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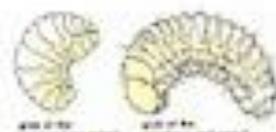
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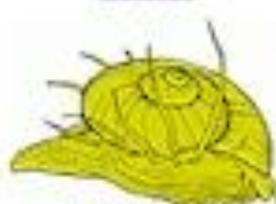
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Types of Skeletal Systems

Changes in movement occur because muscles pull against a support structure, called the skeletal system

-Zoologists recognize three types:

-Hydrostatic skeletons

-Exoskeletons

-Endoskeletons

Hydrostatic Skeletons

Are found primarily in soft-bodied invertebrates,
both terrestrial and aquatic

Locomotion in earthworms

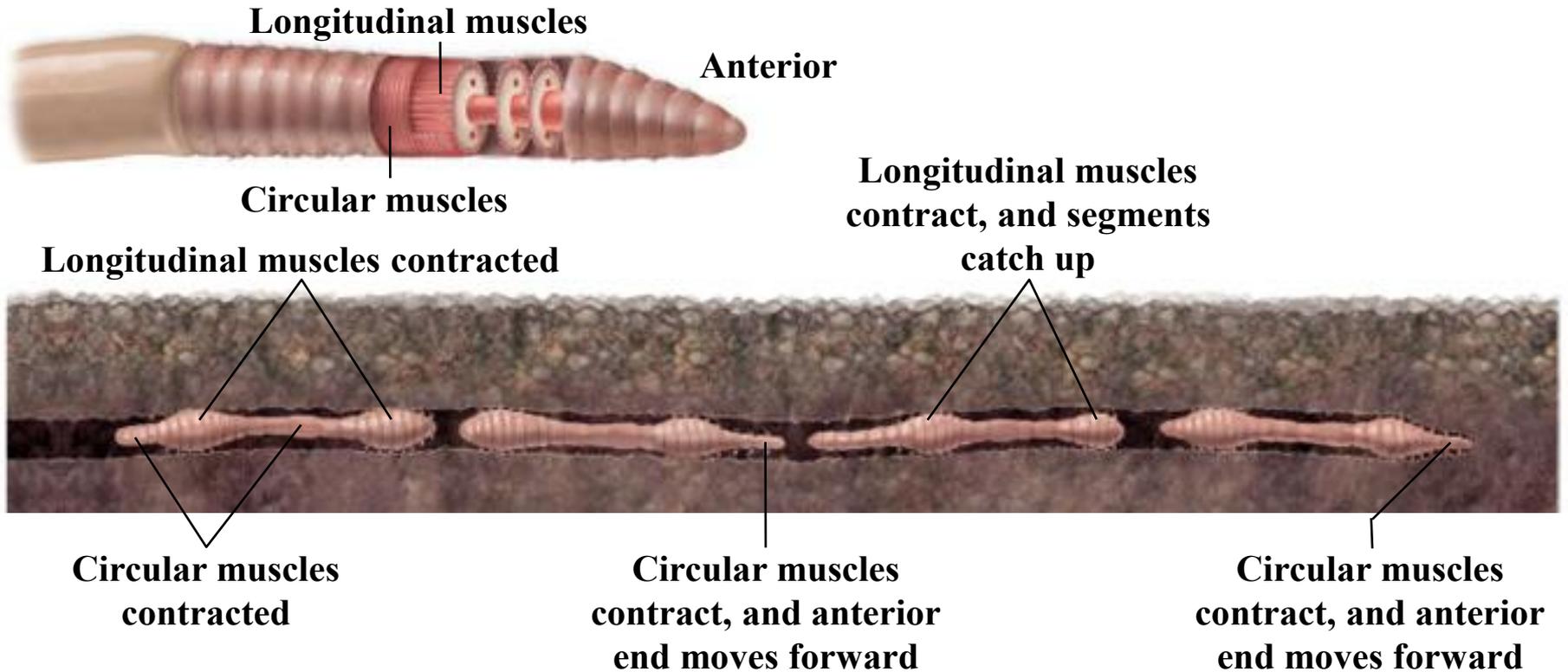
-Involves a fluid-filled central cavity and surrounding circular & longitudinal muscles

-A wave of circular followed by longitudinal muscle contractions move fluid down body

-Produces forward movement

Hydrostatic Skeletons

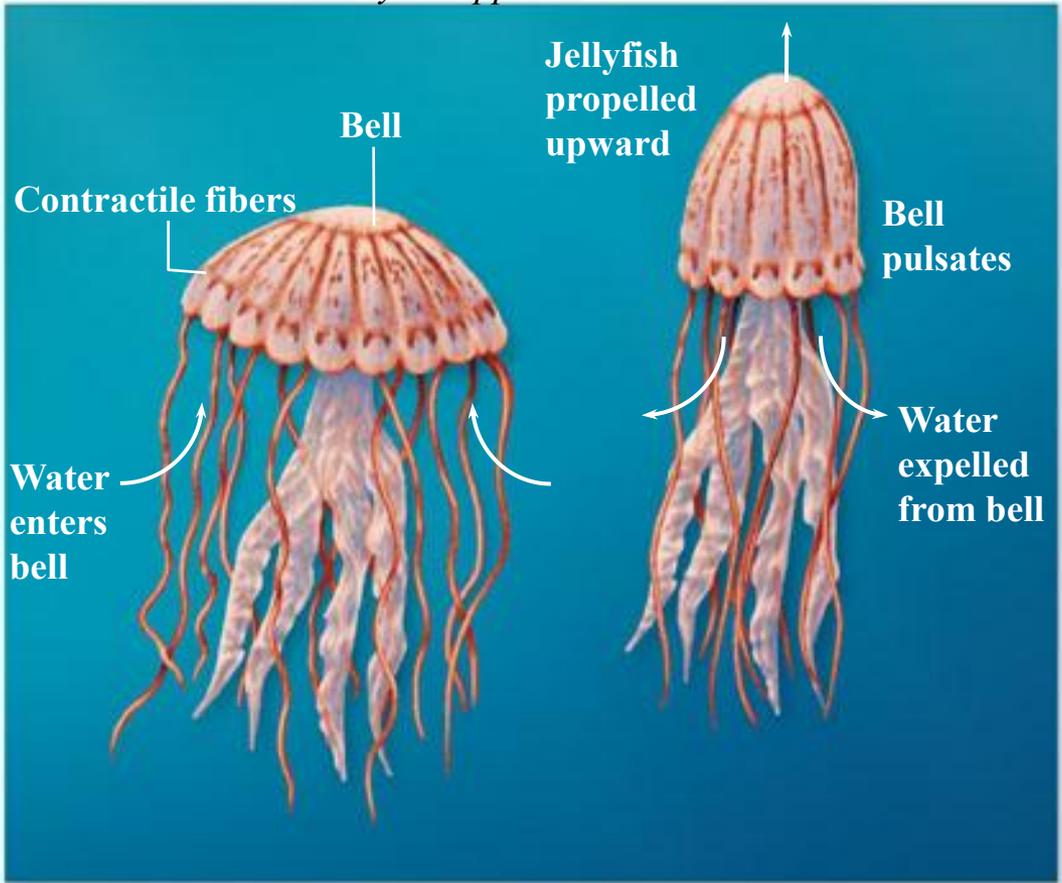
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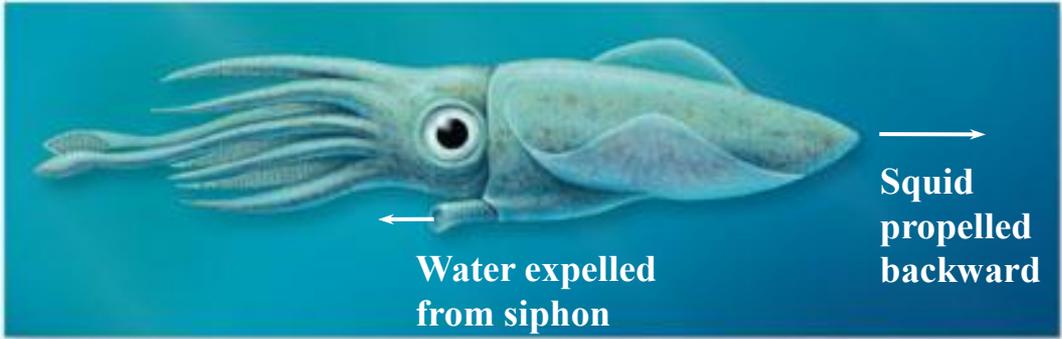
Hydrostatic Skeletons

Locomotion in aquatic invertebrates

- Occurs by fluid ejections or **jetting**
- Jellyfish produce regular pulsations in bell
 - Squeezing some of water contained beneath it
- Squids fill mantle cavity with sea water
 - Muscular contractions expel water forcefully through the siphon, and the animal shoots backward



a.



b.

Exoskeletons

The **exoskeleton** surrounds the body as a rigid hard case

- Composed of chitin in arthropods

An exoskeleton provides protection for internal organs and a site for muscle attachment

- However, it must be periodically shed, in order for the animal to grow

- It also limits body size

Endoskeletons

Endoskeletons are rigid internal skeletons that form the body's framework and offer surfaces for muscle attachment

-Echinoderms have calcite skeletons, that are made of calcium carbonate

-Bone, on the other hand, is made of calcium phosphate

Locomotion in Water

Water's buoyancy reduces effect of gravity

Some marine invertebrates move about using hydraulic propulsion

All aquatic invertebrates swim

- Swimming involves using the body or its appendages to push against the water

- An eel uses its whole body

- A trout uses only its posterior half

Locomotion on Land

Terrestrial locomotion deals mainly with gravity

Mollusks glide along a path of mucus

Vertebrates and arthropods have a raised body, and move forward by pushing against the ground with jointed appendages – legs

- Vertebrates are tetrapods; all arthropods have at least six limbs

- Having extra legs increases stability, but reduces the maximum speed

Locomotion on Land

The basic walking pattern of quadrupeds generates a diagonal pattern of foot falls

