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# HOW DIPTERA MOVE THEIR WINGS: A RE-EXAMINATION OF THE WING BASE ARTICULATION AND MUSCLE SYSTEMS CONCERNED WITH FLIGHT

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[Plates 1–3]

## CONTENTS

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The accepted mechanical model for dipteran wing movements is not compatible with the observations of unanaesthetized flies in tethered flight. In this paper a new model is proposed together with previously undescribed morphological features in support of it. A direct coupling is demonstrated between the indirect flight muscles, consisting of a wing base stop mechanism and a locking of the first axillary sclerite onto the parascutal shelf during the downstroke. We propose that wingbeat amplitude is controlled by axillary muscles which alter the downward force on the wing. We also describe the anatomical basis of the automatic changes in the wing stroke during the wingbeat. These are shown to be a direct consequence of the attachment between the fourth axillary sclerite and the scutellar lever arm. By virtue of their attachments to the sclerite, the fourth axillary muscles are shown to have potential control over the tonic characteristics of these automatic changes. The calypters are connected to the third and fourth axillary sclerites and this suggests an aerodynamic function for these structures which has not previously been proposed. A detailed analysis of the anatomy of the non-fibrillar muscles has allowed a complete functional characterization to be made which is consistent with our new model. The functions given to many of the muscles in this analysis are supported by physiological evidence from other studies. Muscular control of a switch mechanism comprising the radial stop and pleural wing process is discussed, as is the control of a wing base proprioceptor.

## 1. Introduction

This study arose out of a comparison of the neuromuscular basis of song production in different *Drosophila* species (J. A. Miyan and A. W. Ewing, unpublished). Individual species within this genus produce specific sound patterns by using low amplitude vibrations of one or both wings (Spieth 1952; Shorey 1962; Bennet-Clark & Ewing, 1967; Ewing & Bennet-Clark 1968). It is difficult to reconcile the observed wing movements of song with the accepted mechanical model for flight (Boettiger & Furshpan 1952; Pringle 1957) although attempts have been made (see, for example, Bennet-Clark & Ewing 1968; Ewing 1979). The amplitude of these movements is very small (30°) when compared with those in flight (approximately 170° full amplitude) and invites a model that does not require the indirect power muscles or the action of the 'click' mechanism (reviewed by Pringle 1957). This is supported by recent physiological recordings which demonstrate that many dorsoventral muscle units (Ewing 1977) and three of the five dorsal longitudinal muscle motor units are inactive during song production (Miyan & Ewing 1985*b*). The frequency of stimulation to these active units is much higher during song than flight and is well above that required for tetanus (Boettiger & Furshpan 1950). In this state of excitation, these muscles would normally produce thoracic oscillations at a frequency determined by tension in the 'click' mechanism (Pringle 1957). However, although there are wing movements during song production which would be expected to trigger such oscillations (Boettiger 1957), none are observed. The low amplitude nature of song is also a puzzle as the 'click' mechanism should ensure much greater amplitude wing movements.

Pringle's (1949, 1954, 1957) analysis of the physiological properties of insect fibrillar muscle demonstrated that these muscles were 'deactivated' (that is, showed zero tension) by quick releases from load and showed a delayed tension response to such releases. Boettiger & Furshpan (1954*a*, *b*) demonstrated that there was a 'reactivation' (that is, an increase in the rate of rise of tension) of these muscles by stretching after rapid shortening. Boettiger (1957) further demonstrated that after rapid shortening, fibrillar muscle tension continues to fall even after muscle length has stabilized. When the muscle is restretched, the maximum length of the muscle

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is attained with a return of only one third of the maximum tension. The remaining tension is rapidly gained at the top of the stretch. These properties of fibrillar muscle were conveniently incorporated into the mechanical system of the 'click' mechanism proposed for flight, but they did not allow for any smooth, sinusoidal movements as would be required for example in song production. Boettiger (1957) did, however, identify the bumble bee flight system as operating in the absence of a 'click' mechanism. He therefore had to acknowledge the fact that fibrillar muscle could operate in a smooth manner, in which case the physiological properties mentioned above would not be used.

No alternative to the 'click' mechanism has been proposed even after recent detailed morphological studies of the wing base articulation (Wisser & Nachtigall 1983) and this has left the *Diptera* isolated from other orders of flying insects in terms of their flight mechanics. The flight systems most studied outwith the *Diptera* have been those of the locust and dragonfly, and in both a large element of elasticity was found to be important for the conservation of energy. For instance Weis-Fogh (1960, 1961) showed that there was an 86% conservation of energy during the upstroke in locusts which was entirely attributable to elastic elements of the system. The bistable 'click' mechanism proposed by Boettiger & Furshpan (1952) incorporated a lateromedial elastic element, operating on both the upstroke and the downstroke, that relied on the spring action of the dorsal thoracic plate (scutum) and the pleural wing process. The important difference between the two types of model is that in the 'click' system, the muscles must work against an increasing force over the first half of both the upstroke and the downstroke, while in the former system there is muscular work on one half cycle only and very little work once the oscillations have been initiated.

We have been prompted to re-examine the dipteran flight system with particular reference to the mechanics of the wing movements, the role of elasticity and conservation of energy, and the action of the indirect flight muscles. A second important consideration has been the role of the non-fibrillar muscles in flight and in song. These latter muscles have often been cursorily treated by various authors although they are undoubtedly important. Although there is a high degree of homology, there are interesting quantitative differences between species with regard to these muscles. In our analysis we have attempted to concentrate upon the mechanical effects based mainly upon morphological evidence. We also propose an alternative to the 'click' mechanism for dipteran flight which takes into account aspects of fibrillar muscle physiology and relates this to a number of important morphological features not previously described.

## 2. Materials and methods

Nineteen species of *Diptera* were examined. Of these, 12 were examined in fine detail; the remainder were members of species groups already represented and were examined to confirm the generality of specific details within a group.

Specimens of *Eristalis tenax*, *Tipula* sp., *Scatophaga* sp., *Coelopa pilipes*, *C. frigida*, *Tabanus distinguendus*, *T. sudeticus*, and *Haematopota pluvialis* were wild-caught by the authors and Richard Steele, Ken Thomson and Philip Whitfield. Specimens of *Musca domestica*, *Calliphora erythrocephala*, *Sarcophaga argyrostoma*, *Lucilia sericota* and *Protophormia terraenovae* were supplied by the Parasitology Subdepartment of Edinburgh University. Specimens of *Glossina m. morsitans* were provided by the Tsetse Research Laboratory, Bristol, and specimens of *Drosophila virilis*, *D. melanogaster*, *D. buzzatii*, *D. funebris* and *D. mercatorum* were collected from our own stocks.

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Flies were fixed in either alcoholic Bouin (after Pantin 1946) or cocodylate-buffered glutaraldehyde before dissection. To observe morphological changes during flight, flies were stimulated into escape flight by mild agitation of their container and were then shaken into a polystyrene beaker of liquid nitrogen. More than 60% of flies were frozen in natural flight, this being recognized by the characteristic leg postures adopted in flight. Selected flies were then stored in absolute acetone over a molecular sieve (BDH type 4A) at −70 °C for two weeks to ensure complete dehydration. They were then critical point dried and prepared for scanning electron microscopy. Some dissected preparations were also processed for scanning electron microscopy to study particular details.

All drawings were made by using a camera lucida attachment fitted to a WILD M5 stereo microscope. Light micrographs were taken on a WILD M8 stereo-microscope fitted with a WILD MPS 51/45 photomicrographic attachment. Scanning electron microscopy was performed using a Cambridge Stereoscan 250 microscope belonging to the science faculty of Edinburgh University.

Dissections were routinely performed on dehydrated specimens in absolute alcohol. A number of approaches were used to obtain views from more than a single direction. (i) Flies were bisected longitudinally and pinned through the head and abdomen onto a bed of Sylgard (Dow Corning) so that the cut face was uppermost. Muscle blocks could then be individually removed with forceps to reveal underlying structures. (ii) A whole thorax was cut transversely, anterior to the transverse ridge. The abdomen was cut off and the preparation pinned, anterior end uppermost. Muscle blocks could again be pulled out with forceps. (iii) Entry was made through the scutum by cutting a hole with fine scissors.

Simple manipulations of freshly killed (by ether or decapitation) and fixed animals was used to confirm some of the mechanisms deduced from the morphology.

## 3. Thoracic skeletal components of the flight system

For the purposes of the following sections it should be noted that we have used *Glossina m. morsitans* as our primary species. This is due to the clarity of the wing base structures and muscle attachments which, although present in similar form in other species, are, however, somewhat obscured by heavy coatings of connective tissue. Where there are differences in morphology between species, these are made clear in the text and figures.

A close examination of the thorax reveals a number of distinguishable regions (figure 1) whose borders are marked by cuticle density changes, cuticle-membrane borders, lines of weakness, joints and colour differences. The ventral thorax consists of the sternum (1) to which are attached the meso- and the metathoracic legs, and the anepisternum (2) which forms the anterior region with the attached prothoracic legs. Above the sternum, stretching dorsally and posteriorly, is the pleural plate (3) which forms the pleural wing process (p.w.p.) at its dorsal end. Its posterior edge is fused with the epimeron (4) which joins onto the postnotum (5). Sitting on top of the postnotum and joined by flexible cuticle and membrane, is the scutellar lever (6), consisting of the scutellum and an anteroventral arm projecting to a position medial and adjacent to the p.w.p. Also medial to the p.w.p., running longitudinally, is a triangular length of cuticle, the parascutal shelf (7), that has a loose hinge connection to the scutum (8) and the scutellar lever (6). The scutum is the main dorsal thoracic plate that stretches from the pronotum (9) to its joint (the scutoscutellar suture) with the scutellum. Running across the

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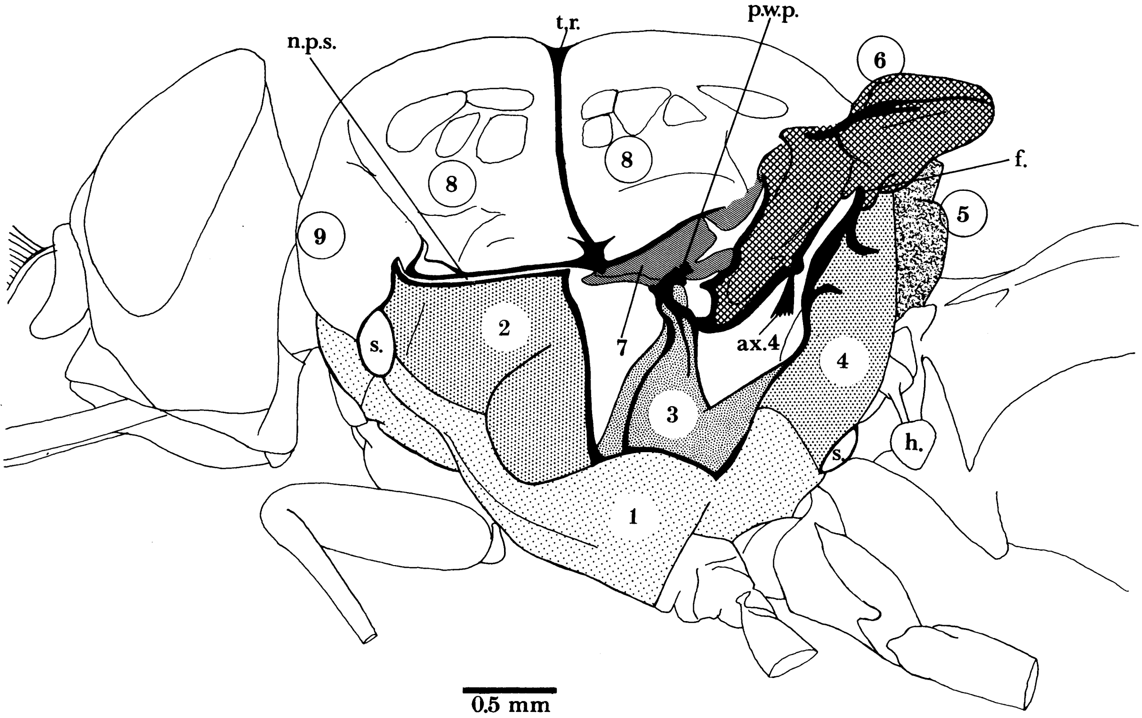

FIGURE 1. Lateral view of the thorax of *G. m. morsitans* showing the main thoracic components concerned with flight. Key: 1, sternum; 2, anepisternum; 3, pleural plate; p.w.p., pleural wing process; 4, epimeron; 5, postnotum; 6, scutellar lever; 7, parascutal shelf; 8, scutum; 9, pronotum; t.r., transverse ridge; n.p.s., notopleural suture; s., spiracles; ax. 4, fourth axillary sclerite; h., haltere; f., fulcrum for movements of the scutellar lever. The dorsal attachments of the d.v.ms are outlined on the scutum.

middle of the scutum is the transverse ridge, a structural member that gives greater strength to the scutum. There are a number of additional strengthening ridges that are not obvious from an external examination. The dorsal edge of the anepisternum is lined with a ridge that has a parallel partner on the corresponding edge of the scutum (the prescutal ridge). The two ridges are separated by membrane which forms the notopleural suture (Snodgrass 1935). The anterior thorax consists of the pronotum which is a strong cuticular plate fused with the anepisternum ventrally and with the scutum dorsally. There is a certain degree of relative movement between dorsal and ventral thorax due to the membraneous sutures and gaps. However, due to the solid pronotum, there is a fulcrum for this movement at the common join between scutum, pronotum and anepisternum. Thus, there must be a line of weakness between the dorsal edge of the pronotum and the scutum.

On the anterior edge of the scutellar lever arm is a region of heavy sclerotization which forms the articulating surface of the post-median notal wing process (p.m.n.p., after Matsuda 1970). A corresponding region on the parascutal shelf is also sclerotized to give the articulating surface of the anterior notal wing process (a.n.p.), which lies dorsal to the p.m.n.p. Their relationship is shown in figure 2.

An internal examination of the thorax reveals that the prescutal ridge extends forwards to join with the ridge of the contralateral side at the midline behind the head. It extends posteriorly to fuse with the transverse ridge from which another ridge projects backwards along the edge of the scutum to form part of the hinge to the parascutal shelf. The transverse ridge ends proud

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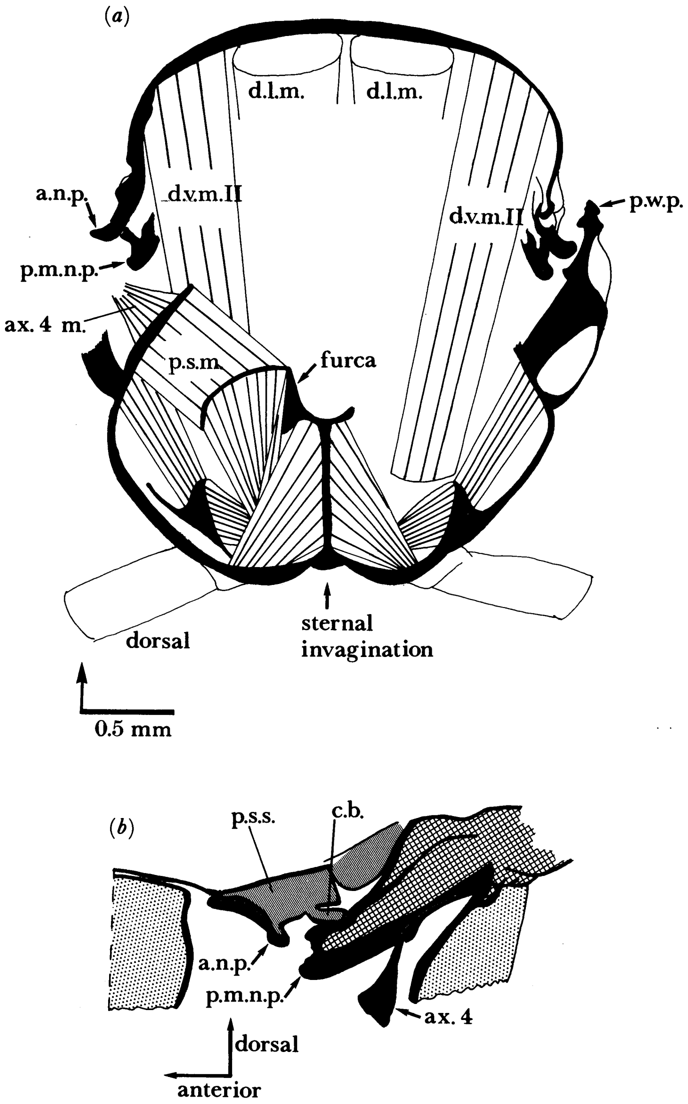

FIGURE 2. (*a*) Transverse section through the thorax of *G. m. morsitans* at the level of the transverse ridge. This shows the arrangement of the post-median (p.m.n.p.) and anterior (a.n.p.) notal processes along with the pleural wing process (p.w.p.) and some of the thoracic musculature. Notice the action of the pleurosternal muscles (p.s.m.) on the p.w.p. (see later). The right p.s.m. has been removed. The other muscles attached to the sternum and furcum are concerned with leg movements while the fourth axillary muscles (ax. 4 m.) are dealt with in a later section. (*b*) The arrangement of the notal processes from a lateral view with the p.w.p. removed. Note the cuticular bridge (c.b.) between the parascutal shelf (p.s.s.) and the scutellar lever arm.

of the scutum, projecting a short distance into the cavity of the thorax. This projection forms the attachment for one of the non-fibrillar muscles (see later). In the posterior thorax, the epimeron is bounded by ridges which form the fulcrum for the scutellar lever. The contralateral epimeral ridges form the other half of the pair of surfaces about which the lever is rotated. The epimeral cuticle is also the attachment for the posterior dorsoventral muscle. The postnotum is attached to the scutellum posterior to the fulcra and forms the attachment for the dorsal longitudinal muscles which, thus, are responsible for rotations of the lever that elevate the p.m.n.ps. The two sternal plates come together at the ventral midline and then invaginate

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together giving a strong internal ridge along the floor of the thorax which is used for the attachment of certain muscles (figure 2). There is an elevated region of this ridge that expands dorsally to give rise to the furca which form the major attachments for leg muscles and the pleurosternal muscles (figure 2 and see later).

