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Thoracic Musculature of *Sericoderus lateralis* (Coleoptera, Corylophidae): Miniaturization Effects and Flight Muscle Degeneration Related to Development of Reproductive System

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Abstract—The thoracic musculature of adult *Sericoderus lateralis* is described based on histological sectioning and 3D computer reconstruction. The thoracic musculature of Corylophidae is not strongly affected by miniaturization: *S. lateralis* has an almost complete set of muscles found in large Cucuiformia beetles. The intravital flight muscle degeneration related to the development of the reproductive system is described.

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The hooded beetles (Corylophidae) are among the smallest beetles and the smallest free-living insects, therefore the study of their morphology is important for discussing the problem of miniaturization in insects. The structure of hooded beetles is very poorly known: the adult morphology was reflected only in taxonomic publications (Matthews, 1899; Paulian, 1950; Bowstead, 1999; Ślipiński et al., 2009), whereas the structure of the larvae was briefly described only for some genera (Boving and Craighead, 1931; Paulian, 1950; Pakaluk, 1985; De Marzo, 2000; Ślipiński et al., 2009). The latest publication of Polilov and Beutel (2010) contains a detailed description of external and internal morphology of adults and larvae of *Sericoderus lateralis* but still provides insufficient data on the musculature.

Many beetles demonstrate various types of intraspecific dimorphism with respect to reduction of the wing apparatus (Thayer, 1992); however, only the external aspects of such modifications were studied in most cases. Degeneration of the wing musculature during the adult stage was described for many beetles (Chapman, 1956; Reid, 1958; Atkins and Farris, 1962; Stegwee et al., 1963; Borden and Slater, 1968, 1969; Bhakthan et al., 1970; Muda et al., 1981; Tada et al., 1991; Rankin et al., 1994; Linders et al., 1995; Desender, 2000). Although intraspecific wing dimorphism is present in some species of Corylophidae (Bowestead, 1999), no wingless forms are known among representatives of the genus *Sericoderus*; the musculature of the flightless individuals was not studied.

This communication continues the series of papers devoted to the morphology of the smallest insects and the phenomenon of miniaturization (Polilov, 2005, 2007, 2008; Polilov and Beutel, 2009; 2010).

MATERIALS AND METHODS

We studied the adults of *Sericoderus lateralis* (Gyllenhal, 1827) (Coleoptera, Corylophidae) collected in June 2007 at the Venevitinovo biological field station, Voronezh Province; in July 2007 in the environs of Khosta, Krasnodar Territory; in June 2008 in the environs of Jena, Germany. The material was fixed in formalin-ethanol-acetic acid mixture and stored in 70% ethanol. Manual dissection in glycerol was used for quick assessment of the musculature. For a detailed study, the material was dehydrated and embedded in Araldite M; 1-μm sections were obtained using a Microm HM 360 microtome and stained with toluidine blue and pyronin. The serial transversal sections were documented on a Zeiss Axioskop. The aligned images were loaded into Bitplane Imaris software, and 3D reconstruction was performed using the manual segmentation mode. The 3D models were processed and visualized in Alias Maya.

The muscles are named and numbered according to the recent assessment of the coleopteran musculature (Kéler, 1963; Larsén, 1966; Beutel and Haas, 2000).

Table 1. The distribution of *S. lateralis* individuals with normally developed musculature and those lacking the principal wing muscles

Locality	Number of ind.			
	females		males	
	with muscles	without muscles	with muscles	without muscles
Venevitinovo, VI.2007	31	3	13	3
Khosta, VII.2007	45	3	0	2
Jena, VII.2008	33	4	7	6
Total	109	10	20	11
	119		31	

The following abbreviations are used: O (origin): the attachment site of the basal end of the muscle; I (insertion): that of the distal end of the muscle; F (function): the function of the muscle.

RESULTS

Populations of *S. lateralis* include individuals with a complete set of thoracic muscles and those lacking a considerable part of metathoracic muscles. The fractions of individuals with reduced muscles and the sex ratio in these fractions vary strongly in the three samples studied (Table 1). However, the individuals lacking a large part of wing musculature in all the samples were mostly females with two mature or nearly mature eggs or males with a completely developed reproductive system. Degeneration of the musculature was not observed in juvenile beetles of both sexes. No changes besides muscle degeneration were observed in the morphology of the wing apparatus. The musculature of the thoracic segments of *S. lateralis* is described below.

