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Musculature of the Ovipositor of *Timia erythrocephala* Wiedemann, 1824 (Diptera, Ulidiidae)

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Abstract—The structure of the ovipositor sclerites and musculature was investigated in *Timia erythrocephala* Wiedemann, 1824 (Ulidiidae), whose larvae are saprophagous. The ovipositor musculature of this species is compared with that of the previously investigated Tephritidae. Based on morphological analysis, characters common to Ulidiidae and primitive Tephritidae and supposedly plesiomorphic for Tephritidae are revealed. Abdominal segment VII in *Timia* is compact and consists of tergite and sternite VII fused into a syntergosternite with a visible suture. The preserved suture between the sternite and tergite of segment VII should be regarded as an intermediate state in the process of syntergosternite formation in tephritoid flies, which was completed already in *Lenitovena*.

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This communication continues the series of papers on the morphology of the ovipositor sclerites and muscles in tephritid flies with different larval trophic specialization, in relation to the adaptations to laying eggs into different substrates.

The muscles of the ovipositor and its adaptations to different types of substrate were previously studied in several species of tephritid flies with phytophagous larvae: *Rhagoletis pomonella* (Walsh) (Dean, 1935), *Ceratitis capitata* (Wiedemann) (Hanna, 1938), *Urophora affinis* Frauenfeld and *U. quadrifasciata* (Meigen) (Berube and Zacharuk, 1983), *Campiglossa plantaginis* (Haliday) (Ovtshinnikova, 2010), *Bactrocera depressa* Shiraki (Ovtshinnikova, 2011), *Carpomya schineri* (Loew) (Ovtshinnikova, 2012), and *Oxyna parietina* (Linnaeus, 1758) (Ovtshinnikova and Ovchinnikov, 2015), and also in *Lenitovena trigona* Matsumura (Ovtshinnikova, 2008) which has saprophagous larvae. As a result, the structure of the ovipositor skeleton and muscles was found to be correlated with larval biology.

We have studied the ovipositor skeleton and muscles of *Timia erythrocephala* Wiedemann, 1824 of the family Ulidiidae, whose larvae are saprophagous.

MATERIALS AND METHODS

The main method of research was manual dissection of insects preserved in 70% ethanol. Seven specimens were dissected with microknives in water under the Leica MZ 9_5 stereomicroscope. The illustrations are based on processed drawings made with an eyepiece grid micrometer, and also on photos obtained with the image capture function of the Leica MZ 9_5 trinocular head. The muscles are designated according to the previously used system (Ovtshinnikova, 2008).

Timia erythrocephala Wiedemann, 1824
(Figs. 1–11)

Material. Seven females, **Russia,** *Volgograd Prov.,* Lake Elton, on *Tamarix*, 20.VI.2003 (O.G. Ovtshinnikova).

The female abdomen consists of 6 segments, with tergites I and II merged; segments VII–XI are modified into an extensible ovipositor. Segment VII (the main segment of the ovipositor) forms a sclerotized, dorsoventrally flattened conical sheath that accommodates the retracted part of the ovipositor; an indistinct suture is present between sternite VII and tergite VII. The apodemes of sternites VI and VII are absent. Tergite VI has small paired dorsomedian outgrowths. A vast membranous area is present between segments VII and VIII. The aculeus is sclerotized; it includes sclerites of segment VIII, the postgenital segments, and the cerci.

