

A STUDY OF CANINE AND EQUINE SKELETAL MUSCLE

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Fig. 1.

**Femurs of Greyhounds and other dogs, indicating
their sizes over the range of liveweight studied.**

Greyhounds



1.17kg
3 weeks ♀
femur weight : 4.95g
femur length : 5.10cm



11.0kg
17 weeks ♀
femur weight : 69g
femur length : 16.8cm



30kg
4 years ♂
femur weight : 139g
femur length : 22.3cm

Other Dogs



1.26kg
8 weeks ♀
femur weight : 6.77g
femur length : 6.9cm



9.9kg
23 weeks ♀
femur weight : 46g
femur length : 15cm



46.5kg
8 years ♂
femur weight : 276g
femur length : 28cm

Fig. 2.

**Femurs of Thoroughbreds and other horses, indicating
their sizes over the range of liveweight studied.**

Thoroughbreds



♂
0.69 kg
154 days 'in utero'
femur weight : 4.7g
femur length : 5.5cm

♀
58.7 kg
346 days 'in utero'
femur weight : 992g
femur length : 28cm

♀
458 kg
3 years
femur weight : 2,660g
femur length : 45cm

Other Horses



CLYDESDALE
496 kg
7 years ♀
femur weight : 3,680g
femur length : 47.4cm



SHETLAND PONY
154 kg
4 years ♂
femur weight : 510g
femur length : 24.5cm



WELSH MOUNTAIN PONY
2.98 kg ♂
158 days 'in utero'
femur weight : 21g
femur length : 8.7cm

Table 2 Lengths of the femur, tibia and fibula, humerus, radius and ulna of dogs and horses in cm.

Type of animal	Live-weight	Sex	Femur	Tibia & Fibula	Humerus	Radius & Ulna	Type of animal	Live-weight	Sex	Femur	Tibia & Fibula	Humerus	Radius & Ulna
Young Greyhounds	377	♀	4.1	3.6	4.1	4.6	Young Thoroughbreds	691	♂	5.5	5.3	4.2	6.3
	927	♀	5.5	5.2	5.7	6.1		13,429	♀	17.6	18.1	14.1	20.2
	1,056	♀	5.5	5.0	5.6	6.0		19,000	♀	20.0	21.3	-	-
	1,174	♀	5.1	5.1	5.3	5.7		23,872	♂	22.6	23.8	16.8	26.0
	1,423	♂	7.6	7.2	7.4	8.3		29,000	♂	22.9	24.2	-	-
	2,280	♂	8.3	7.9	8.1	9.3		30,965	♀	22.4	23.5	-	-
	5,712	♀	12.6	13.0	12.1	14.1		33,500	♂	24.0	25.9	-	-
	11,000	♀	16.8	17.2	15.3	18.5		40,500	♀	27.0	27.7	21.1	31.2
	15,250	♀	18.8	20.3	17.4	21.4		42,962	♀	26.4	27.3	20.59	31.2
	19,750	♂	20.9	22.2	19.1	23.4		58,664	♀	28.4	29.1	22.1	33.8
	23,500	♀	21.6	22.2	20.0	23.9		432,727	♂	47.6	43.4	36.2	50.2
Adult Greyhounds	25,000	♀	21.8	22.2	19.7	24.1	Adult Thoroughbreds	-	-	-	-	-	-
D*	25,300	♂	21.8	22.5	-	-	Young other horses	-	-	-	-	-	-
	28,000	♂	23.6	23.9	-	-	Welsh Mt.	2,977	♂	8.7	7.9	6.8	9.1
D*	28,500	♀	21.0	24.2	21.2	25.4	Welsh Mt.	109,091	♂	30.7	28.7	22.5	32.9
	30,000	♂	23.5	24.3	22.5	25.9	Welsh Mt.	114,546	♀	29.7	28.3	22.6	32.5
Young other dogs							Welsh Mt.	118,182	♂	30.8	29.0	-	-
Cairn Terrier	1,256	♀	6.9	6.8	6.6	7.3	Welsh Mt.	153,727	♂	31.2	28.4	20.0	32.6
Boxer X	6,585	♀	11.8	11.9	11.3	13.0	Welsh Mt.	178,182	♂	36.1	31.6	27.4	37.1
Boxer X	8,500	♂	13.1	14.2	13.1	15.9	Welsh Mt.	203,636	♂	35.2	30.9	26.3	36.1
Boxer X	9,900	♀	15.0	15.5	13.6	16.6	Shetland	280,000	♂	31.4	27.5	-	-
Adult other dogs							Shetland	369,091	♂	47.1	42.5	-	-
Collie X	10,400	♀	14.2	14.8	15.5	13.5	TB X **	432,727	♂	42.5	37.4	31.9	42.6
Afghan	25,100	♀	25.6	27.0	28.0	23.2	TB X **	445,455	♀	41.9	37.0	-	-
Afghan	31,900	♂	25.7	26.0	27.0	24.0	Connemara X	496,364	♀	47.4	36.4	36.5	49.8
Great Dane	46,500	♂	28.1	29.9	30.9	26.5	Clydesdale	521,818	♂	44.5	39.3	-	-
							TB X **	534,545	♀	43.5	38.5	-	-

D* Detained Greyhounds

TB X ** Thoroughbred Crosses

Table 3 Allometric equations comparing the growth of the combined lengths of the propodial and epipodial skeleton of the limbs of dogs and horses relative to liveweight. The weight ranges for computations being: birth to 30 kg for Greyhounds, birth to 47 kg for other dogs, 13.4 to 433 kg for Thoroughbreds and 109 to 535 kg liveweight for other horses.

Type of animal	Number of observations	Growth ratio b*	Se b	log a	r**	Significance of difference of b from .333
Hindlimb						
Greyhounds	16	0.434	0.012	-0.253	0.9944	P < 0.001
Other dogs	8	0.428	0.028	-0.292	0.9872	P < 0.05
Thoroughbreds	10	0.259	0.016	0.516	0.9847	P < 0.005
Other horses	13	0.247	0.030	0.516	0.9259	P < 0.02
Forelimb						
Greyhounds	14	0.408	0.013	-0.138	0.9942	P < 0.001
Other dogs	8	0.415	0.024	-0.169	0.9901	P < 0.02
Thoroughbreds	6	0.256	0.022	0.513	0.9850	P < 0.025
Other horses	7	0.281	0.046	0.314	0.9397	N.S.

* Regression coefficient b, standard error Se b.

** Correlation coefficient r.

Table 4 Values of the combined propodial and epipodial skeletal lengths in cm calculated from the allometric equations of Table 3 for dogs of 0.5 kg and 30 kg liveweight.

	0.5 kg		30 kg	
	Mean	95% limits	Mean	95% limits
Greyhounds				
Hindlimb	8.29	7.66 - 8.97	49.0	46.3 - 51.9
Forelimb	9.20	8.51 - 9.94	48.9	45.9 - 52.1
Other dogs				
Hindlimb	8.56	6.82 - 10.74	49.3	44.6 - 54.4
Forelimb	8.93	7.36 - 10.8	48.9	44.9 - 53.2

Table 5 Values of the combined propodial and epipodial skeletal segments in cm for horses calculated from the allometric equations on Table 3 for Thoroughbreds from 13.4 kg to 433 kg and other horses from 109 to 535 kg liveweight.

	50 kg			500 kg		
	Mean	95% limits	Mean	95% limits	Mean	95% limits
Thoroughbreds	Hindlimb	54.2	52.3 - 56.0	98.4*	88.9 - 108.7	
	Forelimb	52.0	48.6 - 55.6	91.6	79.9 - 109.8	
Other horses	Hindlimb	47.2	42.10 - 53.0	83.3*	78.4 - 88.5	
	Forelimb	42.8	35.8 - 51.1	81.6	72.2 - 92.3	

* Values significantly different ($P < 0.05$) between each type of horse.

Table 6 Allometric equations comparing the growth in length of propodial with epipodial skeletal segments in dogs (Greyhounds: birth to 30 kg, other dogs: birth to 46.5 kg liveweight) and horses (Thoroughbreds: 0.7 kg to 430 kg, other horses: 3.0 kg to 500 kg liveweight).

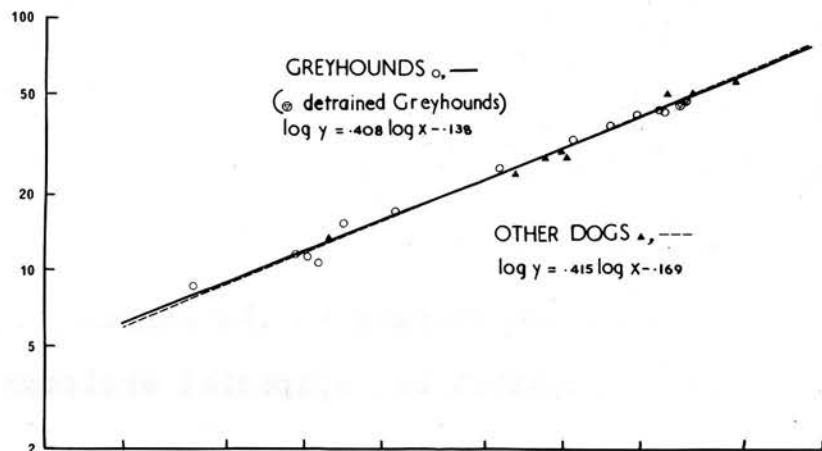
Comparison	Type of animal	Number of observations	Growth ratio b*	Se b	log a	r**	Significance*** of difference in b.
Femur v Tibia and Fibula							
	Greyhounds	16	0.920 ⁺	0.014	0.087	0.9984	NS
	Other dogs	8	0.966	0.022	0.027	0.9982	
	Thoroughbreds	11	0.992	0.031	0.001	0.9956	NS
	Other horses	14	1.031	0.035	0.005	0.9932	
Humerus v Radius and Ulna							
	Greyhounds	14	0.932 ⁺	0.011	0.012	0.9992	NS
	Other dogs	8	0.971	0.029	-0.031	0.9974	
	Thoroughbreds	7	1.015	0.025	-0.193	0.9985	NS
	Other horses	8	0.984	0.053	-0.125	0.9974	

* Regression coefficient b, standard error Se b. ** Correlation coefficient r.
 + Values of b followed by this superscript are significantly different (P<0.05) from 1.
 *** Significance of difference in b between breeds, tested by the test quotient t.
 NS = not significant.

Fig. 3.

Growth changes in the combined lengths of the propodial and epipodial skeleton of dogs.

HUMERUS + RADIUS
& ULNA LENGTH (cm)



FEMUR + TIBIA
LENGTH (cm)

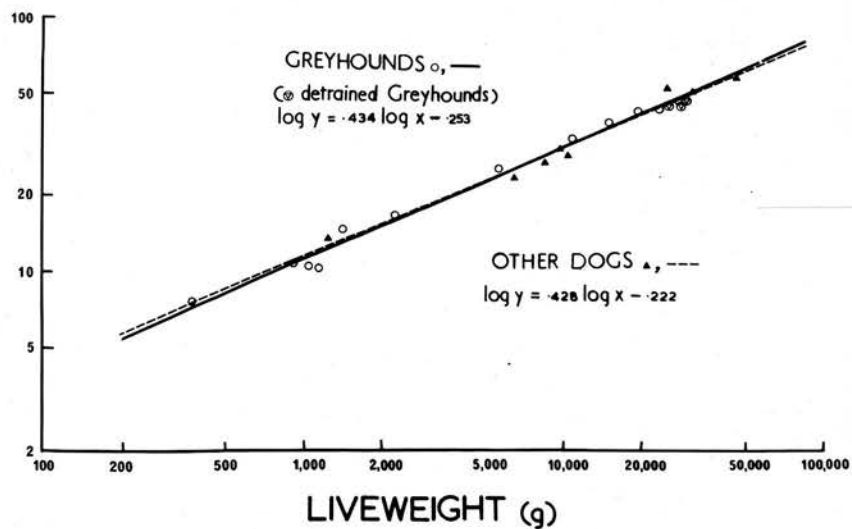
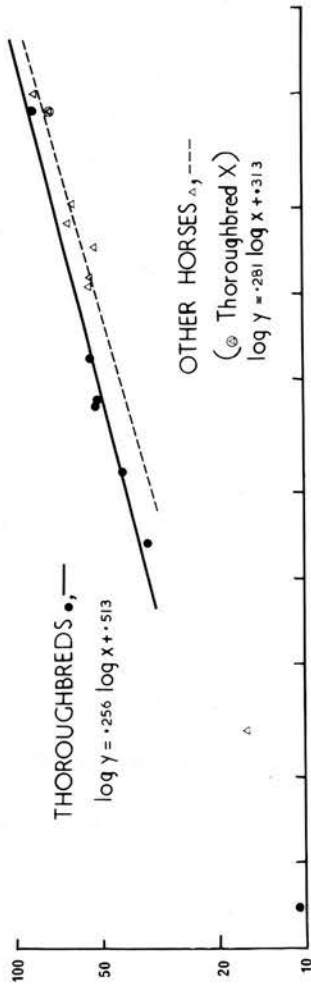


Fig. 4.

Growth changes in the combined lengths of the propodial and epipodial skeleton in Thoroughbreds from 13.4 kg to 433 kg and other horses from 109 kg to 545 kg liveweight.

HUMERUS + RADIUS
& ULNA LENGTH (cm)



FEMUR + TIBIA
LENGTH (cm)

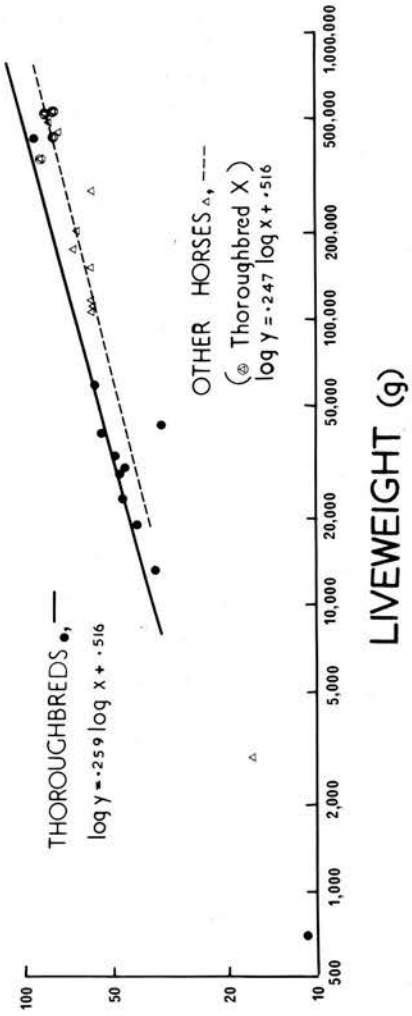
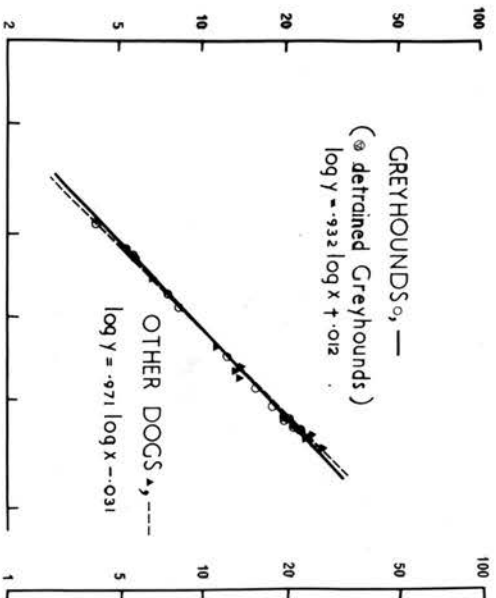


Fig. 5.

Allometric equations comparing the increase in length of the humerus relative to that of the radius and ulna; and femur relative to that of the tibia in dogs and horses.

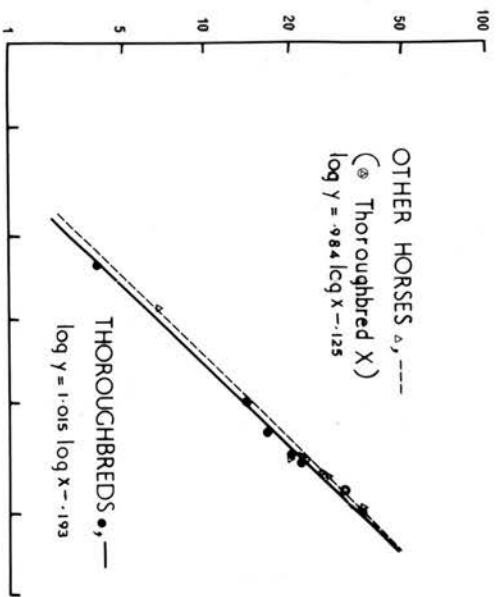
DOGS

HUMERUS
LENGTH (cm)



HORSES

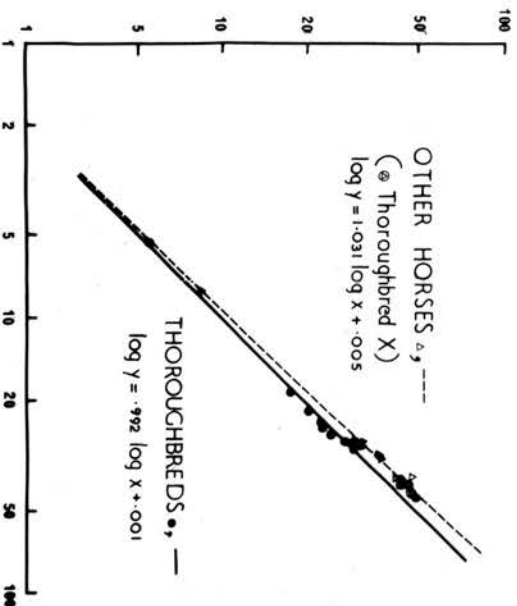
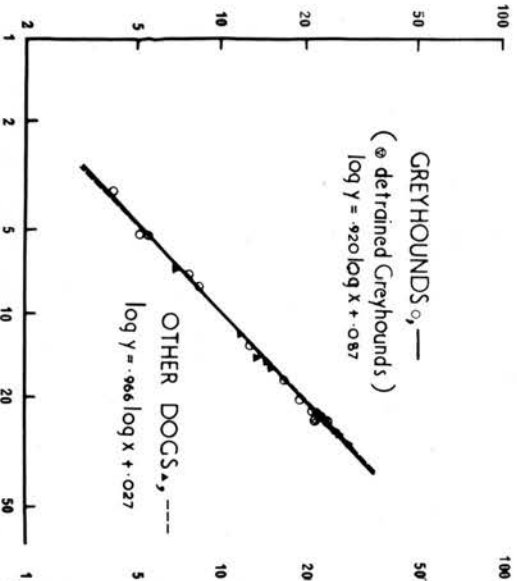
OTHER HORSES Δ , ----
 (⊗ Thoroughbred X)
 $\log y = .964 \log x - .125$



RADIUS & ULNA LENGTH (cm)

RADIUS & ULNA LENGTH (cm)

FEMUR
LENGTH (cm)



TIBIA LENGTH (cm)

TIBIA LENGTH (cm)

Table 7 The weights and volumes of the femur, tibia and fibula, humerus and radius and ulna of dogs and horses.

Type of Animal	Live-Weight (R)	Femur Volume (cm ³)	Tibia & Fibula Weight (R)	Tibia & Fibula Volume (cm ³)	Humerus Weight (R)	Humerus Volume (cm ³)	Radius & Ulna Weight (R)	Radius & Ulna Volume (cm ³)
Young Greyhounds	377	1.98	1.3	1.1	2.72	2.3	2.01	1.8
Young Greyhounds	927	5.71	3.0	3.0	7.3	5	6.1	4.5
Young Greyhounds	1,056	5.70	3.9	3.0	7.7	6	6.3	4.9
Young Greyhounds	1,174	4.95	4.0	2.8	6.41	4.0	5.4	3.2
Young Greyhounds	1,423	12.07	7.9	7.0	13.4	10.5	11.2	9
Young Greyhounds	2,280	16.92	12.8	10.1	19	13	16	12
Young Greyhounds	5,712	44	34	26	41	33	40	30
Young Greyhounds	11,000	69	54	31	64	47	62	44
Young Greyhounds	15,250	85	74	52	76	50	75	52
Young Greyhounds	19,750	107	94	65	102	74	100	72
Young Greyhounds	25,500	90	75	50	86	57	69	43
Adult Greyhounds	24,150	103	70	65	101	68	95	60
Adult Greyhounds	25,000	121	114	80	113	70	90	60
Adult Greyhounds	25,200	137	110	80	135	90	95	60
Adult Greyhounds	25,300	126	105	80	116	90	90	60
Adult Greyhounds	28,000	137	119	85	126	95	105	70
Adult Greyhounds	28,500	141	117	85	126	95	105	70
Adult Greyhounds	29,750	172	110	110	162	113	125	83
Adult Greyhounds	30,000	149	126	110	142	100	125	83
Adult Greyhounds	37,000	165	120	110	142	100	125	83
Young other dogs	1,256	6.8	4.9	4	6.4	5	5.5	4.5
Young other dogs	6,585	33	25	19	34	25	30	22
Young other dogs	8,500	40	35	27	40	30	35	26
Young other dogs	9,900	46	41	28	44	29	40	26
Young other dogs	10,400	40	35	25	39	30	35	22
Young other dogs	25,100	137	118	77	129	94	112	68
Young other dogs	31,900	146	118	79	148	102	123	78
Young other dogs	33,000	119	82	75	125	87	123	68
Young other dogs	46,500	276	276	198	278	256	243	162
Young Thoroughbreds	691	4.7	3.0	3.0	3.7	3.0	3.0	3.0
Young Thoroughbreds	13,429	178	120	90	100.6	80	92	72
Young Thoroughbreds	19,000	280	200	200	200	182	240	180
Young Thoroughbreds	23,872	407	280	230	211	182	240	180
Young Thoroughbreds	29,000	465	330	280	280	240	240	180
Young Thoroughbreds	30,965	487	340	280	280	240	240	180
Young Thoroughbreds	33,500	503	350	380	355	335	370	180
Young Thoroughbreds	40,500	730	470	410	410	384	440	370
Young Thoroughbreds	42,962	655	590	480	410	384	440	370
Young Thoroughbreds	58,664	992	800	530	595	471	482	470
Young Thoroughbreds	432,727	2,880	2,290	1,790	1,844	1,650	1,660	1,270
Adult Thoroughbreds	2,977	21	20	14	12.5	9	8	12
Adult Thoroughbreds	22,000	400	380	470	490	470	400	410
Adult Thoroughbreds	109,091	736	710	470	420	470	400	410
Adult Thoroughbreds	114,546	618	490	410	394	340	320	350
Adult Thoroughbreds	118,182	782	670	510	520	470	470	410
Adult Thoroughbreds	153,727	815	670	550	400	560	470	410
Adult Thoroughbreds	178,182	1,042	890	500	400	560	470	410
Adult other horses	178,182	1,132	990	750	660	660	660	550
Adult other horses	203,636	1,127	980	680	480	790	570	400
Adult other horses	229,091	945	840	440	440	440	620	400
Adult other horses	280,000	925	730	560	560	560	620	400
Adult other horses	369,091	3,135	2,750	1,930	1,790	1,790	620	400
Adult other horses	432,727	2,032	1,620	1,220	920	920	620	400
Adult other horses	445,455	1,955	1,530	1,160	930	930	620	400
Adult other horses	496,364	3,680	2,880	2,170	1,690	1,690	620	400
Adult other horses	521,818	2,576	2,970	1,530	1,090	1,090	620	400
Adult other horses	534,545	2,360	1,810	1,320	990	990	620	400

Table 8 Logarithmic regression equations comparing the increase in weight with increase in volume of the femur, tibia and fibula, humerus and radius and ulna of dogs and horses.

Bone	Type of animal	Number of observations	Growth ratio b*	Se b	log a	r**
Femur						
	Greyhounds	20	1.048 +	0.017	0.058	0.9977
	Other dogs	9	1.011	0.027	0.112	0.9975
	Thoroughbreds	11	1.200 +C	0.039	-0.482	0.9953
	Other horses	17	1.016 C	0.023	0.018	0.9961
Tibia and Fibula						
	Greyhounds	17	1.033	0.020	0.092	0.9973
	Other dogs	8	1.046 +	0.018	0.071	0.9991
	Thoroughbreds	11	1.013	0.025	0.015	0.9973
	Other horses	14	1.000	0.028	0.081	0.9955
Humerus						
	Greyhounds	18	1.017	0.017	0.122	0.9979
	Other dogs	9	0.982	0.031	0.158	0.9965
	Thoroughbreds	7	0.984	0.012	0.106	0.9996
	Other horses	7	0.973	0.027	0.165	0.9982
Radius and ulna						
	Greyhounds	14	1.040	0.021	0.096	0.9976
	Other dogs	8	1.067	0.027	0.065	0.9980
	Thoroughbreds	7	1.021	0.027	0.013	0.9982
	Other horses	8	0.962	0.035	0.192	0.9961

* Regression coefficient b, standard error Se b.

+ Values of b followed by this superscript are significantly different ($P < 0.05$) from 1.

C Values of b followed by this superscript are significantly different ($P < 0.001$) from one another.

** Correlation coefficient r.

Table 9 Regression equations comparing the growth of the proximal hindlimb muscles plus the femur with the distal hindlimb muscles plus the other bones of the hindlimb in Greyhounds from birth to 30 kg, other dogs from birth to 46.5 kg; Thoroughbreds from 13.4 kg to 430 kg and other horses from 3.0 kg to 530 kg liveweight.

Type of animal	Number of observations	Growth ratio b*	Se b	log a	r**	Significance of difference in b***
Greyhounds	18	1.205 +	0.024	0.061	0.9968	} NS
Other dogs	9	1.103	0.059	0.239	0.9901	
Thoroughbreds	6	1.195	0.167	-0.304	0.9630	} NS
Other horses	7	1.074	0.036	0.352	0.9966	

* Regression coefficient b, standard error Se b.

** Correlation coefficient.

*** Significance of the difference in b between breeds tested by the test quotient t.

NS Not significant.

+ Growth ratio significantly greater ($P < .05$) than 1.

Fig. 6.

Changes in weight of the proximal hindlimb muscle plus the femur with increasing weight of the distal hindlimb muscle plus the other bones in dogs.

WEIGHT OF
PROXIMAL HINDLIMB
MUSCLE + FEMUR
(g)

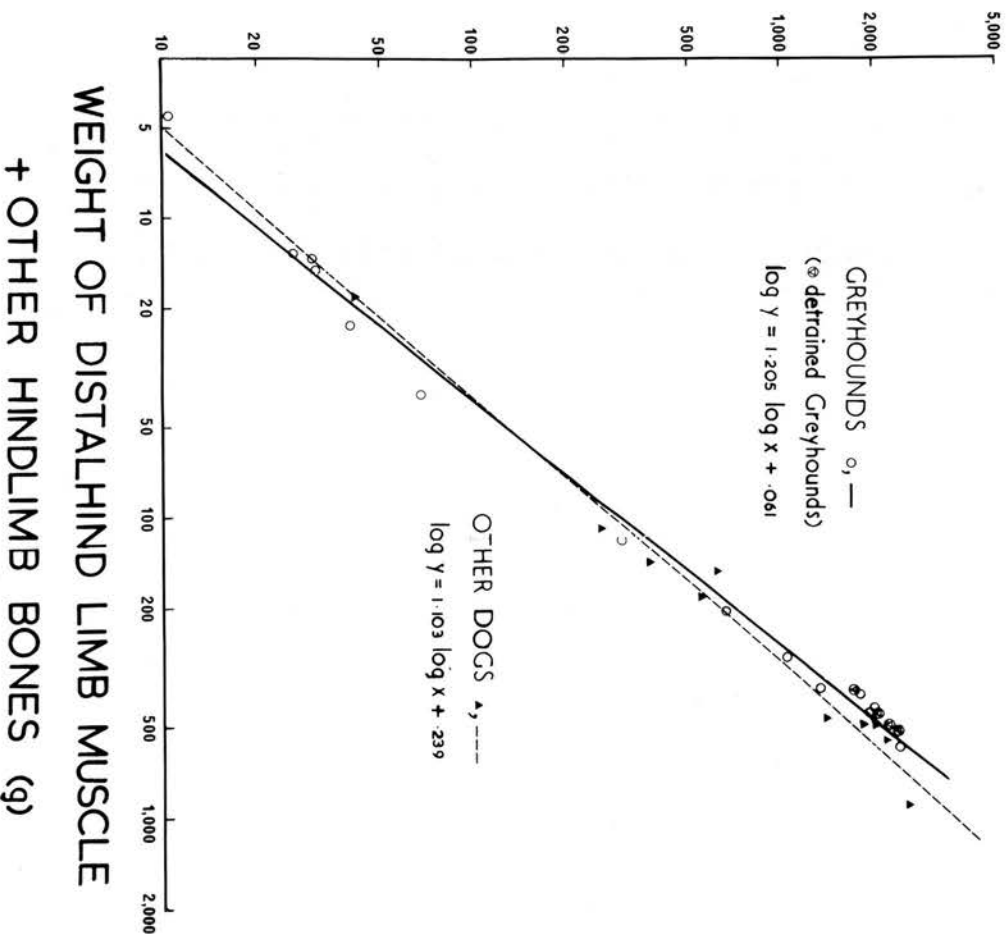


Fig. 7.

Changes in weight of the proximal hindlimb muscle plus the femur with increasing weight of the distal hindlimb muscle plus the other bones in Thoroughbreds from 13.4 kg to 430 kg and other horses from 3.0 kg to 530 kg liveweight.

WEIGHT OF
PROXIMAL HINDLIMB
MUSCLE + FEMUR
(g)

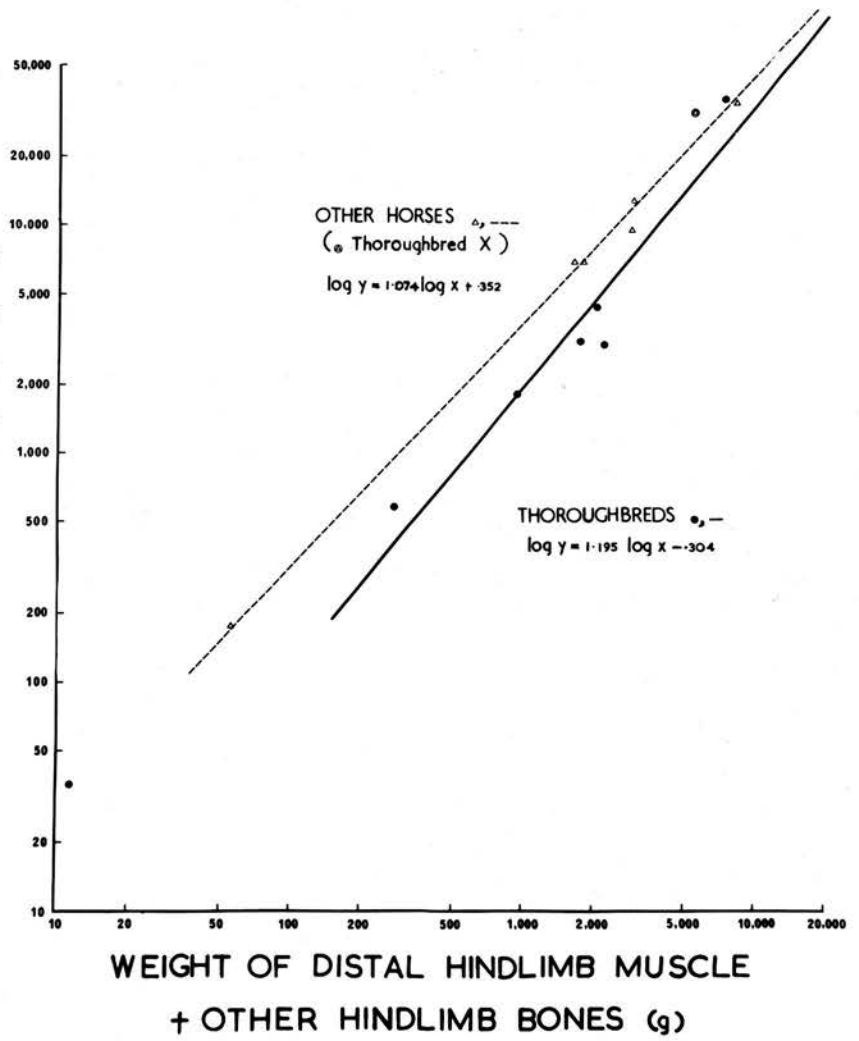


Table 10 The weights and percentage of liveweight of total muscle, total bone and total fat in 18 Greyhounds and 9 other dogs.

Live weight (g)		Age status	Sex	Total muscle weight (g)	Total bone weight (g)	Total fat weight (g)	Liveweight (g)	Breed	Age status	Sex	Total muscle weight (g)	Total bone weight (g)	Total fat weight (g)
377	Young	♀	97.4 (25.8)*	60.8 (16.1)*	2.24	(.06)*	1,256	Cairn Terrier	Young	♀	327.5(26.1)*	151.9 (12.1)*	48 (3.82)*
927	Young	♀	260.4 (28.1)*	148.6 (16.0)*	2.19	(.24)*	6,585	Boxer X	Young	♀	2,120 (32.2)*	823 (12.5)*	158 (2.40)*
1,056	Young	♀	327.5 (31.0)*	156.2 (14.8)*	8.53	(.81)*	8,500	Boxer X	Young	♂	3,024 (35.6)*	979 (11.5)*	223 (2.62)*
1,174	Young	♀	296.3 (25.2)*	156.0 (13.3)*	15.6	(1.3)*	9,900	Boxer X	Young	♀	4,183 (42.3)*	1,120 (11.3)*	72 (.73)*
1,423	Young	♂	300.4 (21.1)*	266.3 (18.7)*	0	(0)*	10,400	Collie X	Adult	♀	4,453 (42.8)*	1,031 (9.9)*	116 (1.12)*
2,280	Young	♂	606.7 (26.6)*	436.4 (19.1)*	19.8	(.86)*	25,100	Afghan	Adult	♀	12,639 (50.4)*	3,276 (13.1)*	407 (1.62)*
5,712	Young	♀	2,080 (36.4)*	958 (16.8)*	9.0	(.16)*	31,900	Afghan	Adult	♂	14,509 (45.5)*	3,698 (11.6)*	111 (.35)*
11,000	Young	♀	4,338 (39.4)*	1,561 (14.2)*	24.0	(.22)*	33,000	Labrador	Adult	♀	11,250 (34.1)*	3,470 (10.5)*	183 (.56)*
15,250	Young	♀	7,206 (47.3)*	1,920 (12.6)*	97.0	(.64)*	46,500	Great Dane	Adult	♂	20,875 (44.9)*	7,396 (15.9)*	478 (1.03)*
19,750	Young	♂	9,563 (48.4)*	2,531 (12.8)*	19.0	(.10)*							
23,500	Young	♀	12,455 (53.0)*	2,272 (10.3)*	196	(.83)*							
24,150	Adult D*	♀	13,297 (55.1)*	2,550 (10.6)*	210	(.87)*					43.5	12.2	0.94
25,000	Adult	♀	14,088 (56.4)*	2,819 (11.3)*	0	(0)*					6.0	2.4	0.50
25,200	Adult	♂	14,692 (58.3)*	3,306 (13.1)*	0	(0)*							
25,300	Adult D*	♂	14,422 (57.0)*	3,123 (12.3)*	65	(.26)*							
28,500	Adult D*	♀	15,742 (55.2)*	3,259 (11.4)*	185	(.65)*							
29,750	Adult	♀	17,983 (60.4)*	4,310 (14.5)*	0	(0)*							
30,000	Adult D*	♂	17,213 (57.4)*	3,684 (12.3)*	70	(.23)*							
Mean percentage of all adults			57.1	12.2	0.28								
SD			1.85	1.30	0.35								
Mean percentage of detrained (D*) adults			56.2	11.7	0.50								
SD			1.20	0.82	0.31								
Mean percentage of trained adults			58.4	12.9	0								
SD			2.00	1.6	0								

* Percentage of liveweight.

Table 11 The weights and percentage of liveweight of total muscle, total bone and total fat in 7 Thoroughbreds and 6 other horses.

THOROUGHBREDS

OTHER HORSES

Liveweight (g)	Age status	Sex	Total muscle weight (g)	Total bone weight (g)	Total fat weight (g)	Liveweight (g)	Breed	Age status	Sex	Total muscle weight (g)	Total bone weight (g)	Total fat weight (g)
691	Young	♂	274.6 (39.7)*	111.7 (16.2)*	0 (0)*	2,977	Welsh Mt.	Young	♂	1,272 (42.7)*	384 (12.9)*	7.23 (0.24)*
13,429	Young	♀	2,806 (20.9)*	3,004 (22.4)*	0 (0)*	109,091	Welsh Mt.	Young	♂	37,803 (34.7)*	13,286 (12.2)*	1,984 (1.82)*
23,872	Young	♂	8,809 (36.9)*	5,847 (24.5)*	16 (0.07)*	114,546	Welsh Mt.	Young	♀	39,051 (34.1)*	11,373 (9.9)*	630 (0.55)*
40,500	Young	♀	16,257 (40.1)*	11,497 (28.4)*	0 (0)*							
42,962	Young	♀	16,789 (39.1)*	10,876 (25.3)*	0 (0)*	203,636	Shetland	Adult	♂	85,054 (41.8)*	27,402 (13.5)*	5,169 (2.5)*
58,664	Young	♀	23,679 (40.4)*	15,295 (26.1)*	0 (0)*	432,727	Thoroughbred X	Adult	♂	170,880 (39.5)*	34,564 (8.0)*	1,902 (0.44)*
432,727	Young	♂	191,883 (44.3)*	53,855 (12.4)*	4,306 (1.00)*	496,364	Clydesdale	Adult	♀	223,997 (45.1)*	70,420 (14.2)*	873 (0.18)*

* Percentage of liveweight.

Mean percentage of all adults

SD

42.1
2.8

11.9
3.4

1.04
1.27

Table 12 Logarithmic regression equations comparing the growth of total muscle and total bone with liveweight and total muscle plus bone weight in Greyhounds from birth to 30 kg liveweight, other dogs from birth to 46.5 kg; Thoroughbreds from 13.4 kg to 430 kg and other horses from 109 kg to 500 kg liveweight.

Dependent variable	Type of animal	Number of observations	Independent variable = liveweight				Independent variable = muscle plus bone weight			
			Growth ratio b*	Se b	log a	r**	Growth ratio b*	Se b	log a	r**
Total muscle	Greyhounds	18	1.222 c	0.019	-1.248	0.9980	1.077 cd	0.009	-0.410	0.9994
	Other dogs	9	1.143 c	0.046	-1.002	0.9945	1.029 d	0.013	-0.228	0.9994
	Thoroughbreds	6	1.161	0.082	-1.198	0.9901	1.119 cd	0.017	-0.748	0.9995
	Other horses	5	1.143	0.052	-1.177	0.9970	1.024 d	0.029	-0.235	0.9988
Total bone	Greyhounds	18	0.911 cd	0.022	-0.521	0.9950	0.800 cd	0.021	0.111	0.9945
	Other dogs	9	1.029 d	0.045	-1.042	0.9930	0.921 d	0.042	-0.326	0.9927
	Thoroughbreds	6	0.804	0.080	0.271	0.9810	0.780 c	0.034	0.562	0.9963
	Other horses	5	0.985	0.191	-0.866	0.9470	0.909	0.111	-0.189	0.9784

* Regression coefficient b, standard error Se b.

c Values of b followed by this superscript are significantly different ($P < 0.05$) from 1.

d Values of b followed by this superscript are significantly different ($P < 0.05$) from one another.

** Correlation coefficient r.

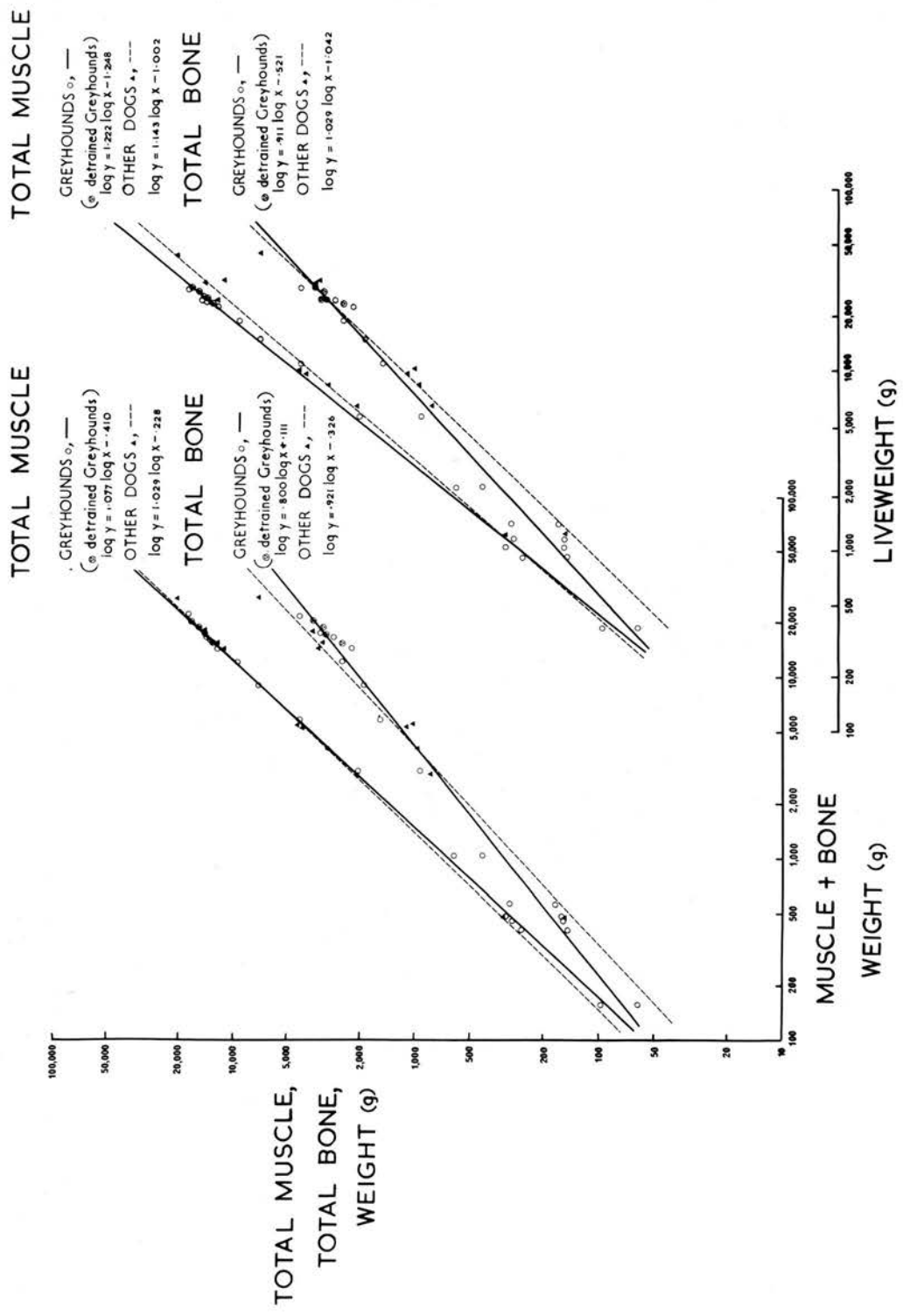
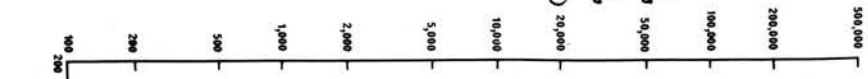


Fig. 9.

Allometric equations comparing the growth of total muscle and total bone relative to liveweight and total muscle plus bone weight between Thoroughbreds from 13.4 kg to 430 kg and other horses from 109 kg to 500 kg liveweight.

TOTAL MUSCLE,
TOTAL BONE,
WEIGHT (g)



TOTAL MUSCLE
THOROUGHBREDS \bullet , —
 $\log y = 1.119 \log x - 0.748$
OTHER HORSES \circ , ---
(\circ Thoroughbred X)
 $\log y = 1.024 \log x - 0.235$

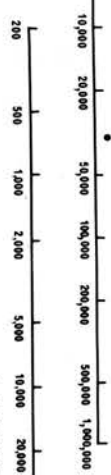
TOTAL BONE
THOROUGHBREDS \bullet , —
 $\log y = 0.780 \log x + 0.562$
OTHER HORSES \circ , ---
(\circ Thoroughbred X)
 $\log y = 0.909 \log x - 0.169$

TOTAL MUSCLE

THOROUGHBREDS \bullet , —
 $\log y = 1.161 \log x - 1.198$
OTHER HORSES \circ , ---
(\circ Thoroughbred X)
 $\log y = 1.143 \log x - 1.177$

TOTAL BONE
THOROUGHBREDS \bullet , —
 $\log y = 0.604 \log x + 0.271$
OTHER HORSES \circ , ---
(\circ Thoroughbred X)
 $\log y = 0.985 \log x - 0.855$

MUSCLE + BONE
WEIGHT (g)



LIVWEIGHT (g)

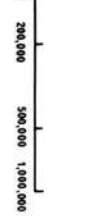


Table 13 Weights of muscle groups and their percentage of liveweight and total muscle weight in adult dogs. Muscles are grouped according to the articulations over which they act and their weights refer to one side of the animal only.

Type of Dog	Live- weight (g)	Total muscle weight (g)	Sex	Distal forelimb		Brachial		Pectoral Girdle		Longissimus		Femoral		Distal hindlimb						
				Percentage of Live- weight	Weight (g)	Percentage of Live- weight	Weight (g)	Percentage of Live- weight	Weight (g)	Percentage of Live- weight	Weight (g)	Percentage of Live- weight	Weight (g)	Percentage of Live- weight	Weight (g)					
Grey-hound (D)	24,150	13,297	♀	0.73	1.30	855	3.5	6.43	1,190	4.9	8.95	685	2.8	5.15	1,661	6.9	12.5	223	0.92	1.67
Grey-hound	25,000	14,088	♀	0.63	1.11	850	3.4	6.03	1,285	5.1	9.12	813	3.3	5.77	1,832	7.3	13.0	249	1.00	1.77
Grey-hound	25,200	14,692	♂	0.77	1.32	956	3.8	6.51	1,125	4.5	7.66	973	3.9	6.62	1,901	7.5	12.9	244	0.97	1.66
Grey-hound (D)	25,300	14,422	♂	0.68	1.20	900	3.6	6.24	1,266	5.0	8.78	719	2.8	4.99	1,953	7.7	13.5	244	0.96	1.69
Grey-hound	27,200	-	♂	-	-	-	-	-	-	-	-	-	-	-	2,041	7.5	-	-	-	-
Grey-hound	27,500	-	♂	-	-	-	-	-	-	-	-	-	-	-	2,321	8.4	-	-	-	-
Grey-hound	28,000	-	♂	-	-	-	-	-	-	-	-	-	-	-	2,530	9.0	-	-	260	0.93
Grey-hound (D)	28,500	15,742	♀	0.71	1.28	1,041	3.7	6.61	1,295	4.5	8.23	815	2.9	5.18	2,148	7.5	13.7	270	0.95	1.72
Grey-hound	29,750	17,983	♀	0.77	1.28	1,120	3.8	6.23	1,522	5.1	8.46	1,422	4.8	7.91	2,267	7.6	12.7	310	1.00	1.72
Grey-hound (D)	30,000	17,213	♂	0.68	1.18	1,132	3.8	6.58	1,605	5.4	9.32	863	2.9	5.01	2,287	7.6	13.3	279	0.93	1.62
Grey-hound	30,000	-	♂	-	-	-	-	-	-	-	-	-	-	-	2,135	7.1	-	-	-	-
Grey-hound	33,608	-	♀	-	-	-	-	-	-	-	-	-	-	-	2,475	7.4	-	-	-	-
Grey-hound	37,000	-	♂	-	-	-	-	-	-	-	-	-	-	-	2,724	7.4	-	-	-	-
Mean %				0.71	1.24		3.68	6.38		4.93	8.65		3.34	5.80		7.61	13.08		0.96	1.69
SD				0.05	0.08		0.16	0.21		0.33	0.57		0.75	1.10		0.54	0.48		0.03	0.05
Mean	190.1	190.1		0.71	1.24	958.5	3.5	6.25	1,327	4.94	8.65	898.6	3.35	5.85	2,175	7.62	13.1	259.9	0.86	1.69
Collie X	10,400	4,453	♀	0.65	1.53	240	2.3	5.39	354	3.4	7.95	205	2.0	4.60	594	5.7	13.2	85	0.82	1.91
Afghan	25,100	12,639	♀	0.88	1.74	947	3.8	7.49	947	3.8	7.49	685	2.7	5.42	1,743	6.9	13.8	270	1.10	2.14
Afghan	31,900	14,509	♂	0.62	1.37	1,021	3.2	7.04	1,065	3.3	7.34	820	2.6	5.65	1,924	6.0	13.3	278	0.87	1.92
Labrador	33,000	11,250	♀	0.69	2.04	804	2.4	7.15	861	2.6	7.65	458	1.4	4.07	1,312	4.0	11.7	261	0.79	2.32
Great Dane	46,500	20,875	♂	0.85	1.88	1,438	3.1	6.88	2,155	4.6	10.3	910	2.0	4.36	2,339	5.0	11.2	434	0.93	2.08
Mean %				0.74	1.71		2.96	6.79		3.54	8.15		2.13	4.82		5.52	12.64		0.90	2.07
SD				0.12	0.27		0.62	0.81		0.73	1.23		0.53	0.68		1.09	1.12		0.12	0.17
Mean	221.8	221.8		0.75	1.74	890	3.03	6.98	1,076	3.6	8.44	616	2.10	4.83	1,582	5.38	12.4	265.6	0.90	2.08

D = Detained Greyhounds

+ Values bearing this superscript are significantly different (P < 0.02) between the two types of dog.

Table 14 Weights of muscle groups and their percentage of liveweight and total muscle weight in adult horses*. Muscles are grouped according to the articulations over which they act and their weights refer to one side of the animal only.

Type of animal	Live- weight (K)	Total muscle weight (K)	Sex	Distal forelimb		Brachial		Pectoral girdle		Longissimus		Femoral		Distal hindlimb							
				Live- weight (K)	Percentage of Total muscle	Live- weight (K)	Percentage of Total muscle	Live- weight (K)	Percentage of Total muscle	Live- weight (K)	Percentage of Total muscle	Live- weight (K)	Percentage of Total muscle	Live- weight (K)	Percentage of Total muscle						
Thoroughbred	432,727	191,883	♂	2,378	0.55	1.24	9,945	2.29	5.18	13,080	3.0	6.82	5,400	1.2	2.8	34,392	7.9	17.9	3,772	0.87	1.97
Thoroughbred	470,909	-	♀	-	-	-	-	-	-	-	-	-	-	-	-	39,978	8.4	-	-	-	-
Thoroughbred	470,909	-	♀	-	-	-	-	-	-	-	-	-	-	-	-	33,388	7.1	-	-	-	-
Thoroughbred	483,636	-	♀	-	-	-	-	-	-	-	-	-	-	-	-	41,645	8.6	-	-	-	-
Mean \bar{x}	-	-	-	0.55	1.24	-	2.29	5.18	-	3.0	6.82	1.2	2.80	-	8.0+	17.9	-	-	0.87	1.97	
SD	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.81	-	-	-	-	-	-
Mean	153,727	-	♂	-	-	-	-	-	-	-	-	-	-	-	-	38,337	8.1	-	-	-	-
Shelland pony	203,636	85,054	♂	1.165	0.57	1.37	4,730	2.4	5.63	6,561	3.2	7.71	2,024	0.99	2.3	12,236	6.0	14.4	1,604	0.79	1.89
Shelland pony	280,000	-	♂	-	-	-	-	-	-	-	-	-	-	-	-	14,320	5.1	-	-	-	-
Thoroughbred X	369,091	-	♂	-	-	-	-	-	-	-	-	-	-	-	-	28,594	7.7	-	3,311	0.90	-
Thoroughbred X	432,727	170,880	♂	2,058	0.48	1.20	8,504	2.0	4.98	12,645	2.9	7.40	4,133	0.96	2.42	30,473	7.0	17.8	2,975	0.69	1.74
Connemara X	445,455	-	♀	-	-	-	-	-	-	-	-	-	-	-	-	26,742	6.0	-	-	-	-
Clydesdale	496,364	223,997	♀	6,922	1.4	3.09	11,480	2.3	5.13	16,540	3.3	7.38	5,482	1.1	2.45	33,068	6.3	14.8	3,857	0.78	1.72
Thoroughbred X	521,818	-	♂	-	-	-	-	-	-	-	-	-	-	-	-	37,218	7.1	-	3,611	0.69	-
Thoroughbred X	534,545	-	♀	-	-	-	-	-	-	-	-	-	-	-	-	41,253	7.7	-	3,608	0.68	-
Mean \bar{x}	-	-	-	0.82	1.89	-	2.23	5.25	-	3.13	7.50	1.02	2.42	-	6.41+	15.67	-	-	0.76	1.78	
SD	-	-	-	0.51	1.05	-	0.21	.34	-	0.21	.19	0.07	0.04	-	1.05	1.86	-	-	0.09	0.09	
Mean	3,381	0.89	2.11	8,261	2.19	5.16	11,915	3.16	7.44	3,879	1.03	2.42	25,690	6.65	15.8	3,161	0.74	1.76	-	-	

* The values for all the muscle groups of Thoroughbreds, except the femoral group are those for the largest (young) Thoroughbred in which these values were assessed.

+ Values bearing this superscript are significantly different ($P < 0.05$) between the two types of horse.

Table 15 Logarithmic regression equations comparing the growth of six muscle groups relative to liveweight in Greyhounds from birth to 37 kg, other dogs from birth to 47 kg; Thoroughbreds from 0.7 kg to 480 kg, and other horses from 3.0 to 530 kg liveweight.

Muscle Group	Type of animal	Number of observations	Growth ratio b*	Se b	log a	r**	Significance *** of difference between groups
Distal forelimb	Greyhounds	18	1.103+	0.042	-2.612	0.9885	} NS
	Other dogs	9	1.097	0.041	-2.553	0.9951	
	Thoroughbreds	7	1.020	0.077	-2.237	0.9862	} NS
	Other horses	7	1.041	0.103	-2.441	0.9763	
Brachial	Greyhounds	18	1.203+	0.171	-2.364	0.9984	} Greyhounds
	Other dogs	9	1.158+	0.044	-2.233	0.9950	
	Thoroughbreds	7	1.052	0.057	-1.908	0.9928	} NS
	Other horses	7	1.014	0.044	-1.780	0.9953	
Pectoral girdle	Greyhounds	18	1.153+	0.034	-2.032	0.9931	} Greyhounds
	Other dogs	9	1.208+	0.057	-2.370	0.9922	
	Thoroughbreds	7	1.042	0.090	-1.802	0.9817	} NS
	Other horses	6	0.987	0.050	-1.481	0.9948	
Longissimus	Greyhounds	18	1.420+	0.031	-3.336	0.9961	} Greyhounds
	Other dogs	9	1.255	0.124	-2.829	0.9677	
	Thoroughbreds	7	0.994	0.158	-1.916	0.9424	} NS
	Other horses	6	0.690+	0.092	-0.360	0.9664	
Femoral	Greyhounds	24	1.357+	0.018	-2.715	0.9980	} Greyhounds
	Other dogs	21	1.315	0.032	-2.662	0.9943	
	Thoroughbreds	19	1.150+ c	0.032	-1.972	0.9935	} NS
	Other horses	17	1.049 c	0.028	-1.457	0.9947	
Distal hindlimb	Greyhounds	19	1.227+	0.023	-3.016	0.9971	} NS
	Other dogs	9	1.130	0.043	-2.616	0.9949	
	Thoroughbreds	8	1.108 c	0.057	-2.528	0.9920	} NS
	Other horses	10	0.960 c	0.020	-1.943	0.9983	

* Regression coefficient b, standard error Se b.

+ Values of b bearing this superscript are significantly different ($P < 0.05$) from 1.

c Values of b for similar muscle groups bearing this superscript are significantly different ($P < 0.02$) from one another.

** Correlation coefficient r.

*** Significance of difference between adjusted means of groups tested by analysis of covariance; NS = not significant.

Table 16 Weights (in g) of 6 muscle groups of Greyhounds and other dogs at 0.5 kg and 30 kg liveweight, calculated from the allometric equations given in Table 15.

	0.5 kg		Liveweight		30 kg	
	Greyhounds	Other dogs	Greyhounds	Other dogs	Greyhounds	Other dogs
Distal forelimb	2.32	2.56	212	228		
95% limits*	(1.76 - 3.06)	(1.84 - 3.56)	(177 - 254)	(200 - 260)		
Brachial	7.64	7.81	1,052	894		
95% limits*	(6.83 - 8.54)	(5.47 - 11.14)	(977 - 1,132)	(776 - 1,030)		
Pectoral girdle	12.02	7.77	1,349	1,092		
95% limits*	(9.64 - 15.0)	(4.90 - 12.3)	(1,168 - 1,559)	(909 - 1,313)		
Longissimus	3.14	3.62	1,050**	616**		
95% limits*	(2.55 - 3.86)	(1.34 - 9.79)	(918 - 1,202)	(414 - 916)		
Femoral	8.86	7.71	2,293**	1,680**		
95% limits*	(7.80 - 10.1)	(6.52 - 9.12)	(2,146 - 2,450)	(1,412 - 1,999)		
Distal hindlimb	1.98	2.72	300	277		
95% limits*	(1.70 - 2.30)	(1.92 - 3.85)	(273 - 330)	(242 - 319)		

* Probability of a value outside these limits < 0.05 .

** Values followed by this superscript are significantly different ($P < 0.05$) between the two types of dog.

Table 17
Weights (in kg) of 6 muscle groups of
Thoroughbreds and other horses at 50 kg
and 500 kg liveweight, calculated from
the allometric equations given in Table 15.

