THE SKELETO-MUSCULATURE OF THE THORAX (MESOSOMA) OF THE QUEEN AND WORKER WOOD ANT

R.G. Smith, Department of Biological Science,
North East London Polytechnic, Romford Road, London E 15.

Introduction

The body region described in this paper consists of the three thoracic segments plus the propodeal (first abdominal) segment which has become completely fused to them. In order to avoid an inexact use of the word thorax for this region, the term mesosoma (Michener, 1944) is used. In females the mesothoracic, metathoracic and propodeal regions form a very compact box, which is solidly fused together in the worker, while in the queen the meso- and metanota are free. This "fused complex" is referred to as the holmus (Haupt, 1938).

The study of the worker was originally carried out on specimens of Formica lugubris Zetterstedt obtained from North Yorkshire. Due to a move to Essex it was easier to obtain specimens of Formica rufa L., so work on the queen was carried out on this species. A study of specimens of both species showed no significant difference in the skeleto-musculature.

The Prothorax

The prothoracic skeleton in both the queen and worker is almost identical in structure, the only significant difference being the shape of the pronotum (Pn). In the queen it covers the anterior and antero-lateral regions of the mesosoma, but in the worker, with the reduction of the mesonotum, the pronotum covers the antero-dorsal region as well. Three other sclerites (two cervico-propleura and the prosternum carrying internally the prothoracic endosternum) are found in the prothorax, they are very closely associated to form the propectus which serves as an exceedingly mobile suspensorium for the head and front legs. The cervico-propleuron (C-P, Fig. 1) is bent so as to present two faces, a lateral and a ventral face, the former being partially hidden under the ventral margin of the pronotum. Anteriorly the cervico-propleuron bears on its internal surface a biramous cuticular outgrowth. The anterior hollow occipital process (OP) articulates with the head. While the solid posterior cervical arm (CA) serves as the point of insertion of three muscles (m6, m11, m17), which according to Snodgrass (1942) are in most insects inserted on a distinct cervical sclerite. In the Hymenoptera it is now generally accepted that the lateral cervical sclerites have fused with the propleura to form the cervico-propleura (for a review of this topic see Smith, 1966). Along the dorsal and postero-lateral edge the cervico-propleuron has become invaginated to form respectively, the submarginal apodeme (SmA) and cervico-propleural plate (C-PP). Where these two invaginations meet is the small cervico-propleural platform (C-PPt) on which the lateral extremity (ASPE) of the prothoracic endosternum is strongly bound. The bottom of the cervico-propleural plate bears the peg-like coxal process (CP), on which

articulates the fore coxa. The prosternum (Fig. 2) presents two faces, a small diamond shaped face that is visible along the postero-ventral edge of the two cervico-propleura. Springing from its posterior edge is the much larger triangular shaped face. This latter face carries the prothoracic endosternum (PE), externally its origins are marked by two pits(PEP). These mark the roots of two T-shaped invaginations which have fused medially to form the main body of the endosternum which is shaped like the Greek letter Π. The cuticle of the main body is drawn out to form eight cuticular wings which greatly increase the surface area for the attachment of ten pairs of muscles (m4, m5, m8, m9, m14-17, m19, m21). In addition the two pits divide the prosternal sclerite into an anterior basisternum (Bs) and minute posterior sternellum (Stn).

Functionally the prothoracic muscles (Fig. 5) fall into five groups. (All muscles are paired and occur in both queen and worker).

Group 1: Muscles that move the head on the propectus

Mesonotal prephragmatic levator (ml) (in the queen it is paired but it is a single muscle in the worker);median cervico-propleural levator and rotator (m2); lateral cervico-propleural levator and rotator (m3); prothoracic endosternal levator (m4); prothoracic endosternal depressor (m5).

Group 2: Muscles that move the propectus on the pronotum

Anterior retractor and rotator (m6); posterior retractor and rotator (m7); anterior protractor (m8); posterior protractor (m9).

Group 3: Muscles that move the fore-coxa on the coxal process

Cervico-propleural promotor (m10); diagonal rotator (m11); basisternal rotator(m12); pronotal remotor (m13); first (m14) and second (m15) prothoracic endosternal lateral remotor; prothoracic endosternal mesal remotor (m16).

