

THE LOCUST JUMP

III. STRUCTURAL SPECIALIZATIONS OF THE METATHORACIC TIBIAE

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SUMMARY

1. The flexor and extensor tibiae muscles of the mesothoracic leg have a constant lever ratio of about 2:1 throughout joint rotation.
2. The mesothoracic tibiae can only flex to 25° about the femora, while the metathoracic tibiae, because of their specialized geometry, can flex almost parallel to the femora.
3. Full metatibial flexion increases the mechanical advantage of the flexor muscle relative to the extensor at full flexion, and increases the vertical component of the thrust produced by tibial extension in a jump.
4. A region in the dorsal proximal cuticle of the metatibia is stiff when stretched but buckles when compressed. The tibia is thus rigid under extensor stress, but bends under flexor stress.
5. Metatibial bending can enable the proximal region of the tibia to become fully flexed even if the distal region is prevented from flexing fully, and may reduce the inertial shock to the femur when the tibia reaches full extension in a kick.

INTRODUCTION

The locust jumps and performs defensive kicks by the rapid and forceful extension of its metathoracic tibiae. Before the movement the tibiae are held flexed for 300–600 ms while flexor and extensor muscles co-contract (Heitler & Burrows, 1976*a*). This enables the production of almost isometric tension in both muscles. The extensor muscle can develop force up to 1.6 kg, while the flexor muscle can only produce 0.07 kg (Bennet-Clark, 1975), but the flexor muscle develops greater torque than the extensor muscle (Brown, 1967) and thus holds the tibia flexed. This is because of structural specializations of the femoral–tibial joint which give the flexor muscle a great mechanical advantage over the extensor muscle when the tibia is flexed. The most important specialization is a cuticle invagination in the distal ventral femur which increases the lever ratio of the flexor muscle when the tibia is flexed, and fits into a pocket in the distal flexor tendon to form a partial catch mechanism (Heitler, 1974). It was estimated that 0.015 kg of flexor tension can maintain the tibia flexed against 1.6 kg of extensor tension. The tibia thus remains flexed during co-contraction until a massive inhibition of flexor excitor motoneurons and an excitation of flexor

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inhibitor motoneurons causes relaxation of the flexor muscle and allows the tibia to extend (Heitler & Burrows, 1976*a*).

In this paper further specializations in the structure of the tibiae are described. The gross anatomy of the proximal metathoracic tibiae is related to the joint specializations described in the previous paper (Heitler, 1974), and a comparison drawn with the non-jumping mesothoracic legs. A region of flexible cuticle in the dorsal proximal tibia is described and suggestions are made for the role of this flexible cuticle in jumping and kicking.

MATERIALS AND METHODS

The anatomy of the tibiae of adult *Schistocerca americana* (formerly *S. gregaria*; Dirsh, 1974) of either sex was studied by making scale drawings from dissected locusts. All dimensions given in the text and figures are scaled to conform to a locust whose metathoracic tibiae measure 21 mm from the femoral-tibial joint to the tibial-tarsal joint. The stiffness of the tibia was measured by dissecting it free from the femur and embedding the proximal joint region in De Khotinsky cement. Force was then applied at right angles to the end of the tibia using a Bionix F-200 transducer, and the resulting deflexion measured against a scale marked in degrees. Observation under the microscope revealed no movement of the embedded region, indicating that the deflexion was due entirely to bending in the tibia. Cuticle structure was investigated using a scanning electron microscope and a polarizing microscope. Cuticle distortion during a defensive kick was studied using a 'Hycam' moving film camera operating at 200 frames/s with an effective exposure time of about 1.6 ms for each frame.

RESULTS AND DISCUSSION

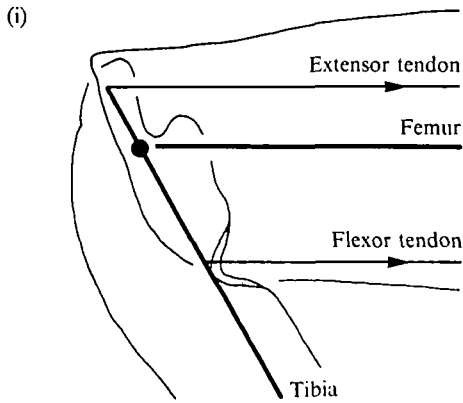
Anatomy of the proximal tibia

The structure of a mesothoracic tibia is first described. This is regarded as representing a 'typical' walking limb. Next a metathoracic tibia is described, and the differences are discussed to demonstrate the specialized nature of the latter in terms of its function in jumping and kicking.