The Thoracic Musculature of the Flying Individuals of S. lateralis

Prothorax (Fig. 1). Dorsal musculature. *m1* (m. pronoti primus): O: anterior part of notum; I: median part of postocciput, together with *m2*; F: levator of head. *m2* (m. pronoti secundus): O: median part of notum; I: postocciput, together with *m1*; F: levator of head. *m3* (m. pronoti tertis) absent. *m6* (m. pronoti quartos): O: phragma; I: median part of notum; F: depressor of pronotum. Ventral musculature. *m9* (m. prosterni primus): O: furca; I: posterior margin of gular plate; F: depressor of head. *m10* (m. prosterni secundus): O: furca; I: cervical region; F: depressor of head. Dorsoventral musculature. *m12* (m. dorsoventralis primus): O: anterolateral part of notum; I: cervical region; F: depressor of head. *m13* (m. dorsoventralis secundus) and *m14* (m. dorsoventralis tertius) absent. *m15* (m. dorsoventralis quartos): O: cervical region; I: notum, in front of *m12*; F: levator of head. *m16* (m. dorsoventralis quintus): O: furca; I: lateral part of phragma; F: levator of prothorax. Lateral musculature. *m17* (m. notopleuralis): O: lateral part of notum; I: upper part of trochanteropleural apodeme; F: stabilization of trochanteropleural apodeme. *m18* (m. pronotomesepisternalis): O: posterior part of notum, lateral of *m6*; I: intersegmental membrane, in front of mesepisternum; F: depressor of prothorax. Leg musculature. *m22* (m. nototrochantinalis): O: lateral part of notum; I: trochanter, by thin tendon; F: rotation of trochanter. *m23* (m. notocoxalis): O: lateral part of notum; I: anterior and lateral margins of base of coxa; F: abduction of coxa. *m24* (m. episternocoxalis): O: trochanteropleural apodeme; I: anterior margin of coxa; F: rotation of coxa. *m25* (m. epimerocoxalis) absent. *m30* (mm. furcacoxales): O: furca; I: posteromedian margin of coxa; F: abduction of coxa. *m31* (m. pleurotrochanteralis): O: trochanteropleural apodeme; I: trochanter, by thin tendon; F: depressor of trochanter. The internal leg muscles were not studied owing to their very small size.

Mesothorax (Fig. 2). Dorsal musculature. *m39* (m. mesonoti primus): O: prothoracic phragma, I: mesothoracic phragma; F: closing of elytra. *m40* (m. mesonoti secundus): O: median part of prothoracic phragma, I: lateral part of mesothoracic phragma; F: opening of elytra, antagonist of *m39*. Ventral musculature. *m42* (m. mesosterni primus): O: prothoracic furca; I: mesothoracic furca; F: retractor of prothorax. *m43* (m. mesosterni secundus) absent. Dorsoventral musculature absent. Lateral musculature. *m47* (m. notopleuralis): O: pleural process; I: anterolateral margin of notum; F: depressor of notum. *m52* (m. epimerosubalaris) absent. *m53* (m. pleuroalaris): O: mesepisternum, I: third axillary plate; F: movement of third axillary plate. *m54* (m. pleuroalaris b) merged with *m53* or absent. *m55* (m. furcopleuralis): O: apex of furca; I: pleural ridge; F: stabilization of furca. Leg musculature. *m60* (mm. notocoxale): O: phragma; I: posterior margin of coxa; F: opening of elytra. *m61* (m. episternocoxalis), O: episternum; I: anterior margin of coxa; F: movement of coxa. *m62* (m. coxobasalaris): O: basalar plate; I: anterior margin of coxa,

