A STUDY OF MYOFIBRIL SARCOMERE STRUCTURE DURING CONTRACTION

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ABSTRACT

In the present investigation of cross-striated muscle fibers of axolotl, we succeeded in observing in one field of vision of the electron microscope all the stages of myofibril contraction. This allowed us to avoid errors in establishing the sequence of individual contraction stages. Our studies reveal a new contraction stage which appears at the shortening of the sarcomere below 74 per cent of the “resting length” but prior to the formation of typical “maximally shortened” sarcomeres, characterized by strong “contraction bands.” At this stage, in the center of the sarcomere, at either side of the M line, a “secondary anisotropic” band arises which widens with further sarcomere contraction. At either side of this band, at the place of the former (“primary”) anisotropic band, a “secondary isotropic” band is formed. A scheme of successive stages of contraction of the sarcomere is presented. The mechanisms of contraction for the first stage (from 100 to 79 per cent of the “resting length”) and for the last stage (from 74 to 58 per cent of the “resting length”) seem to be different. While the sliding of myofilaments with respect to one another can be assumed for the first stage, it is the spiralization of these structures which is the most likely explanation for the last stage. (An Abstract in German also appears at the end of this article.)

INTRODUCTION

The process of contraction of muscle tissue is one of the most interesting riddles in living Nature. Despite prolonged, intensive investigations of this phenomenon by a large group of physiologists, biochemists, biophysicists, and morphologists, the nature of this process is only vaguely understood at present.

Since the time of Merkel (12) and Engelmann (2) the contraction of striated muscle has been related to changes in the size and structure of sarcomeres, and these changes have often been described in detail in the literature. Changes in the sarcomere fine structure during the process of muscle fiber contraction have also been described (1, 7, 8, 10, 14, 19, and many others). Several hypothetical schemes of muscle contraction have been set forth (7, 8, 10, 20). The common feature of almost all these hypotheses (e.g. of the Hodge and Huxley groups) is that they are based on the widely accepted scheme of changes in the sarcomere structure during the process of isotonic contraction. This scheme can be expressed in three main stages: first, shortening of the isotropic and H bands; second, general decrease in density of the sarcomere; third, “disappearance” of all bands and the development of “contraction bands” in the region of the Z line. It is based on data from phase contrast, polarized light, and electron microscopy obtained on both living and fixed objects.
The most objective data on living processes can certainly be obtained from studying their dynamics in living objects. The light microscope, however, because of its low resolution power, cannot provide detailed information on the changes in the myofibril fine structure during the process of contraction. Electron microscopy, while revealing the ultrafine structure of individual details of the muscle fiber, has its own disadvantages: the entire work must be carried out on fixed objects, and the size of the object that can be examined is limited by a relatively small field of vision and the small area of ultrathin sections (of the order of 1 mm², and often much smaller). A comparison of the data obtained on living objects (light microscopy) with those of electron microscopy allows us to conclude that most of the pictures of myofibril contraction obtained with the electron microscope reflect the living state of the tissue more or less adequately. In the study of the dynamics of such a complicated process as the contraction of muscle tissue, it is the second disadvantage that is the greatest hindrance: the restricted field of vision. Any part of the tissue—the sarcomeres in this case—is well known to be heterogeneous with respect to the size of its individual structures (18, and others). In addition, if the images of individual contraction stages are taken from different sections, one is not absolutely sure that all these sections have undergone the same treatment while being prepared (compression during cutting and subsequent straightening, etc.). Thus, the data obtained from different preparations are comparable only to a very limited degree.

When studying changes in sarcomere structure during contraction, the investigator, in arranging the pictures obtained from different preparations in a certain sequence, cannot be absolutely sure of the correctness of the position assigned the various stages in this sequence. In order to set up a scheme that would reflect the sequence correctly, it is important to see the whole series of changes in one and the same preparation and in the same field of vision. Usually, however, one fails to see all the stages (from a non-contracted sarcomere to a strong contraction with the development of "contraction bands") in one field of vision, since large areas of the given muscle fiber (if not the whole fiber) are at the same phase of contraction.

