

sis was found to accumulate 4 elements – Al, V, Ti, and Sc. The data is given in the table. The range of values found for 16 other plant species growing in that area for these particular elements is also included.

Aluminium is accumulated by *Alternanthera sessilis* up to about 10 times more than other plants in the same area. Roots accumulate more Al than shoot portions. Normal Al concentration in the land plants is given by BOWEN¹ as 500 ppm. CHENERY⁴ has documented certain

Trace Elements in *Alternanthera sessilis*

Element, ppm	Roots		Shoots	
	<i>A. sessilis</i>	Others	<i>A. sessilis</i>	Others
Aluminium	7100	212–730	2910	200 – 750
Vanadium	31	–	11	0.3 – 4.5
Titanium	550	20–51	93	27 – 43
Scandium	2.1	–	2.5	0.06– 1

Al accumulators which contain up to 15% Al_2O_3 in leaves, though more common Al accumulators have about 0.2%. HESS⁵ found 5000 ppm Al in the leaves of the mangrove *Rhizophora harrisonii*.

Alternanthera sessilis also seems to accumulate V and Ti, again the roots storing more than the leaves. Degree of enrichment in the leaves here is not as great as in the case of Al. Other plant species have been reported to contain less than 1 ppm V and 1–2 ppm Ti by BOWEN¹ and UNDERWOOD².

Scandium is accumulated by *Alternanthera sessilis* to a lesser degree compared to other plants in that area. Roots and shoots seem to store the same amount of Sc. BOWEN¹ gives the average Sc concentration in the land plants as only about 0.008 ppm, which makes *Alternanthera sessilis* accumulating property about 2000 times more than average. To the best of our knowledge, there are not Ti and Sc accumulator plants reported so far.

⁴ E. M. CHENERY, J. Soil Sci. 2, 97 (1950).

⁵ P. R. HESSE, Pl. Soil 19, 205 (1963).

Lengthening of lobster muscle fibres by two age-dependent mechanisms¹

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Summary. Fibres of the lobster accessory flexor muscle elongate by 2 mechanisms: an increase in sarcomere length, which is restricted to their early development and by the addition of serial sarcomeres of a relatively constant size, which prevails throughout the life of the animal.

Vertebrate muscle fibres, after their early developmental stages, grow in length by adding sarcomeres of a constant size to the ends of the muscle fibres^{2–5}. In fact adult muscle fibres can change in length not only by adding sarcomeres but also by removing them from the ends of muscle fibres^{6,7}.

On the other hand crustacean muscle fibres grow longer by the continuous lengthening of individual sarcomeres during early developmental stages^{8,9} and throughout adult life¹⁰. On this basis, crustaceans such

as lobsters which continue to grow in mass might therefore be expected to have unusually long sarcomeres to account for the increase in fibre length. But if the sarcomeres maintain a fairly constant length throughout adult life then the lengthening of fibres must be attributed to the addition of sarcomeres. We find the latter to be the case for fibres of the limb accessory flexor muscle in lobsters.

Material and methods. Lobsters (*Homarus americanus*) were held in running sea water tanks at ambient temperature (ca. 23°C) at Woods Hole. The accessory flexor muscle in the first walking leg was exposed and fixed at rest length in aqueous Bouin's solution in which it was also stored. All measurements were made with an ocular

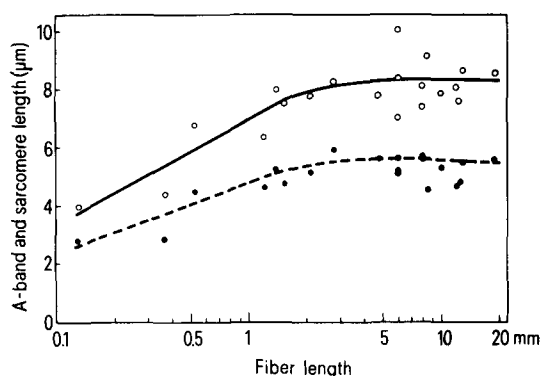


Fig. 1. Relationship between the mean A-band (closed circles) and sarcomere (open circles) lengths of a proximal fibre from the distal head of the accessory flexor muscle and the log of its fibre length. The curve fitting the points for the A-band (dashed line) and the sarcomere (continuous line) lengths is drawn by eye.

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³ G. GOLDSPIK, J. Cell Sci. 3, 539 (1968).

⁴ G. E. GRIFFEN, P. E. WILLIAMS and G. GOLDSPIK, Nature 232, 28 (1971).

⁵ P. E. WILLIAMS and G. GOLDSPIK, J. Cell Sci. 9, 751 (1971).

⁶ G. GOLDSPIK, C. TABARY, J. C. TABARY, C. TARDIEU and G. TARDIEU, J. Physiol., Lond. 236, 733 (1974).

⁷ Z. F. MUHL and A. F. GRIMM, Experientia 31, 1053 (1975).

⁸ G. D. BITTNER, J. exp. Zool. 167, 439 (1968).

⁹ C. K. GOVIND, H. L. ATWOOD and F. LANG, J. exp. Zool. 189, 395 (1974).

¹⁰ G. D. BITTNER and D. L. TRAUT, Personal communication (1976).

micrometer and the following procedure was followed: a single muscle fibre was 'floated' on a glass microscope slide (in 70% alcohol) and its length measured. Next it was teased into myofibrils and 5 consecutive sarcomeres were measured in 3 separate regions along the fibre usually at the center and towards the ends of the fibre. These 15 measurements gave the mean sarcomere length of the muscle fibre. Sarcomere lengths from the 3 different regions of a muscle fibre varied by less than 20% and such variability has been shown to occur naturally in crab muscle fibres¹¹.