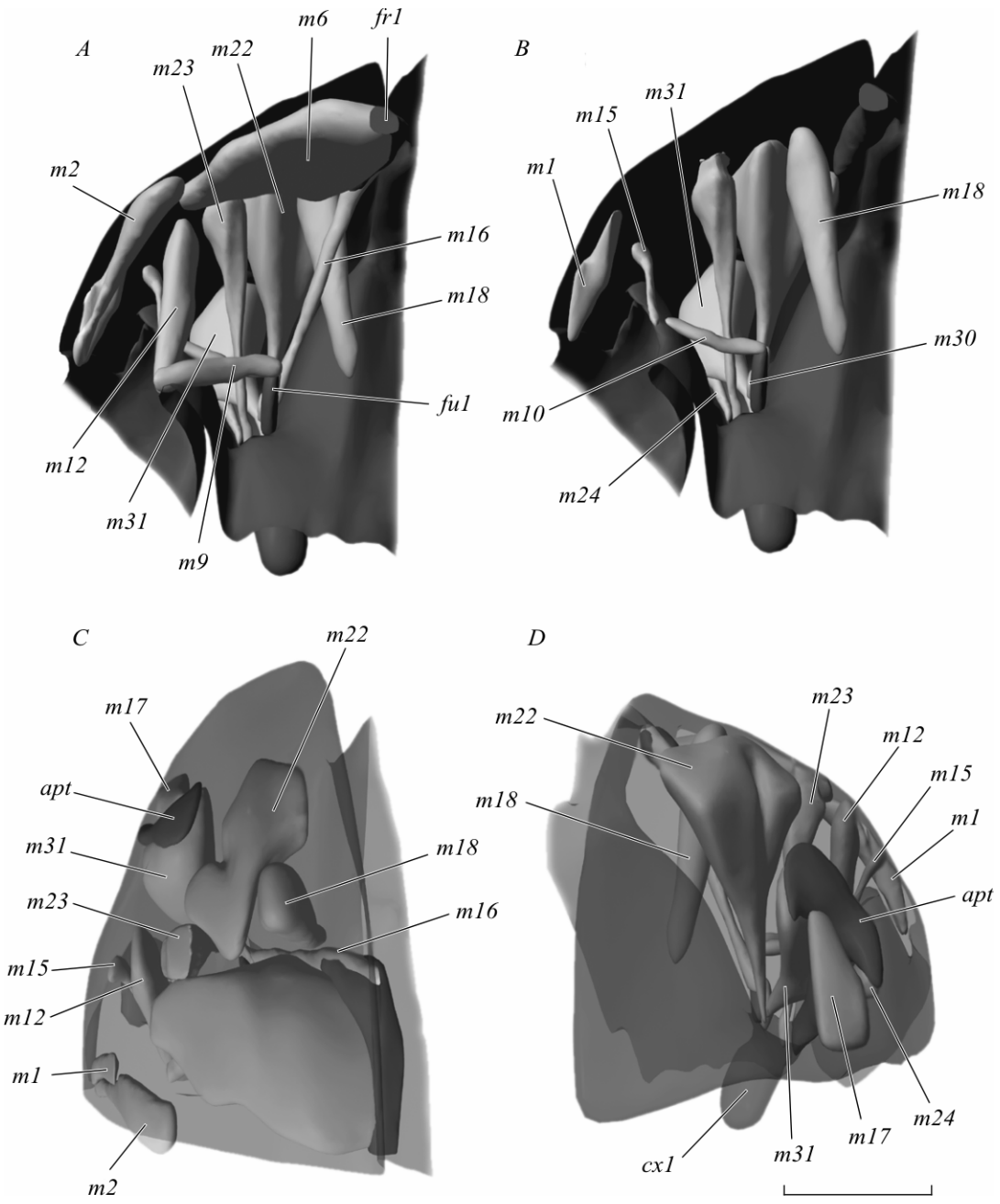

Fig. 1. The prothoracic musculature of adult *S. lateralis*, 3D: median section in lateral view (*A*, *B*); right half of the body in dorsal (*C*) and lateral view (*D*). *apt*, trochanteropleural apodeme; *cx1*, fore coxa; *fr1*, prothoracic phragma; *fu1*, prothoracic furca. For designations of muscles, see text. Scale bar 100 μm.

together with *m61*; F: movement of basalar plate. *m65* (m. furcocoxalis anterior): O: furca; I: anterior margin of coxa; F: movement of coxa, *m66* (m. furcocoxalis lateralis) absent. *m67* (m. furcocoxalis posterior): O: furca; I: posterolateral margin of coxa; F: retractor of coxa. *m70* (m. episternotrochanteralis) absent. *m71* (m. trochanterobasalaris): O: basalar plate; I: trochanter, by thin tendon; F: adduction of trochanter and movement of basalar plate. *m72* (m. furcotrochanteralis): O: furca; I: trochanter, by thin tendon; F: adduction of trochanter. The internal leg muscles were not studied.