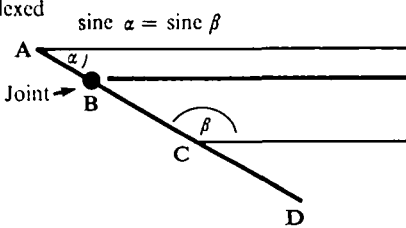
Mesothorax. In a mesothoracic tibia 8.5 mm long, the distance from the extensor tendon to the femoral-tibial pivot is 0.37 mm (line *AB* in Fig. 1*a*), and from the flexor tendon insertion to the joint pivot is 0.77 mm (line *BC*). The two tendon insertion points of the femoral-tibial joint, the joint pivot itself, and the tibial-tarsal joint are approximately co-linear. The flexor and extensor tendons remain parallel to each other and the femur throughout joint rotation, and thus the sine of the angle that the extensor tendon makes to the tibia (α in Fig. 1*a*) is always equal to the sine of the angle that the flexor tendon makes to the tibia (β in Fig. 1*a*). Therefore the lever ratio between the two muscles is constant throughout joint rotation, with a mechanical advantage of about 2:1 in favour of the flexor muscle. The mechanical advantage of both muscles relative to a load at right angles to the end of the tibia varies sinusoidally with joint rotation. The tibia can extend almost 180° to the femur, but cannot flex to an angle of less than about 25° because the proximal ventral surface of the tibia then collides with the distal ventral surface of the femur.

Metathorax. The most proximal part of the metathoracic tibia, from the insertion of

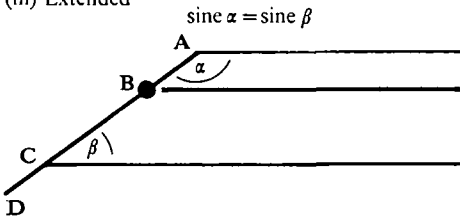
(a) Mesothoracic leg



(ii) Flexed



(iii) Extended



(b) Metathoracic leg

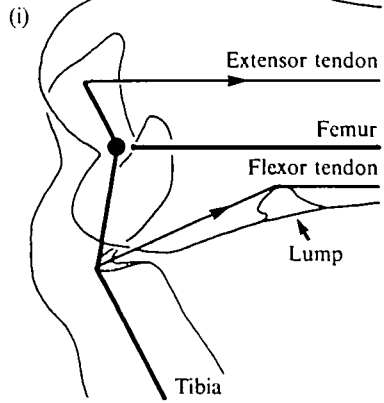
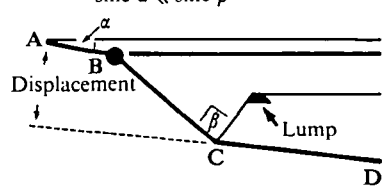
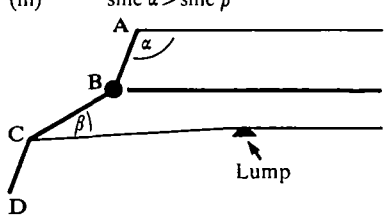
(ii) $\text{sine } \alpha \ll \text{sine } \beta$ (iii) $\text{sine } \alpha > \text{sine } \beta$ 

Fig. 1. A stick diagram comparing the basic structure of (a) a mesothoracic femoral-tibial joint with (b) a metathoracic one. The drawings are not to scale. Thick lines represent the mechanical analogues of the joint structures, thin lines the tendons. In (i) the outline of the femora and tibiae have been drawn in to show the relation of the mechanical analogue to the actual joint. The tibiae are shown in the flexed position (ii) and the extended position (iii).

the extensor tibiae tendon to the joint pivot (line AB in Fig. 1*b*) is parallel to the main line of the tibia distal to the flexor tendon insertion (line CD), but displaced from it dorsally in the sagittal plane by about 2 mm (the dimensions are given in detail in Heitler, 1974). The immediate consequence of this displacement is that the metathoracic tibiae, unlike the mesothoracic, *can* flex to a position almost parallel to the femur, since collision is avoided by the tibial displacement (compare Fig. 1*a* (ii) with 1*b* (ii)).

