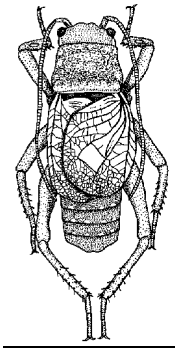

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A PRELIMINARY STUDY OF THE RESPIRATORY AND ALIMENTARY SYSTEMS OF THE EARLY CRETACEOUS "FLEA" *SAUROPHTHIRUS LONGIPES* PONOMARENKO, 1976 (INSECTA, ?APHANIPTERA, SAUROPHTHIRIDAE)

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The respiratory and alimentary systems of female *Saurophthirus longipes* display an unusual combination of plesiomorphic and specialized characters. All three pairs of tracheal trunks are retained, unusually wide, grouped as two tight clusters of three trunks at each body side, and opening into two pairs of enlarged spiracles on the mesothorax and the 8th abdominal segment. The proventriculus is enlarged as well, sclerotized, with no acanthae discernible; the midgut is simple, sac-like; the hindgut is also simple, short, straight, with no rectum differentiated. These observations suggest that the previously advanced hypothesis of Mesozoic "fleas" as parasites of the wing membrane of pterosaurs needs revision.

KEY WORDS: Mesozoic "fleas," pterosaur parasite, tracheae, amphipneustic, proventriculus, midgut, hindgut, Lower Cretaceous.

О. Д. Стрельникова, А. П. Расницын*. Предварительные результаты изучения дыхательной и пищеварительной системы раннемеловой «блохи»

***Saurophthirus longipes* Ponomarenko, 1976 (Insecta, ?Aphaniptera, Saurophthiridae) // Дальневосточный энтомолог. 2016. N 327. С. 1-7.**

Предварительные данные по дыхательной и пищеварительной системе самок *Saurophthirus longipes* демонстрируют необычное сочетание примитивных и специализированных черт. Присутствуют все три пары продольных трахейных стволов, но они гипертрофированы, объединены в два плотных блока и открываются в две пары гипертрофированнын дыхалец. Провентрикулус гипертрофирован, средняя кишка простая мешковидная, задняя также простая, короткая, прямая, не дифференцированная. Полученные данные требуют уточнения существующих представлений о паразитизме мезозойских «блох» на крыловой мембране птерозавров.

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INTRODUCTION

Saurophthirus longipes Ponomarenko, 1976 (Fig. 1) has been described from the Early Cretaceous of Transbaikalia as a hypothetical parasite of pterosaurs related to fleas (Ponomarenko, 1976). It is a wingless, comparatively big insect, ca. 12 mm long, not compressed laterally, with very long and thin, clinging legs, a piercing-and-sucking beak, antennae similar to those of fleas in the segment shape but much longer, and a soft, extensible abdomen. *Saurophthirus* has been allied (Ponomarenko, 1976) with *Tarwinia australis* Riek, 1970, described shortly before as a basal flea from the Lower Cretaceous of Australia (Riek, 1970). A similarity to *T. australis* in the structure of the legs and antenna, and the homonomous meso- and metathorax, which precluded a possible relationship with Diptera, allowed Ponomarenko to place *Saurophthirus* in the order Aphaniptera (Ponomarenko, 1976). The hypothesis has been subsequently supported by new fossils of Saurophthiridae and a related more basal family Pseudopulicidae from the Middle Jurassic and Lower Cretaceous of China (Gao *et al.*, 2012, 2013, 2014, 2016; Huang *et al.*, 2012, 2013; Huang, 2014). Because the taxonomy of all these fossils is still debatable, we refer to them as Mesozoic “fleas”.

