

Review

Supercontracting muscle: producing tension over extreme muscle lengths

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Summary

Muscle mechanics dictates a trade-off between the ability of a muscle to generate isometric force and its length. This intrinsic trade-off is the result of the need for overlap between thick and thin filaments upon extension of the sarcomere and of the limitations imposed by the physical interference between the thin filaments and the thick filaments with the Z-disk upon contraction. However, previously published data indicate that chameleons are able to produce a nearly constant tongue retraction force over a wide range of tongue extension lengths, made possible by the presence of supercontracting muscle in the tongue retractors. Investigation of the length/tension properties and ultrastructure of the tongue retractor in a closely related agamid lizard (*Pogona*

vitticeps) indicates that the ability to generate tension at extreme elongation is probably a derived feature for chameleons. Whereas chameleons are unique among vertebrates in possessing supercontracting muscle, this seems to be a common phenomenon in invertebrates. However, the presence of supercontracting muscle in chameleons and in several invertebrate groups seems to be coupled to the need to generate tension over large changes in muscle length and might be a more general solution for this problem.

Key words: supercontraction, lizard, transmission electron microscopy, contractile properties, muscle.

Introduction

Muscle mechanics, based on the sliding filament model of muscle contraction (Huxley and Niedergerke, 1954; Huxley and Hanson, 1954), dictates a trade-off between the ability of a muscle to generate isometric force and its length. This intrinsic trade-off is the result of the need for overlap between thick and thin filaments upon extension of the sarcomere and of the limitations imposed by the physical interference of thin filaments and thick filaments with the Z-disk upon contraction (Hanson and Huxley, 1955). At extreme elongation or shortening of the muscle, no muscle force can be generated (e.g. Ramsey and Street, 1940; Podolsky, 1964; Gordon et al., 1966). Typical vertebrate striated muscle will consequently be limited to operate at a fairly narrow range of sarcomere lengths situated around the optimal sarcomere length that allows maximal force output (see Burkholder and Lieber, 2001).

Some vertebrates, however, do show extreme muscle elongation under natural circumstances. In animals with ballistic tongues, such as frogs and lungless salamanders, the tongue retractor undergoes considerable lengthening during prey capture (Deban et al., 1997; Nishikawa, 2000). Chameleons are probably best known for their ability to project

their tongue up to twice body length (>1000% of the tongue resting length) while catching prey (Wainwright et al., 1991; Meyers and Nishikawa, 2000; Schwenk, 2000). Clearly, such extreme elongation would take the muscle beyond the plateau in its length/tension relationship and, thus, preclude it from producing any more force (Gordon et al., 1966).

However, there are other types of muscle that are able to shorten and maintain tension over a much wider length range than the typical cross-striated muscle of vertebrates. Z-disks are absent from smooth muscle, so it is capable of generating tension to lengths of less than one-third of the optimal muscle length (i.e. the length at which force production is maximal) (see Gordon and Siegelman, 1971; Small et al., 1990). The drawbacks associated with smooth muscle are its low contraction velocity and its lower maximal force output for a given cross-sectional area (i.e. approximately one-third of that of cross-striated muscle) (Gordon and Siegelman, 1971). Yet chameleons are known to eat large prey (Broadley, 1973; Schleich et al., 1996), so they must be able to exert large retraction forces at any given tongue projection distance. Moreover, a reasonably rapid retraction of the tongue with

adhering prey is probably important since this reduces the time available for the prey to escape. These constraints clearly exclude smooth muscle from playing an important role in the tongue retractor of these animals.

Recently, it has been demonstrated that chameleons have overcome this constraint and are indeed able to generate large, nearly constant forces over a wide range of tongue extension lengths *in vivo* (Herrel et al., 2001). The morphological basis for this remarkable behaviour is in the muscle ultrastructure. On the one hand, the filaments are positioned in such a way that extensive overlap between thick and thin filaments occurs at maximal extension (Herrel et al., 2001). On the other hand, perforations are present in the Z-disks (Rice, 1973; Herrel et al., 2001) and allow the myosin filaments to move through the Z-disks and engage in cross-bridge cycling with thin filaments of the adjacent sarcomere (Fig. 1) (Osborne, 1967). This phenomenon has been observed in several species of chameleon, and it has been proposed as a primitive trait for the group as a whole, closely linked to their extreme sit-and-wait life-style (Herrel et al., 2001).

In the present paper, we investigate the evolutionary origin of the highly specialised chameleon tongue retractor muscle and its properties by examining the ultrastructure and physiological properties of the homologous muscle (i.e. the tongue retractor) in a closely related agamid lizard (*Pogona vitticeps*). In addition, we review published accounts of extreme shortening capacity in vertebrate and invertebrate muscles and try (i) to investigate the relationships thereof with the presence of supercontracting striated muscle and (ii) to determine whether alternative solutions for the problem of generating tension at extreme elongation exist.