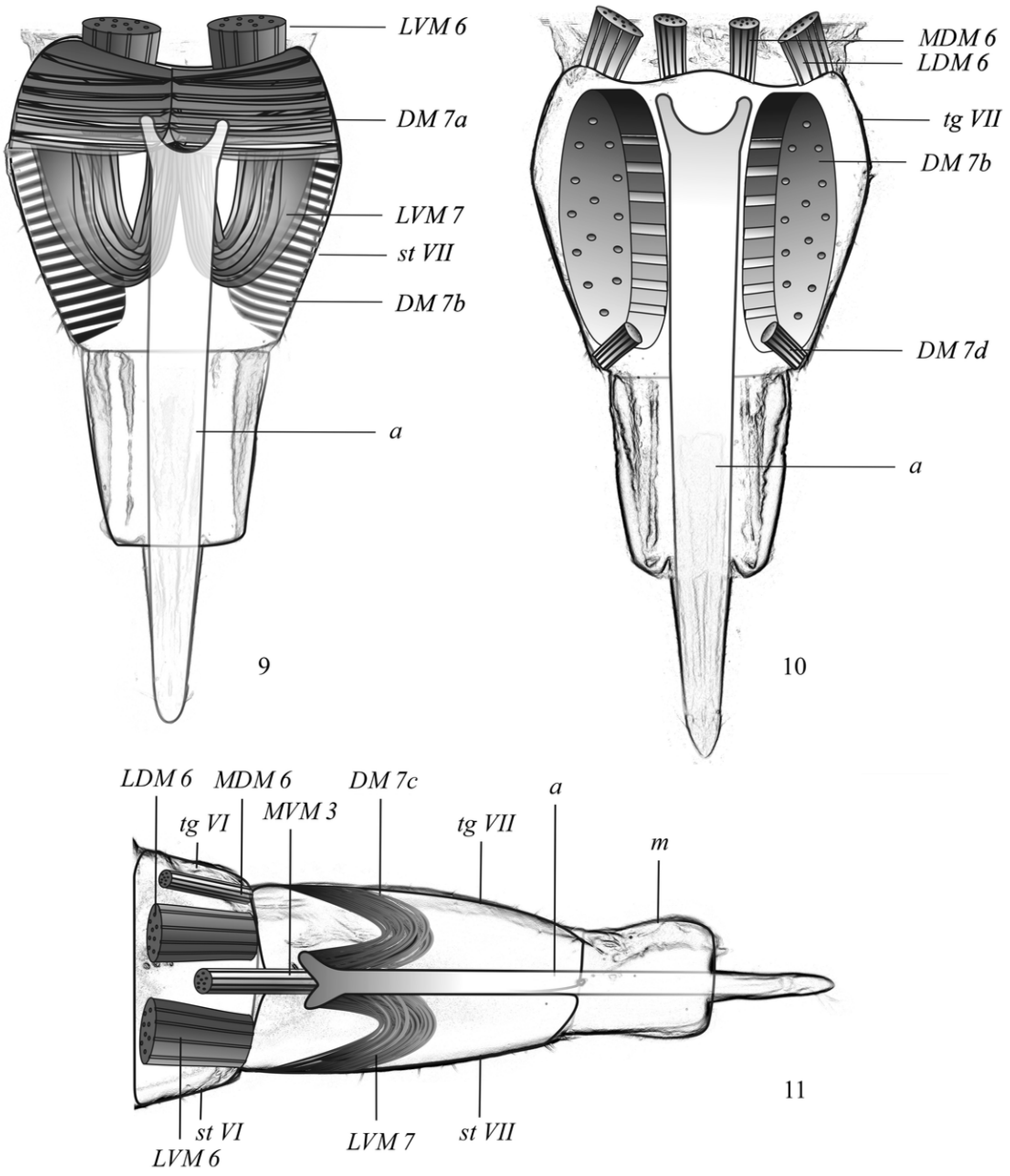
The muscles of the abdominal segments and ovipositor in *T. erythrocephala* females may be subdivided into several groups: (1) abdominal muscles; (2) pregenital muscles, connecting segment VII with the preceding abdominal segments; (3) ovipositor mus-

Figs. 1–8. *Timia erythrocephala* Wiedemann, 1824, female: (1) habitus, lateral view; (2–8) ovipositor: (2) dorsal view; (3) ventral view; (4) laterocaudal view; (5) lateral view; (6) partly extended, lateral view; (7) completely extended, lateral view; (8) completely extended, dorsal view.

cles, including muscles of segment VII and the apical ovipositor segments.

The abdominal segments have tergal, sternal, and tergo-sternal muscles.

Tergal muscles: DM 1a, *DM 1b*, and *DM 2–DM 5*. Two pairs of muscles are attached to abdominal tergites I–II: the powerful paired abdominal retractors *DM 1a*, extending from the median part of abdominal tergite II to the protrusions of the basal margin of tergite I, and the smaller abdominal retractors *DM 1b*, connecting the lateral protrusions of the basal margin of abdominal tergite I to the lateral parts of the basal margin of tergite II. The flat and short paired abdominal flexors and retractors *DM 2*, *DM 3*, *DM 4*, and *DM 5* extend as wide though weak and inconspicuous bundles from the median part of the preceding abdominal tergite to the basal margin of the next tergite.



Figs. 9–11. *Timia erythrocephala* Wiedemann, 1824, ovipositor: (9) dorsal view; (10) ventral view; (11) lateral view; *a*, aculeus; *m*, membrane; *tg*, tergite; *st*, sternite; *DM*, dorsal muscles; *LDM*, lateral dorsal muscles; *MDM*, median dorsal muscles; *LVM*, lateral ventral muscles; *MVM*, median ventral muscles.

Sternal muscles: LVM 1–5, *MVM 1*, and *MVM 2*. The powerful paired flexors and retractors *LVM 1–5* connect the consecutive abdominal sternites. Sternites I and II are connected medially by one additional pair of muscles: *MVM 1* and *MVM 2*.

Pleural muscles: TSM. The abdominal flexors *TSM* connect the abdominal sternites to the corresponding tergites, covering the pleural membrane in a thin layer, and constrict the abdomen dorsoventrally.

