

## Diversity of culicomorphan dipterans in the Eocene Kishenehn Konservat-Lagerstätte (Montana, USA) and its palaeoecological implications

Viktor A. Baranov, Joachim T. Haug, Dale E. Greenwalt, and Ralph Harbach

### ABSTRACT

This report highlights the eight new morphotypes of culicomorphan dipterans from 46-million-year-old Kishenehn Formation (Montana, USA)

This report highlights the eight new morphotypes of culicomorphan dipterans from the 46-million-year-old Kishenehn Formation (Montana, USA). Five of these morphotypes are non-biting midges of the family Chironomidae (cf. *Conchapelopia*, cf. *Psectrotanypus*, *Hintelmanniella noncatafractata* sp. nov., cf. *Tanytarsus*, and *Rheotanytarsus lacustris* sp. nov.), one morphotype is a biting midge of the family Ceratopogonidae (cf. *Alluaudomyia*), one is a phantom midge of the family Chaoboridae (*Chaoborus kishenehnicus* sp. nov.), and the last one is a true mosquito, family Culicidae (*Neoculex*). We discuss implications of the diversity and abundance of representatives of Culicomorpha in the Formation for understanding the palaeoecology of the deposit. Abundance of Chaoboridae and presence of the seemingly surface skating Chironomidae indicate a large, lacustrine habitat.

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## INTRODUCTION

Fossil deposits with outstanding preservation of soft-bodied animals, the so-called Konservat-Lagerstätten (Grimaldi and Engel, 2005), are among the most lauded sources of data about environments of the past. Konservat-Lagerstätten often capture components of ecosystems not preserved elsewhere, such as animals without hard body parts, life-like behaviour, and interactions of organisms or traces of their activities (Arratia et al., 2015). Lagerstätten are often also very good in preserving small and fragile animals, such as representatives of the hyper-diverse group Insecta, which are otherwise rare in sedimentary rocks (Grimaldi and Engel, 2005; Greenwalt et al., 2014). Insects are excellent proxies of environmental conditions and can be used to reconstruct ecosystems of the past (Merrit and Cummins, 1996; Grund, 2006). One such exemplary indicator is the flies (Diptera). Diptera is a monophyletic group with at least 160,000 extant species comprised of gnats, midges, mosquitoes, and myriads of related flies (Marshall, 2012). Due to this diversity and abundance, flies can serve as important indicators of environmental conditions in both modern and fossil ecosystems (Grund, 2006).

A relatively recently recognized Konservat-Lagerstätte with diverse and abundant dipteran fossils is the Middle Eocene Coal Creek Member of the Kishenehn Formation in north-western Montana, USA. So far, 23 species of Diptera representing 21 large families have been reported from the Kishenehn Formation (Greenwalt et al., 2019). Here we deal with representatives of the Culicomorpha (midges and mosquitoes), which make up over 50% of the fossil insects in the formation. Several species of the culicomorphan ingroups Culicidae and Dixidae have already been described (Harbach and Greenwalt, 2012; Greenwalt et al., 2014; Greenwalt and Moulton, 2016). In total, five major culicomorphan families have been recorded in the Kishenehn Formation: Ceratopogonidae, Chaoboridae, Chironomidae, Culicidae, and Dixidae (Greenwalt et al., 2014, 2019). The Kishenehn Formation is in fact one of the richest sources of fossil mosquitoes (Culicidae) in the world (Harbach and Greenwalt, 2012). Two of the 27 known fossil species of Culicidae were described from the Kishenehn, with nearly 100 specimens collected from the formation. About 10 of these are blood-

engorged, the only such specimens known to science. Particularly spectacular was an engorged mosquito that contained host heme in its blood meal (Greenwalt et al., 2013). Here we report previously undescribed representatives of Culicomorpha, including forms of Chaoboridae, Chironomidae, and Ceratopogonidae from the formation, as well as one of the very few fossil larvae of Culicidae known from the fossil record. We also discuss implications of the diversity and abundance of representatives of Culicomorpha in the Kishenehn Formation for understanding the palaeoecology of the deposit.

## MATERIAL AND METHODS

### Imaging

Specimens were imaged using either a Canon EF-S 18–55 mm macro lens or a Canon MP-E 65 mm f/2.8 1–5x macro lens. Exact methods follow those of Haug et al. (2011). Images were taken with additional light-spot polarized illumination, with a CanonEos Rebel Canon EOS 5D MKIII camera on a repro-stand. Some specimens were imaged using a Keyence VHX-6000 digital microscope, either with ring light illumination or cross-polarized co-axial illumination (Haug et al., 2018). All images are vertical stacks and horizontal composites done with inbuilt microscope software (in case of VHX-6000) or Photoshop Elements CS 11 panorama functionality and PICOLAY open software ([www.picolay.de](http://www.picolay.de)). Body dimensions of specimens were measured from photos with ImageJ (public domain, Schindelin et al., 2012). In total, we have examined 428 specimens of Culicomorpha from the Kishenehn Formation.

### Geological Setting

The Coal Creek Member of the Kishenehn Formation, which contains well-preserved fossils of Insecta, is estimated to be  $46.2 \pm 0.4$  MYA (Middle Eocene) based on single-crystal laser fusion  $Ar^{40}/Ar^{39}r$  dating of 12 biotite grains from tephra (Constenius, 1996). Climate at the location of the fossil deposition in the Middle Eocene was tropical or near tropical (Wolfe, 1995; Pierce and Constenius, 2001; Zachos et al., 2001; Huber and Caballero, 2011; Greenwalt et al., 2014). It appears that most of the smaller fossils were deposited in the littoral and profundal area of a large lake, while larger fos-

sils (mostly representatives of Vertebrata) that occur in the formation were preserved in the profundal area of the waterbody (Constenius et al., 1989; Pierce and Constenius, 2014; Greenwalt et al., 2014).

Fossiliferous shales are made up from varves (annual layers) composed of two or three distinct components: (i) eolian siliciclastic particles; (ii) a black layer of the algae-derived carbonaceous materials; +/- (iii) a distinct layer of small amorphous particles between the latter two layers, probably formed as a result of  $\text{CaCO}_3$  precipitation (Greenwalt et al., 2014). Precipitation of  $\text{CaCO}_3$  seems to have been caused by the annual warming of the littoral area (probably during spring) prior to subsequent blooms of algae and/or cyanobacteria (Greenwalt et al., 2014). Massive annual algal blooms were a regular occurrence in the ancient lake of the Kishenehn Formation and appear to be the main factor responsible for the fine-scale preservation of the fossil insects, due to the production of a large amount of mucopolysaccharides by cyanobacteria (Greenwalt et al., 2014, 2019). Mucopolysaccharides are known to entrap and 'stabilize' insects' bodies in both other fossil settings and extant aquatic habitats (Dunn et al., 1997; Martínez-Delclòs et al., 2004). The antimicrobial activity of mucopolysaccharides and the anoxic environment created by algal blooms have been shown to provide protection against the decomposition of dead insects (Martínez-Delclòs et al., 2004).

### Taxonomy

Wherever possible, we decided not to use Linnean ranks ('rankless taxonomy'). Ranks (or "categories" sensu Mayr, 1942, p.102) represent arbitrary constructs in a way that do not hold 'comparative values' (Mayr, 1942, p. 291, line 3) and, in our view, do not contribute to an easier understanding of the phylogenetic relations among species and higher groups (Haug et al., 2020).

Three new species are formally described herein, and a new 'genus-level' name is also established. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system of the ICZN. The ZooBank Life Science Identifiers (LSIDs) can be resolved, and the associated information viewed through any standard web browser, by appending the LSID to the prefix <http://zoobank.org/>.

The morphological terminology largely follows Marshall et al. (2017) and Borkent and Sinclair (2017), and specifically follows Harbach and

Knight (1980) for mosquito anatomical terminology and abbreviations and Borkent (2012) for culicomorphan pupae. Yet, to enhance the understandability for non-experts, we amended some of the special morphological terms with more general terms. As Insecta is an accepted ingroup of Crustacea s.l., 'crustacean' terms given in square brackets were necessary to provide a wider frame of correspondence (Baranov et al., 2019a, 2019b, 2020). In this paper, we deal mostly with morphotypes, i.e., distinct morphological groups of organisms. We assume most if not all of them represent a single species, but representatives of some morphotypes are too poorly preserved to know for certain. We call all the remnants of the pupal life stage 'pupa/pupae' although many of the specimens are actually 'pupal exuviae', the integument left after emergence of the adult fly.

### Data Availability

All fossil specimens have been deposited in the palaeobiology collection of the National Museum of Natural History, Washington, DC, USA (USNM). A complete list of all accessed specimens that were studied is provided in Appendix 1.

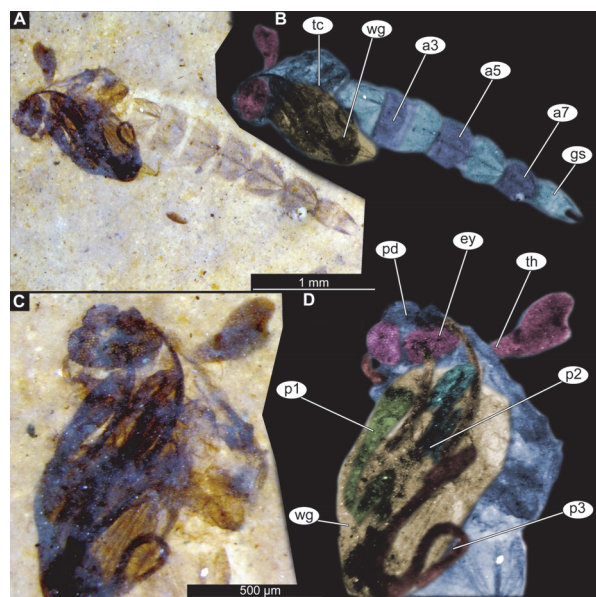
### SYSTEMATIC PALAEOLOGY

Eight new morphotypes of culicomorphan dipterans from the Kishenehn Formation are recorded here. Five of the morphotypes are non-biting midges, i.e., representatives of Chironomidae, one morphotype is a biting midge, i.e., a representative of Ceratopogonidae, one is a phantom midge, i.e., a representative of Chaoboridae, and the last one is a true mosquito, i.e., a representative of Culicidae.

DIPTERA Linnaeus, 1758  
 CHIRONOMIDAE Newman, 1838  
 TANYPODINAE Thienemann and Zavřel, 1916  
*CONCHAPELOPIA* Fittkau, 1957  
 cf. *CONCHAPELOPIA*  
 Figures 1A-D, 2A-C, 3A-C

**Material.** This morphotype is represented by numerous specimens (see Appendix Table 1 for the full list). These specimens are representatives of Chironomidae, based on the following combination of characters: antennae extending posteriorly past the head of the pupa; maxillary palpi directed laterally; trunk end without articulated terminal paddles (Figure 1A–D) (Borkent, 2012).

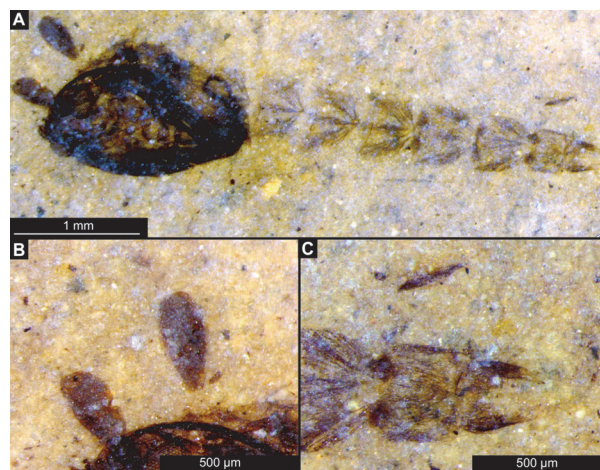
**Remarks.** This morphotype of Chironomidae is exclusively represented by early and late pupae (pharate adults); therefore, we have refrained from



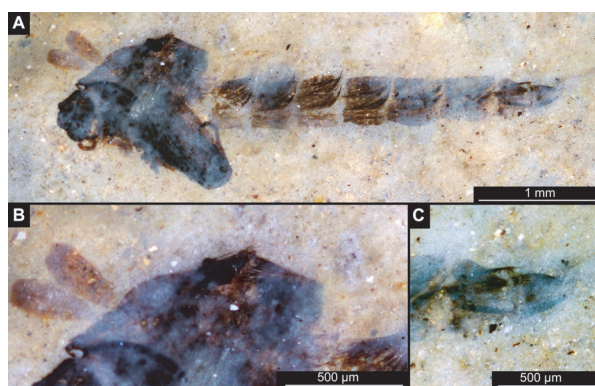
**FIGURE 1.** Representatives of Chironomidae cf. *Conchapelopia*. Male pupa. USNM 621057. A, Habitus, unmarked. B, Habitus, marked. C, Head and thorax, unmarked. D, Head and thorax, marked. Abbreviations: a3–a7, abdominal units (segments) three through seven; ey, compound eyes; gs, genitals; p1, forelegs; p2, midlegs; p3, hindlegs; pd, pedicellus; tc, thorax; th, thoracic horn (respiratory organ); wg, wing.

a formal description of a species (Figures 1A-D, 2A-C, 3A-C).

**Taxonomic attribution.** Within Chironomidae, this morphotype most closely resembles representatives of the extant group *Conchapelopia* Fittkau, 1957 based on the following combination of characters: thoracic horn trumpet-shaped with plastron plate (surface for retention of the air film, providing



**FIGURE 2.** Representatives of Chironomidae cf. *Conchapelopia*. Male pupa USNM 626009. A, Habitus. B, Thoracic horns. C, Male genitalia (hypopygium).



**FIGURE 3.** Male pupa of Chironomidae cf. *Conchapelopia* (USNM 626057). A, Habitus. B, Thoracic horns and notum of the thorax. C, Male genitalia (hypopygium).

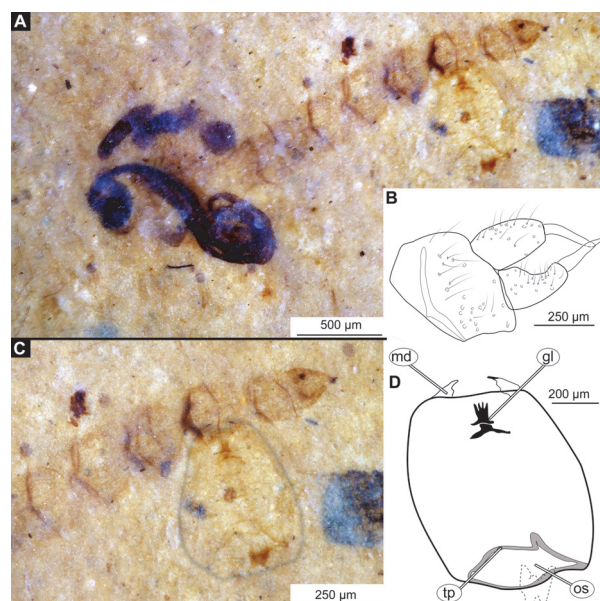
a gas exchange interface); plastron of the thoracic horn occupying about 40% of the internal volume of the entire structure; thoracic comb present behind the respiratory organ, row of curved cuticular hooks absent from tergite of abdominal unit two, abdominal unit one with a longitudinal, sclerotized mark present on the tergite; no lateral filaments visible on abdominal units 2–6; bifurcated spinules present on the abdominal tergite; abdominal unit 8 not extended posteriorly on each side by more than 0.2 of its median length; anal lobes (based on preserved genitals, and the shape of the imprint of the posterior abdomen) much longer than wide, tapering posteriorly (Figures 1A-D, 2A-C, 3A-C) (Langton, 1991). The combination of these characters indicates affinity with extant representatives of *Conchapelopia*, but unfortunately, many important characters, such as the shape and armament of the anal lobes, are poorly preserved. Therefore, a precise taxonomic affinity of this morphotype at the genus level cannot be provided.

