THE JUMPING MECHANISM OF *XENOPSYLLA CHEOPIS*

III. EXECUTION OF THE JUMP AND ACTIVITY

By MIRIAM ROTHSCHILD
Ashton, Peterborough

J. SCHLEIN
Department of Medical Entomology, The Hebrew University, Jerusalem

K. PARKER
Physiological Flow Studies Unit, Imperial College, London S.W.7

C. NEVILLE
Department of Zoology, University of Bristol

AND S. STERNBERG
Department of Entomology, Israel Institute for Biological Research,
Ness Ziona, Israel

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[Plates 39–43]

CONTENTS

The flea's hind legs are the chief source of jumping power, but in species which execute large jumps, take-off is accelerated by elastic energy released from a resilin pad (homologous with the wing hinge ligaments of flying insects) situated in the pleural arch. A central click mechanism, operated by a rapid twitch of the trochanteral depressor (the starter muscle), synchronizes the separate sources of energy which power the jump. Ciné photos confirm the morphological evidence that the flea takes off from the trochanters, not the tarsi.

The loss of wings, associated with a lateral compression of the body and the shortening of the pleural ridge (which thus lowers the position of the pleural arch) together with modifications of the direct and indirect flight muscles, are some of the main morphological features associated with the change from a flying to a saltatorial mode of progression. The flea's take-off basically resembles that of other Panorpoid insects (Diptera, Mecoptera, etc.). The release of elastic energy from the pleural arch is a system by which the force used to move the wings of flying insects is rapidly fed back into the legs and adds power to the jump.

INTRODUCTION

> 'A while ago Socrates asked Chaerephon
> how many of its own feet a flea leaped....'
>
> ARISTOPHANES (*The Clouds*)

The saltatorial powers of fleas have excited wonder and admiration in philosophers and naturalists, as well as the man-in-the-bedroom, who dabs at the insect hopefully with a tablet of soap. Pliny noted them 'skipping merrily in victualling houses', and a notable French courtesan remarked 'Quand à moi ce n'est pas la morsure, c'est la promenade....' According to Buxton with Hopkins (1927) the placid natives of Aitutake, struck by fleas' restlessness and irritating habits, drew the reasonable conclusion that they were the souls of deceased white men....

At the turn of the century Russell† (1913) compared the muscular prowess of a 'performing' flea with that of a man dragging two elephants round Lords Cricket ground, and more recently the jumping *Xenopsylla cheopis* (Roths.) was likened to someone 'with a sorbo rubber ball in his hip joint, bouncing himself off his knees to the top of the Post Office Tower, and repeating the performance 10000 times, scarcely pausing for breath'. Rothschild & Neville (1967) in a preliminary account of the jump, and with dubious poetic licence, described fleas as 'insects which fly with their legs', since the wing hinge ligament, originally situated on the dorsum, had become displaced laterally, making its incorporation into the jumping mechanism possible. The shortening of the pleural ridge, especially marked in Pulicoid fleas, associated with the lateral position of the pleural arch, is no doubt the most important modification involved in making the change possible. The muscles, which were once specialized to produce wing power, are now adapted to load energy into the resilin cap. No energy is dissipated through the wings (which are suppressed), and the elastic energy is turned back, by way of the cuticular lines of force and the massive trochanteral depressor, the starter muscle, into the jump.

The first morphological description of the jumping muscles of the flea was made by Jacobson (1940), who studied those of the legs and thorax of *Ceratophyllus styx* (Roths.). He also noted that although the jump itself is too rapid for the eye to follow, fleas take an appreciable time 'collecting' themselves beforehand. Snodgrass (1946) confirmed Jacobson's description, and both authors agreed that the back legs are the principal jumping organs. Snodgrass (p. 317), however, denied that fleas crouch down prior to take-off or make preliminary movements. Both authors thought that the downward flexion of the femur effects the jump, rather than the extension of the tibiae. Snodgrass added: 'the size of the leg depressor muscles attached on the trochanters leaves little doubt that the action of the femora is most important, but the size of the femora themselves and the tibial muscles they contain would indicate that the extension of the tibiae plays also an important part in the spring. Probably the leap is effected by a simultaneous extension of both femora and tibiae.' Our own interest in the saltatorial powers of the

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† This booklet was mainly written by N. C. Rothschild although he was not a joint author.

flea was aroused by the observation that fleas frequently hold their legs aloft when they jump (plate 40*a*), a fact which was confirmed by photographs carried out at the R.A.F. experimental station at Farnborough (Rothschild 1965, 1969). The fleas, by interrupting a beam of light, took their own picture. It was also revealed by this means that fleas spread their legs widely during their descent, presumably to improve their landing performance (plate 40*a*, inset). In 1967 the B.B.C. arranged for a high speed film to be taken on our behalf by Eric Lucey. In this instance the fleas were *Spilopsyllus cuniculi* (Dale), supplied by us from Ashton stock. This film confirmed the previous observations that the fleas spread their legs widely during the descent and somersaulted in the air if they took off from an uneven surface.† Bennet-Clarke & Lucey (1967) deduced correctly that resilin (plate 43*c*; figures 4*a*, *b*) was present in the pleural arch. They assumed that the fleas took off from their tarsi, not the trochanter. It is extremely likely that some fleas are able to do this, particularly if they are jumping off the middle legs, which lack both pleural arch and lines of force, but there is no evidence of this in the film in question, nor the one taken subsequently by the B.B.C. (1973) for their Horizon programme. It is very noticeable, however, that the angle of the body varies considerably at take-off, some specimens after their initial crouch point their head skywards, reminiscent of a rocket on a launching pad. From a study of the exoskeleton and musculature we concluded that, at any rate the big jumpers, generally take off from the trochanter and femur, not the feet (tarsi), and an attempt was made to photograph the jump in such a way that this deduction could be supported by evidence from a ciné film sequence.

MATERIAL AND METHODS

Only *Xenopsylla cheopis* (Roths.) was used in studying the mechanism of the jump, since cultures of this flea were always available. They were reared on rats at 28 °C at 70–80 % humidity at the Biological Institute at Ness Ziona, Israel, and at Ashton. Other species such as the cat flea *Ctenocephalides felis* (Bouché) are superior performers, jumping four or five times the height of *X. cheopis* and probably developing accelerations in excess of 400 *g*. Occasional observations were made on other species, in particular those with greatly reduced saltatorial powers, collected in the wild at Ashton and Oxford. A culture of *Echidnophaga myrmecobii* Roths., an Australian marsupial stick-tight flea, was maintained on hamsters at Ashton.

The photographs were taken with a Hitachi rotating prism ciné camera on standard 16 mm ciné film. The framing rate of the camera is variable (maximum 10000 frames per second) and the sequence used to illustrate this paper (plate 39) was taken at 3500 frames per second.

These fast framing rates result in short exposure times and it was found to be impossible to provide enough front illumination without killing the fleas. This was solved by back lighting, using a single floodlight, overdriven by a Mole Major power supply, focused on the image plane and directly into the objective of a lower power microscope. The light was focused by means of a spherical flask filled with a copper sulphate solution which provided a simple but effective filter. The light from the microscope was shone directly into the aperture of the ciné camera.

A narrow, pyramid-shaped perspex platform was placed in a glass box containing a number of freshly emerged fleas. The camera was focused on the top of the platform, taking advantage

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† Watson (1938) noted briefly that fleas often turned over in mid air and landed facing in the opposite direction from which they had come.

of the fleas' natural inclination to climb to the top of objects in their immediate vicinity prior to jumping (plate 39*a*). It was noticed that other fleas climbing onto the platform often stimulated the flea already there to take off. This observation provided the solution to the principal problem of the photographic study: anticipating the jump in time for the camera to run up the speed (approximately $\frac{1}{2}$ s, compared with a total time of filming for 100 ft of film of about 1 s).

The sequence of frames showing the jump were analysed frame by frame to give the position of the flea relative to the jumping platform. These measurements are shown in figure 3*a*. The known dimensions of the platform provided a convenient scale for the distance, and the time between frames was accurately measured by means of timing marks produced by the camera on the edge of the film.

The velocity of the flea is the slope of the measured position against time curve, and was calculated by simple differencing, $v(t) = \Delta x(t)/\Delta t$. The acceleration, the slope of velocity against time curve, was also calculated by differencing the calculated velocities, $a(t) = \Delta v(t)/\Delta t$. These calculated curves are shown in figure 3*b*, *c*.

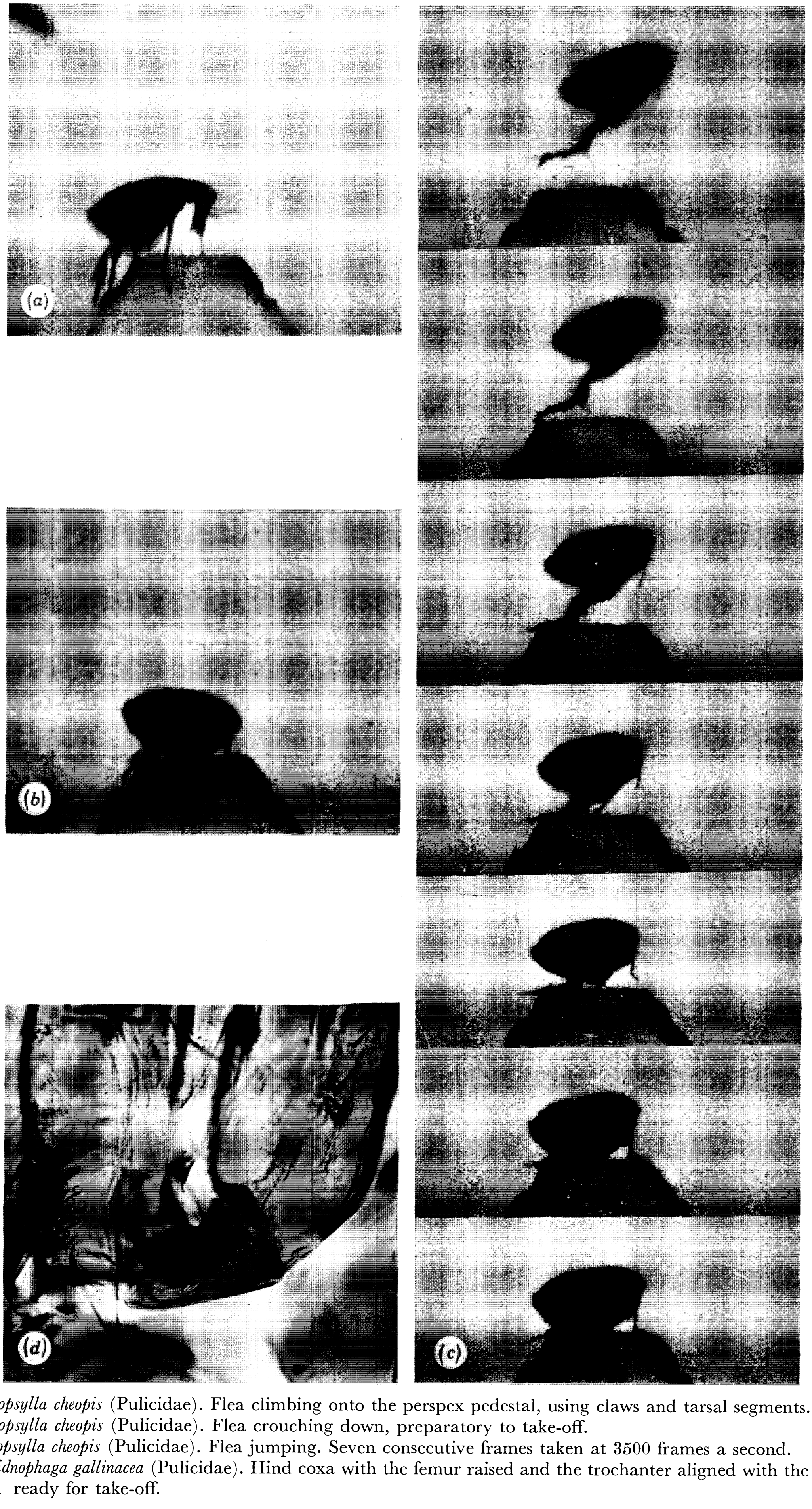
The apparatus for counting the number of jumps executed by fleas confined in a receptacle consisted of a glass tube with a very thin, tightly stretched membrane at the bottom. This membrane was placed in an insulated cavity directly over a microphone. The output of the microphone was fed into an electronic circuit which could detect peaks in the input signal. Each time a peak was detected, the circuit produced a signal which triggered a mechanical counter. As the flea jumped from the taut membrane (similar to a drumhead) it made a sharp sound which was picked up by the microphone and counted. The level of peaks counted by the circuit was variable so that it was possible to differentiate between the rather loud take-off sounds and the slightly softer sounds of their landing and the much softer sounds of walking, falling, etc.