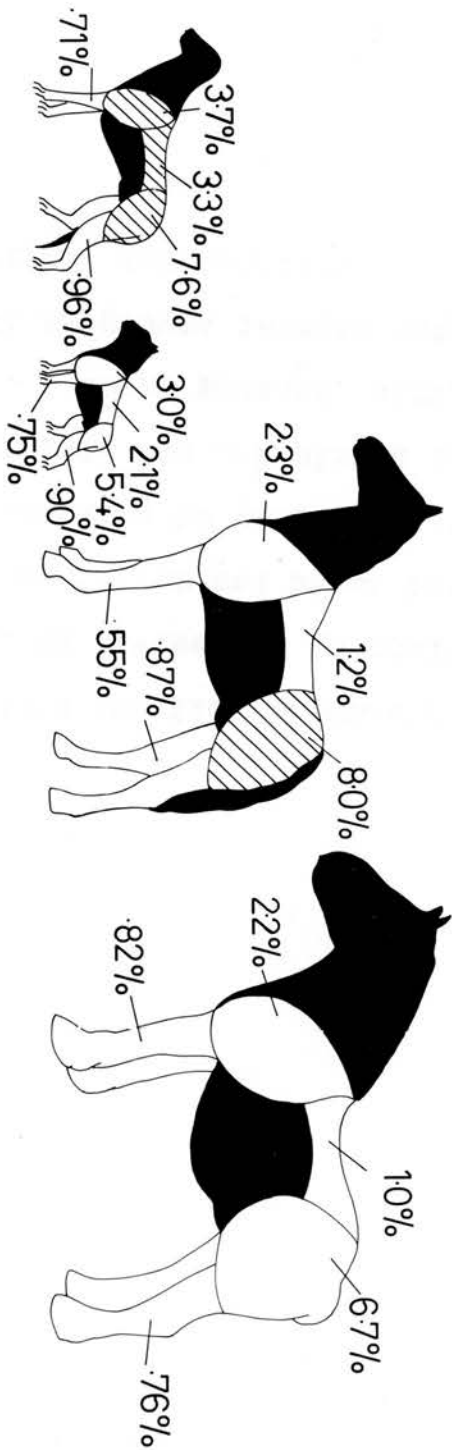
Muscle group	Liveweight		Thorough- breds	Other horses	Thorough- breds	Other horses
	50 kg	500 kg				
Distal forelimb	.36	.28	3.77	3.10		
95% limits*	(.25-.52)	(.18-.45)	(1.91-7.41)	(1.75-5.51)		
Brachial	1.08	.97	12.2	9.97		
95% limits*	(.82-1.4)	(.79-1.18)	(7.4-20.2)	(7.8-12.7)		
Pectoral girdle	1.24	1.44	13.6	13.9		
95% limits*	(.78-1.93)	(1.10-1.86)	(6.13-30.3)	(10.1-19.2)		
Longissimus	.57	.76	5.61	3.74		
95% limits*	(.26-1.23)	(.47-1.23)	(1.39-22.6)	(2.08-6.70)		
Femoral	2.70	2.96	38.2	33.2		
95% limits*	(2.41-3.03)	(2.67-3.29)	(29.5-49.5)	(30.0-36.7)		
Distal hindlimb	.48	.39	6.12	3.65		
95% limits*	(.37-.61)	(.36-.43)	(3.81-9.81)	(3.35-3.97)		

* Probability of a value outside these limits 0.05.

Fig. 10.

Topographical location of muscle groups and their proportion of liveweight in adult Greyhounds, other dogs, Thoroughbreds and other horses. Muscles are grouped according to their skeletal attachments and the proportions are calculated for one side of the body only. Where present, significant differences ($P < 0.02$) in groups between "athletes" and "non-athletes" are indicated.

MUSCLE GROUPS AS PROPORTIONS OF LIVELWEIGHT

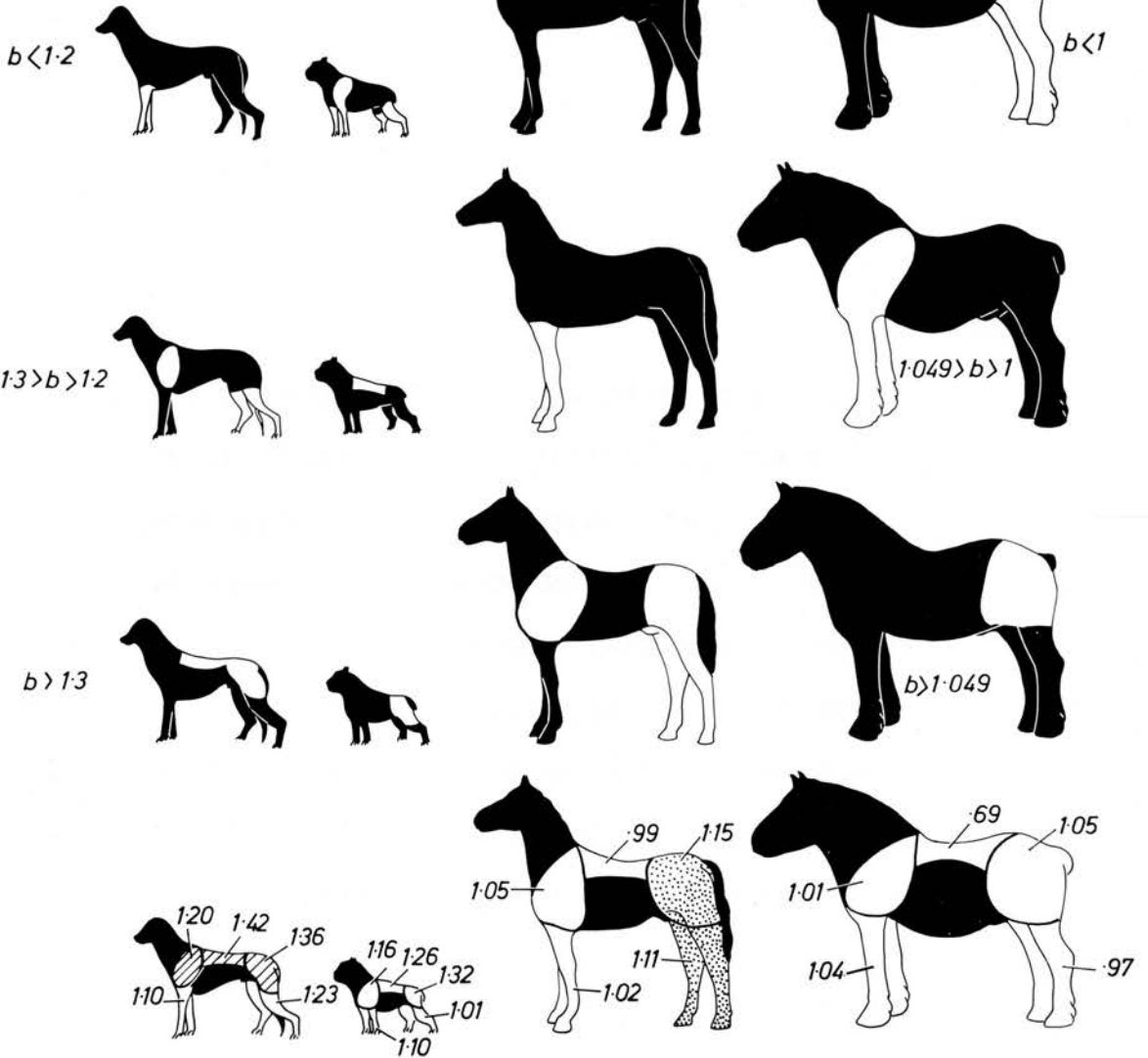


 groups significantly different

Fig. 11.

Growth changes in muscle distribution relative to liveweight in Greyhounds from birth to 37 kg; other dogs from birth to 47 kg, Thoroughbreds from 0.7 kg to 480 kg and other horses from 3.0 kg to 530 kg liveweight. Muscle groups are graded according to their growth ratio -b-. Significant differences in values of b ($P < 0.02$) and adjusted group means ($P < 0.05$) between "athletes" and "non-athletes" are indicated.

MUSCLE GROUPS vs BODY WEIGHT



 GROUPS SIGNIFICANTLY DIFFERENT

 REGRESSION COEFFICIENTS SIGNIFICANTLY DIFFERENT

Table 18 Logarithmic regression equations comparing the growth of six muscle groups relative to total muscle weight in 18 Greyhounds from birth to 30 kg, 9 other dogs from birth to 47.0 kg; 7 Thoroughbreds from 0.7 kg to 430 kg, and 6 other horses from 3.0 kg to 500 kg liveweight.

Muscle Group	Type of Animal	Growth ratio b*	Se b	log a	r**	Significance*** of difference between groups
Distal forelimb	Greyhounds	0.904+	0.029	-1.488	0.9917	Other dogs P < 0.05
	Other dogs	0.953	0.041	-1.567	0.9937	
	Thoroughbreds	0.984	0.059	-1.649	0.9913	NS
	Other horses	1.056	0.089	-2.071	0.9863	
Brachial	Greyhounds	0.984+	0.460	-1.132	0.9995	NS
	Other dogs	1.010	0.026	-1.208	0.9976	
	Thoroughbreds	1.016	0.025	-1.303	0.9985	Thoroughbreds P < 0.05
	Other horses	1.019	0.027	-1.392	0.9986	
Pectoral girdle	Greyhounds	0.944+c	0.018	-0.856	0.9970	NS
	Other dogs	1.055 c	0.036	-1.305	0.9961	
	Thoroughbreds	1.016	0.034	-1.244	0.9972	NS
	Other horses	0.993	0.023	-1.106	0.9990	
Longissimus	Greyhounds	1.161+	0.020	-1.884	0.9976	Greyhounds P < 0.05
	Other dogs	1.109	0.078	-1.772	0.9833	
	Thoroughbreds	0.953	0.153	-1.328	0.9410	NS
	Other horses	0.700+	0.072	-0.128	0.9795	
Femoral	Greyhounds	1.109+c	0.012	-1.324	.9991	NS
	Other dogs	1.042 c	0.024	-1.077	.9982	
	Thoroughbreds	1.063+	0.015	-1.080	.9995	NS
	Other horses	1.048+	0.027	-1.033	.9987	
Distal hindlimb	Greyhounds	1.005	0.014	-1.765	.9984	NS
	Other dogs	0.986	0.023	-1.617	.9981	
	Thoroughbreds	1.060	0.062	-1.868	.9914	NS
	Other horses	0.964	0.016	-1.549	.9995	

* Regression coefficient b, standard error Se b

+ Values of b bearing this superscript are significantly different (P < 0.05) from 1.

c Values of b for similar muscle groups bearing this superscript are significantly different (P < 0.05) from one another.

** Correlation coefficient r.

*** Significance of difference between adjusted means of groups tested by analysis of covariance; NS = not significant.

Table 19 Logarithmic regression equations comparing the growth of six muscle groups relative to total muscle weight in dogs aged up to 15 months postnatal age (young dogs) comprising 11 Greyhounds from birth to 23.5 kg, 4 other pups from birth to 9.9 kg liveweight; and in horses less than 2 years of postnatal age (young horses) comprising 7 Thoroughbreds from 0.7 kg to 430 kg and 3 other horses from 3 kg to 115 kg liveweight.

Muscle group	Type of animal	Growth ratio b*	Se b	log a	r**	Significance*** of difference between groups
Distal forelimb	Greyhounds	0.930	0.053	-1.555	0.9858	NS
	Other dogs	0.975	0.060	-1.626	0.9962	
	Thoroughbreds	0.984	0.059	-1.649	0.9913	
	Other horses	0.981	0.029	-1.780	0.9996	
Brachial	Greyhounds	0.978	0.013	-1.117	0.9992	NS
	Other dogs	0.974+	0.003	-1.087	1.0000	
	Thoroughbreds	1.016	0.025	-1.303	0.9985	
	Other horses	0.999	0.065	-1.321	0.9979	
Pectoral girdle	Greyhounds	0.907+c	0.028	-0.760	0.9958	NS
	Other dogs	1.092 c	0.070	-1.414	0.9959	
	Thoroughbreds	1.016	0.034	-1.244	0.9972	
	Other horses	0.951	0.034	-0.957	0.9994	
Longissimus	Greyhounds	1.206+	0.018	-2.001	0.9990	NS
	Other dogs	1.092	0.243	-1.726	0.9537	
	Thoroughbreds	0.953	0.153	-1.318	0.9410	
	Other horses	0.543+	0.002	-0.452	0.9999	
Femoral	Greyhounds	1.134	0.018	-1.389	0.9989	NS
	Other dogs	1.053	0.027	-1.117	0.9994	
	Thoroughbreds	1.063+	0.015	-1.080	0.9995	
	Other horses	1.090+	0.005	-1.187	1.0000	
Distal hindlimb	Greyhounds	1.043	0.019	-1.863	0.9984	Other dogs P<0.01
	Other dogs	1.037	0.013	-1.763	0.9999	
	Thoroughbreds	1.060	0.062	-1.868	0.9914	
	Other horses	0.998	0.010	-1.674	0.9999	

* Regression coefficient b, standard error Se b.

+ Values of b bearing this superscript are significantly different (P< 0.05) from 1.

c Values of b for similar muscle groups bearing this superscript are significantly different (P< 0.05) from one another.

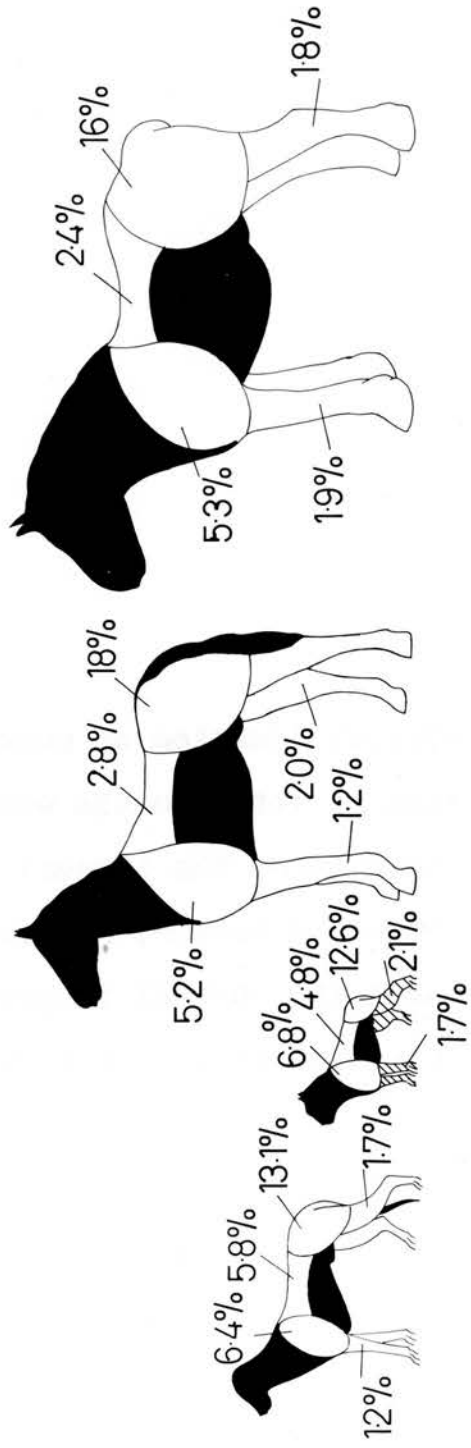
** Correlation coefficient r.

*** Significance of difference between adjusted group means tested by analysis of covariance; NS = not significant.

Fig. 12.

Topographical location of muscle groups and their proportion of total muscle weight in adult Greyhounds, adult other dogs, the largest Thoroughbred investigated and adult other horses. Where present, significant differences ($P < 0.005$) in groups between "athletes" and "non-athletes" are indicated.

MUSCLE GROUPS AS PROPORTIONS OF TOTAL MUSCLE WEIGHT



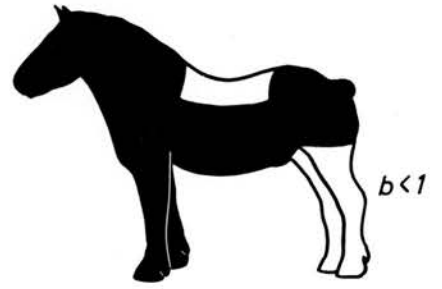
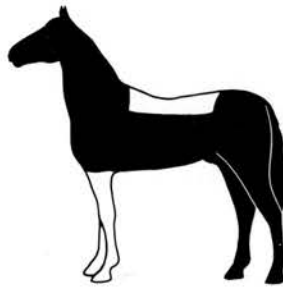
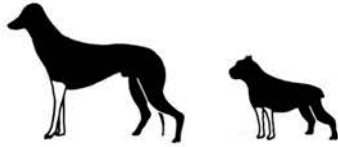
 groups significantly different

Fig. 13.

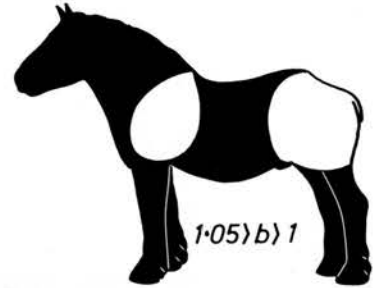
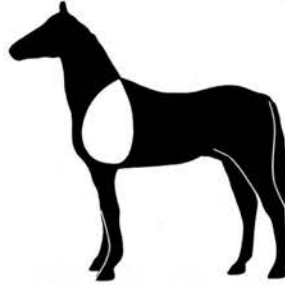
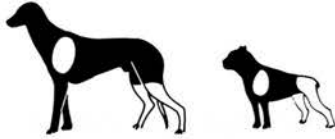
Growth changes in muscle distribution relative to total muscle weight in Greyhounds between birth and 30 kg, other dogs between birth and 47 kg; Thoroughbreds between 0.7 kg and 430 kg and other horses between 3.0 kg and 500 kg liveweight. Muscle groups are graded according to the values of their growth ratios $-b-$. Significant differences in values of b ($P < 0.05$) and the adjusted group means between "athletes" and "non-athletes" ($P < 0.05$) are indicated.

MUSCLE GROUPS vs. TOTAL
MUSCLE WEIGHT

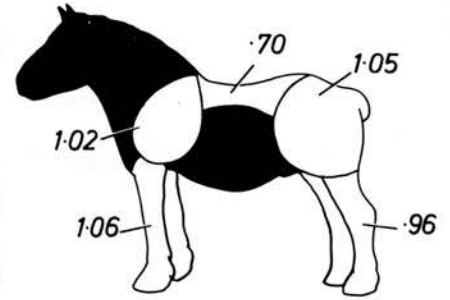
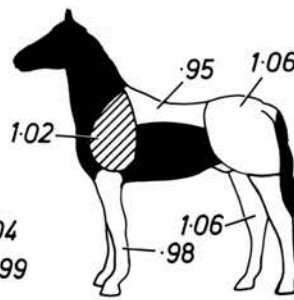
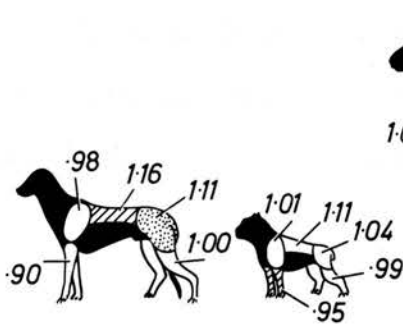
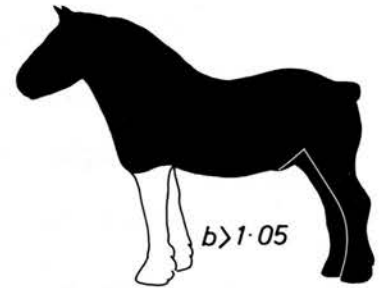
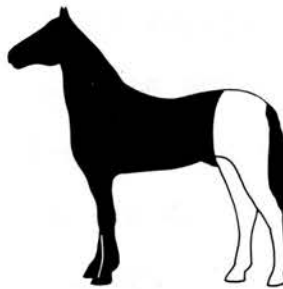
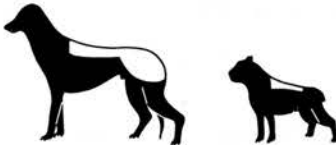
$b < 0.96$



$1 > b > .96$



$b > 1.1$



 GROUPS SIGNIFICANTLY
DIFFERENT

 REGRESSION COEFFICIENTS
SIGNIFICANTLY DIFFERENT

Fig. 14.

Allometric equations comparing the growth of brachial and femoral muscle groups and m. longissimus, relative to total muscle weight between Greyhounds and other dogs.

BRACHIAL MUSCLES
WEIGHT (g)

FEMORAL MUSCLES,
M. LONGISSIMUS,
WEIGHT (g)

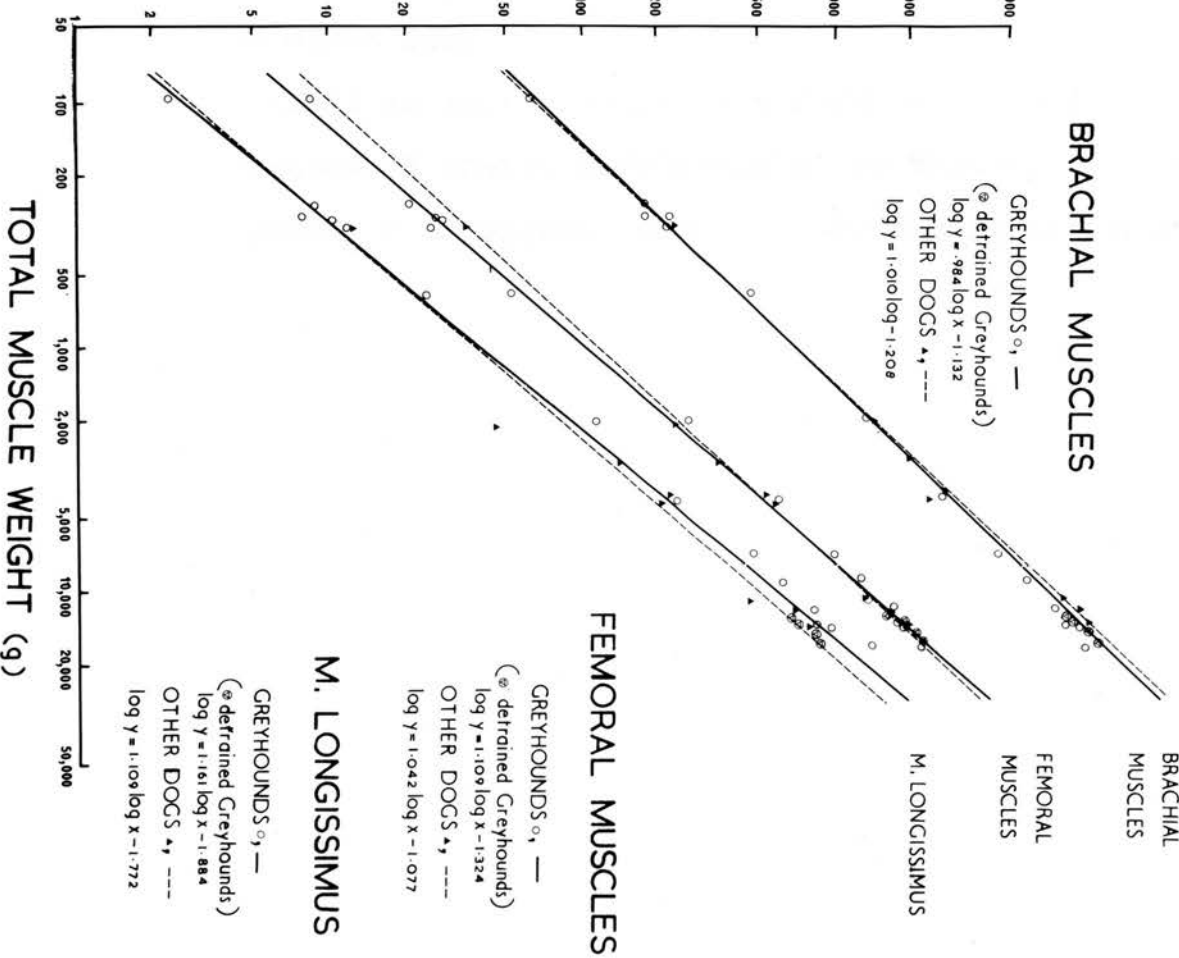


Fig. 15.

**Allometric equations comparing the growth of brachial,
femoral and distal forelimb muscle groups relative
to total muscle weight between Thoroughbreds
and other horses.**

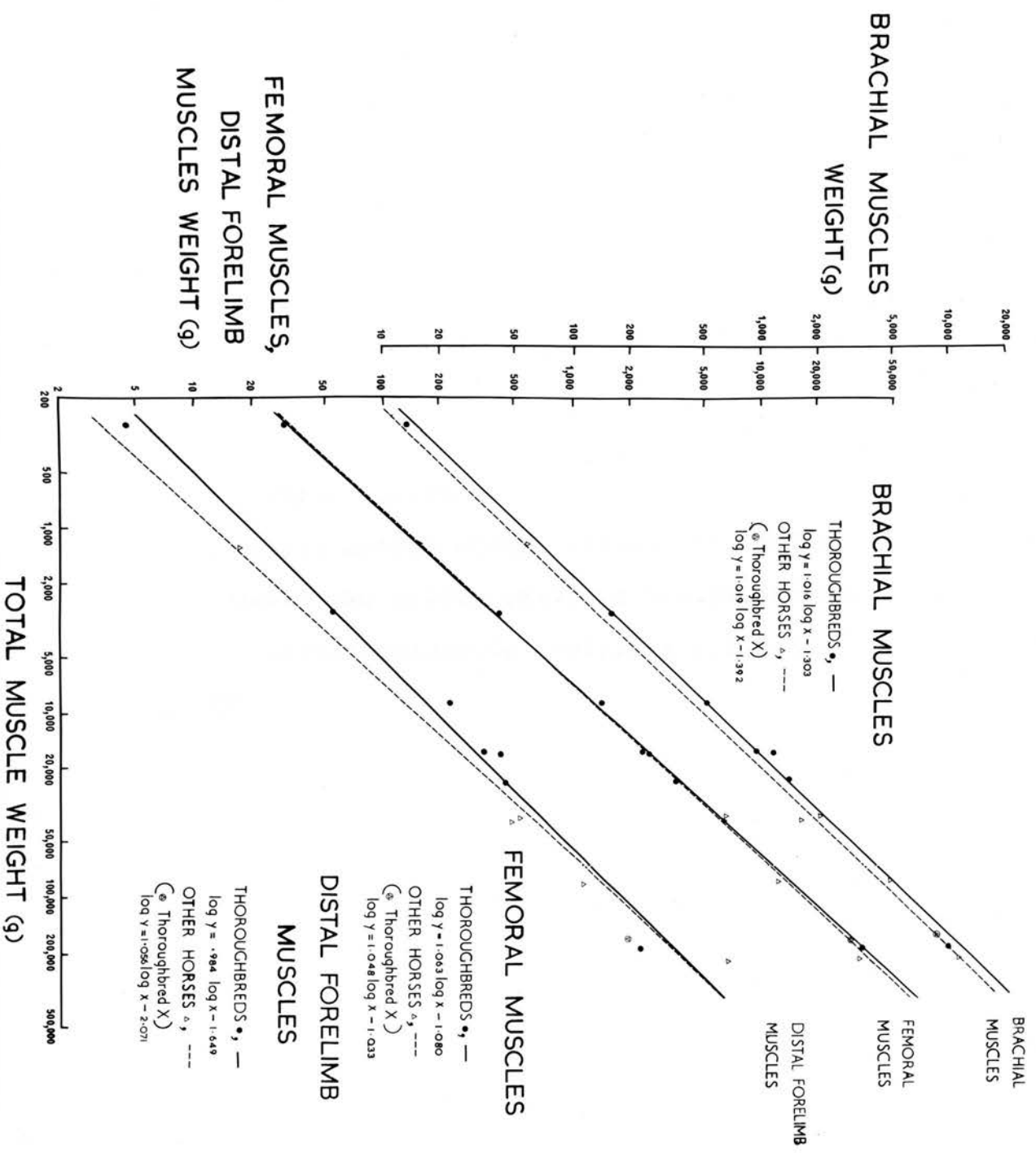


Table 20 Logarithmic regression equations comparing the growth of the proximal hindlimb muscle group with the distal hindlimb muscle group in 19 Greyhounds from birth to 30 kg, 9 other dogs from birth to 47 kg; 7 Thoroughbreds from 13.4 kg to 430 kg and 10 other horses from 3.0 kg to 530 kg liveweight.

Type of animal	Growth ratio b*	Se b	log a	r**	Significance*** of difference between groups
Greyhounds	1.108	0.014	0.623+	0.9986	} Greyhounds P < 0.01
Other dogs	1.051	0.041	0.643	0.9948	
Thoroughbreds	1.148	0.064	0.370	0.9922	} NS
Other horses	1.102	0.024	0.615+	0.9982	

* Regression coefficient b, standard error Se b.
 + Values of b bearing this superscript are significantly different (P < 0.05) from 1.
 ** Correlation coefficient r.
 *** Significance of the difference between groups, tested by analysis of covariance; NS = not significant.

Fig. 16.

Allometric equations comparing the growth of the proximal hindlimb muscle relative to the distal hindlimb muscle in Greyhounds between birth and 30 kg, other dogs between birth and 47 kg; Thoroughbreds between 13.4 and 430 kg and other horses between 3.0 kg and 530 kg liveweight.

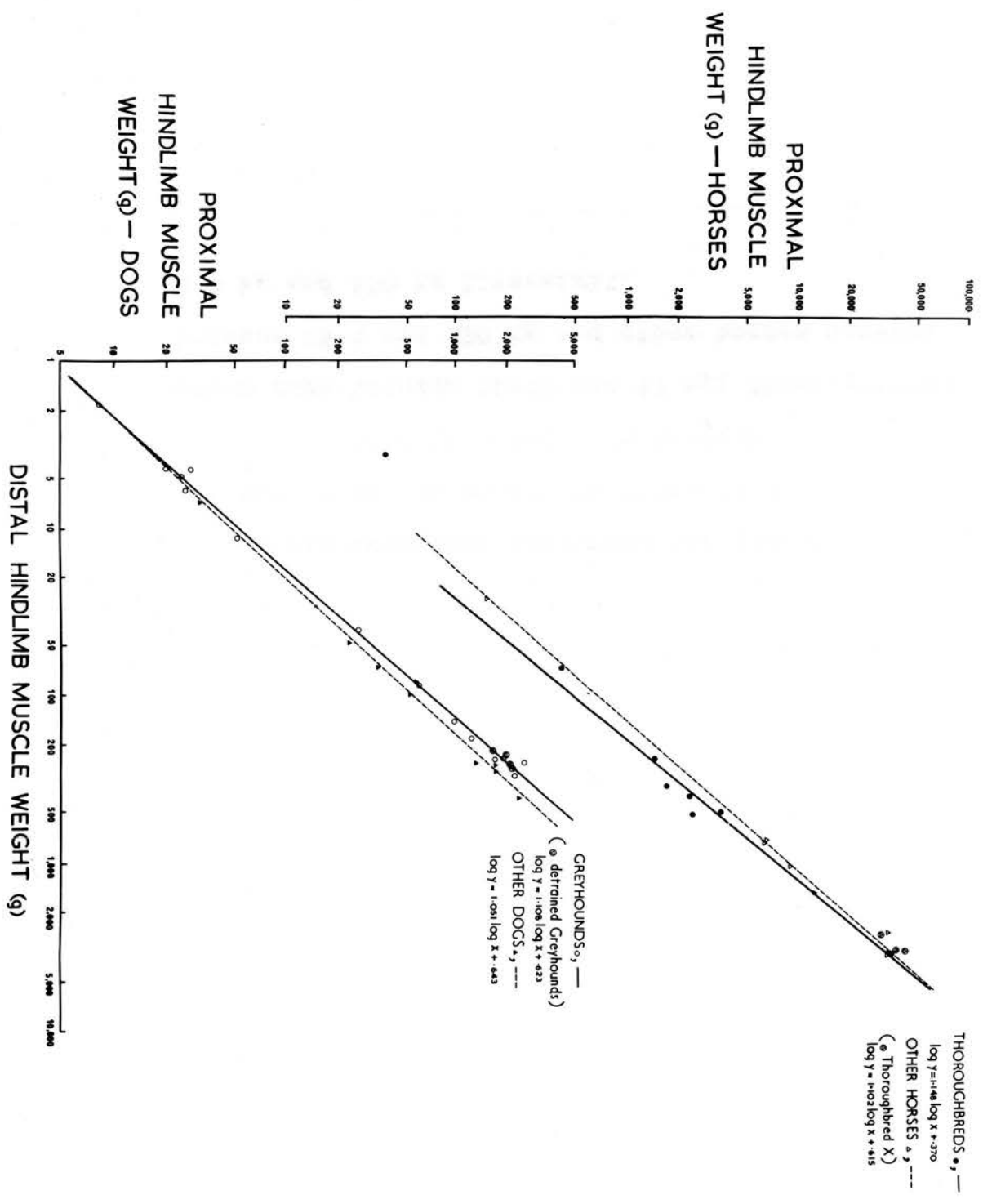


Table 21 Weight in g of total forelimb bone, total hindlimb bone, humerus and femur and their percentage of liveweight, total bone and where relevant total forelimb and total hindlimb bone in adult Greyhounds and adult other dogs.

Type of Dog	Live-weight (kg)	Total bone weight (kg)	Sex	Total forelimb bone			Total hindlimb bone			Humerus			Femur			Hind-limb bone weight
				Weight (g)	Live-weight (%)	Total bone (%)	Weight (g)	Live-weight (%)	Total bone (%)	Weight (g)	Live-weight (%)	Total bone (%)	Fore-limb bone weight	Weight (g)	Live-weight (%)	
Greyhound (D)	24,150	2,550	♀	302	1.25	11.8	283	1.17	11.1	101	0.42	3.96	33.4	0.43	4.04	36.4
Greyhound	25,000	2,819	♀	342	1.37	12.1	338	1.34	12.0	113	0.45	4.00	33.0	0.48	4.29	35.8
Greyhound	25,200	3,306	♂	406	1.61	12.3	340	1.35	10.3	135	0.54	4.08	33.3	0.54	4.14	40.3
Greyhound	25,200	-	♂	-	-	-	-	-	-	-	-	-	-	-	-	137
Greyhound (D)	25,300	3,123	♂	363	1.43	11.6	350	1.38	11.2	116	0.46	3.71	32.0	0.50	4.03	36.0
Greyhound	27,500	-	♂	-	-	-	-	-	-	-	-	-	-	-	-	126
Greyhound	28,000	-	♂	-	-	-	-	-	-	-	-	-	-	-	-	135
Greyhound (D)	28,500	3,259	♀	305	1.07	9.36	386	1.35	11.8	126	0.44	3.87	41.3	0.49	4.33	36.5
Greyhound	29,750	4,310	♀	486	1.63	11.3	472	1.59	11.0	182	0.54	3.76	33.3	0.58	3.99	36.4
Greyhound (D)	30,000	3,684	♂	439	1.46	11.9	405	1.35	11.0	142	0.47	3.85	32.3	0.49	4.04	36.8
Greyhound	30,000	-	♂	-	-	-	-	-	-	-	-	-	-	-	-	149
Greyhound	33,608	-	♀	-	-	-	-	-	-	-	-	-	-	-	-	139
Greyhound	37,000	-	♂	-	-	-	-	-	-	-	-	-	-	-	-	157
	Mean %				1.40	11.5		1.36	11.2		0.47	3.89	34.0	0.45	4.12+	165
	SD				0.20	0.99		0.12	0.56		0.05	0.13	3.12	0.04	0.14	1.54
	Mean	3,293		377.6	1.59	11.5	367	1.37	11.2	127.9	0.47	3.88	33.9	0.49	4.11	139.9
Collie X	10,400	1,031	♀	101	0.97	9.80	112	1.08	10.9	39	0.38	3.78	38.6	0.38	3.9	39.6
Collie	11,000	-	♀	-	-	-	-	-	-	-	-	-	-	-	-	40
Collie	12,000	-	♀	-	-	-	-	-	-	-	-	-	-	-	-	39
Collie X	14,000	-	♀	-	-	-	-	-	-	-	-	-	-	-	-	39
Collie	14,000	-	♂	-	-	-	-	-	-	-	-	-	-	-	-	45
Collie	22,000	-	♀	-	-	-	-	-	-	-	-	-	-	-	-	0.38
Afghan	25,100	3,276	♀	401	1.60	12.2	372	1.48	11.4	129	0.51	3.94	32.2	0.55	4.18	0.46
Afghan	31,900	3,698	♂	453	1.42	12.2	385	1.21	10.4	148	0.46	4.00	32.7	0.46	3.95	146
Labrador	33,000	3,470	♀	399	1.21	11.5	346	1.05	9.97	125	0.38	3.60	31.3	0.36	3.43	119
Great Dane	46,500	7,396	♂	892	1.92	12.1	793	1.71	10.7	278	0.60	3.76	31.2	0.59	3.73	276
	Mean %				1.42	11.61		1.30	10.7		0.47	3.81	33.2	0.43+	3.84+	75
	SD				0.36	1.03		0.28	0.54		0.09	0.16	3.08	0.09	0.28	36.7
	Mean	3,774		449.2	1.53	11.9	401.6	1.37	10.6	143.8	0.49	3.81	32.0	0.49	3.81	143.6

D = Detained Greyhounds

+ Values followed by this superscript are significantly different ($P < 0.05$) between the two types of dog.

Table 22 Weight in g of total forelimb bone, total hindlimb bone, humerus and femur and their percentage of liveweight, total bone and of total forelimb bone for the humerus and total hindlimb bone for the femur in adult horses*

Type of animal	Live-Weight (g)	Total Weight (g)	Sex	Total forelimb bone			Total hindlimb bone			Humerus			Femur			Hind-limb bone weight	
				Weight (g)	Percentage of Live-weight	Total bone	Weight	Percentage of Live-weight	Total bone	Weight	Percentage of Live-weight	Total bone	Weight	Percentage of Live-weight	Total bone		
Thoroughbred	432,727	53,855	♂	5,961	1.37	11.1	7,023	1.62	13.0	1,844	0.43	3.42	30.9	2,880	0.67	5.3	41.0
Thoroughbred	458,182	-	♀	-	-	-	-	-	-	-	-	-	-	2,650	0.58	-	-
Thoroughbred	470,909	-	♀	-	-	-	-	-	-	-	-	-	-	2,272	0.48	-	-
Thoroughbred	470,909	-	♀	-	-	-	-	-	-	-	-	-	-	2,414	0.51	-	-
Thoroughbred	483,636	-	♀	-	-	-	-	-	-	-	-	-	-	2,360	0.49	-	-
Mean % (of adults)	-	-	-	-	1.37	11.1	-	1.62	13.0	-	0.43	3.42	30.9	-	0.51	5.3	41.0
SD	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mean	153,727	-	♂	-	-	-	-	-	-	-	-	-	-	2,424	0.51	-	-
Welsh Mountain	178,182	-	♂	-	-	-	-	-	-	-	-	-	-	510	0.33	-	-
Shetland	203,636	27,402	♂	2,442	1.20	8.91	2,712	1.33	9.90	790	0.39	2.88	32.4	1,127	0.55	4.11	41.6
Welsh Mountain	229,091	-	♀	-	-	-	-	-	-	-	-	-	-	945	0.41	-	-
Shetland	280,000	-	♂	-	-	-	-	-	-	-	-	-	-	925	0.33	-	-
Thoroughbred	369,091	-	♂	-	-	-	-	-	-	-	-	-	-	3,135	0.85	-	-
Thoroughbred	432,727	34,564	♂	4,231	0.98	12.2	4,843	1.12	14.0	1,380	0.32	3.99	32.6	2,032	0.47	5.88	42.0
Comma X	445,455	-	♀	-	-	-	-	-	-	-	-	-	-	1,955	0.44	-	-
Clydesdale	496,364	70,420	♀	7,872	1.59	11.2	8,652	1.74	12.3	2,300	0.46	3.27	29.2	3,680	0.74	5.23	42.5
Thoroughbred	521,818	-	♂	-	-	-	-	-	-	-	-	-	-	2,576	0.49	-	-
Thoroughbred	534,545	-	♀	-	-	-	-	-	-	-	-	-	-	2,360	0.44	-	-
Mean %	-	-	-	-	1.26	10.8	-	1.40	12.1	-	0.39	3.38	31.4	-	0.52	5.07	42.0
SD	-	-	-	-	0.31	1.70	-	0.32	2.06	-	0.07	0.56	1.91	-	0.17	0.90	0.45
Mean	4,848	1.28	11.0	5,402	1.55	12.2	1,490	0.43	3.38	30.7	1,853	0.53	5.16	42.2	-	-	-

* The values of the weights given for Thoroughbreds are, with the exception of those for the femur, those for the largest (young) Thoroughbred in which these values were assessed.

Table 23 Logarithmic regression equations comparing the growth of forelimb bone with total bone, hindlimb bone with total bone, humerus with total forelimb bone and femur with total hindlimb bone in Greyhounds from birth to 30 kg, other dogs from birth to 47 kg; Thoroughbreds from 0.7 kg to 430 kg and other horses from 3.0kg to 500 kg liveweight.

Dependent variable	Independent variable	Number of observations	Type of animal	Growth ratio b*	Se b	log a	r**
<u>Forelimb bone</u>	<u>Total bone</u>	18	Greyhounds	0.956+	0.015	-0.776	0.9981
		9	Other dogs	1.019	0.035	-0.984	0.9958
		7	Thoroughbreds	0.997	0.024	-0.878	0.9986
		6	Other horses	0.989	0.029	-0.914	0.9982
<u>Hindlimb bone.</u>	<u>Total bone</u>	18	Greyhounds	1.060+c	0.017	-1.141	0.9980
		9	Other dogs	0.957 c	0.016	-0.813	0.9990
		7	Thoroughbreds	1.034	0.036	-0.926	0.9970
		6	Other horses	0.975	0.031	-0.791	0.9975
<u>Humerus</u>	<u>Forelimb bone</u>	18	Greyhounds	0.987	0.011	-0.444	0.9989
		9	Other dogs	0.946	0.027	-0.361	0.9972
		7	Thoroughbreds	1.018	0.016	-0.609	0.9993
		7	Other horses	1.019	0.013	-0.566	0.9996
<u>Femur</u>	<u>Hindlimb bone</u>	18	Greyhounds	0.985	0.009	-0.404	0.9993
		9	Other dogs	0.999	0.014	-0.448	0.9993
		7	Thoroughbreds	1.021	0.011	-0.495	0.9997
		8	Other horses	1.006	0.030	-0.425	0.9973

* Regression coefficient b, standard error Se b.

+ Values of b bearing this superscript are significantly different ($P < 0.05$) from 1.

c Values of b bearing this superscript are significantly different ($P < 0.05$) from one another.

** Correlation coefficient r.

Table 24 Ratios of brachial muscle weight to humerus weight and femoral muscle weight to the femur in adult dogs.

Type of dog	Liveweight (g)	Sex	Brachial ratio	Femoral ratio
Greyhound	24,150	♀ D*	8.47	11.3
Greyhound	25,000	♀	7.52	15.1
Greyhound	25,200	♂↗	7.08	13.9
Greyhound	25,200	♂↗	-	14.3
Greyhound	25,300	♂↗ D*	7.76	16.2
Greyhound	27,500	♂↗	-	17.2
Greyhound	28,000	♂↗	-	18.5
Greyhound	28,500	♀ D*	8.26	15.2
Greyhound	29,750	♀	6.91	13.2
Greyhound	30,000	♂↗ D*	7.97	15.3
Greyhound	30,000	♂↗	-	15.4
Greyhound	33,608	♀	-	15.8
Greyhound	37,000	♂↗	7.71	16.5
	Mean		7.71+	15.22+
	SD		0.58	1.82
Collie X	10,400	♀	6.15	14.9
Afghan	25,100	♀	7.34	12.7
Afghan	31,900	♂↗	6.90	13.2
Labrador	33,000	♀	6.43	11.0
Great Dane	46,500	♂↗	5.17	8.5
	Mean		6.40+	12.1+
	SD		0.82	2.43

D* Detained Greyhounds.

+ Values followed by this superscript are significantly different ($P < 0.01$) between each type of dog.

Table 25 Ratios of brachial muscle weight to humerus weight and femoral muscle weight to femur in adult horses.

Type of horse	Liveweight (g)	Sex	Brachial ratio	Femoral ratio
Thoroughbred *	432,727	♂	5.39	11.9
Thoroughbred	470,909	♀	-	17.6
Thoroughbred	470,909	♀	-	13.8
Thoroughbred	483,636	♀	-	17.7
	Mean of adults		-	16.4
	SD		-	2.22
Shetland	153,727	♂	-	14.3
Shetland	203,636	♂	6.06	10.9
Shetland	280,000	♂	-	15.5
Thoroughbred X **	369,091	♂	-	9.12
Thoroughbred X **	432,727	♂	6.16	15.0
Connemara X	445,455	♀	-	13.7
Clydesdale	496,364	♀	5.0	8.99
Thoroughbred X **	521,818	♂	-	14.4
Thoroughbred X **	534,545	♀	-	17.5
	Mean		5.74	13.3
	SD		0.64	2.95

* Young Thoroughbred

** Thoroughbred cross.

Table 26 Logarithmic regression equations comparing the growth of the brachial muscles with that of the humerus in Greyhounds from birth to 30 kg, other dogs from birth to 47 kg; Thoroughbreds from 0.7kg to 430 kg and other horses from 3.0 kg to 500 kg liveweight; and the growth of femoral muscles relative to the femur in Greyhounds from birth to 37 kg, other dogs from birth to 47 kg; Thoroughbreds from 0.7 kg to 480 kg and other horses from 3.0 kg to 530 kg liveweight.

Muscle Group	Bone	Type of Animal	Number of observations	Growth ratio b*	Se b	log a	r**
Brachial	Humerus	Greyhounds	18	1.378+c	0.049	0.055	0.9900
		Other dogs	9	1.149+c	0.057	0.479	0.9915
		Thoroughbreds	7	1.020	0.086	0.394	0.9825
		Other horses	7	1.029	0.041	0.622	0.9960
		Greyhounds	24	1.418+c	0.048	0.270	0.9876
		Other dogs	21	1.271+c	0.047	0.450	0.9871
Femoral	Femur	Thoroughbreds	19	1.232+	0.106	0.049	0.9421
		Other horses	16	1.132	0.076	0.634	0.9699
		Greyhounds	24	1.418+c	0.048	0.270	0.9876

* Regression coefficient b, standard error Se b.
 + Values of b bearing this superscript are significantly different ($P < 0.05$) from 1.
 c Values of b bearing this superscript within each limb are significantly different ($P < 0.05$) from one another.
 ** Correlation coefficient.

Table 27 Heart weight (in g) and its percentage of liveweight and total muscle weight in adult dogs.

Type of dog	Liveweight (g)	Sex	Total muscle weight (g)	Weight	Heart Percentage of:	
					Live-weight	Total muscle
Greyhound	24,150 D*	♀	13,297	334	1.38	2.51
Greyhound	25,000	♀	14,088	419	1.68	2.97
Greyhound	25,200	♂	14,692	365	1.45	2.48
Greyhound	25,300 D*	♂	14,422	326	1.29	2.26
Greyhound	28,500 D*	♀	15,742	422	1.48	2.68
Greyhound	29,750	♀	17,983	460	1.55	2.56
Greyhound	30,000 D*	♂	17,213	449	1.50	2.61
	Mean percentage				1.48 ⁺	2.58 ⁺
	SD				0.12	0.22
	Mean			396	1.48	2.58
	Mean percentage of (D*) detrained Greyhounds				1.41 ⁺	2.52
	SD				0.90	0.18
Collie X	10,400	♀	4,453	108	1.04	2.43
Afghan	25,100	♀	12,639	258	1.03	2.04
Afghan	31,900	♂	14,509	330	1.03	2.27
Labrador	33,000	♀	11,250	272	0.82	2.42
Great Dane	46,500	♂	20,875	414	0.89	1.98
	Mean percentage				0.96 ⁺	2.23 ⁺
	SD				0.10	0.21
	Mean			276	0.94	2.17

+ Values with this superscript are significantly different ($P < 0.02$) between breeds.

Table 28 Heart weight (in g) and its percentage of liveweight and total muscle weight in horses.

Type of horse	Liveweight (g)	Sex	Total muscle weight (g)	Weight	Heart	
					Live-weight	Total muscle
Thoroughbred	432,727	♂	191,883	3,689	0.85	1.92
Welsh Mountain	178,182	♂	-	1,200	0.67	-
Shetland	203,636	♂	85,054	1,471	0.72	1.73
Arab	305,455	♀	-	2,170	0.71	-
Piebald	318,182	♀	-	2,405	0.76	-
Thoroughbred X	369,091	♂	-	3,310	0.90	-
Exmoor X	480,000	♂	-	3,850	0.80	-
Clydesdale	496,364	♀	223,997	3,510	0.71	1.57
Cob	547,273	♂	-	4,410	0.81	-
	Mean percentage				0.76	1.65
	SD				0.07	0.11
	Mean			2,791	0.73	1.61

* Values are those for the largest young Thoroughbred in the series.

Table 29

Logarithmic regression equations comparing the growth of heart relative to liveweight in Greyhounds from birth to 30 kg, and other dogs from birth to 47 kg liveweight; Thoroughbreds from 0.7 kg to 430 kg and other horses from 3.0 kg to 550 kg liveweight; and the growth of heart weight relative to total muscle weight in Greyhounds from birth to 30 kg, other dogs from birth to 47 kg; Thoroughbreds from 0.7 kg to 430 kg and other horses from 3.0 kg to 500 kg liveweight.

Independent variable	Type of animal	Number of observations	Growth ratio b*	Se b	log a	r**
Liveweight						
Greyhounds		18	0.987	0.040	-1.844	0.9873
Other dogs		9	0.998	0.036	-2.027	0.9955
Thoroughbreds		8	0.969	0.034	-1.808	0.9962
Other horses		12	0.968	0.021	-1.982	0.9876
Total muscle						
Greyhounds		18	0.808 ⁺	0.030	-0.835	0.9891
Other dogs		9	0.868 ⁺	0.033	-1.134	0.9951
Thoroughbreds		7	0.916	0.073	-1.190	0.9846
Other horses		5	0.921 ⁺	0.025	-1.392	0.9989

* Regression coefficient b, standard error Se b.

+ Values of b followed by this superscript are significantly different ($P < 0.05$) from 1.

** Correlation coefficient r.

Fig. 17.

**Changes in heart weight with increasing liveweight
and total muscle weight in Greyhounds and other dogs.**

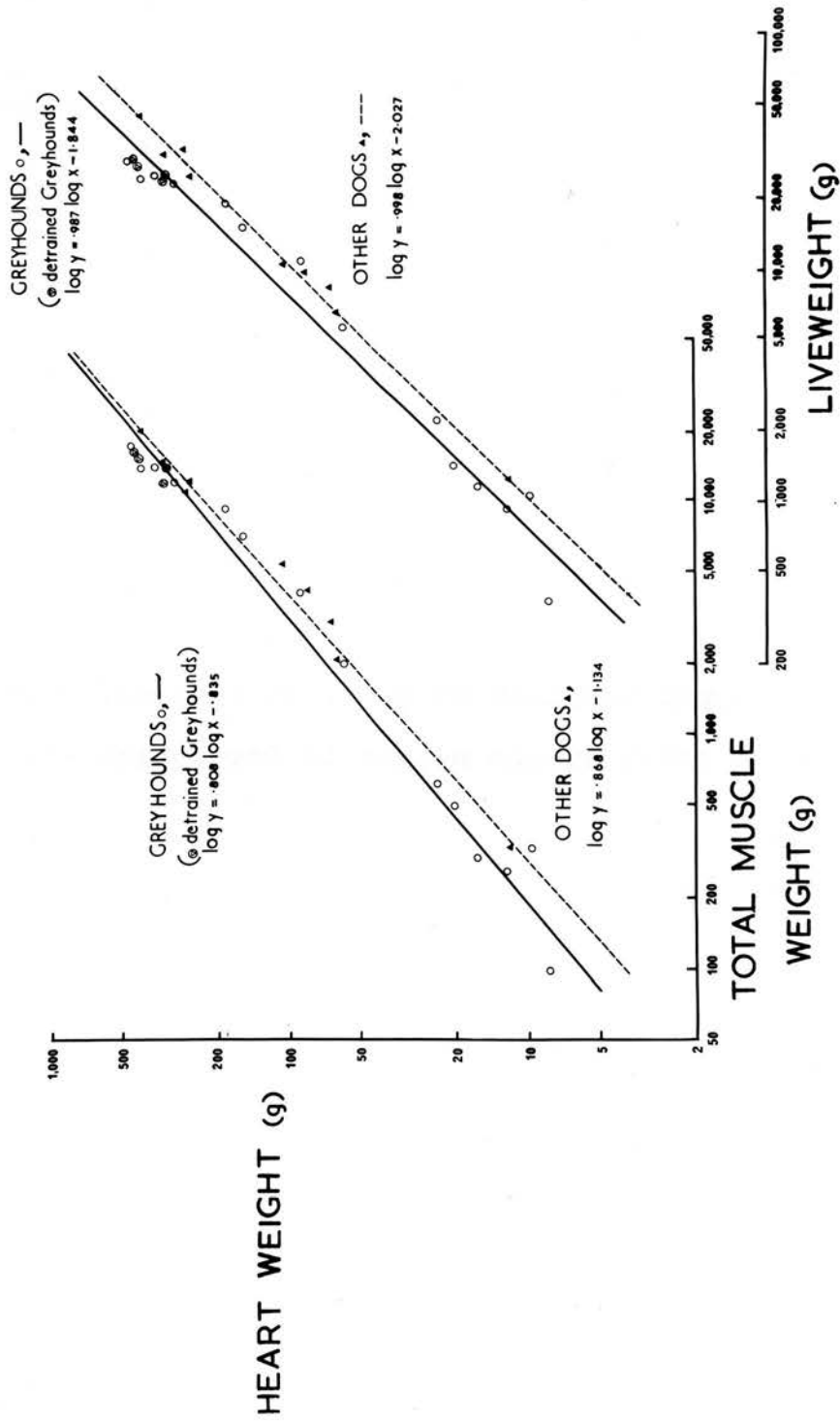


Fig. 18.

**Changes in heart weight with increasing liveweight
and total muscle weight in Thoroughbreds and other
horses.**

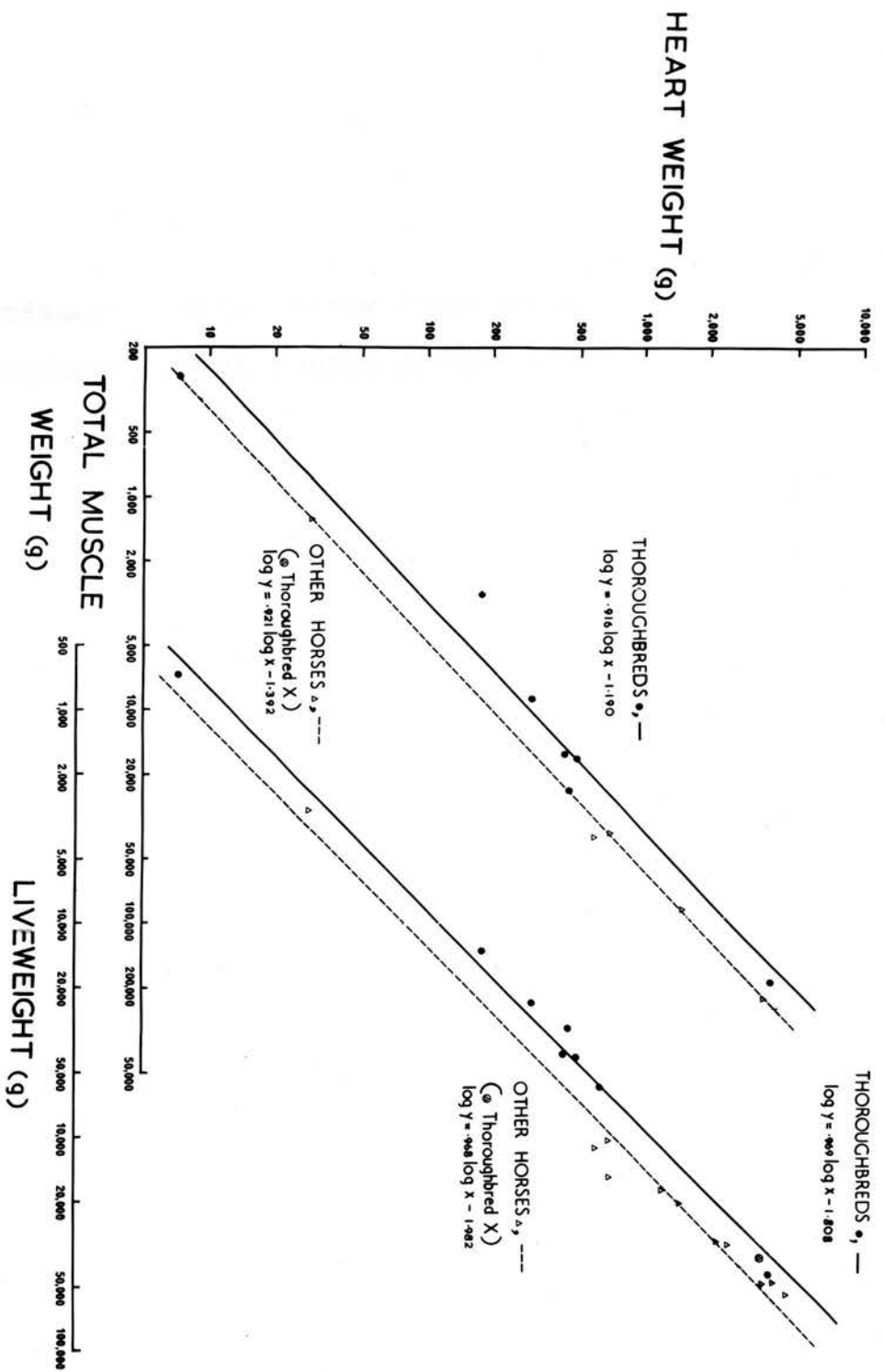


Table 30 Logarithmic regression equations comparing the growth of m. semitendinosus with the femoral muscles in Greyhounds from birth to 37 kg, other dogs from birth to 47 kg; Thoroughbreds from 0.7 kg to 480 kg and other horses from 3.0 kg to 530 kg liveweight.

