isolated fossil scales as those of Culicidae, however, is uncertain. SEM examination of the scales along the posterior margins of the wings of Chaoboridae and Corethrellidae may indicate these as candidates (it is unknown whether they have thin cross-ribs or not, although they are not apparent in the SEM photo of *Mochlonyx cinctipes* (Coquillett) by Ogawa (2007: fig. 2.43B). In addition, Hartkopf-Fröder et al. (2011) suggested that the purported culicid came to the fossil flowers to feed on pollen. However, considering that members of the Chloranthaceae do not have nectaries, this seems unlikely. No extant Culicidae feed (or appear capable of feeding) on pollen.

The fossil at hand provides a good lateral view of the ventral surface of the third palpal segment, which has numerous fine spicules (Fig. 1E). In other Culicidae this area bears thin-walled pegs to more elongate, often capitate sensilla which are known to be CO₂ receptors (McIver 1970; McIver & Charlton 1970; McIver & Hudson 1972). We could not detect any such sensilla on the fossil. Borkent & Grimaldi (2004) noted the presence of numerous pegs on the third palpal segment of the holotype but it was uncertain whether these were thin-walled or not.

A second specimen of *B. antiquus*, found just 11 years after the first report, certainly suggests that further material will become available in the future (if not already present in collections), including hopefully a male and specimens in superior condition. We are confident that future specimens will corroborate the relationships of *Burmaculex* and provide further insights into the diversification of this interesting lineage of blood-feeding flies.

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