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An unexpectedly abundant new genus of black flies (Diptera, Simuliidae) from Upper Cretaceous Taimyr amber of Ugolyak, with discussion of the early evolution of birds at high latitudes

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Abstract

Ugolyakia kaluginae gen. et sp. nov. is described from Ugolyak (Santonian Taimyr amber), based primarily on its unbranched Rs and developed katepisternal sulcus. It is attributed to the tribe Simuliini, although it lacks calcipala and spiniform seta on the costal vein characteristic of most genera of the tribe. Possession of a claw with a large subbasal tooth and absence of significant sclerotization of the sternites suggest that *U. kaluginae* females were blood-sucking avian parasites. Black flies make up 3% of all insect inclusions and 5% of all identifiable dipterans in Ugolyak amber. Only two Late Cretaceous black fly specimens were previously known: a poorly preserved female

from Yantardakh (Santonian Taimyr amber) and a complete one from Turonian New Jersey amber. Feathers found at nearly all Cretaceous black fly sites (and at all formations with records of Simuliini) were younger than the Hauterivian. Ugolyak black flies are thought to have inhabited the same environments as Cretaceous ornithurine birds and most likely fed on them. These insects can then be used as an indicator of this bird community, allowing a better understanding of the Late Cretaceous forest ecology of Northern Asia. The inferred presence of Ornithuromorpha at high latitudes by the Early Cretaceous implies that their high growth rate may have evolved as an adaptation to a short yearly period of productivity (probably as a compensation for the poor flight ability of their young). This further implies that advanced ornithuromorphs might have originated at higher latitudes; later, aquatic ornithuromorphs occupied niches in lower latitude regions with tropical climates such as the Chinese Jehol biota, to which they were preadapted. The inferred seasonality at higher latitudes during cold spells of the Early Cretaceous could further be viewed as a prerequisite for the evolutionary origin of the granivory.

Key words: Simuliidae; Aves; Ornithuromorpha; Taimyr amber; Late Cretaceous; Early Cretaceous.

1. Introduction

Today, the Simuliidae (black flies) is not a large family of Diptera, but they have medical and veterinary importance as blood-feeding parasites, mostly of mammals, but also of birds. It currently includes 2,248 valid species: 2,232 extant and 16 fossil. They are found on all continents except Antarctica (Adler and Crosskey, 2017). Despite their

importance, knowledge of their relationships lags far behind that of many other Diptera (Currie and Grimaldi, 2000). Understanding the abundance of the family in Late Cretaceous Ugolyak amber will elucidate the early history of this group. Preliminary study of the Ugolyak species revealed distinctive claws characteristic of extant black flies that feed on birds. The Turonian *Archicnephia ornithoraptor* (Currie and Grimaldi, 2000) has such claws, as do all recorded Eocene black flies (Crosskey, 2002). This is of particular interest as no Cretaceous vertebrates have been found north of southern Yakutia (over 1300 km southeast of Ugolyak), and the nearest Cretaceous bird fossils are from southern Siberia (well known findings from the Kemerovo region and a dubious record from Buryatia) and Mongolia, at least 2000 km south of Ugolyak. Cretaceous ornithurine (modern type) birds were likely mostly associated with near-shore environments (Zhou, 2004). This is inferred by possible taphonomic factors indicating that those birds and the Ugolyak simuliids inhabited the same environments. These insects can then be used as a proxy for this bird community, allowing better understanding of that aspect of the Late Cretaceous forest ecology of Northern Asia.

1.1. Black fly impression fossils.

Cretaceous and Jurassic occurrences of black flies were recently summarized (Perkovsky and Sukhomlin, 2016a); their ages (by Dmitriev, 2017 and Martin et al., 2016) and quantities are shown in SI Table 1.

Kalugina (1991) attributed the Tithonian *Kovalevimyia lacrimosa* Kalugina, 1991 to the subfamily Kovalevimyinae Kalugina, 1991 on the basis of the following character states: 11-segmented antennae; mouthparts of the female approximately equal in length to the clypeus; length of the lower part of the katepisternum is less than its height; a branched Rs; C, R and M veins hairy; and a long, S-shaped stem of M_{1+2} . Kalugina (1991) referred the Berriasian-Valanginian *Gydarina karabonica* Kalugina, 1991 and

the Aptian *Baisomyia incognita* Kalugina, 1991 to the subfamily Gymnopauidinae Rubtsov, 1956. Crosskey and Howard (1997) disagreed, and referred *Kovalevimyia* to the tribe Prosimuliini Enderlein, 1921 of the subfamily Simuliinae Newmann, 1834. Currie and Grimaldi (2000) assigned both *Kovalevimyia* and *Baisomyia* to the tribe Prosimuliini on the basis of wing characters, but Grimaldi and Engel (2005) stated that *Baisomyia* belongs to the tribe Simuliini. According to Adler and Crosskey (2017) in their latest catalog of black flies, all three genera are related to the subfamily Simuliinae, genera *Gydarina* Kalugina, 1991, while *Kovalevimyia* is related to the tribe Prosimuliini, and *Baisomyia* to the tribe Simuliini.

