THE JUMP OF THE FLEA: A STUDY OF THE ENERGETICS AND A MODEL OF THE MECHANISM

By H. C. BENNET-CLARK

Department of Zoology, University of Edinburgh

AND E. C. A. LUCEY

Research Film Unit, Institute of Animal Genetics, University of Edinburgh

INTRODUCTION

The jump of the flea has long been regarded as a zoological problem because it was not easy to explain the jump of so small an animal in terms of the known properties of muscle and the flea's anatomy. In this paper we present an hypothesis whereby the structure of the flea may be reconciled with its power of leaping.

The present work stemmed from film taken by one of us under the sponsorship of the British Broadcasting Corporation. The original suggestion that this film be made came from the Hon. Miriam Rothschild and it would not have been made without her interest in this problem. The actual film used for this work was made later and at lower speed and higher magnification in order to examine events preceding the jump.

MATERIAL

The rabbit flea, *Spilopsyllus cuniculus* Dale, was used for photographic records. Living specimens were provided by the Hon. Miriam Rothschild.

Spilopsyllus is a small flea about 1·5 mm. long weighing about 0·45 mg. It is a member of the Pulicoidea, generally supposed to be the more primitive superfamily in the order Siphonaptera and characterized by the presence of internal skeletal rods on the metapleuron but not on the mesopleuron (Rothschild & Hopkins, 1953).

Prepared slides and preserved specimens of *Spilopsyllus* were examined. Other specimens were examined for comparison purposes, notable among these were living *Hystricopsylla talpae, Xenopsylla cheopis* and a single specimen of *Pulex irritans*.

Photographic methods (undertaken by E.C.A.L.)

A Fastax type WF 17 camera with 3 in. f/2 Wollensak lens and extension tubes was used together with H.P.S. neg. film stock. This camera has a revolving prism shutter and is capable of taking exposures up to 8000 frames/sec. (f.p.s.). For the records at high magnification a speed of 1000 f.p.s. was used, giving nearly 5 sec. of filming. The exposure at 1000 f.p.s. is 0·33 msec. A time marker recorded intervals of 1 msec. on the edge of the film.

The fleas were confined in a cell 6 × 6 × 1·5 mm., the full width being in the field of view. In early attempts a grille of alternately connected fine wires embedded in

Araldite formed the floor of the cell. The grille could be energized by a pulse from an inductive circuit energized at about 30 V. It was hoped that the fleas would thus be induced to jump.

It was found impossible to induce the fleas to jump predictably; the reason for this will be examined later. A compromise had therefore to be made between the magnification and film speed; the greater anatomical detail revealed at high magnification is offset by the smaller number of fleas in the field and hence the lower probability of a jump being photographed.

For photography, incident illumination was provided by four 12 V., 50 W. lamps, overrun at 22 V., and a 100 W. Zirconium arc lamp provided transmitted light background illumination.

It was found that the warmth and light stimulated the fleas to heightened activity. A total of 300 ft. was taken at 1000 f.p.s., giving over twenty usable jumps.

After development the film was examined frame by frame on a Lytax film analyser, tracings were made at various intervals before and during the jump.

<div align="center">RESULTS</div>

<div align="center">I. <i>The normal jump</i></div>

Tracings made from the films allowed analysis of the course of a normal jump of *Spilopsyllus*.

Before the jump the flea gathers its hind legs until the femora are nearly vertical. This stage is complete at least 0·10 sec. before the jump. The flea then remains stationary until about 0·02 sec. before the jump when the fore and middle legs are folded back and the front end of the animal is pushed upwards (Fig. 1).
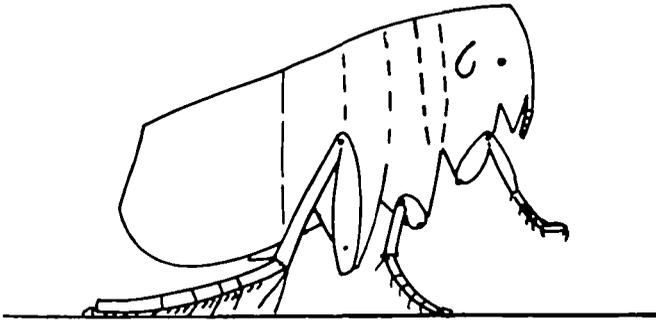

Fig. 1. *Spilopsyllus* about 1 msec. before leaping. The hind femora are vertical and the hind tarsi and tibial spurs are close to or in contact with the substrate. The flea is 1·5 mm. long.

At the moment of jumping the hind femora are rotated downwards through 90° to 120°, full depression being reached in under one frame. Simultaneously, the hind tibiae extend from a position at 45° to the femora to about 130° from the femora (Fig. 2). The impulse drives the flea upwards and forwards, the usual angle of trajectory being 50° to the horizontal; but in the jumps that were examined this was highly variable, several nearly vertical jumps being observed.

The attitude of the flea in flight is also somewhat variable. In several instances the flea was seen to rotate to a vertical attitude head-upwards about 5 msec. after the impulse, in several others to be head-downwards after the same time and in others to rotate about the longitudinal axis at about one turn per 10 msec. The axis of the rota-

tion did not appear to depend on the initial angle of the trajectory but on the roughness of the substrate.

There was no invariable rule that the flea performed a simple somersault during its jump as has been suggested by Rothschild & Clay (1952).
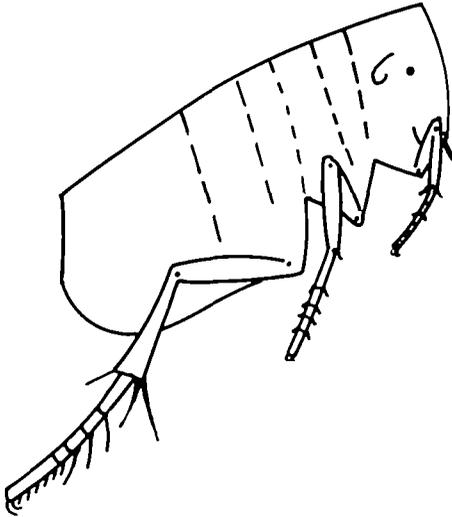

Fig. 2. *Spilopsyllus* in the first millisecond of the jump. The hind femora have rotated through 90°, the hind tarsi maintain the original position relative to the tibiae, which have rotated about 85° on the femora.
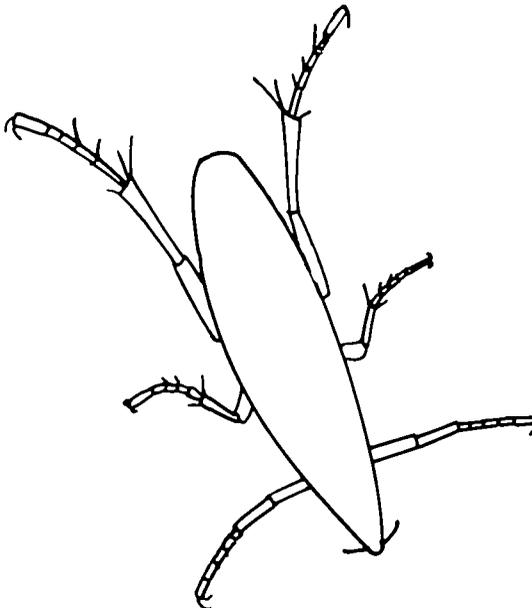

Fig. 3. *Spilopsyllus* descending 40 msec. after the start of the jump. The hind legs are spread apart, the front two pairs are spread outwards.

