

The backward jump of a box moss mite

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Indotritia cf. *heterotrichia*, a box moss mite 800 µm in length, combines the abilities to curl up and to jump. Despite the lack of specialized legs and of extensor muscles in its knee joints, the backward leap is characterized by a short take-off time (ca. 0.5 ms). This is apparently facilitated by a catch mechanism made up of a small hook on each forefemur that hitches on the rim of the anterior shield of the body and maintains the forelegs in a flexed position during a prejump phase. While the animal is propelled backwards, its body simultaneously spins in a forward direction: it is supposed that, at take-off, the hindlegs initiate a forward rolling of the body, which is powered by internal hydraulic pressure, before the hook disengages from the shield rim and triggers a sudden backward impulse. The non-parabolic trajectory of the flight can be described with a model where the air resistance due to the spin (Magnus effect) and to the translatory motion is taken into account.

Keywords: acari; catch mechanism; defence; fast movements; hydraulic pump; kinematic model

1. INTRODUCTION

Leaping arthropods provide numerous examples of morphological and biomechanical adaptations that improve their jump performances (review by Alexander & Bennet-Clark (1977), Furth & Suzuki (1992) and Gronenberg (1996)). Among arachnids, the jump mechanism has only been investigated in detail in the salticid spider *Sitticus pubescens* (Parry & Brown 1959) and in the moss mite *Zetorchestes falzonii* (Krisper 1990). A peculiarity of all arachnids is that they lack extensor muscles in some of their leg joints: legs are stretched by internal hydraulic pressure (Blickhan & Barth 1985; Shultz 1989). *S. pubescens* uses its non-specialized hindlegs to jump, resulting in low performances in comparison with *Z. falzonii*, which uses all its legs and benefits from a 'catch mechanism' associated with its enlarged and elongated hindlegs. A catch mechanism allows energy generated by the relatively slow action of muscles to be stored in elastic structures and released instantaneously when the catch is disengaged (Gronenberg 1996).

We report here on the jumping capacity of a box moss mite, *Indotritia* cf. *heterotrichia*, which like *Z. falzonii* relies on all its legs to leap, but has morphologically unchanged hindlegs like *S. pubescens*. The animal, 800 µm in length, was collected on a small New Guinea island. As with other box moss mite species for which the ability to jump has been reported (Shubart 1967), *Indotritia* cf. *heterotrichia* is a soil-litter-dwelling organism. Given the physical structure of the habitat, it is likely that the jump is a defensive mechanism rather than a method of locomotion.

Box moss mites are able to curl up owing to a movable and foldable sternal region (Grandjean 1967). Leaping box moss mites are the only known example of leg-jumping arthropods with soft and extensible body–sternum articulation (other leg-jumping arthropods that possess a foldable thoracic region are female chalcid wasps (Gibson 1986), but their body–sternum articulation is less extensible than that in *Indotritia* cf. *heterotrichia*). This feature, coupled with the anecdotal nature of previous descriptions, led us to attempt a more detailed study of the jump of *Indotritia* cf. *heterotrichia* by means of: (i) high-speed, close-up video recordings of the take-off and flight; (ii) a kinematic analysis of the flight; and (iii) histological observations combined with scanning electron micrographs of the animal and of a non-jumping box moss mite. Our results indicate that the jump impulse is driven by an unexpected adaptive process, namely a catch mechanism associated with the forelegs.

2. MATERIALS AND METHODS

We investigated the jumping behaviour of *Indotritia* cf. *heterotrichia* from recordings made at 1000 and 2000 images per second with a Kodak Ektapro high-speed video camera mounted on a stereomicroscope (magnification up to ×60). Intense heat-free light was provided by an optical-fibre ring light fitted to a modified 750 W Elmo slide projector where the light was cooled through a water stream. Mites were put on a plaster substrate, and leaps were stimulated by touching the animal with a fine paintbrush. To study the take-off mechanism, 17 close-up recordings were made, and 12 other jumps were filmed in totality for analysis of the trajectory.