In the present investigation we succeeded in obtaining all the stages of sarcomere contraction in a relatively small area of one and the same muscle fiber. Excitation was achieved by pricking the fiber with a thin entomological needle; this action produced a local injury in the muscle fiber and caused local myofibril contraction. Myofibrils located farther away from the excitation site turned out to be in a less contracted state than those located nearer to this site, and vice versa. Between these extremes there were myofibrils which showed the whole sequence of intermediate stages of contraction. There are reasons for believing that the unusual patterns of contraction observed are not a result of pathological changes produced by the application of such a relatively strong excitation as pricking the muscle fiber, since even the extreme stages of contraction (light sarcomeres, limited by "contraction bands") met with in the areas near the excitation site are described in the literature (9) as reversible physiological states of contraction. A description of the regions of the muscle fiber located still nearer to the excitation site and therefore exposed to an irreversible change is beyond the scope of the present communication and will be presented elsewhere.

**MATERIAL AND METHODS**

Experiments were carried out on the flexor tibiae primordialis muscle of the axolotl. The excitation was achieved in a spinal animal by pricking the muscle with a thin entomological needle, and immediately after excitation the tissue was fixed in buffered 1 per cent OsO₄ solution. Further treatment of the material was as described earlier (4). Sections were cut on a Sitte ultramicrotome of the Reichert firm (C. Reichert Optische Werke, Antriegesellschaft, Wien) and most of the sections were stained with lead hydroxide by the Watson method (22). The preparations were examined in the electron microscope UEM-100 at an accelerating voltage of 60 kv.

**OBSERVATIONS**

A section of a stimulated muscle fiber is shown in the electron micrograph in Fig. 2. The whole sequence of changes in the sarcomere structure upon contraction can be seen. Myofibrils located in the upper part of the picture are in the least contracted state, while those in the bottom part are in the most contracted state.

The direction of the process (from the top to the bottom) is beyond any doubt due to the regular shortening of sarcomeres normally arranged in line or in phase. The whole process is conventionally divided into several stages gradually changing...
Figure 1
A scheme of successive stages of isotonic contraction of the sarcomere. S, length of the sarcomere; RL, "resting length"; H, H band; Hc, H sub-band; A-I, "primary anisotropic" band; A-II, "secondary anisotropic" band; I-I, "primary isotropic" band; I-II, "secondary isotropic" band.
from one to another, though in its “final” expression each stage is characterized by the structure specific only for this particular stage.

**First Stage (1 in Fig. 1; M1 in Figs. 2 and 3)**

Myofibrils located in the upper part of Fig. 2 (M1), when judged by the ratio of the length of the I band to that of the sarcomere, are in the so-called “resting state,” the length of their sarcomeres (in axolotl, 1.9 to 2.2 μ) being the “resting length.” Light isotropic and dark anisotropic bands can be clearly seen. The H zone is considerably narrowed (~20 per cent of the sarcomere length), i.e., actin filaments at this stage are inserted between myosin filaments for a relatively large distance (6, 8, 10). In Fig. 3 the M line can be seen in the middle of the H zone. On either side of this line, narrow (~320 A) “halves” of the sub-bands H which are lighter than the H zone are seen (L zone of Sjöstrand and Andersson-Cedergren, 18) (Fig. 3). In less contracted sarcomeres the H sub-bands are more clearly seen. The Z line is distinct against the background of light I bands.

The borders between iso- and anisotropic bands are clearly defined. Within the myofibrils, between loosely arranged filaments of the I band, dark granules 250 to 350 A in diameter can clearly be seen after staining the sections with lead hydroxide. What portion of these granules represent RNP particles cannot be decided at present; it is very likely that at least a part of them are glycogen-bearing (17, 22). The secondary cross-striation (“bridges”) with a period of about 350 A is most strikingly seen in the anisotropic band. In the I band the “bridges” are less evident.

**Second Stage (2 in Fig. 1; M2 in Figs. 2 and 3)**

As one examines Fig. 2 from the top to the bottom, one can observe a decrease in the I band size with the decrease of the sarcomere length (down to 89 per cent, taking the “resting length” as 100 per cent). The A band size also decreases, but very insignificantly (by about 2 per cent). The width of the H band, however, rapidly diminishes and reaches its minimal value around 1300 A, showing no further change during all the subsequent stages of contraction. The H sub-band becomes indistinguishable against the background of the narrowing H band. Thus, the H band narrowed to 1300 A takes the place of the H sub-band (Fig. 3).

The M line becomes more clear cut than at the first stage, and, on the basis of our preparations, it can be assumed that this band is a row of thickenings located in central areas of myosin filaments.

Actin filaments, or, more correctly, those parts of them that are located in the I band, being already rather folded or coiled at the preceding stage, become still more coiled, especially in the zone directly adjoining the Z line (Fig. 3). In this zone some homogeneous substance of a considerable density begins to concentrate between the myofilaments.

