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The structure of the myosin elements in vertebrate smooth muscles

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[Plates 15 and 16]

Low-angle X-ray diffraction experiments with living relaxed and contracting guinea-pig taenia coli muscles have led to the discovery of a meridional reflexion at about 14.3 nm whose presence establishes the existence of a regular assembly of myosin molecules in the form of filamentous elements (Lowy, Poulsen & Vibert 1970). From measurements of the shape of the 14.3 nm reflexion it is possible to deduce that in the axial direction the diffracting elements must be at least 500 nm long, while in a direction perpendicular to the fibre axis these elements must diffract coherently over a lateral distance of at least 60 nm. The latter feature can be straightforwardly interpreted in terms of the lateral register of the cross bridges across the faces of the ribbon-like myosin elements seen in the electron microscope by Lowy & Small (1970), Small, Lowy & Squire (1971) and Small & Squire (1972).

The intensity of the 14.3 nm reflexion varies in patterns from muscles in various relaxed and contracted states. Nevertheless, we have detected no significant changes in the shape of this reflexion when the muscle passes from a resting to a contracted state, when it is loaded with weights from 1 to 10 g, or when it is incubated at different temperatures in Ringer solutions made hypertonic to various extents by the addition of sucrose. These observations suggest that the structure of the myosin elements responsible for the 14.3 nm reflexion persists unchanged regardless of the states of the muscle investigated. In our view this can be interpreted to indicate that the ribbons are present in relaxed muscles and interact with actin during contraction.

Introduction

During recent years rapid progress has been made in structural studies of vertebrate smooth muscles. This is best illustrated by viewing the situation in the light of our knowledge of striated muscles. A comprehensive account of the latter is given in Huxley's (1971) Croonian lecture from which the following is taken.

In striated muscles, actin and myosin are present in separate, overlapping filaments. The myosin molecules are so organized that cross-bridges (containing the molecule's ATPase and actin binding properties) project from the surface of the filament with an axial periodicity of about 14.3 nm. In the respective filaments, both the actin and myosin molecules are arranged with a definite structural polarity. Thus the actin molecules point in the same direction in each of the two strands of the double helical structure but the filaments themselves are attached to the Z line in such a way that the molecules face in opposite directions on either side of the Z line. As regards myosin, the cross-bridges face in opposite directions on either side of the mid-point of the filament. Hence both kinds of molecules are so placed that their active sites always have the same orientation relative to one another. These several features provide the main structural basis for a sliding filament mechanism where the actin and myosin filaments in an actively shortening muscle slide past one another while their lengths do not change appreciably.

X-ray diffraction studies with intact striated muscles show that the axial periodicities due to the arrangement of the actin and myosin molecules remain practically constant during contraction. However, the intensity of the 14.3 nm myosin reflexion decreases, and this can be interpreted in terms of a movement of cross-bridges which results in a decrease in the degree of axial order of these structures. It is also known that during contraction only a relatively small number of cross-bridges are attached to actin at any given time.

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With respect to most of the features outlined above the situation in vertebrate smooth muscles has been shown to be essentially similar (Lowy *et al.* 1970; Lowy & Small 1970; Small *et al.* 1971; Small & Squire 1972; Vibert, Haselgrove, Lowy & Poulsen 1972). The outstanding points which remain to be clarified concern the way the myosin molecules are organized into filamentous structures, and how the actin filaments are arranged with the appropriate polarity. This paper describes and discusses what is known at present about the structure of the myosin filaments, particularly from low-angle X-ray diffraction studies of the guinea-pig's taenia coli muscle. The methods we have used are given in the papers cited above and some further details will be found in the legends to figures 1 and 2.

Results and interpretations

It is well known that the taenia coli muscle of the guinea-pig (t.c.g.p.) shows myogenic spontaneous activity when isolated and maintained in its physiological state, that is in an isotonic Ringer solution at 37 °C. This activity is manifested mechanically under isometric conditions either as rhythmic responses occurring about 1/min, or as irregular fluctuations of a tonic tension level. It follows that in order to study the t.c.g.p. in a resting state its spontaneous activity has somehow to be suppressed. For X-ray experiments there is also the requirement that this suppression should be effective for the time needed to obtain a pattern, which is usually between 2 and 6 h.

We found that lowering the temperature provided the best experimental condition for the study of resting muscles in that this treatment is in most cases completely reversible. However, we also found great variations in the behaviour of different muscles: some showed signs of spontaneous activity at temperatures as low as 10 °C, while some were completely inactivated already at 15 °C. Accepting this variability, we attempted to study resting muscles at temperatures between 5 and 15 °C, and contracting muscles between 15 and 37 °C.

