INSECTA MUNDI A Journal of World Insect Systematics

0300

'Retournement' of the aedeagus in Curculionidae (Coleoptera, Curculionoidea)

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Date of Issue: May 10, 2013

CENTER FOR SYSTEMATIC ENTOMOLOGY, INC., Gainesville, FL

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Insecta Mundi 0300: 1-5

ZooBank Registered: urn:lsid:zoobank.org:pub:636D2AA9-8BA1-48F4-8D93-C7999711DE68

Published in 2013 by
Center for Systematic Entomology, Inc.
P. O. Box 141874
Gainesville, FL 32614-1874 USA
http://www.centerforsystematicentomology.org/

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Abstract. Retournement or turning of the aedeagus about its longitudinal axis through about 180° during development is known in Chrysomeloidea (Coleoptera). This change in the orientation of the organ may be observed during the postembryonic development. This change produces certain morphological effects. By observing these morphological features in the imago the retournement may be inferred. Such morphological features in Curculionidae (Coleoptera) are here recorded. From this it has been inferred not only that retournement of the aedeagus is included in the ontogeny of curculionids, but also that the change of orientation of the organ occurs by the same mechanism as in Chrysomeloidea. These inferences attest the notion of a close phyletic relationship between the superfamilies Curculionoidea and Chrysomeloidea.

Introduction

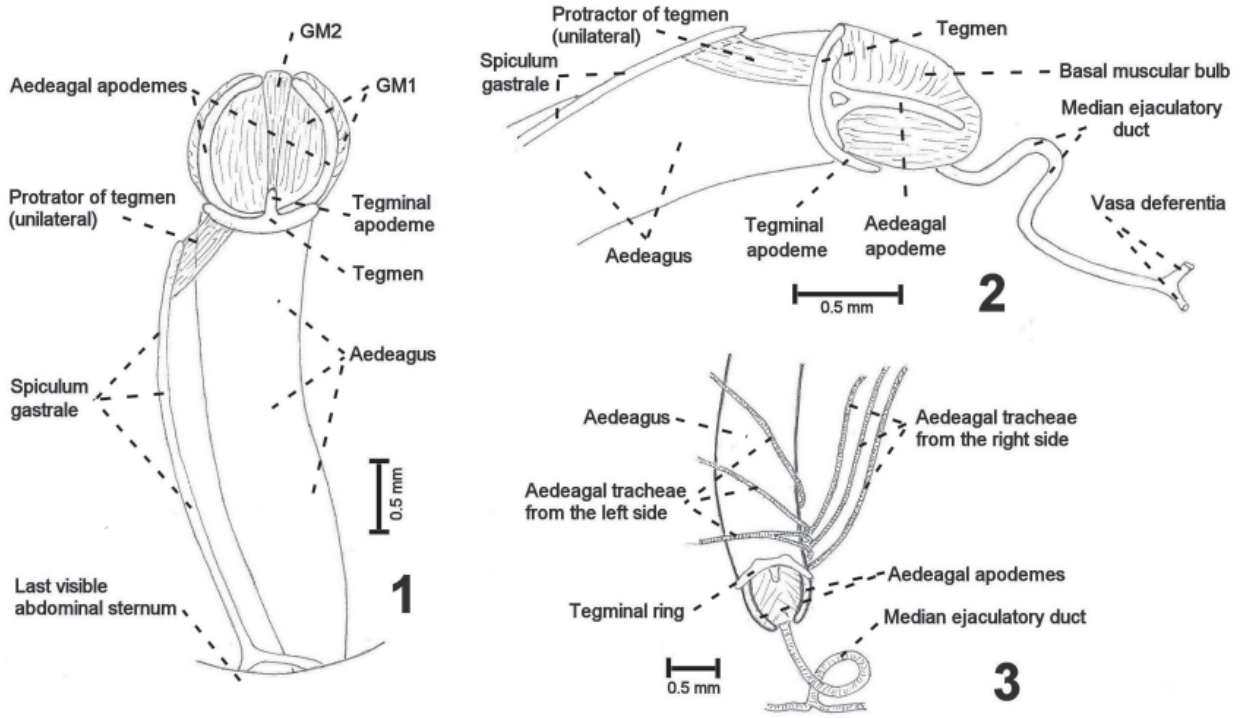
'Retournement' of the aedeagus is the rotation of the developing aedeagus about its longitudinal axis through about 180° during the post-embryonic development. This change of orientation of the aedeagus is irreversible and generally clockwise when viewed from behind, though in some cases it may be counter-clockwise, and is. prevalent, if not universal, among Chrysomeloidea (Verma 1994).