TANYPODINAE Thienemann and Zavřel, 1916  
*PSECTROTANYPUS* Kieffer, 1909  
 cf. *PSECTROTANYPUS*  
 Figures 4A-D, 5A-B

**Material.** This morphotype is represented by numerous specimens (see Appendix Table 1 for the full list). These specimens are representatives of Chironomidae, based on the following combination of pupal characters: antennae extending posteriorly past the head of the pupa; maxillary palpi directed laterally; strongly sclerotized arches from the anterior parts of the abdominal tergites; terminus of trunk without articulated terminal paddles (Figures 4A-D, 5A-B).

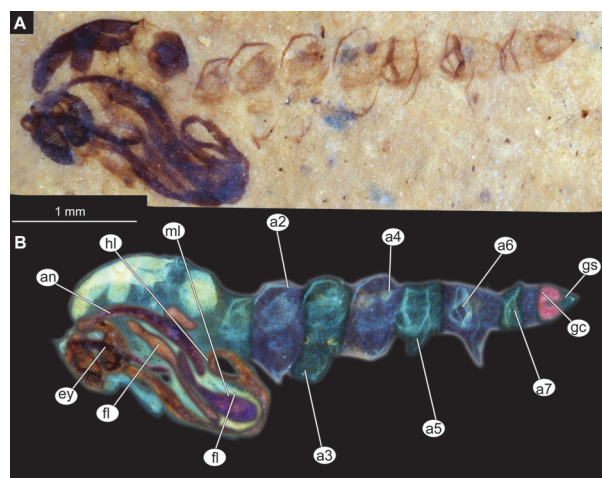
**Remarks.** This morphotype of Chironomidae is represented by early or late pupae (pharate adults)





**FIGURE 4.** Representatives of Chironomidae cf. *Psectrotanypus*. Male pupa and larva. USNM 624474.1. A, Habitus of the pupa. B, Male genitalia (hypopygium). C, Head capsule of the larva attached to the abdomen of the pupa. D, Schematic drawing of the larval head capsule. Abbreviations: gl, gula; md, mandible; os, occipital sclerite; ts, pit of tentorium.

and a single larval head capsule with partially preserved abdominal cuticle. Because some crucial characters (anal lobes, male genitalia (hypopygium), wings) were not preserved, we have refrained from a formal description of a species (Figures 4A-D, 5A-B).



**FIGURE 5.** Representatives of Chironomidae cf. *Psectrotanypus*. Male pupa USNM 624474.2. A, Habitus, unmarked. B, Habitus, marked. Abbreviations: a2–a7, abdominal units (segments) two through seven; an, antenna; ey, compound eyes; gc, gonocoxite (II); gs, genitals; p1, forelegs; p2, midlegs; p3, hindlegs.

**Taxonomic attribution.** It was difficult to interpret the early or late pupae (pharate adults) of this morphotype within Chironomidae due to the lack of preserved wings, legs, anal lobes, and other important structures. Fortunately, it is quite common for pupae of Chironomidae to have their fourth-instar larval exuviae attached to the end of their abdomen, and one of the specimens from the Coal Creek Member (USNM 624474) has just that, a partially preserved larval exuviae still attached to the pupa (Figure 4A-D) (Armitage et al., 1995). We therefore assume that this larva belongs to the same individual as the pupa. The head capsule of this larva provided us with a means to further elucidate the identity of this morphotype. Based on the preserved larval characters, this morphotype is a representative of Tanypodinae, based on the distinct gula present behind the submentum of the head capsule (Figure 4C-D) (Cranston and Epler, 2013). This morphotype most closely resembles representatives of *Psectrotanypus* Kieffer, 1909, based on the following combination of characters: head capsule longer than wide but less than two times as long, mandible elongate, not curved, labial endites (ligula) with four teeth (Figure 4C-D) (Cranston and Epler, 2013). Association with this larval head capsule, as well as several features of the pupae (e.g., strongly sclerotized arches from the anterior parts of the abdominal tergites) and a similar habitus of male genitalia (hypopygium), visible through the late pupal cuticle, indicate that this morphotype is closely related to *Psectrotanypus* Kieffer, 1909 or being an ingroup, though it is impossible to further ascertain due to the many important characters not available (Roback, 1971; Langton, 1991).

CHIRONOMINAE Macquart, 1838

CHIRONOMINI Macquart, 1838

*HINTELMANNIELLA* Baranov and Haug, gen. nov.

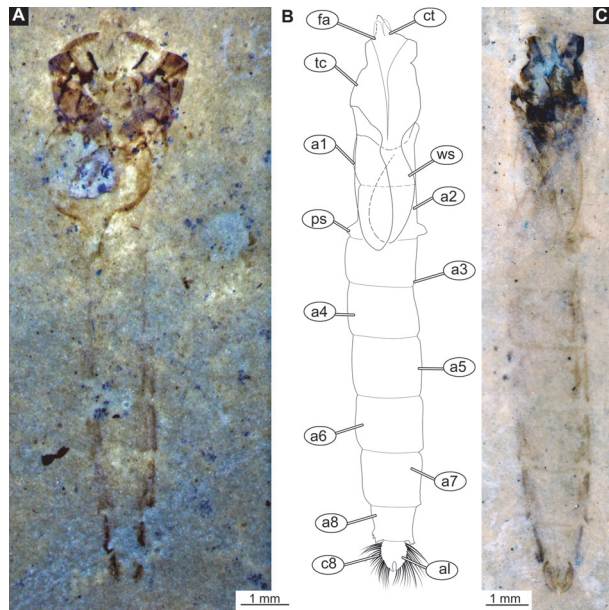
Figures 6A-C, 7A-D, 8A-D, 9A-E

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**Etymology.** This genus is named after Mr. Robert Johann Heinrich Hintelmann (1918–1984) and Mrs. Elisabeth Hintelmann for their contribution to the development of zoological science in Germany, expressed by support provided towards early career researchers in zoological systematics through the R.J.H. Hintelmann Wissenschaftspreis für Zoologische Systematik.

**Type species.** *Hintelmanniella noncatafractata* Baranov and Haug, sp. nov.

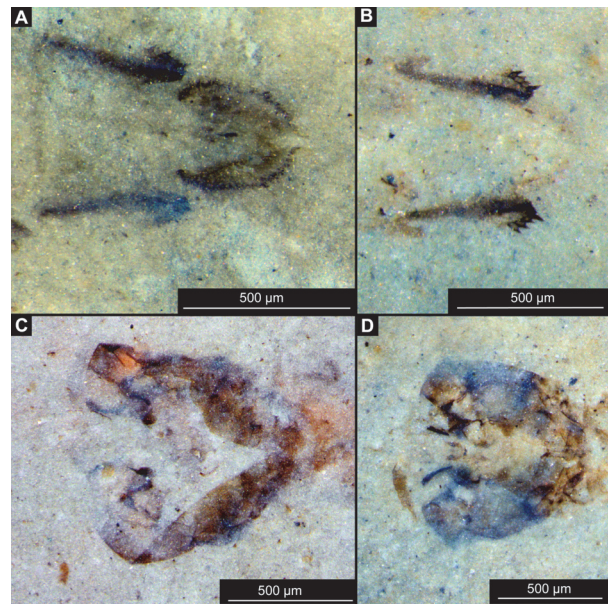
**Diagnosis (based on adult males and pupal exuviae).** The pupa of this species can be easily distinguished from all other known pupae of the



**FIGURE 6.** *Hintelmanniella noncatafractata* sp. nov. (Chironomidae). Pupa. Paratype USNM 717431 (A–B) and paratype USNM 717494 (C). A, Habitus of the pupa. B, Schematic drawing of the pupa, marked. C, Habitus of the pupa. Abbreviations: a1–a8, abdominal units (segments) one through eight; ct, cephalic tubercles; al, anal lobes; c8, posterolateral comb of abdominal unit 8; fa, frontal apotome; tc, thorax.

group Chironomidae based on the following combination of characters: highly rugose cuticle of the thorax; tergite of the abdominal unit 2 lacks armament (Figures 6A–C, 7A–D), most notably it has no row of hooks on the posterior margin; remaining abdominal tergites without armament/shagreen as well; abdominal unit 2 with prominent pedes spuri B (lateral protrusions of the tergite 2) (Figure 6B); abdominal unit 8 with prominent posterolateral comb comprised of 4–7 strongly sclerotized large spines and a number of smaller spines inserted between them; anal lobes with well-developed fringe of setae (Figure 7A–B).

Pharate males can be distinguished from the other representatives of the Chironomidae based on the combination of genitalia (hypopygium), with its broad inferior volsella and gonostylus narrow proximally, broadest medially tapering distally again, resembling those of *Lipiniella* Shilova, 1961. Hind-tibial combs also resemble those of *Lipiniella* (Figure 8D) (Wiederholm, 1989). The new species has relatively short antennae, short wings and extremely robust and short hindlegs.



**FIGURE 7.** *Hintelmanniella noncatafractata* sp. nov. (Chironomidae) Pupa. Paratype USNM 717428 (A), paratype USNM 722339 (B), specimen 722340 (C), specimen USNM 722377 (D). A, Anal lobes. B, Anal lobes and posterolateral comb of abdominal unit 8. C, Thorax. D, thorax.

#### *HINTELMANNIELLA NONCATAFRACTATA*

Baranov and Haug, sp. nov.

Figures 6A–C, 7A–D, 8A–D, 9A–E

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**Material.** Holotype USNM 717431 pupa and associated adult male: paratypes, adult male USNM 624424 and pupa USNM 624644 – male in a state of eclosion, and pupal exuvium (partial) USNM 717428 and additional pupae USNM 722339 and USNM 717494. Additional material – see Appendix Table 1.

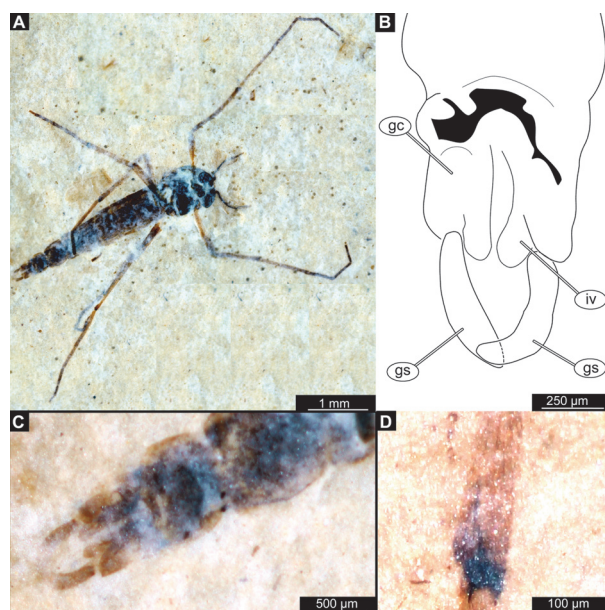
**Etymology.** Named ‘*noncatafractata*’ from Latin for ‘not armoured’, in reference to the complete lack of any armament (hooks or shagreen) on the tergites of the abdominal units.

**Diagnosis.** As for the genus per monotypy.

**Pupa.** (Figures 6A–C, 7A–D). Habitus. Medium-sized pupa, with flattened, comma-shaped body (in lateral aspect). Body length 5.9–9.2 mm ( $n = 23$ ); length of head and thorax combined 1.3–2.3 mm ( $n = 23$ ); abdomen length 4.4–7.4 mm ( $n = 23$ ). Body differentiated into presumably 20 segments, ocular segment plus 19 post-ocular segments (Figure 6A–C).

Anterior part of the body is composed of head and thorax, visible as a single globose structure. Antenna is missing or incomplete on the available specimens (Figure 7A–D). Frons of the head bears

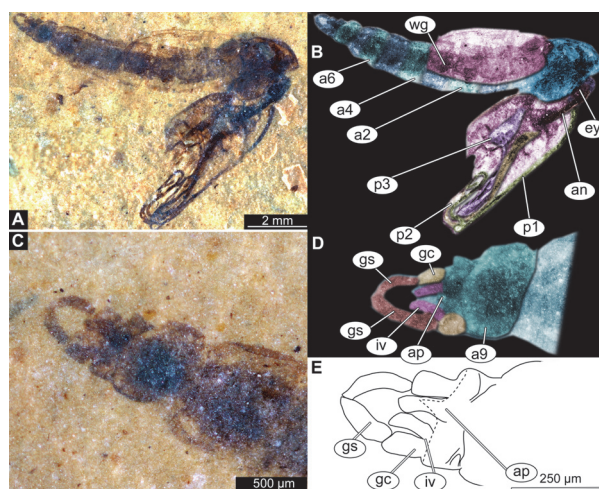




**FIGURE 8.** *Hintelmanniella noncatafractata* sp. nov. (Chironomidae). Adult males. Paratype USNM 717431 (A–C), specimen USNM 624424 (D). A, Habitus. B, Schematic drawing of male genitalia (hypopygium). C, Male genitalia (hypopygium). D, Hindtibial combs. Abbreviations: gc, gonocoxite; gs, gonostylus; iv, inferior volsella (lateral protrusion of gonocoxite).

two conical cephalic tubercles, without visible setae; ocular segment and post-ocular segments 1–5 (presumably) forming a distinct capsule (head capsule); mouthparts located ventrally, short, ending before attachment of the anterior ambulatory appendages (Figures 6A–C, 7A–D). Thorax bears wings and ambulatory appendages (legs) (Figures 6A–C, 7A–D). Thoracic horn (respiratory organ) not preserved. Cuticle of the thorax thick and rugose, wrinkled. No setae visible on the thorax. Developing wings reaching beyond the thorax to the abdomen. Legs not preserved in the available specimens (Figures 6A–C, 7A–D, 9A–B). Abdomen (posterior trunk). Tergites of the abdominal units 1–9 without visible armament or shagreen. Most notably, tergite 2 without any armament, including complete absence of a row of hooks on the posterior edge of the tergite. Lateral edges of the abdominal units slightly darker than the rest of the cuticle. Comb at the posterolateral edge of tergite 8 with 4–7 strong, wide spurs, and, occasionally, a number of smaller denticles nested between the spines (Figure 7A–B). Anal lobes with a dense fringe of setae with over 50 well-preserved setae present.