In the first msec. after the impulse the hind legs are left partially extended at about 30° below the long axis of the flea, although this is difficult to see from the records. The front two pairs of legs at this time are held nearly vertically below the body, partly extended.

In a later part of the jump, after 20–30 msec., the front legs are brought forwards and the middle legs are brought upwards till they stand out horizontally either side of the body. Finally the hind legs are swung apart and the tarsi rotated outwards (Fig. 3). The flea lands in this configuration regardless of the attitude or the trajectory or any bouncing on the walls of the cell. On a smooth surface it tumbles about before coming to rest.

II. *The velocity of the trajectory*

From various records calculations were made of the normal velocity of the ballistic part of the jump.

The velocity during the first 5 msec. after the impulse varied between 0·8 and 1·2 m..sec.$^{-1}$.

A reasonable figure for the velocity is 1 m..sec.$^{-1}$.

In a vertical jump, the deceleration will be the sum of air resistance and gravitational force. Equation (1) can be used to calculate the height reached, assuming that air resistance is about half gravitational acceleration:

$$s = v/2f_t \tag{1}$$

where f_t is the deceleration due to air resistance and gravity, v is the initial velocity, and s is the height attained.

In the present case f_t is $14\cdot72 \times 10^2$ cm..sec.$^{-2}$ and hence

$$s = \frac{1\cdot00 \times 10^4}{2 \times 14\cdot72 \times 10^2} = 3\cdot5 \text{ cm.}$$

This corresponds moderately well with the observed performance; the jumps appear to be typical of the performance of this species.

III. *The impulse at the start of the jump*

About twenty jumps were recorded which were suitable for analysis. Even at the film-speed used, where frames were about 1·0 msec. apart, leg movements were so rapid that it was impossible to work them out in detail.

The duration of each exposure being about 0·33 msec., it was possible to plot the initial acceleration of the animal by measurement of the length of the blur on different records. It was concluded from this that the flea accelerated to its peak speed in between 0·75 and 1·0 msec.

The acceleration can be calculated from the formula

$$v = ft, \tag{2}$$

where v is the velocity, f is the acceleration and t is the time from rest.

For the present case, where

$$v = 1\cdot00 \text{ m..sec.}^{-1} \text{ and } t = 7\cdot5 \times 10^{-4} \text{ sec., } f = 1\cdot33 \times 10^5 \text{ cm..sec.}^{-2}.$$

As the acceleration due to gravity is 981 cm..sec.$^{-2}$, this represents the formidable acceleration of 135 gravities. Where t is 1 msec., the force is 102 gravities.

Assuming that the weight of the flea is 0·45 mg. and the velocity after impulse is 1·00 m..sec.⁻¹, the energy of the impulse can be calculated. The energy of the impulse is the same as the momentum of the moving flea and is given by

$$e = \tfrac{1}{2} mv^2 \qquad (3)$$

where e is the energy in ergs, m is the mass in grams and v is the velocity in cm..sec.⁻¹. Substituting values given above,

$$e = 0\cdot5 \times 0\cdot45 \times 10^{-3} \times 1\cdot00 \times 10^{4} \text{ ergs} = 2\cdot25 \text{ ergs}.$$

Various suggestions can now be made about the nature of the muscular mechanism responsible for the jump.

First, as the impulse only lasts about 0·75 msec. and the latent period of the muscle is maybe about 3 msec. (Roeder & Weiant, 1950), it is most unlikely that a conventional muscle can provide an appreciable pull during the duration of the impulse; the only cases where substantial energy has been derived from such rates of contraction have been resonant systems and in which the mechanical nature of the muscle loading has been very critical (Machin & Pringle, 1959).

Thus one is forced to the conclusion that the jump impulse is derived from the release of energy that was stored in some manner before the jump occurs.

This conclusion becomes very attractive where an attempt is made to reconcile the energy requirements of the jump impulse with the energy that can be produced by the available muscles.

Using Machin & Pringle's (1959) figure of 6×10^5 ergs.g..muscle⁻¹.sec.⁻¹ for the flight muscle of *Bombus terrestris* and assuming a flea of weight 0·45 mg. of which 20 % is actively involved muscle, the rate of energy production per flea is only 56 ergs.sec.⁻¹.

As the jump requires 2·25 ergs, it follows that the flea must be storing the energy for nearly 0·05 sec. before each jump, assuming that the muscle is capable of this very high rate of energy production.

We have many film records showing fleas preparing to jump. In all of these there is a period (described in section I of the results) lasting between 0·10 and 0·25 sec. in which the flea sits with its hind femora raised to the vertical position before jumping. If observed by eye, living fleas walking about appear to stop, tuck up their back legs, pause momentarily, and then jump. This phenomenon has been observed before but its significance was not appreciated (Jacobson, 1940).

When *Xenopsylla* is cooled to about 6° C. the period before the jump is protracted and may last many seconds.

The time taken to store the energy required for the jump would explain why we could not induce fleas to jump by means of an electrical stimulus.

IV. *The energy store*

The anatomy of the metathorax of fleas has been studied in detail (Jacobson, 1940; Snodgrass, 1946) and shows various peculiarities. The main depressor of the trochanter, and hence of the telopodite, arises on the metanotum and the main pull that causes the jump occurs between the metanotum and the depressor tendon at the coxo-trochanteral articulation.

Consistent with this is the thickening of the notum, pleuron and exterior of the coxa in a straight line parallel to the axis of the muscle tendon (Snodgrass's no. 63 t). Cleared specimens were examined and an articulation of coxa to trochanter of coxa to pleuron and also an articulation between the meta pleuron and the metanotum was found. For a general diagram of this area, see Fig. 5.