The most important advantage of full tibial flexion in relation to the function of rapid tibial extension is the reduction in the lever arm of the extensor tibiae muscle that results. This lever is proportional to the sine of the angle that the extensor tendon makes with the tibia, which in the metathoracic legs can be as low as 5° , as opposed to 25° in the mesothoracic legs. The reduced lever arm enables the extensor muscle to

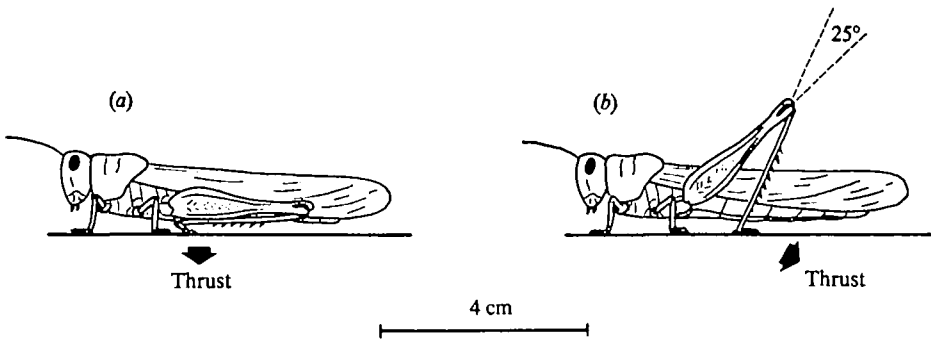


Fig. 2. (a) A locust with its metathoracic tibiae fully flexed and parallel to the ground. The initial thrust upon extension is directly downwards. (b) A locust with its metathoracic tibiae held at 25° to the femur. The thrust upon extension is now largely directed backwards.

develop high force with low torque. A similar reduction in the lever arm of the flexor muscle, which would occur with the geometry of the mesothoracic legs, is avoided in the metathoracic legs because the flexor tendon slides over the femoral lump, and the angle that it makes with the tibia (β in Fig. 1b) changes with joint rotation to reach a maximum of 90° in the fully flexed position. Thus when the metathoracic tibiae are flexed the flexor lever arm is maximal, and the extensor lever arm is minimal (quantitative data given in Heitler, 1974). Full flexion of the tibia thus confers a mechanical advantage to the comparatively weak flexor muscle which helps it to hold the tibia flexed against the much stronger extensor muscle.

Another advantage of full tibial flexion is that it reduces the gap between the distal tibia and the proximal femur. Just before the take-off in a jump the flexed femur-tibia is positioned parallel to the ground (Bennet-Clark, 1975), and so the initial thrust exerted by the unfolding tibiae is directly downwards (Fig. 2a). As the tibiae continue to extend, the thrust develops a backward component propelling the locust forwards, so that the final take-off angle of the locust is usually about 45° (Pond, 1972). This is the optimum angle to ensure that the locust will cover a maximum distance in the jump. The energy of the jump can be accounted for completely by the energy produced in the extension of the metathoracic tibiae (Bennet-Clark, 1975). Were the metathoracic tibiae, like those of the mesothorax, able to flex only to an angle of 25° about the femora, there would be a gap of about 10 mm between the distal end of the tibia and the proximal femur. The femora could not then be positioned parallel to the ground before the jump, but would have to be cocked at an angle of about 45° (Fig. 2b). This would reduce the vertical component and increase the backward component of the thrust derived from metatibial extension, and thus reduce the angle of take-off, unless compensated by some other power source, such as a significant thrust from the pro- or mesothoracic legs.

Bending in the metathoracic tibia

When the tibia is stressed as in a jump or kick, it is a very rigid structure (Fig. 3a). Under these conditions the ventral surface of the tibia is under compression and the dorsal surface is under tension (Fig. 4a). If the tibia is stressed in the opposite direction