**Adult male.** Medium-sized midge with long legs and long abdomen ending with prominent external genitalia. Wings present on several specimens, rel-



**FIGURE 9.** *Hintelmanniella noncatafractata* sp. nov. (Chironomidae). Holotype USNM 624644. Emerging adult male with remnants of the pupa. A, Habitus, unmarked. B, Habitus, marked. C, Male genitalia (hypopygium), unmarked. D., Male genitalia (hypopygium), marked. E, Male genitalia (hypopygium), schematic drawing. Abbreviations: a2–a9, abdominal units (segments) two to nine; an, antenna; ap, anal point (abdominal unit X remnants); ey, compound eyes; gc, gonocoxite (II); gs, gonostylus; iv, inferior volsella (lateral protrusion of gonocoxite); p1, forelegs; p2, midlegs; p3, hindlegs; wg, wings.

atively short in relation to the body. Paratype USNM 717431 (Figures 8A–D, 9A–E). Paratype USNM 624644, paratype male, with the remnants of the pupa and partial imprint of the wing. Paratype USNM 717431 is preserved mostly in dorsal aspect. Body length 4.8 mm. Paratype USNM 624644 is preserved in lateral aspect, 6.2 mm long. Head. Ocular segment and post-ocular segments 1–5 (presumably) forming distinct capsule (head capsule) (Figures 8A, 9A–B). Ocular segment recognizable by a pair of large compound eyes. Eyes without macro- or microtrichia. Eyes have a short, wedge-shaped dorso-medial extension. Clypeus and labrum together 160  $\mu$ m long, rectangular. Post-ocular segment 1 recognizable by its appendages, antennae [antennulae]. Antenna ca. 1 mm long. It was impossible to distinguish the borders between most of the antennal elements (flagellomeres); pedicellus around 110  $\mu$ m long and last flagellomere about 450  $\mu$ m long (Figure 8A). Antennal ratio (AR) (length of the terminal flagellomere divided by the combined lengths of the rest of the flagellomeres) = 0.81. Each antenna bears plumage of long setae. Post-ocular segment 1 is embedded in matrix and impossible to examine. Post-ocular segment 2 (intercalary segment) with-

out externally recognizable structures. Post-ocular segment 3 bears no recognizable appendages (mandibles) (Figure 8A). Post-ocular segment 4 recognizable by its appendage, maxilla [maxillula]. Maxilla recognizable by maxillary palpi that consist of five elements (palpomeres), with palpomeres 1 and 2 hidden behind the labrum; lengths of elements 3 through 5: 96  $\mu\text{m}$  ( $n = 1$ ), 100  $\mu\text{m}$  ( $n = 1$ ), 110  $\mu\text{m}$  ( $n = 1$ ) (Figure 8A). Post-ocular segment 5 recognizable by its appendages, forming the labium (conjoined left and right maxillae). Labium mostly obscured in holotype, no details visible (Figures 8A, 9A-B). Thorax (Figures 8A, 9A-B) bears three pairs of the ambulatory appendages (fore-, mid- and hindlegs) on the pro-, meso-, and metathorax, respectively. Each leg consists of coxa, trochanter, femur, tibia, and tarsomeres 1–5. Wings poorly preserved on both available adult males. Paratype USNM 717431 with wings 2.4 mm long and paratype USNM 624644 with wings 3.4 mm long (Figures 8A, 9A-B). Prothorax horseshoe-shaped (with arms of ‘horseshoe’ facing ventrally), narrow. Prothorax bears first pair of thorax appendages (forelegs). Foreleg element lengths ( $n = 2$ ): femur 1000  $\mu\text{m}$ , tibia 1005–1300  $\mu\text{m}$ , tarsomere 1 960–1300  $\mu\text{m}$ , tarsomere 2 520–640  $\mu\text{m}$ , tarsomere 3 440–470  $\mu\text{m}$ , tarsomere 4 360–370  $\mu\text{m}$ , tarsomere 5 170  $\mu\text{m}$  ( $n = 1$ ). Claws present, non-serrate, no pulvilli visible. Mesothorax with wings poorly preserved, 2.4–3.4 mm long, venation not distinguishable. Wing length to body length ratio 0.5–0.56. Midleg element lengths: femur 1200  $\mu\text{m}$  ( $n = 1$ ), tibia 1300  $\mu\text{m}$  ( $n = 1$ ), tarsomere 1 750  $\mu\text{m}$  ( $n = 1$ ), tarsomere 2 500  $\mu\text{m}$  ( $n = 1$ ). Other elements not preserved. Claws present, non-serrate, no pulvilli visible (Figure 8A). Metathorax bears a pair of ambulatory appendages (hindlegs). Hindleg element lengths ( $n = 2$ ): femur 1010–1360  $\mu\text{m}$ , tibia 1060–1290  $\mu\text{m}$ , tarsomere 1 530–710  $\mu\text{m}$ , tarsomere 2 170–280  $\mu\text{m}$ , tarsomere 3 200–440  $\mu\text{m}$ , tarsomere 4 200–290  $\mu\text{m}$ , and tarsomere 5 110–220  $\mu\text{m}$ . Hindtibial comb separated into two parts, each part with the comb bearing a strong spur (Figure 8D). Claws present, non-serrate, no pulvilli visible (Figure 8A).

Abdomen (posterior trunk). Comprised of 10 units, only eight of which are represented as fully developed abdominal segments; units 9 and 10 incorporated into male genitalia (hypopygium). Abdominal units 1–8 roughly rectangular in shape. Only a few setae, visible in the lateral aspect, preserved on the abdomen (Figure 9A). Abdominal element 9 together with male genitalia (hypopygium) form a male copulatory apparatus (Figures 8B-C, 9C-E).

Male genitalia (hypopygium) (male genitalia, appendages of abdominal unit 8 and following units). Unit 9 broadly rounded posteriorly (Figures 8B-C, 9C-E). Unit 10 represented by a triangular anal point, with pointed end. Gonocoxite (2) cylindrical, 145–220  $\mu\text{m}$  long ( $n = 4$ ). Inferior volsella of the gonocoxite (lateral protrusion of gonocoxite) relatively long, 110–240  $\mu\text{m}$  ( $n = 4$ ), club-shaped, broadest distally (Figure 9C-E). Gonocoxite and gonostylus without a mobile articulation, conjoined (Figures 8B, 9C-E). Gonostylus narrow, arched, with blunt, rounded, distal end, 200–260  $\mu\text{m}$  long ( $n = 4$ ) (Figures 8B, 9C-E).

**Possible adult female.** Single, poorly preserved specimen, which might represent a female of *H. noncatafractata* (paratype USNM 72223). This female can be associated with the males of *H. noncatafractata* based on the similar hindtibial combs. A characteristic pupa of *H. noncatafractata* is present next to the female, suggesting that it may have just emerged from it. Body length of the female 4.3 mm, length of the poorly preserved wing 2.8 mm.

**Remarks.** The following characteristics of the adult male of this morphotype point to it being a representative of Chironomidae based on a specific combination of characters of the pupae: overall similar habitus, antennae with more than six elongate elements (flagellomeres), second element of antennae (pedicellus) conspicuously larger than the other elements, antenna with strong plumage, ocelli absent, head without functional mouthparts, thorax without distinct pre-halter lobe at the base of the true halter, scutum without distinct V-shaped suture, slender-bodied fly, tarsomere one on all (preserved) legs considerably longer than tarsomere 2, tergite of abdominal unit I without strong fringe of lateral setae (Marshall et al., 2017) (Figures 8A-D, 9A-E).

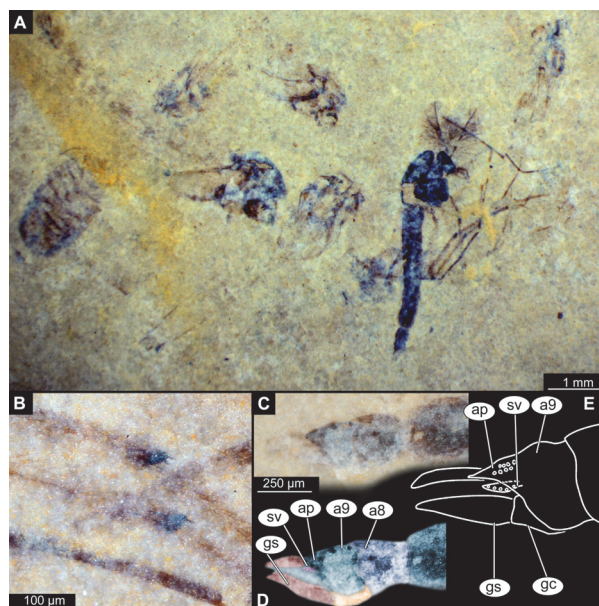
Within Chironomidae, this morphotype is an ingroup of Chironominae, due to a specific combination of characters: gonostylus and gonocoxite conjoined rigidly, no articulation visible (Wiederholm, 1989). While specimens lack wings, and therefore crucial diagnostic characters are missing, we can assume that this midge is a representative of Chironomini. This assumption is based on the absence of a prominent medium volsella (lateral protrusion of gonocoxite), and an anal point without prominent spinules, arranged in longitudinal rows (Wiederholm, 1989) (Figures 8B, 9C-E). Further interpretation within Chironomini is not possible, due to the insufficient preservation of the antennae and wings of the male. The new species has relatively short antennae, short wings and relatively



robust and short hindlegs. These traits are exhibited by midges inhabiting the intertidal zone of the seas or living as a surface skater in hypersaline habitats (Armitage et al., 1995; Qi et al., 2018) with salinities up to 40‰ (Armitage et al., 1995; Qi et al., 2018; Shadrin et al., 2019). In the new species, these traits are less developed than in the known intertidal and marine representatives of Chironomidae, i.e., *Pontomyia* spp., *Clunio* spp., *Dicrotendipes sinicus* Qi and Lin, 2018 and *Baeotendipes noctivagus* Kieffer, 1911 (Qi et al., 2018). It is therefore probable that this combination of traits indicates that adults of *H. noncatafractata* sp. nov. might have led a surface-skating lifestyle on waterbodies in the Kishenehn Formation.

**Association of the life stages.** Pupae of the new species are associated with the adult males via paratype USNM 624644, a male, preserved in a state of eclosion from the pupa. While only the thorax of the pupa is preserved in this specimen, it exhibits characteristic strongly sclerotized, wrinkled cuticle, present in all other pupae of *H. noncatafractata* sp. nov. These pupae exhibit a character combination characteristic for Chironomidae: antennae extending posteriorly past the head of the pupa; maxillary palpi directed laterally; trunk end without articulated terminal paddles (Borkent, 2012). The pupa furthermore exhibits characteristic traits of pupae of Chironomini: wings without nose or a pearl row; all legs are curved under the wings; abdominal units 2–8 without strong spines; tergites of the abdominal units without paired patches of shagreen; tergite 8 with comb of strong, posterolateral spurs; abdominal units 8 and 9 do not form a disc-like structure, anal lobes with numerous simple setae, one pair of the lamellar lateral setae without posterolateral spurs; anal lobes without terminal macrosetae (Wiederholm, 1986). Remarkably, pupae of the new species are lacking armament of the abdominal tergites (Figure 6A–C). Most crucially, they lack traces of the hook row on the posterior edge of tergite 2, present in almost all other pupae of Chironomini (Wiederholm, 1986; Langton, 1991).

One notable exception from this rule is a pupa of the northern Australian group *Anuncotendipes* Cranston, 1999. Pupae of *A. australotropicus* Cranston, 1999 and *A. kakadu* Cranston, 1999 both lack a hook row on tergite 2 of the abdomen (Cranston, 1999). *Anuncotendipes* is clearly an ingroup of the *Harnischia*-group (Cranston, 1999). This is evident from the morphology of the known larvae of *Anuncotendipes*, as noted by Cranston (1999). Despite sharing the absence of the hook



**FIGURE 10.** Representatives of Chironomidae cf. *Tanytarsus*, specimen USNM 722523. Adult male. A, Habitus of the adult male and remnants of a water boatman nymph (Corixidae). B, Hindtibial combs. C, Male genitalia (hypopygium), unmarked. D, Male genitalia (hypopygium), marked. E, Male genitalia (hypopygium), schematic drawing. Abbreviations: a8–a9, abdominal units (segments) eight and nine; an, antenna; ap, anal point (abdominal unit X remnants); gs, gonostylus; sv, superior volsella (lateral protrusion of gonocoxite).

row, these ingroups of Chironomidae are not very similar to *H. noncatafractata* sp. nov.

TANYTARSINI Zavřel, 1916 [in Thienemann and Zavřel, 1916]

TANYTARSUS van der Wulp, 1874

cf. TANYTARSUS

Figure 10A–E

**Material.** This morphotype of Chironomidae is represented by a single adult male and several probably related pupae on a single slab of shale (specimen USNM 722523). As we could not ascertain the state of some important characters, most notably wing venation, we have refrained from a formal description of this morphotype.

**Remarks.** Medium-sized fly with midge-shaped body, long legs and long abdomen ending with prominent external genitalia. Wings lost in the only preserved adult male, Holotype: USNM 722523. Specimen preserved mostly in dorsolateral aspect. Body length 4.8 mm.

**Adult male.** Ocular segment and post-ocular segments 1–5 (presumably) forming distinct capsule (head capsule) (Figure 10A–E). Ocular segment recognizable by a pair of large compound eyes.

