

The jump of the click beetle (Coleoptera, Elateridae)—a preliminary study

M. E. G. EVANS

Zoology Department, University of Manchester

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(With 1 plate and 9 figures in the text)

A preliminary account is given of the jump of the click beetle, *Athous haemorrhoidalis* (F.). The jump is normally made from an inverted position. It involves a jack-knifing movement whereby a prosternal peg is slid very rapidly down a smooth track into a mesosternal pit. The muscles which produce this movement are allowed to build up tension by a friction hold on the dorsal side of the peg. The anatomy of this jumping mechanism is briefly described. Ciné recording showed that the jump was usually nearly vertical and could exceed 0·3 m in height; the beetle normally rotated several times head over tail during a jump. The jump was produced by a very rapid upwards movement of the beetle's centre of gravity during the jack-knifing action. In a typical jump, a 4×10^{-5} kg beetle could be subjected to an upwards acceleration of 3800 m/s^{-2} (380 g). The minimum work done and the power output of the muscles causing jumping have been calculated. A simple mechanical model has been constructed to simulate a jump, and several possible ways in which the jumping mechanism could operate have been discussed.

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Introduction

An inverted click beetle, or skipjack, can produce a violent jack-knifing action which results in a nearly vertical leap of up to 0·3 m from a hard surface. The particular interest of this jump is its performance without the use of legs. Some other insects can produce "legless" jumps—notably the Collembola—but the mechanism found in the click beetles is unique. Most animal jumping mechanisms involve leg extension. Amongst the insects, recent studies of the energetics of jumping have been carried out on the locust by Brown (Alexander, 1968) and on the flea by Bennet-Clark & Lucey (1967). The latter study is of particular interest in that the flea is a very small animal and has evolved an energy storage mechanism. The click beetle also uses an energy store, but of quite a different type.

The Elateridae are a widespread and successful family of about 10,000 species. As far as is known, most Elateridae can jump, but outside this family the only beetles which may have the clicking mechanism are the closely related Trixagidae. The method of jumping has intrigued many generations of entomologists, and Straus-Durckheim paid special attention to it in his anatomical monograph of 1828. More recent studies have been made by Binaghi (1942) and d'Aguilar (1961), and the latter author has summarized much of the previous literature.

Material

Most of this study has been concerned with *Athous haemorrhoidalis* (F.), but the jumping of *Agriotes pallidulus* (Ill.), *Hypnoidus riparius* (F.) and *Corymbites cupreus* (F.) has also been observed. In addition, museum specimens of a number of large, exotic species were examined in order to compare their skeletal anatomy with that of the British species.

Adults of *Athous* were collected during May and June by sweeping grass and low herbage, especially in woodlands. On warm, humid days the beetles were found clinging to the tops of grass blades. If one attempted to catch a beetle, its usual reaction was to drop into the undergrowth of grassroots and litter. If it landed upside-down on a smooth, level patch of ground, and could not quickly right itself with the aid of its legs, it would jump to avoid capture. Normally the beetle would rock its body until the legs gained sufficient purchase on slight irregularities of the surface for it to right itself. Occasionally, a beetle would jump directly from its vertical perch on the grass stem. A beetle can rarely perform its normal righting movements if it is placed on an artificially smooth, level surface such as a table top, and in this situation it will eventually jump.

Methods

Anatomical

Longitudinal and transverse serial sections of material double embedded in celloidin and wax were cut and stained for detailed examination. Dissections of the musculo-skeletal system were carried out on wax embedded whole specimens.

Photographic

16 mm colour, and black and white films were taken of the jump, and were analysed frame by frame using conventional techniques. Bolex and Beaulieu cameras (with extension tubes where necessary) were used for speeds up to 64 frames per second (f.p.s.). A Fastax WF 17 camera with extension tubes was used to take high speed ciné pictures at up to 3750 f.p.s. on Kodak 4X negative film. This was uprated in development so that an illumination could be used which did not kill the beetles. Camera speeds were confirmed with a time marker. The high speed photography was carried out by the staff of the photographic laboratories of the Engineering Department of Manchester University. Speeds of 5000–6000 f.p.s. were also used, but due to the small period of time at which the camera was running at these speeds, it proved very difficult to obtain reasonable results. It was not always easy to make the beetles jump when stimulated, and they would often jump either before or after the film was run. The heat of the lights was a useful stimulus, but the mechanical stimulus of slight pressure proved more reliable. In order to measure accurately the amount of movement, jumps were photographed either against a background of graph paper or above a reflecting surface. In all, several thousand feet of film were used.

Photomicrographic

High power photographs of the surface structure of the cuticle in the peg and track regions were taken of silver coated specimens on the Stereoscan microscope of the Department of Textile Technology, UMIST (University of Manchester, Institute of Science and Technology).

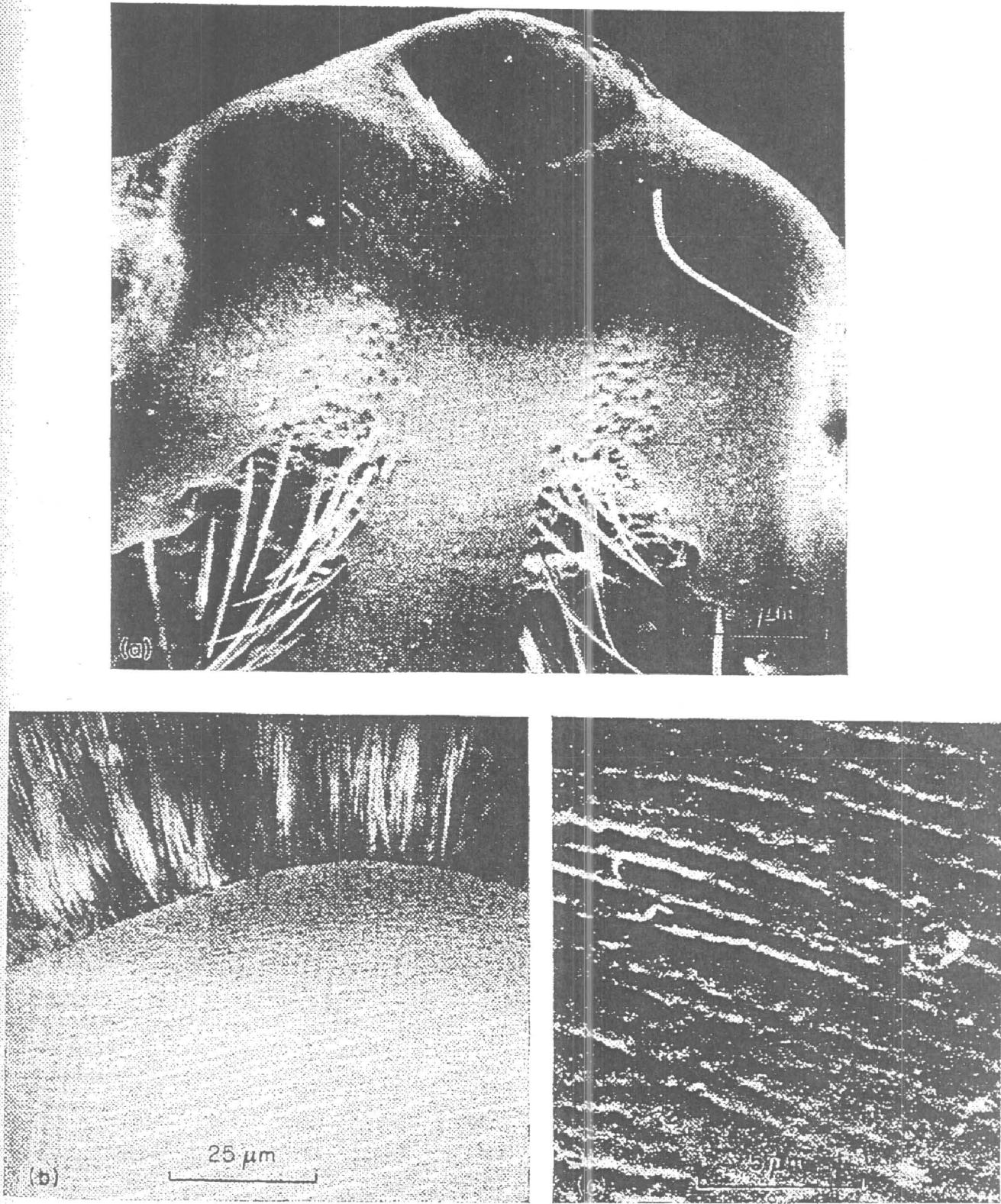


PLATE I. Stereoscan micrographs of the peg and track of *A. haemorrhoidalis*.

