THE JUMPING MECHANISM OF *XENOPSYLLA CHEOPIS*
I. EXOSKELETAL STRUCTURES AND MUSCULATURE

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(*Communicated by J. W. S. Pringle, F.R.S. – Received* 12 *March* 1975)

[Plates 25–36]

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The jumping apparatus of the flea, which includes highly modified direct and indirect flight muscles, is described: attention is drawn to the various specializations of the exoskeleton which stiffen the thorax and also provide the 'click' mechanism triggering take-off.

A finger-like invagination of tall cells within the cavity of the developing pleural arch of the pharate adult secretes the resilin pad. This is illustrated with coloured photographs.

It is suggested that winglessness of a Mecopteran-like ancestor pre-adapted fleas to a parasitic life-style, and that a jumping mode of progression was a primitive feature of the whole Order. Scattered throughout the Siphonaptera today are species which have secondarily lost the pleural arch and with it the power to execute large jumps. These are usually found among fleas parasitizing mammals inhabiting caves, subterranean burrows and runs, high aerial nests and snow or ice-bound habitats. Large pleural arches are associated with fleas infesting large mobile hosts.

Vol. 271. B. 914. [Published 30 October 1975

1. INTRODUCTION

Our investigation of the jumping mechanism of the flea (Rothschild, Schlein, Parker & Sternberg 1972; Rothschild *et al.* 1973) revealed the necessity for a redescription of the musculature, cuticular ridges, and associated structures of the thorax and metacoxa. In the following account we have followed Snodgrass' general (1935) scheme, with certain modifications which he introduced in his excellent study 'The skeletal anatomy of fleas' (1946).

TABLE 1. LABELLING OF THE THORACIC MUSCLES OF FLEAS, COMPARED WITH THE GENERAL SCHEME PROPOSED BY SNODGRASS (1935)

no. of muscle in present publication	Wenk (1953) and Lewis (1961)†	Jacobson (1940)	Snodgrass (1935, 1946)‡	
1	21b	—	—	Prothorax
2	22	—	A (DMcl)	
3	27	—	A (1A)	
4	—	—	B (2B)	
5	—	—	B (3B)	
6	23	—	F (F)	
7	24	—	H (H)	
8	31	—	H	
9	—	m3 (1st leg)	K (K)	
10	36	m2 (1st leg)	L (L)	
11	—	—	L	
12	35	m1 (1st leg)	M (2M)	
13	37	dvm	M (1M)	
14	25	—	A (mA)	Mesothorax
15	28	—	A (1A)	
16	—	—	B (4B)	
17	—	—	F (F)	
18	—	—	G (G)	
19	32	—	H (H)	
20	38	—	J (J) D 70	
21	39	—	K (K)	
22	29§	—	L (L)	
23	—	—	N (N)	
24	42 abcd	dvm, trs	—	
25	26	—	A (mA)	Metathorax
26	43	pm	E (3E″) 58	
27	33	—	H (H)	
28	—	—	H (H)	
29	30	—	L (L)	
30	47b‖	bm‖	M (1M) 63b‖	
31	47c‖	—	M (2M) 63c‖	
32	47a, d	dvm, trs, m	P, Q 63d	
33	44	m3	59	
34	45	m2	60	
35	46	m1	61	
36	—	m cox 1, 2, 3	0, 62a, b	
37	—	—	—	

† The numbers of the muscles designated by Wenk and Lewis are continuous.

‡ The letters refer to Snodgrass (1935) and the numbers 58–70 to Snodgrass (1946).

§ We consider Lewis's muscle 29 the same as his 40, and we failed to find 34 and 41.

‖ Lewis, Jacobson and Snodgrass failed to find muscles inserting on the anterior rim of the coxa, but Lewis has now confirmed their presence. Some fibres attached to the trochanteral depressor and originating on the metepisternum (63b) as shown by these authors, are present in Ceratophylloid but not in Pulicoid fleas. These fibres lie nearer the centre of the flea's body than 30 and 31.

We have also compared the account of the thorax of *Xenopsylla* by Lewis (1961) and the jumping muscles of the Sand Martin flea (*Ceratophyllus styx* Roths.) by Jacobson (1940) with our own observations (see table 1). It is a curious coincidence that none of these three authors (nor Bennet-Clarke & Lucey (1967) who accepted Snodgrass' description as correct) noted the pleurocoxal muscles inserted on the anterior dorsal margin of the hind coxa, but Robert Lewis has very kindly confirmed their presence using his own material and methods. Wenk (1953) has produced an accurate description of the cervical muscles and the head capsule of *Ctenocephalides canis* (Curtis).

No attempt has been made to provide a study of the musculature and exoskeleton of the whole animal, nor have we described the muscles of the femur, tibia and tarsus of the legs. We have allocated numbers to certain muscles in order to aid our description and simplify identification, but they are merely a matter of convenience and in no sense represent a permanent scheme. Prior to this study the importance of the link-plates in stiffening the thorax, and their role in aligning the various hook and socket devices had not been appreciated.

In this paper we are not concerned with the sequence of events in the flea's jump, which will be described later (Rothschild *et al.* 1975, p. 506 of this volume).

2. MATERIAL AND METHODS

Xenopsylla cheopis (Roths.) was reared at Ashton, England, on white rats. The stock was obtained from the Institute of Biological Research, Ness Ziona, Israel. *Echidnophaga myrmecobii* Roths. was obtained in Australia on wild rabbits, and subsequently reared on hamsters at Ashton. Living specimens of *Ceratophyllus gallinae* (Schrank), *C. rusticus* Wagner and *C. styx*, *Ischnopsyllus octactenus* (Kolenati), *Spilopsyllus cuniculi* (Dale) and *Nosopsyllus fasciatus* (Bosc) were collected in the Ashton and Oxford areas. Living *Cediopsylla simplex* (Baker) were received from Professor Nixon Wilson, Iowa, U.S.A.

Two methods were adopted for examining the muscles:

(i) Serial sections were cut at 8 μm. The material was fixed in Bouin Brazil and stained with a modified Mallory's triple stain. A small number of pupae, which are exceptionally difficult to fix satisfactorily, were stained with Delafields haematoxylin.

(ii) The muscles were dissected with flattened needles and *in vitro* staining used when necessary.

For obtaining specimens with the femur and link-plates raised and the exoskeletal catches in the clamped position, fleas were made to jump into hot fixatives. Occasionally specimens were sectioned which had been killed with Bouin Brazil and which had died with femurs raised, but the majority of fleas die with muscles and legs relaxed. The electron micrographs were taken with a Philips EM 200. Light photographs were taken with a Zeiss Photomicroscope. Three objectives were used, a ×10, ×25 and ×40, in conjunction with an optivar setting of 1.25 and a 3.2 projective.

3. THE JUMPING APPARATUS OF THE FLEA

The morphological modifications associated with the saltatorial mode of progression fall into three main groups, although it is probably true to say that every part of the flea has been affected by its jumping ability.

(*a*) Gross morphology and build of the body and legs (plates 30*a*, 32*a*, *b*, *c*);
(*b*) Modified structures of the exoskeleton (plates 25*b*, *c*, 26*f*, 27*f*, 29–36; figures 3–5, 12);
(*c*) Musculature and tendons (plates 25–28, 29*f*; figures 6–11, 13–15).

(*a*) *General build of the body and legs* (plates 25, 27, 32*a*, *b*, *c*; Rothschild *et al.* 1975, plate 39*d*)

The flea's body is compressed laterally and is leaf, or spear, or dart-shaped. The legs are long, and the third pairs of coxae usually very large. In *X. cheopis* – a Pulicoid flea (plate 32*c*) among which are found the best jumpers – the thorax and abdomen are compact, the mesocoxa and second pair of legs are greatly reduced, and the ratio of metacoxa to body size, and length of leg to body length, is greatest. These small compact fleas are essentially body parasites and hence have developed a close attachment to the host. The consistently good jumpers among the Pulicoids are the species which parasitize large animals such as cats, dogs, hares and rabbits, wart hogs, wombats, buffaloes, porcupines, badgers and man himself. The majority of such fleas have a more heavily tanned cuticle than the indifferent performers or 'nest' fleas, probably a reflection of their more active and hazardous life-style.

The massive coxa of the hind leg is the most impressive feature of *X. cheopis*. Other important points to note are the large tracheal air sacs in the tibia and first tarsal segment (plate 35*d*) which presumably add to buoyancy when the insect is airborne, and the group of the long stout spines at the distal end of the tibia which assist in the thrust of the leg against the ground as it straightens during the jump.

The trochanter (and part of the femur in some cases) is flattened along the ventral surface (plate 29*e*), since this is the portion of the leg which is pressed against the substratum at take-off (page 507 of this volume and Rothschild *et al.* 1972, 1973). The modification is very striking in *Echidnophaga* but not at first apparent, since the trochanter is partly retracted within the coxa when the leg is relaxed (plate 30*f*). If the femur is raised, the trochanter is pulled into the horizontal position and its long flat ventral surface aligned with the substratum by virtue of the large membranous infolding of the cuticle near the distal corner of the coxa (plate 27*a*, *b*, *d* (x)). This can be stretched to nearly double the width of the trochanter itself (plate 27*b*, *d* (x)). The device operates in all fleas but it is most highly developed in Pulicoidea.

The trochanter is set at a slight angle to the coxa so that if the femur and tibia are flicked upwards before or after take-off, they can lie against the coxa and can thus be carried aloft, above the level of the notum, with the claws pointing forwards (Rothschild *et al.* 1975, plate 40). It has been suggested (Rothschild 1965) that in this position, with a pair of legs carried aloft, the jumping flea has a better chance of becoming entangled in the host's pelt should it land successfully on a moving animal, since the organs of attachment are then arranged all round their body (plate 32*b*). It should be noted that the post trochanteral portions of fore-, mid- and hind-legs can be rotated upwards and are not infrequently held at rest in this most unusual position. Photographs of stationary fleas show they can prepare for feeding or rest with at least one pair of legs held aloft (Rothschild & Clay 1952, plate xxxiii).

Snodgrass pointed out that the sternal articulation of the flea's meso- and meta-thoracic legs is unique: 'The sclerotic mesal wall of the coxa is deeply emarginate above, leaving a

FIGURE 1. *Xenopsylla cheopis*. Parasagittal section of the metathorax and hind coxa (posterior view). Diagram to show main jumping muscles. The tendon of the trochanter and the trochanteral depressor are coloured red. The levator, epipleural and pleurocoxal muscles are coloured blue.

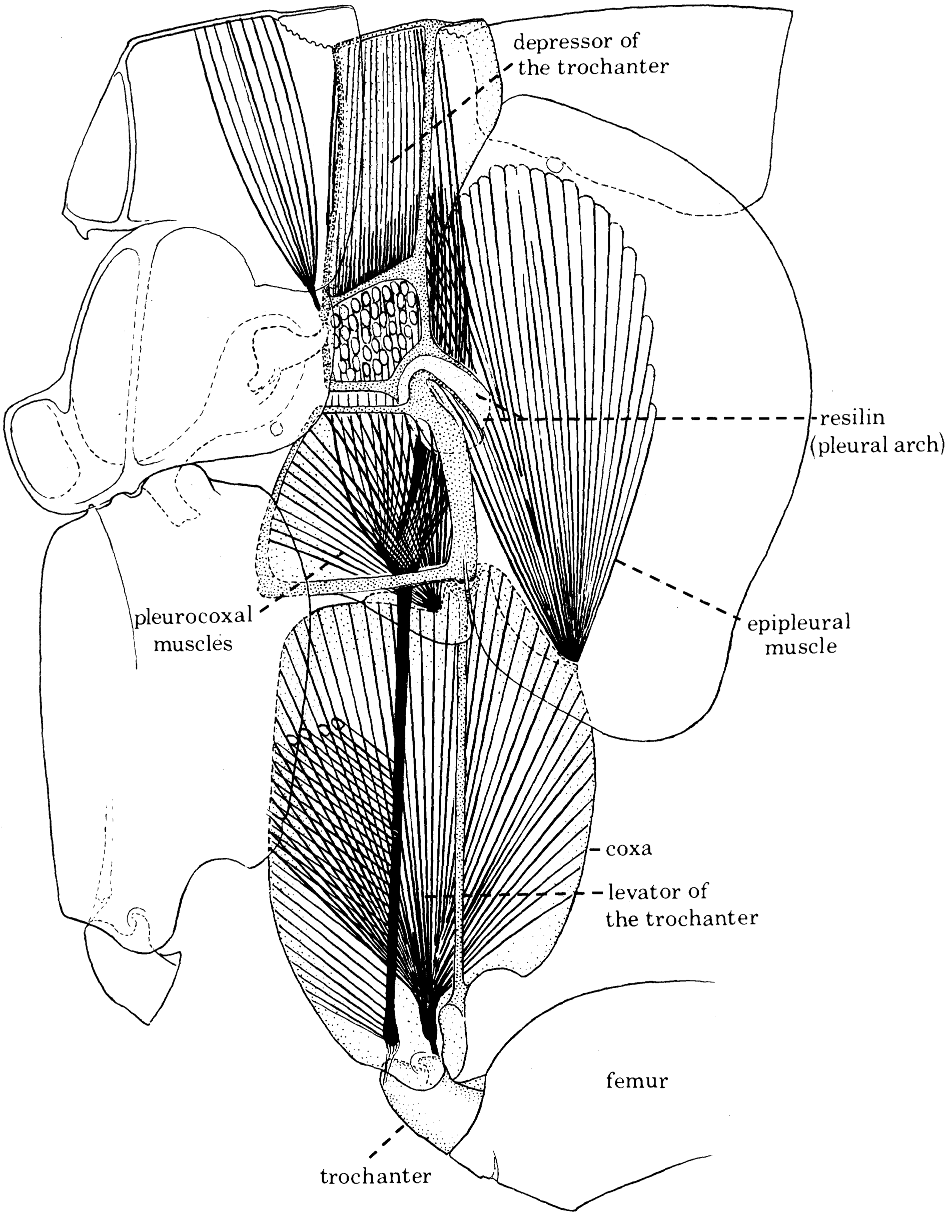

FIGURE 1. For description see opposite.

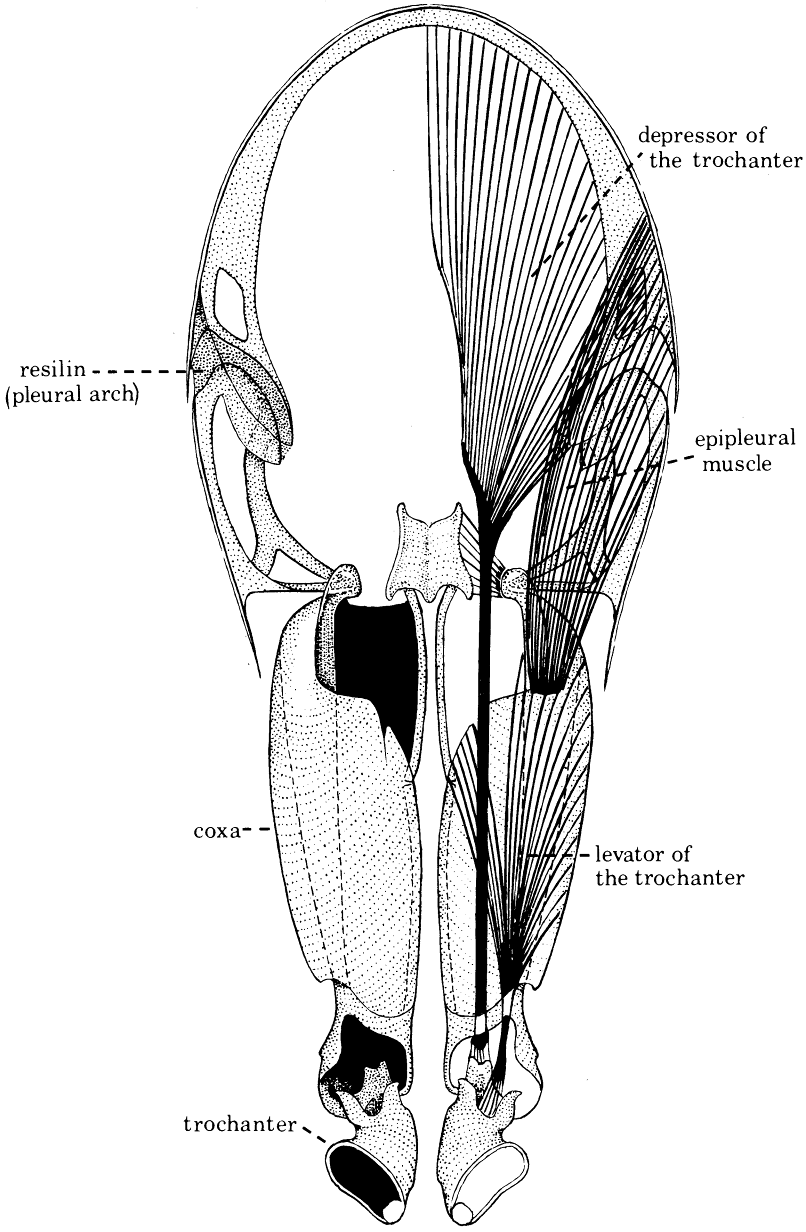

FIGURE 2. For description see opposite.

wide membranous area between the coxa and the sternum. In this membrane is an oval or fusiform articular sclerite [our plates 29*e*, 30*h* a, figures 4, 12, 13, up.in.rd.] with a strong median thickening that articulates at one end on the sternum and at the other in the angle of the coxal emargination.' In fact this sclerite articulates in the angle of the fork of the two lateral branches of the inner internal coxal rod† (plates 28*c*, *e*a, 29*e*a). Snodgrass (1946) remarks that the coxa may be said to be hinged on a transverse axis between the pleurum and sternum, but the hinge is by no means a rigid one. In our opinion this arrangement also permits the flea to spread its legs widely, but in a controlled manner, during the descending period of the jump (Rothschild *et al.* 1975, plate 40*a*, inset). It is very striking that the articular sclerite is variable both in degree of sclerotization and length (plate 34*c*, *d*, a), according to the life-style of the fleas concerned (see p. 488). It is short, narrow, and well sclerotized in the majority of free-living Pulicoids (plates 29*e*a, 30*d*, 31*b*, *c*, figures 4, 12, up.in.rd.) including *X. cheopis*.

(*b*) *Modified structures of the exoskeleton* (plates 29–35, figures 3–5, 12)

This includes the pleural arch (plates 25, 26, 28–35, p, figures 1–5, 10, 16 pl.a), the heavily sclerotized notal, pleural and coxal ridges (plates 29*c*, *e*, 30*a*, 31*c*, 32*a*, *c*, 33*a*, figures 3–7) which together form the 'lines of force' (plate 25*b*), and a variety of hooks, pegs and catches (plates 27*f*, 29*a*, *b*, *e*, 30*f*, *g*, 31*a*, k4, figures 3, 4) which serve to press or clamp the various segments or sclerites together, thus, for example, ensuring rigidity of the thorax, and the trochanteral/femoral articulation, and the pressing or bracing of the hind coxa against the abdomen.

(i) *The pleural arch* (plates 25, 26, 28–35, p; figure 16, pl.a.)

The developing pleural arch of fleas is situated at the apex of the inflexion which forms the pleural ridge (plates 25, 26, 28). In the pharate adult it is a hollow sphere or semi-sphere, developed at the point of junction of the inflexions of the notal ridge, the pleural ridge and the accessory ridges of the metanotal areas. It is obviously homologous with the wing-hinge ligament of flying insects, which also contains resilin.

In the pharate adult stage, this pleural arch cavity is lined with a layer of cells which is one cell thick in places, but in others consists of a thick covering (plates 26*b*, 28*a*, *b*) several cells in depth. A finger-like invagination of taller cells pushes into the cavity from the posterior basal corner (plate 26*d*), near the terminal portion of the pleural ridge. These cells secrete the pure resilin which form the inner portion of the arch itself. During development it can be seen as a peg-like structure of resilin (plates 26*a*, 28*b*) enclosed within an excessively fine epicuticle which in turn is encapsuled within the cuticular covering of the arch (plate 26*e*, *f*). As development continues, more and more resilin is laid down until the space between the top of the pleural ridge and the dome of the arch is filled with the resilin pad (plates 26*e*, *f*, 28*a*, *b*, Rothschild *et al.* 1975, plate 43*c*). Electron micrographs have shown that the central

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† Described in Rothschild & Traub (1971) as 'coxal inner internal rod'. Although the articular sclerite is a rod, that portion with which it articulates should be described as a ridge.

FIGURE 2. *Xenopsylla cheopis*. Transverse section of the metathorax and hind coxa. Diagram of the main jumping muscles to show the relative position of the trochanteral depressor (red) and the levator and epipleurals (blue). The trochanteral depressor lies nearer the centre of the body, while the epipleural and levator muscles are essentially a lateral system.

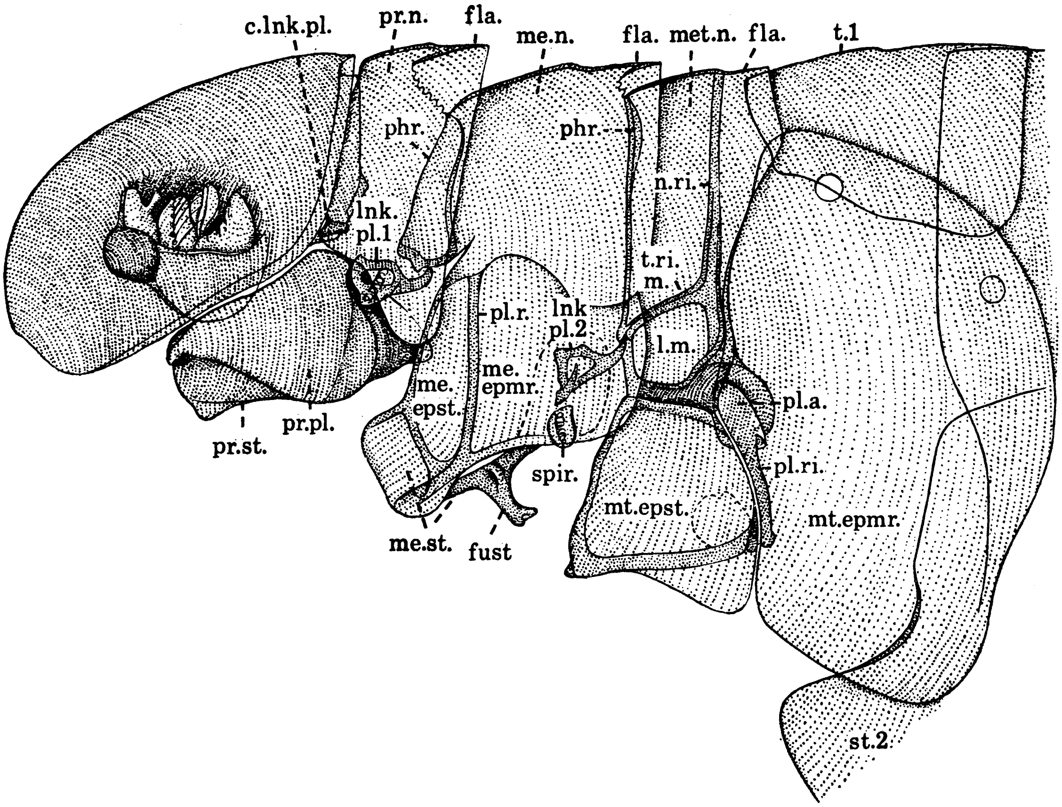


FIGURE 3. *Xenopsylla cheopis*. Head and thorax: exoskeleton.

DESCRIPTION OF PLATE 25

(*a*) *Spilopsyllus cuniculi* (Pulicidae). Parasagittal section viewed by polarized light, cut near the centre of the metacoxa to show the tergotrochanteral depressor muscle and tendon. The trochanter is lowered and the muscle relaxed. The untanned cuticular portion of the tendon stains red and the tanned portion yellow.

(*b*) *Xenopsylla cheopis* (Pulicidae). Parasagittal section viewed by polarized light showing the relation between the resilin arch and the cuticular line of force. (The notal ridge has accidentally been severed where it normally meets the tergum.)

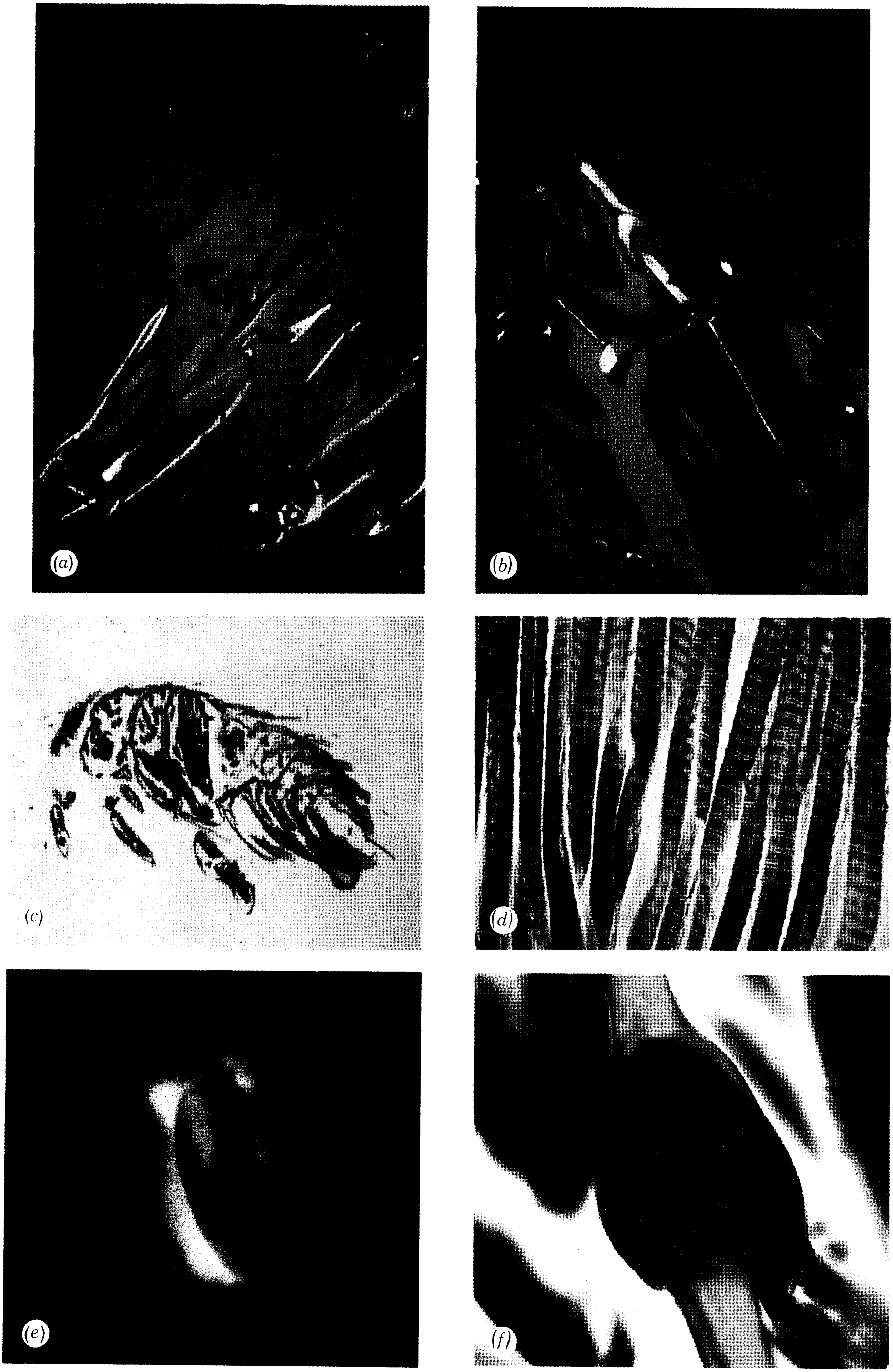
(*c*) *Xenopsylla cheopis* (Pulicidae). Parasagittal section viewed by polarized light, cut near the outside of the body to show the resilin (red) of the pleural arch, held between the notal and pleural ridges (yellow). Portions of the epipleural muscles are visible (blue/black).

(*d*) *Spilopsyllus cuniculi* (Pulicidae). Parasagittal section showing striped muscle fibres of the trochanteral depressor. In this species muscle stains blue with Mallory's triple stain.

(*e*) *Xenopsylla cheopis* (Pulicidae). The pleural arch was dissected out and photographed by ultraviolet light. The hyaline portion of the arch glows with a greenish-blue fluorescence characteristic and diagnostic of resilin. It is photographed lying partly on its side, and the broken pleural ridge is seen as a black stump on the right. (Dissection by Charles Neville.)

(*f*) *Xenopsylla cheopis* (Pulicidae). Parasagittal section showing the helmet-shaped mass of resilin situated between the pleural ridge and the notal ridge. The sharp line of demarcation, characteristic of resilin, between the notal ridge and the pleural arch is well shown. One of the muscles attached inside the pleural arch can be seen on the right of the picture.