Type of animal	Number of observations	Growth ratio b*	Se b	log a	r**
Greyhounds	24	1.032 ⁺ c	0.007	-1.294	0.9995
Other dogs	21	0.985 c	0.010	-1.176	0.9991
Thoroughbreds	19	1.074 ⁺ c	0.014	-1.337	0.9984
Other horses	17	1.012 c	0.014	-1.126	0.9985

* Regression coefficient b, standard error Se b.

+ Values of b followed by this superscript are significantly different ($P < 0.05$) from 1.

c Values of b bearing this superscript within a species are significantly different ($P < 0.05$) from one another.

** Correlation coefficient r.

Fig. 19.

**Cartesian transformation of body shape in the dog.
The outlines are scaled to the same body length.
The figures represent neonatal and three year old
male Greyhounds and are adapted from photographs
taken by the author.**

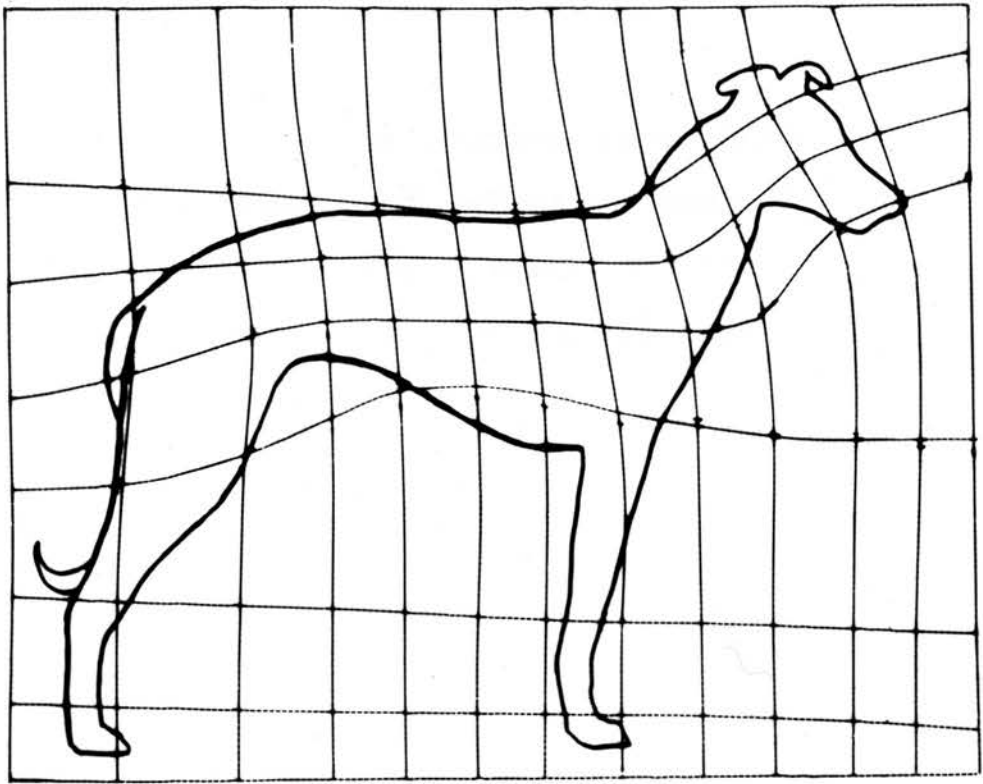
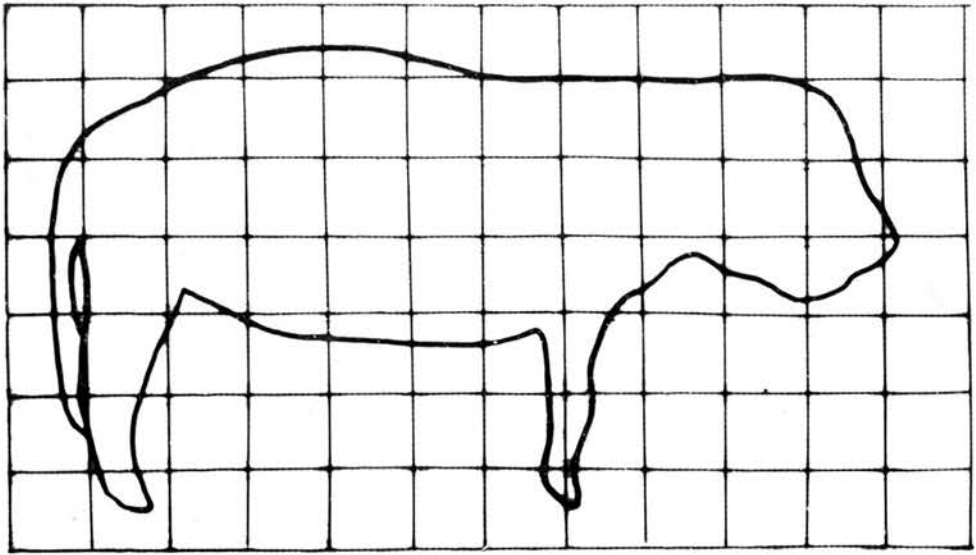


Fig. 20.

Cartesian transformation of body shape in the horse.

The outlines are scaled to the same body length.

The figures represent a neonatal female and a four year old male Thoroughbred, both are adapted from photographs taken by the author.

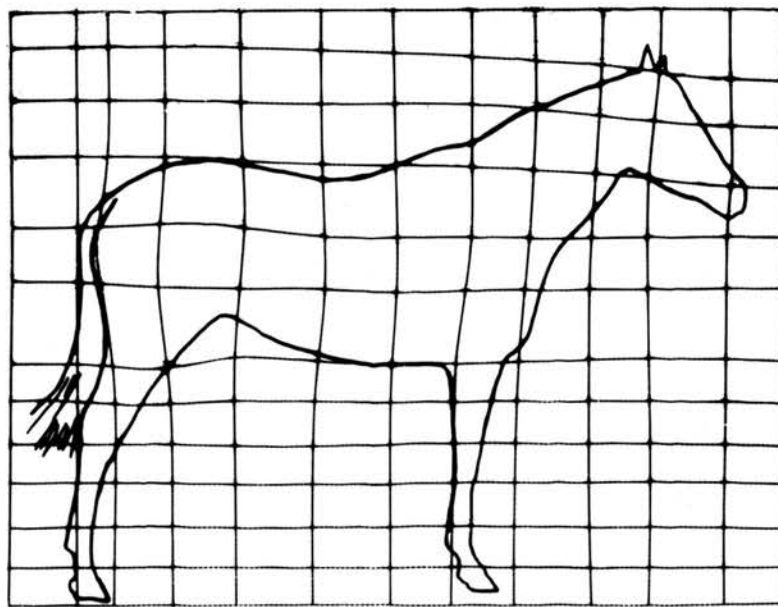
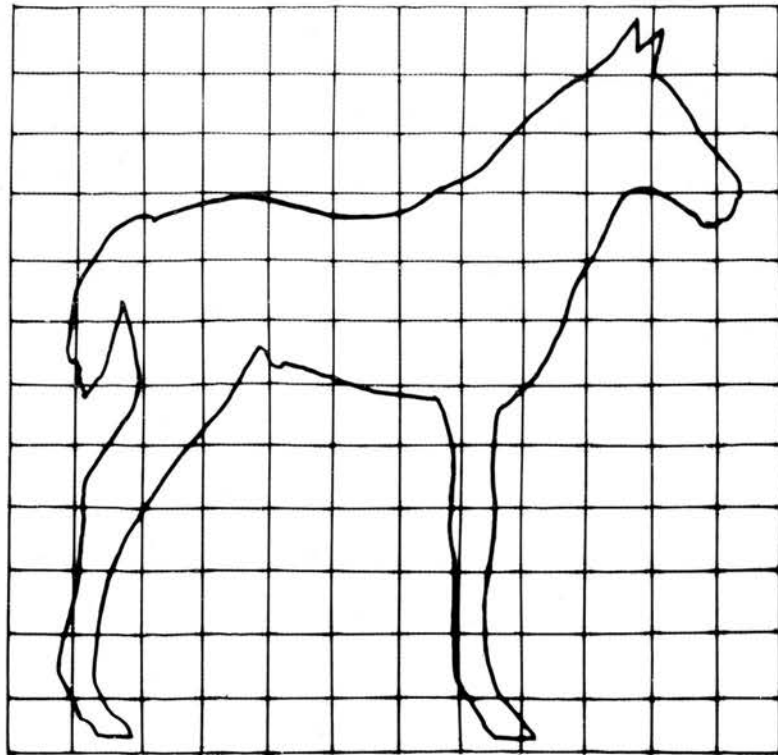


Table 31 Number of samples of m. semitendinosus, m. diaphragma and m. pectoralis transversus taken from 74 horses and 59 dogs and used for histometric and histochemical analysis.

	M. semiten- dinosus	M. dia- phragma	M. pectoralis transversus
Young Greyhounds (Weights .22 to 23.4 kg)	12	12	12
Adult Greyhounds (Weights 19 to 37 kg)	21	10	9
Young other dogs (Weights .46 to 9.9 kg)	16	14	12
Adult other dogs (Weights 7.7 to 46.5 kg)	10	7	8
Young Thoroughbreds (Weights 11 to 433 kg)	24	17	20
Adult Thoroughbreds (Weights 446 to 598 kg)	10	6	10
Young other horses (Weights 2.3 to 207 kg)	12	9	12
Adult other horses (Weights 153 to 560 kg)	20	14	22



Table 32 Comparison of the fresh with the frozen transverse sectional areas (TSA); and mean fibre area of the transverse section with that of a superficial sample, of *m. semitendinosus* from 21 young Thoroughbreds.

Live-weight (g)	TSA (mm ²)		Mean fibre area (µm ²)	
	Fresh	Frozen	Total section	Superficial sample
11,000	176	174	265	280
13,429	91	91	115	118
16,000	232	224	194	196
19,000	147	153	253	270
23,872	489	475	529	533
24,000	423	415	512	510
28,000	417	419	420	422
29,000	392	401	320	314
30,965	582	569	390	383
31,500	545	544	442	445
32,000	592	596	493	492
33,500	504	516	524	522
34,500	487	469	368	368
34,800	389	386	435	445
38,636	976	1005	1146	1146
39,000	589	569	583	573
40,500	647	646	1101	836
42,000	321	320	426	406
42,962	789	782	856	758
50,000	474	460	434	431
58,664	660	674	718	679
Mean	472.5	470.9	501.0	482.4

Table 33 Regression equations comparing the TSA of
 m. semitendinosus with liveweight in dogs and horses.

Number of obser- vations	Type of animal	Growth ratio b*	Se b	log a	r**
33	Greyhounds	0.814	0.023	5.359	0.9875
26	Other dogs	0.745	0.042	5.457	0.9643
28	Thoroughbreds	0.957 ^c	0.052	4.333	0.9638
30	Other horses	0.669 ^c	0.033	5.743	0.9670

* Regression coefficient b, standard error Se b
 c values of b bearing this superscript are significantly
 different ($P < 0.01$) from one another

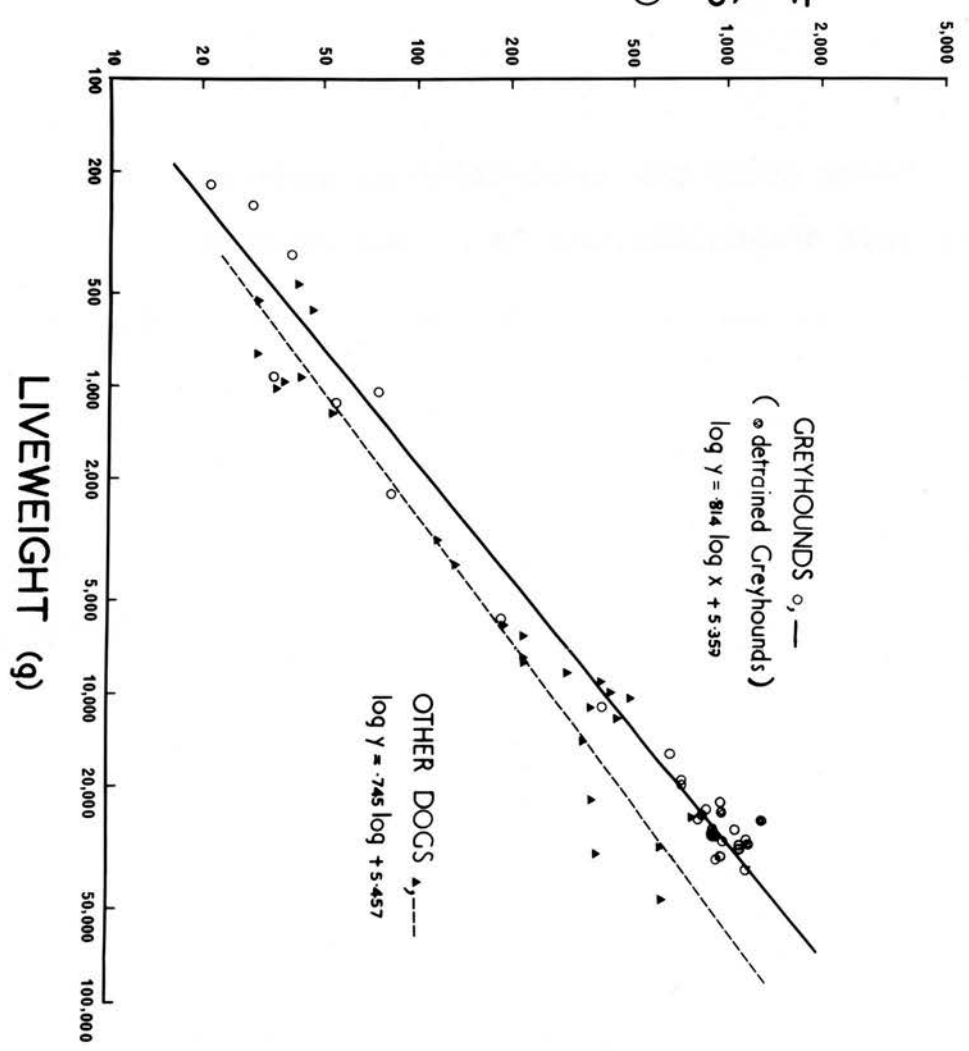
** Correlation coefficient r.

Fig. 21.

**Changes in TSA of m. semitendinosus with increasing
liveweight in Greyhounds and other dogs.**

TSA. OF
M. SEMITENDINOSUS

($\times 10^6 \mu\text{m}^2$)



GREYHOUNDS \circ , —
(\circ detraigned Greyhounds)
 $\log Y = .814 \log X + 5.359$

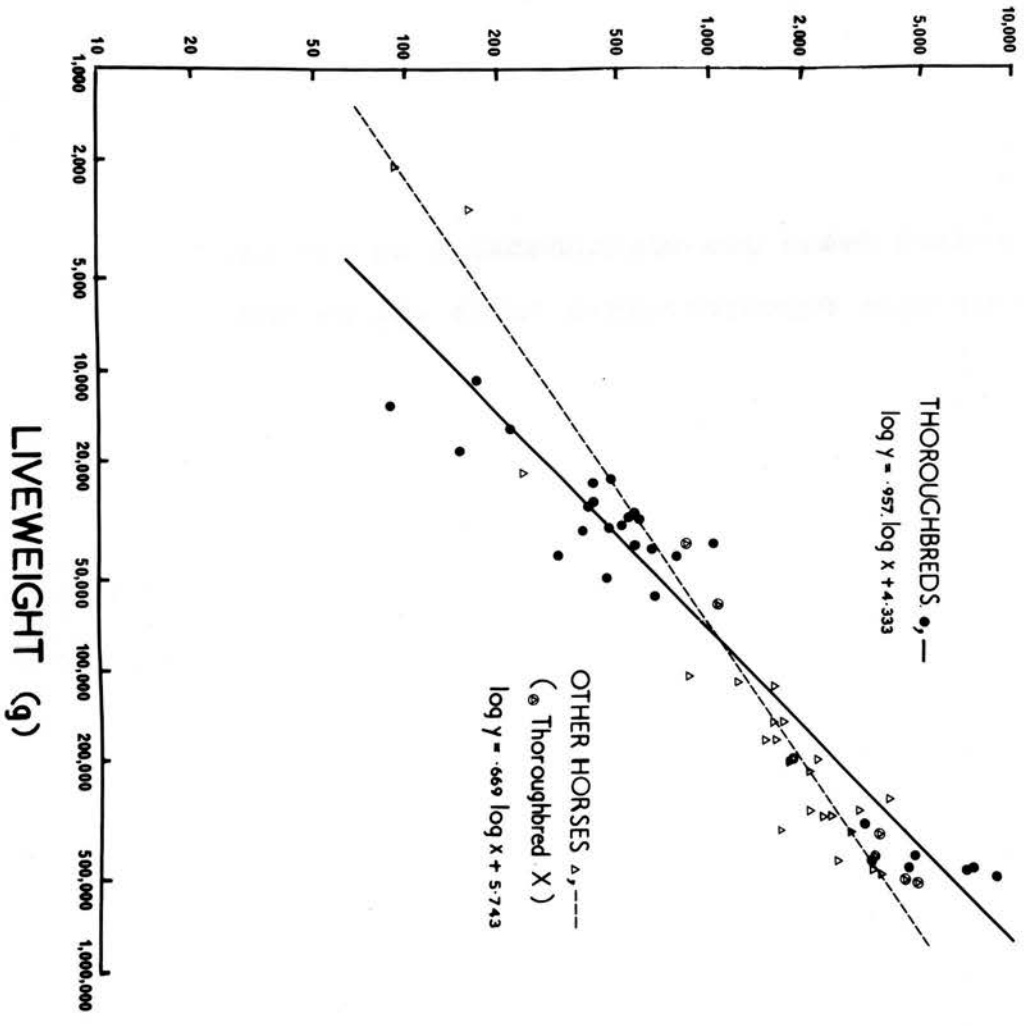
OTHER DOGS \triangle , ---
 $\log Y = .745 \log X + 5.457$

LIVWEIGHT (g)

Fig. 22.

Changes in TSA of m. semitendinosus with increasing liveweight in Thoroughbreds and other horses.

M. SEMITENDINOSUS
T.S.A. OF
($\times 10^6 \mu\text{m}^2$)



THOROUGHBREDS ●, —
 $\log Y = .957 \log X + 4.333$

OTHER HORSES △, ----
(⊗ Thoroughbred X)
 $\log Y = .669 \log X + 5.743$

LIVEWEIGHT (g)

Table 34 The total number of fibres in m. semitendinosus of adult dogs.

<u>Greyhounds</u>				<u>Other dogs</u>		
Live-weight (g)	Sex	Fibre numbers (x 1,000)	Breed	Live-weight (g)	Sex	Fibre numbers (x 1,000)
19,000	♀	280	Collie	7,742	♀	132
22,300	♀	295	Collie X	10,400	♀	184
24,150	♀	230	Collie	11,000	♀	139
24,884	♂	348	Collie	12,000	♀	188
25,000	♀	322	Collie	14,100	♀	136
25,200	♂	209	Collie	22,000	♀	155
25,300	♂	529	Afghan	25,100	♀	214
27,200	♂	313	Afghan	31,900	♂	194
27,500	♂	282	Labrador	33,000	♀	175
28,000	♂	232	Great Dane	46,500	♂	248
28,500	♀	329				
28,864	♂	328				
29,750	♀	404				
30,000	♂	352				
30,000	♂	319				
31,200	♂	348				
31,400	♂	346				
33,523	♀	306				
33,608	♀	260				
34,091	♂	320				
37,000	♂	355				
Mean		28,407		21,370		177
SD		4,321		12,681		37

Difference between means of liveweight and total fibre numbers significant at the 5% and 0.1% levels respectively.

Table 35 The total number of fibres in m. semi-tendinosus of adult horses.

Thoroughbreds			Breed	Other horses		
Live-weight (kg)	Sex	Fibre numbers (x 1,000)		Live-weight (kg)	Sex	Fibre numbers (x 1,000)
445	♀	1,140	Shetland	157	♂	548
471	♀	2,242	Welsh Mt.	178	♂	610
471	♀	1,245	Shetland	204	♂	783
484	♀	1,598	Welsh Mt.	229	♀	798
509	♂	2,136	Shetland	280	♂	1,127
			Connemara X	305	♀	838
			Arab	305	♀	899
			Connemara X	318	♀	610
			Piebald	318	♀	971
			Exmoor	356	♂	1,029
			Connemara X	445	♀	887
			Pony	480	♂	636
			Clydesdale	496	♀	1,168
			(Mean	313		839)
			(SD	109		20)
			Thoroughbred X	356	♀	739
			Thoroughbred X	369	♂	1,516
			Thoroughbred X	433	♂	910
			Thoroughbred X	522	♂	1,171
			Thoroughbred X	535	♀	1,149
			(Mean	443		1,097)
			(SD	83		294)
Mean	476	1,672		349		910
SD	23	503		117		251

The means of the Thoroughbred crosses are significantly greater ($P < 0.05$) than those of the other horses. The means of the other horses without the Thoroughbred crosses are significantly less ($P < 0.01$ for liveweight and $P < 0.001$ for total fibre numbers) than in the Thoroughbreds. There is no significant difference between the means of the Thoroughbred crosses and the Thoroughbreds. The means of the Thoroughbreds are significantly greater ($P < 0.05$ for liveweight and $P < 0.001$ for total fibre numbers) than the means of both types of other horses combined.

Table 36 Regression equations comparing the total number of fibres in m. semitendinosus with liveweight, and the TSA of m. semitendinosus with the mean fibre area of that muscle.

Independent variable	Dependent variable	Type of animal	Growth ratio b*	Se b	log a	r**	Significance *** of difference between groups
Total number of fibres	Body weight						
	33	Greyhounds	0.078	0.022	5.147	0.5316	Greyhounds
	26	Other dogs	0.101	0.023	4.813	0.6229	P<0.01
	28	Thoroughbreds	0.181	0.038	5.165	0.6774	Thoroughbreds
	30	Other horses	0.215	0.093	4.766	0.6877	P<0.01
TSA of m. semitendinosus	Mean fibre area						
	33	Greyhounds	1.088	0.031	5.179	0.9875	Greyhounds
	26	Other dogs	1.126	0.042	4.802	0.9840	P<0.01
	28	Thoroughbreds	1.185	0.053	5.497	0.9751	Thoroughbreds
	30	Other horses	1.258	0.107	5.021	0.9120	P<0.01

* Regression coefficient b, standard error Se b
 ** Correlation coefficient r
 *** Significance of the difference between groups tested by analysis of covariance;

Table 37 Predicted TSA and total fibre numbers of m. semitendinosus in dogs of 0.5 kg and 30 kg liveweight calculated from the logarithmic regression equations on Tables 33 & 36.

	Liveweight	
	0.5 kg	30 kg
<u>TSA (mm²)</u>		
Grevhounds		
Mean	36.0	1,008*
95% limits ⁺	(30.5 - 42.5)	(924 - 1,100)
Other dogs		
Mean	29.4	620*
95% limits ⁺	(23.3 - 37.0)	(510 - 754)
<u>Total fibre numbers (x 1,000)</u>		
Greyhounds		
Mean	228*	314*
95% limits ⁺	(195 - 267)	(288 - 341)
Other dogs		
Mean	122*	184*
95% limits ⁺	(104 - 141)	(163 - 208)
<u>Mean fibre area (µm²)</u>		
Grevhounds		
Mean	159*	3,248
95% limits ⁺	(134 - 188)	(2,975 - 3,547)
Other dogs		
Mean	254*	3,542
95% limits ⁺	(201 - 320)	(2,915 - 4,305)

+ Probability of a value outside these limits < 0.05.

* Values of predictions for similar muscles followed by this superscript are significantly different ($P < 0.05$) between each type of dog.

Table 38 TSA and total fibre numbers of m. semitendinosus in horses of 50 kg and 500 kg liveweight calculated from the logarithmic regression equations on Tables 33 & 36

	Liveweight	
	50 kg	500 kg
<u>TSA (mm²)</u>		
Thoroughbreds		
Mean	676	6,124*
95% limits ⁺	(592 - 772)	(4,703 - 7,974)
Other horses		
Mean	770	3,595*
95% limits ⁺	(683 - 869)	(3,188 - 4,053)
<u>Total fibre numbers (x 1000)</u>		
Thoroughbreds		
Mean	1,036*	1,572*
95% limits ⁺	(940 - 1,143)	(1,293 - 1,912)
Other horses		
Mean	597*	980*
95% limits ⁺	(512 - 698)	(840 - 1,144)
<u>Mean fibre area (µm²)</u>		
Thoroughbreds		
Mean	670*	4,435
95% limits ⁺	(595 - 753)	(3,713 - 5,298)
Other horses		
Mean	1,304*	3,710
95% limits ⁺	(1,132 - 1,502)	(3,246 - 4,240)

+ Probability of a value outside these limits < 0.05.

* Values of predictions for similar muscles followed by this superscript are significantly different (P < 0.05) between each type of horse.

Table 39 Mean fibre areas in μm^2 of m. semitendinosus, m. diaphragma and m. pectoralis transversus of dogs.

Type of animal	Live-weight (g)	Sex	m.semi-tendinosus	Mean fibre area in:		m.pectoralis transversus	(N*)
				(N*)	m.dia-phragma		
Greyhounds							
Young dogs	222	♂	116		253		233
	260		128		257		130
	377		141		163		160
	927		158		328		339
	1,056		263		410		321
	1,174		183		360		294
	2,280		479		420		361
	5,712		915		821		710
	11,000		1,500		1,179		1,250
	15,250		2,460		1,109		1,684
	19,750		2,155		1,488		1,569
23,500	2,595		2,193		2,604		
Adult Greyhounds							
All adults	Mean		3,179	21	1,801	10	3,468
	SD		546		361		473
Males	Mean		3,203	13	1,982	5	3,458
	SD		530		445		329
Females	Mean		3,140	8	1,621	5	3,531
	SD		605		120		548
Detained Adults	Mean		3,330	4	1,955	4	3,505
	SD		821		526		371
Trained adults	Mean		3,144	17	1,699	6	3,439
	SD		489		194		523
Other dogs							
Young dogs	464	♂	288		470		-
	527		252		675		571
	573		335		455		-
	785		233		344		339
	931		303		562		423
	976		379		469		358
	1,010		232		438		598
	1,235		472		617		623
	3,180		938		-		-
	3,843		716		617		798
	6,000		1,687		781		967
	6,585		1,232		1,237		1,450
	7,960		1,870		-		-
	8,500		1,841		1,542		1,618
	9,023		2,370		1,071		1,532
9,900	1,931		1,933		1,913		
Adult other dogs							
All adults	Mean		2,602	10	1,427	7	3,111
	SD		552		199		1,456
Males	Mean		2,767	3	1,534	2	3,763
	SD		410		361		123
Females	Mean		2,532	7	1,385	5	2,720
	SD		618		138		1,564

N* Number of adult samples.

Table 40 Logarithmic regression equations comparing the mean fibre area of m. semitendinosus, m. diaphragma and m. pectoralis transversus with liveweight in the dog and horse.

Dependent variable	Number of observations	Type of animal	Growth ratio b*	Se b	log a	r**	Significance of difference between groups ***
Mean fibre area of m. Semitendinosus	33	Greyhounds	0.737 c	0.023	0.212	0.9847	NS
	26	Other dogs	0.644 c	0.042	0.666	0.9534	
	34	Thoroughbreds	0.821 d	0.039	-1.032	0.9659	NS
	32	Other horses	0.454 d	0.038	0.982	0.9072	
Mean fibre area of m. diaphragma	22	Greyhounds	0.463 c	0.024	1.181	0.9738	NS
	21	Other dogs	0.349 c	0.036	1.690	0.9110	
	23	Thoroughbreds	0.789 d	0.047	-0.936	0.9644	NS
	23	Other horses	0.504 d	0.049	0.647	0.9139	
Mean fibre area of m. pectoralis transversus	21	Greyhounds	0.661	0.034	0.532	0.9763	Other dogs P<0.01
	20	Other dogs	0.579	0.047	0.950	0.9501	
	30	Thoroughbreds	0.871 d	0.064	-1.232	0.9330	NS
	34	Other horses	0.517 d	0.056	0.712	0.8514	

* Regression coefficient b, standard error Se b

c,d Values of b bearing these superscripts within each muscle of dogs and horses respectively, are significantly different (P<0.05) from one another

** Correlation coefficient r

*** Significance of difference between groups tested by analysis of covariance;

NS Not significant.

Table 41 Mean fibre areas (in μm^2) of m. semitendinosus, m. diaphragma and m. pectoralis transversus of dogs at 0.5 kg and 30 kg liveweight calculated from the allometric equations on Table 40.

	Liveweight	
	0.5 kg	30 kg
M. semitendinosus		
Greyhounds		
Mean	159*	3,248
95% limits ⁺	(134 - 188)	(2,975 - 3,547)
Other dogs		
Mean	254*	3,542
95% limits ⁺	(201 - 320)	(2,915 - 4,305)
M. diaphragma		
Greyhounds		
Mean	270*	1,794
95% limits ⁺	(229 - 317)	(1,602 - 2,010)
Other dogs		
Mean	429*	1,789
95% limits ⁺	(354 - 518)	(1,487 - 2,152)
M. pectoralis transversus		
Greyhounds		
Mean	207	3,100
95% limits ⁺	(166 - 258)	(2,638 - 3,643)
Other dogs		
Mean	326	3,485
95% limits ⁺	(249 - 426)	(2,825 - 4,300)

+ Probability of a value outside these limits < 0.05 .

* Values of predictions for similar muscles followed by this superscript are significantly different ($P < 0.05$) between each type of dog.

Table 42 Mean fibre areas in μm^2 of m. semitendinosus, m. diaphragma and m. pectoralis transversus of horses.

Type of animal	Live-weight (g)	Sex	Mean fibre area in:			(N*)		
			m.semi-tendinosus	m.dia-phragma	m.pector-alis trans-versus			
Thoroughbreds								
Young horses	11,000	♀	265	244	161			
	13,429	♀	115	-	-			
	16,000	♂	194	273	332			
	19,000	♀	233	382	319			
	23,872	♂	329	398	407			
	24,000	♀	512	357	448			
	28,000	♂	420	-	408			
	29,000	♂	320	372	378			
	30,965	♀	390	354	414			
	31,500	♂	442	-	648			
	32,000	♀	493	318	468			
	33,500	♂	524	264	302			
	34,500	♀	368	-	-			
	34,800	♀	435	-	-			
	38,636	♂	1,146	572	1,149			
	39,000	♂	583	-	309			
	40,500	♀	1,101	763	852			
	42,000	♂	426	366	418			
	42,962	♀	856	516	1,208			
	50,000	♀	434	320	568			
	58,664	♀	716	-	1,044			
	337,000	♀	2,967	1,978	2,328			
	420,000	♂	3,513	3,670	-			
	432,727	♂	2,821	2,392	3,584			
Adult Thoroughbreds								
All adults	Mean		4,675	10	4,246	6	4,664	10
	SD		1,350		1,250		897	
Entire males	Mean		4,277	2	3,926	1	4,236	2
	SD		113		-		362	
Castrated males	Mean		-		3,109	1	4,310	1
	SD		-		-		-	
Females	Mean		4,649	8	4,610	4	4,836	7
	SD		1,469		1,400		1,034	
Detrained adults	Mean		5,498	4	-		5,286	2
	SD		1,653		-		1,122	
Trained adults	Mean		4,126	6	4,246	6	4,508	8
	SD		859		1,250		846	
Other horses								
Young horses	2,150	♂	503	283	425			
	2,977	♂	372	243	442			
	22,000	♀	403	-	581			
	109,091	♂	1,916	1,135	2,090			
	114,546	♀	1,925	2,222	1,842			
	118,182	♂	2,196	1,473	2,809			
	153,727	♂	2,674	2,061	1,715			
	178,182	♂	2,959	-	5,208			
	207,273	♂	3,040	2,451	2,278			
T'bred X	39,000	♀	916	386	582			
T'bred X	62,000	♀	1,010	-	882			
T'bred X	203,636	♀	1,263	1,305	1,136			
Adult other horses								
All adults	Mean		3,285	20	2,901	14	4,424	22
	SD		757		734		1,814	
Thoroughbred crosses	Mean		3,365	5	3,289	3	3,821	6
	SD		921		1,173		876	
Other adults	Mean		3,258	15	2,796	11	4,654	16
	SD		730		607		2,057	
Entire males	Mean		3,541	3	3,024	2	3,454	1
	SD		432		677		-	
Castrated males	Mean		3,502	9	2,974	7	4,671	10
	SD		951		852		2,027	
Females	Mean		2,944	8	2,751	5	4,293	11
	SD		498		709		1,778	

N* Number of adult samples.

T'bred X Thoroughbred cross.

Table 43 Mean fibre areas in μm^2 of m. semitendinosus, m. diaphragma and m. pectoralis transversus of horses at 50 kg and 500 kg liveweight calculated from the allometric equations on Table 40.

	Liveweight	
	50 kg	500 kg
M. semitendinosus		
Thoroughbreds		
Mean	670*	4,435
95% limits ⁺	(595 - 753)	(3,713 - 5,298)
Other horses		
Mean	1,304*	3,710
95% limits ⁺	(1,132 - 1,502)	(3,246 - 4,240)
M. diaphragma		
Thoroughbreds		
Mean	591*	3,635
95% limits ⁺	(511 - 684)	(2,913 - 4,537)
Other horses		
Mean	1,036*	3,306
95% limits ⁺	(809 - 1,326)	(2,534 - 4,314)
M. pectoralis transversus		
Thoroughbreds		
Mean	726*	5,393
95% limits ⁺	(597 - 883)	(4,056 - 7,172)
Other horses		
Mean	1,384*	4,554
95% limits ⁺	(1,103 - 1,738)	(3,666 - 5,654)

+ Probability of a value outside these limits < 0.05 .

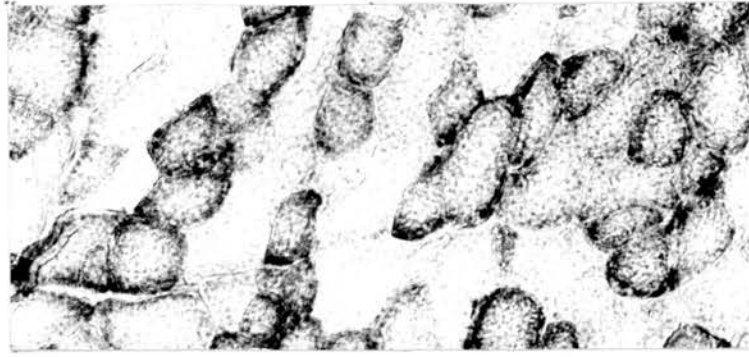
* Values of predictions for similar muscles followed by this superscript are significantly different ($P < 0.05$) between each type of horse.

Figs. 23 - 26.

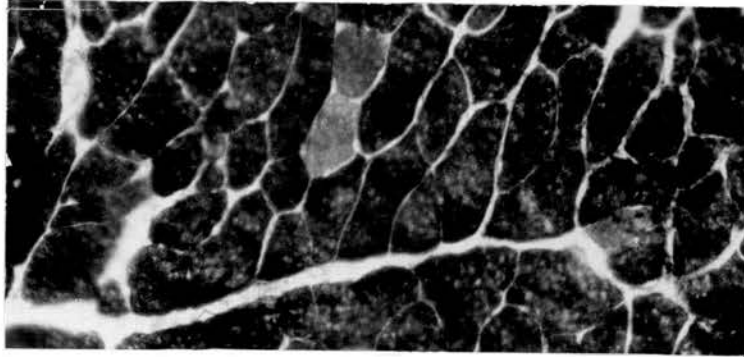
Transverse serial fresh frozen sections from the caudal superficial region of m. semitendinosus from a 318 kg six year old Piebald pony mare, demonstrating SDHase (Fig. 23), GPase (Fig. 24), myosin ATPase (Fig. 25) and fibre outlines with Erlich's haematoxylin (Fig. 26).

AH.SH.PH., AH.SL.PH. and AL.SH.PH fibres are apparent.

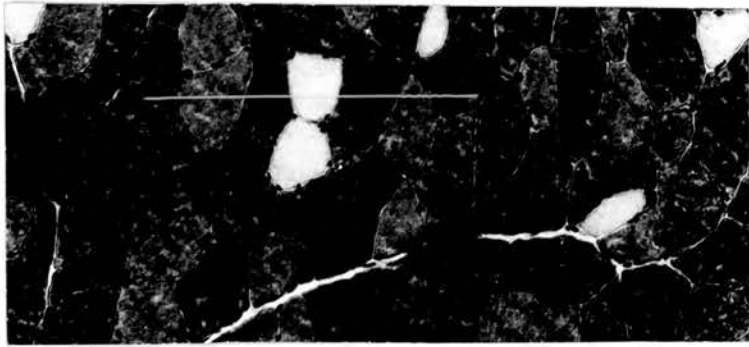
23



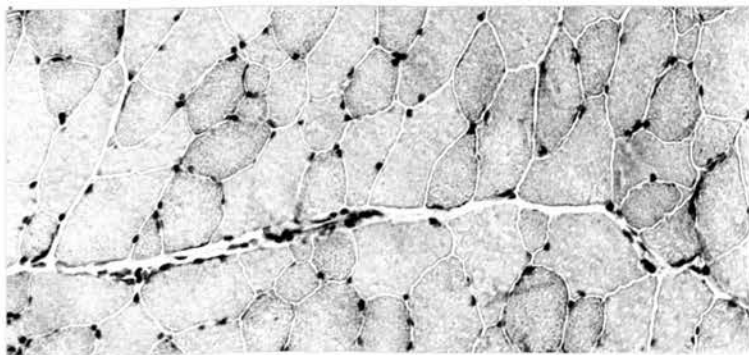
24



25



26



100 μ m

Figs. 27 - 29.

Transverse serial fresh frozen sections from the caudal superficial region of m. semitendinosus from a 318 kg six year old Piebald pony mare, demonstrating SDHase (Fig. 27), GPase (Fig. 28) and myosin ATPase (Fig. 29) activity. These coloured photographs correspond to Figs. 23, 24 and 25 respectively.



3 SLIDES

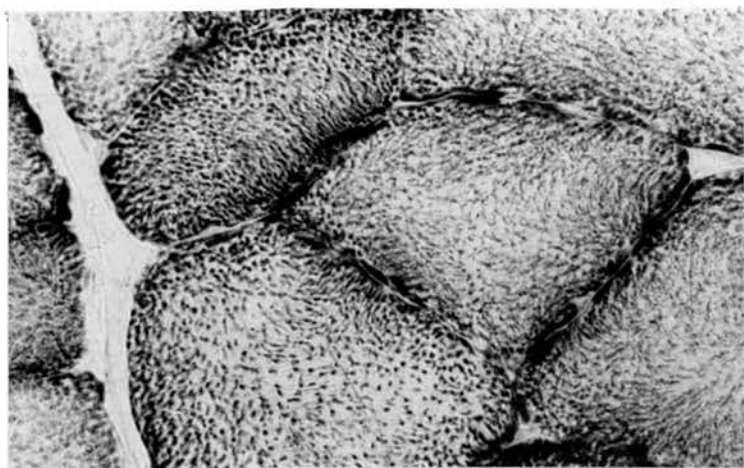
To-Go

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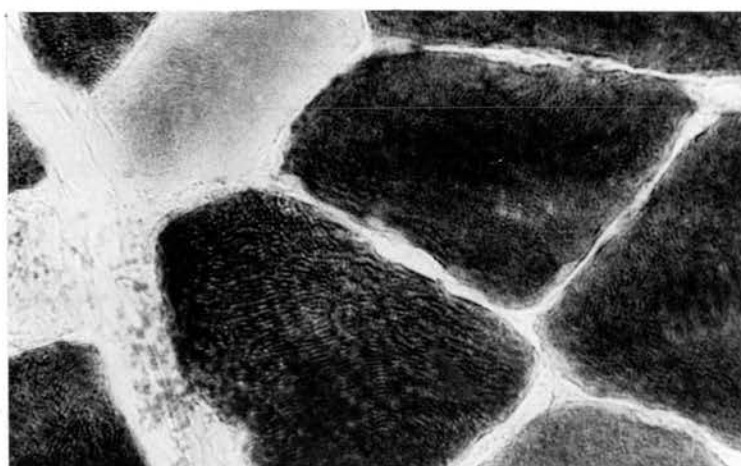
Figs. 30 - 32.

Transverse serial fresh frozen sections from the superficial region of m. pectoralis transversus of a 25 kg adult male Greyhound demonstrating SDHase (Fig. 30), GPase (Fig. 31) and myosin ATPase (Fig. 32) activity. The AH.SH.PH. fibres and AL.SH.PL. fibres show the disposition of the deposits from the reactions.

30



31



32



50 μ m

Figs. 33 and 34.

Transverse fresh frozen sections from the superficial region of m. pectoralis transversus of a 5 year old 25 kg detrained adult male Greyhound (Fig. 33) and from the superficial caudal region of m. semitendinosus of a 3 year old 458 kg Thoroughbred mare (Fig. 34) demonstrating capillaries.

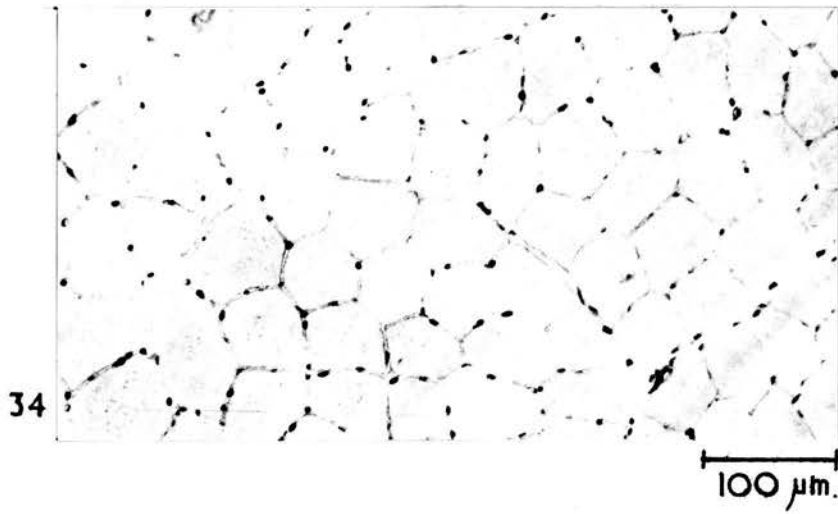
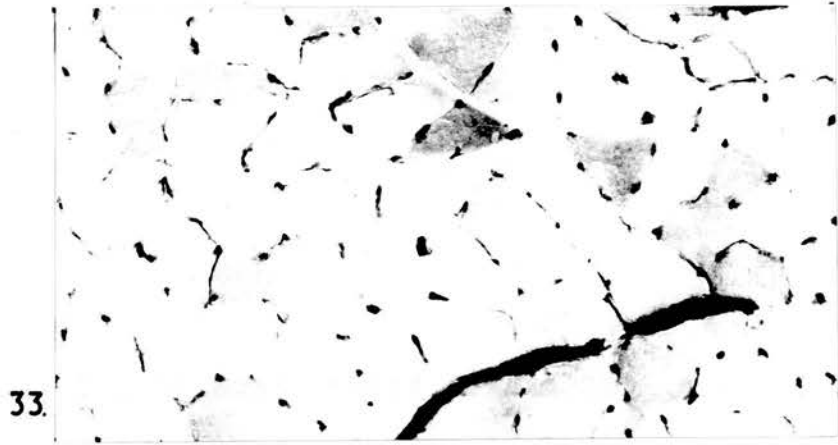


Table 44 QUANTITATIVE HISTOCHEMISTRY OF CANINE SKELETAL MUSCLE

Proportion of transverse section and transverse sectional areas of samples of m. semitendinosus, m. diaphragma and m. pectoralis transversus occupied by myosin ATPase low-reacting (AL) fibres.

GREYHOUNDS				OTHER DOGS					
Sex	Body weight (kg)	% AL numbers	% AL area	Breed	Sex	Body weight (kg)	% AL numbers	% AL area	
<u>MUSCULUS SEMITENDINOSUS</u>									
D*	19	1.8	1.6	Collie		8	22	22	
	22	1.3	0.92	Terrier X		10	20	14	
	24	9.7	5.0	Collie		11	28	18	
	25	3.4	3.3	Collie		12	34	27	
D*	25	1.7	1.1	Collie		14	19	13	
	25	2.5	1.9	Collie		22	12	10	
	25	2.1	1.6	Afghan		25	15	11	
	27	4.3	3.2	Afghan		32	10	7.0	
D*	28	2.1	1.6	Labrador		33	12	15	
	28	2.6	1.1	Great Dane		47	8.9	5.4	
	29	2.7	2.1						
	29	0.97	0.82						
D*	30	0.52	0.58						
	30	0.33	0.32						
	30	2.5	1.5						
	31	5.3	5.1						
	31	2.5	2.8						
	34	4.8	3.3						
	34	3.1	1.2						
	34	4.5	2.8						
	37	4.8	3.3						
	Mean	3.00	2.2			Mean	18.1	14.2	
	SD	2.1	1.3			SD	8.2	6.7	
<u>MUSCULUS DIAPHRAGMA</u>									
D*	24	39	25	Terrier X		10	46	47	
	25	29	23	Collie		11	55	72	
D*	25	27	31	Collie		12	52	42	
	25	16	13	Collie		14	54	41	
D*	29	23	13	Collie		22	59	48	
	30	20	27	Afghan		25	42	49	
D*	30	19	16	Afghan		32	60	59	
	34	29	30						
	34	30	27						
	37	34	29						
	Mean	26.6	23.4			Mean	52.6	51.1	
	SD	7.1	6.9			SD	6.6	10.9	
<u>MUSCULUS PECTORALIS TRANSVERSUS</u>									
D*	24	42	22	Terrier X		10	56	56	
	25	14	12	Collie		11	60	78	
D*	25	16	13	Collie		12	56	56	
	25	12	9	Collie		14	47	38	
D*	29	13	9	Collie		22	56	48	
	30	12	6	Afghan		25	42	36	
D*	30	17	17	Afghan		32	51	48	
	34	18	11	Great Dane		47	50	44	
	37	25	20						
	Mean	18.8	13.2				Mean	52.3	50.5
	SD	9.6	5.4			SD	5.9	13.3	

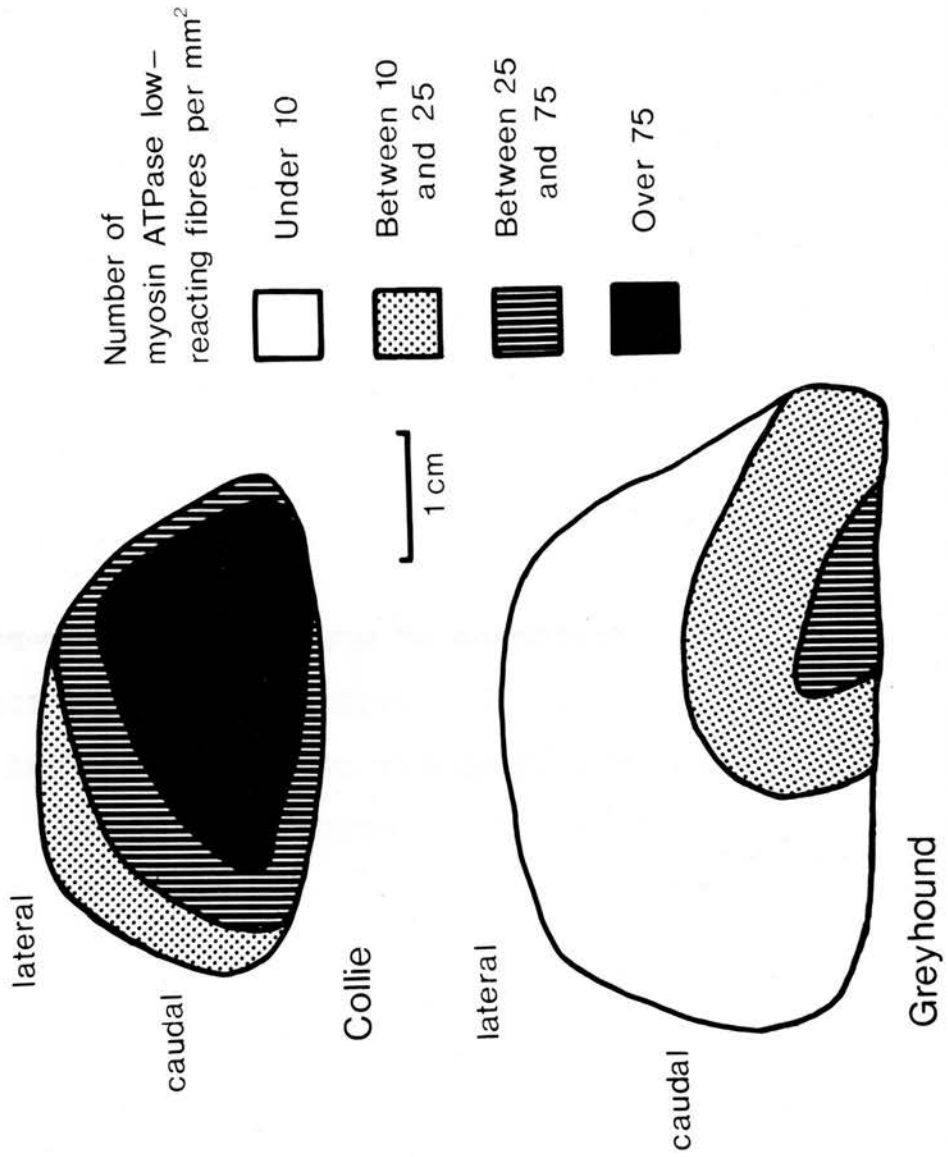
Difference between the means of % AL numbers and % AL areas for the same muscle in the two types of dog are significant at the 0.1% level.

D* Detained Greyhounds.

Fig. 35.

The incidence of myosin ATPase low-reacting (AL) fibres in the complete transverse section of m. semitendinosus of a Greyhound and Collie both adapted for a liveweight of 30 kg.

DENSITY OF MYOSIN ATPase LOW-REACTING
 FIBRES IN COMPLETE TRANSVERSE SECTIONS
 OF M. SEMITENDINOSUS OF DOGS OF 30 KG. BODY WEIGHT



Figs. 36 and 40.

Transverse fresh frozen sections from the superficial caudal (Fig. 36) and deep medial (Fig. 40) region of m. semitendinosus of a 28 kg, 3 year old male Greyhound demonstrating ATPase activity.

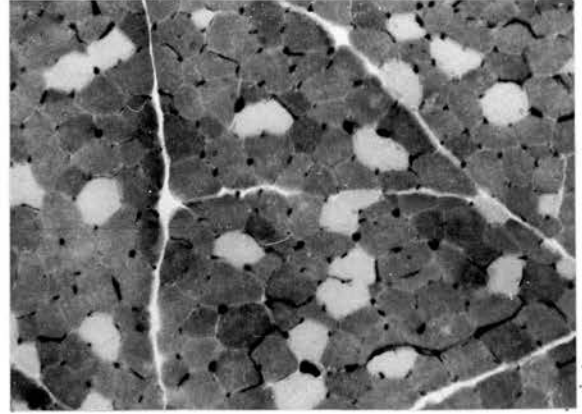
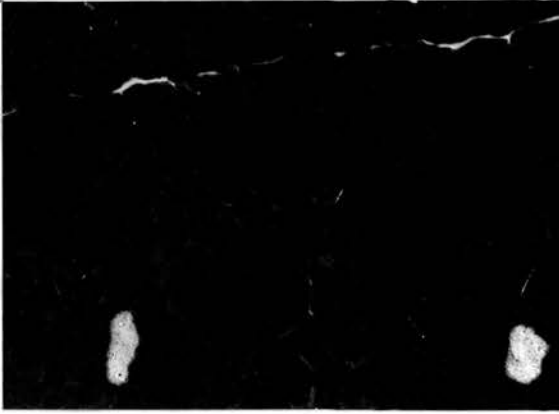
Figs. 37 - 39.

Transverse fresh frozen serial sections from the superficial caudal region of m. semitendinosus of an 8 kg, two year old Collie bitch; demonstrating myosin ATPase (Fig. 37), SDHase (Fig. 38) and GPase (Fig. 38) activity. AH.SH.PH. and AL.SH.PL. fibres are apparent.

Fig. 41.

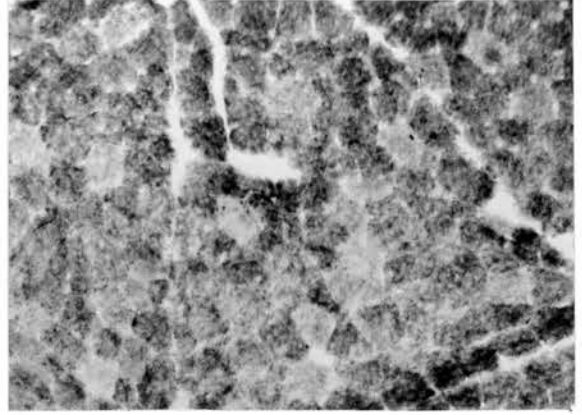
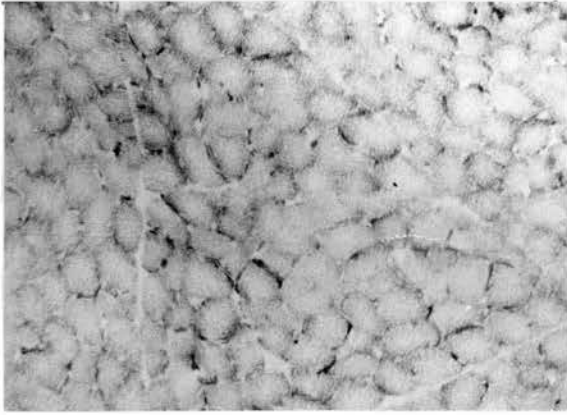
Transverse fresh frozen section from the deep medial region of m. semitendinosus from the same transverse section as Fig. 37.

36



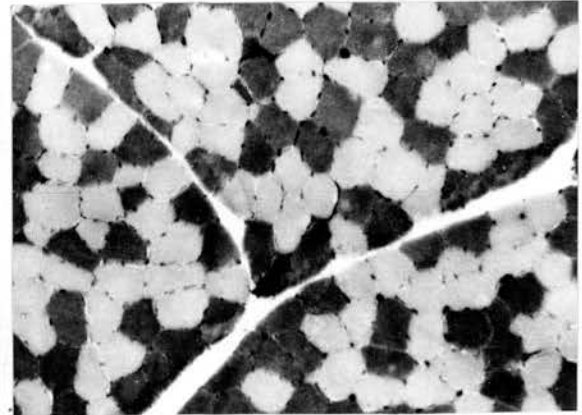
37

38



39

40



41

100μm

Fig. 42.

Transverse fresh frozen section from m. diaphragma of a 25 kg adult male Greyhound demonstrating myosin ATPase activity.

Fig. 43.

Transverse fresh frozen section from m. diaphragma of a four year old 32 kg adult male Afghan demonstrating myosin ATPase activity.

Figs. 44, 46 and 47.

Transverse serial fresh frozen sections from m. pectoralis transversus of a 25 kg adult male Greyhound demonstrating the activity of myosin ATPase (Fig. 44) SDHase (Fig. 46) and GPase (Fig. 47).

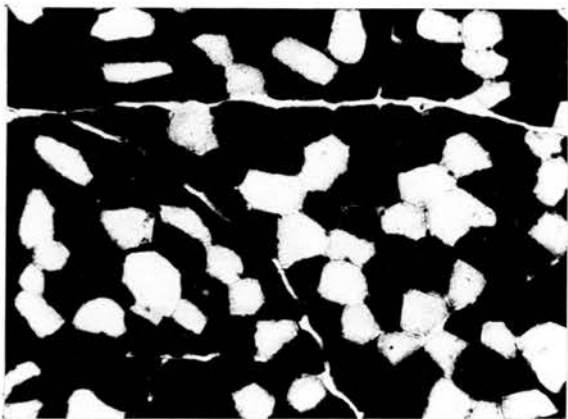
Fibres are either AH.SH.PH. or AL.SH.PL.

Figs. 30 - 32 and 42 are also from the same animal.

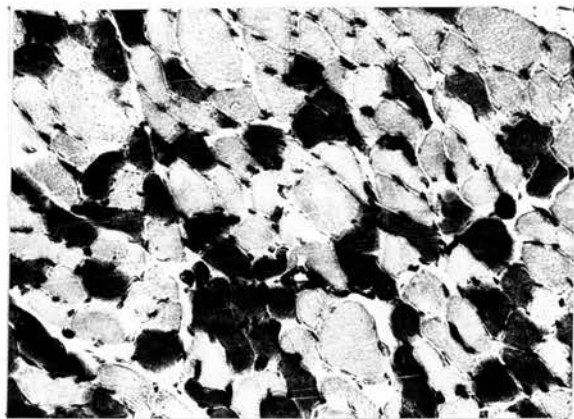
Fig. 45.

Transverse fresh frozen section from m. pectoralis transversus of a 10 year old, 22 kg female Collie demonstrating myosin ATPase activity.

42.



43



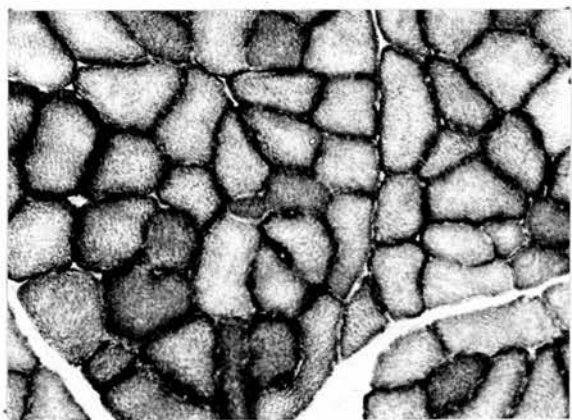
44.