Group 4: Muscle between prothoracic endosternum and cervical apodeme (m17); muscle between mesonotal prephragma and pronotum (m18), in the queen it has two areas of insertion on the pronotum.

Group 5: Propectal depressor of the fore leg trochanter (m19a and b).

The Holmus

It is within the holmus that the major skeleto-muscular differences between the winged queen and wingless worker occur. The structure of the queen's holmus (Fig. 3) will be described first - details of the wings and wing sclerites have not been included, while the notal sclerites are only briefly mentioned. Dorsally most of the holmus of the queen is covered by the enlarged mesonotum, which is divided, by a line of flexure (TsA, ScA) into an anterior scutum (Scu) and a posterior scutellum (Scl). The axillae (Ax) represent the postero-lateral areas of the scutum that have become fused to the scutellum. From the anterior margin of the scutum hangs the crescent-shaped mesothoracic prephragma (MsPr). The postphragma (MsPo) is a large U-shaped sclerite projecting far back into the cavity of the propodeum. Its only attachment with the mesonotum is by means of the narrow tapered lateral arms (LA), which attach to the lateral

extremities of the scutellum at the point where it meets with the axillae. The arm is continued anterior to its attachment with the mesonotum, being fused at its tip to the dorsal edge of the mesopleuron. Arising from the arm is a short upturned projection (x) to which muscle 24 is attached. With the mesothorax providing the power for flight, the metanotum (Mtn) is reduced to a narrow transverse sclerite lying behind the scutellum. Laterally the metanotum bears two arms, the anterior one supporting the first axillary sclerite while the posterior one serves as the point of attachment of muscle 42. The lateral, ventral and posterior surfaces of the holmus are occupied by the mesopleura, metapleura and propodeum. The larger area is covered by the mesopleura which are separated ventrally by the mesothoracic median groove. The interpretation of the ventral meso- and metathoracic areas given by Richards (1956) is followed, although they are labelled pleura in this paper after Daly (1964). Laterally each mesopleuron is divided by the posterior oblique sulcus (POS1) into a dorsal (DMspA) and ventral mesopleural area (VMspA). The dorsal and posterior edges of the former are cut off as the subalar area (SaA) by the transpleural sulcus (Trs - Daly, 1964). Lying within the subalar area is the metathoracic spiracle (S2), in other Hymenoptera its position is in the membrane lying between the mesopleuron and metapleuron (Tonapi, 1958). The anterior edge of the mesopleuron is marked off by the transverse groove (TG) which is dorsally notched (SN) and here sits the mesothoracic spiracle (S1). Only the dorsal metapleural area (DMtpA) of the metapleuron is fully demarcated. Its posterior boundary is the metapleural-propodeal suture (Mtp-Prs), which marks the position of the internal propodeal phragma (PrPh). This suture ends ventrally in the metapleural pit (MtpP), which marks the position of the internal finger-like metapleural pit apodeme. Running anteriorly across the metapleuron from the pit is the posterior oblique sulcus (POS2). Anteriorly the metapleuron is divided from the mesopleuron by the lateral (LMs-MtS) and ventral meso-metathoracic sutures. At its dorsal extremity the suture opens as the meso-metathoracic cleft (Ms-MtC). Below the level of the metapleural pit the metapleural-propodeal suture is lost, although it is still present in some ants (Tulloch, 1935). The tergal plate of the propodeum (Pr) is large, being separated from the metapleuron dorsally. On either side it bears the propodeal spiracle (A1). The ventral surface of the holmus bears five large apertures. The two anterior being the middle coxal cavities into which the ball-shaped heads of the middle coxae fit. Each coxa articulates with two processes, the coxal process (MCP) which lies almost vertically below the second on the lateral mesopleural wall. An identical arrangement holds for the hind coxal cavities. Lying between the hind coxal cavities is the propodeal aperture, it bears dorsally two propodeal teeth (PrT) on which the petiole (Pt) articulates. A thin coxo-propodeal bar (C-PrB) separates each hind coxal cavity from the propodeal aperture. This bar carries internally a thin cuticular rod (CR) on which originates muscle 53. Internally, rising from the meso-

thoracic median groove is the mesothoracic endosternum. It consists of a large vertical plate (VP1) carrying on its postero-dorsal edge the two mesofurcal arms (MsfA). Each arm is distally drawn out to form a thin cuticular wing, which is much larger in the queen than the worker, having muscle 36 attached to it. The two arms are joined together by the mesofurcal bridge at the base of the wings. The metathoracic endosternum is composed of three parts - an anterior, transverse, vertical plate arising from the anterior edge of the ventral surface of the metapleuron, a vertical plate (VP2) arising from the metathoracic median groove and thirdly the two divergent metafurcal arms (MtfA). Each arm is distally enlarged to form the metafurcal plate (MtfP), which is closely applied to the back of the corresponding mesofurcal wing and dorsally fused to the metapleural pit apodeme.

