

New data on classification of Hippoboscidae (Diptera): Genus *Lipoptena* Nitzsch, 1818

Новые данные по классификации Hippoboscidae (Diptera): род *Lipoptena* Nitzsch, 1818

A.A. Yatsuk*, T.A. Triseleva*, A.V. Matyukhin*, E.P. Nartshuk**
А.А. Яцук*, Т.А. Триसेлева*, А.В. Матюхин*, Э.П. Нарчук**

* A.N. Severtsov Institute of Ecology and Evolution, Leninskii Prosp. 33, Moscow 119071 Russia. E-mail: sasha_djedi@mail.ru, <https://orcid.org/0000-0003-0913-7823>; triselyova@yandex.ru, <https://orcid.org/0000-0003-1384-756X>; amatyukhin53@mail.ru, <https://orcid.org/0000-0002-4787-7681>.

** ФГБУН Институт проблем экологии и эволюции им. А.Н. Северцова Российской академии наук, Ленинский пр-т 33, Москва 119071 Россия.

** Zoological Institute, Russian Academy of Sciences, Universitetskaya Nab. 1, Saint Petersburg 199034 Russia. E-mail: chlorops@zin.ru, <https://orcid.org/0000-0001-8300-4928>.

** ФГБУН Зоологический институт Российской академии наук, Университетская наб. 1, Санкт-Петербург 199034 Россия.

Key words: Abdomen morphology, Diptera, Hippoboscidae, *Lipoptena*, *Lipoptenella*, keds.

Ключевые слова: Морфология брюшка, Diptera, Hippoboscidae, *Lipoptena*, *Lipoptenella*, мухи-кровососки.

Abstract. Based on morphological and molecular analysis, a new classification of the genus *Lipoptena* Nitzsch, 1818 has been proposed. The subgenus *Lipoptenella* Bequaert, 1942 has been promoted to the rank of genus. In the genus *Lipoptena*, the morphological groups «*cervi*» and «*capreoli*» are distinguished, not matching in composition with the groups early identified by Maa [1969b]. A key has been compiled for the genera of the subfamily Lipopteninae and keys for all species of the genera *Lipoptenella* and *Lipoptena*.

Резюме. На основании морфологического и молекулярного анализа предложена новая классификация рода *Lipoptena* Nitzsch, 1818. Подрод *Lipoptenella* Bequaert, 1942 повышен до ранга рода. В роде *Lipoptena* выделены морфологические группы «*cervi*» и «*capreoli*», не совпадающие по составу с группами, ранее выделенными Маа [1969b]. Составлен определительный ключ для родов подсемейства Lipopteninae и ключи для всех видов из родов *Lipoptenella* и *Lipoptena*.

Introduction

Hippoboscidae Samouelle, 1819 is a specialised group of blood-sucking ectoparasites with three related families: Glossinidae Theobald, 1903, Streblidae Kolenati, 1863 and Nycteribiidae Samouelle, 1819 [Hennig, 1973]. According to another view, Streblidae and Nycteribiidae are subfamilies of Hippoboscidae [Zhang, 2013]. Widely distributed throughout the world, these flies transmit many dangerous diseases in mammals [Bequaert, 1954; Doszhanov, 1980, 2003; Ganez et al., 2002; Farajollahi et al., 2005; Buss et al., 2016; Lee et al., 2016; Skvarla et al., 2019; Werszko et al., 2020; Tiawsirisup et al., 2023] and birds [Khametova et al., 2018; Čisovská Bazsalovicsová et al., 2023]. Periodic findings of bird parasitic flies on mammals and, conversely, parasites of mammals on birds suggest a diversity of biocenotic

contacts between animals and, accordingly, the great epidemiological and epizootological significance of hippoboscids [Matyukhin, 2012].

The family Hippoboscidae is divided into four subfamilies [Maa, Peterson, 1987]. Lipopteninae Speiser, 1908 and Hippoboscinae Brues & Melander, 1932 mainly parasitize on mammals, while Ornithomyiinae Bigot, 1853 and Ornithoicinae Hennig, 1973 — on birds [Hennig, 1973; Doszhanov, 1980, 2003; Dick, 2018]. The subfamily Lipopteninae is divided into tribes Lipoptenini, including *Lipoptena* Nitzsch, 1818 and *Neolipoptena* Bequaert, 1942, and Melophagini, formed by the genus *Melophagus* Latreille, 1802. Representatives of this subfamily are characterised by absent wings (Melophagini) or wings that break off at the base (Lipoptenini), as well as by narrow eyes, compared to other hippoboscids. Their humeral tubercles do not protrude forward [Doszhanov, 2003].

Hippoboscidae have a large number of unique morphological and physiological adaptations, most of which are closely related to their ectoparasitic lifestyle [Petersen et al., 2007]. The morphology of the abdomen is important in the life of Hippoboscidae flies. The larva develops in the abdomen and females lay a prepupae [Hagan, 1948; Meier et al., 1999]. Changes in the abdominal morphology affect the ability of the abdomen to stretch. Also, at present, more and more evidence suggests that the changes in the attachment apparatus of the louse flies legs, namely: claws, pulvilli and empodium, which allow flies to live and effectively move in the fur and feathers of the host, determine the evolution within the family [Yatsuk et al., 2023].

The first major revision of this group was carried out by Bequaert [1942a], who described the genus *Neolipoptena* and identified some groups within the

genus *Lipoptena* Nitzsch, 1818. Currently, the genus *Neolipoptena* is represented only by the species *Neolipoptena ferresi* Bequaert, 1935 [Dick, 2018]. It differs from other genera in reduced tergites and their location in the posterior third of the abdomen [Bequaert, 1942a].

The genus *Lipoptena* currently includes 29 species [Dick, 2018]. These flies have been divided into several groups according to the morphological characteristics of the species [Maa, 1963, 1965, 1969 a,b; Dick, 2018]. At the same time, the morphology of their abdomen and head is quite diverse, but the tergites are not reduced. Usually *Lipoptena* flies have ocelli, and on the tarsus one of the pair claws and one of the pulvillus under this claw are larger than another one [Doszhanov, 2003].