- Left hind leg, right foreleg, right hind leg, left foreleg

- Allows running by a series of leaps

Some vertebrates are also effective leapers

- Kangaroos, rabbits and frogs have powerful leg muscles

Red-necked wallaby



Locomotion on Land

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Locomotion in Air

Flight has evolved among animals four times

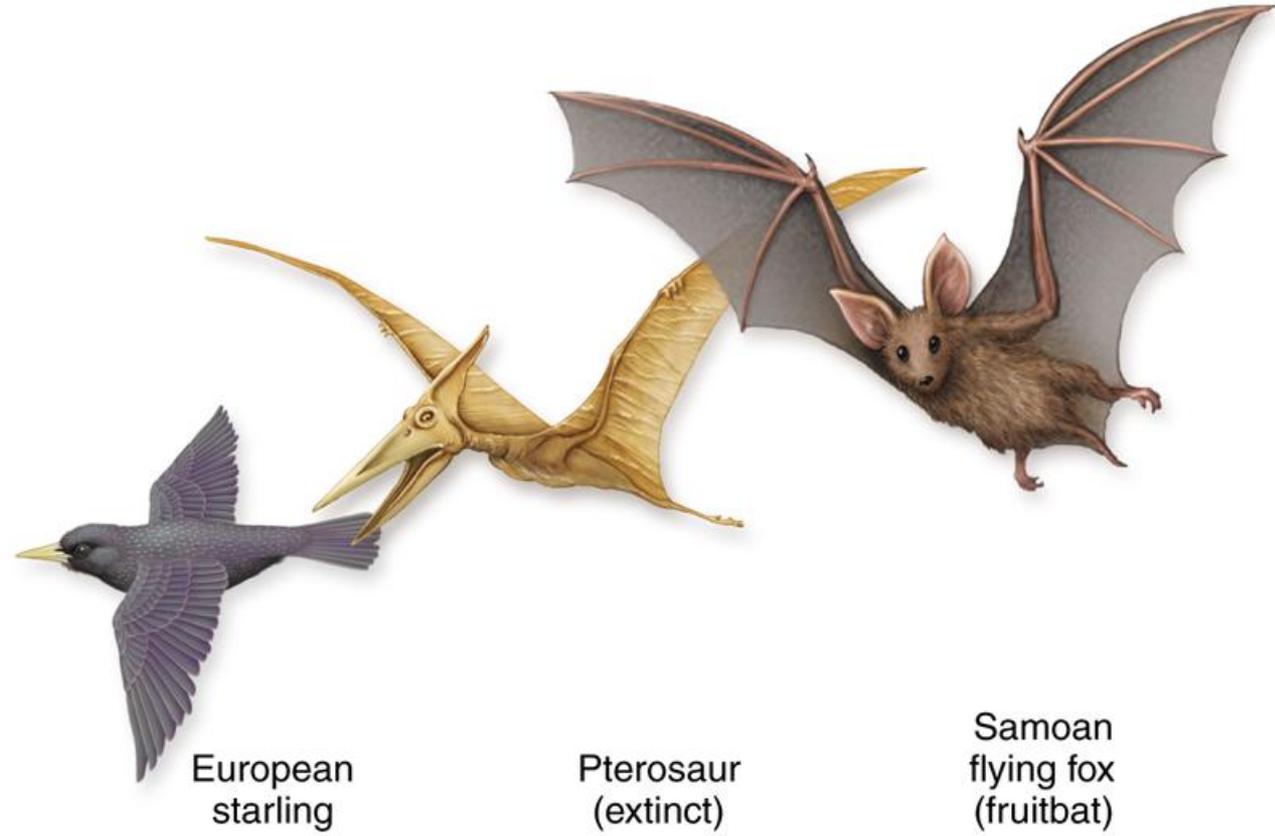
- Insects, pterosaurs (extinct flying reptiles), birds, and bats

- Propulsion is achieved by pushing down against the air with wings

In birds and most insects, wing raising and lowering is achieved by alternate contraction of extensor muscles (elevators) and flexor muscles (depressors)

Locomotion in Air

These different vertebrates all have lightened bones and forelimbs transformed into wings



ASYNCHRONOUS MUSCLE

Asynchronous muscle, the basalar flight muscle of the beetle *Cotinus mutabilis*

Synchronous wing muscles from the locust, *Schistocerca americana*.

Because of delayed stretch activation and shortening deactivation, a tetanically stimulated beetle muscle can do work when subjected to repetitive lengthening and shortening. The synchronous locust muscle, subjected to similar stimulation and length change, absorbs rather than produces work.

Approximately three-quarters of the known insect species have asynchronous flight muscles (Dudley, 1991).

Asynchronous muscles are high-frequency muscles. The wing-stroke frequency during flight of insects using asynchronous muscle ranges from approximately 20 Hz in large belostomatid bugs (Barber and Pringle, 1966) to 500–1000 Hz in small midges (Sotavalta, 1947, 1953).

But high-frequency muscles need not be asynchronous. Among **high-frequency, synchronous muscles** are the shaker muscle of the rattlesnake rattle (up to 90 Hz; Schaeffer et al., 1996; Rome and Lindstedt, 1998), the toadfish soundproducing muscle (over 200 Hz; Fine, 1978; Fine and Mosca, 1989; Rome et al., 1996), the muscles used in stridulation by the katydid *Neoconocephalus robustus* (200 Hz; Josephson and Halverson, 1971) and the tymbal muscle used in sound production by the cicada *Okanagana vanduzeei* (550 Hz; Josephson and Young, 1985).

In synchronous muscles, the myofibrils are enveloped by a layer of sarcoplasmic reticulum; in asynchronous muscles, the sarcoplasmic reticulum is sparse and scattered. Muscle activation in both synchronous and asynchronous muscle results from the release of Ca²⁺ from the sarcoplasmic reticulum in response to fiber depolarization; relaxation follows re-uptake of the released Ca²⁺ by the sarcoplasmic reticulum. High-frequency operation requires brief contractions. The short twitch duration in synchronous muscle is achieved in part by hypertrophy of the sarcoplasmic reticulum and by a reduction in the diameter of the contractile myofibrils (Josephson and Young, 1987).

Think mitochondria within the fibers. Energy demand.

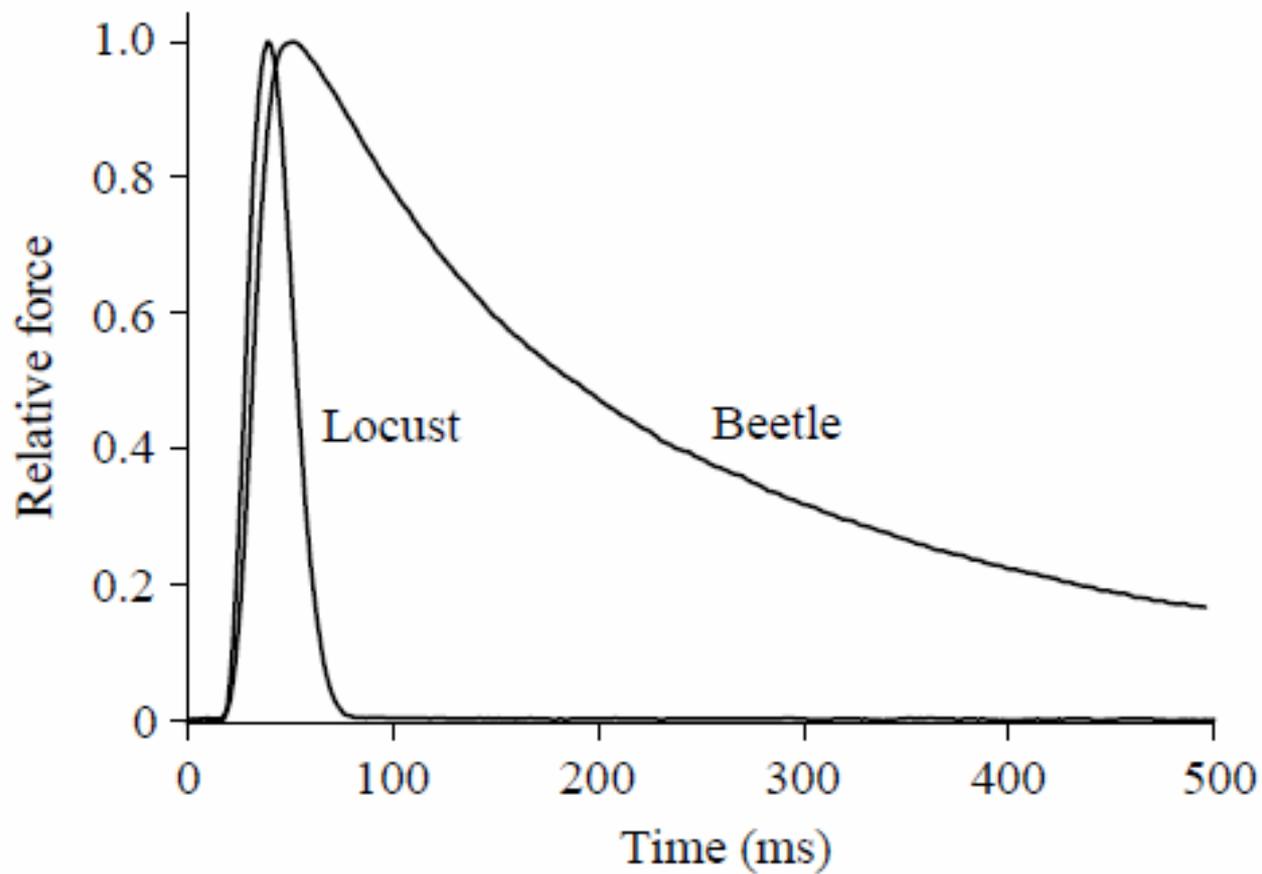


Fig. 2. Isometric twitches from beetle and locust flight muscle at 30 °C.

Table 1. *Structural features of beetle (Cotinus mutabilis) and locust (Schistocerca americana) flight muscle*

	Beetle	Locust
Myofiber cross-sectional area (μm^2)	8069 \pm 520 (20)	3206 \pm 219 (20)
Myofibril cross-sectional area (μm^2)	3.7 \pm 0.1 (36)	0.82 \pm 0.03 (36)
% Muscle fiber as		
Myofibril	58.1 \pm 1.2 (6)	65.0 \pm 2.7 (4)
Mitochondria	36.7 \pm 1.6 (6)	23.5 \pm 2.1 (4)
SR and T system	1.6 \pm 0.1 (6)	9.6 \pm 0.5 (4)
Tracheoles	1.2 \pm 0.2 (6)	0.5 \pm 0.2 (4)
Other	2.4 \pm 0.5 (6)	0

Values are means \pm S.E.M. (*N*).

SR, sarcoplasmic reticulum.

The sample sizes, *N*, for myofiber area and myofibril area are the total number of fibers analyzed from muscles of 2–6 individual animals. The sample sizes for fractional volume are the number of muscles examined, each from a different animal. Five fibers were analyzed for each muscle.

See Stokes et al. (1994) for details of the stereological methods used.