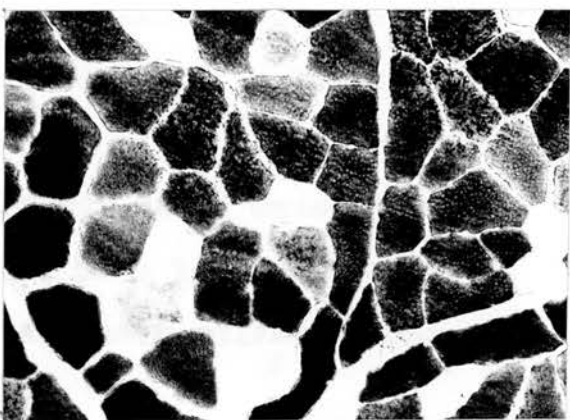
45



46.



47



100μm

Table 45 QUANTITATIVE HISTOCHEMISTRY OF EQUINE SKELETAL MUSCLE

Proportion of transverse section and transverse sectional areas of samples of m. semitendinosus, m. diaphragma and m. pectoralis transversus occupied by myosin ATPase low-reacting (AL) fibres.

THOROUGHBREDS				OTHER HORSES				
Sex	Body weight (kg)	% AL numbers	% AL area	Breed	Sex	Body weight (kg)	% AL numbers	% AL area
<u>MUSCULUS SEMITENDINOSUS</u>								
	445	4.4	2.0	Shetland	♂	154	13	5.1
	458	2.8	2.7	Welsh Mountain	♂	178	19	7.7
	471	5.3	1.7	Shetland	♂	204	12	7.8
D*	471	6.2	2.8	Welsh Mountain	♂	229	8.4	4.4
	484	10	5.5	Shetland	♂	280	20	9.6
	484	7.8	3.6	Connemara X	♂	305	12	7.9
D*	535	3.8	3.8	Arab	♂	305	15	7.0
D*	560	0.15	0.25	Connemara X	♂	318	12	11
D*	598	5.7	3.4	Piebald	♂	318	13	7.1
				Thoroughbred X	♂	356	11	6.5
				Exmoor X	♂	356	15	13.0
				Thoroughbred X	♂	369	12	5.0
				Thoroughbred X	♂	433	10	4.7
				Connemara X	♂	445	13	8.0
				Welsh Mountain	♂	458	12	9.1
				Exmoor X	♂	480	4.6	2.5
				Connemara X	♂	480	19	6.1
				Clydesdale	♂	496	14	9.3
				Thoroughbred X	♂	522	9.1	2.9
				Thoroughbred X	♂	535	6.6	3.0
	Mean	5.1	2.9			Mean	12.5	6.9
	SD	2.8	1.5			SD	3.9	2.8

Difference between means of % AL numbers and % AL areas is significant at the 0.1% level.

<u>MUSCULUS DIAPHRAGMA</u>								
	445	73	73	Shetland	♂	154	73	83
	458	58	61	Welsh Mountain	♂	178	68	73
	471	61	70	Shetland	♂	204	79	82
	496	67	69	Welsh Mountain	♂	229	63	75
	509	74	78	Shetland	♂	280	74	84
	585	68	69	Arab	♂	305	62	72
				Connemara X	♂	318	76	81
				Piebald	♂	318	69	75
				Thoroughbred X	♂	369	61	64
				Welsh Mountain	♂	458	83	84
				Connemara X	♂	480	77	78
				Clydesdale	♂	496	76	76
				Thoroughbred X	♂	522	70	73
				Thoroughbred X	♂	535	67	30
	Mean	66.8	70			Mean	71.3	73.4
	SD	6.4	5.6			SD	6.7	13.8

There is no significant difference between the means of the % AL numbers and % AL areas of the two types of horse.

<u>MUSCULUS PECTORALIS TRANSVERSUS</u>								
	445	27	15	Shetland	♂	154	49	38
	458	25	16	Welsh Mountain	♂	178	50	45
	471	29	10	Shetland	♂	204	37	32
D*	471	25	10	Welsh Mountain	♂	229	30	21
	484	29	18	Shetland	♂	280	43	34
	484	30	21	Pony	♂	305	38	28
D*	496	36	21	Arab	♂	305	38	36
D*	509	29	13	Connemara X	♂	318	47	37
	535	37	26	Piebald	♂	318	54	35
	585	36	23	Thoroughbred X	♂	356	37	29
				Pony	♂	356	46	34
				Thoroughbred X	♂	369	47	32
				Pony	♂	407	55	58
				Pony	♂	420	54	50
				Thoroughbred X	♂	433	33	21
				Connemara	♂	445	60	54
				Exmoor X	♂	480	22	14
				Clydesdale	♂	496	42	31
				Thoroughbred X	♂	521	45	38
				Thoroughbred X	♂	535	41	20
				Percheron X	♂	535	47	40
				Thoroughbred X	♂	560	44	32
	Mean	30.3	17.3			Mean	43.6	34.5
	SD	4.5	5.5			SD	8.9	10.8

Difference between means of % AL numbers and % AL areas is significant at the 0.1% level.

D* Horses out of training.

Table 46 The mean proportional numbers and areas of AL fibres in m. semitendinosus, m. diaphragma and m. pectoralis transversus of adult Thoroughbreds, adult Thoroughbred crosses and adult other horses and a comparison between corresponding values of the three types of horse using Student's 't' test.

	Number of observ- ations		% AL numbers	% AL areas
M. Semitendinosus.				
Thoroughbreds	9	Mean	5.13 b	3.03
		SD	2.85	1.58
Thoroughbred crosses	5	Mean	9.80 b	4.60 a
		SD	1.92	1.67
Other horses	15	Mean	13.5	7.73 a
		SD	3.96	2.60
M. Diaphragma.				
Thoroughbreds	6	Mean	66.8	70.0
		SD	6.37	5.59
Thoroughbred crosses	3	Mean	66.0	55.7 b
		SD	4.58	22.7
Other horses	11	Mean	72.7	78.3 b
		SD	6.57	4.82
M. Pectoralis transversus.				
Thoroughbreds	10	Mean	30.3 d	17.3 c
		SD	4.50	5.46
Thoroughbred crosses	6	Mean	41.2 d	28.7 c
		SD	5.31	6.98
Other horses	16	Mean	44.5	36.7
		SD	9.87	11.3

a,b,c,d, Values followed by the same superscript within a muscle are significantly different ($P < 0.025$; $P < 0.01$; $P < 0.005$ and $P < 0.001$ respectively) from one another.

Table 47 The incidence of fibre types in musculus semitendinosus of the adult horse as differentiated by the succinate dehydrogenase reaction.

THOROUGHBREDS		OTHER HORSES						
Sex	Body weight (kg)	% SH**	% AH.SH***	Breed	Sex	Body weight (kg)	% SH**	% AH.SH***
♀	458	100	97	Shetland	♂	154	54	41
♂	471	63	58	Welsh Mountain	♂	178	55	36
♂	484	58	48	Shetland	♂	204	34	22
D*	535	42	38	Welsh Mountain	♀	229	46	38
D*	560	99	99	Shetland	♂	280	51	31
D*	598	74	68	Connemara X	♀	305	46	34
				Arab	♀	305	58	43
				Piebald	♀	318	62	49
				Thoroughbred X	♀	318	62	49
				Exmoor X	♂	356	52	41
				Thoroughbred X	♂	356	82	67
				Thoroughbred X	♂	369	38	26
				Thoroughbred X	♂	433	76	66
				Connemara	♀	445	80	67
				Welsh Mountain	♂	458	100	88
				Exmoor X	♂	480	43	38
				Connemara X	♂	480	83	64
				Clydesdale	♀	496	65	51
				Thoroughbred X	♂	522	79	70
				Thoroughbred X	♀	535	51	44
				All adult other horses		Mean	60.8	48.2
						SD	17.9	17.5
				Thoroughbred cross adults		Mean	59.2	49.4
						SD	17.6	18.4
				Trained Thoroughbreds		Mean	61.4	18.6
						SD	47.8	17.9

Difference between means of the percentage of SH fibres is not significant between types.
 Difference between means of the percentage of AH SH fibres is significantly different (P < 0.05) between types.

- D* Horses out of training.
- ** Fibres having a high reaction for succinate dehydrogenase.
- *** Fibres having a high reaction for both myosin ATPase and succinate dehydrogenase.

Figs. 48 and 49.

Transverse fresh frozen serial sections from the superficial caudal region of m. semitendinosus of a 458 kg 3 year old Thoroughbred mare demonstrating myosin ATPase (Fig. 48) and SDHase (Fig. 49) activity.

Figs. 50 and 51.

Transverse fresh frozen serial sections from the deep medial region of m. semitendinosus from the same animal as Figs. 48 and 49, demonstrating myosin ATPase (Fig. 50) and SDHase (Fig. 51) activity.

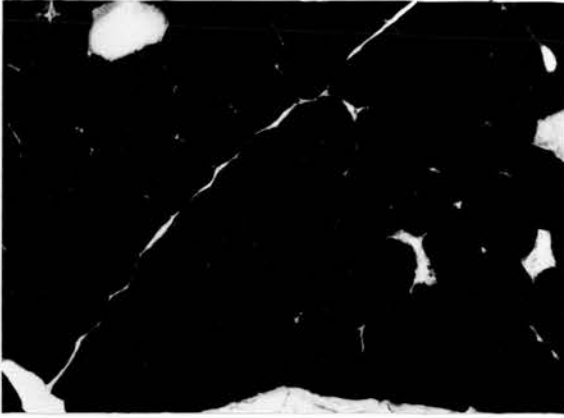
Figs. 52 and 53.

Transverse fresh frozen serial sections from the superficial caudal region of m. semitendinosus of a 318 kg six year old Piebald pony mare demonstrating myosin ATPase (Fig. 52) and SDHase (Fig. 53) activity.

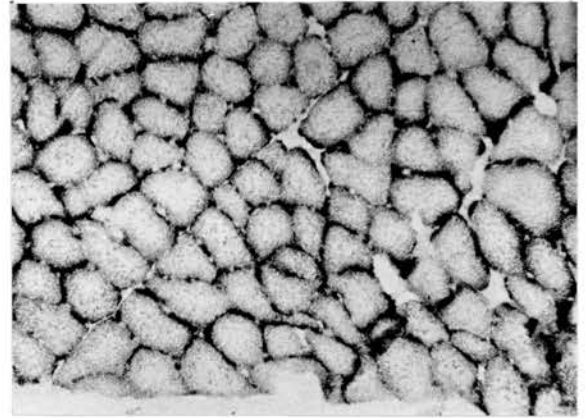
Figs. 54 and 55.

Transverse fresh frozen serial sections from the deep medial region of m. semitendinosus from the same animal as Figs. 52 and 53 and also Figs. 23 - 29, demonstrating myosin ATPase (Fig. 54) and SDHase (Fig. 55) activity.

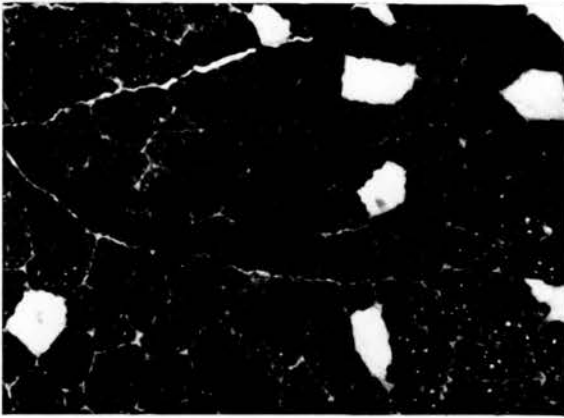
48.



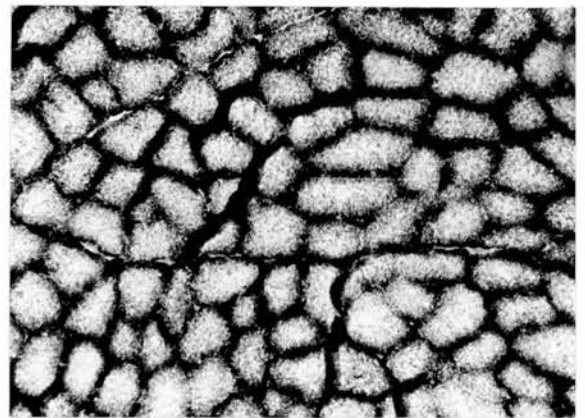
49



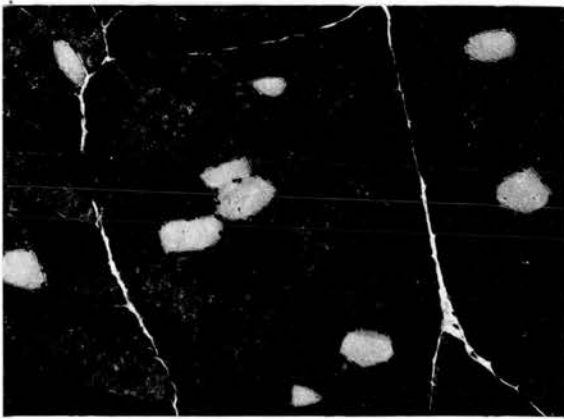
50



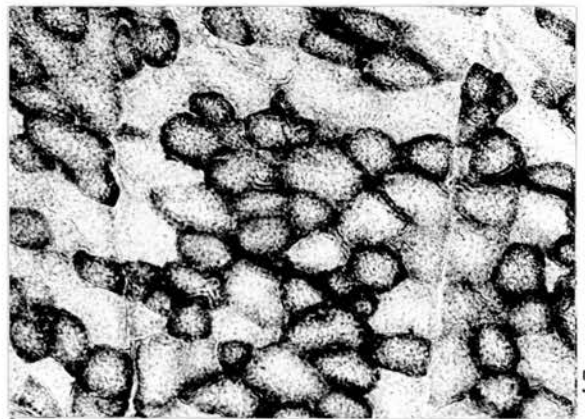
51



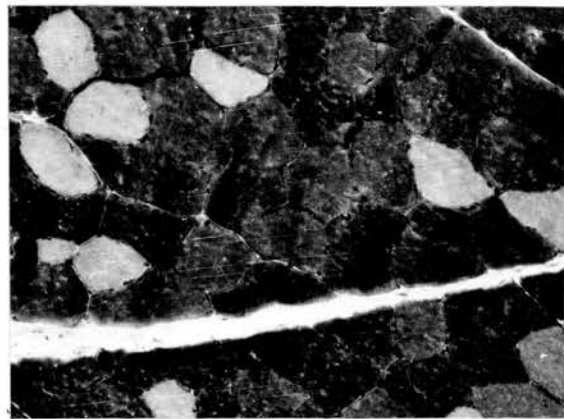
52.



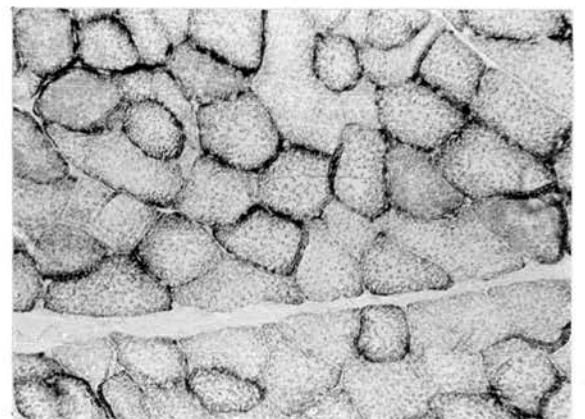
53



54



55



100μm

Fig. 56.

Transverse fresh frozen section from m. diaphragma of a 458 kg, three year old Thoroughbred mare demonstrating myosin ATPase activity.

Figs. 57 - 59.

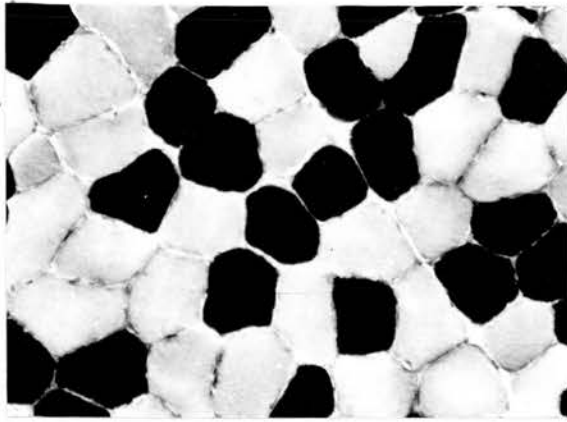
Transverse fresh frozen serial sections from m. diaphragma of a 318 kg six year old Piebald pony mare demonstrating myosin ATPase (Fig. 56), SDHase (Fig. 57) and GPase (Fig. 58) activity. Some AL fibres have a lower GPase activity than AH fibres.

Figs. 60, 62 and 63.

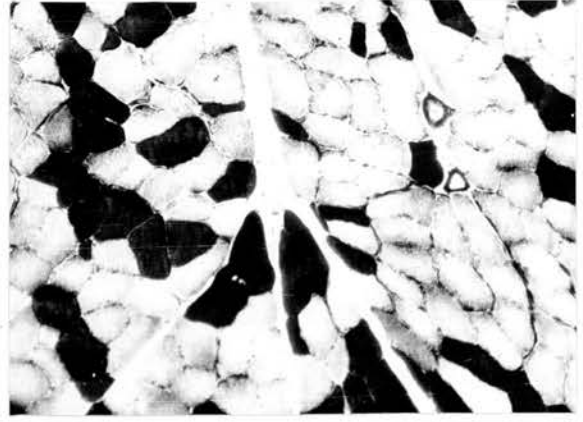
Transverse fresh frozen serial sections from m. pectoralis transversus of a 458 kg, three year old Thoroughbred mare demonstrating myosin ATPase (Fig. 60) SDHase (Fig. 62) and GPase (Fig. 63) activity. These sections are taken from the same animal as Figs. 48 - 51 and 56.

Fig. 61

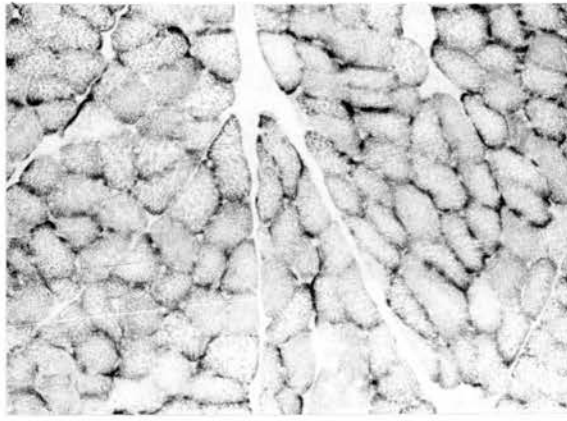
Fresh frozen transverse section from m. pectoralis transversus of a 318 kg, six year old Piebald mare demonstrating myosin ATPase activity. This section is taken from the same animal as those for Figs. 23 - 29, 52 - 55 and 57 - 59.



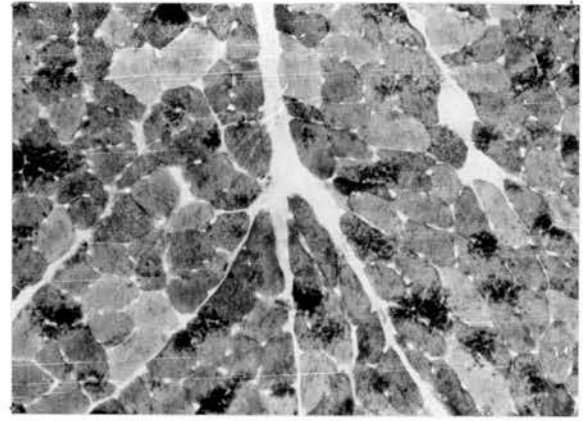
56



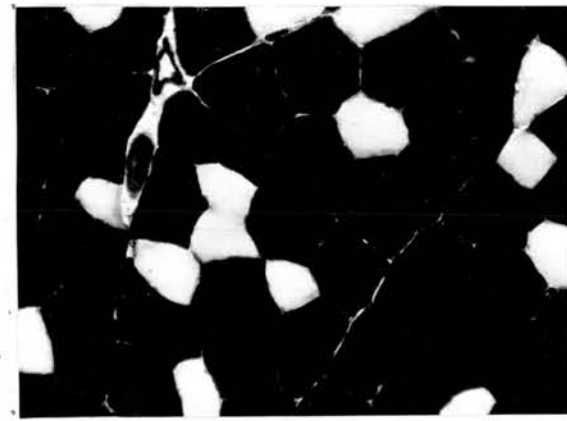
57



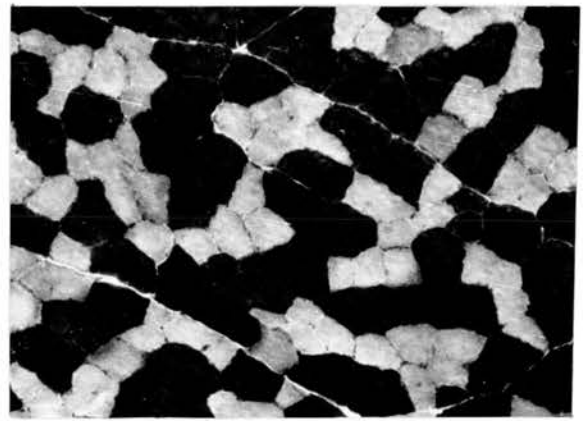
58



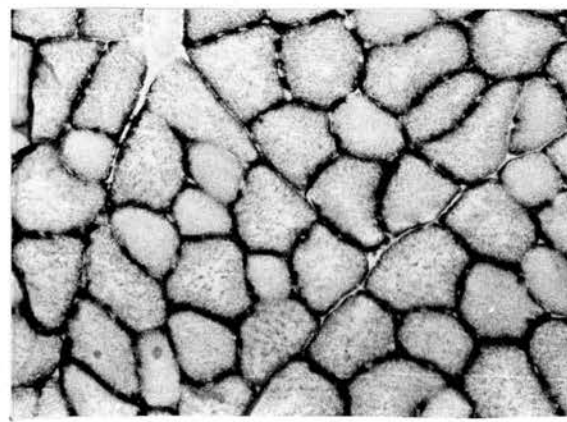
59



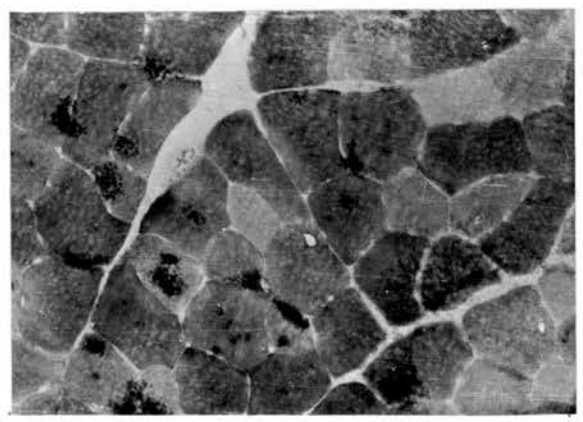
60



61



62



63

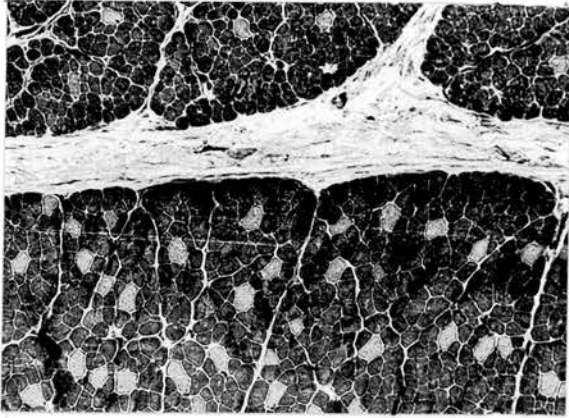
100μm

Figs. 64 - 66.

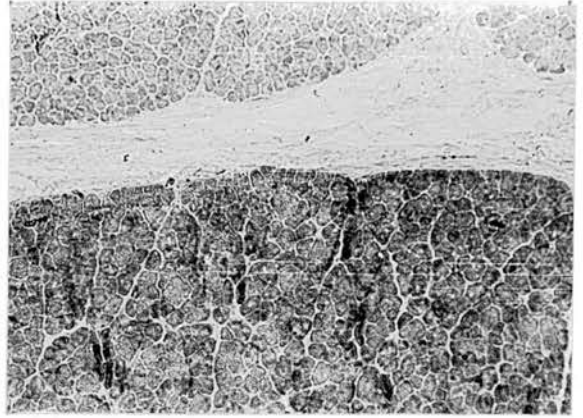
Transverse fresh frozen serial sections from the superficial caudal region of m. semitendinosus and m. diaphragma of a 0.46 kg, two day old male Labrador demonstrating myosin ATPase (Fig. 64), SDHase (Fig. 65) and GPase (Fig. 66) activity.

Figs. 67 - 69.

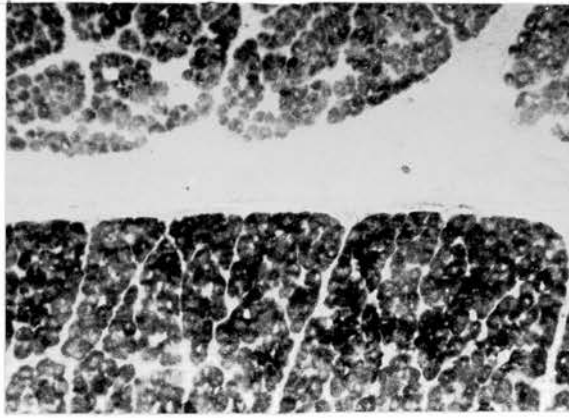
Transverse fresh frozen serial sections from the superficial region of m. pectoralis transversus of a 0.26 kg neonatal male Greyhound demonstrating myosin ATPase (Fig. 67), SDHase (Fig. 68) and GPase (Fig. 69) activity.



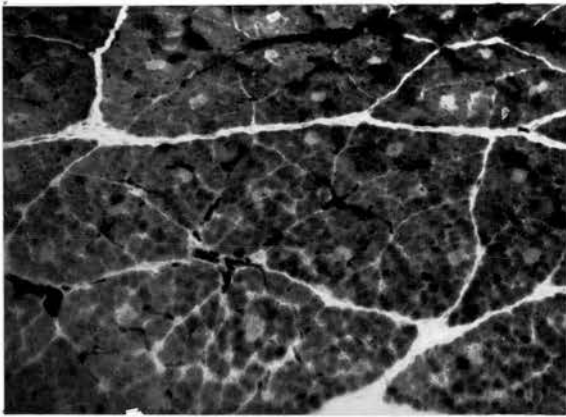
64



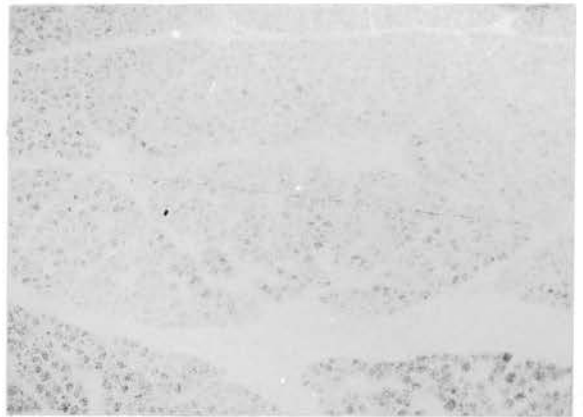
65



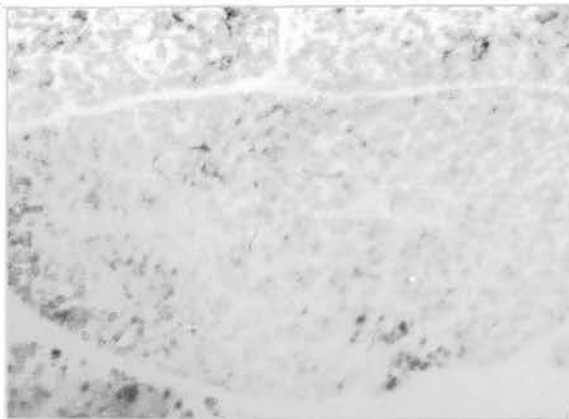
66



67



68



69

100μm

Table 48 Percentage number of, and area of, myosin ATPase low-reacting fibres in m. semitendinosus, m. diaphragma and m. pectoralis transversus of young dogs.

Type of dog	Live-weight (kg)	Age (days)	Myosin ATPase low-reacting (AL) fibres					
			m. semitendinosus		m. diaphragma		m. pectoralis transversus	
			% Numbers	% Area	% Numbers	% Area	% Numbers	% Area
Greyhound	0.222	1	3.0	4.2	7.5	9.8	6.1	4.3
Greyhound	0.260	1	1.8	3.50	4.4	8.10	2.02	2.9
Greyhound	0.377	7	1.9	4.4	3.4	7.6	2.3	5.6
Greyhound	0.927	1	2.0	2.3	8.2	6.2	4.2	2.6
Greyhound	1.06	14	1.6	2.8	8.1	8.9	2.4	3.2
Greyhound	1.17	21	1.5	4.3	16.0	34.0	2.4	4.5
Greyhound	2.28	42	22.02	22.0	36.0	40.0	23.0	28.0
Greyhound	5.71	77	20.02	14.0	27.0	24.0	28.0	23.0
Greyhound	11.0	119	16.01	11.0	32.0	16.0	29.0	17.0
Greyhound	15.3	168	8.7	8.2	33.0	23.0	23.0	22.0
Greyhound	19.8	175	8.1	6.7	35.0	31.0	30.0	27.0
Greyhound	23.5	365	7.9	5.7	39.0	24.0	23.0	13.0
Labrador	0.464	2	4.0	4.4	8.7	11.0	*	*
Collie X	0.527	14	4.0	4.7	9.3	9.5	5.7	6.1
Labrador	0.573	2	3.6	3.8	6.2	6.7	*	*
Collie X	0.785	23	6.2	7.4	38.0	40.0	24.0	21.0
Collie X	0.931	21	7.0	7.9	36.0	38.0	22.0	33.0
Collie	0.976	42	29.2	21.0	45.0	39.0	41.0	44.0
Labrador	1.01	14	3.04	4.0	16.0	14.0	13.0	14.0
Collie X	1.24	35	16.2	17.0	39.0	33.0	40.0	30.0
Collie X	3.18	106	43.9	30.0	*	*	*	*
Collie X	3.84	106	26.2	24.0	49.0	48.0	32.0	37.0
Collie X	6.00	183	36.5	31.0	43.0	52.0	58.0	32.0
Boxer X	6.59	91	18.6	12.0	54.0	41.0	52.0	35.0
Terrier X	7.96	152	27.2	21.0	*	*	*	*
Boxer X	8.50	133	26.5	17.0	53.0	49.0	46.0	43.0
Collie	9.02	183	34.5	31.0	49.0	50.0	52.0	44.0
Boxer X	9.90	161	16.8	15.0	51.0	51.0	53.0	42.0

* No data.

Table 49 Logarithmic regression equations comparing the rate of increase in total sectional area and total area occupied by myosin ATPase low reacting (AL) fibres in m. semitendinosus of 9 Greyhound and 16 other pups less than 12 kg liveweight.

Type of dog	Dependent variable	Growth ratio b*	Se b	log a	r **
Greyhounds	Total sectional area	0.676	0.075	-0.251	0.9595
	Total AL area	1.062	0.185	-2.683	0.9083
Other dogs	Total sectional area	0.821 ^{ac}	0.056	-0.774	0.9694
	Total AL area	1.321 ^{bc}	0.111	-3.356	0.9537

* Regression coefficient b, standard error Se b.

a Value of b significantly greater ($P < 0.02$) than 0.666

b Value of b significantly greater ($P < 0.02$) than 1.

c Values of b bearing this superscript are significantly different ($P < 0.002$) from one another.

Table 50

Logarithmic regression equations comparing the areas of samples of m. semitendinosus, m. diaphragma and m. pectoralis transversus occupied by myosin ATPase low-reacting (AL) fibres with liveweight in dogs and horses (non-significant regressions are excluded).

Dependent variable	Type of animal	Number of observations	Regression coefficient	Se b*	log a	r **
% AL area in m. semitendinosus	Other horses	32	0.186	0.089	-0.267	0.356
	Greyhounds	22	0.189	0.055	0.539	0.614
% AL area in m. diaphragma	Other dogs	21	0.344	0.071	0.292	0.746
	Thoroughbreds	23	0.180 c	0.030	0.832	0.790
	Other horses	23	0.343 c	0.044	-0.020	0.862
% AL area in m. pectoralis transversus	Greyhounds	21	0.279	0.072	-0.060	0.665
	Other dogs	20	0.272	0.070	0.527	0.677
	Other horses	34	0.250	0.046	0.142	0.696

* Regression coefficient b, standard error Se b. (all values of b are significantly greater ($P < 0.05$ than 0))

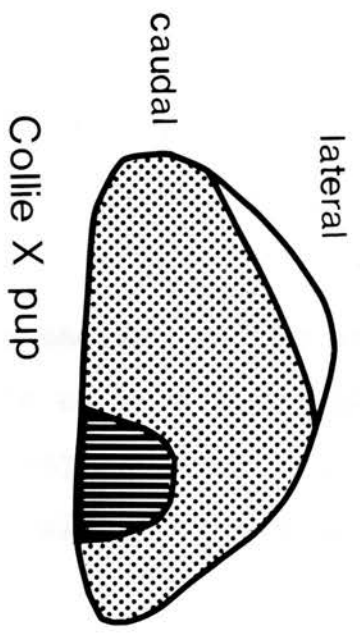
c Values of b bearing this superscript are significantly different ($P < 0.01$) from one another.

** Correlation coefficient r.

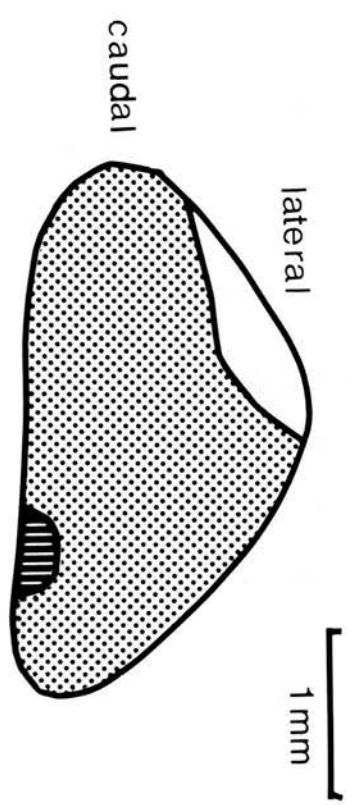
Fig. 70.

The incidence of myosin ATPase low-reacting (AL) fibres in the complete cross section of m. semitendinosus of a neonatal Greyhound and Collie adjusted to a liveweight of 0.5 kg.

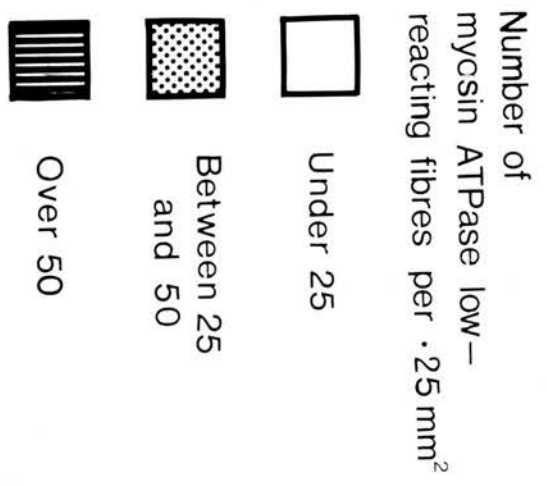
DENSITY OF MYOSIN ATPase LOW-REACTING
 FIBRES IN COMPLETE TRANSVERSE SECTIONS
 OF M. SEMITENDINOSUS OF DOGS OF 0.5 KG. BODY WEIGHT



Collie X pup



Greyhound pup



Figs. 71 and 73.

Transverse fresh frozen sections from the superficial lateral (Fig. 71) and deep medial (Fig. 73) regions of *m. semitendinosus* of a 0.26 kg neonatal male Greyhound demonstrating myosin ATPase activity.

Figs. 72 and 74.

Transverse fresh frozen sections from the superficial lateral (Fig. 72) and deep medial (Fig. 74) regions of *m. semitendinosus* of a 0.46 kg, two day old male Labrador demonstrating myosin ATPase activity.

Figs. 75 and 77.

Transverse fresh frozen sections of *m. diaphragma* (Fig. 75) and *m. pectoralis transversus* (Fig. 77) from the same animal as Figs. 71 and 73, demonstrating myosin ATPase activity.

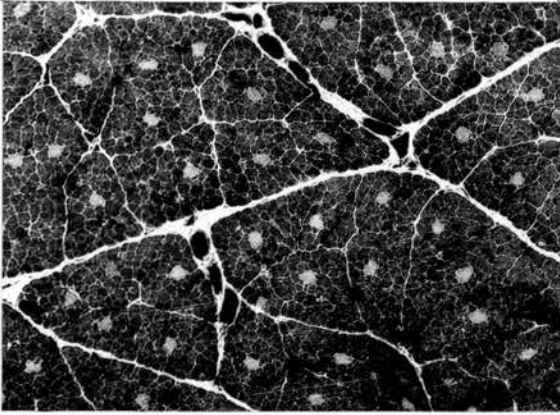
Fig. 76.

Transverse fresh frozen section of *m. diaphragma* from a 0.46 kg, two day old male Labrador demonstrating myosin ATPase activity.

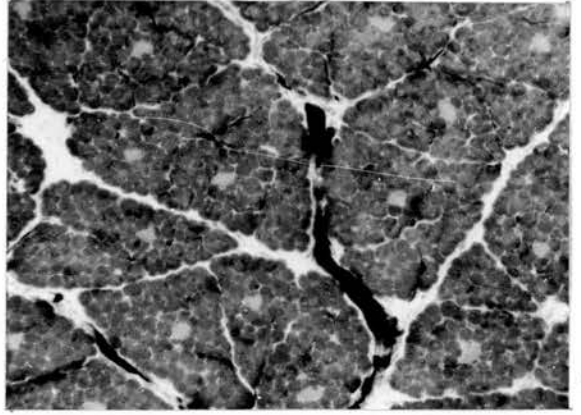
Fig. 78.

Transverse fresh frozen section of *m. pectoralis transversus* from a 0.53 kg, two week old female Collie cross pup, demonstrating myosin ATPase activity.

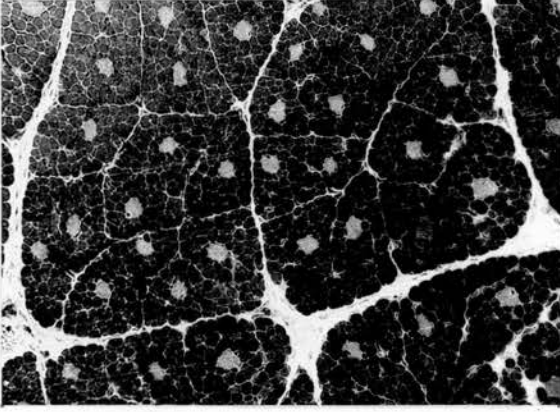
71



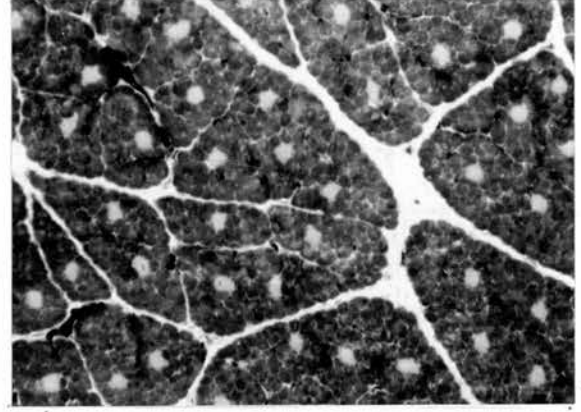
72



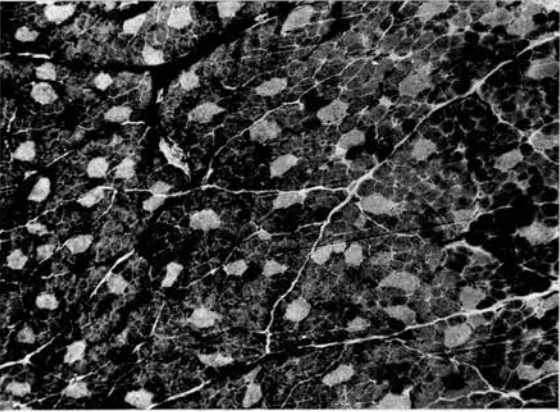
73



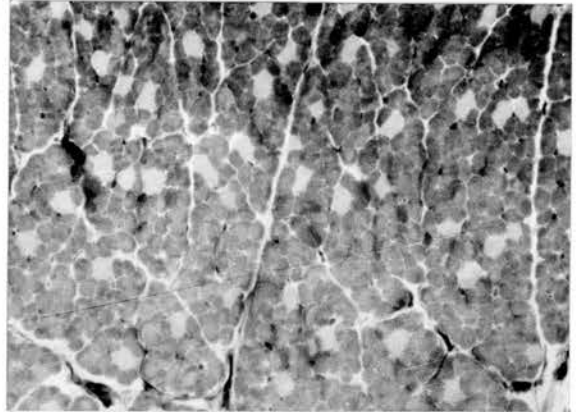
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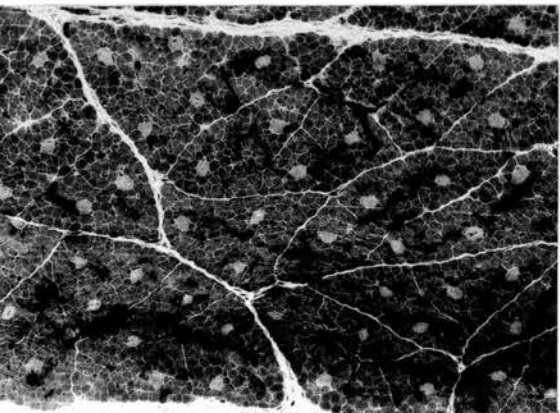
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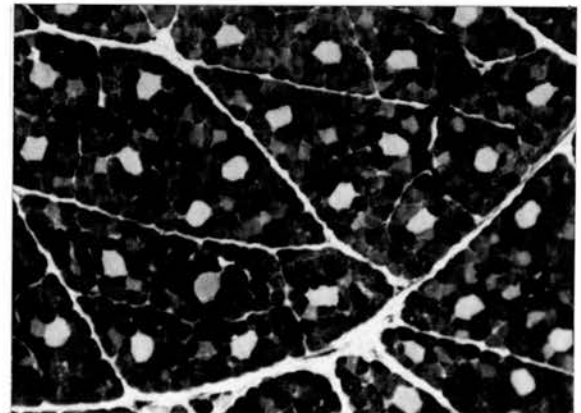
76



77



78



100μm

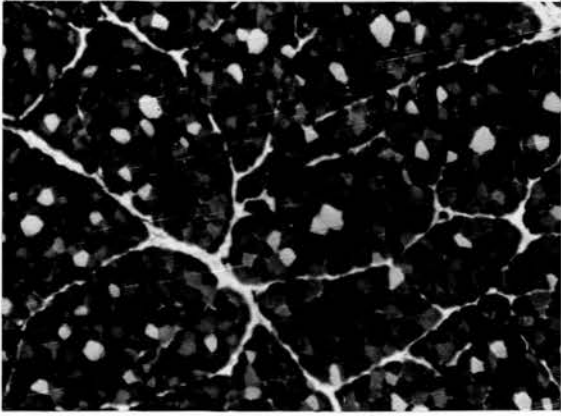
Figs. 79, 81 and 83.

Fresh frozen transverse section from the superficial caudal region of *m. semitendinosus* (Fig. 79), *m. diaphragma* (Fig. 81) and *m. pectoralis transversus* of a 2.3 kg, six week old male Greyhound demonstrating myosin ATPase activity. Fibres with an "intermediate" reaction for myosin ATPase are apparent.

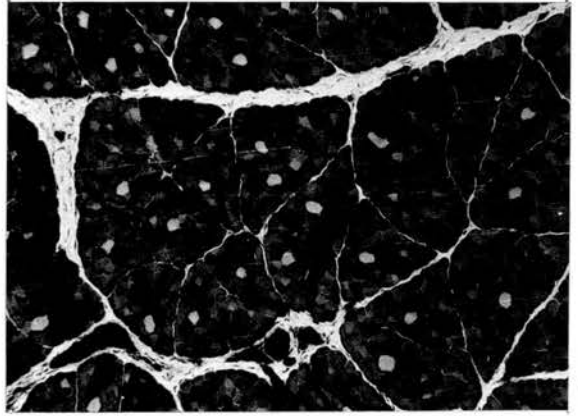
Figs. 80, 82 and 84.

Fresh frozen transverse sections of the superficial caudal region of *m. semitendinosus* (Fig. 80) *m. diaphragma* (Fig. 82) and *m. pectoralis transversus* (Fig. 84) of a 0.79 kg, four week old female Collie demonstrating myosin ATPase activity. Fibres with an intermediate reaction for myosin ATPase may be seen.

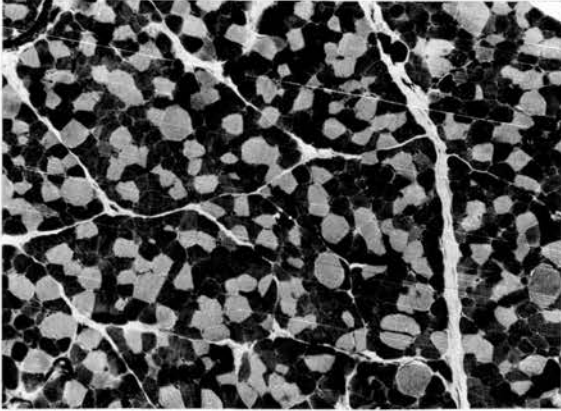
79



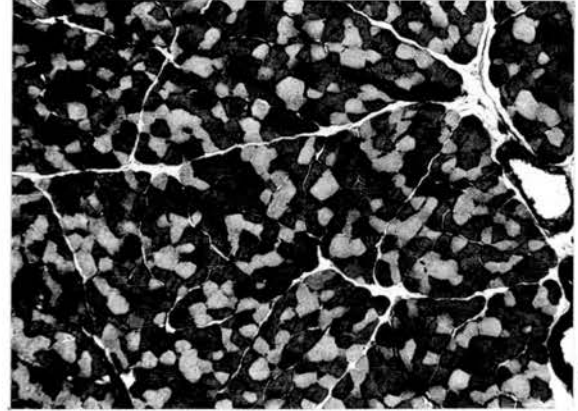
80



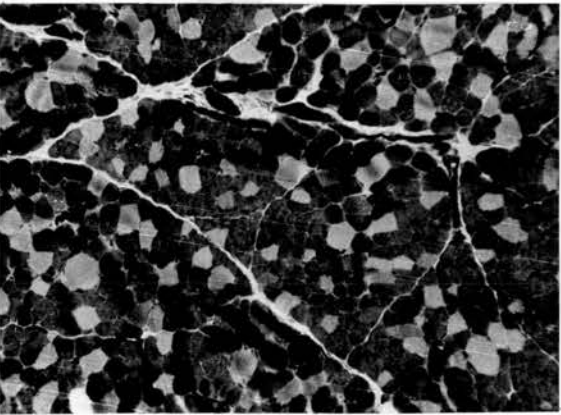
81



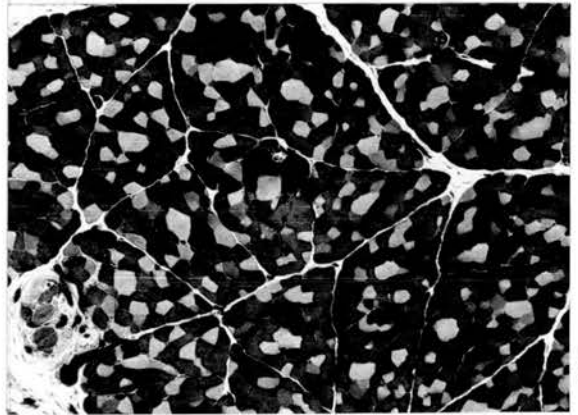
82



83



84



100 μ m

Fig. 85.

**Changes in the numbers of myosin ATPase low-reacting
fibres with increasing liveweight in m. semitendinosus
of Greyhounds and other dogs.**

MYOSIN ATPase LOW-REACTING FIBRES
IN M. SEMITENDINOSUS

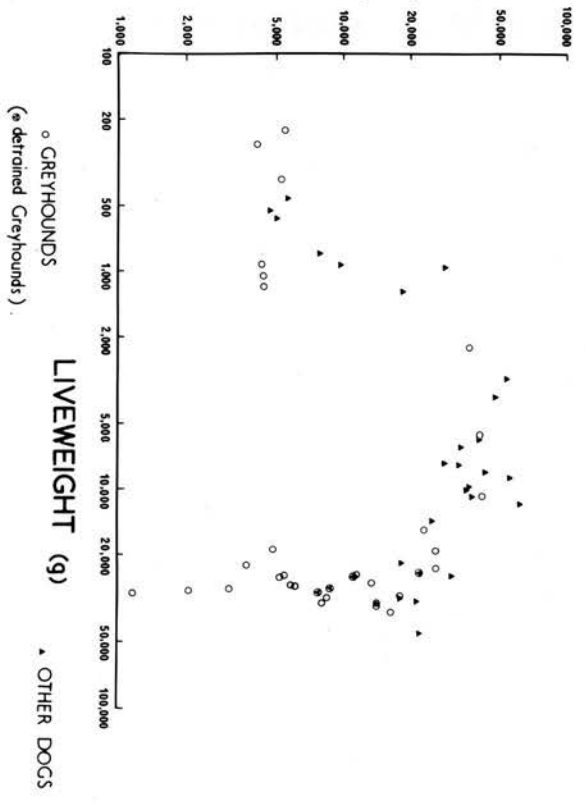


Fig. 86.

Changes in the numbers of myosin ATPase low-reacting fibres in m. semitendinosus of Greyhounds and other dogs with increasing age.

TOTAL NUMBER OF
 MYOSIN ATPase LOW-REACTING FIBRES
 IN M. SEMITENDINOSUS

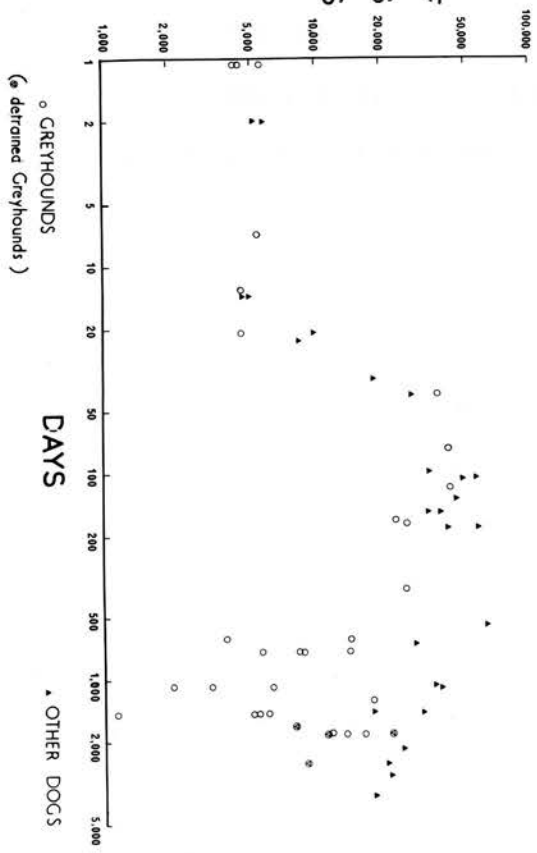


Fig. 87.

**Growth changes in the proportion of myosin ATPase
low-reacting fibres in m. semitendinosus of
Greyhounds and other dogs.**

PERCENTAGE NUMBERS OF
MYOSIN ATPase LOW-REACTING FIBRES
IN M. SEMITENDINOSUS

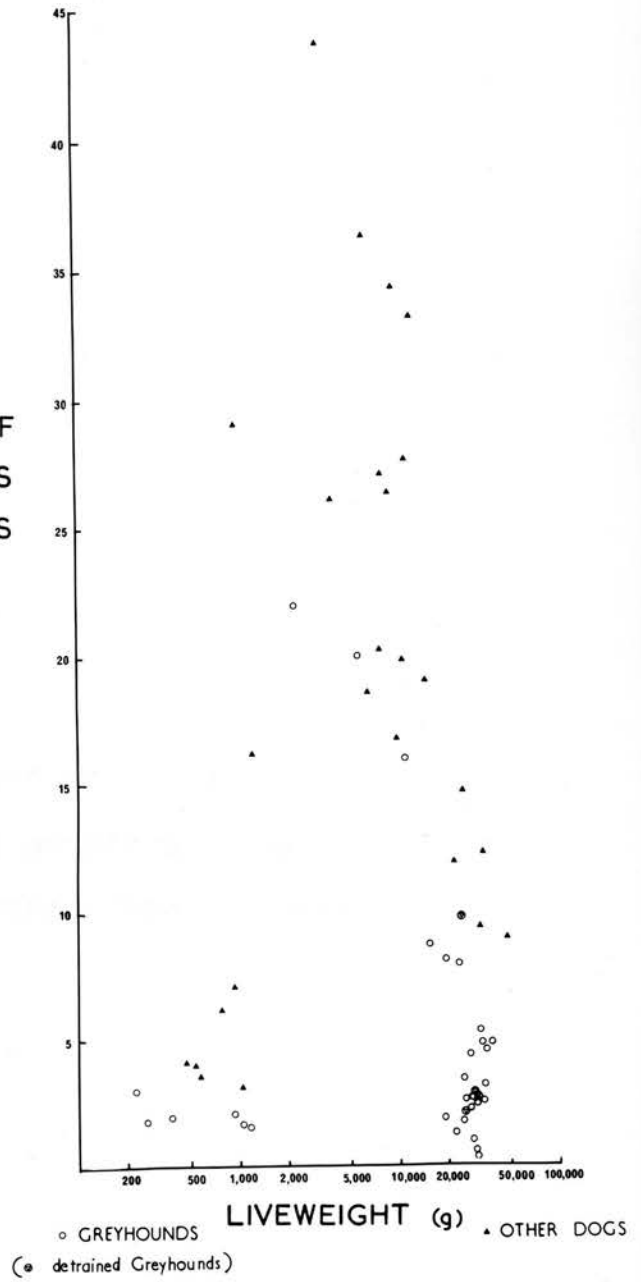


Fig. 88.

The incidence of myosin ATPase low-reacting (AL) fibres in the complete transverse section of m. semitendinosus of a Collie and Greyhound adjusted to a liveweight of 0.6 kg.

DENSITY OF MYOSIN ATPase LOW-REACTING FIBRES IN COMPLETE TRANSVERSE SECTIONS OF M. SEMITENDINOSUS OF DOGS OF 6.0 KG. BODY WEIGHT

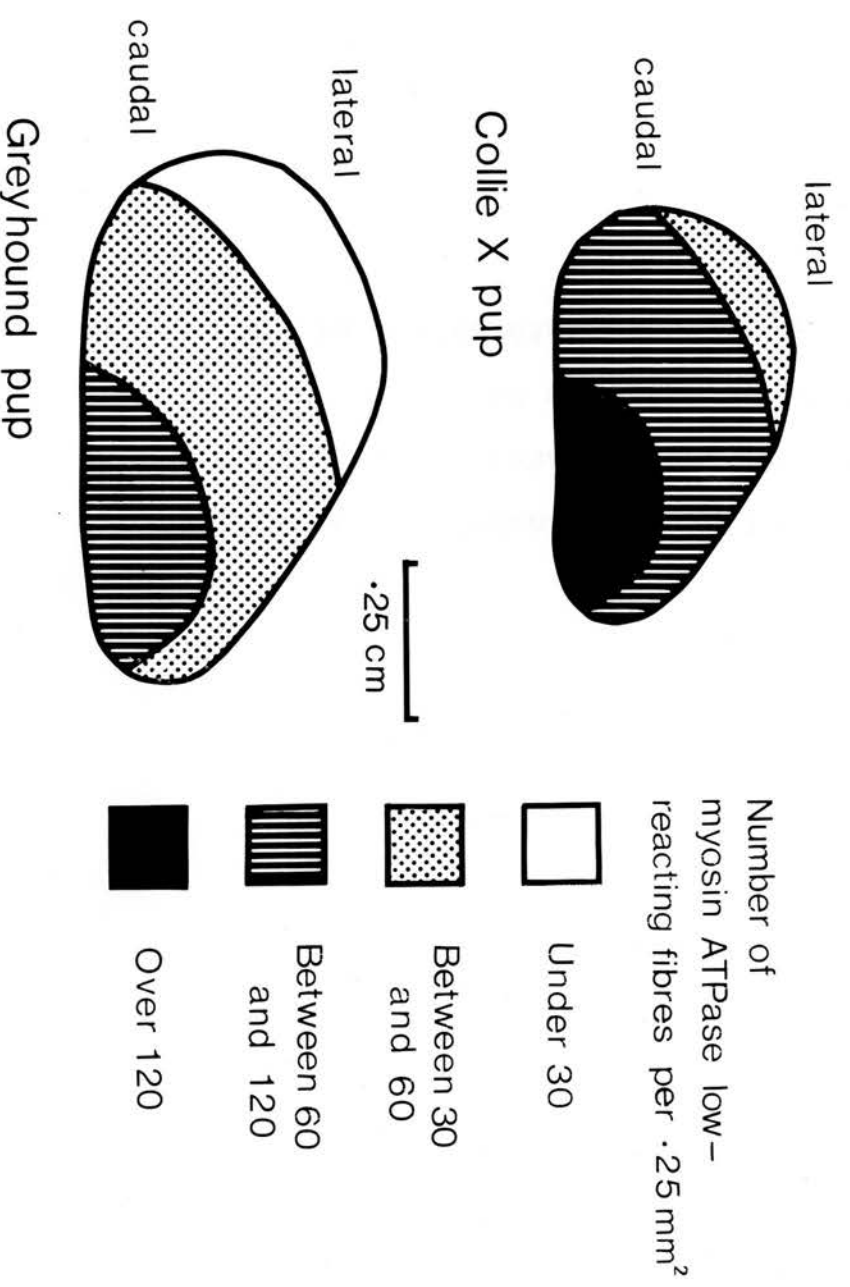


Fig. 89.