The main features of the thoracic skeleton have now been described. It can be seen that contractions of the dorsal longitudinal muscles cause a rotation of the scutellar lever, as was described by Boettiger & Furshpan (1952). The action of the dorsoventral muscles is not immediately obvious although they would produce some rotation of the lever, counter to that of the d.l.ms, as a result of their downward pull on the scutum. To understand the action of the d.v.ms and how the movements of the lever are transmitted to the wings, we have to look at the relationship of the various wing base sclerites to the notal processes.

## 4. The wing base sclerites and wing movements

### (a) *The first and second axillary sclerites*

The post-median notal process of each lever arm is connected to the anterior notal process by the first axillary sclerite (ax. 1, figure 3). This is an X-shaped structure having four radial projections. The p.m.n.p. locates in the notch formed by the two ventral arms while the notch between the anterior arm of the ventral pair and the next dorsal arm is the location of the a.n.p. The cleft between the two dorsal arms is occupied by a projection of the second axillary sclerite (ax. 2). As the p.m.n.p. is raised by the action of the d.l.ms, ax. 1 rotates about its articulation with the a.n.p. until its medial arm stops against the parascutal shelf. At this point, ax. 1 inhibits further rotation of the shelf about its hinge joint to the scutum, and the whole of the scutum is thus raised by the continuing movement of the p.m.n.p. It can now be seen that the action of the d.v.ms is focused upon the scutellar lever as there is a direct stretching of these muscles by the latter part of the sequence (figure 4). Contractions of the d.v.ms will cause the reverse cycle of events producing, in the process, a direct stretching of the d.l.ms.

The second axillary sclerite has a ventral, anteriorly projecting peg that locates in a socket below the dorsal crest of the pleural wing process (p.w.p.) (figure 4). This joint restricts the movements of ax. 2 to a single plane. The two sclerites (ax. 1 and ax. 2) are joined to the base of the radial wing vein; ax. 2 runs along the posterior edge of the vein while ax. 1 is joined to the very end of the vein. It would appear that ax. 1 is the main, force-transmitting element while ax. 2 determines the plane of the movements resulting from that force.

The rotation of ax. 2 is restricted during the lower half of the wing beat cycle as the pivot point for wing movements switches from the peg–socket joint of the sclerite to the p.w.p. to a groove on the crest of the p.w.p. into which a ventral projection of the radial vein locates (figures 4, 5). This effectively acts like a wing stop and operates a few degrees below the horizontal wing position. The wing bends along the radial vein and the forces produced cause some bending of the p.w.p. which thus stores elastic energy and returns it to the wing on the upstroke (see also later). In addition, there is a raising of the scutum by ax. 1 and the parascutal shelf (figure 5), as already described, which would presumably cause energy storage in non-wingbase structures, such as the cuticular flexion point along the anterior scutum, which would also be returned to the wing on the upstroke. A third source of stored energy for the upstroke is the inward movement of the lateral scutum during the downstroke. This latter energy can be controlled by contractions of the pleurosternal muscles which cause a simultaneous

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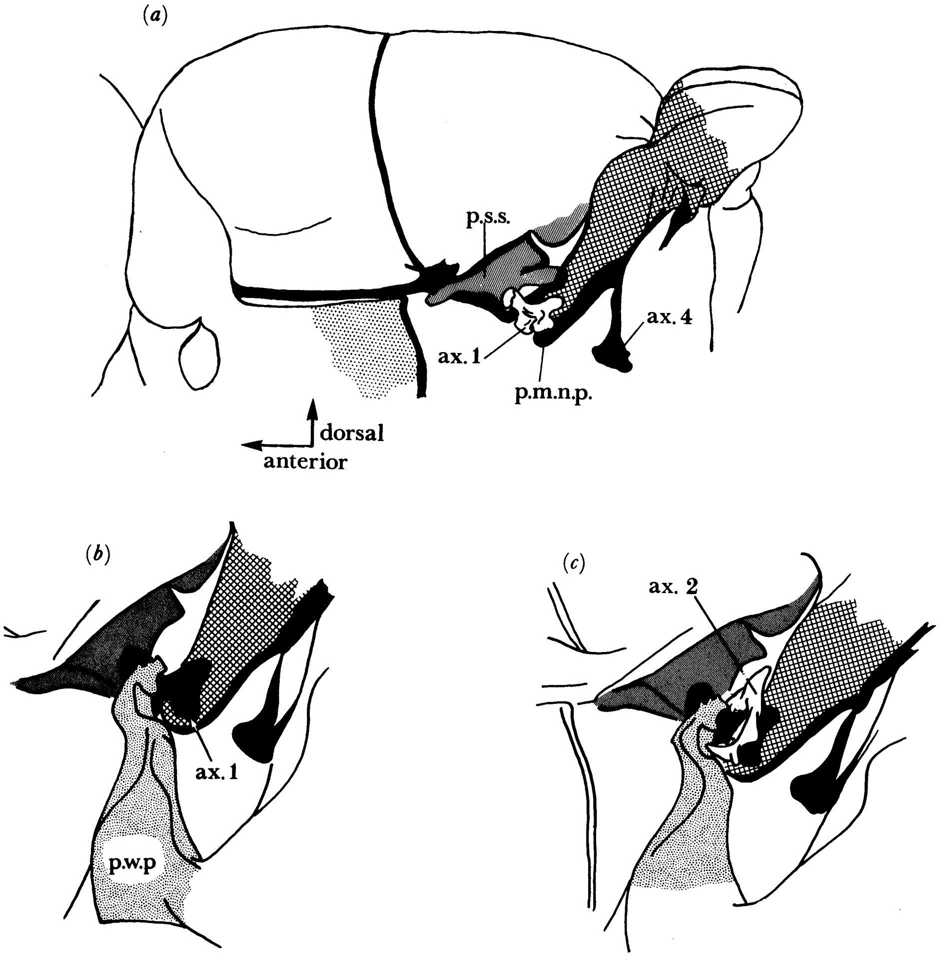

FIGURE 3. Lateral view of the thorax of *G. m. morsitans* showing the arrangement of the first (ax. 1) and second (ax. 2) axillary sclerites. (*a*) Ax. 1 with overlying p.w.p. removed. This sclerite articulates about the two notal processes. (*b*) Ax. 1 with position of p.w.p. (*c*) Ax. 1 and ax. 2 showing the location of the socket joint of ax. 2 in the p.w.p. The ventral peg of ax. 2 is held in the socket by tough connective tissue.

inward movement of the p.w.ps of the two sides (see also later). In previous descriptions of the flight system (for example, Boettiger & Furshpan 1952; Pringle 1957; Wisser & Nachtigall 1983) it has been argued that as the wing passes the mid-point, where the outward force exerted by the scutum is greatest, there is a sudden switch or 'click' that coincides with a change from opposing to accelerating force from the scutum. This occurs as a result of the parascutal shelf hinging up and down relative to the scutum. However, we have described a locking mechanism of ax. 1 on to the parascutal shelf that inhibits such a 'clicking' system (figure 4) and have also demonstrated a lack of the changes in acceleration and velocity (of the wing) predicted by these models (Miyan & Ewing 1985*a*). Thus, there is a storage of elastic energy during the downstroke that is released on the upstroke. There appears to be a similar mechanism on the latter part of the upstroke, for the start of the downstroke. An outward force is exerted on the p.w.p. due to the inward rotation of ax. 2. This will oppose the inward forces of the pleurosternal muscles, and possibly result in outward bending of the p.w.p., thus, storing energy for the downstroke. In addition, there is a constant outward force from the scutum as a result of the action of both sets of indirect muscles (Boettiger & Furshpan 1951, 1952) and this stores energy

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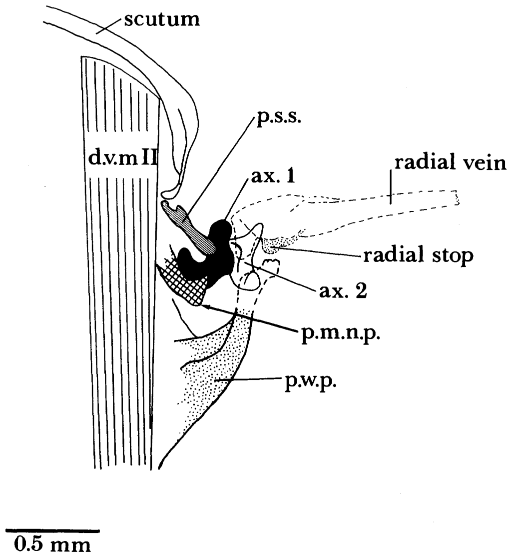

FIGURE 4. Anterior view of a transverse section of the thorax of *G. m. morsitans* at the wing base showing the arrangement of the first and second axillary sclerites (ax. 1 and ax. 2) with the parascutal shelf (p.s.s.), post-median notal process (p.m.n.p.), pleural wing process (p.w.p.) and scutum. The position of the radial wing vein is shown by the dotted line as is the dorsal region of the p.w.p. that would otherwise obscure the underlying structures. Note the medial arm of the ax. 1 which locks on to the p.s.s. during the downstroke causing a direct lifting of the scutum and d.v.m. stretch.

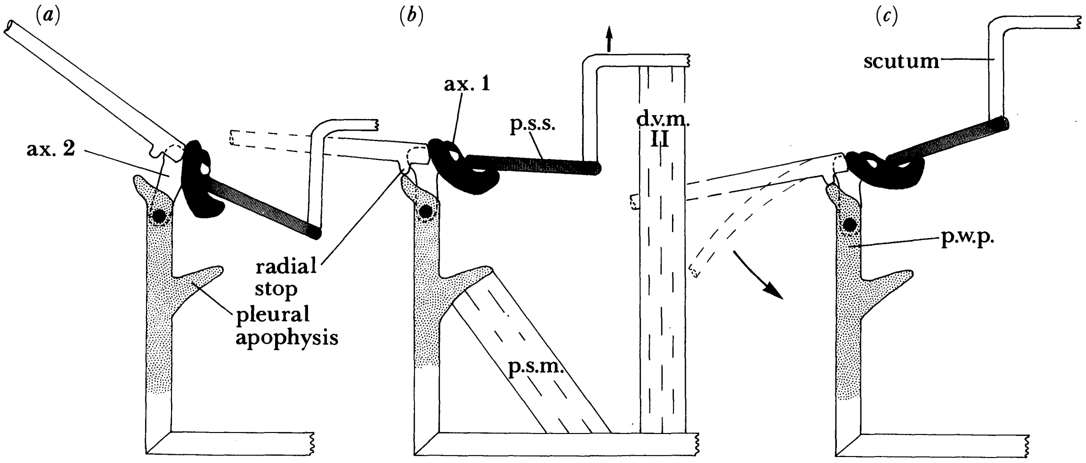

FIGURE 5. Diagrammatic representation of part of a wing cycle based on the anatomy illustrated in figure 4. During the downstroke, rotation of the wing about the joint of ax. 2 with the p.w.p. causes ax. 1 to lock onto p.s.s. thereby inhibiting the latter from further rotation relative to the sclerite. P.s.s.–ax. 1 effectively becomes a single unit for the latter part of the cycle causing a direct lifting of the scutum. At about the horizontal position, the radial stop engages the p.w.p. and the wing bends (dotted line in (*c*)) about the radial vein causing elastic energy to be stored in the p.w.p. and other structures (see text). Notice that a 'click' on the downstroke is inhibited by ax. 1.

as force is applied by the rotating ax. 2. On a qualitative assessment of the two halves of the wingbeat, it appears likely that the forces exerted during the downstroke and, therefore, the energy stored, are greater than those exerted during the upstroke which may be largely an expression of the release of stored energy. This is reflected in the relative muscular involvement in the two half cycles (see later).

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### (*b*) *The third and fourth axillary sclerites*

The third axillary sclerite (ax. 3) provides the basal support for the posterior wing regions and is also the pivotal sclerite for wing retraction and extension, rotating about its articulation with ax. 2. Ax. 3 articulates posteriorly with the fourth axillary sclerite (ax. 4) and the two form the attachments for the calypters (or squamae) as shown in figure 6. It can be seen that ax. 4 is attached to both lobes of the calypters, along the entire length of the medial lobe (the

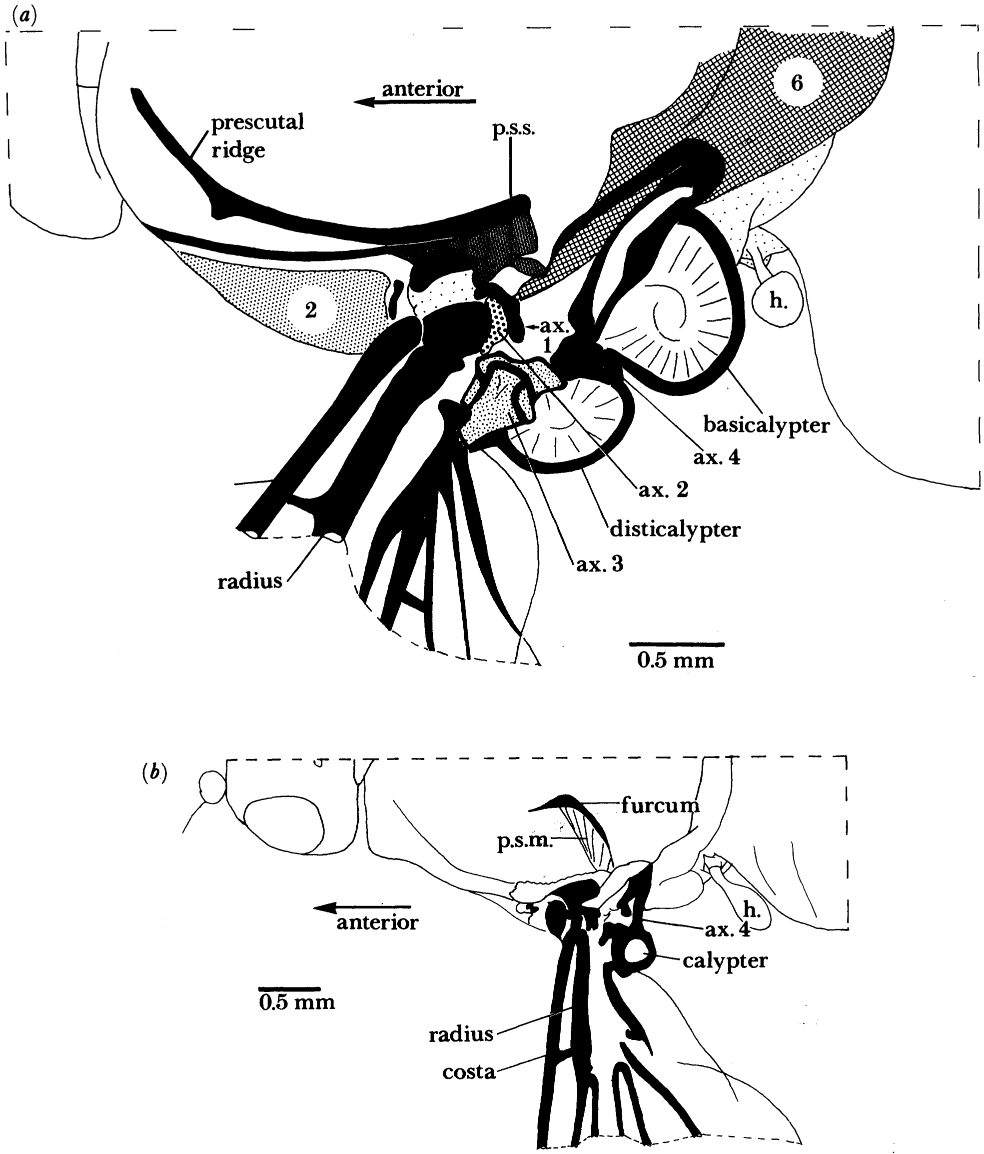

FIGURE 6. Dorsal view of the wing base of (*a*) *G. m. morsitans*, a calypterate, and (*b*) *C. frigida*, an acalypterate fly. Notice the arrangement of the sclerites in (*a*), particularly ax. 4 and its attachments to the scutellar lever (6) and the two calypters. Its articulation with ax. 3 is its linkage for wing synchronous control over wing movements. Ax. 3 rotates about ax. 2 and forms the fulcrum for wing extension–retraction movements. It is doubtful whether either ax. 1 or ax. 2 have any influence on these movements. Ax. 1 is the transmitter of the force from the scutellar lever to wing via its articulation with the anterior notal process of the parascutal shelf (p.s.s.). This force is transmitted to the radial vein of the wing.