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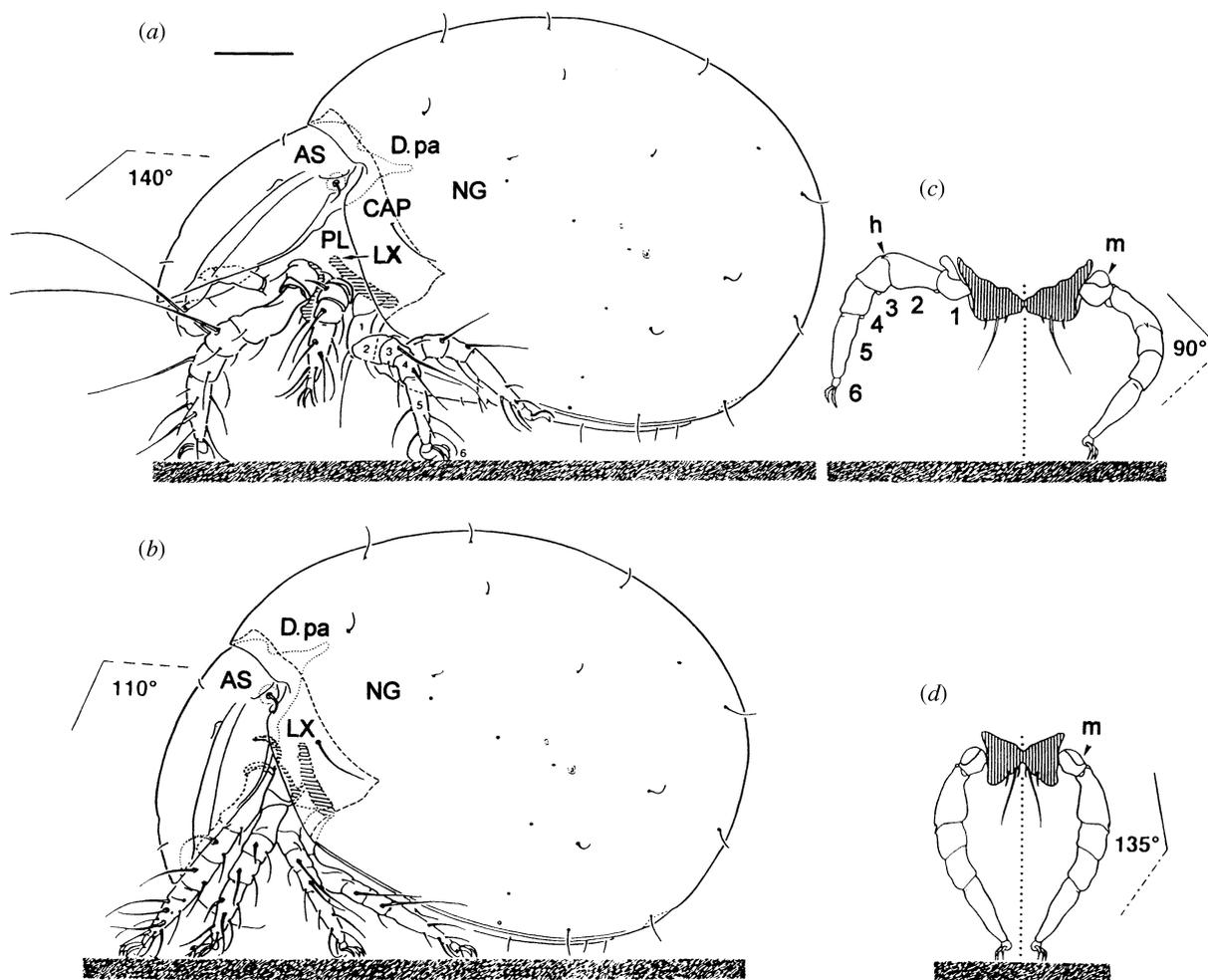


Figure 1. Adult *Indotritia* cf. *heterotrichia*. (a, b) Lateral view of the whole animal during walking (with four legs asymmetrically lifted from the ground) and in prejump position, respectively. The prosoma comprises an anterior shield (aspidosoma, AS) (long axis: unbroken line) covering the mouthparts, whereas the abdomen (opisthosoma, NG) consists of a large, ovoid mass (long axis: line with dashes) and of elongated ventral plates. A flexible cuticle, characterized by an ample pleural region (PL), connects the two body parts and supports a coxisternal plateau (hatched) bearing the legs (leg segments: 1, trochanter; 2, femur; 3, patella; 4, tibia; 5, tarsus; 6, claw). This construction allows the coxisternal plateau to move up into a chamber (CAP) enclosing the legs when the mite curls up. This motion is controlled mainly by abdominal muscles inserted on apophysis LX of coxisternal elements 3. Alternatively, the partial extension of legs I, coupled with contraction of abdominal muscles attached laterally to the anterior shield, will flex the shield and pull down the abdomen, as occurs in the prejump position. D.pa, posterolateral apophysis of the anterior shield. (c, d) Front view of legs I during walking and partly extended in the prejump position, respectively. Leg curvature was estimated using the angle between femur (long axis: unbroken line) and tarsus (long axis: line with dots and dashes). m, membrane of the coxisternal element 1 (hatched) and trochanter joint; h, femoral hook. Reconstructed from video screen. Scale bar, 100 μ m.

