length of a severed muscle, aggravated further by the frailty of the Psoas origin. Here the boundary between attachment and muscle tissue proper is indefinite. Consequently, damage to the slight muscle in this locality with resultant measurement of an apparently shorter unit cannot be excluded. On the other hand, a firm bone to tendon attachment of M. Gastrocnemius at its origin, together with its clearly demarcated terminal passage from muscle to tendon, facilitate separation of this muscle as a unit.

Details concerning the rate of length growth are presented in Table 10 and Figure 7. Rate of growth of M. Psoas is larger than that for M. Gastrocnemius throughout the period studied. In both muscles the rate at birth is greater than for any subsequent group. At this stage the Psoas growth rate is nearly three times as large as that for M. Gastrocnemius. Subsequent to birth, the Psoas curve falls almost vertically until 480 gm. live-weight, after which it falls off more gradually. Although the Gastrocnemius curve shows the same general trend, the flattening out is more gradual throughout. Both curves conclude on a nearly parallel course with only a slight decrease in rate of growth in the last few groups.

TABLE 10.

Rate of growth of muscle length.

Group.	M. Gastrocnemius.	M. Psoas.	Group.	M. Gastrocnemius.	M. Psoas.
Birth..........	0·009,219	0·023,587	Gram.		
Gram.			600	0·002,382	0·005,812
100	0·007,755	0·019,366	1200	0·001,363	0·003,458
150	0·006,273	0·015,369	1800	0·000,941	0·002,484
220	0·005,055	0·012,241	2400	0·000,697	0·001,913
320	0·003,887	0·009,371	3000	0·000,557	0·001,579
480	0·002,921	0·007,072	Mature.......	0·000,544	0·001,550

Discussion.

It is well known that the vertebral column in the ox, sheep, and pig, has a larger rate of growth than the bones of the limb, particularly for the lumbar and sacral regions in which M. Psoas is situated. Hence, it is to be expected that the Psoas muscle will lengthen to a relatively greater degree than M. Gastrocnemius. If length is considered as a percentage of the length of each muscle at birth, it is seen that the relative proportions are more or less the same throughout the period studied. The respective figures are as follows:—

	Relative Length of Muscle with Growth.					
	Birth.	100 gm.	150 gm.	220 gm.	320 gm.	480 gm.
M. Gastrocnemius..........	100	109	152	206	253	303
M. Psoas..................	100	132	158	190	243	296
	600 gm.	1200 gm.	1800 gm.	2400 gm.	3000 gm.	Mature.
M. Gastrocnemius..........	330	410	500	550	590	620
M. Psoas..................	324	375	460	533	581	588

Perhaps a species difference is responsible for the discrepancy, on account of the specialised mode of progression in the rabbit. This possibility is enhanced by the fact that Appleton has measurements in the domestic rabbit, " which show that the growth in length of the tibia after birth is for a time considerably more rapid than that of the femur " (Hammond and Appleton, 1932, p. 378.) This is in contrast with the other domestic animals in which the reverse is true. As length of the Gastrocnemius muscle may be considered equivalent to length of tibia, which increases to a relatively greater extent than in other animals, the explanation advanced of a species difference is likely to be correct.

Another possibility is that, as a consequence of formalin fixation, the Psoas muscle incurs a greater degree of shrinkage in length than M. Gastrocnemius. Such shrinkage would tend to obscure the experimental results. By virtue of the longitudinal arrangement of the Psoas fibres as compared with a pinnate structure in the Gastrocnemius muscle, it is possible that fixation many induce a differential effect on length of muscle.

3. *Width.*

(Literature: Page 339.)

Width of muscle is considered as a general measurement. For this purpose the width has been calculated as a mean value of measurements at the five sites measured, and compared throughout the period of lifetime studied in the rabbit (Table 11).

TABLE 11.

Width of muscle.

Groups of Rabbits.		No. of Rabbits.	Mean Width M. Gastroc.	Sig. Test (W. Prec. Group).	Mean Width M. Psoas.	Sig. Test (W. Prec. Group).
No.	Class.					
			Cm.		Cm.	
1	Birth	10	0·32	—	0·41	—
	Gram.					
2	100	5	0·33	N.S.	0·43	N.S.
3	150	5	0·41	X	0·52	N.S.
4	220	5	0·49	X	0·60	N.S.
5	320	5	0·61	XX	0·78	N.S.
6	480	5	0·79	XX	0·95	N.S.
7	600	10	0·99	XX	0·99	N.S.
8	1200	10	1·30	XX	1·55	XX
9	1800	10	1·57	XX	1·96	XX
10	2400	10	1·64	XX	2·10	X
11	3000	10	1·78	XX	2·28	XX
12	Mature	10	1·82	N.S.	2·34	N.S.

Along its length, M. Psoas major takes origin from the body of the last thoracic vertebra, and all lumbar vertebrae, as well as from the transverse processes of the last-named. As the muscle must be damaged along its medial margin during removal, it is evident that width will be influenced by the degree of damage inflicted in different animals. Furthermore, in order to obtain an individual unit, it was deemed advisable to make a separation where the terminal portion of M. Psoas major joins with M. Iliacus,

TABLE 12.

Width of Gastrocnemius muscle.

Site in Muscle.	Birth.			100 Gm.			150 Gm.			220 Gm.			320 Gm.			480 Gm.		
	Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.	
		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.
A..........................	0·26	—	—	0·28	—	—	0·29	—	—	0·37	—	—	0·47	—	—	0·58	—	—
B..........................	0·37	XX	XX	0·36	XX	XX	0·45	XX	XX	0·58	XX	XX	0·72	XX	XX	0·91	XX	XX
C..........................	0·39	N.S.	XX	0·39	N.S.	XX	0·49	X	XX	0·63	XX	XX	0·78	XX	XX	1·01	XX	XX
D..........................	0·34	XX	XX	0·34	X	XX	0·45	X	XX	0·53	XX	XX	0·65	XX	XX	0·87	XX	XX
E..........................	0·22	XX	XX	0·25	XX	N.S.	0·34	XX	XX	0·35	XX	N.S.	0·43	XX	XX	0·61	XX	N.S.

Site in Muscle.	600 Gm.			1200 Gm.			1800 Gm.			2400 Gm.			3000 Gm.			"Mature".		
	Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.	
		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.
A..........................	0·77	—	—	0·99	—	—	1·16	—	—	1·23	—	—	1·32	—	—	1·36	—	—
B..........................	1·15	XX	XX	1·51	XX	XX	1·79	XX	XX	1·87	XX	XX	2·03	XX	XX	2·06	XX	XX
C..........................	1·23	XX	XX	1·59	X	XX	1·91	XX	XX	1·98	XX	XX	2·18	XX	XX	2·21	XX	XX
D..........................	1·05	XX	XX	1·41	XX	XX	1·73	XX	XX	1·83	XX	XX	2·00	XX	XX	2·08	XX	XX
E..........................	0·76	XX	N.S.	1·00	XX	N.S.	1·25	XX	XX	1·30	XX	N.S.	1·35	XX	N.S.	1·39	XX	N.S.

TABLE 14.

Width of Psoas muscle.

Site in Muscle.	Birth.			100 Gm.			150 Gm.			220 Gm.			320 Gm.			480 Gm.		
	Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.	
		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.
A.	0·31	—	—	0·35	—	—	0·43	—	—	0·46	—	—	0·58	—	—	0·81	—	—
B.	0·39	XX	XX	0·43	XX	XX	0·48	N.S.	N.S.	0·59	XX	XX	0·77	XX	XX	0·87	N.S.	N.S.
C.	0·43	XX	XX	0·46	N.S.	XX	0·53	N.S.	XX	0·63	N.S.	XX	0·85	N.S.	XX	1·02	XX	XX
D.	0·45	N.S.	XX	0·46	N.S.	XX	0·56	N.S.	XX	0·64	N.S.	XX	0·87	N.S.	XX	1·02	N.S.	XX
E.	0·44	N.S.	XX	0·42	X	XX	0·58	N.S.	XX	0·66	N.S.	XX	0·82	N.S.	XX	1·02	N.S.	XX

Site in Muscle.	600 Gm.			1200 Gm.			1800 Gm.			2400 Gm.			3000 Gm.			"Mature".		
	Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.		Width Cm.	Significance Test.	
		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.
A.	0·86	—	—	1·30	—	—	1·67	—	—	1·74	—	—	1·83	—	—	1·81	—	—
B.	0·94	XX	XX	1·55	XX	XX	1·93	XX	XX	2·07	XX	XX	2·19	XX	XX	2·23	XX	XX
C.	1·03	XX	XX	1·67	X	XX	2·08	X	XX	2·30	XX	XX	2·47	XX	XX	2·47	XX	XX
D.	1·05	N.S.	XX	1·65	N.S.	XX	2·18	N.S.	XX	2·30	N.S.	XX	2·55	N.S.	XX	2·64	XX	XX
E.	1·07	N.S.	XX	1·59	N.S.	XX	1·93	XX	XX	2·07	XX	XX	2·36	XX	XX	2·53	N.S.	XX

not more caudally where a common stout tendon serves as insertion for both muscles. These facts must be taken into consideration in interpreting the data.

In M. Gastrocnemius, only in the first group at 100 gm. live-weight and in the final stage in the mature animal is the increment not significant. However, in the Psoas muscle, increase in the value of muscle width from group to group is insignificant in all the earlier groups up to 600 gm. live-weight, as well as in the mature animals. Perhaps the factors mentioned above are partly responsible. In general, the muscles widen until 3,000 gm. live-weight, but over the final six months of the lifetime of the experimental animals (i.e., 3,000 gm. to maturity 3,072 gm.), no widening can be demonstrated.

Apart from width as a general measure, it is of interest to consider the relationship between width at any site along the length of the muscle, relative to the other sites studied.

M. Gastrocnemius.

In Table 12 and Figure 8 are given details of width within M. Gastrocnemius. The muscle shows a distinct belly, as width at mid-points C, B, and D, is always greater than towards the origin (A) and insertion (E). Except at birth and 100 gm. live-weight, the middle of the muscle (C) is the significantly widest portion throughout.

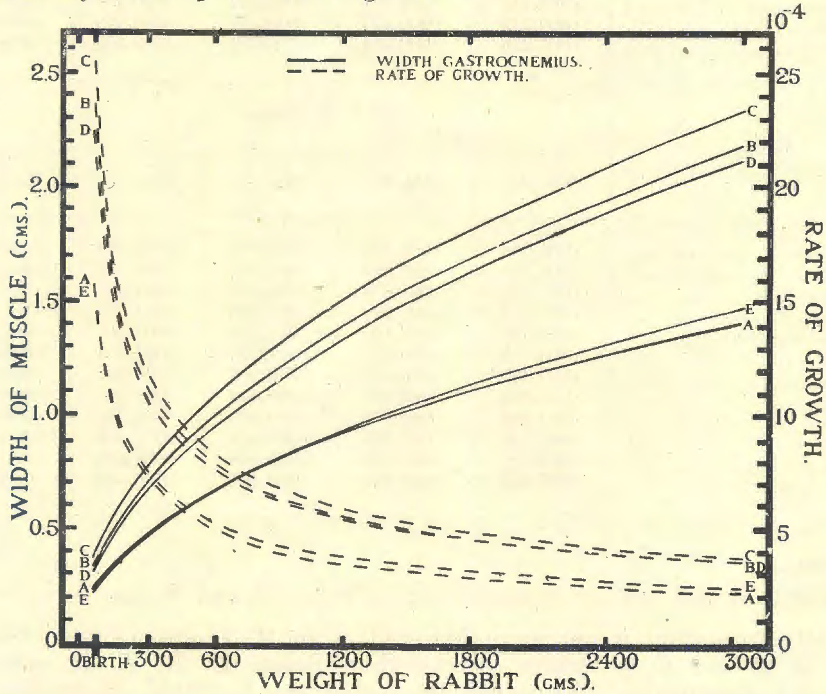


Fig. 8.—Width of muscle.

In Table 13 and Figure 8 are to be found details concerning rate of growth. Always greatest at birth, and corresponding to absolute width in order C, B, D, E, A, the curves descend steeply until 320 gm. live-weight, thereafter flattening and becoming nearly horizontal from 1,800 gm. A clear picture is presented of a greater growth force in mid-muscle producing larger increments of width increase as the animal grows, than at both ends of the muscle.

TABLE 13.

Rate of growth of muscle width.

Group.	M. Gastrocnemius.				
	Site A.	Site B.	Site C.	Site D.	Site E.
Birth	·001,575	·002,367	·002,547	·002,247	·001,563
100 gm.	·001,307	·001,978	·002,124	·001,887	·001,312
150 gm.	·001,064	·001,622	·001,739	·001,556	·001,082
220 gm.	·000,879	·001,348	·001,444	·001,300	·000,904
320 gm.	·000,711	·001,099	·001,175	·001,066	·000,741
480 gm.	·000,576	·000,897	·000,958	·000,875	·000,608
600 gm.	·000,501	·000,784	·000,836	·000,768	·000,534
1200 gm.	·000,355	·000,562	·000,597	·000,555	·000,386
1800 gm.	·000,289	·000,461	·000,489	·000,458	·000,318
2400 gm.	·000,248	·000,397	·000,421	·000,396	·000,275
3000 gm.	·000,222	·000,357	·000,378	·000,358	·000,248
Mature	·000,220	·000,354	·000,374	·000,354	·000,246
Group.	**M. Psoas.**				
	Site A.	Site B.	Site C.	Site D.	Site E.
Birth	·002,050	·002,459	·002,712	·002,779	·002,665
100 gm.	·001,716	·002,051	·002,265	·002,322	·002,213
150 gm.	·001,410	·001,679	·001,857	·001,904	·001,803
220 gm.	·001,175	·001,394	·001,543	·001,583	·001,491
320 gm.	·000,960	·001,135	·001,258	·001,291	·001,208
480 gm.	·000,785	·000,925	·001,027	·001,054	·000,979
600 gm.	·000,687	·000,808	·000,897	·000,921	·000,852
1200 gm.	·000,494	·000,577	·000,642	·000,660	·000,604
1800 gm.	·000,406	·000,473	·000,526	·000,541	·000,492
2400 gm.	·000,350	·000,407	·000,454	·000,466	·000,422
3000 gm.	·000,316	·000,366	·000,408	·000,420	·000,379
Mature	·000,313	·000,362	·000,404	·000,415	·000,375

M. Psoas.

Width of this muscle is considered in Table 14 and Figure 9.

Belly formation is not as pronounced as in M. Gastrocnemius, though width at D and C is always greater than points E, B, A, in order of decreasing magnitude. No doubt the value for E would be smaller, to approximate width at A, if the common muscle termination had been severed more caudally.