Metathorax (Fig. 2). Dorsal musculature. *m79* (m. metanoti primus): O: mesothoracic phragma; I: metathoracic phragma; F: depressor of wing. *m80* (m. metanoti secundus): O: scutum; I: metathoracic phragma; F: depressor of wing. Ventral musculature. *m82* (m. metasterni primus) absent. Dorsoventral muscula-

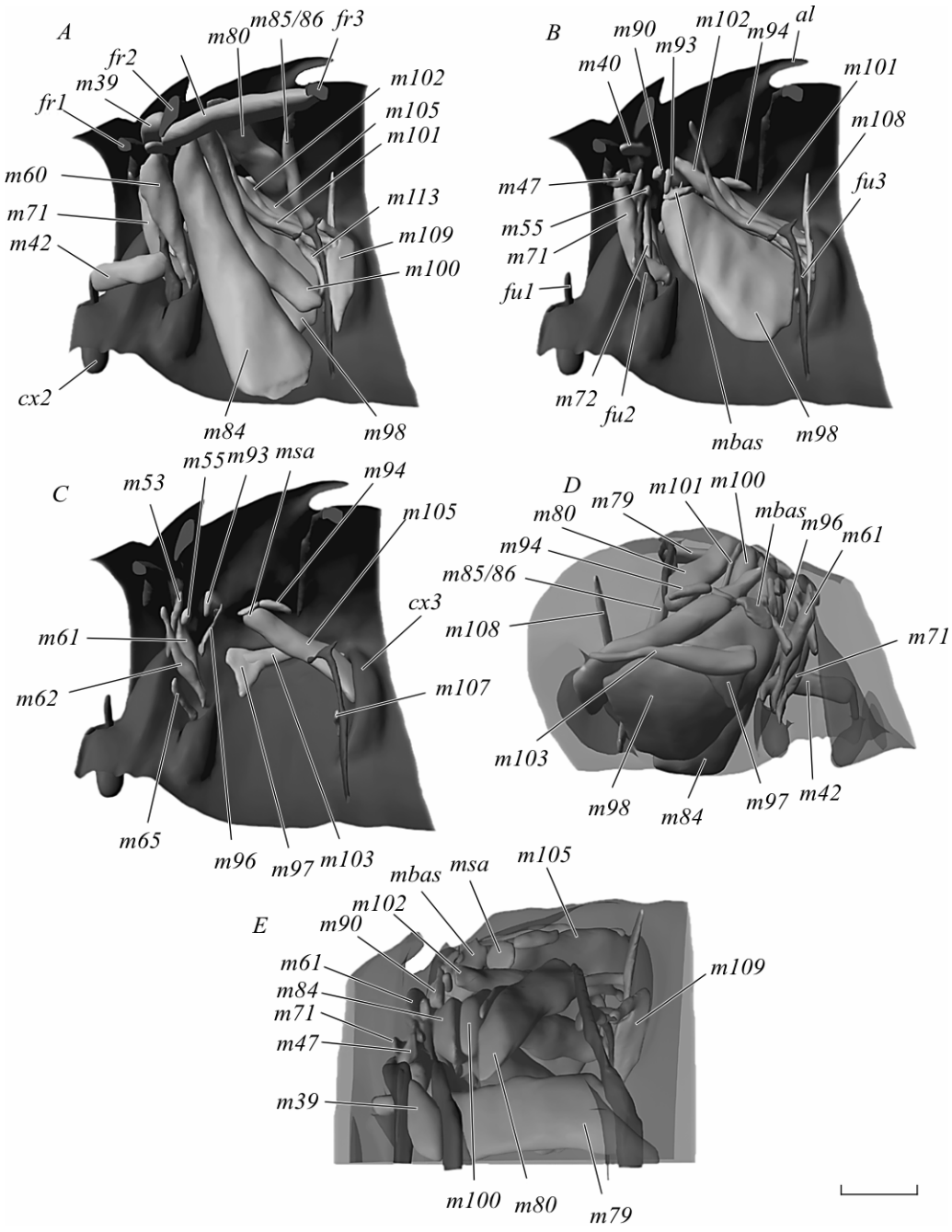

Fig. 2. The meso- and metathoracic musculature of adult *S. lateralis*, 3D: median sections (*A–C*); lateral view (*D*); right half of the body in dorsal view (*E*). *al*, alacrista; *cx2,3*, middle and hind coxae; *fr1,2,3*, phragmata of pro-, meso-, and metathorax; *fu1,2,3*, furcae of pro-, meso-, and metathorax; *mbas*, muscle disc of basalar plate; *msa*, muscle disc of subalar plate; *scl2*, mesoscutellum. For designations of muscles, see text. Scale bar 100 μm.