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basicalypter) and at one end of the lateral lobe (the disticalypter). Movements of this sclerite will thus cause direct changes in the relative orientations of the calypters to each other, to the wing and to the body of the fly. This may have important implications for the aerodynamic functions of these structures (see later). Movements of ax. 4 will also be transmitted to ax. 3 which will respond by rotating about its articulation with ax. 2 and ax. 4; as a component of this rotation is in the vertical plane, there is control, via ax. 4, of the angle of attack of the wing. There is a direct linkage between the scutellar lever and this sclerite (figure 7). The mechanical basis of the automatic changes in the wing during the wing beat as a result of this linkage can be seen. Ax. 4 is under wing-synchronous control from the scutellar lever, therefore its effects upon ax. 3 will also be wing-synchronous. These will be most marked at the top and bottom of the wing beat due to the relative changes between scutellar lever and ax. 4 that result from the flexibility between them. During the downstroke, ax. 4 rises with the p.m.n.p. causing an outward and upward force to be exerted on ax. 3; the wing is therefore extended further and angled, leading edge downward. At the bottom of the stroke, there is a sudden reversal in the movement of the p.m.n.p. causing a rapid elevation of the radial vein followed by a phase-lagged elevation of the posterior wing region, the lag being maintained during the upstroke. There is a retraction of the wing accompanying the upstroke due to the depression of ax. 4 pulling back on ax. 3. At the top of the upstroke, there is again a rapid reversal in movement of the p.m.n.p. which is accompanied by a correspondingly rapid elevation of the posterior wing region as the p.m.n.p. is travelling down towards ax. 4. These changes are precisely those observed in intact flies in tethered flight (for example, Nachtigall 1966, 1968). In addition to these automatic changes, there is a certain amount of muscular control over the degree of pronation and supination (twisting) of the wing by the fourth axillary muscles, the third axillary and the first axillary muscles (see later).

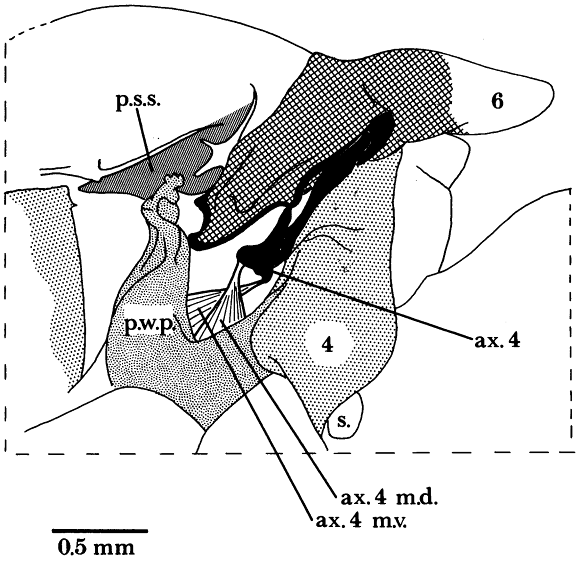

Figure 7. Lateral view of the thorax of *G. m. morsitans* showing the attachment of the fourth axillary sclerite (ax. 4) to the scutellar lever (6). Notice the two sets of fourth axillary muscles, one attaching dorsally on the sclerite (ax. 4 m.d.) and one ventrally (ax. 4 m.v.). These muscles have direct control over the overall characteristics of the wing beat by tonic contractions (see text).

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## 5. The pleural wing process and the radial stop

The wing stop mechanism has already been described but the components of the stop are also implicated in a probable switch mechanism which can alter the wing beat characteristics (Pfau (1973) for *Sarcophaga bullata*) or disengage the wings from the flight motor (Chowdhury & Parr (1981) for *Glossina m. morsitans*). The crest of the p.w.p. has dorsal projections, the number and form of which are characteristic for a given species (figure 8, plate 1). Of the species examined three basic types of structure are identified: those with only a single location for the radial stop on the p.w.p. are found in *Drosophila*, *Coelopa*, and *Eristalis* species; those with two possible locations for the radial stop are found in *Sarcophaga*, *Calliphora*, *Musca*, *Lucilia*, *Phormia*, *Glossina* and *Tabanus* species and those with no apparent location, but with a smooth, spherical surface on which the correspondingly smooth radial stop makes its contact, are found in *Tipula* species (figure 8). The details of a particular species' structures are characteristic and show little individual variation.

The p.w.p. rises dorsally from the sternum and bends sharply at its apex to give rise to a lateral knob that overhangs the ventral thorax. This knob carries the dorsal projections which form the engaging surfaces for the radial stop (a ventral projection at the base of the radial wing vein). Pfau (1973) recognized two positions which could be taken by the radial stop on the p.w.p. However, although he worked with living flies, these were anaesthetized with $CCl_4$ and he did not observe a 'natural' separation between the two structures which he therefore had to hypothesize to give the fly potential control over the switching between the two positions. We have observed such a separation in anaesthetized flies frozen in flight by immersion in liquid nitrogen (figure 9, plate 2). There is a clear separation of the two structures during the upper portion of the wing beat as would be predicted by the location of the socket joint of ax. 2 in the p.w.p. (see also figure 4). Thus, there is a real potential for the fly to control the switching of the radial stop from one to other of the positions on the p.w.p.

A study of the p.w.p. in a number of species shows that a choice of locations does not exist in all *Diptera*. This is true of *Tipula*, *Drosophila*, *Coelopa* and *Eristalis* sp. which all appear to have a single location. *Eristalis tenax* is unusual in its morphology as there is a suggestion of two possible locations on the radial stop itself rather than the p.w.p. (figure 8). These may correspond to positions of the p.w.p. brought about by tension changes in the pleurosternal muscles which would produce movements of the p.w.p. in a transverse plane. It would be predicted from this that the two positions correspond to two different, but stable wing beat frequencies.

Pfau (1973) suggested that the 'gear' changing brings about changes in wing beat frequency, amplitude and intensity. He described muscular control over the position of the p.w.p. along a longitudinal axis of the animal and assumed that the radial stop, and wing, come down to the same position on the axis. We have discovered that this is not the case. The p.w.p. is

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### Description of plate 1

Figure 8. Scanning electron micrographs of the wing base of (*a*) *D. virilis*, (*b*) *E. tenax*, (*c*) *S. argyrostoma*, (*d*) *H. pluvialis*, (*e*) a tipulid, showing the characteristic structures of the dorsal crest of the pleural wing process (p.w.p.), radial stop (r.s.) and pterale C (pt. C) in each species. The so-called 'switch' mechanism is perhaps most clearly seen in *S. argyrostoma* and *H. pluvialis*. The anterior margin of the wing has been cut away in *E. tenax* to reveal the structures beneath it.

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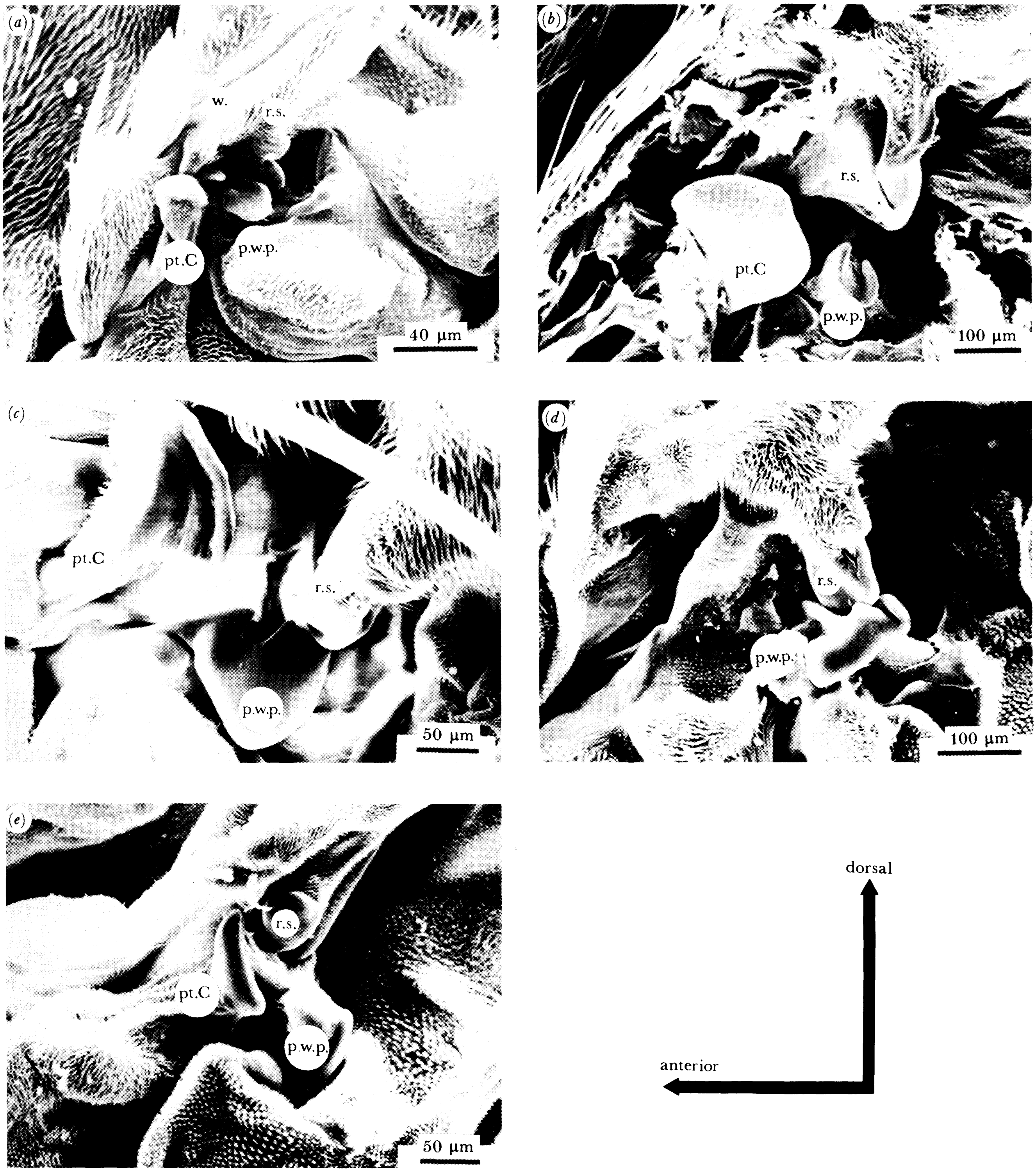

FIGURE 8. For description see opposite.

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Figure 9. Scanning electron micrograph of the wing base of *D. virilis* showing the natural separation between the p.w.p. and radial stop (r.s.) during the upper part of the wing beat.

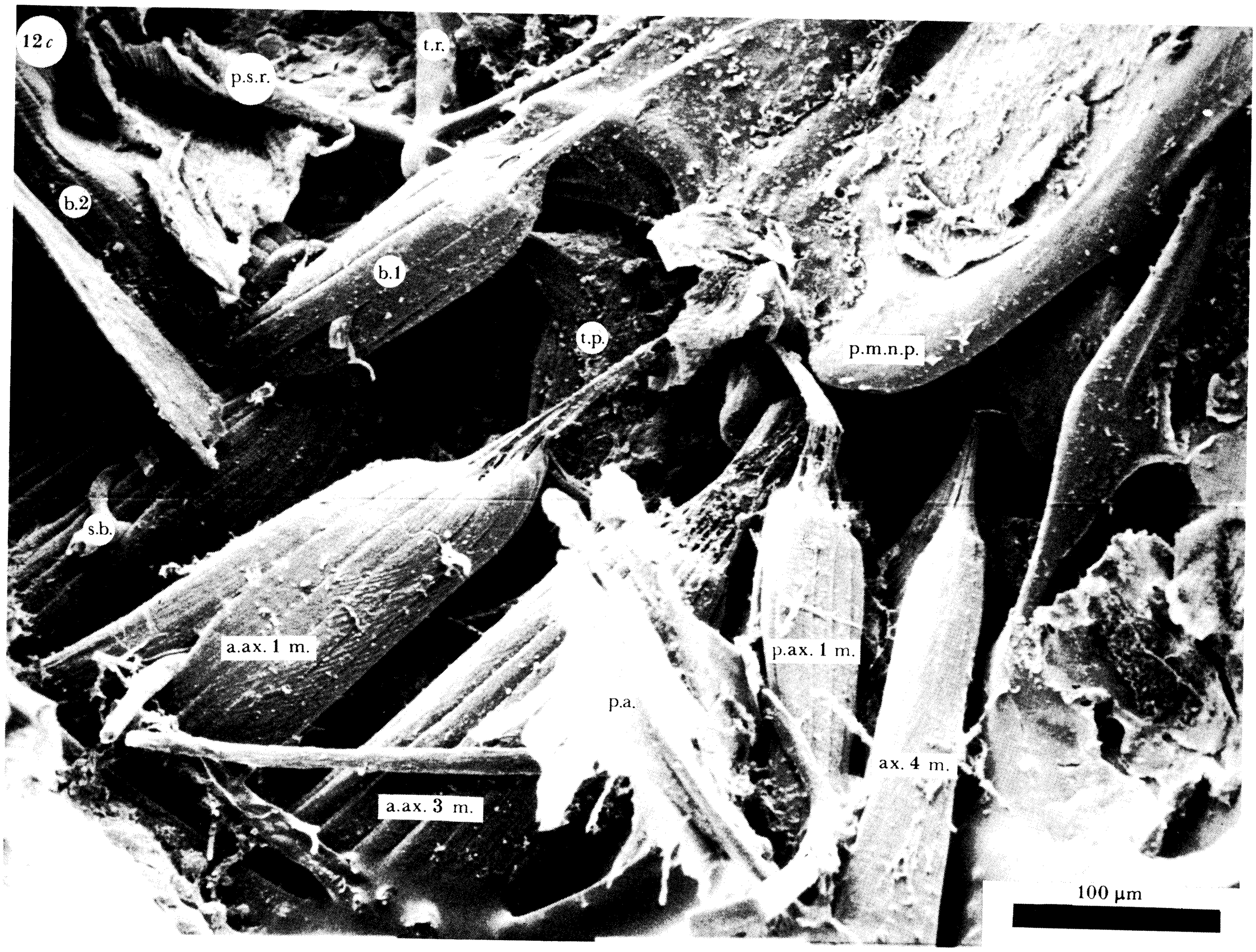

Figure 12 (*c*). For description see opposite.

