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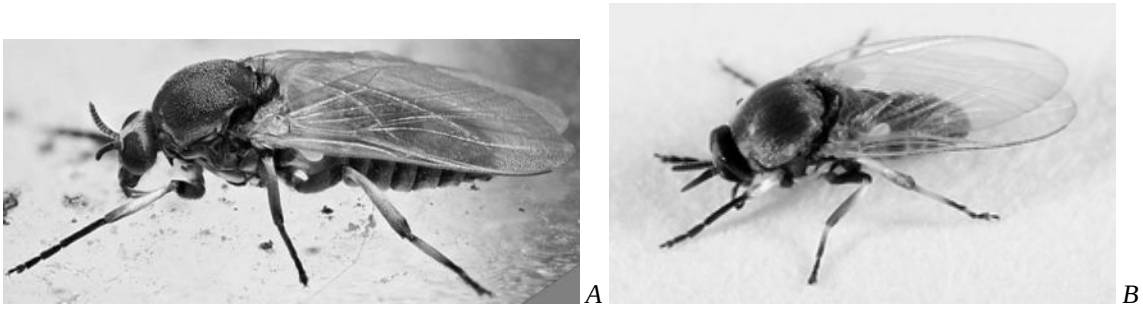
The Adaptation of Bloodsucking Black Flies to Feeding on Warm-blooded Animals

Simuliidae morphological adaptations to suck the blood are combined into several groups: habitus, sensory vesicle of maxillary palp (Lutz's organ), mouthparts, claws adaptations. Habitus adaptations can be traced in smaller absolute body sizes, relatively large head sizes, reduction of 2–6 abdomen sternites, presence of wide wings. The sensory organ adaptations are associated with a size decrease of the sensory vesicle during the transition from the ornithophilia to the mammalophilia of Simuliidae. Adaptations in the mouthparts structure are associated with the presence of hooks on the labrum, fringes with downward directed spinules on the distal margin of the hypopharynx, developed teeth on the maxillas and mandibles apical margins. The structure of females claws is adapted to various groups of hosts of the blood feeders – birds, mammals. Probably that the initial type of black flies hematophagy was ornithophilia.

Key words: black flies, feeding adaptation, homoiothermal tetrapodes.

Scientific Problem Statement and its Significance. According to some researchers [1; 6; 7; 18; 22], the adult Simuliidae initial type of feeding, as in all modern chironomids, was the sap feeding (they cut the stems of inshore plants by their mouthparts and fed on plant juices and secretes). The peculiarities of larvae feeding, like their insufficiency to accumulate a sufficient amount of nutrients for the sexual products development, could be the reason for the appearance in black flies females of necessity for additional blood feeding, as a high-quality source of proteins and fats. The sap feeding black flies, are few, for example, *Cnephia pallipes* Fries, *Prosimulium alpestre* Dorogostajski et Rubtsov. In general in the world's Simuliidae fauna, there are known 37 species which feed on plant juice, from 2204 recent [2; 22]. They have relatively smaller head sizes (head width equal to 2/3 of the thorax width), longer legs, presence of the 2nd – 6th sternites, relatively narrow wings (Fig. 1 A), underdeveloped teeth on the mandible and maxilla (fig. 2 A) [1; 4; 8; 19].



A *B*

Fig. 1. *Females. General View: A – Cnephia pallipes, B – Simulium sp. [3]*

In most species, females have bloodsuckers mouthparts of a piercing-cutting type with developed maxillas and mandibles teeth (fig. 2 B).

It should be noted that among the black flies with a bloodsucking type mouthparts, not all females feed on blood to oviposit the first portion of eggs. The first oviposition can be autogenous, on account of the females fat body reserves, which accumulated by larvae during the development. But black flies cannot accumulate a fat body in the adult phase, therefore all subsequent ovipositions are accompanied by obligatory blood sucking.