The border between the A and I bands, which is fairly straight and well defined at the first stage, becomes more diffuse and less distinct. This complicates the measuring of individual bands. The indistinctness of this border in strongly contracted sarcomeres is ascribed by Sjöstrand and Andersson-Cedergren (18) to the formation of the “transitory zone” in which a gradual thinning of myofilaments takes place in the direction from the A to the I band.

**Third Stage (3 in Fig. 1; M3 in Figs. 2 and 4)**

Sarcomeres undergo still further contraction at this stage (up to ~79 per cent of the “resting length”) and possess a very specific structure: anisotropic bands lighten (diminish in density) considerably; isotropic bands, now reduced to narrow zones along the Z lines, become much darker, so that the densities of the I and A bands become equal and the bands become indistinguishable from each other at low magnifications. One

**Figure 2**

A field of the muscle fiber of the axolotl where all the stages of sarcomere shortening are presented. M1, the first stage (“resting length”); M2, the second stage; M3, the third stage; M4a, M4b, M4c, the fourth stage; M5, the fifth stage. × 5600.
gets the impression that the decrease in A band density is a result of the thinning of myosin filaments. The increase of the I band density might be explained by an increased folding or even coiling of the actin filaments and their consequent closer packing. The H band (or the rest of the H sub-band) remains the same as in the preceding stage (1300 Å). The M line likewise shows no change.

Fourth Stage (4a, 4b, and 4c in Fig. 1: M4a, M4b, and M4c in Figs. 2, 5, 6, and 7)

At this stage the sarcomere structure undergoes extremely interesting alterations. With the further decrease in general density of the zone in which the anisotropic band had been located, two dark lines appear in the center of the zone, on either side of the M line (Fig. 5). The light space between them (1300 Å) corresponds to the narrowed H band of the preceding stage. The width of these lines when they first appear is the same as that of the M line, i.e. 600 to 650 Å; their density is somewhat lower than that of the M line. This gives the impression that these newly formed lines are the rows of thickened areas in myofilaments at the border with the H band. It is characteristic for these lines to show a secondary periodicity in their structure which corresponds to that of the remaining sarcomere portion (~350 Å).

In what remains of the isotropic band a homogeneous substance continues to accumulate, while myofilaments are folding still more. As a result, this entire region including the Z line and adjacent areas of isotropic bands takes on the appearance of the intercalated discs of cardiac muscle fibers. Fawcett and Selby (3) report that the dense material immediately subjacent to the membranes of intercalated discs “has the same appearance and density as that forming the Z bands and is probably of the same composition.” This resemblance of these structures seems not to be fortuitous but to be due to the similarity of the function they perform: excitation conduction to contractile structures. The thickness of the Z line itself remains unchanged. Under low magnifications of the electron microscope, as well as under the light microscope, the appearance of the “contraction bands” marks this moment. With further sarcomere shortening, the width of the two lines (described above) adjacent to the H band rapidly increases, the distance between them remaining the same (~1300 Å) (Figs. 4, 5, and 6).

The remaining sarcomere portion in the region of the former anisotropic band becomes less electron opaque. Myofilaments in this region lose their regular longitudinal orientation, so that the margin between what remains of the I band and this region becomes increasingly indistinct.

As a result of these changes, two clearly distinguishable zones appear in the sarcomere: a dark one, in the center of the sarcomere, some 0.5 μ in width, and a light one along the ends of the sarcomere. The remarkable resemblance of such sarcomeres to those with non-contracted myofibrils attracts attention at first sight: the dark center of the sarcomere (as though forming a “secondary anisotropic” band, A-II), and two broad light zones along the edges (as though comprising a “secondary isotropic” band, I-II). This resemblance, however, is only superficial, and sarcomeres at this stage of contraction can easily be distinguished from non-contracted ones by such indices as the following: (a) the size of the sarcomere is considerably reduced (down to 74 per cent of the “resting length” at the onset of this stage, and down to 63 per cent (1.2 μ) at its end); (b) the distribution of myofilaments in the newly formed “secondary anisotropic” (A-II) band is never so regular as in the usual “primary anisotropic” (A-I) band; (c) a dark homogeneous substance and a dense network of folded myofilaments of the isotropic band are present in the region of the Z line (representing early stages in the development of “contraction bands”); (d) the density of the I-II band is always much greater than that of the “actual” I-I band, and the density of the A-II band is always lower than that of the A-I band; (e) when the sarcomere contracts, its A-II broadens.