(a) Antero-ventral view of anterior mesosternum, with mesosternal lip at top. The track is in the midline, and leads downwards towards the pit. (b) Dorsal view of the posterior end of the peg skid, showing the parallel ridges on the step riser which form the friction hold (see Fig. 4). The posterior rim of the peg hold is uppermost. (c) Detail of peg hold enlarged to show the ridges.

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Results

The anatomy of the jumping mechanism

A jump is normally made from an inverted position in which the beetle rests on its pronotum and elytra. Jumping is preceded by the arching of the back, whereby the middle of the body is raised slightly from the ground (Fig. 1). As this happens, the head is retracted

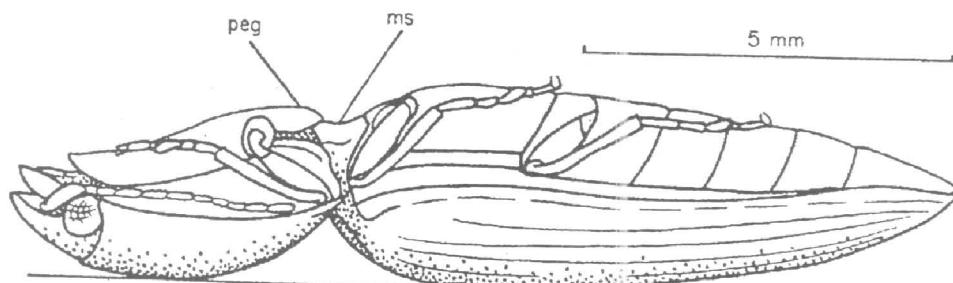


FIG. 1. Side view of *Athous haemorrhoidalis* with the back arched and the peg set on the lip of the mesosternum (ms) ready for jumping.

and the antennae and legs are usually withdrawn and held against the body. Back arching is made possible by the mobile articulation between the prothorax and mesothorax. It is maintained by a posterior extension of the prosternum in the midline—the peg—which rests on the anterior margin of the mesosternum. This is facilitated by a small step on the dorsal side of the distal end of the peg which provides a friction hold (Fig. 4 and Plate I). In normal circumstances, when the beetle is not jumping or preparing to jump, the prosternal peg fits part way into a deep pit just behind the anterior margin of the mesosternum, and the prothorax and mesothorax are fitted tightly together.

The necessity of the peg for jumping can easily be demonstrated by removing its tip in an otherwise intact beetle. The beetle then performs slow arching and flattening movements as it attempts to set the peg onto the mesosternal lip, and it is unable to jump. When an intact beetle has set its peg and has reached the back arched position, it is ready to jump. This position may be maintained for less than half a second, or it may be held for several minutes, but a certain minimum time in this position is necessary and jumping is never immediate. After it is set to jump, however, the beetle will jump immediately it is stimulated to do so. Such a stimulus produces a rapid "jack-knifing" of the body as its curvature is violently reversed (Fig. 2). This is accompanied by the plunging of the peg into the pit as its friction hold suddenly gives. The peg is halted by the impact of prothoracic bumpers on mesothoracic buffers. The peg base forms a median bumper which collides with a buffer

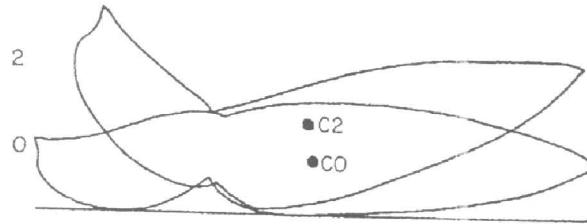


FIG. 2. Profiles of *Athous* to show the jumping (jack-knifing) action. The beetle is inverted and shown lying on a hard surface. The profiles represent two frames taken from a high speed ciné film, and are 0·64 ms apart. Frame numbers are shown on the left; frame 0 shows the beetle in the set position just before jumping. The beetle's centre of gravity in the set position, C_0 , rises to C_2 in frame 2, which is just off the ground. (Scale as for Fig. 3.)

formed by the lip of the mesosternum (Fig. 4); other, more lateral buffers are formed by the mesepisternal rims (Fig. 6(a)). The beetle is then flung off the ground (Fig. 3). The head and appendages are released immediately the jump takes place.

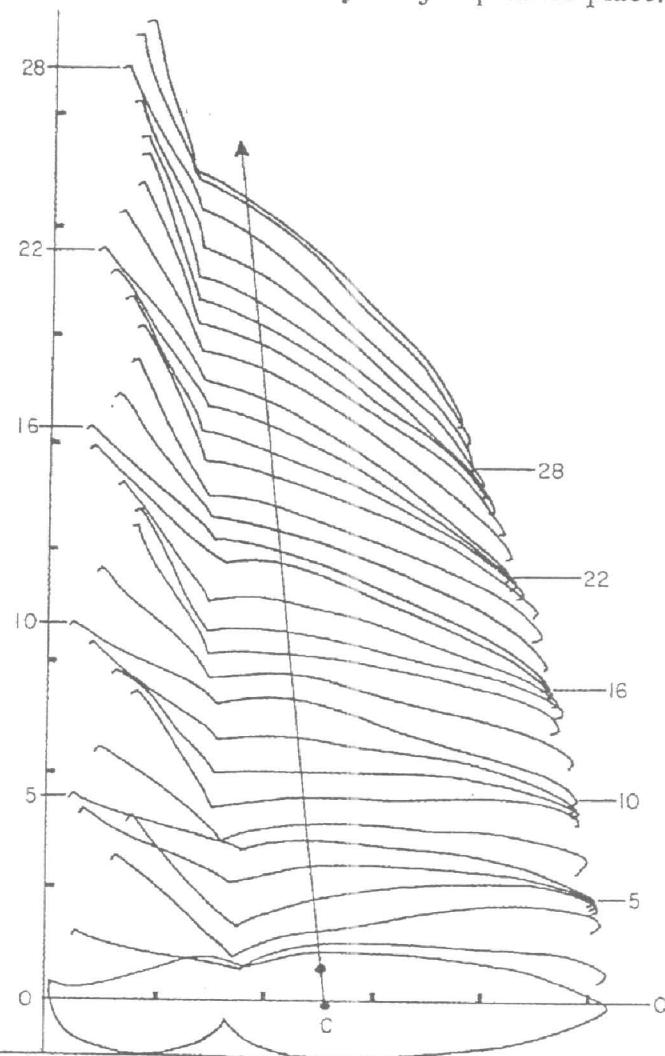


FIG. 3. Profiles of *Athous* taken from the first 30 frames of the same film from which Fig. 2 is taken. Frame numbers are shown on the vertical axis, and the graduations on the axes represent the lines on the one-tenth inch graph paper which formed the background to the film of the jump. Except for frame 0, only the ventral surface of the beetle's profile is shown. The direction of movement of the beetle's centre of gravity (C) is also indicated.

