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GEOGRAPHICAL VARIATION IN *APODEMUS SYLVATICUS* AND *A. FLAVICOLLIS* (*RODENTIA, MURIDAE*) IN EUROPE, WITH SPECIAL REFERENCE TO DANISH AND LATVIAN POPULATIONS

BY

ERIK URSIN

København 1956
kommission hos Ejnar Munksgaard

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CONTENTS

Synopsis.

The following characters have been investigated: The length of tail, hind foot, and skull in relation to the length of head and body; the length of the tooth row and, in some cases, the length of individual teeth; the number of tail rings (literature only); the colour patterns of the chest and, more peripherically, other pelage characters.

In *A. sylvaticus* there seems to be, in western Europe, a more or less gradual change in the proportionate length of several parts of the animal from the north-east towards the west and the south. The western and southern populations are more like *A. flavicollis* than are the north-eastern ones.

A flavicollis shows a considerable local variation in proportionate length of several parts of the body. Regular geographical variation was observed in the shape of the collar which reaches its highest development in north-western Europe.

Four European species of *Apodemus*, namely, *A. mystacinus*, *A. flavicollis*, *A. sylvaticus*, and *A. microps* are shown to be to some extent distinguishable from each other by the proportionate length of various parts of the body.

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Introduction.

The present investigation is based primarily on material belonging to the Zoological Museum of the University of Copenhagen which possesses large collections from Denmark and Latvia. The Danish material was collected by several persons and during many years while the entire Latvian material was collected by Dr. HANS JOHANSEN in August-December 1938 and in July-August 1939. The author is indebted to Dr. MAGNUS DEGERBØL, keeper of vertebrates, and to Dr. JOHANSEN, for permission to work up the collections. Material from other countries has been studied, although not in detail, in the British Museum where the staff of mammalogists was most helpful during my short stay. Dr. K. ZIMMERMANN has been kind enough to place at my disposal an interesting series of skins of *Apodemus flavicollis* from Norway, belonging to the Humboldt University of Berlin. Financial support was rendered by the Danish State Research Foundation, by the University of Copenhagen, and by the JAPETUS STEENSTRUP Foundation. The English language was revised by Mrs. AGNETE VOLSÖE.

The condylobasal length of skulls and the alveolar length of the upper tooth row were measured by the author. A test has shown that the tooth row measurements do not differ essentially from those of MILLER (1912). Body measurements were carried out by several persons, usually on fresh material. Some Danish specimens preserved in alcohol were measured by the author. Hind foot measurements do not include claws. The head-and-body of Danish specimens was measured to the anus, and the tail was measured from the anus to the tip, excluding hairs. Latvian specimens were measured to (and from) the base of the tail. The difference in the measuring technique seems, however, to have affected the results very little.

In the map, Fig. 1, are indicated the Danish localities from which material is available. The localities in Latvia are Antini (57°00′ N. 23°30′ E.), Planupe (57°00′ N. 23°20′ E.), and Koknese (56°40′ N. 25°30′ E.).

The Tail.

The tail length of the two species in Denmark and Latvia is shown in Tables 1—2. As far as sufficient material is available it has been divided into size groups according to length of head and body (Tables 3—4). The contents of Tables 3 and 4 are shown

diagrammatically in Fig. 2. Within the range of body length of the available material there seems to be an almost straight-line relationship between body length and tail length. Small specimens of both species have proportionately longer tail than larger

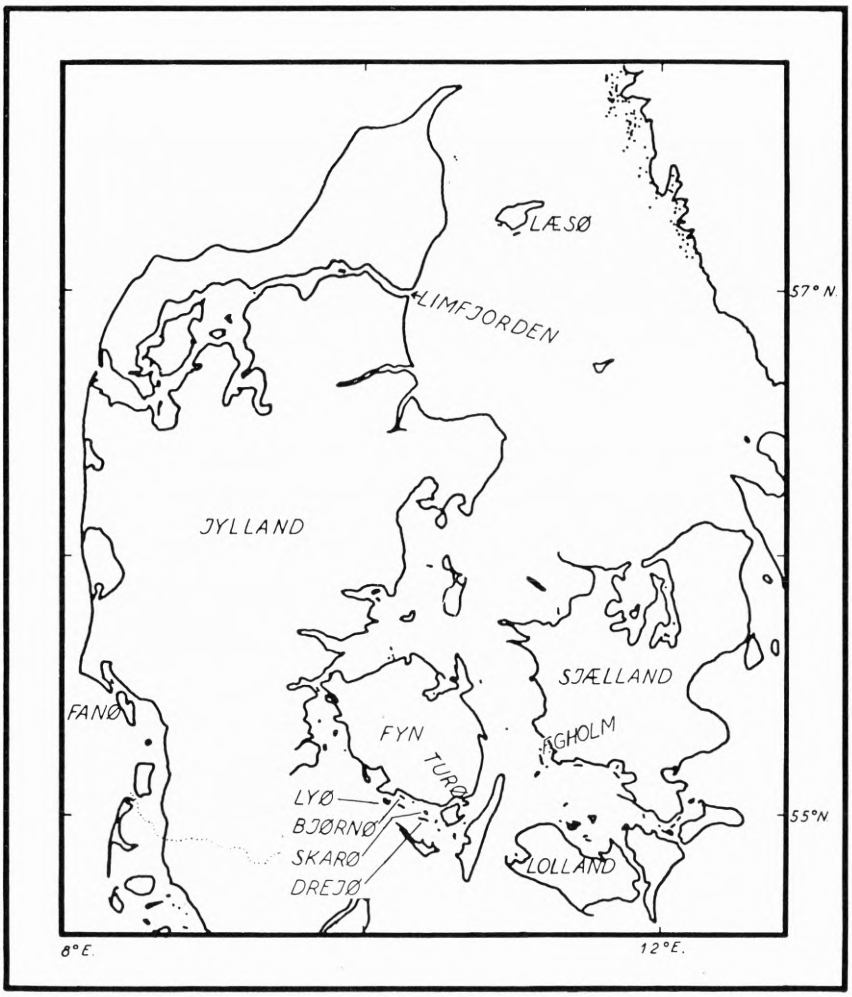

Fig. 1. Map of Denmark with indication of the localities referred to in text.

ones. There is in Denmark and Latvia not much overlapping of the relative tail length of the two species. Only the smaller size-groups of *A. flavicollis* from Koknese (Latvia) are within the range of *A. sylvaticus*.

A comparison of series of *A. sylvaticus* of equal body length shows for most size-groups that the tail is significantly longer in Sjælland than in Jylland. The specimens from two small Danish islands, Skarø and Drejø, resemble those from Jylland while the Latvian series (from Antini) is more like that from Sjælland.

The two series of Latvian *A. flavicollis* (from Antini and Koknese) are distinct from each other. The difference is significant for most size-groups in spite of the small number of observations from Koknese. The Danish series (from Sjælland and Jylland) bear most resemblance to that from Koknese. Both in Sjælland and Jylland the tail is signi-

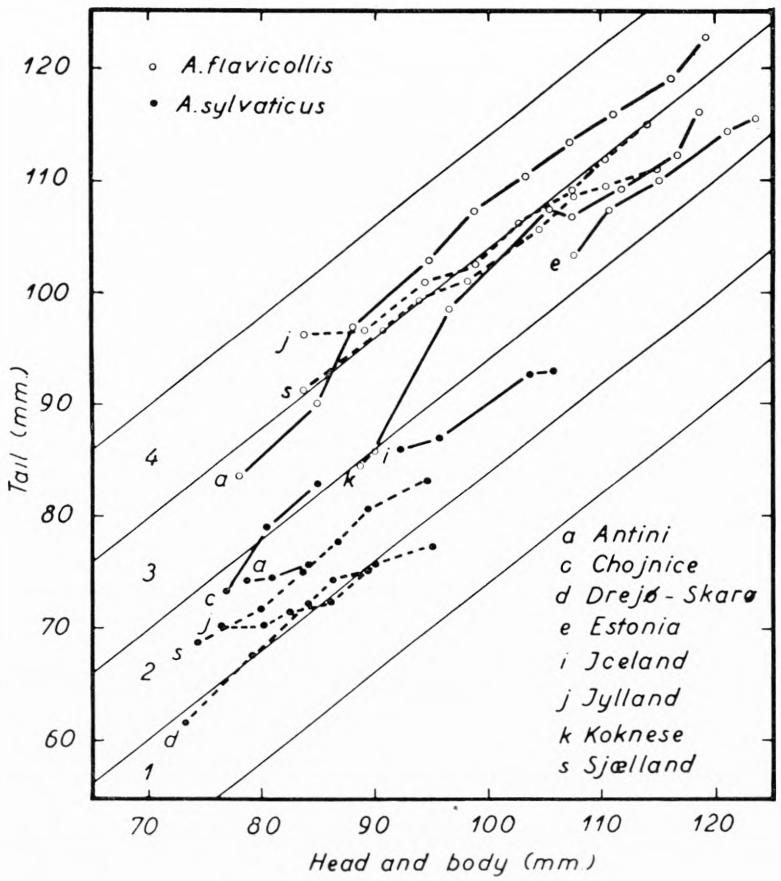

Fig. 2. Cf. text p. 5.

ficantly shorter than in Antini. The tail length is probably not identical in the two Danish series (cf. the diagram, Fig. 2) because in the present material the tail for all size groups was found to be longer in Jylland than in Sjælland. The difference is, however, difficult to prove statistically because generally the standard deviation of the mean is approximately as large as the difference between the means. Significance is, however, approached when the tail/body ratio is calculated for each specimen of the two series and the mean values of this ratio are compared. For Jylland is found $t/b = 1.0395 \pm 0.0127$ and for Sjælland $t/b = 1.0105 \pm 0.0082$. The difference is significant at the 5 % level.

TABLE 1. Measurements of *Apodemus sylvaticus*. Mean values and standard

Locality		Tooth-wear	Head & body		Tail	
			N.	M. ± S.D.	N.	M. ± S.D.
Latvia	Antini	All stages of wear	12	82.08 ± 1.57	12	74.17 ± 2.08
Denmark	Jylland		113	85.49 ± 0.66	109	72.91 ± 0.34
	Sjælland		34	84.77 ± 1.30	34	75.74 ± 1.42
	Fanø		9	85.83 ± 2.36	9	76.94 ± 1.55
	Læsø		8	90.00 ± 2.14	8	81.88 ± 2.74
	Egholm		7	93.93 ± 3.22	7	83.93 ± 1.81
	Skarø		13	85.19 ± 1.85	11	72.50 ± 1.78
	Drejø		15	82.50 ± 2.18	13	69.81 ± 2.38
	Bjørnø		11	86.14 ± 2.53	8	71.88 ± 3.59
	Lyø		8	86.25 ± 3.63	7	68.21 ± 3.84
	Bornholm		16	86.17 ± 1.25	11	73.86 ± 3.69
	Various islands		30	90.26 ± 1.41	25	75.10 ± 1.13
Latvia	Antini	Teeth worn	1	86	1	66
Denmark	Skarø		1	95	0	
	Other loc.		8	96.25 ± 2.95	7	81.07 ± 3.47
Denmark	Drejø	m^3 developing	1	66	1	53

[1] Cf. Figs. 2, 7 and 11; text p. 8.

TABLE 2. Measurements of *Apodemus flavicollis*. Mean values and standard

Locality		Tooth-wear	Head & body		Tail	
			N.	M. ± S.D.	N.	M. ± S.D.
Latvia	Antini	All stages of wear	148	104.0 ± 0.9	143	110.5 ± 1.0
	Koknese		20	104.0 ± 3.0	20	101.7 ± 3.3
	Planupe		10	116.0 ± 3.3	7	111.8 ± 2.5
Denmark	Jylland		42	103.0 ± 1.4	40	106.5 ± 1.6
	Sjælland		82	104.8 ± 1.0	77	105.6 ± 1.0
	Lolland		13	106.3 ± 2.8	12	107.5 ± 2.5
	Turø		8	95.0 ± 5.4	7	88.9 ± 5.6
	Fyn		6	102.5 ± 3.7	5	101.5 ± 1.9
	Various islands		15	105.5 ± 2.8	12	105.8 ± 2.1
Latvia	Antini	Teeth worn	11	117.5 ± 1.8	10	121.0 ± 1.7
	Koknese		4	116.2 ± 6.9	4	115.0 ± 4.4
	Other loc.		2	120	2	117
Denmark	Various loc.		9	115.8 ± 3.5	5	118.4 ± 2.5
Latvia	Antini	m^3 developing	7	76.8 ± 2.0	6	79.2 ± 2.5
	Koknese		3	88.2 ± 1.8	3	79.2 ± 1.8

deviations of the mean for various localities in Denmark and Latvia.

Hind foot		m^{1-3}		Condylob. length			Length group[1]		
N.	M. ± S.D.	N.	M. ± S.D.	N.	Head & body	M. ± S.D.	Tail	Hind foot	Condylob. length
12	20.67 ± 0.17	11	3.52 ± 0.03	9	83	21.38 ± 0.26	1	1	1
113	20.82 ± 0.08	34	3.81 ± 0.03	32	(87)	22.21 ± 0.17	2	1	2
34	20.79 ± 0.20	20	3.83 ± 0.04	19	..	22.22 ± 0.29	1	1	..
9	20.17 ± 0.34	0	..	0	..	..	2	0	..
8	21.12 ± 0.20	0	..	0	..	..	2	1	..
7	21.50 ± 0.22	4	3.90 ± 0.06	5	94	22.75 ± 0.49	2	1	1
13	20.88 ± 0.18	10	3.56 ± 0.03	6	(88)	21.90 ± 0.20	2	1	1
15	20.17 ± 0.30	11	3.50 ± 0.03	6	89	21.90 ± 0.20	1	1	1
11	20.68 ± 0.23	5	3.82 ± 0.06	5	86	21.50 ± 0.55	1	1	1
8	20.75 ± 0.25	6	3.82 ± 0.04	3	91	22.00 ± 0.65	1	1	1
16	21.19 ± 0.29	10	3.84 ± 0.05	10	..	22.02 ± 0.17	2	1	..
30	21.13 ± 0.15	14	3.90 ± 0.04	12	(93)	22.95 ± 0.33	1	1	2
1	20	1	3.6	1	86	22.7	..	..	..
1	21.2	1	3.5	1	95	22.7	..	..	..
8	21.50 ± 0.38	11	3.96 ± 0.05	9	..	23.72 ± 0.28	2	1	..
1	17.5	1	3.7	0	..	..	..	..	..

deviations of the mean for various localities in Denmark and Latvia.

Hind foot		m^{1-3}		Condylob. length			Length group		
N.	M. ± S.D.	N.	M. ± S.D.	N.	Head & body	M. ± S.D.	Tail	Hind foot	Condylob. length
146	24.99 ± 0.10	137	4.42 ± 0.01	75	106	25.60 ± 0.20	4	4	3
19	23.74 ± 0.37	18	4.29 ± 0.04	11	112	25.55 ± 0.30	3	2	2
9	25.11 ± 0.52	8	4.49 ± 0.05	4	119	27.68 ± 0.43	3	3	3
42	24.12 ± 0.17	24	4.30 ± 0.03	19	104	25.77 ± 0.25	4	3	3
82	24.49 ± 0.12	57	4.30 ± 0.02	21	107	25.73 ± 0.22	3	3	3
13	24.81 ± 0.29	23	4.26 ± 0.03	18	104	25.59 ± 0.38	3	3	3
8	23.50 ± 0.46	4	4.22 ± 0.03	2	106	23.90	2	3	..
6	24.67 ± 0.40	0	..	0	..	..	3	4	..
15	24.63 ± 0.31	5	4.28 ± 0.09	4	101	25.50 ± 0.80	3	3	3
8	25.94 ± 0.40	11	4.55 ± 0.04	8	119	27.44 ± 0.19	4	4	3
4	24.75 ± 0.48	4	4.38 ± 0.05	2	113	26.45	3	3	..
2	25.75	2	4.65	1	122	28.7	..	..	..
9	24.86 ± 0.40	11	4.39 ± 0.05	10	..	27.28 ± 0.20	..	3	..
7	22.86 ± 0.34	7	4.26 ± 0.05	3	73	20.17 ± 0.07	3	4	..
2	23.00	3	4.13 ± 0.04	1	80	22.1	..	..	..

TABLE 3. *Apodemus sylvaticus*. Length of tail in relation to length of head & body.

Head & body (Intervals)	Latvia			Denmark								
	Antini			Jylland			Sjælland			Skarø & Drejø		
	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.
65—79	..	..	..	24	76	70.21 ± 1.00	8	74	68.75 ± 3.50	6	73	61.67 ± 2.39
70—84	9	79	74.17 ± 2.64	58	80	70.26 ± 0.58	14	80	71.79 ± 2.22	12	79	68.75 ± 2.06
75—89	10	81	74.50 ± 2.39	77	83	71.59 ± 0.55	24	84	75.00 ± 1.51	16	84	72.19 ± 1.55
80—94	8	84	75.62 ± 1.64	73	86	72.57 ± 0.64	24	87	77.71 ± 1.29	17	86	74.26 ± 1.21
85—99	..	..	..	47	91	75.90 ± 0.94	17	90	80.74 ± 1.14	11	90	75.23 ± 1.06
90—104	..	..	..	28	95	77.32 ± 1.32	7	95	83.21 ± 2.02	..	..	..