(Photographs by Miriam Rothschild. All sections were cut at 8 μm and stained with a modified Mallory's triple stain.)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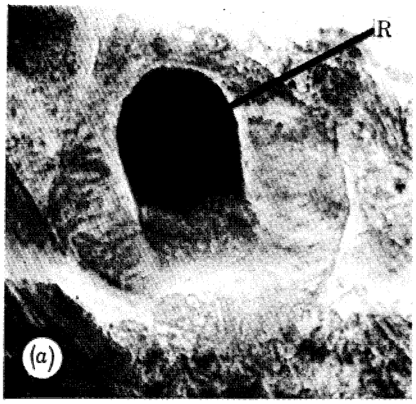
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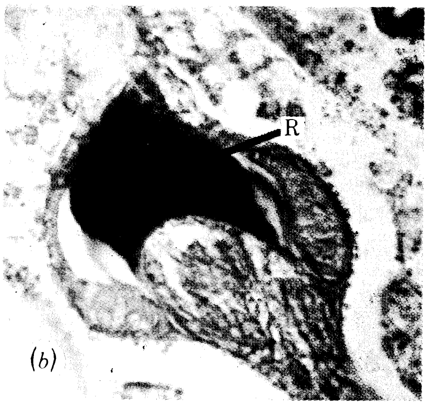
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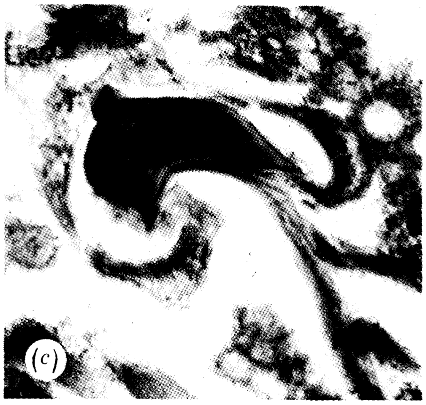
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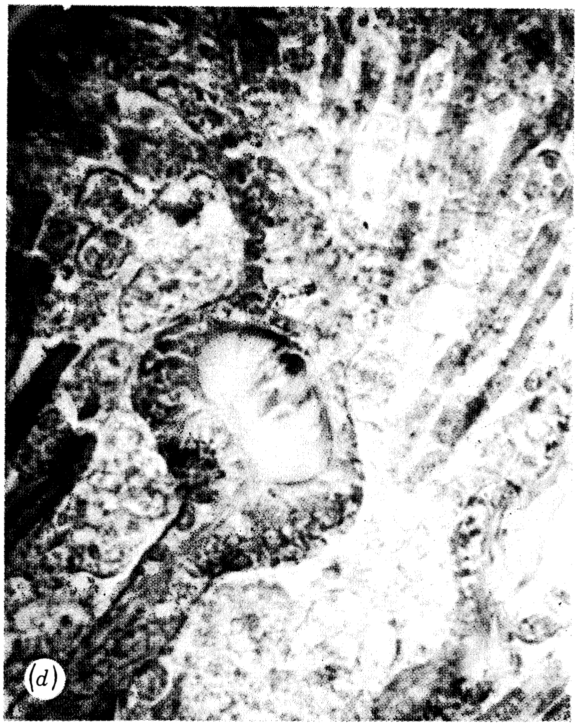
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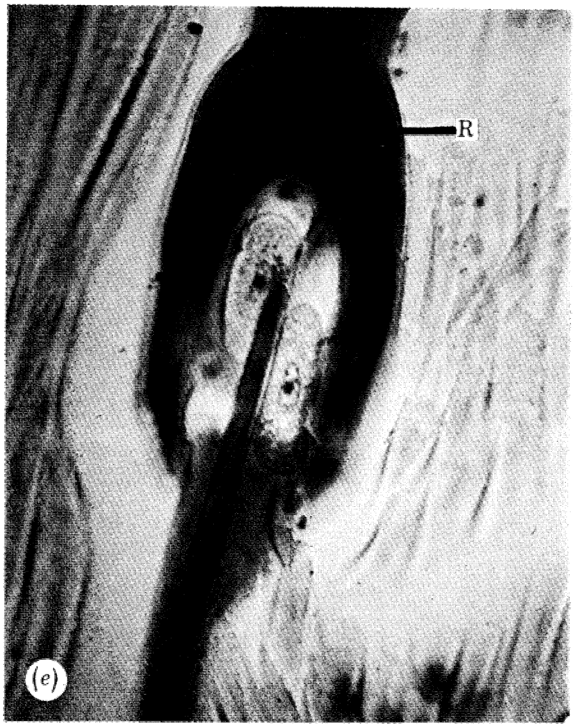
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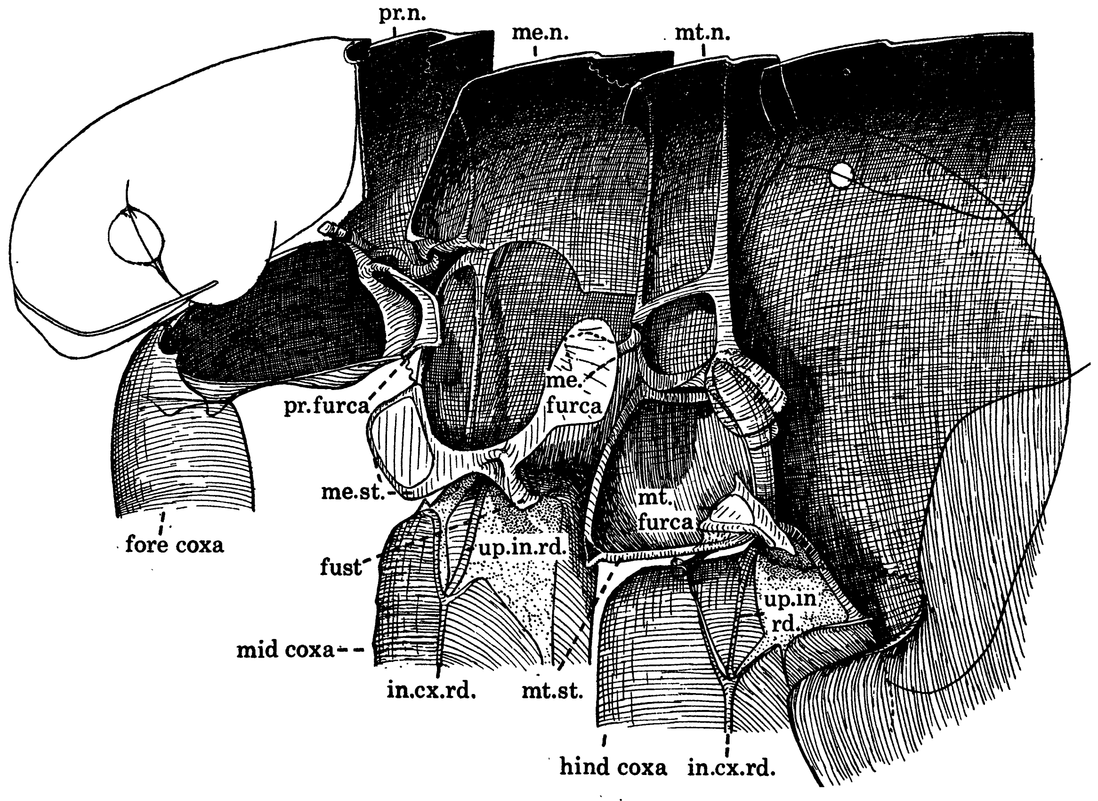


FIGURE 4. *Xenopsylla cheopis*. Head and thorax: exoskeleton (inner surface) depicting the meso- and metafurca, the hook of the central click mechanism (fust), and the articular sclerite (up.in.rd.) of the coxa. The development of the metafurca should be compared with that shown in non-jumpers which have lost the pleural ridge (plate 33*d*, fu).

DESCRIPTION OF PLATE 26

(*a*) *Spilopsyllus cuniculi* (Pulicidae). Pharate adult. Resilin forming in the cavity of the pleural arch, capping the finger-like invagination of tall cells in the base of the wall. The cuticle surrounding the resilin has not yet been laid down.

(*b*) *Nosopsyllus fasciatus* (Ceratophyllidae). Pharate adult. Resilin developing in the pleural arch, at a later stage than that shown in (*a*).

(*c*) *Nosopsyllus fasciatus* (Ceratophyllidae). Resilin developing in the pleural arch. In this photograph an area of fusion between the surrounding cuticle (not yet developed) and the resilin can be seen in the form of a knob at the apex of the arch.

(*d*) *Nosopsyllus fasciatus* (Ceratophyllidae). Early pharate adult. The development of the pleural arch and ridge before the secretion of resilin by the group of tall cells seen at the base of the arch. These form the finger-like invagination which secretes the resilin cap.

(*e*) *Chaetopsylla rothschildi* (Vermipsyllidae). Adult. Parasagittal section through the pleural arch showing the characteristically abrupt junction between resilin and cuticle, and two fat-body cells squeezed into the cavity of the arch.

(*f*) *Xenopsylla cheopis* (Pulicidae). Adult. Parasagittal section in the region of the pleural arch showing the notal ridge, transverse ridge of the metanotal area, and the arthrodial membrane slot (stained blue) in which the tip of the link-plate rotates. Immediately above the slot are a group of sensilla.

(Photographs by Miriam Rothschild.)

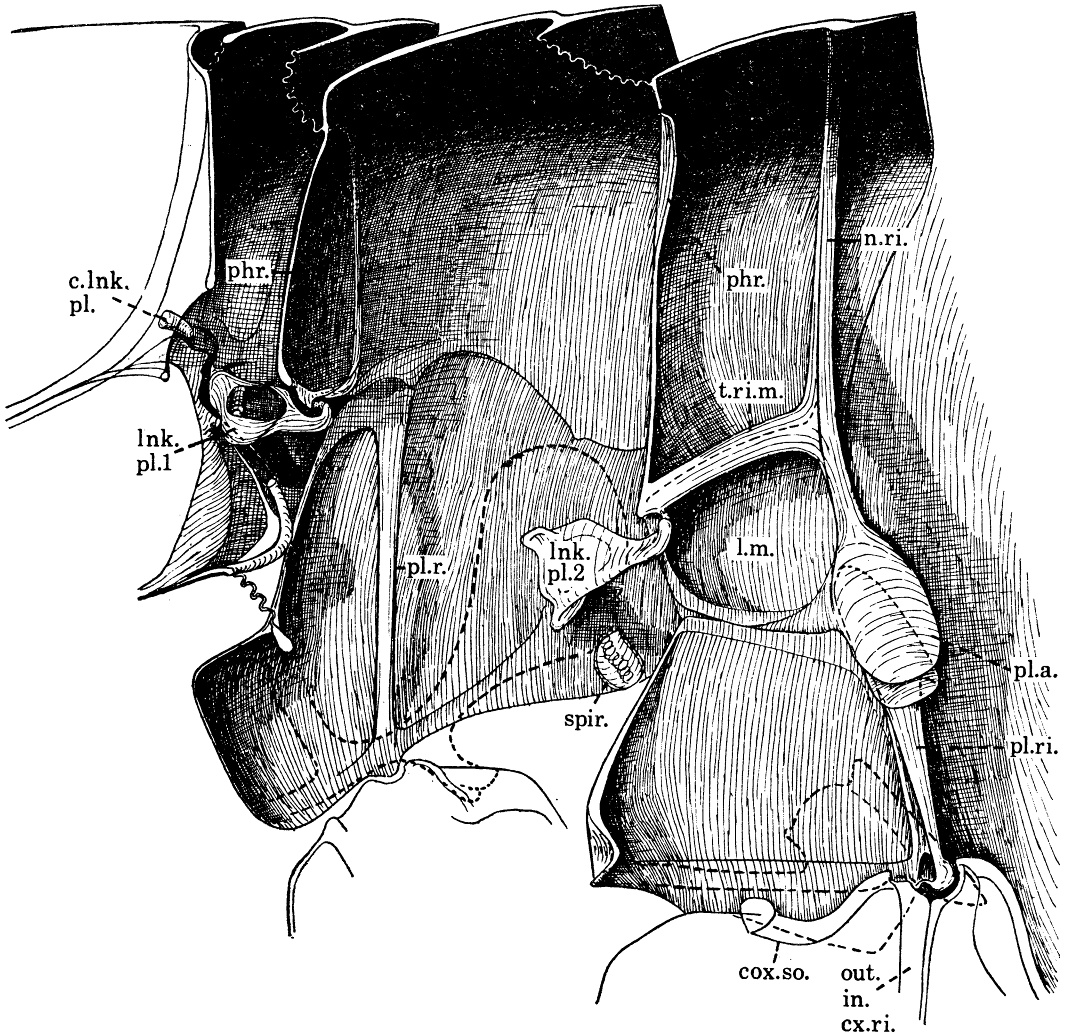


FIGURE 5. *Xenopsylla cheopis.* Thorax: exoskeleton to show the position and relation of the link-plates, the articulation of the pleural ridge with the coxa and location of the inner wall of the coxal guide socket of the jumping leg.

DESCRIPTION OF PLATE 27

(*a*) *Spilopsyllus cuniculi* (Pulicidae). Sagittal section of the base of the metacoxa. The insertion of the trochanteral depressor seen when the femur is lowered and the tendon relaxed. Note: (i) the membrane at the end of the coxa (x) which is heavily folded inwards; (ii) the internal knob of the trochanteral hook which is lying well separated from the tendon; (iii) the muscles of branch 32d of the trochanteral depressor, relaxed and hanging in folds.

(*b*) *Ancistropsylla nepalensis* (Ancistropsyllidae). Sagittal section of the base of the metacoxa. The insertion of the tendon of the trochanteral depressor seen when the femur is nearly fully raised. Note: (i) the membrane at the end of the coxa (x) previously infolded, now fully extended; (ii) the internal knob of the trochanteral hook pressed against the tendon, thus preventing overcentring; (iii) the muscles of branch 32d of the trochanteral depressor fully stretched within the coxa. Also note the semicircle of six sensilla which are always present in this position. (This photograph should be compared with (*a*).)

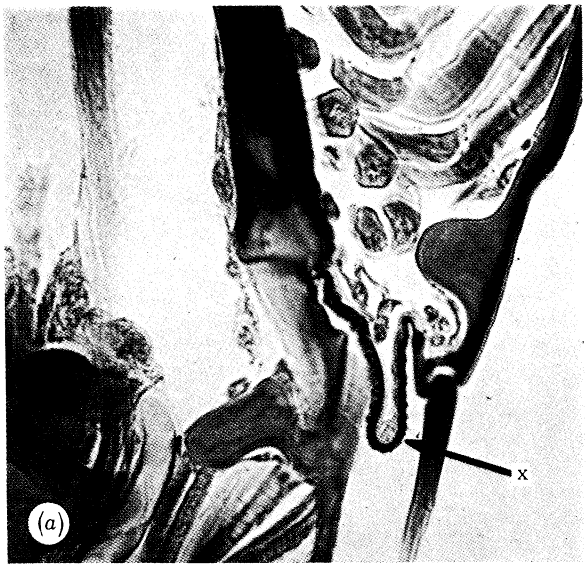
(*c*) *Xenopsylla cheopis* (Pulicidae). The rim of the coxa showing the insertion of muscles 30, 31 and 26. Arthrodial membrane stains blue: the red stain indicates untanned, and therefore flexible cuticle, at the point of insertion.

(*d*) *Xenopsylla cheopis* (Pulicidae). Sagittal section of the base of the metacoxa. The membrane of the end of the coxa (x) is fully extended and the internal knob of the trochanteral hook is pressed limpet-like against the tendon.

(*e*) *Xenopsylla cheopis* (Pulicidae). Parasagittal section of the rim of the metacoxa. The end of the pleural ridge is attached to arthrodial membrane (the recoil mechanism) in its socket in the rim of the metacoxa. Note the sensilla towards the left of the socket.

(*f*) *Xenopsylla cheopis* (Pulicidae). The trochanter of the metacoxa (whole mount). The tendons of the trochanteral depressor and the levator muscles can just be seen faintly to the right and left of the main hooks, at the points of their insertions. The black 'spot' is the clamp between femur and trochanter. The group of sensilla along the ventral surface of the femur are marked by a pale (untanned) area.

(Photographs by Miriam Rothschild.)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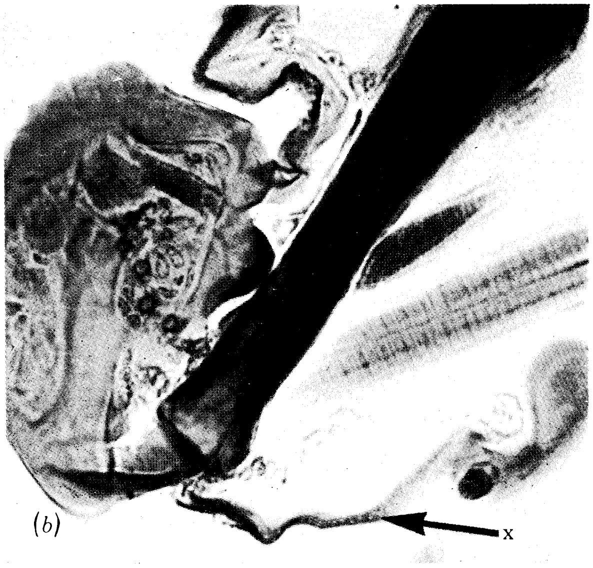
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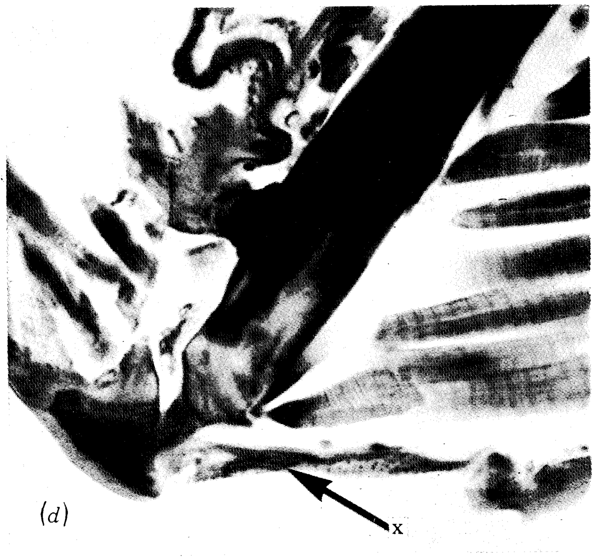
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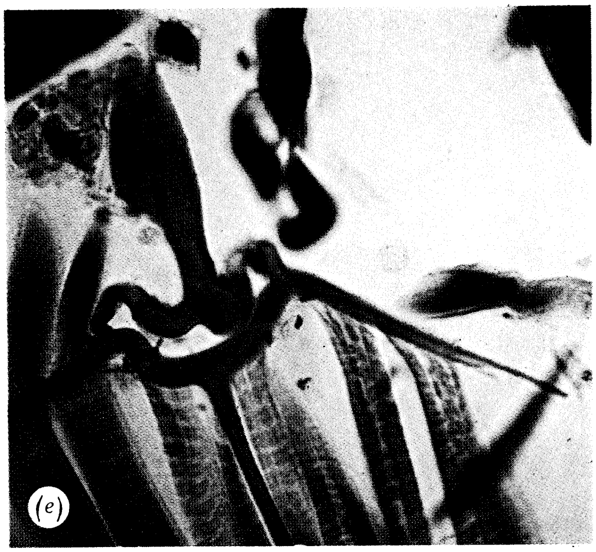
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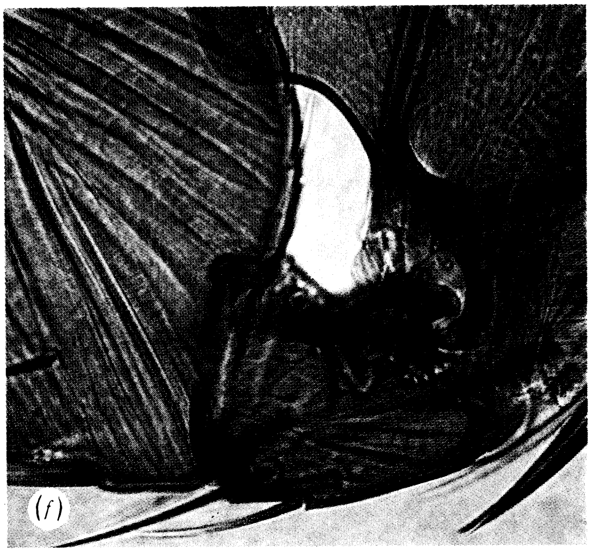

(f)


(a)


R
(b)


a
(c)


(d)


a
(e)

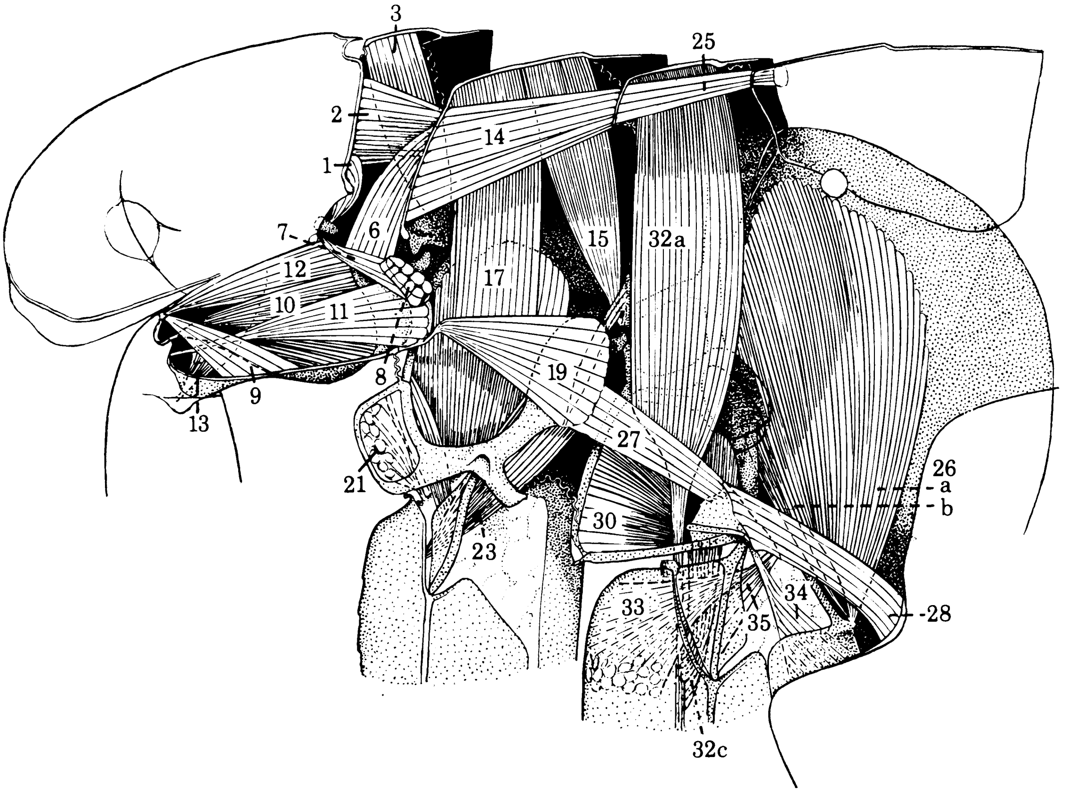


FIGURE 6. *Xenopsylla cheopis*. Thoracic muscles, and those of the upper portions of the coxae.

DESCRIPTION OF PLATE 28

(*a*) *Ctenocephalides felis* (Pulicidae). Pharate adult. Parasagittal section of the metathorax, showing the developing pleural arch. Much of the cuticle round the arch has been laid down but is untanned and stains red. The point of articulation of the pleural ridge and coxa has tanned and stains yellow.

(*b*) *Nosopsyllus fasciatus* (Ceratophyllidae). Early pharate adult showing the secretion of resilin in the pleural arch before the cuticular outer capsule has been laid down.

(*c*) *Ctenocephalides felis* (Pulicidae). Pharate adult. Parasagittal section through the meso- and metacoxa showing the developing articular sclerite (a) where it joins the inner internal rod of the coxa. The nerve cord shows the 2nd and 3rd thoracic ganglia and five of the abdominal ganglia, lying immediately above the coxae. The faint structures to the left of the picture are developing mouthparts.

(*d*) *Xenopsylla cheopis* (Pulicidae). Adult. Parasagittal section through the metathorax and outer surface of the metacoxa to show the massive epipleural muscles, the levator of the coxa and lines of force. The fan-like disposition of the levator is well shown with the pear-drop shaped tendon.

(*e*) *Nosopsyllus fasciatus* (Ceratophyllidae). Adult. Parasagittal section through the metacoxa to show the different widths of the various muscle fibres. Those of the sternocoxal muscle (33) are the widest and the rotator of the trochanter, which originates along the inner internal rod, are slender and narrow. The fibres of the coxal branch of the depressor (32d) normally insert along the tendon, but they have been severed at this point by the action of the section cutting knife.

(Photographs by Miriam Rothschild.)

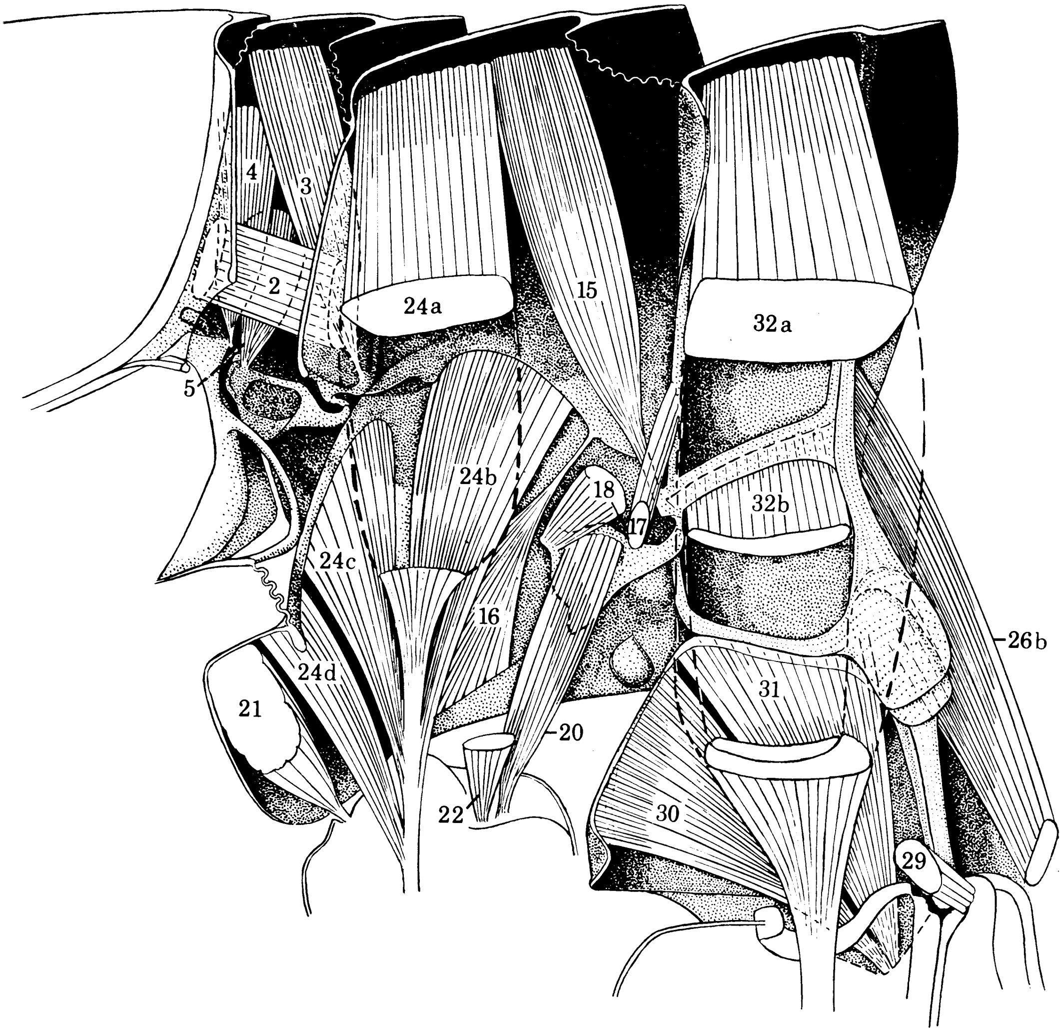


Figure 7. *Xenopsylla cheopis*. Thoracic muscles showing the branches of the trochanteral depressor (indirect flight muscles) in the meta- and mesothorax and the insertion of the direct flight muscles on the upper rim of the meso- and metacoxa.

Description of plate 29

(*a*) *Xenopsylla cheopis* (Pulicidae) (whole mount). The hook (h) of the unpaired click mechanism engaged in the median sinus of the metepisternum. With the hook in this position the flea is cocked for take-off (compare with (*b*)).

(*b*) *Xenopsylla cheopis* (Pulicidae) (whole mount). The hook of the unpaired click mechanism disengaged and in the relaxed position (compare with (*a*)).

