

Musculature of the male genitalia and systematic position of the family Athericidae (Diptera)

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The musculature of the male genitalia of *Atherix ibis* Fabricius (Athericidae) is described and compared with that of Tabanidae (Tabanoidea), Rhagionidae and Coenomyiidae (Xylophagoidea). Comparative studies confirm that Athericidae should be considered a separate family and included in the Tabanoidea.

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Introduction

The Athericidae are a small family of Brachycera Orthorrhapha. Previously, the representatives of Athericidae were included in the family Rhagionidae (superfamily Tabanoidea) (Hennig, 1967, 1973; Steyskal, 1974; etc.). The prevailing view is that Athericidae are a separate family (Stuckenberg, 1973; Nagatomi, 1984; Hackman & Väisänen, 1985; Krivosheina & Zaitzev, 1989). Stuckenberg (1973) has transferred the Rhagionidae to Xylophagoidea leaving only Athericidae and Tabanidae in the superfamily Tabanoidea.

The musculature of the male genitalia has been described for some species of Rhagionidae (*Rhagio montanus* Becker, *Chrysopilus dives* Loew, *Ch. helvolus* Meigen), Coenomyiidae (*Anacanthaspis bifasciata* Röder) and Tabanidae (*Tabanus autumnalis brunnescens* Linnaeus, *Hybomitra nigricornis* Zetterstedt, *Haematopota pluvialis* Linnaeus, *Chrysops dissectus* Loew, *Silvius latifrons latifrons* Olsoufieff) (Ovtshinnikova, 1989). It has been found that the muscles of the male genitalia of Rhagionidae and Coenomyiidae (Xylophagoidea) are similar and those of Rhagionidae and Tabanidae basically different. Thus, the muscles of the male genitalia do not support close relationship between Rhagionidae and Tabanidae and confirm Stuckenberg's opinion that the Rhagionidae should be transferred to the Xylophagoidea.

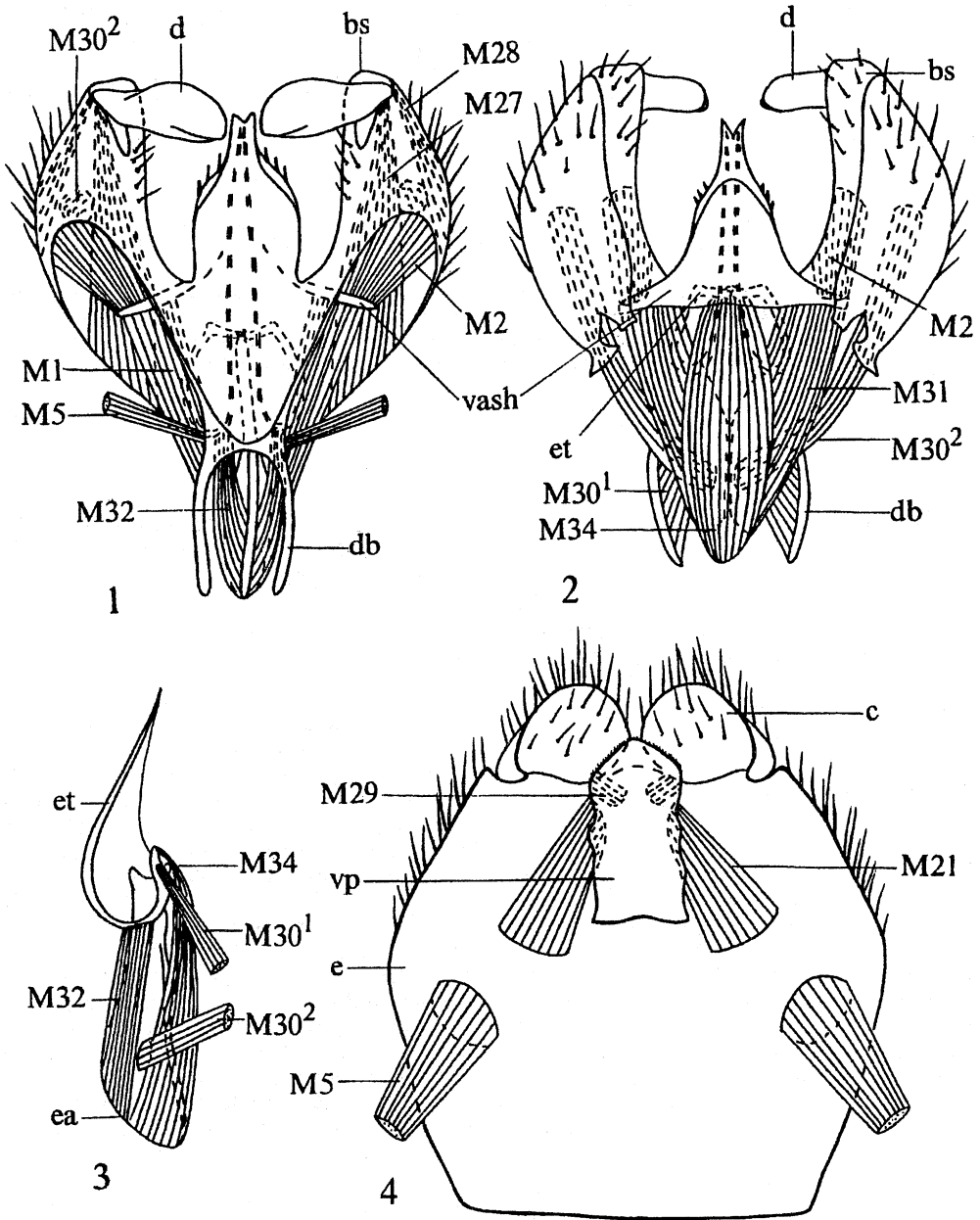
The muscles of the male genitalia of Athericidae (*Atherix ibis* Fabricius) are described in this paper.