ture. *m84* (m. dorsoventralis primus): O: anterior part of metanotum and lateral part of mesothoracic phragma; I: ventrite; F: levator of wing. *m85* (m. dorsoventralis secundus) and *m86* (m. dorsoventralis tertius) merged: O: apex of metendosternite; I: metathoracic phragma; F: correction of relative position of notum and metendosternite. Lateral musculature. *m90* (m. pleura-praealaris): O: prealar sclerite; I: pleural ridge; F: unfolding of wing. *m93* (m. notobasalaris): O: lateral margin of notum; I: muscle disc of basalar plate; F: stabilization of basalar plate. *m94* (m. epimerosubalaris): O: epimere; I: subalar plate; F: movement of basalar plate. *m95* (m. pleuroalaris a) merged with *m96*: O: anterior part of pleural ridge;

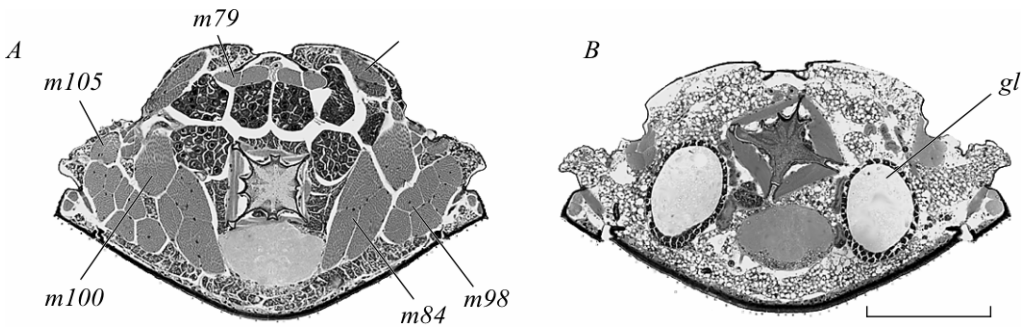

Fig. 3. Transversal sections through the metathorax of *S. lateralis* with normally developed musculature (*A*) and reduced wing muscles (*B*). *gl*, accessory glands. For designations of muscles, see text. Scale bar 200 μm.