3. RESULTS

(a) Take-off

The mite leaped when touched by a predator, when disturbed by a stimulus such as sudden exposure to light, or when it encountered a fibrous walking surface (e.g. filter paper). Two or three leaps could be made successively. After that, if the disturbing stimulus persisted, the animal curled up.

Close-up recordings showed that before taking off, the animal stopped walking and stood on all eight legs with the four forelegs (pairs I and II) directed forwards and the four hindlegs (pairs III and IV) directed backwards. Then it brought the anterior shield (AS in figure 1) closer to the abdomen (NG in figure 1), decreasing the angle between them from ca. 140° (during walking) to 110°.

During this partial curling up, legs I were brought close to each other and the femoral hooks presumably caught the rim of the AS (figures 1 and 2), while the coxisternal plateau on which the legs are inserted was lifted (a mechanism that allows full retraction of the legs inside the body when the animal completely curls up). The prejump phase lasted 65 ± 24 ms ($n=17$).

The take-off could be recorded on only one blurred image at 2000 frames per second ($n=17$), so that we estimated its duration to be 0.5 ms. The NG was obviously pushed upwards initiating a forward rolling of the body, and the angle between the AS and the NG reached a value similar to that observed during walking (figure 1). The mite was always propelled backwards despite the forward spin of the body.

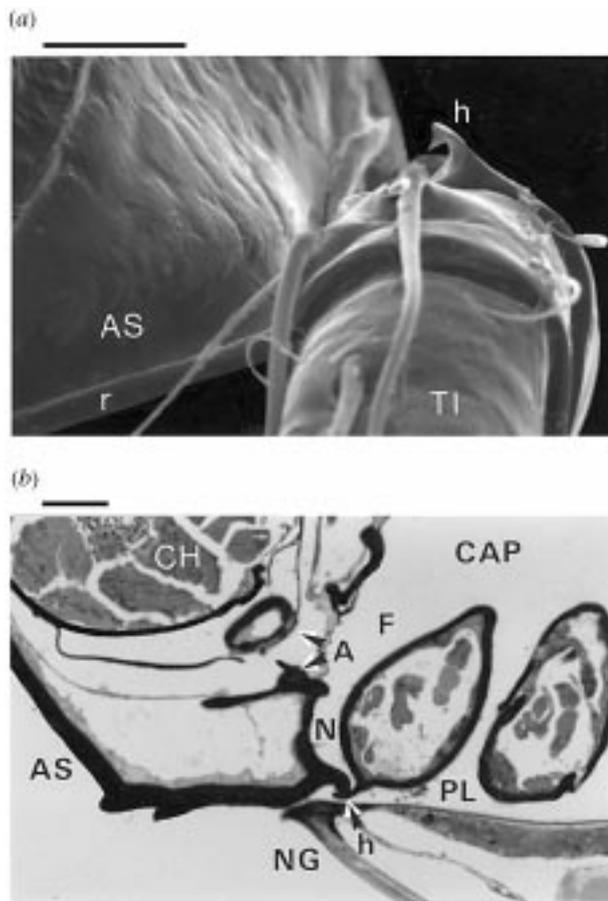


Figure 2. The femoral hook of *Indotritia cf. heterotrichia*, a possible catch system involved in the jump. (a) Scanning electron micrograph of the anterior shield (AS) and of the foreleg, in apical view; left side, partial. The femoral hook (h) has a broad basis located dorsodistally on the segment and a tip curved in a ventral and lateral direction so that it can catch the thickened rim (r) of the aspodosomal shield. TI, tibia. (b) Longitudinal, oblique section of the anterior part of the body in a mite not completely curled up; left side, partial. The femoral hook (h) is hitched on the rim of the AS at a level located a little way behind the middle of the shield. The section goes through the following main structures: F, forefemur; N, aspidosomal recess for foreleg; PL, pleural membrane; A, articular elements of the buccal cone (infracapitulum) and anterior shield joint; and CH, chelicera. Other labels as in figure 1. Scale bar, 20 μm .

(b) Flight

While airborne, the body spun forwards 12–18 times in the plane of the trajectory, a movement often accompanied by a lateral rotation. The mite landed in any position, bounced several times and was found in a curled up posture. After a few seconds it started to walk again.

Parallax effects and the obliquity of spinning were negligible in two jumps we filmed in totality. A typical trajectory, corrected for parallax, is shown in figure 3. Its parameters are used in the model below (the detailed establishment of the model is provided in Appendix A).

