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Hematophagous Insects in the Fossil Record

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Abstract—Hematophagous insect fossils are reviewed. The origin of hematophagy in various dipteran groups is discussed.

INTRODUCTION

Bloodsucking, or hematophagy, is a relatively rare feeding habit in insects. If hematophagous insects are defined as those possessing piercing-and-sucking mouthparts and preying on much larger animals, then there are only four orders in which this feeding habit is important. These are sucking lice (Anoplura), true bugs (Heteroptera), true flies (Diptera), and fleas (Siphonaptera); absolutely all lice and fleas are obligatory bloodsuckers, whereas among bugs and flies, only 10% of families include bloodsuckers. In other orders, hematophagy occurs sporadically, for example, in chewing lice (*Menacanthus stramineus* parasitizing poultry, Askew, 1971) and moths (*Calpe eustrigata* parasitizing wild ungulates, Bänziger, 1968), but these are just single, bizarre cases.

The first mention in fossil remains of a Recent mosquito species, *Aedes ciliaris* L., in Quaternary copal was made in the second half of the 18th century (Bloch, 1776). Hundreds of species of hematophagous insects have been described since then from various deposits of all continents except the Antarctic.

In the paleontological record, hematophagous insects of different orders are represented much more disproportionally (Fig. 1). Fossils of sucking lice and fleas are extremely uncommon, which is understandable, since these insects are closely connected with their hosts and, thus, their chance to be successfully buried in deposits of inland water bodies (the main type of fossil insect localities) or in fossil resins is slim. The lice have been known from the Cenozoic only, being found on fossils of ground squirrels in the Pleistocene of Siberia (Dubinin, 1948) and as lice eggs on hair in Eocene Baltic amber (Voigt, 1952). Little more is known about fossil fleas; only fossils of adult fleas belonging to Recent genera have been found in Eocene Baltic amber (Peus, 1968) and Miocene Dominican amber (Lewis and Grimaldi, 1997). *Tarwinia* has been discovered in the Lower Cretaceous of Australia (Jell and Duncan, 1986), although this insect differs in habit from modern fleas, it has much in common with them, above all the laterally compressed body and saltatory legs. Two more ancient genera from the Mesozoic of Transbaikalia considerably differ from modern fleas and only provisionally, with some reservation, may be allocated to "pre-fleas". More than ten *Saurophthirus* specimens have been found in the Lower Cretaceous deposits of the locality of Baissa; the dorsoventrally flattened body and long tenacious legs make this genus similar to Nycteribiidae and Polyctenidae, bloodsucking flies and bugs connected with bats (Ponomarenko, 1976). Ponomarenko suggested that *Saurophthirus* could parasitize on pterosaurs, being attached with its long tenacious legs to their leathery membrane. In spite of differences in habit, a similar life-style was reconstructed by Rasnitsyn for representatives of the genus *Strashila* from the Upper Jurassic (Rasnitsyn, 1992). This conclusion has been made on the basis of morphological adaptations of *Strashila* to parasitic life, i.e., long legs with tibiotarsal forceps and long claws, hypognathous head, and weakly sclerotized extensible abdomen. An incomplete skeleton recently discovered in Baissa (Zherikhin *et al.*, 1999) may indirectly support this hypothesis, if it belongs to a flying reptile rather than a bird.

Among Heteroptera, bloodsuckers are bed bugs (Cimicidae), bat parasites (Polyctenidae), and some assassin bugs (Reduviidae Triatominae); rare representatives of some families are facultative hematophages (Myers, 1929). Only Reduviidae have been recorded as fossils in the Lower Cretaceous of China, although these were not bloodsucking forms (Hong, 1987).

Bloodsucking dipterans have received most study. If, according to the above definition, we exclude from consideration group with a diet restricted to hemolymph of relatively small insects, then at present we can name 14 extant dipteran families having to a certain degree imaginal bloodsucking, of which 12 have been already identified in the paleontological record.

