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Mechanisms Modeling the Double Rotation of the Elytra in Beetles (*Coleoptera*)

Leonid Frantsevich

Schmalhausen-Institute of Zoology, *B. Chmielnicki str.* 15, *Kiev*-30, 01601, *Ukraine*

Abstract

We recorded transient movements, *i.e.* opening and closing, of beetle elytra. The beetles were tethered from below and filmed under a skew mirror; two markers were glued on each elytron at the apex and at the base. Body-fixed 3D traces of the apical and basal markers were reconstructed. The trace of the basal marker was, as a rule, non-parallel to the apical trace. The costal edge of the elytron uniformly supinated in the course of adduction of the apical marker. We found two essential attributes of double rotation: (1) the elytron to body articulation is approximately a spherical mechanism; (2) transient opening and closing possess single degree of freedom. The double rotation was modeled with two mechanisms: (1) a flexagon model of the Haas and Wootton's type simulated the elytral movement relative to the movement of one facet of the flexagon; (2) a screw and nut model provided traces as two sectors of a helical thread, one sector was phase shifted with respect to other one. Screw guideways in a spherical mechanism give rise to discrepancies. Exact solution for a spherical mechanism with two guideways was proposed. The modeling revealed the attribute (3): the elytron is actuated by two linked but differently directed drives. Experimental investigations on the elytron to body articulation may be oriented at search of those mechanisms.

Keywords: insect flight, insect thorax, flexagon, screw and nut joint

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1 Introduction

The main function of fore wings, or elytra, in beetles is to conceal and protect folded membranous hind wings and the soft abdomen. The elytra are tightly closed above the wings and abdomen during the predominant part of the adult beetle's life. Flight activity in beetles is a short event. Before flight, the elytra open sidewards and release the wings free. After flight, the wings and elytra restore their closed position.

Contribution of the elytra to aerodynamic forces during flight has been measured experimentally and evaluated by modeling on restrained and freely flying beetles[1–5]. This contribution, with respect only to lift, appeared to be significant in beetles which flap their elytra in synchrony with the wings. Flight oscillations of the elytra are passive, which are transmitted from the vigorously oscillating dorsal part of the metathorax, the wing-bearing segment, via a mechanical linkage to the dorsal part of the mesothorax, the elytra-bearing segment[4,6–9].

Transient movements, *i.e.* opening and closing, are the only active movements performed by the elytra. The anterior wingless thoracic segment, the prothorax, is also involved in transient movements. The joint between the pro- and mesothorax moves an angle for 20° to 30° during transients[10,11]. If a beetle is tethered at the prothorax[3,8,12] then the mesothorax is non-stationary during transients. Own movements of the elytra relative to their articulation with the mesothorax will be blurred. The same is true for freely flying beetles.

Stationary recordings of the opening and closing became possible when a beetle was tethered at the ventral side of the meso- and metathorax[13,14]. We recorded 3D trajectories of dot markers glued on different parts of the elytron. We investigated in total 39 specimens of 18 species, 11 families of two main suborders of *Coleoptera*. In many cases we revealed the phenomenon of double rotation of the elytron during active transient movements. Results relevant for the present article are

Corresponding author: Leonid Frantsevich
E-mail: leopup@izan.kiev.ua

summarized in Section 3.

The elytron to body articulation is multicomponent and very compact. 3D shapes of structural components are complicated, their verbal descriptions or flat images are vague and till now have not been formalized in kinematic models. The preliminary goals of modeling are (a) to understand the adaptive value of the double rotation and (b) to derive essential attributes of the mechanism actuating the opening–closing elytra.