Mechanism of the jump

(*a*) *Photographic evidence*

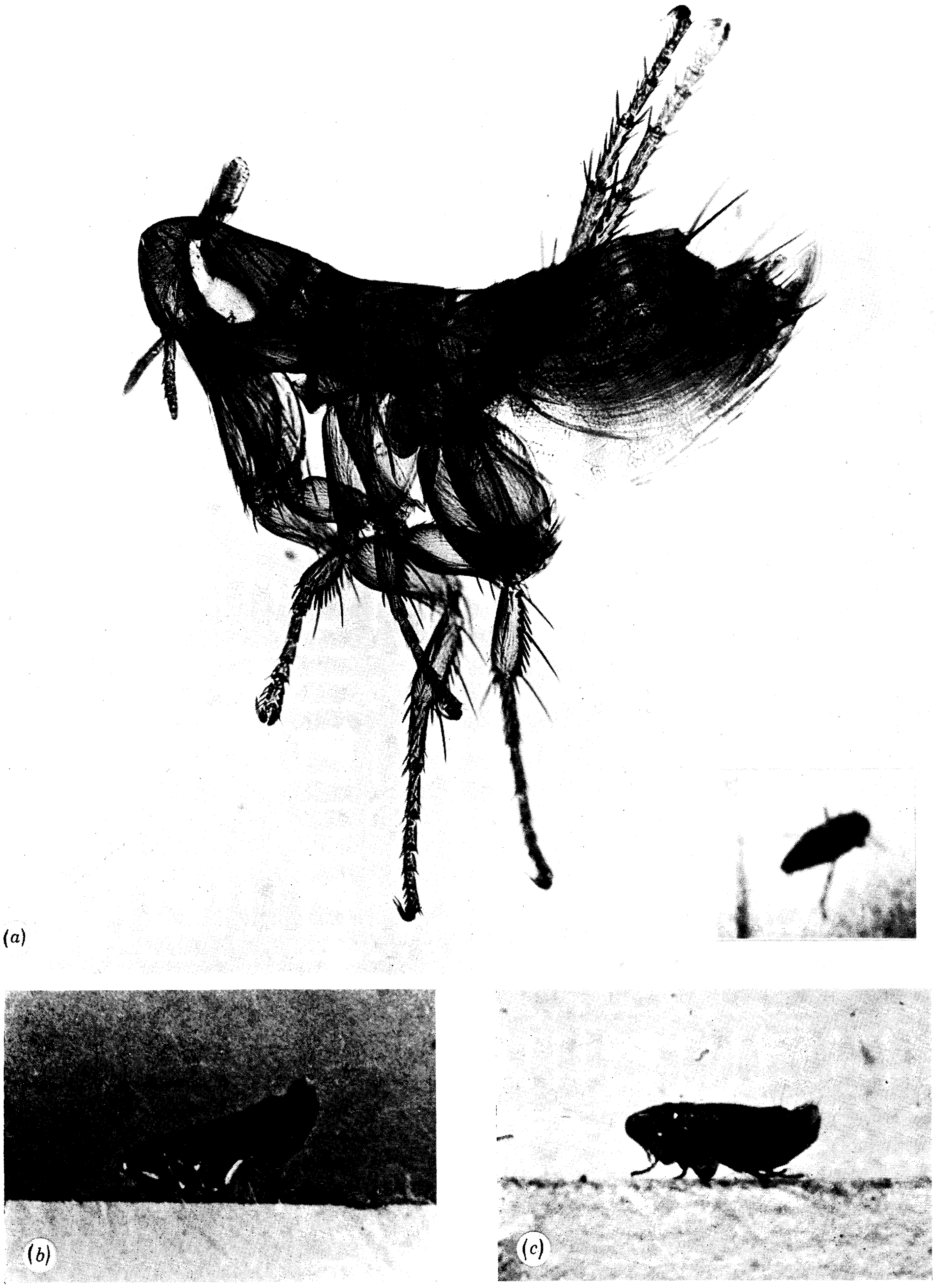
The photographic sequence confirms that fleas do not jump off the tarsi of the hind legs but their trochanters (plate 39*c*, figure 1). Owing to the shape of the platform from which the fleas jumped, the legs below the trochanter could be seen trailing over the edge of the flat top (plate 39*c*; figure 1), and therefore left no doubt about the function of the trochanter in the execution of the jump. The role of the middle leg is not so clear. When fleas are forced to jump into fixatives the middle leg (not the hind leg only) is frequently found to be turned upwards from the trochanter, suggesting that this latter portion of the leg was used for take-off, and the photographic evidence indicates this, but is not clear enough to be conclusive. However the angle at which fleas sometimes leave the ground, clearly seen in the B.B.C. sequence, suggests that they prop themselves up on their fore- and mid-legs, tripod fashion, and it seems probable that in this case the mid-tarsi as well as the fore-tarsi, are resting on the ground in the more conventional manner.

Since the acceleration of the flea is directly proportional to the force it exerts, the calculated acceleration is of particular interest. It should be noted that the differencing of discrete measurements involves fundamental uncertainties, particularly at the beginning and end of the jump when the acceleration shown in figure 3*c* is the straightforwardly calculated value which

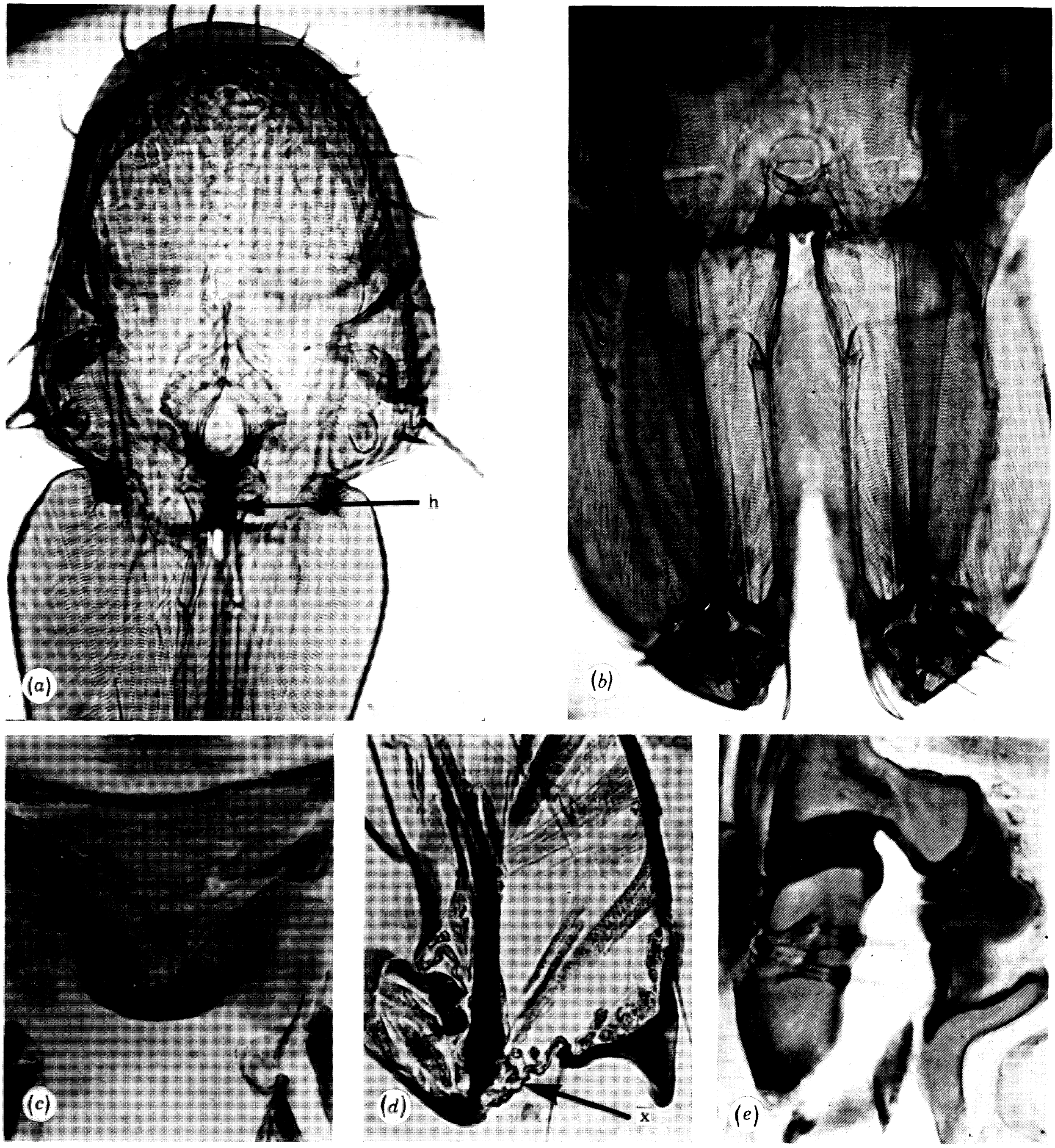


(*a*) *Xenopsylla cheopis* (Pulicidae). Flea climbing onto the perspex pedestal, using claws and tarsal segments.
(*b*) *Xenopsylla cheopis* (Pulicidae). Flea crouching down, preparatory to take-off.
(*c*) *Xenopsylla cheopis* (Pulicidae). Flea jumping. Seven consecutive frames taken at 3500 frames a second.
(*d*) *Echidnophaga gallinacea* (Pulicidae). Hind coxa with the femur raised and the trochanter aligned with the substratum ready for take-off.

(Photographs (*a*, *b* and *c*) by K. Parker; (*d*) by Miriam Rothschild.)