TABLE 4. *Apodemus flavicollis*. Length of tail in relation to length of head & body.

Head & body (Intervals)	Latvia						Denmark					
	Antini			Koknese			Jylland			Sjælland		
	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.
70—84	9	78	83.6 ± 2.9	..	..	..	..	..	..	..	..	..
75—89	10	85	90.0 ± 1.9	..	..	..	4	84	96.2 ± 5.6	4	84	91.2 ± 6.2
80—94	18	88	96.9 ± 2.6	7	89	84.6 ± 3.1	6	89	96.6 ± 4.6	11	91	96.6 ± 2.0
85—99	35	95	102.8 ± 1.4	6	90	85.8 ± 3.4	12	95	100.8 ± 2.4	17	94	99.2 ± 1.6
90—104	52	99	107.1 ± 1.1	5	96	98.5 ± 4.0	18	99	102.5 ± 1.8	27	98	101.0 ± 1.2
95—109	77	103	110.4 ± 0.9	6	106	107.5 ± 1.3	23	103	106.2 ± 1.6	44	104	105.8 ± 1.0
100—114	75	107	113.3 ± 0.8	8	108	106.9 ± 1.1	24	108	109.0 ± 1.5	50	108	108.6 ± 1.0
105—119	68	111	116.0 ± 0.8	9	112	109.2 ± 1.9	17	110	111.9 ± 2.0	44	110	109.3 ± 1.1
110—124	43	116	119.1 ± 1.0	6	117	112.5 ± 3.2	10	114	115.0 ± 2.5	21	115	111.0 ± 1.6
115—129	24	119	122.9 ± 0.9	4	119	116.2 ± 3.2	..	..	..	..	..	..

In Tables 5—8 are compiled from the available literature the measurements of *A. sylvaticus* (L.), *A. flavicollis* (MELCH.), *A. mystacinus* (DANFORD and ALSTON), and *A. microps* KRATOCHVÍL and ROSICKÝ from various localities in Europe and the non-European Mediterranean area. In Fig. 3 the tail length has been plotted against the length of head and body. Material from the British Isles was kept separate in Fig. 4 owing to the high degree of specialization obtained on many small islands. In the diagrams, Figs. 2—4, is drawn a series of straight lines approximately parallel to the graphs of the body/tail relationship in Fig. 2. The intervals between successive lines are numbered 1—5 so that the most short-tailed animals are found in interval 1 and the most longtailed ones in interval 5. Accordingly, they are said to belong to group 1 and group 5 respectively. Most populations of *A. sylvaticus* belong to group 3 and,

TABLE 5. *Apodemus sylvaticus* (and *A. microps*). Published measurements of European (excl. British) and Mediterranean populations.

Reference	Subspecies	Locality	N.	Measurements					Length group[1]		
				Head & body	Tail	Hind foot	Skull C.B.	No. of tail rings	Tail	Hind foot	Skull C.B.
STEIN 1938 p. 507	*sylvaticus*	Frankfurt Oder	8	81.5	74.2	..	..	..	2	..	..
ZIMMERMANN 1936 p. 125	—	Houthem, Holland	9	93.6	88.3	22.1	..	156	2	2	..
— — —	—	Langeoog, Friesian Isl.	7	92.3	98.2	23.0	..	161	4	3	..
— — —	—	Wesermünde	7	88.9	80.8	21.6	..	150	2	2	..
— — —	—	Sylt, Friesian Islands	7	87.3	82.3	21.3	..	144	2	1	..
— — —	—	Lüneburg	76	90.8	81.3	20.8	..	143	2	1	..
— — —	—	Bellinchen (Mark)	6	89.4	76.1	21.3	..	151	2	1	..
— — —	—	Buch (Mark)	36	86.1	78.8	20.7	..	143	2	1	..
— — —	—	Reipzig (Mark)	7	82.4	74.0	22.3	..	131	2	3	..
— — —	—	Zempelburg, Poland	17	80.5	77.5	..	..	163	2	..	..
— — —	—	Jugoslavia	14	86.4	83.2	20.9	..	..	3	1	..
— — —	*dichrurus*	—	26	93.6	89.2	22.2	..	..	2	2	..
— — —	*sylvaticus*	Bulgaria	17	93.3	81.7	23.1	..	173	2	3	..
HAGEN 1954 p. 11	*dichrurus*	S. Sicily	7	93.6	86.3	22.0	23.8	174	2	2	2
— — —	—	Saloniki, Greece	9	96.8	88.5	23.2	24.8	..	2	3	3
— — —	—	Lewadia, Greece	6	97.5	93.3	22.8	25.0	..	3	2	3
— — —	—	Ossagebirge, Greece	8	102.6	100.5	23.4	..	..	3	2	..
— — —	—	NE Sicily	12	103.2	96.4	23.7	26.4	163	2	3	4
VON LEHMANN 1954 p. 24	*sylvaticus*	Liechtenstein	11	97	90	22.3	..	..	2	2	..
HEINRICH 1951 p. 107	—	Holstein	29	81.8	76.4	20.9	..	..	2	1	..
— — —	—	Oberbayrische Ebene	20	89.8	89	21.8	..	..	3	2	..
— — —	—	Bayrische Oberpfalz	40	90	89.9	21.8	..	..	3	2	..
— — —	—	Bodensee	11	91	91	22	..	..	3	2	..
— — —	—	Berchtesgaden	9	91	91	21.6	..	..	3	1	..
— — —	—	Allgäu	19	87	88.8	21.9	..	..	3	2	..
NEUHÄUSER 1936 p. 226	*tauricus*	Asia Minor	10	98.2	101.2	21.3	23.5	..	2	1	2
HILZHEIMER 1911 p. 16	*flavo-brunneus*	Württemberg	5	99.0	85.4	21.8	..	..	2	1	..
HEINRICH 1929 p. 189		Chojnice, Poland, total	17	80.5	77.5	..	..	..	3	..	..
— — —		— h. & b. 70–84	12	77.0	73.6	..	..	..	2	..	..
— — —		— — 75–89	10	80.5	79.1	..	..	..	3	..	..
— — —		— — 80–94	10	85.1	83.2	..	..	..	3	..	..
HEROLD 1951 p. 237		Rhön, Germany	56	83.7	82.5	22.2	..	158	3	3	..
ZIMMERMANN 1953 p. 37	*dichrurus*	Crete	35	93.5	89.4	21.7	23.3	175	3	1	2
BARRETT-HAMILTON 1900 p. 426	*hayi*	Morocco	9	96.1	97.3	22.1	..	..	3	1	..
HANZÁK & ROSICKÝ 1949 p. 26	*sylvaticus*	Slovakian mountains	10	86.5	84.4	21.5	..	..	3	2	..
HANZÁK, priv. communication	—	Böhmen-Böhmerwald	12	93.0	86.3	22.3	22.2	..	2	2	1
KRATOCHVÍL & ROSICKÝ 1953 p. 5	—	Krkonoše	13	93.2	84.9	21.9	..	..	2	2	..
— — —	—	Jižní Čechy	7	93.8	88.5	21.9	..	..	2	1	..
— — —	—	Linkov	10	94.9	89.3	21.9	..	..	2	1	..

[1] Refering to the diagrams.

TABLE 5 (continued).

Reference	Subspecies	Locality	N.	Measurements				No. of tail rings	Length group[1]		
				Head & body	Tail	Hind foot	Skull C.B.		Tail	Hind foot	Skull C.B.
KRATOCHVÍL & ROSICKÝ											
1953 p. 5	*sylvaticus*	Jeseníky	18	95.6	84.5	22.2	..	..	2	2	..
— — —	—	Přerov	8	97.7	83.4	21.7	..	..	2	1	..
— — —	—	Lednicko	8	92.3	87.1	21.4	..	..	2	1	..
— — —	—	Velkomeziříčsko	11	96.1	86.1	22.3	..	..	2	2	..
— — —	—	Rožnavsko	26	90.1	80.1	21.7	..	..	2	2	..
— 1952 p. 60	—	Č.S.R., total	120	93.6	84.0	21.9	..	..	2	1	..
— — —	*Apodemus microps*	Southern Slovakia	19	87.9	79.3	19.2	..	..	2	— 1	..
FELTEN 1952 p. 191	*sylvaticus*	Rhein/Main	146	88.3	85.3	21.6	22.1	162	3	2	2
DEGERBØL 1939 p. 42	*grandiculus*	Iceland, total	31	99.6	90.0	23.3	23.7	144	2	2	2
		—, h. & b. 85–99	14	92.1	86.5	..	23.3	..	2	..	2
		— — 90–104	17	95.8	87.2	..	..	..	2	..	..
		— — 95–109	18	103.6	92.8	..	..	..	2	..	..
		— — 100–114	17	105.8	92.9	..	24.0	..	2	..	1
MILLER 1912 p. 805	*sylvaticus*	Bergen, Norway	10	96.1	98.3	22.1	..	..	3	1	..
— — —	—	Liége, Belgium	10	94.3	92.3	22.0	..	..	3	2	..
— — —	—	Gers, France	10	93.1	85.5	20.5	..	..	2	0	..
— — —	—	Brunswick, Germany	10	94.3	87.1	21.3	..	..	2	1	..
— — —	—	Gageni, Roumania	7	93.0	85.3	21.5	..	..	2	1	..
— — —	—	Bern, Switzerland	10	96.0	93.7	22.2	..	..	3	2	..
— — —	—	Ticino, Switzerland	7	96	97.4	22.5	..	..	3	2	..
— — p. 809	*callipides*	Leon, Spain	10	100.3	92.3	23.0	..	..	2	2	..
— — —	—	Luchon, Haute-Garonne	8	98.7	102.5	22.7	..	..	3	2	..
— — —	—	Ariège, France	10	98.2	100.8	22.7	..	..	3	2	..
— — p. 811	*dichrurus*	Sorrento, Italy	5	100.8	94.6	21.9	..	..	2	1	..
— — —	—	Genoa, Italy	7	102.8	87	22	..	..	2	1	..
— — —	—	Greece	6	100.2	101.0	22.1	..	..	2	1	..
— — —	—	Nîmes, France	10	104.2	97.9	22.9	..	..	3	2	..
— — —	—	Granada, Spain	8	105.8	109.5	24.1	..	..	3	3	..
— — —	—	Alicante, Spain	10	104.4	103.2	23.2	..	..	3	2	..
— — —	*creticus*	Crete	6	84.6	87.8	21.5	..	..	3	2	..

[1] Refering to the diagrams.

particularly, to group 2. Group 1 and group 4 are sparsely represented. In *A. flavicollis* group 3 dominates, seconded by group 4 and even by group 5. Group 2 is represented only by two short series without much importance. Thus the overlapping of the relative tail length of the two species is considerable. *A. mystacinus* is represented by 5's and large 4's and, therefore, overlaps with the most long-tailed forms of *A. flavicollis*. *A. microps* from the Č.S.R. (group 2) does not differ in tail length from *A. sylvaticus*. British *Apodemus,* with the exception of the unquestionable flavicollis from

TABLE 6. *Apodemus flavicollis*. Published measurements of European and Near-Eastern populations.

Reference	Subspecies according to quoted author	Locality	N.	Measurements				No. of tail rings	Length group[1]		
				Head & body	Tail	Hind foot	Skull C.B.		Tail	Hind foot	Skull C.B.
STEIN 1938 p. 507	*flavicollis*	Frankfurt Oder	14	106.0	108.1	..	..	..	3	..	..
ZIMMERMANN 1936 p. 125	—	Usedom, Pommern	24	103.8	102.0	24.6	..	..	3	3	..
— — —	—	Mecklenburg	5	103.4	106.4	24.4	..	201	3	3	..
— — —	—	Bellinchen (Mark)	18	102.3	103.8	24.5	..	203	3	3	..
— — —	—	Buch (Mark)	17	98.1	102.9	23.4	..	210	4	3	..
— — —	—	Reipzig (Mark)	15	100.8	100.8	23.9	..	209	3	3	..
— — —	—	Lüneburg	19	100.0	103.0	..	..	197	3	..	..
— — —	—	Zempelburg, Poland	5	99.0	104.4	..	..	..	4	..	..
— — —	—	Tatra	8	98.3	103.1	24.6	..	193	4	4	..
— — —	—	Jugoslavia	11	102.5	105.2	23.8	..	..	3	3	..
— — —	*brauneri*	Jugoslavia	22	99.0	101.2	23.5	..	..	3	3	..
— — —	*flavicollis*	Bulgaria	35	99.0	99.7	24.5	..	204	3	4	..
VON LEHMANN 1954 p. 24	—	Liechtenstein	3	104	115	24	..	..	4	3	..
HEINRICH 1951 p. 115	—	Holstein	59	100.2	105.2	..	..	..	4	..	..
— — —	—	Bodensee	18	103	111	..	..	..	4	..	..
— — —	—	Allgäu	6	94.1	101.3	..	..	..	4	..	..
— — p. 122	*alpinus*	Steiermark	8	98	115.9	24.4	..	..	5	4	..
— — —	*flavicollis*	Steiermark	4	100	103.2	23.9	..	..	3	3	..
— — p. 115	*alpinus*	Berchtesgaden	38	96.7	112.6	..	..	..	5	..	..
— — —	—	Allgäu	36	95.1	117.5	..	..	..	5	..	..
NEUHÄUSER 1936 p. 226	*saturatus*	NE Asia Minor	3	108	115	24.0	25.2	..	4	2	2
REINWALDT 1927 p. 33		Estonia, total	35	113.3	107.7	24.9	26.4	..	3	3	2
		— h. & b. 100–114	21	107.6	103.2	24.6	25.4	..	3	3	2
		– — 105–119	21	110.8	107.4	24.6	25.7	..	3	3	2
		— — 110–124	20	115.0	109.8	24.9	26.4	..	3	3	2
		— — 115–129	13	121.2	114.3	25.3	27.3	..	3	3	2
		— — 120–134	10	123.7	115.7	25.6	28.0	..	3	3	3
HILZHEIMER 1911 p. 16	*fennicus* + *wintoni*	Finland	6	110.2	104.8	24.3	..	..	3	3	..
HEINRICH 1929 p. 192		Chojnice, Poland	5	99.0	104.4	..	..	..	4	..	..
BARRETT-HAMILTON 1900 p.426	*princeps*	Bustenari, Roumania	16	107.9	108.5	23.9	..	..	3	2	..
KRATOCHVÍL and ROSICKÝ											
— 1953 p. 4		Krkonoše, Č.S.R.	23	103.2	101.8	24.3	..	..	3	3	..
— — —		Střední Čechy, Č.S.R.	9	103.5	105.2	24.8	..	..	3	4	..
— — —		České Středohoří, Č.S.R.	27	108.9	106.1	25.0	..	..	3	3	..
— — —		Jeseníky, Č.S.R.	97	103.7	99.1	24.7	..	..	3	4	..
— — —		Beskydy, Č.S.R.	7	103.0	98.6	23.7	..	..	3	3	..
— — —		Lanžhot, Č.S.R.	15	105.4	103.0	24.4	..	..	3	3	..
— — —		Českomoravská, Č.S.R.	7	98.5	98.0	24.2	..	..	3	3	..
— — —		Rožnavsko, Č.S.R.	86	105.4	104.3	24.3	..	..	3	3	..
— — —		Nízké Tatry, Č.S.R.	11	105.3	107.1	24.3	..	..	3	3	..
— — —		Vysoké Tatry, Č.S.R.	10	106.1	98.2	24.6	..	..	2	3	..

TABLE 6 (continued).

Reference	Subspecies according to quoted author	Locality	N.	Measurements					Length group[1]		
				Head & body	Tail	Hind foot	Skull C.B.	No. of tail rings	Tail	Hind foot	Skull C.B.
KRATOCHVÍL and ROSICKÝ											
— 1953 p. 4		Belanské Tatry, Č.S.R.	7	102.1	100.1	23.7	..	..	3	3	..
— — —		Vihorlat a okolí, Č.S.R.	16	107.4	111.3	24.5	..	..	4	3	..
— 1952 p. 60–61		Č.S.R., total	378	104.6	101.5	24.6	..	..	3	3	..
FELTEN 1952 p. 197		Rhein/Main	58	99.4	107.2	23.8	24.8	201	4	3	3
MILLER 1912 p. 830	*flavicollis*	Haute-Garonne, France	5	110	106.2	24.8	..	..	3	3	..
— — —	—	Haute-Savoie, France.	6	98.8	100.3	25.5	..	..	3	5	..
— — —	—	Harz, Germany	5	106.8	110.6	25.3	..	..	4	4	..
— — —	—	Bustenari, Roumania.	10	109.3	108.3	24.4	..	..	3	3	..
— — —	—	St. Cergues, Vaud, Swz.	6	108.5	102.3	25.9	..	..	3	4	..
— — —	—	Les Plans, Vaud, Swz.	4	102.7	119.7	25.7	..	..	5	5	..
Zool. Mus. Berlin (unpubl.)	subsp. nov.?	Lillehammer, Norway.	10	99.6	98.2	..	..	..	3	..	..

[1] Refering to the diagrams.