The late Aptian dipteran larvae from Koonwarra, Australia (~75° south latitude in Aptian by Martin et al., 2016) definitely belong to Simuliidae (Jell and Duncan, 1986), however Borkent (1997) determined the wing Mem AAP3 (NMVP 103203) from Koonwarra, previously considered a black fly, to be from a male biting midge *Leptoconops* Skuse, 1889 (Ceratopogonidae).

1.2. Black flies in amber.

The first Late Cretaceous black fly *Archicnephia ornithoraptor* Currie and Grimaldi, 2000 was described from Turonian New Jersey amber. The first black fly in fossil resin from the Cretaceous of Asia, *Simuliites yantardakh* Perkovsky and Sukhomlin, was described in the collective group *Simuliites* Kalugina, 1986 from a very incomplete specimen from Yantardakh (Kheta Formation, Santonian) (Perkovsky and Sukhomlin, 2016a).

In addition to these Cretaceous occurrences, nine species of black flies are known from the upper Eocene Baltic and Rovno ambers. They were assigned to three extant genera: *Greniera* Doby and David, 1959, *Simulium* Latreille, 1802 (i.e., subgenus *Hellichella* Rivosecchi and Cardinali, 1975) and *Ectemnia* Enderlein, 1930. These are

Greniera affinis (Meunier, 1904), *G. importuna* (Meunier, 1904), *G. pulchella* (Meunier, 1904), *Simulium* (H.) *oligocenicum* Rubtsov, 1936 and *Ectemnia cerberus* (Enderlein, 1921) from Baltic amber, and *G. yankovskyi* Perkovsky and Sukhomlin, 2015, *G. ukrainica* Perkovsky and Sukhomlin, 2015 and *Simulium* (H.) *polessicum* (Perkovsky and Sukhomlin, 2016b) **comb. nov.** from Rovno amber. Detailed analysis of photographs taken by Pepinelli and Currie (2017) shows that *Ectemnia lithuanica* Yankovsky and Bernotiene, 2005 from Baltic amber does not belong to the genus *Ectemnia*, and should be regarded as Simuliini incertae sedis.

1.3. Number of fossil simuliid taxa.

Before the discovery of the Ugolyak specimens reported here, 16 species in 9 genera of fossil simuliids had been reported, including seven species in six genera from the Mesozoic.

2. Material and methods

The samples that we examined are from the collection of the A.A. Borissiak Paleontological Institute RAS, Moscow (PIN) from Ugolyak locality (Kheta Formation, Santonian, 84-86 Ma) situated on the Taimyr peninsula [72°1'47.07" N, 101°19'47.53" E] (Fig. 1). It is located on the left bank of the Severnyi Ugolyak River, 9.5 km upstream from its mouth, a tributary of the Ugolyak River, which is a left tributary of the Khatanga River. Amber was collected there in 1977 by I.D. Sukacheva during an expedition of the Palaeontological Institute. Controversy over the age of the Ugolyak locality was discussed by Perkovsky and Makarkin (2015). Photographs were taken with Leica M165C stereomicroscope with Leica DFC 420 camera. Black fly systematics follows Adler and Crosskey (2017).

3. Systematic paleontology

Order Diptera Linnaeus, 1758

Family Simuliidae Newmann, 1834

Subfamily Simuliinae Newmann, 1834

Tribe Simuliini Newmann, 1834

Genus *Ugolyakia* Perkovsky et Sukhomlin, gen. nov.

lsid:zoobank.org:act:870E5DEA-7BCA-45BA-8311-3C5D9F7E6680

Figs. 2-4.