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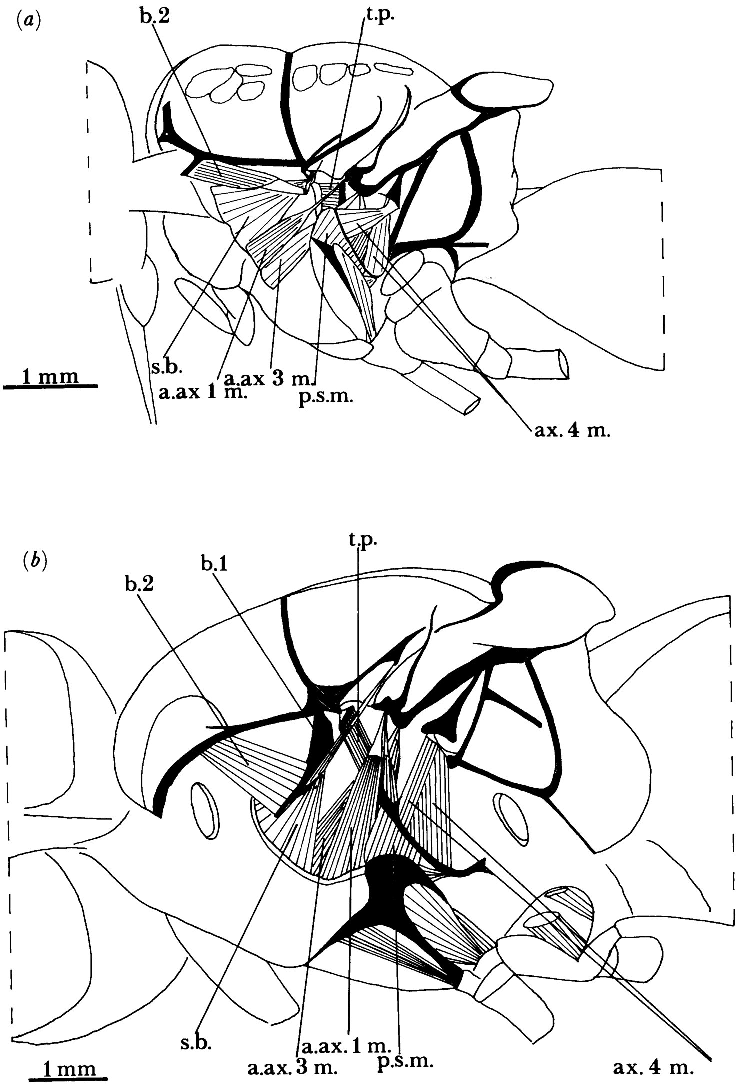

Figure 12. The non-fibrillar muscles of: (*a*) *G. m. morsitans*, (*b*) *E. tenax*, and (*c*) *D. virilis* (s.e.m.) illustrating the variations between species. Note that the t.t.m. is not included in these figures as it obscures many of the muscles. The first basalar muscle (b. 1) is not labelled in (*a*) owing to its small size. However, it is located just anterior and dorsal of the tergopleural muscle (t.p.) and posterior to the second basalar muscle (b. 2). Abbreviations: s.b., sternobasalar muscle; p.s.m., pleurosternal muscle; ax. 1 m., ax. 3 m., ax. 4 m., axillary muscles.

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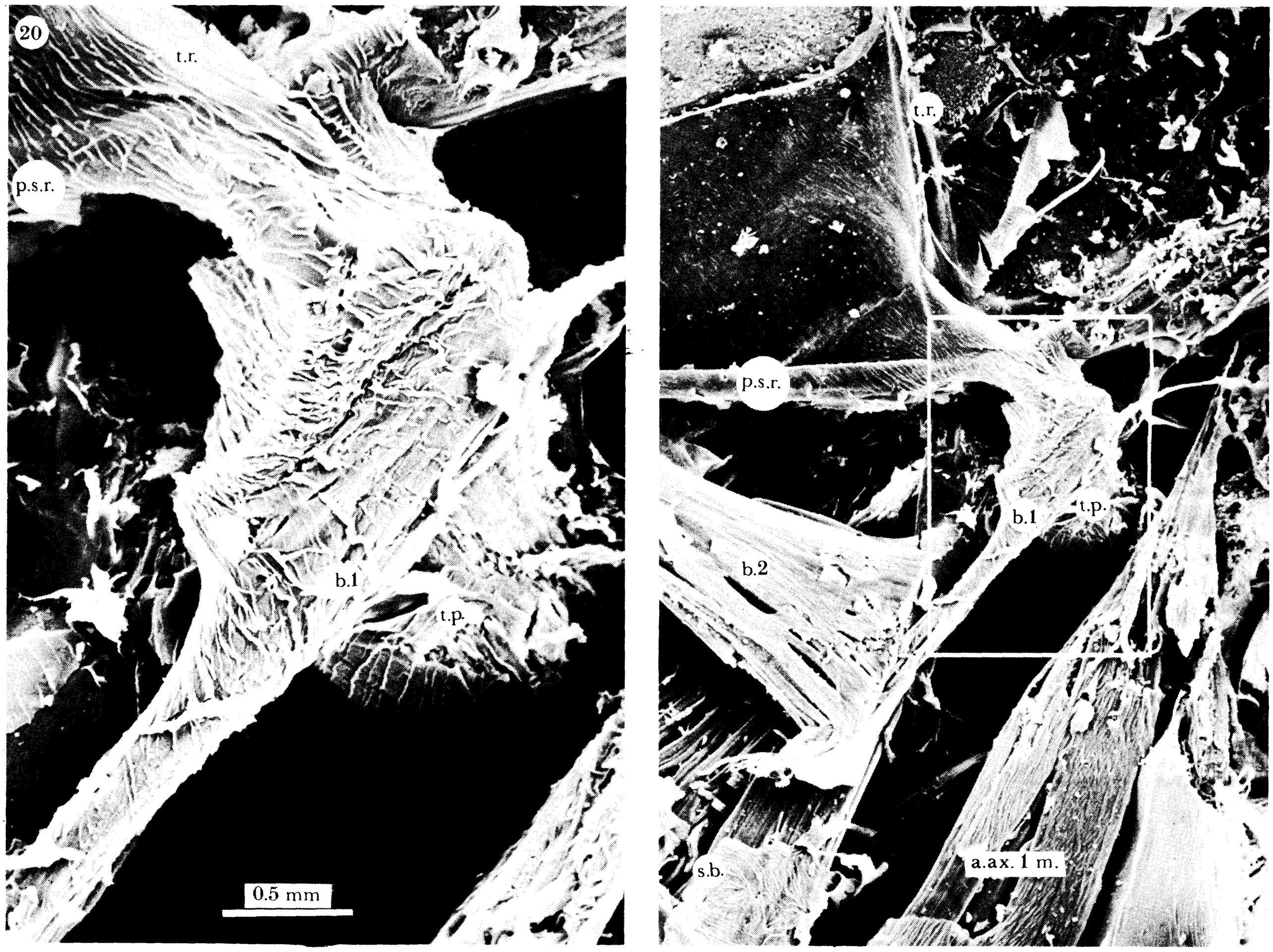

FIGURES 14 AND 20. For description see opposite.

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restricted to movements in the transverse axis via the action of the pleurosternal muscles. There is no control over longitudinal movements and such movements would be difficult, if not impossible against the structural impediment of the pleural plate. The second basalar muscle was given the function of 'gear' control by Pfau (1973) but has subsequently been identified as part of a system controlling a wing base receptor organ (Miyan & Ewing 1984; and next section). Control over the radial stop switch must be by control of the twisting of the wing base, specifically of the radial vein. This implies that one of the major functions for this mechanism is to produce standard changes in the wing stroke, angle of attack, pronation and supination characteristics of the wing beat, causing sudden controlled changes in flight; for example, from cruising to fast forward, hovering to forward (or backward) flight.

Manipulating the wings of *Sarcophaga argyrostoma* with forceps and locating the radial stop into each position on the p.w.p. gives the impression that such changes in position not only cause wing twisting but also change the stroke plane of the wing. There is a tendency for one position to cause an earlier engagement of the stop than occurs in the other position during the wing beat. It is possible that one will cause a greater storage of elastic energy than the other as the wing must 'bend' the p.w.p. to a greater extent to achieve the same amplitude of movement. This may result in frequency changes due to changes in resonance of the system.

Twisting of the wing or radial vein can be accomplished by control over the first axillary sclerite which is fused to the base of the radial vein. This sclerite conveniently has two muscles attached to one of its arms; contractions of each cause a twisting of the sclerite, pronation or supination dependent on which muscle is active. This, and other mechanisms are discussed in the next section. Wing retraction produces a circular movement of the radial stop about the p.w.p. In a stable retracted position, the stop is located in an invagination of the thoracic cuticle at the wing base. It is interesting to note that the wing base must be lifted to locate the radial stop on to the p.w.p. during wing extension and also lifted before wing retraction. This appears to fit with the wing base lifting observed in free flies immediately before and after flight.

## 6. Muscular components of the flight system

### (*a*) *The indirect muscles*

These have normally been separated into two functional groups: the three dorsoventral muscle groups are the indirect wing elevators and the dorsal longitudinal muscles form the indirect wing depressors (figure 10). Based on the mechanical components of the flight system already described, and the attachments of these muscles, there is little doubt that the d.l.ms produce a rotation of the scutellar lever that raises the p.m.n.p. and thereby depresses the wing. The d.l.ms have an anterior attachment on the pronotum and across the dorsal scutum, the two dorsal muscles attaching posterior to the transverse ridge. Thus, they will produce a certain

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### Description of plate 3

Figure 14. Scanning electron micrograph of a transverse section through the thorax of *G. m. morsitans* at the level of the wing bases. The bilaterally symmetrical pair of pleurosternal muscles (p.s.m.) is clearly seen along with the dorsal attachments on the pleural apophyses (p.a.). The furcae are obscured by the body of the muscles (see also figure 2).

Figure 20. Scanning electron micrograph of the first basalar muscle (b. 1) and the tergopleural muscle (t.p.) of *E. tenax* showing the firm attachment between the two muscles.

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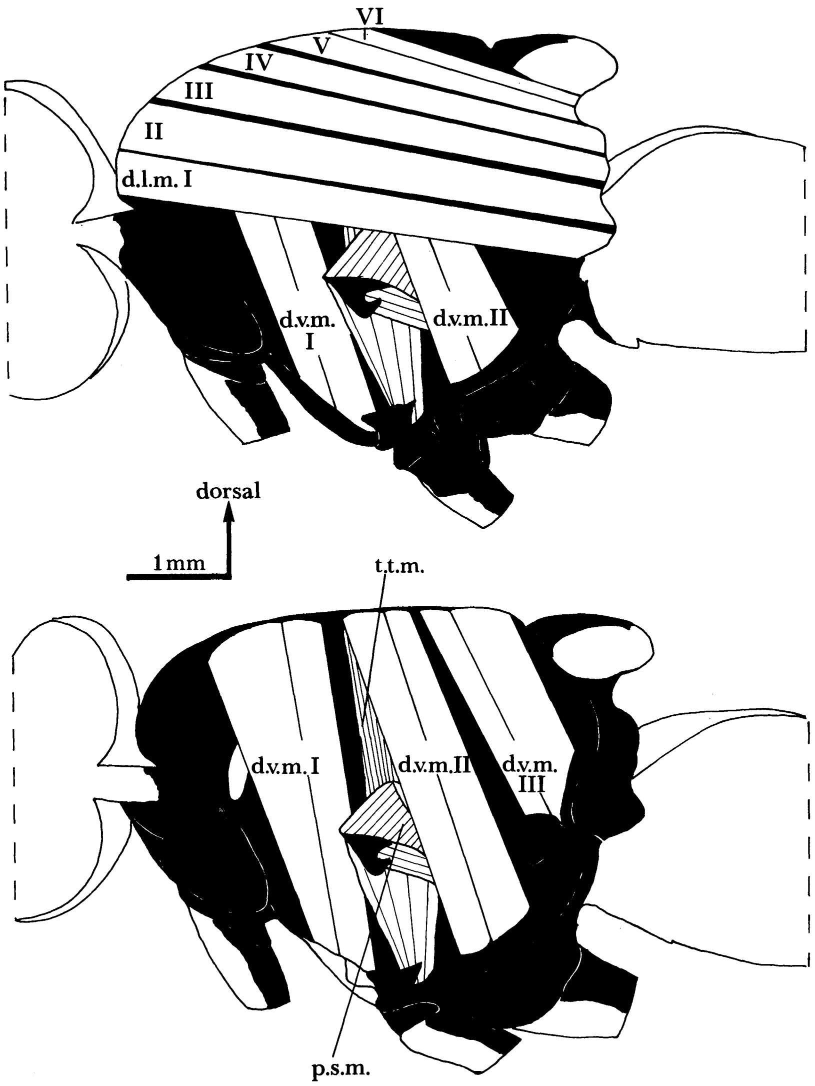

FIGURE 10. The typical morphology of dipteran indirect flight muscles is shown in this longitudinal section through the thorax of *S. argyrostoma* at the midline in (*a*) and with the dorsal longitudinal muscles (d.l.ms) removed in (*b*). Abbreviations: d.v.m., dorsoventral muscles; t.t.m., tergotrochanteral muscle; p.s.m., pleurosternal muscle.

downward pull on the scutum as well as pulling on the postnotum. Owing to the lifting of the lateral scutum during the downstroke of the wing, the downward forces on the scutum by the d.l.ms will result in some distortion of the dorsal thorax and a large increase in the lateral component of forces produced in the scutum. This force will be transmitted to the wing base articulation (Boettiger & Furshpan 1952) and therefore contributes towards the tension and energy of the system.

During wing depression, the locking mechanism of ax. 1 onto the parascutal shelf causes the scutum to be raised at this point and has the effect of stretching the middle dorsoventral muscle (d.v.m. II) directly as this is attached on the lateral scutum adjacent to the wing base and just posterior to the transverse ridge. The anterior dorsoventral muscle (d.v.m. I) presents a problem in that the mechanical system allows for little stretching of this muscle, partly due to the action

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of the d.l.ms, which resist any upward movement of the anterior scutum, and partly due to the rigidity of the anterior scutum as a result of its attachment to the immovable pronotum. From high speed films of tethered flight, it was not possible to measure any relative movement between anterior scutum and ventral thorax. It may be that this muscle is devoted to the job of maintaining a constant lateral force via a downward pull on the scutum. This would follow from the idea that all the indirect muscles are under constant tetanic stimulation and, unless stretched to induce contraction (Pringle 1949) produce a constant, tetanic force (Boettiger & Furshpan 1950; Boettiger 1957).

The posterior dorsoventral muscle (d.v.m. III) has attachments on the epimeron and posterior scutum and will receive similar stretching to that of d.v.m. II as a result of wing depression. In addition, rotation of the scutellar lever during wing depression will cause the posterior edge of the scutum to be lifted which will reinforce d.v.m. stretching produced at the wing base.

There appears to be a disproportionate muscular investment in wing depression compared with wing elevation, which may reflect the larger forces opposing this movement. A scan over the species examined shows that this investment is greatly exaggerated in the tabanids and in *Eristalis tenax* (figure 11) which have 15 and 9 distinguishable d.l.m. fibre bundles, respectively, in longitudinal section, and additional bundles spreading laterally from the midline. All other

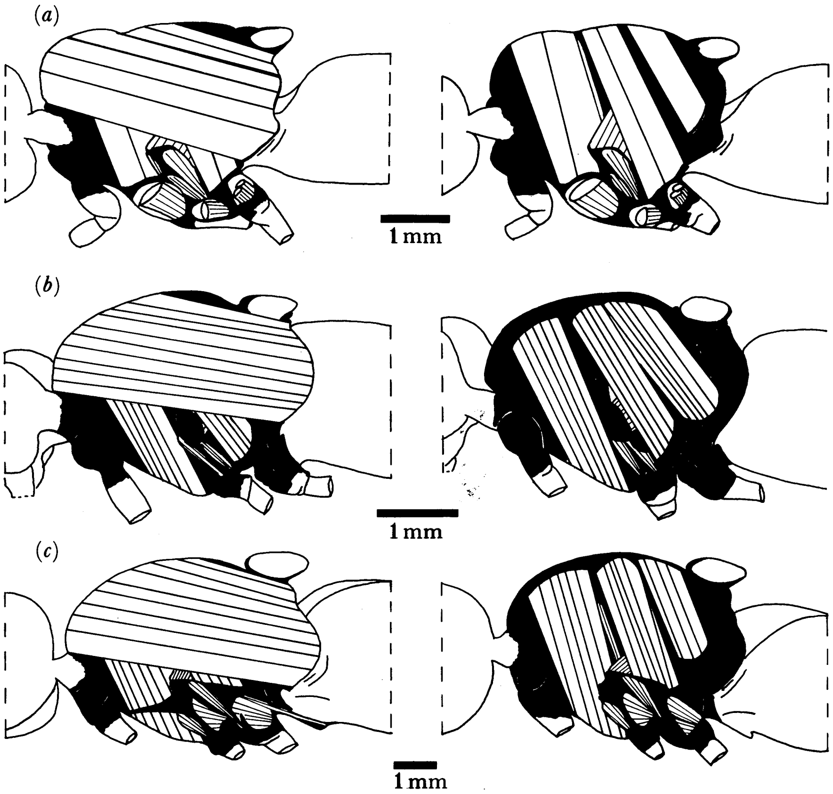

FIGURE 11. The indirect flight muscles of: (*a*) *G. m. morsitans*, (*b*) *T. sudeticus*, and (*c*) *E. tenax*. *G. m. morsitans* does not possess a t.t.m. (see figure 10) and has a large d.v.m. I compared with *S. argyrostoma*. *E. tenax* and *T. sudeticus* are exceptional in having a greater number of d.l.m. fibre bundles (9 and 10, respectively) than the normal complement of six. Some tabanids have as many as 15 distinguishable bundles. These species are also interesting as their muscles show none of the shrinkage that is characteristic of Bouin fixation.