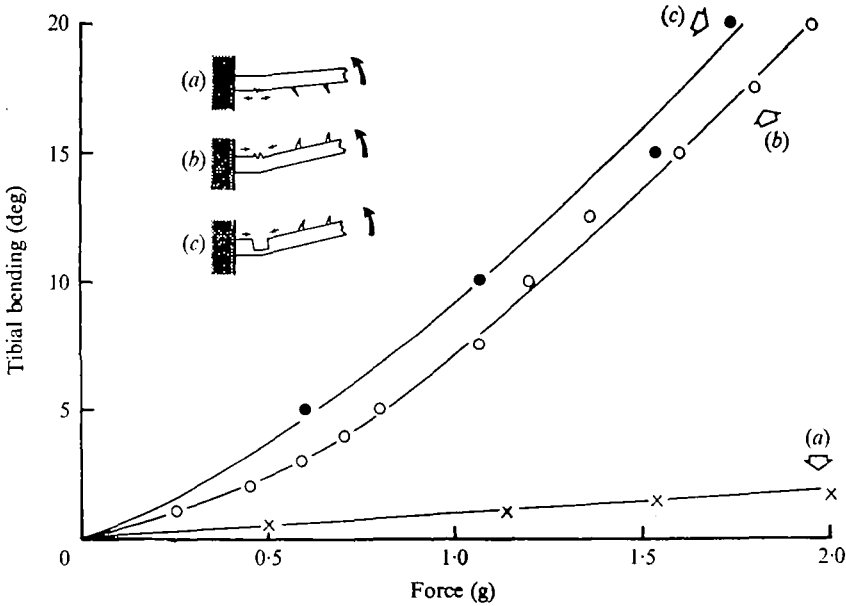


Fig. 3. The stiffness of the tibia under various loading conditions (shown as insets: the thick arrows show the loading, the wavy line indicates the flexible cuticle, and the small arrows show the direction of stress). The proximal tibia has been embedded in cement to within 1 mm of the dorsal band of flexible cuticle, and force is applied at right angles to the tibia 14.5 mm from this region. This figure shows data for one typical tibia taken from a 17 day adult male. (a) The tibia is stressed as in a jump. (b) The loading is the reverse of that encountered in a jump. (c) The loading is the same as that in (b), but the entire dorsal region of flexible cuticle has been cut out.

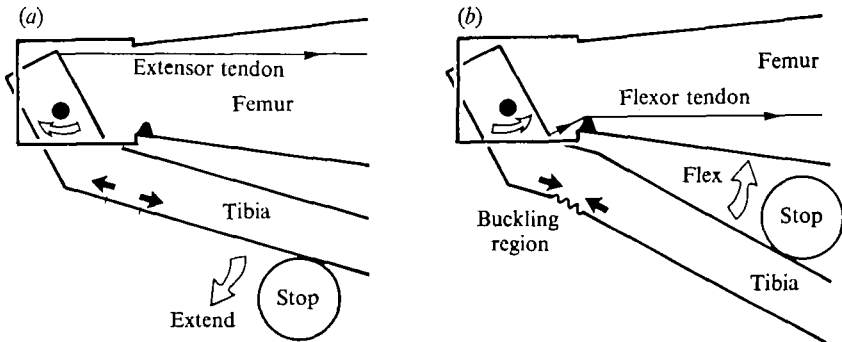


Fig. 4. Buckling of the metathoracic tibia. (a) There is tension in the *extensor* tendon, but a mechanical stop prevents the tibia extending. The dorsal cuticle is stiff under tension stress, and the tibia remains rigid. (b) There is tension in the *flexor* tendon, but a mechanical stop prevents the tibia flexing. The dorsal cuticle now buckles under compression stress, so that the tibia bends.