Current data on the morphology and molecular phylogeny of Hippoboscidae flies show some inconsistencies in the Lipoptenini taxonomy. The purpose of this study was to clarify the taxonomic status of some representatives of the genus *Lipoptena*.

Material and Methods

The total DNA was extracted from whole flies using Diatom-200 reagents (Isogen, Moscow) according to the manufacturer's manual. Polymerase chain reaction (PCR) was performed using primers LCO1490 and HCO2198 [Folmer et al., 1994]. Thermal cycling consisted of an initial denaturation step at 94 °C for one min, followed by six cycles of 1 min at 94 °C, one min at the annealing temperature 45 °C and one min at 72 °C; followed by 40 cycles of 1 min at 94 °C, one and a half min at the annealing temperature 55 °C and one and a half min at 72 °C; with a final extension at 72 °C for six min. Amplification products were purified through precipitation by ethyl alcohol solution with the addition of five M sodium acetate. Electrophoresis and reading of amplification product nucleotide sequences were carried out on an automatic ABI PRISM 3130 sequencer (Applied Biosystems, United States) using BigDye Terminator reagent kit 3.1 (Applied Biosystems). The study was conducted using the «Joint Usage Center Instrumental methods in ecology» at the IEE RAS.

Two sequences of *L. cervi* were obtained (ON858176, ON858178) (Table 1). The analysed fragment consisted of 591 base pairs (bp) of the mtDNA COI gene. Other sequences were taken from the NCBI database (www.ncbi.nlm.nih.gov) (Table 1).

Phylogenetic analyses of the obtained sequences and of the sequences from NCBI were performed using GTR+G as the best-fit model of Maximum Likelihood method (ML) with 1000 bootstrap replicates in MEGA 5.1 software package [Tamura et al., 2011] and GTR model (1set nst = 6 rates = gamma and invgamma for 990000 generations at a recording 100) in MrBayes ver. 3.0 [Ronquist, Huelsenbeck, 2003] software package. A representative of the sister family Glossinidae (*Glossina fuscipes* Newstead, 1910) was taken as an outgroup.

Morphological analysis was carried out according to the works of Bequaert [1942 a, b], Maa [1963, 1965, 1969 a, b], Doszhanov [1980, 1997, 2003] and

Skvarla et al. [2019]. All species of the genus *Lipoptena* listed in Dick [2018] were analysed: *L. arianae* Maa, 1969, *L. axis* Maa, 1969, *L. binoculus* (Speiser, 1908), *L. capreoli* Rondani, 1878, *L. cervi* (Linnaeus, 1758), *L. chalcomelaena* Speiser, 1904, *L. couturieri* Seguy, 1935, *L. depressa* (Say, 1823), *L. doszhanovi* Grunin, 1974, *L. efovea* Speiser, 1905, *L. fortisetosa* Maa, 1965, *L. grahami* Bequaert, 1942, *L. guimaraesi* Bequaert, 1957, *L. hopkinsi* Bequaert, 1942, *L. iniqua* Maa, 1969, *L. japonica* Bequaert, 1942, *L. mazamae* Rondani, 1878, *L. nirvana* Maa, 1969, *L. paradoxa* Newstead, 1907, *L. pauciseta* Edwards, 1919, *L. pteropi* Denny, 1843, *L. pudui* Peterson & Maa, 1970, *L. rusaecola* Bequaert, 1942, *L. saepes* Maa, 1969, *L. saltatrix* Maa, 1969, *L. sepiacea* Speiser, 1905, *L. sigma* Maa, 1965, *L. sika* Mogi, 1975, *L. timida* Maa, 1969, *L. weidneri* Maa, 1969.

The present work is registered in ZooBank (www.zoobank.org) under LSID urn:lsid:zoobank.org:pub:00747F72-9303-471D-A1E7-F74549F6E74C

Results

Data analysis revealed a significant difference between individual groups of species within the genus *Lipoptena* in the morphology of some features. The species *L. depressa*, *L. guimaraesi*, *L. mazamae*, *L. pteropi* and *L. pudui* can be divided into a separate group based on the morphology of the abdomen, in which all tergites, except tergite 1+2, are displaced to the posterior third of the abdomen. In addition, the species *L. pteropi* differs from other species in this group due to a one reduced pulvillus on each tarsus and absence of setae on the membranose area of the abdomen preceding the displaced tergites.

In the species *L. binoculus*, *L. capreoli*, *L. couturieri*, *L. grahami*, *L. paradoxa*, *L. saltatrix* and *L. weidneri* one pulvillus is reduced on all tarsi. *L. iniqua* and *L. sepiacea* have one reduced pulvillus on the tarsi of the first and second legs and absent simple ocelli. In the species *L. chalcomelaena* all pulvilli are reduced. All these species can be classified into the second group. The abdominal tergites, unlike the previous group of the genus *Lipoptena*, are not displaced in these flies. Additionally, *L. binoculus* and *L. paradoxa* lack simple ocelli, and *L. sepiacea* and *L. paradoxa* have short or vestigial palpus.

The remaining studied species of the genus *Lipoptena* correspond to the following key characters: the tergites are not reduced or displaced, the simple ocelli are developed, one of the claws on the tarsi and one of the pulvilli under this claw are larger than the other one.

The phylogenetic analysis showed that all of the constructed dendrograms match at the key nodes. The divergence of superfamilies does not contradict the phylogeny of dipterans from the modern studies [Pape et al., 2011; Lambkin et al., 2013; Narayanan et al., 2019] and, in particular, Hippoboscidae flies [Petersen et al., 2007; Liu et al., 2018; Moya, 2019; Yatsuk et al., 2023].