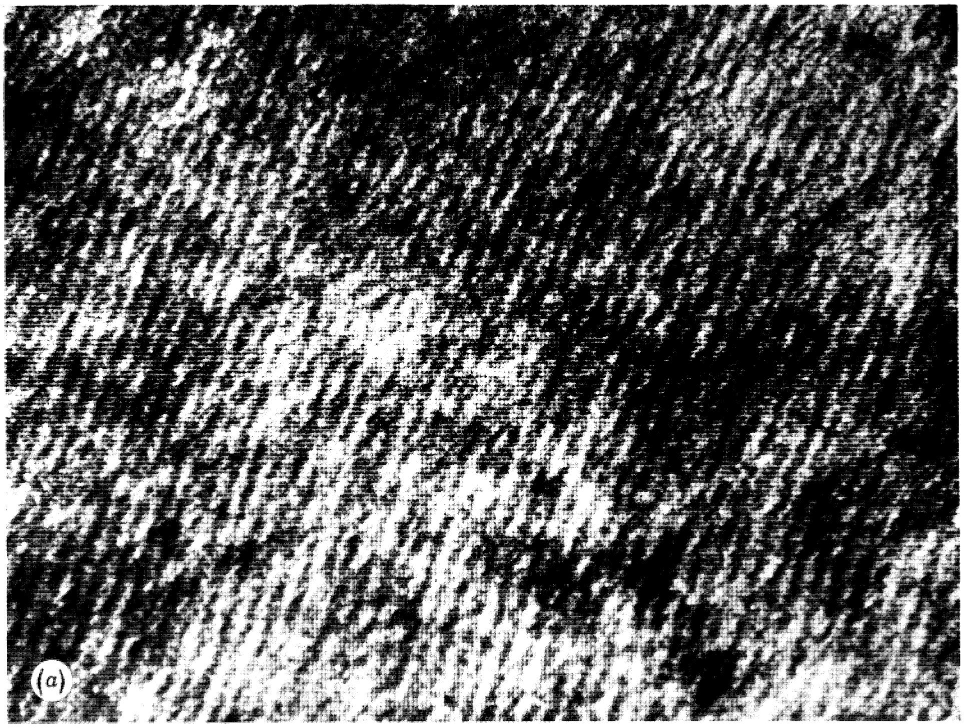


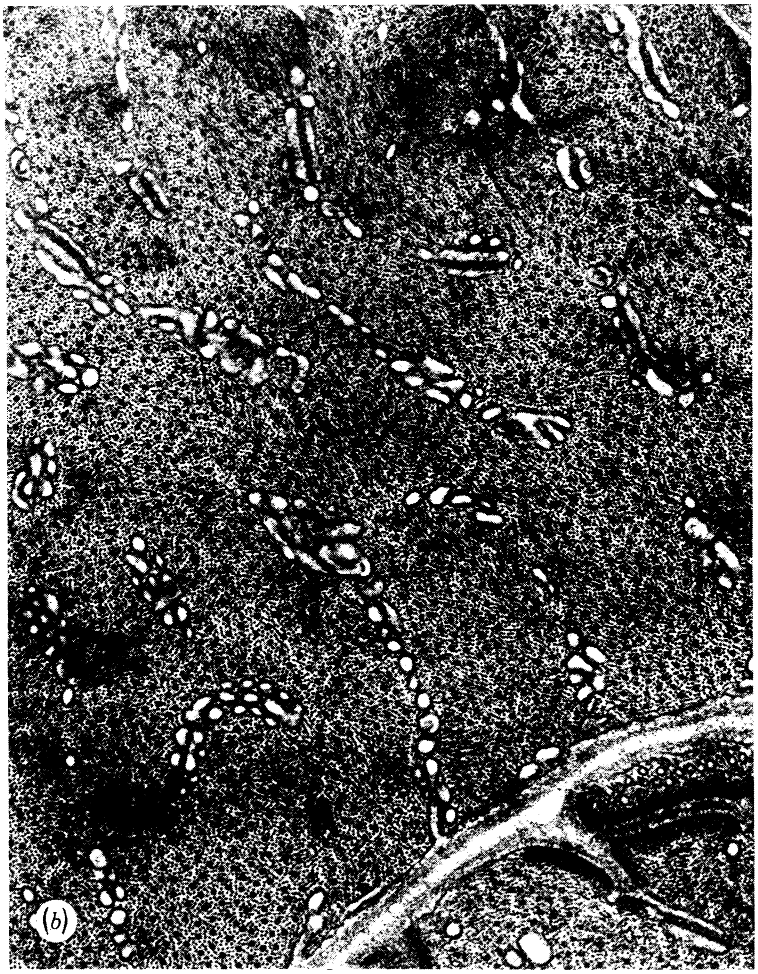
(*a*) *Leptopsylla segnis* (Leptopsyllidae) Flea which jumped into a fixative and remained with both hind legs elevated and the claws facing forwards. The antennae are frequently raised out of their grooves when the flea jumps. (Photograph by G. Bradbury.) *Inset: Nosopsyllus fasciatus* (Ceratophyllidae). The flea is descending after a jump; the legs are spread widely at this stage. (The flea triggered the camera by interrupting a beam of light during the jump.) (Photograph by RAF Experimental Station, Farnborough.)
(*b*) A Ceratophyllid bird flea at rest with the first and second pair of legs elevated and the trochanters aligned close to the substratum. (Photograph by C. Porter.)
(*c*) A Ceratophyllid bird flea at rest with the legs in a normal position. Even in this attitude the hind trochanter is touching, or nearly touching, the substratum. (Photograph by C. Porter.)



(*a*) *Xenopsylla cheopis* (Pulicidae). Transverse section through the thorax in the region of the 2nd thoracic link-plate to show the hook of the click mechanism *in situ*.
(*b*) *Xenopsylla cheopis* (Pulicidae). Transverse section through the metathorax and metacoxa with the femurs raised to show the 'lines of force' between the pleural arch and trochanter. The tendon of the trochanteral depressor is seen as a faint line between the coxal ridges.
(*c*) *Xenopsylla cheopis* (Pulicidae). Transverse section of the thorax showing the membranous socket of the median hook of the click mechanism. Note the two sensilla on either side of the socket.
(*d*) *Echidnophaga gallinacea* (Pulicidae). Parasagittal section (stained) of the distal end of the metacoxa with the trochanter raised. The coxal membrane is partly extended and the internal knob of the hook is pressing against the tendon of the trochanteral depressor.
(*e*) *Spilopsyllus cuniculi* (Pulicidae). Parasagittal section through the lateral metanotal area showing the sensory setae lying immediately outside the point of insertion of the 2nd thoracic link-plate and the abrupt interpolation of arthrodial membrane in the heavily sclerotized ridges. This permits the rotation of the link-plates.

(Photographs by Miriam Rothschild.)





(*a*) *Xenopsylla cheopis* (Pulicidae). Pleural arch showing region with chitin microfibrils embedded in a resilin matrix. Electron micrograph (magn. × 350000).
(*b*) *Xenopsylla cheopis* (Pulicidae). Transverse section through the epipleural muscles (original magn. × 30000).
(Photographs by C. Neville and B. Luke.)

represents the lowest possible value. It may very well underestimate the actual initial value of acceleration for that jump.

Looking at figure 3*c*, the calculated acceleration at the first frame of the jump sequence is 60*g* (60 times the acceleration of gravity). As mentioned, this represents the lowest bound; the actual acceleration at this frame could be much higher. From the second frame, where the calculated acceleration is free from uncertainty, to the fifth frame, the last frame at which the flea is in contact with the jumping platform, the acceleration increases. The peak value is 140*g*, which, assuming the mass of the flea to be 0.2 mg*, corresponds to a maximum force of 28 dyn.

TABLE 1. JUMPING ACTIVITY OF *XENOPSYLLA CHEOPIS* ON FIRST DAY OF EMERGENCE† (50–60 % R.H.)

(Monitored with automatic meter.)

	unfed fleas							
	30 °C (5 trials)		20 °C		30 °C		40 °C	
number of specimens tested and temperature ...	10♂	10♀	single ♀	10 ♀♀	single ♀	10 ♀♀	single ♀	10 ♀♀
number of jumps during first 30 min	1710.0	2076.2	9.4	641.4	99.3	1435.4	156.0	2435.4
average number of jumps per 30 min period	1414.7	1212.8	1.62	497.1	29.5	1106.0	32.4‡	1176.9‡
duration of experiment/h	2½	2½	4	4	4	4	4	4
total number of jumps	7073.5	6064.0	12.9	3976.8	236.0	8848.0	259.2	9415.2

	in container stirred every 30 min				fleas (10 ♀♀) fed for 30 min			
	experimental 30 °C		control 30 °C		30 °C		fed through membrane, 30 °C	
number of specimens tested and temperature ...	single ♀	10 ♀♀	single ♀	10 ♀♀	on rat	unfed	whole blood	unfed
number of jumps during first 30 min	75.2	1348.8	99.3	1239.2	1716.2	1435.4	847.6	1093.0
average number of jumps per 30 min period	45.0	755.2	29.5	669.4	1351.8	1106.0	616.9	848.2
duration of experiment/h	4	4	4	4	4	4	2½	2½
total number of jumps	306.0	6041.6	236.0	5355.2	10814.4	8848.0	3084.5	4241.0

† Jumps decline sharply on the second day when tested continuously.
‡ Fleas inactive at the end of experiment.

(*b*) *Temperature and jumping activity*

Single unfed freshly emerged fleas of either sex, and groups of ten female fleas, were enclosed in 1 in glass tubes and the number of jumps executed were counted by means of the automatic meter (p. 502). Counts were made at 30 min intervals for 2½ and 4 h, and an average of five repetitions of each experiment were recorded (table 1). Comparisons were made between ten males and females at 30 °C and single females and ten females at 20, 30 and 40 °C, and also between fed and unfed fleas.

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* Average mass of 50 unfed males 0.20 mg; 50 fed males 0.24 mg; 50 unfed females 0.30 mg; 50 fed females 0.36 mg.

The following results should be noted:

(1) unfed male fleas executed a total of about 100 more jumps each in a 2½ h period than female fleas, but were less active during the initial 30 min period;

(2) solitary fleas were considerably less active than fleas confined in groups of ten;

(3) the fleas were more active at 40 °C than at 30 °C, and more active at 30 °C than at 20 °C;

(4) maximum activity, i.e. approx. 250 jumps (at 40 °C) in 30 min was recorded in freshly emerged unfed females;

(5) feeding on the rat, activity was greater than in unfed fleas, but fell by 50 % when the fleas were fed on whole blood via a membrane;

(6) additional mechanical disturbance (stirring the container) slightly increased jumping activity over a 4 h period.

In previous experiments, using the automatic meter, we extended these recordings for 3 days. Activity dropped considerably during the second day, but vigorous jumping continued up to the third day, even in unfed fleas.

TABLE 2. LENGTH (mm) OF 50 CONSECUTIVE JUMPS (AT 15 °C) OF FED MALE AND FEMALE FLEAS AND LANDING PERFORMANCE

species		max. jump	min. jump	mean	landing facing point of departure (100 jumps) (%)	landing on feet (♂♂) (100 jumps) (%)
Spilopsyllus cuniculi						
European rabbit flea	♀	184	53	112	26	—
	♂	199	21	65	14	—
Nosopsyllus fasciatus						
European rat flea	♀	98	33	73	24	78
	♂	109	19	55	22	
Xenopsylla cheopis						
Oriental rat flea	♀‡	147	71	114	14	64
	♂	230	54	101	22	
Ceratophyllus styx						
Sand Martin flea (both sexes)		200	60	125	—	—
Echidnophaga gallinacea‡						
hen stick-tight flea (both sexes)		130	93	116	—	—
Isochopsyllus octactenus§						
bat flea (both sexes)		66	5	26	—	—

† The mean mass of 15 specimens was 210 μg.

‡ *E. gallinacea* is a much smaller species than any of the others tested, measuring about 0.8 mm on eclosion compared with approximately 3 mm in the case of *C. styx* or *N. fasciatus*.

§ This species lacks a true pleural arch, but some resilin is present in the structure, and is seen clearly in serial sections. These fleas were harassed to encourage them to jump.

If 100 unfed *X. cheopis* are confined in a glass tank which is lit from one end by a 60 W electric light, the fleas move across to the shady side of the receptacle by walking, running and intermittent jumping. If a glue-coated lid is placed at a height of 7.6 cm (3 in), no jumping fleas get caught at 10 °C (50 °F), but at 27 °C (80 °F) they are much more active and 32 % are found sticking to the surface. If single fleas are used in this experiment the glass has to be tapped to keep them moving. This suggests that muscle power (rather than resilin power) is responsible for the increased jumping performance at raised temperatures. Fleas rarely move towards the shade in a straight line. Other species than *X. cheopis*, which also move away from a bright source of light, follow subtly different dispersal patterns, some scattering much more widely and erratically than others, even if released from the same point. Certain species of fleas change their response to light and shadow after feeding. Males on the whole can execute larger jumps, but the average distance covered is less than that of the females. The latter, probably because of their heavier abdomens, have a somewhat less efficient landing performance, and more often land facing the 'wrong' way, i.e. the direction from which they came (tables 2 and 3). In these circumstances they then orientate themselves by shuffling round, and after a brief pause jump off towards the shade.

TABLE 3. LANDING PERFORMANCE

	X. cheopis		*N. fasciatus*
100 jumps	♂	♀	♂
landing on feet	64	52	78
landing on head	6	4	0
landing on side	24	30	17
landing on back	6	14	5

TABLE 4. *XENOPSYLLA CHEOPIS*: JUMPING PERFORMANCE WITH AMPUTATED LEGS

(Duration of experiment 1 h.)

	amputation†							
	of whole legs				of tarsi only			
10 ♀♀	foreleg	midleg	hindleg	control	foreleg	midleg	hindleg	control
number of jumps in first 30 min	581.8	55.4	3.6	1697.8	1426.2	943.2	1020.6	1679.6
average of total 30 min jumping	486.1	36.1	1.8	1574.4	1407.2	968.1	1029.4	1663.1
duration of experiment/h	1	1	1	1	1	1	1	1
average number of deaths at end of experiment	2.8/10	9/10	9.8/10	0/10	0/10	0/10	0/10	0/10
total jumps	972.2	72.2	3.6	3148.8	2814.4	1936.2	2058.8	3326.2

† This includes part of the tibia.