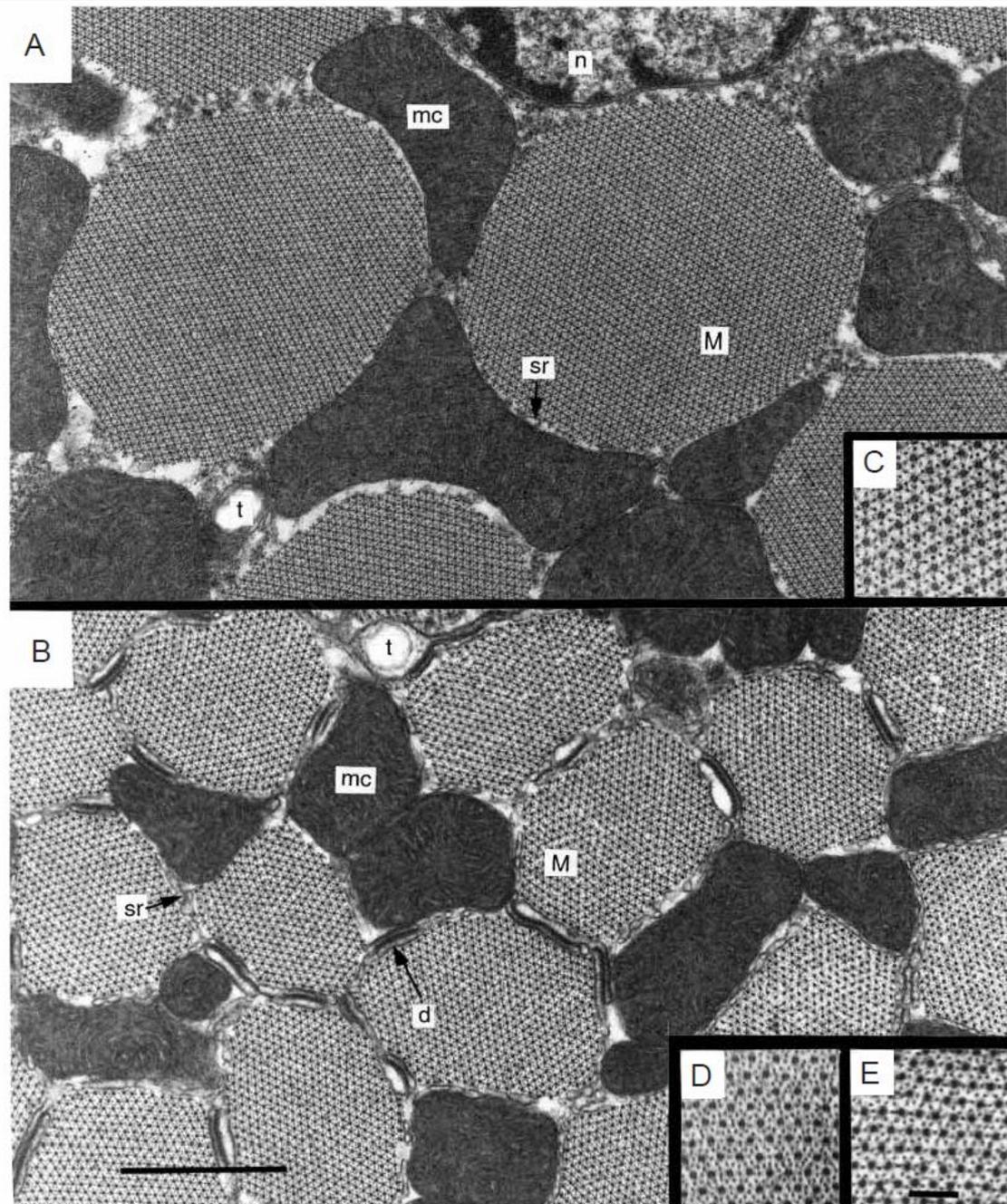


Fig. 3. Ultrastructure of asynchronous (A) and synchronous (B) flight muscle from *Cotinus mutabilis* and *Schistocerca americana* respectively. The beetle muscle is the basalar; the locust muscle the tergosternal. (A,B) Transverse sections at identical magnification. Scale bar, 1 μm . Insets C–E are at greater magnification to show myofilament arrays. The scale bar in E, which also applies to C and D, is 0.1 μm . d, dyad; M, myofibril; mc, mitochondrion; n, nucleus; sr, sarcoplasmic reticulum; t, tracheole.

ROBERT K. JOSEPHSON

TABLE 1

Time required to activate a myofibril, calcium diffusion rate limiting

Assumptions:	
myofibrillar calcium concentration at $t = 0$	1×10^{-7} M/L
calcium concentration surrounding the myofibril at $t = 0$	1×10^{-3} M/L
myofibrillar calcium concentration for maximum activation	1.2×10^{-5} M/L
calcium diffusion coefficient	1.4×10^{-7} cm ² sec ⁻¹
Calcium diffusion time:	$1.1 \text{ msec} \times (\text{myofibrillar diameter, } \mu\text{m})^2$

TABLE 2

Time required to terminate activity, calcium diffusion rate limiting

Assumptions:	
myofibrillar calcium concentration at $t = 0$	1.2×10^{-5} M/L
calcium concentration surrounding the myofibril at $t = 0$	1×10^{-7} M/L
threshold calcium concentration for contractile activity	1.26×10^{-6} M/L
calcium diffusion coefficient	1.4×10^{-7} cm ² sec ⁻¹
Calcium diffusion time:	$9.1 \text{ msec} \times (\text{myofibrillar diameter, } \mu\text{m})^2$



Fig. 4B A longitudinal section of a fiber from a singing muscle of the katydid *Neoconocephalus robustus*. The abbreviations are as in figure 3, the scale as in figure 4C. (Micrograph kindly supplied by D. R. Stokes.)

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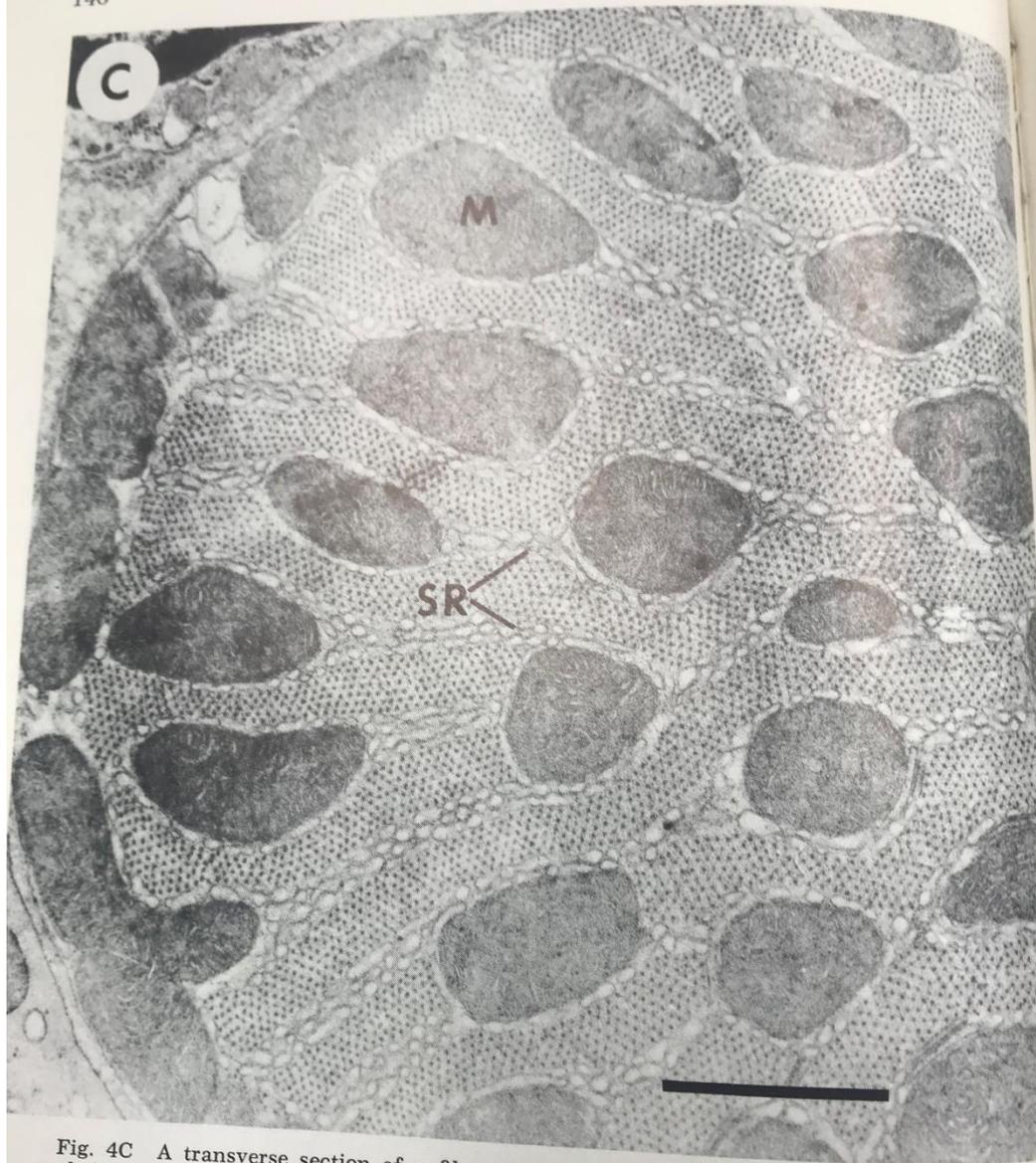


Fig. 4C A transverse section of a fiber from a singing muscle of the katydid *Neoconocephalus robustus*. The abbreviations are as in figure 3. Scale bar indicates 1 μ m. (Micrograph kindly supplied by D. R. Stokes.)

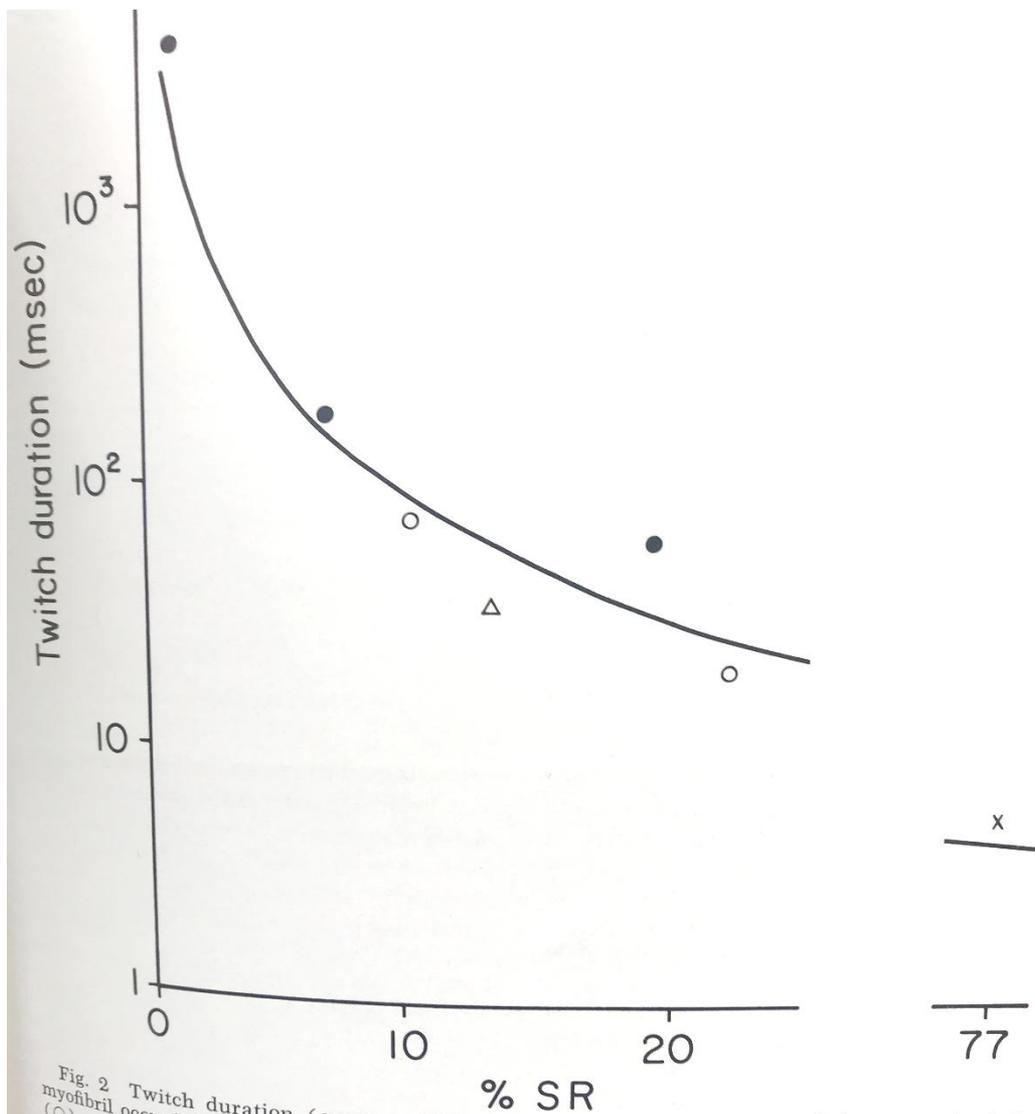


Fig. 2 Twitch duration (onset to 50% relaxation) as a function of the percent of the myofibril occupied by SR, 20°C. (●) — leg muscles from *Schistocerca* (Cochrane et al., '72). (○) — mesothoracic dorsal longitudinal muscle of the katydid, *Neoconocephalus robustus* (Stokes et al., '75). These data have been adjusted to 20° using a Q_{10} of 2.2 (Josephson et al., '75). (Δ) — frog sartorius; contraction time from Close ('72b), SR volume from Peachey ('65). (x) — sonic muscle of the lobster *Homarus*; contraction time from Mendelson ('69) adjusted to 20° with Q_{10} assumed to be 2.2, SR volume from Rosenbluth ('69). The solid line is arbitrarily drawn and gives twitch duration proportional to the SR volume to the negative three-halves power, the proportionality constant being selected to fit the data points.