In general, the muscle widens from A to B to C to D, but narrows from D to E. With two possible exceptions, it is shown that the muscle is always significantly narrowest at site A (near the origin).

Rate of growth (Table 13 and Figure 9) bears a close resemblance to that of M. Gastrocnemius, but the rate is higher throughout for the Psoas muscle. Growth rate is greatest at birth, then the curve falls almost vertically until 320 gm. live-weight. From this stage it drops more gradually until 1,800 gm. live-weight to assume a nearly horizontal level for the final two groups. As in M. Gastrocnemius, the rate of growth is highest about the middle of the muscle (D, C). Towards the ends the growth rate is lower, least of all near the muscle origin at A.

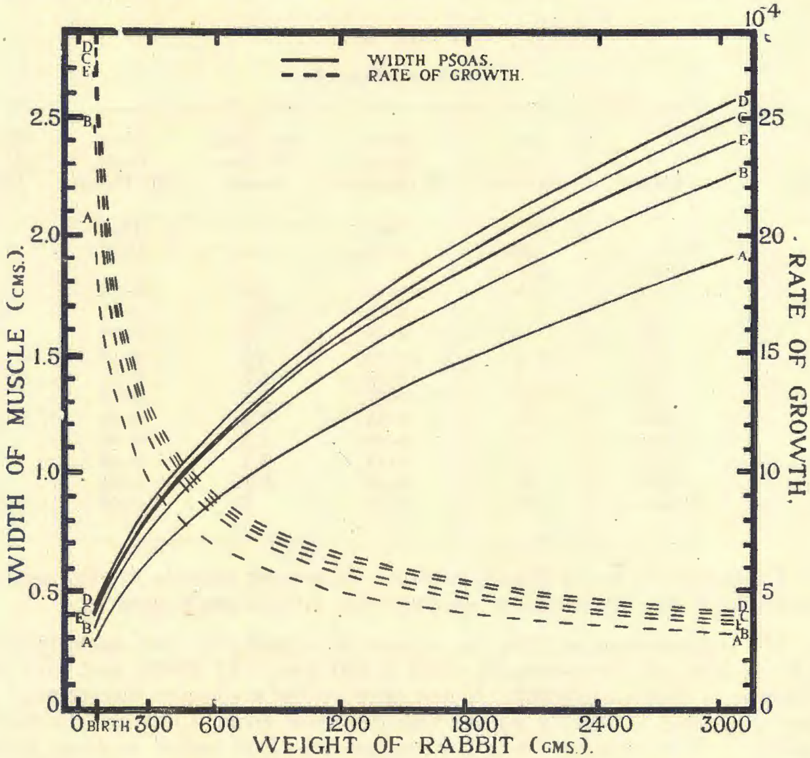


Fig. 9.—Width of M. Psoas.

Discussion.

In the Longissimus dorsi muscle of various domestic animals, it has been inferred that width and depth increase after length has become stabilised. In this experiment muscle length has been shown to increase up to a live-weight of 3,000 gm., yet no widening of muscle has been demonstrated in the six months' period which elapsed after this stage. Explanation is complicated by view of the fact that different species, as well as different muscles, are involved. For example, it is not possible to assess the developmental age of the rabbits studied in terms of the corresponding period, of say the sheep or pig.

Clearly, the structural arrangement (and form) of a muscle is largely dependent on the function the muscle is required to perform in the animal body. Why is M. Gastrocnemius relatively short, with a pronounced belly, as compared with the long Psoas muscle, which has a slightly more discreet spreading about its middle? More information is required regarding the nature of muscular contractility in the different muscles. Obviously a wide field is open for investigation of muscular function and efficiency, as related to form and structural composition.

4. *Depth.*

(Literature: Page 339.)

The next dimension to be considered is depth (or thickness).

TABLE 15.

Depth of muscle.

Groups of Rabbits.		No. of Rabbits.	Mean Depth M. Gastrocn.	Sig. Test (W. Prec. Group).	Mean Depth (M. Psoas).	Sig. Test (W. Prec. Group).
No.	Class.					
			Cm.		Cm.	
1............	Birth......	10	0·11	—	0·06	—
	Gram.					
2............	100	5	0·12	N.S.	0·06	N.S.
3............	150	5	0·13	N.S.	0·07	N.S.
4............	220	5	0·16	X	0·08	N.S.
5............	320	5	0·20	XX	0·11	N.S.
6............	480	5	0·26	XX	0·14	N.S.
7............	600	10	0·31	XX	0·15	N.S.
8............	1200	10	0·35	XX	0·24	XX
9............	1800	10	0·40	XX	0·30	XX
10............	2400	10	0·43	XX	0·33	XX
11............	3000	10	0·44	N.S.	0·34	N.S.
12............	Mature....	10	0·42	X	0·36	N.S.

In Table 15 are to be found details concerning muscle depth, considered as a measure of the mean value of five sites within each muscle.

In M. Gastrocnemius, the increment is significant for each succeeding group from 150 gm. live-weight until 2,400 gm. At 3,000 gm. live-weight the increase is not significant, hence it may be a chance variation. It is, however, puzzling to find a significant decrease from 3,000 gm. live-weight to maturity. This positive result when group 12 is tested against group 11 may be due to the accident of a low figure in the final group. When this variation in depth (0·02 cm.) is taken into consideration, it will readily be appreciated how slight need be an error in measurement to produce this apparent contradiction. Hirzel (1936) found an actual decrease in depth in some heavier classes of sheep. His observations that animals packing on fat very rapidly reach a high weight due to fat growth, as distinct from muscle growth, may have some bearing on the anomaly observed.

Mean depth of the Psoas muscle shows an increase which is, however, distributed unevenly over the lifetime of the rabbits studied. The increase becomes significant only when a live weight of 1,200 gm. has been achieved and the increments at both 3,000 gm. live-weight and maturity are again insignificant.

M. Gastrocnemius.

With regard to the variations in depth within this muscle, Table 16 and Figure 10 present a picture of a more or less uniformly deep muscle which tapers markedly towards its insertion. E is always the shallowest portion of

TABLE 16.

Depth of Gastrocnemius muscle.

Site in Muscle.	Birth.			100 Gm.			150 Gm.			220 Gm.			320 Gm.			480 Gm.		
	Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.	
		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.
A.	0·10	—	—	0·12	—	—	0·11	—	—	0·15	—	—	0·17	—	—	0·22	—	—
B.	0·12	XX	XX	0·13	XX	XX	0·15	XX	XX	0·20	XX	XX	0·25	XX	XX	0·31	XX	XX
C.	0·13	XX	XX	0·14	N.S.	XX	0·16	N.S.	XX	0·21	N.S.	XX	0·25	N.S.	XX	0·32	N.S.	XX
D.	0·12	XX	XX	0·12	N.S.	XX	0·14	X	XX	0·16	XX	N.S.	0·21	XX	XX	0·28	XX	XX
E.	0·08	XX	XX	0·08	XX	XX	0·09	XX	X	0·09	XX	XX	0·10	XX	XX	0·15	XX	XX

Site in Muscle.	600 Gm.			1200 Gm.			1800 Gm.			2400 Gm.			3000 Gm.			"Mature."		
	Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.	
		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.
A.	0·32	—	—	0·39	—	—	0·42	—	—	0·44	—	—	0·45	—	—	0·42	—	—
B.	0·35	XX	XX	0·38	N.S.	N.S.	0·42	N.S.	N.S.	0·45	N.S.	N.S.	0·44	N.S.	N.S.	0·40	N.S.	N.S.
C.	0·33	XX	N.S.	0·37	N.S.	X	0·44	XX	XX	0·47	N.S.	XX	0·48	X	N.S.	0·45	XX	X
D.	0·33	N.S.	N.S.	0·36	N.S.	XX	0·42	XX	N.S.	0·46	N.S.	N.S.	0·49	N.S.	X	0·47	N.S.	XX
E.	0·20	XX	XX	0·23	XX	XX	0·28	XX	XX	0·30	XX	XX	0·34	XX	XX	0·35	XX	XX

TABLE 18.

Depth of Psoas muscle.

Site in Muscle.	Birth.			100 Gm.			150 Gm.			220 Gm.			320 Gm.			480 Gm.		
	Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.	
		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.
A	0·03	—	—	0·03	—	—	0·03	—	—	0·04	—	—	0·06	—	—	0·07	—	—
B	0·05	XX	XX	0·04	XX	XX	0·06	XX	XX	0·06	XX	XX	0·08	XX	XX	0·11	XX	XX
C	0·06	XX	XX	0·06	XX	XX	0·08	XX	XX	0·09	XX	XX	0·10	XX	XX	0·14	XX	XX
D	0·07	XX	XX	0·07	XX	XX	0·09	XX	XX	0·11	XX	XX	0·13	XX	XX	0·18	XX	XX
E	0·09	XX	XX	0·09	XX	XX	0·11	XX	XX	0·12	XX	XX	0·17	XX	XX	0·21	XX	XX

Site in Muscle.	600 Gm.			1200 Gm.			1800 Gm.			2400 Gm.			3000 Gm.			"Mature".		
	Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.		Depth Cm.	Significance Test.	
		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.		Preceding Site.	Site A.
A	0·09	—	—	0·15	—	—	0·19	—	—	0·20	—	—	0·22	—	—	0·24	—	—
B	0·12	XX	XX	0·19	XX	XX	0·25	XX	XX	0·27	XX	XX	0·28	XX	XX	0·29	XX	XX
C	0·16	XX	XX	0·24	XX	XX	0·31	XX	XX	0·34	XX	XX	0·34	XX	XX	0·37	XX	XX
D	0·18	XX	XX	0·27	XX	XX	0·34	XX	XX	0·40	XX	XX	0·40	XX	XX	0·42	XX	XX
E	0·21	XX	XX	0·33	XX	XX	0·40	XX	XX	0·47	XX	XX	0·48	XX	XX	0·50	XX	XX

the muscle. Significance is present throughout, from birth to maturity. Depth in the middle of the muscle (C and B) is greater than towards the ends (D and A) until 1,800 gm. live-weight. At this stage the initially steep curves for C and B flatten abruptly to cross under those for D and A. As a result M. Gastrocnemius is deepest at D and A respectively, in the final group.

These changes are explained by a study of the rate of growth (Table 17, Figure 10). The growth rate is greatest at birth, for all the sites, A to E. Although the curves at B and C fall almost vertically until 480 gm. live-weight, they do not subsequently flatten to the same degree as those for D, A, and E, consequently cross over them to assume a lower level. At birth, there is a striking difference between the rate of growth at the highest point B and the lowest point E, but the difference is very slight in the final groups, when the growth impetus is nearly played out.

TABLE 17.

Rate of growth of muscle depth.

Group.	M. Gastrocnemius.				
	Site A.	Site B.	Site C.	Site D.	Site E.
Birth	·000,583	·001,035	·000,977	·000,635	·000,403
100 gm	·000,476	·000,835	·000,776	·000,514	·000,329
150 gm	·000,382	·000,637	·000,589	·000,407	·000,264
220 gm	·000,311	·000,479	·000,446	·000,328	·000,214
320 gm	·000,247	·000,334	·000,318	·000,258	·000,171
480 gm	·000,197	·000,222	·000,220	·000,204	·000,136
600 gm	·000,170	·000,164	·000,169	·000,174	·000,117
1200 gm	·000,117	·000,067	·000,082	·000,118	·000,080
1800 gm	·000,094	·000,034	·000,050	·000,093	·000,064
2400 gm	·000,079	·000,018	·000,033	·000,078	·000,054
3000 gm	·000,070	·000,010	·000,024	·000,069	·000,048
Mature	·000,070	·000,009	·000,023	·000,069	·000,048

Group.	M. Psoas.				
	Site A.	Site B.	Site C.	Site D.	Site E.
Birth	·000,201	·000,293	·000,381	·000,447	·000,542
100 gm	·000,174	·000,249	·000,321	·000,374	·000,452
150 gm	·000,149	·000,208	·000,265	·000,308	·000,370
220 gm	·000,129	·000,175	·000,222	·000,256	·000,308
320 gm	·000,109	·000,145	·000,183	·000,209	·000,250
480 gm	·000,093	·000,121	·000,150	·000,171	·000,204
600 gm	·000 084	·000,107	·000,132	·000,150	·000,178
1200 gm	·000,064	·000,079	·000,096	·000,108	·000,128
1800 gm	·000,055	·000,065	·000,079	·000,088	·000,104
2400 gm	·000,049	·000,057	·000,069	·000,076	·000,090
3000 gm	·000,045	·000,052	·000,062	·000,069	·000,082
Mature	·000,045	·000,051	·000,061	·000,068	·000,080

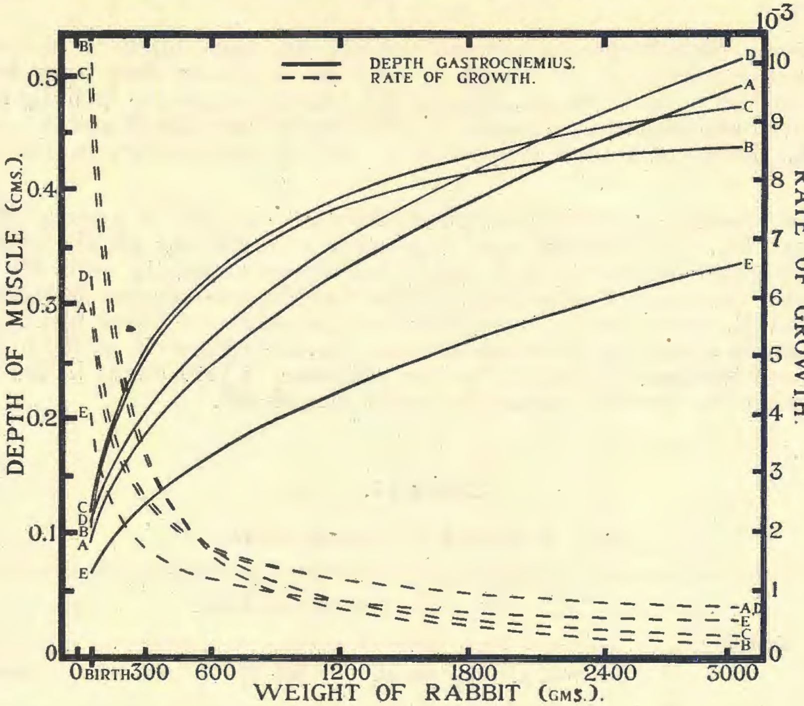


Fig. 10.—Depth of M. Gastrocnemius.

