



## *Libanoculex intermedius* is not a mosquito (Diptera: Culicidae): It is a chaoborid (Chaoboridae)

RALPH E. HARBACH

Department of Science, Natural History Museum, Cromwell Road, London SW7 5BD, UK.

[✉ r.harbach@nhm.ac.uk](mailto:r.harbach@nhm.ac.uk); [ORCID: https://orcid.org/0000-0003-1384-6972](https://orcid.org/0000-0003-1384-6972)

Mosquitoes comprise a large and abundant group of extant species, the Culicidae, which occur throughout the world except in the Polar Regions, high mountains and isolated islands. All males and the females of many species feed exclusively on plant liquids. However, the females of most species feed on the blood of living animals, and many of those are the vectors of pathogens that cause various diseases in humans. Adult mosquitoes are slender, long-legged flies that are easily recognized by their long proboscis and the presence of scales on most parts of the body.

Fossil mosquitoes are uncommon. Some are known from compression fossils and some are known from amber inclusions. Twenty-eight indisputable fossil mosquitoes have been formally described and named: Gilka *et al.* (2021) described the twenty-eighth species and provided an informative tabulation of the 27 previously known fossil species. Three of those species are representatives of three extinct genera that existed in the Upper Cretaceous Epoch of the Mesozoic Era. Twenty species of the extant genera *Anopheles* Meigen, 1818, *Culex* Linnaeus, 1758, *Culiseta* Felt, 1904, *Coquillettidia* Dyar, 1905 and *Toxorhynchites* Theobald, 1901a, and five species from three extinct genera, are known from the more recent Cenozoic Era.

The discovery of the three Cretaceous species confirms the view of Edwards (1923) that the Culicidae probably evolved in the Mesozoic. The oldest fossil mosquitoes, *Burmaculex antiquus* Borkent & Grimaldi, 2016 (Burmaculicinae) and *Priscoculex burmanicus* Poinar, Zavortink & Brown, 2019 (Anophelinae) are embedded in Myanmar (Burmese) amber from the mid-Cretaceous (89.3–99.6 Mya)<sup>1</sup> and *Paleoculicis minutus* Poinar, Zavortink, Pike & Johnston, 2000 is embedded in Canadian amber from the Upper Cretaceous, Campanian Age (72.1–83.6 Mya). *Burmaculex antiquus* has the general appearance and body structure of extant mosquito species (and so do the other two oldest fossil species), which includes an elongated labium with enclosed stylet-like mouthparts. The legs of *Burmaculex antiquus* are covered with scales, but other areas, except for the costa and posterior margin of the wing, apparently lack scales. *Priscoculex burmanicus*, in addition to bearing a predominance of anopheline characters, e.g. the abdomen without scales, bears some unique features, including antennal flagellomeres with scales and wing veins with both slender scales and setae. *Paleoculicis minutus* is the next oldest fossil mosquito. Morphological features indicate that *Paleoculicis minutus* shares a closer affinity with culicine mosquitoes than it does with anopheline mosquitoes, which suggests that this ancestral lineage is younger than the lineage that gave rise to the subfamily Anophelinae. That aside, *Priscoculex burmanicus*, *Anopheles dominicanus* Zavortink & Poinar, 2000 and *Anopheles? rottensis* Statz, 1944 are the only other fossil anopheline mosquitoes. The age of *Priscoculex burmanicus* is noted above, *Anopheles dominicanus* is contained in Dominican amber from the Miocene (5.33–23.03 Mya) and *Anopheles? rottensis* is from the Oligocene of Germany (23.03–33.9 Mya). From the available fossil evidence, it appears that extant groups of the Culicidae evolved in the Cenozoic.

Recently, a new distinctive fossil fly, *Libanoculex intermedius* Azar, Nel, Huang & Engel, 2023, was described as “the earliest known fossil mosquito” from two adult males embedded in Lebanese amber dated to the Barremian Age (125.0–129.4 Mya) of the Lower Cretaceous. At a glance, the fly does not have the general appearance of a mosquito, with striking differences not in agreement with the current diagnosis of the Culicidae. Most notably, the overall construction of the mouthparts is unlike that of all “true” fossil and extant mosquito species.

