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ADVANCES IN THE BIOLOGY OF SHREWS

edited by
Joseph F. Merritt
Gordon L. Kirkland, Jr.
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CARNEGIE MUSEUM OF NATURAL HISTORY
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PREFACE

In 1988 we decided to organize an international colloquium on the biology of the Soricidae at Powdermill Biological Station of the Carnegie Museum of Natural History, the site of a number of previous scientific meetings. It was clear from past conferences at Powdermill that the number of participants had to remain small to enhance communication and productivity. Participants were selected to represent the nearly worldwide distribution of soricids.

The International Colloquium on the Biology of the Soricidae, held 8–14 October 1990, welcomed 55 biologists representing 14 countries—Canada, Czechoslovakia, Finland, France, Germany, Israel, Japan, The Netherlands, Poland, Russia, South Africa, Sweden, the United Kingdom, and the United States. The colloquium encompassed many fields of soricid biology, including ecology, anatomy, physiology, behavior, biogeography, and evolution and systematics. A session dedicated to field and laboratory methods was also included in the program. Topics presented were diverse, ranging from physiological ecology and population dynamics of Eurasian shrews to comparative allozyme and albumin evolution in the Soricidae.

The colloquium was declared a great success by all participants, largely due to the high quality of presentations and the relaxed atmosphere of the Powdermill setting which fostered considerable informal discussion between sessions and in the evenings. The intellectual stimulation of the gathering was further heightened by the crisp autumn days and colorful foliage of the Appalachian Mountains of western Pennsylvania.

Our goal as conveners and editors was to produce a volume of proceedings indicative of the current research and state of knowledge in soricid biology, and to stimulate additional research on this group of mammals. We believe these objectives were met at the colloquium and are formally summarized in the contents of this volume.

In order to conserve costs of publication, figures and tables appear at the end of each article.

ACKNOWLEDGMENTS

The International Colloquium on the Biology of the Soricidae was made possible by funds from the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. We are indebted to James E. King, Director, for his support of the colloquium and publication of this volume.

This colloquium and its success also depended on the support of many people. We are deeply indebted to our friends, Ingrid and Bill Rea and Theresa and Tom Nimick for hosting receptions, and to M. Graham Netting and Ingrid and Bill for providing lodging in their homes for several of the participants, who will never forget their gracious and kind hospitality. The colloquium ran smoothly due to the expert preparation of the facilities by the Powdermill maintenance staff—Gilbert Lenhart, Albert Lenhart, and Lloyd Moore. Participants were housed in cabins at Powdermill and in cottages provided by Donald Ankney and the Laurel Mountain Camp. Robert Leberman and Robert Mulvihill kindly gave *ad libitum* bird-banding demonstrations for the participants. Terri Kromel and Kathy Matt worked long hours in a variety of roles ranging from tour guides and travel agents to medical technicians. Theresa Gay Rohall, the projectionist, kept all speakers on schedule. Dyana Kessel of Ligonier Travel and Tours assisted participants with domestic and international travel arrangements. Individual participants increased their body mass by upwards of 3 kg during the week due to the copious amounts of delicious food provided by Pat Piper and the staff of Ligonier Country Catering and by our hosts for the evening receptions, Ingrid and Bill Rea and Theresa and Tom Nimick.

Transportation between the colloquium site and Pittsburgh and Dulles International Airports was accomplished through help from Gordon L. Kirkland, Jr., Kathy Matt, Joseph Merritt, Santiago Reig, Bob Rose, Duane Schlitter, and Jeff Wilcox. We are indebted to the creative talents of Nancy Perkins of the Section of Exhibit Design and Production, Carnegie Museum of Natural History, for designing the colloquium logo.

We thank the participants for their cooperation in submitting manuscripts and revisions in a timely fashion. We thank the many reviewers of individual manuscripts, whose suggestions for revision contributed significantly to the quality of papers in this volume. We are most grateful to Robert S. Hoffmann and Jane Junge, who although unable to attend the colloquium, did yeoman service through their meticulous editing of several manuscripts. We offer special thanks to Colleen Hannakan and Julia Zeyzus for reworking some of the illustrations.

Lastly, special thanks go to the late C. J. McCoy, Editor, and Mary Ann Schmidt, Assistant Editor of scientific publications for Carnegie Museum of Natural History, for preparing this volume for publication.

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Participants in the International Colloquium on the Biology of the Soricidae, 8–14 October 1990, Powdermill Biological Station of Carnegie Museum of Natural History. Photograph by Frans J. M. Ellenbroek.

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LATITUDINAL VARIATION IN THE LIFE HISTORIES OF *SOREX ARANEUS* AND *S. CAECUTIENS* IN FINLAND

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ABSTRACT

Reproduction of *Sorex araneus* and *S. caecutiens* was studied at three localities in Finland: Loppi (61°N), Sotkamo (64°N), and Kilpisjärvi (69°N). Population turnover was most rapid at Kilpisjärvi. Shrews did not survive two winters at any of the localities. Breeding began and ended in latitudinal order with the shortest breeding season at Kilpisjärvi; there shrews began reproduction under climatically more severe conditions than elsewhere. Overwintered females produced two litters at Kilpisjärvi and three at Loppi. Litter size increased with increasing latitude. Young shrews matured in the year of birth only at Kilpisjärvi, where during most years some young females attained sexual maturity before winter and gave birth to one litter. Attainment of sexual maturity was not density dependant. Mature shrews were not heavier at Kilpisjärvi than in other areas. Seasonal trends in body weight at Kilpisjärvi differed from other populations. Immatures there were heavier in late summer, but they did not gain weight toward autumn. In early winter, their weight decreased more than in southern areas indicating that severe environment adversely affected shrews during times of low snow cover.

INTRODUCTION

This paper reports on life history characteristics of the common shrew, *Sorex araneus*, and the masked shrew, *S. caecutiens*, in three different latitudinal regions of Finland: (1) Loppi, 61°N, in southern Finland; (2) Sotkamo, 64°N, in central Finland; and (3) Kilpisjärvi, 69°N, in northern Finland (Fig. 1). Finland stretches for 1000 km in meridional direction from 60°N to 70°N. Environmental conditions vary considerably in different parts of the country, owing to the influences of both latitude and altitude. Most of Finland belongs to an ancient peneplain area, which is close to sea level. The average altitude of Finland is only 152 m, but northwesternmost parts of the country are in the Scandinavian mountain chain where highest peaks reach above 1300 m.

The common shrew is the most numerous mammalian species in Finland, and its distribution covers all of the country (Siivonen, 1956, 1974; Skarén and Kaikusalo, 1966; Kaikusalo, 1991). Of the six soricid species occurring in Finland, *S. caecutiens* is second in abundance in most of the country. Its numbers decrease toward the south and west (Skarén and Kaikusalo, 1966; Kaikusalo 1991). However, we caught sufficient specimens of both species in all three study areas so that life history characteristics of the two species could be compared at different latitudes in Finland.

STUDY AREA AND MATERIALS

Loppi and Sotkamo are in the northern coniferous taiga forest zone, whereas study sites in the Kilpisjärvi region include both subalpine mountain birch forest and low alpine tundra. The upper boundary of the birch zone lies at about 600 m. Sampling localities at Kilpisjärvi ranged in altitude from 473 m to 1029 m. Field studies thus were carried out in both the alpine and the subalpine regions. Sampling localities at Loppi averaged 120 m (range 100–183 m). At Sotkamo they averaged 200 m (range 120–326 m). In southern Finland trapping was performed at Ojajoki Field Station of the Finnish Forest Research Institute in Loppi, and in the northernmost part of Finland at Kilpisjärvi Biological Station.

At Kilpisjärvi small mammals, predominantly rodents, have been studied continuously since 1946 (e.g., Kalela, 1949, 1957, 1962; Tast, 1966, 1984, 1991; Tast and Kalela 1971; Viitala, 1977). In connection with these investigations, a large sample of shrews has been collected and reported on elsewhere (Kalela et al., 1971*b*; Kaikusalo, 1980; Kaikusalo and Hanski, 1985; Hanski and Kaikusalo, 1989; Henttonen et al., 1989).

This paper is based on material collected (a) at Kilpisjärvi in 1964–1989 consisting of 1,958 common and 302 masked shrews, (b) at Sotkamo in 1966–1989 with 1,564 common and 149 masked shrews, and (c) at Loppi in 1972–1989 with 2,560 common and 75 masked shrews. The proportion of masked shrews in the total shrew sample was statistically highly significantly smaller in southern Finland than elsewhere ($\chi^2 = 170.8$; $P < 0.001$).

The shrews could easily be divided into two age groups. Overwintered animals weighed distinctly more than young of the year and had worn teeth. Furthermore, their tails usually had suffered from winter and were lacking hair at the end.

The three study areas differ markedly in climate, especially in the lengths of winter and summer. The first lasting snow usually falls in the middle of October at Kilpisjärvi, in the middle of November at Sotkamo, and in the middle of December at Loppi (Kolkki, 1966). Snowmelt takes place at Kilpisjärvi in early June, at Sotkamo in early May, and at Loppi in early April (Kolkki, 1966). The growing season (+5°C) at Kilpisjärvi is approximately 95 days long in the birch forest belt (480 m) and less than 80 days in the low alpine belt (740 m) according Hiltunen (1980). It is about 150 days at Sotkamo and about 170 days at Loppi (Tuhkanen, 1980).

RESULTS AND DISCUSSION

Breeding Season

Overwintering common and masked shrews at all localities

were immature animals which had been born during the previous summer and had not attained sexual maturity. When male shrews reach sexual maturity, very rapid growth of the testes takes place. Mature common shrew males have testes exceeding 4 mm in length (Saure et al., 1971). Males attained sexual maturity first at Loppi in the middle of March, and then at Sotkamo and Kilpisjärvi at almost the same time at the turn of March to April (Table 1). Females reached sexual maturity about three weeks later than males at all study areas. So, for example, none of the females obtained in April at Sotkamo and Kilpisjärvi were mature (Table 2). A small difference in the onset of reproduction of females at Sotkamo and at Kilpisjärvi was observed.

Owing to relatively small samples of masked shrews, we report only the dates of first mature animals caught. Sexually active males were first trapped at Loppi on 3 March, at Sotkamo on 28 March, and at Kilpisjärvi on 17 April. Mature females were first obtained at Loppi on 12 April, at Sotkamo on 27 April, and at Kilpisjärvi on 16 May. The breeding season lasted longer in southern Finland than in central and northern parts of the country (Tables 1 and 2). Postbreeding females were caught at Kilpisjärvi as early as late July, and from the middle of August they formed the majority among overwintered females (Table 2). At all three study areas, postbreeding females formed 50% or more of overwintered females by September. Perhaps the fact that postbreeding females were obtained over a fairly long period indicates that there may be annual variation in the termination of the breeding season.

The latest date on which reproductively active masked shrews (i.e., males with large testes and lactating females), were caught was as follows: males at Loppi on 2 October, at Sotkamo on 30 September, and at Kilpisjärvi on 13 September; and females at Loppi on 2 October, at Sotkamo on 3 October, and at Kilpisjärvi on 22 September.

The breeding season was shortest in the areas with the longest and most severe winters. However, differences in the dates of the onset of reproductive activity were less than expected on the basis of climatic factors. Snowmelt takes place at Kilpisjärvi about two months later than at Loppi. Nevertheless, first litters at Loppi were produced approximately one month earlier than at Kilpisjärvi. Thus, common shrews were able to attain sexual maturity in northern Finland under conditions in which they remained immature in central and southern Finland. According to Skarén (1973), in study areas at Iisalmi in central Finland (63°30'N), female common shrews when pregnant for the first time in spring had visible embryos when mean temperatures reached +5°C. Our observations at Loppi and Sotkamo fit well with this, but at Kilpisjärvi breeding began at much colder temperatures. Average dates when mean temperatures reach +5°C are 30 April at Loppi, 10 May at Sotkamo, and 5 June at Kilpisjärvi (Kolkki, 1966; Fig. 1). Correspondingly, breeding ceased at Kilpisjärvi first, but again the difference was much smaller than expected from climate.

Among birds with wide latitudinal ranges, similar observations on the onset of reproduction at a much earlier phenological phase in the north than in the south have been made (e.g., Slagsvold, 1975). Two hole-nesting migratory passerine birds, *Phoenicurus phoenicurus* and *Ficedula hypoleuca*, begin egg-laying at Kilpisjärvi about two weeks earlier than in southern Finland when compared with birch leafing (Järvinen, 1983, 1989).

Winter Reproduction

In our data only one observation gives a hint of possible sexual activity during winter. In 1989, on 11 February, a mature, sexually active common shrew male was trapped at Kilpisjärvi. Among small rodents living in the same area, and under similar ecological conditions beneath the snow, winter breeding has been recorded several times (Tast and Kaikusalo, 1976; Kaikusalo and Tast, 1984; Tast 1991). Heikura (1984) collected one lactating female common shrew in March. Therefore, shrews occasionally reproduce under winter conditions in central Finland.

Reproduction in the Year of Birth

The sexes differed markedly in the attainment of sexual maturity in the year of birth (Table 3). Male young-of-the-year matured only occasionally at all three study areas, whereas a large proportion of juvenile females produced offspring in the northernmost study area (Kilpisjärvi). Differences between sexes were statistically highly significant both for common shrews ($\chi^2 = 75.21$, $P < 0.001$) and for masked shrews ($\chi^2 = 9.45$, $P < 0.01$). One-sixth of females of both species at Kilpisjärvi reproduced in the year of birth, while practically all males and females in other areas remained immature until the following summer. Latitudinal differences in attainment of sexual maturity in the year of birth were highly significant both for common shrews ($\chi^2 = 86.55$, $P < 0.001$) and for masked shrews ($\chi^2 = 11.97$, $P < 0.01$).

Observations of Heikura (1984) and Hyvärinen (1984) were consistent with ours, as they found that at latitude 65°N no juveniles matured before winter. In contrast, Skarén (1979) observed that 5.5% of young female common shrews were pregnant or nursing in June–September at a locality at almost the same latitude as Sotkamo. Henttonen et al. (1989) found that at Pallasjärvi (68°N) in midsummer 1986, 9% of young *S. araneus* females and 21% of *S. caecutiens* were pregnant. There are contradictory opinions of maturation of young shrews before wintering. Several authors have not usually caught mature individuals in the summer of their birth (Pucek, 1960; Vogel, 1972; Heikura, 1984; Hyvärinen, 1984). Others have shown that young females take part in reproduction (Snigirevskaja, 1947; Karaseva and Ilenko, 1960; Stein, 1961; Shvarts, 1962; Dokuchaev, 1989; Sheftel, 1989). Stein (1961) pointed out that young-of-the-year produced offspring during years of population lows. Several subsequent studies, including those of Sheftel (1989) and Dokuchaev (1989), confirmed that population densities affect the maturation of young shrews. Obviously at Kilpisjärvi, however, factors other than population density must have affected the sexual maturation of shrew females. Sexually active young-of-the-year females were captured there over a nine-year period, including four successive summers in 1966–1969 (Table 4).

Common shrew population densities were studied at Kilpisjärvi by Kaikusalo and Hanski (1985) and Henttonen et al. (1989) during the years 1964–1988. In Table 4, their spring density estimates are given as well as changes in population densities from spring to autumn during those summers. Evidently there is no correlation between population density and attainment of sexual maturity in the natal year. Of the three years with low population densities, in 1980 no sexually active young-of-the-year females were captured, whereas in 1968 and 1966 their proportion was highest in the years when 20 or more juvenile females were obtained. And, on the other hand, the two years with high population densities differed distinctly; in 1981, 1.8% of young-of-the-year females attained sexual maturity, whereas in 1969, the proportion was 15.6%. In the two other years with high spring population densities, 1973 and 1974, so few young-of-the-year females were trapped that it was not reasonable to consider those years in detail.

Obviously the proportion of young-of-the-year females breeding in the summer of birth increases with latitude. At latitudes 61°N and 64°N, almost no sexually mature juvenile females were captured, whereas their proportion at latitude 69°N was about one-sixth in both *S. araneus* and *S. caecutiens*. Shvarts (1962) found on the Jamal Peninsula (70°–73°N) in the high Arctic that about one-third of young *S. araneus*, *S. arcticus*, and *S. daphaenodon* females bred in the year of birth.

However, the influence of young-of-the-year breeding on population dynamics of shrews is apparently not very pronounced. Table 4 does not show any correlation between proportion of young female shrews breeding and change in population density from spring to autumn. Among small rodents the situation is different. The reproduction of young voles and lemmings strongly affects population fluctuations in our study areas (Kalela, 1957, 1962; Kalela et al., 1961, 1971*a*; Tast, 1966, 1982, 1991; Koponen, 1970; Henttonen et al., 1977; Laine and Henttonen, 1983).

Population Turnover and Seasonal Weight Variation

There was a complete annual turnover in both common and masked shrew populations in all study areas. Figure 2 presents our data on the proportion of overwintered common shrews in biweekly samples. Before June all shrews in every study area were overwintered ones born during the previous summer. Young shrews were captured first at Loppi in early June, and in the latter half of June in the other study areas. After June the percentage of overwintered animals in samples decreased rapidly. At Kilpisjärvi no overwintered shrews were obtained after early October. The population turnover took longest in southern Finland (Loppi), where no mature shrews were captured after December. Thus, overwintered shrew numbers declined in latitudinal order beginning in northernmost parts of Finland. No shrews survived two winters.

The rapid turnover is also evident from seasonal mass variation presented in Fig. 3. Because molt substantially influences the body mass of shrews, molting animals were excluded. We also excluded all mature females. In small-sized shrews, embryos and milk glandular tissue greatly affect mass and it is difficult to correct for these factors to permit reasonable comparisons.

Immature shrews were distinctly smaller than mature ones. There was no overlap in body mass. All shrews in all samples taken in January and February were immature (Tables 1, 2; Fig. 3). When immature shrews attained sexual maturity in spring, they gained considerable weight. Thereafter shrews grew continuously becoming largest at about midsummer. After that, body mass began to decrease. By autumn, mass loss continued and old, overwintered animals disappeared totally from populations. Their poor survival rate presumably was connected with loss of mass. Obviously for shrews a most critical period is late autumn and early winter when temperatures are already low and the snow cover is not yet so thick that its insulating effect is sufficient.

At Kilpisjärvi those young females that attained sexual maturity in the year of birth were very short-lived. The last were captured in September. Thus, they disappeared from populations at the same time as overwintered shrews. It seems evident that shrews cannot simultaneously be good at survival and reproduction. Apparently energy costs during reproduction are too great. Shrews are not able to store fat for winter when breeding. As a result, the overwintering population consists exclusively of immature animals which do not reproduce until the summer following their birth.

In the survival strategies of overwintering small homeotherms, brown adipose tissue (BAT) has an important role. Before winter, BAT mass increases distinctly in both shrews and small rodents living in boreal and subalpine regions (e.g., Hyvärinen, 1968, 1969; Hissa and Tarkkonen 1969; Pasanen, 1969, 1971; Pasanen and Hyvärinen, 1970; Feist, 1980, 1984; Wunder, 1984; Merritt, 1986; Zegers and Merritt, 1988). Obviously the poor survival of those animals that reproduced before winter is a result of reduced fat storage due to energy costs during reproduction, especially lactation, as stated, for example, by Randolph et al. (1977) and Sauer and Slade (1988). Animals living fast are dying young (Jones, 1990).

Unexpectedly, no geographical variation in the body mass of mature shrews was found in our study areas (Fig. 3). However, in late summer, immatures at Kilpisjärvi were distinctly heavier than those in central and southern Finland. This could be an adaptation to severe environmental conditions in the northernmost study area. At Loppi and Sotkamo, immature shrews had rather constant body mass throughout autumn and winter. At Kilpisjärvi, shrews lost much of their body mass in the autumn before permanent snow cover. Later, when insulating snow cover was thick enough, heat loss was smaller, and shrews gained weight.

Litter Size

Both *S. araneus* and *S. caecutiens* exhibited a trend of increasing litter size with increasing latitude (Table 5). Litters were largest at Kilpisjärvi and smallest at Loppi, differences being highly significant for *S. araneus* both when all samples were treated together ($\chi^2 = 86.62$, $P < 0.001$; 20 d.f.) and when samples were compared in pairs: Kilpisjärvi-Loppi ($\chi^2 = 62.02$, $P < 0.001$; 10 d.f.), Kilpisjärvi-Sotkamo ($\chi^2 = 22.41$,

$P < 0.02$; 10 d.f.), and Sotkamo-Loppi ($\chi^2 = 24.88$, $P < 0.001$; 7 d.f.). Masked shrew samples were smaller, especially at Loppi, but differences between samples were just below significance level.

At Kilpisjärvi a portion of juvenile females reproduced in the year of birth. Litters produced by overwintered females in both species were larger than those of young-of-the-year. Differences in litter sizes between different-aged females were highly significant when both species were treated jointly ($\chi^2 = 26.87$, $P < 0.01$; 10 d.f.) and in *S. caecutiens* ($\chi^2 = 17.75$, $P < 0.01$; 9 d.f.), while in *S. araneus* the difference was slightly below significance level.

The average litter size of *S. araneus* in Lake Ladoga territory in northwestern Russia close to the Finnish border was 6.6 (Ivanter and Ivanter, 1984). The figure is the same as that for common shrews at Loppi, which is located at almost the same latitude. In central Finland at Iisalmi (63°30'N), average litter size of common shrews was 7.8 (Skarén, 1973). This figure is almost the same as that at Sotkamo in our data. Skarén (1973) also found that mean litter size in Finnish common shrews was greater than that in central Europe. Dokuchaev (1989) reported litter size data for *S. caecutiens* from two areas in Siberia. In Omolon (66°N), litters averaged 8.6, whereas the mean was 7.5 in Chelomdzha (60°N). Hanski (1989), when comparing litter sizes in Eurasian *S. caecutiens*, demonstrated a clear trend of increasing number of embryos with increasing latitude.

In many birds and small mammals a positive correlation between the number of offspring and latitude has been observed (e.g., Lack, 1947, 1948; Cody, 1966; Owen, 1979). Of small mammals living in our study areas, this correlation has been documented in the voles *Microtus oeconomus* (Tast, 1966, 1982) and *M. agrestis* (Kalela, 1957; Tast, 1980). However, our shrews differed from the general view of small mammals, as there were no mass differences between shrews from different areas. Among small mammals (<500 g), litter size increases with body mass (Tuomi, 1980). This also explains latitudinal trends in litter sizes of *M. agrestis* and *M. oeconomus* (Kalela, 1957; Tast, 1966, 1980).

Number of Litters

Figure 4 gives the proportions of pregnant and lactating female common shrews in the three study areas. At Kilpisjärvi (Fig. 4a) two peaks are seen both for pregnant and lactating shrews indicating that overwintered females produce two litters. In data from Loppi (Fig. 4c) three distinct peaks show that three litters are commonly produced in southern Finland. Some females apparently give birth to four litters. At Sotkamo in central Finland two litters appears to be the norm (Fig. 4b). Differences in the numbers of litters between northern and southern Finland are a result at least partially of the fact that overwintered shrews survive longer in southern Finland (Fig. 2) with a difference of about two months in the disappearance of cohorts between Kilpisjärvi and Loppi.

In all three study areas the interval between successive peaks between both pregnant and lactating females was distinctly longer than expected based on the known length of the gestation period. This suggests that postpartum estrus does not occur commonly. Our observations support the results of Vogel (1972) that the gestation period is prolonged when the female is nursing her previous litter.

Young female common shrews attaining sexual maturity in the summer of their birth year usually produced only one litter. Parturition occurred almost exclusively in August. In all of our samples, only one female gave birth to two litters in the summer of her birth.

The intensity of reproduction in shrews in our study areas was less than that in small rodents. Voles and lemmings typically give birth to several litters in succession with intervals of three weeks (the length of their gestation period) suggesting postpartum estrus. During most years, all young-of-the-year attain sexual maturity in early summer and reproduce (Kalela, 1957, 1962; Kalela et al., 1961, 1971*a*; Tast, 1966, 1991; Henttonen et al., 1977). This may explain why population fluctuations of small rodents typically are distinctly more pronounced than among shrews.

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Table 1.—*Seasonal variation in the proportion (%) of different cohorts of overwintered male common shrews.*

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
						Loppi						
Immature	100	96	24									
Premature		4	48									
Mature			28	100	100	100	100	100	97	53		
Postbreeding									3	47	100	100
n	20	28	29	43	51	51	43	55	36	15	4	3
						Sotkamo						
Immature	100	100	58									
Premature			42	8								
Mature				92	100	100	100	100	95	62		
Postbreeding										5	38	
n	17	13	12	12	42	37	13	19	22	8	0	0
						Kilpisjärvi						
Immature	100	94	78	5								
Premature			22									
Mature		6		95	100	100	100	100				
Postbreeding									100			
n	38	18	27	19	31	27	52	10	12	0	0	0

Table 2.—*Seasonal variation in the proportion (%) of different cohorts of overwintered female common shrews.*

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
						Loppi						
Immature	100	100	90	5								
Premature			10	54	5							
Mature				41	95	100	100	80	49	18	9	
Postbreeding								20	51	82	91	100
n	25	28	30	22	59	62	39	70	45	22	11	3
						Sotkamo						
Immature	100	100	100	14	3							
Premature				86	10							
Mature					87	100	100	85	31	13		
Postbreeding								15	69	87	100	
n	12	14	7	7	31	34	21	27	26	8	1	0
						Kilpisjärvi						
Immature	100	100	100	67								
Premature				33	91	2						
Mature							9	98	97	69	12	
Postbreeding									3	31	88	
n	35	27	26	42	35	66	40	55	17	0	0	0

Table 3.—*Distribution of young common and masked shrews in three study areas according to their sexual state in the summer of birth.*

		Common Shrews				Masked Shrews			
		Males		Females		Males		Females	
Site	Latitude	Mature	Immature	Mature	Immature	Mature	Immature	Mature	Immature
Loppi	61°N	1	316	1	497	0	20	1	22
Sotkamo	64°N	0	210	0	144	0	32	0	39
Kilpisjärvi	69°N	2	555	78	437	0	64	9	46

Table 4.—*Comparisons between spring population density and proportion of young female common shrews attaining sexual maturity in the year of birth at Kilpisjärvi. Only years with 20 or more juvenile females captured are included. In addition, three other years with mature juvenile females obtained are presented. Population densities and changes are according to Kaikusalo and Hanski (1985) and Henttonen et al. (1989).*

Year	% Sexually Active Juvenile Females	Population Density	Change from Spring to Autumn	*n*
1964	4.5	moderate	no change	44
1966	21.7	low	increase	23
1967	10.0	moderate	decrease	20
1968	30.8	low	increase	185
1969	15.6	high	no change	45
1973	22.2	high	increase	9
1974	50.0	high	decrease	2
1980	0.0	low	increase	50
1981	1.8	high	increase	55
1985	0.0	moderate	increase	23
1987	100.0	moderate	no change	1

Table 5.—*Litter size of* S. araneus *and* S. caecutiens *in three study areas. Young shrews produced litters in the year of birth only at Kilpisjärvi. All other figures pertain to litters of overwintered females.*

	Sorex araneus			*Sorex caecutiens*		
	n	Mean	Range	*n*	Mean	Range
Loppi	123	6.6 ± 0.14	4–11	8	7.4 ± 0.56	5–10
Sotkano	43	7.9 ± 0.20	6–11	19	7.4 ± 0.34	4–10
Kilpisjärvi						
old females	69	8.7 ± 0.25	3–13	26	8.9 ± 0.38	3–12
young females	15	7.4 ± 0.27	6–9	5	6.2 ± 0.66	4–8

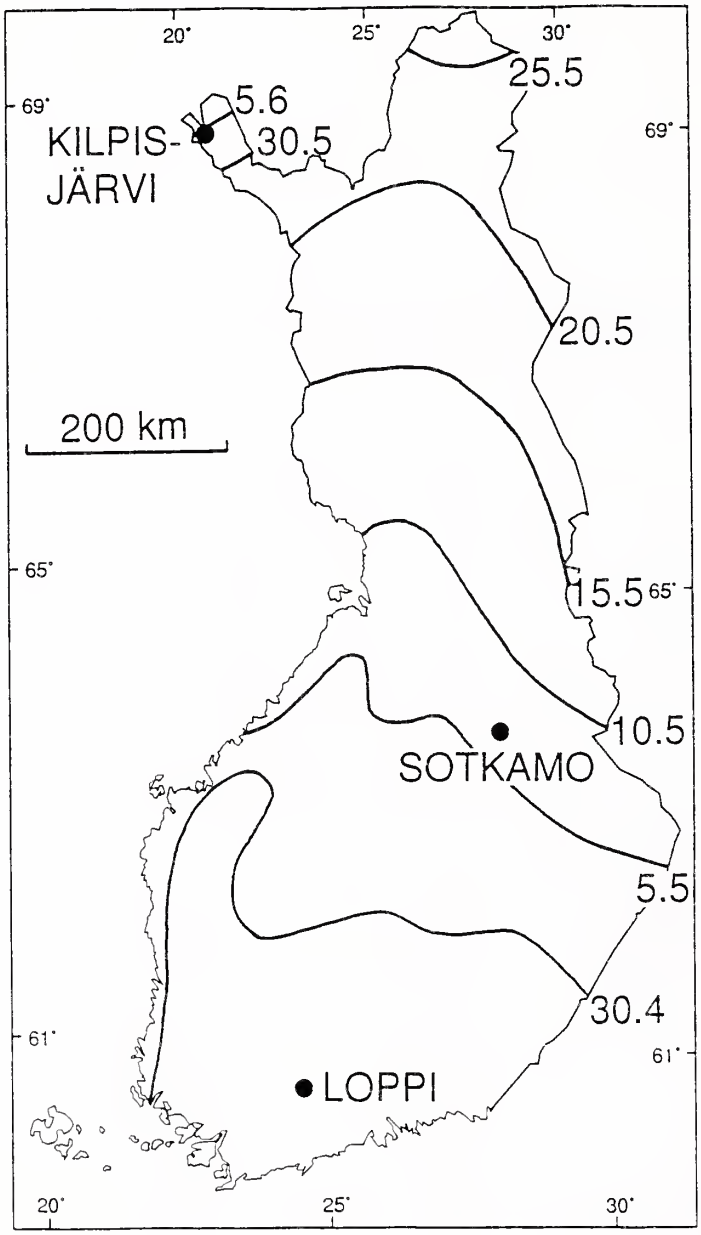


Fig. 1.—The locations of study areas and the average dates when mean temperatures reach +5°C in spring in different parts of Finland (Kolkki, 1966).

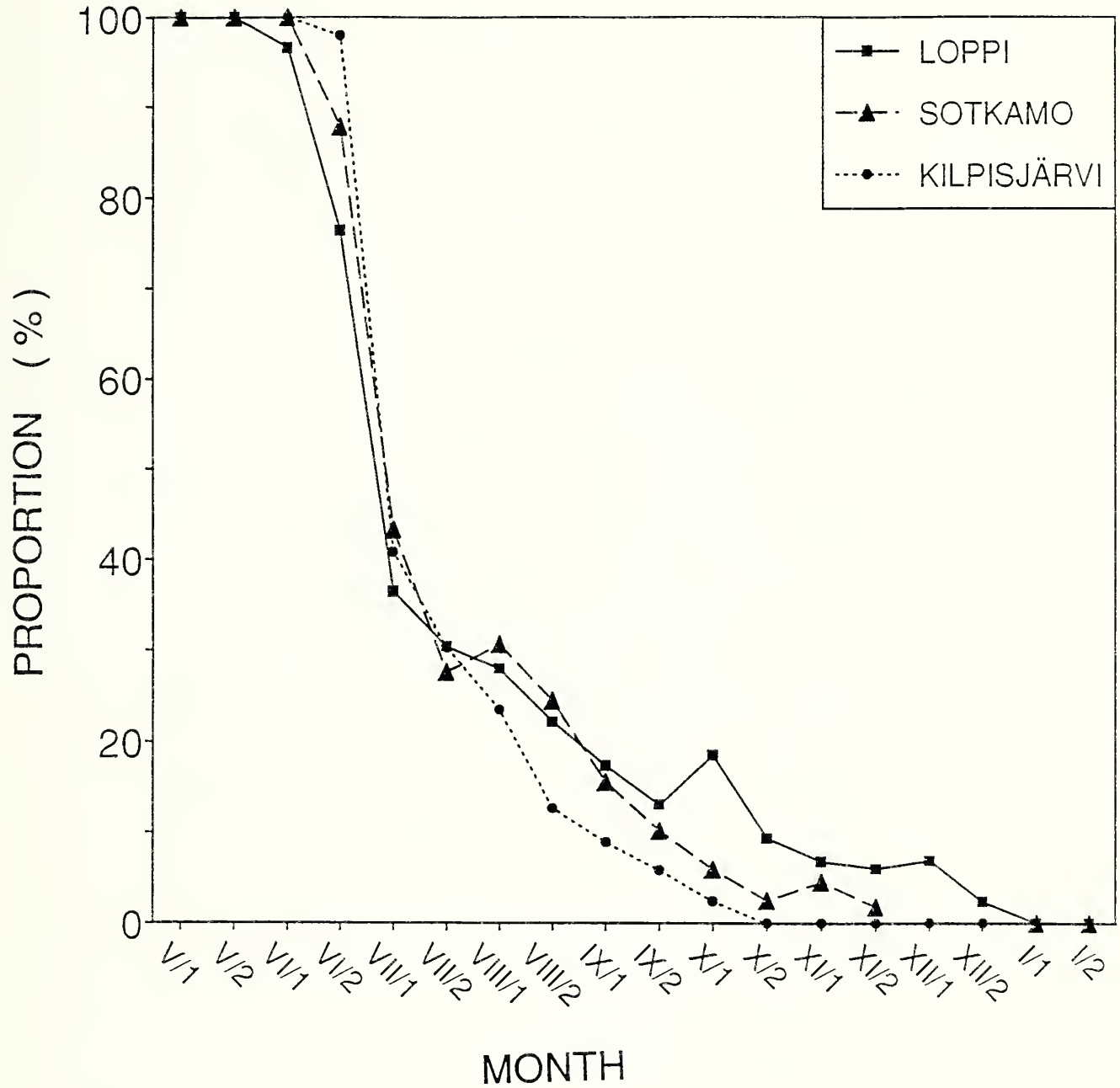


Fig. 2.—The proportion of overwintered common shrews as a percentage of total samples in three study areas in biweekly periods. All shrews in all areas were those overwintered before June.

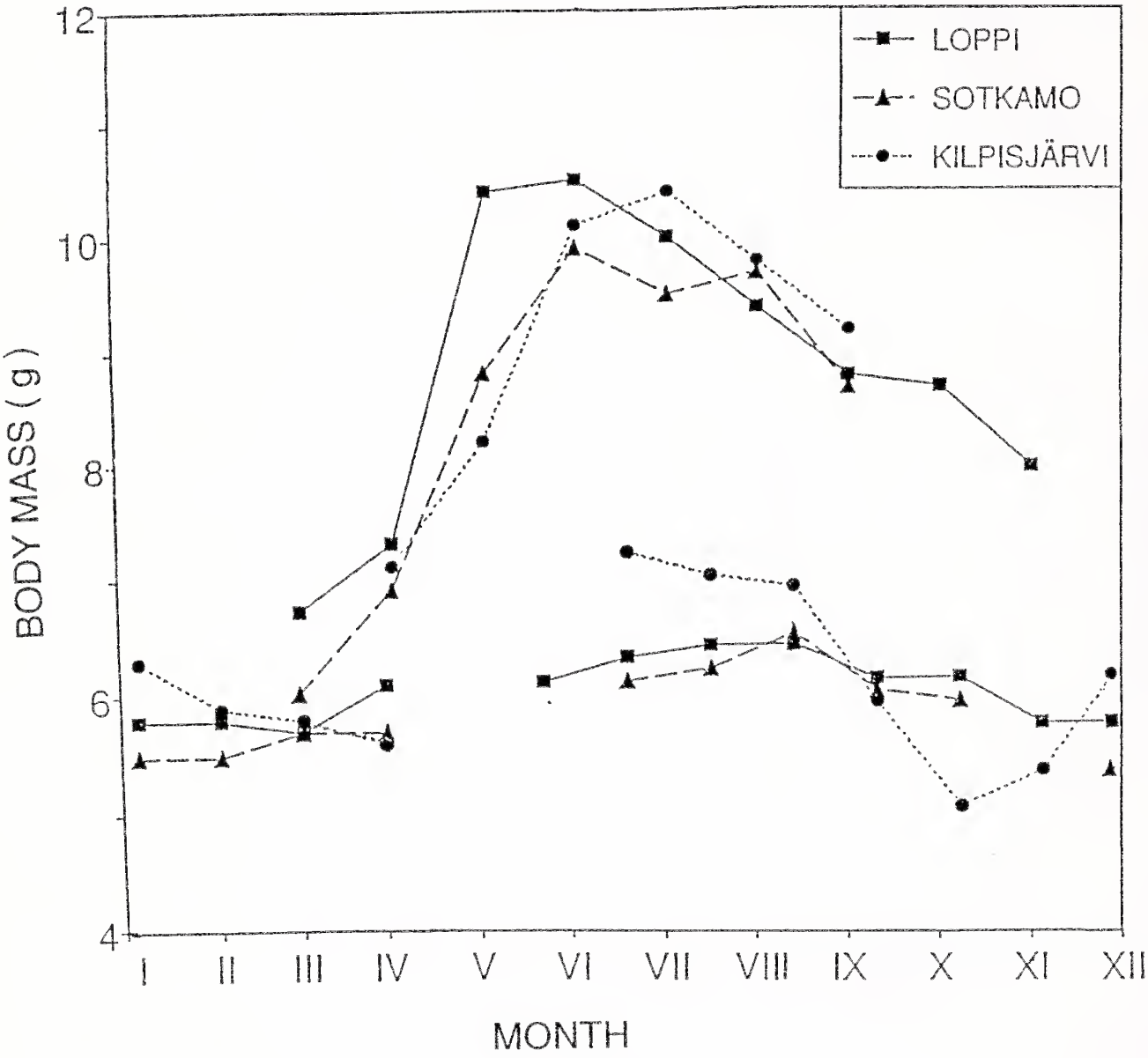


Fig. 3.—Seasonal variation in body mass of mature (upper curves) and immature (lower curves) common shrews in three study areas.

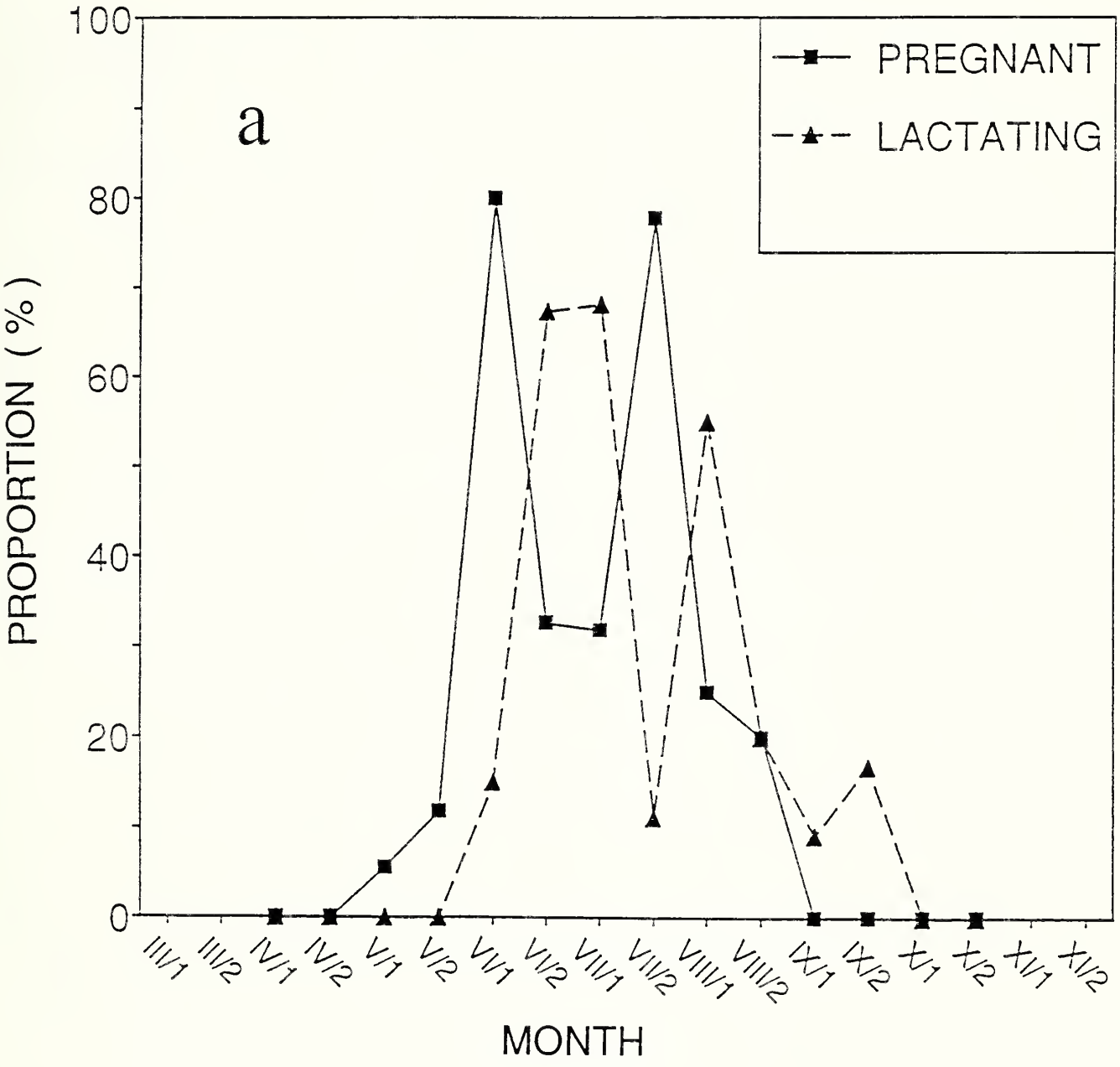
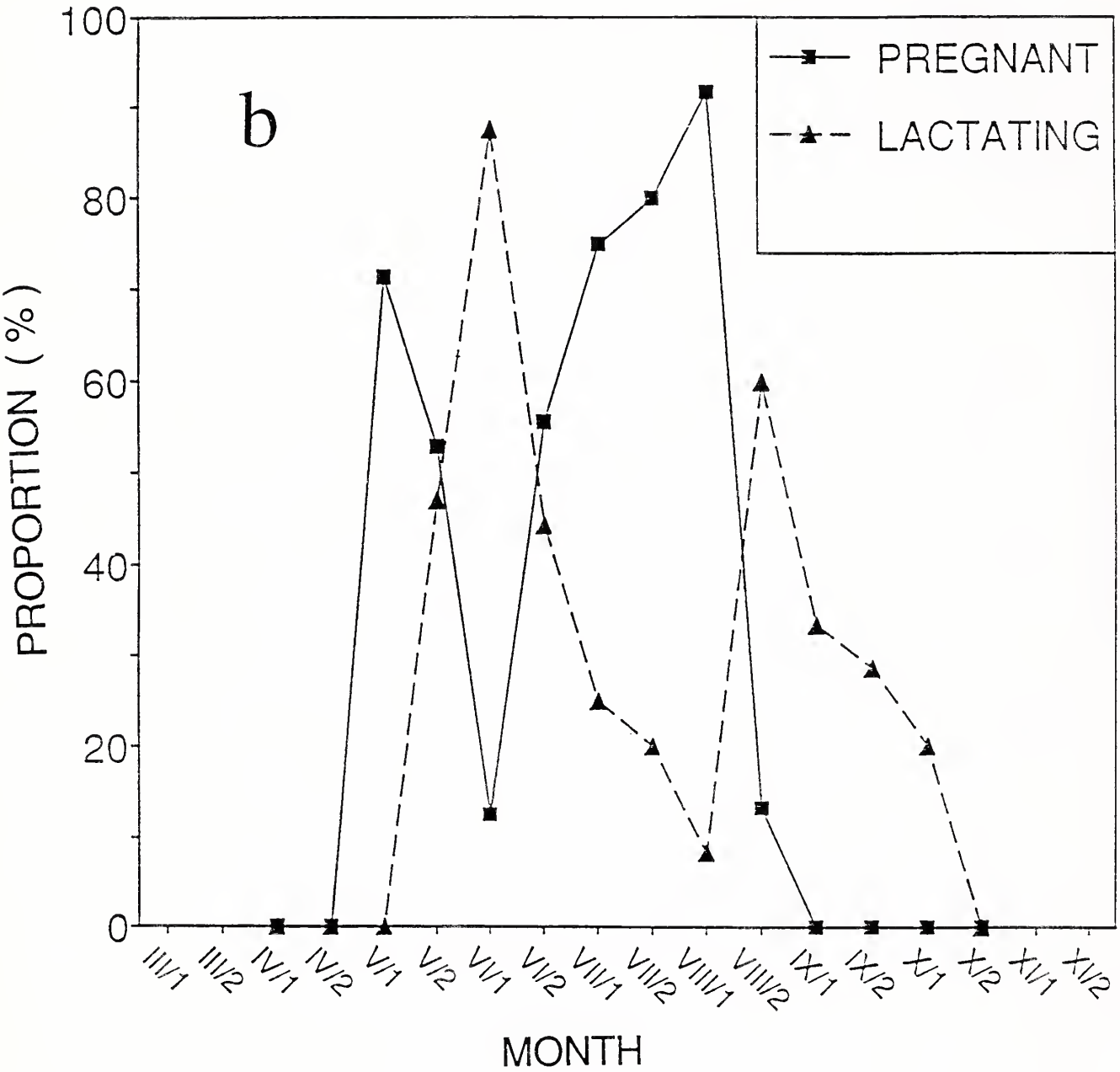
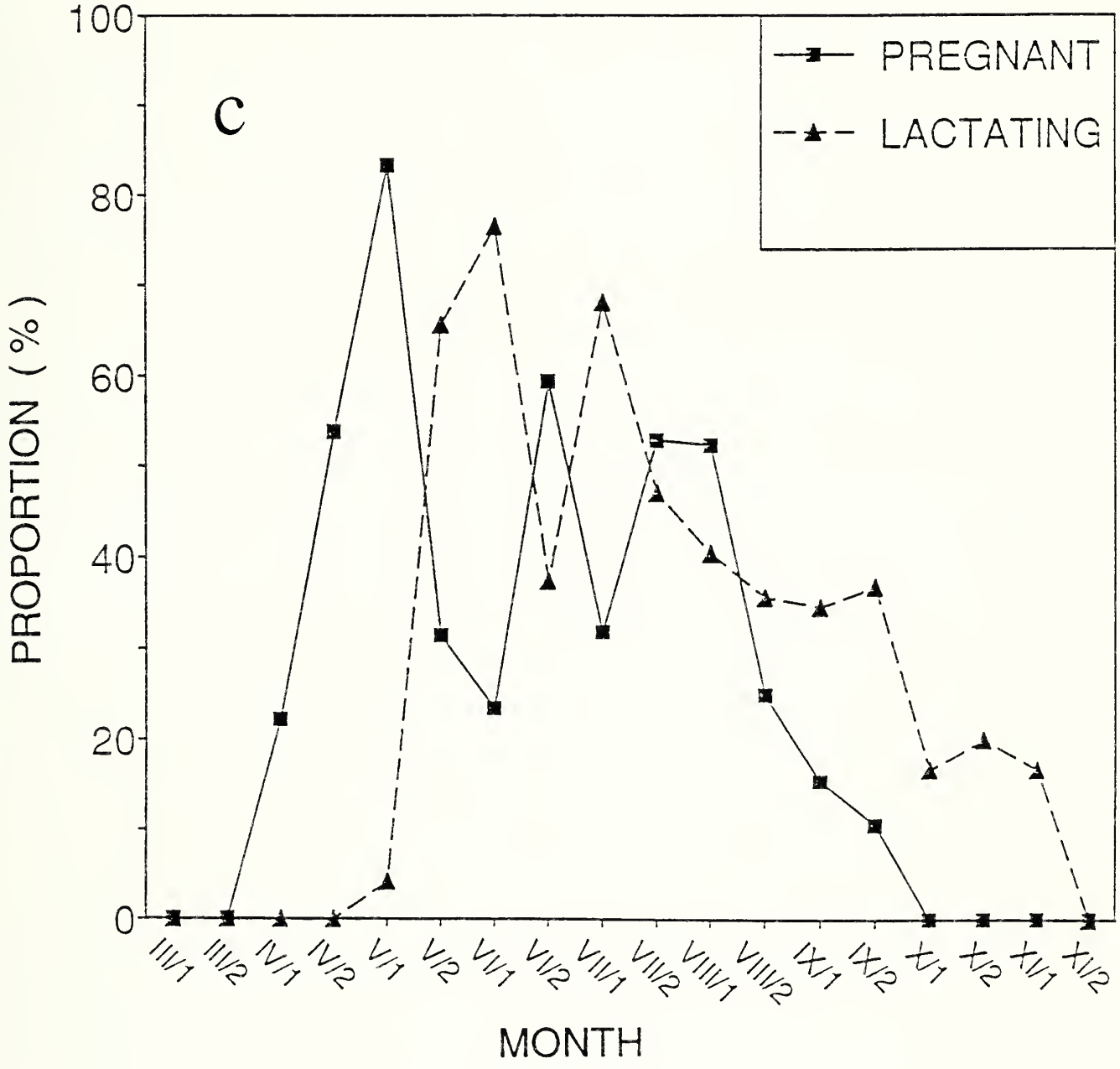


Fig. 4.—The proportion of pregnant and lactating common shrew females in the overwintered cohort during different times of the breeding season. a, Kilpisjärvi; b, Sotkamo; c, Loppi.


b
PREGNANT
LACTATING
PROPORTION (%)
100
80
60
40
20
0
III/1
III/2
IV/1
IV/2
V/1
V/2
VI/1
VI/2
VII/1
VII/2
VIII/1
VIII/2
IX/1
IX/2
X/1
X/2
XI/1
XI/2
MONTH


C
PREGNANT
LACTATING
PROPORTION (%)
100
80
60
40
20
0
III/1
III/2
IV/1
IV/2
V/1
V/2
VI/1
VI/2
VII/1
VII/2
VIII/1
VIII/2
IX/1
IX/2
X/1
X/2
XI/1
XI/2
MONTH

POPULATION BIOLOGICAL CONSEQUENCES OF BODY SIZE IN *SOREX*

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ABSTRACT

All *Sorex* species have high metabolic rates and high food requirements, but there is substantial size-dependent variation among species. Large species, with body weight around 10 g, have roughly twice the food requirements of small species (<5 g), whereas the latter have smaller body energy reserves and higher mass-specific metabolic rates. Consequently, small species starve in a shorter period of time than large ones. The consequenees of these differences as they relate to behavioral, population, and eommunity ecology, and biogeography of shrews are reviewed. In a mosaic of habitat patches varying in productivity, large species are typically confined to more productive patches, apparently because of their relatively high food requirements. Small species with smaller food requirements may survive and reproduce in less productive patches. Populations of small species have higher extinction rates than populations of large species because of the greater sensitivity of small species to environmental stochasticity. *Sorex minutus*, a small species, has significantly higher colonization ability than the larger species *S. caecutiens* and *S. araneus*. Small species have relatively unstable local populations which shift in space, whereas larger species have more stable local populations.

INTRODUCTION

The *Sorex* species which inhabit the forests of northern temperate regions comprise a well-defined guild of small insectivorous mammals with similar body form but much variation in body size. The species range from the smallest extant mammals, *Sorex minutissimus* and *Sorex hoyi*, which weigh 2 to 3 g, to species such as *S. isodon* and *S. palustris*, which weigh 10 g or more. The questions posed in this paper are: What are the population biological consequences of body size in *Sorex* shrews, and to what extent are ecological differences among the species correlated with differences in body size? As body size profoundly affects almost all aspects of animal life (Peters, 1983; Schmidt-Nielsen, 1984), differences in body size of shrews comprise a useful "null hypothesis" of observed differences in their population biology. Differences in body size themselves may be explained by diverse biological factors; however, if a population variable is clearly size-dependent, this provides a useful starting point for further studies.

Body-size differences among syntopic species have received much attention as a possible mechanism facilitating the coexistence of competitors (MacArthur, 1972; Diamond, 1975), and in life-history studies of mammals (Eisenberg, 1981; Harvey and Read, 1988; Harvey and Pagel, 1989). In contrast, comparative studies focusing on body-size differences are much fewer in behavioral ecology and population dynamics.

"Large" and "small" species of shrews are frequently compared in this paper. Large species are defined as those with adult weight of 10 g or more, whereas small species are those that weigh less than 5 g. The distinction is arbitrary. Continental shrew assemblages include species which are evenly distributed between 2 and 12 g. "Small" and "large" species are defined for two reasons. First, in a behavioral experiment (Hanski, 1985, and below), "small" and "large" shrews showed opposite responses to a change in environmental conditions, suggesting that species at the ends of the body size continuum also diverge in some aspects of behavior and population biology. The second reason is pragmatic; the two most abundant shrews in northern Europe, those for which much information is available, represent a large species (*Sorex araneus*, adult mass ca 9 g) and a small species (*S. minutus*, adult mass ca 3 g).

This paper concerns primarily two variables correlated with body size: mass-specific metabolic rate, which decreases with increasing size, and per capita food requirement, which increases with body size. The very small size of *Sorex* species and their exceptionally high mass-specific metabolic rates (Vogel, 1980; Hanski, 1984) suggest that all traits and variables related to feeding and assimilation of food are critical to survival. Therefore, first the size dependency of metabolic rate and per capita food requirement in shrews is quantified. Then the consequences of body-size differences to behavioral ecology, population dynamics, and community structure and biogeography are reviewed. The emphasis will be on population dynamics.

METABOLIC CONSEQUENCES OF BODY SIZE IN SHREWS

Table 1 gives results on body mass, metabolic rates, food requirements, and calculated starvation times for five European species of *Sorex*. The per capita food requirement of the smallest species is about half that of the largest species, whereas the calculated starvation time of the largest species is about twice as long as that of the smallest species, reflecting a parallel difference in mass-specific metabolic rates of these species (Table 1). The measurements in Table 1 were made at 23°C; at lower temperatures, differences among the species are probably amplified.

Because the calculations in Table 1 make no allowance for possible differences in foraging efficiencies of different-sized species, information on the killing and handling times of small and large prey items (beetles) by different species of shrews (Fig. 1) is included. The profitabilities of the two kinds of prey

are expressed as the percentage of 24 h that the shrew must spend to kill, handle, and ingest enough prey items to survive. The results point to three main conclusions (Fig. 1). First, the time required for killing, handling, and ingesting prey, but excluding search time, which is difficult to quantify under natural conditions, is a substantial fraction of the 24 h (about half of which shrews typically spend sleeping; Saarikko and Hanski, 1990). These results are valid only for the kinds of prey items used in the experiment, and shrews may occasionally "save time" by locating and overwhelming larger prey items. Second, if relatively large prey items are available, larger species need to spend less time than smaller ones in foraging to satisfy daily energy requirements, but if small prey items dominate, the situation is reversed. And third, small species do about equally well on small and large prey items, but large shrews do much better if they are able to use large prey items (Fig. 1).

Behavioral Responses to Variation in Food Availability

The results presented in Table 1 and Fig. 1 suggest that shrews may often be hard-pressed to satisfy daily energy requirements. *Sorex* species have a short cycle of only 2–3 hours of alternating sleep and foraging (Saarikko and Hanski, 1990); however, if food availability decreases, they typically respond by increasing the length of the foraging period (J. Saarikko and I. Hanski, personal observation). Another characteristic of *Sorex* activity is short rest periods, which interrupt active foraging and typically last 5–10 min (in *Sorex araneus*). Saarikko and Hanski (1990) present evidence that shrews enter a short rest period when their digestive tract is full, and they would probably not be able to consume and digest more food economically. Similar observations have been made for hummingbirds, among which are the smallest species of birds (Diamond et al., 1986; Karasov et al., 1986). The digestive tract of shrews probably works at a high rate most or all of the time (Saarikko and Hanski, 1990).

Variation in the digestive physiology of shrews, especially differences between small and large species, may be critical. If metabolic requirements, which increase with increasing body size, increase at a slower rate than the cross-sectional area of the gut (Saarikko and Hanski, 1990), small species in particular may live close to a limit set by digestive physiology. Hanski (1984) found that assimilation efficiency increased with decreasing body size down to middle-sized species, but decreased in the smallest species (*S. minutissimus*). Buckner (1964) obtained similar results for another small species, *S. hoyi*. Hanski (1984) suggested that the smallest species maximize energy acquisition by high throughput rate of foodstuffs at the cost of decreased assimilation efficiency. These speculations should be tested with physiological studies.

Size-dependent differences in starvation times (Table 1) are expected to have consequences in the response of shrews to temporal changes in food availability. Hanski (1985) modelled the expected responses of small and large shrews to short-term, unpredictable food shortages ("energy crises"), assuming that at the start of a food shortage a shrew must decide whether to continue foraging or to rest until the food shortage is over (or the shrew is dead). Hanski (1985) concluded that to maximize chances of survival, a shrew should rest if

$$1 - (1-p)^T > p/[p+(1-p)q],$$

where T is the starvation time in hours, p is the probability that food availability will return to a high level in the next hour, and q is the probability that a foraging shrew will die in the next hour when food availability is low. The left side of this inequality gives the probability of surviving the period of food shortage if the shrew rests, and the right side gives the corresponding probability if the shrew continues to forage. This model makes two testable predictions: 1) because T increases with body size (Table 1), larger species are more likely than small ones to decrease activity during periods of low food availability; and 2) the shorter the average length of food shortage (larger p), the more likely the response will be decreased activity. In an experiment comparing small and large species under the same conditions, it was found that, as predicted, small shrews increased activity while large species decreased activity in response to short-term food shortages (Fig. 2). The average duration of food shortages had also the predicted effect on activity of *S. araneus*. Foraging bouts were longer when food availability was constantly rather than temporarily low (Hanski, 1992; J. Saarikko and I. Hanski, personal observation).

One option not considered in the above model, but which is available to shrews in nature, is food caching. Both short-term (Crowcroft, 1957; Goulden and Meester, 1978) and long-term (seasonal) caching (Platt, 1976; Martin, 1984) have been observed in shrews. Short-term caching is especially common in small species of shrews (Hanski, 1989*a*). Food caching may replace the function of body energy reserves in small species, and bridge short-term gaps in food availability. Food caching may also decrease the frequency of interaction of small species with larger and competitively superior species. Comparative studies of food caching in small and large species are needed.

Population Dynamics and Body Size

Comparative studies of colonization and extinction dynamics of three species (*S. araneus*, *S. caecutiens* and *S. minutus*) have been conducted on small islands in lakes in eastern Finland since 1982 (Hanski, 1986; Hanski and Kuitunen, 1986; Hanski and Peltonen, 1988; Peltonen and Hanski, 1991). The islands vary in size from less than 1 ha to hundreds of hectares. Populations of shrews occupying smaller islands have substantial risk of extinction (Peltonen and Hanski, 1991). However, extinctions are compensated for by the establishment of new populations, and species occur on the islands in a dynamic equilibrium between extinction and colonization (Hanski, 1986).

These field studies provide quantitative data on dispersal, colonization, and extinction rates in the three species (Table 2). Dispersal rate is measured as the fraction of individuals in the mainland population which disperse to islands. Colonization and extinction rates refer to the fractions of previously empty and occupied islands which became occupied and empty,

respectively, during one year. The term colonization ability refers to the capacity of an individual or a group of individuals to establish a new local population on an empty island, conditional on arrival at the island.

Dispersal

Larger species show a somewhat higher rate of dispersal to islands (Hanski and Peltonen, 1988) than smaller species, as expected from their longer starvation times (Table 1) and faster swimming rates (Skarén, 1980; Hanski, 1986), but the difference is not significant (Table 2). Unfortunately, results on dispersal rates confound the dispersal ability of a species with the inclination to start overwater dispersal in the first place. Michielsen (1966) found in a comparative study that *S. minutus* had greater dispersal tendency than *S. araneus*, which may have compensated (in our study) for its lower overwater dispersal ability. Studies have revealed that *S. araneus* generally avoids entering water (Hanski and Peltonen, 1988). In many, but not all years, dispersers are smaller and probably socially subordinate individuals, which are apparently forced out of the mainland population by stronger conspecifics (Hanski et al., 1991).

Colonization

There were no interspecific differences in colonization rates, which are determined by dispersal rate and colonization ability (Table 2). *Sorex minutus* may have a somewhat lower dispersal rate than the two larger species, but unexpectedly the results indicate that it has a significantly higher colonization ability than the other species (Table 2). Why should small shrews make good colonizers? These results should be confirmed with studies on other populations and other species. Three observations could be tested or could lead to testable predictions. First, during the five years of our study, we observed only one pregnant shrew dispersing to an island. This shrew was *S. minutus* (Hanski, 1986). Pregnant females are potentially good colonizers, as there is then no need to find a mate before founding a colony. Second, the low per capita food requirements of *S. minutus* (Table 1) and other small species may improve their colonization ability by enhancing survival of newly-dispersed individuals on islands (the same applies to dispersers crossing unfamiliar terrain on land). This could be tested by determining survival rates of shrews experimentally introduced on islands. Third, Michielsen (1966) found in a population ecology study of *S. araneus* and *S. minutus* that the latter species, in spite of smaller size, had a substantially larger home range. This was unexpected, because generally home range size is positively correlated with body size (McNab, 1963). Michielsen (1966) suggested that differences in the diets of the two species might explain these anomalous results. An alternative explanation is that smaller species are generally less territorial and have less well-defined home ranges than large species. Territoriality may be less profitable for small than large species because the food resources of the former are scattered and hence less defendable (Davies and Houston, 1984). Hawes (1977) also reported extensive movements in two small *Sorex* species in British Columbia. Weak and poorly defined home ranges should increase the probability of individuals wandering to new areas.

Extinction

Extinction rate in the three species increases with decreasing body size, and the interspecific differences are highly significant (Table 2). Such a relationship between body size and extinction rate was expected because of the shorter starvation times of the smaller species (Table 1), which make them more susceptible than large species to temporal variation in food availability. Furthermore, an analysis of species' incidence functions, which describe the pattern of occurrence on islands of different size, strongly suggested that extinction rates decrease much faster with increasing island area (and hence with increasing population size) in large species than in small species (Fig. 3; Hanski, 1991). This result also indicates a greater role of environmental stochasticity in small species than in large species (Hanski, 1991). Michielsen's (1966) observation that the average rate of mortality is higher in *S. minutus* than in *S. araneus* is consistent with this conclusion.

To summarize, the smallest species (*S. minutus*) had the highest rate of extinction but also the best colonization ability and probably a high dispersal tendency. The extinction proneness of the small species is probably due to short starvation time and hence great sensitivity to temporal changes in food availability, whereas its good colonization ability may be due to small per capita food requirements and possibly to dispersal of pregnant females. Colonization ability is associated with high extinction rates of local populations in this species because high extinction rates select for increased colonization rates (Brown, 1951; Southwood, 1962). Only highly dispersive species may survive regionally if local populations frequently go extinct (Hanski, 1992).

COMMUNITY STRUCTURE

Size Distributions in Coexisting Species

Assemblages of coexisting shrews show good separation in body size. Principal component analyses of measurements of the skull and postcranial skeleton in a five-species assemblage from Finland and a four-species assemblage from Alberta, Canada, are given in Fig. 4. In both assemblages, there is little overlap in size (PC I in Fig. 4), and adjacent species in a size ranking show almost equal size ratios, or "community-wide character displacement" (Strong et al., 1979). Such body-size differences reduce interspecific competition. Experiments have demonstrated interspecific competition between species with similar body sizes (Hawes, 1977; Neet and Hausser, 1990), but not between species with different body sizes (Ellenbroek, personal communication). The distribution of body sizes in coexisting shrews is comparable to patterns found in granivorous, desert-dwelling rodents (Bowers and Brown, 1982; Hopf and Brown, 1986; Brown, 1987) and mustelids (Dayan et al., 1989). Nonetheless, exactly how body-size differences facilitate coexistence in shrews is not entirely understood (Hanski and Kaikusalo, 1989; Hanski, 1992).

In the skull measurements, there are pairs of

morphologically similar species, such as *isodon–arcticus*, *caecutiens–monticolus*, and *minutus–cinereus* (Fig. 4). The North American species deviate in skull shape from the Eurasian species, as indicated by the position of the species along PC II (Fig. 4). Such differences may reflect phylogenetic divergence, as most of the species on the two continents belong to different subgenera (George, 1988). The even spacing of species differing in size, which is evident in the assemblages of extant shrews (Fig. 4), may also have been a common feature of shrew assemblages in the past. A well-studied late Pliocene assemblage from Poland has five species, *Sorex minutus*, *S. bor* (an extinct species), and three other extinct *Sorex* species (Rzebik-Kowalska, 1994). *Sorex bor* was a small species, intermediate in size between *S. minutus* and *S. caecutiens*. The three remaining species included a species comparable in size to *S. araneus*, and two larger species, roughly the size of *S. mirabilis* (B. Rzebik-Kowalska, personal communication).

Habitat Selection

Large species of shrews have greater per capita food requirements than small species (Table 1). Assuming that the larger species are not more efficient in foraging than the smaller species (Fig. 1), there must be habitats in which food availability is so low that large shrews cannot survive and reproduce but small species can. Therefore, the numerical dominance of large shrews should increase with increasing habitat productivity. Habitat selection of small, medium, and large species of shrews in an extensive set of data from Eurasia is summarized in Fig. 5. These results support the idea that small species dominate in the least productive habitats, whereas large species dominate in the most productive habitats. The absolute density of small species varied little among habitat types (B. Sheftel and I. Hanski, personal observation), which has two possible explanations. Either the more productive habitats are not intrinsically better for small species than the less productive habitats, or small species are competitively excluded or suppressed in numbers by larger species in the more productive habitat types. This question cannot be settled without experiments. However, previous studies have demonstrated that interspecific competition is common in shrews (Michielsen, 1966; Hawes, 1977; Malmquist, 1985; Neet and Hausser, 1990). Many large species of shrews prefer to feed on earthworms if available (Rudge, 1968; Okhotina, 1974; Pernetta, 1976). Earthworms often have a much higher biomass than all other prey types combined (Terhivuo, 1988), but they are typically either very scarce or entirely absent from more barren habitat types, making the existence of large shrew species in these habitats more difficult.

Biogeography and Body Size

The assemblages of *Sorex* inhabiting coniferous forests in north-temperate Eurasia and North America show one major difference: the dominant species in Eurasia is large (*S. araneus*), whereas the dominant species in North America is small (*S. cinereus*, Fig. 4). The presence of *Blarina*, a very large shrew, in North America is not a likely explanation because *Blarina* occurs only in the southern part of the coniferous forest zone and is very different ecologically from *Sorex* (van Zyll de Jong, 1983, and references therein).

I have suggested that this difference may be a consequence of the generally greater productivity of coniferous forests in most of Eurasia compared to those of North America (Hanski, 1989*b*). Such a difference in productivity would favor larger species in Eurasia and smaller species in North America, in the same way as differences in productivity of habitat types favor small or large species (Fig. 5). Less productive forest types probably tend to have lower availability of large prey items than more productive forest types, which would also be a disadvantage to large shrews (Fig. 1). One particular consideration is the scarcity of earthworms in northern coniferous forests in most of North America, due to their almost complete disappearance during Pleistocene glaciations.

The above hypothesis is supported by the exceptions. In eastern Siberia, where the landscape is barren and dominated by larch forests away from river valleys, the dominant shrew is a middle-sized species (*S. caecutiens*), which is not very different in size from *S. cinereus* in North America (Fig. 4). On the other hand, in coniferous forest regions of eastern North America, including Nova Scotia and New Brunswick, where rainfall is high and forests presumably productive, the dominant species is *S. fumeus*, which is only slightly smaller than *S. araneus* (Kirkland and Schmidt, 1982).

Latitudinal changes in the size of shrews do not agree with Bergmann's rule. On the contrary, the size of species and the average size of shrews in local assemblages both tend to decrease with increasing latitude (Hanski, 1989*b*, has analyzed geographical changes in the size of *Sorex caecutiens* as an example). I suggest that the reason for the generally smaller size of shrews in the north is decreasing food availability with increasing latitude. Latitudinal changes in climate may be relatively unimportant for shrews because they spend the winter under snow cover, where temperatures are relatively constant regardless of surface ambient temperature.

Character Displacement?

Sorex araneus, the dominant species in Europe and western Siberia, is absent from eastern Siberia. In eastern Siberia, the dominant species is *S. caecutiens*, which is larger there than in Europe. However, another transcontinental species, *S. isodon*, is smaller in eastern Siberia than in Europe (Fig. 6). These changes in body size may be due to interspecific interactions, *S. isodon* and *S. caecutiens* possibly shifting toward the size of *S. araneus* in eastern Siberia in the absence of that species. That *S. isodon* and *S. caecutiens* change in size in opposite directions supports this interpretation. However, in view of the difficulties of demonstrating character displacement (e.g., Grant, 1975), the above example is cited not as conclusive proof but as a demonstration that shrews provide suitable material to study character displacement.

Discussion

I have attempted to show that comparisons between small

and large species of shrews can be rewarding in the study of behavioral ecology and population dynamics. In explaining behavioral and ecological differences among congeneric species, expectations based on body size differences comprise a useful "null hypothesis."

One field not covered here is the life histories of shrews, for which there are relatively few data. Available data suggest relatively little variation in life histories among species varying in body size. All *Sorex* species are basically "biennials," maturing in their second summer and almost never surviving a second winter. All shrews may have several litters per year, the number being limited by the length of the season. Variation in litter size appears not to be related to body size (e.g., Sheftel, 1989). Sheftel (1989) suggested, from extensive study of eight coexisting *Sorex* species in central Siberia, the hypothesis that competitively inferior species have a greater intrinsic rate of increase than competitively superior species, which facilitates the coexistence of these species. The main evidence was that species that attain high abundance early each season also peak earlier during the general four-year cycle of small mammals in central Siberia (Sheftel, 1989). This hypothesis is worth further study, although surprisingly the competitive ranking of species in Sheftel's hypothesis was not correlated with body size.

The main theme of this paper, which I advance as a working hypothesis, is that small shrews live a more precarious life than large ones. Table 3 summarizes the key elements of this hypothesis. At the individual level, a crucial difference is the shorter starvation times of small shrews, which is reflected in the individuals' behavioral responses to spatially and temporally varying food abundance. At the population level, smaller species are expected to show more temporal variation in population size and a higher rate of extinction of local populations. Hanski (1989*b*) demonstrated that temporal variation in population size was indeed greater in small (*S. minutus* and *S. caecutiens*) than in large (*S. araneus*) species. The results reviewed in this paper conclusively demonstrate the greater extinction-proneness of local populations of small species. Finally, at the metapopulation level (Gilpin and Hanski, 1991), the hypothesis predicts higher turnover in populations of small species, with populations of small species going extinct relatively frequently but new ones being established at a correspondingly high rate. There is direct evidence for the good colonization ability of *Sorex minutus*, a small species. In agreement with these results, it has been found that *S. minutus*, which is typically less abundant than *S. araneus* in most of Europe, is nonetheless more frequent on large islands in the Baltic and elsewhere in northwest Europe (Williamson, 1981; Malmquist, 1985; Peltonen et al., 1989).

The hypothesis of high turnover rate in small species of *Sorex* provides a fresh perspective to the population ecology puzzle of *Sorex minutissimus*, the smallest species of *Sorex* and one of the smallest extant mammals. *Sorex minutissimus* is widely distributed in the Palearctic region but is apparently very rare throughout its entire range. The rarity of *S. minutissimus* is unlikely to be a trapping artifact, because pitfall traps suitable for small *Sorex* are regularly used to catch shrews in Europe and Siberia. Applying the present hypothesis to *S. minutissimus*, I suggest that it occurs as small and very ephemeral local populations, continuously shifting from one place to another. If this is correct, *S. minutissimus* must have exceptionally high dispersal and colonization rates. Perhaps the same traits which make *S. minutus* a good colonizer are even more strongly expressed in and enhance the colonization rate of *S. minutissimus*. However, practically nothing is known about the population biology of this species.

The first extant species of *Sorex* to appear in the fossil record are *S. minutus* and *S. minutissimus* (B. Rzebik-Kowalska, personal communication), which are the two smallest species in Europe. The great evolutionary age of the smallest *Sorex* is in striking contrast with the hypothesized precarious life of individuals and populations. The solution to this apparent paradox may lie in the same factor that allows metapopulations to survive in spite of frequent local extinctions: high rates of dispersal and colonization. High dispersal rate has two consequences that tend to preserve the status quo of the species. First, other things being equal, the geographical range of the species increases with increasing dispersal rate. *Sorex minutus* and especially *S. minutissimus* have large geographical ranges. The probability of extinction of a species is expected to decrease with increasing size of its geographical range for two reasons: the total number of individuals, and the diversity of environmental conditions under which these individuals live, increase with increasing geographical range. Second, a species with high dispersal rate is probably less likely to evolve than a species with restricted dispersal, because high dispersal rate increases gene flow between populations. In summary, high dispersal rate increases gene flow and thereby decreases speciation rate, and it increases the size of the geographical range of the species, which decreases the risk of extinction. I suggest that these factors help explain the relatively great age of the smallest species of *Sorex*.

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Table 1.—*Body mass, metabolic rate, food consumption, mass-specific food requirement, and starvation time in five species of European* Sorex. *Food consumption was measured in carbon. Measurements were made at 23°C. Starvation time is defined as the time during which a starving shrew is expected to lose 20% of its initial carbon content. The values given here are mean values (for sample sizes and other details, see Hanski, 1984).*

Species	Mass g	Metabolic Rate J/h	Food Requirement for 24 h Period		Starvation Time in Hours
			mg C	% body mass	
S. minutissimus	2.5	778	410	94	5.1
S. minutus	2.7	813	420	89	5.4
S. caecutiens	4.9	1148	600	70	6.9
S. araneus	8.9	1626	850	55	8.8
S. isodon	11.1	1845	960	49	9.7

Table 2.—*Comparison between* Sorex araneus, S. caecutiens, *and* S. minutus *in dispersal rate, colonization ability, colonization rate, and extinction rate (from Peltonen and Hanski, 1991, and I. Hanski, personal observation). The figures are numbers of individuals (dispersal rate) or colonization/extinction events (the other three variables). The expected numbers are given in brackets. The test result is from* χ^2 *test or from Monte Carlo (MC) randomization test.* P *gives the significance level (NS stands for nonsignificant result at 5% level).*

Variable	*araneus*		*caecutiens*		*minutus*		Test	*P*
Dispersal rate[a]	41	(36.4)	13	(12.1)	4	(9.5)	3.83	NS
Colonization ability[b]	5	(7.4)	2	(3.5)	5	(1.1)	MC	0.004
Colonization rate[c]	5	(3.0)	2	(4.5)	5	(4.5)	2.78	NS
Extinction rate[d]	1	(5.6)	3	(1.8)	6	(2.6)	MC	0.004

[a]Expected values were calculated by multiplying the observed number of dispersers by the proportions of the species on the mainland (pooled data for five mainland study sites located around the lake).

[b]The success of individuals that have reached an empty island in establishing a new population (the expected figures were calculated from the products of the numbers of dispersers times the numbers of empty islands).

[c]The rate of establishment of new populations (the expected figures were calculated from the numbers of empty islands).

[d]The rate of disappearance of existing populations (the expected figures were calculated from the numbers of island populations). Data were available for five years, and the colonization and extinction events were scored from one year to another. Data on dispersal rate were obtained by trapping shrews on small islets without local populations. Dispersal may also occur in winter over ice, but we have no data on winter dispersal. For further explanation see Peltonen and Hanski (1991).

Table 3.—*The working hypothesis is that small species of* Sorex *have relatively unstable local populations but survive regionally as metapopulations. The arrow means "contributes to."*

Level of Organization	Traits and Variables
Stability of **local populations** is decreased by...	— Small body size → low interference competitive ability → **low density** in productive habitats where superior competitors abundant → **high risk of extinction** — Small body size and high metabolic rate → short starvation time → **high risk of extinction of local populations** due to environmental stochasticity
Stability of **metapopulations** is increased by...	— Small body size → small per capita food requirement → individuals may **establish local populations** also in unproductive habitat patches — Good colonization ability (reasons discussed in the text) → **high colonization rate**
Stability of **species** over evolutionary time is increased by...	— Unstable local dynamics → **low rate of speciation** — Stable metapopulation dynamics → **low rate of species extinction**

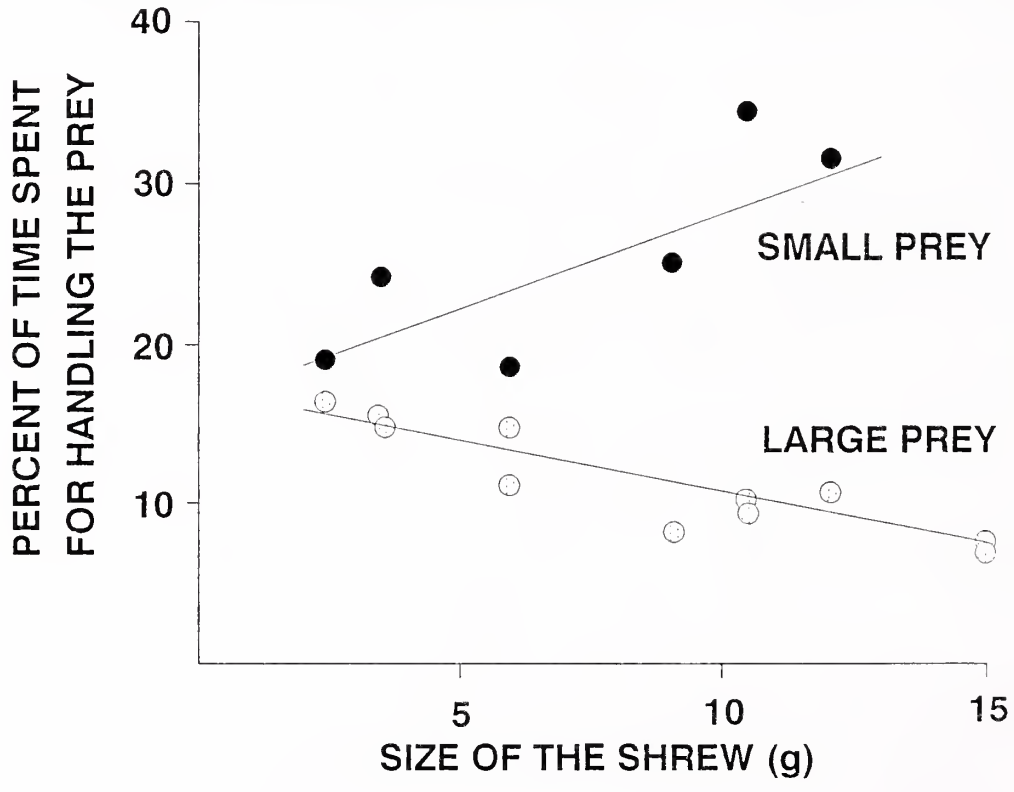

Fig. 1.—The percentage of 24 hours spent handling (including killing and ingesting) prey items to satisfy daily energy requirements in different-sized shrews (on the horizontal axis; the same species as in Table 1, all roughly equally represented). The small prey were *Cercyon* spp. (Coleoptera, fresh weight 1–2 mg), and the large prey were *Sphaeridium* spp. and *Aphodius fossor* (Coleoptera, fresh weight 15–35 mg). Each point gives the mean value for ten trials. The regression lines have significantly different slopes (small prey: $t = 2.69$, $P < 0.05$; large prey: $t = -6.10$, $P < 0.001$). Results from Hanski (1991*a*, personal observation).

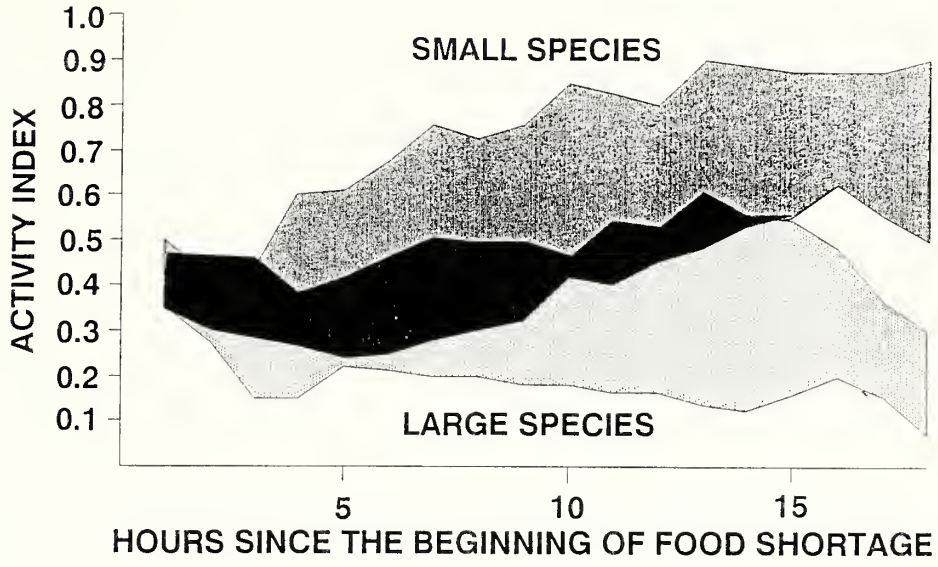

Fig. 2.—Activity of small (*S. minutus* and *S. caecutiens*; three individuals, seven experiments) and large shrews (*S. araneus* and *S. isodon*; five individuals, eight experiments) during an "energy crisis," a period of time during which an individual's energy budget was made experimentally negative by regulating the amount of food to a level 5% less than the requirement, both monitored continuously using an infrared gas analyzer and a computer-controlled feeder. Activity index measures the level of movement activity on an arbitrary scale but adjusted to 0.5 for each individual at the beginning of the experiment to eliminate individual differences. The shaded regions indicate the range of observations for small and large species. For further details see Hanski (1985).

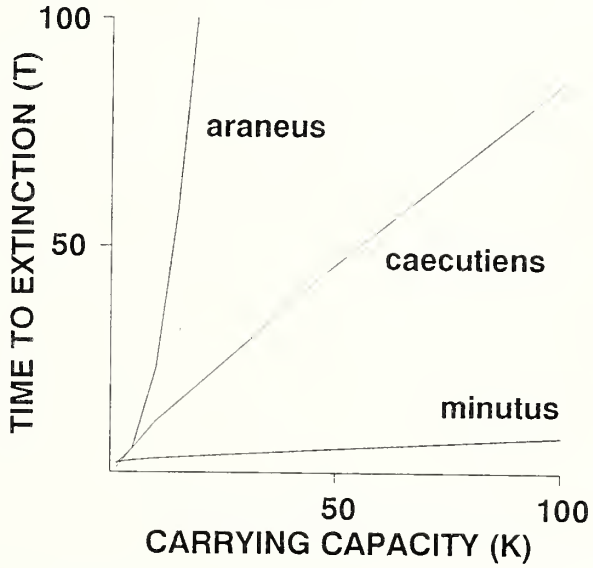

Fig. 3.—The relationship between mean time to extinction (T, in generations) and the environmental carrying capacity (K) in *S. araneus*, *S. caecutiens*, and *S. minutus*, based on an analysis of their incidence functions on islands in two lakes (Hanski, 1991). The carrying capacity is assumed to be proportional to island area, and it corresponds to the equilibrium population size which the species may attain on the island.

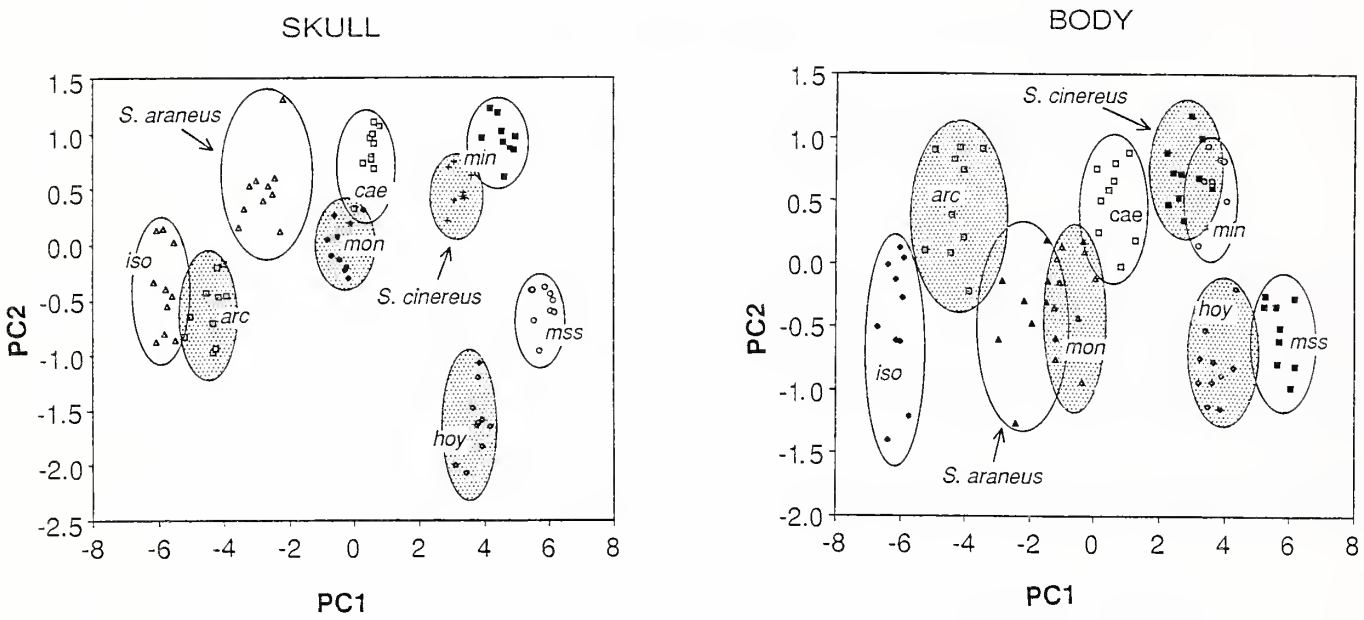

Fig. 4.—Principal component analysis of skull and postcranial skeletal measurements of *Sorex* species from comparable regions of coniferous forest in Finland and Alberta, western North America. The first principal component (horizontal axis) reflects the general size of the species. The Finnish species are (from the largest species on the left to the smallest species on the right) *S. isodon*, *S. araneus*, *S. caecutiens*, *S. minutus*, and *S. minutissimus*; the North American species are *S. arcticus*, *S. monticolus*, *S. cinereus*, and *S. hoyi* (H. Virtanen and I. Hanski, personal observation). The ellipses were drawn to enclose all conspecific individuals (ten young individuals per species). The species abbreviations consist of the first three letters of the species' name (excepting mss for *minutissimus*).

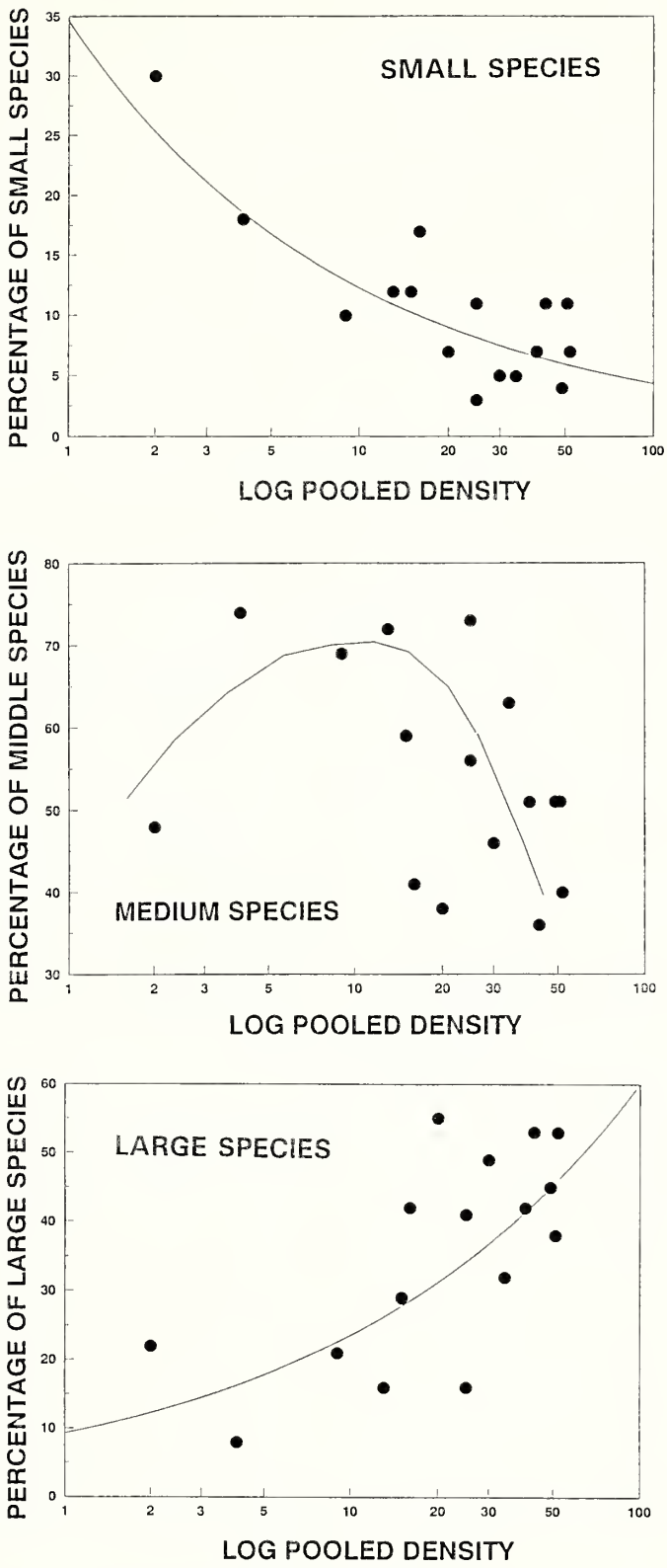

Fig. 5.—Percentages of small, medium, and large species of *Sorex* against the logarithm of their pooled density in 16 habitat types in Eurasia (the pooled density is used as a measure of habitat productivity). The data come from 38 boreal forest localities distributed throughout Russia. The material includes 11 species, which were divided among small (adult weight less than 4 g: *S. minutus*, *S. minutissimus*, *S. gracillimus*, and *S. cinereus*), medium (adult weight 5–6 g: *S. caecutiens*, *S. tundrensis*, and *S. daphaenodon*), and large species (adult weight more than 8 g: *S. araneus*, *S. isodon*, *S. roboratus*, and *S. unguiculatus*; from B. Sheftel and I. Hanski, in preparation).

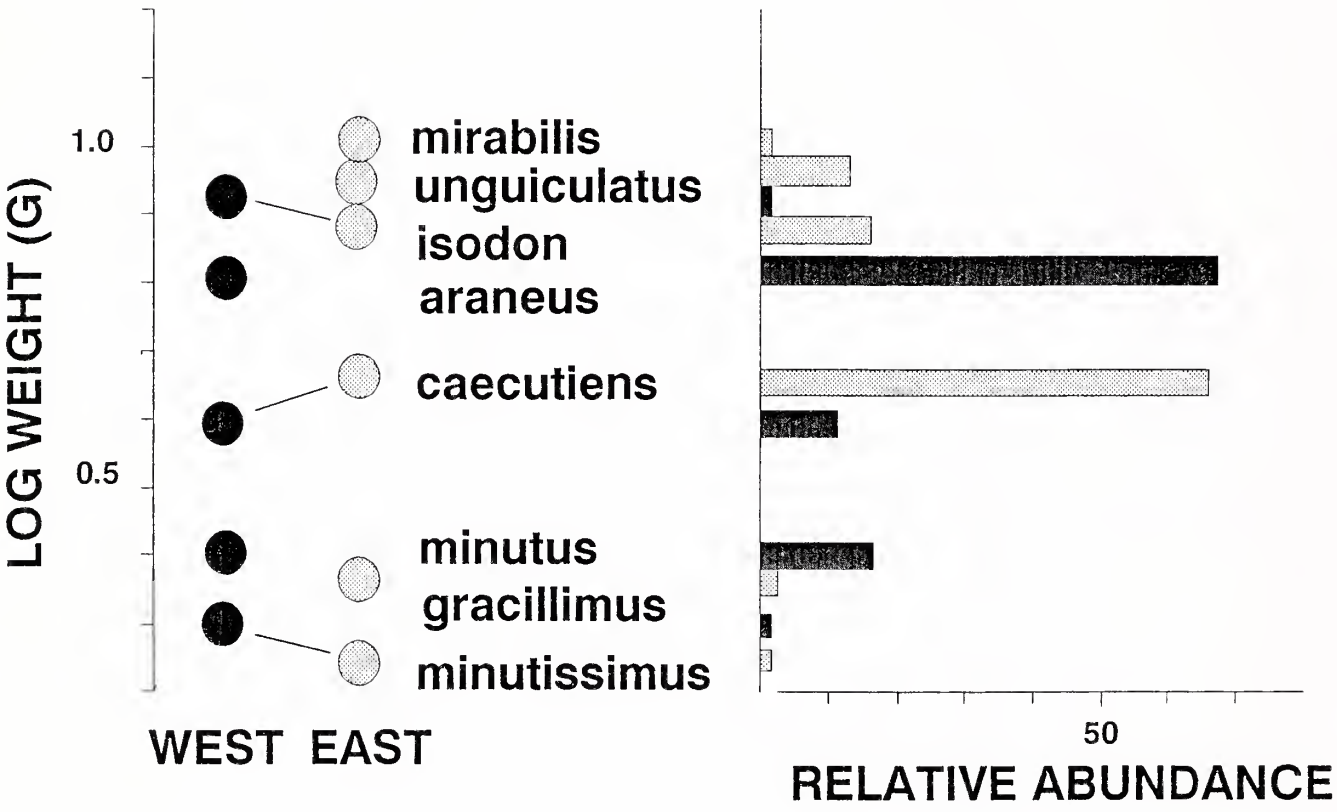

Fig. 6.—Body sizes (fresh mass) and relative abundances of *Sorex* in Karelia (west, dark shading) and the Russian Far East (east, light shading), in the western and eastern edges of the Eurasian coniferous forest, respectively. Data for Karelia are from Ivanter (1976) and for the Far East from Okhotina (1974).

POPULATION DYNAMICS OF THE SHORT-TAILED SHREW, *BLARINA BREVICAUDA*

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ABSTRACT

Short-tailed shrew, *Blarina brevicauda*, populations in east-central Illinois displayed relatively uniform low amplitude annual population cycles in three habitat types over 18 years of continuous study. There was no indication of multiannual or erratic high-amplitude population fluctuations. Fluctuations of shrew populations were not synchronous with those of two species of microtine rodents, both of which underwent erratic high-amplitude fluctuations in abundance. Generalist predators appear to be the primary source of shrew mortality; mortality rates were relatively constant throughout the year. Snakes do not appear to be major predators of nestling juvenile shrews, as they are for voles in the region. *Blarina brevicauda* does not appear to be a major predator on voles, including nestling juveniles. Annual population fluctuations are only weakly correlated with precipitation. Precipitation appears to have a greater influence on adult mortality than on reproduction.

INTRODUCTION

Most species of shrews, including the short-tailed shrew *Blarina brevicauda*, appear to display either annual fluctuations in population density (Blair, 1940, 1948; Getz, 1989) or irregular high-amplitude population fluctuations (Harper, 1929; Manville, 1949; Buckner, 1966; Smith et al., 1974; Grant, 1976; Yahner, 1983; Henttonen et al., 1989; Korpimäki and Norrdahl, 1989*a*). However, shrew populations in boreal regions of Fennoscandia and Siberia display multiannual fluctuations, sometimes in synchrony with those of microtine rodent populations. Specialist predators (e.g., weasels) have been suggested to be responsible for the multiannual shrew–rodent population fluctuations (Hansson and Henttonen, 1985; Henttonen, 1985; Henttonen et al., 1987, 1989; Sonerud, 1988; Korpimäki and Norrdahl, 1989*b*). Korpimäki (1986) further concluded that where only the spring decline phases of vole–shrew populations were in synchrony, nomadic avian predators were responsible for the declines. Sheftel (1989) on the other hand, suggested that cyclic fluctuations of shrews observed in central Siberia may result from intrinsic regulatory factors, rather than from predation effects. In more southern regions of Scandinavia both microtine rodent and shrew population fluctuations are annual (Hansson, 1984).

The above observations have been used to support the hypothesis that presence of fewer species of generalist predators in northern regions is responsible for the more pronounced multiannual population fluctuations of small mammals commonly observed in these regions (Hansson and Henttonen, 1985; Henttonen et al., 1987). In southern regions more species of generalist predators produce annual population cycles. Elsewhere in Europe and in North America microtine rodents have been observed to undergo both erratic and multiannual fluctuations in population density (Hansson and Henttonen, 1985; Taitt and Krebs, 1985; Getz et al., 1987). However, no evidence has been presented regarding presence or absence of synchrony between shrew and microtine rodent population fluctuations. Such evidence would provide a further test of the influence of generalist and specialist predators on population fluctuations of small mammals.

Blarina brevicauda has been proposed as an important predator on microtine rodents (Eadie, 1944, 1948, 1952). Although the efficiency of *B. brevicauda* as a predator on free-living adult voles has been questioned (Barbehenn, 1958; Lomolino, 1984), the shrews may feed on nestling juveniles. If *B. brevicauda* does feed extensively on nestling voles, one might expect fluctuations of sympatric populations of these shrews and voles to resemble typical predator–prey interaction curves.

Blarina brevicauda has high moisture requirements (Chew, 1951) and is usually associated with mesic habitats (Pruitt, 1953, 1959; Getz, 1961). One would therefore expect population densities in drier habitats to be positively correlated with precipitation.

During the course of a continuing long-term study of prairie vole, *Microtus ochrogaster*, and meadow vole, *M. pennsylvanicus*, population fluctuations in east-central Illinois (Getz et al., 1987), data are being obtained regarding population fluctuations of *B. brevicauda*. Detailed data are presented for the period of January 1972 through December 1989. These data have been analyzed to determine the pattern of population fluctuations of *B. brevicauda* (multiannual or annual), and to determine factors responsible for the observed fluctuations. Based on (1) observations of shrew–vole population fluctuations in southern Scandinavia, (2) the potential for predator–prey interactions between *B. brevicauda* and voles, and (3) the existence of high-amplitude fluctuations of vole populations in the study region, I predicted *B. brevicauda* would display high-amplitude population fluctuations in synchrony with those of the voles.

STUDY AREAS

All study sites were located in the University of Illinois Biological Research Area (Phillips Tract) and in Trelease Prairie, both 6 km NE Urbana, Illinois (40°15'N, 88°28'W). Populations of *B. brevicauda* were monitored in bluegrass (*Poa pratensis*), alfalfa (*Medicago sativa*), and restored tallgrass

prairie habitats. Three to eight different study sites were monitored at a time (Getz et al., 1987).

The four bluegrass sites (0.5 ha, 0.8 ha, and two each 1.0 ha) were released from domestic grazing in June 1971; by August 1971 there was a dense cover of bluegrass. The bluegrass study sites were mowed approximately 25 cm above the surface during the summer at 2–3 year intervals to control weed growth. Vegetation in the bluegrass sites varied little throughout the study. Relative abundance of plants in the bluegrass habitat was bluegrass (70%); dandelion, *Taraxacum officinale* (14%); wild parsnip, *Pastinaca sativa* (4%); and goatsbeard, *Tragopogon* sp. (3%); and approximately 20 other species with relative abundances of less than 1% (Getz et al., 1979).

Four different alfalfa sites were used (three each 1.0 ha, one 1.4 ha); all initially included at least 75% alfalfa. Other species gradually increased in prominence; during the last year of use of each site the common species included, in addition to alfalfa, bluegrass, goldenrod, timothy (*Phleum pratense*), brome grass (*Bromus* sp.), clover (*Trifolium repens* and *T. pratense*), and plantain (*Plantago* sp.).

Four tallgrass sites were studied: two 0.5 ha each, one 0.7 ha, and one 2.0 ha. The relative abundances of plants in the latter two sites were big bluestem (*Andropogon gerardi*, 17%), bush clover (*Lespedeza cuneata*, 16%), ironweed (*Vernonia* sp., 12%), Indian grass (*Sorghastrum nutans*, 10%), milkweed (*Asclepias* sp., 9%), goldenrod (*Solidago* sp., 9%), bluegrass (5%), switch grass (*Panicum* sp., 5%), little bluestem (*Andropogon scoparius*, 2%), and approximately ten other species with relative abundances of less than 1%. Vegetation in the two 0.5-ha areas was similar to that in the other two, except that Indian grass was the predominant grass (≈50%) and big bluestem less common (≈5%). The tallgrass study areas were burned in May 1974, 1979, 1984, and 1987 to control invading shrubs and weeds, and to maintain the prairie grasses.

In the bluegrass study sites vegetative cover 0.1–1.0 m above the surface and a dead-litter mat at the soil surface were dense throughout the year. Although herbaceous cover (1.0–2.0 m above the surface) was dense year-round in tallgrass, the soil surface was more open in this habitat than in bluegrass. The mat of dead vegetation at the soil surface in tallgrass was not as dense as that in bluegrass. However, it should provide shrews protection from avian and large mammalian predators. Vegetative cover was dense in alfalfa from April through December. Because of the growth form of the forbs, the soil surface was relatively open. Owing to dominance of forbs, which lost their leaves in winter, the alfalfa habitat provided poor cover during winter in comparison with bluegrass and tallgrass habitats. Approximately 75% of the soil surface of alfalfa sites was exposed from January to March, and dead vegetation over the remaining surface area rarely was higher than 10 cm.

The only other small mammals that occurred more than sporadically in the study areas were prairie and meadow voles, and the western harvest mouse, *Reithrodontomys megalotis*. Of the two other species of shrews present in the region, less than 25 individuals of the least shrew, *Cryptotis parva*, and only three southeastern shrews, *Sorex longistrostris*, were captured. Mammalian predators occurring on the study areas were raccoons, *Procyon lotor*; mink, *Mustela vison*; least and long-tailed weasels, *Mustela nivalis* and *M. frenata* respectively; striped skunks, *Mephitis mephitis*; red and gray foxes, *Vulpes vulpes* and *Urocyon cinereoargenteus* respectively; and domestic cats, *Felis catus*. Other predators included Great Horned Owls, *Bubo virginianus*; Eastern Screech Owls, *Otus asio*; Red-tailed Hawks, *Buteo jamaicensis*; Rough-legged Hawks, *B. lagopus*; Northern Harriers, *Circus cyaneus*; and fox snakes, *Elaphe vulpina*.

Methods

Trap stations were spaced at 10-m intervals; each had one wooden multiple-catch live trap (Burt, 1940) baited with cracked corn. Traps were examined in early morning and late afternoon for three days each month. Traps were covered with vegetation during summer. Owing to the effectiveness of the insulation provided by wood (1.25 cm-thick redwood), bedding material was not placed in traps in winter.

All live *B. brevicauda* were toe-clipped for individual identification when first captured. Owing to difficulty in determining sex and reproductive condition of *B. brevicauda* by external examination, sex and reproductive condition of live shrews usually were not recorded. From 1977 to 1990 shrews that died in traps were necropsied in the field for sex and reproductive condition (males, testis size; females, size of uterus or presence of embryos). Testis length (mm) was visually estimated; uterine size was visually estimated as less than or greater than 2 mm in diameter.

Some *B. brevicauda* can escape from the Burt multiple-catch trap by lifting the door with their nose (Getz, 1961). Accordingly, our data are conservative estimates of population densities of *B. brevicauda*. Population densities were based on the minimum number known alive during each trapping session.

Monthly weather data were obtained from the Illinois State Water Survey weather station located 6 km SW of the study areas.

Results

Trap Mortality

Although many shrews escaped from our traps, mortality was still a serious problem during the study. A total of 5,981 individuals were captured, of which 4,256 (71.2%) were alive at first capture; 796 of these eventually died in the traps. Thus, trap mortality accounted for 42.2% of the total losses from the population. The three habitats differed in overall trap mortality: bluegrass, 43.4% (n = 3,952); alfalfa, 28.3% (n = 1,047); tallgrass, 51.8% (n = 982). There was no evidence that trap mortality in a specific study site differed significantly from that of other sites in the same habitat type. Likewise, trap mortality did not differ seasonally. Despite having a significant impact upon the overall shrew populations and with considerably fewer losses in alfalfa than in tallgrass and bluegrass, trap mortality did not appear to have imposed a serious bias on conclusions.

Population Fluctuations

Blarina brevicauda populations in all three habitat types displayed essentially an annual cycle of abundance; there was no indication of multiannual cycles (Fig. 1). Populations in individual study sites within each habitat type also displayed annual population cycles. The mean annual peak densities for the 18 years of the study were 25.6 ± 2.08 (10.0–37.1), 20.1 ± 2.61 (4.3–54.0), and 15.6 ± 1.47 (2.0–18.4)/ha in bluegrass, alfalfa, and tallgrass, respectively. The mean annual low densities for the three habitat types were 2.6 ± 0.48 (0–8.0), 0.1 ± 0.00 (0–5.0), and 0.4 ± 0.10 (O–3.2)/ha, respectively. The mean annual amplitude of fluctuations (mean of the difference between the annual peak and low densities for each year) were 23.1 ± 1.89 (9.0–39.2), 21.0 ± 2.61 (4.3–54.0), and 15.1 ± 1.48 (3.0–28.8)/ha, respectively.

Peak densities deviated little from year to year from the 18-year mean in each habitat: bluegrass, 7.1 ± 1.16/ha (27.7% of the mean peak density); alfalfa, 7.5 ± 1.86/ha (35.5%); tallgrass, 4.8 ± 0.89/ha (30.8%). The only years of unusually high peak densities were 1981–83 in bluegrass and 1987 in alfalfa (Fig. 1). The annual peak density exceeded the mean peak density eight of the 18 years in bluegrass and nine years in alfalfa and tallgrass.

The modal month of annual peak densities was July for bluegrass and October for alfalfa and tallgrass. The month of the peak density deviated from the modal month by two or more months 15 times in 18 years: bluegrass, 1973 (September), 1981 (December), and 1989 (November); alfalfa, 1972 (August), 1974 (July), 1975 (August), 1983 (July), 1984 (August), 1986 (August), 1987 (July), 1988 (May), and 1989 (August); tallgrass, 1975 (August), 1979 (December), and 1983 (August).

There was no significant synchrony in terms of deviation of the annual peaks from the 18-year mean peaks (higher, >5/ha above the mean peak; lower, >5/ha below; or no deviation, ≤5/ha above or below) among the three habitats (Table 1). Similarities among all three habitats existed for only three years: 1975 and 1979, no deviation; 1980, below. There were five years of similarities between bluegrass and alfalfa (three, no deviation; one, lower; one, higher), seven between bluegrass and tallgrass (six, no deviation; one, higher), and three between alfalfa and tallgrass (two, no deviation; one, higher) (Table 1).

Overall population densities and amplitudes of fluctuation were higher in bluegrass than in alfalfa or tallgrass. The one major exception was May–September 1987 when population densities in alfalfa were more than twice those in bluegrass (Fig. 1). The generalized annual population cycle differed among the three habitats (Fig. 2). Overwintering densities in bluegrass were approximately 2.5 times those in the other two habitats at the annual low density in early March. Thereafter, population densities in all three habitats increased, bluegrass and alfalfa at essentially the same rate, through June. Actual population densities in bluegrass were higher during the increase phase than in the other two habitats during these months. The bluegrass populations continued to increase to the annual peak in July, followed by a gradual decline to October and November after which numbers declined rapidly to the winter low. Alfalfa densities stabilized from June through September with an increase to the annual peak in October. Thereafter the numbers declined rapidly to the winter low. Tallgrass population densities increased gradually from April through October and then declined rapidly to the winter low.

Mean January–March population density correlated significantly with the annual peak density in bluegrass and tallgrass (Spearman's rank correlation test: $r_s = 0.52349$, $P = 0.0258$ and $r_s = 0.53120$, $P = 0.0282$, respectively). January–March density and the annual peak in alfalfa did not correlate significantly ($r_s = -0.03204$, $P = 0.9028$).

Comparisons were made between annual peak population densities and total precipitation for the following periods: (1) previous September–December, (2) January–August of the same year, (3) April–August of the same year, and (4) April–August of the previous year. January–August precipitation correlated significantly with peak annual density the same year in bluegrass ($r_s = 0.54724$, $P = 0.0230$), but not in alfalfa or tallgrass. Annual peak densities did not correlate with the amount of precipitation during any of the other time periods.

Comparisons were also made of deviations in annual peak densities from the 18-year mean peak density with deviation of total January–August precipitation from the 70-year mean for the study region (Table 1). Deviations of more than 5/ha, above or below the mean peak density for the habitat were considered to be significant. In two of the seven years when precipitation was below average, the peak density in bluegrass was more than 5/ha below the mean peak (Table 1). The peak density was higher than the mean peak for the 18 years in three of the nine years when precipitation was higher than the mean. Peak densities in alfalfa were significantly lower than the mean in four of the seven years with less than average precipitation. There was no consistent relationship between deviation of the annual peak density in alfalfa in those years when precipitation was above average. Likewise, there was no consistent relationship between variation in the annual peak densities and precipitation, whether above or below the mean, in tallgrass sites.

Precipitation during the period April–August 1988 was the lowest on record for the region of the study areas (27.7 cm below the mean of 48.6 cm for this period). The alfalfa population peaked in May–June (27/ha, 6.9/ha above the 18-year mean) and in June in bluegrass and tallgrass, 2.6 and 10.6/ha below the mean peaks, respectively. Unlike most other years, population densities in all three habitats declined to very low levels in July–August. Except for a slight recovery in alfalfa in October–November 1988, populations in all three habitats remained very low through July 1989 (Fig. 1).

Annual peak densities of *B. brevicauda* were compared with mean vole population densities of *M. ochrogaster* and *M. pennsylvanicus* combined (both species are potential prey) during April–July, the period when most female *B. brevicauda* were pregnant or lactating. Food, in the form of nestling voles, during this time period would have the greatest potential to result in higher annual *B. brevicauda* population densities. Vole population density in April–July did not correlate significantly with annual peak *B. brevicauda* densities in any of the three

habitats (Kendall's Tau = −0.1184, −0.3629, and 0.0075, bluegrass, alfalfa, and tallgrass, respectively; significance at 0.05 = 0.468).

Survival

Overall 30-day survival rates (those animals alive one month that survived until the next month) were highest in bluegrass (47.5%) and lowest in alfalfa (33.4%); survival in tallgrass (42.5%) was only slightly lower than that in bluegrass. Mean monthly survival rates were consistently higher in both bluegrass and tallgrass than in alfalfa, except for September when survival in tallgrass was 3.4% lower in tallgrass than alfalfa (Table 2).

Survival curves for the three habitat types (Fig. 3) indicated slightly, but nonsignificantly, higher (χ^2 = 5.63, d.f. = 2, P > 0.05) survival the first month following initial capture in tallgrass than in alfalfa and bluegrass. The second month following the initial capture survival was significantly lower in alfalfa than in the other two habitats (χ^2 = 11.6, d.f. = 2, P < 0.01). Thereafter, survival did not differ among the three study areas. The mean persistence times (considering an individual to have entered the population halfway between the previous trapping period and that in which first caught, and to have survived 0.5 month following the last capture) were 1.76 (n = 2.844), 1.55 (n = 830), and 1.69 (n = 567) months for bluegrass, alfalfa, and tallgrass respectively. The mean persistence time for all three habitats combined was 1.71 months (n = 4,241). Fourteen individuals survived 12 months; one survived 17 months. Only 6.0% survived at least four months.

Reproduction

Males were considered to be reproductively active if the testes were three or more mm long. Testes usually were one or less mm in length during presumed nonreproductive periods. A three-fold increase in size therefore was used as an indicator of reproductive activity. Females were considered reproductively active if embryos were present or if horns of the uteri were two or more mm in diameter. Because relatively few females were observed to have embryos, enlarged uteri was the more common indicator of reproductive activity. Uteri of presumed nonreproductive females were less than 0.25 mm in diameter. Although these are arbitrary indicators, they provide the best evidence of reproductive activity obtainable under field conditions. *Blarina brevicauda* did not enter live traps until at least three-fourths grown; thus, young of the year normally could not be distinguished from older adults. This may have resulted in underestimation of the proportion of the adult population that was reproductive during late summer–early autumn. Neither could recruitment of young into the population be used as an indicator of reproductive activity. Data from all three habitats have been grouped together for analysis. The two sexes of the population were considered to be reproductive when approximately 40% of the individuals of each sex displayed evidence of reproduction.

Reproductive activity of males increased to more than 40% approximately two months prior to that of females (January and March, respectively) and declined to less than 40% two months prior to that of females (July and September) (Table 3). There were no differences in the male or female breeding periods among the three habitats. Reproductive activity of both males and females was lowest in December (11.7 and 7.4%, respectively).

There were four years in which precipitation deviated markedly from the 70-year mean during January–August (January–August 1980, 24% lower; May–August 1982, 13% higher; May–August 1983, 13% higher; and April–August 1988, 57% lower). There was no evidence of major differences in reproductive activity (sexes combined) associated with amount of precipitation during these periods: 1980, 72.9%, n = 59; 1982 and 83 (combined) 76.7%, n = 146; 1988, 50.0%, n = 32.

Discussion

Blarina brevicauda populations in east-central Illinois displayed a distinct annual cycle in bluegrass, alfalfa, and tallgrass habitats. Annual peak densities were higher in bluegrass than in the other two habitats. In none of the habitats did the amplitude of population fluctuation exceed ten-fold for any year, the minimum amplitude normally ascribed to multiannual population cycles (Taitt and Krebs, 1985). The annual peak densities for each habitat varied from the mean for that habitat by only 27.7–35.5%. Although population fluctuations in all three habitat types were annual and there was relatively little annual variation in amplitudes of fluctuation in each, annual population cycles among the three habitats were not synchronous. The annual peak normally occurred in July in bluegrass and in October in alfalfa and tallgrass. Synchrony was also compared in terms of deviations of more than 5/ha above or below the mean peak for each habitat. All three populations were in synchrony in only three years; synchrony between any two habitats occurred during only 5–7 of the 18 years of the study. All but four involved peak densities which did not deviate from the mean peaks for each habitat.

Higher overwinter and resultant peak summer densities in bluegrass than in alfalfa and tallgrass most likely result from a combination of differences in winter cover and food availability in the three habitat types. The denser surface vegetation cover afforded by bluegrass, combined with the potential for more ready availability of overwintering invertebrates, favors winter survival. Survival was approximately 20% higher in bluegrass than in alfalfa and tallgrass during the months of December and January. Food availability would also be high early in the spring in bluegrass, supporting rapid population growth. Alfalfa plants started growing in early March; thus, insect and other invertebrate herbivore populations, and in turn food availability for shrews, would also increase in early spring. Rapid population growth in alfalfa, starting from a low density, therefore would be expected. Tallgrass vegetation does not begin its major growth until mid-May. Later food availability, combined with a low winter population density, may be the reason for the slower growth of *B. brevicauda* populations in tallgrass than in the other two habitats. Given the higher starting

density and rapid rate of increase, population densities in bluegrass would be expected to achieve higher peak densities before the annual decline in reproduction slowed or stopped population growth. Owing to lower starting population densities (both alfalfa and tallgrass) and/or slower population growth rates (tallgrass), population densities were lower in alfalfa and tallgrass than in bluegrass at the end of the breeding period, when population growth stopped.

Survival rates did not change during the spring, summer, and autumn in a way that could account for the summer halt of population growth and the autumn decline in numbers. Although the indicator of female reproductive activity (enlarged uteri) remained high until September, actual production of young declined to low levels in August (see below). Thus, the primary reason for termination of annual population growth and the annual late summer–autumn decline of *B. brevicauda* populations appears to be a decline in reproduction; increased mortality does not appear to be involved. Eventual death of most of the breeding adults in midsummer may have resulted in a large proportion of the population being comprised of young of the year at this time. Thus, a change in the age structure and the resultant influence on reproduction may be a factor in the late autumn population decline of *B. brevicauda*. There was increased reproductive activity of both males and females in September and October. This may represent reproductive activation of young of the year. Confirmation of these predictions will require detailed analysis of reproductive activity of young of the year and of the timing of disappearance of the spring–early summer breeding adults from the population.

Survival of *B. brevicauda* was lower in alfalfa than in the other two habitats throughout the year. Even though vegetation cover is much less in winter in alfalfa than in bluegrass and tallgrass, mortality rates in alfalfa during December–March did not differ from those during spring–autumn, when vegetation cover was more dense. The sparse vegetation cover near the ground surface in alfalfa, as contrasted to the more dense cover at the ground surface of bluegrass and tallgrass, appears a likely factor in the year-round higher mortality rates in alfalfa. Avian and large mammalian predators probably would be more efficient in alfalfa during summer and autumn than in bluegrass or tallgrass. During spring–early autumn small mammalian predators (e.g., weasels) and perhaps snakes may also be more efficient predators in alfalfa than in the other two habitats owing to the more open unobstructed ground surface in the former.

Overall persistence (in situ mortality and emigration from the study site were not separated) on the study areas ranged from 1.55 months in alfalfa to 1.76 months in bluegrass; mean persistence for all habitats combined was 1.71 months. This is approximately the same persistence times for the two species of voles in the same habitats (Getz et al., 1979). Although differential food availability among the habitats may also be a factor in both vole and shrew survival (Cole and Batzli, 1979), it appears that voles and shrews are equally subject to mortality and emigration; predation within the study site is presumed to be the primary source of disappearance of voles. Approximately 3.3% of *M. ochrogaster* emigrated from a study site (Getz et al., 1990*a*); data are not available regarding emigration of *B. brevicauda*. Appearance of a few new adult *B. brevicauda* during the winter suggests that at least some emigration does take place.

There was no correlation between the annual peak shrew densities and April–July population densities of voles. Three of the four years (1981, 1982, and 1987) of highest shrew population densities were during periods of relatively low spring–early summer vole population densities (Getz et al., 1987; unpublished data). Vole populations were relatively high during spring–early summer 1983 when shrew densities were also very high. Furthermore, there were no concurrent rapid declines in *B. brevicauda* and vole populations. Most of the distinct population declines of *M. ochrogaster* in the various study sites were during late winter (28); eight were during spring, and five during the summer. Declines of *M. pennsylvanicus* also occurred primarily in late winter (17); seven were in spring, three in summer, and only one in autumn. All *B. brevicauda* declines occurred in autumn–early winter (Fig. 2). *Microtus ochrogaster* never declined in autumn–early winter and *M. pennsylvanicus* only once.

I conclude from these observations that: (1) *B. brevicauda* is not a significant predator on voles, including juveniles in the nest. At least voles do not constitute a major food source for *B. brevicauda* during the breeding period. (2) Population fluctuations of voles and *B. brevicauda* in east-central Illinois are not regulated in the same manner. Although there is no evidence for multiannual population cycles of voles in east-central Illinois (Getz et al., 1987), both *M. ochrogaster* and *M. pennsylvanicus* undergo high-amplitude, but erratic, fluctuations in numbers. During these periods of high-amplitude fluctuations in vole densities *B. brevicauda* populations displayed relatively uniform, low-amplitude fluctuations in abundance. There is anecdotal evidence of least weasel involvement in some of the vole population declines (Getz et al., unpublished data). However, because voles and *B. brevicauda* do not decline concurrently, variation in predation by these specialist predators does not appear to be involved in population regulation of *B. brevicauda*. The above observations agree with those of Korpimäki and Norrdal (1989*b*), who concluded that least weasels are not important predators on shrews. Neither was there evidence to suggest that avian predators contributed to either vole or *B. brevicauda* declines. Hawks were rarely observed flying over the study areas, including during periods of population decline, and few owls were known to roost within the vicinity of the study areas. Pellets of owls and hawks were not examined for prey utilization.

The results of this study also support the conclusions of Hansson (1984) and Henttonen et al. (1989), that where voles do not display multiannual cycles, generalist predators are more important sources of mortality than where distinct multiannual population cycles occur. In the latter regions specialist predators are involved in generating multiannual vole cycles and as a consequence shrew populations also display distinct multiannual cycles. Generalist predators on voles in east-central Illinois include house cats, large avian predators, and snakes. Snakes are especially important sources of mortality on nestling juvenile voles (Getz et al., 1990*b*). However, snakes do not

appear to be a primary source of shrew mortality. Snakes are active until mid-October, at which time both juvenile vole survival and the general population density increase. Although *B. brevicauda* populations begin declining in August in bluegrass, when snakes are active, the declines in alfalfa and tallgrass do not begin until November, after snakes have entered hibernation. If snakes are a major source of mortality on shrews, they take adults throughout the spring, summer, and early autumn and do not feed selectively on nestling juveniles.

January–August precipitation and peak *B. brevicauda* densities correlated only in bluegrass. Peak densities tended to be below the 18-year mean in both bluegrass and alfalfa during those years when precipitation was below the January–August mean. However, there was no consistent relationship between peak densities in these two habitats and precipitation above the January–August mean, nor between deviation in precipitation above or below the mean and peak shrew densities in tallgrass. Thus, the relationship between precipitation and annual population cycles of *B. brevicauda* in east-central Illinois is weak.

The extreme drought of 1988 afforded additional opportunity to evaluate the effects of precipitation on *B. brevicauda* populations. During the January–May period (before the summer drought), 43.8% of the females (n = 16) were reproductive, but during June–September 92.3% (n = 13) were reproductive. Comparable data for these periods over the entire study are 53.9 (n = 191) and 60.9% (n = 409), respectively. Although sample sizes for 1988 were small, the drought apparently had no major impact on reproduction.

Survival data were analyzed in terms of adults present in June 1988 (start of the drought) that survived to July (thereafter sample sizes were too small to be meaningful). For all habitats combined 9.3% (n = 75) survived from June to July. This is much less than the 41.1% (n = 200) June–July survival recorded over the entire study. Thus, increased adult mortality appears to be the major response to the drought conditions resulting in the early population decline in the summer of 1988. Reasons for high mortality were not obvious. The vegetation, including grasses and forbs, in both bluegrass and tallgrass was extremely dry and decimated by the drought. Very little green vegetation was present in either habitat from late June through July. In contrast, the alfalfa plants were robust and succulent throughout the drought. Although invertebrate abundance was not sampled, insect populations most likely would have remained high in alfalfa. Although no data are available, it is difficult to perceive the other two habitats as supporting equally high insect populations. The upper 5–10 cm of soil in all three habitats was extremely dry and hard-packed. June–July mortality was higher in alfalfa than in the other two habitats; none of the 24 individuals present in June survived to July (9.8% of the 51 animals present in June survived to July in bluegrass and tallgrass). I suggest that the reasons for the early rapid decline in *B. brevicauda* populations during the drought of 1988 resulted from adult mortality influenced by factors other than food availability. Water deprivation, combined with low humidities, may have been responsible for the increased mortality at this time (Pruitt, 1953, 1959; Getz, 1961).

Reproduction in *B. brevicauda* populations in east-central Illinois is limited primarily to March–July. Males become reproductive in January, but females do not do so until March, at which time food resources are assumed to be sufficient to support the demands of production of young. At this time vegetation growth resumes and invertebrates presumably become more available. Although testes start regressing in July, with reproductive activity becoming very low by August, female reproductive activity (mostly enlarged uteri rather than pregnancy) extends into September. There is undoubtedly a period of time following birth of the last litter before uterine size regresses to the nonreproductive state. Further, males probably would not successfully mate following regression of their testes in August. As indicated above, I could not separate the effects of loss of older breeding animals from the population on the perceived overall proportion of the population in reproductive condition in late summer. A greater proportion of the population being comprised of young of the year may be responsible for lower reproductive activity within the population at this time. Regardless of the reason, I conclude the main breeding period of *B. brevicauda* in east-central Illinois to be spring–early summer (March–July). Reproduction apparently was not influenced by variation in precipitation; this differs from the results of Pankakoski (1985), who found a positive relationship between reproductive success and precipitation for *Sorex araneus* in Finland.

There is no evidence for major autumn breeding success. However, approximately 21% of the females and 29% of the males appear to be reproductive into October. Owing to the short life span (Fig. 3), approximately 2% of the young born in October would be expected to survive to the spring breeding period. Thus, even though reproduction is low in autumn, young produced at this time may become the breeders the next spring. Overall survival rates are too low for many young produced during the spring–early summer breeding period to survive until the next year.

In summary, *B. brevicauda* displays low-amplitude annual population fluctuations in east-central Illinois. Population fluctuations of *B. brevicauda* differ, and are influenced by different factors, from those of voles in east-central Illinois; the latter displayed erratic multiannual fluctuations. There is no indication of predator–prey interactions between voles and *B. brevicauda* sufficient to affect population fluctuations of either the shrew or voles. Although several generalist predators feed on both voles and shrews in east-central Illinois, snakes do not appear to influence *B. brevicauda* population fluctuations as they do those of voles.

The annual peak density and population cycle of *B. brevicauda* are assumed to be influenced primarily by (1) population density at the beginning of the spring breeding period, (2) timing of the annual increase in food availability, and (3) a midsummer decline in reproduction. Population density at the beginning of the spring breeding period will be higher in those habitats providing good overwinter vegetation cover and food availability than where such conditions do not exist. Further, population growth will be more rapid where and when food availability increases early in the breeding period

than where such increases in food availability occur later. The combined effects of population density at the beginning of the breeding period and timing of food availability determine the peak density achieved before reproduction declines, thereby stopping population growth for the year. The annual nature of the population cycle appears to be generated by the marked decline in reproduction beginning in July. Variation in mortality is not involved. I propose that most of the overwintering breeding adults may finally have been lost from the population by July. Further, young of the year may not become reproductive until autumn. If so, a decline in food availability and/or the early onset of winter may result in such a brief autumn breeding period that population growth cannot be maintained. Thus, it is possible that the annual population cycle of *B. brevicauda* results from (1) the normal mortality of overwintering adults, (2) delay in reproductive maturity of young of the year, and (3) conditions unfavorable to sustain high levels of reproduction during the winter.

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Table 1.—*Synchrony in the deviation of the annual peaks of* Blarina brevicauda *from the 18-year mean peak for each habitat type. L, >5/ha below the mean peak; H, >5/ha above the mean peak; 0 ≤5/ha above or below the mean peak. Relationship between actual deviation (in parentheses) in the annual peak population density (*n*/ha) and deviation of the January–August precipitation from the 70-year mean total (65 cm) for those months.*

Year	Bluegrass	Alfalfa	Tallgrass	Precipitation (% Deviation)
1972	0(−5)	L(−15)	0(−2)	−30
1973	0(+3)	H(+7)	0(0)	+33
1974	0(+2)	0(0)	L(−6)	+4
1975	0(+4)	0(0)	0(+3)	+1
1976	0(+3)	L(−17)	0(+1)	−19
1977	0(−4)	L(−10)	H(+8)	−26
1978	0(−2)	H(+7)	0(+1)	−16
1979	0(−2)	0(−3)	0(−4)	+8
1980	L(−10)	L(−8)	L(−7)	−24
1981	H(+17)	0(+2)	0(−4)	+9
1982	H(+13)	0(+3)	H(+7)	+13
1983	H(+16)	H(+10)	0(+1)	+13
1984	H(+6)	0(−5)	L(−8)	0
1985	L(−6)	L(−7)	0(+4)	+4
1986	L(−12)	0(0)	0(+3)	−16
1987	L(−6)	H(+33)	H(+14)	+5
1988	0(−3)	H(+6)	L(−10)	−30

Table 2.—*Mean monthly survival (% present that month surviving to next month) of* Blarina brevicauda, *1972–1989. Sample sizes in parentheses.*

Month	Habitat Type			Total
	Bluegrass	Alfalfa	Tallgrass	
January	57.9(154)	27.8(18)	30.6(49)	49.3(221)
February	45.1(153)	28.6(14)	47.6(21)	44.1(188)
March	58.6(116)	41.7(12)	44.4(18)	55.5(146)
April	47.5(202)	22.6(31)	47.6(21)	44.5(254)
May	41.6(320)	27.3(77)	38.3(47)	38.7(444)
June	44.5(474)	28.1(153)	49.0(49)	41.1(676)
July	50.9(556)	36.4(154)	57.5(80)	48.7(790)
August	54.6(533)	39.8(161)	58.3(127)	52.2(821)
September	48.4(481)	43.9(132)	40.5(153)	46.1(766)
October	46.4(470)	32.0(128)	37.1(170)	41.9(768)
November	39.5(435)	25.6(78)	35.0(123)	37.0(636)
December	42.6(258)	22.8(35)	29.2(65)	38.3(358)
Mean	47.5	33.4	42.5	44.4

Table 3.—*Percent male and female* Blarina brevicauda *displaying evidence of reproductive activity (see text), as determined by necropsied animals from all study sites combined. Sample size in parentheses.*

Month	Percent Reproductive		
	Males	Females	Combined
January	45.0(20)	5.9(51)	16.9(71)
February	62.5(24)	5.3(19)	37.2(43)
March	92.3(13)	78.5(14)	85.2(27)
April	85.7(28)	77.4(31)	81.4(59)
May	83.3(72)	84.2(76)	83.8(148)
June	62.5(72)	74.2(128)	70.0(200)
July	38.5(91)	55.5(117)	48.1(208)
August	15.4(65)	42.5(87)	30.9(152)
September	26.5(49)	66.2(77)	50.8(126)
October	28.7(108)	21.4(145)	24.5(253)
November	18.6(140)	13.0(154)	15.6(294)
December	11.7(77)	7.4(95)	9.3(172)

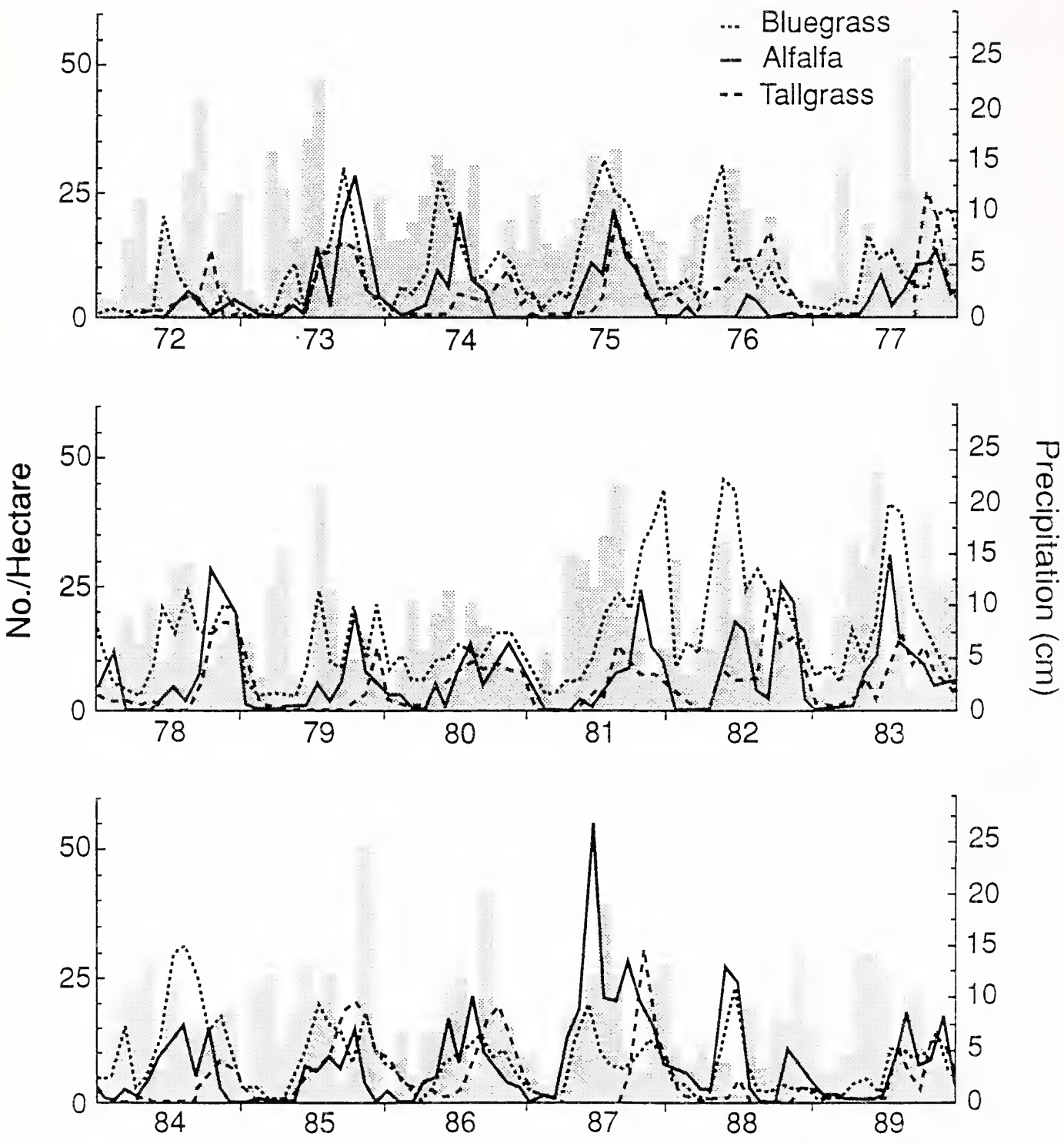

Fig. 1.—Population fluctuations of *Blarina brevicauda* in three habitat types in east-central Illinois and total monthly precipitation (stippled bar graphs).

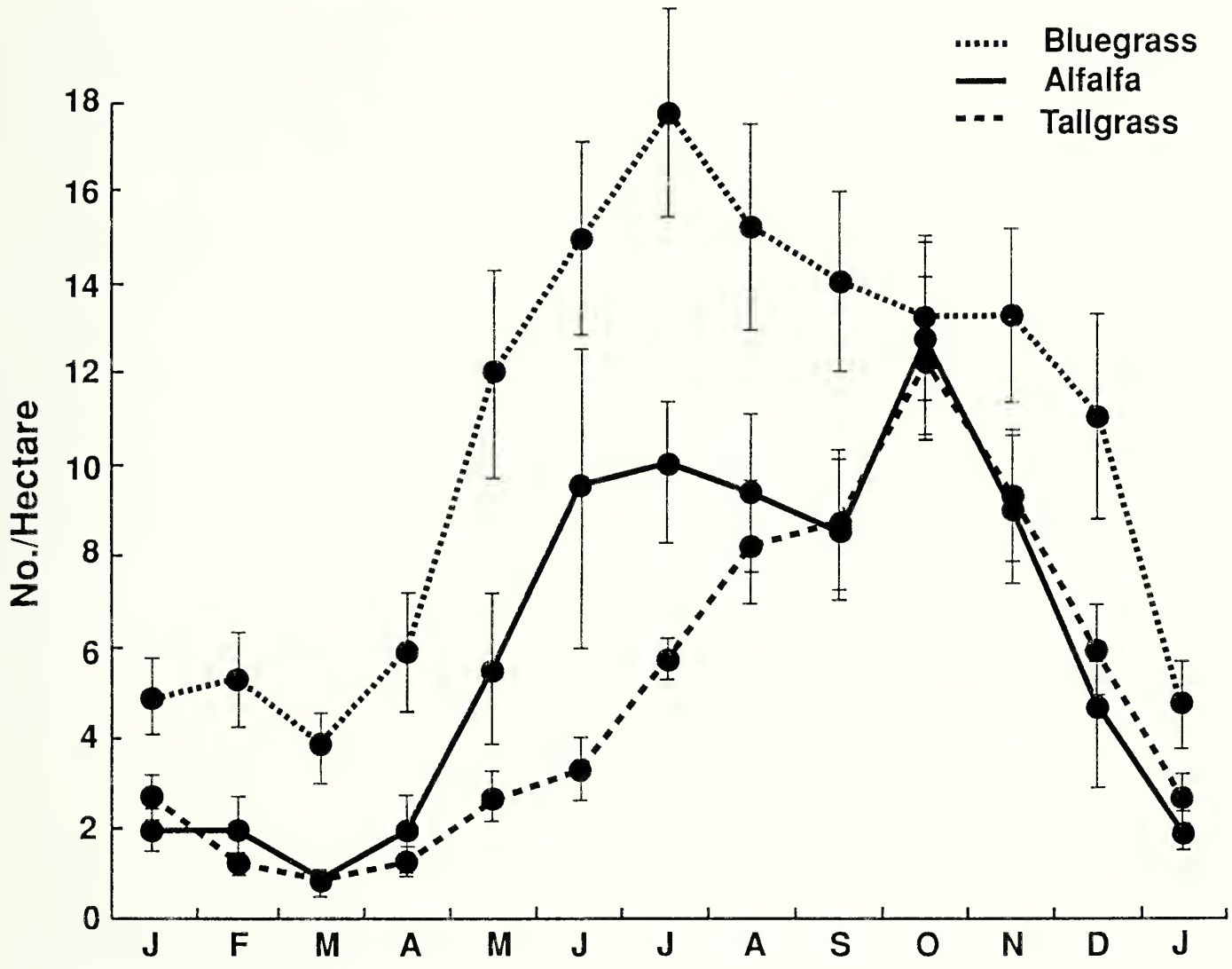

Fig. 2.—Generalized annual population cycles of *Blarina brevicauda* in three habitat types in east-central Illinois. Data represent monthly mean (±SEM) population densities from all study sites in each habitat for 1972–1989.

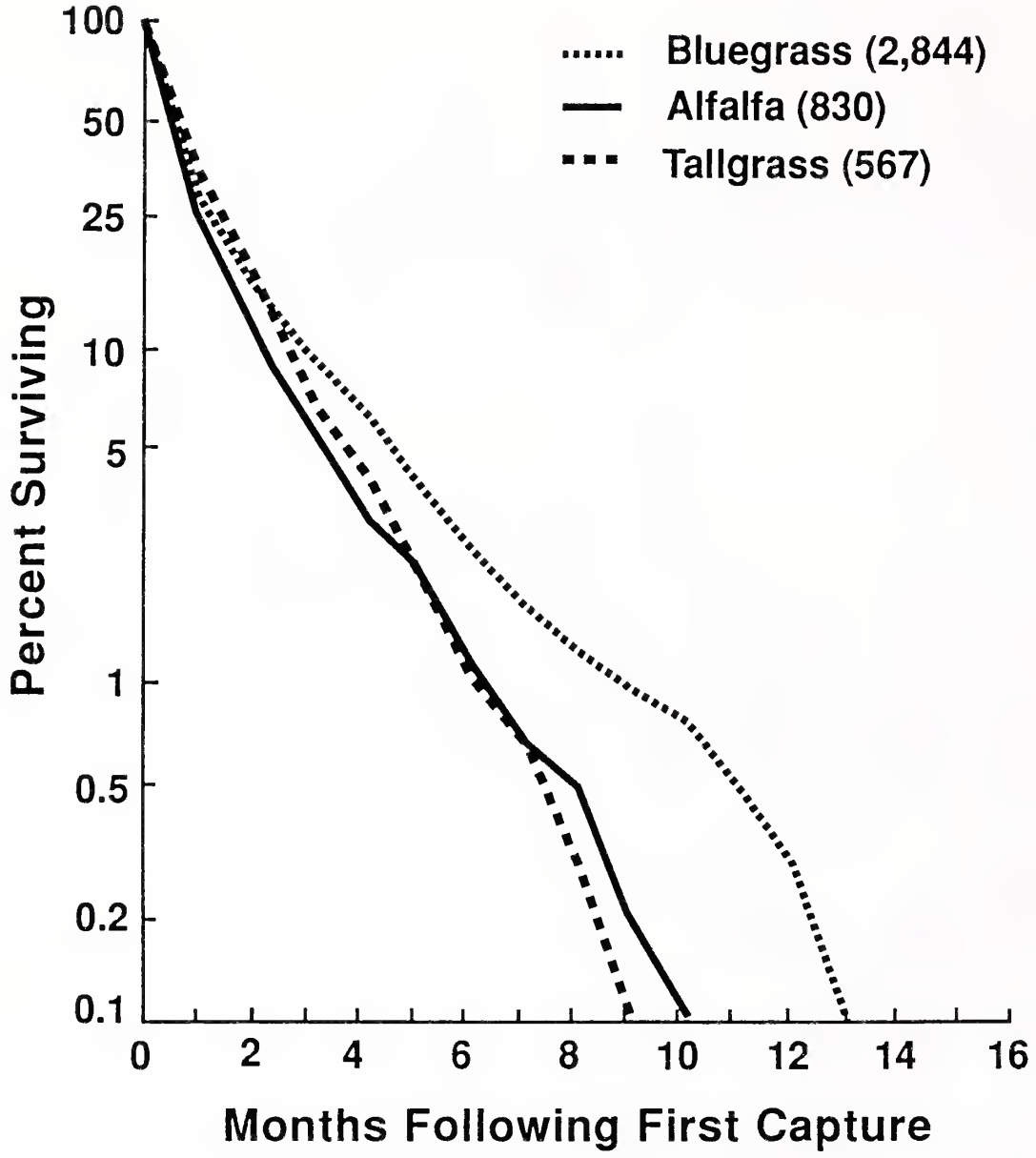

Fig. 3.—Survival of *Blarina brevicauda* following first capture for individuals alive at first capture. Sample sizes in parentheses.

A LIVE-TRAPPING STUDY OF TWO SYNTOPIC SPECIES OF *SOREX*, *S. CINEREUS* AND *S. FUMEUS*, IN SOUTHWESTERN PENNSYLVANIA

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ABSTRACT

This study examined the population biology of two syntopic soricids, *Sorex cinereus* (masked shrew) and *S. fumeus* (smoky shrew), in southwestern Pennsylvania. I used dry pitfalls as live-traps; two 1-ha areas were trapped (100 traps each) for three summers. Traps were opened for 6–8 h once a week and checked every 1.5 h. Fifty-six individual shrews were captured, marked, and released. More shrews were caught during the first summer. No individual was recaptured more than four times and only two individuals were recaptured between summers. Low capture rates were due both to inefficiency of the pitfall traps and to a real decline in density.

INTRODUCTION

Although many species of *Sorex* are found in a variety of habitats, and may constitute a substantial portion of small mammal communities in terms of species diversity, their high metabolic rates, small size, and concomitant low survival rates in live traps have limited studies of their population biology. Shrews rarely survive more than 2–3 hours in a trap and many shrews are not heavy enough to be reliably trapped in most traditional box traps, thus sample sizes are small. Most of what is known about shrews comes from studies in which shrews were kill-trapped. Although such information is valuable, it conveys little about the behavior of shrews.

Many studies of shrews have been designed to define microhabitat and diet of sympatric species to examine the importance of intra- and interspecific competition in structuring insectivore assemblages (Spencer and Pettus, 1966; Brown, 1967; Wrigley et al., 1979; Churchfield, 1984; French, 1984; Whitaker and French, 1984; MacCracken et al., 1985; Ryan, 1986). It has been suggested that competition may be important in structuring insectivore communities, based on the absence of habitat and dietary overlap (e.g., Whitaker and French, 1984) and competitive release on islands (Ellenbroek, 1980; Malmquist, 1986). However, important questions of spatial and temporal activity patterns have not been addressed.

Some investigators have successfully examined insectivore communities using innovative live-trapping methods, including the Longworth trap (Chitty and Kempson, 1949), and dry pitfall traps (Buckner, 1966) combined with frequent trap checks (every 1.5–3 hours). However, most (Croin-Michelson, 1966; Ellenbroek, 1980; Churchfield, 1984) live-trapping studies of shrews have been conducted in Britain and Europe.

The objectives of this study were to examine the ecology of two sympatric species of *Sorex*, *S. cinereus*, (masked shrew), and *S. fumeus*, (smoky shrew) using dry pitfall traps as live traps. In western Pennsylvania, these two species are sympatric with two or three other species of *Sorex*, *Blarina brevicauda*, and several other species of small mammals. My primary study objectives were to collect data on changes in population density, reproductive parameters, home range size and exclusivity, and temporal activity patterns. Another goal of this study was to quantify the efficiency of pitfall traps as live traps, as it is known that pitfall trapping is the most effective method of collecting shrews (e.g., Williams and Braun, 1983). The relationship of these two species to their microhabitat and to each other was further examined by quantifying microhabitat parameters.

METHODS

Study Species.—*Sorex cinereus* is a small shrew which rarely weighs over 5 g, whereas *S. fumeus* weighs between 5–10 g. *Sorex fumeus* is found throughout northeastern North America primarily in forests. *Sorex cinereus* is more catholic in habitat requirements and can be found in a variety of habitats from forests to bogs (Merritt, 1987). Both species are sympatric over much of their ranges with other *Sorex* species. Breeding begins in March and continues through July or August. Juveniles may breed in their first summer. Home ranges of individuals (*S. cinereus*) overlap only slightly and do not change with season (Buckner, 1966). Population density varies from year to year, ranging from 1/ha to over 124/ha (Merritt, 1987). Most shrews live less than one month. Those that survive the juvenile and subadult stages live 13–18 months, breed during the spring and summer, and die before the end of summer (Hamilton, 1940; Buckner, 1966). Individuals are active day and night, and moderate rainfall increases activity significantly (Doucet and Bider, 1974; Vickery and Bider, 1977).

Trapping Procedure.—The study was conducted during 1985 through 1987 at Powdermill Biological Station, Carnegie Museum of Natural History's field station in southeastern Westmoreland County, Pennsylvania. The study area is heavily wooded with second growth deciduous forest, dominated by sugar maple (*Acer saccharum*), tulip poplar (*Liriodendron tulipifera*), and American beech (*Fagus grandifolia*). Two study grids, located approximately 1 km apart on an east-facing slope, were similar in plant species composition. However, one grid (Moul Spring) was 30 m higher in elevation than the other (Calverley Lodge) and had steeper topography.

Shrews were trapped in dry pitfall traps placed 10 m apart in a 10 x 10 array (two 1-ha grids). Pitfall traps were made from #10 size cans (22.86 cm x 12.3 cm), buried up to the rim

near a log or pile of rocks within 1 m of the measured trap station. Traps were closed between trapping sessions by placing a section of log, slightly smaller in both diameter and height, in the can and placing a square of roofing shingle (12.7 x 12.7 cm) over the top. Each can was punctured through the bottom to allow water drainage. In some areas where traps were near streams, water collected in the cans during nonsampling periods and had to be removed.

Trapping was conducted on the two grids 1 day/week for 6–8 h/day during May through August. During March, April, September, October, and November of these years, trapping was conducted 1 day/month for 6–8 h/day. Trapping was conducted only during daylight hours, as it has been shown by previous investigators that diurnal trapping is successful (Churchfield, 1980, 1984). Open traps were provided with ground beef, which presumably acted as a food source (not a bait) once the animal was trapped, and a piece of moss which provided both cover and moisture. Traps were checked approximately every 1.5 h. Using this regime, only two shrews died in traps during the study.

All shrews were individually marked at first capture by toe clipping. Species determination, body mass, time and location of capture, sex, reproductive condition, and tooth pigmentation were recorded for every capture. Males were identified either by the presence of visible testes or an everted penis, and females were identified by the presence of visible nipples. Individuals that were not sexually active could not be sexed. Males were classified as having either visible or nonvisible testes, and nipple size in females was described as small, medium, or large. Pregnancy and lactation in females also were recorded when apparent. Soricid teeth are pigmented, but tooth wear gradually removes the pigment. Therefore, approximate age can be determined by examining the amount of pigmentation on the teeth (Hamilton, 1940; Rudd, 1955). In this study, shrews with heavy pigmentation were assumed to be young of the year, and those with medium and light pigmentation were older (animals that had overwintered). Juveniles were also distinguished from adults by body mass: *S. cinereus* that weighed less than 3 g and *S. fumeus* that weighed less than 5 g were classified as juveniles.

Microhabitat Analysis.—Microhabitat data were collected at each of the 200 trapping stations using a method similar to that of Dueser and Shugart (1978) and Porter and Dueser (1982) and described in detail in Chandler (1989). Data from the two grids were pooled for the microhabitat analysis. When appropriate, transformed (log or square root transformations) variables were used in order to meet the assumption of normality. Stations where shrews occurred and stations where shrews were absent, and stations where only *S. cinereus* occurred and stations where only *S. fumeus* occurred were compared using Discriminant Function Analysis (DFA). All statistical analysis were performed using SAS (SAS Institute Inc., 1985).

Results and Discussion

Trapping.—Three species of shrews, *S. cinereus*, *S. fumeus*, and *B. brevicauda* were caught on each grid during the three years of the study (Table 1). Trap success was low (0.5%); during 5,301 trap days, 112 *Sorex* and 32 *Blarina* were captured. Trap success on both grids was highest at the beginning of the study, declined through the summer of 1985, and remained low during 1986 and 1987 (Fig. 1). Of the 144 captures, 46 were recaptures. Of those, 32 were recaptures of *Sorex* and most were recaptures of *S. cinereus*. Shrews were captured simultaneously in a trap four times during the study, resulting in the death of two shrews. No individual was recaptured more than four times. Many of the recaptures occurred in the same trap or traps adjacent to the original capture site, suggesting that shrews had regular runways.

Trap mortality in this study compared favorably to that reported in previous live-trapping studies of *Sorex*. Estimates of trap mortality have been between 0.04% (Hawes, 1977) and 8% (Churchfield, 1980). In previous studies, traps were checked frequently (every 1.5–3 h) or an appropriate food source was left in the trap (Buckner, 1966; Croin-Michielsen, 1966; Hawes, 1977; Churchfield, 1980; Ellenbroek, 1980). Furthermore, several investigators have opened traps only during daylight hours, thus avoiding the problem of other nocturnal small mammals occupying the traps (Croin-Michielsen, 1966; Hawes, 1977; Churchfield, 1980; Ellenbroek, 1980).

Density was estimated by the minimum number known to be alive method (MNA; Krebs et al., 1969). Initially, density in June exhibited a high of 13 *S. cinereus* and 6 *S. fumeus*/ha, but declined through the summer of 1985 and remained relatively constant during 1986 and 1987 (Fig. 1). Density was 3/ha for *S. cinereus* and 1–3/ha for *S. fumeus*. This estimate of density should be considered conservative, as the recapture rate was low and because there was incomplete sampling of individuals.

Reported shrew densities range from 3/ha to 124/ha (Hamilton, 1940) and changes in density between and within years are well-documented (e.g., Buckner, 1966). The high density recorded at the beginning of this study, followed by lower densities in subsequent years, is consistent with the notion that shrew densities change between years. It seems unlikely that individuals remembered the location of traps between years, but this factor may have contributed to the initial decline in capture success during the summer of 1985. Churchfield (personal communication) and Crowcroft (1957) have suggested that shrews regularly shift runways, and that this may influence trap success when traps cannot be moved.

The age structure of the population changed during each summer, as evidenced by changes in mass and tooth pigmentation. During May and June most animals captured were adults, based on both weight of animals and tooth pigmentation. During this period, animals were relatively heavy and few had completely pigmented teeth. However, during July and August the population was dominated by subadults and juveniles, as indicated by lower average weights, and fully-pigmented teeth in most individuals. Weights for *S. cinereus* ranged from 2.2–5.6 g, and for *S. fumeus* from 5.0–9.0 g. Most reproduction occurred in May, June, and July, because it was only during these months that shrews could be sexed by enlarged nipples in females or enlarged testes in males. Juveniles first appeared in June and were present through

August, which indicates late spring or early summer reproduction and supports the conclusions of previous investigators (e.g., Owen, 1984).

Diel activity, measured by time of day when shrews were captured, occurred throughout the day, although there were periods of greater and lesser activity. Because trapping effort after dark was minimal, no observation on differences in activity during day and night could be made within or between the grids. There was no significant correlation between activity of the two species (Grid 1, $r = 0.155$, NS; Grid 2, $r = 0.033$, NS). Both species were most active during the morning and late afternoon and early evening hours. This is similar to the findings of Buckner (1966), Croin-Michielsen (1966), and Pernetta (1977) for syntopic species. It may be that activity in shrews is constrained because of their high metabolic rates, so that a difference in activity periods is unlikely to be detected. On the other hand, given the low population density, the potential for direct interaction between these species was probably slight in most years.

Microhabitat Analysis.—The grids were established in sites having similar plant species composition (Jacard's similarity index = 0.83), and density of shrews on the two grids was similar, so data from both grids were combined for the microhabitat analyses. Data were partitioned into two groups for discriminant function analysis (DFA): stations where shrews were captured versus stations where shrews were not captured, and stations where only *S. cinereus* were captured versus stations where only *S. fumeus* were captured. In the first analysis, there was significant discrimination between sites where shrews were captured and sites where shrews were not captured (Wilks' Lambda = 0.70, d.f. = 27, $F = 1.64$, $P < 0.03$; Fig. 2). In this case the canonical variate described a gradient of stations with low tree densities (poor habitat) to stations with high woody species richness and higher woody stem density (good habitat). Both species were caught more often in areas with high woody stem density, and less often in open areas with low woody stem density. In the second analysis, there was no significant discrimination between traps where only *S. cinereus* occurred and traps where only *S. fumeus* occurred (Wilks' Lambda = 0.58, $F = 1.33$, d.f. = 27, NS).

None of the variables which have traditionally been described as important components of shrew habitat (e.g., fallen logs, Hamilton, 1940) were important in the DFA. This lack of variation in microhabitat is not surprising considering the history of the region. Both study areas were selectively cut approximately 50 years ago, and there are no differences in soil types or slopes on the grids. Consequently, the vegetation on the grids is of uniform age and type. Both species of shrews in this study are primarily forest dwellers, although *S. cinereus* has more catholic habitat preferences than *S. fumeus* (Merritt, 1987). Of course, the relatively small sample size of shrews captured in this study hampered the detection of differences in microhabitat use.

Acknowledgments

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Table 1.—*Number of captures by sex of* Sorex cinereus, S. fumeus, *and* Blarina brevicauda *during a three-year live-trapping study in western Pennsylvania. Values in parentheses indicate number of recaptures.*

Species	Males	Female	Gender Unknown
S. cinereus			
Grid 1	5(3)	15(8)	29(12)
Grid 2	2(1)	11(2)	24(6)
Total	7(4)	26(10)	53(18)
S. cinereus Total 86(32)			
S. fumeus			
Grid 1	5(0)	2(1)	8(1)
Grid 2	4(0)	0(0)	7(1)
Total	9(0)	2(1)	15(2)
S. fumeus Total 26(3)			
B. brevicauda			
Grid 1	0(0)	0(0)	5(1)
Grid 2	2(0)	9(7)	16(3)
Total	2(0)	9(7)	21(4)
B. brevicauda Total 32(11)			

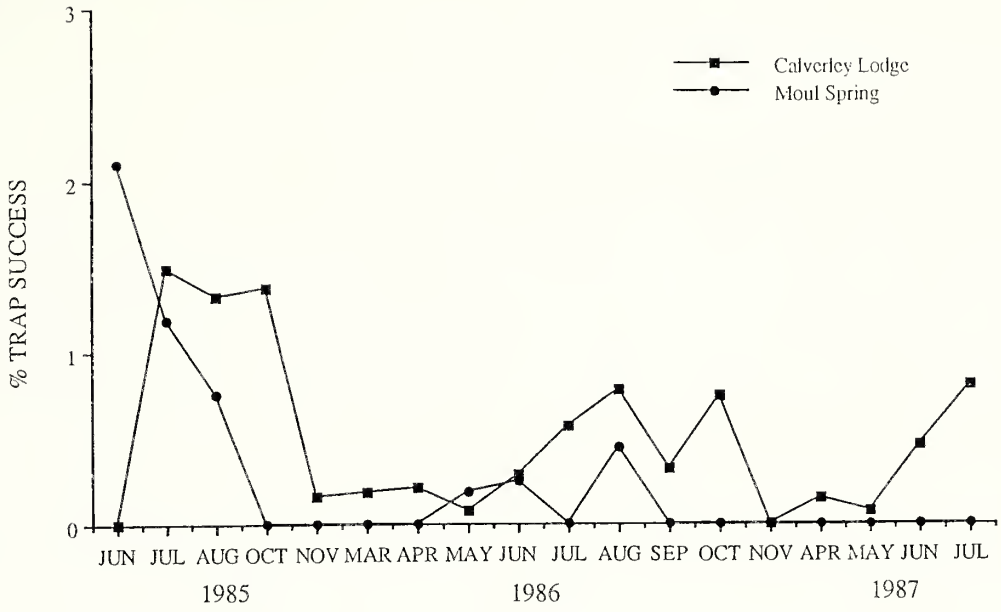

Fig. 1.—Percent trap success on each grid during each month of the study. Trap success was calculated based on the number of captures/total trap hours for the month.