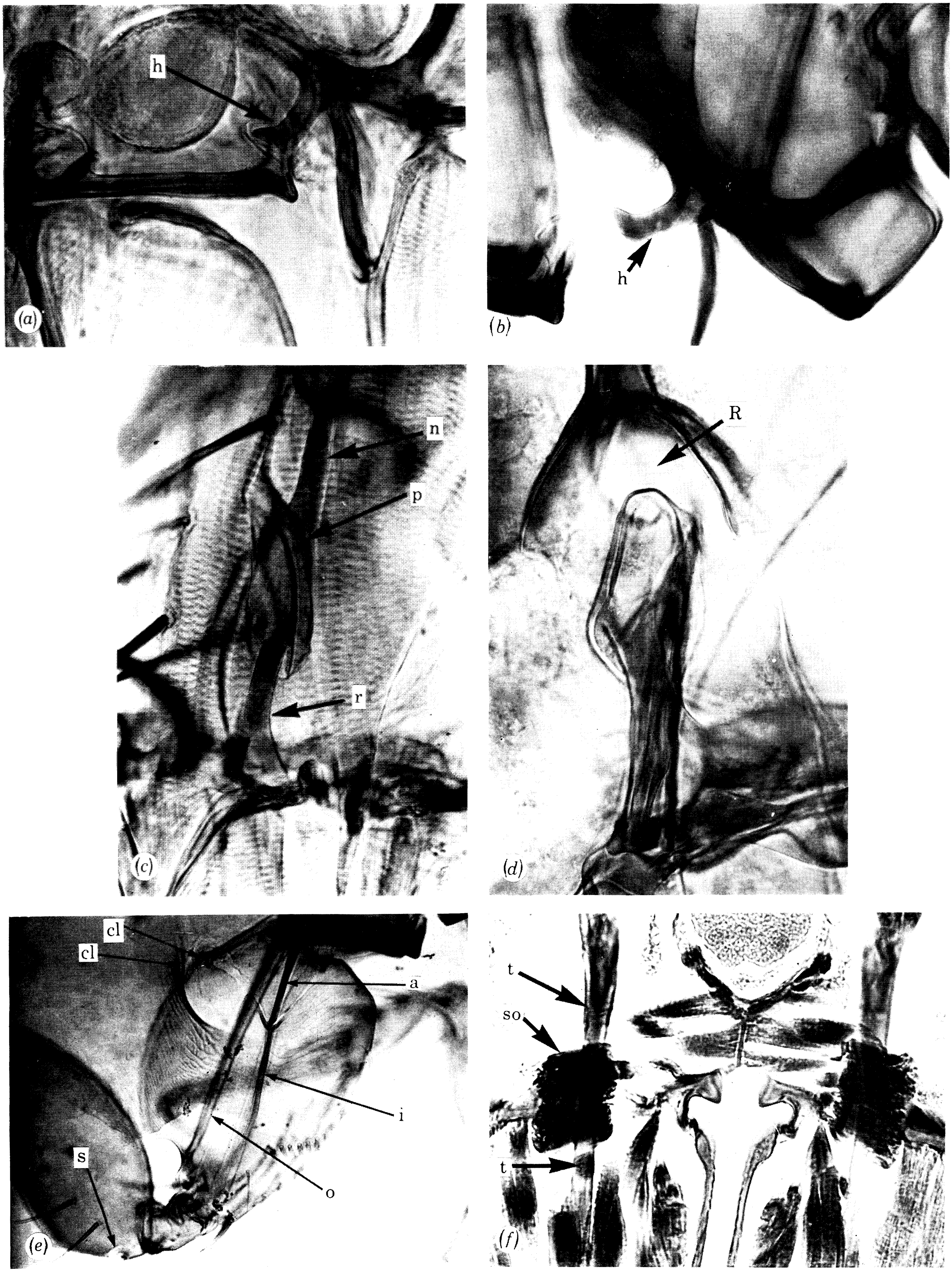
(*c*) *Xenopsylla cheopis* (Pulicidae). A transverse section of the thorax (unstained) showing the lateral situation of the pleural arch (p), and its junction with the notal (n) and the pleural ridges (r). The striped muscle fibres of the trochanteral depressor can be seen on the right of the picture; also the point at which the tendon passes from thorax to coxa.

(*d*) *Synosternus pallidus* (Pulicidae). The very large resilin cap (R) and powerful stout pleural ridge of this Pulicoid species, parasitizing hedgehogs, is well shown. Note the absence of the furca (see also plates 30, 33*d*).

(*e*) *Xenopsylla cheopis* (Pulicidae) (whole mount). Metacoxa: outer coxal ridge (o), inner internal coxal rod (i), articular sclerite (a), coxal/abdominal clamp (cl), sensilla on ventral surface of femur (s). Note that both coxal rod and ridge are straight and the articular sclerite short and non-membranous. They should be compared with those shown on plates 30*h* and 34*d*.

(*f*) *Xenopsylla cheopis* (Pulicidae). Transverse section through the thorax and coxae to show the tendons (t) of the trochanteral depressor passing through the funnel-shaped sockets (so) into the coxa. These sockets appear black on the photograph because they are composed of untanned cuticle and therefore, like the tendon itself, when treated with Mallory's triple stain, colour pillar box red. Tanned cuticle stains yellow and appears lighter in tone. In whole mounts the sockets are deceptively transparent, except for the internal wall which is sclerotized.

(Photographs by Miriam Rothschild.)



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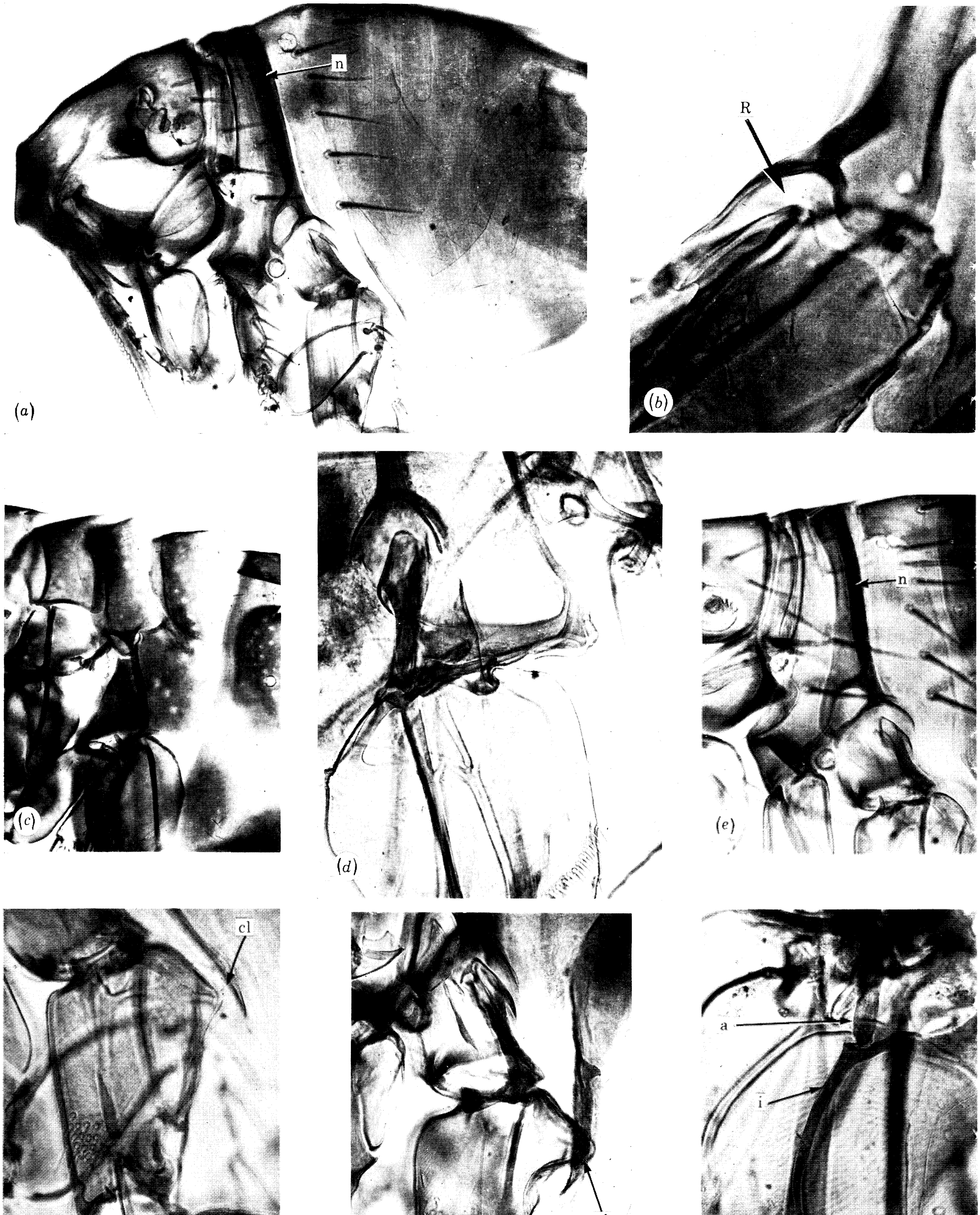

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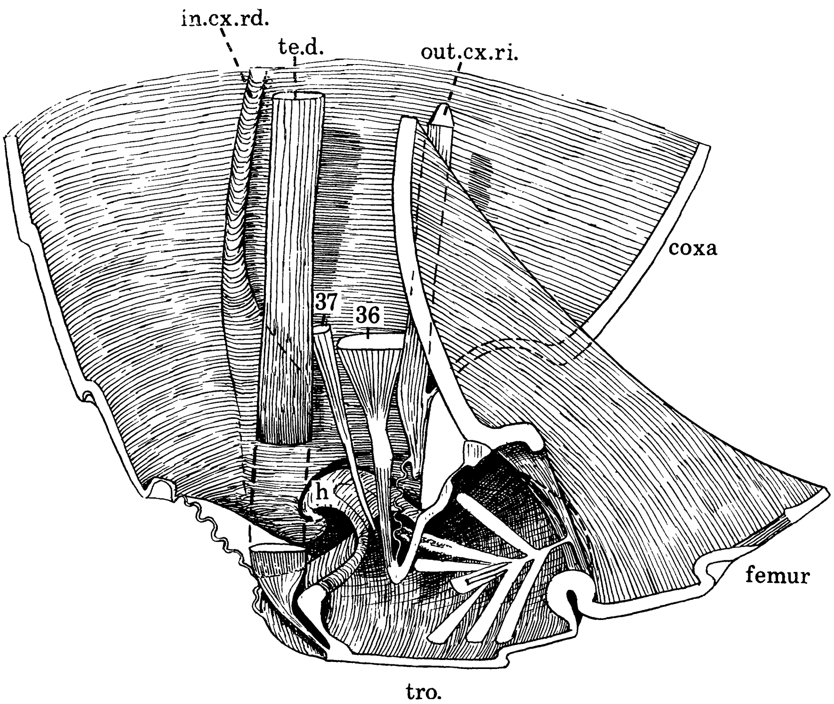


FIGURE 8. *Xenopsylla cheopis*. Trochanteral-coxal joint. Transverse section showing the attachment of the tendon of the trochanteral depressor, the levator of the trochanter and muscle 37 which rotates the hooks into their sockets prior to elevation of the femur.

DESCRIPTION OF PLATE 30

(*a*) *Echidnophaga myrmecobii* (Pulicidae) (whole mount). A parasite of Dasyuridae. Head, thorax and portion of the abdomen. The shape and sclerotization of the metanotal area should be compared with that of *Delopsylla crassipes* (plate 31*c*).

(*b*) *Tunga monositus* (Tungidae) (whole mount). A parasite of mice. Pleural arch. The arch is highly modified and the resilin (R), although present, is reduced in bulk and lacks the typical helmet shape.

(*c*) *Glaciopsyllus antarcticus* (Ceratophyllidae) (whole mount). A parasite of the silver-grey fulmar. Meso- and metathorax showing the absence of the pleural arch and notal ridge.

(*d*) *Synosternus pallidus* (Pulicidae) (whole mount). A parasite of hedgehogs, also often found on foxes. Pleural arch and associated structures. Note the unpaired hook of the click mechanism on the top right hand side of the picture, seen through an overlying sclerite, and the strengthened rim of the coxa (left) above the coxal abdominal clamp. There is a short, articular sclerite and a massive pleural arch – features associated with good jumpers.

(*e*) *Echidnophaga gallinacea* (Pulicidae) (whole mount). A parasite of domestic poultry, etc. Meso- and metathorax. The powerful vertical notal ridge (n) and large lump of resilin in the pleural arch are shown. The link-plates are lacking, but the mesofurca is visible above the spiracle.

(*f*) *Echidnophaga myrmecobii* (Pulicidae) (whole mount). A parasite of Dasyuridae. Metacoxa illustrating the coxal abdominal clamp (cl). The trochanter is deeply inserted within the coxa but when the femur is raised this is pulled out and forms a horizontal take-off surface, parallel to the substratum (Rothschild *et al.* 1975, plate 39*d*). The black cuticular trochanteral/femoral clamp shows up clearly.

(*g*) *Echidnophaga ambulans* (Pulicidae) (whole mount). A parasite of *Tachyglossus*. Pleural arch and metacoxa showing two sinuses in the coxal/abdominal clamp (cl).

(*h*) *Moeopsylla sjoestedti* (Pulicidae) (whole mount). The upper portion of the metacoxa showing the articular sclerite and the strongly bowed inner coxal rod. The habits of this enigmatical species, which parasitizes wart hogs, are not known. The pleural arch is very large but the flea has several characteristics associated with a semi-sessile life-style. The heavily bowed rod (i) is often a feature of species with ambulatory habits lacking a pleural arch (compare with plate 34*d*), but in such cases the articular sclerite (a) is longer compared with the coxal ridge.

(Photographs by Miriam Rothschild and J. V. Brown.)

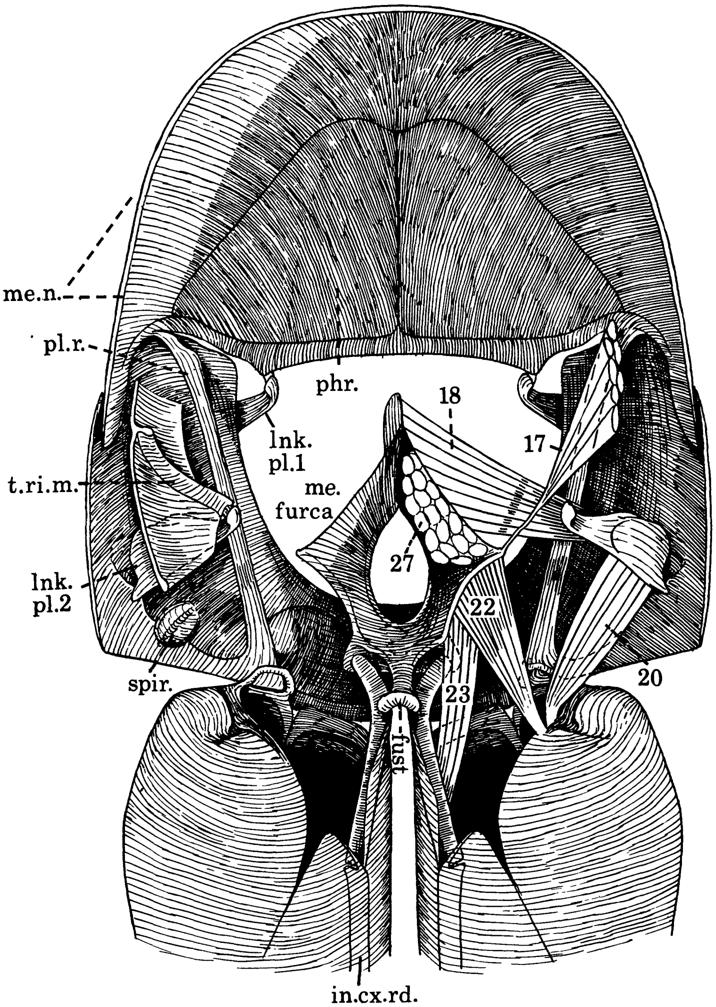


FIGURE 9. *Xenopsylla cheopis*. Metathorax: transverse section to show the relation between metafurca, link-plates, the central hook of the click mechanism (fust) and the articulation of the pleural ridge with the coxa (posterior aspect). The position of muscles 18 and 20 (from the link-plate to the metafurca and coxa) should be noted.

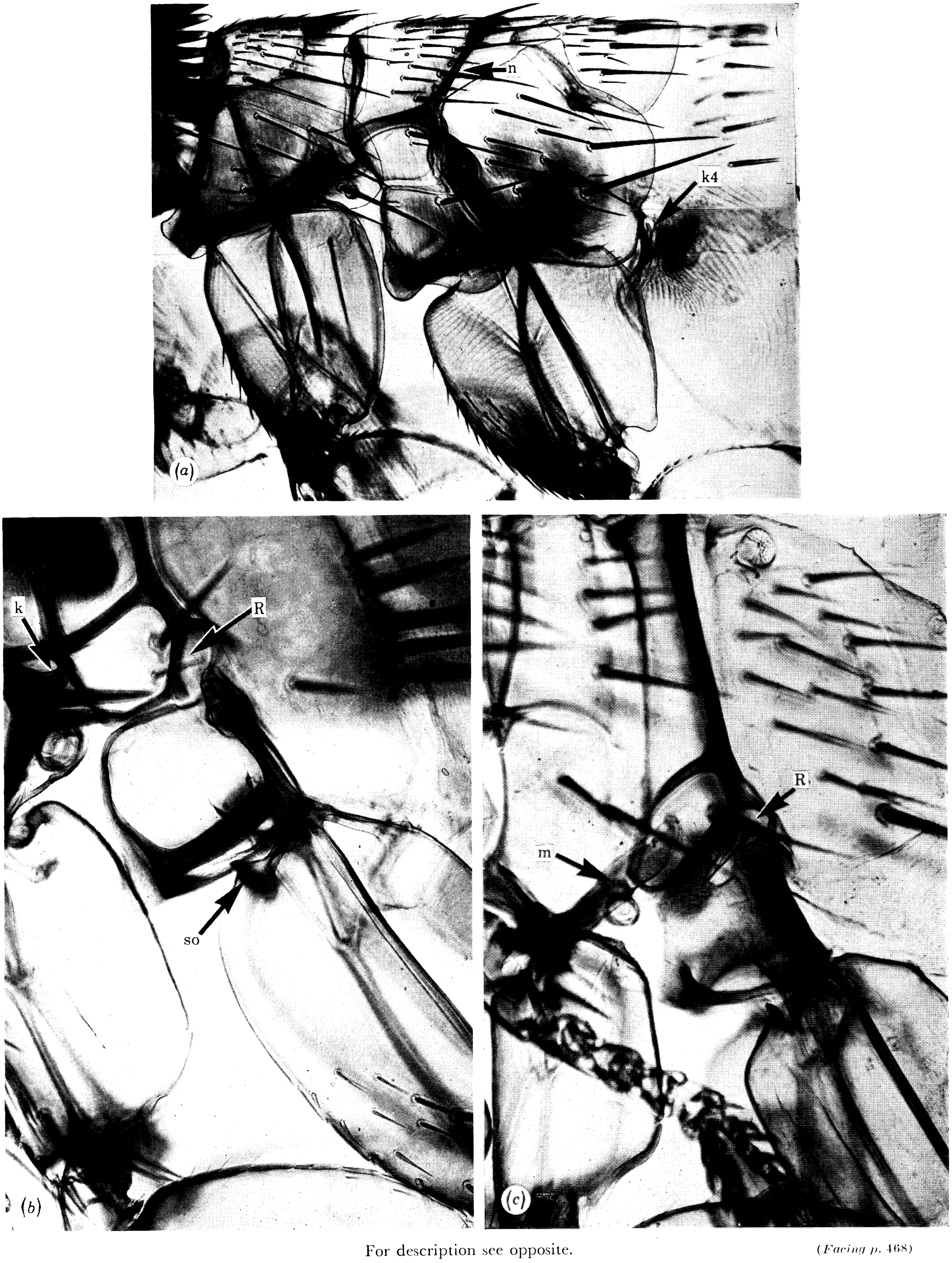
DESCRIPTION OF PLATE 31

(*a*) *Medwayella dryadosa* (Pygiopsyllidae) (whole mount). A parasite of squirrels. Meso- and metathorax showing the pleural arch and pleural ridge, and the V-shaped formation of the notal ridges (n). This should be compared with the vertical notal ridges of the Pulicoid fleas (see below). The so-called 4th link-plate (k4) (found only in this family and not homologous with the thoracic link-plates) can be seen on the border of abdominal sternite II. The variation between species, of the sclerotization of the ridges surrounding the lateral metanotal area, should be noted.

(*b*) *Pariodontis riggenbachi wernecki* (Pulicidae) (whole mount). A parasite of porcupines. Region of the pleural arch. Note the link-plate (k) on the left hand side of the picture and the strongly sclerotized ventral portion of the metepisternum. The dorsal wall of the socket is also heavily sclerotized, particularly where it clamps into the margin of the metepisternum.

(*c*) *Delopsylla crassipes* (Pulicidae) (whole mount). A parasite of *Pedetes* (spring hare). Region of the pleural arch. Note the powerful vertical notal ridge and absence of the thoracic link-plate. The hook-like structure, apparently in the link-plate position, is the terminal portion of the mesofurca (m). The transverse ridge of the metanotal area is weak and sloping, probably a modification associated with the loss of the link-plate. This photograph should be compared with plate 30*a*.

(Photographs by R. Traub and J. V. Brown.)



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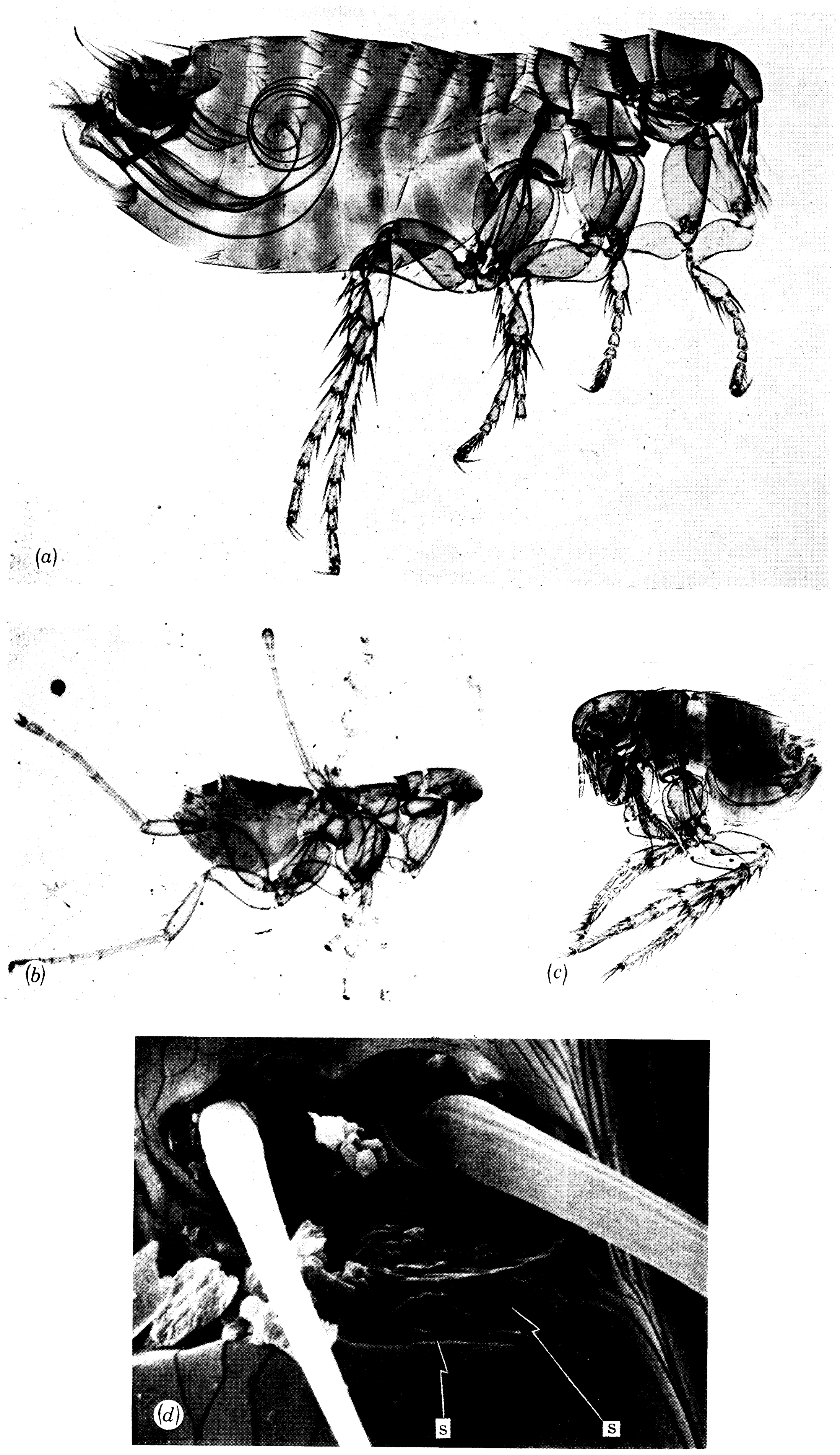

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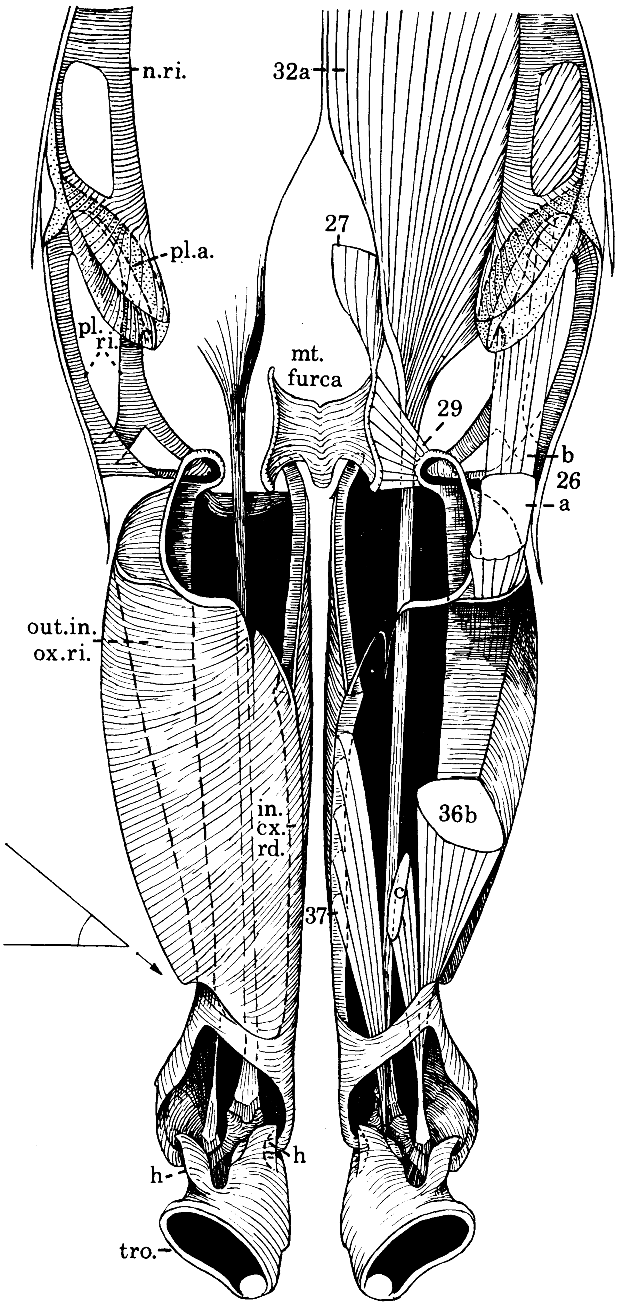


FIGURE 10. *Xenopsylla cheopis*. Metathorax, metacoxa and trochanter. Transverse section (posterior aspect) in the region of the pleural arch to show the relation of the trochanteral depressor and levator muscles and the insertion of the trochanteral hooks. In this relaxed position the trochanteral depressor tendon is not pulled down into the coxal socket.

DESCRIPTION OF PLATE 32

(*a*) *Ceratophyllus fringillae* (♂) (Ceratophyllidae) (whole mount). This bird flea, which is a good jumper, illustrates the typical body build of a Ceratophylloid flea. Compared with *P. porcinus* (c) the abdomen is elongated and the legs comparatively short. Other points to notice are the relatively sloping notal ridges, and the wide mesocoxa.

(*b*) A bat flea (♀) with the middle leg flicked up above the dorsum in a characteristic 'take-off' position. Note the long spindly legs (of which one is missing) characteristic of this family and many cave-dwelling insects.

(*c*) *Pulex porcinus* (♂) (Pulicidae) (whole mount). The typical short abdomen and relatively huge legs of the Pulicoid flea, with narrow mesocoxa, heavily sclerotized vertical notal ridge and large metanotal area, is well illustrated by this New World species, parasitizing peccaries.

(*d*) *Xenopsylla cheopis* (Pulicidae). The external surface of the sensilla on the underside of the femur. They are covered by fine cuticular plates indicated by the arrows.

(Photographs (*a*)–(*c*) by Miriam Rothschild; photograph (*d*) by Miriam Rothschild and B. Martin.)