(*c*) *Amputation experiments*

Fleas can still jump if the fore legs, or middle legs or hind legs are removed (table 4), but few survive the amputation of the hind legs for more than 1 h. Without the third pair of legs, fleas only jump feebly and about three or four times during the 60 min experimental period. Amputation of the fore legs, understandably, has less effect than either the removal of the mid and hind legs. The morphology of the mesothorax and the mesocoxa, especially the trochanteral depressor muscle, leaves no doubt that they play a part in jumping, but since they lack both resilin and the cuticular lines of force, it is evident that their ability in this direction is limited. The removal of the tarsi has naturally less effect on activity than the removal of the whole leg, but it is interesting that amputation of the mid tarsi reduces the number of jumps more drastically than that of the hind tarsi. This rather supports the idea that the middle leg is important for stabilizing and supporting the body for take-off, and without it the flea has difficulty in balancing itself during the preparatory phase, and is less inclined to jump.

It is worth noting that in the case of the Muscoid fly *Calliphora vicina* Robineau-Desvoidy the mesothoracic (not the metathoracic) legs provide the major thrust for the jump which occurs at the beginning of flight (Mulloney 1969). If these are amputated the flies can still jump, although not as well as those missing the metathoracic legs. Understandably the performance of amputees is less effective than that of intact flies. In the Scorpion fly *Panorpa* (Hasken 1939) both meta- and mesothoracic legs take part in the thrust at take-off.

Both the rabbit flea (*S. cuniculi*) and rat flea (*Nosopsyllus fasciatus* (Bosc)) can survive in a domestic refrigerator for several weeks in a glass tube, with the temperature fluctuating around freezing point. They can be rattled like tiny pebbles in the receptacle, but if it is warmed in the palm of the hand for a few moments and they thaw out, they immediately begin jumping about. *X. cheopis*, which is a flea adapted to high temperatures, does not survive freezing.

(*d*) *How fleas jump*

In the absence of neurophysiological evidence, discussion on how fleas jump must remain to some extent hypothetical. We now suggest that the following series of events occur.

(i) *Preparation*

(1) A flea crouches down, lowering the head towards the substratum, arching the back and contracting the body (plate 39*b*).

(2) The femur is raised by contraction of the levator of the trochanter, thus bringing the trochanter and femur of the third leg into contact with the substratum (plate 39*b*, *c*; figure 1). This movement, possibly assisted by the contraction of other muscles, moves the trochanteral 'hooks' into their sockets and establishes the hinge line for the subsequent jump (figure 4*b*, line of force). The levation of the femur pulls the tendon of the trochanteral depressor muscle into the heel of the trochanter (figure 4*b*) and the distal portion of the apodeme is held taut between the internal clamp of the trochanteral 'hook' and the stretched muscle fibres of 32d (plate 41*b*, *d*; figure 6). The expanded proximal portion of the apodeme is wedged into the funnel-shaped socket in the upper edge of the coxa (figures 4*b*, 6*a*); the apodeme of the trochanteral depressor muscle is thus preloaded.

(3) Contraction of the longitudinal and oblique muscles of the thorax rotate the link-plates and align the pro- meso- and meta-nota (figures 4*a*, *b*); contraction of the ventral longitudinal muscles engages the medial or thoracic hook (plate 41*a*, h; figures 4*a*, *b*) of the click mechanism and various other catches, thus stiffening the thorax and pressing the coxa against the abdominal sternum (Rothschild & Schlein 1975, this volume p. 476).

(4) Contraction of the epipleural muscles compresses the resilin within the pleural arch and aligns the pleural ridge with the ridge on the coxa (plate 41*b*; figures 4*a*, *b* 'line of force'). It is possible (as we suggested previously (Rothschild, Schlein, Parker & Sternberg 1972)) that once the medial thoracic hook is engaged, the muscles responsible for the compression of the resilin can relax, leaving it compressed within the pleural arch.

(ii) *Take-off*

(5) Levator and longitudinal muscles relax, thus removing any restraint on the descent of the femur.

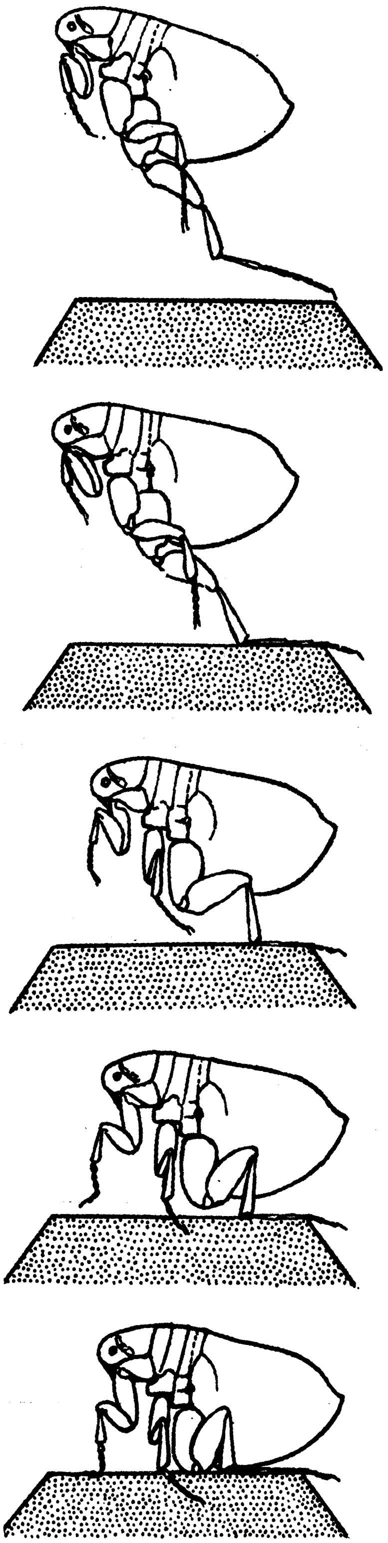

FIGURE 1. *Xenopsylla cheopis*. Outline drawing of the ciné film sequence of frames 2–6, showing take-off.

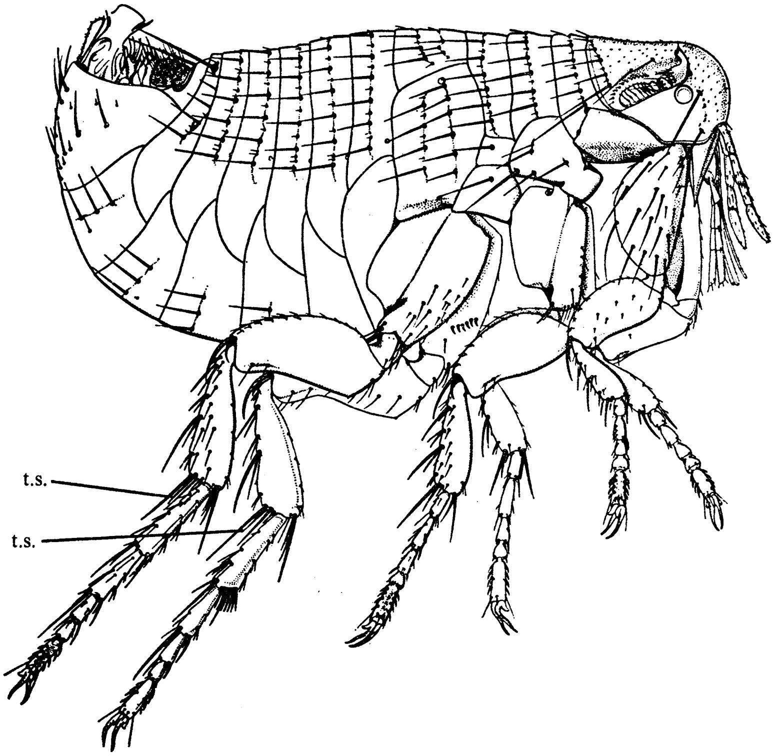

FIGURE 2. *Xenopsylla cheopis.* Outline drawing to show the powerful tibial spines (t.s) which assist in take-off, and the flat jumping surface of the trochanter, and the adjoining portion of the femur (Karl Jordan).

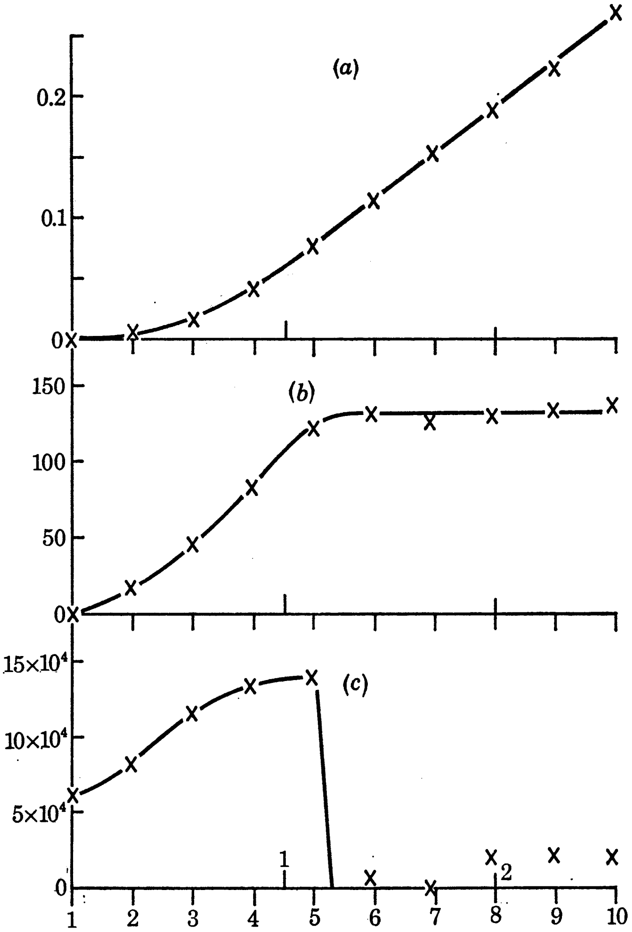

FIGURE 3. *Xenopsylla cheopis.* Position, velocity and acceleration measured from ciné film of a flea jumping (plate 39) (framing rate, 3500 frames per second). (*a*) Vertical position measured relative to jumping platform; data points refer to the individual frames; (*b*) vertical velocity calculated from measured position; points represent averaged instantaneous velocity; (*c*) vertical acceleration calculated from averaged velocity. Note that the solid line indicates that the acceleration can vary discontinuously as contact with the platform is broken.