The junction or articulation between the notal and pleural ridges is described by Snodgrass as looking 'like a ball-and-socket joint for movement between the notum and pleuron; but the two parts are so closely united that an effort to separate them always results in a break, leaving the head of the pleural ridge still in the grasp of the notal ridge'.

In the living or newly killed *Spilopsyllus*, the articulation between pleuron and notum is seen to be surrounded by a pad of transparent cuticle. When the metathorax is split sagittally and the halves are immersed in very dilute methylene blue (under 0·01 %) the pad stains the deep sapphire colour that characterizes resilin (Weis-Fogh, 1960).

Frozen sections of the resilin pad show it to be apparently free from lamellae. It is thus of the pure resilin 'tendon' type described by Weis-Fogh (1960) and thought to have an elastic efficiency of 96 % (Jensen & Weis-Fogh, 1962), even at frequencies of 200 cyc./sec.

The resilin pad of *Spilopsyllus* is elliptical in side elevation and of nearly constant thickness. In newly killed specimens the ellipse is 85–100 μ high, 65–75 μ long and the thickness of the pad is 25–30 μ. The volume is from

$$1\cdot04 \times 10^{-4} \text{ mm.}^3 \text{ to } 1\cdot75 \times 10^{-4} \text{ mm.}^3$$

For the estimation of energy-storing potential, live or newly killed fleas were used, in which the resilin is in a hydrated state. Hydrated resilin, at pH 6·8, breaks after a 140 % elongation at a tension of 30 kg..cm.^{2}. A cubical test piece of side 1 mm. thus delivers a mean 150 g. over 1·4 mm., an energy of 2·06 × 10^4 ergs.mm.$^{-3}$. If stretched 100 % the force is 15 kg..cm.$^{-2}$ (the material is non-linear in its elasticity), the mean force 75 g..mm.$^{-2}$ is delivered over 1 mm. and the energy is 7·4 × 10^3 ergs. These values are calculated from the data of Weis-Fogh (1961), and in the estimation of what follows an intermediate figure of 1·5 × 10^4 ergs.mm.$^{-3}$ is used as this seems entirely feasible.

The pad has a volume of about 1·4 × 10^{-4} mm.^{3}. Its energy-storing potential is thus 2·1 ergs per leg, 4·2 ergs per flea.

The energy store is thus adequate to account for the jump and for the frictional losses that may occur.

V. *The jumping mechanism*

A model of one side of a flea metathorax was made to aid in visualizing the mechanism involved in the storage and release of the energy of the jump impulse.

The model is based on *Pulex irritans*. Snodgrass's plates for *Hystricopsylla* and other fleas were used. The planes of rotation and limits of movement of all joints were found by observation with newly killed *Spilopsyllus* and *Xenopsylla*, and confirmed with *Pulex* (Fig. 4).

In the fleas examined the notum and pleuron were very inflexible, having thick

ridges running in the dorso-ventral direction. The resilin pad lies between the pleural ridge and the notum. The area anterior and posterior to the resilin pad is comparatively thin and free from ridges (*Pulex*). It would thus appear that compression of the notal ridge on the pleuron will cause either compression or shear of the resilin pad. Thus the pleural ridge is capable of up-and-down movement or of sideways rotation, inwards or outwards.
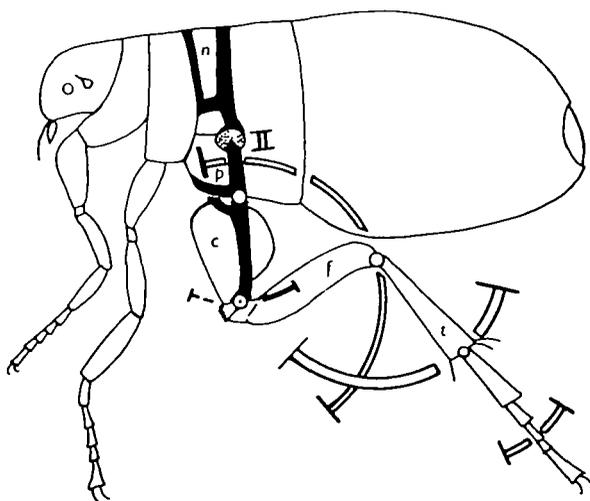

Fig. 4. Diagram of *Pulex* to show the principal skeletal elements in the metathorax and the angles through which the various joints of the hind legs can be rotated. *c*, Coxa; *f*, femur; *n*, notum; *p*, pleuron; *t*, tibia. (Forward rotation of the coxa is restricted, see the text.)

The two pleural ridges are connected together by a wide band of thickened cuticle which is attached to each near the coxal articulation and passes round the front of the metathorax. This is termed the 'sternal ridge' and tends to restrict anterior–posterior movement of the pleural ridge (Fig. 4).

The coxal articulation is somewhat complex. There is a socket at the top of the coxal ridge. The coxa can thus be rotated about 20° forward and 30° backward from the position where coxal and pleural ridges are in line. The coxa may also be twisted around the axis of pleural and coxal ridges as the sternal articulation of the coxa is via a sclerite which is flexibly articulated at one end to the sternum and at the other to the mesial ridge of the coxa.

On the anterior upper margin of the coxa (in Pulicoidea) there is an outward facing tooth of thickened cuticle; if the front of the coxa is rotated outwards and forwards the tooth engages on the sternal ridge that joins the two pleural ridges and forward movement of the coxal is thus prevented (Figs. 5, 6).

The articulation between coxa and trochanter consists of a pair of roller- and-socket joints. The joint allows rotation of the femur from a line about 10° forward of the axis of the coxa (when fully lifted) to a line 120° below the coxal axis (when fully depressed). Depression is effected by a large tendon attached to the forward edge of the trochanter, the trochanter being a mechanical unit with the femur for purposes of depression and lifting (Snodgrass, 1946).

The articulation of the tibia on the femur allows extension to a line nearly parallel with the femoral axis and flexion of about 120°.