Traditionally, dipterous insects are subdivided into two groups: the more primitive Orthorrhapha (midges and lower flies) and Cyclorrhapha (higher flies). In all bloodsucking representatives of orthorrhaphous dipterans, the mouthparts are arranged in a similar pattern (Snodgrass, 1943): the labium forms a nonpiercing pro-

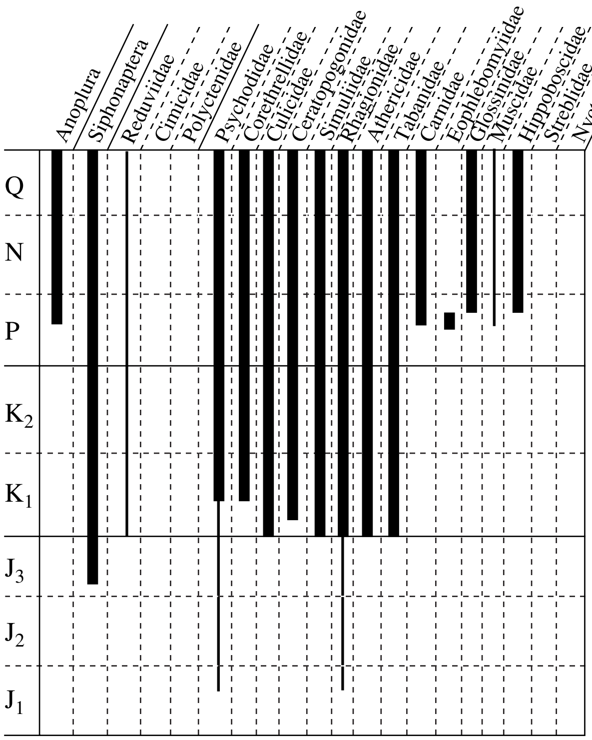

Fig. 1. Hematophagous insects in the paleontological record (thin lines denote nonhematophagous forms).

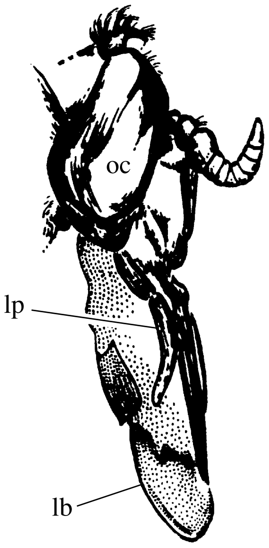

Fig. 2. Female head of *Palaeoarthroteles mesozoicus* (after Kovalev and Mostovski, 1997).

tecting sheath, whereas all other parts, i.e., the labrum, mandibles, maxillae, and hypopharinx, are either cutting or piercing and, thus, active during feeding. In the cyclorrhaphous flies, the morphological basis of bloodsucking mouthparts is changed and notably reduced: the mandibles and maxillae are absent, and the skin is border with the labella furnished with teeth.

All known cyclorrhaphous hematophagous flies are of Cenozoic origin, and bloodsucking representatives of all orthorrhaphous families have been recorded from as early strata as the Early Cretaceous (Fig. 1). All hematophagous midges have also been reported from as early strata as the Early Cretaceous: sandflies Psychodidae Phlebotominae and some mothflies Psychodinae (Hennig, 1972; Azar *et al.*, 1999); Corethrellidae (Szadziewski, 1995); mosquitoes Culicidae (with some doubt, from the Early Cretaceous, according to the personal communication of R. Coram, and, undoubtedly, from the Late Cretaceous, Poinar *et al.*, 2000); biting midges (Borkent, 1997); and blackflies Simuliidae[1] (Kalugina, 1991).

The lower hematophagous brachycerous flies are also known from the Early Cretaceous. Rhagionidae, a primitive family, possibly ancestral to all brachycerans, were common by the Early Jurassic; but only in the Glushkovo Formation, Transbaikalia, there are forms that are supposed to be hematophagous (Kovalev and Mostovski, 1997). The female of *Palaeoarthroteles mesozoicus* (Fig. 2) had a massive proboscis, which was longer than the head capsule, and elongate and downcurved palps, i.e., features that suggest exactly this diet. An alternative hypothesis may suggest preying, but there are no adaptations to this life-style, such as modified legs bearing spines and robust bristles; thus, hematophagy is more acceptable (Stuckenberg, pers. comm.). This is especially interesting, since other characters speak in favor of the primitiveness of this genus. In particular, the antennae retaining the eight-segmented postpedicel are an initial pattern for the brachycerous flies.