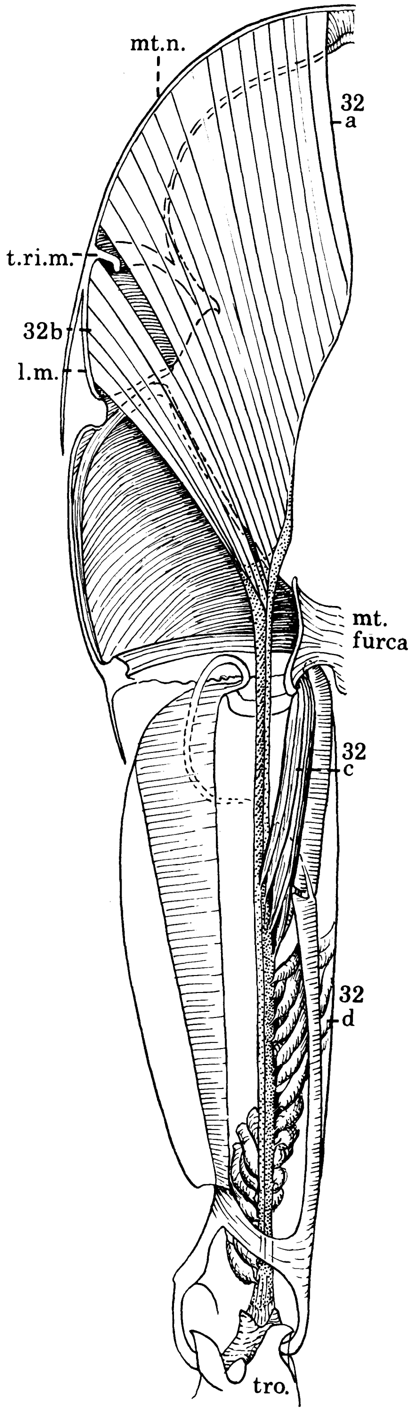
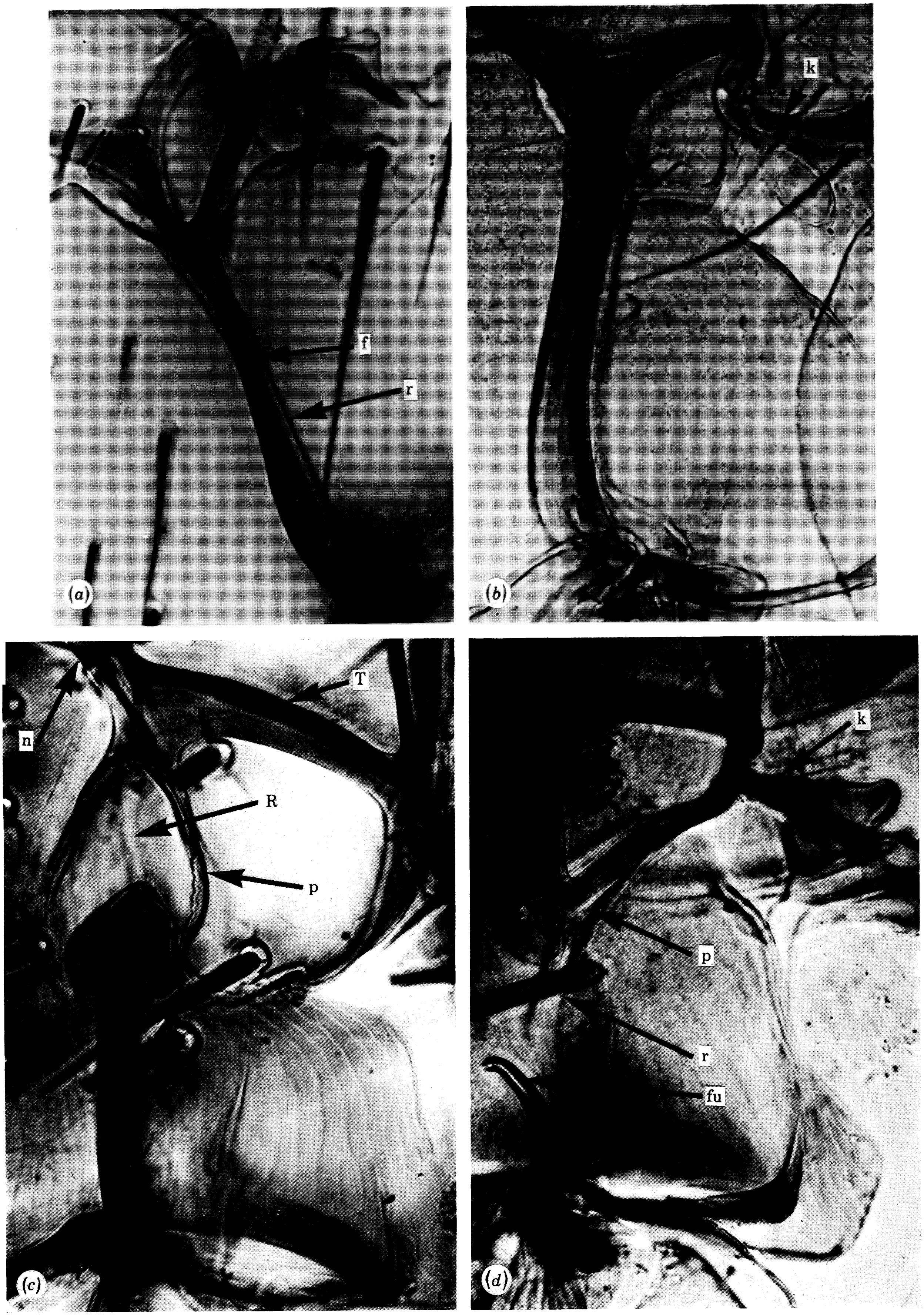


FIGURE 11. *Xenopsylla cheopis*. Metathorax, metacoxa and trochanter. Transverse section to show the relation of branches a, b, c and d of the trochanteral depressor. (Posterior aspect.)

DESCRIPTION OF PLATE 33

Whole mounts of pleural ridge and pleural arch of (*a*) *Choristopsylla tristis* Roths. (Pygiopsyllidae), a tree opossum flea; (*b*) *Ceratophyllus rusticus* (Ceratophyllidae), a bird flea; (*c*) *Ancistropsylla nepalensis* (Ancistropsyllidae), a deer flea; (*d*) *Rhadinopsylla cedestis* (Hystrichopsyllidae), a gerbil flea. Resilin in the highly modified pleural arch (p) is lacking in the opossum flea and bird flea, but the pleural ridgefold (f) is well developed in both species, suggesting these fleas, which inhabit high aerial nests, although poor jumpers, are mobile species. In *Rhadinopsylla*, not only the arch is lacking but the pleural ridge (r) itself is obliterated for much of its length – a condition often associated with the development of a large spur-like projection of the furca (fu). The 2nd thoracic link-plate (k) is well developed. This family of fleas contain typically static species, inhabiting the underground nests of hosts such as moles, shrews, voles and jirds. A very large cap of resilin (R) is present in the arch in *Ancistropsylla*, and one can deduce it is an exceptionally good jumper. The notal ridges (n) are slanting as in most Ceratophylloid fleas.

(Photographs by Miriam Rothschild.)



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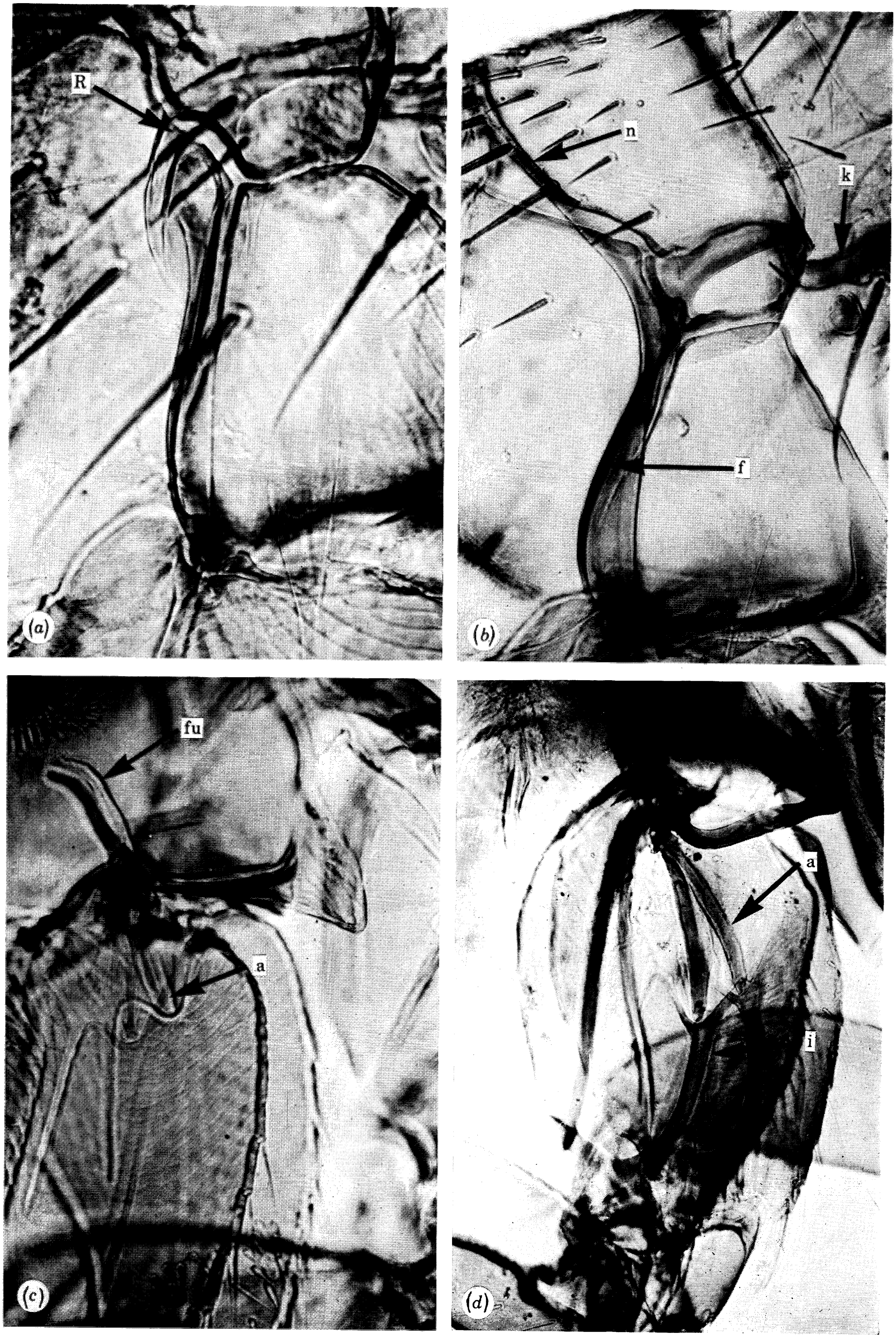

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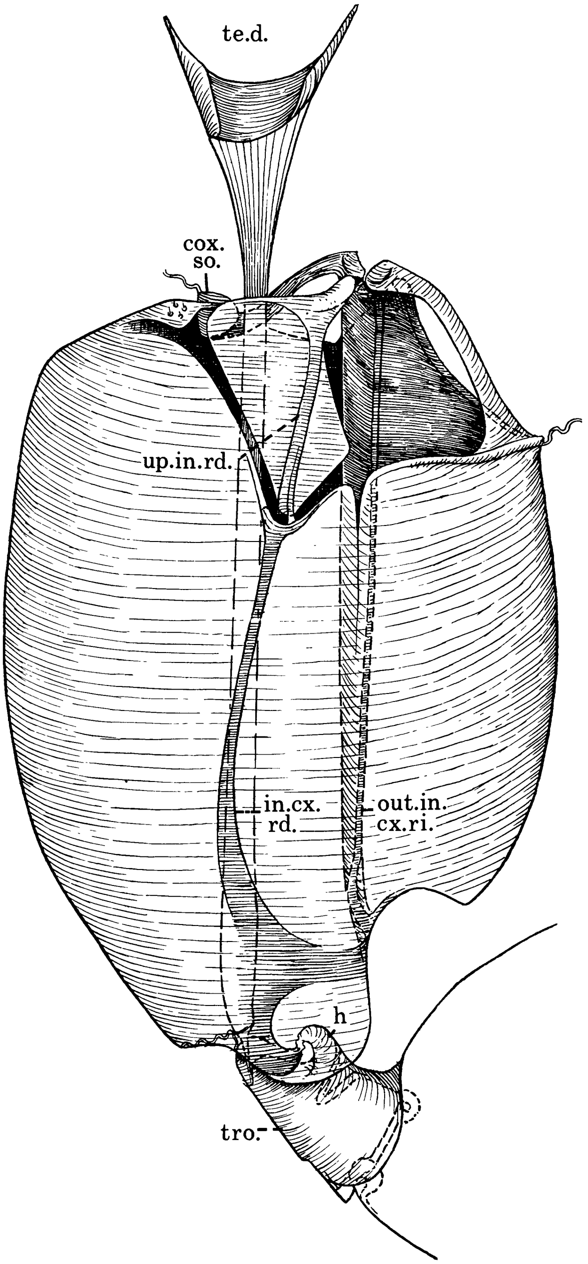


FIGURE 12. *Xenopsylla cheopis*. Metacoxa: lateral view of exoskeleton to show the relation of the coxal ridges, the trochanteral hook and the ridge which forms the coxal-abdominal catch. The femur is relaxed and thus the tendon of the trochanteral depressor is not pulled down into the coxal socket. It should be noted that the untanned portion of the socket is not shown (compare with plates 29*f*, 31*b*, *c*).

DESCRIPTION OF PLATE 34

(*a*) *Ctenophthalmus bisoctodentatus* (Hystrichopsyllidae). A parasite of moles. The pleural arch showing reduced resilin, typical of fleas parasitising mammals with a subterranean life-style.

(*b*) *Ceratophyllus rusticus* (Ceratophyllidae). A bird parasite infesting house martins. Metathorax illustrating the absence of pleural arch, heavily bowed pleural ridge and the sloping V-shaped notal ridges typical of Ceratophyllid fleas.

(*c*) *Stenischia mirabilis* (Hystrichopsyllidae). A parasite of shrew-moles. Metacoxa showing the marked development of the metafurca associated with fleas which have lost the pleural ridge. In addition the coxal rod is lost, only a weakly sclerotized articular sclerite remains. This suggests that the flea has not only lost the power to jump, but is also a very inactive species.

(*d*) *Glaciopsyllus antarcticus* (Ceratophyllidae). A parasite of birds. Metacoxa showing the elongated articular sclerites (a) and short, bowed inner coxal rod (i). This bird flea, despite the lack of pleural arch and its inability to jump, is known to be an active species.

(Photographs by Miriam Rothschild.)

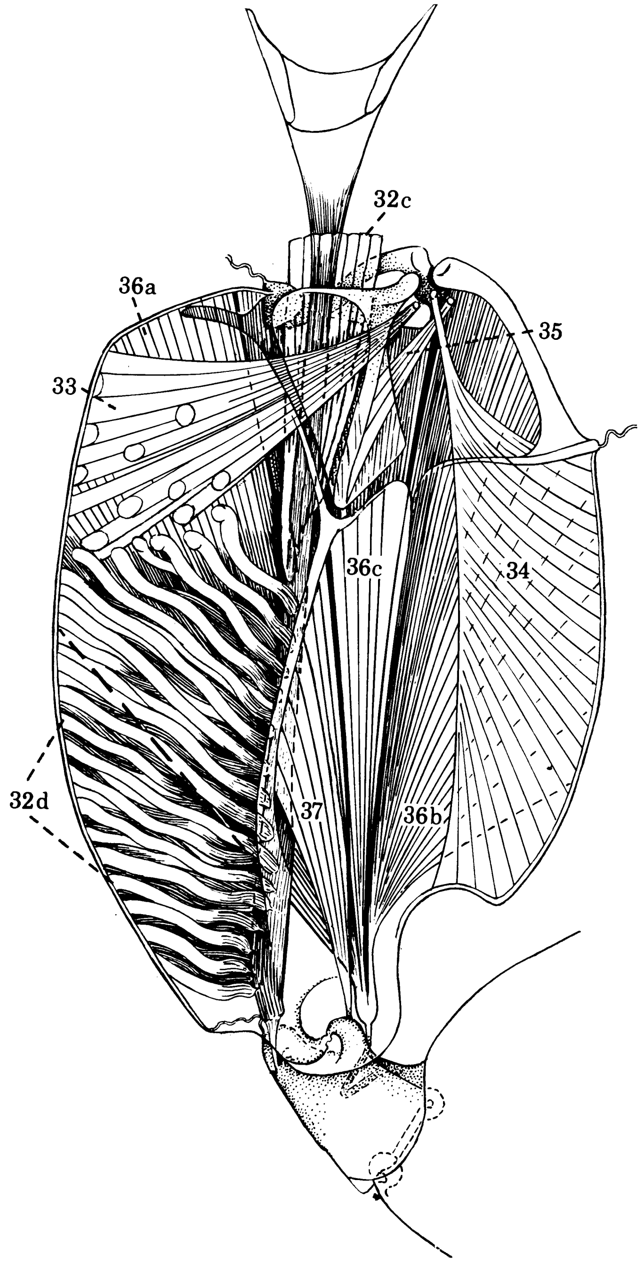


FIGURE 13. *Xenopsylla cheopis.* Metacoxa: lateral view seen from the inner surface. Dissection showing the muscles and tendon of the trochanteral depressor and levator.

DESCRIPTION OF PLATE 35

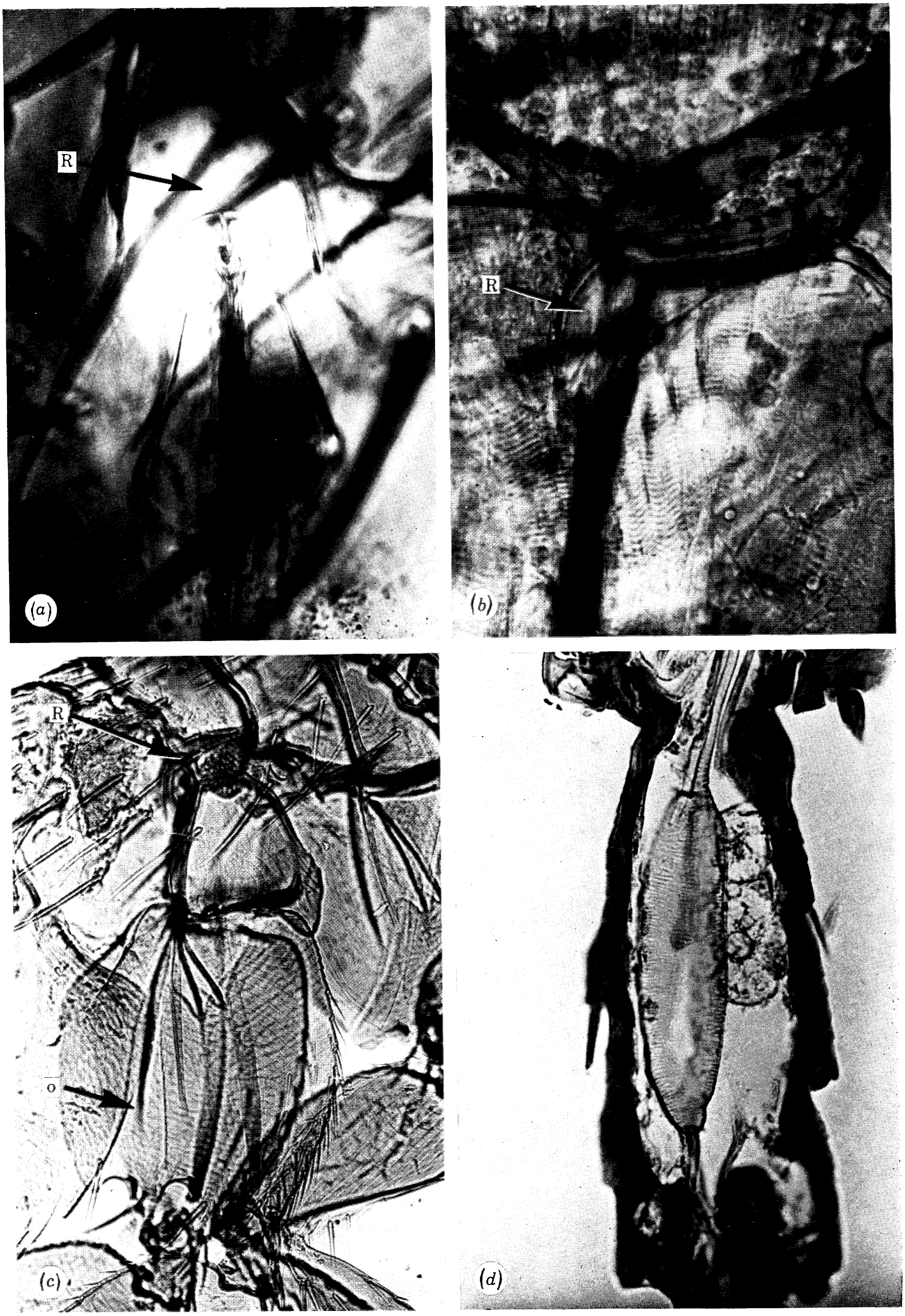
(*a*) *Vermipsylla alakurt* (Vermipsyllidae) (whole mount). The pleural arch showing a high domed mass of resilin (R).

(*b*) *Ischnopsylla octactenus* (Ischnopsyllidae). The greatly reduced pleural arch, showing a small remnant of resilin (R) flanking the pleural ridge. The photograph shows a living specimen. In fixed and stained material resilin in this species colours pale pink not bright red.

(*c*) *Ctenophthalmus nobilis nobilis* (Ctenophalmidae). Pleural ridge and metacoxa to show reduced resilin (R) in the pleural arch and the fading ridges (O) of the meta- and mesocoxa, characteristic of many fleas living in underground burrows. In this photograph the tendons of the trochanteral depressors show up more distinctly than the coxal ridges.

(*d*) *Spilopsyllus cuniculi* (Pulicidae). Longitudinal section through the 1st tarsal segment, showing an inflated tracheal air sac and two fat-body cells.

(Photographs by Miriam Rothschild.)



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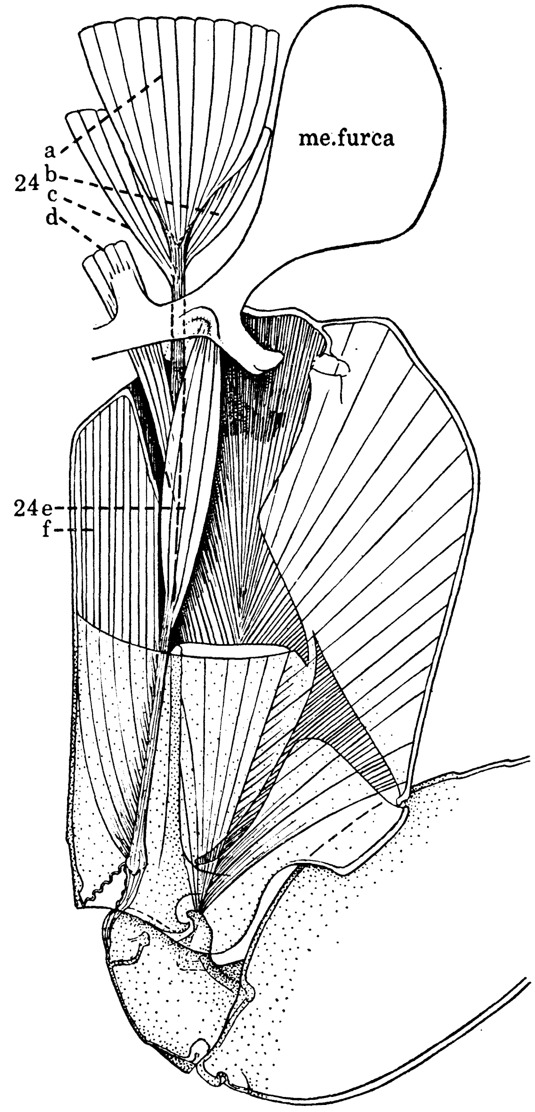

FIGURE 14. *Xenopsylla cheopis*. Mesocoxa to show the trochanteral depressor and its branches a–f, and the levator (not labelled).

portion consists of pure resilin grading into an outer portion of chitin microfibrils embedded in a resilin matrix. The excessively fine epicuticle divides this portion from the cuticular outer covering, which is moulded round it by a secretion of the shorter cells lining the cavity. The sharp junction between the cuticle and resilin (plate 26*e*, *f*) so characteristic of resilin, is in this case very understandable since they are everywhere separated by two exceptionally fine approximating layers of epicuticle. There are, however, signs of some sort of fusion between the two layers at the apex of the arch (plate 26*c*). In this way the resilin is held firmly sandwiched between

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DESCRIPTION OF PLATE 36

Xenopsylla cheopis (Pulicidae). Coxal joint showing the slight angle at which the coxa and femur are set and the ridges and striations of the cuticle (magn. × 1120).

(Photograph by Howard Hinton.)

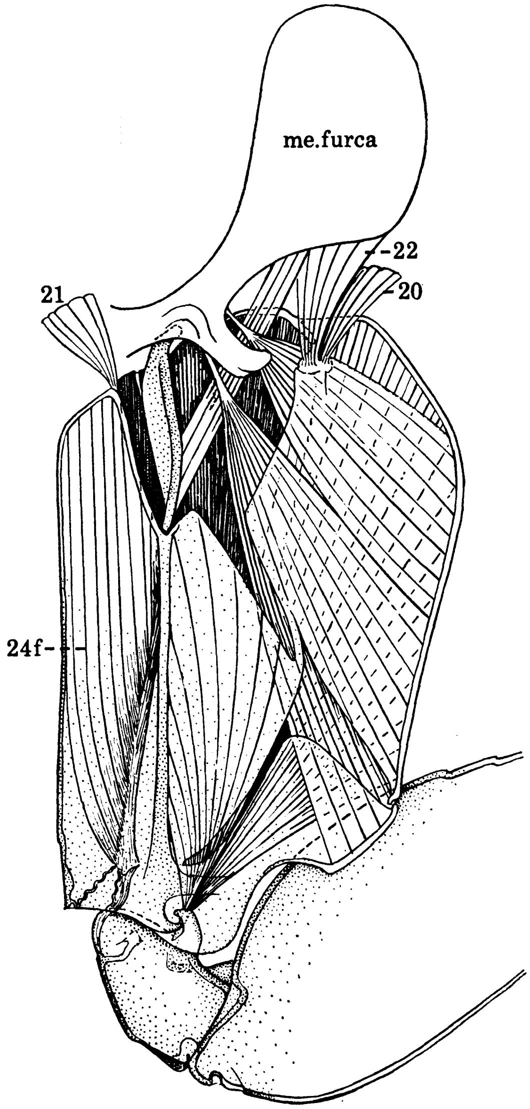

FIGURE 15. *Xenopsylla cheopis*. Mesocoxa to show the levator and insertion of the indirect flight muscles on the rim of the coxa.

the cuticular pleural ridge (which is not detached anywhere from the pleural wall as in the case of the pleural rod of the mesothorax) and the notal ridge. The pleural ridge is thus partially hooded by resilin and cavities are formed between the resilin pad and its points of attachment. Squeezed within these cavities, in all species so far examined, are two large fat-body cells (plate 26*e*).

The resilin can already be identified in the pupal stage (plate 28*b*) but the cuticular portion of the arch is secreted comparatively late in development. In the pharate adult, considerably after the pleural ridge begins to tan, the cuticular outer covering of the arch still consists of secretory cells and the cuticular 'helmet' has not been formed (plates 26*a*, *b*, 28*a*). Before tanning, the cuticle stains red, both inside the secretory cells in the form of droplets, and after it has been laid down, round the resilin (plate 28*a*) in a continuous sheath.

Resilin was identified by examining the structure in ultraviolet light, when it fluoresces with a characteristic blue light which intensifies in an alkaline medium (plate 25*e*) NH_4OH.

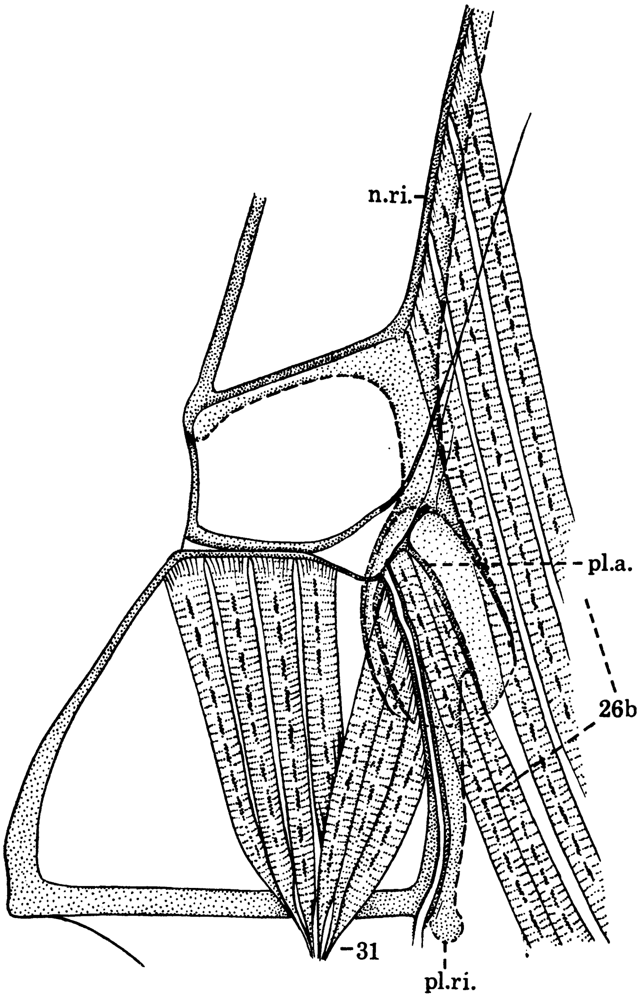

FIGURE 16. *Xenopsylla cheopis*. Diagram of the pleural arch to show the origin of muscle fibre beneath the arch and along the notal and metepisternal ridges and the pleural ridge.

It stains turquoise blue with toluidine blue or brilliant red with azo-carmine (plates 25*f*, 26*a–f*). It is isotropic if unstained, and unstrained viewed by polarized light.

(ii) *Cuticular ridges* (*lines of force*) (plate 25*b*, *c*)

The two pleural arches are interconnected in *X. cheopis* and other Pulicoid fleas by the notal ridge (plates 30*a*, 31*a–c*n, 32*c*) which thus forms a powerful arch or saddle over the back. The ventral ends of pleural ridges in their turn are inserted into sockets in the top of the coxae (plate 27*e*, figures 5, 9) which are thus articulated with the powerful outer coxal ridge (figure 10) and are in turn braced against the trochanteral articulations. This series of vertical ridges from notum to trochanter form the 'line of force' (plate 25*b*) along which energy travels when the compressed resilin expands suddenly. The pleural arch, cuticular ridges and epipleural muscles, form a 'booster' system for the jump. It is important for the jumping performance of the flea that the resilin arch is placed on the periphery of the thorax (plates 25*c*, 29*c*, figures 2, 10, pl.a).

(iii) *Link-plates and catches* (plates 29*a*, *b*, *e*, h, cl, 31*a*k4 figures 3 lnk.pl., 4, fust.)

When the flea jumps it is essential that the thorax is rigid and the legs pressed firmly against the body for take-off. There are various cuticular catches, hooks, pegs, and so forth, which link or press the various segments together and which are involved in stiffening the body when it is 'cocked' for take-off; probably only one central curved peg is directly concerned with the click mechanism of the jump. There are also certain internal structures which are of great importance in bracing the trochanteral depressor tendon for the jump. The two pairs of so-called thoracic link-plates (Snodgrass 1946; Hopkins & Rothschild 1971; Rothschild 1975) are small, movable sclerites which strengthen the connexion between the three thoracic segments and also align them with great precision. These sclerites (plates 31*b*, 33*b*, *d*, 34*b* k, figures 3–5,9 lnk.pl.) can be pulled backwards (1st thoracic link-plate) and rotated upwards (1st and 2nd thoracic link-plate) thus raising the relevant segment and clamping the mesonotum under the pronotum and the metanotum under the mesonotum (Rothschild *et al.* 1975, figures 4*a*, *b*, p. 509). The upward rotating movement of the link-plates (brought about by the action of the ventral longitudinal muscles) is possible because of the abrupt interpolation of a highly flexible arthrodial membrane (plate 26*f*, also Rothschild *et al.* 1975, plate 41*e*) in the pro- and mesonotum (figure 3) and in the sclerotized ridge in the upper corner of the lateral metanotal area and mesopleuron, into which the tips of the link-plates are inserted. Their action automatically aligns various pegs or clamps with their respective sockets, which also serve to link the segments together.