TABLE 7. Published measurements of British and Icelandic populations of *Apodemus*.

Reference	Subspecies according to quoted author	Locality	N.	Measurements			Length group[1]	
				Head & body	Tail	Hind foot	Tail	Hind foot
BARRETT-HAMILTON 1900 p. 423	*intermedius*	Great Britain	93	92.4	86.9	22.6	2	2
MILLER 1912 p. 804	*sylvaticus*	Ireland	5	97	83.7	22.3	2	2
— — —	—	Isle of Man	10	95	84	22.2	2	2
— — —	—	Cromarty, Scotland	5	95.6	87.2	22.6	2	2
— — —	—	Oxfordshire, England.	10	96.5	90.1	22.1	2	2
— — —	—	Scilly Islands	6	95.5	88	22.2	2	2
— — p. 824	*hebridensis*	Lewis, Outer Hebr.	4	108	97.5	24.6	2	3
— — p. 825	*hirtensis*	St. Kilda	3	99.3	92.3	24.1	2	3
— — p. 826	*fridariensis*	Fair Isle	10	108.5	102.4	(24-26.2)	3	3
— — p. 831	*wintoni*	Herefordshire,Engl.	6	108.6	107.5	24.1	3	3
BARRETT-HAMILTON and HINTON 1911 p. 517	*sylvaticus*	East Aberdeenshire, Sc.	6	94	92.2	21.6	3	1
— — p. 516	—	Surrey, England	40	87.6	86.2	21.9	3	2
— — —	*butei*	Bute, Inner Hebr.	17	88.1	78.4	22.0	2	2
— — p. 537	*hamiltoni*	Rum, Hebr.	5	103.8	95.6	24.2	2	3
— — —	*cumbrae*	Gr. Cumbrae, Inner Hebr.	6	93	90.3	22.8	3	3
— — —	—	Tiree, Hebr.	4	102.5	84.2	23.1	1	2
— — —	*maclean*	Mull, Inner Hebr.	5	97	87.4	23.2	2	3

[1] Refering to the diagrams.

TABLE 7 (continued).

Reference	Subspecies according to quoted author	Locality	N.	Measurements			Length group[1]	
				Head & body	Tail	Hind foot	Tail	Hind foot
BARRETT-HAMILTONandHINTON								
— 1911 p. 537	*maclean*	Jura, Hebr.	3	97.6	78.5	22.6	1	2
— — —	—	Islay, Hebr.	9	93.3	81.6	22.5	2	2
— — —	*fiolagan*	Arran, Inner Hebr.	9	98.3	84.5	23.5	2	3
— — —	*hebridensis*	Lewis, Outer Hebr.	7	90.4	85.8	23	2	3
— — p. 536	—	— — —	14	95.8	87.8	23.2	2	3
— — p. 541	*hirtensis*	St. Kilda	42	111	100	25.0	2	3
— — p. 544	*fridariensis*	Fair Isle	6	109.5	103.2	24.1	3	2
— — —	*granti*	Yell, Shetland	9	101.5	91.8	24.0	2	3
— — p. 550	*wintoni*	England	32	103.9	109.5	23.8	4	3
MONTAGU 1922 p. 935	*ghia*	Gigha, Hebr.	3	95.8	..	23.4	..	3
— — p. 936	*tural*	Islay, Hebr.	13	93.6	84.6	23.1	2	3
— — —	*larus*	Jura, Hebr.	4	90.8	89.9	22.8	3	3
PEARSON 1944 p. 139	*sylvaticus*	England	162	88.6	90.3	22.9	3	3
DEGERBØL 1939, p. 42	*grandiculus*	Iceland	31	99.6	90.0	23.3	2	2

[1] Refering to the diagrams.

TABLE 8. *Apodemus mystacinus*. Published measurements of European and Near-Eastern populations.

Reference	Subspecies	Locality	N.	Measurements				Length group[1]		
				Head & body	Tail	Hind foot	Skull C B.	Tail	Hind foot	Skull C.B.
ZIMMERMANN 1953 p. 33	*epimelas*	Balkan	23	115	127	26.7	28.72	5	5	5
— — —	*mystacinus*	Asia Minor, Syria, Palestine	12	119	128	24.9	27.57	4	3	3
— — —	*smyrnensis*	Western Asia Minor	3	110	126	25	27.9	5	3	4
— — —	*euxinus*	Northern Asia Minor	6	117	129	25.2	27.42	5	3	3
— — —	*rhodius*	Rhodos	9	113	128	25.8	27.85	5	4	4
— — —	—	Crete	24	109	120	24.7	27.56	4	3	4
AHARONI 1932 p. 232	*pohlei* (as *A. flav.*)	Syria	9	106.2	122.8	24.4	27.8	5	3	5

[1] Refering to the diagrams.

England (*A. f. wintoni* (BARRETT-HAMILTON)) are within and cover the range of continental *A. sylvaticus*. The British insular forms which by ELLERMAN (1951, see below) have been referred to *A. flavicollis* have not particularly long tails.

The geographical variation of the tail length in *A. sylvaticus* and *A. flavicollis* is shown in the maps, Fig. 5. In *A. sylvaticus* group 1 in western Europe is restricted to

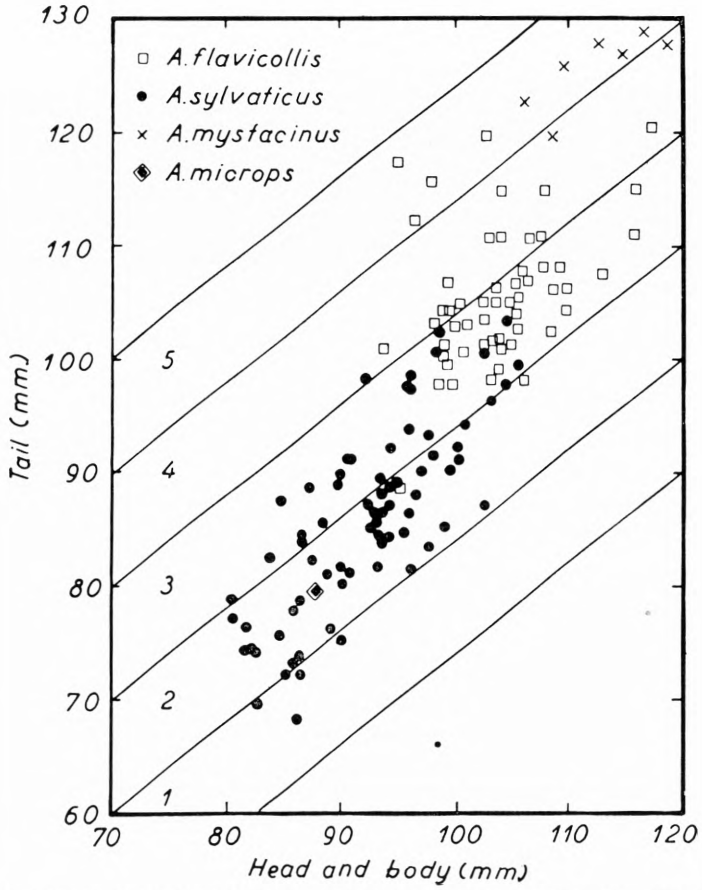

Fig. 3. European (excluding British) and Near-Eastern populations. Cf. text p. 8.

the north-eastern range of the species (Latvia and Danish islands). The occurrence of group 1 populations on two Scottish islands is probably not reliable because the available series contain only 3 and 4 specimens, respectively. Jylland and northern Germany are dominated by group 2 while in southern Germany and in the Mediterranean region groups 2 and 3 seem to be of approximately equal abundance. Groups 2 and 3 also dominate in the British Isles. The series from Langeoog (Friesian Islands), belonging to group 4, is unique among European *A. sylvaticus*.

A. flavicollis does not show the same regular geographical variation as *A. syl-*

vaticus. In *A. flavicollis* groups 3 and 4 seem to be equally represented in northern and southern Europe. In the Alpine region, however, populations occur with an extraordinarily long tail (group 5). They have been described as *A. f. alpinus* HEINRICH 1951. They are known only from HEINRICH's localities in southern Germany and perhaps from Vaud in Switzerland (MILLER 1912). Von LEHMANN's few specimens from Liechtenstein (large 4's) may be *alpinus*, too. *A. f. pohlei* AHARONI from Syria is very long-tailed, but it is probably an *A. mystacinus*. ELLERMAN's objection (1951 p. 568) that as regards dental characters it is a true *A. flavicollis*, does not seem valid

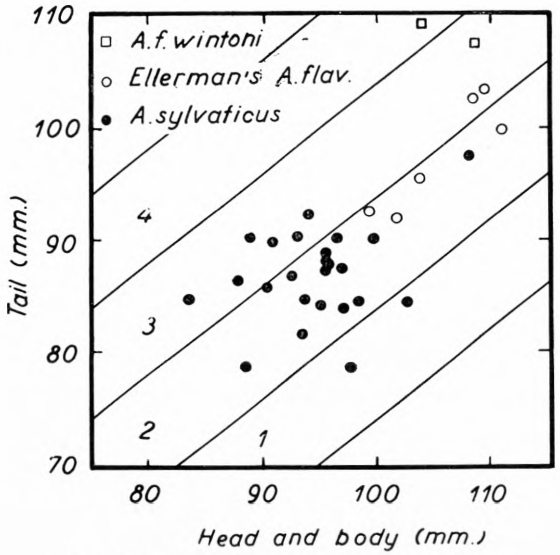

Fig. 4. British populations. Cf. text p. 10.

because ZIMMERMANN (1953) has shown a considerable overlapping of the dental characters of *A. flavicollis* and *A. mystacinus*.

Tail rings were not counted during the present investigation but information is available in the literature (Tables 5 and 6, Fig. 6). In *A. sylvaticus* the same geographical variation occurs in the number of rings as in the tail length. Accordingly, the number of rings does not seem to vary geographically in a regular way in *A. flavicollis* in which the tail length also does not vary. Tail ring counts of *A. f. alpinus* are not available.

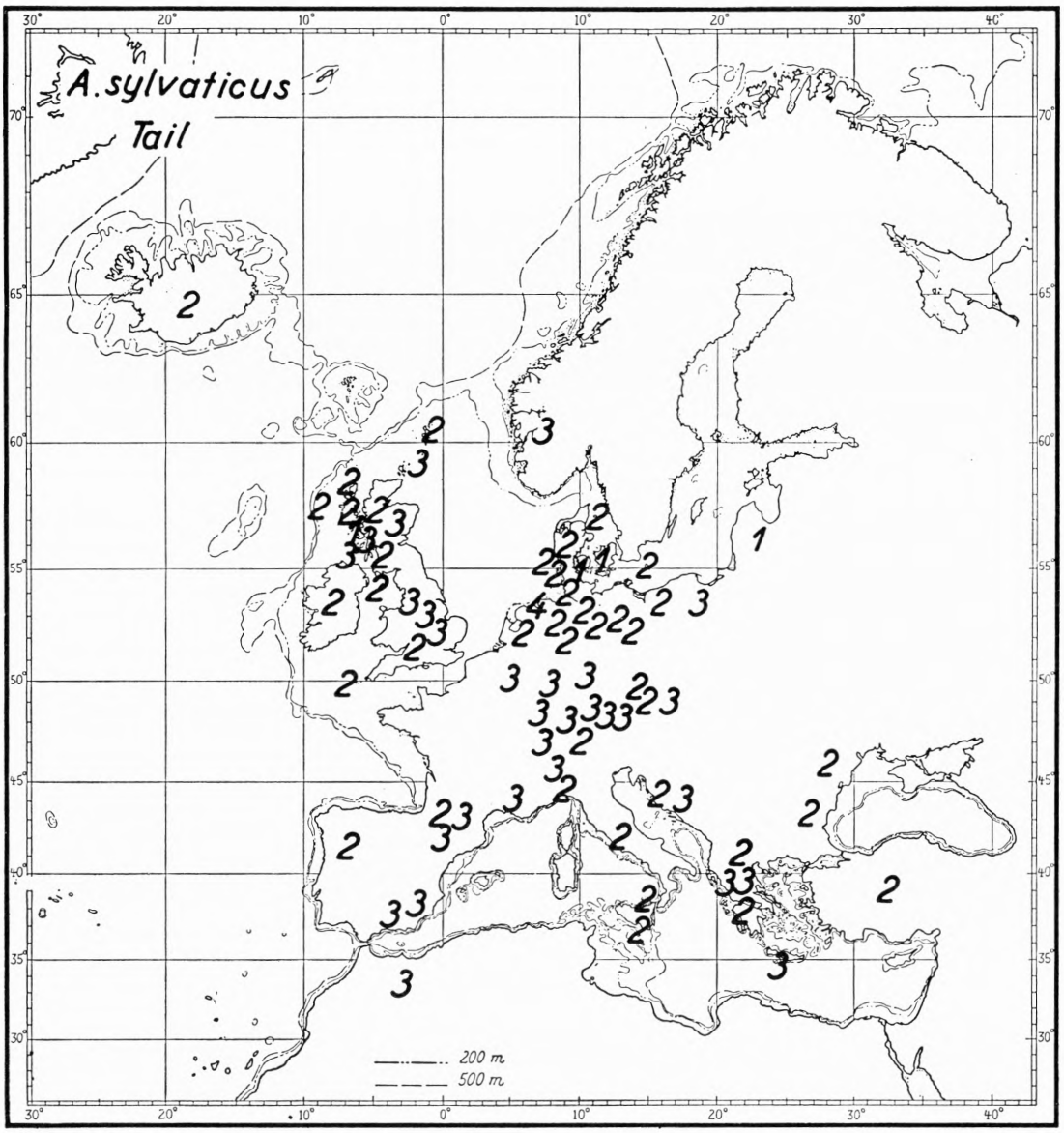

Fig. 5. Relative length of tail. The figures refer to the grouping adopted in Figs. 3 and 4. "1" indicates the shortest tails, "5" the longest.

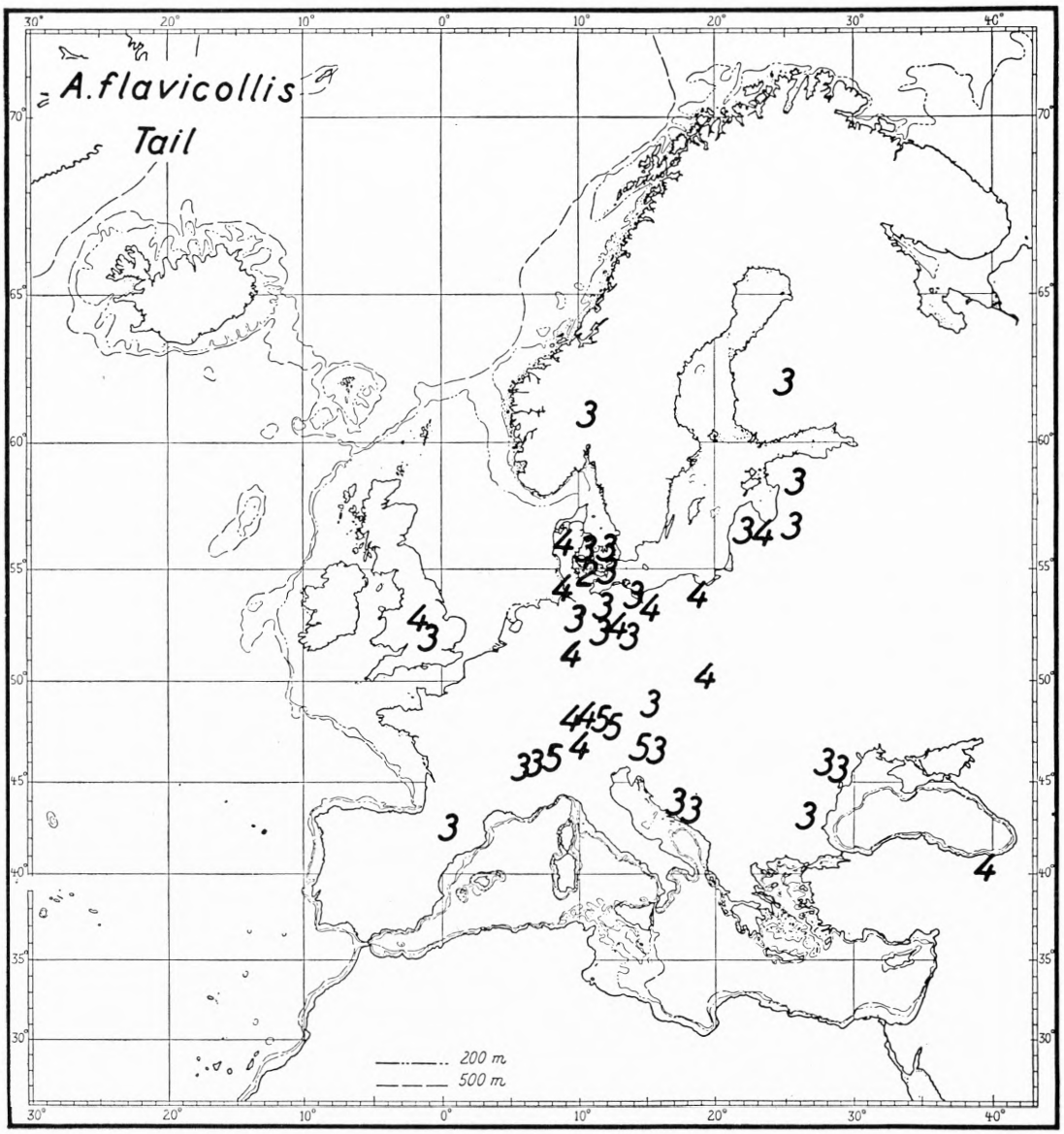

Fig. 5.