Eyes without micro- or macrotrichia. Labrum and clypeus not preserved. Post-ocular segment 1 recognizable by its appendages, antennae [antennulae]. Each antenna bears a dense plumage of long setae. Lengths of the individual elements of the antenna as follows ( $n = 1$ , USNM 722523): first and second flagellomeres only partially visible/obscured, third 50  $\mu\text{m}$ , fourth 40  $\mu\text{m}$ , fifth 45  $\mu\text{m}$ , sixth 25  $\mu\text{m}$ , seventh 40  $\mu\text{m}$ , eighth 35  $\mu\text{m}$ , ninth 40  $\mu\text{m}$ , tenth 40  $\mu\text{m}$ , eleventh 40  $\mu\text{m}$ , twelfth 48  $\mu\text{m}$ , and thirteenth 825  $\mu\text{m}$ . Frons (frontal sclerite) of post-ocular segment 1 impossible to examine as it is embedded in matrix. Post-ocular segment 2 (intercalary segment) without externally recognizable structures. Post-ocular segment 3 bears no recognizable appendages (mandibles). Post-ocular segment 4 recognizable by its appendage, maxilla [maxillula]. Maxilla recognizable by maxillary palpi, which normally consist of five elements (palpomeres), with palpomeres 1 and 2 hidden behind the head; lengths of elements 3 and 4 ( $n = 1$ ) 160  $\mu\text{m}$  and 180  $\mu\text{m}$ , respectively. Palpomere 5 not preserved. Post-ocular segment 5 recognizable by its appendages, forming the labium [conjoined left and right maxillae]. Labium mostly obscured on all specimens, no details visible. Thorax (Figure 10A) bears three pairs of the ambulatory appendages (fore-, mid- and hindlegs) on the pro-, meso- and metathorax, respectively. Each leg consists of coxa, trochanter, femur, tibia and tarsomeres 1–5. Wings not preserved. Prothorax horseshoe-shaped (with arms of ‘horseshoe’ facing ventrally), narrow. Prothorax bears first thoracic appendages (forelegs). Lengths of foreleg elements: femur 870  $\mu\text{m}$  ( $n = 1$ ), tibia 640  $\mu\text{m}$  ( $n = 1$ ), tarsomere 1 1000  $\mu\text{m}$  ( $n = 1$ ), tarsomere 2 530  $\mu\text{m}$  ( $n = 1$ ), tarsomere 3 440  $\mu\text{m}$  ( $n = 1$ ), tarsomere 4 280  $\mu\text{m}$  ( $n = 1$ ). Mesothorax with wing not preserved. Lengths of midleg elements as following: femur 670  $\mu\text{m}$  ( $n = 1$ ), tibia 1300  $\mu\text{m}$  ( $n = 1$ ); other elements not preserved. Metathorax bears a pair of ambulatory appendages (hindlegs). Lengths of hindleg elements as following: femur 1200  $\mu\text{m}$  ( $n = 1$ ), tibia 1400  $\mu\text{m}$  ( $n = 1$ ), tarsomere 1 670  $\mu\text{m}$  ( $n = 1$ ), tarsomere 2 400  $\mu\text{m}$  ( $n = 1$ ), tarsomere 3 300  $\mu\text{m}$  ( $n = 1$ ), tarsomere 4 320  $\mu\text{m}$  ( $n = 1$ ). Tibia with two separate combs (Figure 10B).

Abdomen (posterior trunk) comprised of 10 units, only 8 of which are represented as fully developed abdominal segments. Units 9 and 10 incorporated into hypopygium. Abdominal units 1–8 roughly rectangular in shape. No setae preserved on specimen (Figure 10C–E). Abdominal unit 9 together

with hypopygium forms the male copulatory apparatus.

Male genitalia (hypopygium) (appendages of abdominal unit 8 and following units): unit 9 broadly rounded posteriorly, trapezoidal in shape (Figure 10 C–E). Unit 10 represented by anal point, poorly preserved, seemingly parallel-sided, with two prominent rows of spinulae (eight in two rows of four). Gonocoxite (2) cylindrical, 170  $\mu\text{m}$  long. Superior volsella of gonocoxite (lateral protrusion of gonocoxite) oval, elongate with a row of setal tecae. Gonocoxite and gonostylus without a flexible articulation, conjoined (Figure 10C–E). Gonostylus narrow, curved, with pointed distal end, 220  $\mu\text{m}$  long (Figure 10C–E).

**Taxonomic attribution.** Males of this morphotype can be recognized as representatives of Chironomidae based on a specific combination of characters: overall similar habitus, body slender, antennae with more than six elongated elements (flagellomeres), second element of antenna (pedicellus) conspicuously larger than the rest of the antennal elements, antenna with strong plumage, ocelli absent, head without functional mouthparts, thorax without distinct pre-halter lobe at the base of the true halter, scutum without distinct V-shaped suture, tarsomere 1 on all (preserved) legs is considerably longer than tarsomere 2, tergite of abdominal unit 1 without fringe of strong lateral setae (Marshall et al., 2017). Within Chironomidae, this morphotype is an ingroup of Chironominae, due to a specific combination of characters: gonocoxite and gonostylus conjoined rigidly, no articulation visible (Wiederholm, 1989). Although the available specimen lacks wings, and therefore crucial diagnostic characters are missing, we can assume that this midge is a representative of Tanytarsini. This assumption is based on the combination of a prominent oval superior volsella and anal point with spinulae arranged in longitudinal rows (Wiederholm, 1989) (Figure 10E). Within the Tanytarsini, this morphotype is most similar to *Tanytarsus* van der Wulp, 1874, based on the following combination of characters: maxillary palpus elements are considerably longer than wide, mid- and hindtibiae with separated combs, anal point without two anteriorly directed processes and with a group of spines (Langton and Pinder, 2007). General shape of the superior volsella and characteristic spinulae of the anal point arranged into two longitudinal rows are reminiscent of the condition in extant representatives of *Tanytarsus*, such as *T. gracilentus* Holmgren, 1883 [in Holmgren and Aurivillius, 1883] (Gitka, 2011a). Numerous fossil adult repre-

representatives of *Tanytarsus* are known from amber, but differences in amber taphonomy from that of the Kishenehn Formation makes them difficult to compare to the specimens discussed here (Gilka, 2010; 2011b; Gilka, et al. 2013; Zakrzewska and Gilka, 2015; Zakrzewska, et al. 2020). Pupae on the same slab as the adult male appear to be representatives of *Tanytarsini* based on the armament of the abdominal tergites and can potentially represent the same morphotype as the male. Unfortunately, these pupae are too poorly preserved to be able to ascertain if they represent the same species.

*RHEOTANYTARSUS* Thienemann and Bause, 1913 [in Bause 1913]

*RHEOTANYTARSUS LACUSTRIS* Baranov and Haug, sp. nov.

Figures 11A-E, 12A-E

zoobank.org/D0cBcF87-28EF-41B5-A812-CA8D5DFAF245

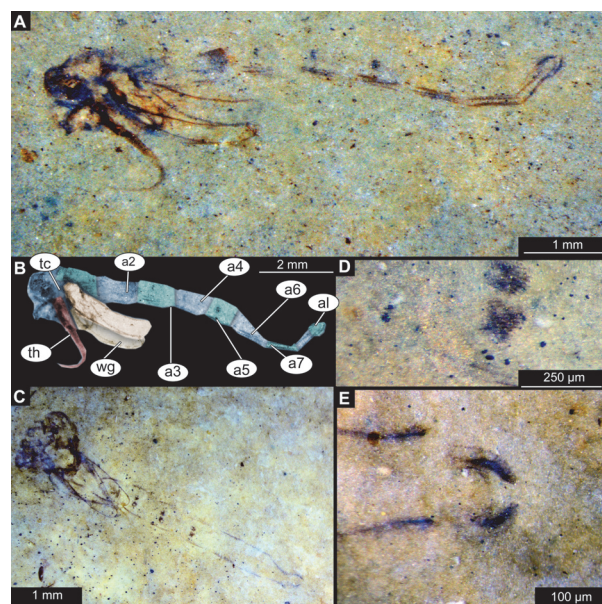
**Diagnosis (based on adult males and pupal exuviae).** This new species can be easily distinguished from all other species of *Rheotanytarsus* based on the specific combination of characters of adult males and pupae: adult male with extremely short medium volsella (lateral protrusion of gono-

coxite) and blunt gonostylus. Pupae associated with the adults are well preserved with thoracic horn parallel-sided and bare; tergites 2–5 of abdominal units with paired, circular patches of spinules present; tergite 2 with shagreen split into two groups; comb of abdominal unit 8 with four strong, thorn-like, strongly sclerotized spurs.

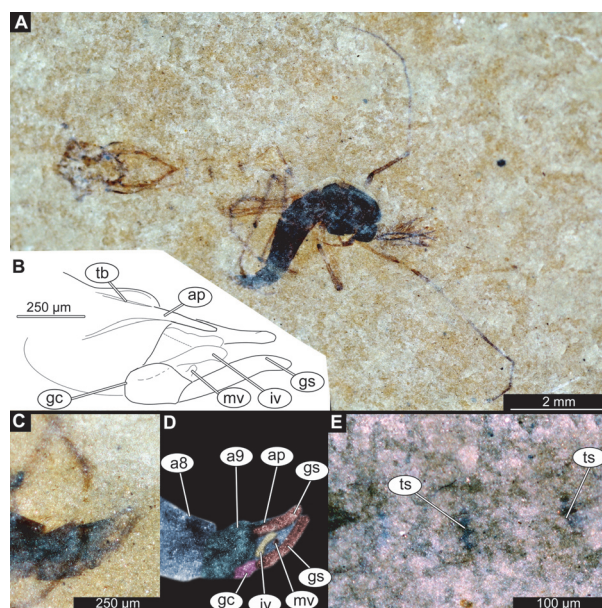
**Etymology.** Named *lacustris* after the lake deposits of the Kishenehn Formation the specimens were found in.

**Type material.** Holotype: USNM 717577 adult male and its pupal exuvium; paratypes, pupae: USNM 722460, USNM722479, USNM624824 and USNM 623669. Additional material: 76 additional pupae were examined; see Appendix Table 1 for additional material.

**Pupa.** Habitus. Medium-size, with flattened, comma-shaped body (in lateral aspect). Body length, 5.1–7.0 mm ( $n = 17$ ); length of head and thorax combined, 0.9–1.7 mm ( $n = 17$ ); abdomen length, 4.0–5.5 mm ( $n = 17$ ). Body differentiated into presumably 20 segments, ocular segment plus 19 post-ocular segments (Figure 11A-C); anterior



**FIGURE 11.** *Rheotanytarsus lacustris* sp. nov. (Chironomidae). Pupa. Paratypes USNM 722460 (A–B) and USNM 623669 (C–E). A, Habitus, unmarked. B, Habitus, marked. C, Habitus, unmarked. D, Abdominal tergite III with armament of shagreen. E, Anal lobes and postero-lateral comb of abdominal unit 8. Abbreviations: a2–a7, abdominal units (segments) two to seven; al, terminal lobes; tc, thorax; th, thoracic horn (respiratory organ); wg, wing.



**FIGURE 12.** *Rheotanytarsus lacustris* sp. nov. (Chironomidae). Adult male and pupa. Holotype USNM 717577 (A–E). A, Habitus, unmarked. B, Schematic drawing of male genitalia (hypopygium). C, Male genitalia (hypopygium), unmarked. D, Male genitalia (hypopygium), marked. E, Abdominal tergite II with armament of shagreen. Abbreviations: a8–a9, abdominal units (segments) eight and nine; ap, anal point (remnants of tergite X); gc, gonocoxite (II); gs, gonostylus; iv, inferior volsella (lateral protrusion of gonocoxite); mv, median volsella (lateral protrusion of gonocoxite); tb, tergal bands; ts, shagreen of tergites.



part of the body composed of head and thorax, visible as a single globose structure; thorax bears wings and ambulatory appendages (legs) (Figure 11A-C). Ocular segment and post-ocular segments 1–5 (presumably) forming a distinct capsule (head capsule); antennae missing or incomplete on the available specimens; frons of the pupae with a pair of small cephalic tubercles; mouthparts located ventrally, short, ending before attachment of the fore ambulatory appendages (Figure 11A-C). Only three specimens of *Rheotanytarsus lacustris* have well-preserved thoracic horns (USNM 722460, 722479 and 624824). Thoracic horn long (0.6–2.0 mm,  $n = 3$ ), with parallel-sided base, tapering towards the apical end. Thoracic horns smooth, without spikes or setae. Wings reaching beyond the thorax to the abdomen. Legs not preserved in the available specimens (Figure 11A-C).

Abdomen (posterior trunk). Comprised of 10 units, only eight of which are represented as fully developed abdominal segments; units 9 and 10 incorporated into hypopygium. Tergites of abdominal units 2–5 with paired circular patches of spinules at anterior margin (Figure 11D-E). Tergite 2 with a rectangular field of shagreen on posterior margin, split by an area of smooth cuticle medially. Tergites of the units 6–9 without visible armament. Combs at the posterolateral edge of tergite 8 with four strong, wide spurs (Figure 11E). Anal lobes with a dense fringe of setae although setae not preserved per se, rather only their tecae at the edge of the lobe.

**Adult male.** Medium-sized midge, with long legs and long abdomen ending with prominent external genitalia. Wings are lost in the only preserved adult male, Holotype: USNM 717577 (Figure 12A-E). The specimen preserved mostly in dorsolateral aspect. Body length 4.8 mm.

Ocular segment and post-ocular segments 1–5 (presumably) forming distinct capsule (head capsule) (Figure 12A-E). Ocular segment recognizable by pair of large compound eyes. Eyes without micro- or microtrichia, with well-preserved ommatidia. Frons (frontal sclerite) of post-ocular segment 1 impossible to examine as it is embedded in matrix. Labrum and clypeus 240  $\mu\text{m}$  long, rectangular. Post-ocular segment 1 recognizable by its appendages, antennae [antennulae]. Antenna 1200  $\mu\text{m}$  in length, impossible to distinguish the borders between the antennal elements (flagellomeres). Each antenna bears dense plumage of long setae. Post-ocular segment 2 (intercalary segment) without externally recognizable structures. Post-ocular segment 3 bears no recognizable

appendages (mandibles) (Figure 12A-E). Post-ocular segment 4 recognizable by its appendage, maxilla [maxillula]. Maxilla recognizable by maxillary palpi. Maxillary palpus consists of five elements (palpomeres) with palpomeres 1 and 2 hidden behind the labrum; lengths of elements 3 through 5: 140–150  $\mu\text{m}$  ( $n = 2$ ), 200  $\mu\text{m}$  ( $n = 1$ ) and 170  $\mu\text{m}$  ( $n = 1$ ), respectively. Post-ocular segment 5 recognizable by its appendages, forming the labium [conjoined left and right maxillae]. Labium mostly obscured on holotype, with details not visible (Figure 12A). Thorax (Figure 12A) bears three pairs of the ambulatory appendages (fore-, mid- and hindlegs) on the pro-, meso-, and metathorax, respectively. Each leg consists of the following elements (proximal to distal): coxa, trochanter, femur, tibia, tarsomeres 1–5. Wings lost (Figure 12A). Prothorax horseshoe-shaped in frontal view (with arms of ‘horseshoe’ facing ventrally), narrow. Prothorax bears first thoracic appendages (forelegs). Lengths of foreleg elements as follow ( $n = 2$ ): femur 1120–1130  $\mu\text{m}$ , tibia 890–1130  $\mu\text{m}$ , tarsomere 1 1120–1280  $\mu\text{m}$ , tarsomere 2 760–790  $\mu\text{m}$ , tarsomere 3 550–650  $\mu\text{m}$ , tarsomere 4 300–490  $\mu\text{m}$ , and tarsomere 5 410  $\mu\text{m}$  ( $n = 1$ ). Mesothorax with wings poorly preserved, 2.6 mm long, venation not distinguishable. Lengths of midleg elements as follow ( $n = 1$ ): femur 1250  $\mu\text{m}$ , tibia 1040  $\mu\text{m}$ . Other elements have not been preserved. Metathorax bears a pair of ambulatory appendages (hindlegs). Lengths of hindleg elements as follow ( $n = 1$ ): femur 770  $\mu\text{m}$ , tibia 1150  $\mu\text{m}$ , tarsomere 1 700  $\mu\text{m}$ , tarsomere 2 480  $\mu\text{m}$ , tarsomere 3 220  $\mu\text{m}$ , and tarsomere 4 240  $\mu\text{m}$  (Figure 12A).