There are 2 clusters within Hippoboscidae on dendrograms (Fig. 1). The first cluster is formed by rep-

Table 1. Sequence data
Таблица 1. Данные сиквенсов

Genus and species name	Sequences number	Data source	Data link
<i>Crataerina hirudinis</i> (Linnaeus, 1758)	MW590962, MW590970	NCBI	Lehikoinen et al., 2021
<i>Crataerina pallida</i> (Olivier in Latreille, 1812)	EF531196	NCBI	Petersen et al., 2007
<i>Glossina fuscipes</i> Newstead, 1910	KP979584	NCBI	Votycka et al., 2015
<i>Hippobosca longipennis</i> Fabricius, 1805	MK405667	NCBI	Mihalca et al., 2019
<i>Hippobosca equina</i> Linnaeus, 1758	EF531207	NCBI	Petersen et al., 2007
<i>Hippobosca equina</i> Linnaeus, 1758	OR054157	NCBI	Yatsuk et al., 2023
<i>Hippobosca rufipes</i> von Olfers, 1816	EF531207	NCBI	Petersen et al., 2007
<i>Icosta ardea</i> (Macquart, 1835)	OR064837, OR064838	NCBI	Yatsuk et al., 2023
<i>Lipoptena cervi</i> (Linnaeus, 1758)	ON858177, ON858179, ON858181	NCBI	Yatsuk et al., 2023
<i>Lipoptena cervi</i> (Linnaeus, 1758)	ON858176, ON858178	NCBI	The current study
<i>Lipoptena cervi</i> (Linnaeus, 1758)	KR362257	NCBI	Jaakola et al., 2015
<i>Lipoptena cervi</i> (Linnaeus, 1758)	MF496025	NCBI	Sochova et al., 2017
<i>Lipoptena depressa</i> (Say, 1823)	JF871918	NCBI	Unpublished
<i>Lipoptena depressa</i> (Say, 1823)	KR686276	NCBI	Hebert et al., 2016
<i>Lipoptena fortisetosa</i> Maa, 1965	MK405668, MK405669	NCBI	Mihalca et al., 2019
<i>Lipoptena fortisetosa</i> Maa, 1965	MN807844, MN807846	NCBI	Kurina et al., 2019
<i>Lipoptena mazamae</i> Rondani, 1878	EF531205	NCBI	Petersen et al., 2007
<i>Melophagus ovinus</i> (Linnaeus, 1758)	NC_037368	NCBI	Liu et al., 2017
<i>Olfersia spinifera</i> (Leach, 1817)	KC700567, KC700570	NCBI	Levin, Parker, 2013
<i>Ornithoctona erythrocephala</i> (Leach, 1817)	JQ246707	NCBI	Marinho et al., 2012
<i>Ornithoica aequisenta</i> Maa, 1966	HIPMJ021-19	BOLD	ZSM Collection of Manfred Sommerer
<i>Ornithoica exilis</i> (Walker, 1861)	HIPMJ022-19	BOLD	ZSM Collection of Manfred Sommerer
<i>Ornithoica momijamai</i> Kishida, 1932	OR045887, OR045888, OR045889	NCBI	Yatsuk et al., 2023
<i>Ornithoica stipituri</i> (Schinner, 1868)	HIPMJ018-19	BOLD	ZSM Collection of Manfred Sommerer
<i>Ornithoica turdi</i> (Latreille, 1812)	OR064834	NCBI	Yatsuk et al., 2023
<i>Ornithoica unicolor</i> Speiser, 1900	OR064840, OR064841	NCBI	Yatsuk et al., 2023
<i>Ornithomya anchineura</i> Speiser, 1905	MZ261718	NCBI	Levesque-Beaudin & Sinclair 2021
<i>Ornithomya avicularia</i> (Linnaeus, 1758)	OR064829, OR064830, OR064831, OR064832	NCBI	Yatsuk et al., 2023
<i>Ornithomya biloba</i> Dufour, 1827	MF496010	NCBI	Sochova et al., 2017
<i>Ornithomya biloba</i> Dufour, 1827	OR054213	NCBI	Yatsuk et al., 2023
<i>Ornithomya candida</i> Maa, 1967	OR064839	NCBI	Yatsuk et al., 2023
<i>Ornithomya chloropus</i> Bergroth, 1901	OR054225, OR064835, OR064836	NCBI	Yatsuk et al., 2023
<i>Ornithomya comosa</i> Austen, 1930	OR064833	NCBI	Yatsuk et al., 2023
<i>Ornithomya fringillina</i> Curtis, 1836	MW590981	NCBI	Lehikoinen et al., 2021
<i>Ornithophila gestroi</i> (Rondani, 1878)	KJ174684	NCBI	Gutierrez-Lopez et al., 2015
<i>Pseudolynchia canariensis</i> (Macquart, 1840)	OR054156	NCBI	Yatsuk et al., 2023

representatives of the subfamily Ornithoicinae, the genus *Ornithoica* Rondani, 1878. The second cluster is divided into two subclusters. The first includes representatives of the subfamily Ornithomyinae, the genera *Crataerina* von Olfers, 1816, *Ornithoctona* Speiser, 1902, *Ornithophila* Rondani, 1879 and *Ornithomya* Latreille, 1802. The second subcluster is formed by representatives of the tribe Olfersini, the genera *Icosta* Speiser, 1905, *Olfersia* Leach, 1817 and *Pseudolynchia* Bequaert, 1926 and mammalian parasites represented by the genera *Melophagus* Latreille, 1802, *Hippobosca* Linnaeus, 1758 and *Lipoptena*. At the same time, the species *L. depressa* and *L. mazamae*, the representatives of the subgenus *Lipoptenella* Bequaert, 1942 are separated from other representatives of the genus *Lipoptena*, *L. cervi* and *L. fortisetosa*.

Analysis of genetic distances (Table 2) between genera with pairwise comparison of groups showed

that within Hippoboscidae the genetic distance between individual genera ranges from 8.14 between *Ornithomya* and *Crataerina* to 15.34 between *Melophagus* and *Ornithoctona* (Table 2). The distance between *Lipoptenella* and *Lipoptena* is 11.8, which corresponds to the genetic distance between genera within the studied family.