As regards the X-ray pattern, we shall here be concerned mainly with the meridional reflexion at about 14.3 nm (figure 1) whose presence establishes the existence of a regular assembly of myosin molecules in the form of filamentous elements (Lowy *et al.* 1970). We found that this reflexion varies in *intensity* depending on the state of the muscle: it is strongest in resting and weakest in contracting muscles (figure 2). Other things being equal, stretching the muscle tends to stimulate contractile activity. Low temperatures and/or hypertonic solutions produce the opposite effect (figures 1 and 2). Arguing by analogy from observations on frog skeletal muscles (Huxley & Brown 1967) it may be assumed that most of the intensity of the 14.3 nm reflexion comes from the myosin cross-bridges. On this assumption the results with the t.c.g.p. indicate that low temperatures and hypertonic solutions suppress cross-bridge movement, but they give no clue as to the mechanism(s) involved.

Whilst the intensity of the 14.3 nm myosin reflexion decreases on activation, the reverse is true of the actin layer lines (Vibert *et al.* 1972). This provides an additional diagnostic feature for the evaluation of the muscle's state. As regards the equatorial reflexion at about 12 nm (figure 1) which is due to the lattice arrangement of the actin filaments (cf. Elliott & Lowy 1968), no consistent changes have so far been detected in its intensity, shape or spacing during contraction.

From measurements of the *shape* of the 14.3 nm myosin reflexion it is possible to deduce that in the axial direction the diffracting elements must be at least 0.5 μm long, while in a direction perpendicular to the fibre axis these elements must diffract coherently over a lateral distance

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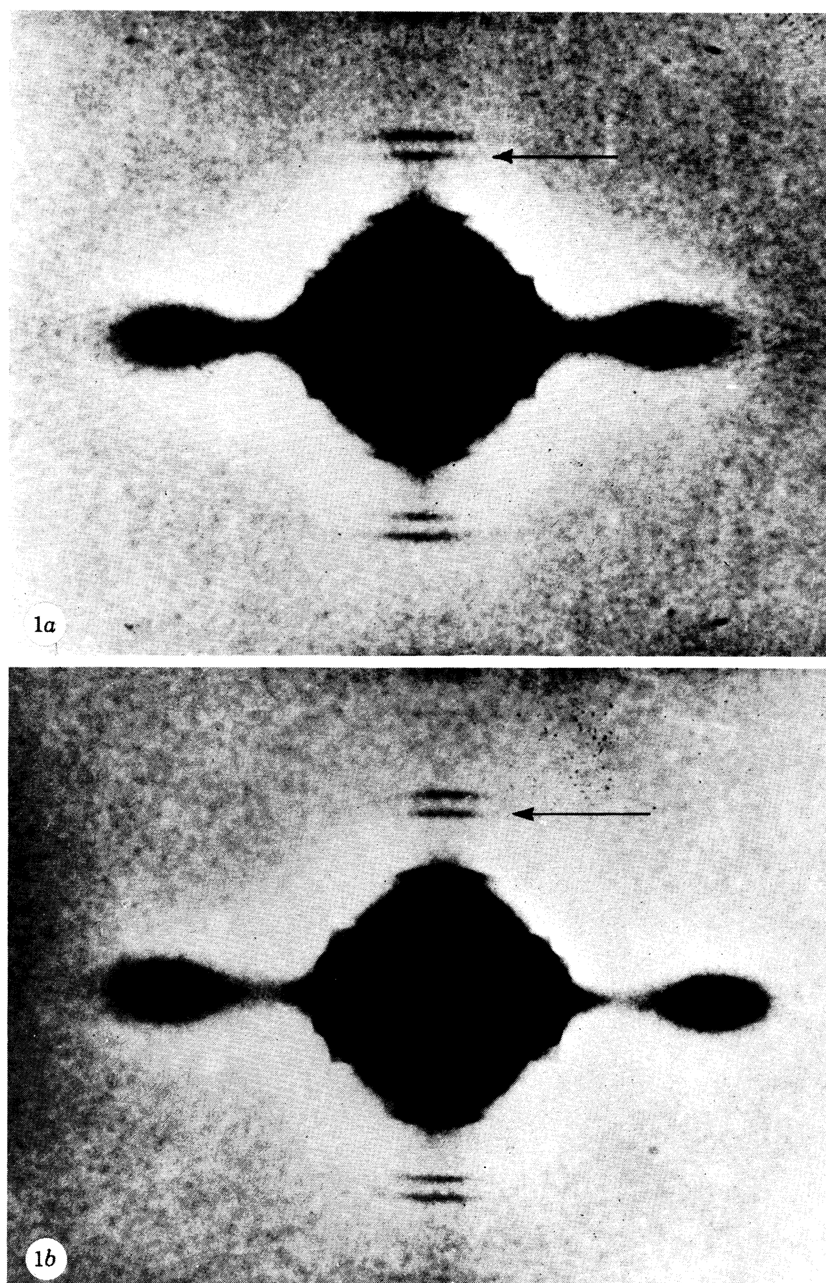