The movement of the peg into the pit is extremely rapid—less than one millisecond for most jumps and about half of this for the highest jumps. The anterior wall of the pit forms a guide for the peg which ensures that the violent blow of the prothorax on the mesothorax is accurately located. This anterior wall forms a track along which the skid—a dorsal raised area of the peg—slides. The track forms an arc which is centred in the middle of the transverse axis linking the prothoracic pivots, and thus the sliding peg will accurately follow the track profile (Fig. 4). Since the movement of the peg skid needs to be so rapid, sliding friction has been reduced to a minimum by the extreme smoothness of the track. Even magnifications of well over 10,000 on stereoscan photographs failed to reveal any details—apart from scratches—on the track surface (Plate I(a)).

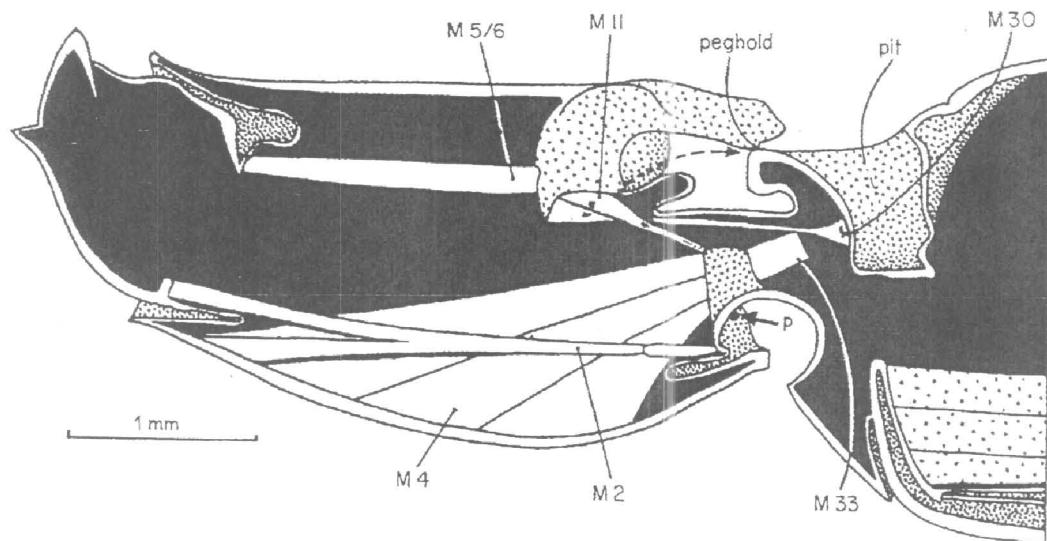


FIG. 4. Longitudinal section (semi-diagrammatic, with the ventral side uppermost) through the anterior half of *Athous* to show the muscles involved in jumping. The peg hold is shown resting on the mesosternal lip at the beginning of the track which leads into the pit. The horizontal pivot axis (P), upon which the prothorax swings, is arrowed. The direction of movement of the peg base (bumper) towards the mesosternum (buffer) is shown as a dotted line.

The peg skid has a dual function. Its posterior margin forms a friction hold against the smooth anterior lip of the mesosternum, and its dorsal face moves along the track and has a low sliding friction. A common form of sculpturing on the peg skid of Elateridae is a regular series of small punctures. These are visible on some parts of the skid of *A. haemorrhoidalis*, but at the posterior margin, the friction hold is formed by a series of parallel ridges about 1 μm apart (Plate I(b), (c)). These become less pronounced and fade out more posteriorly; the sliding surface of the skid is fairly smooth. Tension in the large M₄ muscle (which causes the body to jack-knife) can be built up whilst the ridged lip of the peg skid is held against the very smooth lip of the mesosternum. Tension is released when the peg skid slips over the mesosternal lip, and the smooth skid slides rapidly along the very smooth track until the bumpers hit their buffers.

The mesosternum is a massive, thick-walled sclerite whose lateral margins meet the sidewalls of the mesothorax. Each sidewall is also massively constructed and consists of a mesepisternum and mesepimeron which reach the elytron dorsally, where they make a good fit with its deep side margin, the epipleuron (Fig. 5). Thus there is a strong arc of sclerites on either side of the mesosternal buffer which links it with the tough elytra. The elytra are not only interlinked with the mesothoracic sidewalls, but are interlocked in the midline at the suture, and are held closed by the mesoscutellar catch.

The cuticle of the prothorax is also very thick and this is particularly noticeable at the base of the prosternal peg, which forms a bumper. The fore coxae lie on either side of the peg base, and a suture between the prosternum and the sidewall extends forwards from the mesal side of each coxal base (Fig. 5). This suture can open sufficiently, particularly anteriorly, to allow a slight amount of movement between the prosternum and the sidewall. The margins of this suture are linked by varying amounts of elastic and flexible cuticle (Fig. 9), and one possible interpretation of this in relation to jumping will be suggested later.

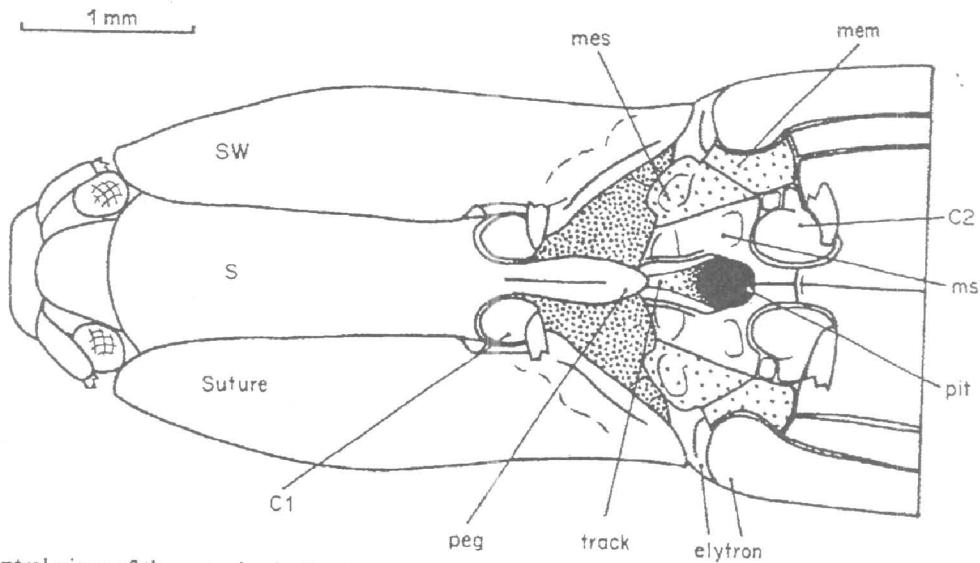


FIG. 5. Ventral view of the anterior half of *Athous*. The peg is shown resting on the beginning of the mesosternal track leading into the pit (as in Fig. 4). The arthrodial membrane between the prothorax and mesothorax is shown heavily dotted, whilst the mesepisternum (mes) and mesepimeron (mem) are lightly dotted. Other structures: c₁, first coxa; c₂, second coxa; ms, mesosternum; s, prosternum; sw, prothoracic sidewall.