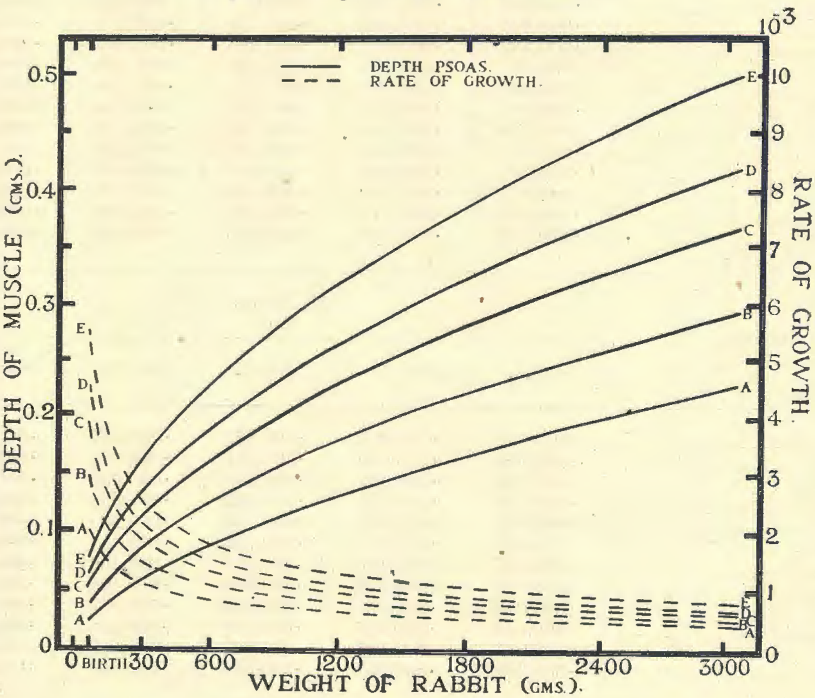


Fig. 11.—Depth of M. Psoas.

M. Psoas.

Depth of the Psoas muscle is considered in Table 18 and Figure 11. In contradistinction to M. Gastrocnemius, M. Psoas is thinnest near its origin (A) and thickens uniformly along its length, so that it is always thickest towards the insertion (E). When the measurements at each site are compared, all the variations are found to be significant for each group from birth to maturity.

Interpreted in terms of growth rate (Table 17 and Figure 11), the thickest portions of the muscle grow fastest throughout—in order E, D, C, B, A, respectively. Rate of increase is greatest at birth, falls rapidly until 220 gm. live-weight, then subsides more gradually to become almost stationary from 1,200 gm. live-weight onwards. When compared with the data for M. Gastrocnemius, rate of growth of Psoas is found to be initially less, yet it does not decrease to the same degree in the final stages. Whereas the early developing Gastrocnemius muscle has a relatively high rate of growth early in life, the later maturing Psoas muscle maintains an initially lower growth impetus over later stages of life.

Discussion.

In neither muscle has it been possible to show an increase in depth from 2,400 gm. live-weight to 3,000 gm., nor in the six months' period subsequent to the latter stage. From the data presented, the conclusion is drawn that depth of muscle has become stable even before length and width. Yet Hammond (1936) and McMeekan (1940-41) showed that, in the ox, sheep and pig, M. Longissimus dorsi increases in depth after the cessation of widening of the muscle. Is it possible a different mechanism regulates the inter-relationship in different muscles, and in different species?

Another question that arises is the reason for the varying shape of the two muscles studied. Whereas the Psoas muscle is thickest near the insertion and tapers uniformly to become thin and sheet-like at its origin, M. Gastrocnemius is relatively thick from its origin along the greater part of the muscle, only tapering out suddenly near its insertion. Speculation is unlikely to be profitable in the absence of knowledge concerning the nature of the contractile process, its speed, and duration.

5. *The inter-relation of weight, length, width, and depth of muscle.*

Discussion.

A diagrammatic representation of the changes in growing muscle is shown in Figure 12. Length seems to be the major factor in determining mass of muscle, not only by virtue of its relatively greater magnitude, but also because the effect of increasing width and depth is automatically increased as the muscle becomes longer.

The weight and the dimensions considered are by no means proportional at the various stages. Weight increases to a markedly greater degree than length, width, and depth, especially from about 600 gm. live-weight onwards. However, not only shape but also the composition of muscle determines weight, as models of identical form but of different composition (e.g., tin, lead) are obviously of dissimilar weight. Hence weight cannot be related to shape unless the changing chemical composition and density are also known. Herein lies a difficulty in assessing the relative importance of length, width, and depth, in terms of increasing weight of muscle.

Although the chemical composition of muscle has not been considered in this study it is well known that muscle changes in composition as an animal becomes older. For instance, Hammond (1932) found a decrease in the percentage of water, a slight increase of protein and ash, and a marked increase of fat. A knowledge of these variations is essential for evaluating the relative importance of the dimensional changes in effecting the increase in muscle mass. Nevertheless, it is of interest to discuss the relative changes of these dimensions in terms of the general order of development in post-natal life (Table 19, Figure 13).

TABLE 19.

Relative growth, as percentage of measurement at birth.

Group.	Gastrocnemius Muscle.				Psoas Muscle.			
	Weight.	Length.	Width.	Depth.	Weight.	Length.	Width.	Depth.
Birth	100	100	100	100	100	100	100	100
100 gm.	117	109	103	107	143	132	105	97
150 gm.	244	153	128	118	246	158	128	123
220 gm.	471	206	156	147	395	190	148	140
320 gm.	883	253	193	178	798	243	193	180
480 gm.	1,556	303	252	233	1,435	296	235	237
600 gm.	2,000	330	309	282	1,773	324	248	250
1,200 gm.	3,800	410	406	318	4,182	375	388	400
1,800 gm.	5,900	500	491	364	7,818	460	490	500
2,400 gm.	7,420	550	513	382	10,500	533	525	550
3,000 gm.	9,280	590	556	400	13,446	581	570	567
Mature	9,440	620	569	382	14,664	588	585	600

That weight develops to a much greater extent than length, width, or depth, is clearly indicated. Reference to Table 19 reveals how this divergence becomes increasingly pronounced as the animal ages. As the Psoas muscle has previously been shown to have a later period of growth than M. Gastrocnemius, it is not surprising that this same trend is again revealed. Thus, in the mature rabbit, the relative weight of the Psoas muscle has increased roughly one and a half times as much as that for M. Gastrocnemius.

In both muscles the length growth surpasses both width and depth up to 600 gm. live-weight. This conforms to expectation, but it is surprising that this supremacy is maintained in the Gastrocnemius muscle throughout the lifetime of the animal. Even in the final stages length is still on the up-grade. In this muscle the trend for width and depth is similar in the initial groups, but from 600 gm. live-weight depth increases at a lesser rate than width. There is an increasing divergence as the animal grows, so that in the mature rabbit the curve for depth lies far below that for width. Thus a gradient exists in the Gastrocnemius muscle as regards the order of development. Firstly, developing earliest and most is the growth in length, next width, and lastly depth.

In the Psoas muscle, growth in length, width, and depth up to 600 gm. live-weight behave similarly to M. Gastrocnemius. However, in the succeeding groups, the respective curves cross and re-cross. Apparently the order of development of the various dimensions closely resemble each other after a body weight of 600 gm. has been attained.

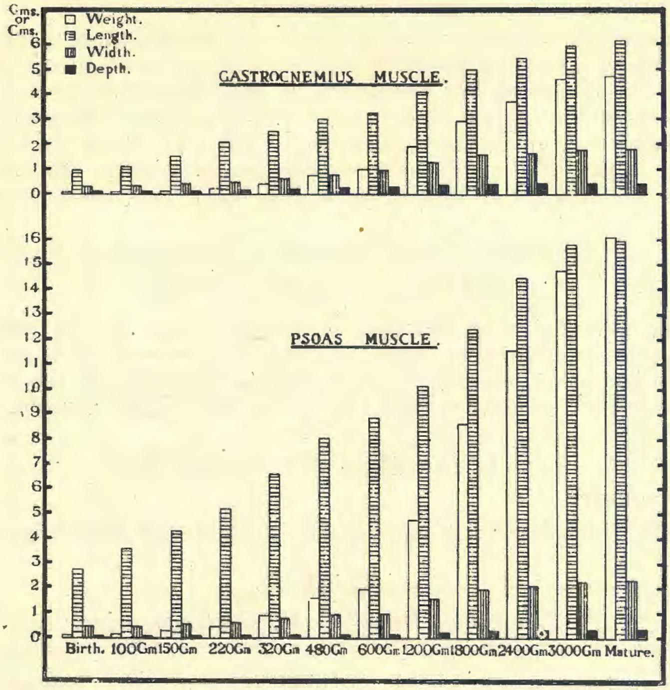


Fig. 12.—Changes in mass and dimensions of muscle.

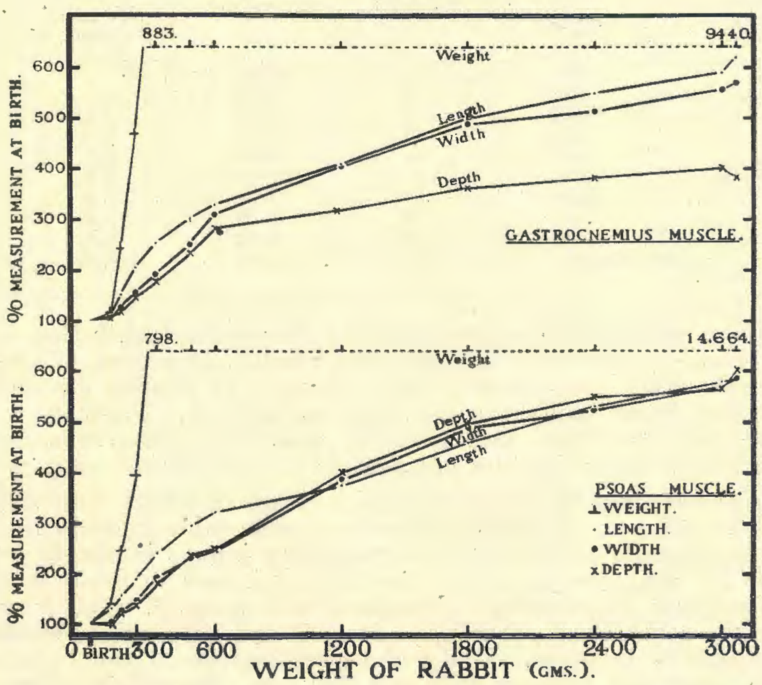


Fig. 13.—Relative growth, as percentage of measurement at birth.

This comparison shows that the order of development varies in different muscles. Inherent structural differences such as those previously described, together with the resulting variation in the respective growth mechanism, make it necessary to treat each muscle on its merits. Hence it is unwise to make assumptions, in terms of muscle in general, from this limited study. Before this is possible it will be necessary to carry out a more detailed investigation of skeletal musculature, of widely varying structure and function

(c) Growth and development of muscle bundle.

(Literature pages 339-341).

Having demonstrated changes in morphology of the growing muscle unit, as a whole, one may now consider the constituent units of muscle tissue. As far as is possible, morphological changes in the muscle bundle have been studied in similar manner to the individual muscle.

1. *Length of Muscle Bundle.*

M. Gastrocnemius.

Length of fasciculus is considered in Table 20 and Figure 14.

TABLE 20.

Length of Bundle—M. Gastrocnemius.

Groups of Rabbits.		No. of Rabbits.	Mean Bundle Length.	Significance Test.	
No.	Class.			(W. Prec. Group).	(W. Group 4).
	Gm.		Cm.		
4.............	220	5	0·73	—	—
5.............	320	5	0·95	XX	XX
6.............	480	5	1·01	N.S.	XX
7.............	600	10	0·93	N.S.	XX
8.............	1,200	10	0·90	N.S.	XX
9.............	1,800	10	1·00	XX	XX
10.............	2,400	10	0·99	N.S.	XX
11.............	3,000	10	0·94	N.S.	XX
12.............	Mature......	10	0·97	N.S.	XX

It was not possible to determine the changes in length that occur in the early stages of life (up to 150 gm. live-weight). Dissection of these filamentous short bundles is difficult. Even though the bundles are handled carefully, they break easily because they are so frail. Probably a sectioning method may facilitate measurement, provided precautions are taken to ensure the sectioned bundles are straight in the finished preparations.

It is seen that there is a definite increase in length from 220 gm. live-weight to 320 gm. Although there is no detectable increase in the groups following, bundle length in these succeeding groups is always greater than for the 220 gm. group. A peculiar feature is seen in group 9 where there is a significant lengthening as compared with group 8. This is undoubtedly due to the accident of a low figure at 1,200 gm. live-weight together with a high figure at 1800 gm. Under the circumstances it can be said that the bundle lengthens between 220 and 320 gm. live-weight after which no further increase in length takes place.

As the length of the Gastrocnemius bundle was not determined for the first three groups, it is not possible to calculate the rate of growth from birth onwards. However, these changes in growth rate of bundle length may be deduced from a study of the foregoing data. Although growth must be extremely active in the initial groups, it loses its impetus relatively early in life (320 gm. live weight). Presumably, after a high initial rate of growth at birth, the rate of lengthening must decrease markedly to become stationary from 320 gm. to maturity. Such a picture is not at variance with the view that the bundle rapidly lengthens at birth and shortly afterwards, until achieving stability at 320 gm. live-weight.

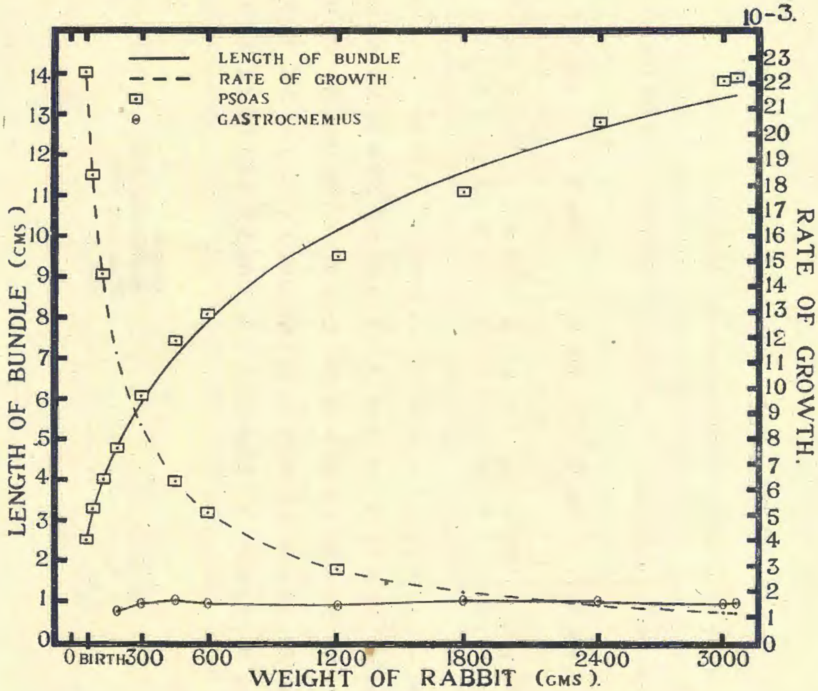


Fig. 14.—Length of muscle bundle.