Like Chrysomeloidea, Curculionoidea are pseudotetramerous in their tarsi. The two superfamilies are phylogenetically close, which will be covered at some length under the section "Discussion" in this communication. This phyletic closeness suggests the possibility of aedeagal 'retournement' among Curculionidae; hence this study.

Progress of the 'retournement' during development has been observed and recorded in two chrysomelids, *Galerucella birmanica* (Jacoby, 1859) (Verma 1969), and *Aspidomorpha miliaris* (Fabricius, 1775) (Verma and Kumar 1972). Occurrence of the aedeagal rotation during development has been inferred in a number of chrysomeloid species from the observation of certain morphological changes, as seen in the adult, from the developmental turning of the aedeagus (Kumar and Verma 1971, 1980; Pawar and Verma 1977). For the present study we searched for similar morphological changes in adult curculionids.

Material and methods

Fresh specimens of a fairly large curculionid species, *Xanthochelus superciliosus* Gyllenhal, 1834 were dissected under magnification, and examined. A few dissections of a smaller species, *Myllocerus*



Figures 1-3. *Xanthochelus superciliosus* aedeagus. **1)** Aedeagal apparatus of adult in ventral view. The muscles GM1 and GM2 have been labeled following Burke (1959). **2)** Basal part of the aedeagal apparatus in lateral view, from the right side. **3)** Tracheal supply to the aedeagus base in ventral view.

fabricii Guerin, 1843 have also been done. Figures were drawn using a camera lucida, and extent of magnification in the figures was recorded with the help of a micrometer scale.

Observations

In both species of curculionids examined, a long spiculum gastrale, which arises posteriorly from the terminal abdominal sternum and extends forward beneath the aedeagus, is tilted upward and to the right side of the aedeagus in its anterior part (Fig. 1-2). Arising from its anterior tip is a unilateral muscle, the retractor of the spiculum. This muscle attaches to a tegminal ring at the base of the aedeagus. The tegminal ring is provided with a short apodeme.

