

THE HYDRAULIC MECHANISM OF THE SPIDER LEG

BY D. A. PARRY AND R. H. J. BROWN

Department of Zoology, University of Cambridge

(Received 12 February 1959)

INTRODUCTION

Hinge joints occur in the legs of various arthropods, notably *Limulus* (Snodgrass, 1952); arachnids; diplopods, chilopods and pauropods (Manton, 1958*b*). At a hinge joint flexion is muscular, but the anatomical form of the joint rarely permits the presence of antagonistic extensors (see Manton, 1958*a*, fig. 151 for an exception). In the recent account of the leg muscles of the house spider *Tegenaria* sp., Parry (1957) suggested that extension might be due to hydraulic forces in the leg. Manton (1958*b*) attributed to the same cause the full extension of the arachnid leg when the limb tip is off the ground but considered that extension during a propulsive stroke was passive and due to the ground reaction on the limb and so, indirectly, to depressor muscles.

In the present paper support is given to the idea that active extension occurs at the hinge joints of the *Tegenaria* leg and that the mechanism is a hydraulic one. First, we measure the internal pressure in the leg of intact spiders and find it to be surprisingly high. Secondly, we establish an empirical relation between the internal pressure of the leg and the torque at the hinge joints. Thirdly, we measure the torques actually developed at the hinge joints when a spider accelerates a mass attached to the leg, and use the relation between torque and pressure to show that the measured torques can be accounted for by the pressures which occur in the leg.

MEASUREMENT OF INTERNAL PRESSURE

Methods

The pressure inside the leg of an intact living spider can be measured by taking advantage of the thin flexible articular membranes at the two hinge joints. This principle is employed in two ways:

(a) *Direct observation of the membrane* (Fig. 1). A sleeve is sealed over the leg and the membrane observed through a binocular microscope. To measure the *maintained resting pressure*, the pressure in the sleeve is slowly raised until the membrane just collapses. To measure *transient pressures* developed when the spider is struggling, the sleeve pressure is raised to a predetermined value above the resting pressure so that the membrane collapses, and the spider is then stimulated. The reinflation of the membrane indicates that the internal pressure equals or exceeds the sleeve pressure.

(b) *Use of a high impedance transducer.* The Cambridge Instrument Company very kindly lent us one of their photo-electric transducers and associated equipment. The principle of this instrument is illustrated in a purely formal way in Fig. 2. The stiffness of the diaphragm is such that the instrument is almost isometric, a pressure change of 1 cm. Hg producing a volume change of 5×10^{-3} mm.³ (cf. the joint volume of the spider which is about 0.5 mm.³). One leg of a living spider is sealed into the cavity as shown, the stop-cock, *S*, is opened and a zero recorded. The pressure is then raised to a pressure *P*, above the internal resting pressure of the spider, so that the articular membrane collapses. The stop-cock *S* is then closed and the recorder started. The spider is stimulated with a paint brush or a puff of air and the excess of internal pressure above *P* is thus recorded against time.

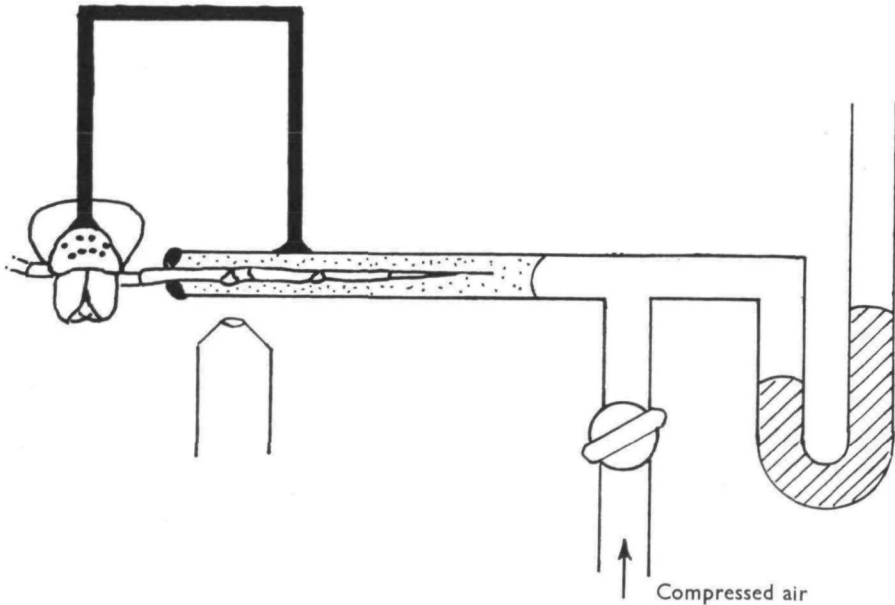


Fig. 1. Method of mounting a spider for observation of the articular membrane during the application of external pressure.