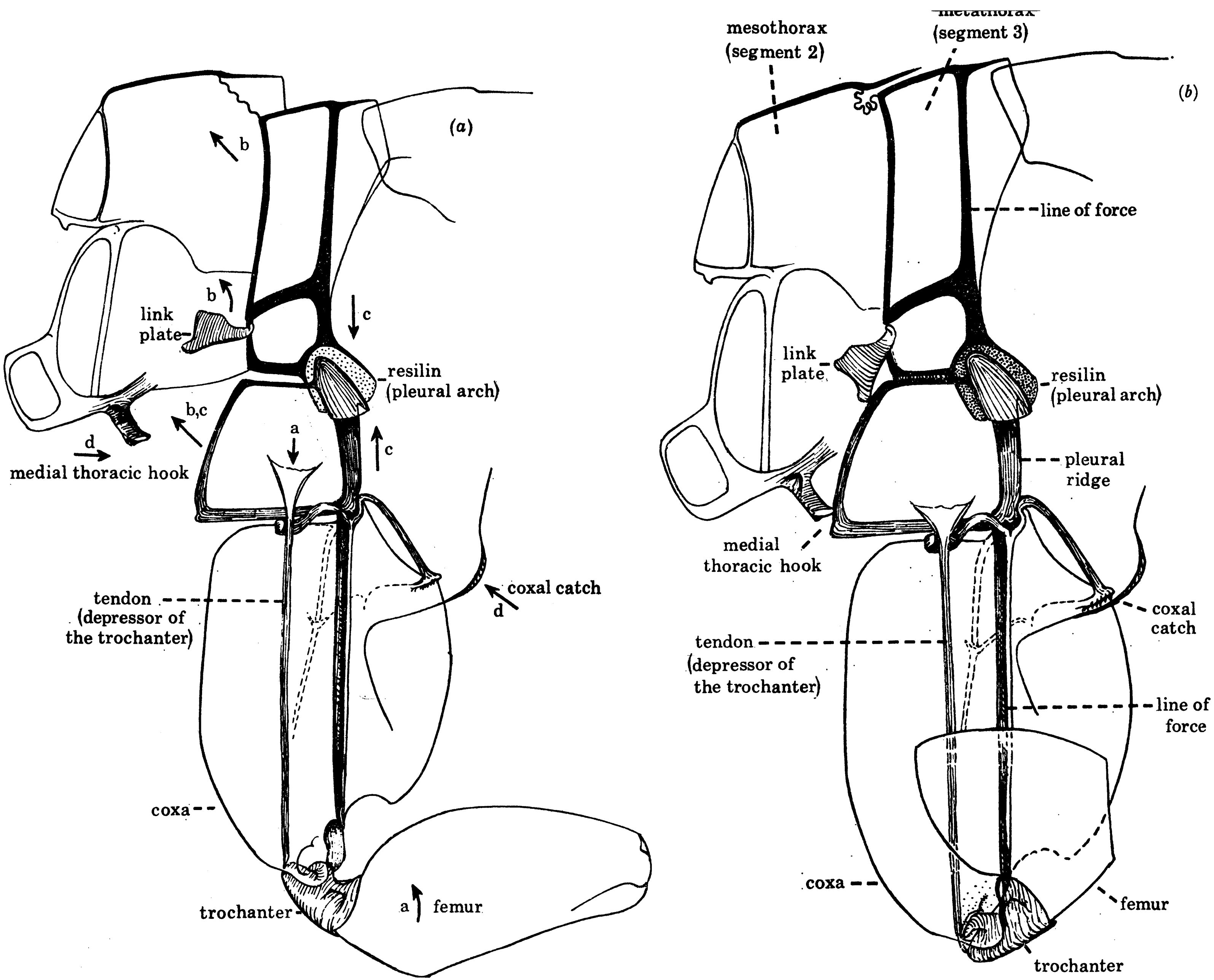

Figure 4. *Xenopsylla cheopis*. (*a*) Diagram to show, from the lateral aspect, the position of the cuticular ridges, link-plates, clamps and other stiffening devices in the relaxed position. (*b*) The same diagram as figure 4*a*, only with the femur raised ready to jump. The link-plate has been rotated upwards, thus aligning the meso- and metathoracic segments; the thoracic hook-like peg is partly engaged in the metepisternal sinus; the ridges of the coxal abdominal clamp are approximated, and the tendon of the depressor is pulled down into the heel of the trochanter.

(6) The jump is initiated by a rapid twitch of the trochanteral depressor muscle. Because the pull through the apodeme of this muscle is nearly in line with the coxal trochanteral hinge, the contraction is initially isometric and serves merely to increase the existing tension in the apodeme.

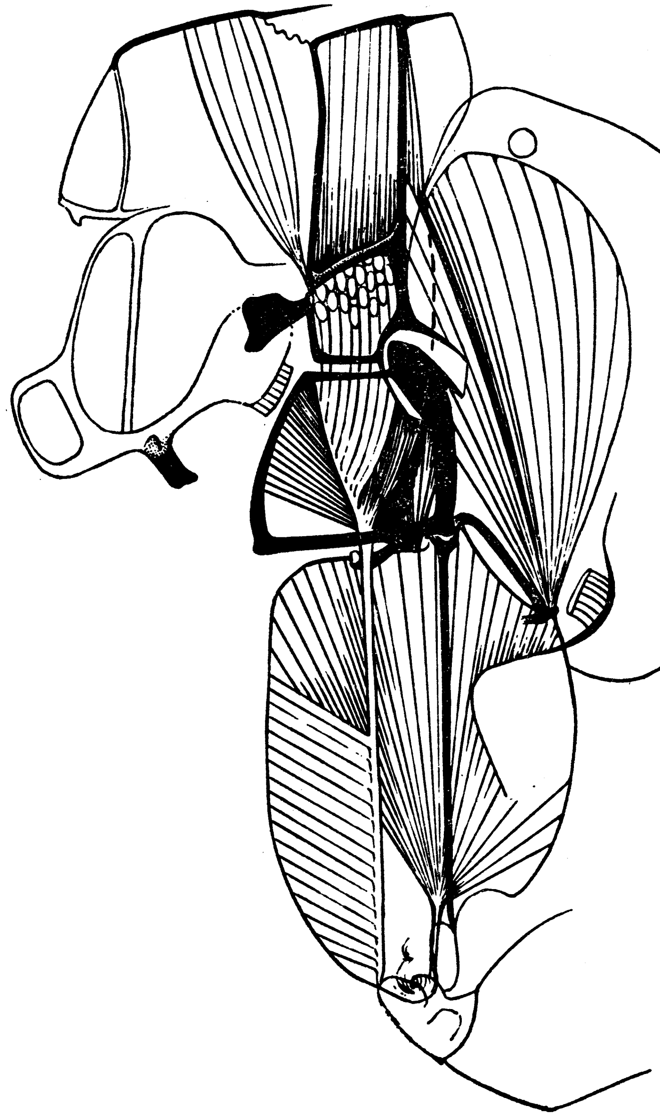

Figure 5. The same as figure 4, showing the trochanteral depressor muscle, the levator of the trochanter and the epipleurals.

(7) As the twitch tension rises, depression of the central region of the notum expands the thorax laterally sufficiently to disengage the medial hook. Once this happens the elastic energy stored in the resilin pad is released and moves the aligned pleural and coxal ridges (lines of force, figure 4*b*) downwards relative to the notum, adding its energy to that produced by the trochanteral depressor muscle. The trochanter is thus pressed against the substratum.

(8) Rotation of the trochanter and femur increases the leverage of the depressor apodeme, and the elastic energy stored in both the resilin pad and the depressor apodeme is fed into the jump, producing an increasing acceleration.

(9) As the leg straightens, the trochanter and femur leave the ground and the remaining force is exerted through the tibia assisted by the powerful tibial spines (figure 2).

The dense sarcoplasmic reticulum of the trochanteral depressor muscle† (Cullen 1975) suggests that this muscle is capable of producing a very rapid twitch. Species of flea which have secondarily lost the pleural arch and lack resilin can still jump, though more feebly than *Xenopsylla*. In these insects, as in flies (Nachtigall & Wilson 1967), the jump results from a rapid twitch of the trochanteral depressor muscle. In *Xenopsylla* the preliminary compression of the resilin in the pleural arch, and the preloading of the depressor apodeme by the engaging of its proximal portion in the coxal socket, add further energy which is not derived from the trochanteral depressor muscle. A mechanism of this sort, where energy from three different sources has to be released simultaneously within fractions of a millisecond, requires to be triggered by a single mechanism. It is suggested that this is brought about by the release of the medial hook.

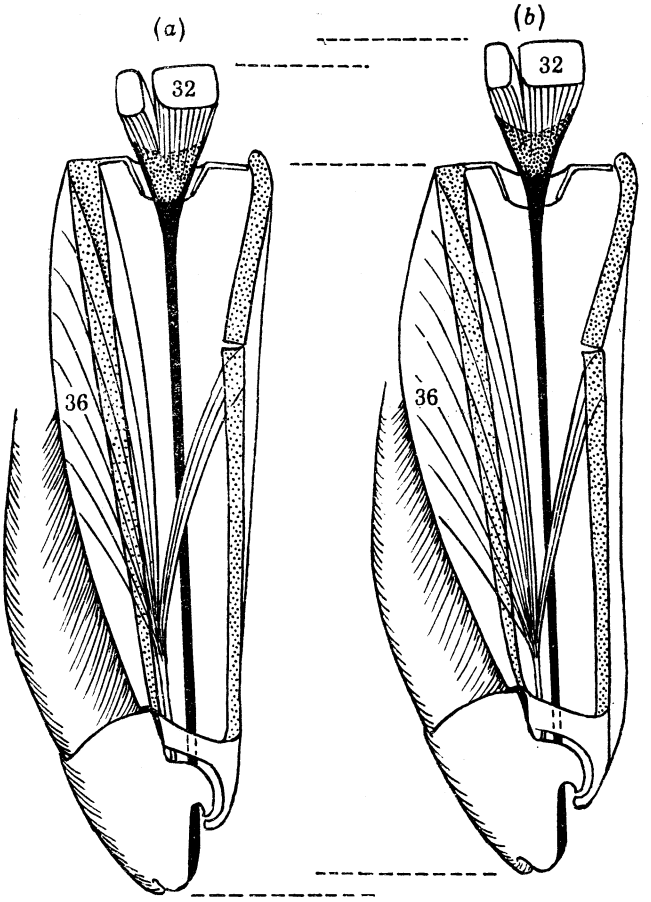

FIGURE 6. *Xenopsylla cheopis*. Diagrams showing (*a*) the position of the trochanteral depressor (32) when the femur is raised; (*b*) the distortion of the coxa when the levator and the trochanteral depressor are fully contracted. The tendon is pulled out of the socket.

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† Only one e.m. photograph of a transverse section (plate 42*b*) of the epipleural muscles is available. This suggests that the sarcoplasmic reticulum is also dense, but not so dense as that of the trochanteral depressor. Clearly no definite opinion can be formed from a single photograph.

The muscles involved in providing energy for the jump thus form two rather distinct systems. The trochanteral depressor muscle lies nearer the centre of the flea's body and is primarily responsible for the take-off. The epipleural muscles (modified flight muscles) lie near the outside of the body and are primarily responsible for compression of the resilin of the pleural arch. Their contraction also maintains alignment between the coxa, pleural and notal ridges. The epipleural muscles and the trochanteral levator muscles which preload the depressor apodeme must contract before take-off, whereas the trochanteral depressor muscle both supplies its own energy to the jump and triggers the whole process by releasing the catch of the medial link.

The release of elastic energy from the pleural arch increases the energy of the jump, but this mechanism is not a replacement for the usual method of take-off which basically resembles the take-off of muscid flies and scorpion flies. It is essentially a system by which the force normally used in moving the wings is fed back rapidly into the legs. In view of the acceleration now developed during the jump the long narrow tarsi could not support the strain and the initial take-off occurs by contact of the trochanter and femur with the ground. The presence of ventral femoral sensilla throughout the order suggests this habit is characteristic of all fleas, not only the good jumpers.

Discussion

A jumping mode of progression which can also function as an escape mechanism is found in several orders of insects apart from the fleas (Siphonaptera). The most familiar examples of these are locusts and grasshoppers (Orthoptera), click beetles and flea beetles (Coleoptera), leaf hoppers (Homoptera) and the moss flies (Mecoptera). There are many Diptera (flies) and Hymenoptera (wasps, etc.) which can also execute small jumps, and many flying insects initiate take-off by first leaping into the air. It has been shown that when their wings are removed such insects can still jump about (Hasken 1939; Nachtingall & Wilson 1967).

In grasshoppers the coxa are relatively tiny and the femur is greatly enlarged. As in fleas the trochanter is rigidly fixed to the latter joint. Before the jump the tarsus rests on the ground and the leg is bent sharply at the trochanteral tibial articulation, so that tibia and femur are almost parallel in position. The jump is the result of straightening the leg, and at the final moment of take-off the various joints are aligned and the leg almost vertical. Presumably

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Description of plate 43

(*a*) *Schistocerca gregaria* (Acrididae). Late 4th instar nymph. Wing hinge ligament: parasagittal section through the thorax showing the secretion of resilin in progress in the wing hinge ligament.