Diagnosis. Relatively small black flies (Fig. 2A). Head width slightly less than thorax width. Frons relatively narrow (Fig. 2B). Antenna short, with 10 antennomeres (Fig. 2D). Maxillary palp short, 3rd palpomere large (Fig. 2C). Scutum convex, black, evenly covered with hairs, silvery spots absent. Katepisternal sulcus developed, possibly evanescent anteriorly; distal part of katepisternum almost twice as long as height (Fig. 2H). Wing relatively elongated, over twice as long as wide (Fig. 2F). Costa (C) pubescent throughout with short hairs; subcostal vein with short hairs; Rs not branched; b-r cell long; b-m cell present (Fig. 2E). Stem vein covered with long hairs. R1 with small hairs, extended almost to margin. Abdominal sternites from II to VII reduced, replaced by membrane. Calcipala pedisulcus absent (Fig. 2G). Hind tarsomere 3 with elongate, ventrally projecting lobe. Claw with large subbasal tooth.

Type species: *Ugolyakia kaluginae* Perkovsky et Sukhomlin, sp. nov. (by present designation).

Etymology. The name of the genus derives from the locality. Gender feminine.

Ugolyakia kaluginae Perkovsky et Sukhomlin, sp. nov.

Isid:zoobank.org:act:644BE1C2-E6B3-4706-9D62-756DC1B29A68

Material. Holotype PIN 3631/37. A nearly complete female missing only the apex of the left wing. Syninclusion: PIN 3631/38, a male non-biting midge (Diptera: Chironomidae: Orthoclaadiinae). Paratypes (all females): PIN 3631/23, syninclusion: PIN 3631/38, aphid (Homoptera, Aphidinea); PIN 3631/42; syninclusions: PIN 3631/39, a female non-biting midge (Diptera: Chironomidae), PIN 3631/40, Diptera, PIN 3631/41: 2 Diptera (1 Brachycera, 1 Nematocera). Nontype material: PIN 3631/34 and PIN 3631/35 in a single piece of amber; additional syninclusion: PIN 3631/36, Coleoptera.

Diagnosis. As for the genus (*vide supra*).

Description. Head. Relatively large, width at base slightly smaller than width of thorax (Fig. 3B). Head length almost 2 times shorter than scutum length (Fig. 3A). Frons long, about 1/3 head length, narrow, minimal width 1.7 times less than maximum width (Fig. 3C). Pedicel slightly longer than and as wide as 3rd antennomere (Fig. 3G). Third palpomere large, more than twice wider than 4th, 5th palpomere shorter than 3rd, 4th palpomeres together (Fig. 3F). Mouthparts strongly prognathous, almost half head length in lateral view.

Thorax. Katepisternum well developed, not pubescent, with relatively shallow sulcus (Fig. 3D). Anepisternal membrane not pubescent.

Wing. Basal radial cell (br) long, 1/3 length of Rs (Fig. 4B). Basal medial cell (bm) clearly expressed (Fig. 3E). M1, M2 connected at lower edge of cell, forming stipes.

Legs dark (Fig. 4A). Tibial spurs well developed, length less than width of tibia at attachment point (Fig. 4C). Basitarsus 1 cylindrical, dark.

Abdomen. Cerci rectangular; length twice width. Triangular anal lobes seen in paratype PIN 3631/23 (Fig. 4C). Width of anal lobes in side view exceeds that of cercus, ventral edge of anal lobes very elongated. Widths of 3rd, 4th, 5th tergites three times larger than lengths (Fig. 3B).

Measurements in mm. Holotype: body length 2.40; head length 0.45, head width 0.52; frons length 0.17, minimum frons width 0.07, maximum frons width 0.11; length of antenna 0.37; length of maxillary palp 0.38, length of 3rd palpomere 0.12, width of 3rd palpomere 0.09; length of 4th palpomere 0.09, length of 5th palpomere 0.17; length of mouthparts 0.25; scutum length 0.91, scutum width 0.78; length of wing 2.14, width of wing 0.84; length b-r cell 0.45.

Paratype PIN 3631/23: body length 2.49; head length 0.46, head width 0.42; length of antenna 0.48; length of maxillary palp 0.39, length of 3rd palpomere 0.12, width of 3rd palpomere 0.07, length of 4th palpomere 0.12, length of 5th palpomere 0.15; length of mouthparts 0.26; scutum length 0.71; wing length 1.96, wing width 0.84; length of b-r cell 0.45; length of stem M1, M2 0.03; width of cercus 0.08, length of cercus 0.05; length of anal lobes 0.05, width of anal lobes 0.10.

Paratype PIN 3631/42: body length 2.23; head length 0.47; length of maxillary palp 0.35, length of 3rd palpomere 0.10, width of 3rd palpomere 0.09, length of 4th palpomere 0.10, length of 5th palpomere 0.15; length of mouthparts 0.17; scutum length 0.75, scutum width 0.78; length of wing 1.98, width of wing 0.88; length of b-r cell 0.38; width of cercus 0.08, length of cercus 0.04.