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dipterans examined have six distinct d.l.m. fibre bundles. The indirect flight muscles of *Glossina morsitans* are initially small but undergo a rapid growth after the first blood meal. There does not appear to be any difference between the flight ability of these flies before and after the meal although there are cuticular changes which result in a harder, heavier thorax after the meal which must have effects upon the mechanical properties of the flight system (D. Saunders, personal communication).

### (*b*) *The non-fibrillar flight muscles*

There are up to 17 distinct bundles of muscles directly concerned with the flight system other than the fibrillar muscles (figure 12, plate 2). A major problem with previous analyses of their function has been that they have usually dealt with the isolated action of each muscle. However, this may have little correspondence with the actual function when put in the context of normal behaviour. In addition there has been little attempt to relate the action of the muscles to specific wing base structures. The following analysis attempts to identify the functions of the muscles by using detailed morphological data.

#### (i) *The tergotrochanteral muscle*

There is a substantial amount of evidence that this muscle is concerned with escape jumps and is part of the giant fibre escape system (Power 1948; Nachtigall & Wilson 1967; Mulloney 1969; Levine & Tracey 1973; Tanouye 1977; Tanouye & Wyman 1979, 1980; King & Wyman 1980; Koto *et al.* 1981; Thomas & Wyman 1982). The activation of this muscle is correlated with a simultaneous activation of the d.l.m. motoneurons (Tanouye & Wyman 1980) such that its contractions may well initiate the wing movements at the start of flight following the escape jump. Its attachments would certainly support this idea as it is fixed onto the lateral scutum adjacent to the wing base. Its contractions would therefore cause a rapid elevation of the wings causing the d.l.ms to be stretched and thereby initiating the oscillations of flight. That this muscle is not essential for the start of flight, and probably not used for flight starting outwith escape reactions, is illustrated by its absence in *Glossina* and by the initiation of flight even after its insertions have been cut in other species (King 1983; Nachtigall & Wilson 1967).

Ventrally, the fibres of the tergotrochanteral muscle converge to a single tendon that attaches onto a medial projection of the trochanter within the coxa of the mesothoracic leg (figure 13). As the leg is oriented laterally, contractions of the muscle will cause a sudden extension of the leg resulting in the observed jump. Although there are reports of this muscle receiving multiple innervation (for example, Heide 1983), detailed studies have only identified a single motoneuron, associated with the giant fibre pathway, that excites this muscle (Tanouye & Wyman 1980; Thomas 1980, 1981).

There is variation in the size of this muscle between species. In the species examined, *Coelopa* have the largest, along with *Scatophaga*, and *Eristalis* have the smallest. There may be a correlation in the behaviours of the species in that some species may use this muscle for non-escape behaviours. For example, *Coelopa* and *Scatophaga* use jumping to catch prey. It would be interesting to study the physiology of this muscle in these species and compare it with that found in *Drosophila* where activation appears to be exclusively via the giant fibre pathway (Tanouye & Wyman 1980; Tanouye & King 1983).

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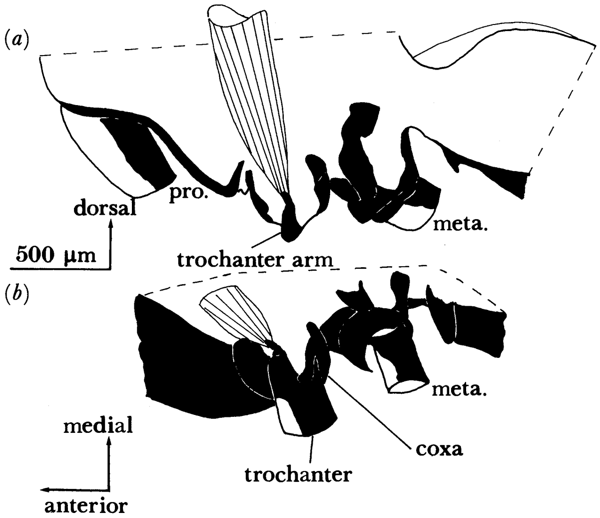

Figure 13. Ventral attachment of the t.t.m. There is a single tendinous attachment to the medially projecting arm of the mesothoracic trochanter. There appears to be a cuticular stop on the coxa which prevents extension of the leg beyond vertical. Abbreviations: pro. and meta. are pro- and metathoracic leg stumps.

### (ii) *The pleurosternal muscles*

These are also called the furcoentopleural muscles (Williams & Williams 1943; Ewing 1977) or the musculus latus (Ritter 1911; Nachtigall & Wilson 1967). From a simple mechanical point of view, these muscles have been implicated in tensioning the thoracic flight box (Pringle 1957) and therefore of controlling its resonant frequency which translates directly into wing beat frequency. Nachtigall & Wilson (1967) produced direct evidence of the muscles' involvement with novel recordings of the movement of the lateral thoracic walls correlated with the activity recorded from the muscles.

It is fairly clear from their anatomy what these muscles do (figure 14, plate 3, and see also figure 2). The two muscles show a bilaterally symmetrical arrangement; they are attached ventrally to the paired furcae, parts of the sternal invagination, and are thus coupled together. Dorsally, each muscle attaches onto the pleural apophysis, a medially projecting torsion bar of the pleural plate. Contractions of these muscles, presumably synchronized centrally, produce an inward pull on the pleural plates that is transmitted to the p.w.p. at their dorsal ends. Thus, they must produce tension in the wing base articulation, as described earlier. There is probably very little movement, if any, of the pleural apophyses relative to the pleural plates due to the rigidity of the attachment. Thus, there will be little effect upon the action of the posterior, non-fibrillar muscles that have their ventral attachments on the apophyses (see later). There is in addition to the main pleurosternal muscle, a small laterally projecting muscle that attaches on the furca and the thoracic joint of the pleural apophysis. Its function is unknown and difficult to deduce from the available evidence.

### (iii) *The first axillary muscles*

There are two muscles in this group that have dorsal attachments on the medial arm of the first axillary sclerite (ax. 1). There is a large anterior muscle that has its ventral attachment along the anepisternal ridge and a small posterior muscle that attaches on the pleural apophysis (figure 15). Mechanically the two muscles are antagonists in their actions on ax. 1. The anterior

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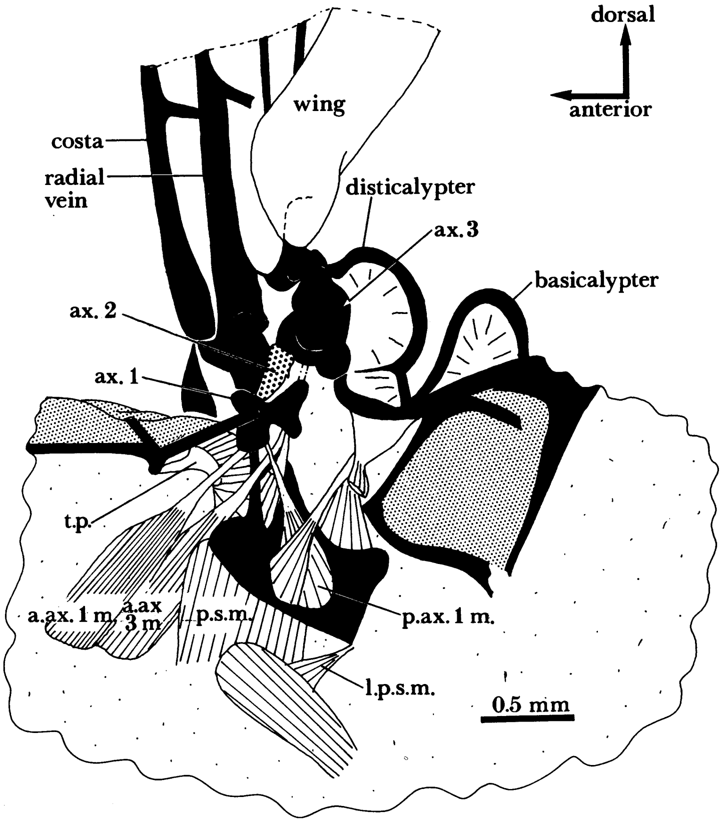

Figure 15. The axillary muscles of *G. m. morsitans* along with their attachments on the wing base sclerites. Note the paired first and third axillary muscles (anterior (a.), and posterior (p.), ax. 1 m. and ax. 3 m.; the posterior third axillary muscle is not labelled), and the lateral pleurosternal muscle (l.p.s.m.).

muscle causes a pronatory rotation and the posterior muscle a supinatory rotation of ax. 1 about its articulation with the a.n.p.

From the mechanical role of ax. 1 discussed earlier, these muscles must have a direct effect upon the twisting of the wing during the wing beat. As the wing is depressed, the tension in these muscles will increase as the arm of the first axillary moves away from their ventral attachments. They can thus tonically influence the characteristics of the wing beat by the degree of their contraction. In addition, they will produce a net elevating force on the wing which will depend for its magnitude on which muscle is active, the larger muscle presumably giving a greater force. Contraction of the anterior muscle will contribute towards a retraction of the wing as well as a greater supination of the wing during the wing beat. Heide (1975) showed that this muscle was active during extreme turning reactions in which the wing on the ipsilateral side to the active muscle was folded in, indicating that this muscle is involved in the retraction of the wing in a flying animal. The posterior muscle will produce some extension as well as pronation of the wing.

### (iv) *The third axillary muscles*

These are similar to the first axillary muscles in being paired, having a larger anterior muscle attached to the anepisternal ridge (posterior to the attachment of the anterior first axillary muscle) and a posterior muscle attached to the pleural apophysis, dorsal and anterior to the

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attachment of the posterior first axillary muscle (figure 15). Dorsally, the two muscles form a single tendon that attaches to the anterior edge of the third axillary sclerite (ax. 3). These muscles are the main wing retractors, rotating the wing backwards about the articulation of ax. 3 with ax. 2. In the process of retracting there is a supination of the anterior wing as the radial vein rotates over ax. 2 which cannot follow the retraction due to its joint with the p.w.p.

The third axillary muscles have an additional effect upon an extended wing owing to the relation between their tendon attachment with ax. 3 and the main wing joints (figure 16). Because the tendon passes below the ridge of the p.w.p. and ends distal to it, contractions of these muscles will produce a downward force on the wing which will increase the downstroke amplitude and also the magnitude of the upstroke recoil. This is supported by the findings of Heide (1975, 1983). He recorded the activity of these muscles during turning reactions and found that they were active during turns in which only one wing was beating, the other wing folded right back. In this condition only the ax. 3 muscles on the side of the folded wing are active, although not receiving wing-synchronized excitation. Such synchronized activity is observed during turning reactions in which both wings are beating but one has a greater amplitude of movement than the other. The muscles on the ipsilateral side to the wing with the greater amplitude are now active and do receive wing-synchronous activity (Heide 1975, 1983). This is probably due to the wing-stimulated receptor, pterale C (Miyan & Ewing 1984).

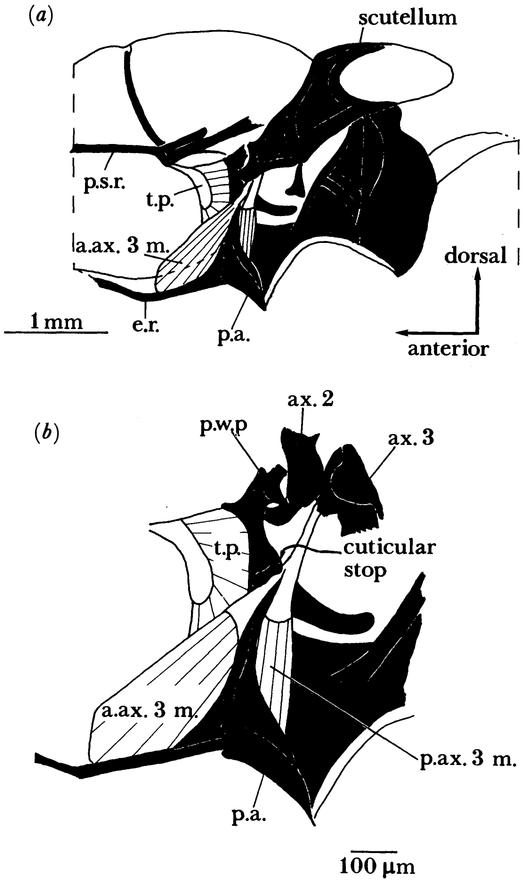

Figure 16. Low (*a*) and high (*b*) power drawings of the third axillary muscles of *G. m. morsitans* showing the cuticular stop that maintains the line of action of these muscles relative to the pleural wing process (p.w.p.) and second axillary (ax. 2) pivot when the wing is extended. Abbreviations: p.s.r., prescutal ridge; e.r., episternal ridge; t.p., tergopleural muscle; p.a., pleural apophysis.

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Thus the functions deduced from the morphology have an appropriate correlate in the physiological characteristics of the muscles. One interesting point that must come out of these results is that if the third axillary muscles are active in the absence of wing retraction, there must be a mechanism for maintaining the extended position. Heide's recordings (1975, 1983) give the clue in the correlations found between the activities of the third axillary muscles and those of the sternobasalar muscle during turning reactions (see later section for latter muscle).

### (v) *The fourth axillary muscles*

The number of distinct muscles belonging to this group is correlated with the size of the calypters (or squamae). Calypterate flies, having large calypters possess four muscles, while acalypterate flies, with very reduced appendages appear to have only two muscles. Of the species examined *Drosophila*, *Coelopa* and *Scatophaga* belong to the second group.

The number of muscles devoted to ax. 4 would suggest an important role for it in wing movement, or related (possibly aerodynamic) characteristics. All the ax. 4 muscles originate on the pleural apophysis (figure 17). We recognize two groups: a single bundle that attaches onto the ventral edge of ax. 4, and a single bundle (acalypterates) or group of three bundles (calypterates) that form a common tendinous attachment onto the dorsal edge of ax. 4. Williams & Williams (1943) identified four ax. 4 muscles in *Drosophila repleta* corresponding to the bundles found in calypterate flies. We were unable to find more than two bundles in the *Drosophila* species examined (see materials and methods for list).

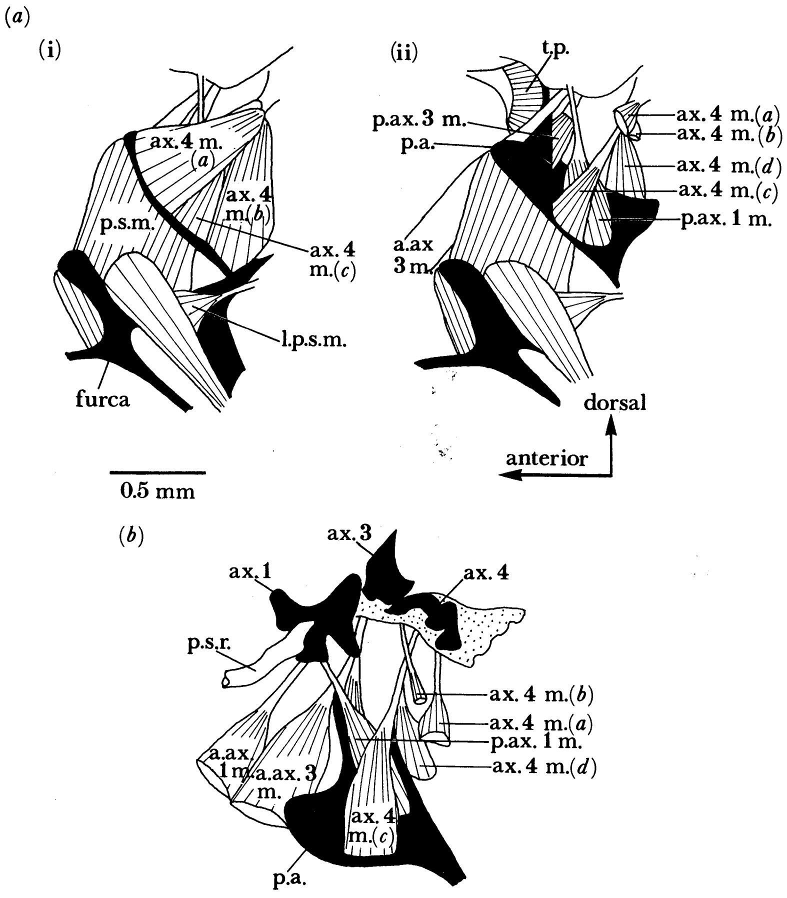

FIGURE 17 (*a*, *b*). For description see opposite.