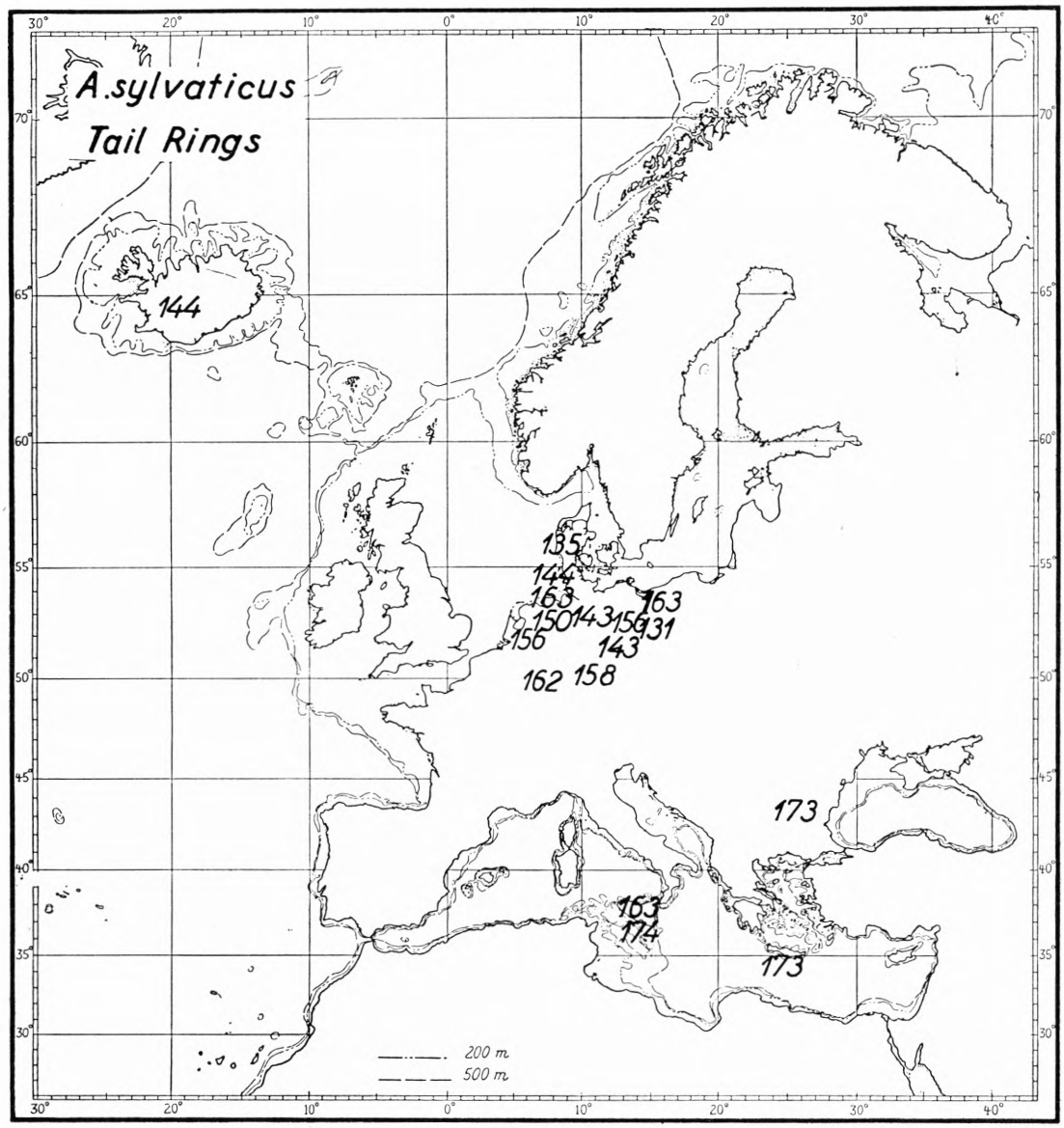

Fig. 6. Cf. text p. 15.

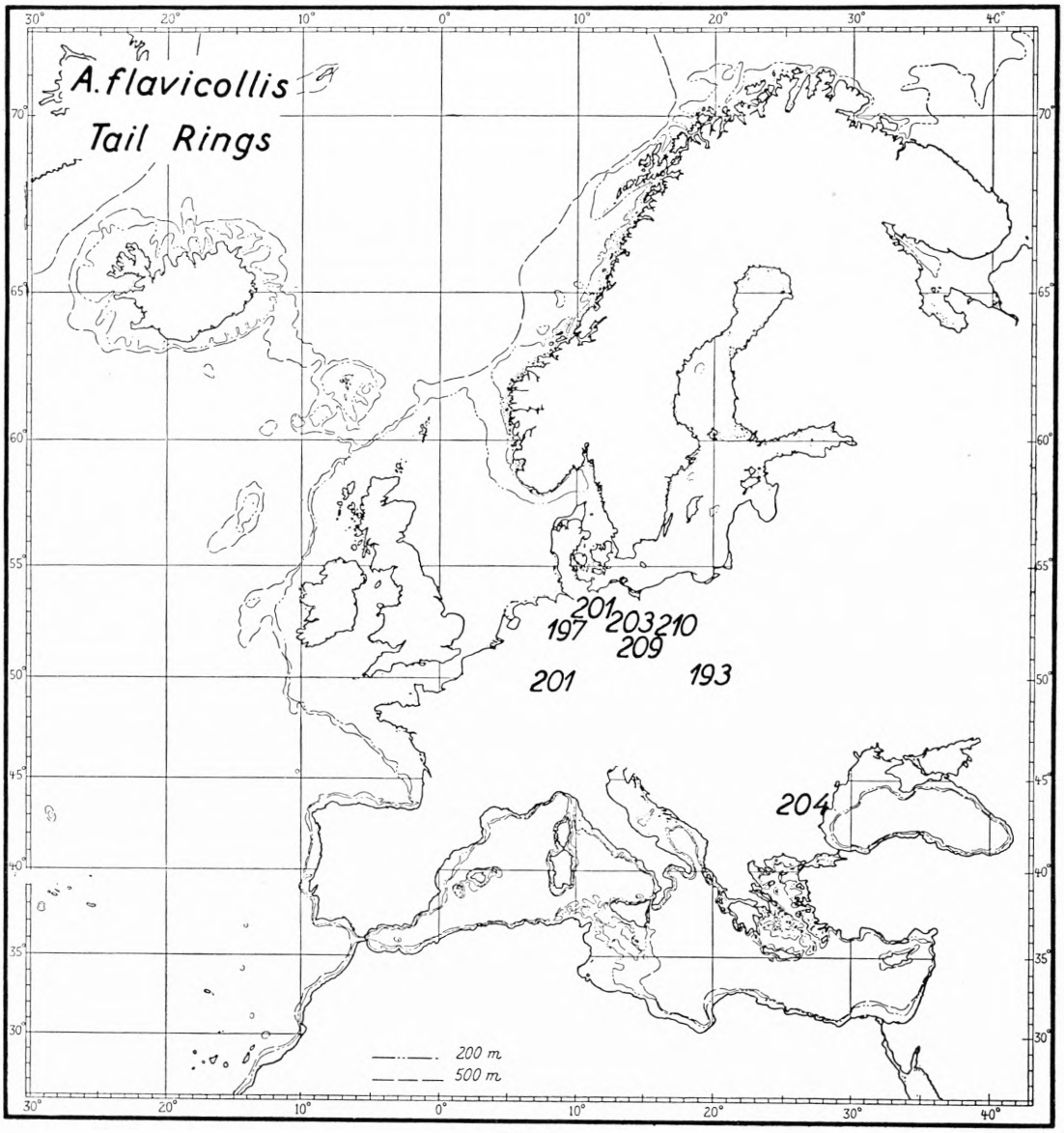
A. flavicollis
Tail Rings
201
197
203
210
209
201
193
204
200 m
500 m

Fig. 6.

The Hind Foot.

The length of the hind foot of *A. sylvaticus* and *A. flavicollis* in Denmark and Latvia is shown in Tables 1—2 and, divided into groups according to body size, in

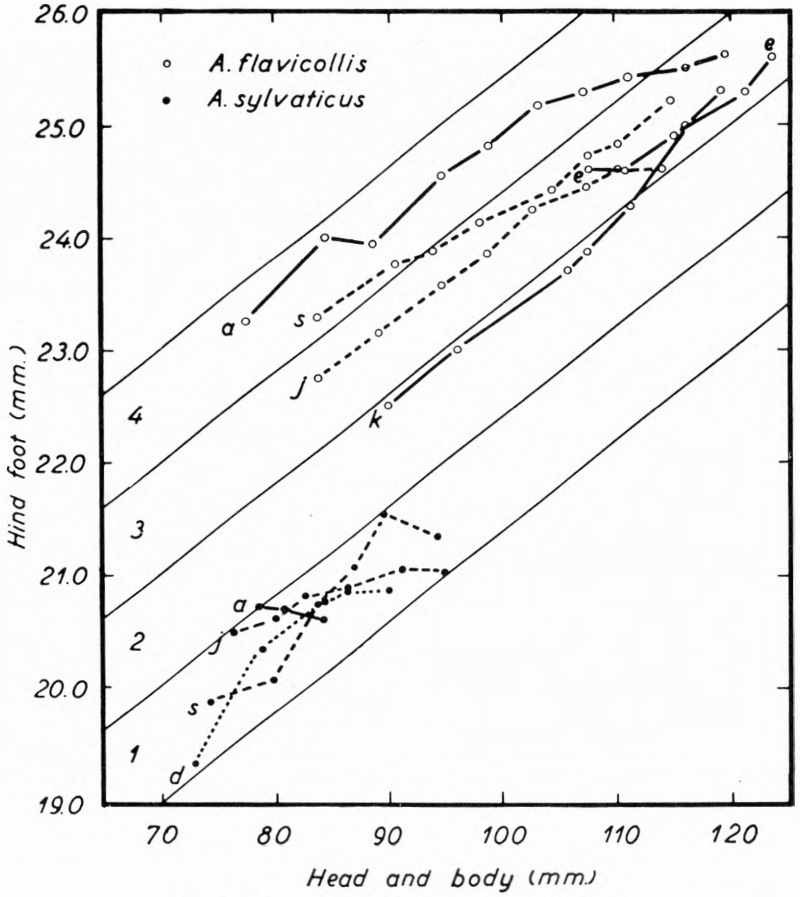

Fig. 7. Lettering as in Fig. 2. Cf. text p. 20.

Tables 9—10. The contents of the latter tables are shown diagrammatically in Fig. 7. A straight-line relationship between the body length and the length of the hind foot seems to be approximated. The oblique straight lines in Fig. 7 show the relationship and indicate a convenient grouping of the material. In both species the hind foot seems to be proportionately longer in small examples than in large ones. It is relatively shorter in *A. sylvaticus* than in *A. flavicollis*. The material of *A. sylvaticus* is not sufficient to demonstrate differences, if such occur, between Danish and Latvian series

TABLE 9. *Apodemus sylvaticus*. Length of hind foot in relation to length of head & body.

Head & body (Intervals)	Latvia			Denmark								
	Antini			Jylland			Sjælland			Skarø & Drejø		
	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.
65—79	..	..	..	24	76	20.50 ± 0.19	8	74	19.88 ± 0.50	7	73	19.36 ± 0.46
70—84	9	79	20.72 ± 0.11	58	80	20.62 ± 0.10	14	80	20.07 ± 0.31	14	79	20.36 ± 0.25
75—89	10	81	20.70 ± 0.10	81	83	20.80 ± 0.08	24	84	20.75 ± 0.26	18	84	20.78 ± 0.18
80—94	8	84	20.62 ± 0.19	77	86	20.89 ± 0.09	24	87	21.08 ± 0.19	19	86	20.87 ± 0.14
85—99	..	..	..	51	91	21.07 ± 0.12	17	90	21.56 ± 0.16	13	90	20.88 ± 0.18
90—104	..	..	..	28	95	21.04 ± 0.16	7	95	21.36 ± 0.26	..	..	..

TABLE 10. *Apodemus flavicollis*. Length of hind foot in relation to length of head & body.

Head & body (Intervals)	Latvia						Denmark					
	Antini			Koknese			Jylland			Sjælland		
	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.
70—84	11	78	23.27 ± 0.31	..	..	..	..	..	..	..	..	..
75—89	11	84	24.00 ± 0.23	..	..	..	4	84	22.75 ± 0.63	5	84	23.30 ± 0.49
80—94	19	89	23.95 ± 0.21	..	..	..	6	89	23.17 ± 0.36	11	91	23.77 ± 0.24
85—99	36	95	24.56 ± 0.17	6	90	22.50 ± 0.57	12	95	23.58 ± 0.31	18	94	23.89 ± 0.23
90—104	55	99	24.82 ± 0.14	5	97	23.00 ± 0.63	19	99	23.87 ± 0.24	28	98	24.14 ± 0.21
95—109	79	103	25.18 ± 0.10	7	106	23.71 ± 0.57	25	103	24.26 ± 0.21	47	104	24.44 ± 0.18
100—114	77	107	25.29 ± 0.11	9	108	23.89 ± 0.46	26	108	24.46 ± 0.18	53	108	24.73 ± 0.17
105—119	67	111	25.42 ± 0.12	9	111	24.33 ± 0.44	18	110	24.61 ± 0.19	47	110	24.84 ± 0.17
110—124	41	116	25.51 ± 0.18	5	116	25.00 ± 0.45	10	114	24.60 ± 0.28	22	115	25.23 ± 0.18
115—129	22	120	25.64 ± 0.24	3	119	25.33 ± 0.68	..	..	..	..	..	..

or between Danish series mutually. The hind foot length of *A. flavicollis* is liable to considerable variation. It is shortest in Koknese and longest in Antini. The Danish series (Jylland and Sjælland) are intermediate between the Latvian ones. The graph for Sjælland runs throughout above that for Jylland although the difference between these localities is not statistically significant. It seems, however, as if the *A. flavicollis* of Sjælland is characterized by a slightly shorter tail (see above) and longer hind foot than is found in that occurring in Jylland. The hind foot length in Antini is for most groups of body size significantly different from that found in the other three localities. The Koknese values are significantly different from those for Sjælland, but not for the Jylland values with which they slightly overlap in the larger specimens.

The diagrams, Figs. 8—9, show the body/hind foot relationship in non-British and British *Apodemus* populations. The diagrams are based on Tables 1—2 and 5—8.