The model was made as simple as possible, only the left side of the metathorax being built. The heavily sclerotized ridges were made from $\frac{1}{8}$ in. diameter steel welding rod, the remainder from $\frac{1}{16}$ in. rod. all junctions being silver-soldered. The lateral coxo-pleural articulation was made of a $\frac{1}{4}$ in. diameter ball-bearing and a brass conical socket, the mesial sternal articular sclerite being simulated by a length of welding rod held by short lengths of flexible P.V.C. tubing.
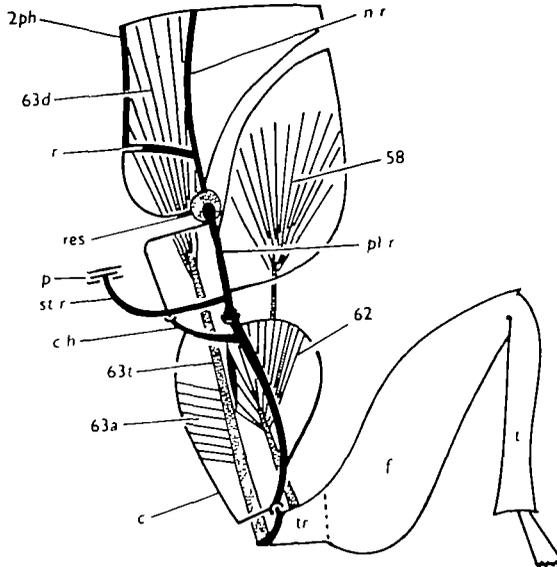

Fig. 5. Diagram of the principal muscles and lateral skeletal elements of the left side of the metathorax of a pulicoid flea, based on Snodgrass (1946) and on observation. Key (following Snodgrass): *c*, coxa; *c.h*, coxal hook; *f*, femur; *n.r*, notal ridge; *p*, 'pivot' point of sternal ridge; *pl.r*, pleural ridge; *r*, horizontal accessory ridge of metanotum; *res*, resilin pad (lobe of notal ridge in Snodgrass); *st.r*, sternal ridge; *t*, tibia; *tr*, trochanter; muscle 58, coxal remotor; 62, trochanter levator; 63 *a*, trochanter depressor; 63 *d*, dorso-ventral muscle; 63 *t*, tendon of trochanter levator and dorso-ventral muscle; *2ph*, metathoracic phragma.

The resilin pad between pleural and notal ridges was simulated by an industrial 'Metalastic' coupling of high elasticity, which was bolted in place.

The model was about 400 times the size of the insect, measuring 30 cm. from dorsal surface to the coxo-trochanteral articulation and 7 cm. from the resilin pad to the mid-line.

Muscles were simulated by nylon cords, only four muscles being incorporated (Fig. 5). These muscles were the largest muscles illustrated by Snodgrass (1946) and his numbering is followed here . The course of the muscles followed that shown in his drawings as this seemed a reasonable basis for experiment.

The muscles were the trochanter levator (62) the trochanter depressor (63 *a*), the associated dorso-ventral muscle (63 *d*) and the coxal remotor (58).

The individual action of the 'muscles' of the model is fairly predictable. The trochanter depressor (63 *a*) and levator (62) act antagonistically. Similarly, if the trochanter is held (by 62), the coxal is moved to and fro by 58 and 63 *d*.

When the muscles act simultaneously, however, the situation becomes more complex. If the trochanter is fully lifted by the levator (62) it cannot be depressed by 63 *d*

as the tendon (63 *t*) passes behind the axis of the articulation (see Fig. 6A). If, then, 62 is relaxed whilst maintaining tension on 63 *d* the trochanter is not depressed as the articulation has over-centre properties. However, muscle 63 *d* does act, under these conditions, as a coxal promotor.

When the femur is fully lifted by 62 and the muscle 63 *d* is pulled, the trochanter is not depressed owing to the over-centre properties of the trochanter–coxa articulation. Instead, the coxa is rotated forward until the tooth on the upper, outer coxal margin engages with the sternal ridge that joins the two pleural ridges (shown in Fig. 6B).
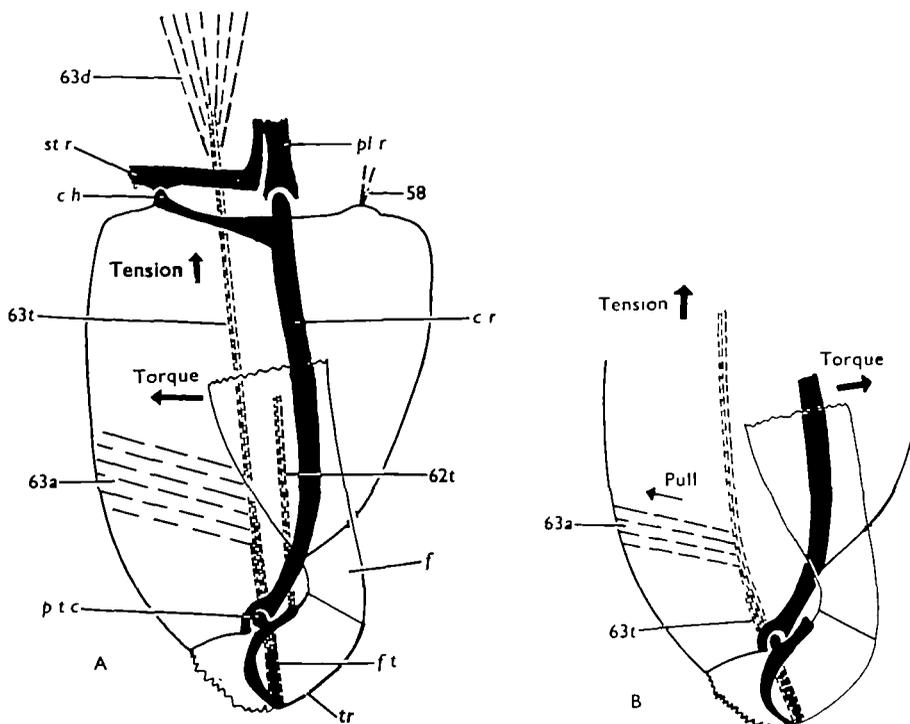

Fig. 6. Diagrams of forces in muscles and tendons of the left hind coxa and of torque on the hind femur. In both cases the femur (*f*) is fully raised and 63 *d* is contracted. 63 *t* is under tension (arrowed). In A, the tendon (63 *t*) passes behind the pivot (*p.t.c.*) of trochanter (*t*) on coxa, 63 *a* being relaxed. Torque on the femur is such as to lift it (arrowed). In B, 63 *a* has contracted and pulled 63 *t* in front of the pivot. Torque on the femur depresses it. Symbols as in Fig. 5, with *c.r*, coxal lateral ridge; *ft*, flexible part of 63 *t*; 62 *t*, tendon of trochanter levator; *p.t.c.*, pivot of trochanter on coxa.