Atherix ibis Fabricius (Figs 1-4)

Material. Finland: 1 ♂, Kuusamo 7367: 601, 50 m downstream from Patoniva, 7.VII.1990; 1 ♂, Isoniemi, 11.VII.1990 (Keijo Karvonen leg.)

The male genitalia of Athericidae may be characterized as follows. Their dorsal part is formed by the epandrium (9th and 10th tergum: Stuckenberg, 1973) with proctiger (10th sternum) and cerci. The epandrium looks like a large plate connected to the proctiger by a membrane. The ventral part of the genitalia is formed by the hypandrium (9th sternum) with basistyli and movably connected dististyli. The 9th sternum is fused with the basistyli. The basistyli have long dorsal processes. The aedeagal complex consists of the aedeagal sheath with the ventral plate and the ejaculatory apodeme with ejaculatory ("endophallic") tines and very small ejaculatory sclerites. The ejaculatory tines are attached to the basal part of the ejaculatory apodeme, which looks like a long plate. The ejaculatory sclerites and ejaculatory tines are connected by narrow hyaline processes and membrane surrounding the basal part of the ejaculatory complex (the "wall of the endophallus": Bonhag, 1951).

Muscles of the male genitalia of Athericidae include muscles of the aedeagal complex (the aedeagal sheath and the ejaculatory complex), hypandrial complex (dististyli),



Figs 1-4. *Atherix ibis* Fabricius: 1, hypandrium, dorsal view; 2, hypandrium, ventral view; 3, aedeagal complex, lateral view; 4, epandrium, ventral view. Abbreviations: bs, basistyli; c, cerci; d, dististyli; db, dorsal processes of basistyli; e, epandrium; ea, ejaculatory apodeme; et, ejaculatory tines; M1-M34, muscles; vash, ventral plate of aedeagal sheath; vp, ventral plate of proctiger.

epandrial complex (epandrium, proctiger, cerci) and tergosternal muscles.

The aedeagal complex includes 7 muscle pairs: M1, M2, M30¹, M30², M31, M32 and M34. The aedeagal sheath is moved by two muscle pairs, M1 and M2. The powerful retractors of the aedeagal sheath M1 are attached to the basal border of the lateral part of the ventral plate of the aedeagal sheath and the basal part of the dorsal processes of basistyli. The powerful protractors of the aedeagal sheath M2 are attached to the latero-basal part of the ventral plate of the aedeagal sheath and the basistyli.