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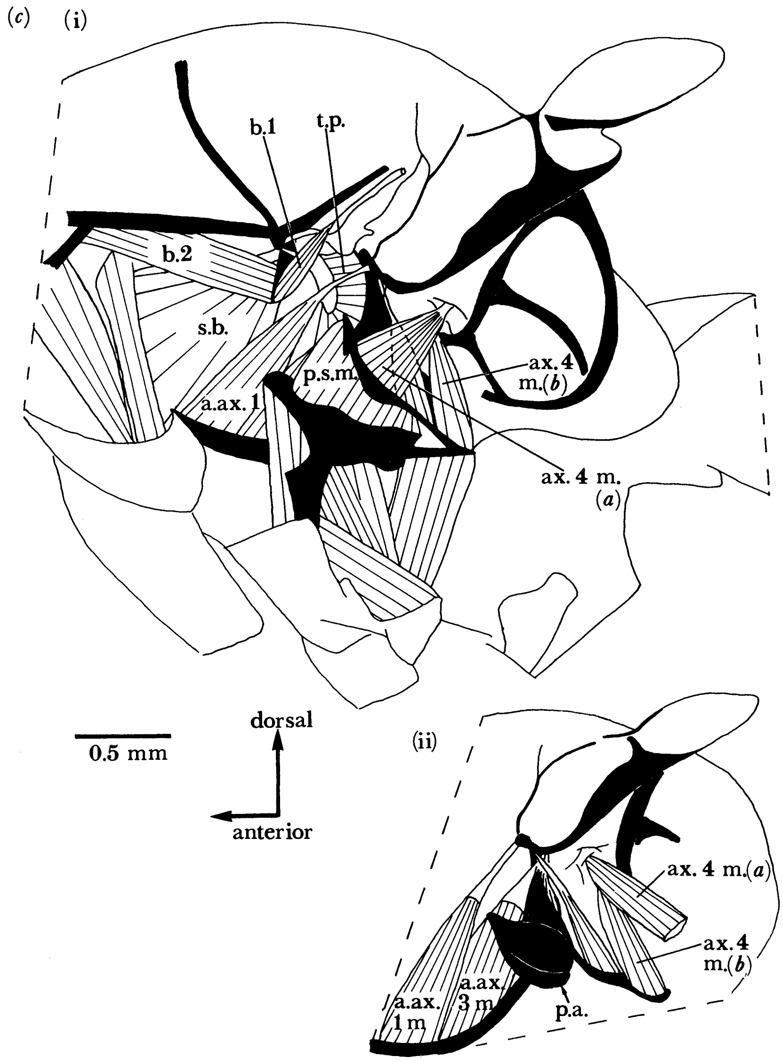

Figure 17. The fourth axillary muscle complex.

(*a*) (i) and (ii) Successive dissections of the fourth axillaries of *G. m. morsitans*. The pleural apophysis (p.a.) forms the ventral attachment for all of the muscles along with the posterior first and third axillary muscles (p. ax. 1 m. and p. ax. 3 m.). The tergopleural muscle (t.p.) is attached on the dorsal region of the pleural wing process (p.w.p.).

(*b*) The fourth axillary muscles of *S. argyrostoma* showing the divergence of the attachments of ax. 4 m. (*a*), which attaches ventrally, and ax. 4 m. (*b*)–(*d*) which attach dorsally on the fourth axillary sclerite (ax. 4). Abbreviations: p.s.r., prescutal ridge; p.s.m., l.p.s.m., pleurosternal, and lateral pleurosternal muscles.

(*c*) (i) The non-fibrillar muscles of *C. figida*, an acalypterate fly (compare with figure 12). Abbreviation: s.b., sternobasalar muscle. (ii) Dissection of the fourth axillary muscles showing only two muscle bundles.

The important role of ax. 4 in the automatic changes during the wing beat has already been discussed as a consequence of its attachment to the scutellar lever. Owing to their attachment to ax. 4, the calypters must undergo synchronized changes also and must therefore be re-examined for their aerodynamic role in flight. In previous work, they seem to have been ignored. Their importance is indicated by the increased musculature applied to ax. 4 in calypterate flies with large, double-lobed calypters.

Contractions of ax. 4 muscles pull the sclerite inward, causing a partial retraction of the wing which will be antagonized by activation of the sternobasalar muscle. In such a case, the resultant

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effect will depend upon which group of ax. 4 muscles is active. If the muscles attached to the dorsal edge are active, there will be a twisting of the sclerite along its longitudinal axis causing the calypters to be lifted and the third axillary sclerite to be depressed at its posterior edge. Conversely, if the ventral muscle is active, there will be a twisting in the opposite direction causing the calypters to be depressed and ax. 3 to be elevated.

The physiological recordings made by Nachtigall & Wilson (1967) and Heide (1975) do not contradict these ideas although they did not record from all the members of this group under the different flight conditions. Heide's (1975) findings that members of this group are active during turning reactions in which both wings are beating supports the idea that the calypters may be used additionally for aerodynamic purposes.

### (vi) *The basalar muscles*

These muscles are normally grouped together as wing extensors although the first basalar has not normally been ascribed any function (Nachtigall & Wilson 1967; Ritter 1911; Heide 1971; Williams & Williams 1943). We have discovered that the first and second basalar muscles are involved in the control of a wing base proprioceptive organ (Miyan & Ewing 1984) and that the sternobasalar muscle is the wing extensor.

The arrangement of the muscles and sclerite is shown in figure 18. The basalar sclerite is separated from the anepisternal plate, scutum and pleural plate by flexible membrane and is capable of some movement relative to them. Posterior to the arm of this sclerite is the receptor called pterale C (after Ritter 1911) which is embedded in membrane. The two structures are linked such that movements of the basalar sclerite produce rotations of pterale C (pt. C) about a loose articulation on the p.w.p. Contractions of the second basalar muscle cause an anterior swing, away from the thoracic wall, while contractions of the first basalar muscle will cause the opposite movement. The movements of pt. C by these muscles effectively changes the position in the wing beat cycle at which the receptor is stimulated by the descending wing.

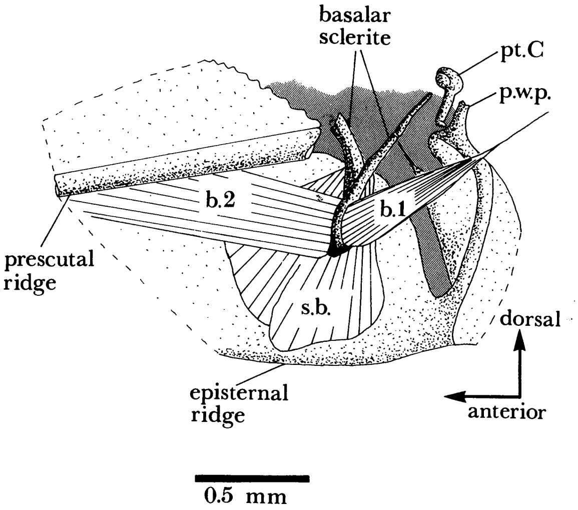

FIGURE 18. The basalar muscle of *G. m. morsitans*. The first and second basalar muscles (b. 1 and b. 2) form an antagonistic pair controlling the position of a receptor, pterale C (pt. C, after Ritter 1911) about its articulation with the pleural wing process (p.w.p.), via their action on the posterior arm of the basalar sclerite. The sternobasalar muscle (s.b.) acts on the anterior basalar and extends the wing by force transmitted through membrane.

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It appears from the relative masses of the muscles that the first basalar might well be acting as a simple spring to return pt. C to its rest position against the thorax. This is exaggerated in *Glossina* in which Schlein (1970) failed to identify the presence of the first basalar muscle. We have, however, found it to be present in this species although it is much reduced. Examination of this muscle in flies fixed in flight and those at rest, demonstrates that it is only functional in the extended wing state (figure 19), that is, when pt. C has been swung into its 'active' position by the second basalar muscle.

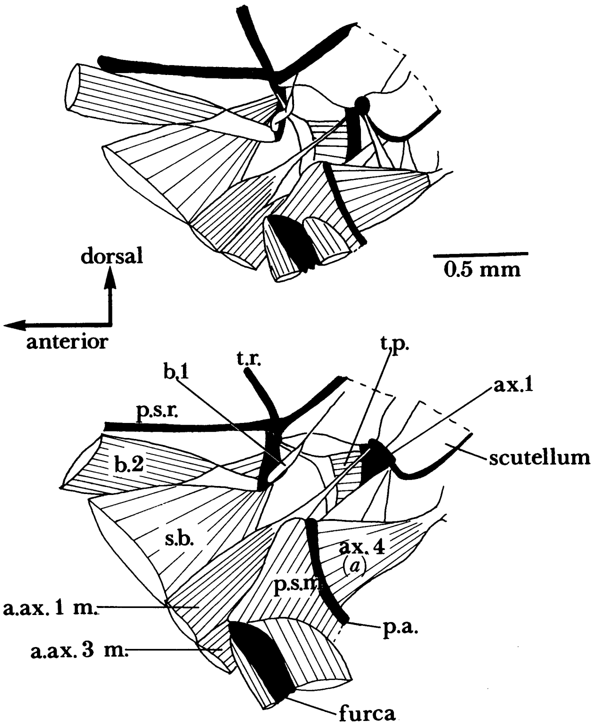

FIGURE 19. Some of the non-fibrillar muscles of *G. m. morsitans* showing the 'deactivation' of the first basalar muscle (b. 1) when the wing is folded (*a*) and its 'active' state when the wing is extended (*b*).

In syrphids (hoverflies) the first basalar muscle is firmly attached to the tergopleural muscle (see later) in such a way that contractions of either will have an effect upon the attached structures of both (figure 20, plate 3). This arrangement would probably give the first basalar muscle a greater spring action as its otherwise long tendinous attachment to the scutum is partly relieved of applied force (see also later).

A very different situation is encountered in tabanids in which the first basalar muscle is greatly enlarged, having almost the same dimensions as the second basalar (figure 21). Tabanids are peculiar in having no receptor structure comparable to pt. C. The basalar sclerite in this species is also much more rigid and movements of any of the three muscles attached to it (the first, second and sternobasalar muscles) produce extension movements of the wing. It appears therefore that in tabanids the basalar muscles are devoted to precise control over wing extension–retraction movements.

The sternobasalar muscle in all species is devoted to wing extension, achieving this by pulling on the membrane at the anterior edge of the wing. There is a degree of variation in the size

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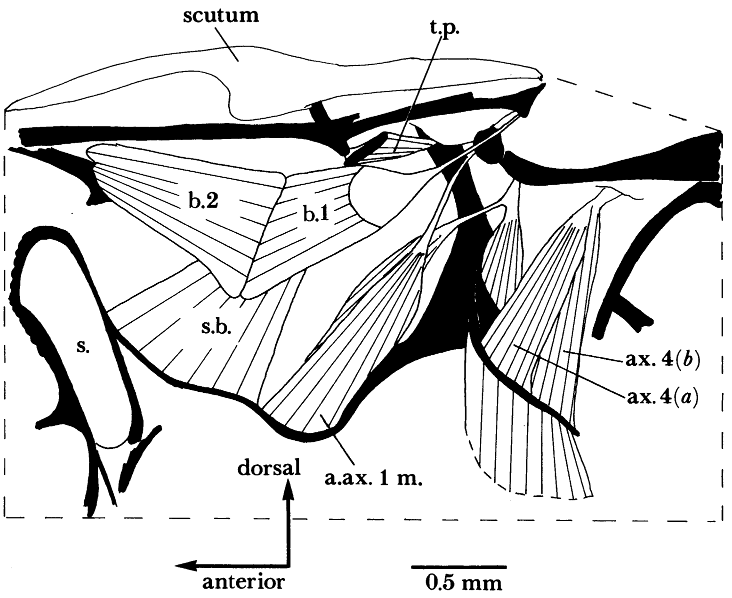

FIGURE 21. Some of the non-fibrillar muscles of *Tabanus distinguendus*, showing the greatly enlarged first basalar muscle (b. 1). Tabanids do not have a structure comparable with pterale C in other dipterans, therefore it is likely that b. 1 is involved, along with b. 2 and s.b., with the precise control of wing retraction–extension. It will prove interesting to examine the flight characteristics of this species group and determine to what extent they actually make use of such precise control (for example, as a swing-wing aircraft?).

of this muscle between species. For example, of the two species of *Coelopa* examined, *C. pilipes* has a much larger muscle than *C. frigida*. The significance of this difference is not obvious but a behavioural correlation may be one possibility, namely the use of this muscle in wing flicking displays. The sternobasalar muscle is often observed as a twin-bundled muscle but there seems to be no difference in the functions of the two halves although Ritter (1911) makes some distinction.

The functional difference in the basalar muscles discussed here are supported by the findings of Tanouye & King (1983) that only the sternobasalar muscle is involved in wing extension as part of the giant fibre escape response. They did make the point that they would have expected the second basalar muscle to be involved as it is innervated by the largest motor axon to any 'direct' flight muscle. This may be related, however, to the speed of conduction required for its reflex links with pt. C (Miyan & Ewing 1984).

### (vii) *The tergopleural muscle*

This muscle has also been called the third and fourth basalar muscle (Williams & Williams 1943; Ewing 1979) but, as it has no attachments to the basalar sclerite, we have adopted the present name. In most species this muscle is composed of two bundles, originating in a shallow evagination of the pleural plate and forming a single, stiff tendon that attaches onto the medial projection of the transverse ridge of the scutum. In tabanids and *Eristalis*, this muscle is a single, tightly packed, parallel bundle, originating in a similar pleural evagination but inserting onto a rigid bar which is fixed onto the transverse ridge with tough connective tissue that allows a degree of rotation of the bar relative to the ridge (see figures 20 and 21).

Wisser & Nachtigall (1983) discussed the functions of this muscle in terms of a 'bracing'

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action between the scutum and pleural plate, providing an additional, more direct tension to the wing base articulation to that supplied by the pleurosternal muscles. This function is doubtful however when the findings of Boettiger & Furshpan (1950, 1951, 1952) are studied. They found that contractions of either set of indirect muscles (d.l.ms or d.v.ms) produced an outward movement of the lateral scutum which, coupled with the inward movement of the pleural wing process by the pleurosternal muscles, would give the required tension. Boettiger & Furshpan (1950) assumed that the indirect muscles are under constant tetanic stimulation and this was confirmed by Boettiger (1957) from direct measurements, which also demonstrated the constant force that would result to be translated directly into lateral force. The use of a direct tensioning system of the sort proposed by Wisser & Nachtigall (1983) is therefore probably not required although it may be important in non-flight behaviours.

In our morphological studies, we have found that the tergopleural muscle may produce small relative movements between scutum and p.w.p. and thereby cause a rotation of the first axillary sclerite, this rotation not being subject to the same wing-synchronous changes as those experienced by the first axillary muscles. In this case it may well be the element responsible for determining selection of position of articulation of the radial stop on the p.w.p. and, hence, of the angle of attack of the wing over the wing beat. Figure 20 shows the attachment of the first basalar muscle to the tergopleural muscle in *Eristalis tenax*. Assuming that contractions of the tergopleural muscle produce a supination of the wing, the effect of the first basalar attachment will be to bring pterale C closer in to the thorax, taking a more posterior location than its normal extended position. This may maintain the receptor's trigger point in the cycle which will depend upon pt. C being stimulated by a portion of the wing more posterior and hence lower than the raised anterior margin.

## 7. DISCUSSION

In this paper we describe some new anatomical findings concerning the dipteran wing base structures and their associated musculature. This morphological data, along with experimental work published elsewhere (Miyan & Ewing 1985*a*), leads us to propose a novel mechanism for dipteran flight which differs substantially from the generally accepted model first proposed by Boettiger & Furshpan (1952). This latter model incorporates a bistable thoracic 'click' mechanism acting on both the up and downstroke of the wing beat. By contrast, our model envisages no such 'click' mechanism and we suggest that elastic energy is stored during the latter portion of the downstroke to be released during the upstroke (figure 22). The new model does not involve the rapid length changes and pauses implicit in the former model and which have been thought important owing to the physiological properties of insect fibrillar muscle (Pringle 1949, 1957, 1981). The specific property of fibrillar muscle referred to is the delayed tension response to stretch activation. In this, fast stretches cause a delayed increase in tension while fast releases from load cause a sudden 'deactivation', or loss of tension, in the muscle. Thus, the wing movements produced would have rapid up and down strokes with pauses at the top and bottom of the beat, giving a greater lift generation than movements with a more sinusoidal component (Pringle 1981).