The pivots which form the articulation between the prothorax and mesothorax are two smooth knobs on the underside of the posterior margin of the pronotum (Fig. 6(b), (c)). They rest on a pair of smooth depressions on either side of the midline at the front margin of the mesothorax (Fig. 6(a)). On either side of the pivots, pronotal flanges project backwards into elytral cavities on either side of the mesoscutellum. The rounded root of each elytron lies immediately under each flange. Because of these flanges, the prothorax cannot be swung either upwards or downwards until it has slid forwards sufficiently on its pivots to enable the posterior edges of the flanges to clear their elytral cavities as they tilt upwards (Fig. 7). When the beetle is set to jump (in the back arched position), the flanges locate the pivots in their correct positions, and prevent the pivots from sliding backwards into their original locked positions. A subsidiary pivot is present on the sidewalls of the mesothorax—the antero-dorsal rim of the mesepisternum. These rims are smooth, shining rails which fit into corresponding grooves in the prothoracic sidewalls. They enable the prothorax to slide forwards on the mesothorax; they form a second bumper-buffer system, and they also provide a pivot at the end of the jumping swing of the prothorax if the normal pronotal pivots slide off their mounts.

Musculature (Fig. 4)

Muscle nomenclature follows Evans (1961) who tried to standardize this for the whole muscle system of a beetle. More recently, Larsen (1966) had made a comprehensive comparative study of the thoracic muscles of beetles, and his numbering system will also be quoted. Larsen has described the thoracic musculature of *Corymbites aeneus* (L.), and this is very similar to that of *A. haemorrhoidalis* particularly with respect to the jumping muscles.

The largest muscles in the prothorax are the dorsal intersegmental muscles, M4, which together account for about one third of the weight of the head and prothorax, and between 6 % and 9 % of the whole beetle. These muscles produce the jump. Each muscle originates

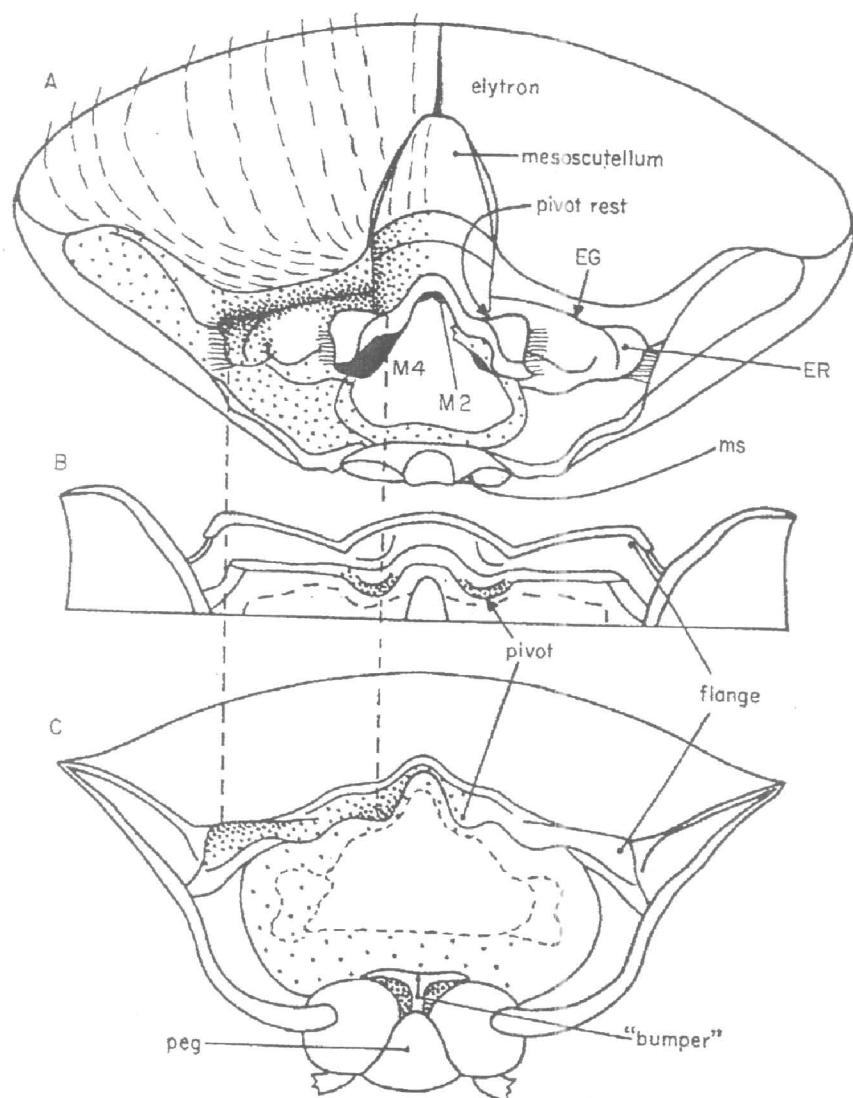


FIG. 6. Details of the pivot region of *Athous*.

(a) Anterior view of the mesothorax showing the attachments of muscles M2 and M4. (b) Ventral view of the posterior rim of the prothorax. (c) Posterior view of the prothorax. EG, Elytral groove; ER, elytral root; ms, mesosternum.

over a wide area of the pronotum on either side of the midline, and inserts by a wide apodeme at the bottom of the inwardly projecting spike on the mesonotal rim (i.e. ventrally on the most lateral part of the first phragma).

The antagonistic muscle is the median dorsal muscle (M2a and b) which originates both on the anterior pronotum and on the back of the head. It lies just beneath the pronotum and inserts on the middle of the mesothoracic rim (i.e. medially on the first phragma). Its narrow apodeme contains a translucent, thickened region which attaches the muscle to the most dorsal part of the mesothoracic rim. M2 is much smaller than M4, and is responsible for both head retraction and back arching before the jumping mechanism is set. It is important to note that it inserts dorsally to the transverse axis through the pivots, and the back of the pronotum is arched to allow it the highest possible insertion; conversely, the

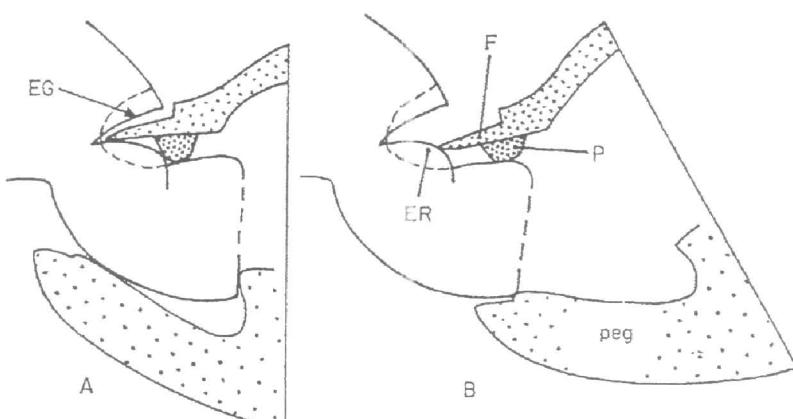


FIG. 7. Diagrams showing the relative positions of the pronotal pivots and flanges and the peg and track.
(a) "Resting" position, seen in normal walking. (b) Set position, seen just before jumping. F, Pronotal flange; P, pivot; other labels as in Fig. 6.

jumping muscle M4 inserts on the mesothoracic rim as far ventrally as is possible. Thus, a reasonable mechanical advantage is obtained.

The prothoracic ventral muscles (M5 and M6), which run from the profurcae to the cervical sclerites and the back of the head, also act as head retractors. Two small, intersegmental muscles are found ventrally. The mesothoracic ventral muscles (M30) arise on the posterior sides of the profurcae, and are connected to the mesofurcae by long, narrow apodemes; the lateral intersegmental muscle (M11) runs between the profurca and the ventral end of the most lateral part of the mesonotal rim (i.e. just ventral to the insertion of M4). Both M30 and M11 could move the prothorax in relation to the mesothorax, and they may form part of a possible trigger mechanism.