Discussion

As follows from the description of the genus, representatives of *Lipoptena* have developed simple ocelli, palpus slightly shorter than the fronts, the tarsi have a pair of simple claws, one of which is smaller than the other [Bequaert, 1942a; Doszhanov, 1980, 2003], one of the pulvilli may also be smaller [Maa, 1969a] or one or both pulvillus may be reduced [Doszhanov, 1980]. On the female abdomen there are from 2 to 5 median tergites (tergites 3–7), in males from 1 to 4 [Bequaert, 1942a;

Table 2. Distances between groups
Таблица 2. Дистанции между группами

Genera	<i>Ornithoica</i>	<i>Ornithomya</i>	<i>Ornithoictona</i>	<i>Lipoptena</i>	<i>Crataerina</i>	<i>Hippobosca</i>	<i>Melophagus</i>	<i>Icosta</i>	<i>Pseudolynchia</i>	<i>Ornithophila</i>	<i>Glossina</i>	<i>Olfersia</i>
<i>Ornithomya</i>	13.29											
<i>Ornithoictona</i>	14.38	11.39										
<i>Lipoptena</i>	13.63	12.64	14.25									
<i>Crataerina</i>	13.34	8.14	12.36	13.35								
<i>Hippobosca</i>	13.3	14.6	14.57	11.21	14.60							
<i>Melophagus</i>	13.33	14.08	15.34	12.92	14.43	12.84						
<i>Icosta</i>	14.17	14.32	14.14	14.12	15.11	13.66	15.00					
<i>Pseudolynchia</i>	13.26	13.67	14.31	12.66	14.20	12.46	11.55	11.03				
<i>Ornithophila</i>	12.72	13.43	14.31	14.69	13.97	13.45	13.10	14.83	13.10			
<i>Glossina</i>	14.09	15.69	16.72	15.82	16.67	17.11	16.21	17.41	16.03	17.76		
<i>Olfersia</i>	13.57	13.55	13.62	11.29	12.99	11.19	11.90	11.72	11.81	13.79	15.86	
<i>Lipoptenella</i> stat.n.	14.03	13.82	15.98	11.80	13.79	12.70	11.78	14.89	13.56	15.46	17.30	12.82

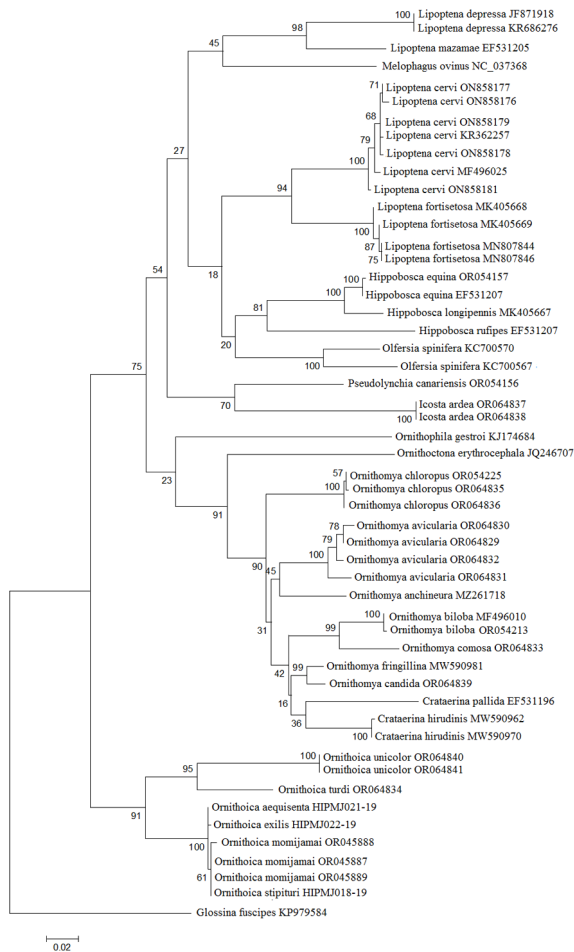


Fig. 1. Reconstructed phylogenetic tree of the family Hippoboscidae with the species of the genus *Glossina*. as an external group, using MEGA 5.1 Maximum likelihood (ML). Bootstrap support is depicted at the nodes. The scale is the genetic distance between haplotypes.

Рис. 1. Полученное филогенетическое древо для семейства Нипробосцидае с видом рода *Glossina*, в качестве внешней группы, с помощью метода максимального правдоподобия (ML) в MEGA 5.1. Уровень поддержки бутстреп обозначен в узлах. Масштабная шкала — генетическое расстояние между гаплотипами.

Doszhanov, 1980]. To date, based on morphological data, *Lipoptena* species have been divided into several groups: (a) *L. japonica*, *L. cervi*, *L. efovea*, *L. nirvana*, *L. sigma*, *L. saepes*, *L. pauciseta*, *L. rusaeicola*, *L. fortisetosa*, *L. axis*, *L. timida*; (b) *L. pteropi*; (c) *L. couturieri*, *L. saltatrix*, *L. grahami*, *L. weidneri*, *L. chalcomelaena*, *L. capreoli*, *L. arianae*; (d) *L. hopkinsi*, *L. sepiacea*, *L. iniqua*, *L. binoculus*, *L. paradoxa*; (e) *L. depressa*, *L. guimaraesi*, *L. mazamae* and the remaining without the group *L. doszhanovi*, *L. pudui*, *L. sikae* [Maa, 1969b; Dick, 2018].