The horseflies (Tabanidae) are also known from as early strata as the very Early Cretaceous (Martins-Neto and Kucera-Santos, 1994; Coram *et al.*, 1995; Ren, 1998). A specimen from the Early Cretaceous of Transbaikalia also belongs to a horsefly (Mostovski *et al.*, 2003). This identification is supported by the large size of this fly, its massive body with relatively slender legs, the shape of the head with a somewhat swollen clypeus, and the elongated proboscis with well-developed stilets. The postpedicel is enlarged basally, being able to accommodate fields of olfactory receptors, and curved apical segments of the palps appear to be covered with forwardly directed sensillae; the latter feature is also characteristic of Recent hematophagous horseflies (Stuckenberg, pers. comm.).

First athericids (Athericidae) was described by Stuckenberg (1974) from Eocene Baltic amber. Isolated wings from the Lower Cretaceous deposits of Trans-

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[1] After Kalugina (Kalugina and Kovalev, 1985), we place the genus *Simulimima* from the Early–Middle Jurassic of Transbaikalia, making some reservation, within Eoptychopteridae, mainly due to its giant size (its length excluding thoracic horns is 12 mm), which is absolutely nontypical of Recent and fossil blackflies. Thus, the earliest record of unquestionable blackflies has been made in the Glushkovo Formation, Transbaikalia, which is likely to be of Late Jurassic age (e.g., Kovalev, 1990).

Table 1. Feeding specialization of bloodsucking dipterous insects

Family	Bloodsuckers' hosts						Nonhematophagous species
	Mammalia	Aves	Reptilia	Amphibia	Pisces	Insecta	
Psychodidae	+	+	+	+			+
Corethrellidae	+	+		+			+
Culicidae	+	+	+	+	+		+
Ceratopogonidae	+	+	+	+	+	+	+
Simuliidae	+	+					+
Rhagionidae	+						+
Athericidae	+	+		+			+
Tabanidae	+	+	+				+
Carnidae	+	+					+
Muscidae	+						+
Glossinidae	+		+				
Hippoboscidae	+	+					
Streblidae	+	+					
Nycteribiidae	+						

baikalia and England should be allocated to this family as well (Mostovski *et al.*, 2003).

The orthorrhaphous and cyclorrhaphous dipterans differ from each other in the type of hematophagy. There are only free-living, i.e., periodically attacking, bloodsuckers among Orthorrhapha, and the imaginal hematophagy is characteristic of females only,[2] whereas such uniformity has not been recorded within the cyclorrhaphous flies, where both males and females are hematophages (Beklemishev, 1951). Amid the cyclorrhaphous flies, there are also free-living, both facultative and obligatory, bloodsuckers with free-living larvae, these are some Muscidae (only nonbloodsucking forms are known as fossils,[3] the oldest come from the Eocene of the United States, Cockerell, 1921). Glossinidae, vectors of sleeping sickness in Africa, known from the Oligocene of the United States (Grimaldi, 1992) and, presumably, related extinct Eophlebomyiidae from the Eocene of the United States (Cockerell, 1924, 1925) also belong to periodically attacking bloodsuckers. Carnidae, which have been recorded from Eocene Baltic and Miocene Dominican amber (Grimaldi, 1997), are referred to ambushing bloodsuckers inhabiting nests and lairs and having free-living larvae; the life long parasitism of others (multi-interrupted, once-interrupted, and non-interrupted variants are possible) is connected with the transition to laying pupae and discontinuing independent larval feeding, cases of imaginal endoparasitism are known (*Ascodipteron* females in Streblidae, Askew, 1971). The louse flies Hippoboscidae recorded in the Oligocene of Germany (Statz, 1940) as well as Streblidae and Nycteribiidae, which are unknown as fossils, are ectoparasites.

There are some data in the literature on representatives of one more cyclorrhaphous family, Phoridae, that attack people (Disney, 1994) or suck the contents of the abdomen of satiated Culicidae females. The scuttle-flies are suspected to be bloodsuckers of earthworms (Disney, pers. comm.), but how wide the hematophagy is distributed and whether this diet is obligatory or facultative is still an open question. In the paleontological record, the true scuttle-flies have been recorded from as early strata the Paleocene (Evenhuis, 1994).