The jump

The jumping action is accompanied by an audible "click" which gives the beetle its common English name, and this suggested a simple way of obtaining some idea of the speed of this action. The sound produced was recorded on magnetic tape and played back onto a U-V recorder. This established a single major peak amplitude which was produced over about a millisecond. More detailed analysis using a storage oscilloscope showed that this peak could have a duration as short as 0.25 ms. The sound may arise from the parts of the dorsal hinge as they disengage. However, the two most probable ways in which it might be produced are either the sudden slipping of the peg over its friction hold, or the violent impact of the peg bumper on the mesosternal buffer. The short, sharp sound produced seems to favour the latter explanation, but this is by no means certain.

A preliminary visual record was made using ciné film exposed at 64 f.p.s. to establish the height reached and the trajectory of the jump. The jump is often almost vertical, and if a beetle leaps from a level surface, it will usually land close to its take-off point. The highest jump of *A. haemorrhoidalis* recorded on film was 0.263 m, but specimens have been observed to jump over 0.3 m. Of course, many jumps are much less than this, but on several occasions a beetle jumping from a smooth, hard surface (glass) leaped to between 0.18 and 0.26 m in each of ten consecutive jumps. Conversely, jumps from a soft substrate were much lower, and jumping from a surface such as soft cotton wool was barely possible; obviously, the reaction of the substrate is necessary to provide the lifting thrust.

For the films taken at 64 f.p.s., the take-off speed was estimated from the distance moved by the centre of gravity between frames 1 and 2. (In all the films, frame 0 is the last frame before jumping, in which the beetle is still in the set position.) The trajectory was very symmetrical, and the beetle fell at an acceleration very close to g , the acceleration due to gravity. Thus air resistance seems to have had little effect, and the expression

$$h = \frac{v^2 \sin^2 \theta}{2g}$$

can be applied to the trajectory, where h m is the height reached, v m/s is the take-off velocity and θ° is the angle the trajectory at take-off makes with the horizontal. As the jump is nearly vertical,

$$h \approx \frac{v^2}{2g}.$$

v has been calculated from this expression in order to compare it with the velocity estimated from the films, and these are given in Table I. Besides a series of jumps made by *A. haemorrhoidalis*, Table I also includes six jumps made by two small species of Elateridae.

TABLE I

Species	Jump	h (m)	Measured v (m/s)	Calculated v (m/s)
<i>A. haemorrhoidalis</i> (Length $10\text{--}12 \times 10^{-3}$ m)	1	0.223	1.92	2.09
	2	0.23	2.11	2.12
	3	0.23	2.11	2.12
	4	0.263	2.11	2.26
	5	0.238	2.27	2.16
	6	0.238	2.27	2.16
	7	0.218	2.11	2.07
	8	0.261	2.11	2.26
	9	0.245	1.92	2.19
<i>Agriotes pallidulus</i> (Length $4\text{--}5 \times 10^{-3}$ m)	1	0.075	1.06	1.21
	2	0.085	1.28	1.29
	3	0.093	1.28	1.35
<i>Hypnoidus riparius</i> (Length $4\text{--}5 \times 10^{-3}$ m)	1	0.014	0.42	0.52
	2	0.023	0.48	0.67
	3	0.021	0.58	0.64

It can be seen that in most cases there is reasonable agreement between the measured and calculated take-off velocities, and that in 12 out of the 15 jumps the measured velocity is smaller than that calculated. A slight error in the calculated v is due to the not quite vertical trajectory. Errors in the v estimated from the films include:

- (1) Deviations of the film speed from 64 f.p.s. (slight, as this was checked against time).
- (2) Inaccuracies of measurement against the graph paper background due to the movement of the beetle in a plane at a slight angle to the plane at right angles to the optical axis (slight).

- (3) Difficulty of measuring the small distance between frames 1 and 2 against the slightly blurred background (slight).
- (4) The drop in v due to its measurement over a 1/64 second interval which may itself be nearly 1/64 s after take-off; this is probably the major error.

In order to obtain a more accurate measurement of v , but more particularly to try to observe the jumping action, high speed ciné films of the jump of *Athous* were made. These established take-off speeds of up to 2.5 m/s, or even of 2.7–2.8 m/s within the first millisecond after take-off. The jumping action occurred in slightly less than 2 frames at the fastest speeds used, 3100 and 3750 f.p.s.; 2 frames represent times of 0.64 ms and 0.53 ms respectively. It seems likely that for a normal high jump, the jumping action takes place in about half a millisecond, or less, but for purposes of calculation the upper time limits quoted above will be used.

The jumping action is shown in Fig. 2 where profiles of the beetle taken from the first and third frames of a jump have been superimposed. In frame 0, the beetle is set to jump, and in frame 2 it is just clear of the ground. It can be seen that the prothorax swings through a much larger angle than the hindbody, and that the angled base of the elytra is the last part of the beetle to retain contact with the ground. Frame 2 shows the approximate position in which the peg bumper hits the mesosternal margin. A longer sequence from the start of the same jump is shown in Fig. 3. The profile of the whole beetle is again shown in frame 0, but in successive frames, only the upper (ventral) margin of the body has been drawn. The successive positions shown are 0.32 ms apart, and the whole sequence covers a period of just under 10 ms.

In the example illustrated in Fig. 3, the centre of gravity rises at 85° rather than at 90° to the horizontal, and as the jump is continued the beetle rotates head over tail. Jumps always show this same direction of rotation, although very occasionally there may be no rotation at all. A jump of 0.26 m lasts about half a second, and the beetle usually somersaults at least six times; for jumps of this height the rotation rate varied between 12 and 20 revolutions per second. The jump is clearly not a single somersault as supposed by previous workers such as Binaghi (1942). Rotation normally occurs in the plane about the transverse, horizontal axis (pitch), but some specimens were observed to be also rotating about their longitudinal, horizontal axes (roll). No observed jumps showed any rotation about the midvertical axis (yaw). The amount of roll rotation seemed to depend on the degree of transverse tilt exhibited by the beetle at take-off, and this in turn depended upon the substratum.

Another complicating feature of the jump was the return movement of the prothorax after it had struck the mesothorax, and then been flung forwards as far as the still contracted M4 muscle would allow, and then been pulled back again (Fig. 3). This occurred in the first few milliseconds after take-off, and subjected the head to some astonishing changes of acceleration. Much of the energy involved in this vibration is wasted, and it is hoped to examine the problem of rotational energy losses in a later publication. The aerodynamics of the leap are obviously complex, and have not been investigated. However, the result of the leap from the beetle's point of view is simple. It either lands the right way up, or it returns to earth still inverted, when it will jump again. If it lands on a hard surface, the whole beetle will bounce. The attitude of a beetle on landing was shown in a series of tests to be not significantly different from chance, and this conclusion agrees with

the results of a more extensive series of tests by d'Aguilar (1961) on three species of *Agriotes*.

Acceleration and force produced

Since in the jump illustrated in Figs 2 and 3 a velocity (v) of 2.4 m/s is attained in not more than 0.64 ms, the acceleration must have been at least

$$2.4/(6.4 \times 10^{-4}) = 3800 \text{ m/s}^{-2} \text{ (380 g).}$$

This is the highest acceleration recorded for any jumping animal, although that produced by the human flea (Bennet-Clark & Lucey, 1967) is of the same order (320 g). The force required to give this acceleration to the beetle (mass $40 \text{ mg} = 4 \times 10^{-5} \text{ kg}$) would be $4 \times 10^{-5} \times 3800 = 0.15 \text{ N}$ (15 g weight).