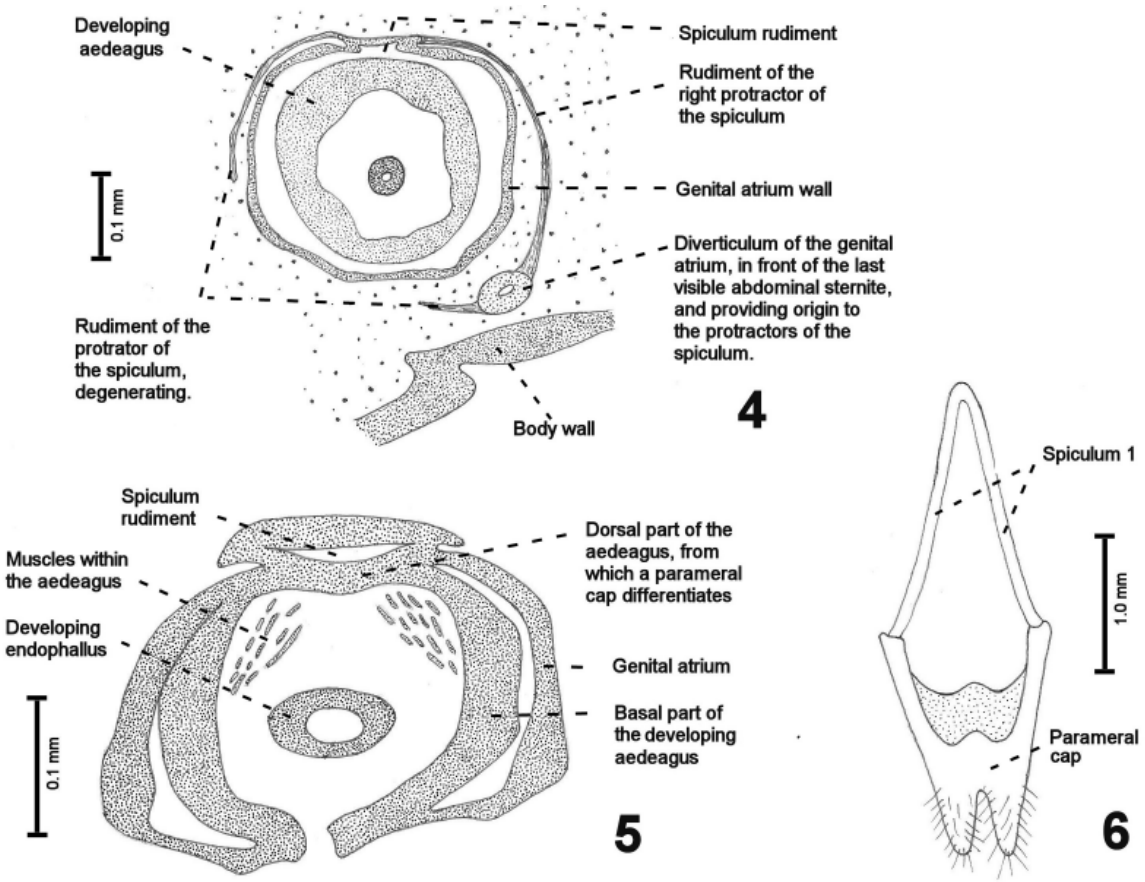
The tracheal supply, reaching the base of the aedeagus, is twisted, i.e. the tracheae, from the right side, enter the muscular mass at the base of the aedeagus on the left side, and those from the left side reach the aedeagal base to enter the muscular mass on the right side (Fig. 3). The nature of the twisted tracheal supply to the aedeagus indicates a clockwise 'retournement' of the organ, when looked at from behind. The relative orientation of the right and left aedeagal tracheae, on completion of the rotation of the aedeagus in the clockwise direction, is well explained and illustrated in Kumar and Verma (1971).

The median ejaculatory duct presents a spiral coiling, when the aedeagus is in repose (Fig. 2-3). In all dissections the aedeagus appeared deversed to the right side. ('deversed' means having an inclined orientation of the aedeagus in repose.)

Discussion

The developmental phenomenon of 'retournement' of the aedeagus has been inferred from the following morphological features in the adult male curculionids:

(i) Twisted nature of the tracheal supply for the aedeagus.
(ii) Spiral coiling of the median ejaculatory duct.



Figures 4-6. **4)** Diagrammatic cross section through a basal part of the aedeagal apparatus in a young pupa of *Galerucella birmanica* (after Verma 1969). **5)** Cross section through a basal part of the developing genital tube in a pupa, within 24 hours of pupation, of *Galerucella birmanica* (after Verma 1969). **6)** Spiculum 1 with parameral cap in *Aeolesthes induta*, dorsal view (after Kumar and Verma 1980).

(iii) The asymmetrical tilting, upward and towards the right side, of the spiculum gastrale.
(iv) The unpaired muscle arising from the anterior tip of the spiculum attaches to the tegminal ring.

From similar adult morphological features the 'retournement' has been inferred in several Chrysomeloidea (Kumar and Verma 1971, 1980; Pawar and Verma 1977).

It may be noted that there is a close similarity between the mechanism of the 'retournement' in Chrysomeloidea and that in Curculionidae. In the former the 'retournement' has been attributed to a unilateral pull on the dorsal face of the genital tube (= aedeagus + genital atrium) by the right protractor of the spiculum 1, while its counterpart of the left side undergoes degenerative changes (Fig. 4) (Verma 1969; Verma and Kumar 1972). This leads to a rotation of the developing aedeagus in the clockwise direction, as viewed from the caudal end. In some cases the right protractor degenerates, resulting in a counterclockwise 'retournement'.

In many Chrysomeloidea there are two spicula in the aedeagal apparatus, one behind the other. They have been referred to as spiculum 1 (the more anterior one), and spiculum 2 (Kumar and Verma 1980). It may be clarified here that the structure, which has been referred to as spiculum 2 , is the homologue of the spiculum gastrale in curculionids.

