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Skeleto-muskular mechanism of the halteres of the melon fly, *Dacus* (*Strumeta*) *cucurbitae* COQUILLETT

(Diptera: Trypetidae)

With 4 text figures

The halteres are extremely specialized structures whose exact physiology and mode of action is not yet clearly understood. Every possible sensory function has been assigned to them by earlier workers, and as reviewed by MELIN (1941), the halteres have even been thought of as organs of respiration and sound production.

There are two main schools of thought regarding the function of the halteres. Some workers (VON BUDDENBROCK 1919, and his subsequent followers) consider them as sensory organs of stimulation, 'Stimulationsorgane', whose discharge of energy serves to tone up the motor activity. Other more recent workers (FRAENKEL & PRINGLE 1938; PRINGLE 1948) regard them as sensory organs of equilibrium functioning in the manner of a gyroscope. However, as pointed out by CHADWICK (1953) there is justification for each of these points of view, provided that neither is interpreted as excluding the other.

Each haltere of *Dacus* (*Strumeta*) *cucurbitae* COQUILLETT, is composed of three portions, viz., a swollen 'base', a narrow elongated tubular 'stalk', and an apical more or less globular thin-walled 'end-knob'. Basally, the haltere is movably articulated with the metathorax. It has been suggested (PRINGLE 1948) that the stalk is formed by two fused veins, one of which may involve the Radius vein.

Articulation of the Haltere

Axillary sclerites

The axillary sclerites are much modified and intimately associated with the base of the haltere. Unlike the forewing where there are four of them, the number of axillary sclerites of the haltere is only three. Eventhough highly modified, their true identities are easily brought out when their relationships are carefully studied. There is no account available in literature of the axillary sclerites of the halteres of any cyclorrhaphous Diptera. As a matter of fact, BONHAG's (1949) work on the horse-fly, is the only available reference on the axillary sclerites of the halteres of Diptera. However, as will be evident from the following account, some of his observations are not wholly indisputable.

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First axillary sclerite: (Figs. 1a, 1b, 3; $1Ax_3$)

It is a very slender and gently curved sclerite anteriorly articulating with the anterior notal wing process (ANP_3), its posterior end extending close to the third axillary sclerite. Its entire surface abuts against the dorso-mesal margin of the second axillary sclerite ($2Ax_3$).

BONHAG (1949) considers the first axillary sclerite as articulating with the third axillary which, however, is an interesting observation requiring extensive study in the entire insect series before it can be accepted.