Materials and methods

Force measurements

The length/tension properties of the tongue retractor muscles were investigated in two live, anaesthetised adult *Pogona vitticeps* (snout-to-vent length 99.07 mm and 107.85 mm). In this experiment, the animals were deeply anaesthetised with ketamine (200 mg kg⁻¹ body mass), and bipolar stainless-steel electrodes were implanted bilaterally into the tongue retractor muscle (mm. hyoglossus). The animals were kept under deep anaesthesia by administering additional ketamine (half the original dose) every 2–3 h.

In the experiments, the animal was mounted upside-down in a purpose-built holder, the hyoid was immobilised in the resting condition, and the anterior tongue pad was sutured to a muscle lever (Cambridge Technology model 6650 force lever connected to an Aurora Scientific Series 305B lever system controller). Initially, the muscle was twitch-stimulated (Grass S48 stimulator connected to a Grass SIU5 stimulus isolation unit), and stimulation voltage was increased until maximal force output was obtained (at 12 V). In all subsequent experiments, muscles were stimulated at 15 V to ensure maximal muscle recruitment.

For both individuals, the muscle length was varied and the

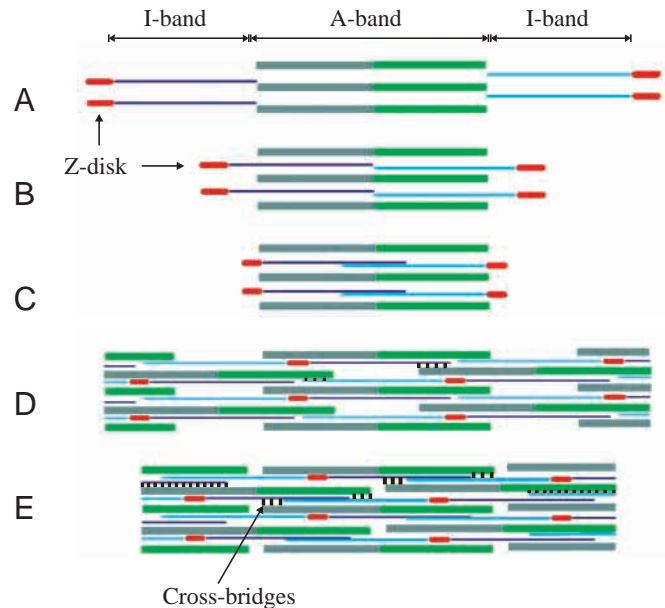


Fig. 1. Schematic diagram illustrating the process of supercontraction. (A) Here, the muscle is completely extended, resulting in no overlap between thick and thin filaments. (B) Muscle in the contracted state, overlap between thick and thin filaments is optimal. (C) Muscle in an even further contracted state; thin filaments overlap and thick filaments abut on the Z-disk. In normal vertebrate cross-striated muscle, no force can be generated at this stage. (D) Muscle in supercontraction. The thick filaments have passed through the holes in the Z-disks and are starting to engage in bonding with the thin filaments of the adjacent sarcomere. (E) Muscle in complete supercontraction. After this stage, the thick filaments will physically interact with each other and the muscle can no longer generate force. The green bars represent the thick filaments, the blue bars the thin filaments and the red bars the elements of the Z-disk. In the sarcomere, polarities are such that the dark green part of the thick filament can engage in binding with the dark blue thin filament and the light green part of the thick filament with the light blue thin filament. Hypothetical cross-bridges formed between filaments of adjacent sarcomeres (in black) are indicated in D and E. Modified after Osborne (1967) and Hardie (1976).

passive tension was recorded. At each length, the muscle was twitch-stimulated (15 V, 2 ms pulse duration) and the tongue retraction force was recorded. For at least three twitches in both individuals, muscle twitch kinetics (maximal isometric tension, time to peak tension, half-relaxation time) was recorded. Next, the muscle was kept at resting length (see below) and stimulated with tetanic trains of 300 ms (2 ms pulse duration) of increasing frequency. The fusion frequency (60 Hz) and tension at fusion were determined. Subsequently, tongue length was varied and the passive tension recorded; the muscle was then stimulated with 300 ms tetanic trains at 60 Hz and the active tension recorded. Throughout the experiment, the temperature of the animal was kept at 32 °C by a heat lamp and continuously monitored with a YSI telethermometer and thermocouple. After all recordings, the animals were killed by injection of a lethal dose of ketamine (twice the anaesthetic dose).

During all physiological experiments, muscle resting length was defined as the length of the muscle at rest (i.e. with the tongue lying at rest in the mouth). Extensions of the muscle thus involve stretching of the muscle beyond this length and correspond to tongue extensions observed during prey capture *in vivo*.