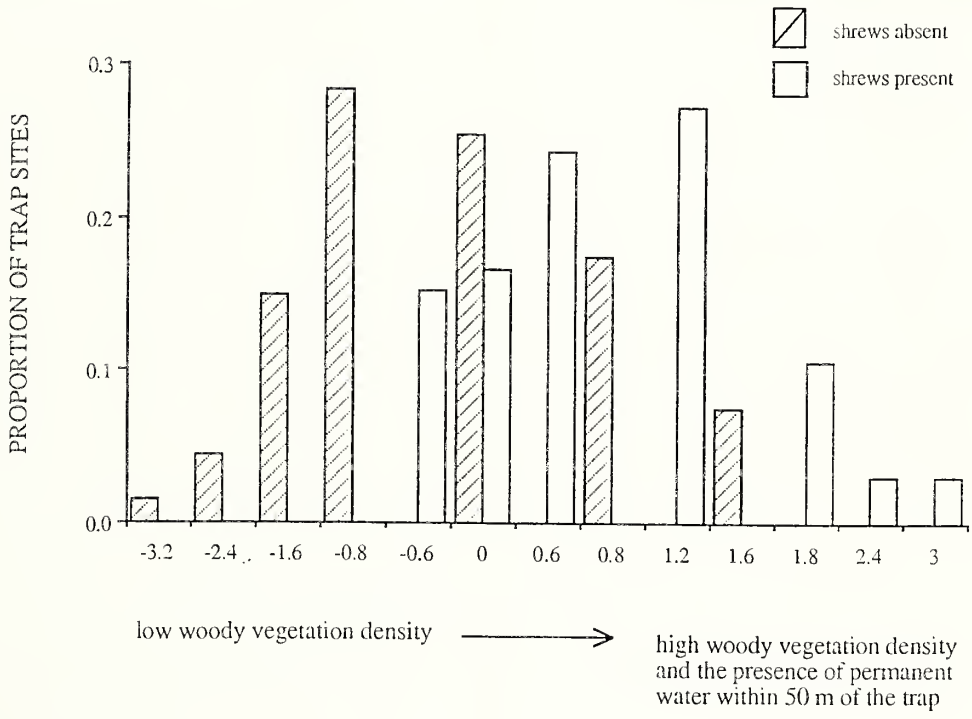

Fig. 2.—Stations where shrews were captured and those where shrews were not as they occur along the discriminant axis. There was significant separation of these two groups along this axis (Wilks' Lambda = 0.792; d.f. = 27, $F = 1.638$, $P < 0.03$).

SPATIAL DISTRIBUTION OF NINE SPECIES OF SHREWS IN THE CENTRAL SIBERIAN TAIGA

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ABSTRACT

A guild of nine shrew species was studied in the middle Yenisei River taiga region of central Siberia in order to assess the ecological distribution and relative abundances of individual species in 11 habitat types over an eight-year period. The spatial distribution of shrews was analyzed in two-dimensional ecological space, as defined by the method of ecological ordination of vegetation, with the use of Ramensky ecological scales. There was little overlap in the spatial optima of the nine species. Species with the broadest ecological niches had ecologieal optima in less productive habitats, whereas species with narrower niches had optima in more productive habitats. Species occupying similar habitats tended to differ in body size. It is hypothesized that in the course of competition between species of similar sizes, the subordinate species can survive only in most productive habitats, which represent ecological refugia.

INTRODUCTION

The ecological distribution of small mammals represents an important characteristic of their community. Particularly interesting is the analysis of habitat distribution of sympatric congeneric species. Congeneric species often have similar ecologies and similar food habits. Thus the ecological distribution of such species is related to the sharing of food resources, a process which facilitates the coexistence of congeneric species.

Shrews represent good subjects for such analyses. They feed mostly on invertebrates, but due to their high metabolism and resulting large consumption of food, shrews do not have high selectivity of food items. This increases the potential importance of microhabitat distribution in their coexistence. Central Siberia (Russia) represents one of the most suitable sites for such investigations, being populated by eight *Sorex* species and *Neomys fodiens*. However, traditional methods of analysis of ecological distribution often cannot offer a conclusive picture of similarity of ecological requirements of coexisting species. That is why I attempted to employ Ramensky ecological scales (Ramensky et al., 1956) in addition to traditional methods for the analysis of spatial distribution of shrew species.

Nine species of shrews (eight *Sorex* and *N. fodiens*) inhabit the area. Such a high diversity of species is produced in part by the reciprocal introgression of east Palearctic and west Palearctic species in this region, and by the region's relatively high biotopic diversity, which permits coexistence of a great number of congeneric species.

Three species—*Sorex araneus*, *S. minutus*, and *Neomys fodiens*—have western origins. The ranges of *S. araneus* and *S. minutus* extend from the Atlantic to the Baikal region; *Neomys fodiens* reaches the Pacific. Six other species are usually considered to have eastern origins (Shvarts, 1989). *Sorex isodon*, *S. caecutiens*, and *S. minutissimus* range from northern Europe to the Pacific and are often considered to be trans-Palearctic species. *Sorex roboratus* and *S. daphaenodon* usually are accepted as east Palearctic species, and *S. tundrensis* is a Holarctic species. With the exception of *S. tundrensis*, which is known from northeasternmost Europe and western Alaska, the ranges of these species are largely limited to Siberia.

MATERIALS AND METHODS

Thirty 20-m-long ditches for capturing small mammals were established in habitats adjacent to the Mirnoe field station in central Siberia (see Study Area). Each ditch was equipped with two catching cans, located 5 m from the ends. At sites where the high water table prevented excavation of ditches, 20-m-long polyethylene drift fences equipped with catching cans were constructed. Results of trapping by ditches and fences could be considered identical. This viewpoint is confirmed by some experiments (Tupikova et al., 1961). Sampling of small mammals was carried out from 20 June to 3 September of 1976–1983.

A detailed geobotanical description was prepared for each ditch and used in the analysis of the spatial distribution of shrews on the basis of "Ramensky ecological scales" (Ramensky, 1925). The idea of this approach is based on using the characteristics of vegetation as an indirect integrated indicator of physical-chemical conditions of environment. Plants can react to very minute variation in environmental conditions, which can hardly be detected by any physical methods. According to the rule of ecological individuality of plants, suggested by Ramensky (1925), each plant species can be classified on the basis of its response to various environmental factors. The school of Ramensky distinguishes the following factors: the soil moisture regime, soil nutrients (richness), seasonality of moisture, grading pressure, altitude position, and illumination conditions (Ramensky et al., 1956). Vorobjev (1959) added temperature and climatic conditions. Belgard (1950), using some of the listed factors, also considered the periodic floods of river waters and correspondence to vegetation type. Some other investigators (e.g., Ellenberg, 1952; Mras and Samek, 1966) suggest distinguishing soil moisture regime, richness, temperature regime, aeration, acidity, nitrogen content, and climatic conditions. A detailed analysis of different approaches to the ecological ordination of vegetation was presented by Whittaker (1967). Most investigators accept soil moisture and richness as the main factors influencing the

vegetation of an area.

By using the "Ramensky ecological scales" approach, it is possible to map habitat variation in a two-dimensional space based on soil moisture and richness. In the work of Ramensky et al. (1956) for numerous plant species, some quantitative values or weights (in relative units) are given. These correspond to variation of soil moisture and richness, and are thus suitable for describing the ecological distribution of species. A relatively wide range of variation is typical for low abundances and a narrow range for high abundance. There is a nonlinear dependence between the relative units describing ranges of soil moisture and richness and physical parameters. Ramensky derived these relative units from the sequence of species that were ranked by a physical gradient which permitted subdivision of this row into equal parts with each species receiving a value. Thus, starting from the detailed geobotanical description of habitat, one can find its coordinates in two-dimensional factor space (soil moisture and richness, for example).

Study Area

Investigations were carried out at Mirnoe, the northern ecological station belonging to the Severtsov Institute of Evolutionary Animal Morphology and Ecology. The station is situated on the bank of the Yenisei River in central Siberia (62°N, 89°E). Details of geographic and climatic characteristics of the site were described in Sheftel (1989). Investigations were carried out in the principal habitats on both banks of the Yenisei River. Eleven habitats were sampled.

1. Bog forest is distinguished by sparse population of *Pinus sylvestris*, *P. sibirica*, and *Picea obovata*, sometimes with addition of *Larix sibiricus* and *Betula alba*. Trees do not exceed 5–6 m in height. Undergrowth is poorly developed. Dwarf shrubs include *Ledum palustre*, *Chamaedaphne calyculata*, *Vaccinium vitis-idaea*, and *V. myrtillus* in relatively dry places. Herbaceous species include *Carex globularis*, *Equisetum sylvaticum*, *E. pratense*, *Trientalis europaea*, and *Empetrum nigrum*. The moss cover reaches 100%, with a dominance of *Sphagnum* sp. and *Polytrichum commune*, and sometimes *Pleurosium schreberi*. Two drift fences and one ditch were situated in different sections of bog forest.

2. Boreal coniferous (taiga) forest habitat are characterized by *Pinus sibiricus* and *Picea obovata*, with *Betula alba* and sometimes *Populus tremula*. The height of the trees is 10–20 m. Among young trees dominants are Siberian pine. Undergrowth, formed by *Sorbus aucuparia* and *Rosa acicularis*, is sparse. Ground cover species include *Vaccinium myrtillus*, *Linnaea borealis*, *Majantemum bifolium*, *Equisetum sylvaticum*, *E. pratense*, *Trientalis europaea*, and *Lycopodium complanatum*. Moss cover is from 60–90% with *Hylocomium splendens*, *Pleurosium schreberi*, and *Polytrichum commune* as dominants. Six ditches were installed in this habitat.

3. Grass–moss small-leaved forests are formed following the cutting of taiga forests or spontaneous forest fires. Common trees include *Betula alba* and *Populus tremula*. Larch is commonly encountered on burned sites. Siberian pines and Siberian spruce are ubiquitous. The last two species are also common among young trees. Undergrowth is formed from *Sorbus aucuparia*, *Rosa acicularis*, *Lonicera altaica*, and *Juniperus sibirica*. Typical ground cover species include *Equisetum pratense*, *Calamagrostis obtusata*, *Vaccinium myrtillus*, *Pyrola incornata*, *Linnaea borealis*, *Dryopteris linneana*, and *Majantemum bifolium*. Moss cover is 30–50%; *Hilocomium splendens* prevails. Five ditches were placed in this habitat type.

4. Taiga forest edge contains mainly solitary *Pinus sibirica* with dense young growth of birches. Undergrowth includes *Rosa acicularis*, *Rubus idaeus*, and *Lonicera altaica*. Ground cover is represented by *Chameron angustifolium*, *Tanacetum boreale*, *Trifolium pratense*, *Ranunculus borealis*, *Vicia cracca*, *Rubus arcticus*, *Calamagrostis obtusata*, *Galium boreale*, and others. Two ditches were placed in this habitat.

5. The anthropogenic meadow habitat is distinctive. The part of the meadow near the station formed in the place of old vegetable gardens. Here *Urtica dioica*, *Actium lappa*, *Agropyron repens*, *Heraclium dissectum*, *Stellaria media*, *Taraxacum officinale*, *Achillea millefolium*, and other herbs are common. In meadows used for haying, *Poa angustifolia*, *P. pratense*, *Ranunculus borealis*, *R. acer*, *Tanacetum boreale*, *Agrostis alba*, *Chamaenerion angustifolium*, *Thalictrum minus*, and *Leucanthemum vulgare* prevail. On the higher more xeric part of the meadow there are trees dominated by birches with occasional Siberian and common pines. Herbaceous plants include *Poa angustifolia*, *Trifolium pratense*, *T. repens*, *Alchemilla* sp., *Ranunculus boreale*, *Achillia millefolium*, *Chamerion angustifolium*, *Brunella vulgaris*, *Selena repens*, and *Antennaria dioica* are usual. Three ditches were placed in different sections of the anthropogenic meadow.

6. Riparian spruce forests occupy high portions of the floodplain and first terrace on both banks of the Yenisei River. The dominant species is *Picea obovata*, with small admixtures of birches and *Abies sibirica*. Trees are 20–25 m high. Undergrowth plants are *Rosa acicularis*, *Ribes acidum*, and *Lonicera altaica*. Herbaceous cover includes *Athyrium filix-femina*, *Cardamine macrophylla*, *Equisetum pratense*, *Calamagrostis obtusata*, *Cypripedium guttatum*, and *Aconitum septentrionale*. Moss cover is up to 50%, with *Rhytidiadelphus triquetrum* as the dominant. Three ditches were situated there.

7. Osier bed habitat along the bank of the Yenisei River consists mainly of *Salix viminalis* and *S. saposhnicovii*. Bushes and trees are up to 10–12 m in height. Herbaceous cover is formed by *Urtica dioica*, *Solanum depilatum*, *Cacalia hostata*, *Filipendula ulmaria*, *Artemisia vulgaris*, *Angelica sylvestris*, *Bromus inermis*, *Thalictrum simplex*, and others. Two ditches were constructed there.

8. The floodplain forest occupies the central wet part of flood land on the west bank of the Yenisei River. Trees (*Picea obovata* and *Abies sibirica*) up to 20–22 m high are separated by up to 40 m. The second layer of trees is formed from *Alnus fruticosa* and birches. Very dense and high (3 m) undergrowth includes *Alnus fruticosa* and *Padus racemosa* accompanied by *Ribes acidum* and *R. niger*, *Swida alba*, and *Rosa acicularis*. Young trees (*Abies sibirica*) are solitary. Common herbaceous species include *Athyrium filix-femina*, *Cardamine macrophylla*, *Veratrum lobelianum*, *Aconitum septentrionale*, *A. volubile*,

Cacalia hostata, *Paris quadrifolia*, and *Urtica dioica*. Moss (mainly *Rhytidiadelphus triquetrum* and *Climacium dendroides*) covers up to 30%. In this habitat one ditch and one fence were installed.

9. A seasonally-flooded hillock meadow is a shallow depression near a stream in the floodplain of the Yenisei River. Herbaceous cover is formed from *Calamagrostis langsdorffii*, *Carex caespitosa*, *C. acuta*, *Veronica longifolia*, *Geum aleppicum*, *Ptarmica cartilaginea*, *Veratrum lobelianum*, *Rumex aquaticus*, and *Bromus inermis*. *Spirea salicifolia* is present in dry patches. One drift fence was installed at this place.

10. The riparian meadow of the floodplain on the east bank of the Yenisei River supports solitary shrubs of *Salix viminalis*, *Padus racemosa*, and *Sorbaria sorbifolia*. Herbaceous cover includes *Heracleum dissectum*, *Angelica sylvestris*, *Pleurospermum uralense*, *Artemesia vulgaris*, *Phalaroides arundinacea*, *Thalictrum simplex*, *Vicia cracca*, *Tanacetum boreale*, *Calamagrostis langsdorffii*, *Sanguisorba officinalis*, *Gallium boreale*, and others. Here two ditches were established.

11. Marshy alder thickets are situated next to the bottomland meadow in a broad depression among the riparian spruce forest. Trees are mainly *Alnus incana*, 10–12 m high. Herbaceous cover includes *Filipendula ulmaria*, *Urtica dioica*, *Carex caespitosa*, *Calla palustris*, *Ranunculus repens*, *Veratrum lobelianum*, *Cardamine macrophylla*, *Chrysosplenium alternifolium*, plus others. One drift fence was installed here.

Results

In studying the distributions of shrews within habitats, I determined their mean abundances from 1976–1983. This region is characterized by a four-year cycle in shrew populations (Sheftel, 1989), and thus the data encompass two complete cycles. Included are two peaks (1977, 1981), two population lows (1978, 1982), two periods of population growth (1979, 1983), and two prepeak situations (1976, 1980). A total of 24,032 shrews were captured, and the distributions of the nine species by habitat are given in Table 1. The highest relative abundances were in the marshy alder thicket and herbaceous spruce–riparian forest; the lowest were in the bog forest and dry anthropogenic meadow (Table 1). *S. araneus* was dominant in almost all habitats, especially in those with well-developed herbaceous cover such as the taiga forest edge, anthropogenic meadow, grass–moss small-leaved forest, and bottomland meadow (Table 1). Many of those habitats were formed under anthropogenic influence. Second in overall relative abundance was *S. caecutiens*, which was the most abundant soricid in the bog forest. The proportion of this species (>40%) was also high in the boreal coniferous (taiga) forest (Fig. 1). *Sorex tundrensis* was dominant in riparian willow thickets and in floodplain forest with bushes (35.7% and 25.7% of shrews, respectively). No other species were dominant and their fraction was always less then 16%.

Thus, in anthropogenic grassy habitats *S. araneus* prevailed; in natural habitats with moss cover, *S. caecutiens*; and in most typical floodplain habitats, *S. tundrensis*. In the herbaceous spruce forest, marshy alder thickets, and hillock meadow, *S. araneus* dominated, but the degree of dominance was less pronounced here due to high species richness (Table 1).

To find the ecological valency of species, we calculated the width of the spatial ecological niche according to the formula:

$$\beta = \frac{Y_i^2}{\sum_a n_{ia}^2}$$

where n is the number of individuals of ith species captured in habitat a and y is the total number of individuals of ith species captured (Levins, 1968). The ecological niche width was calculated separately for each year. Table 2 gives the averaged values for this parameter.

On the basis of the calculated spatial niche widths, species can be conditionally divided into two groups: eurytopic (niche width >10) and stenotopic (niche width <10). Differences in the ecological niche width between species belonging to different groups in most cases were statistically significant. It is noteworthy that within both eurytopic and stenotopic groups, species exhibited considerable variation in abundance.

The ecological distributions of the shrews were plotted in two-dimensional ecological space with the Ramensky scales of moisture and richness as coordinates. The detailed geobotanical descriptions of all 30 capture sites permitted calculation of values for moisture and richness; after that, all 30 points were mapped on the described two-factor space (richness as abscissa, moisture as ordinate). The area delimited by coordinates of soil richness and moisture show ecological habitats occupied by shrews (Fig. 2)

Analysis of distribution of shrews revealed that the most abundant species, such as *S. araneus*, occupied practically all ecological space. Accordingly, I marked only those points where the abundances of such species exceeded mean values over the year. This procedure was used for all nine species of shrews. As an example, Fig. 3 illustrates the distribution of shrews in 1981. There is broad overlap in the contours for different species. This pattern of overlap was evident in the other years.

Then for each species, I plotted contours for each of the eight years of observations (1976–1983) and separated their common part (ecological optimum), which contained habitats with stable high preferences by each species, independent of the population dynamics phase, weather conditions, etc. (Fig. 4). If representatives of given species were not observed in a particular year (e.g., *S. daphaenodon* in 1978) or the number of catches was quite small and animals were caught only in one or two ditches, then I used data for fewer years. That is why the distribution of *S. daphaenodon* is based on only six years of data and those of *S. roboratus* and *N. fodiens* on data for seven years.

When the ecological optima for all species were mapped onto common ecological space (Fig. 5), they were found to be largely discrete. Partial overlap was found only between *S. araneus* and *S. minutus* and also between *S. caecutiens* and *S. minutissimus*. The majority of species had one highly preferred habitat. Only the smallest species (*S. minutissimus*) and the

largest (*N. fodiens*) had more than one preferred zone, each with two. Habitats supporting maximum annual abundance of shrews are considered to represent the ecological niche space for each species.

In Fig. 5, species having one optimum are aligned in the following order: *Sorex caecutiens* (#2), *S. araneus* (#1), *S. minutus* (#3), *S. isodon* (#5), *S. tundrensis* (#6), *S. roboratus* (#7), and *S. daphaenodon* (#8). Optima for *S. caecutiens*, *S. araneus*, and *S. minutus* are similar for moisture but show a progressive increase in soil richness. The optima of the remaining species differ little in soil richness but show a progressive increase in moisture from *S. isodon* to *S. daphaenodon* (Fig. 5).

In the analysis of these species sequences (Fig. 5), an interesting pattern is evident: each pair of species neighboring in the ecological space is very different in size. For example, relatively small *S. caecutiens* is a neighbor of large *S. araneus*, which in turn has a slightly overlapping space optimum with very small *S. minutus*. Then follows large *S. isodon*, followed by relatively small *S. tundrensis*. Similar conditions are evident for the large *S. roboratus* and, at the end of the chain, the small *S. daphaenodon*.

If we compare the length of the upper tooth row for the neighboring species (Table 3), we find that their ratio is at least equal to or somewhat bigger than 1:1.2. This is slightly less than observed by Hutchinson (1959), although shrews with such dimensional differences nevertheless prefer different habitats. A considerable difference in size is observed in the pair *S. araneus–S. minutus*, and this was the only pair with partial overlap of spatial optima.

Discussion

In this paper I have attempted to combine the continuum concept of plant community ecology with the theory of ecological niches in animal community studies. The possibilities and prospects of using ordination methods in such investigations are reviewed in detail in Austin (1985). Previous attempts to apply such methods to study the spatial distribution of animals were analyzed in Shvartz and Sheftel (1990), thus I will not use ecological ordination. I will only stress, that, using the parameters of soil moisture and richness as spatial coordinates in studying the ecological distributions of nine shrew species, all of which are terrestrial, yielded better results than have been obtained for other groups, such as birds, whose distributions are strongly influenced by other factors (Kozlenko, 1987).

Using ordination methods demonstrates that all observed shrew species have preferred sites in ecological space, which either do not overlap, or overlap only slightly, between different species. Such sites correspond to the center of the spatial ecological niche (Schoener, 1970).

The majority of species have one such center. Only *S. minutissimus* and *N. fodiens* had two. In the first case this can be explained by the preference of *S. minutissimus* for ecotonal habitats. This species is quite common at the borders of taiga and swamp, taiga and meadow, etc. As these habitats are quite separated on the ordination map, *S. minutissimus* has several sites with consistently high density. It is interesting that the smallest North American shrew *Sorex (Microsorex) hoyi* also prefers edge habitats (Spencer and Pettus, 1965). For *N. fodiens*, the two preferred habitats are bottomland rich meadow and weedy places in former vegetable gardens. For these two places the common factors are the presence of long-stemmed grasses and the proximity of the Yenisei River. Distance from water is likely an important factor for location of preferred *N. fodiens* habitat.

Species having one optimum are aligned practically along one line in the following order from poor, dry soils to moist, rich soils: *S. caecutiens*, *S. araneus*, *S. minutus*, *S. isodon*, *S. tundrensis*, *S. roboratus*, *S. daphaenodon*. The ecological optima for the first three species are situated at about the same conditions of moisture along the increasing soil richness axis. The others prefer sites with relatively high soil richness but differ in terms of increasing moisture.

Species whose centers of optima are at low soil richness exhibit maximum width of the ecological niche space, while those who prefer rich, moist biotopes have minimal width of ecological niche space (Table 2). For this reason inhabitants of poor habitats more often can be detected in rich habitats than vice versa.

In studying the spatial distribution of shrews, the majority of authors have arrived at the conclusion that preferred habitats differ among species. If body size of one species is larger than that of another, then it is supposed that the larger species forces the smaller into poorer habitat (Dickman, 1988). In the case of similar-sized species, e.g., *S. araneus* and *S. coronatus* (Neet and Hausser, 1990) or *S. vagrans* and *S. obscurus [=monticolus]* (Hawes, 1977) their ecological distributions are believed to be determined by competition. Neet and Hausser (1990) support this statement by their experiments with species removal. On the other hand, Hutchinson (1957) concludes that each species must have a refugium, where it is a favored competitor in relation to other species. In these studies only pairs of species were considered. In reality shrew communities are often composed of several species. Those investigators who worked with such communities (Getz, 1961; Brown, 1967; Spencer and Pettus, 1965) found that all species are mainly separated in space. Wrigley et al. (1979) noted that shrew species of the same community differ in size. Among species of similar size, abundance of one species exceeds other species abundances considerably. Churchfield (1984), Whitaker and French (1984), and Shvartz and Demin (1986) studied the feeding habits of different species in multispecies *Sorex* communities, and found that the differences in animal sizes are quite important for division of food resources, an essential condition for species coexistence.

In the present work I have arrived at the conclusion that, in the case of mutual coexistence of congeneric species of *Sorex*, on the one hand each species has a preferred habitat that is unique for this species; on the other hand neighboring habitats are occupied by *Sorex* species of different body size. The question of the role of interspecies competition in determination of such ecological distributions remains open. To solve it I analyzed published data on the ecological distribution of shrews in Siberia (Yudin, 1980; Yudin et al., 1976; Yudin et al., 1979;

Shvetzov, 1977; Sheftel, 1983). In general, the ecological distributions of species in the present study agree quite well with published data. As a rule, exceptions are noted in northern communities with low species richness. Thus, *S. roboratus* in the northern Yenisei River taiga in the absence of *S. araneus* occupies small-leaved and coniferous forests with developed herbaceous cover, while it normally did not occupy these habitats in the middle Yenisei River taiga region in the presence of *S. araneus* (Sheftel, 1983). In the same way, *S. tundrensis* in the northern forest and southern tundra in the absence of *S. caecutiens* occupied wet, mossy habitats (Yudin, 1980). Moraleva (1987) observed that, with increasing abundance of *S. caecutiens* (in years of peak abundance), *S. tundrensis* was forced out from habitats where this species was common in the prepeak year. During peak population growth of the dominant species *S. araneus* and *S. caecutiens*, the density of species with a narrow-space ecological niche (e.g., *S. roboratus*, *S. tundrensis*, *S. daphaenodon*) decreased.

Conclusions

Multispecies communities of shrews include coexisting species of both similar and different sizes. Each species has its own spatial optimum (center of ecological niche space) which is nearly always separated from that of other species. Neighboring habitats are occupied by species with different body sizes. Other studies have shown that species of small body size are forced by larger species into poorer habitats, where particular dimensional features of food objects enhance the survival of the larger species (Demin and Glazov, 1990). When species with similar body sizes occur in the same area, this can lead to parapatry with a narrow contact zone and pronounced segregation between habitats (Neet and Hausser, 1990; Hawes, 1977). In the case where ranges of similar-sized species overlap significantly, one species can live only in a suppressed state in the most productive habitats, which represents a kind of ecological refugium.

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Table 1.—*Distribution of shrew species in 11 different habitats during one abundance cycle 1978–1981 (individuals per 100 pitfall-nights).*

Habitats	Species									Total
	Sorex araneus	*Sorex caecutiens*	*Sorex minutus*	*Sorex minutissimus*	*Sorex isodon*	*Sorex tundrensis*	*Sorex roboratus*	*Sorex daphaenodon*	*Neomys fodiens*	
Bog forest	8.8	19.8	0.8	0.6	1.2	0.5	0.2	0.1	—	32.0
Boreal coniferous forest	34.1	29.4	1.6	0.7	1.1	0.9	0.8	0.1	0.1	68.8
Grass–moss small-leafed forest	43.7	29.8	5.6	0.8	1.7	1.5	1.5	0.1	0.1	84.8
Border of taiga forest	65.1	18.1	5.1	0.4	2.9	1.5	0.2	—	0.3	93.6
Dry meadow	21.3	7.6	2.0	0.5	1.1	2.3	0.1	—	0.2	35.1
Herbaceous riparian spruce forest	49.4	36.1	8.2	0.4	3.5	2.5	2.0	0.3	0.4	102.8
Riparian willow thickets	20.2	7.9	4.6	0.6	4.0	23.8	4.0	0.3	1.3	66.7
Floodplain forest with bushes	15.5	14.8	4.5	0.5	4.4	18.1	10.6	1.0	0.9	70.3
Seasonally flooded hillock meadow	14.7	11.8	5.7	0.4	4.5	7.0	5.0	1.1	0.7	50.9
Riparian high grass meadow	42.0	12.5	12.1	0.5	2.9	7.3	—	—	2.3	79.6
Marshy alder thickets	48.2	24.9	16.9	1.0	13.4	5.3	—	—	1.7	111.4

Table 2.—*Size of spatial ecological niche and average annual shrew abundance. Data represent an average for an eight-year period.*

Species	Size of Spatial Niche	Mean Relative Abundance
Sorex araneus	20.7 ± 1.18	33.7
Sorex caecutiens	19.4 ± 1.64	22.0
Sorex minutus	14.6 ± 1.25	4.2
Sorex minutissimus	10.4 ± 1.50	0.4
Sorex isodon	13.7 ± 1.00	3.1
Sorex tundrensis	8.3 ± 0.89	3.8
Sorex roboratus	4.9 ± 0.89	1.1
Sorex daphaenodon	3.7 ± 0.64	0.3
Neomys fodiens	5.0 ± 0.82	0.4

Table 3.—*Relation between the length of upper intermediate teeth in* Sorex *species (40 specimens for each species).*

Species	Length of Upper Teeth (mm)	Ratio of Length
araneus / caecutiens	2.82 ± 0.018 / 2.38 ± 0.018	1.18 ± 0.012
araneus / minutus	2.82 ± 0.018 / 1.93 ± 0.018	1.43 ± 0.016
isodon / minutus	2.85 ± 0.022 / 1.93 ± 0.018	1.48 ± 0.018
isodon / tundrensis	2.85 ± 0.022 / 2.30 ± 0.024	1.24 ± 0.016
roboratus / tundrensis	2.70 ± 0.022 / 2.30 ± 0.024	1.17 ± 0.055
roboratus / daphaenodon	2.70 ± 0.022 / 2.23 ± 0.018	1.21 ± 0.014

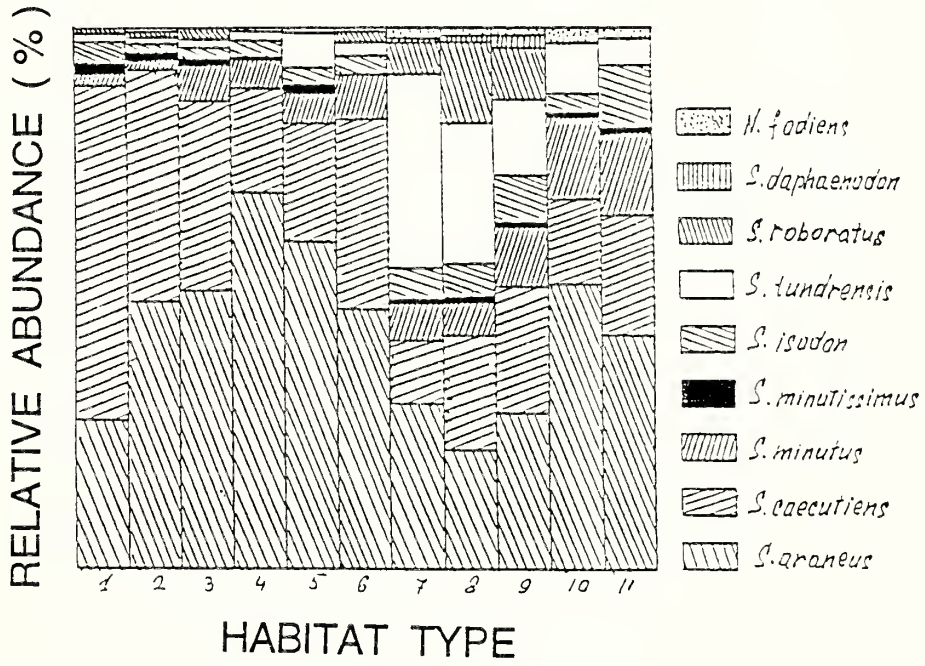

Fig. 1.—Relative abundance (%) of shrew species in the different habitats. 1, bog forest; 2, boreal coniferous forest; 3, grass–moss small-leaved forest; 4, border of taiga forest; 5, dry anthropogenic meadow; 6, herbaceous riparian spruce forest; 7, riparian willow thicket; 8, floodplain forest with bushes; 9, seasonally flooded hillock meadow; 10, riparian high grass meadow; 11, alder thickets.

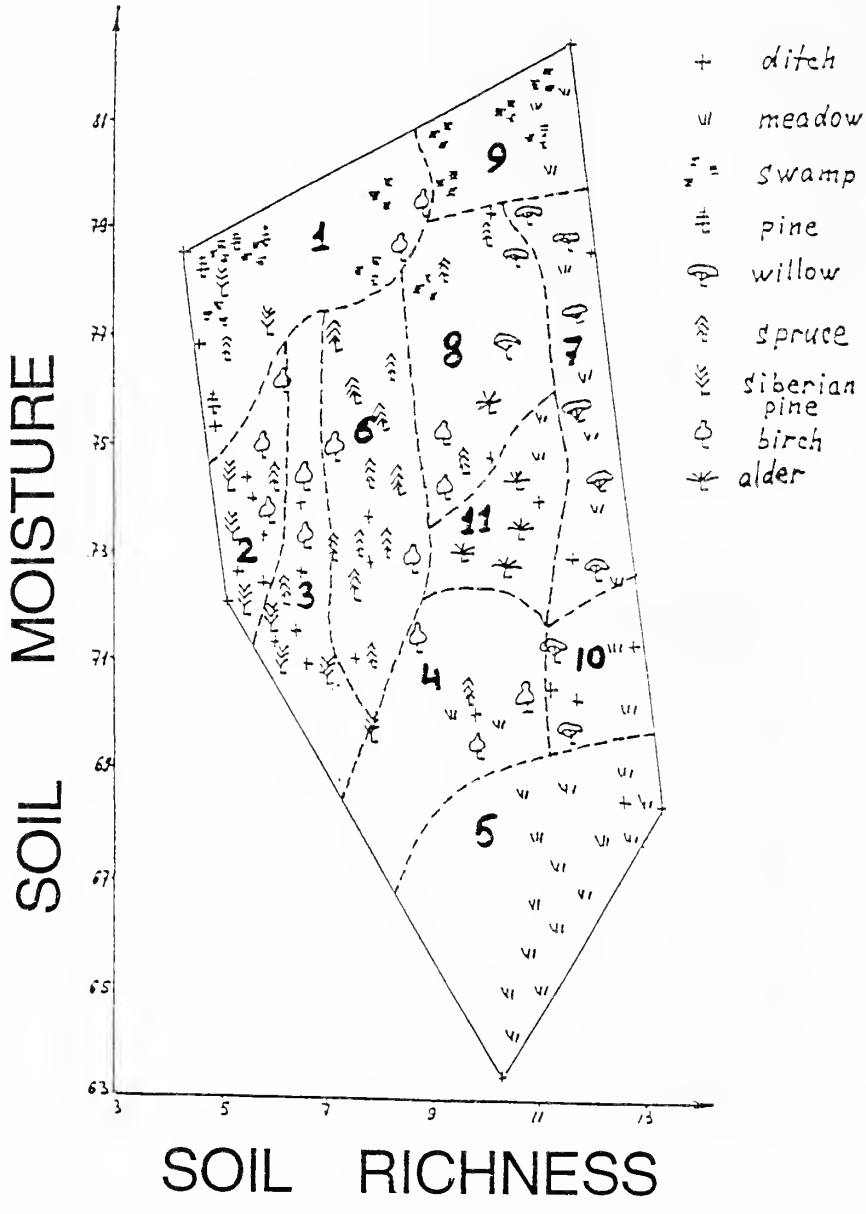

Fig. 2.—Observed ecological space with coordinates of soil richness and moisture according to Ramensky et al. (1956). (The order number of specific habitat is the same as in Fig. 1).

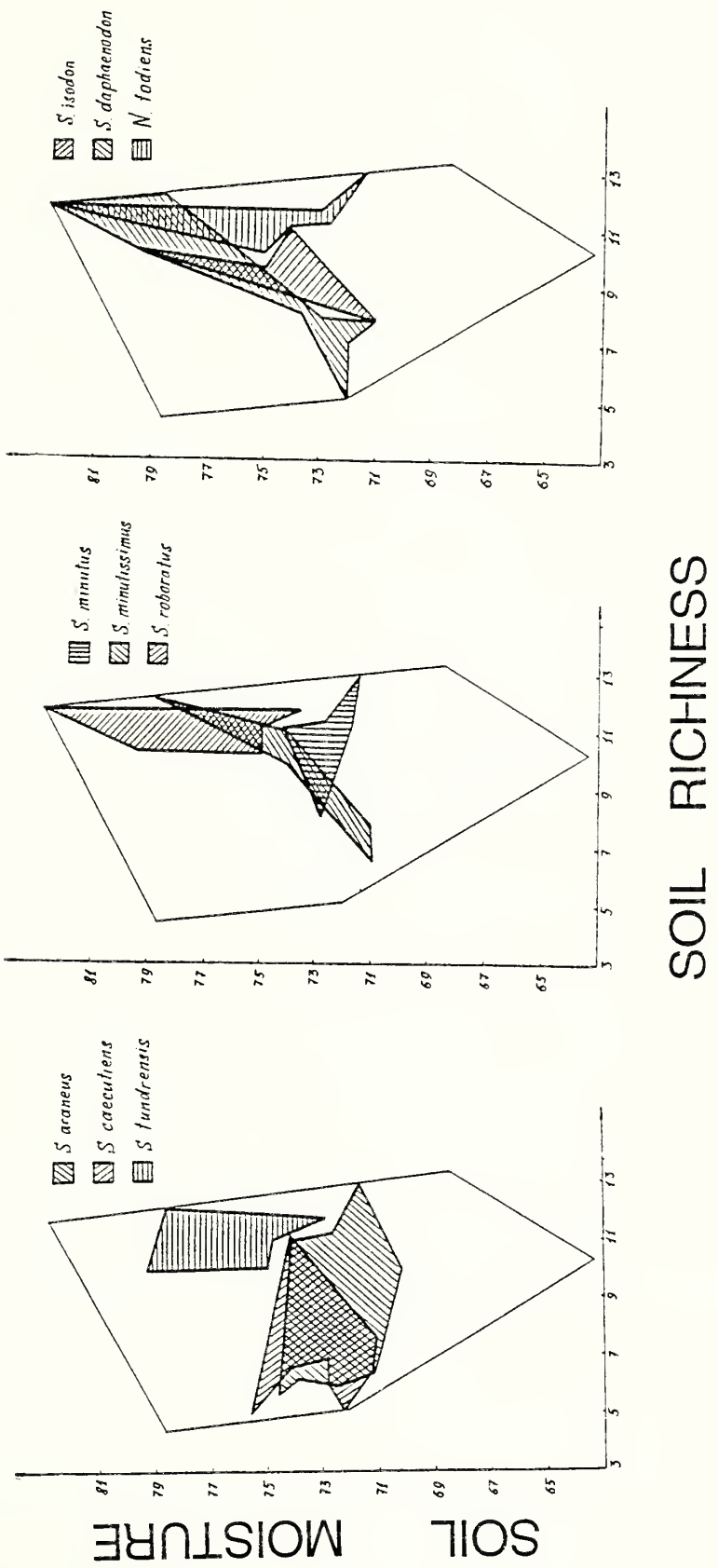

Fig. 3.—Map of the ecological distribution of nine species of shrews in 1980.

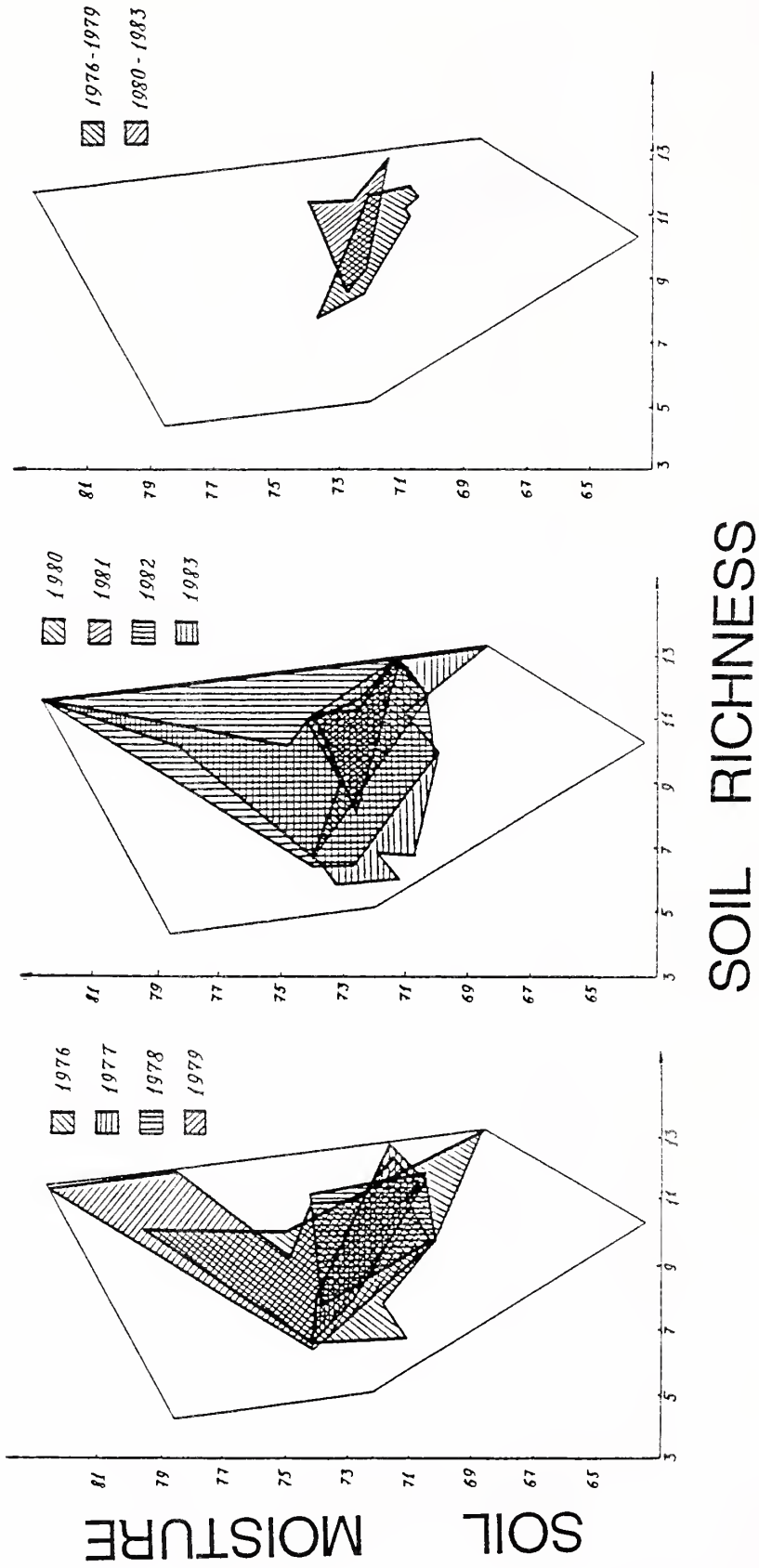

Fig. 4—Optimal ecological conditions of soil moisture and soil richness for *Sorex minutus* for the years 1976–1979.

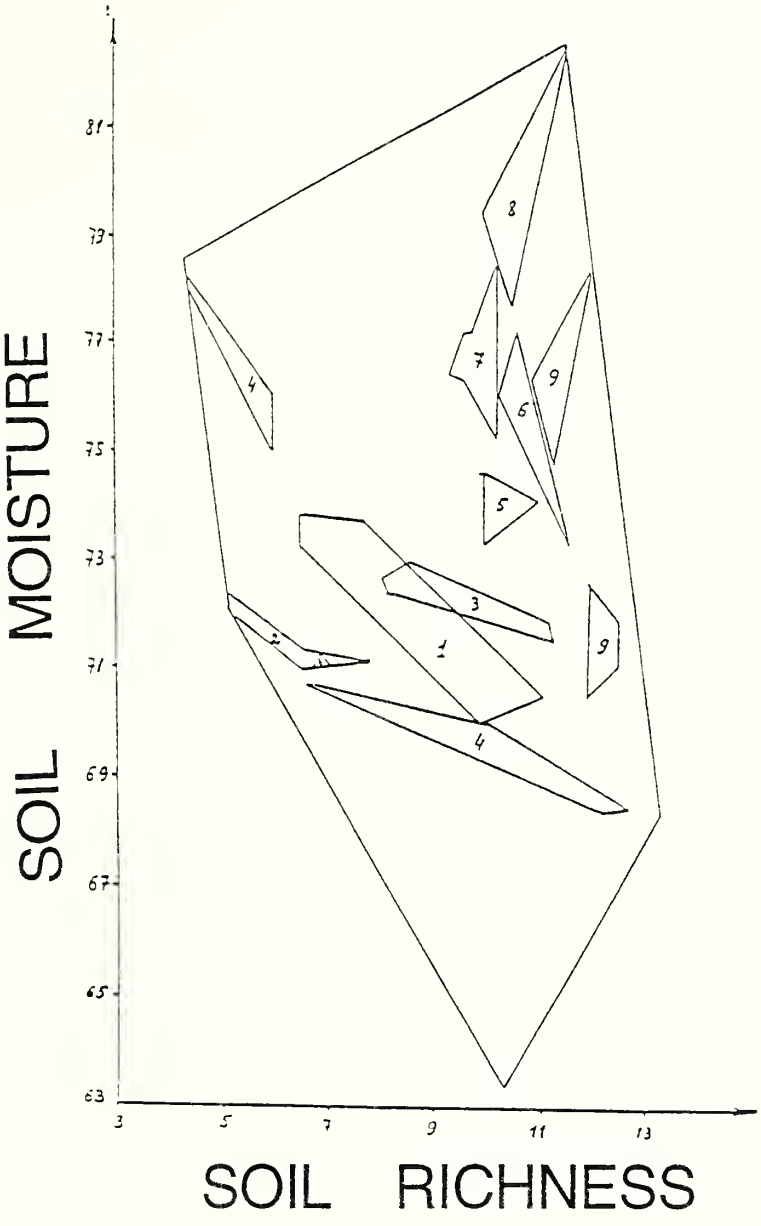

Fig. 5.—Map of ecological distribution of nine species of shrews in two-dimensional ecological space. 1, *Sorex araneus*; 2, *S. caecutiens*; 3, *S. minutus*; 4, *S. minutissimus*; 5, *S. isodon*; 6, *S. tundrensis*; 7, *S. roboratus*; 8, *S. daphaenodon*; 9, *Neomys fodiens*.

COMMUNITY ORGANIZATION OF SHREWS IN TEMPERATE ZONE FORESTS OF NORTHWESTERN RUSSIA

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ABSTRACT

The ecological distributions of six species of *Sorex* were studied during 12 years in the Novgorod region of northwestern Russia. Data on the biotopic distribution and estimated pattern of spatial association in multispecies communities of shrews were analyzed using cluster analysis. Results concerning the coexistence of closely-related species and the permissible limits of size similarities for such species are consistent with studies of Gause and Hutchinson. Species that were most similar in spatial distribution differed substantially in body size. Analysis of soil invertebrates revealed a relationship between population structure of soil invertebrates and biotopic distribution of shrews.

INTRODUCTION

Shrews (Soricidae) are small insectivorous mammals which often occur in assemblages of five or more species (Kirkland, 1991). Within the study area in northwestern Russia, as well as in regions of Siberia and the Far East, soricid species are rather uniform in morphology and ecology, which theoretically should hinder their coexistence. However, the species diversity of soricid assemblages usually is substantially higher than that of associated groups of small rodents (Sheftel, 1994). Most shrew species share a similar mode of life; they forage for invertebrates in the upper soil layers and forest litter. Our attention therefore was focused on the food resources of shrews as a basic factor determining the structural organization of multispecies communities.

MATERIALS AND METHODS

Data on the biotopic distribution of six species of *Sorex* (Table 1) were collected from 1975 to 1987 at a research station near Valdai (57°59'N, 33°10'E), Novgorod region, Russia. Specimens were caught with snap traps and in ditches (20 m in length). Trapping was concentrated in three periods: May–June, July, and August–September. Sampling effort totalled 37,632 trapdays and 1,259 ditchdays.

Geobotanical characteristics of the vegetation cover (ca 2,300 descriptions) of almost all traplines and ditches were recorded using the succession classification system of Razumovsky (1981) for the Moscow district. Razumovsky's classification scheme for describing native vegetation cover is a system of communities defined by floristic criteria (similar to the Braun-Blanquet method) and the ordination in space of moisture and soil richness factors. We used indicator species of plants for classifying plant communities in accordance with Razumovsky's system; however, we adapted this scheme slightly to meet the specific conditions of the study area and to facilitate data processing.

Soil invertebrates were collected near the trap stations. Samples of forest litter and soil layers were taken from 25 × 25 cm squares. Ten to 12 samples were taken in each habitat. Three hundred twenty samples yielded ca 10,000 invertebrates, which were scored, weighed, and measured in the laboratory. Eleven size classes of invertebrates were defined on the basis of 2-mm size intervals. The median size class was calculated for all habitats.

Skull morphology was examined in six species of soricids: *Neomys fodiens* (n = 20), *Sorex araneus* (n = 69), *S. caecutiens* (n = 39), *S. isodon* (n = 16), *S. minutus* (n = 45), *S. minutissimus* (n = 31). Only animals born in the same year were used, and the sexes were pooled. The following measurements were taken with an ocular micrometer (magnification 16X) to nearest 0.05 mm: length of mandibular symphysis (Fig. 1a), length of "arm" of mandible (from tip of I_1 to anterior edge of coronoid process, Fig. 1b), tip of first incisor to posterior tip of angular process of mandible (Fig. 1c), distance between anterior edge of M_1 and lower condylar facet (Fig. 1d), length of lower toothrow (Fig. 1e), and length of upper toothrow.

All measurements were taken by the second author. Means and standard deviations were calculated. Cluster analysis was used to present data on the spatial distribution of shrews. A value equal to 1.0 minus the correlation coefficient for the pairs of species was taken as a measure of the coupling. This measure helped to compare the ecological distributions of shrew species and did not depend on their abundance.

RESULTS

Abundance and Size Distribution of Soil Invertebrates

Samples of soil invertebrates tended to be dominated by smaller size classes (<4 mm; Fig. 2). The dominance of small forms was pronounced in habitats with low primary productivity (Fig. 2 a,b) such as pine forest on peat-moss bogs (oligotrophic marshes) and dry spruce forest (Fig. 2 a,b). Larger size classes were better represented in richer habitats such as taiga forests (Fig. 2 c,d).

The biomass of invertebrates approximated a normal distribution with very small and very large types constituting only a minor portion of the entire biomass. The distribution of biomass among size classes was more balanced in low productivity habitats (Fig. 3 a,b). In more productive plant

communities, the distribution of invertebrate biomass featured a peak of medium-sized items (Table 2, Fig. 3 c,d).

Biotopic Distribution of Shrews

Cluster analysis of snap trap data grouped four shrew species having similar ecological distributions (*Neomys fodiens*, *Sorex isodon*, *S. minutus*, *S. araneus*, Fig. 4a). These are listed in order of decreasing moisture of their preferred habitats. These species preferred rich, humid habitats dominated by grassy plant associations such as floodplains and drained lowland bogs, or European broad-leaved and coniferous-broad-leaved forests. *Sorex isodon* and *S. minutus*, which were most similar in their biotopic distribution, differ considerably in size (Fig. 5).

The distributions of *S. caecutiens* and *S. minutissimus* differed from this group. They preferred typical taiga forests; however, the small sample size of *S. minutissimus* (Table 1) limited comparisons with other species.

Cluster analysis of the data obtained from ditches showed very similar results (Fig. 4b). Three clusters are recognizable: two species of floodplain habitats (*N. fodiens*, *S. isodon*), two species of European broad-leaved and coniferous-broad-leaved forests (*S. araneus*, *S. minutus*), and two species of typical taiga (*S. caecutiens*, *S. minutissimus*). The correlation coefficients for the first two species pairs were 0.89 and 0.69, respectively, and differed from zero ($P < 0.003$ and $P < 0.07$).

In the second cluster, *S. minutus* grouped closer to *S. araneus* than to *S. isodon*. This may be due to the lesser resolution of captures in ditches and to the complicated conditions of the narrow floodplain of the Valdaika River, resulting in a combination of the data obtained close to the water and in the moister plant associations.

Similar results were also obtained when we analyzed the combined data from snap traps and ditches of Putchkovsky (1969*a*). There was negative correlation between the pairs of typical taiga shrews and shrews inhabiting richer biotopes. The distribution of *S. araneus* differed substantially from both taiga species and species inhabiting humid and rich habitats (Fig. 4c).

To conclude, the cluster analysis of biotopic distribution of shrews identified two groups of biotopically similar species: one group inhabiting rich, humid, grassy associations and European broad-leaved and mixed coniferous-broad-leaved forests (European faunal element with *S. araneus*, *S. minutus*, *N. fodiens*, and an eastern element, *S. isodon* [Shvarts, 1989]), and the other group inhabiting the taiga-type habitats (*S. caecutiens*, *S. minutissimus*, both representatives of the eastern element). Species with the most similar biotopic distributions were characterized by considerable difference in body size.

Morphometric Analysis of Feeding Apparatus of Coexisting Species of Shrews

The divergence of coexisting species in size of preferred food items is apparently related to differences in size of parts of the feeding apparatus (Hutchinson, 1959). Simberloff and Boecklen (1981) raised doubts regarding the significance of Hutchinsonian ratios; however, subsequent statistical analysis by Losos et al. (1989) lend support to the significance of these interspecific size ratios.

The ranges of ratios for five dimensions of the feeding apparatus (Fig. 1, b–e and length of upper toothrow) for pairs of species within the same faunal elements were: *N. fodiens/S. araneus* = 1.1–1.24; *S. araneus/S. minutus* = 1.32–1.39; *S. isodon/S. caecutiens* = 1.18–1.21; *S. caecutiens/S. minutissimus* = 1.16–1.29 (Shvarts and Demin, 1986). The ratios for pairs of species from different faunal elements were markedly smaller: *S. isodon/S. araneus* = 0.99–1.04; *S. minutus/S. minutissimus* = 1.04–1.12. The differences between species in pairs, *S. isodon–S. araneus* and *S. minutus–S. minutissimus*, for all jaw characters were not significant ($P > 0.1$). The coexistence of such species within individual habitats should be limited in accordance with ideas of Hutchinson (1959).

In the larger shrews (*N. fodiens*, *S. isodon*, *S. araneus*), the dimensional ratios were smaller than in the smaller species. This is, perhaps, connected with the fact that in case of shrews feeding on larger items, it is not the increase in the absolute length of jaws that is of primary importance but the increase in the power of the masticatory musculature. This is amply confirmed by the higher values for the ratios of dimensions of symphysis in the large shrews by comparison with the small species: *N. fodiens/S. isodon* = 1.3; *S. araneus/S. caecutiens* = 1.3; *S. caecutiens/S. minutus* = 1.14; *S. minutus/S. minutissimus* = 0.97. The analysis of the skull measurements showed also that the maximum size differences were between coexisting species, particularly between *S. isodon* and *S. minutus*, and *S. caecutiens* and *S. minutissimus* (Fig. 5).

Discussion

We compared the results of the morphometric analysis with data on density of individual shrew species in different habitats. The abundant species were *S. isodon* and *S. minutissimus*, two members of the Asian faunal element whose existence in multispecies soricid communities may have been influenced by competition with similar-sized species of the European faunal element (e.g., *S. araneus* and *S. minutus*, respectively).

Of the three most numerous species of shrews, *S. araneus* and *S. minutus* are members of the European faunal element and differ considerably in size (Fig. 5). This size difference apparently is sufficient for *S. caecutiens*, a member of the Asian faunal element, to coexist. Average ratios of jaw elements of the three species were *S. araneus/S. caecutiens* = 1.16–1.21, and *S. caecutiens/S. minutus* = 1.12–1.18. These are on the low end of "acceptable" Hutchinsonian ratios (Hutchinson, 1959). It is not known whether the size interval between *S. araneus* and *S. minutus* existed prior to the invasion of *S. caecutiens* or whether it represents an evolutionary response as has been demonstrated for Pleistocene *Sylvaemus* (= *Apodemus*) of the Near East (Tchernov, 1979). Based on the numbers of individuals collected, the data from our study suggest that *S. caecutiens* is more successful as a member of the Valdai Hills shrew community that either of the other two members of the Asian faunal element, *S. isodon* and *S. minutissimus* (Table 1).

The most closely associated species biotopically were *S. araneus* and *S. minutus*, which differ considerably in size. These two species of the European faunal element were clearly associated with nemoral or broad-leaved deciduous forest habitats. Unlike *S. minutus*, *S. caecutiens* was associated with taiga habitat and clearly preferred sites with continuous moss cover. *Sorex araneus* was considerably less abundant in such habitats. Despite the small number of *S. minutissimus* trapped, the species appeared to be closely associated with *S. caecutiens* (Fig. 4b). The spatial distributions of these two species in the Valdai Hills was thus similar to that reported by Putchkovsky (1969*a*) for these species in the taiga of the Onega Peninsula, approximately 770 km NE.

Sorex isodon was the most stenotopic shrew in the Valdai Hills. Its distribution was clearly restricted to humid, rich floral communities in grass bogs and meadow stages of the floodplains. Being a bit larger than *S. araneus*, *S. isodon* is adapted to coexistence with *S. minutus* and both had their highest densities in floodplain habitats. In regions of extensive floodplain habitats, *S. isodon*, which is usually rare in Europe, is numerically superior to *S. araneus* (Putchkovsky, 1969*b*). The data suggest that optimal habitats for *S. isodon* are humid and rich communities with well-developed grass cover, whereas *S. araneus* prefers drier broad-leaved deciduous (nemoral) forest communities (Sheftel, 1994).

Neomys fodiens is semiaquatic, inhabiting floodplains and seldom occurring elsewhere, except when displaced by rising flood waters. About 50% of the food items consumed by *N. fodiens* are aquatic organisms, which are less available to other species (Churchfield, 1984). The biomass of aquatic invertebrates must not be great or opportunities for water shrews to forage in aquatic habitats must be limited in the study area. How else can one explain that small number of *N. fodiens* in the floodplain? According to our data, taking into account all three study periods, there were 0.4/5.2/4.4 animals per ten ditches/days for *N. fodiens* and 0.7/9.8/11.2 for *S. araneus*. The absence of a satisfactory explanation for this case has allowed some authors to consider as peculiar the fact that the water shrew is not the most numerous shrew species in habitats adjacent to lakes (Churchfield, 1984).

The results of our analysis of organization of the shrew community agree with those of Sheftel (1994). It is important to note the fact that his work established not only the same patterns of organization in a nine-species shrew community, but also similar species optima in ecological space represented by soil humidity and soil richness.

The results of our morphometric and ecological analyses did not reveal the reasons for the clear numerical superiority of *S. araneus* over other species in our study (Table 1). In addition, the causes of changes in the role of one or other species in different habitats should be analyzed in more detail. Frequently, the abundance of species can differ substantially in adjacent habitats. For example, in taiga forests of the European part of Russia, *S. araneus* frequently is replaced by *S. caecutiens*.

We asked, what are the factors that determine the numerical domination of one or other species of shrews? In attempting to answer this question, we analyzed the numerical and biomass distributions of size classes of invertebrates in four habitats. We compared habitats on the basis of the median size class for biomass and number of invertebrates. There was a shift in the main biomass and number of invertebrates from smaller to larger size classes with increasing soil richness (Fig. 2, 3). Over the range of the poorest to the richest habitats there was a shift towards the larger items (Table 2). The distribution of shrew species by habitat mirrored shifts in resource abundance. The proportion of smaller-sized species of shrews was greater in poorer habitats, whereas larger species were dominant in richer habitats with more abundant prey items (Table 2). This may explain the phenomenon of different species of shrews being numerically dominant in adjacent habitats.

Two species (*S. araneus* and *S. caecutiens*) tend to dominate soricid communities in the region of the Valdai Station and in adjacent regions of European Russia. In this study, their numerical relationship is changed as invertebrate resources increased in biomass and shifted towards larger-sized prey. Thus the ratio between the numbers of *S. araneus* and *S. caecutiens* was 0.77 in dry pine forest, 2.28 in dry *Picea abies* forests, 3.65 in temporarily wet *Picea* forests, and 16.08 in forests of the river floodplains (Table 2). *Sorex araneus* was numerically dominant in the richest and medium-rich habitats but was substantially less abundant and comprised a smaller portion of the shrew community in poorer areas, where *S. caecutiens* frequently was the numerically dominant species (Table 2). Our data suggest that characteristics of the food resource base (number and biomass of different-sized invertebrates) govern the numerical superiority of individual shrew species.

A Model of Organization of Multispecies Community of Shrews

A relationship between abundance and body size of soil invertebrates was shown by Gilarov (1944) (Fig. 6a). Furthermore, Tseitlin (1985) demonstrated that the slope of the regression line was very similar for soil invertebrates of the tundra, coniferous forests, oak woods, and other zonal habitats. We may therefore assume that the size distribution of invertebrates shows a similar pattern in all north temperate habitats.

If we propose (Fig. 6a) that $\lg N = b - a \lg L$, and the biomass of each size class $B = k L^4 N$ (where L is the linear size of invertebrates; B its biomass; b, free term in the equation; and a and k, proportionate factors), then $\lg B = \lg k L^4 N = 3 \lg L + \lg k - \lg N$, or $\lg B = \lg N + 3/a(b - \lg N) + \lg k = 3b/a + \lg k + [1 - (3/a)]\lg N$. The dependence of the individual mass distribution on the size of the objects is shown in Fig. 6b.

On the basis of graphs and equations, the relationship between the biomass and body size of invertebrates was figured (Fig. 6c). As mentioned earlier, the highly abundant small-sized invertebrates have a very small total biomass. Large-sized invertebrates occur in low density but have a high individual mass. While a small-sized prey has a low energy value, a large-sized prey is probably rarely encountered as a result of its low abundance. As can be seen from the relationship between total

biomass and body size of invertebrates, the most economical strategy for predators such as shrews should be feeding on medium-sized invertebrates. However, if the same food source allows more than one species of shrews to coexist in the same biotope, then specialization of different species on different portions of the food resource spectrum must be expected. As the total biomass of both very small and very large invertebrates is relatively low, the number of predator species specialized on these prey groups will be also lower than the number of those feeding on abundant medium-sized prey.

The model allows some generalizations concerning the formation of shrew community and the rules of its organization.

1. The spatial distribution of shrews and their average annual population levels should be the result of a coevolutionary process within a community of several species of different sizes. The amount of competition between species is a function of overlap in the size of preferred food items, which is apparently closely correlated with jaw size (Pianka, 1978). Similar-sized members of the community should therefore occupy different habitats. But different-sized members of a community may coexist due to divergence in different size classes of food items.

2. In shrew communities with three or more species of shrews, certain species will be mainly adapted to feeding on invertebrates of the medium-sized classes. The greater abundance of such species may produce the impression of ecological plasticity in these shrews. In the case of two syntopic species, the one with a prey-size distribution corresponding to the main invertebrate biomass reserves will be dominant in number.

3. In the case of a secondary contact between species originating from different faunal provinces, those species for which no competitors of corresponding size are present should be the most successful.

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Table 1.—*Number of shrews caught in different habitats near the research station of the Institute of Geography, Russian Academy of Sciences.*

Species	Captured in Snap Traps	Captured in Ditches	Total
Sorex araneus	1,060	632	1,692
Sorex caecutiens	83	258	341
Sorex minutus	112	143	255
Sorex isodon	10	43	53
Sorex minutissimus	3	6	9
Neomys fodiens	17	103	120

Table 2.—*Relationship in structure of the population of soil mesofauna and shrews. Small species are* Sorex caecutiens, S. minutus,*and* S. minutissimus*; average number data indicate the number of mammals per ten pitfall-days.*

Type of Habitat	Biomass Median (mm)	Number Median (mm)	Share of Small Species (%)	Average Number	
				S. caecutiens	*S. araneus*
Pinus sylvestris–Vaccinium vitis-idaea–Pleurozium schreberi	8.8	2.4	60.8	2.00	1.53
Picea abies–Pleurozium schreberi	9.9	2.6	56.9	1.03	2.35
Picea abies–Oxalis acetosella	10.4	4.9	42.4	0.66	2.53
Picea abies (+*Alnus incana*)*–Geum rivale+Filipendula ulmaria*	11.3	5.3	16.5	0.25	4.02

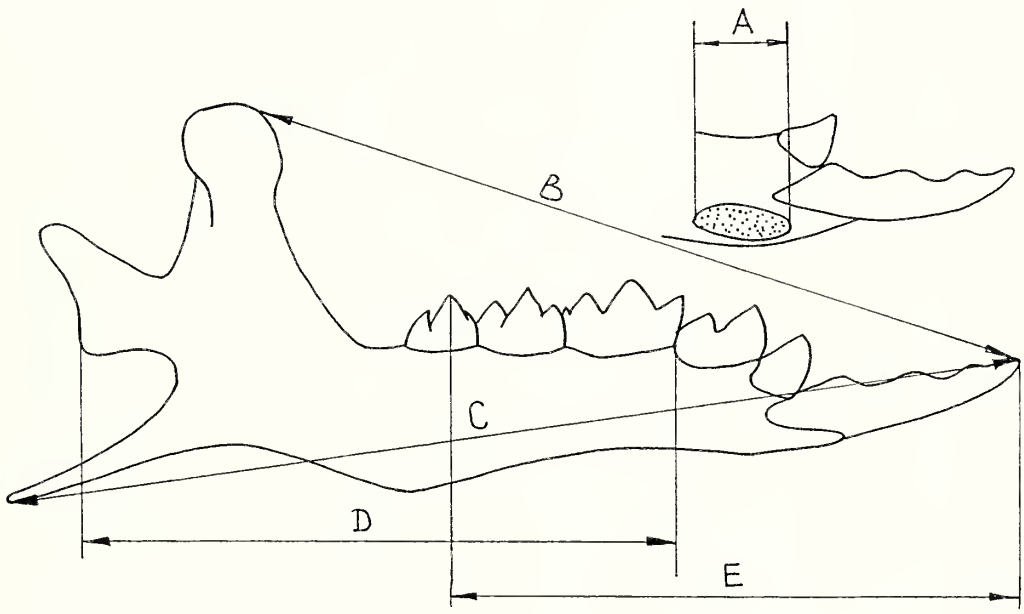

Fig. 1.—Measurements of the lower jaw of a shrew used for morphological analysis. a, length of lower jaw symphysis; b, length of the arm of the lower jaw (from the top of the incisor of the lower jaw to the anterior edge of the coronoid process); c, tip of first incisor to posterior tip of angular process of the mandible; d, distance between the front border of the molars of the lower jaw and the lower tip of the coronoid process; e, length of the lower toothrow.

Fig. 2.—Histograms of number/size class of soil invertebrates in the plant associations studies: a, *Pinus sylvestris*, *Sphagnum fuscum*; b, *Pinus sylvestris*, *Vaccinium vitis-idaea*, *Pleurozium schreberi*; c, *Picea abies*, *Oxalis acetosella* (taiga type); d, *Picea abies* + *Alnus incana*, *Geum rivale* + *Filipendula ulmaria*.

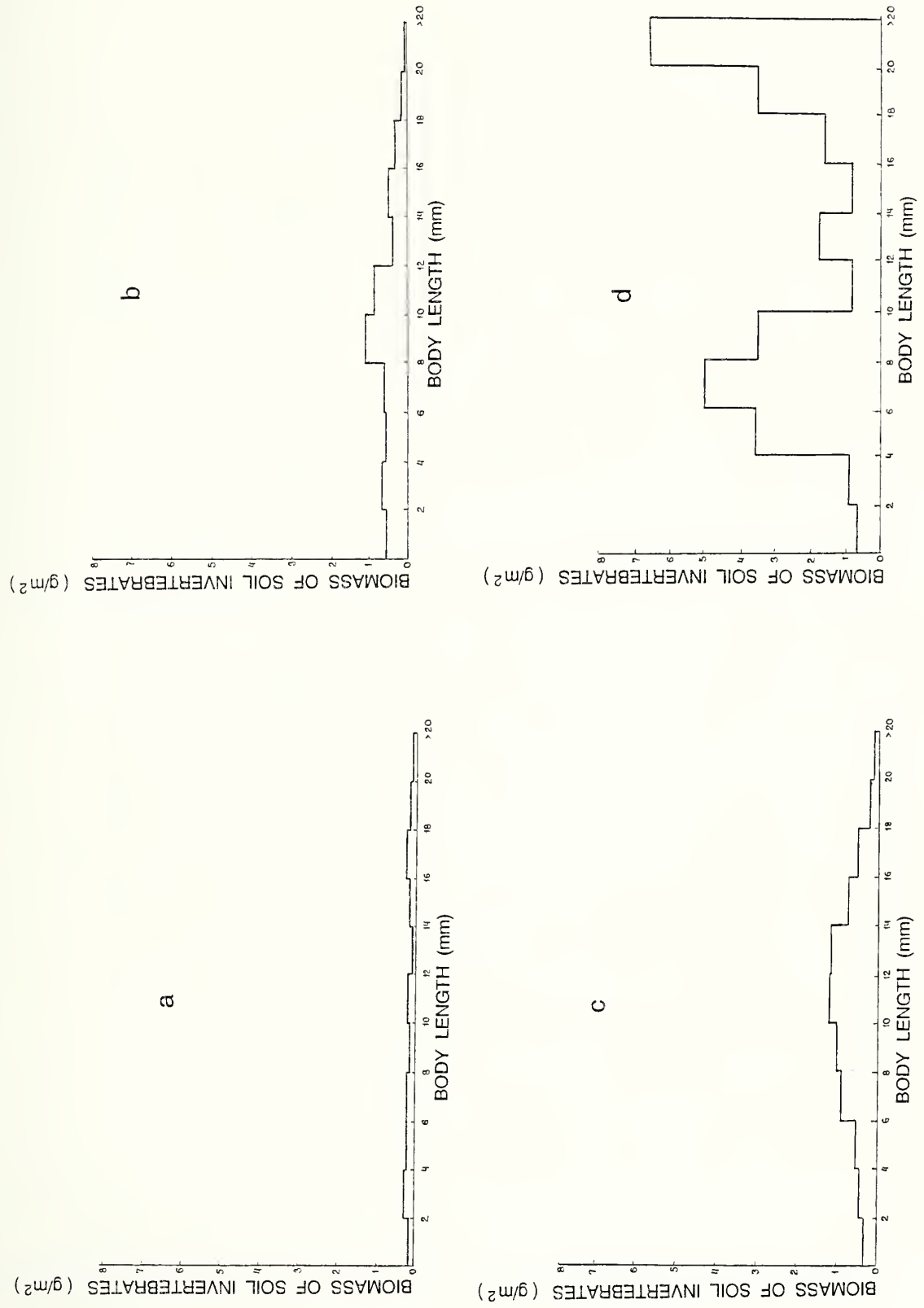

Fig. 3.—Histograms of biomass/size class of soil invertebrates in the plant associations studies: a, *Pinus sylvestris, Sphagnum fuscum*; b, *Pinus sylvestris, Vaccinium vitis-idaea, Pleurozium schreberi*; c, *Picea abies, Oxalis acetosella* (taiga type); d, *Picea abies* + *Alnus incana, Geum rivale* + *Filipendula ulmaria*.

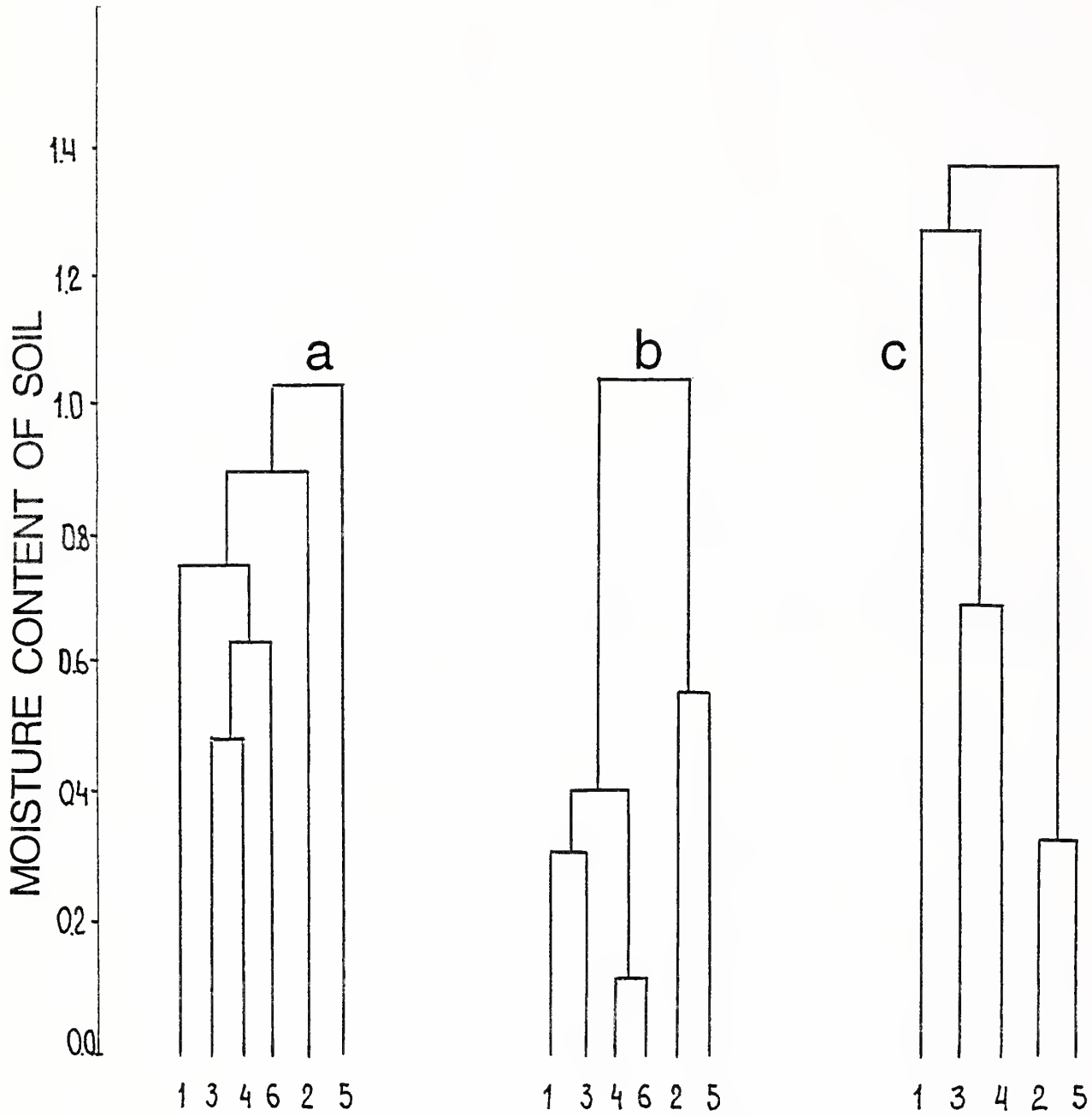

Fig. 4.—Cluster analysis of the data on the biotopic distribution of shrews in the study area. a, data from snap trapping; b, data from ditches; c, data of Putchkovsky (1969*a*). Numbers refer to the following species: 1, *Sorex araneus*; 2, *S. caecutiens*; 3, *S. minutus*; 4, *S. isodon*; 5, *S. minutissimus*; 6, *Neomys fodiens*.

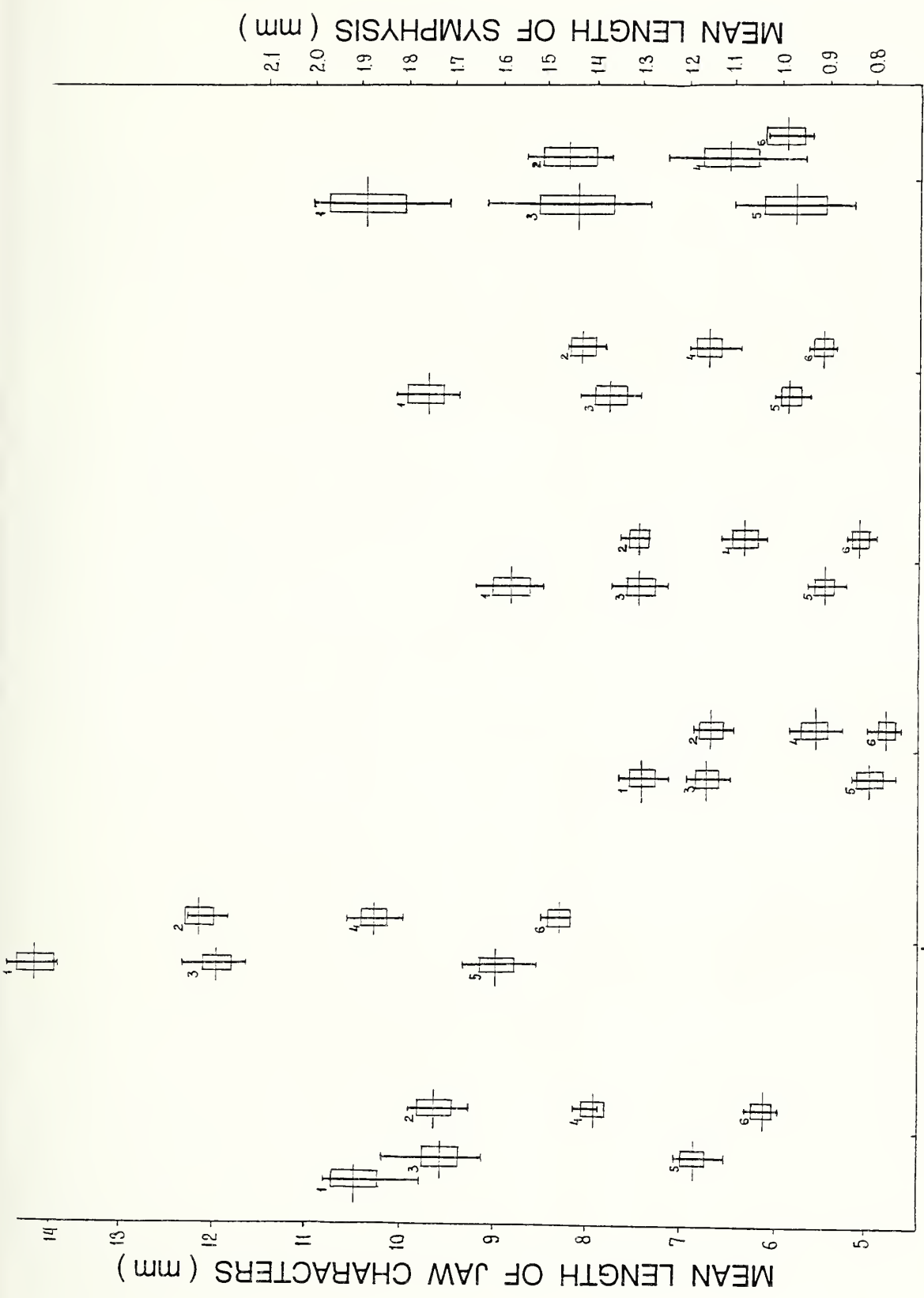

Fig. 5.—Means (±1 SD) of jaw characters in the shrews studied. 1, *Neomys fodiens*; 2, *Sorex isodon*; 3, *S. araneus*; 4, *S. caecutiens*; 5, *S. minutus*; 6, *S. minutissimus*. Characters: A, length of the arm of the lower jaw (from the tops of the incisor of the lower jaw to the anterior edge of the coronoid process); b, tip of first incisor to posterior tip of the angular process of the mandible; c, distance between the front border of the molars of the lower jaw and the lower tip of the coronoid process; d, length of the lower toothrow; e, length of the upper toothrow; f, length of the lower jaw symphysis.

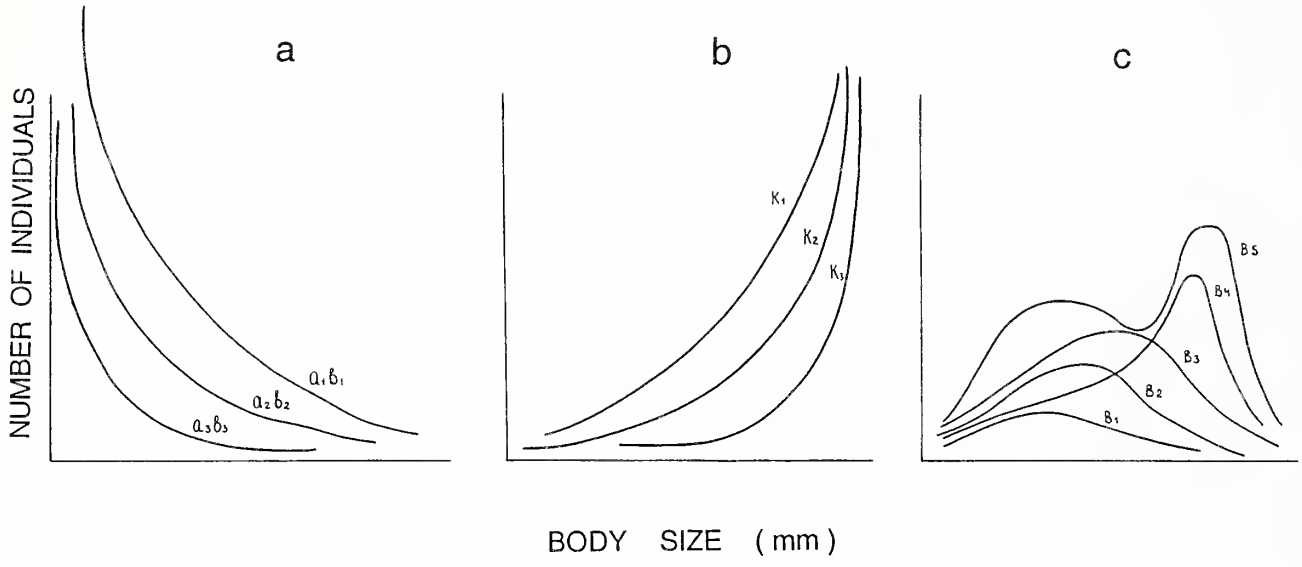

Fig. 6.—Numbers and individual mass of invertebrates in relation to body size and biomass distribution.

TERRITORIALITY IN JUVENILES OF THE COMMON SHREW (*SOREX ARANEUS*) IN PREPEAK AND PEAK YEARS OF POPULATION DENSITY

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ABSTRACT

The results of the study of the territoriality and spacing behavior of immature common shrews *Sorex araneus* in the middle Yenisei taiga are presented and discussed for prepeak (1984) and peak (1985) years. Using information obtained from 100 live traps and 60 pitfalls on a square grid, shrews were mobile in summer, but became sedentary by autumn. Three groups of animals—transients, settlers (short-term occupants of the grid), and residents—were delimited. The percentages of these groups remained constant irrespective of the increase of the total population density. The decrease of the home-range size in August in the peak year was accounted for mainly by settlers reducing their exploratory behavior. The decrease of the residents' home ranges in September may be one reason for the dramatic population crash in the winter period. The change in territoriality observed during the study is likely to be one of the main prerequisites for regular four-year cycling in population density.

INTRODUCTION

Many alternate causal mechanisms have been hypothesized to account for population fluctuations of small mammals. Four behavioral hypotheses were reviewed by Gaines and McClenaghan (1980): social subordination (Christian, 1970), genetic-behavioral polymorphism hypothesis (Chitty, 1967; Krebs, 1978, 1979), presaturation-saturation dispersal hypothesis (Lidicker, 1975), and social cohesion hypothesis (Bekoff, 1977). A resident fitness hypothesis (Anderson, 1989) and social fence hypothesis (Hestbeck, 1982, 1988) are also worthy of mention.

All hypotheses of population dynamics have been based on investigations of small rodents, mainly Microtinae (*Microtus* and *Clethrionomys*). Studies of the dispersal, territoriality, and spacing behavior of Soricidae are numerous, but most do not concern the variation of those parameters in relation to long-term population dynamics (Shillito, 1963; Michelsen, 1966; Hawes, 1977; Churchfield, 1980; Ellenbroek, 1980; Malmquist, 1986). Such research, especially in cyclic populations, is of great interest due to special biological features of the Soricidae. One of the most important features of *Sorex* shrews is that they usually do not breed in the year of their birth (Pucek, 1959; Kaikusalo and Hanski, 1985; Sheftel, 1989). Therefore, until the next spring all immatures are equal in their social status in the population, which usually is associated with sexual maturation (Gaines and McClenaghan, 1980; Boyce and Boyce, 1988).

The other characteristic feature of the soricid shrew is its solitary and aggressive nature (Crowcroft, 1957; Eisenberg, 1964; Moraleva, 1989). Stability of social interaction occurs only for mother and young. But at the end of lactation relations between mother and young and between siblings become aggressive (Dehnel, 1952; Moraleva and Pavlova, 1983; Michalak, 1988) and most immature animals disperse from their natal home ranges. In populations of common shrews, specific interaction between adults and immature animals was observed (Moraleva, 1989). Although breeding adult rodents achieve dominant rank (Gaines and McClenaghan, 1980), immature common shrews are able to pressure adult males and cause their emigration (Moraleva, 1989). Interaction between immature animals and adult females was more complicated. Immature shrews avoided encounters with adult females but at the same time dispersing females avoided the home ranges of immatures (Moraleva, 1989). Old adults disappeared from the population between July and October (Crowcroft, 1956; Michelsen, 1966; Pernetta, 1977; Churchfield, 1979, 1980; Moraleva, 1983, 1989). The influence of adult shrews on the dispersal and spacing behavior of immatures is less compared with rodents. That is the reason why it is possible to consider intraspecific interactions separately for sex and age groups. In this study, the interaction between adult and immature common shrews, considered previously (Moraleva, 1989), is examined critically during the summer period, when the territorial population structure is forming.

It is known that the shrew population of the present study possesses a four-year density cycle (Sheftel, 1989). We studied the spacing behavior during the summer of peak and prepeak years, keeping in mind that these data could be of some significance for the understanding of the general mechanism of population dynamics.

METHODS

Studies were conducted at the Northern Ecological Station, Mirnoe, of the A. N. Severtsov Institute of Evolutionary Morphology and Ecology of Animals, Russian Academy of Sciences. The station is located on the eastern bank of the Yenisei River, at the eastern edge of the western Siberian plain. The study area has a typical taiga landscape and is characterized by a continental climate (Sheftel, 1989).

Shrews were live trapped on the eastern bank of the Yenisei River, about 1.5 km from the river. The live-trapping area is typified by a mixed forest with *Pinus sibirica*, *Picea obovata*, and *Populus tremula* as the dominant tree species. The understory is dominated by *Vaccinium myrtillus*, *Equisetum sylvaticum*, and *Equisetum pratense*. Mosses, mainly *Pleurozium schreberi* and *Hylocomium splendens*, cover

40–50% of the area.

Live trapping was carried out with handmade, box-type live traps and pitfall traps with food and moss provided to increase the survival of shrews in the traps. A piece of porous, spongy material (Porolon) was placed on the bottom of the pitfall to absorb extra moisture. The pitfalls were covered to prevent rain water from entering.

Within the study area, 100 live traps were arranged in a square grid with a 15-m interval between traps (ten traps in a line). In addition, 60 pitfall traps were placed in seemingly favorable spots about 30 m apart. The live traps and pitfalls were examined every six to nine hours, and the shrews captured were marked by toe clipping. In 1984, the live-trapping periods were 23 June to 3 July, 6–15 August, and 14–19 September. In 1985, the trapping periods were 7–17 July, 1–12 August, and 14–19 September. We replaced traps in September 1985 to determine the boundaries of small home ranges. The date, time, and point of capture of each shrew were recorded. Shrews were classified as juveniles (sexually immature, current-year animals) or adults (sexually mature, over-wintered animals—Dehnel, 1949); gender was determined only for adult shrews. Dead shrews were autopsied. For statistical analysis we employed the Student *t*-tests and χ^2 test.

Results

All marked animals were divided into two groups—those never recaptured, and those captured more than one time. These categories were considered a reasonable approximation to evaluate dispersing and residential animals (Table 1). The difference in values obtained for peak and prepeak years was not significant ($P > 0.05$; $T_{st} = 0.42$). The number of newcomer animals sharply decreased in September and all (four and two) were recaptured. That is evidence for the end of dispersal at this time.

Some dispersing animals marked on the grid were recaptured outside the grid in the trapping ditches (Sheftel, 1989). These data give us an opportunity to estimate the distance of the movements of shrews. In 1984, two animals were captured in five and eight days after the first capture at 1.5 and 2 km away from the grid. In 1985, one animal was found 1.5 km away after 44 days. These results are in agreement with those previously reported (Moraleva, 1983). For both prepeak and peak years the majority of animals marked in July disappeared gradually by September and the base of the shrew population in September was composed of animals marked in August (Table 2). The difference in the proportion of animals marked in July that remained until September for different years may be affected by the fact that the term of trapping in 1984 occurred two weeks earlier than in 1985.

Several variations of spacing behavior of immature individuals can be recognized (Fig. 1a). There were some animals in the population that moved widely across the study grid (Fig. 1a). Most such animals usually were recorded only in one trapping period (e.g., nos. 216, 295) and single individuals (e.g., no. 179), during two trapping periods (July and August). This shows that such animals can occupy an area beyond the grid. The other type of spacing behavior is shown in Fig. 1b. These animals also moved widely but mainly within the grid. It is typical for them to investigate the site more thoroughly after crossing some distance (ca 80–100 m). Figure 1c depicts animals that appeared on the study grid in June (no. 52) or in August (nos. 226, 327). At the beginning they moved more widely and were likely to search the area in which to establish a home range. By the next trapping period in August or September they settled down in small home ranges. Figure 1d shows the sites of captures and borders of home ranges of resident shrews which lived there for a long time and never were recorded beyond these boundaries. Such animals usually were recorded all through the trapping periods in summer 1984 (Fig. 1d, lower portion), or in 1985 (Fig. 1d, upper portion). One animal (no. 81) survived the winter and was recaptured in the summer of 1985 within the same home range.

Thus, changes in the type of spatial behavior could be recognized through the transformation from wide, active movements to the restricted movements within the single home range. This pattern prompted us to use the maximum distance between capture points instead of an area estimate to express home range size. In this analysis we used animals which were captured more than three times in August and two times in September. The animals captured only on the last line of traps were not included (Table 3). The decrease of the home range size reflects the end of the exploratory period by September and the stabilization of the home ranges in both years (1984: $P < 0.01$, $T_{st} = 2.7$; 1985: $P < 0.001$, $T_{st} = 5.3$). The home range sizes in August ($P < 0.01$, $T_{st} = 2.9$) and September ($P < 0.01$, $T_{st} = 3.1$) decreased in the peak year in comparison with the prepeak year.

Numbers of individuals with different spacing behavior types are evaluated in Fig. 2. The analysis of histograms (χ^2 test) showed a significant difference ($P < 0.05$, $\chi^2 = 13.6$) between Augusts in prepeak and peak years. The differences in the distribution can be related to the increasing proportion of animals with a home range size of 20–40 m during the peak year. In the prepeak year, the proportion of animals with a home range size of 40–80 m was higher than in the peak year.

For the calculation of population density a strip half the width of the mean specific range of movement was added to the area of the grid. Chitty (1948) proposed the formula

$$A = L^2 + 4\,(Lr + \tfrac{1}{4}\pi r^2)$$

where A is the effective or true trapping area, L is the length of a side of the square trapping grid (the spaced-out area, within the confines of which the traps are arranged), and r is the radius of mean territory when it is assumed to be circular. The surface of the practical trapping area was 18,225 m^2 (135 m × 135 m). The means of territory size were calculated as a maximum distance between two points of recapture (Table 3). Half of this distance was considered as a radius (r) of activity ranges. Population density was expressed as the number of individuals per ha (Table 4). For purposes of density calculations we used the total number of individuals present on the grid more than three days.

The maximum density of shrews occurred in early August, so the competition for space at that time should be the most

intensive. Interaction between shrews in prepeak and peak years can be considered as competition between the "old" resident shrews marked during a previous trapping period (June or July) with established home ranges, and a second group of individuals appearing and settling down in August.

In the prepeak year the density of "old" residents in August was 3.6 shrews/ha. Their home ranges were exclusive and a considerable portion (about 80%) of the study grid was unoccupied. In contrast to that in August of the peak year, the density of "old" residents was four times more, 14.2 shrews/ha. Their home ranges covered 54% of the area of the study grid and the overlap was about 17% of the whole territory occupied. During both years, "old" residents disappeared gradually during August. Some of them showed dispersal trends because their last captures were outside of their home ranges near the border of the study grid.

For a comparison of the average numbers of recaptures per individual in different years, we used the animals which were caught in the first five days of the trapping period in August (Table 5). In the prepeak year (1984) the total number of recaptures per individual (7.9) for August was significantly greater ($P < 0.001$) than this parameter for "old" residents (2.9). However, there was no difference of these values (4.5 vs 3.8) for the peak year ($P > 0.05$, $T_{st} = 1.60$). The total number of recaptures per individual in the prepeak was significantly greater than the total in the peak ($P < 0.001$, $T_{st} = 3.7$), but at the same time there was no significant difference between "old" residents ($P > 0.05$, $T_{st} = 0.74$). Thus residential animals were captured in the same frequency in prepeak and peak years, but the frequency of recaptures was reduced in the peak years for those animals which appeared just in August.

The proportion of animals that persisted on the grid in August is shown in Fig. 3. The animals staying on the grid longer than ten days (to September or to the next year) are considered as residents. Animals of the intermediate type, called settlers, searched for territories and attempted to settle down. The differences in proportions of those types in the prepeak and peak years was not statistically significant ($P > 0.05$, $\chi^2 = 2.2$).

There were no significant differences in home range sizes in August between prepeak and peak years for residential animals (Table 6). At the same time the home range size of settlers decreased significantly in the peak year ($P < 0.05$, $T_{st} = 2.51$). Hence, the high density of "old" residents leads to reducing search activity of settlers.

On the other hand, settler shrews in August exhibited overlapping home ranges to a greater extent with "old" residents than did residents (those shrews remaining until September). The settlers, together with "old" residents, were captured in 41% of the traps, and residents in 26%. Intraspecific competition forced the shrews to avoid the home ranges of "old" residents and the most successful tactic was to settle in any unoccupied space between the home ranges of residents.

The final position of home ranges in September is shown in Fig. 4. In the prepeak year four new animals appeared in our grid. Two of them (nos. 259 and 279) settled in small home ranges. The home range of no. 279 overlapped with the home range of no. 182. Two other shrews (nos. 282 and 277) moved all over the grid as they tried to establish their own home ranges. In September of the peak year two new animals appeared—nos. 2511 and 2312. They both lived near the borders of the grid and were residents (Fig. 4). All animals of that time were strictly resident and stayed within small areas. Only two individuals (nos. 92 and 269) went beyond their home ranges a short distance; two others (nos. 189 and 212) moved widely enough and came to neighboring home ranges.

In September, when the border of home ranges stabilized, we calculated the area of home ranges (Table 7) using the exclusive boundary method (Ward, 1984). The size of home ranges varied between 440 and 1013 m^2 in 1984 and between 225 and 900 m^2 in 1985. The average size was smaller in the peak year ($P < 0.05$). These data are in agreement with those of Michelsen (1966), who found the winter home ranges of shrews to vary between 370 and 630 m^2.

Discussion

Our data show that the population structure of immature shrews of *S. araneus* in the Yenisei taiga was similar to other populations investigated and also labile on a seasonal basis (Shillito, 1963; Michelsen, 1966; Buckner, 1969; Pernetta, 1977; Churchfield, 1980, 1984). Shrews were mobile in summer and sedentary in autumn. However, the seasonal changes of population structure occurred more rapidly in this study than in European populations, probably due to the shorter warm period. In this study, the first litters began dispersing as late as 20 June (Sheftel, 1989), and all animals became residents by the middle of September.

Aggressive interaction in the natal nest stimulates dispersal of young (Dehnel, 1952; Moraleva and Pavlova, 1983; Michalak, 1988). As Michelsen believed, the young (at least of the first litters) occupy the optimal home ranges during the first weeks following dispersal. The investigation of interactions between adult females and immatures shows that the young of the first litters avoided the home ranges of breeding females and preferred to settle in unoccupied territories (Moraleva, 1989). By the time of the dispersal of the second litter (the end of June to the beginning of August), the majority of adult females have abandoned their home ranges and become transients. By early August, the population density as well as competition for space by immature shrews reached maximum levels and simultaneously the final rearrangement of individual territories of immatures occurred. Some residential animals disappeared from the grid. Probably some shrews perished, while others were forced to move as they were replaced by immigrants. Thus, the residential status of shrews did not determine the "winner" in competition for space. Individual features are likely to determine the result of interaction. The successful result of the competition for space may be dependent, for example, on the type of nervous system, body mass, or some other features. Hanski et al. (1991) suggested that the individual's competitive ability may be related to the biting strength of the jaw rather than body mass.

As a result of the sharp competition for space in August, territorial structure without overlapping home ranges was formed by September. By that time the dispersal process had actually finished and only scattered individuals kept searching for home ranges (Fig. 4). In September, the population consisted predominantly of shrews, mostly of the second litter, that had settled the grid in August. Hence, the actual role of the early- and late-born young in the maintenance of the population could be different. This evidence is in agreement with the idea (Pernetta, 1977) that the late-born young are the most important cohort in the population structure.

Individual variation in behavior is the rule rather than the exception in most species of animals (Slater, 1981; Ims, 1989), and should be especially important in shrew populations where individuals tend to be equal in age and sexual maturity, and prevailing ecological conditions seem uniform. Differences in spacing behavior of immature common shrews during summer is demonstrated here. Some shrews chose home ranges rapidly and maintained them without change throughout the year until the end of the next period of reproduction. Those individuals are similar to residents which were described by Inoue (1988) for *Sorex unguiculatus*. The opposite type of behavior was shown by transient animals, often moving a considerable distance. The maximum distance moved was about two km in our study but *S. araneus* is known to move even greater distances (Tegelstrom and Hanssen, 1987) and even to disperse over water (Hanski et al., 1991). All other kinds of territorial behavior in summer, demonstrated in Fig. 1, could be considered as variants of exploratory behavior, when animals tried to establish their home ranges. At the same time these different behavioral patterns could be imagined as a succession of actions; hence, different movement patterns reflect the different stages of settlement. At first, the shrews could move extensively like a transient, but subsequently the radii of their trips become shorter and at the end they choose their home ranges and become residents. On the other hand, some residents could be forced to disperse and become transient.

Frequently distribution diagrams show the relationship between home range length (Fig. 2) and the type of territorial behavior (Fig. 1). Home range length for residents (Fig. 1d) extends to 40 m, supporting the results of other authors: 17.8 m (Dickman, 1980), 22–24 m (Michelsen, 1966), and 11.4 and 30 m in different types of habitat (Yalden, 1974). Animals whose home ranges are 40 m to 80–100 m in length can be considered to be settlers searching for new home ranges in which to settle. This type of territorial behavior is shown in Fig. 1b, c. The animals moving wider than 80–100 m (nos. 216, 268—Fig. 1a) seems to be intermediate between transients and settlers.

Dispersal and social behavior in rodent populations are functions of age, reproductive status, and ecological conditions (Christian, 1970; Fleming, 1979). The dispersal of young is greatly influenced by philopatry as well as dominant rank and aggressiveness of adults, competition for breeding success, avoidance of inbreeding, and so on (for review, see Gaines and McClenaghan, 1980; Stenseth, 1983; Anderson, 1989). In contrast to rodents, all offspring of shrews are equal in breeding and social conditions and are able to force out adult males. In early August, offspring become independent from the influence of adult females (Moraleva, 1989), so dispersal of immatures was induced by internal factors only. The differences in dispersal trends of individual animals can be genetic in nature (Krebs et al., 1973; Krebs, 1978, 1979) or nongenetic, including maternal effects (Hilborn, 1975; Kawata, 1987) or developmental stability (Zakharov et al., 1991).

In this study density fluctuated from 7 to 36 shrews and correlated approximately with published results. For August–September, Shillito (1963) found density of the common shrew 24–28 shrews/ha, Yalden (1974) 42 shrews/ha, and Dickman (1980) 39 shrews/ha. In contrast, Michelsen (1966) calculated only the total number of shrews of territories present. Hence, our results for September are well-suited for comparison with Michelsen (1966), as at that time shrew dispersal became reduced and total number of territories could be actually evaluated. Our parameters for August were higher at the expense of the animals temporarily occupying the study grid. Population density (about 18 shrews/ha) observed by Michelsen (1966) actually did not change for the two-year investigation and correlated with the density characteristics of our population in the peak year (Table 4).

The difference in population structure for the prepeak and peak years can be considered a special subject. In the peak year the population density increased approximately two times in comparison with the prepeak year. The proportion of animals with different trends of dispersal remains constant irrespective of the variation in total population density (Table 1, Fig. 3). This is evidence that there is no correlation between the proportion of animals dispersing and the density of the population for the prepeak and peak years. As we later found, there was such a correlation in the years of low population density (Moraleva, unpublished data).

The increase in population density in the peak year led to reduction of home range size (Table 3). The decrease of the home range size in August as well as number of recaptures per individual (Table 5) was due mainly to settlers, which can be considered an indication of inhibition of exploratory behavior. This agrees with the Johnson (1988) model, predicting the decrease in exploration when density increased. The size decrease of the residential home ranges in September may be one of the reasons for the dramatic population crash in the winter period.

Because the region studied is characterized by significant spatial heterogeneity (Sheftel, 1989, 1994), models based on this factor (Lidicker, 1975, 1985; Hestbeck, 1982, 1988) are of interest for the analysis of the population dynamics.

Our data suggest that in the prepeak year the home ranges of the first generation animals do not cover the space completely. There are vacant areas remaining that permit other shrews to move and establish home ranges. The possibility of avoiding extra contacts as vacant areas are occupied decreases the stress level in the population. This pattern of distribution allows more "experienced" animals to find and occupy the best habitats. The same type of spacing (when more experienced animals were located in the optimal habitats) was found for the white-footed mouse (Morris, 1989). On the conditions of such

distribution, relatively few animals (in the first instance from poor habitats) are thought to perish in the extreme winter period. Intensive reproduction during the next spring produced a first generation of shrews that numbered about two times more in peak than in prepeak years. As a result of four times greater coverage by home ranges, exploration behavior was inhibited in the peak year. The most successful strategy is the fast selection of any vacant space in any type of habitat. In the peak year young shrews occupied all kinds of habitats, including suboptimal ones. According to the social fence hypothesis (Hestbeck, 1982, 1988), when population density rises above the carrying capacity, further population regulation is achieved through resource exhaustion. The reduction of the home range is believed to lead to resource exhaustion, making it impossible for some individuals to survive winter. When environmental resources become depleted in winter, animals probably begin to move. Obviously, shrews from the poorest habitats or those with smallest home ranges or the weakest individuals were the first to leave their home ranges ("saturation dispersal" according to Lidicker, 1975). Those individuals usually must cross the home ranges of residential animals, resulting in some extra stress and depletion of energy. The mobile animals are the first to die. Step by step, more and more animals perish during winter and density depression occurs.

This study of immature common shrews in prepeak and peak years supports the viewpoint that change in territoriality and spacing behavior can be one of the reasons for regular four-year cycling in the population dynamics of *S. araneus*.

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Table 1.—*Number and percentage of capture-recaptured* Sorex araneus *based on the period in which first trapped and marked in prepeak (1984) and peak (1985) years.*

	1984			1985		
Trapping period	6/23–7/3	8/5–8/15	9/14–9/19	7/7–7/17	8/1–8/13	9/14–9/19
Captured one time	19 (49%)	44 (44%)	—	42 (45%)	79 (49%)	—
Recaptured	20 (51%)	55 (56%)	4 (100%)	52 (55%)	82 (51%)	2 (100%)
Total	39	99	4	94	161	2

Table 2.—*Number and percentage of* Sorex araneus *in September in prepeak (1984) and peak (1985) years divided according time of marking.*

	1984	1985
Total in September	25	40
Marked in July	2 (8%)	13 (32.5%)
Marked in August	19 (76%)	25 (62.5%)
Marked in September	4 (16%)	2 (5%)

Table 3.—*Average home range size of* Sorex araneus *(in m between extreme capture points) in prepeak (1984) and peak (1985) years.*

	1984		1985	
	August	September	August	September
$\bar{X}$	65.6	32.5	44.4	16.5
SD	38.8	33.8	34.1	10.6
SE	6.2	9.4	4.2	1.9
n	39	13	67	31

Table 4.—*Population density of* Sorex araneus *(number of individuals per ha) in prepeak (1984) and peak (1985) years.*

	1984			1985		
	July	August	September	July	August	September
Radius	19.0	32.9	16.3	25.3	22.3	7.4
True trapping area (m^2)	29,619	39,466	27,669	33,688	31,626	22,159
Number of individuals	20	60	25	50	115	40
Density	6.8	15.2	9.0	14.8	36.4	18.1

Table 5.—*Number of recaptures per individual for* Sorex araneus *caught in first five days of trapping period in August in prepeak (1984) and peak (1985) years.*

	1984		1985	
	Total	"Old" Residents	Total	"Old" Residents
$\bar{X}$	7.9	2.9	4.5	3.8
SD	6.50	2.42	2.64	3.99
SE	0.99	0.9	0.34	0.69
n	44	8	60	35

Table 6.—*Average home range size of* Sorex araneus *in August for resident and settlers in prepeak (1984) and peak (1985) years.*

	1984		1985	
	Residents	Settlers	Residents	Settlers
$\bar{X}$	52.4	89.3	44.0	48.4
SD	19.9	47.3	30.0	30.0
SE	6.0	13.1	8.3	6.3
n	12	14	14	24

Table 7.—*Average home range size of* Sorex araneus *in September in prepeak (1984) and peak (1985) years (m^2).*

	1984	1985
$\bar{X}$	613.8	417.6
SD	203.7	204.3
SE	64.5	38.6
n	11	29

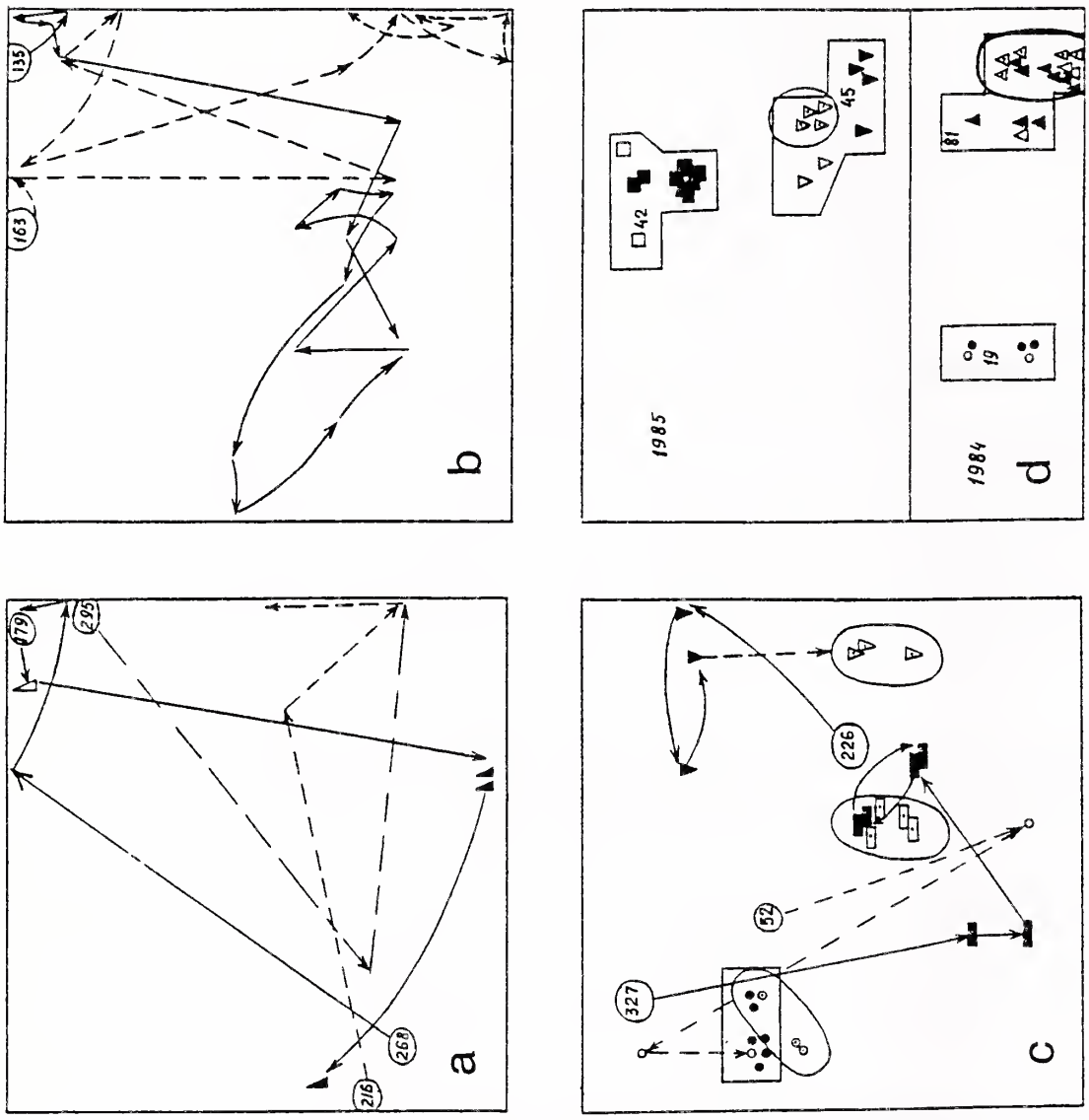

Fig. 1.—Variation in spatial behavior (a–d) of individually marked common shrews. The circled numbers indicate the points of first capture, arrows indicate the subsequent captures. Empty symbols indicate the points of capture in July, black symbols indicate August, symbols with a dot inside indicate September, solid lines indicate borders of home ranges.

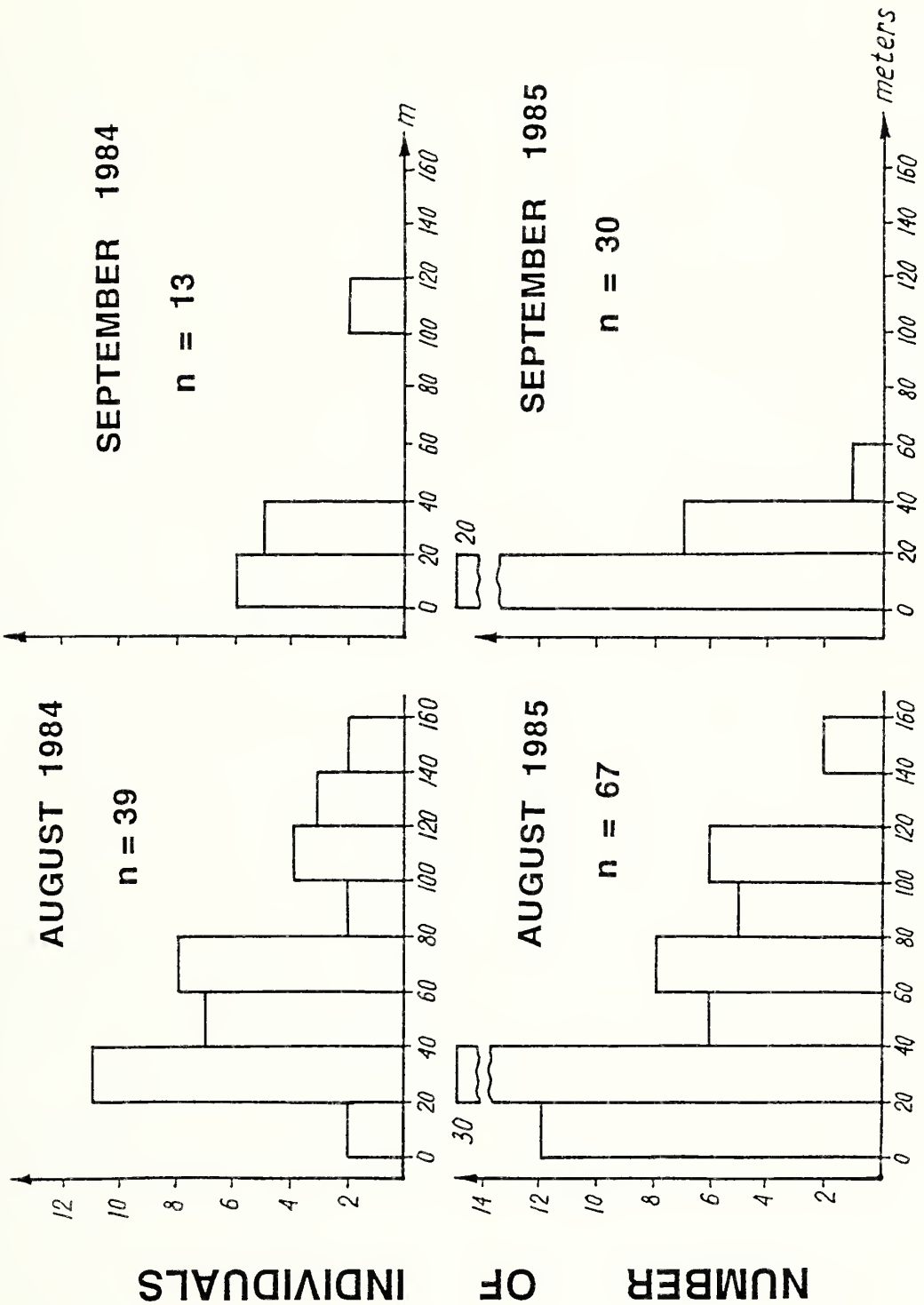

Fig. 2.—Home range sizes of common shrews in August and September in prepeak (1984) and peak (1985) years.

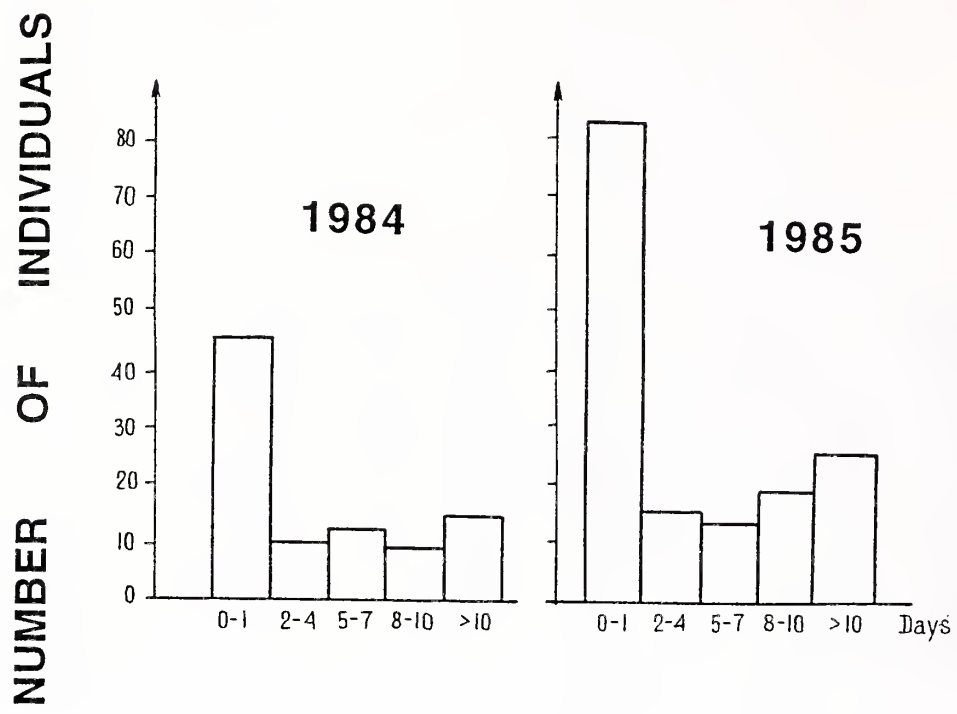

Fig. 3.—The duration (in days) spent by common shrews within the grid in August in prepeak (1984) and peak (1985) years.

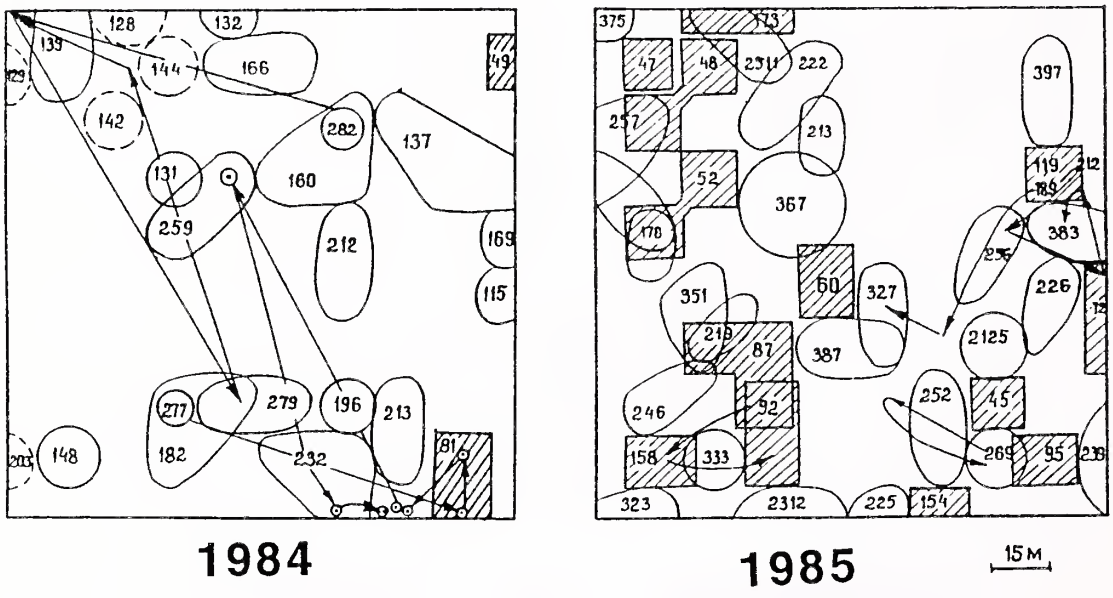

Fig. 4.—Movements and home ranges of individually marked common shrews in September of prepeak (1984) and peak (1985) years. All symbols, lines, and numbers as in Fig. 1. Dashed line indicates borders of supposed home ranges of animals captured in August 1984 and then 1985. Shaded areas indicate home ranges of animals marked in June and July.

FORAGING STRATEGIES OF SHREWS, AND THE EVIDENCE FROM FIELD STUDIES

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ABSTRACT

This paper outlines aspects of the feeding ecology of ten soricid species in an attempt to elucidate the foraging strategies of wild shrews using information gathered from field studies. Shrews are shown to be wide-spectrum feeders but the diet of each species is dominated by a few major prey taxa which are common and abundant. Shrews exhibit quantitative rather than qualitative specialization. While each species predominantly uses a single foraging mode with respect to prey location, this is not exclusive. Within the constraints of body size each species exploits a wide range of prey sizes which is attributed to encounter rates with invertebrates. Prey selection was related more to availability than to size or food value as a guide to profitability. While shrews take certain prey in proportion to their abundance, other prey appear to be underutilized, and the reasons for this are explored. Evidence of prey-switching and differential patch use is investigated. Shrews are found to be excellent opportunists with elements of dietary specialization and partial selection in addition to generalization. The feeding and foraging strategies that they employ allow exploitation of a full range of terrestrial and semiterrestrial habitats, and permit rapid adaptation to spatial and temporal changes in prey availability.

INTRODUCTION

With their high metabolic rates, voracious appetites, and continuous daily and year-round activity, shrews are of considerable interest with respect to their feeding ecology and foraging strategies. Questions arise about the ability of these small predators to locate sufficient food to satisfy their daily requirements, their selection of prey, their response to changing availability of prey, and their relationships with competitors. Shrews are diverse in form and in body size, and they have a wide geographical distribution, occurring in a range of terrestrial and semiterrestrial habitats. So, aside from their intrinsic interest they serve as useful models in the study of predator-prey interactions.

There have been numerous studies of the diets of soricids and we have considerable knowledge of the feeding habits of many species, such as *Sorex minutus* (Grainger and Fairley, 1978); *Sorex araneus* (Rudge, 1968); *S. cinereus*, *S. fumeus*, *S. palustris* and *Blarina brevicauda* (Hamilton, 1930); *Neomys fodiens* (Wołk, 1976; Churchfield, 1985; Kuvikova, 1985); and *Crocidura russula* (Bever, 1983). Fewer studies have investigated their feeding habits in relation to prey availability (e.g., Pernetta, 1976; Churchfield, 1982). Increasing interest is being shown in the community ecology of shrews and ecological separation between species, using diet and habitat use as indicators of niche overlap (Terry, 1981; Churchfield, 1984, 1991; French, 1984; Whitaker and French, 1984; Ryan, 1986). But there has been little effort to answer many basic questions about the foraging behavior and prey selection of wild shrews, and to develop theories about their foraging strategies based on data from field studies. This is in contrast to the growing literature on optimal foraging theory involving laboratory-based experiments on shrews (e.g., Barnard and Brown, 1981, 1985; Pierce, 1987). These studies suggest that shrews are more selective in their feeding habits than field studies have previously indicated.

Using data on the diets of ten soricid species from different geographic regions and habitats, and of different body sizes, this paper attempts to formulate some general theories about the feeding ecology and foraging strategies of shrews which can be derived from field studies of wild populations. In particular, it investigates prey selection by shrews.

Methods

Study Animals

Ten species of shrews, representative of different geographic ranges, body sizes, and foraging modes were studied (Table 1). They included three European species from Britain, three species from North America, two from subtropical Africa, and two large species from tropical Africa. Eight of these species are truly terrestrial and two species (*Neomys fodiens* and *Sorex palustris*) possess adaptations for a semiaquatic mode of life. While the shrews came from a diversity of habitats (grassland, scrub-grassland and forest), each species was collected from a single habitat type using live-trapping techniques. The aim of the investigation was not to provide basic data on the diets of these soricids but to explore trends within these species which might provide insight into the foraging strategies of shrews, making use of data available from field-based studies.

Diet Analysis

The feeding habits of each species were studied by stomach and/or fecal analysis. For seven of the species, alimentary tracts were available from 86 specimens ranging from 8 to 16 individuals per species (Table 1). From these specimens, stomachs and intestines were dissected and the complete contents removed for analysis of prey remains. The remaining three species (*Sorex araneus*, *S. minutus*, and *N. fodiens*) were part of longer-term population studies and, in order to avoid kill-trapping, their diets were studied through fecal analysis. The feces produced by a shrew captured in a live-trap constituted a single sample. A mean of 14 pellets per sample was obtained from *S. araneus*, 12 from *N. fodiens*, and six from *S. minutus*. Further details of the technique of fecal

analysis and a critique of the method can be found in Churchfield (1982). Reference collections of potential prey items were used to facilitate identification of invertebrate remains. From these it was possible not only to identify the types of prey consumed, but also their size ranges since, even in fecal samples, sufficiently large fragments of most prey were found.

Large numbers of diet samples were available from *S. araneus*, *S. minutus*, and *N. fodiens* (Table 1), covering different seasons. Fewer were available from the other species and coverage was more limited. The number of different prey taxa found will be affected by the number of samples examined, but sample number need not be great to provide a reliable indication of dietary diversity. Figure 1 shows the relationship between the number of fecal samples examined in random order and the cumulative number of prey taxa found for four species of shrews where dietary diversity was particularly high. Ninety percent of the prey types were recorded by the fifth sample in *Myosorex cafer*, by the seventh sample in *Neomys fodiens*, by the ninth sample in *Sorex araneus*, and the eleventh in *Crocidura hirta*. However, in view of the number of samples available, only *Sorex araneus* and *S. minutus* were selected for more detailed consideration.

Both stomach and fecal analyses are subject to criticism on the basis that the samples collected represent only a small component of the total diet, and that quantitative assessment is difficult or impossible when only small fragments of prey remains are found. Criticisms of the technique are discussed in Churchfield (1982). A major problem is the disparity between the number of prey taken and the volume they represent. Small prey, such as Formicidae and Isoptera, may have a high encounter rate and be eaten in large numbers, but their individual energy content is low compared with a large prey type, such as an orthopteran which has a lower encounter rate and is probably more difficult to catch and handle. Using stomach and fecal analysis and assessing the diet in terms of the frequency of occurrence of different prey items clearly creates a bias towards small prey items and does not give a true reflection of which prey types constitute the bulk of the diet. Therefore, the relative volume of each prey identified in stomach and fecal samples was assessed by eye and recorded. Results were expressed in terms of percentage composition by volume and percentage of dietary occurrences (the number of occurrences of a named prey item as a proportion of all occurrences).

Results and Discussion

Dietary Diversity and Specialization

Shrews feed on a wide range of invertebrates and in all but one of the ten species examined, the number of different prey taxa identified in the diet exceeded 12. The relatively low dietary diversity of some species, notably *C. poensis*, may be related to sample sizes. With the exception of a single incidence of bird remains in *N. fodiens*, no vertebrate parts were found. Plant material occurred in small amounts in some samples but will not be considered further here. The greatest dietary diversity, with 36 different prey taxa, was found in *N. fodiens*, which exploits both terrestrial and aquatic prey (Fig. 2). Most invertebrate taxa are consumed by shrews, and the many detailed diet studies of other soricid species by various workers confirm this (e.g., Hamilton, 1930; Rudge, 1968; Whitaker and Mumford, 1972; Whitaker and Maser, 1976; Grainger and Fairley, 1978; Bever, 1983; Churchfield, 1984; Whitaker and French, 1984). This suggests that shrews are wide-spectrum feeders, exhibiting little selection for prey type.

However, the many different prey recorded were not consumed in equal proportions and the bulk of the diet of each species comprised between two and five dominant prey types, each of which contributed at least 10% of occurrences and together made up at least 50% of dietary occurrences (Fig. 2). Despite differences in sample size, the number of dominant taxa was remarkably consistent. So, some degree of specialization or selection did occur. The identity of these major prey types differed according to the species of shrew, habitat and geographic location. Coleoptera and Araneae were particularly important prey for many temperate soricids, whereas Coleoptera, Orthoptera, Isoptera, Formicidae, and Diplopoda were dominant prey for the tropical and subtropical species.

Individual species tended, then, to take large proportions of a few prey taxa and smaller but fairly constant amounts of other prey. While the actual value of these components of the diet may differ from location to location, each species appeared to have its own typical prey specialties. For example, Coleoptera, Lumbricidae, insect larvae (Coleoptera, Diptera, and Lepidoptera), and Araneae together comprised a mean of 77% (SE = 9.1) of occurrences in the diet of *S. araneus* during three years of sampling in a grassland habitat. The observation that each species has prey specialties is confirmed by studies of coexisting shrews, such as *S. araneus*, *S. minutus*, and *N. fodiens*, where each species has its own distinct dietary profile in the proportions of different prey taxa eaten (Churchfield, 1984, 1991).

Foraging Mode

Prey specialization among individual species may be due to the adoption of a particular foraging mode which affects their encounters with certain prey types. Shrews are mainly active on or just below the ground surface, and this is reflected in the foraging modes identified for the eight terrestrial species studied here (Fig. 3). Most terrestrial species were found to be both epigeal and hypogeal, exploiting soil-dwelling invertebrates as well as surface-dwelling prey. However, the proportions of prey taken in each mode differed. Some species were almost exclusively epigeal (e.g., *C. viaria*, *C. poensis*) whereas others showed increasing subterranean activity, culminating in *S. araneus*. Temperate-zone species tended to show a greater degree of subterranean foraging than tropical or subtropical species. It is possible that differences in soil compaction, organic content, and/or abundance of soil-dwelling invertebrates, or a combination of factors, between tropical and temperate soils affect foraging modes of shrews.

Caution must be taken in interpretation of such results because of the disparity between the frequency of occurrence of different prey and their volume. The former takes into account the encounter rate of prey in that each occurrence is recorded, but small, frequently-eaten prey are likely to be

overemphasized. The latter takes into account the bulk of the prey, so large prey which may be encountered and eaten comparatively infrequently will be overemphasized. The disparity between the two was not found to be significant except in those species which had a particular foraging mode or dominant prey type, notably *S. araneus*, which consumed large quantities of earthworms. If the volume as well as the incidence of these prey is taken into account, then 74% of the diet of this shrew comprised subterranean prey, compared with only 42% in terms of the total occurrences.

The predominance of particular foraging modes within individual species can be associated with body size and anatomical adaptations (Hutterer, 1985). *Sorex minutus* is a small, lightly-built species, best suited for foraging on the ground surface and among vegetation. *Sorex araneus* is larger, more robust and better adapted for pushing into the soil. *Myosorex cafer*, another hypogeal, earthworm-eating soricid, is very similar. Despite their size, the two large tropical species (*C. viaria* and *C. poensis*) took few soil-dwelling invertebrates. This may reflect the scarcity of such prey relative to surface-dwelling prey, or the unsuitability of this foraging mode in hard tropical soils in the absence of special adaptations for burrowing, or both.

More obvious specializations are possessed by soricid species, including *N. fodiens* and *S. palustris*, which have evolved a semiaquatic existence and whose diets include a range of freshwater prey, mostly invertebrates (e.g., Hamilton, 1930; Wołk 1976; Churchfield, 1985). Nevertheless, *N. fodiens* and *S. palustris*, at least, still retain the epigeal and hypogeal foraging modes to a greater or lesser extent (Fig. 4). *Sorex palustris* appeared to be more of a specialist aquatic forager than *N. fodiens* since over 80% of its diet (both in terms of percentage dietary occurrences and prey volume) were aquatic in origin, compared with some 50% for *N. fodiens*. So, although dietary specialization occurs within species with respect to foraging mode, it is not complete or exclusive.

Prey Size Selection

Optimal foraging theory predicts that a predator should feed more selectively when profitable prey are abundant, and ignore unprofitable prey (e.g., Cowie, 1977; Krebs et al, 1977). Laboratory experiments on *S. araneus* suggest that size is a guideline of prey profitability, and that there is clear selection for larger prey (Barnard and Brown, 1981). Shrews preferred larger prey, but this depended on the encounter rate. If encounter rates for large prey were low, shrews became unselective. In the wild, shrews are presented with a great diversity of prey types and sizes. Is there any evidence that prey is selected because of size?

In the wild, all shrews catch and eat invertebrates of a wide range of body sizes. Even very small shrews take prey 30 mm or more in length, such as lumbricids and the larger Lepidoptera and Diptera larvae, in addition to tiny prey 3 mm in length. Some of the largest shrews may feed extensively on tiny prey 3–5 mm in length (e.g., Isoptera, Formicidae). Figure 5 shows the percentage composition by volume of prey of different size ranges found in the diets of the eight species of terrestrial soricids. Although there is no clear relationship between the size of the shrew and the prey taken, the bulk of the diet of the smallest shrews (*S. minutus*, *S. vagrans*, and *S. monticolus*) comprised small prey 3–10 mm in body length. *Sorex minutus*, with a mean body mass of 3.5 g, clearly preferred smaller prey.

The largest shrews, exemplified by *C. poensis* with a mean body mass of 16.0 g, took increasing quantities of larger prey. Medium-sized shrews 8–11 g took a more even spread of prey sizes. Clearly, body size (or, more appropriately, jaw size) influences the prey which can be tackled, but considerable variation occurs between species in the same size range. For example, *C. viaria*, despite being a large shrew of about 14 g, took great quantities of very small prey (Formicidae and Isoptera), in contrast to *C. poensis*. Unlike *S. minutus*, which rarely if ever eats earthworms, *S. vagrans* was found to take these large prey, despite the small size of those studied here (4.3 g body mass).

Thus, it is difficult to make generalizations concerning prey size selection since certain species clearly have a propensity for particular prey types, regardless of their size and their individual energetic considerations. The consumption of Formicidae by *C. viaria* suggests selection for these prey since *C. poensis*, which came from a similar area where these invertebrates are also extremely abundant, consumed few of them. Similarly, the consumption of large quantities of earthworms, which are relatively large prey, by *S. araneus* suggests a preference since they were not eaten to the same extent by *S. minutus* or *N. fodiens* living in the same habitat.

So, despite the choices available, wild shrews do not select the largest prey they can tackle but take greater numbers of apparently less profitable prey, such as formicids. Some even seem to specialize in less profitable prey. This suggests either that shrews do not relate profitability with prey size or that availability or encounter rate are key factors in prey consumption.

Prey Selection and Availability

The feeding habits of shrews vary according to habitat and location with respect to the identity of the major prey types consumed and their relative contributions to the diet (Rudge, 1968; Whitaker et al., 1983). There are also seasonal oscillations, although these are often of small magnitude (Pernetta, 1976; Churchfield, 1982, 1984). But, for a given location and habitat, different prey taxa assume a characteristic proportion of the diet of each soricid species. Figure 6 shows the mean percentage contribution of each major prey type to the diet of syntopic populations of *S. araneus* and *S. minutus* over a three-year period. Despite some seasonal differences in their relative importance, Lumbricidae, Coleoptera, Diptera larvae, and Araneae remained the four dominant prey types in the diet of *S. araneus*, and Araneae, Coleoptera, Hemiptera, and Lepidoptera larvae remained the major prey of *S. minutus*. Other taxa were secondary in importance. Is this an indication of prey selection or merely a reflection of availability and encounter rate?

There is some evidence to suggest that availability (and hence encounter rate) has an important influence on the incidence of certain prey in the diet. For example, changes in

seasonal abundance of adult Coleoptera, reflected in numbers captured in pitfall traps, were closely accompanied by changes in their composition in the diet of *S. araneus* (Fig. 7). In fact, there is a significant correlation between dietary incidence and the abundance of these prey (Fig. 8).

Despite signs of seasonal changes in the abundance of other prey and attempts to monitor their occurrence in field samples and in diets, no other positive, statistically significant correlations were found (Churchfield et al., personal observation). For example, Araneae were common prey of shrews throughout the year but they had a highly seasonal occurrence in field samples, with low numbers in winter and high numbers in summer. However, this was not reflected in the diet of *S. araneus*. Regardless of changing abundance, this species took a fixed proportion of these prey, around 11.0% of dietary occurrences. This may reflect the inability of *S. araneus* to catch these athletic prey, many of which are out of reach among the vegetation. Araneae featured much more prominently in the diet of *S. minutus* which is smaller and more agile on and above the ground surface than is *S. araneus*, but sample sizes were insufficient to permit further analysis of correlation for this species.

Similarly, Isopoda varied in availability according to season and habitat. Although they were certainly eaten more frequently by *S. araneus* in habitats where they were abundant than where they were scarce, there was little correlation between diet and availability because this shrew tended to take a fixed proportion of these prey (mean 5%, maximum 10%, of dietary occurrences). These prey had a clumped distribution and should be easy to catch and so could be highly profitable, and they were eaten in large quantities by *S. minutus* and *N. fodiens* in the same habitat. Clearly *S. araneus* is discriminating against them. It has been shown that certain isopod species are not favored by *S. araneus* (Crowcroft, 1957). *Sorex araneus* appears to avoid isopods when other prey are abundant. *Neomys fodiens*, with its larger jaws, may be better adapted for eating these prey. *Sorex minutus* may overcome these problems by selecting smaller species and/or individuals which are not so heavily chitinized.

It thus appears that feeding habits of shrews are not simply a matter of availability, for there are also elements of palatability which affect prey choice, and these differ among soricid species. For instance, Diplopoda were rarely eaten by *Sorex* species, and yet they were readily taken by *Neomys*, *Crocidura*, and *Myosorex*.

Prey Selection, Profitability, and Encounter Rate

Since the bulk of prey eaten by shrews are locally common and abundant invertebrates, why don't shrews specialize further and restrict their feeding habits to the most profitable prey? The consumption of Isopoda and Diplopoda, which have among the lowest energy values and the highest ash contents of any invertebrates (Cummins and Wuycheck, 1971) seems to contradict optimal foraging theory. Of all the major prey taxa commonly eaten by shrews, Coleoptera are among the most profitable in terms of high energy but low ash and water content (Cummins and Wuycheck, 1971; Churchfield, 1991). While they ranked within the first three most frequently consumed prey in the diets of the eight terrestrial shrews studied here, and were preferred by *S. araneus* (Fig. 8), no species fed exclusively on these prey.

The answer must lie in the encounter rate of such prey and the daily energy requirements of shrews, which dictate not only that a target number of prey must be captured daily in order to survive, but also that frequent meals are required. Profitable prey such as Coleoptera cannot be sufficiently abundant or catchable to enable them to serve as the sole dietary item. Although the probability of locating such a preferred prey may be high, the risk of not doing so may still be too great when starvation is imminent. Despite clumping of prey, shrews are likely to encounter invertebrate taxa one at a time and thus not be in a position to choose between them. While they are searching for the most profitable prey, they encounter other invertebrates which may be worth eating as a short-term solution. Small invertebrates, for instance, are far more numerous than large ones. The mere abundance (and encounter rate) of Formicidae and Isoptera in tropical regions may explain why they are dominant prey for some soricids. Although individually they may be classed as unprofitable prey, collectively they have higher energy contents per gram than Isopoda or Diplopoda, and much lower ash contents (Cummins and Wuycheck, 1971).

Difficulty of capture may also be an important factor in prey selection. Many important and profitable prey, such as carabid and staphylinid beetles and Araneae, are strong, agile and fast-running. Following detection, successful capture rates may be low, and so shrews may have to rely on easier prey much of the time. Given their energetic constraints, shrews simply cannot afford to be too selective.

Nevertheless, selection can still operate after a prey is captured, by eating only the most profitable parts of it. Observations of wild and captive shrews show that hungry individuals feed rapidly and fail to eat entire prey, discarding portions of legs, head capsules, and chitinous exoskeleton, and pressing on quickly to locate the next prey. This suggests that handling cost and profitability may indeed be taken into account, as optimal foraging theory suggests.

Whether selectivity increases with increasing satiation in wild shrews is not known, but this seems likely. Less desirable prey may be eaten early in a foraging bout when the shrew is very hungry, but ignored in favor of more preferred prey as the risk of starvation recedes.

All these factors would explain why shrews do not specialize more, and why shrews of different body sizes do not exhibit more selection in their prey sizes, particularly the larger shrews. Wild shrews seem to operate on a strategy of partial selection: they eat more of the most profitable prey if they are available but do not ignore other prey.

Prey Switching

How do shrews react to declining availability of major prey items? Because shrews feed on common and usually abundant prey it is rare for a particular prey taxon not to feature in the diet at any one time. Nevertheless, seasonal changes in

abundance do occur, and it may then be necessary for shrews to switch prey. An example of this is provided by the changing abundance of Coleoptera and the effect that this produced on the feeding habits of *S. araneus*. Density of these prey declined in winter. Their declining prominence in the diet was compensated for by an increase in the importance of certain other prey, namely Diptera larvae, Gastropoda, and Myriapoda. Individually none of these prey types compensated for the decline in Coleoptera, but collectively there was correlation between changing dietary occurrence of Coleoptera and the importance of these three alternative prey (Fig. 9). Again, no other prey type showed such a relationship with changing abundance. For example, Lumbricidae always featured prominently in the diet of *S. araneus* and, although they showed some seasonal variation in dietary occurrence, this was not consistent with changing importance of particular alternative prey. Again, Araneae were fairly consistent in the diet and their incidence was not related to other prey.

By retaining a diverse diet the amount of prey-switching need only be small. A decrease of 25% in the dietary occurrence of Coleoptera as a result of declining abundance required a change of only 3% in each of the eight other major prey taxa consumed to compensate for it, and this was hardly noticeable in diet samples. In the three taxa where a change was detected, only an 8% difference in each was required to compensate.

Response to Changing Population Density and Competition

Optimal foraging theory predicts that predators should become less selective in the presence of competition from conspecifics, and laboratory experiments have demonstrated this (Barnard and Brown, 1981). But there was no evidence of this in wild *S. araneus* in response to increasing population density and competition. The highly diverse diets of all shrews tend to obscure any possible differences in dietary composition within the same species, although changes in dietary diversity and niche overlap between species in different communities have been described (Churchfield, 1991). However, the abundance of invertebrates in many habitats suggests that intra- and interspecific competition may not occur (Churchfield, 1982; Churchfield and Brown, 1987). There is evidence that the availability of certain prey types affects the relative abundance of different shrew species. For example, *S. araneus* is rare in acid moorland while *S. minutus* is relatively abundant. This has been attributed to the dearth of earthworms, a major prey for *S. araneus*. *Sorex minutus* is able to subsist on small arthropods which are abundant in this habitat (Butterfield et al., 1981).

Patch Use

Most soricids appear to have stable home ranges which they occupy for most, if not all, their lives, although males may vacate their normal home ranges in response to the breeding season and the need to locate females (Pernetta, 1977; Churchfield, 1980*a*). Social interactions, including competition for food, and habitat characteristics may also affect the use of home ranges (Platt, 1976; Hawes, 1977; Neet and Hausser, 1990). But there is no evidence that shrews move home ranges solely in response to food supply. For example, in a recent field study in which abundances of major prey types differed between neighboring areas, and where *S. araneus* and *S. minutus* were free to move among these areas, there was no evidence that the shrews were attracted to sites where Coleoptera, for example, were most abundant (Churchfield et al., personal observation).

However, there is evidence that shrews use parts of their home ranges differentially in response to changing abundance and distribution of prey. They certainly respond to clumps of prey. This is clear enough during live-trapping studies when resident shrews can be attracted time after time to a food source in a trap. Experimental studies in outdoor enclosures with simulated natural environments also show that shrews will revisit or concentrate on sites where prey have recently been found (Churchfield, 1980*b*). Even diet studies of wild shrews show this to be the case. Dipteran larvae, such as Bibionidae, have a clumped distribution in the soil around plant roots where they feed. Fecal analyses of *S. araneus* showed that these prey were eaten in considerable numbers whenever a patch was located. Up to 15 larvae were found per fecal sample. Attraction to clumped prey may also occur in tropical soricids, such as *C. viaria*, which feeds extensively on Isoptera and Formicidae. However, in the absence of field experiments to investigate patch or home range use in response to food distribution little more can be concluded.

Conclusions

All soricid species examined exhibited high dietary diversity, but with some specialization with respect to the dominant prey types exploited. While each species showed some specialization for a particular foraging mode, this was not exclusively used. Each species took a wide range of prey sizes. There was some selection for prey size but this was not strictly related to the body mass of the shrew. Prey selection was related more to availability and encounter rate than to size or food value as a guide to profitability. Elements of catchability and palatability also influence prey choice. Shrews are true opportunists. They show elements of specialization and partial selection for prey on the basis of dietary composition, foraging mode, size, and profitability, in addition to generalization. This permits rapid adaptation to spatial and temporal changes in prey availability.

Acknowledgments

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Table 1.—*The soricid species examined in the present study including body sizes and geographic origins.*

Species	Mean Body Mass (g)	Collection Site	Sample Size (*n*)
Sorex araneus	8.2	Southern England	240
Sorex minutus	3.5	Southern England	35
Neomys fodiens	11.9	Southern England	169
Sorex vagrans	4.3	Sierra Nevada, California	16
Sorex monticolus	5.5	Sierra Nevada, California	10
Sorex palustris	11.7	Sierra Nevada, California	15
Myosorex cafer	10.0	Eastern Zimbabwe	13
Crocidura hirta	10.0	Northern Zimbabwe	14
Crocidura viaria	14.3	Burkina Faso	10
Crocidura poensis	16.0	Southeast Nigeria	8

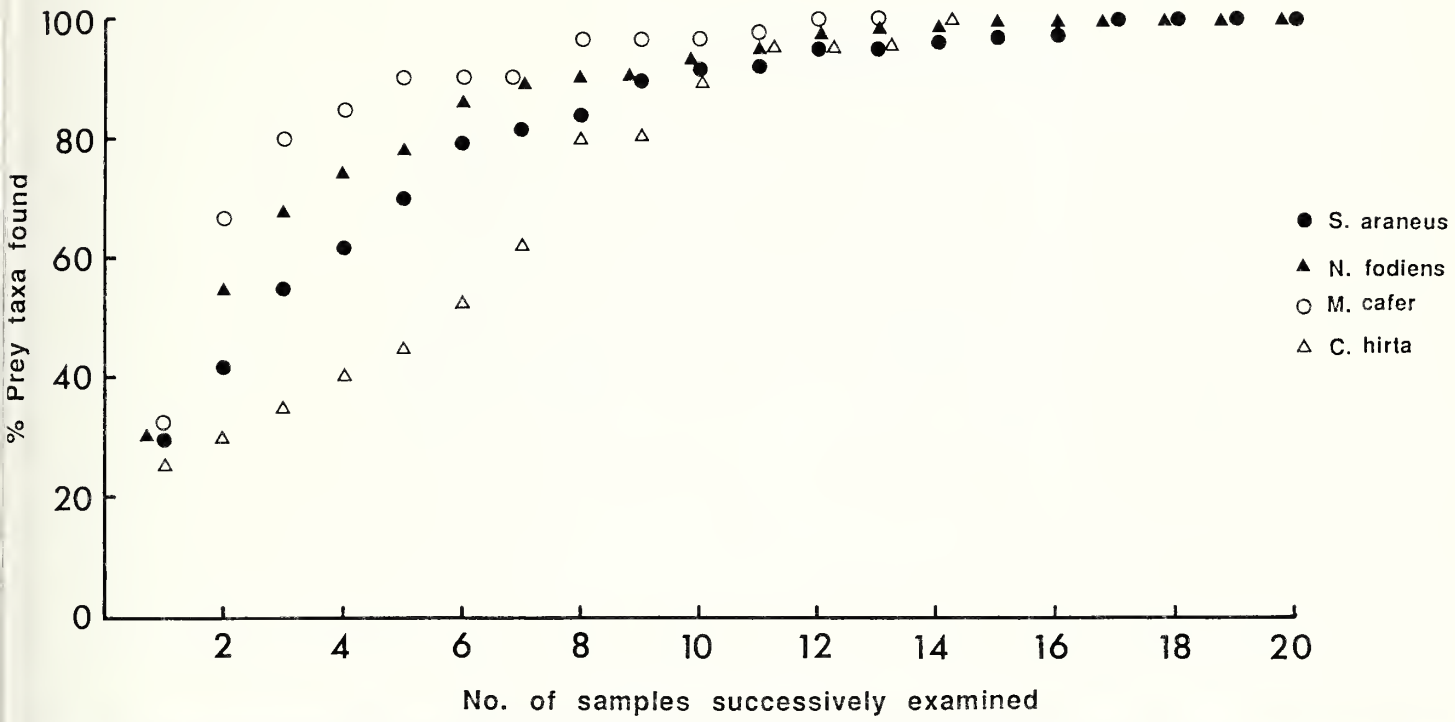

Fig. 1.—The relationship between the number of diet samples examined and the number of prey taxa found.

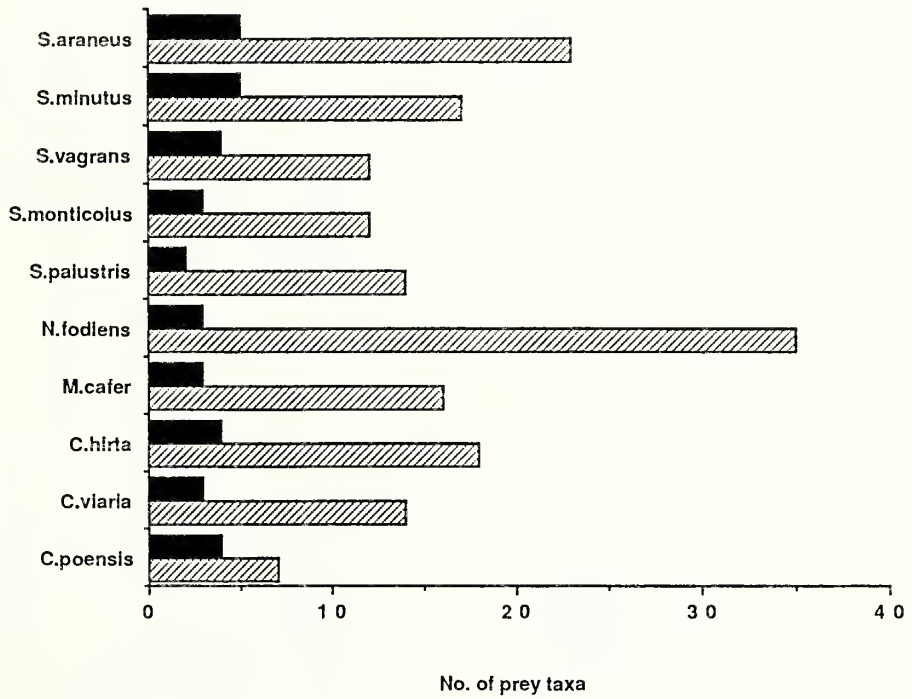

Fig. 2.—Dietary diversity and the number of dominant prey types in ten species of shrews. Hatched bars represent the total number of prey taxa identified; solid bars represent the number of dominant taxa.

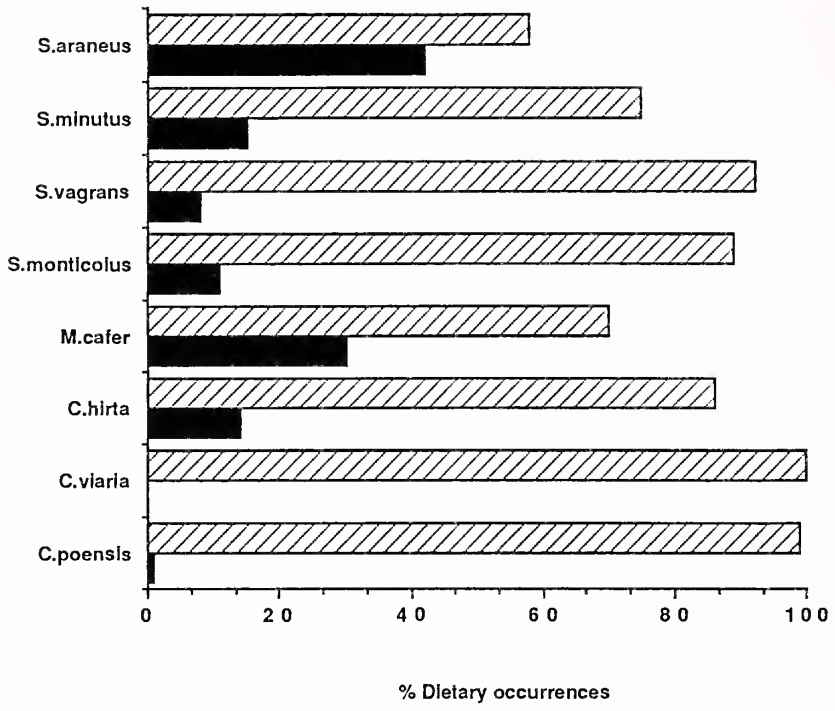

Fig. 3.—Foraging modes of terrestrial shrews: the percentage dietary occurrences of surface-dwelling (epigeal: hatched bars) and soil-dwelling (hypogeal: solid bars) prey in the diets of eight terrestrial soricids.

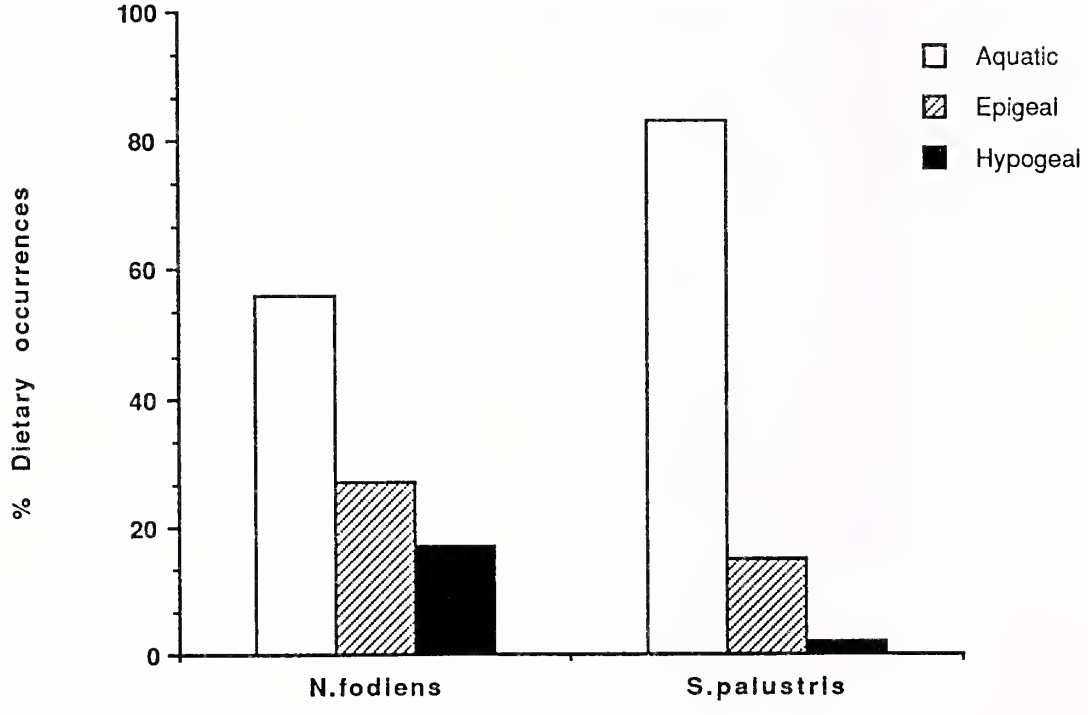

Fig. 4.—Foraging modes of two semiaquatic soricids, *Neomys fodiens* and *Sorex palustris*.

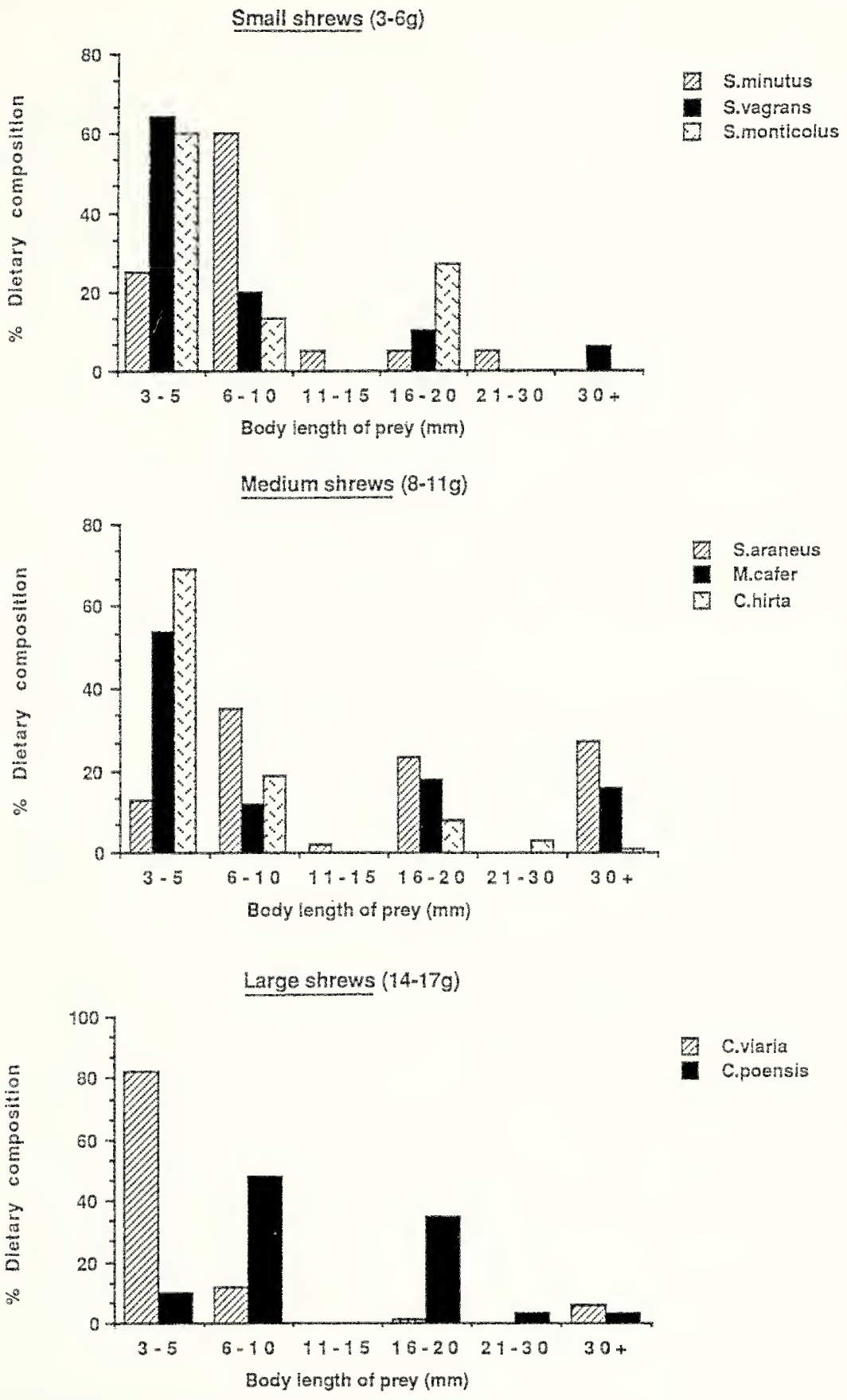

Fig. 5.—The percentage composition by volume of prey of different body lengths in the diets of small, medium, and large shrews.