RESULTS

Resting pressures. When a spider is immobilized with one leg in a sleeve, it maintains a positive pressure of approximately 5 cm. Hg which we call the resting pressure. The following figures (each a mean of four successive determinations) indicate the sort of variation encountered in different spiders: 4, 5, 5, 8, 9, 11, 11 cm. Hg. In the absence of other evidence we presume that these pressures are typical of the resting spider when supporting its own weight in normal life.

Transient pressures. When a spider, mounted as indicated in Fig. 2, is stimulated by a puff of air or by a paint brush the internal pressure rises to several times the resting value and then falls again in a time which rarely exceeds 1 sec. and is usually

about $\frac{1}{8}$ sec. A transducer record showing an unusually high transient pressure is shown in Fig. 3. The peak pressures which have been recorded in this way are as follows:

Spider A	11, 15, 17, 17, 19, 20, 22, 23, 24 cm. Hg
Spider B	16, 24, 27, 39, 39+ cm. Hg
Spider B (next day)	16, 20, 23, 24, 25, 25, 45 cm. Hg
Spider C	25, 25, 30, 30, 40 cm. Hg

It will be seen that pressures of up to 45 cm. Hg have been recorded.

Comparable results have been obtained by the simpler method (a) described above. The maximum sleeve pressures against which a spider was observed to re-inflate its articular membrane was 40 cm. Hg. This was repeated on the same spider on two successive days.

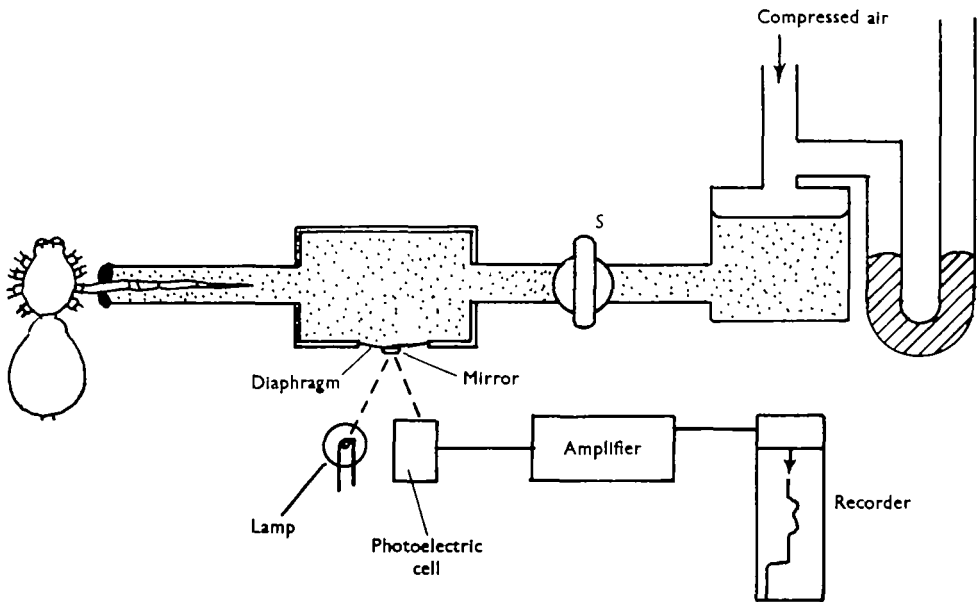


Fig. 2. Measurement of transient pressures in the leg of a spider using a high impedance photo-electric transducer.