Outside the British Isles the relative length of the hind foot of *A. sylvaticus* is fairly distinct from that of the other species considered. *A. sylvaticus* is largely confined to groups 1 and 2 (cf. the figures). *A. microps* (known from Slovakia only) has an

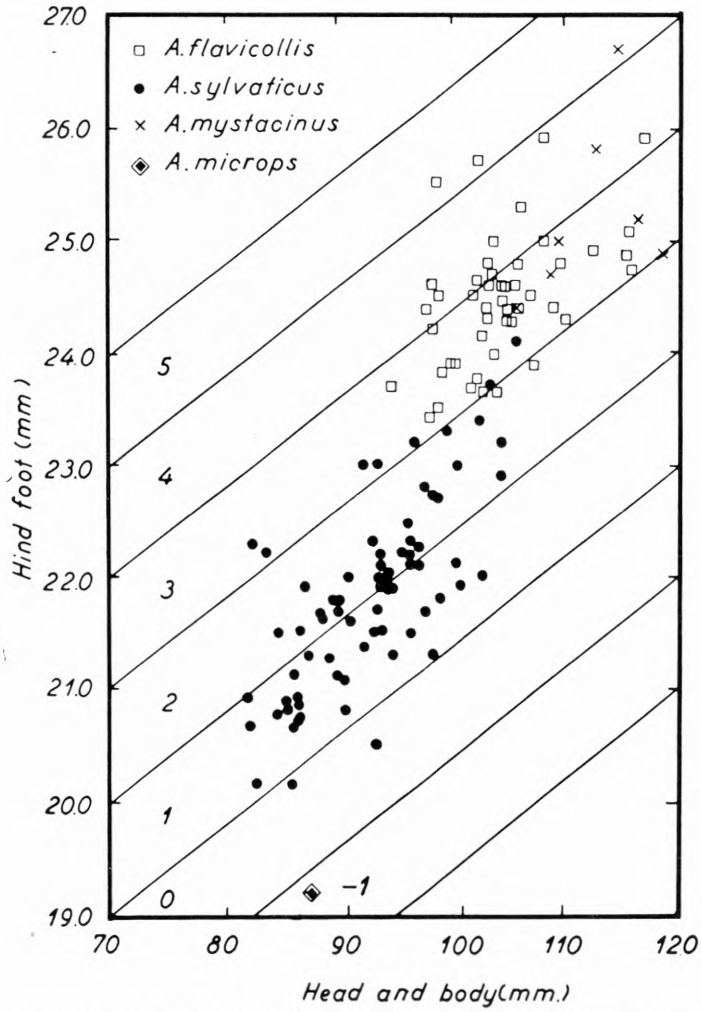

Fig. 8. European (excluding British) and Near-Eastern populations. Cf. text p. 22.

extremely short hind foot (group — 1). *A. flavicollis* and *A. mystacinus* are represented in group 3 and sparsely in groups 4 and 5. The three series of *A. flavicollis* with the longest hind foot were collected in the Swiss-French frontier region. One of these series is further characterized by a very long tail (*A. f. alpinus*?). The various subspecies of *A. mystacinus* are separated primarily by pelage characters (cf. ZIMMERMANN 1953, p. 32). It seems, however, that the proportionately long hind foot is a

useful additional distinguishing character for the continental European form, *A. m. epimelas* NEHRING. The English *A. f. wintoni*, without doubt a *flavicollis*, has a comparatively short hind foot (group 3, only slightly above group 2) while many other British *Apodemus* populations have longer feet (cf. Fig. 9). ELLERMAN (1951) referred several specialized British insular forms to *A. flavicollis* owing to their large skull while previous authors have referred all British *Apodemus* except *A. f. wintoni* to *A. sylvaticus* or erected new species for them. ELLERMAN's British *A. flavicollis* except *A. f. wintoni* have been given a separate signature in the diagrams. They are generally

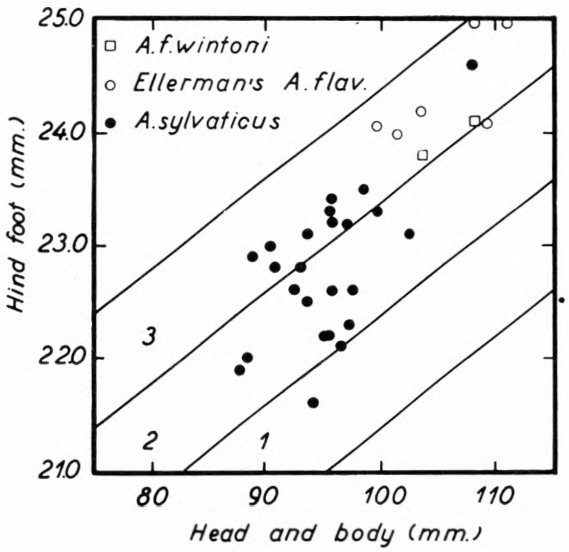

Fig. 9. British populations. Cf. text p. 23.

characterized by an extraordinarily long hind foot. This supports ELLERMAN's opinion that they ought to be referred to *A. flavicollis*. However, throughout the British Isles, there is a tendency in *A. sylvaticus* towards prolongation of the hind foot as compared with conditions in other northern European populations. On small British islands there is also a tendency towards large size (BARRETT-HAMILTON and HINTON 1911). The populations which ELLERMAN referred to *A. flavicollis* perhaps represent the extreme development of this evolutionary line. The isolated populations may also be regarded as belonging to a "fringing form" (RICHARDS 1935). RICHARDS called attention to the interesting phenomenon that within several species of animals the isolated populations on small islands off the British coast have peculiarities in common although they are exposed to quite different climatic conditions on the northern islands compared with those on the southern ones. Like BARRETT-HAMILTON and HINTON (1911—21 p. 436) he considered them survivors of a fauna element which previously inhabited the British mainland. The problem is complicated, and probably cannot be solved at present. There is, however, not much doubt that the British *Apodemus* populations

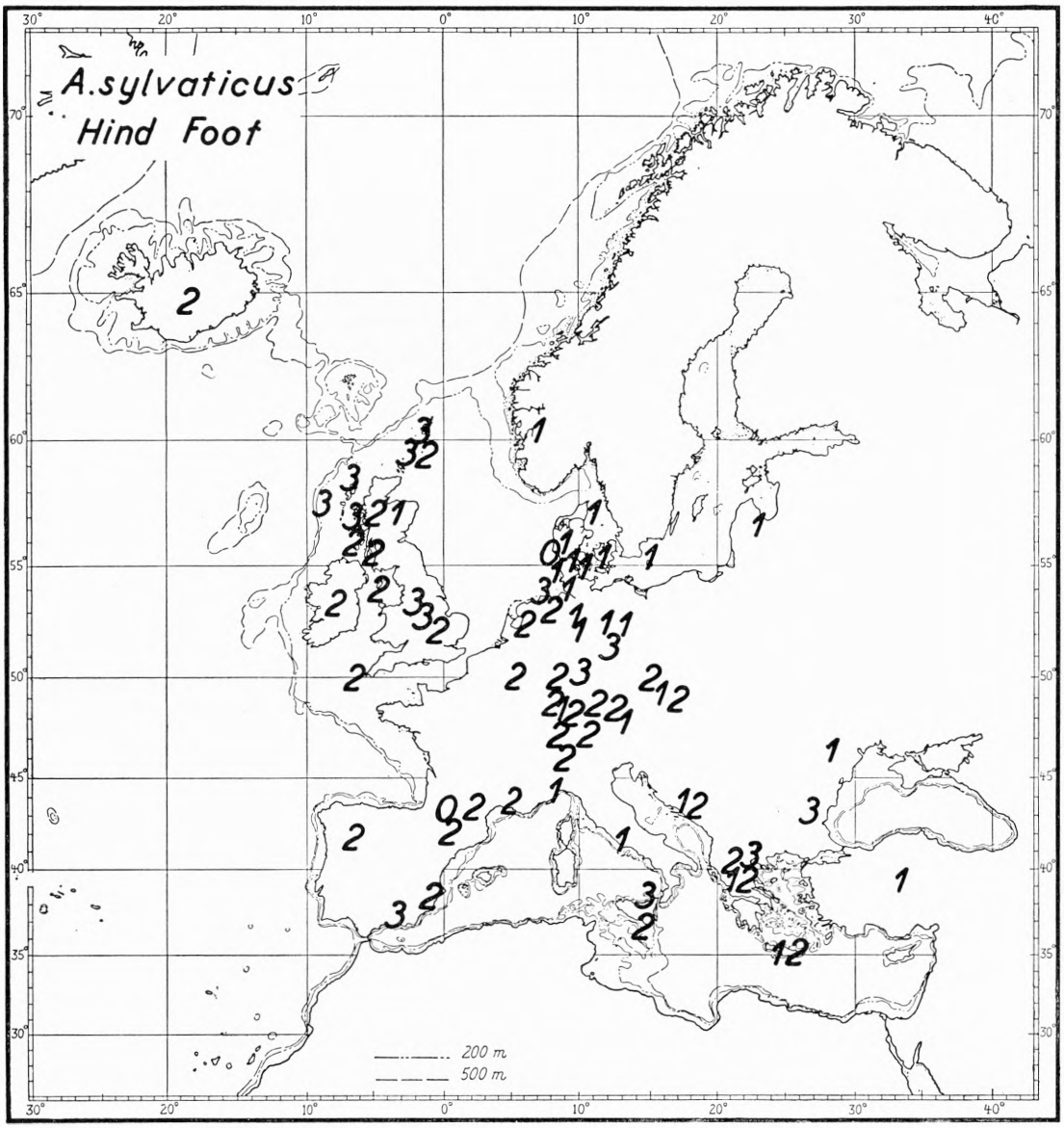

Fig. 10. Relative length of hind foot. "0" indicates the shortest hind feet, "5" the longest. Based on the diagrams, Figs. 8 and 9.

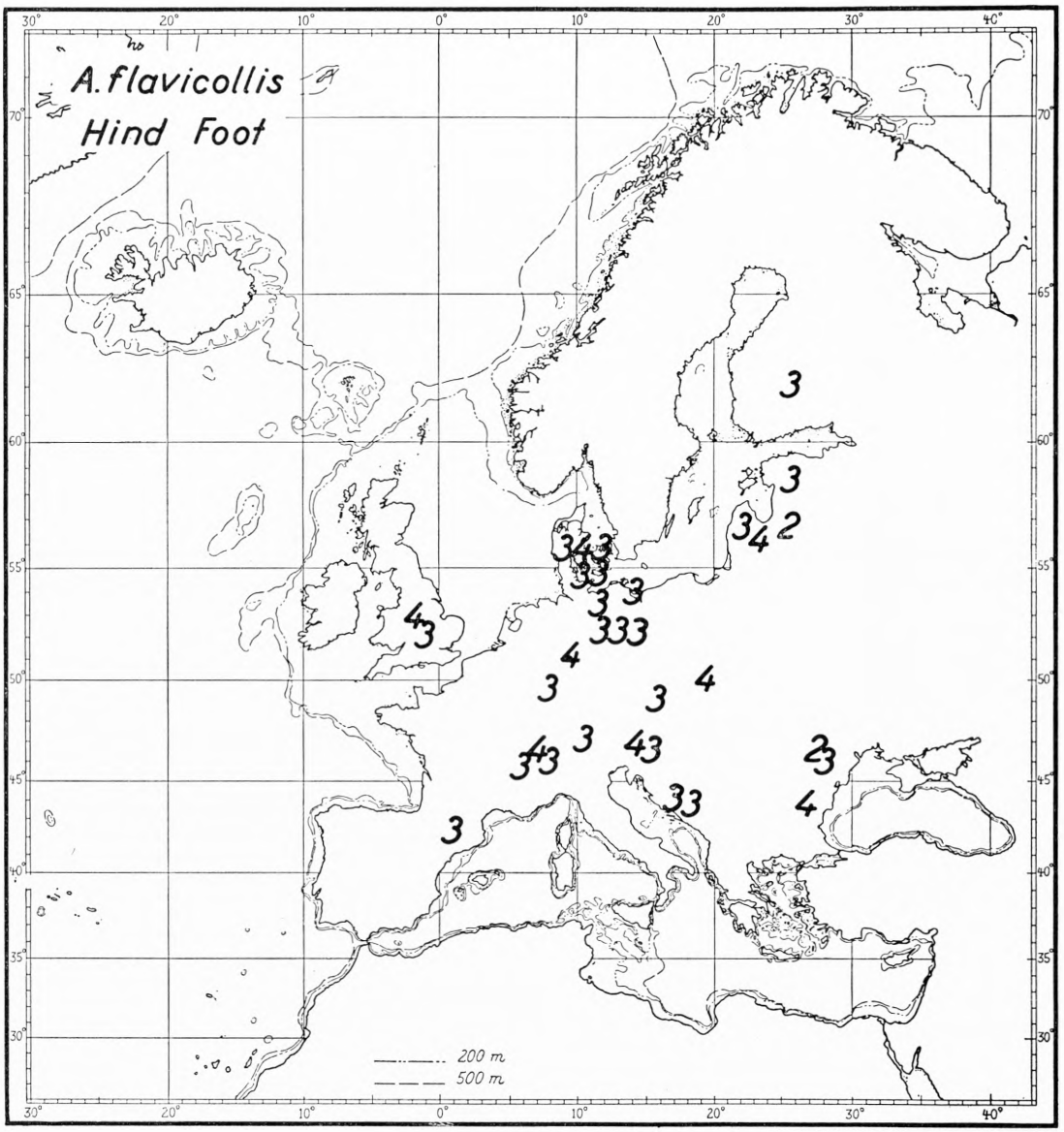

Fig. 10.

are of high age because they are so divergent from each other that a recognizable form seems to exist on almost every island where the genus is represented. Provisionally, it seems most adequate to consider all British *Apodemus* except *A. f. wintoni* as representatives of *A. sylvaticus*.

The geographical variation of the hind foot length of *A. sylvaticus* and *A. flavicollis* is shown in Fig. 10. In the former the hind foot is shortest in Denmark, northern Germany, and Latvia where group 1 predominates. In central Europe group-2-series are in majority. In southern Europe and in Great Britain even group 3 is represented. The pattern of variation is approximately the same as for the tail length (Fig. 5). However, the occurrence of short-tailed and short-footed populations in southern Europe (e. g. Gers, France: tail, group 2; hind foot, group 0, if the measurements are reliable) perhaps indicates the existence of a more complicated pattern of variation than described here.

A regular geographical variation of the hind foot length does not seem to occur in European *A. flavicollis* although individual populations differ considerably from each other. Populations with an extremely long hind foot and others with an extremely short one may occur close to each other, for instance in Latvia (see above).

The Condylobasal Length.

The condylobasal length of the skull in *A. sylvaticus* and *A. flavicollis* from Denmark and Latvia is shown in Tables 1—2 and, in relation to body size, in Tables 11—12 and Fig. 11. As in previous diagrams the relation between the measurements seems to approach a straight line. The condylobasal length is usually proportionately greater in *A. flavicollis* than in *A. sylvaticus*. The Koknese *flavicollis* is, however, within the range of *A. sylvaticus*. The difference in condylobasal length between the Koknese

TABLE 11. *Apodemus sylvaticus*. Condylobasal length in relation to length of head & body.

Head & body (Intervals)	Latvia			Denmark								
	Antini			Jylland			Islands except Skarø & Drejø			Skarø & Drejø		
	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.
70— 84	6	79	21.17 ± 0.34	..	..	..	..	..	..	..	..	..
75— 89	7	82	21.50 ± 0.31	22	83	21.91 ± 0.20	12	85	21.83 ± 0.36	..	..	..
80— 94	7	84	21.64 ± 0.26	21	85	22.12 ± 0.18	18	88	22.28 ± 0.21	8	88	21.88 ± 0.19
85— 99	..	..	..	11	91	22.59 ± 0.16	19	92	22.55 ± 0.20	9	90	22.06 ± 0.18
90—104	..	..	..	7	98	22.93 ± 0.21	15	96	22.97 ± 0.20	..	..	..
95—109	..	..	..	..	..	..	9	100	23.39 ± 0.31	..	..	..

TABLE 12. *Apodemus flavicollis*. Condylobasal length in relation to length of head & body.

Head & body (Intervals)	Latvia						Denmark								
	Antini			Koknese			Jylland			Sjælland			Lolland		
	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.	N.	Head & body	M. ± S.D.
70– 84	4	75	20.98 ± 0.81	..	..	..	..	..	..	..	..	..	..	..	..
75– 89	4	86	23.18 ± 0.63	..	..	..	..	..	..	..	..	..	..	..	..
80– 94	6	88	23.17 ± 0.47	..	..	..	..	..	..	..	..	..	..	..	..
85– 99	11	94	24.04 ± 0.36	..	..	..	5	94	24.66 ± 0.43	..	..	..	..	..	..
90–104	19	100	24.55 ± 0.18	..	..	..	9	100	25.51 ± 0.33	..	..	..	10	96	24.35 ± 0.23
95–109	38	104	25.35 ± 0.13	..	..	..	11	102	25.57 ± 0.27	12	104	25.32 ± 0.21	6	102	25.35 ± 0.51
100–114	44	108	25.76 ± 0.14	..	..	..	11	106	25.88 ± 0.18	13	108	25.78 ± 0.20	5	106	26.06 ± 0.49
105–119	43	111	26.35 ± 0.11	8	111	25.19 ± 0.28	7	109	25.83 ± 0.22	15	112	26.12 ± 0.22	6	113	26.87 ± 0.26
110–124	27	116	26.97 ± 0.13	6	116	25.68 ± 0.55	5	116	26.50 ± 0.45	..	..	..	6	118	27.25 ± 0.29
115–129	16	120	27.36 ± 0.16	..	..	..	2	120	27.20	..	..	..	..	..	..

series and other series of *A. flavicollis* is statistically significant except for the comparison Koknese-Jylland.

The diagram, Fig. 12, shows the ratio between the condylobasal length and the length of head and body in European and Near-Eastern populations of *A. sylvaticus*, *A. flavicollis*, and *A. mystacinus*, compiled from Tables 1, 2, 5, 6, and 8. Material from the British Isles is not available. The skull of *A. mystacinus* is very large (groups 3—5) as compared with other forms. *A. flavicollis* is usually found in group 3 but also occurs scattered in group 2. *A. sylvaticus* has usually a proportionately short skull (groups 1 and 2), but a few series have skulls of medium or large size. Two short series of *A. s. dichrurus* from Greece are referred to group 3, but perhaps it is not advisable to lay stress on such scattered observations. Of considerable interest is HAGEN's (1954) observation to the effect that two distinct forms of *A. sylvaticus* occur in Sicily. The form observed in southern Sicily is an ordinary *A. sylvaticus* which according to its colour may be referred without difficulty to *A. s. dichrurus* Raf. It has a group 2 skull and is further characterized by the total absence of collar and pectoral spot. The form collected in north-eastern Sicily is vividly coloured with brown back and almost white under-parts. Is has a distinct pectoral spot. The skull is extremely large, as in *A. mystacinus*, and seems to have a somewhat angular appearance like that of *A. flavicollis*. The pelage characters resemble those of *A. f. princeps* (BARR.-HAM.). The length of the hind foot is within the range of overlapping of *A. sylvaticus* and *A. flavicollis*, while the tail length and the number of tail rings is as in *A. sylvaticus*. The present author suspects that the *Apodemus* of north-eastern Sicily is, in fact, an aberrant form of *A. flavicollis* which species is otherwise not known from Sicily. However, to avoid confusion it is probably advisable to retain the dubious Sicilian form as an *A. sylvaticus* until more material becomes available.