An attempt was made to measure directly the force produced by a beetle jumping. The jump was made from a small, perspex platform mounted directly onto a mechanical transducer. The signal was recorded on magnetic tape, and then played back into a pen-recorder with a 30 : 1 reduction of speed. Jump height ($h \text{ m}$) was recorded on a graph paper background. The forces ($F \text{ N} = F \times 10^2 \text{ grams weight}$) for six jumps made by three different beetles are given in Table II.

TABLE II

Specimen and jump	Weight $M \times 10^{-6} \text{ kg}$ (mg)	Jump height $h(\text{m})$	Measured force $F \text{ N}$ ($F \times 10^{-2} \text{ g wt}$)	Calculated force $F \text{ N}$ ($F \times 10^{-2} \text{ g wt}$)	Calculated jack-knifing time* $t \times 10^{-3} \text{ s(ms)}$
1	32	0.23	0.062	0.113	0.6
2a	29	0.22	0.07	0.098	0.6
b	29	0.05	0.034	0.022	1.3
3a	29.4	0.15	0.048	0.068	0.8
b	29.4	0.26	0.064	0.118	0.6
c	29.4	0.23	0.06	0.104	0.6

* Strictly, the time for the centre of gravity to travel through 1 m, which is approximately equivalent to its movement from frame 0 to frame 2 in Fig. 2.

The force of the jump may also be calculated theoretically from the weight of a beetle and the height of its jumps, provided that the acceleration distance, $l \text{ m}$ is known (as v and t were not measured directly). This distance l , is the distance the centre of gravity of a beetle is moved from its set position to its take-off position (frame 0 to frame 2 in Fig. 2). To measure l approximately, enlarged profiles of frame 0 and frame 2 were cut out of thick cardboard and suspended in various positions to determine their centres of gravity. This was done for two high jumps (one of which is shown in Figs 2 and 3). In both cases, the centre of gravity was displaced anteriorly as well as vertically, although the jumps were nearly vertical. Because the anterior displacements were different in each jump (perhaps due to different body angles to the lens), the average vertical displacement of $6.5 \times 10^{-4} \text{ m}$ (0.65 mm) was assumed to represent l , and this value has been used to calculate F and t for the jumps shown in Table II.

Since the height of the jump is $v^2/2g$ (p. 327) the velocity of take-off is $\sqrt{2gh}$. By one of the standard equations for motion under constant acceleration, the time required to attain this velocity from rest in a distance l is

$$2l/\sqrt{2gh} = \sqrt{2l^2/gh}$$

Similarly, the acceleration involved would be

$$v^2/2l = gh/l,$$

and the force mgh/l .

(Since these equations assume constant acceleration, and since the acceleration over distance l is almost certainly not constant, values derived for force and time can only be approximate.)

It can be seen from Table II that apart from jump 2b, the theoretical forces produced are always greater than those measured. 2b is the smallest jump, and would have taken the longest time to produce its impact upon the transducer. It seems likely, therefore, that the signals from the other jumps were produced too rapidly to be fully recorded on the equipment. Either the mechanical transducer or the pen-recorder (or both) reacted too slowly to record the full force. This interpretation is supported by the fact that the rise times of the traces from the pen-recorder were all about 2 ms, about three times longer than the calculated jack-knifing time.

Minimum energy and power produced

The minimum kinetic energy acquired by the beetle at take-off is $\frac{1}{2}Mv^2$. If we consider the jump shown in Figs 2 and 3, the beetle's mass M is 4×10^{-5} kg, and v is 2.4 m/s. Then the minimum amount of work done by the jump muscles is

$$\frac{1}{2} \times 4 \times 10^{-5} \times 2.4^2 = 1.15 \times 10^{-4} \text{ J.}$$

The weight of the M4 muscles in a specimen of 4×10^{-5} kg was $3.36 \text{ mg} = 3.36 \times 10^{-6}$ kg.

Thus the work done per unit weight of M4 muscles was

$$1.15 \times 10^{-4} / 3.36 \times 10^{-6} = 34.2 \text{ J/kg.}$$

This energy was expended in the jack-knifing period of 0.64 ms. Therefore the power exerted per unit weight of jumping muscle was

$$34.2 / 0.64 \times 10^{-4} = 5.3 \times 10^4 \text{ W/kg} \quad (53 \text{ W/g}).$$

This is a minimum figure which assumes 100% efficiency in the mechanical system, and it can be shown that the efficiency is far lower than this. It also represents only translational energy; rotational energy is additional, and in order to make the point it has been ignored. It is hoped to compare the translational and rotational energies involved in a subsequent publication.

A simple mechanical model

In order to gain a clearer understanding of the jumping action, a two-dimensional model was constructed (Fig. 8). This was based on the shape of a sagittal section of the beetle, and was cut out of thick plywood. The peg and track profiles were accurately reproduced, as was the position of the (necessarily single) pronotal pivot. The profiles of the elytra and pronotum were also closely similar to those of the beetle, although the front and back ends of the model were shortened to lighten it. The main muscles concerned