Transmission electron microscopy

For transmission electron microscopy, the mm. hyoglossus of three adult *Pogona vitticeps* (mass 30 ± 9.1 g) and one adult female *Chameleo calytratus* (mass 84 g) was removed under deep anaesthesia (ketamine, 200 mg kg^{-1} body mass). Tissue samples were removed from the middle third of the muscle and cut in two. The animals were killed with an overdose of ketamine after removal of the muscle. Tissue samples were fixed in 6.25 % glutaraldehyde in 0.1 mol l^{-1} sodium cacodylate buffer (pH 7.4) for 24 h. One half of the muscle sample was fixed in its resting position (i.e. unfolded for the chameleon), and the other half was extended to approximately 160 % of its resting length and tied onto a wooden stick using surgical wire (only for *P. vitticeps*). Samples were then immersed in 2.5 % glutaraldehyde in 0.1 mol l^{-1} sodium cacodylate buffer containing 0.05 % calcium chloride (pH 7.4).

Several small blocks of tissue taken from the middle part of the muscle were cut from the samples and thoroughly washed three times for 10 min in 0.1 mol l^{-1} sodium cacodylate buffer containing 7.5 % saccharose and 0.05 % calcium chloride. Next, the tissue was postfixed for 2 h at 4°C in 1 % osmium tetroxide in 0.033 mol l^{-1} veronalacetate buffer containing 4 % saccharose (pH 7.4). After postfixation, samples were rinsed three times for 10 min in 0.05 mol l^{-1} veronalacetate buffer containing 6 % saccharose sodium cacodylate buffer (pH 7.4) and dehydrated through a graded series of ethanols. The samples were then embedded in Durcupan. Suitable areas of longitudinal and cross sections of the striated muscle were selected on Toluidine-Blue-stained semi-thin sections. Subsequently, ultrathin sections were stained with lead citrate and uranyl acetate and examined in a Philips CM10 electron microscope. Photographs were taken of all samples at different locations for several sections within each sample.

For at least five sarcomeres of two different tissue samples in all three individuals, sarcomere length, thick filament length, thin filament length and filament overlap were measured on longitudinal sections. Reported values are means \pm standard deviations (S.D.).

Results and discussion

The results from the present study indicate that the tongue retractor muscle (m. hyoglossus) in the agamid lizard *P. vitticeps* corresponds to the typical vertebrate cross-striated type. At resting length, the m. hyoglossus reached peak tension in 23.9 ± 3.3 ms (two individuals, three twitches per individual). The half-relaxation time of the m. hyoglossus was 23 ± 1.4 ms ($N=6$). The contraction kinetics was indicative of a fast-twitch muscle (see Marsh and Bennett, 1985; Herrel et al., 1999). A

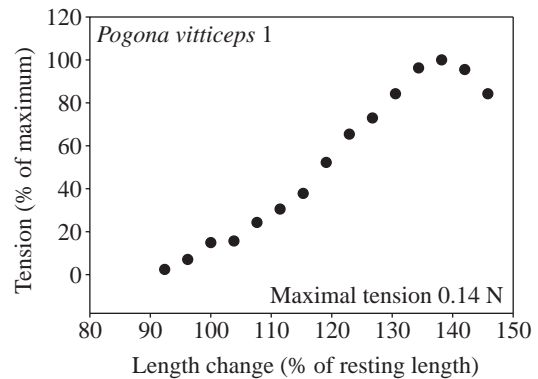


Fig. 2. Length/tension diagram for the m. hyoglossus of an adult *Pogona vitticeps*. In these experiments, the tongue of the lizard was attached to a force lever, its length was changed, the muscle was tetanically stimulated and the forces were recorded. The length/tension diagram for *P. vitticeps* is similar to that reported for other animals with typical cross-striated muscle, showing a rapid increase in tension, a distinct optimal length for contraction and a decrease in tension if the muscle is extended beyond its optimal length.

maximal twitch force of 0.023 ± 0.01 N ($N=6$) was achieved at 150 % of muscle resting length. The tetanic length/tension diagram shows the typical shape reported for vertebrate cross-striated muscle, with a fairly rapid rise in active tension, an optimal length for force production and a subsequent decrease in active tension (Fig. 2). Forces were highest (0.21 ± 0.11 N, $N=2$) at 140 and 170 % of muscle resting length in the two animals and decreased at shorter or longer lengths.

Ultrastructural investigations indicate that the Z-disks in *P. vitticeps* are of the normal continuous type (Fig. 3). The sarcomere structure is similar to that observed for the cross-striated muscle fibres in the leg muscle of lizards (Robertson, 1956). Well-defined H-, A- and I-bands are present in the resting and extended muscle samples. Sarcomere length ($2.08 \pm 0.1 \mu\text{m}$, $N=30$) as well as thick ($1.51 \pm 0.04 \mu\text{m}$, $N=30$) and thin ($0.95 \pm 0.05 \mu\text{m}$, $N=30$) filament lengths are similar to those observed for other vertebrates (see Table 1 in Burkholder and Lieber, 2001). Filament overlap is complete (overlap zone $0.68 \pm 0.03 \mu\text{m}$ on one side, $N=30$) in the resting sample, with actin filaments almost abutting on each other (Fig. 3A), so little or no tension can be generated at resting length, as was shown in the physiological experiments. At approximately 150 % of whole muscle extension, filament overlap is still large (overlap zone $0.57 \pm 0.02 \mu\text{m}$, $N=30$), without the thin filaments physically interfering with one another (Fig. 3B). Note, however, that the actual extension of the sarcomeres was only approximately 120 % for a whole muscle extension of 150 %.