The median unpaired hook-like peg (plate 29*a*, *b*, figures 3, 4, 9 fust., also Rothschild *et al.* 1975, plate 41*a*, *c*) which fixes the mesothorax to the metathorax provides the principal click mechanism of *Xenopsylla*. In this group it consists of a heavily sclerotized hook-like protuberance (with a slightly bifid tip) of the base of the mesofurca which is inserted in a membranous socket in the metepisternum (plate 29*a*, *b*, figure 9), when the flea is 'cocked' for take-off. The size of this peg varies from species to species, and there is a certain degree of correlation between its thickness, length, and the development of the knuckle-like terminal portion, and the amount of resilin in the pleural arch.

A mechanism (there may be two in some species) for fixing the hind coxa against the abdomen is present in all fleas, but it is most highly developed in good jumpers (plates 29*e* cl, 30*f*, *g*). This also shows some bewildering modifications (see p. 484). In *Xenopsylla* it consists of a ledge-like protuberance in the upper third of the hind margin of the hind-coxa, which is pressed against a sclerotized ridge on the 2nd abdominal sternum when the flea is ready for take-off.

There is a funnel-shaped guide socket through which the tendon of the depressor passes from thorax to coxa, which is situated in the upper portion of the coxa (plate 29*f*), and which probably plays an important part in the mechanism of the jump. The inner (mesal) wall of this funnel is heavily sclerotized (the only portion visible in mounted material since the untanned areas are transparent (plate 31*b* so, figures 2, 5, 10)), and a peg-like portion of it projects above the margin of the coxa and fits into a membranous sinus in the base of the metasternum. This also serves to fix the coxa in position when the flea is collected for take-off. Here again a strongly developed sclerotized guide socket is correlated with a large pleural arch. In addition the point at which the cuticular process at the base of the pleural ridge fits into an acetabulum on the upper margin of the coxa is larger and more heavily tanned in good jumpers. Snodgrass (1946) describes the two trochanteral hooks (plate 27*f*, figures 8, 10, 11, 13) which slot into the distal end of the coxa as 'The usual type of dicondylic coxal articulation with a transverse hinge axis on the end of the coxa'. He also noted that the coxal ridges are braced against the trochanteral articulations. When the femur is raised, both trochanteral hooks become deeply engaged in their sockets in the basal portion of the coxa, and this action also serves to press an internal cuticular knob at the base of the outer hook against the base of the tendon of the depressor (plate 27*a*, *b*, *d*). The tendon is pulled down into the heel of the trochanter (figure 8), and the membranous portion between the coxal wall and the trochanter fully stretched (plate 27*d*, x). The cup-shaped knob clamps, limpet-like, against a slight depression in the surface of the tendon, thus preventing any chance of 'overcentring' (plate 27*b*, *d*) and also probably serving as a shock absorber. This portion of the tendon is, chronologically, the first to develop red-staining cuticle in the pharate adult stage.

The most heavily tanned clamp in the flea is the curious black 'soldering' device between femur and trochanter (plates 27*f*, 30*f*). This is a permanent brace, allowing some slight movement between femur and trochanter, but not the freedom permitted by a hook which can be partially withdrawn from a socket when the insect is in the relaxed position. Clearly this area must take the full impact of the leg striking the substratum and needs strong support. No other portion of the exoskeleton except the claws, and various spines such as the pronotal and genal combs, is so densely tanned.

At the site of all the important external clamping and strengthening devices are small groups of trichoid sensilla. In the third thoracic segment these are found in association with (*a*) link-plates (plate 26*f*); (*b*) area of meso- and metanotal approximation; (*c*) trochanteral hooks (plate 27*b*); (*d*) coxal/abdominal sternal clamp; (*e*) unpaired mesopleural/metepisternal hook-like peg (Rothschild *et al.* 1975, plate 41*c*); (*f*) coxal/metepisternal peg; (*g*) area of pleural articulation with the coxal socket (plate 27*e*), and (*h*) associated with the tendon guide socket. In addition there is an interesting group of campaniform sensilla (in this case covered by a thin layer of cuticle (plates 27*f*, 32*d*, s) in an unusual, probably unique position, on the underside of the femur, situated near the trochanter. These sensilla are no doubt associated with the flea's habit of jumping off its trochanters and femur – rather than its feet. There are, of course, numerous other campaniform sensilla in various parts of the fleas' anatomy, but these are of a more usual type.

(iv) *Recoil mechanism and shock absorbers*

The cuticle of the pharate adult *Xenopsylla* stains a uniform bright red with Mallory's triple stain. When the cuticle tans, this scarlet hue is replaced by a golden yellow colour. Arthrodial membrane and the immensely fine epicuticle stain blue. During adult life there are small areas in which the cuticle remains untanned and stains red. One may speculate that these flexible areas function as shock absorbers, or provide strong support without rigidity. Characteristic areas of untanned cuticle are found at the point of insertion of muscles – for instance, the epipleural muscles in the anterior margin of the coxa (plate 27*c*). A different type of insertion is present in the form of a strip of untanned cuticle interpolated behind the group of sensilla on the underside of the femur. Again, the end of the knob where it is clamped against the base of the trochanteral depressor tendon consists of untanned cuticle whereas the base is well tanned (plate 27*b*). Arthrodial membrane supports the base of the pleural ridge where it articulates with the coxa (plate 27*e*), and may well exert a protective function during recoil. We have already drawn attention to the points of insertion of the link-plates which are partly formed by arthrodial membrane, and the outer portion of the tendon guide-sockets which are untanned cuticle. The heavily tanned (almost black) trochanteral femoral clamp (plate 27*f*) is surrounded by a small area of untanned cuticle.

(*c*) *Musculature and tendons* (plates 25*a*, *b*, *d*, 27*a–e*, 28*a*, *c–e*, figures 1, 2, 6–11, 13–16)

(i) *General considerations*

The musculature of the flea's thorax, due to the loss of wings and the various adaptations to the parasitic life-style, is highly modified. Some of the direct and indirect flight muscles have been retained, but their area of origin has shifted and various sclerites which would have provided useful 'landmarks' have been altered or altogether obliterated. The homologies of certain muscles are therefore extremely doubtful. Thus we have suggested homologies between the tergo-pleural muscles (2*b* and 3*b*) found in the wing-bearing segments of other insects, and our thoracic muscles 4 and 5 (figure 7), but such deductions must be regarded as speculative.

We would have much preferred to have adopted or modified the numbering or lettering of any of the existing systems, rather than re-number them ourselves, but in view of the type of discrepancies between the various accounts, we felt that such a procedure would create additional confusion. As we have pointed out (p. 459) the numbers are a matter of mere convenience, and do not in any way represent a permanent scheme. As far as the mechanism of the jump is concerned, the one important difference between our observations and those of previous authors concerns the presence of the two muscles which we have described arising along the ridge of the metepisternum (30 and 31), inserted on the anterior dorsal rim of the metacoxa (see p. 466). In existing descriptions they have been missed, i.e. mistaken for branches of the trochanteral depressor (Snodgrass's 63b), which are inserted on the tendon within the coxa, and originate along the transverse ridge of the lateral metanotal area. In Pulicoid fleas 63b is lacking altogether, but some fibres† (lying mesad of our muscle 31) inserted on the tendon, originate along the ridge of the mesosternum (internal to our muscles 30 and 31) as described by Snodgrass (1946), and are present in various Ceratophylloid fleas including bat fleas, Hystrichopsyllids and Ancistropsyllids.

The importance of muscles 30 and 31 lies in their situation external to the trochanteral depressor, for they are part of the 'booster' complex which controls the compression of resilin and the maintenance of the series of cuticular ridges forming the line of force.

The structure of the trochanteral depressor muscle (the starter muscle) is highly specialized. Cullen (1975) (p. 491 of the present volume) shows that it is similar to the tubular leg muscles of other insects, but exhibits two notable features.

(i) More sarcoplasmic reticulum (s.r.) than in any other insect muscle so far examined by electron microscopy;

(ii) The s.r. is arranged in three distinct configurations in a form not observed hitherto in insect muscle. Both the large volume and surface area of s.r. are undoubtedly specializations concerned with the rapid contraction necessary for the jump.

There is some variation in different species of fleas in the number of individual muscle fibres in the trochanteral depressor and the epipleurals. In *X. cheopis* there are between 70 and 78 in the former and 69 and 83 in the latter (table 2), but this is greatly exceeded in other species.

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† These were discovered after the publication of the Glossary of volume V of the *Catalogue of the Rothschild Collection of Fleas* and are not mentioned in that description of the metathorax.

TABLE 2. THE NUMBER OF FIBRES IN THREE MUSCLES OF *XENOPSYLLA CHEOPIS* (FIVE SPECIMENS)

mesothorax: depressor of the trochanter (thoracic branches)	45	49	37	40	44
metathorax: depressor of trochanter (thoracic branches)	71	78	73	70	70
metathorax: epipleural muscle (III segment)	70	83	77	69	68

The most impressive structure of the flea's jumping apparatus is the massive tendon of the trochanteral depressor. From our stained sections it looks like a red bar skewering the coxa from mid-line to base (plate 25*a*, figures 1, 2). In species which contain a large volume of resilin in the pleural arch, such as *X. cheopis*, the tendon has the greatest width (seen in lateral aspect since it is flattened from side to side and is not circular in transverse section), especially at the distal end where it is inserted in the trochanter (figure 10). The tendon of the levator presents a great contrast, for it is short and shaped like a peardrop, and is somewhat reminiscent of the handle of a fan, the muscle fibres spreading out fanwise from the point of insertion over the outer surface of the coxa (plate 28*d*).

(ii) *Numbering and location of the muscles*

In table 1 we provide a comparison of the numbering and lettering of the muscles described in the thorax and the jumping (3rd) leg by Lewis (1961), Jacobson (1940), Snodgrass (1946) and ourselves. We also append a brief description of the insertion and origins of these muscles. Snodgrass arranged his muscles in main groups designated in the text by a letter, quite separate from his labelling of figures. The letters in parentheses after our number refer to these main groups, not his diagrams.

Xenopsylla cheopis *the muscles of the thorax and metacoxa*

(plates 25, 27, 28, figures 1, 2, 6–11, 13, 16)

(The letters indicate the identification of the muscles according to the division into groups by Snodgrass (1935) and figures 58–70 refer to Snodgrass' labelling, 1946.)

1st segment (prothorax)

No. 1. *Cervical muscle* (= 21b of Wenk), figure 6 (1). Originates on the postocciput, above and lateral to the foramen magnum; inserts on the cervical link-plate (cervical sclerite).

No. 2. *Longitudinal median muscle* (A, Dmcl), figure 6 (2). Extends from 1st phragma to postoccipital area, separated here into two branches: the different direction of the fibres suggests that each branch exercises a different function.

No. 3. *Oblique latero-dorsal muscle* (A, 1A), figure 6 (3). Originates on the upper part of the pronotum; inserts on the lower lateral margins of the first phragma.

No. 4. *Tergopleural muscle I* (B, 2B), figure 7 (4). Originates on the pronotum on its anterior lateral side; inserts in the membrane between the upper edge of the propleurum and the 1st thoracic link-plate.

Our suggested homology between Snodgrass' muscle 2B 'which goes from the lateral tergal margin to the basalare' is highly speculative. We are not suggesting thereby that the 1st thoracic link-plate is a modified basalar sclerite (Rothschild 1975).

No. 5. *Tergopleural muscle II* (B, 3B), figure 7 (5). Originates posterior to and below I on the lateral pronotum; inserts on the upper posterior apex of the 1st thoracic link-plate. Note that this muscle was not observed by Snodgrass. In his description of the thorax (1946, p. 21) he says 'no muscles were observed attached on the first link-plates'. We consider this muscle is probably homologous with 3B of Snodgrass (1937) 'going from the tergum to the wing process'.

No. 6. *Lateral intersegmental muscle* (= oblique intersegmental muscle) (F, F), figure 6 (6). Originates on the first phragma; inserts on the upper part of the profurca (Wenk, 24).

No. 7. *Ventral muscle* (H, H), figure 6 (7). Originates on the upper anterior side of the profurca; inserts beside the foramen magnum (Wenk, 24).

No. 8. *Ventral transverse muscle* (H), figure 6 (8). Connects the upper inner parts of the profurca.

No. 9. *Sternocoxal muscle I* (= sternal promotor of Snodgrass) (K, K), figure 6 (9). Originates on the median anterior half of the prosternum; inserts on the inner upper rim of the coxa above the coxal articulation.

No. 10. *Sternocoxal muscle II* (= sternal remotor of Snodgrass) (L, L), figure 6 (10). Originates on a large area of the prosternum; inserts on the outer rim of the coxa, below the coxal articulation.

No. 11. *Sternocoxal muscle III* (included in Snodgrass' description of the sternal remotor) (L), figure 6 (11). Originates on the profurca; inserts on the coxal rim near the insertion of 10(B).

No. 12. *Pleurocoxal muscle I* (M, 2M), figure 6 (12). Originates along the upper surface of the propleuron; inserts on the upper inner margin of the coxal rim.

No. 13. *Pleurocoxal muscle II* (M, 1M), figure 6 (13). Originates on the upper anterior surface of the propleuron; insertion on the mesal rim of the coxa, below the coxal articulation.

2nd segment (mesothorax)

No. 14. *Longitudinal median dorsal muscle* (A, mA), figure 6 (14). Connects the first phragma to the second phragma.

No. 15. *Oblique latero-dorsal muscle* (A, 1a), figure 6 (15). Originates on the posterior dorsal half of the mesonotum; inserts on the lower inner margin of the second phragma.

No. 16. *Tergopleural muscle* (B, 4B), figure 7 (16). Extends from a small protuberance on the lower posterior part of the mesonotum to a pleural suture between the base of the pleural rod and the second thoracic link-plate.

No. 17. *Lateral intersegmental muscle* (F, F), figures 6, 9 (17). Originates on one side of the lateral protrusion of the mesofurca; attaches on the other side to the anterior inner edge of the metanotum, above the articulation of the 2nd thoracic link-plate.

No. 18. *Pleurosternal muscle* (G, G), figures 7, 9 (18). Originates on the upper anterior flap of the 2nd thoracic link-plate; inserts on the upper anterior margins of the mesofurca. Lewis and Snodgrass describe only one muscle attached to the 2nd thoracic link-plate of fleas. The suggested homology with Snodgrass' muscle G, the pleurosternal muscle, is again speculative.

No. 19. *Ventral longitudinal muscle* (H, H), figure 6 (19). Originates on the greater part of the lateral surface of the mesofurca; inserts by a tendon to the lower posterior angle of the profurca.

No. 20. *Tergal remotor of the leg* (J, D70), figures 7, 9, 15 (20). Originates on the anterior surface of the 2nd thoracic link-plate; inserts on the posterior part of the base of the mid-coxa.

No. 21. *Sternal promotor of the leg* (K, K), figures 6, 15 (21). Originates on the mesosternum; inserts on the outer anterior rim of the coxa.

No. 22. *Sternal remotor of the leg* (L, L), figures 7, 9, 15 (22). Originates on the posterior lower surface of the mesofurca; inserts behind the mid line of the base of the mid-coxa.

No. 23. *Adductor muscle of the coxa* (N, N) figures 6, 9 (23). Originates on the lower part of the mesofurca; inserts on the inner anterior rim of the mid-coxa.

No. 24. *The depressor of the trochanter* (mesothorax) figures 7 (24); 14–15 (24). There are three thoracic branches which insert on the trochanteral depressor tendon above the level of the coxa. (a) is the largest, a notal branch originating on the anterior portion of the lateral and dorsal walls of the mesonotum; (b) originates on the anterior part of the mesepisternum and the upper part of the mesosternum. Branches of (b) and (c) are continuous but may perform different functions. Three branches (d), (e) and (f) join the tendon below the level of the coxa. (d) originates on the margin of the metasternum and mesepisternum and descends to insert on the tendon about one-third from the coxal dorsal margin. (e) originates under the mesofurca and inserts along the tendon after (below) the insertion of branch (d). (f) originates along the anterior border of the coxa and inserts along the tendon extending from below the attachment of branch (e), to near the distal end of the trochanter.

3rd segment (*metathorax*)

No. 25. *Longitudinal dorsal muscle* (A, mA), figure 6 (25). Connects the second and third phragma.

No. 26. *Epipleural muscle or coxosubalar* (E, 3E″, 58), figures 1, 2, 6, 10, 16 (26). Branch (a) originates on the greater part of the surface of the metepimeron. (b) originates along the notal ridge and some fibres in the posterior concavity, under the pleural arch. Both branches insert on the posterior basal part of the hind coxa, on the ridge which forms the coxal/abdominal catch.

No. 27. *Ventral longitudinal muscle I* (H, H), figures 6, 9, 10 (27). Originates on the inner posterior side of the mesofurca and inserts on the upper part of the metafurca.

No. 28. *Ventral longitudinal muscle II* (H, H), figure 6 (28). Connects the posterior upper margins of the metafurca to the crescent-shaped sclerotization in the 2nd abdominal sternite forming the coxal/abdominal catch.

No. 29. *Sternal remotor of the leg* (L, L), figures 7, 10 (29). Originates on the outer (lateral) surface of the metafurca; inserts on the coxal socket of the pleural ridge.

No. 30. *Pleurocoxal muscle I* (M, 1M, 63b), figures 1, 6 (30). Originates on the anterior part of the metepisternum; inserts in a depression in the outer rim of the coxa, anterior to the pleural/coxal articulation.

No. 31. *Pleurocoxal muscle II* (M, 2M, 63*c*), figures 7, 16 (31). Originates on the posterior half of the metepisternum; inserts on the upper part of the coxa alongside no. 30.

No. 32. *The depressor of the trochanter* (P, Q, 63d), figures 1, 2, 7, 10, 11, 13 (32). There are two thoracic branches which insert on the trochanteral depressor tendon above the level of the coxa: (a) which originates on the metanotum and occupies the entire area anterior to the notal ridge, except for a narrow median dorsal strip, and (b) which originates along the transverse ridge of the lateral metanotal area (figures 3, 5 t.ri.m.). Both insert at the thoracic end of the tendon. (c) (homologous with 24e (figure 14)) originates under the metafurca and inserts along the tendon about one third of the way from the coxal margin. (d) originates along the anterior border of the coxa and inserts along the tendon from below the attachment of (c) to the distal end of the tendon, which inserts within the anterior end of the trochanter. This muscle is homologous with 24f (figure 14) but it originates over a wider area of the anterior coxal border. In the trochanteral depressor of the mesothorax there is a branch 24d (figure 14) which originates on the margin of the metasternum and metepisternum and inserts on the tendon. This muscle (see above, p. 478), designated 63b by Snodgrass, does not exist in the metathorax of Pulicoid fleas.

No. 33. *Sternocoxal muscle I* (rotator and promotor) (59), figures 6, 13 (33). Originates on the posterior angle of the metafurca. Broad insertion within the coxa of the upper third of the anterior mesal wall of the coxa.

No. 34. *Sternocoxal muscle II* (remotor and rotator) (60), figures 6, 13 (34). A broad origin along the posterior mesal wall of the coxa. Insertion on the metafurca above the coxal articulation. The homologous muscle in the mesocoxa (not numbered by us in figure 15) is split into two.

No. 35. *Sternocoxal muscle III* (61), figures 6, 13 (35). Originates on the inner face of the articular sclerite of the inner internal rod (figure 10, 12). Inserts on the metafurca near no. 33.

No. 36. *The levator of the trochanter* (0, 62a, b), figures 1, 2, 8, 10, 13 (36). Large branches (a) and (b) originate, spreading fanwise, over most of the lateral inner surface of the hind coxa. Branch (c), mesal branch, originates along the posterior fork of the inner internal rod. All three branches join a short pear-drop shaped tendon which inserts behind the axis of the coxo-trochanteral articulation, near the lateral hook of the trochanter. In the pharate adult the division of 36a and b into two main branches is much more distinct than in the adult flea.

No. 37. *The rotator of the trochanter*, figures 8, 10, 13 (37). Originates along most of the upper surface of the inner internal rod of the coxa. It inserts in the membrane in front of the inner (mesal) hook of the trochanter. This muscle pulls up the hook (rotates the trochanter) when the femur is elevated.

4. COMPARISON WITH OTHER SPECIES: THE SECONDARY LOSS OF THE PLEURAL ARCH AND JUMPING ABILITY

The Pulicoidea have a closer association with the body of the host than the Ceratophylloidea which visit, rather than live continuously, in the fur of the host. The latter superfamily have a more elongated, less compact body and relatively shorter legs. The bat fleas, however (Hopkins & Rothschild 1956, plates 18–20), which are mostly blind cave dwellers (living as larvae in bat guano and climbing the walls to reach their hosts), have developed long, delicate, spindly legs (plate 32*b*), which is a feature of many troglodyte insects (Jefferson 1974). A high proportion of Pulicoid fleas (Hopkins & Rothschild 1953) have a large hind coxa and a greatly reduced midcoxa, whereas those of Ceratophylloid fleas are of approximately equal width, and, occasionally, even narrower than the midcoxa in some bat fleas (e.g. *Porribius caminae* Roths.). Undoubtedly the middle leg plays a more important role in jumping, and maintaining balance in take-off, in the Ceratophyllid fleas. Furthermore the pleural ridge is not so drastically shortened and the notal and transverse ridge of the metanotal area form a V-shaped, instead of a right-angled join with the pleural ridge – due to the notal ridge sloping backwards (plates 32*a*, 34*b*) as in *Ceratophyllus*, *Paractenopsyllus*, *Cratynius*, etc. This is a less specialized condition than the vertical notal ridge of *Pulex*, *Spilopsyllus*, *Moeopsylla* and *Echidnophaga* (plates 30*a*, 31*c*, 32*c* and Hopkins & Rothschild 1953). The importance of the vertical ridges in good jumpers is emphasized in the latter genus (plate 30*a*, *e*). Here the thorax has been greatly reduced in connexion with its sessile habits (Jordan & Rothschild 1906), and the shape of the coxa is strongly modified. Nevertheless a long, straight, heavily sclerotized notal ridge has been retained (plate 30*a*, *e*), and the coxal ridge is displaced towards the back of the leg, thus forming a vertical line of force when the flea is braced for take-off. This arrangement is most characteristic of Pulicoid fleas, but here and there one encounters unrelated genera which have also developed a striking vertical ridge. Similarly, scattered throughout the order, are sporadic examples of fleas without a pleural arch (plates 33*a*, *b*, *d*, 34*b*) in which the resilin is greatly reduced or lacking altogether, and this is associated with the modification of other features characteristic of good jumpers such as the heavy sclerotization of notal and coxal ridges. There is, however, only one described Pulicoid flea, *Xenopsylla papuensis* Jordan (Traub 1972, pl. 17, fig. 92), which has lost all but mere traces of resilin in the pleural arch, but it still retains many features of good jumpers. A recent discovery of a blind *Xenopsylla* from New Guinea (Traub in litt.) displays more of the features which we have come to associate with 'nest' fleas in other groups (Rothschild 1966).

Surprisingly few observations have been made on the jumping powers of fleas lacking the pleural arch. Species such as *Ceratophyllus rusticus* (plate 33*b*) and *Ischnopsyllus octactenus* (a blind species (plate 35*b*)) both of which retain only remnants of resilin, can execute small jumps (personal observations) but are, on the whole, poor performers (Rothschild *et al.* 1975, p. 504 and table 2). This probably applies to many similar species although some, of course, may be crawlers only. Thus Holland (1949) remarks in passing that no specimens of the rather sluggish *Tarsopsylla* 'were noted to jump vigorously'. Hůrka (1963) says that freshly hatched *Ischnopsyllus intermedius* (Rothschild) (a species with a greatly reduced pleural arch) sometimes reacted by jumping if blown upon, 'otherwise a rare phenomenon in this flea family'. Hase (1931) recorded small jumps for a blind archless bat flea *Myodopsylla wolffsohni salvasis* Jordan, and Weidner (1937) records that two specimens of *I. hexactenus* (Kolenati) escaped capture by jumping.

There is a remarkable lack of uniformity in the morphological details associated with the reduction or loss of the arch – even if it is in response to the same specialized situation, e.g. high aerial nests built by hosts such as squirrels or swallows†, or life in bat caves. Nevertheless, the tendency to respond similarly to a special circumstance or a given hazard in the environment, occurs within a framework imposed by the basic morphological characteristics of the family, subfamily or group. Thus if a Ceratophyllid flea secondarily becomes a nest flea and responds among other things by the loss of the pleural arch, it will generally retain an elongated pleural ridge (plates 30*c*, 33*a*), a slanting notal ridge – even if the sclerotization is greatly reduced – and the relatively broad midcoxa characteristic of the family.

In addition there are modifications of the coxal ridges in poor jumpers. In many species associated with hosts (plate 35*c*) living in burrows or underground nests, such as *Ctenophthalmus*

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† Fleas with arboreal hosts or bird hosts which build high aerial nests may be forced along opposite evolutionary paths – either developing bigger and better pleural arches or losing them altogether.

nobilis nobilis Roths. (Ctenophthalminae) the outer coxal ridge is less heavily sclerotized and peters out before it reaches the trochanteral joint, thus obliterating or partly obliterating the line of force. In *Stenischia mirabilis* Jordan (Rhadinopsyllinae) a flea lacking both pleural arch and pleural ridge, the coxal ridge is also missing (plate 34*c*).

Ceratophyllid fleas which have lost the arch, such as *Glaciopsyllus antarcticus* Smit & Dunnet, *Ceratophyllus rusticus* and *C. arcuegens* Holland, tend to develop a long articular sclerite of the metacoxa, associated with a wide, heavily sclerotized, bowed, inner internal rod of the metacoxa (plates 30*h*, 34*d*) and a massive deep curved pleural ridge-fold (plate 33*a*). These features may be correlated with walking as opposed to jumping – either wandering or migrating from open nests on the ground, or climbing up or down vertical surfaces (Smit 1972), and such Ceratophyllid nest fleas are rarely blind.

The various linking devices show considerable variation between species. In a number of Pulicoid fleas such as *Echidnophaga* in which the thorax is greatly reduced (plate 30*a*, *e*) in connexion with their semi-sessile life-style, an associated loss of one or both link-plates occurs. However in bat fleas, including those which do not jump, the link-plates are large and elongated, probably an adaptation associated with their long flexible sinuous thorax. In *Echidnophaga* and related genera, and also in Ceratophyllid fleas, the mesofurcal peg and the click mechanism have developed along a slightly different pattern. (A comparison of these variations will be made in a later paper.) In some big jumpers such as *Moeopsylla*, the upper margin above the metacoxal catch is bar-like and heavily sclerotized (plates 30*d*, 31*b*). In several species of *Echidnophaga* there are two sternal sockets which accommodate hook-like protuberances and expansions of the metacoxa (plate 30*f*, *g*), but in others there is a sclerotized nipple on the sternum which fits into a coxal slot. In Pygiopsyllids (plate 31*a*) a spur or furca, arising near the base of the pleural ridge, is inserted into a strongly sclerotized socket on the anterior edge of sternum II, above the 4th link-plate† (4k). In Pygiopsyllids with reduced resilin, this furca is also reduced or absent, and the stout socket (or squamulum) of the 4th link-plate less heavily tanned. At death most of the hooks and catches are released from their sockets and are rarely seen in position in mounted specimens. Hence the true nature and function of these structures have not previously been fully recognized and appreciated. The loss of jumping ability is associated with a reduction in sclerotization and size of these various linking and bracing devices and the hooks and soldering devices. But in many cases such structures must also play a role in walking and climbing, as well as jumping.

Closely associated with the function of the link-plates is the development of the lateral metanotal area and its sclerotized ridges. The reduction of this region in many species lacking a pleural arch (plate 30*c*) has attracted the attention of several morphologists (Traub 1972; Johnson 1957). Now that the essential role of the rigid thorax in the mechanism of the jump is appreciated, together with the necessary alignment of certain linking and clamping devices, this modification is understandable, since it is the corner of the lateral metanotal area which accommodates the 2nd thoracic link-plate. In species with a rigid thorax such as *Echidnophaga gallinacea* (Westwood) and *Neotunga*, not only the lateral metanotal area but the link-plates themselves are reduced or altogether lacking, despite the big resilin pleural arch (plate 30*a*, *e*).

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† In Pygiopsyllids there is an additional abdominal peg-and-socket device designated by Jordan the 4th link-plate (plate 31*a*). This structure is not homologous with the thoracic link-plates. We followed Snodgrass in renumbering the link-plates the 1st and 2nd thoracic link-plates (Rothschild & Traub 1971).

A large lateral metanotal area is not required in non-jumpers; if the thorax is in itself sufficiently rigid, it can also be dispensed with by fleas which jump well.