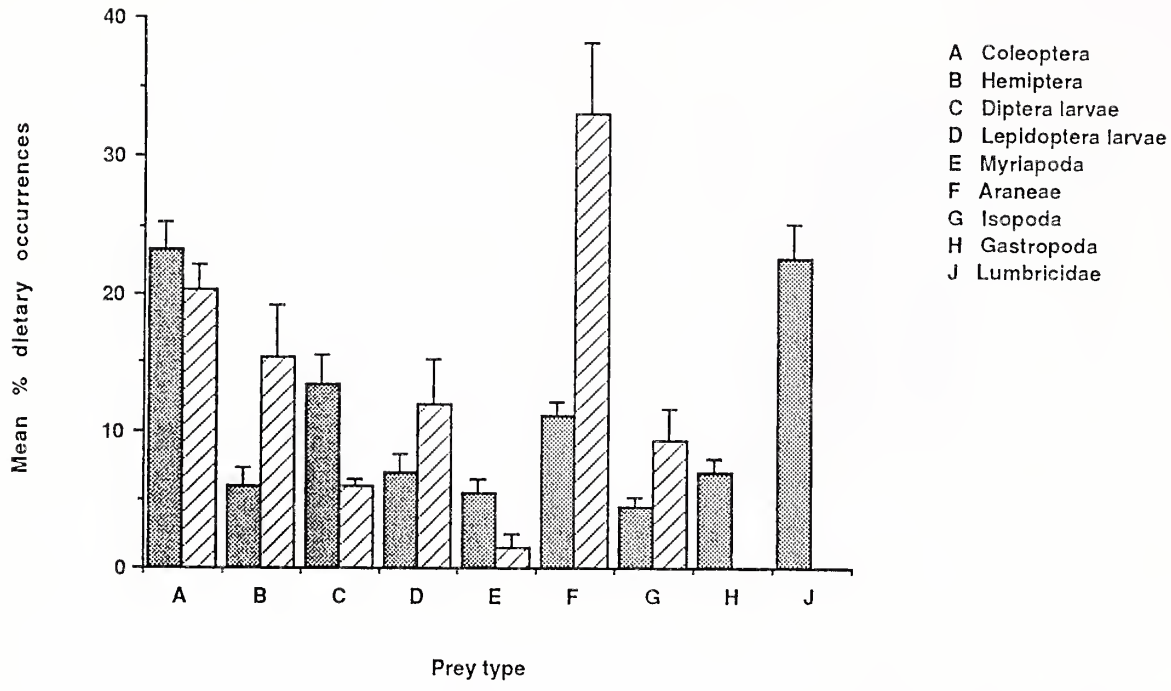

Fig. 6.—The mean percentage dietary occurrences of nine major prey types in the diets of *S. araneus* (shaded bars) and *S. minutus* (hatched bars) over a three-year period, with standard errors.

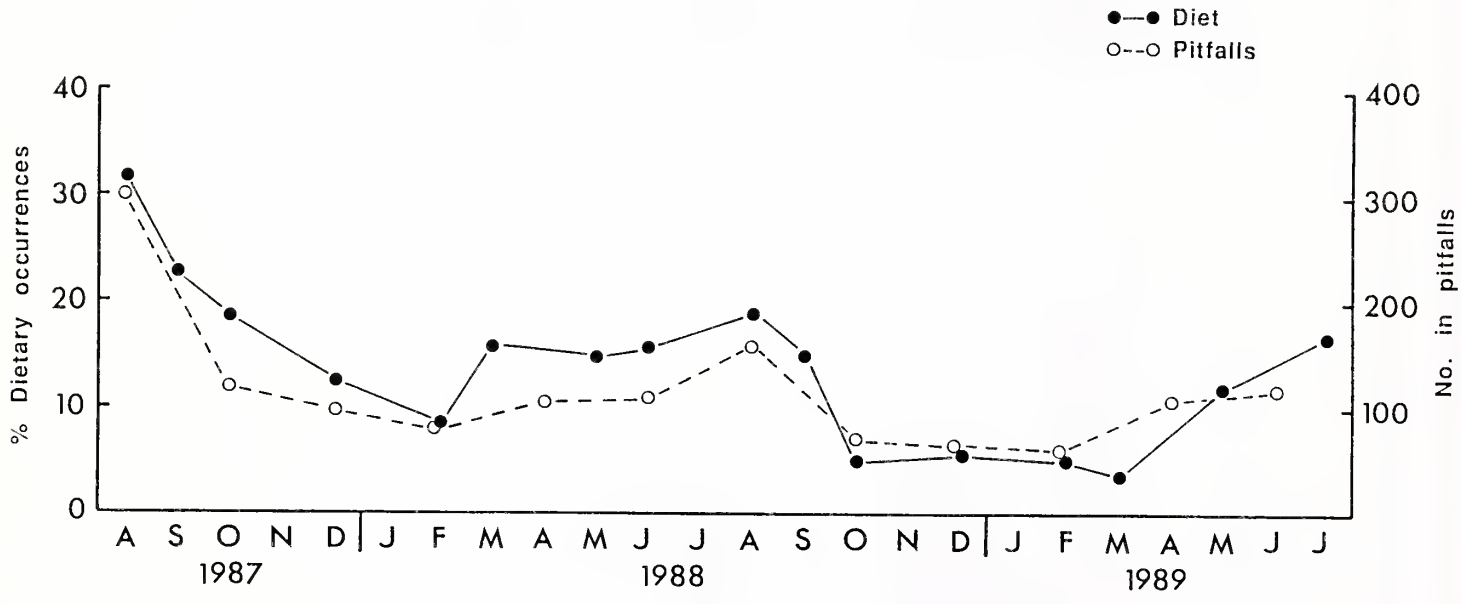

Fig. 7.—The percentage dietary occurrences of adult Coleoptera in the diet of *S. araneus*, and their incidence in pitfall samples.

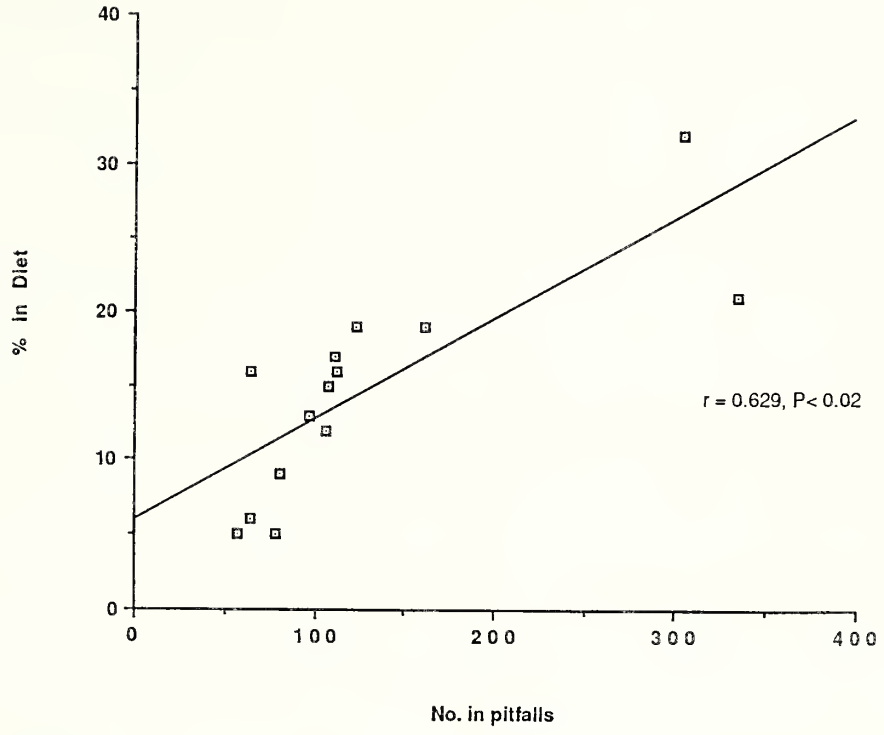

Fig. 8.—The relationship between the availability of Coleoptera and their occurrence in the diet of *S. araneus*.

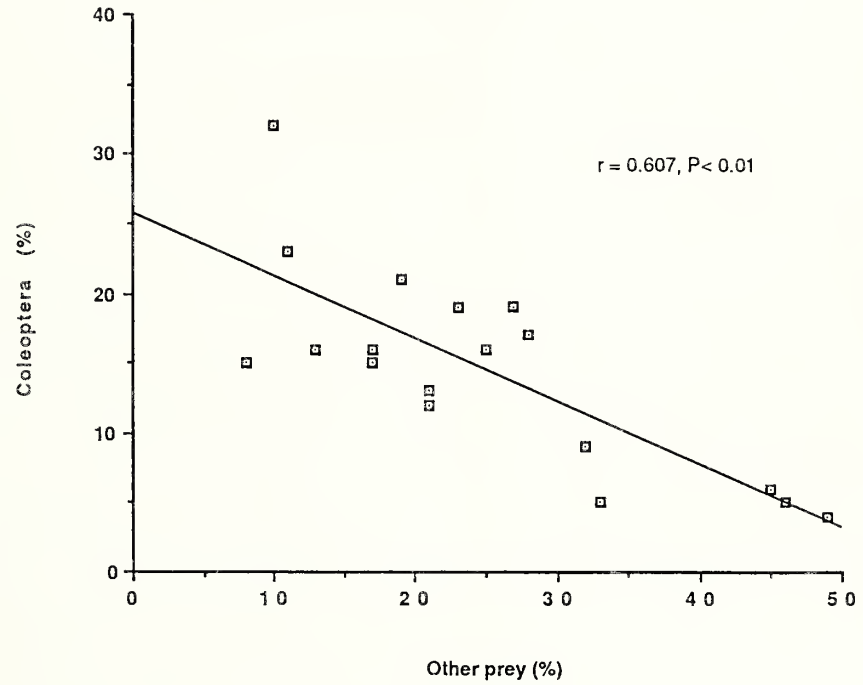

Fig. 9.—Prey switching in *S. araneus*: declining occurrences of Coleoptera in the diet were compensated for by increases in other prey (Diptera larvae, Gastropoda, and Myriapoda).

THE TERRITORIAL AND DEMOGRAPHIC STRUCTURES OF A COMMON SHREW POPULATION

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ABSTRACT

Territorial and demographic structure (age and sex) were determined in a long-term population study of the common shrew (*Sorex araneus* L.) using live-trapping, mark, and recapture techniques. Territorial behavior among overwintered females varied based on age and reproductive activity. Home ranges of overwintered females averaged 1300 m^2 (range, 800–1700 m^2). After the reproductive period, females began to move and home range structure disappeared. Home ranges of settled juveniles (young-of-the-year) overlapped significantly; their mean area in different years varied from approximately 360 to 500 m^2. Concomitantly, there were young transient individuals in the population without home ranges. Contrary to previous observations that shrews move randomly, *Sorex araneus* in this study had distinct home ranges but these often overlapped.

INTRODUCTION

Rodents and shrews inhabit forests and play essential but different roles in terrestrial ecosystems. Territorial behavior, although often studied in rodents, has been investigated very little in shrews. Data on shrews are scarce and often contradictory. Karasewa (1955) and Nikitina and Korchagina (1966) described shrews as wandering animals, not associated with any territory, and having no defined home ranges. More recently, other investigators using live traps have concluded that shrews do have home ranges and defend territories (Shillito, 1963; Michielsen, 1966; Yalden, 1974; Pernetta, 1977; Ellenbroek, 1980). Radioactive marking has been used to evaluate daily activity of shrews only with respect to short-term stays within areas. More recently, studies of territoriality of shrews in the Enisey taiga (Moraleva and Sheftel, 1980; Moraleva, 1983) have provided information on the influence of season and age on this phenomenon.

The aim of the present work was to investigate territoriality in a population of the common shrew (*Sorex araneus* L.) in the taiga of northwestern Russia.

MATERIALS AND METHODS

This study was conducted from 1986 to 1989 on the northeastern shore of Ladoga Lake in southern Karelia near the Russia–Finland border (61°22'N, 31°58'E). The territorial behavior of small mammals was evaluated based on live-trapping of marked animals in experimental enclosures (Ivanter and Makarow, 1988). Study sites were secondary forests near forest Lake Kurkunlampi. Plant cover was a mosaic of spruce, birch, and mixed forest associations: "*Piceetum oxalidosum*," "*Betuletum myrtilloso-mixtoherbosum*," "*Betuletum graminoso-myrtillosum*," and "*Piceeto-pinetum myrtilloso-herbosum*."

Traps were open from June to September during dry weather and were closed during rain and very cold weather to prevent mortality of shrews. Animals were sampled in the periods 26–30 June, 10–19 July, and 11–22 August 1986; 18–24 August 1987; 16 June–20 August 1988; 21–26 June, 13–18 July, 17–22 August, and 8–13 September 1989. Spring-loaded live traps were used and baited with rye bread and sunflower oil.

The study plots were quadrats of 1 ha (1986–1987) and 2 ha (1988–1989). Traps were set in a grid with 10 m intervals between traps. Traps were checked every two hours during daylight hours and were closed at night. Captured animals were marked by toe-clipping. Records were made of sex, age, weight, reproductive condition, date, and time and point of capture.

The inclusive boundary strip method (Burt, 1943; Evans and Holdenreid, 1943; Stickel, 1954) was used to determine the home ranges. Single captures of the animals outside their own ranges, and captures of dispersing individuals, were not taken into account.

Live-trapping data were supplemented by data on relative abundance from snap-trap lines and pitfall traps operated concurrently in the study area.

RESULTS AND DISCUSSION

General Characteristics of the Population

The number of *Sorex araneus* marked varied greatly from year to year (Table 1). Because of the border effect, the total number of animals marked in the study area was greater than the actual population density. The proportion of animals caught several times varied from year to year, ranging from 58 to 77%. Thus, temporary inhabitants of the trapping area should not have greatly influenced estimates of abundance. Using the number of shrews in the sampling grid in August as an index of shrew density, we concluded that population density exhibited a 12-fold change during the five years of observations (Table 1). Shrew captures were highest in 1986 and 1989 and lowest in 1987; 1988 marked the beginning of an increase in shrew abundance. Differences in the seasonal dynamics of shrews between the two peak years (1986 and 1989) are explained by unusual weather conditions in 1989; an early and warm spring in 1989 resulted in earlier reproduction. Data on abundance obtained from live-trapping were consistent with data from pitfall and snap-trap sampling (Table 2).

The population of shrews changed gradually during the summer–autumn period (Fig. 1). Distinct differences were obvious between July and August and were related to high mortality of adults marked in June. The proportion of newly-caught animals decreased gradually, reaching a minimum in September after the end of reproduction.

The sex and age structure of the population varied only

slightly by year (Fig. 2). In general, the proportion of animals that overwintered did not exceed 25% of the total number of marked animals.

The habitat distribution of animals did not vary significantly through the years. The mosaic nature of the vegetation on the study area smoothed differences in numbers, because home ranges of many animals were located in two or three neighboring habitats. Thus, estimation of habitat differences on the basis of number of captures was more illustrative than by number of individuals marked in each habitat. The greatest number of captures was in the meadow-sweet brush woods (in August 1989 with an average of 3.1 captures per trap). There were fewer shrews in the mixed forest (1.3 captures per trap). Ferny birch forest and thick spruce forest with needle fall on the ground were poorly settled (0.5 captures per trap in both forest types). Occupation of the latter habitat started only in July, and in June there were only 0.2 captures per trap. Increased abundance of shrews was accompanied by increased numbers of animals captured in every habitat, but to a greater extent in preferred ones.

Variation of Territorial Behavior in Animals of Different Sex and Age

The majority of overwintered shrews disappeared from the study site during June and July, and the number of overwintered shrews did not exceed ten specimens per hectare in August. The behavior of overwintered males was very different from that of overwintered females.

Overwintered Females.—Movements of overwintered females were less than movements of any other age and sex group. Overwintered females had well-defined home ranges which averaged 1300 m^2 (range 800–1700 m^2, $n = 9$). Home ranges were observed only in the most highly populated areas, and home ranges rarely overlapped (Fig. 3). As a rule, only one female was caught at a given trap. Traps visited by two females never exceeded 10% of all traps that caught overwintered females. Only once were three different females caught in the same trap.

The majority of adult females spent all the reproductive period in the same home range, but the configuration of home ranges varied. Some females changed their home range during the interval between litters, but new home ranges were in a state of dynamic equilibrium, that is, as one range changed, the borders of the surrounding ranges also changed. Consequently, minimal overlap of ranges was maintained, suggesting that the home ranges functioned as territories. After the reproductive season, some females left their ranges and either moved randomly over surrounding territories or left the area entirely (Fig. 4).

Overwintered Males.—Overwintered males were the most mobile members of the population. The majority did not have a consistent home range and moved randomly over the study plot, often through the home ranges of several females. Habitat preference was not well-expressed, although capture sites were often in low-lying areas. The distance between points of sequential captures was often 100 m and more.

Territorial behavior of males ranged between two extremes: 1) chaotic movements not connected with specific home ranges, with animals present on the study grid for very limited periods of time (Fig. 5); and 2) animals limited to large but defined home ranges. Males basically were segregated from each other and seldom shared home ranges, once again suggesting the presence of territoriality. In 1989, of 40 traps in which males were captured, 33 traps caught only one individual, four caught two different individuals, one caught three, and only two caught four different individuals.

The-Young-of-the-Year (Subadults).—Movements were variable among subadult shrews. Some had small, well-defined home ranges; others moved randomly within the study grid. Analysis revealed a relationship between these two patterns. Young born early in the year tended to occupy distinct home ranges. Specimens initially captured early in summer established their home ranges almost at once and occupied them throughout the period of observation. Sometimes individuals left their home range briefly but always returned (see Fig. 6, specimen no. 80). Occasionally, a home range changed, but the major part of it remained constant. In contrast, individuals that appeared on the study grid later in the summer did not have as much of a choice of home ranges. During years of high populations, all suitable habitat was occupied by resident shrews which forced young shrews to move actively in search of unoccupied habitat in which to establish home ranges.

There are three possible methods for acquiring a home range: 1) find and occupy a free space in favorable habitat, 2) occupy an established home range (see Fig. 6, animal no. 142), or 3) establish a home range in suboptimal habitat. Young shrews searching for unoccupied space generally moved through the most favorable habitats. As a result of differences in movements between resident and dispersing individuals, there were differences in numbers of shrews in various habitats. The occurrence of an animal in suboptimal habitat (e.g., the fern–birch forest) usually did not result in establishment of a home range. Young of the year found moving through the study site were those who did not find unoccupied habitat during the period of observation (Fig. 6, specimen no. 270).

During the gradual occupation of the study site, all favorable habitats became occupied and were divided into individual home ranges. The mean area of the home ranges in different years ranged from 360 m^2 to 500 m^2. In years of high shrew density, establishment of home ranges occurred earlier, usually in July (Fig. 7), and in years of low numbers, it occurred in August and September. Sometimes the full occupation of all suitable habitats did not take place due to extremely low numbers of animals (Fig. 8).

The number of young-of-the-year inhabiting the study area changed with time (Fig. 1). The change occurred because of mortality of animals or their disappearance from the study area. With the appearance of new individuals, the borders of previously established home ranges changed. This produced the impression of substantially overlapping home ranges of neighbors, whereas in reality the home range of the earlier occupant was compressed.

Conclusions

The results of the study suggest that a population of the common shrew, *Sorex araneus*, is a complex and dynamic

system, in which groups of individuals of different ages and sexes coexist and exhibit differential territorial behavior. The population of the common shrew in southern Karelia in this study was less stable than populations investigated in Holland (Michielsen, 1966) and England (Shillito, 1963; Buckner, 1969; Pernetta, 1977). However, animals in the present study were more closely associated with apparent territories than were those in the taiga forests of Siberia (Moraleva, 1983, 1988, 1989). The unique characteristic of the population investigated here was that home ranges of overwintered females and young-of-the-year in the same preferred habitats were distributed independently and overlapped greatly.

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Table 1.—*Number of common shrews marked on the study grid. The study area was 1 ha in 1986–1987 and 2 ha in 1988–1990. x = no sampling.*

Year	June	July	August	September
1986	8	48	44	x
1987	x	1	3	x
1988	x	22	39	x
1989	79	113	73	60
1990	15	x	25	x

Table 2.—*Mean number of common shrews in forests of the Ladoga Lake region per 100 snap trapnights and 10 pitfall nights in 1985–1990.*

Method of Sampling	1985	1986	1987	1988	1989	1990
Snap trap lines	3.6	6.5	2.2	2.3	10.0	2.2
Pitfall traps	9.2	10.4	3.2	4.2	9.0	no trapping

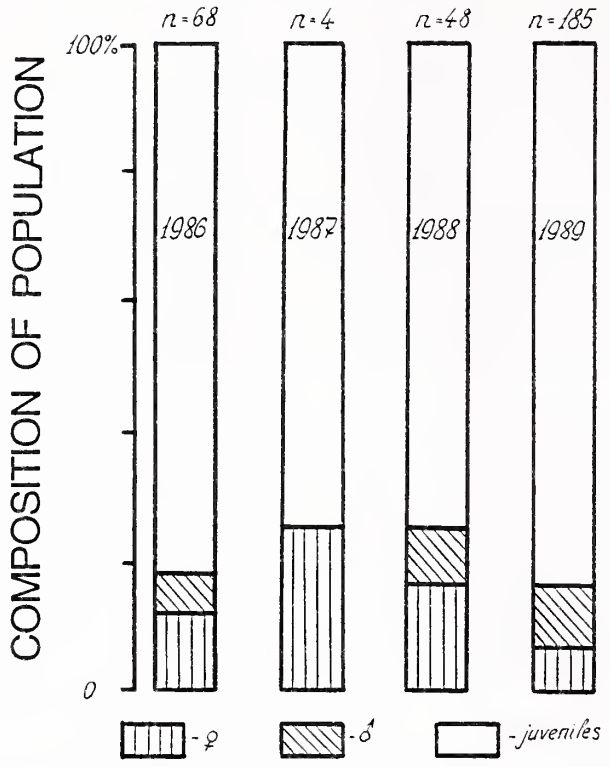

Fig. 1.—Sex and age structure of the common shrew population from 1986–1989.

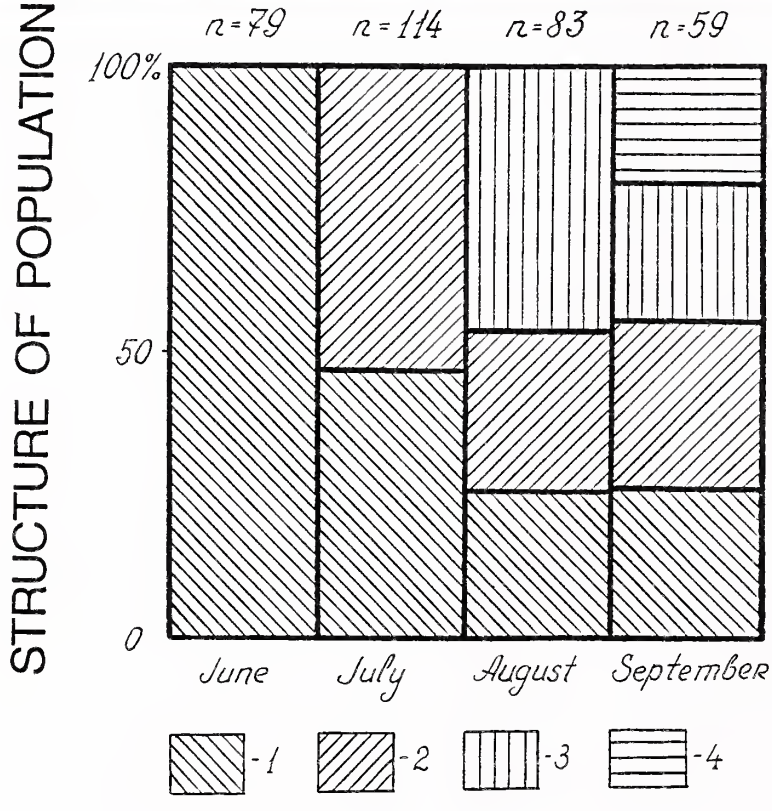

Fig. 2.—Change of structure of the common shrew population on the study grid from June through September, 1989 (in all age groups). The individuals were marked in: 1) June, 2) July, 3) August, 4) September.

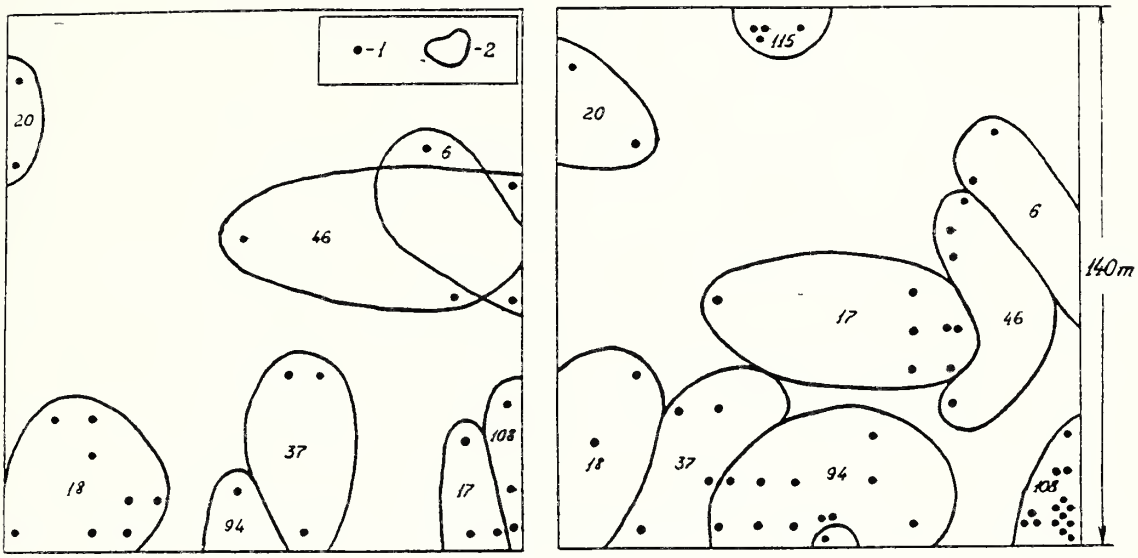

Fig. 3.—Home ranges of overwintered females in June (left) and July 1989. 1) stations of capture, 2) boundaries of home ranges.

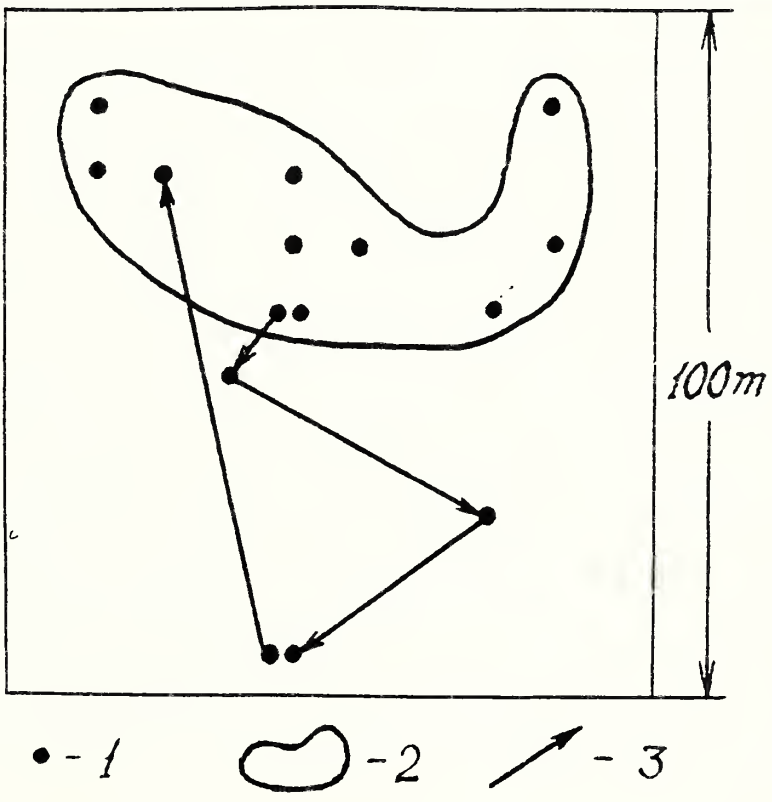

Fig. 4.—Home range of overwintered female no. 5 in June–July and its movements in August 1986. See the legend of Fig. 3.

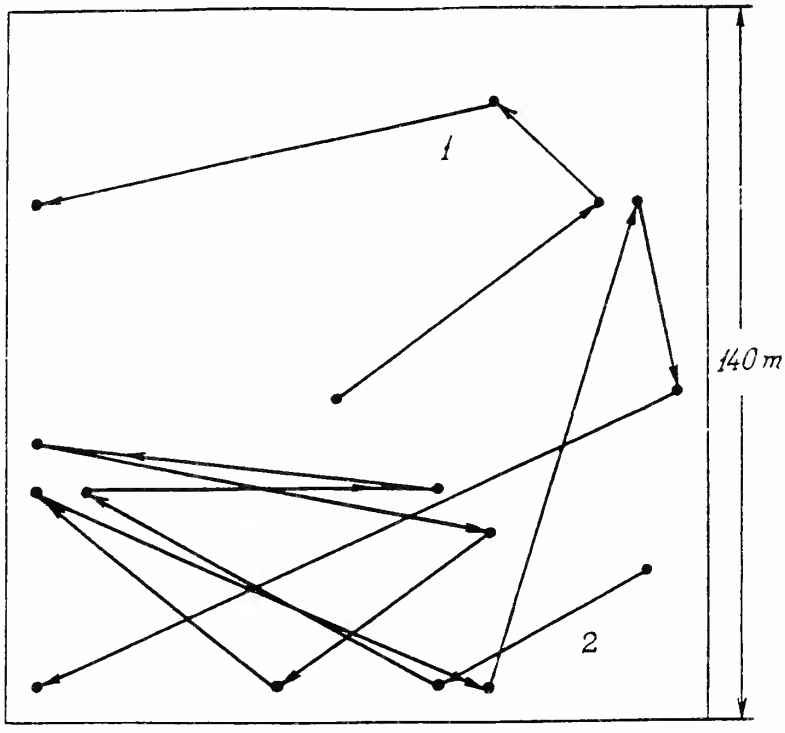

Fig. 5.—Two types of territorial behavior of males (22 June–18 July 1989). 1) random movements (no. 55), 2) extended stay within definite territory (no. 28).

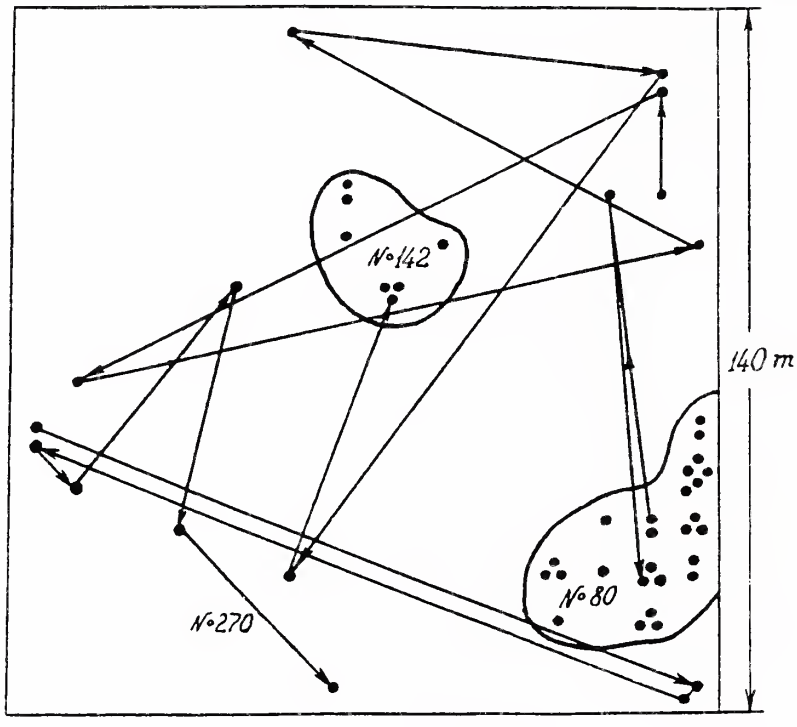

Fig. 6.—Location of capture of young-of-the-year marked in June (no. 80, 23.06–11.09), July (no. 142, 16.07–14.09), and August (no. 270. 21.08–8.09) 1989.

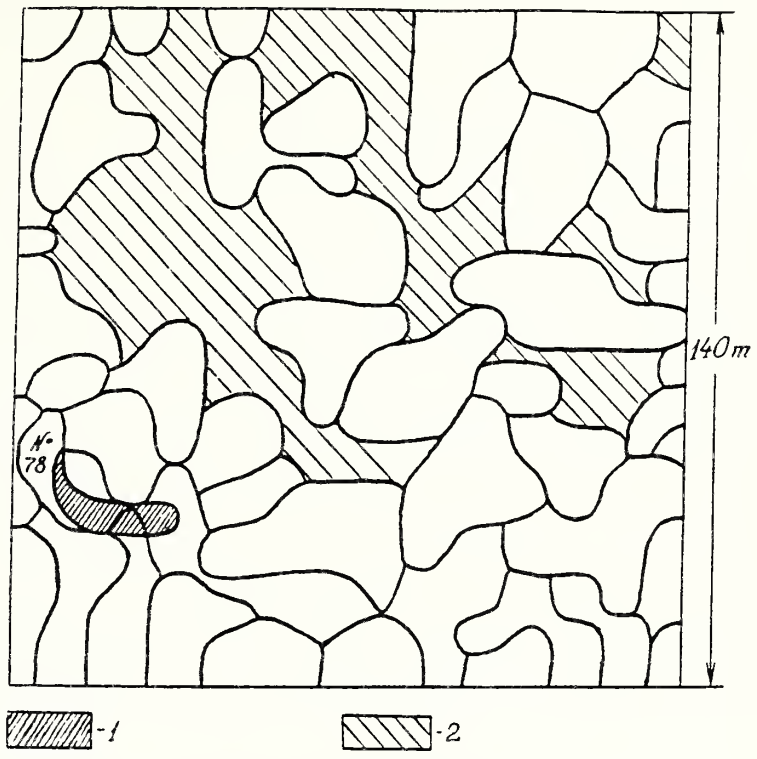

Fig. 7.—Home ranges of young-of-the-year in July 1989 (high shrew density). 1) imaginary overlap of home ranges caused by the disappearance of animal no. 78 during study, 2) space occupied by animals.

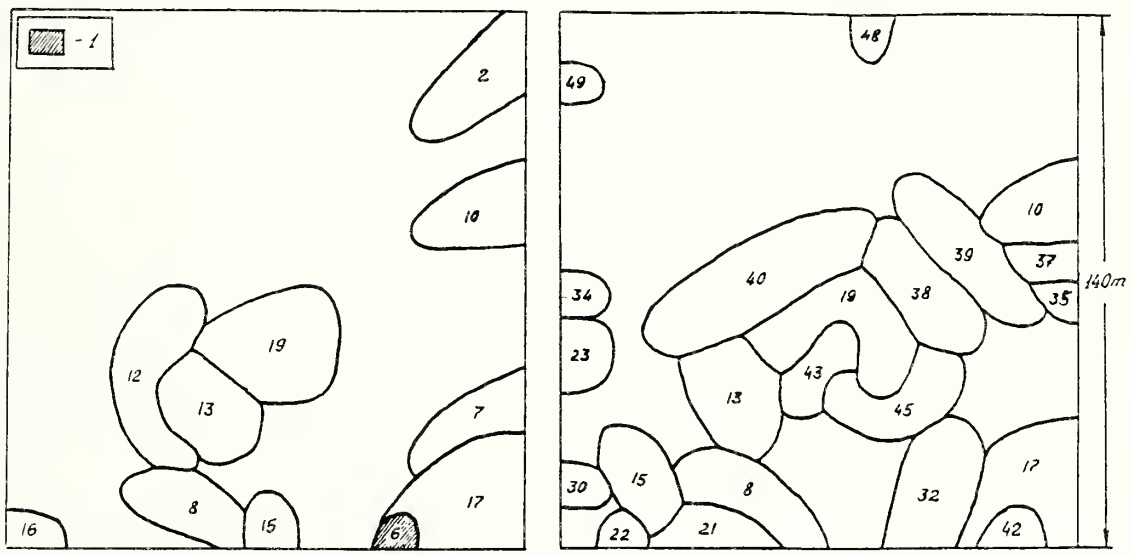

Fig. 8.—Home ranges of young-of-the-year in June (left) and July (right) 1988 (low shrew density). 1) imaginary overlap of home ranges as result of the compression of the home range of animal no. 17.

PARASITISM BY GASTROINTESTINAL HELMINTHS IN THE SHREWS *SOREX ARANEUS* AND *S. CAECUTIENS*

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ABSTRACT

We studied parasitism by gastrointestinal helminths (trematodes, cestodes, and nematodes) in *Sorex araneus* (n = 114) and *Sorex caecutiens* (n = 105) in Finnish Lapland. The large-sized *S. araneus* had significantly higher overall infection levels than the smaller species *S. caecutiens*, even when the size difference of shrews was taken into account. Similarly, most helminth species were significantly more prevalent in *S. araneus* than in *S. caecutiens*. Adult males tended to have higher overall infection levels than juvenile males, but significant differences between the sexes were few. Infection level/body size ratios, possible indicators of parasite pathogenicity, did not differ consistently between the age groups or sexes of shrews. Several helminth species, especially cestodes, showed significant differences in prevalence between age groups, but not between sexes of shrews. We were unable to find a clear effect on weight of shrews due to heavy helminth infections.

INTRODUCTION

The most conspicuous features of shrews of the genus *Sorex* are their small body size and high metabolic rate (Vogel, 1976). Since shrews also have small energy reserves (Vogel, 1980), the high metabolic rate inevitably implies severe energetic constraints and high risk of starvation. One of the effects of gastrointestinal parasites on hosts may be decreased efficiency of absorption and digestion, which can be compensated for by increased food consumption or use of energy reserves (Munger and Karasov, 1989). Adverse effects of parasites could be especially severe for shrews, as shrew populations seem to be largely food limited (Kaikusalo and Hanski, 1985) and probably experience frequent energy crises. Furthermore, the common shrew *Sorex araneus*, which has unusually high burdens of gastrointestinal helminths (Haukisalmi, 1989), is expected to be more severely affected than other species of *Sorex*.

Hanski (1989) suggested that heavy investment in reproduction may increase the vulnerability of adult male shrews to biotic and abiotic factors. For example, adult males seem to have a low social position in the population (Moraleva, 1989). Increased susceptibility to parasitism or increased pathogenicity of parasites may be another consequence of intense reproductive effort. As an extreme example, Lee and Cockburn (1985) have shown that because of very intense reproduction, males of some *Antechinus* species (insectivorous marsupials) are attacked by various pathogens and parasites, which contributes to the disappearance of males after the mating season. Female investment in pregnancy and lactation increases their energy requirements (Glazier, 1985) and food consumption, which may also lead to increased levels of parasitism.

We describe herein parasitism by gastrointestinal helminths in *Sorex araneus* and *S. caecutiens* in Finnish Lapland. Specifically, we examine differences in infection levels between the species (Haukisalmi, 1989), the level of parasitism in relation to age and sex of shrews, and the potential of endoparasites to affect the condition of shrews. In addition to the number of parasite species and individuals, we present data on helminth biomass; such data could elucidate the energetic constraints of parasites on shrews.

MATERIALS AND METHODS

One hundred fourteen common shrews (*Sorex araneus*) and 105 masked shrews (*S. caecutiens*) were trapped in 1988–1990 at Pallasjärvi (68°03', 24°09'), western Finnish Lapland. Most of the specimens (*S. araneus*, 78%; *S. caecutiens*, 70%) were obtained between June and October; only a few were caught in midwinter (December–February). The shrews were collected in old taiga forests characterized by a thick moss layer and dominance of spruce (*Picea abies*) and blueberry (*Vaccinium myrtillus*) (for details, see Henttonen et al., 1987, 1989).

The shrews were usually found dead in live-traps, which were primarily used for catching voles as the interval between checking traps was mostly six and sometimes eight hours. After capture, the shrews were frozen for later examination. The contents of stomach and intestines were searched for helminths under a binocular microscope. Identification of parasites was based on the monographs of Žarnowski (1960), Vaucher (1971), Vaucher and Durette-Desset (1973), and Genov (1984). Earlier data on shrew helminths in Finland was provided by Vaucher (1971), Vaucher and Durette-Desset (1973), and Haukisalmi (1989).

Multiway contingency tables (log-linear models, Fienberg, 1970) were used to analyze dependence between the occurrence of the common helminths (H), and age (A) and sex (S) of shrews. For each parasite species we selected the best (= simplest) model that fit the observed data (χ^2 test, $P > 0.05$). Fienberg (1970) and Harris (1984) described the process of selecting the best model in multiway contingency tables. In log-linear models interactions are indicated by combined variables (e.g., AH), and lack of interactions by separating the variables with a comma (e.g., A,H). The highest order model (SAH), which includes all possible interactions, is accepted if its fit to the data is significantly ($P < 0.05$) better than the fit of model SA, AH, SH, which includes all but the highest order effect (Harris, 1984).

The number and volume of all helminths and the number of helminth species in each host were used to describe overall

infection levels. Ratios of these parameters to weight (without alimentary tract) of shrews were also calculated. Davidson et al. (1980) have shown these ratios to be good indicators of parasite pathogenicity in white-tailed deer (*Odocoileus virginiana*). Significance of differences between and within shrew species in overall infection levels was checked by Kruskal-Wallis test.

The index of helminth volume was obtained as a product of mean length and width of helminths, based on the measurements of ten individual worms or on published data. This measure of volume is obviously crude but is satisfactory for the present purpose. Because of their highly non-normal distributions, logarithmic transformations were performed on the number and volume of parasites in partial correlation analyses.

Results

Differences Between Species

Seventeen species of gastrointestinal helminths parasitized *Sorex araneus* and *S. caecutiens* at Pallasjärvi, including four species of trematodes, nine of cestodes, and four of nematodes (Table 1). All 17 species parasitized *S. araneus*, whereas only 13 species were found in *S. caecutiens*. The nematodes of the genus *Longistriata* were the most prevalent helminths in both shrew species. Most of the helminth species had significantly higher prevalence in *S. araneus* than in *S. caecutiens*. The cestode *Hymenolepis schaldybini* was the only species having higher prevalence in *S. caecutiens* (Table 1). The overall infection levels also tended to be higher in *S. araneus*, especially in juveniles (Table 2). In adult males, some parameters were higher in *S. araneus*, but in adult females there were no significant interspecific differences.

Differences Between Age Groups and Sexes

The number of helminth species (*S. caecutiens*), number of individual parasites (both shrew species) and volume of helminths (*S. caecutiens*) per host were significantly higher in adult males than in juvenile males (Table 2). However, when infection indices were expressed as ratios of host body weight, adult males rarely showed higher infection levels than juveniles. Furthermore, the number of parasite species per host weight was significantly higher in juvenile males and females of *S. araneus* than in adults; such differences were not observed in the original values. In females there were no significant differences between age groups in the original infection indices. Adult males showed consistently higher overall infection levels than adult females, but significant differences between the sexes were rare.

The log-linear models showed that occurrence of the common cestodes depends on the age, but usually not on the sex, of shrews (Table 3). *Choanotaenia crassiscolex* and *Hymenolepis* sp. had higher prevalence in juveniles, whereas *H. schaldybini*, *H. scutigera*, and *H. infirma* were more prevalent in adults (Fig. 1). The full-order model SAH for *H. infirma* (host *S. araneus*) was accepted, since it gave a significantly ($\chi^2 = 8.3$, d.f. = 1, $P < 0.01$) better fit to the data than the model SA, AH, SH. In *H. infirma,* the age-dependence differed between male and female shrews so that adult males, but not females, had higher prevalence than juveniles. The occurrence of nematodes was independent of age and sex of the host, with the exception of *Longistriata pseudodidas* in *S. caecutiens* (Table 3, Fig. 1).

Infection Parameters and Weight of Shrews

Because infection level may be determined by the size of the host, comparisons between weight and parasite burden could be confounded by the effect of varying size of shrews. Therefore, body length of shrews was controlled in correlation analyses between the various infection parameters and weight of shrews (partial correlation). Since the weight and body length of males and females did not differ significantly in either of the shrew species, sexes were pooled.

Significant correlations between overall infection parameters and weight of shrews were few (Table 4), i.e., no consistent evidence of impaired condition of shrews due to gastrointestinal parasites was found. We also performed partial correlation analyses for the weight of juvenile shrews and various helminth species with at least ten occurrences (zero observations were excluded), but none of the correlations was found to be significant.

Discussion

The results confirm earlier observations by Haukisalmi (1989) that *Sorex araneus* has much higher infection levels of gastrointestinal helminths than *S. caecutiens*. The larger size of *S. araneus* implies higher absolute food requirements (Hanski, 1984), which should increase the colonization rate of helminths. In addition, *S. araneus* is expected to have higher numbers of helminths because of its long and voluminous intestinal tract. However, when the size difference between the two shrew species is taken into account, *S. araneus* still shows significantly higher infection levels than *S. caecutiens*, especially in juveniles. This suggests that high infection levels in *S. araneus* are due to either its generalized diet or high abundance (Haukisalmi, 1989), rather than to large body size. In addition, harmful effects of parasites may be greater in *S. araneus* than in *S. caecutiens* (c.f. Davidson et al., 1980). Soveri et al. (1994) have shown that histopathological changes, some of which could be caused by helminths, are very common in *S. araneus*. Unfortunately, we do not know the prevalence of such changes in *S. caecutiens*.

Hanski (1989) raised the question of the role of parasites in permitting the coexistence of competing shrew species. Our findings favor the idea that coexistence is facilitated by large species of shrew being more severely affected by parasites. This conclusion is supported by the fact that interspecific differences in infection levels were most pronounced in juveniles, which show strict interspecific territoriality (Croin Michielsen, 1966; Hawes, 1977). On the other hand, *S. araneus* is expected to be better adapted to helminths than the small species since the bulk of the helminth population circulates through it (Hanski, 1989; Haukisalmi, 1989).

Adult males, especially of *S. caecutiens*, had higher overall infection levels than juvenile males, but in females there were

no significant differences between age groups. This seems to support the idea that the intense reproductive effort of adult males is accompanied by a high risk of being affected negatively by biotic factors (Hanski, 1989). The data presented by Kisielewska (1961) and Erkinaro and Heikura (1977) also showed that adult males are especially susceptible to infection by intestinal and extra-intestinal endoparasites, respectively.

If the high overall infection levels of adult males were due to intense reproduction resulting in impaired resistance, there should be increased infection levels in most helminth species, including species with direct (nematodes) and indirect (cestodes) transmission. The patterns of age dependence of parasite species were variable: some cestodes were most prevalent in adult shrews, some in juveniles, and the occurrence of nematodes usually did not depend on the age of host. High infection levels thus seem to reflect specialization of particular helminth species on adult shrews, rather than general impairment in resistance of adults. For example, high overall infection in adult males (Table 2) seems to be due primarily to a single cestode species, *H. infirma*, which occurs in very high numbers in both shrew species (Table 1) and which is most prevalent in adult males (Fig. 1). Factors not directly related to reproductive effort, i.e., diet, longer exposure time, and greater amounts of food consumed, could also contribute to high infection levels in adult shrews.

Kisielewska (1961) suggested that susceptibility to endoparasite infections could contribute to the rapid disappearance of males of *S. araneus* after the breeding season (Moraleva, 1989; see also Lee and Cockburn, 1985). However, the infection level/body weight ratios, which are possible indicators of parasite pathogenicity (Davidson et al., 1980), suggest that harmful effects of helminths are not more severe in adult shrews than in juvenile shrews.

Studies of the effect of helminths on the condition and weight of hosts have yielded contradictory results. Low body weight of snowshoe hares (Keith et al., 1985, 1986) and rabbits (Yuill, 1964; Jacobsen et al., 1978; Dunsmore, 1981) were associated with the presence of high numbers of helminths. On the other hand, some studies report only minor changes in physiological parameters of hosts (cotton rat, Briese and Smith, 1980; white-footed mouse, Munger and Karasov, 1989) or practically no effect at all (mountain hare, Iason and Boag, 1988; willow ptarmigan, Thomas, 1986).

Our analysis showed that within shrews of equal size the body weight generally did not correlate significantly either with the overall infection levels or infection levels of various helminth species. We could not find any support for the assumption that biomass of parasites has more severe energetic effects on shrews than the number of parasite species and individuals. We conclude that gastrointestinal helminths do not have detectable effects on the condition of shrews.

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Table 1.—*Gastrointestinal helminths recovered from* Sorex araneus *(n = 114) and* S. caecutiens *(n = 105) at Pallasjärvi, optimum microhabitats, median volume index, number of infected hosts (n), and mean (± SD) number of parasites in infected hosts.* [st]*, stomach;* [1,2,3]*, three parts of the intestines; *,**,***, if the number of infected hosts differs between the shrew species, the higher value is marked with asterisks (χ^2 test): *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.*

Helminth species	Volume	*S. araneus*		*S. caecutiens*	
		n	$\chi \pm$ SD	*n*	$\chi \pm$ SD
Trematoda					
Brachylaimus fulvus[st]	0.7	4	1.0 ± 0.0	0	— —
Opisthioglyphe sobolevi[2]	0.1	2	2.0 ± 0.0	2	1 ± 0.0
Rubenstrema opisthioglyphe[3]	3.9	2	23.0 ± 22.0	0	— —
Pseudoleucochloridium soricis[3]	0.5	3	29.0 ± 28.3	0	— —
Cestoda					
Choanotaenia crassiscolex[1]	7.0	44***	5.3 ± 9.4	3	1.3 ± 0.6
Hymenolepis furcata[1]	3.6	6	3.0 ± 4.9	1	1 —
H. schaldybini[2,3]	1.5	37	6.8 ± 8.0	48*	11.1 ± 12.0
H. singularis[2]	3.6	10	4.9 ± 6.9	6	6.2 ± 6.5
H. scutigera[2,3]	0.4	72***	28.6 ± 30.0	13	4.0 ± 4.1
Hymenolepis sp.[2]	0.3	45*	28.5 ± 34.7	25	11.7 ± 16.2
H. infirma[3]	0.0	30	84.5 ± 102.1	29	43.3 ± 71.5
H. globosoides[2]	18.0	11*	1.8 ± 1.3	1	1 —
Dilepis undula[1,2,3]	0.4	11*	1.5 ± 0.7	0	— —
Nematoda					
Capillaria sp.[st]	0.5	15*	1.0 ± 0.0	4	1.0 ± 0.0
Longistriata depressa[1]	0.1	84*	18.8 ± 20.0	54	7.5 ± 6.6
L. pseudodidas[1]	0.1	80*	9.1 ± 7.7	54	5.8 ± 5.7
Parastrongyloides winchesi[3]	0.1	22*	4.4 ± 3.5	6	2.7 ± 2.1

Table 2.—*Infection indices describing the total helminth burden of shrews. Values for number of species and ratio of number of species to host weight are arithmetic means (± SD), other values are medians. All indices show significant (P < 0.01) differences among the eight categories of shrews (Kruskal-Wallis test).* ^{a,s,h}*, if infection parameters differ significantly (P < 0.05) between the age groups (a), sexes (s), or host species (h), the higher value is marked with the respective symbol.*

	S. araneus				*S. caecutiens*			
	Males		Females		Males		Females	
	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
n	47	21	37	9	46	19	29	13
Number of species	4.1^{h}	4.6^{h}	4.3^{h}	3.7	1.9	3.4^{a}	2.1	3.0
	(1.3)	(2.0)	(1.7)	(1.2)	(1.1)	(1.0)	(1.2)	(1.6)
Species/weight (×10)	8.2^{ah}	6.4	8.3^{ah}	5.2	6.1	7.3	6.6	6.8
	(2.5)	(2.7)	(3.4)	(2.1)	(3.8)	(2.2)	(3.7)	(3.8)
Number of helminths	59^{h}	107^{ash}	52^{h}	38	12	33^{a}	16	20
Helminths/weight	10.3^{h}	15.4^{sh}	10.0^{h}	4.9	3.7	4.9	5.3	5.0
Volume of helminths	26^{h}	29	22^{h}	11	5	27^{a}	4	16
Volume/weight (×1000)	5.2^{h}	4.0	4.0^{h}	2.2	1.6	5.6^{a}	1.3	3.3

Table 3.—*Best log-linear models for dependence between the occurrence of helminths (H), and sex (S) and age (A) of shrews (see text).* ^{a}*, full-order model; goodness-of-fit test is not possible.*

	S. araneus				*S. caecutiens*			
Helminth Species	Model	d.f.	χ^2	*P*	Model	d.f.	χ^2	*P*
C. crassiscolex	S,AH	3	3.1	0.38	—	—	—	—
H. schaldybini	S,AH	3	3.2	0.36	S,AH	3	3.1	0.37
H. scutigera	S,AH	3	3.8	0.29	—	—	—	—
Hymenolepis sp.	S,AH	3	5.3	0.15	S,AH	3	0.8	0.84
H. infirma	SAH^{a}				S,AH	3	4.2	0.24
L. depressa	S,A,H	4	5.0	0.28	S,A,H	4	6.5	0.70
L. pseudodidas	S,A,H	4	3.8	0.43	S,AH	3	0.4	0.94
P. winchesi	S,A,H	4	3.1	0.53	—	—	—	—

Table 4.—*Partial correlations between three infection indices and weight (without alimentary tract) of juvenile and adult shrews, controlled for the effect of body length. Logarithmic transformations were performed on the number and volume of helminths. *, P < 0.05.*

	No. of Species	No. of Helminths	Helminth Volume
S. araneus			
Juvenile			
1988 (*n* = 29)	0.36	−0.00	0.18
1989 (*n* = 34)	−0.24	−0.37*	−0.28
Adult (*n* = 18)	−0.14	0.27	0.23
S. caecutiens			
Juvenile			
1988 (*n* = 25)	−0.30	−0.30	−0.09
1989 (*n* = 22)	0.20	−0.015	−0.07
Adult (*n* = 22)	0.41	0.26	0.51*

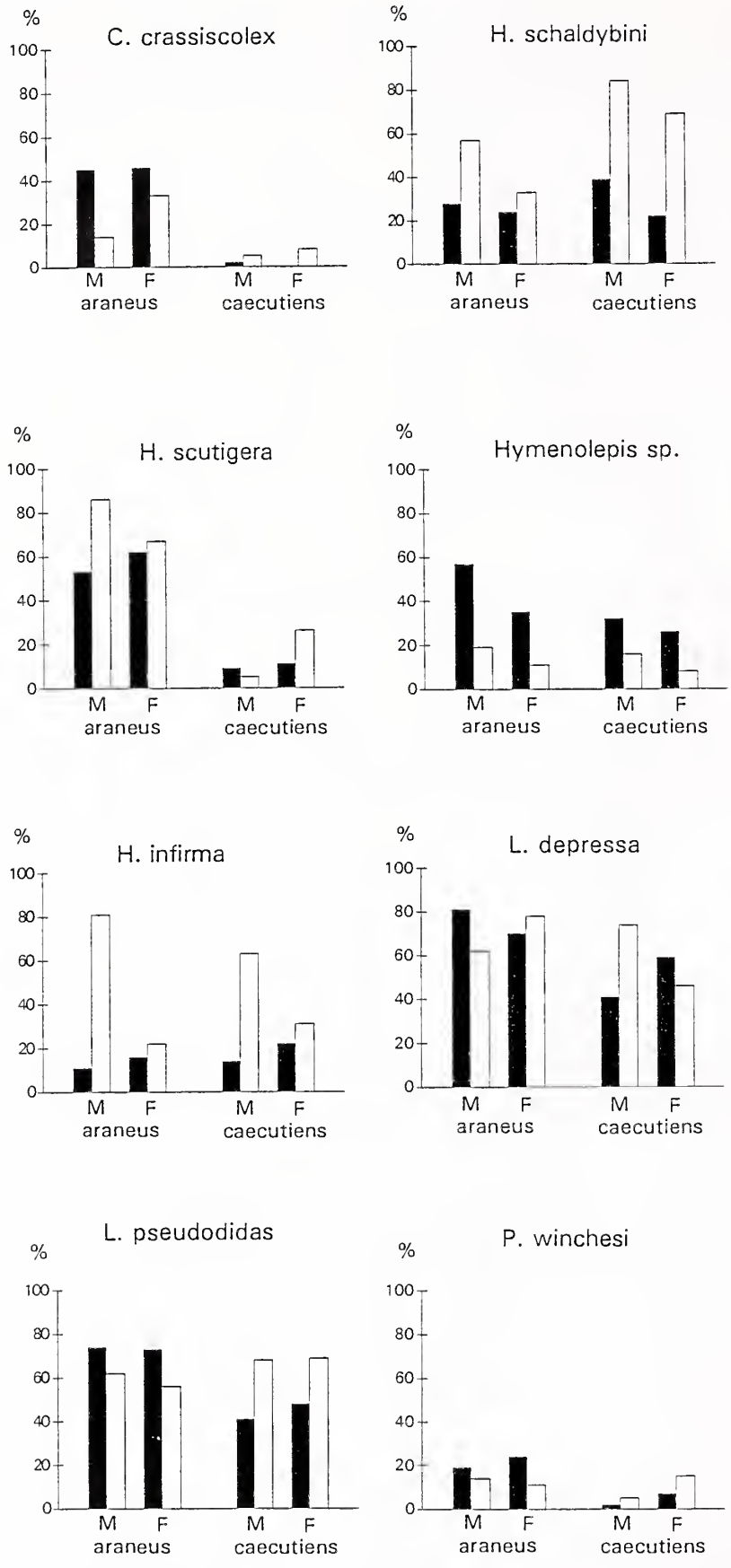

Fig. 1.—Prevalence of common helminths in the shrews *Sorex araneus* and *S. caecutiens*. M, males; F, females. Black bars, juveniles; white bars, adults.

THE MASKED SHREW, *SOREX CINEREUS*, IN A RELICTUAL HABITAT OF THE SOUTHERN APPALACHIAN MOUNTAINS

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ABSTRACT

We analyzed habitat features in relation to the abundanee of *Sorex cinereus* at ten high-elevation sites (1082–1524 m) in Virginia, USA. Each site contained red spruce (*Picea rubens*), an indicator of boreal habitat. *S. cinereus* comprised 89.4% of 434 shrews captured, and it was the only species captured at all sites. Captures of *S. cinereus* were significantly correlated ($P < 0.05$) with soil moisture-holding capacity, soil organic matter, and total understory vegetation, but otherwise no suite of habitat characteristics was present that could be correlated with the abundance of *S. cinereus*. Characteristics that provided cover, e.g., rocks, stumps, and fallen trees, were important, but features that provided suitable habitat at one site were often replaced by other features at other sites. Our data indicate that habitat characteristics that promote shaded, moist habitat are critical to *S. cinereus*, and that such features may be especially important in a relictual forested habitat in the southern Appalachian Mountains.

INTRODUCTION

The late John E. Guilday (1972:233) observed that the Appalachian Mountains provide "...a tongue of 'more northerly' environment into the Carolinean lowlands of the South." The northern conditions present at high altitudes in the southern Appalachians allow boreal species, such as *Sorex palustris*, *Glaucomys sabrinus*, and *Microtus chrotorrhinus*, to exist far south of their centers of distribution. These species had greater, more continuous ranges in the Appalachians during periods of glacial cooling, but in the southern Appalachians all now have highly disjunct, fragmented ranges (Hall, 1981). Both the populations and the habitats in which they occur are considered relicts of the ice age.

In contrast, other northern species that reach into the southern Appalachians have broader distributions. The range of the masked shrew, *Sorex cinereus*, the most widely distributed member of the genus in North America, is centered in the transcontinental coniferous forest. In addition to southern extensions into montane forests of the Appalachian and Rocky mountains, it also occurs northward into the tundra (Junge and Hoffmann, 1981). Indicative of its boreomontane distribution, the masked shrew has not been taken below 610 m elevation in Virginia (Pagels and Handley, 1989).

Numerous studies have described *S. cinereus* as a habitat generalist. In Canada, van Zyll de Jong (1983) reported *S. cinereus* from alder and willow thickets; along margins of marshes, bogs, and streams; and in deciduous and coniferous woods up to the timberline. In Manitoba, Wrigley et al. (1979) captured *S. cinereus* in herbaceous and shrubby areas, deciduous and coniferous forests, dry prairie, sparse weeds on sand dunes, and spruce–aspen–juniper savannas. In Wyoming, *S. cinereus* is known from willow–sedge savannas, and wet, grass–sedge meadows (Negus and Findley, 1959; Clark, 1973), in spruce–fir forests (Raphael, 1988), and in numerous other habitats from sagebrush to an alpine rockslide (Brown, 1967). Additional habitat types include hardwood floodplains (French, 1984) and old fields (French, 1984; Whitaker, personal communication) in Indiana; old fields, marshes, hardwood swamps, spruce swamps, spruce burns, and bogs in northern Michigan (Pruitt, 1953, 1959; Getz, 1961; Ryan, 1982); swamp hardwood forests in the Northeast (Hill, 1982); farmstead shelterbelts in Minnesota (Yahner, 1982); and a high-altitude grassy area in Tennessee (Tuttle, 1964).

The masked shrew is also a generalist in terms of its diet, which consists of adults and larvae of numerous insect taxa and other invertebrates such as earthworms, sowbugs, centipedes, spiders, mollusks, and vertebrates, including young mice and salamanders (van Zyll de Jong, 1983; French, 1984). Getz (1961) suggested that because of its small size *S. cinereus* is able to forage effectively for invertebrates that are present in almost all areas, and that food availability may not be a critical factor in its local distribution. Several studies have suggested that moisture is the most important factor influencing the local distribution of *S. cinereus* (Pruitt, 1953, 1959; Getz, 1961; Spencer and Pettus, 1966; Wrigley et al., 1979; Hill, 1982). Pruitt (1953, 1959) observed that *S. cinereus* can only permanently inhabit those microhabitats in which the humidity approaches saturation. Getz (1961) concluded that the primary importance of cover, whether it be leaf litter, moss, or vegetation, was its effect on humidity.

Our objectives were to characterize habitat features in relictual habitat of the southern Appalachian Mountains and to relate these features to the abundance of *S. cinereus*. We expected that *S. cinereus* would occur at all sites. However, because all sites were forested, we hypothesized that if differences did exist in the abundance of *S. cinereus*, our analyses would indicate a suite of habitat features, notably those that promote high moisture, associated with high *S. cinereus* abundance.

METHODS

The ten study sites in western Virginia possessed vegetation features, for example *Picea rubens* and northern hardwood species, usually associated with a boreal fauna (Payne et al., 1989). All sites exceeded 1000 m elevation. Mean elevation of the eight Highland County sites was 1160 m (Hi-12, 1097 m; Hi-12+, 1082 m; Hi-13, 1127 m; Hi-14, 1127 m; Hi-14+, 1158 m; Hi-16, 1188 m; Hi-18, 1219 m; Hi-21, 1280 m), and

1501 m (CC, 1478 m; and WT, 1524 m) at the two Grayson County sites.

Mammal sampling and habitat measurements were centered on points that appeared to best represent the habitat. Small mammals were trapped with arrays of pitfall traps and terrestrial drift fences as described by Bury and Corn (1987) and similar to those of Kirkland and Sheppard (1994). The pitfall arrays at each site consisted of two triads of pitfalls spaced 20–25 m apart. A triad consisted of three 5-m strips of aluminum flashing forming drift fences 24.5 cm high radiating approximately 120° outward from each other, beginning 2–3 m from a central point. Two #10 tin cans were buried to ground level at each end of the drift fence, one on each side. Each pair of cans was considered one trap. A plastic insert fitted with a wire handle was placed in each can to facilitate removal of specimens. The pitfalls were filled with 15% formalin solution to drown and preserve captured animals. Traps were checked at approximately three-week intervals from August to November 1988, and from March to November 1989. All specimens were deposited in the Virginia Commonwealth University Mammal Collection (VCU).

The line-intercept method (Canfield, 1941) was used to measure most habitat features. Transects for all habitat measurements were centered on pitfall arrays, but transects were not necessarily the same for different sets of data collected on different dates. One hundred measurements of understory features were taken at 1-m intervals along transects that extended 25 m in the four major compass directions. Measurements of the understory recorded at the 100 points included surface and underground rock, moss, lichens, ferns, herbs, tree seedlings, and dead wood (fallen trees, stumps). A pole with a spike was driven into the ground to a depth of 10 cm to determine the presence or absence of underground rock. A rock was counted as a surface rock if its greatest length was at least 10 cm.

Soil pH, field capacity, or the moisture-holding capacity of the soil (after Salter and Williams, 1967), and percent organic matter (after Ball, 1964) were determined for ten soil samples taken randomly from each site.

Observations of the overstory included presence, species composition, and layering of the canopy and subcanopy. All trees, including standing dead trees, with a diameter at breast height (dbh) of at least 10 cm were counted within a circumscribed area (60 m diameter) at each site to determine density of the forest stand. Stand age was determined from 40 increment cores per site taken from trees with a dbh of 10 cm or greater which were closest to 3-m points along 30-m transects, again directed in the four major compass directions. Canopy openness was estimated using a tube held overhead.

Average linkage cluster analysis (Ludwig and Reynolds, 1989) was used to determine communities based on the following habitat measurements: soil features, tree species and density, understory features, and understory vegetation. Analyses of variance and Tukey multiple range tests were used to determine if significant differences in habitat variables existed among the sites. Regression analyses were used to determine if correlations existed between habitat features and *S. cinereus* captures.

Results

A total of 434 shrews representing six species was captured. *Sorex cinereus* comprised 89.4% of shrew captures and was the only species taken at all sites (Table 1). In addition, seven rodents were captured: *Peromyscus maniculatus* (2), *Synaptomys cooperi* (1), *Microtus pennsylvanicus* (1), and *Clethrionomys gapperi* (3).

Five overstory species accounted for over two-thirds of the 1,590 trees counted: *Picea rubens* (31%), *Acer rubrum* (11%), *Fagus grandifolia* (9%), *Betula lutea* (9%), and *Betula lenta* (8%) (Table 2). *Picea rubens* was present at all sites, *A. rubrum* and *F. grandifolia* at eight sites, and *B. lenta* and *Prunus serotina* at seven sites. Overstory diversity (Shannon index, H′) was generally high at all sites except Hi-14 and WT which were characterized by an abundance of *P. rubens* (Table 2).

Soils from Hi-16, CC, and WT had similar features including low pH, high field capacity, and high organic matter content (Table 3). The field capacities at CC and WT were significantly different from those at other sites ($P < 0.05$). Three communities were identified in a cluster analysis of the sites using soil features. Sites CC and WT were each established as separate communities. The other sites were clustered as a third community at 50% dissimilarity. Percent organic matter of soils, field capacity of soils, and total understory vegetation were the only individual microhabitat features significantly correlated to captures of *S. cinereus* ($P < 0.05$, $r^2 = 0.72$, 0.52, and 0.43, respectively).

Shrubs were absent at four of the ten sites (Table 4). *Kalmia latifolia* was the most prevalent shrub species, especially at Hi-16 and Hi-18, sites with relatively high understory diversity. Herbs were present at all sites, with a notable abundance of *Houstonia* sp. at WT and grasses at Hi-21. Surface rocks were present at six sites, but they were particularly large at CC and WT, two of the sites with significantly higher numbers of *S. cinereus* (Table 4). Total vegetation (total understory variables minus rock, fallen trees, and stumps) at the sites ranged from 41 at Hi-14+ to 279 at WT. A cluster analysis of sites using understory features (Table 4) identified three communities. Sites Hi-16 and Hi-18 were paired as one community, and WT, the most dissimilar site, was established as a separate community. The remaining sites were clustered as a third community. The communities showed no relation to those based on *S. cinereus* captures.

Mean stand age ranged from 47.7 years at Hi-14+ (mean dbh = 0.30 m) to 108.0 years at WT (mean dbh = 0.28 m) (Table 5), but stand age was not correlated to mean dbh. Analysis of variance determined that there was no significant difference in dbh among the sites; however, WT was significantly older than all other stands ($P < 0.001$). All sites had at least three trees 70 years of age or older and one tree 80 years of age or older.

Total tree density ranged from 312 trees/ha at Hi-13 to 734 trees/ha at Hi-14 (Table 5). No relationship was observed between the total density of trees and the diversity of the stands

or tree density and the relative abundance of *S. cinereus*. Basal area, the product of tree density and dbh, ranged from 15.3 m^2/ha at Hi-13 and CC to 30.5 m^2/ha at Hi-14. No relationship was observed between total tree density and basal area of stands or the relative abundance of shrews.

All sites possessed a layered canopy; however, the extent of layering and number of layers varied among sites (Table 6). A high overstory layer was present at almost all of the sampling points, but the canopy was not completely closed at any site. Mean canopy openness ranged from 7.9% at Hi-13 to 44.0% at Hi-21. Sites Hi-21 and WT were significantly more open than other sites ($P < 0.05$). Foliage height diversity (FHD) (Aber, 1979; McPeek et al., 1983) showed little variation among the sites, with the exception of WT which had a significantly lower FHD than other sites (Table 6). Not surprisingly, FHD was found to be negatively correlated to understory vegetation ($P < 0.05$, $r^2 = 0.57$). As noted, however, only total understory vegetation, not FHD, was significantly correlated with *S. cinereus* captures.

Measurements of selected structural features of the understory of all sites are given in Table 7. Of the sites with greatest *S. cinereus* captures, Hi-16 had relatively large numbers of stumps and fallen trees, and CC and WT had many large surface boulders that approached one m in their greatest dimension (Table 7).

Discussion

The influence of habitat on populations of small mammals has received much attention in recent years (August, 1983; McPeek et al., 1983; Seagle, 1985; Adler, 1985, 1987; Hanski and Kaikusalo, 1989). Many studies have focused on the effects of habitat structure and the roles of both microhabitat and macrohabitat (Price, 1978; Yahner, 1982; Morris, 1987; Bowers and Flanagan, 1988).

Price (1978) and Yahner (1982) noted that the availability of suitable microhabitats may determine abundances of species on a local scale. Other studies (Morris, 1987; Bowers and Flanagan, 1988) have suggested that the density of small mammal populations may more closely reflect habitat variability at the macrohabitat level. Adler and Wilson (1987) noted that habitat generalists utilize different habitat types over their entire distributional range, but on a local scale, they may be particularly efficient at exploiting diverse resources and responding readily to environmental fluctuations. The variation in abundance of *S. cinereus* among our sites in basically a single type of habitat supported these views. Further, as Getz (1961) surmised, amount of cover is more important than type of cover in determining the distribution and abundance of *S. cinereus*. Our data suggest that various features of a habitat, both micro- and macro-, are important in supplying suitable habitat for *S. cinereus*. Our results support the findings of Getz (1961) and Pruitt (1953, 1959) that greater numbers of *S. cinereus* are found in association with features that promote shaded, moist conditions, i.e., features that one would hypothesize to be important to a northern species. Our findings concur with Snyder and Best (1988) and Yahner (1982), who reported a positive relationship between vegetation density and the abundance of *S. cinereus* in diverse habitats in Minnesota. Importantly, however, as we also found in this relictual forested habitat, features that provide suitable habitat are variable, and not all such variables must be present at the same time or in equal abundances. Illustrating this point, several cluster analyses were performed using different groups of habitat variables; however, the clusters showed no concordance with *S. cinereus* captures or with one another. These analyses indicate that no single set of habitat variables, such as soil features, understory features, or vegetation, was responsible for the differences in *S. cinereus* densities among the sites.

Although the three sites with greatest *S. cinereus* captures—Hi-16, CC, and WT—were each separated into distinct soil and understory vegetation communities, they were similar in that they had structural features that provided suitable habitat. Site Hi-16 had few rocks, but a high number of fallen trees and stumps, and relatively heavy shrub cover (Table 4, 7). Site WT had the lowest FHD, but had large boulders and an abundance of herbs and evergreen tree seedlings. Site CC did not have a particularly heavy understory; however, there were several large boulders at the site (Table 7). Site CC also had dense thickets of rhododendron which were counted as part of the subcanopy due to their height. Rhododendron undoubtedly had the same effect as shrubs on the microhabitat in terms of shading and cover.

In summary, because all of our sites were in a single kind of habitat, i.e., a relictual forest, we cannot suggest that the sites with the greatest numbers of *S. cinereus* provided better habitat than we would have found had we sampled other habitats. In the forest type we studied both micro- and macrohabitat features were important in contributing to a suitable environment for *S. cinereus*. Such features, although they demonstrated much variability among sites, were those that promoted shaded, moist conditions.

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Table 1.—*Captures of shrews at each site. Relative abundance (captures per 100 trapnights) is indicated under numbers captured. Total trapnights were 3,564 at CC and WT, and 3,660 at all other sites.*

Species	Site										Total
	12	12+	13	14	14+	16	18	21	CC	WT	
Sorex cinereus	17	28	24	36	14	68	18	43	64	76	388
	0.46	0.77	0.66	0.98	0.38	1.86	0.49	1.17	1.80	2.13	5.37
S. fumeus	1	3	2	1	1	2	—	—	4	6	20
	0.03	0.08	0.05	0.03	0.03	0.05	—	—	0.11	0.17	0.28
S. dispar	—	—	—	—	—	—	—	—	—	1	1
										0.03	0.01
S. hoyi	—	—	—	—	—	1	3	3	1	—	8
						0.03	0.08	0.08	0.03		0.11
Cryptotis parva	—	—	—	—	—	—	—	—	—	1	1
										0.03	0.03
Blarina brevicauda	1	1	1	—	4	3	1	2	3	—	16
	0.03	0.03	0.03		0.11	0.08	0.03	0.05	0.08		0.22
Total	19	32	27	37	19	74	22	48	72	84	434
Richness	3	3	3	2	3	4	3	3	4	4	6
Evenness	0.37	0.41	0.38	0.17	0.64	0.26	0.52	0.37	0.33	0.28	0.26
Diversity (H′)	0.18	0.19	0.18	0.05	0.30	0.16	0.25	0.18	0.20	0.17	0.20

Table 2.—*Density of trees per hectare (first line) and relative frequency (total of one species/total of all species; second line) of live overstory species.*

Species	Site									
	12	12+	13	14	14+	16	18	21	CC	WT
Picea rubens	39	21	109	595	198	117	106	71	64	448
	0.07	0.05	0.35	0.81	0.33	0.25	0.27	0.21	0.13	0.91
Acer rubrum	85	28	7	64	25	195	209	11	0	0
	0.14	0.07	0.02	0.09	0.04	0.42	0.53	0.03	—	—
Fagus grandifolia	28	110	11	43	237	0	0	4	60	14
	0.05	0.27	0.04	0.06	0.39	—	—	0.01	0.13	0.03
Betula lenta	209	103	7	0	0	103	53	21	0	7
	0.35	0.25	0.02	—	—	0.22	0.13	0.07	—	O.01
Betula lutea	103	0	14	0	0	18	4	0	326	11
	0.17	—	0.04	—	—	0.04	0.01	—	0.70	0.02
Tsuga canadensis	85	74	135	0	0	7	11	0	0	0
	0.04	0.18	0.43	—	—	0.02	0.03	—	—	—
Prunus serotina	21	57	11	14	92	0	11	4	0	0
	0.14	0.14	0.04	0.02	0.15	—	0.03	0.01	—	—
Robinia pseudoacacia	0	0	0	0	35	0	0	71	0	14
	—	—	—	—	0.06	—	—	0.22	—	0.03
Crataegus sp.	0	0	0	0	0	0	0	106	4	0
	—	—	—	—	—	—	—	0.34	0.01	—
Acer saccharum	21	11	7	0	0	0	0	14	0	0
	0.04	0.03	0.02	—	—	—	—	0.04	—	—
Quercus rubrum	0	0	0	18	11	0	0	14	0	0
	—	—	—	0.02	0.02	—	—	0.04	—	—
Amelanchier arborea	0	0	0	0	4	7	4	0	7	0
	—	—	—	—	0.01	0.02	0.01	—	0.01	—

Table 2 (cont.)

Species	Site 12	12+	13	14	14+	16	18	21	CC	WT
Acer pennsylvanicus	0	0	11	0	0	4	0	0	11	0
	—	—	0.04	—	—	0.01	—	—	0.02	—
Abies fraseri	0	0	0	0	0	0	0	0	7	0
	—	—	—	—	—	—	—	—	0.01	—
Magnolia acuminata	0	0	0	0	0	7	0	0	0	0
	—	—	—	—	—	0.02	—	—	—	—
Carya sp.	0	4	0	0	0	4	0	0	0	0
	—	0.01	—	—	—	0.01	—	—	—	
Sorbus americana	0	0	0	0	0	0	0	0	4	0
	—	—	—	—	—	—	—	—	0.01	—
Acer spicatum	0	0	0	0	0	0	0	0	4	0
	—	—	—	—	—	—	—	—	0.01	—
Total density	591	408	312	734	602	459	398	316	487	488
Dead trees	88	78	14	21	103	152	149	46	99	110
Richness	8	8	9	5	7	9	7	9	9	5
Evenness	0.86	0.85	0.67	0.44	0.73	0.66	0.64	0.78	0.51	0.27
Diversity (H′)	2.58	2.55	2.13	1.03	2.05	2.09	1.80	2.48	1.61	0.63

Table 3.—*Mean soil pH, mean field capacity (amount of water expressed as percent of soil dry weight), and mean percent organic matter at each site. Numbers below are one standard error of the mean.*

	Site 12	12+	13	14	14+	16	18	21	CC	WT	$\bar{X}$
pH	3.7	4.4	4.0	4.1	3.8	3.7	3.9	4.1	3.5	3.3	3.9
	0.07	0.07	0.06	0.08	0.05	0.03	0.06	0.08	0.05	0.02	0.03
Field capacity	34.9	41.4	50.2	41.9	39.6	47.3	40.7	29.5	103.0	176.5	60.5
	0.9	1.7	2.9	1.5	1.3	7.5	4.7	1.9	7.9	19.8	4.9
Organic matter	12.5	8.3	13.1	10.2	10.2	26.0	11.1	9.3	20.3	35.3	15.6
	1.2	0.9	2.1	0.3	1.0	6.4	2.8	0.8	1.4	5.1	1.2

Table 4.—*Occurrences of understory variables at 100 points at each site.*

	Site									
	12	12+	13	14	14+	16	18	21	CC	WT
Surface rock	0	0	0	0	1	1	20	15	12	7
Underground rock	7	7	17	4	16	16	57	52	21	21
Fallen trees	8	9	9	15	7	13	13	7	4	9
Stumps	1	0	1	3	1	5	1	2	0	0
Shrubs	0	0	0	17	1	33	69	10	0	7
Evergreen tree seedlings	15	3	5	1	2	38	1	7	3	42
Deciduous tree seedlings	11	16	8	6	22	18	19	13	15	9
Herbs	37	35	23	9	5	4	7	51	30	78
Ferns	44	24	27	5	8	19	18	44	52	44
Lycopodium	7	0	5	0	0	1	4	0	0	35
Mosses	6	4	27	9	4	19	16	9	15	64
Total vegetation	120	82	95	47	41	132	127	]34	115	279
Total understory	136	98	122	57	67	167	225	210	152	316
Diversity (H')	0.78	0.72	0.83	0.86	0.78	0.89	0.87	0.83	0.76	0.86

Table 5.—*Mean dbh, mean age, and estimated basal area calculated from measurements made on 40 trees per site. Total density was derived from total tree counts at each site. Numbers below are one standard error of the mean.*

	Site										
	12	12+	13	14	14+	16	18	21	CC	WT	$\bar{X}$
DBH (m)	0.23	0.24	0.25	0.23	0.22	0.22	0.27	0.30	0.20	0.28	0.24
	0.017	0.019	0.021	0.021	0.021	0.017	0.014	0.025	0.014	0.019	0.004
Age (yrs)	59.7	71.73	77.9	53.2	47.7	66.7	62.0	48.8	64.4	108.0	66.0
	3.12	4.05	4.69	1.88	2.00	3.47	2.08	3.45	5.42	5.33	5.6
Density	591	408	312	734	602	459	398	316	487	488	480
Basal area (m^2/ha)	24.6	18.5	15.3	30.5	22.9	17.4	22.8	22.3	15.3	30.0	21.7

Table 6.—*Occurrence of subcanopy and canopy layers, and mean canopy openness from 100 points at each site. Foliage height diversity (FHD) indices (see Aber, 1979) were calculated from the number of layers of the subcanopy and canopy.*

	Site									
	12	12+	13	14	14+	16	18	21	CC	WT
Subcanopy										
High	46	51	15	23	18	56	7	35	61	21
Low	2	0	0	1	1	8	0	0	5	1
Overstory										
High	98	100	99	100	100	100	100	67	98	88
Medium	50	59	52	47	61	28	30	14	23	3
Low	9	16	6	7	11	5	5	2	0	0
FHD	0.52	0.54	0.44	0.48	0.49	0.52	0.37	0.44	0.46	0.28
Canopy openness	12.8	15.4	7.9	14.4	10.1	13.3	16.0	44.0	20.2	33.2

LIFE HISTORIES OF THE SORICIDAE: A REVIEW

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ABSTRACT

Data on adult body mass, litter size, gestation length, neonate mass, age when eyes open, age and mass at weaning, growth rate to weaning, maximum life span, and length of the breeding season were compiled primarily from the published literature for 93 soricid species representing 12 genera. Body mass and litter size were the most frequently reported traits, and most information was found on *Crocidura* and *Sorex* species. Both litter size and the length of the breeding season differed significantly among all species, all genera, and between subfamilies. However, when the analyses were restricted to *Crocidura* and *Sorex*, *Crocidura* were larger as adults and neonates, had smaller litters, opened their eyes earlier, and had longer breeding seasons. Signifieant correlations between female adult body mass and other traits were not common. However, a number of developmental traits consistently covaried with one another. Litter size was negatively correlated with length of the breeding season among populations, among species, and among genera, but not within any one species. Overall, the life histories of the Soricidae are diverse. For example, across all populations average male body mass and litter size ranged from 1.7 g to 117.0 g, and 1.2 to 9.8, respectively.

INTRODUCTION

Species of the family Soricidae occur almost worldwide and in a variety of habitats ranging from deserts to tropical rain forests (Hutterer, 1985). Thus, one might expect diverse life history tactics to have evolved to cope with different environmental conditions. There have been numerous reviews on the life histories of mammals. Most of these have examined large data bases and have emphasized differences and covariation among traits at higher taxonomic levels (families, orders; e.g., Eisenberg, 1981; Stearns, 1983). Most have found that body size is a key trait because many other traits vary with it. However, other traits can covary if body size effects are removed (e.g., Harvey et al., 1989). Although differences among taxa and allometric relationships seem well-established at higher taxonomic levels, the ecological correlates for differences among groups are not always evident. For example, Gittleman (1986) found only a few dietary and vegetational effects that could explain life-history variation among carnivore families.

Life-history traits may also be influenced by the degree of seasonality. Boyce (1979) stated that seasonality is important in explaining: 1) fat and resource storage mechanisms, 2) geographic variation in litter size, 3) rapid somatic growth patterns, and 4) the evolution of large body size, especially in homeothermic vertebrates. Some support for these postulates has been reported by Boyce (1978; 1988), May and Rubenstein (1984), Cameron and McClure (1988), and Zeveloff and Boyce (1988). These studies have demonstrated that mammalian litter size or body size, or both, increase with increasing latitude or highly seasonal evapotranspiration rates and temperature regimes. However, Millar (1984) found that adult mass and neonate mass, litter size, age at weaning, and developmental rates in mice of the genus *Peromyscus* were not significantly correlated with the length of the breeding season. Rather, he found that survival increased as the length of the breeding season decreased.

Most comparative studies on life histories in the Soricidae have focused on a few species in a few genera (e.g., Vogel, 1972*a*, 1972*b*). Recent studies have emphasized differences in longevity, litter size, reproductive effort, and postnatal development in species of *Crocidura* and *Sorex* (Vogel, 1980; Genoud, 1988; Genoud and Vogel, 1990). These studies have suggested that these differences may apply broadly to the two extant subfamilies (Crocidurinae and Soricinae).

In this paper, I review the life histories of the Soricidae by examining 11 life-history traits and the length of the breeding season. Each variable was tested for differences at three levels: among species, among genera, and between subfamilies. Similarly, I examined how the traits covaried with one another, and with the length of the breeding season within species, among populations, among species, and among genera. Other ecological correlates were not considered because most species for which life-history data were available appear to fit into the "terrestrial" habitat grouping as tentatively classified by Hutterer (1985). Also, many species appear to have similar diets.

METHODS

Life-History Traits

The literature was searched for data on adult body mass, litter size, gestation length, neonate mass, age when the eyes open, age and mass at weaning, growth rate to weaning, maximum life span, and length of the breeding season. When possible, I consulted original sources, but some secondary sources were used. Unpublished data were also included and are cited as such.

Data on adult body mass were compiled for males, females, or both sexes combined having a minimum sample size of two per population. Most are means (although a few median and modal values are included), primarily representing adults caught during the breeding season. Some authors were not explicit on how data were presented, and some samples may have included juveniles and pregnant females. Measures of combined mass for males and females were available for *Crocidura crossei*, *C. flavescens*, and *Suncus murinus*, but were not used because males are over 33% heavier than females. Most other species were much less sexually size dimorphic, usually exhibiting less than a 20% difference between sexes.

Litter size estimates are primarily mean values from embryo counts, with an *n* of two or more from each population. These estimates were supplemented with a few neonate counts from laboratory matings for species that had little or no other litter size data. Two additional studies (Johnston and Rudd, 1957; Forsyth, 1976) gave estimates based on counting neonates in natural nests. Four other studies (Hoffmeister and Goodpaster, 1962; Hutterer, 1976; Baxter and Lloyd, 1980; Michalak, 1987*b*) that determined litter size from counting neonates conceived in the wild, but born in the laboratory, were also included. Litter size estimates from placental scar counts were very rare and only two studies (Hamilton, 1940; Connor, 1966), which combined placental scar counts and embryo counts, were used.

The length of gestation was usually determined under laboratory conditions, where it was measured as the number of days between a mating and subsequent parturition. In at least one species, *Suncus etruscus*, gestation can be longer if it is coincident with lactation (Vogel, 1970), so such estimates were not used. In two additional studies (Pearson, 1944; Crowcroft, 1957), minimum gestation length was determined by noting the time between capture of a wild gravid female and the birth of her litter in the laboratory. However, in many cases, the methodology used to determine the length of gestation was not described.

All neonate weights are mean values for one or more litters measured in the laboratory, except for the data of Forsyth (1976) who inspected nests in the wild. Most young soricids open their eyes over several days and therefore a range was usually reported. Median values for this trait were compiled.

Weaning is a gradual, transitional period for most mammals and has been measured in a variety of ways. Most investigators who described their methodology have defined the age at weaning as two or more days after the young were first seen eating solid food. Only two studies (Dryden, 1968; Michalak, 1987*b*) used the quantitative method of King et al. (1963). Other studies probably gave ages when weaning was forced and the young survived.

Body mass at weaning and growth rate to weaning also represent values from laboratory studies. If not given, growth rates were calculated by subtracting neonate mass from mass at weaning and then dividing by the number of days of lactation.

Estimates of maximum life span were compiled mainly from mark-recapture studies, although a few were based on toothwear indices (e.g., Dapson, 1968). Other traits such as age at maturity, survival, and number of litters per season were not compiled, primarily because they are rarely reported in the literature. Length of the breeding season was defined as the number of months in which pregnant or lactating females were caught under natural conditions.

Statistical Analysis

Most analyses were performed using SPSS-X (Statistical Package for the Social Sciences-Extension; SPSS, Inc., 1988). Means are given ± 1 standard error (SE). Species means were calculated from population values, generic means were calculated from the constituent species means, and subfamily means were calculated from the constituent generic means, following Harvey et al. (1989). This averaging procedure minimizes bias if, for example, some genera are species-rich while others are species-poor. However, 70% of the species used here were from the genera *Crocidura* or *Sorex*. For this reason, I analyzed the data for all species, as well as those only from the above two genera.

Analysis of life-history data at lower taxonomic levels (below the family level) is usually not recommended because taxa are closely related genetically and, therefore, do not serve as independent points (Harvey and Clutton-Brock, 1985). In a bivariate analysis, this would increase the level of significance. I analyzed the data at various levels to find differences and correlations that were common to all levels, reasoning that if the relationship occurred at all levels, it was likely real. All data were log (base 10) transformed before analyses, except growth to weaning, which as a proportion was arcsine transformed (Sokal and Rohlf, 1981). For correlation analyses, a minimum *n* of five was required. Also, significant correlations between growth rate to weaning and the traits it was derived from (neonate mass, mass at weaning, and age at weaning) should be viewed with caution because of possible autocorrelation.

Nomenclature

Taxonomically, the Soricidae is one of the most difficult of all mammalian families (Pruitt, 1957; Croin Michielsen, 1966) and the number of included species varies with the authority. In this study, a species name was retained if it was recognized by Honacki et al. (1982), Nowack and Paradiso (1983), or Corbet and Hill (1986). Using the above authorities, the following generic names were changed: *Megasorex gigas* was placed in *Notiosorex*, *Microsorex hoyi* was placed in *Sorex*, and *Surdisorex* species were placed in *Myosorex*. Similarly, the following species names were changed: *Crocidura occidentalis* to *C. flavescens*, *C. hildegarde* to *C. gracilipes*, *C. nigeriae* to *C. poensis*, *C. jouvenetae* to *C. crossei*, *C. deserti* to *C. hirta*, *Cryptotis floridanus* to *C. parva*, *Sorex personatus* to *S. cinereus*, *S. obscurus* to *S. monticolus*, and *S. roboratus* to *S. vir*. Recently, three new species pertinent to this review have been recognized: *Crocidura canariensis* (Hutterer et al., 1987), *C. zimmermanni* (Vogel et al., 1986), and *Sylvisorex vulcanorum* (Hutterer and Verheyen, 1985). These new names are recognized herein. The results of studies by Hellwing (1970; 1971; 1973*a*; 1973*b*) and Mover et al. (1988) on "*Crocidura russula*" were attributed to *C. suaveolens* following Catzeflis et al. (1985).

Results

More than 260 species of Soricidae are recognized, but life-history data were found for only 93 (Table 1). The data were highly heterogeneous, with 35 species represented by estimates for only one trait, whereas others had estimates for two or more traits. Most data were for species of the genera *Crocidura* and *Sorex*. Adult mass and litter size were the most frequently reported traits.

Differences Among All Species

A one-way analysis of variance showed that mean adult male mass differed among species ($F = 52.5$, $P < 0.0001$, $n = 51$) and ranged from 1.8 g (*Suncus etruscus*) to 65.2 g (*S. murinus*) (Table 1). Similarly, adult female mass differed among species ($F = 46.4$, $P < 0.001$, $n = 45$) and ranged from 2.0 g (*S. etruscus*) to 42.8 g (*S. murinus*). Combined body mass for both sexes also differed among species ($F = 27.0$, $P < 0.0001$, $n = 54$) and ranged from 2.1 g (*S. etruscus*) to 22.0 g (*Crocidura hirta*). Depending on which adult mass category was used, 27 to 37 species were under 10 g, 14 or 15 species were between 10 and 20 g, and only 4 or 5 species were greater than 20 g.

Mean litter size differed among species ($F = 10.5$, $P < 0.001$, $n = 59$) and ranged from 1.2 (*Crocidura grayi*) to 8.7 (*Sorex tundrensis*). Only 20 of 59 species (33.9%) had mean litter sizes of five or more.

Mean gestation length differed among species ($F = 30.1$, $P < 0.0001$, $n = 14$) and ranged from 18.0 days (*Sorex isodon*) to 31.5 days (*Crocidura canariensis*). Gestation lengths were more or less evenly distributed over that 14-day range. Neonate mass differed among species ($F = 20.0$, $P < 0.0001$, $n = 22$) and ranged from 0.24 g (*Sorex minutus* and *Suncus etruscus*) to 2.84 g (*Suncus murinus*). Only six of 22 species (27.3%) produced neonates that weighed one gram or more. The age at which young opened their eyes differed among species ($F = 9.1$, $P < 0.0001$, $n = 17$) and ranged from 8.6 days (*Suncus murinus*) to 22.0 days (*Neomys anomalus* and *N. fodiens*). Ages in other species were more or less evenly distributed across this range.

The age at weaning differed among species ($F = 2.8$, $P < 0.005$, $n = 21$) and ranged from 18.0 days (*Crocidura hirta* and *C. suaveolens*) to 30.0 days (*Sorex cornatus*). Only six of 21 species (28.6%) weaned their offspring on or before 20 days of age. Body mass at weaning differed among species ($F = 12.0$, $P < 0.001$, $n = 17$) and ranged from 2.1 g (*Crocidura bicolor*) to 30.4 g (*Suncus murinus*). Thirteen of the 21 species (76.5%) weaned their young when they were less than 10 g. Growth rates to weaning differed among species ($F = 3.1$, $P < 0.05$, $n = 17$) and ranged from 0.06 g/day (*C. bicolor*) to 1.39 g/day (*Suncus murinus*). Fourteen of 17 species (82.4%) had growth rates of 0.5 g/day or less.

Maximum life spans did not differ significantly among species and averaged 16.8 months for all species. Length of the breeding season differed among species ($F = 3.4$, $P < 0.0005$, $n = 27$) and ranged from 4.4 months (*Sorex caecutiens*) to year-round (*Scutisorex somereni*). Other species were more or less evenly distributed across this range.

Differences Among Crocidura *and* Sorex *Species*

When only *Crocidura* and *Sorex* species were considered, there were fewer differences than when all 93 species were considered. Maximum life span was not significantly different among species as before. Age at weaning and growth rate to weaning also were not significantly different. Despite the exclusion of the lightest and heaviest species (*Suncus etruscus* and *S. murinus*, respectively), male mass, female mass, and the combined mass of both sexes all showed differences among species ($F = 36.0$, $n = 42$; $F = 30.9$, $n = 35$; $F = 26.5$, $n = 41$; $P < 0.0001$, respectively). Similarly, neonate mass and mass at weaning differed among species ($F = 4.7$, $n = 14$; $F = 6.0$, $n = 12$; $P < 0.01$, respectively). Litter size, gestation length, age when eyes open, and length of the breeding season were also different among species ($F = 9.8$, $n = 43$, $P<0.0001$; $F = 23.7$, $n = 9$, $P < 0.0001$; $F = 3.8$, $n = 10$, $P<0.05$; $F = 2.4$, $n = 16$, $P < 0.05$, respectively).

Differences Among Genera

Mean male mass differed among genera ($F = 2.4$, $n = 8$, $P < 0.05$) and ranged from 4.7 g (*Cryptotis*) to 33.5 g (*Suncus*). Litter size also differed among genera ($F = 11.3$, $n = 11$, $P < 0.0001$) and ranged from 1.9 (*Scutisorex*) to 6.8 (*Neomys*). Only *Blarina*, *Neomys*, and *Sorex* had mean litter sizes exceeding five. Gestation length differed among genera ($F = 6.9$, $n = 6$, $P < 0.01$) and ranged from 20.3 days (*Blarina*) to 29.7 days (*Crocidura*). Age when the eyes opened differed among genera ($F = 6.0$, $n = 7$, $P < 0.01$) and ranged from 11.6 days (*Suncus*) to 22.0 days (*Neomys*). Age at weaning differed among genera ($F = 3.9$, $n = 7$, $P < 0.05$) and ranged from 19.2 days (*Suncus*) to 28.7 days (*Neomys*). Maximum life span differed among genera ($F = 7.9$, $n = 7$, $P < 0.01$), ranging from 13.5 months (*Neomys*) to 27.0 months (*Crocidura*). Length of the breeding season differed among genera ($F = 2.8$, $n = 10$, $P < 0.05$) and ranged from 5.0 months (*Notiosorex*) to year-round (*Scutisorex*). The following traits did not differ among genera: female mass, combined mass of both sexes, neonate mass, mass at weaning, and growth rate to weaning.

Differences Between Crocidura *and* Sorex

Adult mass of males and females showed that *Crocidura* were larger than *Sorex* (Table 2). *Sorex* females gave birth to larger litters of smaller neonates after a shorter gestation period compared to *Crocidura* females. *Crocidura* juveniles opened their eyes and are weaned earlier than *Sorex* juveniles. *Crocidura* lived longer and had longer breeding seasons than *Sorex*. Combined mass, body mass at weaning, and growth rate to weaning did not differ between genera.

Differences Between the Two Subfamilies

Of the 12 variables only two showed significant differences between the two subfamilies (Table 3). The Crocidurinae produced smaller litters but had longer breeding seasons compared to the Soricinae.

Correlations Between Length of the Breeding Season and Life-History Traits

Within Species.—Since the data were heterogeneous, only a few species and only female mass and litter size were examined in relation to the length of the breeding season within species. Within *Blarina brevicauda*, *Sorex araneus*, *S. cinereus*, or *Suncus murinus*, neither female mass nor litter size was

significantly correlated with the length of the breeding season.

Among All Populations and Only in Crocidura *and* Sorex *Populations.*—Among all populations, both male and female weights were significantly correlated with the length of the breeding season $r = 0.60$, $n = 36$; $r = 0.56$, $n = 39$, respectively; $P < 0.001$), whereas combined weights were not. Litter size was negatively correlated with the length of the breeding season ($r = -0.66$, $n = 80$, $P < 0.001$) (Fig. 1). The only other significant correlation was between age at weaning and length of the breeding season ($r = -0.88$, $n = 6$, $P < 0.05$). Among *Crocidura* and *Sorex* populations, the only trait that was correlated with the length of the breeding season was litter size ($r = -0.57$, $n = 54$, $P < 0.001$).

Among All Species and Only in Crocidura *and* Sorex *Species.*—Among all species, length of the breeding season was negatively correlated with both litter size and the age when eyes open ($r = -0.80$, $n = 27$, $P < 0.001$; $r = -0.61$, $n = 13$, $P < 0.05$, respectively). Male mass, female mass, gestation length, and neonate weight were positively correlated with the length of the breeding season ($r = 0.50$, $n = 23$; $r = 0.43$, $n = 22$; $r = 0.61$, $n = 12$; $r = 0.53$, $n = 15$; $P < 0.05$, respectively). Using *Crocidura* and *Sorex* species only, length of the breeding season was negatively correlated with litter size ($r = -0.79$, $n = 16$, $P < 0.001$) but positively correlated with gestation length ($r = 0.76$, $n = 7$, $P < 0.05$).

Among All Genera.—Among all genera, the length of the breeding season was correlated only with litter size ($r = -0.83$, $n = 10$, $P < 0.01$). Samples were too small for analysis by subfamily.

Correlations Among Life-History Traits

Within Species.—In *Blarina brevicauda*, *Sorex araneus*, *S. cinereus*, and *Suncus murinus*, no significant relationships were found between female mass and litter size. However, in *S. murinus* there was a negative correlation between litter size and gestation length ($r = -0.78$, $n = 9$; $P < 0.05$).

Among All Populations and Only Among Crocidura *and* Sorex *Populations.*—Of the possible 36 correlations, only 16 were significant among all populations (Table 4). Female mass was associated with only three other traits, but many developmental traits were correlated with one another. Larger females appeared to produce smaller litters (Fig. 2), but gave birth to and weaned larger young. Larger litters were associated with smaller young at birth and weaning, shorter gestation lengths, and later ages when eyes open. Gestation length was positively associated with neonate mass, but negatively associated with age at weaning and age when eyes open. Neonate mass was positively correlated with mass at and growth to weaning, but negatively correlated with age at weaning and age when eyes open. Earlier age when eyes open was associated with earlier age at weaning, and greater mass at weaning was positively correlated with growth to weaning.

Ten correlations were significant when only *Crocidura* and *Sorex* species were used (Table 4). The patterns were similar to those above except that the following relationships were no longer significant: litter size and neonate mass, litter size and mass at weaning, female mass and neonate mass, female mass and mass at weaning, gestation length and neonate weight, gestation length and age at weaning, and neonate mass and age at weaning. Also, in this comparison litter size was negatively correlated with maximum life span.

Among All Species and Only Among Crocidura *and* Sorex *Species.*—Of the 36 possible correlations, only 12 were significant among all species (Table 5). Greater female mass was associated with larger neonates, which grew more rapidly and weighed more at weaning. Litter size was negatively correlated with both gestation length and neonate mass, but positively correlated with both the age when eyes open and age at weaning. Gestation length was negatively correlated with the age when eyes open. Neonate mass was positively correlated with both mass at weaning and growth rate to weaning. The later the young opened their eyes, the later they were weaned. Also, the more rapid the growth to weaning, the heavier the young were when weaned.

Using only *Crocidura* and *Sorex* species, 13 correlations were significant (Table 5). The patterns were the same as above with the following exceptions: litter size was negatively correlated with both growth rate to weaning and maximum life span. Also, age at weaning was not significantly correlated with litter size.

Among Genera.—Eight correlations were significant among genera (Table 6). Female mass was positively correlated with neonate mass, mass at weaning, and growth to weaning. Litter size was negatively correlated with gestation length. Neonate mass was positively correlated with both mass at weaning and growth to weaning. Age at weaning was positively correlated with the age when eyes open. Also, mass at weaning was positively correlated with growth to weaning. Samples were too small for analyses within each subfamily.

Influences of Adult Female Mass.—Ideally, the effects of body size should be controlled for, because previous studies have shown that it covaries with many other traits. In this study, body mass was usually correlated with one or three other traits (Tables 4, 5, and 6). Due to the structure of the data, adequate sample sizes for a partial correlation analysis (holding female mass constant) could be done using only species means with all species (Table 5). Controlling for female mass did alter some of the covariation among traits (Table 7). For example, the positive correlations between neonate mass and both mass at weaning and growth to weaning were no longer significant. Also, five new relationships became apparent: gestation length was positively correlated with both neonate mass and mass at weaning, neonate mass was negatively associated with both age when eyes open and age at weaning, and growth to weaning was positively correlated with age when eyes open.

When correlations with length of the breeding season were considered, a number of changes occurred. Length of the breeding season was still negatively correlated with litter size and positively correlated with gestation length. However, the correlations between length of the breeding season, female mass, neonate mass, and age when eyes open were no longer significant. Also, length of the breeding season was negatively associated with growth to weaning.

Discussion

Quality of the Data Base

This study has many of the drawbacks inherent in this type of review. First it must be assumed that the 93 species examined are representative of the approximately 260 soricid species. Also, sample sizes were often small and some traits were measured in slightly different ways in different studies. Other difficulties with this type of review have been addressed by P. Harvey and colleagues (Clutton-Brock and Harvey, 1984; Harvey and Mace, 1982; Harvey and Clutton-Brock, 1985). Among other things, they have pointed out that rarely are numbers of mammalian species evenly distributed across genera. Most of the life-history data collected were from *Crocidura* (39 species) and *Sorex* (32 species). Other genera were represented by one to four species. There is also a geographic bias. Species found in Europe and North America tended to be overrepresented relative to species in other areas.

Another bias which has large statistical implications involves the genus *Suncus*. This genus is represented in this study by two species: *S. etruscus* and *S. murinus*. Both male and female adult weights show that they are the smallest and largest species, respectively, in the family. Adult males of *S. etruscus* weigh as little as 1.3 g (Fons, 1970), but *S. murinus* males can reach 177.0 g (Louch et al., 1966). In the latter species, body mass varies considerably from area to area. Those from Bangladesh are heavier than those from Sri Lanka which in turn are heavier than those from Japan (Tsubota et al., 1986). *Suncus murinus* is also unusual because growth and development of the young appear to be phenotypically plastic. Dryden and Ross (1971) found that a higher quality diet increased the growth rate and accelerated some development changes compared to young on a lower quality diet.

Length of Breeding Season

Length of the breeding season ranged from four months to year-round among all populations. Most breeding seasons are continuous, although in at least one species (*Soriculus caudatus*) it is bimodal, occurring before and after the monsoon in Nepal (Mitchell, 1977). Considering all species, length of the breeding season was significantly different and common to all three taxonomic levels (among species, among genera, and between subfamilies). Similarly, when only *Crocidura* and *Sorex* species were considered, length of the breeding season was different among species as well as between genera. On average, members of the Crocidurinae have longer breeding seasons than members of the Soricinae.

In *Blarina brevicauda*, *Sorex araneus*, *S. cinereus*, and *Suncus murinus*, length of the breeding season was not correlated with either female mass or litter size. Four traits among all populations, six among all species, and three among all genera were significantly correlated with the length of the breeding season. Common to all levels was a negative relationship between litter size and length of the breeding season. At the species level, this negative correlation occurs even if the data are adjusted for the effects of female mass. Among all populations of *Crocidura* and *Sorex*, and among all *Crocidura* and *Sorex* species, one and three traits were correlated with the length of the breeding season, respectively. Common to both levels was a negative relationship between litter size and length of the breeding season.

The relationship between litter size and length of the breeding season in small mammals remains unclear. A number of studies have shown that litter size increases with increasing latitude (or altitude) within species (Spencer and Steinhoff, 1968; Innes, 1978; McLaren and Kirkland, 1979; Halfpenny, 1980). Usually, the negative relationship between the two variables is much stronger among species than within species (Lord, 1960; Innes, 1978; McLaren and Kirkland, 1979). However, whether latitude (or altitude) accurately predicts the length of the breeding season is unknown. Millar (1984) found a significant negative correlation between litter size and length of the breeding season in 15 species of *Peromyscus*, but not in *P. maniculatus*. He also found that many other traits did not vary with the length of the breeding season. Thus, soricids appear to fit a similar pattern in that litter size and length of the breeding season are negatively correlated, but only at or above the species level, and few other traits covary with length of the breeding season.

Differences in Life-History Traits

Considering all species, only litter size was different and common to all three taxonomic levels. The number of traits that were different decreased as the taxonomic level increased (ten among species, six among genera, one between subfamilies). This result is not surprising because the amount of variation decreased as data were averaged over each successively higher taxonomic level. Since litter size was the only trait that differed at all levels, this suggests that there is a considerable amount of variation in the other traits that are independent of the two subfamilies. In a broader mammalian survey, Stearns (1983) found that ten traits were significantly different among four orders as well as among eight families.

When only *Crocidura* and *Sorex* species were used, eight traits differed among species and seven traits between the two genera. Traits common to both levels indicate that *Crocidura* are larger as adults (both males and females) and as neonates, have smaller litters and open their eyes earlier than *Sorex*. This suggests that these two groups have evolved distinct life histories. Earlier, Vogel (1972*a*, 1972*b*) pointed out similar differences in a comparison (mainly) of *C. russula* and *S. araneus*.

The contrasting life histories of *Crocidura* and *Sorex* species, as well as between crocidurine and soricine species, appear to be related to their metabolic rates (Vogel, 1976, 1980; Genoud, 1988). These authors found that the Crocidurinae have lower metabolic rates than the Soricinae and this may be related to the respective Paleotropic versus Holarctic origins of the two subfamilies. They also suggested that this is related to differences in reproduction, development, and longevity. For example, *Crocidura* species usually have litter sizes less than five, whereas *Sorex* species usually have litter sizes greater than five. These patterns may have ultimately resulted from differences in climate (warm versus cold) or resource

availability (unpredictable versus seasonally predictable) (Genoud, 1988).

Correlations Among Life-History Traits

Considering all species, the number of significant correlations decreased with increasing taxonomic level. Among populations, among species, and among genera, 16, 12, and 8 correlations were significant, respectively. Seven relationships were common to all three levels. Larger females produced larger neonates and weaned larger young compared to smaller females. These relationships have been found in broader surveys (Millar, 1977; Read and Harvey, 1989). Litter size was negatively correlated with gestation length and this pattern is also evident across all eutherian orders (Read and Harvey, 1989). Larger neonates grew more rapidly and were weaned at a greater weight than smaller neonates. Also, age when eyes open was positively correlated with age at weaning, and weight at weaning was positively correlated with growth to weaning. These latter relationships have not been examined in broader surveys, but Modi (1984) found no significant relationships between either growth rate to or age at weaning with age when eyes open in 15 taxa of *Peromyscus*.

When only *Crocidura* and *Sorex* were used, three more significant correlations were found and common to both the population and species levels. Litter size was negatively correlated with maximum life span, but positively correlated with age when eyes open. Gestation length was also negatively correlated with age when eyes open. The negative tradeoff between litter size and life span has been found across eutherian orders (Read and Harvey, 1989). Modi (1984) found a negative correlation between litter size and age when eyes open.

A number of the patterns of covariation were found among species whether the effects of female mass were controlled for or not (Tables 5 and 7). This suggests that these relationships occur independently of adult mass. For example, there was a negative correlation between litter size and neonate mass whether the influence of female mass was adjusted for or not. This situation is evident across all eutherian orders (Read and Harvey, 1989). However, when female mass was adjusted for, a number of new relationships were evident. For example, gestation length became significantly correlated with neonate mass. Thus, among soricids, covariation among other traits may or may not be independent of adult female mass.

Future Research Needs and Summary

A number of important traits were not quantified in this review. For example, age at sexual maturity can have a profound effect on the rate of increase of a population (Cole, 1954). Under laboratory conditions, young females of *Blarina brevicauda*, *Crocidura russula*, *Cryptotis parva*, and *Suncus murinus* can conceive at approximately 30 days of age (Blus, 1971; Hellwing, 1971; Mock and Conaway, 1976; Dryden, 1969, respectively). Mock and Conaway (1976) also reported that *C. parva* males could breed at 36 days of age. In a review of the literature, Jeanmarie-Besançon (1988) found that the number of females maturing in the year of their birth was highly variable under natural conditions, especially among *Sorex* species. He concluded that *Crocidura* species were more likely to breed as young-of-the-year than *Sorex* species. This situation may be the result of their respective Paleotropic versus Holarctic origins. However, not all European populations of *Crocidura* breed in the year of their birth (Bishop and Delany, 1963), and all studies on age at sexual maturation in *Crocidura* have been conducted in temperate regions. Similar studies are needed in tropical regions.

Another trait that has been relatively neglected is the number of litters per season or per lifetime. Necropsies of snap- or pitfall-trapped specimens have led most investigators to conclude that females produce at least two litters each season. This is based on the observation that females can be pregnant and lactating simultaneously and thus undergo a postpartum estrus. A postpartum estrus has been documented in seven soricid genera: *Blarina* (Lutz, 1964), *Cryptotis* (e.g., Blair, 1938), *Crocidura* (e.g., Hutterer et al., 1987), *Myosorex* (Baxter and Lloyd, 1980), *Neomys* (Michalak, 1987*a*), *Sorex* (e.g., Skarén, 1979), and *Suncus* (Dryden, 1969). However, determining the number of litters based on necropsied samples has drawbacks and this trait may be best measured by mark-recapture studies (Innes and Millar, 1987). Buckner (1966) used the latter technique and found that female *Blarina brevicauda*, *Sorex arcticus*, and *S. cinereus* averaged about two litters per lifetime (range = 1–5). Additional live-trapping studies to quantify this trait as well as survival rates could prove useful.

Generalizing across all species, adult soricids are small, with most weighing <10.0 g. Neonates are small, usually weighing <1.0 g. Juveniles are usually weaned when body mass is only 2.0 g below adult mass. Growth rate to weaning is usually <0.3 g/day. Gestation length and age at weaning are variable, with both traits ranging from about 18 to 30 days. The age when eyes open ranges from 8 to 22 days. Litter size is extremely variable, but most species have litters of less than five. Maximum life span averaged 17 months across all species. Length of the breeding season is variable, but usually exceeds four months.

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APPENDIX

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Table 1.—*Life-history traits and length of the breeding season for 93 species of the Soricidae. Means are given ±1 standard error (SE)*

Species	Male Mass (g)	Female Mass (g)	Combined Mass (g)	Litter Size	Gestation Length (Days)
Blarina brevicauda	18.1 ± 0.5 (25)	17.0 ± 0.5 (27)	16.9 ± 1.4 (11)	5.4 ± 0.2 (24)	20.3 ± 0.5 (4)
B. carolinensis				5.4 (1)	
Crocidura attenuata			7.4 (1)		
C. beatus	10.5 (1)	10.5 (1)			
C. bicolor	4.7 ± 1.2 (2)	5.7 (1)		4.0 (1)	
C. bottegi		2.0 (1)	3.2 (1)		
C. canariensis			7.5 (1)	2.1 (1)	30.0 (1)
C. crossei	9.8 (1)	6.3 (1)		3.0 (1)	
C. dolichura			5.5 (1)		
C. douceti			4.3 (1)		
C. flavescens	45.4 ± 9.8 (2)	24.8 (1)		3.5 ± 0.5 (5)	
C. foxi			21.0 (1)		
C. fuscomurina	5.0 (1)		3.0 (1)		
C. gracilipes	12.2 (1)	10.8 (1)		3.0 (1)	
C. grandiceps			21.9 (1)		
C. grayi	11.1 (1)	10.5 (1)		1.2 (1)	
C. hirta	16.9 (1)	15.1 (1)	22.0 (1)	3.9 ± 0.2 (6)	
C. horsfieldi				3.3 (1)	
C. jacksoni	12.7 (1)				
C. jouveneta	9.8 (1)			2.5 (1)	
C. kivuana				1.7 (1)	
C. lanosa				3.3 (1)	
C. leucodon			7.9 (1)	4.0 ±0.8 (3)	31.5 ± 0.5 (2)
C. littoralis			21.0 (1)	3.0 (1)	
C. lusitania			4.1 (1)		
C. luna	9.5 (1)				
C. mariquensis	11.0 (1)	9.0 (1)	11.0 (1)	3.6 ± 0.2 (3)	
C. nanilla	3.4 (1)	2.3 (1)			
C. nigricans	21.0 (1)				
C. nigrofusca				3.3 (1)	
C. niobe		12.5 (1)			
C. olivieria	66.4 ± 16.0 (3)	34.9 ± 7.4 (2)		3.1 ± 0.3 (6)	
C. osorio			5.7 (1)		
C. poensis	14.2 ± 3.0 (2)	14.6 (1)	19.8 ± 3.3 (2)	2.3 (1)	
C. russula	10.6 ± 0.6 (7)	11.2 ± 0.7 (5)	13.0 ± 1.5 (3)	3.8 ± 0.2 (13)	29.7 ± 0.3 (3)
C. suaveolens	7.3 ± 0.3 (3)	7.7 ± 0.2 (4)	7.9 ± 0.8 (3)	4.0 ± 0.7 (4)	27.6 ± 0.5 (5)
C. tarfayensis			6.5 (1)		
C. theresae				3.7 ± 1.2 (2)	
C. viaria	17.7 (1)		16.5 ± 0.5 (2)	3.5 (1)	
C. whitakeri			5.5 (1)		
C. zimmermani			7.7 (1)		
Cryptotis magna				3.0 (1)	
C. parva	4.7 ± 0.02 (8)	5.0 ± 0.2 (6)	4.4 ± 0.1 (3)	4.2 ± 0.3 (11)	22.0 ± 0.4 (4)
Diplomesodon pulchellum			8.9 (1)		
Myosorex baboulti					
M. norae	23.7 (1)	25.1 (1)			
M. polulus	19.5 (1)	17.6 (1)			
M. varius			12.5 ± 1.1 (4)	2.9 ± 0.1 (3)	
Neomys anomalus	11.9 ± 1.0 (2)	14.0 ± 0.7 (2)	10.9 ± 0.7 (2)	7.2 ± 1.7 (3)	
N. fodiens	14.6 ± 1.2 (5)	14.9 ± 0.9 (4)	16.4 ± 1.5 (5)	6.3 ± 0.6 (11)	20.8 ± 0.9 (5)
Notiosorex crawfordi	5.4 (1)		4.1 ± 0.4 (2)	3.9 ± 0.2 (2)	
N. gigas			13.1 ± 2.2 (2)		

and the number of populations are in parentheses. See Methods for further explanation. Sources for each species appear in Appendix.

Neonate Mass (g)	Age Eyes Open (Days)	Age at Weaning (Days)	Mass at Weaning (g)	Growth Rate (g/day)	Life Span (Months)	Breeding Season (Months)
0.8 (1)	12.0 (1)	20.6 ± 1.5 (5)			17.2 ± 1.5 (6)	6.6 ± 0.3 (10)
						7.0 (1)
0.8 ± 0.6 (2)	13.0 ± 2.1 (3)	19.3 ± 3.2 (3)	2.1 ± 0.9 (2)	0.06 ± 0.20 (2)		
0.8 (1)						
						9.0 ± 3.0 (2)
1.0 (1)	13.0 (1)	18.0 (1)				
0.8 ± 0.1 (2)	11.7 ± 1.3 (3)	20.5 ± 0.5 (2)	7.0 (1)	0.30 (1)		
						8.0 (1)
2.1 ± 0.2 (2)	15.0 (1)	23.5 ± 3.5 (2)	16.4 ± 4.4 (2)	0.65 ± 0.28 (2)		
1.0 ± 0.1 (4)	10.7 ± 1.2 (3)	20.0 ± 0.6 (3)	8.2 ± 0.9 (2)	0.37 ± 0.04 (2)	27.0 (1)	7.5 ± 0.5 (2)
0.7 ± 0.1 (3)	10.8 ± 1.4 (4)	18.0 ± 1.1 (4)	6.5 ± 2.1 (2)	0.32 ± 0.13 (2)		7.0 (1)
1.4 (1)		20.0 (1)	13.7 (1)	0.62 (1)		
0.3 ± 0.1 (6)	14.3 ± 0.3 (4)	20.0 ± 0.6 (3)	3.2 (1)	0.15 (1)	11.0 (1)	7.5 ± 0.5 (2)
2.5 (1)						
1.0 (1)	17.0 (1)	22.0 (1)			16.0 (1)	9.0 (1)
0.6 (1)	22.0 (1)	28.0 (1)	9.3 (1)	0.31 (1)		5.0 (1)
0.7 ± 0.1 (2)	22.0 ± 0.6 (3)	29.3 ± 1.3 (4)	11.2 ± 0.8 (3)	0.50 ± 0.07 (2)	13.5 ± 5.5 (2)	6.5 ± 0.5 (2)
						5.0 (1)

Table 1 (cont.)

Species	Male Mass (g)	Female Mass (g)	Combined Mass (g)	Litter Size	Gestation Length (Days)
Scutisorex somereni				1.9 (1)	
Sorex alpinus	7.7 (1)	8.5 (1)			
S. araneus	9.8 ± 0.4 (14)	9.9 ± 0.4 (16)	9.2 ± 0.3 (32)	6.7 ± 0.2 (22)	21.5 ± 0.7 (6)
S. arcticus	8.0 ± 0.4 (4)	8.0 ± 0.4 (4)		6.7 ± 0.3 (10)	
S. bendirri		15.3 ± 0.8 (2)			
S. caecutiens	6.5 ± 0.6 (2)	6.0 (1)	5.9 ± 0.1 (2)	7.4 ± 0.4 (8)	
S. cinereus	4.2 ± 0.1 (22)	4.4 ± 0.2 (24)	3.9 ± 0.3 (15)	6.5 ± 0.3 (31)	
S. coronatus	8.6 ± 0.3 (3)	9.4 ± 0.3 (3)		4.9 ± 0.5 (5)	24.0 (1)
S. daphaenodon				6.2 ± 0.4 (3)	
S. dispar	5.0 ± 0.4 (4)	4.8 ± 0.5 (2)	4.9 ± 0.2 (6)	3.5 ± 1.5 (2)	
S. fumeus	7.7 ± 0.3 (15)	7.2 ± 0.3 (12)	7.6 ± 0.1 (2)	4.6 ± 0.4 (9)	
S. gaspensis	3.2 (1)		4.0 ± 1.1 (2)	5.7 ± 0.0 (2)	
S. granarius			6.6 (1)		
S. hoyi	3.2 ± 1.0 (4)	3.1 ± 0.7 (3)	3.8 ± 0.7 (4)	5.7 (1)	
S. isodon	12.3 ± 0.7 (3)	11.9 ± 0.6 (3)		6.7 ± 0.6 (3)	18.0 (1)
S. longirostris	3.1 (1)	2.6 (1)	3.1 ± 0.2 (9)	4.0 ± 0.3 (4)	
S. macrodon			10.6 (1)		
S. merriami	5.0 (1)	5.9 (1)		6.0 (1)	
S. milleri	4.1 (1)	3.5 (1)			
S. minutissimus	2.0 ± 0.3 (2)	2.5 (1)			
S. minutus	4.5 ± 0.2 (7)	4.4 ± 0.2 (8)	3.9 ± 0.2 (9)	6.1 ± 0.4 (13)	25.0 (1)
S. mirabilis			15.0 (1)		
S. monticolus	6.9 ± 0.2 (3)	5.9 (1)		6.4 ± 1.1 (4)	
S. nanus			2.6 (1)	6.5 (1)	
S. ornatus	5.2 (1)	5.0 (1)	5.1 (1)		
S. pacificus				4.2 (1)	
S. palustris	13.3 ± 0.8 (9)	11.7 ± 0.6 (8)	12.7 ± 1.5 (3)	5.5 ± 0.3 (5)	
S. sinuosus	6.1 ± 0.1 (2)	5.6 ± 0.2 (2)	5.8 ± 0.5 (2)		
S. trowbridgii	4.7 ± 0.2 (3)	5.2 (1)	7.4 ± 0.2 (2)	4.1 ± 0.5 (3)	
S. tundrensis			6.3 (1)	8.7 ± 1.2 (2)	
S. unguiculatus			13.2 (1)		
S. vagrans	6.4 ± 0.4 (4)	6.6 ± 0.7 (3)	6.9 (1)	5.9 ± 0.2 (9)	20.0 (1)
S. vir				7.5 ± 0.1 (2)	
Soriculus caudatus				4.8 (1)	
S. nigrescens			15.2 (1)	4.9 (1)	
Suncus etruscus	1.8 ± 0.0 (2)	2.0 ± 0.1 (2)	2.1 ± 0.3 (2)	3.9 ± 0.2 (2)	28.0 ± 0.0 (2)
S. murinus	65.2 ± 10.2 (9)	42.8 ± 6.3 (10)		2.9 ± 0.2 (18)	29.6 ± 0.5(11)
Sylvisorex granti			3.8 (1)	1.6 (1)	
S. lunaris				2.6 (1)	
S. megalura		5.3 (1)	4.0 (1)	1.8 (1)	
S. vulcanorum			3.5 (1)		

Neonate Mass (g)	Age Eyes Open (Days)	Age at Weaning (Days)	Mass at Weaning (g)	Growth Rate (g/day)	Life Span (Months)	Breeding Season (Months)
						12.0 (1)
0.4 ± 0.1 (4)	193.5 ± 0.5 (4)	23.4 ± 0.8 (7)	7.6 ± 0.5 (4)	0.31 ± 0.01 (4)	14.9 ± 0.8 (7)	6.1 ± 0.3 (12)
					16.5 ± 1.5 (2)	5.3 ± 0.5 (4)
					16.0 (1)	4.4 ± 0.3 (5)
0.3 (1)	18.0 (1)	20.0 (1)	3.5 (1)	0.16 (1)	20.5 ± 2.5 (2)	5.3 ± 0.4 (8)
0.6 (1)		30.0 (1)	8.6 (1)	0.27 (1)	20.0 ± 1.0 (1)	8.0 ± 2.0 (2)
					17.0 (1)	5.7 ± 0.7 (3)
0.9 (1)	16.0 (1)	22.0 (1)	7.3 (1)	0.29 (1)	16.0 (1)	5.0 ± 0.0 (2)
						6.0 ± 0.0 (2)
0.2 ± 0.1 (2)		26.3 ± 2.0 (3)	3.2 (1)	0.10 (1)	16.3 ± 1.2 (3)	6.4 ± 0.5 (7)
		21.0 (1)			16.0 (1)	
					16.0 (1)	
						7.0 (1)
					16.0 (1)	
					18.0 (1)	8.0 ± 1.0 (2)
0.4 ± 0.1 (2)	21.0 (1)	22.0 ± 1.5 (3)	3.9 ± 0.4 (2)	0.15 ± 0.0 (2)	19.0 ± 3.0 (3)	6.5 ± 1.5 (2)
						6.0 (1)
0.2 ± 0.1 (2)	14.5 ± 0.5 (2)	19.5 ± 0.5 (2)	2.2 ± 0.1 (2)	0.10 ± 0.01 (2)	17.0 (1)	6.0 (1)
2.8 ± 0.2 (8)	8.6 ± 0.2 (5)	18.9 ± 1.0 (8)	30.4 ± 5.5 (6)	1.39 ± 0.26 (6)		10.4 ± 1.0 (7)

Table 2.—*Life-history traits and length of the breeding season compared between* Crocidura *and* Sorex. *Data were derived from Table 1 by averaging species means for each genus. Means are given ±1 SE and the number of species are in parentheses.* [a] $P < 0.05$; [b] $P < 0.01$; [c] $P < 0.001$.

Variable	*Crocidura*	*Sorex*	t-value
Male mass (g)	15.1 ± 3.4(20)	6.3 ± 0.6 (22)	3.5[b]
Female mass (g)	12.6 ± 2.2(14)	6.7 ± 0.7 (22)	2.9[a]
Combined mass (g)	10.6 ± 1.5(21)	6.9 ± 0.8 (20)	1.9
Litter size	3.1 ± 0.2 (21)	5.9 ± 0.3 (22)	7.8[c]
Gestation length (days)	29.7 ± 0.8 (4)	21.7 ± 1.3 (5)	4.4[b]
Neonate mass (g)	1.1 ± 0.2 (8)	0.5 ± 0.1 (6)	3.7[b]
Age eyes open (days)	12.4 ± 0.7 (6)	18.6 ± 1.1 (4)	5.1[b]
Age at weaning (days)	19.9 ± 0.7 (7)	23.5 ± 1.3 (7)	2.6[a]
Mass at weaning (g)	9.0 ± 2.1 (6)	5.7 ± 1.0 (6)	1.0
Growth rate (g/day)	0.39 ± 0.1 (6)	0.21 ± 0.1 (6)	1.6
Life span (months)	27.0 (1)	17.1 ± 1.7 (13)	4.1[a]
Breeding season (months)	7.9 ± 0.4 (4)	6.1 ± 0.3 (12)	2.7[a]

Table 3.—*Life-history traits and length of the breeding season compared between the Crocidurinae and Soricinae. Data were derived from Table 2 by averaging genus means within each subfamily. Means are given ±1 SE and the number of genera are given in parentheses.* [a] *Mann-Whitney U test;* [b] $P < 0.01$.

Variable	Crocidurinae	Soricinae	U_s-Value[a]
Male mass (g)	23.4 ± 5.4 (3)	9.6 ± 2.6 (5)	14.0
Female mass (g)	15.4 ± 4.0 (4)	10.8 ± 2.9 (4)	5.0
Combined mass (g)	7.6 ± 2.0 (5)	10.9 ± 2.0 (6)	21.0
Litter size	2.7 ± 0.3 (5)	5.1 ± 0.5 (6)	30.0[b]
Gestation length (days)	29.3 ± 0.5 (2)	21.2 ± 0.4 (4)	11.0
Neonate mass (g)	1.4 ± 0.2 (3)	0.6 ± 0.1 (4)	12.0
Age eyes open (days)	13.7 ± 1.7 (3)	16.7 ± 2.2 (2)	9.0
Age at weaning (days)	20.4 ± 0.8 (3)	23.2 ± 2.0 (3)	10.0
Mass at weaning (g)	12.7 ± 3.7 (2)	6.4 ± 2.1 (3)	5.0
Growth rate (g/day)	0.57 ± 0.2 (2)	0.26 ± 0.1 (3)	5.0
Life span (months)	20.0 ± 3.5 (3)	14.7 ± 1.5 (2)	8.0
Breeding season (months)	9.3 ± 0.9 (4)	6.2 ± 0.4 (6)	24.0[b]

Table 4.—*Correlations among life-history traits (excluding male mass and combined mass) among all populations (lower triangle) and only among* Crocidura *and* Sorex *populations (upper triangle). Only significant* r*-values are reported and the number of populations appears in parentheses.* [a] $P < 0.05$; [b] $P < 0.01$; [c] $P < 0.001$.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
(1) Female mass	—	−0.43[b] (58)							
(2) Litter size	−0.45[c] (80)	—	−0.77[b] (12)		0.74[b] (11)				−0.50[a] (17)
(3) Gestation length		−0.81[c] (30)	—		−0.73[a] (10)				
(4) Neonate mass	0.91[b] (8)	−0.56[b] (31)	0.43[a] (24)	—	−0.52[a] (18)		0.68[b] (20)	0.68[b] (20)	
(5) Age eyes open		0.73[c] (22)	−0.76[c] (22)	−0.60[c] (31)	—	0.64[b] (19)			
(6) Age at weaning			−0.51[b] (29)	−0.33[a] (38)	0.71[c] (34)	—			
(7) Mass at weaning	0.95[b] (7)	−0.51[a] (24)		0.86[c] (32)			—	0.90[c] (20)	
(8) Growth to weaning				0.74[c] (27)			0.91[c] (27)	—	
(9) Life span									—

Table 5.—*Correlations among life-history traits (excluding male mass and combined mass) among all species (lower triangle) and only among* Crocidura *and* Sorex *species (upper triangle). Only significant* r*-values are reported and the number of species appears in parentheses.* [a] $P < 0.05$; [b] $P < 0.01$; [c] $P < 0.001$.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
(1) Female mass	—			0.86[b] (11)			0.89[b] (10)	0.92[c] (10)	
(2) Litter size		—	−0.78[a] (9)	−0.66[a] (14)	0.74[a] (10)			−0.58[a] (12)	−0.67[a] (12)
(3) Gestation length		−0.79[b] (14)	—		−0.84[a] (6)				
(4) Neonate mass	0.90[c] (17)	−0.52[a] (21)		—			0.70[a] (12)	0.76[b] (12)	
(5) Age eyes open		0.68[b] (17)	−0.71[a] (11)		—	0.65[a] (10)			
(6) Age at weaning		0.49[a] (21)			0.76[c] (17)				
(7) Mass at weaning	0.94[c] (15)			0.82[c] (17)			—	0.96[c] (12)	
(8) Growth to weaning	0.89[c] (14)			0.78[c] (16)			0.95[c] (16)	—	
(9) Life span									—

Table 6.—*Correlations among life-history traits (excluding male mass and combined mass) among genera. Only significant* r*-values are reported and the number of genera are given in parentheses. (Missing rows and columns are the result of nonsignificant values.)* [a] $P < 0.05$; [b] $P < 0.01$.

	(1)	(2)	(4)	(5)	(7)
(1) Female mass	—				
(2) Litter size		—			
(3) Gestation length		−0.82[a] (6)			
(4) Neonate mass	0.92[b] (7)		—		
(5) Age eyes open				—	
(6) Age at weaning				0.92[b] (7)	
(7) Mass at weaning	0.99[b] (5)		0.93[a] (5)		—
(8) Growth to weaning	0.96[a] (5)		0.92[a] (5)		0.94[a] (5)

Table 7.—*Correlations among life-history traits controlling for female body mass among all species. Only significant* r*-values are reported and the number of species occurs in parentheses. (Missing rows and columns are the result of nonsignificant values.) Compare with Table 5 (lower triangle).* [a] $P < 0.05$; [b] $P < 0.01$; [c] $P < 0.001$.

	(1)	(2)	(3)	(4)	(6)	(7)
(1) Litter size	—					
(2) Gestation length	−0.82[b] (9)	—				
(3) Neonate mass	−0.85[c] (14)	0.63[a] (9)	—			
(4) Age eyes open	0.67[c] (12)	−0.75[a] (8)	−0.63[a] (12)	—		
(5) Age at weaning	0.52[a] (15)		−0.69[b] (14)	0.82[c] (12)		
(6) Mass at weaning		0.63[a] (9)			—	
(7) Growth to weaning				0.65[a] (10)	0.76[b] (11)	—
(9) Breeding season	−0.82[c] (19)	0.71[a] (9)				−0.77[b] (9)

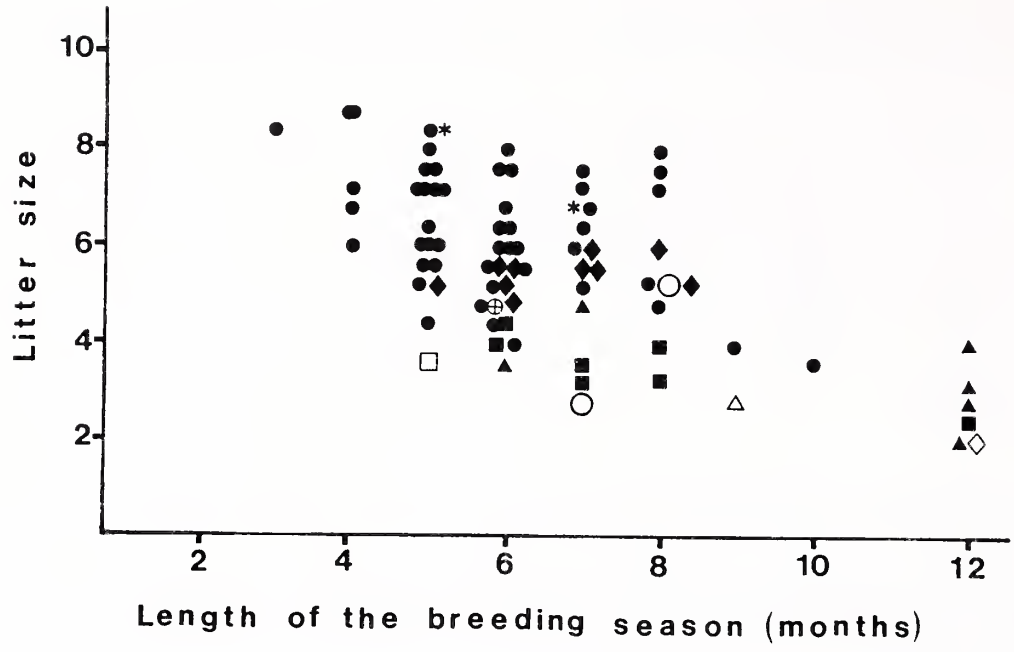

Fig. 1.—Relationship between litter size and length of the breeding season among populations. Symbols for each genus are as follows: *Blarina* ◆; *Crocidura* ■; *Cryptotis* ○; *Myosorex* ▲; *Neomys* *; *Notiosorex* □; *Scutisorex* ◇; *Soriculus* ⊕; *Sorex* ●; *Suncus* △.

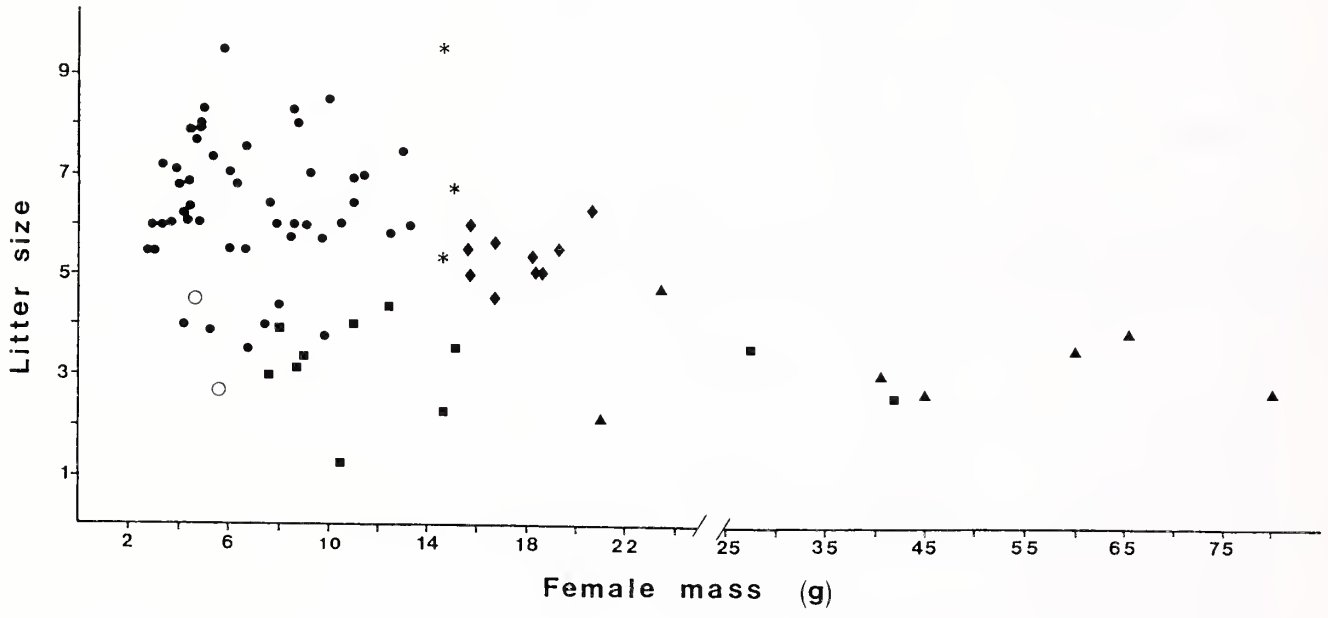

Fig. 2.—Relationship between litter size and adult female mass among populations. Symbols for each genus are as follows: *Blarina* ◆; *Crocidura* ■; *Cryptotis* ○; *Neomys* *; *Sorex* ●; *Suncus* △. Note that the scale of the x-axis changes after 25 g.

SHREWS AS INDICATORS OF HEAVY METAL POLLUTION

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ABSTRACT

Heavy metal (Cu, Ni, Zn, Cd, Cr, Hg, Pb) concentrations were analyzed in small mammals trapped near the sources of pollution and on control sites in southern Finland. Shrews (*Sorex* and *Neomys*) had higher heavy metal concentrations in their livers and kidneys than voles. In *S. araneus*, the most common species of shrew in southern Finland, heavy metal concentrations decreased with increasing distance from the source of pollution. Some heavy metals (Cd, especially) accumulated with increasing age of individual shrews. Heavy metal accumulation in shrew tissues tended to increase with increasing soil acidity. The biological effect of heavy metal pollution was studied by assessing developmental stability in skull morphology of *S. araneus*. Developmental stability was usually reduced in the polluted areas, possibly due to toxic effects of heavy metals. *S. araneus* may be a useful bioindicator of pollution in terrestrial ecosystems because it is a relatively localized animal with high potential of reproduction and also is abundant in areas intensively affected by human activities.

INTRODUCTION

Small mammals have been used in field studies to indicate accumulation of toxic compounds such as heavy metals. For example, the effect of automobile exhaust lead residues along roadsides has been studied by analyzing lead concentrations in small mammals (Quarles et al., 1974; Getz et al., 1977; Goldsmith and Scanlon, 1977). Interspecific differences among small mammals in the accumulation efficiency of heavy metals have been found. Herbivorous or granivorous voles and mice accumulate smaller amounts of toxic compounds in their bodies than predatory mammals such as shrews (Goldsmith and Scanlon, 1977; Hunter and Johnson, 1982; Andrews et al., 1984, 1989; Forsyth and Peterle, 1984; Beyer et al., 1985; Hunter et al., 1987; Hegstrom and West, 1989; Ma, 1989), although some contradictory results exist (Roberts and Johnson, 1978).

Small mammals can achieve high population densities, thereby yielding adequate sample sizes for studies of heavy metal bioaccumulation with reasonable work effort. Shrews may be particularly useful in this respect because they have high consumption rates due to their high metabolic rates (Hanski, 1984). Some species, such as the common shrew, *Sorex araneus*, eat large quantities of earthworms (Lumbricidae; e.g., Pernetta, 1976), which in turn accumulate high concentrations of heavy metals (Ireland, 1983; Morgan and Morgan, 1988; Ma, 1989).

The aim of this study was to evaluate the usefulness of shrews in studying heavy metal pollution. We compare shrews and rodents living in the same polluted area and then focus on different species of shrews to find the most effective indicator. We also examine differences between sexes and age groups of shrews in this respect. Heavy metal accumulation in shrews evidently depends on the amount of metals in both soil and food resources, which again may be affected by physical factors, such as the distance from the point source of pollution and soil pH. We present some data for these relationships here.

Negative detrimental effects attributed to high heavy metal concentrations in the tissues of small mammals have been reported, including shrews. These include histopathological changes of the kidneys due to Cd and Pb, and increased relative organ weights and decreased body size (Goyer et al., 1970; Nicholson et al., 1983; Andrews et al., 1984; Ma, 1989). However, the polluted environment may stress an animal population, even if acute poisoning effects are not observed. The level of this stress can be assessed by analyzing the developmental stability of the population (Yablokov, 1986; Zakharov, 1989). In stressing environments, developmental stability of the population is reduced, which results in an increased level of fluctuating asymmetry in morphological traits (Leary and Allendorf, 1989), increased number of phenodeviants (exceptional forms of some meristic character; Zakharov, 1989), and in some cases in increased amounts of total phenotypic variability (Soulé, 1982; Zakharov, 1984; Pankakoski et al., 1987). Reduced developmental stability due to toxic compounds in the environment has been shown in fish and seal populations (Valentine and Soulé, 1973; Valentine et al., 1973; Jagoe and Haines, 1985; Zakharov, 1989; Zakharov et al., 1989). In our earlier study (Pankakoski et al., 1992) we demonstrate that heavy metal pollution may also affect the developmental stability of shrew populations. We summarize the results of that earlier paper here, along with some new analyses. When assessing developmental stability in shrew populations our hypothesis is that the progeny of female shrews exposed to heavy metals has a decreased level of developmental stability. The change in level of developmental stability implies the biological meaning of pollution for that shrew population.

METHODS

We analyzed concentrations of several heavy metals (Cu, Ni, Zn, Cd, Cr, Hg, and Pb) in the livers and kidneys of small mammals trapped near sources of pollution and in control sites in southern Finland. We present here results of the five most common species in southern Finland. Three of these are insectivorous species, namely the common shrew *S. araneus*, pygmy shrew *S. minutus*, and water shrew *Neomys fodiens*; the two others are herbivorous rodents, viz., the field vole *Microtus*

agrestis, and red-backed vole *Clethrionomys glareolus*.

Field Studies and Descriptions of Study Sites

The trapping was conducted (August 1987 and 1988) on polluted sites near the metal works and on control sites. The control sites have the average background level of heavy metals in south Finland; completely clean areas are not found anywhere in Finland (Rühling et al., 1987), but these were known to be much less contaminated than the polluted sites.

The three main study areas were as follows:

1) *Tikkurila.*—A lead smeltery in the city of Vantaa (60°16'N, 25°03'E) and its control area in northern part of the city of Espoo, ca 20 km west of Tikkurila. From the late 1920s until the early 1980s the lead smeltery in Tikkurila heavily polluted the soil (Erviö and Lakanen, 1973); high levels of lead have been recorded in mushrooms there (Liukkonen-Lilja et al., 1983). In Tikkurila the traps were set on verges between a grain field and a mixed forest of *Populus tremula*, *Betula* spp., *Salix* spp., *Picea abies*, and *Pinus silvestris*. The dense ground vegetation layer was comprised of several species of grasses and herbs. The control area in Espoo was a forested area, where soil analyses and accumulation of metals in moss bags (for the latter method, see Mäkinen, 1977) has shown low levels of heavy metals (Marttinen and Edgren, 1984; Kinnunen et al., 1985). In Espoo the moist mixed forest was dominated by *Picea abies*, *Betula* spp., and *Populus tremula*; the undergrowth was mostly *Vaccinium myrtillus*, mosses, and different species of grasses.

2) *Harjavalta.*—An industrial town in southwestern Finland (61°19'N, 22°07'E) and control sites at 10 and 20 km distances in rural areas, in Panelia and Eurajoki communes. According to earlier studies, the Harjavalta works (copper, sulfuric acid, and fertilizer factories) spread several heavy metals (especially Cd, Cu, and Ni) over a wide area (Hynninen, 1986). By using the moss bag method, Hynninen (1986) showed significantly elevated concentrations of several heavy metals as far as 9 km from the works. The rate of accumulation is very high around the works, but it rapidly decreases with increasing distance (Hynninen, 1986; Hynninen and Lodenius, 1986). Small mammals were trapped at a distance of 1–2 km from the factories, as closer to the works the undergrowth was too sparse due to pollution to give vegetative cover for mammals. Trapping was performed on several restricted areas, including shrubby sites (*Betula* and *Salix* spp.) along the edges of fields and along a small creek, abandoned old fields, and moist mixed forest (dominated by *Betula* spp., *Pinus silvestris* and *Picea abies*) with several species of herbs and grasses in the ground vegetation layer. The two control sites were situated against the prevailing winds that transport the metals (Hynninen, 1986; Hynninen and Lodenius, 1986) southwest of Harjavalta in mixed forests dominated by *Picea abies*, *Betula*, and *Salix*. In the undergrowth *Vaccinium myrtillus* and *V. vitis-idaea* dominated, along with grasses and herbs.

3) *Koverhar.*—An iron and steel works in Hanko, in southern Finland (59°53'N, 23°13'E) and its control area 4 km away in Tvärminne. Iron and lead concentrations in lichens are clearly increased at the distance of 2 km and slightly increased still at 5 km from the works (Helminen et al., 1986). Soil is much more alkaline in Koverhar than is common in Finnish forests due to the addition of lime in the iron smelting process (Fritze, 1991). The trapping habitats were similar both in Koverhar and its control area: moist mixed forest situated at the seashore and dominated by *Alnus glutinosa*, *Betula* spp., and *Pinus silvestris*. The soil was wet and the undergrowth was comprised of several species of moist habitat grasses and herbs, such as *Filipendula ulmaria*, *Phragmites australis*, and *Equisetum palustris*. Ten soil samples each from Koverhar and its control area were analyzed for heavy metals and pH.

Small mammals were trapped with metal or plastic pitfall traps which were partly filled with water to kill the animal (Pankakoski, 1979). Snap traps baited with bread or cheese also were used in Tikkurila and its control area in Espoo. The small mammals caught were put in plastic bags and deep-frozen.

Soil acidity (pH) was measured in samples (usually ten samples/area) from the lower part of humus layer (above the leaching layer). The pH was measured at +23°C in a mixture of 15 ml soil and 25 ml distilled water using a Knick Co. analyzer.

In Tikkurila 16 sample plots (area 50 × 25 cm, 30 cm deep) were dug up and hand sorted for earthworms in the field. The numbers of species and individuals were counted later. Soil samples were taken at 3 cm depth in each plot and analyzed for lead. Eight sample plots were similarly studied in Pornainen (60°28'N, 25°20'E) 25 km northeast from Tikkurila in a habitat similar to that in Tikkurila.

Laboratory Studies

The small mammals were weighed and sexed, and the livers and kidneys were removed for analysis of heavy metals. These organs usually accumulate more heavy metals than other soft tissues. The age grouping of shrews was determined by the general size of the individual, the color and condition of the coat, especially the coat of the hind feet and tail (Crowcroft, 1957), and by the level of tooth wear (Pankakoski, 1989). Juvenile shrews were defined as individuals trapped in their year of birth; adults were born in the previous summer (Crowcroft, 1957; Pankakoski, 1989). Juveniles were almost always immature, all adults were mature.

Heavy metals in small mammals were analyzed using a SpectraMetrics SpectraSpan IIIB plasmaemission spectrophotometer (Cd, Cr, Ni, Pb), atomic absorption spectrophotometer (AAS; Cu, Zn), or gold film mercury analyzer (Hg; Jerome Instrument Corporation, Model 511). Tissues were dried overnight at +105°C, weighed, and digested in 10 ml of a 1:4 mixture of $HClO_4$ and HNO_3 under a reflux cap. In order to obtain sufficient quantities of *S. minutus* kidney for analyses, it was necessary to pool organs from 3–4 individuals of the same age and sex. Heavy metals in soil samples and earthworms were analyzed using atomic absorption spectrophotometer. Heavy metal concentrations (mg/kg) are expressed on a dry weight basis.

Earthworms sampled in Tikkurila and Pornainen were kept alive on moist absorbent paper in a refrigerator for some days to make them empty their guts. Samples comprising 1–19

individuals of *Aporrectodea caliginosa*, the commonest lumbricid there, were deep-frozen in small plastic tubes and later analyzed for lead (AAS).

Statistical comparisons of heavy metal concentrations were based on median values and nonparametric tests (Mann-Whitney U-test, Kruskal-Wallis test, and Spearman rank correlation coefficient), because the data mostly were not normally distributed. There were usually some individuals with very high concentrations, the fact that violates the assumptions of parametric tests and artificially raises the arithmetic mean.

Developmental stability of *S. araneus* was assessed by using the numbers of small paired foramina in the skull and from mandible measurements (for the method, see Pankakoski and Hanski, 1989). The foramina were counted as a blind test without knowing the trapping place of the animal. The metrical measurements of both mandibles were taken by using a video camera connected to a digitizer and a microcomputer (Pankakoski and Hanski, 1989). In developmental stability analyses we used Friedman's nonparametric test to compare variances of several traits. Numbers of asymmetric traits or phenodeviants were compared with one-way analysis of variance. For the details of analyzing developmental stability, see Pankakoski et al., (1992).

Results

Inter- and Intraspecific Comparisons

Differences in heavy metal concentrations between shrews and voles in Tikkurila and its control area in northern Espoo are presented in Table 1. In both areas the concentrations of Cd, Pb, and Hg were higher in *S. araneus* and *N. fodiens* than in *C. glareolus* and *M. agrestis*. Copper concentrations seemed to be higher in *S. araneus* than in the other species, but this difference was usually not significant. *Neomys fodiens* may accumulate high amounts of Hg, as observed in the small sample from the control area in Espoo; the median of Hg concentrations in liver was 4.47 mg/kg (Table 1).

Excepting Ni, heavy metal concentrations in liver did not differ significantly between *S. araneus* and *S. minutus* (Harjavalta sample, juveniles; Table 2). Concentrations of all metals but Zn, however, were significantly higher in the kidneys of *S. araneus*.

Sorex araneus adults tended to have higher concentrations of heavy metals than juveniles (Table 3). The difference was greatest in Cd (both liver and kidney), but significant also in Zn, Cu, and Hg (liver). Chromium and Pb did not exhibit higher concentrations in adults, but Pb in kidneys was significantly higher in juveniles. No differences were observed in heavy metal accumulation between the sexes of shrews.

The Effect of Distance from the Pollution Source

In *S. araneus* trapped less than 1 km from the lead smeltery in Tikkurila the concentration of Pb in the liver decreased as the distance from the pollution source increased (Fig. 1). The Pb in both soil and earthworms (*Aporrectodea caliginosa*) also decreased according to increasing distance in the same area (Fig. 2A). The total number of earthworms, however, increased by increasing distance from the lead smeltery in Tikkurila (Fig. 2B). Some sample plots close to the smeltery were devoid of earthworms. The median for Pb concentrations in 16 soil samples from Tikkurila was ten times higher than the corresponding median for the eight samples taken in similar habitat at a rural site (Table 4). Lead concentrations were almost 20 times higher in *A. caliginosa* from Tikkurila than in control samples (Table 4). Because earthworms are an important food resource for the common shrew, our results imply one pathway of Pb, from soil through earthworms to shrews.

On a larger scale, the effect of emissions from the metal industry in Harjavalta was demonstrated in tissues of *S. araneus* sampled at 10 and 20 km from Harjavalta. However, the decreasing trend was evident; hence, the lowest concentrations usually were from the control site at 20 km from the factories (Fig. 3).

Heavy Metal Bioaccumulation and Soil pH

Bioavailability of several heavy metals is higher in acidified soils than in soils with high pH (e.g., Andersson and Nilson, 1974; Roberts et al., 1978; Beyer et al., 1987; Scheuhammer, 1991). In Tikkurila, its control area in Espoo, and in the Harjavalta area soil pH ranged from 4.2 to 5.4 (Table 5), which is not beyond normal variation in Finnish soils. The range is due mainly to differences in soil types: forest soils are more acidic than old field and arable soils. On the other hand, as seen in Table 5, the mean ($\pm$SD) soil pH values had much greater range in Koverhar and its control area (7.60 ± 0.28 and 4.59 ± 0.29, respectively; $P < 0.001$, t-test). Due to addition of lime during the smelting process at the Koverhar steel factory, much calcium is distributed to the surroundings and, consequently, the soil pH was highly significantly elevated near the works (see also Fritze, 1991).

If soil pH affects heavy metal concentrations, the lower pH values at the control sites than at the polluted sites of Tikkurila and Harjavalta should increase heavy metal concentrations of shrews there. However, the concentrations show the opposite trend, at least in Harjavalta, i.e., lower values were from control sites (Fig. 3). There was much more Pb in shrews in Tikkurila than in the control area in Espoo, but the Cd and Zn concentrations were higher in Espoo (Table 6). The strong influence of the heavy metal pollution source may overcome the impact of pH in these study sites.

Top soil layers near the Koverhar metal works contained higher concentrations of heavy metals than the soil in the control area (significant for Pb and Zn, ten samples on both sites; Cd concentrations were below the detection level in both sites; Fig. 4). However, shrews on the *control* site had a significantly *greater* burden of Pb in liver and kidneys, and of Zn, Cu, and Ni in the kidneys (Fig. 4; for the corresponding medians, see Table 7). The accumulations of Cr in all tissues and of Cd and Zn in the livers of *S. araneus* from Koverhar were greater than in the control area (Fig. 4; for Cd, see Table 7). The fact that Pb, especially, had higher concentrations in the control area is perhaps related to the differences in the soil pH of the two sites.

Heavy Metals and Developmental Stability of Shrew Populations

The biological effect of heavy metal pollution was assessed by comparing developmental stability in morphological skull characters of *S. araneus* in polluted and control areas. The stress of heavy metal pollution should decrease the level of developmental stability in shrew populations (see Pankakoski et al., 1992). Figure 5 summarizes the data from the three main study areas, Tikkurila (A), Harjavalta (B), Koverhar (C), and their control areas. Comparisons of heavy metal concentrations among these sites are presented in Tables 6 and 7 and Fig. 3 and 4.