The ultrastructure of the tongue retractor muscle in *C. calytratus* (Fig. 4) is different from that in *P. vitticeps* and resembles that of *C. melleri*, with clear perforations in the Z-disks (see Herrel et al., 2001). However, the unusually short sarcomere and filament lengths reported for *C. melleri* were not observed in *C. calytratus*. In this species, the sarcomere ($2.28 \pm 0.21 \mu\text{m}$, $N=10$) and thick ($1.44 \pm 0.21 \mu\text{m}$, $N=10$) and

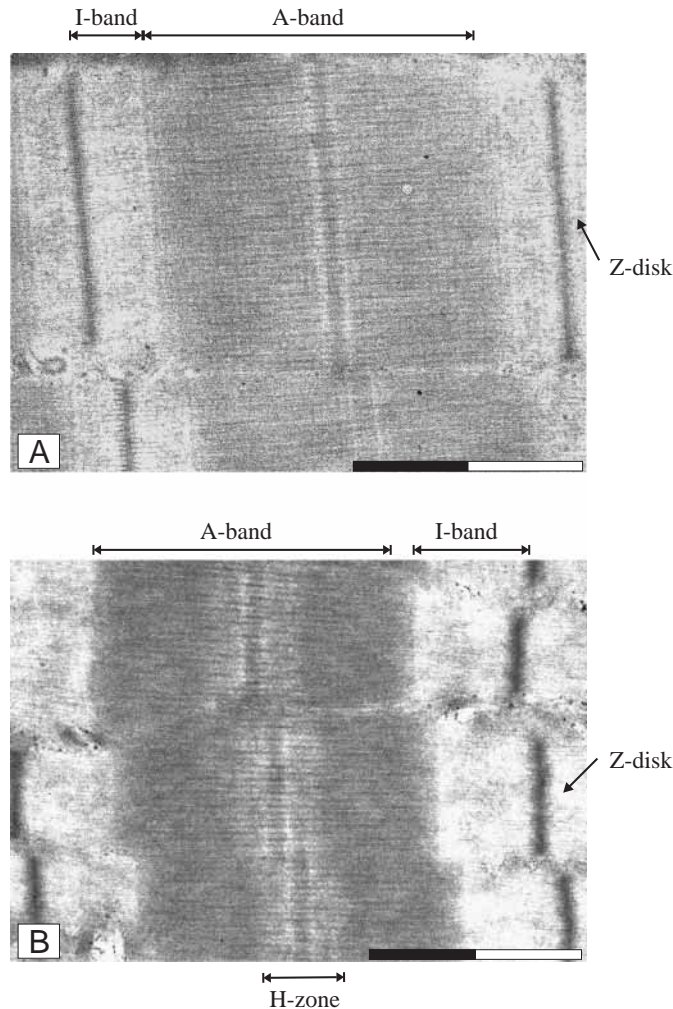


Fig. 3. Transmission electron micrograph (longitudinal section) through the tongue retractor muscle (m. hyoglossus) of an adult *Pogona vitticeps*. (A) Muscle in the resting condition. Note how the thin filaments almost abut in the middle of the A-band. The Z-disk is of the normal continuous type typical of vertebrate cross-striated muscle. (B) Section through a muscle in the extended condition (140% of whole muscle resting length). Note how the sarcomeres are extended to only approximately 120% of their resting length. Even in the extended condition, the overlap between thick and thin filaments is large, allowing the muscle to generate near-maximal tension. Scale bar, 1 μ m.

thin ($1.04 \pm 0.11 \mu\text{m}$, $N=10$) filament lengths are generally similar to those observed for *P. vitticeps*. A rough comparison between the data gathered for *C. calyptratus* and data collected from the picture of the ultrastructure of the tongue retractor in an unspecified species of chameleon published by Rice (1973) (sarcomere length $2.28 \pm 0.04 \mu\text{m}$, thick filament length $1.65 \pm 0.03 \mu\text{m}$, thin filament length $0.74 \pm 0.04 \mu\text{m}$; $N=5$; see Fig. 1 of Rice, 1973) indicates that the values of sarcomere and filament lengths obtained for *C. melleri* (Herrel et al., 2001) were potentially incorrect. Further investigations are under way to determine the ultrastructure in additional specimens of