Most of the modern species feed on the warm-blooded (homoiothermic) animals. Females suck blood once a few days, which depends on the term development of eggs. The search of hosts for the blood feeding is purposeful and occurs in three stages [1; 22]. Remote search is due to reaction of the sensory vesicle of maxillary palps, when the females detect the specific bird or mammal odor. Search on the middle distance occurs in the process of the hosts of the blood feeders approaching, when the female catches the carbon dioxide molecules, which are released by animals during breathing. A close search occurs by the using the organ of vision – the females find a group of animals, choose a particular animal from the group and the best place on the animal's body. The search for the host with the help of the olfactory organ in the first stages and the reaction to sweat and carbon dioxide makes it impossible to feed on the poikilothermic tetrapods for the black flies.

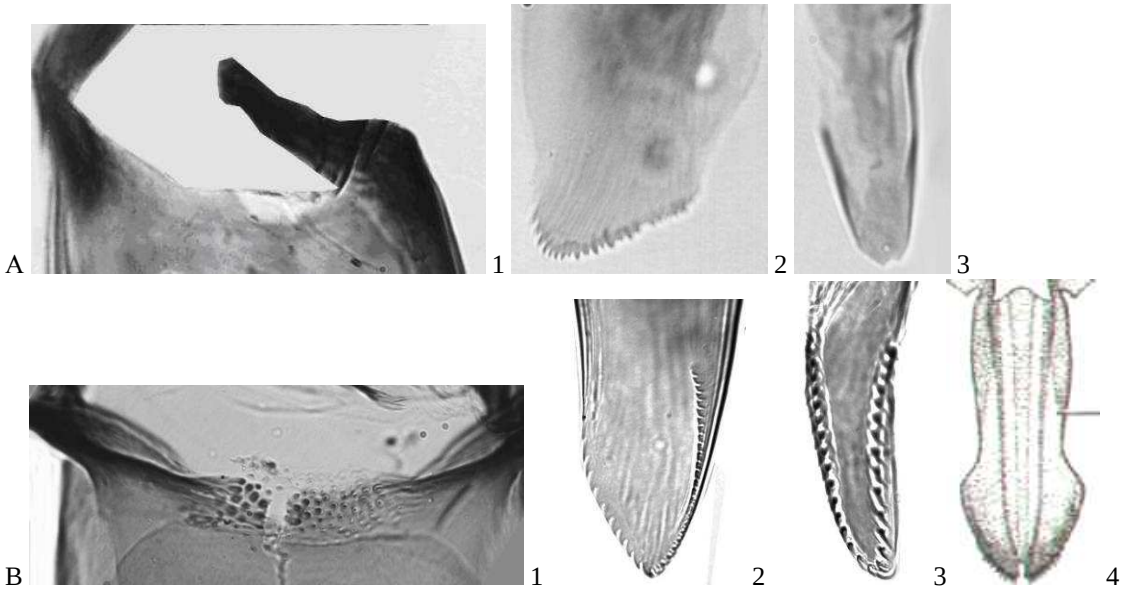


Fig. 2. *Structures of the Mouthparts: A – Cnephia pallipes, D – Simulium paramorsitans: 1 – proximal margin of the cibarium, 2 – mandibular teeth, 3 – maxilla teeth, 4 – hypopharynx [1]*

Formulation of the Article Purpose and Objectives. The aim of the study was to establish the morphological adaptations of Simuliidae bloodsucking species females to feed on warm-blooded animals.

Materials and Methods. In our work were used the traditional methods of total black flies micropreparations studying in Canadian balsam under a light microscope, due to the need to use a standard serial material. The collections of the Zoological Institute of the Russian Academy of Sciences, the National Research Center for Biological Resources of the National Academy of Sciences of Belarus, the Donetsk National University and the Lesya Ukrainka Eastern European National University were used to carry out the research. The materials for the work were long-term studies, generalizations of morphological and biological black flies adaptations to living conditions and also analysis of literary sources.

Statement of the Main Material and Substantiation of the Research Results. All the black flies morphological adaptations to sucking blood can be combined into several groups: habitus, sensory organ (sensory vesicle), mouthparts, claws adaptations.

1) Habitus adaptations. Bloodsuckers are more compact compared to phytophages (Fig. 1 B), the average size of *Cnephia pallipes* females is 3,8–4,0 mm, and the average size of the genus *Simulium* females is 2,5–3,5 mm [14].