The lengths tabulated in Table 21 are those of fasciculi at sites A, B, C, D, E, along the length of the muscle. In Figure 15, a graphical representation gives a picture of the mean bundle length at the various sites. For reasons which will soon be evident, three curves are compiled from the data, for the groups from 600 gm. live-weight to maturity, from 320 to 480 gm., and at 220 gm. live-weight.

At 220 gm. live-weight there is a tendency for a progressive increase in length from A to E i.e. the shortest bundles occur at A. Although there is the same general trend at 320 gm. live-weight, and at 480 gm., no significant difference can be shown between sites A and B. For all the subsequent groups, however, B is in each case shorter than A, with a progressive increase in length at the succeeding points C, D and E. Here, as in the earlier groups, the bundles nearer the insertion are always longer than those nearer the origin of the muscle, but the shortest bundles are always

TABLE 21.

Length of Bundle—Gastrocnemius Muscle.

Site in Muscle.	220 Gm.			320 Gm.			480 Gm.			600 Gm.			1,200 Gm.			1,800 Gm.			2,400 Gm.			3,000 Gm.			"Mature"		
	L. Cm.	Sig. T.		L. Cm.	Sig. T.		L. Cm.	Sig. T.		L. Cm.	Sig. T.		L. Cm.	Sig. T.		L. Cm.	Sig. T.		L. Cm.	Sig. T.		L. Cm.	Sig. T.		L. Cm.	Sig. T.	
		P. S.	S. A.		P. S.	S. A.		P. S.	S. A.		P. S.	S. A.		P. S.	S. A.		P. S.	S. A.		P. S.	S. A.		P. S.	S. A.		P. S.	S. A.
A.	0·68	—	—	0·91	—	—	0·98	—	—	0·91	—	—	0·91	—	—	0·99	—	—	0·98	—	—	0·98	—	—	0·97	—	—
B.	0·72	X	X	0·91	NS	NS	0·98	NS	NS	0·88	X	X	0·84	X	X	0·93	XX	XX	0·92	XX	XX	0·86	XX	XX	0·91	XX	XX
C.	0·75	X	XX	0·95	XX	XX	1·00	NS	NS	0·92	XX	NS	0·86	NS	NS	0·97	X	NS	0·94	NS	X	0·92	XX	XX	0·95	XX	NS
D.	0·76	NS	XX	0·97	X	XX	1·02	NS	XX	0·96	XX	XX	0·91	NS	NS	1·03	XX	X	1·02	XX	X	0·98	XX	NS	1·00	XX	X
E.	0·76	NS	XX	0·99	X	XX	1·05	X	XX	0·99	X	XX	0·97	X	X	1·09	XX	XX	1·08	XX	XX	0·98	NS	NS	1·04	XX	XX

ABBREVIATIONS :—

L. .... Length.
Sig. T. .... Significance Test.
P. S. .... Preceding Site.
S.A. .... Site A.

found at B. Probably there is a change in the relative length of the bundles at sites A and B in older as opposed to younger animals. Confirmation of this fact may be obtained, if a technique can be devised for measuring the bundles in very small animals, which are not represented in these data.

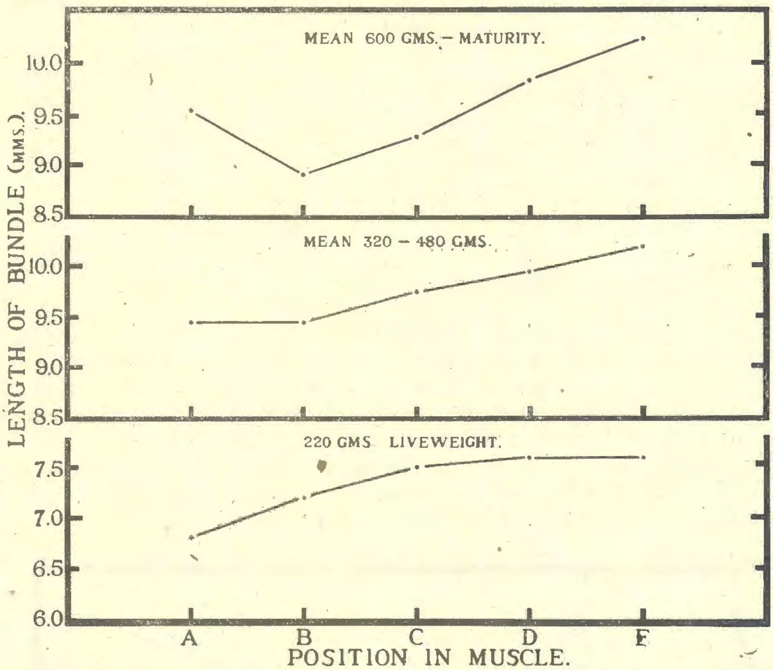


Fig. 15.—Length of bundle, M. Gastrocnemius.

Angle of Bundle in M. Gastrocnemius.

During dissection it was observed that the angle of bundles to the long axis of the Gastrocnemius muscle varies appreciably from the earlier to later groups. A method is available for calculating this angle, namely, the mathematical formulation that Sine of angle $= \frac{\text{Side opposite the angle.}}{\text{Hypotenuse.}}$ Applying this formulation to the muscle, it follows that Sine of angle of bundle to long axis of M. Gastrocnemius equals—

$$\frac{\text{Depth of muscle.}}{\text{Length of bundle.}}$$

In Table 22 are shown the respective values of this angle from 220 gm. live-weight onwards. In the young animal the fasciculi are steeply inclined in relation to the long axis of the muscle, but as the animal grows the bundles assume a progressively more obtuse relationship to the long axis. This is shown graphically in a diagrammatic form in Figure 16. The apparent reversal of trend in the mature animal is the possible result of an error or abnormality. Probably the measurement of the depth of muscle for this group is implicated, as the same anomaly is there apparent.

TABLE 22.

Angle of Bundle to Long Axis of M. Gastrocnemius.

Groups of Rabbits.		Number of Rabbits.	Mean Angle Sites A-E. (Degrees).
No.	Class.		
4	220 gm.	5	12·8
5	320 gm.	5	12·2
6	480 gm.	5	14·8
7	600 gm.	10	19·4
8	1,200 gm.	10	22·9
9	1,800 gm.	10	23·6
10	2,400 gm.	10	25·9
11	3,000 gm.	10	28·1
12	Mature	10	25·7

Apart from these general changes in the relative position of the Gastrocnemius bundles, a well-defined gradient exists between the fascicular angles at varying sites within the muscle (Table 23). For all the groups, the angle is slight near the origin at site A, but it becomes larger along the muscle to reach a maximum value at mid-muscle (B or C). Towards the muscle insertion the angle again decreases from C to D to E, so much so that the bundles at the terminal site are more nearly longitudinally inclined than anywhere else within the muscle.

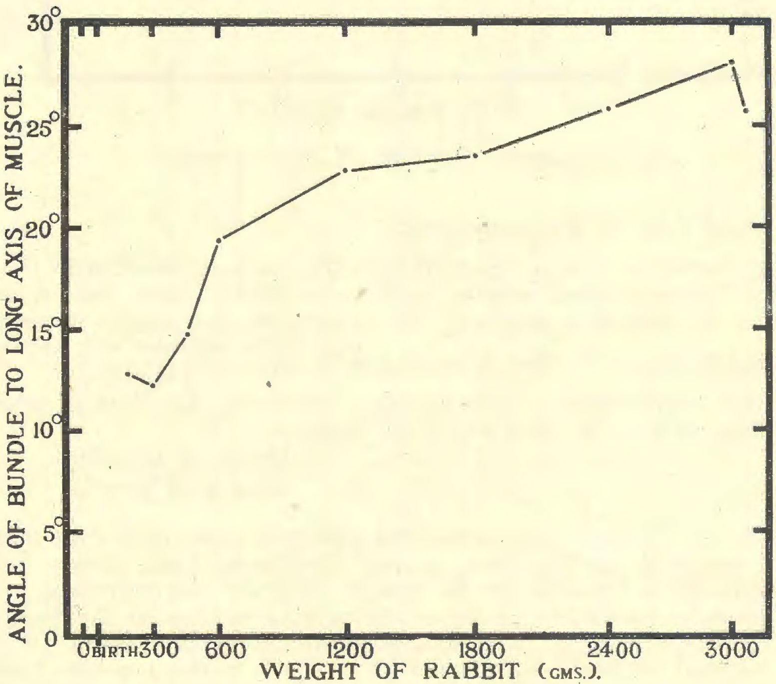


Fig. 16.—Angle of bundle to long axis of M. Gastrocnemius.

TABLE 23.

Angle of Bundle to Long Axis of M. Gastrocnemius at Sites A, B, C, D and E.

Site in Muscle.	Group.								
	220 Gm.	320 Gm.	480 Gm.	600 Gm.	1,200 Gm.	1,800 Gm.	2,400 Gm.	3,000 Gm.	Mature.
A..........	12·5°	11·0°	13·0°	20·5°	25·0°	25·0°	26·5°	27·5°	25·5°
B..........	16·0°	16·0°	18·5°	23·5°	27·0°	27·0°	29·5°	31·0°	27·0°
C..........	16·5°	15·5°	18·5°	21·5°	25·5°	27·0°	30·0°	31·5°	28·5°
D..........	12·0°	12·5°	16·0°	20·0°	23·5°	24·0°	27·0°	30·0°	28·0°
E..........	7·0°	6·0°	8·0°	11·5°	13·5°	15·0°	16·5°	20·5°	19·5°

M. Psoas.

Table 24 and Figure 14 show that, in contradistinction to M. Gastrocnemius, there is a steady increase in bundle length throughout the growth of the animal. Significance is reached at 320 gm. live-weight, but the increment at 600 gm. and at maturity is not significant.

TABLE 24.

Length of Bundle—M. Psoas.

Groups of Rabbits.		No. of Rabbits.	Mean Bundle Length.	Significance Tests.	
No.	Class.			(W. Prec. Group).	(W. Group 1).
			Cm.		
1..............	Birth........	10	2·53	—	—
2..............	100 gm.....	5	3·25	N.S.	N.S.
3..............	150 gm.....	5	4·00	N.S.	XX
4..............	220 gm.....	5	4·78	N.S.	XX
5..............	320 gm.....	5	6·08	X	XX
6..............	480 gm.....	5	7·41	X	XX
7..............	600 gm.....	10	8·12	N.S.	XX
8..............	1,200 gm.....	10	9·51	XX	XX
9..............	1,800 gm.....	10	11·13	XX	XX
10..............	2,400 gm.....	10	12·75	XX	XX
11..............	3,000 gm.....	10	13·83	XX	XX
12..............	Mature......	10	13·85	N.S.	XX

Details of rate of growth are presented in Table 25 and Figure 14. The rate of length increase is highest at birth, decreases sharply to 220 gm. live-weight, thenceforth more gradually to become almost stationary in the ultimate groups. As is to be expected from the muscle structure, these data closely approximate those dealing with length of M. Psoas.

Discussion.

Length of bundle is shown to be an early developing character in M. Gastrocnemius. It is remarkable that Gastrocnemius bundles achieve their maximum length so early in life (320 gm. live-weight—52 days), with no further change until maturity (3,072 gm. live-weight—416 days). It is of interest to discuss this finding in relation to muscle length and depth, both of which have been shown to increase until the final stages in the lifetime of the series of animals studied.

TABLE 25.

Rate of growth of length of bundle—M. Psoas.

Group.	Growth Rate.
Birth	·022,457
100 gm.	·018,383
150 gm.	·014,490
220 gm.	·011,418
320 gm.	·008,599
480 gm.	·006,348
600 gm.	·005,125
1,200 gm.	·002,880
1,800 gm.	·001,979
2,400 gm.	·001,464
3,000 gm.	·001,171
Mature	·001,145

How does the Gastrocnemius muscle lengthen, if this is not due to lengthening of the component muscle bundles? Over the period from 320 gm. live-weight to maturity this muscle has been shown to lengthen from 2·50 cm. to 6·15 cm., i.e., an increase of 3·65 cm.

By what mechanism do the bundles change their relative position in the growing muscle? The mean fascicular angle changes progressively from 12·2° to 25·7° over the same period. Not only do the bundles maintain constant length, but the changing position of the bundles also tends to reduce their effective length in terms of the long axis of the muscle. An unequal rate of growth of the two aponeuroses to which the ends of the bundles are attached may offer a possible solution. For example, if the aponeurosis of origin (superficial) has a relatively greater growth rate distally along the muscle, the fascicular angle will become more obtuse. At the same time the muscle will be thickened to a degree corresponding with the degree of tilting invoked by this process. Alternatively, if the aponeurosis of insertion (deep) has a relatively greater rate of growth proximally along the muscle the same effect will be produced. Presumably both processes play a part in the growing muscle, the aponeurosis of origin extending down towards the muscle insertion, while the aponeurosis of insertion extends upwards towards the muscle origin.

In general, it appears that the varying position assumed by the bundles as the animal grows will contribute more to thickening of the muscle than to an increase in length. If this is so increase in length of the muscle will be dependent upon a thickening of the bundles, and ultimately of the innumerable fibres comprising these bundles. Contradictory as it may seem, lengthening of the muscle is apparently due to a thickening of the bundles (or fibres), whereas thickening of the muscle is at least partly due to an apparent lengthening of the bundles, as the result of a change in their relative position.

In M. Psoas, where a different process is at work, increase in muscle length can be attributed to a straightforward lengthening of the individual fasciculi. Increase in the depth of this muscle must depend largely upon progressive thickening of these bundles as the animal grows older and larger.

2. *Number of fibres comprising the bundle.*

For counting the number of muscle fibres comprising the individual bundle, cross-sections were prepared by cutting frozen sections at the centre of the muscle (site C). The fibres of twenty bundles, selected at random, were counted from each muscle. The results are shown in Table 26.

TABLE 26.

Number of muscle fibres per bundle.