Analysis of morphological data showed, that the first new group we identified includes species from groups (e) and (b) and *L. pudui*, which remained without a group. In the Bequaert's [1942a] study, the subgenus *Lipoptenella* was isolated, which included species *L. depressa*, *L. moschi* (Pallas 1777), *L. mazamae* and *L. pteropi* (synonym *L. gracilis* Speiser 1903). The subgenus *Lipoptenella* was represented in our phylogenetic analysis by the species *L. depressa* and *L. mazamae*. The genetic distance between them and neighbouring genera corresponds to the genus level. According to the genetic distance, as well as the position of *L. depressa* and *L. mazamae* on the phylogenetic tree and the unique features of the abdomen morphology of species from the subgenus *Lipoptenella*, we propose to elevate the subgenus *Lipoptenella* Bequaert, 1942 to the rank of a genus, including, respectively, *L. depressa*, *L. guimaraesi*, *L. mazamae*, *L. pteropi* and *L. pudui*. The species *L. mosshi* included by Bequaert [1942a] is now considered a synonym of *L. cervi* (Linnaeus, 1758) [Soös, Hürka, 1986].

The genus *Neolipoptena* may be the closest genus to *Lipoptenella*. This is indicated by the fact that the tergites are displaced to the posterior third of the abdomen. Their hosts belong to the same subfamily Capreolinae Brookes, 1828 [Bequaert, 1942a; Maa, 1969b]. However, to fully clarify the issue about the phylogenetic relationships of this genera, a molecular genetic study is required.

Species *L. binoculus*, *L. capreoli*, *L. chalcomelaena*, *L. couturieri*, *L. grahami*, *L. iniqua*, *L. paradoxa*, *L. saltatrix*, *L. sepiacea* и *L. weidneri*, allocated to the second group, probably also may be separated into a distinct genus on the basis of serious differences in their attachment apparatus and palpus from those described for the genus *Lipoptena*, as well as the absence of simple ocelli in some species. But now we do not have enough data to determine their status. Therefore, we combine them into the separate group «*capreoli*» within the genus *Lipoptena*. Accordingly, this group included representatives from the old morphological groups (c) and (d).

We propose to combine the remaining species *L. arianae*, *L. axis*, *L. cervi*, *L. doszhanovi*, *L. efovea*, *L. fortisetosa*, *L. hopkinsi*, *L. japonica*, *L. nirvana*, *L. pauciseta*, *L. rusaecola*, *L. saepes*, *L. sigma*, *L. sikae* and *L. timida* into the «*cervi*» group.

Diptera Linnaeus, 1758:

Hippoboscidae Samouelle, 1819:

Lipopteninae Speiser, 1908

Lipoptenella Bequaert, 1942 **stat.n.**

Type species: *Melophagus depressus* Say, 1823, by original designation.

Hosts. Mammals. Deers (Tragulidae Milne-Edwards, 1864; Cervidae Goldfuss, 1820: Capreolinae Brookes, 1828).

Description. Flies of small sizes.

Head. The eyes are oval. There are simple ocelli. Palpi shorter than forehead. The antennae are small, the parafrontals are wide.

Thorax. The humeral tubercles do not protrude forward. The prothorax is separated from the mesothorax by a suture. The transversal suture runs obliquely to the scutellar suture. Scutellum with rounded posterior edge. Dorsal chaetotoxicity of the thorax is poorly developed.

Wings. The costa ends long before the top of the wing. Three longitudinal veins. The wings break off at the base when the fly reaches a host.

Legs. The claws on the paws are simple. Pulvilli are developed.

Abdomen. Pleurisy 1 large. Pleurisy 2 is very elongated. Tergites 3-5 are displaced to the posterior third, except for tergite 1+2. The abdomen has a large membranous area between tergite 1+2 and displaced tergites.

Differential diagnosis. This genus belongs to the subfamily Lipopteninae due to its oval eyes and three veins wings breaking off at the base. The genus *Lipoptenella* stat.n. differs from the genus *Lipoptena* due to tergites 3-5 displaced to the posterior third of the abdomen.

Representatives of *Lipoptenella* stat.n. differ from representatives of the genus *Melophagus* due to the width of the eyes, which exceed the width of the antennae, and the presence of wings, and from representatives of *Neolipoptena* due to the presence of tergites 3-5.

Given below keys to genera of the subfamily Lipopteninae and species of the genera *Lipoptenella* and *Lipoptena* are

based on Bequaert [1942a, b], Maa [1965, 1969a, b], Doszhanov [1980, 2003], Salvetti et al. [2020], Oboňna et al. [2022], Visagie [1993].

KEY TO GENERA OF THE SUBFAMILY LIPOPTENINAE

1. The membranous area of the dorsal part of the abdomen (representing dorsum of abdominal segment 3) is naked. Tergites are located in the posterior third 2
— Tergites are located on the abdomen in the usual way .. 3
2. Displaced tergites are reduced (hard to distinguish) *Noelipoptena*
— At least some of the tergites are not reduced
..... *Lipoptenella* stat.n.
3. The eyes are narrow: narrower than the antennae, the length of the eye exceeds the width by 3-4 times. Wings and halteres are absent *Melophagus*
— Eyes wide: wider than the antennae. Wings may be broken off, but not reduced..... *Lipoptena*

KEY TO SPECIES OF THE GENUS LIPOPTENELLA

1. Membranous area of abdominal dorsum without setae. 3 wide tergites in both sexes. Each leg with 1 vestigial and 1 fully developed pulvillus *L. pteropi*
— Membranous area of abdominal dorsum extensively setose. 2 wide tergites in female, 1 in male. Each leg with pair of fully developed pulvilli 2
2. Membranous area of abdominal dorsum with not more than 55 setae, usually less 3
— Membranous area of abdominal dorsum with not less than 80 setae, usually more 4
3. Palpus not more than 2.5 times as long as wide, distinctly shorter than frons. Body length less than 1.4 mm
..... *L. mazamae*
— Palpus about 4 times as long as wide, and slightly longer than frons. Body length 1.4-1.7 mm *L. puidi*
4. Apical spur of tibia 1 as stout as major apical spur of tibia 2. Tergite 5 only represented by 1-3, usually 2 setae which arise from membrane rather than sclerite. Brazilian Subregion *L. guimaraesi*
— Apical spur of tibia 1 very thin, seta-like, distinctly thinner than major apical spur of tibia 2. Tergite 5 represented by small setiferous sclerite, usually also by an arcuate series of setae leading to spiracle 5 at each side. Rocky Mtn Subregion or Californian Subregion *L. depressa*