Abdomen (posterior trunk). Comprised of 10 segments (abdominal units), only eight of which are represented as fully developed abdominal segments; units 9 and 10 incorporated into male genitalia (hypopygium). Abdominal units 1–8 roughly rectangular in shape. Only a few setae, visible in the lateral aspect, preserved on the abdomen (Figure 12A-D). Abdominal unit 9 together with hypopygium forms male copulatory apparatus (Figure 12B-D).

Male genitalia (hypopygium) (male genitalia, appendages of abdominal unit 8 and following units). Unit 9 broadly rounded posteriorly (Figure 12B-D). Unit 10 represented by strong, parallel-sided anal point, with two parallel crests running atop of it. Gonocoxite (2) cylindrical, 220  $\mu\text{m}$  long. Inferior volsella (lateral protrusion of gonocoxite) of the gonocoxite relatively long (230  $\mu\text{m}$ ) and curved outwards, towards gonostylus. Medium volsella is



visible as a short stump at the base of the gonocoxite. Gonocoxite and gonostylus without a flexible articulation, conjoined (Figure 12B-D). Gonostylus narrow, curved, with blunt, rounded, distal end, 230  $\mu\text{m}$  long (Figure 12B-D).

**Remarks.** Pupa and adult of the new species are directly associated with each other on the slab with the holotype, where the adult male can be seen eclosing from the pupal exuviae. The adult male of this morphotype is a representative of Chironomidae based on the following combination of characters: overall similar habitus, body slender, antennae with > 6 elongate elements (flagellomeres), second element of antennae (pedicellus) conspicuously larger than the rest of antennal elements, antennae with strong plumage, ocelli absent, head without functional mouthparts, thorax without distinct pre-halter lobe at the base of the true halter, scutum without distinct V-shaped suture, tarsomere 1 on all (preserved) legs is considerably longer than tarsomere 2, tergite of abdominal unit 1 without fringe of strong lateral setae (Marshall et al., 2017). Within Chironomidae, this morphotype is a representative of the ingroup Chironominae, due to the following combination of characters: gonostylus and gonocoxite are conjoined rigidly, no articulation visible (Wiederholm, 1989). While the specimen lacks wings, and therefore crucial diagnostic characters are missing, we can assume that this midge is a representative of Tanytarsini. This assumption is based on prominent oval superior and medium volsellae (lateral protrusions of gonocoxite), and anal point with prominent spinules arranged in longitudinal rows (Wiederholm, 1989; Figure 12B). Within the group Tanytarsini, this morphotype is most similar to *Rheotanytarsus* Thienemann and Bause, 1913, based on the following combination of characters: maxillary palpal elements are considerably longer than wide, mid- and hindtibiae with double combs, anal point without rows of spines (Langton and Pinder, 2007).

The new species has a peculiar combination of characters of the male genitalia (hypopygium), such as a gonostylus with a broadly rounded apical end (similar to *R. buculicaudus* Kyerematen and Sæther, 2000) and a very short median volsella (similar to *R. verticillus* Kyerematen, Andersen and Sæther, 2000) and a relatively parallel-sided anal point (similar to *R. pallidus* Kyerematen, Andersen and Sæther, 2000). In general, the combination of the hypopygial characters exhibited by the new species is somewhat reminiscent of *R. barrengaryensis* Cranston, 1997, particularly in terms of the

parallel-sided anal point, and bluntly rounded gonostylus. In contrast to *R. barrengaryensis*, however, the new species has an outwardly bending inferior volsella and a very short medium volsella (Cranston, 1997).

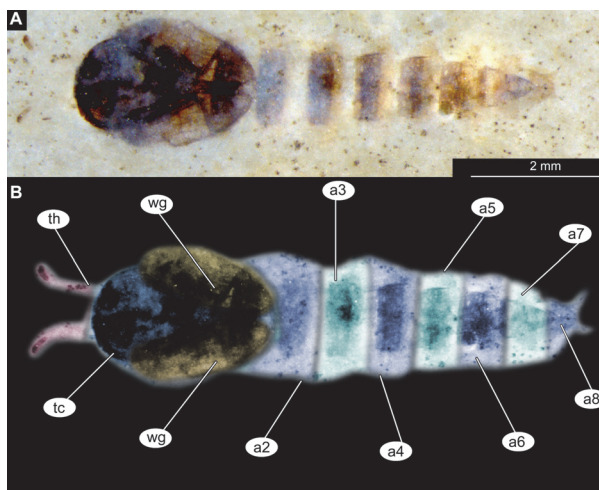
Pupae of the new species are similar to the pupa of *R. barrengaryensis* in the following aspects: thoracic horn bare with a medial bend; tergites of abdominal units 2–5 with circular anterior patches of spinules; shagreen of the tergite 2 medially divided by a stretch of smooth cuticle; tergite 6 without anterior patch of spinules; anal lobe with more than 20 setae in fringe (Cranston, 1997; Kyerematen and Sæther, 2000).

Numerous species of *Rheotanytarsus* are known from amber, but differences in amber taphonomy relative to that of the Kishenehn Formation makes them hard to compare to the specimens discussed here (Zakrzewska and Gilka, 2015; Zakrzewska et al., 2020).

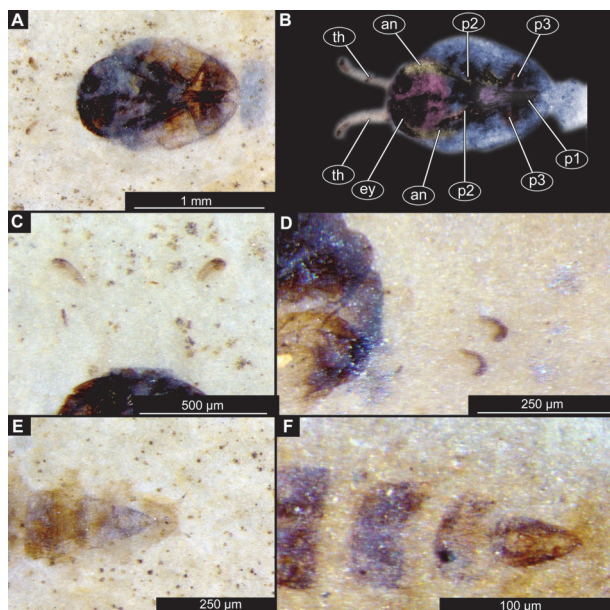
DIPTERA Linnaeus, 1758  
CERATOPOGONIDAE Newmann, 1834  
*ALLUAUDOMYIA* Kieffer, 1913  
cf. *ALLUAUDOMYIA*  
Figures 13A-B, 14A-F

**Material.** This morphotype is represented by numerous early and late pupae (pharate adults) (see list in Table 1).

**Taxonomic attribution.** This morphotype is an ingroup of Ceratopogonidae based on a specific combination of characters: antennae extended posteriorly from the head; maxillary palpus directed



**FIGURE 13.** Representatives of Ceratopogonidae cf. *Alluaudomyia*. Pupa. USNM 623317. A, Habitus, unmarked. B, Habitus, marked. Abbreviations: a2–a8, abdominal units (segments) two to eight; tc, thorax; th, thoracic horn (respiratory organ); wg, wing.



**FIGURE 14.** Representatives of Ceratopogonidae cf. *Alluaudomyia*. Pupa. USNM 623317 (A–B), USNM 623326 (C), USNM 624879 (D–F). A, Thorax, unmarked. B, Thorax, marked. C, Thoracic horns. D, Thoracic horns. E, End of abdomen. F, Male genitalia (hypopygium). Abbreviations: an, antenna; ey, compound eyes; p1, forelegs; p2, midlegs; p3, hindlegs; th, thoracic horn (respiratory organ).

posteriorly; thoracic horns without transverse striation ('undivided'), with two rows of pores; end of the abdomen without articulated terminal paddles, end of abdomen bearing two spine-like protrusions (Figures 13A–B, 14A–F). It is difficult to further interpret the morphotype within Ceratopogonidae due to the poor preservation of the thorax and armament of the abdominal units. Nevertheless, a thoracic horn with two parallel rows of pores (Figure 14C–D) and a slightly bifid distal end indicates that this morphotype is like *Alluaudomyia* Kieffer, 1913 (Art Borkent, pers comm.; Borkent, 2014a).

DIPTERA Linnaeus, 1758

CHAOBORIDAE Edwards, 1912

CHAOBORUS Lichtenstein, 1800

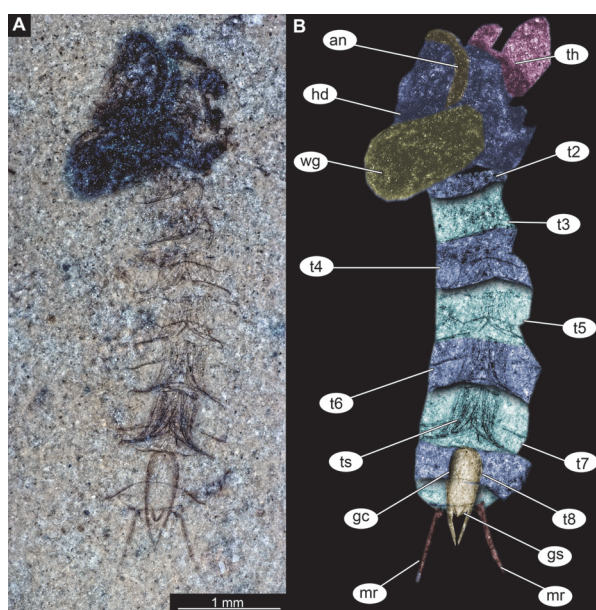
CHAOBORUS KISHENEHNICUS Baranov and Haug sp. nov.

Figures 15A–B, 16A–F, 17A–D, 18A–D, 19A–D, 20A–D, 21A–B, 22A–D

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**Etymology.** The name '*kishenehnicus*', meaning of or pertaining to Kishenehn, refers to the geological formation in which the species was found.

**Diagnosis (based on adult males).** This species is easily distinguished from all other species of *Chaoborus* based on a specific combination of



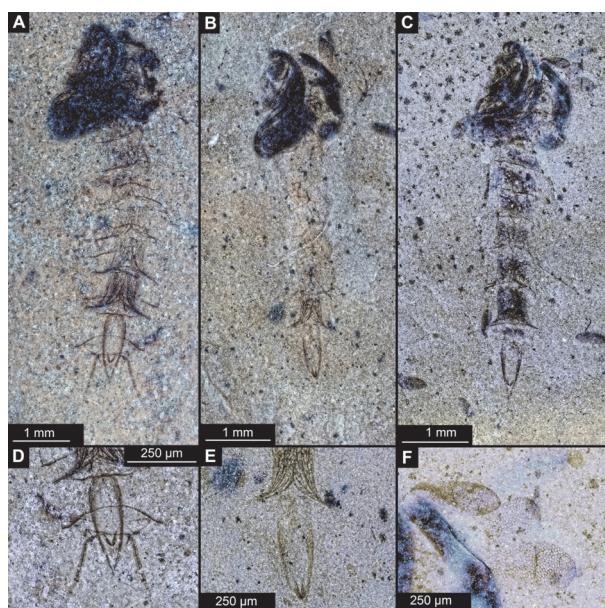
**FIGURE 15.** *Chaoborus kishenehnicus* sp. nov. (Chaoboridae). Pupa. USNM 623080. A, Habitus, unmarked. B, Habitus, marked. Abbreviations: a2–a8, abdominal units (segments) two to eight; an, antenna; gc, gonocoxite; gs, genitalia; mr, medial rib of the anal paddle; p3, hindlegs; pd, pedicellus; th, thoracic horn (respiratory organ); ts, tergal setae; wg, wing.

characters (Figures 15A–B, 16A–F, 17A–D, 18A–E, 19A–D, 20A–D, 21A–B, 22A–D): adult male without lobe or paired, strong setae on the inner surface of the apical part of the gonocoxite; pulvilli absent or very minute, and thus invisible in the fossil specimens; legs with at least the proximal part of the femur much lighter than the rest of the leg (Figures 18A–E, 19A–E, 20A–D).

**Type material.** Holotype: USNM 626053, adult male; paratypes: USNM 623065, USNM 717303; adult female USNM 624863; USNM 595142 (pupa). Additional material consisting of 140 adult or pharate males and pupae and seven females are listed in Appendix Table 1.

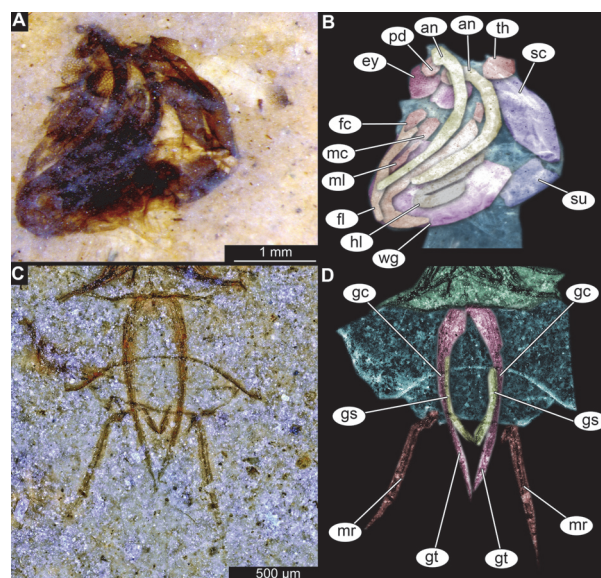
**Pupa.** Habitus. Medium-sized, with flattened, comma-shaped body (in lateral aspect). Body length 2.6–3.9 mm ( $n = 28$ ); abdomen length 1.9–3.1 mm ( $n = 28$ ); length of thorax 0.8–1.3 mm ( $n = 28$ ), body differentiated into presumably 20 segments, ocular segment plus 19 post-ocular segments (Figures 15A–B, 16A–F, 17A–D); anterior part of the body composed of head and thorax, visible as a single globose structure; thorax bears wings and ambulatory appendages (legs) (Figures 15A–B, 16A–F, 17–D); ocular segment and post-ocular segments 1–5 (presumably) forming a distinct capsule (head capsule); mouthparts located ventrally and short, ending before attachment of the first





**FIGURE 16.** *Chaoborus kishenehnicus* sp. nov. (Chaoboridae). Pupa. USNM 623080(A, D), USNM 624863 (B, E), USNM 623356 (C, F). A–C, Habitus, unmarked. D–E, Genitals. F, Thoracic horn (respiratory organs).