Blood-sucking species of black flies have a relatively large head (head width is equal to the thorax width), shorter legs, sternites are reduced from the 2nd to the 6th (fig. 3), which is associated with the necessity to stretch the abdomen during the blood feeding (fig. 4). They have relatively wide wings to soar in air currents (fig. 5), as far as the range of the passive dispersion is quite significant [1; 8; 10; 11; 19].

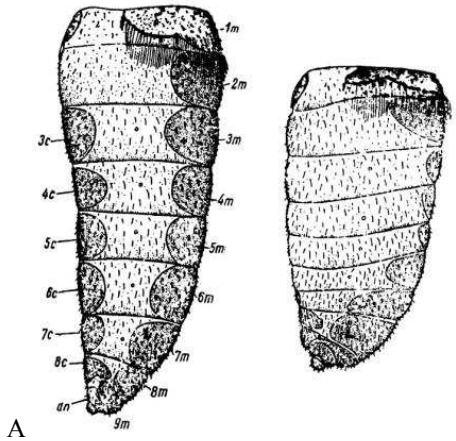
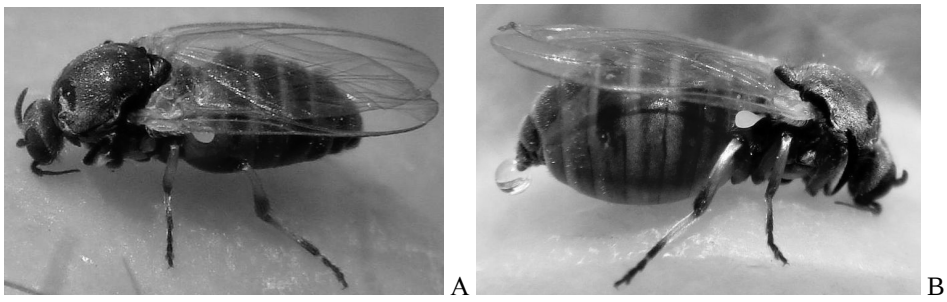


Fig. 3. *The Abdomen of Black Fly Female [19]: A – nonbloodsucking species, B – blood-sucking species*



A B

Fig. 4. *The Black Fly Simulium sp. [20] Before the Beginning of Bloodsucking (A) and at the end of Bloodsucking (B)*

A B

Fig. 5. *Wings of the Black Flies: A – Cnephia [12]; B – Simulium Aureum [16]*

2. Adaptation to the search a host for the blood feeding is the development of the sensory vesicle of the maxillary palp, which is located in front of the head (fig. 6). The size of the sensory vesicle differs among different groups of black flies. Ornithophilic black flies of the genus *Simulium* the subgenera *Eusimulium, Nevermannia, Hellichiella, Byssodon*, have a rounded and large 3rd segment of the maxillary palp (length 0,13–0,17 mm, width 0,08–0,11 mm), which contains a large sensory vesicle (length 0,06–0,08 mm, width 0,04–0,05 mm) densely covered with sensitive papillae. In teriophilian black flies of the genera *Stegopterva, Simulium* the subgenera *Schoenbaueria, Wilhelmia, Obucovia, Boophthora, Simulium*, the 3rd segment of the maxillary palp is small, elongate (length 0,10–0,14 mm, width 0,05–0,07 mm), contains a small sensory vesicle (length 0,03–0,06 mm, width 0,02–0,04 mm) densely covered with sensitive papillae.