As taxonomists normally do when presented with an unknown organism, I ran *Libanoculex intermedius* through several identification keys. First, using the key of Carpenter & LaCasse (1955), which includes dixid and chaoborid

<sup>1</sup> The ages provided for fossil taxa follow the geological timescale determined by the International Commission on Stratigraphy (ICS). These ages generally differ slightly from those provided with the published descriptions of fossil mosquitoes.

midges as subfamilies of the Culicidae, the fossil fly, based on having “Mouth parts short; wings with veins clothed for the most part with long hairs, scales almost confined to the fringe”, keys to the subfamily Chaoborinae. The alternative, “Mouthparts prolonged into the form of a proboscis; wings with scales on veins”, would, but does not, lead the fossil fly to the subfamily Culicinae. Second, using the key to the families of the North American Diptera (McAlpine 1981), the fly keys to couplet 15, which distinguishes the Culicidae (flies with scales present on wing veins, head, and legs and usually on other parts of body; proboscis long, extending far beyond clypeus) from the Chaoboridae and Dixidae (flies with scales absent from wing veins and other parts of body, though conspicuous hairs frequently present; proboscis short, barely extending beyond clypeus). *Libanoculex intermedius* does not exhibit the diagnostic characters of the Culicidae and is distinguished from dixid midges and is identifiable as a chaoborid in the next couplet (16) of the key. Finally, using the key for the identification of the subfamilies and genera of North American chaoborids (Cook 1981), *Libanoculex intermedius* keys out in the first couplet: Clypeus long, nearly as long as height of rest of head capsule... subfamily Eucorethrinae, which only includes the extant *Eucorethra underwoodi* Underwood, 1903. The couplet includes three other characters – halter with numerous setae on stem and knob; postpronotum undivided medially; tergite 9 [tergum IX] of male produced in two posteriorly directed spine-like processes. Those characters do not appear to be features of the fossil fly described by Azar *et al.* (2023). However, whereas the first two characters are uncertain, tergum IX is unmistakably a short bi-lobed sclerite (see Azar *et al.* fig. 1K) as in most extant male mosquitoes.

The clypeus of mosquitoes is a rounded snout-like projection that forms the frontal part of the head from which the mouthparts project. In contrast, the clypeus of *Libanoculex intermedius* is much longer. The labium (prementum) of mosquitoes is developed into a long porrect or downwardly curved proboscis that extends well beyond the clypeus, and the maxillary palpi project anteriorly (forward) from the base of the clypeus alongside the proboscis. *Libanoculex intermedius* does not have a “true” proboscis – the labium is extremely short, barely extending beyond the clypeus. Furthermore, the maxillary palpi are elbow-shaped appendages that project laterally (outward) from near the distal end of the clypeus. Azar *et al.* stated that the clypeus is bare in mosquitoes. Not true. Clypeal setae are present in *Burmaculex antiquus* and some extant species (e.g. species of *Trichoprosopon* Theobald, 1901b), and clypeal scales are present in many other species. Indeed, the mouthparts of the fossil fly bear a remarkable structural resemblance to the mouthparts of the extant *Eucorethra underwoodi*.

All adult mosquitoes feed exclusively on fluids, by means of suction, because the food canal in both sexes is a very fine capillary tube with an internal diameter that only allows the passage of liquids. I agree with Azar *et al.* that *Libanoculex intermedius* seems to have been capable of feeding on liquids, including blood, but its mouthparts are not developed for piercing and sucking as they are in mosquitoes. Surely the triangular, denticulate mandibles and apically toothed laciniae of *Libanoculex intermedius* are constructed for abrading and lacerating, not piercing and suction.

The labrum and labium of male mosquitoes are developed as well as they are in females, but the other mouthparts are less developed. The hypopharynx is fused with the inner wall of the labium. Maxillae are present in all extant males, but they are devoid of teeth and are more weakly developed than in females. Mandibles are present in some males of some groups and absent in others; when present, they are much shorter than the labium and vary greatly in length in species of different genera and subgenera (Marshall & Staley 1935; Marshall 1938; Snodgrass 1959; Wahid *et al.* 2007). It appears that atrophy of the maxillae, and in particular the mandibles, has progressed with the evolution of the early ancestors of the extant taxa. It is not too difficult to imagine that ancestral males of the Culicidae once had maxillae and mandibles like the females that gradually became less developed with a switch from blood feeding to feeding exclusively on plant juices. However, whether or not ancestral male mosquitoes were blood feeders has no practical relevance to the taxonomic classification of *Libanoculex intermedius*.