The pleural arch displays many subtle modifications. In some of the best jumpers like the cat flea (*Ctenocephalides felis* (Bouché)) the resilin forms a rather broad arch, while a narrow, high, domed structure is seen in *Ancistropsylla* (plate 33*c*) and *Vermipsylla* (plate 35*a*). When the arch is lost it is always the posterior portion which is the last to disappear (plate 30*b*). In stained serial sections of some fleas which have apparently no arch whatsoever, a 'remnant' of resilin seems to be incorporated in the dorsal end of the pleural ridge, and shows up by virtue of its staining properties. Most reduced arches stain less brightly and densely than the large resilin pads. Even in species lacking a pleural arch the tendon of the trochanteral depressor muscle is an impressive structure and it comes as no surprise to find that some species without the 'booster' mechanism can still hop up to 50 times their own body length (Rothschild *et al.* 1975, table 2, p. 504). There is the usual variation seen between species (even between individual specimens). One of the widest tendons at the distal end (near the point of insertion) so far measured is that of *Moeopsylla*, which has a very broad arch, while that of *Ancistropsylla*, which is narrow and domed, is relatively slender (plate 27*b*) (225 μm compared with 525 μm). There is also some correlation between body size and tendon size, illustrated for example by *Vermipsylla alakurt* Schimkewitsch, which is a big flea (Hopkins & Rothschild 1956, pl. 11*e*, *f*), and *Hystrichopsylla talpae* (Curtis), an even larger species, almost double the length of *Moeopsylla*, with far less resilin, but a tendon measuring up to 625 μm across. The areas of the tendons which show tanning of the cuticular portions are more extensive in some good jumpers, but this feature is often related to the degree of tanning in the species as a whole. Thus *Ancistropsylla*, a deer flea which is presumably exposed to relatively little risk of damage from the host's de-fleaing activities, is altogether less heavily tanned, and the tendons correspondingly less sclerotized, despite its ability to execute large jumps.

As we have said, there is variation in the number of fibres in the trochanteral depressor muscle. Some species in the genus *Pleochaetis* have a very large number, whereas in sessile fleas such as *Tunga monositus* Barnes & Radovsky (1969) the fibres in the trochanteral depressor are reduced and the number in the epipleural muscles greatly exceeds them. Likewise the size of the sarcomeres differs from species to species. There is one curious feature common to the Pulicoid fleas so far examined by serial section, and that is the affinity of their muscle fibres for aniline blue (plate 25*d*). This is generally, though by no means invariably, lacking in Ceratophyllid fleas, especially bird fleas, for, treated with exactly the same process, their muscle fibres scarcely take up the blue stain at all. The reason for this difference is not understood, but when more fleas have been sectioned, it may be possible to confirm the impression we have gained that in some circumstances there is a correlation between good jumping performance and muscle affinity for aniline blue.

The two groups of fleas in which there are the greatest number of species lacking a pleural arch are the Ischopsyllidae (bat fleas) (Hopkins & Rothschild 1956) and the Hystrichopsyllidae (Hopkins & Rothschild 1962, 1966). In the Rhadinopsyllinae (Hopkins & Rothschild 1962, figs. 863–884) the loss follows a pattern characteristic of this subfamily. All these species lack both the pleural arch and a continuous pleural ridge (plate 33*d*, r), the inner coxal ridges and rods are drastically reduced, and the fleas are blind. Blindness is linked to nocturnal hosts, independently of whether they are nest fleas (Traub 1972), but both loss of eyes and pleural arch are frequently found together; many Hystrichopsyllids are closely associated with their hosts in such locations. Basically eyes are characteristic of fleas which reach the host by active means in the open, and one can assume that Ceratophyllids like *Glaciopsyllus* and *Libyastus* spp., despite the absence of the pleural arch, and the greatly reduced notal ridges (plate 30*c*), are well sclerotized and still migrate and disperse from nests.

Some other peculiar modifications of the thorax are found in certain genera of archless fleas. *Wenzella obscura* Traub (a parasite of *Heteromys* (Traub 1972, pl. 14; Hopkins & Rothschild 1962, pl. 8*a*, *b*)) has a strongly angled pleural ridge, associated in this case with an immensely elongated downward projecting triangle of the metanotum; *Conorhinopsylla nidicola* Jellison (Hopkins & Rothschild 1962, pl. 7*c*), a parasite of *Neotoma*, has an abnormally long, thin pleural ridge and virtually no notal ridge. Both lack the lateral metanotal area. In some extreme examples of highly modified non-jumpers such as *Stenischia mirabilis* (Rhadinopsyllinae) the midcoxa is narrower (Hopkins & Rothschild 1962, pl. 9e) than that of most Pulicoid fleas.

In the Hypsophthalmidae (Ceratophylloid fleas (Hopkins & Rothschild 1956)) there are some interesting examples of convergent or parallel evolution since features characteristic of the Pulicoid semi-sessile rabbit fleas are found in the family (Traub 1972). *Chimaeropsylla potis* Roths. has, in common with *S. cuniculi*, heavily serrated anchoring mouthparts, a modified frons (a shortened and angled fronto-clypeal region and lengthened genal region (Hopkins & Rothschild 1956, pl. 28*c*)) and lacks holding organs on the inner surface of the male antennae. The whole family, even those such as *Chiastopsylla pitchfordi* Ingram which has a reduced pleural arch, and is said to be a nest flea (Traub 1972), possesses the type of vertical notal ridge characteristic of Spilopsyllinae rabbit fleas.

The Pulicoid fleas, as we have noted (p. 482) are the superfamily which is most definitely associated with the body of the host. Even species like *Tunga*, sessile once they have reached their destined feeding site, retain resilin in the pleural arch and are said to be prodigious jumpers (Bonnet 1867). Certainly *Echidnophaga myrmecobii* leaps unerringly 5 or 6 in on to a passing hamster (personal observation), and the astonishing host-finding ability of the rabbit flea *S. cuniculi* has been demonstrated in the field (Mead-Briggs 1964). Vibrations and contrasting light and shadow are probably the main cues on which the Pulicoid fleas depend for making the final contact with their host, even though the smell of urine (Vaughan & Mead-Briggs 1970) and body odours may attract them into the vicinity of the animal. On the other hand fleas which have lost the pleural arch generally come into contact with their hosts in burrows, underground runs or nests, when the latter are using their sleeping quarters or tending their young.

5. DISCUSSION

One of the most outstanding characteristics of fleas is their uniformity. This strangely circumscribed and isolated Order is a small one, comprising only about 2000 species and subspecies, with probably not more than 500 still to be discovered and described. There can be no doubt that the group is monophyletic, and from whatever Mecopteran-like ancestor (Tillyard 1935; Hinton 1958; Rothschild 1975) they may have descended, all members of the Siphonaptera must have already lost their wings and adopted a saltatorial mode of progression when the Order, as defined today, came into being. Among the free-living Mecopterans there are species such as *Boreus hiemalis*† (L.), *Apteropanorpa tasmanica* Carpenter or *Apterobittacus*

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† The proportion of the femur to the coxa (see p. 513 of this volume) suggests that *Boreus* jumps more like a grasshopper than a flea.

apterus McLachlan which have degenerate or non-functional wings, and progress by hopping or walking. Perhaps a tendency to winglessness preadapted the ancestor of the flea to a parasitic life-style. The great development of the jumping mode of progression was accompanied in the flea by a shift of the wing-hinge ligament (part of the pleural arch) from a dorsal to a mid-thoracic position (Rothschild 1969; Rothschild & Traub 1971; Rothschild *et al.* 1972) and an associated reduction in the length of the pleural ridge. This change of position was linked to the lateral compression of the body, which enables the flea to slip easily through the host's pelt. It is interesting that resilin is present in the wing-hinge ligament of the degenerate wings of *Boreus* and would appear to be secreted in a similar manner to that of the pleural arch of fleas, and not as in the locust (Neville 1963).

The original members of the Order must all have possessed other highly specialized features such as the sensillum (= pygidium), combs of blunt, spine-like setae, proventricular spines, a rectal ampulla with six rectal pads, four malpighian tubules, one unbranched pair of salivary glands, adhesive suckers lining the male antennae, horizontally† ridged or striated cuticle (plate 36) and link-plates. Furthermore the copulatory organ of the flea, which has been described as the most complicated sexual apparatus in the world, is basically similar throughout the Order, although diversified by a plethora of variations. Despite their uniform and conservative morphology, species and groups of species are characterized by a bewildering number of minor specializations, which have been imposed on this ground plan, first forming the framework of the superfamilies and then reflecting the different life-styles and characteristics of particular hosts.

There are no two link-plates alike, even in closely related species! These endless variations on a central theme are often difficult to interpret. Nevertheless it is surprising that an important structure such as the hook of the 'click' mechanism should vary so much, and apparently so capriciously. It is more understandable that modifications like the reduction of sclerotized ridges, the reduction of clamps, the loss of eyes, loss of resilin in the pleural arch, etc., are scattered throughout the order in response to convergent life patterns or behaviour of the host. Thus the building of high aerial nests, colonial habits or nocturnal activity of the mammals concerned, may call forth similar structural responses in their fleas, which may nevertheless pertain to quite unrelated families.

Although these superimposed modifications are sometimes difficult to understand, in other cases the correlation is obvious. Thus the sessile female *Tunga monositus* which, once it has reached the host, remains fixed in the mouse's ear for the rest of her life, has a greatly reduced number of fibres in the trochanteral depressor muscle, but still retains massive epipleurals, which are required for compressing the resilin in the pleural arch – an operation essential for the initial jump onto the passing host.

It is more difficult to assign or apportion the roles of walking, running, climbing or jumping in the development or loss of the sclerotized ridges of the coxa – often because of the lack of information relating to the habits of the fleas. In the case of two related species of rabbit fleas, *Spilopsyllus cuniculi* and *Cediopsylla simplex*, both of which have been bred in captivity (Rothschild & Ford 1973) it is possible to compare their relative activity. Both have powerful sclerotized notal ridges but *C. simplex* is a better jumper than *cuniculi*, and altogether a more mobile flea. The articular sclerite of its metacoxa is well tanned and the inner rod sclerotized. In the

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† In some parts of the body these striations or ridges are vertical or even whorled.

latter species, which is sessile for very long periods, the articular sclerite is membranous and the ridge below the point of articulation virtually missing. A better understanding of the habits of fleas would throw light on various, at present apparently meaningless, modifications. Thus the curious sclerotized reinforcements at the base of the metacoxa in *Glaciopsyllus* (plate 34*d*) may be, in some ways, a response to movement across the ice-covered rocky ledges on which the host is said to nest. This species has been observed walking about in vacated nests and over the snow at −20 °C! (Murray, Orton & Cameron 1967, and private communication).

In adult fleas there are two different sets of ecological factors which mould the evolution of the insect. On the one hand there is the specialized and peculiar environment of the body of a warm-blooded mammal or bird, and on the other, the relatively unsheltered and fluctuating conditions found in the open, or in the nest or burrow of the host. The development of the wing-hinge ligament for the purpose of boosting the jump reflects this dual environment, for resilin is relatively unaffected by temperature and is eminently suitable as an energy store for an insect which jumps on and off an animal with a blood temperature of 38 °C (100 °F). Thus no warming up process equivalent to 'wing buzzing' is required when a flea leaps off the cold ground on to a passing host.

Although the jump of the flea is an effective escape mechanism, and these insects – even blind species such as *Ischnopsyllus octactenus* and *I. intermedius* (Hůrka 1963) – respond to harassment by leaping (Rothschild *et al.* 1975, p. 504) this function is relatively of minor importance for saltatorial performance is rarely retained solely as a means of avoiding destruction by the host. The nest flea escapes by hiding in debris, or possibly in the case of those with heavy dorsal incrassations, in cracks and crannies in rocks and the walls of burrows. There are blind fleas, however, such as *Cryptopsylla ingrami* de Meillon (Hopkins & Rothschild 1956) with a well developed pleural arch and vertical lines of force for which speculative jumping must play quite a significant role. Undoubtedly this mode of progression remains, *par excellence*, a device by which the newly hatched unfed flea reaches a passing host in the open.

The fact that fleas lacking a pleural arch can still leap, suggests that the winged ancestor of the Order took off with a small jump, like the Muscid flies of to-day (Nachtigall & Wilson 1967; Mulloney 1969). Nature then parsimoniously turned back the flight mechanism of the ancestral flea into the mechanism of the jump, thereby perfecting and boosting take-off and producing their prodigious saltatorial performance. It is also of no little satisfaction to the morphologist that the largest and fastest moving mammalian hosts elicit in their fleas the larger lumps of resilin.

Our sincere thanks are due to Professor R. Traub for the loan of specimens and helpful discussions concerning the function of various morphological structures. Dr Charles Neville has given us constant advice and is practically a joint author of this section as well as of part III.

Mr F. G. A. M. Smit has also helped us with material from the Rothschild Collection, much information from the literature, has checked our drawings of the exoskeleton and criticized the text. Mr Bob Ford has cared for the various flea cultures throughout, Dr Michael Hardy collected living bat fleas for us, and Professor Nixon Wilson rabbit fleas from the U.S.A. We are grateful for all their assistance.

We also wish to thank Mr J. V. Brown for his help with the photographs (plates 30, 31), Mr B. Martin for the scanning micrograph (plate 32*d*), Professor Howard Hinton, F.R.S., for plate 36, and Mrs Lynn Wright for skilful dissections of link-plates and trochanters.

Finally we are both greatly indebted to Professor John Pringle, F.R.S., for space in his department, and his constant interest, encouragement and perspicacious comment.

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List of abbreviations used on plates

a	articular sclerite
cl	clamp
f	pleural ridge-fold
fu	furca
h	hook (thoracic catch) of click mechanism
i	inner coxal rod
k	link-plate
k4	4th link-plate
m	mesofurca
n	notal ridge
o	outer coxal ridge
p	pleural arch
r	pleural ridge
R	resilin
s	sensilla
so	coxal socket
t	tendon of trochanteral depressor muscle
T	transverse ridge of metanotum
x	coxal membrane

List of abbreviations used on text figures

c.lnk.pl.	cervical link plate
cox.so.	coxal socket
fla.	flange
fust	thoracic 'catch' or hook of click mechanism
h	trochanteral hook
in.cx.rd.	inner coxal rod
l.m.	lateral metanotal area
lnk. pl. 1	1st thoracic link-plate
lnk. pl. 2	2nd thoracic link-plate
me.epmr.	mesepimeron
me.epst.	mesepisternum
me.n.	mesonotum
me.st.	mesosternum
mt.spimr.	metepimeron
mt.epst.	metepisternum
mt.n.	metanotum
n.ri.	notal ridge
out.in.cx.rd.	outer internal coxal ridge
phr.	phragma
pl.a.	pleural arch
pl.r.	pleural rod
pl.ri.	pleural ridge
pr.n.	pro-notum
pr.pl.	propleurum
pr.st.	prosternum
spir.	spiracle
te.d.	tendon of trochanteral depressor muscle
t. 1	1st tergum
t.ri.m.	transverse ridge of metanotum
tro.	trochanter
up.in.rd.	upper internal rod (coxal) or articular sclerite

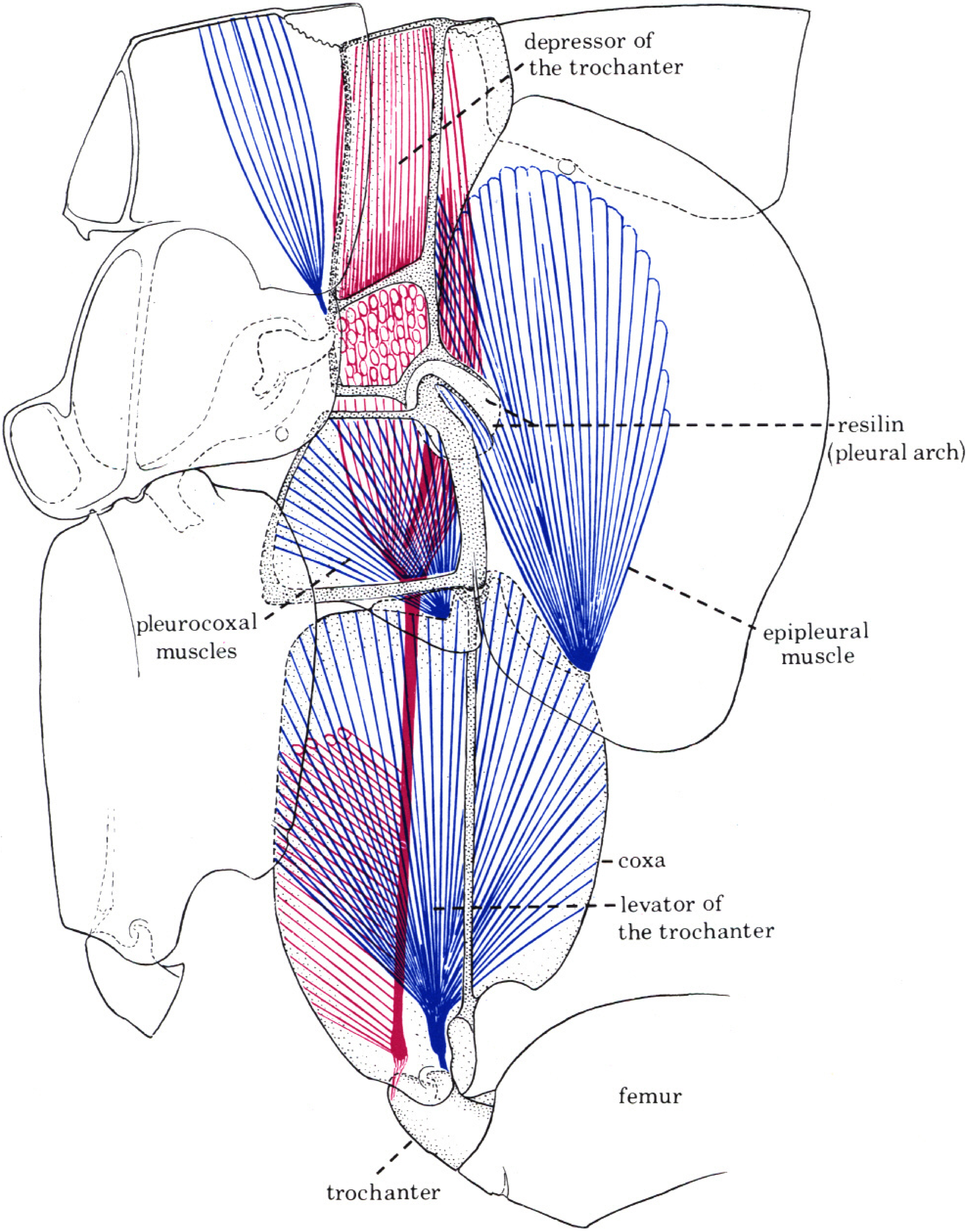
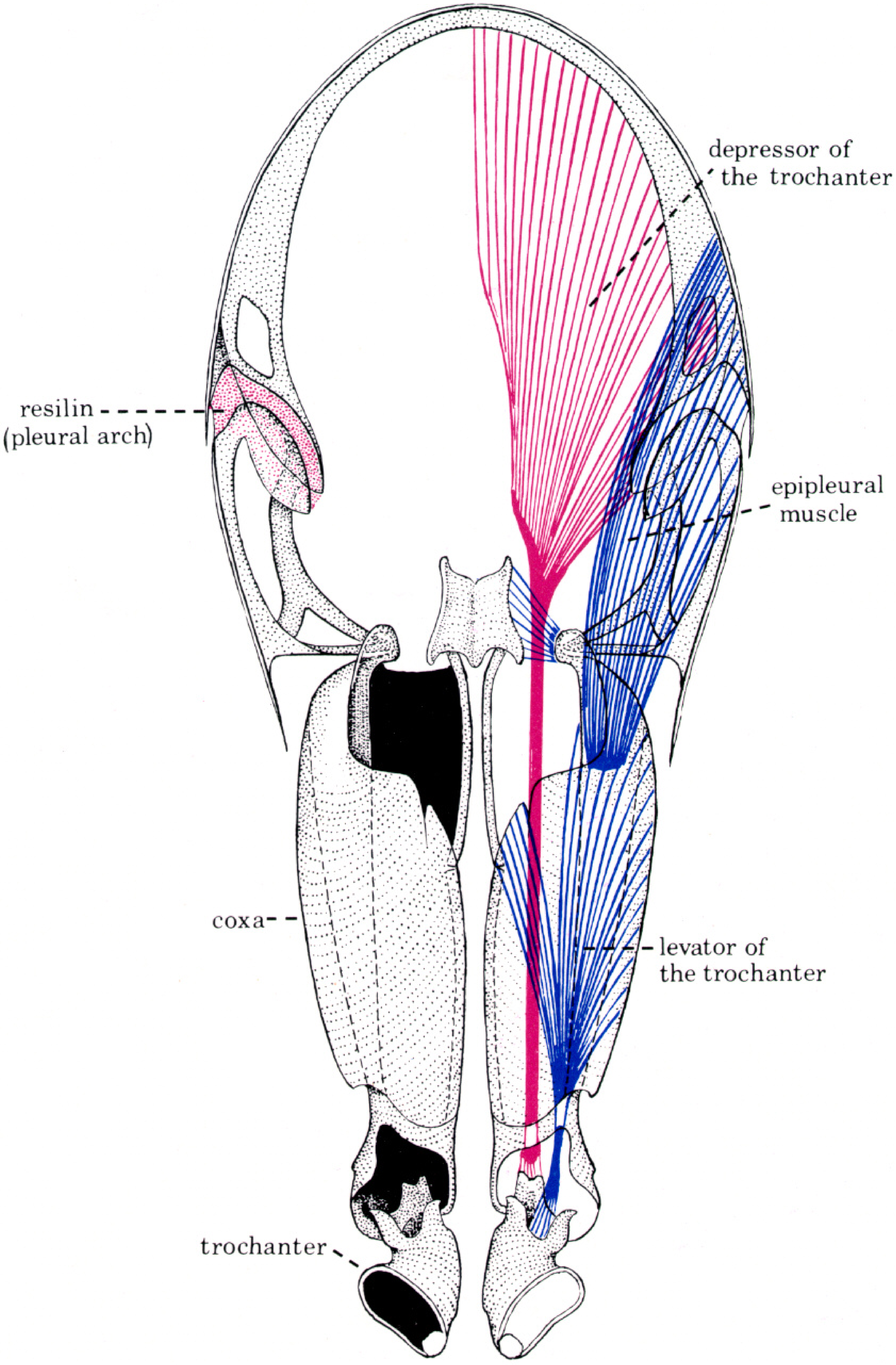


FIGURE 1. For description see opposite.