FIGURE 1. Low-angle X-ray diffraction patterns from the taenia coli muscle of the guinea-pig mounted isometrically. The patterns were recorded on a camera of length 36 cm. Fibre axis vertical. Exposure time 5 and 3 h for (*a*) and (*b*) respectively. (*a*) Muscle in resting state at 9 °C in an isotonic Ringer solution of composition given by Bülbring & Golenhofen (1967). Average resting tension 2 gf. (*b*) Muscle in resting state at 35 °C in a calcium-free Ringer solution containing 2 mmol/l EGTA and sucrose to give a tonicity of 480 milliosmolar. Average resting tension 2 gf. Note that in both patterns the intensity of the 14.3 nm reflexion from myosin (arrow) is about the same as that of the 13 nm collagen reflexion next to it. (The much stronger reflexion nearest to the central scatter is the 26 nm reflexion due to collagen.) Note also that the 14.3 nm reflexion has much the same shape in the two patterns, and that the spacing of the equatorial reflexion decreases from about 11.5 nm in isotonic Ringer to about 9.5 nm in hypertonic Ringer. The patterns in figures 1 and 3 are reproduced by a technique described in Vibert *et al.* (1972).

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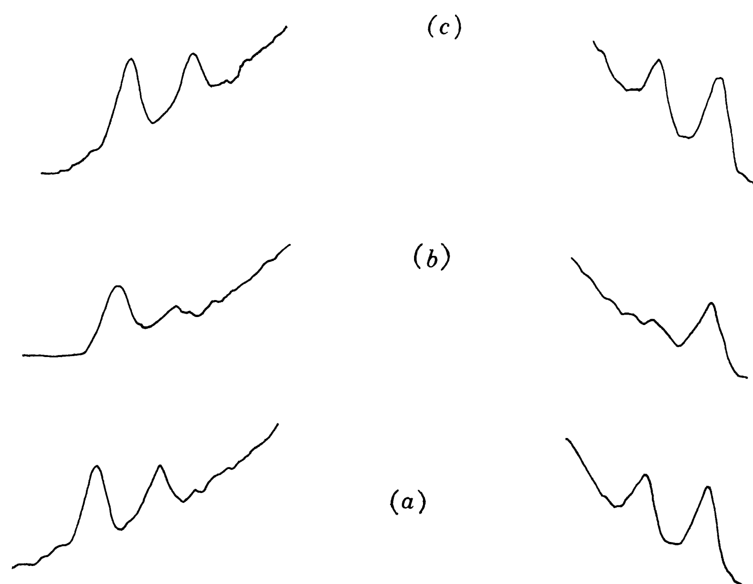

FIGURE 2. Densitometer traces along meridian of X-ray patterns from taenia coli muscles mounted isometrically. The inner peaks correspond to the 14.3 nm reflexion from myosin, the outer peaks to the 5th order reflexion from collagen at 13 nm. Muscle in isotonic Ringer solution: (*a*) at 9 °C, muscle holding an average resting tension of 1 gf; (*b*) at 32 °C, muscle producing a peak *active* tension of 8 gf; and (*c*) at 10 °C, muscle holding an average resting tension of 1 gf.