Except for the margins of the wing, *Libanoculex intermedius* is completely devoid of scales (there is no evidence of dislodged scales in the surrounding resin). Scales are absent from the abdomen of *Burmaculex antiquus*, as well as *Priscoculex burmanicus* and most extant anophelines, but they otherwise, like all other mosquitoes, have scales on various other areas of the body, at least on the legs (McAlpine 1981) as in *Burmaculex antiquus*. Legs with scales is a synapomorphy for the Culicidae.

Azar *et al.* (2023) provided two photographic images of the habitus of the holotype of *Libanoculex intermedius*, a principally ventral view (fig. 1A) and a principally dorsal view (fig. 1B). They also provided a photographic image and a line drawing of the genitalia (figs 1K and 2E, respectively). There is something amiss about the different aspects of the genitalia, but first it should be noted that they are quite simple compared to culicids and outwardly resemble the genitalia of extant Chaoboridae. That aside, the image shown in figure 1K, labelled as a ventral view, differs from the ventral view shown in figure 1A. Whereas terga VIII and IX (the latter, as indicated above, is distinctly bi-lobed and

bears numerous spine-like setae) are visible in figure 1K, only a single sclerite, undoubtedly sternum VIII, is visible in figure 1A. Because terga VIII and IX are visible in the dorsal view shown in figure 1B, it seems that the image in figure 1K was obtained by focusing through the ventral side of the genitalia shown in figure 1A to image the opposite (dorsal) side, which corresponds with the dorsal aspect of the genitalia shown in figure 1B. If this is correct, then the fly was either trapped in resin before any genital rotation or the genitalia do not rotate. It is important to note that the abdominal structures caudad of segment VII undergo a 180° rotation in all male culicids and chaoborids except *Eucorethra*, in which the genitalia apparently remain in a non-rotated position (Cook 1956; Belkin 1962). If this is correct, would the lack of rotation in *Eucorethra* be considered a plesiomorphy or a reversal? If the former, then *Eucorethra* would surely be the sister of Chaoboridae + Culicidae, which share the synapomorphy of rotation. Finally, the illustration shown in figure 2E appears to be a combination of dorsal and ventral structures.

The data matrix which Azar *et al.* (2023) used to elucidate relationships includes 15 morphological characters coded for six taxa: Dixidae, Corethrellidae, Chaoboridae, *Libanoculex intermedius*, *Burmaculex antiquus* and “crown-Culicidae” (= all extinct and extant mosquitoes except *Burmaculex antiquus*). The cladogram generated by the phylogenetic analysis is expressed parenthetically as Dixidae + (Corethrellidae + Chaoboridae + (*Libanoculex intermedius* + (*Burmaculex antiquus* + crown-Culicidae))), from which the authors concluded that *Libanoculex intermedius* is an extinct member of the Culicidae (it could equally be interpreted as a separate family that is sister to Culicidae). Regrettably, the characters used for the cladistic analysis are fraught with problems (see below). Firstly, only two of the 15 characters are exclusively for males, three are exclusively for females and the others are presumably for both sexes. Because the authors only included the segmentation of the maxillary palpus of females in their data set, a note is needed here about the maxillary palpi of culicid males. Only 11 male fossil mosquitoes are known. Eight are from the Eocene (33.9–56.0 Mya) and two from the Oligocene (23.0–33.9 Mya) of the Cenozoic; only one is older – *Paleoculicis minutus* (72.1–83.6 Mya, Campanian, Upper Cretaceous, Mesozoic). The maxillary palpus of all of these males, and the female of *Burmaculex antiquus*, consists of five palpomeres that extend forward along the sides of the proboscis (it is reasonable to assume that the maxillary palpus is similarly developed in the unknown male of *Burmaculex antiquus*). Furthermore, unlike the male of *Libanoculex intermedius*, palpomeres 2 and 3 are ankylosed in the 11 fossil males and form the longest part of the palpus. Specific problems with the 15 characters used in the phylogenetic analysis are propounded in the following list (numbers are the character numbers of the authors).