There are 5 muscle pairs of the ejaculatory complex: M30¹, M30², M31, M32 and M34. Retractors of the ejaculatory tines and the ejaculatory apodeme M30¹ connect the basal part of the ejaculatory tines at the articulation of the ejaculatory apodeme to the distal part of the dorsal processes of the basistyli. Long protractors of the ejaculatory apodeme M30² are attached to the middle part of the ejaculatory apodeme and the basistyli. The powerful protractors of the ejaculatory apodeme M31 are attached to the distal part of the ejaculatory apodeme and the basal border of the ventral plate of the aedeagal sheath. Protractors of the ejaculatory apodeme M32 connect the ejaculatory tines at the point of bend and the ejaculatory sclerites with the distal part of the dorsal surface of the ejaculatory apodeme. The muscles of the ejaculatory tines M34 connect the basal end of the ejaculatory tines at the articulation of the ejaculatory apodeme to the distal part of the ventral surface of the ejaculatory apodeme.

The hypandrial complex includes two muscle pairs (M27 and M28) originating on the dististyli. The powerful adductors of the dististyli M27 are attached to the middle part of the basal border of the dististyli and basistyli. The less powerful abductors of dististyli M28 are attached to the lateral part of the basal border of the dististyli and the lateral part of the basistyli.

There is one small tergosternal muscle pair M5 attached to the lateral border of the basal part of the dorsal processes of the basistyli and the lateral part of the epandrium.

The epandrial complex includes two muscle pairs, M21 and M29. The proctiger retractors M21 are attached to the proctiger and the epandrium, Small retractors of the cerci M29 are attached to the basal border of the cerci and the distal part of the proctiger.

Discussion

Comparison of the musculature of the male genitalia of Coenomyiidae, Rhagionidae, Tabanidae and Athericidae confirm the following. The muscles of the dististyli (M27, M28) and the muscles of the epandrial complex (M21, M29) of Athericidae, Coenomyiidae, Rhagionidae and Tabanidae are similar. The tergosternal muscles M5 of Athericidae and Tabanidae are similar. In contrast, Rhagionidae and Coenomyiidae have two tergosternal muscles, M5¹ and M5². The muscles M5¹ and M5² connect, respectively, the basal and the distal part of the dorsal processes of the basistyli with the epandrium. Tergosternal muscles in Athericidae and Tabanidae are weakened. They have only one tergosternal muscle pair which is less powerful than M5¹ in Coenomyiidae and Rhagionidae.

The M33 and M35 muscles of the hypandrial complex are well developed in Tabanidae, but not in Athericidae. There are no M35 muscles in Coenomyiidae and Rhagionidae, but M33 muscles are found in some of them. The M33 muscles in Coenomyiidae, Rhagionidae and Tabanidae connect the hypandrium with the basistyli. The M35 muscles in Tabanidae connect the distal part of the dorsal processes of the basistyli with the lateral borders of the hypandrium. The lack of the M33, M35 and M5² muscles in Athericidae indicate that the M33 muscle pair in Tabanidae is divided into M33 and M35. Thus, the homologization of the M35 muscles of Tabanidae with the M5² muscles of Coenomyiidae and Rhagionidae is impossible. The M5² muscles cannot change their point of attachment from the epandrium to the hypandrium.

The lack of the M33 muscles in Athericidae is shared with Xylophagoidea (Rhagionidae, Coenomyiidae) and distinguish these families from Tabanidae. But this fact is not significant because of inconstant M33 muscles in all Brachycera Orthorrhapha.

There are two muscle pairs of the aedeagal sheath M1 and M2 in Athericidae and Xylophagoidea. In contrast, only one muscle pair M2 is found in Tabanidae. Tabanidae have no M1 muscles. Moreover, the M2 muscles pair of Tabanidae is less powerful than M2 muscle pair of Xylophagoidea. Thus, the aedeagal sheath of Athericidae is very mobile, more than that of Tabanidae. It is ap-

parent that the Tabanidae have a reduced musculature of the aedeagal sheath.