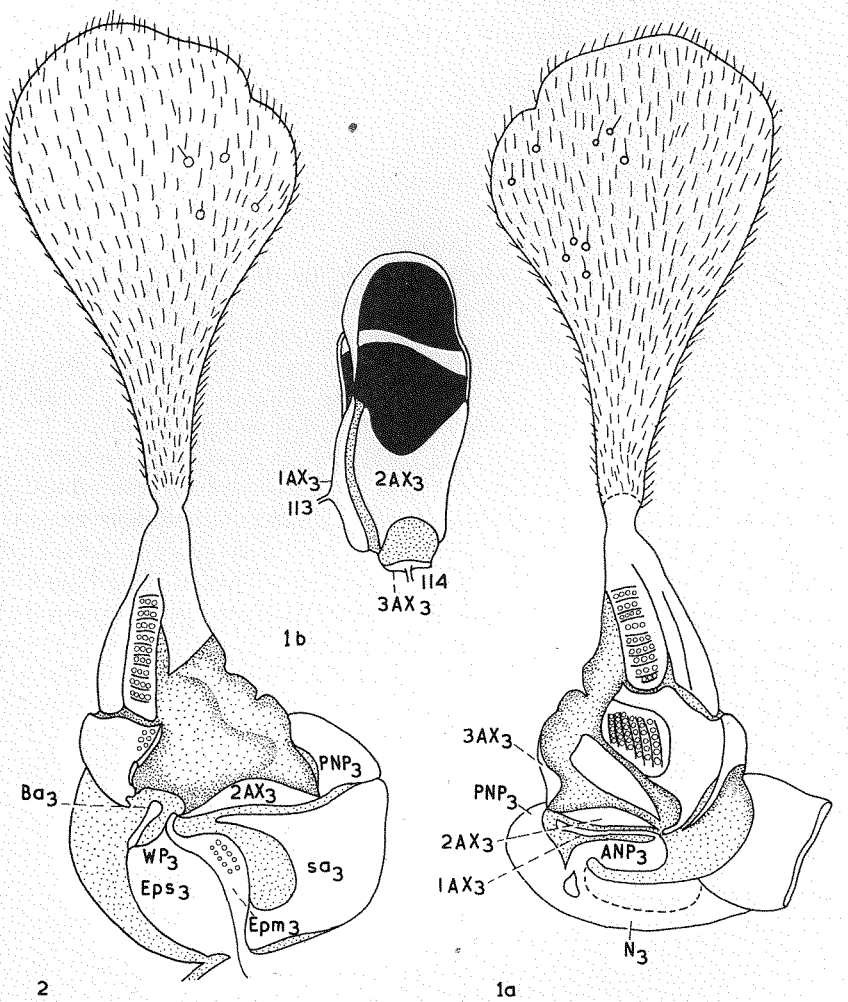

Fig. 1a. Dorsal view of left haltere. — Fig. 1b. Basal inner view of haltere. — Fig. 2. Ventral view of left haltere. ANP_3, anterior notal wing process; 1 Ax_3, 2 Ax_3, 3 Ax_3, first, second and third axillary sclerites respectively; Ba_3, basalar sclerite; Eps_3, episternum; Epm_3, epimeron; N_3, alinotum; PNP_3, posterior notal wing process; Sa_3, subalar sclerite; WP_3, metapleural wing process

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Second axillary sclerite: (Figs. 1a, 1b, 3; $2Ax_3$)

It is the largest and the main pivotal sclerite of the haltere base. It is the only sclerite with a dorso-ventral orientation within the membranous base of the haltere. Dorsally, it is in apposition with the first axillary sclerite. Ventrally, it is clearly articulated with the pleural wing process (WP_3). Posteriorly, it is articulated with the third axillary sclerite. The second axillary is intimately associated with the haltere base.

Third axillary sclerite: (Figs. 1a, 1b, 3; $3Ax_3$)

The small third axiallary sclerite is, more or less, triangular with its base towards the metathorax. The anterior margin of its base articulates with the second axillary, while the posterior margin articulates with the posterior notal wing process (PNP_3).

Epipleurites

Basalar sclerite: (Figs. 2, 3; Ba_3)

It is a very minute finger-like sclerite incompletely detached from the upper met-episternal portion of the pleural sclerite (pl_3). The apical portion of the basalar sclerite is free and is situated close to the meta-pleural wing process.

Subalar sclerite: (Figs. 2, 3; Sa_3)

It is relatively more developed than the basalar, and is roughly triangular in outline. The elongated apex of the subalar sclerite is wedged in the narrow space between the haltere base and the met-epimeral portion of the pleural sclerite (pl_3). The subalar is incompletely detached from the met-epimeral portion of the pleural sclerite.

Musculature

There has been a widely accepted notion among entomologists that the haltere is operated by means of a single muscle (vide, PRINGLE 1948, TIEGS 1955). On the basis of this assumption various interpretations of the movement of the haltere have been put forward. It has also been accepted that there is a great similarity and correlation in the frequencies of the movement of the wing and the haltere. This observation attracted the attention of the present writer, and to find out the reason, be probed deeper into the matter. His observations clearly show that the similarity in the frequencies of movement of the wing and the haltere, owes its existence to a corresponding similarity of the basal mechanism involved in the respective movements.

As would be very clear from the description which follows, the haltere is acted upon by a greater number of muscles than hitherto described by various workers. It cannot be denied of course, that in view of the great functional changes undergone by the haltere, there has been considerable modification in its skeleto-muscular system. This, however, fails to eclipse the basic similarity of the skeleto-muscular system of the haltere with that of the wing.