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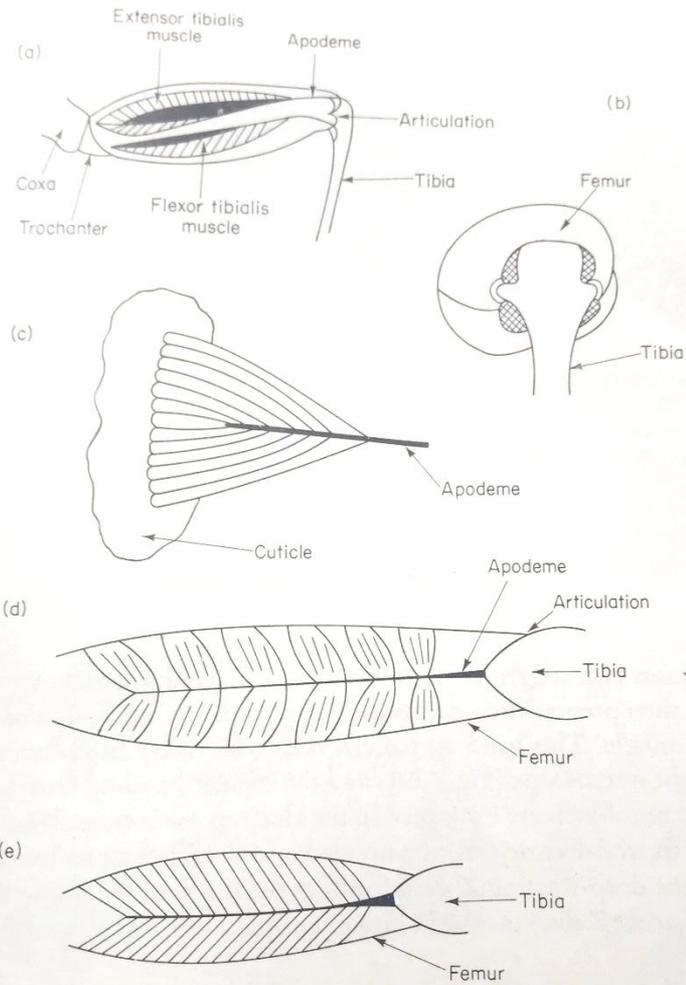


FIG. 1.1. The structure and arrangement of some insect skeletal muscles. (a) Main femoral musculature of a typical insect. The apodemes are inserted above and below the tibial articulation, which thus restricts movement into the vertical plane in relation to the femur. (b) The femur/tibia dicondylic joint. The cross-hatched area is flexible cuticle known as the articular corium. (c) Isolated single unit insect muscle (e.g. a coxal muscle). (d) Multi-unit muscle with separate muscle units (e.g. stick insect flexor tibialis). (e) Undivided multi-unit muscle (e.g. flexor tibialis of cockroach and Lepidoptera. From Huddart (1971b).

where a considerable ground sarcoplasm is present and where contraction speed and mechanical output are considerably lower than that seen in flight muscle.

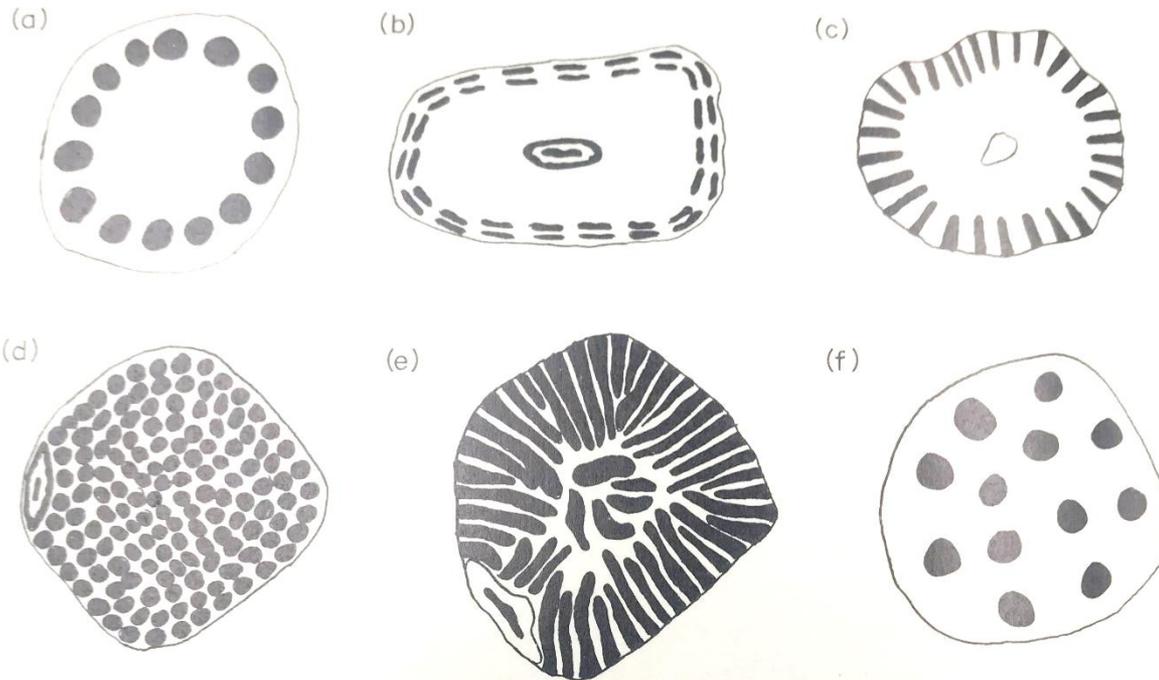


FIG. 1.2. The distribution of myofibrils in some skeletal muscle fibres. (a) *Anodonta* (Mollusca); (b) *Octopus* (Mollusca); (c) hirudinean (Annelida); (d) insect leg muscle and vertebrate skeletal muscle; (e) cockroach flight muscle; (f) *Thyone* (Echinodermata). (a), (b), (c) and (f) redrawn from Hoyle (1957) and Florey (1966), (d) and (e) drawn from fresh material (frozen sections examined with phase contrast).

TABLE 1.6. ULTRASTRUCTURAL DIFFERENCES SHOWN BY SOME SELECTED FAST AND SLOW ARTHROPOD MUSCLES

Animal and muscle	Sarcomere length (μm)	Dyads per sarcomere	Sarcoplasmic reticulum	T system	Actin/myosin ratio	Reference
Lobster Phasic Tonic	4 9	2-4 2	extensive extensive	regular regular	3 : 1 6 : 1	Jahromi and Atwood (1969a)
Cockroach (coxa) Phasic Tonic	3-4 7.3	2-4 irregular	extensive reduced	regular at A band at Z and A band	3 : 1 6 : 1	Jahromi and Atwood (1969b)
Dragonfly (dorso/ventral muscles) Phasic (non-respiratory) Tonic (respiratory)	5 5.5	frequent few	extensive sparse	regular poorly developed	10-12 : 1 9-10 : 1	Mill and Lowe (1971)

TABLE 6.6. SOME ELECTRICAL CHARACTERISTICS OF SELECTED INSECT MUSCLE FIBRES

Insect	Muscle	Membrane capacity ($\mu\text{F}/\text{cm}^2$)	Resistance R_m (Ω)	Time constant T_m (sec)	Length constant (mm)	Diameter (μ)	Reference
<i>Romalea</i> (Orthoptera)	Extensor tibialis	2.2	3000	6.6	1.7	70-100	Cerf <i>et al.</i> (1959)
<i>Schistocerca</i> (Orthoptera)	Extensor tibialis	2.0	8000	1.6	2.8	70-100	Usherwood (1962)
<i>Locusta</i> (Orthoptera)	Flight muscle	5.3	1500	8	0.6-1.2	70-100	Hagiwara and Watanabe (1954)
<i>Aeschna</i> (Odonata)	Coxal depressor	47	530	2.5	0.53	—	Malpus (1968)
<i>Philosamia</i> (Lepidoptera)	Intersegmental	5.9	2629	16.8	—	—	Yamagushi <i>et al.</i> (1972)

TABLE 1.1. PHYSICAL CHARACTERISTICS OF THE MYOFIBRILS OF SOME TYPICAL VERTEBRATE SKELETAL MUSCLES

Animal and muscle	Myofibril diameter (μm)	Actin length (μm)	Myosin length (μm)	Sarcomere length (μm)	Reference
Mouse biceps brachii	0.4-1.2	c. 1	c. 1.5	2.8	Goldspink (1968, 1970)
Chick pectoralis	1	1	1.5	2.2	Hagopian (1970), Mendell (1971)
Bovine semitendinosus	1.8	1.3	1.7	2.4	Henderson <i>et al.</i> (1970)
Human vastus lateralis	1.0	0.9	1.3	2.0	Gollnick <i>et al.</i> (1969)
Frog semitendinosus	0.7	1.0	1.2	2.2	Knappeis and Carlson (1968)
Rat gastrocnemius	0.8	1.0	1.2	2.6	Walker <i>et al.</i> (1968)
Frog sartorius	0.6	1.0	1.7	2.9	Huxley (1964)
	0.5-1.0	0.8	1.2	1.9	Armstrong (1970c)
Rat psoas	0.6	1.0	1.3	2.6	Schiaffino and Margreth (1969)
Pigeon breast (white fibre)	0.6-1.2	0.75	1.2	1.7	Grinyer and George (1969)
Cat extraocular (slow fibre)	0.7-1.2	1.1	1.3	2.4	Cheng-Minoda <i>et al.</i> (1968)

Animal and muscle	Myofibril diameter (μm)	Actin length (μm)	Myosin length (μm)	Sarcomere length (μm)	Reference
<i>Lumbricus</i> , body wall	2.8×0.3	2	2.8	5.2	Mill and Knapp (1970)
<i>Ips</i> (Coleoptera) flight muscle	0.5-2.0	0.8	1.0	1.8	Bhakthan <i>et al.</i> (1971)
Dragonfly respiratory muscle	1.0	1.8	2.0	5.0	Mill and Lowe (1971)
<i>Homorocoryphus</i> (Orthoptera) indirect flight muscle	0.8	1.0	1.9	2.4	Anstee (1971)
Blowfly (<i>Phormia</i>) flight muscle	2.3	1.1	2.2	2.8	Smith and Sacktor (1970)
Cockroach intersegmental abdominal muscle	0.8-1.0	2.0	3.6-4.1	8.0	Smith (1966)
Cockroach tergo-coxal	1.0-2.0	1.5	2.7	3.0-4.0	Hagopian and Spiro (1968)
Rosechafer (Coleoptera) tergo-sternal	2.0	1.5	2.6	3.2	Saita and Camatini (1967)
<i>Eurypelma</i> (Arachnida) tarsal levator	0.8	1.8	2.5	2.8-3.6	Sherman and Luff (1971)
tarsal depressor	0.7-1.0	2.3	4.0	5.6-6.8	
Crayfish deep abdominal extensor (phasic)	0.5-1.2	0.8	1.5	2.0	Jahromi and Atwood (1967)
Crayfish claw closer	1.0-1.5	1.2	2.0	2.5	Huddart and Oates (1970b)
<i>Portunus</i> carpopodite flexor (phasic fibre)	0.6	1.3	2.8	4.0	Armstrong (1970c)
<i>Carcinus</i> , claw closer	0.5-1.0	0.7	1.3	2.0	Bradbury (1973b)
<i>Sagitta</i> (Chaetognatha) longitudinal muscle	0.8	0.8	1.4	2.0	Duvert (1969)
<i>Balanus nubilus</i> (Crustaceae) giant fibre	2.5	2.3	4.0	6.5	Hoyle <i>et al.</i> (1965)

adjacent sarcomeres overlap through the holes in the Z disc. This allows the muscle to shorten down to about 25% of resting length. More recently the phenomenon of supercontraction has been reported in a vertebrate skeletal muscle. Rice (1973), working on chameleon tongue muscle, has reported a contraction down to about 16% of extended length. In this muscle the Z discs are fragmented, consisting of strips of material about 300 Å wide, allowing the myosin filaments of adjacent sarcomeres to overlap through the slits in the Z disc. Figure 9.4 shows supercontraction and non-shortening in muscles