Let us consider now the feeding preferences of the families in question, mainly on the basis of Downes' (1958) data (table). It turns out that only among higher flies there are families some members of which are entirely bloodsucking. Within the Orthorrhapha, all bloodsucking females necessarily consume nectar, as nonbloodsucking males do; in addition, all these families include nonbloodsucking forms, although, for example, in Culicidae and Tabanidae, these are rare species and genera within bloodsucking groups, whereas in Psychodidae and Rhagionidae, hematophagous members have been reported in some lineages only.

The range of potential hosts is rather wide and varies in different families, but absolutely all families of bloodsucking dipterans parasitize on mammals; more rarely, on birds; and still much rarely, on reptiles and amphibians, and Ceratopogonidae and Culicidae occa-

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[2] Except for the biting midges (Shakirzyanova, 1951; Silva and Grünwald, 1999). In both cases, laboratory examination of the male abdomen contents showed the presence of blood. The ratio of males with blood in their abdomens reached 3.6%. Interestingly, male mouthparts, including the mandibles, are fully developed, although they are shorter than in females and lack some teeth and sensillae (Silva and Grünwald, 2000).

[3] However, the only distinctive feature of hematophages, i.e., spines on the labella, is hardly visible in fossils.

sionally attack fishes (mudskippers). The most narrowly specialized family is Nycteribiidae, which feeds exclusively on bats. Ceratopogonidae possess the widest range of hosts that include various vertebrates as well as large insects, which are attacked by biting midges as if they were vertebrates and hemolymph of which is sucked out while the prey is still alive; this process may take several days (a unique case in the dipterans). There are predaceous biting midges hunting for proportionally-sized small insects, which are killed before they start sucking their hemolymph. As usual, there are non-bloodsucking forms within this family, including aphagous and nectarophagous species; rare representatives consume pollen grains rather than blood or hemolymph as a source of protein.

The history of the biting midges is well studied, mainly due to the efforts of Borkent (e.g., 1995, 2000) and Szadziewski (1996). Ceratopogonidae found in Early Cretaceous resins of Austria, Lebanon, and Spain; in Late Cretaceous resins of Siberia, Europe, and North America; and in Sakhalin, Baltic, Chinese, and Mexican Tertiary ambers (Evenhuis, 1994); unlike inclusions in resins, compression fossils of biting midges are very rare (Kalugina, 1991; Borkent, 1997). The number of fossil species of the biting midges is twice as great as that of all other fossil hematophagous dipterans combined; of 5000 known species of biting midges, about 200 are extinct, whereas there are not more than 100 fossil species known in the other 11 families.

Such an abundant fossil material supports a hypothesis formulated on the basis of the modern biting midge behavior (Downes, 1978) that bloodsucking on mammals is an initial feeding habit of the biting midges, and preying on insects is secondary (Borkent, 1995; Szadziewski, 1996). Both of the most primitive lineages, Austroconopinae and Leptoconopinae, representatives of which consume blood of vertebrates, have been discovered before others, in the Early Cretaceous, where other modern subfamilies have not been recorded, and the extant genus *Leptoconops* has been found in Early Cretaceous Lebanese amber. Known morphological features of extinct genera of these subfamilies as well as those of the Cretaceous genus *Protoculicoides*, the systematical position of which is unclear, create no problems in treating these taxa as bloodsuckers of vertebrates. Mouthparts having finely serrate mandibles and inversely serrate maxillae combined with simple claws are unequivocally taken as evidence for bloodsucking on vertebrates. Frankly, some controversies emerge; for instance, a spine is present on the first tarsomere in *Austroconops gladis* (Lebanese amber), a feature, which, within the Recent biting midges, is characteristic of predators feeding on proportionally-sized insects. Recently, the subfamily Lebanoculicoidinae (Borkent, 2000) possessing the most primitive wing venation within the family have been established; the structure of the mouthparts is unknown. However, there is no strong evidence against the hypothesis that hematophagy is a plesiomorphic feeding type of biting midges.