Further contraction of the dorso-ventral muscle causes distortion of the Metalastic coupling, with upward movement of the pleural ridge (Fig. 7). In the model the coxa rotates outwards, as the sternal articulation is held at a constant distance from the dorsal surface; this does not appear to be the case in the flea and it is probable that here the coxa rotates inwards till the mesial surfaces of both coxae are pressed together. Such a condition can be seen on a living, constrained flea.

'Muscle' (63 *d*) can be fastened and the model remains set with a distorted thorax, the trochanter levator being relaxed. If now, the trochanter depressor (63 *a*) is pulled gently, the tendon (63 *t*) can be pulled in front of the coxo-trochanter articulation

(Fig. 6B) and the trochanter and femur then snap downwards, the energy being derived from the elastic return of the Metalastic coupling acting through the contracted dorso-ventral muscle (63 d).

The snap movement produced by the model has several features that suggest that it is an adequate model of the jump of the flea.
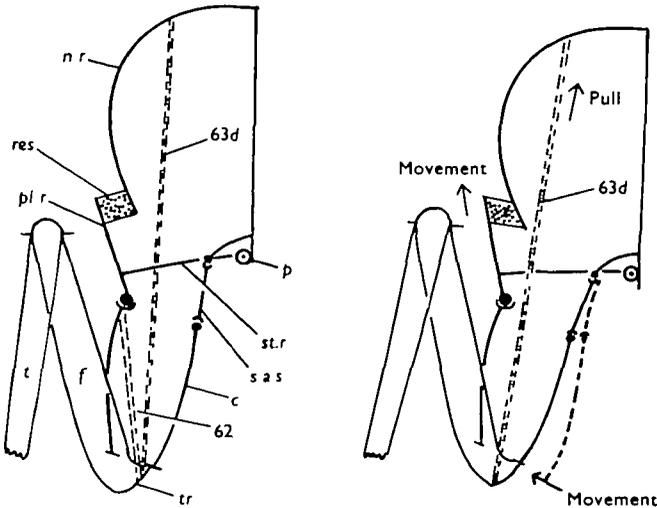

Fig. 7. View from behind of the left half of a model thorax. At A, the femur (f) is shown fully lifted by 62. In B, 63 d has contracted, pulling the coxa (c) upwards. As a consequence, the pleural ridge moves upwards and distorts the resilin pad (res). The coxa rotates outwards, the sternal articular sclerite rotating also. The original position of the inner wall of the coxa is shown dotted. Symbols as in Fig. 5. s.a.s., Sternal articular sclerite.

The major objection to direct muscular involvement in jumping was the time course of the process. In the model the only muscular movement at the jump is a triggering by 63 a which acts nearly normal to the axis of the principal tendon (Fig. 6B) and hence would have little affect on the rate of movement of the leg. The major antagonist to the jumping movement is the trochanter levator. In the model this may be relaxed as soon as the dorso-ventral muscle starts to contract and before any distortion of the thorax has occurred.

The stored energy is dissipated, in the model, via muscle 63 d, which is in the isometric condition and hence develops its full isometric tension.

VI. *The force of the jump*

The force of locust jumps has been calculated elsewhere (Brown, 1963; Hoyle, 1955). The present case is easier as the acceleration is so large that gravitational acceleration can be neglected. Force may hence be calculated from

$$F = mf, \tag{4}$$

where F is the force on both legs, m is the mass of the flea and f is the acceleration of the flea. As the acceleration has already been calculated in terms of g, force can be calculated directly in grams.

In the present case

$$m = 4\cdot5 \times 10^{-4}\,\text{g.,}$$
$$f = 135\,g$$
$$F = 4\cdot5 \times 10^{-4} \times 1\cdot35 \times 10^2\,g = 61\cdot0\,\text{mg. weight.}$$

This gives the mean force on each leg as $30\cdot5$ mg. If the force is constant, the distance over which it is delivered is given by

$$s = ft^2/2 \tag{5}$$

where f is the accelerating force, t is the time which the force acts and s is the distance over which the force acts. In the present case, for the greater acceleration, in $0\cdot75$ msec.,

$$f = 1\cdot33 \times 10^5\,\text{dyn.}$$
$$t = 0\cdot75 \times 10^{-3}\,\text{sec.}$$

So $\qquad s = \frac{1}{2}(1\cdot33 \times 10^5 \times (0\cdot75)^2 \times 10^{-6}) = 0\cdot37$ mm.

In the case where acceleration is over 1 msec., $f = 10^5$ dyn. and the distance is $0\cdot5$ mm., the force being $22\cdot5$ mg., on each leg.

VII. *Forces in the flea and during the impulse*

An attempt will be made in this section to calculate the mechanical advantage of the leg and to relate this to the forces that could be expected from the muscle and the resilin pad. Calculation of this type is possible because we have shown that the muscle, $63\,d$, is in the isometric condition, where its properties are predictable (Weis-Fogh, 1956) and because the properties of resilin are known (Weis-Fogh, 1960).

The leg effects the impulse by $90°$ depression of the femur and $85°$ extension of the tibia. This is seen in single frames of the film (Figs. 1, 2) and a general representation is given in Fig. 8.

Measurement of male *Spilopsyllus* gave the mean length of the trochanter and femur, between articulations, as $0\cdot33$ mm., of the tibia as $0\cdot33$ mm. and of all the tarsi as $0\cdot5$ mm. The apex of the tibia bore spines $200\,\mu$ long, the first tarsus spines were as $180\,\mu$ long, the second tarsus spines were $130\,\mu$ long and the third tarsus spines $80\,\mu$ long. The fourth tarsus and apical tarsus bore many spines from $50\,\mu$ to $30\,\mu$ long.

The point of the attachment of the trochanter depressor tendon ($63\,t$) is $60\,\mu$ from the centre of the articulation between trochanter and coxa. The attachment of $63\,t$, trochanter pivot and femur-to-tibia pivot are in line along the leg (Fig. 8).

By drawing a series of diagrams, as in Fig. 8, showing leg position for different positions of the flea along its trajectory, the distance moved by $63\,t$ can be related to the distance travelled by the flea. This is done in Fig. 9; it will be seen that for $0\cdot37$ mm. movement of the flea on a $60°$ trajectory, $34\,\mu$ movement of $63\,t$ is required, a mean mechanical advantage of $10\cdot9:1$. For $0\cdot5$ mm. movement, $60\,\mu$ movement of $63\,t$ is required, a mechanical advantage of $8\cdot3:1$.

Similar curves drawn for a $45°$ trajectory give the following figures: for $0\cdot37$ mm. movement of the flea, $31\,\mu$ at the tendon, mechanical advantage $12:1$; for $0\cdot5$ mm. at the flea $62\,\mu$ at the tendon, mechanical advantage $8\cdot1:1$.