Developmental stability was usually reduced in areas where shrews have high heavy metal concentrations in their tissues (Fig. 5). This was indicated by the tendency towards higher levels of fluctuating asymmetry and total phenotypic variability, as well as the higher numbers of asymmetric traits and phenodeviants in the polluted areas (Tikkurila and Harjavalta, Fig. 5A, B). In the Harjavalta area there was a parallel trend in most characteristics; the columns in Fig. 5B are highest in Harjavalta (indicating high level of disturbances during development, i.e., *low* developmental stability) and they decrease with increasing distance, as was the case also in heavy metal concentrations. In Koverhar (Fig. 5C), the result of developmental stability in "polluted" and control areas is controversial (reduced developmental stability at the control site), as were also the concentrations of most heavy metals in the shrews (more heavy metals at the control site; see Fig. 4). When there was a significant difference between Koverhar and its control area, developmental stability was lower in the control area (high columns in Fig. 5C: FA of foramina and PV of mandibular measurements).

Discussion

Searching for an Indicator Species

A good indicator species for heavy metal pollution accumulates high concentrations of different metals in its tissues. Such a species is also useful in slightly polluted areas. The indicator species should also occupy a wide range of habitats and be abundant enough to provide adequate sample sizes.

Shrews Versus Rodents.—In our study, shrews had clearly higher concentrations of the most toxic heavy metals (Cd, Pb, and Hg) than the rodents in the same area. This agrees with the studies by Goldsmith and Scanlon (1977), Hunter and Johnson (1982), Andrews et al. (1984, 1989), Beyer et al. (1985), and Hunter et al. (1987). Shrews and voles have similar Zn concentrations. In mammalian tissues, Zn is usually effectively controlled by regulatory systems, which may be violated by high levels of Cd (Bremner, 1974; Czarnowska and Gworek, 1980; Włostowski, 1987).

At least when Cd, Pb, or Hg are considered, shrews are better indicators than the rodents. The higher concentrations are doubtless due to the higher amount of these metals in the largely animal foods eaten by shrews (Hunter et al., 1989). The Pb concentration in soil, earthworms, and shrews in Tikkurila demonstrate the probable pathway of Pb into the shrew. Earthworms are regarded as the main heavy metal source for shrews (Ma, 1989; Ma et al., 1991).

Different Species of Shrews.—Dissimilar heavy metal concentrations in *S. araneus* and *S. minutus* perhaps reflect differences in the diets between the two species. Earthworms accumulating high concentrations of heavy metals are more important food items for *S. araneus* than for *S. minutus* (Pernetta, 1976; Butterfield et al., 1981; Bauerová, 1984). Furthermore, the kidneys of one *S. minutus* specimen usually were too small for an adequate analysis of heavy metals, making the pooling of samples of the same age group necessary. This increased the number of individuals needed in the study. Because most heavy metal concentrations were lower in the kidneys of *S. minutus* than in *S. araneus*, the latter species is a more appropriate indicator of heavy metal pollution.

Neomys fodiens may be an effective indicator of Hg, as indicated by high concentrations in the Espoo sample (Table 1). A similar result was obtained by Bergbom (1987) in south Finland. However, *N. fodiens* is a habitat specialist and is usually too rare for adequate sample size. We conclude that *S. araneus* is a better bioindicator for heavy metal pollution of terrestrial ecosystems than other species of small mammals in south Finland. It is also abundant in areas with intensive human impact.

Accumulation of Heavy Metals in S. araneus.—The dependence of heavy metal accumulation on age in *S. araneus* accords well with earlier studies. Accumulation in several species of small mammals is most evident for Cd (McKinnon et al., 1976; Johnson et al., 1978; Way and Schroeder, 1982; Włostowski, 1987; Hunter et al., 1989). The increased level of Zn in older individuals may be connected with increased Cd in them (see above). In our study Pb concentrations did not increase according to the age of the individual, as is also the case in studies by McKinnon et al. (1976), Anderson et al. (1981), and Cloutier et al. (1986). Contradictory results have been presented by Way and Schroeder (1982) and Scanlon et al. (1983). Because concentrations of most heavy metals in adult shrews were at least as high as in juveniles, they may be more appropriate indicators for low heavy metal concentrations in the environment than juveniles. On the other hand, juvenile shrews have smaller home ranges and usually reach higher densities than adults (Croin Michielsen, 1966), both characteristics being useful for an indicator animal of heavy metal pollution. For comparisons of heavy metal concentrations on several sites, the age groups must be treated separately.

Shrews are short-lived animals with high potential of reproduction. Their relatively small home ranges (compared to those of larger mammals or birds) exposes them to local environmental conditions. In the present study, shrews indicated changes in heavy metal concentrations occurring at relatively short distances, as was found in the Tikkurila Pb area (Fig. 1). In earlier studies a similar decrease has been observed in Pb concentrations of soil and mushrooms there (Erviö and Lakanen, 1973; Liukkonen-Lilja et al., 1983). It is noteworthy that the decrease in Pb accumulation with increasing distance was demonstrated also in shrews, more mobile animals than earthworms.

Heavy Metal Accumulation and Soil pH

Several heavy metals move into organisms more readily from acidified soils than from soils with higher pH, as shown in plants (Andersson and Nilson, 1974; Nuorteva et al., 1986), in earthworms (Ma, 1982; Ma et al., 1983; Beyer et al., 1987; Morgan and Morgan, 1988) and in small mammals (Roberts et al., 1978; Ma, 1989). This effect is especially evident in Pb, where concentrations are higher in organisms living in places with low soil pH and/or low concentration of Ca ions (Johnson et al., 1978; Roberts et al., 1978; Andersen, 1979; Beyer et al, 1987; Scheuhammer, 1991).

In Koverhar both high pH and high amount of Ca-ions in the soil may be responsible for the low rate of accumulation of several heavy metals in *S. araneus*, although these metals show high concentrations in the soil there. In the control area at the distance of 4 km, where the soil pH is "normal" (i.e., much lower) and the soil is less polluted, heavy metal accumulation (especially Pb) in shrews was more intensive. In the other study areas (Tikkurila, Espoo, and Harjavalta area), where the differences in soil pH between the polluted and control sites were smaller, the effect of pH on heavy metal accumulation could not be demonstrated.

Developmental Stability

In the present study developmental stability was reduced in those shrew populations which showed highest heavy metal concentrations. This suggests that their toxic effects may stress the shrew populations. It is possible that Pb (high concentrations both in Tikkurila and Koverhar) is especially important in this respect. Other differences in habitat quality may also affect developmental stability. The high level of developmental stability in the shrews from control area of Espoo perhaps partly indicates the benefits of a forest habitat for *S. araneus*. However, the final cause-and-effect relationship between heavy metals and developmental stability cannot be proved by field studies alone.

Although the concentrations of heavy metals in natural small mammal populations are relatively easy to analyze, it is difficult to indicate changes in viability or breeding success caused by their toxic effects. If the concentrations are too low to increase mortality or to cause histopathological tissue alterations, their negative effects cannot be demonstrated by traditional methods. By analyzing developmental stability it seems possible to assess the *biological effect* of toxic compounds on small mammal populations also in moderately polluted areas (Pankakoski et al., 1992).

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Table 1.—*Comparison of heavy metal concentrations (mg/kg) in the livers of four small mammal species from Tikkurila (lead smeltery area) and Espoo (control area) populations. All age groups are combined, and median and maximum (highest concentration in the sample; in parentheses) values are given. In Tikkurila, the animals were trapped within a radius of 500 m from the lead smeltery.* n, *number of individuals. Statistical significance in all tables and figures is indicated by the following symbols: o,* $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. *The first column of asterisks (a) after the concentrations of* Neomys fodiens, Clethrionomys glareolus, *and* Microtus agrestis *indicates significant difference from those of* Sorex araneus; *the second column of asterisks (b) indicates significant difference of* C. glareolus *and* M. agrestis *from those of* N. fodiens *(Mann-Whitney U-tests). Because the age structure in samples of* S. araneus *differed between Tikkurila and Espoo, see Table 6 for comparison of concentrations between these localities.*

	S. araneus	*N. fodiens*		*C. glareolus*			*M. agrestis*		
Tikkurila			(a)		(a)	(b)		(a)	(b)
Cd	2.90 (29.20)	0.74 (13.42)	**	0.29 (1.71)	**		0.09 (0.69)	***	*
Pb	15.95 (233.4)	12.80 (45.62)		3.64 (9.43)	***	**	1.69 (6.78)	***	***
Zn	86.44 (130.1)	86.42 (131.3)		95.71 (107.0)	o		89.86 (100.0)		
Cu	23.41 (45.79)	16.02 (37.20)	**	19.54 (39.53)	o		18.58 (32.67)		
Hg	0.10 (0.29)	0.13 (0.20)		0.03 (0.07)	*	***	0.00 (0.09)	**	***
n	24	13		8			11		
Espoo									
Cd	6.77 (18.00)	6.26 (6.97)		0.00 (0.87)	***		0.00 (0.00)		
Pb	4.15 (7.55)	2.67 (3.03)		0.00 (2.73)	***		0.00 (1.22)		
Zn	102.21 (130.1)	78.90 (85.22)		109.33 (132.9)			105.28 (116.3)		
Cu	24.13 (30.30)	10.89 (11.30)		17.64 (28.51)	***		13.67 (18.63)		
Hg	0.13 (0.29)	4.47 (5.94)		0.02 (0.07)	***		0.06 (0.07)		
n	28	3		22			3		

Table 2.—*Heavy metal concentrations (mg/kg) in two shrew species,* S. araneus *and* S. minutus, *given as median and (maximum) values. Only juveniles trapped near the works in Harjavalta were included. If the difference between the species was significant (Mann-Whitney U-tests,* P, *asterisks) the greater value is in italics. Sample sizes:* S. araneus n = *24 (except in zinc, in which liver* n = *50, kidney* n = *33);* S. minutus *liver* n = *25, kidney* n = *8 (pooled samples).*

Heavy Metal	*S. araneus*		*S. minutus*		*P*
Liver					
Cd	5.55	(23.04)	5.51	(10.43)	
Cr	0.00	(4.79)	0.00	(13.40)	
Pb	1.41	(5.14)	0.00	(17.61)	o
Zn	76.94	(310.1)	82.98	(176.5)	
Cu	20.76	(30.27)	21.43	(44.44)	
Ni	0.26	(7.24)	*3.39*	(68.08)	***
Kidneys					
Cd	*7.49*	(24.83)	0.00	(2.86)	***
Cr	*10.00*	(31.30)	0.99	(2.37)	***
Pb	*13.76*	(26.67)	9.74	(13.42)	*
Zn	71.43	(329.9)	54.63	(64.29)	o
Cu	*38.11*	(67.74)	19.43	(25.71)	***
Ni	*1.30*	(23.00)	0.00	(0.71)	**

Table 3.—*Heavy metal concentrations in the two age groups of* S. araneus *from Harjavalta (medians, mg/kg). If the difference between the species was significant (Mann-Whitney U-tests,* P, *asterisks), the greater value is in italics.*

Heavy Metal	Juveniles	Adults	*P*
Liver			
Cd	5.55	*29.09*	***
Cr	0.00	0.23	
Pb	1.41	1.79	
Zn	71.25	*78.81*	***
Cu	20.76	*31.81*	***
Ni	0.26	0.64	
Hg	0.06	*0.20*	***
Kidneys			
Cd	7.49	*46.66*	***
Cr	10.00	8.53	
Pb	*13.76*	7.53	**
Zn	67.86	90.59	o
Cu	38.11	40.84	
Ni	1.30	2.92	
n	24	18	

Table 4.—*Lead concentrations (mg/kg) in soil and in the earthworm* Aporrectodea caliginosa *in Tikkurila (lead smeltery area) and Pornainen (control area). Median values and ranges (in parentheses) of 16 plots in Tikkurila (in* A. caliginosa *only ten plots, as earthworms were absent in the six plots closest to the smeltery) and eight plots in Pornainen are presented.* P = *significance in Mann-Whitney tests.*

	Tikkurila		Pornainen		*P*
Soil	1781	(411–79960)	18.2	(13–542)	***
A. caliginosa	925.5	(554–2200)	50.0	(0–139)	***

Table 5.—*Soil pH (mean, standard deviation, and sample size) at the study areas. The pH of the trapping points that yielded the greatest catches of shrews is presented in Espoo and Harjavalta (the latter consists of three points, ten analyses in each).*

Locality	Distance from the Source of Pollution (km)	Mean pH	±SD	*n*
Tikkurila	<0.1	5.29	±0.107	10
Control in Espoo	20	4.21	±0.586	10
Harjavalta	1–2	5.36	±0.360	30
Control 10	10	4.72	±0.418	10
Control 20	20	4.18	±0.172	10
Koverhar	0.5	7.60	±0.284	10
Koverhar	1.5	5.54	±0.777	10
Control	4	4.59	±0.293	10

Table 6.—*Heavy metal concentrations (mg/kg) in the liver of juvenile* S. araneus *around a lead smeltery (Tikkurila) and a rural control area (Espoo), given as median and (maximum) values. The greater concentration is in italics, if the difference was statistically significant (Mann-Whitney U-tests,* P, *asterisks).*

Metal	Tikkurila		Espoo		*P*
Cd	2.64	(7.1)	*4.97*	(18.0)	*
Pb	*15.55*	(233.4)	4.66	(7.6)	***
Zn	85.08	(128.7)	*102.57*	(130.1)	***
Cu	23.15	(36.8)	23.50	(30.3)	
Hg	0.10	(0.3)	0.10	(0.3)	
n	22		18		

Table 7.—*Heavy metal concentrations (mg/kg) in the liver and kidneys of juvenile* S. araneus *in Koverhar and its control area at a distance of 4 km, given as median and (maximum) values. If the difference is significant (Mann-Whitney U-tests,* P, *asterisks), the greater value is in italics.*

Heavy Metal	Koverhar		Control		*P*
Liver					
Cd	1.47	(4.23)	1.10	(3.02)	
Cr	*0.00*	(1.80)	0.00	(0.55)	*
Pb	1.57	(4.68)	*3.92*	(5.25)	***
Zn	*89.82*	(97.45)	79.89	(131.3)	*
Cu	19.01	(23.74)	20.27	(32.93)	o
Ni	0.00	(0.00)	0.00	(0.00)	
Kidneys					
Cd	*2.07*	(6.18)	0.00	(7.50)	**
Cr	*1.82*	(8.57)	0.00	(4.29)	*
Pb	0.00	(8.82)	*9.31*	(30.00)	***
Zn	109.1	(134.5)	*144.0*	(225.0)	***
Cu	38.71	(57.69)	*50.09*	(120.0)	***
Ni	0.00	(4.29)	*0.00*	(37.50)	*
n	21		16		

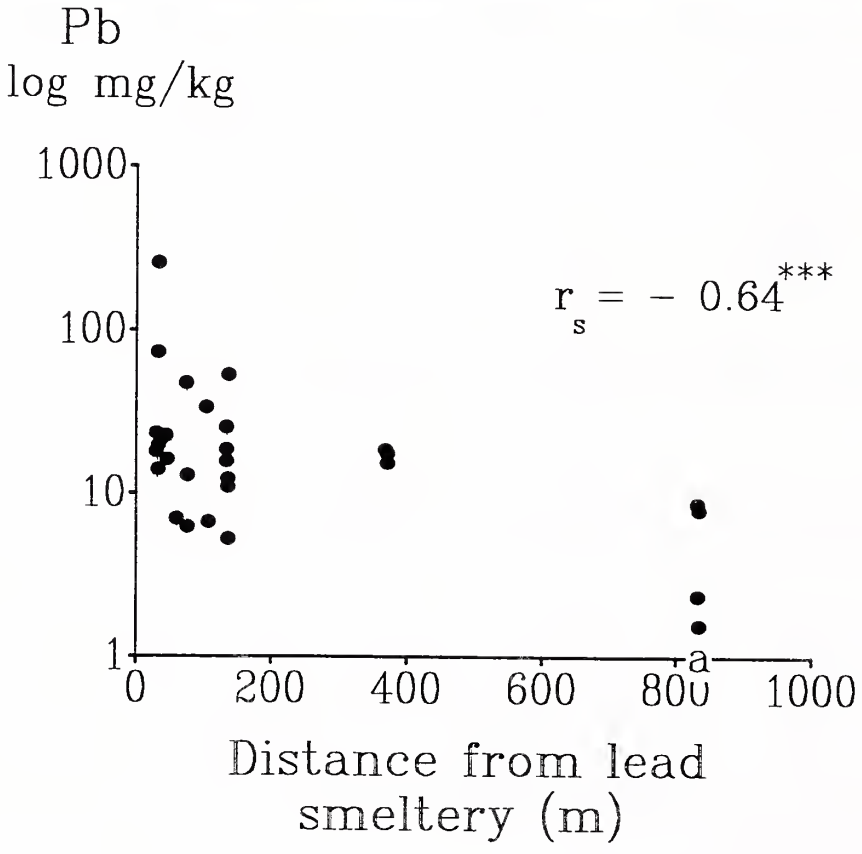

Fig. 1.—The dependence of lead concentration in the liver of *S. araneus* on the trapping distance from the lead smeltery in Tikkurila. a, four individuals with concentration under the determining level (ca 0.05 mg/kg Pb); r_s, Spearman rank correlation coefficient. Notice that the vertical axis is in log scale.

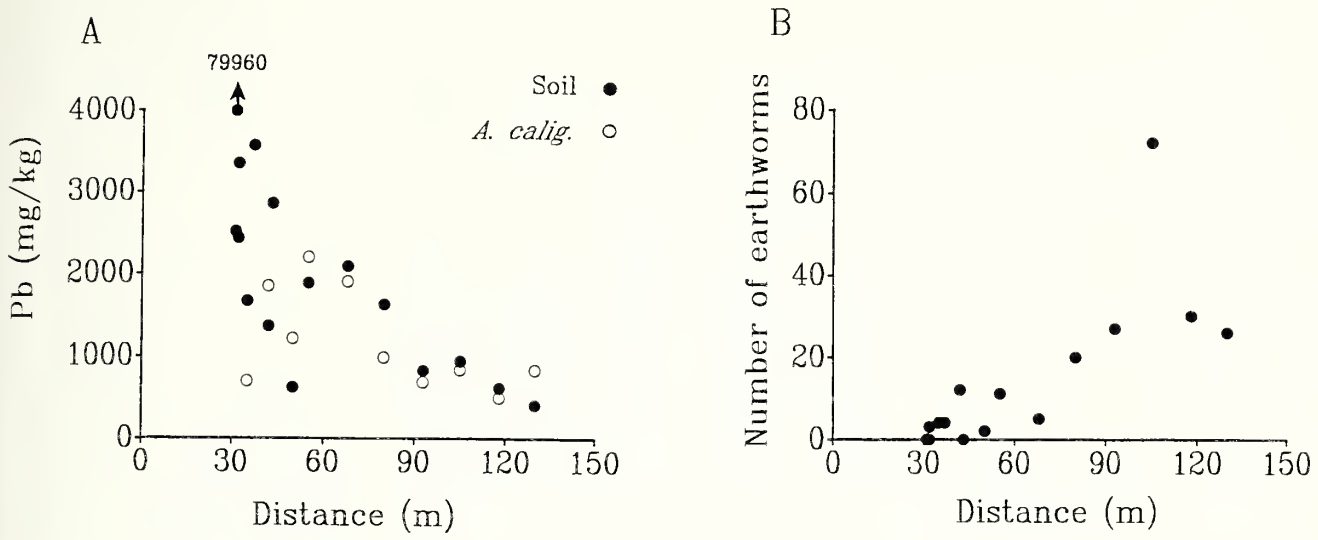

Fig. 2.—The effect of distance from the smeltery on soil and earthworm (*Aporrectodea caliginosa*) lead concentrations (A) and on the total number of earthworms (all species; B). Tikkurila, May–June 1990: from 16 plots measuring 25 × 50 cm. The lead concentrations of earthworms represent median values of 1–9 samples analyzed in each plot. Each sample comprised of 1–19 individuals of *A. caliginosa*. This species was present only in ten plots at the greatest distance from the smeltery (A). Spearman rank correlation coefficients with distance: soil Pb $r_s = -0.80^{**}$ (16 plots), *A. caliginosa* Pb $r_s = -0.47$ (ten plots), total number of earthworms $r_s = +0.86^{***}$ (16 plots). In *A. caliginosa* the Pb concentration value (705 mg/kg) at the nearest distance (35 m) was based on only one small juvenile individual; excluding this individual the Spearman rank correlation coefficient with distance is $r_s = -0.78^{*}$ (nine plots).

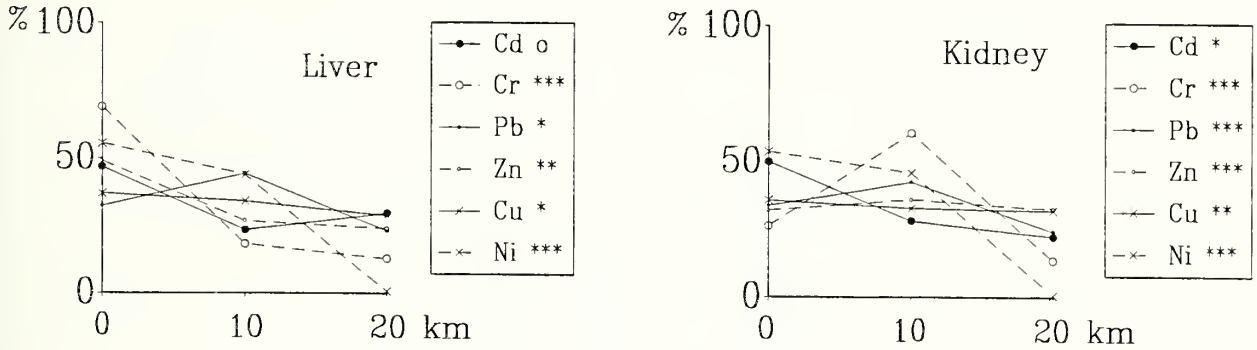

Fig. 3.—Relative concentrations of heavy metals in tissues of *S. araneus* (only juveniles) at three distances from Harjavalta metal works. To make different metals (with different scales) comparable, the concentrations are presented in percentages; 100% is the sum of concentrations (median values) in the three sites: at the Harjavalta works (0 km), control area at 10 km, and control area at 20 km. If the concentrations are equal in each trapping area, the relative value is 33.3% in each. The asterisks indicate significant differences among the three areas (Kruskal-Wallis tests). Number of individuals: Harjavalta works, $n = 24$; control 10 km, $n = 19$; control 20 km, $n = 20$.

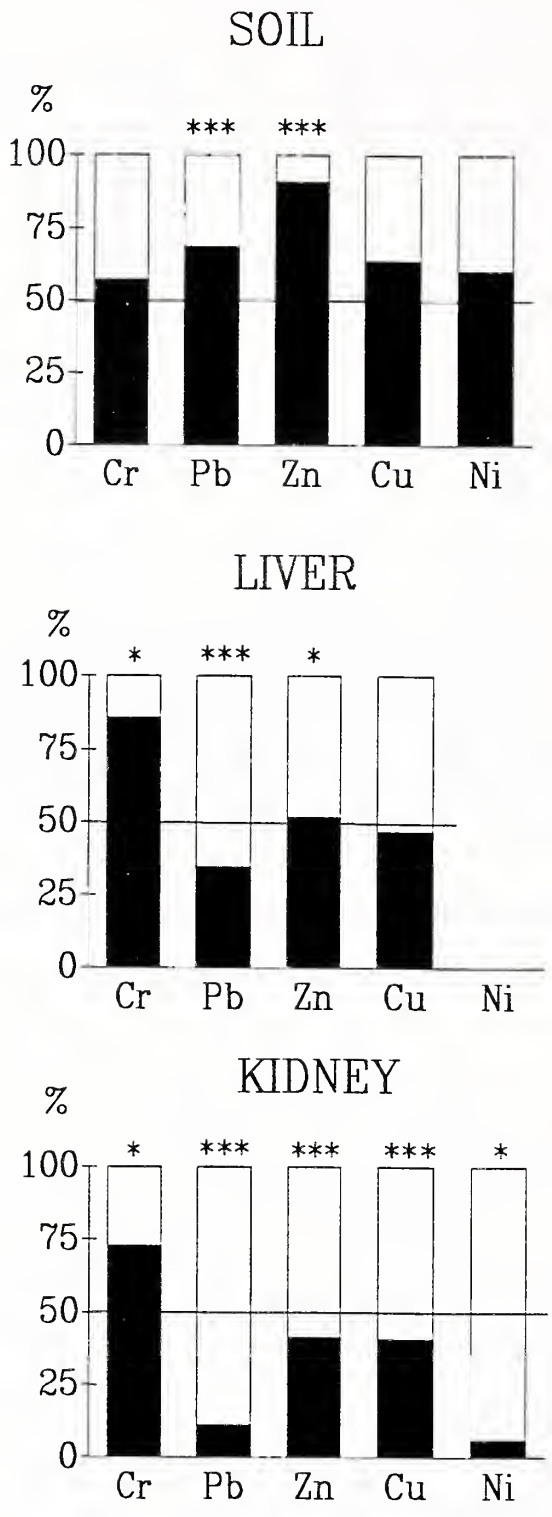

Fig. 4.—Comparison of relative concentrations of heavy metals in soil and tissues of *S. araneus* (only juveniles) between Koverhar works (n = 21) and its control area (n = 16). To make different metals (with different scales) comparable, the concentrations are presented in percentages; 100% is the sum of concentrations at Koverhar works and at its control area. If the concentrations are equal on both sites, the black (Koverhar) and white (control) areas of the bar are equally high (50%). The asterisks indicate significant differences between the two areas (Mann-Whitney tests). The relative values are based on mean values of the concentrations, as several of the median values (shown in Table 7) were 0.

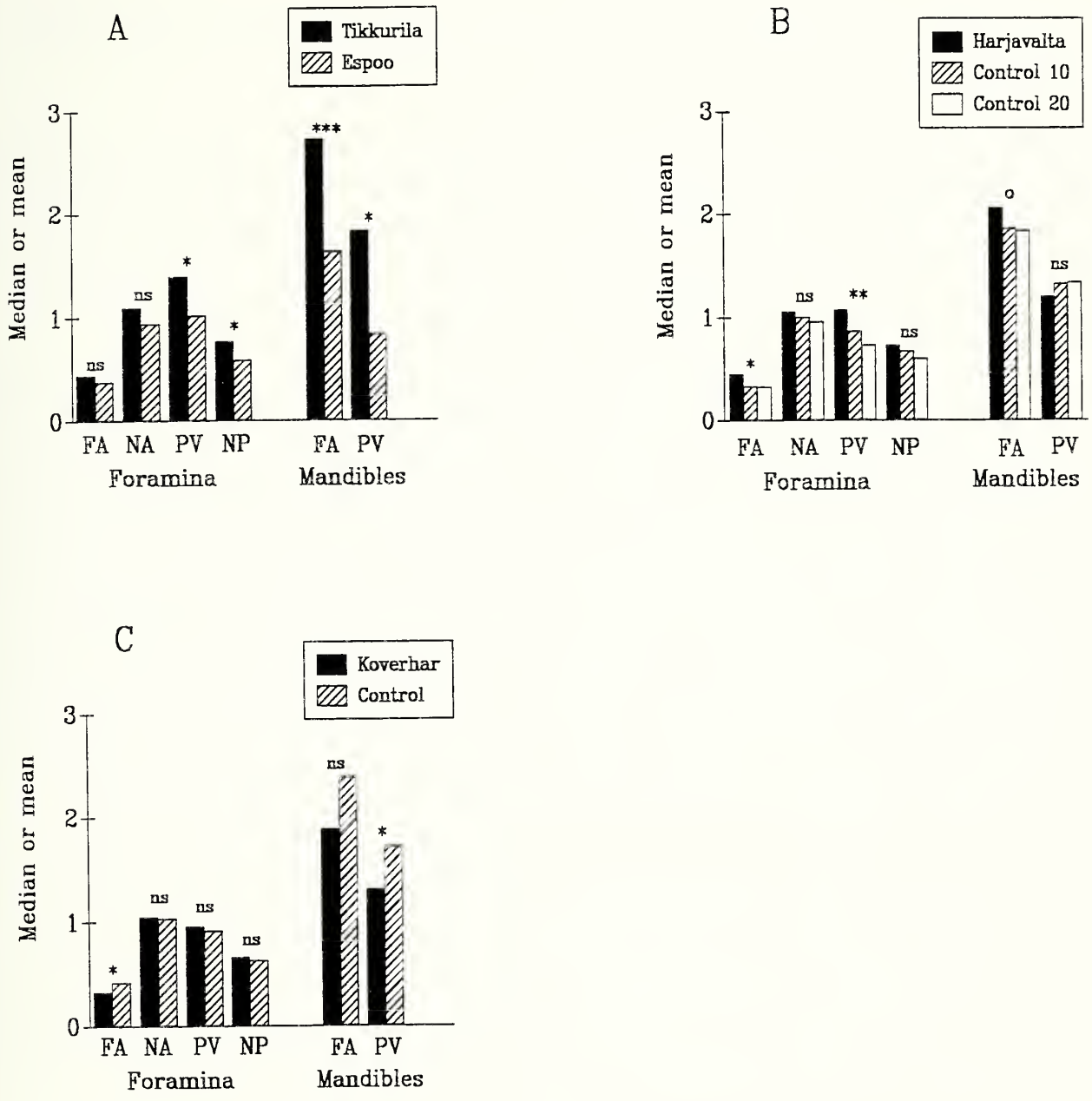

Fig. 5.—Comparison of developmental stability in the morphometrical traits of *Sorex araneus* between the polluted and control areas. High columns indicate low developmental stability. A, Tikkurila lead area and control in Espoo; B, Harjavalta and two control areas at 10 and 20 km distances; C, Koverhar and control. Developmental stability was measured by fluctuating asymmetry (FA), number of asymmetric traits per individual (NA), number of phenodeviants per individual (NP) and by total phenotype variability (PV). For the details, see text. The values on the y axis are medians (FA, PV; mandibular PV median × 0.1) or means (NA, NP; mean × 0.1). The asterisks indicate significant differences between the areas (FA, PV: Friedman tests; NA, NP: t-tests or ANOVAs). Number of individuals: Tikkurila n = 22, Espoo n = 18; Harjavalta n = 50, control 10 km n = 19, control 20 km n = 20; Koverhar n = 46, control n = 53.

HISTOPATHOLOGY OF THE COMMON SHREW *SOREX ARANEUS* IN FINLAND

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Abstract

Twenty-eight common shrews (*Sorex araneus*) were captured in two areas in Finland during the winter and spring of 1989 and 1990 for histopathological analysis. The prevalence of histopathological changes were 59% in the liver, 46% in the intestines, 42% in the lungs, 21% in the heart, and 10% in the brain. Three shrews (11%) did not show any histopathological changes, but 57% of shrews had changes in more than one organ. The most common findings were inflammation of the biliary ducts of the liver, enteritis, mild inflammation in the lungs, and parasitic cysts in the kidneys. The prevalence of histopathological changes in these shrews was higher than in vole samples from the same localities. Because shrews have high metabolic rates and are dependent on continuous food intake, even short or mild diseases can be fatal or weaken their condition. Thus, diseases may contribute to the population fluctuations observed in shrews.

Introduction

Attempts have been made to explain the dynamics of shrew populations by reference to the weather (Formozov, 1948; Ivanter, 1975; Pankakoski, 1985), food availability (Kaikusalo and Hanski, 1985) and predation (Hansson, 1984; Henttonen, 1985; Korpimäki, 1986). In contrast, analyses by Henttonen et al. (1989) of the long-term dynamics of shrew populations in northern and central Finland did not give any conclusive results with regards to weather and predation. There are no previous reports on diseases in shrews, although some work has been conducted on the role of diseases in the regulation of sympatric vole populations. Elton et al. (1935) reported a protozoan infection of the brain to cause high mortality among field voles (*Microtus agrestis*), and Descôteaux and Mihok (1986) found that high prevalence of antibodies and high titers to some viruses were characteristic of meadow voles (*Microtus pennsylvanicus*) which were captured late in the population decline. We report here the first results concerning the histopathology of the common shrew, *Sorex araneus*. Although diseases are often studied by isolating the causative agent, many agents are difficult to isolate (e.g., viruses, protozoa, certain bacteria, and toxins) and special methods are needed for them. By contrast, pathological changes in tissues may be found easily, and thus systematic histopathological monitoring of the main organs in a sufficiently large sample may give valuable information of the disease status at the population level.

Materials and Methods

Twenty-eight common shrews were captured with live traps, most of them (22) at Luhanka, central Finland, in January–April 1989, and the rest (six) from Evo, southern Finland, in March 1990. The 23 animals (11 females and 12 males), which were trapped in January–March, were typical overwintering nonbreeding juvenile shrews whose mean weight was 5.5 g $\pm$ 0.5 ($x \pm$ SD). Five additional animals were trapped immediately after the snowmelt, in April 1990. Of these, two males (5.9 and 7.2 g) were in breeding condition and three females (5.2, 5.2, and 6.2 g) were maturing. The 28 shrews were trapped in old-field habitats; some were already dead when found in the traps and the rest were euthanized with ether immediately after capture. In both winters, local microtine populations were declining from a peak phase in the preceding summer. During the winter trapping, the shrews were rather common but after the snowmelt their populations also crashed.

The animals were dissected and tissue samples were taken from the lungs (two lobes from the right side), liver (near the edge of the largest lobe), the whole heart, right kidney, part of small intestines and brain (transversal section from the middle), and stored in buffered 10% formalin. One histological slide including all the organs mentioned above from each animal was stained with hematoxylin-eosin. Each slide was studied thoroughly with a light microscope. If leukocytes (mainly lymphocytes, eosinophils, or neutrophils) were increased in one or some of the visual fields of lungs, the increase was categorized as small; but if they were increased highly in some of the visual fields or evenly (although slightly) through the section, the increase was categorized as moderate.

Results

The histopathology of shrews is shown in Table 1. In addition, the unpublished data which represents a mean of several samples of field voles collected at the same time at Luhanka are presented as a comparison in Table 1. There were three shrews (11%) in which no histopathological changes were found. This may be an overestimation, however, as not every organ could be examined in all the animals. Histopathological changes were found in more than one organ in 57% of the 28 shrews.

Discussion

The results show numerous histopathological changes in common shrews, with about 90% of the shrews being affected. The changes were more common than in material obtained from the declining field vole population at the same time (Table 1), except in the lungs, where a small increase of leukocytes was more often found in voles. Another noticeable feature was that in 57% of shrews more than one organ was affected. The high prevalence of changes was striking, since the shrew samples consist mainly of overwintering, immature shrews, and adult shrews are expected to have even higher prevalence (compare

Haukisalmi et al., 1994).

The changes in the liver, which plays an essential metabolic role in mammals and also functions in the excretion of gall via the biliary ducts, were very common and clearly defined. Gall excretion may have been disturbed in the affected animals, and this could have hampered the absorption of lipids and thereby interfered with energy metabolism. One reason for the liver pathology could be coccidiosis; coccidian-like parasites were found in three individuals. Liver coccidiosis is a severe disease in rabbits (Soulsby, 1982), but its effects on shrews are unknown. Common shrews in Finland can also harbor a cestode, *Choanotaenia hepatica*, in their biliary ducts (Haukisalmi, 1989), and this could have been another reason for the changes, although this parasite was not found in any of the slides.

Inflammatory processes in the intestines (enteritis) were also quite common (46%). An animal suffering from enteritis is usually very sick, because a loss of electrolytes and water via the intestines quickly results in dehydration, which can be fatal. Absorption of nutrients is disturbed and chronic enteritis results in starvation. In shrews, which have high metabolic rates and need constant supplies of food (Hanski, 1984), even small reductions in absorption could be fatal. Intestinal helminths are abundant in common shrews in Finland (Haukisalmi, 1989), and these may contribute to the high prevalence of enteritis. Other common etiological agents for enteritis are bacteria, viruses, protozoa, and toxic substances (Jones and Hunt, 1983).

The increase of leukocytes in lungs indicates inflammatory process, usually infection. Lung infections, although common, were usually mild, but even these can be harmful to shrews, whose need for oxygen is great and respiratory rates are high (Nagel, 1994). They can at least contribute to energy losses through an acceleration in the respiratory rate and changes in behavior. Parasites, which were found in three individuals, may also be important agents in these changes. Mas-Coma (1977) commented that a lung nematode *Paracrenosoma skrjabini*, which parasitizes in *S. araneus*, is found in Russia and central Europe but no lung parasites are known in shrews from Finland. Bacteria and viruses are also common in respiratory infections (Jones and Hunt, 1983).

The parasitic cysts, evidently of protozoan origin, found in many kidney samples are probably not dangerous to their hosts, but interstitial nephritis, an inflammation of the kidney parenchyme, can alter many functions in the kidney and can therefore be harmful.

The heart of the common shrew requires a high energy supply since heart rate can be over 600/min (Nagel, 1985, 1994). Consequently any change in the structure of the heart is potentially dangerous. Even the slightest decrease in function can cause trouble, at least in terms of energy costs.

It is difficult to say if live-trapping under- or overestimates the proportion of diseased animals in the population. If an animal is really sick it will probably not move much and will die before entering a trap. In such cases, sampling with live-trapping certainly underestimates the role of diseases. But if the disease is mild, the animal may move more because of changes in behavior or to compensate for the energy losses. For these reasons, one should be cautious when interpreting prevalence values at the population level.

Conclusions

Although it is premature to interpret the real significance of histopathological findings for shrew populations, we summarize the following: 1) the histopathological changes were common and many of them were fairly severe; 2) over half of the animals had more than one organ affected, and the synergistic effects of multiple tissue or organ pathology could be important; 3) even brief or mild diseases can be fatal or debilitating in shrews, which have high metabolic rates and are dependent on nearly continuous food intake; and 4) the interaction between sublethal diseases and unfavorable environmental conditions may be important.

We conclude that diseases may contribute to the fluctuations in common shrew populations. The significance of diseases likely increases when the populations are dense and the environmental conditions (weather and food availability) are poor. Stress and deficiencies in food impair resistance and immunological mechanisms and predispose the animals to diseases, which in turn increases energy losses. Diseased animals are also easier prey for predators. Whether the ultimate reason for death is disease, starvation, or predation, there could be many interacting primary factors involved.

Acknowledgments

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Table 1.—*Histopathology in organs of the common shrew collected in winter and early spring from two locations in southern and central Finland and mean numbers of several field vole,* Microtus agrestis, *samples from the same period of the same study area in central Finland.*

Organ	Prevalence (%) and Number Examined (in parentheses)							
	Female Shrews		Male Shrews		Total Shrews		Total Voles	
Liver	54	(13)	64	(14)	59	(27)	37	(117)
biliary or peribiliary inflammation, proliferation	31		57		44		3	
marks of restricted inflammation or mononucleated cells	23		7		15		27	
coccidian-like parasites	8		14		11		0	
cirrhosis	0		7		4		0	
parasitic cysts	0		0		0		14	
Intestines	43	(14)	50	(10)	46	(24)	15	(117)
enteritis	43		50		46		15	
Lungs	33	(12)	50	(12)	42	(24)	53	(117)
small increase in leukocytes	17		25		21		41	
moderate or noticeable increase in leukocytes	8		17		13		9	
parasites	17		8		13		0	
fungal cysts	0		0		0		13	
Kidneys	14	(14)	31	(13)	30	(27)	13	(117)
parasitic cysts	14		31		22		0	
interstitial nephritis	7		23		15		3	
degeneration, infarct, necrosis or calcification	0		0		0		13	
Heart	14	(14)	29	(14)	21	(28)	1	(117)
parasitic cysts	7		21		14		0	
inflammation	7		0		4		1	
degeneration	0		7		4		0	
Brain	10	(10)	9	(11)	10	(21)	6	(69)
inflammation	0		9		5		0	
mononucleated cells	10		0		5		0	
parasitic cysts	0		0		0		6	

VARIATION IN BRAIN MORPHOLOGY OF THE COMMON SHREW

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ABSTRACT

Common shrews (*Sorex araneus*) were trapped on study grids located in mixed deciduous forests of western Siberia and 60 km west of Moscow. The patterns of seasonal changes in masses of body, brain, and brain regions were similar in both populations, but there were some differences in absolute values. The regions of the brain differed in their responses to winter and drought conditions by showing greater variation in the phylogenetically recent regions (sueh as neocortex) than in the phylogenetically ancient regions of the brain, such as olfactory bulbs and myelencephalon. Water content decrease was not the only reason leading to brain size decrease over winter. Dry mass of the brain declined in this period, primarily because forebrain mass declined by 21% (neocortex especially, 28%). During a period of mass gain in spring the most considerable increase was observed in the hippocampus (+33% of wet mass, +26% of dry mass). The most noticeable mass changes occurred in this region and only as reproductive activity began. My research indicates broad macromorphologieal variability occurs in the brain of the common shrew. This variation is associated with age, sex, and different environmental factors such as geographic, seasonal, and extreme climatic (summer drought) parameters. The possibility is explored that seasonal (and other) variation in brain mass (previously reported by this author for voles) may represent a more generalized mammalian pattern of adaptive mechanism of winter-active small mammals employed to conserve energy during harsh climatic conditions.

INTRODUCTION

The study of seasonal morphological changes of nonhibernating small mammals at intermediate and high latitudes is important in understanding the adaptive strategies and environmental relations of these animals. Dehnel (1949) was the first to find seasonal changes of the skull height in *Sorex araneus*. Seasonal changes found in the volume of the braincase (Pucek, 1955) suggested that analogous variations should take place in the volume of the brain. This was demonstrated for mass and volume of the brain in *Sorex minutus* (Cabon, 1956) and in *S. araneus* (Bielak and Pucek, 1960). The data on seasonal changes of brain size were surprising because of the widely adopted viewpoint of the stability and sufficient protection of the brain from extreme environmental factors. The complex of seasonal changes in shrews, and of skull and brain changes especially, has been considered by investigators as a specific adaptation to winter conditions of this group of animals only. But detailed investigations of brain variability in voles have shown the existence both of seasonal changes in brain size (similar to that of shrews) and of significant alterations in brain structure and proportions (Yaskin, 1980, 1984, 1989). Histological changes in the skulls of rodents similar to those of shrews were also recorded (Quay, 1984). Seasonal changes in brain morphology, accompanied by the changes in its size and cranial capacity, are considered to be a general pattern for a large group of Palearctic and Nearctic species of small mammals (Yaskin, 1984). This report deals with original data on seasonal, annual, and geographic variability in brain size and brain macromorphology of the common shrew, *Sorex araneus*.

MATERIALS AND METHODS

Two populations of *Sorex araneus* were sampled circumannually. The study areas were situated in the floodplain biotope of the Pyshma River (western Siberia) and in mixed forest near the Moskwa River 60 km west from Moscow. Perhaps the most significant climatic characteristic of the western Siberian site was the high variability between the seasons. The locality near Moscow features a milder climate with smaller seasonal temperature gradients.

Animals were obtained through frequent inspection of live traps and metal cylinders. All captured shrews were measured, weighed, and then dissected as soon as possible after death. The braincase height was taken to the nearest 0.1 mm using a dial caliper. The brain mass was determined after its separation from the spinal cord at the posterior attachment of the pyramids. After being weighed to the nearest 1 mg, the brain was immersed in 10% formalin in which it was kept at room temperature for a period of more than one month. The method of determination of the mass of brain regions (Latimer, 1950; Dmitrieva, 1969) was used for quantitative investigation of peculiarities of brain structure. The brain and principal brain regions of 217 (Siberian locality) and 53 (Moscow region) individuals of common shrews were weighed. To convert brain regions after formaldehyde fixation into their respective fresh masses, a conversion index was calculated (k = fresh brain mass/fixed brain mass). The index diverged in animals of different ages, so it was calculated for each individual separately. Weighed wet brain parts were transferred to weighing glasses and evaporated in an oven at a temperature of 60°C for 48 h. This proved to be sufficient time to dry the tissue to a constant mass. After drying, the brain parts were weighed to an accuracy of 0.2 mg. The absolute water mass of the fresh brain was determined as the difference of the fresh brain and the sum of dry masses of brain regions. Water content was calculated as the percentage of absolute water mass to fresh brain mass. The significance of the differences was assessed by the Student's t-test of the differences in mean values for two independent groups.

RESULTS

The observation of winter reduction of skeleton size in

shrews (Dehnel, 1949) has been confirmed for different species and populations, although some geographic peculiarities of the processes have been found (Z. Pucek, 1965; Hyvärinen and Heikura, 1971; Mock, 1994).

According to my data the mean height of the braincase in young common shrews from the Moscow region was 6.01 ± 0.048 mm in summer. The reduction in the braincase during the autumn and winter was expressed by a decrease in its height in February ($\bar{X}$ = 4.94 ± 0.040 mm) of 17.8% ($P < 0.001$) in relation to summer. During the spring "jump in growth" mean height of braincase increased by 8.5% ($P < 0.001$), and in overwintered adult shrews was 5.36 ± 0.056 mm. A comparison of these data with some other populations has indicated that the population under study was characterized by a great winter regression in the height of the braincase.

Figure 1 shows the changes in the mean body and brain masses for both sexes in different seasons during the life cycle of common shrews from western Siberia. These curves agree with data on the Białowieza population (Poland) obtained previously by Z. Pucek (1965). The reduction in the brain mass during the winter was expressed by a decrease in its mass in February (Fig. 1) of 21.2% ($P < 0.001$) relative to July. From October to February the brain mass decreased by 17% ($P < 0.001$). The corresponding values obtained by Z. Pucek (1965) in Białowieza were 23.6% and 15.0%. The mass of the brain increased in the spring; however, the summer brain mass in overwintered adults was almost 16% ($P < 0.001$) lower relative to that of young from the same season. A similar value (14.6%) was given by Z. Pucek (1965).

As can be seen from Fig. 1, the brain tended to lose mass before the decrease in body mass. In the period from June to September, brain mass decreased by 11% ($P < 0.001$). In contrast, the body mass loss began in September.

The relative brain mass (Fig. 1) maintained approximately the same level in young shrews from summer and winter. The fundamental changes in the relative brain mass took place from March, since the brain mass gain within the spring-to-summer period was smaller than the corresponding spring-to-summer body mass increase.

A comparison of seasonal body and brain mass changes in the two populations under study (Table 1) shows that animals from the Moscow region were characterized by more pronounced winter regression in brain mass than were those from western Siberia. No differences in body mass were found. There were no regional differences in brain mass of young shrews from summer; however, the winter brain masses in young and overwintered adults from the Moscow region were statistically lower (by 6.3–6.8%; $P < 0.01$) than those of western Siberian individuals of corresponding age.

The water content of an organism tends to decrease with age. There is also information on the lowering water content of tissues in small mammals during a winter period (M. Pucek, 1965; Sawicka-Kapusta, 1974). Seasonal variations in the brain mass of shrews are due to changes in water content and dry matter (M. Pucek, 1965). My data indicated that both dry brain mass and water content decreased during autumn and winter. In shrews of six to ten months of age in March, the mean dry mass of the brain was 13.0% ($P < 0.001$) lower than in animals one to three months old in summer. The absolute water mass was 25.4% lower ($P < 0.001$) and water content was 2.36% lower ($P < 0.01$). During the period of rapid growth in spring, the dry brain mass in shrews aged seven to 11 months increased by 10.8% ($P < 0.001$) (Fig. 3), and the water mass increased by 16.2% ($P < 0.001$) during this period. From the winter to summer, the brain water content increased by 0.75% ($P < 0.05$). The present results indicated that the decrease in the brain mass of common shrews during the winter was caused both by water and dry matter loss. Water loss was more pronounced, but even more importantly, the dry matter, whose mass was absolutely less in winter than in summer, was also subject to seasonal variation.

Although many investigations have been dedicated to studies of age-dependent variability of brain region ratios in mammals, the problem of variation in the morphology of the brain according to fluctuations in environmental parameters is still obscure. Seasonal changes in brain region ratios previously were observed in rodents in the genera *Clethrionomys* and *Microtus* (Yaskin, 1980, 1984).

The patterns of seasonal changes in the masses of different regions of the brain in common shrews were diverse (Fig. 2; Table 2). The most pronounced winter loss of mass occurred in the forebrain (−31.5%; $P < 0.001$), and especially in the neocortex (−37.4%; $P < 0.001$). The masses of the hippocampus, paleocortex, striatum, and mesencephalon+diencephalon decreased for this period by 20–29%. On the contrary, no noticeable winter regression in the masses of such regions as olfactory bulbs, myelencephalon, and cerebellum were observed. During a period of gain in mass in spring, the rate of mass increase was different in different brain structures. The most considerable increase was observed in the hippocampus (+32.6%; $P < 0.001$). This region showed the most noticeable sexual differences in its mass that occurred only as reproductive activity began.

Although the seasonal variations in the absolute masses of different brain regions were substantial, the seasonal changes in the ratio of brain regions were also appreciable. During winter the relative mass of the forebrain declined; the most intensive decrease was observed in the neocortex (−18.4%; $P < 0.001$). By contrast, the relative mass of myelencephalon increased by 32.6% ($P < 0.001$). The relative mass of the olfactory bulbs and cerebellum increased significantly simultaneously. The highest relative mass increase during the winter-to-summer period was found in the hippocampus (+15.2%; $P < 0.001$).

The quantitative ratio of different regions of the brain is altered during the winter and does not return in overwintered adults to the state observed in young. The proportions of the brain were considerably different. In overwintered shrews, the relative masses of the forebrain, neocortex, paleocortex, and striatum were lower than in young nonwintered shrews (during the spring mass gain, the mass of these regions did not reach the autumnal level), while the relative masses of the cerebellum and myelencephalon were higher. There were no noticeable differences in masses of the hippocampus, mesencephalon+diencephalon, and bulbus olfactorius.

The pattern of seasonal dry mass changes of different brain regions (Fig. 3, Table 3) did not exactly coincide with the pattern of that before drying (Fig. 2, Table 2), but the general picture was similar. Seasonal changes were comparatively more pronounced in the dry mass of forebrain (−21.2%; $P < 0.001$), and the neocortex lost as much as 27.6% ($P < 0.001$) of its dry matter. Winter regression in dry mass of the bulbus olfactorius, myelencephalon, and cerebellum was not observed. Dry masses of the forebrain and such parts as the neocortex, paleocortex, and striatum in overwintered adults did not reach the level characterized for young before winter, while the dry mass of another forebrain region, the hippocampus, was similar in both age groups. In overwintered adults the dry matter mass of the cerebellum and myelencephalon was appreciably higher compared to that in the young.

Some sexual differences in these variations were observed. Brain mass of females was lower than in males, but usually only in summer months. The hippocampus showed the most substantial sexual differences in its size that occurred only as reproductive activity began. The absolute and relative masses of this region in males were higher by 5–7% ($P < 0.05$) than in females.

In addition, certain changes of brain mass and brain structure in common shrews were correlated with effects of the 1975 summer drought (western Siberia locality) when the body masses of young shrews in June–August were on the average lower by 8% than in other years. The brain mass was lower by 5% in July 1975 ($P < 0.05$). The differences disappeared in October. Some differences were also found in proportions of the brain. The ratio of forebrain to whole brain mass in young shrews from the summer drought was 6.3% lower ($P < 0.01$) with respect to other years.

Discussion

Both wet and dry masses of some brain regions in overwintered shrews were higher than in young ones of the previous summer, while the total brain mass of adults was significantly lower. This indicates that the brain regions have different regularity in age-dependent patterns of development. Some parts, such as the forebrain, decreased in size with age, whereas others (the cerebellum and myelencephalon) increased significantly. Therefore, Dehnel's phenomenon (Dehnel, 1949) does not affect some of the brain regions. The present data on seasonal variations of brain morphology in common shrews agree to a considerable extent with the results obtained in the bank vole, *Clethrionomys glareolus* (Yaskin, 1980, 1984).

The comparison of the age-related mass variability of different brain regions in shrews with known data on alterations of learning abilities of mammals as aging progresses (Obrazcova, 1964) leads to the suggestion that the greater dimensions of the forebrain and neocortex in young shrews may be related to their higher need to react to environmental perturbations.

Lowering of the vital activities may be accompanied by consequent cessation of some organismal function, the phylogenetically younger functions ending first (Astvazaturov, 1939). My results illustrated such a fundamental strategy concerning morphophysiological alterations in the brain. The forebrain suffers the most impressive mass regression during the winter (and drought also), the phylogenetically youngest part of the brain (neocortex) in particular. The mass of the relatively phylogenetically ancient bulbus olfactorius and myelencephalon remained constant during the winter period.

My results revealed the broad morphological variability of such a highly specialized and relatively stable organ as the brain. This variation is correlated with age, sex, and different environmental factors such as geographic location, season, and extreme climatic parameters, such as drought conditions.

The similarity in morphological brain changes in winter and during drought conditions suggests that these variations represent a more generalized mammalian pattern of adaptive mechanisms. It seems that these morphological changes are advantageous as a nonspecific adaptive mechanism by conferring an adaptive advantage of conservation of energy during the harsh winter and summer drought periods.

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Table 1.—*Seasonal and age changes in brain and body mass of* Sorex araneus *from western Siberia and Moscow region. Values given are mean ±SE.*

Season	Site	Sample Size	Body Mass (g)	Brain Mass (mg)
Summer (VI–VIII)	Siberia	103	7.06 ± 0.09	258 ± 1.9
	Moscow	10	7.36 ± 0.12	262 ± 3.6
Autumn (X)	Siberia	32	6.47 ± 0.19	236 ± 2.5
	Moscow	6	6.02 ± 0.25	235 ± 3.7
Winter (II–III)	Siberia	18	5.33 ± 0.17	207 ± 3.8
	Moscow	18	5.23 ± 0.08	193 ± 2.4
Summer (VI–VIII)	Siberia	62	9.27 ± 0.28	221 ± 2.2
	Moscow	9	19.91 ± 0.31	207 ± 2.1

Table 2.—*Seasonal and age changes (in percent) in the wet mass of the brain regions in common shrews,* Sorex araneus, *from western Siberia. 1, autumn–winter regression; 2, spring "jump of growth"; 3, differences between nonwintered and overwintered animals; im, immature; m, mature.*

Brain Regions	Summer (im)→ Winter (im) 1		Winter (im)→ Summer (m) 2		Summer (im)→ Summer (m) 3	
	%	*P*	%	*P*	%	*P*
forebrain	−31.5	<0.001	+17.1	<0.001	−19.8	<0.001
neocortex	−37.4	<0.001	+18.4	<0.01	−25.9	<0.001
hippocampus	−29.2	<0.001	+32.6	<0.001	−6.1	>0.05
paleocortex	−28.1	<0.001	+12.5	<0.05	−19.18	<0.05
striatum	−27.6	<0.001	+5.7	>0.05	−23.4	<0.001
bulbus olfactorius	−4.2	>0.05	−2.8	>0.05	−10.1	>0.05
mesencephalon + diencephalon	−20.1	<0.05	+22.3	<0.01	−2.3	>0.05
cerebellum	−8.3	>0.05	+22.8	<0.01	+12.6	<0.05
myelencephalon	+1.9	>0.05	+10.0	<0.05	+12.2	<0.05

Table 3.—*Seasonal and age changes (in percent) in the dry mass of the brain regions in common shrews from western Siberia. Designations as in Table 2.*

Brain Regions	Summer (im)→ Winter (im) 1		Winter (im)→ Summer (m) 2		Summer (im)→ Summer (m) 3	
	%	*P*	%	*P*	%	*P*
forebrain	−21.2	<0.001	+15.7	<0.001	−8.8	<0.05
neocortex	−27.6	<0.001	+18.2	<0.01	−14.3	<0.01
hippocampus	−19.7	<0.01	+25.6	<0.001	+0.9	>0.05
paleocortex	−19.5	<0.001	+12.7	<0.05	−9.3	<0.05
striatum	−20.9	<0.01	+9.5	<0.05	−8.3	<0.05
bulbus olfactorius	−5.1	>0.05	+9.1	>0.05	+3.4	>0.05
mesencephalon+diencephalon	−16.9	<0.01	+18.1	<0.05	−1.9	>0.05
cerebellum	−4.8	>0.05	+21.5	<0.01	+15.6	<0.05
myelencephalon	+4.6	>0.05	+13.2	<0.01	+18.4	<0.01

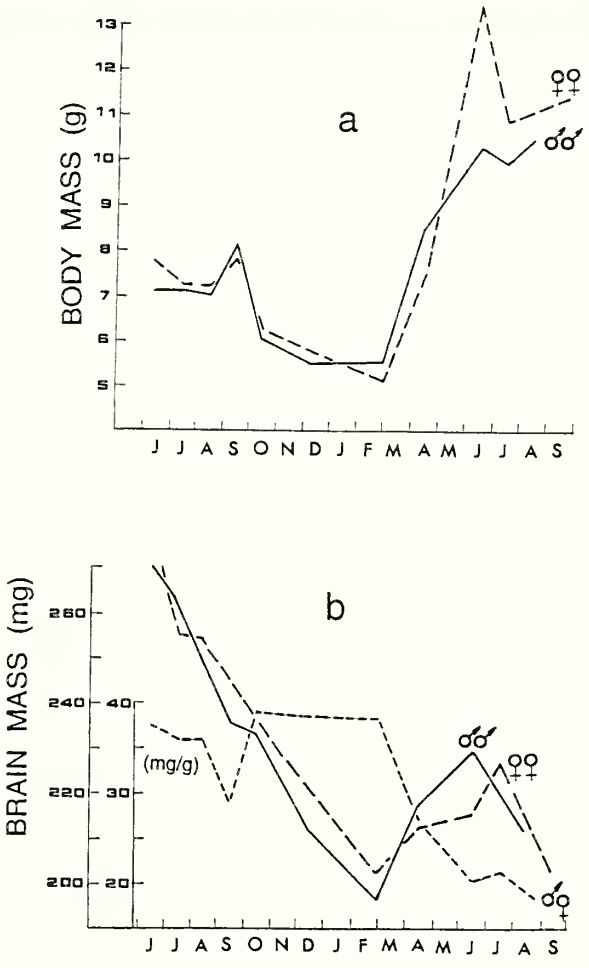

Fig. 1.—Seasonal and age changes in the body mass (g). a, absolute (mg); and b, relative (mg/g) brain mass of the common shrew (*Sorex araneus*) from western Siberia. At the beginning of the curves, the shrews are young nonwintered animals and at the end of the curves, adult wintered animals.

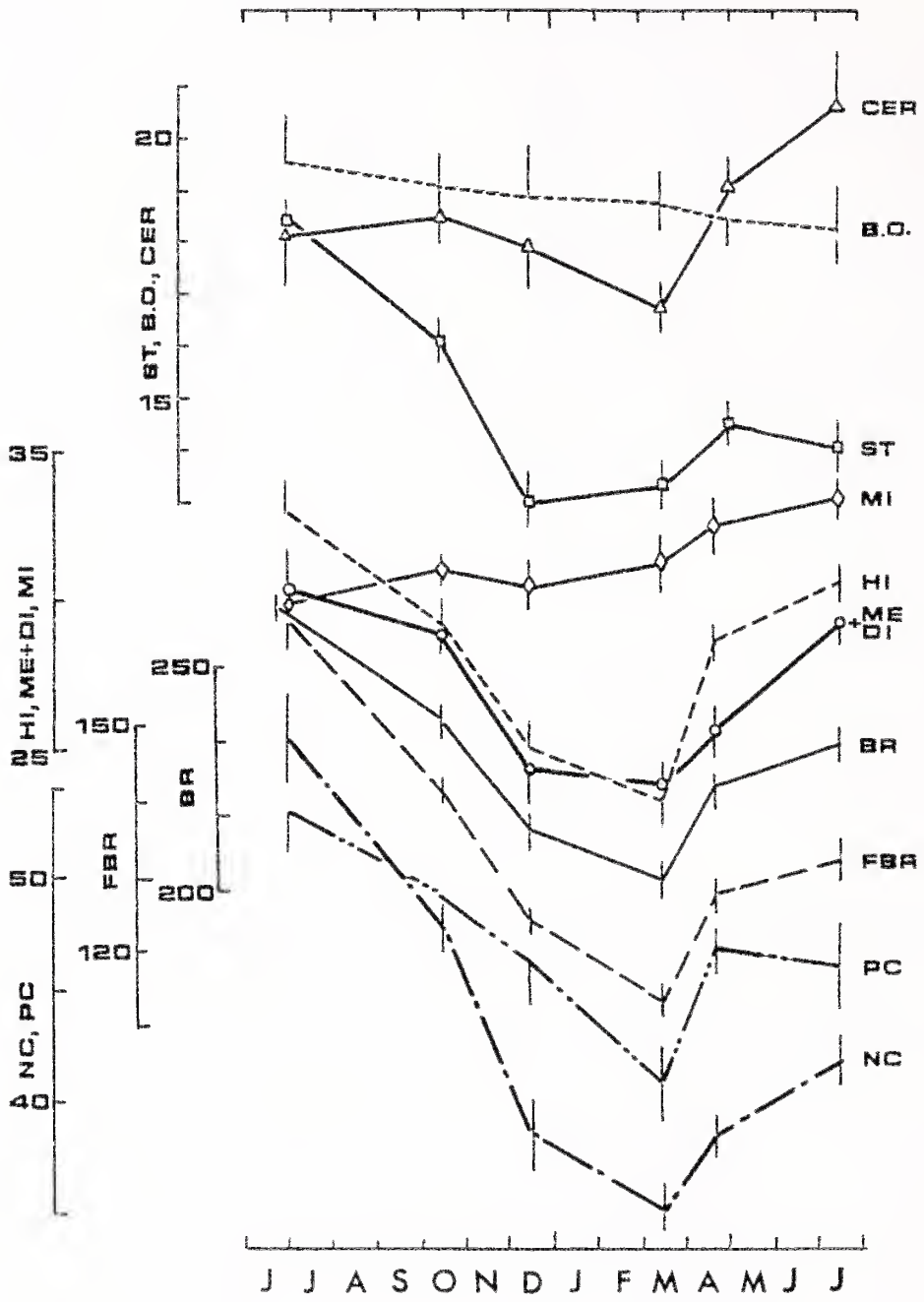

Fig. 2.—Seasonal and age changes in the wet mass (mg) of the brain and its regions in common shrews (western Siberia). At the beginning of the curves, the shrews are young nonwintered animals and at the end of the curves, adult wintered animals. BR, brain; FBR, forebrain; NC, neocortex; HI, hippocampus; PC, paleocortex; ST, striatum; B.O., bulbus olfactorius; ME+DI, mesencephalon+diencephalon. The ends of the vertical lines indicate ±SE.

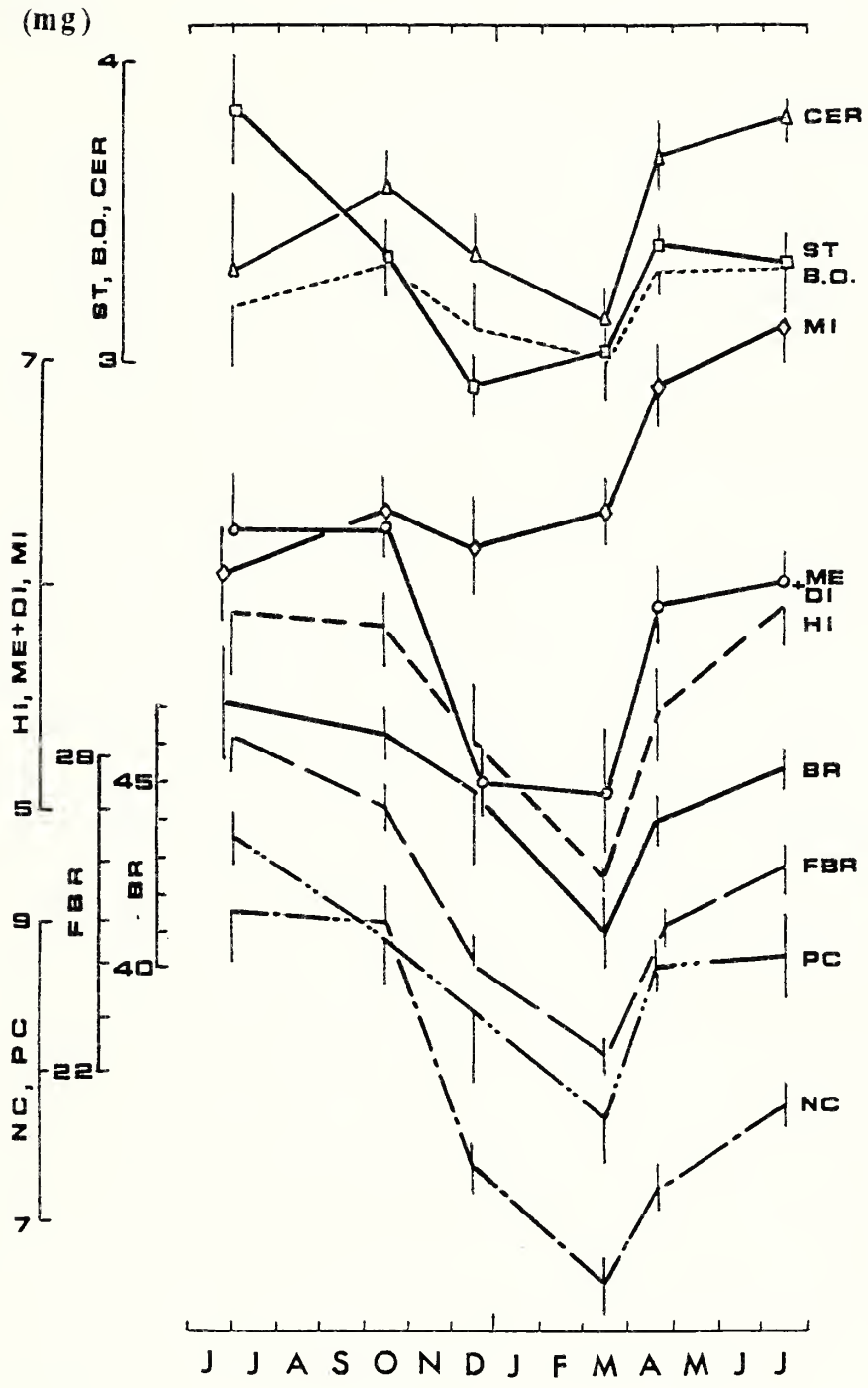

Fig 3.—Seasonal and age changes in the dry mass (mg) of the brain and its regions in common shrews (western Siberia). Designations as in Fig. 2.

THERMAL BIOLOGY OF FREE-RANGING SHREWS AS REVEALED BY COMPUTER-FACILITATED RADIOTELEMETRY: ENERGETIC IMPLICATIONS

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ABSTRACT

Seasonal changes in core body temperature of northern short-tailed shrews (*Blarina brevicauda*) residing in a natural outdoor enclosure were monitored by radiotelemetry techniques. The study was conducted at the biologieal station of the Carnegie Museum of Natural History, southwestern Pennsylvania, during autumn, winter, spring, and summer of 1989–1990. Radiotransmitters were surgically implanted within the peritoneal cavity of shrews. Each monitoring period lasted five days, during which time body temperature readings were recorded every 15 min using a computer subsystem. A temperature "pulse" of the implanted shrew was relayed from an outdoor enclosure to a lab-based receiver interfaced with a hardware-software DATACOL-AVM subsystem. At the laboratory, instantaneous body temperature readings were automatically tabulated by an Apple II+ computer. Body temperature of shrews was maintained continuously at euthermy, and averaged 38.3°C (n = 1,470 readings) ranging from 34.4–42.2°C during the year-long study. Minimum body temperatures occurred during summer while maximum temperatures occurred during autumn (P = 0.001). Shrews compensated for the high cost of continuous euthermy by minimizing thermal conductance through an increase in pelage insulation. Soricids respond to the winter physical environment by coupling of anatomical, behavioral, and physiological modifications of their thermoregulatory constitution.

INTRODUCTION

The overwinter survival of small, nonhibernating mammals is largely contingent on their ability to cope with extreme cold coupled with a reduced availability of food and water. In north-temperate and boreal regions of North America, the winter period may last up to 7½ months with minimum ambient temperatures frequently reaching −40°C (Merritt, 1984). In response to these selection pressures, small mammals have evolved behavioral, anatomical, and physiological adjustments which permit their overwinter survivorship (Wang and Hudson, 1978; Vogel, 1980; Feist, 1984; Hanski, 1984, 1989; Hyvärinen, 1984; Merritt, 1984, 1986; Wunder, 1984; Hutterer, 1985; Heller et al., 1986; Zegers and Merritt, 1988*a*, 1988*b*).

Wunder (1984) postulated that during winter, small mammals exhibit a variety of behavioral, physiological, and anatomical compensatory mechanisms to cope with reduced food and increased cold. These mechanisms included avoidance behavior (i.e., migration, use of ameliorating microclimates, torpidity, increased thermal insulation) and resistance (i.e., increased thermogenesis by changes in basal metabolic rate, nonshivering thermogenesis, shivering, and increases in level of activity).

Blarina brevicauda, the largest North American shrew, is distributed throughout much of the eastern half of North America, where it is one of the most abundant mammals. This semifossorial soricid is most common in mesic forests possessing a well-developed layer of leaf litter and humus, but can be found in a diverse array of plant assemblages (George et al., 1986). Research on the population dynamics of *B. brevicauda* derived from field studies in Ontario, Manitoba, Minnesota, and Pennsylvania reveals good overwinter survivorship in regions characterized by ambient temperatures reaching −40°C (Buckner, 1966). The apparent success of *B. brevicauda* in coping with harsh winter climates derives from a complex suite of behavioral, anatomical, and physiological mechanisms which contribute to their thermoregulatory constitution (Merritt, 1986; Merritt and Adamerovich, 1991; Bozinovic and Merritt, 1992).

Merritt (1986) described two resistance mechanisms (sensu Wunder, 1984) in *B. brevicauda*—increased resting metabolic rate and nonshivering thermogenesis during winter. Also, by employing radiotelemetry techniques on free-ranging shrews, Merritt and Adamerovich (1991) demonstrated that *B. brevicauda* did not possess the capability to undergo torpor, and did not display communal nesting as a means of energy conservation during winter. Randolph (1973), and more recently Bozinovic and Merritt (1992), reported a lower rate of heat loss in *B. brevicauda* during winter, compared with summer-caught shrews. This increased insulation during winter is reported as a plausible avoidance mechanism to cold by small mammals (Wunder, 1984).

In order to assess accurately the ecology and behavior of free-ranging species of mammals, researchers have employed radiotelemetry techniques. Such applications have been applied to many mammals in order to understand their activity, movements, survival, and thermal physiology (Amlaner and MacDonald, 1979; Cochran, 1980; Mech, 1983; Kenward, 1987). However, radiotelemetry is limited in use for many species of small mammals due to the comparatively large size of transmitters. Because of this limitation in technology, only two studies have been conducted on members of the family Soricidae. Cawthorn (1989) detailed the ecology and activity patterns, and Merritt and Adamerovich (1991) examined temperature regulation in the largest North American soricid, *B. brevicauda*. Several questions concerning the thermal biology of shrews have surfaced as a result of these initial studies, and prompted further refinement in techniques designed to elucidate daily body temperature fluctuations of the northern short-tailed shrew. Thus, the objective of our study was to determine the thermoregulatory patterns of *B. brevicauda* and assess the

energetic implications of the maintenance of continuous euthermy in this soricid. The thermal biology of free-ranging shrews was elucidated during autumn, winter, spring, and summer of 1989–1990 at Powdermill Biological Station by employing computer-facilitated radiotelemetry techniques.

Methods

Northern short-tailed shrews were live-trapped at Powdermill Biological Station, Carnegie Museum of Natural History, southeastern Westmoreland County, Pennsylvania (Merritt, 1986). The collection site (elevation, 400 m) encompassed a secondary growth forest of hawthorn (*Crataegus* sp.), crab apple (*Pyrus coronaria*), black locust (*Robinia pseudoacacia*), sugar maple (*Acer saccharum*), and black cherry (*Prunus serotina*). Upon capture, shrews were marked by toe clipping, sexed, weighed, and their reproductive status recorded if evidenced by external criteria.

Candidates for surgery were maintained in the animal facility for two days on *Tenebrio* larvae, cat food, and water ad libitum. Shrews were then anesthetized by using methoxyflurane (Pitman-Moore, Inc.) inhalation therapy. A radiotransmitter battery package (AVM Instrument Company, Inc., Livermore, California) encapsulated in "Elvax" paraffin coating material (The Mini-Mitter Company, Inc., Sunriver, Oregon) was surgically implanted within the peritoneal cavity of the shrew by access through an incision in the ventro-lateral abdominal wall. Each 2.6–3.0 g encapsulated radiotransmitter battery package was pretuned to a specific frequency ranging between 150–151 MHz. To ensure that frequencies did not drift during the study, temperature-sensitive transmitters were calibrated before and after use by immersion in a water bath of known temperature (ranging from 22–42°C) as recorded by a YSI 2100 Telethermometer. Following surgical implantation, the peritoneum and outer skin were closed using 4–0 Ethicon silk. The shrew was retained in the animal facility for two days following surgery, and then released in an outdoor enclosure. The body mass of the shrew was recorded before release.

The purpose of the outdoor enclosure was to restrict the movements of shrews to facilitate telemetry measurements and also to minimize loss of implanted animals due to dispersal or predation. The outdoor enclosure, placed in a maple–cherry–locust forest, measured 4.8 × 2.5 × 1.4 m; it was constructed of ¼" clear plexiglass framed by "2 × 4" outdoor lumber (Merritt and Adamerovich, 1991). The interior of the enclosure consisted of a layer of soil 1.5 m deep provided with rocks, logs, sticks, ferns, and herbs, to simulate the natural environment. The enclosure was covered with 2 cm^2 polypropylene net to restrict predators, while permitting normal precipitation to reach the inside environment. The bottom of the enclosure consisted of small-gauge fiberglass screening set upon a 40-cm deep base of no. 2B gravel to permit drainage and prohibit burrowing activities of shrews and other small mammals. A soil embankment graded from the surrounding ground to the side of the enclosure in order to maintain a soil temperature inside the enclosure that approximated that of the outside soil. Within the enclosure, three wooden nest boxes were positioned along three walls and supplied with grasses and leaves. Nest boxes were buried slightly below ground level, and a feeding station sheltered within a plastic canister was positioned adjacent to each box.

Three different temperature regimes were recorded in the enclosure during the study periods by a three-point thermograph (Model 4030; Qualimetrics, Inc., Sacramento, California). Temperatures were recorded 1.5 m above ground surface (ambient), on ground surface, and in a subsurface tunnel. Snow depth was also measured within the enclosure. Shrews residing in the enclosure were provided with 5.0 g of *Tenebrio* larvae equivalent to ca 31.5 Kcal per day (Merritt and Adamerovich, 1991).

Each seasonal monitoring period lasted from 5–6 days. Within the enclosure, pulse signals from shrews with transmitters were received and conveyed at 15-min intervals via a Yagi antenna to an LA 12-DS portable telemetry receiver in line with a two-stage repeater transmitter. The signals then were transmitted and received in the laboratory (160 m from the enclosure) by another LA 12-DS receiver. This lab-based receiver was facilitated by a DATACOL-AVM hardware–software subsystem (AVM Instrument Company, Inc.) that converted pulse interval signals into instantaneous body temperature readings and automatically displayed and tabulated these data on an Apple II+ computer.

Results

Seasonal Changes in Body Temperature

The highest core body temperature for *B. brevicauda* occurred during autumn. Body temperature of one adult *B. brevicauda* (22.6 g) monitored from 6–10 November 1989 averaged 41.2°C and ranged from 40.0–42.4°C (n = 362 readings; Fig. 1). Temperatures at ground level ranged from −1 to 3°C during this time. The range in body temperatures of this shrew represented the greatest fluctuation, and also the highest level of body temperature of a shrew for all seasons studied. Of the 362 body temperature readings spanning five days, only three were above 42.0°C, indicating such temperatures were probably spurious readings, and thus were declared as outliers in the sample.

Body temperatures of *B. brevicauda* (adult, 23.9 g) during the winter period (10–15 January 1990) averaged 38.4°C and ranged from 37.2–40.0°C (n = 423 readings; Fig. 2). Temperatures on the ground surface within the enclosure ranged from −1 to −0.5°C for the six-day study period and snow cover was intermittent reaching a maximum depth of only 30 cm. This shrew exhibited a conservative thermoregulatory budget with 96% of the readings between 38.0–39.0°C.

Body temperatures for *B. brevicauda* (adult, 23.9 g) during the spring period (5–10 April 1990) were similar to those of winter and averaged 38.5°C (range, 37.0–39.6°C, n = 322 readings; Fig.3.). Temperatures on the ground surface of the enclosure ranged from 9–15°C. As was the case with the shrew during the winter trial (Fig. 2), body temperature fluctuations were minimal, with 93% of the readings between 38.0–39.0°C.

Body temperature fluctuations for *B. brevicauda* (subadult, 18.15 g) during the summer period (7–11 August 1990) averaged 35.4°C and ranged from 34.4–36.0°C (n = 363

readings; Fig. 4). Ground temperature during this period ranged from 17.5–23.0°C. This shrew exhibited the most conservative level of core body temperatures of all shrews tested, with only 3% (12/363) of the readings outside of 35.0–36.0°C. In contrast to *B. brevicauda* monitored during the autumn trial (Fig. 1), this shrew exhibited the lowest core body temperature of all shrews tested during the study.

A one-way ANOVA revealed significant differences in body temperature through the year [F (3,146.9) = 14,165.77; $P < 0.0001$]. The a posteriori Student-Newman-Keuls test revealed significant differences in body temperature between seasons ($P < 0.05$), except between winter and spring (38.4 vs 38.5 respectively, $P > 0.05$). Thus, a comparison between body temperature and time of day for each seasonal trial was clearly random. Results should be interpreted with some caution due to the fact that each seasonal trial, although composed of many data points (temperature readings), consisted of only one shrew. Further, shrews were commonly derived from different cohorts, thus age of a given shrew would likely influence the thermal biology of a seasonal trial. All shrews were judged to be in a nonreproductive state during the trial periods.

Evaluation of the Technique

Results of the present study indicate that seasonal changes in core body temperature of *B. brevicauda* can be evaluated satisfactorily by use of computer-facilitated radiotelemetry techniques. All shrews recovered well from the methoxyflurane inhalation therapy and the surgical procedure as evidenced by a 100% survivorship.

The intraperitoneal positioning of a radiotransmitter (less than 15% of body mass) caused no apparent short-term aberrations in behavior or physiology of northern short-tailed shrews. Postoperative gross inspection of the peritoneum and associated organs revealed no pathological effects attributable to the presence of the implant. Body temperatures of implanted shrews, confined to a natural outdoor enclosure, are realistic approximations of those core body temperatures exhibited by shrews residing in the natural environment. This fact was confirmed by periodic recording of body temperatures by use of rectal probes during the period in which shrews were implanted with transmitters.

Major shortcomings of the technique described herein are associated with the cost of temperature transmitters (ca $380 each). In most cases, the cost of employing this technology prohibits large sample sizes, thus restricting the data base and compromising the validity of results. Further, this "economic factor" contributes to a reluctance of investigators to use this technology in an "unrestrictive" field situation. Technological advances in the field of radiotelemetry coupled with use of outdoor enclosures may result in increased use of this technique with members of the family Soricidae.

Discussion

The family Soricidae is composed of some 266 species belonging to 20 different genera (Churchfield, 1990). This family is distributed on all continents except Australia, Antarctica, and central and southern South America. Of the family Soricidae, the subfamily Crocidurinae exhibits a tropical distribution centered in Africa and Asia, while the subfamily Soricinae exhibits a Holarctic and northern Neotropical distribution (Corbet and Hill, 1980; Nowak and Paradiso, 1983).

Members of the Soricinae inhabiting northern regions are faced with extreme cold and scarcity of food and water during the long winter period (Merritt, 1986; Sheftel, 1989). Members of this subfamily possess high surface area/volume ratios, and are typified by elevated mass-independent metabolic rates. Small endotherms equipped with the ability to exhibit physiological heterothermy would surely possess an adaptive edge for coping with harsh climatic perturbations. However, physiological heterothermy is uncommon within the Soricinae (Dawson, 1973; Vogel, 1976, 1980; Genoud, 1985, 1988; Merritt and Adamerovich, 1991).

Results of our study and those of an earlier work (Merritt and Adamerovich, 1991) clearly indicate that during autumn, winter, and spring, *B. brevicauda* (a member of the subfamily Soricinae) did not exhibit physiological heterothermy as do various members of the more southerly subfamily Crocidurinae (Genoud, 1988). Instead, body temperatures recorded at 15-min intervals ranged from 37.4–41.8°C during autumn, winter, and spring. Maximum body temperature occurred during the autumn period. This increase in thermogenic capacity represented a response to cold cues received at ground surface (the foraging zone of the shrew) and is due, in part, to nonshivering thermogenesis mediated by brown adipose tissue (Merritt, 1986).

Body temperature of *B. brevicauda* recorded during the summer period did show a slight departure from euthermy, ranging from 34.2–36.0°C. This slight decline in core body temperature may represent a thermogenic response to warm temperatures encountered by the shrew on the ground surface while foraging. Conclusions and implications of this occurrence are tenuous, complicated by a low sample size coupled with the fact that the single individual monitored during the summer period was a subadult.

Our results demonstrated that *B. brevicauda* did not undergo a state of torpor or heterothermy as a means of energy conservation during winter. Here we evaluate the role of resistance (increased activity) and avoidance (changes in pelage insulation) as compensatory mechanisms influencing the amount of energy allocated to maintenance or respiration in the short-tailed shrew during winter. We compare our results with the general model proposed by Wunder (1975). This model predicts the amount of energy used for maintenance (R), given body weight (W) in grams, ambient temperature (T_A) in °C and the degree of running activity in km/h. The model is expressed as:

$$R = a\,M_{basal} + M_{TR} + M_{activity}$$

where a is a coefficient that modifies the metabolic rate for the posture associated with activity, M_{basal} is the basal metabolic rate, M_{TR} is the metabolic rate associated with temperature regulation below the thermoneutral zone, and $M_{activity}$ is the metabolic rate due to the level of activity. In a mathematical form the model is expressed as:

$$T = a(3.8\ W^{-0.25}) + 1.05W^{-0.5}$$
$$[(38 - 4W^{0.25}) - T_A] + (8.46\ W^{-0.40})\ V$$

where V (km/h) is the velocity of running.

Assuming *B. brevicauda* with a weight of W = 20.0 g under conditions of resting metabolic rate (i.e., a = 1.0, V = 0, winter $T_A = -1.0°C$, and summer $T_A = 20°C$ [see Results]), the model predicts that during summer, R = 54.65 cal/g h (1.09 Kcal/animal h), while during winter, R = 155.90 cal/g h (3.12 Kcal/animal h). Using the values of M_{basal} reported by Merritt (1986), i.e., 13.74 cal/g h during summer, and 16.63 cal/g h during winter, the values of thermal conductance (TC) documented by Bozinovic and Merritt (1992), i.e., 2.117 cal/g h °C during summer, and 1.532 cal/g h °C during winter, a mean value of body temperature (T_B) = 38.6°C (see Results). Using the model of Wunder (1975) in the form:

$$R = a\ M_{basal} + TC\ (T_B - T_A),$$

the amount of energy used for maintenance during summer is 53.11 cal/g h (1.06 Kcal/animal h), while during winter the energy devoted to maintenance is 77.29 cal/g h (1.50 Kcal/animal). The amount of energy used for maintenance (R) measured during winter was 48% lower than predicted by the model (Wunder, 1975). During summer energy used for maintenance (R) was practically the same as predicted by the model (Fig. 5).

Results of our radiotelemetry research revealed that *B. brevicauda* was a continuously euthermic species (Fig. 1–4). Our analysis of energy allocated to maintenance indicated that winter individuals compensate for the large difference between body temperature and temperatures encountered during foraging by morphological, physiological, and behavioral compensatory mechanisms. These changes are especially important for species of soricids that possess small body sizes because the cost of continuous endothermy is extremely high (Vogel, 1980; Genoud, 1988; McNab, 1991; Merritt and Adamerovich, 1991). Our research indicates that the avoidance and resistance tactics delimited herein act synergistically to enhance winter survivorship for *B. brevicauda* and may explain in part the evolutionary success of shrews inhabiting cold regions of the world.

Acknowledgments

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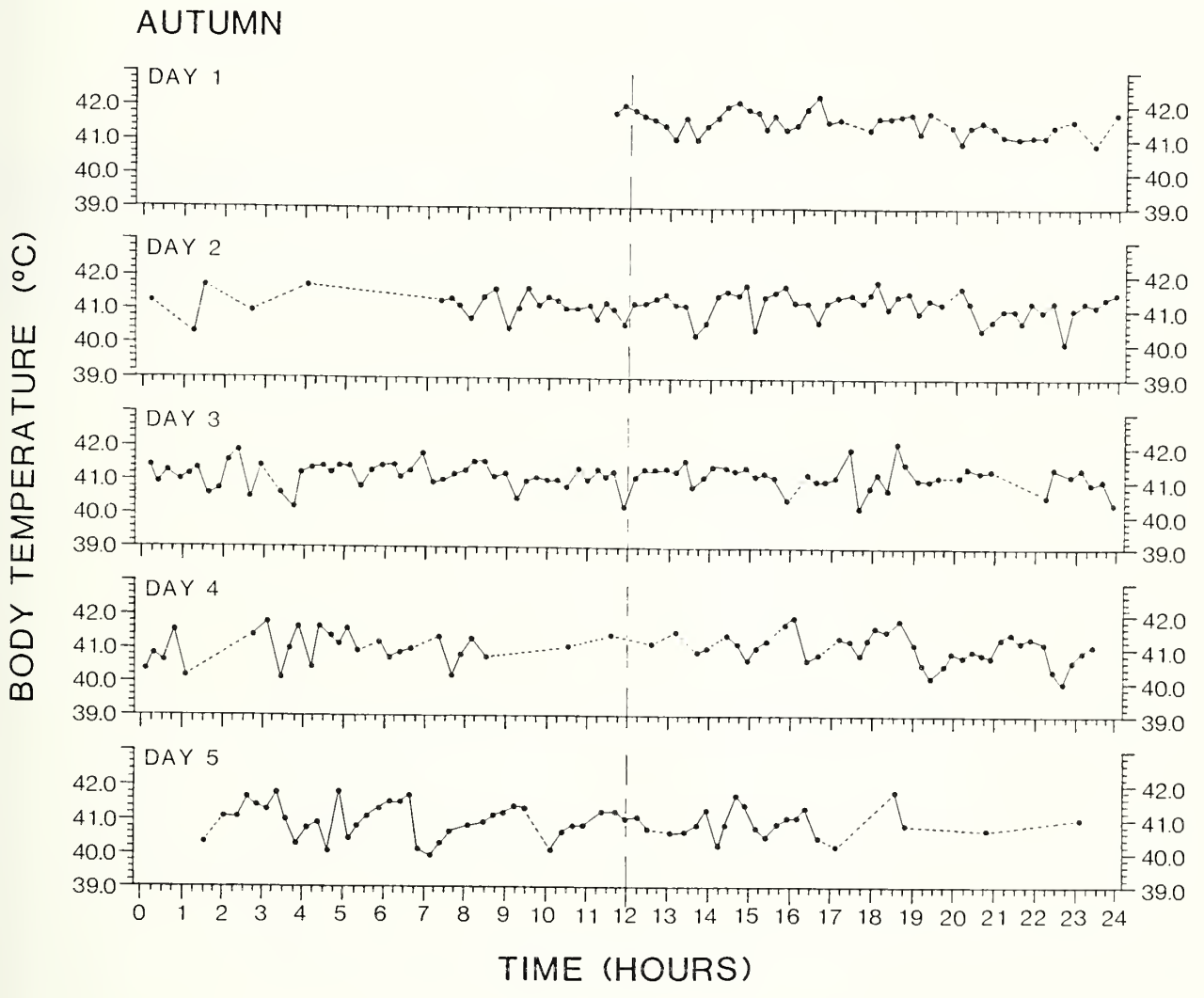

Fig. 1.—Core body temperature of one adult *Blarina brevicauda* (22.6 g) monitored by radiotelemetry techniques during autumn (6–10 November 1989) in a natural outdoor enclosure at Powdermill Biological Station. Average body temperature was 41.2°C based on 362 readings. Dashed lines represent period of malfunctioning transmitter or incomplete transmission of signal.

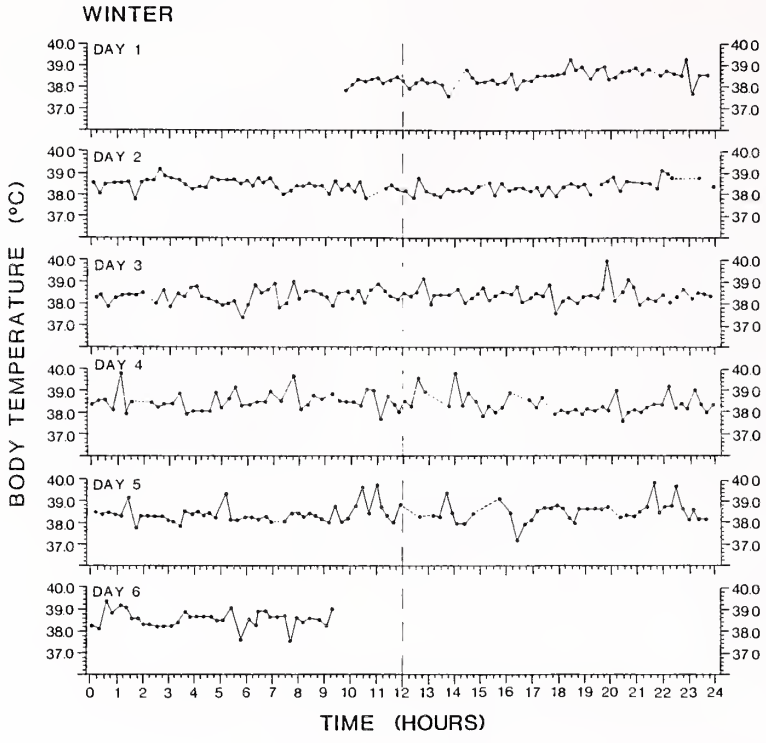

Fig. 2.—Core body temperature of one adult *Blarina brevicauda* (23.9 g) monitored by radiotelemetry techniques during winter (10–15 January 1990) in a natural outdoor enclosure at Powdermill Biological Station. Average body temperature was 38.4°C based on 423 readings. Dashed lines represent period of malfunctioning transmitter or incomplete transmission of signal.

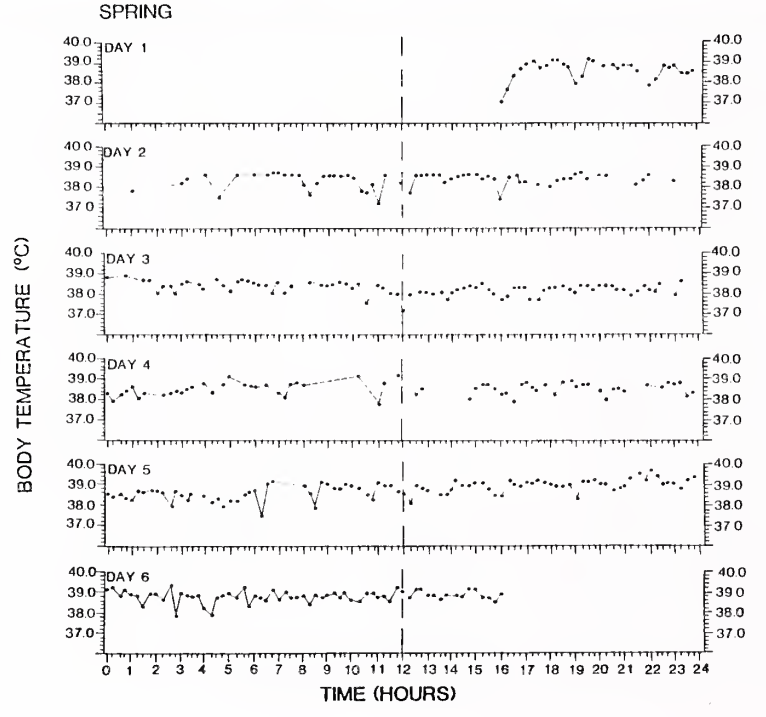

Fig. 3.—Core body temperature of one adult *Blarina brevicauda* (23.9 g) monitored by radiotelemetry techniques during spring (5–10 April 1990) in a natural outdoor enclosure at Powdermill Biological Station. Average body temperature was 38.5°C based on 322 readings. Dashed lines represent period of malfunctioning transmitter or incomplete transmission of signal.

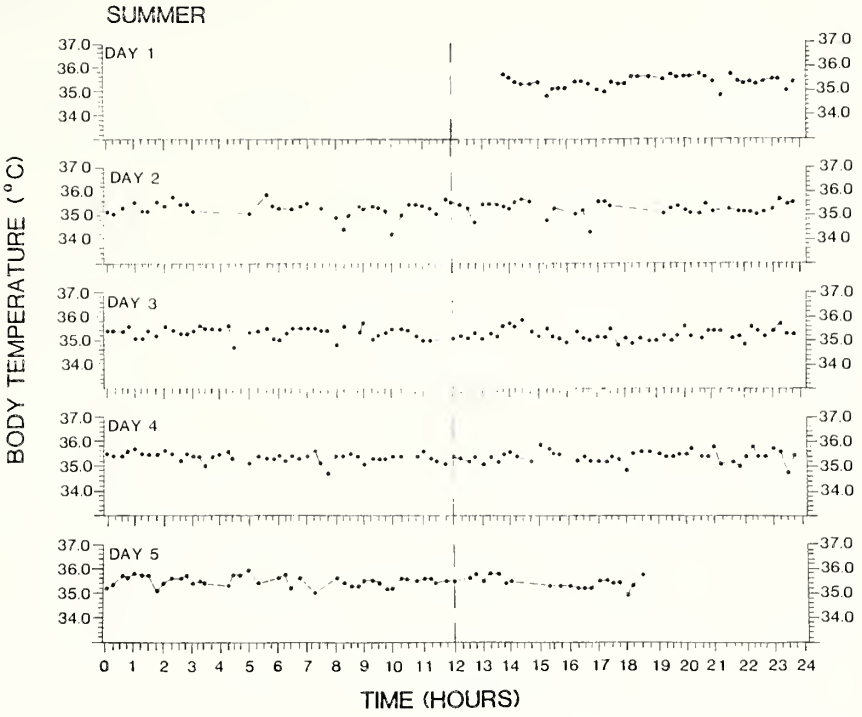

Fig. 4.—Core body temperature of one subadult *Blarina brevicauda* (18.15 g) monitored by radiotelemetry techniques during summer (7–11 August 1990) in a natural outdoor enclosure at Powdermill Biological Station. Average body temperature was 35.4°C based on 363 readings. Dashed lines represent period of malfunctioning transmitter or incomplete transmission of signal.

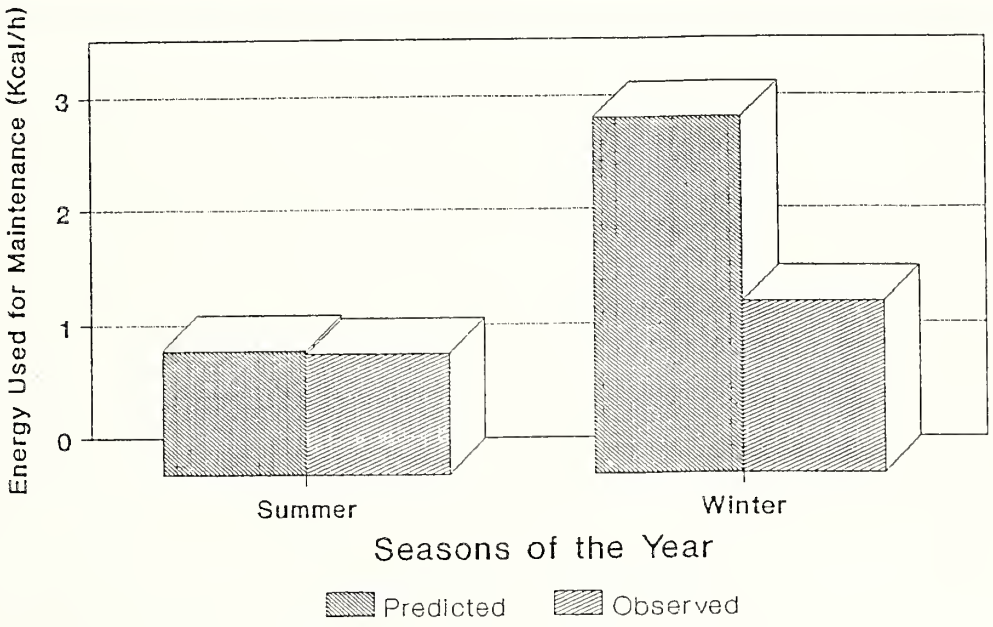

Fig. 5.—Predicted and observed energy used for maintenance during summer and winter in *Blarina brevicauda*. Values for predicted energy use are according to the model of Wunder (1975).

THE DEVELOPMENT OF THE SKULL OF *SUNCUS MURINUS*

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ABSTRACT

The ontogenetic changes of the shape of skulls of *Suncus murinus* were deseribed using 20- and 25-day embryos, newborn, and adult shrews. The length, width, and height of skulls and distances between specific points were measured in four embryonic stages (20-, 25-, 27-, and 29-day embryos) and four postnatal stages (newborn, 9-, and 14-day infants and adults). Most linear measurements of the skull reached 20%, 60%, and 90% of the adult value in 20-day embryos, neonates, and 14-day infants, respectively. The eye and the cochlear capsule developed early, whereas the growth of the mandible was retarded. The postglenoid grows profoundly after 14 days.

INTRODUCTION

The head of *Suncus murinus*, the musk shrew, has several unusual characters including a long and movable snout, small eyes, primitive ossified otic capsules, no zygomatic arch, double jaw articulation, and extraordinarily well-developed temporal muscles. An adult *Suncus* has a flat skull that is long and narrow (Fig. 1), whereas an early embryo has fundamentally different features (Fig. 3), such as a spherical head with relatively large eyes. We described skulls of three ontogenetic stages and adult *Suncus murinus*, and examined the development in five embryonic and three postnatal stages by analyzing the linear measurements of the cartilaginous and bony skulls.

MATERIALS AND METHODS

Relatively few studies on skull development of shrews have been reported (Parker, 1885; Ärnback Christie-Linde, 1907; Roux, 1907; de Beer, 1929), largely because the shrew is difficult to breed and maintain in captivity. We used musk shrews supplied by the Central Institute for Experimental Animals (Kanagawa, Japan), which keeps a colony of animals originally from Okinawa, Japan, and Tainan, Taiwan. The gestation period of *S. murinus* is 30 or 31 days. One 20-day and three 25-day embryos, one newborn, one 9-day, and one 14-day infants were fixed in 4% formaldehyde, stained with 0.01% Alcian Blue and 1% Alizarine red-S, and then cleared with 0.5–1% KOH and glycerol (Kelly and Bryden, 1983). Salivary glands, brown fat, and viscera, except eyes, were removed from skinned animals before staining and clearing. Two other embryos, which were larger than the 25-day embryo, were obtained from pregnant shrews captured in Taiwan. We estimated that the ages of these two embryos were 27 and 29 days. Five macerated skeletons were made from adult specimens which were trapped in Taiwan. The exact ages of these adults were unknown, but we plotted the adult measurements against 68 days post fertilization because *Suncus* is reported to reach adult weight between 30 and 40 days after birth (Shigehara, 1985). Records and images of specimens were retained as a database (Masuda and Yohro, 1990) in a microcomputer.

To quantify the growth of the skeletal system in *S. murinus*, a series of linear measurements was taken on lateral- and dorsal-plane photographs of cleared specimens and of dried skulls. To minimize distortions of measurements from photographs due to three-dimensional specimens, three photographs were taken in a stable condition at different times, dimensions were measured five times for each photograph, and the averages were calculated. Skull measurements, defined below and illustrated in Fig. 1, were defined in lateral view unless otherwise noted. Abbreviations are: GL, the greatest length of skull (distance between anterior tip of the snout and posterior end of the occipital bones); CBL, condylobasal length (distance from anterior edge of premaxilla to the most posterior projection of the occipital condyles); CB, cranial breadth (the greatest width of braincase, as seen in dorsal view); H, height (maximum height); E, diameter of an eye ball; CC, diameter of the cochlear capsule, as seen in ventral view; PG, postglenoid length (distance between posterior end of the occipital bones and glenoid fossa); FL, bony facial length (distance between anterior tip of the snout and posterior edge of the infraorbital foramen); ML, the distance between the tip of the lower incisor and posterior end of the angular process; HP, the greatest height of the mandible. More precise measurements could be taken on cleared skulls during the prenatal period by identifying six specific points (Fig. 2): AT, anterior tip of the snout; ET, the posterior end of the ethmoturbinale; AH, ala hypochiasmatica; PA, processus alaris; E, portion of the basal plate where the distance between the cochlear capsules is the narrowest; PE, posterior end.

RESULTS

Skeletal Development

Twenty-Day Embryo.—In the 20-day embryo (Fig. 3), the basic cranial structures have already been chondrified. The central stem has already chondrified with no visible separation between parts. The anterior nasal septum unites posteriorly with the parachordal plate, which is perforated by the foramen hypophyseos. The nasal septum is narrow and the parachordal region broadened in width posteriorly. The medial end of the ala hypochiasmatica, which will join the ala orbitalis in later

stages, and the processus alaris project on each side of the central stem. The medial end of the ala orbitalis has two branches, pila praeoptica and pila metoptica, which end freely. The former is short and relatively broad, and the latter is slender and directed to the ala chiasmatica. However, a considerable gap remains between the pila metoptica and the ala chiasmatica. Spherical cartilago pterygoideus is situated anterior to the processus alaris on both sides. The ala temporalis is chondrified anterolaterally to the processus alaris separately as a Y-shaped slender structure, but there remains a wide gap between the arms of the "Y." The cochlear capsule connects anteriorly with the commissura alicochlearis, which unites with the processus alaris to form the lateral border of the carotid foramen.

In lateral view, the lamina parietalis lies dorsal to the otic capsule and connects anteroventrally to the otic capsule with the associated commissura parietocapsularis and posteriorly to the pila occipitale with its commissura parieto-occipitalis. However, there is no connection between the lamina parietalis and the ala orbitalis in the 20-day embryo.

The tectum nasi (nasal roof) has already chondrified and fully continued ventrally to the paries nasi, whereas the paries nasi (wall of the nasal capsule) and the solum nasi (nasal floor) are not completely developed. In the solum nasi, the lamina transversalis anterior, cartilago paraseptalis, and the lamina transversalis posterior are visibly separated from anterior to posterior. The lamina transversalis anterior connects anteriorly to the nasal septum, whereas the lamina transversalis posterior connects laterally to the paries nasi. The middle portion of the nasal skeleton has practically no floor, thus resulting in an extensive fenestra basalis. Posteroventral to the nares, three pairs of fringes project from the midventral line. On the dorsal aspect, the processus alaris superior projects ventrocaudally from the cupula anterior. The paries nasi connect to the ala orbitalis and with the associated commissura orbitonasalis.

The cochlear capsule is almost chondrified, but the canalicular part has chondrified only the portion surrounding the semicircular canals. The basal plate and the cochlear capsule are connected to the thin commissura basicapsularis anterior and the commissura basicapsularis posterior.

The caudolateral corner of the parachordal plate gives rise to the pilae occipitale. Relatively broad cartilaginous plates lie on the upper ends of the pila occipitale. We have not identified a separate chondrification center of this structure, tentatively identified as the supraoccipital cartilage, which is separated from the otic capsule by the fissura occipito-capsularis superior. The supraoccipital cartilage on both sides is medially suspended by a slender cartilaginous thread, which originates at the flexion between hindbrain and midbrain. This slender bridge, which can be observed only for a short period, soon disappears at the middle portion but remains as a slender process on both sides from the supraoccipital cartilage.

The premaxilla, the maxilla, the frontal, the parietal, and the squamosal are already present. The squamosal has begun ossifying from the anterior portion, which contributes to the articular facets. The lower jaw is first formed by the Meckel's cartilage, which articulates with a small incus, then the second, osseous jaw forms laterally to the Meckel's cartilage, starting anteriorly. The Meckel's cartilages unite anteriorly into a pointed synchondrosis. The stapes is chondrified in most parts except at the basis stapedius. A slender secondary cartilage is present at the site of the coronoid process of the mandible.

Twenty-Five-Day Embryo.—By 25 days, further chondrification and ossification of the embryo has occurred (Fig. 4). A pair of spherical cartilages is found between the pila metoptoica and the central stem, and the processus alaris has grown laterally to join with the commissura alicochlearis, the processus ascendens, and the processus pterygoideus of the ala temporalis. A small slit, which does not stain well with Alcian blue, can be seen between the ala temporalis and the other two cartilaginous elements. The median head of the ala temporalis gives rise to a tiny forward projection. The cartilago pterygoideus attaches dorsally to the ossified pterygoid dorsally. A small secondary cartilage is evident at the anterior portion of the pterygoid. The commissura basicapsularis is separated by a foramen into commissura basicapsularis anterior and commissura basicapsularis medialis.

The premaxilla and maxilla expand their ossifications and the underlying cartilaginous paries nasi are becoming resolved. The sulcus of the nasolacrimal duct remains between the lamina transversalis anterior and the paries nasi. The ethmoid plate starts to chondrify from the tectum nasi downwards, and the turbinals have begun developing.

All dermal bones, nasal, palatine, vomer, lacrimal, and pterygoid, are ossifying. Chondral ossification has begun in the exotympanic, basioccipital, and exoccipital. The supraoccipitale has already ossified by 25 days; however, whether it ossifies cartilaginously or dermally is unclear. In mammals the supraoccipital is supposed to be ossified from a broad cartilaginous band which makes the dorsal border of the foramen magnum, whereas in *Suncus* a series of cartilaginous islands is seen in the 20-day but not in the 25-day embryo. The ossification of the exoccipitale extends to the lateral edge of the hypoglossal foramen. Slender secondary cartilages are seen at the tip of coronoid process, condylaris, and angularis of the mandible. Upper and lower incisor development are visible as calcification of dentin.

Newborn.—In the skull of newly born musk shrew (Fig. 5), most parts have ossified and the cartilaginous portion has degenerated, but borders of most bones still can be distinguished. The following structures remain cartilaginous in this stage: nasal skeleton, interorbital septum, parietal plate, canalicular part of the otic capsule, commissura basicapsularis medialis, most of the styloid process, connection between the processus alaris and the alisphenoid, part of the basal plate between the basisphenoid and the basioccipital, commissura basicapsularis posterior, and base of the pilae occipitale between the basioccipital and the exoccipital. The cartilaginous nasal capsule is resolved on its dorsal surface because of the ossification of the frontal and the parietal, whereas the turbinal area and the anterior rostrum remain cartilaginous. The parietal plate degenerates anteriorly and ossifies independently to form a part of the occipital bones (indicated by an asterisk in Fig. 6), which is covered laterally by the squamosal and visible only in the separated occipital bones of a macerated skull. The

Meckel's cartilage is still present and articulates with the incus; however, anterior to the tooth row the cartilaginous bar has disappeared from the lingual surface of the mandible. Secondary cartilages of the mandible broaden and form the distal ends of the three processes.

Ossifications are seen in the basisphenoid, alisphenoid from the ala temporalis, orbitosphenoid from the ala orbitalis, cochlear capsule, goniale, crus longum of incus and collum mallei, and the tips of turbinals. The long and slender hamulus of the pterygoid projects posteriorly. The ethmoid plate begins ossifying at the middle. The squamosal has two facets to articulate with the coronoid process of the mandible. The goniale is a small spicule of bone lying close to the ventral border of the Meckel's cartilage. The ossification of the dorsal border of the foramen magnum, presumably the supraoccipital, proceeds radially and anteriorly. The interparietal is absent, as is any remnant of the jugal.

Adult.—Only features that differ between embryos and adults will be mentioned here because Sharma (1958), Dötsch (1982, 1983*a*, 1983*b*) and Inamura et al. (1984) have already described the adult skull of *Suncus murinus* in great detail. In the adult skull most bones are fused and only a few sutures can be recognized, such as the spheno-occipital, the parieto-occipital, and the parieto-squamosal sutures. The general shape of the skull is flat and long (Fig. 6), the bones are thick, and the sagittal crest, the lambdoid crest, the lateral crest, the zygomatic process of the maxilla, and the paroccipital process are well-developed. There is a great gap between the squamosal and the zygomatic process of the maxilla, and the orbital fossa and the temporal fossa are confluent. The jugal, the zygomatic arch, and the auditory bulla are absent, and the tympanic remains a ring throughout life. The first upper incisor develops a large, hook-like crown and the comparable lower incisor is also well-developed and curved upward. A part of the cartilaginous nasal skeleton projects anterior to the premaxilla. The prominent coronoid process of the mandible flares posterodorsally and laterally, whereas the angular process extends posteriorly as a delicate spicule. The condylar process is short with ventral and dorsal facets.

Differential Growth Rate During Ontogeny

Most measurements of the skull increased linearly with age, and reached 90% of the adult value by 14 days after birth. Measurements were plotted against age in Fig. 7. In the 20-day embryo and in the newborn, most cranial values (greatest length, condylobasal length, cranial breadth, postglenoid length, and facial length) were about 20% and 55% of adult values, respectively. Regressions of cranial measurement (CBL, CB, H) against age showed that condylobasal length increased with age with a slope of 0.80, whereas the cranial breadth and cranial height showed much lower slopes of 0.34 and 0.14, respectively.

The diameter of the eye ball achieved 59% and 80% of the adult size in the 20-day embryo and in the newborn respectively, whereas auditory organs (CC and TT) showed about 37% and 88% of development by that time. The slope of the regression line of the eye was very small (0.017), but the eye continued to increase in size until adulthood. The mandibular measurements (ML and HP) were 10% and 50% in the 20-day embryo and the newborn, respectively. The slope of the regression line of the length of the mandible against age was 0.37, which was the same as that of the bony facial length of the skull. The height of the mandible had a slope of 0.27, which was twice that of the cranial height.

The postglenoid length was only 63% of the adult value in the 14-day infant, although it had showed similar percentages as the other skull measurements in the 20-day embryo and newborn. The proportion of PG to the condylobasal length decreased from 50% in the 20-day embryo to 25% in the 14-day infant, but then increased again to 38% in the adult. In the postglenoid region, the proportion behind the commissura basicapsularis medialis decreased from 16.3% to 11.9% between the 25-day embryo and the newborn (Fig. 8).

Growth rates of different parts of the cartilaginous basicranial axis varied extensively (Fig. 8). Between the 20-day embryo and the 25-day embryo, every part except the facial region, which is the distance between AT and ET, increased in proportion to total length, whereas parts of the facial region decreased. However, between the 25-day embryo and the newborn, only the distance between AT and ET increased its proportion (from 0.4% to 1.1%) and contributed to the lengthening of the skull. By contrast, the proportion of bony facial length to condylobasal length consistency remained about 50% during development.

Discussion

According to previous studies on the growth of *S. murinus* (Dryden, 1968; Shigehara, 1980, 1985), early postnatal development is rapid, but this animal is thought to be born in a relatively undeveloped condition (Shigehara, 1985). We have shown here that most linear measurements have reached 60% of adult values in newborn and 90% values by postnatal day 14. However, not all parts of the skull appear to grow at an equivalent rate. Sensory organs such as the eyeball and cochlear capsule began developing early and also stopped growing earlier than other skull features. In the adult, eye balls are small (diameter of 1.64 mm in the adult), the auditory region lacks bony bullae, and the tympanic rings are exposed without any bony supports.

By contrast, the mandible starts its growth later than the skull, but develops well. Markedly long and slender angular processes and well-developed coronoid processes were observed in the adult. Among the measurements, the height of the mandible did not reach 90% of the adult value by 14 days after birth, which means that the coronoid process continues to increase its size after postnatal day 14. This observation agrees with the experimental data, which showed that the development of the coronoid process depends on the external stress of the masticatory muscles (Washburn, 1947). The retardation of the growth of the mandible in early postnatal stages can be explained by the retardation of the development of the masticatory muscles, because in newborn *Suncus*, ratios of the masticatory muscles against those of the adult are very low (Yamada and Yohro, 1988); 1.46% (masseter muscle), 1.43%

(temporal muscle), 3.16% (medial pterygoid muscle), 7.53% (lateral pterygoid muscle), 2.74% (digastric muscle), compared with those of *Mus musculus* (house mouse); 8.68, 10.76, 10.55, 13.59, and 21.00%, respectively.

Fearnhead et al. (1955) showed that the ratio of the postglenoid length against the condylobasal length is markedly high in the Soricidae, with an average of 41.84%. In this study, we showed that the ratio of the postglenoid length against the condylobasal length decreased from the 20-day embryo to the 14-day infant but increased thereafter. Postnatal growth of the postglenoid length is more pronounced than that for the face. The increase in length of the postglenoid beyond 14 days after birth does not depend on the elongation of the cranial base, but on the growth of the postcochlear region. The paroccipital process developed as an insertion for the pars cephalica of the trapezius muscle. The squamosal and the parietal are elongated and contributed to increase the area for insertion of temporal and masseter muscles.

Consequently, different parts of the skull develop in different stages—the sensory organs developed in the prenatal stages, the skull height and the basicranial region elongated around birth, and bony additions occurred in the postglenoid region and mandible after postnatal day 14. In newborn animals, skull length, skull height, and postglenoid length have reached about 50% of adult values. The width and facial length, in contrast, were 61% and 68% of their adult size, respectively. Growth in the transverse direction is limited after birth and, as a result, the skull gains a more slender appearance as development progresses toward adulthood.

Acknowledgments

We thank T. Hijikata (Department of Anatomy, Tokyo University) for providing cleared postnatal specimens, S. Kuratani (Department of Biochemistry, Baylor University) for comments on the description of the chondrocranium of the musk shrew, T. Sakai (Department of Anatomy, Juntendo University) for suggestions in the early stages of this study, and A. W. Crompton (Museum of Comparative Zoology, Harvard University) for comments.

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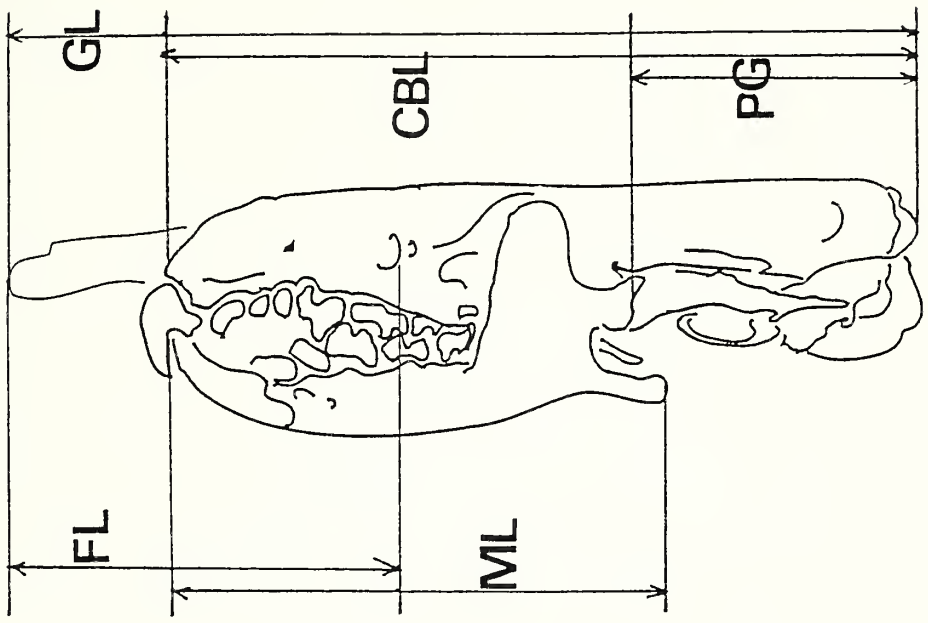

Fig. 1.—An adult skull of *Suncus murinus* from lateral view with specific points for measurements. See text for abbreviations.

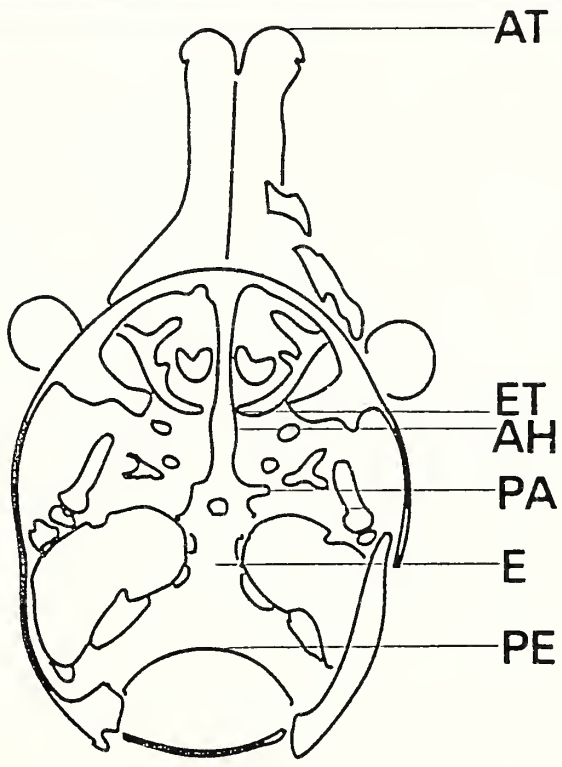

Fig. 2.—A chondrocranium of the 20-day embryo of *Suncus murinus* from dorsal view with specific points for measurements. See text for abbreviations.

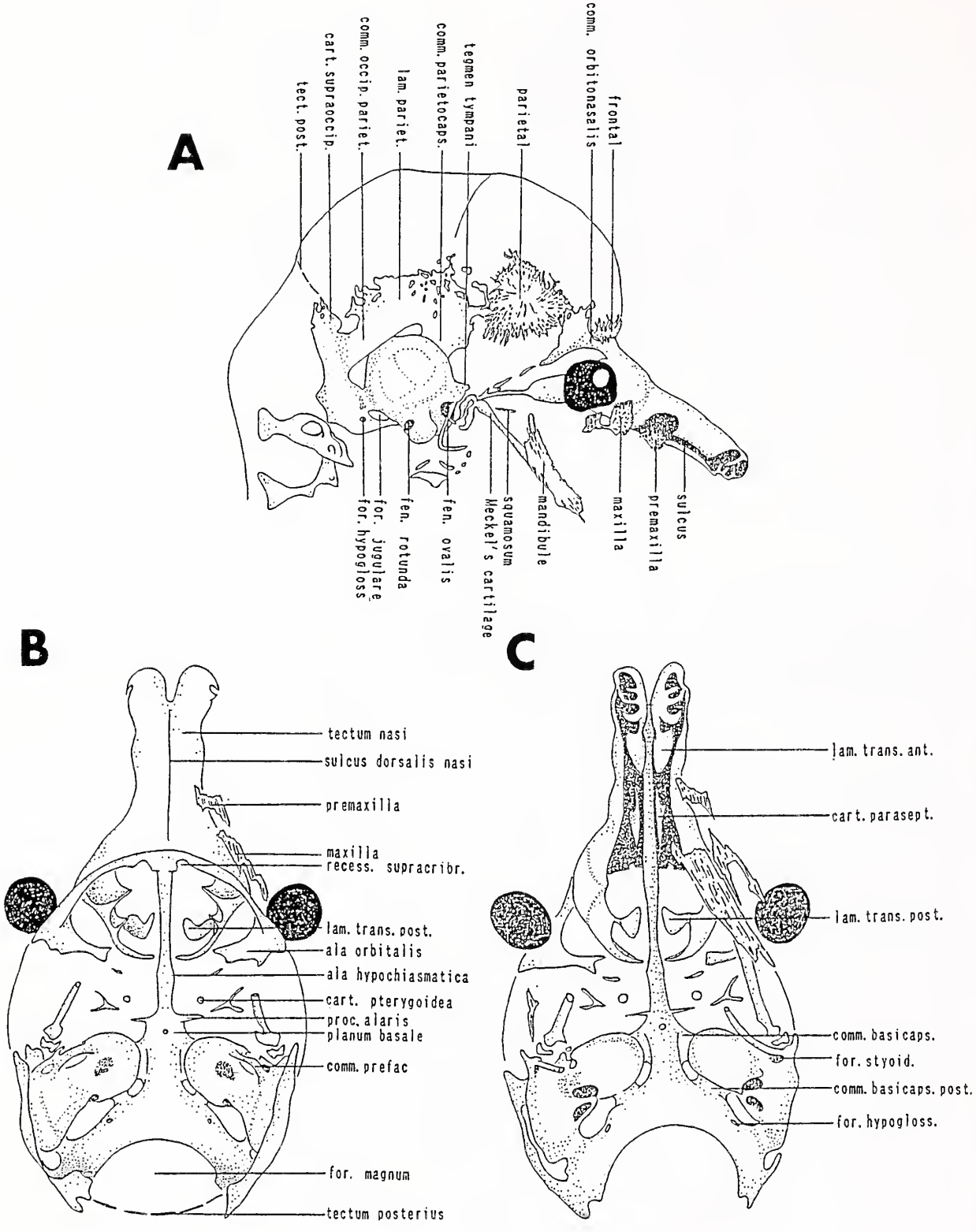

Fig. 3.—Skull of a 20-day embryo of *Suncus murinus*. Drawings of a cleared specimen in lateral (A), dorsal (B), and ventral (C) aspects.

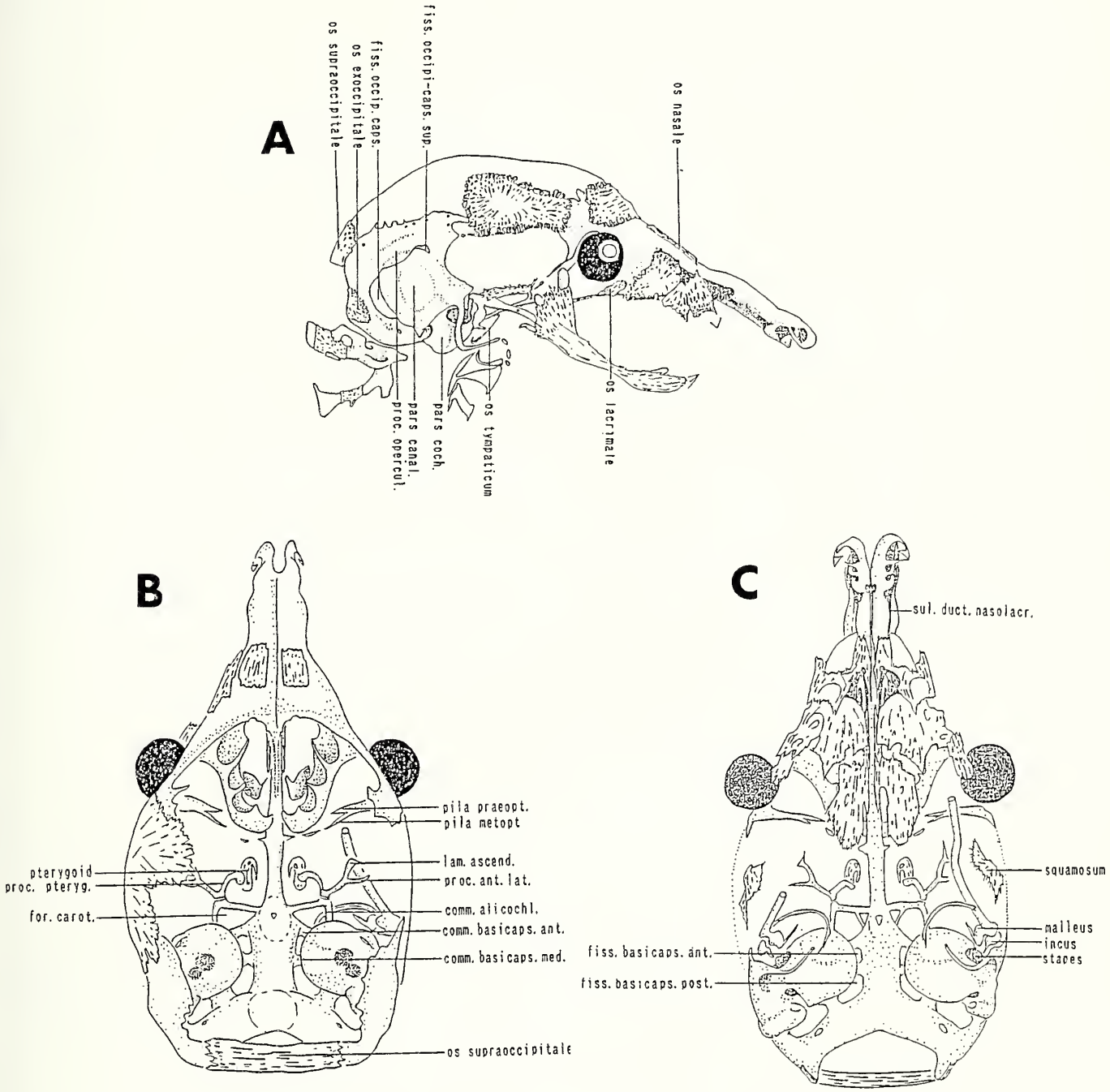

Fig. 4.—Skull of a 25-day embryo of *Suncus murinus*. Drawings of a cleared specimen in lateral (A), dorsal (B), and ventral (C) aspects. Right parietal and the anterior part of Meckel's cartilage are removed.

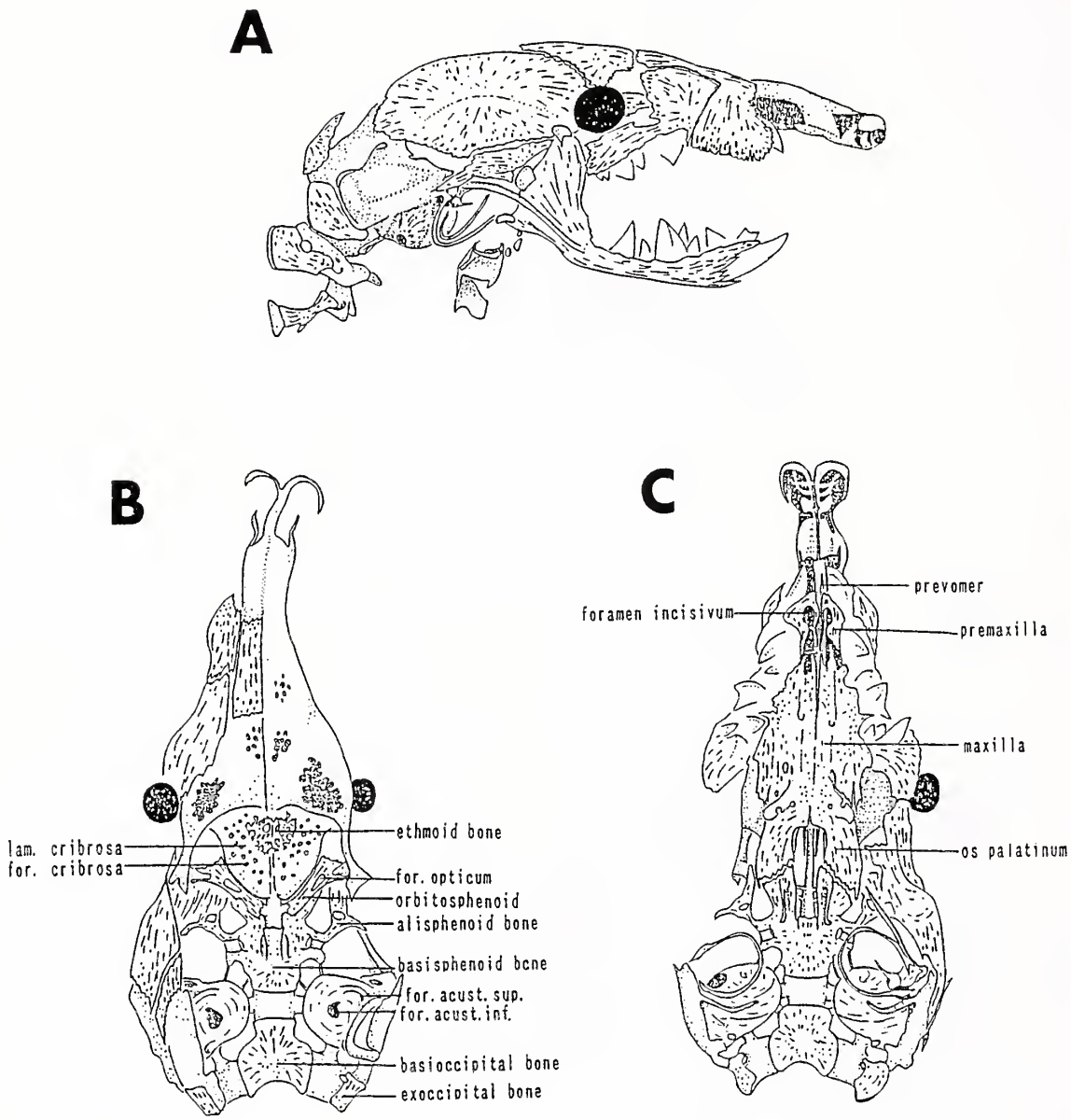

Fig. 5.—Skull of a newborn *Suncus murinus*. Drawings of a cleared specimen in lateral (A), dorsal (B), and ventral (C) aspects. Dorsal bones except a part of left side are removed.

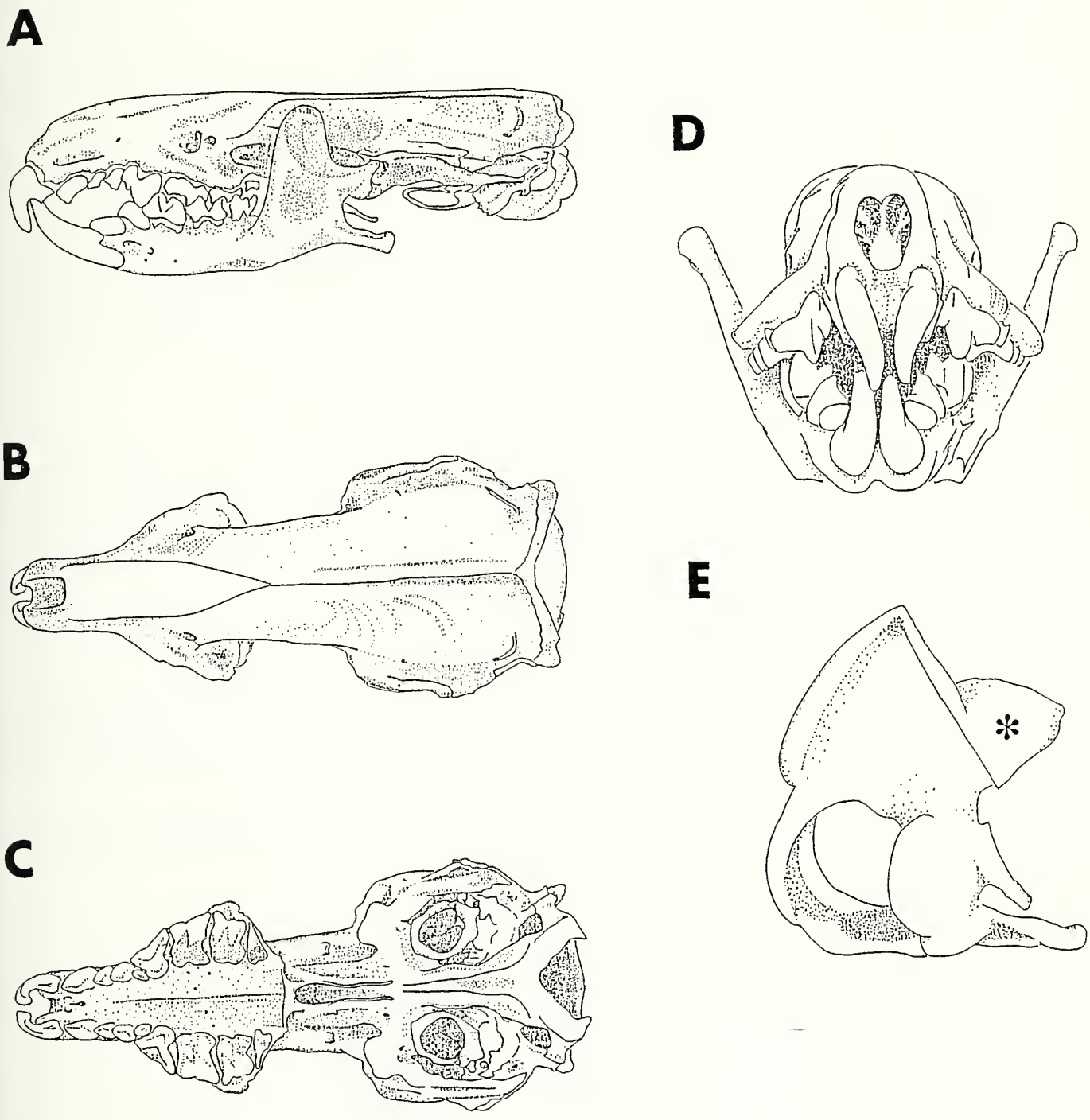

Fig. 6.—Skull of an adult male *Suncus murinus*. Drawings of a macerated skull in lateral (A), dorsal (B), ventral (C), and anterior (D) aspects. E: Posterolateral aspect of the right side of an occipital complex in a young *Suncus*. The asterisk indicates the anterior wing of an occipital bone, which is covered by the squamosal laterally and cannot be seen from outside. The anterior of the occipital bone can be observed only in the macerated skull of a young animal.

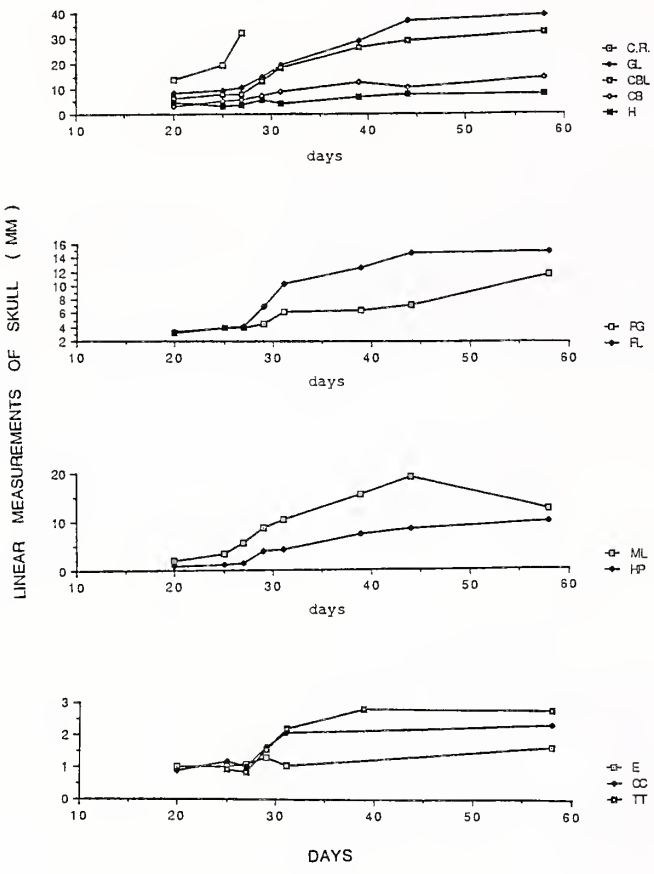

Fig. 7.—Linear measurements (mm) of skulls of *Suncus murinus* against age (gestation day). CB, condylobasal length; CC, diameter of a cochlear capsule; CBL, condylobasal length; C.R., cranio-rostral length; FL, facial length; GL, greatest length; E, diameter of the eye; HP, mandibular length; ML, mandibular height; PG, postglenoid length; TT, diameter of a tympanic ring.

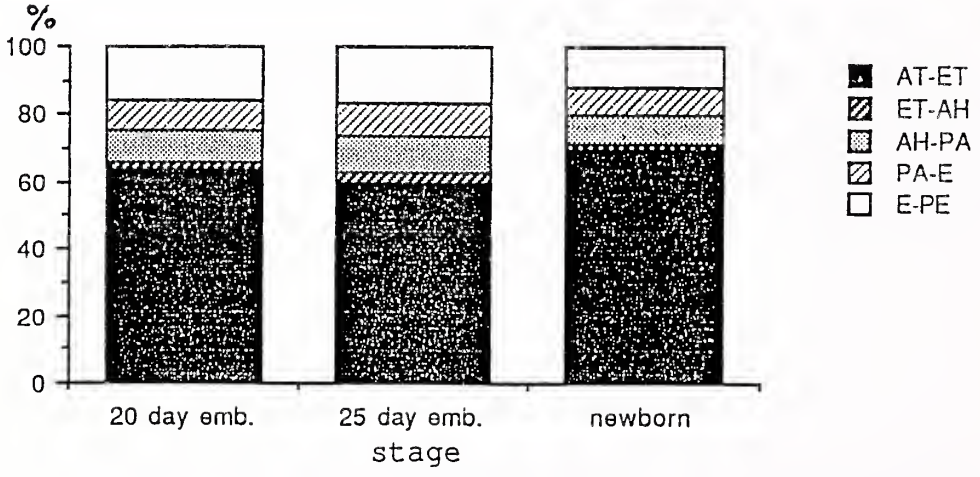

Fig. 8.—Proportions long axial segments in *Suncus* chondrocranium. AH, ala hypochiasmatica; AT, anterior tip; E, eye; ET, ethmoturbinal; PA, processus alaris; PE, posterior end.

CHARACTERISTICS OF THE BREEDING SEASON IN THE COMMON SHREW (*SOREX ARANEUS*): MALE SEXUAL MATURATION, MORPHOLOGY, AND MOBILITY

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ABSTRACT

A population of *Sorex araneus* near Oxford, England, was studied during the breeding season of 1990. Several phenotypic traits that may potentially influence male mating success were monitored among marked individuals. These included morphological characteristics such as body size, testes size, sperm count, seminal vesicle size, and lateral gland length; also, timing of sexual maturation, relative mobility, and parasite load were examined. Male body mass increased significantly between March and April, and was strongly correlated with body length in May, when both body mass and length were also correlated with seminal vesicle mass (an indicator of androgen activity). Body length in May was negatively correlated with gut parasite load. Early maturing males were found to develop the largest testes but had relatively small lateral glands in May. Male shrews were significantly more mobile than females during the breeding season; individual mobility was associated with body size in both sexes, and with testes size among males.

INTRODUCTION

Little is known about the mating system of the common shrew (*Sorex araneus*). Behavioral studies in the field are essentially limited to an old fashioned live-trapping methodology (the species is too small for radio collars), and in captivity, common shrews are not easily maintained and bred (Mercer and Searle, 1994). Nevertheless, common shrews are unlikely to be more difficult to study than any other shrews of the subfamily Soricinae, which comprises some 102 species (Hutterer, 1985). The common shrew itself is one of the most abundant small mammals in the northern Palearctic region. Furthermore, this species is one of the few mammals for which it has been demonstrated unambiguously that, in nature, multiple paternity can occur within a single litter (Searle, 1990; Tegelström et al., 1991).

In this paper we review what is known about the breeding season of the common shrew, based largely on long-term mark-release-recapture studies (for behavioral analysis), and systematic snap-trap collections (for studies of reproductive physiology). Attributes of the breeding season in this species vary somewhat according to geographical location; the emphasis in this paper, however, is on common shrews in southern Britain. We also present the results of our own initial field studies which are more specifically directed towards an understanding of the mating system of the common shrew. Given that multiple paternity occurs in this species, we are particularly interested in competition among males for mates and the morphological and behavioral characteristics which may maximize male mating success.

Characteristics of the Breeding Season in the Common Shrew

The common shrew, a seasonal breeder, has a long immature phase when males and females are extremely similar in their behavior and morphology (Michielsen, 1966; Buckner, 1969; Searle, 1985), followed by a relatively short adult phase, when sexual dimorphism becomes apparent. Thus, in Britain, almost all individuals become sexually mature in the spring following their birth, and die within the same year (e.g., Adams, 1910; Middleton, 1931; Brambell, 1935).

With a gestation period of 20 days, a lactation period of about 23 days, and a postpartum estrus (e.g., Dehnel, 1952; Searle, 1984*a*), females could potentially produce numerous litters of up to ten young (see Mercer and Searle, 1994) during the March–October breeding season (Middleton, 1931; Brambell, 1935; Crowcroft, 1957; Michielsen, 1966). In reality, however, it is the first two or three litters which are the most important; adult females become scarce and erratic breeders thereafter (Brambell, 1935; Tarkowski, 1957).

Onset of Sexual Maturity.—It is generally agreed that male common shrews attain sexual maturity (as defined by presence of sperm in the testes) three to four weeks before females have their first recognized ovulation (Brambell, 1935; Crowcroft, 1957; Michielsen, 1966; Skarén, 1973). In southern Britain, some males reach maturity in March (Brambell, 1935), and first conceptions occur in late April or May (Brambell, 1935; Crowcroft, 1957; Searle, 1984*b*) with a high degree of synchrony of the first estrus within a particular locality (Brambell, 1935; Tarkowski, 1957).

Features associated with the onset of sexual maturity include an increase in body size (Adams, 1910; Brambell, 1935; Michielsen, 1966; Shillito, 1963*a*), and onset of the spring molt (Crowcroft, 1957; Shillito, 1963*a*; Skarén, 1973). In addition, sexual maturity of males is characterized by rapid growth of the testes and accessory sexual organs (Middleton, 1931; Brambell, 1935) and maximal development of the lateral glands (Crowcroft, 1957; Michielsen, 1966; Searle, 1985).

The body weight at which sexual maturity is reached has been reported as ranging from 7.7 g to 9 g (Middleton, 1931; Brambell, 1935; Crowcroft, 1957; Shillito, 1963*a*; Michielsen, 1966). Adult males and nonpregnant parous females ultimately attain a body mass of around 12 g (Brambell, 1935). Adult

body length ranges from about 70–85 mm among common shrews in Britain (Crowcroft, 1957).

From birth until the end of February the testes are minute, weighing less than 5 mg combined (Brambell, 1935). They develop rapidly, however, and become evident externally as a bulge at the base the tail by March or April (Crowcroft, 1957). By the end of April the testes are fully grown (Brambell, 1935) with a combined fresh weight in excess of 200 mg (Middleton, 1931; Garagna et al., 1989).

The increased androgen production associated with development of mammalian testes is known also to influence development and activity of sebaceous scent glands (Clarke and Frearson, 1972; Yahr et al., 1979). In the common shrew, lateral glands (situated on either side of the body) develop into large active structures at sexual maturity in the male (but not the female: Searle, 1985), producing a characteristic odor (Crowcroft, 1957; Michielsen, 1966; Skarén, 1973). In older males the skin around the lateral glands and over the testes may become bare (Searle, 1985; Mercer and Searle, 1994).

Range and Movements.—In addition to these physical changes associated with sexual maturity, there are also modifications of behavior. In particular, changes in the range and movements of individuals have been revealed by live-trapping studies. Over the winter months, immature animals generally have nonoverlapping and stable home ranges of approximately 30 m diameter (Shillito, 1963*b*; Michielsen, 1966; Buckner, 1969). The dimensions of the home range may vary according to vegetation type, but within one population, males and females have ranges of similar size (Buckner, 1969; Michielsen, 1966).

With the onset of sexual maturity, females do not drastically modify their movements, but males become very active and may abandon their original home ranges (e.g., Shillito, 1963*b*; Michielsen, 1966; Churchfield, 1980). During spring and summer the male shrews are generally regarded as nomadic. Shillito (1963*b*), for example, reports a range of up to 144 m in diameter, and the majority of males on her study site disappeared from the area, temporarily or permanently, as a result of their ranging behavior. It is uncertain, however, whether males are truly nomadic, or merely establish large, stable home ranges.

Determinants of Male Mating Success

On the basis of current understanding of morphology, development, and behavior of the common shrew during the breeding season as reviewed above, several characteristics emerge as potentially important in determining male mating success. One such factor is individual timing of maturation relative to other males. Among other species, advantages established among early maturing individuals (for example, with respect to body size) may be maintained or exaggerated, as competition commonly prevents compensatory growth among those maturing later (Clutton-Brock, 1988). Relative adult body size may be an important determinant of mating success among common shrews if the aggressive behavior between adult males in captivity (Moraleva, 1989) is expressed during competition for mates.

Although less well-studied among mammals than body size, variation in testes size may also influence the outcome of male competition for mates. It is now realized, for example, that male fertilizing capacity may be limited under certain circumstances (Dewsbury, 1982; Small, 1988) and that sperm competition is widespread among mammals (Ginsberg and Huck, 1989; Møller and Birkhead, 1989). The testes of the common shrew are considerably larger than expected for a typical mammal of its size, implying that sperm competition has been influential in their evolution (Kenagy and Trombulak, 1986). Testes size or sperm count (or both) may therefore correlate with insemination success.

The activity of the lateral glands may also have some influence on the mating success of male common shrews. Although the function of the lateral glands is uncertain in shrews, sexual selection has apparently influenced the relative size and activity of particular (sexually dimorphic) sebaceous glands in other mammals (Jannett, 1986). Male mobility may also be a sexually selected trait when females are widely distributed in space (Schwagmeyer, 1988), as is typically the case among populations of the common shrew.

Here, in a step toward a more detailed understanding of the mating system of the common shrew, we explore the way in which these variables are related, based on our preliminary study of common shrews in a population in southern Britain.

Study Area and Methods

The study site, a 2-ha strip of rough grassland on Little Wittenham Nature Reserve, Oxfordshire, England (Ordnance Survey grid reference: SU567/932), was bounded by a river to the north and a road to the west, grazed meadow to the south and a larger area of mixed woodland to the east. In addition to common shrews, several species of small mammals were recorded at the site: moles (*Talpa europaea*), pygmy shrews (*Sorex minutus*), woodmice (*Apodemus sylvaticus*), and bank voles (*Clethrionomys glareolus*). Likely predators at the site included a kestrel (*Falco tinnunculus*), seen regularly over the area, and domestic cats from nearby houses.

The first period of live trapping was conducted between 19–30 March 1990. The study area was divided into two overlapping areas, each of which was trapped for five consecutive days using 96 numbered Longworth traps provided with hay bedding and set in a grid at approximately 10-m intervals. Puparia of *Calliphora* (killed by freezing, see Little and Gurnell, 1989) were used as bait. Traps were locked open at night, except for one night during each five-day trapping period, when traps were baited additionally with approximately 15 g of moist minced ox heart. During the day, traps were visited at 1–2 h intervals between 0700 h and 1900 h. When set overnight, traps were emptied at 0530 h. No trap deaths occurred with this regime.

All common shrews were weighed, sexed, and the body length and tail length measured. These latter measurements were difficult to make on live animals under field conditions, and although results were consistent, our measurements of body length of live animals are not necessarily directly comparable with those of dead animals. The degree of sexual maturation

and stage of molt were noted. Each animal was individually marked by toe clipping and released.

Males were subsequently ranked with respect to timing of sexual maturation. Ranking was based on relative size of the testes bulge, stage of spring molt, and body size during late March. In general, these parameters were closely associated with one another. Shared ranks were assigned where no clear differences were evident.

There were insufficient data to calculate accurate home-range areas but the relative mobility of shrews captured four or more times was estimated using three parameters: the farthest distance between any two (of four or more) capture points (FD), the farthest distance between any of the first four capture points (FD[4]), and the mean distance moved between four or more consecutive captures (MDM). In addition, distances moved between consecutive captures were classified either as zero (animal recaptured in same trap as previous capture), short (animal recaptured 10–19 m from previous capture point), medium (animal recaptured 20–29 m from previous capture point), or long (animal captured 30 m or more from previous capture point).

Traps were removed on 30 March and the population left undisturbed until around the time of first estrus, which was determined by the first occurrence of nape scars (an indication of mating, see Crowcroft, 1957). Previous studies in Oxfordshire indicate a high level of synchrony among females within a site with respect to first conception (Searle, 1984*b*).

During April (23–27), traps were replaced in their original positions over four consecutive nights, again baited with moist minced ox heart and opened at 0530 h. All male common shrews captured were weighed, their position of capture noted, and then transferred to captivity. These animals were sacrificed between 28 April and 7 May to provide detailed information on their reproductive condition, body size, lateral gland size, and parasite load. Each was weighed, and measurements of body length, tail length, combined lateral gland length, and fresh mass of the testes were recorded. Sperm counts were made on the right epididymis by a method derived from Searle and Beechey (1974). The sperm count is given in terms of the total number of sperm in the caput epididymis. Fresh mass of the seminal vesicle was recorded as an indicator of androgen activity (Grocock and Clarke, 1974). Males were ranked according to relative number and size of cestodes and nematodes in the intestine.

Statistical Analysis

Parametric distributions were assumed for all characters except maturity and parasite load. Product-moment correlation coefficients, regression equations, and t-tests were used for parametric data; Spearman rank correlation coefficients were used for nonparametric data; and two-tailed tests were used throughout.

Results

Morphology During the Breeding Season

During March, 26 common shrews were captured and individually marked. Mean male body mass (±SE), 8.5 ± 0.2 g (n = 11), and mean female body mass, 7.5 ± 0.1 g (n = 15), differed significantly at this time (t = 5.11, d.f. = 24, P < 0.001), while body length, 71.2 ± 1.8 mm and 71.3 ± 1.5 mm for males and females, respectively, did not. There was no significant correlation between body mass and body length during March for either sex.

In April, body masses had increased significantly (males: t = 5.52, d.f. = 17, P < 0.001; females: t = 31.21, d.f. = 14, P < 0.001). Furthermore, male and female body masses remained significantly different (t = 3.10, d.f. = 15, P < 0.01). The mean body mass increase for nine recaptured males over this period was 1.5 ± 0.3 g and the mean body mass overall 10.2 ± 0.3 g (n = 11). The mean female mass increase was 1.4 ± 0.2 g and the mean body mass 9.0 ± 0.3 g (n = 9).

Correlations between male morphological characters measured throughout the breeding season are presented in Fig. 1. There are three values for body mass; those recorded in late March, late April, and early May, respectively. The May values (recorded after a short period of maintenance in captivity) are significantly correlated with body mass measured during March (r = 0.76, n = 9, P < 0.05), but not during April (note, however, that the mean body mass values during late April, 9.56 ± 0.22 g, and early May, 10.20 ± 0.33 g, were not significantly different). In contrast with the March data, however, male body masses in May were strongly correlated with their body lengths (r = 0.81, n = 11, P < 0.005). Both body mass and length in May were significantly correlated with seminal vesicle mass (body mass: r = 0.68, n = 11, P < 0.05; body length: r = 0.89, n = 11, P < 0.0005). Testes mass in May was correlated with body mass in April at the time of recapture (r = 0.70, n = 9, P < 0.05) but not with body mass in May after a short period of maintenance in captivity. Testes mass of these sexually mature individuals was not correlated with seminal vesicle mass or sperm count. Lateral gland length was not correlated with adult body size or seminal vesicle mass, but was negatively correlated with body mass increase between March and April (r = 0.80, n = 11, P < 0.05) and positively correlated with sperm count (r = 0.60, n = 11, P < 0.05).

Mobility During the Breeding Season

Individual shrews were caught between one and 14 times each. The number of captures per trap hour did not differ significantly for males and females. Measures of mobility are based on 16 individuals that were captured on four or more occasions during late March.

During March, male shrews were found to be significantly more mobile than females. Mean farthest distance moved between any two of the first four captures (FD[4]) for males was 38 ± 5 m, and for females 20 ± 4 m (t = 2.98, d.f. = 14, P < 0.01). Mean distance moved between consecutive captures was 25 ± 3 m for males, and 12 ± 2 m for females, (t = 3.65, d.f. = 108, P < 0.001). Mean farthest distance moved between any two capture points (FD) for males was 59 ± 12 m and for females 25 ± 7 m (t = 1.89, d.f. = 14, P < 0.1). Maximum recorded distance moved between consecutive captures for males was 100 m, and for females 43 m. In

general, males made a greater proportion of long distance movements (>30 m) between consecutive captures, whereas females were more likely to be captured in the same trap on consecutive occasions (Fig. 2a, b; $\chi^2 = 13.27$, d.f. = 3, $P < 0.01$).

The mean distance moved between the March and April trapping periods was also calculated for the 18 marked shrews that were recaptured. Again males were found to have moved considerably greater distances than females. The mean distance moved from last capture in March to the first capture in April was 58 ± 11 m for males and 20 ± 6 m for females ($t = 2.66$, d.f. = 16, $P < 0.02$). All females recaptured in April were found within 30 m of the area in which they had been captured during March (although several females were absent in April and may therefore have moved longer distances off the study site). Of nine recaptured males, three were found within 30 m of the area where they were last captured in March. Two of these males were unusual in several respects. The first was the latest male to reach maturity and showed no mass increase over April. In May, this male was relatively small, had relatively small seminal vesicles and testes, but had well-developed lateral glands. The second male was also relatively small, with small seminal vesicles; additionally, this male had the highest gut parasite load among those examined. The greatest distance moved by any recaptured male from its last point of capture was 110 m. Two marked males were not recovered from the study site.

Timing of Sexual Maturation

Early maturing males were found to have attained the greatest testes masses in May (Spearman rank correlation coefficient $r_s = 0.83$, $n = 9$, $P < 0.02$) but they also had the smallest lateral glands ($r_s = 0.71$, $n = 9$, $P < 0.05$). Male maturity rank was not correlated with mobility scores during March or with distance moved between the March and April trapping sessions.

Morphology and Mobility

There was a strong trend during March for the heaviest males to move the greatest distances between any two of their first four capture points (FD[4]: $n = 8$, $r^2 = 0.477$, $F_{1,8} = 5.47$, $P = 0.06$). No such trend was found among females. Male body mass (March, April, May) was not correlated with the distance moved between March and April trapping sessions. There was, however, a strong trend for males with the largest testes to move the greatest distances during this period ($n = 8$, $r^2 = 0.412$, $F_{1,8} = 4.93$, $P = 0.06$). Body length was correlated with farthest distance moved during March (FD) for all individuals ($n = 16$, $r^2 = 0.350$, $F_{1,8} = 7.52$, $P < 0.02$) and for both males and females when considered separately (Fig. 3a; males: $n = 8$, $r^2 = 0.544$, $F_{1,8} = 7.16$, $P < 0.05$. Fig. 3b; females: $n = 8$, $r^2 = 0.784$, $F_{1,8} = 21.74$, $P < 0.005$).

Parasite Load

No relationship was found between gut parasite load and body mass, testes mass, seminal vesicle mass, or lateral gland length. When one heavily infested shrew was removed from the analysis, however, gut parasite load was negatively correlated with body length ($r_s = 0.73$, $n = 9$, $P < 0.05$). We found no significant correlations between gut parasite load and measures of male mobility during the breeding season.

Discussion

Morphological Relationships

The values obtained for morphological variables such as body mass, body length, and testes mass in general agree well with those described by previous authors (Adams, 1910; Middleton, 1931; Brambell, 1935; Shillito, 1963*a*; Michielsen, 1966).

The relationships between seminal vesicle mass and body size suggest that the degree of androgen production may influence growth rates of maturing males and hence adult body size. The lack of significant correlation between testes and seminal vesicle masses, however, indicates that large testes do not necessarily secrete the most androgens. Studies on chromosomally abnormal shrews also suggest that testes size is a poor indicator of androgen production (Searle, 1984*c*; Searle and Wilkinson, 1986).

Testes mass (measured in May) was related to body mass at the time of recapture (April), but was apparently unrelated to sperm count. Sperm output is related to testes size in several mammalian species (rams, Abdou et al., 1978; mice, *Mus musculus*, H. Hauffe, personal communication; kangaroo rats, *Dipodomys ordii*, Hoditschek and Best, 1983; rats, Lino, 1972), although this is not always the case (e.g., Carter et al., 1980).