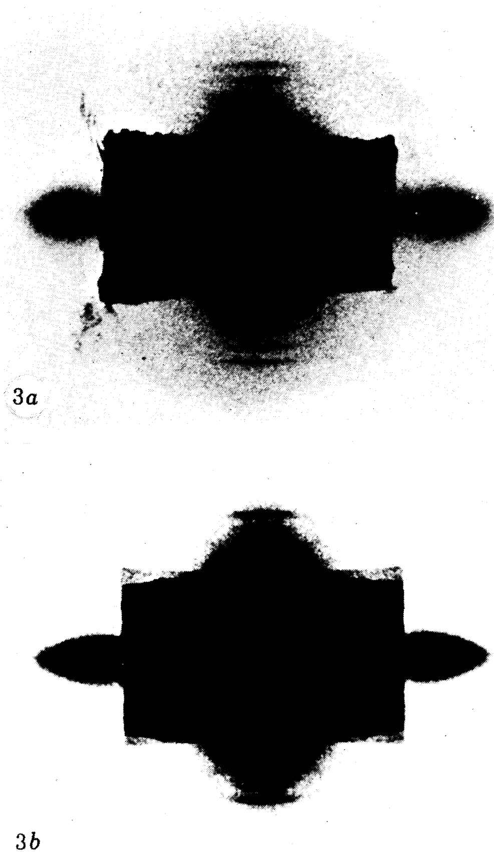

FIGURE 3. Low-angle X-ray diffraction patterns from which the traces shown in figure 2 are taken: (*a*) resting muscle at 9 °C; (*b*) contracting muscle at 32 °C. Note that in spite of a clear change in intensity, the shape of the 14.3 nm reflexion is much the same in the two patterns.

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at least 60 nm in at least one dimension. Previously (results quoted in Lowy & Small 1970), we set the value of this minimum lateral dimension at about 30 nm on the basis of the close similarity of the equatorial breadths of the 14.3 nm reflexion and those meridional reflexions due to collagen, fibrils of the latter showing a diameter of about 30 nm in sectioned material of the t.c.g.p. However, further measurements indicate that the breadth of the 14.3 nm reflexion and of the collagen reflexions correspond to a diffracting unit of at least 60 nm in t.c.g.p. muscles either alive or glutaraldehyde fixed. Following dehydration, and embedding measurements of the collagen reflexions show that the collagen fibrils have shrunk to a value nearer 30 nm. Under these conditions the 14.3 nm reflexion is rather weak so that accurate measurement is no longer possible. Nevertheless, on the information now available, the results from living muscles leave little doubt that one of the lateral dimensions of the myosin diffracting unit is at least 60 nm.

In our experiments with muscles maintained at various temperatures no changes can be detected in either the equatorial or meridional breadths of the 14.3 nm reflexion. It would appear therefore that the structure of the myosin elements giving rise to the 14.3 nm reflexion persists unchanged regardless of the state of activity of the muscle. The same can be deduced from experiments in which other means were used to change the state of the muscle. Thus the shape of the 14.3 nm reflexion remains unchanged when the muscle is loaded with weights from 1 to 10 g; or when incubated at different temperatures in Ringer solutions made hypertonic to various extents (up to 500 milliosmolar) by the addition of sucrose.

The X-ray results demonstrate that in the t.c.g.p. we are dealing with myosin elements at least 0.5 μm long on which structures with an axial repeat of 14.3 nm are in lateral register over a distance of at least 60 nm. It has been possible to visualize such very long elements in the electron microscope (Lowy & Small 1970), and to identify them as the myosin elements by the presence on their surface of cross-bridges which show an axial periodicity of about 14 nm (Small *et al.* 1971). Furthermore, these myosin elements were found to be ribbon shaped, about 10 nm thick, and with a lateral width that varies from 20 to 110 nm (Lowy & Small 1970). The cross-bridges are located on the two ribbon faces; they are organized laterally (with a separation of about 10 nm) in rows across each ribbon face, and the rows are spaced axially at a constant period of about 14 nm (Small *et al.* 1971).

The lateral register of the cross-bridges across the ribbon faces would readily account for the 60 nm equatorial breadth of the 14.3 nm reflexion. The observation that this feature of the X-ray pattern persists regardless of the state of the muscle strongly suggests that the ribbons represent the normal form of the myosin elements. We are aware that this interpretation is subject to a qualification which concerns the origin of the lateral register of the 14.3 nm periodicity. This will be dealt with in the course of the following discussion.

Discussion

The ribbon form of the myosin elements described above is not accepted by Rice, McManus, Devine & Somlyo (1971); Somlyo, Somlyo, Devine & Rice (1971) and Somlyo, Devine & Somlyo (1971) who experimented mostly with the portal-anterior mesenteric vein of the rabbit. These workers claim that myosin is normally present in large round filaments (diameter about 18 nm) with irregular outlines, and that these filaments are organized in a quasi-regular lattice (nearest neighbour spacing about 70 nm). They consider that the latter feature might account for the equatorial breadth of the 14.3 nm reflexion. They believe that the ribbons are artefacts

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resulting from the aggregation of the round filaments due to two conditions, both of which are said to reduce the separation between the round filaments. These conditions are excessive stretching of the muscle and treatment with hypertonic solutions.