The present author has followed TIEGS (1955) regarding the broad grouping of the muscles in order to facilitate comparison with the musculature of the wing.

Tergal muscles

These muscles are wanting in the metathorax of the melon fly. BONHAG (1949) in the horsefly, MILLER (1950) in *Drosophila melanogaster*, NUSSBAUM (1960) in *Basilia nana*, SNODGRASS (1956) in the honey-bee, and ALAM (1951) in *Stenobracon deesae* report a similar condition.

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Dorso-ventral muscles

Indirect levator of the haltere: (Fig. 4; No. 108)

This muscle consists of two branches (*a* and *b*) arising on the ventro-mesal aspect of the basisternal surface of the second intersegmental ridge. It is inserted through a long and thin tendon on the under-surface of the convex base of the anterior notal wing process. On contraction, it pulls down the convex basal area of the anterior notal wing process, thereby raising the haltere. It is homologous with the 'dorso-ventral muscle, No. 56' of the horse-fly (BONHAG 1949), and the 'muscle of the haltere, No. 77' of *Drosophila melanogaster* (MILLER 1950). However, since MILLER gives no account of either its origin or insertion, it is not possible to be definite about its homology.

Tergal depressor of the trochanter: (Fig. 4; No. 109)

Besides being the depressor muscle of the trochanter, it also serves as an indirect levator of the haltere, by pulling down the alinotum on contraction.

Pleural (epipleural) muscles

First extensor of the haltere: (Fig. 4; No. 110)

This small muscle arises on the lateral portion of the second intersegmental ridge (metepisternal surface) just mesal to the origin of the Occlusor of the metathoracic spiracle, and is inserted on the antero-dorsal aspect of the internal apodeme of the basalar sclerite. On contraction, it pulls the haltere slightly forwards, its action being transmitted to the base of

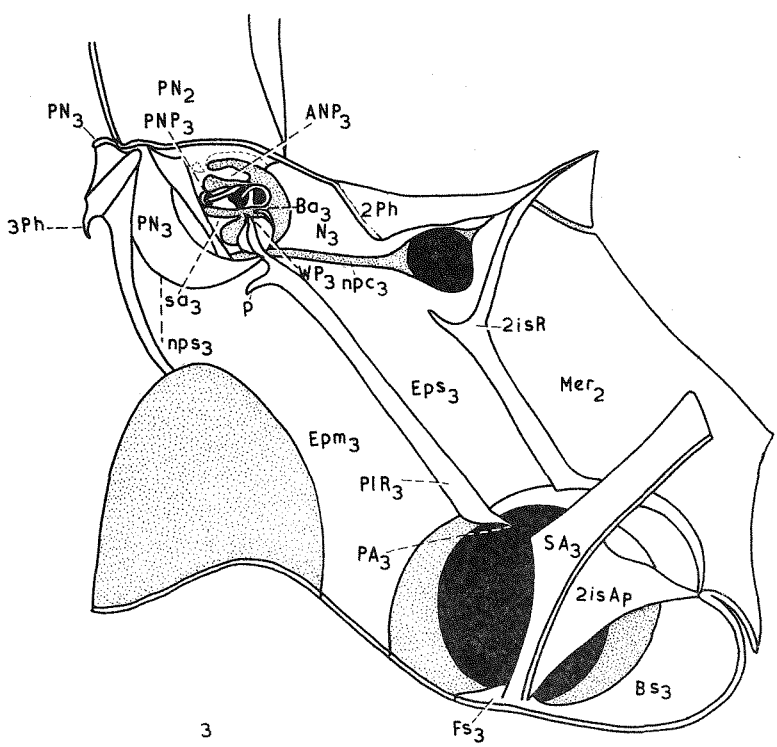

Fig. 3 (siehe Fig. 4)