The mechanical advantage at different points on the impulse stroke is the slope of

the curve of distance moved by flea v. distance moved by $63\,t$. The curve of mechanical advantage is shown in Fig. 9. Resilin has non-linear properties, the strain per unit stress being less at full elongation than at half elongation. As the mechanical advantage of the joint decreases over the power stroke it follows that, if the force in the resilin pad decreases in a similar way, the force at the leg will be nearly constant and hence acceleration will be constant. Prediction of the distortion undergone by short lengths
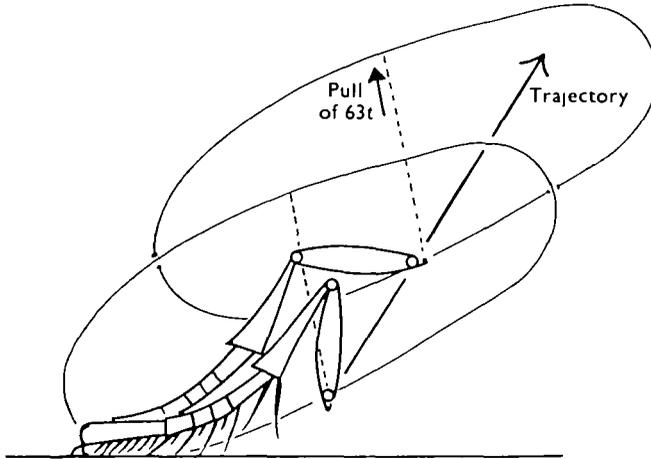

Fig. 8. Diagram showing starting and finishing position of the hind leg of a flea on a trajectory 60° above the substrate. The femur rotates through 90° and the tibia through 85° on the femur for a total movement of 0·5 mm. The axis of the trochanter depressor is shown dotted. Dimensions in the text.
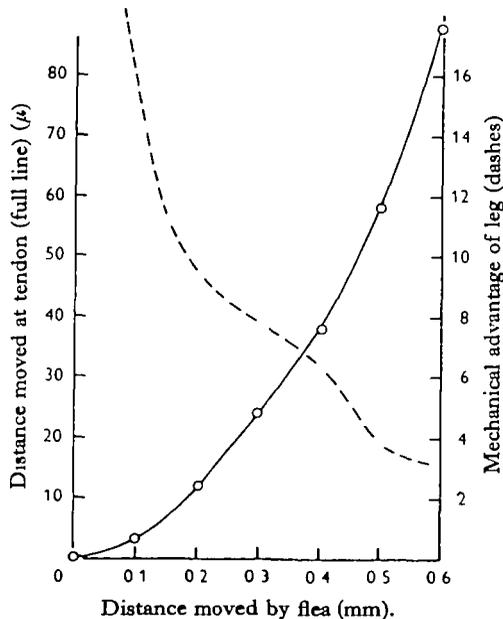

Fig. 9. The full line shows distance moved by flea and distance moved by depressor tendon $63t$, derived from diagrams similar to Fig. 8. The dashed line shows the slope of the full line and gives the mechanical advantage throughout the power stroke of the leg.

of elastic material under stress is difficult and it is not proposed to examine this aspect in any greater detail.

The dorso-ventral muscle, 63 d, is inserted over the whole of the dorsal surface of the notum enclosed between the notal ridge (*n.r* in Fig. 5), the metathoracic phragma (*2ph*) and the metathoracic accessory ridge of the metanotum (*r*). This is a surface 80 μ long and 0·28 mm. high in *Spilopsyllus*. The cross-sectional area is 2·2 × 10⁻⁴ cm.². The isometric tension in locust flight muscle is 1·6 kg..cm⁻². at 11° C. and rises to an estimated 3 kg..cm.⁻² at 25° C. and to 4 kg..cm.⁻² at 35° C. (Weis-Fogh, 1956). However, these last two figures may not be realistic as the muscle yielded in his experiments at 2–2·5 kg..cm.⁻². The maximum tension was produced near the normal length of the muscle in the body of the insect.

Using the upper figure the maximum tension expected in dorso-ventral muscle of the flea would be 2·2 × 10⁻⁴ × 4 × 10³ g. This is 0·88 g.; a realistic figure would be from 0·44 g. to 0·66 g.

If 0·66 g. is applied to an elastic spring the mean force of recovery is 0·33 g. A force of 0·33 g. applied over 34 μ gives 1·12 erg. Applied over 60 μ, 1·98 ergs is given. It was shown earlier that 34 μ movement at tendon 63 t moved the flea 0·37 mm. and that 60 μ at 63 t moved the flea 0·5 mm.

An energy dissipation at 1·12 ergs per leg or 2·24 ergs per flea is that calculated to produce a velocity of 1 m.sec⁻¹ after 0·75 msec. in a flea weighing 0·45 mg. No allowance is made for energy loss due to friction. The other case—where the flea accelerates in 1 msec. over 0·5 mm., 1·98 ergs per leg being available and giving 3·96 ergs per flea—is 75 % more than the 2·25 ergs required in section III.

The dorso-ventral muscle has a length of about 0·30 mm. The movement of 34 μ required to store the energy will only be 0·11 of the length; if the energy is stored in 0·2 sec., this is about 0·55 lengths.sec.⁻¹ and the muscle should be able to approach its isometric tension.

The tendon must be capable of transmitting a pull of up to 0·8 g. The tendon in *Spilopsyllus* is approximately 13 μ in diameter near the trochanter and 11·5 μ near the thorax. Using Jensen & Weis-Fogh's (1962) measurements for tensile strength of locust tibial cuticle of 9·6 kg..mm.⁻², the tendon has a strength distally of 1·27 g. and proximally of 0·84 g. Brown (1963) has estimated the tensile strength of locust tibial extensor tendon as 18 kg..mm.⁻², so it seems likely that the flea tendon is strong enough for the proposed mechanism.

Energy losses should be quite slight. The trochanter depressor tendon slides through the haemolymph but, as the velocity of tendon movement is only 20 cm..sec.⁻¹ at the end of the jumping stroke, losses from this cause are likely to be negligible.

It is assumed that the tibia is free to rotate on the femur. While it is difficult to justify this, the total tendon movement in the tibia is only about 20 μ, and this is only constrained by what may be a relaxed muscle. The problem of tibial flexion is considered in the next section.

The muscular system and anatomy is, as far as can be calculated, appropriate to the mechanism that has been put forward.

VIII. *Attitude after the impulse and glide path*

In the flea the trajectory and attitude are highly variable, somersaults and rolling being the rule rather than the exception; this is also found in small locusts which cannot use wings as stabilizers (Brown, 1963).