2 Definitions

The origin of the body-fixed Cartesian reference is set at the apex of the scutellum, a small triangular plate seen between the basal parts of the closed elytra. The direction of the transverse axis q is between any two symmetrical landmarks on the beetle's body. The longitudinal axis p is roughly tangential to the basal parts of the elytra and the ventral plate of the meso- and metathorax. The vertical axis v is perpendicular to q and p. Positive directions are respectively to the right, anterior and dorsal. Also we define the plane $q0p$ as the equatorial, $q0v$ as frontal, $p0v$ as sagittal. In spherical coordinates, the azimuth φ is counted in $q0p$ clockwise from the positive semiaxis p, the elevation ψ is counted upwards from $q0p$.

We discern in the elytron a big rigid blade, and a tiny antero-medial process – the root, which articulates with the mesothorax (Fig. 1). Closed elytra link together down the sutural (medial) edge, the opposite, lateral one is named the costal edge. Posteriorly, both edges converge in the apex. The outward movement of the elytron with respect to the body is the abduction, and the reverse inward movement is the adduction.

Performing abduction or adduction, the apex moves down a flat circular trajectory with respect to the body. The axis of this rotation is named as the Rotation Axis of Abduction–Adduction (RAAM). The angle of rotation of the apical marker about RAAM, counted forwards from the closed position, is designated with ε. The blade of the elytron is able to secondary torque around the radius-vector from the root to the apex, or approximately around the sutural edge. Direction of the torque when the costal edge elevates is named supination, inward depression is named pronation. A trajectory of any marker outside the sutural edge is the combination of abduction–adduction with supination–pronation.

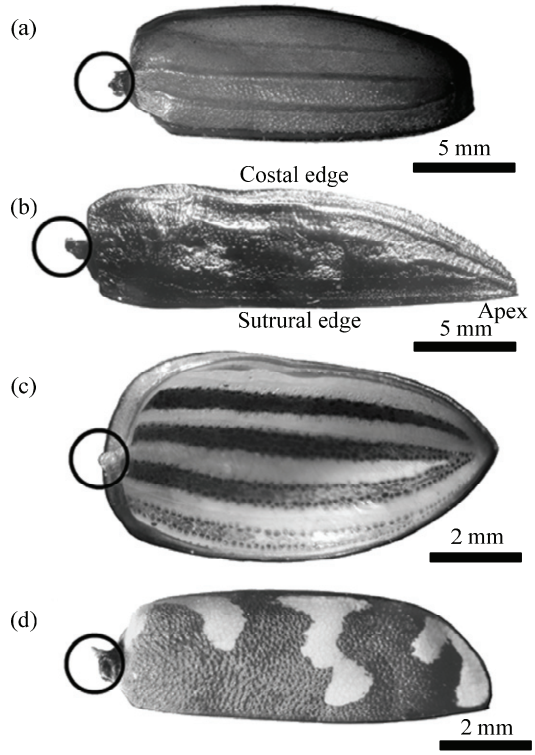

Fig. 1 Elytra in beetles. (a) *Melolontha melolontha* (Scarabaeidae); (b) *Chalcophora mariana* (Buprestidae); (c) *Leptinotarsa decemlineata* (Chrysomelidae), view from below; (d) *Cicindela hybrida* (Cicindelidae). Roots of the elytra are enclosed in annuli.

3 Results: Experimental background

(1) Tethered beetles were filmed under a skew mirror which can provide images from two directions.

(2) An apical dot marker P was glued to the apex of the elytron, and a shoulder marker Q was a thin rod glued tangentially to the base of the elytron and pointing sidewards (Figs. 2a and 2b). Their coordinates were traced frame by frame (Figs. 2c and 2d).

(3) 3D traces of both markers were reconstructed in the body-fixed space (Figs. 2e and 2f).

(4) The shape of the apical trace reflected different steps of transient movements: (a) small initial elevation of the linked elytra before broad opening; (b) broad outward swing (abduction) during opening; (c) captured trace points of passive flight oscillations shaped as "mushroom heads"; (d) reverse inward swing (adduction) during closing and (e) small final depression after closing, reverse to elevation. The broad outward and inward swings were processed in synchrony for the apical and shoulder traces.

(5) The apical trace in the given elytron was a flat