At the end of this stage, when A-II reaches its maximal width of ~0.5 μ (i.e. about 40 per cent

Figures 3 and 4

Myofibrils of the axolotl muscle fiber at the first (M1), second (M2), and third (M3) stages of contraction. In the center of the H band (H) the H sub-band is seen (Hc). × 31,000.
of the sarcomere length), the density of this band begins to decrease (4c in Fig. 1, M4c in Figs. 2 and 7) and its borders with I-II become indistinct. The electron opacity of the M line gradually decreases. The whole complex of structures in the Z region becomes still darker. During these changes the size of the sarcomere remains unchanged (i.e., 63 per cent of the "resting length").

Fifth Stage (5 in Fig. 1; M5 in Figs. 2 and 8)

At this stage the sarcomere shortens by 5 per cent more and reaches its minimal stage of 1.1 μ, which is some 38 per cent of the "resting length." It is impossible now to differentiate I-II, A-II, and the M line, since the whole sarcomere from one margin to the other is of uniform density, although a somewhat darker area is sometimes preserved at the place of the A-II band. Myofilaments seem to be wave-shaped and possibly coiled. "Contraction bands" (Z and the adjacent zone) are completely developed and clearly seen against the background of light sarcomeres.

Dark granules, which are always seen among the myofilaments of the I band at the first contraction stages, are met with much less frequency at the fifth stage, and their location is restricted to the zone of "contraction bands."

DISCUSSION

With the procedure of muscle fiber excitation employed, we succeeded in following up the whole set of subsequent changes in sarcomere structure during contraction.

The fact that this whole series of changes has been followed up on the same preparation in the same field of vision is of great importance. This allowed us to find the right place for each stage in the total sequence of changes.

The first and second contraction stages have often been described in the literature. As to the mechanism of contraction working at these stages, of all the schemes set forth the most likely one seems to us to be that proposed by Huxley (8). According to this hypothesis, filaments of the I band slide between myosin filaments of the A band in the process of sarcomere contraction (1 and 2 in Fig. 1). This leads to a reduction of the I and H bands while the A band remains relatively the same. The reason for the progressive decrease in density of the A band is obscure. Several assumptions could be set forth to explain this phenomenon. We think it unlikely that it is due to a simple decrease of the osmiophilia of myofilaments. From a thorough examination of the sarcomere fine structure at different contraction stages, we gain an impression rather that the decrease in A band density is a result of contraction of the myofilament diameter. But since no exact measurement of myofilament thickness has been carried out during sarcomere contraction, this assumption remains untested. At any rate, no thickening of myofilaments takes place during sarcomere contraction, as was thought by Sjöstrand and Andersson-Cedergren (18). If some thinning of myofilaments (myosin) does take place, it starts and proceeds more intensely in the rapidly narrowing H band, so that by the time the H band and the sub-band H become indistinguishable from each other (Fig. 3; 2 in Fig. 1), the difference in the thickness of different regions of myosin filaments is most clearly manifested.

The nature of the M line remains unclear at present. As judged by our preparations, as well as by the photographs of other workers (8, 15, 16, 18, and others), it can be assumed that this line is a row of thickenings arranged in the middle of myosin filaments. It is likely that these thickenings consist of myosin, since they are extracted (at least in stretched or feebly contracted myofibrils) during the extraction of myosin (10). Huxley’s experiments have shown that after the extraction of myosin from myofibrils in the "resting state" and at the contraction to 75 per cent of resting length, some material remains in the middle of the former A band (that is, at the place of the M line). It would seem that these results contradict the suggestion of the myosin nature of the M line, but we

Figures 5 and 6

Myofibrils of the axolotl muscle fiber at the fourth stage of contraction. M4a, the myofibril at the very beginning of this stage: on either side of the M line two dark lines appear. M4b, the myofibril with well developed "secondary anisotropic" (A-II) and "secondary isotropic" (I-II) bands. × 31,000.
think it possible that the myosin of this line, as well as that of the remaining portion of the myofilament, may possess different solubilities in specific solvents. The experiments of Hanson and Huxley (6), for example, have shown that with a more complete myosin extraction the M line also disappears (cf. Figs. 17b, 18b, and 20 in the paper cited). Sjöstrand and Andersson-Cedergren, however, consider that no conclusion as to the chemical composition of structures can be drawn from their solubility alone, since solubility can depend on the molecular and substructural organization of the given formation. In this connection, Sjöstrand and Andersson-Cedergren believe as well that no sharp differences can be assumed in the chemical composition of myofilaments in the I and A bands (despite observations to the contrary) and that the myofilaments of the I band may contain some amount of myosin.