Sexual Maturation

Individual timing of maturity at the onset of the breeding season was significantly correlated with two morphological characters of potential importance in determining reproductive success among adult male shrews. Early maturing males tended to develop larger testes but had relatively small lateral glands in May. The significance of testes size has already been discussed. The size of the lateral glands was inversely proportional to weight increase between March and April, such that large lateral glands were associated with both late development and slow growth rate. Interestingly, lateral gland length was also positively correlated with sperm count in these males. It is difficult to speculate on the significance of results relating to the lateral glands without knowing their function. However, in view of the positive correlation found between early development and adult testes size, these results were unexpected and as such warrant further investigation.

Relationships Between Morphology and Mobility

Our results agree with those of previous studies with respect to general sex differences in mobility during the breeding season. During March, male shrews were found to be generally more mobile than females. Similarly, those males recaptured in April were generally found to have moved greater distances from their previous points of capture than had recaptured females.

The spatial distribution of female common shrews during the breeding season, coupled with relatively short periods of sexual receptivity (Crowcroft, 1957), suggest mobility to be an important correlate of male mating success. During March we found a strong trend for heavier males to have greater mobility scores (farthest distance moved between any of first four capture points, FD[4]), whereas no such trend was found among females. Furthermore, those males which moved the farthest distances in April had, in general, developed the largest testes.

While body mass was associated with mobility during March among male shrews only, another measure of mobility (the farthest distance moved between any two [of four or more] capture points, FD) was significantly correlated with body length among both males and females (body length was unrelated to body mass at this time). Hence, regardless of sex or stage of maturation, longer-bodied subadults ranged farther distances overall than did shorter-bodied individuals (male and female body lengths were not significantly different at this time). If subadults are actively territorial, then such a difference between large and small individuals might feasibly be brought about by dominance relations, raising the question of cause and effect (i.e., do large individuals become dominant and monopolize larger territories, or do dominant individuals become larger as a result of gaining access to larger territories?). Alternatively, there may be no strict territoriality as such, and differences in ranging behavior may simply result from larger individuals having increased foraging requirements. In future studies we aim to measure the reproductive success of individual common shrews in natural populations using the method of DNA fingerprinting. This information will be related to various individual characteristics such as relative mobility, body size, and timing of maturity, in order to obtain a more detailed picture of the mating system of the common shrew.

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	Body mass (March)	Body mass (April)	Body mass (May)	Body mass increase (March-April)	Body length (March)	Body length (May)	Testes mass (May)	Sperm count (May)	Seminal vesicle mass (May)
Body mass (April)	n.s.								
Body mass (May)	*	n.s.							
Body mass increase (March-April)	n.s.	**	n.s.						
Body length (March)	n.s.	n.s.	n.s.	n.s.					
Body length (May)	n.s.	n.s.	**	n.s.	n.s.				
Testes mass (May)	n.s.	*	n.s.	n.s.	n.s.	n.s.			
Sperm count (May)	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		
Seminal vesicle mass (May)	n.s.	n.s.	*	n.s.	n.s.	***	n.s.	n.s.	
Lateral gland length (May)	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	*	n.s.

Fig. 1.—Correlations between male morphological characters. Abbreviations: n.s., $P > 0.05$; *, $P < 0.05$; **, $P < 0.005$; ***, $P < 0.0005$.

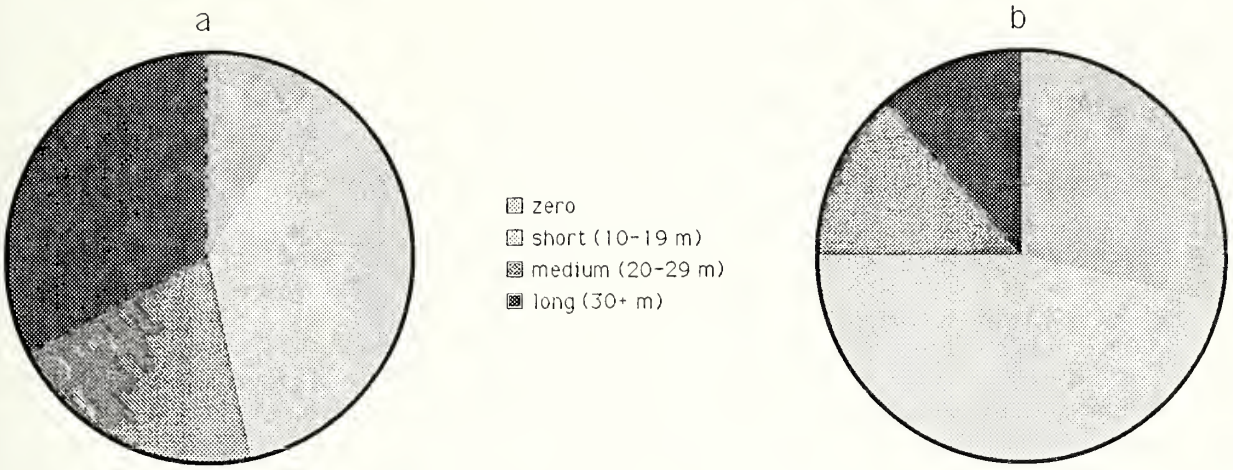

Fig. 2.—The relative frequency of movements of different distances made by common shrews between consecutive captures in March: a, males and b, females ($\chi^2 = 13.27$; d.f. = 3, $P < 0.01$).

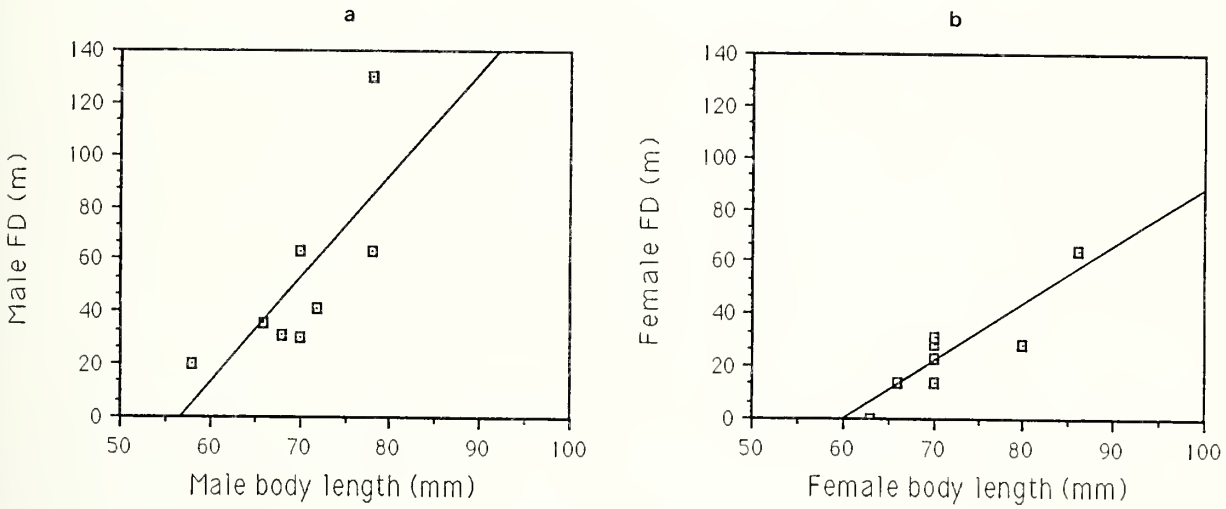

Fig. 3.—Relationship between body length of common shrews and farthest distance (FD) moved between capture points (≥4) during March: a, males ($y = 3.98x - 227$, $r^2 = 0.544$, $F_{1,8} = 7.16$, $P < 0.05$), and b, females ($y = 2.21x - 134$, $r^2 = 0.784$, $F_{1,8} = 21.74$, $P < 0.005$).

VISUAL AND HEARING BIOLOGY OF SHREWS

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ABSTRACT

The morphology and ontogenetic development of the shrew eye and ear correspond to a common mammalian pattern. Generally, the qualitatively normal strueture of the eye and the ear predispose shrews to normal seeing (light-dark and color discrimination) and hearing (tuned to frequencies of about 12–24 kHz). These assumptions were confirmed by behavioral experiments. The small size of these sense organs, however, constrains and reduces the range, sensitivity, and resolution capabilities of perception. No structural or dimensional modifications of components of the sensory organs which would enhance or shift their functional capacities were noted. Shrews can be considered visually and acoustically unspecialized (generalized) mammals.

INTRODUCTION

The introduction of sophisticated research methods and sensitive analytical devices into biology in last few decades has led to the realization that the sensory world of mammals may be quite different from that of man, and that we still know little even about our own senses. Many discoveries in sensory biology were achieved by the combined efforts of ethologists, physiologists, morphologists, and ecologists, as well as physicists and chemists, and have gained wide publicity outside zoological circles. Pheromones, echolocation, ultra- and infrasonic communication, magnetic orientation, electroreception, infrared perception, and seismic registration are among discoveries which have marked the opening of new horizons in understanding of animal sensory life.

Bats and dolphins, as well as laboratory and domestic mammals, became popular model organisms in studies of the structure and function of particular sensory systems. Compared to those groups of mammals, insectivores in general and soricids in particular remained of peripheral interest to sensory biologists. Consequently, knowledge of the sensory biology of shrews remains limited. Several studies of some aspects of perception in soricids, such as the demonstration of primitive echolocation (see below), have become widely known among mammalogists. Yet there has been little followup of these pioneering studies. Previous studies of sensory biology seem to support the generally accepted assumption that shrews represent a primitive stage in mammalian evolution. For a variety of reasons few studies of shrew sensory biology have been reported.

We dedicated a decade to study of the peripheral structures of the visual and auditory systems of shrews. Since we do not expect to continue this research, we here summarize the present state of knowledge in this field. It is not the purpose of this paper to review detailed morphological descriptions published previously. Only descriptive information which is new, updated, or relevant to further reasoning is provided. New accumulated knowledge and new comparative data allow new interpretations of some older descriptive facts.

VISUAL SYSTEM

Vision

Vision in shrews as in other microphthalmic mammals has been regarded as poorly developed (Walls, 1942; Rochon-Duvigneaud, 1943; Sharma, 1957) or even considered nonfunctional (Rood, 1958). These conclusions were based on anatomical studies of the eye and observations of behavior. Experimental evidence of light perception in shrews was found in studies of the photoperiodicity of circadian and circannual rhythms of activity (Crowcroft, 1964; Gebczynski, 1965; Buchalczyk, 1972; Siegmund and Sigmund, 1983; Rissman et al., 1987; Sigmund et al., 1987).

Crocidura suaveolens could be trained to distinguish between light (100–450 lux) and dark (Braniš, 1988). In further experiments, neither the intensive light of a camera flash nor moving objects or moving prey behind glass could elicit a behavioral response in *Sorex araneus*, *S. minutus*, *Neomys fodiens*, *N. anomalus*, or *C. suaveolens* (Braniš, 1981).

Color discrimination ability in shrews was postulated on the basis of morphological studies which revealed high numbers of retinal cones (Braniš, 1981). Recently, the ability to discriminate colors, at least in the range from 471–622 nm, was evidenced through behavioral conditioning experiments in *Neomys fodiens* (Kodejsova, 1989; Sigmund et al., 1989).

Ocular Anatomy

Some aspects of the morphology of the eye of shrews were described as early as the 1930s and 1940s by Schwartz (1935), Kolmer and Lauber (1936), Walls (1942), Rochon-Duvigneaud (1943), and Cei (1946). Detailed quantitative and new and updated qualitative information was presented by Braniš (1985*a*, 1985*b*), where also further references are given.

The eyes of shrews are situated laterally in the front half of the head, with both optic axes diverging at an angle of about 100°. The orbit is not developed and the eyeball is deeply immersed in the massive Harderian gland. The eyeball (Fig. 1) is approximately spherical but its diameter varies considerably from species to species (Table 1).

The sclera covers about 65% of the eyeball surface. The only visible part of the eye in vivo is the strongly convex cornea, which has a structure very similar to that of other mammals. The corneal epithelium, however, is not differentiated into zones with several cell layers. It is composed of only one to three layers of loosely packed cells. This thin

epithelium is covered by a distinctly multilaminar keratinized layer. Its cornification was confirmed by specific histological staining (rhodamin B-toluidin blue) as well as by transmission electron microscopy (Fig. 2, 3) (Braniš, 1989). This cornification may protect the eye during burrowing. However, similar corneal cornification has not been observed in other fossorial mammals (see Burda et al., 1990).

The vascular layer of the eye is composed of a thin and heavily pigmented choroid, a rudimentary ciliary zone with an almost imperceptible ciliary muscle, and a thin iris with the sphincter muscle at its pupilary margin (Fig. 1).

The lens occupies about one half of the eye's axial diameter. It is biconvex with the flatness index amounting to between 1/32 and 1/47. The lens is normally developed; however, its suspensory ligament (zonule of Zinn) is made up of only sparse, thin filaments. The focusing apparatus of the eye in shrews is simple and resembles that of reptiles (cf. Duke-Elder, 1958).

The retina in *Sorex*, *Neomys*, and *Crocidura* is 0.12–0.14 mm thick at the posterior pole of the eye. Despite this reduced thickness, all of the typical retinal layers are developed. Both types of receptors, rods and cones, are present (Fig. 4, 5) in species-specific ratios and densities which are within the range of values found in other mammals (Table 1) (Braniš, 1981). The total retinal areas of the examined shrews ranged from 0.7–2.1 mm^2 and contained between 220,000 and 465,000 receptors per mm^2. No area or fovea centralis was observed in any shrew retina. The ultrastructure of the retina in shrews has been described by Grün and Schwammberger (1980) and Sigmund et al. (1987).

Visual Pathways and Centers

The optic nerves of *Crocidura suaveolens* and *Sorex araneus* are about 0.1 mm in diameter and contain about 3,800 and 6,000 myelinated axons, respectively (Braniš, 1985*a*).

The primary visual brain centers, geniculate lateral body, pretectal area, and optic tectum are well-developed in *Crocidura suaveolens*. These centers exhibit typical axonal degeneration after bilateral enucleation which indicates that they receive direct visual innervation (Sigmund et al., 1984). In addition, the lamination of the superior colliculus, which mediates reflex movements triggered by light, was described as relatively well developed in *Sorex shinto* (Sato, 1977). These findings have been interpreted as further evidence for an anatomically complete visual system in shrews which may play a role in the lives of shrews.

Development of the Eye

Ontogenetic (prenatal and postnatal) development of the eye was studied in *Sorex araneus* (Braniš, 1985*b*, 1986) and (prenatal development only) in *Suncus murinus* (Sprando et al., 1989). The eye primordium was first indicated by the presence of optic vesicles broadly continuous with the third brain ventricle in the *Sorex* embryo aged about 11 days (gestation lasts 21 days). The optic cup with a closed lens vesicle was present in embryos 13–15 days old. In 16-day-old embryos, the retina had begun to differentiate into the primitive neuroblastic and marginal layers. The retinal pigment epithelium layer contained densely packed melanin granules. A small number of nerve fibers appeared in the optic nerve primordium. The hyaloid artery and the annular vessel system were highly developed at that stage. The inside of the lens vesicle became gradually occluded by extending primary lens fibers. By days 17 or 18, the anterior segment of the eye formed and the eyelids developed. The lens vesicle was filled with primary lens fibers, and secondary lens fibers appeared laterally. Before birth, at gestational day 20, the eyelids were fused, the eyeball wall was organized, and the retina had differentiated into three layers.

The whole eye differentiates very quickly during the first three postnatal weeks. The diameter of the eyeball grows rapidly up to the tenth day after birth, when it reaches about 80% of the adult ocular dimensions. The choroidal pigment emerges first on day 8, and the adultlike pigmentation appears on postnatal days 18–20. The cornea becomes stratified at the age of 12–16 days after birth. The retinal layers develop progressively during the initial postnatal weeks. On day 13, the two types of visual receptors are discernible at the light microscopic level. At the time of eyelid opening, postnatal days 18–19, the retina is fully formed. The first myelinated axons in the optic nerve are visible at ten days after birth. At the time of eyelid opening, only about 25% of the axons are myelinated.

In general, the eye in both *Sorex araneus* and *Suncus murinus* develops normally; no part of it appears to be developmentally retarded.

Auditory System

Hearing Physiology

No audiological (behavioral or electrophysiological) studies have been conducted to directly and explicitly ascertain the characteristics of hearing (frequency tuning, hearing range, sensitivity, resolution, and sound localization capabilities) in any soricid species.

In the absence of direct data, some characteristics of hearing may be deduced from general bioacoustic principles, characteristics of vocalization, behavioral ecology, and functional morphology of the auditory apparatus. This deduction is based upon the generally accepted correlation between tuning of the auditory system and all of the aforementioned aspects. These factors will be discussed sequentially.

Physical Constraints

What an animal should hear, and what it can hear are determined and constrained by the physical principles of acoustics. For production of high tones, small resonance cavities (larynx, mouth, nose) are needed, whereas voluminous organs are required to produce low tones. Similarly, smaller and lighter receiving structures, including the ear canal, middle ear cavity, ear drum, and auditory ossicles, should resonate at higher frequencies than the larger structures of larger animals. Small mammals like shrews would be expected to have their smaller auditory as well as vocalization organs tuned to higher frequencies.

Small mammals have small heads with a short interaural distance. Consequently, they are typically not able to localize sound due to the negligible difference in time of arrival of a stimulus at the two ears, and therefore make use of the difference in frequency-intensity spectra of a sound reaching the two ears (Heffner and Masterton, 1980). The frequency-intensity difference cue is available even to a small mammal provided that it can perceive frequencies high enough to be effectively shadowed by the head and pinnae (Heffner and Masterton, 1980). High frequencies are, however, more attenuated in the environment than low frequencies. Hence it is advantageous for mammals to have their hearing tuned to the lowest frequency that can be accurately localized. For example, in *Sorex araneus*, with an average interaural distance (measured around the head) of about 22 mm, the frequency of a corresponding wave length which could be effectively shadowed by the head and thus localized, is about 15 kHz (Table 2).

Vocalization

The vocalizing and auditory systems in each species have coevolved and are tuned to each other. This also must be true to permit active acoustic orientation or echolocation. Consequently, frequency characteristics of calls used for intraspecific communication and echolocation should provide us with information on the frequency tuning of hearing.

Hutterer and Vogel (1977) demonstrated in some crocidurine shrews that the species-specific main frequency of defensive, or fright calls (32–14 kHz) was inversely related to the body size (9–120 g). It is not known whether these calls are aimed at conspecifics only, and therefore whether such calls serve as a correlate of hearing capabilities. However, there is no such problem with courtship calls. The main frequency of these calls is about 10 kHz in *Neomys fodiens*, and about 15 kHz in *Crocidura russula* (Hutterer, 1978). Unfortunately some earlier papers (e.g., Hutterer, 1976), though valuable, cannot be considered here since ultrasonic calls were not recorded.

Frequencies of sounds considered to be echolocation calls ranged from 30–60 kHz in three *Sorex* species (Gould et al., 1964), 18–60 kHz with the majority of the energy between 20–40 kHz in *S. vagrans* (Buchler, 1976), and about 30–50 kHz in *Blarina brevicauda* (Gould et al., 1964; Tomasi, 1979). Grünwald (1969) found two *Crocidura* species vocalizing up to 46 kHz, but the main frequencies were about 20 kHz.

Acoustic Behavior

Shrews are relatively vocal animals (Gould, 1969; Hutterer, 1978) and there is no doubt that vocalization and hearing are important for intraspecific communication during activities such as courtship, mother-offspring contact, and agonistic behavior. This notwithstanding, the vocal repertoire of shrews is not as complex as in higher mammals (Hutterer and Vogel, 1977).

It has been suggested that *Crocidura*, in contrast to *Sorex*, may use hearing to locate prey (Burda and Bauerova, 1985), but this hypothesis has not been experimentally tested. It is doubtful whether hearing plays a crucial role to warn of predators, and surely not at a great distance. Higher frequency sounds at natural intensities are soon attenuated in the environment; low-frequency sounds apparently are not perceived, and in any case they cannot be localized by shrews. Shrews are able to produce and perceive high-frequency sounds. Echolocation would certainly be of great use for these mammals with poor eyesight. It will be argued that due to the short basilar membrane and small numbers of receptors, the hearing of shrews must limit discrimination capacities. The analysis of echoes would be thus too crude for echolocation to be useful in hunting. Gould et al. (1964), Buchler (1976), and Tomasi (1979) demonstrated echolocation during orientation by the soricine shrews *Sorex* and *Blarina*. According to these authors the primary use of echolocation by shrews was for exploration of the environment; *Blarina* in Tomasi's experiments were able to distinguish by means of echolocation between closed and open tunnels. Grünwald (1969) was not able to document echolocation in *Crocidura*. The usual interpretation of these conflicting results is that soricine shrews echolocate and crocidurine shrews do not. We do not question the results, but we feel the experiments should be repeated using representatives of both subfamilies under the same conditions, preferably in the same laboratory.

Examination of the ears of many wild-caught shrews of several species did not reveal diseases or disorders which could substantially affect the hearing function (Burda, 1978). Either these conditions are very rare or such cases are immediately eliminated by natural selection. This observation may be considered indirect evidence that a functioning auditory system is important for survival and success in shrews.

Functional Morphology

Outer ear.--The structure of the outer ear of shrews has been described by Boas (1912) and Burda (1980). The auricle of shrews (Fig. 6) approximates the hypothetical prototype of a primitive mammalian auricle (see Boas, 1912). The relative length and surface area, degree of divergence from the head, intensity of hair cover, and resulting exposure of the auricle are genus-specific. *Crocidura* and *Suncus* have relatively larger, less hairy, and more diverted and exposed auricles than *Sorex* or *Neomys* (Burda, 1980). The difference may be explained by Allen's rule (Burda, 1980; see also Nagel, 1994): the Crocidurinae originated in warmer southern climates whereas the Soricinae originated in cooler northern areas. Desert shrews of the genus *Notiosorex* (Soricinae) also have conspicuous auricles (Walker, 1975). In addition, the crocidurine shrews are surface-dwelling whereas the soricine shrews are more fossorial (Burda and Bauerova, 1985). Fossorial and subterranean mole shrews (*Anourosorex squamipes*) have auricles completely concealed in the fur (Walker, 1975). Yet it would be hasty to conclude that the pinnae in these forms became small and hidden in the fur primarily to avoid interference with burrowing so as not to "act as shovels collecting the dirt." We suggested that a prerequisite for the reduction of the auricles in subterranean mammals is abandonment of the necessity for keeping the auricles for sound collecting, amplifying, and binaural localization (Burda et al., 1990), and perhaps even for thermoregulation.

The cutaneous muscles of the head and neck and the

auricular muscles exhibit a primitive arrangement in shrews which approximates an archetypal mammalian condition (Burda, 1979*a*). The auricular muscles are somewhat larger in *Crocidura suaveolens* than in *Sorex araneus*, which may be related to the larger size and greater deflection of auricles in the former species (see also Burda and Bauerova, 1985). It is not clear whether the auricles of shrews are movable. The position of the auricles at the sides of the head, the relatively small, undeveloped auricular muscles, and the steady, lively, fast, and violent motion of the head characteristic of shrews, are conditions not fully consistent with movable auricles.

The outer earcanal (external meatus) in shrews is cartilaginous along its entire course. It is relatively long: 4.5–8 mm in *Sorex minutus* and *Neomys fodiens*, respectively (Burda, 1980). For comparison, the meatus length in the Norway rat is 5.7 mm (Plassmann and Brändle, 1992). If the ear canal is considered a resonating pipe, the meatus in *S. araneus*, for example, would resonate at about 13 kHz (see Table 2). However, the length of the meatus is primarily determined and constrained by the distance between the outer ear canal opening (auricle) and the ear drum (tympanic bone). Since shrews retain the primitive condition of tympanic bones being situated on the ventral side of the head, the meatus has to be relatively long (Burda, 1979*b*, 1980).

Middle ear.--Detailed morphological descriptions of the middle ear structures in shrews have been provided by Burda (1979*b*), Fleischer (1973), and Henson (1961), (see also literature cited therein).

The tympanic bulla in shrews (at least in *Sorex*, *Neomys*, and *Crocidura*) is largely ligamentous and nonossified. The only bone it contains, excluding the paries cochlearis, is the tympanic ring or annulus tympanicus, which makes a frame for the tympanic membrane or ear drum. The areas of the pars tensa of the ear drum and the estimated volumes of the middle ear cavity in some shrew species are given in Table 2 (based on Burda, 1979*b*). Using the formulas of Plassmann and Brändle (1992) the resonance frequency of these structures was estimated and included in Table 2.

Although the computed values are only rough approximations (Plassmann and Brändle, 1992), it is remarkable how similar these values are for different parts of the ear in each species. The mean resonance frequencies vary predictably when a size-graded series of shrew species is compared (Table 2). We assume that the ear structures have the lowest impedance at the resonance frequency, therefore the resonance frequency and the frequency range of best hearing sensitivity should correlate. The estimated values also agree with frequency characteristics of vocalizations used for intraspecific communication.

The vibration of the ear drum is transferred to the cochlea by the auditory ossicles. The vibratory amplitude is increased and the impedance from air to cochlear fluid is matched by the acoustic lever action of the ossicles, expressed by the "lever ratio," and by condensation of energy from the larger ear drum to the smaller footplate of the stapes, expressed by the "area ratio." These ratios in some shrew species are given in Table 2. The values of the area ratio in shrews are the highest known among mammalian species (see Burda 1979*b*; Plassmann, 1989). The lever-ratio values were determined according to Plassmann (1989) (see Fig. 7). The "final transformation ratio" is defined as the product of the two ratios (Møller, 1974). Theoretically, a value of about 63 indicates efficient transmission of energy (Møller, 1974). Taking into account that this value (=63) is based on approximations, and that we did not measure the actual ear drum area but the area enclosed by the tympanic ring, one conclusion is that the middle ears of shrews fit the theory remarkably well.

The auditory ossicles in shrews (Fig. 7) are firmly connected with each other and, through the gonial, with the tympanic ring. Ossicles of similar form and arrangement are also found in other small and "ultrasonic" forms like bats and mice (Fleischer, 1973).

Cochlea of the inner ear.--The structure of the cochlea of shrews has been described from different points of view and using different methods of study by Platzer (1964), Platzer and Firbas (1966), Firbas and Platzer (1969), Fleischer (1973), Burda (1978, 1979*b*), Sigmund (1985), and Walther (1987), (see also references therein).

The cochlea of shrews is low and flat. It has 1.5 turns in *Sorex* and *Neomys*, and 1.75 turns In *Crocidura*. The secondary spiral lamina is well-developed. The low number of cochlear coils is considered a primitive trait in mammals. A low and flat cochlea with well-developed secondary spiral laminae is characteristic of mammals with good high-frequency hearing (Fleischer, 1973).

The length of the basilar membrane varies from 2.9–4.5 mm in four soricid species (Table 3) and may be correlated with the size of the pinna in the examined Soricidae and with body size at the subfamily level. *Crocidura* has a longer basilar membrane and a larger pinna than would be found in a soricine shrew of comparable body size. An analogous situation was found among acoustically unspecialized mice and rats (Muridae) and discussed in detail (Burda et al., 1988).

Parameters of many elements of the cochlear partition, such as thickness of the basilar membrane, height of the organ of Corti, and length of the stereocilia of hair cells, change from the base toward the apex of the cochlea in *Sorex araneus* and *Crocidura russula* in the same predictable manner as in other acoustically unspecialized mammals (Walther, 1987). Apart from some differences in the structure of the basilar membrane between *S. araneus* and *C. russula*, the functional significance of which is not clear, the cochleas of both species are structurally unspecialized organs. Local specializations or discontinuities in cochlear morphometrical baso-apical gradients, which would account for extension of the region where the best frequency is represented and thus for better hearing resolution in the respective frequency range, have been reported in bats and gerbils but were not observed in shrews (Walther, 1987; Walther and Bruns, 1987).

The density of cochlear receptors in the species of shrews examined amounted to about 390 outer hair cells and 110 inner hair cells per 1 mm (Table 3). These densities are somewhat higher than the "mammalian average" (Burda and Braniš, unpublished data). This may be due to the smaller size of cells in smaller mammals compared to larger ones (see Burda et al.,

1988). While the density of outer hair cells increased from the base to the apex of the basilar membrane, the density of inner hair cells reached maximum at about 60% of the basilar membrane length from the basal end in *Sorex araneus* (Burda and Braniš, unpublished data). A similar pattern of receptor distribution has been found in house mice and many other mammals (Burda and Braniš, unpublished data; Burda et al., 1988).

The total number of cochlear receptors in mammals is determined primarily by the length of the basilar membrane, which shows greater interspecific variation than does the mean density of receptors. The absolutely shorter basilar membrane in shrews can accommodate only a smaller number of receptors (Table 3). This may have functional consequences: either the dynamic range of the shrew ear may be relatively limited, or frequency and intensity discrimination (sensitivity) of hearing may be relatively poor (cf. Wever, 1974; Burda et al., 1988).

In shrews, the cuticular plates of the cochlear hair cells are arranged in a conspicuous geometric pattern on the reticular lamina along the entire organ of Corti (Fig. 8). Such a geometrically regular arrangement is typical of basal parts of the Corti organs in many mammalian species and of the entire Corti organs of bats. This is a feature typical of Corti organs tuned to high frequencies (Burda, 1979*b*). Considering some additional features, like the presence of the secondary spiral lamina and the massive spiral ligament throughout the cochlear duct, we conclude that even the apical parts of the Corti organ are tuned to relatively high frequencies. The hearing range of shrews is apparently shifted to higher frequencies.

The spiral cochlear ganglia in *Sorex minutus* and *S. araneus* contain 6,440 and 7,090 neuron cells, respectively (Sigmund, 1985). The ratios between the numbers of cochlear neurons and counts of cochlear receptors are within the range of values found in murids (Burda et al., 1988).

The postnatal development of the organ of Corti has been studied in *Sorex araneus* (Braniš and Burda, unpublished data). The reticular lamina of the Corti organ in this species matures in a way similar to that of murids (Burda, 1985; Burda and Braniš, 1988). At birth, the triad of cuticular plates of outer hair cells is narrow at the apex and wide at the base of the cochlear spiral. During maturation it grows at the apex and decreases at the base to reach its mature dimensions. At a certain point along the organ of Corti the mature values are present at birth, and the dimensions of this area do not change significantly during further development. In murids there is an exact correlation between the location of this point and the region where the maximum density of inner hair cells is found. This area also corresponds to the cochlear region activated by the frequency range of greatest auditory acuity (Burda, 1985; Burda and Braniš, 1988). This developmental "turning point" in *S. araneus* also was localized at the place of the maximum density of inner hair cells. The width of the triad of outer hair cells was about 17 μm at this place. The region of basilar membrane with a comparable dimension is where the frequencies (octave) of 16–32 kHz are represented in the rat, the house mouse, and the cat (Burda, 1985; Burda and Braniš, 1988, and unpublished data for morphometry; Ehret, 1975; Liberman, 1982; and Müller, 1988, for tonotopy). Consequently, based on assessment of only this parameter, we assume that the cochlear partition in *S. araneus* is tuned to frequencies of about 16–32 kHz.

Conclusions

The components of the visual system in the shrews examined appear to be structurally normally developed. The retina is of a diurnal type with both rods and cones. The ontogenetic development of the eye appears to be normal and no part of the eye can be considered developmentally retarded. The morphological substrate for functional light perception is provided. The small size of the eyeball and consequently small retinal surface accommodates a limited number of receptors. There is neither a fovea nor an area centralis in the retina of shrews. The accommodating apparatus of the eye is very simple and probably nonfunctional. These quantitative aspects indicate that visual acuity may be very limited in shrews.

Shrews are capable of light-dark discrimination on the basis of long- and short-term stimulation. They are unable visually to discern moving objects or sudden brief light stimuli. The controversy may be explained in terms of functional morphology. The cone-rich retinas of shrews provide a morphological basis for color discrimination. The ability to distinguish colors has been demonstrated in behavioral tests. Due to the small size of the perceptive retinal surface, shrews probably have only the ability to perceive color changes in the environment as stimuli affecting circadian and/or circannual rhythms. Binocular fixation of color images seems to be unlikely.

The structure of the outer, middle, and inner ear in shrews generally conforms to a primitive eutherian pattern. The size of ear structures in soricine shrews follows a slightly different, yet parallel, allometric curve to that of crocidurine shrews. Assuming that the resonance frequency of ear structures is determined by their dimensions, frequency tuning was calculated for each structure independently according to physical formulas and formulas given in the literature. It was shown that all structures in each particular species are tuned to roughly the same frequency. The dimensions of auditory system components remained proportional and follow the general mammalian plan. Neither the high-frequency hearing of shrews nor the structure of their ear which makes high-frequency hearing possible should be considered evolutionary adaptations (sensu Sluys, 1988).

In summary, hearing in shrews is correlated with vocalization and both are tuned to the same frequencies. The tuning is determined by the dimensions of auditory components and those structures in turn are determined by overall size and strict conformity to a general pattern. *Crocidura* can theoretically enhance auditory sensitivity in the range of higher frequencies by changes in structural dimensions without abandoning the general pattern. These changes may have occurred due to environmental factors encountered by living in warmer habitats (Allen's rule), or by a less fossorial existence, more open habitats (with other acoustic properties), and by different hunting strategies. Hearing undoubtedly is important for shrews as evidenced by behavioral observations and by the

fact that no pathologic cases were found in nature. Echolocation cannot be ruled out; it may be useful, but its discrimination capacities would be relatively limited. The actual role of hearing and its significance for shrews have yet to be thoroughly tested in controlled experiments.

Generally, the qualitatively normal structure of the eye and ear predispose shrews to normal vision and audition. Their small size, however, presumably reduces and constrains the range or sensitivity or resolution capabilities of visual and acoustic perception. No structural or dimensional modifications of the respective sensory organs which would adaptively enhance their functional capacities or change their tuning were noted. Shrews can thus be considered visually and acoustically unspecialized (generalized) mammals. The ecological niche of shrews apparently exerts little selective pressure for vision and audition, therefore the eye and ear have retained small dimensions and limited functional capacities.

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Table 1.—*Morphometry of the eye in shrews.*

Species	Eyeball Diameter[a]	Retinal Thickness[b]	Retinal Area[c]	Rod/Cone Ratio	Receptor Density[d]	Axons Number[e]
S. minutus	0.93	119	1.2	7/1	245,000	—
S. alpinus	0.72	138	0.7	8/1	221,000	—
S. araneus	1.14	139	1.6	6/1	220,000	6,000
C. suaveolens	1.14	145	1.4	12/1	300,000	3,800
C. leucodon	1.20	140	1.4	15/1	390,000	—
N. anomalus	1.29	137	1.8	16/1	410,000	—
N. fodiens	1.49	140	2.0	17/1	465,000	—

[a] Equatorial diameter of eyeball (mm).
[b] Thickness of central retina (μm).
[c] Retinal area (mm^2).
[d] Number of receptors per 1 mm^2.
[e] Number of axons in the optic nerve.

Table 2.—*Morphometrical and functional characteristics of the outer and middle ears of shrews.*

Species	a Body Mass (g)[a]	b Inter-aural Distance (mm)[b]	c f (kHZ)[c]	d Meatus Length (mm)[d]	e f (kHZ)[e]	f Meatus Area (mm^2)[f]	g Middle Ear Volume (mm^3)[g]	h f (kHz)[h]	i Mean Eardrum Radius (mm)[i]	j f (kHz)[j]	k f (kHz)[k]	l Area Ratio[l]	m Lever Ratio[m]	n Final Ratio[n]
Sorex minutus	4	15	22.9	4.5	19.6	0.95	3.13	23	0.68	19.6	21.3 (1.9)	49:1	1.33:1	65.2:1
Crocidura suaveolens	5	19	18	5.2	17	1.41	6.48	18.7	0.84	15.9	17.4 (1.2)	55:1	1.37:1	75.3:1
Sorex araneus	8	22.5	15.2	6.8	13	1.33	7.64	16.9	0.81	16.4	15.4 (1.7)	51:1	1.17:1	59.7:1
Neomys fodiens	13	27	12.7	8.0	11	1.77	11.15	15.5	0.94	14.2	13.3 (1.9)	46:1	1.44:1	66.2:1

[a] Based on Burda (1979*b*).
[b] Measured around the head; mean values based on measurements of five specimens in each species.
[c] Frequency effectively shadowed by the head: f = c/d where c = 343m/s, d = interaural distance (column b).
[d] Based on Burda (1980).
[e] Resonance frequency of the meatus: $f = c/4 \cdot \ell$ where c = 352.9 m/s, ℓ = meatus length (column d).
[f] Mean values of measurements made in five specimens in each species.
[g] Calculated from dimensions given in Burda (1979*b*).
[h] Resonance frequency of the outer and middle ear computed according to Plassmann and Brändle (1992):

$$f = x\sqrt{\frac{m}{VL}}$$

where x = constant = 56,166, m = meatus area (column g), V = middle ear volume (column g), L = 1.5r + 0.96 where r = radius of the meatus.
[i] Based on Burda (1979*b*).
[j] Resonance frequency of the eardrum computed according to Plassmann and Brändle (1992): f = Y/r where y = eonstant = 13.32, r = radius of the cardrum.
[k] Mean frequcncy (and standard deviation) of values in columns b, e, h, j.
[l] Eardrum area : stapedial footplate area; see Fig. 7 (this paper) and Burda (1979*b*).
[m] Lever ratio of the malleus : incus; calculated from dimensions given in Burda (1979*b*), see Fig. 7 (this paper).
[n] Final ratio scnsu Møller (1974) (theoretically expected value = 63); product of the lever and area ratios (columns l, m).

Table 3.—*Length of the basilar membrane, density, and total counts of cochlear receptors in shrews (based on Burda, 1979b).*

	Sorex minutus	*Crocidura suaveolens*	*Sorex araneus*	*Neomys fodiens*
Length of basilar membrane (mm)	2.9	4.0	3.95	4.5
Density of outer hair cells per 1 mm of basilar membrane length	400	380	396	384
Density of inner hair cells per 1 mm of basilar membrane length	109	107	112	106
Total number of outer hair cells	1,161	1,522	1,563	1,734
Total number of inner hair cells	315	430	442	479

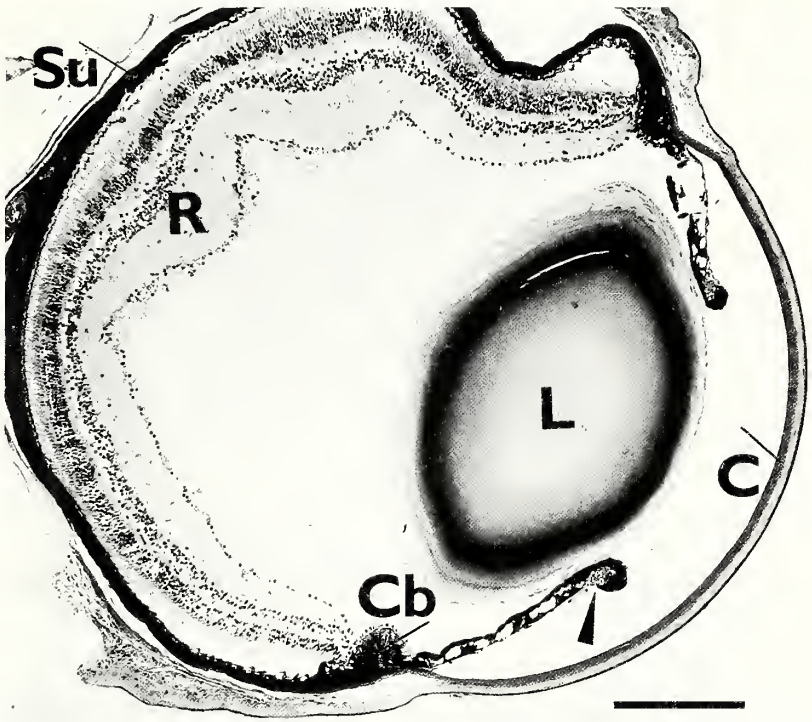

Fig. 1.—Sagittal section through the eyeball of *Sorex araneus*. C, cornea; Cb, ciliary body; L, lens; R, retina; Su, sclerouveal complex. Arrow points to sphincter pupillae muscle. Semithin section; toluidin blue; bar = 0.2 mm.

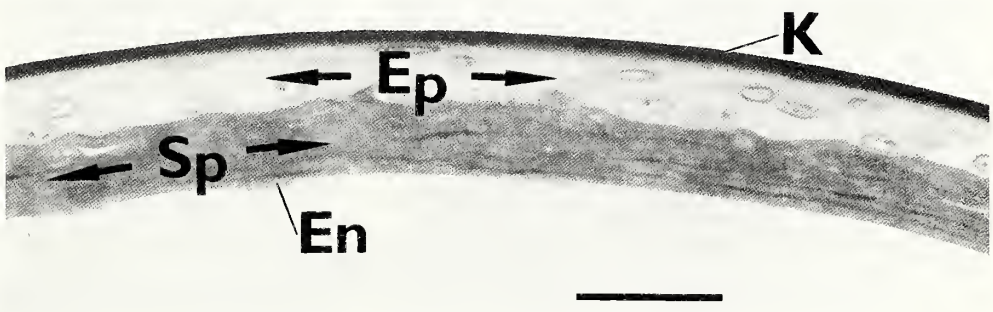

Fig. 2.—Sagittal section of the cornea of *Sorex araneus*. En, corneal endothelium; Ep, corneal epithelium; K, keratinized layer; Sp, corneal matrix (substantia propria corneae). Semithin section; toluidin blue; bar = 30 μm.

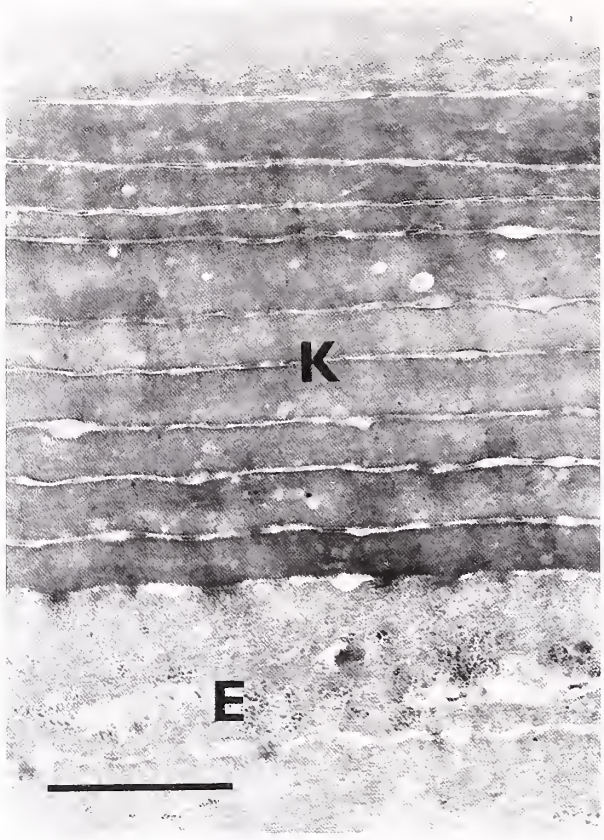

Fig. 3.—Electromicrograph of the corneal surface in *Sorex araneus*. E, epithelium-cell layer; K, keratinized lamaellae. Bar = 10 μm.

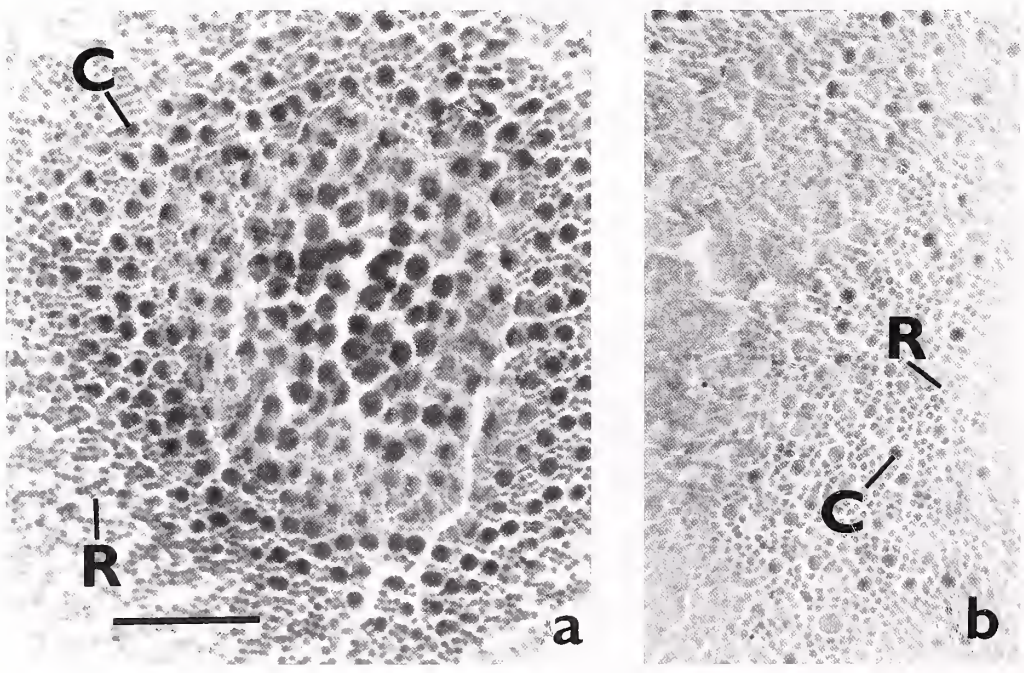

Fig. 4.—Tangential section of the retinal receptor layer (LM). a, *Sorex araneus*. b, *Crocidura suaveolens*. R, rods; C, cones. Note the difference in the density of rods and cones in both species. Paraffin section 6 μm thick; Held hematoxyline; bar = 25 μm.

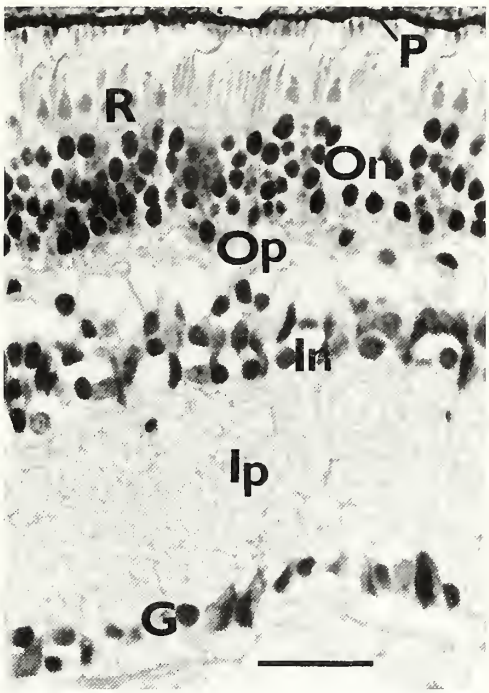

Fig. 5.—The retina of *Sorex araneus*. P, pigmented epithelium; R, receptor layer; On, outer nuclear layer; Op, outer plexiform layer; In, inner nuclear layer; Ip, inner plexiform layer; G, ganglion cell layer. Note both types of visual cells, rods and cones, in the receptor layer. Semithin section; toluidin blue; bar = 30 μm.

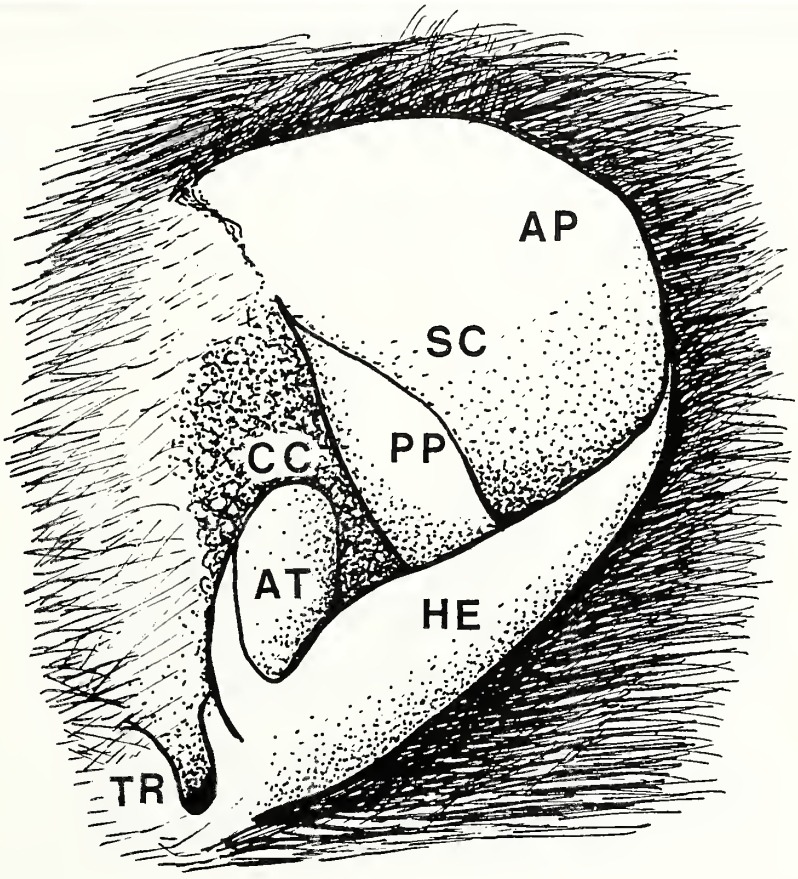

Fig. 6.—The auricle of a shrew (semischematic drawing). AP, apex auriculae; AT, antitragus; CC, cavum conchae; HE, helix; PP, plica principalis; SC, scapha; TR, tragus.

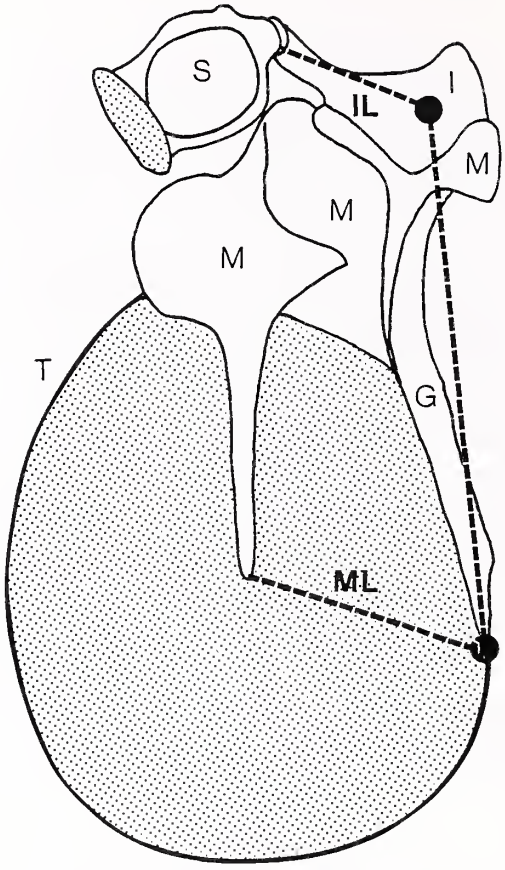

Fig. 7.—The sound-conducting apparatus of the middle ear of a shrew (*Sorex araneus*) (semischematic drawing). I, incus; G, goniale; M, malleus; S, stapes; T, tympanic ring. Indicated is the lever system of the ossicles: IL, incudial lever; ML, mallear lever; dotted sections indicate the ear drum and the stapedial footplate.

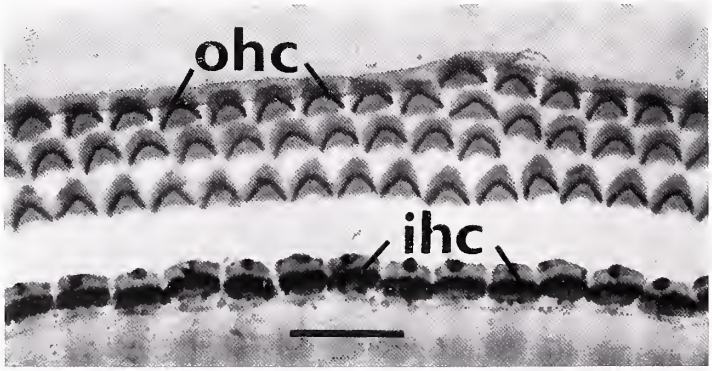

Fig. 8.—Surface specimen of the Corti organ in *Sorex araneus*. ihc, one row of inner hair cells; ohc, three rows of outer hair cells. Note a disturbance of a regular geometric pattern caused by a supernumerary outer hair cell. Stained in toto by toluidin blue and Ehrlich hematoxyline; bar = 30 μm.

RELATIONSHIP OF MANDIBULAR MORPHOLOGY TO RELATIVE BITE FORCE IN SOME *SOREX* FROM WESTERN NORTH AMERICA

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ABSTRACT

Based on the reported decreasing size of the median tine on I^1 from north to south, combined with the progressive enlargement of certain cranial characters along that gradient, we hypothesized that bite force among several taxa of *Sorex* along the Pacific Coast should be related inversely to latitude and should be greatest in taxa without a median tine. We tested these hypotheses with 12 taxa of *Sorex* from western North America. Condylobasal length was highly correlated with mass of the masticatory musculature. Thus, bite force in shrews can be described by $\cos \Theta A/B$, where $\Theta = 90° - \alpha$ (α = the angle subtended by a line from the apex of the coronoid process through the distalmost extension of the lower condylar facet and a line parallel to the ventral edge of the dentary), A is the coronoid-condyloid length, and B is the length from the lower condyloid process to any point of interest on the dentary. Based on this formula, variation in bite force at the tip of I_1 and at the metaconid of M_1, accounted for by factors other than body size, was relatively small across the taxa. However, differences in bite force among taxa, other than that related to size, are related largely to coronoid-condyloid length and to angle Θ. Bite force per se seems correlated positively with absence or reduced size of the tine on I^1, greater appression of I^1s, greater aridity of habitats, and greater hardness of foods eaten by shrews.

INTRODUCTION

Mammals possess a wide variety of cranial morphologies and dental batteries usually closely tied with their foraging ecologies. Differences in jaw morphology and associated musculature commonly are sufficient to explain differences in diets and foraging behavior even among closely related taxa (Freeman, 1979, 1981; Kiltie, 1982, 1984; Humphrey et al., 1983; Herring, 1985) including insectivores (Nikolskaya, 1965). Because of their high rates of metabolism and nearly continuous activity, shrews (Soricidae) require a constant supply of food (Genoud, 1988). These demands "should exert relatively strong selection for food gathering and processing" (Pearson, 1988:1).

Some dentary specialization has occurred among soricids as they have evolved large and procumbent I^1s (first upper incisors) and some have red iron-bearing enamel (secondarily lost in others) that by differential erosion produces sharp cutting edges on the teeth (Dötsch and Koenigswald, 1978; Vogel, 1984). Median tines on I^1, first recorded by Baird (1858) who considered them of taxonomic importance, also may have a dietary function (possibly related to the hardness of food items—Carraway, 1990). Presence and position of tines have been used to separate strongly similar syntopic shrews (Hoffmann, 1971; Hennings and Hoffmann, 1977; Carraway, 1990). Carraway (1990) found considerable variation in the size, shape, and position of the tines within and among some taxa that possessed them; there was some correlation with latitude. Several closely related taxa that possess relatively large tines, posteromedial ridges, or closely appressed I^1s without tines or ridges are syntopic in western Oregon. If tines have a dietary function, such a function may be manifested through differences in bite force, thus permitting use of different food resources and avoidance of excessive competition among these taxa. We considered this hypothesis by measuring bite force in several taxa of *Sorex* without tines and with tines of different morphologies, and we tested the hypothesis that bite force relative to the size of the animal was not related to the presence, size, or position of median tines. Subsequently, we analyzed jaw mechanics in these taxa in an attempt to explain observed differences in bite force and we attempted to relate our findings to information available on food items used by these shrews.

MATERIALS AND METHODS

Specimens and Measurements.—The tongue, hyoid apparatus, and associated musculature; salivary glands; and eyes were dissected free, and the brain aspirated from freshly skinned skulls of frozen specimens referable to *Sorex monticolus setosus* (n = 54), *S. s. sonomae* (n = 28), *S. s. tenelliodus* (n = 88), *S. p. pacificus* (n = 20), and *S. vagrans* (n = 25—sensu Carraway, 1990); and *S. m. alascensis* (n = 12) and *S. trowbridgii* (n = 29—sensu Jackson, 1928) from Alaska, Washington, or Oregon. Prepared skulls were weighed to the nearest 0.0001 g on a Mettler AE 240 digital balance, placed in a dermestid colony for 2–5 days for removal of soft tissues, cleaned of frass, and reweighed. We considered the net value between the two weights to be an index to the mass of the temporalis muscle because the temporalis constitutes 61–70% of the total masticatory musculature (Dötsch, 1983, 1985). All specimens ultimately were prepared as complete skeletons or as skins and partial skeletons for deposit in the Oregon State University, Department of Fisheries and Wildlife mammal collection (OSUFW).

Condylobasal length was measured with a Fowler Max-Cal electronic caliper to the nearest 0.01 mm. Length of the mandible (parallel to the ventral edge of the right dentary) from the lower condylar facet (the pivot during closure of the soricine jaw—Fearnhead et al., 1955) to the tip of I_1 (first lower incisor) and to the metaconid of M_1 (first lower molar), coronoid-condyloid length, and the angle (α) subtended by a line from the apex of the coronoid process through the distalmost extension of the lower condylar facet and a line along the ventral edge of the right dentary (Fig. 1a) were measured

with an ocular micrometer or ocular protractor mounted in a Bausch and Lomb binocular microscope. The same linear and angular dimensions were measured on skulls of museum specimens for *S. b. bairdii* (n = 16—sensu Carraway, 1990); and *S. preblei* (n = 22), *S. palustris* (n = 13), *S. bendirii palmeri* (n = 21), *S. merriami* (n = 13—sensu Jackson, 1928), and additional *S. m. alascensis* (n = 17) on deposit in the Oregon State University, Department of Fisheries and Wildlife mammal collection. All 12 taxa were classified according to the presence, size, and position of the median tine on I^1 by LNC.

Jaw Mechanics and Bite Force.—The soricine jaw (Fig. 1b) may be considered a type I lever (MacDonald and Burns, 1975) with the lower condylar facet serving as the fulcrum (Fearnhead et al., 1955) and with the muscle moment arm (coronoid-condyloid length) set at an acute angle to the resistance moment arm (lower condylar facet to the tip of I_1 or to the metaconid of M_1). This can be represented by the simple formula:

$$\text{bite force} = \cos \theta \, A/B \qquad (1)$$

where, $\theta = 90° - \alpha$, $\cos \theta$ is the proportion of the force vector directed at a right angle to the muscle moment arm, A is the length of the muscle moment arm, and B is the length of the resistance moment arm. We regarded values calculated by use of this formula to be an index to bite force, because we considered the force applied in the closure of the jaw to be that supplied solely by the temporalis muscle and the direction of that force to be parallel to the ventral edge of the dentary. Thus, if the force applied to the muscle moment arm remains constant, bite force may be increased by lengthening the muscle moment arm in relation to the length of the resistance moment arm, by decreasing the length of the resistance moment arm in relation to the length of the muscle moment arm, or by altering θ such that it becomes more acute (α becomes more obtuse).

Analysis.—Means of bite force, and means of linear and angular variables were calculated for each taxon. From these summary statistics (Table 1) linear regressions in STATGRAPHICS (Statistical Graphics Corporation, 1987) were performed to ascertain the degree of relationship between bite force and other variables as a method of evaluating the contribution of each of the variables to bite force. Deviations (Fons et al., 1984) from the "average" shrew were calculated to provide an index to the degree of allometry of the jaw among shrew taxa; this was presented as the percentage of the expected "average" shrew.

Results and Discussion

Morphology of the Median Tine on I^1.—Sorex sonomae (both subspecies) and *S. merriami* have no median tines (Fig. 2a, b, c); the anterior cusps of I^1s usually are parallel and appressed (for a greater proportion of their length in *S. sonomae*). *Sorex pacificus* has parallel cusps on I^1s separated by a ridge that extends along as much as 50% of the posteromedial edge of each cusp (Fig. 2d). *Sorex bendirii* and *S. palustris* have median tines (contrary to previously reported absence of a tine in the latter—Verts and Carraway, 1984; Jameson and Peeters, 1988) set within the pigmented area between divergent I^1s (Fig. 2e, f). *Sorex trowbridgii* and *S. vagrans* have short, somewhat obtuse tines set above the pigmented area at about 20–30° to the long axis of I^1s; in both species the tines commonly are not in direct opposition (Fig. 2g, h). Tine morphology is extremely variable in *S. vagrans*, but I^1s usually are parallel and not greatly divergent (Carraway, 1990); in *S. trowbridgii*, I^1s are widely divergent (Carraway, 1987). *Sorex monticolus* (both subspecies), *S. bairdii*, and *S. preblei* have relatively long, acutely pointed tines set within the pigmented area on I^1s (Fig. 2i, j, k, l). The coastal forms *S. monticolus* and *S. bairdii* exhibit a cline in angle of the tine from about 15–20° in *S. m. alascensis* from Alaska to about 15° in *S. m. setosus* from Washington to about 10° in *S. bairdii* from Oregon. Thus, a cline from most-divergent to least-divergent I^1s is apparent.

Mass of the Masticatory Musculature.—Mean (± SE) proportions of the weight of prepared skulls composed of soft tissues removed by dermestids ranged from 70.9 ± 0.3% to 76.6 ± 0.3% for the seven taxa analyzed. Also, the relationship between the weight of soft tissues removed to condylobasal length (Fig. 3) was significant (r^2 = 0.9613; $P < 0.0001$). The narrow range of proportions and this strong relationship indicate that the weight of the masticatory musculature is proportional to the size of the animal, a situation identical to that found for European soricids (Dötsch, 1985). Turnbull (1970:243–244) opined that although "muscle pull is not necessarily always directly proportional to muscle weight (or mass)...in general there is an approach to direct proportionality between muscle mass and force and that this is a reasonable first approximation of the actual condition." Consequently, we chose to ignore muscle pull in considering other factors that affected bite force and to consider condylobasal length as an index to muscle mass to examine other relationships. Because our findings paralleled those of Dötsch (1985) we considered it appropriate to extrapolate the direct relationship of muscle mass to condylobasal length to taxa for which we had no direct measure of muscle mass, thereby permitting use of prepared museum specimens in subsequent analyses. Kiltie (1982:189) believed that "reasonable predictions of relative bite force can be made if the parameters involved are estimated by the same criteria for the species being compared."

Relative Bite Force Among 12 Taxa of Sorex *from Western North America.*—Bite force at the tip of I_1 (Fig. 4a) was poorly correlated with condylobasal length (r^2 = 0.2775; $P > 0.07$), but at the metaconid of M_1 (Fig. 4b) the correlation was stronger (r^2 = 0.6118; $P < 0.05$). For shrew taxa that do not possess a median tine on I^1 and in which I^1s are parallel and appressed (*S. s. sonomae*, *S. s. tenelliodus*, and *S. merriami*) bite force at I_1 was 106–112% (104–111% at M_1) of that expected on the basis of size (as indexed by condylobasal length). For the taxon that possesses a posteromedial ridge on I^1 and in which I^1s are parallel but slightly separated (*S. pacificus*) bite force at I_1 was 104% (104% at M_1) of expected. For the taxon with a rather blunt, high-set tine on I^1 and separated but parallel I^1s (*S. vagrans*), bite force at I_1 was 99% (99% at M_1) of expected. For taxa with a long, low-set tine and slightly divergent I^1s (*S. bairdii*, *S. m. alascensis*, *S. m. setosus*, and *S. preblei*), bite force at I_1 was 93–103% (94–103% at M_1) of expected (Fig. 4a, b). Lastly, for taxa with a low-set tine and widely divergent I^1s or with a blunt tine and

widely divergent I^1s (*S. bendirii*, *S. palustris*, and *S. trowbridgii*), bite force at I_1 was 92–94% (93–96% at M_1). Thus, except for *S. bairdii*, it appears that shrews with the more parallel and less divergent I^1s (Fig. 2) have progressively greater bite force. Also, there was a north–south increase in bite force among *S. m. alascensis*, *S. m. setosus*, *S. bairdii*, *S. pacificus*, *S. s. tenelliodus*, and *S. s. sonomae* (Fig. 4), taxa distributed along the Pacific Coast. These trends support those predicted by Carraway (1990).

Mechanisms Responsible for Differences in Bite Force.—If the mass of masticatory musculature for all 12 taxa we examined is correlated as strongly with condylobasal length as it was for the seven taxa for which we have a direct measure of muscle mass, then the relationship between condylobasal length and the variables described in equation 1 should provide insight into morphological differences among taxa that produced differences in bite force. Disproportionately shorter resistance lever arms were not responsible for greater bite forces calculated for species without a median tine, with a posteromedial ridge, or with a small tine, because the distance from the lower condylar facet to neither the tip of I_1 nor the metaconid of M_1 deviated from expected based on condylobasal length by more than 3%, most by no more than 1% (Fig. 5a, b). In only *S. palustris* and *S. bendirii* was the resistance arm shorter than expected by as much as 3% (Fig. 5a, b). In *S. merriami* and *S. s. sonomae*, both without median tines, the coronoid-condyloid length was 110% and 109% of expected on the basis of condylobasal length, respectively (Fig. 5c). In both *S. s. tenelliodus* and *S. pacificus* the length was 103% of expected. In *S. bairdii*, the geographical intermediate between the latter three taxa and the long-tined taxa to the north, the coronoid-condyloid length was 101% of expected. In *S. bendirii*, *S. palustris*, *S. m. setosus*, *S. m. alascensis*, *S. trowbridgii*, *S. vagrans*, and *S. preblei*, the coronoid-condyloid length was only 92–100% of expected (Fig. 5c). Thus, those species that have the greatest bite force may have developed it by evolving longer coronoid processes. However, if all else remains equal, an increase in the height of the coronoid process would not only increase the length of the muscle moment arm, but it also would reduce angle θ so that the force vector to the muscle moment arm would be more acute. Indeed, angle θ was 90–96% of expected for *S. merriami*, *S. bairdii*, *S. s. tenelliodus*, *S. s. sonomae*, and *S. pacificus*, taxa (except *S. bairdii*) without tines or with only a ridge, and 102–110% of expected for the remaining taxa (Fig. 5d). However, on the basis of the coronoid-condyloid length, angle θ was only 92–96% of expected for *S. merriami*, *S. bairdii*, *S. s. tenelliodus*, and *S. pacificus* (Fig. 5e). Thus, in these four taxa, bite force was increased not only by lengthening the muscle moment arm but also by further reducing angle θ. In *S. s. sonomae*, bite force was enhanced by the longer muscle moment arm, but reduced slightly by the small increase in angle θ relative to that expected on the basis of greater length of the muscle moment arm (Fig. 5e). Except for *S. bendirii*, angle θ in the remaining species was 101–105% of expected on the basis of the length of the muscle moment arm (Fig. 5e). *Sorex bendirii*, the largest member of the genus in North America, not only has a muscle moment arm only 96% of expected on the basis of size (Fig. 5c), but angle θ is 110% of expected on the basis of length of the muscle moment arm (Fig. 5e), explaining the least relative bite force at I_1 (Fig. 4a) among the 12 taxa examined. The somewhat greater relative bite force at M_1 for *S. bendirii* may be explained by a shorter length of mandible to M_1 than expected (Fig. 5b). Because of the shorter-than-expected coronoid-condyloid length and greater-than-expected angle θ, bite force in *S. palustris* (Fig. 4) no doubt would be even less than observed had not the length of both resistance moment arms been less than expected on the basis of condylobasal length (Fig. 5a and 5b).

Bite Force, Tine Morphology, Diet, and Habitat of Shrews.—*Sorex merriami* is a shrew of the sagebrush (*Artemisia*) desert and short-grass prairie (Brown, 1967; George, 1990) and *S. sonomae* is a shrew of the fogbelt of the Pacific Coast (Carraway, 1990). Foods eaten by *S. merriami* consist largely of Lepidoptera larvae, beetles (Coleoptera: Carabidae and Tenebrionidae), and cave crickets (Orthoptera: *Ceuthophilus*—Johnson and Clanton, 1954). Because of the small size of this shrew (Armstrong and Jones, 1971) and its relatively large hard-bodied prey, possession of greater bite force than a similar-sized shrew that occupies more mesic habitats seemingly would be a distinct advantage. Snails and slugs (Gastropoda) and large beetles (Coleoptera: Cicindelidae), abundant in coastal habitats occupied, are primary foods of *S. sonomae* (Maser, 1973; Whitaker and Maser, 1976). Greater bite force in this species likely is an advantage in piercing the calcareous shells of snails and the tough skin of slugs, and immobilization of beetles. In both *S. merriami* and *S. sonomae*, I^1s are appressed for some or most of their length because of the absence of encumbering tines, thereby permitting the rapid piercing of prey to subdue it. Although the function of the I^1s in piercing is attributed to shrews in general (Pernetta, 1977), such would seem a particularly desirable attribute for shrews that feed on large or especially hard or tough-skinned prey.

Sorex pacificus (sensu Carraway, 1990), the shrew with the next strongest bite force, is often found in moist, wooded areas with fallen decaying logs and brushy vegetation (Bailey, 1936). Its diet consists of 29 of the 47 food items found in stomachs of five species of shrews examined, with internal organs of adult insects comprising 28.6% by volume of its stomach contents (Whitaker and Maser, 1976). It also immobilizes and caches cicindelids then later consumes their softer parts (Maser, 1973). This diet, combined with a greater-than-expected bite force (Fig. 4), suggests that the parallel, only slightly separated I^1s are an adaptation for capturing, immobilizing, killing, and eviscerating hard-bodied prey.

Sorex trowbridgii usually is considered a forest-dwelling species; it occurs in all stages of the sere, and is most abundant near logs surrounded with large quantities of ground litter where other species of shrews are absent (Dalquest, 1948; Jameson, 1955; Whitaker and Maser, 1976; Terry, 1981). It is considered to have the least specialized diet of shrews in western Oregon; it consumed all 47 food items found in stomachs of five species of shrews. Centipedes (Chilopoda) were the most common food (Whitaker and Maser, 1976).

Sorex vagrans is associated with grasslands and meadows (Terry, 1981) and, within these habitats, also tends to be a food generalist with 30 of the 47 food items occurring in its diet (Whitaker and Maser, 1976); no identified item comprised >14% by volume of stomach contents. Also, *S. vagrans* is able to shift its diet depending on habitat conditions (Whitaker et al., 1983). The strongly divergent I^1s (possibly related to the obtuse tines set at about 20–30° to the long axis of the I^1s) in *S. trowbridgii*, the extremely variable tine morphology observed in *S. vagrans* (Carraway, 1990), and the less-than-expected bite force in both species (Fig. 4) may be related to their generalized diets.

Habitat relationships of the relatively rare *S. preblei* are poorly understood. Specimens have been collected in a wide variety of habitats ranging from marshes and riparian areas to sagebrush-steppe (Bailey, 1936; Verts, 1975; Hoffmann and Fisher, 1978; Larrison and Johnson, 1981; Tomasi and Hoffmann, 1984; Williams, 1984; Ports and George, 1990). The remaining long-tined shrews (*S. bairdii* and both subspecies of *S. monticolus*) usually are species of montane and coastal forests (Bailey, 1936; Dalquest, 1948; Williams, 1955; Hennings and Hoffmann, 1977; Wrigley et al., 1979; Terry, 1981). The diet of *S. monticolus* consisted of 58.8% by volume of insect larvae and soft-bodied invertebrates (S. Churchfield, personal communication) as would be expected based on its less-than-expected bite force and mesic habitat affinity. Apparently, nothing is known regarding the diets of *S. preblei* and *S. bairdii*. However, based on the less-than-expected bite force and probably mesic habitat of *S. preblei*, we suggest that its diet may consist of soft-bodied prey. Conversely, the greater-than-expected bite force of *S. bairdii* suggests harder prey despite its association with habitats subject to high levels of precipitation. We are unable to offer a reasonable explanation of how the elongate tine, set nearly parallel to the long axis of the anterior cusp of I^1 (Fig. 2), might function in capturing and dispatching prey.

At the opposite end of the bite-force spectrum from shrews without median tines are *S. bendirii*, a shrew of marsh areas with standing water (Pattie, 1969), and *S. palustris*, a shrew of riparian zones (Beneski and Stinson, 1987). Of five species of shrews examined in western Oregon by Whitaker and Maser (1976), *S. bendirii* had the most specialized diet; at least 25% of the prey consumed were aquatic with mayfly naiads (Ephemeroptera) and earthworms (Oligochaeta: Lumbricidae) the top foods. Aquatic organisms were primary food items in stomachs of *S. palustris* (Conaway, 1952; Linzey and Linzey, 1973; Whitaker and French, 1984). The soft-bodied prey likely require little effort either to subdue or to dispatch; thus, specializations of jaw mechanics to enhance bite force seemingly are unnecessary. In contrast, the widely divergent I^1s (reminiscent of those of *S. trowbridgii*) suggest a more generalized diet than reported.

Conclusions

Because mass of the masticatory musculature is so strongly correlated with size (as indexed by condylobasal length), and because muscle mass can be used as an index to force applied, differences in mandibular morphology seem nearly wholly responsible for differences in bite force among taxa of *Sorex* in western North America. Differences in bite force among taxa, other than that related to size, are related largely to coronoid-condyloid length and to angle ϴ. Bite force per se seems correlated positively with the absence or reduced size of the tine on I^1 and the corresponding greater appression of the I^1s (accounting at least in part, for the observed north–south increase in bite force among several taxa), greater aridity of habitats, and greater hardness of foods eaten by shrews.

We suggest that both the characters that caused us to investigate the role of bite force in avoidance of competition among syntopic shrews (appressed I^1s and lack of tines on I^1s) and the characters primarily responsible for an increase in bite force (a more acute angle ϴ, a longer muscle moment arm, and shorter resistance moment arms) are derived morphological characters. Phylogenies based on morphometric (Findley, 1955) and allozymic electrophoretic (George, 1988) studies are congruent, with *S. trowbridgii* and *S. merriami* placed in an unnamed subgenus (George, 1988) and the remaining taxa that we investigated placed in the subgenus *Otisorex*. Therefore, we offer as evidence of the derived condition, the character states of presence of appressed I^1s and lack of tines on I^1s in members of two subgenera (*S. merriami* in the unnamed subgenus and *S. sonomae* in *Otisorex*). In addition, the north–south cline in tine morphology in closely related taxa (large, acutely angled tines in *S. monticolus* to short, less acutely angled tines in *S. bairdii* to posteromedial ridges in *S. pacificus* to complete absence of tines in *S. sonomae*) along the Pacific Coast (Carraway, 1990) adds support to our contention. Finally, for characters responsible for an increase in relative bite force, we offer as supportive evidence of the derived condition, the occurrence of a more acute angle ϴ, a longer muscle moment arm, and shorter resistant moment arms in some but not all taxa of both subgenera (Fig. 5). The derived condition, and the apparent relationship among bite force, tine morphology, diet, and conditions of the physical environment, suggest that the state of these characters among the several taxa examined are adaptive to current ecological conditions. We believe that the correlations of bite force and tine morphology with ecological conditions were sufficient for us to reject our hypothesis that these characters and factors were unrelated. Consequently, bite force, as it affects diet, probably is sufficient to explain avoidance of excessive competition among the several syntopic taxa of *Sorex* in western Oregon.

We suggest that the imprecision of the correlations we found was related more to the lack of knowledge of diets and habitat affinities of the specific populations of shrews that we studied than to the crudeness of our measures of bite force or our classification of tine morphology. We also suggest that precise and species-specific information on shrew behavior relative to their capturing, dispatching, and dissecting prey may provide explanations for discrepancies we observed in the postulated relationships.

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Table 1.—*Means (± SE) of linear (mm) and angular (degrees) skull dimensions, mass (g) of masticatory musculature removed by dermestids, and calculated indices to bite force for 12 taxa of western* Sorex.

Taxon	*n*	Condylobasal Length	Length of Mandible: Tip of I_1 (*B*)	Length of Mandible: Metaconid of M_1 (*B*)	Coronoid-condyloid Length (*A*)	Angle ϴ	Mass: Masticatory Musculature[a]	Index to Bite Force[b]: Tip of I_1	Index to Bite Force[b]: Metaconid of M_1
Sorex s. sonomae	28	21.41 ± 0.14	13.44 ± 0.10	7.85 ± 0.06	5.15 ± 0.05	28.50 ± 0.54	0.64 ± 0.02	0.34 ± 0.00[c]	0.58 ± 0.01
S. s. tenelliodus	88	19.84 ± 0.04	12.22 ± 0.04	7.17 ± 0.02	4.42 ± 0.02	28.60 ± 0.27	0.50 ± 0.01	0.32 ± 0.00[c]	0.54 ± 0.00[c]
S. merriami	13	15.91 ± 0.10	9.36 ± 0.05	5.67 ± 0.04	3.44 ± 0.03	31.15 ± 0.93		0.31 ± 0.00[c]	0.52 ± 0.01
S. pacificus	20	19.64 ± 0.06	12.38 ± 0.06	7.17 ± 0.03	4.36 ± 0.03	28.00 ± 0.50	0.46 ± 0.01	0.31 ± 0.00[c]	0.54 ± 0.00[c]
S. bendirii	21	23.57 ± 0.13	15.13 ± 0.09	8.08 ± 0.05	5.17 ± 0.05	30.86 ± 0.68		0.29 ± 0.00[c]	0.55 ± 0.01
S. palustris	13	19.70 ± 0.15	11.78 ± 0.12	6.80 ± 0.04	3.92 ± 0.04	32.00 ± 0.71		0.28 ± 0.00[c]	0.49 ± 0.01
S. trowbridgii	29	17.15 ± 0.05	10.17 ± 0.03	6.00 ± 0.02	3.29 ± 0.02	34.76 ± 0.33	0.22 ± 0.01	0.27 ± 0.00[c]	0.45 ± 0.00[c]
S. vagrans	25	16.27 ± 0.06	9.42 ± 0.06	5.66 ± 0.03	3.23 ± 0.02	35.56 ± 0.44	0.20 ± 0.01	0.28 ± 0.00[c]	0.46 ± 0.00[c]
S. monticolus setosus	54	17.29 ± 0.04	10.41 ± 0.04	6.12 ± 0.02	3.49 ± 0.01	33.36 ± 0.35	0.29 ± 0.01	0.28 ± 0.00[c]	0.48 ± 0.00[c]
S. m. alascensis	29	17.60 ± 0.06	10.63 ± 0.06	6.20 ± 0.03	3.42 ± 0.02	33.48 ± 0.28	0.24 ± 0.02[d]	0.27 ± 0.00[c]	0.46 ± 0.00[c]
S. bairdii	16	18.55 ± 0.21	11.29 ± 0.18	6.59 ± 0.10	3.95 ± 0.07	30.38 ± 0.81		0.30 ± 0.00[c]	0.52 ± 0.01
S. preblei	22	14.61 ± 0.07	8.43 ± 0.04	5.06 ± 0.02	2.72 ± 0.02	35.95 ± 0.54		0.26 ± 0.00[c]	0.43 ± 0.00[c]

[a] Taxa for which values are missing were museum specimens.
[b] Bite force = $\cos \ominus A/B$.
[c] SE < 0.005.
[d] $n = 12$.

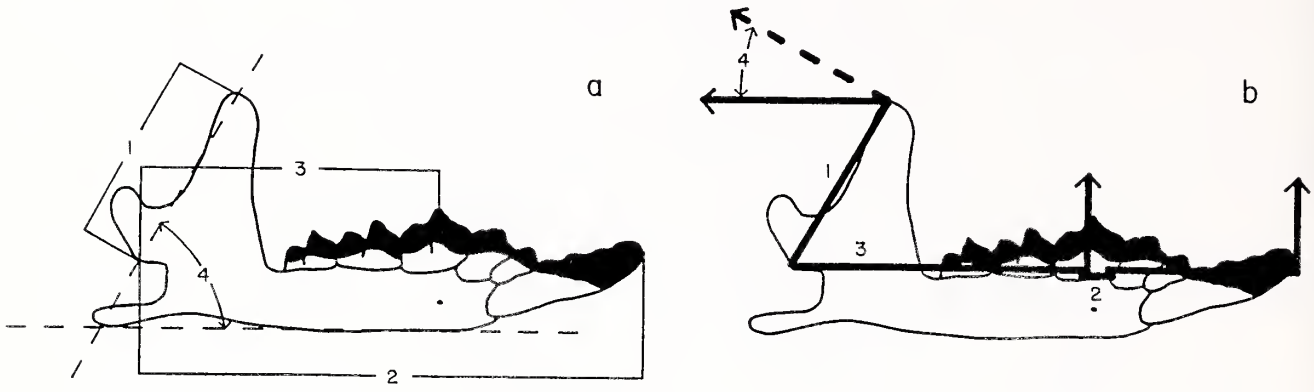

Fig. 1.—Camera-lucida tracings of lateral view of mandibles of a typical *Sorex* overlain with: a, dimensions and angle measured: 1, coronoid-condyloid length; 2, length of mandible to tip of I_1; 3, length of mandible to metaconid of M_1; 4, angle α and b, with lever arms and angle used in calculating bite force: 1, muscle moment arm; 2 and 3, resistance moment arms; 4, angle $\theta = (90° - \alpha)$.

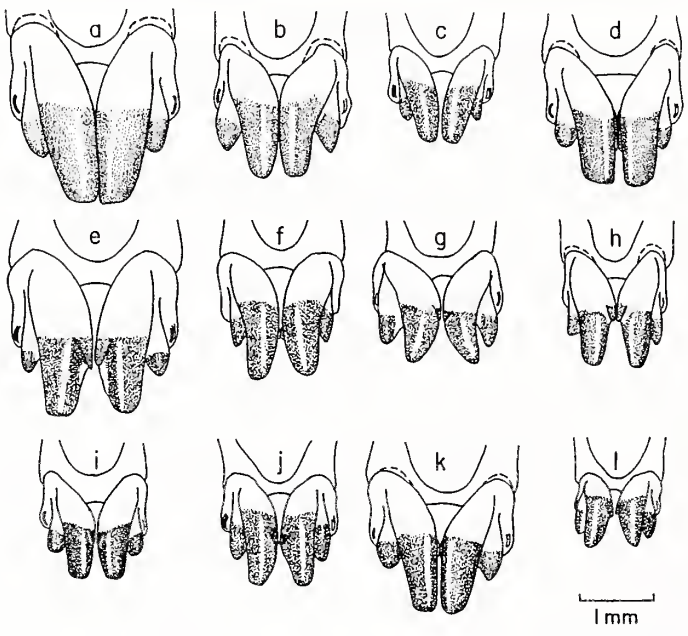

Fig. 2.—Camera-lucida tracings of anterior view of I^1s of 12 taxa of *Sorex* from western North America for which bite force was measured: a, *S. s. sonomae* (PSM 14424); b, *S. s. tenelliodus* (OSUFW 7286); c, *S. merriami* (OSUFW 3546); d, *S. pacificus* (OSUFW 4837); e, *S. bendirii* (OSUFW 7382); f, *S. palustris* (OSUFW 4857); g, *S. trowbridgii* (PSM 5892); h, *S. vagrans* (SDNHM 16971); i, *S. monticolus setosus* (PSM 2075); j, *S. m. alascensis* (OSUFW X-1719); k, *S. bairdii* (OSUFW 9041); and l, *S. preblei* (OSUFW 3859).

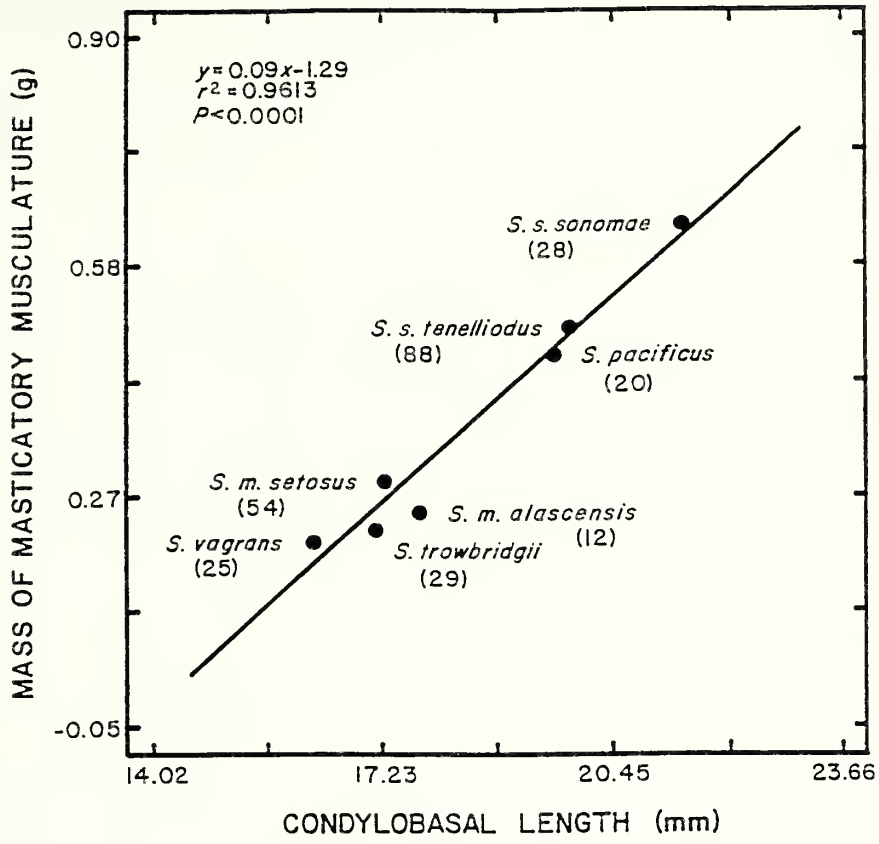

Fig. 3.—The relationship between mean condylobasal length and mean mass of the masticatory musculature for seven taxa of *Sorex* from western North America (*n* in parentheses).

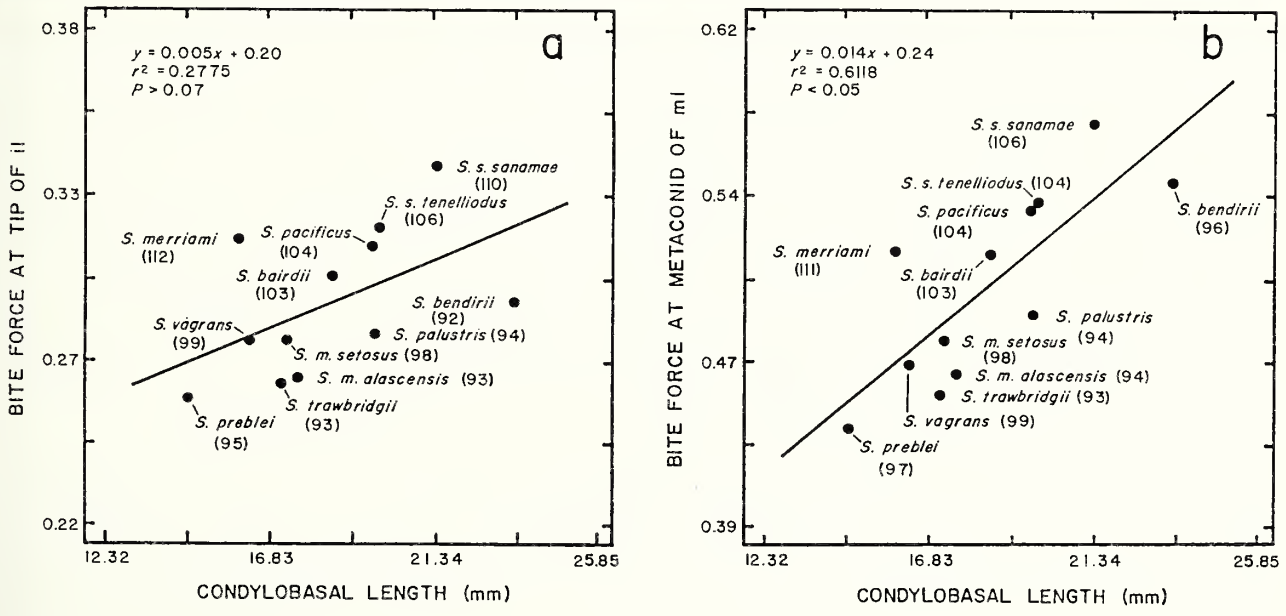

Fig. 4.—The relationship between condylobasal length and a, bite force at tip of I_1 and b, bite force at the metaconid of M_1 for 12 taxa of *Sorex* from western North America. Percent deviation from "average" shrew (value expected based on condylobasal length) in parentheses.

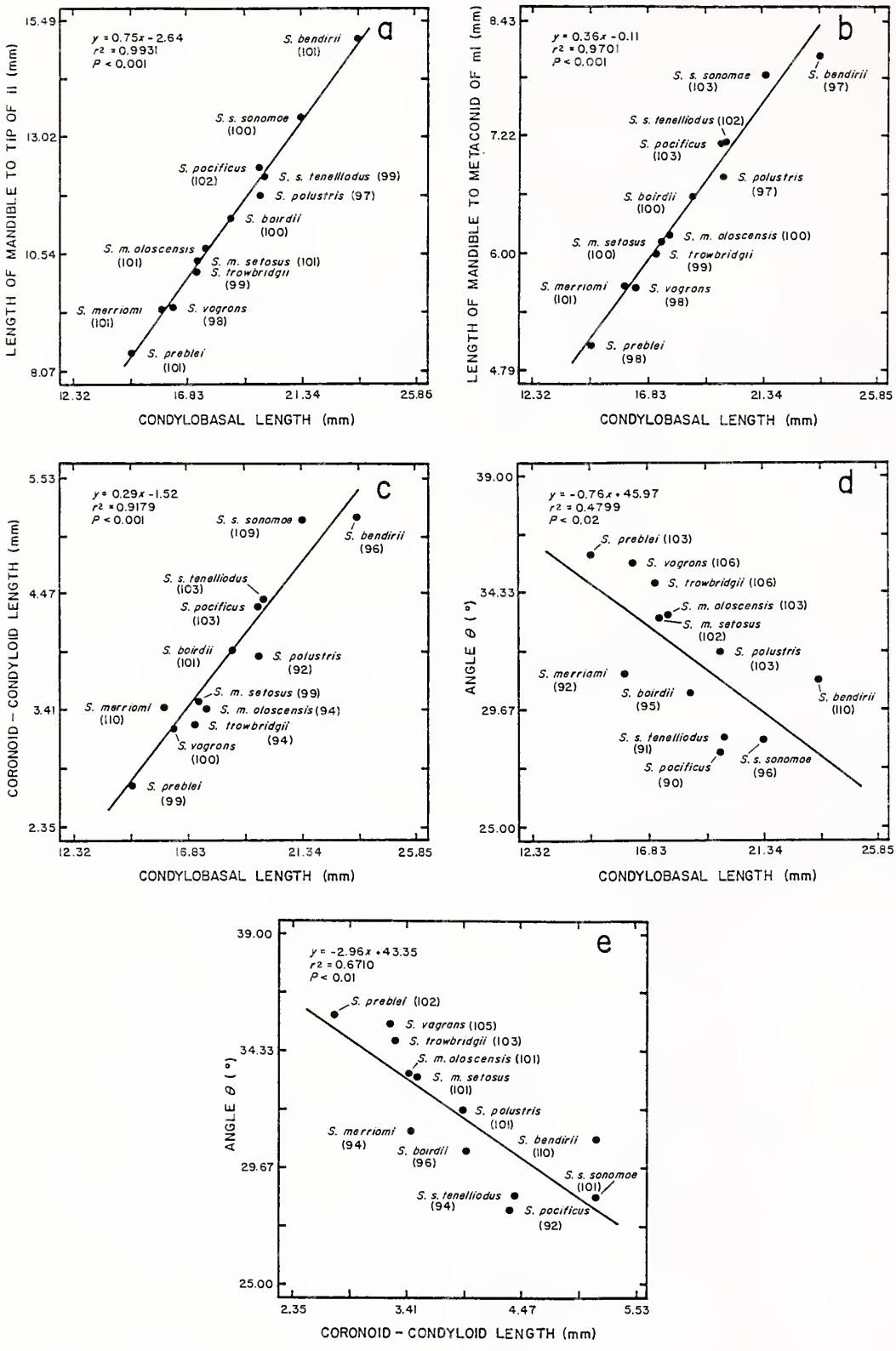

Fig. 5.—The relationship between condylobasal length and a, length of mandible to tip of I_1; b, length of mandible to metaconid of M_1; c, coronoid-condyloid length; d, angle θ; and e, between coronoid-condyloid length and angle θ. Percent deviation from "average" shrew (value expected based on condylobasal length) in parentheses.

ULTRASTRUCTURE OF THE OLFACTORY EPITHELIUM OF THE SHORT-TAILED SHREW, *BLARINA BREVICAUDA*

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ABSTRACT

The ultrastructure of the olfactory epithelium has been investigated in many vertebrates including mammals of several orders. Although these reports indicate that there are basic similarities as well as significant differences, epithelial organization does not appear to eorrelate with evolutionary development or ecological niche, especially among mammals. Few reports on the ultrastructure of insectivore olfactory epithelium are available; therefore, we investigated the fine structure of the olfaetory epithelium of *Blarina brevicauda*, the short-tailed shrew. This species was especially appropriate because its brain has relatively well-developed olfactory regions. The olfactory epithelium from several male shrews was prepared for transmission electron microscopy and investigated in detail. The basic strueture of the shrew olfactory epithelium is similar to that reported for other mammals. A distinctive supporting cell with a different ultrastructure was noted among the more numerous and typical supporting eells. The shrew olfactory epithelium is not distinctive in its organization or complexity compared to that of other mammals, but it does appear to provide the anatomical substrate for significant olfactory sensation.

INTRODUCTION

Schultze (1856, 1862) provided the earliest histological description of the vertebrate olfactory epithelium and distinguished three types of cells—receptor, supporting, and basal cells. Since that time, numerous reports have appeared supporting those observations, and more detailed studies have been made using electron microscopy (Seifert, 1970; Graziadei, 1973). These basic cell types have similar morphology in a wide variety of vertebrates including the Insectivora (Wohrmann-Repenning, 1975). However, significant differences have been detected between species even within orders of mammals (Gemmell and Nelson, 1988). There have been few studies of the ultrastructure of the olfactory epithelium in the Insectivora (Graziadei, 1966) and none of these have involved the Soricidae.

Since morphometric studies of the olfactory system of shrews have supported the hypothesis that olfaction is of prime importance in these animals (Baron et al., 1983, 1987; Larochelle and Baron, 1989; Stephan et al., 1984), we supplemented previous investigations by examining the fine structure of the shrew olfactory epithelium. The purpose of our study was to make detailed observations on the olfactory epithelium of *Blarina brevicauda* and to relate that data to what is known about the fine structure of the olfactory epithelium in other mammals.

MATERIALS AND METHODS

Ten *Blarina brevicauda* were collected in the vicinity of Norfolk, Virginia, by live-trapping. Only adult males weighing at least 16 g were used in these studies. Animals were maintained in the laboratory less than 24 hours prior to being sacrificed. During this period the shrews received canned cat food and water ad libitum. Sacrifice was by transcardiac perfusion of fixative in anesthetized animals. The shrews were briefly etherized to facilitate handling and then injected intraperitoneally with 0.2 ml of 2.5% tribromoethanol. Two shrews were sacrificed without etherization to verify that this brief exposure to ether had no observable effect on olfactory epithelium morphology. A 22-gauge needle was inserted into the left ventricle and the vascular system was perfused with about 10 ml of a room temperature solution of 0.9% sodium chloride, 1% sodium nitrite, 5 mg heparin, and 0.05 M phosphate buffer pH 7.4, followed by 100 ml of room temperature 1.25% glutaraldehyde, 1% formaldehyde (from paraformaldehyde) in 0.1 M cacodylate buffer pH 7.4. The perfusion lasted about 30 minutes. Following removal of the brain, the roof of the nasal cavity was excised and turbinates covered with olfactory epithelium were gently removed and placed in fixative containing 2.5% glutaraldehyde, 2% formaldehyde in 0.1 M cacodylate buffer pH 7.4. During this dissection of the turbinates the epithelium was kept covered with fixative. The olfactory epithelium was fixed overnight at 4°C. Following a 30-min rinse in 0.1 M cacodylate buffer pH 7.4 with three changes, the tissues were post-fixed for 2 h at 4°C in 2% osmium tetroxide in 0.1 M cacodylate buffer pH 7.4. The tissues were then rinsed in buffer as before, dehydrated in 10-min steps through a graded ethanol series followed by 100% acetone, infiltrated for 6 h with a 1:1 mixture of epoxy resin and acetone, and for 12 h with 100% epoxy resin. The olfactory epithelium was embedded in flat molds oriented so that cross sections of the epithelium could be cut. Following 48-h polymerization of the epoxy resin (Polybed 812, Polysciences, Warrington, Pennsylvania) at 65°C, the blocks were trimmed for sectioning. One-micron sections were cut with glass knives, mounted on glass slides, and stained with methylene blue/azure II (Richardson et al., 1960). These sections were photographed with a Nikon Biophot microscope. Silver thin sections were cut with a diamond knife using an LKB III ultramicrotome, picked up on naked copper grids,

stained with uranyl acetate and lead citrate, and photographed with a JEOL 100 CXII transmission electron microscope.

Results

Light Microscopic Observations

The olfactory epithelium of the short-tailed shrew varied in thickness from about 17 μ to over 60 μ in different areas of the nasal cavity. In some instances, thick and thin epithelia, both containing olfactory receptor neurons, were located directly adjacent to each other, typically on opposite sides of the supporting vascular and connective tissue matrix of the turbinate (Fig. 1). The epithelial structure was pseudostratified columnar and the nuclei of the three basic cell types, supporting, receptor, and basal, formed distinct layers (Fig. 1). In some animals, many receptor cells were more darkly stained than supporting or basal cells. In other animals, all three cell types were stained to the same degree. Although no systematic study was done, it appeared that the dark receptors were generally not as well fixed as receptors in epithelial regions where all three cell types were the same density. The dark staining could be due to ischemic changes in the cells that occurred during the perfusion before fixative reached those areas. Dendrites topped by olfactory vesicles were common. Supporting cells had abundant cytoplasm. Their nuclei were uppermost in the epithelium and were rounded and lightly stained. In some animals, a relatively small percentage of supporting cells were distinctly pale. The apical surface of these pale cells typically protruded above the adjacent supporting cells. In other areas of the nasal epithelium or in other animals, all supporting cells had the same degree of staining, but there was a small number of cells identical in other respects to the pale cells. These distinctive supporting cells were designated type 2 and the more common supporting cells type 1. Pale supporting cells were more common in areas of epithelium where dark receptors were present, so it is possible that the pale appearance was also due to ischemic changes. No secretory granules were observed in supporting cells. Basal cells had little cytoplasm and also exhibited varying degrees of staining. Mitotic figures were present in this layer. Large groups of axons with surrounding Schwann cells were common in the lamina propria.

Electron Microscopic Observations

Receptor neurons varied in cytoplasmic density (Fig. 2) with some cells having more electron-dense cytoplasm than others. Dark cells were found together in various regions of the olfactory epithelium and often appeared to be less well fixed than less dense receptors. The olfactory vesicle was rounded or cylindrical with 10–15 cilia and contained numerous small, empty, membrane-bound structures of a vesicular or tubular nature. Ciliary microtubule structure had the common 9 + 2 configuration. The dendrite contained many mitochondria and also often had basal body rootlets (Fig. 3). The perikaryal cytoplasm contained numerous mitochondria, sparse profiles of rough endoplasmic reticulum, and a prominent Golgi apparatus (Fig. 2, 4). Type 1 supporting cells had irregular, long, and often branched microvilli on their apical surfaces (Fig. 2, 3, 5). The apical cytoplasm was filled with smooth endoplasmic reticulum that was often aligned in parallel arrays (Fig. 2, 3). Occasional dense granules were observed in the apical cytoplasm. Adjacent supporting cells often appeared to share gap junctions (Fig. 4). Type 2 supporting cells had an apical projection with microvilli that extended above the adjacent supporting cells (Fig. 5). The apical cytoplasm of this type 2 supporting cell lacked the profuse smooth endoplasmic reticulum of the more numerous type 1 supporting cell. The type 2 cell also appeared to have more mitochondria. In some areas of the olfactory epithelium the type 2 cells had cytoplasm with very low electron density. This was common in areas where the receptors had increased density and may have been due to ischemia prior to fixation. In areas with optimal fixation, the type 2 cells had similar cytoplasmic density as the type 1 cells and the receptors. This type 2 cell is similar to a "pale" cell (Kratzing, 1978) and a "microvillar" cell (Moran et al., 1982) previously reported.

Basal cells often had pale cytoplasm that contained many polyribosomes and little rough endoplasmic reticulum (Fig. 6). The nucleus had less heterochromatin than either the supporting or receptor cells. Some basal cells had darker cytoplasm, more nuclear heterochromatin, and processes that surrounded receptor cell axons (Fig. 7).

Discussion

Despite the observation that the olfactory structures constitute a very large proportion of the brain in *Blarina* (Baron et al., 1983, 1987; Stephan et al., 1984), there does not appear to be a corresponding increase in complexity of the organization of the olfactory epithelium. In its general features, the olfactory epithelium of *Blarina brevicauda* is similar to that of other mammals (Arstila and Wersall, 1967; Frisch, 1967; Andres, 1969; Graziadei, 1973; Seifert, 1970; Yamamoto, 1976; Kratzing, 1978; Gemmell and Nelson, 1988). In the only previous ultrastructural study of the olfactory epithelium of an insectivore, Graziadei (1966) reported that the structure of the olfactory epithelium in the mole, *Talpa europaea*, was similar to that of other vertebrates. The structure of the olfactory epithelium of *Blarina* differs from that reported for the mole. The olfactory epithelium of the mole was only 30 μ thick compared to a maximum of 60 μ in *Blarina*. The olfactory vesicle of the mole exhibited relatively few cilia, less than five, compared to as many as 15 observed in the shrew. No distinctive variation in supporting cell morphology, such as that of the type 2 cell, was reported for the mole. The significance of these differences with regard to the evolutionary development of the mammalian olfactory system is not apparent at this time. The organization of the olfactory epithelium of *Blarina* exhibits a complexity that appears to be a sufficient anatomical substrate to support significant olfactory sensitivity. Although it has been suggested that the degree of olfactory system development in shrews may not necessarily indicate a high level of olfactory acuity (Sigmund and Sedlacek, 1985), the basis for such a conclusion does not rest on sufficient behavioral data at the present time. The possible correlation of olfactory system structural complexity and level of olfactory acuity with an

animal's ecological niche and degree of social interaction remains to be resolved by further investigation.

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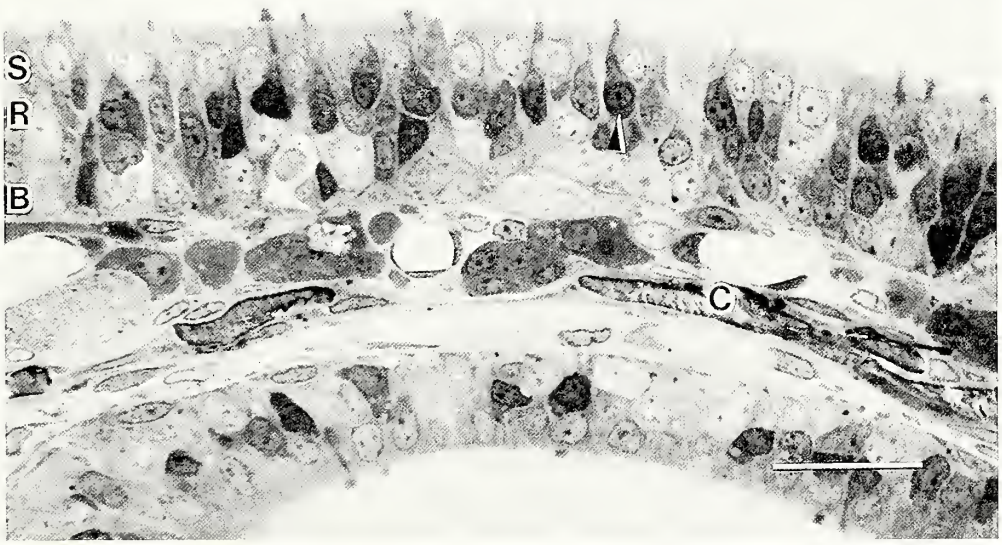

Fig. 1.—Two areas of olfactory epithelium of different thickness are separated by the lamina propria and cartilaginous (C) supports of the turbinate. Cell nuclei of supporting cells (S), receptor cells (R), and basal cells (B) can be distinguished. Receptor cells, their dendrites, and olfactory vesicles are distinct (arrow). Bar equals 50 μ.

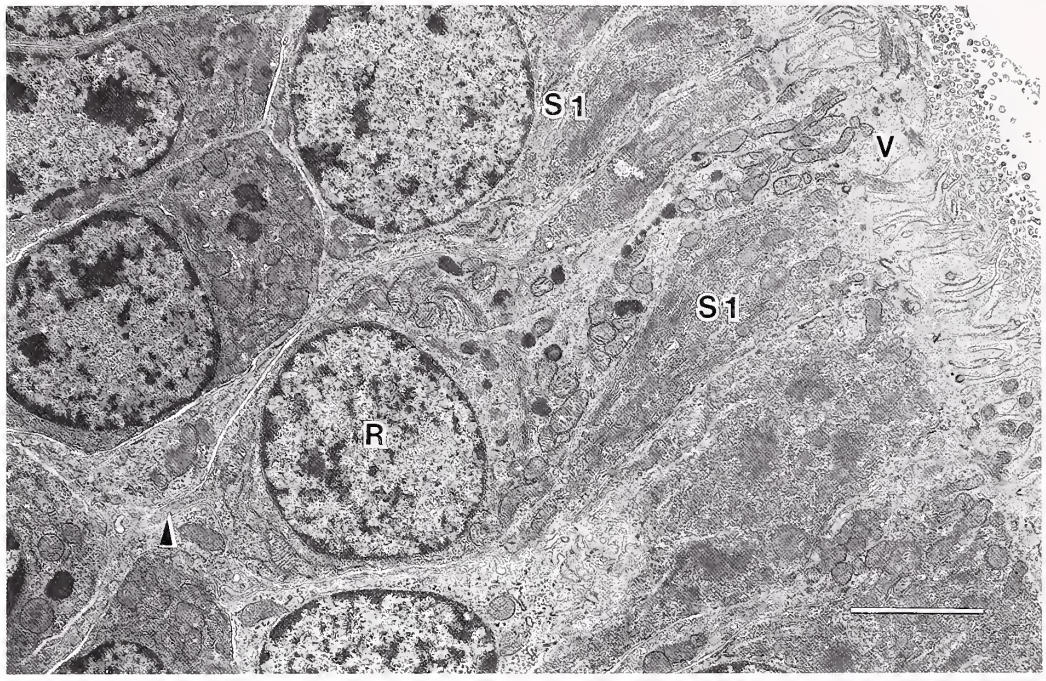

Fig. 2.—This receptor cell (R) has a prominent Golgi apparatus, numerous mitochondria in the dendrite, several cytoplasmic dense bodies, and several cilia emerging from the olfactory vesicle (V). Type 1 supporting cells (S1) with extensive smooth endoplasmic reticulum surround the receptor. A process resembling the axon emerges from the basal surface of the receptor (arrow). Bar equals 3 μ.

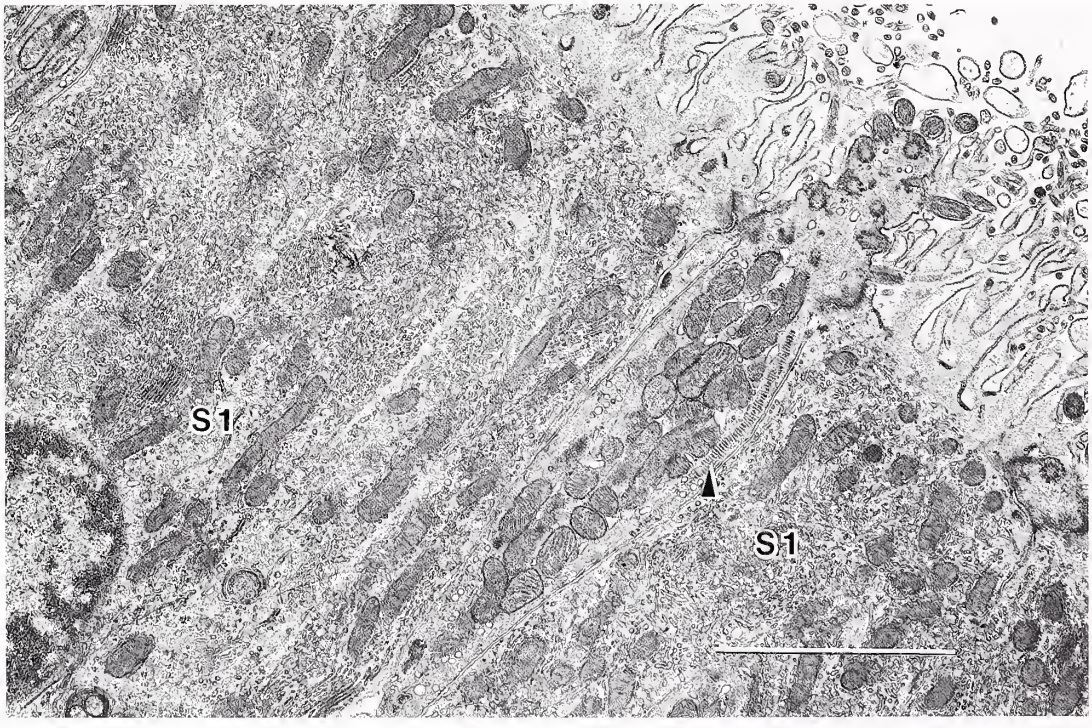

Fig. 3.—The olfactory vesicle of this receptor has a more cylindrical, rather than spherical shape. A basal body rootlet (arrow) is present in the dendrite. The adjacent type 1 supporting cells (S1) have profuse smooth endoplasmic reticulum and irregular, complex microvilli. Bar equals 3 μ.

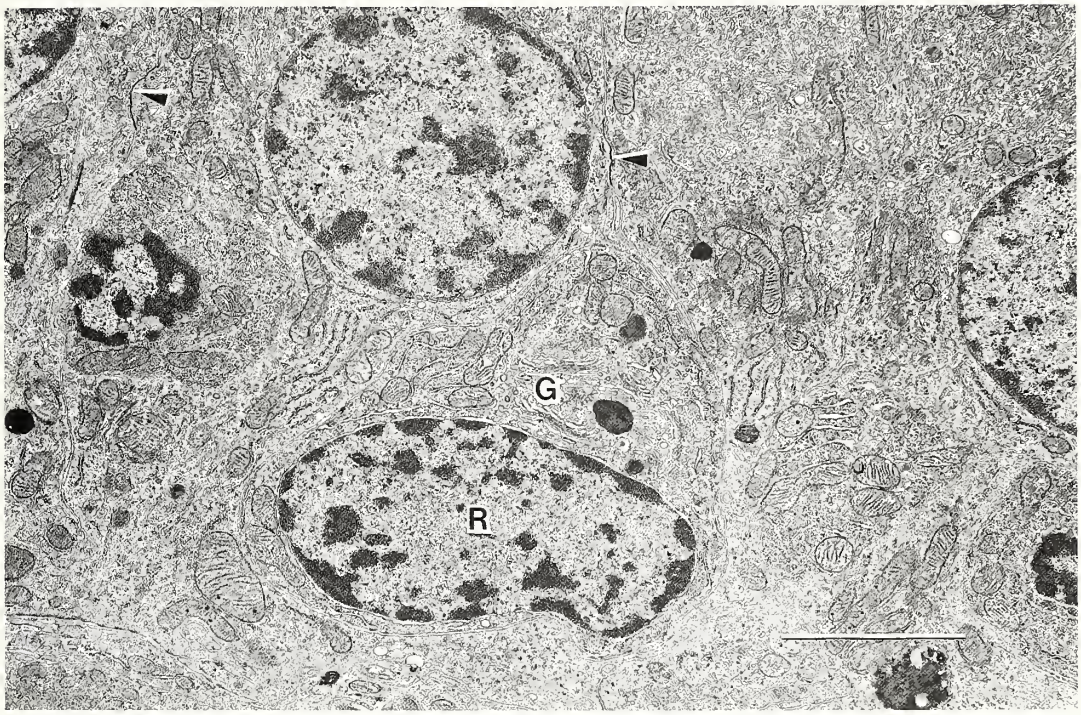

Fig. 4.—The receptor cell (R) perinuclear cytoplasm contains a well-developed Golgi apparatus (G). There are apparent gap junctions between adjacent supporting cells (arrows). Bar equals 3 μ.

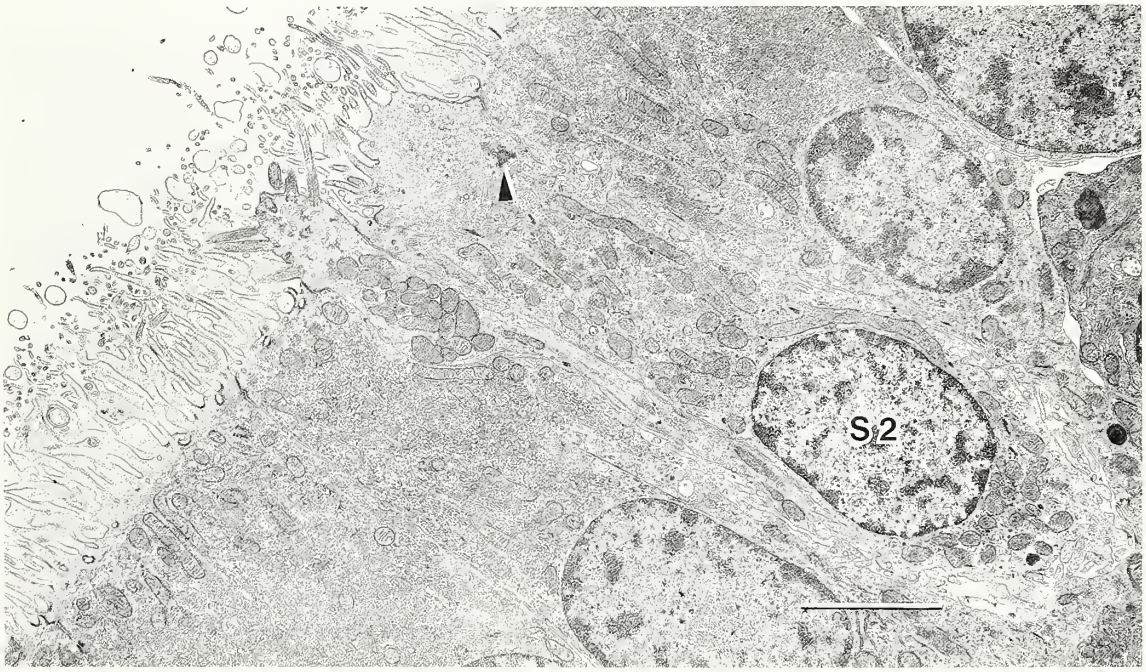

Fig. 5.—This type 2 supporting cell (S2) lacks the profusion of smooth endoplasmic reticulum present in the adjacent supporting cells. The apical portion of the cell has microvilli and projects above the adjacent type 1 supporting cells. There is a centriole in the apical cytoplasm of the type 2 supporting cell (arrow). Bar equals 3 μ.

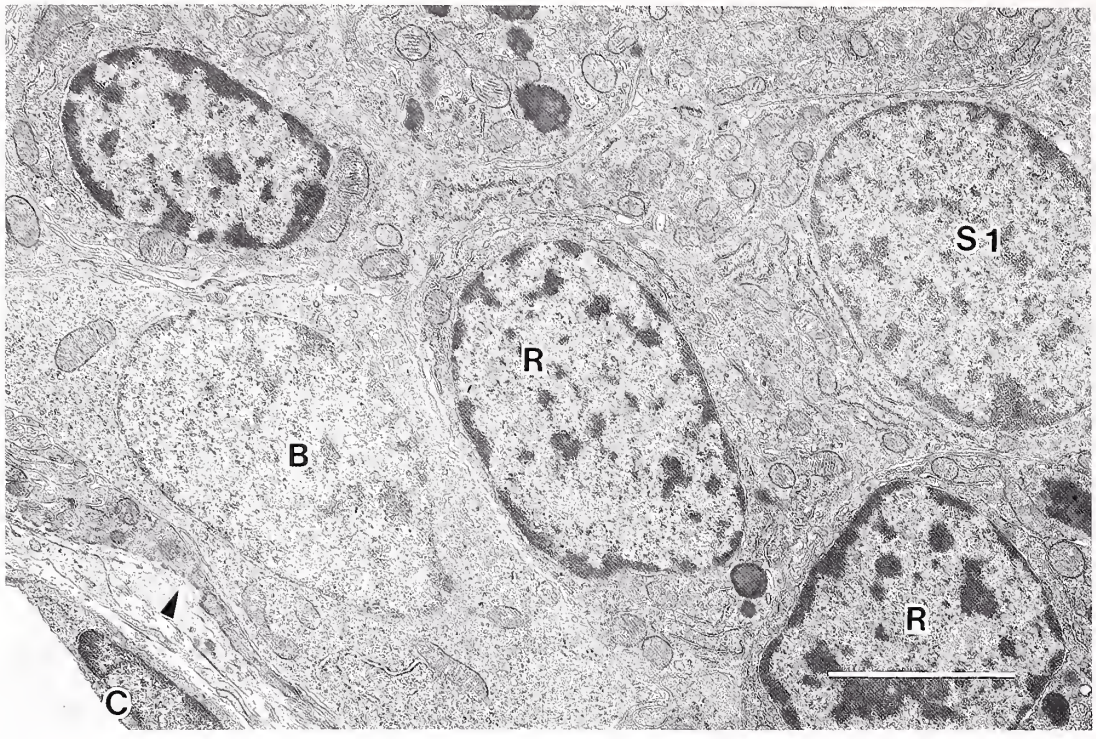

Fig. 6.—This basal cell (B) has many polyribosomes and few other cytoplasmic organelles. Receptor cells (R) and a supporting cell (S1) are nearby. Near the basal cell is the basal lamina (arrow) and a capillary (C) in the lamina propria. Bar equals 3 μ.

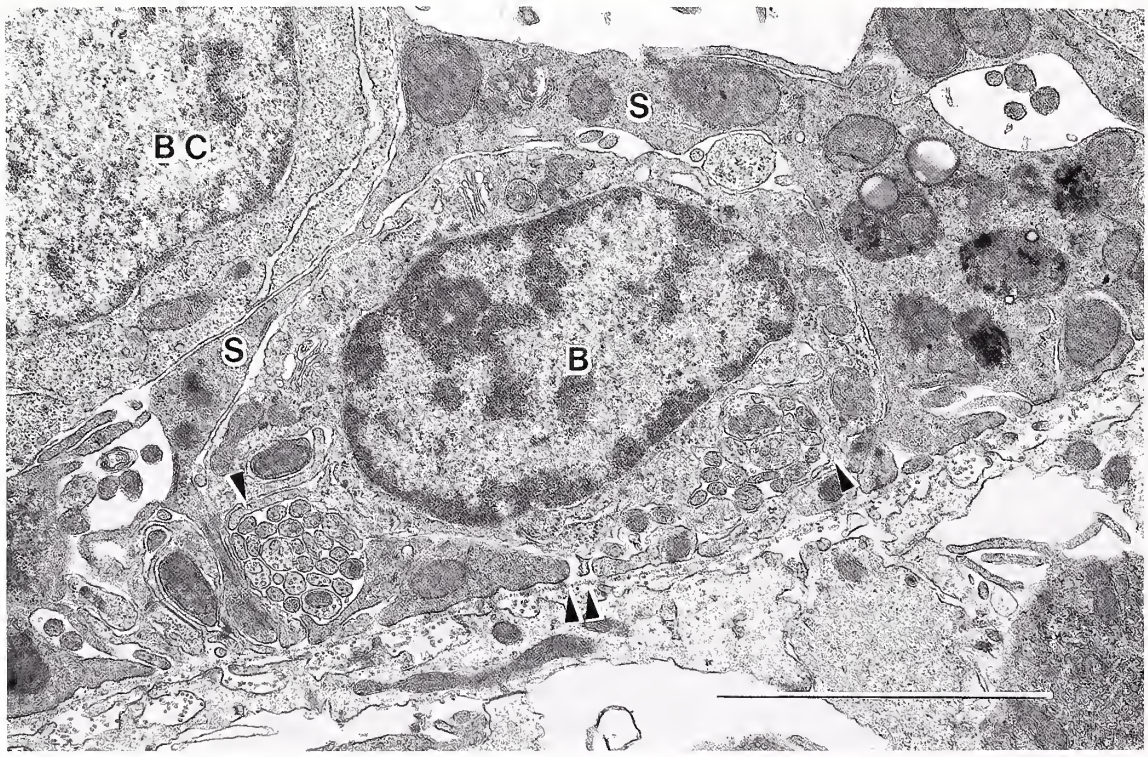

Fig. 7.—Several receptor cell axons (A) are surrounded by processes (arrows) of this distinctive basal cell (B) with denser cytoplasm and nucleus. An adjacent basal cell (BC) has the more typical morphology. Type 1 supporting cell processes (S) encompass the basal cell. The basal lamina (double arrow) is evident. Bar equals 3 μ.

COMPARISON OF PIGMENT AND OTHER DENTAL CHARACTERS OF EASTERN PALEARCTIC *SOREX* (MAMMALIA: SORICIDAE)

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ABSTRACT

Phylogeny of shrews is based mainly on morphological characters (chiefly cranial and dental characters), and more recently biochemical characters (electrophoretic and karyological). However, many dental characters that are useful for identification of different species are of little phylogenetic value. Parallel evolution appears to be frequent, probably often due to ecological adaptations. In this study skulls of eight species of shrews of the genus *Sorex* from the Palearctie were analyzed. Nine characters and 17 measurements were recorded from each skull. The characters and measurements were compared with those of European species of *Sorex*. Each character is discussed in terms of usefulness for identification, and phylogenetic and ecological relationships. The two most useful identification characters, the frontal shape of the upper incisors and the shape of the upper antemolars, were shown to have limited phylogenetic value, in many cases because of parallel evolution.

INTRODUCTION

Identification of shrew species is based mostly on quantitative and qualitative skull characters, particularly dental characters. Only qualitative dental characters will be considered in this work. However, to evaluate the correct number of species and of their relationships, it is necessary to combine skull characters (both metric and descriptive) with other morphological characters, and also with karyological and electrophoretic data.

Although the number of European species of *Sorex* is well-known, this is not true for Asian members of the genus. However, many taxonomic publications (Yudin, 1971; Corbet, 1978; Hutterer, 1979; Dolgov, 1985; Hoffmann, 1987) have dealt with this problem. Corbet and Hill (1986) recognized 22 Asian species, whereas Honacki et al. (1982) recognized 24.

The red-toothed shrews of the genus *Sorex* in the Palearctic may be classified into four geographic distribution groups (Dolgov, 1967; Corbet, 1978; Honacki et al., 1982; Corbet and Hill, 1986). Distribution group A includes species with wide distributions in the Palearctic taiga zone (*S. araneus*, *S. caecutiens*, *S. daphaenodon*, *S. isodon*, *S. minutissimus*, *S. minutus*, *S. roboratus* [includes *S. vir*, Hoffmann, 1985] and *S. tundrensis*). Six of these species occur in the Russia, whereas *S. daphaenodon* and *S. roboratus* are not known west of the Ural Mountains. Also, six of these species occur east to the Pacific Ocean, whereas *S. araneus* and *S. minutus* are not known east of the Yenisei River and Lake Baikal. Distribution group B includes species occurring only in far eastern Siberia (*S. cinereus*, [according to Ivanitskaya and Kozlovsky {1985}, a complex of three species], *S. gracillimus*, *S. mirabilis*, and *S. unguiculatus*). Distribution group C includes the Caucasian species *S. raddei*, *S. satunini* (replaces *S. caucasicus* Zaitsev, 1988) and *S. volnuchini*. Distribution group D includes species found only in the central mountain ranges of southern Siberia: *S. asper* from Tien Shan and *S. buchariensis* (should, according to Hoffmann [1987], be included in *S. thibetanus*) from Pamir. *Sorex roboratus* from Altai is a synonym of *S. vir* (here in group A), but the name *roboratus*, Hollister (1913) has precedence over the name *vir*, Allen (1914). Because *S. alpinus* occurs outside Europe only in the Carpathian Mountains, it is not considered in this study, which includes only species in groups A, B (excluding *S. cinereus* complex and *S. mirabilis*), and C.

METHODS

Skulls of *S. daphaenodon* (n = 7), *S. gracillimus* (n = 7), *S. raddei* (n = 10), *S. roboratus* (n = 7), *S. satunini* (n = 7), *S. tundrensis* (n = 12), *S. unguiculatus* (n = 7), and *S. volnuchini* (n = 10) were examined under a dissecting microscope. Specimens of *S. raddei*, *S. satunini*, and *S. volnuchini* were obtained from the Zoological Institute, Russian Academy of Sciences, St. Petersburg. Specimens of the remaining species were obtained from the Swedish Museum of Natural History, Stockholm. In addition to qualitative characters, 17 cranial and mandibular characters were measured on each skull (Fig. 1) by use of an image analyzer (MOP Videoplan, Kontron image analysis division, Zeiss). These measurements were compared with the corresponding measurements of nine European species of *Sorex* (Dannelid, 1990) by using the principal component analysis and the PLS (partial least squares) discriminant analysis (Wold et al., 1983; Ståhle and Wold, 1988) of the SIMCA (soft independent modelling of class analogy) pattern recognition package (Wold et al., 1984).

The qualitative characters examined were: A) the accessory medial tines on the upper incisors, which differ among species in size and position in the pigmented field and thus can be valuable as a species character (Heptner and Dolgov, 1967; Hoffmann, 1971; Diersing and Hoffmeister, 1977; Hennings and Hoffmann, 1977; Junge and Hoffmann, 1981; Dannelid, 1989) as can the incisor tips (either parallel or divergent). These two characters are connected: species with medial tines high up in the pigmented area usually have divergent incisor tips, whereas those with medial tines placed lower usually have parallel incisor tips (Fig. 2); B) the five teeth posterior to the incisor, usually known as unicuspids, are herein termed antemolars (Reumer, 1984). The relative sizes of these teeth, compared to each other, are usually constant within the species and have been used in species identification (Fig. 3); C) the

hypocones are small cusps situated on the posterolingual parts of P^4, M^1, and M^2. They may be either unpigmented or weakly pigmented (Fig. 4*a*). In *S. daphaenodon* they are heavily pigmented (Fig. 4*b*). Usually, smaller species have unpigmented hypocones and larger species pigmented hypocones, but the large species *S. roboratus* has completely unpigmented hypocones; D) the position of the lacrimal foramen relative to the posterior cusps of M^1 (or rarely the anterior cusps of M^2) which differs slightly among species, and is sometimes used as a taxonomic character (van Zyll de Jong, 1980); E) all *Sorex* species have four cusps (the tip of the incisor is here also regarded as a cusp) on the lower incisor. *Sorex minutus* and its possible ecological equivalents (*S. gracillimus*, *S. volnuchini*) have sharp cusps and little difference between the first depression and the others (Fig. 5*a*). However, most other species have blunt cusps and a more shallow depression between the first two cusps than between the rest (Fig. 5*b*); F) the second tooth in the lower jaw, herein called A_1 (Reumer, 1984) is in *S. araneus* and some other species triangular in appearance, whereas in other species it has a more elongate shape. This character is visible only in young animals; in old animals with worn teeth the difference disappears; G) Dannelid (1989) recognized three pigment patterns on the first three teeth in the lower jaw: the "*araneus*" pattern, where the border between pigmented and unpigmented areas runs straight and unbroken on I_1, A_1, and P_4; the "*minutus*" pattern, where there is a pigment gap on P_4; and the "*alpinus*" pattern, where the pigment on P_4 starts at the base of the tooth. These pigment patterns are useful only for some species (e.g., *S. minutus* never shows an *araneus* pattern). None of the non-European species studied in this work showed an *alpinus* pattern; H) although the mental foramen has been used for taxonomic purposes, the position on the mandible varies not only interspecifically but also intraspecifically; in some instances there is variation in its position between the left and the right mandible of an animal. Most species have the mental foramen situated under the trigonid of M_1; and I) the intensity of color of the pigment on the teeth was examined. Most species have what herein is called medium pigmentation, whereas *S. minutus*, *S. gracillimus*, and to some extent *S. volnuchini* have lighter pigmentation and *S. minutissimus* has darker pigmentation.

Results

Sorex daphaenodon

A: The medial tines are small (smaller than in *S. araneus*) and positioned in the lower part of the pigmented field, close to the middle of this area; the tips of incisors are blunt and parallel (Fig. 2a). B: A^1–A^4 decrease in size evenly posteriorly (although sometimes A^1 and A^2 are of the same size); A^5 is clearly smaller and always pigmented (Fig. 3a). C: In all other species the hypocones on the upper molars are either unpigmented or very weakly pigmented. In *S. daphaenodon* much of the occlusal area of those teeth is pigmented and the hypocones are as strongly pigmented as the other molar cusps. This is by far the easiest way to recognize this species (Fig. 4b). D: The lacrimal foramen is positioned over the metacone of M^1. E: The lower incisor has blunt cusps. F: The lower antemolar is triangular (although not to the extent in *S. araneus*). G: The pigmentation pattern on I_1–P_4 is mostly an *araneus* pattern, but there is sometimes a small gap in the pigmentation between A_1 and P_4. H: The mental foramen is positioned centrally under the trigonid of M_1. I: The pigmentation is medium (as in *S. araneus*) or a little darker, although one aberrant individual has extremely light pigmentation.

Sorex gracillimus

A: The medial tines are small, situated in the uppermost part of the pigmented area; the tips of the incisors are sharp and divergent. Compared with *S. minutus*, the medial tines are smaller, situated higher in the pigment field, and the incisor tips are more divergent. Also, the upper border of the pigmented area is oblique (straight in the similar species *S. minutus* and *S. volnuchini*, Fig. 2b). B: The upper antemolars differ from those of *S. minutus* in that A^1–A^3 are approximately the same size (A^3 is not larger than A^2 as in *S. minutus*); A^4 and A^5 are smaller, but the difference in size between these two teeth is not as great as in *S. minutus* (A^5 is larger than in *S. minutus* and pigmented) (Fig. 3b). C: The hypocones of P^4–M^2 are unpigmented. D: The lacrimal foramen is over the metastyle of M^1. E: The lower incisor is sharp-cusped, almost indistinguishable from that of *S. minutus* (Fig. 5a). F: The lower antemolar is elongate, nontriangular. G: The pigmentation pattern on I_1–P_4 is a *minutus* pattern. H: The mental foramen is positioned under the trigonid of M_1, mostly in an anterior position. I: The pigmentation is light (similar to *S. minutus* or a little darker).

Sorex raddei

A: The medial tines are small and situated high in the pigmented area; the incisor tips are slightly divergent (Fig. 2c). B: The upper antemolars are variable, with A^1–A^2 large, A^2 thicker than A^1, A^3–A^5 gradually diminishing in size, and A^5 unpigmented or weakly pigmented. However, one specimen has similar-sized A^1–A^3 and another has similar-sized A^3–A^5. These variations are probably not due to tooth wear, because the specimens are subadults with little wearing of the tooth (Fig. 3c). C: The hypocones are weakly pigmented on M^1–M^2, never on P^4. D: The lacrimal foramen is over the metastyle of M^1 (somewhat farther back than in the sympatric *S. satunini*). E: The lower incisor is intermediate between blunt-cusped and sharp-cusped types. The cusps are mostly blunt, but some individuals have cusps almost as sharp as those of *S. minutus*, *S. gracillimus*, and *S. volnuchini*. F: The lower antemolar is triangular and sometimes weakly two-cusped. G: The pigmentation of I_1–P_4 is an *araneus* pattern. H: The mental foramen is under the anterior part of M_1, sometimes under P_4–M_1. I: The pigmentation is medium.

Sorex roboratus

A: The medial tines are fairly large to small, and very low in the pigmented field. The often longish appearance gives this

species the appearance of a gigantic *S. minutissimus*; the tips of the incisors are blunt and parallel (Fig. 2d). B: The upper antemolars are grouped into three size classes (A^1–A^2, A^3–A^4, and A^5), much as in *S. araneus* (Fig. 3d). C: The hypocones of P^4–M^2 are unpigmented. D: The lacrimal foramen is over the metacone (rarely the metastyle) of M^1. E: The lower incisor is blunt-cusped, the cusps sometimes higher and more distinct than in other blunt-cusped forms. F: The lower antemolar is elongate, nontriangular, sharp-cusped, and rarely weakly two-cusped. G: The pigmentation of I_1–P_4 is an *araneus* pattern, but not so constant as in *S. araneus* and *S. raddei*. H: The mental foramen is under the trigonid of M_1, in a posterior position. I: The pigmentation is medium.

Sorex satunini

A: The medial tines are large and positioned in the lower half of the pigmented field, often close to the center of that field; the tips of the incisors are blunt and parallel. The incisors of *S. satunini* appear very similar to those of *S. araneus* in frontal view (Fig. 2e). B: The upper antemolars are similar to those of *S. araneus*, with antemolars in three size groups (A^1–A^2, A^3–A^4, and A^5). A^2 is often thicker than A^1, A^3 is larger than A^4, and A^5 is large and pigmented. It was not always possible to distinguish *S. satunini* from the sympatric *S. raddei* (Fig. 3e). C: The hypocones are pigmented on M^1–M^2, sometimes also on P^4. D: The lacrimal foramen is over the metacone (rarely the metastyle) of M^1 (more anteriad than in the sympatric *S. raddei*). E: The lower incisor is blunt-cusped. F: The lower antemolar is weakly triangular. G: The pigmentation of I_1–P_4 is sometimes an *araneus* pattern, but this is not a consistent character. H: The mental foramen is positioned centrally under the trigonid of M_1, sometimes a little farther back. I: The pigment color is medium.

Sorex tundrensis

A: The upper incisor is similar to those of *S. araneus* and *S. satunini*, differing only in that the medial tines are smaller, sometimes very small, and rarely absent (Fig. 2f). B: A^1–A^2 are of similar size, A^3–A^5 diminish gradually in size posteriorly, and A^5 is large and pigmented, similar to the condition in *S. araneus* (Fig. 3f). C: The hypocones are unpigmented on P^4 and pigmented on M^1–M^2. D: The lacrimal foramen is over the metacone of M^1. E: The lower incisor is blunt-cusped. F: The lower antemolar is triangular. G: The pigment pattern on I_1–P_4 is mostly an *araneus* pattern. H: The mental foramen is positioned posteriorly under the trigonid of M_1, or between the trigonid and the talonid of M_1. I: The pigment color is medium.

Sorex unguiculatus

A: The medial tines are absent (or in some cases rudimentary in the upper half of the pigmented area); the tips of the incisors are blunt and slightly divergent (Fig. 2g). B: The upper antemolars gradually decrease in size posteriorly, except for A^3 which is larger than A^2; A^5 is large and pigmented (Fig. 3g). C: The hypocones are sometimes weakly pigmented on M^1 and M^2. D: The lacrimal foramen is above the metastyle (sometimes the metacone) of M^1. E: The lower incisor is blunt-cusped (Fig. 5b). F: The lower antemolar is triangular. G: An *araneus* pattern sometimes occurs on I_1–P_4. H: The mental foramen is under the trigonid of M_1. I: The pigment color is medium.

Sorex volnuchini

A: The medial tines are situated lower in the pigmented field than in *S. minutus* and *S. gracillimus* (but still in the upper half); they are otherwise similar to those species, with relatively sharp, widely divergent incisor tips (Fig. 2h). B: The upper antemolars are almost indistinguishable from those of *S. minutus*. A^1–A^3 are large, with A^3 larger than A^2. A^4 is smaller, and A^5 is very small. However, A5 is mostly larger than in *S. minutus* (although not so large as in *S. gracillimus*) (Fig. 3h). C: The hypocones on P^4–M^2 are always unpigmented. D: The lacrimal foramen is above the metastyle of M^1. E: The lower incisor is sharp-cusped and similar to the lower incisors of *S. minutus* and *S. gracillimus*, but the first cusp (= tip of incisor) is often stronger and more upturned than in those species. F: The lower antemolar is elongate and nontriangular. G: The pigment pattern on I_1–P_4 is variable; however, an *araneus* pattern never occurred. H: The mental foramen is under the trigonid of M_1, somewhat farther back than in *S. minutus*. I: The pigment color is light, slightly darker than in *S. minutus* and *S. gracillimus*.

Measurements for 17 characters in the eight species examined are presented in Table 1. For comparison, the corresponding measurements (from Dannelid, 1990) for nine western European species are given in Table 2. A PCA on all 210 individuals of the 17 species resulted in separation of the shrews into two groups: one consisting of smaller species (*S. caecutiens*, *S. gracillimus*, *S. minutissimus*, *S. minutus*, and *S. volnuchini*), and another consisting of the remaining species of which *S. roboratus* and *S. unguiculatus* were separated as the largest. The first projection of the PCA (X = PC 1, Y = PC 2; Fig. 6a) explained 74.7% of the variance. Overall, the PCA was 81.6% of the total variance. A PLS discriminant analysis on the same matrix (Fig. 6b) explained 33.2% of variance and the separation of the species in the plot was similar to the separation in the PCA.

Discussion

Dental characters are usually regarded as "good" characters. Even if a skull is badly damaged or recovered from an owl pellet, it is usually possible to find at least part of the dentition intact. In old animals, however, the teeth are worn to a considerable degree, and many dental characters may be obscured. Furthermore, cranial and dental characters can be used not only for identification, but also for phylogenetic inference and for deduction of ecological valences.

The characters of the anterior aspect of the upper incisors are useful for identification of species. The position of the medial tines in the pigmented field rarely varies, and the appearance of the incisor tips is also constant among species.

Species with the medial tines in the upper half of the pigmented area include *S. minutus*, *S. gracillimus*, *S. volnuchini* (the latter two species are probably ecological equivalents to *S. minutus*), *S. raddei*, *S. samniticus*, and *S. isodon*. In the last species, the medial tines are very small; they are smaller still in *S. unguiculatus* wherein the medial tines are rudimentary or absent (but situated in the upper half, when present). Finally, the European *S. alpinus* shows no trace of medial tines. Although the small species *S. minutus*, *S. gracillimus*, and *S. volnuchini* all have medial tines in the upper part of the pigmented area, the position of these structures is not identical. *Sorex gracillimus* has medial tines placed higher than *S. minutus*, whereas *S. volnuchini* has the tines in a lower position. Also, in *S. gracillimus* the upper border of the pigmented area is oblique, whereas this border is relatively straight in *S. minutus* and *S. volnuchini*. Species with medial tines in the lower half of the pigmented area include *S. araneus*, *S. coronatus*, *S. granarius*, *S. daphaenodon*, *S. satunini*, *S. tundrensis* (all members of the *S. araneus/arcticus* group defined on karyological grounds, Hausser et al., 1985), *S. minutissimus*, *S. roboratus*, and *S. caecutiens*. The last species shows some variation in the position of the medial tines (Dannelid, 1989).

The phylogenetic value of the characters of the anterior aspect of the upper incisors is limited, as all members of the monophyletic *S. araneus/arcticus* group have similar upper incisors. However, *S. minutus* and *S. gracillimus* have almost identical incisors, but are considered distantly related based on both karyological data (Tada and Obara, 1988) and the shape of the glans penis (Dolgov and Lukyanova, 1966). Therefore, this is probably an instance of parallelism. There also may be some ecological significance to the characters of the upper incisors. Some shrews dig in the ground and may construct burrows (Pelikan, 1960). If the incisors are involved in digging, then large medial tines situated low in the pigment field would adapt the incisors for digging. This hypothesis is supported by comparison between *S. araneus* and *S. minutus*. *Sorex araneus* spends a lot of time underground, whereas *S. minutus* functions more as an epifaunal predator (Croin-Michielsen, 1966). *Sorex araneus* also has larger medial tines than *S. minutus* which are situated in the lower part of the pigmented field, whereas in *S. minutus* they are situated in the upper half of the field. Moreover, the American *S. vagrans*, which does not make burrows (Terry, 1981), has minute medial tines situated very high on the incisors above the pigment field (Junge and Hoffmann, 1981), a condition that does not occur in Eurasian species. However, *S. trowbridgii*, which may burrow (Terry, 1981), has small medial tines in the upper part of the pigment field (Junge and Hoffmann, 1981), and *S. unguiculatus*, which is semifossorial (Yoshino and Abe, 1984; Hutterer, 1985), may have rudimentary medial tines. Thus, although digging may be related to the shape and position of the medial tines, other selective factors are obviously involved.

The identification value of characters of the upper antemolars is good. This character is relatively constant, and only *S. raddei* has a distinct degree of variation. The upper antemolars gradually decrease in size posteriad without apparent gaps in size in *S. alpinus*, *S. caecutiens*, *S. daphaenodon* (A^1 and A^2 often equal in size, might have a size gap between A^4 and A^5), *S. gracillimus*, *S. isodon*, and *S. unguiculatus* (A^3 larger than A^2). This situation is often combined with a (relatively) large A^5. The upper antemolars are arranged in three size groups (A^1–A^2, A^3–A^4, and A^5) in *S. araneus*, *S. roboratus*, *S. satunini* (A^3 mostly larger than A^4), and sometimes *S. raddei*. The upper antemolars are arranged in three different size groups (A^1–A^3, A^4, and A^5) in *S. minutissimus*, *S. minutus*, *S. volnuchini*, and sometimes *S. raddei*. The condition of A^1 and A^2 being of similar size and the other antemolars decreasing posteriorly occurs in *S. tundrensis* and *S. raddei*. The condition of A^3 being larger than A^2 occurs in *S. minutus* (but not *S. gracillimus*), *S. unguiculatus*, and *S. volnuchini*. The phylogenetic value of the antemolar characters is probably not great. In the subgenus *Otisorex*, A^4 is usually larger than or equal in size to A^3; whereas, in the subgenus *Sorex*, A^3 is usually larger than A^4 (Diersing, 1980). However, that study chiefly concerned North American members of the genus, and Diersing (1980) also included in the subgenus *Sorex* species such as *S. merriami* and *S. trowbridgii* which, on electrophoretic grounds, are not considered to belong in this subgenus (George, 1988). No member of the subgenus *Sorex* has A^4 larger than A^3; however, several species have A^3 and A^4 of equal size. The ecological significance of antemolar characters is obscure. The antemolars do not contact the underlying dentition of the lower jaw (posterior part of I_1, A_1) when the jaw is occluded (Dõtsch, 1985). They might, however, come in direct contact with prey.

The pigmentation on the hypocones of P^4–M^2 is excellent for distinguishing between *S. daphaenodon* and other species, but is otherwise limited. Dannelid (1989) reported that, among the European species, only *S. araneus* and *S. coronatus* have pigmented hypocones on the upper molars; pigmented hypocones on specimens of *S. caecutiens* and *S. isodon* from Kamchatka were later observed. *Sorex minutus* and its possible ecological equivalents never have pigmented hypocones on upper molars, and even a large species such as *S. roboratus* has completely unpigmented hypocones. Species of the chiefly North American *Otisorex* complex have unpigmented hypocones on P^4–M^2. This character probably has no phylogenetic value. The ecological significance of this character is obscure. The hypocones are small cusps and probably do not serve any major function. Many shrew species show reduction of the hypocones. The strong pigmentation of the hypocones and the strong pigmentation on the upper molars of *S. daphaenodon* is difficult to explain. The diet of this species includes a large proportion of beetles (Yudin, 1962). However, other species have the same dietary specialization without exhibiting the same pigmentation. Both *S. araneus* and *S. alpinus* eat a large proportion of land snails (Churchfield, 1984; Kuvikova, 1986) that might be even harder to crush than beetles; nevertheless, these species have normal pigmentation on the upper molars. As far as is known, the diet of *S. daphaenodon* is similar to the diets of *S. araneus*, *S. alpinus*, *S. isodon*, and *S. tundrensis*.

The position of the lacrimal foramen has limited identification value. Most species have the lacrimal foramen situated over the metacone or the metastyle of M^1, and only in

S. alpinus is it in a more posteriad position. The phylogenetic value of this character is nil, and it probably has no ecological significance.

The identification value of characters of the lower incisor is good within limits. Two distinct morphological types occur. Most species have blunt cusps and a much more shallow depression between first and second cusps than between the others. *Sorex minutus* and its possible ecological equivalents (*S. gracillimus*, *S. volnuchini*) have sharper cusps and depressions between the cusps of almost equal size. This pattern is also sometimes found in *S. raddei*. The phylogenetic value of this character is probably low. Sharp cusps may be the result of at least two instances of parallel evolution. This character probably has some ecological significance. The sharp-cusped forms, *S. minutus*, *S. gracillimus*, and *S. volnuchini*, are small shrews with lightly pigmented teeth (slightly darker in *S. volnuchini*). They also have I^1 with small medial tines situated in the upper half of the pigment field. They probably all live as epifaunal predators, and the limitation of burrowing activities might make it possible for them to maintain sharp cusps on I_1. This does not mean that all species of *Sorex* that seldom burrow possess lower incisors with sharp cusps; however all burrowing (and some nonburrowing) species are characterized by lower incisors with blunt cusps.

The characters of the lower antemolar have limited identification value. Some species, chiefly of the *S. araneus/arcticus* group but also *S. raddei* and *S. unguiculatus*, have a triangular A_1 when not worn; other species have a more elongated A_1. The phylogenetic value of this character is probably limited; e.g., not all members of the *araneus/arcticus* group have a triangular A_1. Based on karyology *S. granarius* is regarded as more primitive than *S. araneus* and *S. coronatus* (Volobouev and Catzeflis, 1989); however, it does not have a triangular A_1. It might be argued that a triangular A_1 is a synapomorphy for more advanced members of the *S. araneus/arcticus* group, and that the similar shape of the tooth in *S. raddei* and *S. unguiculatus* is due to parallelism. This character has obscure ecological significance. Species with a triangular A_1 usually eat a large proportion of lumbricids and it is possible that a triangular A_1 gives a better hold on the prey if it is transversely placed in the mouth. However, lumbricids are also important food items in many species that have a nontriangular A_1. The highest proportion of lumbricids is eaten by *S. mirabilis*, occurring in 82.5% of the specimens (Okhotina, 1969). Unfortunately the shape of the A_1 of *S. mirabilis* is unknown to the author.

The pigment pattern on I_1–P_4 has good identification value in some cases, such as when comparing *S. araneus* and *S. minutus*, but many species have an intermediate pattern. The phylogenetic value of this character is probably low, except that the *S. alpinus* pattern might be an autapomorphy for *S. alpinus*. This character probably has no ecological significance.

The position of the mental foramen has limited identification value (many species have the mental foramen situated below the trigonid of M_1). This character probably has no phylogenetic or ecological significance.

The identification value of the pigmentation intensity is limited; most species of *Sorex* have teeth with approximately the same pigmentation, and some show intraspecific variation. For the smaller species, however, it may be a useful character as *S. minutus* and *S. gracillimus* have lighter pigmentation than other species (*S. volnuchini* is a little darker), whereas *S. minutissimus* has the darkest tooth pigmentation of the Eurasian species. The pigmentation character probably has no phylogenetic value. It may, however, have some ecological significance. Red tooth pigment contains iron (Dötsch and Koenigswald, 1978) which may make the teeth more resistant to wear (Selvig and Halse, 1975; Vogel, 1984). However, C. Dötsch (personal communication) believes that red-pigmented enamel is weaker than white enamel, in which case its function must be explained differently. The greatest amount of iron is present on the incisors and on the occlusal surfaces of the molars, especially so on the lower incisor of *S. araneus* (Dötsch and Koenigswald, 1978). If burrowing is responsible for part of the tooth wear on the incisors, it is conceivable that species that spend little time underground (like *S. minutus* and *S. gracillimus*) would have lightly pigmented incisors. The overall lighter pigmentation of the teeth of these species also may reflect a diet of less sclerotized food. Crocidurines, which lack tooth pigmentation, do not, however, eat softer food than soricines; they may in some instances be adapted for even more powerful food crushing (Dötsch, 1985). But crocidurines have a lower metabolic rate than soricines, and thus probably consume less food, which could account for less tooth wear (Vogel, 1984). Also, carcass feeding (Schlüter, 1980) and burrowing might be responsible for tooth wear during the winter in soricines; the more austral crocidurines come in contact with partly frozen carcasses and soil to a lesser extent than soricines. The function of the red pigment might not be only resistance against abrasion. Different rates of tooth wear between the harder red enamel and the softer white enamel creates sharp cutting edges (Vogel, 1984). Tooth wear is not continuous throughout life, but is more pronounced in overwintered adults than in juveniles (Pankakoski, 1989). Shrews with worn teeth do not switch to a softer diet, at least not in *Crocidura russula* (Bever, 1983). If the same is true for *Sorex*, as seems likely, it is conceivable that chewing with teeth heavily worn after the winter causes an even higher rate of abrasion.

For a discussion of habitat and food preferences, the size of the species is an important factor. I have therefore grouped the species studied according to size, based on cranial measurements (see tables 1 and 2). Because size relationships are important in interspecific comparisons, it is essential to compare sympatric populations whenever possible. For example, if measurements of a Siberian species such as *S. tundrensis* are compared to those of European populations of a widespread species such as *S. araneus*, measurements of *S. tundrensis* will not be compared with those of sympatric populations of *S. araneus*, which differ considerably in size from European populations (Hoffmann, 1985). The species studied (17 of the 30 Palearctic species) were divided into seven size classes. *Sorex minutissimus*, the smallest species, does not overlap much in size with other species. The second size class

consists of *S. minutus*. *Sorex caecutiens*, *S. gracillimus*, and *S. volnuchini* make up the next size class. The two latter species are morphologically very similar to *S. minutus*; as none of these three species overlap in distribution, they are considered possible ecological vicars. *Sorex minutus* and *S. volnuchini* probably are related, whereas *S. gracillimus* might be the result of parallel evolution in eastern Siberia. *Sorex caecutiens* has smaller mandible measurements than *S. volnuchini* and in some cases also *S. gracillimus*. *Sorex tundrensis* is usually a little smaller than *S. araneus*, as is also *S. granarius* of Spain; these two species constitute the next size class. *Sorex araneus*, *S. coronatus*, *S. satunini*, and *S. daphaenodon* are all related, not greatly different in size. *Sorex samniticus* and *S. alpinus* of Europe are also of the same size class, though the latter species is intermediate between this size class and the next which is made up of *S. isodon* and *S. raddei*. *Sorex raddei* has larger mandibular measurements than *S. isodon* from Europe. The final size class consists of *S. roboratus* and *S. unguiculatus* (*S. mirabilis*, not included in this study, is larger). A more useful division may be into two groups: "smaller species" (size classes 1–3) and "larger species" (size classes 4–7).

Although many species of *Sorex* may occur in the same area, there is little distributional overlap among species in the same size class. The only overlaps found in the eastern Palearctic are as follows: *S. caecutiens* and *S. gracillimus* (size class 2) occur sympatrically in eastern Siberia; *S. araneus* and *S. daphaenodon* (size class 5) occur sympatrically in Siberia between the Ural Mountains and Lake Baikal; and *S. roboratus* and *S. unguiculatus* (size class 7) occur sympatrically in eastern Siberia. Also, *S. caecutiens* overlaps in northeastern Siberia with members of the *S. cinereus* complex which may be approximately the same size.

The diets of species of *Sorex* show some variation between size classes. *Sorex minutissimus* (size class 1) eats many different kinds of invertebrates but avoids lumbricids and gastropods (Skarén, 1978). *Sorex minutus* (size class 2) also avoids lumbricids and eats relatively few gastropods (Churchfield, 1984). *Sorex caecutiens* (and the North American *S. cinereus*) eats a small amount of lumbricids (Yudin, 1962; Whitaker and Mumford, 1972). Species in size classes 4 to 6 all have diets based largely on lumbricids, coleopterans, and in some cases terrestrial gastropods (Yudin, 1962; Pernetta, 1976; Skarén, 1979; Churchfield, 1984; Kuvikova, 1986). Of the larger forms, *S. roboratus* concentrates on coleopterans (Yudin, 1962), whereas *S. unguiculatus* and *S. mirabilis* feed heavily on lumbricids (Okhotina, 1969; Yoshino and Abe, 1984). Thus, two different feeding types can be recognized among the Eurasian species of *Sorex*. The smaller shrews (size classes 1–3) probably live as epifaunal predators, not burrowing much. They eat any animal matter they can overpower but avoid lumbricids and (class 1) gastropods. Two distinct complexes of ecological equivalents might be involved here. These are separated from each other by dental characters, particularly by the shapes of the upper and the lower incisors. *Sorex minutissimus* (and the American *S. hoyi*) makes up one of these complexes; *S. minutus*, *S. gracillimus*, and *S. volnuchini* the other. These complexes are not equivalent to size classes 1 and 2 because the size of *S. hoyi* more closely resembles a small *S. minutus* than *S. minutissimus*. Larger shrews (classes 4–7) are often more or less semifossorial, and they often heavily rely on lumbricids and coleopterans in their diets. *Sorex caecutiens* (size class 3) and the American *S. cinereus* occupy an intermediate position. They eat few lumbricids, and may live as epigeal predators (Yoshino and Abe, 1984; Aitchison, 1987), at least in the absence of other small shrews.

The qualitative characters discussed were all characters chosen with respect to their identification value. No single character separates all species, but a combination of characters is often very useful. All nine European species of *Sorex* (except *S. araneus* and *S. coronatus*) can be separated by the characters cited herein, if the skull is in good condition and the geographic origin of the specimen is known. However, all characters are not equally useful. The best identification characters are the shape of the upper incisors (including the medial tines) and the shape of the upper antemolars. Other characters, such as the pigmentation of the hypocones on the upper molars (for separating *S. daphaenodon*) and the shape of the lower incisors (for separating *S. minutus* and its possible ecological equivalents), are of more limited value. Finally some characters like the relative position of the lacrimal and mental foramina are of very limited usefulness and can only be used in combination with other characters.

Diersing (1980) listed four qualitative cranial and mandibular characters for separation of the subgenera *Sorex* and *Otisorex*. However, none of these characters is constant and no single morphological character can be used for absolute separation of *Sorex* and *Otisorex*. Such characters seem to exist in electrophoretic studies (George, 1988). Unfortunately, the phylogenetic value of identification characters seems to be very limited. The characters useful for identification and the characters good for phylogenetic analysis are not the same. Parallel evolution appears to have taken place frequently, in many instances probably due to similar ecological forces. It is likely that the different shapes of the upper and lower incisors among different species of *Sorex* reflect different ways of living. Incomplete knowledge about the ecology of many species of *Sorex* prevents us, however, from relating different types of incisors to different ecological niches. Future work in this field, combined with studies of the relationships between different size classes of *Sorex* should help understanding of ecological niche separation within the genus.