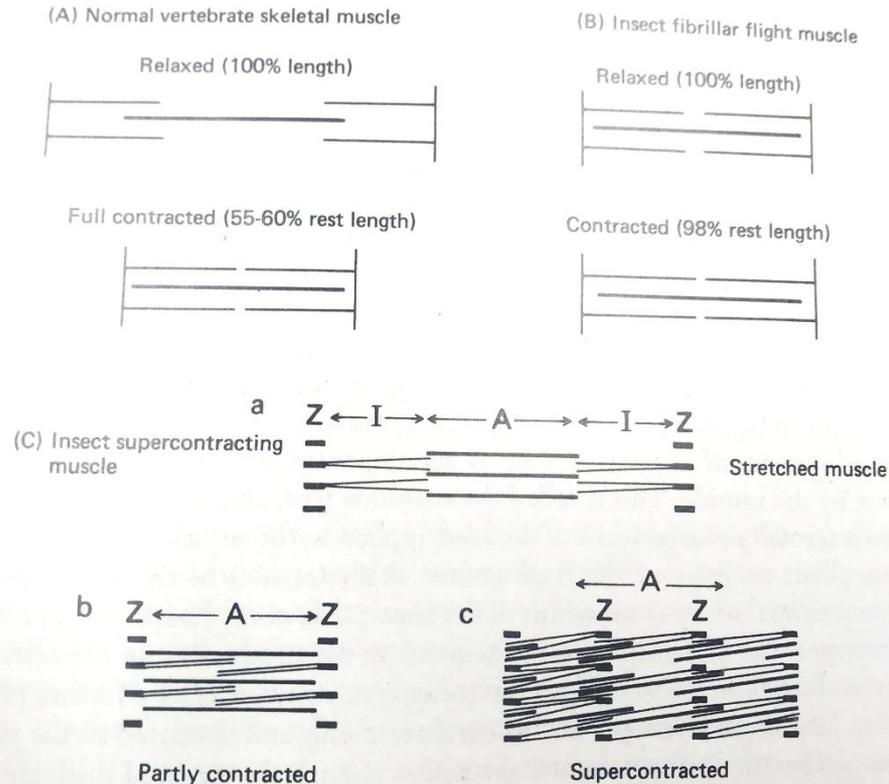


FIG. 9.4. Shortening properties during activation in some skeletal muscles. Fibrillar flight muscle hardly shortens at all, while supercontracting muscle shortens down to about 16% resting length compared with the conditions in normal vertebrate skeletal muscle, where an approximate contraction to 60% resting length is seen. C redrawn from Osborne (1967).

Invertebrate Muscles: Muscle Specific Genes and Proteins

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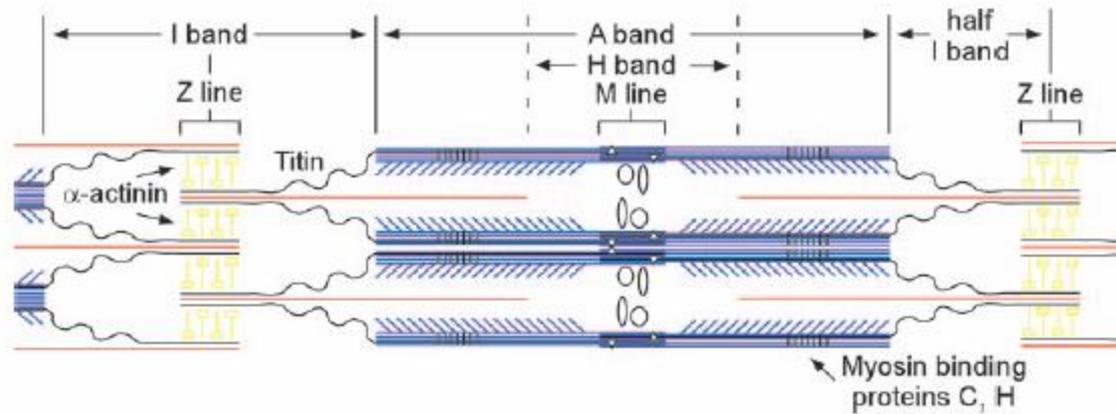


FIG. 5. Thick and thin filament arrangement in vertebrate striated muscle sarcomere. Also shown are the sarcomere associated proteins α -actinin, titin, myomesin, M-protein, and myosin binding proteins C and H. Red, actin; blue, myosin; yellow, α -actinin; triangle, titin serine/threonine protein kinase activity; ellipse and circle in M line, myomesin and M-protein, respectively.

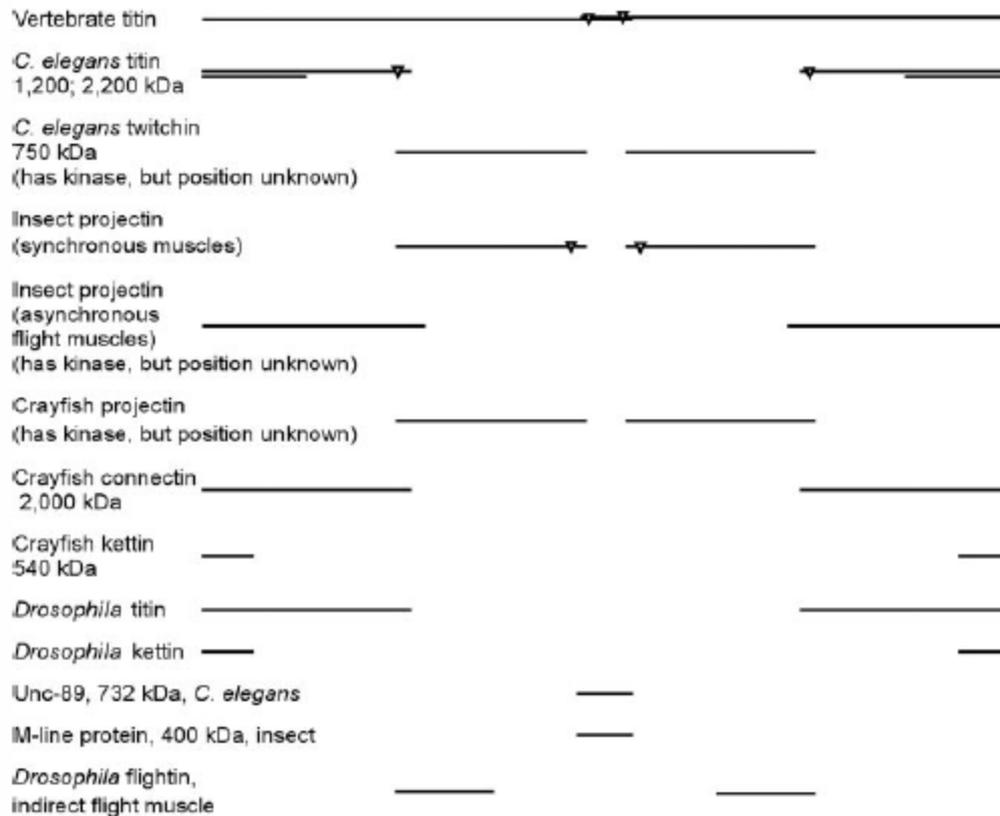
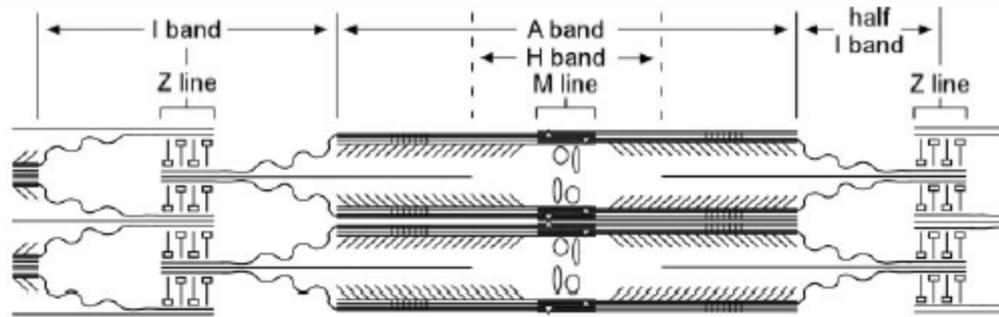
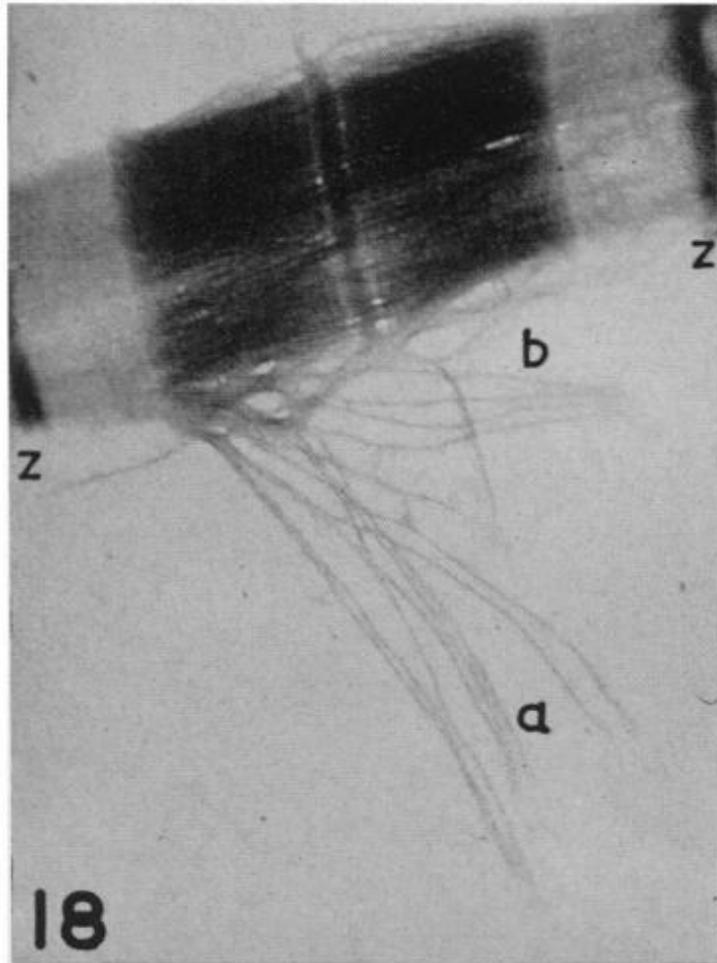
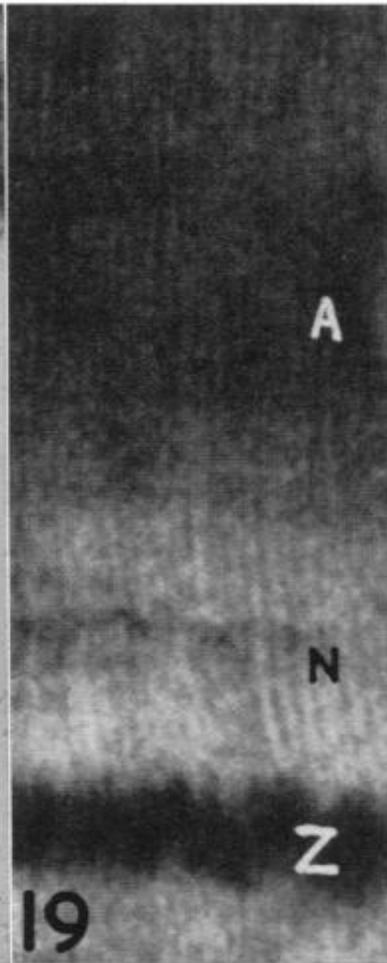