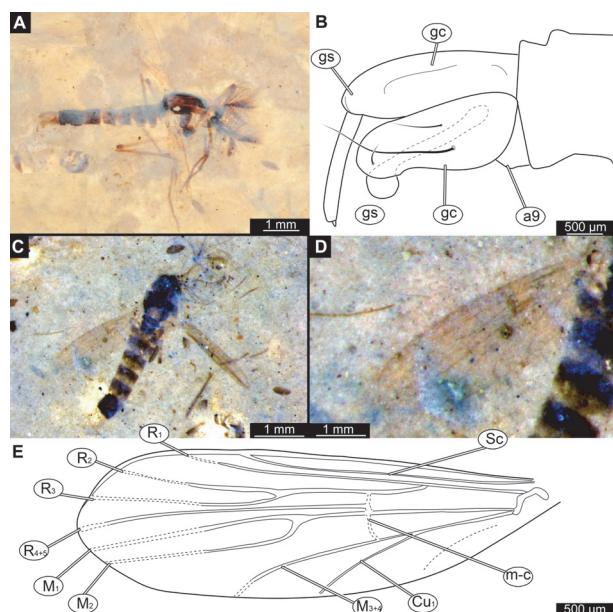
ambulatory appendages (forelegs) (Figures 15A-B, 16A-F, 17A-D). Ocular segment recognizable by its appendage derivative, clypeo-labral complex, and a pair of large compound eyes. Labrum and clypeus are present, but their shape is obscured by deformation of the specimens, since most of the pupae are preserved in lateral aspect (Figures 15A-B, 16A-F, 17A-D). Post-ocular segment 1 recognizable by its appendages, antennae (antennulae). Antennae curved around the head, ending beneath the head, at about mid-length to 0.8 of the length of the wings. Antennae attached to the massive, rounded pedicellus (antennal element 2) (Figure 16A-B). Post-ocular segment 2 (intercalary segment) without externally recognizable structures. Post-ocular segment 3 bears no recognizable appendages (mandibles) (Figure 16A-B). Post-ocular segment 4 recognizable by its appendage, maxilla [maxillula]. Maxilla recognizable by maxillary palpus. Palpi are poorly preserved on the available specimens. Post-ocular segment 5 is recognizable by its appendages, forming the labium [conjoined left and right maxillae]. Labium mostly obscured on all specimens, with no details visible (Figure 16A-B). Thorax bears three pairs of ambulatory appendages (fore-, mid- and hindlegs) on the pro-, meso-, and metathorax, respectively. Thoracic segments forming a single semi-globose structure, closely enveloping the head of the pupa. Ambulatory appendages of the thorax folded



**FIGURE 17.** *Chaoborus kishenehnicus* sp. nov. (Chaoboridae). Pupa. USNM 595142. A, Thorax, unmarked. B, Thorax, marked. C, Male genitalia (hypopygium) unmarked. D, Male genitalia (hypopygium), marked. Abbreviations: an, antenna; ey, compound eyes; fc, forecoxa; gc, gonocoxite; gs, genitals; mc, midcoxa; mr, medial rib of the anal paddle; p1, forelegs; p2, midlegs; p3, hindlegs; pd, pedicellus; sc, scutum; su, scutellum; th, thoracic horn (respiratory organ); wg, wing.

around and under the wings (Figure 15A-B). Prothorax bears thoracic horns (modified first spiracle). Thoracic horns spindle-shaped, widest at mid-length, tapering apically into a short tube (300–650 µm,  $n = 13$ ) (Figures 16A-B, 17A-B). Thoracic horn with a honeycomb-shaped surface texture and small apical opening (Figures 16A-B, 17A-B). Prothorax bears first thoracic appendages (forelegs). Forelegs running posteriorly, upwards anteriorly to the upper edge of the eye and then downward to the apical edge of the wing (Figure 17B). Mesothorax bears a pair of wings and a pair of ambulatory appendages (midlegs). Midlegs situated medially to foreleg. Midlegs are also looping around the wing, distal part of the loop lying on the abdomen, beyond the distal end of the wing. Distal parts of the midlegs loop again under the wing (Figures 15A-B, 16A-F). Metathorax bears a pair of ambulatory appendages (hindlegs); halteres not visible in the fossils. Hindlegs almost entirely hidden behind the coxae of the fore- and midlegs and wings (Figure 17A-B).

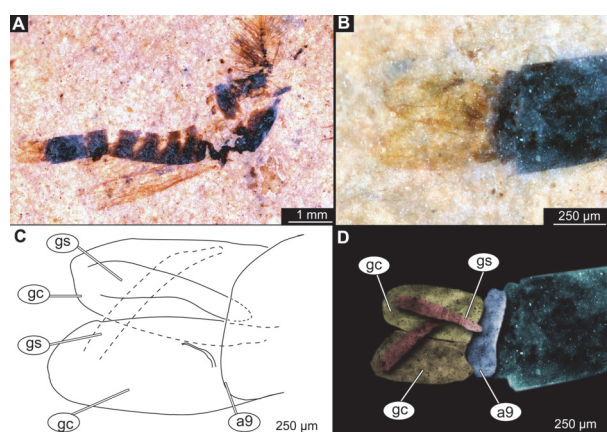
Abdomen (posterior trunk). Abdominal units 1–8 with setae of the pharate adult tergites visible through the pupal cuticle. Setae radiating from the abdominal midline, outwards, forming pointed



**FIGURE 18.** *Chaoborus kishenehnicus* sp. nov. (Chaoboridae). Adult males. Holotype: USNM 626053 (A–B) and paratype USNM 623065 (C–E). A, C, Habitus, unmarked. B, Schematic drawing of the male genitalia (hypopygium). D, Wing. E, Wing, schematic drawing. Abbreviations: Cu1, cubital vein one; gc, gonocoxite (II); gs, gonostylus; M<sub>1</sub>–M<sub>3+4</sub>, median veins one through three+four; m-cu, crossvein median-cubital; R<sub>1</sub>–R<sub>4+5</sub>, radial veins one through four+five; Sc, subcostal vein; a9, abdominal unit IX.

ends, at the dorso-posterior part of each abdominal unit (Figures 15A–B, 16D–E, 17C–D). Trunk end (abdominal unit 9 plus remnants of abdominal unit 10) bears genitalia and remnants of two anal lobes (paddles). Anal lobes of all studied specimens consist only of a single, medial rib, membranous parts of the terminal paddles and rest of the ribs seem to have been lost. Genitalia (appendages of abdominal unit 8) present as well as a tight cluster of gonocoxal setae (Figures 16D–E, 17C–D).

**Adult male.** Medium-sized fly with midge-shaped body, long legs, and long abdomen ending with prominent external genitalia. Wings are relatively well preserved in Holotype. USNM 626053 and paratype USNM 623065 males (Figures 18A–E, 19A–D). Wings with poorer preservation are relatively frequent in the available material. The specimens are preserved mostly in dorsolateral aspect, but some midges are preserved in mostly lateral aspect (Figures 18A–E, 19A–D). This orientation gave us the opportunity to examine different characters. Ocular segment and post-ocular segments 1–5 (presumably) forming distinct capsule (Figures 18A, C, 19A). Ocular segment recognizable by a



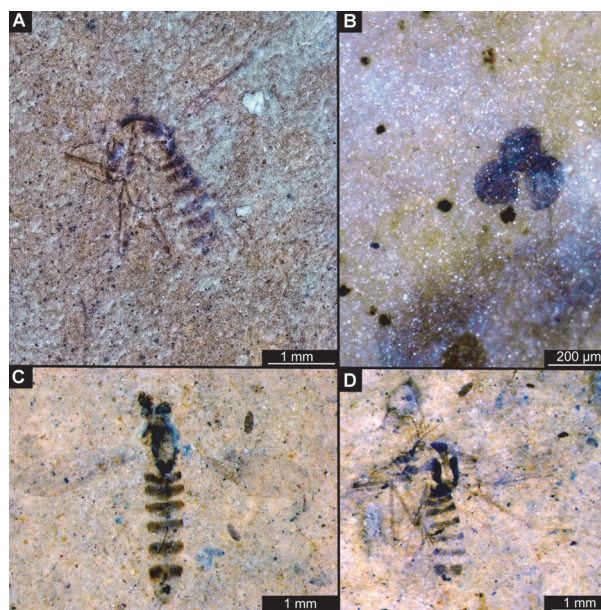
**FIGURE 19.** *Chaoborus kishenehnicus* sp. nov. (Chaoboridae). Adult males. Paratype, USNM 717303. A, Habitus. B, Male genitalia (hypopygium), unmarked. C, Schematic drawing of the male genitalia (hypopygium). D, Male genitalia (hypopygium), marked. Abbreviations: gc, gonocoxite (II); gs, gonostylus; a9, abdominal unit IX.

pair of large compound eyes. Eyes without micro- or macrotrichia, with long, wedge-shaped dorso-medial extension (six ommatidia long and four ommatidia across). Eyes well preserved with individual ommatidia visible (Figure 18A, C), Frons (frontal sclerite) of post-ocular segment one impossible to examine as it is embedded in the matrix. Labrum rectangular, longer than wide, as evident from observation of specimens USNM 622981 and USNM 624754 (labrum 176–276  $\mu\text{m}$  long). Post-ocular segment 1 recognizable by its appendages, antennae (antennulae). Each antenna with two proximal elements (scape and pedicellus) and 13 additional elements (flagellomeres). Pedicellus donut-shaped (squashed sphere with invagination on the top), 130–240  $\mu\text{m}$  in diameter ( $n = 5$ ). Flagellomeres widest at mid-length, tapering apically (Figures 18A, C, 19A). Each flagellomere with a whorl of setae at its ‘equator’ (Figures 18A, C, 19A). Each whorl contains at least 12 setae. Lengths of individual elements of the antenna as follow ( $n = 3$ ): first flagellomere 35–88  $\mu\text{m}$ , second 26–68  $\mu\text{m}$ , third 27–74  $\mu\text{m}$ , fourth 26–70  $\mu\text{m}$ , fifth 39–65  $\mu\text{m}$ , sixth 29–63  $\mu\text{m}$ , seventh 43–77  $\mu\text{m}$ , eighth 47–77  $\mu\text{m}$ , ninth 40–66  $\mu\text{m}$ , tenth 45–61  $\mu\text{m}$ , eleventh 56–91  $\mu\text{m}$ , twelfth 57  $\mu\text{m}$  ( $n = 1$ ), two specimens (USNM 626083, USNM 624754) with flagellomere 13 preserved, but the border between it and flagellomere 12 is unclear, length of two flagellomeres together 192–317  $\mu\text{m}$  (Figures 18A, C, 19A). Post-ocular segment 2 (intercalary segment) without externally recognizable structures. Post-ocular segment 3 bears no recognizable append-



ages (mandibles) (Figures 18A, C, 19A). Post-ocular segment 4 recognizable by its appendage, maxilla [maxillula]. Maxilla recognizable by maxillary palpi. Maxillary palpus consists of five elements (palpomeres), with palpomeres 1 and 2 hidden behind the labrum and clypeus; lengths of elements 3 through 5 ( $n = 2$ ): 123–146  $\mu\text{m}$ , 113–167  $\mu\text{m}$  and 116–125  $\mu\text{m}$ , respectively. Post-ocular segment 5 recognizable by its appendages, forming the labium [conjoined left and right maxillae]. Labium mostly obscured on all specimens, no details visible (Figures 18A, C, 19A). Thorax (Figures 18A, C, 19A) bears three pairs of the ambulatory appendages (fore-, mid-, and hindlegs) on the pro-, meso-, and metathorax, respectively. Each leg consists of the following elements (proximal to distal): coxa, trochanter, femur, tibia, tarsomeres 1–5. Prothorax horseshoe-shaped in lateral view (with arms of ‘horseshoe’ facing ventrally), narrow. Prothorax bears the first pair of thoracic appendages (forelegs). Lengths of foreleg elements as follow: femur 550–860  $\mu\text{m}$  ( $n = 3$ ), tibia 930–1240  $\mu\text{m}$  ( $n = 4$ ), tarsomere 300–440  $\mu\text{m}$  ( $n = 3$ ), tarsomere 2 175–345  $\mu\text{m}$  ( $n = 3$ ), tarsomere 3 140–230  $\mu\text{m}$  ( $n = 3$ ), tarsomere 4 280  $\mu\text{m}$  ( $n = 1$ ), tarsomere 5 370  $\mu\text{m}$  ( $n = 1$ ) (Figures 18A, C, 19A). Mesothorax of several specimens have wings relatively well preserved, but complete venation was only preserved in specimen USNM 623065. Even for this specimen, it is impossible to trace where exactly the vein reaches the edge of the wing (Figure 18D, E). Wing length (tip to arculus) 1.7–2.5 mm ( $n = 13$ ). Radial 1 vein is long, terminating closer to radial 2 vein than to the subcostal vein (Figure 18D, E).  $R_4 + 5$  ending at the level with  $M_1$  and  $M_2$ .  $Cu_1$  is slightly bent at the distal third. Crossveins barely visible.

Lengths of midleg elements as follows: femur 740–1280  $\mu\text{m}$  ( $n = 3$ ), tibia 730–1220  $\mu\text{m}$  ( $n = 3$ ), tarsomere 1 400–460  $\mu\text{m}$  ( $n = 2$ ), tarsomere 2 350  $\mu\text{m}$  ( $n = 1$ ). Other elements have not been preserved in any of the available specimens (Figures 18A, C, 19A). Metathorax bears a pair of altered wings (halteres) and a pair of ambulatory appendages (hindlegs). Lengths of hindleg elements as follow: femur 550–860  $\mu\text{m}$  ( $n = 3$ ), tibia 930–1240  $\mu\text{m}$  ( $n = 4$ ), tarsomere 1 300–440  $\mu\text{m}$  ( $n = 3$ ), tarsomere 2 175–345  $\mu\text{m}$  ( $n = 3$ ), tarsomere 3 140–230  $\mu\text{m}$  ( $n = 3$ ), tarsomere 4 280  $\mu\text{m}$  ( $n = 1$ ), tarsomere 5 370  $\mu\text{m}$  ( $n = 1$ ). Posterior trunk consisted of 10 units, only eight of which are represented as fully developed abdominal segments; units 9 and 10 incorporated into hypopygium. Abdominal units 1–8 roughly rectangular in shape. No setae pre-



**FIGURE 20.** *Chaoborus kishenehnicus* sp. nov. (Chaoboridae). Probably associated females. USNM 624863 (A, B), USNM 623071 (C), USNM 717284 (D). A, C, D, Habitus. B, Spermathecae.

served on a specimen (Figures 18B, 19B-D). Abdominal unit 9 together with hypopygial structures, forming a male copulatory apparatus.

Male genitalia (hypopygium) (appendages of abdominal unit 9 and following units). Unit 9 broadly rounded posteriorly, trapezoidal in shape (Figures 18B, 19B-D). Gonocoxite (2) cylindrical 320–450  $\mu\text{m}$  long. Phalopodemes can be seen impressed on unit 9 (Figures 18B, 19B-D). Gonocoxite and gonostylus with a mobile articulation (Figures 18B, 19B-D). No penis valve preserved. Gonostylus narrow, parallel-sided, with pointed, narrow, distal end, 230–315  $\mu\text{m}$  long (Figures 18B, 19B-D).