As in the case of another kind of smooth muscle, namely the anterior byssus retractor of *Mytilus* (a.b.r.m.) (Elliott & Lowy 1961), we found in our X-ray experiments with the t.c.g.p. that stretching does not affect the separation of the actin filaments. There is therefore no reason to believe that the spacing between the myosin filaments will be changed under these conditions. The distance between the actin filaments is indeed decreased in hypertonic solutions in both the t.c.g.p. (Elliott & Lowy 1968) and the a.b.r.m. (J. Lowy & P. J. Vibert, unpublished results). But if this were to lead to the aggregation of myosin elements in the t.c.g.p. one might expect that a mixture of round filaments and ribbons would be present under conditions of varying hypertonicity and that such a state of affairs could have an appreciable effect on the shape of the 14.3 nm reflexion. However, our experiments with t.c.g.p. muscles in Ringer solutions of varying hypertonicity showed no signs of a shape change in that reflexion. It may also be pointed out here that ribbons were seen in the original electron microscope studies (Lowy &

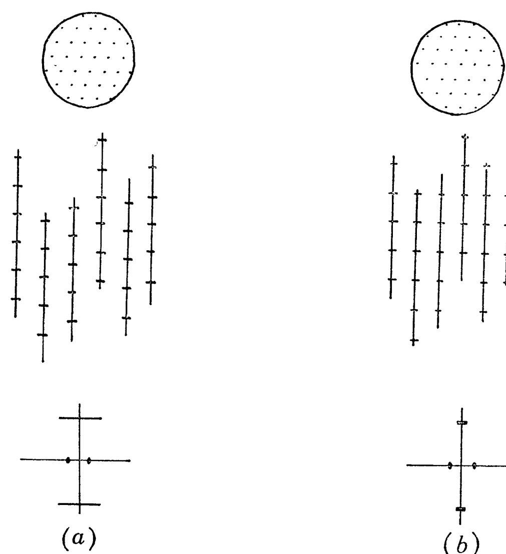

FIGURE 4. Diagram showing that the equatorial breadth of a meridional reflexion depends on the lateral extent of the region in which the elements whose periodic arrangement gives rise to the reflexion are in register. In both cases illustrated, filamentous elements with an axial periodicity are so arranged that, when projected on to a plane perpendicular to the fibre axis, they form a two-dimensional hexagonal array. This gives rise to one or more equatorial reflexions in the diffraction pattern. In (*a*) there is no lateral register between adjacent filaments with respect to their axial periodicity, i.e. random axial displacements of filaments exist: the meridional reflexion(s) arising from the axial periodicity has a breadth corresponding to the transform of a single filament. In (*b*) adjacent filaments are so alined that, at least over a limited region, a three-dimensional array is formed. The meridional reflexion(s) now has a narrower breadth corresponding to the lateral extent of this three-dimensional array. Note that this effect on the breadth of the reflexion is independent of the nature of the two-dimensional array formed by projecting the structure down the fibre axis on to a horizontal plane. Thus an array characterized by short-range order, or by a purely random distribution, could equally well be associated with a meridional reflexion of small breadth. The accuracy with which the filaments must be in register can be estimated from a knowledge of the number of orders of the axial repeat that show the narrow breadth corresponding to the three-dimensional array. In the case of the taenia coli myosin pattern with its axial repeat $C = 14.3$ nm, both the 14.3 nm and the 7.15 nm (i.e. $l = 1$ and $l = 2$) meridional reflexions show the narrow breadth. The maximum axial deviation Δ from the ideal position for each filament is given approximately by $C/\Delta = 4\,l'$ (Vainshtein 1966), where l' is the layer line order at which the three-dimensional array ceases to influence the breadth of the reflexions. Thus setting $l' \geqslant 3$, $C = 14.3$ nm, we obtain $\Delta \leqslant \pm 1.2$ nm.

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Small 1970) when the t.c.g.p. was maintained in *isotonic* Ringer solutions before fixation, and that further electron microscope work has demonstrated that the presence of ribbons does not depend on whether the muscle has been loaded with weights of 1 or 10 g before fixation (Small & Squire 1972).

These considerations can be interpreted to indicate that stretching or hypertonic solutions do not lead to an aggregation of myosin elements into ribbons. There remains the question of the possible significance of a lattice arrangement of the myosin elements. This is dealt with in figure 4 which demonstrates that the arrangement of the myosin elements in a regular lattice has no effect on the equatorial breadth of the 14.3 nm reflexion. This is determined solely by the fact that the structures responsible for the 14.3 nm periodicity (i.e. the cross-bridges) are in register (to within about 2.5 nm axially) over a distance of about 60 nm laterally. It is not easy to envisage such a situation in the case of the round filaments without any clear evidence for a connecting structure equivalent to the M line present in certain striated muscles. However, if it turns out that even in the absence of such a structure the required degree of register between round filaments is somehow maintained, then the X-ray results by themselves cannot provide conclusive evidence for or against the existence of the ribbons. It might be noted here that during the assumed aggregation of round filaments into ribbons an M line structure would be compressed. This could upset the lateral register of the cross bridges and hence produce an effect on the shape of the 14.3 nm reflexion.