In the worker, the loss of the flight machinery has resulted in the holmus (Fig. 3) becoming skeletally simplified to form a continuously sclerotised box in which sulci and sutures, on the dorsal and lateral surfaces, are poorly developed. On the ventral surface, the holmus structure is as for the queen, only the subpleural signum (SSg) being absent. In identifying the dorsal and lateral regions certain landmarks become important - metathoracic spiracle, metapleural pit and internal propodeal phragma (Reid, 1941). The metapleural pit and associate sutures and sulci allow us to identify the dorsal metapleural area, which is continuous dorsally with the tuberculate area (TuA, containing the metathoracic spiracle). The tuberculate area bears internally the origin of muscle 47 and is probably homologous to the posterior part of the subalar area in the queen which bears this same muscle. If this is so, then the sulcus which marks its anterior boundary will be the remains of the transpleural sulcus, and the sulcus running anteriorly from its anterior end, across the mesopleuron is the posterior oblique sulcus. The extent of the meso- and metanota is difficult to determine. A fine line, the mesonotal-mesopleural suture (Msn-MspS), running anterodorsally from the tuberculate area may represent the remains of the boundary between the mesonotum and mesopleuron. At the base of the hood-shaped mesonotum, lying between the tuberculate areas, is a strong groove which could be the boundary between the meso- and metanota. If so, then the thin strip of cuticle lying between the groove and metanotal-propodeal suture (Mtn-PrS) is all that remains of the metanotum. Laterally it is continuous, posterior to the tuberculate area, with the dorsal metapleural area. Internally the meso- and metathoracic endosterna are very similar to those of the queen.

The muscles of the holmus (Fig. 6) can functionally be divided into thirteen groups (all muscles which are paired are found in the queen, the worker lacks muscles 22, 23, 25-29, 36, 38-42).
Group 1: Muscles that move the propectus on the holmus - First (m20) and second (m21) mesofurcal retractors.
Group 2: Mesothoracic indirect flight muscles - Dorso-longitudinal (m22); dorso-ventral (m23); furcal retractor of the postphragma (m24), not all workers examined had this muscle.

Group 3: Mesothoracic direct flight muscles - Basalar (m25); first (m26) and second (m27) pleuroaxillary; subalar (m28); pleural depressor of the scutellum (m29).
Group 4: Muscles that move the middle coxa - Pleural promotor (m30); meso-endosternal/mesopleural promotor (m31); dorsal meso-endosternal remotor (m32); ventral meso-endosternal remotor (m33).
Group 5 - Mesothoracic depressor of the middle leg trochanter (m34), in the queen its origin is on the mesofurca but in the worker it is on the mesopleuron.
Group 6 - Mesospiracular occlusor muscle (m35).
Group 7 - Furcal bracing muscles - Mesothoracic pleurofurcal muscle (m36); interfurcal (m37).
Group 8: Metathoracic direct flight muscles - Basalar (m38); pleuro-axillary (m39); pleurosubalar (m40); coxosubalar (m41); metapleural depressor of the metanotum (m42).
Group 9: Muscles that move the hind coxa - Metapleural promotor (m43), in the worker also partially originates on the mesopleuron; ventral meta-endosternal promotor (m44); dorsal meta-endosternal remotor (m45).
Group 10 - Metathoracic depressor of the hind leg trochanter (m46).
Group 11 - Metaspiracular occlusor muscle (m47).
Group 12: Muscles that move the petiole on the holmus - Median levator (m48); propodeal lateromotor (m49); meta-endosternal lateromotor (m50); metafurcal depressor (m51).
Group 13: Propodeal spiracular muscles - Occlusor (m52); dilator (m53).