PIN 3631/34: length of body 2.6; wing length about 1.8, wing width 0.8.

Etymology. Named in remembrance of the late Dr. Nadezhda Kalugina, for her work on extinct black flies.

4. Remarks

These specimens are referred to the subfamily Simuliinae and the tribe Simuliini (Crosskey, 1990) by their unbranched Rs, developed katepisternal sulcus, relatively large head, antenna with 10 antennomeres, and the length of their mouthparts equal to that of the clypeus.

5. Taxonomic position of new genus

The new genus differs from typical Simuliini in the ratio of height to width of the distal part of the katepisternum. The height of the distal part of the katepisternum in *Ugolyakia* gen. nov. is less than its width; this height is usually equal to the width in the tribe. This and the shape of the wing, which is narrower than in all other Simuliini, is similar in *Ugolyakia* gen. nov. to the conditions seen in the genus *Gymnopais* Stone, 1949 of the tribe Prosimuliini. The absence of a calcipala is also characteristic of representatives of the tribe Prosimuliini, but they have a branched Rs and never possess a 10-segmented antenna (except in the aberrant triploide *Prosimulium isos* Rubtsov, 1956). Previously, two genera of Cretaceous Simuliini were known: *Baisomyia* Kalugina 1991 and *Archicnephia* Currie and Grimaldi, 2000. *Ugolyakia* gen. nov. differs from the Early Cretaceous genus *Baisomyia* by its larger head size (its head to thorax ratio is the same as in extant genera); number of antennomeres (10, not 9), approximately equal sizes of the 1st, 2nd and 3rd antennomeres (in *Baisomyia*, the 2nd

antennomere is twice as long as the 3rd), and narrower wings. The hairlike macrotrichia of the wing veins is a common feature.

Archicnephia Currie and Grimaldi, 2000 from Turonian New Jersey amber and *Ugolyakia* gen. nov. share the hairlike costal macrotrichia, absence of a calcipala and pedisulcus, hind tarsomere 3 with elongate, ventrally projecting lobe, and presence of a large subbasal tooth on the claw. However, the Ugolyak black flies are approximately twice as large (the New Jersey black fly body length is 1.0 mm, head width is 0.22 mm, head length 0.56 mm, scutum length 0.5 mm). The 3rd palpomere of the Ugolyak black flies is twice as wide as the 4th palpomere, while the New Jersey black fly 3rd palpomere is globose and 4 times wider than its 4th palpomere. Ugolyak black flies have cylindrical, rather than spindle-shaped antenna, short antennal macrotrichia; shorter mouthparts (the New Jersey black fly's mouth appendages are longer than the clypeus). Ugolyak black flies have narrower wings, 2.3-2.6 times longer than wide, while the wing length of the New Jersey black fly is 1.8 times longer than its width. Finally, the Ugolyak black flies have shorter hairs on C, Sc, and R1 veins, a common stem of M1 and M2 veins, narrower hind tibiae, and well-developed tibial spurs.

The differences between the new genus and 19 extant genera of Simuliini are shown in the SI Table 2.

Simuliites yantardakh Perkovsky and Sukhomlin, 2016a from Yantardakh (the most famous locality of the Kheta Formation) was recently described based on a female lacking its legs, wings and abdomen. Although it bears an obvious similarity to the type species of the new genus, they can be only meaningfully compared when more complete fossils from Yantardakh are found. Ugolyak black flies differ from the Yantardakh specimen by the length of antenna (0.37-0.48 mm, versus 0.53 mm in the case of *S. yantardakh*) and the width of antennomeres: the 2nd and 3rd antennomeres are neither

wider nor longer than the 4th one. One genus of Sisyridae and one of Rotoitidae occur at Ugolyak and Yantardakh, but no common species was known before *Baeomorpha quattoruno* Gumovsky, 2018 (Perkovsky and Makarkin, 2015; Gumovsky et al., 2018).

6. Discussion

6.1. Early evolution of the Simuliidae.

The oldest known Diptera fossils are from the early Anisian (early Middle Triassic) Grès à Voltzia Formation (Upper Buntsandstein) of the northern Vosges Mountains in northeastern France (Lukashevich et al., 2010).

It was supposed that the Triassic *Anisinodus crinitus* Lukashevich et al., 2010 is close to the ancestors of the Chironomidae-Ceratopogonidae and Simuliidae lineages, yet it lacks their apomorphies (Lukashevich et al., 2010).