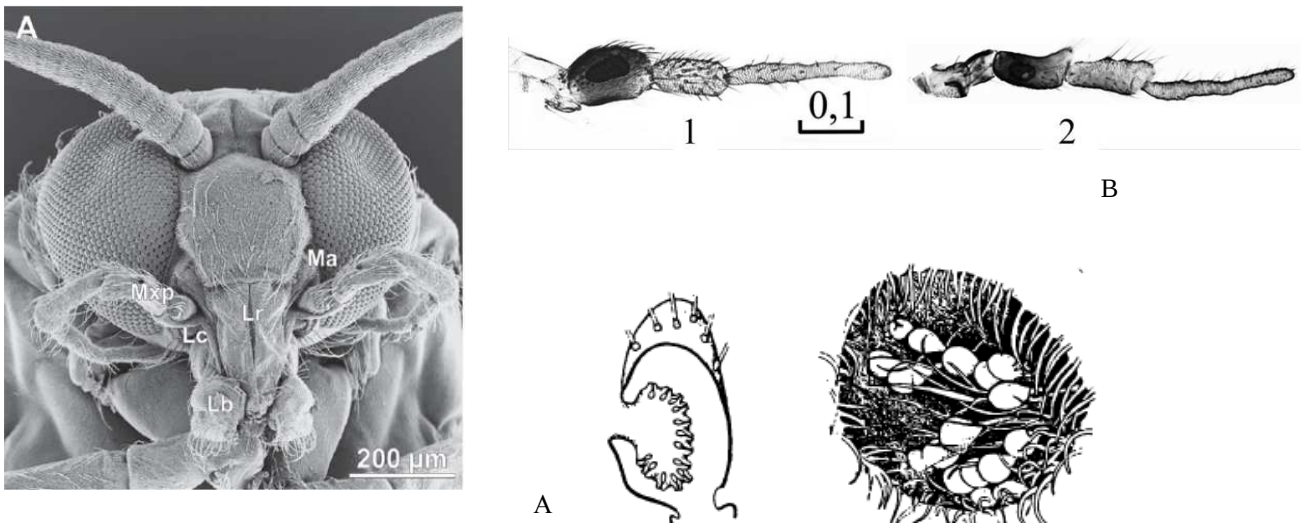


Fig. 6. *Structure of the Head [15] (A), the Simuliidae Maxillary Palp (B): 1 – Simulium Verna, 2 – Simulium Noellery and the Structure of the Sensory Vesicle (C) [6]*

Such differences in the structure of the black flies sensory vesicle of different trophic specialization can be explained by the generally smaller relative sizes of birds compared to mammals and, correspondingly, the need to have a large relative surface of the olfactory organ for prey search. A large sensory vesicle

demanded a large segment in which it located. The further expansion process of trophic specialization and the transition to feeding on mammals that had relatively large size and led a herd lifestyle resulted in a decrease of the olfactory organ sensory surface area and, correspondingly, a decrease the sensory vesicle and the trird segment of the maxillary palp.

3. Black flies have piercing-cutting type of mouthparts with developed maxillas and mandibles teeth. This type of mouthparts has four features. First, the presence of two or three branched hooks on the labrum (fig. 7), which attached to the skin of the host and keep the insect during feeding (males and nonbloodsucking species have setae). The second, presence of a fringes with setae on the distal margin of the hypopharynx (fig. 2. B 4), which fix the mouthparts on the wound margin. The labia hooks and the hypopharynx setae stretch the wound in different directions to increase it. Third, the fringes of spines presence on the proximal margin of the cibarium (fig. 2. B 1). Fourth, the presence of well-developed teeth on the maxillas and mandibles apical margins, which cut the integument of the host and forming a wound by cutting movements. During feeding blood enters the mouth from the wound, but not from the capillary, as mosquitoes do. The proboscis immerses in the integument of the host to 0,4 mm depth [21].

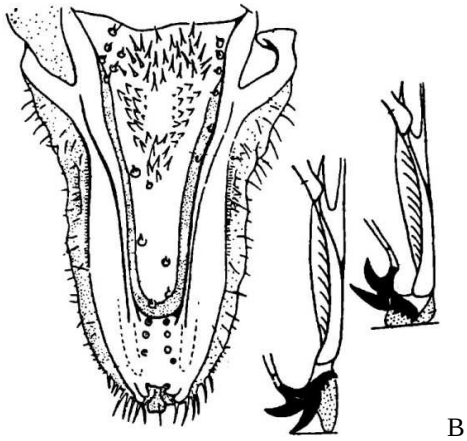


Fig. 7. *The Structure of the Simuliidae Labrum [21]: A – General View, B – Labrum Terminal Teeth*

4. Clear adaptive changes associated with imago feeding reveal in the claw structure (Fig. 8). The claws on the females legs are different structure, because they are adapted to the body integument of various groups of hosts for blood feeding – birds and mammals. Ornithophilic black flies of the subgenera *Eusimulium, Nevermannia* have a developed thumblike lobe at the base of the claw (fig. 9 A). The slit size on the claw corresponds to the diameter of the barbules on the avian feathers, it allows the female to clamp one or two barbules of the feather with two separated claws and hold on to it.