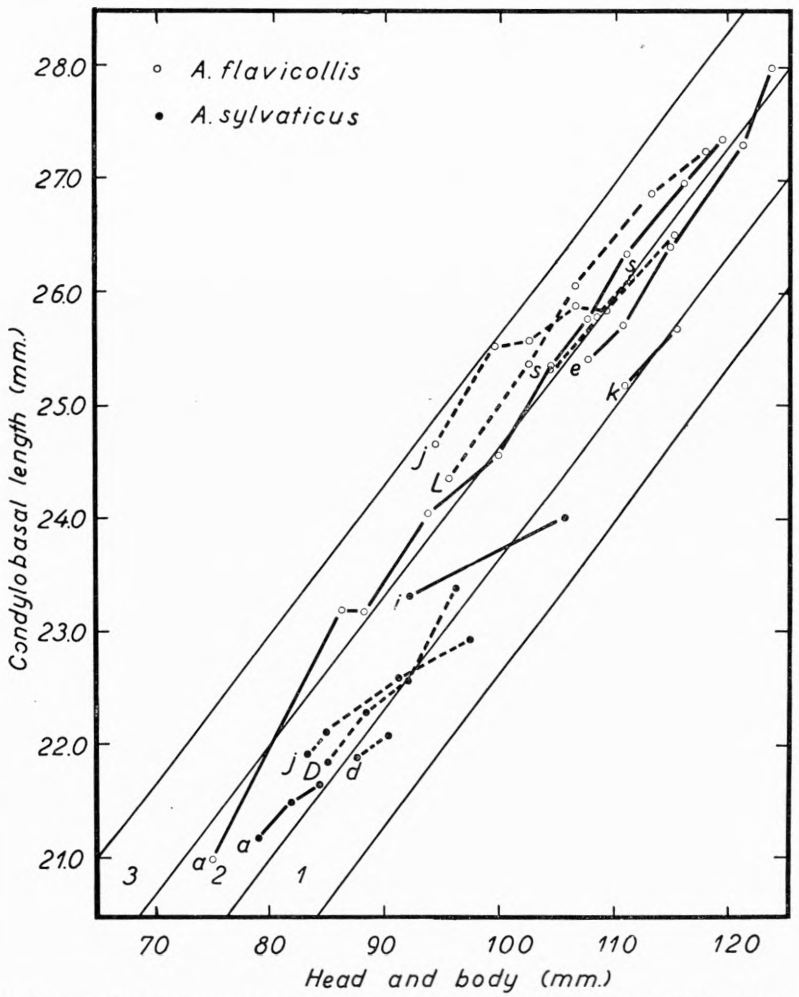

Fig. 11. Lettering as in Fig. 2 except L: Lolland, and D: Danish islands excluding Skarø and Drejø.

The Teeth.

The mean alveolar length of the maxillary tooth row in *A. sylvaticus* and *A. flavicollis* from Denmark and Latvia is shown in Tables 1—2. Specimens with worn teeth seem to have a slightly longer tooth row than younger ones. The difference has been proved statistically for the Antini *flavicollis* (Table 2) in which it was found to be significant at the 1 $^{0}/_{00}$ level. The dimensions of individual teeth probably do not change with age. However, as the teeth become worn they may change their position a little and it seems as if the roots become more protruding. The difference between

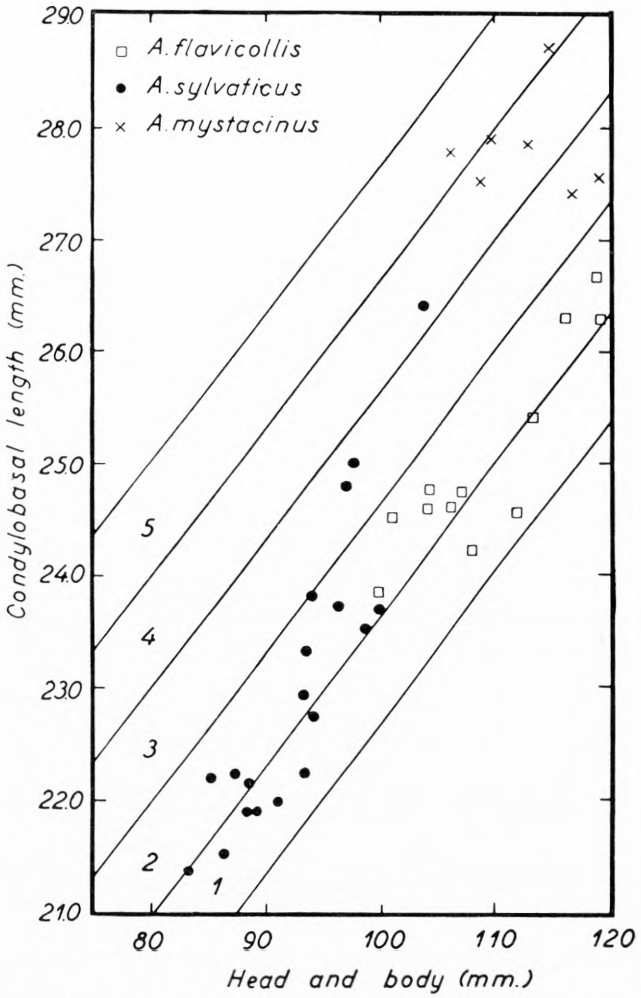

Fig. 12. European and Near-Eastern populations. Cf. text p. 27.

young and old animals is, however, not very great. In most series the increase in tooth row length amounts to about 0.1 mm.

A. sylvaticus. Two groups of localities may be distinguished in Denmark and Latvia (Table 1). One has a mean length of the tooth row of 3.50—3.56 mm. It contains the single Latvian locality from which material is available (Antini) and two small Danish islands, Skarø and Drejø, situated near eachother south of the island of Fyn. They cover 1.9 and 4.1 sq. km., respectively. Another group contains all Danish localities except Skarø and Drejø; the mean length of the tooth row ranges from 3.81—3.90 mm. The difference between the two groups of localities is highly significant for most of the possible comparisons between individual series. Differences

TABLE 13. *Apodemus sylvaticus.* Micrometer readings of the length (M. ± S. D.) of individual molars and of the tooth rows. Crown measurements. Unit: 0.0374 mm.

Locality	N.	Maxillary tooth row				Mandibular tooth row			
		m^1	m^2	m^3	m^{1-3}	m_1	m_2	m_3	m_{1-3}
Lyø.....	6	48.00 ± 1.21	31.83 ± 0.60	22.00 ± 0.52	98.50 ± 1.12	45.00 ± 1.26	31.67 ± 0.43	25.33 ± 0.34	101.17 ± 1.54
Bjørnø ..	5	49.00 ± 0.49	32.60 ± 0.26	22.20 ± 0.49	100.80 ± 0.49	47.00 ± 0.45	32.00 ± 0.45	25.60 ± 0.41	102.00 ± 0.55
Sjælland.	11	48.91 ± 0.53	30.73 ± 0.36	22.36 ± 0.45	100.82 ± 0.74	46.18 ± 0.63	31.00 ± 0.19	24.91 ± 0.28	100.27 ± 0.71
Jylland..	11	47.91 ± 0.86	31.00 ± 0.49	22.82 ± 0.54	99.82 ± 1.68	46.45 ± 0.58	31.18 ± 0.69	24.27 ± 0.52	99.82 ± 1.33
These combined	33	48.55 ± 0.42	31.30 ± 0.25	22.52 ± 0.25	100.12 ± 0.64	46.15 ± 0.28	31.24 ± 0.27	24.88 ± 0.23	100.55 ± 0.57
Skarø ...	10	46.00 ± 0.70	29.60 ± 0.62	20.60 ± 0.31	94.70 ± 1.14	43.00 ± 0.56	29.60 ± 0.62	23.50 ± 0.27	94.81 ± 1.36
Drejø ...	11	46.64 ± 0.58	29.73 ± 0.45	19.09 ± 0.56	93.73 ± 1.00	45.09 ± 0.44	29.64 ± 0.28	22.18 ± 0.44	96.00 ± 0.60
Antini (Latvia)	11	44.36 ± 0.53	30.45 ± 0.37	21.64 ± 0.43	93.64 ± 0.82	42.27 ± 0.49	29.27 ± 0.38	24.18 ± 0.38	94.82 ± 0.88

TABLE 14. *Apodemus sylvaticus.* Relative size of individual molars and of the tooth rows (micrometer readings). Cf. Table 13.

	Maxillary tooth row				Mandibular tooth row			
	m^1	m^2	m^3	m^{1-3}	m_1	m_2	m_3	m_{1-3}
Normal Danish populations.....	100	100	100	100	100	100	100	100
Skarø.....	95	95	92	95	93	95	94	94
Drejø.....	96	94	85	94	98	95	89	95
Antini.....	91	97	96	94	92	94	97	94

TABLE 15. *Apodemus sylvaticus.* P-values for comparison of the length of teeth in various localities. As "normal" Danish populations are considered the specimens from Lyø, Bjørnø, Sjælland, and Jylland. Cf. Tables 13 and 14 and text p. 31.

Teeth	19–20 degrees of freedom			41–42 degrees of freedom		
	Comp. with Skarø	Comp. with Antini		Comp. with normal Danish populations		
	Drejø	Skarø	Drejø	Antini	Skarø	Drejø
m^1.....	> 0.1	0.1	0.01	0.001	0.01	0.05
m^2.....	> 0.1	> 0.1	> 0.1	0.1	0.01	0.01
m^3.....	0.05	0.1	0.01	0.1	0.001	0.001
m^{1-3}.....	> 0.1	> 0.1	> 0.1	0.001	0.001	0.001
m_1.....	0.01	> 0.1	0.001	0.001	0.001	0.05
m_2.....	> 0.1	> 0.1	> 0.1	0.001	0.01	0.01
m_3.....	0.1	> 0.1	0.01	> 0.1	0.01	0.001
m_{1-3}.....	> 0.1	> 0.1	> 0.1	0.001	0.001	0.001

between localities belonging to the same group are not significant. The material of specimens with worn teeth is scarce, but indicates the same difference between the two groups. A closer examination shows that the mutual resemblance of series with short tooth rows (Antini, Skarø, and Drejø) is superficial only. Micrometer readings of the crown length of individual teeth and of the entire tooth row have been carried out for Antini, Drejø, Skarø, Bjørnø, Lyø, Sjælland, and Jylland. The mean values and standard deviation of the means are shown in Table 13. The four Danish localities which may be considered "normal" (Lyø, Bjørnø, Sjælland, and Jylland) have been treated separately, but the values for these localities combined have been calculated, too. In Table 14 the mean values for the short-toothed series are expressed as percentages of the mean values for "normal" Danish populations. The statistical significance of the differences is shown in Table 15, expressed as P-values. (A P-value of 0.01 corresponds to significance at the 1 % level, etc.). Usually, the P-value expresses only the probability of the existence of a real difference. When, as on the present occasion, the number of degrees of freedom is constant for a series of comparisons the P-values also give some information about the relative size of the differences. When comparing Skarø and Drejø we find only one difference which is significant at the 1 % level, namely, in m_3 which is shorter in the Drejø series. It is hardly advisable to lay stress on the doubtful difference observed in m^3 ($P = 0.05$) because when eight possible combinations are available a single difference at the 5 % level is not unlikely to occur, even if no real difference exists. The comparison Antini-Drejø shows conspicuous differences between these localities. m 1 of both jaws is significantly shorter in the Antini series while m 3 is significantly longer. The mean values for Skarø seem to indicate a reduction particularly of m^3 and m_1. A comparison with "normal" Danish populations clearly shows this tendency. In a way, the Skarø series is intermediate between those from Antini and Drejø each of which shows reduction of the same end of both tooth rows, namely, the front end in the Antini series and the hind end in the Drejø series. It is noteworthy that although not all differences between "normal" populations and such with short tooth rows are statistically significant, all the observed mean values are actually lower in the short-toothed series than in the "normal" ones (Table 14).

It is difficult to decide on the relationship between the short-toothed and the long-toothed populations. If we dare adopt the point of view that evolution within the *Murinae* generally tends towards reduction of the hind part of the tooth row (although Simpson (1945) finds it extremely difficult to trace the evolutionary trends within the group) we may consider the Antini population a primitive form while the Drejø population is a particularly advanced form. The Skarø population, however, does not fit into this scheme because its maxillary tooth row is of the "advanced" type while the mandibular tooth row is "primitive". At any rate, it does not seem warranted to believe in any close relationship between the Antini form and the two insular short-toothed forms. The latter are probably microgeographical races developed after the isolation of the islands from the continent about 7000 years ago (cf. Ursin 1949a and b, with further references). They may be even younger because

TABLE 16. *Apodemus sylvaticus*. Length (in mm.) of the maxillary tooth row in Europe, excluding Denmark and Latvia, and in Asia Minor.

Reference	Name used by quoted author	Area	N.	m^{1-3}
MILLER 1912	*A. s. sylvaticus*	Ireland	10	3.82
— —	—	Scotland	6	3.83
— —	—	England	16	3.84
— —	—	Scilly Islands	4	3.95
— —	—	Jersey	3	4.00
— —	—	Norway	11	3.75
— —	—	Holland-Belgium	9	3.87
— —	—	Northern France	12	3.83
— —	—	Germany	23	3.81
— —	—	Austria-Hungary	3	3.93
— —	—	Roumania	4	3.85
— —	—	Switzerland	20	3.98
— —	*A. s. sylv.? A. s. dichrurus?*	Turin, Italy	10	3.98
— —	*A. s. callipides*	Southern France	9	3.93
— —	—	Spain-Portugal	8	4.00
— —	*A. s. creticus*	Crete	4	3.90
— —	*A. s. dichrurus*	Southern France	9	3.98
— —	—	Genoa, Italy	7	3.83
— —	—	Sorrento, Italy	7	3.94
— —	—	Spain	21	4.07
— —	—	Balearic Islands	6	4.27
— —	—	Sicily	21	4.17
— —	—	Greece	9	3.89
— —	*A. hebridensis*	Lewis, Outer Hebrides	3	4.07
— —	*A. hirtensis*	St. Kilda	9	4.11
— —	*A. fridariensis*	Fair Isle	10	4.16
NEUHÄUSER 1936	*A. s. tauricus*	Asia Minor	10	3.85
FELTEN 1952	*A. s. sylvaticus*	Rhein/Main	144	4.0
Dr. HANZÁK (private communic.)	—	Böhmen-Böhmerwald	12	3.75
Zool. Mus. Copenhagen[1]	*A. s. grandiculus*	Iceland	21	4.02
Brit. Mus. London[2]	*A. s. mosquensis*	Volsk, Saratov, Russia	8	3.40

[1] Degerbøl's material (1939). Alveolar measurements by the present author.
[2] Measured by the author.

there is no evidence that the recent mammalian fauna of the Danish islands is as old as the islands themselves. On the contrary, *A. sylvaticus* is known to be able to invade islands without use of any landbridge, because it occurs on the island of Læsø (see Fig. 1) which according to JESSEN (1897, p. 9) has not been connected with the mainland since several thousand years ago it was submerged. The reduction of the tooth row in the two Danish insular populations is somewhat similar to that previously observed in the Lyø stock of *Microtus agrestis* in which was observed a tendency towards simplification of the second maxillary tooth. According to HINTON (1926)

and ZIMMERMANN (1952) evolution within the *Microtinae* seems continuously to work towards simplification of the molar structure so that the Lyø *M. agrestis* is probably an advanced form while the variety with complicated molar structure occurring in Scandinavia (COLLETT 1912, p. 123; URSIN 1949a) is more likely to be an ancient one, as already suggested by ZIMMERMANN (1950) who lists the Scandinavian *M. agrestis* among the "fringing forms" of the species. It is tempting to regard the relationship of the "advanced" *A. sylvaticus* from Drejø and the, as it seems, "ancient" Antini form in a similar way. This would, however, probably be premature, because the geographical variation of the length of the tooth row of the species, particularly in eastern Europe, is imperfectly known.

The available information of the geographical variation of the tooth row length in *A. sylvaticus* has been listed in Table 16 and is shown in a map, Fig. 13, too. Fairly low mean values (about 3.85 mm.) are found in Denmark, northern Germany and France, the British mainland, Ireland, and perhaps in south-eastern Europe and Asia Minor. Higher values are primarily found on the small islands off the British coast and in southern Europe. The affinities of the Czechoslovakian populations seem doubtful. HANZÁK and ROSICKÝ (1949) found very low values, but Dr. HANZÁK has informed me that the material may have included several specimens of *A. microps* KRAT. & ROS. 1952. Dr. HANZÁK most kindly forwarded 12 tooth row measurements of true *A. sylvaticus*, but even these show a low mean value (3.75 ± 0.04 mm.). *A. microps*, also measured by Dr. HANZÁK, has an extremely short tooth row (3.31 ± 0.03 mm.; N. = 10). The difference between the values for the two species is highly significant. HANZÁK and ROSICKÝ (l. c.) also found very short tooth rows in *A. flavicollis* (see below). Perhaps their method of measuring is not quite identical with that adopted by MILLER (1912) who is responsible for most of the information available. The occurrence of long-toothed forms in southern Europe roughly corresponds with the distribution of *A. s. dichrurus* RAF. and *A. s. callipides* CABR. MILLER's series of *A. s. sylvaticus* from Switzerland, however, has a long tooth row (3.98 mm.) and so has FELTEN's German material from the Rhein/Main area (4.0 mm.). The Antini series (3.52 mm.) is unique in continental western Europe. It may have affinities to *A. s. mosquensis* OGNEV which is known to the present author only from a series of skulls from Volsk, Saratov, Russia, seen in the British Museum. The latter series, however, may as well belong to the species which is known as *A. microps*. Even the Antini series may belong to *A. microps* although it has not the extremely short hind foot which seems to characterize the Slovakian *A. microps*. Still another possibility is that the Antini series represents a local form, a microgeographical race without more importance to systematics than the two Danish insular forms with short tooth rows.