This method of obtaining mean sarcomere length cannot fully compensate for the degree of contraction or stretch of the muscle fibre during fixation: a more reliable indicator of growth is the A-band length which remains constant during length changes in the sarcomere. Hence the mean A-band length of a fibre was obtained following the above procedure but with fewer (8–10) measurements per fibre.

The number of sarcomeres in a muscle fibre was calculated by dividing the mean sarcomere length into the fibre length.

Results and discussion. The limb accessory flexor muscle in crustaceans consists of two widely separated muscle bundles, the proximal and distal heads, attached to the terminal regions of the tendon that runs the length of the meropodite¹². The distal head has fibres attached on one side of the tendon only, thus the most proximal and the most distal fibre, may be positively identified from animal to animal and we have followed the growth of these two sets of fibres. Similar results were obtained from an identified fibre in the proximal head. Growth of these lobster muscle fibres was monitored from the first post-larval (4th) stage which measured 11.5 mm (rostrum to telson) and weighed less than 0.1 g, to an adult which was 390 mm in total length and weighed approximately 4.4 kg.

From the post-larval stage to the adult, fibres of the accessory flexor muscle show a nearly 50fold increase in length, with the distal head fibres growing from 0.4 mm to 17–19 mm and the proximal head fibre from 0.4 mm to 20 mm. The fibres elongate in two phases as seen when fibre length is plotted against mean A-band and sarco-

mere lengths for the proximal fibre of the distal head (Figure 1). The fibre length was plotted on a log scale to emphasize the early developmental stages which otherwise would have been greatly compressed in the range of fibre lengths sampled. There is an initial period when the fibre grows by increasing A-band and sarcomere lengths until it is about 3 mm long. Thus during early development the mean sarcomere length increases from around 4 μ m in a 0.2 mm fibre to reach adult size of 8–10 μ m in a 3 mm fibre. Growth of the fibre beyond 3 mm does not appear to depend on increases in A-band and sarcomere lengths as seen in Figure 1. This pattern of growth was also seen in the other 2 sets of fibres examined.

Figure 1 also suggests that increase in sarcomere length cannot fully account for the corresponding increase in fibre length in the early developmental stages, e.g., for a 10fold increase in fibre length (0.3–3 mm) there is only a doubling in sarcomere length (4–8 μ m). Thus during early development the fibre elongates not only by increasing sarcomere length but also by adding sarcomeres. However, the mechanism of adding sarcomeres becomes striking only after sarcomere length has reached its maximum size and this is seen when fibre length is plotted against the number of sarcomere as in the proximal fibre of the distal head (Figure 2). Addition of sarcomeres of a nearly constant size lengthens the fibre from 3 mm to its maximum size of 19 mm. Similar results were obtained for the other 2 sets of fibres sampled in this study.

We conclude that elongation of fibres in the lobster accessory flexor muscle occurs via two separate mechanisms. The mechanism of increasing sarcomere length occurs only in the early stages while that of adding sarcomeres occurs throughout the life of the animal.

Other lobster limb muscles may also grow by adding sarcomeres as indicated by preliminary data on the claw closer muscle. Here fibre length also varies with the size of the animal while sarcomere length is relatively constant (LANG and GOVIND, unpublished observations).

However, for some crayfish and crab muscle fibres, BITTNER and TRAUT¹⁰ have shown that growth in length is solely by elongating individual sarcomeres while keeping their numbers constant. In this study the authors sampled fibres from a specific region of the crayfish propodite opener muscle which had fibres of uniform length and not from amongst the entire muscle in which fibre lengths varied by as much as 20–25%, as was done in an earlier study⁸.

This sampling technique which more accurately reflects the relationship between fibre length and sarcomere length, has been refined in the present study by examining single identifiable muscle fibres from the various growth stages. It is therefore unlikely that differences in sampling techniques alone can account for the dissimilar growth mechanisms in crayfish and lobster fibres.

As to why lobster limb muscles grow by adding sarcomeres while crayfish muscles do not, it is worth noting that lobsters are larger animals than crayfish and hence have longer muscle fibres. Increasing the length of the sarcomere to its maximum size, which may be genetically specified, accounts for the linear growth of muscle fibres in crayfish but not for the comparatively long fibres in lobsters. Hence the mechanism of adding sarcomeres which must prevail during early development in lobsters and crayfish, remains active throughout the entire life span of a lobster.

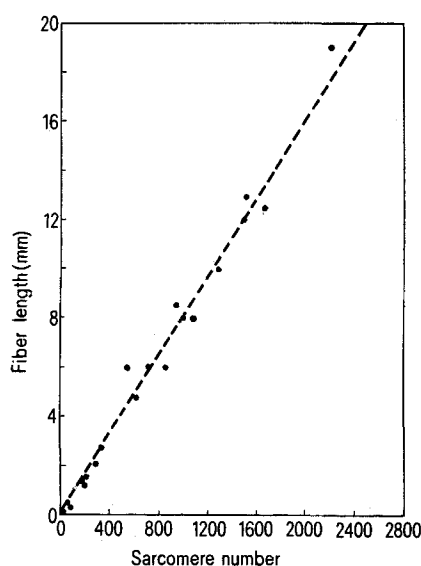


Fig. 2. Relationship between the length of a proximal fibre from the distal head of the accessory flexor muscle and its sarcomere number. Regression line is $y = 0.0083x - 0.1171$, $N = 20$, $r = 0.99$, $p < 0.01$.

¹¹ C. FRANZINI-ARMSTRONG, *J. Cell Sci.* 6, 559 (1970).

¹² M. J. COHEN, *Comp. Biochem. Physiol.* 8, 223 (1963).