In the process of sarcomere transition from the first to the second stage, the M line becomes more distinct. The cause of this seems to be a progressive myosin concentration in this line, and it is suggested that this derives from the thinning (cf. above) and shortening (by 2 to 5 per cent) of the myosin filaments.

In an analysis of the changes in the I band, it should be stressed that myofilaments of this band, which, according to Huxley and Hanson, consist of actin, though arranged relatively irregularly at the first contraction state, are conspicuously folded or coiled with further sarcomere contraction. The impression is gained that these filaments form dense spirals in the region of the Z line (2 to 5 in Fig. 1; Figs. 4 to 8), and we propose that these spirals participate in the development of the "contraction bands."

With further contraction (the fourth stage) and decrease in density of the whole sarcomere, a new "secondary anisotropic" band (as we have called it provisionally) appears. Judged by its osmiophilia, it can be assumed that this new band is of a myosin nature. No special experiments to determine the nature of these bands were carried out; the investigations of other authors (6, 9, 10, 20, and others) unfortunately do not include experiments with myofilaments at the contraction stage described (the fourth). Therefore, in order to define the actual composition of the A-II band special investigations are required (treatment with specific solvents, investigations in polarized light, and the use of antibodies against actin and myosin (11, 13)).

Another striking event at the fourth contraction stage is the widening of the "secondary anisotropic" band. Such widened A-II bands have a length of about 0.5 \( \mu \), i.e. they are less than half the length of the A-I at the "resting length." Sjöstrand and Andersson-Cedergren (18) present a diagram of "A band" length changes in relation to the length of the sarcomere. It follows from the diagram that when the sarcomere length changes from 2.0-2.3 \( \mu \) ("resting length") to 0.8-1 \( \mu \) (strong contraction), the "A band" length decreases by more than 50 per cent (from \( \sim 1.3 \mu \) to \( \sim 0.6 \mu \)). Thus, the length of the short "A band" of Sjöstrand and Andersson-Cedergren corresponds to the same part of the sarcomere as the A-II band in our investigation. We think it evident that these authors, seeing the images of very much shortened sarcomeres, assumed that the dark band (A-II) in the middle of the sarcomere was the usual but very strongly shortened (more than two times) anisotropic band. As mentioned above, the dark band in the center of the strongly shortened (to 69-74 per cent of the "resting length") sarcomere cannot be regarded as the usual anisotropic band.

\( ^3 \) The anisotropic band (A-I) actually shortens somewhat with the shortening of the sarcomere, but this shortening does not exceed 2 to 5 per cent of the initial length of this band. According to Villafranca (21), the A band length undergoes very insignificant changes when the sarcomere length changes from 1.4 to 1.5 \( \mu \), i.e. approximately 7 per cent.

Figure 7

Myofibrils of the axolotl muscle fiber at the end of the fourth (M4c) stage of contraction. The density of the A-II band begins to decrease and its borders with the I-II band become indistinct. \( \times 31,000 \).

Figure 8

Myofibrils at the fifth (M5) stage of contraction. The A-II and I-II bands are scarcely distinguishable from one another. "Contraction bands" are clearly seen against the background of light sarcomere. \( \times 31,000 \).
since this structure appears anew and widens and does not narrow with the contraction of the sarcomere.

The structural basis for the appearance of the A-II band remains unknown. It seems very likely, however, that these bands are the manifestation of the spiralization or folding of myosin filaments or of constituting subunits of the former anisotropic bands (A-I). This spiralization, it is suggested, begins at the border of the H band (4 in Fig. 1) and involves ever increasing lengths of myosin filaments, thus accounting for the increase in density of a gradually widening central zone in the sarcomere (4a and 4b in Fig. 1; Figs. 5 and 6).

The former isotropic band (I-I), as was mentioned above, having narrowed to a narrow line in the Z region (3 and 4a in Fig. 1; Figs. 4 and 5), gradually fuses with the lighter zone of the I-II band (4b in Fig. 1). Actin filaments in the process of their shortening form bendings or folds in the region of the Z line and thus participate in the formation of the “contraction bands” (3 to 5 in Fig. 1; Figs. 6 to 8). Huxley and Hanson (6, 10) consider that the “folding” of actin filaments proceeds in the center of the sarcomere while that of myosin filaments takes place in the Z region. In our opinion, this situation cannot take place in the sarcomere, since at the moment of development of the first but distinct “contraction bands” the “primary isotropic” band is still present between the Z line and the somewhat narrowed (by 2 to 5 per cent) A-I, so that there is no direct contact between myosin filaments and the Z line, as Huxley believes. Hanson’s investigations (5) carried out on insect muscles also permit one to suggest that it is just actin filaments which participate in the formation of the “contraction band” in the Z region (Cz), since Cz is isotropic in polarized light, while “contraction bands” in the M region (Cm) are anisotropic (owing, it seems, to the “folding” of myosin filaments). It is possible that in insect muscles possessing a small amplitude of length fluctuations while at work, Cm is analogous to A-II of higher animals.