Growth changes in the TSA and total area of myosin ATPase low-reacting fibres in m. semitendinosus of Greyhounds and other dogs with regression equations and regression lines for young dogs less than 12 kg liveweight.

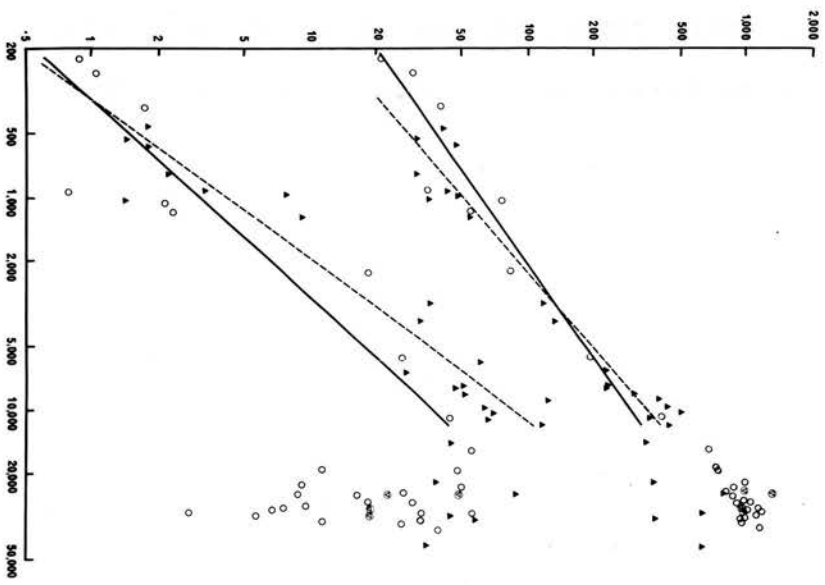
TOTAL SECTIONAL AREA
OF M. SEMITENDINOSUS

(mm²)

TOTAL AREA OF
MYOSIN ATPase LOW-REACTING FIBRES
IN M. SEMITENDINOSUS

(mm²)

LIVEWEIGHT (g)



OTHER DOGS Δ , ---
 $\log Y = .821 \log X - .774$

GREYHOUNDS \circ , —
(de trained Greyhounds)
 $\log Y = .876 \log X - .251$

OTHER DOGS Δ , ---
 $\log Y = 1.321 \log X - 3.356$

GREYHOUNDS \circ , —
(de trained Greyhounds)
 $\log X = 1.082 \log X - 2.683$

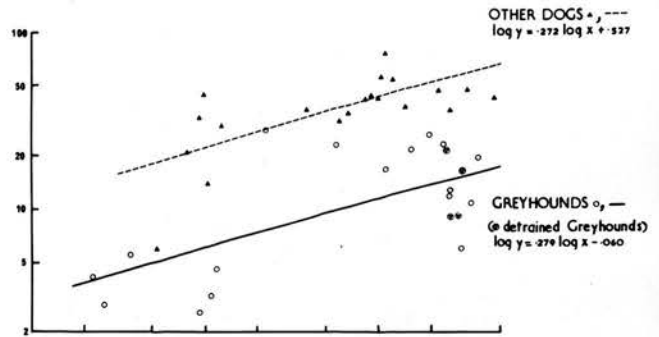
REGRESSION EQUATIONS AND LINES REFER TO YOUNG DOGS LESS THAN 12 KG LIVEWEIGHT

Fig. 90.

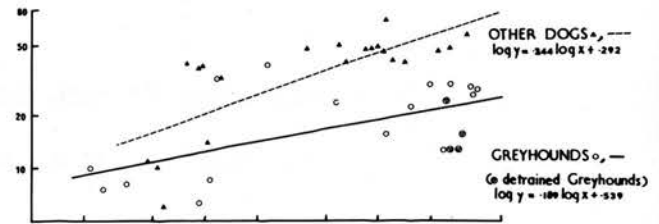
**Growth changes in the proportion of myosin ATPase
low-reacting fibres in m. semitendinosus,
m. diaphragma and m. pectoralis transversus of
Greyhounds and other dogs.**

PERCENTAGE AREA OCCUPIED BY
MYOSIN ATPase LOW-REACTING FIBRES
IN SAMPLES OF:-

M. PECTORALIS TRANSVERSUS



M. DIAPHRAGMA



M. SEMITENDINOSUS

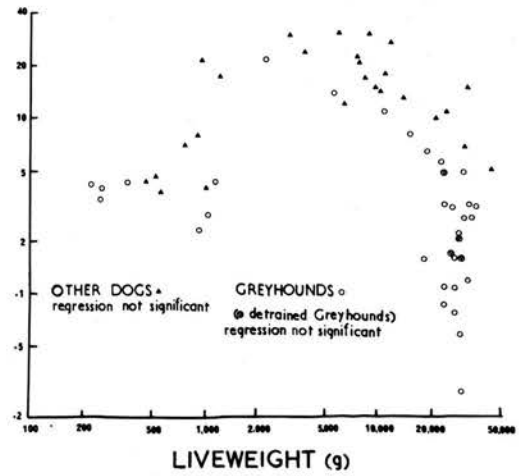


Table 51 Percentage of fibres sampled low in succinate dehydrogenase activity (SL), glycogen phosphorylase activity (PL), and myosin ATPase activity (AL), and percentage of area of samples occupied by AL fibres; in m. semitendinosus, m. diaphragma and m. pectoralis transversus of young horses.

Type of horse	Live-weight (kg)	Sex	Age *	M. semitendinosus				M. diaphragma				M. pectoralis transversus			
				SL	PL	AL	AL Area	SL	PL	AL	AL Area	SL	PL	AL	AL Area
Thoroughbred	11	♂	338	0	0	2.2	2.4	0	1	41	41	0	0	7.5	8.7
Thoroughbred	13	♂	274	89	0	1.7	1.6	**	**	**	**	**	**	**	**
Thoroughbred	16	♂	337	54	0	0.60	0.70	0	0	23	24	0	0	19	22
Thoroughbred	19	♂	326	47	0	0.81	0.71	0	2	35	43	0	0	21	25
Thoroughbred	24	♂	314	83	0	3.9	2.5	0	0	32	51	47	0	8.9	8.6
Thoroughbred	24	♂	318	33	0	1.9	1.2	0	0	26	33	0	0	13	12
Thoroughbred	28	♂	285	72	0	2.3	3.2	**	**	**	**	0	0	7.5	7.1
Thoroughbred	29	♂	326	46	0	1.7	2.2	0	2	36	64	0	0	18	22
Thoroughbred	31	♂	311	66	0	0.87	0.71	0	0	36	45	17	0	10	8.5
Thoroughbred	32	♂	321	62	0	1.4	1.0	**	**	**	**	0	0	22	18
Thoroughbred	32	♂	317	65	0	2.0	1.4	0	0	41	57	0	0	24	19
Thoroughbred	34	♂	330	53	0	4.2	2.6	0	0	41	49	0	0	22	18
Thoroughbred	35	♂	274	50	0	3.7	2.2	**	**	**	**	**	**	**	**
Thoroughbred	35	♂	341	62	0	2.4	6.8	**	**	**	**	**	**	**	**
Thoroughbred	39	♂	339	46	0	6.1	2.4	0	0	49	33	0	0	14	11
Thoroughbred	39	♂	338	35	0	1.9	1.4	**	**	**	**	0	0	15	16
Thoroughbred	41	♂	340	61	0	6.6	3.6	0	0	43	56	0	0	24	18
Thoroughbred	42	♂	338	**	**	1.7	1.5	**	**	40	41	**	**	21	19
Thoroughbred	43	♂	338	64	0	7.4	8.0	0	0	45	41	0	0	42	41
Thoroughbred	50	♂	338	52	0	1.3	0.7	0	0	41	42	0	0	34	28
Thoroughbred	59	♂	346	**	**	3.6	3.4	**	**	**	**	**	**	31	21
Thoroughbred	337	♂	703	46	4	3.7	1.9	0	0	69	76	0	0	24	9.1
Thoroughbred	420	♂	896	51	0	7.2	3.7	0	1	79	84	**	**	**	**
Thoroughbred	433	♂	886	49	0	2.3	1.2	0	1	67	63	0	0	43	29
Connemara X	2	♂	160	0	0	5.7	5.8	0	0	10	10	0	0	10	10
Welsh Mountain	3	♂	158	0	0	3.7	3.4	0	0	8.8	13	0	0	8.4	6.4
Dartmoor	22	♂	339	**	**	3.5	2.5	**	**	**	**	**	**	22	18
Thoroughbred X	39	♂	326	62	0	0.78	0.4	0	42	42	33	0	0	24	16
Thoroughbred X	62	♂	348	67	0	1.8	1.1	**	**	**	**	0	0	37	32
Welsh Mountain	109	♂	855	63	0	15	5.2	0	4	56	61	17	46	46	39
Welsh Mountain	115	♂	703	50	0	8.7	4.2	0	6	60	65	0	0	41	35
Welsh Mountain	118	♂	703	50	0	25	8.8	0	70	70	72	0	0	51	23
Welsh Mountain	154	♂	703	51	0	7.2	3.7	0	0	66	70	0	0	29	19
Welsh Mountain	178	♂	703	**	**	10	4.3	**	**	**	**	**	**	52	42
Thoroughbred X	203	♂	460	64	0	13	8.5	0	0	62	64	0	44	44	33
Fell X	207	♂	703	46	0	11	4.8	0	3	65	68	0	0	37	27

* Age is calculated in days from conception, (338 days is added to postnatal ages).

** No data.

Figs. 91 - 93.

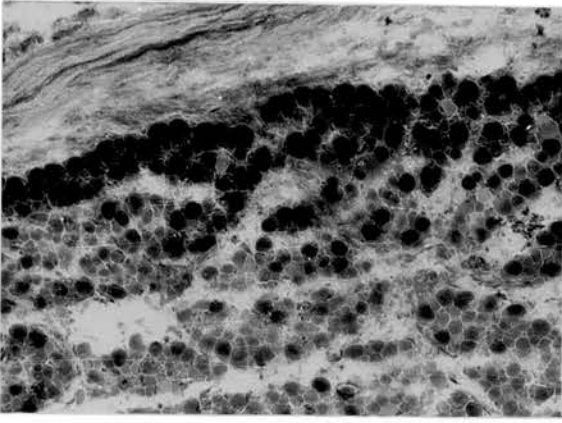
Fresh frozen transverse serial sections from the superficial caudal region of m. semitendinosus of a 2.2 kg, 160 day "in utero" male Connemara cross pony demonstrating myosin ATPase (Fig. 91), SDHase (Fig. 92) and GPase (Fig. 93) activity.

Figs. 94 and 95.

Fresh frozen transverse serial sections from m. diaphragma of the same animal as Figs. 91 - 93, demonstrating myosin ATPase (Fig. 94) and GPase (Fig. 95) activity.

Figs. 96 and 97.

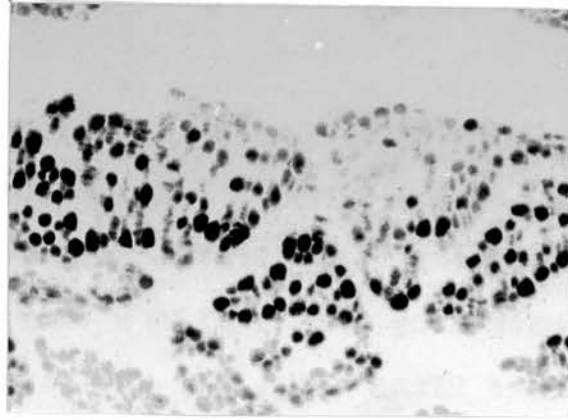
Fresh frozen transverse serial sections from the superficial region of m. pectoralis transversus of the same animal as Figs. 91 - 95 demonstrating myosin ATPase (Fig. 96) and GPase (Fig. 97) activity.



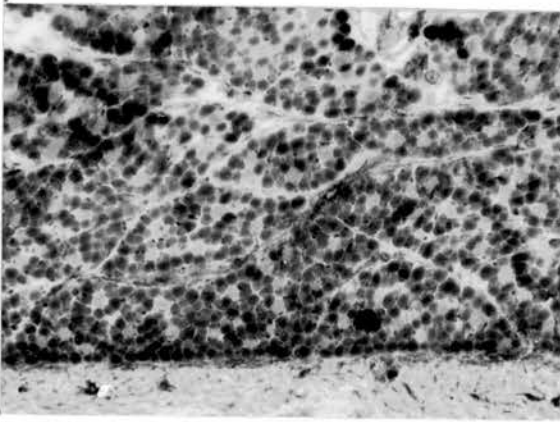
91.



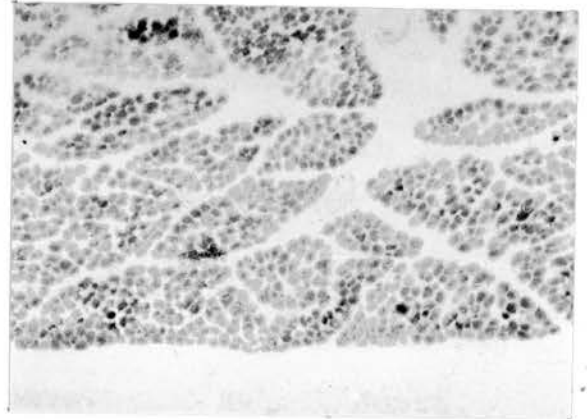
92.



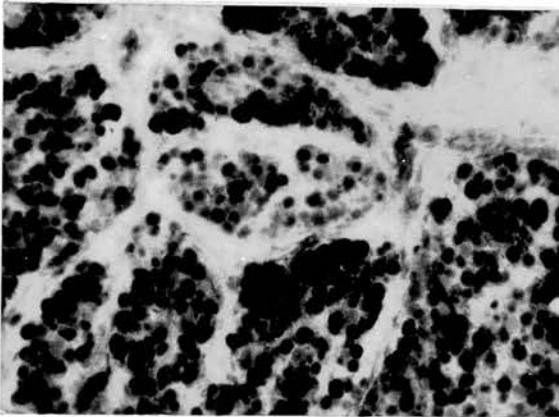
93.



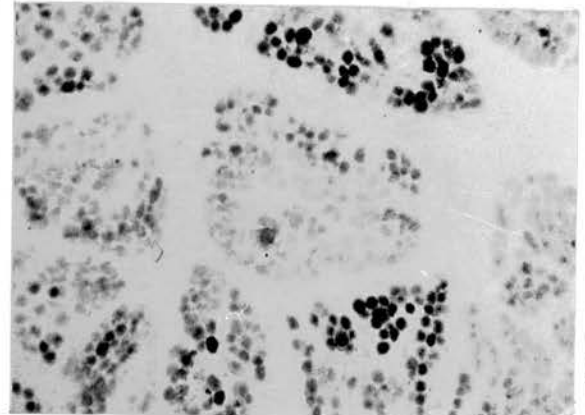
94.



95.



96.



97.

100µm

Figs. 98 and 99.

Transverse fresh frozen serial sections from m. semitendinosus of a 24 kg, 318 day "in utero" female Thoroughbred demonstrating myosin ATPase (Fig. 98) and SDHase (Fig. 99) activities.

Figs. 100 and 101.

Fresh frozen transverse serial sections from m. diaphragma of the same animal as Figs. 98 and 99 demonstrating myosin ATPase (Fig. 100) and SDHase (Fig. 101) activity.

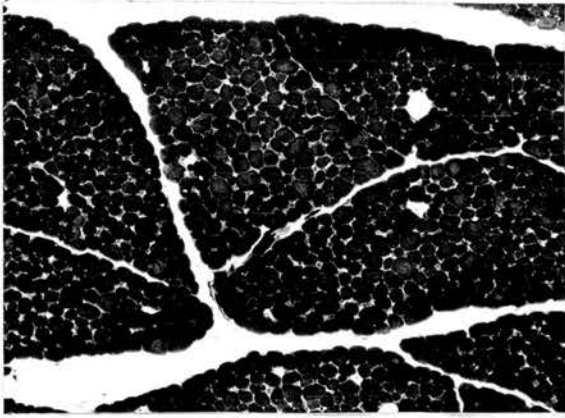
Fig. 102.

Fresh frozen transverse section from the deep medial region of m. semitendinosus of the same animal as Figs. 98 - 101 demonstrating myosin ATPase activity.

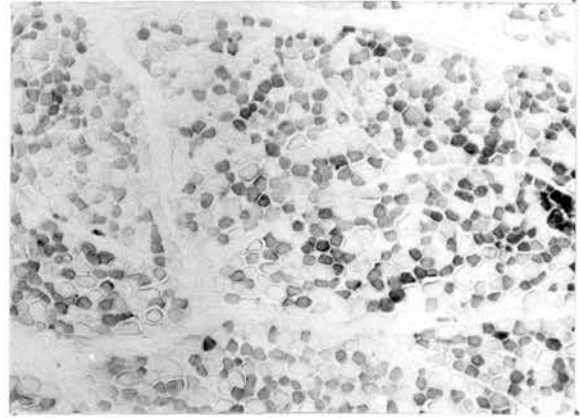
Figs. 103 - 105.

Fresh frozen transverse serial sections from the superficial region of m. pectoralis transversus of a 32 kg, 317 day "in utero" female Thoroughbred demonstrating myosin ATPase (Fig. 103), SDHase (Fig. 104) and GPase (Fig. 105) activity.

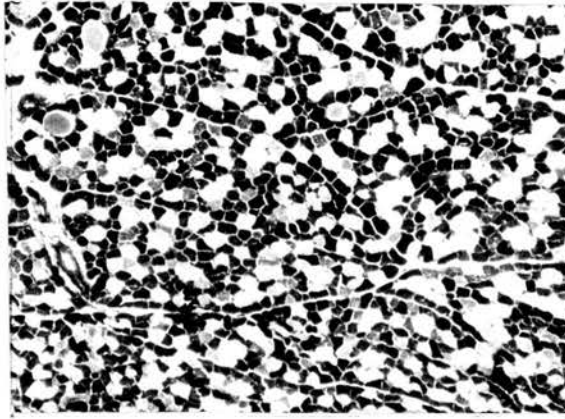
98.



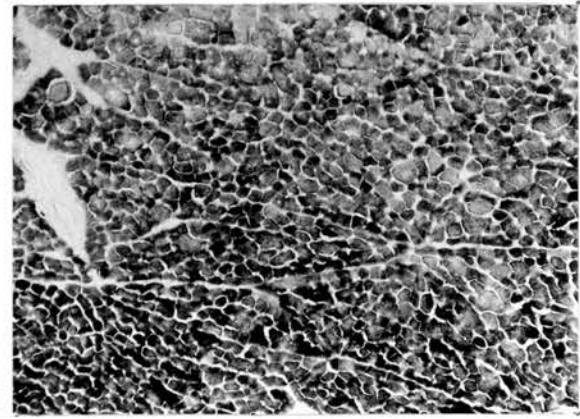
99



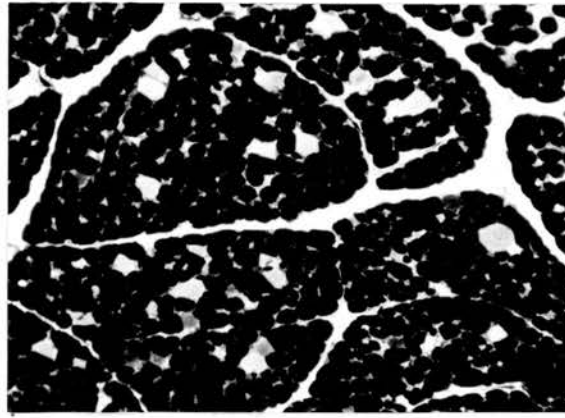
100.



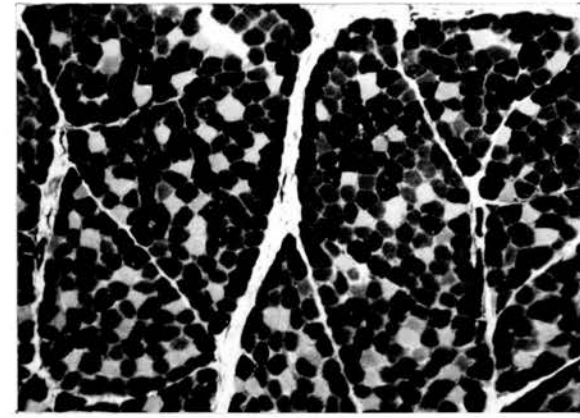
101



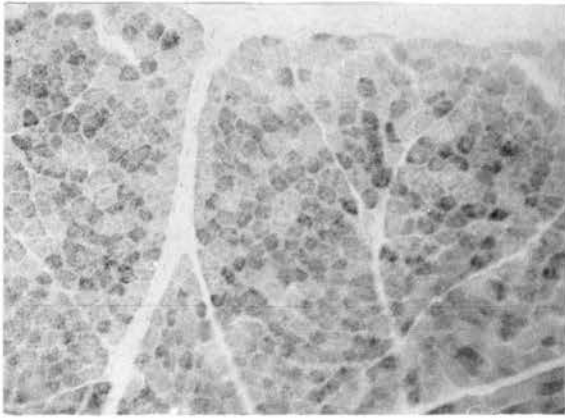
102



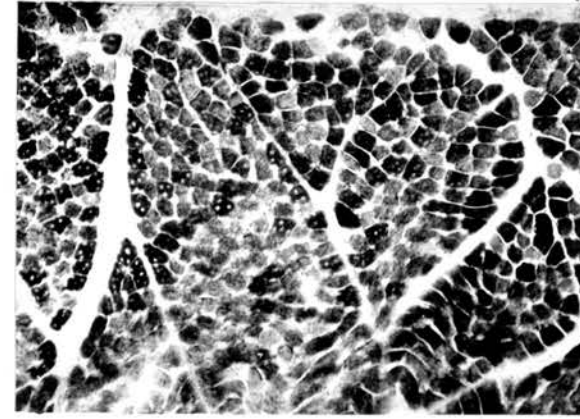
103



104



105



100 μm

Figs. 106, 108 and 110.

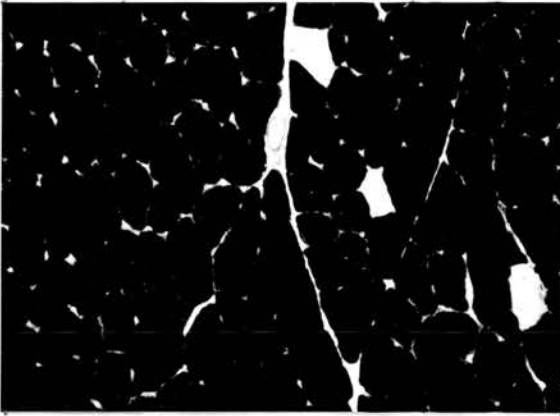
Fresh frozen transverse sections from the caudal superficial region of *m. semitendinosus* (Fig. 106), *m. diaphragma* (Fig. 108) and *m. pectoralis transversus* (Fig. 110) of a 337 kg yearling Thoroughbred female demonstrating myosin ATPase activity.

Figs. 107, 109 and 111.

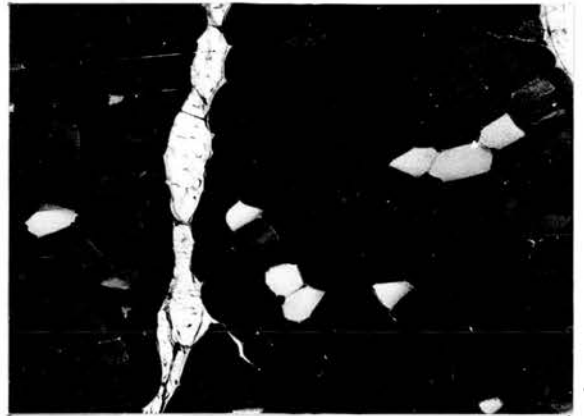
Fresh frozen transverse sections from the caudal superficial region of *m. semitendinosus* (Fig. 107), *m. diaphragma* (Fig. 109) and *m. pectoralis transversus* (Fig. 111) of a 115 kg, yearling female Welsh Mountain pony demonstrating myosin ATPase activity.

An "intermediate" reaction for myosin ATPase may be seen in some fibres.

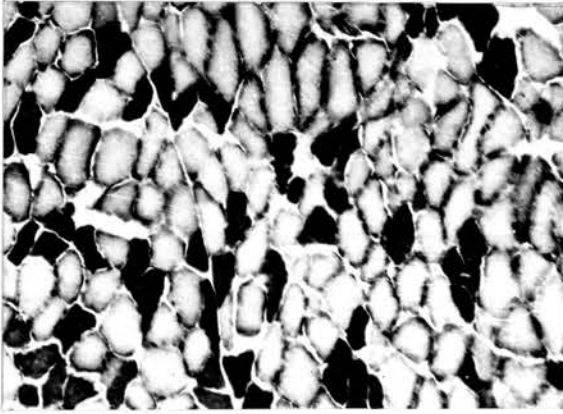
106.



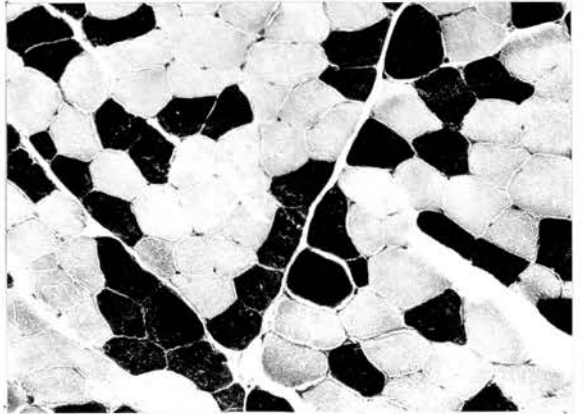
107



108



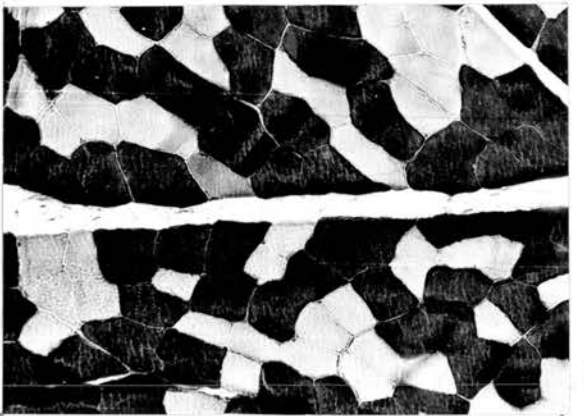
109



110



111



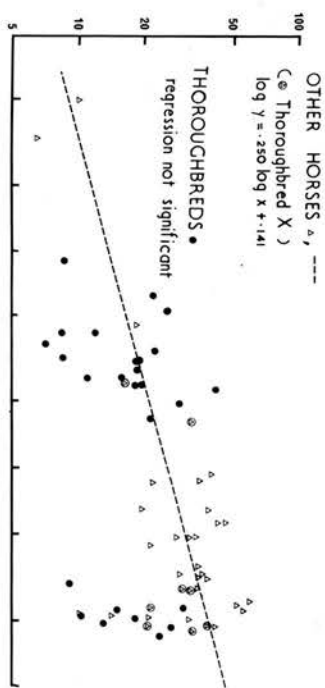
100 μm

Fig. 112.

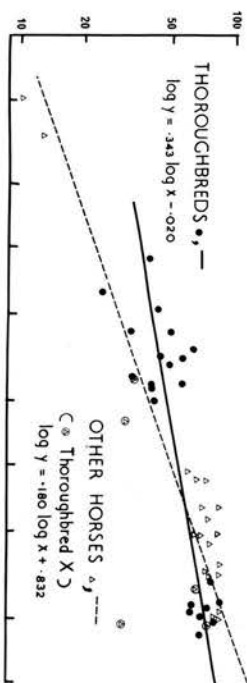
Growth changes in the proportion of myosin ATPase
low-reacting fibres in m. semitendinosus,
m. diaphragma and m. pectoralis transversus of
Thoroughbreds and other horses.

PERCENTAGE AREA OCCUPIED BY
MYOSIN ATPase LOW-REACTING FIBRES
IN SAMPLES OF :-

M. PECTORALIS TRANSVERSUS



M. DIAPHRAGMA



M. SEMITENDINOSUS

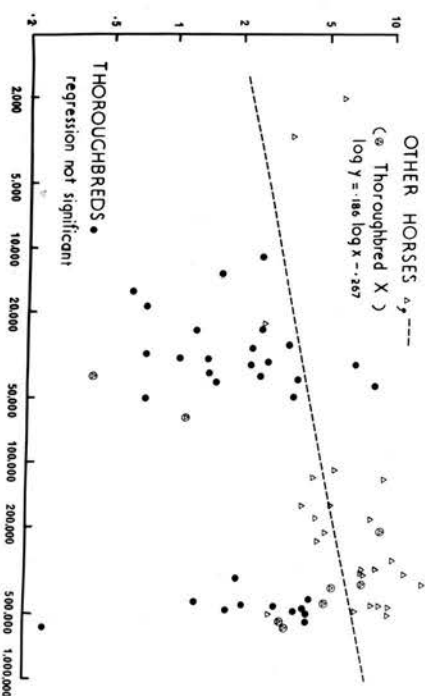


Table 52 Total numbers of fibres, and of wosin ATPase low-reacting (AL) fibres in m. semitendinosus of the dog.

Arc status of Greyhounds	Liver-weight (g)	Sex	Total number of fibres (x 1000)	Total number of AL fibres	Type of dog	Liver-weight (g)	Sex	Total number of fibres (x 1000)	Total number of AL fibres
Young	222	♂	185	5,477	Young Labrador	464	♂	143	5,775
Young	260	♂	280	4,133	Young Collie X	527	♀	120	4,766
Young	317	♀	280	5,197	Young Labrador	573	♀	141	5,006
Young	927	♀	219	4,304	Young Collie X	785	♀	122	8,212
Young	1,056	♀	289	4,498	Young Collie X	931	♀	141	9,901
Young	1,174	♀	300	4,407	Young Collie	976	♀	99	28,901
Young	2,126	♀	173	37,522	Young Labrador	1,010	♀	151	4,584
Young	3,712	♀	208	41,366	Young Collie X	1,235	♀	114	18,518
Young	11,000	♀	270	42,170	Young Collie X	3,180	♀	126	55,254
Young	13,250	♀	274	23,920	Young Collie X	3,843	♀	186	48,678
Young	13,500	♀	331	26,705	Young Collie X	6,000	♀	114	41,563
Young	23,500	♀	337	26,513	Young Boxer X	6,585	♀	183	34,002
Young	13,000	♀	280	4,949	Young Terrier	7,960	♀	120	33,268
Adult	22,300	♀	295	3,749	Young Boxer X	8,500	♀	167	44,269
Adult	24,150	♀	230	22,355	Young Collie	9,023	♀	156	57,332
Adult	24,884	♀	322	11,802	Young Boxer X	9,900	♀	222	37,331
Adult	25,000	♀	322	5,405	Adult Collie X	7,742	♀	132	29,333
Adult	25,200	♀	209	5,228	Adult Collie	10,400	♀	184	36,433
Adult	25,300	♀	529	11,166	Adult Collie X	11,000	♀	139	38,480
Adult	27,200	♀	313	13,605	Adult Collie	12,000	♀	188	63,242
Adult	27,500	♀	282	5,934	Adult Collie	14,100	♀	136	23,841
Adult	28,000	♀	232	6,064	Adult Collie	22,000	♀	155	18,435
Adult	28,500	♀	329	8,903	Adult Afghan	25,100	♀	214	31,482
Adult	28,864	♀	328	3,175	Adult Afghan	31,900	♀	194	18,308
Adult	29,750	♀	404	2,083	Adult Labrador	33,000	♀	175	21,533
Adult	30,000	♀	352	1,165	Adult Great Dane	46,500	♀	248	22,144
Adult	30,000	♀	319	7,950					
Adult	31,200	♀	348	18,317					
Adult	31,400	♀	346	8,647					
Adult	33,523	♀	306	14,591					
Adult	33,608	♀	260	8,022					
Adult	34,091	♀	320	14,397					
Adult	37,000	♀	355	16,973					

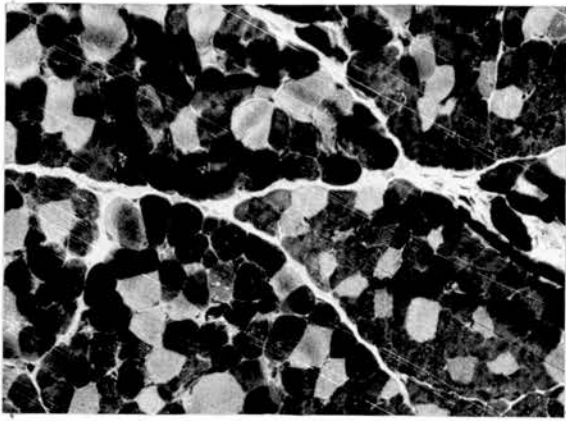
D* Detained Greyhounds.

Figs. 113, 115 and 117.

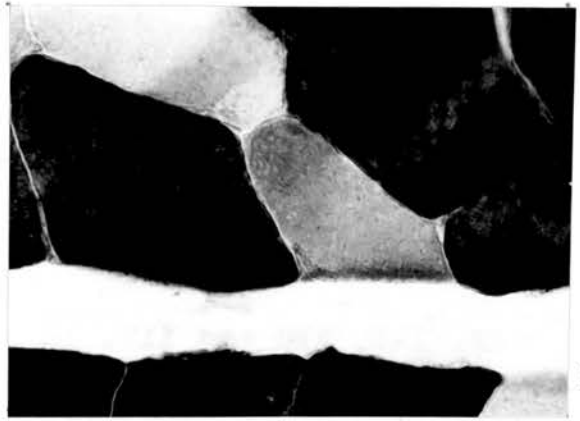
Fresh frozen transverse serial sections from the superficial region of m. pectoralis transversus of a 2.3 kg six week old male Greyhound demonstrating myosin ATPase (Fig. 113), SDHase (Fig. 115) and GPase (Fig. 117) activity. Fibres with an "intermediate" reaction for myosin ATPase are apparent.

Figs. 114, 116 and 118.

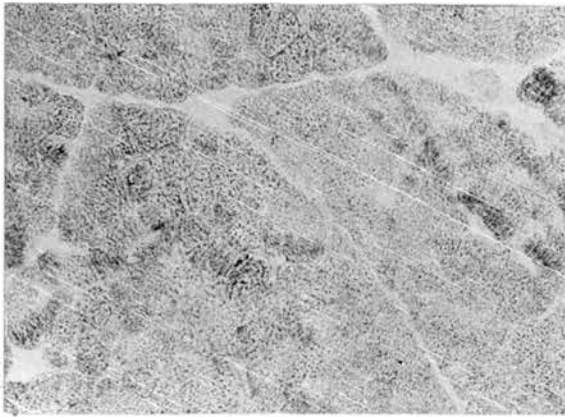
Fresh frozen transverse serial sections from m. pectoralis transversus of a 115 kg, yearling female Welsh Mountain pony demonstrating myosin ATPase (Fig. 114), SDHase (Fig. 116) and GPase (Fig. 118) activity. A fibre with an "intermediate" reaction for myosin ATPase is apparent.



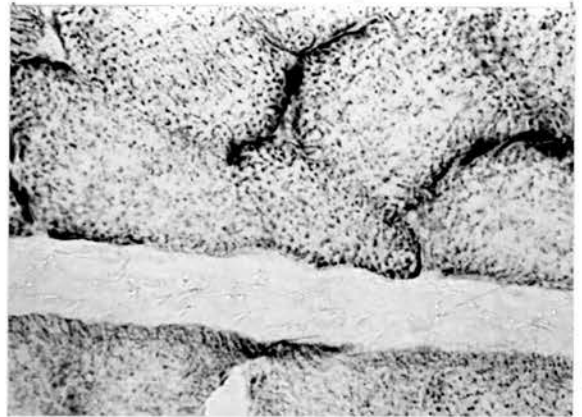
113



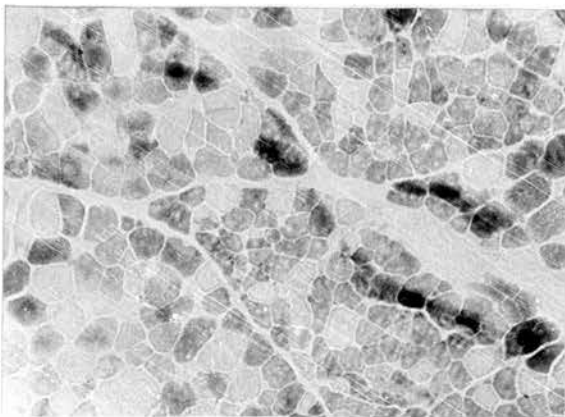
114



115

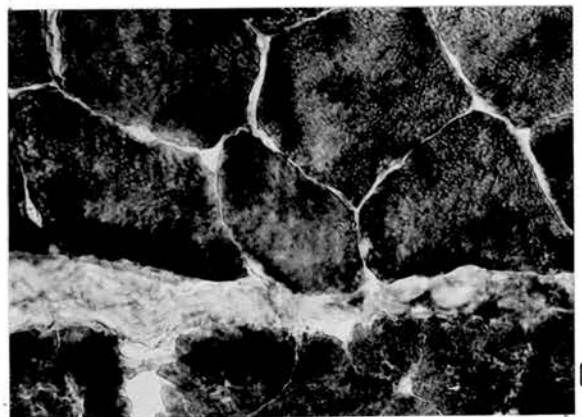


116



117

100 μm



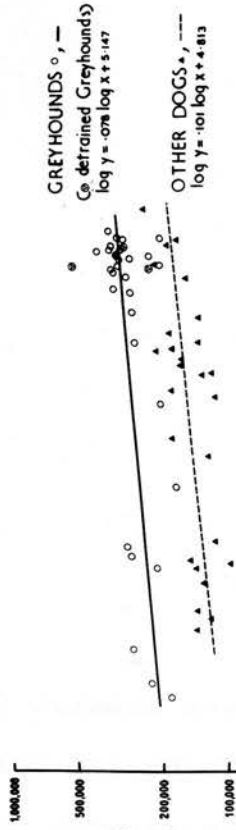
118

50 μm

Fig. 119.

**Growth changes in the total numbers of fibres and
total number of myosin ATPase low-reacting fibres
in m. semitendinosus of Greyhounds and other dogs.**

TOTAL NUMBER OF FIBRES
IN M. SEMITENDINOSUS



TOTAL NUMBER OF
MYOSIN ATPase LOW-REACTING FIBRES
IN M. SEMITENDINOSUS

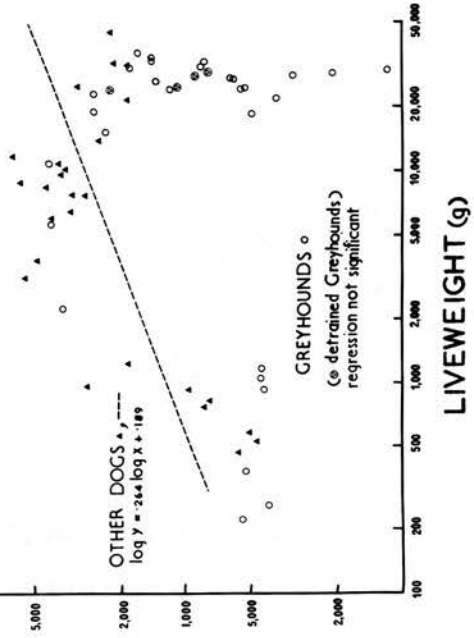


Table 53 Mean areas in μm^2 of myosin ATPase low-reacting (AL) and high-reacting (AH) fibres, in m. semitendinosus, m. diaphragma and m. pectoralis transversus of dogs.

Type of animal	Live-weight (g)	Sex	M. Semitendinosus			M. Diaphragma			M. Pectoralis transversus		
			AL	AH	(N*)	AL	AH	(N*)	AL	AH	(N*)
Young Greyhounds											
	222	♂	163	114		328	244		163	238	
	260		250	126		409	250		189	129	
	377		337	137		364	156		160	154	
	927		181	157		250	336		339	345	
	1,056		471	260		450	407		321	433	
	1,174		535	178		775	281		294	548	
	2,280		489	469		461	397		361	430	
	5,712		641	983		718	858		710	582	
	11,000		1,024	1,588		693	1,408		1,250	773	
	15,250		2,315	2,474		981	1,171		1,684	1,659	
	19,750		1,778	2,188		1,338	1,568		1,569	1,432	
	23,500		1,872	2,657		1,355	2,733		2,604	1,474	
3 Smallest Greyhounds											
	Mean		250	126		367	217		171	174	
	SD		87	12		41	53		16	57	
Adult Greyhounds											
All adults											
	Mean		2,358	3,212 (21)		1,602	1,972 (10)		1,992	3,727 (9)	
	SD		571	577		373	470		478	745	
Males											
	Mean		2,476	3,226 (13)		1,732	2,037 (5)		2,543	3,576 (4)	
	SD		577	540		354	547		237	337	
Females											
	Mean		2,167	3,189 (8)		1,472	1,886 (5)		2,151	3,848 (5)	
	SD		540	672		380	446		223	991	
Detrained adults											
	Mean		2,174	3,402 (4)		1,521	2,330 (4)		2,361	3,974 (4)	
	SD		121	908		526	435		221	959	
Trained adults											
	Mean		2,401	3,167 (17)		1,655	1,716 (6)		2,297	3,529 (5)	
	SD		628	501		275	340		374	557	
Young Other dogs											
	464	♂	310	287		570	460		-	-	
	527		295	251		688	659		615	568	
	573		361	333		489	453		-	-	
	785		277	230		360	334		296	362	
	931		339	301		594	544		632	365	
	976		268	425		408	520		386	339	
	1,010		307	230		371	451		638	592	
	1,235		499	466		525	675		471	725	
	3,180		646	1,167		-	-		-	-	
	3,843		645	742		605	627		924	740	
	6,000		1,450	1,823		871	713		1,142	724	
	6,585		815	1,327		935	1,587		969	1,978	
	7,960		1,424	2,041		-	-		-	-	
	8,500		1,148	2,090		1,420	1,678		1,506	1,714	
	9,023		2,106	2,508		856	1,281		1,317	1,762	
	9,900	1,692	1,979		1,918	1,949		1,523	2,350		
3 Smallest other dogs											
	Mean		322	290		582	524		615	568	
	SD		35	41		100	117		-	-	
Adult other dogs											
All adults											
	Mean		1,930	2,526 (10)		1,380	1,456 (7)		2,963	3,240 (8)	
	SD		350	754		330	365		1,400	1,777	
Males											
	Mean		1,880	2,860 (3)		1,375	1,718 (2)		3,334	4,184 (3)	
	SD		462	419		586	961		1,300	1,200	
Females											
	Mean		2,100	2,668 (7)		1,381	1,352 (5)		2,740	2,674 (5)	
	SD		442	696		279	386		1,557	1,935	

*N = number of adult samples.

Table 54 Allometric equations comparing the growth of myosin ATPase high-reacting (AH) fibres with myosin ATPase low-reacting (AL) fibres in m. semitendinosus, m. diaphragma and m. pectoralis transversus of the dog and horse.

Muscle	Type of animal	Number of observations	Growth ratio b*	Se b	log a	r **
M. semitendinosus						
	Greyhounds	33	1.299 c	0.078	-0.882	0.9485
	Other dogs	26	1.153 c	0.062	-0.371	0.9671
	Thoroughbreds	32	1.039	0.064	0.072	0.9467
	Other horses	32	1.004	0.090	0.315	0.8982
M. diaphragma						
	Greyhounds	22	1.235	0.154	-0.666	0.8734
	Other dogs	21	0.929	0.128	0.237	0.8583
	Thoroughbreds	23	0.981	0.069	-0.042	0.9510
	Other horses	23	0.916	0.071	0.204	0.9416
M. pectoralis transversus						
	Greyhounds	21	1.066	0.084	-0.118	0.9459
	Other dogs	20	1.024	0.108	-0.055	0.9131
	Thoroughbreds	30	1.288 cd	0.061	-0.687	0.9697
	Other horses	34	0.938 d	0.054	0.387	0.9512

* Regression coefficient b, standard error Se b.

c Values of b bearing this superscript are significantly different ($P < 0.025$) from 1.

d Values of b bearing this superscript are significantly different ($P < 0.001$) from one another.

** Correlation coefficient r.

Table 55 Mean areas in μm^2 of myosin ATPase low-reacting (AL) and high-reacting (AH) fibres, in m. semitendinosus, m. diaphragma and m. pectoralis transversus of horses.

Type of animal	Live-weight (kg)	Sex	M. Semitendinosus		M. Diaphragma		M. Pectoralis transversus		
			AL	AH (N*)	AL	AH (N*)	AL	AH (N*)	
Young Thoroughbred			290	280	247	242	187	159	
	11.0								
	13.4		107	115	-	-	-	-	
	16.0		211	194	289	268	384	320	
	19.0		233	255	474	332	375	304	
	23.9		341	537	636	286	394	408	
	24.0		317	516	461	321	428	451	
	28.0		362	421	-	-	387	410	
	29.0		266	321	661	211	448	362	
	31.0		330	391	443	304	347	422	
	31.5		318	443	-	-	545	677	
	32.0		336	502	444	232	370	499	
	33.5		320	558	312	231	246	317	
	34.5		222	374	-	-	-	-	
	34.8		410	437	-	-	-	-	
	38.6		442	1,192	378	761	948	1,170	
	39.0		429	587	-	-	321	307	
	40.5		599	1,166	784	747	613	929	
	42.0		310	428	370	363	364	433	
	43.0		795	862	477	548	1,191	1,220	
	50.0		293	441	330	313	465	621	
	58.7		663	718	-	-	720	1,189	
	337.0		1,555	3,021	2,190	1,506	874	2,792	
	420.0		1,834	3,638	3,911	2,856	-	-	
	432.7		1,444	2,853	2,254	2,671	2,426	4,443	
3 Smallest Thoroughbreds									
	Mean		203	196	268	255	286	240	
	SD		92	83	30	18	139	114	
Adult Thoroughbreds									
All adults			Mean	3,373	4,827 (9)	4,529	3,678 (6)	2,665	5,417 (10)
	SD		2,190	1,420	1,396	1,225	816	1,344	
Entire males			Mean	2,223	4,605 (2)	-	-	2,927	4,218 (2)
	SD		271	361	-	-	266	929	
Castrated males			Mean	-	-	3,633	3,021 (2)	2,290	5,288 (2)
	SD		-	-	738	346	791	985	
Females			Mean	3,699	4,891 (7)	4,977	4,007 (4)	2,703	5,859 (6)
	SD		2,416	1,633	1,505	143	987	1,438	
Horses in training			Mean	2,370	4,229 (5)	-	-	2,725	5,400 (8)
	SD		1,816	946	-	-	778	1,415	
Horses out of training			Mean	4,627	5,575 (4)	-	-	2,426	5,483 (2)
	SD		2,150	1,686	-	-	1,273	1,492	
Young other horses									
	2-15		336	513	310	279	322	436	
	2-98		306	374	350	232	336	451	
	22-00		265	393	-	-	471	607	
Thoroughbred X			470	920	307	443	404	637	
Thoroughbred X			62.0	398	-	-	761	954	
	109.1		630	2,145	1,229	1,015	1,750	2,383	
	114.5		873	2,025	2,422	1,924	1,555	2,041	
	118.2		788	2,670	1,518	1,370	1,243	4,431	
	153.7		1,386	2,774	2,202	1,790	1,130	1,952	
	178.2		1,006	3,186	-	-	4,199	6,305	
Thoroughbred X			207.3	1,402	3,232	2,567	2,239	857	
	203.6		815	1,331	1,335	1,255	1,336	2,834	
Adult other horses									
All adults			Mean	1,705	3,569 (20)	3,126	2,688 (14)	3,516	4,959 (22)
	SD		422	891	797	117	1,813	1,883	
Thoroughbred crosses			Mean	1,460	3,579 (5)	3,444	2,979 (3)	2,649	4,639 (6)
	SD		424	963	1,199	1,064	752	1,162	
Others			Mean	1,787	3,566 (15)	3,039	2,609 (11)	3,841	5,079 (16)
	SD		402	902	707	1,228	2,000	2,111	
Entire males			Mean	1,827	4,034 (4)	2,817	3,679 (3)	3,739	4,849 (2)
	SD		624	1,629	643	204	291	168	
Castrated males			Mean	1,616	3,618 (7)	3,339	2,385 (5)	5,605	5,160 (9)
	SD		477	548	983	908	1,768	2,352	
Females			Mean	1,723	3,324 (9)	3,103	2,446 (6)	3,584	4,814 (11)
	SD		303	698	781	673	2,064	1,719	

*N = Number of adult samples.

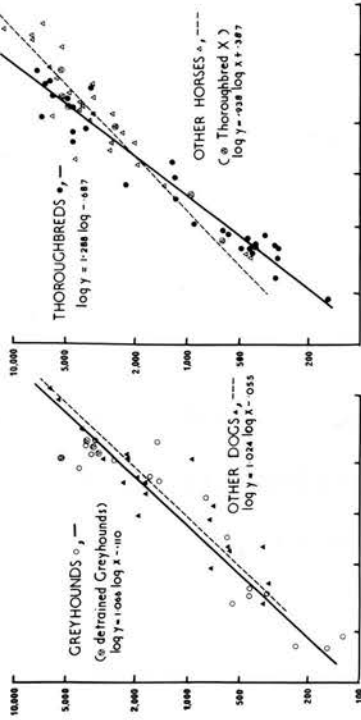
Fig. 120.

**Change in area of myosin ATPase high-reacting (AH)
relative to myosin ATPase low-reacting (AL) fibres
during growth in the dog and horse.**

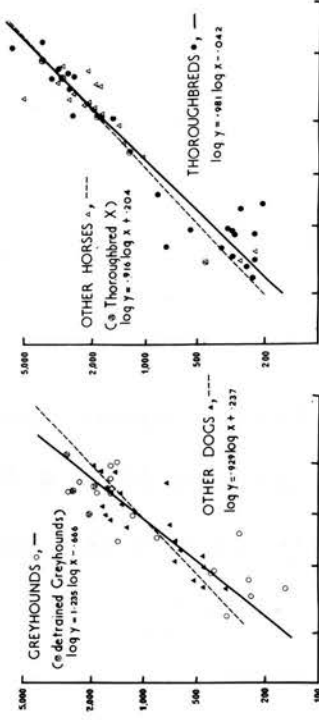
HORSES

DOGS

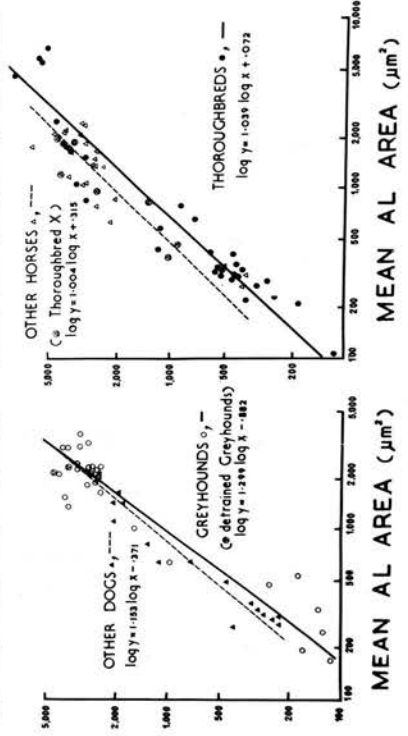
MEAN AH AREA
IN M. PECTORALIS TRANSVERSUS
(μm^2)



MEAN AH AREA
IN M. DIAPHRAGMA
(μm^2)



MEAN AH AREA
IN M. SEMITENDINOSUS
(μm^2)



MEAN AL AREA (μm^2)

MEAN AL AREA (μm^2)

Table 56 Capillary - fibre ratios and mean area per capillary (in μm^2) in m. semitendinosus, m. diaphragma and m. pectoralis transversus of dogs.

Type of animal	Live-weight (g)	Sex	M. Semitendinosus		M. Diaphragma		M. Pectoralis transversus	
			Capillary/fibre ratio	Area/capillary (N*)	Capillary/fibre ratio	Area/capillary	Capillary fibre ratio (N*)	Area/capillary (N*)
Young Greyhounds	222	♂	-	-	0.09	3,333	0.09	3,378
	260	♂	-	-	0.07	3,827	0.01	9,146
	377	♂	-	-	0.06	2,569	0.07	2,329
	1,056	♂	-	-	0.14	3,024	0.06	5,000
	1,174	♂	0.07	2,660	0.34	1,065	0.13	2,206
	2,280	♂	0.73	659	0.44	964	0.35	1,027
	5,712	♂	0.75	1,214	0.72	1,147	0.59	1,198
	11,000	♂	1.06	1,410	0.91	1,298	0.86	1,448
	15,250	♂	1.19	2,068	0.89	1,253	1.31	1,276
	19,750	♂	1.46	1,480	1.20	1,242	1.82	1,234
	23,500	♂	1.65	1,569	1.19	1,850	1.56	2,168
Young Greyhounds	Mean		0.99	1,581 (7)	0.55	1,961 (11)	0.62	2,765 (11)
	SD		0.53	636	0.45	1,039	0.67	2,423
Adult Greyhounds								
All adults	Mean		2.22	1,435 (13)	1.78	1,075 (8)	2.14	1,556 (8)
	SD		0.17	248	0.32	195	0.18	207
Males	Mean		2.22	1,468 (7)	1.75	1,084 (4)	2.08	1,554 (4)
	SD		0.20	260	0.31	238	0.20	186
Females	Mean		2.22	1,397 (6)	1.81	999 (4)	2.20	1,559 (4)
	SD		0.15	252	0.36	141	0.16	255
Detained adults	Mean		2.17	1,514 (4)	1.81	1,194 (4)	2.05	1,708 (4)
	SD		0.22	234	0.47	209	0.19	88
Trained adults	Mean		2.23	1,399 (9)	1.74	956 (4)	2.23	1,405 (4)
	SD		0.16	259	0.11	85	0.14	176
Young other dogs	464	♂	0.02	38,462	0.03	15,615	-	-
	527	♂	0.15	1,689	0.45	1,493	-	-
	573	♂	0.05	6,173	0.10	4,464	-	-
	785	♂	0.30	765	0.50	688	0.36	952
	931	♂	-	-	-	-	0.20	2,083
	976	♂	0.63	604	0.57	817	0.47	765
	1,010	♂	0.68	340	-	-	0.47	1,284
	1,235	♂	0.68	691	0.54	1,152	0.58	1,087
	3,180	♂	0.91	1,029	-	-	-	-
	3,843	♂	-	-	0.71	874	0.97	819
	6,000	♂	1.04	1,618	0.87	896	0.97	995
	6,585	♂	1.17	1,053	1.06	1,170	1.08	1,341
	7,960	♂	1.95	962	-	-	-	-
	8,500	♂	1.41	1,309	1.21	1,279	1.15	1,409
	9,023	♂	1.10	161	0.83	1,289	1.00	1,539
	9,900	♂	1.88	1,030	1.57	1,230	1.53	1,249
Young other dogs	Mean		0.86	3,992 (14)	0.70	2,581 (12)	0.80	1,229 (11)
	SD		0.62	10,028	0.44	422	0.41	375
Adult other dogs								
All adults	Mean		1.88	1,372 (9)	1.48	1,190 (6)	2.17	1,486 (7)
	SD		0.27	244	0.25	401	0.90	397
Males	Mean		2.12	1,355 (2)	1.67	1,949 (1)	3.00	1,692 (2)
	SD		0.10	175	-	-	1.27	436
Females	Mean		1.82	1,377 (7)	1.44	1,038 (5)	1.83	1,403 (5)
	SD		0.27	272	0.26	169	0.57	399

D* Detained Greyhounds.

N* Number of observations.

+ Absence of visible reaction for capillaries.

Table 57 Capillary - fibre ratios and mean area per capillary (in μm^2) in m. semitendinosus, m. diaphragma and m. pectoralis transversus of horses.