A series of models of whole fleas have been constructed; these are all propelled by a large internal rubber band operating on a 'trochanter' depressor tendon via an 'over-centre' joint—the release of the energy stored in the rubber band may be triggered from outside the model.

The models differ in the disposition of the joints of the hind legs; changes have been made in the angle through which the femoral–tibial articulation can rotate. No attempt was made to produce active extension of the tibia.

If the leg is rigid from the trochanter onwards, the model always somersaults markedly; this is a consequence of torque reaction to the impulse (Fig. 10*a*).

When the tibial articulation is freed so that the tibia can rotate from 135° to the femoral axis until it is parallel to the femur, the jump is comparatively free from somersaults and rolling. It is essential that the tibial and tarsal spurs of the flea should be represented on the model; series of pins have been fastened at appropriate points. It is also essential that tibia and tarsi should act as a rigid unit.
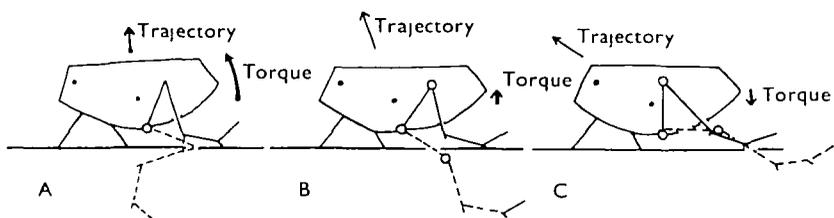

Fig. 10. Diagram of the trajectory and final torque on three types of model flea. The centre of gravity is indicated as a central spot; trajectory is a radial arrow and torque an arc at the posterior end. The starting position of the legs is shown as a full line, the final position is in dashes, and pivots are shown as circles. At A the leg is rigid from the trochanter. At B and C the starting-point of the power stroke differs.

When the angle of the femur to the substrate is altered, or when the position of the femur before the impulse is altered, the glide path varies. In Fig. 10*b* the femur starts from a position 50° above the model's longitudinal axis and rotates through 90°; the glide path is about 60° to the substrate. If the femur starts from a position normal to the long axis of the model, and rotates through 90°, the glide path is about 30° to the substrate (Fig. 10*c*). In both cases the torque on the model is small.

The glide path in either case can be altered by altering the attitude of the model with respect to the substrate; if the model starts in a nose-up attitude, the glide path becomes more nearly vertical, but the tendency to somersault increases.

If one leg is placed on a raised part of the substrate or if the substrate is not flat, the model rolls in flight owing to lateral assymmetry of the impulses. Similar effects would be found if the two legs were not depressed simultaneously. In the models the legs were mechanically coupled but this is apparently not the case in the flea.

The case where the flea lands facing the point of departure (Rothschild & Clay, 1952) is a consequence of simultaneous somersaulting and rolling, not simple

somersaulting as was suggested. The present films and experiments suggest that a straight trajectory is exceptional.

From the performance of the models, it appears that the jump can be explained by assuming that there is active rotation of the limb at the coxa–trochanter articulation and passive rotation at the femoro-tibial articulation; this assumption differs from that made by Snodgrass (1946) and is more consistent with the known properties of muscles.

IX. *Experiments on living and dead fleas*

For these experiments specimens of *Xenopsylla cheopis* were used.

Fleas may be examined while alive by sticking them to a length of 'Sellotape' wound sticky-side-out around a microscope slide. The flea is firmly held, surgery may be performed, and the flea can then be removed with ease.

If a newly killed flea is placed on its side on the sticky slide the joints may be manipulated. If the femur is rotated upwards and the resilin pad is pushed toward the centre of the thorax, the femur is depressed. If the femur is raised as far as possible and held in place and the resilin pad is then pushed as before, the femur does not move downwards when released. Under these circumstances, femoral depression continues if the femur is first depressed through about 10° by manipulation with a needle.

These two observations are similar to those found with the model and are consistent with the suggested mechanism of thoracic wall distortion and the over-centre joint.

Living fleas have been operated upon with small pieces of razor blade. If either the notal ridge or the pleural ridge is cut on both sides of the thorax the flea walks in a fairly normal manner and raises and lowers the femora, but cannot jump. Attempts to transect the resilin pad were unsuccessful. A flea treated unilaterally will still jump but the performance is less spectacular.

When a cut is made along the whole of the forward edge of the coxa in such a position as to transect muscle 63 *a* (which runs from the forward edge of the coxa to the tro-chanter-depressor tendon 63 *t*), the flea cocks its leg so that the femur is vertical. The femur then twitches forwards and this movement may be continued, with the flea stationary, for as long as 10 sec. The animal seems incapable of depressing the tro-chanter. These results are consistent with the proposed mechanism for releasing the over-centre joint.

X. *Prediction of performance of other fleas*

The performance of *Spilopsyllus cuniculi* has already been considered. Live speci-mens of *Hystricopsylla talpae* and *Pulex irritans* were collected by M. B. Usher and *Xenopsylla cheopis* was available in laboratory culture.

A survey of the size of the resilin pad and weight of the flea was carried out with a view to estimating the jumping performance. Newly killed specimens were used to estimate the size of the pad as in §IV. The value, $1·5 \times 10^4$ ergs.mm.³, for energy storage by resilin, is again used. The results are given in Table 1. The estimate of velocity was made by use of equation (1), the deceleration being taken as $1·2 g$ for the large *Hystricopsylla* and $1·5 g$ for the others; this is an assumption considered in §II for *Spilopsyllus* and it may be a considerable underestimate for *Pulex*. As will be seen from Table 1, there is a considerable range of estimated performance.

Hystricopsylla is about 5 mm. long. In twenty jumps a height of 3 cm. was observed

on two occasions. The sample of *Xenopsylla* could escape from a jar 7·5 cm. high but not one from 12·5 cm. high. The one specimen of *Pulex* (at present not common) jumped to the top of the 'pooter' in which it was collected, a height of 13 cm. Male *Pulex* weigh probably up to 1 mg. and females up to 1·5 mg. But the available energy may be as much as 30 ergs, which would propel the animal up to 20 cm.

Table 1.