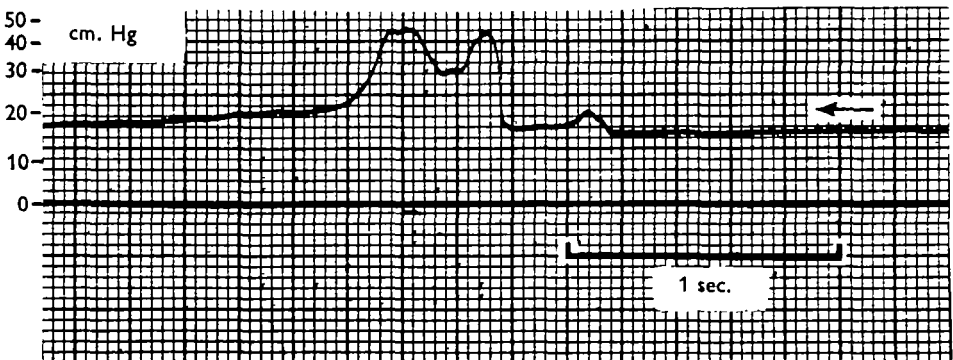


Fig. 3

RELATION BETWEEN PRESSURE AND TORQUE AT A JOINT

Direct determination

A leg is removed at the coxa-trochanter joint where normal autotomy occurs (Parry, 1957) and waxed into the end of a Perspex tube with a 1:1 beeswax-resin mixture (Krogh & Weis-Foch, 1951). The tip is cut off and the leg perfused with 1.3% magnesium chloride to relax the muscles. The tip is then sealed with wax and the Perspex tube mounted in the way shown in Fig. 4, thus enabling the relationship between internal pressure and torque at the joint to be determined under static conditions for different joint angles.

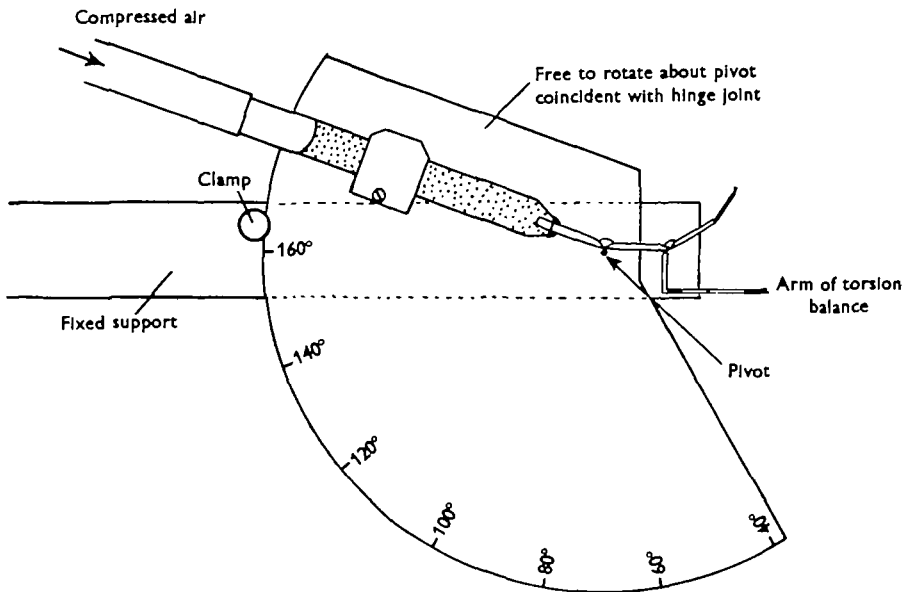


Fig. 4. Measurement of the relation between the internal pressure of the leg, the joint angle and the torque developed at the hinge joint.

Fig. 5 shows the relationship between pressure and torsion balance reading for the femur-patella joint ('upper joint') and the tibia-basitarsus joint ('lower joint') of a particular leg whose size is indicated by the fact that the distance between the two joints was 11 mm. The distance between the upper joint and the torsion balance pivot was 10 mm.; that between the lower joint and the pivot was 8 mm. For a given joint angle (θ) the relation between pressure (P) and torque (C) is linear, that is $C = k_{\theta} P$, where k_{θ} decreases as θ increases. If C is expressed in dyne-cm. and P in dynes/cm.², k_{θ} has the dimension cm.³ and its value for the selected values of θ is shown in the figure.