Summary

The skeletomusculature of the mesosomal region in both the queen and worker is described. Within the prothorax the only major skeletal difference is the shape of the pronotum. Both females contain the same number of prothoracic muscles. It is within the remaining mesosomal segments (holmus) that the major skeletomuscular differences occur, this being associated with the loss of the flight apparatus in the worker. Dorsally and laterally the worker's holmus has become skeletally simplified with sutures and sulci poorly developed. The worker lacks those holmus muscles which are in the queen associated with the flight machinery.

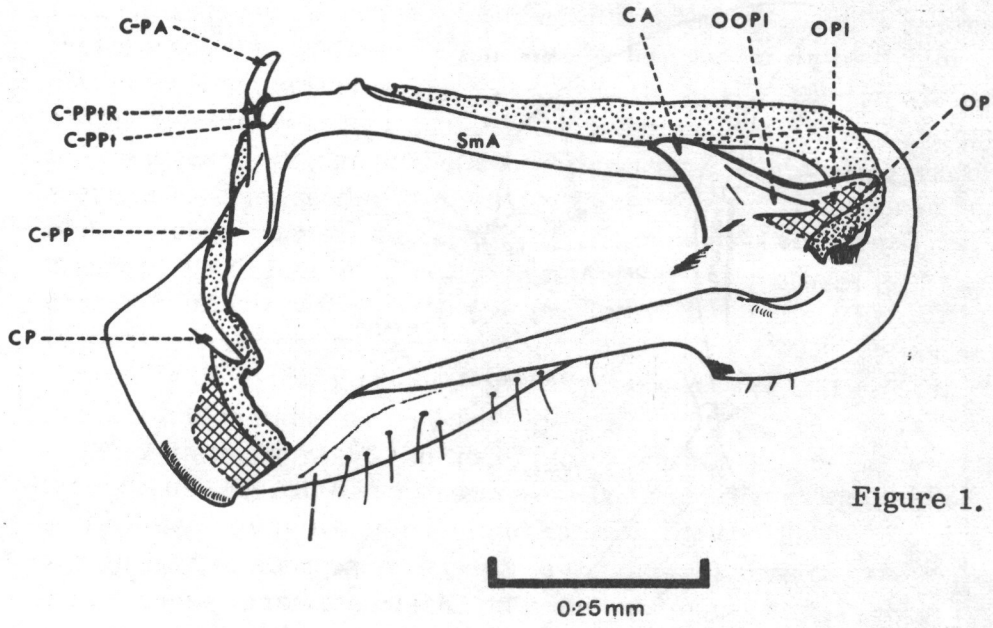
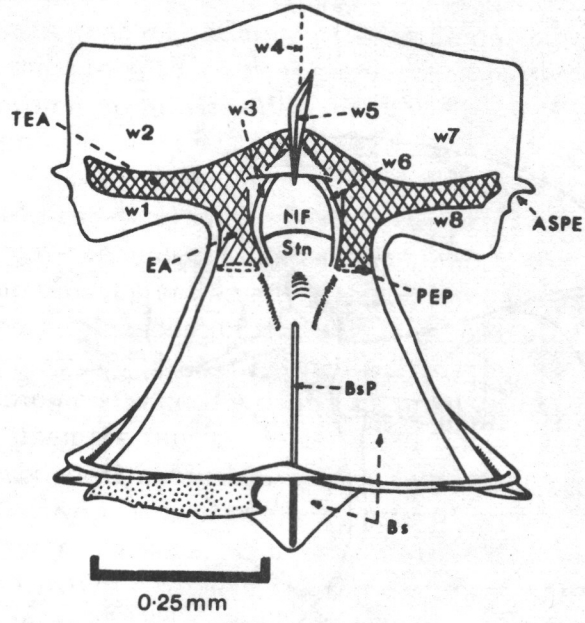


Figure 1.