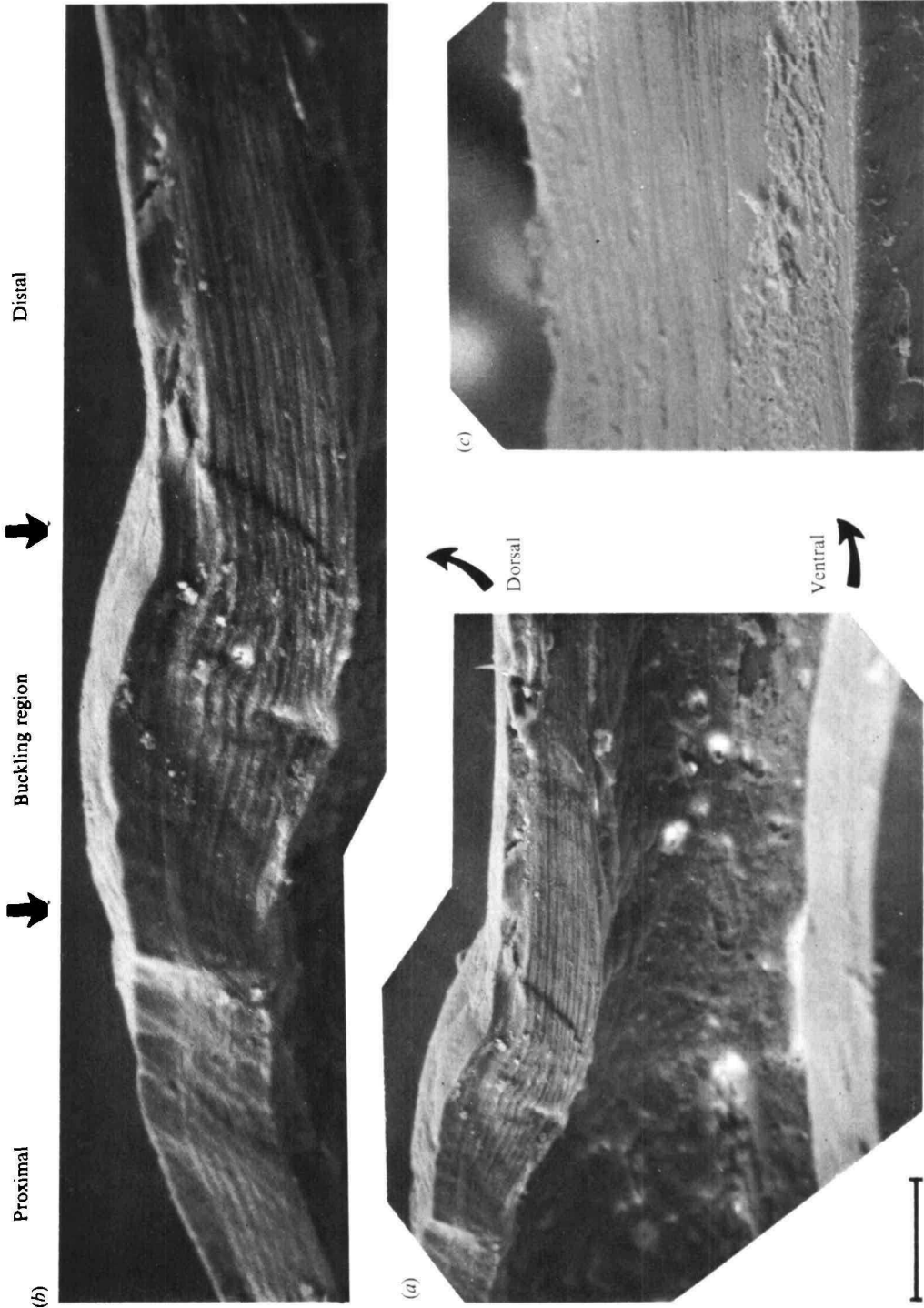
however, it is much less rigid (Fig. 3*b*). This is because there is a small region of lightly sclerotized cuticle in the proximal dorsal tibia (Bennet-Clark, 1975) which can buckle under compression (Fig. 4*b*). The specializations in the proximal region of the tibia which cause this differential stiffness can be seen by examining the cut surface of cuticle from a tibia sectioned longitudinally in the sagittal plane. On the ventral side

of the tibia no lamellations or growth layers are visible to the scanning electron microscope (Fig. 5*a, c*), although they are present in the cuticle (Neville, 1967). This is due to the heavy sclerotization of exo- and endocuticle which binds the cuticle in this region into a rigid beam of uniform high shear strength, thus increasing the compressive strength of the ventral tibia (Jensen & Weis-Fogh, 1962). It is this ventral region which is under compressive stress during a jump. On the dorsal surface, however, endocuticular striations representing the growth layers are apparent, indicating a difference in shear strength between the lamellate (i.e. Bouligand structure night growth) and the preferred orientation (day growth parallel to the tibial axis) layers of the endocuticle. The entire dorsal cuticle, which is under tension in a jump, is less heavily sclerotized than the ventral cuticle, and therefore has reduced compressive strength. In one particular region of this dorsal cuticle, however, the striations are thickened and separated, leading to an overall swelling of the cuticle (Fig. 5*b*). This feature is also visible in polarizing photomicrographs of sections of the cuticle made from a tibia that had been fixed in the normal unstrained state (Fig. 6*a*). Sections made from a tibia that had been fixed in the strained state show that it is in this thickened region that the buckling of the cuticle takes place which enables the tibia to bend (Fig. 6*b*), and so this region would appear to show particular compressive weakness. Indeed, the entire dorsal region of flexible cuticle can be removed without greatly affecting the stiffness of the tibia when it is stressed so that this region comes under compression (Fig. 3*c*). When stressed in this sense the intact tibia is effectively no longer a tube: the stiffness derives almost entirely from the sclerotized ventral cuticle acting as a beam.