Indirect determination

It can be shown that if the torque C is due to the internal fluid pressure, k_{θ} is numerically equal to $\Delta V/\Delta\theta$, where ΔV is the small change in the volume of the joint due to a small change of angle $\Delta\theta$. The relation between ΔV and $\Delta\theta$ is measured,

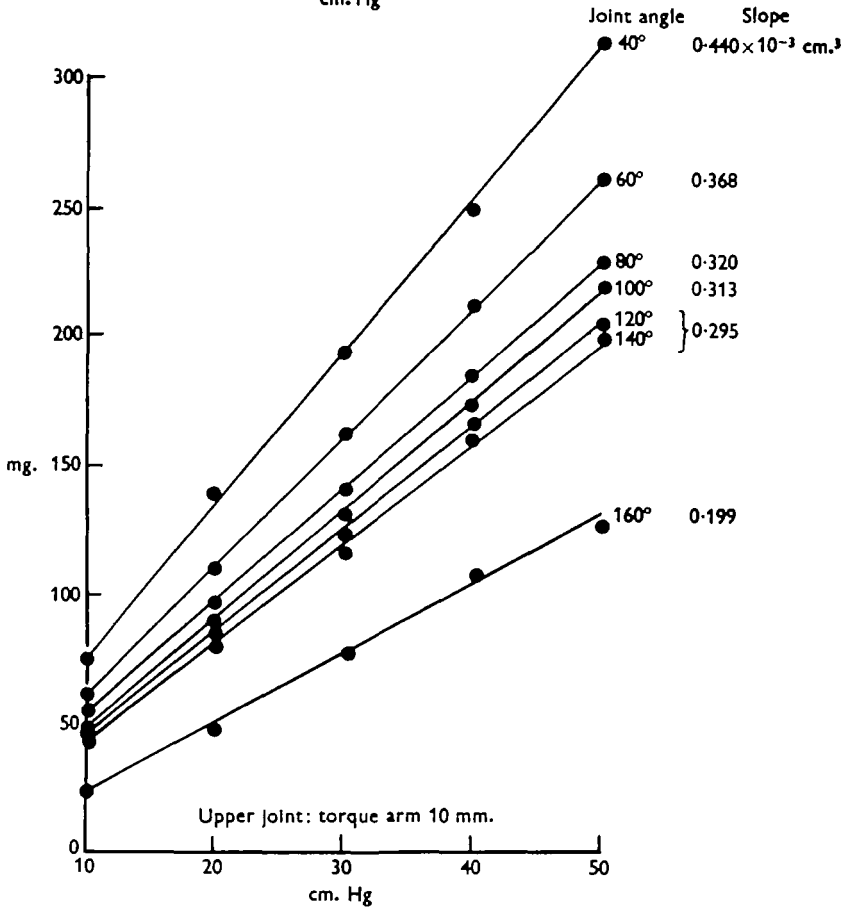
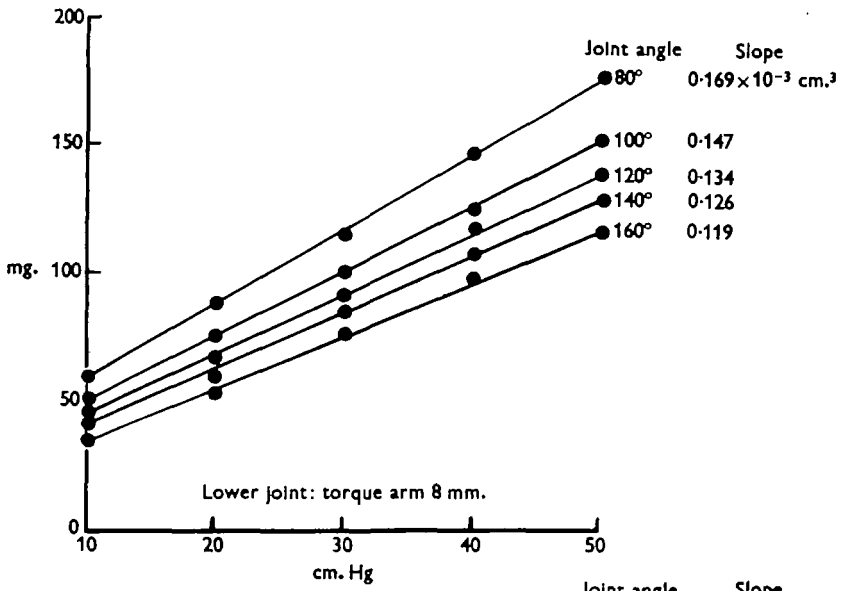


Fig. 5. Relation between the internal pressure and the torsion balance reading for different joint angles. The 'torque arm' is the distance between the joint and the arm of the balance (see Fig. 4).

using the apparatus shown in Fig. 6. At a given pressure the joint angle is increased in 20° stages from 40° to 160° and the movement of the bubble is measured with a travelling micrometer. A second series of readings is taken as the angle is decreased, and a mean for each angle is determined. In the event, the difference between the ascending and descending readings was negligible.