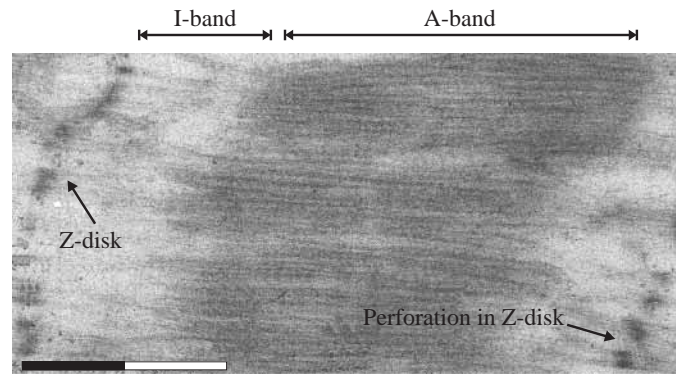


Fig. 4. Transmission electron micrograph (longitudinal section) through the tongue retractor muscle (m. hyoglossus) of an adult *Chameleo calyptratus*. Note the perforations in the Z-disks (arrow) characteristic of supercontracting muscle. Scale bar, 1 μ m.

C. calyptratus and in other species of chameleon to test the generality of these findings.

These results indicate that the supercontractile capacity of the tongue retractor is probably a unique and derived feature of chameleons. The tendency to generate maximal force when the muscle is stretched and the considerable filament overlap upon extension are already present in the sister group to chameleons, the agamids. Functionally, this seems obvious since the task of the tongue retractor is to retract the tongue after it has been protracted during prey capture or transport (see Schwenk and Throckmorton, 1989; Herrel et al., 1997). Also, in other vertebrates that use their tongue to capture prey, such as frogs, the tongue retractor produces maximal tension when extended (Peters and Nishikawa, 1999). Whether this is linked to the predominance of the use of the tongue during prey capture (where it is greatly extended) or is a general consequence of the lingual transport mode of most terrestrial vertebrates remains to be seen. This could be tested by investigating the physiological properties and ultrastructure of the tongue retractor in scleroglossan lizards, which use their jaws to capture prey but still use their tongue during prey transport (e.g. scincids, lacertids).

The supercontractile mechanism thus seems to have originated within the evolution of chameleons and is probably the consequence of their highly specialised arboreal sit-and-wait foraging strategy. Being cryptic, arboreal sit-and-wait predators, the ability to project the tongue ballistically was undoubtedly a key innovation that allowed the radiation of these animals. Because of the arboreal cryptic life-style, chameleons were no longer able to lunge for prey and had to rely exclusively on tongue retraction to move the prey back to the mouth. The importance of large prey, typical for sit-and-wait predators (Pough et al., 2001), put further constraints on the function of the tongue retractors and presumably triggered the evolution of supercontractile properties in the chameleon tongue.

Given that the ballistic tongue projection mechanism of chameleons was probably an essential first step in the

development of the unusual muscle properties of the tongue retractors, one can speculate whether other vertebrates with ballistic tongues also show similarly specialised tongue retractor muscles. Both frogs (Nishikawa, 1999, 2000) and lungless salamanders (Deban et al., 1997; Deban and Wake, 2000; Wake and Deban, 2000) have tongues that elongate greatly during prey capture and that are probably subject to similar constraints on the function of the tongue retractor muscles. In frogs, there are two major tongue protrusion strategies during which the tongue is extended to more than 100% of its resting length: inertial elongation and hydrostatic elongation (Nishikawa, 1999). However, experiments on muscle physiology (Peters and Nishikawa, 1999) and investigations of the muscle ultrastructure (Nishikawa et al., 1999) both indicate that neither of these strategies is accompanied by the highly specialised muscle ultrastructure observed in chameleons. Although, in both cases, the tongue needs to retract to approximately 50% or more of its resting length, the major difference between frogs and chameleons is the lack of the need for a continuous substantial force production during retraction in frogs. Inertial elongators will typically use extensive forward body and jaw movements when capturing large prey (Anderson, 1993; Anderson and Nishikawa, 1996; Nishikawa, 2000), thus reducing any constraint on force production. Hydrostatic elongators, in contrast, although they do not lunge at their prey, are typically small-prey specialists feeding primarily on ants and termites (Ritter and Nishikawa, 1995). Although, in these animals, at extreme *in vivo* tongue extensions, filament overlap and thus force production is minimal, they do not need to produce large forces to retract their tiny prey.

Lungless salamanders, in contrast, are not ant specialists and typically do not lunge at prey. Although the prevalence of larger prey in the diet of these animals is unknown, they are extremely successful at capturing medium-sized prey placed at a variety of distances from the mouth (Deban and Dicke, 1999). Moreover, many of these species are arboreal or rock climbers, so lunging is not an option. The most specialised species, such as those of the genus *Hydromantes*, can extend their tongue over distances of more than one body length (Deban et al., 1997). Not surprisingly, the tongue retractor muscle in these animals is rather unusual. As in chameleons, the muscle is extremely long, but instead of being tightly coiled and packed into the mouth, it extends all the way back to the pelvic girdle, with part of the muscle lying in a big loop in the space in front of the heart (Deban et al., 1997). Given the similarities with chameleons, we suggest that these animals are prime candidates for possessing similar muscular specialisations, including supercontractile muscle in their tongue retractor. However, nothing is known about the physiology or ultrastructure of the tongue retractor in these animals, so future research will have to determine whether this is actually the case.