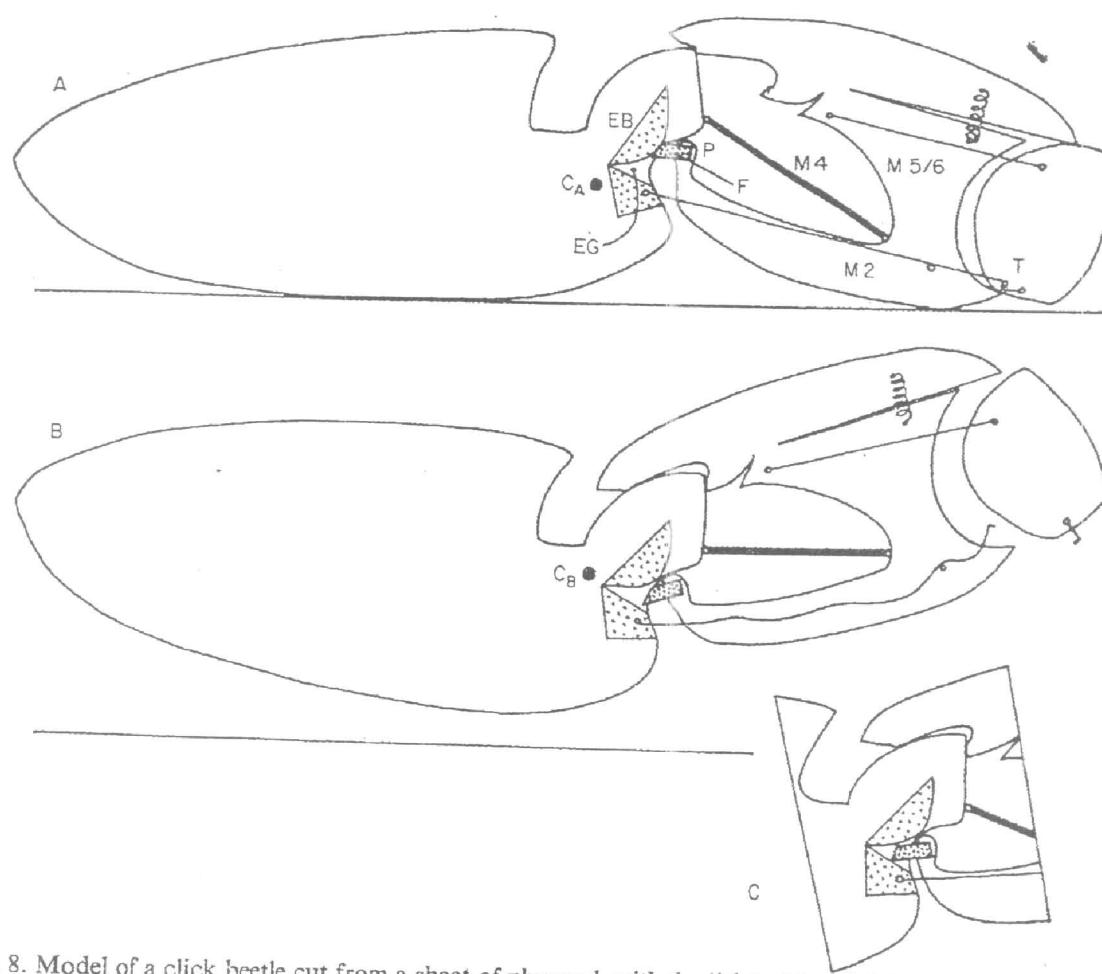


FIG. 8. Model of a click beetle cut from a sheet of plywood, with the "elytral base" (EB), "elytral groove" (EG) and "flange" (F) added as a second layer. The main muscles are simulated by elastic bands, and the "suture" is held shut by a weak spring. C, Centre of gravity of model; T, trigger; other letters as in Figs 6 and 7.

(a) Model in set position before the jump. (b) Model in the jack-knifed position. (c) Detail of model in "resting" position showing pivot region (compare with Fig. 7(a)).

with jumping were simulated with elastic bands. The pronotal flanges which fitted into the anterior elytral cavities were simulated by a single process on the pivot which projected backwards into a notch, in the "locked" (non-jumping) position of the beetle. The model was placed on a flat, polished surface. In the inverted position, its dorsal surface (i.e. elytra and pronotum) rested on a basal ledge (the "ground"). If the model was bent into the back-arched position (Fig. 8(a)) and then released, the peg bumper would swing rapidly through a small arc to hit its buffer (Fig. 8(b)), and the whole model would "jump" a few centimetres horizontally along the polished surface.

The first problem is to explain why the model jumps. There seem to be two possible explanations. The model either levers itself off the "ground" in a similar manner to a legged jump, or it bounces itself up by the ground reaction to an impulse resulting from the bumper impact. One drawback to the latter theory is that the impulse generated would be a vector quantity (having both magnitude and direction), and the model jumps at right angles to the direction of the impulse. The impact theory was tested on the model by fixing a cushion of cork or of a soft material to the buffer to diminish the impact

upon the mesothorax. The model still jumped about the same distance, so the jack-knifing movement itself must be more important than any effect of the impact.

An animal which uses its legs to jump, raises the centre of gravity of its body through an acceleration distance in order to acquire a particular take-off velocity. The model click beetle does the same by changing its shape relative to the "ground". When the model's centres of gravity were determined in the set position (8(a)) and the jumping position (8(b)), it was found that in position 8(b) the centre of gravity of the 0.5 m long model had risen by 0.02 m. Thus moving from 8(a) to 8(b) rapidly enough (using a strong elastic band as M4) gave the model a take-off velocity. (Of course, if the jumping action took place off the "ground", there was nothing to react against, and the prothorax and hindbody merely rotated around the model's centre of gravity; since this was not raised, no jump occurred.) This seems to be a likely explanation of how the living beetle jumps, for it shows this rapid change from the 8(a) to 8(b) positions before it leaves the ground. The centres of gravity were determined for cardboard profiles of two different jumps (one was of frames 0 and 2 in Fig. 2), and they each showed an appropriate rise from the set to the take-off position. This rise is the acceleration distance, l , and I have already used this to estimate the force produced by a jump.

The second problem is to explain the operation of the catch and release system whereby position 8(a) is attained and apparently released at will. The ordinary resting or walking position of the body is that in which the peg is fitted part way into the pit, and in which the pronotal pivots have been moved as far posteriorly as possible on the mesonotum (8(c)). This gives a close fit between the prothorax and mesothorax which is presumably maintained by contracted longitudinal muscles; it may be termed the "locked" position, since the prothorax cannot be bent into the back-arched position (8(a))—on a preserved specimen—without forcing it. The arching movement is prevented by the posterior pronotal flanges not being able to turn in their anterior elytral cavities (Fig. 7); this has been simulated on the model by the single flange on the pivot. On the model, the pivot must be slid forwards before the prothorax can swing from position 8(c) to 8(a), and it is difficult to do this by any direct "muscular" system. In the living beetle, one can suppose that this slight protraction of the prothorax may be produced by a slight increase in the turgor pressure of the blood (perhaps produced abdominally) accompanied by a temporary relaxation of the longitudinal muscles. When the pronotal pivot has been correctly located, the median dorsal muscle (M2) can swing the prothorax to position 8(a). The flange now serves to prevent any backwards sliding of the pivot as muscle M2 operates (except as a result of great pressure), for it presses back against the rounded elytral base (EB and ER in Figs 8(a) and 7(b)).

To maintain the prothorax in this position, and to allow the jump muscle, M4, to build up tension, the peg skid lip must be set against the lip of the track; to accomplish this, either the peg, or the whole prothorax, must be slightly depressed (i.e. moved dorsally). It was noticed in both living and preserved specimens that the tip of the peg in an inverted specimen could be slightly depressed by slightly raising the anterior rim of the sternum and so opening the suture anteriorly, while the cuticle between the first coxae at the peg base acted as a stiff hinge. In each suture, the sternum was linked to the sidewall by varying amounts of flexible and elastic cuticle. Anteriorly, where there was a large amount of flexible cuticle (Fig. 9(a)), most movement was possible; posteriorly, there was relatively more elastic cuticle (Fig. 9(b)), and less displacement of the sternum was possible. The

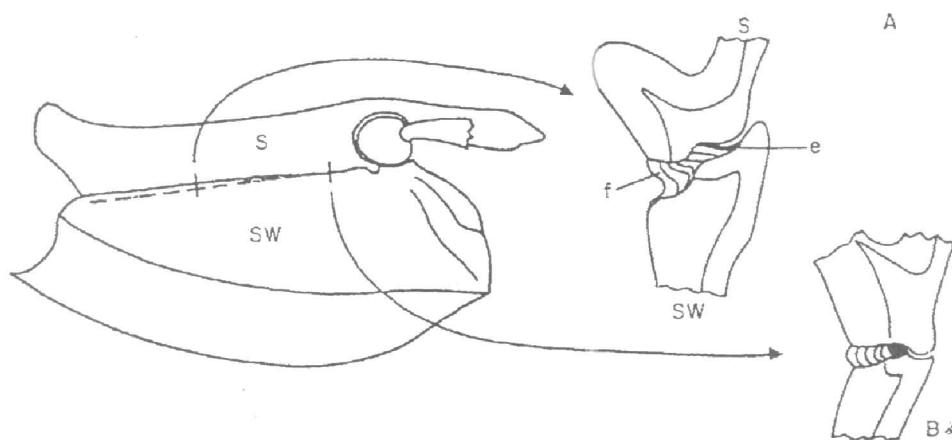


FIG. 9. Side view of prothorax of *Athous* (ventral side uppermost) with sections through two regions of the suture between the sternum (S) and the sidewall (SW). (a) is anterior to (b), which is near the posterior end of the suture. The distribution of flexible cuticle (f) and elastic cuticle (e) is shown in (a) and (b).

elastic cuticle presumably resisted sternal movement. The sutures were simulated on the model by a narrow gap held shut by a spring.