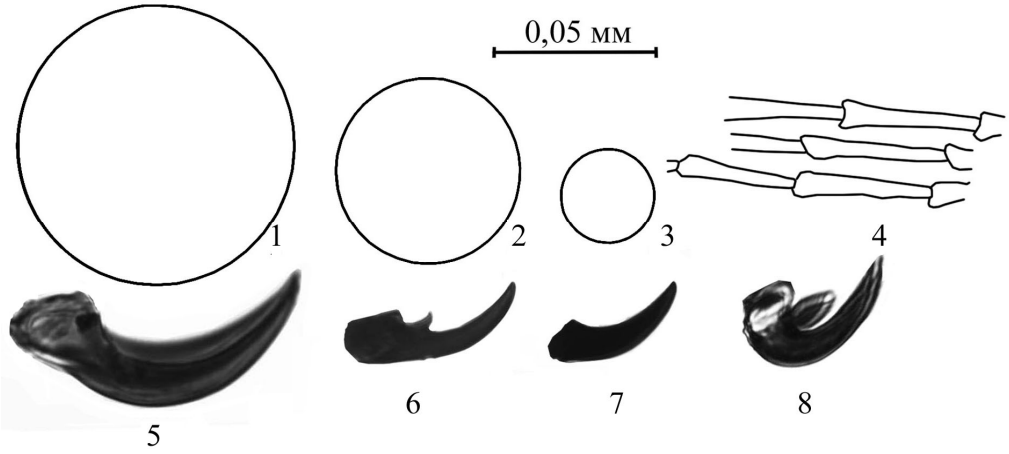
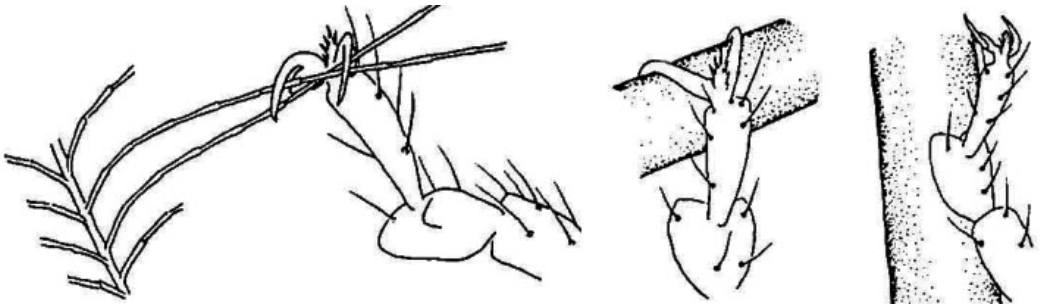


Fig. 8. *Correspondence of the Skin Derivatives of Hosts for Blood Feeding and Claws of Black Flies Females (from Gryaznov, [12], with Changes). Hair Diameter: 1 – From the Cow's Ear, 2 – From the Cow's Body, 3 – From the Human Body, 4 – Chicken Feathers; Claws 5 – Females Simulium (Wilhelmia) Equinum, 6 – females Simulium Ornatum, 7 – Females Simulium (Boophthora) erythrocephalum, 8 – Females Simulium (Nevermannia) Verna*

In the mammalophilic species from subgenera *Wilhelmia, Boophthora, Simulium*, claw is simple, without thumblike lobe. The claw inner bend corresponds to diameter of the mammalian hair. Females are fixed on mammalian hair by putting the separate claws on one side of the hair at right angles to the last segment of the tarsomere (Fig. 9 B).