Further consideration of the pre-fixation conditions used by the two groups of investigators reveals the following situation. Rice *et al.* (1971) and Somlyo *et al.* (1971) were able to see round filaments regardless of whether the muscles were spontaneously active or relaxed, that is, respectively, in muscles incubated before fixation at room temperature in isotonic Ringer solutions, or in calcium-free Ringer solutions containing procaine. Under these conditions Small & Squire (1972) did not succeed in preserving adequately the structure of the myosin elements either in the form of round filaments or ribbons. Ribbons were consistently seen in muscles relaxed in isotonic Ringer solutions at 4 °C (Lowy & Small 1970).

Leaving aside the discrepancy between the results of Rice *et al.* (1971) and Somlyo *et al.* (1971), and those obtained by Small & Squire (1972) which cannot at present be resolved, one is led to consider the possibility that the ribbons could form on cooling. But our X-ray results indicate that this is not likely. As was argued in the case of the effect of hypertonic solutions, one might have expected that under conditions of varying temperatures a mixture of ribbons and round filaments would be present, and that this could affect the shape of the 14.3 nm reflexion. We have seen no sign of a shape change in that reflexion in our experiments where muscles were maintained in isotonic Ringer solutions at temperatures varying from 0 to 37 °C. However, the intensity of the 14.3 nm reflexion increases markedly at the lower temperatures. We therefore suggest that the ribbons are not formed on cooling but are seen at low temperatures because this somehow allows the myosin ribbons to be adequately preserved by chemical fixation. Conceivably, under these conditions the spontaneous cycling of cross-bridges is effectively suppressed.

On the other hand, muscles in isotonic Ringer solutions at room temperature are active, that is the cross-bridges cycle spontaneously as evidenced by the fact that the 14.3 nm reflexion is very weak. From the electron microscope work it would appear that under these conditions the myosin ribbons are not adequately preserved by the chemical fixation procedures used hitherto.

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Our view is that one of the main reasons why the ribbon form of the myosin elements could be studied in a relatively intact state was because low temperatures and hypertonic solutions were found to effectively suppress cross-bridge movement. In fact cross-bridge order could be better preserved than in frog or rabbit skeletal muscles, and in the best t.c.g.p. preparations (Small *et al.* 1971; Small & Squire 1972) cross-bridge order is almost as good as in insect flight muscles (cf. Reedy 1968). This made it possible to demonstrate that in the t.c.g.p. the cross-bridges are arranged on a two-dimensional lattice, as well as to obtain good evidence that they face in opposite directions on opposite ribbon faces (Small *et al.* 1971; Small & Squire 1972). These structural findings provide very powerful support for the proposal of a sliding filament mechanism where the actin filaments move in opposite directions along opposite ribbon face (Lowy & Small 1970). Given this particular kind of sliding system, it becomes all the more important to understand how the actin filaments are arranged with the appropriate polarity. One way of investigating this in sectioned material would be to label the actin filaments with heavy meromyosin. The results from such experiments could also contribute significantly toward the final solution of the problem concerning the form of the myosin elements.

The difficulties involved in obtaining direct X-ray evidence relevant to the myosin problem in vertebrate smooth muscles will have been obvious throughout this discussion. In that connexion one might perhaps emphasize the point that so far only one reflexion has been available for study. After the discovery of the ribbons there was at first some hope that the lateral separation of cross-bridges in the rows across the ribbon faces would give some diffraction. But we have seen no signs of this in living muscles. We are now exploring the situation in rigorized material where it is at least conceivable that the order of the cross-bridges might be improved by their attachment to actin. Experiments with iodoacetic acid indicate that in the t.c.g.p. a mechanical condition of rigor can exist which resembles that found in vertebrate skeletal muscles (Lowy & Mulvany 1972).

We thank E. B. Neergaard for introducing us to the technique used for reproduction of the X-ray patterns, and P. Boldsen and Mrs I. Lunde for carrying out the photographic work involved. We thank also Miss K. Eskesen, Mrs L. Nychel, Mr F. Marquard and Mr J. Pedersen for excellent technical assistance. This work was supported by grants from Statens Naturvidenskabelige Forskingsråd and Statens Laegevidenskabelige Forskningsråd.