The buckling is probably made possible by a reduction in the cross-linkage between the interlamellar protein and the chitin microfibrils, thus allowing movement between the laminae in this region. This would not greatly affect the tensile stiffness of the cuticle, which derives largely from the microfibrils (Jensen & Weis-Fogh, 1962), but it would produce a considerable reduction in compression stiffness, since shear resistance is reduced and the cuticle as a whole could buckle into an S shape without subjecting the individual laminae to tensile stress. This is exactly what happens when the tibia bends (Fig. 6*b*). Little is known about the biochemistry of the flexible cuticle. The sections do not fluoresce under ultraviolet illumination, and so are unlikely to contain resilin (Andersen & Weis-Fogh, 1964). The bending plane looks similar in structure to the patch of tough flexible cuticle adjacent to the pad of pure resilin in the locust wing hinge (Weis-Fogh, 1960). This patch does not contain resilin either, but has coarse, densely packed protein fibrils between the chitin laminae.

One clear function of the bending plane is to enable the proximal joint region of the tibia to be flexed fully even if some structural block prevents the distal tibia flexing against the proximal femur (as in Fig. 4*b*). This flexion is essential during the co-

Fig. 5. Scanning electron micrographs of the cut surface of the proximal cuticle of a hind tibia which has been split sagittally. (*a*) Low magnification showing both dorsal and ventral surfaces. (*b*) The dorsal cuticle at higher magnification. Striations which look like growth layers are visible. This must reflect differences in the shear strength of the preferred orientation and lamellate zones of the cuticle. In the middle of the section is a region where the striations are thicker. This is the region that buckles under compression. (*c*) The only striations visible in the highly sclerotized ventral cuticle are knife marks. Calibration: (*a*) 120 μm , (*b*) 70 μm , (*c*) 25 μm .