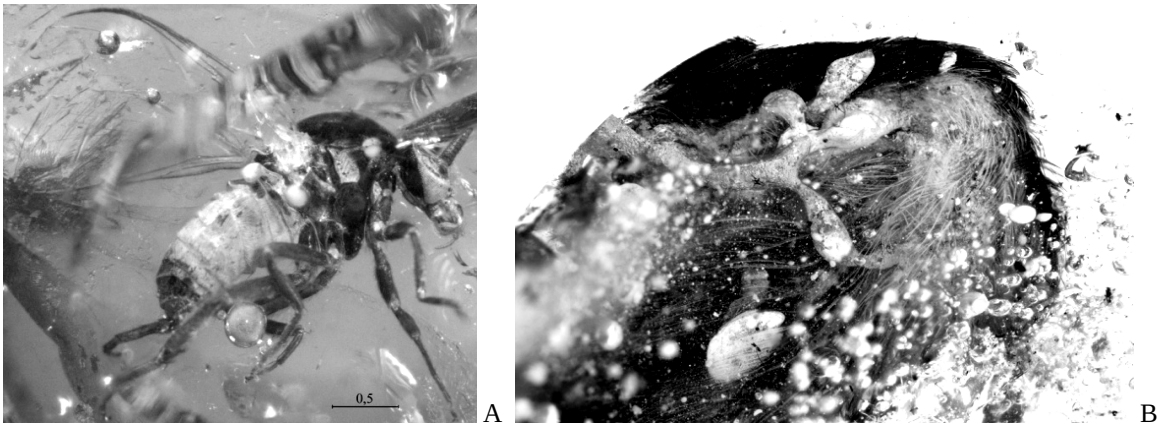


A B C

Fig. 9. *Methods of Fixing Black Flies Females on Hosts for Blood Feeding (From Gryaznov, [12], with Changes): A – Ornithophilic Species on the Barbules of the Avian Feather, B – Mammalophilic Species on Mammalian Hair; C – Ornithophilic Species on Mammalian Hair*

In females that feed on both birds and mammals (*Stegopterna, Tetisimulium, Simulium* species-group *ornatum*), there is a small basal thumblike lobe of the claw. On birds, they can grab the barbules, on mammals they don't use a claw, but hold on the surface of the hair using the underside of the III tarsomere (fig. 7 B) [12].

Considering the question of black flies hematophagy and imago adaptation to it, we can't pass by the historical aspect of black flies feeding. Black flies are known from the Lower-Middle Jurassic [13] and even then they had bloodsucking type mouthparts. In recent years have appeared many findings of black flies fossils in the Mesozoic ambers of the Late Cretaceous period from the north of Eurasia [17]. All investigated black flies of this period had a tarsomere claw with a basal thumblike lobe, in modern species such feature is characteristic for ornithophilic species. In addition, amber of the same age of the Northern Hemisphere (North American Arctic) were massively found the remains (bones and feathers) of birds living along the coast of the seas and fresh water bodies [4; 5] and could be the hosts for black flies feeding. Thus, it could be traced the connection between Cretaceous birds and their ectoparasites – black flies. Understanding the black flies adaptation to feeding on warm-blooded animals will help to clarify the general pathways of the simuliid evolution.



A B

Fig. 10. *Fossils in Cretaceous Amber: A – Black Fly; B – Bird Wing [4]*

Conclusions and Prospects for Further Research. Thus, the Simuliidae morphological adaptations to suck the blood can be combined into several groups: habitus, sensory vesicle (Lutz's organ), mouthparts, claws adaptations. Habitus adaptations can be traced in smaller absolute body sizes, relatively large head sizes, reduction of 2–6 abdomen sternites, presence of wide wings. The sensory vesicle adaptations are associated with a size decrease of the sensory vesicle during the transition from the ornithophilia to the mammalophilia of Simuliidae. Adaptations in the mouthparts structure are associated with the presence of

hooks on the labrum, fringes with downward directed spinules on the distal margin of the hypopharynx, developed teeth on the maxillas and mandibles apical margins. The structure of females claws is adapted to various groups of hosts of the blood feeders – birds, mammals. Probably, that the initial type of black flies hematophagy was ornithophilia.