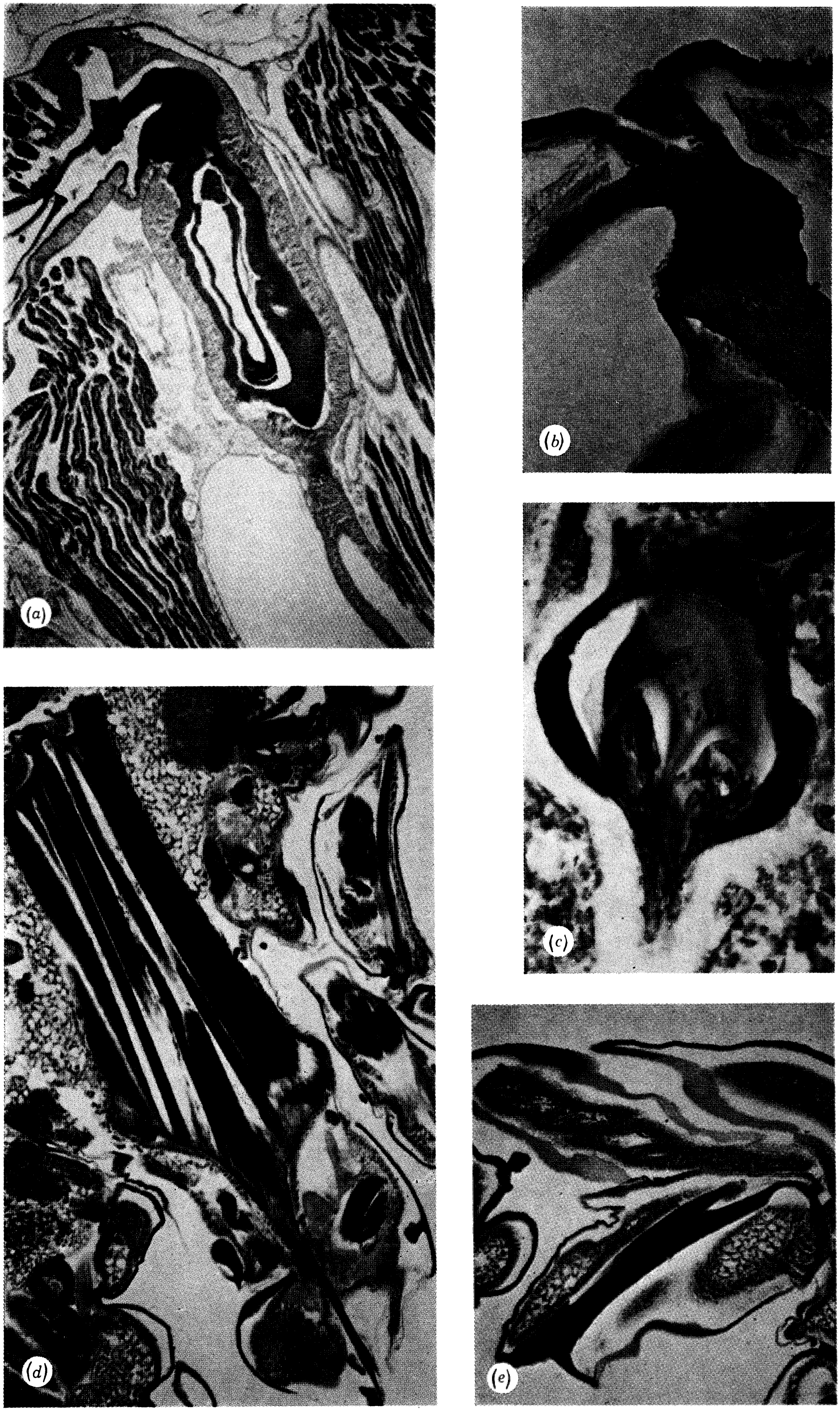
(*b*) *Boreus hiemalis* (Boreidae). Adult ♂. Wing hinge ligament: parasagittal section through the base of the degenerate wings, showing resilin in the wing hinge (staining red) enveloped in blue-staining epicuticle.

(*c*) *Spilopsyllus cuniculi* (Pulicidae). Pharate adult. Parasagittal section showing resilin in the developing pleural arch. In serial sections stained with toluidine blue and light green, resilin colours turquoise blue and cuticle light green. At this stage the cuticular lining of the pleural arch cavity has not been secreted, but some cuticle is present at the point where the pleural ridge meets the pleural arch.

(*d*) *Javesella dubia* (Delphacidae). Nymphal stage. Trochanteral depressor muscle and tendon. Parasagittal section through the metathorax and metacoxa, showing the origin of fibres along the cuticular in-folding and the attachment of the tendon in the trochanter.

(*e*) *Javesella dubia* (Delphacidae). Nymphal stage. Parasagittal section showing the infolding sclerite of the metathorax (= 'Unsprungeplatte') which probably contains resilin. Active secretion of the cuticle is in progress.

(Photographs by Miriam Rothschild.)


(a)
(b)
(c)
(d)
(e)

nearly all the work in jumping is done by the extensor muscle of the trochanter, which is the largest of the leg muscles (Brown 1963), and said to exhibit half the tensile strength of steel. If the leg is restrained during contraction of these muscles the apodemes are snapped. At the apex of its jump the locust frequently begins to fly forward, but at other times merely spreads its wings and parachutes down, thus improving landing. Resilin is present in the wing hinge ligament (plate 43*a*). Like the flea, it spins and somersaults in the air, if the take-off surface is uneven. Despite the help of its wings it sometimes pitches on its head and back (Hoyle 1958; Brown 1963).

The click beetle (*Melanotus communis* (Gryll)) apparently uses its remarkable jumping powers as an escape mechanism rather than a mode of progression, and its legs and leg muscles appear to play no part in take-off or landing. Prior to jumping it lies on its back, arches its body and jack-knives itself vertically into the air by suddenly flattening out. A resilin energy store (Sanassi 1969) and a click mechanism (Evans 1972) are combined to effect this jump. It lands, near the point of departure, on the back, head or sides. Evans (1973) noted the high acceleration inflicted upon the brain during the first part of the jump of *Athous haemorrhoidalis* (Fab.) when the head and prothorax were 'bouncing' on the hind body; peak acceleration was estimated during the initial jump at approximately 2300*g*.

Leaf hoppers (Homopterans) are also spectacular jumpers. Although this was not suggested by Weber (1929), Pesson (1951) or Sander (1957) who described the jumping muscles of various Homopterans, the Aleuroids, like fleas, probably take off from the trochanter, not the tarsi. In their case the tergotrochanteral depressor tendon is inserted in the proximal corner of the metacoxa, which would greatly facilitate such a take-off. An extremely interesting modification is found in certain Fulgoroidea and Psylloidea, where the jumping muscle originates along a massive infolding of the furca of the sternum or pleurum, actually extending up into the dorsum (plate 43*d*, *e*). Examination of serial sections of nymphs of *Javesella dubia* Kirsch (Delphacidae) by polarized light suggests (but does not prove) that resilin is present in this sclerite (= Unsprungsplatte (Sander 1957)). A much more conventional arrangement, when the main branch of the tergotrochanteral muscle originates along the dorsum, is found in the Cicadas. The variation seen within this order emphasizes the remarkable uniformity of the Siphonapteran saltatorial musculature.

The jump of *Boreus* has not yet been studied. The presence of resilin in the wing hinge ligament (plate 43*b*) of the reduced and non-functional wings of this species, raises some interesting queries. Would such a relatively large lump of resilin have survived in this situation if it performed no special function? Is the fact that *Boreus* – popularly known as the snow flea – is active in winter at low temperatures, significant in this connexion? However the enormously elongated femur and long tibia in this genus and the morphology of the trochanter, suggests that the jump is executed in the manner reminiscent of the grasshopper rather than the flea. It is worth noting that the tendon of the trochanteral depressor in both meso- and metacoxa of *Boreus* is more sclerotized and therefore presumably more rigid than in the fleas. In an interesting paper on the thorax of another Mecopteran *Panorpa communis* L. (Hasken 1939, p. 328) the author remarks that the insect's take-off resembles a jump off and that if the wings are removed this jumping movement becomes even more marked. The tibial spurs, as in fleas, are used to assist take-off. The trochanteral depressor tendon, and the muscles inserting on it, are described as very powerful.

As we have suggested (p. 487, present volume) the Mecopteran-like ancestors of fleas may well have been preadapted to a parasitic mode of life by a tendency to lose their wings. Fleas, however, seem to be the only known example of winged insects which have developed a saltatorial mode of progression by incorporating their flight mechanisms into the jumping mechanism. This appears to have been achieved by turning the force used for moving the wings (elevation by the trochanteral depressor as well as forward movement by the indirect flight muscles) and the released elastic energy, back into the sclerotized ridges, and thus into boosting take-off. The most important evolutionary modification which made the change possible would appear to be the lateral compression of the flea's body which at the same time facilitated rapid passage through the pelt of the host and thereby altered the position of the pleural arch from the dorsal to a lateral situation.

Certainly in fleas their jumping ability constitutes a highly successful method of active host finding (see Rothschild & Schlein 1975, p. 486). Ioff (1950) for example has described the life-cycle of *Vermipsylla alakurt* Schimkewitsch, which emerges from the pupa on high arctic meadow lands at the onset of cold weather, and jumps from the freezing soil onto passing ungulates. As many as 7000 specimens have been recorded from a single sheep. Bates (1962) describes *Ceratophyllus styx* jumping onto model birds 'hovering' in front of the cliff face, after emerging from the empty nesting burrows of their hosts. Such conditions emphasize the fact that resilin is less temperature-dependent than muscle, and must be of considerable adaptive value for an insect which passes frequently from the cold ground to the warm-blooded host.

We are especially grateful to Professor John Pringle, F.R.S. for his sustained interest and help with the problem of the flea's jump, and for his many ingenious and intuitive suggestions on the mechanisms involved. We would also like to acknowledge the help of Dr Roger Abbott who discussed the problem with us on numerous occasions, and at considerable length. Mr Bob Ford bred the fleas we used, and helped with various experiments involving living material. We would like to thank Professor George Varley for specimens of *Javesella dubia* and Professor George Dunnet for the *Ceratophyllus rusticus*. We are also grateful to Dr Michael Cullen for examining and commenting upon our e.m. photograph of the epipleural muscles.