KEY TO SPECIES OF THE GENUS LIPOPTENA

1. One or two pulvilli reduced or vestigial (group «*capreoli*») 2
— Pulvilli normally developed (group «*cervi*») 12
2. All pulvilli reduced *L. chalcomelaena*
— Not all pulvilli reduced 3
3. 2 scutellar setae *L. binoculus*
— More scutellar setae 4
4. Anterior pulvilli of all legs reduced or vestigial 6
— Other features: anterior pulvilli of 1 and 2 legs vestigial, pulvilli of leg 3 both vestigial 5
5. Male: median length of sternite 1 hardly less than that of its lateroposterior lobe. Inner and outer margin of that lobe distinctly though weakly curved. Apices of pleurites 1-2 in dorsal view rounded. Female: posterior margin of pleurite 1 subequal in length to inner posterior margin of pleurite 2. Ocelli absent *L. iniqua*

- Male: median length of sternite 1 markedly exceeding that of its lateroposterior lobe. Inner and outer margins of that lobe straight or very nearly straight. Apex of dorsum of pleurite 2 acute, apex of pleurite 1 angulate. Female: posterior margin of pleurite 1 distinctly shorter than inner posterior margin of pleurite 2. Ocelli absent *L. sepiacea*
6. Palpus vestigial, not or barely protruding beyond anterior margin of frons, and in lateral view, hardly longer than wide. Claws slightly asymmetrical, ocelli absent.....
..... *L. paradoxa*
- Palpus well developed, distinctly protruding beyond anterior margin of frons. Other features 7
7. Body length more than 2.4 mm 8
- Body length less than 2.4 mm 10
8. Extremely hairy body and legs. 8–13 humerals setae. Lateral setae of mesonotum forming continuous patch with acrostichals between humeral callus and scutoscutellar suture. 8–10 (in 4–5 pairs) scutellar setae *L. couturieri*
- Body less hairy. Less humerals setae. Lateral setae arranged differently. 8 or less scutellar setae 9
9. Body moderately dark *L. saltatrix*
- Pale body and legs *L. capreoli*
10. Body length more than 2.3 mm. Mesonotum setae: 5–7 humerals, 7–9 acrostichals, 9–13 laterocentrals (in 2 series), 3–6 postalars (about 1/2 of them are small), 2–3 prescutellars (1 large plus 1–2 small), 9–12 mesopleurals, 4–8 scutellars (in 2–4 pairs) *L. saltatrix*
- Body length less than 2.3 mm. Other features 11
11. Mesonotum setae: 3–4 humerals, 5–8 acrostichals, 3–4 laterocentrals (in single series), 3–5 postalars, 1 major plus 0–2 minor prescutellars, 7–8 mesopleurals, 4–5 scutellars (in 3 pairs). Legs are not densely hairy *L. weidneri*
- Mesonotum setae: 7–8 acrostichals, 7–10 laterocentrals (in 2 series), 4 postalars, 2 prescutellars, 6 scutellars (2 very long). Densely hairy legs *L. grahami*
12. Few mesonotum setae (like 3 humerals, 7 acrostichals, 4 laterocentrals, 3 postalars, 2 prescutellars, 6–7 mesopleurals, 6 scutellars or less) 13
- Other features: larger number of mesonotum setae 21
13. Only longitudinal suture on the mesoscutum 17
- Prescutellar and longitudinal sutures or grooves on mesoscutum 14
14. Longitudinal and transversal sutures of mesonotum sutures ending at same level, both not reaching scutellar suture ..
..... *L. timida*
- Longitudinal and transversal sutures of the mesonotum almost reaching scutellar suture 15
15. 6 scutellar setae *L. efovea*
- 4 scutellar setae 16
16. All four tergites are normally developed. Body length 1.6–2.2 mm *L. hopkinsi*
- Tergite 1 is represented by row of strong setae. Body length 1.3–1.6 mm *L. rusaecola*
17. Body length less than 2 mm 18
- Body length 2 mm or more 20
18. Posterior (inner) margin of pleurite 2 distinctly concavely curved *L. fortisetosa*
- Posterior margin of pleurite 2 straight 19
19. Median pregenital plate of female gently narrowed behind. Female sternite 1 weakly divergent behind ... *L. pauciseta*
- Median pregenital plate of female strongly narrowed behind. Female sternite 1 strongly divergent behind *L. indica*
20. 7–8 acrostichals setae. Pleurite 1 kidney-shaped with 8–11 long setae *L. nirvana*
- 5–6 acrostichals setae. S-shaped posterior margin of female pleurite 2 *L. sigma*

21. Prescutellar and longitudinal sutures on mesoscutum.....
..... *L. cervi*
- Only longitudinal suture on mesoscutum 22
22. Body length 2 mm or more 23
- Body length less than 2 mm *L. sikae*
23. 12 scutellar setae. Pleurite I without clear edges. Pleurite 2 big and round *L. doszhanovi*
- 6–8 scutellar setae. Other features 24
24. 42–52 laterocentrals mesonotum setae *L. arianae*
- Less laterocentrals mesonotum setae 25
25. 9–14 laterocentrals mesonotum setae *L. saepes*
- 28 laterocentrals mesonotum setae *L. japonica*

Acknowledgements

The work was performed as part of the State Research Projects of the A.N. Severtsov Institute of Ecology and Evolution RAS (No. FFER-2024-0018) and Zoological Institute RAS (No. 122031100272-3).