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Sources and Literature

1. Adler P. H. The Black Flies (Simuliidae) of North America / P. H. Adler, D. C. Currie, D. M. Wood. – New York : Cornel University Press, 2004. – 942 p.
2. Adler P. H. World blackflies (Diptera: Simuliidae): a comprehensive revision of the taxonomic and geographical inventory [2016] / P. H. Adler, R. W. Crosskey. – 2016. – 126 p. [Elektronik resourse]. – Mode of access : https://www.clemson.edu/cafls/biomia/pdfs/blackflyinventory.pdf
3. Antrim N. H. Simulium sp. / N. H. Antrim. – 2008 [Elektronik resourse]. – Mode of access : http://www.pbase.com/tmurray74/image/98798665
4. Becker R. Bird wings trapped in amber are a fossil first from the age of dinosaurs / Becker R. // Nature. – 2016 [Elektronik resourse]. – Mode of access : http://www.nature.com/news/bird-wings-trapped-in-amber-are-a-fossil-first-from-the-age-of-dinosaurs-1.20162.
5. Bono R. K. A Large Ornithurine Bird (*Tingmiatornis arctica*) from the Turonian High Arctic: Climatic and Evolutionary Implications / R. K. Bono, J. Clarke, J. A. Tarduno, D. Brinkman // Scientific Reports. – 2016 [Elektronik resourse]. – Mode of access : https://www.nature.com/articles/srep38876
6. Crosskey R. W. The natural history of blackflies / R. W. Crosskey. – Chichester, U.K., 1990. – 711 p.
7. Currie D. C. Morphology and systematics of primitive Simuliidae (Diptera: Culicomorpha) / D. C. Currie. – Edmonton : Univ. of Alberta, 1988. – 331 p.
8. Davies L. The taxonomy of British black-flies (Diptera, Simuliidae) / L. Davies // Trans. Roy. Entomol. Soc. London. – 1966. – Vol. 118. – Pt. 14. – P. 413–511.
9. Gryaznov A. I. Autogenous blood-sucking species of blackflies (Diptera, Simuliidae) [Avtogennost krovososushcich vidov moshek (Diptera, Simuliidae)] / A. I. Gryaznov // 9 Congress All-Union. Entomol. Society, oct., 1984: theses. doc. – Kyiv, 1984a. – P. 130–131 [In Russian].
10. Gryaznov A. I. The morphology of the abdominal sclerites female blood-sucking blackflies Simuliidae [Morfologiya bryushnych skleritov samok krovososushcich moshek Simuliidae] / A. I. Gryaznov // Morphology and Ecology of Diptera – potential vectors of infectious diseases. – Ivanovo, 1984b. – P. 51–73 [In Russian].
11. Gryaznov A. I. The number of ovariol in the ovaries of bloodsucking midges (Diptera, Simuliidae) and its relation to the nutritional and reproductive behavior of females [Chislo ovariol v yaichnikakh krovososushcich moshek (Diptera, Simuliidae) I yego sviaz s pishchevym I reproduktivnym povedeniem samok] / A. I. Gryaznov // Zool. Journal. – 1995. – T. 74, Вып. 2. – P. 51–73 [In Russian].
12. Houston S. Cnephia / S. Houston. – 2009 [Elektronik resourse]. – Mode of access : http://bugguide.net/node/view/250053/bgpage
13. Kalugina N. S. New Mesozoic Simuliidae and Leptoconopidae and the origin of blood-sucking in the lower Diptera [Novye mezozoiskie Simuliidae i Leptoconopidae I proischozhdenie krovososaniia u nizshici dvukrylykh nasekomykh] / N. S. Kalugina // Paleontological Journal. – 1991. – № 1. – P. 81–84 [In Russian].
14. Kaplich V. M. Keys to the black flies (Diptera: Simuliidae) of Polesie [Opredelitel moshek (Diptera: Simuliidae) Polisia] / V. M. Kaplich, E. B. Sukhomlin, A. P. Zinchenko. – Minsk : Novoe znanie, 2012. – 477 p.
15. Krenn H. W. Form, function and evolution of the mouthparts of blood-feeding Arthropoda / H. W. Krenn, H. Aspȍck // Arthropod Structure & Development. – 2012. – Vol. 41. – P. 101–118.
16. Lindsey J. K. Simulium aureum Fries 1824 (Family Simuliidae) / J. K. Lindsey. – 2010 [Elektronik resourse]. – Mode of access : http://www.commanster.eu/commanster/Insects/Flies/SpFlies/Simulium.aureum.html
17. Perkovsky E. E. The First Record of Late Cretaceous Blackflies (Diptera: Simuliidae) in Asia (Yantardakh, Taimyr) / E. E. Perkovsky, E. B. Sukhomlin // Paleontological Journal. – 2016. – Vol. 50 (9). – P. 997–1000.
18. Rubtsov I. A. Adaptive character of taxonomic features variability [Adaptivnyi kharakter izmenchivosti taksonomicheskikh priznakov] / I. A. Rubtsov // Zool. Journal. – 1970. – Vol. 49. – Issue. 9. – P. 635–646 [In Russian].
19. Rubtsov I. A. Black flies (family of Simuliidae). Fauna of the USSR. Insects Diptera [Moshki (sem. Simuliidae). Fauna SSSR. Nasekomye dvukrylye] / I. A. Rubtsov. – M. ; L. : AN SSSR, 1956. – T. 6. – Issue 6. – 860 p.
20. Solé J. M. Simuliidae / J. M. Solé. – 2011 [Elektronik resourse]. – Mode of access : ttp://www. biodiversidadvirtual.org/insectarium/Simuliidae-img195803.html