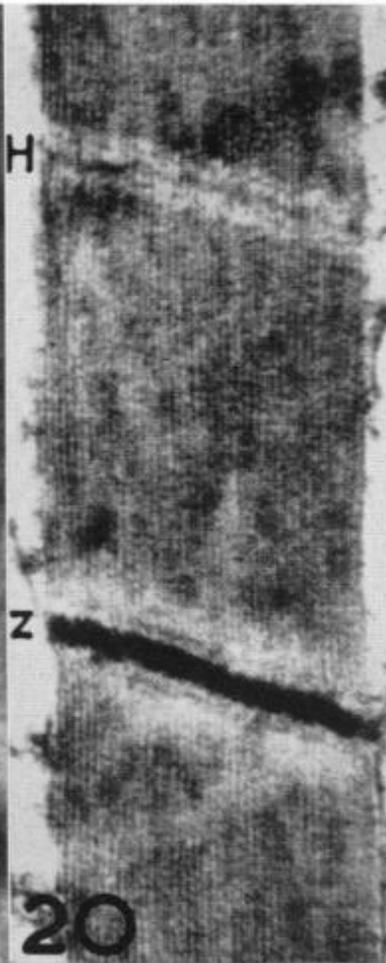
FIG. 8. Sarcomere location of the major invertebrate giant muscle proteins. *Top*: a repeat of the vertebrate sarcomere shown in Fig. 5. *Bottom*: position of vertebrate titin and major invertebrate giant proteins. Triangles represent serine/threonine kinase position when known. Line lengths are not proportional to protein molecular weight.



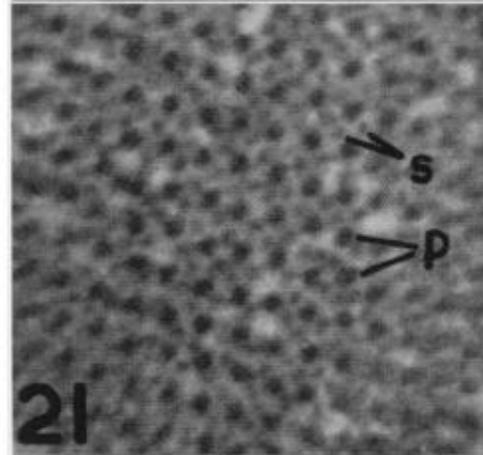
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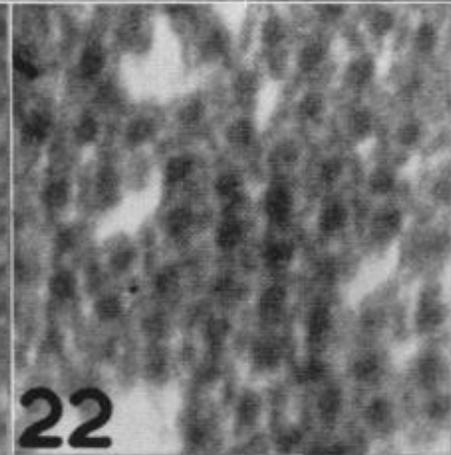
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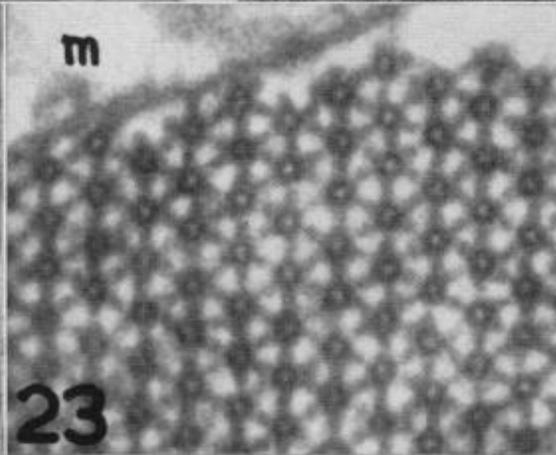
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Diversity of Striated Muscle

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SYNOPSIS. A broad comparative survey has been made correlating ultrastructure of cross-striated fibers with contractile properties in both invertebrates and vertebrates. Most of the muscles were found to be heterogeneous in fiber-composition as indicated by: length of sarcomere, extent of SR, number of invaginating tubules, numbers of mitochondria, etc. Z discs and M bands have markedly different structures in different fibers. The general concept of the "fibrillar" nature of striated muscle is challenged. It is suggested that following excitation the responses of individual sarcomeres, or parts of sarcomeres, are relatively independent. The possibility that all striated muscles contain a very thin elastic filament in parallel with actin and myosin, which may also be contractile, is raised.

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Isolation, Electron Microscopy and 3D Reconstruction of Invertebrate Muscle Myofilaments

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Abstract

Understanding the molecular mechanism of muscle contraction and its regulation has been greatly influenced and aided by studies of myofilament structure in invertebrate muscles. Invertebrates are easily obtained and cover a broad spectrum of species and functional specializations. The thick (myosin-containing) filaments from some invertebrates are especially stable and simple in structure and thus much more amenable to structural analysis than those of vertebrates.

Comparative studies of invertebrate filaments by electron microscopy and image processing have provided important generalizations of muscle molecular structure and function. This article reviews methods for preparing thick and thin filaments from invertebrate muscle, for imaging filaments by electron microscopy, and for determining their three dimensional structure by image processing. It also highlights some of the key insights into filament function that have come from these studies.

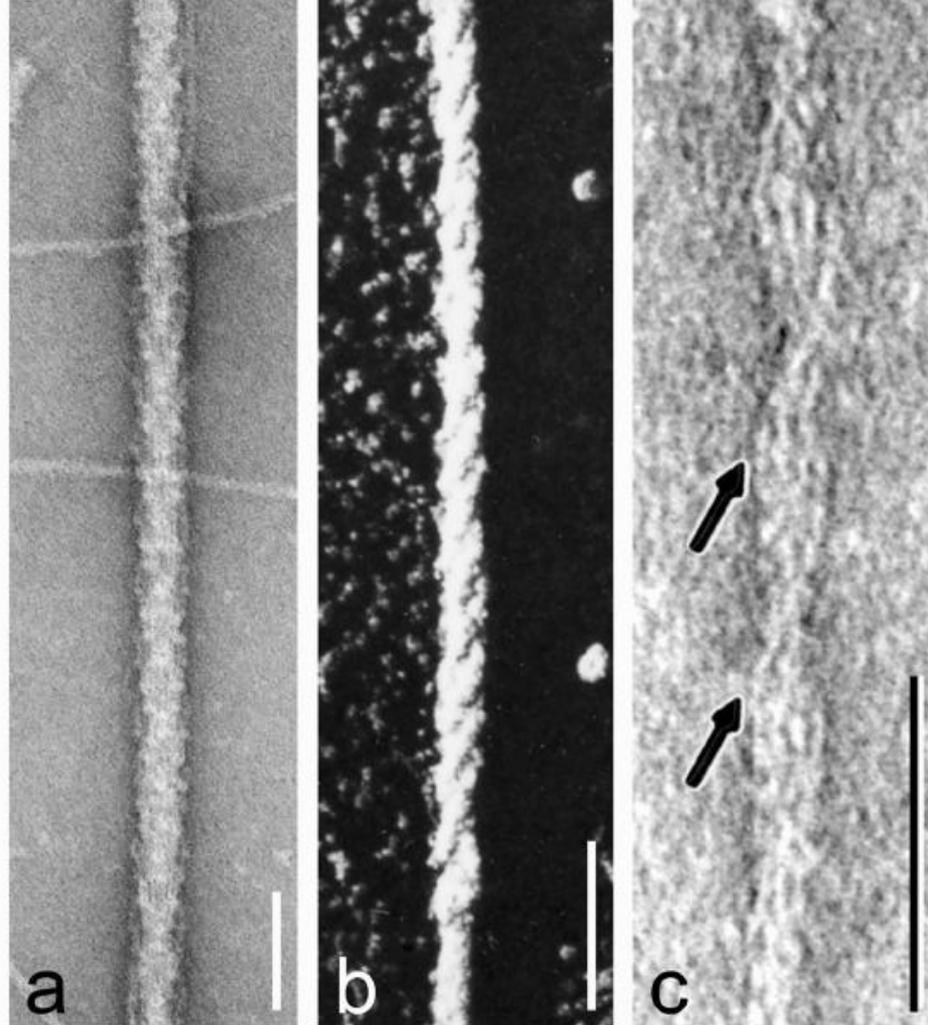


Figure 2.

Negative staining and shadowing. (a) unpurified tarantula thick filaments, with thin filaments in background (from [4]); (b) metal-shadowed tarantula thick filament showing right-handed helical tracks (from [5] with permission); (c) negatively stained thin filament from frog cardiac muscle (from [103] with permission); this vertebrate image is chosen for the clarity with which it reveals tropomyosin (arrowed strands), although it was invertebrate filaments that first demonstrated the tropomyosin-shift mechanism unequivocally [12]. In (a,c), protein is white and stain dark; in (b) metal is white. Scale bars: a, b (100 nm), c (50 nm).

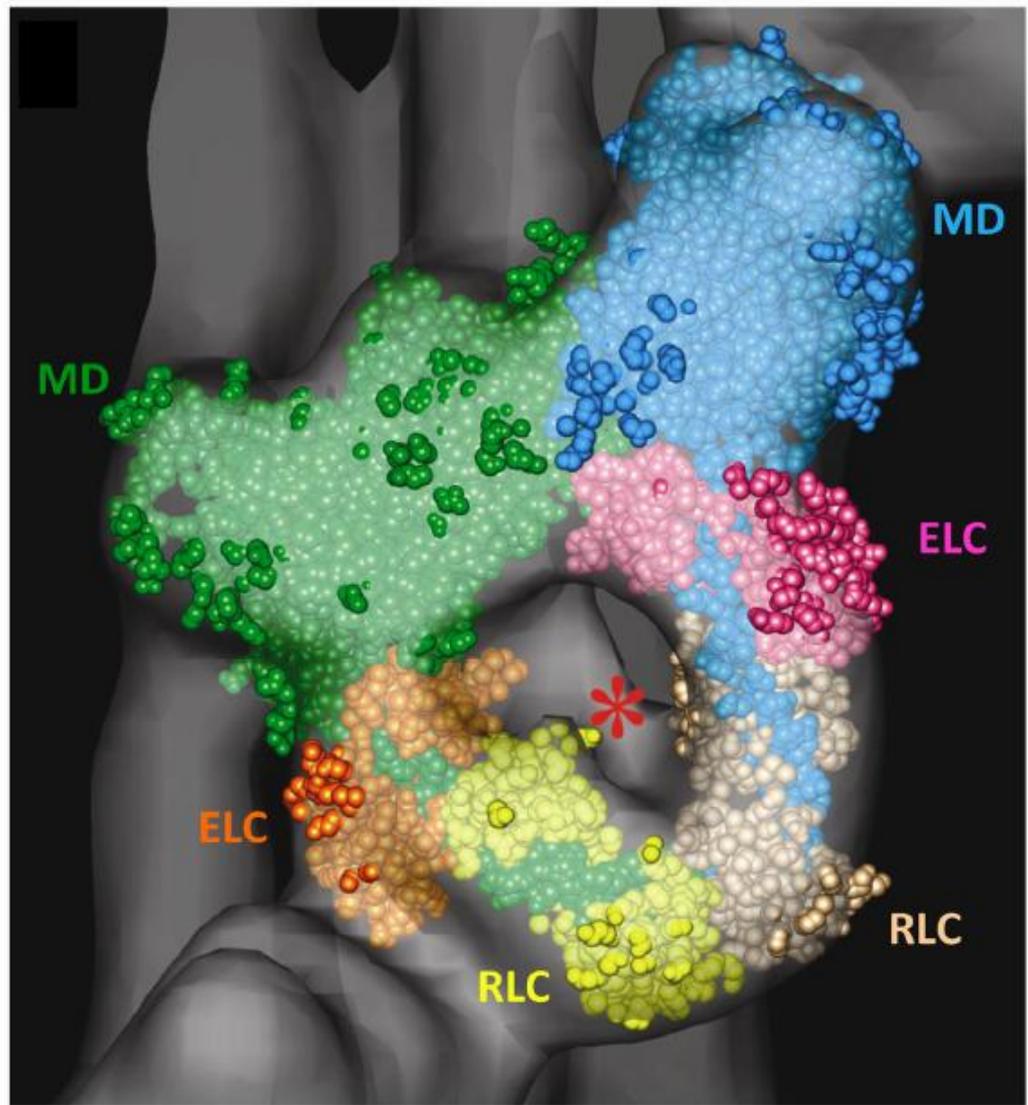


Figure 6. Fitting of myosin head atomic structure into repeating J-motif in tarantula reconstruction (Fig. 5e). Motor domain (MD), essential light chain (ELC) and regulatory light chain (RLC) of blocked head are in green, orange and yellow; those of free head are blue, pink and beige. Asterisk indicates rod-like volume of density that represents the start of the S2 portion of the myosin tail. Modified from [50].