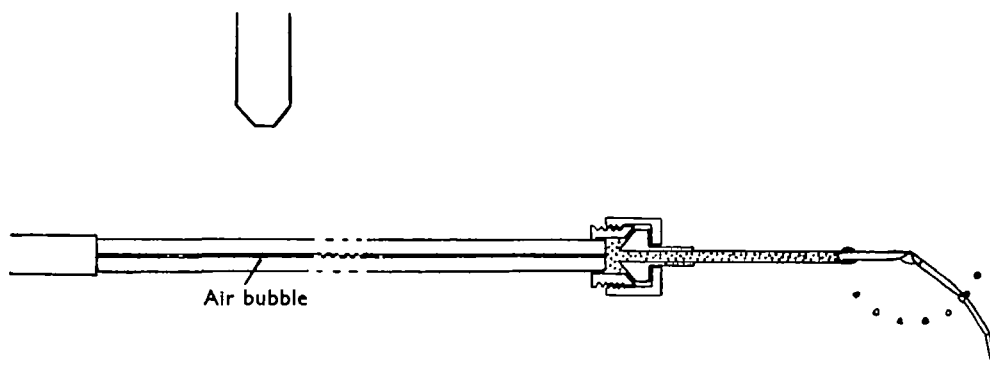


Fig. 6. Measurement of the relation between a change of joint angle and the consequent change in joint volume.

The results shown in Fig. 7 were obtained from the same leg as those of Fig. 5 and so $k_\theta (= C/P)$ can be directly compared with $\Delta V/\Delta\theta$:

Joint angle	40°	60°	80°	100°	120°	140°	160°
Upper joint $\left\{ \begin{array}{l} C/P \\ \Delta V/\Delta\theta \end{array} \right.$	0.44 —	0.37 0.31	0.32 0.29	0.31 0.27	0.30 0.26	0.29 —	0.20 mm. ³ — mm. ³ /radian
Lower joint $\left\{ \begin{array}{l} C/P \\ \Delta V/\Delta\theta \end{array} \right.$	— —	— 0.20	0.17 0.18	0.15 0.15	0.13 0.14	0.13 0.13	0.12 mm. ³ — mm. ³ /radian

The agreement between the direct and indirect determinations of k_θ is good, although there is a small consistent discrepancy in the measurements of the upper joint. In the next section the values for k_θ obtained by direct measurement are used.

FORCES DEVELOPED DURING EXTENSION

The extension torques developed at the hinge joints in normal walking are those producing a force at the foot (likely to be greatest in the fourth pair of legs which push forwards) together with those associated with accelerating and raising the distributed mass of the leg (likely to be greatest in the first pair of legs which straighten forwards). No attempt has been made to measure these torques. Instead, the leg of an intact living spider was loaded with additional mass in the form of a brass ring of 45 mg. and photographed by high-speed cinematography (Brown & Popple, 1955) while it was extending in a horizontal plane about the upper hinge joint. Analysis of the film provides the angular acceleration of the leg, from which the torque developed at the hinge joint can be determined. The pressure

needed to produce this torque can be calculated from the data given in the last section and can in turn be compared with the pressures which have actually been measured in living spiders.

This method of measuring the torque is only a rough one: no account can be taken of internal friction (including tension in the flexor muscles); and a frame interval of 6 msec. is not short enough to give an accurate measure of acceleration.