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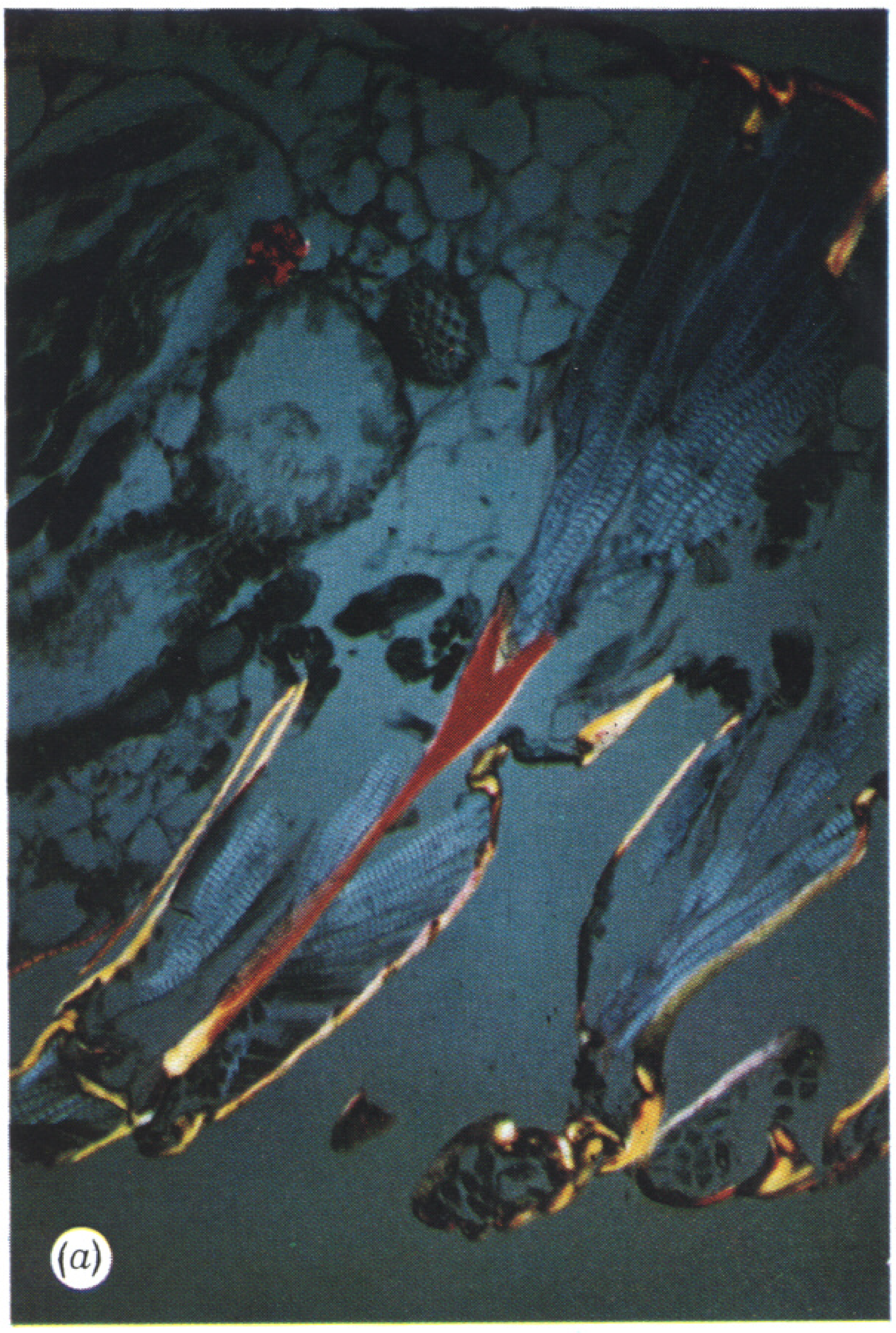
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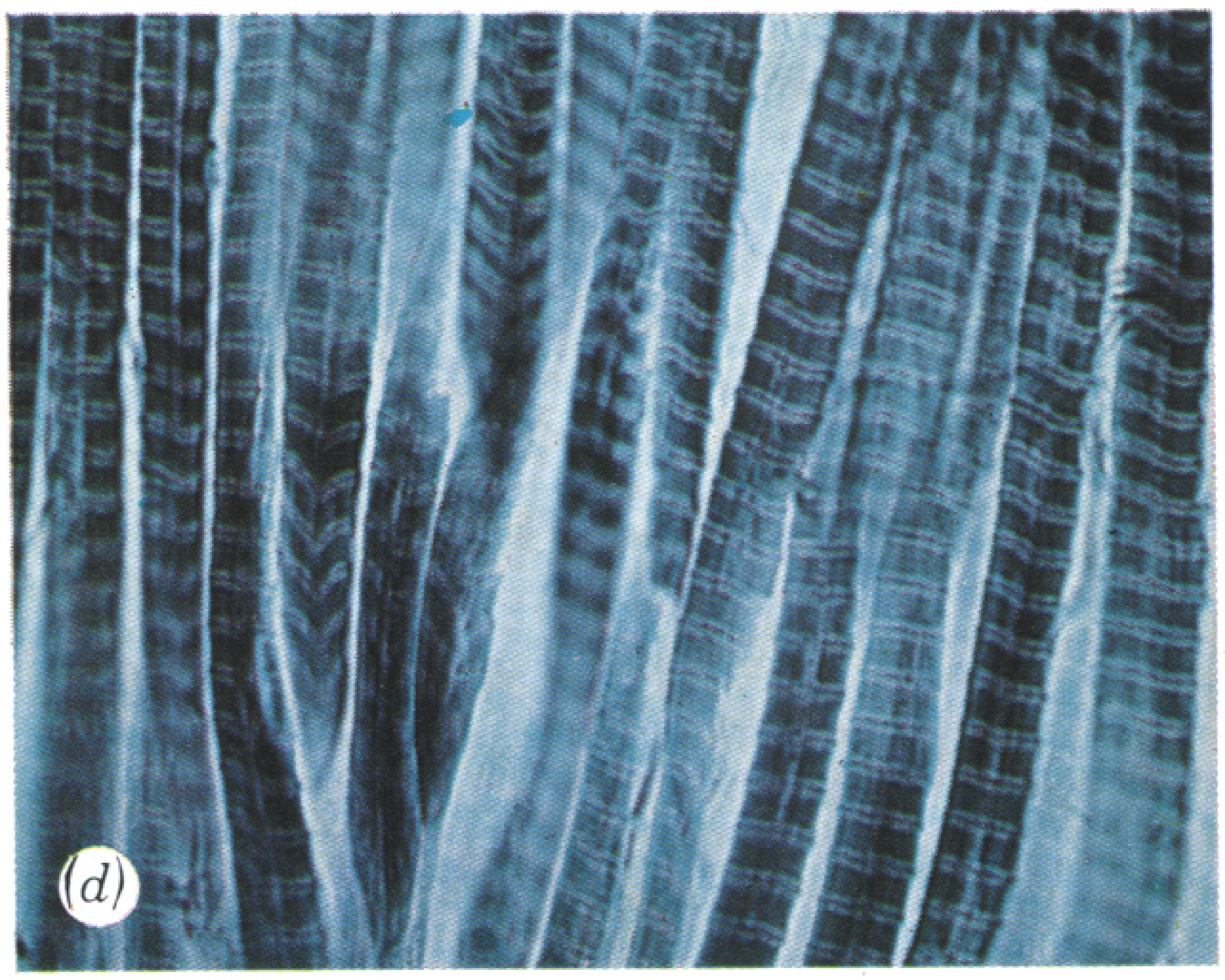
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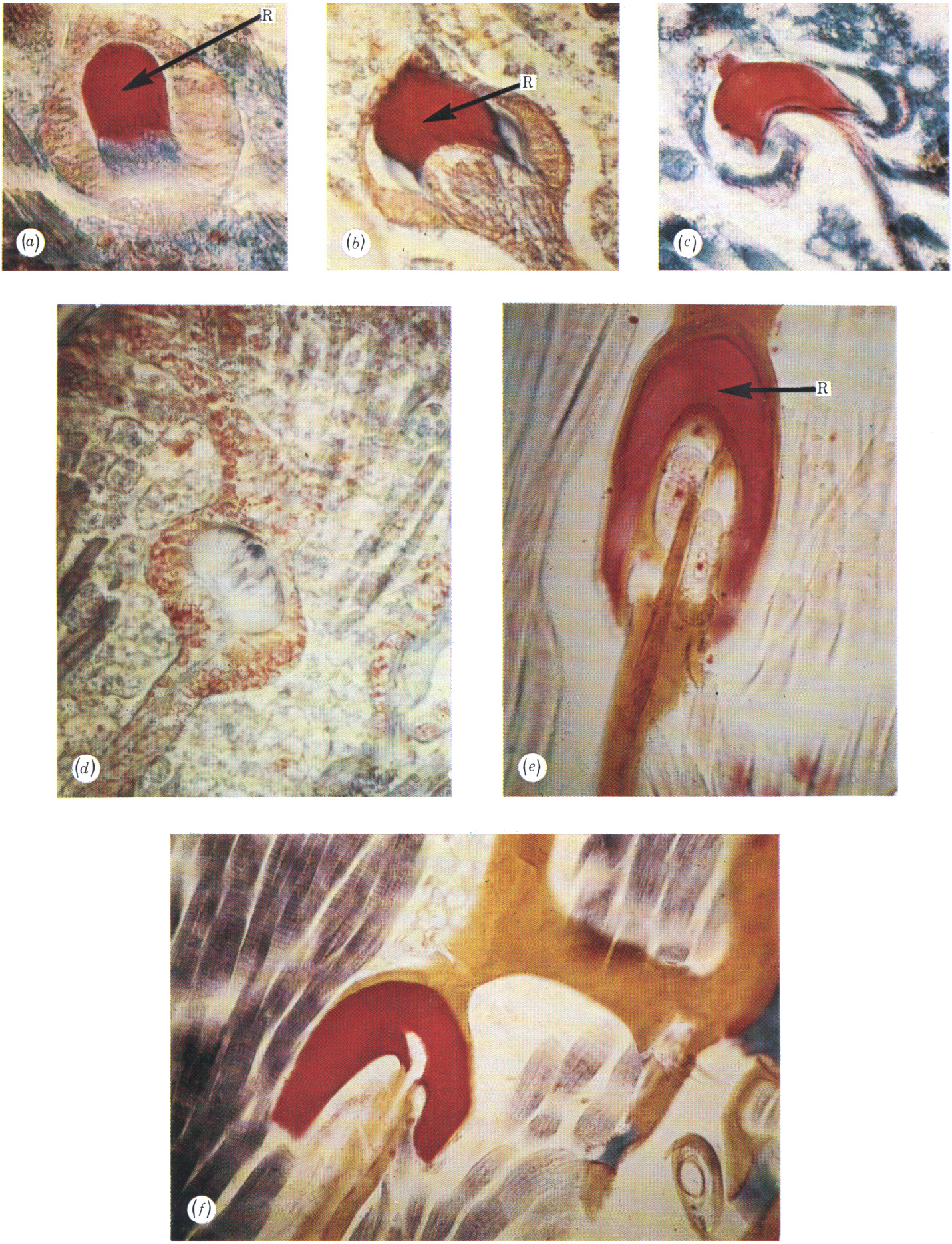
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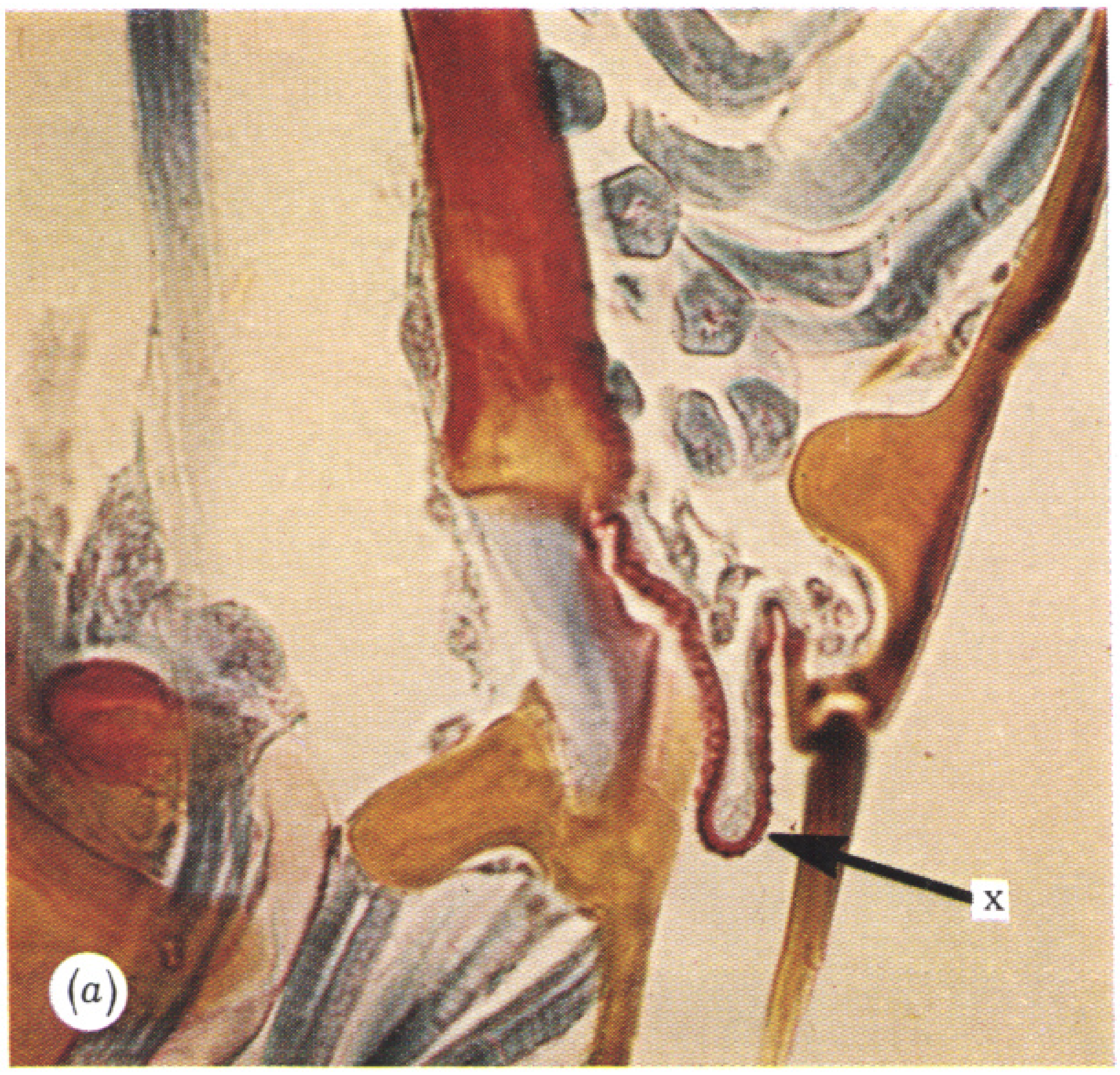
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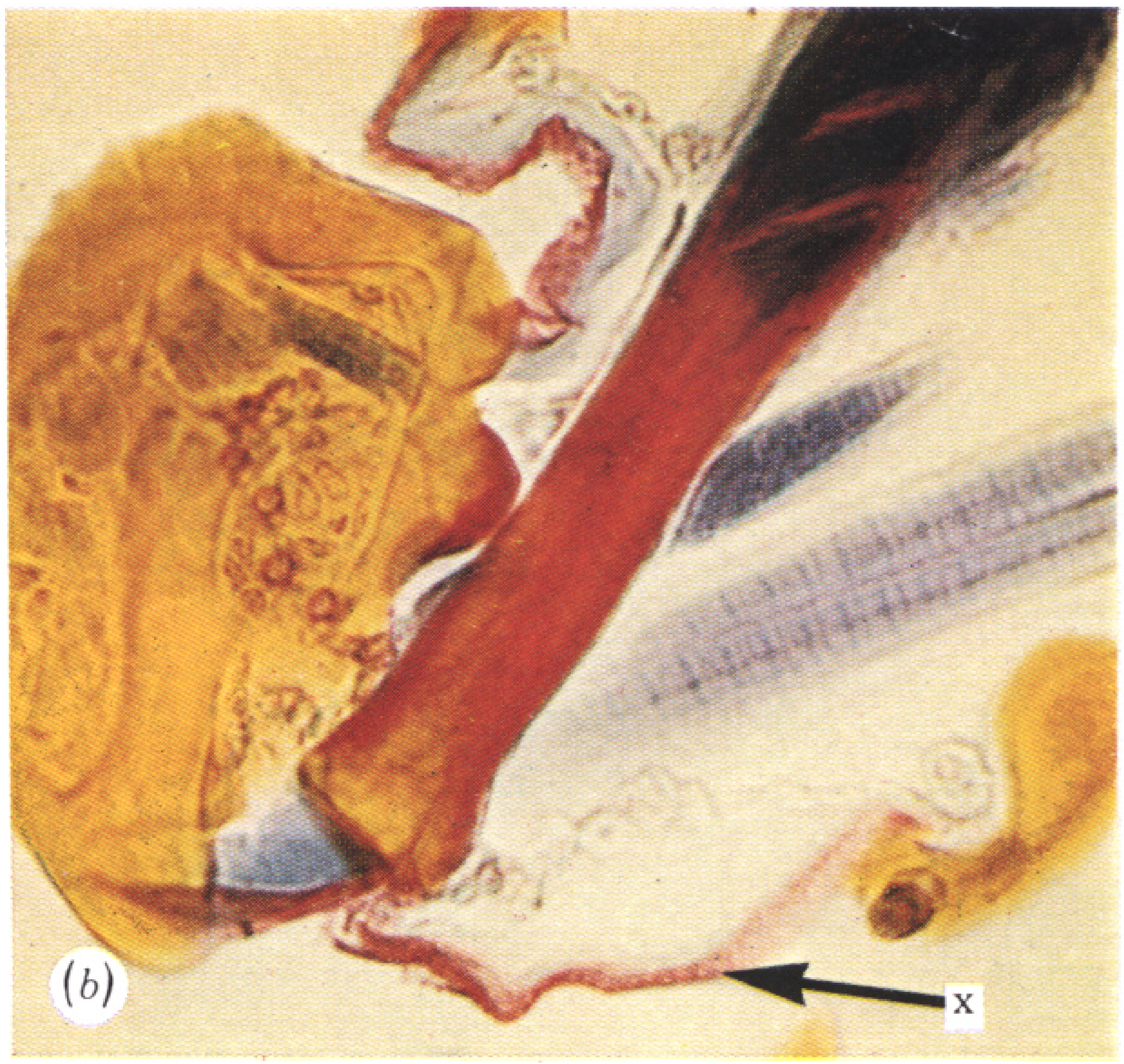
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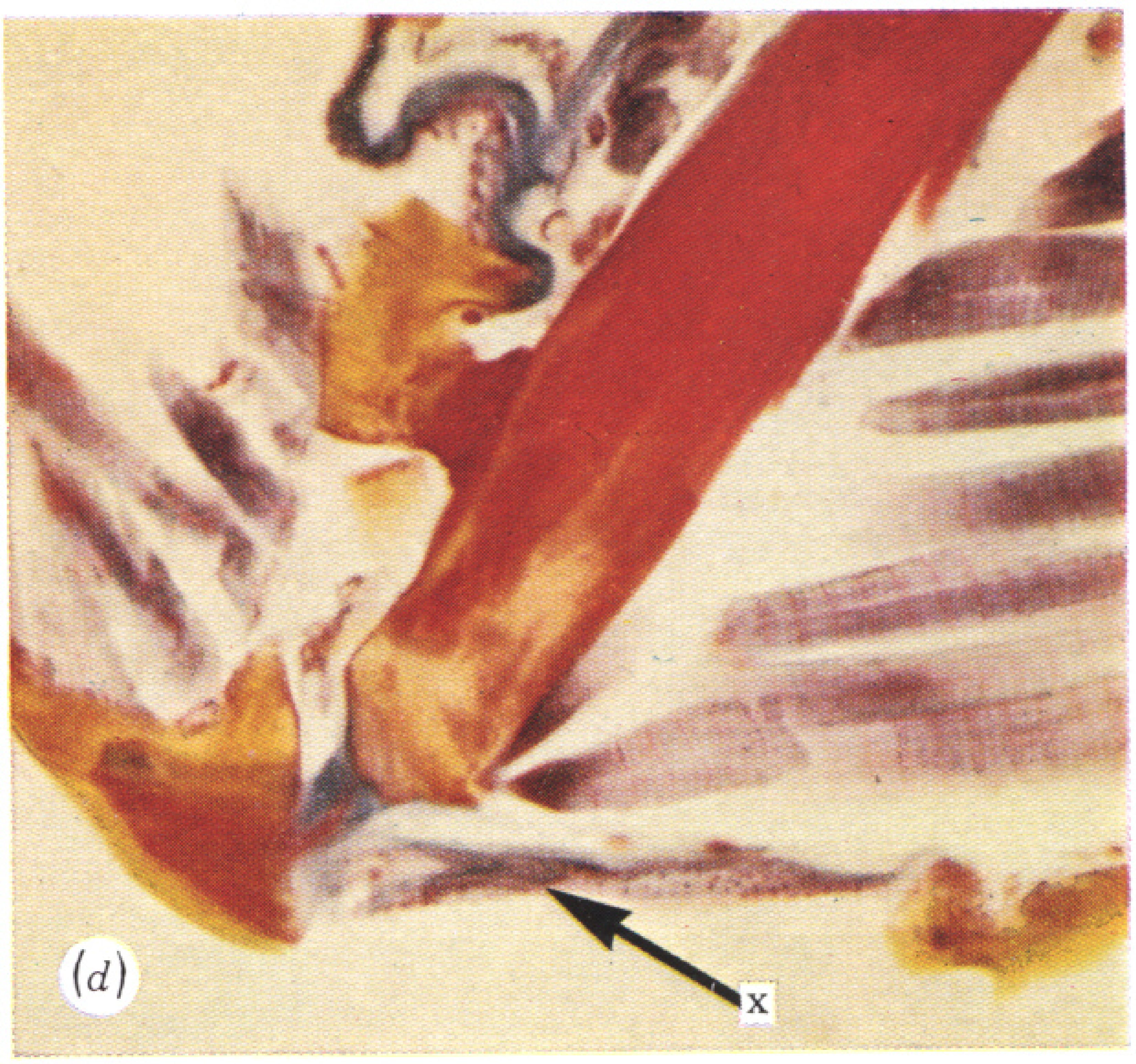
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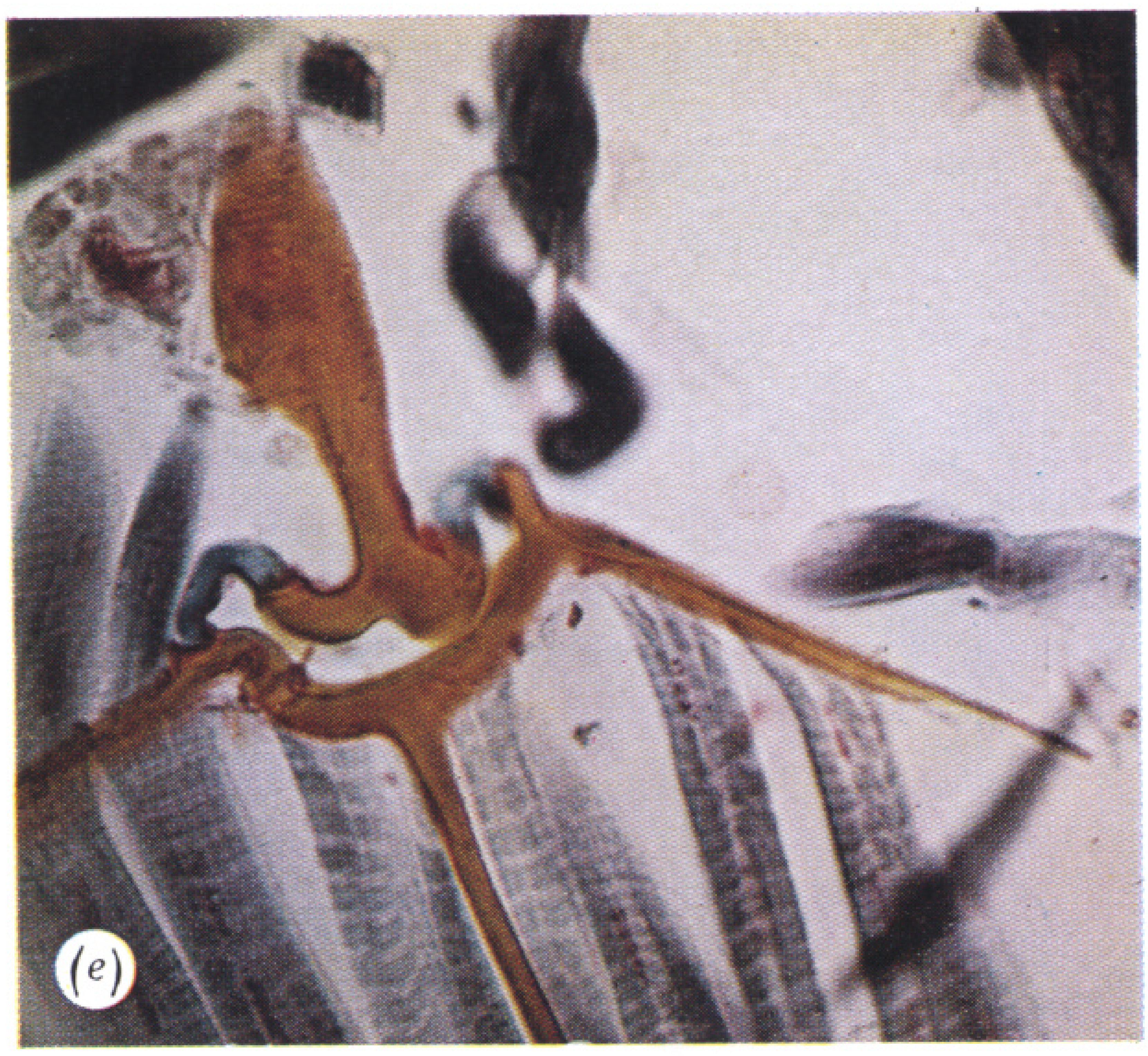
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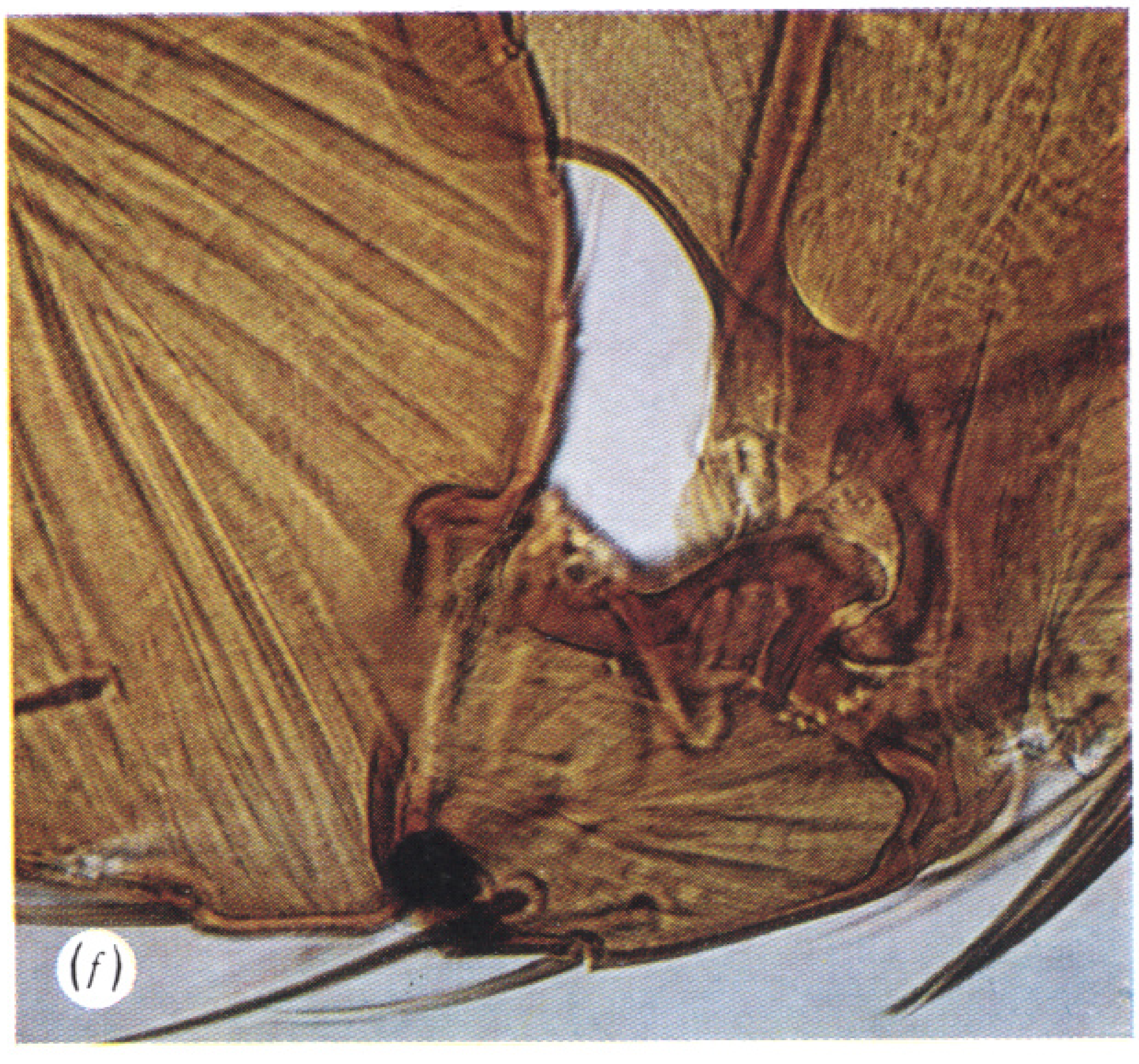
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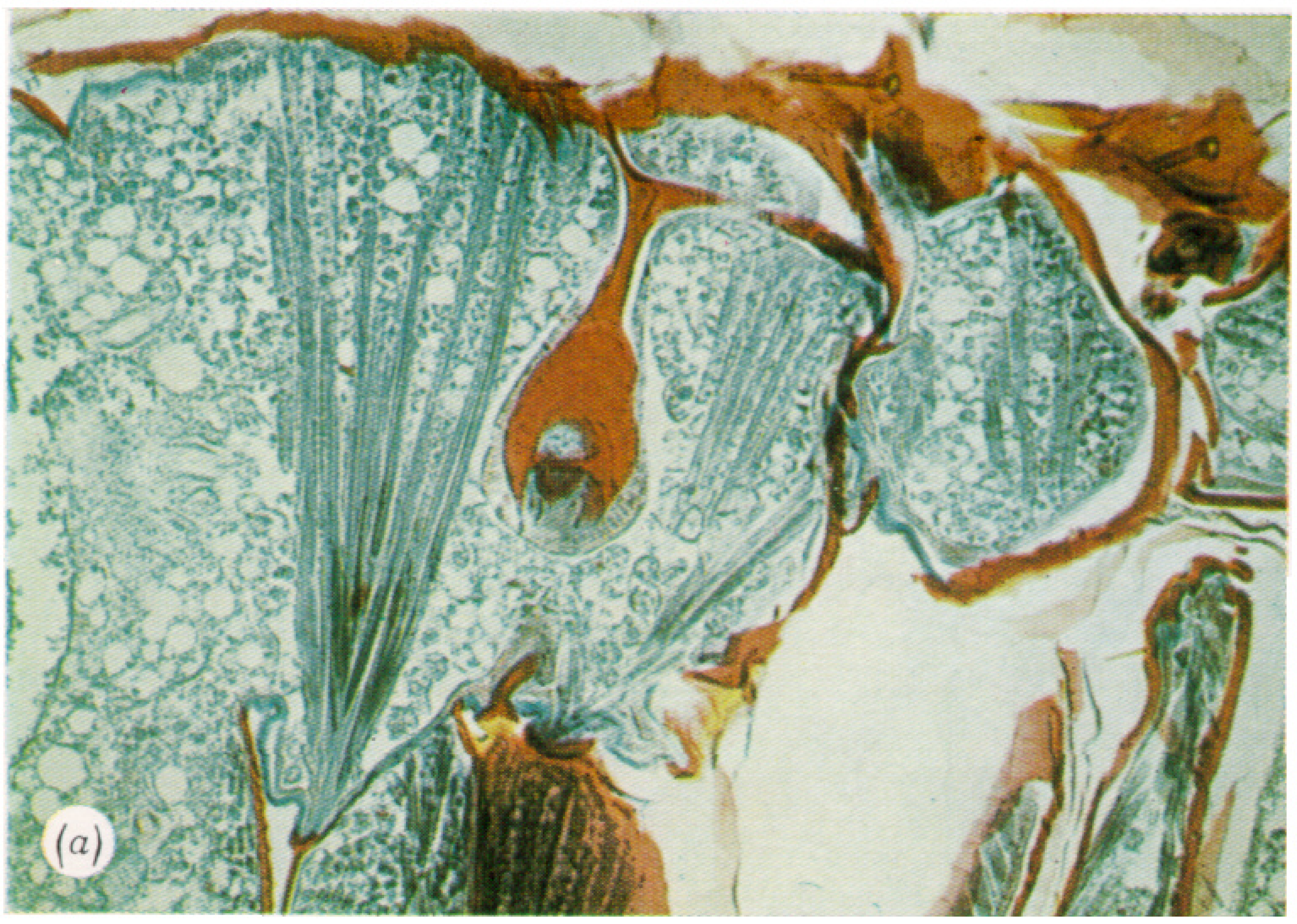
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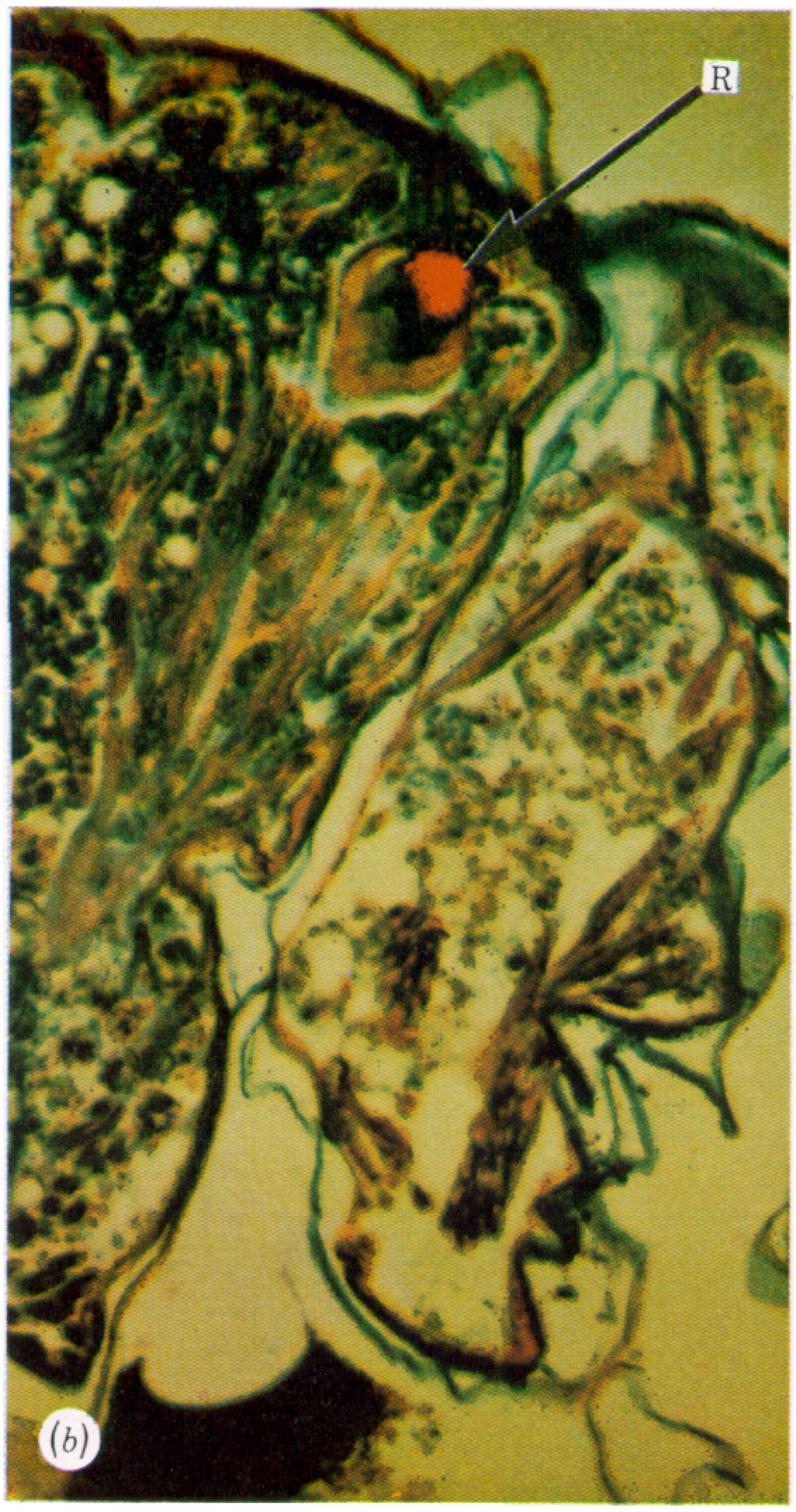
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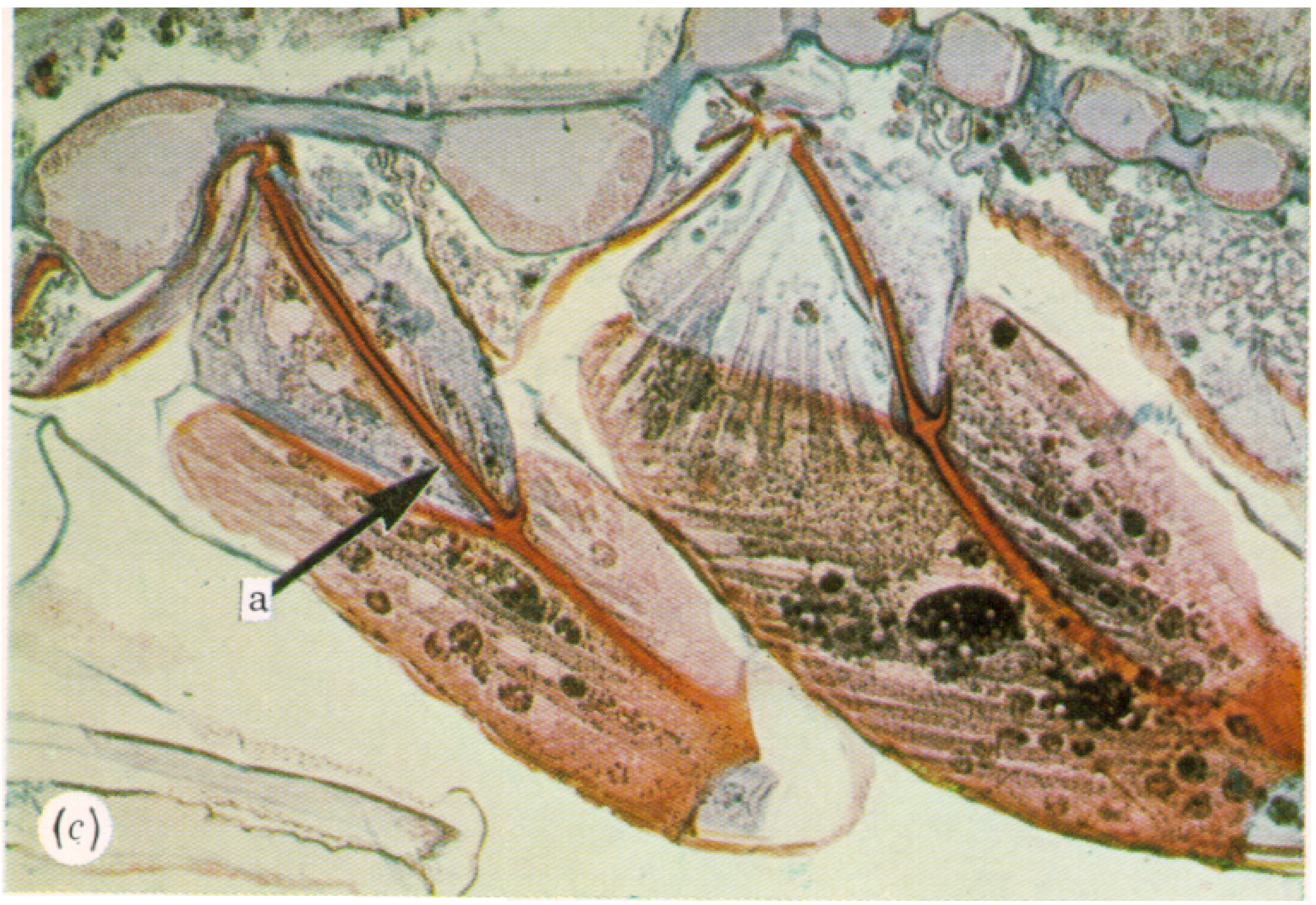
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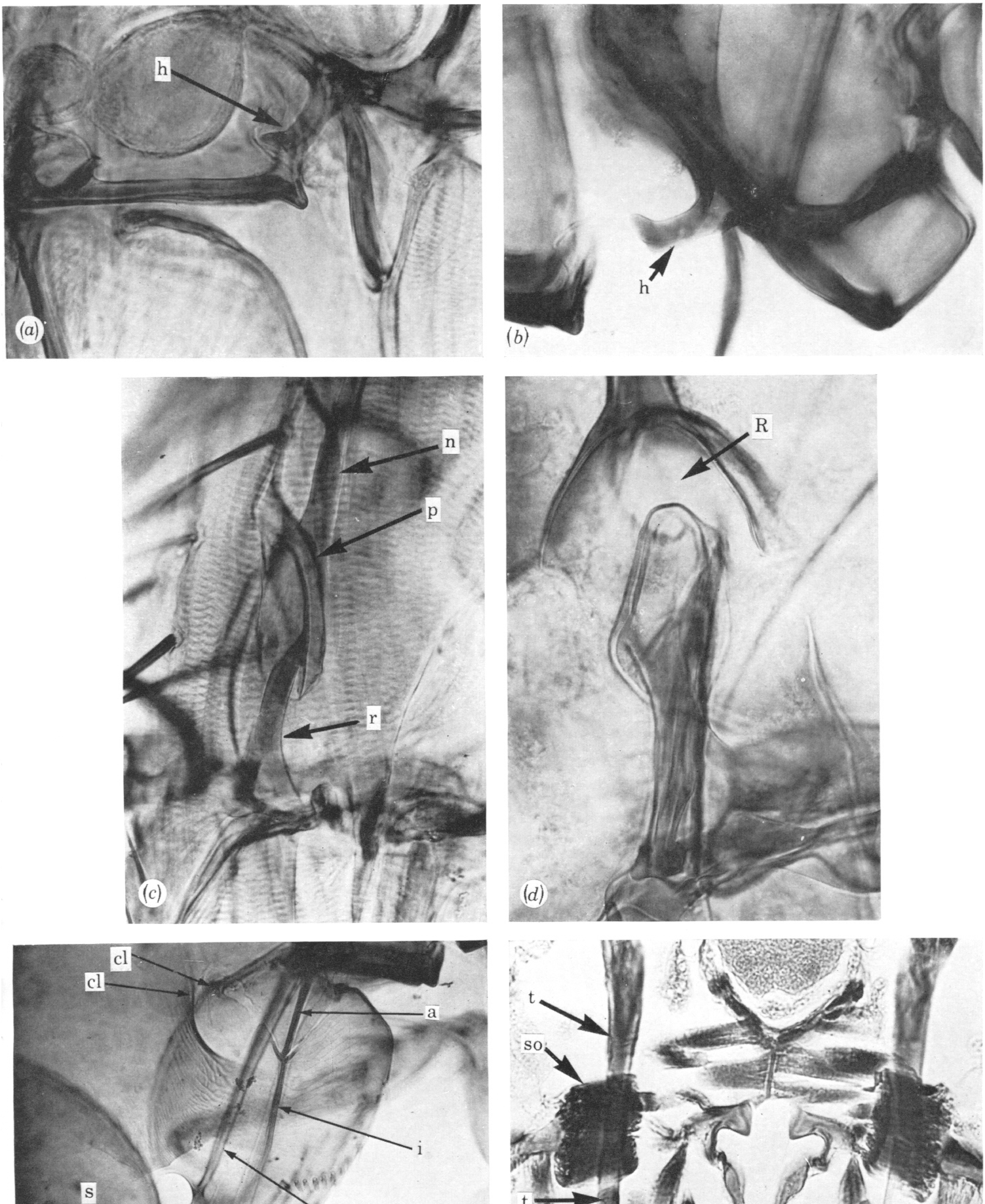
(c)