Thus, our observations which contradict Huxley’s views are in agreement in this respect with the opinion of Sjöstrand and Andersson-Cedergren (18), for they believe that “contraction bands” in the region of the Z line are an “aggregation of the I band part of the myofilaments.”

Between the folded (or coiled) myofilaments of the parts of the I band adjoining the Z line, some homogeneous, dense substance accumulates which participates in the development of “contraction bands.” The nature of this substance is quite unknown.

At the end of the fourth stage (4c in Fig. 1; Fig. 7), while the size of the sarcomere remains unchanged, a gradual decrease in density of the A-II band and the M line takes place and “contraction bands” become still darker. It is impossible at present to suggest even a hypothetical scheme for the changes in ultrastructure at this stage. The alterations in sarcomere ultrastructure taking place at the transition to the fifth (last) stage of contraction (5 in Fig. 1; Fig. 8), when only folded filaments and strong “contraction bands” can be seen in the region of the Z lines along the whole sarcomere, are still vague.

Thus, suggesting a scheme of the interrelation between the changes in ultrastructure of a sarcomere during its contraction, we draw the conclusion that at the first stages of contraction, i.e. from the “resting length” to and including the third stage (1 to 3 in Fig. 1), the hypothesis of Huxley (sliding of two filament types with respect to each other) is the most likely explanation. At further stages of contraction (the fourth and fifth, 4a, 4b, 4c, and 5 in Fig. 1) this mechanism is evidently replaced by another, namely the folding or coiling of myofilaments. This second mechanism was also assumed by Huxley. He confined it, however, to the sarcomeres of those types which are presented in our scheme (Fig. 1) under the numbers 4c and 5. But, as shown above, an obligatory (fourth) stage, characterized by neoformation of secondary “anisotropic” and “isotropic” bands, comes between these final stages and the third stage (3 in Fig. 1). At this fourth stage, coiling (if we admit its existence) proceeds most intensely, since at this time the sarcomere shortens extensively (79 per cent → 74 per cent → 63 per cent). At the last stage (5, Fig. 1; Fig. 8) the shortening is insignificant (63 per cent → 58 per cent).

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Mit Hilfe einer neuen Technik—Reizung der Muskelfaser des Axolotl durch einen Na
delstich—gelingt es, im Elektronenmikroskop alle Stadien der Myofibrillenkontraktion
im selben Gesichtsfeld darzustellen. Dadurch werden mögliche Fehler, wie sie sich aus
einer Bestimmung der Reihenfolge der Kontraktionsstadien aus verschiedenen Bereichen
des Präparates ergeben können, vermieden. Es wird ein neues Kontraktionsstadium be-
schrieben, das auftritt, wenn das Sarkomer auf weniger als 74 Prozent der Ruhelänge ver-
kürzt ist aber noch nicht das durch starke "Kontraktionsstreifen" charakterisierte Bild des
"maximal verkürzten" Sarkomers zeigt. In diesem Stadium entsteht im Zentrum des
Sarkomers, an beiden Seiten des M-Streifens, die "sekundäre anisotrope" Scheibe, die
sich bei weiterer Verkürzung des Sarkomers verbreitert. Auf beiden Seiten dieser Scheibe,
an Stelle der ehemaligen ("primären") anisotropen Scheibe, bildet sich die "sekundäre
isotrope" Scheibe. Die aufeinandergeschalteten Stadien der Sarkomerenkontraktion wer-
den in einem Schema dargestellt. Der Kontraktionsmechanismus der ersten Stadien—
von 100 Prozent auf 79 Prozent der Ruhelänge—scheint sich von dem der letzten Stadien—
von 74 Prozent auf 58 Prozent der Ruhelänge—zu unterscheiden. Man kann für die ersten
Stadien ein Gleiten der Protofibrillen gegen einander annehmen. Für die letzten Stadien
ist eine Spiralisierung der Protofibrillen die wahrscheinlichere Erklärung.

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