Generally speaking, there is an opinion, which was expressed by Martini (1932) and supported by some modern researches (Downes, 1978; Nagatomi and Soroida, 1985), that hematophagy is an initial feeding habit of dipterans as a whole. One of the main pieces of evidence is the presence of a complete set of mouthparts in the hematophagous orthorrhaphans that inherited it from their ancestors, the scorpion flies, whereas the mouthparts underwent a considerable reduction in the majority of other dipteran groups. Indeed, the mandibles are usually absent from males and often from females of most of orthorrhaphans; however, the full set is characteristic of not only hematophages. Initially, amongst non bloodsucking groups, the mandibles have been recorded only in predaceous Blephariceridae females[4] (Peterson, 1916), but this list has been notably extended owing to families in which not only cases of hematophagy but even predation have not been recorded (Nagatomi and Soroida, 1985). Not only female mandibles (rudimentary, as in some Vermileonidae and Nemestrinidae, or somewhat reduced, as in Pelecorhynchidae) but also the mandibles of both sexes in the families Dixidae and Chaoboridae have been described; in chaoborids that have not been under suspicion concerning their bloodsucking habit, the development of mandibles compares well with that in bloodsuckers of the related family Corethrellidae (Cook, 1956). Additionally, all families of the orthorrhaphous Diptera with recorded hematophagy include non-bloodsucking species and genera possessing the full set of the mouthparts; consequently, the hematophagy of the orthorrhaphous dipterans is impossible without this full set, but such a completeness does not mean the presence of hematophagy.

Reasons against hematophagy as the ancestral diet of dipterans seem to be stronger (e.g., Szadziewski, 1996). Thus, within other insect orders, the ancestral feeding mode is typical of both sexes, not only of females, as in the orthorrhaphous dipterans (the cyclorrhaphous flies cannot be used as evidence because of their obviously advanced position).

Regrettably, direct paleontological data on the initial, Triassic (and even Early Jurassic), phase in the dipteran evolution are scarce, fragmentary, and absolutely insufficient for making conclusions about a plesiomorphic diet; thus, we can add nothing to this discussion, except for “a note about not finding bloodsucking families” not only in the Triassic, but throughout the Jurassic (or nearly so, if the Glushkovo Formation is the Late Jurassic, not Early Cretaceous).

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[4] By the way, Downes (1978) treats Blephariceridae as bloodsuckers and considers the predation on proportionally-sized insects subsequent sucking of hemolymph principally similar to true hematophagy, thus disregarding the fact that the victim is killed. Therefore, Downes is in fact mixing both cases, when discussing the primary nature of the hematophagy as a dipteran feeding habit.

Within the families Psychodidae and Rhagionidae, undoubted bloodsuckers appeared only in the Early Cretaceous, although the families themselves existed at least as early as the Early Jurassic (Ansorge, 1996; Mostovski and Jarzembowski, 2000). Within the infraorder Culicomorpha, to which the majority of bloodsucking midges belong, the families in question have been recorded only from as later strata as the Early Cretaceous, although representatives of both culicomorph superfamilies Dixidae, Chaoboridae, and Chironomidae have been known from as early strata as the Triassic or the Early Jurassic (Lukashevich, 1996; Krzemiński and Jarzembowski, 1999). To explain this phenomenon, the idea is periodically expressed that bloodsucking disappeared in all primitive groups of the infraorder Culicomorpha later, which seems to be inconsistent.