MATERIAL AND METHODS

The object of our study, *Saurophthirus longipes*, is currently represented by 15 specimens, all from deposits of the Zaza Formation at the Baissa locality in the upper reaches of the Vitim River (West Transbaikalia). Six female specimens were selected for the study: PIN No. 3064/2378, 2380, 2381, 2383, 1898 (holotype), and 4210/6965. Other specimens were either insufficiently preserved or (one male) had the abdomen sclerotized and therefore obscuring the soft internal structures. All the material is kept at the Arthropoda Lab, Borissak Paleontological Institute, RAS, in

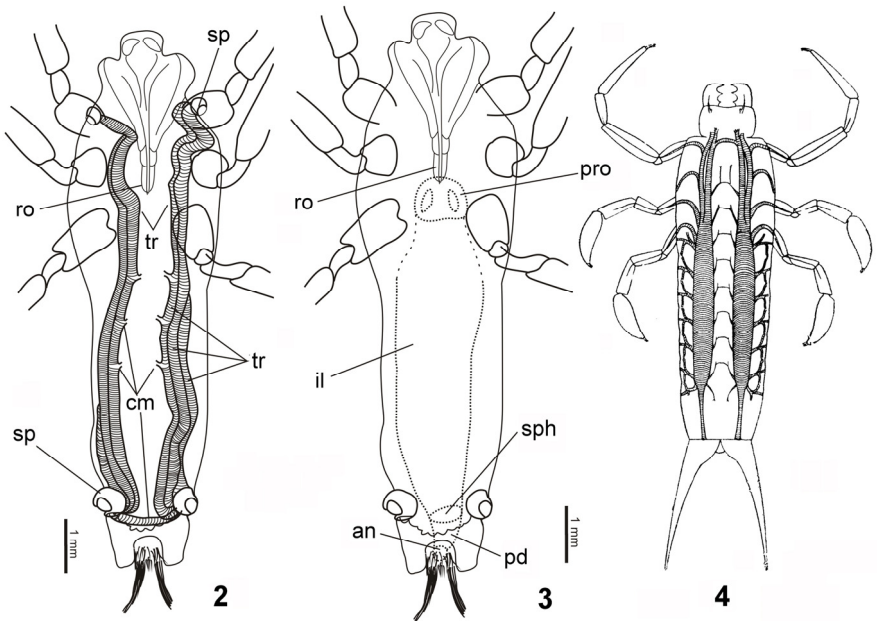
Moscow. The fossils were studied under a MPS-2 microscope either dry of wetted with 95% alcohol, and photographed with a Leica DFC 420 camera attached to a Leica M165 C microscope. The photos were combined using Helicon Focus 5.1.28 and Kolor Autopano Giga 3.0.5 and further contrasted when necessary with Adobe Photoshop CS6 and FastStone Image Viewer 5.5.

Herein we briefly report preliminary results of our work. A more detailed ongoing study, using a wider range of modern tools, will be published elsewhere.

Fig. 1. *Saurophthirus longipes*, holotype PIN no. 3064/1898, general view (photo by David Grimaldi, with permission).

RESULTS

The specimens studied reveal three pairs of longitudinal tracheal trunks, tightly clustered at each body side as a bundle of three trunks, each bundle ca. 1/3 as wide as the abdomen (Fig. 2). Spiral thickenings, the tenidia, are visible in many places, clearly indicating that these are indeed tracheae. The tracheal trunks lie dorsolaterally and open posteriorly as a pair of giant spiracles on the 8th abdominal segment. Anteriorly they are traceable to a pair of large mesothoracic spiracles, which are identified with less certainty, being obscured by sclerotized thoracic structures. One fossil preserves a thick transverse commissure connecting the posterior spiracles. Other commissures, branching off the main trunks towards the body median, are harder to see; their arrangement is probably metameric. Such visible commissures originate somewhat posteriorly of the transverse bands of spines present dorsally on the meso- and metathoracic and first four abdominal segments. The tracheal trunks occasionally intertwine, bend, and form loops near spiracles.



Figs. 2–4. Overview schemes of internal structure of Cretaceous fossil insects: 2 – respiratory system of *Saurophthirus longipes* (symbols: cm – commissures, ro – rostrum (beak), sp – spiracles, tr – tracheal trunks); 3 – alimentary system of *Saurophthirus longipes* (symbols: an – anus, il – midgut, pro – proventriculus, ro – rostrum, pd – proctodeum, sph – sphincter); 4 – larval respiratory system of *Coptoclava longipoda* Ping (Coleoptera, Coptoclavidae) from Early Cretceous of Baissa, Transbaikalia (after Ponomarenko, 1961, with permission).