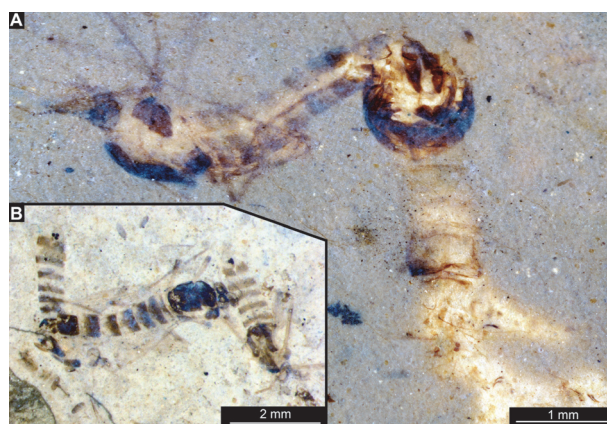
**Adult female (probable association).** Medium-sized fly, with midge-shaped body, long legs and long abdomen ending with a prominent cercus. Body length 2.5–3.5 mm ( $n = 5$ ). Wings with poorer preservation are relatively frequent in the available material. The specimens are preserved mostly in dorsolateral aspect, but some midges are preserved in mostly lateral aspect (Figure 20A-D).

Ocular segment and post-ocular segments 1–5 (presumably) forming distinct head capsule (Figure 20A-D). Ocular segment recognizable by pair of large compound eyes. Eyes without micro- or macrotrichia, with long, wedge-shaped dorsomedial extension (6 ommatidia long and 4 ommatidia across). Eyes well preserved with individual ommatidia structure visible (Figure 20A, C-D). Post-ocu-

lar segment 1 recognizable by its appendages, antennae [antennulae]. Each antenna with one proximal element (pedicellus) and 11 additional elements (flagellomeres) still visible. Pedicellus around 50–70  $\mu\text{m}$  in diameter ( $n = 2$ ), while flagellomeres are widest at mid-length, tapering apically. Lengths of individual elements of the antenna are as follow ( $n = 4$ ): first flagellomere 35–70  $\mu\text{m}$ , second 30–55  $\mu\text{m}$ , third 45–70  $\mu\text{m}$ , fourth 50–65  $\mu\text{m}$ , fifth 40–50  $\mu\text{m}$ , sixth 45–60  $\mu\text{m}$ , seventh 40–65  $\mu\text{m}$ , eighth 50–65  $\mu\text{m}$ , ninth 45–86  $\mu\text{m}$ , tenth 87–190  $\mu\text{m}$ , eleventh 115–125  $\mu\text{m}$  ( $n = 2$ ). Labrum rectangular, longer than wide, 220–240  $\mu\text{m}$  long ( $n = 2$ ). Post-ocular segment 2 (intercalary segment) without externally recognizable structures. Post-ocular segment 3 bears no recognizable appendages (mandibles) (Figure 20A). Post-ocular segment 4 recognizable by its appendage, maxilla [maxillula]. Maxilla recognizable by maxillary palpi. Maxillary palpus consists of five elements (palpomeres), with palpomeres 1 and 2 hidden behind the labrum and clypeus; lengths of elements three through five ( $n = 1$ ): 145  $\mu\text{m}$ , 160  $\mu\text{m}$ , and 160  $\mu\text{m}$ , respectively. Post-ocular segment 5 recognizable by its appendages, forming the labium [conjoined left and right maxillae]. Labium mostly obscured on all specimens, no details visible.

Thorax (Figure 20A, C-D) bears three pairs of the ambulatory appendages (fore-, mid-, and hindlegs) on the pro-, meso-, and metathorax, respectively. Each leg consists of the following elements (proximal to distal): coxa, trochanter, femur, tibia, tarsomeres 1–5. None of the females have well-preserved legs fit for proper measurements. Prothorax horseshoe-shaped (with arms of ‘horseshoe’ facing ventrally), narrow, bears first pair of thoracic appendages (forelegs). Mesothorax of several specimens have wings relatively well preserved but complete venation is not visible on any of them. Wing length (tip to arculus) 2.0–2.7 mm ( $n = 7$ ). Metathorax bears a pair of altered wings (halteres, both well visible) and a pair of ambulatory appendages (hindlegs).

Posterior trunk consists of 10 segments (abdominal units), only nine of which are represented as fully developed abdominal segments. Abdominal units 1–8 roughly rectangular in shape (Figure 20A). Abdominal units 9 and 10 are reduced, forming the copulatory apparatus of the female. Paired cerci attached to the end of abdomen, but they are poorly or not at all preserved in most of the available specimens. Most complete cerci can be seen in specimen USNM 623071. A triple spermatheca, situated within abdominal unit

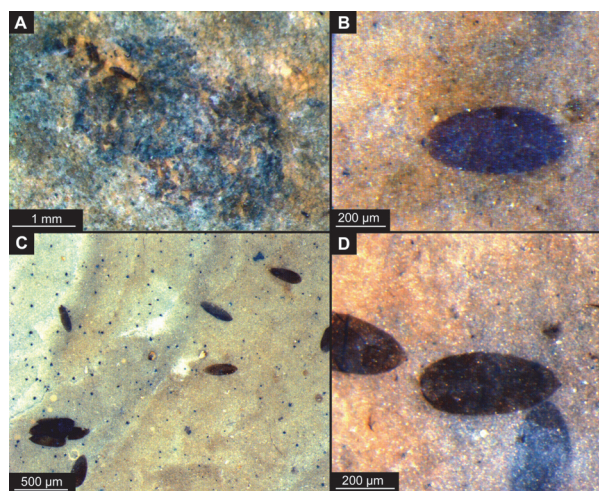


**FIGURE 21.** *Chaoborus kishenehnicus* sp. nov. (Chaoboridae). A, Adult male eclosing from the pupa (USNM622875). B, Male and probably associated female side-by-side, with additional female present (USNM623038).

8, well visible in many specimens through the outer cuticle due to its strong sclerotization (Figures 20B, 21A-B).

**Egg clutches (probable association).** We have found a number of the fossilized structures resembling euarthropodan eggs (Figure 22A-D). Large clusters of such eggs are arranged in a spiral pattern, characteristic for the eggs of extant representatives of *Chaoborus* (Strickman, 1980). Therefore, we hypothesize that these fossils might represent egg clutches of *C. kishenehnicus* sp. nov.

**Remarks.** We interpret this new species as an ingroup of Chaoboridae based on a specific combination of characters. Pupa: end of abdomen with a



**FIGURE 22.** *Chaoborus kishenehnicus* sp. nov. Probably associated egg masses and individual eggs. A, USNM 623795, egg mass. B, USNM 624281, egg. C, USNM 624174, eggs. D, USNM 624230, eggs.



pair of large, articulated paddles, supported by a sclerotized area of cuticle, called the medial rib; mouthparts short, not reaching beyond coxae of anterior legs; bundles of the diagonally oriented setae visible on the tergites of the abdominal units (Borkent, 2012). Adult male: with radial 1 vein long, terminating closer to radial 2 vein, longer than to the subcostal vein. Pupae associated with the adults by the genitalia of the pharate specimens visible via the pupal cuticle (Figures 15-17) and by the direct association of the eclosing male with the pupa (Figure 21A). Pupae associated with the adults are mostly well preserved, but are always missing some crucial characters, most notably the mesal and lateral longitudinal ribs of the terminal paddle. Therefore, pupae cannot be used for a differential diagnosis. Pupae can be associated with adult males by the virtue of genitalia of pharate males' genitalia. Adult females are poorly preserved, but wing venation similar to that of males, can indicate that they are also representatives of *C. kishenehnicus* sp. nov. (Figure 21B).

Within Chaoboridae, the new species is an ingroup of *Chaoborus*, based on a specific combination of characters (listed separately for each life stage). Pupa: with spindle-shaped thoracic horns, more than three times longer than wide, terminal paddles with prominent median rib almost reaching the edge of the lobe. It is notable that pupae have their terminal paddles only partially preserved, with most of the ribs and membrane absent from all available specimens. This type of preservation is apparently common in pupae of the fossil pupae of *Chaoborus*, as it is also the common type of anal paddle preservation in the Oligocene *Chaoborus tertarius* von Heyden, 1862 (Borkent, 1978; 1A-C, 2A-C). *Chaoborus kishenehnicus* is the second formal record of a fossil species of Chaoboridae in the United States, after the record of *Chaoborus* pupae from the Middle Eocene Tallahatta Formation (Johnston and Borkent, 1998; Borkent, 2014b).

This new species is highly reminiscent of many modern representatives of *Chaoborus* (Cook, 1956). The lack of crucial characters, such as well-preserved pulvilli or coloration, does not allow the identification of the new species as a representative of any of the ingroups of *Chaoborus* ('subgenera') (Cook, 1956; Sæther, 1970).

DIPTERA Linnaeus, 1758  
 CULICIDAE Meigen, 1818  
 CULICINAE Meigen, 1818  
 CULICINI Meigen, 1818  
 CULEX Linnaeus, 1758

## NEOCULEX Dyar, 1905

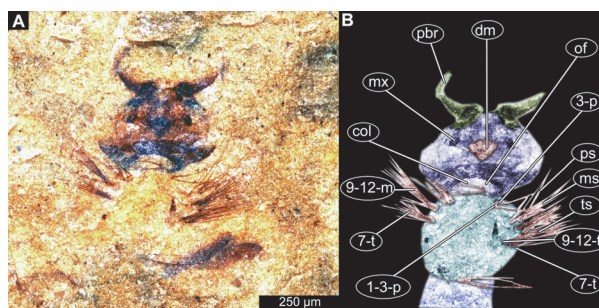
### Figure 23A-B

**Material.** This morphotype is represented by a single, partial fossil of a larva (USNM 623914) (Figure 23A-B). The fossil consists of the head, thorax, and remnants of abdominal units 1 and 2.

**Larva.** Head: broader than long; antennae and setae missing; mouthbrushes (palatal brushes) distinct, dense; dorsomentum and maxillae visible but not sharply defined; collar weakly developed, circular. Thorax: pro-, meso- and metathoracic segments clearly demarked by pleural setal groups, setae of prothorax and lateral setae of meso- and metathorax are well preserved.

**Taxonomic attribution.** The larva is a representative of Culicidae based on a specific combination of visible characters: head capsule well-developed, with prominent mouthbrushes (palatal brushes), maxillae borne on transverse margin of the head capsule lateral to the dorsomentum; head, thorax, and first abdominal unit not conjoined, thorax bulbous and wider than the head and abdomen, lateral clusters of the long setae present on the thorax and abdominal units (Harbach, 2007; Borkent and Sinclair, 2017).

Within Culicidae, this morphotype is most similar to extant species of the group *Neoculex* Dyar, 1905. The most important character supporting this interpretation is the very short seta 3-P in the cluster of setae 1-3-P on the prothorax. Adults of the related group *Culiseta* are known from the Kishenehn Formation (Harbach and Greenwalt, 2012), but setae 1-3-P are equally long in extant species of that group. Short setae 3-P also occur in most extant species of the groups *Aedinus* Lutz, 1904 [in



**FIGURE 23.** Head and thorax of a larval representative of *Culex* (*Neoculex*) (Culicidae), specimen USNM 623914. A, Habitus, unmarked. B, Habitus, marked. Abbreviations: Col, collar; Dm, dorsomentum; MS, mesothoracic setae; Mx, maxilla; OF, occipital foramen; IPBr, palatal brush; PS, prothoracic setae; TS, metathoracic setae; 1-3-P, setal group 1-3-P; 3-P, seta 3-P; 7-T, seta 7-T; 9-12-M, setae 9-12-M (mesothoracic pleural setal group).

Lutz and Bouroull, 1904], *Anoedioporpa* Dyar, 1923, *Belkinomyia* Adames and Galindo, 1973, *Carrollia* Lutz, 1905, *Melanoconion* Theobald, 1903, *Micraedes* Coquillett, 1906, *Microculex* Theobald, 1907, and *Tinolestes* Coquillett, 1906. However, the representatives of those ingroups, except for a few species that extend into subtropical areas, are confined to the Neotropical Region. *Neoculex* is predominantly an Old-World group, but several extant species occur in the Nearctic Region.

Larvae of most extant representatives of *Neoculex* inhabit shallow vegetated areas of permanent and temporary bodies of groundwater, but some species have been found in rock holes, crab holes, tree holes, bamboo internodes and artificial containers. Adult females are known to feed on frogs, birds and river rats (Belkin, 1962; Becker et al., 2010).

## DISCUSSION

### Taxonomic Diversity of the Group Culicomorpha in the Kishenehn Formation

Culicomorphan flies represent most fossils in the Kishenehn Formation. In particular, Greenwalt et al. (2014) have stated that in the unbiased collection of the Kishenehn material, fossils initially thought to be representatives of Chironomidae make up 50.5% of all insect fossils. Upon closer examination of the available material, it became clear that about 50% of these supposed fossils of Chironomidae are representatives of a single species of phantom midges (Chaoboridae), here named *Chaoborus kishenehnicus* sp. nov., or pupae of a biting midge (Ceratopogonidae) of the group *Alluaudomyia*. In total, we here examined 428 specimens of the culicomorphans from the formation. Among these, 113 specimens (26%) were pupae of Ceratopogonidae (*Alluaudomyia* sp.), 140 (33%) of the specimens were representatives of Chaoboridae (*C. kishenehnicus* sp. nov.), 175 (41%) were representatives of Chironomidae, and one specimen (0.2%) was a larval representative of Culicidae.

This subsample of representatives of Culicomorpha from the formation is not strictly representative, as we have pre-selected the studied specimens based on the quality of their preservation. These preliminary data do, however, reflect prevalence of representatives of Ceratopogonidae, Chaoboridae and Chironomidae in the fossil fauna of the formation.

In total, there are now 14 morphotypes of the culicomorphans recorded from the formation (Harbach and Greenwalt, 2012; Greenwalt and Moulton, 2016; Greenwalt et al., 2019; data herein). Nine of these morphotypes represent formally described species. Among the latter are two species of Culicidae, four of Dixidae, two of Chironomidae and a single species of Chaoboridae (Harbach and Greenwalt, 2012; Greenwalt and Moulton, 2016; Greenwalt et al., 2019; data herein). In general, the species diversity of Culicomorpha in the formation is relatively low, which, in combination with their high abundance, provides us with additional information on the palaeoenvironment of the formation.

### Palaeoecological Implications of the Culicomorphan Diversity in the Kishenehn Formation

We have attempted to use the diversity of the fossil culicomorphans in the Kishenehn Formation to better understand the palaeoecology of this deposit. We have used both insights on the taphonomy of culicomorphans and extrapolated autecology of the individual morphotypes. The formation is relatively young (Middle Eocene) and the majority of the recorded culicomorphan morphotypes closely resemble their modern relatives. Therefore, we think it is feasible to extrapolate the autecology of these morphotypes based on their extant relatives (Grund, 2006; Stebner et al., 2017).

The majority of the recorded culicomorphan morphotypes have extant relatives associated with open lake habitats. Extant species of *Chaoborus* often inhabit ponds and lakes, often fishless or with a low-density of fishes (Sæther, 1997). *Rheotanytarsus*, *Tanytarsus*, *Conchapelopia*, and *Psectroanypus* all contain large numbers of extant species, with diverse autecologies, but all of them have at least some representatives that inhabit lacustrine habitats (Langton, 1991). Extant representatives of *Alluaudomyia* (biting midges) inhabit a wide variety of habitats, often stagnant waters (Borkent, 2014a). Likewise, extant representatives of Culicidae occupy a spectrum of aquatic environments, and most of them feed on suspended particulate matter and microorganisms, which they extract from the water with filamentous mouth brushes (Belkin, 1962).