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ABBREVIATIONS USED IN FIGURES

h	medial thoracic hook	x	coxal membrane
t.s.	tibial spurs		

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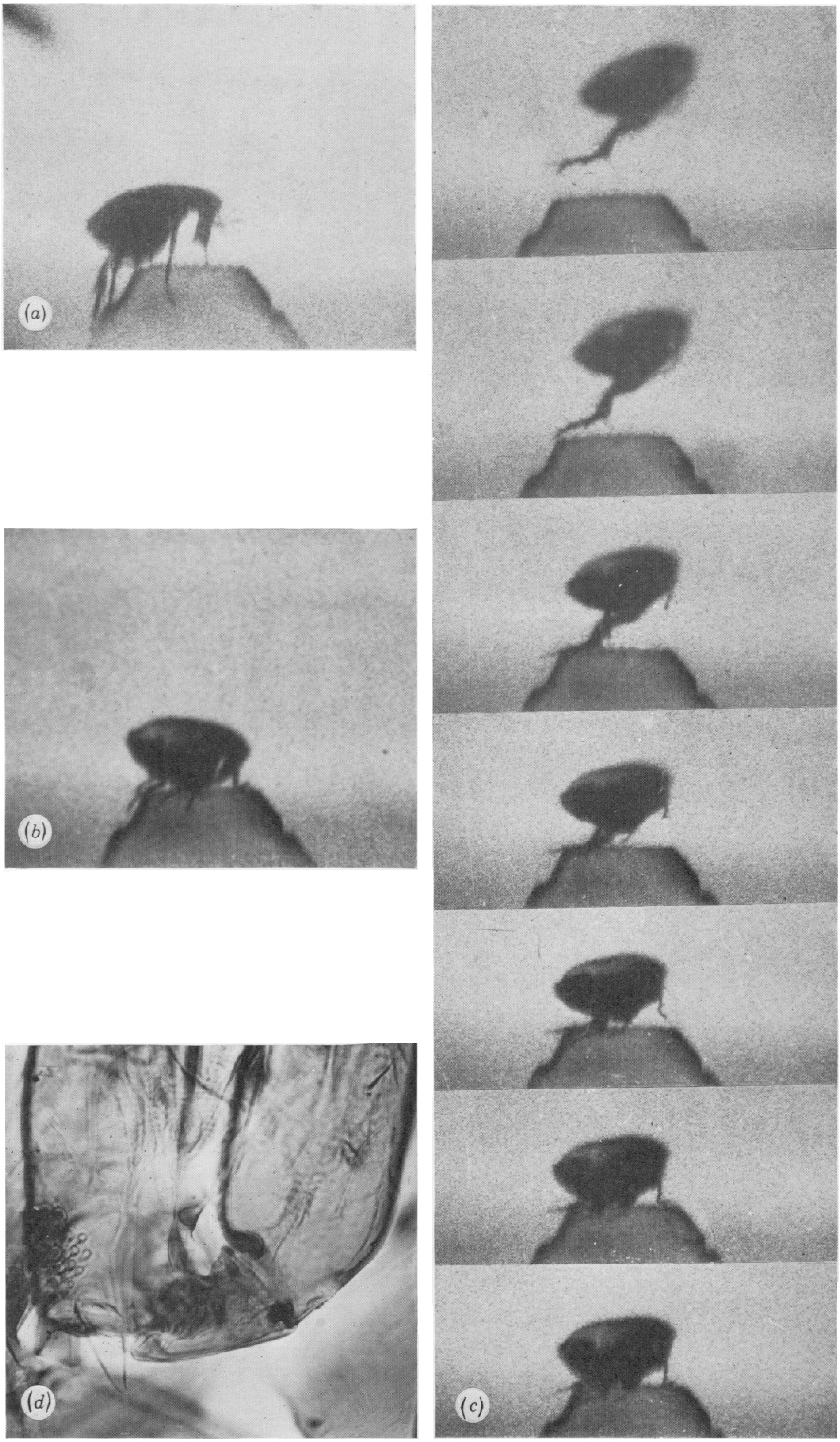
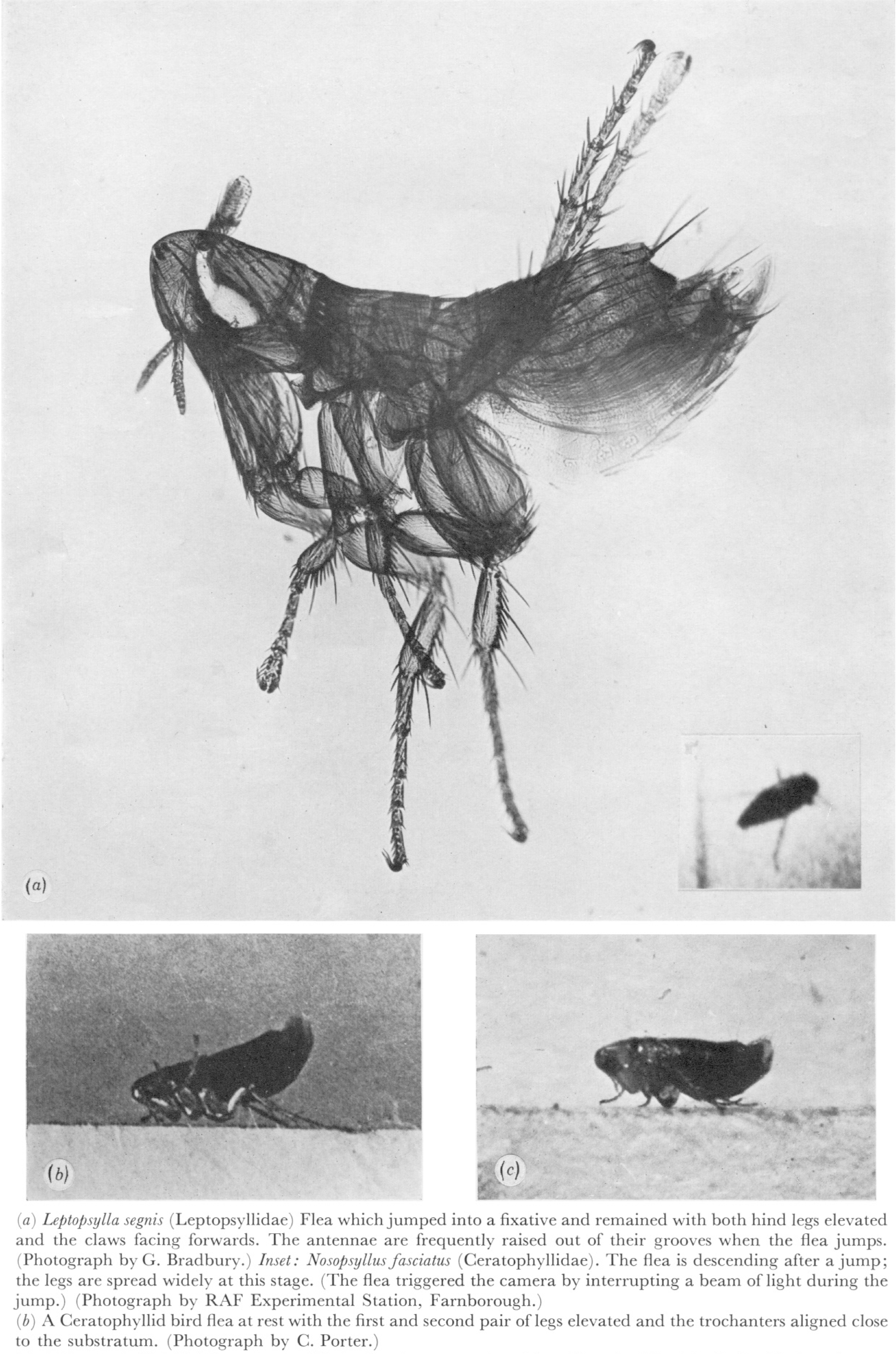


(*a*) *Xenopsylla cheopis* (Pulicidae). Flea climbing onto the perspex pedestal, using claws and tarsal segments.
(*b*) *Xenopsylla cheopis* (Pulicidae). Flea crouching down, preparatory to take-off.
(*c*) *Xenopsylla cheopis* (Pulicidae). Flea jumping. Seven consecutive frames taken at 3500 frames a second.
(*d*) *Echidnophaga gallinacea* (Pulicidae). Hind coxa with the femur raised and the trochanter aligned with the substratum ready for take-off.



(*a*) *Leptopsylla segnis* (Leptopsyllidae) Flea which jumped into a fixative and remained with both hind legs elevated and the claws facing forwards. The antennae are frequently raised out of their grooves when the flea jumps. (Photograph by G. Bradbury.) *Inset: Nosopsyllus fasciatus* (Ceratophyllidae). The flea is descending after a jump; the legs are spread widely at this stage. (The flea triggered the camera by interrupting a beam of light during the jump.) (Photograph by RAF Experimental Station, Farnborough.)
(*b*) A Ceratophyllid bird flea at rest with the first and second pair of legs elevated and the trochanters aligned close to the substratum. (Photograph by C. Porter.)
(*c*) A Ceratophyllid bird flea at rest with the legs in a normal position. Even in this attitude the hind trochanter is touching, or nearly touching, the substratum. (Photograph by C. Porter.)

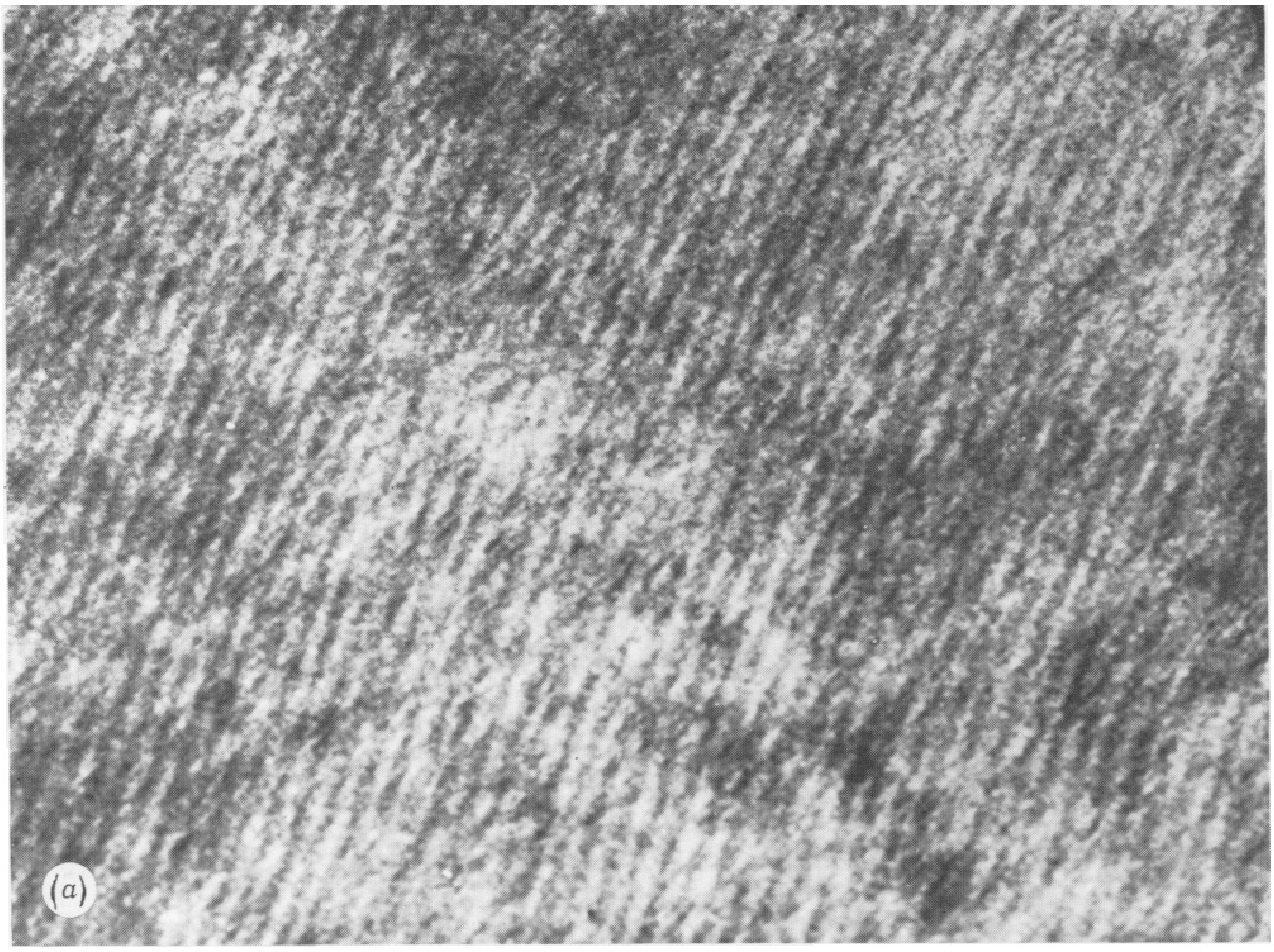
(*a*) *Xenopsylla cheopis* (Pulicidae). Transverse section through the thorax in the region of the 2nd thoracic link-plate to show the hook of the click mechanism *in situ*.