The relict family Ptychopteridae (sensu Lukashevich, 2012) was considered by Kalugina (1991) to be the ancestral group for many fossil and modern Diptera. It includes the extinct monotypic subfamily Eoptychopterinae (Early Jurassic-Early Cretaceous), that was widely distributed in the Mesozoic. Eoptychopterinae shares the habitus and antenna structure of the Simuliidae, by which Kalugina (1991) considered Simuliidae had derived directly from ptychopterids. However, revision of the genus *Eoptychopterina* Kalugina (in Kalugina and Kovalev, 1985) by Lukashevich (2004) showed that *Eoptychopterina* had specialized mouth parts, suggesting that while they may appear closely related, *Eoptychopterina* and black flies perhaps shared common ancestors rather than representing a single lineage (Lukashevich, 2004).

Primitive features of the wing and katepisternum indicate that Parasimuliinae separated from early black flies before other subfamilies, although reliable fossils of this subfamily have not been identified. Discovery of *Simulimima grandis* Kalugina (in Kalugina and Kovalev, 1985), a black fly pupa from the Lower Jurassic of Siberia, which has all of the character states of extant Prosimuliini (Simuliinae) is very important for understanding the origin of black flies. It is not related to Limoniidae, as supposed by Currie and Grimaldi (2000) (see discussion of abdomen size below). Crosskey (1991) provides convincing arguments in favor of attributing this pupa to the genus *Prosimulium* Roubaud, 1906, which shows that the subfamily Simuliinae existed in the Middle Jurassic. According to Borkent (2012a), *Simulimima* is sister to all known modern and fossil black flies, supported by extant Simuliidae having a relatively shortened abdomen (ratio of wing length to the length of abdominal segments 3–9 of about 0.7), and *Simulimima grandis* having a proportionally longer abdomen (this ratio 0.33) (Borkent, 2012a). However, reexamination of the *S. grandis* holotype showed that it is a pupal exuvium with an extended abdomen, so that intersegmental membranes are in places longer than the tergites themselves, resulting in a modified shape of the abdomen, increasing its length more than 1.5 times its length in life (Lukashevich, 2004, p. 302), so the actual ratio would be not 0.33, but at least 0.5; in Prosimuliini, such moulted skins are usually much longer than live pupae (Crosskey, 1991). At the same time, a *Simulium* (*Hellichella*) sp. pupa from Baltic amber (Perkovsky et al., in prep.) has a ratio of not more than 0.65, and the smallest ratio of pupae depicted in Adler et al., 2004 is 0.55–0.6. In our opinion, the difference between the ratio of 0.5 in *Simulimima* and 0.55 or even 0.65 in the other black flies is not sufficient to consider *Simulimima* to be sister to all other black flies. Thus, we can assume that the family Simuliidae and the

tribe Prosimuliini originated in the Early Jurassic and Simuliini not later than the Early Cretaceous (Evenhuis, 1994).

6.2. Biological and taphonomic peculiarities important for understanding the significance of numerous black flies in Ugolyak.

Ugolyakia kaluginae gen. et sp. nov. females were probably blood-sucking ornithophiles, as suggested by their bifid claws, which were presumably adapted to attach to the barbs of bird feathers (the claws are simple in mammalophilic taxa). In extant black flies that feed on bird blood, the size of the claw slit corresponds to the diameter of feather barbula, allowing the female black fly to grip one or two of these with two separated claws. This proposed relationship between the claw's structure and ornithophilia is, however, "rather strong, but not absolute" (Currie and Grimaldi, 2000, p. 480), as there are non-blood-sucking species with a large subbasal claw tooth (e.g., *Simulium baffinense* Twinn, 1936, *Cnephia eremites* Shewell, 1952, *Cnephia pallipes* (Fries, 1824), *Metacnephia borealis* (Malloch, 1919). Nevertheless, other evidence supports the notion that *Ugolyakia kaluginae* gen. et sp. nov. was a blood-sucking species, i.e., its female tergites are strongly chitinous and clearly visible, while the sternites are slightly chitinous and indistinct. The thickening of the anterior wing veins is indicative of active flight. The wings of the three examined type specimens have clear signs of thickening of the anterior wing veins, in particular of the C, Sc, R1, Rs and b-r cells. The anterior crowding or thickening of the anterior wing veins, which results in a more deformable area posteriorly, promotes fast flight, maneuverability, and greater weight-supporting force on the upstroke (Ennos, 1989; Pepinelli et al., 2013). Reduction of sternites of abdominal sclerites indicates the ability of the abdomen to expand

significantly during feeding, and the wing morphology indicates the possibility of taking off after filling with blood, further consistent with hematophagy.