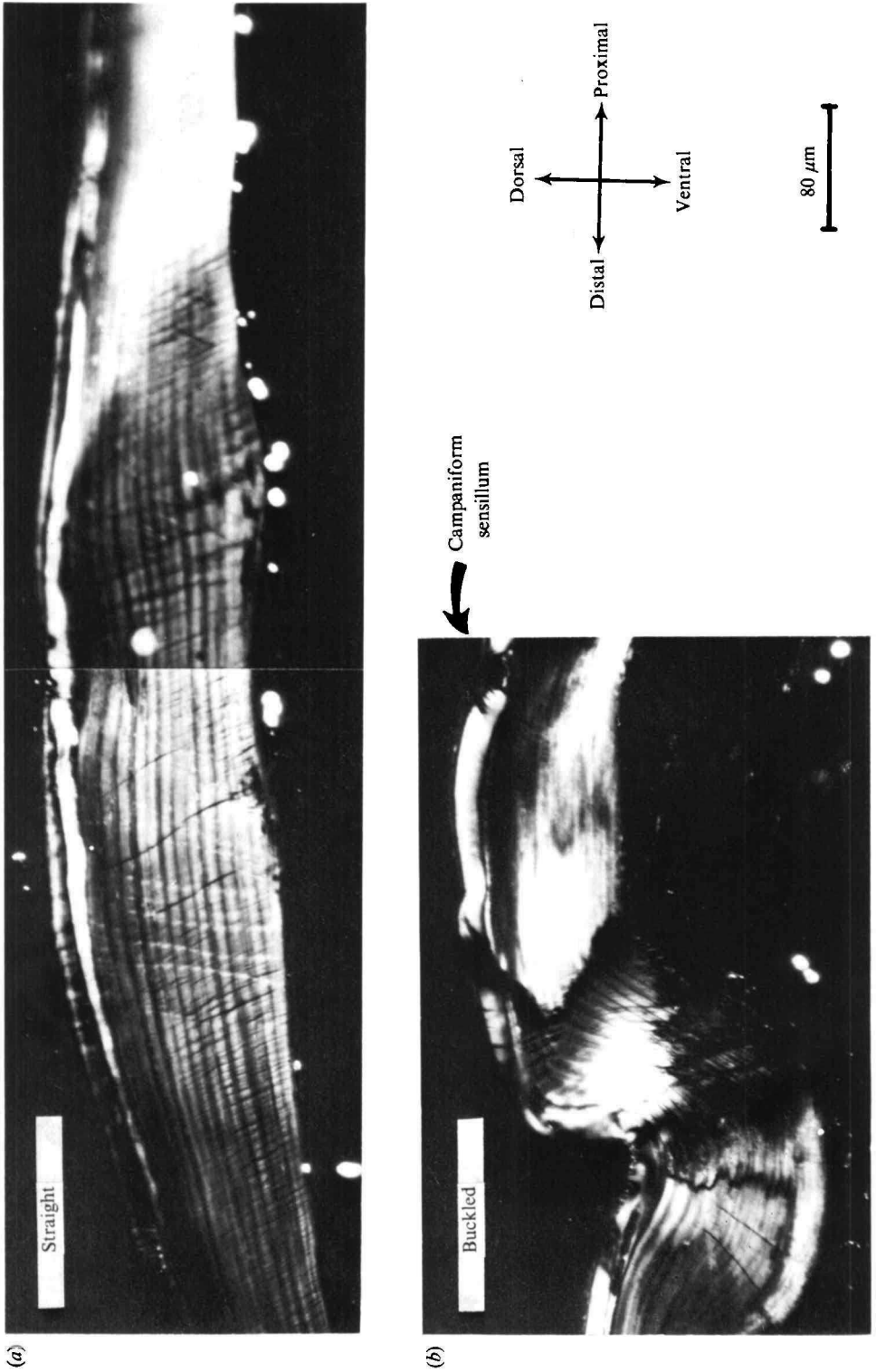


Fig. 6. Polarizing photomicrographs of the dorsal proximal cuticle of the tibia. (a) The tibia has been fixed in the unstrained state. (b) The tibia has been fixed while strained. A campaniform sensillum is present in this section.