Although such movements are predicted, none are seen in anaesthetized, tethered, flying flies (Miyan & Ewing 1985*a*; figure 23). Observed wing movements show a downstroke which is much longer and slower than the upstroke. There is little change in velocity during the major

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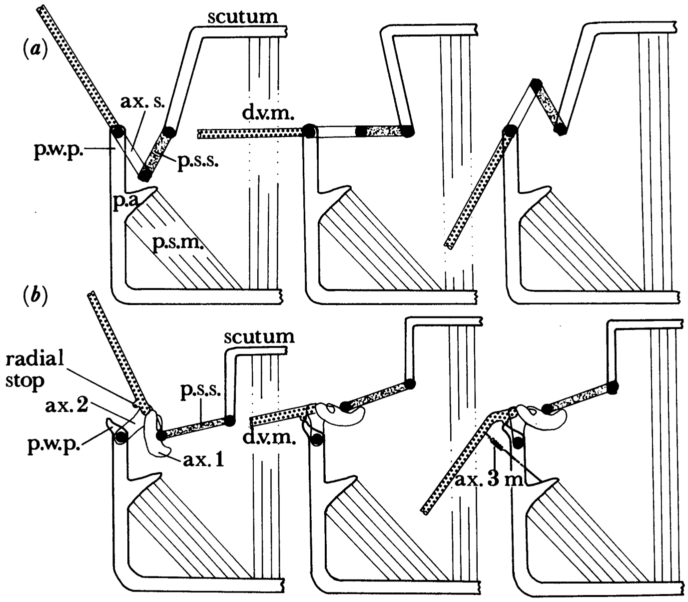

Figure 22. Diagrammatic comparison of the 'click' model (*a*) and the model proposed by the authors (*b*). Note the radial stop–p.w.p. mechanism that leads to wing bending, the amplitude of which can be controlled by the tonic contractions of the third axillary (and probably other) muscles (ax. 3 m.). Note also the ax. 1 lock onto p.s.s. which prevents any bistability and leads to direct stretching of the d.v.ms. Elastic energy is stored in the p.w.p., radial vein and other thoracic elements to be released on the upstroke. Abbreviations: p.s.m., pleurosternal muscle; p.s.s., parascutal shelf; d.v.m., dorsoventral muscle; ax. s., axillary sclerites as a single unit; p.a., pleural apophysis.

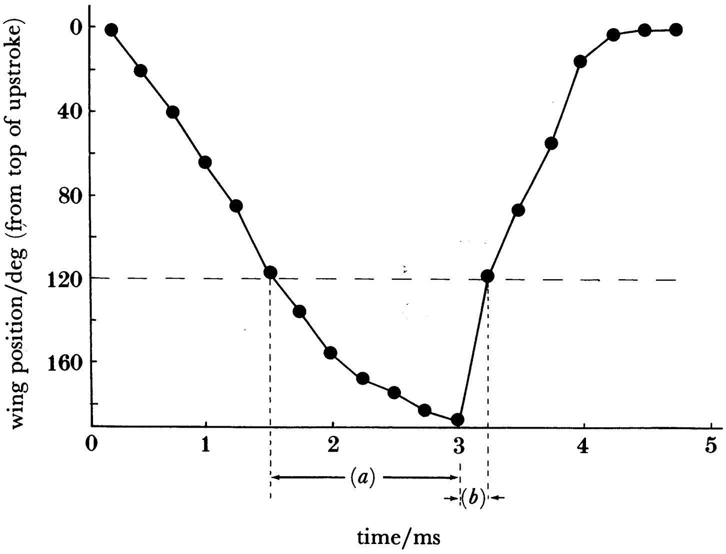

Figure 23. Typical analysis of wing movements during tethered flight for *D. virilis*. The broken line across the plot is the approximate position at which the radial stop engages the pleural wing process on the downstroke, and disengages on the upstroke. The intervals (*a*) and (*b*) are very unequal although representing equal angular displacement of the wing. They suggest a strong elastic recoil at the beginning of the upstroke (see text). The observed wing movements do not support the 'click' model for dipteran flight (Boettiger & Furshpan 1952; Pringle 1957).

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part of the upstroke in contrast to the more sinusoidal components in the downstroke. There is no indication of the predicted changes in velocity in either half cycle and there is a marked discontinuity at the bottom of the downstroke where a sudden, rapid acceleration is observed on the upstroke.

We have demonstrated a wing base stop mechanism consisting of the radial stop and pleural wing process (p.w.p.). We have also described the locking mechanism of the first axillary sclerite (ax. 1) onto the parascutal shelf (p.s.s.) during the lower part of the downstroke that results in lifting of the dorsal scutum and consequent stretching of the dorsoventral muscles (d.v.ms). This locking immediately precedes the wing stop being engaged, which occurs approximately 15–25° below the horizontal position of the wing. As the d.v.ms are stretched after the ax. 1 lock is engaged, these muscles will not be activated until the last part of the downstroke. This is in contrast to d.l.m. activation due to stretching which occurs at the beginning, and throughout the upstroke. However, it is possible that the delay before onset of tension, as a result of the rapid stretching in the d.l.ms, may be of a duration that would allow the upstroke to be completed before any great force was produced by them. The speed of the upstroke is therefore advantageous and possibly even necessary if a blocking force on the upstroke, due to contractions of the d.l.ms, is to be avoided. This speed would be enhanced by the addition of elastic forces which, we propose, are stored during the downstroke, to the forces produced by the d.v.ms. Thus, the observed movements and their anatomical basis make use of the special properties of fibrillar muscle (Boettiger 1957).

The wing stop described in this paper has been illustrated by various authors (for example, Pfau 1973; Wisser & Nachtigall 1983) but has not been implicated as part of an important mechanical system. This may well stem from the misconception that the wing articulates about a set fulcrum on the p.w.p., and from a commitment to the bistable 'click' model for dipteran flight. The functional significance of the stop becomes clear when correlated with the mechanical system of the wing base articulation and thoracic components. It is this relationship that is the basis for the direct stretching, and activation, of the d.v.ms and their antagonism to the d.l.ms. The mechanical arrangement causes a much more direct effect of the two sets of indirect muscles upon the wings, and upon each other, than is provided by previous models which rely upon thoracic distortions for these effects. It also forms the basis for a system of elastic energy storage, on both halves of the wing beat but with a greater component during the downstroke. The pleural wing process appears to be a major contributor to this system and it would be of interest to analyse its structure and compare it with the resilin found in other elastic systems (for example, the flight system of the locust: Weis-Fogh (1961); the jump of the flea: Bennet-Clark & Lucey (1967)).

That the downstroke requires greater muscular work is clear from the musculature devoted to this movement. The amount of work contributed by the d.v.ms to the upstroke is a problem that does not seem capable of solution with the available evidence. We have found it impossible to measure any movements of the anterior scutum during the wing beat and propose that the anterior d.v.m. (d.v.m. I) is not directly involved in powering the upstroke. Rather, it is probably devoted to maintaining lateral tension in the scutum by a constant downward force. It will be interesting to investigate the dynamics of wing movements in those species, such as tabanids and syrphids, which have a much greater d.l.m. complement than normal. Such species appear to be specialist fliers and may therefore hold significant clues as to the functional significance of the indirect muscles. It will also be of interest to find some means of measuring

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the exact muscle tension in a flying fly to determine the precise cycle of events during the wing beat, particularly at the bottom of the downstroke and beginning of the upstroke. The techniques for such a study do not appear to exist at the present time.

A significant feature of our model is that it is the first that provides a convincing mechanism for the control of wing beat amplitude. Owing to their line of action relative to the p.w.p.–ax. 2 joint, the third axillary muscles can potentially influence the amplitude of the downstroke by the degree of their contraction. The force that they produce will affect the entire wing cycle but the direction of that force will depend upon the position of the wing. Thus, at the top of the upstroke there will be a slight medially directed force, translated into a small downward force during the major part of the downstroke. The magnitude of the force is determined by its line of action relative to the wing joint, and as this is very close to the joint during the upper part of the stroke, the force will be correspondingly small. However, about the horizontal position of the wing, there will be a maximum downward force that will tend to pull the wings down further than if the muscles were inactive. This is supported by the physiological recordings from these muscles during turning reactions in which both wings are beating, one with a greater amplitude than the other (Heide 1971, 1975, 1983). Heide (1975) found that the muscles on the side with the greater amplitude were active while those on the side with the lower amplitude were silent. Heide's recordings from these muscles during extreme turning reactions, in which one wing is folded, point to the other function of these muscles, that of wing retraction. In the former situation, a mechanism is required to oppose the retracting action and this is provided by the wing extensor, the sternobasalar muscle. This muscle's activity is strongly correlated with the third axillary muscle (Spüler & Heide 1978; Heide 1983) and has also been found to be an integral part of the giant fibre escape response (Tanouye & King 1983) in which it causes a fast extension of the wings, full extension being achieved within the first six wing beats (Nachtigall 1966; Nachtigall & Wilson 1967).

In addition to the main wing movements, we have identified the mechanical basis of the automatic changes in the wing observed during the wing beat. This is centred on the fourth axillary sclerite (ax. 4) and its attachment to the scutellar lever and third axillary sclerite (ax. 3). Via these articulations, ax. 4 affects the wing movements in a controlled way over the entire stroke. We have also shown that there is potential control over these changes by the fourth axillary muscles. These would produce tonic changes during the entire cycle as they are probably incapable of high frequency contraction–relaxation cycles. These muscles would also have parallel control over the cyclical characteristics of the calypters by virtue of the latter's attachments on the fourth and third axillary sclerites. This attachment suggests implications for the possible aerodynamic roles of these structures which have been previously ignored. The rim of each calypter is heavily sclerotized giving the whole structure a rigidity that would probably be maintained in free flight conditions. Thus, they would provide a surface that could conceivably be used similarly to the flaps of aircraft, for 'braking', or for lift control.

We have described a switch mechanism, previously identified in *Sarcophaga bullata* by Pfau (1973) and in *Glossina morsitans* by Chowdhury & Parr (1981). This is controlled by muscles acting upon the radial vein, rotating it about its length and, thus, determining the position taken by the radial stop on the pleural wing process for the lower part of the wing beat. The muscles involved are the first axillary and the tergopleural muscles which exert their effects upon the first axillary sclerite. A second set of muscles has been identified as controlling a wing base proprioceptor, pterale C (after Ritter 1911). The functions of all the muscles are listed in table 1. By using the anatomical evidence it has been possible to infer the actions of all the

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TABLE 1. THE FUNCTIONS OF THE NON-FIBRILLAR MUSCLES AS DEDUCED FROM THE MORPHOLOGY

(Notice the difference between the functions of a muscle when manipulated on its own (isolated action) and when analysed in the context of a wing held in an extended position and inhibited from retracting. The physiological evidence of other workers confirms many of these classifications (see text).)

| muscle group or sclerite name | | number of bundles | isolated action | action on extended wing | | sclerite function |
|---|---|---|---|---|---|---|
| axillary 1 | ax. 1 m. (a.) | 1 | wing retraction | supination | wing elevation | attachment of radial vein<br>main force transmitter to wing<br>wing twist fulcrum |
| | ax. 1 m. (p.) | 1 | | pronation | | |
| axillary 2 | | 0 | no muscles attached to this sclerite | | | pivot for upper part of wing beat at its joint with the p.w.p. |
| axillary 3 | ax. 3 m. (a.) | 1 | wing retraction | wing depression | | main wing retraction articulation<br>attachment of calypters<br>control of automatic changes during beat via ax. 4 and scutellar lever |
| | ax. 3 m. (p.) | 1 | | | | |
| axillary 4 | ax. 4 m. (d.) | 1 or 3 | partial wing extension | calypter lift<br>rear of wing depressed | wing retraction | control of calypters<br>automatic changes during stroke via scutellar lever and ax. 3 |
| | ax. 4 m. (v.) | 1 | | calypter depression<br>rear of wing elevated | | |
| basalar 1 | | 1 | posterior and inward movement of pt. C | pt. C position control | | pt. C control via posterior arm of sclerite |
| basalar 2 | | 1 | anterior and outward movement of pt. C | pt. C position control | | pt. C control via posterior arm of sclerite |
| sternobasalar | | 1 or 3 | wing extension | forward and downward movement of wing | | wing extension via anterior basalar |
| tergopleural | | 1 or 2 | wing extension | supination of wing via action on ax. 1 | | — |
| pleurosternal | | 1 or 2 | medial flexion of p.w.p. | wing depression, tensioning wing articulation | | — |
| tergotrochanteral | | | extension of mesothoracic leg | wing elevation | | — |

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non-fibrillar muscles and many of these are confirmed or supported by the physiological evidence from other workers. For example, the giant fibre escape response has confirmed the action of the tergotrochanteral muscle in extending the mesothoracic leg and initiating the escape jump (Tanouye & Wyman 1980) which had previously been deduced from force measuring experiments and leg ablation experiments (Nachtigall & Wilson 1967). In the same escape response, there is an extension of the wings mediated by the sternobasalar muscle (Tanouye & King 1983). It is interesting to note that Tanouye & King (1983) found no giant fibre activation of the second basalar muscle, nor of the first and third axillary muscles. These muscles were found to receive descending influences from the brain, but at a much higher stimulation threshold than the giant fibre system. K. Gotz and G. Heide (unpublished) and Heide (1983) found that the first and third axillary muscles were activated by visual turning stimuli and therefore were probably involved in the resulting turning reactions of the fly. The visual stimuli would certainly have a brain pathway and would probably not influence the giant fibre system. Thus the results of the above-mentioned groups of workers fit with the morphological analysis presented in this paper.

During the course of this study, we received much support and interest from our colleagues, in particular from Geoffrey Harper who gave detailed criticisms and patient discussions. It is also a pleasure to thank the staff of the Tsetse Research Institute (Bristol), the Parasitology Department (Edinburgh), Richard Steele, Ken Thomson and Philip Whitfield for the supply of living specimens, and the S.E.R.C. for supporting the work (grant number GRB 61429).

A note of thanks is added here for the anonymous referee who directed us to the work of Matsuda (1970) and put us right on the nomenclature of the post-median notal process, which we had, in common with many other workers, mistaken for the posterior notal process.

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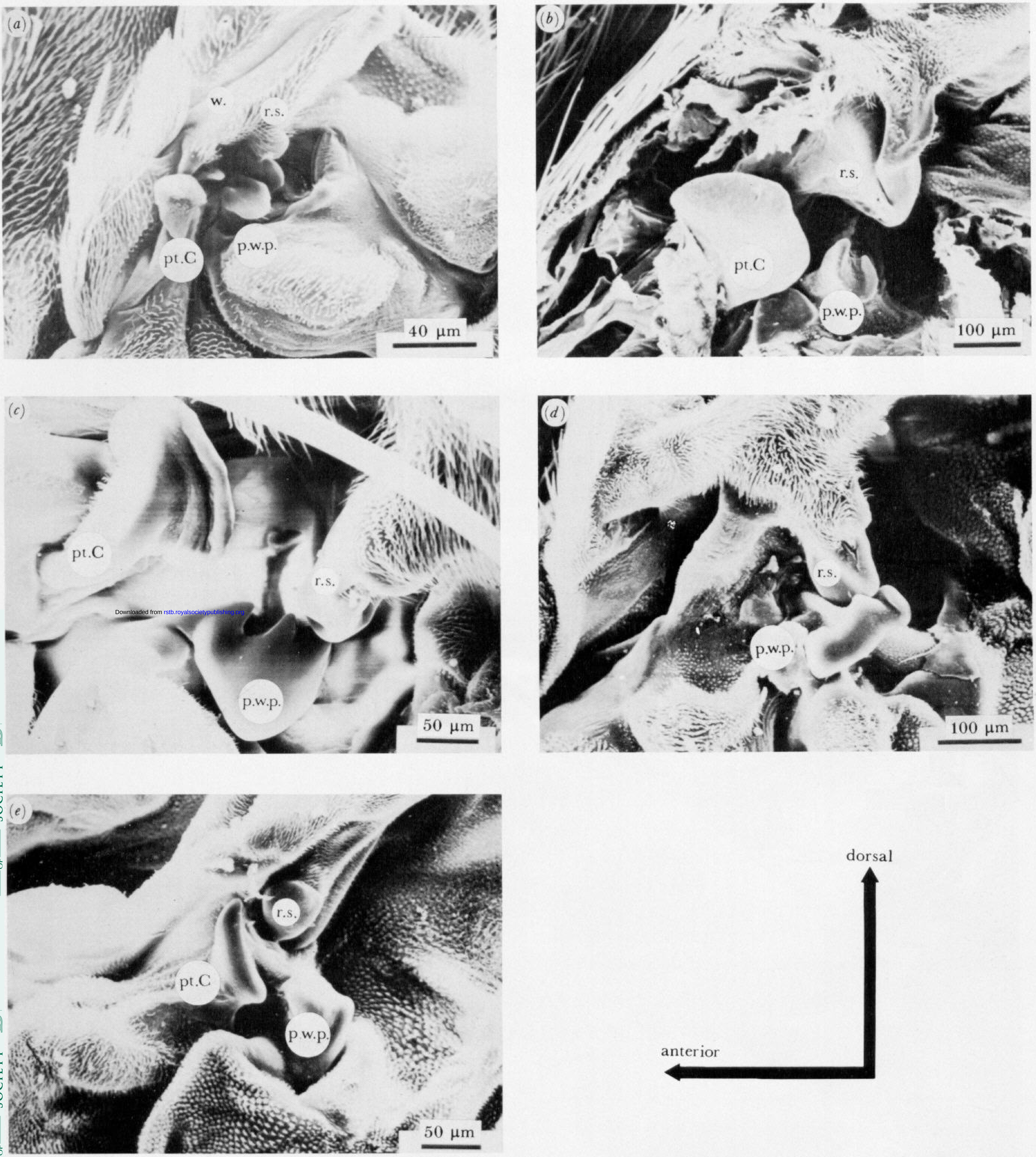

FIGURE 8. For description see opposite.