Groups of Rabbits.		Number of Rabbits.	Fibres. (M. Gastroc).	Significance Test (W. Group 1)	Fibres (M. Psoas.).	Significance Test (W. Group 1).
No.	Class.					
1............	Birth......	10	48	—	92	—
7............	600 gm..	10	51	N.S.	91	N.S.
8............	1,200 gm..	10	52	N.S.	87	N.S.
9............	1,800 gm..	10	60	N.S.	95	N.S.
10............	2,400 gm..	10	54	N.S.	91	N.S.
11............	3,000 gm..	10	50	N.S.	94	N.S.
12............	Mature....	10	51	N.S.	87	N.S.

It is not possible to differentiate the number of fibres per bundle between birth and maturity, both in M. Gastrocnemius and in M. Psoas. Not one of the variations is significant so that all may be due to chance alone. Thus the differentiation of muscle fibres has ceased at birth, and the post-natal growth of muscle must be attributed to an increase in size of the fibres existing at birth.

When the two muscles are compared, it is seen that M. Gastrocnemius has consistently less fibres per bundle than M. Psoas Nevertheless, Gastrocnemius bundles will not necessarily be more slender than those of the Psoas muscle, as differences in fibre diameter must also be taken into account. This aspect is discussed in the following section.

3. *Cross-sectional area of muscle bundle (" grain ", texture).*

This has been calculated from the number of fibres per bundle, together with the mean fibre diameter for each group (Table 27, Figure 17). If the fibre is presumed to be circular in outline, the mean cross-sectional area can be calculated from the mean fibre diameter. This, multiplied by the average number of fibres constituting the bundle, gives the average cross-sectional area of the muscle bundle.

In both muscles " grain " increases more or less uniformly from birth to 3,000 gm. live-weight, with only a slight increase from 3,000 gm. to maturity. All increments are significant in M. Psoas, except for the mature animal, but in M. Gastrocnemius significance is just missed at both 2,400 gm. live-weight and 3,000 gm.

TABLE 27.

Cross-sectional area of muscle bundle.

Groups of Rabbits. No.	Groups of Rabbits. Class.	No. of Rabbits.	Mean Area. (M. Gastroc.).	Significance Test. (W. Prec. Group).	Mean Area. (M. Psoas.)	Significance Test. (W. Prec. Group).
			Sq. Mm.		Sq. Mm.	
1............	Birth......	10	·004,880	—	·005,212	—
7............	600 gm..	10	·052,877	XX	·027,339	XX
8............	1,200 gm..	10	·090,983	XX	·057,560	XX
9............	1,800 gm..	10	·181,098	XX	·108,428	XX
10............	2,400 gm..	10	·199,320	N.S.*	·133,238	XX
11............	3,000 gm..	10	·221,077	N.S.*	·152,538	X
12............	Mature....	10	·246,405	X	·153,952	N.S.

* Here significance at P = 0·05 is just missed.

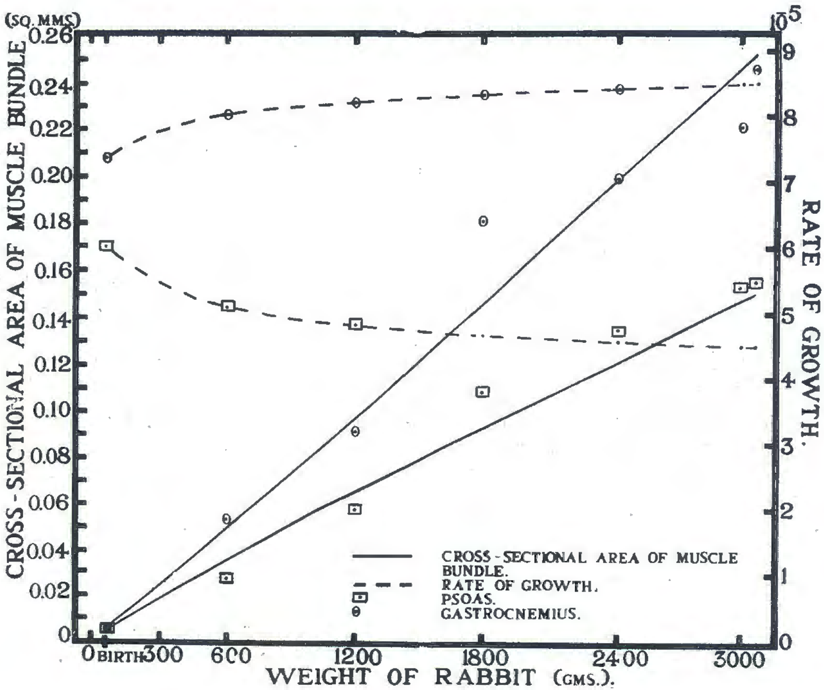


Fig. 17.—Cross-sectional area of muscle bundle.

Comparison of the two muscles shows that at birth M. Psoas has slightly bigger bundles, but they become increasingly smaller than those of M. Gastrocnemius in the succeeding stages from 600 gm. live-weight to maturity. Thus, in general, M. Psoas is a finer grained muscle, this difference becoming accentuated as the animal grows older.

The reason for this is evident from a study of rate of growth (Table 28, Figure 17). M. Gastrocnemius has always a greater growth rate than M. Psoas. Gastrocnemius bundles show a pronounced increase between birth and 600 gm. live-weight, after which the rate slackens to become almost stationary from 2,400 gm. onwards. On the other hand, M. Psoas is growing fastest at birth and the growth rate then drops markedly to 600 gm. live-weight. From 600 gm. the curve declines more gradually to become flat in the ultimate stages.

TABLE 28.

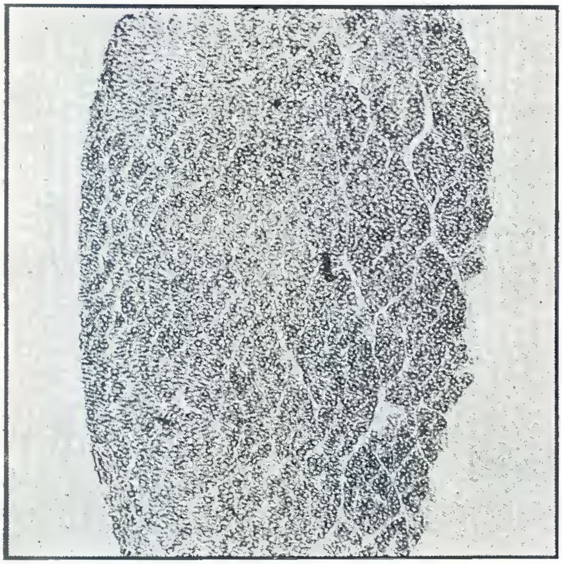
Rate of growth of cross-sectional area of muscle bundle.

Group.	M. Gastrocnemius.	M. Psoas.
Birth	·000,074	·000,060
600 gm.	·000,080	·000,051
1,200 gm.	·000,082	·000,048
1,800 gm.	·000,083	·000,047
2,400 gm.	·000,084	·000,046
3,000 gm.	·000,085	·000,045
Mature	·000,085	·000,045

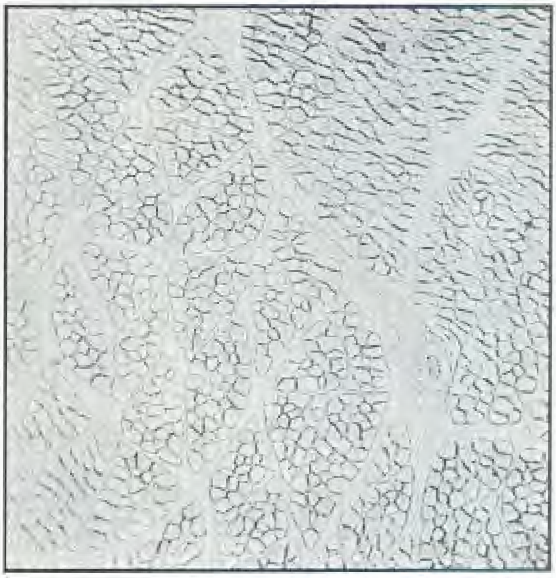
PLATE III.

The effect of age on the coarseness of texture in the Gastrocnemius muscle.
(All to the same magnification 50 × .)

Unstained cross-sections cut by the freezing method. Large bundles, consisting of a smaller number of thicker fibres, than in the Psoas muscle.



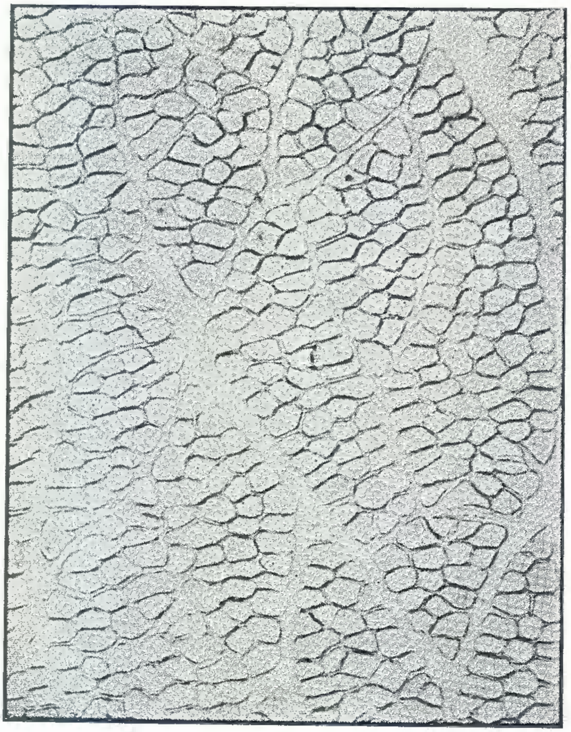
Birth.



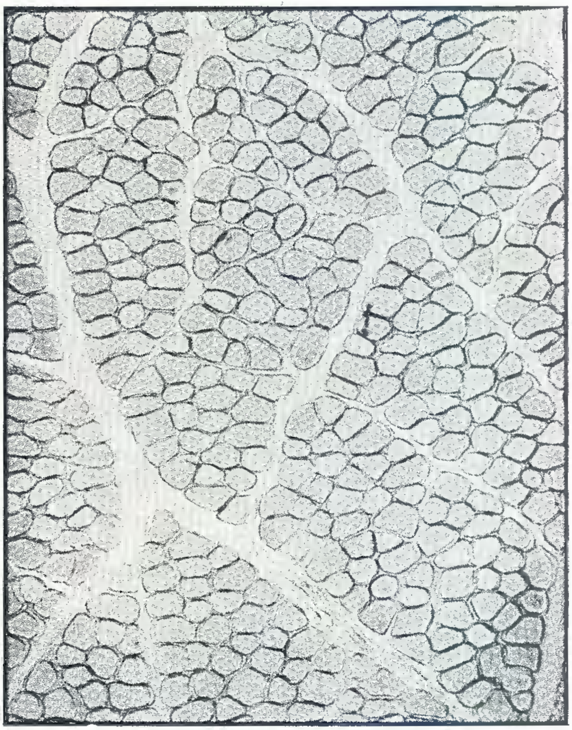
600 gm. live-weight.

1,200 gm. live-weight.

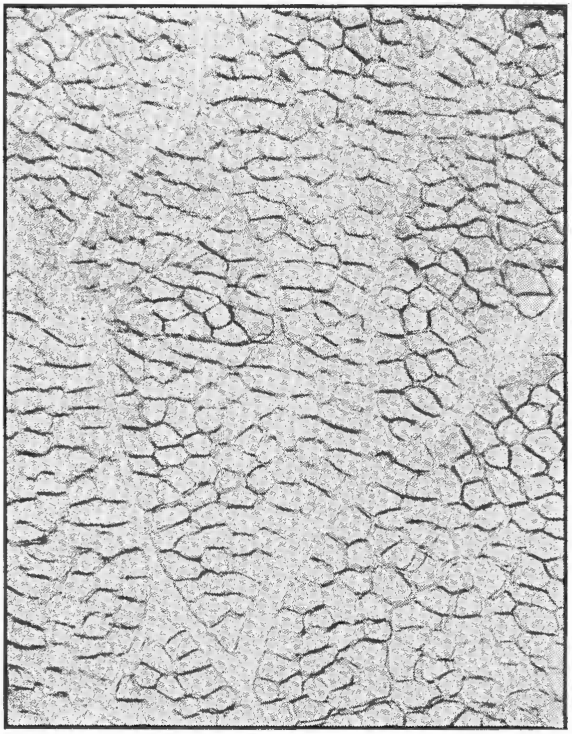
1,800 gm. live-weight.



2,400 gm. live-weight.



3,000 gm. live-weight.

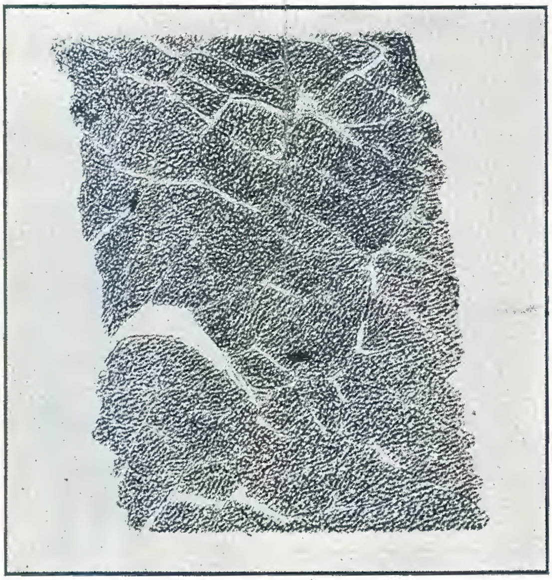


" Mature."

Plate IV.

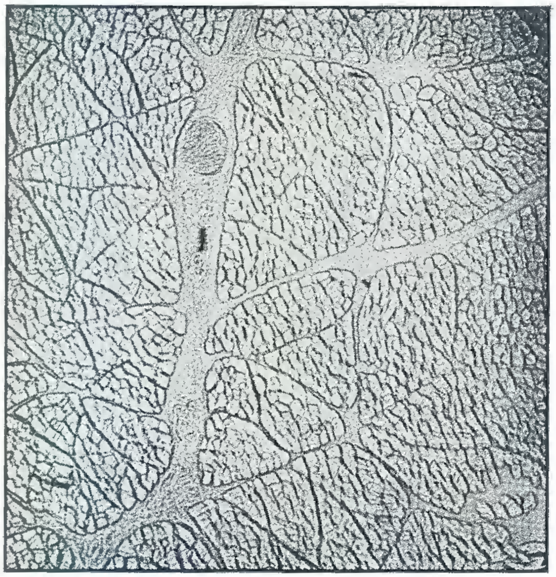
The effect of age on the coarseness of texture in the Psoas muscle.
(All to the same magnification 50 ×.)