I: third axillary plate; F: folding of wing. *m96* (m. pleuroalaris b) merged with *m95*. *m97* (m. sternoepisternalis): O: pleural ridge; I: lateral margin of ventrite; F: stabilization of pleurite. *m98* (m. sternobasalaris): O: ventrite, lateral of *m84*; I: muscle disc of basalar plate; F: pronator and depressor of wing. Leg musculature. *m100* (m. nototrochantinalis): O: scutellum; I: trochanter; F: levator of wing. *m101* (m. notocoxalis anterior): O: notum; I: posterolateral margin of coxa; F: levator of wing. *m102* (m. notocoxalis posterior): O: notum, lateral of *m100*; I: lateral margin of coxa; F: levator of wing. *m103* (m. episternocoxalis): O: episternum; I: anterolateral margin of coxa; F: stabilization of episternum. *m104* (m. coxobasalaris) absent. *m105* (m. coxosubalaris): O: posterior margin of coxa; I: subalar plate; F: movement of subalar plate and supination of wing, *m107* (m. furcocoxalis anterior): O: metendosternite; I: anteromedian margin of coxa; F: promotor of coxa. *m108* (m. furcocoxalis lateralis): O: metendosternite; I: lateral margin of coxa or posterior margin of pleurite (could not be precisely determined); F: stabilization of metendosternite. *m109* (m. furcocoxalis posterior): O: metendosternite; I: posterior margin of coxa; F: promotor of coxa. *m113* (m. furcotrochanteralis): O: metendosternite; I: trochanter, by thin tendon; F: depressor of hind leg. The internal leg muscles were not studied.

The Thoracic Musculature of the Flightless Individuals of S. lateralis

The prothoracic and mesothoracic muscles are the same as in the flying individuals (see above).

Metathorax. Muscles *m79*, *m80*, *m84*, *m98*, *m100*, *m101*, *m102*, and *m105* are absent; the remaining muscles are the same as in the flying individuals. The space freed by the reduced muscles in the metathorax is occupied by the reproductive system (Fig. 3).

DISCUSSION

The Effect of Miniaturization

Comparison of the composition of thoracic muscles in different members of Cucujiformia (Table 2) shows that *S. lateralis*, despite its minute size, has an almost complete set of muscles typical of large representatives of related groups: 46 pairs of thoracic muscles, whereas other examined representatives of Cucujiformia have 47–53 pairs (Beutel and Haas, 2000). The modifications not found in other studied groups of Cucujiformia are the absence of *m82* (m. metasterni primus) and the merging of *m85* (m. dorsoventralis secundus) and *m86* (m. dorsoventralis tertius).

An almost complete set of thoracic muscles was also described in the feather-winged beetle *Mikado* sp. (Polilov and Beutel, 2009). Despite its very small size, *Mikado* showed only one reduction that is unknown in larger members of Staphylinoidea, namely the absence of *m108* (m. furcocoxalis lateralis). There are 45 pairs of thoracic muscles in *Mikado* and 45–51 pairs in larger Staphylinoidea.

The only reduction observed in both *S. lateralis* and *Mikado* sp. is the absence of *m52* (m. epimerosubalaris); however, this muscle is absent in most of the studied Staphylinoidea where it is functionally substituted by *m60* (m. notocoxale).

A considerable reduction of the number of thoracic muscles in *Mengenilla chobauti* (Strepsiptera) as compared to *Dytiscus marginalis*, described by Osswald and co-authors (2009), may be explained by the fact that comparison was made between taxonomically and ecologically remote groups, so that the apparent reduction of muscles may be unrelated to miniaturization. In addition, since the nomenclature of the larval muscles is poorly developed, subunits of large muscles could

Table 2. The musculature of thoracic segments of *S. lateralis* and some Cucujiformia (partly based on data of Beutel and Haas, 2000)