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Table 1.—*Means (in mm) ± SD of cranial and mandibular characters recorded from skulls of eight species of* Sorex *from the eastern Palearctic.*

Character	*daphaenodon*	*gracillimus*	*raddei*	*roboratus*	*satunini*	*tundrensis*	*unguiculatus*	*volnuchini*
Condylobasal length	17.06 ± 0.46	15.10 ± 0.34	17.68 ± 0.52	19.30 ± 0.51	17.20 ± 0.47	16.16 ± 0.48	18.85 ± 0.42	14.68 ± 0.35
Breadth of rostrum over upper incisors	1.38 ± 0.21	1.06 ± 0.10	1.24 ± 0.12	1.51 ± 0.11	1.23 ± 0.11	1.39 ± 0.19	1.26 ± 0.09	1.04 ± 0.06
Maxillary breadth	5.20 ± 0.27	3.65 ± 0.19	5.20 ± 0.14	5.46 ± 0.13	5.15 ± 0.31	4.46 ± 0.22	5.33 ± 0.30	4.23 ± 0.15
Interorbital breadth	3.65 ± 0.43	3.12 ± 0.24	3.66 ± 0.08	3.83 ± 0.07	3.46 ± 0.11	3.48 ± 0.14	4.13 ± 0.19	2.89 ± 0.11
Cranial height	6.03 ± 0.37	4.54 ± 0.31	5.60 ± 0.22	6.05 ± 0.42	5.43 ± 0.32	5.74 ± 0.26	6.43 ± 0.37	4.64 ± 0.28
Length of upper antemolars	2.40 ± 0.12	2.19 ± 0.10	2.45 ± 0.15	2.54 ± 0.11	2.16 ± 0.09	2.14 ± 0.21	2.64 ± 0.20	1.82 ± 0.11
Length of upper molariform teeth	4.27 ± 0.13	3.61 ± 0.21	4.18 + 0.25	4.68 ± 0.26	4.20 ± 0.28	4.08 ± 0.18	4.82 ± 0.24	3.59 ± 0.13
Cranial breadth	8.76 ± 0.29	7.31 ± 0.20	9.29 ± 0.26	9.43 ± 0.40	8.72 ± 0.16	8.44 ± 0.23	10.08 ± 0.23	7.36 ± 0.21
Width of M^1–M^2	4.53 ± 0.12	3.27 ± 0.17	4.78 ± 0.23	5.04 ± 0.16	4.68 ± 0.19	4.17 ± 0.23	5.01 ± 0.19	3.89 ± 0.12
Palatal length	6.97 ± 0.17	5.96 ± 0.26	7.47 ± 0.19	7.82 ± 0.27	7.03 ± 0.28	6.43 ± 0.20	7.56 ± 0.35	6.01 ± 0.17
Glenoid width	4.80 ± 0.13	4.10 ± 0.31	5.32 ± 0.20	5.07 ± 0.19	4.84 ± 0.15	4.68 ± 0.18	5.55 ± 0.16	4.42 ± 0.26
Length of mandible	8.52 ± 0.21	6.86 ± 0.29	8.90 ± 0.40	9.75 ± 0.28	8.45 ± 0.37	7.71 ± 0.23	9.21 ± 0.42	7.05 ± 0.24
Height of coronoid process	4.36 ± 0.24	3.04 ± 0.15	4.37 ± 0.38	4.47 ± 0.09	4.35 ± 0.08	3.96 ± 0.11	4.80 ± 0.14	3.25 ± 0.18
Distance between coronoid process and upper articular facet on mandibular condyle	2.94 ± 0.18	2.37 ± 0.18	3.12 ± 0.16	3.18 ± 0.19	3.08 ± 0.14	2.75 ± 0.17	3.35 ± 0.10	2.48 ± 0.18
Length of lower incisor	3.41 ± 0.18	2.71 ± 0.15	3.47 ± 0.17	3.65 ± 0.56	3.59 ± 0.12	3.38 ± 0.13	3.60 ± 0.27	2.72 ± 0.20
Length of mandibular toothrow except incisor	4.99 ± 0.16	4.08 ± 0.22	5.30 ± 0.12	5.29 ± 0.06	5.12 ± 0.14	4.57 ± 0.13	5.26 ± 0.28	4.31 ± 0.17
Greatest condylar depth	2.11 ± 0.16	1.46 ± 0.16	2.01 ± 0.16	2.29 ± 0.18	1.96 ± 0.17	1.86 ± 0.11	2.42 ± 0.13	1.65 ± 0.12

Table 2.—*Means (in mm) ± SD of cranial and mandibular characters recorded from skulls of nine species of* Sorex *from Europe.*

Character	*alpinus* (*n* = 19)	*araneus* (*n* = 19)	*caecutiens* (*n* = 19)	*coronatus* (*n* = 19)	*granarius* (*n* = 13)	*isodon* (*n* = 19)	*minutissimus* (*n* = 7)	*minutus* (*n* = 19)	*samniticus* (*n* = 13)
Condylobasal length	17.70 ± 0.45	17.05 ± 0.64	15.27 ± 0.55	17.26 ± 0.48	15.84 ± 0.49	17.77 ± 0.60	11.85 ± 0.52	14.06 ± 0.72	16.58 ± 0.48
Breadth of rostrum over upper incisors	1.14 ± 0.14	1.39 ± 0.14	1.12 ± 0.15	1.50 ± 0.12	1.32 ± 0.15	1.25 ± 0.19	0.90 ± 0.08	0.96 ± 0.09	1.27 ± 0.10
Maxillary breadth	4.83 ± 0.16	4.54 ± 0.36	3.80 ± 0.19	4.90 ± 0.19	4.62 ± 0.19	4.78 ± 0.31	3.63 ± 0.15	3.49 ± 0.18	4.93 ± 0.15
Interorbital breadth	3.94 ± 0.13	3.40 ± 0.24	2.96 ± 0.14	3.47 ± 0.15	3.52 ± 0.12	3.67 ± 0.23	2.55 ± 0.08	2.66 ± 0.11	3.51 ± 0.07
Cranial height	5.58 ± 0.24	5.55 ± 0.30	5.07 ± 0.31	5.44 ± 0.24	5.19 ± 0.16	6.13 ± 0.60	3.41 ± 0.28	4.40 ± 0.35	5.00 ± 0.24
Length of upper antemolars	2.81 ± 0.11	2.44 ± 0.12	2.13 ± 0.12	2.34 ± 0.15	2.01 ± 0.07	2.56 ± 0.15	1.33 ± 0.09	1.83 ± 0.13	2.11 ± 0.10
Length of upper molariform teeth	4.37 ± 0.12	4.08 ± 0.27	3.40 ± 0.19	4.09 ± 0.14	3.98 ± 0.17	4.09 ± 0.15	3.04 ± 0.09	3.15 ± 0.23	4.40 ± 0.18
Cranial breadth	9.03 ± 0.20	8.50 ± 0.47	7.79 ± 0.45	8.85 ± 0.24	8.44 ± 0.25	9.31 ± 0.43	5.98 ± 0.11	6.94 ± 0.28	8.63 ± 0.14
Width of M^1–M^2	4.69 ± 0.15	4.46 ± 0.36	3.66 ± 0.11	4.76 ± 0.15	4.60 ± 0.13	4.62 ± 0.23	3.53 ± 0.08	3.37 ± 0.17	4.96 ± 0.16
Palatal length	7.78 ± 0.22	7.18 ± 0.27	6.39 ± 0.24	7.58 ± 0.29	6.97 ± 0.27	7.79 ± 0.31	4.95 ± 0.17	5.76 ± 0.25	7.40 ± 0.16
Glenoid width	5.07 ± 0.26	4.83 ± 0.26	4.10 ± 0.18	4.97 ± 0.25	4.81 ± 0.16	4.90 ± 0.24	3.62 ± 0.34	3.79 ± 0.17	5.19 ± 0.14
Length of mandible	9.00 ± 0.41	7.72 ± 0.31	6.67 ± 0.26	8.17 ± 0.24	7.95 ± 0.30	8.41 ± 0.34	5.40 ± 0.14	6.08 ± 0.22	8.31 ± 0.31
Height of coronoid process	3.71 ± 0.13	4.04 ± 0.15	3.19 ± 0.12	4.21 ± 0.13	3.76 ± 0.18	4.27 ± 0.18	2.75 ± 0.07	2.69 ± 0.19	4.11 ± 0.11
Distance between coronoid process and upper articular facet on mandibular condyle	2.52 ± 0.15	2.70 ± 0.19	2.29 ± 0.12	3.02 ± 0.17	2.62 ± 0.21	2.94 ± 0.17	2.07 ± 0.03	2.04 ± 0.12	2.82 ± 0.10
Length of lower incisor	3.20 ± 0.14	3.45 ± 0.19	3.15 ± 0.12	3.58 ± 0.14	3.12 ± 0.18	3.43 ± 0.17	2.31 ± 0.09	2.50 ± 0.17	3.38 ± 0.07
Length of mandibular toothrow except incisor	5.17 ± 0.21	4.71 ± 0.22	4.01 ± 0.13	4.74 ± 0.13	4.38 ± 0.11	5.00 ± 0.20	3.23 ± 0.13	3.68 ± 0.21	4.77 ± 0.18
Greatest condylar depth	2.03 ± 0.12	1.76 ± 0.13	1.53 ± 0.07	1.99 ± 0.15	1.81 ± 0.10	1.82 ± 0.14	1.28 ± 0.06	1.34 ± 0.10	1.82 ± 0.09

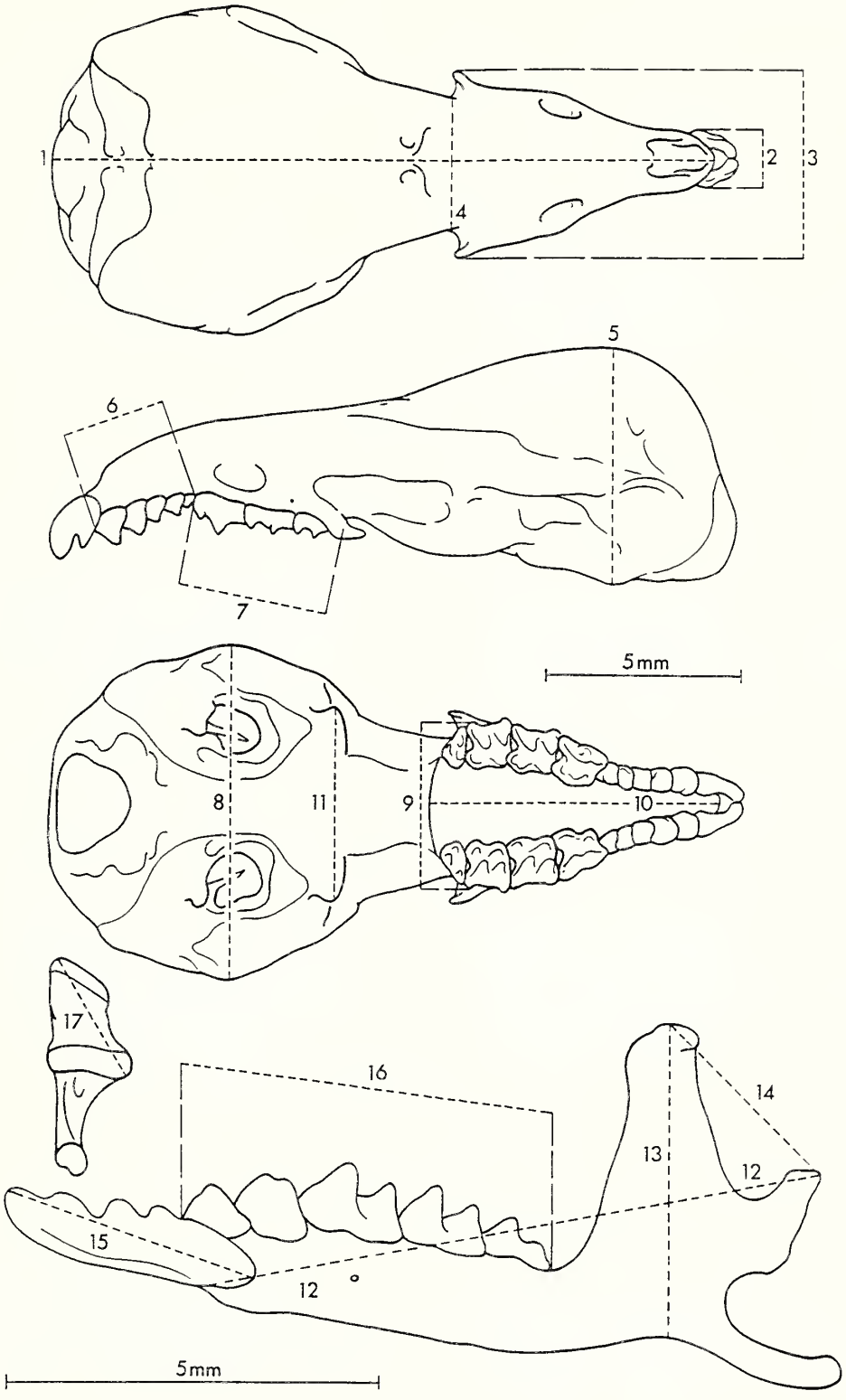

Fig. 1.—Illustration of a skull of *Sorex* indicating skull dimensions measured. 1, condylobasal length; 2, breadth of rostrum over upper incisors; 3, maxillary breadth; 4, interorbital breadth; 5, cranial height; 6, total length of left upper antemolars; 7, total length of left upper molariform teeth; 8, cranial breadth; 9, width of M^2–M^2; 10, palatal length; 11, glenoid width; 12, length of left mandible; 13, height of left coronoid process; 14, distance between left coronoid process and upper articular facet of left mandibular condyle; 15, length of left lower incisor; 16, length of left mandibular toothrow (except incisor); 17, greatest condylar depth on left mandible.

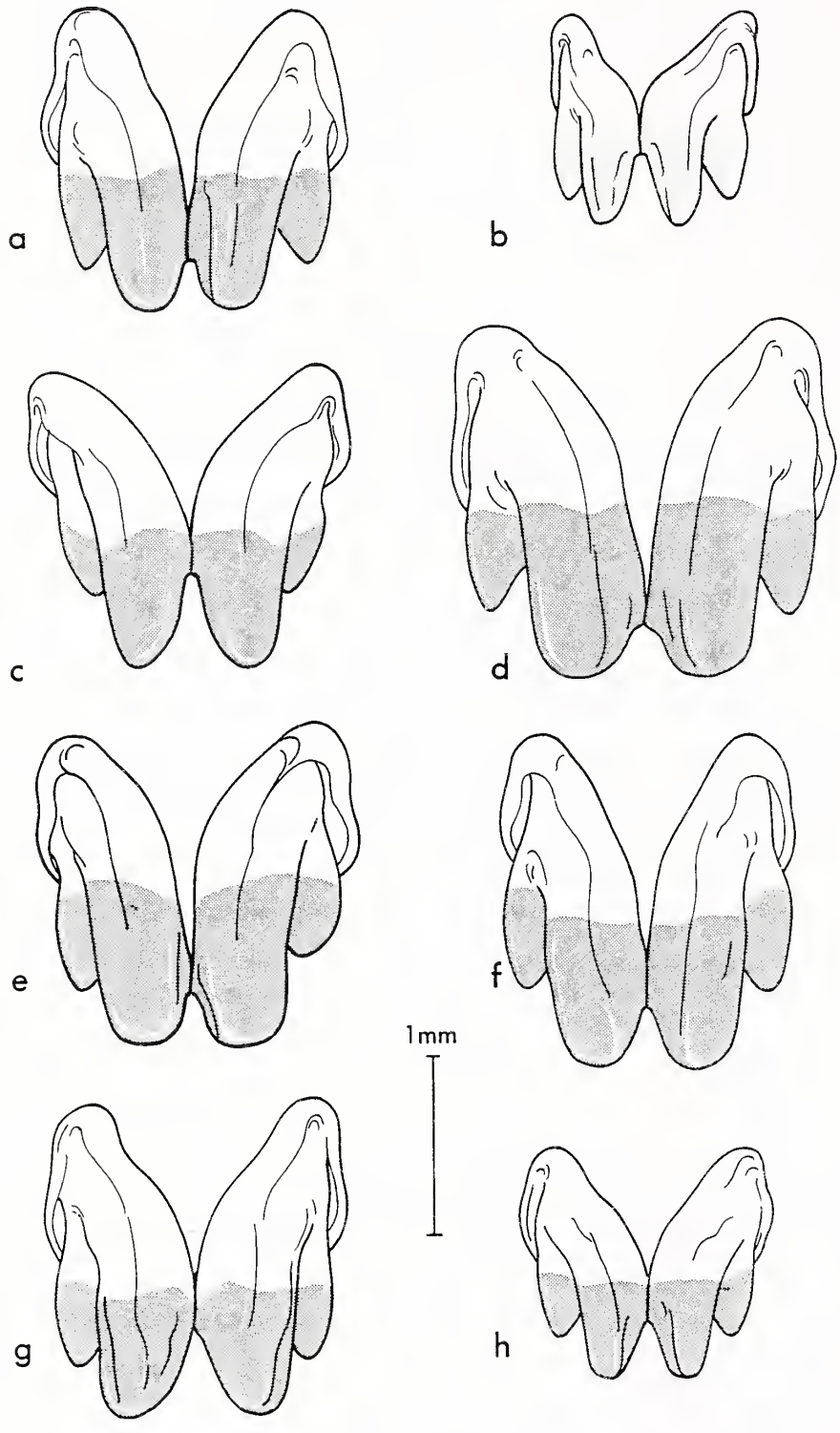

Fig. 2.—Frontal view of upper incisors of: a, *Sorex daphaenodon*; b, *S. gracillimus*; c, *S. raddei*; d, *S. roboratus*; e, *S. satunini*; f, *S. tundrensis*; g, *S. unguiculatus*; h, *S. volnuchini*.

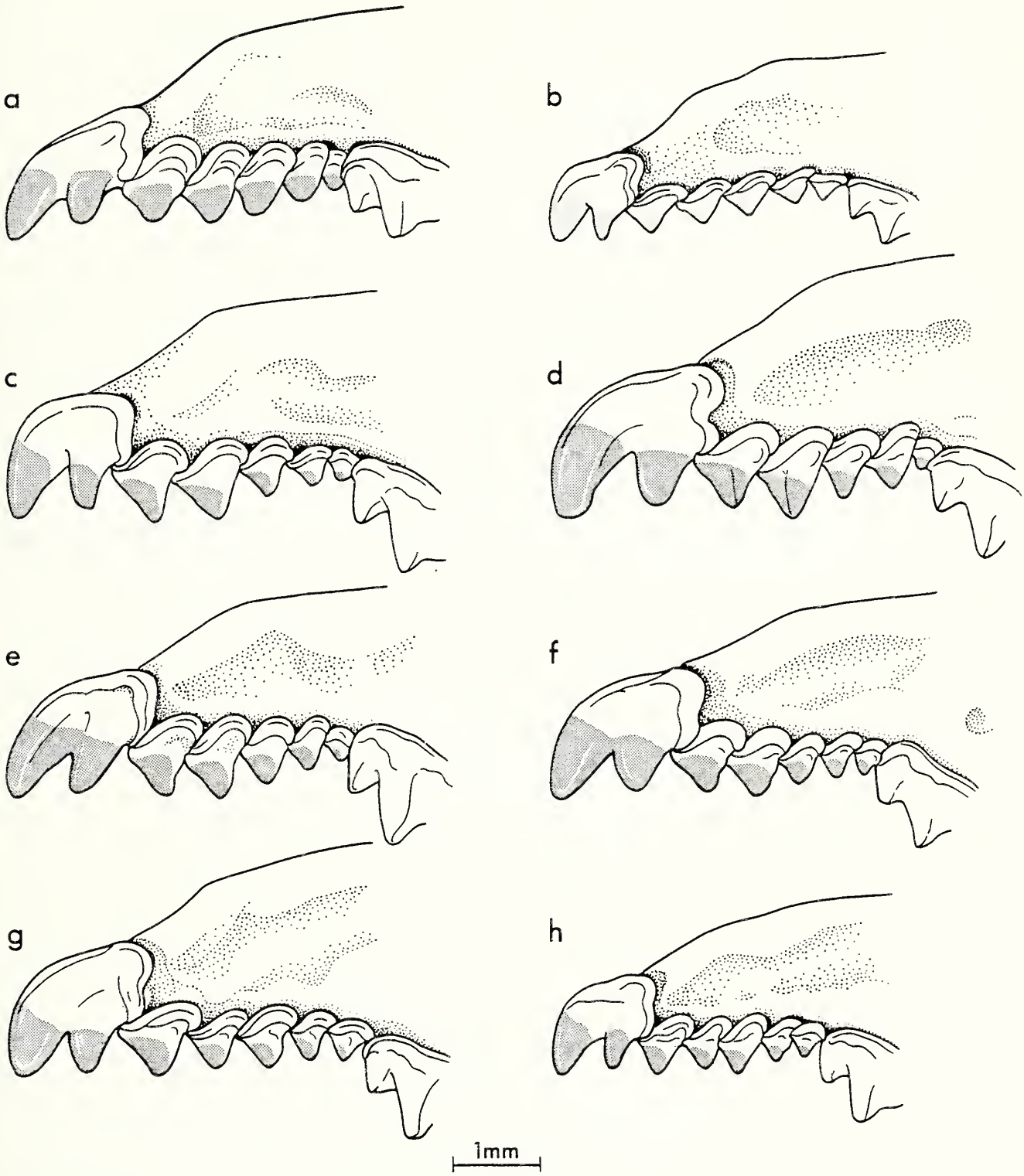

Fig. 3.—Lateral view of left upper antemolars of: a, *Sorex daphaenodon*; b, *S. gracillimus*; c, *S. raddei*; d, *S. roboratus*; e, *S. satunini*; f, *S. tundrensis*; g, *S. unguiculatus*; h, *S. volnuchini*.

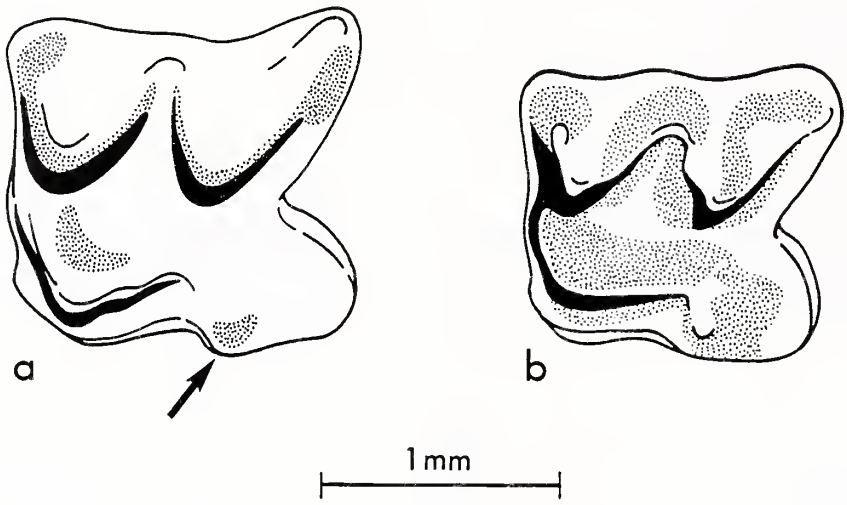

Fig. 4.—Occlusal view of left M^1 of: a, *Sorex araneus*; b, *S. daphaenodon*. Arrow points to hypocone.

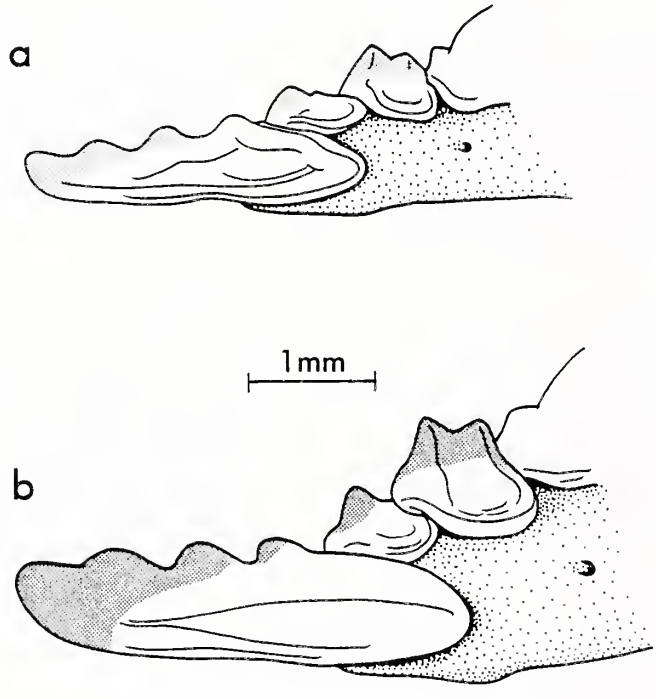

Fig. 5.—Lateral view of left lower incisor of: a, a sharp-cusped form (*Sorex gracillimus*); b, a blunt-cusped form (*S. unguiculatus*).

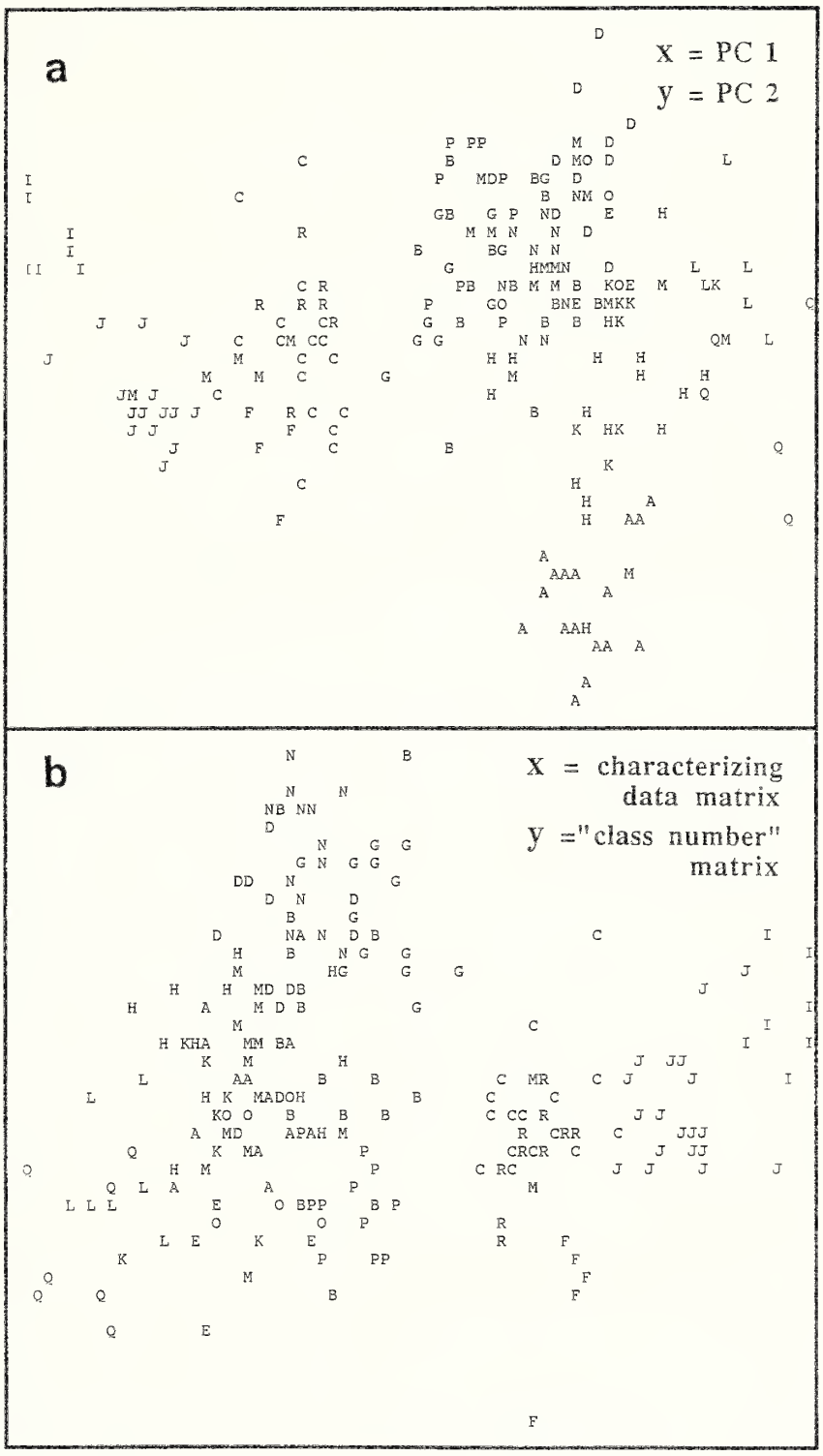

Fig. 6.—PCA and PLS discriminant analyses on 17 Eurasian *Sorex* presented in plot form: a, PCA plot (first projection, smaller species to the left, larger species to the right); b, PLS plot (larger species to the left, smaller species to the right). Symbols indicate: A, *Sorex alpinus*; B, *S. araneus*; C, *S. caecutiens*; D, *S. coronatus*; E, *S. daphaenodon*; F, *S. gracillimus*; G, *S. granarius*; H, *S. isodon*; I, *S. minutissimus*; J, *S. minutus*; K, *S. raddei*; L, *S. roboratus*; M, more than one individual at the same spot; N, *S. samniticus*; O, *S. satunini*; P, *S. tundrensis*; Q, *S. unguiculatus*; R, *S. volnuchini*.

FUNCTION OF THE FEEDING APPARATUS IN RED-TOOTHED AND WHITE-TOOTHED SHREWS (SORICIDAE) USING ELECTROMYOGRAPHY AND CINERADIOGRAPHY

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ABSTRACT

Electromyography and cineradiography of masticatory action in crocidurine and soricine shrews elucidated feeding strategies in relation to their unusual skull features. Multichannel EMG demonstrated differences in masticatory rates as well as in EMG activity levels of masticatory muscles between the two soricid groups. Parts 1 and 2 of M. temporalis primarily exerted pressure on food while the pinnated part 3 of the muscle produced a force concentration along one line of action and, thus, acted as a guiding muscle. M. masseter and M. pterygoideus medialis, as a complex, adducted the jaws with lateral components of movements. The dorsal part of M. pterygoideus lateralis supported the digastric as a jaw opener. The activity of M. pterygoideus medialis in an intermediate phase between the power phase and jaw opening was correlated with jaw tilting. Graphic presentation of masticatory orbits as well as distance calculations from markers in dorsoventral, lateral, and frontal planes illustrated jaw movements. Rotational movements at the inferior articulation of the double jaw joint during jaw opening were intensified in soricines, thus providing better alignment of the teeth for effective grinding movements. In crocidurines foreeful transverse motions were gained due to the anatomy of the articulation and the masticatory muscles.

INTRODUCTION

Detailed experimental studies in the last two decades on mastication in mammals of various feeding types abound with electromyographical data and models of three-dimensional jaw movements (for reviews, see Gans et al., 1978; Gorniak, 1985). Based on these studies, many investigators have pointed out that one chewing cycle pattern is probably common to all mammals (Hiiemae, 1978; Butler, 1983). The skulls of soricids are in some respects unique among mammals; there is no zygomatic arch, and the lower jaws have a "double mandibular articulation" and a "fossa temporalis interna." These features are related to masticatory muscle function (Dötsch, 1982, 1983*a*, 1986). Furthermore, striking differences in the anatomy of the double jaw joint between the shrew subfamilies (Dötsch, 1983*b*) make it clear that there is a need for additional information concerning the masticatory behavior of soricids. None of the previous anatomical studies of the feeding apparatus of shrews reported details of their chewing patterns (see review in Dötsch, 1982), and only two investigations mentioned jaw movements of soricids (Fearnhead et al., 1954; Gasc, 1963).

Feeding has been studied in the insectivorous bat *Myotis lucifugus* (Kallen and Gans, 1972) and in the insectivore *Tenrec ecaudatus* (Oron and Crompton, 1985). However, a member of the shrews (Insectivora, Soricidae) has never been studied electromyographically. A comparison of mastication between the insectivorous tenrecs and soricids also should provide an understanding of early mastication in mammals. Tenrecs as well as soricids have no zygomatic arch. It should then be determined if a "general mammalian chewing pattern" (Hiiemae, 1978) does exist.

Comparative studies on the functional morphology of mastication in mammals (among others, Storch, 1968; Bühler, 1977) and papers on the philosophy of this subject (Herring, 1988) have shown that studies in mastication should be more than sampling experimental data across mammalian orders and families. Moreover, representatives of both soricid subfamilies (Crocidurinae, Soricinae) occupy a variety of different food niches and environments (Hutterer, 1985). Hence, it would be instructive to know both the way distinct forms of the shrew masticatory apparatus and its functions are linked, and whether there are differences in the chewing patterns of white-toothed (Crocidurinae) and red-toothed (Soricinae) shrews.

MATERIALS AND METHODS

Twelve specimens of *Suncus murinus* (ranging from 30 to 50 g) and seven of *Crocidura flavescens* (ranging from 30 to 80 g), both members of the subfamily Crocidurinae, and four specimens of *Blarina brevicauda* (ranging from 21 to 27 g), a member of the subfamily Soricinae, were used for electromyography (EMG) and cineradiography. The white-toothed shrews were from breeding populations whereas the red-toothed shrews were wild-caught animals. The animals were trained to take food (mealworms, pieces of chicken breast and heart, and soft commercial cat food) during the experiments after a period of fasting.

Electromyography

Electrodes (up to 12, 37, or 50 μm bipolar nickel-chromium wires, Clark, Medical Instruments) were implanted under halothane anesthesia with a 21-gauge hypodermic needle (for details see Dantuma and Dötsch, 1989*a*) to simultaneously record activities of right and left masticatory muscles (Dötsch and Dantuma, 1989*a*). The electrodes were placed in the following muscles: M. digastricus, M. masseter, M. pterygoideus medialis, and three parts of M. temporalis. The M. pterygoideus lateralis was too small for electrode implantation. The exact positions of the electrodes were later determined by dissection.

The EMG signals were amplified with a Princeton Applied Research 113 preamplifier at a frequency range of 30 Hz to 10 kHz. The synchronization pulses of the film frames were generated by a mechanism of a 16-mm camera (Arriflex) on Kodak Ektachrome film. The pulses and the EMG signals were displayed on a Tektronix R 5103 N oscilloscope and a multichannel chart recorder (Siemens Oscillomink B), and stored on a 14-channel tape recorder (Bell & Howell CEC/VR 3369) at a speed of 15 or 7.5 ips. A mirror placed at 45° to the lateral side of the animal allowed a split view (lateral and ventral) recording. The EMG signals were digitized with an A/D converter and then analyzed with an IBM computer using programs that determined the percentage distribution of muscle activity (written by R. Dantuma). Maximal jaw opening was determined by frame-by-frame analysis and served as a basis for the grouping of masticatory cycles.

It was impossible to do EMG of the masticatory muscles of shrews in the same way as in larger animals (Weijs and Dantuma, 1975; De Gueldre and De Vree, 1988). The small size of the shrews restricted application of multipin connectors. Consequently, we developed an alternative system (Dantuma and Dötsch, 1989*a*). After implantation, the electrodes formed a 30-cm cable leading out at the dorsal region of the head. Their free ends were soldered to a connector. The cable was then protected with silicone rubber (Silastic 285R). The connector was suspended from a rotating unit when the shrews were not in experiments. This allowed the animals to move relatively freely in their cages.

Cineradiography

To follow the complicated jaw movements radiographically, dental parapulpar pins (TMS Link Series, self-shearing, gold-plated, stainless steel pins) were implanted in the skulls of the shrews (Dantuma and Dötsch, 1989*b*). The standardized size and shape of the pins, and the stability of pin position made all marks comparable. Also, for any given pin two marks were defined, screw-head and end. This is especially important for small objects. The shrews were filmed during feeding with an Arriflex 16-mm camera at 50 frames/sec. The radiographic films (Agfa Gevapan 30) were taken with a Siemens X-ray apparatus equipped with a 70-mm lens (Tridoros optimatic 800, with a Sirecon-2 image intensifier, 48–56 kV, pulse duration 1 msec) in either a dorsoventral or lateral projection. The cineradiographic films were analyzed frame by frame with an "Old Delft" variable speed analytical projector.

The X and Y coordinates of 20 marks on the film frames, i.e., those belonging to one masticatory cycle, were digitized with a Calcomp 2500 digitizer, and recorded on an IBM-compatible computer. Dorsoventral and lateral two-dimensional X-ray photographs (displaced at an angle of 90°) were also taken and their X and Y coordinates determined. A PC program then calculated the X/Y/Z coordinates using these coordinates, another (both programs were written by H. Amesz-Voorhoeve) rotated the three-dimensional coordinates onto the two-dimensional projection of the film frames and recalculated their X/Y/Z coordinates. Graphic presentation of the masticatory orbits as well as distance calculations from the markers in dorsoventral, lateral, and frontal planes illustrated jaw movements.

Results and Discussion

Morphology

The masticatory apparatus of the white-toothed *Crocidura flavescens* and *Suncus murinus* and the red-toothed *Blarina brevicauda* differ with respect to the double mandibular articulation and masticatory musculature. Because the skull structures and masticatory muscles were described in Dötsch (1982, 1983*a*, 1983*b*), only a brief summary of their essential features is included.

The two condylar facets of the jaw articulation in crocidurines are connected by a bony ridge. The dorsal facet carries a large articular disc which extends to the ventral facet (Dötsch, 1983*b*). The pterygoid bone does not contribute to the formation of the glenoid fossa. The condylar facets of soricines are clearly separated, and the disc covers only the dorsal facet. The jaw articulation with its glenoid fossa is relatively larger than that in crocidurines (Dötsch, 1983*b*). In soricines, the pterygoid bone is part of the glenoid fossa.

The mass of masticatory muscles relative to total body mass in white-toothed shrews is larger than in red-toothed shrews (Dötsch, 1982, 1983*a*). The percentage of M. pterygoideus lateralis of the total masticatory musculature is greater in *Blarina* than in *Crocidura* and *Suncus*. In contrast, M. masseter and M. pterygoideus medialis in the white-toothed shrews are somewhat larger than in *Blarina*. M. digastricus in the white-toothed shrews is slightly smaller. Morphologically, M. temporalis showed the greatest differences among the species investigated. Its three main parts, as well as M. suprazygomaticus and M. zygomaticomandibularis, are well-developed in crocidurines (Dötsch, 1983*a*). The characteristic pinnation of part 3 is particularly well-expressed in *Suncus* and *Crocidura*. The large part 1 of M. temporalis which attaches anteriorly at the coronoid process is, in these species, mainly longitudinally oriented whereas in *Blarina* it faces laterally to the coronoid process.

In spite of differences in some aspects of tooth morphology among the species studied, in all shrews the upper dental arch is wider in the molar region than is the lower arch. This produces unilateral occlusion along labial parts of the molars at the ipsilateral side. According to the general anatomy in *B. brevicauda* described above, I predicted a greater variety of movements would be possible in this species than in the white-toothed shrews.

Masticatory Patterns

As in other mammals with anisognathous jaws, mastication is unilateral in shrews. A masticatory sequence included initial grasping of food, followed by chewing and repositioning cycles. The results indicate that the stage of the reduction sequence as well as food size and food consistency determined the lengths of these cycles. Mealworms were masticated with the most regular changing of the ipsilateral active side, in a course of five to seven cycles per side. The soft cat food mixed with

small resistant particles was chewed slightly more irregularly. Food of homogeneous, tough consistency such as pieces of chicken heart and chicken breast was preferentially chewed on one side of the jaws during the reduction sequence. Changing to the other side was infrequent.

Masticatory patterns and chewing frequencies in mammals are determined essentially by the consistency of food and the individual's bite (Herring and Scapino, 1973; Hiiemae, 1978; Thexton et al., 1980; Fish and Mendel, 1982). The masticatory cycle time of shrews varied with the type of food presented. For example, in *C. flavescens*, the mean chewing cycle duration was shortest on soft cat food (212.0 ± 18.4 msec). Chewing on mealworms averaged 242.8 ± 7.6 msec, on pieces of chicken heart 238.4 ± 15.2 msec, and on pieces of chicken breast 231.0 ± 20.2 msec.

A comparison of the masticatory rates of several shrew species revealed correlation with subfamily, independent of body size. The white-toothed *Crocidura flavescens* masticated at a rate of 4.6 orbits per second, *Suncus murinus* at 5.5, and *Crocidura russula* at 5.9. The red-toothed *Sorex araneus* chewed at a rate of 7.1 orbits per second, the European water shrew *Neomys fodiens* at 7.7, *Blarina brevicauda* at 7.9, and *Cryptotis parva* at 7.7. Thus, chewing rates were significantly higher in soricines than in crocidurines. Differences were tested by the Mann-Whitney U test of significance ($\alpha = 0.05$). An association with the anatomical differences in the jaw articulation and the masticatory musculature as well as in the muscle activities (EMG) is possible. Additionally, Vogel (1981) has shown that the two subfamilies of the Soricidae have different metabolisms.

Usually, masticatory cycles are divided into closing (fast and slow closing, FC and SC) and opening phases (slow and fast opening, SO and FO, Hiiemae, 1978). A "general mammalian chewing pattern" postulated by Hiiemae involves a closing stroke and an opening stroke. Subsequent studies (reviewed by Gorniak, 1985, except the article on *Tenrec ecaudatus* by Oron and Crompton, 1985) suggested deviations from the presumed generalized pattern owing to differences in dentition, jaw articulation, and jaw musculature (De Gueldre and De Vree, 1988). Because of the absence of a zygomatic arch, in both tenrecs and in soricids, it is of interest to determine the significance of muscle activity and jaw movements in these animals.

In *S. murinus* (Dötsch, 1986), I found similar percentages for opening (61–66%) and closing phases (34–39%), compared to a cycle for shrews and tenrecs (Oron and Crompton, 1985). However, if these percentages are compared with those in other shrew species, differences between the two soricid subfamilies become apparent. Depending on the food that was chewed, in *B. brevicauda* percent time for opening (30.6–44.2%) and closing (55.8–69.4%) phases were reversed in contrast to those recorded for *C. flavescens* and *S. murinus* (opening 52.6–64.7%, closing 35.3–47.4%). Gamble (1979) reported a percentage of 62% for closing and power stroke (definition of terms in Gamble's work) and 38% for opening in *B. brevicauda*.

In the white-toothed shrews, the long opening phase is affected by prolongation of the slow opening phase (Dötsch, 1986). In cats, tree shrews (*Tupaia*), and fruit bats, the significance of the SO phase is related to food transport by the tongue (Thexton et al., 1980; Mendel et al., 1981; Fish and Mendel, 1982; De Gueldre and De Vree, 1988). If there is a long FO/FC complex (for example in cats, Thexton et al., 1980) and a short SO phase, the food is chewed with the cheek teeth. Meeting the conditions in shrews, the very long SO phase, especially in *S. murinus*, is associated with movements at the mobile symphysis and of the tongue (Dötsch, 1986). Given the configuration of the jaw-joint in *Blarina*, the more obliquely-oriented masticatory muscles, and the occlusal surfaces of the cheek teeth, a greater variety of jaw movements is postulated in this genus. Additionally, food may be chewed better in red-toothed shrews (Dötsch, 1982). This might affect the longer time needed for jaw closing.

Electromyography

The stage of the reduction sequence and the type of food determined the length of masticatory cycles. These, in turn, affected the EMG pattern which generally varies with each cycle. This made it difficult to average the myograms.

Figure 1 presents myograms of right and left masticatory muscles of *C. flavescens* during chewing on pieces of chicken heart in the middle of a chewing series. The EMG levels of the muscles on the ipsilateral (active) and the contralateral (balancing) sides were asymmetrical. A clear asynchronous EMG pattern occurred in the large M. temporalis. The right, relatively small, pinnated part 3 of M. temporalis (M.TE3R) fired in the power phase before the left muscle (M.TE3L) was activated. The large M. temporalis 2 started almost simultaneously on both sides in the closing phase. The EMG level, however, in the first four cycles was higher in the right portions of M. temporalis than in the left. This indicated that the right side was the ipsilateral chewing side. In the last three cycles, left M. temporalis parts (M.TE3L, M.TE2L) were highly active, expressing the fact that the left jaw was the active side.

Another pattern occurred in M. pterygoideus medialis and in M. masseter. The right M. masseter (M.MASR) and M. pterygoideus medialis (M.PTMR) were in the closing phase longer than the contralateral muscles. Additionally, the EMG levels of M. masseter and M. pterygoideus medialis on the balancing side were higher than on the active side. M. digastricus showed main activity during the opening phase, which was slightly intensified on the active side. In two of the cycles (Fig.1), the left M. digastricus (M.DIGL) showed activity in an intermediate phase between the power phase and fast opening. The first of these cycles was a reversal of the ipsilateral side from right to left. The intermediate activity of M. digastricus occurred simultaneously with a strong action of the left M. pterygoideus medialis and a weaker action of the right M. pterygoideus medialis. In general, M. pterygoideus medialis may be firing in the power phase and in an intermediate phase during slow opening.

These observations suggest that M. temporalis with its main parts 1 and 2 is the primary muscle exerting pressure on food.

The pinnated part 3 was mainly acting as a guiding muscle. M. masseter and M. pterygoideus medialis are primary adductors of the jaws. M. digastricus is a jaw opener with lateral components of movement. Table 1 summarizes the activity of the masticatory muscles in *C. flavescens*. The number of pluses for the degree of muscular activity in a respective phase of a cycle showed the trends of muscle functions. M. pterygoideus lateralis is two-headed. The activity of the superior head was recorded by chance. Depending on the food that was chewed, it showed high levels of activity during the power phase and the fast opening phase.

Previous observations on dried skulls and muscles (Dötsch, 1982) confirmed the presumption that the superior M. pterygoideus lateralis supports M. digastricus as a jaw opener. This also occurs in *Tenrec ecaudatus* (Oron and Crompton, 1985), although it is not clear if the superior or inferior head of the muscle was recorded. The M. pterygoideus lateralis muscle weight in soricines was greater than in crocidurines (Dötsch, 1983*a*). The inferior M. pterygoideus lateralis would primarily cause laterally directed jaw closing movements. If crocidurines and soricines are compared, M. pterygoideus lateralis presumably will be more active in movements with guiding components in *Blarina* than in *Crocidura* or *Suncus*. In this context, M. mylohyoideus of *C. flavescens* (by chance punctured) was highly active in the intermediate phase and during fast jaw opening. From the line of action observed, this muscle inverted the mandibles so they rotated along a longitudinal axis. The resulting outward tilting of the mandibles can be seen as movements at the loose symphysis separating the lower incisors (Dötsch, 1986). The simultaneous action of M. pterygoideus medialis and M. mylohyoideus in the intermediate phase are considered to be responsible for rotational movements of the jaws.

Cineradiography

Figure 2a shows the positions of the implanted pins that served as markers for following complex jaw movements cineradiographically. Number 1 is a calculated midpoint between points 21 and 22 in the centers of left and right articulations. These points, 21 and 22 (not presented in the figure), are not implanted markers but estimated points. Calculation of the X/Y/Z coordinates of the cineradiographic film frame markers allowed estimation of distance changes between the pin points (Dantuma and Dötsch, 1989*b*). These changes showed the moving jaws during mastication and thus reproduced the movement pattern.

Principally, each orbital movement varied from the other. Figure 2b shows the movement orbits of points on the tip of the coronoid process and at the lower jaws in frontal view from one masticatory cycle. This cycle was the second in a series of three successive cycles (Fig. 2c, d) taken while *B. brevicauda* masticated a mealworm. The rotation of both lower jaws about the midline of the head (Fig. 2b, frontal view, line 1/2) is clearly demonstrated in these figures. The mobile symphysis enables relatively independent rotational movement of the mandibles. Points 9 and 10 on the tip of the coronoid process of the ipsilateral left side moved much more medially than points 15 and 16 on the contralateral side (Fig. 2b, c). Larger rotation of the lower jaw at the inferior jaw articulation produced stronger outward deflection of the coronoid process on the working side during jaw opening. This was associated with movements of the various M. temporalis parts acting on the coronoid process of the lower jaw. The markers on the mandibular ramus, which lie anterior to the jaw joints, however, differed less in their movement pattern on left and right sides (Fig. 2d). The relatively weak M. masseter/M. pterygoideus medialis complex acting on the mandibles would effect slight differences of movement on the working and the balancing side.

Conclusions

Chewing in soricids involves a combination of jaw movements that includes shearing, crushing, and grinding functions. The movements of the lower jaws in shrews vary from cycle to cycle and are conditioned by the double jaw joint and the mobile symphysis. This is reflected in the complex EMG patterns of the masticatory muscles. Additionally, masticatory muscle functions as well as jaw movements do not suggest a simple classification into a carnivorous, omnivorous, or herbivorous feeding type. The dissimilarities in the masticatory patterns of white-toothed and red-toothed soricids are explained by differences in the structure of the jaw joint and of the chewing muscles.

In all shrews, M. temporalis is the primary muscle exerting pressure on the food while M. masseter and M. pterygoideus medialis act as a complex to adduct the jaws with lateral components of movement. The superior part of M. pterygoideus lateralis supports M. digastricus as a jaw opener. M. pterygoideus medialis shows an immense repertory of muscle activity in most cycle phases. Its action in an "intermediate" phase is correlated with movements between the power phase and jaw opening which can be seen as tilting of the mandibles. A strong outward rotation of the coronoid process during opening is coupled with rotation at the inferior articulation of the double jaw joint. The large parts 1 and 2 of M. temporalis produce the main force that is concentrated in the crocidurines on the tip of the coronoid process. In soricines, the lines of force are laterally directed along the process. The pinnated part 3 of M. temporalis provides a force concentration along one line of action (Gamble, 1979). It functions most likely with M. suprazygomaticus and M. zygomaticomandibularis (the latter two muscles were too small for experiments) in stabilization of the lower jaw, especially in the area of the double joint. Given the anatomy, strong rotational movements will be prevented in crocidurines but forceful transverse motions will be enhanced. Rotational movements are intensified in soricines and will provide better alignment of the molars for effective grinding masticatory movements.

The unique skull features of all shrews, such as the absence of a zygomatic arch, the existence of a double mandibular articulation, and a fossa temporalis interna, result in a variety of muscle activities and jaw movements. The variation of feeding behavior is greater in soricids than in other mammals, even than in the closely-related tenrecs (Oron and Crompton,

1985) which also have no zygomatic arch. Therefore, a "typical" mammalian chewing pattern (Hiiemae, 1978) is not common to all mammals.

Finally, different metabolisms in the two soricid subfamilies (Vogel, 1981) indicate divergent biological strategies. The different feeding strategies of red-toothed and white-toothed shrews are reflected in anatomical differences of the masticatory apparatus. Considering the disparity and universal presence of soricines and crocidurines and their adaptation to different ecological niches (Hutterer, 1985), variation in food acquisition and masticatory behavior of these "primitive" insectivores was undoubtedly a basis for successful evolution.

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Table 1.—*Activity of the masticatory muscles during jaw closing and opening in* Crocidura flavescens. *For each muscle, symbols are as follows: First row, three pluses, main activity in a distinct phase; two pluses to one plus, high level to low level activity; plus/minus, occasional activity; minus, no activity. Second.row, I, ipsilateral, and C, contralateral activity; I=C, I synchronous C; I←C, I later than C, I→C, I before C. Third row, iEMG levels of ipsilateral and contralateral muscles in the main activity phases; I<C, I lower than C; I>C, I higher than C; I≙C, I similar to C.*

	Closing		Opening	
	Masticatory Cycle Phases			
	Fast	Slow	Slow	Fast
	"Power" Phase		Intermediate	Opening
M. digastricus	+		± to -	+++ I=C I>C
M. pterygoideus medialis	+++ I←C I<C		++ to + I=C I≙C	±
M. masseter	+++ I←C I<C		± to −	−
M. temporalis 1 M. temporalis 2	+++ I=C I>C		−	−
M. temporalis 3	+++ I→C I>C		−	−
(M. pterygoideus lateralis)	+++		−	++

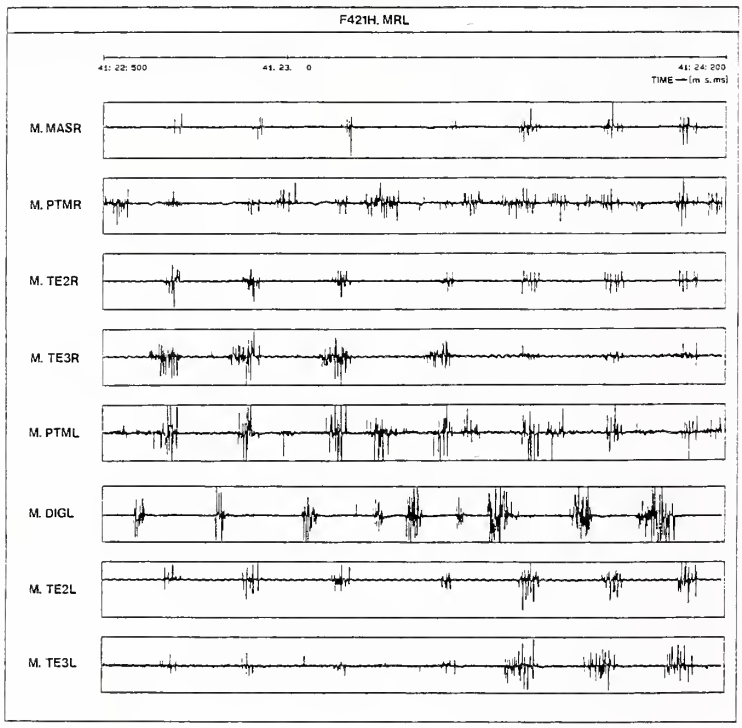

Fig. 1.—*Crocidura flavescens*. Original electromyograms from the middle of a chewing series, the animal was feeding on pieces of chicken heart. Reversal of ipsilateral side from right to left. M.MASR, right M. masseter; M.PTMR and PTML, right and left M. pterygoideus medialis; M.DIGL, left M. digastricus; M.TE2R and TE2L, right and left M. temporalis 2; M.TE3R and TE3L, right and left M. temporalis 3.

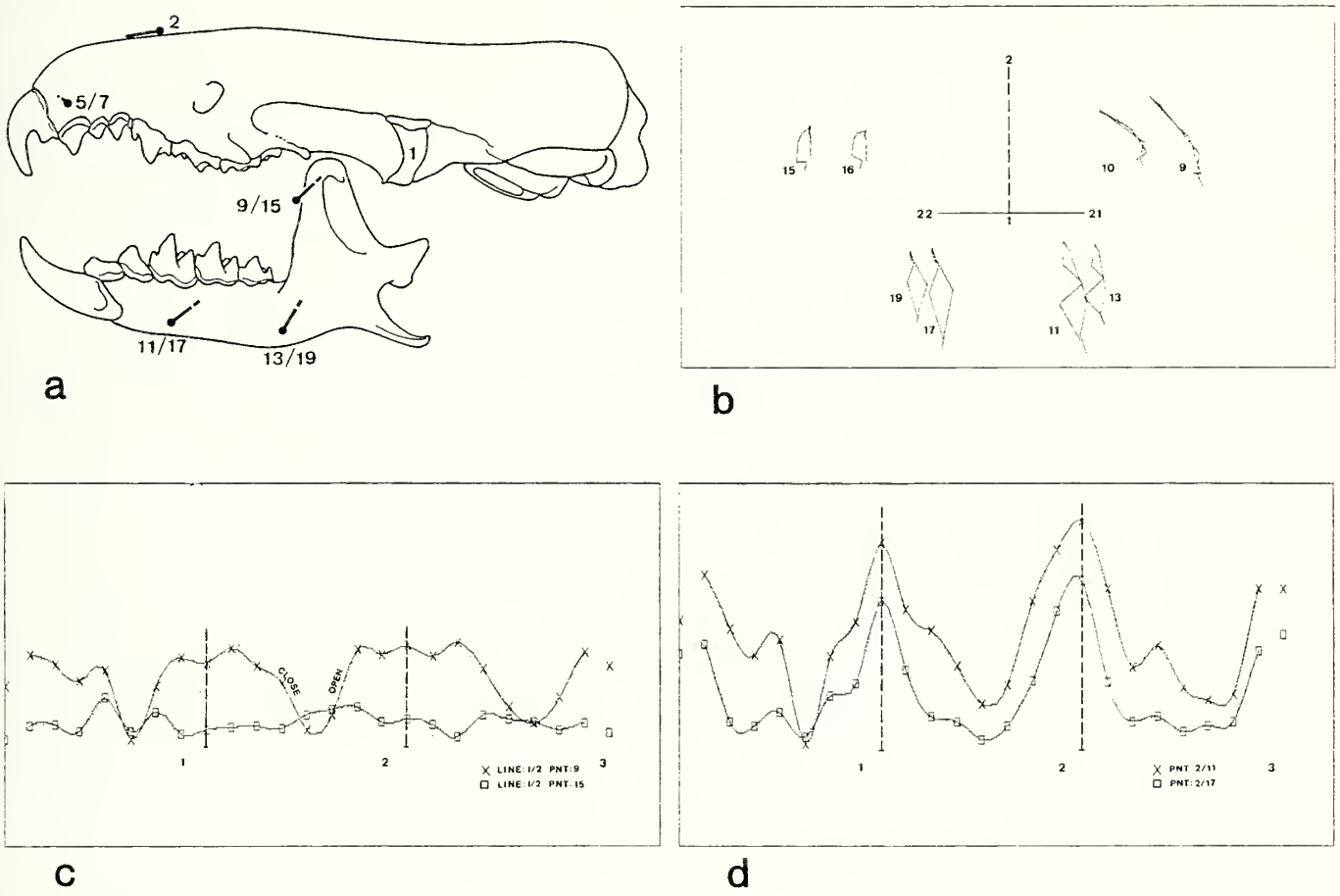

Fig. 2.—a. Positions of implanted parapulpar pins in the skull of *C. flavescens*. 1, calculated midpoint between the centers of right and left jaw articulations; 2, screw-head point of the pin on the midline of the skull; 5/7, left and right screw-head points of the pins in the rostrum; 9/15, left and right markers on the tip of the coronoid process; 11/17, anterior, and 13/19, posterior left and right lower jaws. b. Movement orbits of marker points in frontal view of *Blarina brevicauda* chewing a mealworm. Ipsilateral side is to the left. Left (9, 10) and right (15, 16) points in the coronoid process; left (11, 13) and right (17, 19) points in the mandibles; 21 and 22 are estimated markers in the centers of the articulations. c. Calculations of distance changes between points on the coronoid processes (9/15) and the midline of the skull (line 1/2), frontal view. d. Distance changes between point 2 and left and right mandible markers (11/7), frontal view. Movement orbits from cycle 2 are shown in b.

COMPARATIVE EMBRYONIC DEVELOPMENT OF THE SORICIDAE

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ABSTRACT

Embryonic and fetal development was studied in *Sorex vagrans* and *S. cinereus* using embryos from wild-caught, pregnant females. A total of 103 embryos and fetuses were classified to developmental stage based on external morphological features and crown–rump measurements; and developmental changes in skeletal, neural, respiratory, and digestive systems characterized for each stage. These data were compared to the developmental pattern of the mouse *Mus musculus*. Differences were observed in timing of neural tube closure, and skeletal and respiratory developmental events. All embryological changes occurred at a later developmental stage in *Sorex* than in *Mus*. Results substantiate allometric or evolutionary relationships between taxa.

INTRODUCTION

Members of the mammalian Order Insectivora are considered to be the most primitive living eutherians. Their primitive status is based on ancestral dental and skull characteristics retained by extant species. These mammals are insectivorous, as were early Cretaceous forms.

Within the Order Insectivora, members of the Family Soricidae (Subfamily Soricinae) are considered the most primitive (Repenning, 1967; Vogel, 1980, 1981). Developmental studies of postnatal growth in one species, *S. araneus*, indicate that young are born in an immature, nidicolous state, more similar to the developmental sequence of metatherians than to that of other eutherians (Vogel, 1972, 1980, 1981). This developmental evidence is interpreted as further support for the hypothesis that insectivores are evolutionarily very primitive mammals. The similarity in fetal development at birth between the Soricinae and marsupials represents a plesiomorphic, or primitive, relationship rather than an apomorphic, or derived, relationship (Lillegraven, 1976; Marshall, 1979). Members of the Subfamily Soricinae, therefore, may be the most primitive extant eutherians with which to study ontogenetic correlates to metatherians.

Although a comparative atlas on the staging of mammalian embryos has recently been published (Butler and Juurlink, 1987), no insectivores were included among the species studied. Several studies have addressed prenatal development in insectivores (Štěrba, 1977, 1985), yet to date, no comprehensive atlas of embryonic development has been produced on any member of the Genus *Sorex*. Initial studies are presented here for two members of this genus, *S. vagrans* and *S. cinereus*.

MATERIALS AND METHODS

Shrews were collected in pitfall traps between April 1985 and August 1990 in western Montana. Reproductive tracts from all females were removed and immediately fixed in 10% calcium chloride-buffered formalin. Those containing obvious embryos were handled in one of two ways. The smallest swellings were separated and processed for histological analysis in their entirety, whereas larger swellings ($> 3 \times 5$ mm) were opened to remove the fetuses prior to processing. Each larger embryo and fetus was photographed and classified by developmental stage based on external morphological features and crown–rump measurements, employing Theiler's (1989) criteria for *Mus musculus*, Streeter's (1942, 1945, 1948, 1949, 1951) and O'Rahilly's (1973) for the human embryo, and Štěrba's work (1977, 1985) for insectivores. A total of 103 embryos and fetuses (74 *S. vagrans* and 29 *S. cinereus*) were classified. From these, two or three individuals representing each ontogenetic stage recognized by Theiler (1989) were dehydrated, embedded in paraffin, serially sectioned at either 3 or 8 μm, and stained with hematoxylin and eosin for histological examination. Developmental stages of skeletal, neural, respiratory, and digestive systems were characterized for each individual. These embryological data were compared with the ontogenetic time frame observed by Štěrba (1977) for *Sorex araneus* and the developmental pattern exemplified by *M. musculus* as outlined by Rugh (1968) and Theiler (1989).

RESULTS

The prenatal growth rates of *S. vagrans* and *S. cinereus*, expressed as crown–rump length as a function of developmental stage, closely parallel one another (Fig. 1). Ontogenetic changes described for each developmental stage depicted in Fig. 1, with the exception of Theiler Stage 12, are outlined below. The ontogenetic stage and approximate day of development follow Štěrba (1977) for insectivores, and thus is not consistent with the developmental time frame of Theiler stages for *Mus*; Theiler stages were used solely as an index of morphological criteria for development. Certain ontogenetic stages observed fell between those described by Štěrba and are thus approximated by indicating a "+" value (e.g., Ontogenetic Stage 2+).

Ontogenetic Stage 2 (Theiler Stage 13): [Approximately Day 10 post-coitus (p.c.); S. vagrans*]*

External features.—[Crown rump (CR) measurement of one embryo = 1.3 mm]. Neural folds are forming along the length of the embryo leaving the anterior and posterior regions open as an exposed neuropore. Somites are readily visible (Fig. 2a).

Internal anatomy.—The forebrain anlage is thickening and flexing, bending the anterior portion of the embryo. Somites are readily apparent (a total of nine in the embryo sectioned), and

initial heart formation is occurring (Fig. 2a, b). The gut is developing, with an expansion in the foregut region (Fig. 2b).

Ontogenetic Stage 2+ (Theiler Stage 14):
[Approximately Day 11 p.c.; S. cinereus*]*

External features.—[Mean crown-rump measurement ($\bar{X}$CR) = 1.6 mm, range 1.4–1.8 mm]. Two branchial bars are evident, and the forming heart bulges from the ventral surface. The forelimb bud is barely discernible, and the tail curves to the right (Fig. 2c). The anterior neuropore has closed, whereas the posterior neuropore remains open.

Internal anatomy.—Nephric ducts and vesicles are forming in conjunction with the thoracic somites. In the hindgut region the aorta is paired.

Ontogenetic Stage 3 (Theiler Stage 16):
[Approximately Day 12 p.c.; S. vagrans*]*

External features.—[$\bar{X}$CR = 3.0 mm, range = 2.9–3.1 mm]. The posterior neuropore is still open. Front limb buds are prominent, and hind limb buds are evident as distinct bulges. The lens plate is indented to form a pit, whereas the otic vesicle has completely closed and is separated from the epidermis. Branchial bars 1 and 2 are enlarged and convex, whereas numbers 3 and 4 are concave and only apparent from the presence of the cervical sinus. The tail is beginning to elongate and terminates in an enlarged stump (Fig. 3a, b).

Internal anatomy.—Bronchial buds are forming as branches from the laryngotracheal tube (Fig. 3c), and the thyroid diverticulum is prominent. Rathke's pouch appears as a distinct evagination from the roof of the oral cavity. The digestive tract has formed as a narrow tube running the length of the embryo with a slight expansion forming as the stomach anlage. Mesonephric ducts and tubules are in evidence along the latter third somites of the embryo.

Ontogenetic Stage 3+ (Theiler Stage 17):
[Approximately Day 13 p.c.; S. vagrans *and* S. cinereus*]*

External features.—[$\bar{X}$CR: *S. vagrans* = 3.6 mm, range 3.0–4.3 mm; *S. cinereus* = 2.8 mm, range 2.7–3.0 mm]. The eye lens vesicle is conspicuous, forming a deep pocket. Both forelimb and hindlimb buds are enlarging, and the tail is elongating (Fig. 3d).

Internal anatomy.—The surface epithelial layer is invaginating to form a lens pocket (Fig. 3e). The liver anlage is forming blood sinuses, and there are a large number of mesonephric tubules. The heart has formed single atrial and ventricular chambers, but these are not subdivided (Fig. 3f).

Ontogenetic Stage 4 (Theiler Stage 19):
[Approximately Day 14 p.c.; S. vagrans*]*

External features.—[$\bar{X}$CR = 4.4 mm, range 4.2–4.8 mm]. The most characteristic feature of this developmental stage is the formation of a footplate on the forelimb. A distinct constriction marks the presumptive wrist. The hindlimb, slower to form, is still represented by an expanded bud. Three brain regions, telencephalon, mesencephalon, and rhombencephalon, are clearly visible, and the nostrils have formed adjacent to a nasolacrimal groove. Somites are distinct, particularly in the tail region which has elongated (Fig. 4a).

Internal anatomy.—The tongue has not yet elevated from the floor of the mouth. Major bronchi of the lungs are forming lined with pseudostratified columnar epithelium (Fig. 4c). The liver is a diffuse organ consisting of large sinusoids filled with nucleated erythrocytes (Fig. 4f). The stomach is enlarging, lined internally with pseudostratified, columnar epithelium and externally with a single layer of cuboidal cells. The matrix of the stomach is densely packed with undifferentiated cells (Fig. 4f). Mesonephric development is marked by the appearance of glomerular bodies (Fig. 4b). The eye lens has detached from the surface ectoderm and has completed closure (Fig. 4e). All vertebrae are in the precartilage coalescence stage, and the ribs are beginning to chondrify (Fig. 4d, Table 1).

Ontogenetic Stage 4+ (Theiler Stage 20):
[Approximately Day 14 p.c.; S. vagrans*]*

External features.—[$\bar{X}$CR = 6.4 mm, range 6.1–6.6 mm]. The hindfoot plate has formed on an elongating limb being displaced from the body, and the forefoot plate has begun to show signs of digitation. Eye pigmentation is distinct, and the otic vesicle is deeply invaginated (Fig. 5a).

Internal anatomy.—Semilunar ganglia are very prominent. The eye lens is forming, but there is only slight development of lens fibers (Fig. 5b). Mitoses are apparent in cells of the lens. The major bronchus is branching and rapidly elongating. There are numerous mesonephric tubules, and the metanephric tissue has begun to develop. Primary renal calyces are present, and metanephric ducts are forming (Fig. 5c). The gonad is at its earliest stage of differentiation; in the animals examined (all males) an outline of the seminiferous tubules is apparent. Vertebral tissue is condensing above and around the notochord.

Ontogenetic Stage 5 (Theiler Stage 21):
[Approximately Day 15 p.c.; S. vagrans*]*

External features.—[$\bar{X}$CR = 6.6 mm, range 6.3–7.0 mm]. Marked changes have occurred with further development of the eye, and conspicuous formation of the ear pinna. The forelimb has constricted further at the wrist, and hand rays are forming with distinct indentations demarcating the presumptive digits. The hindlimb has also further differentiated with a constricture at the ankle and a hint of digit formation. Somites are clearly visible in the tail region, and hair tracts, which are progenitors of whiskers, are noticeable on the snout (Fig. 6a, b).

Internal anatomy.—A small number of bronchioles are branching off of the bronchi, lined with pseudostratified, columnar epithelium (Fig. 6c). The stomach has continued expansion and is thickly lined with pseudostratified cells. Circular muscle layers are beginning to differentiate, but there is no glandular development. All valves are present in the heart, and the pituitary gland is differentiating (Fig. 6f). Gonadal development is proceeding rapidly with the appearance of discrete seminiferous tubules (Fig. 6d, e). Skeletal development

has proceeded to varying stages of chondrification, with caudal vertebrae lagging behind (Fig. 6g, h, i; Table 1).

Ontogenetic Stage 6 (Theiler Stage 22):
[Approximately Day 17 p.c.; S. vagrans *and* S. cinereus*]*

External features.—[$\bar{X}$CR: *S. vagrans* = 8.4 mm, range 7.5–8.7 mm; *S. cinereus* = 7.6 mm, range 7.4–7.8 mm]. Two features characterize this developmental stage. A prominent umbilical hernia appears, and the digitation of the foot plates has continued. The ear pinna has expanded, and hair follicles cover most of the body. The tail still curves to the right (Fig. 7a, b, c).

Internal anatomy.—Marked development has occurred in all internal organ systems by this stage. The tongue has risen up, and been undercut by the lower jaw, with concurrent formation of the epiglottis; the secondary palate is still open. The lung has become distinctly lobed, and extensive branching of the bronchioles has occurred, although the lung tissue remains compacted (Fig. 7l). The bronchioles are lined by simple columnar epithelium. The esophagus, lined with a stratified layer of cuboidal cells with round nuclei, opens into an expanded stomach lined with tall, pseudostratified, columnar cells with very elongated nuclei. Two or three clearly distinct layers of circular smooth muscle cells are differentiating in the stomach wall, although no longitudinal layers are evident (Fig. 7o). The lining of the intestinal tract has an appearance similar to that of the stomach, though it is thrown into folds. A portion of the small intestine lies externally as a component of the umbilical hernia. The choroid plexus is well-developed, and projects deeply into the lateral ventricle (Fig. 7k). Further pituitary development and folding have reduced the size of Rathke's pouch (Fig. 7h). Rapid development of the cervical (Fig. 7i) and cranial (Fig. 7j) nerves is evident, and anlagen of both the upper and lower incisors are visible. Gonadal development has proceeded with further rounding in the walls of the seminiferous tubules and the presence of large, prominent gonocytes within the lumina (Fig. 7m, n). Ovarian development has proceeded as well, although follicular development is not evident. Skeletal ossification has begun medially in the upper limbs, and in the cervical vertebrae, whereas other skeletal tissues are still in precartilaginous stages or are beginning to progress through stages of chondrification (Fig. 7d, e, f, g; Table 1).

Ontogenetic Stage 7 (Theiler Stage 25):
[Approximately Day 19 p.c.; S. vagrans*]*

External features.—[$\bar{X}$CR = 12.0 mm, range 11.5–12.4 mm]. The eyelids are fused. The umbilical hernia has disappeared, and the skin is noticeably wrinkled. Hindlimbs are tightly curled into the body (Fig. 8a, b, c, h).

Internal anatomy.—Palatine processes have fused resulting in formation of the secondary palate. Lung tissue has become less compacted as the terminal bronchioles begin opening into terminal saccules through transitory ducts (Fig. 8i, j, k). The upper and lower incisors have differentiated into precalcified enamel and dentin layers—the bell stage of development (Fig. 8f). Formation of the eye has progressed significantly; cells of the lens are rapidly laying down fibers, the ciliary body has formed, and the eyelids have closed (Fig. 8l). The thymus has greatly enlarged with the proliferation of small, darkly stained lymphocytes in the cortical region. The medullary region is still reduced and contains lightly-staining epithelial reticular cells (Fig. 8g). By this stage all vertebral types (though not every vertebra) are undergoing ossification as are the proximal regions of long bones of upper and lower limbs, and bones of the skull (Table 1). Skeletal elements of the fore- and hindfeet are undergoing chondrification (Fig. 8d, e; Table 1).

Ontogenetic Stage 7+ (Theiler Stage 26):
[Approximately Day 20 p.c.; S. vagrans*]*
(This stage marks the final growth sequence before birth.)

External features.—[$\bar{X}$CR = 12 mm, range 11.4–12.6 mm]. The most diagnostic feature at this stage is the withdrawal of limbs away from the body. As in Stage 25 the eyes are essentially invisible with the closure of the eyelids (Fig. 9a, b).

Internal anatomy.—Overall development is similar to that described for the previous stage. The gastrointestinal tract has differentiated providing many of the cellular characteristics seen in the adult. The esophagus is lined with stratified, squamous epithelial cells which give way to columnar cells in the stomach. Six to eight layers of circular muscle invest, and support, the stomach, and the first longitudinal folds (rugae) are apparent (Fig. 9j). Gastric pits are evident as are sporadic Goblet cells, although the submucosal glandular tissue has not yet developed. A proliferation of thin-walled villi lined with columnar epithelial cells, and surrounded by two or three layers of circular smooth muscle, predominate in the small intestine (Fig. 9k). However, no lacteals are visible at this stage. The lungs are becoming less compacted, but alveolar development is not yet evident. Branching of bronchioles ends in terminal saccules (Fig. 9n, o). There is continued development in all of the endocrine glands. The medulla of the thymus has enlarged, and a few of the thyroid follicles appear to be invested with colloid. Pancreatic islands are well-differentiated, and pituitary cells of the Pars distalis (adenohypophysis) are enlarging slightly, and becoming more rounded (Fig. 9f). Rathke's pouch has been further reduced. Seminiferous tubules of the testis are encapsulated with a single layer of fibrocytes, and the basement membrane is forming. Large numbers of spermatogonia are evident within the tubules, and there is much interstitial tissue, although the interstitial cells are not easily distinguishable from support tissues (Fig. 9l, m). A thick pad of multilocular fat tissue has formed in the intrascapular region. The eye appears similar to that of the previous stage; the iris rudiment is present, but has not differentiated further (Fig. 9c). Ear ossicles are well-formed, and vestibular sensory hairs are visible (Fig. 9i). All vertebral types are ossifying further as are the ribs, appendicular long bones, and bones of the skull. Chondrification is continuing in the fore- and hindfeet. (Fig. 9d, e, g, h; Table 1).

Discussion

Both *S. vagrans* and *S. cinereus* are born in an altricial condition similar to that described for *S. araneus* (Vogel, 1972). Although the timing of developmental changes and rate of growth in *S. cinereus* parallel that observed in *S. vagrans* (Fig. 1), overall fetal size attained at comparable stages is slightly smaller. This difference is most likely due to the smaller adult body size of *S. cinereus*. In wild populations adult *S. cinereus* weigh on average 39% less than adult *S. vagrans* (4.6 g vs. 7.6 g).

The general ontogenetic pattern appears similar to that previously described for the laboratory mouse, *M. musculus* (Rugh, 1968; Theiler, 1989). When Štěrba's (1977, 1985) results on *S. araneus* are taken into consideration, the time at which comparable developmental stages are reached in these soricids is estimated to be later. However, if the degree of internal organogenesis is correlated with the stage of development, as exemplified by external body form characteristics, there is close correlation between the soricids and *M. musculus* with a few notable exceptions.

Staging of soricid embryos in the present study was based on two criteria: first, comparison of external characteristics with those described for *Mus* (Theiler, 1989), and second, consideration of actual age attained as proposed by Štěrba (1977). Although dates of conception were not known, the completeness of developmental stages available, and their close correlation with Theiler's and Štěrba's described stages, suggest that this method can be used to accurately sequence soricid developmental stages. Use of developmental characteristics to classify embryos rather than relying solely on CR measurements is of critical importance. Embryos of the same age, particularly at the later stages of development, may vary several millimeters in length even within a litter. Also, it is recognized that at comparable stages of development embryo length may vary greatly between species (ten Donkelaar et al., 1979; Butler and Juurlink, 1987). Some variation in the age assigned to various stages in the present study may have occurred due to variability in developmental rates, particularly between littermates (ten Donkelaar et al., 1979; Juurlink and Fedoroff, 1980), but this is considered to be negligible. Given these assumptions, several developmental differences are apparent in soricids.

Vogel (1972) described in detail the reduced skull ossification at birth in *S. araneus* and *Neomys fodiens*, a condition paralleling that observed in neonate marsupials. A similar situation is found in the present study. In comparison to *Mus* (Rugh, 1968), the timing of chondrification and/or ossification of a few cranial bones, vertebrae, long bones of the hind limb, and feet, occurs later in the soricids (Table 1). Other developmental events in *Sorex* occur at a later embryonic age as well. The posterior neuropore which closes in *Mus* at Theiler Stage 16 (ten days p.c.), remains open past Stage 17 in soricids, which approximates Day 13 p.c. In all cases closure is complete by Stage 19, or approximately Day 14 p.c. in soricids. Eye development also appears to lag behind that observed in *Mus*. Lens fiber formation and growth of the iris are retarded.

A significant difference occurs in the development of the lungs. In soricids, alveolar growth does not occur by birth. The final stage of development in near-term fetuses consists of terminal saccules (Fig. 8j, 9o). Lung tissue remains more compacted and possesses fewer terminal saccules per area than in *Mus*. Although Theiler (1989) described an "alveolar explosion" in *Mus* at this stage (Stage 26, just prior to birth), more detailed descriptions of lung development in the mouse (Engel, 1953) and rat (Burri, 1974, 1985) suggest that true alveolar formation has not yet occurred. However, lung tissue in these species does become markedly less dense, and terminal saccules become numerous as the progenitors to alveoli (Burri, 1974).

Štěrba (1984) argued that the altricial ontogenetic pattern, exemplified by the genus *Sorex*, is the primary evolutionary pattern from which the precocial pattern, as exemplified by *Mus*, developed. This suggests that the difference in developmental rates between *Mus* and *Sorex* represents acceleration in development in *Mus*, rather than retardation in *Sorex*. This argument is convincing considering that in altricial species of the genus *Sorex*, considerable developmental maturation occurs during the postnatal period. A comparison of ontogenetic time patterns in other insectivores (e.g., *Crocidura* and *Talpa*: Štěrba, 1977; *Suncus*: Vogel, 1972) further supports this thesis. Taken collectively these studies thus suggest that development in *Sorex* species falls between the Crocidurinae and the Muridae.

The very altricial condition of newborn *Sorex* has also been suggested as supporting this group's phylogenetic relationship to marsupials (Vogel, 1981). Developmental similarities between *Sorex* and *Neomys*, and a generalized marsupial, *Didelphis*, have been demonstrated (Vogel, 1972, 1981). Those studies and the present one illustrate differences in many prenatal development stages relative to typical nidicolous eutherians such as *Mus*. However, the influence of allometric scaling on developmental processes should not be overlooked. Štěrba (1984) proposed a thesis which addressed the limiting factors of adult body size and physiological longevity. He attempted to explain the occurrence of nidicolous and nidifugous (precocial) ontogenetic patterns by ecological selective pressures which influence the development of r- and K-strategies of reproduction. These selective pressures, he suggested, determine the ontogenetic pattern, which then secondarily becomes evolutionarily "fixed." Much broader comparative embryological studies on additional soricids and similarly-sized advanced eutherians should further clarify this relationship.

Acknowledgments

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Table 1.—*Chondrification and/or ossification of tissues.* [a] *Ontogenetic Stage (OS) and approximate developmental day (D) after Štěrba (1977).*

Skull Bones:		
Basioccipital, basisphenoid, exoccipital, tympanic (endochondral bones which pass through a chondrification stage); maxillary, palatine, premaxillary, pterygoid (dermal bones which ossify directly from connective tissue)		
	OS5(~D15)[a]	chondrified—early/middle condensation stages
	OS6(~D17)	chondrified—middle/late condensation stages
	OS7(~D19)	ossification occurring
	OS7+(~D18)	continued ossifieation
Vertebrae:		
Cervical	OS4(~D14)	preeartilage coalescence
	OS5	chondrified—late condensation stage
	OS6	ossification—early stage
	OS7	continued ossification
	OS7+	continued ossification
Thoracic	OS4	precartilage coalescence
	OS5	chondrified—early condensation stage
	OS6	chondrified—early condensation stage

	OS7	ossification occurring
	OS7+	continued ossification
Lumbar	OS4	precartilage coalescence
	OS5	chondrified—middle condensation stage
	OS6	chondrified—middle condensation stage
	OS7	ossification occurring
	OS7+	continued ossification
Sacral	OS4	precartilage coalescence
	OS5	chondrified—middle/late stages
	OS6	chondrified—late stage/early ossification
	OS7	continued ossification
	OS7+	continued ossification
Caudal	OS4	precartilage coalescence
	OS5	precartilage coalescence
	OS6	precartilage/early chondrification
	OS7	ossified—early stages
	OS7+	continued ossification
Ribs	OS4	chondrified—early stage
	OS5	chondrified—early stage
	OS6	chondrified—early stage
	OS7	ossification occurring
	OS7+	continued ossification
Appendicular Skeleton:		
Humerus	OS5	chondrified
	OS6	ossification occurring
	OS7	continued ossification
	OS7+	continued ossification
Ulna/Radius	OS5	chondrified
	OS6	ossification occurring
	OS7	continued ossification
	OS7+	continued ossification
Carpals, Metacarpals, Phalanges		
	OS6	prechondral/earliest chondrification stages
	OS7	chondrification—early stages
	OS7+	chondrification continuing
Femur	OS5	chondrification—early stage
	OS6	chondrification—middle stage
	OS7	ossification occurring
	OS7+	continued ossification
Tibia/Fibula	OS5	chondrification—early stage
	OS6	chondrification—middle stage
	OS7	continued ossification
	OS7+	continued ossification
Tarsals, Metatarsals, Phalanges		
	OS6	prechondral/earliest chondrification stages
	OS7	chondrification—middle stage; (epiphyses in prechondral stage)
	OS7+	chondrification continuing

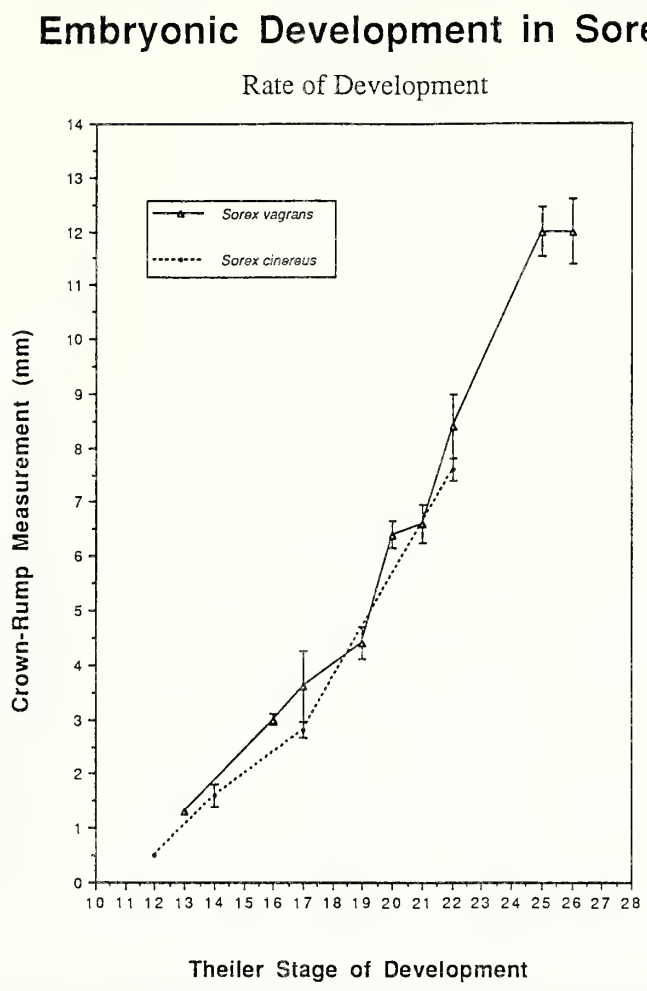


Fig. 1.—Crown-rump measurement as a function of Theiler developmental stage in *Sorex vagrans* and *Sorex cinereus*.

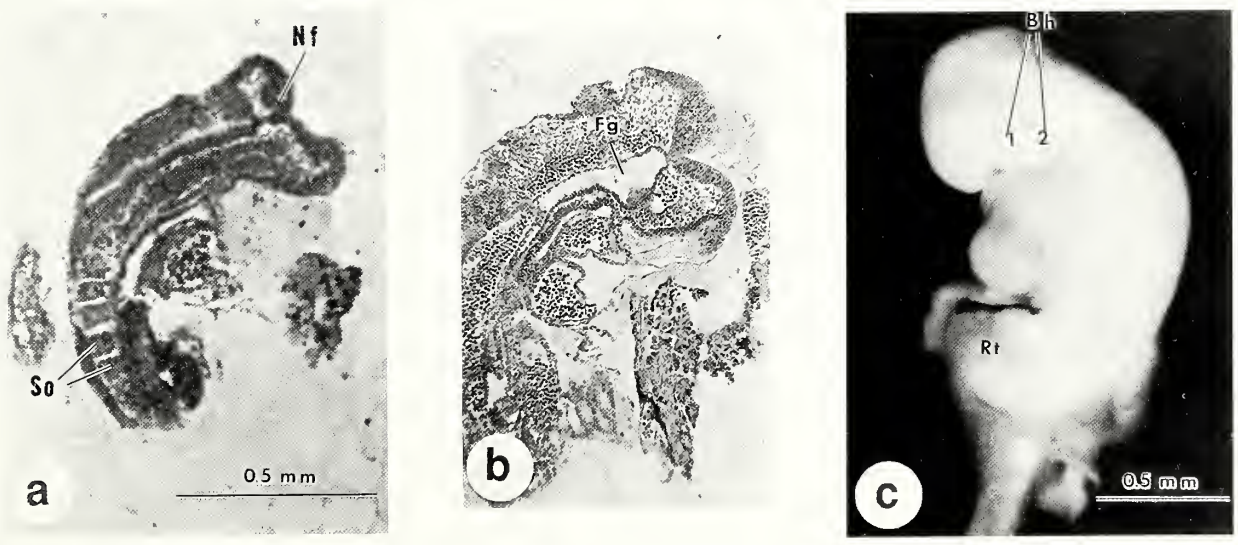


Fig. 2.—a, b, Ontogenetic Stage 2 in nine-somite embryo of *Sorex vagrans*. So, somite; Nf, neural folds; Fg, foregut. c, Ontogenetic Stage 2+ in embryo of *Sorex cinereus*, left side view. Bh, branchial bars; Rt, tail curved to right.

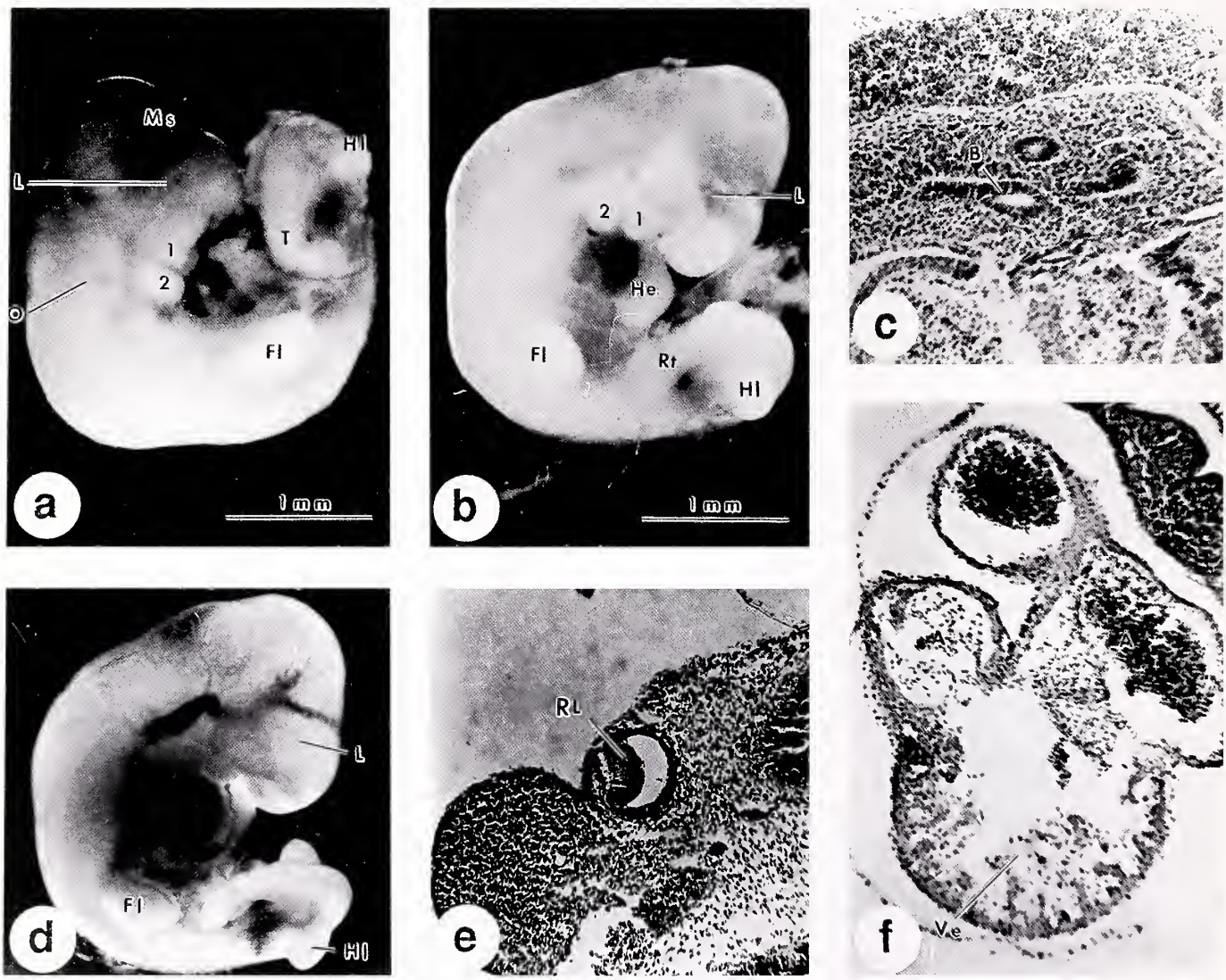


Fig. 3.—a–c, Ontogenetic Stage 3 in *Sorex vagrans*. a, b, Embryo, right side views. L, lens pit; Ms, mesencephalon; 1, first branchial bar, 2, second branchial bar; O, otic vesicle; T, tail; He, heart; Fl, front limb bud; Hl, hind limb bud; Rt, tail curvature to the right. c, Lung. B, bronchial bud. d, Ontogenetic Stage 3+ in *Sorex vagrans*, embryo, right side. L, lens pit; Fl, front limb bud; Hl, hind limb bud. e, Eye showing retinal layer (RL). f, heart. Ve, unpaired ventricle; A, incompletely partitioned atrial chambers.

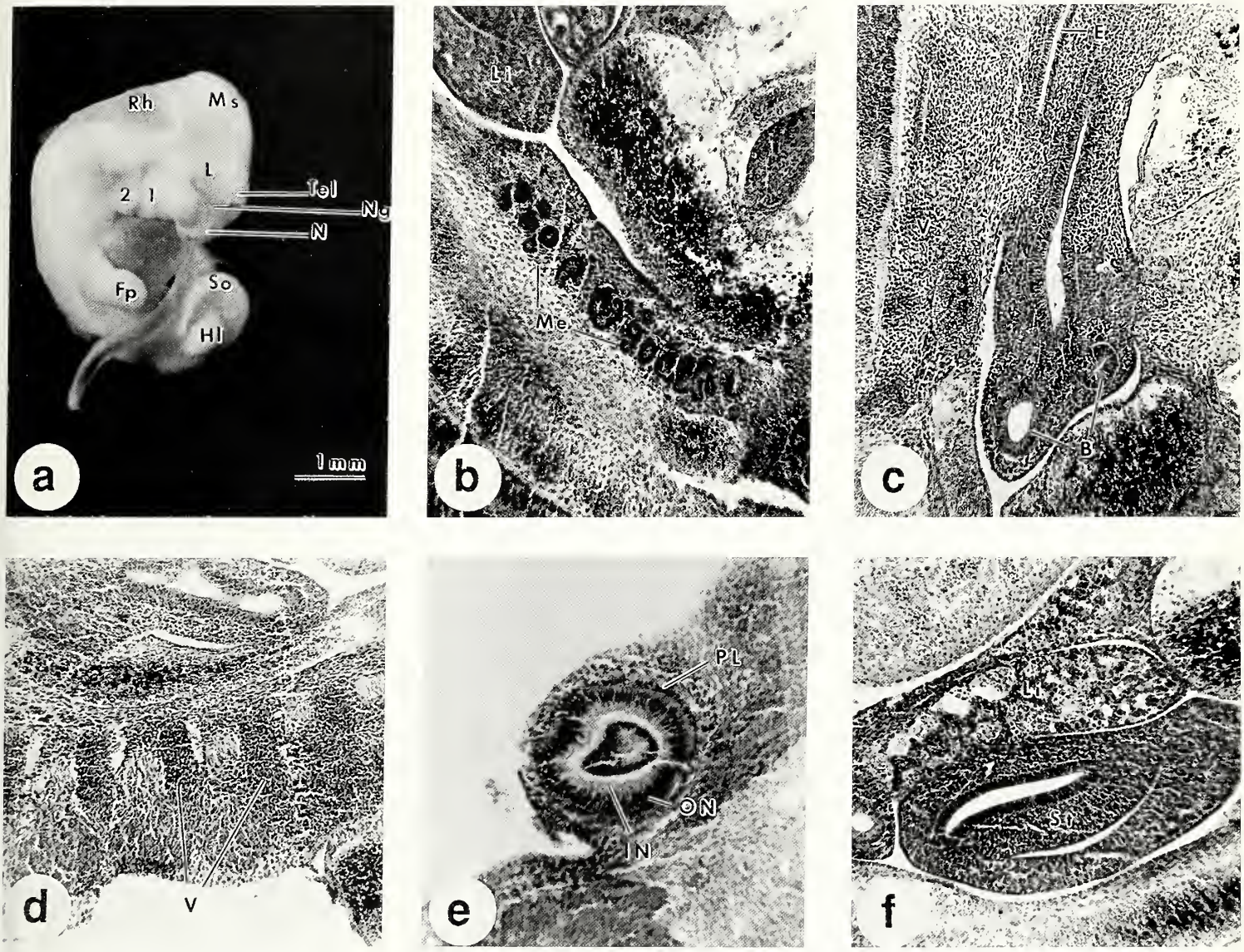


Fig. 4.—Ontogenetic Stage 4 in *Sorex vagrans*. a, Embryo, right side. Tel, telencephalon; Ms, mesencephalon; Rh, rhombencephalon; 1, first branchial bar; 2, second branchial bar; L, lens (L), Ng, nasolacrimal groove; N, nostrils; Fp, forelimb bud forming handplate; Hl, hindlimb bud undifferentiated; So, tail somites. b, Me, mesonephric development; Li, liver. c, Lung. B, bronchi; V, thoracic vertebrae; E, esophagus. d, V, Thoracic vertebrae. e, eye. PL, pigment layer; IN, inner neuroblastic layer; ON, outer neuroblastic layer. f, St, stomach; Li, liver.

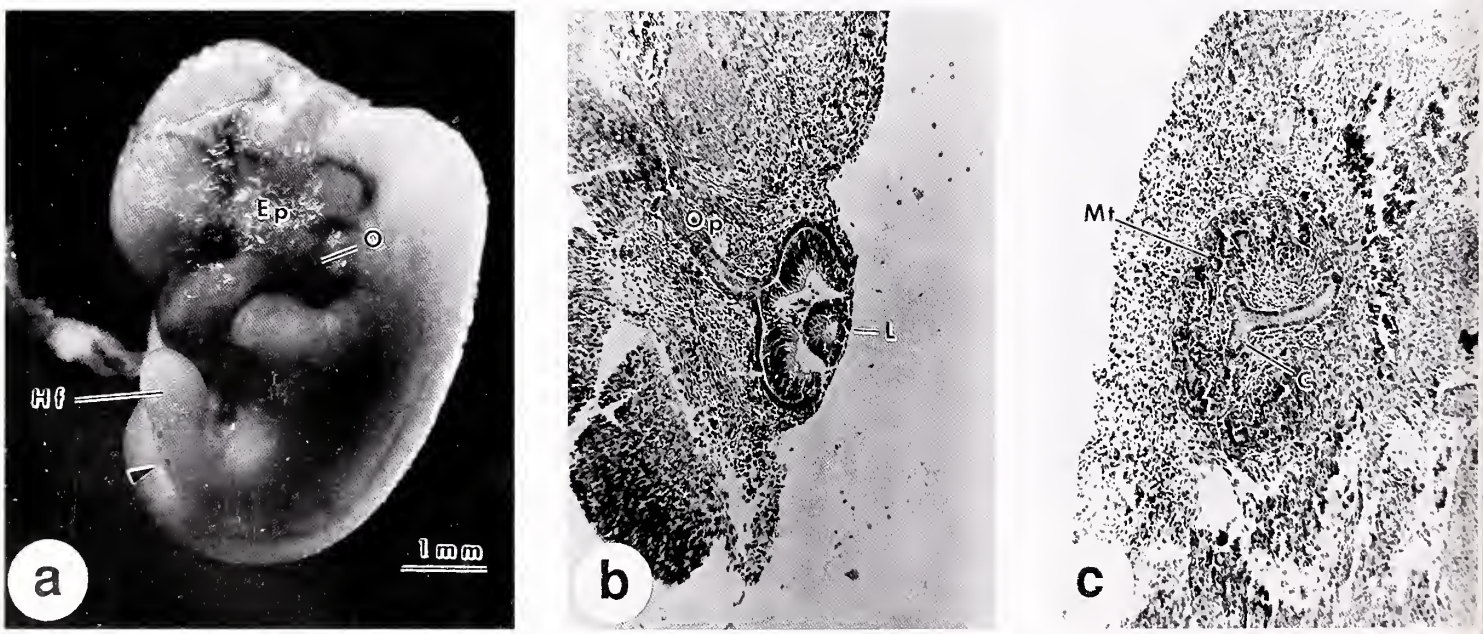


Fig. 5.—Ontogenetic Stage 4+ in *Sorex vagrans*. a, Embryo, left side. Ep, eye pigmented; Hf, hindfoot plate forming on elongating limb (arrow); O, otic vesicle. b, Eye. L, lens; Op, optic nerve. c, Kidney. Mt, metanephric ducts; C, renal calyx.

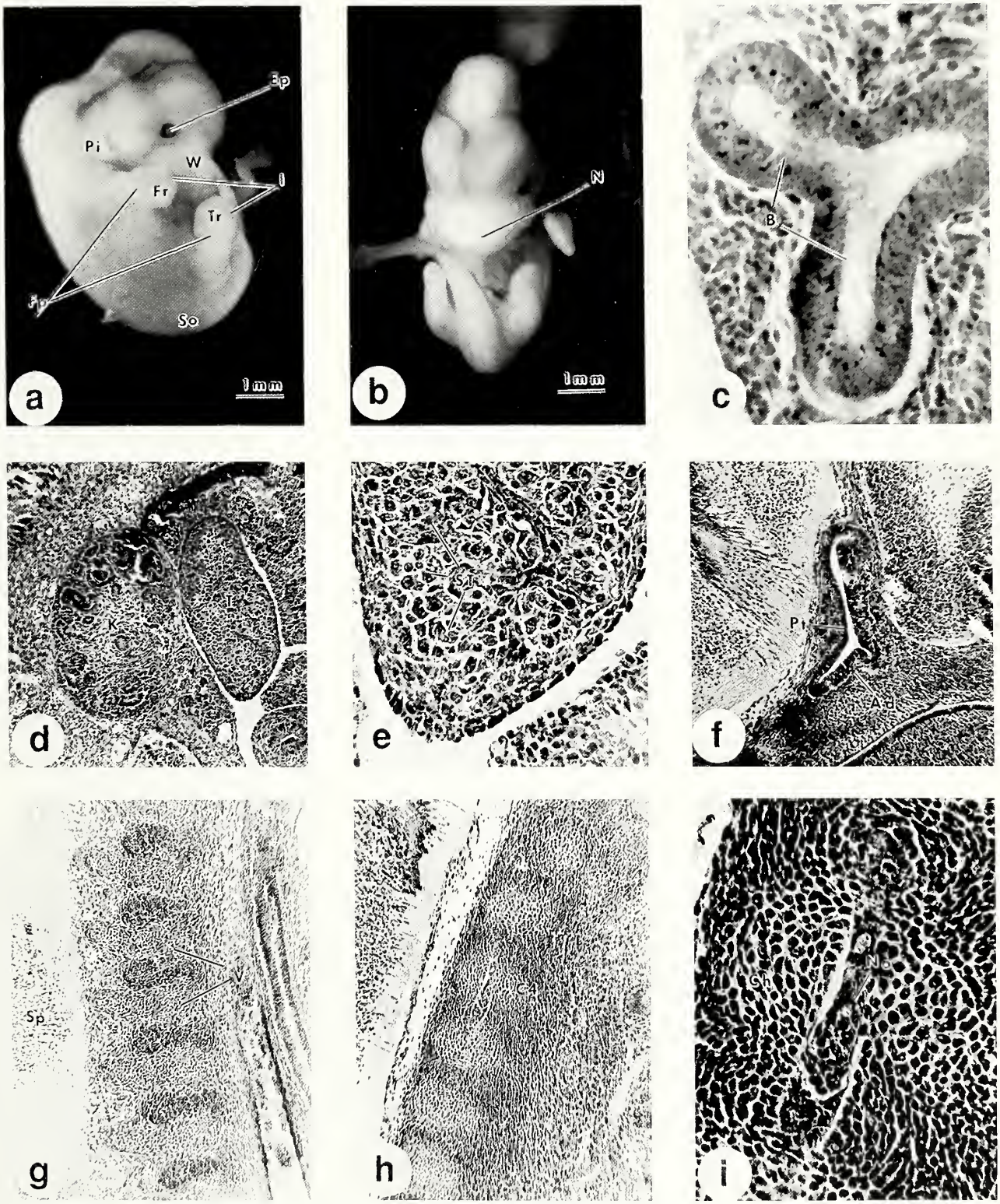


Fig. 6.—Ontogenetic Stage 5 in *Sorex vagrans*. a, b, Embryo, right and frontal views. Ep, eye pigmented; Pi, ear pinna; W, whiskers; Fp, foot pads; Fr, forelimb rays; Tr, toe rays; I, footplate indentations; So, somites; N, nostrils. c, Lung. B, bronchi. d, K, kidney with nephric ducts developing; T, testis. e, Enlargement of testis section shown in *d*. St, developing seminiferous tubules. f, Pituitary gland. Pt, pars tuberalis; Ad, adenohypophysis. g, V, thoracic vertebrae; Sp, spinal cord. h, Cervical vertebrae, C4 identified. i, Enlargement of C4. Ch, chondrification center; No, notochord.

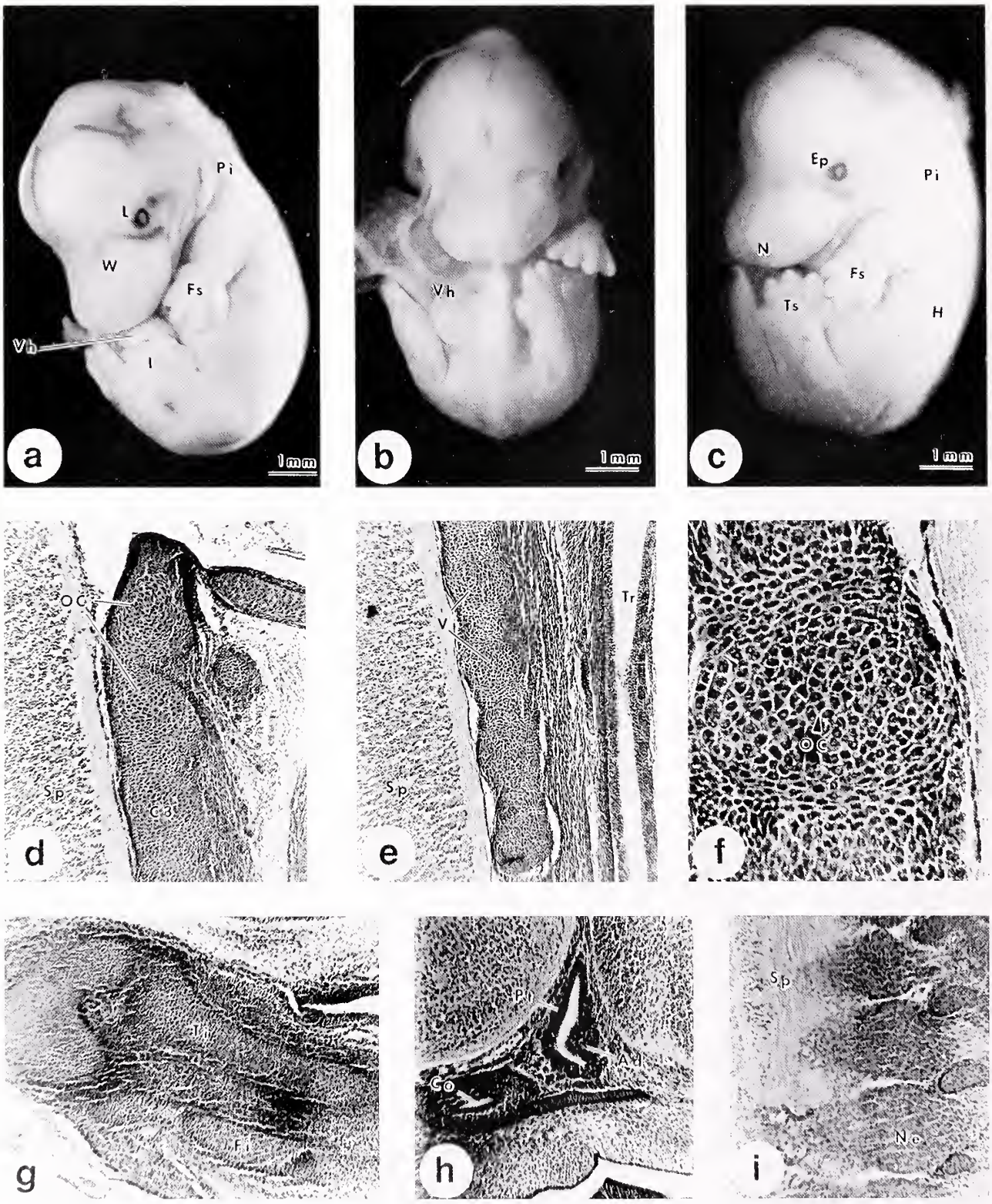
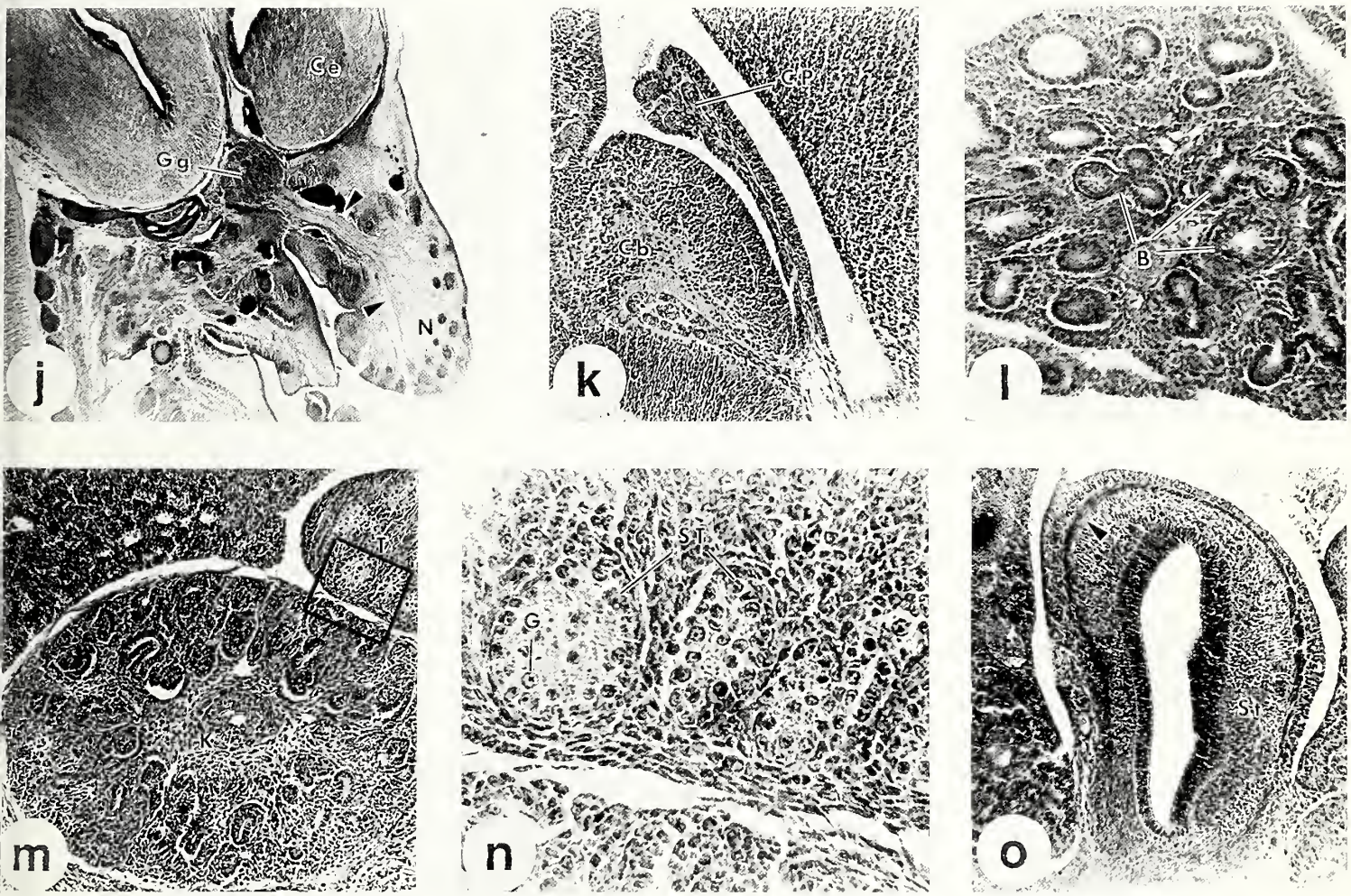


Fig. 7.—Ontogenetic Stage 6 in *Sorex vagrans*. a, b, c, Embryos, frontal view flanked by two views of right side. Pi, ear pinna; L, lens; W, whiskers; Fs, forefoot plate indented; I, hindfoot plate indenting; Vh, umbilical hernia; Ep, eye pigmentation; N, nostrils; Ts, toes separating at slightly later stage 22; H, hair follicles prominent. d, Cervical vertebrae, C3 identified. OC, ossification centers; Sp, spinal cord (Sp). e, V, thoracic vertebrae; Sp, spinal cord; Tr, trachea. f, Enlargement of ossification center (OC) of thoracic vertebrae. g, Hindlimb showing tibia (Ti), and fibula (Fi), undergoing chondrification. h, Pituitary folding upon itself. Pt, pars tuberalis; Ad, adenohypophysis; Co, cochlea of ear ossicles. i, Spinal nerves (Ne) developing in



association with the spinal cord (Sp). j, Frontal head region. Ce, cerebrum; N, nose with hair follicles and well-developed ganglion Gasseri (Gg) with nerve tracts radiating distally (arrows). k, Choroid plexus of brain (CP), directed anteriorly from the cerebellum (Cb). l, Lung tissue illustrating branching of bronchioles (B). m, Kidney (K) with continued duct development, and testis (T). n, Enlargement of testis section shown in *m* illustrating discrete seminiferous tubules (ST), and the presence of gonocytes (G). o, Cross section of stomach (St) with development of circular muscle layers (arrow).

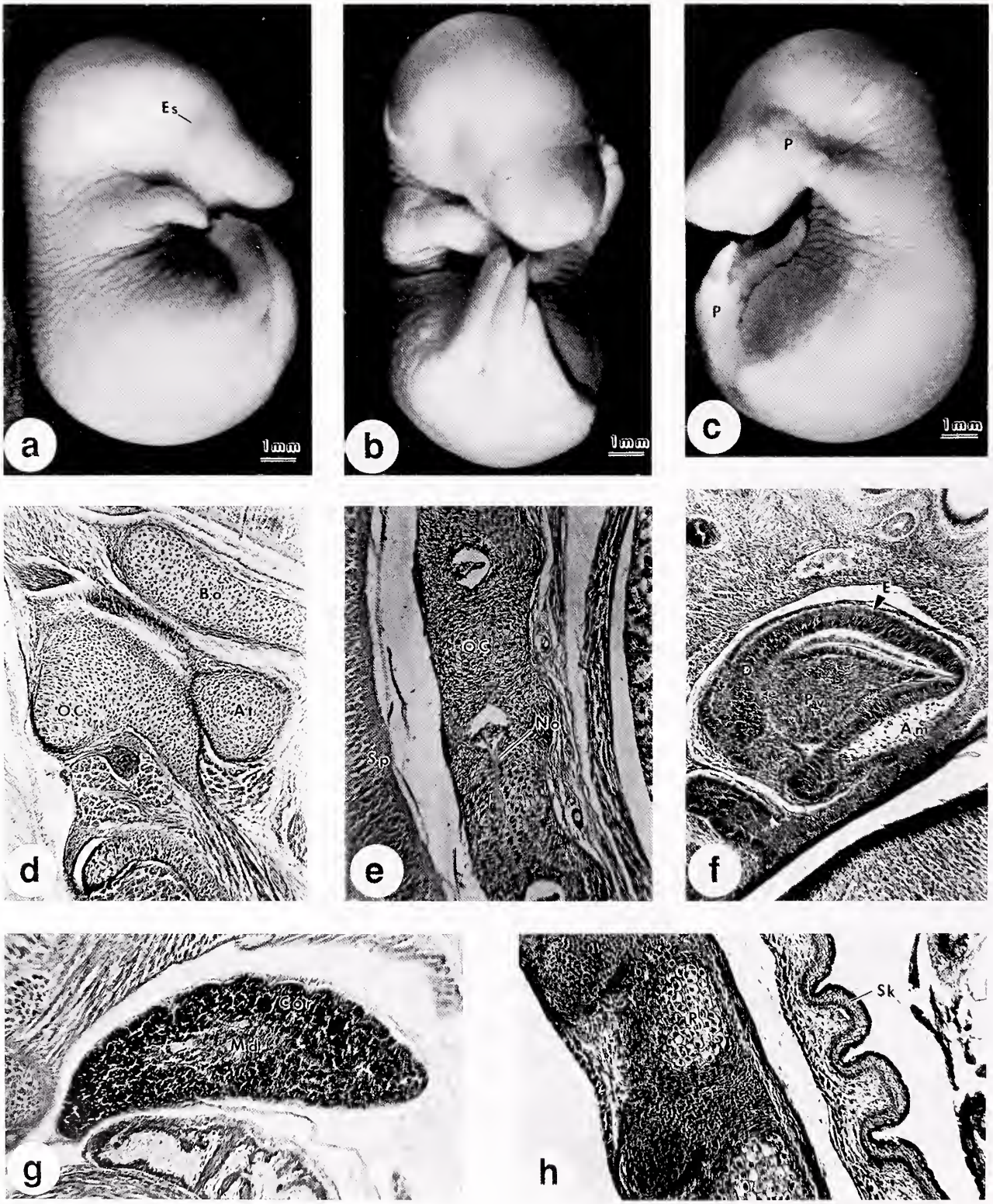
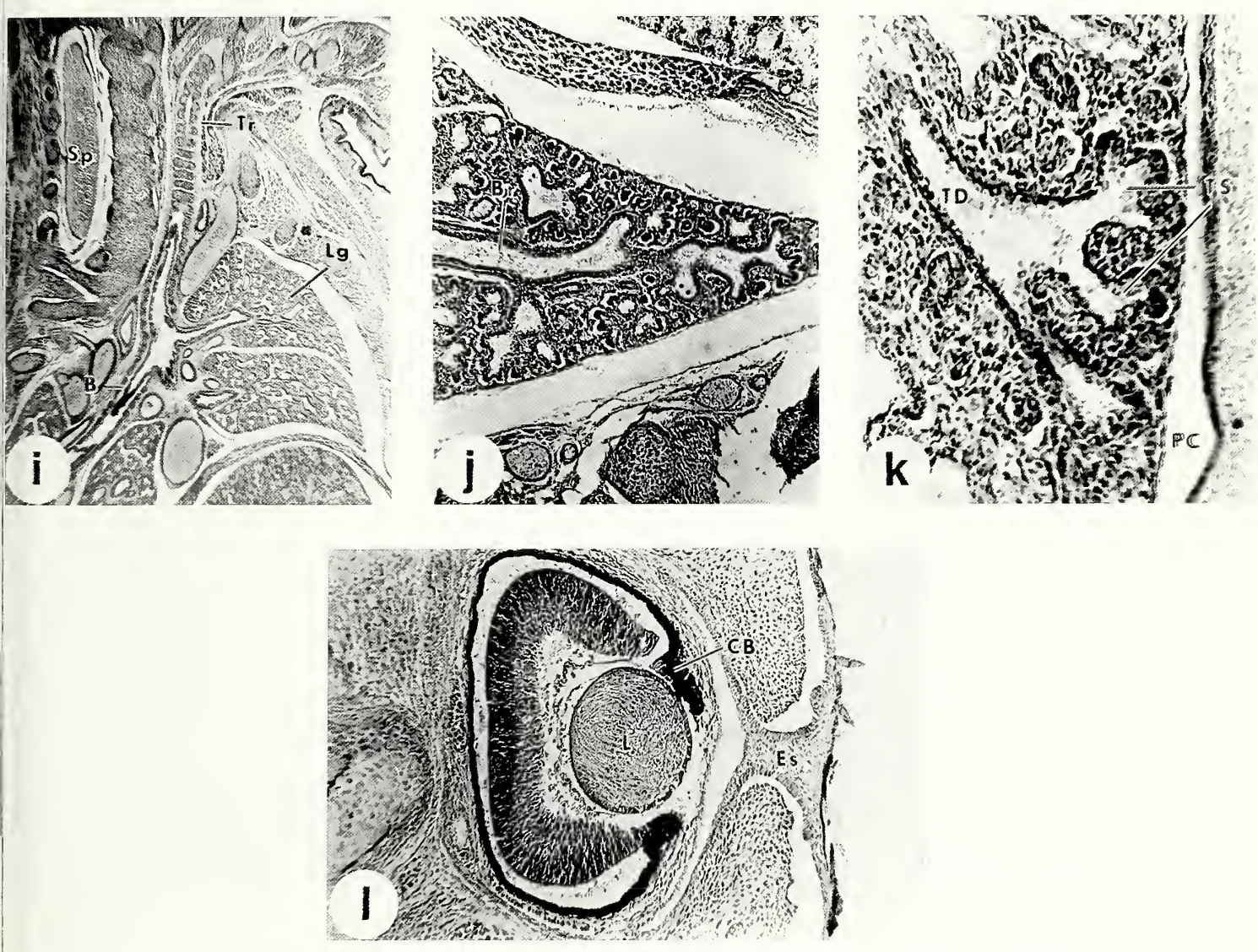


Fig. 8.—Ontogenetic Stage 7 in *Sorex vagrans*. a, b, c, Embryo; right side, frontal, and left side views. Es, eyelid fused; P, fingers and toes parallel. d, Junction of skull and spinal column. Bo, basioccipital bone ossifying; OC, ossification center of atlas; At, anterior arch of atlas. e, Lumbar vertebrae. OC, ossification center; No, notochord; Sp, spinal cord. f, Tooth formation showing development of enamel (E), dentin (D), pulp (Pv), and ameloblast layers (Am). g, Thymus illustrating



medullary (Md) and cortical (Cor) regions. h, Thoracic region showing folding of outer skin surface (Sk) and underlying ribs (R). i, Complete respiratory tract. Tr, trachea; Lg, lung lobes; B, primary bronchus; Sp, spinal cord. j, Enlargement of lung lobe illustrating branching of secondary bronchus (Br). k, Enlargement of section shown in *i* showing transitory ducts (TD), terminal saccules (TS), and pleural cavity (PC). l, Sagittal section through eye. L, lens; CB, ciliary body; Es, fused eyelid.

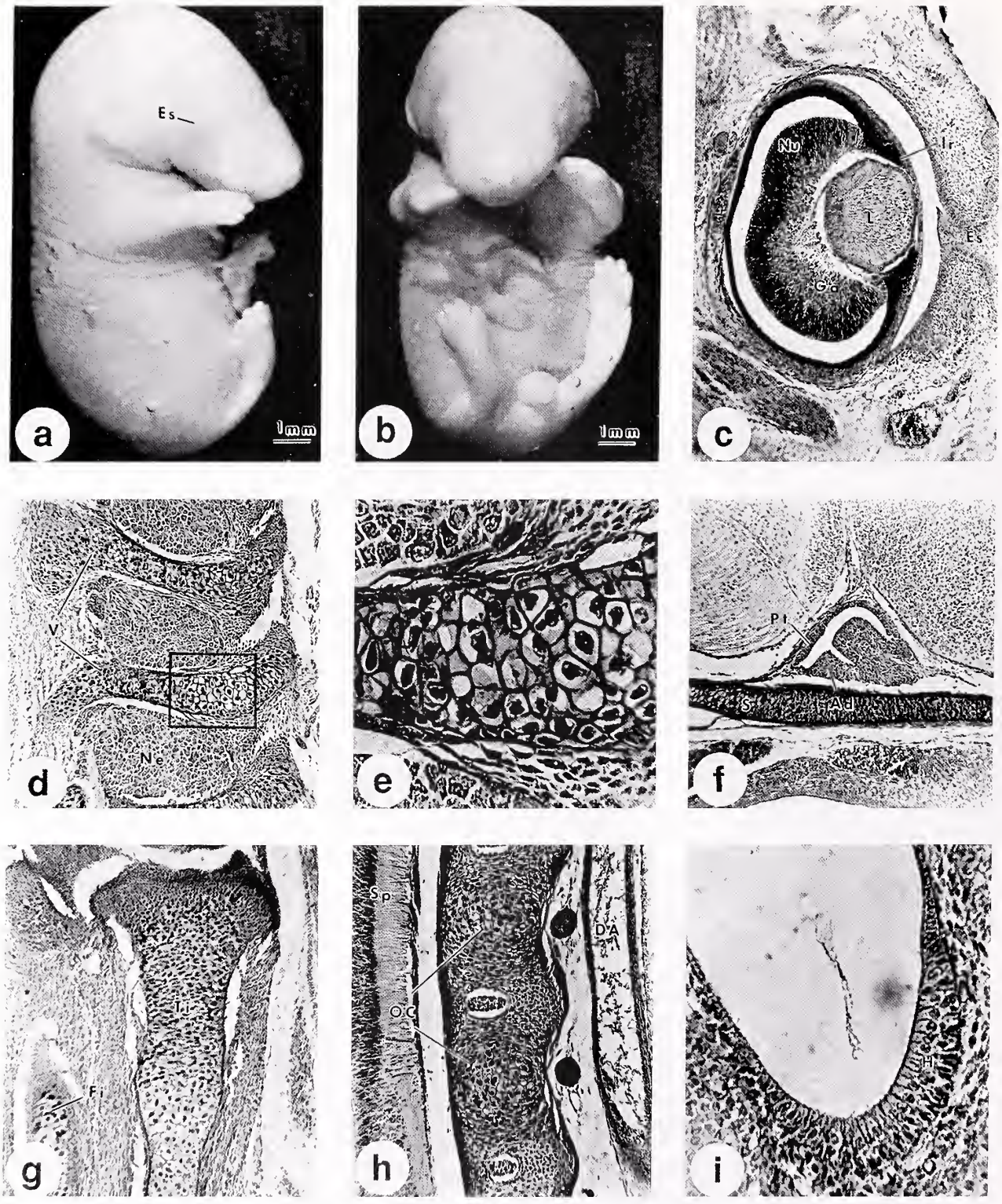
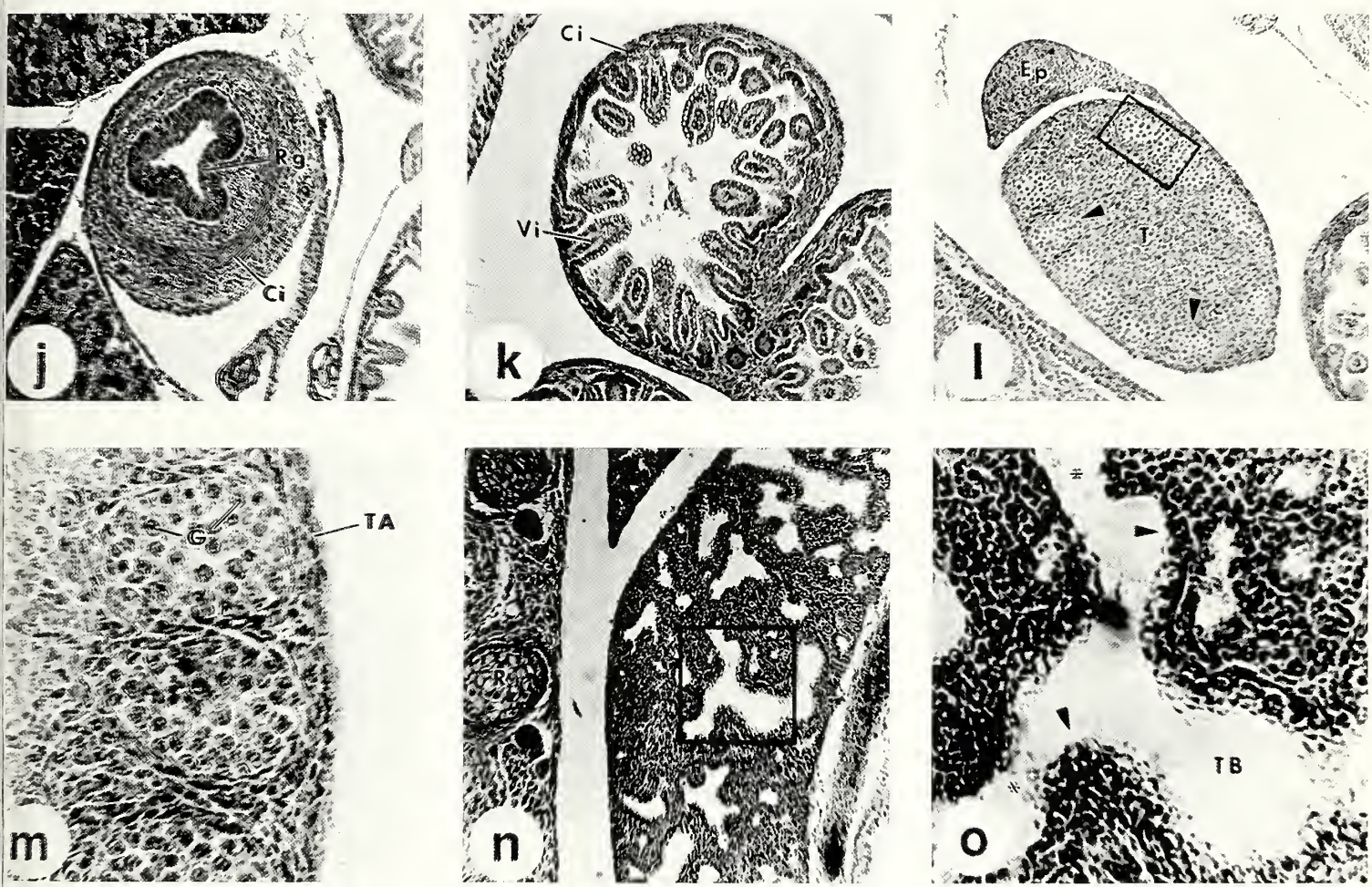


Fig. 9.—Ontogenetic Stage 7+ in *Sorex vagrans*. a, b, Embryo, right side and frontal views. Es, eyelid fused. c, Sagittal section through eye. L, lens; Ir, iris; Nu, nuclear layer of retina; Ga, ganglion layer of retina; Es, fused eyelid (Es). d, V, cervical vertebrae; Ne, spinal nerve. e, Enlargement of cervical vertebrae shown in *d* illustrating progressive ossification. f, Pituitary gland continuing to fold. Pt, pars tuberalis; Ad, adenohypophysis; S, sphenoid bone. g, Proximal region of tibia (Ti) and fibula (Fi) illustrating ossification. h, Thoracic vertebrae. OC, ossification centers; DA, dorsal aorta; Sp, spinal cord. i, Vestibule of inner ear illustrating sensory hair cells (H). j, Cross section of stomach; development of folds (Rg, rugae) and increased



layering of circular smooth muscles (Ci). k, Cross section of small intestine. Vi, villus; Ci, circular smooth muscles. l, Longitudinal section of testis (T) and epididymis (Ep); seminiferous tubules are distinct (arrows). m, Enlargement of seminiferous tubules shown in section *l*. TA, tunica albuginea; G, gonocytes. n, Lung lobe illustrating slightly more porous tissue. R, rib. o, Enlargement of lung section shown in *n*. TB, terminal bronchiole opening into transitory ducts (*); transition into smooth-walled channels of transitory ducts (arrows).

BROWN FAT AND THE WINTERING OF SHREWS

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ABSTRACT

The relationship between mass of the interscapular brown fat and body mass was studied in six species of shrews and four species of rodents in Finland. Both anatomical location and changes in amount of brown fat were studied in *Sorex araneus*, *Sorex minutus*, and *Neomys fodiens*. The fatty acid composition of brown fat lipids was also measured in *Sorex araneus* and *Neomys fodiens*. The distribution of brown fat in shrews was very extensive, and nearly all the fat tissue was brown fat. For animals caught during the same season, logarithmic values for relative weights of interscapular brown fat of different species were strongly and negatively correlated with body weight. In *Neomys fodiens* the proportion of brown fat was higher than expected on the basis of body mass. In the smallest shrew species the mass of brown adipose tissue can be as much as 20% of the body mass. The proportion by weight of interscapular brown fat to total brown fat in spring was estimated to be about 30%. The fatty acid composition of brown fat lipids in shrews resembled the lipid composition in marine mammals. The very high proportion of 20- and 22-carbon fatty acids was assumed to be connected to the diet of shrews. Of special interest is the finding that brown fat is located between the muscles of the limbs. Warming of the blood coming from the extremities is assumed to be one explanation for the successful wintering of shrews.

INTRODUCTION

To survive extremely cold winters, shrews have developed means of adapting to low temperatures. Because shrews are very small and their insulation is poor (Hissa and Tarkkonen, 1969), their only effective means of thermoregulation in a cooling environment is to increase the metabolic rate. In Soricinae the metabolic rate per unit body mass is generally 2–3 times higher than that of a nonsoricine of the same size (Morrison et al., 1959; Vogel, 1976; Nagel, 1985). Furthermore, the metabolic potential of different tissues in shrews is very high compared to that in other small mammals (Hyvärinen and Pasanen, 1973). In shrews, elevation of a high basal metabolism is uneconomical but necessary. During the Finnish winter, shrews live continuously in temperatures below the thermoneutral zone. In these harsh conditions shivering thermogenesis is not a solution (see Wunder, 1984). Brown adipose tissue (BAT) is known to be the main factor responsible for heat production in small mammals (for reviews see Himms-Hagen, 1976; Rothwell and Stock, 1984). Previously studied seasonal variations in the amount or metabolism of BAT in shrews have been related only to interscapular brown fat (IBAT) (Buchalzyk and Korybska, 1964; Hissa and Tarkkonen, 1969; Pasanen and Hyvärinen, 1970; Pasanen, 1971), which is only part of the total BAT in small mammals. In *Clethrionomys gapperi* and *Microtus pennsylvanicus*, IBAT makes up only 16–25% of the total BAT (Anderson and Rauch, 1984). In this work, the distribution of BAT in the common shrew (*Sorex araneus*) was studied. To compare the role of BAT in shrews of different sizes, the weights of IBAT in several shrew species and in other small mammals were measured. The fatty acid composition of shrew BAT was compared with that of nonsoricine mammals.

MATERIALS AND METHODS

Specimens were obtained by snap trapping or with pitfalls near Joensuu or in Rautjärvi, eastern Finland. Eleven *S. araneus* and four *Sorex minutus* were trapped in April–May 1984 and 13 *S. araneus*, three *S. minutus*, and one *Neomys fodiens* in January–February 1985. Sixteen *S. araneus*, ten *S. minutus*, eight *Sorex caecutiens*, and two *Sorex minutissimus* were obtained in a pitfall catch in September 1989. In that same catch were also two *Micromys minutus*. Ten young *S. araneus* and six *S. minutus* were taken in July 1984 and July 1990; and two *Neomys fodiens*, two *Sorex isodon*, and three *Myopus schisticolor* were captured near Joensuu at the end of August 1989.

Mass of IBAT was determined for all animals except the shrews captured in April–May 1984. An attempt was made to determine the weights of the other brown adipose tissues, but this was too inaccurate because those adipose tissues were intermixed with other tissues. For mapping the distribution of different types of BAT, animals captured in April–May 1984 were skinned, the internal organs, stomach and intestines removed, and the bodies were cut into 4–5 pieces from head to tail. The pieces were fixed in Bouin fixative, decalcified in 6% HNO_3 (Romeis, 1948), and embedded in paraffin. The pieces were cut into 8 μm transverse or sagittal sections and stained with Lillie's (1951) allochrome method or with hematoxylin-eosin.

Succinic dehydrogenase activity was demonstrated histochemically using freshly frozen cryostatmicrotomy slices (Burstone, 1962). Burstone's method was used to determine the location of BAT.

To measure fatty acid composition, the IBAT of four *S. araneus* and two *N. fodiens* captured in July was extracted with chloroform methanol (2:1). The lipids were hydrolyzed and the fatty acids methylated using the BF_3-method (Metcalfe et al., 1966). Samples were analyzed by gas chromatography on a Hewlett-Packard gas chromatograph (model 5890) using a fused silica OV-1 capillary column.

RESULTS

The mass of IBAT of shrews captured in September in Rautjärvi was dependent on the size of the species, with the

highest relative weights of IBAT found in the smallest species (Table 1, Fig. 1). When correlations of the logarithmic values for the relative IBAT weights and the body weights of different shrew and microtine rodent species from the same time of year were calculated, the correlation coefficient was −0.94 (Fig. 1). Values for *Clethrionomys glareolus* and *Microtus agrestis* were taken from the work of Pasanen (1971). The proportion of the body mass made up by IBAT increased from autumn to winter in *S. araneus* (Fig. 2). There was only one *N. fodiens* specimen taken in winter, but for that animal the relative IBAT weight was 3%, compared to 1.3% for two young *N. fodiens* caught in late summer. In *N. fodiens* relative IBAT weight was also higher than in other small mammals of the same size (Fig. 1).

The anatomical locations of BAT in *S. araneus* were (with one exception) typical for the other mammals studied (Fig. 3). Inter- and subscapular brown fat formed the major concentrations, but the amount of BAT around the kidneys, below the braincase, between the muscles of the neck, in the thorax area, in the iliac and inguinal areas, and in the limbs totaled about twice that in the interscapular area. Brown fat between the muscles of the limbs has not been observed in other mammals. Between the muscles of the thigh were especially large amounts of BAT (Fig. 4, 5) surrounding the large arteries, veins, and nerves like a jacket (see Smith, 1961). The proportion of total BAT to body weight was 4–10% in *S. araneus* and 6–12% in *S. minutus*. If the distribution of BAT is about the same in the smaller *S. minutissimus*, the proportion of the body mass made up by BAT would be 15–20%. According to histological structure, all adipose tissue of *S. araneus* and *S. minutus* is classified as BAT.

Compared to other terrestrial mammals, the fatty acid composition of interscapular brown fat lipids in *S. araneus* and *N. fodiens* includes a very high proportion of 20- and 22-carbon fatty acids. Therefore, the amount of polyunsaturated fatty acids is very high and the number of double bonds per mole (Δ/mole) is about two in *N. fodiens* and about 1.6 in *S. araneus* (Table 2).

Discussion

The capacity for nonshivering thermogenesis has been shown to be inversely related to body mass, age, and acclimation temperature (Rothwell and Stock, 1984). Brown fat is mainly responsible for nonshivering thermogenesis (NST) in cold-adapted mammals. Rothwell and Stock (1984) estimated that the contribution of BAT to thermogenesis is 60% or more. Therefore, the negative correlation of relative IBAT mass and body mass is to be expected. It is possible, however, that in the smallest winter-active mammal of Europe, *S. minutissimus*, the proportion of BAT is so great (15–20% of body weight) that it may be one factor limiting the body size. Foster and Frydman (1978) demonstrated in the laboratory rat that BAT can produce heat at a rate equivalent to 500 W/kg. The aerobic power of muscle is about 60 W/kg during maximal exercise (Rothwell and Stock, 1984). Although shrews are capable of producing enough heat to live in cold environments, energy costs may become too high for survival. When non-BAT tissues of shrews reach a higher metabolic capacity than those of other small mammals (Hyvärinen and Pasanen, 1973), the amount of food that must be consumed in cold becomes too great. The animal cannot eat enough to provide the energy it is producing (see Hanski, 1984).

The mass of BAT differs in members of the same species living at different latitudes (Pasanen, 1969) as well as at the same location at different times of the year. Furthermore, winter conditions greatly influence BAT weights (Pasanen, 1971). For example, Anderson and Rauch (1984) recorded higher relative IBAT mass in *C. gapperi* and *M. pennsylvanicus* from Manitoba, Canada, than in voles from Finland (Hissa and Tarkkonen, 1969; Pasanen, 1971). The main reason for this variation may be adaptation to the severity of the winter. Because geographic location and seasonal changes greatly influence relative IBAT weights, IBAT weights of different species should be compared only for animals captured at the same time of year in similar climatic conditions. In early autumn the IBAT weights are very similar between years (Pasanen, 1971).

The fatty acid composition of BAT lipids in shrews does not resemble that of other terrestrial mammals, but is similar to that of marine mammals, wherein C_{20} and C_{22} fatty acids make up more than 30% of the total fatty acids. In *S. araneus* this proportion is over 20% and in the water shrew 30%. In the IBAT tissue of hamsters, for example, 95–99% of the fatty acids belong to the C_{16} and C_{18} series (Smalley, 1970). Although the proportion of saturated fatty acids is high, the proportion of polyunsaturated fatty acids is also high. In general, the brown fat of mammals contains more saturated fatty acids than the white fat (Smith and Horwitz, 1969). The diet of shrews may affect the unusual fatty acid composition.

The proportion of the body mass of *N. fodiens* made up by BAT is greater than expected on the basis of body mass. In one animal captured in February, IBAT made up 3% of the body mass and the total BAT may have been about 10% of total mass. *Neomys fodiens* is a diving mammal and it can be assumed that a high proportion of BAT is an adaptation for diving in cold water. In the muskrat (MacArthur, 1986), also a diving mammal, total BAT is about 0.8% of body weight. Based on the body weight (about 1 kg), however, the proportion of BAT should be much smaller. Anderson and Rauch (1984) measured the weights of BAT from different parts of the body of red-backed and meadow voles. They found that the weight of IBAT is about 16–25% of total BAT. In *S. araneus* and *S. minutus* the proportion of IBAT was about 30%. This result, however, is an approximation made on the basis of histological observations.

The distribution of BAT between muscles and other tissues and the small size of shrews makes it impossible to accurately estimate the weights of different types of BAT. In addition, BAT in shrews cannot be classified according to anatomical location because BAT is found nearly everywhere. In fact, white adipose cells are uncommon and virtually all the adipose tissue in *S. araneus* and *S. minutus* is BAT. Especially unusual is the location of BAT in the limbs, surrounding blood vessels and nerves, where it warms blood coming from the thin uninsulated paws and legs. BAT is also abundant below the

braincase, and probably warms blood from the nose. This warming of blood returning from the extremities may facilitate successful overwintering of shrews.

Because white adipose tissue is virtually absent in shrews, at least in *S. araneus* and *S. minutus*, I assume that brown adipose tissue also performs the functions of white fat. This assumption is supported by the finding of comparatively low GDP-binding rate of the brown fat of *Sorex vagrans* (Tomasi et al., 1987). Normally, GDP-binding of BAT is correlated with the capacity for nonshivering thermogenesis (see Horwitz, 1989). In *Sorex* species, BAT must also function as a site for lipid storage. Especially in overwintered adults and in young shrews at the time of weaning, the lipid content of BAT is very high compared with that of voles (Pasanen, 1971; Pasanen and Hyvärinen, 1970). In shrews, the metabolic capacity of BAT per unit mass is highest in autumn (Hyvärinen and Pasanen, 1973) when the lipid content and relative weight of IBAT are lowest (Pasanen, 1971). It is possible that during the winter fatty acids are liberated into the blood stream for use in other tissues. The activity of lipase-esterase enzyme is much higher in the BAT of *S. araneus* than in that of voles (Pasanen, 1971), although the cytochrome c content is the same or lower (Hyvärinen and Pasanen, 1973). In general, lipid metabolism seems to be more important in shrews than in voles during winter (Hyvärinen, 1984). In *Blarina brevicauda*, nonshivering thermogenesis increased 54% from August to January (Merritt, 1986), indicating the important role of BAT in the overwintering of that shrew species.

Tomasi (1984) observed that the rate of thyroxine utilization is much higher in shrews than in rodents, and assumed that it plays a role in the high metabolism of shrews. According to histological results, the thyroid gland of *S. araneus* is very active during the autumn critical period but is inactive during overwintering (Hyvärinen, 1969). The only endocrine gland studied which is not inactive in winter is the adrenal medulla (Hyvärinen, 1984). During winter, all physiological functions of *S. araneus* are organized as economically as possible. BAT, adaptations of the sympathetic nervous system, and lipid metabolism in general provide the main physiological adaptations for shrews to the harsh winters of northern latitudes.

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Table 1.—*Relative IBAT weights (% of body mass) of nonwintered small mammals captured in late August or in September in eastern Finland, or in the vicinity of Oulu, and overwintering small mammals in January–February 1986 near Joensuu.* [a] *September 1989 in Rautjärvi (61°20'N, 29°20'E);* [b] *late August 1989 in Lieksa (63°N, 30°E);* [c] *material of Pasanen (1971) captured in September 1966–70 near Oulu (65°N, 26°E).*

	August–September			January–February		
Species	*n*	Body mass (g)	% IBAT	*n*	Body mass (g)	% IBAT
Sorex minutissimus	2[a]	1.9	5.20			
Sorex minutus	10[a]	2.9	2.56 ± 0.22	3	2.2	2.67 ± 0.30
Sorex caecutiens	3[a]	4.1	1.35 ± 0.10			
Sorex araneus	16[a]	6.7	1.23 ± 0.09	11	5.5	2.29 ± 0.22
Micromys minutus	2[a]	8.05	1.15			
Sorex isodon	2[b]	10.5	1.12			
Neomys fodiens	2[b]	11.4	1.37	1	10.2	3.01
Myopus schisticolor	3[b]	13.7	0.65 ± 0.11			
Clethrionomys glareolus	50[c]	15.7	0.51			
Microtus agrestis	82[c]	25.8	0.38			

Table 2.—*Fatty acid composition (mean %) of interscapular brown fat of* Neomys fodiens *and* Sorex araneus *captured during summer.*

Fatty Acid	*Neomys fodiens* *n* = 2	*Sorex araneus* *n* = 4
[C]12:0	0.41	0.42
12:1	0.26	0.06
13:0	0.80	1.58
13:1	0.18	0.02
14:0	1.10	4.03
14:1	0.26	0.40
15:0	0.95	0.74
15:1	0.19	0.69
16:0	17.93	18.73
16:1	4.72	3.59
17:0	2.38	1.20
17:1	1.84	2.08
18:0	12.43	10.57
18:1	13.88	18.56
18:2	8.47	14.55
18:3	0.35	0.14
18:4	0.22	0.08

Table 2 (cont.)

19:0		0.33
19:1		0.22
20:0		0.04
20:1	0.78	0.81
20:2	0.40	0.48
20:3	1.36	0.69
20:4 and 20:5	17.97	8.68
22:4		0.16
22:5	4.80	2.31
22:6	8.52	6.91
Number of double bonds per mole (Δ/mole)	1.9-2.1	1.4-1.5

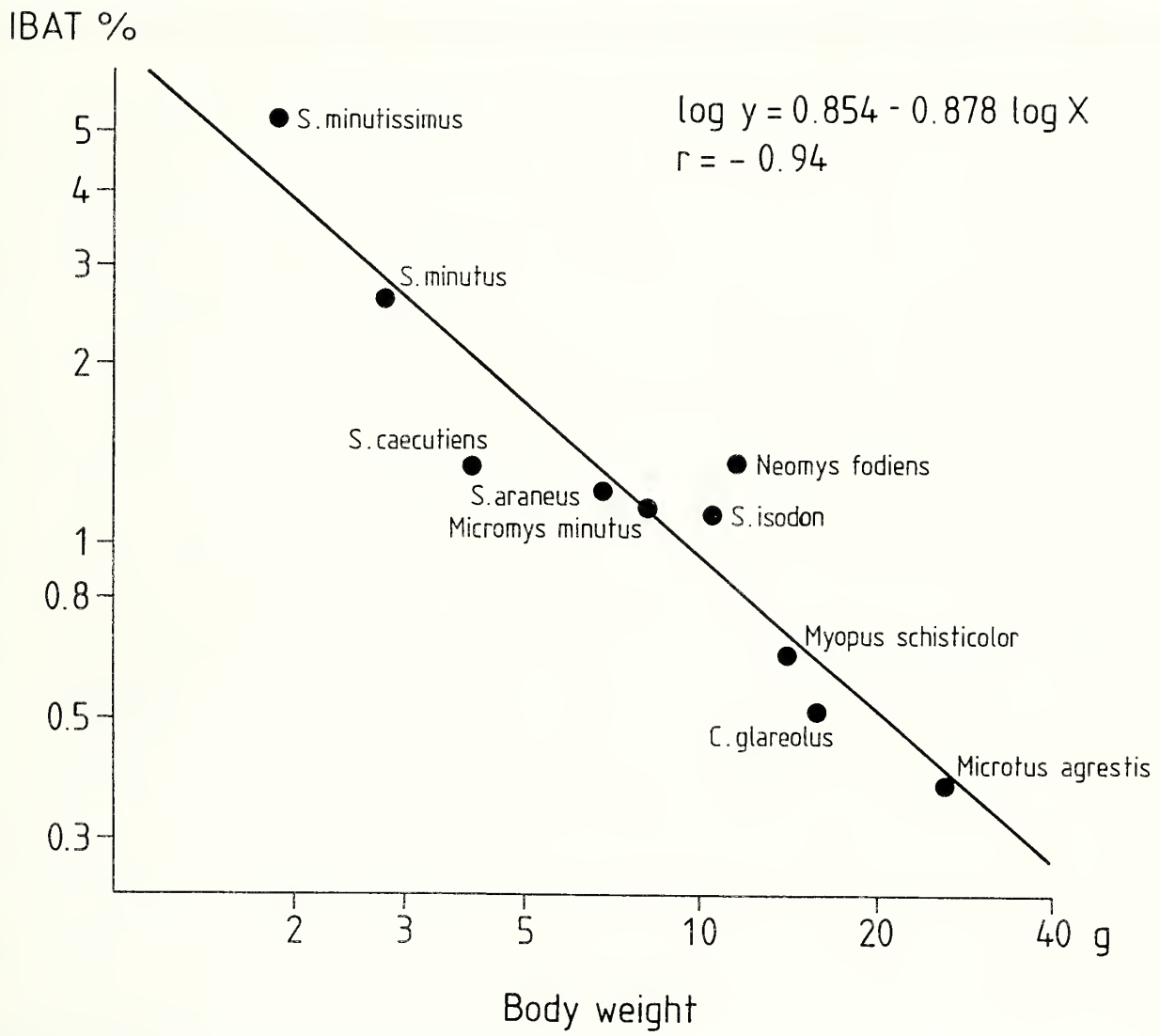

Fig. 1.—The relationship of relative IBAT weight and body weight of ten small mammal species captured in August–September (material in Table 1).

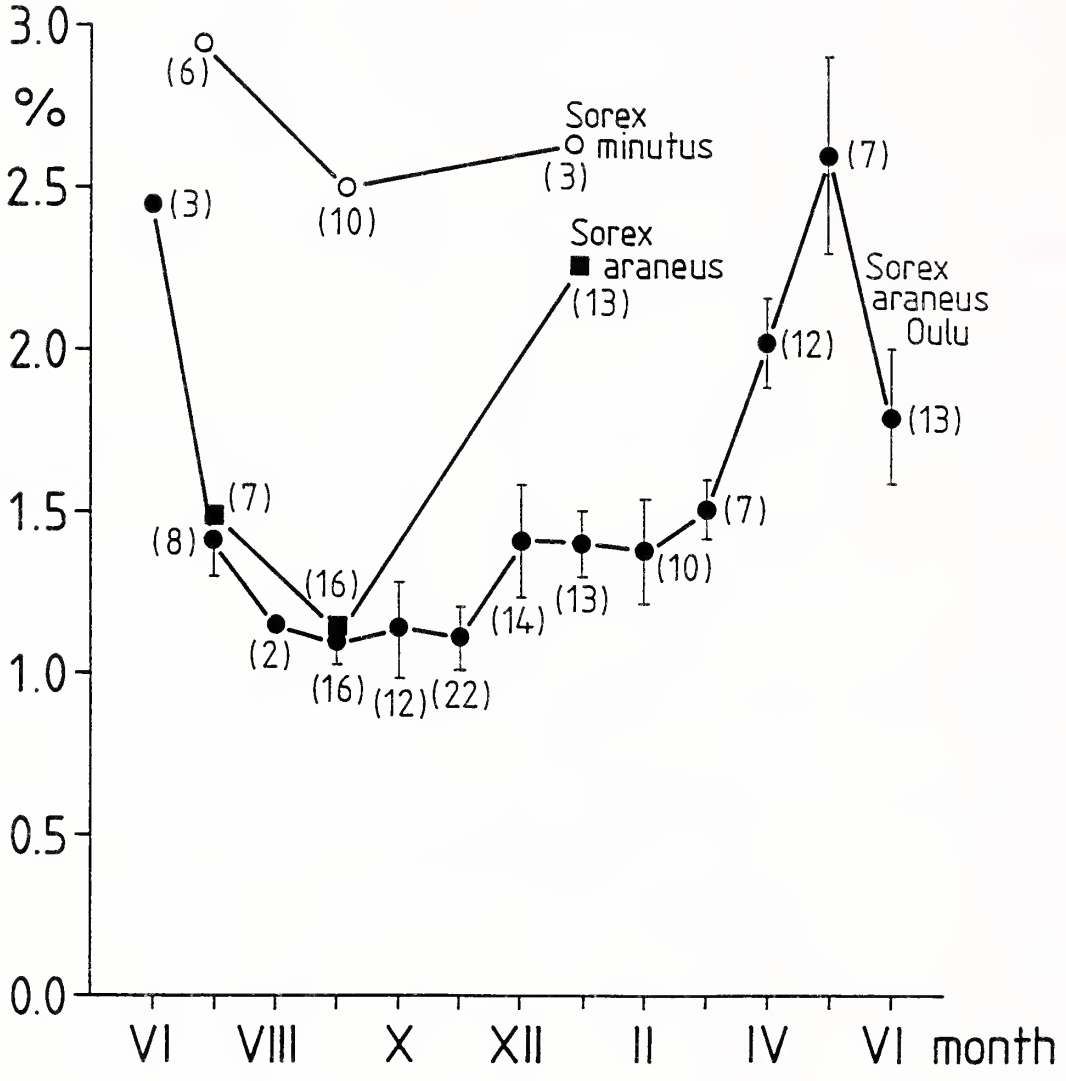

Fig. 2.—Seasonal changes in IBAT weight of *Sorex minutus* and *Sorex araneus* in the vicinity of Joensuu (for material, see Table 1) and *Sorex araneus* in the vicinity of Oulu (± SE; Pasanen and Hyvärinen, 1970). Number of individuals in parentheses.

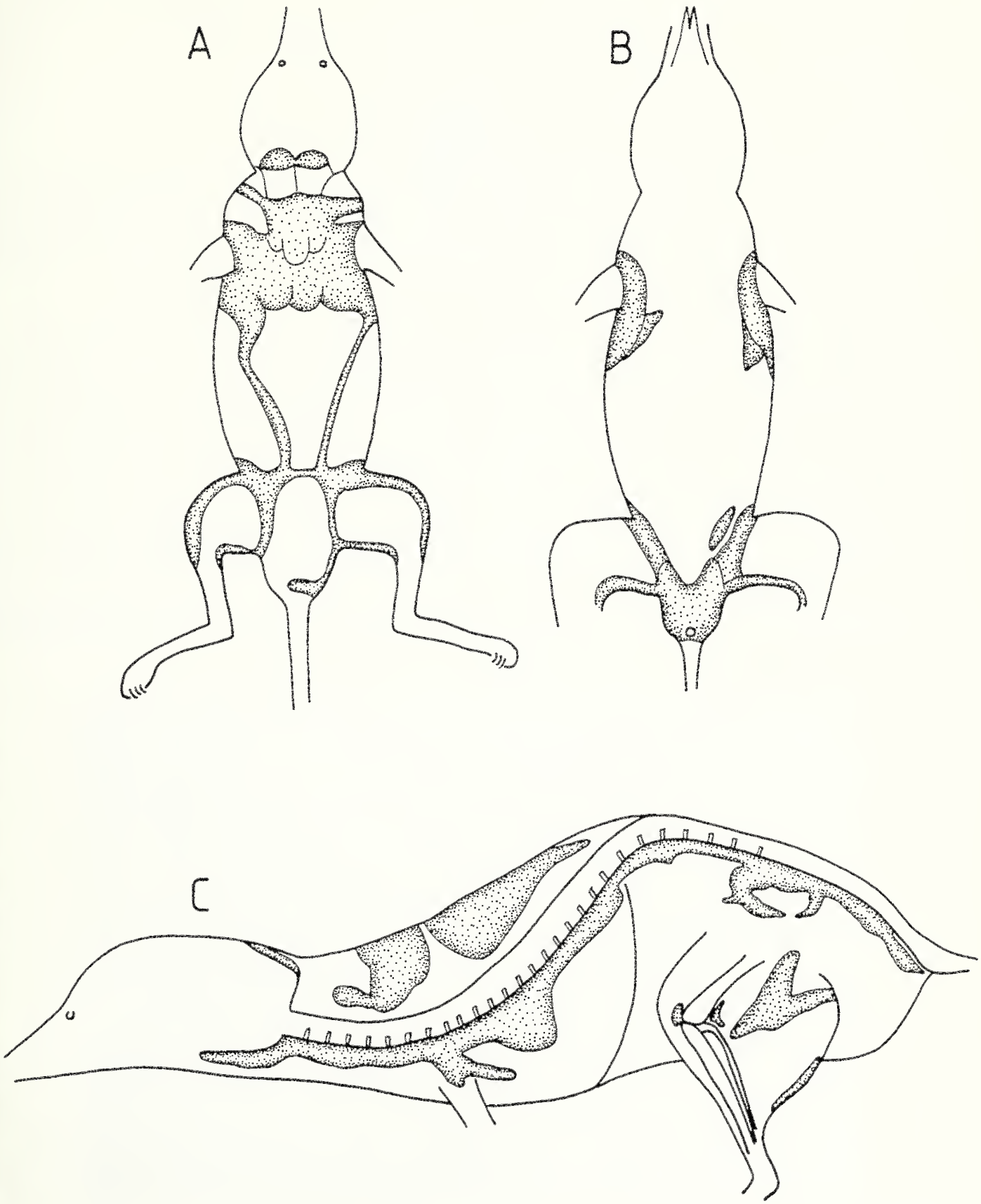

Fig. 3.—Schematic diagram showing anatomical location of BAT in shrews. Dorsal view (A) and ventral view (B) of *Neomys fodiens* captured in February. Sagittal section of *Sorex araneus* showing distribution of BAT in trunk and hind foot (C).