A. flavicollis. The Antini series has a longer tooth row than other series from Denmark and Latvia with the exception of that from Planupe. The difference between Antini and the third Latvian locality, Koknese, is statistically significant at the 1 $^0/_{00}$ level if the whole material is compared irrespective of the age of the animals. If the few old animals with worn teeth are compared the difference is significant at the 5 $^0/_0$

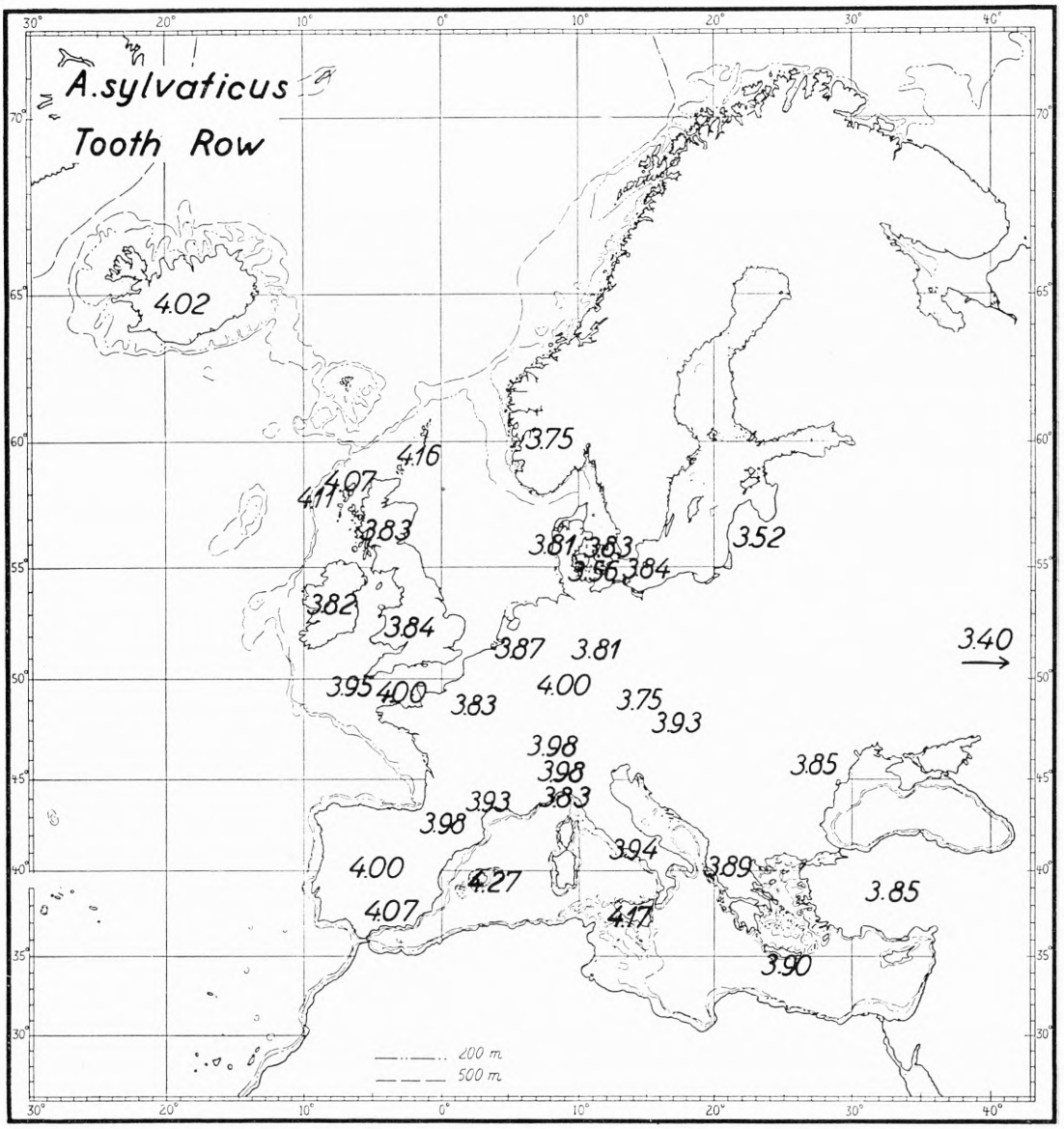

Fig. 13. Length (in mm.) of the tooth row. Cf. text p. 33.

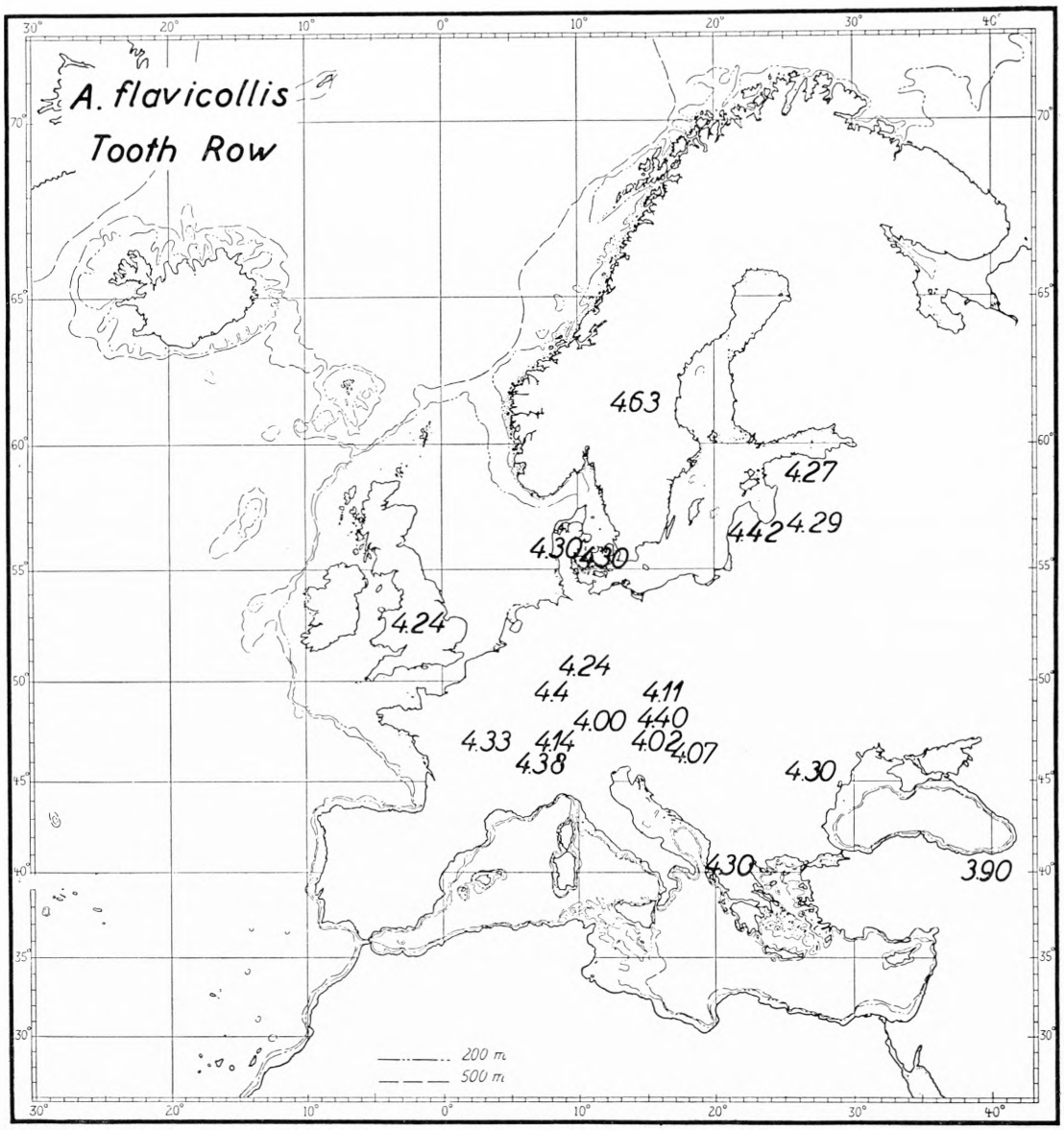
A. flavicollis
Tooth Row
4.63
4.27
4.42
4.29
4.30
4.30
4.24
4.24
4.4
4.11
4.00
4.40
4.33
4.14
4.02
4.07
4.38
4.30
4.30
3.90
200 m
500 m

Fig. 13.

TABLE 17. *Apodemus flavicollis*. Published measurements of the maxillary tooth row in Europe and Asia Minor.

Reference	Subspecies	Area	N.	m^{1-3}
MILLER 1912	*flavicollis*	Sweden	7	4.63
— —	—	Denmark	4	4.35
— —	—	France	6	4.33
— —	—	Germany	10	4.24
— —	—	Austria-Hungary	9	4.40
— —	—	Roumania	12	4.30
— —	—	Switzerland	25	4.38
— —	—	Greece	6	4.30
— —	*wintoni*	England	9	4.24
REINWALDT 1927	*flavicollis*	Estonia	16	4.27
NEUHÄUSER 1936	*saturatus*	NE Asia Minor	3	3.90
HANZÁK and ROSICKÝ 1949	*flavicollis*	Č. S. R.	16	4.11
HEINRICH 1951	*alpinus*	Allgäu	10	4.00
— —	—	Steiermark	8	4.02
— —	*flavicollis*	Bodensee	8	4.14
— —	—	Steiermark	3	4.07
FELTEN 1952	—	Rhein/Main	57	4.4

level only. The difference between Antini (all stages of tooth wear) and the Danish series is highly significant, too.

The available information about the geographical variation of the length of the tooth row of *A. flavicollis* in Europe is listed in Table 17 and shown in a map, Fig. 13. The range of the mean values is considerable although perhaps partly due to variation in the method of measuring and of the age of the animals measured. The mean values of MILLER's measurements are within the range of variation of the Latvian and Danish series with the single exception of the extremely high value for Sweden. No regular geographical variation is seen in MILLER's material. REINWALDT's series from Estonia, consisting predominantly of old animals, is like that from Koknese and, therefore, distinct from the Antini series. Several figures referring to central Europe (HANZÁK and ROSICKÝ, HEINRICH) are low. HANZÁK and ROSICKÝ, however, also give very low values for *A. sylvaticus* (see above) so that another method of measuring than that adopted by MILLER may be suspected. According to NEUHÄUSER (1936) the tooth row of *A. f. saturatus* from Asia Minor is extremely short. The long tail and the occasional existence of a complete collar seem to be the only *flavicollis* characters left in this form which is supposed (NEUHÄUSER) to be closely related to the Caucasian *A. f. fulvipectus* OGNEV.

Like other parts of the body the length of the tooth row of *A. flavicollis* seems to be subject to considerable local variation although no regular geographical variation can be traced at present.

Pelage Characters.

A. sylvaticus. Several authors have paid attention to the occurrence of the buff or orange pectoral spot which has been observed to vary geographically. According to LÖHRL (1938, p. 128) and HEINRICH (1951, p. 105) it occurs in southern Germany in about 90 % of the specimens, but is usually absent in north-eastern Germany. HEROLD (1951, p. 238) found it to be rare in Rhön, central Germany. ZIMMERMANN (1936, p. 127) who collected most of his material in Brandenburg, found that in most specimens the spot was absent or only slightly indicated. In Latvia (Antini) the spot is just traceable in a few of the 12 specimens available, completely absent in the others. The 88 Danish skins may be divided into three groups. The majority (49 specimens) have a large pectoral spot which is sometimes prolonged caudally to the belly. In 18 skins the spot proper is absent, but a buff midventral line is developed behind the front legs. The same pattern was observed in 2 among 35 German skins in the British Museum. The remaining 21 Danish skins are like the Latvian ones: the spot is absent or only traceable. The difference between Latvian and Danish series is obvious even when skins from the same season are compared. 57 English skins (Brit. Mus.) had the spot well developed while it was absent or only traceable in 2 skins. A series of 12 skins from Switzerland contained 11 specimens with a large spot and 1 without spot.

The above evidence seems to show that in north-eastern Europe and in central Germany a form occurs which is characterized by the absence of the pectoral spot in most specimens. North-west of this region (Denmark, Gr. Britain) and south of it, too, (southern Germany, Switzerland) the spot or a midventral line is usually developed. Matters are, however, even more complicated: The smaller of the two *Apodemus* forms occurring in Sicily (the true *A. s. dichrurus*) has no pectoral spot while the larger one (which is perhaps an *A. flavicollis*?) has a large spot (HAGEN 1954, p. 8). The *A. s. dichrurus* of Crete in this respect is like the smaller of the Sicilian forms. The geographical variation of the pectoral spot seems to follow other lines than the variation of several other characters described above.

The present investigation has not added much to the knowledge of the variation of other pelage characters. The under-parts seem to be slightly more whitish in Latvia than in Germany, Switzerland, the British mainland, and Denmark. The general pallor of the back and sides of the Mediterranean populations (*A. s. dichrurus*) has been described by several authors, particularly by MILLER (1912). The colour of the differentiated forms restricted to small islands off the British coast has been described by a. o. BARRETT-HAMILTON and HINTON (1911—21).

Apodemus flavicollis. The geographical variation of the ventral breast-band or collar has been studied particularly by BARRETT-HAMILTON (1900) who found that the populations of north-western Europe including England usually have a broad collar, while those living in south-eastern Europe often have a pectoral spot only.

TABLE 18. *Apodemus flavicollis*. Shape of the collar in Denmark and Latvia.
Groups: 1. Pectoral spot only.
2. Pectoral spot faintly connected with the sides of the body.
3.–6. Broad collar: 3. Pectoral spot extending about 5 mm. behind the collar.
4. Pectoral spot extending about 8 mm. behind the collar.
5. Pectoral spot extending 10—15 mm. behind the collar.
6. Pectoral spot extending to belly (cf. Table 19).

			Group					Total
			1.	2.	3.	4.	5.	
Latvia	Locality	Antini	13	27	29	28	7	104
		Planupe	1	1	2	3	..	7
		Koknese	3	5	6	1	..	15
		Various localities	1	..	2	..	..	3
		Total	18	33	39	32	7	129
	Season	July-September	11	22	26	23	5	87
		October-December	7	11	13	9	2	42
	Head & body	No. measured	18	33	39	32	7	129
		Mean length	112.8	110.1	107.6	108.9	110.4	109.4
		Standard dev. of mean	1.8	1.6	1.4	1.3	3.8	0.7
Denmark	Locality	Sjælland	..	..	52	17	2	71
		Jylland	..	1	7	4	..	12
		Lolland	..	..	3	5	10	18
		Various islands	..	1	6	2	1	10
		Total excl. Lolland	..	2	65	23	3	93
	Season (Lolland omitted)	January-June	..	..	16	6	1	23
		July-December	..	2	49	17	2	70
	Season (Lolland)	January-June	..	..	2	3	6	11
		July-December	..	..	1	2	4	7
	Head & body (Lolland omitted)	No. measured	..	1	43	20	2	66
		Mean length	..	107.5	107.5	109.5	110.0	108.2
		Standard dev. of mean	..	..	1.2	1.6	..	0.9
	Head & body (Lolland)	No. measured	..	..	3	5	7	15
		Mean length	..	..	99.2	109.5	106.1	105.8
		Standard dev. of mean	..	..	4.5	5.4	2.8	2.4

He created the subspecific names *wintoni* and *princeps* for these forms. Owing to a misunderstanding of MELCHIOR's Danish text (1834) he did not realize that two forms of *Apodemus* occur in Sjælland which is considered the type locality for *A. flavicollis*. He considered the latter a synonym of "*Mus sylvaticus typicus*" because he had seen specimens of this form from Sjælland. MILLER (1912) restricted the name *A. f. wintoni* to cover the English population and used *A. f. flavicollis* for all other western European populations.

TABLE 19. *Apodemus flavicollis.* Shape of the collar in Europe. Material belonging to the British Museum, London, and to the Zoological Museums of the Universities of Berlin and Copenhagen. Grouping as in Table 18 (which see).