The trajectory can be described by the equations $d^2y/dt^2 = \lambda_0 dz/dt - \mu dy/dt$ and $d^2z/dt^2 = -[g + \lambda_0 dy/dt + \mu dz/dt]$, where y is the horizontal position of the centre of mass, z is its vertical position, t is the time, λ_0 is the air resistance coefficient per unit mass due to the spin

(Magnus effect; see, for example, White & Schulz (1977)), μ is the air resistance coefficient per unit mass due to the translatory motion (fluid friction), and g is the acceleration due to gravity. The air resistance coefficients obtained for the jump depicted in figure 3 were $\lambda_0 = 5.0 \text{ s}^{-1}$ and $\mu = \mu_0 v^{0.41}$, where the velocity $v = ((dy/dt)^2 + (dz/dt)^2)^{0.5}$, and with $\mu_0 = 7.19$.

The spin of the body further increases the air resistance, thus causing a reduction of the total kinetic energy and leading to a non-parabolic trajectory (figure 3). We found that 56% of the initial kinetic energy of rotation and 40% of the initial kinetic energy of translatory motion were lost at the end of the jump shown in figure 3. The kinetic energy of rotation at $t=0$ is 17% of the total energy.

(c) Anatomical data

As Wilson (1970) did for leaping spiders, it was in the hope of disclosing enlarged muscles presumably involved in the jump that we made a comparison of the musculature of *Indotritia cf. heterotrichia* with the one of a non-jumping box moss mite, *Rhysotritia duplicata*.

Like other box moss mites (Sanders 1982), *Indotritia cf. heterotrichia* possesses two sets of dorsoventral muscles, the coxisternal adjustors, which control the coaptation of the AS and of the legs and the NG when the animal curls up (figure 4). Three large sets of ventral muscles, located at the level of abdominal plates, control the internal pressure by bringing the abdominal walls closer. In the jumping mite, the cross-sectional area of the coxisternal adjustors and of one set of abdominal compressors (figure 4) was proportionally more than 1.5 times greater than in *Rhysotritia duplicata* ($n=3$).

In addition, slight differences in the number of muscles originating from the endosternum (a ligament-like structure suspended within the haemocoel) were detected. A peculiar feature of the jumping mite is that the abdominal muscles involved in the leg retraction during curling up (coxisternal retractors; Sanders 1982) are attached to broad lateral apophyses of the coxisternal plateau (LX in figures 1 and 4), which do not exist in *Rhysotritia duplicata*. Another difference regarding the nervous system should be noted: in *Indotritia cf. heterotrichia*, large paired nervous ganglia, attached to the central nervous system by a short peduncle, innervate some extrinsic muscles of legs III and IV (i.e. levators and depressors of trochanters and femora).

4. DISCUSSION

Until now, a definite understanding of the jump technique used by *Indotritia cf. heterotrichia* has been prevented by the small size of the animal and by the speed of the leg movements. Yet a fairly plausible scenario of the jump can be drawn. There is indeed some evidence that a catapult mechanism is involved. First, the take-off time is lower than the contraction time of any muscle (1–20 ms according to Bennet-Clark & Lucey (1967) and Huxley (1974)) and is one of the shortest among jumping animals. It ranks among the times found in the flea (within 1 ms) (Schmidt-Nielsen 1990), the click beetle (about 0.6 ms) (Evans 1972), the collembolan *Hypogastrura socialis* (about 0.6 ms) (Christian 1979) and *Z. falzonii*