In the case of *Hintelmanniella noncatafractata* sp. nov., it is impossible to extrapolate its ecology from extant relatives, as the new species seems to be rather different from all extant species of Chironomini (Wiederholm, 1989; Cranston, 1999).



Nevertheless, the rather unusual combination of the morphological characters of the adult males of the species indicates that they might have been surface-skimmers, as are a number of extant representatives of Chironomidae (Qi et al., 2018). Prominent characters of *H. noncatafractata* that point towards a surface skimming lifestyle include shortened antennae, robust and widened legs (especially femora) and relatively short wings. These traits are conducive to skimming on the water surface, utilising surface tension, and wind to glide along the water surface (Armitage et al., 1995). Most of the surface-skimming representatives of Chironomidae inhabit marine environments, but other surface-skimming insects, such as water bugs (Gerridae), Mayflies (Ephemeroptera), stoneflies (Plecoptera) (Marden and Thomas, 2003), and possibly also the representatives of the extinct group Chresmodidae are (or were) inhabiting open freshwater habitats (Dong et al., 2010). Additionally, some of the glacier and snow dwelling non-biting midges like numerous representatives of Diamesinae (Gilka, Soszyńska-Maj and Paasivirta, 2013), Orthocladiinae (Epler, 2012) and some of Podonominae (Serra-Tosio and Brundin, 1990), do have brachypterous conditions of the wings and similar legs. However, we think that presence of this ecomorphotype in the Kish-

enehn Formation is unlikely due to what we know about the palaeoecology of the deposit (Greenwalt et al., 2013).

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## APPENDIX

List of the specimens examined in the paper.

USNM Number	Taxon	USNM Number	Taxon
USNM 543764	<i>Conchapelopia</i>	USNM 621239	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 553523	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621240	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 595142	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621245	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 595142	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621252	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 619945	cf. <i>Stilobezzia</i>	USNM 621272	cf. <i>Stilobezzia</i>
USNM 619945	cf. <i>Stilobezzia</i>	USNM 621273	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620003	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621308	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620010	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621340	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620056	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621340	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620056	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621354	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620057	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621371	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620086	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621387	<i>Conchapelopia</i>
USNM 620093	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621395	<i>Conchapelopia</i>
USNM 620245	<i>Hintelmanniella noncatafractata</i> sp. nov.	USNM 621398	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620309	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621466	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620368	<i>Conchapelopia</i>	USNM 621479	<i>Conchapelopia</i>
USNM 620385	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621483	cf. <i>Stilobezzia</i>
USNM 620404	Chironominae larvae?	USNM 621483	cf. <i>Stilobezzia</i>
USNM 620470	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621509	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620534	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621526	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620560	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621538	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620770	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621580	<i>Conchapelopia</i>
USNM 620791	<i>Conchapelopia</i>	USNM 621582	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620865	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621592	<i>Conchapelopia</i>
USNM 620922	<i>Conchapelopia</i>	USNM 621661	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620922	<i>Conchapelopia</i>	USNM 621661	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620924	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621718	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 620960	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621753	<i>Conchapelopia</i>
USNM 620960	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621798	cf. <i>Stilobezzia</i>
USNM 620992	<i>Conchapelopia</i>	USNM 621836	cf. <i>Stilobezzia</i>
USNM 621036	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621869	<i>Conchapelopia</i>
USNM 621036	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621902	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 621041	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 621922	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 621057	<i>Conchapelopia</i>	USNM 621985	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 621066	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 622138	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 621066	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 622520	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 621075	<i>Conchapelopia</i>	USNM 622562	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 621089	<i>Conchapelopia</i>	USNM 622589	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 621188	<i>Conchapelopia</i>	USNM 622680	cf. <i>Stilobezzia</i>
USNM 621239	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 622721	<i>Conchapelopia</i>
USNM 621239	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 622737	<i>Conchapelopia</i>

## APPENDIX (continued).

USNM Number	Taxon	USNM Number	Taxon
USNM 622767	Culicomorpha mt2	USNM 623317	cf. <i>Stilobezzia</i>
USNM 622776	cf. <i>Stilobezzia</i>	USNM 623317	cf. <i>Stilobezzia</i>
USNM 622807	<i>Conchapelopia</i>	USNM 623320	cf. <i>Stilobezzia</i>
USNM 622875	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623325	cf. <i>Stilobezzia</i>
USNM 622889	<i>Conchapelopia</i>	USNM 623325	cf. <i>Stilobezzia</i>
USNM 622925	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623326	cf. <i>Stilobezzia</i>
USNM 622927	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623326	cf. <i>Stilobezzia</i>
USNM 622935	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623343	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 622951	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623344	cf. <i>Stilobezzia</i>
USNM 622981	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623346	cf. <i>Stilobezzia</i>
USNM 623003	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623346	cf. <i>Stilobezzia</i>
USNM 623014	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623346	cf. <i>Stilobezzia</i>
USNM 623018	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623350	cf. <i>Stilobezzia</i>
USNM 623028	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623354	cf. <i>Stilobezzia</i>
USNM 623028	<i>Conchapelopia</i>	USNM 623356	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 623038	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623356	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 623039	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623360	cf. <i>Stilobezzia</i>
USNM 623045	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623362	cf. <i>Stilobezzia</i>
USNM 623045	cf. <i>Stilobezzia</i>	USNM 623365	cf. <i>Stilobezzia</i>
USNM 623063	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623365	cf. <i>Stilobezzia</i>
USNM 623065	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623371	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 623066	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623376	cf. <i>Stilobezzia</i>
USNM 623070	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623408	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 623071	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623429	cf. <i>Stilobezzia</i>
USNM 623080	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623445	cf. <i>Stilobezzia</i>
USNM 623080	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623472	cf. <i>Stilobezzia</i>
USNM 623080	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623472	cf. <i>Stilobezzia</i>
USNM 623091	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623474	cf. <i>Stilobezzia</i>
USNM 623094	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623479	cf. <i>Stilobezzia</i>
USNM 623105	cf. <i>Stilobezzia</i>	USNM 623490	cf. <i>Stilobezzia</i>
USNM 623105	cf. <i>Stilobezzia</i>	USNM 623491	cf. <i>Stilobezzia</i>
USNM 623112	cf. <i>Stilobezzia</i>	USNM 623522	cf. <i>Stilobezzia</i>
USNM 623115	<i>Conchapelopia</i>	USNM 623537	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 623116	cf. <i>Stilobezzia</i>	USNM 623538	<i>Conchapelopia</i>
USNM 623116	cf. <i>Stilobezzia</i>	USNM 623538	Tanytopodinae pupa sp.
USNM 623154	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623555	cf. <i>Stilobezzia</i>
USNM 623197	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 623556	cf. <i>Stilobezzia</i>
USNM 623209	cf. <i>Stilobezzia</i>	USNM 623556	cf. <i>Stilobezzia</i>
USNM 623232	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623559	cf. <i>Stilobezzia</i>
USNM 623250	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623561	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 623251	cf. <i>Stilobezzia</i>	USNM 623574	cf. <i>Stilobezzia</i>
USNM 623267	Chironominae larvae?	USNM 623574	cf. <i>Stilobezzia</i>
USNM 623303	cf. <i>Stilobezzia</i>	USNM 623599	Chironomidae sp
USNM 623305	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 623631	<i>Chaoborus kishenehnicus</i> sp. nov.



APPENDIX (continued).

USNM Number	Taxon	USNM Number	Taxon
USNM 623635	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 624802	cf. <i>Stilobezzia</i>
USNM 623669	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 624811	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 623685	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 624823	Culicomorpha mt 2
USNM 623704	Macropelopiini	USNM 624824	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 623820	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 624829	<i>Culicomorpha</i>
USNM 623832	cf. <i>Stilobezzia</i>	USNM 624863	<i>Hintelmanniella noncatafractata</i> sp. nov.
USNM 623895	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 624873	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 623914	Culicidae	USNM 624879	cf. <i>Stilobezzia</i>
USNM 624067	cf. <i>Stilobezzia</i>	USNM 624879	cf. <i>Stilobezzia</i>
USNM 624068	cf. <i>Stilobezzia</i>	USNM 624879	cf. <i>Stilobezzia</i>
USNM 624073	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 624891	cf. <i>Stilobezzia</i>
USNM 624073	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 624894	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624185	cf. <i>Stilobezzia</i>	USNM 624896	cf. <i>Stilobezzia</i>
USNM 624188	<i>Rheotanytarsus</i> sp.	USNM 624898	cf. <i>Stilobezzia</i>
USNM 624241	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 624898	cf. <i>Stilobezzia</i>
USNM 624269	cf. <i>Stilobezzia</i>	USNM 624909	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624277	cf. <i>Stilobezzia</i>	USNM 624917	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624284	Chironominae	USNM 624929	cf. <i>Stilobezzia</i>
USNM 624317	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 624938	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624326	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 624963	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624376	cf. <i>Stilobezzia</i>	USNM 624970	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624380	cf. <i>Stilobezzia</i>	USNM 624982	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624409	Chironominae sp.	USNM 624986	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624415	<i>Hintelmanniella noncatafractata</i> sp. nov.	USNM 625080	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624418	<i>Hintelmanniella noncatafractata</i> sp. nov.	USNM 625099	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 624466	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 625108	cf. <i>Stilobezzia</i>
USNM 624500	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 625108	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624545	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 625114	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624552	cf. <i>Stilobezzia</i>	USNM 625177	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624553	cf. <i>Stilobezzia</i>	USNM 625193	cf. <i>Stilobezzia</i>
USNM 624579	cf. <i>Stilobezzia</i>	USNM 625199	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624644	<i>Hintelmanniella noncatafractata</i> sp. nov.	USNM 625239	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 624657	cf. <i>Stilobezzia</i>	USNM 625395	cf. <i>Stilobezzia</i>
USNM 624658	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 625432	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624665	<i>Hintelmanniella noncatafractata</i> sp. nov.	USNM 625550	cf. <i>Stilobezzia</i>
USNM 624707	cf. <i>Stilobezzia</i>	USNM 625825	cf. <i>Stilobezzia</i>
USNM 624707	cf. <i>Stilobezzia</i>	USNM 625864	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624708	cf. <i>Stilobezzia</i>	USNM 625884	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624708	cf. <i>Stilobezzia</i>	USNM 625889	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624743	cf. <i>Stilobezzia</i>	USNM 626009	<i>Conchapelopia</i>
USNM 624743	cf. <i>Stilobezzia</i>	USNM 626036	<i>Conchapelopia</i>
USNM 624754	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 626053	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 624768	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 626057	<i>Conchapelopia</i>
USNM 624802	cf. <i>Stilobezzia</i>	USNM 626057	<i>Conchapelopia</i>

## APPENDIX (continued).

USNM Number	Taxon	USNM Number	Taxon
USNM 626091	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 717614	cf. <i>Stilobezzia</i>
USNM 626096	<i>Conchapelopia</i>	USNM 717614	cf. <i>Stilobezzia</i>
USNM 626098	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 717642	cf. <i>Stilobezzia</i>
USNM 626121	<i>Conchapelopia</i>	USNM 717642	cf. <i>Stilobezzia</i>
USNM 626155	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 717670	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 626155	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 722238	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 626165	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 722238	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 626284	<i>Culicomorpha pupa</i>	USNM 722238	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 712974	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 722239	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 712977	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 722250	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 712984	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 722252	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717190	<i>Conchapelopia</i>	USNM 722260	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717195	<i>Conchapelopia</i>	USNM 722261	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717238	<i>Conchapelopia</i>	USNM 722261	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717284	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 722263	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717304	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 722263	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717313	<i>Conchapelopia</i>	USNM 722263	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717313	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 722266	<i>Rheotanytarsus lacustris</i> sp. nov.?
USNM 717324	<i>Conchapelopia</i>	USNM 722268	<i>Chaoborus kishenehnicus</i> sp. nov.
USNM 717348	<i>Conchapelopia</i>	USNM 722270	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717368	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 722286	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717406	cf. <i>Stilobezzia</i>	USNM 722286	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717406	cf. <i>Stilobezzia</i>	USNM 722286	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717406	cf. <i>Stilobezzia</i>	USNM 722286	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717423	cf. <i>Stilobezzia</i>	USNM 722288	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717428	<i>Hintelmanniella noncatafractata</i> sp. nov.	USNM 722288	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717431	<i>Hintelmanniella noncatafractata</i> sp. nov.	USNM 722295	<i>Rheotanytarsus lacustris</i> sp. nov.?
USNM 717438	cf. <i>Stilobezzia</i>	USNM 722296	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717438	cf. <i>Stilobezzia</i>	USNM 722297	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717479	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 722297	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717486	cf. <i>Stilobezzia</i>	USNM 722297	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717486	cf. <i>Stilobezzia</i>	USNM 722323	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717509	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 722323	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717518	cf. <i>Stilobezzia</i>	USNM 722335	cf. <i>Stilobezzia</i>
USNM 717534	cf. <i>Stilobezzia</i>	USNM 722352	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717536	cf. <i>Stilobezzia</i> ?	USNM 722353	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717542	cf. <i>Stilobezzia</i>	USNM 722354	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717572	cf. <i>Stilobezzia</i>	USNM 722369	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717577	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 722370	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717591	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 722370	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717592	cf. <i>Stilobezzia</i>	USNM 722371	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717592	cf. <i>Stilobezzia</i>	USNM 722377	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717606	cf. <i>Stilobezzia</i>	USNM 722377	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 717609	cf. <i>Stilobezzia</i>	USNM 722379	<i>Hintelmanniella noncatafractata</i> sp. nov.

APPENDIX (continued).

USNM Number	Taxon	USNM Number	Taxon
USNM 722379	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 722523	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 722397	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 722523	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 722399	Culicomorpha mt 2	USNM 722523	<i>Tanytarsus</i> sp.
USNM 722400	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 722528	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 722401	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 722545	cf. <i>Stilobezzia</i>
USNM 722402	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 722552	cf. <i>Stilobezzia</i>
USNM 722410	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 722556	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 722442	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 722556	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 722453	cf. <i>Stilobezzia</i>	USNM 722556	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 722459	cf. <i>Stilobezzia</i>	USNM 722557	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 722460	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 722557	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 722464	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 722557	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 722465	cf. <i>Stilobezzia</i>	USNM 722557	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 722471	<i>Chaoborus kishenehnicus</i> sp. nov.	USNM 722557	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 722477	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 722560	cf. <i>Stilobezzia</i>
USNM 722479	<i>Rheotanytarsus lacustris</i> sp. nov.	USNM 722561	<i>Rheotanytarsus lacustris</i> sp. nov.
USNM 722521	cf. <i>Stilobezzia</i>	USNM 722568	cf. <i>Stilobezzia</i>