Black flies are not common in amber (Crosskey, 2002; Hoffeins and Hoffeins, 2003; Perkovsky and Sukhomlin, 2015), constituting less than 0.1% of all insects in representative collections of both Eocene and Cretaceous ambers (i.e., a single record for more than 6000 inclusions from Yantardakh). The Ugolyak assemblage, however, differs in its larger representation of Simuliidae, making up 3% of all its insect inclusions, 5% of all dipterans determined to the family level.

Such a high number of black flies in Ugolyak amber might be explained by taphonomic factors. Today, they often inhabit small, flowing freshwater streams surrounded by the forest. They emerge from pupae, and fly and settle on stream bank vegetation to dry. They then find shelter on the trunks of trees, from where they swarm and copulate, after which the females of most species search for a host. Often, the larger the freshwater stream, the further the black flies can fly in search of hosts (Kaplich et al., 2015). With larger streams and rivers creating a large floodplain, black flies could dry off on low plants, then fly out, and their number would then presumably not be so high on the amber tree trunks; when the river valley vegetation consisted mostly from angiosperms, preservation of black flies in fossil resin would be rare. We therefore assume that a small, flowing freshwater streams were next to the Ugolyak amber forest.

Biting midges are other bloodsucking dipterans present in Ugolyak amber. Interestingly, all of these identifiable to the genus level appear to belong to *Culicoides* Latreille, 1809 (Fig. 5). Extant *Culicoides* feed on birds and mammals (one or both: Borkent, 1995). In Yantardakh amber *Culicoides* females comprise just 18.5% of all biting midges (Szadzewski, 1996), in Campanian Canadian amber, 13.3% (Borkent, 1995, 2012b), and all bloodsucking females together (*Culicoides*, *Austroconops* Wirth

and Lee, 1958 and *Leptoconops*) constitute 22% in Yantardakh (Szadziwski, 1996) and 17% in Canadian amber (Borkent, 1995, 2012b).

6.3. Co-occurrences of fossil black flies and feathers.

Feathers (SI Table 1) were found at nearly all Cretaceous black fly sites after the Hauterivian, including all Lagerstätten with Simuliini (Chiappe and Witmer, 2002): Yantardakh (Zherikhin, 1978; “Northern Siberia” in Chiappe and Witmer, 2002), Baissa (Fig. 6A), New Jersey amber (Grimaldi and Case, 1995), the Gurvan-Eren Formation (Fig. 6B; in one layer with *Simuliites brevirostris*: Sinitsa, 1986) and in Koonwarra (feathers figured in Chiappe and Witmer, 2002).

This is significant for Mesozoic North Asia, as it has almost no fossil vertebrate record (except in the extreme south of the subregion).

6.4. Implications for the early evolution of birds at high latitudes.

The most plausible hypothesis is that black flies from Ugolyak fed on ornithuromorph birds, a clade which comprises extant birds and a number of extinct Cretaceous stem taxa (Mayr, 2017). This implies that ornithuromorph birds already inhabited the Arctic in the Early Cretaceous, and is based on two independent premises. First, we only see highly-specialized aquatic forms among ornithuromorph birds of the Cretaceous like the Early Cretaceous *Gansus* Hou and Liu, 1984 (You et al., 2006). In the Late Cretaceous, several lineages of ornithuromorph birds with aquatic specializations are known, including shorebird-like and diving taxa (Mayr, 2017; Agnolin et al., 2017). Enantiornithes, the “opposite” birds and likely a sister clade of ornithuromorphs, are also reported from marine environments (e.g., Chiappe et al.,

2002; Morrison et al., 2005), but they do not display locomotor specializations for an aquatic life-style. The second, and probably more important argument, is that enantiornithine birds or more primitive avian taxa have not yet been found at polar localities. Enantiornithines dominate the ecosystem of the tropical Jehol biota (Zhou, 2004) and other low latitude bird localities, but are less numerous and less diverse in a rich temperate bird community of southern Canada (Longrich, 2009). In the Arctic and Antarctic localities of the Cretaceous, only ornithuromorph birds are known (Tambussi and Acosta Hospitaleche, 2007; Agnolin, 2010; Bono et al., 2016; Agnolin et al., 2017 and see references in these papers).