Currently, all paleontological facts witness against hematophagy as a plesiomorphic feeding habit. To be true, inclusions are still not known in the pre-Cretaceous resins, and it is far more difficult to study mouthparts on compression fossils, so much more that usually only isolated wings were buried. In this connection, the case of Psychodidae, the oldest members of which are described on the basis of isolated wings with plesiomorphic venation from the Lias of Germany is pertinent (Ansorge, 1994). *Liassopsychodina*, unlike all other Phlebotominae described by that time, retained the CuP vein, so Ansorge considered it as an ancestral form and did not place it within Phlebotominae (Fig. 3). However, a paper has been published containing a description of several new genera from Early Cretaceous Lebanese amber (Azar *et al.*, 1999) in which the impossibility of correct conclusions on the systematical placement of the moth flies based solely on the venation is demonstrated. It turns out that characters traditionally treated after Hennig (1972) as apomorphies of various subfamilies, i.e., the reduction of the radial and cubital veins, the development of the eye bridge, the reduction of the elongate mouthparts with developed mandibles, the changing number of segments in the maxillary palps and in the antennae, have been the phlebotomine-like male genitalia, are recorded in the Early Cretaceous in virtually all possible combinations, making allocation to that or this subfamily more difficult and confirming the principle of the archaic polymorphism one more time. The most interesting for us is *Libanophlebotomus*, which is the closest to the German *Liassopsychodina* in the wing venation and may be considered as a transitional link between the latter and the typical sand flies, for instance, *Mesophlebotomites*. The authors put *Libanophlebotomus* within Phlebotominae on the basis of symplesiomorphies and on the strength of all the characters, despite the presence of the CuP vein, which is lacking in the modern sand flies. One may ask the question: What is preventing us from placing the Early Jurassic *Liassopsychodina* within the sand flies and suggesting it to be hematophagous? However, the ground for such an assumption is too feeble.[5] Dipteran bodies are virtually unknown from the Early Jurassic, so the hypothesis about their bloodsucking feeding habit will hardly be confirmed or rejected on the basis of their mouthparts structure or genitalia.

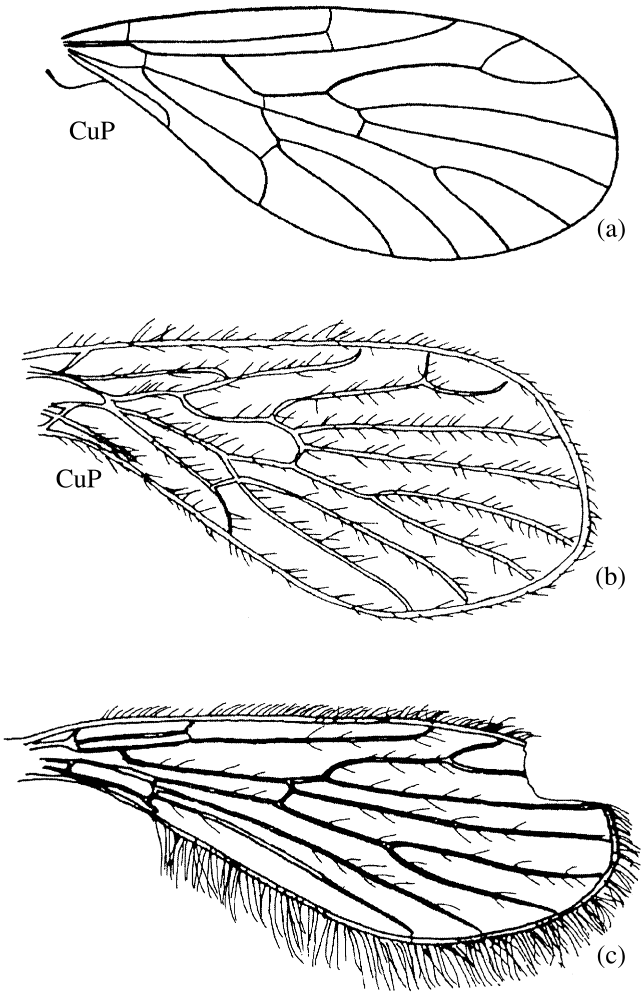

Fig. 3. Wing venation of Psychodidae: (a) *Liassopsychodina pommerana* (after Ansorge, 1994), (b) *Libanophlebotomus lutfallahi* (after Azar *et al.*, 1999), (c) *Mesophlebotomites hennigi* (after Azar *et al.*, 1999).