Whereas the phenomenon of *in vivo* supercontraction which, at least in chameleons appears to be linked to the production of tension with extreme elongation, seems to be rare in

vertebrates, in invertebrates there are many cases in which supercontractile striated muscle has been observed. Some of the best-known cases include the barnacle scutal depressor muscle (Hoyle and McAlear, 1963; Hoyle et al., 1965, 1973), in which the phenomenon of supercontraction was first described, the ventral body wall musculature of the blowfly larva (Osborne, 1967), the visceral muscles of the tsetse fly (Rice, 1970) and of *Drosophila melanogaster* (Goldstein and Burdette, 1971) and a variety of other muscles in insects (e.g. Hardie, 1976; Candia-Carnevali, 1978; Hardie and Hawes, 1982; Cook and Pryor, 1997; Friedländer et al., 1999). In several of the instances cited above, the presence of supercontracting muscle seems to be coupled to the need to generate tension over large changes in length, as seems to be the case in chameleons. In fact, Osborne (1967) stated that 'thus, although the muscles may not change in length by as much as 76% during locomotory activity, the mechanism of supercontraction might allow them to develop a constant tension over a greater range than is possible in vertebrate striated muscle', indicating that tension rather than shortening capacity in itself might be the key element in the evolution of supercontraction. Also, in the barnacle scutal depressor muscle, in which a large, constant force needs to be produced during escape jet locomotion (Hoyle et al., 1965), the presence of supercontractile muscle seems to be coupled to the production of tension of over a wide working range.

In insects, supercontracting muscle typically seems to be associated with hydraulic or hydrostatic systems in which the constraint on the generation of tension probably comes into play as well (e.g. Rice, 1970; Goldstein and Burdette, 1971). Yet, in other insect muscles, no constraint on tension is apparent, and here only the ability to shorten extensively might be the functionally relevant property. Smooth muscle is absent from insects, so in many cases in which this type of muscle would normally be observed (i.e. where speed of contraction and absolute tension are not so important), supercontracting muscle is present (see Candia-Carnevali, 1978; Hardie and Hawes, 1982; Cook and Pryor, 1997; Friedländer et al., 1999). Unfortunately, there have been only two studies of which we are aware investigating the physiological properties of supercontracting muscle in invertebrates (Hoyle and Smyth, 1963; Hardie, 1976), and in only one of these were the length/tension properties of the muscle investigated (Hardie, 1976). The results of that study seem to indicate that, again, supercontractile muscle is able to generate near-maximal tension over a very broad range of shortening distance (see Fig. 5) (Hardie, 1976).

In other invertebrate classes (e.g. cephalopods, nematodes and annelids), one other type of muscle seems to be able to fulfil a similar functional role: obliquely striated muscle. The Z-disk material in these animals is not aggregated into a distinct Z-disk as in cross-striated muscle (Kier, 1985), so cross-bridge cycling can continue beyond the ranges normally observed for cross-striated muscle (Rosenbluth, 1967; Milligan et al., 1997). Despite these theoretical considerations, measurements on the obliquely striated muscle of squid and

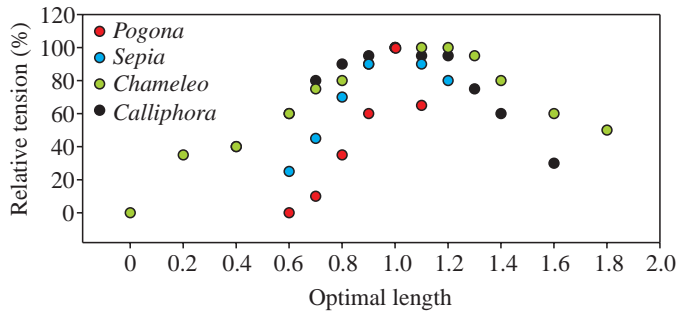


Fig. 5. Summary diagram illustrating the differences in contractile properties between a variety of muscles. Relative tension is plotted against optimal muscle length. The length/tension properties of a typical vertebrate cross-striated muscle are indicated in red (data for the tongue retractor in *Pogona vitticeps*). The length/tension diagram for the obliquely striated mantle muscle in *Sepia officinalis* is depicted in blue (Milligan et al., 1997). The length/tension properties of chameleon (*Chameleo oustaleti*) tongue retractor muscle are depicted in green (Herrel et al., 2001) and the length/tension properties for the body wall muscle of *Calliphora erythrocephala* (Hardie, 1976) are depicted in black. Both the chameleon and the *Calliphora erythrocephala* muscles are of the supercontracting type and are able to generate tension over extreme muscle lengths. Cuttlefish obliquely striated muscle (blue) seems to have intermediate length/tension properties and is able to generate tension over a wider range of muscle lengths than typical vertebrate cross-striated muscles (red).

cuttlefish did not confirm that force could be produced over a much larger range of lengths than in cross-striated fibres (Milligan et al., 1997). However, if data for obliquely striated cuttlefish muscle are compared with data for a typical vertebrate cross-striated muscle and supercontracting muscle (Fig. 5), it becomes apparent that obliquely striated muscle has length/tension properties intermediate between those of cross-striated and supercontracting muscle. In conclusion, we would like to suggest that the combination of extreme performance (i.e. extreme shortening and force generation) apparently resulted in a similar evolutionary 'solution' (i.e. supercontractile muscle) in major groups of invertebrates and in some vertebrates.