1. Scales on the posterior margin of the wing: These scales are absent only in Dixidae. Their presence in the other taxa is uninformative (irrelevant) for establishing a specific relationship of *Libanoculex intermedius* with one or other of those taxa.

2. Wing vein R<sub>2+3</sub>: This vein is “strongly arched” only in Dixidae; therefore, like character 1, the condition of being “straight or slightly curved” in the other taxa is uninformative (irrelevant) for resolving a definite relationship with one or other of those taxa.

3. Wing vein R<sub>1</sub> termination: This vein terminates beyond the level of the splitting of vein R<sub>2+3</sub> in all of the groups except Corethrellidae; therefore, it is uninformative (irrelevant) with regard to Chaoboridae, *Libanoculex intermedius*, *Burmaculex antiquus* and “crown-Culicidae”.

4. Proboscis, length: The coding of this character is subjective. It is not based on quantitative data. Despite that, the development of the mouthparts of *Libanoculex intermedius*, especially the formation of the prementum and clypeus, are not comparable with those of *Burmaculex antiquus* and the “crown-Culicidae”. The subjective coding of length disregards the anatomical characteristics of form, arrangement and relationships of the components of the mouthparts.

5. Labrum (females): This character could not be scored for *Libanoculex intermedius*. In a data set with so few coded characters, it is unlikely that this character contributed to the results.

6. Laciniae: The coding applied to this character is problematic. The two character states are overly simplified and ambiguous. The form (characteristics) of the laciniae should have been explicitly coded with multiple states to eliminate the ambiguity. For example, state 0 is actually two states, “reduced” and “flattened blade”. How are these two conditions comparable, and what is the meaning of “reduced”? State 1 is even more problematic. For example, the pectinate (comb-like) apex of the lacinia of *Libanoculex intermedius* is not a feature of Culicidae, in which the apex of the lacinia bears fine striations, which are absent in some taxa.

7. Maxillary palpus, palpomere 3, length (males): This palpomere is correctly coded in-so-far as it is likely to be as long in the unknown male of *Burmaculex antiquus* as in males of the “crown-Culicidae”. However, the length of the palpomere should have been coded more precisely with regard to its structural association with palpomere 2 (as noted above).

8. Maxillary palpus, length (females): This character also could not be scored for *Libanoculex intermedius*, and may have had no effect on the results of the analysis, depending on how the questionable coding was optimized.

9. Clypeus (setae): Setae are coded as absent in Culicidae and present in the other five taxa. As noted above, setae are present in *Burmaculex antiquus* and some extant mosquitoes, indicating that they were probably present in other extinct species. This character should have been coded as a polymorphism for the “crown-Culicidae”, which would have eliminated the character as an autapomorphy for the group.

10. Maxillary palpus, scales (males): Only the “crown-Culicidae” are coded for the presence of scales on the maxillary palpi. Since the five-segmented palpus of the female of *Priscoculex burmanicus* is without scales, it would seem likely that the palpus of the male would also lack scales, which brings the suitability of this character into question. In comparison, all known “true” fossil and extant mosquito species have scales on their legs (see character 12).

11. Maxillary palpus, segmentation (females): Like characters 5 and 8, this character could not be scored for *Libanoculex intermedius*. Disregarding that, the character is incorrectly scored for the “crown-Culicidae”. The maxillary palpi of female mosquitoes have five or fewer palpomeres, not four with a vestigial fifth palpomere as coded by Azar *et al.* As decisively shown by Harbach & Kitching (1998), “five palpomeres is the maximum number present in both females and males (the standard number in Nematocera), and shorter palpi have evolved through the reduction or loss of distal palpomeres.” Depending on the group, female mosquitoes have maxillary palpi composed of five, four, three, two or one palpomere, and some of those with four, three or two may have, respectively, a vestigial fifth, fourth or third palpomere.

12. Legs, scales: The presence of scales on the legs is an autapomorphy for “true” Culicidae, both fossil and extant species, which excludes *Libanoculex intermedius*.