Type of animal	Live-weight (kg)	Sex	M. Semitendinosus		M. Diaphragma		M. Pectoralis transversus		
			Capillary/fibre ratio	Area/capillary (N*)	Capillary/fibre ratio	Area/capillary (N*)	Capillary/fibre ratio	Area/capillary (N*)	
Young Thoroughbreds									
	23.9	♂	0.98	541	0.98	411	1.01	402	
	28.0		0.98	426	-	-	0.71	596	
	31.0		0.84	464	0.76	464	0.88	424	
	32.0		0.67	740	-	-	-	-	
	34.5		0.40	907	-	-	-	-	
	34.8		0.57	758	-	-	-	-	
	38.6		1.46	1,046	1.08	530	1.10	1,055	
	39.0		-	-	-	-	0.54	309	
	40.5		0.80	1,433	0.98	779	0.64	849	
	42.0		1.10	398	0.77	474	0.79	530	
	43.0		0.45	1,901	-	-	0.85	1,420	
	50.0		0.86	504	0.49	654	-	-	
	58.7		0.94	701	-	-	0.99	1,055	
	337.0		1.66	1,784	1.73	1,142	-	-	
	432.7		1.77	1,592	1.90	1,259	2.29	1,560	
Young Thoroughbreds	Mean		0.96	943 (14)	1.08	714 (8)	0.98	820 (10)	
	SD		0.42	523	0.49	323	0.49	440	
Adult Thoroughbreds									
All adults	Mean		2.83	1,711 (4)	2.49	1,886 (3)	3.01	1,707 (4)	
	SD		0.78	213	0.42	506	0.39	218	
Detained adults	Mean		3.81	2,006 (1)	2.44	1,475 (1)	2.75	1,770 (2)	
	SD		-	-	-	-	0.37	351	
Trained adults	Mean		2.50	1,613 (3)	2.52	2,092 (2)	3.27	1,644 (2)	
	SD		0.52	103	0.59	508	0.19	55	
Young other horses									
	2.15	♂	0.19	2,632	0.13	2,193	-	-	
	2.98		0.49	761	0.45	529	0.59	761	
	22.0		0.72	563	-	-	0.85	680	
Thoroughbred X	39.0		1.18	776	0.86	449	0.92	623	
Thoroughbred X	62.0		-	-	-	-	2.38	370	
	109.1		1.27	1,490	1.15	989	1.64	1,275	
	114.5		1.42	1,359	1.28	1,732	1.33	1,389	
	118.2		1.45	1,518	1.02	1,442	1.85	1,518	
	153.7		1.06	2,532	1.53	1,351	1.36	1,259	
	178.2		-	-	-	-	2.83	1,842	
Thoroughbred X	203.6		0.87	1,450	1.42	921	1.32	862	
	207.3		-	-	1.35	1,821	1.78	1,280	
Young other horses									
All young other horses	Mean			0.96	1,453 (9)	1.02	1,270 (9)	1.53	1,078 (3)
	SD			0.43	733	0.47	595	0.66	246
Thoroughbred crosses	Mean		1.03	1,113 (2)	1.14	685 (2)	1.54	618 (3)	
	SD		0.22	477	0.40	334	0.75	246	
Other young horses	Mean		0.94	1,551 (7)	0.99	1,437 (7)	1.53	1,251 (8)	
	SD		0.49	793	0.51	554	0.68	379	
Adult other horses									
All adults	Mean		1.98	1,582 (13)	1.88	1,600 (11)	2.10	1,749 (12)	
	SD		0.30	202	0.45	450	0.35	369	
Thoroughbred crosses	Mean		1.88	1,749 (5)	1.95	1,676 (3)	2.09	1,848 (5)	
	SD		0.38	182	0.58	422	0.30	272	
Other adults	Mean		2.05	1,478 (8)	1.85	1,572 (8)	2.11	1,677 (7)	
	SD		0.26	137	0.44	485	0.41	432	
Entire males			-	-	2.82	1,220 (1)	-	-	
Castrated males									
	Mean		1.93	1,674 (6)	1.61	1,793 (5)	2.16	1,719 (6)	
	SD		0.34	179	0.28	469	0.21	389	
Females									
	Mean		2.03	1,503 (7)	1.96	1,484 (5)	2.04	1,778 (6)	
	SD		0.30	198	0.32	433	0.47	383	

N* = Number of observations.

Table 58 Logarithmic regression equations comparing the growth of capillary-fibre ratios with liveweight in m. semitendinosus, m. diaphragma and m. pectoralis transversus in dogs and horses.

Muscle	Type of animal	Number of observations	Growth ratio b*	Se b	log a	r **
M. semitendinosus						
	Greyhounds	20	0.815	0.084	-3.276	0.9155
	Other dogs	32	0.718	0.718	-2.742	0.8415
	Thoroughbreds	18	0.431	0.431	-2.070	0.8422
	Other horses	22	0.359	0.359	-1.707	0.9102
M. diaphragma						
	Greyhounds	19	0.659	0.036	-2.702	0.9760
	Other dogs	18	0.600	0.106	-2.336	0.8160
	Thoroughbreds	11	0.376	0.068	-1.794	0.8785
	Other horses	20	0.408	0.038	-1.991	0.9305
M. pectoralis transversus						
	Greyhounds	19	0.880 c	0.061	-3.583	0.9612
	Other dogs	18	0.537 c	0.050	-2.010	0.9361
	Thoroughbreds	14	0.422 c	0.050	-2.241	0.9383
	Other horses	23	0.215 c	0.051	-0.871	0.6774

* Regression coefficient b, standard error Se b.

c Values of b within a species followed by this superscript are significantly different ($p < 0.01$) from one another.

** Correlation coefficient.

Figs. 121 - 126.

Fresh frozen transverse sections from:

m. diaphragma of a 2.2 kg, 160 day "in utero"
male Connemara cross pony (Fig. 121);

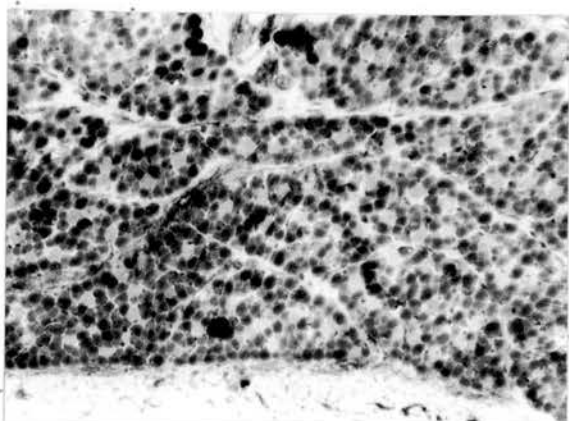
the superficial region of m. pectoralis
transversus of a 0.38 kg, one week old female
Greyhound (Fig. 122);

m. diaphragma of a 25 kg, four year old female
Afghan (Fig. 123);

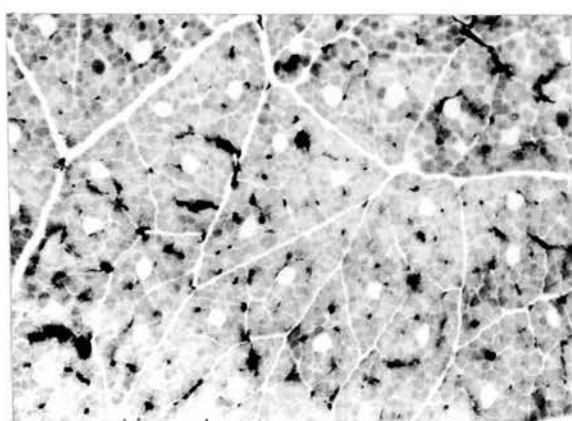
the superficial caudal region of a 28 kg three
year old male Greyhound (Fig. 124);

m. diaphragma of a 318 kg, six year old Piebald
pony mare (Fig. 125);

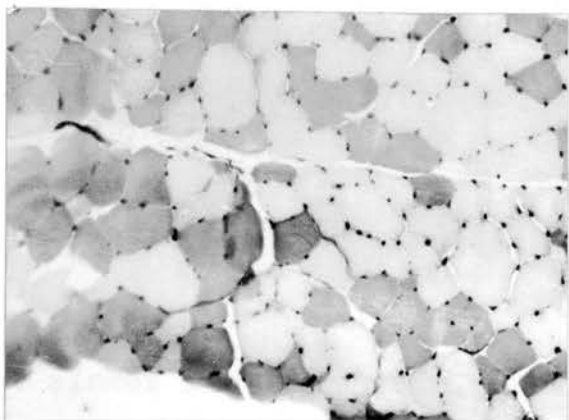
and the superficial region of m. pectoralis
transversus of a 445 kg, six year old Connemara
cross mare (Fig. 126); all treated to demonstrate
capillaries.



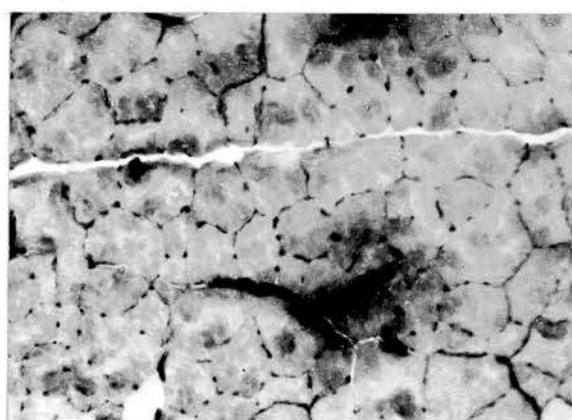
121.



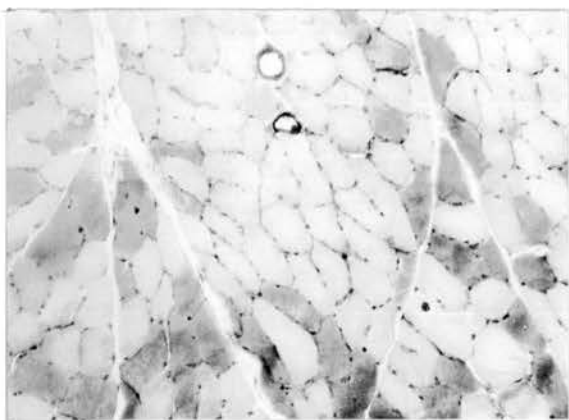
122



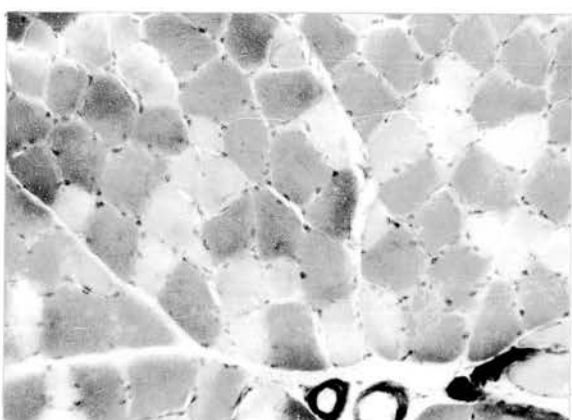
123.



124



125



126

100 μ m

Table 59 Biochemical estimation of succinate dehydrogenase activity (SDHase) in m. semitendinosus, m. diaphragma and m. pectoralis transversus of dogs and horses expressed as mg of INT formazan produced per g of muscle per 15 minutes.

HORSES											
Type of animal	Live-weight (kg)	Sex	M. semi-tendinosus	M. diaphragma	M. pectoralis transversus	Type of animal	Live-weight (kg)	Sex	M. semi-tendinosus	M. diaphragma	M. pectoralis transversus
DOGS											
Greyhound pups											
	260	♂	0.38	0.88	0.66		16,000	♂	1.01	-	0.61
	377	♀	0.42	0.96	-		19,000	♀	0.84	-	-
	1,056	♂	1.45	1.52	1.26		24,000	♀	0.78	3.16	1.41
	1,174	♂	0.62	1.39	0.60		29,000	♂	1.04	-	-
	2,280	♂	0.80	1.49	1.09		31,500	♂	0.86	-	0.84
	5,712	♀	1.09	-	-		50,000	♀	-	1.94	-
	11,000	♂	1.04	1.92	0.90						
	15,250	♂	1.94	2.69	1.20	Thoroughbred adults	458,186	♀	1.78	-	0.61
	19,750	♂	1.65	1.95	0.98		470,909	♀	1.25	-	2.23
	23,500	♀	2.26	2.15	1.43		483,636	♂	1.32	-	1.26
Greyhound adults	D* 24,150 (inside)	♀	2.36 (2.74)	-	-	Other foals					
	25,000	♀	3.54	2.91	-	Thoroughbred X	39,000	♂	1.34	-	1.00
	D* 23,300	♂	3.65	2.91	-		114,546	♀	1.81	3.37	2.12
	D* 28,500	♀	2.23	2.50	-	Other adults	118,182	♂	0.67	1.11	1.17
	(inside)		2.50	-	-						
	D* 30,000	♂	2.06	2.23	-						
	(inside)		2.76	-	-						
	37,000	♂	2.29	3.14	-						
Other pups	6,585	♀	1.49	1.62	-						
	8,500	♂	1.13	1.25	0.83						
Other adults	9,900	♀	1.13	1.73	1.06						
	-		-	-	-						

D* Detained Greyhounds.

Table 60 Classification of fibre types in mammalian muscle.

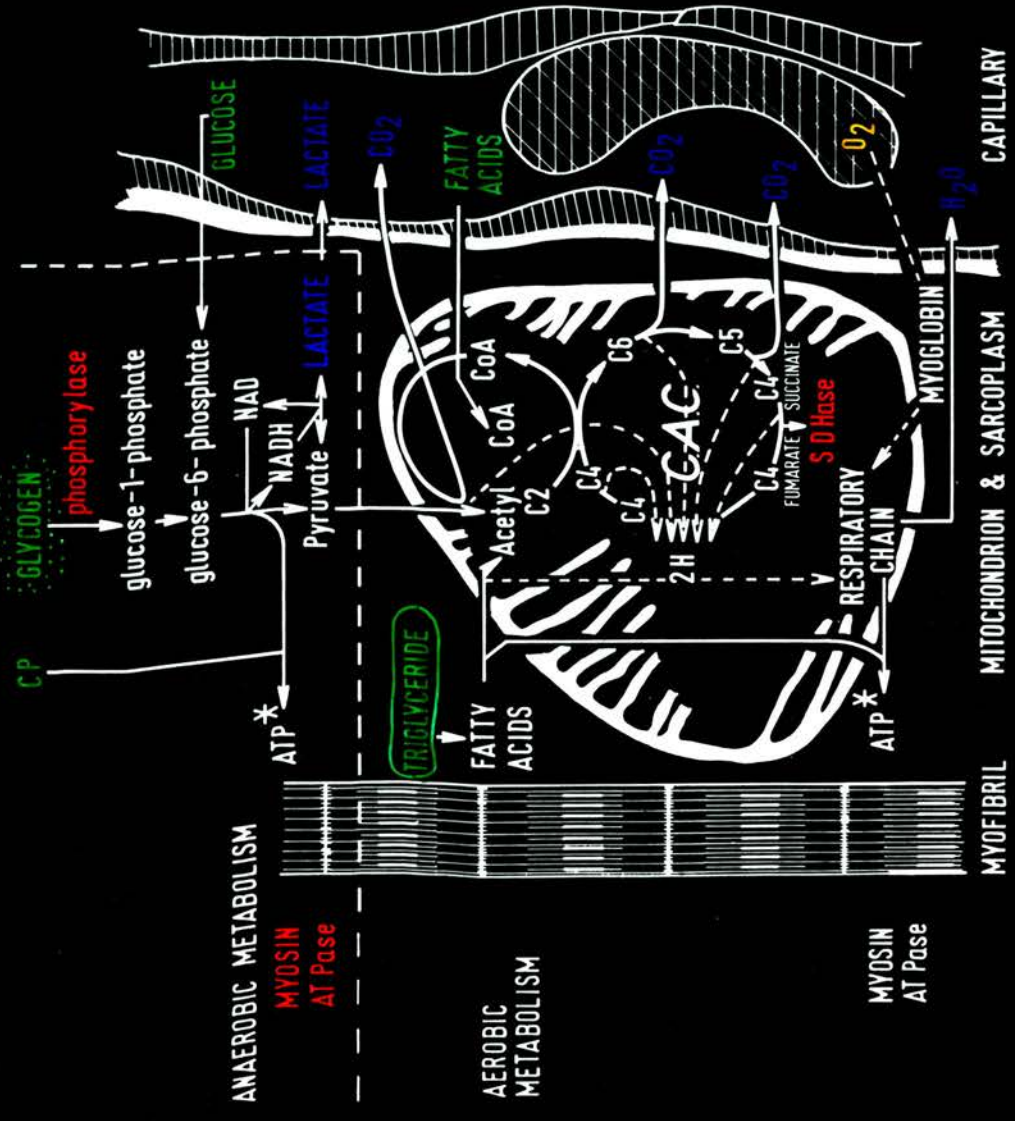
Gunn and Davies (1971)	SLOW-TWITCH AEROBIC		FAST-TWITCH ANAEROBIC		FAST-TWITCH COMBINED FAST-TWITCH OXIDATIVE GLYCOLYTIC	FAST-TWITCH AEROBIC	SLOW-TWITCH COMBINED
	SLOW-TWITCH AEROBIC	SLOW-TWITCH OXIDATIVE	FAST-TWITCH ANAEROBIC	FAST-TWITCH			
Peter et al. (1972)						-	-
Dubowitz and Pearce (1960)	1		11		-	-	-
Stein and Padykula (1962)	B		A		C	-	-
Engel (1962)	1		11		-	-	-
Romanul (1964)	111		1		11	-	-
Padykula and Gauthier (1966)	Intermediate		White		Red	-	-
Moody and Cassens (1968)	Red		White		Intermediate	-	-
Hall-Craigs (1968)	Slow-red		Fast-White		Fast-red	-	-
Edgerton and Simpson (1969)	Intermediate		White		Red	-	-
Brooke and Kaiser (1970)	1		11B		11A	-	-
Yellin and Guth (1970)	β		$\alpha\beta$		α	-	-
Ashmore and Doerr (1971)	β -red		α -white		α -red	-	-
Burke et al. (1971)	Slow		Fast-fatiguable		Fast-fatigue resistant	-	-
Johnson and Pearce (1971)	1		11		111	-	-

Fig. 127.

Outline of anaerobic and aerobic metabolism in muscle. The hatched line separates the metabolic processes which may take place without oxygen from those which need oxygen. (Modified from Davies, 1973).

Key: Energy sources. Marker enzymes. Products.

SUMMARY OF ANAEROBIC AND AEROBIC METABOLISM IN SKELETAL MUSCLE



* ATP is produced most rapidly by anaerobic metabolism, but more ATP is formed per mole of glucose using aerobic metabolism.

Fig. 128.

**Diagrammatic representation of m. semitendinosus
in the dog.**

Fig. 129.

**Diagrammatic representation of m. semitendinosus
in the horse.**

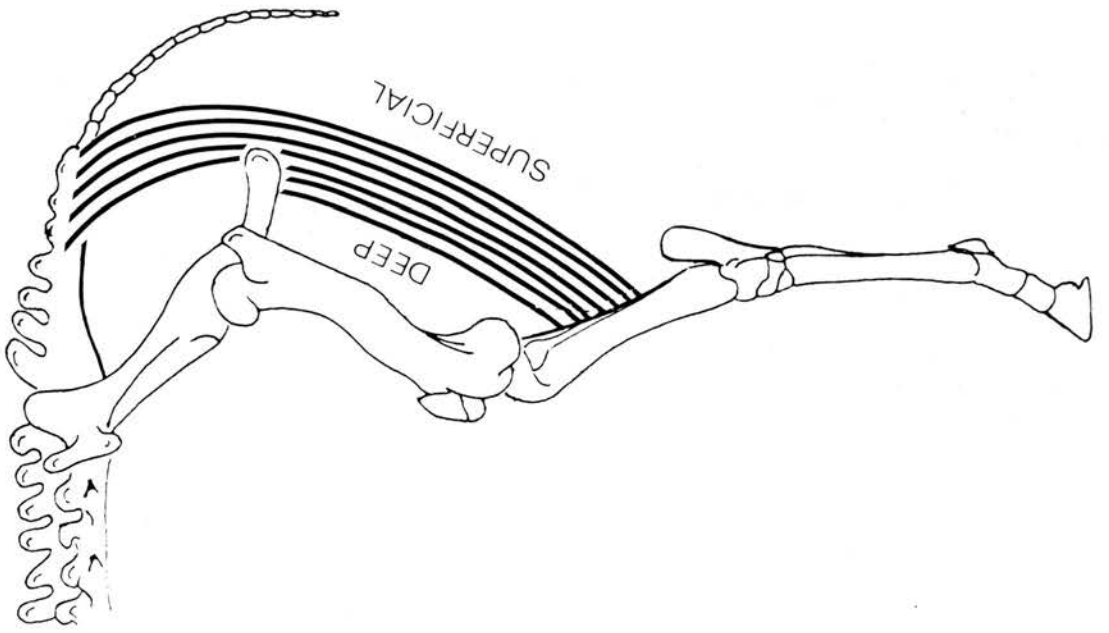
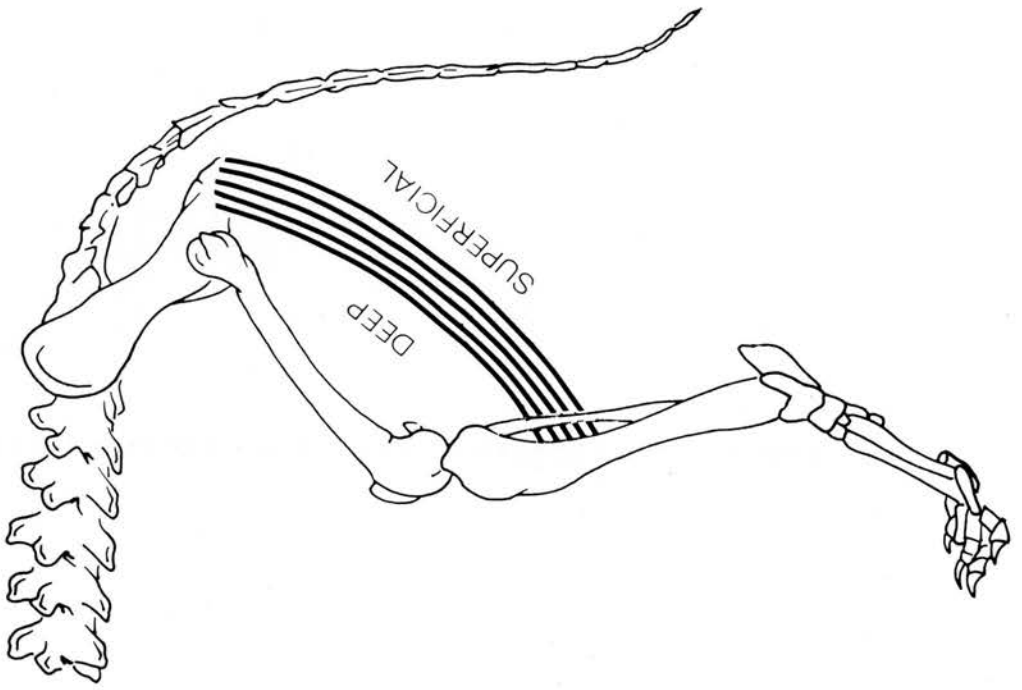


Fig. 130.

**Interrelationships of factors dictating the speed
of running animals.**

SPEED OF RUNNING



COORDINATED GAIT



STRIDE LENGTH

X

STRIDE FREQUENCY

LENGTH OF LIMBS

NATURAL FREQUENCY OF LIMBS

RANGE OF MOVEMENT OF JOINTS

MECHANICAL ADVANTAGE OF MUSCLES

ACCELERATION CAPACITY

INTRINSIC SPEED OF SARCOMERE CONTRACTION

(Force produced by muscle relative to body weight)

INTERNAL MUSCLE ARCHITECTURE

REPETITIVITY OF LIMB MOVEMENT
(Anaerobic and aerobic energy supply mechanisms)

APPENDIX 1

List for recording data obtained from total or partial muscle dissection of the horse. All weights are recorded in grammes, all linear measurements are made in centimetres and all volumes recorded in cubic centimetres.

Breed	Welsh Mountain
Sex	Male
Identification number	E4373
Age (postnatal age plus 338 days)	855 days
Weight	109000
Respiratory system	1190
Heart	695
Abdominal viscera including the digestive system, spleen, and urinogenital system.	30453
Spinal cord	146
Head	8182
Integument comprised of skin, tail, hooves, and where present mammary glands, penis, sheath, testicles and scrotum.	8332

DATA FROM HALF CARCASS

Fat	1984
Fascia, ligaments and scrap (blood vessels, nerves and lymph nodes)	527
Fore limb tendons	110
Hind limb tendons	200

MUSCLES AND CONSTITUENTS OF MUSCLE GROUPS

Cutaneus	399
Cutaneus colli	
Cutaneus trunci	
Attaching fore limb to the body	2666
Sternocephalicus	
Brachiocephalicus	
Trapezius cervicalis	
" thoracalis	
Rhomboides cervicalis	
" thoracalis	
Latissimus dorsi	
Pectorales superficiales	
" profundi	
Serratus dorsalis (cranialis and caudalis)	
" ventralis (cervicis and thoracis)	
Upper fore limb	2018
Deltoideus	
Supraspinatus	
Infraspinatus	
Teres major	
" minor	
Subscapularis	
Coracobrachialis	
Articularis humeri	
Biceps brachii	
Brachialis	
Tensor fascia antebrachii	
Triceps brachii	

Lower fore limb	542
Anconeus	
Extensor carpi radialis	
Extensor digitorum communis	
" " lateralis	
Extensor carpi obliquus	
Flexor carpi radialis	
" " ulnaris	
Ulnaris lateralis	
Flexor digitorum superficialis	
" " profundus	
Costal muscles	848
Levatores costarum	
External intercostals	
Internal intercostals	
Retractor costae	
Transversus thoracis	
Abdominal muscles	1430
Obliquus externus abdominis	
Obliquus internus abdominis	
Rectus abdominis	
Transversus abdominis	
Axial muscles	2010
Omohyoideus	
Sternothyroideus	
Scalenus dorsalis	
" ventralis	
Cervicalis ascendens	

Axial muscles continued

Rectus capitis ventralis major

" " " minor

Rectus capitis lateralis

Spinalis

Longissimus costarum

Longus colli

Intertransversales colli

Splenius

Longissimus capitis et atlantis

Complexus

Multifidis cervicis

Obliquus capitis anterior

" " posterior

Rectus capitis dorsalis major

" " " minor

Multifidis dorsi

Intertransversales lumborum

Coccygeus

Sacro-coccygeus dorsalis

" " lateralis

" " ventralis

Intertransversalis caudae

Retractor ani

Iliopsoas group

638

Psoas major

" minor

Iliacus

Quadratus lumborum

Longissimus (dorsi and cervicis)		856
Upper hind limb		6,423
Semitendinosus	504	
Semimembranosus	590	
Adductor	421	
Biceps femoris	1268	
Sartorius	85	
Gracilis	250	
Pectineus	71	
Quadratus femoris	24	
Quadriceps femoris	1,040	
Tensor fasciae latae	207	
Glutei	1,885	
Obturator internus	78	
externus and		
gemelli		
Lower hind limb		798
Extensor digitorum longus		
" " lateralis		
" " brevis		
Tibialis cranialis		
Peroneus tertius		
Gastrocnemius		
Soleus		
Popliteus		
Flexor digitorum superficialis		
" " profundus		
Muscle subtotal		<u>18628</u>

(appendix 1 p.6)

Diaphragm		548	
Total muscle (subtotal x 2, plus diaphragm)		37,803	
BONES			
Fore limb		1,531	
Hind limb		1,834	
Ribs and costal cartilages		941	
	Bone subtotal	4,306	
Sternum		246	
Vertebrae and pelvis		4,428	
Total bone (subtotal x 2, plus sternum, vertebrae and pelvis)		13,286	
REST plus TOTAL MUSCLE plus TOTAL BONE		105,729	(97% of total body weight)

BONE LENGTHS, WEIGHTS and VOLUMES

	Length	Weight	Volume
Humerus	22.5	490	473
Radius and ulna	32.9	405	397
Femur	30.7	736	712
Tibia and fibula	28.7	473	420

APPENDIX 2

List for recording data obtained from total or partial muscle dissection of the dog. All weights are recorded in grammes, all linear measurements are made in centimetres and all volumes recorded in cubic centimetres.

Breed	Collie x Terrier
Sex	Female
Identification number	C6472
Age	1095 days
Weight	10400
Respiratory system	165
Heart	108
Abdominal viscera	1557
including the digestive system, spleen, and urinogenital system.	
Spinal cord	18
Head	890
Integument	1234
comprised of skin, tail, claws, and where present mammary glands, penis, sheath, testicles and scrotum.	
DATA FROM HALF CARCASS	
Fat	116
Fascia, ligaments and scrap (blood vessels, nerves and lymph nodes)	10
Fore limb tendons	7
Hind limb tendons	14

MUSCLES AND CONSTITUENTS OF MUSCLE GROUPS

Cutaneus trunci	-
Attaching fore limb to the body	354
Sternocephalicus	
Branchiocephalicus	
Latissimus dorsi	
Trapezius cervicalis	
" thoracalis	
Rhomboideus cervicalis	
" thoracalis	
" capitis	
Pectoralis superficialis	
" profundus	
Serratus dorsalis (cranialis and caudalis)	
" ventralis (cervicis and thoracis)	
Omotransversarius	
Upper fore limb	240
Deltoideus	
Supraspinatus	
Infraspinatus	
Teres major	
" minor	
Subscapularis	
Coracobrachialis	
Biceps brachii	
Brachialis	
Tensor fascia antebrachii	
Triceps brachii	

Anconeus

Extensor carpi radialis

Extensor digitorum communis

" " **lateralis**

pollicis longus et indicus

proprius

Flexor carpi radialis

" " **ulnaris**

" **digiti quinti**

" **digitorum brevis**

" " **superficialis**

" " **profundus**

Ulnaris lateralis

Brachioradialis

Pronator teres

Pronator quadratus

Supinator

Abductor digiti quinti

" **pollicis brevis et opponens**

pollicis

" **pollicis longus**

" **digiti quinti**

" **digiti secundi**

Adductor pollicis

Interossei

Lumbricales

Flexor pollicis brevis

Lower fore limb continued

Interflexorii

Palmaris brevis accessorius

Costal muscles 106

Levatores costarum

External intercostals

Internal intercostals

Retractor costae

Transversus thoracis

Abdominal muscles 170

Obliquus externus abdominis

" internus abdominis

Rectus abdominis

Transversus abdominis

Axial muscles 332

Sternothyroideus

Sternohyoideus

Scalenus

Rectus capitis dorsalis

" " lateralis

" " ventralis

Spinalis et semispinalis thoracis

et cervicis

Semispinalis capitis

Iliocostales

Longus colli

Intertransversarii

Rotatores

Splenius

Axial muscles continued

Longus capitis

Longissimus cervicis

" capitis

Multifidus

Transversus costarum

Obliquus capitis caudalis

" " cranialis

Coccygeus

Sacrococcygei

Ischiococcygeus

Levator ani

Intertransversarius dorsalis

coccygeus

Intertransversarius ventralis

coccygeus

Iliopsoas group

45

Psoas major

" minor

Iliacus

Quadratus lumborum

Longissimus (thoracis and lumborum)

205

Upper hind limb

594

Semitendinosus

40

Seminembranosus

63

Adductor

90

Biceps femoris and abductor

100

cruris caudalis

Upper hind limb continued

Sartorius	30
Gracilis	31
Pectineus	5
Quadratus femoris	4
Quadriceps femoris (including articularis genus)	125
Tensor fasciae latae	24
Glutei, piriformis and capsularis coxae	65
Obturator internus, externus and gemelli	17

Lower hind limb

85

Extensor digitorum longus	
" " lateralis	
" " brevis	
" hallucis longus	
Tibialis cranialis	
Peroneus brevis	
Peroneus longus	
Abductor digiti I, II and V	
Adductor digiti I, II and V	
Flexor digitorum superficialis	
" " profundus	
" hallucis brevis	
Gastrocnemius	
Popliteus	
Tibialis caudalis	

Lower hind limb continued

Interflexorii

Lumbricales

Muscle subtotal 2199

Diaphragm 55

Total muscle (subtotal x 2, plus
diaphragm) 4453

BONES

Fore limb 101

Hind limb 112

Ribs and costal cartilages 77

Bone subtotal 290

Sternum 18

Vertebrae and pelvis 433

Total bone (subtotal x 2, plus sternum,
vertebrae and pelvis) 1031REST plus TOTAL MUSCLE plus TOTAL BONE 9750 (94% of
total body
weight)

BONE LENGTHS, WEIGHTS and VOLUMES

	Length	Weight	Volume
Humerus	13.5	39	30
Radius and ulna	15.5	35	22
Femur	14.2	40	30.5
Tibia and fibula	14.8	35	25

Appendix 3.

Appendix 4.

Appendix 5.

Appendix 6.

9. Changes in organ weights in mice exposed to moderate or severe hypoxia. By E. J. CLEGG. *Department of Human Biology and Anatomy, University of Sheffield*

Mice exposed to moderate or severe hypoxia show differing patterns of loss in body weight. At moderately reduced atmospheric pressures weight loss is small and ceases after a few days, but at very low pressures it is continuous (Clegg & Harrison, *Proc. 3rd Int. Congr. Biometereol.* 1966).

In the present experiments groups of litter-mate pairs (experimental and control) of male C57BL mice were killed after periods of up to 7 days' exposure to atmospheric pressures of either 530 torr or 390 torr and changes in the weights of hearts, spleens, livers and kidneys were assessed after covariance adjustment to allow for differences in body weights between groups. At both levels of hypoxia adjusted mean heart and spleen weights were increased over control values, but surprisingly, in comparisons between the two hypoxic groups the responses were greater at the less severe level of hypoxia. Liver weights were significantly decreased only at 390 torr; kidney weights showed no particular trend. Morphometric examination of the spleen showed that in hypoxic animals the amounts of red pulp were increased, the response being generally greater at 530 torr.

Both heart and spleen have been shown to be of importance in adaptive responses to hypoxia and the paradoxical result of this investigation, that the response appears greater when the degree of hypoxia is less, is interpreted as meaning that while at 530 torr adaptive processes are successful, at least in the short term, at 390 torr they are not. At this pressure lack of overall homeostasis itself reduces the extent of specific adaptive responses.

10. The ultrastructure of synovial cells in vitro. By MARY GLEN-BOTT. *Department of Anatomy, St Thomas's Hospital Medical School, London and University of Hong Kong*

Electron microscopy of the synovial membrane reveals two cell types (Barland *et al.*, *J. Cell. Biol.* **14**, 1962). Type A cells have numerous filopodia and vacuoles but little endoplasmic reticulum and their functions are absorptive while type B cells, with abundant endoplasmic reticulum, have a secretory role.

Synovial cells were washed from trypsinized rabbit knee joints using a modification of the method of Fraser & McCall (*Ann. rheum. Dis.* **24**, 1965). The ultrastructure of these cells was compared with those of the intact joint both before and after trypsinization and after the washing procedure was completed. The washed cells were also kept in conditions of culture for periods of 4, 24 and 48 h and examined by electron microscopy. They showed immediate changes in morphology which included increased electron density; more numerous filopodia and evidence of phagocytosis. The two cell types were not now clearly distinguishable. After 4 h in suspension culture all the cells had a similar morphology: with a more rounded outline, indented nucleus, free cytoplasmic ribosomes, Golgi complex and also packed filaments. After 24 and 48 h in culture the cells which attached to a flat surface contained numerous large vesicles and dense bodies.

These results indicate that the two major synovial cell types lose their characteristic morphology while adapting to the altered conditions of culture. The two cell types of the intact joint may represent different functional states of the same cell and some morphological features of the cultured cells indicate that the synovial cell belongs to the same class of cell as the macrophage.

11. A comparative histochemical study of the mammalian diaphragm and M. semitendinosus. By A. S. DAVIES and H. M. GUNN. *Department of Veterinary Anatomy, University of Edinburgh* (Fig. 3)

Histochemical methods for myosin adenosine triphosphatase (ATPase), succinic dehydrogenase (SDHase), phosphorylase and lipids were used on fresh-frozen diaphragm and M. semitendinosus samples from adult mice, rats, rabbits, cats, dogs and horses. Samples of diaphragm

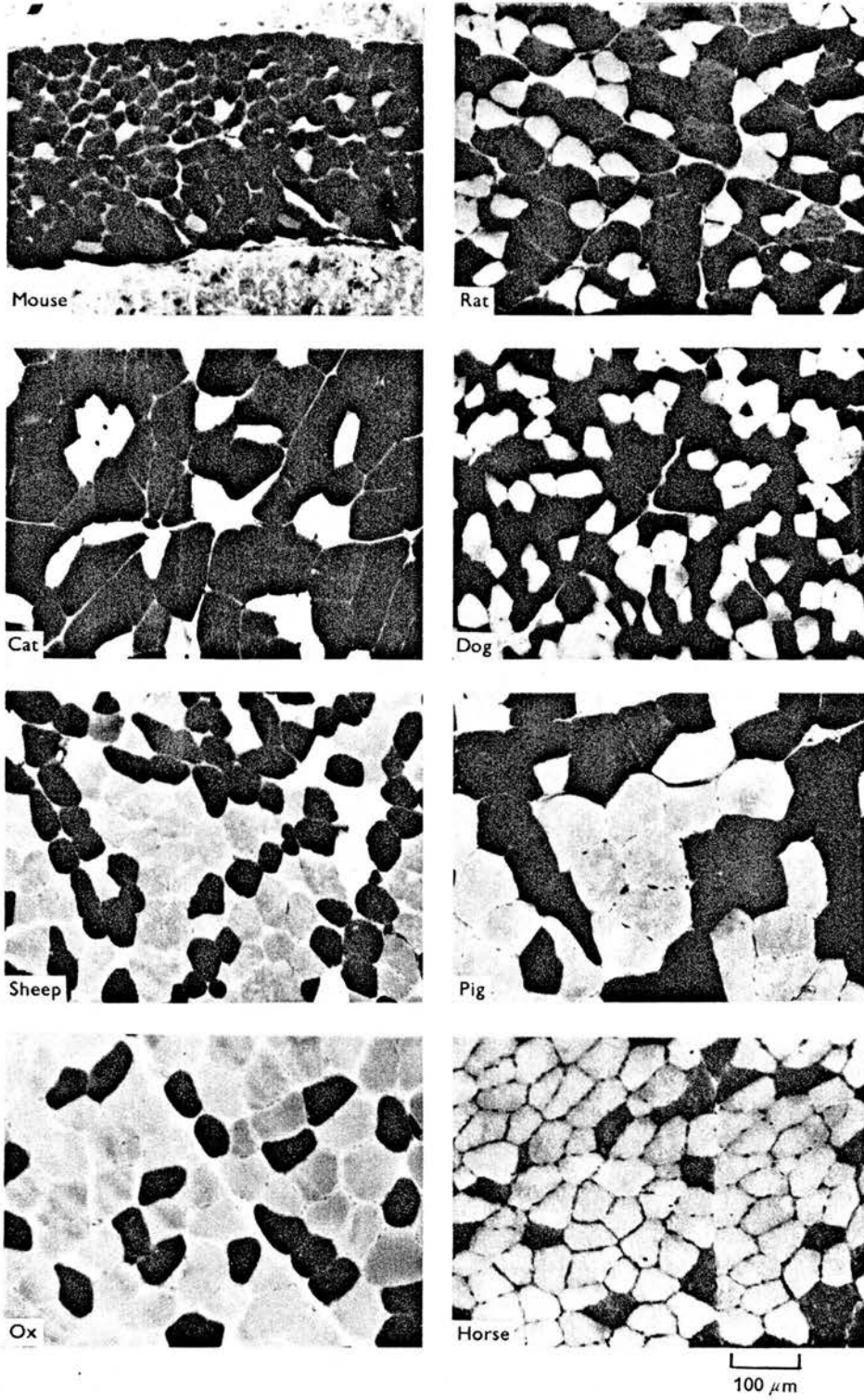


Fig. 3

only were obtained from adult pigs, sheep and cattle. Histochemical profiles of about 400 individual fibres for each sample were determined by tracing transverse serial sections.

In the diaphragm, the percentage of ATPase-high fibres tended to decrease with increasing body size (Fig. 3). The superficial region of *M. semitendinosus* of the smaller animals contained only ATPase-high fibres. With increasing body size, the deep region of mixed fibre population occupied a larger proportion of the muscle and the proportion of its fibres low in ATPase activity increased. The effect of body size on fibre type was much greater in the diaphragm than in *M. semitendinosus*.

The intensity of staining with Sudan Black B, with or without previous acetone extraction, corresponded to SDHase activity in individual fibres. Gauthier & Padykula (*J. Cell Biol.* **28**, 1966) reported decreased sudanophilia of fibres of the mammalian diaphragm with increasing body size. Although this trend was confirmed, the diaphragm of larger mammals was nevertheless composed of fibres of relatively high sudanophilia and SDHase activity. When the SDHase activity of fibres within the diaphragm of each animal was compared, the proportion of high to low activity fibres varied between species, but was not influenced by body size.

In general, the percentage of fibres in the diaphragm with high phosphorylase activity increased with increasing body size. ATPase-high fibres were high in phosphorylase, except in those animals with a lower percentage of phosphorylase-high than ATPase-high fibres. In *M. semitendinosus*, phosphorylase activity corresponded to ATPase activity.

The significance of these results will be discussed.

12. The sphincteric mechanism of the inguinal canal. By P. K. FITZGERALD. *University College, Cork*

Electromyography has now shown that the internal oblique and transversus muscle fibres that arise from the inguinal ligament are on constant guard over the inguinal canal and thereby act as a sphincter for it. These are the only muscle fibres in the abdominal wall that show constant activity. The inguinal sphincter is supplied by the first lumbar nerve. Paralysis of the sphincter may result from central or peripheral lesions of this nerve. Incompetence may result from a variety of conditions ranging from metabolic conditions such as hypovitaminosis to prolonged strain of the sphincteric muscles, e.g. abdominal distension, obesity, urinary obstruction, prolonged standing, chronic cough, etc. The surgical treatment of inguinal hernia resolves itself into (a) removal of the sac, (b) reconstruction of the inguinal canal. In infants since the external ring almost superimposes the internal ring it is often not necessary to open the canal. In adults the competence or incompetence of the inguinal sphincter will determine whether the reconstruction of the canal is advisable or not. If the sphincter is competent a Bassini type of repair is adequate. If the sphincter is incompetent after appropriate means of producing tone in the sphincter fails, then either a mechanical support or a reconstruction of the abdominal wall is indicated. A reconstruction of the abdominal wall will vary with the age of the patient and condition of the musculature. In summary, therefore:

- (1) The inguinal canal is controlled by sphincteric fibres.
- (2) The course and distribution of L1 nerve should be kept in mind in planning operations in the lumbar and low abdominal regions so as to prevent paralysis of the inguinal sphincter.
- (3) The technique for repair of inguinal hernia should depend on the competence of L1 myotome.

13. Sexual differentiation in the brain of the neonatal rat. By H. K. DARRAH, P. C. B. MACKINNON and A. W. ROGERS. *M.R.C. Neuroendocrinology Unit and Department of Human Anatomy, University of Oxford*

Sexual differentiation of the male rat brain occurs under the influence of the testis during the first week of life (Harris, *Endocrinology* **75**, 1964). Differentiation of the female rat brain into a male-type brain however can be simulated by transplanting testicular tissue or injecting androgenic hormones into the neonatal animal. Females treated in this way exhibit male-type behaviour and become acyclic and anovular in adult life. Recent evidence suggests that the

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Histochemical Characteristics of Muscle Fibres in the Diaphragm

By H. M. GUNN and A. S. DAVIES. (*Department of Veterinary Anatomy, University of Edinburgh, Edinburgh EH9 1QH, U.K.*)

This study attempts to define and explain histochemical variations in the muscle fibres of the diaphragm in mammals of various body sizes.

Fresh frozen transverse sections of muscle fibres were treated to demonstrate aerobic metabolism, anaerobic metabolism and lipid distribution. These properties were demonstrated by histochemical methods for succinate dehydrogenase activity, phosphorylase activity and the Sudan Black B method for lipids respectively. Incubation of sections with ATP and Ca^{2+} at pH 9.4 and subsequent treatment with Co^{2+} and ammonium sulphide demonstrated myosin adenosine triphosphatase activity. It may distinguish between fibres with a fast and a slow intrinsic speed of contraction due to the presence or absence of a deposit in the myofibrils.

By using serial frozen sections and back projection, histochemical profiles of about 400 individual muscle fibres were made on each sample taken from the diaphragms of shrews, mice, rats, rabbits, cats, dogs, sheep, humans, pigs, oxen and horses. From these profiles the following types of muscle fibres were found: fast-contracting, aerobic;

fast-contracting, combined; fast-contracting, anaerobic; slow-contracting, aerobic; slow-contracting, combined.

Studies on myosin adenosine triphosphatase showed that the percentage of fast-contracting fibres increased with decreasing body size; this phenomenon can be related to the faster speed of contraction of the diaphragm in smaller mammals.

Biochemical studies have shown that the ability for aerobic metabolism is greater in the diaphragms of smaller mammals. Histochemically this trend was seen, but differences in succinate dehydrogenase activity between fibres were not as distinct as the differences in adenosine triphosphatase activity. The proportion of aerobic and anaerobic fibres varied between species, but was not influenced by body size. Phosphorylase activity tended to show an opposite trend to that of adenosine triphosphatase. The horse had nearly 100% of its fibres high in phosphorylase activity, but in the shrew diaphragm no fibres with phosphorylase activity were seen.

Fast-contracting muscle fibres were also high in phosphorylase activity, showing that faster-contracting fibres used mainly an anaerobic metabolism. In smaller animals the proportion of fibres with high adenosine triphosphatase activity exceeded that of fibres with high phosphorylase activity, so aerobic metabolism may be used by fast-contracting fibres.

Histochemical fibre types in the mammalian diaphragm

A. S. DAVIES AND H. M. GUNN

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Veterinary Studies, Edinburgh*

(Accepted 3 March 1972)

INTRODUCTION

In 1873, Ranvier showed that differences in the colour of femoral muscles of the rabbit could be related to differences in speed of contraction. This relationship has rarely been questioned, even though biochemical advances have shown that the redness is due to iron-containing pigments involved in oxygen and electron transport, and there is no reason to suppose that variations in the structure and function of the contractile myofilaments need be reflected in changes in the colour of the muscle. The advent of histochemical methods which reveal, in single fibres, the enzymes concerned with the release of energy and its connexion to a contractile force, has made the characterization of fibre types in muscle progressively more difficult.

Different levels of succinate dehydrogenase (SDHase) activity in individual muscle fibres were demonstrated by Padykula (1952), Rutenburg, Wohman & Seligman (1953) and Wachstein & Meisel (1955). The patterns obtained with other methods for enzymes of aerobic metabolism corresponded to those for SDHase (Dubowitz & Pearce, 1960*b*; Engel, 1962; Romanul, 1964). It has been claimed that the activity of the anaerobic metabolic enzyme phosphorylase is 'reciprocal' to that of enzymes of aerobic metabolism in skeletal muscle fibres of the rat and human (Dubowitz & Pearce, 1960*a, b*) and the cat (Jinnai, 1960). This concept has been supported by Engel (1962, 1965, 1970) and Suchenwirth & Bundschu (1970) in human muscles; Nishiyama (1966) in respiratory muscles of the rat and cat; Kugelberg & Edström (1968) in rat crural muscles; Moody & Cassens (1968) in the longissimus and trapezius muscles of the pig; and Jasmin, Bokdawala & Desrosiers (1971) in crural muscles of the hamster. However, fibres high in SDHase and moderate to high in phosphorylase activity have been demonstrated in rat crural muscles (Romanul, 1964), in rat femoral muscles and m. soleus of monkey and rat (Bocek & Beatty, 1966), in the thyroarytenoid and cricothyroid muscles of the rabbit (Hall-Craggs, 1968), in guinea-pig crural muscles (Edgerton & Simpson, 1969), in cat crural muscles (Prewitt & Salafsky, 1970), and in the gastrocnemius and soleus muscles of the mouse and the triceps brachii and rectus abdominis muscles of the pig and ox (Ashmore & Doerr, 1971). Using methods for SDHase, glycogen and myosin adenosine triphosphatase (myosin ATPase), Stein & Padykula (1962) established histochemical 'profiles' from transverse serial sections of fibres in rat crural muscles. They showed that some fibres are high in both myosin ATPase and SDHase activity. The existence of this type of fibre confounds the simple division of muscle fibres into two histochemical types as proposed by Engel (1962, 1965, 1970) for human muscles and applied to crural muscles of the guinea-pig by

Karpati & Engel (1967, 1968); their 'Type I' fibres have high activities for the enzymes of aerobic metabolism and show little phosphorylase or myosin ATPase activity, whereas their 'Type II' fibres have low activity for aerobic enzymes and high activity for phosphorylase and myosin ATPase. Edgerton & Simpson (1969) defined three basic fibre types in the crural muscles of the rat and guinea-pig; those with activities high for myosin ATPase, aerobic and anaerobic enzymes, those with activities high for myosin ATPase and anaerobic enzymes and low for aerobic enzymes, and those with activities low for myosin ATPase and anaerobic enzymes and showing 'intermediate' activity for aerobic enzymes. This 'intermediate' fibre frequently has, however, a higher SDHase activity than that of fibres high in myosin ATPase in muscles of the pig and ox (Ashmore & Doerr, 1971). Even this more complex classification does not seem to be generally applicable to all muscle fibres.

The present study was undertaken to resolve some of the apparently contradictory reports on the relationships between histochemical reactions in individual fibres. Patterns of fibre type profiles in one particular muscle have been established in mammals of different body size, using SDHase as an indicator of aerobic capacity, phosphorylase as an indicator of anaerobic capacity, and myosin ATPase as an indicator of the intrinsic speed of contraction of individual fibres. There has been no previous study comparing fibre type profiles in the same muscle of several different species. The diaphragm was chosen because this muscle has a similar function in all mammals and a comparable region, the costal diaphragm, can be sampled in each animal. The results have been briefly reported in a previous communication (Davies & Gunn, 1971).

MATERIAL AND METHODS

Preparation of material

Adult mice, rats, rabbits, cats, dogs and horses were killed by an overdose of anaesthetic. Adult sheep, pigs and cattle were killed by the usual abattoir procedures. The mice, rats and rabbits were laboratory strains reared in cages. The other animals used were from normal domestic and farm environments. The numbers and sex of the animals of each species are shown in Table 1. One sample of the costal diaphragm of each animal was removed within 45 minutes of death. Blocks of muscle, supported between blocks of liver tissue in the case of the smaller animals, were mounted on a cryostat chuck. A 5 mm thick cork sheet interposed between the chuck and the tissue prevented splitting of the tissue when chuck and tissue were rapidly frozen by plunging into dichlorodifluoromethane (Arcton 12, I.C.I.) cooled to its melting-point of -158°C with liquid nitrogen. About ten adjacent serial transverse sections were cut 10 μm thick at -20°C , mounted directly on to coverslips, and allowed to thaw and dry rapidly at room temperature.

Succinate dehydrogenase

Histochemical methods

Sections were incubated for 20 minutes at 37°C in a medium composed of 10 ml of 0.2 M phosphate buffer at pH 7.6, 10 ml of 0.2 M sodium succinate, and 20 ml of nitro blue tetrazolium (1 mg/ml) (Nachlas *et al.* 1957). Gas bubbles frequently formed between the section and the coverslip; these were often eliminated by drying the section between washing and fixation in 4% formaldehyde.

Table 1. Mean transverse-sectional areas of diaphragm muscle fibres

Species	No. of animals			Transverse-sectional area (μm^2)		
	Male	Female	Total	Mean	s.d.	Significance*
Mouse (<i>Mus musculus</i>)	4	0	4	1110	160	$P < 0.05$
Rat (<i>Rattus rattus</i>)	3	1	4	1990	460	N.S.
Rabbit (<i>Oryctolagus cuniculus</i>)	3	0	3	3170	180	N.S.
Cat (<i>Felis catus</i>)	1	1	2	3590	1720	N.S.
Dog (<i>Canis familiaris</i>)	4	1	5	1690	150	N.S.
Sheep (<i>Ovis aries</i>)	0	3	3	1870	300	N.S.
Pig (<i>Sus scrofa</i>)	1	5	6	5680	1170	$P < 0.001$
Ox (<i>Bos taurus</i>)	1	2	3	3790	460	N.S.
Horse (<i>Equus caballus</i>)	3	1	4	2420	560	N.S.
Total	20	14	34	2690	1370	—

* Significance of difference of mean for each species and mean for all species, tested at the 5% significance level by the test quotient t .
N.S. = not significant.

Lipids

Sections were fixed in 4% formaldehyde for 10 minutes and stained with a freshly filtered, saturated solution of Sudan black B in 70% ethanol for 20 minutes. Excess dye was removed by a brief wash in 50% ethanol. Some sections were immersed in acetone for 30 minutes between fixation and staining.

Phosphorylase

Takeuchi's (1956) modification of the method of Takeuchi & Kuriaki (1955) was used. Sections were incubated for three hours at 37 °C in a medium consisting of 75 mg glucose-1-phosphoric acid, 15 mg adenosine-5'-monophosphoric acid, 3 mg glycogen, 22.5 ml distilled water, 15 ml of 0.1 M acetate buffer at pH 5.8, one international unit of protamine zinc insulin and 7.5 ml of absolute ethanol. They were subsequently washed, dried, fixed in absolute ethanol, dried, and stained with dilute Lugol's iodine for three minutes. Because the colour faded, iodine staining was repeated immediately before subsequent use of the section.

Myosin ATPase

The calcium-cobalt method of Padykula & Herman (1955) was modified to improve the buffering capacity of the medium. Sections were fixed for exactly two minutes in cacodylate buffered 4% formaldehyde at pH 7.0. Without fixation, the sections floated off the coverslip, and prolonged fixation affected the characteristics of the enzyme (Stein & Padykula, 1962; Guth & Samaha, 1969). Sections were incubated for 20 minutes at 37 °C in a freshly made medium consisting of 8 ml of 1.0 M tris-(hydroxymethyl)-aminomethane, 4 ml of 0.18 M calcium chloride, and 60 mg ATP disodium salt made up to 30 ml with distilled water, which was then adjusted to a pH of 9.5 with 0.1 N-HCl and made up to a final volume of 40 ml. The final concentration of ATP was therefore 2.4 mM. With two washes in distilled water between treatments, the sections were immersed in 2% cobalt chloride for three minutes and developed in dilute ammonium sulphide for one minute.

Cell outlines

Sections were fixed for 10 minutes in 4% formaldehyde, washed, and stained for 20 minutes in Ehrlich's haematoxylin.

Methods for establishing fibre profiles and transverse-sectional areas

Profiles of about 400 individual fibres in each section were established by first back-projecting a haematoxylin stained section on to a glass screen, enabling a tracing of the fibre outlines to be made on transparent paper. Each serial section was then projected in turn. The histochemical reaction of each fibre was indicated on the tracing; Figs. 3-7 illustrate the type of material used. To estimate the level of activity of enzymes that showed a continuous spectrum of activity between fibres, a simple division into 'high' and 'low' was made for each fibre, relative to the overall level of activity of fibres in each section. It was not considered possible to compare one sample with another, because of difficulties of standardization of the preparation and processing of the material. This is considered to be a source of variation in the quantitative data between samples, and precludes the possibility of a comparison between species based on overall enzyme activity. Fibre transverse-sectional areas were estimated by counting the number of fibres projected within an area of known magnification on the screen.

RESULTS

Qualitative histochemistry

Succinate dehydrogenase

Diformazan deposition occurred as blue dots or irregular areas that appeared to form a network around the myofibrils (Figs. 13, 15, 17, 19). In fibres with a high level of activity, diformazan deposition was highest in the subsarcolemmal region. Diformazan was deposited in larger aggregations in the smaller animals. It was frequently observed that fibres shown in serial section to be myosin ATPase-low had a pattern of intense blue, punctate, clearly defined dots, moderately dense and evenly distributed, whereas the colour of the reaction in ATPase-high fibres was purplish, especially in freshly stained sections. This variation in reaction was not sufficiently consistent to use in identifying fibre types.

Lipids

The density of staining with Sudan black B, with or without previous treatment of the section with acetone, always corresponded to SDHase activity (Figs. 5, 6, 7). SDHase activity was therefore chosen to determine histochemical profiles.

Phosphorylase

Fibres varied in reaction from an intense blue network to a paler blue, to a diffuse pink, to fibres coloured only by the iodine. In all species except the mouse, fibres high in both phosphorylase and SDHase activity were seen (Figs. 4, 6, 17, 18).

Table 2. Percentage of histochemical fibre types in the diaphragm of nine mammalian species

Species	No. of fibres counted	Percentage of fibre types*											Contraction times† ms ± s.d.	
		Ah						Al						
		Sh		Sl		Sh		Sl		Sh	Ph	Ah		
		Ph	Pl	Ph	Pl	Ph	Pl	Ph	Pl					
Mouse	1436	—	93	—	—	—	7	—	—	100	—	93	—	
Rat	1337	7	25	27	2	1	38	—	—	71	35	61	18 ± 1	
Rabbit	1605	21	—	36	—	—	43	—	—	64	57	57	32 ± 4	
Cat	1612	16	—	45	—	—	39	—	—	55	61	61	39 ± 2	
Dog	3573	64	—	—	—	—	36	—	—	100	64	64	65 ± 5	
Sheep	2938	43	—	—	—	43	14	—	—	100	86	43	—	
Pig	2548	17	3	32	3	4	41	—	—	65	53	55	—	
Ox	1879	24	—	—	—	58	18	—	—	100	82	24	—	
Horse	2559	21	—	—	—	77	2	—	—	100	98	21	—	

* Key: Ah, Sh, Ph: high activity of myosin ATPase, SDHase or phosphorylase respectively. Al, Sl, Pl: low enzyme activity.

† Reference for contraction times: Sant'Ambrogio & Saibene (1970).

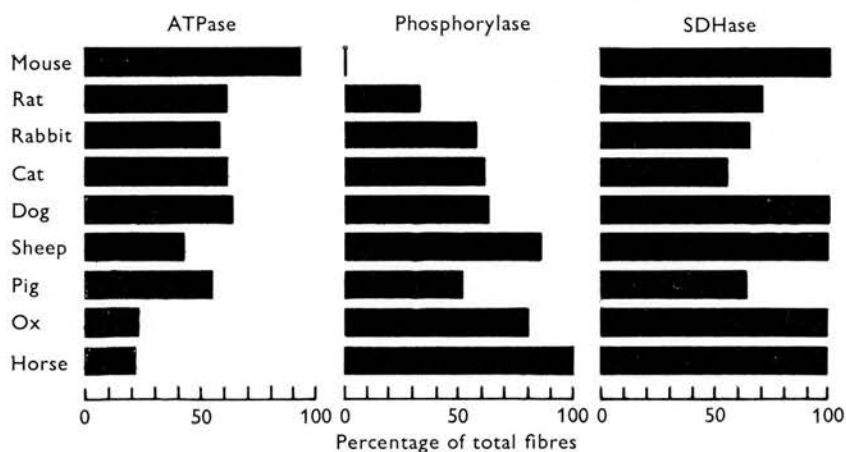


Fig. 1. Histogram showing the number of fibres of each species with high activity of myosin ATPase, phosphorylase and SDHase, as a percentage of total fibres sampled.