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References

Anderson, C. W. (1993). Modulation of feeding behavior in response to prey type in the frog *Rana pipiens*. *J. Exp. Biol.* **179**, 1–11.

- Anderson, C. W. and Nishikawa, K. C. (1996). The roles of visual and proprioceptive information during motor program choice in frogs. *J. Comp. Physiol. A* **179**, 753–762.
- Broadley, D. G. (1973). Predation on birds by reptiles and amphibians in South-Eastern Africa. *Honeyguide* **76**, 19–21.
- Burkholder, T. J. and Lieber, R. L. (2001). Sarcomere length operating range of vertebrate muscles during movement. *J. Exp. Biol.* **204**, 1529–1536.
- Candia-Carnevali, M. D. (1978). Z-line and supercontraction in the hydraulic muscular systems of insect larvae. *J. Exp. Zool.* **203**, 15–30.
- Cook, B. J. and Pryor, N. W. (1997). Structural properties of the intrinsic muscles of the Malpighian tubules of the female stable fly, *Stomoxys calcitrans* L. *J. Entomol. Sci.* **32**, 138–147.
- Deban, S. M. and Dicke, U. (1999). Motor control of tongue movement during prey capture in plethodontid salamanders. *J. Exp. Biol.* **202**, 3699–3714.
- Deban, S. M. and Wake, D. B. (2000). Aquatic feeding in salamanders. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 65–94. San Diego: Academic Press.
- Deban, S. M., Wake, D. B. and Roth, G. (1997). Salamander with a ballistic tongue. *Nature* **389**, 27–28.
- Friedländer, M., Jeger, R. E. and Scholtz, C. H. (1999). Intra-follicular visceral musculature in *Omorgus freyi* (Haaf) (Coleoptera: Trogidae) testes. *Int. J. Insect Morphol.* **28**, 5–11.
- Goldstein, M. A. and Burdette, W. J. (1971). Striated visceral muscle of *Drosophila melanogaster*. *J. Morphol.* **134**, 315–334.
- Gordon, A. M., Huxley, A. F. and Julian, F. J. (1966). The variation of isometric tension with sarcomere length in vertebrate muscle fibres. *J. Physiol., Lond.* **184**, 170–192.
- Gordon, A. R. and Siegman, M. J. (1971). Mechanical properties of smooth muscle. I. Length–tension and force–velocity relations. *Am. J. Physiol.* **221**, 1243–1249.
- Hanson, J. and Huxley, H. E. (1955). The structural basis of contraction in striated muscle. *Symp. Soc. Exp. Biol.* **9**, 228–264.
- Hardie, J. (1976). The tension/length relationship of an insect (*Calliphora erythrocephala*) supercontracting muscle. *Experientia* **32**, 714–716.
- Hardie, J. and Hawes, C. (1982). The three-dimensional structure of the Z-disc in insect supercontracting muscles. *Tissue Cell* **14**, 309–317.
- Herrel, A., Aerts, P., Fret, J. and De Vree, F. (1999). Morphology of the feeding system in agamid lizards; ecological correlates. *Anat. Rec.* **254**, 496–507.
- Herrel, A., Cleuren, J. and De Vree, F. (1997). Quantitative analysis of jaw and hyolingual muscle activity during feeding in the lizard *Agama stellio*. *J. Exp. Biol.* **200**, 101–115.
- Herrel, A., Meyers, J. J., Aerts, P. and Nishikawa, K. C. (2001). Functional implications of supercontracting muscle in the chameleon tongue retractors. *J. Exp. Biol.* **204**, 3621–3627.
- Hoyle, G. and McAlear, J. H. (1963). Mechanism of supercontraction in a striated muscle fibre. *Science* **141**, 712–713.
- Hoyle, G., McAlear, J. H. and Selverston, A. (1965). Mechanism of supercontraction in a striated muscle. *J. Cell Biol.* **26**, 621–640.
- Hoyle, G., McNeil, P. A. and Selverston, A. (1973). Ultrastructure of the barnacle giant muscle fibres. *J. Cell Biol.* **56**, 74–91.
- Hoyle, G. and Smyth, T. (1963). Neuromuscular physiology of giant muscle fibers of a barnacle, *Balanus nubilus* Darwin. *Comp. Biochem. Physiol.* **10**, 291–314.
- Huxley, A. F. and Niedergerke, R. (1954). Structural changes in muscle during contraction. *Nature* **173**, 971–973.
- Huxley, H. E. and Hanson, J. (1954). Changes in the cross-striations of muscle during contraction and stretch and their structural interpretation. *Nature* **173**, 973–976.
- Kier, W. M. (1985). The musculature of squid arms and tentacles: ultrastructural evidence for functional differences. *J. Morphol.* **185**, 223–239.
- Marsh, R. L. and Bennett, A. F. (1985). Thermal dependence of isotonic contractile properties of skeletal muscle and sprint performance in the lizard *Dipsosaurus dorsalis*. *J. Comp. Physiol. B* **155**, 541–551.
- Meyers, J. J. and Nishikawa, K. C. (2000). Comparative study of tongue protrusion in three iguanian lizards, *Sceloporus undulatus*, *Pseudotrapelus sinaitus* and *Chameleo jacksonii*. *J. Exp. Biol.* **203**, 2833–2849.
- Milligan, B. J., Curtin, N. A. and Bone, Q. (1997). Contractile properties of obliquely striated muscle from the mantle of squid (*Allotheutis subulata*) and cuttlefish (*Sepia officinalis*). *J. Exp. Biol.* **200**, 2425–2436.
- Nishikawa, K. C. (1999). Neuromuscular control of prey capture in frogs. *Phil. Trans. R. Soc. Lond. B* **354**, 941–954.