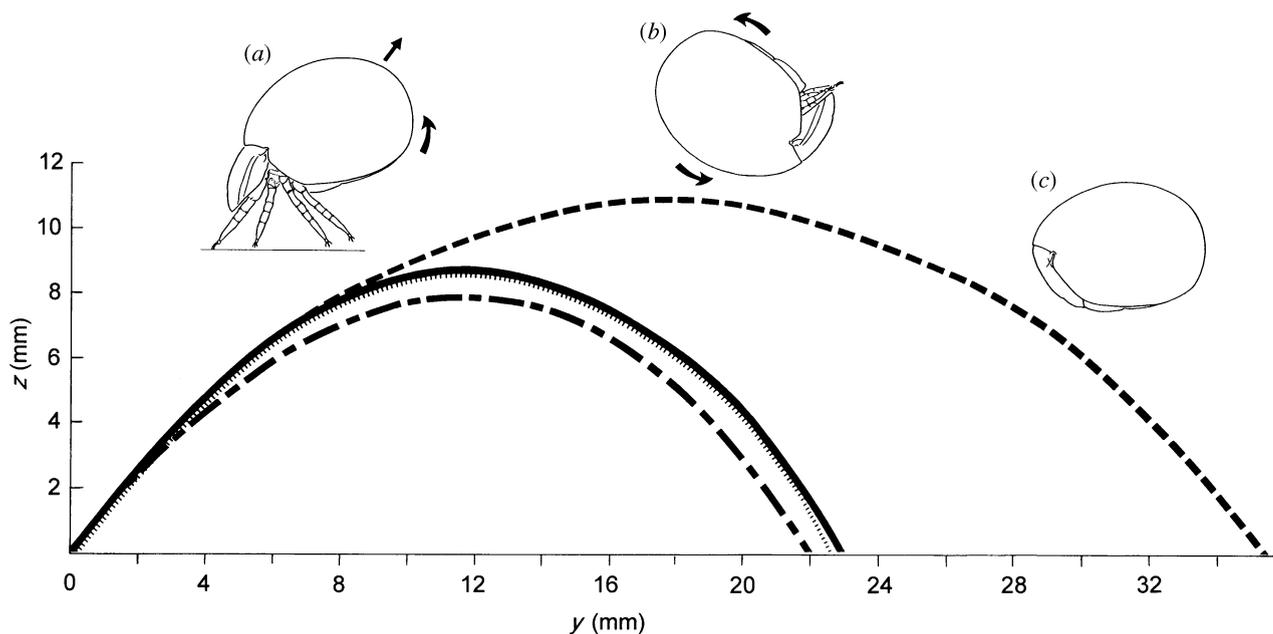


Figure 3. Schematic trajectory of a jumping *Indotritia cf. heterotrichia* (solid line), with a curve (dotted line) modelled using equations (10) and (11) in Appendix A, and two hypothetical curves: a parabolic trajectory without drag and without spin (dashed line) and a trajectory without spin (dot-dashed line). The four curves have identical initial conditions (take-off angle and velocity). Parameters of the jump: take-off angle, 56° ; height, 0.87 cm; range, 2.3 cm; take-off speed, 0.72 m s^{-1} ; duration, 86 ms. Three body postures assumed by the animal are shown: (a) at take-off, the impulse being directed backwards (straight arrow) after a forward rolling has occurred (curved arrow); (b) spinning forwards during the backward flight; and (c) completely curled up after landing.

Table 1. Comparison of jump parameters expressed as average performance in *Indotritia cf. heterotrichia* ($n=12$) and two other leg-leaping Chelicerata

	box moss mite (<i>Indotritia cf. heterotrichia</i>)	salticid spider (<i>Sitticus pubescens</i>) ^b	moss mite (<i>Zetorchestes falzonii</i>) ^c
body mass (mg)	0.09	10	0.04
ballistic parameters			
take-off angle	50°	$<45^\circ$	80°
acceleration distance (mm)	0.15	4.4	0.2
height of jump (cm)	0.9	1.5	8
length of jump (cm)	2.5	2	5
kinematic parameters			
take-off time (ms)	0.5	—	0.2
take-off speed (m s^{-1})	0.6	0.7	1.2
acceleration in g units	120	50	340
power ^a /body mass ratio (W kg^{-1})	844	9	7,450

^aCalculated taking into account the translational and rotational energy.

^bFrom Parry & Brown (1959).

^cFrom Krisper (1990).

(around 0.2 ms). Arthropods with such low take-off times have been shown to possess a catch mechanism. Second, the power generated at take-off (table 1), although modest in comparison with the value observed in *Z. falzonii*, is considerable in comparison with the value of the salticid *S. pubescens*, which does not rely, to our knowledge, on a catch mechanism for its jump. The performance of *Z. falzonii* can be related to the presence of a catapult and of specialized legs; jump performances of *Indotritia cf. heterotrichia* are in agreement with the restrictions

affecting the performances of small animals that have no elongated legs (Bennet-Clark 1977): short legs reduce the acceleration distance and, consequently, the take-off speed.

A catapult involves muscles that load a spring the energy of which is instantaneously released when a catch is disengaged. In fleas, for example, a block of resilin (acting as a spring) is cocked by cuticular locking devices and compressed for 50–100 ms by the trochanter depressor muscle; when some muscles relax, the catches