Species	Weight of individual (mg.)	Estimated volume of resilin in each pad (mm.³)	Estimated total energy store (ergs)	Estimated velocity (sec.⁻¹)	Estimated height of jump (cm.)
Hystricopsylla talpae	4·8	$5·65 \times 10^{-4}$	17·0	84 cm.	3·0
Spilopsyllus cuniculi	0·45	$1·1 \times 10^{-4}$	3·30	1·2 m.	4·9
		$1·4 \times 10^{-4}$	4·20	1·35 m.	6·2
Xenopsylla cheopis	0·40	$1·54 \times 10^{-4}$	4·6	1·5 m.	7·6
Pulex irritans					
Preserved ♀	0·49	$4·1 \times 10^{-4}$	12	2·2 m.	16
	—*	$5·35 \times 10^{-4}$	16	—*	Up to 20 cm.
Preserved ♂	—*	$1·08 \times 10^{-3}$	31·5	—*	Up to 20 cm.

* See text.

These performance figures are estimates; they are in all classes underestimates as the value for the elongation of the resilin that has been chosen is less than the maximum possible. This is felt to be more consistent with the probable properties of the rest of the system and also allows for elastic, frictional and viscous losses.

For interest, the acceleration undergone by *Pulex* over a probable distance of 0·75 mm. would be 320 *g* and the time taken is about 0·66 msec., compared with 0·75 msec. for *Spilopsyllus*; the figures are similar, the difference in performance, however, is significant.

GENERAL DISCUSSION

The problem of rapid locomotion in a very small animal resolves itself into a need for very rapid movement of the limbs. In flying insects this is met by myogenic systems operating into resonant loads (Machin & Pringle, 1959). In a walking insect, where the limbs do not oscillate, a limitation is reached at about 20 steps/sec., which is about the upper limit for walking that has been measured (Wilson, 1965); this leads to a velocity of about 1 cm.sec.⁻¹ for an animal whose legs move 0·5 mm. per step. At this sort of speed, jumping is profitless; it has been seen that a velocity of from 1 m..sec.⁻¹ is needed, and that even at this velocity with a small animal air resistance is probably very significant.

In fact, for an animal of this size to jump, it is necessary to invoke some energy-storage mechanism—the case of the locust is apparently on the lower limit of size for direct muscular contraction and even there the events are too rapid for the full tension of the muscle to be realized (Hoyle, 1953) and the arrangement of the muscle fibres is extremely specialized.

In the flea the full energy-producing potential of the muscle is not realized as the muscle contracts from close to its resting length to its isometric tension; this is not the condition for maximum power (Hill, 1950). The mechanism postulated is unusual in as far as the muscle itself appears to transmit force without change of length; this is, however, an unsatisfactory condition compared with that of a locust or frog where the rate of muscular contraction probably never returns to zero. Argument of this type, indeed, accounts for the far shorter jump of the flea, which has a similar proportion of muscle involved in the jumping mechanism.

Energy-storage mechanisms are common in insects (Weis-Fogh, 1960) and are used to reduce inertial losses in wing mechanisms. The energy store in the flea occurs at just that point at which the winged ancestor might have been expected to have a wing; it is tempting to suggest that the jumping mechanism of the flea is a specialization of the conventional flight mechanism of a higher insect.

In this context, one inexplicable fact emerges. The depressor of the trochanter contains two sections: one is conventional and arises on the coxa; the other is apparently the coxal promotor and arises on the thoracic notum. The real problem of the flea's jump is the conversion of a dorso-ventral muscle, possibly an indirect flight muscle, to a trochanter depressor; it would appear from the foregoing discussion that the rest of the mechanism is typical of a winged insect.

SUMMARY

1. The energy requirement of a jump of 3·5 cm. height by the rabbit flea, *Spilopsyllus cuniculi*, is 2·25 ergs. This must be delivered in 0·75–1·0 msec. over a distance of 0·37–0·5 mm., which is not compatible with direct muscular action.

2. The anatomy of the jumping mechanism has been re-examined and its action studied by high-speed cinematography. The following explanation is offered. The main impulse comes from the depression of the metathoracic femur, whose depressor muscle originates on the notum. In the resting position the attachment of the depressor tendon to the femur is over-centre with respect to the trochanter–femoral joint. When the muscle contracts energy is stored in a resilin pad located between notum and pleuron. This energy is released by a second muscle which pulls the depressor tendon away from the over-centre position, thus enabling it to depress the femur.

3. Operations on live fleas have provided evidence in support of the proposed mechanism.

4. The depressor muscle is capable of providing 1·96 ergs on each side.

5. The resilin pad is capable of storing 4 ergs on each side.

6. Species which are better jumpers have larger resilin pads.

REFERENCES

BROWN, R. H. J. (1963). Jumping arthropods. *Times Science Review*, Summer 1963, pp. 6–7.
HILL, A. V. (1950). The dimensions of animals and their muscular dynamics. *Sci. Prog., Lond.* **38**, 209–30.
HOYLE, G. (1955). Neuromuscular mechanisms of a locust skeletal muscle. *Proc. R. Soc.* B **143**, 343–67.
JACOBSON, H. (1940). Über die Sprungmuskulatur des Uferschwalbenflohes, *Ceratophyllus styx* Roths. *Z. morph. Ökol. Tiere* **37**, 144–54.
JENSEN, M. & WEIS-FOGH, T. (1962). Biology and biophysics of locust flight. V. Strength and elasticity of insect cuticle. *Phil. Trans. R. Soc.* B **245**, 137–69.
MACHIN, K. E. & PRINGLE, J. W. S. (1959). Physiology of insect fibrillar flight muscle. II. Mechanical properties of a beetle flight muscle. *Proc. R. Soc.* B **151**, 204–25.
ROEDER, K. D. & WEIANT, E. A. (1950). The electrical and mechanical events of neuromuscular transmission in the cockroach, *Periplaneta americana. J. exp. Biol.* **27**, 1–13.
ROTHSCHILD, M. & CLAY, T. (1952). *Fleas, Flukes and Cuckoos*. Pp. xiv + 304. London.
ROTHSCHILD, M. & HOPKINS, G. H. E. (1953). *An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Natural History)*, vol. 1. Pp. xv + 361. London.
SNODGRASS, R. E. (1946). The skeletal anatomy of fleas. *Smithson. misc. Collns* **104**, 1–89.
WEIS-FOGH, T. (1956). Tetanic force & shortening in locust flight muscle. *J. exp. Biol.* **33**, 668–684.
WEIS-FOGH, T. (1960). A rubber-like protein in insect cuticle. *J. exp. Biol.* **37**, 889–907.
WEIS-FOGH, T. (1961). Molecular interpretation of the elasticity of resilin, a rubber-like protein. *J. molec. Biol.* **3**, 648–67.
WILSON, D. M. (1965). Proprioceptive leg reflexes in cockroaches. *J. exp. Biol.* **43**, 397–409.