Unstained cross-sections cut by the freezing method. Small bundles, compared with the Gastrocnemius muscle, consisting of a larger number of thinner fibres. Note the marked dissimilarity in size of the component fibres.

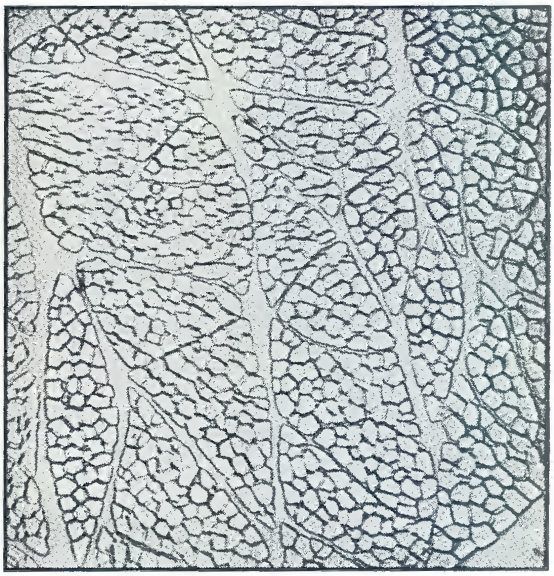


Birth.

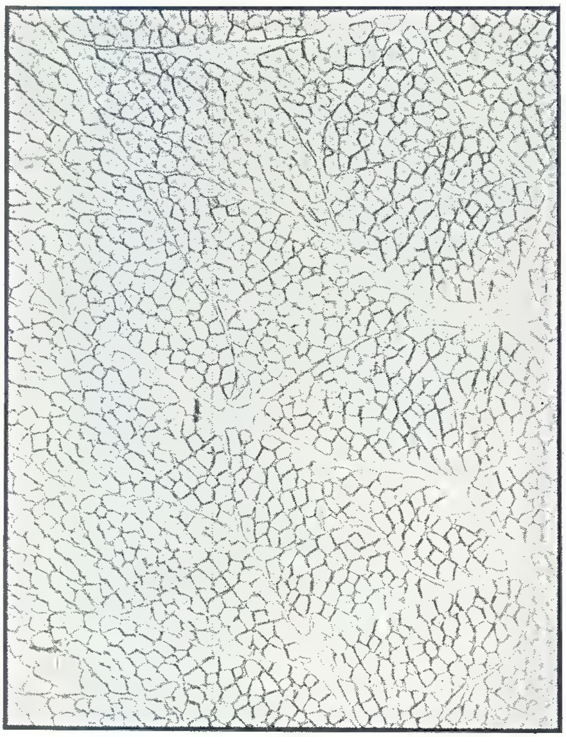
600 gm. live-weight.



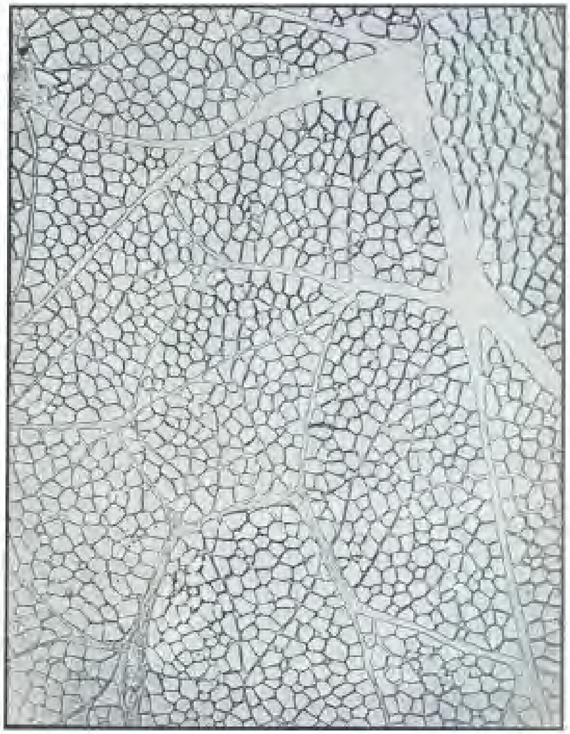
1,200 gm. live-weight.



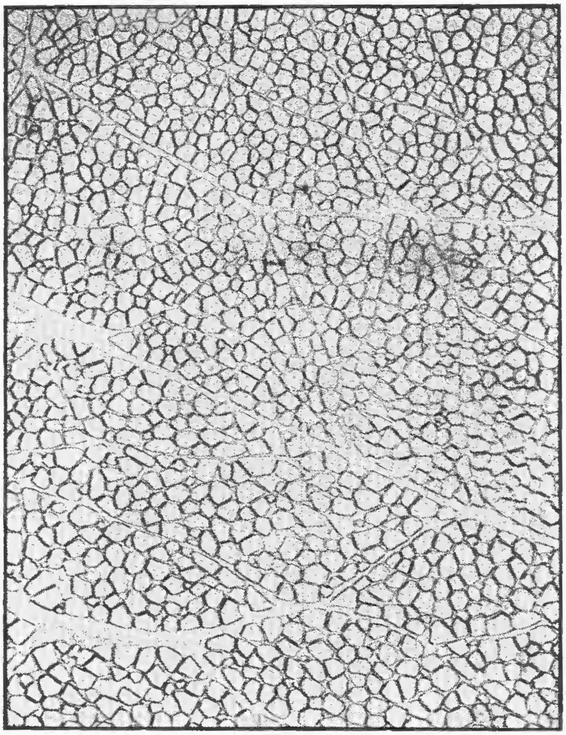
1,800 gm. live-weight.



2,400 gm. live-weight.



3,000 gm. live-weight.



" Mature."

Discussion.

In order to emphasize the growth changes, a diagrammatic representation of the muscle bundle as a whole is shown in Figure 18. Obviously, it is difficult to draw to the same scale, length in terms of centimetres and " thickness " (cross-sectional area) in fractions of a square millimetre. In this diagram length has been correctly scaled for both muscles, so that the proportions are true to life. " Thickness " has been drawn to a larger scale. Again, the relative " thickness " is correct for both muscles, but the proportion of length to " thickness ", considered as separate characters, is false.

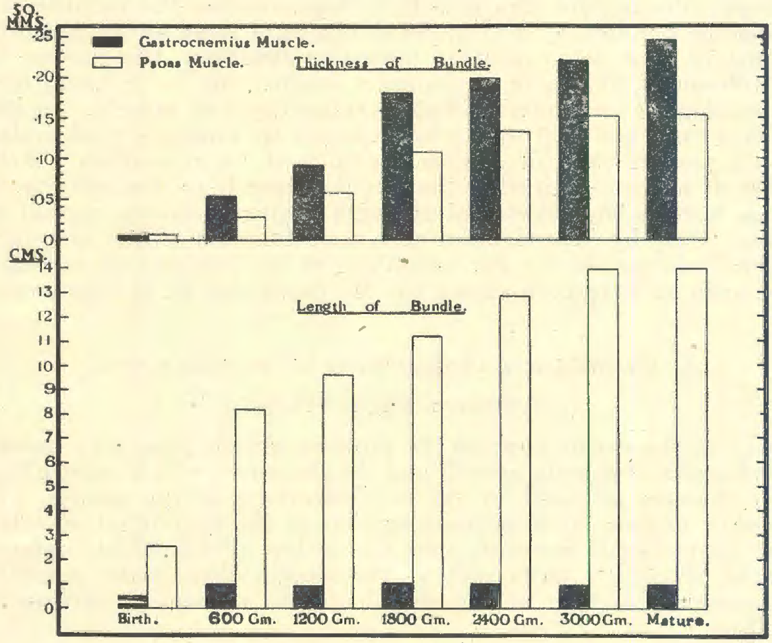


Fig. 18.—Growth of muscle bundle in length and thickness.

Length growth of the two types of bundles is clearly dissimilar. Excluding the period from birth to 600 gm. live-weight, there is virtually no change in length of the Gastrocnemius bundle. On the other hand, the much longer Psoas bundles lengthen, in stages spread more or less evenly, over the period up to 3,000 gm. live-weight. Clearly length growth of the Psoas bundle is a much later developing character than in the Gastrocnemius muscle. The degree of thickening of the bundle is more or less the same in both muscles, but the Gastrocnemius bundles are thicker at all stages of the growth period after birth.

Thus the increase in substance of M. Gastrocnemius, from 600 gm. live-weight to maturity, may be attributed to a thickening of the component bundles. Lengthening of bundles plays no part in this process. By contrast, the Psoas muscle grows largely by lengthening of the bundles. Although thickness growth of the bundles also contributes to enlargement of the muscle, it is probable that the length increase is the more important factor.

From the viewpoint of meat research, interest is also attached to the eating quality of these different types of muscle. It is to be expected that a finely grained muscle will be less stringy or tough (Hammond 1940a; 1940b), but other factors such as the amount of connective tissue and fat have to be considered. M. Psoas (or fillet) is traditionally a delicacy, with probably the most tender meat in the carcass. How far is this to be attributed to fineness of the muscle bundles? The tougher Gastrocnemius muscle has been found to contain a large amount of connective tissue, in addition to the coarseness of grain here revealed, but the respective importance of each factor in determining toughness has still to be decided.

Obviously the texture of a muscle is dependent on the number of fibres constituting the bundles, as well as the thickness of these fibres. As both these factors must be such as to promote muscular efficiency, the reasons for the inherent differences, shown in the muscles studied, are to be found by study of the physiological characteristics of varying types of muscle. In general, thicker fibres (and bundles) are to be expected in a muscle used mainly for maintaining posture than in a muscle employed for movement. No doubt the number of fibres constituting the bundle depends on the activity of contraction, as well as the functional strength required during normal muscle contraction. Only by investigation of muscle function will it be possible to explain the basic reason for the variations in architecture of various types of muscle, such as have been shown for M. Psoas and M. Gastrocnemius.

(*d*) Growth and development of muscle fibre.

(Literature: Pages 341-347.)

A study of the morphology of the growing muscle fibre may throw light on the mechanism of muscle growth and development, which must ultimately depend on changes initiated in the microstructure of the muscle. Hence, it is necessary to pass on to a consideration of the individual muscle fibre. It will be appreciated, however, that the technical difficulties, inherent in measurement of minute units such as the muscle fibre, make it difficult to obtain a complete picture of the morphological changes occurring in the growing fibres.

1. *Length of muscle fibre.*

M. Gastrocnemius.

Evidence has been presented that, in the Gastrocnemius muscle, the component fibres pass right along the length of the bundle from one end to the other (pages 341-342). In order to obtain confirmation of this finding it was necessary to carry out considerable work.

After separating individual bundles from a muscle, the bundles were straightened in a holder made for this purpose and securely fastened in this position. Each bundle was infiltrated in an ascending series of gelatin solutions and embedded in twenty-five per cent. gelatin. Serial sections were cut transversely by the freezing method in a low temperature room. All sections were examined microscopically to ascertain the presence of fibres beginning or ending within the bundle. In addition, in every tenth section, the number of fibres comprising the bundle was counted, as well as measuring the diameter of each fibre within the bundle. The results obtained substantiate the claim that Gastrocnemius fibres extend from one end of the bundle to the other end.

This is of importance, as an estimate of fibre length can be obtained relatively easily by measuring length of bundle. The observations regarding Gastrocnemius bundles have already been discussed (page 392). For purposes of comparison, length of the Gastrocnemius muscle fibre may be considered to be equivalent to bundle length. Therefore, as in the case of bundle length, length of the Gastrocnemius fibre is an extremely early developing character. By the time that the animal has attained a live-weight of 320 gm. fibres have ceased to make any further length growth. Furthermore, a gradient of fibres of varying lengths exists within the muscle. In general, fibres are shorter at B than at A, and show a progressive increase in length at each of the succeeding sites C, D, and E.

M. Psoas.

Unlike the Gastrocnemius muscle, Psoas fibres are usually shorter than the bundle with one or both ends lying freely within the bundle. This makes it difficult to devise a method for obtaining a routine measurement of length of fibre, to be applied in this experiment. No suitable technique was devised, hence it is not possible to present any data concerning the length growth of Psoas muscle fibres. However, from a consideration of bundle length (page 397), it would appear that the fibres constituting these bundles continue to lengthen over a relatively greater period of the lifetime of the animal, than in the Gastrocnemius muscle.

2. *Diameter of Muscle Fibre.*

M. Gastrocnemius.

Fibre diameter is considered in Table 29 and Figure 19.

TABLE 29.

Diameter of Gastrocnemius Muscle Fibres.

Rabbit Group. No.	Rabbit Group. Class.	No. of Rabbits.	DIAM. "A"	Sig. Test Prec. Gr.	DIAM. "B"	Sig. Test Prec. Gr.	DIAM. "C"	Sig. Test Prec. Gr.	DIAM. "D"	Sig. Test Prec. Gr.	DIAM. "E"	Sig. Test Prec. Gr.
			μ		μ		μ		μ		μ	
1	Birth...	10	12·30	—	11·33	—	10·83	—	10·91	—	11·41	—
	Gm.											
7	600	10	33·87	XX	34·74	XX	36·79	XX	39·57	XX	37·12	XX
8	1,200	10	42·23	XX	45·35	XX	48·85	XX	51·18	XX	48·24	XX
9	1,800	10	55·22	XX	58·55	XX	62·30	XX	67·78	XX	66·23	XX
10	2,400	10	59·93	X	65·61	XX	68·06	XX	74·44	XX	74·84	XX
11	3,000	10	64·40	X	72·06	XX	75·48	XX	81·55	XX	81·82	X
12	Mature.	10	67·04	N.S.	75·29	N.S.	77·43	N.S.	85·64	N.S.	87·38	X

Considerable thickening of fibres takes place from birth to maturity. After a period of marked increase from birth to 600 gm. live-weight the curves flatten out progressively in the subsequent groups, so that there is only a slight increase between 3000 gm. and maturity. This flattening of the curves takes place in a graded manner, least and latest at D and E, and in order of increasing flatness C, B, and A. Thickening of fibres near the muscle insertion clearly continues over a longer period of the life of the animal, than at points nearer the muscle origin. Significance is shown for all increments in fibre diameter at each site, except in the mature group of rabbits.

In Table 30 and Figure 19 are to be found details concerning the rate of growth. The growth rate is greatest at birth, then decreases sharply until 600 gm. live-weight, after which the curves flatten less abruptly until 1800 gm., and become nearly horizontal in the concluding groups. It is to be noted the same relative order is preserved throughout, namely D, E, C, B, A, in order of decreasing magnitude.