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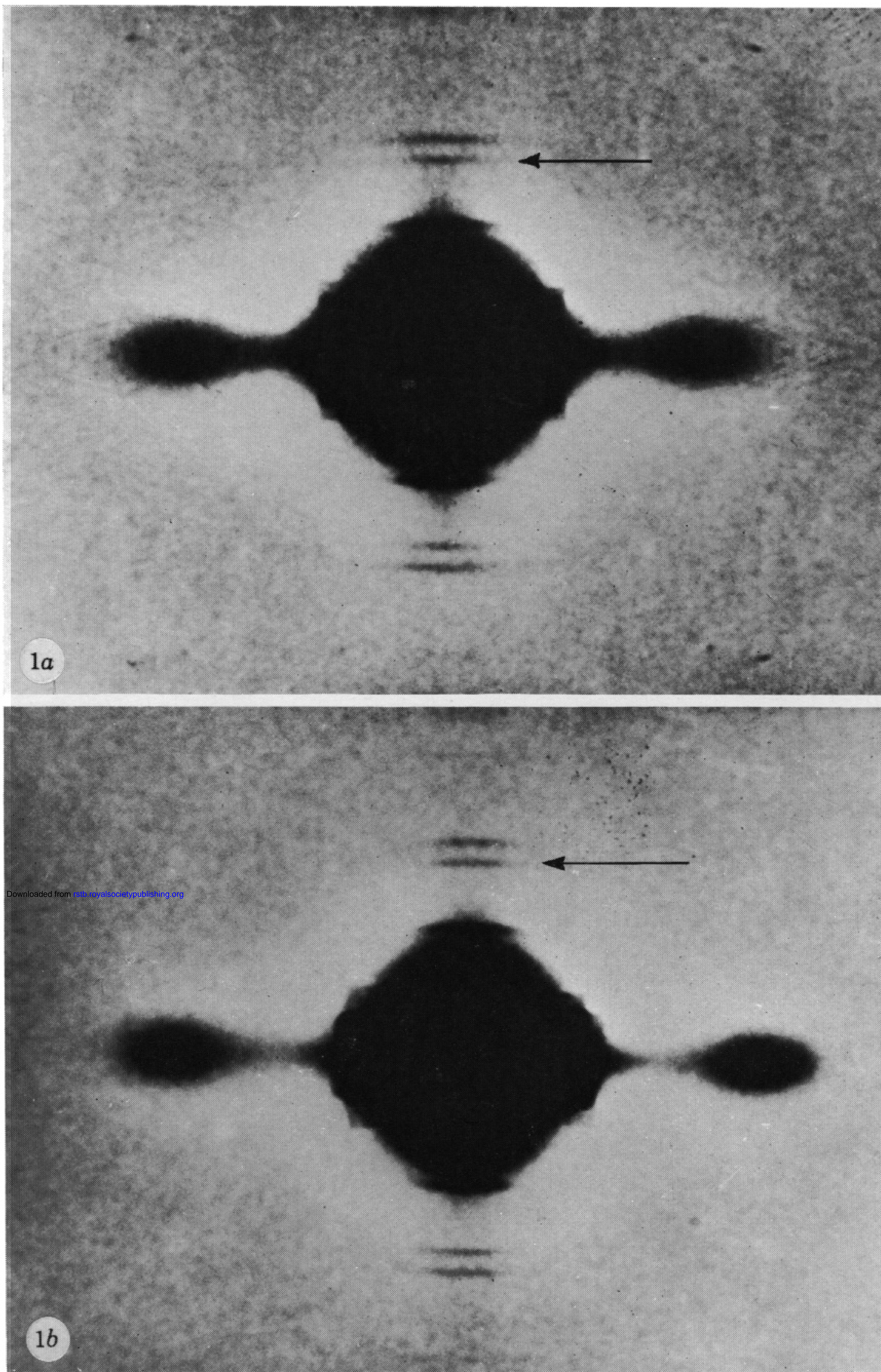

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FIGURE 1. Low-angle X-ray diffraction patterns from the taenia coli muscle of the guinea-pig mounted isometrically. The patterns were recorded on a camera of length 36 cm. Fibre axis vertical. Exposure time 5 and 3 h for (*a*) and (*b*) respectively. (*a*) Muscle in resting state at 9 °C in an isotonic Ringer solution of composition given by Bülbring & Golenhofen (1967). Average resting tension 2 gf. (*b*) Muscle in resting state at 35 °C in a calcium-free Ringer solution containing 2 mmol/l EGTA and sucrose to give a tonicity of 480 milliosmolar. Average resting tension 2 gf. Note that in both patterns the intensity of the 14.3 nm reflexion from myosin (arrow) is about the same as that of the 13 nm collagen reflexion next to it. (The much stronger reflexion nearest to the central scatter is the 26 nm reflexion due to collagen.) Note also that the 14.3 nm reflexion has much the same shape in the two patterns, and that the spacing of the equatorial reflexion decreases from about 11.5 nm in isotonic Ringer to about 9.5 nm in hypertonic Ringer. The patterns in figures 1 and 3 are reproduced by a technique described in Vibert *et al.* (1972).