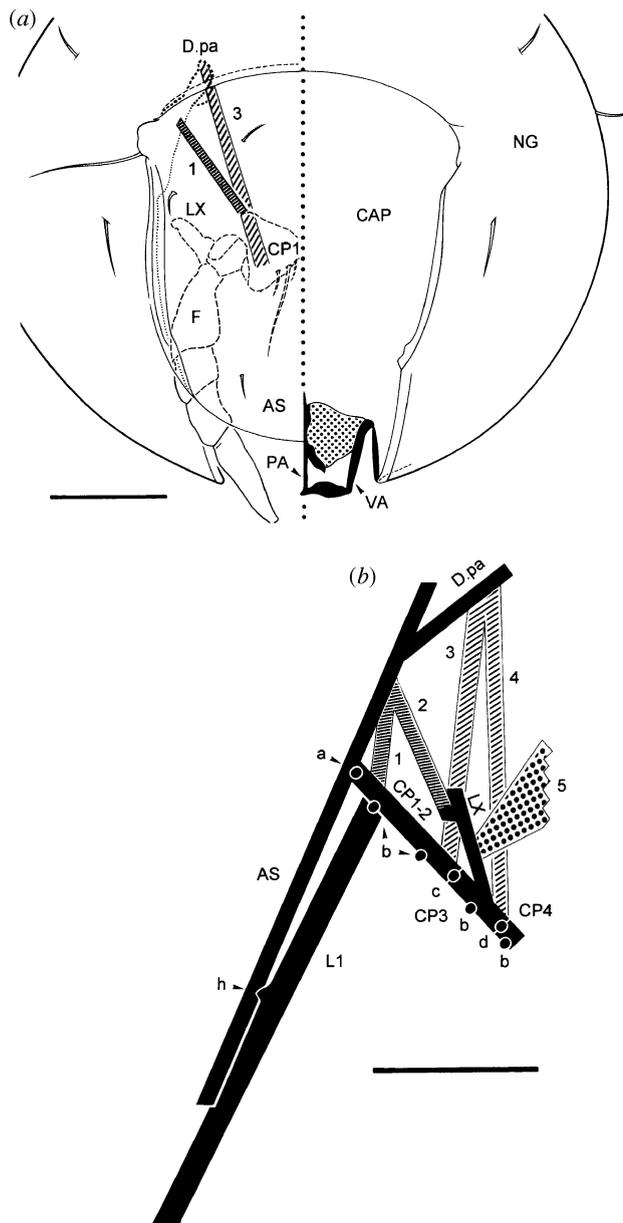


Figure 4. Muscular and cuticular elements possibly involved in the propelling of *Indotritia* cf. *heterotrichia* at take-off. (a) Enlarged muscles. To the left, the coxisternal adjusters (only bands 1 and 3 are schematized in frontal projection) running dorsoventrally from the lateral wall of the AS and from the apophysis D.pa to elements 1–3 of the coxisternal plateau (CPI, element 1; LX, lateral apophysis of element 3). To the right, the abdominal compressors (viewed in cross-section) spread transversally between the ventral plates (anal plate, VA) and the pre-anal apodeme PA. F, forefemur; other labels as in figure 1. (b) Lateral, schematic representation of the AS, of elements of the coxisternal plateau (CPI–4) and of leg I (L1) (the other legs are not shown for clarity). Our hypothesis is that, with the femoral hook (h) of legs I firmly hitched on the rim of the AS, contraction of coxisternal adjusters (1–4), and perhaps also of coxisternal retractors (5) (spread between the lateral wall of the NG and the apophysis LX, they are partly seen), would not shift the coxisternal plateau upwards substantially, but would store elastic strain energy mainly in the plateau. When the femoral hooks disengage, the strain energy stored in the plateau could add to the kinetic energy generated by the hydraulic extension of legs I. a, the coxisternal plateau and anterior shield joint achieved by three arthrodistal membranes

are disengaged (see Gronenberg 1996). Our observations point out some of the structures that may constitute a catapult.

(a) Hydraulic pump

During a prejump phase lasting about 65 ms, the animal partly curls up and brings its legs I closer to each other. Hooks ('h' in figures 1 and 2) that catch the rim of the AS during a complete curling up are present on the femora of these legs. High-speed video images were not sharp enough to distinguish if the hooks caught the rim before the jump, but it seems to be a reasonable assumption as legs I are brought nearer at this time.

Given the total lack of extensor muscles in several leg joints, particularly in the femoro-patellar ('knee') joint (figure 1), we speculate that a hydraulic pump could power leg movements at take-off. Direct evidence of a hydraulic pump would require measurements of haemolymph pressure and of concomitant muscular activities (Shultz 1991), which are prevented by the smallness of the mite. However, besides the partial curling up during the prejump phase, which should generate a rush of haemolymph in the NG, some muscles differentiating *Indotritia* cf. *heterotrichia* from the non-jumping box moss mite *Rhyssotritia duplicata* might contribute to an increase of pressure that would augment the velocity with which the legs could be extended when the flexor muscles are relaxed (Blickhan & Barth 1985). Combined contraction of coxisternal adjusters and abdominal compressors (figure 4) could indeed result in the production of the highest possible haemolymph pressure before leg extension. In fact, the action of these muscles (with respect to pressure generation) appears to be complementary: while the abdominal muscles would increase fluid pressure by transversally compressing the NG (Sanders 1982), contraction of coxisternal adjusters would compress the abdominal contents longitudinally by pulling the coxisternal plateau inwards.