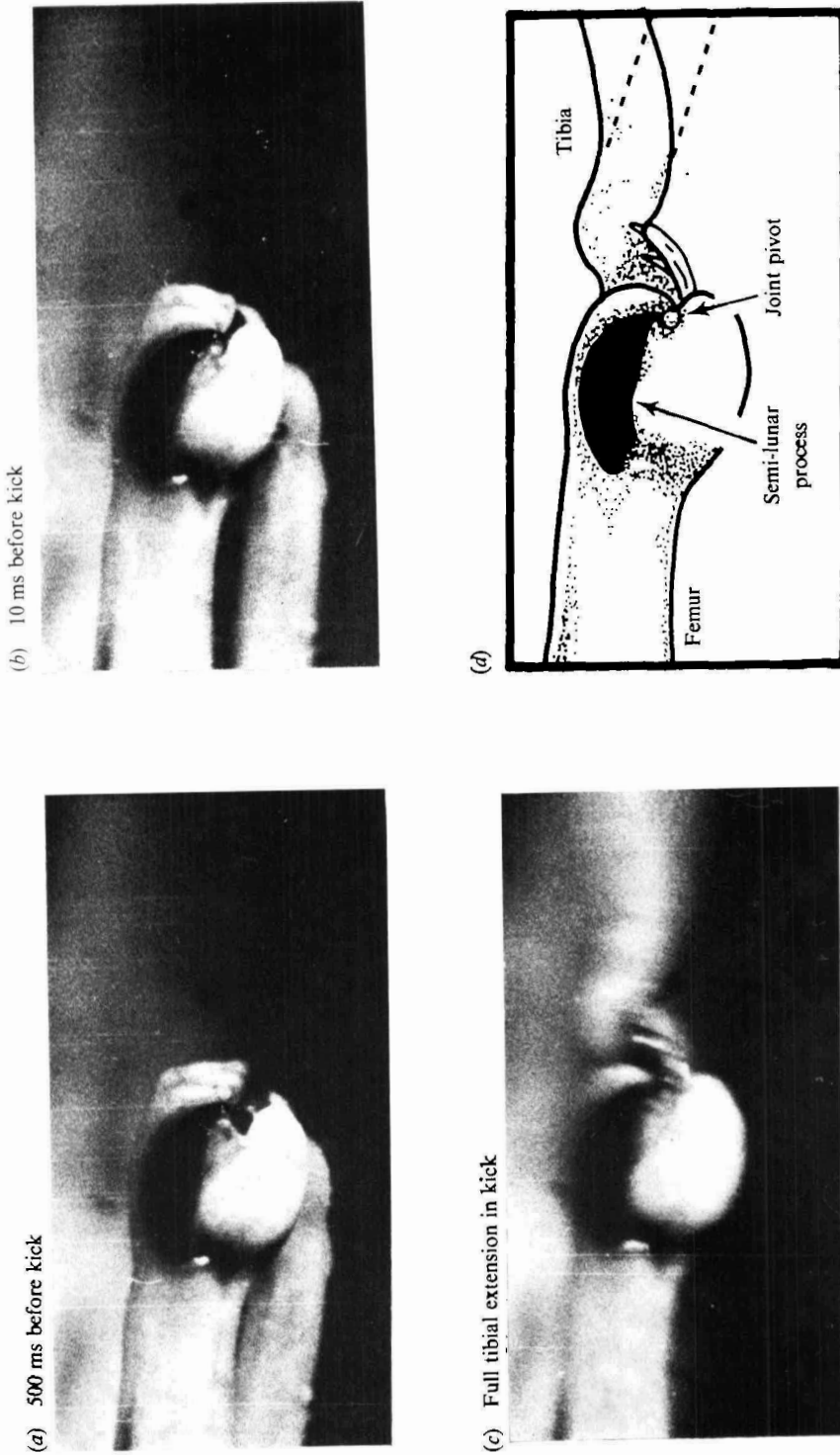


Fig. 7. Photographs taken at 200 frames/s of the metathoracic femoral-tibial joint during a defensive kick. (a) 500 ms before the start of the kick. (b) Just before the start of the kick. The increased gap between the distal femur and the proximal tibia is a good marker of the distortion of the semi-lunar processes. (c) About 5 ms after the start of the kick the tibia is fully extended and the tibia is bending dorsally. *b* and *c* are separated by 10 ms. (d) A tracing made from (c). The dotted lines indicate the position the tibia would have been in, if it were not bent.

contraction of flexor and extensor muscles prior to a jump or kick. The degree of tibial bending that can occur without permanent damage to the tibia varies considerably with the age of the locust. In a mature locust whose cuticle has fully hardened tibial bending of $15\text{--}20^\circ$ may be repeatedly induced without producing a plastic deformation of the tibia, or apparently effecting its ability to withstand the stresses of jumping. In a locust whose cuticle is still soft from the previous moult much greater bending can occur, but extreme strains ($70\text{--}80^\circ$) may result in temporary or permanent deformation of the tibia.

Photographs were taken of the femoral-tibial joint before and during a defensive kick (Fig. 7). During the co-contraction phase before the kick there is no significant buckling of the dorsal cuticle of the tibia, indicating that when the distal tibia can flex fully against the proximal femur there is little ventral bending stress in the tibia. There is nevertheless distortion of the sclerotized femoral semi-lunar processes which support the joint pivot (Fig. 7*a, b*). This distortion is caused by the extensor muscle tension, and stores approximately half of the energy released in the jump or kick (Bennet-Clark, 1975). The exposure time (1.6 ms) is much too long to freeze tibial motion during the actual joint rotation. However, when the tibia reaches full extension it slows, stops, and bounces back. This sequence occurred in the exposure of Fig. 7(*c*). The period of maximum exposure must be when the tibia is stationary, and so the highlight of Fig. 7(*c*) indicates the tibia in its most extended position. The tibia clearly bends dorsally at a point which suggests buckling of the dorsal proximal cuticle (Fig. 7*d*). This bending increases the angular distance over which the tibia comes to rest at extreme extension and so one may conjecture that the forces on the joint structures are reduced by a factor related to the asymmetry of stiffness of the tibia.

Apart from these mechanical functions, the buckling region may also have an affect on nearby sense organs. The tibial subgenual organ is located just under the bending plane, and a group of five campaniform sensilla occur on the tibia just proximal to the bending plane (Fig. 6*b*). These sensilla have their ridges aligned along the long axis of the tibia, and thus would be expected to monitor bending stresses in the tibia (Pringle, 1938). No function has been shown for the sensilla: ablation has no apparent affect on the ability of the locust to jump or kick, and recordings from flexor and extensor motoneurons to the tibial muscles do not reveal any inputs resulting from mechanical stimulation of the individual sensilla. The subgenual organ, on the other hand, plays an important role in the production of the motor programme in the kick and jump (Heitler & Burrows, 1976*b*). Howse (1965) reports a similar arrangement of sensilla and subgenual organ close to a plane of weakness on the tibia of the termite. He suggests that the plane of weakness might serve to focus cuticle strain on the sensilla. If this is true the bending plane on the locust tibia might also have a similar function.

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