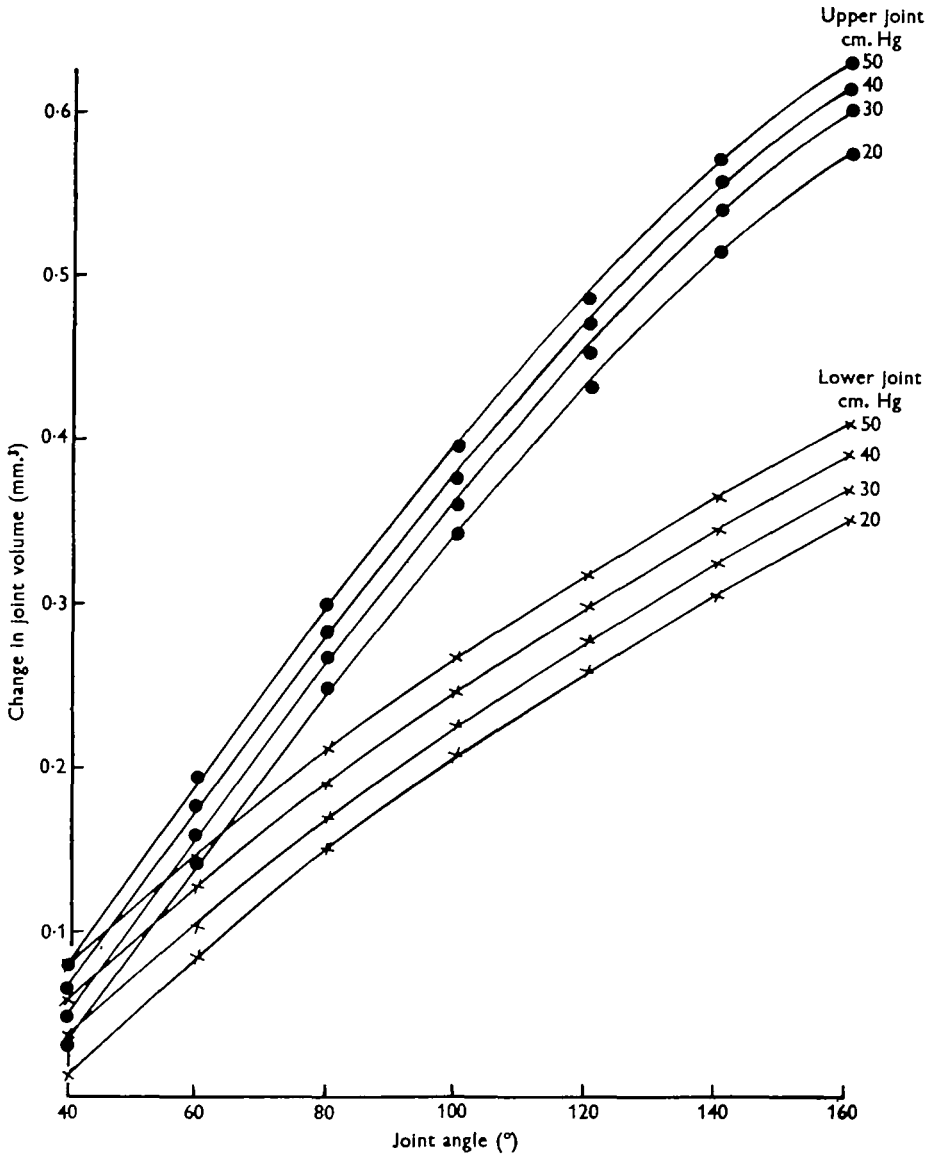


Fig. 7. Relation between changes in joint angle and changes in joint volume at different internal pressures.

From four sequences the following example is selected as involving the greatest acceleration which has been encountered:

t	0	6	12	18	msec.
Angular velocity (ω)	0	20.0	47.5	50.4	radian/sec.
Angular acceleration ($\dot{\omega}$)		3.3	4.6	0.47	$\times 10^3$ radian/sec. ²
Torque ($I\dot{\omega}$)		125	174	17.8	dyne-cm.
Pressure (C/k_{θ})		31	45	5	cm. Hg

In the other three sequences obtained (two different spiders) the maximum torques developed during a 6-msec. period, and the corresponding pressures, were: 130 dyne-cm. (35 cm. Hg); 77 dyne-cm. (18 cm. Hg); and 54 dyne-cm. (13 cm. Hg). It will be seen that the pressures required to produce these torques all lie within the range of pressures which the spiders have been shown to develop. The figures furthermore establish directly that the torques developed at the hinge joints can be considerably greater than are required merely to extend the leg when it is off the ground (cf. Manton, 1958*b*).

DISCUSSION

The hydraulic mechanism

Anatomy. In the spider, prosoma and abdomen are separated by a narrow pedicel (Fig. 8). The prosomal tergum and sternum are relatively rigid plates—the one convex, the other flatter—connected together by an unsclerotized lateral region. The legs are inserted into this lateral region and are without articulations

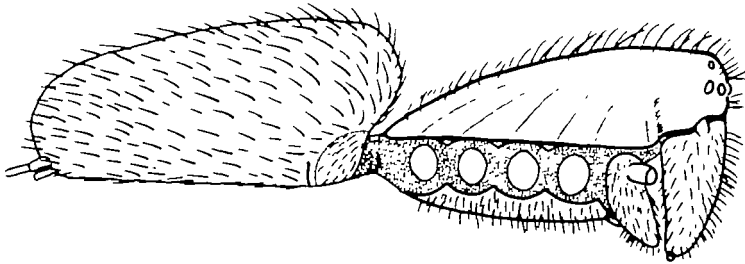


Fig. 8. *Tegenaria atrica* showing the flexible lateral region which intervenes between prosomal tergum and sternum.

with either tergum or sternum, which are therefore free to move apart or come together (see Fig. 8). According to Brown (1939) there are no tergo-sternal muscles, but dorso-ventral muscles run from the tergum to the endo-skeleton, the stomach and the proximal ends of the coxae of the legs.