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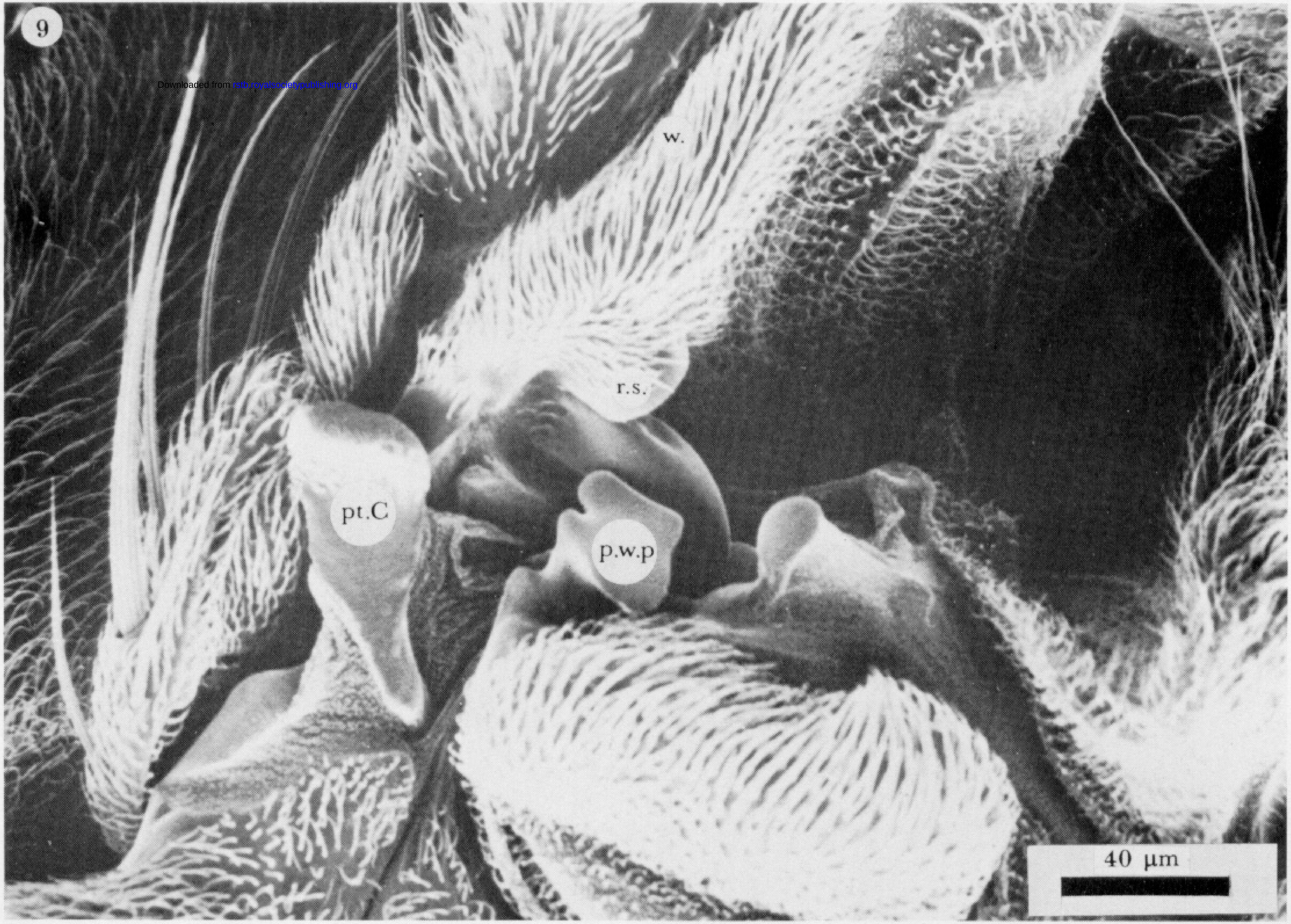

IGURE 9. Scanning electron micrograph of the wing base of *D. virilis* showing the natural separation between the p.w.p. and radial stop (r.s.) during the upper part of the wing beat.

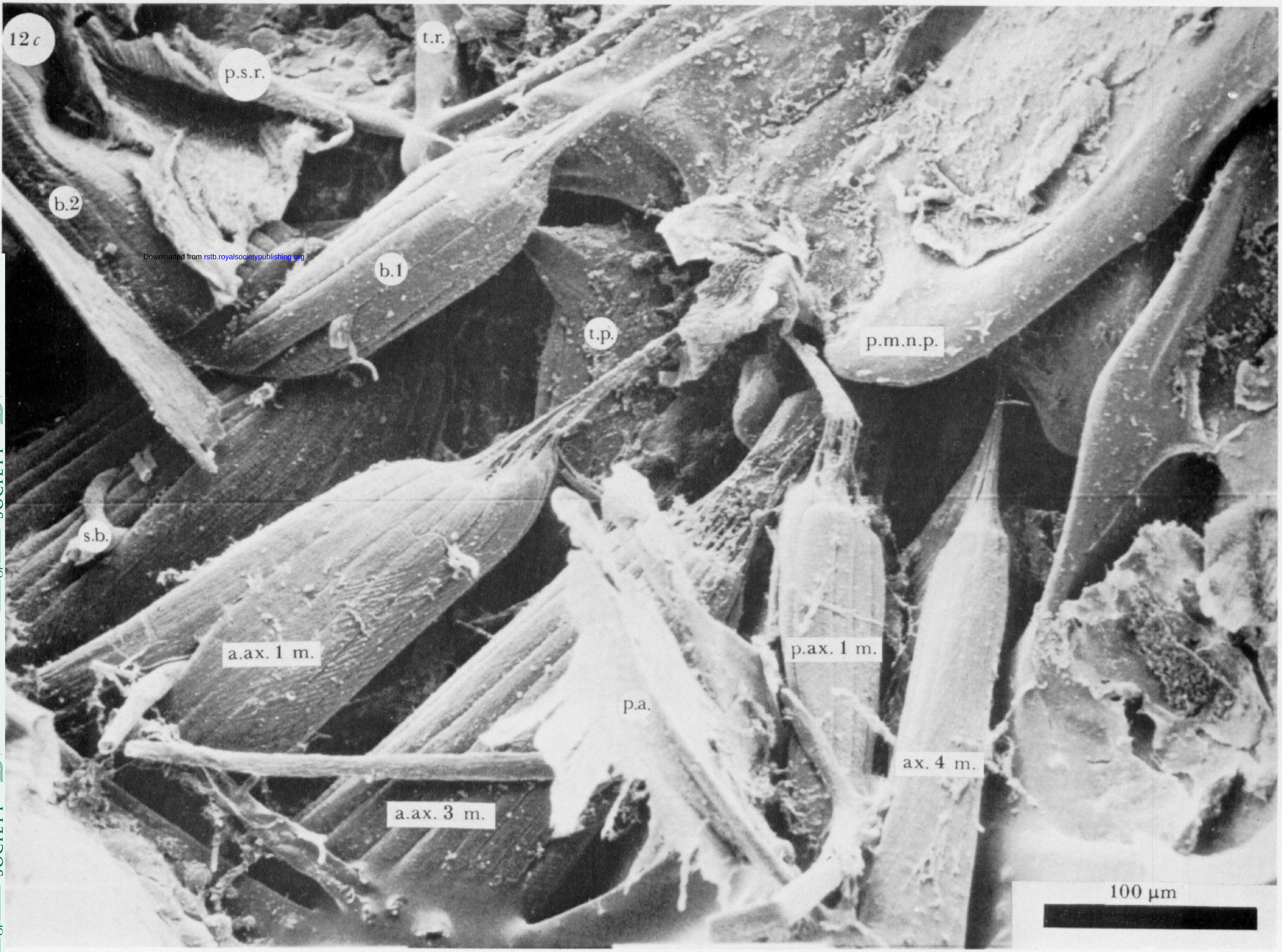

FIGURE 12 (c). For description see opposite.

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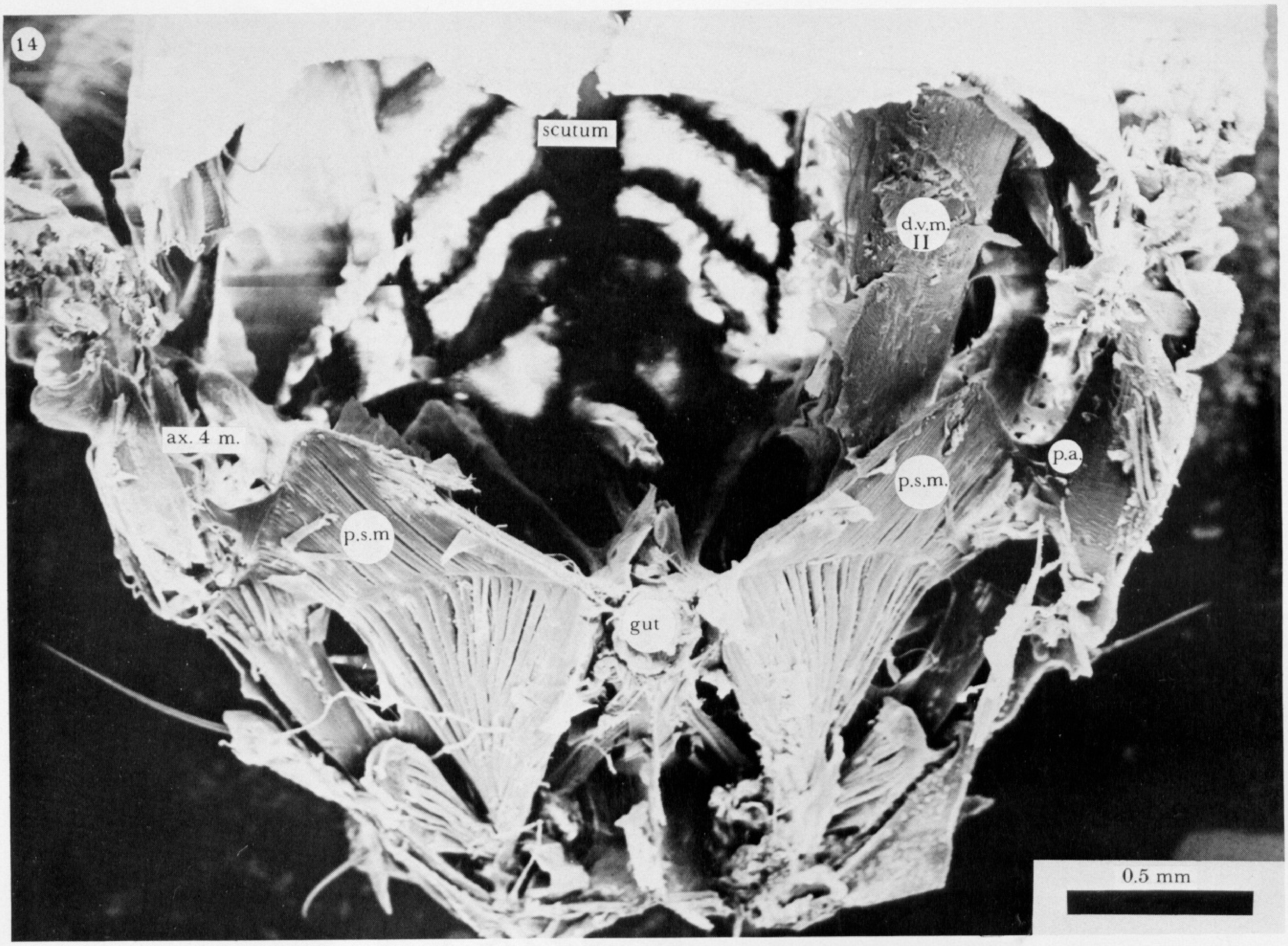

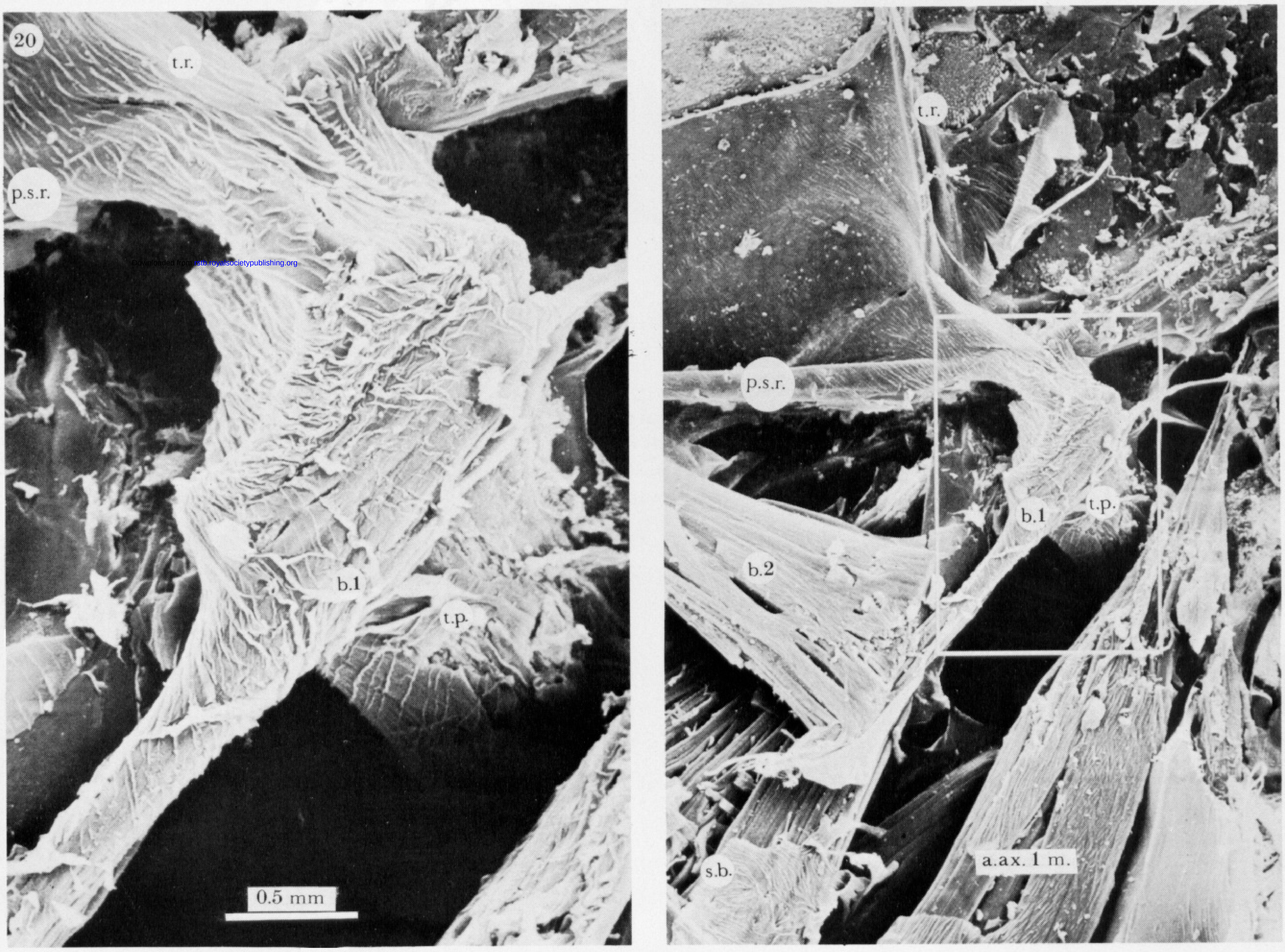

FIGURES 14 AND 20. For description see opposite.

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