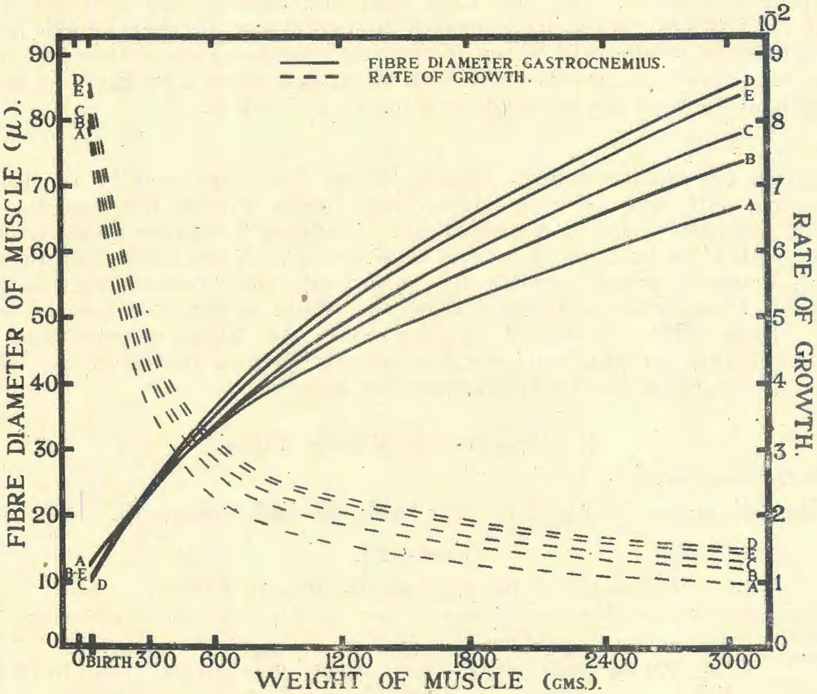


Fig. 19.—Diemeter of Gastrocnemius muscle fibres. [Corrigendum: For legend-abcissa axis substitute WEIGHT OF RABBIT (GMS.).]

TABLE 30.

Rate of Growth of Fibre Diameter in M. Gastrocnemius.

Group.	Site A.	Site B.	Site C.	Site D.	Site E.
Birth	·077,991	·079,868	·081,428	·085,643	·085,249
600 gm.	·023,095	·026,433	·028,272	·031,124	·030,491
1,200 gm.	·015,990	·018,919	·020,535	·022,916	·022,341
1,800 gm.	·012,861	·015,520	·016,990	·019,113	·018,582
2,400 gm.	·010,918	·013,371	·014,732	·016,676	·016,176
3,000 gm.	·009,720	·012,031	·013,317	·015,141	·014,663
Mature	·009,611	·011,907	·013,186	·014,995	·014,522

Relative fibre diameter within the muscle is considered in Table 31 and Figure 20. The most striking feature of the table is that at birth relative fibre diameter presents a pattern different from that of the subsequent groups.

TABLE 31.

Relative Fibre Diameter of Gastrocnemius Muscle.

Site in Muscle.	Birth.			600 Gm.			1,200 Gm.			1,800 Gm.			2,400 Gm.			3,000 Gm.			Mature.		
	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.
	μ			μ			μ			μ			μ			μ			μ		
A..........	12·30	—	—	33·87	—	—	42·23	—	—	55·22	—	—	59·93	—	—	64·40	—	—	67·04	—	—
B..........	11·33	XX	XX	34·74	N.S.	N.S.	45·35	X	X	58·55	X	X	65·61	XX	XX	72·06	XX	XX	75·29	XX	XX
C..........	10·83	N.S.	XX	36·79	XX	XX	48·85	XX	XX	62·30	XX	XX	68·06	X	XX	75·48	XX	XX	77·43	N.S.	XX
D..........	10·91	N.S.	XX	39·57	XX	XX	51·18	N.S.	XX	67·78	XX	XX	74·44	XX	XX	81·55	XX	XX	85·64	XX	XX
E..........	11·41	N.S.	XX	37·12	XX	XX	48·24	X	XX	66·23	N.S.	XX	74·84	N.S.	XX	81·82	N.S.	XX	87·38	N.S.	XX

ABBREVATIONS : Sig. Test.............................. Significance Test.

TABLE 32.

Relative fibre diameter of Psoas muscle.

Site in Muscle.	Birth.			600 Gm.			1,200 Gm.			1,800 Gm.			2,400 Gm.			3,000 Gm.			Mature.		
	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.	Diam.	Sig. Test. Prec. Site.	Sig. Test. Site A.
	μ			μ			μ			μ			μ			μ			μ		
A..........	8·74	—	—	20·28	—	—	31·42	—	—	39·50	—	—	44·99	—	—	46·90	—	—	48·68	—	—
B..........	8·39	N.S.	N.S.	19·40	X	X	28·67	XX	XX	38·19	N.S.	N.S.	42·45	XX	XX	43·58	XX	XX	46·21	X	X
C..........	8·38	N.S.	N.S.	19·34	N.S.	X	28·30	N.S.	XX	36·70	N.S.	XX	41·57	N.S.	XX	43·53	N.S.	XX	45·96	N.S.	XX
D..........	8·32	N.S.	X	19·16	N.S.	XX	27·69	N.S.	XX	37·04	N.S.	XX	42·25	N.S.	XX	44·76	N.S.	X	46·12	N.S.	X
E..........	8·67	N.S.	N.S.	19·37	N.S.	X	29·03	X	XX	38·55	N.S.	N.S.	44·52	X	N.S.	47·56	XX	N.S.	49·95	XX	N.S.

At birth, fibre diameter is greatest near the origin of the muscle (A), and smaller at the subsequent points (B, C, D, E). The significance test shows a positive result throughout. In the later groups, from 600 gm. live-weight to maturity, the thinnest fibres are found near the origin (A), with a significant increase in diameter at the succeeding points B, C, and D. One negative result is shown in both the 600 gm. and the 1200 gm. groups. Excluding birth, the fibres at E are in some groups thinner than at D (600 gm., 1200 gm.), whereas no significant difference is shown for the other groups (1800 gm., 2400 gm., 3000 gm., maturity).

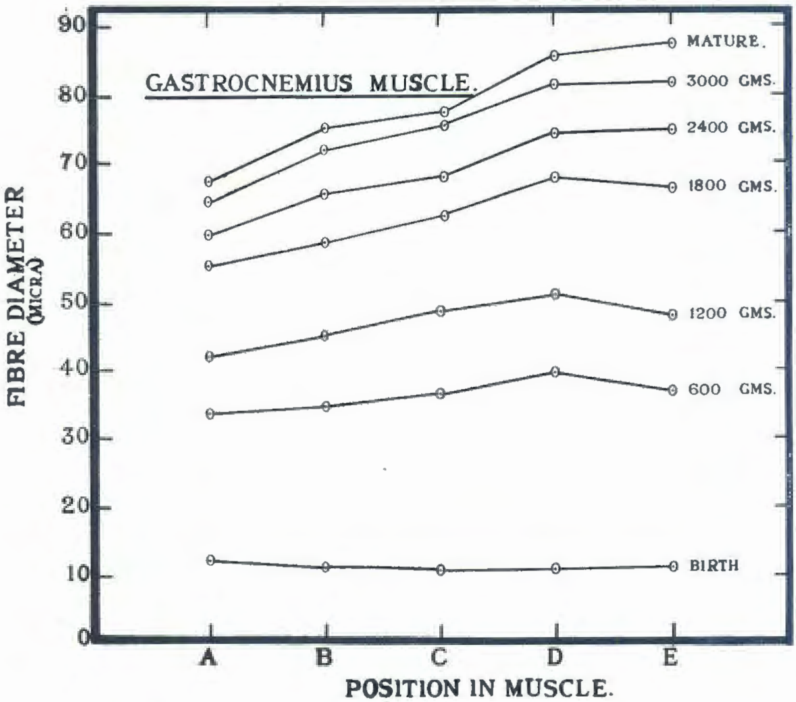


Fig. 20.—Relative fibre diameter of Gastrocnemius muscle.

This latter irregularity may be due to the variation in individual animals comprising the groups (see Appendix Table F). Fibres at the terminal site E are thinner than at D in 8, 6, 7, 6, 6 and 2 animals respectively of the ten rabbits comprising each of the last six groups. Perhaps slight differences in the relative positions at which fibres were taken for measurement from different animals may account for this variation. Under the circumstances, all that can be said is that, in the older animals, there is a tendency for the diameter of fibre to become slightly reduced from D towards the insertion of the muscle.

With reference to the change in relative thickness of the fibres in the older groups as compared with the new-born rabbit, probably this is brought about by the growth gradient shown to exist along the length of the muscle. It has been observed that the rate of thickening of fibres increases in progressive manner from the beginning towards the end of the muscle.

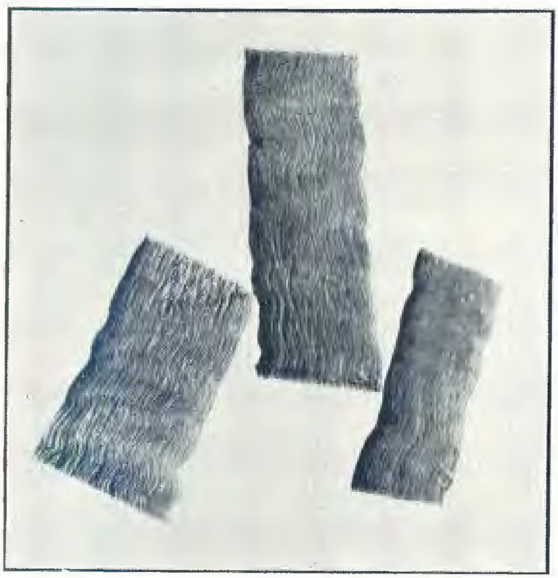
PLATE V.

The effect of age on the diameter of the muscle fibres of M. Gastrocnemius.
(All to the same magnification 200 × .)

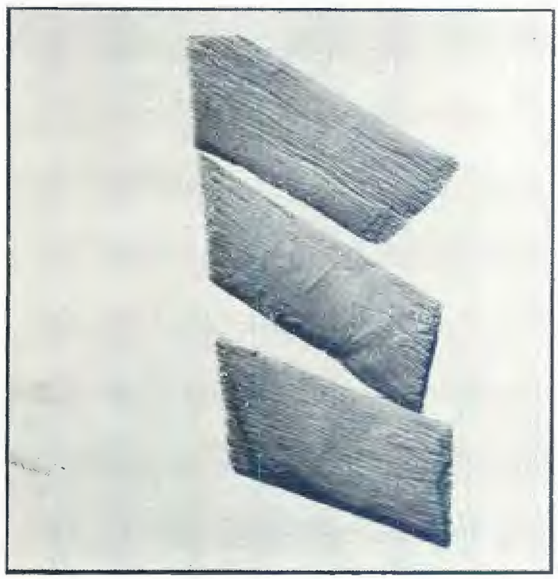
Unstained fibres teased from the formalin-fixed muscle showing striation in both the longitudinal and transverse direction.

Birth.

600 gm. live-weight.



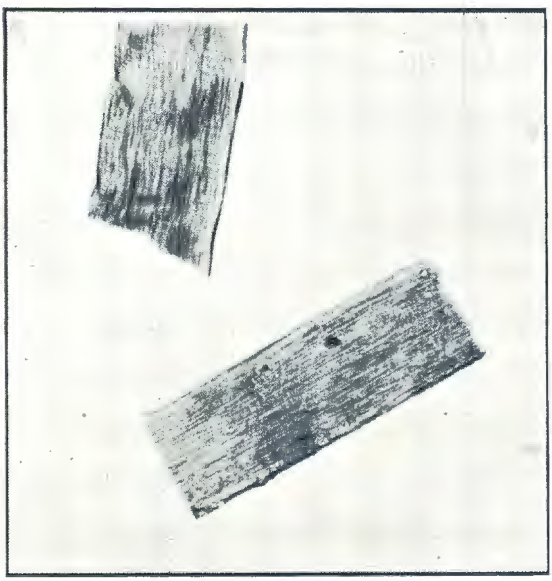
1,200 gm. live-weight.



1,800 gm. live-weight.

2,400 gm. live-weight.

3,000 gm. live-weight.



" Mature."

M. Psoas.

Throughout the life of the animal, Psoas fibres are appreciably thinner than the Gastrocnemius fibres. Although there is a definite increase in fibre diameter, this increase is much less marked than for M. Gastrocnemius (Table 33, Figure 21). The curves are uniformly flatter throughout. From the tests it is seen that there are significant differences at all the stages up to 2400 gm. live-weight. In the two final groups some of the increments do not show significance, hence they may be chance variations. The tendency is for increases in fibre diameter to be less definite from 2400 gm. live-weight onwards than in the Gastrocnemius muscle.

TABLE 33.

Diameter of Psoas Muscle Fibres.

Rabbit Group. No.	Rabbit Group. Class.	No. of Rabbits.	DIAM. "A"	Sig. Test Prec. Gr.	DIAM. "B"	Sig. Test Prec. Gr.	DIAM. "C"	Sig. Test Prec. Gr.	DIAM. "D"	Sig. Test Prec. Gr.	DIAM. "E"	Sig. Test Prec. Gr.
			μ		μ		μ		μ		μ	
1	Birth...	10	8·74	—	8·39	—	8·38	—	8·32	—	8·67	—
	Gm.											
7	600	10	20·28	XX	19·40	XX	19·34	XX	19·16	XX	19·37	XX
8	1,200	10	31·42	XX	28·67	XX	28·30	XX	27·69	XX	29·03	XX
9	1,800	10	39·50	XX	38·19	XX	36·70	XX	37·04	XX	38·55	XX
10	2,400	10	44·99	XX	42·45	XX	41·57	XX	42·25	XX	44·52	XX
11	3,000	10	46·90	N.S.	43·58	N.S.	43·53	N.S.	44·76	X	47·56	X
12	Mature.	10	48·68	N.S.	46·21	X	45·96	X	46·12	N.S.	49·95	X

Rate of growth is considered in Table 34 and Figure 21. At birth, the Psoas growth rate is roughly two-thirds of the rate for M. Gastrocnemius. However, from 600 gm. live-weight to maturity it is only slightly less than the Gastrocnemius growth rate. From the graphs it is seen that the curves are of similar trend in both muscles. After an initial steep decline to the 600 gm. group, the rate of growth subsequently flattens out gradually to become almost horizontal in the final stages. There is a tendency for a gradient to occur along the length of the muscle, whereby the growth rate at the ends (A, E) is higher throughout than in the central portion (B, C, D). These differences are less marked than those encountered in the Gastrocnemius muscle.