In the chrysomelid *Galerucella birmanica* the spiculum 2 is represented by a soft diverticulum of the genital atrium, arising close in front of the last visible abdominal sternum (Verma 1969) (Fig. 4). Spiculum 1 (Kumar and Verma 1980), and simply named as spiculum in Verma (1969) and Verma and Kumar (1972) is actually a tegminal apodeme, which will become evident if the development of this structure in *Galerucella birmanica* (Verma 1969) is kept in view. In this chrysomelid the rudiment of the spiculum

appears as an apodemal invagination at the base of the aedeagal rudiment on the dorsal side (Fig. 5). The basal dorsal part of the aedeagal rudiment develops a parameral cap; hence it should be regarded as representing the tegmen. (For further development and the 'fate' of the parameral cap Verma, 1969 may be referred to). In support of this notion is the spiculum 1 in the cerambycid *Aeolesthes induta* Newman, 1842 carrying a bifid parameral cap dorsally (Fig. 6). It may be recalled that the tegmen in a curculionid includes a short tegminal apodeme.

In the curculionids the unilaterally developed muscle, arising from the anterior tip of the spiculum gastrale and attaches to the tegmen, is comparable to the asymmetrically developed right protractor of the spiculum 1 in Chrysomeloidea (Kumar and Verma 1980), as it arises from the spiculum gastrale/spiculum 2 and attaches to the spiculum 1/tegminal apodeme. If this homology is accepted, it becomes obvious that in a curculionid the muscle, which is responsible in bringing about the 'retournement', not only rotates the genital tube, but also pulls the anterior part of the spiculum gastrale sideways on the right side and upward; hence the tilt in the anterior part of the spiculum.

The morphological features, suggesting the developmental phenomenon of 'retournement' of the aedeagus, seem common, if not universal, among Curculionoidea. The asymmetrical upward and rightward tilting in an anterior part of the spiculum gastrale has been recorded also by Burke (1959) in the cotton boll weevil (*Anthonomus grandis* Boheman, 1843), by Hieke (1966) in the curculionid *Liparus* Olivier, by Francke-Grosmann (1948) in a scolytid (*Dendroctonus micans* Kugel, 1794), by Bissell (1937) in the pecan weevil (*Curculio caryae* Horn, 1873), and by Schoof (1942) in the curculionid *Conotrachelus* Schönherr. These authors also observed a strong muscle band arising from the anterior tip of the spiculum gastrale and attaching to the tegmen on the right side, in contrast to the similar left muscle being weakly developed or absent.

Our communication is not the first to report the aedeagal 'retournement' in Curculionidae. Wanat (2007) has comparatively studied male terminalia in Curculionoidea and other Coleoptera, and has inferred that basal weevil groups, Nemonychidae, Oxycoryninae, and Aglycyderinae exhibit genitalia rotation around the long body axis.

Phyletic closeness between Chrysomeloidea and Curculionidea has been generally recognized. Farrell (1998) worked out phylogeny of Phytophaga, taking into account 212 morphological features and 115 complete DNA sequences. In Farrell's study it was inferred that Chrysomeloidea and Curculionoidea are sister groups. This opinion was expressed also by Marvaldi et al. (2002). Hunt et al. (2007) studied 1900 beetle species through phylogenetic analysis, based on sequences of three genes, and inferred that Chrysomeloidea and Curculionoidea, along with Erotylid series, Cucujid series, and Nitidulidae, appear to belong to the same clade.

The present study, pointing to 'retournement' of the aedeagus in Curculionidae taking place through essentially the same developmental mechanism, is additional evidence supporting the phyletic closeness between the two superfamilies, Chrysomeloidea and Curculionoidea. As Beutel et al. (2010) pointed out, even in the present age of phylogenomics, comparative morphology may still play a vital role in working out phyletic relations.

Acknowledgments

The authors are grateful to Dr. V. V. Ramamurthy, Principal Scientist, Division of Entomology, Indian Agricultural Research Institute, New Delhi for identifying the curculionids, studied. They are also thankful to the Museum Library of Paris for generously helping us in getting access to the required literature. We thank Ron N. Beenen, Naturalis Biodiversity Centre, Leiden, and Jean-François Voisin, Museum National d'Histoire Naturelle, Paris for reviewing the manuscript.

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Received December 9, 2012; Accepted March 29, 2013.