In other respects, it is unclear whether or not the changes affecting the endosternal musculature and the insertion of coxisternal retractors, as well as the presence of peculiar nervous ganglia, are directly related to the hydraulic force generation that the jump would require. However, the following remarks should be noted: (i) endosternal muscles are responsible for much of the pressure generated for leg extension in other arachnids (Palmgren 1981; Shultz 1991); (ii) the clustering of tendons of coxisternal retractors on the apophyses LX is likely to result in a powerful leverage on the coxisternal plateau, suggesting that these muscles might supplement the action of coxisternal adjusters (figure 4); and (iii) the supply of coxisternal locomotors of legs III and IV by ganglia could be regarded as a specialization for minimizing energy losses in the

(not shown; they connect the plateau to the buccal cone, the buccal cone to the chelicerae, and the chelicerae to the AS, respectively); b, coxisterno-trochanteric articulations of the legs; c, ligament between coxisternal elements 1–2 (which are fused together) and the element 3; d, hinge between coxisternal elements 3 and 4. Scale bar, 100 μ m.

hydraulic system if it facilitates the immobilization of proximal leg segments during the propulsive stroke performed by distal segments at take-off.

(b) *Catch mechanism*

Given the assumed activity of the coxisternal adjusters, coupled or not with the activity of coxisternal retractors, a complete retraction of the coxisternal plateau should occur in the absence of an antagonistic force. In fact, femoral hooks of the forelegs could counteract the effects of the coxisternal muscles (figure 4). The functional role of the hooks is obvious when the animal curls up (figure 2): by hitching on the lateral rim of the AS, the hooks contribute to the coaptation of the AS, of the legs and of the NG, and thereby reduce the activity of aspidosomal flexors and adjusters.

If, as we postulate, the femoral hooks are attached to the rim of the AS in prejump position (figure 1), contraction of coxisternal adjusters should store elastic strain energy in the mite's cuticle, particularly in the coxisternal plateau (CPI-4 in figure 4). Clearly, the function of femoral hooks appears to be similar to that of catch mechanisms found in other jumping arthropods: it would allow the mite to store muscular energy during the prejump phase. In *Indotritia cf. heterotrichia*, however, the hook is involved in another task (i.e. the curling up) and is associated with the forelegs instead of hindlegs as usually observed (but see Crowson (1981) for a possible catch mechanism associated with the forelegs in some Coleoptera).

The following observation is consistent with the hypothesis that femoral hooks may act as a catch: in box moss mites, the ability to curl up is independent of the occurrence of femoral hooks, but only box moss mites that possess femoral hooks are known to jump. The ability to leap has been reported in two primitive genera of Oribotritiidae, which include species equipped with femoral hooks, i.e. *Indotritia* (Shubart 1967) and *Austrotritia* (G. Wauthy, personal observations). By contrast, members of the genus *Oribotritia*, also regarded as primitive in the family, lack femoral hooks (Grandjean 1967) and do not jump (S. F. Swift, personal communication). However, a small number of species have been observed to jump, and care should be taken with this generalization: some *Indotritia* and *Austrotritia* species might not possess femoral hooks (several diagnoses do not mention the presence or absence of the character). A more thorough survey of the occurrence of femoral hooks and of their role among box moss mites is necessary to confirm the involvement of these elements in the jump.

According to video recordings and anatomical data, leg movements at take-off can be modelled as follows. During the acceleration time, legs IV and III push the NG upwards and initiate the forward spin of the body, while legs I act initially as a prop preventing the mite from falling over forwards. Once legs IV-II have left the substrate, legs I suddenly push the animal backwards (figure 3); the impulse would occur as a result of the femoral hooks (figure 2), which, when disengaged from the rim of AS, would allow legs I to extend rapidly and thus act as a catch mechanism.

(c) *Attitude in flight*

Backward somersaults and forward spinning are an attitude very unusual in leaping animals. It results not only from the rolling induced by legs IV-II, but also from the backward impulse of legs I directed behind the centre of mass. This attitude has been observed in bristle-tails (Evans 1975) and in some *Z. falzonii* jumps (Krisper 1990), but the former spins fewer times and the latter exhibits such an attitude only occasionally. The forward spinning increases the height of the jump compared with a situation where no spin occurs (Bennet-Clark 1977). However, the ecological importance of an increased height is unclear as the animal lives in the leaf litter where it probably strikes an obstacle before reaching the maximum height of its jump. Another peculiarity of the trajectory is its non-parabolic shape (figure 3). In fact, the air resistance during the translation and the rolling (Magnus effect) of the mite causes important kinetic-energy losses that had to be taken into account in modelling the trajectory.