21. Wenk P. Bionomics of adult black flies / P. Wenk // M. Laird (ed.), Black flies: the future for biological methods in integrated control. – London : Academic Press, 1981. – P. 259–284.
22. Yankovsky A. V. Keys to the black flies (Diptera: Simuliidae) of Russia and adjacent territories (former USSR) [Opredelitel moshek (Diptera: Simuliidae) Rossii i sopredelnykh territorii (byvshego SSSR)] / A. V. Yankovsky. – SPb : RAS, 2002. – 570 p.

Сухомлін Катерина, Зінченко Олександр, Зінченко Марія. Пристосування кровосисних мошок до живлення на теплокровних тваринах. Морфологічні адаптації симуліїд до ссання крові об'єднано в декілька груп: адаптації габітусу, органа чуття (органа Лутца), ротового апарату, кігтиків. Адаптації габітусу простежено в менших абсолютних розмірах тіла відносно більших розмірах голови, редукції 2–6 стернітів черевця, наявності широких крил. Адаптації органа чуття пов'язані зі зменшенням розмірів органа Лутца при переході від орнітофілії до теріофілії симуліїд. Адаптації в будові ротового апарату пов'язані з наявністю гачків на лабрумі, облямівки зі спрямованих донизу шипиків на дистальному краї гіпофаринксу, розвинених зубців на кінцях максил та мандибул. Будова кігтиків самок адаптована до різних груп живителів – птахів, ссавців. Імовірно, що вихідним типом гематофагії мошок була орнітофілія.

Ключові слова: мошки, адаптації до живлення, гомойотермні тетраподи.

Сухомлин Екатерина, Зинченко Александр, Зинченко Мария. Приспособление кровососущих мошек к питанию на теплокровных животных. Морфологические адаптации симулиид к кровососанию объединены в несколько групп: адаптации габитуса, органа чувств (органа Лутца), ротового аппарата, коготков. Адаптации габитуса прослеживаются в меньших абсолютных размерах тела, относительно больших размерах головы, редукции 2–6 стернит брюшка, наличии широких крыльев. Адаптации органа чувств связаны с уменьшением размеров органа Лутца при переходе от орнитофилии к териофилии симулиид. Адаптации в строении ротового аппарата связаны с наличием крючков на лабруме, каймы из направленных вниз шипиков на дистальном крае гипофаринкса, развитых зубцов на концах максилл и мандибул. Строение коготков самок адаптировано к различным группам прокормителей – птиц, млекопитающих. Вероятно, что исходным типом гематофагии мошек была орнитофилия.

Ключевые слова: мошки, адаптации к питанию, гомойотермные четыреногие.

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