Myosin ATPase

Myosin ATPase-high fibres showed a dense brown reaction in which a brown network could usually be seen. These were always distinct from myosin ATPase-low fibres in which only the brown network was seen. Blood vessels were also stained; the reaction of capillary endothelia varied between species (Figs. 3, 9–12). Myosin ATPase-low fibres frequently had an activity of SDHase equal to or greater than adjacent myosin ATPase-high fibres (Figs. 3, 6, 13, 14, 15, 16, 19, 20); it was not therefore possible to grade the activity of SDHase from the myosin ATPase reaction.

Quantitative histochemistry

The data obtained on histochemical profiles of muscle fibres in the diaphragm are shown in Table 2 and Fig. 1. The proportion of myosin ATPase-high fibres decreases in the larger animals (Figs. 9–12). All myosin ATPase-low fibres are high in SDHase activity. A proportion of myosin ATPase-high fibres were classified as SDHase-low only in the rat, rabbit, cat and pig; hence the proportion of SDHase-high fibres is not dependent on body size. All fibres in the diaphragm of the dog (Fig. 8), for instance, are high in SDHase activity. The proportion of fibres high in phosphorylase activity increases in the larger animals. With the exception of all fibres in the mouse and a proportion of fibres in the rat and pig, all myosin ATPase-high fibres are high in phosphorylase activity. In the larger animals some myosin ATPase-low fibres are phosphorylase high. All species except the mouse have a significant proportion of fibres high in both phosphorylase and SDHase.

Mean transverse-sectional areas of diaphragm muscle fibres are shown in Table 1. Only two species are significantly different ($P < 0.05$) from the mean of all the species; the mouse has small fibres and the pig large fibres relative to the other species.

DISCUSSION

Sources of variation

All samples were taken from the costal diaphragm of adult animals, which were of mixed sex and from different environments. There is no published work on the difference in the proportion of histochemical fibre types between sexes. Following artificial exercise in rats (Edgerton, Gerchman & Carrow, 1969) and guinea-pigs (Barnard, Edgerton & Peter, 1970), an increase was observed in the proportion of crural muscle fibres with high activity of enzymes of aerobic metabolism. There was, however, no significant difference in the proportion of myosin ATPase-high fibres. The effect of exercise on fibre types in the diaphragm has not been studied. The mice, rats and rabbits sampled in the present study had had very little exercise and the other species an unknown amount. With present evidence, it is possible that SDHase-low fibres in the diaphragm of the rat, rabbit, cat and pig are present because of lack of normal exercise. Since adult animals were used, the decrease reported in the proportion of myosin ATPase-high fibres in the developing soleus muscle of the guinea-pig, rat and cat (Karpati & Engel, 1967) and pectineus muscle of the dog (Cardinet *et al.* 1969) does not influence the results of this study. The variation in the proportion of myosin ATPase-high fibres between animals within a species is high, but does not obscure the overall effect of body size. We have observed large differences, which are not related to body size, in the proportion of myosin ATPase-high fibres in the diaphragm and limb muscles between breeds of dogs and horses (unpublished observations). The vertebral, sternal and costal regions of the rat diaphragm have been shown to vary in their lipase and SDHase activity (George & Susheela, 1961), respiratory quotient (Susheela & George, 1963) and butyrate oxidation (Susheela & George, 1964). However, Günther (1952, 1953) observed no differences in the proportion of fibres with 'Fibrillenstruktur' and 'Felderstruktur' in these regions of the diaphragm of the rat, mouse and dog, and Nishiyama (1966) stated that there was no variation

between regions of the cat diaphragm in the proportion of fibre types demonstrated by histochemical methods for oxidative enzymes and phosphorylase.

The number of species, their range of body size, and the number of animals of each species used in the present study indicate a consistent pattern of fibre type distribution, but more detailed studies are needed to establish differences between breeds and the manner in which these differences develop.

Transverse-sectional areas of muscle fibres

The diaphragm samples used in our study were all removed before rigor and were therefore contracted. Freezing and section cutting were not considered to alter fibre size appreciably. Transverse-sectional areas were estimated only in regions in which fibres were cut transversely and where the amount of endomysium and perimysium was minimal. We therefore consider that the estimates of transverse-sectional area are comparable between samples and species.

The relation of body size to the transverse-sectional area of fibres in an equivalent muscle of different species has not been studied extensively. Joubert (1956) found that fibre diameters in the gastrocnemius muscle of two sheep, two rabbits, one pig and one ox were not related to body size. George & Naik (1959) studied the pectoralis muscle of 25 species of birds of varying body weight. The mean fibre diameter increased with increasing weight of the muscle, at a rate dependent on the mode of flight. Julian & Cardinet (1961) found that the mean transverse-sectional area of fibres of *m. biceps brachii* of a wide range of breeds of dogs (1.4 kg to 56 kg) was larger in heavier dogs. The dogs used in the present study were in the middle of this weight range. Gauthier & Padykula (1966) reported the results of fibre measurements in the diaphragm of 13 mammalian species, and claimed that there was a direct relationship between fibre diameter and body size. They gave no data for the horse and dog, which we found to have small fibres relative to several smaller species.

Our results suggest that there are large sources of variation in fibre transverse-sectional area apart from body size. The diaphragm of the mouse has a purely aerobic metabolism; small fibres would facilitate a high rate of oxygen diffusion. On this basis, Hill (1956) predicted that the diameter of muscle fibres should vary as the square root of linear body size. However, the fibres in the diaphragms of the species which we have studied do not fit this hypothesis.

Significance of the histochemical reactions used

Succinate dehydrogenase

Patterns of mitochondria, demonstrated by classical methods (Nachlas *et al.* 1957; Scarpelli & Pearse, 1958; Novikoff, Shin & Drucker, 1961) or by electron microscopy in skeletal muscle (Padykula & Gauthier, 1963; Ogata, 1964; Pieper, Feustel & Hubner, 1969) and kidney (Novikoff *et al.* 1961), have in each case been shown to follow the diformazan deposition caused by SDHase activity. Brooke & Engel (1966) provided evidence that nitro BT is selectively adsorbed on to mitochondria and sarcoplasmic reticulum of striated muscle fibres. Since, however, SDHase is believed to be entirely intramitochondrial (Roodyn, 1967), this should enhance the histochemical localization of this enzyme. A limited extent of diformazan deposition away from

sites of SDHase activity, such as lipid droplets (Hitzeman, 1963), should have little effect on the comparison between individual fibres, but the report of a heterogeneous all-or-none deposition in individual mitochondria (Seligman *et al.* 1967) could have more serious implications. It is possible that the SDHase activity of mitochondria from different fibres may vary (Blanchaer, 1964), but the density of diformazan deposited histochemically in a particular fibre after incubation for as long as 20 minutes should depend primarily on mitochondrial density, rather than on the actual level of SDHase activity.

Paul & Sperl (1952) demonstrated a direct relationship between estimates of mitochondrial density, determined by phase microscopy of blenderized tissue, and the oxidative capacity of a variety of muscles from different species. This relationship is supported by observations on the effect of severe exercise on limb muscles, which can produce a twofold increase in the capacity of muscle to oxidize pyruvate (Holloszy, 1967), accompanied by a concomitant increase in mitochondrial density as seen electron microscopically (Gollnick & King, 1969). Similar findings were reported by Kraus, Kirsten & Wolff (1969).

The assumption that the histochemical SDHase reaction indicates the capacity of an individual fibre for aerobic metabolism appears reasonable, although it lacks direct proof.

Sudan black B

Padykula & Gauthier (1963) showed that this stain coloured both triglyceride droplets and phospholipid in muscle fibres of the rat diaphragm. Previous treatment with acetone removed triglyceride droplets but not phospholipid. They showed that the intracellular localization of the stain corresponded to the fat droplets and mitochondria seen electron microscopically. Since acetone extraction of our sections did not affect the density of the staining of an individual fibre relative to others surrounding it, triglyceride droplets appear to be associated with mitochondria in all fibres. The use of Sudan black B as a mitochondrial marker to estimate the dependence of a fibre on aerobic metabolism is as valid as the use of SDHase.

Phosphorylase

Takeuchi & Kuriaki (1955) showed that their method is specific for the enzyme catalysing the successive phosphorylation of the terminal glucose units of the glycogen chain, with the production of glucose-1-phosphate. The method uses the reversibility of this reaction to synthesize a polyglucose, staining blue with iodine, that is distinct from native glycogen, both by iodine staining and by electron microscopic appearance (Takeuchi & Sasaki, 1968). Differences in the colour of iodine staining have been attributed to the progressive increases in chain length during synthesis of the glucose polymer, blue indicating chains of over 30 glucose units, and red indicating chains of 7-13 glucose units (Swanson, 1948). Iodine colours have been used in this study to indicate different levels of phosphorylase activity in individual fibres.

It is accepted that glycogen is the major store of energy for muscular contraction in the absence of oxygen, and that phosphorylation is the first step in glycolysis. The

phosphorylase activity of an individual fibre is therefore a measure of the rate at which it can derive energy for contraction anaerobically.

Myosin ATPase

Padykula & Herman (1955) and Padykula & Gauthier (1963) provided evidence that their histochemical technique was specific for myosin ATPase. This was given strong support by the work of Guth & Samaha (1969), who compared the effects of pre-incubation at pH values of 10.4 and 4.35 on the ATPase activity of both actomyosin extracted from fast and slow muscles of the cat, and individual fibres of these muscles examined histochemically. Their study also provided evidence that fibres shown histochemically to be ATPase-high are fast contracting, and that ATPase-low fibres are slow contracting, a concept supported by work showing that the activity of myosin ATPase is directly proportional to the intrinsic speed of shortening of normal muscles of widely varying speeds of contraction (Bárány, 1967), and of muscles in which the speed of contraction has been altered by cross-innervation (Bárány & Close, 1971). The distinct difference between the histochemical reactions of fast and slow contracting fibres is possibly related to the molecular difference between the myosin of fast and slow muscles demonstrated by Samaha, Guth & Albers (1970).

This evidence appears to justify the designation of ATPase-high mammalian extrafusal fibres as fast-twitch, and ATPase-low fibres as slow-twitch fibres.

Classification of fibre types

The interpretation of histochemical fibre types should relate the reactions directly to the physiological and metabolic characteristics of each fibre. The evidence given above suggests that the profile obtained by determining the SDHase, phosphorylase and myosin ATPase reactions will classify an individual fibre by its capacity for aerobic and anaerobic metabolism, and by its intrinsic speed of contraction. Fig. 2 is an attempt to classify fibre types in the diaphragm by these criteria. Where the incidence of a fibre is less than 5%, it probably plays an insignificant part in the function of the diaphragm, and it is appreciated that a fibre classified as 'anaerobic' or 'aerobic' will usually have a low level of the other type of metabolism. For both fast- and slow-twitch fibres, there are three theoretical possibilities for their metabolism; aerobic, combined aerobic and anaerobic, and anaerobic. Only five of these six possibilities occur in significant proportions. The following trends are observed:

(i) Slow-twitch fibres use aerobic metabolism to a greater extent than fast-twitch fibres, and consequently do not include an 'anaerobic' type.

(ii) The diaphragm of the smaller animals uses a predominantly aerobic metabolism. Although a capacity for aerobic metabolism is maintained in the larger animals, there is also an increasing capacity for anaerobic metabolism.

Our studies demonstrate that fibres may have a high activity of enzymes for both aerobic and anaerobic metabolism. They do not indicate what the absolute levels of the activities of these enzymes might be, but suggest that the relationship between aerobic and anaerobic metabolism in muscle fibres is not necessarily the simple 'reciprocal' one suggested by Dubowitz & Pearse (1960*a, b*). This contention is supported by Gillespie, Simpson & Edgerton (1970), who found greater stores of glycogen in the 'red' region of *m. vastus lateralis* of the guinea-pig, composed of 77% SDHase high

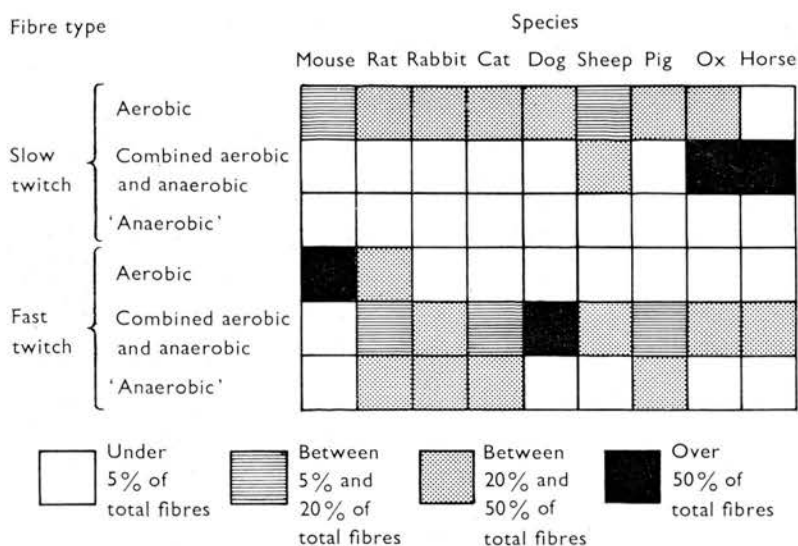


Fig. 2. Incidence of fibre types in the diaphragm.

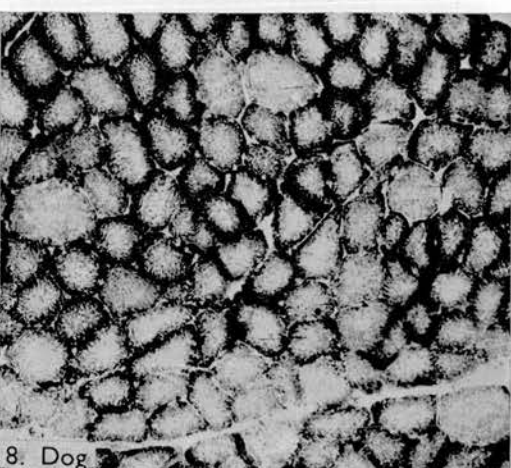
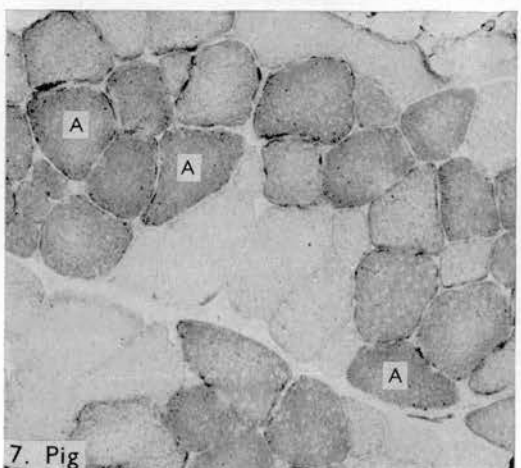
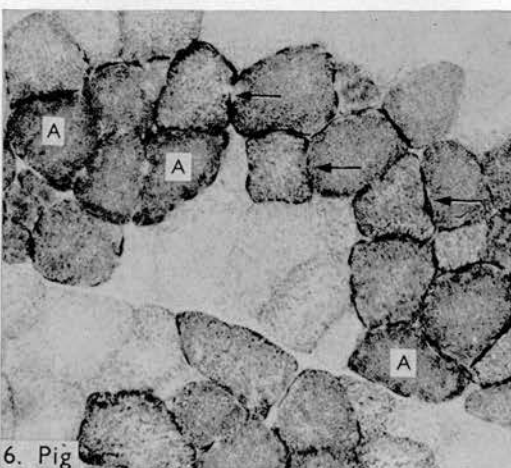
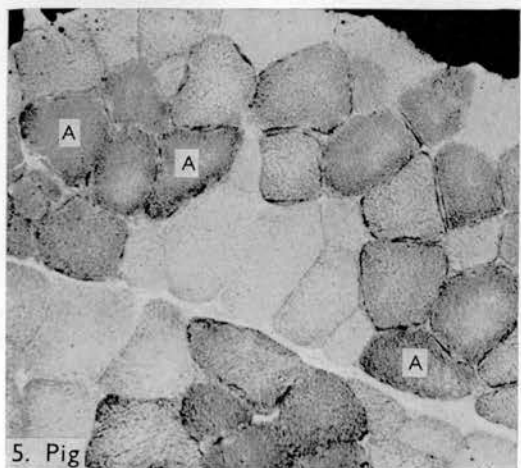
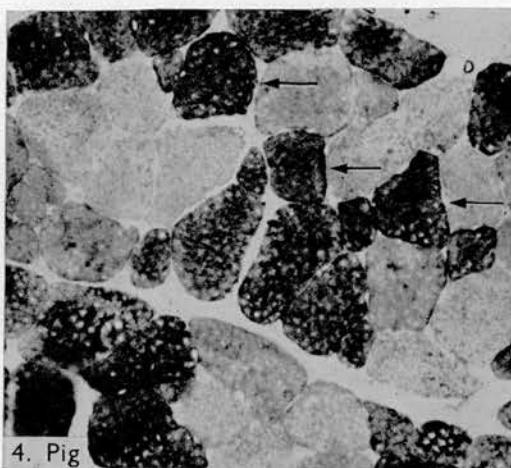
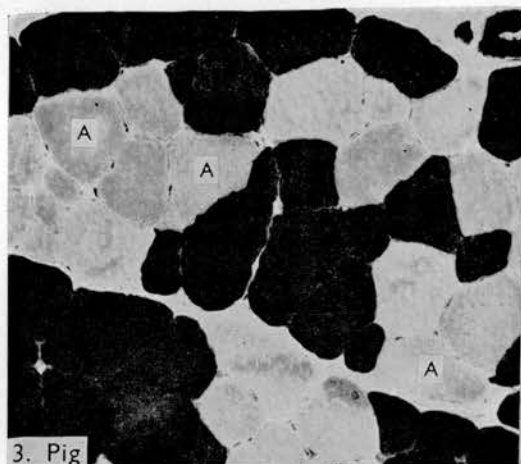
fibres, than in the 'white' region, composed of 29% SDHase high fibres. Edgerton & Simpson (1969) reviewed the various classifications that have been used since 1962 for histochemical fibre types in muscle. They favoured the descriptive terms 'red', 'intermediate' and 'white' in preference to letters or numbers. Fibres low in myosin ATPase activity were described as 'intermediate' in SDHase activity by Stein & Padykula (1962), Edgerton & Simpson (1969) and Jasmin *et al.* (1971) in their studies of crural muscles of rat, guinea-pig and rat, and hamster respectively. Our results, and those of Ashmore & Doerr (1971) for limb muscles of the pig and ox, and Burke *et al.* (1971) for the cat gastrocnemius, show that this type of fibre frequently has SDHase activity equal to or greater than surrounding myosin ATPase high fibres. The term 'intermediate' has, therefore, no general significance.

Muscle fibre types in the diaphragm

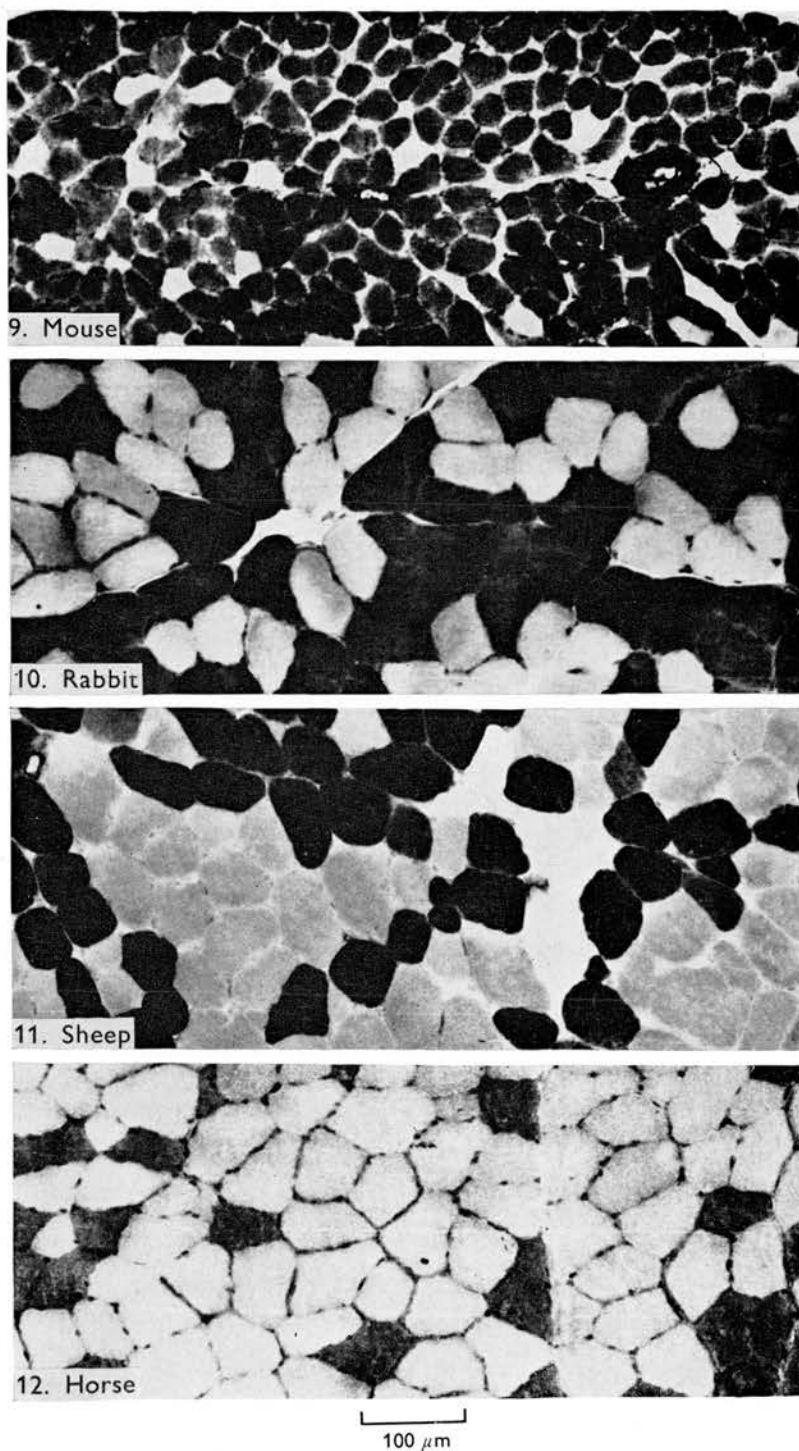
Bullard (1919) stained sections of the cat diaphragm with Sudan III and described equal numbers of 'dark' fibres with many lipid droplets and 'light' fibres of greater diameter and fewer lipid droplets, together with a small number of intermediate fibres. Günther (1952) also recognized the heterogeneity of muscle fibres in the diaphragm. By studying susa-fixed, paraffin embedded sections stained with Heidenhain's

Figs. 3-7. Transverse serial sections of the pig diaphragm stained for myosin ATPase (Fig. 3), phosphorylase (Fig. 4), phospholipid and triglycerides (Sudan black B) (Fig. 5), SDHase (Fig. 6), and phospholipid (Sudan black B) after extraction of triglycerides with acetone (Fig. 7). Arrows indicate fibres high in both phosphorylase and SDHase activity. Fibres marked A have low myosin ATPase activity, but their SDHase activity and Sudanophilia are higher than any myosin ATPase high fibres.

Fig. 8. Transverse section of diaphragm of dog: SDHase.



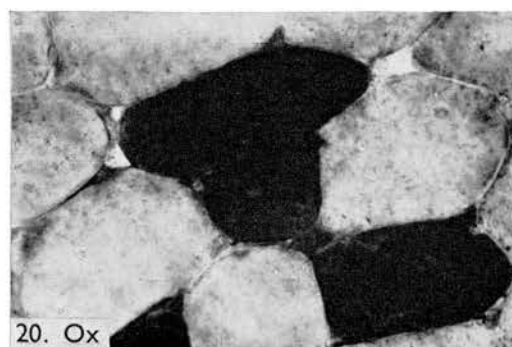
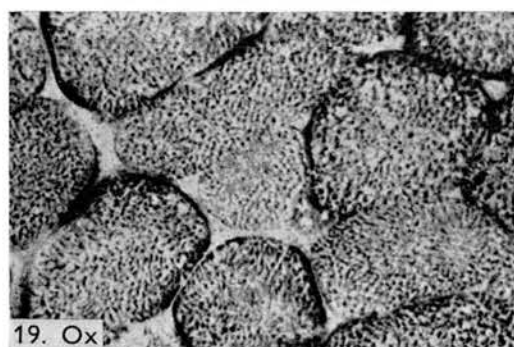
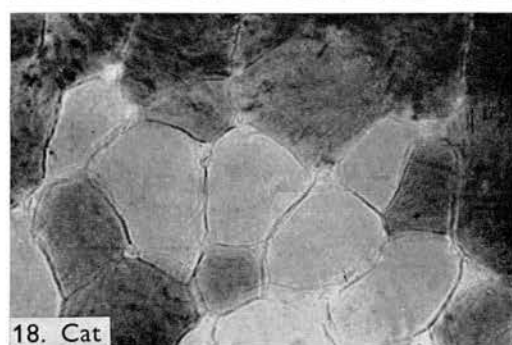
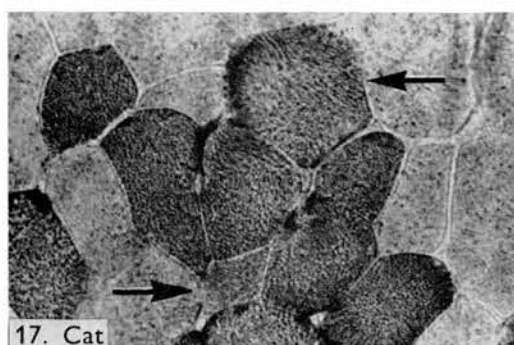
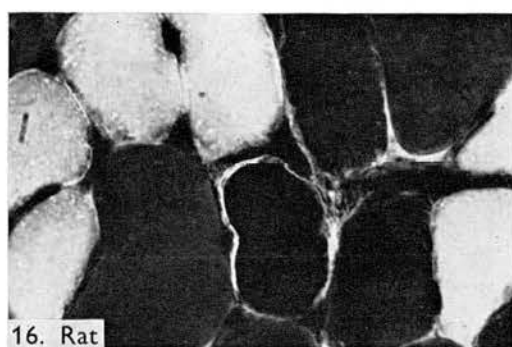
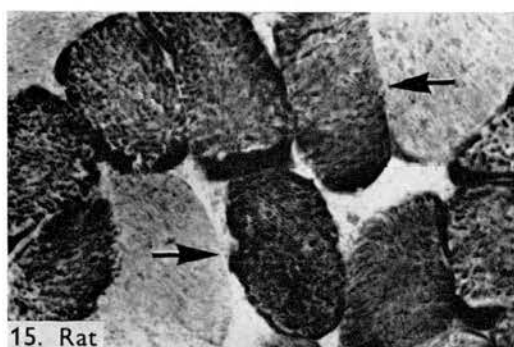
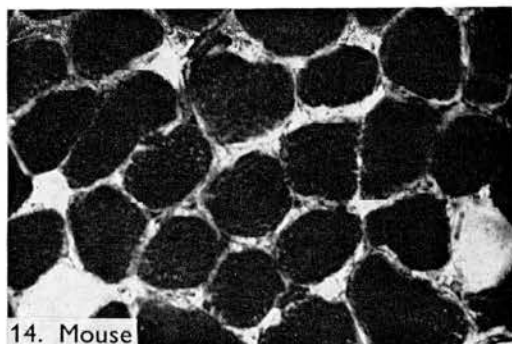
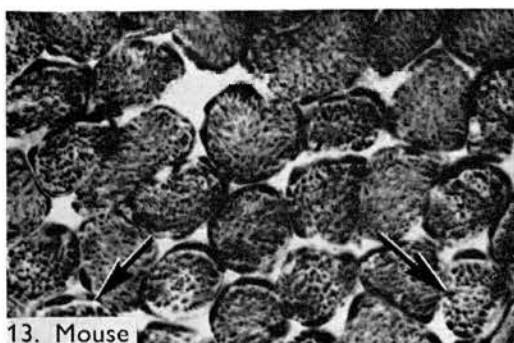
100 μ m



Figs. 9–12. Transverse sections of the diaphragm of the mouse (Fig. 9), rabbit (Fig. 10), sheep (Fig. 11), and horse (Fig. 12); myosin ATPase.

iron-alum haematoxylin, he reported the presence of two distinct populations of fibres in the diaphragm of the rat, mouse, rabbit and hedgehog, and later in the dog and human (Günther, 1953), corresponding in myofibrillar arrangement to the 'Fibrillenstruktur' and 'Felderstruktur' fibres described by Krüger (1952). This morphological difference was considered to be correlated with 'phasic' and 'tonic' contraction respectively; in the rat diaphragm 42% of fibres were classified as 'Felderstruktur', a proportion close to the 39% of ATPase-low fibres that we have observed. However, Günther (1953) found only 5% of the fibres of the diaphragm of the dog to be 'Felderstruktur', compared with our 36% myosin ATPase-low fibres in this species. In an electron microscopic study of the rat diaphragm, Bubenzer (1966) described two fibre types; thin, mitochondria-rich fibres were 'Felderstruktur', and thick fibres with fewer mitochondria, less glycogen and no lipid droplets were 'Fibrillenstruktur'. Muscle fibres in the diaphragm of the mouse, rat, guinea-pig and rabbit were found to vary in their phosphorylase activity by Takeuchi & Kuriaki (1955). Histochemical methods for enzymes of oxidative metabolism in the diaphragm of several mammals (Ogata, 1958) and in the diaphragm of the rat (George & Susheela, 1961; Padykula & Gauthier, 1963) showed a large variation in enzymic activity of individual fibres. Nishiyama (1966) distinguished three fibre types in the rat and cat diaphragm and concluded that phosphorylase was reciprocal to the activity of oxidative enzymes. However, we have observed a significant proportion of fibres in these muscles that contain high levels of both phosphorylase and SDHase activity (Figs. 17, 18).

Padykula & Gauthier (1963) used the myosin ATPase reaction on the rat diaphragm but did not report a variation between fibres. In this muscle, they distinguished by electron microscopy 'red', 'intermediate' and 'white' fibres based on mitochondrial density, fibre diameter, width of Z line, and end-plate morphology (Padykula & Gauthier, 1963, 1970; Gauthier & Padykula, 1966). Gauthier & Padykula (1966) compared fibre types in the diaphragm of the rat, bat, shrew and ox with the electron microscope. They also studied the costal diaphragm of 36 mammalian species using Sudan black B staining of material either fresh frozen, or fixed in formalin or osmium tetroxide, and found that the level of Sudanophilia decreased with increasing body size. The diaphragm of small animals (species of mouse, bat and shrew) was stated to be composed of 'homogeneous red fibres', that of animals intermediate in size (including rat, cat, rabbit, dog and sheep) of 'mixtures of fibre types', and that of the pig and ox of 'homogeneous white fibres'. Our findings differ in that the diaphragms of the dog and sheep are composed more or less uniformly of fibres of high SDHase activity and Sudanophilia (Fig. 8). The diaphragm of the pig is clearly heterogeneous when stained with Sudan black B (Figs. 5, 7). Although they do not show the dense aggregations seen in fibres of smaller animals (Figs. 13, 15), the fibres of the ox and horse diaphragm have relatively high Sudanophilia and SDHase activity (Fig. 19).



100 μ m

Table 3. *Fibre types in muscles of known contraction times*

Species	Muscle	Percentage of fibre type*										Contraction time† (ms)		
		Ah					Al							
		Sh		Sl			Sh		Sl					
		Ph	Pl	Ph	Pl	Pl	Ph	Pl	Ph	Pl	Sh		Ph	Ah
Rabbit	Thyroarytenoid	100	—	—	—	—	—	—	—	—	100	100	100	6
Rat	E.D.L.*	63	—	33	—	4	—	—	—	—	67	100	96	12
Cat	F.D.L.*	33	2	56	—	—	9	—	—	—	44	89	91	27
Rabbit	Cricothyroid	1	77	—	—	4	18	—	—	—	100	5	78	27
Rat	Soleus	14	1	—	—	1	84	—	—	—	100	15	15	36
Cat	Soleus	—	—	—	—	—	100	—	—	—	100	—	—	70

* Key: Ah, Sh, Ph: high activity of myosin ATPase, SDHase or phosphorylase respectively. Al, Sl, Pl: low enzyme activity. F.D.L.: m. flexor digitorum longus. E.D.L.: m. extensor digitorum longus.
† References for contraction times: Cat (Buller, Eccles & Eccles, 1960); rat (Close, 1964); rabbit (Hall-Craggs, 1968).

Comparative physiology

The presence of fast- and slow-twitch fibres in the diaphragm has been indicated by our histochemical demonstration of myosin ATPase-high and low fibres in all animals studied. Physiological evidence for this has been provided by studies on the action potentials in single diaphragmatic muscle fibres of the rabbit (Sant'Ambrogio, Decandia & Gantchev, 1969), and on the firing patterns of single phrenic motoneurons of the cat (Nail, Sterling & Widdicombe, 1969), which demonstrated the presence of two types of motor unit, differing in their threshold for stimulation and in firing frequency. For motor units of the cat gastrocnemius muscle these properties have been shown to be related to contraction times (Burke, 1968).

We have studied fibre types in muscles of known contraction times. The results are shown in Table 3, and confirm the postulation of Edgerton & Simpson (1969) that the proportion of myosin ATPase-high fibres in these muscles bears a reciprocal relationship to the contraction time. The histochemical findings of Barnard, Edgerton, Furukawa & Peter (1971) in guinea-pig hind limb muscles, and of Cardinet,

Figs. 13, 14. Transverse serial sections of the diaphragm of the mouse, stained for SDHase (Fig. 13), and myosin ATPase (Fig. 14). Arrows indicate myosin ATPase-low fibres with similar SDHase (Fig. 13), and myosin ATPase (Fig. 14). Arrows indicate myosin ATPase-low fibres with similar SDHase activity to myosin ATPase-high fibres.

Figs. 15, 16. Transverse serial sections of the diaphragm of the rat, stained for SDHase (Fig. 15) and myosin ATPase (Fig. 16). Arrows indicate fibres high in both SDHase and myosin ATPase activity.

Figs. 17, 18. Transverse serial sections of the diaphragm of the cat, stained for SDHase (Fig. 17) and phosphorylase (Fig. 18). Arrows indicate fibres high in both SDHase and phosphorylase activity.

Figs. 19, 20. Transverse serial sections of the diaphragm of the ox, stained for SDHase (Fig. 19) and myosin ATPase (Fig. 20). The myosin ATPase-low fibres have similar, or higher, SDHase activity compared with the myosin ATPase-high fibres.

Tunell & Fedde (1971) in *m. pectineus* of dogs, support this hypothesis. Table 2 shows the contraction times determined for the diaphragm of the rat, rabbit, cat and dog by Sant'Ambrogio & Saibene (1970). Although their results suggest that contraction time is related to body size, our data show little variation in the proportion of myosin ATPase-high fibres between these species. A histochemical study of the actual diaphragms for which contraction times have been determined will be necessary to resolve this inconsistency.

The proportion of myosin ATPase-high fibres in the semitendinosus muscle also appears to be inversely proportional to body size (Davies & Gunn, 1971), although the effect is not as marked as in the diaphragm. This property of *m. semitendinosus* would be expected by the requirements of dimensional theory (Hill, 1950), for which the limb muscles of larger animals must have lower intrinsic speeds of contraction.

Comparative metabolism

Crosfill & Widdicombe (1961) showed that in mice and rats the frequency of breathing could vary widely for constant alveolar ventilation with little increase in work, and that the rate of work of breathing per gram of body weight was high, compared with that in the larger guinea-pigs, rabbits, monkeys, cats and dogs. Since myosin ATPase activity is probably the rate-limiting step in the conversion of chemical to mechanical energy in muscle (Mommaerts, 1970), their results are consistent with the proportions of myosin ATPase-high fibres that we have seen in the diaphragm of the mouse, rat, rabbit, cat and dog. It is probable, then, that the diaphragms of the larger animals used in our study will have even lower rates of energy conversion than the larger animals studied by Crosfill & Widdicombe (1961).

Kunkel, Spalding, de Franciscis & Futrell (1956) showed that the cytochrome oxidase activity per gram of gracilis muscle of the rat, sheep, pig and ox varied as the -0.24 power of body weight, and therefore directly with the metabolic rate (Kleiber, 1947). Although the respiration rate did not vary with body weight in other muscles, tissue slices from the diaphragm of a series of mice and rats respired at a rate proportional to the -0.15 power of body weight (Bertalanffy & Estwick, 1953). While it is expected, therefore, that the capacity for oxidative metabolism of the diaphragm in our series of animals will also be less with increasing body size, fibres of the diaphragm of the larger animals appear histochemically to be dependent on aerobic metabolism. They do, however, have a capacity for anaerobic metabolism, presumably for brief periods of greater effort.

SUMMARY

Histochemical profiles of individual muscle fibres from the diaphragm of the mouse, rat, rabbit, cat, dog, sheep, pig, ox and horse were classified according to their reaction to methods demonstrating myosin adenosine triphosphatase, succinate dehydrogenase and phosphorylase. Other evidence indicates that the myosin adenosine triphosphatase reaction differentiates between fast-twitch and slow-twitch muscle fibres and that the succinate dehydrogenase and phosphorylase reactions demonstrate the capacity for aerobic and anaerobic metabolism respectively. Fast-twitch fibres, which may use either an aerobic metabolism, an anaerobic metabolism or a com-

bined aerobic and anaerobic metabolism, and slow-twitch fibres, which may use either an aerobic metabolism or a combined aerobic and anaerobic metabolism, have been recognized in the diaphragm.

The diaphragm of smaller animals has a high proportion of fast-twitch fibres and a predominantly aerobic metabolism. The diaphragm of larger animals has a majority of slow-twitch fibres and a capacity for combined aerobic and anaerobic metabolism. Only the mouse and pig have mean fibre transverse-sectional areas significantly different from the mean of all the species studied.

We are indebted to Professor A. R. Muir for assistance in all stages of this study. One of us (A. S. D.) was supported by a grant from the Meat and Livestock Commission.

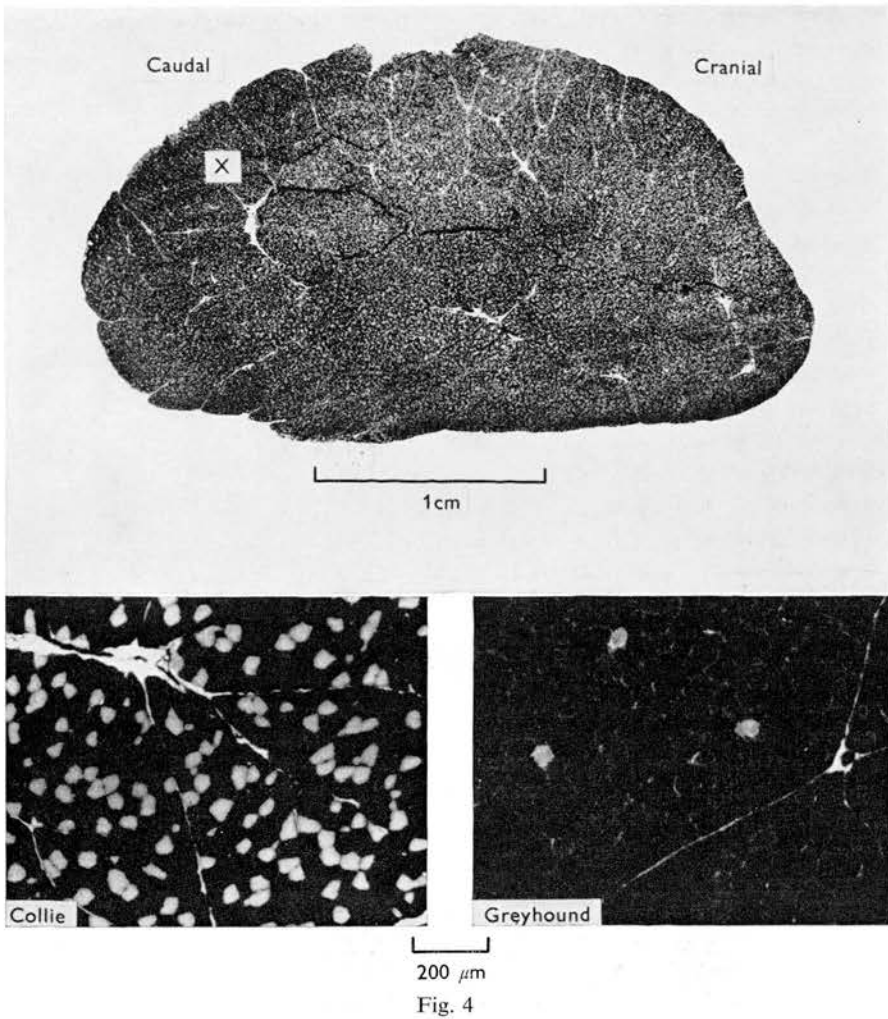
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23. Histochemical differences in the skeletal muscles of different breeds of horses and dogs. By H. M. GUNN (introduced by A. R. MUIR). *Department of Veterinary Anatomy, University of Edinburgh* (Fig. 4).

The proportion of slow-twitch skeletal muscle fibres in the diaphragm and *M. semitendinosus*, as demonstrated by the histochemical reaction for myosin adenosine triphosphatase (myosin ATPase), decreases with increasing body size (Davies & Gunn, *J. Anat.* **112**, 1972). This finding corresponds to a decreasing speed of movement of the diaphragm and limbs with increasing body size.

A study of *M. semitendinosus* in 10 thoroughbreds and 9 other horses, 33 greyhounds and 9 other dogs, has been made. All the animals used were adults. The thoroughbreds and greyhounds had an unexpectedly low proportion of myosin ATPase low reacting (slow-twitch) fibres in relation to their body size.

The fresh frozen complete transverse section of *M. semitendinosus* of a collie, shown in Fig. 4,

has been stained for myosin ATPase. A magnified area from this section, at \times , is shown together with an area from the same region of a greyhound semitendinosus. The deep cranial region of the M. semitendinosus of the dog and horse contains the highest proportion of slow-twitch fibres, occurring as groups of pale staining slow-twitch fibres. This proportion decreases progressively towards the superficial caudal region, where the slow-twitch fibres occur singly.

Complete cross-sections of M. semitendinosus of greyhounds and other large dogs have been compared. The greyhound semitendinosus has more fibres, and a smaller area of its cross-section occupied by slow-twitch fibres, as well as a smaller total number of slow-twitch fibres. The difference between thoroughbreds and other horses parallels this observation.

The significance of these findings will be discussed in relation to the athletic ability of these animals.

24. The effect of denervation on genotypic and compensatory growth of the immature avian salt gland. By J. B. PITTARD and A. D. HALLY. *Department of Anatomy, University of Newcastle upon Tyne.*

Compensatory growth in the paired duck salt gland only follows unilateral ablation of one gland if there is a functional demand on the remaining gland (Jephcott & Hally, *J. Anat.* **106**, 1970). Compensatory growth is therefore an example of functional growth.

What is the role of the secretory nerve in this response? We denervated one gland in 3 day old ducklings, leaving the contralateral gland as control, and used unoperated ducklings as additional controls. We rested the operated birds for 1 day and then divided them into an unstimulated group with water *ad lib.* and a stimulated group which were injected daily with 10 % intravenous saline (20.5 m-equiv. NaCl/kg body weight). We killed the birds at 10 days post hatch and weighed the salt glands.

The mean Salt Gland Index (S.G.I.) (weight of two salt glands (mg)/kg body weight) of unoperated control glands: $291 \pm \text{s.e. } 7$, equalled that of the stimulated denervated glands: $297 \pm \text{s.e. } 13$. By contrast the S.G.I. of stimulated innervated glands rose 80 % to $537 \pm \text{s.e. } 20$.

We concluded that compensatory growth is wholly *dependent* on an intact nerve supply.

In the absence of functional demand unstimulated ducklings doubled their *absolute* body and salt gland weights during the experimental period by 'genotypic' growth.

The unstimulated denervated glands also grew at almost the same rate to reach an S.G.I. of $268 \pm \text{s.e. } 9$, so genotypic growth is largely *independent* of nerve supply.

25. Changes in rat dentine following systemic administration of adrenal glucocorticoid hormone. By P. C. BALL (introduced by C. L. B. LAVELLE). *Department of Conservative Dentistry, University of Birmingham (Fig. 5).*

An investigation into the role played by the adrenal glucocorticoid hormones in the development of the dental tissues is being carried out. One aspect of this investigation involved a study of the mandibular incisors of 50 mature rats which were maintained in a hyperglucocorticoid state by the weekly injection of 0.1 ml Depo-Medrone (methylprednisolone acetate 40 mg/ml).

The systemic administration of high levels of glucocorticoids to rodents is known to result in an increased rate of eruption of the mandibular incisors. This increased eruption rate has been shown in this investigation to be associated with a marked thinning of the dentine walls of the tooth. The quantity of hormone used in this study has also been found to cause vascular changes in the incisor.

In the normal rodent all dentine is avascular. A histological examination of the rat incisors obtained in this investigation demonstrated vascular channels in the dentine of every hormone-treated animal. These blood vessels were situated mainly in the inner layer of newly deposited dentine but some could be traced passing from the pulp deep into the mature dentine. This vascularity of the dentine was found to occur within the first 7 days of administration of the hormone and to persist throughout the length of the experimental period. The photographs (Fig. 5) show two areas of transversely cut pulp and dentine from incisors of rats maintained for

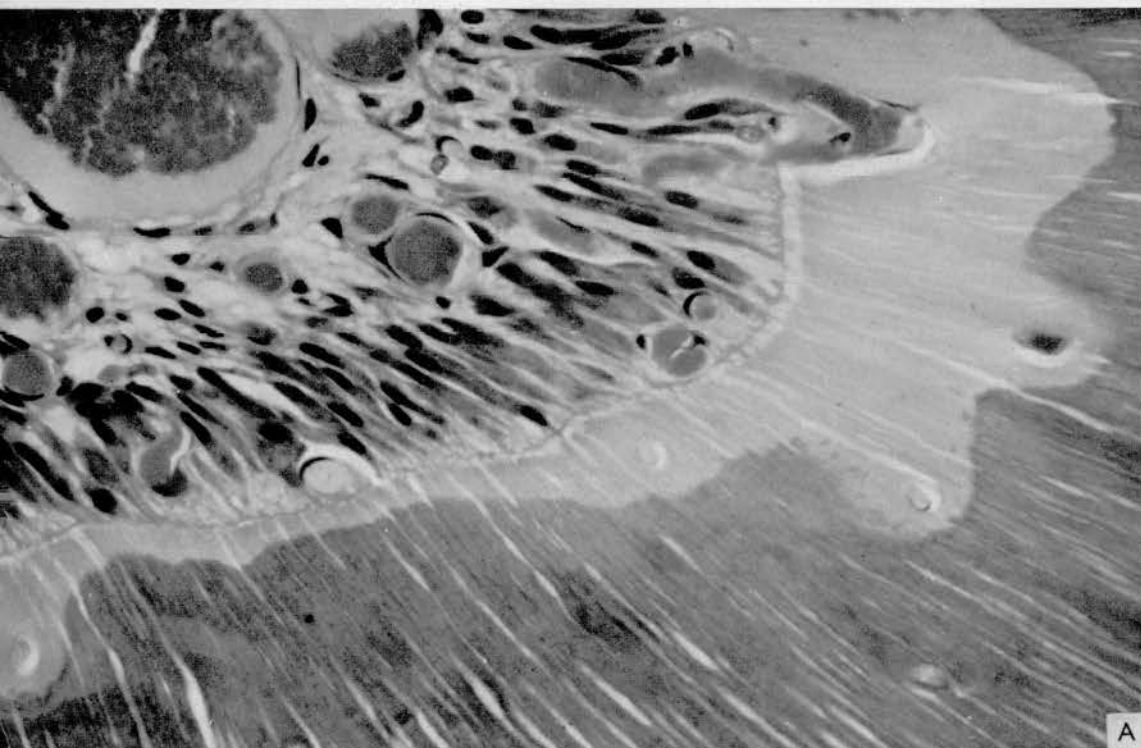


Fig. 5

a 5-week period in the hyperglucocorticoid state. Field A shows one blood vessel looping into the preentine and several other vessels transversely cut ($\times 100$). Photograph B is of a single blood vessel at a magnification of 400 times.

An increase in the vascularity of the peripheral layer of the dental pulp was also noted in these hormone-treated animals.

DEMONSTRATIONS

D 1. The action of metabolic inhibitors on the sexual differentiation of the hypothalamus induced by neonatal androgen. By D. F. SALAMAN (introduced by B. A. CROSS). *Department of Anatomy, University of Bristol.*

Testosterone propionate (TP) given to female rats within the first 10 days of life causes an acyclic pattern of gonadotrophin secretion to develop after puberty with failure of ovulation and permanent sterility. This demonstration illustrates the effects of the selective inhibitors of synthesis, hydroxyurea (DNA), actinomycin D and α -amanitin (RNA) and puromycin (protein) when administered simultaneously with TP to 4 day old female rats. Vaginal smears are taken from puberty and ovarian weight and the presence or absence of corpora lutea, ruptured follicles and eggs in the oviduct at death (90 days) are recorded.

The most effective inhibitor tested was α -amanitin which afforded almost complete protection against a low or moderate dose of TP (30 and 80 μg per rat). Hydroxyurea was partially effective against both doses, puromycin was only marginally effective against the lower dose of TP, while actinomycin D was without effect at either dose.

α -Amanitin is a selective inhibitor of non-ribosomal or informational RNA synthesis while actinomycin D at low doses inhibits ribosomal RNA synthesis preferentially. These results are consistent with an action of TP on hypothalamic messenger RNA rather than ribosomal RNA synthesis.

D 2. Intra-axonal transport of neurohypophysial hormones and related proteins in the rat. By C. W. JONES, G. D. BURFORD and B. T. PICKERING (introduced by B. A. CROSS). *Department of Anatomy, University of Bristol.*

Small-scale chromatographic techniques have been developed for the isolation of isotopically pure oxytocin and vasopressin from the pooled neurohypophysis of four rats. By injecting radioactive amino acid into the CSF through the cisterna magna and killing the animals at various intervals after the injection, the time-course for the appearance of radioactive hormone into the gland and its disappearance from the gland has been determined. From these results we have been able to show that the intra-axonal transport of the hormones has a velocity of at least 1–2 mm/h, and have estimated the daily release rate from the gland to be about 19 mu. oxytocin and 29 mu. vasopressin. Calculations from these estimates allowed us to suggest that the steady-state plasma concentration for each hormone is about 3 $\mu\text{u./ml}$.

Besides the hormones, the neurohypophysis contains a family of cysteine-rich proteins – the neurophysins – which have long been considered as carrier proteins. We have developed a method, using polyacrylamide-gel electrophoresis, to study the neurophysins in individual rat glands. We have shown that the rat, in common with cattle and pigs, has two major and one minor neurophysin. All of these proteins become labelled after an intracisternal injection of [^{35}S]-cysteine and the time-course for the appearance of radioactivity in the two major neurophysins parallels that for the hormones. The minor neurophysin component appears to be a metabolic product of one of the major ones. One of the major components is absent from the glands of rats with hereditary hypothalamic diabetes insipidus (Brattleboro strain) and this finding, together with comparisons of relative amounts of the two proteins, enabled us to suggest that one major neurophysin is biosynthetically associated with vasopressin and the other with oxytocin.

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THE EFFECT OF BODY SIZE AND SELECTION ON SKELETAL MUSCLE

FIBRE TYPES IN MAMMALS

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This study attempts to define and resolve some of the histochemical variations in the muscle fibres of mammals, and to demonstrate how the histochemical properties of muscle fibres may be influenced by selection and growth.

Fibre type profiles have been established in the diaphragm and M. semitendinosus of mammals of different body size, using succinate dehydrogenase as an indicator of aerobic capacity, phosphorylase as an indicator of anaerobic capacity and myosin adenosine triphosphatase as an indicator of intrinsic speed of contraction of individual fibres - fibres having a high activity of this enzyme being fast-twitch and those having a low activity being slow-twitch.

By using transverse frozen serial sections and back projection, histochemical profiles of about 400 individual muscle fibres were made on each sample taken from the diaphragms of adult shrews, mice, rats, rabbits, cats, dogs, sheep, pigs, oxen and horses; and from the semitendinosus muscle of adult mice, rats, rabbits, cats, dogs and horses. From these profiles the following types of muscle fibres were found: fast-contracting, aerobic; fast-contracting, with both aerobic and anaerobic capacity; fast-contracting, anaerobic; slow-contracting, aerobic; and slow-contracting, with both aerobic and anaerobic capacity. The proportion of slow-twitch fibres in the diaphragm and M. semitendinosus increases with increasing body size. This finding corresponds to a decreasing speed of movement of the diaphragm and limbs with increasing body size.

An increase in the proportion of fibres that are low in myosin adenosine triphosphatase activity, was seen in the longissimus muscles from 34 Large White pigs ranging from 1.3 to 93 kg live weight. This finding indicates a modification in the properties of some muscle fibres during growth to enable the animal to support itself.

A study of M. semitendinosus and M. anterior pectoralis in 10 Thoroughbreds and 9 other horses, 33 Greyhounds and 9 other dogs, all the animals used being adults, showed that the Thoroughbreds and Greyhounds - breeds which have been selected to run quickly, had a lower proportion of slow-twitch fibres, in relation to their body size, than animals from other breeds.

AUSWIRKUNG VON KÖRPERGRÖSSE UND ZUCHTWAHL AUF
SKELETTMUSKELFASERTYPEN BEI SÄUGETIEREN

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Zweck dieser Studie sind Definition und Analyse einiger histochemischer Variationen in Muskelfasern von Säugetieren. Es soll gezeigt werden, wie die histochemischen Eigenschaften von Muskelfasern durch Zuchtwahl und Wachstum beeinflusst werden können.

In Diaphragma und M. semitendinosus von Säugetieren verschiedener Körpergröße wurden Fasertypprofile erstellt, unter Verwendung von Succinatdehydrogenase als Indikator aerober Kapazität, Phosphorylase als Indikator anaerober Kapazität und Myosin-Adenosin-Triphosphatase als Indikator der inhärenten Kontraktionsgeschwindigkeiten einzelner Fasern. (Fasern mit hoher Aktivität dieses Enzyms haben hohe, Fasern mit geringer Aktivität geringe Kontraktionsgeschwindigkeit.)

Unter Verwendung tiefgekühlter transversaler Serienschritte und Durchprojektion wurden histochemische Profile von ungefähr 400 einzelnen Muskelfasern aus jeder Probe erstellt, die dem Diaphragma ausgeschnittener Spitzmäuse, Mäuse, Ratten, Kaninchen, Katzen, Hunden, Schafen, Schweinen, Ochsen und Pferden sowie dem M. semitendinosus ausgewachsener Mäuse, Ratten, Kaninchen, Katzen, Hunden und Pferden entnommen waren. Aus diesen Profilen ließen sich folgende Typen von Muskelfasern bestimmen: schnell kontrahierend, aerob; schnell kontrahierend, aerob und anaerob; schnell kontrahierend, anaerob; langsam kontrahierend, aerob; langsam kontrahierend, aerob und anaerob. Der Anteil von Fasern mit langsamer Kontraktion in Diaphragma und M. semitendinosus nimmt mit zunehmender Körpergröße zu. Dieser Befund entspricht der verringerten Geschwindigkeit der Bewegung in Diaphragma und Gliedern bei zunehmender Körpergröße.

Ein zunehmender Anteil von Fasern mit geringer Myosin-Adenosin-Triphosphatase-Aktivität wurde in M. longissimus von 34 Großen weißen Schweinen mit einem Lebendgewicht von 1,3 kg - 93 kg gefunden. Dieser Befund weist auf eine Veränderung der Eigenschaften einzelner Muskelfasern während des Wachstums zur Gewährleistung der Standfestigkeit des Tiers hin.

Eine Studie des M. semitendinosus und M. anterior pectoralis bei 10 Vollblut- und 9 anderen Pferden, 33 Windhunden und 9 anderen Hunden (durchwegs ausgewachsene Tiere) zeigte, daß die Vollblutpferde und die Windhunde, die für schnelles Laufen gezüchtet werden, einen geringeren Anteil von Fasern mit langsamer Kontraktion bezogen auf die Körpergröße aufwiesen als Tiere anderer Züchtungen.

L'EFFET DE LA TAILLE DU CORPS ET DE LA SELECTION SUR LE MUSCLE SQUELETTIQUE

TYPES DE FIBRES CHEZ LES MAMMIFERES

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Cette étude tente de définir et de résoudre certaines variations histo-chimiques dans les fibres musculaires des mammifères et de démontrer comment les propriétés histo-chimiques des fibres musculaires peuvent être influencées par la sélection et la croissance.

Des profils de type fibreux ont été établis dans le diaphragme et les muscles semi-tendineux de mammifères de taille différente, en utilisant la succinate déshydrogénase comme indicateur de la capacité aérobie, la phosphorylase comme indicateur de la capacité anaérobie et l'adénosine triphosphatase de myosine comme indicateur de vitesse de contraction intrinsèque des fibres individuelles - les fibres réagissant beaucoup à cette enzymetant à contraction rapide et celles réagissant moins étant à contraction lente.