Object	1	2	3	6	9	10	12	13	14	15	16	17	18	22	23	24	25	30	31	39	40	42	43	47	52	53	55	60	61
Sericoderus	×	×	–	×	×	×	×	–	–	×	×	×	×	×	×	×	–	×	×	×	×	×	–	×	–	×	×	×	×
Coccinella	×	×	–	×	×	×	×	–	×	×	×	×	×	–	×	×	–	×	×	×	×	×	–	×	×	×	×	×	×
Lytta	×	×	–	×	×	×	×	–	×	×	×	×	×	×	×	×	×	–	×	×	×	×	×	×	×	×	×	×	×
Meloe	×	×	–	×	×	×	×	–	×	×	×	×	×	×	×	×	×	–	×	×	×	×	×	×	–	×	–	×	×
Tenebrio	×	×	–	×	×	×	×	×	–	×	×	×	×	×	×	×	–	–	×	×	×	×	–	×	×	×	×	×	×
Cassida	×	×	–	×	×	×	×	–	–	×	×	×	×	×	×	×	–	×	×	×	×	×	–	×	×	×	×	×	×
Donacia	×	×	×	×	×	×	×	×	–	×	×	×	×	×	×	×	–	–	×	×	×	×	–	×	×	×	×	×	×
Object	65	66	67	70	71	72	79	80	82	84	85	86	90	93	94	95	96	97	98	00	01	02	03	04	05	07	08	09	13
Sericoderus	×	–	×	–	×	×	×	×	–	×	a	a	×	×	×	b	b	×	×	×	×	×	×	–	×	×	×	×	×
Coccinella	–	×	×	×	–	×	×	×	×	×	×	×	×	×	×	b	b	×	×	×	–	×	×	–	–	×	×	×	×
Lytta	×	×	×	×	–	×	×	×	×	×	×	×	×	×	×	b	b	×	×	×	×	×	×	×	×	×	×	×	×
Meloe	×	×	×	–	–	×	–	–	×	–	×	–	–	–	–	b	b	×	–	–	–	×	×	–	–	×	×	×	×
Tenebrio	×	–	×	×	–	×	×	×	×	×	×	×	×	×	×	b	b	–	×	×	×	×	×	×	–	×	×	×	×
Cassida	×	–	×	×	–	×	×	×	×	×	×	×	×	×	×	b	b	–	×	×	–	×	×	×	–	×	×	×	×
Donacia	×	–	×	×	–	×	×	×	×	×	×	×	×	×	×	b	b	–	×	×	–	×	×	–	×	×	×	×	×

Notes: ×, the muscle is present; –, the muscle is absent; the merged muscles are marked with letters *a*, *b*.

be considered as separate muscles in older papers. For example, Osswald and co-authors used data from the paper of Korschelt (1923) who described 92 pairs of thoracic muscles in the *Dytiscus* larva, whereas the adult beetle has only 52 pairs, according to the recent data (Beutel and Hass, 2000).

Thus, miniaturization in beetles leads only to reduction of the number of muscle subunits and fibers but has almost no effect on the set of thoracic muscles. Since the efficiency of a muscle depends on its cross-section, the relative strength of muscles increases as the body size decreases (Gorodkov, 1984), because of which the musculature can easily undergo miniaturization.

Degeneration of the Musculature

The flightless individuals of *S. lateralis* lack all the large muscles raising and lowering the wing, whereas nearly all the muscles involved in folding and fixation of the wing are present.

The absence of signs of muscle degeneration in juvenile (weakly pigmented) beetles with still immature reproductive systems indicates that all the individuals have a complete set of thoracic muscles at the moment of eclosure. Degeneration of muscles in *S. lateralis* probably occurs during the adult life and is caused by the development of the reproductive system. This phenomenon, termed the oogenesis-flight syndrome, was demonstrated for some bark beetles (Chapman, 1956; Reid, 1958; Atkins and Farris, 1962; Borden and Slater, 1968, 1969; Bhakthan et al., 1970), weevils (Muda et al., 1981; Rankin et al., 1994; Linders et al., 1995), ground beetles (Desender, 2000), leaf beetles (Stegwee et al., 1963), and lamellicorns (Tada et al., 1991). Degeneration of muscles in *S. lateralis* undoubtedly has a high adaptive significance: the young beetles disperse actively and start to reproduce once they have found a suitable substrate; a considerable part of the wing musculature is lysed and the freed space is occupied by the reproductive organs. This is particularly important in the case of miniaturization since the reproductive system occupies a much greater relative volume in *S. lateralis* than in large beetles (Polilov and Beutel, 2010). It is interesting that development of the reproductive system causes the same degree of muscle degeneration in males and females of *S. lateralis*. A small fraction of individuals with degenerated wing musculature (13.3% for all the samples) may suggest the ability of *S. lateralis* to restore the lysed muscles, which was shown for *Leptinotarsa decemlineata* (Stegwee et al., 1963), *Ips confusus* (Bhakthan et al., 1971), and *Lissorhoptrus oryzophilus* (Muda

et al., 1981); alternatively, the generative individuals may be found less frequently because the generative phase may be shorter than the juvenile and immature ones. This problem awaits further study.

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