(d)


a
(e)



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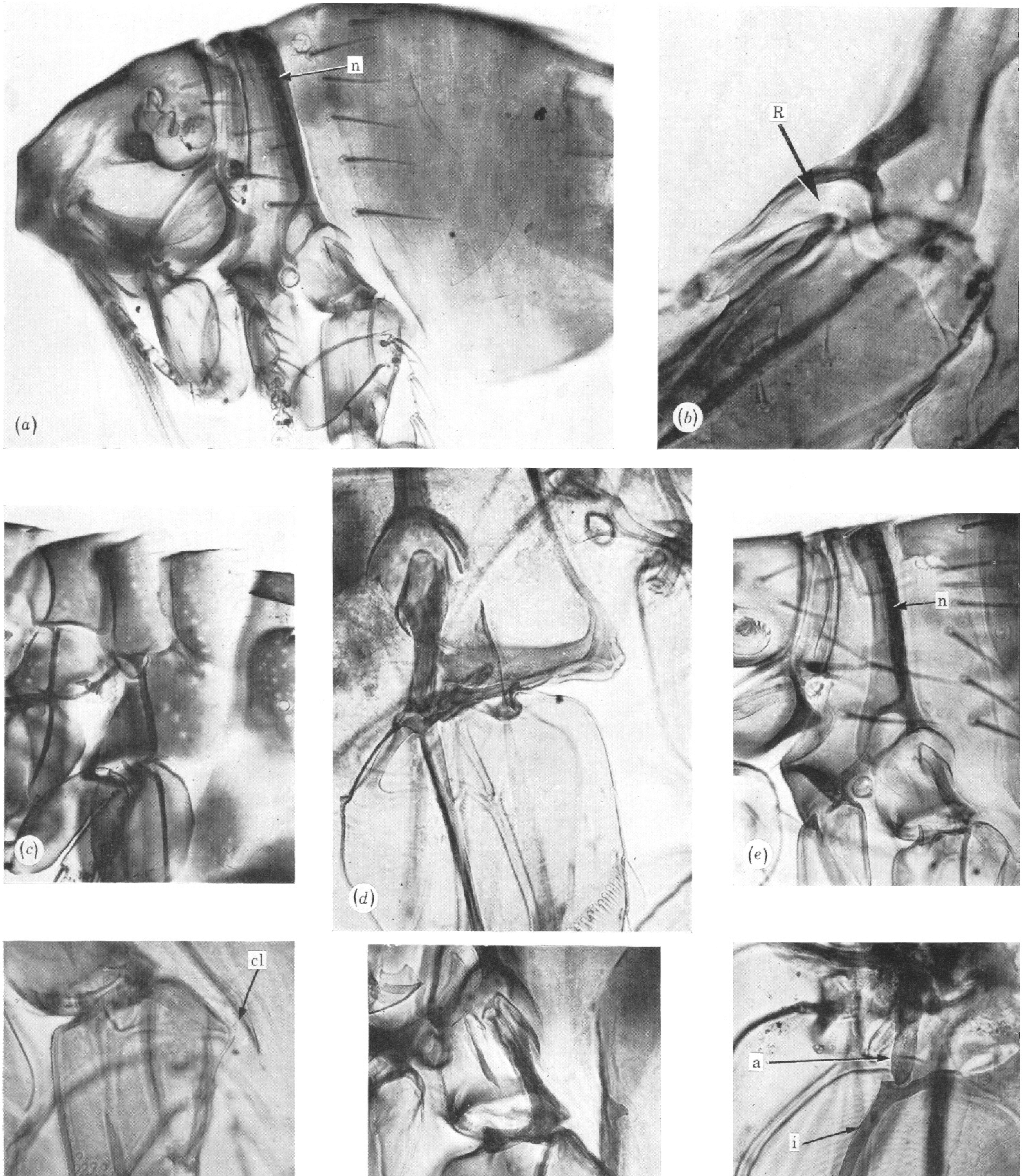

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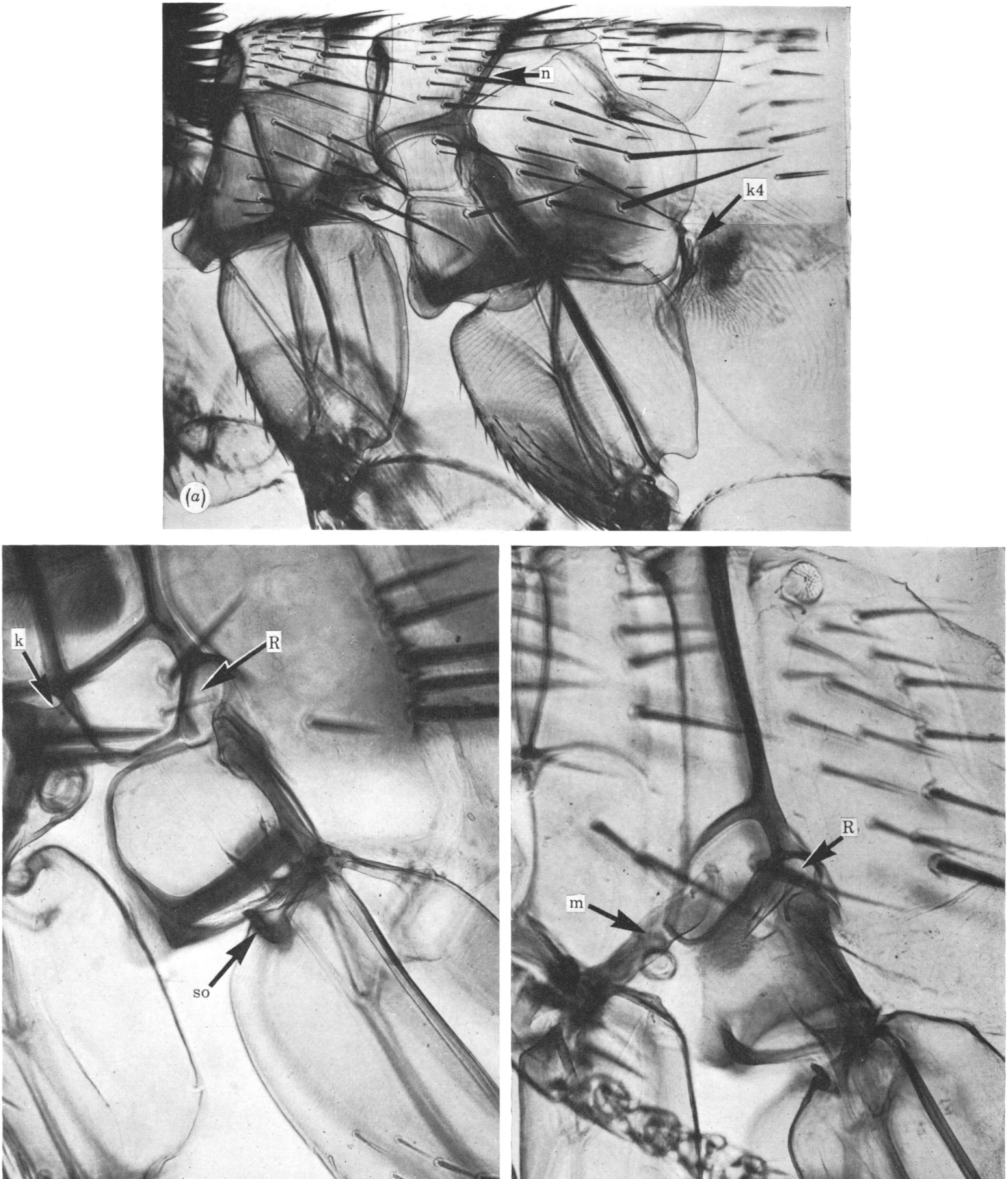

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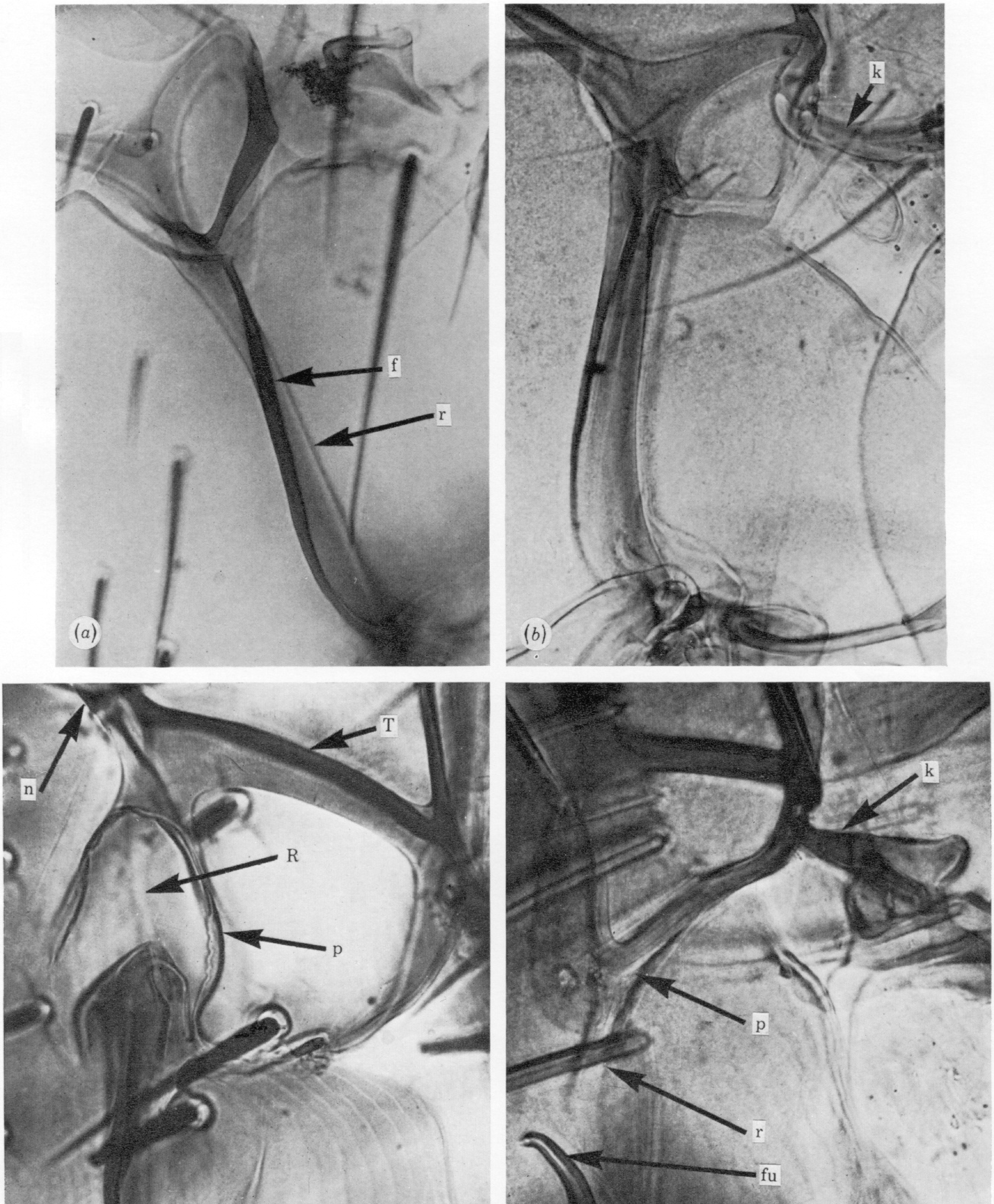
For description see opposite.



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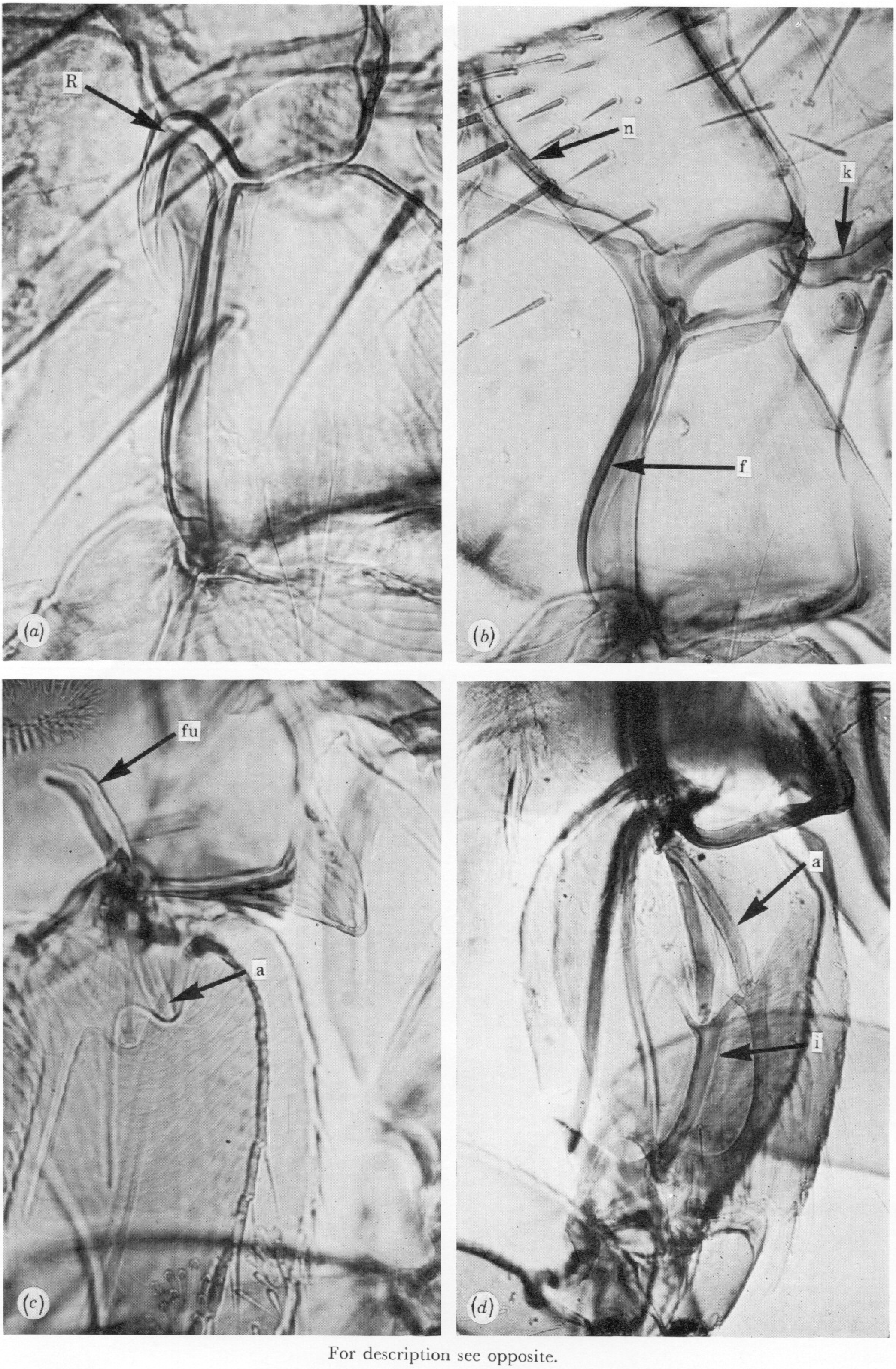

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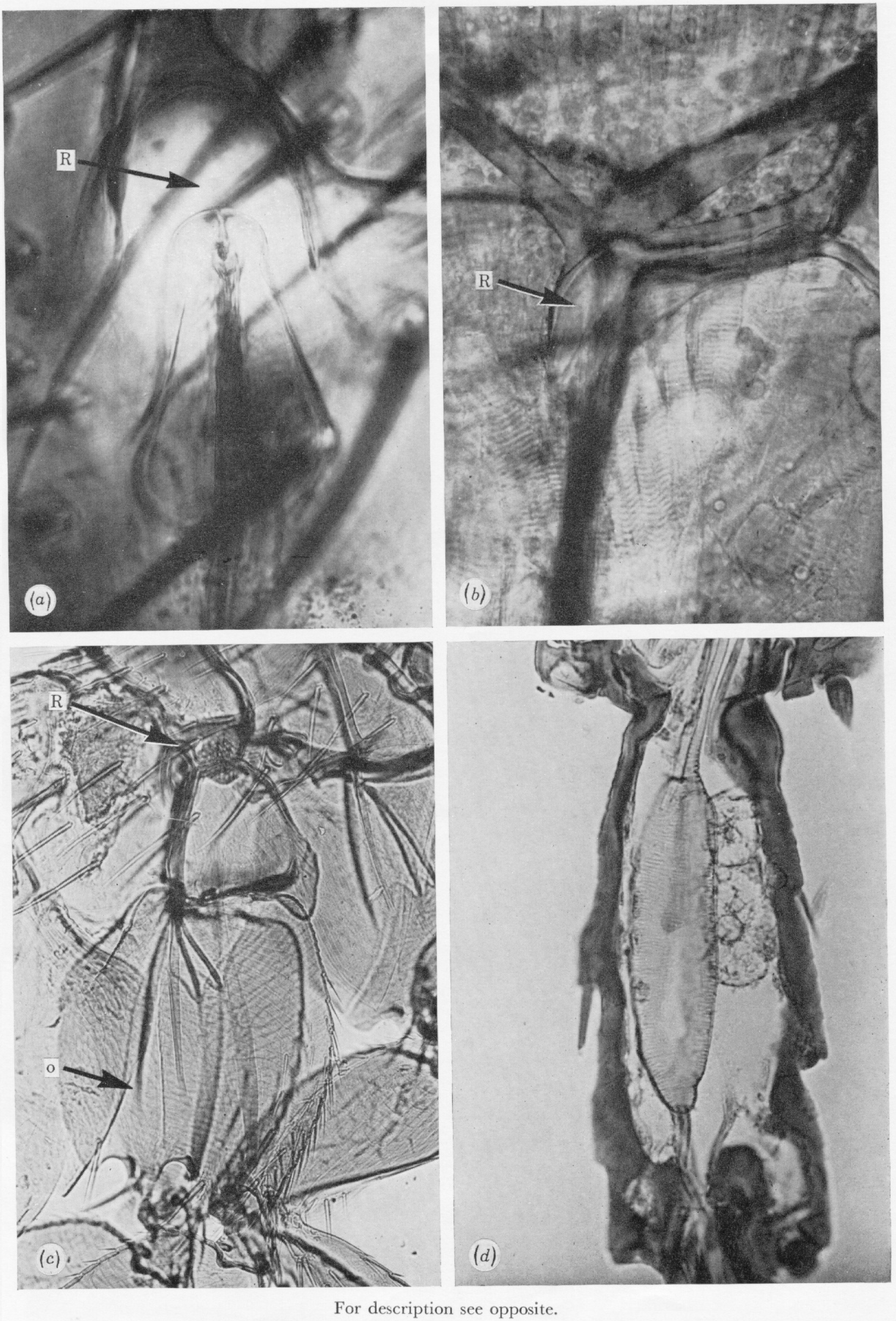

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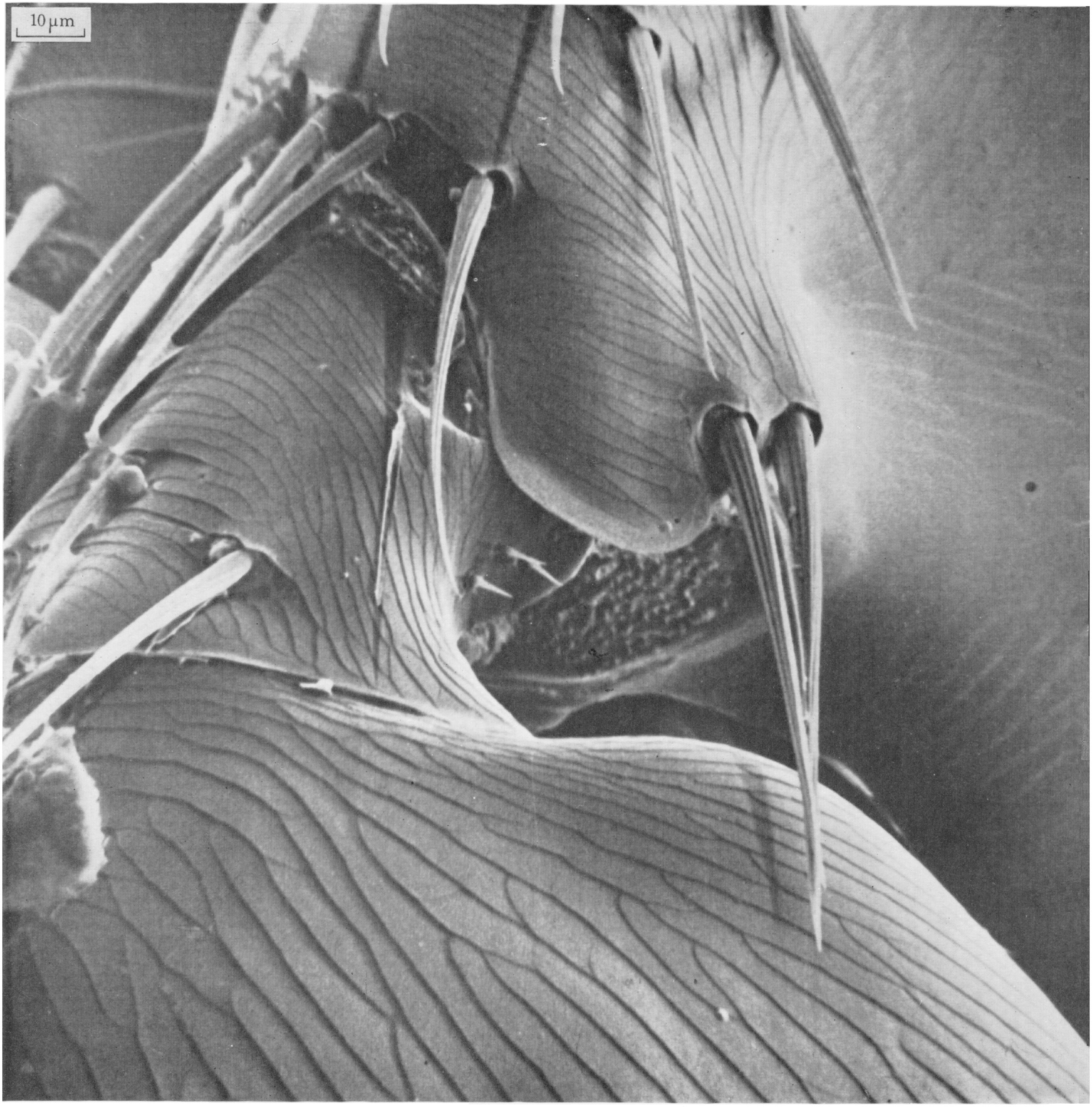

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