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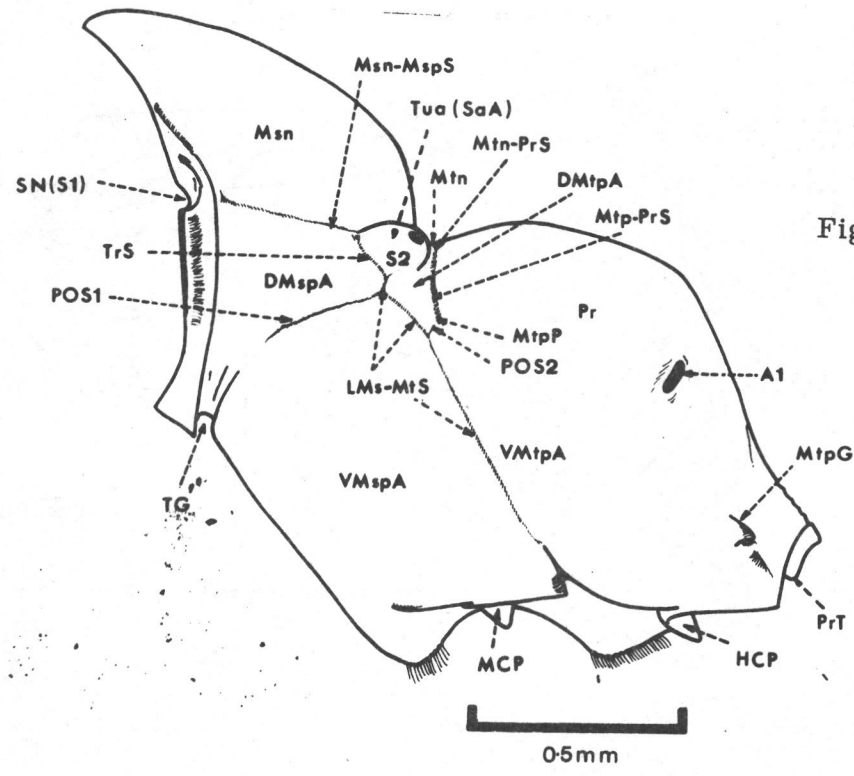

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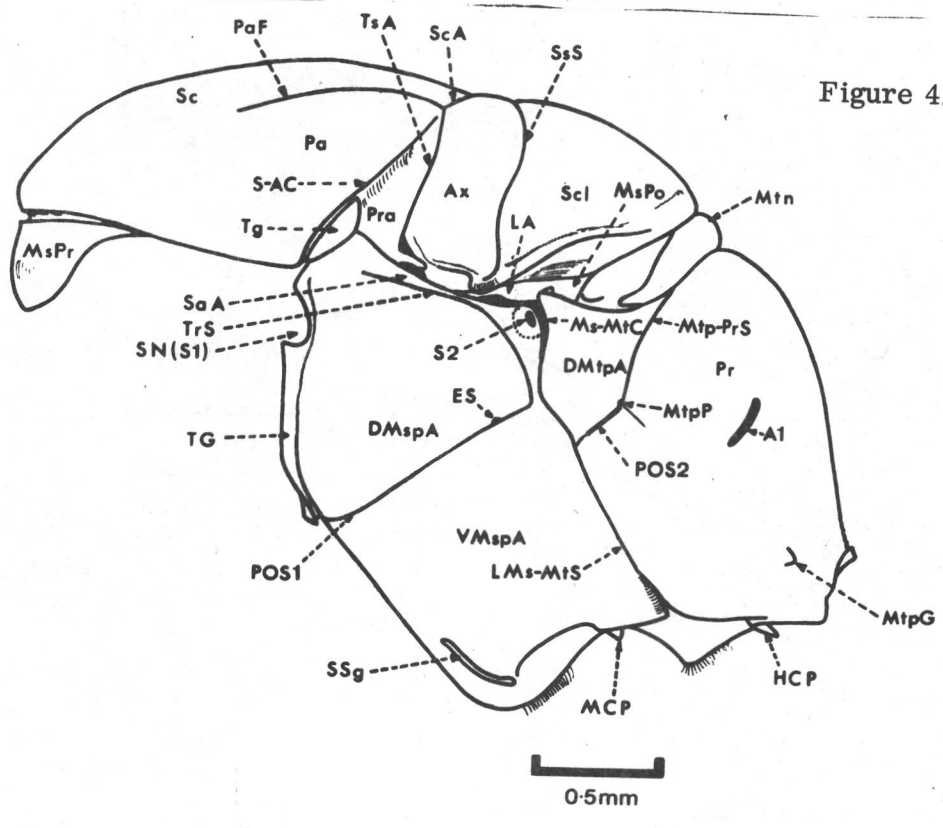