Pregenital muscles, connecting segment VII to the preceding abdominal segments: *MDM 6*, *LDM 6*, and *LVM 6*. The long oblique ovipositor retractors *MDM 6* extend from the mediobasal outgrowths of tergite VI to the median part of the basal margin of tergite VII. The powerful ovipositor retractors *LDM 6* connect the laterobasal margins of tergite VI to the laterobasal margins of tergite VII. The powerful ovipositor retractors *LVM 6* connect the basal margin of sternite VI

to the basal margin of tergite VII. Together, these muscles control the position of the ovipositor during egg laying.

Ovipositor muscles: DM 7a, *DM 7b*, *DM 7c*, *DM 7d*, *LVM 7*, *MVM 3*, and *TSM 8.*

The powerful circular flexors of segment VII, muscles *DM 7a* connect tergite VII and sternite VII basally; when contracted, they constrict the basal portion of the ovipositor. Muscles *DM 7b* are short and powerful flexors of segment VII which connect the lateral parts of its tergite and sternite along nearly the entire length of the ovipositor except the basal and distal portions. Contraction of these muscles constricts the ovipositor dorsoventrally.

The long aculeus retractors *DM 7c* extend from the dorsal part of the basal margin of the aculeus to the middle part of the basal margin of tergite VII. The long paired muscles *DM 7d* connect the median part of the vagina to the laterodistal parts of tergite VII; their contraction retracts the vagina. The long and powerful aculeus retractors *LVM 7* extend from the ventral part of the basal margin of the aculeus to the median part of the basal margin of sternite VII. The very long paired muscles *MVM 3* extend from sternite III along almost all the abdominal segments to the very short hyaline apodeme at the level of sternite VI, and further to the membrane at the ventrobasal margin of the aculeus (where the vagina enters the aculeus). Muscles *TSM* are short, wide, and flat pleural muscles of segment VIII; when contracted, they constrict the distal portion of the ovipositor dorsoventrally.

DISCUSSION

Tephritoid flies demonstrate transition from laying eggs into liquid and semi-liquid substrates (in species with saprophagous larvae) to oviposition onto the surface of plants and inside the plant tissues. The larvae of those species of the family Ulidiidae whose biology is known are saprophages while the larvae of most representatives of the family Tephritidae are endophytophages inhabiting various plant tissues. *Lenitovena trigona* (Matsumura), a species from the genus considered to be primitive within Tephritidae, has saprophagous larvae. As shown by previous studies, the main morphological adaptations of the ovipositor occur in some groups that have switched to laying eggs into fruits, such as *Bactrocera* Macquart, 1835, *Ceratitis* MacLeay, 1829, and *Carpomya* A. Costa, 1854, and into flower buds and capitula of composites (Asteraceae), such as species of the genera *Campiglossa* Rondani, 1870 and *Urophora* Robineau-Desvoidy, 1830, and also *Oxyna parietina* (Linnaeus, 1758) (Ovtshinnikova, 2008, 2010, 2011, 2012; Ovtshinnikova and Ovchinnikov, 2014, 2015).

The family Ulidiidae is believed to be primitive as compared with the advanced and diverse family Tephritidae. Based on comparative morphological analysis of the ovipositor sclerites and muscles of *Timia erythrocephala* (Ulidiidae) and the previously studied species of the family Tephritidae, some characters were revealed which may be considered common to Ulidiidae and primitive Tephritidae (*Lenitovena*) and plesiomorphic for Tephritidae: the presence of the ventral aculeus retractors *LVM 7* and the dorsal aculeus retractors *DM 7c* (which are absent in the advanced members of Tephritidae); the absence of a large and complex apodeme of sternite VII and, correspondingly, the absence of dorsoventral differentiation of the sclerotized cone of the ovipositor; the presence of one pair of muscles *DM 7d* connecting the vagina with segment VII (as opposed to the advanced Tephritidae which have two pair of vaginal muscles); the presence of a simpler variant of the closing mechanism for retention of hemolymph in the abdomen (as compared with that in the advanced phytophagous Tephritidae). This mechanism is formed by muscles *DM 7a*, the powerful circular flexors of segment VII, attached to only slightly modified basal part of its sternite, muscles *DM 7b*, the powerful flexors of segment VII, which connect the lateral parts of its tergite and sternite along nearly the entire length of the ovipositor and pump hemolymph into the apical segments, and muscles *TSM 8* acting as flexors of segment VIII. Thus, the elementary closing mechanism of the ovipositor was formed before transition to laying eggs into plant tissues. Another important feature of *Timia* and *Lenitovena* is the absence of the apodeme of sternite VI and the associated muscles, which are present in the advanced species of Tephritidae.

Unlike that of *Lenitovena*, the flattened segment VII of *Timia* is an incompletely formed syntergosternite consisting of the sternite and tergite separated by a suture. The preserved suture between the sternite and tergite of segment VII should be regarded as an intermediate state in the process of syntergosternite formation in tephritoid flies, which was completed already in *Lenitovena*.

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