En utilisant des sections transversales gelées et la "Back Projection", des profils histo-chimiques d'environ 400 fibres de muscle individuelles furent faits de chaque échantillon pris sur les diaphragmes de musaraignes adultes, souris, rats, lapins, chats, chiens, porcs, moutons, boeufs et chevaux; et du muscle semi-tendineux de souris, rats, lapins, chats, chiens et chevaux adultes. A partir de ces profils, on a découvert les différents types de fibres musculaires suivants: contraction rapide, aérobie; contraction rapide avec à la fois une capacité aérobie et anaérobie; contraction rapide anaérobie; contraction lente, aérobie; et contraction lente avec à la fois une capacité aérobie et capacité anaérobie. La proportion des fibres à contraction lente dans le diaphragme et les muscles semi-tendineux augmente avec l'accroissement de la taille. Cette découverte correspond à un ralentissement de la vitesse du mouvement du diaphragme et des membres avec l'accroissement de la taille du corps.

On a observé chez 34 porcs de type White Large (Blanc gros) dont le poids (vivant) varie de 1,3 kg. à 93 kg., un accroissement dans la proportion des fibres des muscles les plus longs qui ont une activité basse en triphosphatase adénosine de myosine. Cette découverte indique une modification des propriétés de certaines fibres musculaires pendant la croissance, en vue de permettre à l'animal de supporter son propre poids.

Une étude des muscles semi-tendineux et des muscles pectoraux antérieurs de 10 chevaux de race pure et de 9 autres chevaux, de 33 lévriers et de 9 autres chiens (tous ces animaux étant adultes) a montré que les chevaux de race pure et les lévriers - races qui ont été sélectionnés pour courir vite - ont une proportion de fibres musculaires à contraction lente plus basse par rapport à la taille de leur corps, que les animaux d'autres races.

ВЛИЯНИЕ РАЗМЕРА ТЕЛА И СЕЛЕКЦИИ НА ТИПЫ
СКЕЛЕТНЫХ МЫШЕЧНЫХ ТКАНЕЙ МЛЕКОПИТАЮЩИХ.

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Это исследование пытается определить некоторые гистохимические отклонения в мышечных тканях млекопитающих, и показать, как могут влиять на гистохимию мышечных тканей процессы селекции и роста.

Установили профили типов тканей в диафрагме и в полусухожильной мышце млекопитающих разных размеров, используя сукцино-дегидразу как указатель аэробной способности, фосфорилазу как указатель анаэробной способности и миозинаденозинтрифосфатазу как указатель присутствия сократительной скорости отдельных тканей; причем, ткани, отличающиеся высокой активностью этого энзима - быстро-сокращающиеся, а ткани, имеющие низкую активность этого энзима - медленно-сокращающиеся.

Методом проекции поперечных замороженных серийных разрезов установили профили примерно 400 отдельных мышечных тканей на каждой пробе, полученной из диафрагм взрослых беломорских, мышей, крыс, кроликов, кошек, собак, овец, свиней, волков и лошадей; и из полусухожильных мышц взрослых мышей, крыс, кроликов, кошек, собак и лошадей. Изучая эти профили, нашли следующие типы мышечных тканей: быстро-сокращающиеся, аэробные ткани, быстро-сокращающиеся с аэробной и анаэробной способностью; быстро-сокращающиеся, анаэробные; медленно-сокращающиеся, аэробные, и медленно-сокращающиеся, как и с аэробной, так и с анаэробной способностью. Число тканей в диафрагме и в полусухожильной мышце, сокращающиеся медленно, увеличивается с увеличением размера тела; этот вывод соответствует уменьшению скорости движения диафрагмы и членов по мере увеличения размера тела.

В длинных мышцах от 34 больших белых свиней, в пределах от 1,3 до 93 кг живого веса, обнаружили увеличение количества тканей, в которых миозинаденозинтрифосфатазная активность была низкой. Это

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указывает на то, что в процессе роста, вещества некоторых мышечных тканей изменяются, чтобы животное могло стоять.

Изучение полусухожильной мышцы и передней грудной мышцы на 10 чистокровных и на 9 других лошадях, на 33 борзых и на 9 других собаках (причем все изучаемые животные были взрослые) показало, что в чистокровных и борзых - породах, выбранных для быстрого бега - количество медленно-сокращающихся тканей по сравнению с размером тела меньше, чем у животных других пород.

THE EFFECT OF BODY SIZE AND SELECTION ON SKELETAL MUSCLE

FIBRE TYPES IN MAMMALS

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INTRODUCTION

Systems of classification of muscle fibres based on histochemical reactions have largely ignored the functional significance of the methods used. Non-enclosure of fibres has been in terms of colour descriptions (Ogata, 1958), numerals (Dubowitz & Pearse, 1960; Engel, 1962) and alphabetical symbols (Stein & Padykula, 1962; Guth, Samaha & Albers, 1970; Brooke & Kaiser, 1970; Ashmore & Doerr, 1971), based on observations of histochemical reactions in muscle fibres of numerous muscles in a variety of mammals. These systems of classification may be superseded if fibres can be characterised by their mechanical and metabolic properties.

In this study the use of selected histochemical reactions and profile construction has enabled classification of individual fibres to be made according to their intrinsic speed of contraction and their capacity for aerobic and anaerobic metabolism. The myosin adenosine triphosphatase (myosin ATPase) reaction is used to indicate the intrinsic speed of contraction of a fibre - fibres having a high activity of this enzyme being fast-twitch those having a low activity being slow-twitch (Burke, Levine, Tsairis & Zajac, 1973). Succinate dehydrogenase activity is used as an indicator of aerobic metabolism and glycogen phosphorylase as an indicator of anaerobic metabolism. The diaphragm was used to establish histochemical profiles in a variety of mammals because it has a similar function in all the animals studied.

An increase in the proportion of fibres that are low in myosin ATPase activity during postnatal growth has been reported in the pectineus muscle of the dog by Cardinet, Wallace, Fedde, Guffy & Bardens (1969). A similar observation has been made by Karpati & Engel (1967) on the soleus of the rat, guinea-pig and cat. To investigate this phenomenon it was decided to study the effect of increasing body weight on the histochemical characteristics of muscle fibres in the domestic pig, both because the extent of postnatal growth of the pig exceeds that of most other domestic animals, and the skeletal muscle of the pig appears to be unique in its organisation of histochemical fibre types in that one or more bundles of fibres characterised by low activity of myosin ATPase are located within perimysium enclosed fasciculi.

The members of the Thoroughbred breed of horse and Greyhound breed of dog are notably quicker runners than their fellow specific members. These breeds have been selected to run quickly for approximately 300 years in the case of the Thoroughbred and 3,000 years in the case of the Greyhound. The

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possibility that a selection procedure (the criterion of selection being speed of running) may influence the proportions of different types of fibres in the muscles of these breeds is investigated. The results have been reported previously by Davies & Gunn, 1971; Gunn & Davies, 1971; Davies & Gunn, 1972; Davies, 1972 and Gunn, 1973.

MATERIALS AND METHODS

Samples were taken from the costal diaphragm of adult shrews, mice, rats, rabbits, cats, dogs, pigs, sheep, cattle and horses; from the dorsomedial region of *m. longissimus* at the level of the thoraco-lumbar junction from Large White pigs of 1.3 to 93 kg. live weight; and from the left *m. pectoralis transversus* of horses at the manubrium sterni. The samples were removed from each animal within 45 minutes of death. Complete cross-sections of the middle third of *m. semitendinosus* from mice, rats, rabbits, cats, dogs and horses were also taken as soon as possible after death. The outline of the transverse sectional area (T.S.A.) of *m. longissimus* of pigs at the level of the thoraco-lumbar junction, adjacent to the sampling site, was drawn on paper and the T.S.A. measured by the paper weighing method.

After rapid freezing of a block of fresh muscle, about ten adjacent serial sections, 10 μ m thick, were cut transversely to the direction of the muscle fibres. The histochemical methods used are described by Davies & Gunn (1972); they are modifications of the methods used by Nachlas, Tsou, de Souza, Cheng & Seliqman (1957) to demonstrate succinate dehydrogenase activity; Takeuchi & Kuriaki (1955) to demonstrate glycogen phosphorylase activity; and Padykula & Herman (1955) to demonstrate myosin ATPase activity. The serial sections were back projected on to tracing paper so that individual fibres could be outlined and their metabolic profiles constructed. To estimate the level of activity of enzymes that showed a continuous spectrum of activity between fibres, a simple division into high and low was made for each fibre relative to the overall level of activity of fibres in each section. Mean fibre T.S.A. were estimated by counting the number of fibres projected within an area of known magnification and where applicable the mean T.S.A. of each fibre type was determined by cutting out and weighing the tracing paper on which the profiles were constructed.

Low power projection of sections stained for myosin ATPase activity enabled an assessment to be made of the number of myosin ATPase low reacting bundles of fibres in samples from *m. longissimus* of pigs. Using the measurement of the T.S.A. of the whole muscle, an estimate of the total numbers of bundles in the T.S.A. was made. At the same time, the number of myosin ATPase low fibres in each bundle was recorded and the mean number calculated. Similarly, the total number of myosin ATPase low reacting fibres was assessed in the *m. semitendinosus* of dogs by sampling the muscle at 2 mm. intervals across its entire transverse section. The total area of myosin ATPase low reacting fibres was calculated from this figure, and the mean area of myosin ATPase low reacting fibres in the section.

RESULTS

The following types of fibres exist in significant though differing proportions, in the diaphragms of the ten species examined: fast-twitch, aerobic; fast-twitch, with both aerobic and anaerobic capacity; fast-twitch anaerobic; slow-twitch aerobic; and slow-twitch with both aerobic and anaerobic capacity. The proportions of each of these fibre types in the diaphragms of the ten species examined is given in Table 1.

Table 1. Percentage of histochemical fibre types in the diaphragm of ten mammalian species.

Species	No. of animals studied	No. of fibres counted	Percentage of fibre types*											
			AH						AL					
			SH	SL	FA	FL	SA	SL	SH	SL	SA	SL		
Shrew	2	1120	-	100	-	-	-	-	-	-	-	100	100	
Mouse	4	1400	-	100	-	-	-	-	-	-	-	100	100	
Rat	3	1337	7	23	27	2	38	-	-	-	-	33	35	
Rabbit	2	1637	22	-	38	-	60	-	-	-	-	33	33	
Cat	2	1912	18	-	63	-	19	-	-	-	-	43	43	
Dog	4	3373	88	-	-	-	30	-	-	-	-	28	30	
Pig	2	2708	85	-	-	-	15	18	-	-	-	43	40	
Horse	4	2748	17	3	12	3	4	81	-	-	-	11	13	
Sheep	2	1879	24	-	-	-	38	13	-	-	-	28	30	
Cattle	2	2558	21	-	-	-	37	7	-	-	-	21	20	

*AH, SH, SL, FA, FL, SA, SL: high activity of myosin ATPase, 50% or of phosphorylase respectively. AL, SL, FL: low enzyme activity.

Table 1 demonstrates that the proportion of myosin ATPase high reacting (fast-contracting) fibres increased with decreasing body size. Differences in succinate dehydrogenase activity between fibres were not as conspicuous as the difference in myosin ATPase activity, and the proportion of fibres having a high or low succinate dehydrogenase activity did not show a body size correlation. Phosphorylase activity tended to show an opposite trend to that of myosin ATPase activity. The horse had nearly 100% of its fibres high in phosphorylase activity, but in the shrew diaphragm no fibres with high phosphorylase activity were seen.

In the larger species, fast contracting fibres were high in phosphorylase activity, showing that fast-contracting fibres in these species use mainly an anaerobic metabolism. In smaller animals, however, the proportion of fibres with high myosin ATPase activity exceeded that of fibres with high phosphorylase activity, demonstrating that fast-contracting fibres may also use aerobic metabolism.

Observations on the complete cross sections of *m. semitendinosus* of mice, rats, rabbits, cats, dogs and horses of mixed breeds, showed that the caudal superficial region of the muscle of smaller animals contained only myosin ATPase high reacting fibres. With increasing body size, the deep region of mixed fibre population occupied a larger proportion of the muscle and the proportion of its fibres low in myosin ATPase activity increased.

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The transverse sectional area of *m. longissimus* of the pigs studied, increased with increasing body weight in a relationship to the $2/3$ power of body weight. The increase in mean fibre transverse sectional area is directly proportional to the transverse sectional area of the whole muscle in pigs of live weight from 3.7 to 98 kg. The histological appearance of the myosium and perimysium did not suggest a disproportionate development of fibres other than muscle fibres. After ten days of age (3.7 kg live weight this study), growth in T.S.A. of *m. longissimus* of the pig is therefore accounted for by growth of a constant population of muscle fibres.

The number of myosin ATPase low reacting bundles of fibres remained constant throughout growth. However, the mean number of fibres per bundle increased from 1.0 in early postnatal life to 3.2 at 98 kg. live weight (Fig. 1).

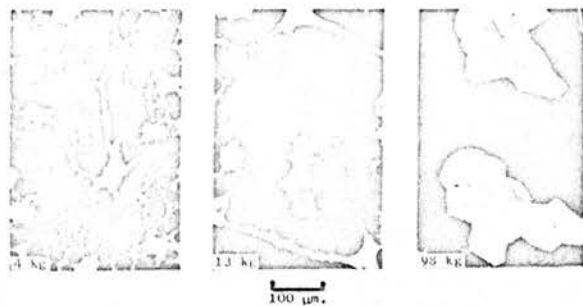


Fig. 1. Fibre types differentiated by the myosin ATPase reaction in *m. longissimus* at three stages of growth.

res with intermediate reaction for myosin ATPase were seen adjacent to the myosin ATPase low bundles". This observation was made frequently in pigs between birth and 15 kg. live weight.

Comparison of the T.S.A. of the muscle occupied by myosin ATPase low reacting fibres with total body weight by means of double logarithmic regressions showed that the area of the muscle occupied by myosin ATPase low reacting fibres bears a linear relationship to body weight ($\log Y = 0.99 \times X$).

The results obtained by assessing the total area of *m. semitendinosus* occupied by slow-twitch fibres in 12 Greyhounds and eight other dogs are given in Table II. The area occupied by slow twitch fibres in the Greyhound is

imals. The proportion of fast-twitch fibres in *m. semitendinosus* also appears to be inversely proportional to body size, although the effect is not marked as in the diaphragm. This property of *m. semitendinosus* is to be expected from dimensional theory (Hill, 1950), according to which the limb muscles of larger animals should have a lower intrinsic speed of contraction.

The unequal distribution of slow-twitch fibres across the transverse section of *m. semitendinosus* results in a higher incidence of slow-twitch fibres in the deep, medial region than the superficial lateral region of the muscle. This allows the deep region to be more suited for a postural function, and the superficial region having a greater mechanical advantage to be more suited for a predominantly propulsive function.

Effect of changing body size during growth on *m. longissimus* of pigs

If an animal maintains roughly the same shape as it grows, the cross-sectional area of any muscle will increase only by a factor of the $2/3$ power of the weight. This was confirmed by the comparison, using double logarithmic regressions, of T.S.A. of *m. longissimus* with total body weight. Although the muscle should become proportionally weaker by this growth, the T.S.A. of the muscle occupied by slow-twitch fibres in fact increases in direct proportion to body weight. Awan & Goldspink (1972) have shown that slow-contracting fibres develop and maintain more tension per μ mole of creatine phosphate used and therefore ergonomically more efficient for postural activity than fast-contracting fibres. Thus, the contractile apparatus of *m. longissimus* adapts to the changing demands placed on it during growth by the relative increase in slow-contracting fibres. Histochemical evidence has been obtained which shows that this adaptation may cause a transformation of the physiological properties of certain fibres.

Effect of selection for speed of running on fibre types

On a body size basis it might be expected that large horses and dogs should have a greater area of their skeletal muscle occupied by slow-contracting fibres than smaller members of their species. However, as Thoroughbreds and Greyhounds have a lower proportion of slow-contracting fibres in their limb muscles than smaller members of their species, a procedure of selection for speed of movement may override the effect of body size. So selection for speed produced, over a large number of generations, animals with subtle differences in their musculature. These differences appear to be neurologically determined since the myosin ATPase activity of a fibre is influenced by its type of innervation. Therefore, the differences seen in the proportion of different types of fibres in the muscles of these animals may be related to differences in their nervous system.

General Discussion

The ratio of slow-contracting to fast-contracting fibres, as determined histochemically, can be related functionally to ontogenetic and phylogenetic case in size, to selection for rapid limb movement and to the functional demands made on different parts of the same muscle.

significantly less than the other dogs at the 0.1% level. In samples from similar areas of *m. pectorales transversus* of five Thoroughbreds and six other horses, the area of slow-twitch fibres was significantly less at the 0.5% level in Thoroughbreds than in other horses.

Table II

QUANTITATIVE HISTOCHEMISTRY OF THE CANINE SEMITENDINOSUS MUSCLE
Proportion of the transverse sectional area occupied by myosin
ATPase low reacting (slow-twitch) fibres

GREYHOUNDS				OTHER DOGS				
Dog No.	Sex	Body Weight (kg)	%	Dog No.	Breed	Sex	Body Weight (kg)	%
1	♀	37	3.3	1	Great Dane	♀	47	5.4
2	♀	26	1.8	2	Collie	♀	14	12.8
3	♀	29	0.8	3	Collie	♀	11	20.6
4	♀	27	3.2	4	Collie	♀	22	10.2
5	♀	31	2.8	5	Labrador	♀	33	14.9
6	♀	34	3.3	6	Terrace X	♀	10	14.7
7	♀	25	3.3	7	Afghan	♀	25	11.0
8	♀	31	5.1	8	Afghan	♀	22	10.0
9	♀	30	0.3					
10	♀	34	2.8					
11	♀	34	1.6					
12	♀	22	0.9					
			MEAN 2.4				MEAN 17.4	
			S.D. 1.4				S.D. 5.3	

DIFFERENCE BETWEEN MEANS IS SIGNIFICANT AT THE 0.1% LEVEL

DISCUSSION

The effect of body size on fibre types in adult animals

The biochemical studies of Bertalanffy & Estwick (1953), on a series of mice and rats, show that the capacity of the diaphragm for aerobic metabolism decreases with increasing body size. On that basis it may be expected that the capacity for oxidative metabolism may be less in the diaphragm of the larger animals in our series, in fact they have a high capacity for aerobic metabolism as shown histochemically, and also a capacity for anaerobic metabolism, presumably for brief periods of high respiratory rate.

The increasing proportion of fast-twitch fibres with decreasing body size may be related to the faster speed of contraction of the diaphragm in smaller

Changes in the characteristics of muscle fibres as basic as the ATPase activity of its myosin and its intrinsic speed of contraction imply considerable adjustment of the motor unit. During normal growth this change may involve either the conversion of a motor neurone, or a localized denervation of a muscle fibre associated with a colonizing re-innervation from a neighbouring motor unit of a different type. These possibilities merit further investigation.

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The identification of factors favouring athletic ability in dogs

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This study compares the skeletal muscle of greyhounds, a breed selected for high-speed running, with other breeds by gross dissection, histometric and histochemical methods to identify any adaptations of their skeletal muscle which would favour their superior athletic capabilities.

Total carcass dissection was carried out on seven adult greyhounds and five other adult dogs. Muscles were grouped into functional units, weighed and the data analysed by analysis of covariance at the 5% level of significance. Total hind-limb muscle and *m. longissimus* weight occupied a greater proportion of total body weight than in the other breeds. This specialization would lead to greater propulsion by the spinal column and hind limb in the greyhound. A greater proportional mass of the hind limb was found above the stifle in the adult greyhound, and this would allow the hind limb to have a higher natural frequency of oscillation than the hind limb of other dogs (Tricker & Tricker, 1967), thus favouring a faster speed of non-forced limb movement. These differences were not found in eleven greyhound and four other pups, and the adult differences can be attributed to a greater growth rate of the functional units in the greyhound.

Another feature of the greyhound is its greater acceleration capability. At similar body masses the transverse sectional area of a muscle may be related to its acceleration capacity. The transverse sectional area of *m. semitendinosus* - a propulsive muscle of the hind limb - was compared in thirty-three greyhounds and twenty-six other dogs (adults and pups) and was found to be significantly greater in the greyhound, due to a greater number of fibres in the muscle.

Adult greyhounds have a higher proportion of myosin adenosine triphosphatase high-reacting (fast-twitch) fibres in their *semitendinosus* muscle than other dogs (Gunn, 1973). A histochemical investigation on *m. semitendinosus* of greyhound and other pups established that the difference in the proportions of myosin adenosine triphosphatase high-reacting (fast-twitch) and low-reacting (slow-twitch) fibres present in the respective adults was not as marked in the pups, either between the two types of dog or across the transverse section of the muscle.

It appears that greyhounds have gross morphological as well as subtle differences in their musculature which favour their greater speed of running. The gross differences develop as a result of the natural growth of

these animals, and the differences in the proportion of slow and fast-twitch fibres seen in the adults, which is neurogenically controlled, are not present at birth.

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Histochemical Observations on Laryngeal Skeletal Muscle Fibres in 'Normal' Horses

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ATROPHY of the left dorsal crico-arytenoid muscle of the horse is associated with laryngeal paralysis (Cole, 1946), and the consequent inability to dilate the rima glottidis sufficiently during exercise may produce a "roaring" sound on inspiration (Cook, 1965).

Cole (1946) provided the following evidence that atrophy of the left dorsal crico-arytenoid is of neurogenic origin. The muscles supplied by the left recurrent laryngeal nerves were atrophic, and in three cases atrophy occurred in the contralateral muscles. Histologically, atrophied muscles showed groups of small diameter fibres. Many horses with atrophy of left laryngeal muscles had smaller diameter recurrent laryngeal nerves on the left side. These nerves showed disintegration of axons and disappearance of myelin sheaths, particularly in small finely myelinated fibres at the periphery.

The present paper attempts to determine whether any neurogenic alterations can be shown in the laryngeal muscles of apparently normal horses. This approach is possible because of the ability to demonstrate various histochemical fibre types in muscle, and because of the experimental evidence that these fibre types are affected by their innervation pattern. This is shown by the effects on muscles of changing their nerve supply, thus

causing the nerve to one histochemical type of muscle to innervate a muscle of a different histochemical type (Dubowitz, 1967; Guth, Samaha and Albers, 1970), and by the reinnervation studies of Karpati and Engel (1968a).

MATERIALS AND METHODS

The larynges from 12 randomly selected horses, six adult cattle, and three greyhounds were obtained from the abattoir and post-mortem room. These animals had no clinical features of laryngeal paralysis, as described by Cook (1965) but only one (No. 10) was examined with an endoscope and it was normal. Both dorsal crico-arytenoid muscles were removed rapidly by severing their origins and insertions, and immediately weighed. The tendinous portion of these muscles and samples of the diaphragm, semitendinosus, anterior superficial pectoral and psoas muscles, were then frozen rapidly in Arcton 12 (I.C.I.) cooled to its melting point of -158°C with liquid nitrogen. Fresh frozen serial sections were cut $10\ \mu\text{m}$ thick on a cryostat.

The methods used are described by Davies and Gunn (1972): they are modifications of the methods used by Nachlas, Tsou, de Souza, Cheng and Seligman (1957) to demonstrate succinate dehydrogenase (SDHase)

TABLE I

POSSIBLE HISTOCHEMICAL FIBRE TYPE PROFILES USING THE ENZYMES MYOSIN ADENOSINE TRIPHOSPHATASE (myosin ATPase), SUCCINATE DEHYDROGENASE (SDHase), AND GLYCOGEN PHOSPHORYLASE (GPase)

Myosin ATPase	SDHase	GPase	Speed of Contraction	Metabolism	% Fibre Types in an Area of Left Dorsal Cric-arytenoid of Horse No. 11
Ah	Sh	Ph	Fast	Combined aerobic and anaerobic	72%
Ah	Sh	Pl	Fast	Aerobic	—
Ah	Sl	Ph	Fast	Anaerobic	—
Ah	Sl	Pl	Fast	—	—
Al	Sh	Ph	Slow	Combined aerobic and anaerobic	27%
Al	Sh	Pl	Slow	Aerobic	1%
Al	Sl	Ph	Slow	Anaerobic	—
Al	Sl	Pl	Slow	—	—

Key: Ah, Sh, Ph: high activity of myosin ATPase, SDHase or phosphorylase respectively.
Al, Sl, Pl: low enzyme activity.

TABLE II

Type of Horse	Number	Age (years)	Sex	Weights of Muscles (g)		Mean Group Size*	
				Left	Right	Left	Right
Pony	1	6	Gelding	4.9	4.8	3.8	—
Pony	2	Aged	Female	7.2	7.3	3.6	3.7
Pony	3	Aged	Gelding	6.3	6.4	3.6	4.1
Pony	4	3	Gelding	6.9	7.1	2.0	3.6
Shetland Pony	5	4	Gelding	2.5	2.6	2.2	1.8
Pony	6	One-half	Male	4.3	4.5	2.1	2.6
Arab x Thoroughbred	7	One-third	Male	5.0	5.1	2.4	1.9
Thoroughbred	8	6	Gelding	4.5	5.1	3.4	2.5
Hunter	9	Aged	Gelding	9.3	8.6	13.9	3.9
Thoroughbred	10	8	Gelding	12.4	10.7	4.7	2.9
Thoroughbred	11	2	Female	6.5	6.7	2.1	1.7
Carthorse	12	Aged	Male	11.3	13.0	9.8	3.5

* Number of ATPase low fibres per group.

activity; Takeuchi and Kuriaki (1955) to demonstrate glycogen phosphorylase (GPase) activity; and Padykula and Herman (1955) to demonstrate myosin adenosine triphosphatase (ATPase) activity. These serial sections were back projected on to tracing paper so that individual fibres could be outlined and their metabolic profiles constructed. The mean transverse sectional areas of each fibre type was determined by cutting out and weighing the tracing paper.

Grouping of fibre types was assessed by counting the fibres with a low activity for myosin ATPase. The counts were made on transverse bands taken across the mid-portion of the dorsal crico-arytenoid muscles from the medial to their lateral borders. The numbers of myosin ATPase low fibres and the number of fibres

forming contiguous groups were counted. A group was defined as a number of fibres in the same fasciculus, that were low in myosin ATPase, and whose sides (rather than angles) were in contact. The mean number of fibres per group and the range of size of groups expressed as a percentage of the total number of ATPase low reacting fibres sampled was used to compare animals.

RESULTS

(a) Normal fibre types in horse muscles

The evidence that succinate dehydrogenase activity indicates aerobic activity; glycogen phosphorylase activity indicates anaerobic activity; and myosin ATPase activity is related to the intrinsic speed of contraction is presented by Davies and Gunn (1972).



Fig. 1. Transverse section of left dorsal crico-arytenoid of a Hunter (horse No. 9), stained for myosin ATPase, showing "type grouping". X 60.

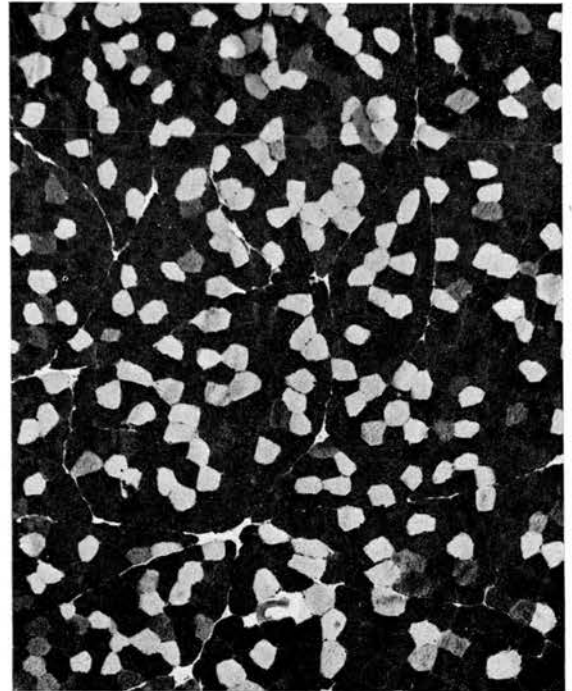


Fig. 2. Transverse section of right dorsal crico-arytenoid of a Thoroughbred gelding (horse No. 8), stained for myosin ATPase, showing a normal mosaic pattern. X 60.

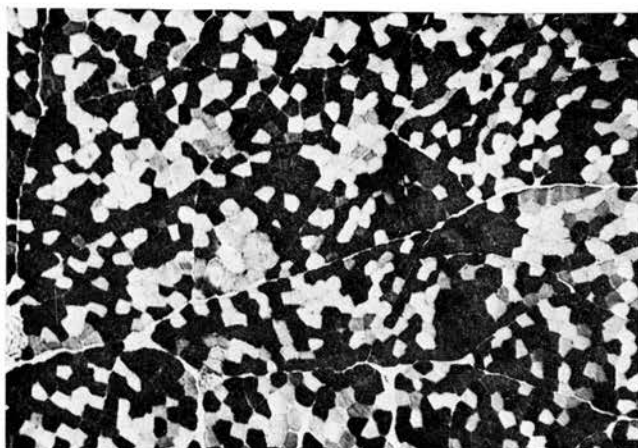


Fig. 3. Transverse section of left dorsal crico-arytenoid of a foal (horse No. 7), stained for myosin ATPase, showing "type grouping". X 60.

Using these reactions, the possible histochemical fibre types are shown in Table I.

Of these, only four types are found in normal equine muscle. They are: Ah, Sl, Ph; Ah, Sh, Ph; Al, Sh, Pl; and Al, Sh, Ph. Myosin ATPase low fibres are frequently characterized by a succinate dehydrogenase reaction in which diformazan deposits occur as intense blue punctate dots, randomly distributed throughout the fibres. In myosin ATPase high fibres, the diformazan deposits are not as clearly defined and tend to be concentrated under the sarcolemma. The proportion of these types of fibres varies between muscles and between regions of certain muscles.

Differences in proportion also occur between breeds and at different ages in the same breed (Gunn, 1972). These differences were not considered to affect the results of the present study because contralateral pairs of muscles were always compared.

(b) Normal fibre types in the dorsal crico-arytenoid muscle

All fibres in the normal dorsal crico-arytenoid muscle, e.g. No. 11, see Table II, have a high activity of succinate dehydrogenase, and therefore only Ah, Sh, Ph; Al, Sh, Pl and Al, Sh, Pl fibres are present. Slow twitch aerobic (Al, Sh, Pl) fibres, comprise less than 7 per cent of the total fibres.

These three fibre types are normally distributed in the mosaic pattern shown in figs. 2 and 4. However, some dorsal crico-arytenoid muscles show replacement of the normal mosaic pattern by groups of myosin ATPase low and high fibres, figs. 1 and 3. It was shown that over 85 per cent of 2,512 myosin ATPase low fibres counted in normal left dorsal crico-arytenoid muscles occurred in groups of less than 10 fibres.

"Normal" muscles in this context were taken as those which showed little differences between the left and right muscles, either in fibre type or in distribution of these fibres. The left dorsal crico-arytenoid of horses, Nos. 5, 6 and 11 (Table II), were "normal" with these criteria.

(c) Abnormalities in the grouping of fibre types in the dorsal crico-arytenoid muscles

Some dorsal crico-arytenoid muscles, e.g. the left from horses Nos. 9 and 7, figs. 1 and 3 respectively, show

that the normal mosaic pattern of figs. 2 and 4 has been replaced by groups of fibres with low myosin ATPase activity. Fig. 5 compares the grouping patterns between a normal and an abnormal distribution by showing the sizes of the groups of contiguous fibres expressed as a percentage of the total number of ATPase low fibres counted.

It can be seen in this histogram, and in other severely affected specimens, that when there is extensive grouping in the left muscle, there is an increase in size of group in the right muscle. Type grouping occurred in a foal, No. 7, in the left dorsal crico-arytenoid, figs. 3, 4 and 6. The dorsal crico-arytenoid muscle has a similar origin and insertion, and should have a similar function in the horse, ox and dog. Abnormal grouping was not seen in the left dorsal crico-arytenoid of six adult cattle and three greyhounds.

Horse No. 9 had the abnormal fibre types: Ah, Sh, Pl; Al, Sl, Ph; and Al, Sl, Pl. As the myosin ATPase low fibres could have either a high or low activity for glycogen phosphorylase, the latter enzyme does not reveal the grouping as clearly as myosin ATPase.

(d) Atrophy

Fresh muscle weights shown in Table II do not indicate any unilateral muscular atrophy. The differences of the weights of the muscles on either side is not significant using Student's 't' test. Indeed, the markedly affected left muscle of horse No. 9 is actually heavier than its partner. So the changes in fibre types and their groupings are expressions of changes in functional properties of the fibres, and there is unlikely to be any marked change in the total number of fibres present.

The main difference in area noted was that the ATPase low fibres in the large groups of horse No. 9 had a mean area of $7,000 \mu\text{m}^2$ which is greater than the mean area of $4,500 \mu\text{m}^2$ for ATPase low fibres in smaller groups of the same animal.

DISCUSSION

The muscle fibre types found in the arytenoid muscles are similar to those fibre types reported in the diaphragm of the horse (Davies and Gunn, 1972). This may be related to the fact that both move rhythmically during breathing (Negus, 1949), and are therefore continually acting muscles.

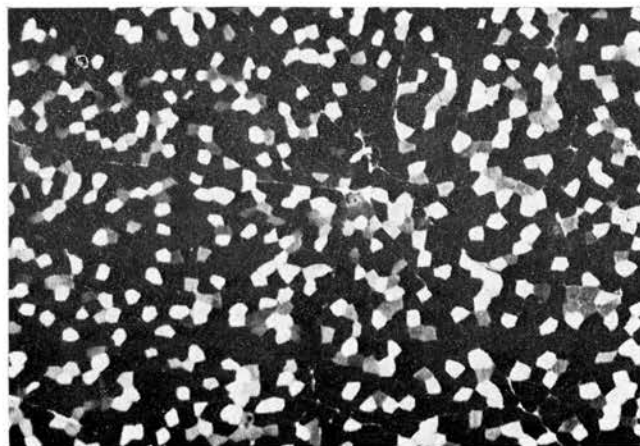


Fig. 4. Transverse section of right dorsal crico-arytenoid of a foal (horse No. 7), stained for myosin ATPase, showing a normal mosaic pattern. X 60.

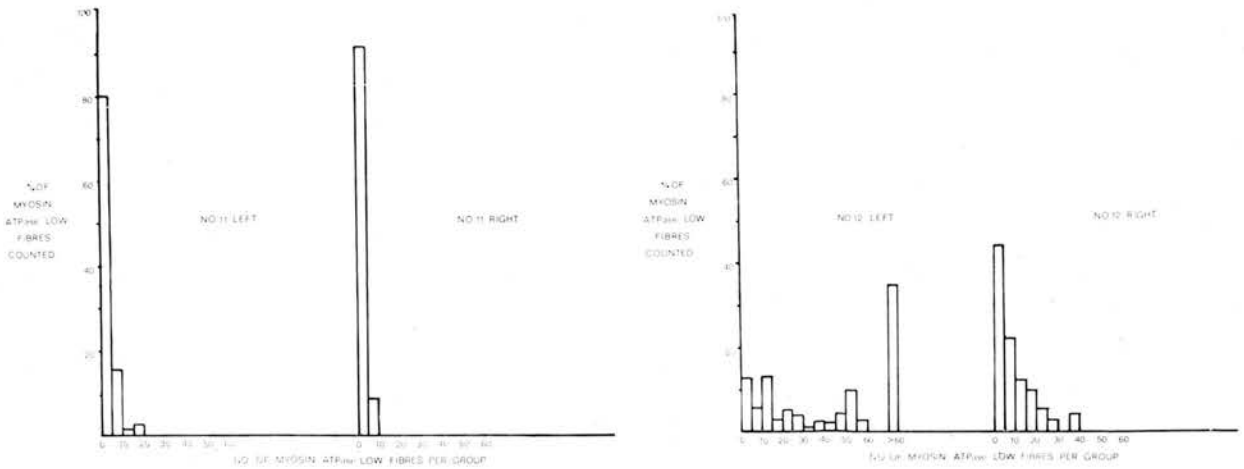


Fig. 5. Frequency distribution of the number of myosin ATPase low fibres per group (frequency interval of 5 fibres), expressed as a percentage of the total myosin ATPase low fibres counted, in the left and right dorsal crico-arytenoid of a normal horse (No. 11), and one showing grouping (No. 12).

Karpati and Engel (1968a) have shown that by crushing a nerve on three separate occasions and by sectioning a nerve and re-suturing it, type grouping of muscle fibres was demonstrated in the limb muscles of the guinea-pig by the myosin ATPase reaction when the muscles were examined 4-6 months after the operative procedures. They showed that the mechanism of completing the re-innervation of these muscles was by collateral branching of successful regenerating nerve fibres.

Type grouping was also shown to occur 2-4 months after experimental sectioning and re-suturing of the nerve supplying the tibialis anterior muscle of the white rat by Edström and Kugelberg (1969). They showed grouping both by the succinate dehydrogenase reaction and by PAS negativity in individual motor units after stimulating single motor units to deplete their glycogen content. However, when the sciatic nerve was sectioned and regeneration not allowed to occur by removing part of the nerve, type grouping did not occur in the soleus and gastrocnemius of the guinea-pig (Karpati and Engel, 1968b).

The enzyme NADH diaphorase can show the dependence of a fibre on oxidative metabolism. Karpati and Engel (1968b) have shown that three weeks after section of the nerve to the soleus and gastrocnemius in guinea-pigs, this enzyme does not differentiate fibre types because of a decline in its activity. One horse, No. 9, had a noticeable fall in activity of the aerobic enzyme used in this study, SDHase, in some of its fibres. Grouping of phosphorylase low fibres did not occur to the same extent as grouping of ATPase low fibres. Studies relating to muscular pathology in the horse should therefore incorporate enzymes of aerobic and anaerobic metabolism as well as myosin ATPase.

Some of the suggested aetiological factors concerned in laryngeal paralyses in the equine are listed by Johnson (1970). Quinlan and Morton (1957) were unable to finish their experiments, but suggest a hereditary predisposition to laryngeal paralysis. Cook (1966) shows that a mycotic infection in the guttural pouch may be associated with laryngeal paralysis. Horse No. 10 had such an infection on the left side which had regressed before death.

This study shows that neurogenic changes occur in the dorsal crico-arytenoid muscles of randomly selected

horses which did not have laryngeal paralysis. Edström and Kugelberg (1969) suggest that as a disease progresses the newly formed groups in "type grouping" become denervated, and so these groups atrophy. This sequence is seen in amyotrophic lateral sclerosis in man.

Group atrophy is seen in the haematoxylin and eosin stained photomicrographs of Cole (1946). The groups seen in the horses studied may have progressed to a stage when they would have atrophied if the animals had been allowed to live longer, and so some of the animals used may eventually have become clinical "roarers".

The work of increasing the respiratory exchange in a large animal is greater than that for a small animal (Crossfill and Widdicombe, 1961). It is possible, therefore, that a slight interference to normal breathing in a large animal, such as the horse, which would not be detected clinically but which increases its work of breathing, may decrease its athletic ability.

Further studies, to find out if these neurogenic changes observed are due to an intermittent disruption in nerve supply or a developmental defect, are required. Observations on the branchial efferent nucleus of the

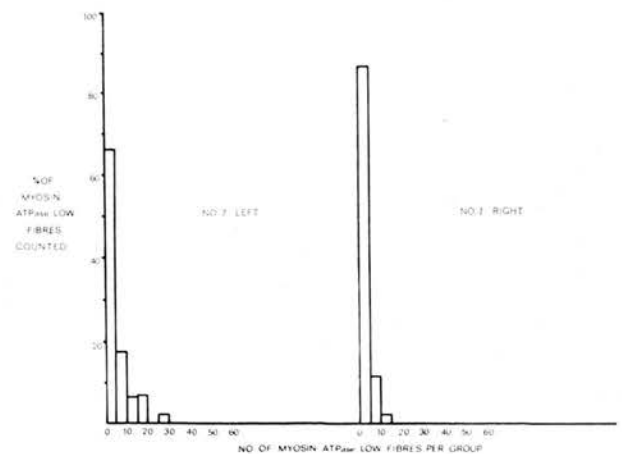


Fig. 6. Frequency distribution of the number of myosin ATPase low fibres per group (frequency interval of 5 fibres), expressed as a percentage of the total myosin ATPase low fibres sampled, in the left and right dorsal crico-arytenoid of a foal (No. 7).

vagus and accessory nerves in the medulla oblongata as well as quantitative estimations of the number of axons in both recurrent laryngeal nerves may show whether the origin of these neurogenic disturbances in the laryngeal muscles are central or peripheral. This may show why the clinical condition of laryngeal paralysis apparently has various aetiologies.

SUMMARY

Histo-chemical fibre types in normal skeletal muscle of the horse are described. Extensive grouping of fibre types and the occurrence of abnormal fibre types have been recognised in the left dorsal crico-arytenoid muscles of randomly selected horses which were not suspected of having abnormal larynges.

Type grouping was observed in the right muscles of those horses that had severely disrupted fibre type patterns in their left dorsal crico-arytenoids and also in the left dorsal crico-arytenoid of a foal. Type grouping was demonstrable in the absence of any asymmetry, either in the weights of the muscles or in the diameters of their fibres.

RÉSUMÉ

Les types histo-chimiques de fibres musculaires striées du Cheval sont décrits.

L'existence de fibres anormales et de groupements anormaux au niveau des muscles crico arytenoïdiens dorsaux gauches, prélevés sur des chevaux choisis au hasard, a été constatée, bien que ces chevaux n'aient point été suspectés d'avoir un larynx anormal.

Le groupement par type fut observé dans les muscles du côté droit des chevaux présentant des anomalies des fibres des muscles crico arytenoïdiens dorsaux gauches et aussi dans le muscle correspondant d'un foal. Ceci en l'absence d'asymétrie, soit dans le poids des muscles soit dans le diamètre de leurs fibres.

ZUSAMMENFASSUNG

Histochemisch definierte Fasertypen des normalen Skelettmuskels beim Pferd werden beschrieben. Eine übermäßige Gruppierung gewisser Fasertypen und das Auftreten abnormer Typen wurde im linken, dorsalen m. crico-arythaenoideus bei zufällig untersuchten Pferden gefunden, bei denen kein Verdacht auf Abnormitäten am Larynx bestand.

Eine Typ-Gruppierung wurde in den rechten Muskeln von Pferden beobachtet, die in ihren linken crico-arythaenoid-Muskeln schwer gestörte Fasertyp-Muster zeigten und auch im linken, dorsalen m. crico-arythaen-

oideus eines Fohlens. Die Typ-Gruppierung war nachzuweisen ohne dass eine Asymmetrie bestand (Muskelgewicht und Faserdurchmesser).

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Further Observations on Laryngeal Skeletal Muscle in the Horse

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EVIDENCE for a progressive neurogenic atrophy in the dorsal cricoarytenoid muscle of several horses with no clinical symptoms of laryngeal paralysis was reported in a previous communication (Gunn, 1972). Because the premonitory signs of a neurogenic atrophy were shown to occur in a four-month-old foal, it was considered unlikely that postnatal environmental factors are important in the aetiology of equine laryngeal paralysis.

The opportunity has since arisen to study the larynges of foetal horses and one horse in which the clinical symptoms of laryngeal paralysis had occurred. It has therefore been possible to determine whether a neurogenic disturbance is present prenatally, and if the change in the pattern of innervation occurs without a significant loss in the numbers of fibres in an obviously atrophic laryngeal muscle.

MATERIALS AND METHODS

The larynges from three randomly selected foetuses, and one horse which had been ventriculectomised eight years previously to alleviate the clinical symptoms of laryngeal paralysis, were obtained from the post-mortem room (Tables I and II).

The methods used were similar to those described previously by Gunn (1972). The right and left dorsal cricoarytenoid muscles of each of the four animals used were removed and weighed. Both halves of the transverse arytenoid and both cricothyroid muscles of the adult horse were also removed and weighed. Complete transverse sections of the mid-bellies of the muscles were prepared for histological examination.

The histochemical methods used for myosin adenosine triphosphatase (myosin ATPase), succinate dehydrogenase (SDHase), and glycogen phosphorylase (GPase)

TABLE I
CHARACTERISTICS OF THE DORSAL CRICOARYTENOID OF FOETAL HORSES

Type of horse	Number	Age (days in utero)	Sex	Weight of muscles (g)		Mean group size*		Percentage of Myosin ATPase low reacting fibres contained in groups greater than 5	
				Left	Right	Left	Right	Left	Right
Thoroughbred	13	330	Male	.8	.8	1.2	1.1	2	0
Thoroughbred	14	338	Female	1.5	1.4	1.4	1.1	9	3
Thoroughbred	15	338	Male	1.2	1.4	1.1	1.1	1	0

* Number of Myosin ATPase low fibres per group.

TABLE II
HORSE NUMBER 16, A 14-YEAR-OLD THOROUGHBRED MARE

	M. Dorsal Cricoarytenoid		M. Transverse Arytenoid		M. Cricothyroid	
	Left	Right	Left	Right	Left	Right
Muscle weight (g)	4.0	11.0	1.7	3.0	6.7	7.9
Mean size of myosin ATPase low groups	3.6	1.7	*	2.8	1.3	1.3
Total fibre number	35500	38600				
Total number of myosin ATPase low fibres	3200	3200				
TSA of muscle occupied by muscle fibres (μm^2)	26×10^6	187×10^6				

* No myosin ATPase low reacting fibres present in this muscle.

were similar to those already described (Gunn, 1972). A high molecular weight dextran was added to the phosphorylase incubation medium after the method of Meijer (1968).

A fibre having a high activity of the enzyme myosin ATPase (Ah) is designated as fast-twitch, and a fibre with a low activity (Al) as slow-twitch. The SDHase and GPase reactions indicate the capacity of a fibre for aerobic and anaerobic metabolism respectively. The symbols Sh and Sl indicate a high or low SDHase enzymic activity, and the symbols Ph and Pl refer to the GPase activity.

Metabolic profiles of individual fibres were constructed and an assessment of grouping of fibre types was carried out. In the adult horse the total number of each type of fibre was measured by counting each fibre in the left dorsal cricoarytenoid, and the total number of fibres in the right muscle was estimated by sampling the entire transverse section at 2 mm intervals.

RESULTS

Fibre types

Late foetal laryngeal muscle contains the same fibre types as those found in normal adult laryngeal muscles, which are: fast-twitch combined aerobic and anaerobic (Ah, Sh, Ph) fibres, slow-twitch combined aerobic and anaerobic (Al, Sh, Ph) fibres, and a few slow-twitch predominantly aerobic (Al, Sh, Pl) fibres (Gunn, 1972). The overall density of reaction products due to the succinate dehydrogenase and glycogen phosphorylase reaction was less in foetal than in adult laryngeal muscle.

While it is recognised that the histochemical methods used do not quantitatively indicate the overall enzyme activity, foetal laryngeal muscle always gave weaker reactions for both these enzymes.

Areas of reduced fibre size were observed in the laryngeal muscles of the adult horse with laryngeal paralysis. In the left dorsal cricoarytenoid and in the two halves of the transverse arytenoid some areas had fibres with reduced activities of succinate dehydrogenase and glycogen phosphorylase.

In a sample of such an area from the left dorsal cricoarytenoid, 13 per cent of the fast-twitch fibres were Sl in contrast to the normal, which contains no such

fibres. Slow-twitch fibres which were Sl (7 per cent) and Pl (29 per cent) are also absent from control specimens.

A significant number of Sl or Pl fibres is abnormal in any region of adult horse laryngeal muscle, as normally all the fibres are aerobic and only 1 per cent do not have anaerobic capacity. This suggests that in regions of severe fibre atrophy, fast-twitch fibres had a reduced capacity for aerobic metabolism, and slow-twitch fibres had a reduced capacity for anaerobic metabolism.

Central nuclei were apparent in some fibres, and fibres having a higher SDHase activity centrally than peripherally were also present. In areas of severe hypotrophy, fibres were surrounded by connective tissue which sometimes contained fat cells.

An interesting observation is that the left half of the transverse arytenoid muscle consists entirely of fast-twitch fibres, while the right half, which is separated from the left by a fibrous raphe, contains some slow-twitch fibres. Further, in the left half 6 per cent of the fast-twitch fibres are Pl, while in the right half 8 per cent of these fibres are Sl, and some fast-twitch fibres do not react for either of the metabolic enzymes. The slow-twitch fibres in the right half include 13 per cent which were Sl, and 44 per cent which were Pl.

The significance of these observations is obscure, but it may be related to the interaction between fibres which insert onto a common raphe.

Abnormalities in the grouping of fibre types

The right dorsal cricoarytenoid muscle of one of the foetuses, horse No. 14 (fig. 1), shows the normal regular pattern of fibre types. However, the contralateral muscle (fig. 2) has groups of fibres with low myosin ATPase activity. Nine per cent of the myosin ATPase low reacting fibres occurred in groups of over five (Table I). The percentage of myosin ATPase low reacting fibres in groups greater than five was much lower in this muscle in the other two foetuses.

Groups of myosin ATPase low reacting fibres were seen in the left dorsal cricoarytenoid (figs. 3 and 4), and in the right half of the transverse arytenoid of the adult horse. These muscles did not have groups of myosin ATPase low reacting fibres as large as those

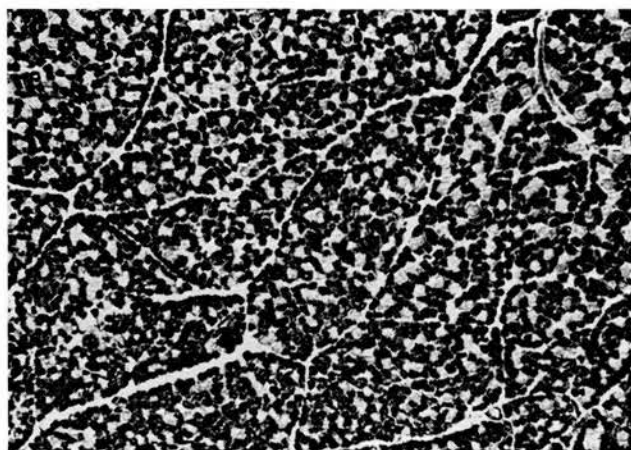


Fig. 1. Transverse section of right dorsal cricoarytenoid of a Thoroughbred foetus (horse No. 14), stained for myosin ATPase. Low reacting fibres occur in a regular pattern. X 60.

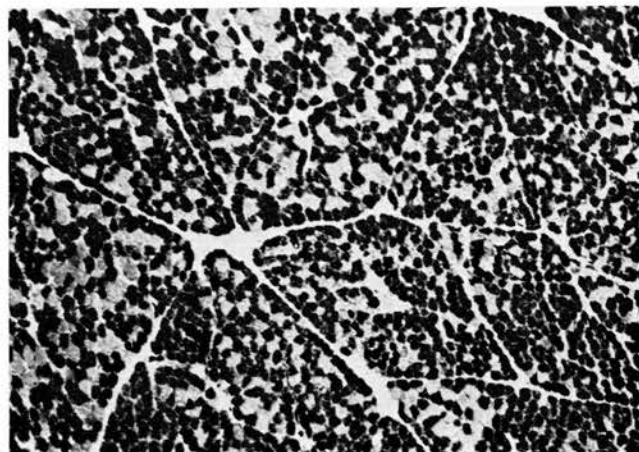


Fig. 2. Transverse section of left dorsal cricoarytenoid of a Thoroughbred foetus (horse No. 14), stained for myosin ATPase. Low reacting fibres are arranged irregularly in groups. X 60.

DISCUSSION

The occurrence of an abnormal pattern of fibre type distribution in the left dorsal cricoarytenoid of a foetal horse suggests a neurogenic disturbance occurring in this muscle before birth. A reduction in the transverse sectional area of the left dorsal cricoarytenoid muscle due to a decrease in size of the individual fibres combined with, in some regions, a decrease in their metabolic capacity, would render the muscle inadequate to cope with a period of high functional demand.

The preferential atrophy of myosin ATPase high reacting fibres seen in this study is similar to that seen by Engel, Brooke and Nelson (1966) in the cat gastrocnemius muscle following experimental denervation.

The occurrence of atrophy in the right half of the transverse arytenoid is similar to the observations by Cole (1946). He shows that the three larynges with the greatest atrophy in the left dorsal cricoarytenoid muscle also had atrophy of their right transverse arytenoid muscles. This may indicate involvement of the right caudal (recurrent) laryngeal nerve as well as the contralateral nerve. Signs of a neurogenic disturbance are not present in the cricothyroid muscles, which are innervated by the cranial laryngeal nerve.

It appears from these studies that the condition of laryngeal paralysis in the horse is congenital in character and progressive in nature. It is a neurogenic disease involving the left caudal laryngeal nerve and possibly the right nerve to a lesser extent.

SUMMARY

An abnormal pattern of fibre type distribution has been observed in the left dorsal cricoarytenoid of a foetal horse. The gross atrophy of the left dorsal cricoarytenoid of a case of equine laryngeal paralysis occurred due to a decrease in mean transverse sectional area of its fibres, in particular a hypotrophy of the

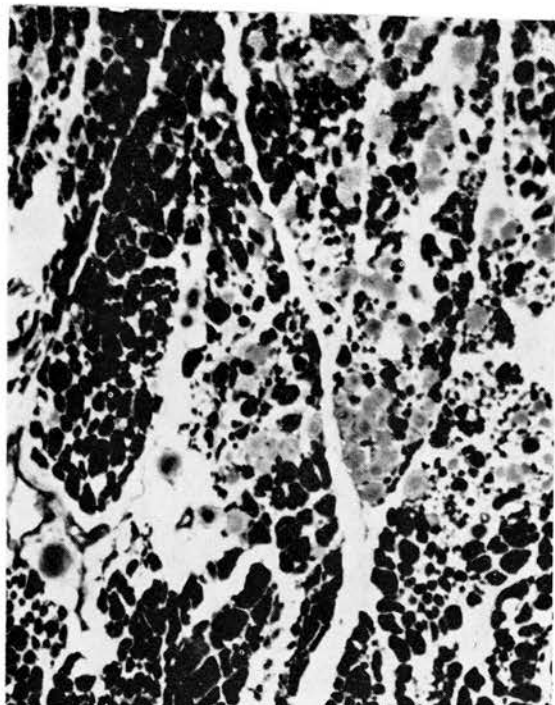


Fig. 3. Transverse section of left dorsal cricoarytenoid of a Thoroughbred mare (horse No. 16), stained for myosin ATPase. Both types of fibres occur in groups. The reduction in mean transverse sectional area of the myosin ATPase high reacting fibres suggests a preferential atrophy of this type of fibre. X 60.

seen in some of the muscles of apparently normal horses (Gunn, 1972).

Groups of myosin ATPase low reacting fibres were not seen in either of the cricothyroid muscles. The entire transverse section of the left transverse arytenoid consisted of bundles of hypotrophic fast-twitch fibres enclosed in thickened fibrous tissue septae.

Atrophy

Atrophy, as shown by the low weights relative to those of the contralateral muscles, was observed in the left dorsal cricoarytenoid and left half of the transverse arytenoid muscles of the adult horse (Table II). Fresh muscle weights of the other pair of muscles and of the dorsal cricoarytenoid muscles of the foetuses shown in Tables I and II do not indicate unilateral muscular atrophy.

Marked reduction of mean fibre transverse sectional area (T.S.A.) was apparent in the complete transverse section of the left dorsal cricoarytenoid, and in the left half of the transverse arytenoid, and in areas of the right half of the transverse arytenoid of the adult horse (figs. 3 and 4). The total number of fibres in both cricoarytenoid muscles was approximately the same (Table II).

Atrophy of the muscle on the left side was due to a decrease in mean T.S.A. of both types of fibre. However, the mean T.S.A. of the myosin ATPase high reacting fibres was $738 \mu\text{m}^2$ on the left side and $5,735 \mu\text{m}^2$ on the right side. The mean T.S.A. of the myosin ATPase low reacting fibres was $990 \mu\text{m}^2$ on the left side and $5330 \mu\text{m}^2$ on the right side.

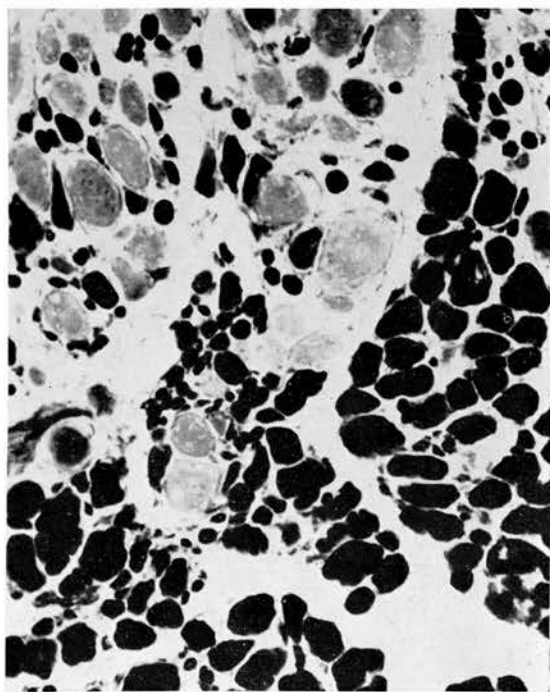


Fig. 4. Same section as Fig. 3. X 150.

myosin ATPase high reacting fibres, rather than a decrease in fibre number.

RÉSUMÉ

Une disposition anormale dans la distribution des fibres a été observée dans le muscle crico arytenoïde dorsal gauche d'un foetus équin.

Dans un cas de paralysie laryngée du cheval l'altération la plus importante constatée au niveau du muscle crico arytenoïde dorsal gauche fut la réduction de la surface moyennée de section des fibres et en particulier une hypotrophie des fibres à myosine-ATPase "high activity", beaucoup plus qu'une réduction dans le nombre des fibres.

ZUSAMMENFASSUNG

Ein abnormer Aufbau der Faserverteilung konnte im linken, dorsalen Cricoarythaenoid eines Pferdefoeten beobachtet werden. Die Atrophie des linken, dorsalen Cricoarythaenoids bei einem Fall von Larynxparalyse trat eher wegen einer Abnahme in der Ausdehnung der Faserfläche auf, insbesondere bestand eine Hypotrophie

der Myosin-ATPase reichen Fasern, als wegen einer Abnahme der Faseranzahl.

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