13. Wing vein R<sub>1</sub>: An anterior curvature of this vein is a unique feature of *Burmaculex antiquus* and is therefore diagnostic for the species. There is no way of knowing whether or not it is an autapomorphic character of the extinct genus or subfamily, but assuming it is, then it is uninformative (irrelevant) with regard to *Libanoculex intermedius* and the other taxa included in the analysis.

14. Wing veins, scales: It seems the presence of scales on the costal vein of *Burmaculex antiquus* was overlooked for coding this character. Disregarding that, the Chaoboridae and Corethrellidae are incorrectly coded as being “without scales”. Chaoboridae have slender hair-like scales on their wing veins (Cook 1956; Belkin 1962). Therefore, it is important to note that this includes *Eucoethra underwoodi*, the earliest extant lineage of the family (Borkent & Grimaldi 2016). As such, it is conceivable that the absence of scales on the wing veins of *Libanoculex intermedius* and *Burmaculex antiquus* may represent independent losses.

15. Meron, development: This character is coded as a synapomorphy of the Chaoboridae and as missing data for *Burmaculex antiquus*. It is therefore uninformative (irrelevant) with respect to the other taxa. Curiously, the image that purports to show the meron in *Libanoculex intermedius* (fig. 1J) is not only difficult to interpret, it is obviously a mirror image of the thoracic region of the whole specimen shown in figure 1A.

The above clearly shows that the phylogenetic analysis of Azar *et al.* (2023) is flawed. The paucity of data for male mosquitoes and the reliance on synapomorphies (for females and males?) has produced a questionable phylogeny. In the tree produced by the authors, there is no valid reason to assume that *Libanoculex intermedius* is a culicid because it is the sister to a lineage comprised of *Burmaculex antiquus* + other fossil and extant Culicidae. It is misleading to rank *Libanoculex intermedius* as a member of an extinct family-group taxon of the Culicidae, that it is somehow comparable to the subfamilies Burmaculicinae, Anophelinae and Culicinae.

The preponderance of morphological features of *Libanoculex intermedius* are shared with the Chaoboridae, not with the Culicidae; consequently, the classification of the fossil fly as a member of an extinct subfamily of the Culicidae is unsupported. The differences are so apparent that a phylogenetic analysis based on “presumed” synapomorphies in light of obvious autapomorphies is pointless.

Azar *et al.* (2023) presumed that the mouthparts of *Libanoculex intermedius* are a precondition for the evolution of a very long prementum concomitant with reduction of the rostrum and development of a fascicle of very long stylets that form a capillary tube for sucking up liquids. But is this assumption to be accepted? Of course not. There are at least three other options: *Libanoculex intermedius* is (1) a member of a lineage that died out prior to the evolution of the lineage that gave rise to the Culicidae; (2) it represents an early lineage of the Chaoboridae, or an offshoot of that lineage; and (3) it is an ancestral lineage of *Eucoethra* or an extinct species of that genus.

In view of all the evidence provided above, it seems tenable that *Libanoculex intermedius* is an ancestral member of the chaoborid subfamily Eucoethrinae. *Libanoculex intermedius* may be a sister group to all Culicidae, but it is not



itself a member of the family. For that reason, *Libanoculex intermedius* (an unfortunate misapplication of the genus and species names) is here formally removed from the Culicidae and transferred to the subfamily Eucorethrinae Cook, 1965 of the Chaoboridae. Attendant with this taxonomic action, the family-group name Libanoculicinae Azar *et al.*, 2023 is recognized as a synonym of Eucorethrinae Cook, 1965.

Based on the presence of stylet-like laciniae, it is reasonable to conclude that the mouthparts of *Burmaculex antiquus* females were developed for piercing and siphoning liquid nourishment, and the male probably had a similarly developed proboscis and mouthparts. Therefore, *Burmaculex antiquus* is correctly classified as a member of an extinct subfamily of Culicidae (subfamily Burmaculicinae) and remains the oldest known fossil mosquito.

For the record, Azar *et al.* (2023) incorrectly attributed the authorship of the family name Culicidae to Billberg (1820). The family name Culicidae was established by Meigen, 1818 (as Culiciformes, the coordinate family-group name formed from the genitive singular of the type genus *Culex* (*Culicis*, combining stem *Culici*-). Culiciformes Meigen, 1818 is the earliest family-group name that established the date of priority for Culicidae, not Billberg (1820, as Culicides).

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