TABLE 34.

Rate of growth of fibre diameter in M. Psoas.

Group.	Site A.	Site B.	Site C.	Site D.	Site E.
Birth.....................	·054,717	·051,898	·051,380	·051,314	·053,530
600 gm.................	·016,861	·015,824	·015,537	·015,754	·016,713
1,200 gm.................	·011,815	·011,052	·010,824	·011,024	·011,757
1,800 gm.................	·009,570	·008,934	·008,738	·008,923	·009,546
2,400 g,..................	·008,166	·007,614	·007,438	·007,612	·008,161
3,000 gm.................	·007,299	·006,798	·006,636	·006,801	·007,303
Mature..................	·007,219	·006,721	·006,562	·006,726	·007,223

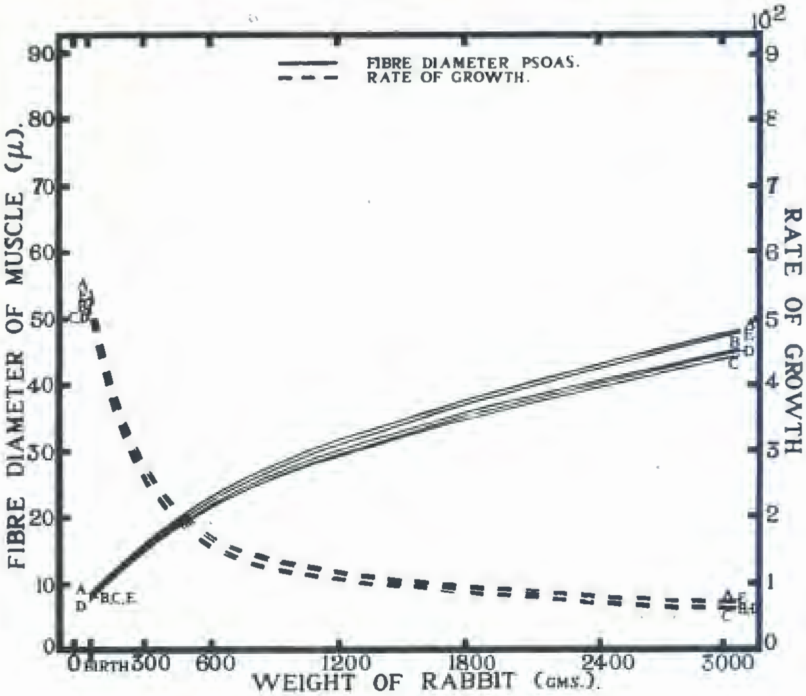


Fig. 21.—Diameter of Psoas muscle fibres.

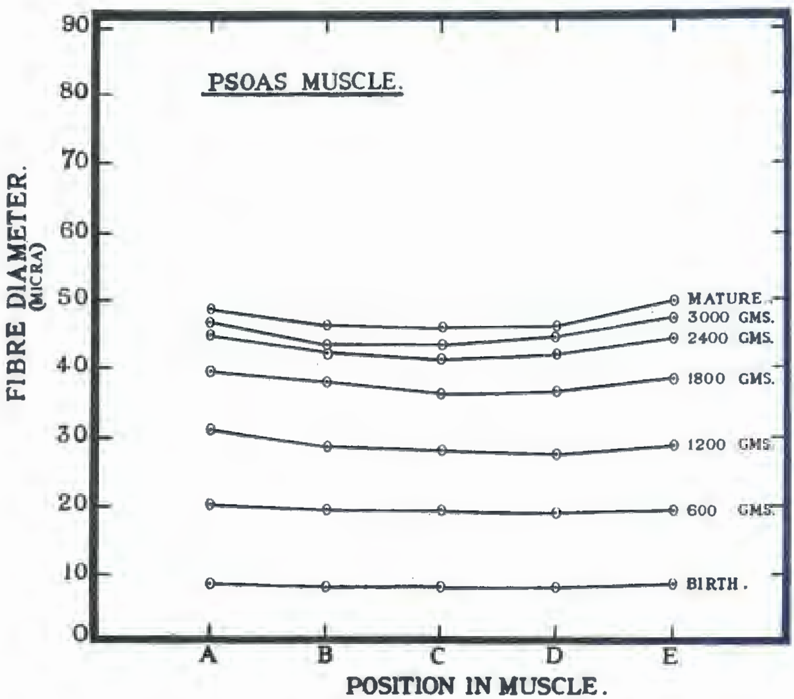


Fig. 22.—Relative fibre diameter of Psoas muscle.

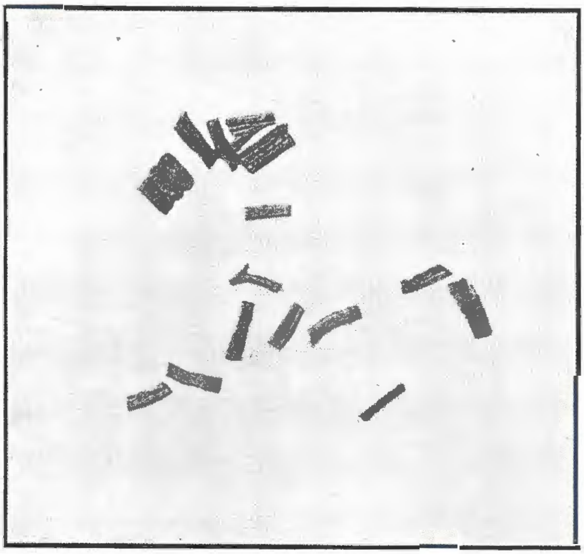
Details of relative fibre diameter within the muscle are presented in Table 32 and Figure 22. The fibres tend to become progressively thinner from A to B to C, but they tend to thicken again towards the other end of the muscle, from C to D to E. In general, fibre diameter at B, C, and D, is significantly less than at site A (two exceptions at birth, one exception at 1,800 gm. live-weight). Only a slight difference is evident between fibre diameter at the two ends of the muscle, as the fibres are significantly thinner at E than at A only in the 600 gm. and 1,200 gm. groups. In all the other groups the variations may be due to chance alone. By comparison with the picture painted for M. Gastrocnemius, thicker fibres are found at the ends of the Psoas muscle, and the central portion of the muscle is composed of thinner fibres.

Plate VI.

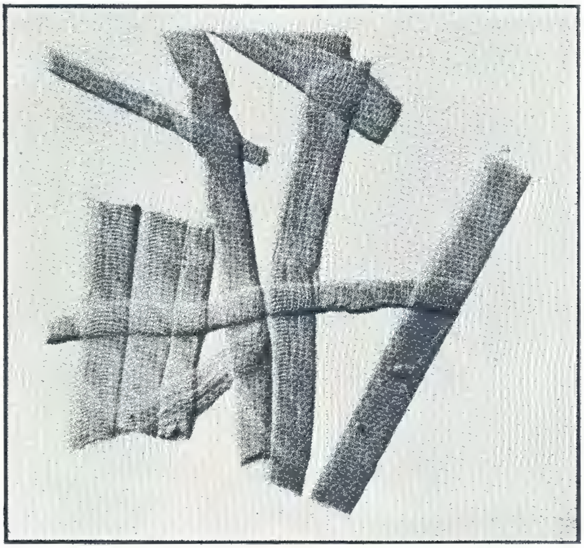
The effect of age on the diameter of the muscle fibres of M. Psoas.

(All to the same magnification 200 × .)

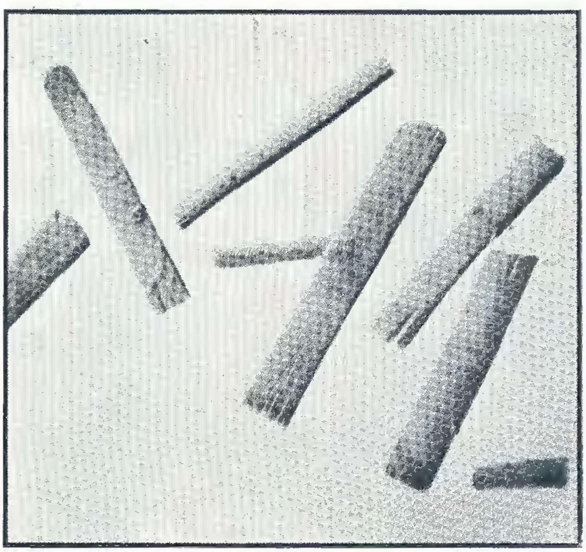
Unstained fibres, teased from the formalin-fixed muscle, showing a characteristic broad cross-striation compared with Gastrocnemius fibres. Note the marked variation in size, here illustrated particularly for the 1,200 gm. group.



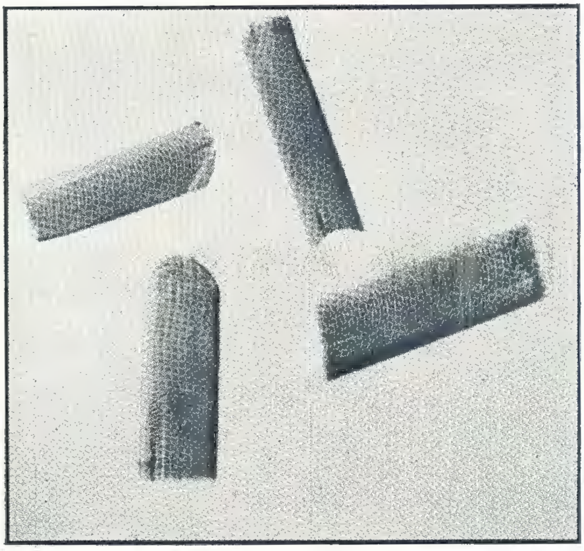
Birth.



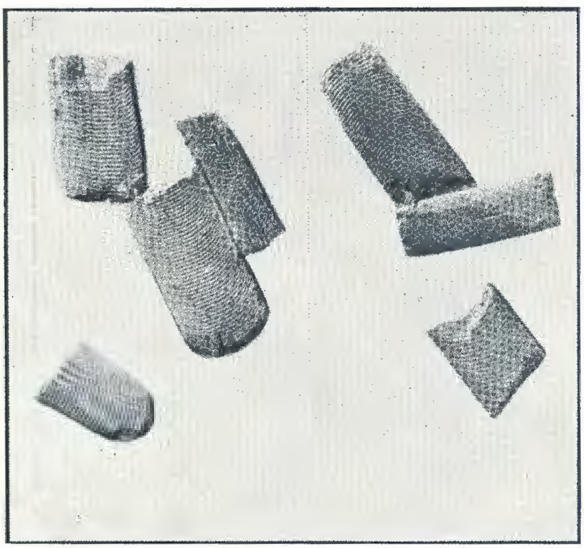
600 gm. live-weight.



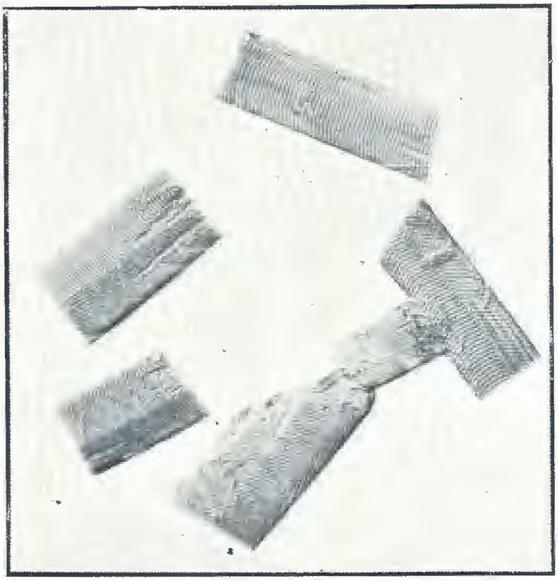
1,200 gm. live-weight.



1,800 gm. live-weight.



2,400 gm. live-weight.



3,000 gm. live-weight.

" Mature."

Discussion.

M. Gastrocnemius. Gastrocnemius fibres attain their maximum development in length very early in life (320 gm. live-weight—52 days). However, the thickness of these fibres continues to increase throughout the lifetime of the animals studied, although a definite increase is not shown between 3000 gm. live-weight and maturity (or over the last six months of the lifetime of these rabbits). Thus, thickening of the fibres must account largely for the muscular development which takes place. Even though M. Gastrocnemius is a relatively early developing unit, its component fibres achieve maturity in thickness growth at a late stage of its development. A diagrammatic representation of the respective changes is shown in Figure 23.

It is understandable that the relative thickness of fibres within the muscle at birth presents a pattern different from that of succeeding groups. Rabbits are born in a comparatively immature condition, with relatively little work for the leg muscles early in life. However, when the animals start walking these muscles are in constant use. Not only does this increased functional activity necessitate thicker fibres, but presumably the nature of this work is such as to also call for the development of stronger and thicker fibres towards the insertion of the muscle, in order to promote efficiency of function. A reason cannot be advanced for this graded thickening of fibres. Information is lacking as regards the part played in the functioning muscle, by the fibres of varying degrees of thickness at different points within the muscle.

From the point of view of obtaining a representative measurement of fibre thickness, it appears that a specimen taken from the middle of the muscle will closely approximate the mean fibre diameter of the whole muscle. Hence, in comparative muscle studies, the labour involved in measuring fibres can be reduced considerably where only a general idea of thickness of fibre is required.

M. Psoas.—Comparison of the number of fibres comprising the muscle bundle shows more or less the same number at later stages of life as at birth. In other words, new fibres are not formed after birth. In the absence of a formation of new fibres, it is reasonable to assume that lengthening of the bundle is brought about by an increase in the length of the existing muscle fibres. Although there is a possibility that the different types of fibre (spindleshaped intrafascicular fibres, blunt tendon-end fibres with one intrafascicular termination) may not contribute evenly to this process, nevertheless it remains true that length increase of fibre, considered as a general measure, will be approximately equal to length increase of bundle. For instance, Buchthal and Lindhard (1939) found that, on the average, fibres shorter than the bundle are more than half the length of the bundle. For convenience, fibre length has been pictured as half the observed length of Psoas bundles in the diagram shown in Figure 23.

By analogy from a study of the development of bundles, Psoas fibres probably lengthen progressively over the lifetime of the rabbit until 3000 gm. live-weight. This appears to be the major difference between the development of the two muscles. Thickness of fibre does not show as marked development as does length of bundle (or fibre), and the curve is flatter throughout the period studied. As thickening of the fibres is relatively