RESEARCH ARTICLE

Muscular tissues of the squid *Doryteuthis pealeii* express identical myosin heavy chain isoforms: an alternative mechanism for tuning contractile speed

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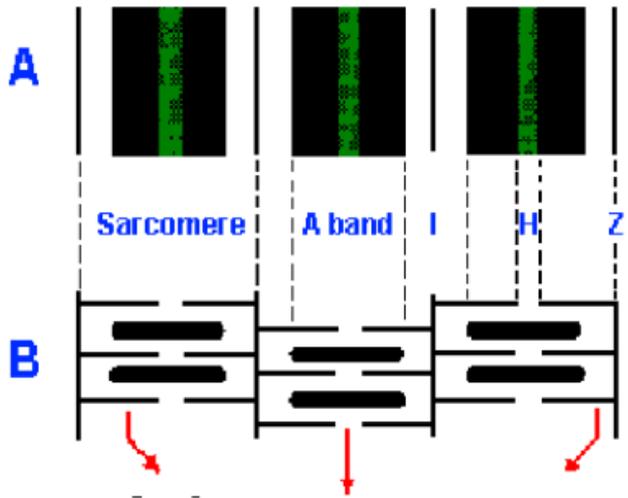
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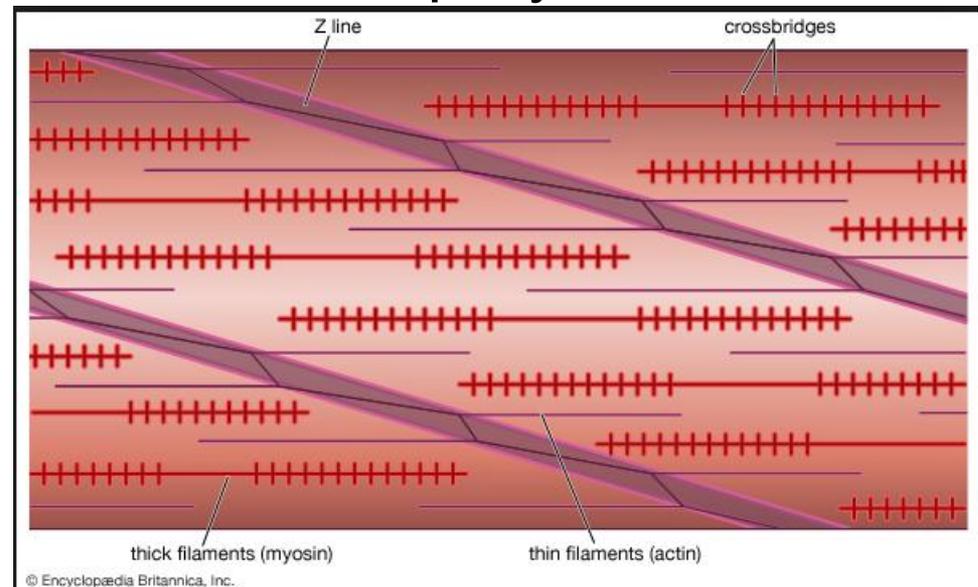
We identified three myosin heavy chain isoforms in squid muscular tissues, with differences arising at surface loop 1 and the carboxy terminus. All three isoforms were detected in all five tissues studied. These results suggest that the muscular tissues of *D. pealeii* express identical myosin isoforms, and it is likely that **differences in muscle ultrastructure, not myosin ATPase activity, represent the most important mechanism for tuning contractile speeds.**

This rapid strike is caused by contraction of transverse muscle in the core of the tentacular stalk. The tentacle transverse muscle is unusual amongst cephalopods, as it includes fibres that are **cross-striated with short thick filaments and sarcomeres (~0.8um thick filament length)**, whereas most cephalopod muscle is obliquely striated with long thick filaments [e.g. the **thick filaments of arm transverse muscle fibres are ~7.4um** (Kier and Curtin, 2002)]. Measurements of shortening velocities in transverse muscle tissue preparations revealed that the transverse muscle of the tentacle contracts nearly 10 times faster than the transverse muscle of the arm [15 vs 1.5 muscle lengths s⁻¹, respectively (Kier and Curtin, 2002)]. This 10-fold greater contractile speed in the tentacles is expected given the observed differences between the transverse muscle ultrastructure in the arms and tentacles. Because the tentacle fibres contain 10-fold more sarcomeres per unit length than the arm muscle and the shortening velocity is proportional to the number of elements in series (Huxley and Simmons, 1973; Josephson, 1975), the contractile speed of the transverse muscle of the tentacle is predicted to be 10-fold faster than that of the arm, which indeed it is (Kier and Curtin, 2002).

cross-striated



obliquely striated



General differences in NMJ physiology of crustaceans

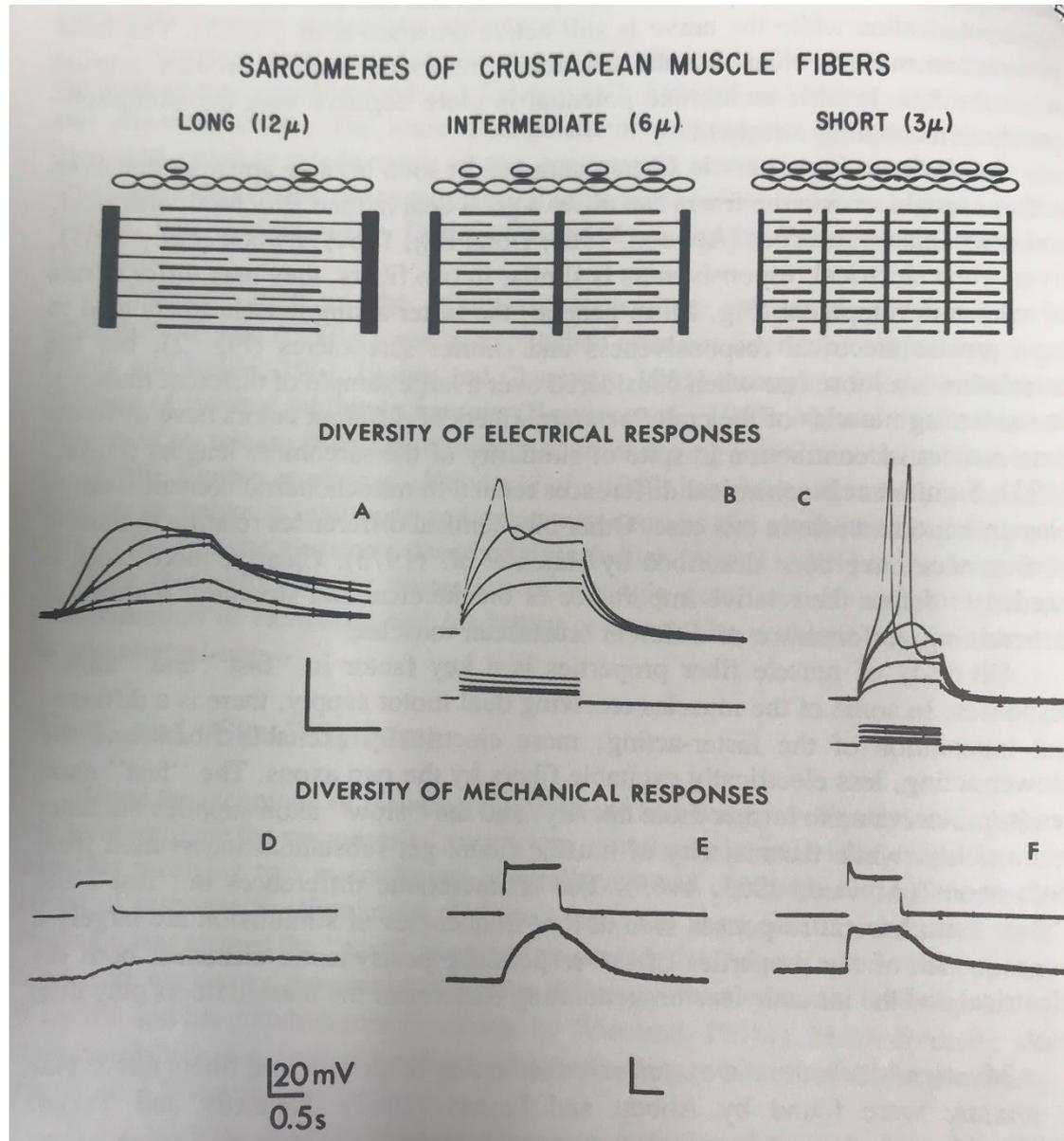


TABLE 1. Correlation of sarcomere type with physiological properties.

Sarcomere type	Rate of isometric tension development	Maximum isometric tension	Membrane resistance	Probability of spike or large graded response
Long (8μ)	Slow (e.g., $1 \text{ kg/cm}^2/\text{sec}$ in <i>Cancer</i>)	Large (e.g., 5 kg/cm^2 in barnacle)	High (e.g., $1170 \Omega \text{ cm}^2$ in <i>Carcinus</i>)	Low
Intermediate ($4-8\mu$)	Intermed. (e.g., $8 \text{ kg/cm}^2/\text{sec}$ in <i>Cancer</i>)	Intermed. (e.g., 4.5 kg/cm^2 in lobster abdomen)	Intermed. (e.g., $300 \Omega \text{ cm}^2$ in <i>Carcinus</i>)	Intermed.
Short (4μ)	Fast (e.g., $40 \text{ kg/cm}^2/\text{sec}$ in <i>Cancer</i>)	Small (e.g., 0.8 kg/cm^2 in lobster abdomen)	Low (e.g., $100 \Omega \text{ cm}^2$ in <i>Carcinus</i>)	High

References: *Cancer*: Atwood et al. (1965); barnacle: Hoyle and Smyth (1963); lobster: Jahromi and Atwood (1969); *Carcinus*: Atwood (1963).