The abdomen is relatively flexible and becomes wrinkled and apparently shrunken when an animal is short of food or water. Millot (1949) describes a thin subcuticular muscle layer; otherwise the abdominal musculature is scanty (Brown, 1939). The heart lies in the abdomen and a single large aorta runs through the pedicel into the prosoma where arteries distribute the blood peripherally.

Resting pressure. Under the conditions of our experiments the haemocoelic pressure in the legs of unstimulated spiders is about 5 cm. Hg and we suggest that the normal resting pressure is of approximately this value. Regarding the production and distribution of this pressure there are three possibilities:

(1) The pressure might be uniformly distributed throughout the prosoma and abdomen and due to muscle tension. This seems unlikely because the isolated abdomen is found to become grossly distended at such a pressure and yet its musculature appears inadequate to maintain the characteristic shape in life. It should be noted that if the prosoma and abdomen were at the same pressure no load would be imposed on the heart, whose systolic pressure need only be sufficient to overcome the peripheral resistance.

(2) The pressure might be limited to the prosoma, the abdomen being at atmospheric pressure. This accords with the observed lack of turgidity in the abdomen but demands that the systolic pressure of the heart should just exceed the prosomal pressure, thus developing considerably more pressure than is usual among arthropods (compare data given in Prosser (1950), Table 67; but note also Harris & Crofton (1957) on the nematode *Ascaris* in which the mean internal pressure is 7 cm. Hg).

There is a little evidence that the heart may in fact produce the required high pressure. The blood flow in a spider's leg can be seen by transmitted light if the leg is sealed into a flat-sided cell filled with a physiological solution (1 l. of spider Ringer is made up with: 144 c.c. M/15 KH_2PO_4 ; 144 c.c. M/15 Na_2HPO_4 ; 347 c.c. 0.54M NaCl; 5.56 c.c. 0.36M $\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$; 5.56 c.c. 0.36M $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$).

If the prosoma is now compressed dorso-ventrally the blood flow in the leg eventually stops. The haemocoelic pressure at which this occurs can be measured in the usual way by determining the external pressure which has to be applied to the leg in order just to collapse the articular membrane. The pressures thus measured will presumably represent the maximum which the heart can produce. Readings were as follows: 10.4, 10.6, 11.2 and 11.6 cm. Hg.

Clearly this needs further investigation, but so far as the available evidence goes, it suggests that the 'maintained pressure' of 5 cm. Hg occurs in the prosoma, but not the abdomen. This being the case it might be expected that some form of valve or sphincter would occur in the pedicel and would play an important part in regulating prosomal pressure.

(3) A third possibility should be mentioned: that the pressure is limited to the legs alone. This would still demand a high heart pressure, and would involve a sphincter at the base of the leg and suitable muscles in the leg, of which there are no signs.

Transient pressure. Pressures of up to 45 cm. Hg, maintained for a fraction of a second, have been measured on a stimulated spider. If two legs are separately sleeved and subjected to the same external pressure, the articular membranes are found to inflate and deflate simultaneously when the spider is stimulated. This suggests that the transient pressure arises in the prosoma rather than in the individual legs (where, as noted above, no muscles seem suitably disposed to produce

it) and it may well be due to the sudden activation of the prosomal muscles and slight dorso-ventral compression. This sudden rise of pressure would, of course, temporarily stop the prosomal circulation, and in this connexion it is interesting to note the well developed aortic valve in the pedicel (see, for example, Millot, 1949, fig. 419, based on the beautiful work of Schneider, 1892).