The muscles of the ejaculatory complex of Athericidae and Tabanidae are very similar and differ from those in Xylophagoidea. The protractors of the ejaculatory apodeme M31 of Tabanidae, Athericidae and Xylophagoidea are similar. Specially for this paper the attachment places of M30¹, M32, M34 in *Tabanus autumnalis brunnescens* were precised. In this additional investigation the same attachment places of these in Tabanidae and Athericidae were confirmed.

The M30¹ muscles of Tabanidae and Athericidae connect the ejaculatory tines at the articulation of the ejaculatory apodeme to the distal parts of the dorsal processes of the basistyli. In contrast, Xylophagoidea have only one muscle pair M30, which connect the basal part of the ejaculatory apodeme with the distal parts of the dorsal processes of the basistyli.

The muscle pair M30² is present in Athericidae and Tabanidae, but these muscles are differently attached. The M30² muscles of Athericidae connect the middle part of the ejaculatory apodeme with the basistyli, unlike M30² of Tabanidae, which connect the distal part of the ejaculatory apodeme with the distal part of the dorsal processes of the basistyli.

Athericidae and Tabanidae are similar in the splitting of M30 muscles into M30¹ and M30², but these muscles are differently attached. We suppose that the splitting occurred in the common ancestor of these families in consequence of lengthening of the ejaculatory apodeme and dorsal processes of basistyli.

The M32 ejaculatory muscles are present in Athericidae, Tabanidae and Xylophagoidea. These muscles connect the ejaculatory apodeme with the ejaculatory tines and small ejaculatory sclerites in Athericidae and Tabanidae and with well developed ejaculatory sclerites in Xylophagoidea. The ejaculatory sclerites of Athericidae and Tabanidae are connected with tines and surrounded by membrane, which makes possible minor shift in the origin of muscles.

There are no ejaculatory tines in Xylophagoidea and the muscles of the ejaculatory tines (M34 in Athericidae and Tabanidae) are absent here. In all probability, the M34 of Athericidae and Tabanidae originated from splitting of the Xylophagoidea muscle pair M32.

The differences in the musculature of the male genitalia of Athericidae and Tabanidae are evident in the hypandrial complex: the lack of M33 in Athericidae and splitting of M33 into M33 and M35 in Tabanidae. In the ejaculatory complex there are differences in the insertion points of M30² muscles.

The greatest similarity in the muscles of the male genitalia of Xylophagoidea (Coenomyiidae, Rhagionidae) and Athericidae, in contrast to Tabanidae, is the presence of the both muscle pairs of the aedeagal sheath M1 and M2 (plesiomorphy). The lack of the M1 muscles of the aedeagal sheath in Tabanidae is the result of reduction.

Comparison of the muscles of the male genitalia of Athericidae, Tabanidae and some representatives of Xylophagoidea (Coenomyiidae, Rhagionidae) confirm that in the arrangement and junction of the muscles Athericidae and Tabanidae are much closer to each other than to Xylophagoidea. The similarity in the structure of the sclerites and muscles of the ejaculatory complex, especially of the ejaculatory tines (apomorphy), strengthens this conclusion. Such complicated structures with homologous muscles cannot evolve independently.

Thus, the common ancestor of Athericidae and Tabanidae had well developed ejaculatory tines with the muscles, the splitting muscles M30 of the ejaculatory apodeme and well developed muscles of the aedeagal sheath (M1, M2) and the hypandrial muscles M33. Then, the reduction of the muscles of the aedeagal sheath and the splitting of the hypandrial muscles M33 (M33 and M35) took place in Tabanidae. At the same time the retention of the muscles of the aedeagal sheath and the reduction of M33 muscles of the hypandrium took place in Athericidae.

This analysis of male genital muscles provides additional evidence for Stuckenberg's (1973) opinion that Athericidae and Rhagionidae are two distinct families and that Athericidae should be included in the Tabanoidea.

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