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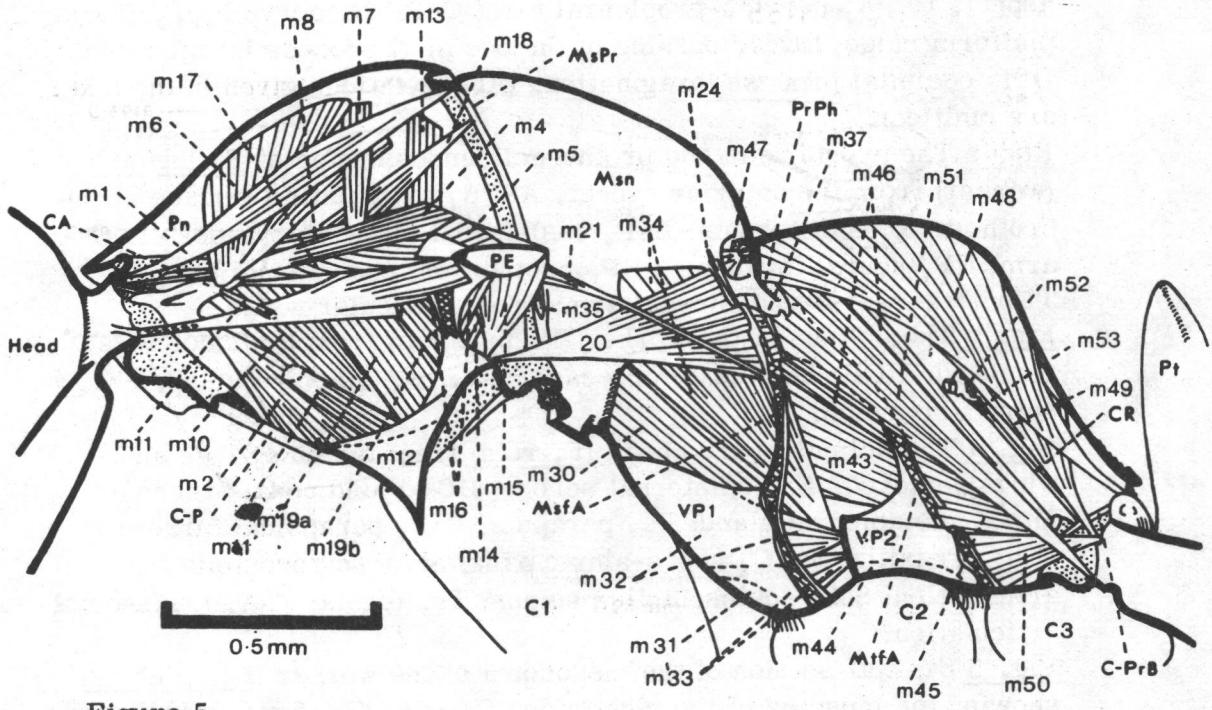

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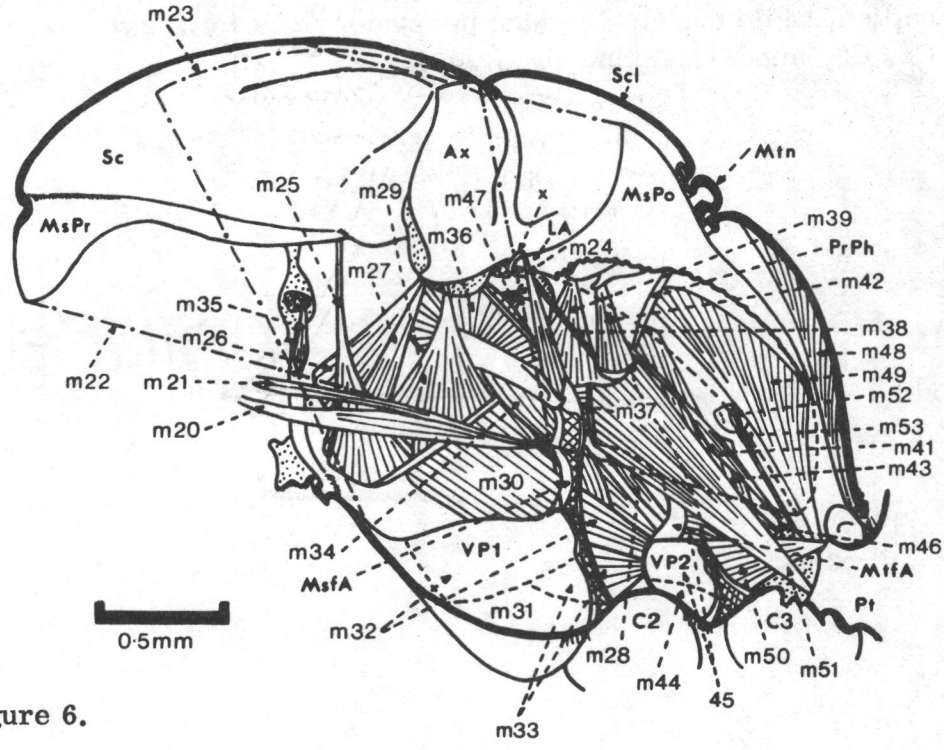