References

- Bequaert J.C. 1942a. A monograph of the melophaginae or ked-flies of sheep, goats, deer and antelopes (Diptera, Hippoboscidae) // Entomologica Americana. Vol.22. No.1. P.1–64.
- Bequaert J.C. 1942b. A monograph of the melophaginae or ked-flies of sheep, goats, deer and antelopes (Diptera, Hippoboscidae) // Entomologica Americana. Vol.22. No.2. P.65–172.
- Bequaert J.C. 1954. The Hippoboscidae or louse-flies (Diptera) of mammals and birds. 2. Taxonomy, evolution and revision of America genera and species // Entomologica Americana. Vol.34. P.1–232.
- Buss M., Case L., Kearney B., Coleman C., Henning J.D. 2016. Detection of Lyme disease and anaplasmosis pathogens via PCR in Pennsylvania deer ked // Journal of Vector Ecology. Vol.41. No.2. P.292–294. <https://doi.org/10.1111/jvec.12225>
- Čisovská Bazsalovicsová E., Víchová B., Oboňa J., Radačovská A., Blažeková V., Králová-Hromádová I. 2023. Bird louse flies *Ornithomya* spp. (Diptera: Hippoboscidae) as potential vectors of mammalian babesia and other pathogens // Vector-Borne and Zoonotic Diseases. Vol.23. No.5. P.275–283. <https://doi.org/10.1089/vbz.2022.0088>
- Moya de R.S. 2019. Implications of a Dating Analysis of Hippoboscoidea (Diptera) for the origins of phoresis in feather lice (Psocoda: Phthiraptera: Philopteridae) // Insect Systematics and Diversity. Vol.3. No.4. P.1–5. <https://doi.org/10.1093/isd/ixz008>
- Dick C.W. 2018. Checklist of world Hippoboscidae (Diptera: Hippoboscoidea). Chicago: Department of Zoology, Field Museum of Natural History. 7 p.
- Doszhanov T.N. 1980. Mukhi-krovososki (Diptera, Hippoboscidae) Kazakhstana. Alma-Ata: Nauka. 280 p. [In Russian]
- Doszhanov T.N. 1997. Mukhi-krovososki (Diptera, Hippoboscidae) iz V'yetnama // Izvestiya ministerstva nauki Akademii nauk Respubliki Kazakhstan. Seriya biologicheskaya i meditsinskaya. Vol.4. P.24–27. [In Russian].
- Doszhanov T.N. 2003. Mukhi-krovososki (Diptera, Hippoboscidae) Palearktiki. Almaty: Nauka. 277 p. [In Russian].
- Farajollahi A., Crans W.J., Nickerson D., Bryant P., Wolf B., Glaser A., Andreadis T.G. 2005. Detection of West Nile virus RNA from the louse fly *Icosta americana* (Diptera: Hippoboscidae) // Journal of the American Mosquito Control Association. Vol.21. No.4. P.474–486. [https://doi.org/10.2987/8756-971X\(2006\)21\[474:DOWNVR\]2.0.CO;2](https://doi.org/10.2987/8756-971X(2006)21[474:DOWNVR]2.0.CO;2)
- Folmer O., Black M., Hoeh W., Lutz R., Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates // Molecular Marine Biology and Biotechnology. Vol.3. No.5. P.294–299.
- Gancz A.Y., Barker I.K., Lindsay R., Dibernardo A., McKeever K., Hunter B. 2002. West Nile virus outbreak in North American owls, Ontario // Emerging Infectious Diseases. Vol.10. No.12. P.2135–2142. <https://doi.org/10.3201/eid1012.040167>