Area	Group						Total
	1.	2.	3.	4.	5.	6.	
Norway	..	..	..	2	3	1	6[1]
England	..	..	..	9	22	..	31
Lolland (Denmark)	..	..	3	5	10	..	18
Estonia-Leningrad	..	..	2	3	..	1	6
Denmark (excl. Lolland)	..	2	65	23	3	..	93
Latvia	18	33	39	32	7	..	129
Central Europe	12	7	12	3	2	..	36
South-eastern Europe	38	19	16	4	2	..	79

[1] Collar proper very broad, about 12 mm. as against usually about 7 mm. in groups 3–5. Four juveniles from the same locality, not included in the table, had very broad collars, too.

Table 18 shows the variation of the shape of the collar in Danish and Latvian populations. The shape does not seem to be influenced by the season of the year or the size (age) of the animals. All Danish skins have a complete collar although in a few specimens it is only slightly traceable. In Latvia, about 15 % of the specimens have a pectoral spot only, and the collar proper is just traceable in further 25 %. In the series from the Danish island of Lolland the collar (or rather: the pectoral spot of the collar) usually extends further caudally than in other Danish series.

The geographical variation of the shape of the collar in Europe is shown in Table 19, based on material investigated by the author. Extreme development of the collar is seen in a small series from Lillehammer, Norway. The collar is very broad in this series, measuring about 12 mm. from the cranial to the caudal border as against about 7 mm. in broad-collared specimens from other localities. The Norwegian skins also show a considerable caudal prolongation of the median part of the collar (the pectoral spot). Such prolongation also occurs in English skins, and partly in those from Lolland, too. In other series from Denmark and in that from the Estonia-Leningrad area a complete and usually broad collar is developed but with a single exception the pectoral spot is not much prolonged caudally. All the above mentioned skins are of the "*wintoni*" type, as BARRETT-HAMILTON (1900) has it. The series from Latvia, from localities scattered over central Europe, and from south-eastern Europe are characterized by a high proportion of skins without complete collar and usually without much caudal prolongation of the pectoral spot. They are of BARRETT-HAMILTON's "*princeps*" type.

BARRETT-HAMILTON and HINTON (1911—21) called attention to the resemblance of the Norwegian *A. flavicollis,* as described by COLLETT (1912) with the English *A. f. wintoni.* REINWALDT (1927, p. 30) further pointed out that the Estonian stock rather more resembled the English and probably also the Norwegian form than the

continental *A. f. flavicollis* as this was described by MILLER (1912, p. 289): "chest spot frequently not forming complete collar". REINWALDT's description seems to show that the Estonian *A. flavicollis* is intermediate between the Latvian and the Danish ones. In Estonia a caudal prolongation of the pectoral spot was not rare but, on the other hand, a few specimens were seen in which a complete collar was not formed. HILZHEIMER's (1911) description of *A. flavicollis* from Finland points even more in the "*wintoni*" direction. HEROLD (1932) found that 16 specimens from the island of Usedom on the South-Baltic coast all had broad collars with the pectoral spot faintly developed. Much like these are 39 specimens from Rhön in central Germany which were described by HEROLD (1951). Rhön seems to be the southernmost locality from which has been described a series with complete collars throughout. FELTEN (1952) in a series of 59 specimens from the Rhein-Main area found only 33 specimens with complete collar. HEINRICH (1951) says that in northern Germany the complete collar is an almost constant character while near Bodensee and in Steiermark several specimens were obtained which had the pectoral spot only. Of particular interest is his long-tailed *A. f. alpinus* which shows an extreme development of the "*princeps*" condition. In this form a complete collar is perhaps never developed. The "large *A. s. dichrurus*" from Sicily (HAGEN 1954) which as already mentioned is perhaps an *A. flavicollis* has a well-developed pectoral spot but no collar. *A. f. saturatus* from Asia Minor "often" has a complete collar (NEUHÄUSER 1936) and, therefore, seems to be of the "*princeps*" type.

All things considered, there is not much doubt that the *A. flavicollis* of north-western Europe is characterized particularly by an extreme development of the collar. Fig. 14 gives a provisional survey of the geographical variation of the chest pattern in western Europe.

There seems to be some correlation between the shape of the collar and the colour of the under-parts, although the geographical variation of the colour in short series is somewhat obscured by seasonal changes. The English form is extremely dark. 14 of the 28 skins seen in the British Museum are darker than the darkest Danish skin. The short series from Norway and from the Estonia-Leningrad area are also darker, on an average, than Danish specimens. Skins from central and south-eastern Europe were not found to be different from Danish skins but perhaps the material was too small. A comparison of Danish and Latvian skins collected from July to December shows that in Latvian specimens the under-parts are more bright white than in Denmark. The series from Lolland does not differ in this respect from other Danish series. HEINRICH's *A. f. alpinus* (1951) is said to have more greyish underparts than *A. f. flavicollis* from the Alpine region. In the colour of the under-parts the former is obviously distinct from other populations with the reduced "*princeps*" collar type.

The back and sides are more reddish in Denmark than in Latvia. It has not been possible to trace the further geographical variation of this character, probably owing to a considerable seasonal variation. English skins, however, seem to be even more reddish than Danish ones.

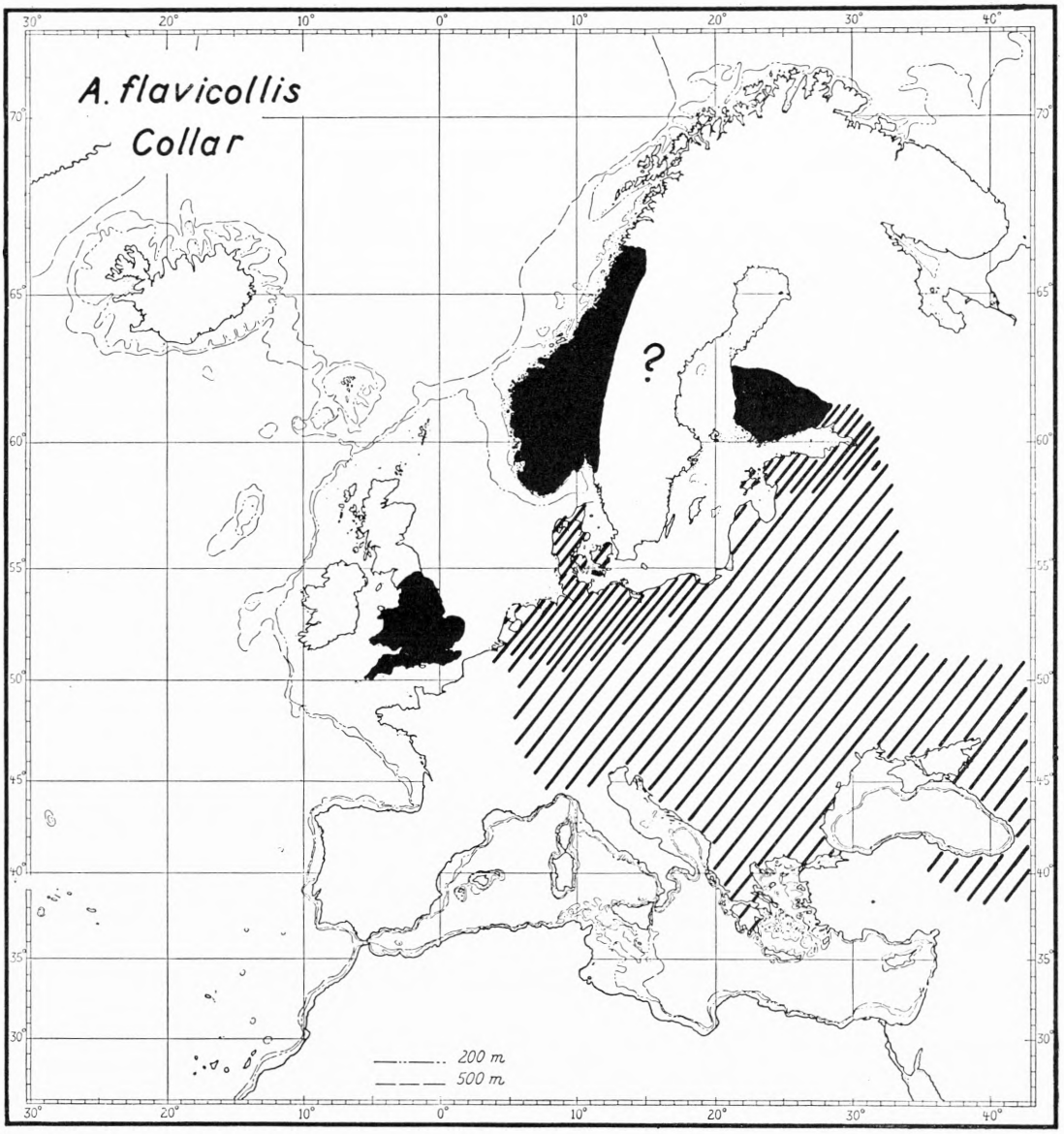

Fig. 14. Provisional survey of the geographical variation in western Europe of the development of the collar and the pectoral spot in *A. flavicollis*. The map is not supposed to be correct in detail. Cf. text p. 39.
Black: Collar broad with long pectoral spot (*"wintoni"* condition).
Dense hatching: Collar complete, usually with short pectoral spot (intermediate form).
Open hatching: Complete collar frequently not formed. Pectoral spot usually short (*"princeps"* condition).

General Remarks.

A. sylvaticus. Populations with a short tooth row, with a low number of tail rings, and with proportionately short tail and hind foot are found in the north-eastern part of western Europe (Denmark and Latvia). The size or relative size of these parts of the body, and the number of tail rings, seem to increase towards the west and the south, the maximum for most characters being reached on some of the small islands off the British coast and in the Mediterranean part of western Europe. The geographical variation of the length of head and body was not considered during the present investigation, but information in the literature (notably MILLER 1912) seems to show that the body size also increases from the north-east towards the west and the south. The large size of several British insular forms recalls the observations by DEGERBØL (1933, 1940) who found large-sized forms of the house mouse (*Mus musculus*) on the Faroe islands and of the badger (*Meles meles*) on a Danish island (Sjælland). Populations with extraordinarily short tooth rows occur in Latvia and on two small Danish islands. These populations do not seem to be closely related because the proportionate length of individual teeth varies considerably from one of these populations to another. The two Danish insular forms are probably microgeographical races developed on the islands where they occur, perhaps as an effect of isolation (a so-called "SEWALL-WRIGHT effect"). The relationship and systematic value of the Latvian short-toothed form is obscure at present. Affinities to *A. s. mosquensis* OGNEV may be suggested but the problem probably cannot be solved until the distribution, variation and systematic value of *A. microps* KRAT. et ROS. become known. *A. microps* is in Slovakia an extremely short-footed and short-toothed form which does not appear to be geographically isolated from populations of *A. sylvaticus.*

A. sylvaticus is widely distributed in the Danish archipelago, but nevertheless no distinguishable insular forms have been traced as yet, except in the two cases of a slight peculiarity in dental characters. In this respect the contrast with British populations is striking. On the small islands north, west, and south of the British mainland a multitude of distinguishable isolated forms occur, many of which have been given subspecific or even specific names of their own. The differences between individual populations may be considered the result of a highly effective isolation of long duration. At present only little is known about the maximum age of these populations. There is, however, not much doubt that it considerably exceeds the 5,000—10,000 years which have probably passed after the Danish archipelago became isolated from the continent. More difficult to understand than the difference between the isolated British populations is their mutual similarity. Most of them seem to have evolved towards the *flavicollis* characters (large animals with proportionately long tail and hind foot), especially on the more remote islands as the Shetlands and Fair Isle. RICHARDS (1935) called attention to the fact that such similarity between British insular forms is probably not to be explained as an effect of climate, because the climate of the islands

north and west of the British mainland is different from that of the Channel Islands. Several authors, as for instance STEJNEGER (1908) and BARRETT-HAMILTON and HINTON (1911—21, p. 436) consider the mammals of these small islands survivors of a previous mammalian fauna which inhabited the British mainland and continental Europe. RICHARDS (1935) termed such remainders "fringing forms". ZIMMERMANN (1950) studied the occurrence of "fringing forms" within European voles (*Microtinae*) and found several interesting examples. If the British insular populations of *A. sylvaticus* are taken to represent a fringing form the populations of southern Europe should perhaps be included in this, too. Except in colour there seems, as mentioned above, to be a certain similarity between the British and the south European *A. sylvaticus,* both of which show several *flavicollis* characters as for instance large size, long feet, and long tooth-rows. The fringing form may be considered an old inhabitant of western Europe that became so mixed up with an eastern relative that most of western or at least central Europe is now inhabited by intermediate forms. The Danish populations may or may not represent the pure eastern form. An investigation of the Scandinavian populations would perhaps throw more light on this problem. It must, however, be remembered that the validity of the theory of "fringing forms" is questioned by DEGERBØL (1940) who found that what might be termed "fringing form characters" occur in the Faroe house mouse which in all probability was introduced by man within historical times.

An alternative explanation of the geographical variation of *A. sylvaticus* in western Europe may be based on the cline concept. The gradual change of the characters of the northern form occurring in Denmark into those of the western (British) and southern (central European and Mediterranean) forms much resembles the features of a cline. However, it seems difficult to explain a cline formation of this type because the climatic change from Denmark towards the west is not the same as the change towards the south. DEGERBØL (1939, p. 41) and HEINRICH (1951) have called attention to the resemblance of the geographical variation in Denmark and Germany of *A. sylvaticus* and *Microtus arvalis.* The frequency of the "simplex" tooth character of the latter species is particularly high in Denmark and decreases rapidly towards the south (ZIMMERMANN 1935, 1952). It is at present difficult to see whether there is a causal connection or only a superficial resemblance between the geographical variation of the two species.

Besides the above two attempts towards an explanation of the geographical variation in *A. sylvaticus* still another seems close at hand. It has special bearing upon the development of the British insular forms. The mutual similarity of these may result from an orthogenetical trend in evolution. The term "orthogenetical" is here used in the wide sense of the word (as by ZIMMERMANN 1952, p. 493), not postulating the existence of any inner urge for directed evolution. Just as in many families of rodents the evolution seems to work towards development of rootless molars (see ELLERMAN 1940—41, or any other monographic work on rodents), there may occur within isolated populations of *A. sylvaticus* an evolutionary trend towards develop-

ment of certain, partly *flavicollis*-like, characters which may prove to be the fittest. If, further, microgeographical races play an important rôle in evolution as suggested by e. g. DOBZHANSKY (1941, p. 175) it does not seem excluded that particularly advanced forms simultaneously have evolved by selection on a number of small islands provided, that the size of the populations (i. e. the size of the islands) is suitable for a highly effective selection to work.

It would probably be premature to revise the nomenclature of the *A. sylvaticus* of western Europe, particularly because the Swedish form which must retain the name *A. s. sylvaticus* (L.) is not known in details. It still seems convenient to use the name *A. s. dichrurus* RAF. for the pallid Mediterranean form. A nomenclatorial separation of the form occurring in Denmark and northern Germany from the vividly coloured populations of central and parts of southern Europe will probably prove to be inconvenient owing to the gradual change of most characters (other than colour?) into those of *A. s. dichrurus*. Therefore, the name *A. s. callipides* CABRERA which seems to have been applied to transitional forms should probably be abandoned.

A. flavicollis. The size and proportions of this species do not seem to be subject to regular geographical variation in western Europa. Local variation is, however, considerable. The only character which has been found to vary geographically throughout the area is the colour pattern of the neck and chest (see Fig. 14). In northern Europe a complete collar is formed in practically all specimens. It is usually much prolonged caudally as a mid-ventral pectoral spot. In central and south-eastern Europe the collar is considerably reduced and often represented by a short pectoral spot only. Intermediate forms with complete although not very broad collar and usually with a short pectoral spot occur in Denmark and in the Estonia-Leningrad area. This geographical variation was observed, although not in detail, by BARRETT-HAMILTON (1900) who applied the subspecific names *wintoni* and *princeps* for the north-western and south-eastern forms, respectively. This terminology is convenient but, unfortunately, it is necessary to retain the name *A. f. flavicollis* (MELCHIOR) for the population occurring on the island of Sjælland which is considered the type locality. This population is intermediate in character. Perhaps it will prove advantageous to use the name *A. f. flavicollis* for the intermediate populations and for those of the *princeps* type so that *A. f. princeps* (BARR.-HAM.) becomes synonymous with *A. f. flavicollis*. The name *A. f. wintoni* (BARR.-HAM.) then covers the English, Norwegian, and Finnish populations. If the two latter turn out to possess peculiarities of their own, making them worthy of subspecific recognition (and they are not unlikely to do so) they should perhaps, with the English "true" *wintoni*, form a "*wintoni*-group" as opposed to a "*flavicollis*-group". The population of the island of Lolland (Denmark), although slightly more *wintoni*-like than other Danish populations, is still intermediate and should be referred to *A. f. flavicollis*. The Alpine longtailed form *A. f. alpinus* HEINRICH, seems to be worthy of subspecific recognition although its distribution and relationship with other central European populations is not yet known in detail.

At present it seems difficult to decide on the origin of the differentiation of the western European *A. flavicollis* into two groups according to chest colour patterns. The restriction of *A. f. wintoni* to the northern or north-western range of the species perhaps indicates an adaptation to the climatic conditions in northern Europe although the climatic similarity of Finland and England is, indeed, not very conspicuous. It is also possible that *A. f. wintoni* is to be considered a "fringing form" which previously had a wider distribution in Europe.

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