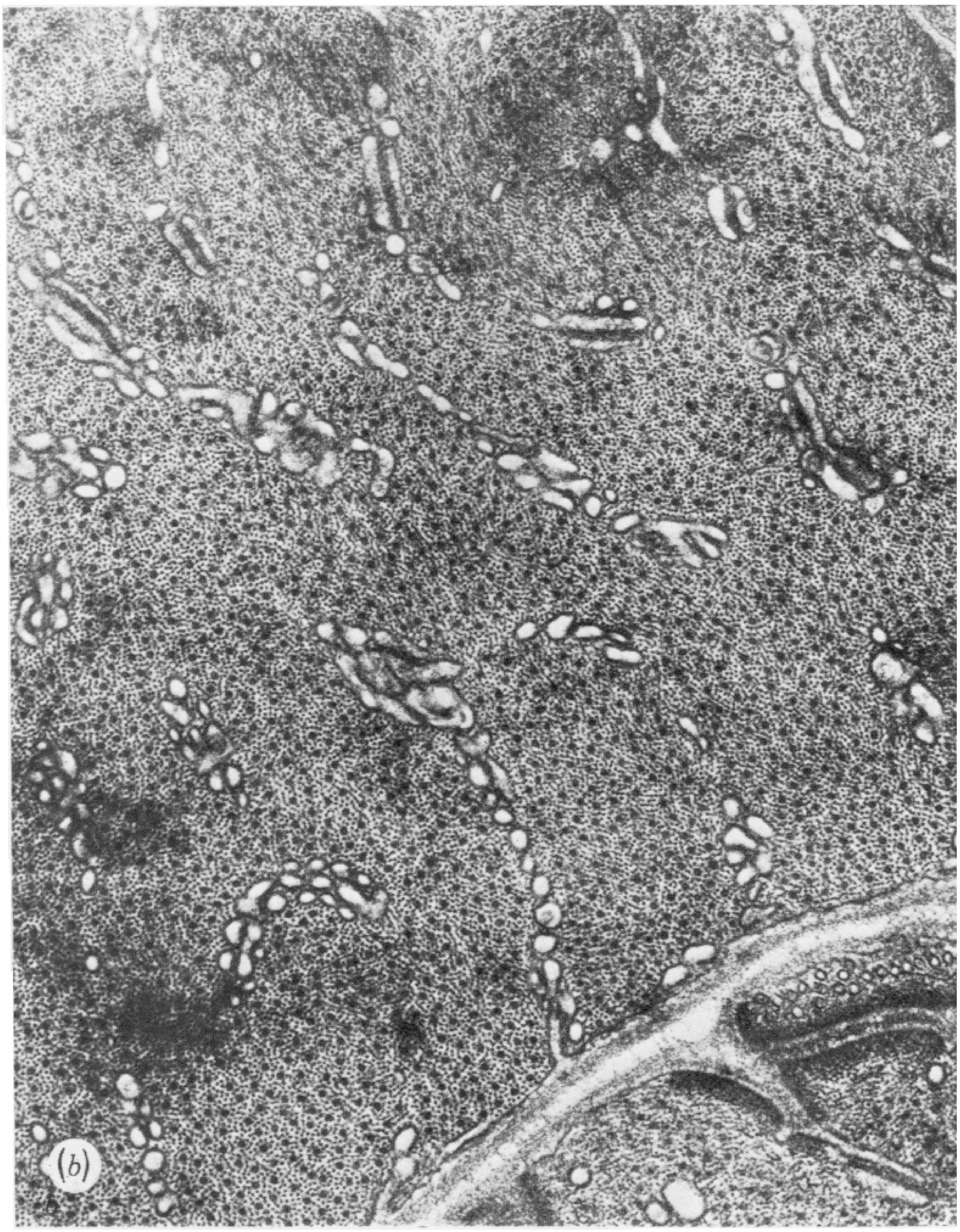
(*b*) *Xenopsylla cheopis* (Pulicidae). Transverse section through the metathorax and metacoxa with the femurs raised to show the 'lines of force' between the pleural arch and trochanter. The tendon of the trochanteral depressor is seen as a faint line between the coxal ridges.

(*c*) *Xenopsylla cheopis* (Pulicidae). Transverse section of the thorax showing the membranous socket of the median hook of the click mechanism. Note the two sensilla on either side of the socket.

(*d*) *Echidnophaga gallinacea* (Pulicidae). Parasagittal section (stained) of the distal end of the metacoxa with the trochanter raised. The coxal membrane is partly extended and the internal knob of the hook is pressing against the tendon of the trochanteral depressor.

(*e*) *Spilopsyllus cuniculi* (Pulicidae). Parasagittal section through the lateral metanotal area showing the sensory setae lying immediately outside the point of insertion of the 2nd thoracic link-plate and the abrupt interpolation of arthrodial membrane in the heavily sclerotized ridges. This permits the rotation of the link-plates.



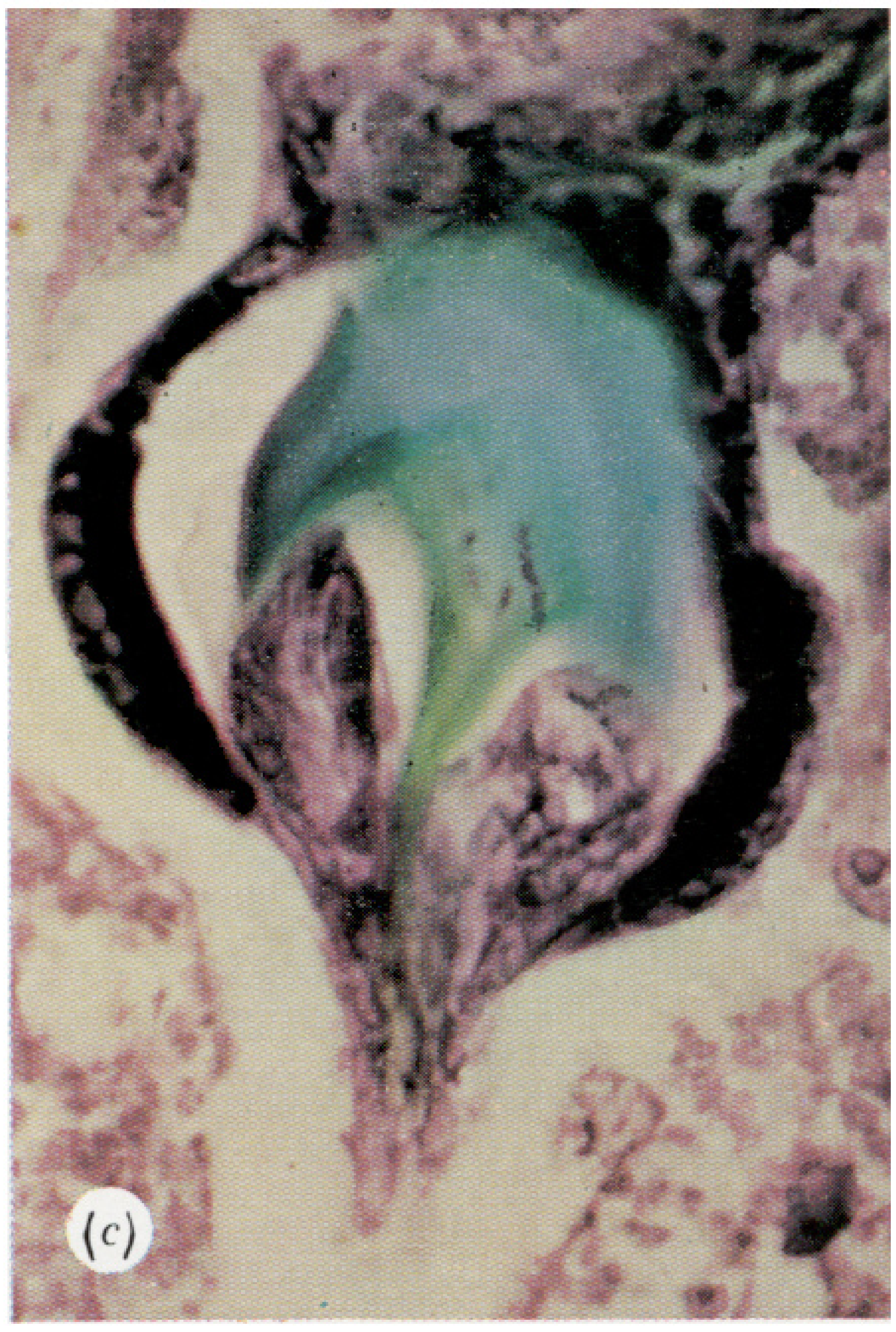


(*a*) *Xenopsylla cheopis* (Pulicidae). Pleural arch showing region with chitin microfibrils embedded in a resilin matrix. Electron micrograph (magn. × 350 000).

(*b*) *Xenopsylla cheopis* (Pulicidae). Transverse section through the epipleural muscles (original magn. × 30 000).


(a)


(b)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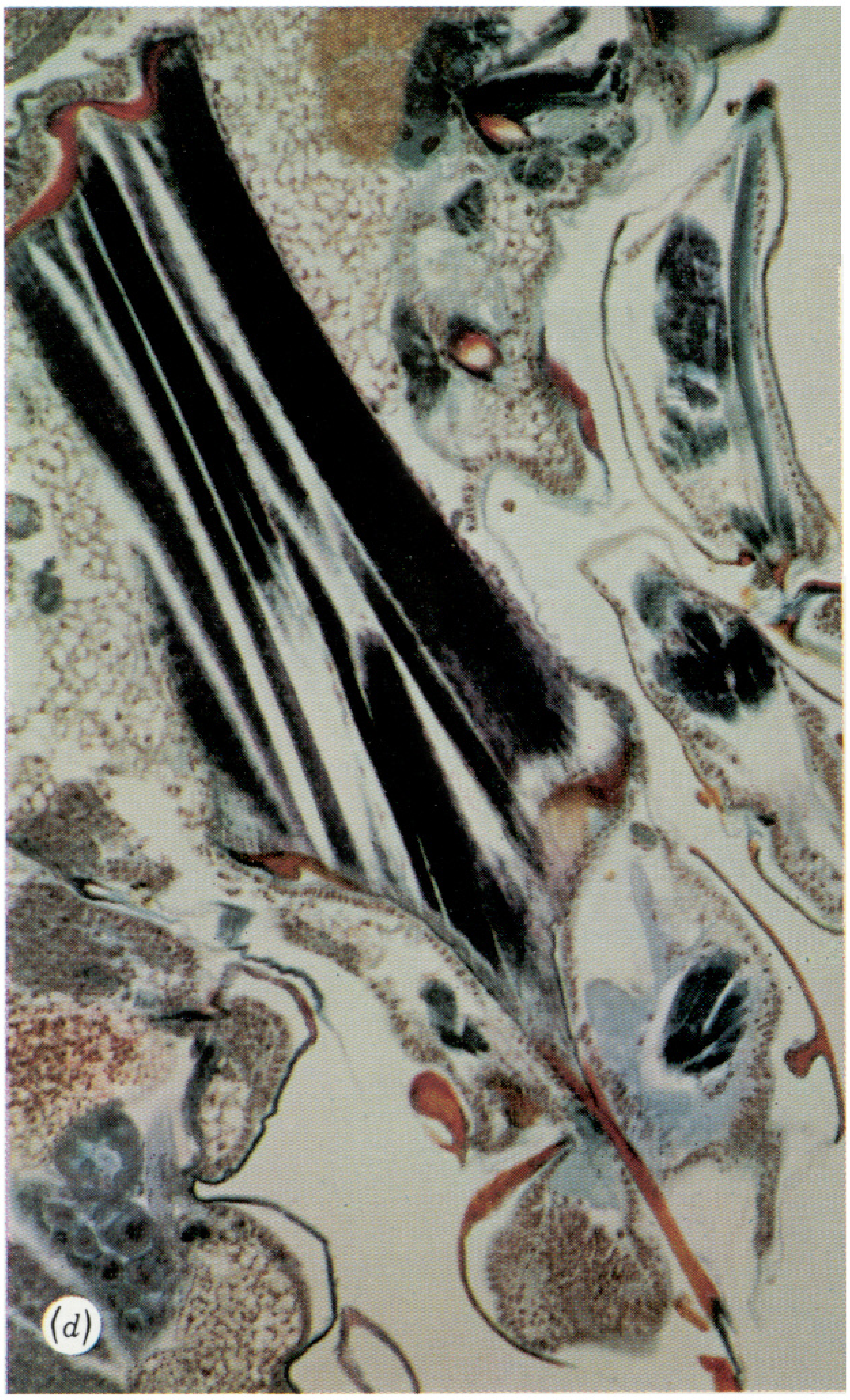
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