Previous authors (e.g., Longrich, 2009; Bono et al., 2016; Agnolin et al., 2017) discussed possible physiological adaptations of ornithuromorphs to life in the Arctic, comparing them with the more primitive, slow-growing enantiornithines (Chinsamy et al., 1998). It is, however, also possible that these physiological adaptations originated in polar environments. The unusually high growth-rates of modern birds and their fossil relatives Ornithuromorpha (Chinsamy et al., 1998) may have gradually evolved as an adaptation to the short productive period of the year, perhaps as compensation for poor flight abilities during earlier stages of ontogenesis. These physiological parameters are already seen in late Early Cretaceous ornithuromorphs (O'Connor et al., 2015), implying an earlier origin of the fast-growing ornithuromorphs. Several cooling spells of the Early Cretaceous predating the flourishing of the Jehol biota have been proposed (Ogg and Hinnov, 2012), and even glaciation is known in the Berriasian to Valanginian (Alley and Frakes, 2003). The proposed hypothesis implies that advanced ornithuromorph birds are not indigenous elements of the Jehol biota, but had their origin in higher latitudes of the *Baeomorpha* Realm (Fig. 7). Characteristic of this realm is a temperate or warm temperate climate and abundant *Baeomorpha* Brues, 1937

(Rotoitidae) and aphid fossils that differ strongly in composition from those of other territories with known rich amber faunas (Gumovsky et al., 2018). Enantiornithines are known only on the border between the *Baeomorpha* and Isoptera realms (Morrison et al., 2005), and so absence of enantiornithines can be added to the diagnosis of the *Baeomorpha* Realm.

All known Mesozoic polar birds were aquatic, and most modern Arctic and Antarctic birds rely on marine resources. At least some of the putative primitive ornithuromorphs which inhabited the Arctic during the Early Cretaceous could have been aquatic (or terrestrial, but linked to aquatic trophic chains), and thus entered lower latitude niches to which they were preadapted, coexisting with previously established tropical biota. Arboreal habitats of the tropics were apparently heavily exploited by enantiornithine birds (Zhou, 2004), which show similarities in limb structure with various modern forest birds (see review in Zelenkov 2017).

The inferred seasonality in the higher latitudes during cold spells of the Early Cretaceous could further be viewed as a prerequisite for the evolutionary origin of the granivory (seed-eating). This feeding specialization occurred in several clades of Cretaceous theropod dinosaurs and is viewed as one of the factors explaining survival of birds at the end of the Cretaceous (Larson et al., 2016). Granivory is known for the basal avian taxa *Jeholornis* Zhou and Zhang, 2002a and *Sapeornis* Zhou and Zhang, 2002b (Zhou and Zhang, 2002a; Zheng et al., 2011) and thus seed-eating (at least optional) may be primitive for birds. A dietary switch to seed-eating may be the only possible way for a primitive bird (which lived on the continent far from sea) to survive cold winters in the higher latitudes.

The abundance of black flies and, by inference, birds in the Santonian Ugolyak communities and not in other studied Taimyr localities could have been due to

landscape differences. Current evidence suggests that Taimyr Santonian angiosperms were associated with river valleys (Nadein and Perkovsky, 2018); the right tributaries of the Kheta and left tributaries of Kotuj run mainly along the Putorana Plateau, which was present in the Cretaceous, bounded by granite canyons, creating a narrow area for the small, flowing freshwater streams surrounded by the amber forest (see above). The Ugolyak is the only known retinite location of the Kheta Formation of the river catchment area in the flat Khatanga lowland where the Cretaceous river valleys were not bounded by granite canyons. This would allow for many small tributaries, similar to today, creating favorable conditions for these Cretaceous birds and/or black flies to live and be preserved.

7. Conclusions

Ugolyakia kaluginae gen. et sp. nov. is described based on several black fly females from Kheta time amber of Ugolyak. Its wing venation (an unbranched R_s), and the developed katepisternal sulcus indicate that *Ugolyakia* gen. nov. belongs to the Simuliini, but two important characters of most genera of the tribe are absent, i.e., calcupala and spiniform costal macrotrichia. The presence of a large subbasal tooth of the claw and the absence of significant sclerotization of the sternites suggest that the females of *Ugolyakia kaluginae* gen. et sp. nov. were blood-sucking avian parasites. Black flies in Ugolyak make up 3% of all inclusions of insects and 5% of all registered Diptera; previously, only two Late Cretaceous amber black flies were known, a small fraction of a percent of the Yantardakh and New Jersey amber correspondingly. Feathers have been found at nearly all black fly fossil sites after the Hauterivian. In our opinion, the abundance of black flies in Late Cretaceous Ugolyak was related to that of

birds, and the abundance of birds was due to the presence of wide river valleys in the Khatanga lowland, a habitat in turn favourable for the development of angiosperm or mixed forest communities (Nadein and Perkovsky, 2018) in which they thrive.