Up to the present, no presumed extinct hematophages have been described from those dipteran groups in which hematophagy is now unknown. It should be emphasized that “the evidence of the primary nature of the hematophagy” in the nonbloodsucking families Chaoboridae and Chironomidae, to which referred Labandeira (1998), is based on phylogenetic analysis, not on the study of the Mesozoic fossils, i.e., it is speculative and is not supported by any facts. It turns out

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[5] The only Mesozoic larva from the Middle–Upper Jurassic of Transbaikalia *Eopericoma zherichini*, which was questionably allocated to Psychodidae (Kalugina and Kovalev, 1985), is probably does not belong to Phlebotominae because of the presence of the terminal sclerotized syphon, which is now characteristic of Psychodinae only.

that there were no bloodsucking members in a family in the past if they are now absent from the family. Nonetheless, the method of actualism may not be considered reliable enough; the absence of bloodsuckers from the modern representatives of a family may be only indirect evidence of their absence in the Mesozoic due to the incompleteness of our knowledge about the biology of many dipterans. Only in the end of the 1960s, was the bloodsucking feeding habit demonstrated in *Corethrella* (Williams and Edman, 1968), being repeatedly confirmed later; simultaneously, the full set of well-developed piercing-and-sucking mouthparts was discovered in two families in which hematophagy was still unknown (Downes and Colless, 1967). An unexpected find of mandibles in some Tanyderidae may be explained by deficiency of data on this odd family, but Chironomidae are probably one of the best studied groups of Diptera, and feeding on proportionally-sized insects, which might be hypothesized on the basis of the mouthpart structure of *Archaeochlus*, is still unknown among them (Cranston *et al.*, 1987). It is now believed that information on the mouthpart structure is insufficient to prove the hematophagous lifestyle, but field observation, analysis of the gut contents and egg development, and/or tests with laboratory animals are essential (Nagatomi and Soroida, 1985).

Leaving the question of the primary feeding habit in dipterans aside, one may agree with Beklemishev that hematophagy of the orthorrhaphous dipterans evolved from entomophagy (Beklemishev, 1951). The entomophagy might form morphological (piercing-and-sucking mouthparts), behavioral (aggressiveness, active search for a victim), and biochemical (digestive enzymes) preadaptations for the transition to hematophagy, and the main preadaptation is piercing-and-sucking mouthparts.

As for the bloodsucking of the higher flies, in accordance with Beklemishev's widely accepted point of view (Beklemishev, 1951), this feeding habit is not inherited from their ancestors, but originated on a different morphological basis of notably reduced mouthparts and is evidently correlated with the expansion of grass bioms like steppes and savannas during the Cenozoic. Extensive herds of large herbivorous mammals induced the origin of insect assemblages utilizing excretes, i.e., coprophagous insects that were licking and scratching various exudates of mammals and gradually turned toward independently obtaining blood.

Consequently, even within the same order of Diptera, the formation of hematophagy occurred independently at a different time (and this is supported by paleontological data) apparently on the basis of preceded trophic specialization and on a different morphological ground. Such an absence of one main direction allowed formulation of the concept of a variety of morphofunctional pathways of trophic specialization formation in insects (Chaika, 1995), according to which different morphofunctional mechanisms may prepare the hematophagy in different taxa on any level.

Yet paleontological data on hematophagous insects had just started to be accumulated by the 1950s, Beklemishev (1951) suggested that only the appearance of homoiothermal animals (not simply vertebrates or even amniotes) stimulated the transition of insects towards feeding on vertebrates, although even today some authors believe reptiles to be the first hosts of dipterous bloodsuckers (Downes, 1978). A natural question arises, why did bloodsuckers originate in the Early Cretaceous (except for the only undoubted Jurassic insect, *Strashila*), although the mammals had emerged much earlier, in the Late Triassic (Carroll, 1993)? Despite the incompleteness of the paleontological record of homoiothermal animals in the Jurassic and the Early Cretaceous, they suggest that exactly during the Early Cretaceous, the mammals and birds become diverse, common, and flourishing, thus leading to the appearance of bloodsuckers. Apparently, the origin of hematophagy does not merely demarcate the time of the origin of the homoiothermal animals, as was thought by Beklemishev, but reflects their transformation into an ecologically important group. Incidentally, possibly pulling bloodsucking sand flies down into the Early Jurassic is not too disastrous for the hypothesis concerning the primary nature of hematophagy on mammals. Phlebotominae are the only lair parasites amongst the orthorrhaphous dipterans, and in the Jurassic, the mammals most likely were predominantly small lair dwellers. Beklemishev wrote that the encounter of parasites and their hosts in a shelter should occur much earlier than on pastureland, which may support the theory in question if the above suggestions regarding hematophagy of Psychodidae are ever confirmed by facts.