It is suggested that after the back arching movement due to muscle M2, one way in which the peg can be set against the track lip is by a slight outwards (i.e. ventrally directed) movement of the anterior prosternum. Contraction of the jump muscle, M4, would then hold it in position. What evidence is there for this view? Firstly, down and upwards swinging of the prothorax due to M2 and M4 is clearly seen if the tip of the peg is removed from a live specimen. It cannot now locate the peg on its track lip, but still attempts to do so with backwards and forwards movements of the peg. Secondly, a momentary opening and closing of the sutures was observed on a live specimen at the end of the back arching movement, just before the peg was set. This was seen under the microscope; unfortunately, definition was not good enough to record this photographically during the jumping sequence.

The next task is to explain how this prosternal movement could be produced. Posteriorly, there are no muscles directly attached to the peg, and the external leg muscles are too near the sternal hinge to be effective. Anteriorly, however, it is possible that the use of the back of the head as a wedge would open the sutures. The head is drawn back immediately the back arching movement commences, for one of the origins of the muscle M2 is on the head. It remains withdrawn when the peg is swung forwards to the track lip. Thus M4 must operate whilst M2 is still contracted. If this is so, further contraction of M2 (and of the ventral muscles M5 and 6) would pull back the head far enough to open the sutures. The model clearly shows how this would happen (Fig. 8(a)), and an association between head retraction and suture opening has been recorded photographically. It was also seen, however, that the sutures are apparently rapidly closed again, and this is more difficult to explain. It could be due to the head moving forwards again as M2 and M5/6 relaxed, but this was not observed under the microscope, neither was any rise of the peg tip—it remained in the set position. Further, the beetle can still jump when the head is completely immobilized. It is more likely that the rapid closure of the suture is due to the continued contraction of the very powerful jump muscle, M4, forcing it shut—or nearly shut. This would hold the peg against the track lip in the set position, whilst distorting

the prothoracic cuticle so that the pronotal pivot slid postero-dorsally. Since the latter pivot is located against the rounded elytral base by flanges, these flanges would have to slide dorsally. This movement, caused by prothoracic distortion, can be observed in a dead specimen by pushing the prothorax against the mesothorax.

It has been suggested above that one way of locating the peg on the track lip is by prosternal movement induced by the head. This is not the only method of location, for the beetle can still jump when the head is immobilized, and this must involve a displacement of the pronotal pivots.

A final question is: how is this mechanism sprung, i.e. released for jumping? The build-up of tension as the peg is held in the set position is part of an energy storing mechanism, and where such a store is found (as in the flea) there is normally a trigger system to release it for the jump. The beetle can hold the set position for periods as short as half a second or less, or as long as several minutes. This also suggests the presence of a trigger mechanism rather than a simple build-up of tension until the peg slipped. This trigger action has not yet been elucidated, but at least three possibilities can be suggested:

- (1) It was seen from the high speed film that a number of muscles are relaxed either as the jump occurs, or immediately afterwards. The antennae, head and legs all start to move outwards once the jump has taken place. In at least one jump, the head moved slightly forwards just before the jump. This suggests that the dorsal and ventral longitudinal muscles are involved in the trigger system. The jump of the model could be triggered by releasing the dorsal (and/or ventral) "muscles" (T in Fig. 8), thus allowing the head to be pushed forwards. Since the suture on the model would not close completely, but was held open by the head, there was enough play on the prosternum to allow the peg tip to rise and so release the jump. The analogue between the model and the living beetle now breaks down, because on the beetle the suture was seen to close after opening. It was not possible to see if it closed completely; if not, the analogue between model and beetle might still hold. If the suture did close completely, another explanation must be sought.
- (2) For instance, the head muscles, M2, may have been just sufficiently powerful to balance the jump muscles, M4, when the latter were partly held by the peg hold. Thus when M2 relaxed, the peg hold would give.
- (3) A third possibility is that the ventral intersegmental muscles act as the trigger. There is certainly activity in this part of the body just before a jump, since the ventral intersegmental membrane moves inwards at this time. As M30 would tend to pull the peg hold directly posteriorly (rather than rotating it into the mesosternal lip as does M4), it may be able to twitch the peg over the lip. This process might be aided by M33 (Fig. 4) which normally acts as an elytral levator. M33 runs between the mesepisternum and the posterior side of the inwardly projecting spike on the mesonotal rim. If it slightly depressed the anterior mesonotum, including the pronotal pivots, the peg would easily slip over its hold.

To summarize, observations of living beetles and manipulation of a simple model suggest that jumping is caused by a very rapid jack-knifing of the body which raises the beetle's centre of gravity by an appropriate distance in an appropriate time.

The sequence of events is as follows:

the pronotal pivots are moved forwards from the locked position; muscle M2 swings the pronotum dorsally so that the peg is withdrawn from the pit; the jump muscle, M4, then swings the pronotum back (ventrally) to approximate the peg lip and the track lip; one way in which the peg lip can be set on the track lip is by a slight depression (dorsally) of the peg tip caused by the sutures being forced open anteriorly by the retraction of the head—which acts as a wedge—by the dorsal and ventral longitudinal muscles; other ways of setting the peg—such as by moving the pronotal pivots—may also be used; once the peg is located, tension built up by the jump muscle, M4, may cause the prothorax to distort slightly, thus forcing the pronotal pivots postero-dorsally. The method of triggering the jump is even more speculative. It may be due to the sudden release of the head by the prothoracic longitudinal muscles, or to a delicate balance between the M2 and M4 muscles, or the ventral intersegmental muscles may be involved. Whatever the trigger mechanism, it causes the peg to slip, and jack-knifing and jumping then follow.

It has already been pointed out that the very large power output during the short act of jack-knifing necessitates an energy storage mechanism. The energy input is due to the build-up of tension in the jump muscles in the period between setting the peg on its friction hold and triggering the jump. The energy must be partly stored in the series elastic component of the muscles. It is probably also stored by the temporary distortion of the prothoracic cuticle caused by the increase in muscle tension. It is intended that the mechanics and energetics of the jump will be considered in more detail elsewhere.

Summary

A preliminary account is given of the jump of the click beetle, *Athous haemorrhoidalis* (F.).

The jump is normally made from an inverted position and involves moving a prosternal peg very rapidly into a mesosternal socket. The peg has a friction hold which catches on the mesosternal lip and thus allows muscle tension to be built up for the jump. When the hold suddenly slips, the underside of the peg slides down a very smooth track until the peg base and prothoracic sidewalls hit the mesosternum and mesepisterna. The skeletal anatomy and the muscles concerned have been described briefly.

The trajectories of a number of jumps were recorded on 16 mm ciné film at 64 f.p.s., whilst a detailed study of the jumping action (jack-knifing) was made using a high speed ciné camera at film speeds of up to 3750 f.p.s. It was established that the beetle usually jumped almost vertically, that it could rise to over 0.3 m, and that it normally rotated head over tail between six and ten times in a half second jump.

Jumping was due to the change of shape produced by the jack-knifing action which raised the beetle's centre of gravity very rapidly through a short acceleration distance. In a typical jump, the take-off velocity of 2.4 m/s was acquired in not more than 6.4×10^{-4} s, involving the whole beetle in an upwards acceleration of about 3800 m/s^{-2} (380 g). For a beetle of 4×10^{-5} kg, this represents a force of 0.15 N (15 grams weight). Attempts to measure the force produced directly by using a mechanical transducer were only partly successful. The minimum amount of work done by the jump muscles in the example quoted was 1.15×10^{-4} J, which represents a minimum power output per unit weight of jump muscle of about $5.3 \times 10^4 \text{ W/kg}$ (53 W/g).

This requires an energy store, and a simple mechanical model is described which simulates a jump. The possible ways in which the jumping mechanism may operate have been discussed.

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