- Hagan H.R. 1948. A Brief Analysis of Viviparity in Insects // Journal of the New York Entomological Society. Vol.56. No.1. P.63–68.
- Hennig W. 1973. Diptera (Zweiflügler) // W. Kükenthal W. (Ed.): Handbuch der Zoologie. 2. Aufl. Bd.IV. Ht.2. Teil 2. Lief.20. Berlin, New York: Walter de Gruyter. 337 S. 143 Abb. <https://doi.org/10.1002/MMNZ.19750510213>
- Khametova A.P., Pichurina N.L., Zabashta M.V., Romanova L.V., Orekhov I.V., Borodina T.N., Adamenko V.I., Zabashta A.V. 2018. Biocenotic structure of natural focus of borreliosis in the Rostov region // Medical Parasitology and Parasitic Diseases. No.4. P.33–39. [In Russian]. <https://doi.org/10.33092/0025-8326mp2018.4.33-39>
- Lambkin C.L., Sinclair B.J., Pape T., Courtney G.W., Skevington J.H., Meier R., Yeates D.K., Blagoderov V., Wiegmann B.M. 2013. The phylogenetic relationships among infraorders and superfamilies of Diptera based on morphological evidence // Systematic Entomology. Vol.38. No.1. P.164–179. <https://doi.org/10.1111/j.1365-3113.2012.00652.x>
- Lee S.H., Kim K.T., Kwon O.D., Ock Y., Kim T., Choi D., Kwak D. 2016. Novel detection of *Coxiella* spp., *Theileria luwenshuni* and *T. ovis* endosymbionts in deer keds (*Lipoptena fortisetosa*) // PLoS ONE. Vol.11. Art.Pe0156727. <https://doi.org/10.1371/journal.pone.0156727>
- Liu Z.Q., Kuermanali N., Li Z., Chen S.J., Wang Y.Z., Tao H., Chen C.F. 2017. The complete mitochondrial genome of the parasitic sheep ked *Melophagus ovinus* (Diptera: Hippoboscidae) // Mitochondrial DNA Part B: Resources. Vol.2. No.2. P.432–434. <https://doi.org/10.1080/23802359.2017.1347832>
- Maa T.C. 1963. Genera and species of Hippoboscidae (Diptera) // Pacific Insects Monograph. Vol.6. 186 p.
- Maa T.C. 1965. A synopsis of the Lipopteninae (Diptera, Hippoboscidae) // Journal of Medical Entomology. Vol.2. No.3. P.233–248. <https://doi.org/10.1093/jmedent/2.3.233>
- Maa T.C. 1969a. Further notes on Lipopteninae (Diptera: Hippoboscidae) // Pacific Insects Monograph. Vol.20. P.205–236.
- Maa T.C. 1969b. A revised checklist and concise host index of Hippoboscidae (Diptera) // Pacific Insects Monograph. Vol.20. P.261–299.
- Maa T.C., Peterson B.V. 1987. Hippoboscidae // Manual of Nearctic Diptera, Vol.2. Ottawa: Agriculture Canada. Research Branch. P.1271–1281.
- Matyukhin, A.V., Zabashta, A.V., Zabashta, M.V. 2012. [Blood-sucking flies of diurnal birds of prey and owls of the Palearctic] // [Birds of Prey in the dynamic environment of the third Millennium: state and prospects]. Proceedings of the VI International conference on falcons and owls of Northern Eurasia. Krivoy Rog. 27–30 September 2012. Krivoy Rog: FL-PChernyavsky D.A. P.530–533. [In Russian].
- Meier R., Kotrba M., Ferrar P. 1999. Ovoviviparity and viviparity in the Diptera // Biological Reviews. Vol.74. No.3. P.199–258. <https://doi.org/10.1017/S0006323199005320>
- Narayanan Kutty S., Meusemann K., Bayless K.M., Marinho M.A.T., Pont A.C., Zhou X., Misof B., Wiegmann B.M., Yeates D., Cerretti P., Meier R., Pape T. 2019. Phylogenomic analysis of Calyptratae: resolving the phylogenetic relationships within a major radiation of Diptera // Cladistics. Vol.35. No.6. P.605–622. <https://doi.org/10.1111/cla.12375>
- Oboňa J., Fogašová K., Fulín M., Greš S., Manko P., Repaský J., Roháček J., Sychra O., Hromada M. 2022. Updated taxonomic keys for European Hippoboscidae (Diptera), and expansion in Central Europe of the bird louse fly *Ornithomya comosa* (Austen, 1930) with the first record from Slovakia // ZooKeys. Vol.1115. P.81–101. <https://doi.org/10.3897/zookeys.1115.80146>
- Pape T., Blagoderov V., Mostovski M.B. 2011. Order Diptera Linnaeus, 1758 // Zhang Z.-Q. (Ed.): Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness // Zootaxa. Vol.3148. No.1. P.222–229. <https://doi.org/10.11646/zootaxa.3148.1.42>
- Petersen F.T., Meier R., Kutty S.N., Wiegmann B.M. 2007. The phylogeny and evolution of host choice in the Hippoboscidae (Diptera) as reconstructed using four molecular markers // Molecular Phylogenetics and Evolution. Vol.45. No.1. P.111–122. <https://doi.org/10.1016/j.ympev.2007.04.023>
- Ronquist F., Huelsenbeck G.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models // Bioinformatics. Vol.19. No.12. P.1575–1574. <https://doi.org/10.1093/bioinformatics/btg180>
- Salveti M., Bianchi A., Marangi M., Barlaam A., Giacomelli S., Bertoletti L., Roy L., Giangaspero A. 2020. Deer keds on wild ungulates in northern Italy, with a taxonomic key for the identification of *Lipoptena* spp. of Europe // Medical and Veterinary Entomology. Vol.34. No.1. P.74–85. <https://doi.org/10.1111/mve.12411>
- Skvarlal M.J., Machtinger E.T. 2019. Deer Keds (Diptera: Hippoboscidae: *Lipoptena* and *Neolipoptena*) in the United States and Canada: new state and county records, pathogen records, and an illustrated key to species // Journal of Medical Entomology. Vol.20. No.10. P.1–17. <https://doi.org/10.1093/jme/tjy238>
- Soős Á., Húrka K. 1986. Catalogue of palaeartic Diptera. Vol.11. Scathophagidae – Hypodermatidae. Budapest: Akadémiai Kiadó. P.215–226.
- Tamura K., Peterson D., Peterson N., Stecher G., Nei M., Kumar S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods // Molecular Biology and Evolution. Vol.28. No.11. P.2731–2739. <http://dx.doi.org/10.1093/molbev/msr121>
- Tiawsirisup S., Yurayart N., Thongmeesee K., Sri-In C., Akarapas C., Rittisorntanoo G., Bunphungbaramee N., Sipraya N., Maikaew U., Kongmakee P., Saedan A. 2023. Possible role of *Lipoptena fortisetosa* (Diptera: Hippoboscidae) as a potential vector for *Theileria* spp. in captive Eld's deer in Khao Kheow open zoo, Thailand // Acta Tropica. Vol.237. Art.106737. <https://doi.org/10.1016/j.actatropica.2022.106737>
- Visagie E.J. 1993. A redescription of *Lipoptena binocula* (Speiser 1908) (Hippoboscidae: Diptera), with notes on its biology and comparisons with the other two flies of this genus in South Africa // Onderstepoort Journal of Veterinary Research. Vol.60. No.1. P.51–58.
- Werszko J., Steiner-Bogdaszewska Ż., Jeżewski W., Szewczyk T., Kuryło G., Wołkowycki M., Wróblewski P., Karbowski G. 2020. Molecular detection of *Trypanosoma* spp. in *Lipoptena cervi* and *Lipoptena fortisetosa* (Diptera: Hippoboscidae) and their potential role in the transmission of pathogens // Parasitology. Vol.147. No.14. P.1629–1635. <https://doi.org/10.1017/S0031182020001584>
- Yatsuk A.A., Triseleva T.A., Narchuk E.P., Matyukhin A.V., Safonkin A.F. 2023. Morphology of the wings and attachment apparatus in the evolution of the family Hippoboscidae (Diptera) // Integrative Zoology. Vol.19. No.5. <https://doi.org/10.1111/1749-4877.12786>
- Zhang Z.-Q. 2013. Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness // Zootaxa. Vol.3703. No.1. P.1–82. <https://doi.org/10.11646/zootaxa.3148.1.1>

Поступила в редакцию 8.4.2023