- Nishikawa, K. C.** (2000). Feeding in frogs. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 117–148. San Diego: Academic Press.
- Nishikawa, K. C., Kier, W. M. and Smith, K. K.** (1999). Morphology and mechanics of tongue movement in the African pig-nosed frog *Hemisis marmoratum*: a muscular hydrostatic model. *J. Exp. Biol.* **202**, 771–780.
- Osborne, M. P.** (1967). Supercontraction in the muscles of the blowfly larva: an ultrastructural study. *J. Insect Physiol.* **13**, 1471–1482.
- Peters, S. E. and Nishikawa, K. C.** (1999). Comparison of isometric contractile properties of the tongue muscles in three species of frogs, *Litoria caerulea*, *Dyscophus guineti* and *Bufo marinus*. *J. Morphol.* **242**, 107–124.
- Podolsky, R. J.** (1964). The maximum sarcomere length for contraction of isolated myofibrils. *J. Physiol., Lond.* **170**, 110–123.
- Pough, F. H., Andrews, R. M., Cadle, J. E., Crump, M. L., Savitzky, A. H. and Wells, K. D.** (2001). *Herpetology*. New Jersey: Prentice Hall. 612pp.
- Ramsey, R. W. and Street, S. F.** (1940). The isometric length/tension diagram of isolated skeletal muscle fibers of the frog. *J. Cell. Comp. Physiol.* **15**, 11–34.
- Rice, M. J.** (1970). Supercontracting and non-supercontracting visceral muscles in the tsetse fly, *Glossina austeni*. *J. Insect Physiol.* **16**, 1109–1122.
- Rice, M. J.** (1973). Supercontracting striated muscle in a vertebrate. *Nature* **243**, 238–240.
- Ritter, D. A. and Nishikawa, K. C.** (1995). The kinematics and mechanism of prey capture in the African pig-nosed frog (*Hemisis marmoratum*): description of a radically divergent anuran tongue. *J. Exp. Biol.* **198**, 2025–2040.
- Robertson, J. D.** (1956). Some features of the ultrastructure of reptilian skeletal muscle. *J. Biophys. Biochem. Cytol.* **2**, 369–380.
- Rosenbluth, J.** (1967). Obliquely striated muscle. III. Contraction mechanism of *Ascaris* body muscle. *J. Cell Biol.* **34**, 15–33.
- Schleich, H. H., Kästle, W. and Kabisch, K.** (1996). *Amphibians and Reptiles of North Africa*. Germany: Koeltz Scientific Publishers.
- Schwenk, K.** (2000). Feeding in lepidosaurs. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 175–292. San Diego: Academic Press.
- Schwenk, K. and Throckmorton, G. S.** (1989). Functional and evolutionary morphology of lingual feeding in squamate reptiles: phylogenies and kinematics. *J. Zool., Lond.* **219**, 153–175.
- Small, J. V., Herzog, M., Barth, M. and Draeger, A.** (1990). Supercontracted state of vertebrate smooth muscle cell fragments reveals myofilament lengths. *J. Cell Biol.* **111**, 2451–2461.
- Wainwright, P. C., Kraklau, D. M. and Bennett, A. F.** (1991). Kinematics of tongue projection in *Chameleo oustaleti*. *J. Exp. Biol.* **159**, 109–133.
- Wake, D. B. and Deban, S.** (2000). Terrestrial feeding in salamanders. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 95–116. San Diego: Academic Press.