5. CONCLUSIONS

As shown in *Indotritia cf. heterotrichia*, morphological demands imposed by jumping appear to be minor in leaping box moss mites. In contrast, jump evolution seems to be bound by other requirements, notably muscular (according to anatomical data) as well as behavioural (as exemplified, for instance, by the raised posture before take-off and by coordinated movements of the legs at take-off), and also mechanical, if a catch system is involved.

Current data for the ability to jump within box moss mites indicate that jump evolution has occurred in two genera emerging at the root of a large branch (Oribotritiidae) in the phylogeny. If such a phyletic limitation is confirmed, the influence of a constraint can be invoked: one would only need one of the demands imposed by jumping to be completed before the achievement of others for a constraint to be met (see Endler & McLellan (1988) and McKittrick (1993)). If the femoral hooks play a role in the jump, their acquisition for a former function (i.e. the protection of the opening of patellar organs as suggested by Grandjean (1967)) could be the key factor of jump evolution.

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APPENDIX A

The observed trajectory can be modelled using the theoretical equations derived below. Given the lift force (F_L), the drag force (F_D) and the gravity (mg , where g is the acceleration of gravity, and m is the body mass) acting on the mite in the z - y plane of a trajectory that is a mirror image of the observed trajectory processed with motion analysis software (figure 5), Newton's equations of motion are:

$$d^2y/dt^2 = -(F_D/mv)(dy/dt) + (F_L/mv)(dz/dt), \quad (1)$$

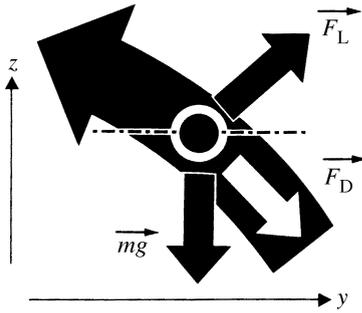


Figure 5. Specular translatory motion of the mite's body (black dot) during a jump performed in the plane z - y , with a schematic representation of the forces acting on the animal (F_L , lift; F_D , drag; and mg , gravity).

$$d^2z/dt^2 = -[g + (F_D/mv)(dz/dt) + (F_L/mv)(dy/dt)]. \quad (2)$$

The expression for F_D is given by

$$F_D = \frac{1}{2} \rho v^2 C_D (\text{Re}) S, \quad (3)$$

(for details, see White (1974)), with

$$C_D \approx A / [(\text{Re})^B],$$

$$\text{Re} = vd/\nu,$$

where v is the velocity, ν is the kinematic viscosity coefficient, d is the mite's diameter, Re is the Reynolds number, S is the frontal surface of the body, ρ is the density of the air, and A and B are constants which were *ca.* 16.8 and 0.61, respectively, in the range of velocities involved, i.e. $0.51 \text{ m s}^{-1} < v < 0.56 \text{ m s}^{-1}$.

For the present case, where $S = \pi(d/2)^2$, $d = 0.1 \text{ cm}$, $n = 1 - B$, $\rho = 1.293 \text{ kg m}^{-3}$, $m = 9 \times 10^{-8} \text{ kg}$ and $\nu = 0.146 \text{ cm}^2 \text{ s}^{-1}$, we can write the equations

$$F_D/mv = \mu_0 v^n = \mu,$$

where μ stands for the drag force divided by the momentum, and

$$\mu_0 = (\rho AS/2m)(\nu/d)^B = 7.194 \text{ m k s}$$

(metre-kilogram-second system of units).

For the sake of comparison, the value of the ratio F_D/mg is 63% at $t=0$.

The expression for F_L is similar to equation (3), but with a different coefficient C_L :

$$F_L = (C_L/8)\pi d^3 \rho v \varpi,$$

where the mean angular velocity was estimated to be $\varpi = 3.6 \times 10^3 \text{ rad s}^{-1}$ from the video record.

We now compute

$$F_L/mv = \lambda_0 \approx 3 \text{ s}^{-1},$$

$$F_L/mg = 18\%.$$

The final expressions for (1) and (2) are therefore:

$$d^2y/dt^2 = -\mu(dy/dt) + \lambda_0(dz/dt), \quad (4)$$

$$d^2z/dt^2 = -[g + \mu(dz/dt) + \lambda_0(dy/dt)]. \quad (5)$$

Equations (4) and (5) can be used to compute the conditions of the centre of mass at any moment of the flight and to trace a theoretical curve that fits the observed trajectory quite satisfactorily (figure 3). The air resistance and spin have a pronounced effect on the shape of the trajectory, as illustrated by figure 3. If both air resistance and spin are neglected, then a parabolic trajectory is obtained whose range and height are both larger. If only the drag is taken into account (i.e. no spin), a non-parabolic trajectory with a range and height which are both smaller is found.

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