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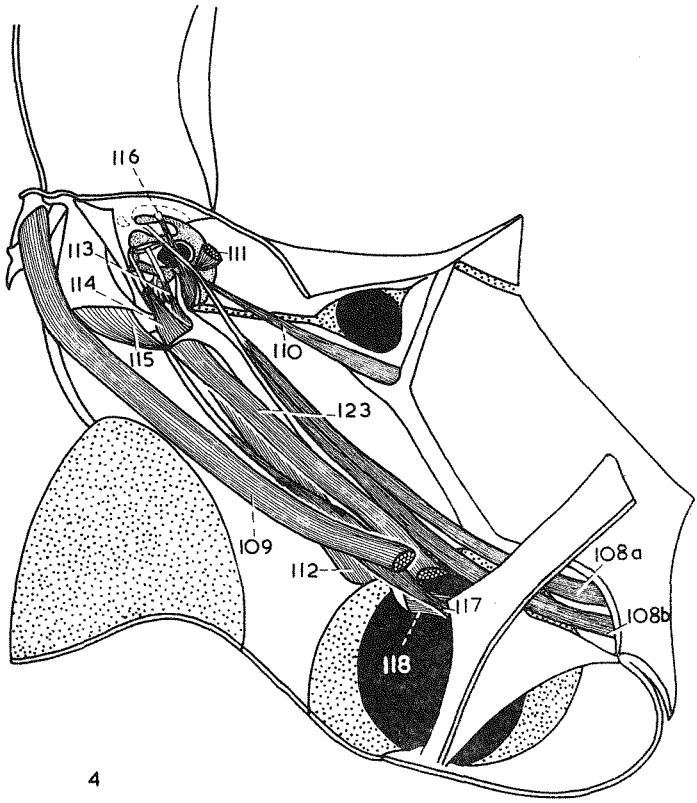

Fig. 3. Inner view of left half of metathorax. — Fig. 4. Same as Fig. 3, showing musculature. Bs_3, meta-basisternum; Fs_3, meta-furcasternum; $2isR$, second intersegmental ridge; $2isAp$, apodeme of the second intersegmental ridge; Mer_2, meron of middle coxa; npc_3, noto-pleural cleft of metathorax; nps_3, notopleural sulcus of metathorax; PA_3, meta-pleural apophysis; $2ph$, $3ph$, second and third thoracic phragmata respectively; PN_2, PN_3, meso-, and metapostnotum respectively; pN_3, lateral concave extension of posterior part of metanotum; p, posteriorly directed projection of the meta-pleural ridge; PlR_3, meta-pleural ridge; SA_3, metasternal apophysis

the latter through the basalar sclerite. It is homologous with the 'anterior pleural muscle of the basalar, No. 57' of the horse-fly (BONHAG 1949). BONHAG is also of the opinion that it is involved in the slight 'promotion' of the haltere.

Second extensor of the haltere: (Fig. 4; No. 111)

This very small muscle arises on the posterior surface of the second phragma slightly ventral to the point where the latter is joined by the trans-postnotal ridge, and is inserted on the antero-dorsal aspect of the basalar apodeme. It functions, more or less, in the same way as the first extensor of the haltere. BONHAG (1949) in the horse-fly, attributes a similar function to the 'tergal muscle of the basalar, No. 59'.

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First flexor of the haltere: (Fig. 4; No. 112)

This muscle arises on the antero-ventral surface of the met-epimeron close to the metapleural ridge, and is inserted on the tip of the subalar sclerite. On contraction, it serves to pull the haltere slightly backwards. Its action is transmitted to the base of the haltere through the subalar sclerite. It is homologous with the 'pleural muscle of the subalar, No. 61' of the horse-fly (BONHAG 1949) where it is also considered to bring about slight 'remotion' of the haltere.