Agreeing with the triggering role of homoiothermal animals on the origin of the hematophagy, we can also assume that already in the Cretaceous, in that epoch of dinosaurs, bloodsuckers found an approach to fundamentally different corneous skin of reptiles, having discovered some weak points like eyelids. Recently, Borkent (1995) has proposed a reconstruction in which he shows that only a large dinosaur might be the host of the biting midge species. Below we will analyze his argumentation.

Many of the nematocerous dipterans, not only bloodsuckers, possess olfactory clavate sensillae on their maxillary palps. It has been shown on the example of Culicidae that these sensillae work also as receptors of carbon dioxide, and the number of these sensillae reflects the host size, since a smaller animal needs a greater development of olfactory organs to be discovered (Chaika, 1997). At least two biting midge species, *Culicoides canadensis* and *C. bullus*, have been described from Late Cretaceous Canadian amber the morphological features of which (a combination of the mouthpart structure and a small number of the clavate sensillae) provide ground for the suggestion that they fed on very large vertebrates. But there are no such large mammals or birds known in the Canadian deposits of this age (apparently, mammals did not exceed the size of opossum; birds, the size of divers or pelicans); thus, so the only candidates left are large dinosaurs, for instance, *Corythosaurus* that was discovered there (Borkent, 1995).

The hypothesis about hematophagy on reptiles in the Cretaceous appears to be correct, but the chain of conclusions, which have been widely cited (e.g., Labandeira, 1998), does not seem to be convincing. First, data on the correlation of the metabolism with the size in birds and mammals are extrapolating over reptiles; however, these are fundamentally different types of metabolism. Second, another explanation is possible; it has been demonstrated on the example of Culicidae that the least number of clavate sensillae is characteristic of ambushing females (despite the size of their victims) that fly for short distances, not of those hunting for large gregarious prey, which are characterized by active watching flight (Chaika, 1997). Consequently, the matter is the hunting strategy rather than the prey size, which cannot be tested in fossils.

If the reptiles are considered to be the first hosts of the hematophagous insects, then the time of the appearance of the bloodsuckers (Late Jurassic–Early Cretaceous) can scarcely be logically explained, since the first reptiles originated in the Late Carboniferous, and the dinosaurs, the most successful of all reptiles, became dominant terrestrial vertebrates already in the Late Triassic (Carroll, 1988). True enough, it is exactly during the Jurassic and the Cretaceous that the dinosaurs because very large and it is obvious that a larger host may be much easier revealed, since it produces a larger amount of specific substances and carbon dioxide; additionally, those giants might be inertially homoiothermal. However, we do not think that exactly that event gave rise to hematophagy, since the corneous skin of reptiles seems to be the most disadvantageous object for experiments of the first bloodsuckers, when compared to the soft skin of mammals. The "reptile" hypothesis would not suit advocates of the primary nature of hematophagy Diptera as well, since the time of their appearance, the lowermost Middle Triassic (Krzemiński *et al.*, 1994), can be linked to some important event in the amniotic world with difficulty.

Reasons that triggered the transition to hematophagy are still unclear. It is believed that insects turn to hematophagy if they do not accumulate nutrients in the amount sufficient for laying their eggs (Rubtsov, 1956). However, such a mechanism may be suggested only for the lower dipterans, since among the majority of other hematophagous insects, males (lice, fleas, bugs, and higher flies) and larvae (lice and bugs) are also bloodsucking; in fleas, the larval diet is rather nutritious as well, they consume dried blood and the excrements of adult fleas. Larvae of many dipterans prey or dwell in highly nutritious substrates as well. Possibly, there was a reverse causal relationship, the transition of dipteran imagoes to hematophagy gave their larvae a way to exploit ill nutritious and/or ephemer substrates, thus leading to further ecological radiation and allowing the reduction of the period of the larval stage or, in the case of the higher pupiparous flies, even elimination of larval feeding in such a changeable world.

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