Black flies from Ugolyak most likely fed on ornithuromorph birds, which implies that they inhabited the Arctic by the Early Cretaceous. The unusually high growth-rates of modern birds and fossil Ornithuromorpha may have evolved as an adaptation to the short yearly productive period (probably as a compensation for poor flight ability of their young). Advanced ornithuromorphs might have had their origin in higher latitudes, later entering niches in tropical Jehol biota to which they were preadapted. The inferred seasonality in higher latitudes during cold spells of the Early Cretaceous may have been a prerequisite for the origin of the granivory in birds.

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Figure captions

Fig. 1. Type locality of *Ugolyakia kaluginae* gen. et sp. nov. (square) and other Cretaceous sites with named adult black fly species, showing co-occurrences of feathers (circles). Map of middle Cretaceous (ca 106 mya) redrawn from Scotese (2014).

Fig. 2. Line drawings of *Ugolyakia kaluginae* gen. et sp. nov. females: 3631/37, holotype (A-E, H), 3631/42, paratype (F) and 3631/23, paratype (G, I). (A) General view. (B) Frons (reconstruction). (C) Maxillary palp. (D) Antenna. (E) Outer wing margin. (F) Wing. (G) Hind basitarsus. (H) Katepisternum. (I) Terminalia.

Fig. 3. Photographs of *Ugolyakia kaluginae* gen. et sp. nov., holotype, 3631/37. (A) Lateral view. (B) Ventral view. (C) Frons. (D) Katepisternum. (E) Wing. (F) Maxillary palp. (G) Antenna.

Fig. 4. Photographs of *Ugolyakia kaluginae* gen. et sp. nov. paratypes 3631/42 (A, B) and 3631/23 (C). (A) General view. (B) Wing. (C) Terminalia and hind tarsus.

Fig. 5. Photographs of female of *Culicoides* sp. (Ceratopogonidae) from Ugolyak. (A). General dorsal view. (B) General ventral view. (C) Head and legs.

Fig. 6. Photographs of feathers from Cretaceous birds. (A) PIN 3064/10593, Baissa. (B) PIN 3149/2150, Gurvan-Eren Formation.

Fig. 7. A possible boundary between the *Baeomorpha* Realm and the Isoptera Realm (Gumovsky et al., 2018). **1. Lower Cretaceous:** 1.1. Golling, Austria; 1.2. Wessex Fm., Isle of Wight, U.K.; 1.3. Levantine amber belt (Lebanon, Syria, Jordan, Israel); 1.4. Choshi, eastern Honshu Isl., Japan; 1.5.a mainly Escucha Fm. (San Just, Arroyo de la Pascueta, La Hoya), 1.5b mainly Utrillas Group (El Caleyú, El Soplao, Peñacerrada, Salinillas de Buradón) – Albion, Spain; 1.6. Begichevo Fm. (Zhdanikha, Kresty) Taimyr Peninsula, Russia; 1.7. Arctic Coastal Plain, Alaska, U.S.A. **2. Upper**

Cretaceous: 2.1. Charentese amber (Archingeay-Les Nouillers, île d'Aix, Cadeul, Puy-Puy, Fouras, etc.), Western France; location for part of 2.4 (middle Cenomanian Anjou amber) is the same; 2.2. Hukawng Valley, Myanmar; 2.3. Agdzhakend, Azerbaijan; 2.4. (part) Fourtou and Salignac, South-eastern France; 2.5. Agapa, Taimyr Peninsula, Russia; 2.6. Timmerdyakh, Yakutia, Russia; 2.7. Raritan Fm., New Jersey and Maryland, U.S.A.; 2.8. Vendée, Western France, 2.9. Shavarshavan, Armenia; 2.10. Kheta Fm. (Yantardakh, Romanikha, Ugolyak), Taimyr Peninsula, Russia; 2.11. Piolenc and Belcodène, Southern France; 2.12. Ajka, Csinger valley, Hungary; 2.13. Eutaw Fm. (Alabama – Santonian), Neuse River near Goldsboro (North Carolina – Campanian), U.S.A.; 2.14. Kuji group – Campanian and Futaba group – Santonian, northern Honshu Isl., Japan; 2.15. Grassy Lake, Alberta, and Cedar Lake, Manitoba, Canada; 2.16. Hell Creek Formation, South Dakota, U.S.A. **3. Controversially dated locality:** Baikura, ?Ognevka Formation, Taimyr Peninsula, Russia.

Highlights

The first complete fossils of black flies are described from North Siberian amber.

These fossils are unusually numerous in Ugolyak (Taimyr).

The fossils are identified as a new genus of Simuliini, *Ugolyakia*.

Ugolyakia fed on the ornithuromorph birds.

Advanced ornithuromorphs might have originated in higher latitudes.