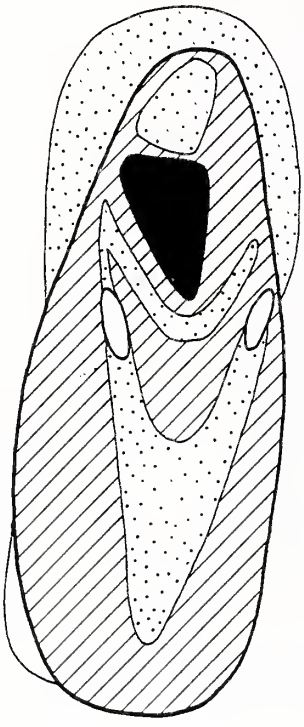

Fig. 4.—Schematic diagram showing the location of BAT (stippled area) in transverse section of the thigh of *Sorex araneus*. Bone = black.

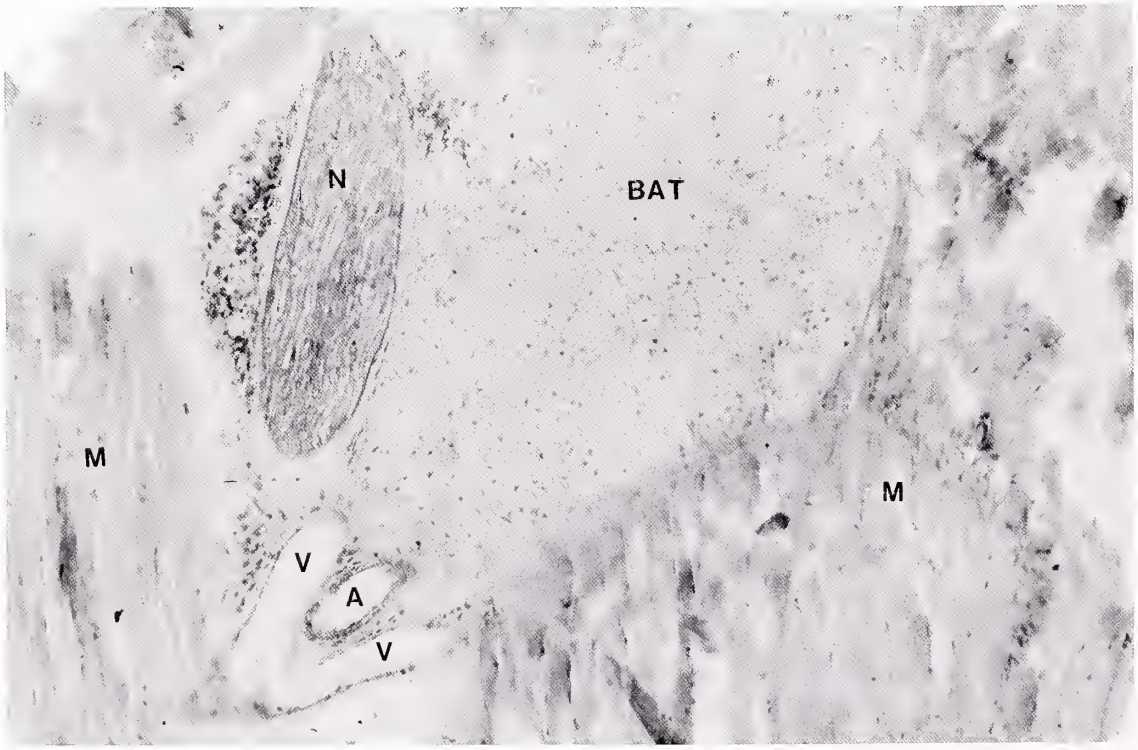

Fig. 5.—Oblique section through the thigh of the common shrew. Brown fat (BAT) surrounding blood vessels and the sciatic nerve. M, muscle; A, artery; V, vein; N, nerve. Allochrome × 200.

EFFECTS OF MELATONIN ON THE CHRONOBIOLOGY OF THE LEAST SHREW, *CRYPTOTIS PARVA*

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ABSTRACT

A principle obstacle to studies describing the mechanisms involved in Dehnel's phenomenon is the difficulty in raising shrews of the genus *Sorex* in the laboratory. The least shrew, *Cryptotis parva*, thrives in captivity and serves as an animal model to investigate the role of melatonin in two chronobiologic events: 1) the capacity of selected age categories to respond to cold, and 2) the autumnal reduction in body length. This study did not confirm a role for melatonin in aiding pubertal (24–33 days old) and old-aged (>300 days) shrews' ability to thermoregulate when exposed to cold. Shrews implanted with melatonin showed significantly smaller lumbar intervertebral discs than did their matched controls.

INTRODUCTION

Shrews of the genus *Sorex* often die in large numbers in the autumn (Adams, 1910). Survivors of this autumnal epidemic then show a decrease in body size (Dehnel, 1949). Understanding these seasonally related events, characterized as Dehnel's phenomenon, offers a challenge with biological implications beyond the soricids. A principle obstacle to studies describing the mechanisms of this phenomenon is the difficulty in rearing *Sorex* shrews in the laboratory. The least shrew, *Cryptotis parva*, thrives in captivity (Mock, 1982), and may serve as an animal model for determining the physiological bases of these occurrences. This study was undertaken to determine the role of melatonin in two of these chronobiologic events—response to cold, and autumnal reduction in body length.

Pearson (1945) thoroughly reviews the so-called autumnal epidemic in older shrews. He concedes that shrews are frequently found dead and discusses in some detail many of the reported causes for this occurrence. He then argues that there is little reason to believe that regulation of the life span of shrews differs significantly from that of other small, prolific mammals. I found Pearson's explanation to be satisfactory until I provided least shrews used in a study of the response of brown fat to cold exposure (Chaffee et al., 1969). Old males died when they were cold stressed in the same manner as other species used in the study. Subsequent experiments to determine the role of age in the least shrew's response to cold found that animals over 300 days old showed significantly greater heat loss than did prepubertal (21–23 days) and young adult (60–90 days) shrews. Surprisingly, heat loss per unit time in pubertal animals (24–33 days) approached that of the older animals (Mock, 1985).

Winter-induced decreases in shrews' body lengths are caused primarily by a reduction in the volume of the nucleus pulposus. Some resorption in the intervertebral disc cartilage may also occur (Hyvärinen, 1969). Many hormones and enzymes have been investigated in an attempt to determine the seasonal acclimatization mechanism (Hyvärinen, 1984). Factors controlling what Hyvärinen and Heikura (1971) call the endogenous seasonal rhythm have not been elucidated.

A scenario can be constructed in which melatonin is an agent in these reported chronobiologic events. Most mammals of temperate and arctic regions have seasonally limited and synchronized reproductive patterns. In many of these species, reproductive cycles depend on changes in photoperiod. The pineal gland and its primary hormone, melatonin, respond to changes in the light-dark cycle and act to inhibit reproduction during certain periods of the year (Reiter et al., 1983). Melatonin probably also functions in thermoregulatory adaptations of northern small mammals (Quay, 1984), and in events associated with the onset of puberty (Sizonenko et al., 1985). The possibility that melatonin is the agent controlling the endogenous seasonal rhythm of shrews serves as the basis for this study.

MATERIALS AND METHODS

All the shrews used in the course of this study were maintained according to a regimen previously described (Mock, 1982) in a breeding colony at Kirksville College of Osteopathic Medicine. Melatonin for implanting was prepared by kneading one part melatonin (Sigma Chemical Co., St. Louis, Missouri) with four parts beeswax (Impression Wax, The Hygenic Corp., Akron, Ohio). Five-milligram lots of the mixture were then compressed into 2.5 mm diameter pellets. The 5-mg control pellets contained beeswax only. The pellets were injected subcutaneously via needles designed for implanting medicated pellets into the pinnal cartilage of cattle. Dosages of 2 mg of melatonin were used in some of the initial cold-stress studies for pubertal animals. The duration of melatonin treatment prior to cold exposure was 8–10 days for old-aged shrews. Duration of treatment for pubertal males varied from 2–8 days and is so indicated in Table 1.

Needle microprobes attached to a digital thermometer (BAT-12, Bailey Instruments Inc., Saddle Brook, New Jersey) were placed subcutaneously along the flanks of restrained shrews of selected ages. Initial temperatures were recorded, and after 5 min, the animals were placed in a cold room (3–5°C) and body temperatures were recorded at regular intervals for 30 min. The temperature value reported was the difference between the initial and final readings.

The intervertebral disc protocol involved allowing the implanted animals to survive for an eight- or ten-day treatment

time. Animals were sacrificed and their vertebral columns fixed in 10% buffered formalin. After proper fixation the tissue ventral to the vertebral column was carefully removed, exposing the lumbar vertebrae and intervertebral discs. A ventral view of the five lowest lumbar discs was measured using a calibrated ocular disc in a dissecting microscope. Agreement of two observers was required before any measurement was recorded. All vertebral columns were given an identification number by a technician who was not involved in the measuring. Observers were unaware of the source or treatment of vertebral columns examined. The matched animals used in the melatonin studies were sibling pairs with the exception of one pair of old females. These animals were one day apart in age and from the same lines with similar histories.

Results and Discussion

A role for melatonin in protecting pubertal and old age shrews from rapid heat loss during exposure to cold was not demonstrated by these experiments (Table 1, 2). However, these findings do reconfirm the previous report that least shrews of selected age classes show limited ability to thermoregulate (Mock, 1985). The age categories for which young shrews show an inability to properly respond to cold are expanded with this study. In fact, the term pubertal probably is inappropriate for describing the affected animals. Captive male least shrews are sexually mature prior to 55 days of age (Mock and Conaway, 1976). The evolutionary advantages of a factor that selectively removes older individuals from a population prior to periods of limited food availability are obvious. It is difficult, however, to envision the benefit of eliminating a major age category of young animals. It is possible that pubertal and young adult least shrews are not found in autumnal populations. Factors similar to those reported for voles may be present that retard sexual development in autumnal offspring exposed to short gestational or lactational photoperiods (Horton, 1984, 1985).

Shrews implanted with melatonin showed significantly smaller intervertebral disc lengths than did their matched controls (Table 3). The primary change in disc size is the reduction in the volume of the nucleus pulposus (Hyvärinen, 1969). The major components of the nucleus pulposus are proteoglycan complexes and the water which they bind (Humzah and Soames, 1988). A likely mechanism to explain these observations is a direct or indirect effect of melatonin on glycosaminoglycans or the proteins to which they are linked.

Acknowledgments

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Table 1.—*Wilcoxon's signed-rank test for evaluating the effects of melatonin on pair-matched, male, pubertal least shrews' response to cold values show body temperature loss (°C) per 30 min at 3–5°C.* $P > 0.05$.

Animal Numbers	Age (Days)	Dosage (mg)	Duration of Treatment (Days)	Control	Melatonin Treated
13532–13534	40	1	8	13.6	22.2
14005–14013	55	1	3	15.1	13.0
14022–14021	36	2	4	18.1	12.1
14123–14124	36	2	4	10.2	7.0
14201–14202	37	2	3	3.9	9.2
14215–14220	36	2	2	15.2	6.7
14224–14221	38	2	4	11.0	22.5
14233–14232	33	2	3	19.1	14.4
14245–14252	31	2	4	12.1	16.0

Table 2.—*Wilcoxon's signed-ranks test for comparing effects of cold treatment on melatonin implanted and control, pair-matched, old-aged least shrews values equal heat loss (°C) per 30 min at 3–5°C.* $P > 0.05$.

Animal Numbers	Sex	Age (Days)	Control	Melatonin Treated	D (°C)
15005–15004	♂♂	443	7.9	12.3	−4.4
15025–15024	♂♂	411	16.9	11.5	5.4
14513–14505	♂♂	531	17.0	13.6	3.4
14551–14554	♂♂	464	14.0	6.2	7.8
14431–14430	♀♀	736	18.6	11.1	7.5
14543–14542	♀♀	501	18.9	21.2	−2.3
14424–14421	♀♀	748	11.8	18.5	−6.7
15000–14553	♂♂	477	20.6	21.8	−1.2
15020–15015	♀♀	458	22.1	19.0	3.1
14541–14532	♂♂	503	20.7	14.6	6.1

Table 3.—*Paired comparisons t-test for comparing the effects of melatonin implants on the total length of the lower five lumbar intervertebral discs in 90-day-old least shrews. Values are in mm. Treatment duration was 8 or 20 days.* $P < 0.001$.

Animal Numbers	Sex	Control	Melatonin Treated	D	D^2
12003–12004	♂♂	2.950	2.475	.475	0.226
12305–12302	♂♂	2.825	2.550	.275	0.076
12311–12310	♂♂	2.250	2.225	.025	0.001
12314–12312	♂♂	2.550	2.300	.250	0.062
12313–12315	♀♀	2.550	2.350	.200	0.040
12324–12322	♀♀	2.750	2.440	.310	0.096
12325–12323	♂♂	2.475	2.175	.300	0.090
12321–12320	♀♀	2.325	2.250	.075	0.006
12502–12501	♀♀	2.285	2.105	.180	0.032
12420–12415	♂♂	2.350	2.260	.090	0.008
12425–12424	♂♂	2.235	2.015	.220	0.048
12500–12503	♀♀	2.315	2.105	.210	0.044
		$\bar{X} = 2.488$	$\bar{X} = 2.271$	$\Sigma = 2.135$	0.503

CAPTIVE BREEDING OF THE COMMON SHREW (*SOREX ARANEUS*) FOR CHROMOSOMAL ANALYSIS

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ABSTRACT

A method is described for systematic breeding of wild-caught common shrews (*Sorex araneus*). In studies over four breeding seasons, 294 animals from 54 litters were known to have been born, 243 of which were successfully weaned. These animals and their parents provided data concerning litter weights and sex ratio of offspring, as well as chromosomal and genetic segregation. By manipulation of photoperiod, sexual maturation of laboratory-born males was induced. It should now be possible to maintain a continuously-breeding laboratory colony for genetic analysis and other studies.

INTRODUCTION

The common shrew, *Sorex araneus*, has always been regarded as difficult to maintain and breed in captivity (see Searle, 1984*a*). One of the first attempts at captive maintenance was that of Adams (1912), but successful breeding was not achieved until the late 1940s by Dehnel (1952). Although common shrews have been bred in captivity intermittently since then (Crowcroft, 1957; Vogel, 1972; Vlasak, 1973; Fedyk, 1980), nobody has established a long-term self-sustaining colony of the type routinely maintained for shrews of the subfamily Crocidurinae (Hellwing, 1971; Oda et al., 1985). In this paper, we describe our methods for the breeding and maturation of common shrews, which we believe would allow such a colony to be established.

Our breeding study extended over four seasons, during which time data were collected on litter size, sex ratio and weight of young, condition of the mothers, and response of laboratory-reared young to photoperiod. In addition, shrews of different chromosomal constitutions were crossed to generate interracial hybrids and to study the inheritance of different chromosomal morphs in this highly variable species.

MATERIALS AND METHODS

Common shrews were bred during 1980, 1981 (J.B.S.), 1988, and 1989 (S.J.M.). The procedures adopted by J.B.S. have already been described (Searle, 1984*a*); thus we concentrate herein on the more recent methods of S.J.M.

Animal Collection.—Wild shrews were collected with unbaited Longworth traps (Chitty and Kempson, 1949) at sites characterized by known frequencies of chromosomal types (Searle, 1983). Females were collected pregnant (late April, May) or prior to their first pregnancy (early April). Mature males were collected at the same times as the females.

Animal Maintenance.—After capture, shrews were kept for up to a week in standard household buckets containing 1–2 cm of moist, milled peat or garden soil, with a covering of hay for concealment and as nesting material. Approximately 25 g of moist, minced ox heart was provided twice daily. Individuals were subsequently transferred to individual, open-air enclosures. These enclosures varied from 0.13 to 0.7 m^2 in basal area (only the larger of these were used for mating or rearing of young) with sides at least 45 cm high. They had a substrate of peat or garden soil, and turf sods were provided as additional cover. Any attempt to keep the turf moist (see Dehnel, 1952, and Searle, 1984*a*) resulted in an infestation of mites, which declined when watering was discontinued. At least one nest box was provided, consisting of an inverted six-inch plantpot filled with hay. In the majority of enclosures, a wire or plastic exercise wheel was provided, and all enclosures had wire mesh tops to prevent loss of animals to predators.

For long-term maintenance and breeding, 25 g of a complex meat-based diet (Searle, 1984*a*) was provided twice daily. More food was given to lactating females and to other animals as their individual needs demanded. Water was provided ad libitum.

Breeding.—Pregnant and lactating females were left undisturbed as much as possible, with a notable increase in food consumption taken to indicate the approximate onset of lactation. Thus for wild-conceived pregnancies, 23 days after such increased food consumption (the length of lactation—Dehnel, 1952; Searle, 1984*a*), the enclosure was first examined for the presence of young, which were considered weaned if their teeth had erupted. Additional signs of weaning were increased activity in the enclosure and disturbance of the food bowl, frequently coupled with vocalization.

At weaning, all animals were removed from the enclosure, weighed, sexed (Searle, 1985*a*), and any distinctive features noted. Female offspring were generally killed and karyotyped soon after weaning to give a guide to the karyotypes of the parents and their male siblings. Siblings lived peaceably together in the same cage if the number of nest boxes provided was at least equal to the number of individuals. After removal of her young, the adult female was immediately exposed to a mature male in her original enclosure. The male was left with the female for 20 days (the gestation period—Dehnel, 1952; Searle, 1984*a*) and then removed to prevent infanticide (in contrast to the method of Genoud and Vogel, 1990, where males were reintroduced before birth to mate at the postpartum estrus). For these captive crosses, the enclosure was examined for a weaned litter 23 days after removal of the male.

Collection of Data.—Animals were killed by cervical dislocation, weighed, and examined for signs of white spotting of the fur. Gender was confirmed by dissection. Body and tail lengths were measured using a variant of Morrison-Scott's pin method (Jewell and Fullagar, 1966). Mitotic preparations were made from bone marrow using the air-drying method of Ford (1966), modified for the shrew by Searle (1983). Mitotic preparations were G-banded by a combined ASG and trypsin method (Searle, 1983), and at least five spreads were scored using the light microscope at 1000X under oil immersion.

Photoperiod Studies.—Nineteen immature males born and reared in captivity were used to assess the effect of photoperiod manipulation on the induction of physical and sexual maturity. At the beginning of this experiment, the age (from weaning) of the animals was between 52 and 69 days, and the ambient photoperiod was approximately 14.5L:9.5D.

For long daylengths (LD), individuals were kept in an animal room in cages, either singly or in small groups, and maintained at a light regime of 16L:8D. For short days (SD), the light regime was 8L:16D, and photoperiod cabinets were used (Grocock and Clarke, 1974). In these cabinets, shrews were housed singly in polypropylene rat cages (350 mm × 200 mm × 200 mm deep), lined with a layer of peat or soil, and the bars replaced with a sheet of perforated metal. Each cage was provided with an exercise wheel, a nest box, and a dish of water. Food was provided twice daily as described above.

The males were subjected to one of three photoperiod regimes. Animals subjected to the first regime (regime A, n = 5, two months LD) were killed before the others to provide an early indication of response to long photoperiods. All of the individuals exposed to regime A derived from one litter, in contrast to those exposed to regimes B and C, which derived from five and six litters, respectively. Animals under regimes B and C were kept for four months, one set of animals (regime B, n = 6) subjected to LD only, whereas the other (regime C, n = 8) had two months SD followed by two months LD. At the end of their photoperiod treatment all animals were killed, and in addition to the normal measurements, fresh weights of testes and seminal vesicles were also recorded.

Results and Discussion

Success of the Breeding Method.—Altogether, 294 young from 54 litters were known to have been born (Table 1). Of these, 243 (44 litters, $\overline{X}$ = 5.5) survived to weaning, including 150 young (24 litters, $\overline{X}$ = 6.3) from natural conceptions and 93 young (20 litters, $\overline{X}$ = 4.7) from crosses in captivity; the maximum litter size recorded at weaning was ten. The difference in size between wild and captive-conceived litters was not significant. No difference in litter size was detected between inter- and intraracial crosses (see also Searle, 1984*a*).

There were strong indications that it is better to bring females into captivity as pregnant animals and cross them after the first litter rather than to attempt to breed nulliparous females. Of ten wild-caught pregnant females collected between 24 April and 22 May 1988, all succeeded in rearing litters, and five subsequently reared litters conceived in captivity. Of five wild-caught nulliparous females collected between 5 and 10 April 1989, none raised a litter to weaning. Of 50 attempted crosses overall, at least 25 (50%) resulted in successful fertilization; when nulliparous females are excluded (nine failed crosses), the success rate rose to 61%. Twenty-one of 81 shrews (12 of 49 females) used for breeding died prematurely; the others were killed after weaning their respective litters.

There was a high frequency of preweaning mortality among wild-conceived young in 1980 and 1981 (40%, excluding those deliberately killed: Table 1), with much of this due to the death of nursing mothers. For wild-conceived young in 1988 and 1989 and laboratory-conceived young, there was far less preweaning mortality. Following weaning, mortality was highest in the first month, at 16% (8 of 49 males). Death was often associated with a disturbance such as movement to another enclosure.

Hair loss was noted in some animals in captivity, usually taking the form of a generalized reduction in the thickness of the fur, especially around the lower back and base of the tail. This was generally associated with dampness in the enclosure, and was frequently improved by replacement of bedding and relocation of the nest boxes. Loss of hair did not seem to affect either longevity or fertility.

Measuring Maturity in the Male.—The degree of maturation in these males was assessed in relation to the following data from wild-caught shrews (Stockley and Searle, 1994). For immature males, body mass is typically in the range of 5–8 g (Crowcroft, 1956) and neither the paired testes nor the seminal vesicles weigh more than 5 mg (Brambell, 1935*b*; note that Brambell erroneously names the seminal vesicles "prostate glands"). Adult males weigh 8–12 g, and typically have a combined testis mass of greater than 100 mg and often exceeding 200 mg; likewise for the seminal vesicles. Seminal vesicle mass is a good indicator of androgen activity (Grocock and Clarke, 1974), and their growth therefore indicates the onset of sexual maturation. Body length is given by Crowcroft (1956) as a reliable indicator of physical maturity in the common shrew. Because the tail does not grow perceptibly after weaning (Table 2), the ratio between body and tail may be used as an indicator of maturity which takes into account natural variation in overall size. From our data (Table 2), body (measured from nose to anus) to tail (measured from anus to tail tip) length ratios tend to lie between 1.6 to 1.9 for immatures, and 2.0 to 2.1 for adults, close to the values that may be extrapolated from Crowcroft (1957).

Animal Weights.—The mean weight of captive-bred offspring at weaning was 7.99 g (n = 15). There was no significant difference, however, between the masses of offspring conceived in the wild and in captivity, or between sexes.

The body weights of nulliparous females were not available for this analysis (see *Success of the Breeding Method*, above), but adult female body masses were measured at the weaning of each litter. There was a significant regression between litter size and body weight of the female at weaning for the first litter (n = 11, r^2 = 0.684, P = 0.0017, d.f. = 10), and the relationship between the size of the second or third litter and body mass of the female at weaning of her previous litter only just fails to achieve significance (n= 5, r^2 = 0.900, P =

0.0516, d.f. = 4; Fig. 1). The extent to which the first relationship is explained by greater mammary development in females with large litters is unknown. No correlation was evident between the size of the first and second litters ($n = 6$, $r^2 = 0.412$, $P > 0.05$, d.f. = 5), and the second relationship is therefore taken to suggest that heavier females produced larger litters. No relationship was found between litter size and mean weanling mass, indicating that smaller litter size is not compensated for by larger weanlings.

Sex Ratio.—Of those offspring sexed on weaning, 57% (119 of 209 animals) were males. Although the sex ratio among weanlings did not differ significantly from 50%, there was a clear tendency towards male bias, which agrees with the findings of Brambell (1935*a*), who gives an average sex ratio of 54% males for wild-caught animals throughout the year (n = 1,064). (Note that male bias determined in nature may partly reflect behavioral differences, particularly in the spring: Crowcroft, 1957; Skarén, 1973; Pucek, 1959.) There were no significant differences in sex ratio between litters conceived in nature and those conceived in captivity.

Response to Photoperiod.—Thirteen males survived to yield data on responses to photoperiod (Table 3, 4), and on the basis of testis and seminal vesicle masses, males subjected to each of the three photoperiod regimes attained sexual maturity. As regards those individuals kept singly (Table 3), it is particularly striking that one individual each from regimes B (four months LD) and C (two months SD, two months LD) had a combined testis mass greater than 250 mg, comparable with males at the height of sexual development. Associated with testis growth, the skin over the testes became bare in some males, as has been recorded in wild-caught individuals (Searle, 1985*a*). One individual from regime C demonstrated regrowth of hair on this bare patch, also consistent with animals in nature (J.B.S., personal observation).

Five animals were housed in groups of three and two animals respectively (see Table 4). Of the three males subjected to two months LD (regime A), one was of immature size and reproductive condition, while the others clearly showed testis and seminal vesicle development. In the other group (four months LD, regime B), one had barely begun to mature, while the other showed clear signs of adulthood, both in reproductive and body growth. Neither individual showed sexual development to the degree found in regime B animals housed singly (Table 3). Inhibition of sexual maturation due to the proximity of another animal is a well-documented phenomenon in both sexes (Lee and McDonald, 1985; Spears and Clarke, 1986), and it is interesting that this may occur in the common shrew despite its normally solitary nature (Croin-Michielsen, 1966). All animals were in good health, and it is considered unlikely that individuals remained immature due to insufficient food supply.

Although no significant differences were found between animals kept singly under regimes B and C, and individual variation was large, some trends should be noted (Table 3). Seminal vesicle mass was similar in the two regimes (indicating similar androgen levels), but testis mass was higher on average under regime B (four months LD). In contrast, the animals under regime C (two months SD, two months LD) had a more adult body-to-tail ratio, with a mean ($\pm SE$) of 1.87 $\pm$ 0.13 (mean for regime B: 1.59 $\pm$ 0.09). In both regimes there were males with adult testis mass and immature body proportions, suggesting sexual and physical maturation are, to an extent, independent processes, although in nature they usually occur concurrently. Pucek (1960) who clearly demonstrated that female common shrews of immature body proportions become sexually mature, made a similar postulation.

The lateral scent gland, which in nature undergoes substantial development only in the male (Searle, 1985*a*), became active in individuals of all three photoperiodic regimes, in parallel with body size and testis development.

Inherited Characters.—Breeding studies have demonstrated that alleles at the *Mpi-1*, *Pgm-2*, and *Pgm-3* enzyme loci segregate in a Mendelian fashion in the common shrew (Searle, 1983, 1985*b*). We report here on segregation studies of other polymorphic features.

Various patterns of distribution of white fur have been noted on the body of the common shrew (Crowcroft, 1955). While white nape patches may be found in adult females as a result of damage during mating (Crowcroft, 1955) and a generalized white peppering is associated with old age (Searle, 1983), the incidence of white patches (commonly found on the ears, but also found in association with the feet, abdomen, and tip of the tail; Crowcroft, 1955) may have a genetic basis. If white spotting results from the expression of an allele at a particular locus, it would seem likely that the gene is analogous or homologous to the recessive, nonpleiotropic white-spotting gene of variable penetrance (*s*), found in several other mammals, e.g., guinea pigs (Searle, 1968).

The results from breeding studies are consistent with the interpretation that white spotting is controlled by an *s*-type gene. A number of offspring from crosses between white-spotted shrews did not display any form of white spotting (data in Searle, 1983), consistent with expression of a recessive trait. The fact that *within an individual* one ear may have white hair and the other not (Crowcroft, 1955) suggests that the white-spotting allele is not fully penetrant.

Breeding studies have also proved invaluable for cytogenetic analysis. In Britain, there are three karyotypic races of common shrew ("Oxford," "Aberdeen," and "Hermitage"), each with a distinctive chromosomal complement. All of these races can be crossed in captivity and it has been demonstrated that litter sizes are similar to those derived from intraracial crosses (Searle, 1984*b*). Furthermore, we have been able to bring Oxford-Aberdeen race hybrids to maturity by photoperiod manipulation (as described above), and to study their fertility (Mercer et al., 1992). Searle (1986) has also examined transmission of variant chromosomes from chromosomal heterozygotes. The results from wild-caught females are unreliable due to multiple paternity (which has itself been demonstrated with the help of this breeding study—Tegelström et al., 1991; see also Searle, 1990), but those from crosses in captivity can be used.

Conclusions

The success of this breeding program may be measured in

terms of percentage of fertile crosses, survival of young to weaning, and postweaning survival. In all of these respects, and especially in terms of the number of young reared, the method has shown itself to be remarkably reliable. Other workers (M. Dodds-Smith, P. Stockley, personal communications) have successfully adopted the same protocol.

Altogether 50% of attempted crosses were fruitful. Collecting adult females during their first pregnancy rather than before enhances the success of subsequent captive crosses. Of those offspring known to have been produced, 87% survived to weaning (excluding those young deliberately killed before weaning), but postweaning mortality was sometimes high, especially if the young were exposed to excessive disturbance.

The sample of animals subjected to photoperiodic manipulation was too small to allow thorough quantification of any of the observed effects. It seems certain, however, that prolonged periods of long days (16L:8D) stimulate sexual maturation (as indicated by testis size and seminal vesicle growth) in young common shrews. Under these conditions, sexual development may occur in the absence of body growth, and both may be inhibited when common shrews under long photoperiod are housed in groups. These observations deserve further study.

We have demonstrated that captive maintenance of the common shrew is feasible at all stages of the life cycle, and most of the technical obstacles to the establishment of a breeding colony have been removed. Shrews can be kept in standard laboratory cages for several months at a time, and early sexual maturation can be induced. The principal problems remain those of the frequency of feeding and the level of mortality, but both of these are likely to be overcome through modification of existing techniques. The benefits of a permanent colony of common shrews for studies of behavior, traditional genetics, and reproductive biology would be substantial. In particular, such a colony would permit a more detailed experimental approach than hitherto possible for the study of the phenomenal chromosomal variation in this species.

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Table 1.—*Success of captive breeding in the common shrew.* [a] *minimum estimates;* [b] *data of Searle (1984a);* [c] *data of S.J.M.;* [d] *total of 23 attempted crosses. Three females were killed during gestation;* [e] *excludes crosses with nulliparous females (nine, all failed);* [f] *includes only one complete litter (of a single animal).*

Where Conceived	Failed Crosses	Preweaning Number of Animals (Litters) Born[a]	Killed	Died[a]	Weaned	At Weaning Mean Litter Size	Proportion Males
Wild[b]	—	80 (15)	8 (1)	29 (6)	43 (8)	5.4	55%
Captive[b]	6[d]	69 (14)	7 (1)	4 (1)	58 (12)	4.8	
Wild[c]	—	110 (17)	0	3 (3)[f]	107 (16)	6.7	55%
Captive[c]	10[e]	35 (8)	0	0	35 (8)	4.4	66%
WILD	—	190 (32)	8 (1)	32 (9)	150 (24)	6.3	—
CAPTIVE	16	104 (22)	7 (1)	4 (1)	93 (20)	4.7	—
TOTAL		294 (54)			243 (44)	5.5	57%

Table 2.—*Body (including head) lengths and tail lengths for a representative sample of adult and immature common shrews. The adults were collected from the vicinity of Oxford (United Kingdom) during 10–25 May 1981. The immatures (the progeny of a variety of crosses involving common shrews from the vicinity of Oxford and Aberdeen, United Kingdom) were reared in captivity and measured within five days of weaning from 27 July to 11 August 1981.*

Age and Sex	*n*	Length (Mean ± S.E., in mm) Body	Tail	Body-to-Tail Ratio
Adult females	10	82.67 ± 0.69	39.92 ± 0.89	2.1
Adult males	10	83.03 ± 0.50	41.61 ± 0.71	2.0
Immature females				
Litter 1	1	66.5	42.5	1.6
Litter 2	4	75.25 ± 0.71	42.52 ± 0.24	1.8
Litter 3	2	71.65 ± 0.05	40.20 ± 0.20	1.8
Litter 4	2	71.85 ± 1.45	40.05 ± 2.75	1.8
Litter 5	4	69.05 ± 0.46	39.65 ± 0.76	1.7
Immature males				
Litter 1	7	70.96 ± 0.37	43.04 ± 0.49	1.6
Litter 2	2	72.85 ± 1.45	44.80 ± 0.60	1.6
Litter 3	3	72.93 ± 0.57	41.53 ± 0.93	1.8
Litter 4	3	69.93 ± 1.09	37.37 ± 1.10	1.9
Litter 5	4	69.68 ± 0.86	40.38 ± 1.28	1.7

Table 3.—*The extent of sexual maturation in male shrews kept singly under different photoperiod regimes.* [a] *age in days from weaning;* [b] *animal died prematurely, and therefore received approximately five weeks less long photoperiod than the other two regime B animals (86 days, as opposed to 123 and 124 days). Its loss of condition is reflected by its low body mass.*

Photoperiod Regime	Age[a]	Combined Fresh Weights (mg)		Body Weight (g)	Body-to-Tail Ratio
		Testes	Seminal Vesicles		
B	191	282	105	9.27	1.51
(4 months LD)	192	124	122	9.09	1.76
	145[b]	156	82	5.64	1.49
Means:	176	187	103	8.00	1.59
C	189	255	100	8.46	1.60
(2 months LD +	191	71	50	8.28	1.84
2 months SD)	191	127	135	10.09	2.32
	192	79	115	8.65	1.60
	182	88	136	8.48	1.97
Means:	189	124	107	8.79	1.87

Table 4.—*The extent of sexual maturation in male shrews kept in groups under different photoperiod regimes.* [a] *age in days from weaning;* [b] *too small to weigh accurately;* [c] *sperm and meiotic division observed in testes;* [d] *no sperm in testes, no indications of meiosis.*

Photoperiod Regime	Age[a]	Combined Fresh Weights (mg)		Body Weight (g)	Body-to-Tail Ratio
		Testes	Seminal Vesicles		
A	112	117	118	8.6	—
(2 months LD)	112	75	29	6.5	—
	112	5	b	6.2	—
B	194	54[c]	12	7.8	1.82
(4 months LD)	194	20[d]	b	7.6	1.37

Fig. 1.—Relationship between the size of the second or third litter and the weight of the mother at the weaning of her previous litter. For two females, the data for both the second and third litters are included on this graph, but for the statistical analysis (see text) single mean values were calculated for these females.

PROPOSED STANDARD PROTOCOL FOR SAMPLING SMALL MAMMAL COMMUNITIES

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ABSTRACT

Accurate estimates of small mammal community structure are difficult to obtain due to numerous sources of variation, including trap type and method of deployment, duration of sampling, and weather conditions. This is particularly true in the case of shrews (Soricidae), which are underrepresented by traditional sampling methods. To foster research on the community ecology of small mammals, particularly shrews, we propose adoption of a standard protocol for sampling small mammals. This sampling protocol involves deploying Y-shaped arrays of ten pitfall traps and drift fences. Each arm, which is anchored on a central pitfall, consists of three pitfalls separated by 5-m sections of drift fence. Pitfalls, not less than 14 cm in diameter and 19 cm deep, should be filled approximately half full of water to quickly drown captured animals. Due to the significant influence of precipitation on sample data, we recommend that arrays be operated for ten consecutive days, which in temperate forest regions will usually encompass at least one precipitation event. Use of the proposed sampling protocol will reduce sources of error related to trap type, method of trap placement, and the trapping skill levels of individual investigators. This will facilitate comparisons of community data between sites and provide better estimates of abundance and structure of soricid communities than nonstandardized sampling methods.

INTRODUCTION

Shrews (Soricidae) are important constituents of small mammal communities in forested regions of the Holarctic and Old World tropics (Kirkland, 1991). Despite their importance in terms of numbers of species and individuals, shrews apparently are underrepresented in many studies of small mammal community structure. A key factor is trap type, which can influence the capture rate of individual species (Cockrum, 1947; Wiener and Smith, 1972; Pizzimenti, 1979; Williams and Braun, 1983) and thus perception of small mammal community structure. Live traps typically underestimate the abundance of shrews (Pucek, 1969), whereas pitfall traps are very efficient in capturing soricids, especially the smallest species (Prince, 1941; MacLeod and Lethiecq, 1963; Wolfe and Esher, 1981). Even old and new models of the Museum Special snap trap differ in their sensitivity to individual species of small mammals, including shrews (West, 1985). Added to variation attributable to trap type is the considerable difference in skill levels of individual investigators in deploying traps, particularly snap traps. Other potential sources of variation include the method of deployment of traps (e.g., randomly vs. systematically placed traps) and interstation distances in grids and transects.

Another potentially important source of error between studies is variation due to weather and moon phase. Not only can precipitation have a significant influence on activity levels of small mammals (Burt, 1940; Sidorowicz, 1960; Mystkowska and Sidorowicz, 1961; Falls, 1968; Drickamer and Capone, 1977; Pankakoski 1979*a*), but hard rains can set off snap traps, particularly those placed in exposed sites, thus reducing probability of capture. Small mammals may respond to high ambient light during the full moon by decreasing activity (Blair, 1951) or by spatially shifting foraging patterns (Bowers, 1988, 1990). As a consequence, samples of small mammals obtained during periods of precipitation or full moon may differ quantitatively and qualitatively from samples obtained during periods of clement weather or new moon.

One consequence of these various sources of variation is that it is often difficult to compare the structure of terrestrial small mammal communities as revealed by different studies. In fact, potential sources of error and variability are so numerous that it seems impossible to expect that valid comparisons of community structure could be made between studies. Nevertheless, we believe extraneous variation between studies can be minimized thereby facilitating valid comparisons. An essential step in this direction would be adoption of a standard protocol for sampling small mammal communities. Use of a standard sampling protocol would alleviate some of the problems normally encountered in comparing estimates of small mammal community structure obtained by different methods, and thereby foster an understanding of regional variation in small mammal community structure. This would be especially important in the case of shrews, which are sensitive to sampling techniques and are often underrepresented in samples obtained by conventional trapping (Wolfe and Esher, 1981).

The sampling protocol proposed herein, which was initially tested in five forest habitats in south-central Pennsylvania, USA, employs Y-shaped arrays of pitfalls and drift fences. Results of sampling from September to November 1987 demonstrated the effectiveness of the proposed standard sampling protocol in capturing shrews. In this paper, we describe the sampling protocol, present the results of initial sampling with the pitfall arrays, compare data obtained by pitfall and snap trap sampling in the same habitats, and provide an annotated list of equipment and supplies needed for the proposed protocol.

DESCRIPTION OF PITFALL ARRAYS AND PROPOSED PROTOCOL

Arrays of ten pitfall traps (minimum size of 14 cm diameter × 19 cm deep) and drift fences (5-m long sections of 25–30 cm wide aluminum flashing, plastic sheeting, or similar material) should be arranged as illustrated in Fig. 1. Each arm of an array consists of three pitfalls connected by sections of drift fence, which extend to the central pitfall. The three arms should be separated by arcs of approximately 120°. This configuration

minimizes directional bias in sampling. Drift fencing should be buried to a depth of 3–5 cm to prevent small mammals from crawling or burrowing underneath.

Pitfalls should be installed so that the rims are flush with or slightly below the soil surface. One problem frequently encountered when installing pitfalls is soil getting into the pitfalls as it is back-filled around the traps. If tapered plastic containers are used for pitfalls, the amount of soil getting into pitfalls during installation can be minimized if two traps are nested before the pitfall is placed in the ground. As soil is filled in around the pitfall, material will fall into the upper pitfall. When this pitfall is removed, the lower one will be clean and its rim will be slightly below the soil surface. Traps should be filled with water to a depth of approximately 9 cm (half full). There should be sufficient water in traps to prevent animals from touching the bottom and thereby jumping out, but not enough water to permit floating animals to reach the rim. Based on experience in the north temperate forest biome, we recommend operating pitfall arrays for ten-day periods, checking them daily. This totals 100 trapnights (TN) of sampling effort per array per sampling period and permits easy calculation of relative abundance as percentage capture success. Operating individual arrays for the same number of nights also facilitates comparison between arrays, either as whole numbers or as percentage capture success. The minimum ten-day sampling period is justified in part by the considerable labor needed to establish an array. However, a more important consideration is to ensure that each sampling period encompasses at least one precipitation event, given the significant influence of precipitation on small mammal activity. The ten-day sampling period is particularly applicable in temperate deciduous forest regions where precipitation is relatively high and evenly distributed throughout the year, and a seven-day cycle of storms or weather fronts occurs.

If there is no precipitation during the first ten days of sampling, we recommend extending the sampling period until there is a precipitation event, and perhaps one or two days after precipitation occurs, or until the capture rate returns to prerainfall levels. In regions of low or highly seasonal precipitation, adjustment in the length of sampling periods should be made to accommodate prevailing local climatic conditions.

Methods and Materials

Arrays of pitfalls and drift fences were initially tested in five forest habitats (two arrays per habitat) on South Mountain, Cumberland County, south-central Pennsylvania, USA. Habitats sampled were mature lowland mixed deciduous forest, midelevation chestnut oak (*Quercus prinus*) forest, ridge forest dominated by chestnut oak and black gum (*Nyssa sylvatica*), three-year-old clearcut, and nine-year-old clearcut. The two clearcuts were in predominantly chestnut oak stands. The ten arrays were run concurrently for 39 days between 22 September and 21 November 1987.

For comparative data from snap trap sampling, we used data obtained by the first author at 18 localities in central Pennsylvania, including two recent (<5-years-old) clearcuts. This sampling included both trapping grids and best site trapping (Kirkland, 1979; Kirkland and Hench, 1980; Cornbower and Kirkland, 1983).

Results and Discussion

Initial Sampling with Proposed Protocol and Comparisons

Initial sampling of small mammals using arrays of pitfalls and drift fences revealed soricids to be considerably more important constituents in the five habitats sampled than was expected based on snap trap sampling (Table 1). Not only did pitfall trapping reveal a significantly higher proportion of soricids in the sample, but there were significant shifts in the perceived structure of the soricid assemblage (Table 1). The snap trap sample was dominated by the large, nearly mouse-size short-tailed shrew (*Blarina brevicauda*), which comprised 77.9% of the shrews taken, whereas this species comprised less than one-third of soricids taken in the pitfall arrays (Table 1). This is consistent with the results of Mengak and Guynn (1987), who found that in South Carolina *Blarina carolinensis* comprised 98% of shrews taken in Museum Special snap traps but only 36% of soricids taken with pitfalls and drift fences. Long-tailed shrews (*Sorex* spp.) were significantly more abundant in the small mammal community and in the soricid assemblage based on pitfall trapping (Table 1).

Noteworthy in pitfall sampling was capture of 37 pygmy shrews (*Sorex hoyi*). This species was first collected in Pennsylvania by pitfall sampling (Kirkland et al., 1987). Previous live and snap trap sampling of small mammals on South Mountain by the first author over a 17-year period failed to capture this species. Yet, *S. hoyi* comprised 10% of the pitfall sample and was approximately evenly distributed in the five habitats sampled (Table 2). These data indicate that sampling with the proposed standard protocol yielded much better estimates of soricid abundance and community composition than conventional snap trap sampling.

As the proportion of soricids in the pitfall sample was larger, the relative importance of rodents was proportionately reduced. When data for the most abundant rodent species were analyzed, the proportions of *Peromyscus* spp. (combined white-footed mouse, *P. leucopus*, and deer mouse, *P. maniculatus*), and southern red-backed vole (*Clethrionomys gapperi*) were significantly lower in the pitfall sample (Table 1). However, when compared in the context of their respective contributions to the rodent assemblage, proportions of these species did not differ between pitfall and snap trap samples (Table 1). This suggests that pitfall samples provide valid estimates of the relative abundance of these species within rodent assemblages but may underestimate their overall abundance. Part of this difference may be related to the behavior of individual species. For example, the tendency of forest-dwelling populations of *Peromyscus maniculatus* and *P. leucopus* to utilize downed trees as routes of travel (Plantz, 1987; Graves et al., 1988), may make them less subject to capture in pitfalls than in snap traps, which are often set at the bases of trees or on logs where these species are active. Pitfall arrays tend to be installed in open areas between trees.

Although total numbers of rodents may be underestimated in pitfall sampling, data for *P. leucopus* and *C. gapperi* (Table 2) indicate that pitfall sampling provides good estimates of relative abundance of rodent species in individual habitats. *Peromyscus leucopus*, an abundant habitat generalist, did not differ in abundance among the five habitats ($\chi^2 = 3.98$, $0.25 < P < 0.50$). *Clethriomonys gapperi*, which is not common in oak forests of south-central Pennsylvania and which evinces positive population responses to clearcutting (Kirkland, 1990), was not equally abundant in the five habitats ($\chi^2 = 45.09$, $P < 0.001$), with 40 of 46 (87.0%) specimens captured in the two clearcut habitats.

We did not capture any eastern chipmunks (*Tamias striatus*) during our initial sampling. Subsequently we have captured only five individuals (all juveniles) in approximately 13,000 TN of pitfall sampling effort in suitable habitats for this species. This suggests that adult chipmunks are not subject to capture by our method of pitfall trapping, perhaps because they can escape from traps before drowning.

No sampling protocol will be optimal for all taxa of small mammals. For example, although our protocol is particularly effective in capturing soricids, it is less efficient in taking small muroid rodents and is inefficient in capturing specimens weighing more than 60 g. One way to address these deficiencies would be to augment pitfall arrays with snap traps, which are more efficient in capturing rodents.

Influence of Precipitation on Perceptions of Small Mammal Abundance and Community Structure

Preliminary data confirmed the significant influence of precipitation on the overall capture rate of small mammals, and the differential responses of shrews and rodents to precipitation (Fig. 2). During periods of no rain, the average daily capture rate for small mammals was 7.4/100 TN, but when it rained ($\geq$0.3 cm), the rate increased to 18.9/100 TN ($\chi^2 = 76.79$, $P < 0.001$). This increase was different for shrews and rodents. On nonrainy nights, capture rates for shrews and rodents (3.8/100 TN and 3.7/100 TN, respectively) did not differ. However, when it rained, capture rates increased significantly to 13.4/100 TN for shrews ($\chi^2 = 95.17$, $P < 0.001$) and 5.4/100 TN for rodents ($\chi^2 = 4.12$, $P < 0.05$). Although the capture rates for shrews and rodents did not differ on nonrainy nights, the capture rate for shrews was significantly higher when it rained ($\chi^2 = 34.63$, $P < 0.001$).

These results indicate that perception of relative abundance and community structure of small mammals can be significantly influenced by precipitation during sampling. Consequently, we believe that it is important to include at least one episode of rainfall ($\geq$0.3 cm) in each sampling period. Ideally, this precipitation should occur during the first hours after sunset when small mammals normally are most active.

Problems: Rocky Substrates and Traps Filling with Water

Use of pitfalls and drift fences may be limited by substrate conditions. For example, Pucek (1981) noted that pitfalls are "impossible to use in rock, gravel, or clay." Nevertheless, Brown (1967) successfully employed pitfalls to sample soricid communities in rockslide habitats in the central Rocky Mountains (USA). However, he used single pitfalls, and thus was not constrained by the limitations imposed by arrays of pitfalls with drift fences.

Pitfalls are also difficult to install in habitats with high water tables. At such sites, it may be necessary to anchor pitfalls to keep them from being forced out of the ground by subsurface water pressure. Metal or plastic tent stakes, or stakes cut from shrubs or trees hooked over the rims of pitfalls work well to secure pitfalls in the ground.

Frequent, heavy rains will cause pitfalls to fill with water, which must be removed. One way to prevent this is to shelter the pitfalls (Handley and Varn, 1994). Another is to put holes in the walls of the pitfalls at the desired maximum depth of water. However, in saturated soil (e.g., bogs), such holes often will cause the trap to completely fill with water.

Capture of Amphibians, Reptiles, and Invertebrates

Drift fences with pitfalls have been used for many years to collect amphibians and reptiles (Gibbons and Semlitsch, 1981; Campbell and Christman, 1982). In fact, the inspiration for development of our pitfall arrays was the success of herpetologists at Carnegie Museum of Natural History's Powdermill Biological Station in capturing large numbers of shrews incidental to sampling amphibians with pitfalls and drift fences (J. F. Merritt, personal communication). Because amphibians may serve as both prey for and competitors with shrews, we have preserved amphibians captured during pitfall sampling. During the initial 39 days of sampling in 1987, we collected 424 amphibians representing nine species. If removed daily, amphibians are in good shape and suitable for fluid preservation.

Substantial numbers of epigeal invertebrates are also collected in pitfalls. Such material has been used to assess the food resource base of soricids (Pernetta, 1976; Churchfield, 1982). We collect invertebrates at the end of each ten-day sampling period by straining pitfall water through a sieve and then preserving them in 10% formalin or 70% ethanol. In summer, warm water may cause some deterioration of invertebrates during a ten-day sampling period, but this is not sufficient to preclude identification to family.

Annotated List of Recommended Supplies and Equipment

Drift Fencing.—A variety of materials, including aluminum flashing, vinyl plastic, tarpaper, corrugated metal, and fiberglass panels, can be used for drift fencing, with factors such as price and local availability determining which material is selected. For example, in Czechoslovakia J. Gaisler (personal communication) uses 1 mm-thick plastic sheeting. This material is used by utility companies to cover buried electrical cables and by construction crews as barriers around excavations. Handley and Varn (1994) use salvaged pieces of aluminum siding for drift fencing. Whatever material is used, it is important that drift fencing be high enough to prevent mammals

from climbing or jumping over, and that it be buried to a sufficient depth to prevent them from crawling or tunneling under. We recommend using material that is at least 25 cm wide. Nine 5-m sections are needed for each standard array (see Fig. 1).

We initially chose aluminum flashing, which although very durable, was expensive (approximately $1.95 per meter of 25.4 cm-wide material or nearly $90 per array in September 1987), somewhat bulky, and did not conform to irregularities in the ground surface. The latter problem was overcome by extensive trenching. The high cost of aluminum flashing also makes it attractive to thieves.

More recently we have used heavy-duty (6 mil-thick) vinyl plastic sheeting as drift fencing. This material is sold in 30.5 m (100 ft) by 30 cm (12 in) wide rolls for approximately $10 per roll, making it considerably less expensive than aluminum flashing. Vinyl plastic is substantially less bulky than the aluminum flashing, is flexible so that it easily conforms to undulating topography, and is therefore considerably easier to install. We cut the vinyl plastic sheeting into lengths slightly longer than 5 m (5.3 m works well). The extra length permits some flexibility in avoiding obstacles while still maintaining the 5-m interval between pitfalls. Any excess is wound on the end stakes for greater stability. We use a staple gun to attach the plastic sheeting to wooden stakes for vertical support. The lower 5–8 cm should not be stapled so that it can be rolled to line the trench. Once inserted in a trench, the plastic is held in place by wooden blocks and nails (see below). Soil is then back-filled into the trench to provide greater stability and to prevent small mammals from crawling or tunneling underneath.

Pitfalls.—Several types of containers may be used as pitfalls; however, these should be at least 14 cm in diameter and 19.5 cm deep. Plastic containers used to transport bulk dairy products (e.g., cottage cheese) are relatively inexpensive and often come with snap-on lids, which are useful in covering traps securely during nonsampling periods. Such plastic containers are slightly tapered so they stack and thus are convenient to carry. In contrast, #10 tin cans, which are approximately the same size, do not stack, lack convenient lids, and unlike plastic containers, do not deform to accommodate roots and rocks. Handley and Varn (1994) used 2-L plastic soda bottles with the tops cut off. European researchers have traditionally employed cones as pitfalls (Pankakoski, 1979*b*). These vary in size but generally are about 14 cm in diameter and 38 cm deep.

Staple Gun.—Needed to secure plastic sheeting to stakes. We have found that 10 mm (⅜ in) staples are an optimal length for attaching 6-mil plastic sheeting.

Blocks of Wood and Nails.—These are essential for securing plastic sheeting in trenches. At least five to eight pieces of wood (1.9 cm × 1.9 cm × 15.3–20.3 cm or ¾ in by ¾ in by 6–8 in) are needed for each 5-m section of drift fence to secure vinyl plastic fencing. Each block has a single hole drilled in the middle to accommodate snugly a large nail or spike which is driven into the ground through the bottom of the vinyl plastic. We recommend 15.3 cm (6 in) nails.

Stakes.—Stakes are essential to the installation of plastic sheeting drift fences since they provide vertical support. They are also needed to stabilize aluminum flashing. At sites where wind is expected (e.g., recent clearcuts, grasslands, or deserts), a greater number of stakes will be required to stabilize drift fencing. Gibbons and Semlitsch (1981) recommended securing aluminum flashing to stakes with plastic cable ties.

Narrow-Bladed Shovels or Drain Spades.—Drain spades are narrow shovels with rounded blades. The cross section of the drain spade approximates the curvature of the pitfalls recommended. As a result, four cuts, one on each side, will loosen a plug of soil which approximates the shape and volume of a pitfall.

Wrecking/Pry Bars or Rock Picks.—Small wrecking/pry bars (46–61 cm long) are useful for prying loose rocks from pitfall excavations and for excavating drift fence trenches. Geologist's rock picks can substitute for the wrecking/pry bars in excavating trenches for drift fences.

Conclusions

Our purpose in proposing a standard protocol for sampling small mammals is to foster research on small mammal community ecology and to facilitate comparison of data. The proposed protocol is designed to minimize a number of sources of error and variation that have made valid comparisons of such data difficult. We recognize that no sampling protocol is perfect. Each has strengths and weaknesses, and there may be conditions under which our proposed sampling protocol is either inappropriate or impractical. Nevertheless, we believe that if our proposed sampling protocol is adopted by a modest number of researchers, the resulting pool of data will lead to a significant enhancement of understanding of the structure of small mammal communities. Because of the efficiency of pitfalls with drift fences in capturing soricids, adoption of our protocol will yield better insight into the abundance and diversity of shrews in small mammal communities.

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Table 1.—*Comparisons of results from sampling of small mammal communities in forested and clearcut habitats with arrays of pitfalls and drift fences at ten localities in south-central Pennsylvania and with Museum Special snap traps at 18 localities in Pennsylvania.* * P < *0.001.*

Community Characteristic	Pitfalls	Snap Traps	z-Value
% Soricids	58.1	16.6	14.616*
Blarina brevicauda as % of total soricids	28.8	77.9	−9.048*
Blarina brevicauda as % of total small mammals	16.7	13.0	−1.704*
Sorex spp. as % of total soricids	71.2	22.1	9.048*
Sorex spp. as % of total small mammals	41.4	3.7	16.832*
Peromyscus leucopus as % of total small mammals	24.1	47.6	−7.677*
Peromyscus leucopus as % of rodents	57.4	57.1	0.077
Clethrionomys gapperi as % of total small mammals	12.4	30.2	−6.607*
Clethrionomys gapperi as % of rodents	29.7	36.2	−1.535
Total Sampling Effort (TN)	3900	6748	
Total Catch	370	841	
Catch/100 TN	9.49	12.46	

Table 2.—*Ecological distribution and community structure of small mammals in five habitat types on South Mountain, Cumberland County, Pennsylvania, as revealed by 39 nights of sampling with ten arrays of pitfalls and drift fences (two per habitat) between 22 September and 21 November 1987.*

	Distribution of Small Mammals by Habitat Type				
Species	Mature Lowland Deciduous Forest	Nine-Year-Old Clearcut	Mid-Altitude Oak Forest	Three-Year-Old Clearcut	Ridge Forest
Blarina brevicauda	17	25	5	9	6
Sorex fontinalis	21	24	15	27	12
S. fumeus	6	9	0	2	0
S. hoyi	6	9	8	10	4
Clethrionomys gapperi	4	17	2	23	0
Peromyscus leucopus	18	15	13	19	24
Microtus pinetorum	8	3	3	3	0
Microtus pennsylvanicus	0	1	0	2	0
Number of species	7	8	6	8	4
Number of specimens	80	103	46	95	46

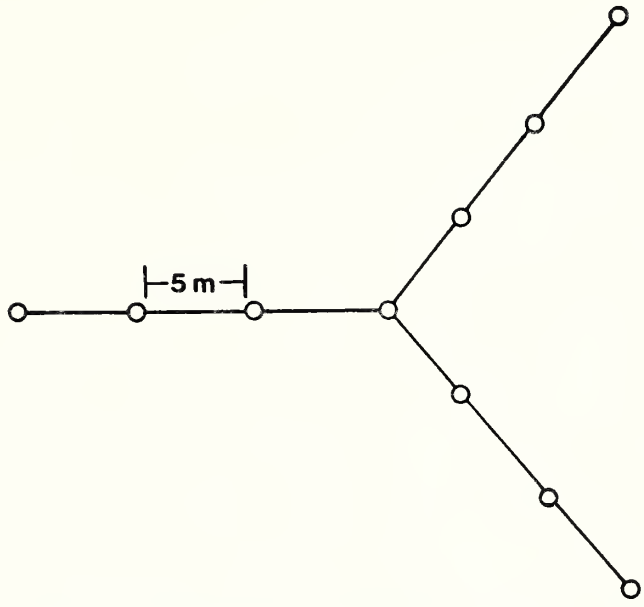

Fig. 1.—Schematic representation of arrangement of pitfalls and drift fences in proposed standard sampling protocol.

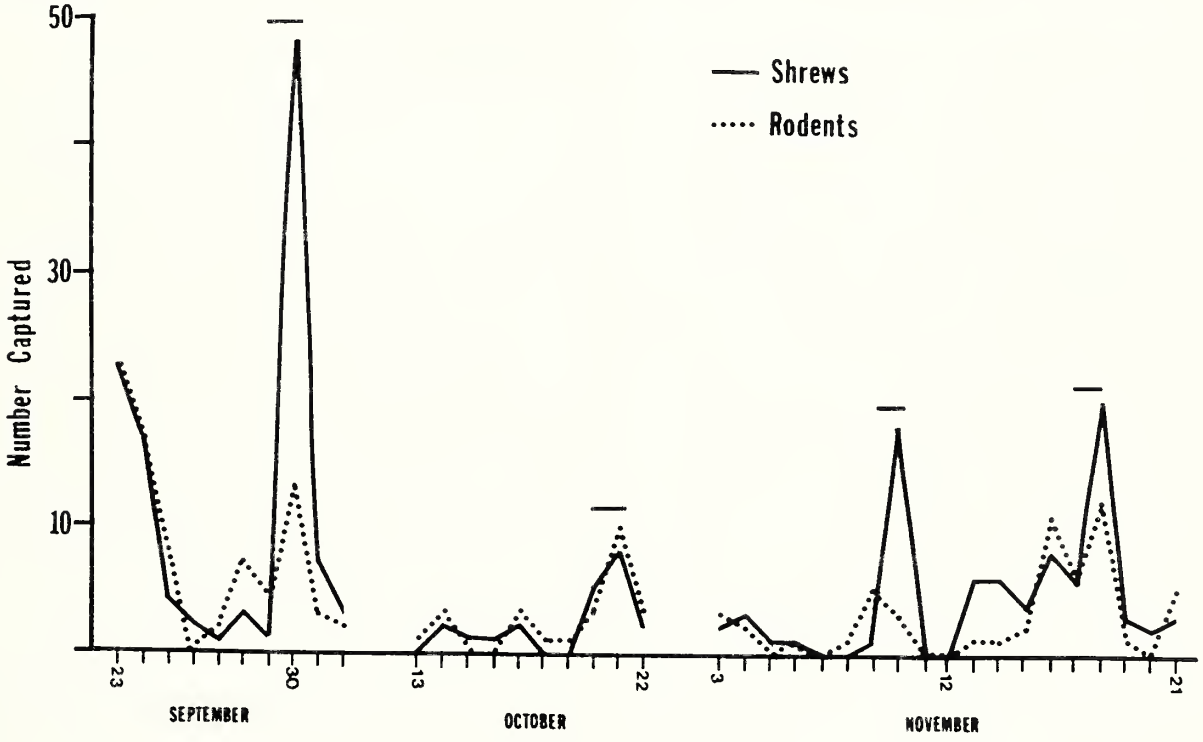

Fig. 2.—Pattern of captures of soricids and rodents during 39 nights of sampling with ten pitfall arrays between 22 September and 21 November 1987 in Michaux State Forest, South Mountain, Cumberland County, Pennsylvania. Precipitation indicated by horizontal bars.

THE TRAPLINE CONCEPT APPLIED TO PITFALL ARRAYS

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ABSTRACT

We describe a small and easily set pitfall array for eapturing and preserving shrews, other small vertebrates, and invertebrates. It is designed to be set in a transect. Because this array can be set quickly it is practical to set many, simulating a trapline. Like a trapline, a transect of pitfall arrays can easily and quickly sample all of the habitat types and give a quick estimate of diversity of species in an area.

INTRODUCTION

During 14 months of sampling the distribution, abundance, and habitat preferences of shrews in coastal South Carolina (July 1989 to September 1990), we successfully used a very compact pitfall array. The whole array fits into a triangle with 2.5-m sides. This small array is inexpensive, seldom vandalized (constructed entirely of salvaged, discarded, rigid materials), lightweight, and conveniently transportable. It can be set quickly (two people can set two arrays per hour in any but the rockiest soil), even in rough terrain and amidst obstacles, and it causes minimal disturbance to habitat. Because of their small size, our arrays even survived the calamity of falling trees with little or no damage when Hurricane Hugo passed through our study area, leveling the forest on 21 September 1989. Arranged in a transect, with 14 arrays (98 pitfalls) per 1000 m, our arrays are equivalent to a trapline, and are particularly good for quick estimates of habitat selection and presence or absence of species of shrews.

MATERIALS AND METHODS

Our pitfalls were 2-liter, heavy-gauge plastic soft drink bottles with the tops cut off. Bottles with reinforced round bottoms, rather than those with rippled bottoms, maintained shape better in the ground, and removal of specimens from them was easier. The topless plastic bottles are 20 cm deep and 11 cm in diameter. At the center of each array we also used one 4-liter plastic container approximately 18 cm deep and 15 cm in diameter. Equivalent-sized metal cans might be used for short-term sampling, but they are not good for long-term projects because they rust. Also, their flat bottoms make removal of specimens more difficult.

Containers were placed in arrays of seven pitfalls each (Fig. 1). The pitfalls were arranged in a three-leaf clover pattern (120° between arms), with the 4-liter container at the center and the 2-liter bottles on either side near the distal end of each arm (drift fence). The drift fences converged at the central pitfall. The fences were made of vinyl or aluminum siding, 1.2 m long by 30 cm high, inserted into a trench 2–5 cm deep to prevent burrowing through litter beneath the fence, and held upright by sticks cut from the forest. An array fits into a triangle a little less than 2.5 m from corner to corner.

Containers were sunk into the ground with lips flush with the surface. Each pitfall was sheltered from rain, falling leaves, sun, and moonlight with a square of vinyl or aluminum siding 30 × 30 cm, leaned over the pitfall, against the drift fence. A larger square of plastic or aluminum, laid flat on the convergent drift fences, sheltered the central pitfall.

In damp ground on swamp borders, we compensated for fluctuating water tables by pegging down the pitfalls. Otherwise, they popped out of the ground. We made hooked pegs from slender sprouts. One long peg on either side of a pitfall effectively held it in place, even when it was totally submerged. If preservative is not used pitfalls can be kept in wet ground by puncturing them so they will fill to the level of the water table.

We filled the pitfalls to about half their depth with 10% formalin to preserve specimens. During sampling, we checked the pitfall traplines at 4–6 week intervals and had little trouble with specimens spoiling except occasionally in flooded pitfalls. At first, we put a skim of mineral oil on the formalin to reduce evaporation and odor. However, we soon eliminated the oil because it was expensive, coated the specimens, and evaporation proved not to be a problem in the humid climate of coastal South Carolina. In spite of the increased odor of the formalin, catch numbers did not decline. If arrays are checked daily (preferably morning and evening), water can be substituted for formalin. Shrews also can be captured in dry pitfalls, but in experiments in 1987 at Mountain Lake Biological Station in southwestern Virginia, we observed a higher capture rate in pitfalls containing liquid, even if no more than a few millimeters deep. Rodents, with the exception of baby voles, can easily jump out of dry pitfalls.

We marked arrays with pink surveyor's tape (highest visibility in forest). To deter vandalism we included with the array marker a waterproof label which stated, "THIS IS A PROJECT OF THE SMITHSONIAN INSTITUTION STUDYING POPULATIONS OF SMALL ANIMALS. FOR MORE INFORMATION PHONE (a number)." A local cooperator responded to telephone queries by reading a brief explanation of the project.

Equipment needed to install the pitfalls and drift fences is minimal. However, two items not ordinarily found in the home or laboratory greatly simplify the job of installation: 1) drain spade with a 5 × 16-in (12.5 × 40-cm) blade, the edge sharpened for cutting roots in the pitfall hole; and 2) posthole digger with a lift diameter of 5 in (12.5 cm), only 1.5 cm greater in diameter than a 2-liter container. This tool expedites removal of soil after the hole has been cut with the drain spade. These tools may be obtained from a large hardware store or

from Forestry Suppliers, Inc. (Box 8397, Jackson, Mississippi 39284-8397). Other equipment will vary with the preference of individual pitfall trappers. We recommend: mattock with combination adz-shaped and ax blades (essential for digging in hard or rocky ground), trowel, pruning shears, gloves (in the South soil often contains roots of poison ivy, *Rhus radicans*), 1-m^2 plastic sheet for removing waste earth from pitfall holes, an extra 2-liter bottle for plugging pitfalls during installation to keep soil out, and a 5-gal (20-liter) plastic container for dispensing formalin into the pitfalls.

Gear for collecting specimens from pitfalls varies with the preference of individual trappers. We used a bucket, 14-in diameter × 8 in deep (35 × 20 cm), for carrying specimens and supplies; plastic bags, ½-gal, 5 × 15 in (2-liter, 12.5 × 37.5 cm); waterproof labels; #2 pencil or pen with waterproof permanent ink; latex gloves; containers of formalin and water; ¼-cup measure; trowel; and pruning shears. Wearing latex gloves, we scooped specimens from pitfalls by hand into a plastic collecting bag, prelabeled with the array number. Then we cleaned out leaves and debris, added water if necessary, and restored the strength of the preservative in the pitfall by adding ¼ cup of 37% formaldehyde solution.

Results

Where we used the 2.5-m arrays in coastal South Carolina, 40–60 km NE of Charleston, for 14 months in 1989 and 1990, flooding often drastically reduced catch during the 4–6 weeks between pitfall checks. Likewise, invertebrates in the pitfalls were a deterrent to capture of shrews. The mammals could use the invertebrates as a platform and scramble out of the pitfalls. Nevertheless, in 22 pitfall arrays we caught shrews: 53 *Sorex longirostris*, 32 *Blarina carolinensis*, and 11 *Cryptotis parva*, and a few rodents including: 7 *Reithrodontomys humulis*, 2 *Oryzomys palustris*, 1 *Ochrotomys nuttalli*, and 1 *Microtus pinetorum*. The miniature arrays were even more effective for capturing amphibians and reptiles. They caught 575 frogs and toads, 190 salamanders, 26 lizards, and 6 small snakes.

The major fraction of the pitfall catch, however, was composed of a broad spectrum of invertebrates, including snails, earthworms, nematodes, centipedes, millipedes, spiders, harvestmen, crayfish, crabs, amphipods, isopods, Coleoptera, Hymenoptera, Orthoptera, Diptera, and even Lepidoptera. Except for Hymenoptera, the insects included both adult and larval stages. Sometimes pitfalls were jammed full to the top with a multitude of one kind of invertebrate such as crayfish, isopod, or beetle. In using pitfalls for invertebrates, entomologists at the Smithsonian Institution prefer as a preservative a solution of 50% antifreeze (ethylene glycol) and 50% water containing detergent or soap, or a solution of 50% alcohol and 50% water containing detergent or soap. For high-quality specimens, pitfalls filled with these weak preservative solutions must be checked at intervals of less than a week.

There is a considerable amount of literature on pitfall trapping. Because of the scale of the pitfalls described, two papers are particularly appropriate to our discussion. Bury and Corn (1987) concluded that pitfall arrays with short drift fences (2.5 m) are no more effective for capturing small mammals than pitfalls without fences. However, they did not distinguish shrews from other small mammals in their comparison. Small scale pitfalls are designed primarily for catching shrews and are relatively ineffective for other small mammals. Furthermore, in the array that Bury and Corn described was a 10-m gap between the fences at their inner ends which largely nullified the value of the drift fences. The resulting array differed little from an array of pitfalls without fences.

Williams and Braun (1983) compared single pitfalls with 1.2 m- and 0.6 m-long drift fences radiating from them, with single pitfalls without drift fences. A pitfall with 1.2-m fences caught 2.5 times as many shrews as a pitfall without fences, and 3.3 times as many as a pitfall with 0.6-m fences.

The use of the pitfall as a sampling tool has been developed, refined, and tested so thoroughly that it is desirable and feasible to propose standards (Kirkland and Sheppard, 1994). We do not pretend that the method we describe here is either new, refined, or tested as much as the larger pitfall arrays. However, it does catch shrews, and it offers a person who works alone or with limited resources a method of sampling shrews that is not labor-intensive and doesn't require as much space as a large array.

Acknowledgments

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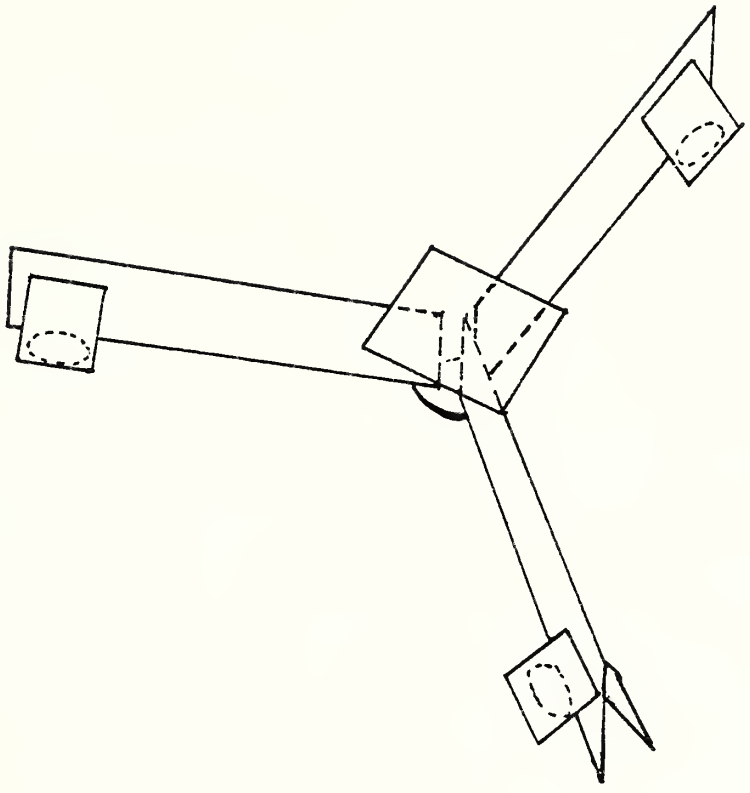

Fig. 1.—Plan for 2.5-m pitfall array, with a 4-liter container in the center and pairs of 2-liter pitfalls near the outer ends of 1.2 m drift fences. Not drawn to scale.

ALBUMIN EVOLUTION IN THE SORICINAE AND ITS IMPLICATIONS FOR THE PHYLOGENETIC HISTORY OF THE SORICIDAE

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ABSTRACT

Results of albumin immunodistance analyses suggest that the Nearctic *Otisorex* and *Sorex trowbridgii* are sister taxa, and Palearctic *Sorex* are more distantly related. The genera *Notiosorex* and *Neomys* are equidistant from the Soricini/Blarinini cluster. Shrews are monophyletic with respect to other Insectivora, although the Croeidurinae and Soricinae diverged soon after shrews diverged from moles. Divergence times estimated from the albumin immunodistance data are eonsiderably older than those estimated from the fossil record, suggesting an Eocene rather than Mioeene divergence of crocidurine and soricine shrews. Shrews, moles, tenrecs/golden moles/hedgehogs, and solenodons represent four relatively equidistant lineages of insectivores that diverged sometime in the late Paleocene or early Eocene.

INTRODUCTION

Living shrews of the family Soricidae are Holarctic and African in distribution, with a few species found in the northern Neotropics and the Orient. Because of their small size and secretive habits, few specimens existed in museums and little phylogenetic work was attempted until very recently. In the last 15 years or so, a virtual explosion of systematic studies has been published on shrews (a summary may be found in the introduction of George [1988] and additional citations in this volume). These new studies, based on allozyme and karyotypic data, reexaminations of fossil series, and morphometric analyses of osteological data, sometimes have yielded conflicting results. Herein we review the phylogenetic conclusions of previous studies, present new results from albumin immunodistance data, and attempt to estimate divergence times for lineages of shrews from these data.

Using albumin immunodistance data, we address four issues in shrew systematics. First, we examine conflicting phylogenetic trees proposed for intrageneric relationships within the genus *Sorex* based on allozymes and morphology, and compare them to the tree generated from the immunodistance data. Allozyme data divide the genus into three major lineages comprising the following species groups (George, 1988): an unnamed subgenus including *Sorex trowbridgii*, *S. merriami*, and *S. arizonae*; the subgenus *Sorex* including Palearctic long-tailed shrews and *S. arcticus* and *S. tundrensis* from the Nearctic; and the subgenus *Otisorex* which consists solely of Nearctic species. These results conflict with previous classifications in several ways, most notably in that the *Sorex trowbridgii* clade had been classified within the subgenus *Sorex* with the Palearctic shrews (Findley, 1955).

Second, we address the question of the phylogeny of tribes within the Soricinae. Allozyme results classified the tribe Neomyini as the sister taxon to the tribes Soricini and Blarinini. However, divergence dates for these taxa could not be calculated from the allozyme data because the data indicated that the genus *Sorex* has a more rapid rate of protein evolution than the other lineages, and the calculation of dates of divergence from genetic distances requires the assumption, or more preferably, the demonstration of roughly equal rates of change among the constituent lineages.

Third, we compare the date of divergence of the Crocidurinae and Soricinae calculated from the immunodistance data to the date estimated from the fossil record. Finally, we examine evolutionary relationships of soricids to other insectivores and mammals, and compare the phylogeny based on immunodistance data to other proposed higher-level mammalian phylogenies.

METHODOLOGY

Following methods described by Sarich (1969) and Maxson and Maxson (1990), antisera to *Sorex vagrans*, *Blarina brevicauda*, *Neomys fodiens*, and *Suncus murinus* albumins were generated in rabbits (*Oryctolagus cunicularis*). For family-level studies, previously prepared antisera to the albumins of *Mogera wogura*, *Scapanus townsendii*, *Condylura cristata* (moles, family Talpidae), *Solenodon paradoxus* (solenodon, family Solenodontidae), *Erinaceus europaeus* (hedgehog, family Erinaceidae), *Eremitalpa granti* (golden mole, family Chrysochloridae), and *Hemicentetes semispinosus* (tenrec, family Tenrecidae) were used. Antisera from a large number of noninsectivores were also available. Additional antigens used were *Sorex palustris*, *S. trowbridgii*, *S. araneus*, *S. caecutiens*, *Cryptotis parva*, and *Notiosorex crawfordii*.

With the exception of a few quantitative precipitin experiments to be discussed below, all the albumin comparisons were carried out by immunodiffusion. This apparently retrogressive decision requires some justification. The several methods (immunodiffusion, quantitative precipitin, microcomplement fixation, radioimmunoassay) that have been used to measure and compare immunological distances among mammalian taxa have long been known to give highly correlated results. In addition, there is much less variation in precision and ultimate phylogenetic resolving power among them than has been thought to be the case. This was demonstrated by the doctoral research of Elizabeth Pierson on higher-taxon (family and above) relationships among bats using immunological comparisons of their transferrins (Pierson,

1986). After preparing antisera, Pierson carried out a series of "preliminary" immunodiffusion comparisons over a few days, then over parts of the next three years she performed micro-complement fixation (MC'F) reactions. The phylogenetic trees resulting from the two data sets were congruent, and little, if any, resolving power was added by the MC'F comparisons. As Pierson wrote (1986:227):

> While immunodiffusion may not offer the quantitation of MC'F, it nevertheless proved to be an extremely useful tool in this study. One of the most striking advantages of the immunodiffusion technique is best illustrated by telling a story. Three years ago when I began the analysis of family level relationships in bats, I spent four days running immunodiffusion experiments to get preliminary indications of results I might get from MC'F comparisons. Upon completion of these first experiments, I sketched the phylogeny suggested by the results. Three years, and many, many MC'F experiments later, the PHYLIP Fitch analysis yielded essentially the same tree. The truly robust MC'F results were equally apparent by immunodiffusion; the taxa that were difficult to place by immunodiffusion also caused problems in MC'F. Thus this quick, and very simple method provided, in general, the same branching order among higher taxa as the much more technically demanding and time consuming MC'F.
>
> There are additional advantages to the Ouchterlony procedure. First, it has greater phylogenetic scope.... Second, MC'F reactions have a very narrow window.... Third, immunodiffusion is an essentially foolproof technique, and will work with samples, like tissue extracts, that can present anti-complementarity problems with the more exacting MC'F procedure....

This is not to say that procedures such as quantitative precipitation, MC'F, and radioimmunoassay do not add resolving power at shorter distances, but we do not believe that they add much at most of the distances with which we are concerned in this study. In addition to these technical advantages, immunodiffusion comparisons have the unique advantage, for molecular data, of being able to be seen through photographs. Thus, it is difficult to consign immunodiffusion data, when presented as actual photographs, to the black box status accorded to immunological data in general. We have added only two technical innovations to the method as originally presented by Goodman (1960). First, the agar gels contained 5% polyethylene glycol (PEG, MW approximately 8000). This markedly increases the strength of more distant reactions, and adds sharpness to the precipitin lines (W. Rainey, personal communication).

Second, we added a fourth component to the usual three, allowing the use of an outgroup in each experiment. For example, to test soricine relationships, we placed, in four wells located clockwise from 12 o'clock, an antiserum to *Sorex* albumin, *Suncus* serum, an antiserum to *Mogera* albumin, and *Solenodon* serum, at appropriate dilutions. *Solenodon* reacts more strongly with anti-*Mogera* than does *Suncus*; with anti-*Sorex*, the two sera react about equally well. Going from an anti-mole reference point to an anti-soricine point, the relative strength of the crocidurine reaction increases, indicating a phylogenetic association between the two shrews. What of the fact that *Solenodon* and *Suncus* react equally with anti-*Sorex*? This is explained by replacing anti-*Mogera* in the pattern with antisera to albumins of other orders such as edentates, whereupon *Solenodon* consistently reacts more strongly than *Suncus*, indicating less change along its albumin lineage. Such arrangements then provide internal rate tests, and, by extension, the phylogenetic relationships of the taxa compared, given one assumption about where the root of the overall tree lies.

The small number of precipitin comparisons (small because of the paucity of shrew material) was conducted using turbidimetric methods. For these comparisons, 0.15 ml of an appropriate antiserum concentration (so that the final optical density at 370 nm and a 1 cm path was < 1.0) was added to each of five tubes containing 0.15 ml of diluted serum (typically, 1:50 in the first tube, 1:100 in the second, and so on). After mixing, the reactions were allowed to equilibrate over 18 hours at 20° C. Isotonic tris-buffered saline (1 ml at pH 7.45) was then added to each tube, the mixture vortexed, and the optical density read in a Zeiss spectrophotometer. Large series of tests have shown that data obtained in this manner are quantitatively equivalent to those obtained using centrifugation and three washings of the precipitate, with final solution in dilute NaOH. The advantage of the turbidimetric procedure lies in its simplicity. Each reduction of 1% in amount of turbidity given in the heterologous, as compared to the homologous, reaction is equivalent to two units of immunological distance (AID).

Results

Within-Sorex *Relationships*

To test alternative hypotheses of subgeneric relationships within *Sorex* (Findley, 1955; George, 1988), antibodies to *Sorex vagrans* were tested against antigens of four species of long-tailed shrews representing the three subgenera, *S. araneus* and *S. caecutiens* (subgenus *Sorex*), *S. palustris* (subgenus *Otisorex*), and *S. trowbridgii* (unnamed subgenus). The allozyme data for these five species (using *Cryptotis parva* and *Notiosorex crawfordii* as outgroups) have indicated (with two synapomorphies) that *Sorex trowbridgii* is the sister taxon to the Palearctic *Sorex* and Nearctic *Otisorex* (Fig. 1a, modified from George, 1988). By contrast, the anti-*Sorex vagrans* albumin comparisons show a slightly stronger reaction with *S. trowbridgii* than with the Palearctic *Sorex* (*araneus* and *caecutiens*; Fig. 1b). The relationship among the three lineages is probably close to a trichotomy. From the immunodiffusion data, we estimate an AID value for the *Sorex vagrans/trowbridgii* branch point of ± 15. Using a calibration of 2.8 AID units per million years (Sarich, 1985), this suggests a divergence time of 5–6 MYBP or latest Miocene. The AID values for *vagrans/araneus* and *vagrans/caecutiens* are in the low 20s, which yields an approximate date for this branch point of 8 MYBP or late Miocene.

The much higher rate of electrophoretic differentiation within *Sorex* compared to other soricines (George, 1986, 1988) makes

it difficult to use those data for any divergence time calculations within the genus. However, divergence must have been younger than the 14 MYBP figure obtained using the standard calibration (George, 1988:453). Thus, our molecular estimates for divergence times among the subgenera of *Sorex* slightly predate the earliest fossils assigned to the genus (5 MYBP, or Miocene/Pliocene boundary; Repenning, 1967; Savage and Russell, 1983). We see no inconsistencies among the three bodies of data, particularly considering that fossil-based dates are necessarily minimum ones, and that the early fossil record of the genus *Sorex* from the Miocene is scant and would benefit from additional paleontological work, especially in Asia (J. Reumer, personal communication).

Soricine Tribal Relationships

The next question to be addressed is tribal relationships within the Soricinae. Albumin immunodistance data were used to test the topology of the tree constructed from allozyme data (Fig. 2a; modified from George, 1986) and to calculate divergence dates for these lineages. Anti-*Sorex* albumin gave, using turbidimetric precipitin comparisons, the following distances: *Blarina brevicauda*, 42; *Neomys fodiens*, 80; *Notiosorex crawfordii*, 88; and *Suncus murinus*, 144. The smaller *Neomys* distance (relative to *Notiosorex*) indicates that the *Sorex/Blarina* lineage and *Neomys* shared a brief period of common ancestry after the divergence of *Notiosorex* (Fig. 2b). This conclusion is also supported by the fact that *Neomys* albumin reacts better with anti-*Blarina* (in immunodiffusion comparisons) than does *Notiosorex* albumin. With anti-*Neomys*, *Sorex* and *Notiosorex* are at the same distances, whereas with the anti-edentate/mole outgroup, *Notiosorex* reacts more strongly than *Sorex*. The Soricini/Blarinini AID value of 42 corresponds to a divergence time of approximately 15 MYBP, or mid-Miocene. For perspective, this is slightly more recent than the divergence of the great apes and Old World monkeys (Sarich and Cronin, 1976). The AID value for the trichotomy is ± 85, which is approximately 30 MYBP or mid-Oligocene.

Repenning (1967), using morphological analysis of living and fossil forms, classified soricines into three tribes: Soricini, Blarinini, and Neomyini. The allozyme data support this three-tribe classification (George, 1986). However, Reumer's (1984) assessment of the fossil evidence suggested that *Notiosorex* and *Neomys* should be classified in separate tribes, the Notiosoricini and Soriculini, respectively. The albumin data are consistent with this latter classification as they place *Neomys* and *Notiosorex* about equidistant from one another and from the soricine/blarinine unit.

Crocidurinae-Soricinae Relationships

Sorex, *Cryptotis*, *Blarina*, *Notiosorex*, *Suncus*, and *Solenodon* albumins were reacted with antisera to the albumins of *Sorex*, *Neomys*, *Mogera*, *Hemicentetes*, *Erinaceus*, *Bradypus* (Xenarthra: Bradypodidae), *Tamandua* (Xenarthra: Myrmecophagidae), and *Cabassous* (Xenarthra: Dasypodidae) in a series of 4-well immunodiffusion reactions. The decrease in the relative distance to *Suncus* when going from nonshrew to shrew comparisons is consistent but not very strongly marked. Thus, the shrews form a monophyletic group, but the distance between the Soricinae and Crocidurinae, relative to those between shrews and nonshrews, is unexpectedly large.

Current interpretations of fossil data place the divergence date of crocidurine and soricine shrews in the early Miocene (Reumer, 1984, 1987, 1989), whereas our data suggest that the divergence took place as early as the Eocene. This conclusion derives from two separate lines of evidence. First, the AID of 144 for this divergence point converts to a time of ± 50 MYBP. Second, soricine-crocidurine albumin cross reactions are only slightly stronger than those between shrews and moles (reactions among the three major mole albumin lineages are also only slightly stronger than those between shrews and moles; D. W. Moore, V. M. Sarich, and T. L. Yates, personal communication). Reactions between shrews and moles are not discernably stronger than those between them and other "insectivores." If shrews and moles are to remain monophyletic units, then the crocidurine-soricine divergence must have followed closely in time the divergence of soricids and talpids, and those among the various "insectivoran" lineages.

Interfamilial Relationships

What about other taxa that have been placed among the insectivores? Most of the pertinent albumin studies have been published, and we briefly review those results. Dermopterans and tupaiids are, in that order, sister groups to the primates (Cronin and Sarich, 1980). Macroscelids align with lagomorphs, and the data indicate that the two groups of elephant shrews, pikas, and rabbits/hares, comprise four lineages that are essentially equidistant from one another (Sarich, 1985).

What are the relationships among the remaining insectivoran taxa? A few conclusions may be drawn from existing data (see previous section for a list of sera and anti-sera compared). Golden moles, represented by *Eremitalpa*, join strongly with tenrecs (*Hemicentetes*), and the resulting clade then joins with hedgehogs (*Erinaceus*). These three taxa may be slightly closer to *Solenodon* than to the shrews and moles, but it is a weak grouping, based on the reactions observed.

Conservatively, with dermopterans and tupaiids placed with primates and macroscelids with lagomorphs, four relatively equidistant "insectivoran" lineages remain: shrews; moles; *Solenodon*; and tenrecs/golden moles/hedgehogs (Sarich, 1993). These four lineages are no closer to one another than they are to the other probable members of one of the two major groups of mammals: lagomorphs/macroscelids, primates, bats, rodents and carnivores/pangolins (ungulates and subungulates making up the other major group of mammals). These probably represent old lineages that had begun diverging sometime in the Paleocene, and finished in the early Eocene.

This lack of precise resolution might be taken as indicative of a basic weakness of the molecular approach. We believe this is an unrealistic conclusion. Quoting Sarich (1985:433):

> ...only three extant orders can be shown in the Paleocene, and it is not clear that for any of these (primates, carnivores, rodents) can the Paleocene lineages

> be associated with extant ones. The real beginnings of diversification leading to extant intra-ordinal lineages would then appear to be no earlier than late Paleocene and early Eocene, and indeed most orders do not even appear in the fossil record until the Eocene.... If the picture just sketched is in fact realistic, it also goes a long way toward answering the question of why it has proved so difficult to determine interordinal affinities among the placentals—to, for example, determine the sister group to rodents. If we are now only allowing some 10 MY to proceed from the adaptive radiation which gave rise to placental orders to the late Paleocene to early Eocene interordinal radiations, then any periods of common ancestry among extant orders are going to be rather brief indeed, and one might argue that we are fortunate to be able to see any, and not worry about our inability to see more. This may be one of those questions that doesn't have accessible answers; the answers (shared, derived characters linking orders) having been destroyed or distorted beyond recognition over time.

A quantitative assessment of this point was made by Nei (1986:134–139), wherein he calculated how much DNA sequence was necessary to resolve, to a given level of confidence, a lineage of length *Y*MY at a time depth of *Z*MY. For $Y = 5$ and $Z = 50$ (time spans appropriate to the relationships involved here), 4,100 base pairs of DNA sequence are needed to achieve resolution at a 95% confidence level. In other molecular studies of higher-order relationships within the Mammalia, few authors have included more than one lipotyphlan insectivore taxon, and none has looked at as many taxa as we have. Therefore, there are difficulties in developing comparisons of our results with those of others. Amino acid sequence data (mainly globins) have been used to argue for a soricid/erinaceid unit which links to talpids (Miyamoto and Goodman, 1986). Those results are at variance with this study and also with morphological data (McKenna, 1975). Miyamoto and Goodman's (1986) conclusion is equivocal because they had only two sequences for the shrew and mole, although their methodology required at least three. Miyamoto and Goodman (1986) and Shoshani et al. (1985) also suggested a shrew/mole/hedgehog unit as a sister group to carnivores and pangolins. Finally, Shoshani's (1986) immunodiffusion data produced some dubious groupings: hedgehogs with bats, primates, and tupaiids; tenrecs and shrews; edentates and lagomorphs. These results show little congruence with other morphological or molecular data and none with ours.

Conclusions

We believe that the problem with congruence lies in a lack of appropriate and extensive rate-testing such as that discussed in the methodology section. That judgment should not be accepted as suggesting that we have never read too much into our data. However, we have tried to be conservative in claims here.

For clearer patterns of relationships to be discerned, future work must sample greater numbers of taxa and, if the primate data are instructive (Nei, 1986), examine thousands of DNA base pairs from each taxon.

Acknowledgments

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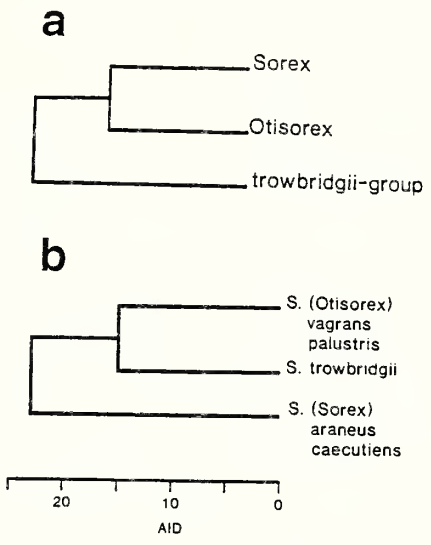

Fig. 1.—Relationships of three subgenera of *Sorex*. a, Tree based on allozymic data (George, 1988). b, Tree based on albumin immunodistance (AID) data from quantitative precipitin comparisons.

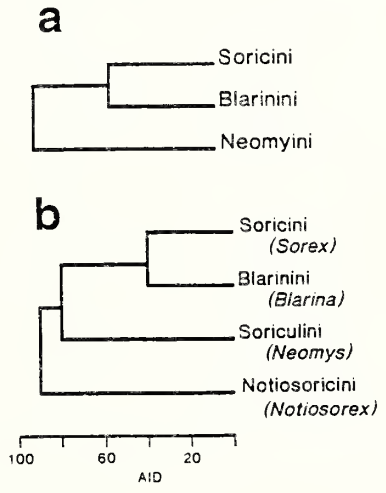

Fig. 2.—Phylogeny of soricine shrews. a, Tree based on allozymic data (George, 1986). b, Tree based on albumin immunodistance (AID) data from quantitative precipitin comparisons.

THE *SOREX* OF THE *ARANEUS-ARCTICUS* GROUP (MAMMALIA: SORICIDAE): DO THEY ACTUALLY SPECIATE?

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ABSTRACT

In shrews of the *Sorex araneus-arcticus* group, the efficiency with which Robertsonian fusions can induce genetic isolation between chromosomal races seems to be linked to the size of the chromosome arms involved as well as to the level of geographic fragmentation of suitable habitats. Only those populations differentiated by incompatible fusions of the longest autosomic arms have reached complete reproductive isolation. Some data suggest that ecological differentiation could be initiated afterwards by competition between the new species.

INTRODUCTION

The *Sorex araneus-arcticus* group is composed of eight species (Table 1) characterized by a common XX-XY_1Y_2 sex chromosome system (bibliography compiled by Reumer and Meylan, 1986; see also Ivanitskaya et al., 1986; Volobouev and van Zyll de Jong, 1988; Wójcik and Searle, 1988). Although they have different karyotypes, they are closely related species. Chromosomal phylogenies and mechanisms responsible for the chromosomal evolution of this group have been suggested (Searle, 1984; Hausser et al., 1985; Halkka et al., 1987; Volobouev, 1989). The main mechanisms advocated are Robertsonian fusion, centromeric shift, and tandem fusion, the first being particularly important in the European species. The karyotype of the Iberian species, *S. granarius*, which is all acrocentric except for the sex chromosomes and a small polymorphic metacentric (*2Na* = 34, *NFa* = 34–36), is considered to represent the ancestral condition (Wójcik and Searle, 1988; Volobouev, 1989; and Volobouev and Catzeflis, 1989).

Chromosomal polymorphism has been found in many species of the *araneus-arcticus* group: *S. daphaenodon* and *S. tundrensis* (Ivanitskaya and Malygin, 1983; Ivanitskaya et al., 1986), *S. arcticus* (Volobouev and van Zyll de Jong, 1988), and especially *S. araneus*, where 12 chromosome arms are involved in an impressive Robertsonian polymorphism, leading to more than 20 karyotypic races each characterized by distinctive metacentric sets. The exact number of races is still difficult to assess because a clear definition of a karyotypic race is lacking. This polymorphism has been thoroughly studied by numerous authors; the most recent review is by Zima et al. (1988).

Robertsonian fusions are thought to be the primary mechanism of this karyotypic differentiation. Attempts have been made on this basis to retrace the evolution of these karyotypic races (Searle, 1984, 1988). Nevertheless, some authors consider that the inverse mechanism of fissions or reciprocal translocations also plays an important part in chromosomal evolution of this species (Halkka et al., 1987).

The *S. araneus-arcticus* group may be involved in a continuous speciation process driven by chromosome rearrangements (Hausser et al., 1985), considering the existence of closely related species and the intraspecific chromosomal polymorphism in the most widely distributed species. However, in a recent review, Bengtsson and Frykman (1990) strongly contested the idea that such simple chromosome mutations as Robertsonian fusions play a major part in speciation. Considering the evidence for selection against genetic isolation of karyotypic races of *S. araneus* in hybrid zones (Fedyk, 1986; Searle 1986*a*; abstracts of unpublished papers of the international meeting "The Population and Evolutionary Cytogenetics of *Sorex araneus*," Oxford, England, August 29–31, 1987, which will be referred here as "in litt."), they suggested that, presently, these races are not undergoing speciation, but rather a "de-speciation" process which increases gene flow between chromosome races. The aim of this work is to mitigate these conclusions, which in my view do not account for the variety of situations encountered.

THE SIZE OF THE ROBERTSONIAN METACENTRICS

The difference among karyotypic races of *S. araneus* is due to Robertsonian fusions of primitive acrocentric chromosomes which correspond, with minor modifications (two centromeric shifts), to those of *S. granarius*. These arms or acrocentric chromosomes are labelled according to the usual letter nomenclature for *S. araneus* first proposed by Halkka et al. (1974) and (unwillingly) modified by Fredga and Nawrin (1977). In this nomenclature, arms are ordered according to their size, *a* being the largest, *u* the smallest (Fig. 1).

Robertsonian polymorphism in *S. araneus* involves every arm from *g* to *r*. Robertsonian fusions are also responsible for a large part of the karyotypic difference between *S. araneus* and its sibling species *S. coronatus*, in addition to two centromeric shifts on the chromosome arms *b* and *f* (Volobouev and Catzeflis, 1989).

Zima et al. (1988) first demonstrated that fusions of arms *g* to *r* do not occur at random in *Sorex araneus*. Their demonstration can be extended to the 15 acrocentric autosomes of *S. granarius*, which show fusions in *S. coronatus* and *S. araneus*. These autosomes can be ordered by size and grouped into three arbitrarily delimited categories: long (*a* to *f*), medium (*g* to *l*), and short (*m* to *q*). Documented fusions in which the longer arm belongs to each of those categories are listed in Fig. 2.

Fusions involving long arms are few compared to their possible number (3/54). This does not mean that long arms fuse

infrequently or with difficulty, but merely reflects self-limitation of the process (Zima et al., 1988). In *S. araneus* and *S. coronatus*, the large metacentrics are spread everywhere and the autosomic arms *a* to *f* are never found in an acrocentric state; the metacentric *af* is common to both species, whereas *bc* is species-specific for *S. araneus* and *ci* is species-specific for *S. coronatus*. Where long arms are fused into metacentrics, they can no longer contribute to new fusions. If fission or reciprocal translocation were generally tolerated in these species, as suggested by Halkka et al. (1987), other combinations of the long arms should be observed.

In contrast to fusions involving long arms, almost every possible fusion involving the short arms was found (14/15). However, in populations of *S. araneus*, these arms frequently remain unfused, or show a high level of intrapopulation Robertsonian polymorphism. These polymorphisms usually characterize local races, e.g., the three such races described for Great Britain (Searle, 1984, 1988).

The medium-sized metacentrics present an intermediate situation; 25 of 51 possible fusions are documented. Those involving relatively long arms are distributed through large groups of populations. For example, *gm* and *hi* are found everywhere in the west European phylogenetic group of karyotypic races (WEPG; Searle, 1984). These occur from the northern slope of the Alps to central Sweden and from Great Britain to Poland, and *jl* occurs in all known populations except in the Valais race (southern Alps and Italy).

Why Have Robertsonian Metacentrics Spread?

The pattern of geographic distribution of metacentric chromosomes suggests that Robertsonian fusions of long arms occurred earlier, or were more successful, than fusions of short arms. It is commonly believed that Robertsonian heterozygotes should have a disadvantage due to increased frequency of nondisjunction at meiosis. They would suffer from partial sterility, which would seriously thwart expansion of metacentrics. Most models of chromosome evolution advocate small demes and inbreeding to explain the initial success of Robertsonian metacentrics (see for example Capanna, 1980, for the superficially similar case of Robertsonian evolution in *Mus domesticus*). In *Sorex araneus*, wherein neither inbreeding nor small isolated demes are likely to occur (Hausser et al., 1985; Bengtsson and Frykman, 1990), meiotic drive, together with high fertility of simple Robertsonian heterozygotes (Garagna et al., 1989), is practically the only mechanism that can account for the success of the metacentrics. Searle (1986*b*) provided support for such a process. Unfortunately, as pointed out by Bengtsson and Frykman (1990), his conclusions rest partially on reconstruction of the male karyotype by comparing karyotypes of females with those of their offspring, and are undermined by his own discovery of multiple paternity in common shrew litters (Searle, 1990). Even though it needs further confirmation, the meiotic drive hypothesis remains the most likely one. Hedrick (1981) demonstrated that even a very weak meiotic drive can have spectacular effects. In *S. araneus*, the link between the size of the metacentrics and their success strengthens the idea that a "mechanical" meiotic process is involved rather than some external selection pressure. Therefore, I suggest that meiotic drive efficiency is dependent to some extent on the size of the fused arms. This hypothesis needs to be tested by crossing heterozygotes for metacentrics of various sizes with homozygotes for the corresponding chromosomes.

Hybrid Zones and Contact Zones

Bengtsson and Frykman (1990) emphasized that selection in hybrid zones between metacentrics increases gene flow rather than increasing genetic isolation. The best documented example of this process is the contact zone between the Oxford race and the Hermitage race in England (Searle, 1986*a*). Both races belong to the WEPG, characterized by the *gm*, *hi*, and *jl* metacentrics (Searle, 1984). Characteristics for the Oxford race are the metacentrics *kq*, *no*, and *pr*, whereas the Hermitage race carries the metacentric *ko*. Metacentric *pr*, elements of which are acrocentric in the Hermitage race, seems to spread relatively freely throughout the 30-km wide hybrid zone, and a sharp decrease of other metacentrics is observed. Also, an increase of the so-called monobrachial hybrids (e.g., *ko–kq*) and of the corresponding acrocentric chromosomes *k*, *n*, *o*, and *q* characterizes populations at the center of the hybrid zone. In this case, the acrocentric state is selected for, because of compatibility with both chromosome races, whereas monobrachial hybrids apparently suffer severe loss of fertility. Thus, a tension zone is maintained wherein polymorphism allows genetic flow between karyotypic races.

In northern Poland (Fedyk, 1986; Fedyk and Leniec, 1987), Sweden (K. Fredga, in litt., 1987), and Finland (Halkka et al., 1987), the contact zones involve metacentrics of different phylogenetic groups, which are defined by different fusions of medium-sized arms. In these cases, "hybrid races" frequently occur between the main phylogenetic groups. These "races" can show a mixture of compatible metacentrics issuing from each phylogenetic group. For example, the northern race of Sweden has both *gm*, which is characteristic of the WEPG, and *hn*, which originated in the east European phylogenetic group, EEPG (Fredga and Nawrin, 1977). This pattern suggests an independent pace of spread of metacentrics, which may be linked to their size. Additionally, "hybrid races" frequently carry local fusions which could have developed through hybridization (S. Fedyk, in litt., 1987). For example, a local race in northeastern Poland shows the metacentric *hk*, whereas the EEPG and WEPG carry *ik* and *hi* (Wójcik, 1986).

These "hybrid races" could act as buffers and decrease the level of difference between forms in direct contact. The contact zones between such forms are sometimes, but not always, characterized by increase in acrocentric frequencies, which suggests the maintenance of genetic flow (Fedyk, 1986). A cline in allele frequencies of MPI through the hybrid zone between northern and central races in Sweden supports this hypothesis (Frykman and Bengtsson, 1984; Bengtsson and Frykman, 1990). Although a very complex structure of hybrid races developed between WEPG and EEPG in northeastern Poland together with an increase in the frequency of acrocentrics, these groups are in direct contact in eastern and southeastern Poland where they show a very narrow contact zone. Interracial

monobrachial hybrids have been found at only one locality, and increase in frequency of the concerned acrocentrics was not observed (J. Wójcik, in litt., 1987). Thus, the "de-speciation" process may be less general than postulated by Bengtsson and Frykman (1990).

Contact Zones in the Alps

The situation in the Alps is schematized in Fig. 3. A succession of karyotypic forms of *S. araneus* is found along the northern slope of the Alps. In the north, the Vaud race occurs as a typical race of WEPG, with metacentrics *gm*, *hi*, *jl*, *kr*, and *no*. In the south, the so-called "Acrocentric" form occurs, where all the arms *g* to *r* are present as acrocentric chromosomes. These populations are nevertheless polymorphic for the metacentric *jl*, which was discovered after their name was given. Between the Rhone and the Arve valleys, intermediate "Vaud-Acrocentric" populations occur, in which *gm* is always present, *no* always absent, and *hi*, *jl*, and *kr* are polymorphic. These three forms are mutually isolated by the presence of *S. coronatus* in the lowest parts of the Rhone and Arve valleys. South of the Bernese Alps, another race is found, the Valais race, characterized by the metacentrics *gi*, *hi*, *kn*, and *lo* (Hausser et al., 1986). Contact zones have been found between the Valais and Vaud races and between the Valais race and the Acrocentric form (Hausser et al., 1991).

These contact zones are different from the Oxford-Hermitage hybrid zone in that they are extremely narrow (less than one kilometer; sympatry was found at only one locality in each case). No hybrids were found either in the vicinity of the Acrocentric-Valais contact zone (25 individuals caught on a transect of about five km) or between Vaud and Valais races (13 individuals on a similar transect; Fig. 4). The arms *g*, *h*, *i*, and *k*, which are implied in metacentrics with monobrachial homologies in the Vaud and Valais races, were never found in an acrocentric condition in any individual of these races.

Although samples are small, two comparisons can be made. First, the Intermediate Vaud-Acrocentric populations occupy an area about 40 km wide between the two parental forms (with 15 individuals out of 24 analyzed being heterozygotes for at least one Vaud metacentric), whereas Valais-Acrocentric intermediates have never been identified. Even if this zone has been accidentally widened by recent isolation of parental forms by *S. coronatus*, the contrast with the Valais-Acrocentric contact zone is striking. Secondly, in the Oxford-Hermitage hybridization zone, the frequency of monobrachial hybrids reaches 10% in the middle of the zone (which is approximately 30 km wide), whereas the frequency of acrocentrics *k* and *o* (arms involved in these monobrachial hybrids) reaches 80% in the same populations. If hybridization occurred, such a pattern should have been detected in the Vaud-Valais contact zone even in a very small sample, because the meiotic problems encountered by monobrachial hybrids are far more severe. A hypothetical hybrid between Vaud and Valais would face in meiosis at worst a multivalent of 11 elements at meiotic metaphase 1, and at best (accounting for the known polymorphic elements of each race), a tetravalent and a multivalent of seven elements (Hausser et al., 1986). By comparison, the monobrachial hybrids between Oxford and Hermitage races only face a tetravalent or a pentavalent, which still is sufficient to induce selection against metacentrics (Searle, 1988).

Thus, these very sharp replacements of one form by another strongly suggest genetic isolation. To test this hypothesis, Taberlet et al. (1991) examined a partial sequence (*279 bp*) of mtDNA (Cytochrome *b*) for 11 individuals of the various taxa found in the western Alps, especially near known or postulated contact zones (numbered localities in Fig. 3). The preliminary results are shown in Fig. 5. Individuals of the Acrocentric, Intermediate, and Vaud karyotypic forms belong to the same clone, along with two Valais individuals of Les Houches near Chamonix (locality 1, Fig. 3). The other Valais individuals, especially those collected near the contact zones with the Vaud race (localities 2 and 3, Fig. 3) belong to another well-differentiated clone. The most parsimonious interpretation of these data is that Valais metacentrics were able to cross the mtDNA clone boundary near Chamonix, where they did not encounter incompatible metacentrics. Congruence between the clone boundary and the karyotypic race limit in the Vaud-Valais contact zones, on the other hand, strengthens the hypothesis of genetic isolation of these races.

The Vaud and Acrocentric populations are not genetically differentiated, as shown by the electrophoretic analysis of 30 loci (Fig. 6; Hausser et al., 1991). Hence, the only difference between the two types of contact zones is the presence of metacentrics with monobrachial homologies in one and not in the other. The chromosome arms involved in the Vaud-Valais differentiation (*g*, *h*, *i*, *j*, *k*, *l*, *n*, *o*) not only are more numerous than the ones implied in the Oxford-Hermitage hybrid zone (*k*, *n*, *o*, *q*), but also include longer elements. These contrasting situations suggest that the size of the fused arms can influence the structure of the contact zone. However, some long elements are involved in the contact zones detected in northern Sweden and in Poland, where genetic exchanges are likely to occur through local "hybrid" races. This apparent contradiction needs to be resolved.

The Role of Geographic Barriers and Filters

The key is in the presence, in northern Europe, of acrocentric chromosomes corresponding to the metacentrics with monobrachial homology in the involved races. These Robertsonian events are recent. Their present incompleteness and the existence of the Acrocentric form suggest that the population that first recolonized northern and central Europe after the last glaciation has mostly acrocentric karyotypes. I suggest that in northern Europe contact between carriers of incompatible metacentrics occurred in highly polymorphic populations, whereas in Switzerland and in southeastern Poland the present metacentric configurations were fully established before contact of the different races.

The sharpness of the Valais-Acrocentric border supports this hypothesis. Despite this clearcut replacement of one form by the other, genetic exchange is attested by the presence of Valais metacentrics on a Vaud-Acrocentric mtDNA substrate. This apparent contradiction is easily resolved if one assumes that

each of the Valais metacentrics has progressed independently into the Acrocentric population through a broad polymorphic "front" similar to the present Vaud-Acrocentric intermediate zone. After glaciation, the upper Arve valley was frequently cut and reopened by extensions and regressions of glacier tongues from Mont Blanc. Temporary isolation would have cut the hypothetical Valais-Acrocentric intermediates from their Acrocentric relatives for a time long enough to allow Valais metacentrics to accumulate and reach a homozygous state (except for *lo*, which is still polymorphic in every Valais population).

Presently, the polymorphic front no longer exists, and the border between the two forms is maintained by a swiftly flowing river, the Torrent des Griaz, that originates from a glacier two km above the trapping area. The torrent presents a 100-m-wide stony and sandy bed, which is almost abiotic due to frequent bursts of water, ice, and mud, which is probably unattractive for shrews and thus rarely crossed by them. Thus, hybrids should be rare. Because they should present a quadruple Robertsonian heterozygosity and, for some of them, even a monobrachial homology (*jl–lo*), hybrids also should have reduced fertility. Nevertheless, one Valais individual was found on the "wrong" side of the river. Such crossings may eventually induce a new polymorphic zone, and the Valais metacentrics may further introgress into acrocentric populations.

This situation indicates that strong geographical barriers such as the Bernese Alps, which have existed for a long time between the Vaud and Valais races, are not a prerequisite for a metacentric to reach homozygosity in a local population. Geographic filters, such as rivers or rocky cliffs, seem to be sufficient to ensure quick elimination of the corresponding acrocentrics. This process, which can be helped by local extinctions and recolonizations (Lande, 1985), is more likely if concerned metacentrics originated from the fusion of large arms which should be, as suggested above, strongly favored by meiotic drive. Geographic filters also help to coordinate the progression of various metacentrics differentially advantaged by meiotic drive. Thus, they may contribute to sharpening the boundary between contiguous races, which eventually leads to complete genetic isolation. The different behavior of metacentrics in the Alps compared to northern Europe may therefore be attributed to the stronger partitioning of habitats in the former region.

Unquestionable evidence for the absence of hybrids between the Vaud and Valais karyotypic races of *Sorex araneus* is lacking. Our knowledge of the contact zones between *S. araneus* Vaud race and *S. coronatus* is far better. In that case, the lack of hybrids is well substantiated in the large sample analyzed from contact zones (331 individuals; Neet and Hausser, 1989). Thus, true specific status exists between these two forms. A prezygotic barrier presumably was developed (Neet and Hausser, 1989). It is very difficult in this case to decide which geographic barrier led to the independent differentiation of *S. coronatus*. Based on its present distribution, the species should have originated in southwestern France or in northwestern Spain (Hausser, 1978). As the Pyrenean glaciers never completely separated France from northwestern Spain during the Pleistocene (Nilsson, 1983), and as *S. coronatus* is not isolated from the diverse chromosomal races of *S. araneus* in biochemical phylogenies (Catzeflis, 1984), it is difficult to advocate a long geographical isolation to explain this speciation. What remains is a set of specific Robertsonian fusions, involving some of the longer arms, and some other chromosomal mutations.

Non-Robertsonian Mutations

Sorex coronatus is chromosomally distinguished not only by seven Robertsonian fusions, but also by two centromeric shifts (Volobouev and Catzeflis, 1989) and differences in the nuclear organizing regions (NORs; Olert and Schmid, 1978). The question remains whether these non-Robertsonian mutations are the threshold between mere intraspecific polymorphism and full speciation?

For the centromeric shifts, the answer is definitely no: in *Sorex araneus*, a small secondary arm occurs on the *j* acrocentric chromosome when it is not fused into *jl* metacentric (Fig. 7a). A centromeric shift seems the best interpretation for this observation, also made in England (Searle, personal communication), but not in the intermediate Vaud-Acrocentric or in the Acrocentric populations (Fig. 7b). Since such a centromeric-shift polymorphism is widely tolerated in populations, it is surely no more efficient than Robertsonian fusions as an isolating mechanism. The data on the NORs of *S. coronatus* were obtained from one male. Halkka and Söderlund (1987) demonstrated that four to six of the eight potential NORs of *S. araneus* were randomly activated in individuals from Finland. Even if the difference in localization of NORs of each species is clear, it is premature to assume that it should have a negative effect on hybrid survival or fertility. *Sorex tundrensis* seems to have NORs similar to those of both *S. araneus* and *S. coronatus* (Ivanitskaya, 1989). Thus, it is hazardous to assign different importance to various types of chromosome mutations in speciation processes. Because Robertsonian fusions are still responsible for the most numerous differences between *S. araneus* and *S. coronatus*, the karyologic differentiation between these species is, in my view, of the same nature as the karyotype differentiations among karyotypic races of *S. araneus*. But, again, it involves longer metacentrics which should have been strongly favored by meiotic drive.

Ecology

From a strictly genetic point of view, the speciation of *S. araneus* and *S. coronatus*, and perhaps of *S. araneus* Vaud and Valais, is achieved with reproductive isolation. Unlike species which evolved through geographical isolation, they are poorly differentiated genetically (Catzeflis, 1984). Additionally, it has been shown that variation in mandible measurements, which provide the only way to distinguish these species morphologically (Hausser and Jammot, 1974), is correlated primarily with the habitat of these shrews. Thus, most of the morphological differentiation between *S. araneus* and *S. coronatus* is a by-product of their parapatric distribution (Hausser, 1984). Neet (1989*a*) found that the interspecific

morphological difference is greater between allopatric populations than in contact zones, wherein interspecific territoriality occurs. The contact zones studied consisted of a mosaic of individual territories occupied by one or the other species (Neet, 1989*b*). These data strengthen the idea that both species exploit the same ecological niche. Such pairs of species in competition should not expect a long future because slight climatic modification may be sufficient to end the equilibrium and lead one of them to extinction. Indeed, *S. coronatus* seems to be expanding at the expense of *S. araneus* (Hausser, 1978).

Some slight ecological differences in microhabitat utilization were nevertheless noted in the contact zones studied, with *S. coronatus* living in significantly drier places (Fig. 8; Neet and Hausser, 1990). This differentiation may be maintained by competition pressure. In removal experiments, the remaining species quickly exploited all available habitats and significant differences were lost. In such a situation, selection should favor increasing ecological differentiation. The presence of sympatric species of the *araneus-arcticus* group in Siberia (Luk'yanova and Rafkin, 1974) suggests that this process occurred in previous stages of diversification of this group.

Conclusions

In the *Sorex araneus-arcticus* group, a succession of relationships between taxa differentiated primarily by Robertsonian fusions was observed. These fusions lead to the meeting of chromosome races bearing incompatible metacentrics (monobrachial homologies). When these incompatible metacentrics are small or few, and the corresponding acrocentrics are still present, selection acts against metacentrics and the resulting tension polymorphism allows genetic flow through the hybrid zone. When some of the incompatible metacentrics are medium-sized, genetic flow occurs in some homogenous and continuous habitats, whereas it seems to be interrupted in strongly partitioned habitats like the Alps. When metacentrics are composed of the longer arms, genetic flow is interrupted, although genetic and ecological differentiation is incomplete in the European species of this group. Thus, the combination of chromosome size-dependent meiotic drive and efficiency of geographic filters leads to a variety of situations, including true speciation.

Acknowledgments

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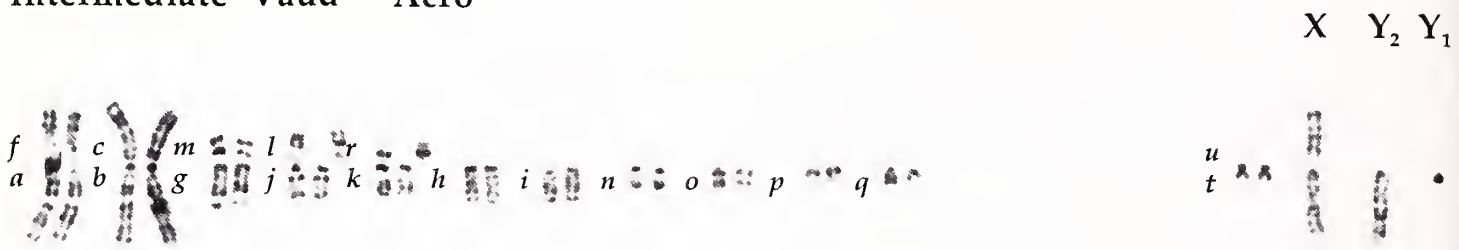
Table 1.—Species of the *Sorex araneus-arcticus* group, their karyotypes and distributions. *2Na*: diploid autosomic number; *NFa*: autosomic fundamental number. These species bear similar X Y_1 Y_2 sex chromosomes. These data were compiled from various sources cited in Reumer and Meylan (1986). The geographic distribution follows van Zyll de Jong (1983) and Dolgov (1985).

Species	*2Na*	*NFa*	Distribution	First Description of Karyotype
Sorex araneus	18–30	36	Pyrenees to Lake Baikal	Sharman, 1956
Sorex arcticus	26	34	Yukon to Newfoundland	Meylan, 1968
Sorex asper	30	52	E. Kazakhstan to W. Sinkiang	Ivanitskaya and Kozlowsky, 1983
Sorex caucasicus	22	42	Northern Turkey, Caucasus	Kozlowsky, 1973
Sorex coronatus	20	40	Northern Spain to Germany	Bovey, 1948
Sorex daphaenodon	24–26	42	Urals to Kamchatka	Fedyk and Ivanitskaya, 1972
Sorex granarius	34	34–36	Western Spain, Portugal	Hausser et al., 1975
Sorex tundrensis	30–34	52–56	Urals to N.W. Canada	Kozlowsky, 1971

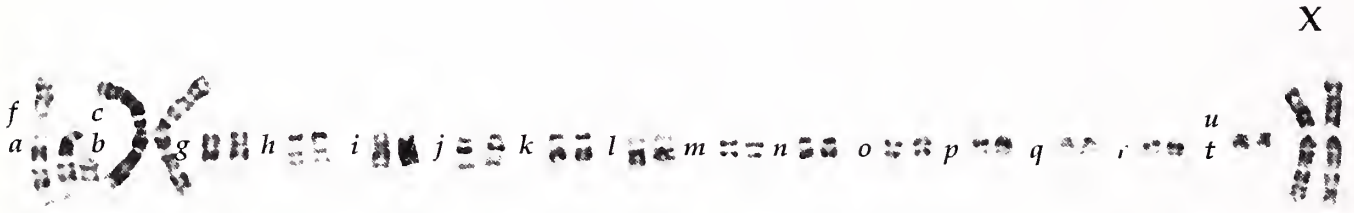
Sorex araneus

Vaud

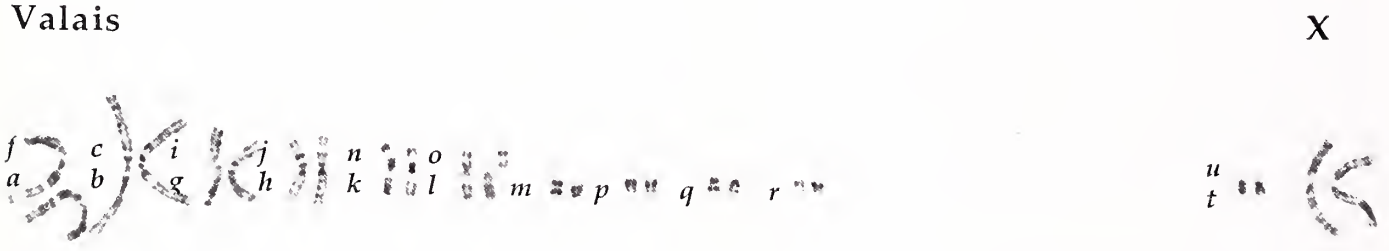
Intermediate Vaud - Acro



Acrocentric form



Valais



Sorex coronatus

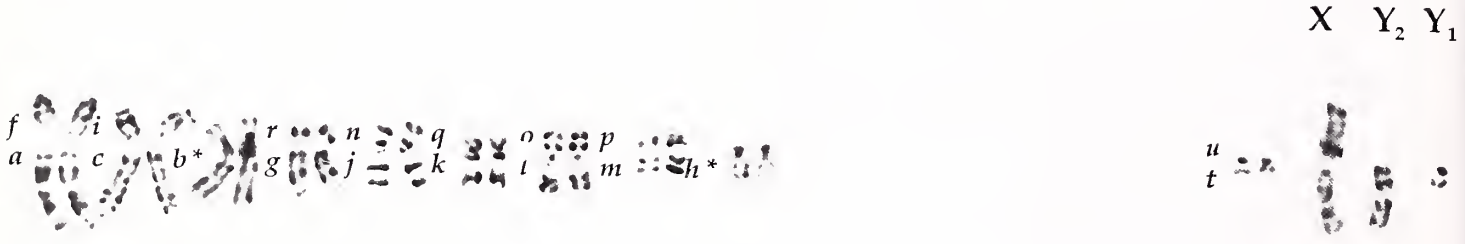


Fig. 1.—Karyotypes of the species, chromosomal races, and forms of the *Sorex araneus* group in the western Alps. Nomenclature of the arms after Fredga and Nawrin, 1977. Asterisks: centromeric shifts in *Sorex coronatus*. Intermediate Vaud-Acrocentric are polymorphic for metacentrics *jl*, *hi*, and *kr*. The acrocentric form is polymorphic for the metacentric *jl*.

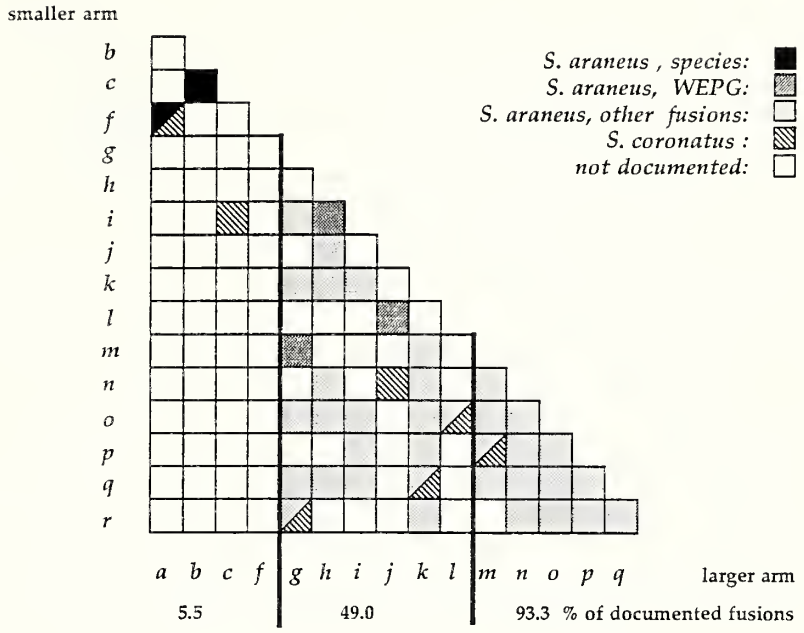


Fig. 2.—Theoretical and observed autosomic Robertsonian fusions in *Sorex araneus* and *S. coronatus*. A primitive acrocentric karyotype similar to that of *S. granarius* is postulated. WEPG: Western European Phylogenetic Group.

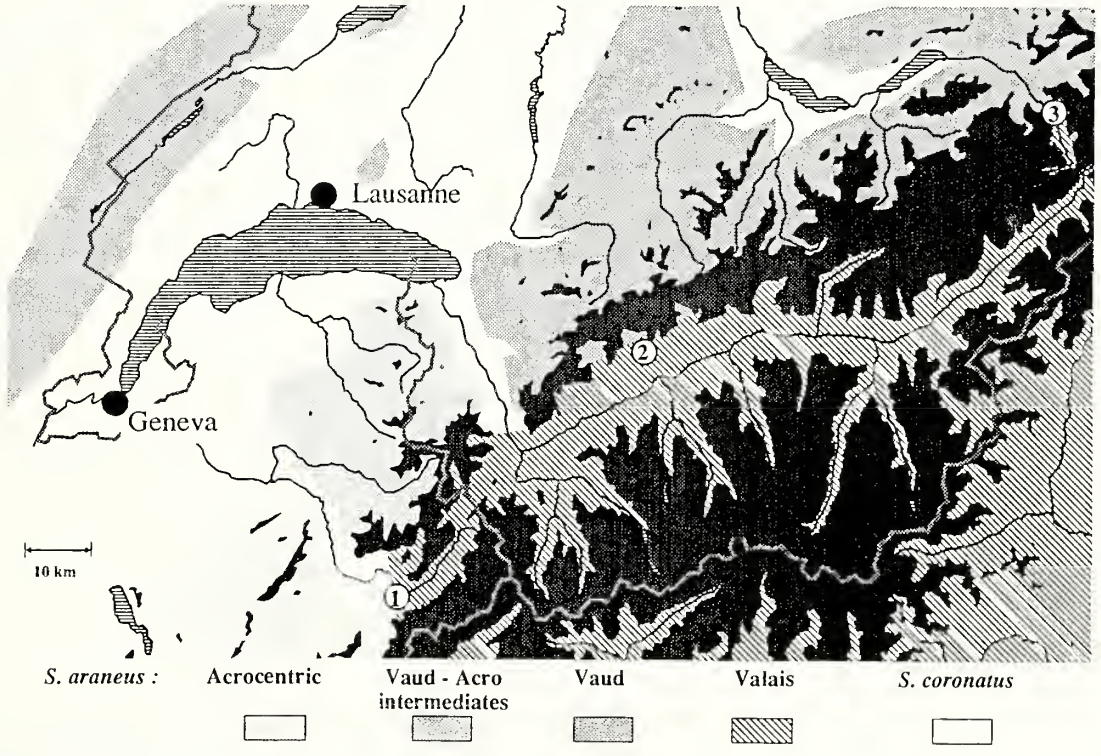


Fig. 3.—Distribution of the species, chromosomal races, and forms of the *Sorex araneus* group in the western Alps. For karyotypes, see Fig. 1. The numbered localities correspond to hypothetized (2) or known (1 and 3) contact zones. Black: above 2000 m; this area is only partially exploited by shrews (up to 2400–2800 m).

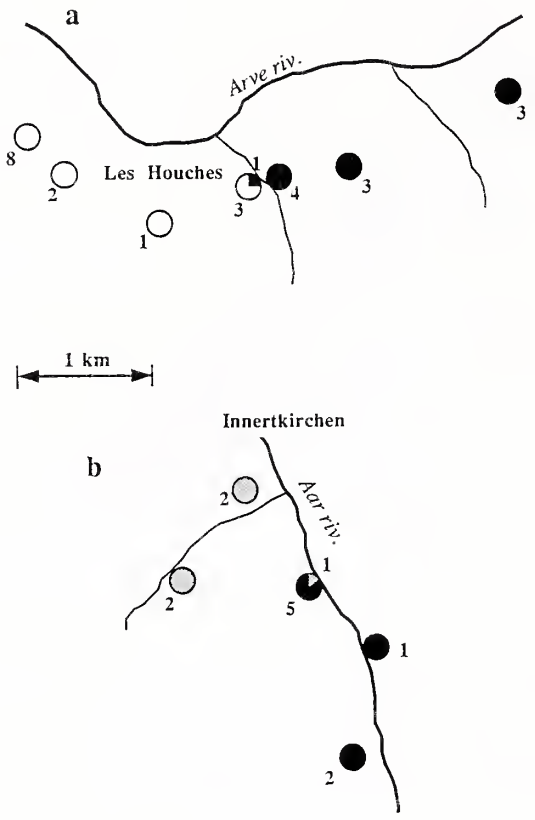


Fig. 4.—Contact zones between the Valais race (black circles) and the Acrocentric form (white circles) of *Sorex araneus* (a) and between the Valais race and the Vaud race (grey circles) of the same species (b). The numbers of karyotypically analyzed individuals are shown. These drawings correspond to localities 1 and 3 on Fig. 3.

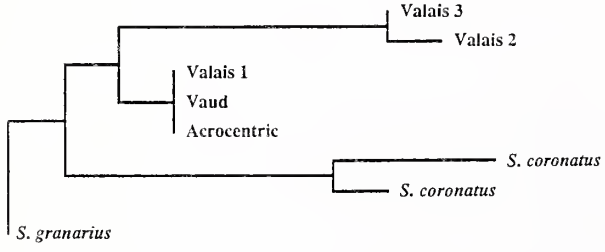


Fig. 5.—Most parsimonious phylogenetic tree obtained by comparison of partial sequences of mtDNA (cytochrome *b*) clones (Fitch parsimony). The length of branches is proportional to the number of substitutions. The tree was rooted with *S. granarius* as the ancestral species. The numbers for the Valais populations correspond to the numbered localities on Fig. 3. After Taberlet et al. (1991).

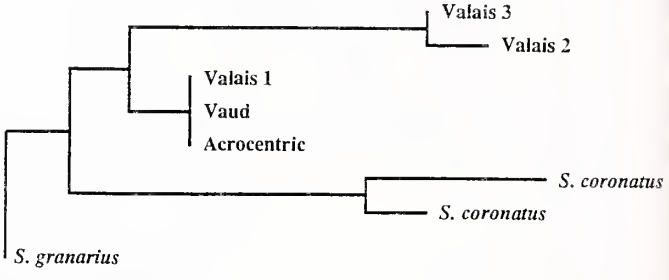


Fig.-6.—UPGMA dendrogram computed from electrophoretic data (30 loci, 88 individuals) of the chromosomal forms presented in Fig. 1. After Hausser et al. (1991).

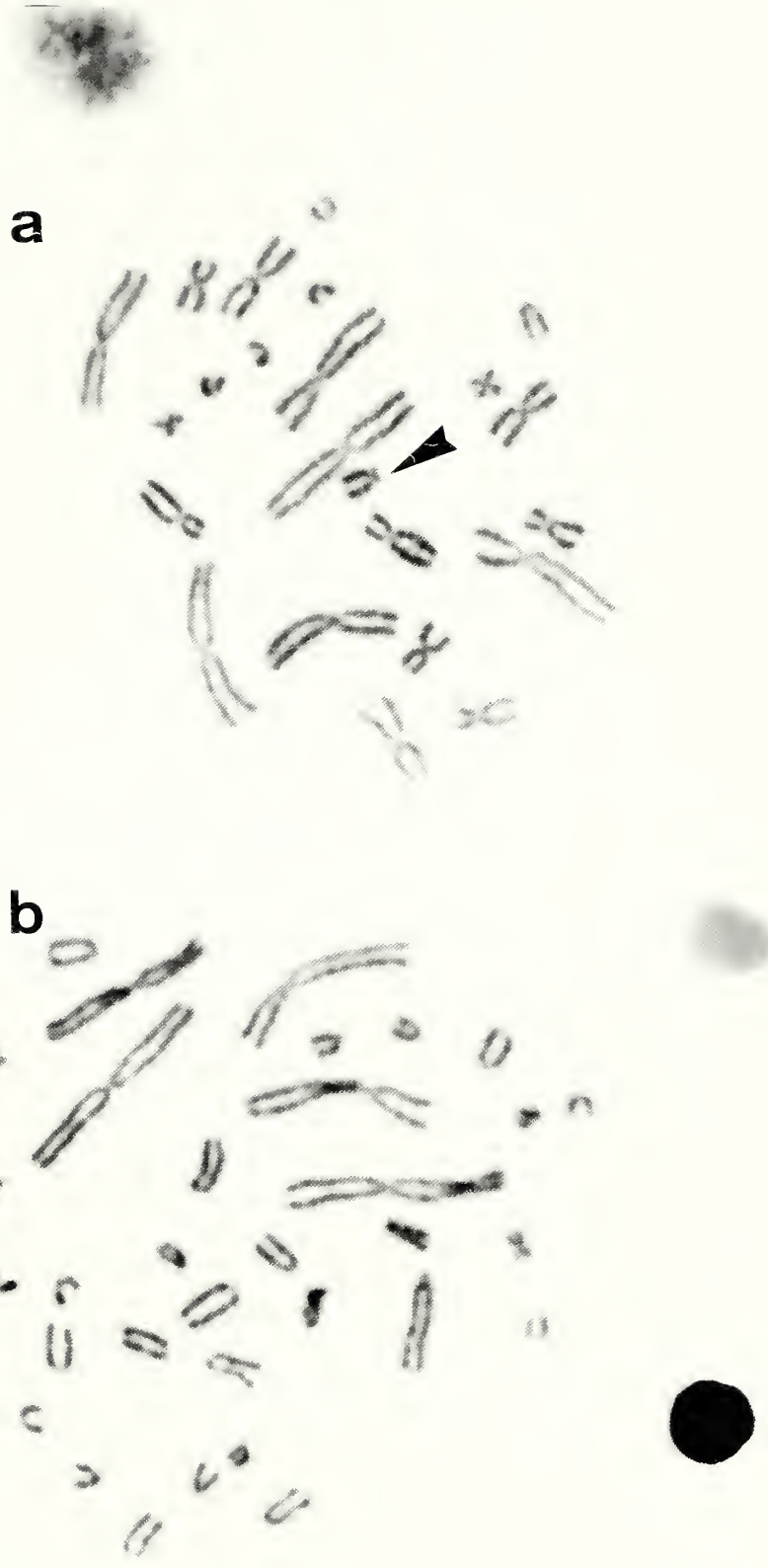


Fig. 7.—(a): Centromeric shift on the chromosome *j* of a heterozygous *j*, *l-jl* female of the Vaud race of *Sorex araneus*. (b) This feature does not exist in this male of the Acrocentric form.

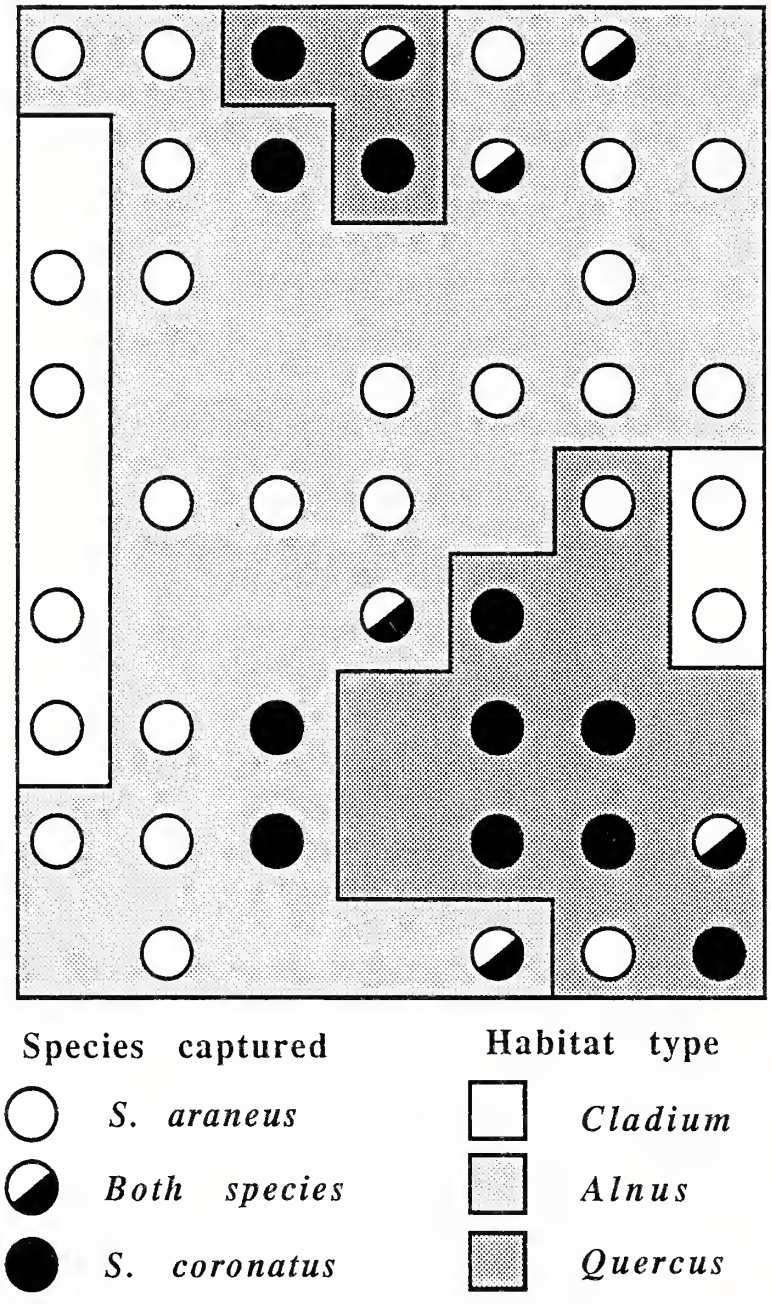


Fig. 8.—Habitat segregation in a 90 x 70 m area of a contact zone between *S. araneus*, Vaud race, and *S. coronatus*. The *Quercus* habitat is drier, the *Cladium* wetter. After Neet and Hausser (1990), modified.

THE PLIO-PLEISTOCENE PATTERNS OF DISTRIBUTION OF THE SORICIDAE IN POLAND

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ABSTRACT

The study of the insectivore fauna from 26 Polish Pliocene, Pleistoeene, and Holocene localities revealed that 15–23 species of shrews were present in the Early and Middle Pliocene, but beginning at the Late Pliocene their number never exceeded ten shrews. However, as genera disappeared from the record, the number of *Sorex* species increased. The greater diversity of shrews in Poland than in southwestern Europe in the past probably is due to the migrations of shrews from Asia.

INTRODUCTION

The origin of shrews (Soricidae) is far from being clear. According to Sigé (1976), some of their morphological characters point to the Paleogene family Nyctitheriidae as their direct ancestor.

The oldest true soricid yet known is *Srinitium marteli* Hugueney, 1976 (Reumer, 1987, 1989). Found in France in the sediments of the Middle Oligocene (about 30 mya), it is representative of the subfamily Crocidosoricinae. This subfamily was erected by Reumer (1987) for the most primitive Oligocene and Miocene forms. So far it is known only from Europe although the Early Miocene *Antesorex* Repenning, 1967 may also be a member of this subfamily. Crocidosoricinae did not survive beyond the Miocene-Pliocene boundary, but gave rise to the fossil American subfamily Limnoecinae as well as to still living subfamilies Crocidurinae and Soricinae (Reumer, 1987, 1989, 1994). Soricinae strongly radiated during the Pliocene, replacing Crocidosoricinae in Europe.

In Poland, there are no materials of shrews from the Oligocene. The only Miocene locality (Bełchatów) containing shrews has not yet been examined. On the other hand, the Pliocene and Pleistocene localities are numerous and very rich in the Soricidae.

This paper is the result of my long, just finished study of the Plio-Pleistocene shrews of Poland (Rzebik-Kowalska, 1975, 1976, 1981, 1989, 1990*a*, 1990*b*, in press). I revised materials described by Kowalski (1956, 1958, 1960*a*, 1960*b*) and Sulimski (1959, 1962) and examined new evidence.

In all, about 26 localities were studied, representing the time from the Early Pliocene to the Holocene, but with a long gap in the Middle Pleistocene, when an important part of Poland was covered several times by the Scandinavian ice sheet (Fig. 1).

The material studied derived from excavations of sediments situated in the karstic caves and channels of Kraków-Wieluń Upland in southern Poland (see maps in Szyndlar, 1984; Wołoszyn, 1987).

Remains of shrews in fossil localities originate from owl pellets. The thanatocoenosis (an assemblage of organisms or their parts brought together in nature after death) of most Polish fossil localities also has this origin (Kowalski, 1964). Some owls nest and seek shelter in caves and devour shrews usually avoided by mammalian carnivores. This explains why a fossil mammalian fauna from a cave almost always includes some shrews. Contrary to diurnal raptors which digest most of their food, owls regurgitate the pellets consisting of fur and bones. These pellets are characteristic in shape and size of particular owl species. Pellets disintegrate quickly, but bones, mainly jaws and teeth, being the hardest and most resistant elements of the skeleton, remain in sediments (Andrews, 1990; Kowalski, 1990).

Although fossil remains are incomplete, their size, morphology of jaws (especially of the coronoid and condyloid processes of the mandible), as well as the number and morphology of teeth, allow for their identification. The knowledge of the fauna of shrews can help, on the other hand, for determination of geologic age and paleoenvironment of the fossil fauna.

PRINCIPAL LOCALITIES

The oldest studied locality, Podlesice, is dated to the Early Pliocene and contains an extremely diverse fauna of shrews. No less than 23 species belonging to about 14–15 genera were found there (Table 1, column A) . Such a large number can arouse doubts as possibly being too high and representing several periods, but studies of the rodents suggest that the fauna from Podlesice is uniform in age (Nadachowski, 1989). It is of course possible that some morphotypes have been determined as separate species, but it does not change the general picture of an extremely rich assemblage of the Soricidae.

The fauna of Podlesice contains forms associated with different biotypes. *Episoriculus*, *Deinsdorfia*, and the talpid *Desmana* are typical of humid or aquatic environments. *Blarinella*, *Sorex*, and probably *Paranourosorex* are restricted to the forest, whereas several species of moles and maybe *Mafia* are inhabitants of open areas. *Petenyia*, *Blarinella*, and some other genera were probably eurytopic.

The thanatocoenosis of Podlesice evidently derives from owl pellets. The high number of taxa must therefore reflect differentiated ecological conditions in an extensive hunting territory of those birds (Webster, 1973; Nilsson, 1984). The composition of the entire fauna points to a climate colder and drier than that of the Miocene, but definitely warmer than the present one.

The next rich locality, Węże 1 (Table 1), contains the fauna of the early Middle Pliocene. It is also rich in shrews. I found 15 species belonging to 12 genera there. Environmental conditions were not very different from those at Podlesice, although the climate might have been more humid, perhaps similar to the present-day Mediterranean.

A rich fauna of shrews is also present in a younger Middle Pliocene locality, Rębielice Królewskie 1A (Table 1, E). The fauna has a similar number of genera (13) and species (20) as are present at Węże 1. Thirteen species are identical in both localities; in contrast only eight species known from Węże 1 and nine from Rębielice Królewskie 1A were present at Podlesice. The shrew fauna from the Middle Pliocene of Poland suggests the same mosaic of biotopes as the Early Pliocene of Podlesice. Among other groups of mammals some at Rębielice Królewskie 1A point to a climate more humid and colder than in Early Pliocene, but still warmer than at present (Kowalski, 1960*b*, 1989).

The number of shrews did not drop to less than ten species until the Late Pliocene faunas at Kielniki 3B (eight) and Kadzielnia 1 (Table 1, F and G), dated to the Plio-Pleistocene boundary (nine). Both suggest a climate similar to the present. Kielniki 3B has six and Kadzielnia 1 seven species identical with those from Węże 1 and Rębielice Królewskie 1A. Among them are *Beremendia fissidens*, *Petenyia hungarica*, and *Sorex minutus*. A new taxon at this time is *Sorex (Drepanosorex) praearaneus*.

Early Pleistocene faunas are known from two localities in Poland, Kamyk and Kielniki 3A (Table 1, H and I). Each of them contains only five species of *Soricidae*. In the slightly older Kamyk fauna, four ancient forms remain: *Blarinoides mariae*, *Beremendia fissidens*, *Petenyia hungarica*, and *Sorex bor* (the absence of *Sorex minutus*, present in all older and younger localities, is undoubtedly accidental, the material being very limited). In the younger Kielniki 3A, *Sorex minutus* is present but *Blarinoides mariae* absent. Present in both localities was *Sorex (Drepanosorex) praearaneus*. A climate similar to the present is suggested by this assemblage.

The fauna of Kozi Grzbiet (Table 1, J) lived in a mild phase of climate near the end of the Early Pleistocene. Shrews increased in diversity, ten species were present again, but their number did not reach that of the Pliocene. At Kozi Grzbiet, *Beremendia* was still present; however, seven or less taxa belonged to the genus *Sorex*, others being *Neomys newtoni* and *Macroneomys brachygnatus*. Woodland was the dominant environment at Kozi Grzbiet.

After a long gap in the Middle Pleistocene, the fossil record begins in the Last Interglacial and continues until the Recent. During this time only shrews still living in Poland were present in our country, except for *Sorex minutissimus* which in the cool period of the Early Pleistocene reached as far as northern France (Heim de Balsac, 1940). Now *S. minutissimus* is restricted to northern Fennoscandia and Russia.

Distribution of the Fauna of Soricidae

From this survey, it is evident that during the Pliocene shrews were extremely diversified in Poland. This is in contrast with the picture known from southwestern Europe, where only the Middle Pliocene localities yielded more than ten species of Soricidae (Fejfar, 1966; Reumer, 1984).

A part of the answer for this high number of species in the fossil faunas of Poland (in relation to those in southern and western Europe) may be the character of the localities. Some localities in Poland containing materials from the Early Pliocene (Zalesiaki 1B or Zamkowa Dolna Cave B) yielded five or less and up to eight taxa of shrews. The absence of some species in a fossil assemblage does not necessarily mean their absence in the area; for example, selection by the predator that accumulated the fossil remains could produce such a result (Lopez-Cardo et al., 1977; Nilsson, 1984; Kowalski, 1990).

The difference in diversity of shrews in the southwestern and northeastern parts of Europe may nevertheless be genuine. The source of new insectivore taxa in the European fauna was, as a rule, Asia. Today the family Soricidae is more diversified in eastern Asia, where nine genera are present (Honacki et al., 1982), than in Europe with only four genera (Niethammer and Krapp, 1990) (see Table 2). Northeastern Europe was more open to the migration from Asia, but some forms probably did not reach the south or west of Europe.

The same is true in the case of the genus *Sorex*. According to earlier publications (Kowalski, 1956; Sulimski, 1959, 1962; Repenning, 1967), *Sorex* was represented by numerous species in the Plio-Pleistocene. Recent research has demonstrated that many of the species considered to be *Sorex* belong to other genera (Reumer, 1984). When corrections are made, it becomes clear that the number of *Sorex* in Pliocene localities of southwestern Europe ranged from zero (Crochet, 1986) to three (Reumer, 1984). At about the middle of the Pleistocene this number increased to four or five in Germany (Koenigswald, 1972, 1973). On the other hand, in the Pliocene of Poland, five localities for *Sorex* species are known from Podlesice, Rębielice Królewskie 1A and four from Kielniki 3B and Kadzielnia. The Kozi Grzbiet locality—at the end of the Early Pleistocene—had as many as seven species.

In general, shrews prefer warm climatic conditions, but the genus *Sorex* is associated mainly with rather cold climates. Today *Sorex* is absent from the tropics, and in the Old World the greatest number of species is known from northeast Asia. Presently, there are no *Sorex* species in the southern part of the Iberian Peninsula, there are three of them in Spain south of the Pyrenees (Niethammer and Krapp, 1990), five in Poland (Pucek, 1984), five in Finland (Hanski and Kaikusalo, 1989), but 13 or less in Siberia (Judin, 1989) (see Table 3). It is therefore possible, even likely, that the cline in the number of *Sorex* species existed in the Plio-Pleistocene and that northeastern Europe was more suitable for these shrews than the western parts of the continent. The morphology of some Polish fossil shrews resembles eastern forms like *Sorex unguiculatus* and *S. caecutiens* rather than *S. araneus*, now widely distributed in Europe. This thesis is supported by the absence of *Crocidura* species in any of the fossil faunas of Poland before the Holocene.

Another reason for the high number of shrew taxa in Poland may be the survival of some forms which lasted longer there

than in the west. *Blarinella*, *Sulimskia*, *Zelceina*, and *Mafia* became extinct in the south and west of Europe at the end of the Middle Pliocene, but survived in Poland until the Plio-Pleistocene boundary at Kadzielnia (Rzebik-Kowalska, 1989, 1990*a*, 1990*b*).

Neomys is first recorded at Kozi Grzbiet (end of the Early Pleistocene in Poland), which is later than its first appearance in western Europe. *Crocidura*, a genus now diversified in Africa but present in both fossil and extant faunas of southern Europe, does not appear as fossil material in Poland earlier than in the Holocene.

Summary

When comparing the presence of fossil shrews in Poland with the western and southern parts of Europe, it becomes evident that: 1) The explosion of Soricidae in Europe, through immigration and radiation, took place earlier than is generally recognized; diversification already had occurred by the start of the Early Pliocene. 2) The comparison of the contemporaneous Plio-Pleistocene localities of Poland and southwestern Europe indicates that the former fauna was more diversified. This was probably due to several introductions from Asia, some of which did not reach the west or south. Also, some species persisted longer in the east, contributing to greater diversity. 3) The abundance of species in northeastern Europe is particularly striking in the case of the genus *Sorex*, where many localities have four or five species, and sometimes as many as seven. In contrast, *Crocidura* was, in all probability, absent during the Plio-Pleistocene north of the Carpathians and its migration and colonization to the west went to the south of these mountains.

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Table 1.—*Fossil Soricidae from the principal Pliocene and Early Pleistocene localities of Poland. Localities: A, Podlesice; B, Zalesiaki 1B; C, Zamkowa Dolna Cave B; D, Węże 1; E, Relielice Królewskie 1A; F, Kielniki 3B; G, Kadzielnia; H, Kamyk; I, Kielniki 3A; J, Kozi Grzbiet; plus sign (+), present at a specific locality; minus sign (−), absent at a specific locality.*

Species	Localities									
	A	B	C	D	E	F	G	H	I	J
Paenelimnoecus pannonicus (Kormos, 1934)	+	+	−	+	+	−	−	−	−	−
Paenelimnoecus sp.	−	−	−	−	+	−	−	−	−	−
Paranourosorex gigas Rzebik-Kowalska, 1975	+	−	−	−	−	−	−	−	−	−
Amblycoptus cf. *topali* Janossy, 1972	−	−	+	−	−	−	−	−	−	−
Episoriculus gibberodon (Petenyi, 1864)	+	+	−	+	+	?	−	−	−	−
Neomysorex alpinoides (Kowalski, 1956)	+	?	−	−	−	−	−	−	−	−
Mafia dehneli (Kowalski, 1956)	+	−	−	−	−	−	−	−	−	−
Mafia cf. *csarnotensis* Reumer, 1984	+	−	−	+	+	−	−	−	−	−
Sulimskia kretozoii (Sulimski, 1962)	+	−	−	+	+	−	+	−	−	−
Blarinoides mariae Sulimski, 1959	+	−	+	+	+	−	+	+	−	−
Beremendia fissidens (Petenyi, 1864)	−	+	+	+	+	+	+	+	+	+
Beremendia minor Rzebik-Kowalska, 1976	−	−	−	−	+	−	−	−	−	−
Zelceina podlesicensis Rzebik-Kowalska, 1990	+	−	−	−	−	−	−	−	−	−
Zelceina soriculoides (Sulimski, 1959)	−	−	−	+	+	−	−	−	−	−
Blarinella dubia (Bachmayer and Wilson, 1970)	+	+	−	−	−	−	−	−	−	−
Blarinella europaea Reumer, 1984	+	+	−	+	+	−	−	−	−	−
Petenyia robusta Rzebik-Kowalska, 1989	+	−	+	−	−	−	−	−	−	−
Petenyia hungarica Kormos, 1934	−	−	−	+	+	+	+	+	+	−
Deinsdorfia reumeri Rzebik-Kowalska, 1989	+	−	−	−	−	−	−	−	−	−
Deinsdorfia insperata Rzebik-Kowalska, 1989	+	−	−	−	−	−	−	−	−	−
Deinsdorfia hibbardi (Sulimski, 1962)	−	−	−	+	+	+	+	−	−	−
Deinsdorfia cf. *kordosi* Reumer, 1984	−	−	−	+	+	−	−	−	−	−
Sorex minutus Linnaeus, 1766	+	+	−	+	+	+	+	−	+	+
Sorex bor Reumer, 1984	+	−	−	+	+	+	+	+	+	−
Sorex casimiri Rzebik-Kowalska n. sp. (in press)	−	+	+	−	+	−	−	−	−	−
Sorex pseudoalpinus Rzebik-Kowalska n. sp. (in press)	−	−	−	+	−	−	−	−	−	−
Sorex polonicus Rzebik-Kowalska n. sp. (in press)	−	−	−	−	+	−	−	−	−	−
Sorex praealpinus Heller, 1930	−	−	−	−	−	+	−	−	−	+
Sorex subaraneus Heller, 1958	−	−	−	−	−	−	+	−	−	+
Sorex runtonensis Hinton, 1911	−	−	−	−	−	−	−	−	−	+
Sorex minutissimus Zimmermann, 1870	−	−	−	−	−	−	−	−	−	+
Sorex (Drepanosorex) praearaneus Kormos, 1934	−	−	−	−	−	+	+	+	+	−
Sorex (Drepanosorex) savini Hinton, 1911	−	−	−	−	−	−	−	−	−	+
Sorex (Drepanosorex) sp.	−	−	−	−	−	−	−	−	−	+
Sorex sp. 1	+	−	−	−	−	−	−	−	−	−
Sorex sp. 2	+	−	−	−	+	−	−	−	−	−
Sorex sp. 3	+	−	−	−	−	−	−	−	−	−
Neomys newtoni Hinton, 1911	−	−	−	−	−	−	−	−	−	+

Table 1 (cont.)

Macroneomys brachyonatus Fejfar, 1966	−	−	−	−	−	−	−	−	+
Soricidae gen. et sp. indet. 1	+	−	−	−	−	−	−	−	−
Soricidae gen. et sp. indet. 2	+	−	−	−	−	−	−	−	−
Soricidae gen. et sp. indet. 3	+	−	−	−	−	−	−	−	−
Soricidae gen. et sp. indet. 4	+	−	−	−	−	−	−	−	−
Soricidae gen. et sp. indet. 5	−	−	−	+	−	−	−	−	−
Soricidae gen. et sp. indet. 6	−	−	−	−	+	−	−	−	−
Soricidae gen. et sp. indet. 7	−	−	−	−	+	−	−	−	−

Table 2.—*Number of Recent genera of Soricidae in Europe and eastern Asia.*

Eastern Asia	Europe
Sorex	*Sorex*
Neomys	*Neomys*
Crocidura	*Crocidura*
Suncus	*Suncus*
Soriculus	
Blarinella	
Anourosorex	
Chimarrogale	
Nectogale	

Table 3.—*Number of* Sorex *species in Recent fauna of Europe and Siberia. Plus sign (+), present in the specific locality; minus sign (−), absent in the specific locality; asterisk (*), south of the Pyrenees. References: [1]Neithammer and Krapp, 1990; [2]Pucek, 1984; [3]Hanski and Kaikusalo, 1989; [4]Judin, 1989.*

Species	Spain*[1]	Poland[2]	Finland[3]	Siberia[4]
Sorex coronatus	+	−	−	−
Sorex granarius	+	−	−	−
Sorex minutus	+	+	+	+
Sorex araneus	−	+	+	+
Sorex caecutiens	−	+	+	+
Sorex alpinus	−	+	−	−
Sorex isodon	−	−	+	+
Sorex minutissimus	−	−	+	+
Sorex cinereus	−	−	−	+
Sorex mirabilis	−	−	−	+
Sorex daphaenodon	−	−	−	+
Sorex unguiculatus	−	−	−	+
Sorex gracilimus	−	−	−	+
Sorex roboratus	−	−	−	+
Sorex tundrensis	−	−	−	+
Sorex beringianus	−	−	−	+
Number of species	3	4	5	13

Time in Millions of years	Chronostratigraphy Global		Biostratigraphy Mammal ages	Localities
- 0	HOLOCENE			Raj Cave, Giebułtów, Józefów
	PLEISTOCENE	Upper	TORINGIAN	Koziarnia Cave, Mamutowa Cave
		Middle		
-1		Early	BIHARIAN	Kozi Grzbiet Kielniki 1 Kielniki 3A, Zamkowa Dolna CaveC Kamyk ~~Kadzielnia~~
-2	PLIOCENE	Upper	VILLANYIAN	Kielniki 3B Zamkowa Dolna Cave A Rębielilice Królewskie 1A and 2
-3		Middle	RUSCINIAN	Zamkowa Dolna Cave B Węże 1 Zalesiaki 1B
-4				
-5		Early		Podlesice
-6	MIOCENE	Upper	TUROLIAN	

Fig. 1.—Correlation of the Pliocene to Holocene terrestrial faunas of Poland.

COMPARATIVE CYTOGENETICS AND SYSTEMATICS OF *SOREX*: A CLADISTIC APPROACH

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Abstract

G- and C-banded chromosomes of 11 *Sorex* species were compared to determine the degree of chromosomal differentiation, types of chromosomal rearrangements, direction of chromosomal evolution, and to propose an ancestral karyotype. Using data on 2N and NF for 30 *Sorex* species, a WISS cladogram was construeted. This phylogenetic tree shows that the genus *Sorex* is divided into three large polytypic groups, which may be regarded as the subgenera *Sorex* s. str., *Otisorex*, and *Homalurus*. The subgenus *Sorex* includes *S. araneus*, *S. coronatus*, *S. asper*, *S. tundrensis*, *S. daphaenodon*, *S. satunini*, *S. arcticus*, and *S. granarius*. The subgenus *Otisorex* consists mainly of the Nearctic species *S. vagrans* and its allies, *S. bendirii*, *S. ornatus*, *S. cinereus*, *S. leucogaster*, and *S. ugyunak*. The subgenus *Homalurus* consists of the Palearctic species *S. alpinus*, *S. minutus*, *S. volnuchini*, *S. bucharensis*, *S. isodon*, *S. unguiculatus*, *S. roboratus*, and *S. caecutiens*. The American species *S. fumeus* and *S. trowbridgii* represent independent phyletic branches on the cladogram. The position of European *S. samniticus* is also rather isolated. Two methods of numerical analysis (UPGMA and WISS) of G-banded karyotypes were carried out for 24 chromosomal races of *S. araneus*. The WISS method allowed for identification of homoplastic events, synapomorphic characters, and the determination of the racial groups more definitely than has been produced by other methods.