Dynamic considerations. By adding mass to the leg of a living spider and finding the acceleration during an extensor movement we have measured the torques which can be developed at a hinge joint. We have then calculated the internal pressure needed to develop these torques, using values for k_θ empirically determined. However, k_θ was measured under static conditions and it remains to be seen whether it can be applied under dynamic ones. Two considerations arise:

(1) When a hinge joint is extending fluid must flow into the joint thus setting up a pressure gradient in the leg so that the pressure in the joint will not be the same as the pressure in the prosoma. A rough application of Poisseuille's equation shows that this gradient may be insignificant. The maximum observed rate of extension of the upper hinge joint was about 50 radian/sec. at a joint angle of about 90° . This is equivalent to a volume change of 15 mm.³/sec. Taking the viscosity of the blood to be 0.05 dyne-sec./cm.² (as in human blood—no direct measurements are available), and the length of the upper part of the leg to be 1 cm., we get:

$$r^4 \Delta p = 0.002 \text{ dyne-cm.}^2,$$

where r = radius of duct and Δp = pressure difference between prosoma and upper hinge joint. Now as the channel is of indeterminate shape no precise value can be assigned to r ; but it can be seen that Δp is negligible provided that the equivalent duct is not less than 0.02 cm. radius, or two-fifths of the actual radius of the femur, which is not unreasonable. However, the matter needs further investigation.

(2) If the prosoma were very indistensible then the withdrawal of a small quantity of fluid would produce a significant fall in pressure. But in the section on anatomy we have pointed out that the prosoma is built in such a way that changes in volume can readily be produced.

Bleeding. It might be thought that, owing to the high pressures occurring in the spider, bleeding would be a serious hazard, and it is the case that spiders readily die from this cause. Perhaps the most frequent form of damage is the loss of a leg and here a special protective mechanism has been evolved (Parry, 1957). But minor damage to the prosoma need not be fatal; the withdrawal of blood together with the relaxation of the prosomal muscles would produce an immediate fall in pressure and the wound might heal in a few days. During this time the spider is not immobilized, but we have no reason to think that ordinary walking necessitates the high pressures which we have measured in uninjured animals, especially if the hind legs (the only ones whose propulsive stroke is an extension) contribute less force than usual.

SUMMARY

1. The blood pressure inside the leg of the house spider *Tegenaria atrica* has been measured. Maintained pressures of about 5 cm. Hg and transient pressures of up to 40 cm. Hg have been found.
2. The relation between the blood pressure in the leg and the extension torque at the hinge joints has been established.
3. Considerable torques can be developed at the hinge joints during extension, for example, when accelerating a mass fixed to the leg. The transient pressures found to arise in the leg are adequate to account for these torques.
4. The hydraulic mechanism is discussed. The available evidence suggests that the pressure found in the legs occurs also in the prosoma but not in the abdomen, in which case the maintained pressure must be due to the heart. This, however, requires further investigation.

We are greatly indebted to the Cambridge Instrument Company for the loan of a photo-electric transducer; and also to many friends who have supplied us with spiders. The spider Ringer was based on determinations of freezing-point depression and sodium and potassium concentration of *Tegenaria* blood made for one of us some years ago by Dr P. C. Croghan and not hitherto published.

REFERENCES

- BROWN, R. B. (1939). The musculature of *Agelena naevia*. *J. Morph.* **64**, 115-66.
- BROWN, R. H. J. & POPPLE, J. A. (1955). Multiple flash photography. *Med. Biol. Illustr.* **5**, 23-8.
- HARRIS, J. E. & CROFTON, H. D. (1957). Structure and function in the Nematodes. *J. Exp. Biol.* **34**, 116-30.
- KROGH, A. & WEIS-FOCH, T. (1951). Respiratory exchange of the desert locust. *J. Exp. Biol.* **28**, 344-57.
- MANTON, S. M. (1958*a*). Evolution of arthropodan locomotory mechanisms, Pt. 6. *J. Linn. Soc. (Zool.)*, **43**, 488-556.
- MANTON, S. M. (1958*b*). Hydrostatic pressure and leg extension in arthropods. *Ann. Mag. Nat. Hist. Series 13*, **1**, 161-82.
- MILLOT, J. (1949). Ordre des Aranéides, in Grassé, P.-P. (directeur): *Traité de Zoologie*, **6**. Paris: Masson.
- PARRY, D. A. (1957). Spider leg muscles and the autotomy mechanism. *Quart. J. Micr. Sci.* **98**, 331-40.
- PROSSER, C. L. (ed.) (1950). *Comparative Animal Physiology*. Philadelphia: Saunders.
- SCHNEIDER, A. (1892). Mélanges arachnologiques. *Tablettes Zoologiques*, **2**, 135-98.
- SNODGRASS, R. E. (1952). *A Textbook of Arthropod Anatomy*. New York: Comstock.