Figure 6.

Fig. 1 Left cervico-propleuron of F. lugubris (worker) from the inner aspect. C-PA, cervico-propleural arm; C-PPtR, cervico-propleural platform ridge; OOPI, opening of the occipital process invagination; OPI, occipital process invagination. (Abbreviations given in the text are omitted).

Fig. 2 The prosternum and prothoracic endosternum of F. lugubris (worker) from the anterior aspect. ASPE, articulating surface of the prothoracic endosternum; BsP, basisternal plate; EA, endosternal arm; NF, neural foramen; PEP, prothoracic endosternal pits; TEA, transverse endosternal arm; w1-8, cuticular wings.

Fig. 3 The holmus of the worker (F. lugubris) from the side, legs removed. HCP, hind coxal process; MtpG, metapleural gland, SN, spiracular notch.

Fig. 4 The holmus of the queen (F. rufa) from the side, legs and wings removed. ES, episternal scrobe; HCP, hind coxal process; MtpG, metapleural gland; Pa, parapsis; PaF, parapsidal furrow; Pra, preaxilla; S-AC, supra-alar carina; ScA, scutoscutellar articulation; SsS, scutoscutellar sulcus; Tg, tegula; TsA, transscutal articulation.

Fig. 5 Sagittal section of the mesosoma of the worker (F. lugubris) showing the muscles of the right side. C1, C2, C3, fore, middle and hind coxa. Muscle 9 is not shown.

Fig. 6 Sagittal section of the holmus of the queen (F. rufa) showing the muscles of the right side. Part of the postphragma is shown in outline only to show the muscles lying underneath. Muscles 22 and 23 which if left in would have covered most of the muscles are shown in outline, while muscle 40 which lies under 42 is not shown at all. C2, C3, middle and hind coxa.

REFERENCES

DALY, H. V. (1964) Skeleto-muscular morphogenesis of the thorax and wings of the honey bee. (Hymenoptera: Apidae). Univ. Calif. Publs. Ent. 39: 1-77, 54 figs.

HAUPT, H. (1938) Zur Kenntnis der Dryinidae. Z. Naturw 92: 13-35, 16 figs.

MICHENER, C. D. (1944) Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bull. Am. Mus. nat. Hist. 82: 157-326, 246 figs., 12 diagrams.

REID, J. A. (1941) The thorax of the wingless and short winged Hymenoptera. Trans. R. ent. Soc. Lond. 91: 367-446, 81 figs.

RICHARDS, O. W. (1956) An interpretation of the ventral region of the Hymenopterous thorax. Proc. R. ent. Soc. Lond. (A) 31: 99-104, 7 figs.

SMITH, R. G. (1966) A study of the mesostomal musculature and skeleton of the ant Formica lugubris Zetterstedt, and certain other Hymenoptera. (PhD Thesis, University of Hull.)

SNODGRASS, R. E. (1942) The skeleto-muscular mechanisms of the honey bee. Smithson. misc. Collns. 103 (2): 1-120, 32 figs.

TONAPI, G. T. (1958) A comparative study of the spiracular structure and mechanisms in some Hymenoptera. Trans. R. ent. Soc. Lond. 110: 489-520, 4 figs., 12 pls.

TULLOCH, G. S. (1935) Morphological studies of the thorax of ant. Entomologica am. 15: 93-130, 8 pls.