TABLE 5. *Muscles with one excitatory axon.*

Muscle	Innervation	Terminals
<i>Panulirus</i> stomach muscle (cardiac portion)	1 E-axon (tonic)	Intermediate output, poor facilitation
Lobster rotator	1 E-axon (tonic);	Low output, good facilitation
Crayfish opener (<i>Procambarus</i>)	1 E-axon (tonic);	Low output, good facilitation; Intermediate output, poor facilitation
<i>Grapsus</i> stretcher	1 E-axon (tonic);	Low output, strong facilitation; Intermediates; High output, poor facilitation
<i>Chionecetes</i> opener	1 E-axon (tonic);	Low output, strong facilitation; Intermediate; High output, poor facilitation
<i>Cancer</i> accessory flexor	1 E-axon (tonic);	Low output, good facilitation; Intermediate output, intermediate facilitation

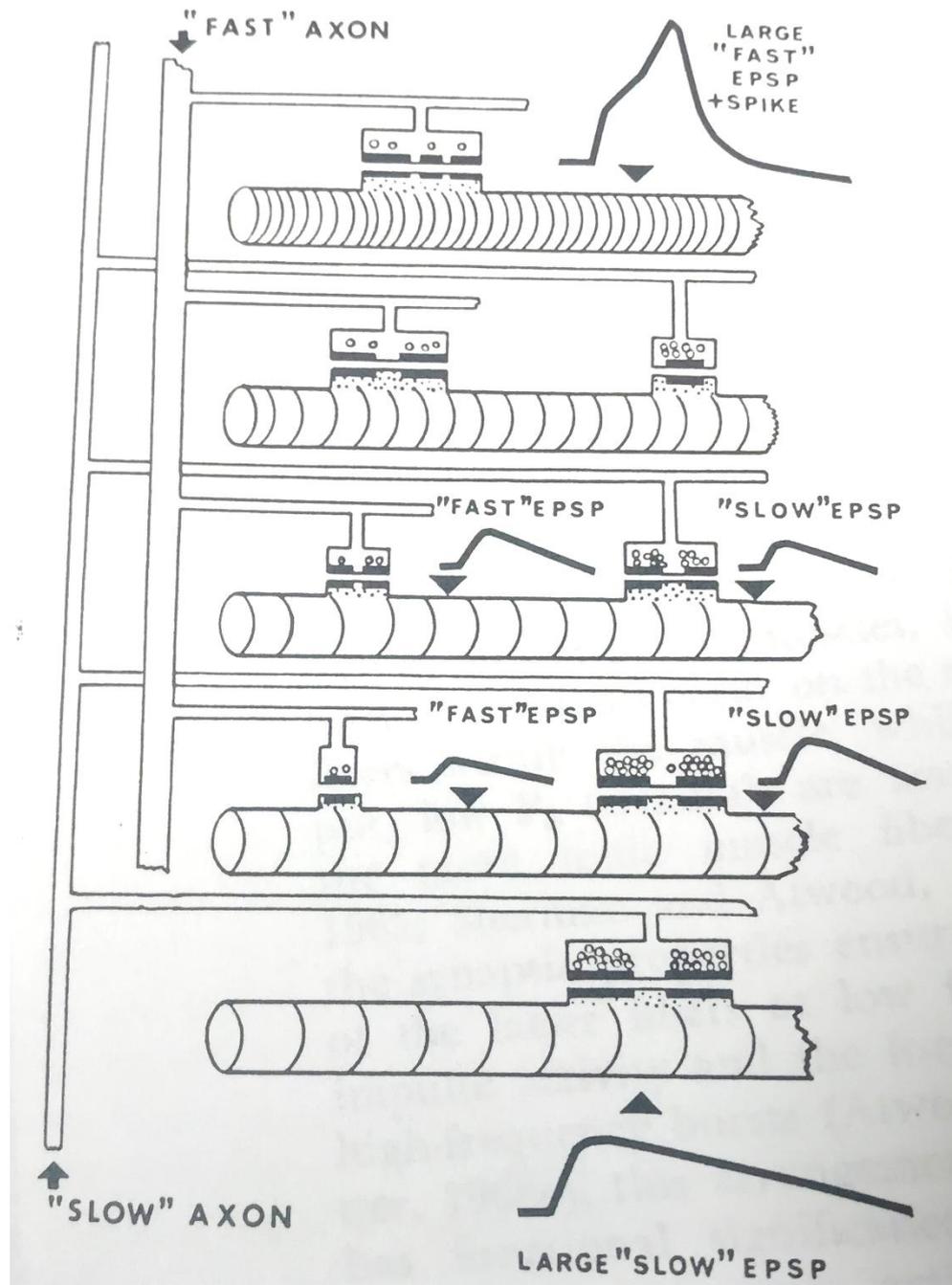


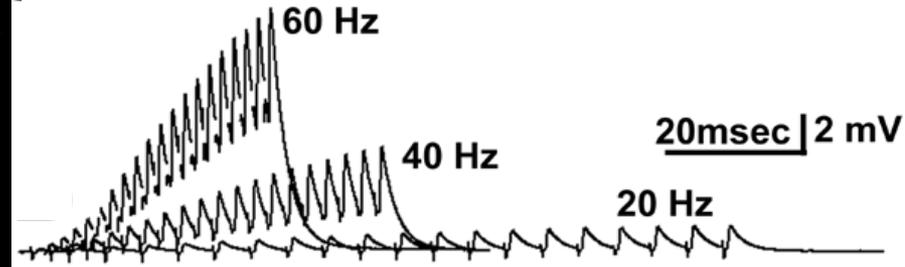
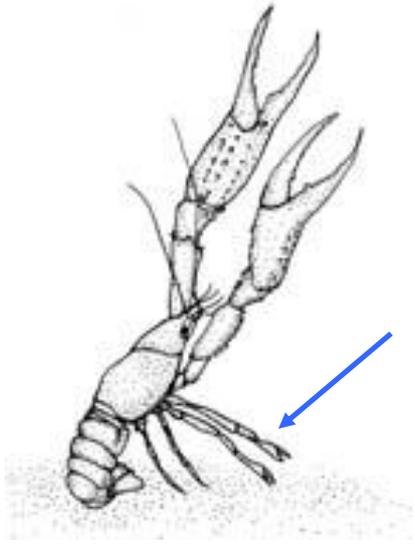
TABLE 7. *Sarcomeres of Grapsus limb buds (stretcher muscle).*

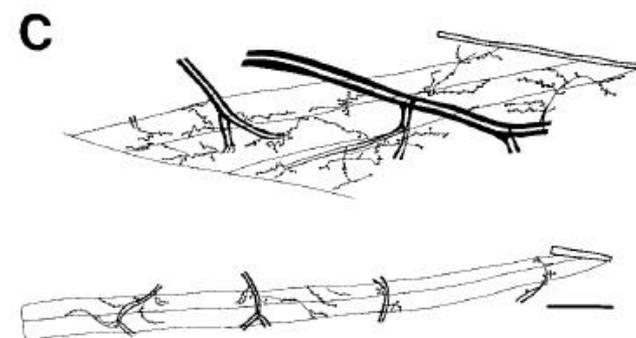
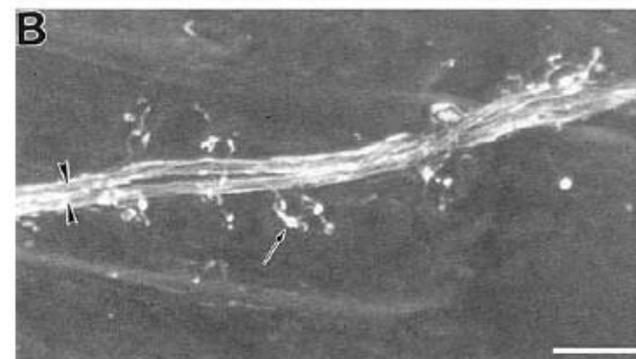
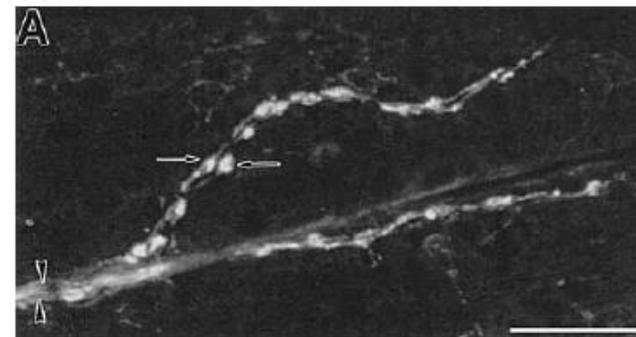
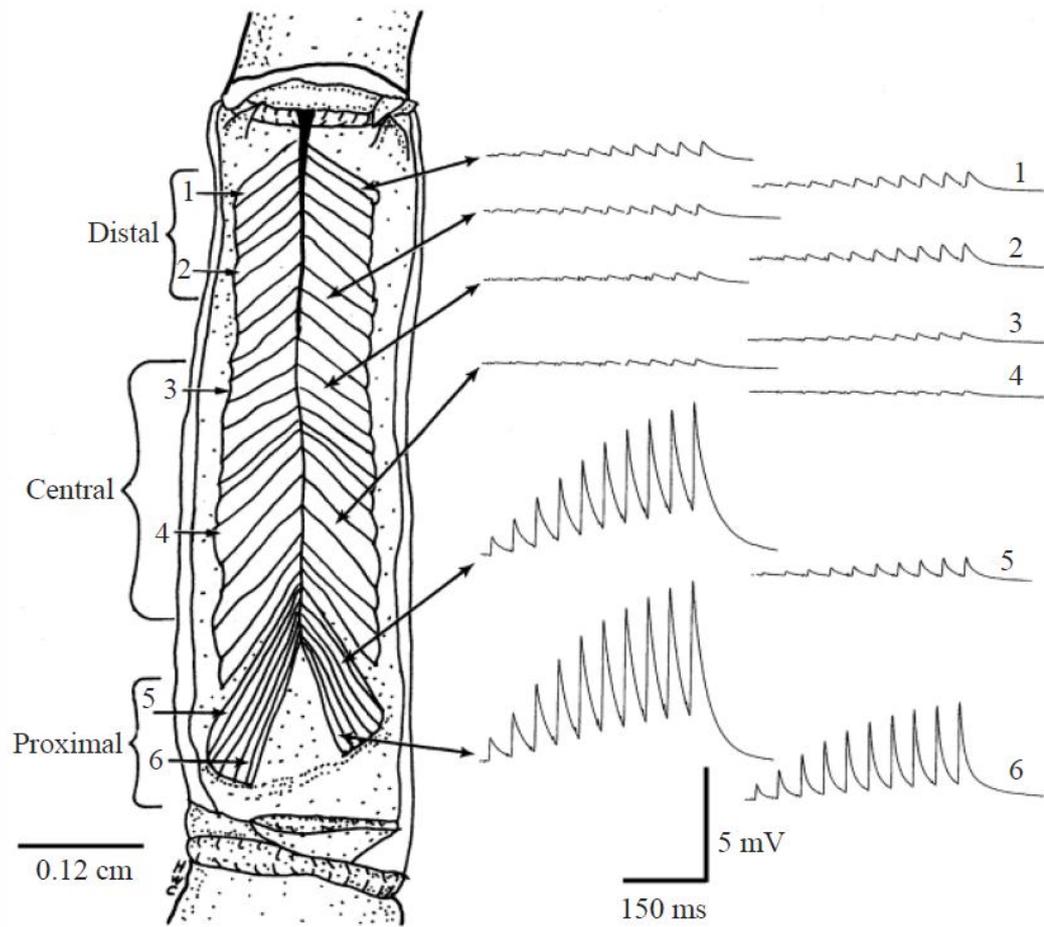
Limb bud length, cm	R value	Mean sarcomere length, μ
0.4	8	3.2
0.6	10.7	4.5
1.1	24.5	4.9
Adult		7.5 (high F_e); 10.7 (low F_e).

(R value; after Bliss, 1960.)

Crayfish







Leg extensor muscle