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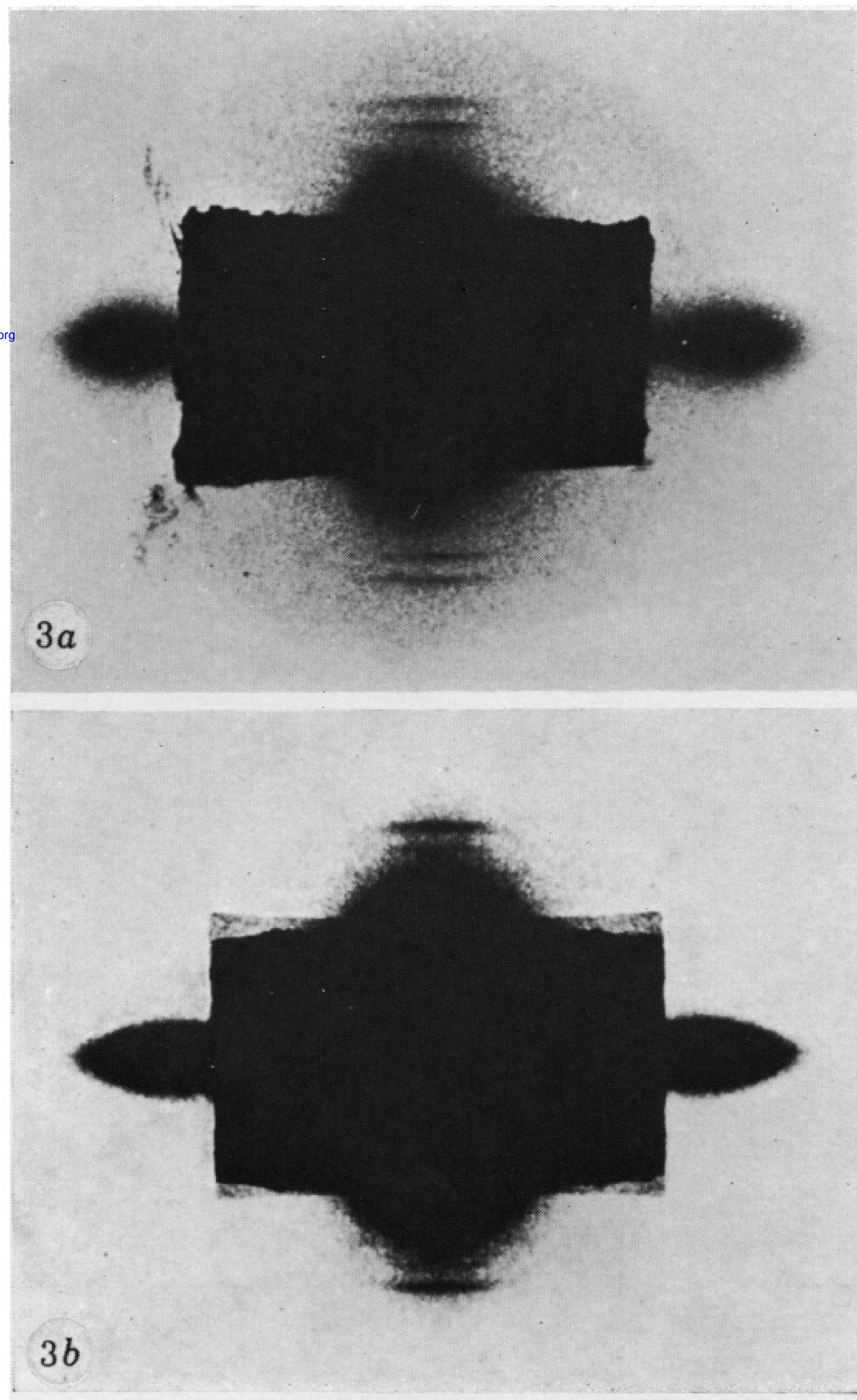

FIGURE 3. Low-angle X-ray diffraction patterns from which the traces shown in figure 2 are taken: (*a*) resting muscle at 9 °C; (*b*) contracting muscle at 32 °C. Note that in spite of a clear change in intensity, the shape of the 14.3 nm reflexion is much the same in the two patterns.

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