Haltere adjustor muscles

Second flexor of the haltere: (Figs. 1b, 4; No. 113)

This very small muscle arises on the basal aspect of the posteriorly directed projection (*p*) of the metapleural ridge incompletely covered over by the third flexor of the haltere, and is inserted on the first axillary sclerite of the haltere base. BONHAG (1949) does not describe this muscle in the horse-fly. The 'pleural muscle of the third axillary sclerite, No. 60a' described by him, however, appears very similar to this muscle. As the muscle is very tiny, and the first and the third axillary sclerites are located very close to each other, it is quite likely that BONHAG (1949) has mistakenly regarded it as inserted on the third axillary sclerite.

Third flexor of the haltere: (Figs. 1b, 4; No. 114)

This small muscle arises on the dorsal margin of the posterior projection of the meta-pleural ridge, and is inserted on the mesal margin of the third axillary sclerite. On contraction, it serves as flexor of the haltere. It is homologous with the 'pleural muscle of the third axillary sclerite, No. 60' of the horse-fly (BONHAG 1949) where it is regarded as a remotor of the haltere.

Depressor of the haltere: (Fig. 4; No. 115)

This is the tergo-pleural muscle arising on the tip of the posterior projection of the meta-pleural ridge, and is inserted on the under surface of the highly concave postero-lateral extension of the alinotum. On contraction, it pulls in the latter, and this action results in the depression of the haltere. Although this concavity of the posterolateral part of the alinotum is a constant feature, it has been neglected by all workers on Diptera as regards its role in the movement of the haltere. The muscle, too, has not been recorded earlier in any dipterous insect.

Tergo-pleural muscle: (Fig. 4; No. 116)

This small muscle arises on the met-episternal surface of the dorsal part of the meta-pleural ridge, and proceeding more or less vertically upwards, is inserted slightly anterior to the anterior notal wing process, on the alinotum. It functions in the same way as its homologue in the mesothorax. It is homologous with the 'tergal muscle of the pleural wing process, No. 62' of the horse-fly (BONHAG 1949).

Pleuro-sternal muscles

Anterior pleuro-sternal muscle: (Fig. 4; No. 117)

It originates on the postero-lateral margin of the metasternal apophysis, and is inserted on the tip of the posteriorly directed projection of the meta-pleural ridge. It functions in the same way as its counter-part in the mesothorax. It is homologous with the 'anterior pleurosternal muscle, No. 63' of the horse-fly (BONHAG 1949), 'pleurosternal muscle, No. 79' of *Drosophila melanogaster* (MILLER 1950), and the 'delicate muscle acting on the haltere' in *Plusiomyia olliffi* (TIEGS, 1955).

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Posterior pleuro-sternal muscle: (Fig. 4; No. 118)

It arises on the postero-lateral margin of the meta-sternal apophysis, and is inserted on the dorsal margin of the meta-pleural apophysis. It functions in the same way as its counter-part in the mesothorax. It is homologous with the similarly labelled muscle 'No. 64' of the horse-fly (BONHAG 1949).

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Summary

The skeleto-muscular mechanism of the halteres of the melon fly *Dacus* (*Strumeta*) *cucurbitae* COQUILLETT, has been described in detail which also happens to be the first account of its type in Diptera Cyclorrhapha. It has been shown that the haltere is acted upon by a greater number of muscles than hitherto known. Comparison has been made with other dipterous insects whereever found possible.

Zusammenfassung

Der Skelett-Muskel-Mechanismus der Halteren des Melonenschädlings *Dacus* (*Strumeta*) *cucurbitae* COQUILLETT wird eingehend beschrieben. Es ist zugleich der erste Bericht über diesen Typ unter den Diptera Cyclorrhapha. Es wird gezeigt, daß die Zahl der Muskeln, die auf die Halteren einwirken, größer ist, als bisher angenommen wurde. Soweit möglich, werden Vergleiche mit anderen Diptera angestellt.

Резюме

Описывается детально скелето-мускулярный механизм жужжалиц у *Dacus* (*Strumeta*) *cucurbitae* COQUILLETT как первое доказательство этого типа у Diptera Cyclorrhapha. Было отмеченно, что жужжальца работают большим числом мускуль чем до сих пор было известно. По возможности даются сравнения с другими двухкрылими.

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