The alimentary system can be traced only partially (Fig. 3). The mouthparts form a piercing-and-sucking beak with strong barbed stylets, which has been amply described (Gao *et al.*, 2013) and needs no further discussion here. The alimentary canal is visible only within the abdomen, being obscured in the head and thorax except for the well sclerotized proventriculus, situated in different specimens at the level of either meso- or metathorax (like with the gut, its place does not appear to be fixed). It is ca. 1/3 as wide as the thorax, roundly trapezoidal, widened posteriorly, with two sublateral windows of obscure nature, without identifiable needle-like acanthae characteristic of fleas and scorpion-flies. The midgut is wide, particularly anteriorly (up to 0.8 of the abdomen width at the level of the 2nd abdominal segment), straight, gradually narrowing towards the 8th segment, where it turns into the hindgut and where an ovate sphincter is sometimes visible, about as wide as the posterior spiracle. The midgut is probably well extensible; it contains no hard particles. The hindgut is straight, with no obvious differentiation into a thin gut and a rectum. It opens into the anus at the 9+10th segment, which bears the cerci and is situated in an emargination of the 8th segment. No traces of the crop, other gut diverticula, the Malpighian tubules, rectal valve, rectal papillae or any parts of the nervous or reproductive systems were observed.

DISCUSSION

The respiratory system of *Saurophthirus longipes*, with only two open spiracle pairs, one on the mesothoracic and another on the 8th abdominal segments, is amphipneustic. This condition appears to be unique among adult Holometabola, which normally are holopneustic, with all 10 spiracle pairs functional, including true fleas and scorpion flies, which are supposed to be the closest relatives of Mesozoic "fleas" (Wigglesworth, 1935; Setty, 1940). The amphipneustic tracheal system is characteristic of the holometabolan larvae developing inside of a substrate, particularly the larvae of dipterans and aquatic beetles, which (beetles) also have strongly inflated tracheal trunks (Schwanwitsch, 1949; Prokin *et al.*, 2013; Yee, 2014) like in *S. longipes*. Among insects, having three pairs of tracheal trunks is a plesiomorphic character, but their close-set arrangement as two bundles, one at each body side, in combination with each trunk being strongly inflated, appears to be a unique apomorphy. The only apparent analogue are respiratory systems of some aquatic beetle larvae, which differ by having only a single, proportionally even more inflated tracheal trunk at each side (Fig. 4).

The above similarity of the respiratory system of *Saurophthirus* to that of aquatic beetle larvae contradicts the hypothesis of aerial respiration inherent in the idea of Mesozoic "fleas" being pterosaur ectoparasites (Ponomarenko, 1976; Gao *et al.*, 2013, etc.), suggesting that it needs to be reconsidered. We cannot exclude the possibility of *Saurophthirus* females having had amphibiotic adaptations. This possibility will be addressed in detail in future publications.

The alimentary system of *S. longipes* also looks unusual for an adult insect, primarily because of its short, straight, and undifferentiated hindgut. A strongly sclerotized proventriculus and sac-like midgut are expected for a blood-sucking insect. At the same time, the visible details of the proventriculus (especially the sublateral "windows") appear unusual and require further study. The putatively closest relatives of Mesozoic "fleas," the true fleas and scorpion-flies, have proventriculi with a single central space and armed with thin cuticular needles, the acanthae, used to disintegrate the cells (erythrocytes, bacteria) contained in the ingested fluid (Setty, 1940; Chauvin, 1949).

CONCLUSION

Our study of impression fossils of female *S. longipes* has revealed unexpectedly many details of the internal structure of these ancient insects, including three pairs of wide tracheae arranged as two tight lateral clusters and opening into two pairs of enlarged spiracles on the mesothorax and the 8th abdominal segment, and the alimentary canal with a large sclerotized proventriculus, wide midgut, and short, simple hindgut. Some of the above traits support the hypothesis of Mesozoic "fleas" being blood-sucking ectoparasites of wing membranes of pterosaurs, some contradict it, and some appear unique among adult Holometabola. This emphasizes a need for a more detailed study of these fossils, using a wider range of modern imaging and analytical tools, which is currently under way.

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