Introduction

Cytogenetic investigations of shrews belonging to the genus *Sorex* have made valuable contributions to the systematics of this group. Karyotypic analyses support the recognition of *S. isodon* (Kozlovsky and Orlov, 1971), *S. satunini* (syn. *S. caucasicus*), *S. volnuchini* (Kozlovsky, 1973*a*, 1973*b*), *S. gracillimus* (Tsuchiya, 1979), *S. tundrensis* (Ivanitskaya and Kozlovsky, 1983), *S. asper* (Ivanitskaya et al., 1986), *S. leucogaster*, and *S. ugyunak* (Ivanitskaya and Kozlovsky, 1985), *S. coronatus* (Olert and Schmid, 1978), and *S. samniticus* (Graf et al., 1979).

At the same time, application of cytogenetic data to questions of *Sorex* subgeneric taxonomy still is relatively underutilized, although there are many unsolved problems to which it could be applied. Most systematists of recent decades have followed Findley (1955), who recognized two subgenera within *Sorex*: the nominate subgenus, which includes most Palearctic and some Nearctic species, and *Otisorex*, including most species from North America. However, this classification does not take into account Stroganov's (1957) recognition of the subgenus *Eurosorex* for *S. bucharensis* and its allies, and Heptner and Dolgov's (1967) recognition of the monotypic subgenus *Ognevia* for *S. mirabilis*. An earlier proposition to place *S. alpinus* in a separate subgenus, *Homalurus* Schultze, 1890, also should be mentioned. Contrary to this "splitting" tradition, Gureev (1971) argued that it is impossible to divide *Sorex* into subgenera on the basis of traditionally-used characters, such as morphology of the postmandibular channel.

Attempts to classify the genus on the basis of different macromorphological features led to conflicting systems, most of which, however, did not gain nomenclatural recognition. For instance, Hoffmann (1971), used the informal category "species group" to divide the two traditional subgenera into three groups each, many of them monotypic. Some years earlier another system of four groups was proposed by Dolgov and Lukjanova (1966) for Palearctic *Sorex* on the basis of glans penis morphology.

The first attempt to revise the subgeneric division of *Sorex* with cytogenetic data was done by Vorontsov and Kral (1986). Those authors created 13 subgenera reflecting proposed genealogical relationships. Unfortunately, all their subgeneric names are formally unavailable. For example, *S. bucharensis* in that scheme was recognized as the subgenus *Yudinia*, but this species is the type species for the subgenus *Eurosorex* (Stroganov, 1957). Also, the closely related species *S. isodon* and *S. unguiculatus* were placed in different subgenera.

All of these schemes of classification, although differing in composition of proposed subgenera and species groups, are similar in one important way: they are not (save Vorontsov and Kral's [1986] system, as these authors thought) cladistic. And it is evident that cladistic analysis of relationships within such a large and complicated group as the genus *Sorex* is urgently desirable.

In the present paper two cladistic interpretations of relationships within *Sorex* based on karyotypic data are considered. The first is an analysis of relations of karyotypic races in *S. araneus*. The second is an analysis of relationships among the *Sorex* species for which data are available.

Phylogenetic Relationships of Karyotypic Races in the Superspecies *Sorex araneus*

Karyotypic races of *Sorex araneus* differ by combinations of autosomal arms arising as a result of different orders of acrocentric chromosome fusions. The first two and the last biarmed autosomal pairs are identical in all races, whereas the other autosomes are acrocentrics or meta-submetacentrics with race-specific combinations of the arms. Twelve karyotypic races of *S. araneus* were known by 1984. At that time the first cladistic analysis of the group was undertaken by Searle (1984) who presented four cladograms. Two alternative cladograms (Searle, 1984, fig. 3) were constructed using the principle of

minimal number of evolutionary steps (Camin and Sokal, 1965). These two schemes differ in the position of race G: in one case it is included in a group with races I, J, K, A, B, and F; in the other case it is included with races C and H. In addition, both schemes unite race K with J and I, and race F with A and B on the basis of only plesiomorphic characters. Therefore the positions of races F and K are equivocal.

In two other cladograms of Searle (1984), constructed on the basis of supposing a hybrid origin of some of the races, uncertainties are decreased. These two schemes differ only in the position of sister groups ED and IJK and clarify the position of race G. But they do not decrease the uncertainty in the positions of F and K. Searle (1984) did not show the taxon-character matrix, but the method of Camin and Sokal (1965) requires that the primitive characters should be defined a priori. In this case it is easy to see that the characters n, p, q, and r (F race) are plesiomorphic with respect to np, qr (A race) and to nq, pr (B race) but it is hardly possible to polarize characters np, nq, qr, and pr. Besides, the DEGCH clade (Searle, 1984, fig. 3b) represents a group of races with continuous geographic ranges (Table 1). The inclusion of races C and H in the same sister group can be explained by insufficient data from the European part of Russia and from western Siberia.

Currently 24 karyotypic races of *S. araneus* have been described (Table 1). Shrews from western Europe and Poland are the best studied: karyotypes of *S. araneus* from more then 50 populations outside of Russia have been studied using G-bands. Therefore, I have reconsidered the cladograms of Searle (1984), taking into account these new data. In addition, features of karyotypic races in the common shrew are convenient for formalization and thus allow various methods of dendrogram construction.

In phenetic and cladistic analyses of relationships among karyotypic races of *S. araneus*, I employed a taxon-character matrix (Table 2) using UPGMA and WISS algorithms, respectively. Two alternative phenograms (Fig. 1*a*, *b*) obtained using the UPGMA algorithm (Sneath and Sokal, 1973) are considered reflections of levels of phenetic similarity of the karyotypic races. At higher levels of these trees, relationships among races agree with those revealed by cladistic analysis (see below). Comparing these two phenograms, there is no disagreement in the composition of UVGS and KBRFANJIMQ groups. In addition, a set of unique characters determines the same position of the L race in both trees. The positions of T, P, O, W races, as well as the ED and HC sister groups, vary between the phenograms. In general, these phenograms identify two groups of karyotypic races in *S. araneus*. One of them (group UVGS) is represented by races known only from Finland, whereas the other one (group KBRFANJIMQ) is geographically less compact, as races forming some of its subgroups (e.g., AN and IMQ) are widely distributed.

Cladistic analysis using the WISS algorithm (after Farris et al., 1970) has evident advantages over the phenetic algorithm. First, it identifies sister groups on the basis of synapomorphies. Second, the method provides a possibility of determining the position of the ancestral karyotype at the base of the cladogram. And lastly, the distance between each pair of nodes in the cladogram reflects the number of Robertsonian fusions, whereas the length of each branch reflects the level of that race's relative karyotypic advancement. Thus, the cladogram obtained using the WISS algorithm reveals both monophyletic groups and levels of relative change from the ancestor (Fig. 2).

The WISS cladogram and phenograms (Fig. 1*a*, *b*) are similar only in recognizing the UV, GS, ED, and IMQ groups and that race L diverges from all other taxa at the very base of the trees. Race T (south Finland) is included with the PW group (east Poland) in one phenogram and is joined with the KBRFA-NJIMQ group in the second, thus sharing features in common with other races from Finland. In contrast, race T in the WISS cladogram is the sister group of the other Finnish races (V, U, S, G), although this race has a great number of autapomorphic characters separating it from other members of the group. Race C (Białowieza) is placed with race H (Novosibirsk) in both of the phenograms and in the cladograms obtained by Searle (1984), whereas the WISS cladogram indicates it has a common ancestor with other races of east and north Poland (W, O, P). Race F (south England) forms a group with race B (south Sweden) and R (north Czechoslovakia) on both phenograms, but the WISS cladogram treats it as a sister form of the K, J, I, Q, and M races. Race K (west Germany) is a member of the BRFANJIMQ group according to the phenograms, whereas after cladistic analysis it is identified as the sister group of the Polish (W, O, P) and Finnish (T, V, U, S, G) races.

The above-mentioned uncertainty of position of the F and K races in Searle's (1984) paper is eliminated by the WISS method, as race K becomes ancestral to the A, N, F, R, B, J, Q, I, M races and race F becomes ancestral to the A, N, R, B races. The Novosibirsk race (H) clusters with race C (Białowieza) in all phenograms and in Searle's cladograms, but forms an independent branch in the WISS cladogram, which makes more sense geographically. The separation of branch H at the base of the cladogram reflects its uncertain position. However, this can be explained by an absence of karyotype data from localities in Siberia and European Russia.

The independent origin of some biarmed autosomes has been previously suggested when distributional patterns of karyotypic races were evaluated (Searle, 1984). Analysis of the composition of monophyletic groups of karyotypic races and their characters reveals with more certainty homoplasies at different levels of evolutionary diversification of chromosomal races of *S. araneus*. For instance, the qr combination, which is an apomorphy uniting races A, I, H, D, probably appeared independently in European (A, I) and Siberian (H, D) subgroups. Other cases of probable homoplasies are characters pr (races B and E), rk (races Q and S), kq (races M and G). Character ok, which is a synapomorphy for the clade ANFRB, appears independently in race U, thus also demonstrating homoplasy. The character hn appears independently at least three times, in the geographically and cladistically separated groups H, C, and VUSQ. Another case of homoplasy is demonstrated by character mn appearing in clades DE and WOP.

The cladistic analysis outlined above allows identification of apomorphic characters in the races under consideration. These characters seem to be indicators of the historical development

of the entire complex. At the present time, four groups of races are recognized in Europe, each group consisting of races of common origin (Fig. 3). In addition, race L, which is known only from Vallais, Switzerland, represents an independent line of karyotypic evolution. This conclusion differs markedly from those of Wojcik and Zima (1987), who recognized seven karyotypic groups in Europe. However, the above authors failed to identify synapomorphic and symplesiomorphic groups among karyotypic races.

Further studies of chromosomal evolution in the common shrew may change the above-suggested phylogeny. However, such changes would most likely affect only those parts of the cladogram that contain Siberian races and the position of races Ms and Mn from eastern Europe.

Phylogenetic Relations Within the Genus *Sorex*

In *S. araneus*, groups of karyotypic races are easily recognized as monophyletic assemblages of subspecies-semispecies taxonomic rank. However, in other representatives of this genus identification of such groups is not so simple. First, chromosome numbers are more or less fully known only for Palearctic species. Second, data on differentially-stained chromosomes of *Sorex* are fragmentary, and serve as a source of data for phylogenetic reconstructions only in some groups of species. At present, chromosome numbers are known for 30 *Sorex* species, but only ten of them have been differentially-stained. Such fragmentary data allow limited speculation on directions of chromosome rearrangement resulting in the present diversity of karyotypes in the genus *Sorex*. Nevertheless, even scant information on G-, C-, and N-banded chromosomes permits a hypothesis of chromosomal evolution in the genus *Sorex*.

Olert and Schmid (1978) explained differences between *S. araneus* and *S. coronatus* by three pericentric and two paracentric inversions and one reciprocal translocation. Later, comparing results obtained from G-banded chromosomes of Siberian populations of *S. araneus* and *S. tundrensis* with the data of Olert and Schmid (1978), Aniskin (1987) proposed that Recent karyotypes are derived from transformations of the hypothetical ancestral karyotype of 46 autosomes, rather than one Recent karyotype being derived directly from another. Various sequences of fusions of the ancestral chromosomes led to the origin of the three species considered here. Additional data on C- and N-banded chromosomes of *S. araneus* and *S. tundrensis* led to the proposal that the ancestral karyotype of these species had not 46, but 50 autosomes (48 acrocentrics and two small metacentrics) (Ivanitskaya, 1985, 1989). Comparison of G-banded chromosomes of four species of shrews with 2N = 42 showed the identical arrangement of G-bands in the autosomes (Ivanitskaya, 1985). In previous studies, some differences in autosome morphology of these species were explained by pericentric inversions (Halkka et al., 1970; Kozlovsky and Orlov, 1971). However, my data do not confirm that the existence of a chromosome rearrangement of this type in the morphology between separate pairs is due to the different position of centromeres without change of the arrangement of G-bands. Supposedly these chromosomes were formed from the same ancestral elements by centromere-telomere fusion with subsequent differentiation of active centromeres.

The karyotypes of *S. minutus*, *S. isodon*, *S. caecutiens*, *S. unguiculatus*, and *S. roboratus* consist of 42 chromosomes but differ in autosomal arms. *Sorex minutus* and *S. isodon* possess a similar pattern of G-bands in the first five pairs of biarmed autosomes; G-bands of the large meta- and submetacentric autosomes of *S. isodon* and of the large acrocentric autosomes in *S. minutus* are similar as well. This cannot be explained by pericentric inversions. It seems more probable that chromosomes in *S. isodon* and *S. minutus*, which are morphologically different, have been formed by centromere-telomere fusions of acrocentric chromosomes of the ancestral karyotype and by conserving as active different ancestral centromeres.

Detailed comparison of G-banded chromosomes of shrews characterized by multiple sex chromosomes (*S. araneus* and *S. tundrensis*), with shrews having diploid numbers of 42 (*S. caecutiens*, *S. isodon*, *S. unguiculatus*, and *S. roboratus*) has yielded only two similarities: Y chromosomes; and the "e" arm of X chromosomes of *S. araneus* and *S. tundrensis* and X chromosomes of shrews having 2N = 42 (Fedyk and Michalak, 1982; Ivanitskaya, 1985). No autosomes or autosome sections of significant length with identical bands are found in these species. This can be explained by the complex structure of shrew chromosomes formed as a result of various types of tandem fusions of a great number of relatively small acrocentric elements. This hypothesis is indirectly confirmed by an investigation of *Sorex* chromosome structure by Schmid et al. (1982), which demonstrated unusual phenomena for mammals, namely diffuse distribution of AT-rich sites of DNA within the length of the chromosomes of *S. araneus* and *S. coronatus*, and the complete absence of structural heterochromatin in the autosomes. AT-rich (or GC-rich) sites of DNA in chromosomes of most mammals are located in centromeric regions. It is possible that the diffusely distributed AT-rich sites in the chromosomes of *Sorex* species with low 2N are regions of the ancestral centromeres.

Thus, these comparative data allow identification of prevalent types of chromosome changes in the evolution of this group. Apparently, no significant changes in heterochromatin quantity have taken place in the process of karyotype divergence, nor have pericentric inversions played an essential role in chromosome rearrangement. The ancestral karyotype of *Sorex* supposedly consisted of a large number of acrocentric chromosomes. As the greatest number of autosome arms found in shrews is 94 (*S. fumeus*), presumably the ancestral karyotype of shrews contained a minimum of 94 small acrocentric autosomes.

Karyotype structure (chromosome number and morphology) can be used for cladistic analysis. As G-band data are not available for all shrew species, use of that character for cladistic analysis is not now possible. However, the hypothesis concerning the direction of chromosome evolution discussed above, the pattern of chromosome rearrangement, and the structure of the proposed ancestral karyotype of shrews makes it possible to use chromosome morphology and chromosome number as characters for cladistic analysis. For this character system the WISS algorithm (Farris et al., 1970) was used.

The initial data include the autosome number of the proposed ancestral karyotype ($2N_p = 94$ with $NF_p = 94$), the number of autosomal arms (NFa), and the number of biarmed autosomes (M) in the karyotypes of Recent species. The height of species *i* (H_i) is the distance between the ancestral karyotype and the karyotype of the *i*th species and was calculated according to the formula

$$H_i = 2N_i - NFa_i + M_i.$$

The distance (D) between species *i* and *j* was accordingly

$$D_{ij} = NFa_i - NFa_j + M_i - M_j.$$

The height of species *k*, which is ancestral to the species *i* and *j*, was calculated as

$$H_k = 0.5\ (H_i + H_j - D_{ij}).$$

The karyotype containing the greater number of chromosomes and greater number of arms was considered more primitive.

Information on karyotypes of 30 species of shrews (Table 3) was included in the analysis. In defining the karyotype ancestral to the *araneus-coronatus-tundrensis* group, data on G-banded chromosomes of these species were taken into consideration. However this correction did not change the tree topology considerably from that based on only 2N and NFa parameters.

Based on the cladogram obtained (Fig. 4), shrews form three polytypic groups. One group includes representatives of the subgenus *Otisorex*: American species of the "*vagrans*" group and, related to them, *S. bendirii*, the Amphiberingian species *S. ugyunak*, and two related American species, *S. ornatus* and *S. vagrans bairdi*. The ancestral karyotype for the subgenus *Otisorex* appears to be related to karyotypes of Recent *S. leucogaster* and *S. cinereus*. Possibly, the karyotype related to *S. cinereus* was also ancestral to a large group of Palearctic species which were initially attributed to the nominate subgenus. Along the line *pa-1–ci-3* (Fig. 4), there are five proposed centromere-centromere and 14 centromere-telomere fusions which define a second polytypic group. This species group is divided into two subgroups. In one of these subgroups (with the terminal species *S. raddei* and *S. gracillimus*), centromere-centromere fusions are the main type of chromosome rearrangements. In the other (*S. alpinus*, *S. minutus*, *S. volnuchini*, *S. bucharensis*), centromere-centromere and centromere-telomere chromosome fusions are substantially equal. Representatives of these subgroups—*S. isodon*, *S. unguiculatus*, *S. roboratus*, *S. caecutiens* (point *cc* on the cladogram) and *S. minutus* (*mi*)—are similar in their patterns of G-bands, i.e., the same ancestral chromosomes formed biarmed autosomes in one group (*cc*) and acrocentric autosomes in the other one (*mi*). It is difficult to imagine that all these events were independent. Moreover, the cladistic algorithm does not allow for the process of differentiation of active centromeres. Thus, considering the G-band data linking these two subgroups, node 3 must be placed at least five evolutionary steps higher. As a consequence, the part of the cladogram situated beyond node 3 represents a more compact group.

The third group in the cladogram is represented by species with multiple sex chromosomes in males. Along the "*pa*"-2 branch of cladogram 19, centromere-telomere fusion should occur. Between nodes 2 and 5, an X autosome translocation and another Robertsonian fusion of ancestral autosomes occurred. Thus, an ancestral karyotype in this group could have included 48 acrocentric and two metacentric autosomes. Three separate evolutionary lines can be identified within this group. The first includes *S. araneus*, *S. coronatus*, *S. asper*, *S. granarius*, and *S. tundrensis*, the last species having an Amphiberingian distribution, whereas the others are Palearctic endemics. Derivatives of the second branch are the Asian species *S. daphaenodon* and the European *S. satunini*. The third subgroup of shrews with multiple sex chromosomes includes the North American *S. arcticus*.

In this scheme two pairs of species, *S. araneus-S. satunini* and *S. arcticus-S. tundrensis*, which were formerly considered closest relatives, belong to different phyletic branches. The American species *S. fumeus* and *S. trowbridgii* represent independent phyletic branches on the cladogram. The position of the European *S. samniticus* is also isolated and does not indicate relationships of this species.

From this karyologically-based cladogram, the following three groups of subgeneric rank are recognized: *Sorex* s. str. with type species *S. araneus* L., *Otisorex* de Kay with type species *S. cinereus*, and *Homalurus* Schultze with type species *S. alpinus*. Thus, the subgenus *Sorex* of earlier authors is divided by karyological data into two unrelated taxa. *Sorex trowbridgii* and *S. fumeus*, which were previously included in this subgenus, are placed distantly on the cladogram which makes it impossible to include them in *Sorex* s. str. Vorontsov and Kral (1986) included each of these species in a monotypic subgenus. However, the question of formal taxonomic treatment of their relationships requires more investigation.

The European species *S. samniticus*, which was considered until recently a subspecies of *S. araneus*, appears on the cladogram close to *S. trowbridgii*, thus forming with the latter a sister group relative to *Sorex* s. str. As they are dissimilar in macromorphology and geographically distant, this probably results from parallel evolution of similar chromosome structures. The karyotype of *S. samniticus* seems to be similar to that interpreted as ancestral for the subgenus *Sorex* s. str. Analysis of G-banded chromosomes is necessary for more accurate determination of the relationships of these two species.

The cladogram constructed herein shows interesting similarity to the phylogenetic tree constructed from analysis of biochemical data by George (1988). Thus, *S. trowbridgii* (together with the karyologically unstudied *S. merriami* and *S. arizonae*) and *S. fumeus* (together with *S. dispar*) are placed distant from each other and from other groups in both schemes. George's (1988) data also indicated monophyly of the subgenus *Otisorex*, which agrees with the cladogram constructed from karyotypic data. But in the cladogram based on allozyme analysis, all Palearctic species represented a compact group.

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Table 1.—*The karyotypic races of the common shrew and their characteristics. The designation of* S. araneus *races used in this paper follows Searle (1984) for ease of comparison with his cladograms.*

Race	Combinations of Autosomal Arms (g–r)	Range of Distribution	Reference
A	hi, gm, jl, ko, np, qr	Northeastern Scotland	Searle, 1984
B	hi, gm, jl, ko, nq, pr	Southern Sweden	Fredga and Nawrin, 1977
C	hn, gr, jl, ik, mp, q, o	Eastern Poland	Fredga and Nawrin, 1977
D	hi, gk, jl, mn, op, qr	Russia, Tomsk region	Aniskin and Volobuev, 1981
E	ho, gk, jl, mn, iq, pr	Russia, south of Krasnoyarsk region	Aniskin and Volobuev, 1981
F	hi, gm, jl, ko, n, p, q, r	Southern England, northern Poland	Searle, 1984; Fedyk, 1986
G	hn, gm, jl, kq, ip, or	Russia, Novosibirsk region	Aniskin and Volobuev, 1981
H	hn, go, jl, ik, mp, qr	Northern Finland, northern Sweden	Halkka et al., 1974
I	hi, gm, jl, kq, no, pr	Central Britain	Searle, 1984
J	hi, gm, jl, kp, nr, oq	Central Sweden	Fredga and Nawrin, 1977
K	hi, gm, jl, k, n, o, p, q, r	West Germany, Czechoslovakia, Hungary, Yugoslavia	Olert and Schmid, 1978; Dulic, 1978; Zima and Kral, 1985
L	gi, hj, lo, kn, m, p, q, r	Switzerland (Valais)	Hausser et al., 1985
Ms	hi, gm, jl, kp, no, qr	Russia, south of Moscow region	Ivanitskaya, 1986
Mn	hi, gm, jl, kr, no, pq	Russia, north of Moscow region	Aniskin and Lukyanova, 1989
N	hi, gm, jl, ko, np, q, r	Western and northeastern Poland	Fedyk, 1986; Wojcik, 1986
O	hk, gr, jl, io, mn, p, q	Northern Poland	Fedyk, 1986; Wojcik, 1986
P	ik, gr, jl, hq, mn, o, p	Northeastern Poland	Fedyk, 1986; Wojcik, 1986
Q	hi, gm, jl, kr, no, p, q	Switzerland (Vaud)	Hausser et al., 1986
R	hi, gm, jl, ko, nr, p, q	Northern Czechoslovakia, Moravia	Zima and Kral, 1985
S	hn, gm, jl, kr, ip, oq	Northeastern Finland	Halkka et al., 1987
T	hk, gq, jl, mo, ip, nr	Southeastern Finland	Halkka et al., 1987
U	hn, gq, jl, ko, ip, mr	Central and southern Finland	Halkka et al., 1987
V	hn, jl, oq, ip, mr, g, k	Southwestern Finland	Halkka et al., 1987
W	hi, gr, jl, ko, mn, p, q	Northeastern Poland	Fedyk, 1986

Table 2.—*Taxon-character matrix of the superspecies* Sorex araneus, *based on the presence (1) or absence (0) of arm combinations in the karyotypic races.*

Characters	Karyotypic races																						
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W
hi	1	1	0	1	0	1	0	0	1	1	1	0	1	1	0	0	1	1	0	0	0	0	1
hn	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
ho	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
jh	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
gm	1	1	0	0	0	1	1	0	1	1	1	0	1	1	0	0	1	1	1	0	0	0	0
gr	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1
gk	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
go	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
gi	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
jl	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
lo	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
ko	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
mn	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1
mp	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
kq	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ik	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
kp	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
kn	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
kr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
hk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
hq	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
gq	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
np	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
nq	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
op	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
iq	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ip	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
nr	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0
qr	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
pr	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
or	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
oq	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0
io	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
mo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
mr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0

Table 3.—*The karyotypic characters of* Sorex *species. 2N is the number of chromosomes in males; 2Na, the number of autosomes; NFa, the number of autosomal arms. * for additional information, see Table 1.*

Species	2N	2Na	NFa	Reference
S. cinereus	66	64	66	Meylan, 1967
S. ugyunak	60	58	62	Ivanitskaya and Kozlovsky, 1985
S. leucogaster	66	64	70	Ivanitskaya and Kozlovsky, 1985
S. ornatus	54	52	76	Brown and Rudd, 1981
S. bendirii	54	52	66	Brown, 1974
S. vagrans	54	52	58–62	Brown, 1974
S. v. bairdi	53–54	51–52	56,60	Brown, 1974
S. fumeus	66	64	94	Meylan, 1967
S. trowbridgii	34	32	38	Brown, 1974
S. samniticus	52	50	50	Graf et al., 1979
S. alpinus	58	56	66	Zima, in litt.
S. minutus	42	40	54	Meylan, 1965*a*
S. volnuchini	40	38	56	Kozlovsky, 1973*a*
S. bucharensis	40	38	56	Ivanitskaya et al., 1977
S. unguiculatus	42	40	70	Takagi and Fujimaki, 1966
S. isodon	42	40	70	Kozlovsky and Orlov, 1971
S. caecutiens	42	40	70	Fredga, 1968
S. roboratus	42	40	66	Ivanitskaya and Malygin, 1985
S. minutissimus	38	36	68	Halkka et al., 1970
S. raddei	36	34	60	Kozlovsky, 1973*b*
S. mirabilis	38	36	60	Ivanitskaya et al., 1986
S. gracillimus	36	34	60	Tsuchiya, 1979
S. arcticus	29	26	34	Meylan and Hausser, 1973
S. granarius	37	34	34–36	Hausser et al., 1985
S. daphaenodon	27	24	42	Fedyk and Ivanitskaya, 1972
	29	26	42	Ivanitskaya et al., 1986
S. satunini	25	22	42	Kozlovsky, 1973*b*
S. coronatus	23	20	40	Meylan, 1965*b*
S. araneus	21–29	18–26	36	Matthey and Meylan, 1961*
S. asper	33	30	52	Ivanitskaya et al., 1986
S. tundrensis	31–37	28–34	52	Kozlovsky, 1971; Kral and Radjably, 1976; Aniskin and Volobouev, 1980; Ivanitskaya and Kozlovsky, 1983
	39–41	36–38	54	Ivanitskaya et al., 1986

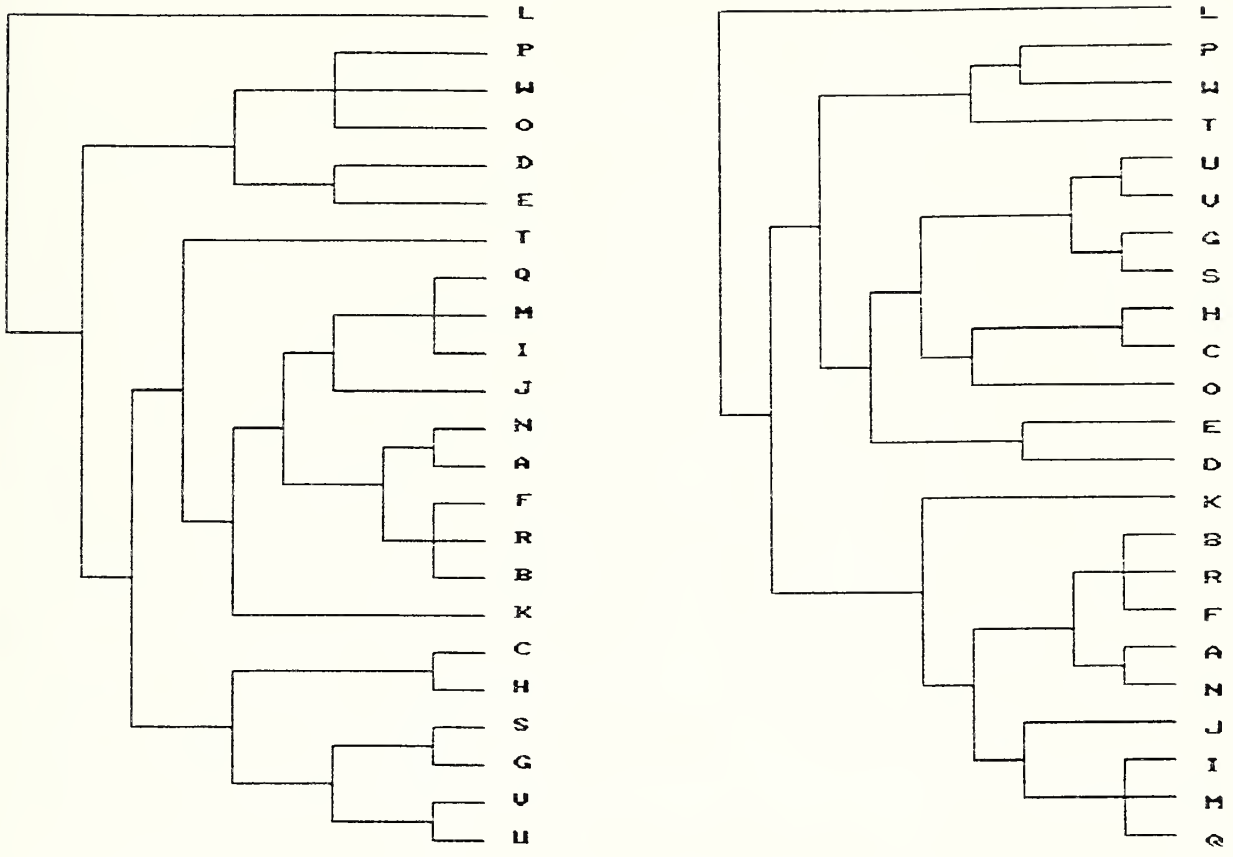

Fig. 1.—Two variants (a, b) of phenograms reflecting the levels of similarity between karyotypic races (A–W) of *Sorex araneus*.

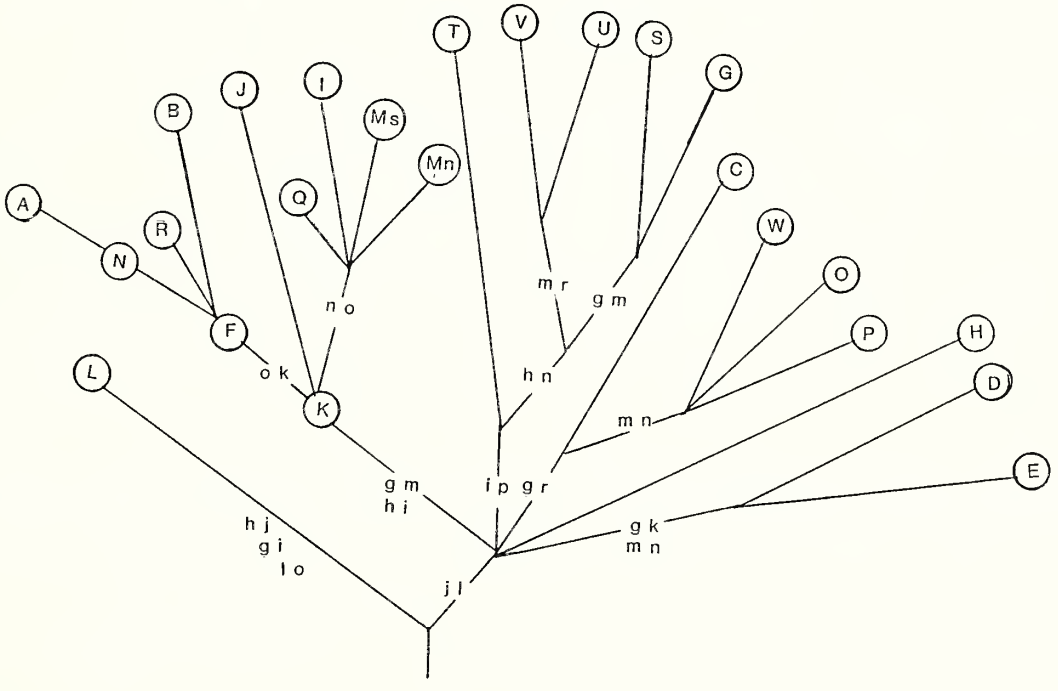

Fig. 2.—Cladogram WISS reflecting phylogenetic relationships of karyotypic races (A–W) of *S. araneus*.

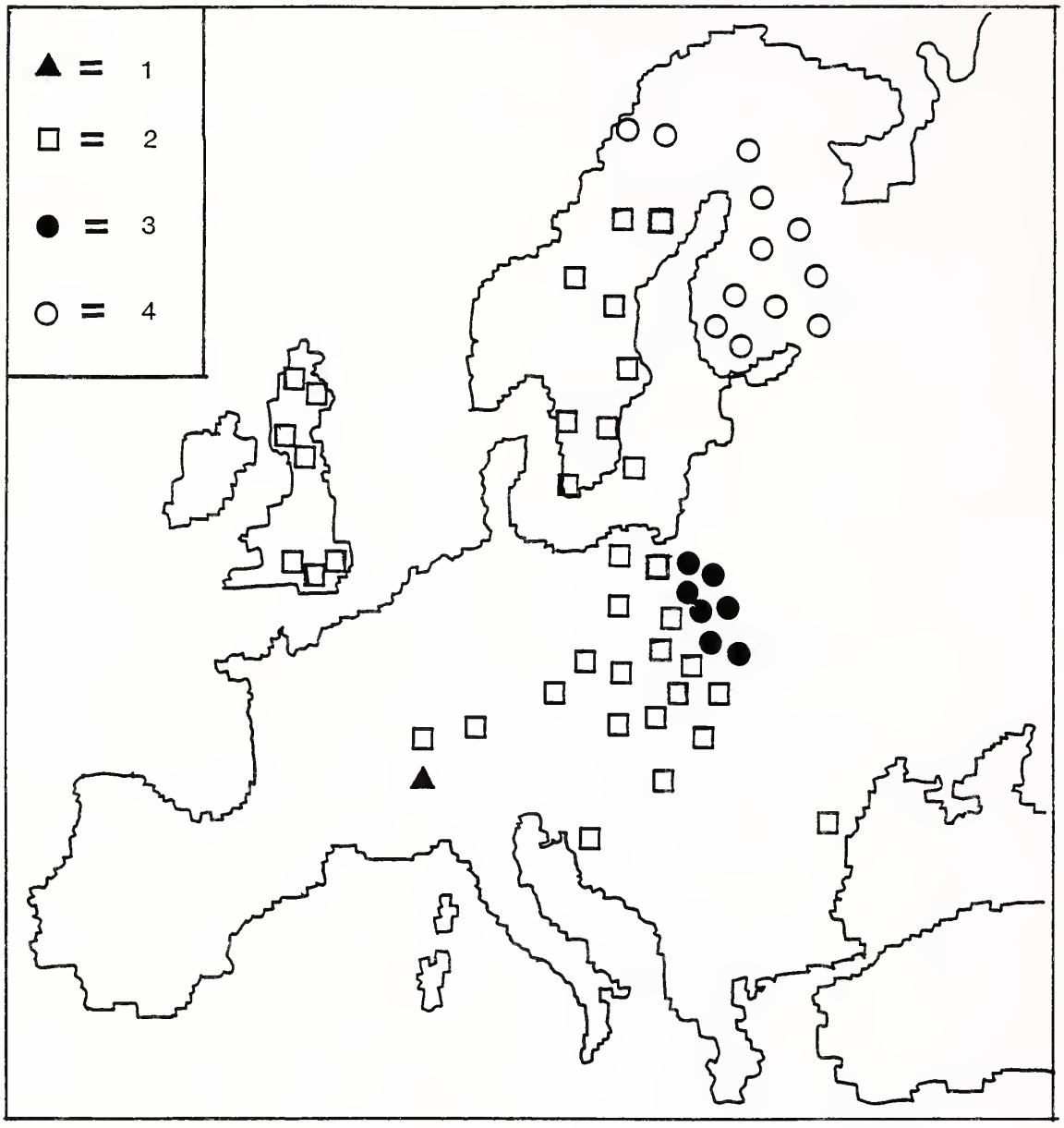

Fig. 3.—Distribution of karyotypic races of *S. araneus* in Europe. Karyotypic races are combined in four groups due to their apomorphies: 1 (triangle) = hj, gi, lo; 2 (open square) = gm, hi; 3 (closed circle) = gr; 4 (open circle) = ip.

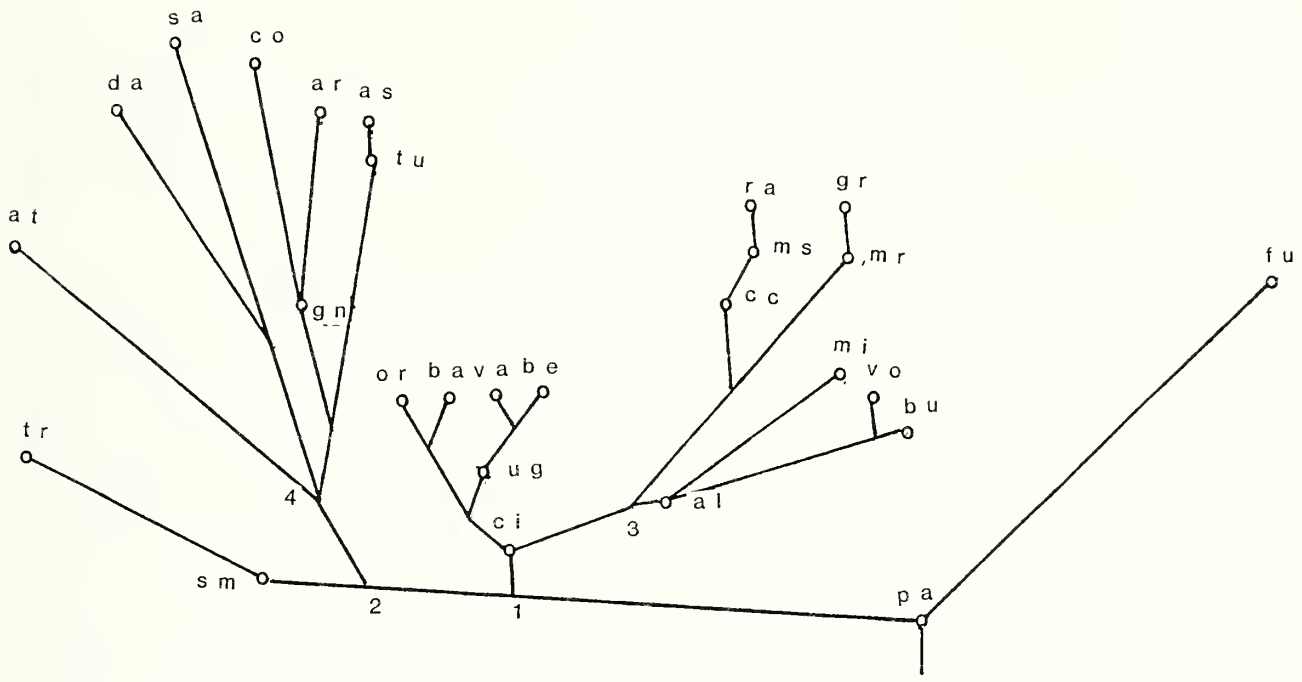

Fig. 4.—Cladogram WISS reflecting phylogenetic relationships of the *Sorex* species: pa, a proposed ancestral *Sorex* karyotype with 2Na = 94; at, *S. arcticus* (2Na = 26); ar, *S. araneus* (2Na = 18–26); as, *S. asper* (2Na = 30); al, *S. alpinus* (2Na = 54); bu, *S. bucharensis* (2Na = 38); be, *S. bendiri* (2Na = 52); ba, *S. bairdi* (2Na = 51–52); cc, *S. caecutiens*, *S. unguiculatus*, *S. isodon*, *S. roboratus* (2Na = 40); co, *S. coronatus* (2Na = 20); ci, *S. cinereus*, *S. leucogaster* (2Na = 64); da, *S. daphaenodon* (2Na = 24, 26); fu, *S. fumeus* (2Na = 64); gr, *S. gracillimus* (2Na = 34); gn, *S. granarius* (2Na = 32); mi, *S. minutus* (2Na = 40); ms, *S. minutissimus* (2Na = 36); mr, *S. mirabilis* (2Na = 36); or, *S. ornatus* (2Na = 52); ra, *S. raddei* (2Na = 34); sm, *S. samniticus* (2Na = 50); sa, *S. satunini* (2Na = 22); tr, *S. trowbridgii* (2Na = 32); tu, *S. tundrensis* (2Na = 28–37); ug, *S. ugyunak* (2Na = 58); va, *S. vagrans* (2Na = 52); vo, *S. volnuchini* (2Na = 38).

THE EVOLUTION OF THE SORICIDAE AS SHOWN BY THE VARIABILITY OF CRANIAL MORPHOLOGY

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ABSTRACT

Three skull variables were examined for their levels of variation within populations of species and of genera of shrews in the Family Soricidae, and among related families of primitive placental mammals. Characters which exhibit highly correlated variability at the population level and over time also manifest the same correlations throughout the geographic range. The amount of variability increases significantly at the generic level compared to the population and species levels, and soricid shrews have slightly more variability in the proportions of the skull than other families of primitive placental mammals.

INTRODUCTION

The pattern of character variability at the population level reflects the early adaptive peculiarities of the populations and expresses the morphological reorganization of organs in phylogenesis. I examined this variability using concrete data. In choosing a methodology, I tried to maintain simplicity and universality for all cases studied in order to reveal the most general principles.

The Order Insectivora and its close relatives were chosen because they comprise an old, diversified, and widely distributed group. I studied the families traditionally grouped in the Order Insectivora, although in the view of many contemporary authors some of these families, e.g., Macroscelididae, should be placed in separate orders. This approach permits broader comparisons and more universal conclusions. Although there is controversy on the number of genera in the Family Soricidae, I recognized 21 genera, which is closest to the position of Sokolov (1973).

MATERIALS AND METHODS

Material came from the author's collection, and the collections of several Russian museums and the British Museum (Natural History).

The choice of characters for study of taxonomic variability presents substantial difficulties (Simpson, 1948), the most fundamental of which are: (1) the choice of individual characters for measurement, (2) the ability to express measurements in comparable units, and (3) the assignment of weights to the characters in order to obtain reliable general averages. In addition, the coefficient of variation of volumetric values calculated using linear measurements is not comparable to that of linear and surface measurements (Schmalhausen, 1935).

Three basic craniometric characters were selected for analysis: the condylobasal length of the skull, the length of the upper toothrow, and the width of the rostrum. These characters can be evaluated quantitatively and are more comparable at all levels of the taxonomic hierarchy. Functionally, they are interpreted as indicators of the distribution of strength for seizing, holding, extracting, and dismembering prey in various ecological situations.

Among the various statistical measurements, special attention is given to the coefficient of variation (CV):

$$CV = \frac{\sigma * 100}{\bar{X}}$$

The CV is abstracted from the absolute value of the characteristic and is an indicator of the strength of the controlling factor (Jablakov, 1966). In this paper, the CV of the measurements of individuals is used to characterize the variability of populations (geographic selection). The average CV of populations is used to characterize the variability of species, the average CV for species is used to characterize the variability of genera, and the average CV for genera is used to characterize the variability of families. In all cases, the averages were weighted according to importance.

$$\bar{X} = \frac{\Sigma W_i X_i}{\Sigma W_i}$$

(Zaks, 1976)

For a more complete description of forms, taxa, and their interactions, I used orthographic regression. The straight line is derived by the method of least squares, according to the formula:

$$tg2\varnothing = \frac{\sum_{i=1}^{n} (X_i - X)(Y_i - Y)}{\sum_{i=1}^{n} (X_i - X)^2 - \sum_{i=1}^{n} (Y_i - Y)^2}$$

This line is called the line of orthographic regression of the gradient line (Linnick, 1962). Generally, the points (P_i) are located in an elongate strip and the angle (λ, the angle of the gradient line to the X axis) is derived simultaneously. The equation for linear regression is as follows:

$$Y = B_0 + B_1 * X$$

The coefficient B_0 characterizes the significance of Y when B_1

= 0. This is a theoretical situation. The angle λ depends on the coefficient B_1 and is used in this paper since it has significance which can be interpolated from the biology of the taxa. To some degree, λ characterizes the changes in skull proportions with allometric growth of the parts of the skull.

The data presented establish general tendencies in a large number of observations. As a rule, the null hypothesis was not checked. Only illustrative examples are provided, not the complete body of data.

Genera such as *Suncus*, *Sorex*, and *Crocidura* are characterized by an abundance of species and wide geographic distributions, permitting a multifaceted comparison of their variability. For this reason, they have been used most frequently for analysis. Individual characteristics change at the population level, as do combinations of characters, in species of the same and different genera.

Results

In *Crocidura suaveolens* from Tadjikistan ("Tiger Ravine" collection), the CV of individual characters (Fig. 1) increased in the sequence: condylobasal length of the skull (2.7), length of the upper toothrow (3.2), and width of the rostrum (3.7). Sometimes the upper toothrow measurements showed the greatest variation. For example, in *C. hirta* from Lake Tanganyika the corresponding CVs were 3.6, 5.1, and 3.1, respectively. The amount of population variability in individual linear characters of the species in the genus *Crocidura* was similar, although it fluctuated within a broad range. The variability of the upper toothrow ranged from 1.7 (*C. fumosa* from Tanzania) to 7.6 (*C. flavescens* from Ethiopia). The mean values of CV for populations of *Crocidura* species (16 populations, 7 species) were 3.1, 3.4, and 3.4, respectively.

In *Crocidura* populations, pairs of characters tend to vary together. This correlation is more pronounced than differences in the variability of characters taken individually. The correlation coefficient between condylobasal length of the skull and the length of the upper toothrow in *C. suaveolens* from "Tiger Ravine" was 0.7. For the condylobasal length and the rostrum width, the correlation coefficient was 0.6, and it was 0.5 for the upper toothrow length and the rostrum width. These differences are not great, but the pattern held for all populations. The average correlation coefficients of these character pairs were 0.80, 0.61, and 0.54, respectively.

These characters are even more consistent within populations of species in the genus *Sorex*. The variability increases in the same sequence as with the *Crocidura*: condylobasal length of skull, length of upper toothrow, and rostrum width. In *S. sinalis* from the Perm region, for example, the CVs of these characters were 1.4, 1.8, and 2.6, respectively. On the average (11 populations, 7 species) the CVs of these characters in *Sorex* were 1.54, 1.90, and 2.30, respectively. The amount of character variability within species of *Sorex* was not significant (range 1.05 to 2.98), indicating that the potential evolutionary capabilities of the lowest evolving units in a genus are similar.

In populations of the genus *Sorex*, the correlation coefficient of the condylobasal length of the skull and the upper toothrow length is greatest, and that between the upper toothrow length and rostrum width is the least. For example, the correlation coefficients of these pairs were 0.70 and 0.20, respectively, in *S. sinalis* from Kamchatka. On average, the variability of craniometric features of populations of the genus *Sorex* was less than that of species of *Crocidura*.

The levels of craniometric variability within populations of *Neomys fodiens* were similar to those of the populations of *Sorex*. The CV of the condylobasal length of the skull in several populations ranged from 1.6 to 2.2, that of the upper toothrow length ranged from 2.1 to 2.4, and the CV of the rostrum width ranged from 1.9 to 2.5. Usually the condylobasal length of the skull was the least variable character, but the variability of all characters was not significantly different.

Populations of species of *Suncus* also show a broad range of character variability, and the amount of variability of each character within populations of a single species is also large. For instance, the CV of the condylobasal length for populations of *Suncus murinus* from Madagascar was 5.2, that of the upper toothrow was 10.2, and that of the width of the rostrum was 4.7. In populations of *S. murinus* from Sri Lanka, the CVs for these characters were 11.5, 10.2, and 12.7, respectively.

Thus, cranial characters of shrews are seen to vary in ways characteristic for the taxa. The absolute values of the characters, the amount of variability of single characters, and the relative variability of several characters within a taxon are specific to that taxon. There are also deviations within taxa and similarities among taxa, which suggests that the variations are influenced not only by the relationships within a taxon but also by the relationships among taxa. This does not reject the theory that closely related species populations show more similar variability in character complexes than do populations that are less closely related.

Populations display character variability through time in much the same manner. In *Crocidura suaveolens* from southwestern Tajikistan, the average CV of the condylobasal length of specimens collected over an eight-year period was 0.8. The CV of the upper toothrow was 1.2 in these specimens and that of the rostrum width was 1.6. There was a definite increase in variability from one character to another. There was a statistically significant difference in the CV of the condylobasal length of specimens taken in 1970 and 1972, and a similar difference in the CVs of the rostrum widths of specimens taken in 1960 and in 1972. In fact, the average indicators for these years were significantly different from the average of all specimens taken in all years, although each character varied differently. This shows some degree of variability in these features over time in a single population.

The differences in character variability over time in this group also correlate with the degree of differences in variability of these characters within a single season. The correlation coefficient between the variability of the upper toothrow length and the rostrum width was the least (0.5) of the three pairs. Fewer differences were found between the condylobasal length of the skull and the rostrum width (correlation coefficient of 0.61). On the other hand, the direction of change of the correlation coefficient agrees with the change in the direction of the gradient line by year. The CV of the angle *L* (defining the

slope of the line) for condylobasal length/rostrum width was 4.0, whereas for the upper toothrow length/rostrum width pair it was 15.1 (Fig. 1). The lower the correlation coefficient for two indicators, the greater the multiyear variability in their proportions and vice versa.

The wide variability of the size of the skull from year to year is illustrated by comparing subadults and overwintering adults of *Sorex* and *Neomys*. In some instances, subadults were larger, in others they were smaller. Obviously, this pattern is connected with variations in favorability of living conditions from year to year (Dehnel, 1952; Dolgov, personal observation).

Geographic variability of species is also related to population and chronological variability. Forms living in temperate zone plains with smooth gradations of environmental conditions typically exhibit clinal variability in metric indicators. The genus *Sorex* is dominant in these parts of the geographic range of the Family Soricidae. Usually the variability is not smooth, but is polyclinal. For example, the variability of the condylobasal length of the skull of *Sorex caecutiens* in the eastern part of its range decreased to the west (Dolgov, 1966, 1972). In the central part of the range, it decreased from south to north and simultaneously to the west. In *S. tundrensis* from the Altai, variability of the condylobasal length decreased to the west, north, and northeast. The variability of this character in *S. sinalis* decreased in the central part of its range from west to east (Dolgov, 1966, 1972).

The direction and amount of change in variability may be similar between characters (homoclinal), or may be different (heteroclinal). For example, the variability of both the condylobasal length and the upper toothrow length of *S. sinalis* increased in the central part of the range, whereas the variability of rostrum width remained the same. The same relationship in the variability of these characters was observed in other widely distributed species, including *S. caecutiens* and *S. tundrensis* (Dolgov, 1966, 1972).

Overall, characters which exhibit highly correlated variability at the population level and over time also manifest the same correlations throughout the geographic range. For example, the condylobasal length of skull and the length of the upper toothrow are homoclinal with respect to each other. Characters which are less correlated with each other at the population level and over time also are heteroclinal over the geographic range.

Forms belonging to families with southern and tropical distributions exhibit a regional-mosaic type of geographic variation. For example, neighboring populations of *Crocidura suaveolens* from the ridges of Tien-Shan, Pamir, and Pamiro-Alaya Mountains and nearby regions of Afghanistan formed a mosaic conglomerate of more or less differing forms without showing vectorized trends (Dolgov, personal observation). A similar example of regional-mosaic variability was provided by *Suncus murinus* (Dolgov, personal observation). The degree of difference in the genic variability was less in the genera *Suncus* and *Crocidura* than in the genus *Sorex*. This corresponds well with the smaller differences in population variability of individual characters in these two genera, and with the smaller differences in correlation coefficients for character pairs for these genera as compared to *Sorex*. Thus, for these genera a pattern is seen between population and geographic variability.

The degree of variability of linear characters of species of the widely distributed genus *Sorex* is greater at the species level than at the population level. For instance, the CV of the condylobasal length of the skull varied from 2.0 (*S. araneus*) to 3.7 (*S. tundrensis*), whereas in the more narrowly distributed species it ranged from 0.6 (*S. gracillimus*) to 1.7 (*S. bedfordae*). But there were instances in which a species with a wide distribution (*S. sinalis*, 2.2) had less variability than one with a smaller distribution (*S. tundrensis*, 3.7).

The indices of regression for *Sorex* at the species level demonstrate a tendency toward correlation of features at the population level related to the geographic variability of pairs of characters. The minimal variability of the angle of the gradient line for the condylobasal length/toothrow length pair is typical. It varied for widely distributed species from 7.3 (*S. caecutiens*) to 13.8 (*S. minutus*). This agrees with the maximum coefficient of correlation in their populations and with their geographic homoclinality.

The CV of the linear characters (condylobasal length, toothrow length, and rostrum width) of the genus *Crocidura* was less at the species level in some cases than it was at the population level. For instance, the CVs of *C. flavescens* were 5.8, 6.0, and 5.7, respectively, and in *C. hirta* the CVs of the same characters were 2.5, 2.6, and 2.6. In other instances (Fig. 1), the CVs of the features at the population level were smaller than they were at the species level (*C. lasiura*: 4.6, 5.9, 6.3) and in still other instances they did not vary significantly (*C. suaveolens*: 2.7, 3.2, 3.0).

The variance of individual characters differs between species to some extent. In some instances the pattern of variability of all characters was of the same sequence (*C. hirta*, *C. flavescens*). In others, the upper toothrow length showed the most variability (*C. leucodon*: 2.7, 41.0, 2.8). Rostrum width was often the most variable character, but the difference between its variability and that of other characters was not great. On the whole, the genus *Crocidura* typically exhibited diversity in the variability of individual characters.

Unlike the linear features, there are species differences in the angle (λ) of the regression line. In individual species the differences are similar in their sequences, but are quantitatively different. The λ of the regression of toothrow length on rostrum width was most variable: 14.8 in *C. fumosa*, 29.9 in *C. suaveolens*, and 37.2 in *C. russula*, whereas the condylobasal length regressed on rostrum width was least variable: 5.9 in *C. lasiura* and 11.8 in *C. suaveolens* (Fig. 1). The variability of species of other genera was similar qualitatively and quantitatively. On the whole, variability of λ at the species level increased, reflecting increases in the versions of the cranial proportions in different geographical populations of a species as compared with the variation in one population over many years.

At the generic level, the amount of variability of characters increases significantly. The CV of the condylobasal length of the skull in the genus *Crocidura* was 23.2, the upper toothrow length was 25.6, and the rostrum width 24.2 (Fig. 1). In the genus *Sorex*, the CVs of the same characters were 12.0, 13.0,

and 15.7, respectively, whereas the species maxima for the characters were 3.7, 4.5, and 5.6, respectively. This shows that variability of characters relative to each other preserves the same sequence at generic and specific levels. The rostrum width is the most variable character, followed by the upper toothrow length and the condylobasal length.

By contrast, the variability of λ (indicative of variability in skull proportions) does not increase significantly at the generic level. In the genus *Crocidura* (22 species examined), the variability of the condylobasal length regressed on upper toothrow length was 8.5, the variability of the condylobasal length regressed on upper rostrum width was 12.9, and that of upper toothrow length regressed on rostrum width was 28.4 (Fig. 1). In 19 *Sorex* species, the variabilities for these regressions were 15.8, 14.4, and 20.8, respectively. This indicates definite stabilization in divergence of proportions of the crania at the generic level.

Evolution of individual characters relative to each other preserves at generic level both variations in populations through time and geographic variation at the species level. Condylobasal length and toothrow length are most strongly correlated geographically and chronologically; the proportions of these characters are similar in both genera and species. Since these characters have minimum impact on the variations of genera and species over time, it is more important that genera and species exhibit independent geographic modification.

This was demonstrated by comparing the average generic and specific values. *Diplomesodon* had the widest rostrum relative to the condylobasal length of the skull; *Sorex* and *Microsorex* (now also called *Sorex*) had the narrowest. All other species in the family, including *Suncus* and *Crocidura*, occupied intermediate positions. The same general relationships among genera were observed in the relationship of the rostrum width relative to the upper toothrow length, although there was less difference among species and *Blarinella* had the narrowest rostrum. The genera of the Family Soricidae have undergone a similar evolution in the relationship of the upper toothrow length relative to the condylobasal length of the skull; no divergence was observed (Fig. 2). The distribution of cranial proportion by average species character is valid for all species of these genera (Fig. 3).

An ecological interpretation of differences in variability of these characters at the generic level is possible. Species of *Sorex* (including the former *Microsorex*) are adapted to the extraction of comparatively slow-moving and soft-bodied prey which are mined from the litter of the boreal forest floor. These species have developed a dolichognathic skull. Species of the genus *Diplomesodon* have a brachyognathic skull, which supports holding and cracking of more mobile, harder-bodied prey found on the surface in arid zones. The species of the genera *Crocidura* and *Suncus* occupy intermediate positions.

In general, the degree of dolichognathicity or brachyognathicity of the skull is associated with aridity of the ranges occupied by the genera: *Diplomesodon* occupies deserts, *Crocidura* and *Suncus* occupy plains, and *Sorex* (including *Microsorex*) live in forests. Thus, the tendencies of variability of characters at the population and species levels are realized in the phylogenetic specificity of form.

Increase or decrease in the size of any character causes preconditions for changes in both the qualitative and quantitative functionality of the other characters. A disproportionate change in a single character relative to the others increases even more the possibility of a qualitative change in function, permitting divergence of many kinds (Dolgov, 1976).

The factors which determine the correlation of character variability at the species and subspecies levels were discussed by Schmalhausen (1940). At the species level, correlations of character variability indicate physiological interrelationships of the individual. Above the species level, they indicate phylogenetic relationships. This is the border between micro- and macroevolution. The continuity of similarities and differences in variability is preserved in this instance.

There was slightly less variability (CV) in the linear measurements in the Family Soricidae (Table 1) than in the same characters at the generic level, especially in the genus *Crocidura* (Fig. 1). Single character variability reflects the peculiarities of genera; for instance, the length of the skull is less variable than the width of the rostrum. The stability of the proportions of the skull noted at the generic level (Table 2) becomes even more pronounced at the family level (Fig. 1).

The stabilization of variation of these characters and their relationships reflects stabilization of the cranial morphotype of shrews at the family level. The similarity of this cranial morphotype in various biologically prosperous genera demonstrates its universality and high biomechanical utility. Variants are most often found in the specializations of individual species.

The Soricidae has more genera than other insectivore families, and soricid shrews are the most widely distributed. They are established in a wide spectrum of landscape zones and biotypes. Regardless of this ability, the variability of individual cranial characters at the family level is the lowest of any family considered here (Table 1). Soricid shrews, however, exhibit the same or slightly more variability in the proportions of the skull than is found in the other families of primitive placental mammals (Table 2).

Variability in individual cranial characters increases above the family level (Fig. 1, Table 1), which reflects a well-defined divergence of families. At the same time, the variability of cranial proportions is not significant (Fig. 1, Table 2). The relation between skull length and rostrum width was most variable in all groups.

Discussion

The families considered here have developed common cranial proportions. According to Schmalhausen (1945), "...this stability is not the absence of variability, but rather it is based on that variability always being led in a specific direction." The stability of the cranial morphotype of shrews at the family level may be the result of variation of stabilizing selection (Schmalhausen, 1946). This is canalizing selection, in which feedback mechanisms support development of a standard phenotype despite changes in genes, genotypes, and fluctuations in external conditions (Waddington, 1957, 1960). A number of

the morphological characters of the skulls of these families are primitive, leading Wilson et al. (1975) to postulate a low rate of evolution for the families listed in Table 1.

Thus, the pattern of character variation, the individual and comparative qualitative characteristics of this variation, and the correlation between the variability of some characters and the independence of others can be traced from the population—the primary evolutionary unit—through the taxonomic hierarchy to species, genus, family, and order. This pattern is considered sequential, the most likely chain of events in the phylogenetic development of characters and their complexes. The morphometric variability of characters and the corresponding variability in their functions emerge as population adaptations and simultaneously produce the prerequisites for evolutionary transformation of organs.

In Chapter 14 of *The Origin of the Species*, Darwin (1859) noted, "The larger and more dominant groups within each class thus tend to go on increasing in size; and they consequently supplant many smaller and feebler groups." These and other indicators of biological progress were also developed by Schmalhausen (1940, 1946) and Heptner (1965), based on taxonomic material. According to these theories, *Sorex*, *Crocidura*, and *Suncus* are biologically progressive genera, since there are many species in each genus, both the genera and their constituent species inhabit geographically wide areas, their karyotypes exhibit polymorphism, and they evolve new forms.

In these theories, biological progress is tied to morphological change. The morphology of shrews corresponds to a high degree with the demands of their environment and "does not require" radical improvements. However, sometimes the environment changes radically, from warmer to cooler or from wetter to drier. In order to survive, it is necessary to constantly conform to new conditions and shrews have "solved" this problem. They possess the capacity for high rates of evolution within their already developed morphotypes and the maximum adaptive variability at the specific and generic levels. This supports morphological adjustment to the environment.

The morphological changes in shrews are not vectorized, but reflect established changes in morphology at lower taxonomic levels. The evolutionary pattern in shrews may be said to be an "indefinitely mobile cladogenesis," as demonstrated by rapid changes in a limited number of morphological variants. If evaluated as directional (vectoral) changes in morphology, they seem to evolve slowly. In actuality, the rate of their evolution may be high. Perhaps it is precisely such an evolutionary mechanism which allowed shrews and their ancestors to pass successfully from a role as the forefathers of placental mammals in the Cretaceous era to a position as one of the most flourishing groups existing today. It can be assumed that even in the early stages of evolution, their morphotypes were highly adapted to their environments.

The possibilities of successful indefinitely mobile cladogenesis are realized by the less specialized genera, such as *Sorex*, *Crocidura*, and *Suncus*. This provides the basis for the assumption that it is precisely these groups which will continue to be the central branches on the evolutionary tree of the Soricidae in the future.

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Table 1.—*Variation in the craniometric characters of members of the Soricidae and related families.*

Family	Condylobasal Length of the Skull (mm) MIN	MEAN	MAX	Upper Toothrow Length (mm) MIN	MEAN	MAX	Rostrum Width (mm) MIN	MEAN	MAX
	σ	CV	N	σ	CV	N	σ	CV	N
Soricidae	11.8	21.95	39.4	5.1	10.02	18.3	2.90	6.57	13.2
	4.53	20.66	20	2.15	21.47	20	1.62	24.64	20
Erinaceidae	29.5	47.67	90.5	15.4	24.67	49.9	9.2	15.83	27.4
	16.39	34.39	6	9.23	37.42	6	5.46	34.49	6
Talpidae	19.5	30.85	56.0	8.90	14.20	30.7	5.80	8.7	17.8
	8.4	27.24	13	5.02	35.37	13	2.82	32.43	13
Potamogalidae	34.7	49.0	67.0	15.1	23.0	32.3	10.3	14.1	18.8
	—	—	2	—	—	2	—	—	2
Tenrecidae	16.2	42.86	112.4	7.60	20.14	59.3	4.90	11.57	28.7
	16.51	38.52	7	9.88	49.14	7	4.10	35.44	7
Solenodontidae	74.3	80.04	83.3	38.7	40.22	41.0	23.8	24.32	24.9
	—	—	1	—	—	1	—	—	1
Chrysochloridae	15.80	23.45	40.3	7.0	10.7	18.7	6.50	8.70	14.1
	6.26	26.70	4	2.67	24.95	4	1.73	19.91	4
Macroscelididae	28.7	43.58	64.1	7.8	22.45	30.5	3.80	6.95	14.4
	12.32	28.27	4	5.08	22.63	4	3.27	47.04	4
All Families	11.80	42.62	112.4	5.10	20.75	59.30	2.90	12.25	28.7
	17.23	40.43	8	9.05	43.62	8	5.38	43.95	8

Table 2.—*Relative proportions of cranial measurements of families of the Soricidae and related families.*

Family	Ratio of Condylobasal Length to Upper Toothrow Length MIN	MEAN	MAX	Ratio of Condylobasal Length to Rostrum Width MIN	MEAN	MAX	Ratio of Upper Toothrow Length to Rostrum Width MIN	MEAN	MAX
	σ	CV	N	σ	CV	N	σ	CV	N
Soricidae	55.00	64.10	68.0	63.00	71.70	82	52.00	57.30	72
	4.05	6.32	20	5.24	7.30	20	6.25	10.91	20
Erinaceidae	55.00	63.00	67	69.00	77.83	90	49.00	65.00	90
	3.92	6.22	6	5.27	6.78	6	13.45	20.70	6
Talpidae	40.00	64.07	83	64.00	77.46	91	47.00	64.15	90
	10.72	16.88	12	8.61	11.11	12	15.64	24.39	12
Potamogalidae	50.0	55.0	60	63.00	68.50	74	59.00	60.50	62
	—	—	2	—	—	2	—	—	2
Tenrecidae	45.00	67.00	75	30.00	69.90	85	30.00	51.14	78
	9.89	14.75	7	16.86	24.14	7	13.43	26.26	7
Chrysochloridae	68.00	71.50	78	72.00	79.00	86	44.00	63.00	85
	4.09	5.72	4	6.52	8.25	4	16.69	26.49	4
Macroscelididae	57.00	62.50	69	82.00	87.00	96	79.00	85.25	100
	—	—	4	—	—	4	—	—	4

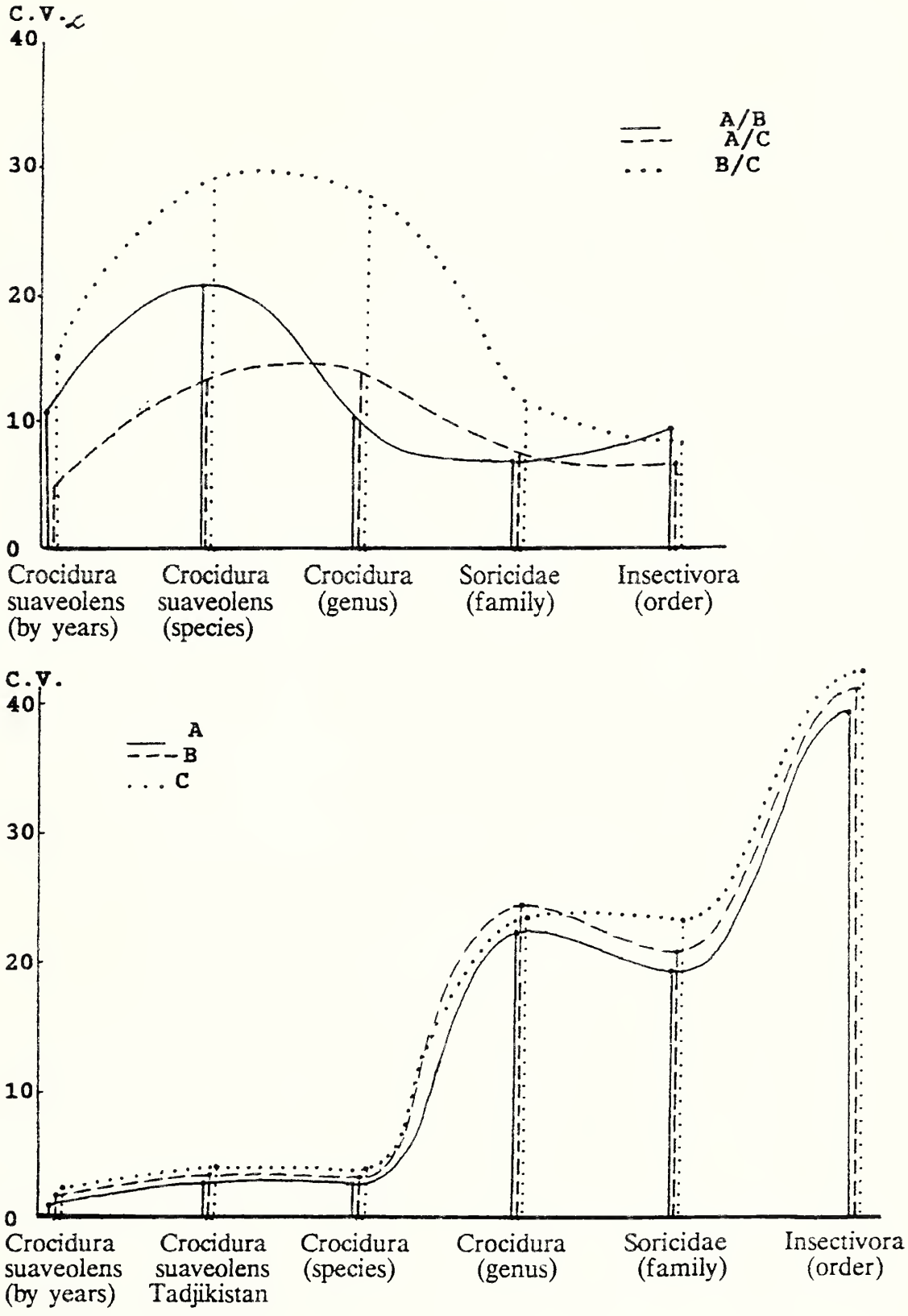

Fig. 1.—The variability of linear characters and proportions (the gradient line angle) of the primitive placental mammals at different levels of taxonomic hierarchy. A, condylobasal length of skull; B, upper toothrow length; C, rostrum width.

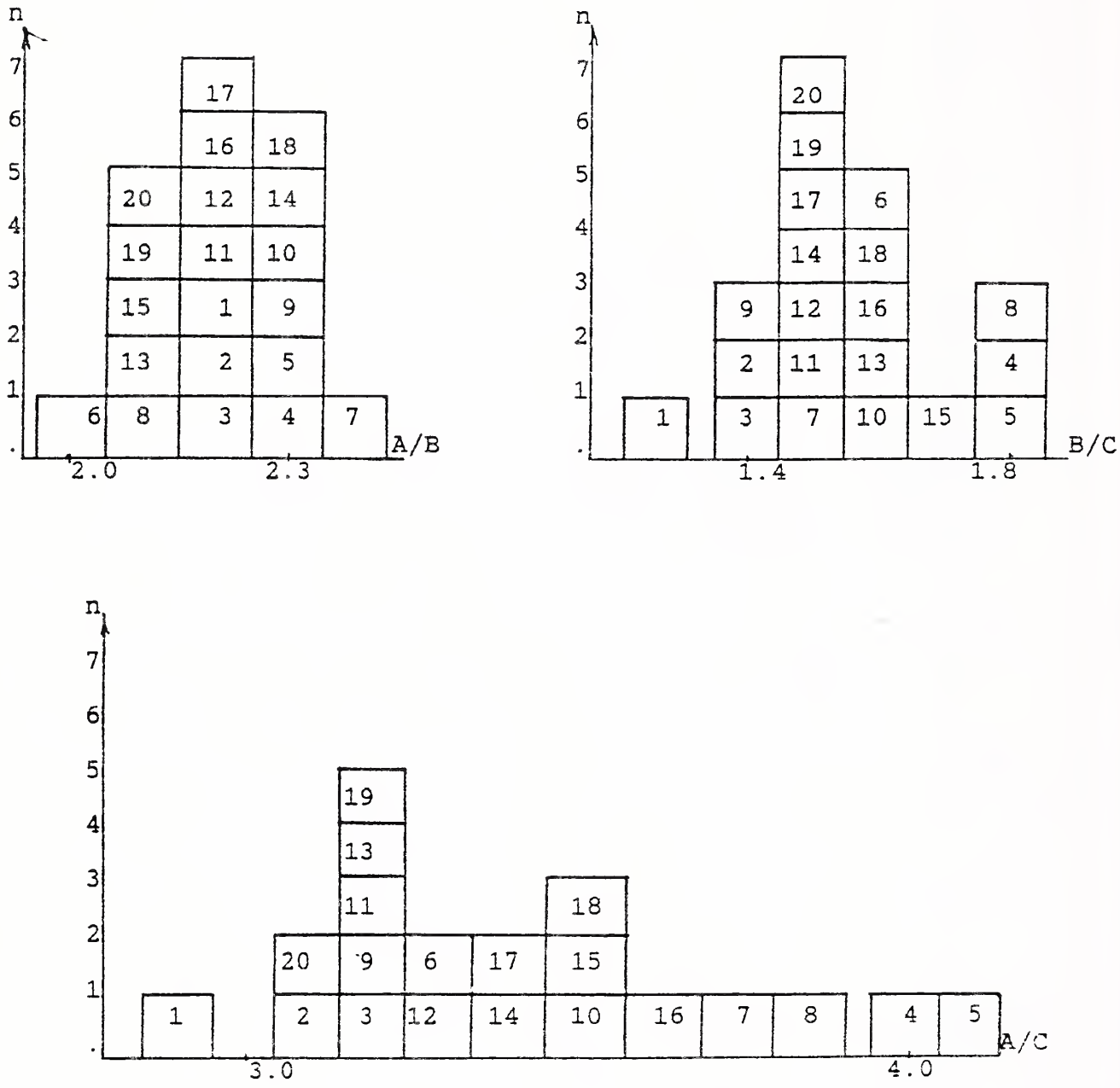

Fig. 2.—The distribution of soricid genera according to craniometric characters, using the letters as defined in Fig. 1. The genera are: 1, *Diplomesodon*; 2, *Crocidura*; 3, *Suncus*; 4, *Microsorex*; 5, *Sorex*; 6, *Anourosorex*; 7, *Feroculus*; 8, *Blarinella*; 9, *Myosorex*; 10, *Surdisorex*; 11, *Scutisorex*; 12, *Solisorex*; 13, *Blarina*; 14, *Cryptotus*; 15, *Neomys*; 16, *Soriculus*; 17, *Notiosorex*; 18, *Chodsigoa*; 19, *Chimarrogale*; 20, *Nectogale*. n = number of genera.

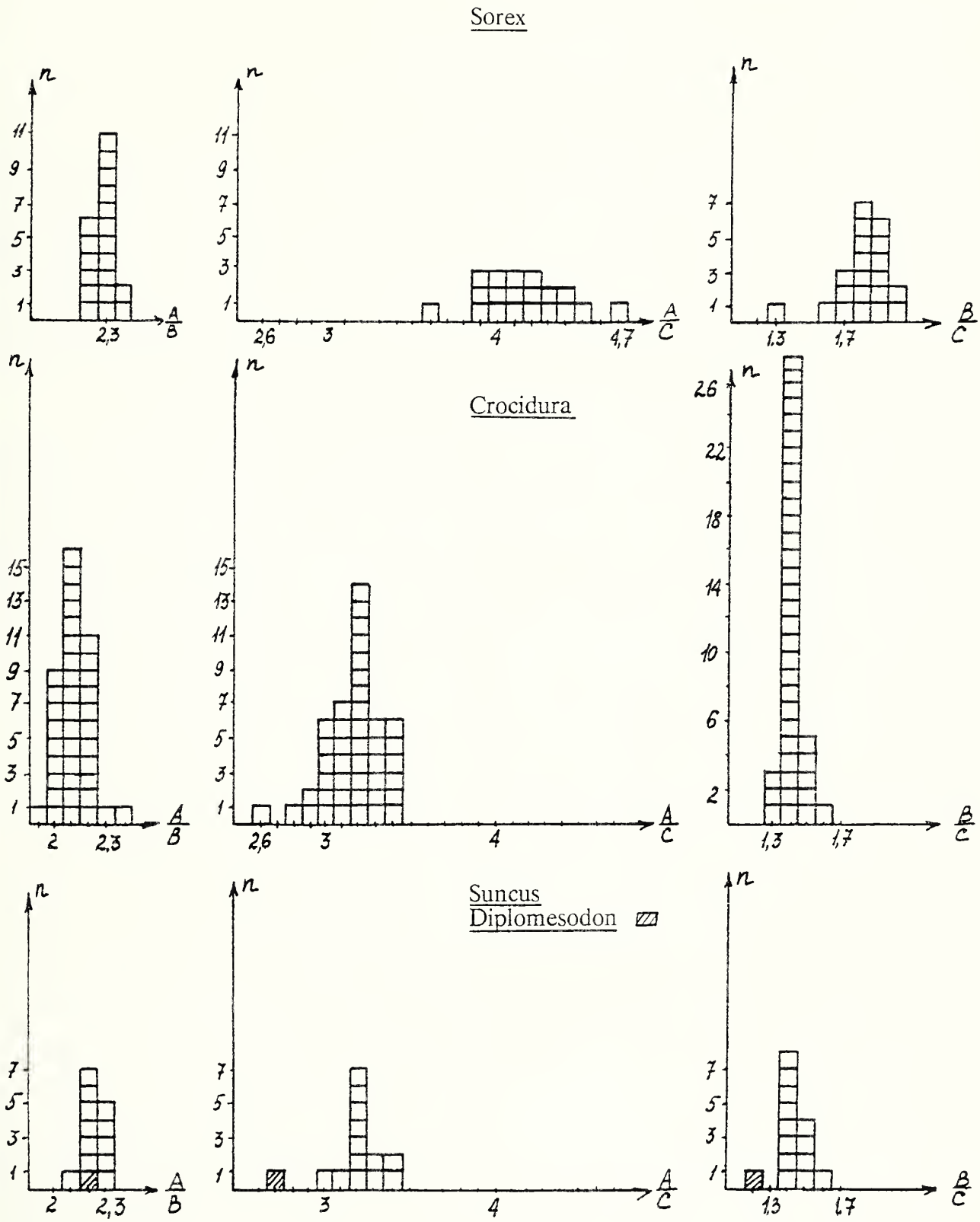

Fig. 3.—The variability of four soricid genera according to craniometric characters, using the letters as defined in Fig. 1.

CHROMOSOMAL EVOLUTION IN THE GENUS *CROCIDURA* (INSECTIVORA: SORICIDAE)

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ABSTRACT

Available *Crocidura* karyotypes (38 taxa) are used to investigate chromosomal evolution in the genus. Intraspecific variability is relatively rare, whereas interspecific differentiation is common. Diploid chromosome numbers range from 2N = 22 to 2N = 60, and fundamental numbers from FN = 34 to FN = 86. Based on comparisons of differentially-stained chromosomes of Palearctic, Afrotropical, and Oriental species, a hypothetical ancestral karyotype is proposed: it has 38 elements consisting mostly of acrocentric or subtelocentric chromosomes, and four metacentrics. Three main chromosomal evolutionary tendencies are recognized. The first retains a karyotype close to the ancestral state with around 40 chromosomes and is found, as expected from its plesiomorphic state, in all zoogeographic regions inhabited by *Crocidura*. The second tendency is to increase both diploid and fundamental numbers, as is characteristic of most African *Crocidura*. The third tendency, which reduces the diploid number mainly through Robertsonian fusions, is apparently restrieted to Eurasian species. The karyological data corroborate a phylogenetic hypothesis derived from biochemical data that the genus *Crocidura* contains two monophyletic clades: an Afrotropical clade and a Palearctic-Oriental clade.

INTRODUCTION

According to Repenning (1967), the two extant subfamilies of Soricidae (Crocidurinae and Soricinae) diverged from a common ancestor during the Oligocene. The genus *Crocidura* appeared later, probably during the Miocene, somewhere in Africa where most of the species now occur (Heim de Balsac and Meester, 1977). Since the Miocene, the genus *Crocidura* has radiated considerably. More than 140 species occur in the Old World from the African continent to the Palearctic and Oriental regions (Hutterer et al., 1982).

Recently, methods such as allozyme electrophoresis have added considerably to knowledge of the evolution of the Soricidae (Catalan, 1984; Catzeflis, 1984), the Soricinae (George, 1986), and the Crocidurinae (Maddalena, 1990*a*). The last author compared Palearctic and Afrotropical *Crocidura* cladistically (Fig. 1). The results suggested the existence of two monophyletic groups, each corresponding approximately to a different zoogeographic region. *Crocidura bottegi* and *C. luna* do not group with either clade, probably because they retain many ancestral isozymes. Based on morphological characters, the two species were also regarded as primitive (Heim de Balsac and Lamotte, 1956, 1957; Butler and Greenwood, 1979).

The first cytogenetical studies of *Crocidura* were done about 40 years ago by Bovey (1949) in Switzerland, and later by Meylan and coworkers (see Reumer and Meylan, 1986, for a review). These early studies showed relatively great interspecific chromosomal variation and a very low level of intraspecific polymorphism. Undifferentially-stained karyotypic preparations were useful for recognizing and characterizing species, but of limited utility for establishing chromosomal homologies. Only recently have differentially-stained karyotypes of *Crocidura* been published (Harada et al., 1985; Tada and Obara, 1986; Hutterer et al., 1987*a*; Grafodatsky et al., 1988; Maddalena, 1990*b*; Maddalena and Vogel, 1990), thus enabling comparative studies.

First we present a synopsis of known *Crocidura* karyotypes, and analyze intra- and interspecific variation. Second, on the basis of comparison of G-banding patterns of European, African, and Asian species, we propose a hypothetical ancestral karyotype for the genus *Crocidura* and discuss how the different extant species evolved from the primitive state. Finally, we compare findings based on chromosomal data with the hypotheses of relationships based on biochemical data (Fig. 1).

SYNOPSIS OF *CROCIDURA* KARYOTYPES

In checklist form, Reumer and Meylan (1986) listed the chromosome formulas of 21 *Crocidura* species. Since then (1991), information for 17 additional species has accumulated. Table 1 includes all karyotypes of *Crocidura* species available, covering about one-fourth of the known species. Unless noted, the scientific names are as in the original papers. In a few cases, the chromosome formula was adapted to standardize chromosomal characteristics, which are the diploid number (2N), the fundamental number of chromosomal arms including the two female sex chromosomes (FN), and the shape of both male (Y) and female (X) sex chromosomes. Species are listed according to geographic origin and by increasing diploid number. The genus *Suncus*, sometimes considered a subgenus of *Crocidura* (Ellerman and Morrison-Scott, 1966; Heaney and Timm, 1983) is not included.

RESULTS AND DISCUSSION

Karyotypic Variability in the Genus Crocidura

Intraspecific Variation.—Intraspecific chromosomal polymorphism has been observed in only six of the 38 known karyotypes (Table 1). These are found in all of the three zoogeographical regions occupied by the genus *Crocidura*. Five cases are non-Robertsonian variations, but in one *C. suaveolens* from Japan, a Robertsonian fusion of two acrocentric chromosomes was described, and the diploid number consequently decreased from 2N = 40 to 2N = 39 (Tsuchiya, 1987). A similar case was recently discovered in a *Crocidura* species from the Mediterranean island of Pantelleria (Vogel et

al., 1992). Apart from these rare events, non-Robertsonian variations are more frequent. Variation of the diploid number involving B-chromosomes have been reported in *C. suaveolens*, *C.* cf. *malayana*, *C. poensis*, and *C. crossei* (Meylan and Hausser, 1974; Maddalena, 1990*b*; Ruedi et al., 1990). According to the classification of Volobuev (1981), these are group II B-chromosomes. Another kind of intraspecific non-Robertsonian polymorphism involves extensive FN variations in the Oriental species *C.* cf. *malayana* and *C.* cf. *fuliginosa* and in the African *C. theresae* (Table 1). This is probably due to a varying amount of heterochromatin, which leads to the formation of additional short chromosomal arms.

The female X chromosome is usually a metacentric of large size, although it is submetacentric or acrocentric in six species (Table 1). Intraspecific variation of the X chromosome has been reported only in *C. suaveolens* (Tembotova, 1983; Ivanitskaya, 1989; Maddalena, 1990*b*). The Y chromosome is generally acrocentric or subtelocentric and of small size. However, in *C. bottegi*, *C. horsfieldi*, *C.* cf. *malayana*, and *C.* cf. *fuliginosa* (Meylan, 1971; Krishna Rao and Aswathanarayana, 1978; Ruedi et al., 1990), it is a relatively large submetacentric element. In *C. dsinezumi*, *C. horsfieldi watasei*, *C. suaveolens*, *C. sibirica*, *C. leucodon*, *C. poensis*, and *C. theresae*, the Y chromosome appears to be entirely heterochromatic based on C-banding (Harada et al., 1985; Tada and Obara, 1986; Grafodatsky et al., 1988; Maddalena, 1990*b*; Maddalena and Vogel, 1990), which is probably the general case in *Crocidura*. The male sex chromosome of *C. suaveolens* provides the only real example of intraspecific polymorphism: it has geographically variable size and shape (Tembotova, 1983; Grafodatsky et al., 1988; Ivanitskaya, 1989; Maddalena, 1990*b*). This is similar to the variation found in *Suncus murinus* (Yong, 1971; Yosida, 1985).

Interspecific Variation.—Chromosomal variation is extensive among the species of *Crocidura* (Table 1). The diploid number ranges from 2N = 22 in *C. pergrisea* to 2N = 60 in *C.* cf. *bicolor*, whereas fundamental numbers vary from FN = 34 to FN = 86. Although only about one-fourth of *Crocidura* species have been karyotyped, some interesting tendencies appear when 2N and FN are plotted together (Fig. 2). Most African species have a high diploid number, generally with around 50 chromosomes and more than 60 chromosomal arms. In contrast, all Palearctic and Oriental species have about 40 chromosomes or less and a relatively low fundamental number. The Thai species *C. attenuata* is a notable exception among Oriental species because it has a chromosome formula similar to African species, with 2N = 50 and FN = 66 (Tsuchiya et al., 1979). But if the karyotype of *C. attenuata* is compared to the conventionally-stained karyotypes of the African species *C. olivieri* and *C. viaria*, which have the same chromosome formula (Maddalena, 1990*b*), it is obvious that they are not homologous. The Oriental species has most biarmed elements larger than the acrocentric chromosomes, whereas the opposite situation characterizes the African species. Unfortunately, a banded karyotype is not available for *C. attenuata*, therefore it is not possible to explain the process responsible for this unusual augmentation of chromosome number.

The African species *C. luna* and *C.* cf. *bottegi* and the Palearctic *C. canariensis* and *C. sicula* share the same chromosome formulas (Table 1), which is probably due to the retention of ancestral characters, even though some differences appear on G-banding (Fig. 3, and Maddalena, 1990*b*).

In most *Crocidura* species, the X chromosome is large, meta- or more rarely submetacentric, representing about 6–8% of the haploid genome (Meylan, 1971; Krishna Rao and Aswathanarayana, 1978; Grafodatsky et al., 1988). However, *C. pergrisea* is an apparent exception in having an acrocentric X chromosome (Grafodatsky et al., 1988). Another peculiarity is found in *C. poensis*, wherein the X chromosome is very large and metacentric, representing about 12% of the total genome. Such unusually large sex chromosomes are known in other mammal groups and have generally been attributed either to the insertion of large blocks of heterochromatin or to the translocation of an autosome onto the sex chromosome (Ohno et al., 1964; Hood and Baker, 1986). In *C. poensis*, most of the X chromosome is euchromatic in C-banding (Maddalena, unpublished data). The heterochromatin portions are restricted to the centromere and to a distal band, both of which are also present in the normal-sized X chromosomes of *C. dsinezumi*, *C. horsfieldi watasei*, *C. suaveolens*, and *C. leucodon* (Tada and Obara, 1986; Grafodatsky et al. 1988). Thus, translocation involving an autosome is the more probable origin of this very long chromosome in *C. poensis*.

Hypothetical Ancestral Karyotype

Among the techniques developed to differentiate chromosomes, G-banding (Seabright, 1971) has become the most popular because of its high resolution power. Thus it is possible to compare the banding pattern of chromosomes of different species and to recognize homologies. We propose here a hypothetical ancestral karyotype on the basis of homologous chromosomes shared between three Palearctic (*C. russula*, *C. suaveolens*, and *C. canariensis*) and three Afrotropical (*C. luna*, *C. olivieri*, and *C. poensis*) species. The results are presented in Fig. 3. *Crocidura* cf. *malayana* (Fig. 4) was the Oriental representative for comparison. According to the parsimony principle, homologous chromosomes shared between Palearctic and Afrotropical species were considered primitive characters, and were retained to reconstruct the ancestral karyotype.

Unfortunately, no true outgroup could be used to root a cladistic analysis, either because the G-banded karyotype of sister taxa is unknown (e.g., *Sylvisorex*) or the karyotypes are too divergent to permit recognition of homologies (e.g., Soricinae, Grafodatsky et al., 1989).

The comparative approach recognized 19 pairs of homologous chromosomes (Fig. 3), giving a formula of 2N = 38 and FN = 54 to FN = 58. Only four pairs of chromosomes would be metacentric, whereas most of the complement would be acrocentric with a variable number of short chromosomal arms (Fig. 5). This model remains approximate because homologies of the smallest chromosomes are difficult to establish, and because few representatives could be compared. However, that the morphologically and biochemically primitive *C. luna* (2N = 36), *C.* cf. *bottegi* (2N = 36), and *C. bottegi*

(2N = 40) possess karyotypes close to the model reinforces our conclusion (Heim de Balsac and Lamotte, 1957; Butler and Greenwood, 1979; Maddalena, 1990*a*; Fig. 1).

Chromosomal Evolution in the Genus Crocidura

Although only 38 of the 149 species of *Crocidura* have been karyotyped (Table 1), several tendencies of chromosome evolution are evident. First, at the intraspecific level, karyological polymorphism is rare, and if present, it is mainly due to non-Robertsonian processes such as the presence of supernumerary chromosomes (B-chromosomes, Fig. 4) or variation in the number of additional heterochromatic arms (Ruedi et al., 1990).

At the supraspecific level, however, there is much more variation. Studies have shown that Palearctic species such as *C. horsfieldi watasei*, *C. leucodon*, and *C. pergrisea* have reduced diploid numbers due to Robertsonian translocations (Harada et al., 1985; Grafodatsky et al., 1988) and perhaps also to tandem fusions (Grafodatsky et al., 1988). In other Palearctic species and a few Oriental species there is karyotypic stability (Table 1), with a chromosome formula close to the hypothetical ancestral type (Fig. 5), even though some differences appear in G-band patterns (Harada et al., 1985; Grafodatsky et al., 1988; Grafodatsky et al., 1989; Maddalena, 1990*b*). As several Eurasian species share a similar karyotype with 2N = 40, Grafodatsky et al. (1988) regarded that formula as the primitive karyotype for *Crocidura*. Those species are *C. suaveolens* (including *gueldenstaedtii*, *cypria*, and *monacha*), *C. sibirica*, *C. dsinezumi*, *C. lasiura*, *C. dracula*, *C. caspica*, and *C.* cf. *fuliginosa*. Other methods should be used to test whether these cytologically similar species represent a monophyletic unit within the Palearctic-Oriental species-group. *Crocidura* cf. *malayana*, which could also be included in this group, differs by the presence of B-chromosomes, which raise the original diploid number of 38 to 40 (Ruedi et al., 1990).

The Oriental *C. attenuata* has a chromosome formula identical to some African species (Tsuchiya et al., 1979; Table 1). However, the morphology of its chromosomes appears different suggesting convergence. However, the process responsible for such an increase of the chromosome number is unknown.

Whereas the chromosome numbers of Palearctic and Oriental species often decrease or remain stable, Afrotropical *Crocidura* show an increase of both diploid and fundamental numbers. This tendency may lead either to karyotypes with mostly acrocentric chromosomes (e.g., giant shrews with 2N = 50 and FN = 66, Maddalena et al., 1989), or to mostly biarmed elements (e.g., *C. wimmeri* with 2N = 50 and FN = 84, Meylan and Vogel, 1982). Exceptions to this general pattern are found in *C. luna*, *C.* cf. *bottegi*, and *C. bottegi* which retain a chromosomal formula close to the hypothesized ancestral type. In *C. lusitania*, the karyotype (2N = 38) consists mainly of metacentric chromosomes (Maddalena, 1990*b*), and is thus interpreted as the result of secondary reduction in the diploid number by a Robertsonian process, whereas the fundamental number remains high (FN = 74) as in other African species.

The divergent karyotypic evolution of Palearctic-Oriental and Afrotropical species is illustrated in Fig. 2 and Fig. 6. These figures show a major difference between species in these zoogeographic regions, and suggest the existence of two distinct lineages among *Crocidura*. This is in full agreement with the previous phylogenetic hypothesis derived from biochemical data (Maddalena, 1990*a*; Fig. 1). Also reinforcing this conclusion is the intermediate condition of *C. russula* from both karyological and biochemical points of view. With 2N = 42 and FN = 60, this species has the highest chromosomal formula among Palearctic species and thus is intermediate between those and the Afrotropical species (Fig. 6). The zoogeographic origin of *C. russula* is probably North Africa (Richter, 1970), from which it entered Europe by crossing the Strait of Gibraltar (Catzeflis, 1984; Vogel and Maddalena, 1987), unlike the four other European species which entered Europe from the east (Catzeflis 1984; Poitevin et al., 1986; Vogel et al., 1986; Maddalena and Vogel, 1990). This zoogeographic pattern is confirmed by the biochemical results, which set *C. russula* well apart from the other European taxa. Other North African species (e.g., *C. whitakeri* or *C. tarfayaensis*) should be investigated to see if they also possess a karyotype intermediate between Afrotropical and Palearctic species. Another contact zone between these zoogeographic regions, which lies in Arabia, should also be more intensively studied.

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Table 1.—*Diploid number (2N), fundamental number (FN) and shape of the female (X) and male (Y) sex chromosome of all the known karyotypes of* Crocidura *species. The abbreviations used are M = metacentric, SM = submetacentric, ST = subtelocentric, and A = acrocentric.*

Species	2N	FN	X	Y	References
Palearctic origin					
C. pergrisea	22	34			1
C. horsfieldi watasei[a]	26	48	SM	A	2
C. leucodon	28	56	M	A	1,3
C. zimmermanni	34	44	M	A	4
C. canariensis	36	56	M	ST	5
C. sicula[b]	36	56	M	ST	6,16
C. suaveolens[c]	40	50	M	A, SM	3,9,10
	40,41,42	50,52,54	M	A	7,16
	39,40	50	M	A	8
C. sibirica	40	50	M	ST	1
C. lasiura	40	54	M	A	11
C. dsinezumi	40	56	SM	ST	2,12
C. russula	42	60	M	A	5,7,16
Oriental origin					
C. horsfieldi[a]	38	48	M	SM	13
C. cf. *malayana*[d]	38,39,40	62–68	SM	M, SM	14
C. cf. *fuliginosa*[d]	40	54–58	SM	SM	14
C. attenuata	50	66			15
Afrotropical origin					
C. luna	36	56	M	ST	16
C. cf. *bottegi*[e]	36	56			16
C. lusitania	38	74	M	A	16
C. bottegi	40	60	SM	SM	17
C. nanilla	42	74	M		16
C. ebriensis[f]	44	66,72	M	A	16,17
C. crossei[g]	44,45	72,73	M	A	16,18

Table 1 (cont.)

C. grandiceps[h]	46	68	M	A	18
C. nigrofusca[i]	48	78	M	A	16
C. olivieri[j]	50	66	M	A	16,17,18,19
C. viaria[k]	50	66	M	A	16,20
C. hirta	50	66	M	A	21
C. flavescens	50	74	M	A	22
C. nigeriae	50	76	M	A	18
C. wimmeri	50	84	M	ST	18
C. theresae	50	82,86	M	A	16,17
C. luna macmillani[l]	50				23
C. lamottei	52	68	M	A	17
C. poensis	52,53	70,72	M	A	16,17
C. hildegardeae	52	76	M	A	16
C. cf. *gracilipes*	52	86	M		18
C. fuscomurina	56	86	M	A	16
C. bicolor[m]	60				23

References:

1. Grafodatsky et al. (1988)
2. Harada et al. (1985)
3. Meylan (1966)
4. Vogel (1986)
5. Hutterer et al. (1987a)
6. Vogel (1988)
7. Meylan and Hausser (1974)
8. Tsuchiya (1987)
9. Tembotova (1983)
10. Ivanitskaya (1989)
11. Orlov and Bulatova (1983)
12. Tada and Obara (1986)
13. Krishna Rao and Aswathanarayana (1978)
14. Ruedi et al. (1990)
15. Tsuchiya et al. (1979)
16. Maddalena (1990b)
17. Meylan (1971)
18. Meylan and Vogel (1982)
19. De Hondt (1974)
20. Vogel et al. (1988)
21. Maddalena et al. (1989)
22. Maddalena et al. (1987)
23. Orlov et al. (1989)

Notes:

a. Reumer and Meylan (1986) considered *C. horsfieldi watasei* from Japan and *C. horsfieldi* from India as different species.
b. Vogel (1988) previously used the name *C. caudata*, now replaced by *C. sicula* (Vogel et al., 1989).
c. *Crocidura russula monacha*, *C. cypria*, and *C. gueldenstaedtii* are conspecific with *C. suaveolens* (Catzeflis et al., 1985).
d. Ruedi et al. (1990) applied these names for two species from peninsular Malaysia which were previously confused in a single taxon (Jenkins, 1976).
e. This female shows a karyotype different from *C. bottegi* (Maddalena, 1990*b*), and represents a distinct species (R. Hutterer, in prep.).
f. This species is mentioned in Reumer and Meylan (1986) as *C. crossei*, but after R. Hutterer (in litt.) the specimens from the Ivory Coast differ from *C. crossei* and probably represent a distinct species for which the name *C. ebriensis* is available. Variations of FN are probably caused by methodological differences in the preparation of karyotypes.
g. Meylan and Vogel (1982) provisionally used the name *C.* cf. *planiceps*, but their voucher specimen probably belongs to *C. crossei* (R. Hutterer, in litt.).
h. Named *C.* cf. *nimbae* by Meylan and Vogel (1982) but Hutterer (1983) referred this specimen to *C. grandiceps*.
i. According to Hutterer et al. (1987*b*) this name antedates *C. zaodon* in the sense of Heim de Balsac and Meester (1977) and Dippenaar (1980).
j. The name *C. olivieri* includes the forms *giffardi*, *kivu*, *manni*, *occidentalis*, and *spurrelli* (Maddalena, 1990*b*).
k. The name *C. bolivari* is a junior synonym of *C. viaria* (Hutterer, 1984).
l. This subspecies may be referable to *C. thalia* (R. Hutterer, in litt.)
m. Certainly not *C. bicolor*, but impossible to identify from text (R. Hutterer, in litt.).

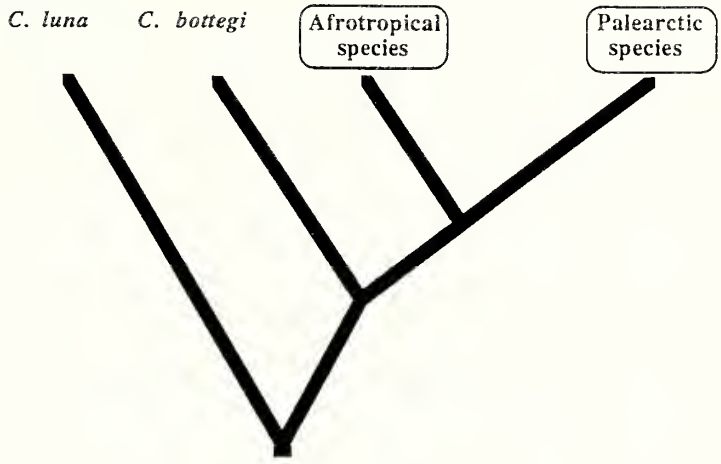

Fig. 1.—Phylogenetic relationships of African and Palearctic shrews derived from a cladistic analysis of electrophoretic characters; the outgroup (not shown) was *Sylvisorex megalura* (after Maddalena, 1990*a*).

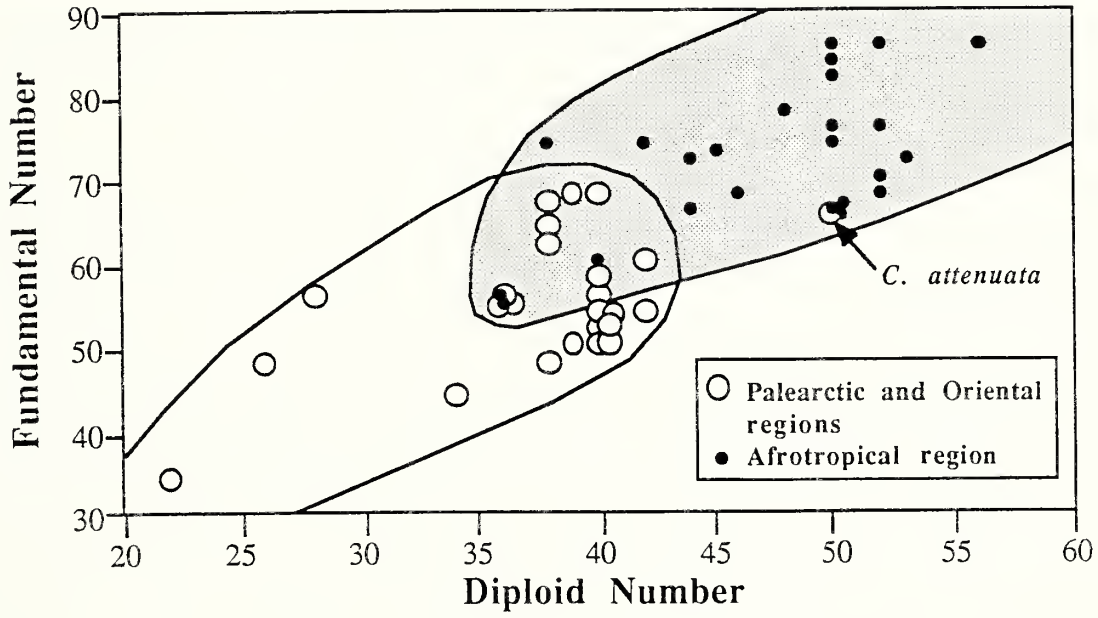

Fig. 2.—Scattergram of diploid and fundamental numbers of *Crocidura* species in Table 1. The geographic origin of the species correlates generally with their chromosome formulas.

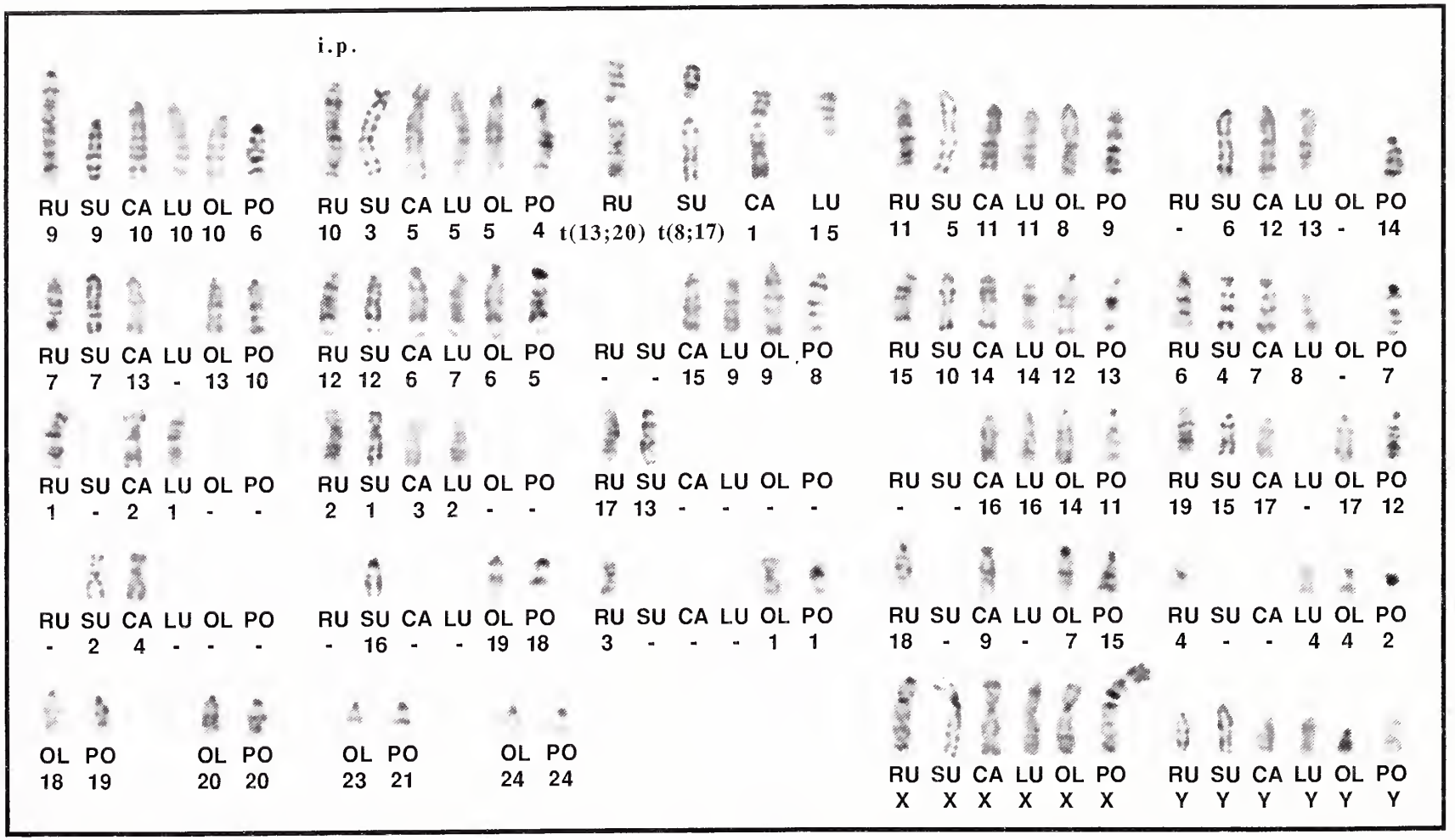

Fig. 3.—Comparative analysis of G-banding patterns of three Palearctic and three Afrotropical species. RU = *C. russula*, SU = *C. suaveolens*, CA = *C. canariensis*, LU = *C. luna*, OL = *C. olivieri*, PO = *C. poensis*, i.p. = pericentric inversion, t = translocation. The presumed homologous chromosomes between Palearctic and Afrotropical species served as the basis for reconstruction of the ancestral karyotype (after Maddalena, 1990*b*).

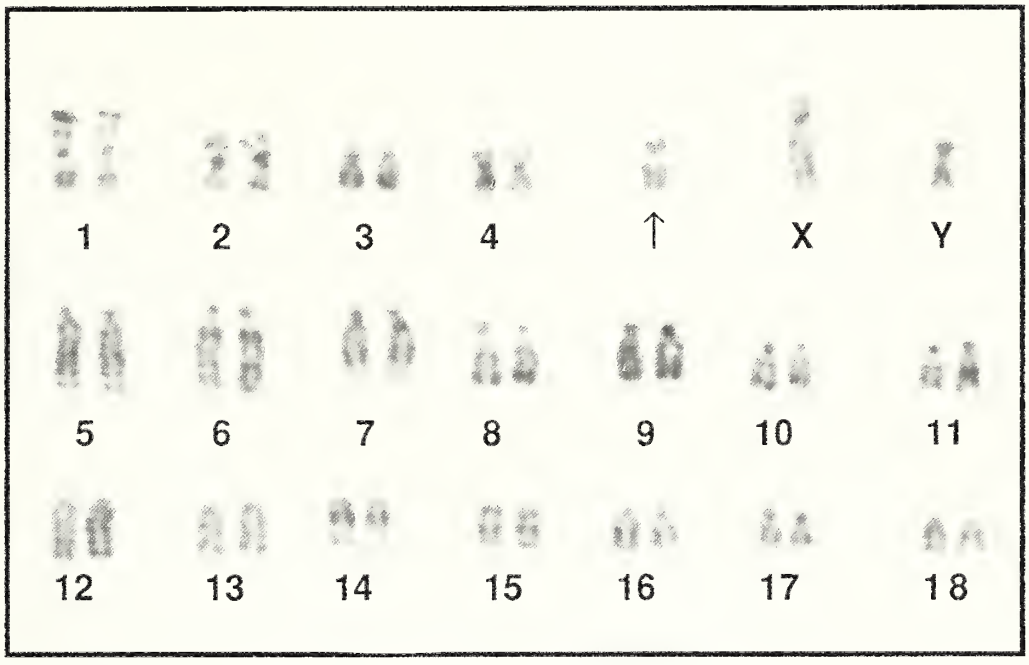

Fig. 4.—G-banded karyotype of *C.* cf. *malayana* from Southeast Asia. This karyotype has nearly the same banding pattern as the Palearctic species in Fig. 3. Supernumerary B-chromosome is indicated by an arrow.

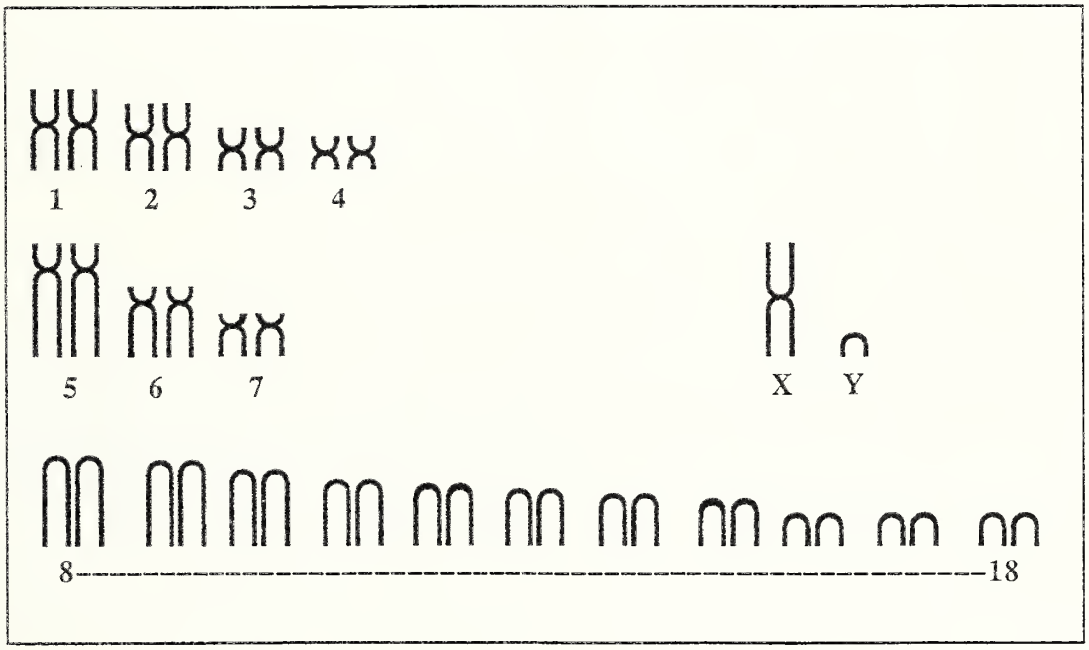

Fig. 5.—Model of the hypothetical ancestral karyotype of *Crocidura* species. The precise diploid and fundamental numbers are not known but should be around 38 and 54–58 respectively.

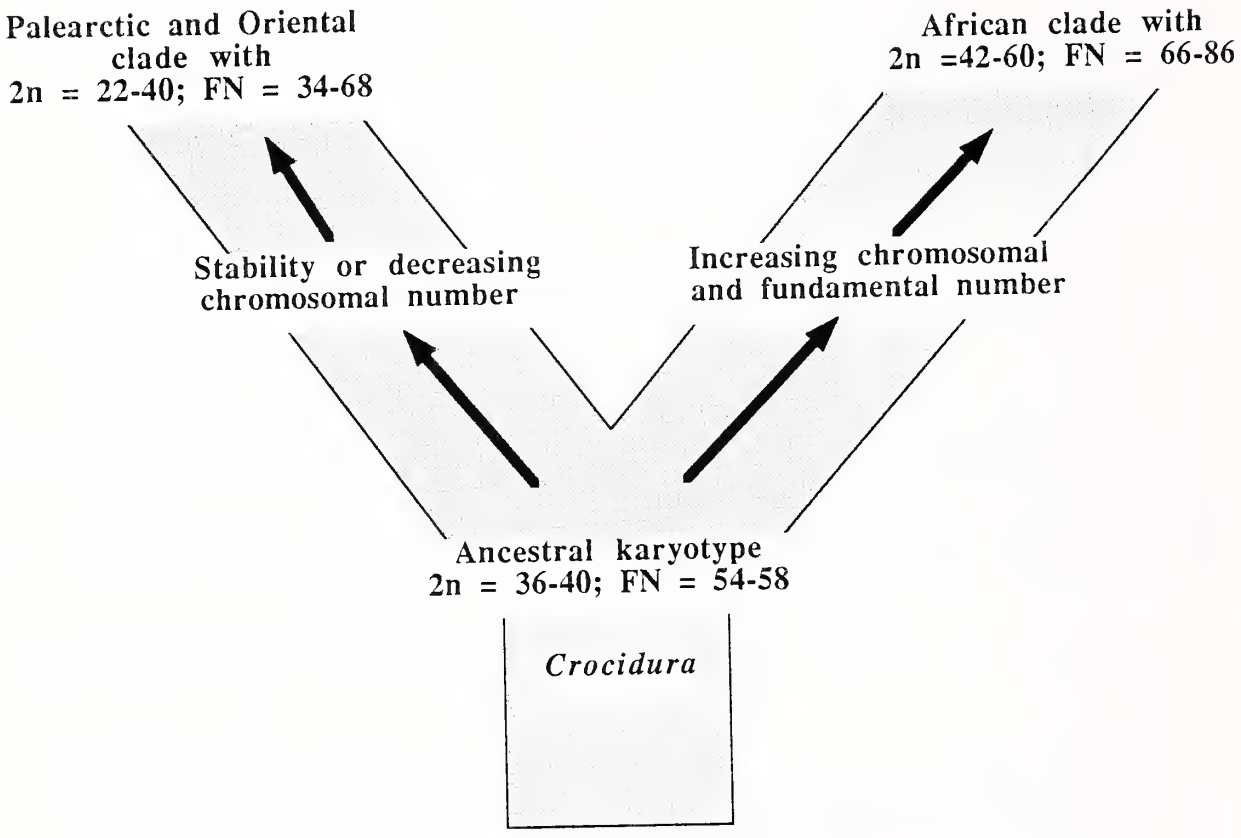

Fig. 6.—Principal lines of chromosomal evolution in the genus *Crocidura*. According to this scheme, karyotypes with 36–40 chromosomes (e.g., *C. bottegi*, *C. luna*) represent primitive characters. The two main clades are defined by opposing chromosomal evolution, one leading to the Afrotropical species with high diploid and fundamental numbers and the other to the Palearctic-Oriental species with stable or low diploid number. Exceptions to this pattern are discussed in the text.

PHYLOGENY AND DISTRIBUTION OF THE CROCIDOSORICINAE (MAMMALIA: SORICIDAE)

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ABSTRACT

Typical features distinguishing the subfamily Crocidosoricinae Reumer, 1987 from other groups of Soricidae are found in the lower incisor, in the lower fourth premolar, in the number of lower antemolars, in the mandibular condyle, and in the upper incisor. Crocidosoricinae are the most plesiomorphic shrews and they gave rise, during the Miocene, to the other subfamilies. A cladogram is presented showing the relationships to some other insectivore families. The Nyctitheriidae are placed as the sister taxon of Heterosoricidae, Plesiosoricidae, and Soricidae; the Heterosoricidae as the sister taxon of Plesiosoricidae and Soricidae; and the Crocidosoricinae as the sister taxon of all other Soricidae.

The Crocidosoricinae originated in Asia, immigrated to Europe at the beginning of the middle Oligocene, and peaked in diversity during the early Miocene. Climatic deteriorations around the early/middle Miocene boundary and the middle/late Miocene boundary, in combination with increased competition by more apomorphic forms, caused an impoverishment, a southward retreat and, finally, the extinction of the Crocidosoricinae.

INTRODUCTION

The subfamily Crocidosoricinae Reumer, 1987 was established for housing a number of morphologically related shrews from Oligocene and Miocene deposits, most of them located in Europe. In the original descriptive paper (Reumer, 1987) the taxonomic relationships were briefly discussed and a number of taxa were mentioned as possible members of the Crocidosoricinae. Ziegler (1989) greatly expanded our knowledge of the subfamily.

Here the Crocidosoricinae will be placed on a firmer foundation, initially with a discussion about the morphological characteristics of the subfamily and the phylogenetic relationships between the Crocidosoricinae and other insectivore taxa. Next, the biostratigraphic and biogeographic distribution of the subfamily will be investigated, using published literature.

The aim of this study is to summarize what is known of the early history of the Soricidae, thereby stimulating further research for the origins and phylogeny of the family.

MATERIALS AND METHODS

This is primarily a literature study. Terminology follows Reumer, 1984, unless otherwise noted. Dental elements from the upper jaw are indicated by superscripted numbers (for example, P^4 or M^1); dental elements from the lower jaw (mandible) by subscripted numbers (for example, P_4 or M_1).

For the compilation of Tables 2, 3, 4, and 5 and for the design of Fig. 2, 3, 4, and 5, I used the following literature sources (numbers in parentheses refer to source indications in Tables 2–5): Aguilar et al., 1986 (1); Agusti et al., 1984 (2); Baudelot, 1972 (3); Bohlin, 1942 (4); de Bruijn and Rümke, 1974 (5); Brunet et al., 1981 (6); Bulot, 1986 (7); Crochet, 1975 (8); Daams and Freudenthal, 1981 (9); Doben-Florin, 1964 (10); Doukas, 1986 (11); Engesser, 1972 (12), 1980 (13); Engesser et al., 1981 (14); Fahlbusch and Wu, 1981 (15); Gaillard, 1899 (16); Gibert, 1975*a* (17), 1975*b* (18); de Giuli et al., 1987 (19); Heizmann et al., 1989 (20); Heizmann and Fahlbusch, 1983 (21); Hugueney, 1974 (22), 1976 (23); de Jong, 1988 (24); Lavocat, 1951 (25), 1961 (26); Li et al., 1983 (27); Rabeder, 1978 (28); Remy et al., 1987 (29); Repenning, 1967 (30); Russell and Zhai, 1987 (31); Stehlin, 1940 (32); Storch, 1988 (33); Sulimski, 1969 (34); Tobien, 1939 (35); Viret and Zapfe, 1951 (36); Yanovskaya et al., 1977 (37); Zapfe, 1951 (38); Ziegler, 1989 (39); Ziegler and Fahlbusch, 1986 (40).

The stratigraphic framework used in the analysis is mostly based on Schmidt-Kittler (1987) for the Oligocene and Mein (1990) for the Neogene (Mio–Pliocene). The Oligocene is subdivided into MP (Mammalian Paleogene) biozones, and the Miocene and Pliocene into MN (Mammalian Neogene) biozones. The early Oligocene is considered to span MP 18 (La Debruge) through MP 22 (Villebramar), the middle Oligocene spans MP 23 (Itardies) through MP 27 (Boningen), and the late Oligocene MP 28 (Pech du Fraysse) through MP 30 (Coderet). The Oligocene/Miocene boundary is placed at the MP 30–MN 1 boundary. The early Miocene as used in this article is defined as spanning MN 1 (Paulhiac) through MN 4 (La Romieu). The middle Miocene spans MN 5 (Pont Levoy) through MN 8 (Anwil), the late Miocene spans MN 9 (Can Llobateres) through MN 13 (El Arquillo), and MN 14–16 is the Pliocene. See Lindsay and Tedford (1990) for a correlation of names of North American, central European and southwest European mammal ages and stages.

MORPHOLOGICAL CHARACTERISTICS

Crocidosoricinae are part of the family Soricidae, which family is here considered sensu stricto, excluding the Heterosoricidae Viret and Zapfe, 1951. The Soricidae are characterized by being generally small-sized Insectivora, by possessing a deeply pocketed internal temporal fossa, by the lack of a zygomatic arch, and by having a dorsoventrally separated mandibular condyle. The subfamily Crocidosoricinae, established by Reumer (1987) has the following diagnosis:

"The lower incisor is cuspulate and relatively small; the

posterior extension of its buccal face is not, or only slightly developed. The P_4 is tetrahedron shaped; its wear surface is V-shaped; there is a (sometimes only weakly defined) posterior groove or sulcus. Sometimes 2, but usually 3–5 lower antemolars. Upper incisor not fissident. Condyle *Crocidura*-like, small, with articular facets that are only slightly separated."

A differential diagnosis was also given, in which the Crocidosoricinae were distinguished from the other subfamilies then recognized:

"The Crocidosoricinae...can be distinguished from the other subfamilies of Soricidae by usually having 3–5 lower antemolars, and by the small lower incisor which lacks a strong buccal extension. They differ from the Soricinae and the Limnoecinae in having a tetrahedron-shaped, more or less symmetric P_4, with a wear-surface that is V-shaped rather than surrounding a posterolingual basin, or comma-shaped. They differ from the Soricinae in having less strongly separated condylar facets."

The recent resurrection (Reumer, 1992) of a fifth soricid subfamily, the Allosoricinae Fejfar, 1966 in addition to the Crocidosoricinae, the Crocidurinae, the Limnoecinae, and the Soricinae, requires an adaptation of this differential diagnosis, discussed later. Several morphological traits of the Crocidosoricinae need a short discussion. The lower incisor ($I_{inf.}$) is generally short. In the normal crocidosoricine situation, the $I_{inf.}$ is bicuspulate and the axes of crown and root are not parallel, but placed under a weak angle, e.g., Ziegler, 1989:table 2, fig. 2 (*Ulmensia ehrensteinensis* Ziegler, 1989); table 4, fig. 4 (*Soricella discrepans* Doben-Florin, 1964); and table 6, fig. 2 (*Florinia stehlini* [Doben-Florin, 1964]). The short crown results in only a slight posterior extension of $I_{inf.}$ at the buccal side of the mandible. In the derived state, the $I_{inf.}$ develops the tendency to elongate buccally and to proceed posteriad below the subsequent dental elements, in some cases reaching below the middle of M_1 (e.g., in *Blarinoides mariae* Sulimski, 1959, a Ruscinian Soricinae: see Reumer, 1984:plate 26).

The tetrahedron-shaped P_4 is included in the diagnosis. The archetypical crocidosoricine P_4 has a V-shaped or Y-shaped wear facet. From the tip, two ridges (posterior arms) run to the posterolingual and the posterobuccal corners of the tooth, enclosing a posterior sulcus. On both posterior arms a small terminal cuspule may be present. This is what Jammot (1983) calls a "type *Myosorex*" P_4, named after the living crocidurine genus *Myosorex*. The posterolingual arm may become elongated (seen for example in the crocidosoricine *Clapasorex sigei* Crochet, 1975), or the posterobuccal (posterolabial) branch may become elongated (seen for example in the crocidosoricine *Carposorex sylviae* Crochet, 1975, and in an advanced form in the subfamily Soricinae; see Crochet, 1975; Reumer, 1987:fig. 2). If both posterior arms reduce, the wear facet becomes triangular, a situation seen in most species of the subfamily Crocidurinae. There are exceptions to this rule. The simple fact that Jammot (1983) called the typical crocidosoricine P_4 after a living Crocidurinae (*Myosorex*) indicates that in this genus apparently the archetypical P_4 remained. It seems better not to speak of a "type *Myosorex*" P_4, but of a crocidosoricine type of P_4, when referring to the type of P_4 with two posterior arms provided with accessory cuspules.

A character not mentioned before is the double-rooted nature of the P_4, although this too is not strictly diagnostic. Most Crocidosoricinae have a double-rooted P_4, the only exception being *Florinia stehlini* (Doben-Florin, 1964) (Ziegler, 1989). On the other hand, members of other subfamilies also may have a double-rooted P_4, such as the living genus *Surdisorex* (Crocidurinae); the fossil *Paenelimnoecus micromorphus* (Doben-Florin, 1964) and *P. crouzeli* Baudelot, 1972 (Allosoricinae); and *Antesorex compressus* (Wilson, 1960) (an Arikareean Soricinae; see Repenning, 1967; Reumer, 1992).

Another character of the Crocidosoricinae is the possession of generally more than two lower antemolars. The number may vary from three to five, with only one exception—the early Miocene *Miosorex pusilliformis* (Doben-Florin, 1964) had only two lower antemolars. This is apparently an early "Reduktionsstadium" (Ziegler, 1989). On the other hand, several shrews are known that possess three lower antemolars and that do not belong to the Crocidosoricinae: e.g., *Alluvisorex arcadentes* Hutchison, 1966, a Barstovian Soricinae from Oregon; *Angustidens vireti* (Wilson, 1960), an early Miocene Limnoecinae from Colorado; *Limnoecus niobrarensis* Macdonald, 1947, a Barstovian Limnoecinae from Nebraska; and the genus *Myosorex*, a living Crocidurinae from Africa (Repenning, 1967). As this latter genus was also found to have retained the crocidosoricine type of P_4, it may be considered a plesiomorphic Crocidurinae or a living relic of the Crocidosoricinae (see also Reumer, 1987). It would be worthwhile to study its isozyme and chromosome constitution in order to reveal its relation to other Crocidurinae.

The mandibular condyle of the Crocidosoricinae is relatively small, it has upper and lower articular facets, and the interarticular area is not very large. This type of condyle is retained in most Crocidurinae and in the American Limnoecinae, albeit sometimes larger. The Soricinae are marked by a development of the condyle in which the interarticular area becomes larger dorsoventrally, the separation of the facets thus becoming more pronounced, and in which the interarticular area shows a lingual (medial) emargination. In the Allosoricinae, the upper articular facet acquires a triangular form.

The upper incisor is invariably single tipped. The development of fissident upper incisors, which can be found in many Soricinae (tribes Soriculini, Beremendini, some Soricini), in *Allosorex* (Allosoricinae), but also in the Heterosoricidae, is apparently an apomorphic feature that has a polyphyletic origin.

In the framework of the present study the presence or absence of pigmentation in the teeth is ignored. Most authors, when describing shrews, mention the presence or absence of pigment as a diagnostic feature. I think that in fossils this character must be treated with utmost care. As a result of the fossilization processes the original absence or presence of a pigment of iron-containing compounds in the enamel may be impossible to reconstruct.

Relationships

Because the Crocidosoricinae are by far the earliest Soricidae, they are critical in discussing the relationship of the Soricidae to other insectivore families and the relationships within the Soricidae. Reumer (1987) hypothesized that the Soricidae (Crocidosoricinae) sprung off from Eocene or early Oligocene Nyctitheriidae, independently from the Heterosoricidae. Nyctitheriidae and Soricidae share several derived characters: elongate and cuspulate lower incisors and a complex condylar facet. The Nyctitheriidae furthermore have a P^4 much like the soricid P^4, and the alveolar pattern of the lower antemolars is identical to that of the Crocidosoricinae; all elements are single rooted, except for the P_4, which is double rooted (Sigé, 1976; Butler, 1988).

On the other hand, there appear many differences: Nyctitheriidae have a zalambdodont dentition, Soricidae are dilambdodont; Nyctitheriidae have strongly molarized premolars, which Soricidae lack; there is a hypoconulid in the nyctitheriid lower molars, which is absent in shrews.

Butler (1988) places the Soricidae (sensu lato) far from the Nyctitheriidae in his postulated phylogenetic tree, and considers the Plesiosoricidae a sister taxon of the Soricidae. These two families share many derived characters: dilambdodont dentition, large first incisors, reduction of the rest of the antemolar dentition, reduction or loss of the hypoconulid, the emphasis on P^4–M_1 shear, and, this is important, the loss of the zygomatic arch (Butler, 1988; Sigé, 1976). Butler (1988:132, fig. 5.6) places the Plesiosoricidae and the Soricidae as a sister group of a group comprising Dimylidae, Talpidae, and Proscalopidae. Sigé (1976:68), however, considers the common characters of Plesiosoricidae and Soricidae as parallelisms, and states: "...*Plesiosorex* réalise pendant l'Oligocène et le Miocène une adaptation parallélisant plus ou moins celle des soricidés."

The Heterosoricidae share many characters with the Soricidae (to which family they were always considered to belong), but there is one important difference. Heterosoricidae do have a zygomatic arch (Gaillard, 1915; Viret and Zapfe, 1951), and lack the specialized masticatory apparatus of the Soricidae (see Repenning, 1967; Reumer, 1987).

Some characters shared by the Heterosoricidae and the Soricidae may prove to be points of convergence. For example, the fissident upper incisor could well have different origins: the emergence of a median tine in the Soricidae versus a spadelike widening of the apex in Heterosoricidae. The condyle, which is of a complex shape in both families, shows dorsoventrally separated facets in the Soricidae, while in the Heterosoricidae the facets show also a conspicuous mediolateral separation. The fact that the molar morphology of the Heterosoricidae (weak posterior emargination, continuous endolophs) strongly resembles that of a highly advanced group of Soricinae (viz., the group with the genera *Petenyia* and *Blarinella*) can only be explained as a convergence.

The presence of many possible convergences hinders the construction of a clear and unambiguous phylogenetic tree or cladogram. It is often impossible to decide whether a certain character (for example, the loss of the zygomatic arch or the formation of a complex condyle) is either a shared derived character (synapomorphy) or a case of parallelism (convergency).

Thus, as a working hypothesis only, the following cladogram is proposed (Fig. 1). The nodes are characterized by the following hypothesized synapomorphies: A: somewhat enlarged first incisors, often serrate (cuspulate); complex condyle; lower antemolar alveolar pattern: all single rooted except for double-rooted P_4. B: demolarization of antemolars except P^4; reduction of antemolars; strongly enlarged first incisors; dilambdodont upper molars; loss or reduction of hypoconulid; P^4–M_1 shear. C: loss of zygomatic arch. D: internal temporal fossa; dorsoventral separation of condylar facets.

Reumer (1987, 1989, 1992) hypothesized that the Crocidosoricinae were ancestral to the other soricids. The emergence of other subfamilies began in the Miocene. The oldest record of a Limnoecinae is *Angustidens vireti* (Wilson, 1960) from the early Miocene (Arikareean) of Colorado (see Repenning, 1967). The oldest record of an Allosoricinae is also from the early Miocene (Orleanian): *Paenelimnoecus micromorphus* (Doben-Florin, 1964) from several localities in Bavaria, Germany (Ziegler, 1989; Reumer, 1992).

The earliest record of a Soricinae is not, as mentioned before (Reumer, 1989), *Paenelimnoecus crouzeli* Baudelot, 1972, because this is an Allosoricinae (Reumer, 1992). The oldest mention of a possible Soricinae in Europe is *?Hemisorex* sp. from the early Miocene (Orleanian, MN3–4) of Stubersheim 3 in Germany (Ziegler, 1989). An unambiguous Soricinae is *Hemisorex robustus* Baudelot, 1967 from the middle Miocene (MN6) of Sansan in France (Baudelot, 1972); this taxon is already highly developed and seems to stand at the base of the lineage leading to *Blarinella* and *Petenyia*. In fact, a comparison of the type material of *H. robustus* and *Blarinella* (*B. dubia* [Bachmayer and Wilson, 1970] and *B. europaea* Reumer, 1984) could reveal that they are congeneric.

Antesorex compressus (Wilson, 1960) seems the earliest American record of a Soricinae; it is from the late Arikareean (late early Miocene) of Colorado (see Repenning, 1967). However, the specimens need to be examined to decide their subfamiliar assignment. The possession of a double-rooted P_4 in *A. compressus* could indicate an affinity to the Crocidosoricinae.

The oldest recorded Crocidurinae was supposedly a late Miocene *Crocidura* sp. from Kenya (see Repenning, 1967). It was described by Butler and Hopwood (1957), but Butler (1985) subsequently suggested that it was probably of Pleistocene age. No other Miocene Crocidurinae have been described; the origin of this subfamily is still unknown.

Morphologically, the Crocidosoricinae can be distinguished from the Limnoecinae by the shape of the P_4, which possesses a comma-shaped wear facet in the Limnoecinae; better separating criteria do not seem to be present, as the majority of limnoecine species have three or four lower antemolars and possess a crocidosoricine type of condyle, albeit rather large.

The Crocidosoricinae are distinguished from the Allosoricinae most readily by the absence or extreme reduction of the entoconids and entoconid crests (entocristids in the terms of Ziegler, 1989) in the latter subfamily, and by the different

condyles; allosoricines have a triangular upper condylar facet. The oldest Allosoricinae retain some crocidosoricine features, such as the double-rooted P_4.

The difference between Crocidosoricinae and Soricinae is found in the P_4 (see above and Reumer, 1987), in the condyle (soricines having well-separated articular facets), and in the lower number of lower antemolars (only *Alluvisorex arcadentes* Hutchison, 1966 retains a minute P_3, see Repenning, 1967). Also, soricines have a more elongate lower incisor, and many have a fissident upper incisor.

The difference between Crocidosoricinae and Crocidurinae is less pronounced. In general, the crocidurines have a simpler P_4, lacking accessory cuspules and a posterior sulcus. Also the number of lower antemolars is lower, but, as already noted above, the living crocidurine *Myosorex* is an exception to the rules.

Biostratigraphy and Biogeography

General Remarks

For a (literature) study of the biostratigraphic and paleobiogeographic distribution of the Crocidosoricinae, a complete listing of assigned taxa is necessary. Table 1 gives a compilation of the genera and species used in the present study, including some taxa that are still of uncertain generic assignment. I do not want to claim the list as being complete and exhaustive. Considerable changes in the list will no doubt occur or be necessary, for the following reasons.

Many articles give faunal lists of a given locality in which the Soricidae are mentioned as "Soricidae indet.," "Soricidae species A and B," or the like. Such records have been excluded from this study, except when authors explicitly claim close relationship to known crocidosoricine taxa. Therefore, many records may have been "overlooked." Furthermore, the identification of species often needs to be viewed with some caution. Certainly, researchers of the last few decades, such as Baudelot, Hugueney, Doben-Florin, Crochet, and Ziegler, who all described Crocidosoricinae, provided us with excellent descriptions and identifications, but many of the earlier records, whatever their morphology, were identified as "*Sorex*." Likewise, Miocene shrews tended to be identified as either "*grivensis*," "*antiquus*," or "*dehmi*." Because I was not able to check all such identifications, I have for the present compilation adhered to the original designations. The appropriate species have, however, been assigned to the genera as currently used (see Ziegler, 1989, who revised a great part of crocidosoricine taxonomy). Thus, records of "*Sorex*" *dehmi* are treated in the lists as *Lartetium dehmi*.

Finally, maps such as the ones reproduced here (Fig. 2–5) more often show the current geographical distribution of vertebrate paleontologists rather than a trustworthy distribution of the taxa under consideration. This produces a bias in the distribution maps.

Oligocene

Figure 2 gives the distribution of Soricidae (Crocidosoricinae) in Oligocene deposits. Table 2 summarizes the records.

The earliest published report (not seen) of a Soricidae is in the early Oligocene of Mongolia: an indeterminate shrew from the Ergilin-Dzo Svita (Yanovskaya, 1977, *in* Russell and Zhai, 1987). If the identification is correct, this find appears to underline the hypothesis of the Asiatic origin of the family, as stated by Butler (1985, 1988) and Reumer (1987).

Sulimski (1969) described the middle Oligocene *Gobisorex kingae* from the Shand-Gol Svita in Mongolia (see also Russell and Zhai, 1987); its biostratigraphic correlation to the three recorded French middle Oligocene finds is unknown. The remains resemble Heterosoricidae, but are best compared to "primitive Miocene species of the genus *Sorex*..." (Sulimski, 1969:68). The sizes of the teeth are relatively large, but compare well to those of, for example, *Soricella discrepans* (see Ziegler, 1989). *G. kingae* has either five single-rooted antemolars, or four such elements including a double-rooted P_4. In the latter case, the posterior root of P_4 is larger than the anterior one, a situation also known in *Ulmensia ehrensteinensis* (Ziegler, 1989). As Sulimski (1969) put it, *Gobisorex* represents an earlier stage of soricine evolution showing some resemblances to heterosoricines. Until I can examine the material (which lacks a mandibular ascending ramus), I can make no definitive choice between Soricidae and Heterosoricidae, and hence accept the opinion of Sulimski that *Gobisorex* is an early soricid ("soricine"). The presence of at least four lower antemolars and the anterior position of the buccal side of $I_{inf.}$ furthermore seem to justify inclusion into the Crocidosoricinae.

The late Oligocene marks the onset of the blooming of the subfamily. An indeterminate find from Yindirte (Taben Buluk) in China (Bohlin, 1942; Russell and Zhai, 1987) and eight reports from Europe (France and Germany) indicate a proliferation of taxa. Two new genera (*Crocidosorex* and *Ulmensia*) are reported, indicating morphological diversification of the subfamily. A possible ninth record, of *Mysarachne picteti* Pomel, 1853 from Chauffours (Puy-de-Dôme, France) was neglected due to the unavailability of the material and of the name (see Lavocat, 1951).

Miocene

Figures 3, 4, and 5 show the geographical distribution of the Crocidosoricinae in, respectively, the early Miocene, middle Miocene, and late Miocene. Tables 3, 4, and 5 list the records concerned.

The early Miocene (MN zones 1–4) shows an extensive proliferation of Crocidosoricinae, both in terms of geographical distribution and in terms of taxonomical diversity. Figure 3 and Table 3 show the presence of eight genera with at least 16 species (plus indeterminate material or material of uncertain affinities), a total of over 60 records. The distributional emphasis (see Fig. 3) is situated in central Europe and France. Figure 4 and Table 4 show the situation in the middle Miocene (MN zones 5–8). There is one report from Asia (Xiacaowan in China; Li et al., 1983), but in Europe the diversity is considerably less than that of the early Miocene, although the geographical distribution seems somewhat enlarged with records from Turkey (three localities; Engesser, 1980) and from

Morocco in northern Africa (Beni-Mellal; Lavocat, 1961). The distributional emphasis has shifted from central Europe to Spain.

Miosorex grivensis is the most successful species, while, apart from the mentioned record from Xiacaowan, the entire genus *Crocidosorex* appears to have vanished. We have less than 40 records from the middle Miocene, including only two genera and four species (plus some indeterminate material).

With the onset of the late Miocene, the subfamily Crocidosoricinae has disappeared almost completely (Fig. 5, Table 5). There are only three late Miocene records, all of *Miosorex grivensis* from Spanish localities (Gibert, 1975*b*; de Jong, 1988). All three are stratigraphically dated to the earliest late Miocene (MN 9); MN zones 10–13 are devoid of Crocidosoricinae.

Pliocene

Finally, there are three closely-linked records that can be attributed to the Pliocene: an island relic from three sites at Apricena in the Italian peninsula of Gargano, that once was an island (Fig. 5, Table 5). It is taxonomically indeterminate (de Giuli et al., 1987).

L. Maul (personal communication, January 30, 1989) mentioned the report of "*?Crocidosorex*" from Akkulaevo in Bashkiria (Russia) by Sukhov, 1970. Apparently the taxon was only mentioned in one table on page 18 of Sukhov's article without any description in the text. Because I have not seen this record, I ignore it beyond this brief mention.

Another Pliocene record concerns *Myosorex meini* described by Jammot, 1977, as a Crocidurinae from three Pliocene localities: Seynes and Balaruc 2 in southern France, and Iles Medas in northern Spain. Crochet (1986), who mentioned the taxon, cited Jammot (1977) who stated that *M. meini* and "*Sorex*" *dehmi* have important affinities. This could imply that *M. meini* is a Crocidosoricinae. I have not seen the original material and Jammot's thesis is unobtainable. Apart from the fact that *M. meini* has never been published as a new taxon according to the rules of the International Code of Zoological Nomenclature and is therefore a nomen nudum, I prefer to adhere to Jammot's original notion of the taxon as a Crocidurinae. It is therefore excluded from the present study.

Discussion

I stated earlier (Reumer, 1989) that the Soricidae probably came to Europe as part of the faunal immigration wave often called "Grande Coupure," about 33 million years ago. In terms of MP (Mammalian Paleogene) biozonation the Grande Coupure is situated between MP 20 and 21 (Tobien, 1987). The oldest shrews from Europe date from the middle Oligocene of France. *Srinitium marteli* Hugueney, 1976 from Saint-Martin-de-Castillon is dated to biozone MP 23 (Schmidt-Kittler, 1987). An indeterminate shrew from Garouillas is correlated to the biozone d'Antoingt, biozone 10 according to Remy et al. (1987), which corresponds to MP zone 25. A find of *Srinitium* sp. from biozone 13 of the Pech du Fraysse, also in France, is still slightly younger (Remy et al., 1987); it is dated to either biozone MP 27 or MP 28.

Engesser and Mayo (1987) mention a "soricid indet." from the Swiss locality of Balm, dated to the assemblage zone of Balm, which is MP 22 (Schmidt-Kittler, 1987). A recent reinvestigation has shown the absence of Soricidae, however, in this locality (Reumer, in press).

The results of the literature survey of the distribution of the Crocidosoricinae (Fig. 2–5; Tables 2–5) show the peak of crocidosoricine diversity in the early Miocene. After the early Miocene, a decline started, leading to a virtual extermination of the subfamily by the onset of the late Miocene (Vallesian, MN zone 9). This finding strongly contradicts my earlier hypothesis (Reumer, 1989) that the climatic deterioration at the Miocene–Pliocene boundary was responsible for the extinction of the Crocidosoricinae on the European continent. I drew a parallel with the climatic event at the Plio–Pleistocene boundary of 2.4 million years ago and its impact on soricid diversity, and with the Pleistocene glacial history.

Because the Crocidosoricinae were almost entirely absent during the late Miocene, the climatic events at the Miocene–Pliocene boundary could, consequently, not have caused the extinction of the subfamily.

Van der Meulen and Daams (1992) studied the paleoecological conditions in the early and middle Miocene, based primarily on the composition of rodent associations from Spanish localities. Their studies resulted in a Relative Humidity Curve and a Relative Temperature Curve for the interval studied (MN zones 3 through 9). A drop in relative humidity is noted in MN 4, followed by a considerable cooling event starting at the onset of MN 5. Both events, but especially the cooling event, coincide with the boundary between early and middle Miocene as used in the present study. I postulate that the considerable drop in crocidosoricine diversity, as noted above, is at least partly caused by the climatic deterioration of MN 4/5 (see Reumer, 1989, for the impact of climatic events on fossil Soricidae).

A second cooling event is noted at the onset of MN 9, leading to temperatures lower than those recorded before. It coincides with an increase in relative humidity. As mentioned above, the Crocidosoricinae disappear almost entirely in MN 9, which marks the beginning of the late Miocene. It is here postulated that this extinction is at least partly caused by the MN 9 cooling event.

Another development paralleled the climatic events of the Miocene: the gradual evolution of advanced types of shrews. As noted above, Limnoecinae and Soricinae are present in America from the early Miocene onwards; in Europe the Allosoricinae are present from the early Miocene and unambiguous Soricinae from the middle Miocene onwards. Such advanced forms must have lived in competition with the Crocidosoricinae; it is therefore likely that the Crocidosoricinae disappeared through the combined influence of climatic deteriorations and increased competition.

Figures 3, 4, and 5 furthermore show a gradual shift of the major distributional areas into a southward direction. In the early Miocene, most Crocidosoricinae lived in central Europe; in the middle Miocene most records are from Spain and other Mediterranean regions; the few late Miocene and Pliocene

records are all from south European localities. This pattern suggests a gradual southward retreat. It parallels the phenomenon observed by Reumer (1984) for the Plio-Pleistocene genus *Episoriculus* and provides further evidence for the impact of climatic cooling trends on the distribution of fossil Soricidae.

Conclusions

The Soricidae most probably originated in Asia and came to Europe right after the early Oligocene "Grande Coupure." Only a few records are known from Oligocene deposits, but then the shrews (subfamily Crocidosoricinae) bloomed during early Miocene times with the main distributional emphasis in central Europe. Climatic deteriorations around MN4/5 coincide with a decline in diversity, and the biogeographic focus moved southward to Mediterranean regions. A second climatic deterioration around MN 9 (earliest late Miocene) coincides with the virtual extinction of the Crocidosoricinae; only an island relic in Italy survived into the Pliocene. Increased competition by more apomorphic groups of shrews (in Europe mainly Allosoricinae and Soricinae) probably contributed to this extinction process.

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Table 1.—*Alphabetic list of the taxa included in the subfamily Crocidosoricinae Reumer, 1987.*

Carposorex sylviae Crochet, 1975

Clapasorex bonisi Crochet, 1975
C. sigei Crochet, 1975

Crocidosorex antiquus (Pomel, 1853)
C. piveteaui Lavocat, 1951
C. thauensis Crochet, 1975

Florinia stehlini (Doben-Florin, 1964)

Gobisorex kingae Sulimski, 1970

Lartetium dehmi (Viret and Zapfe, 1951)
L. petersbuchense Ziegler, 1989
L. prevostianum (Lartet, 1851)

"*Limnoecus*" *truyolsi* Gibert, 1975

Miosorex desnoyersianus (Lartet, 1851)
M. grivensis (Depéret, 1892)
M. pusilliformis (Doben-Florin, 1964)

"*Oligosorex*" *bruijni* Gibert, 1975

"*Sorex*" *collongensis* Mein, 1958
"*Sorex*" *gracilidens* Viret and Zapfe, 1951

Soricella discrepans Doben-Florin, 1964

Srinitium marteli Hugueney, 1976

Ulmensia ehrensteinensis Ziegler, 1989

Table 2.—*List of names and localities of Oligocene Crocidosoricinae used in the analysis. Numbers refer to the articles mentioned in the Materials and Methods section. +, type locality.*

Late Oligocene		
Crocidosorex cf. *thauensis*	Eggingen Erdbeerhecke (Bavaria, Germany)	39
id.	Eggingen Mittelhart (id.)	39
id.	Ehrenstein 4 (id.)	39
id.	Hochheim (Germany)	33
Crocidosorex sp.	Cournon-les-Souméroux (Puy-de-Dôme, France)	6
Ulmensia ehrensteinensis	Ehrenstein 4 (Bavaria, Germany) (+)	39
Ulmensia sp.	Hochheim (Germany)	33, 39
indet.	Yindirte (Taban Buluk, China)	4, 31
indet.	Hochheim (Germany)	33
Middle Oligocene		
Gobisorex kingae	Shand-Gol Svita (Mongolia) (+)	31, 34
Srinitium marteli	St-Martin-de-Castillon (Vaucluse, France) (+)	23
Srinitium sp.	Pech du Fraysse (Quercy, France)	29
indet.	Garouillas (Quercy, France)	29
Early Oligocene		
indet.	Ergilin-Dzo Svita (Mongolia)	31, 37

Table 3.—*List of names and localities of Early Miocene (MN1–MN4) Crocidosoricinae used in the analysis. Numbers refer to the articles mentioned in the Materials and Methods section. +, type locality; *, uncertain taxonomic affiliation.*

Crocidosorex antiquus	Montaigu-le-Blin (Allier, France) (+)	8, 32
id.	Langy (id.)	32
id.	Saulcet (id.)	32
id.	Chaveroches (id.)	32
id.	St-Gérand-le-Puy (id.)	6
id.	Ulm Westtangente (Bavaria, Germany)	20, 39
id.	Tomerdingen (Germany)	35, 39
id.	Oschiri (Sardinia, Italy)	5
Crocidosorex cf. *antiquus*	Budenheim (Germany)	33, 39
Crocidosorex thauensis	Bouzigues (Hérault, France) (+)	8
id.	Paulhiac (Lot-et-Garonne, France)	8
Crocidosorex piveteaui	Marcoin-près-Volvic (Puy-de-Dôme, France) (+)	8
Crocidosorex sp.	Ulm Westtangente (Bavaria, Germany)	20, 39
id.	Weisenau (Germany)	33
Miosorex grivensis	Valdemoros 1A (Calatayud, Spain)	18
id.	Munebrega 1 (id.)	18
id.	Torralba 1 (id.)	18
id.	Villafeliche 4 (id.)	18
id.	Valdemoros 3B (id.)	18
id.	La Romieu (Gers, France)	7, 9
id.	Rembach (Bavaria, Germany)	40
Miosorex aff. *grivensis*	Forsthart (id.)	40
id.	Vieux-Collonges (Rhône, France)	9
Miosorex pusilliformis	Wintershof West (Bavaria, Germany) (+)	10
id.	Stubersheim 3 (id.)	39
id.	Erkertshofen 2 (id.)	39
id.	Petersbuch 2 (id.)	39
id.	Navarrete del Rio (Teruel, Spain)	9
Miosorex cf. *desnoyersianus*	Petersbuch 2 (Bavaria, Germany)	39
Lartetium dehmi	Erkertshofen 2 (Bavaria, Germany)	40
id.	Rauscheröd 1b (id.)	40
id.	Rembach (id.)	40
id.	Forsthart (id.)	40
id.	Vieux-Collonges (Rhône, France)	9
Lartetium petersbuchense	Petersbuch 2 (Bavaria, Germany) (+)	39
id.	Erkertshofen 2 (id.)	39
Florinia stehlini	Wintershof West (Bavaria, Germany) (+)	10
id.	Petersbuch 2 (id.)	39
id.	Erkertshofen 2 (id.)	39
id.	Rauscheröd 1b/1c (id.)	40
Carposorex sylviae	Laugnac (France) (+)	8
Carposorex sp.	Paulhiac (id.)	8
id.	La Brète (Aquitaine, France)	8
id.	Stubersheim 3 (Bavaria, Germany)	39
Clapasorex sigei	Bouzigues (Hérault, France) (+)	8
Clapasorex bonisi	Paulhiac (Lot-et-Garonne, France) (+)	8

Table 3 (cont.)

Soricella discrepans	Wintershof West (Bavaria, Germany) (+)	10
id.	Stubersheim 3 (id.)	39
id.	Erkertshofen 2 (id.)	39
id.	Petersbuch 2 (id.)	39
id.	Budenheim Hessler (Hessen, Germany)	39
id.	Navarrete del Rio (Teruel, Spain)	9
id.	Chaveroches (Allier, France)	22, 39
id.	Dolnice (Czechoslovakia)	39
Soricella cf. *discrepans*	Ulm Westtangente (Bavaria, Germany)	20, 39
Soricella n. sp.	Petersbuch 2 (id.)	39
indet.	Stubersheim 3 (id.)	39
indet.	Aliveri (Greece)	11
indet.	Weisenau (Germany)	33
"*Oligosorex*" *bruijni**	Villafeliche 2A (Calatayud, Spain)	17
id.*	Ateca 1 (+) and 3 (id.)	17
"*Limnoecus*" *truyolsi**	Villafeliche 4 (Calatayud, Spain) (+)	17
id.*	Valdemoros 3B (id.)	17
"*Limnoecus*" sp.*	Vieux Collonges (Rhône, France)	9
"*Sorex*" *collongensis**	id. (id.) (+)	3

Table 4.—*List of names and localities of Middle Miocene (MN5–MN8) Crocidosoricinae used in the analysis. Numbers refer to the articles mentioned in the Materials and Methods section. +, type locality; *, uncertain taxonomic affiliation.*

Crocidosorex sp.	Xiacaowan (China)	27
Miosorex grivensis	Armantes 4 and 7 (Calatayud, Spain)	18
id.	Las Planas 4A and 4B (id.)	18
id.	Manchones (id.)	18
id.	Arroyo del Val 6 (id.)	18
id.	Hostalets de Pierola (Vallès Penedès, Spain)	2, 18
id.	La Grive St. Alban (France) (+)	16, 36
id.	Puttenhausen (Bavaria, Germany)	15
Miosorex aff. *grivensis*	Las Planas 5B, 5H, and 5K (id.)	24
id.	Valalto 2c (id.)	24
id.	Borjas (id.)	24
id.	Villafeliche 9 (id.)	24
id.	Alcocer 2 (id.)	24
id.	Toril (id.)	24
id.	Solera (id.)	24
Miosorex desnoyersianus	Lo Fournas II (Pyrénées Orientales, France)	1
id.	Sansan (Gers, France) (+)	3
Lartetium dehmi	La Grive St. Alban (France) (+)	36
id.	Puttenhausen (Bavaria, Germany)	40
id.	Steinberg (id.)	21
id.	Neudorf a.d. March (=Devinska Nova Ves, Czechoslovakia)	28, 38
Lartetium dehmi africanus	Beni Mellal (Morocco)	3, 26

Table 4 (cont.)

Lartetium prevostianum	Sansan (Gers, France) (+)	3
id.	Lo Fournas II (Pyrénées Orientales, France)	1
id.	Cases de Pène (id.)	1
indet.	Vermes (Jura, Switzerland)	14
indet.	Anwil (Baselland, Switzerland)	12
indet. (comparable to *M. desnoyersianus*)	Steinberg (Bavaria, Germany)	21
indet. (comparable to *M. grivensis*)	Sari Çay (Turkey)	13
id.	Paşalar (Turkey)	13
indet. (comparable to *L. dehmi*)	Çandir (Turkey)	13
"*Sorex*" *gracilidens* (*)	Neudorf a.d. March (=Devinska Nova Ves, Czechoslovakia) (+)	28, 36, 38
"*Limnoecus*" *truyolsi* (*)	Las Planas 4A (Calatayud, Spain)	17

Table 5.—*List of names and localities of Late Miocene and Pliocene Crocidosoricinae used in the analysis. Numbers refer to the articles mentioned in the Materials and Methods section.*

Pliocene		
indet.	Apricena F15, F21b, F21c (Gargano, Italy)	19
Late Miocene (MN9–MN13)		
Miosorex grivensis	Can Ponsich (Vallès Penedès, Spain)	18
Miosorex aff. *grivensis*	Carrilanga 1 (Calatayud, Spain)	24
id.	Pedregueras 2A (id.)	24

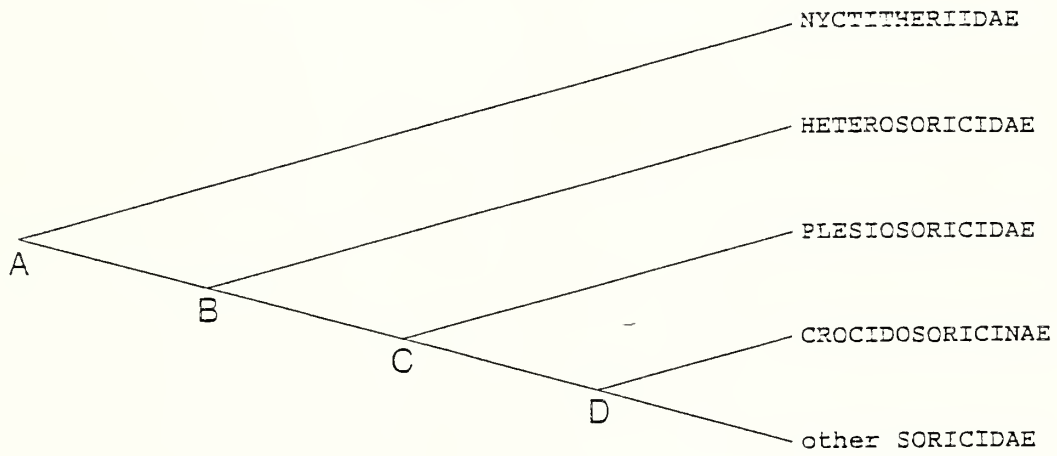

Fig. 1.—Cladogram showing postulated interrelationships of some insectivore higher taxa. The nodes are characterized by hypothesized synapomorphies: A—enlarged, often serrate first incisors; complex condyle; lower antemolars single rooted except for double-rooted P_4; B—demolarization of antemolars except for P^4; reduction of antemolars; strongly enlarged first incisors; dilambdodont upper molars; loss or reduction of hypoconulid; P^4–M_1 shear; C—loss of zygomatic arch; D—internal temporal fossa; dorsoventral separation of condylar facets.

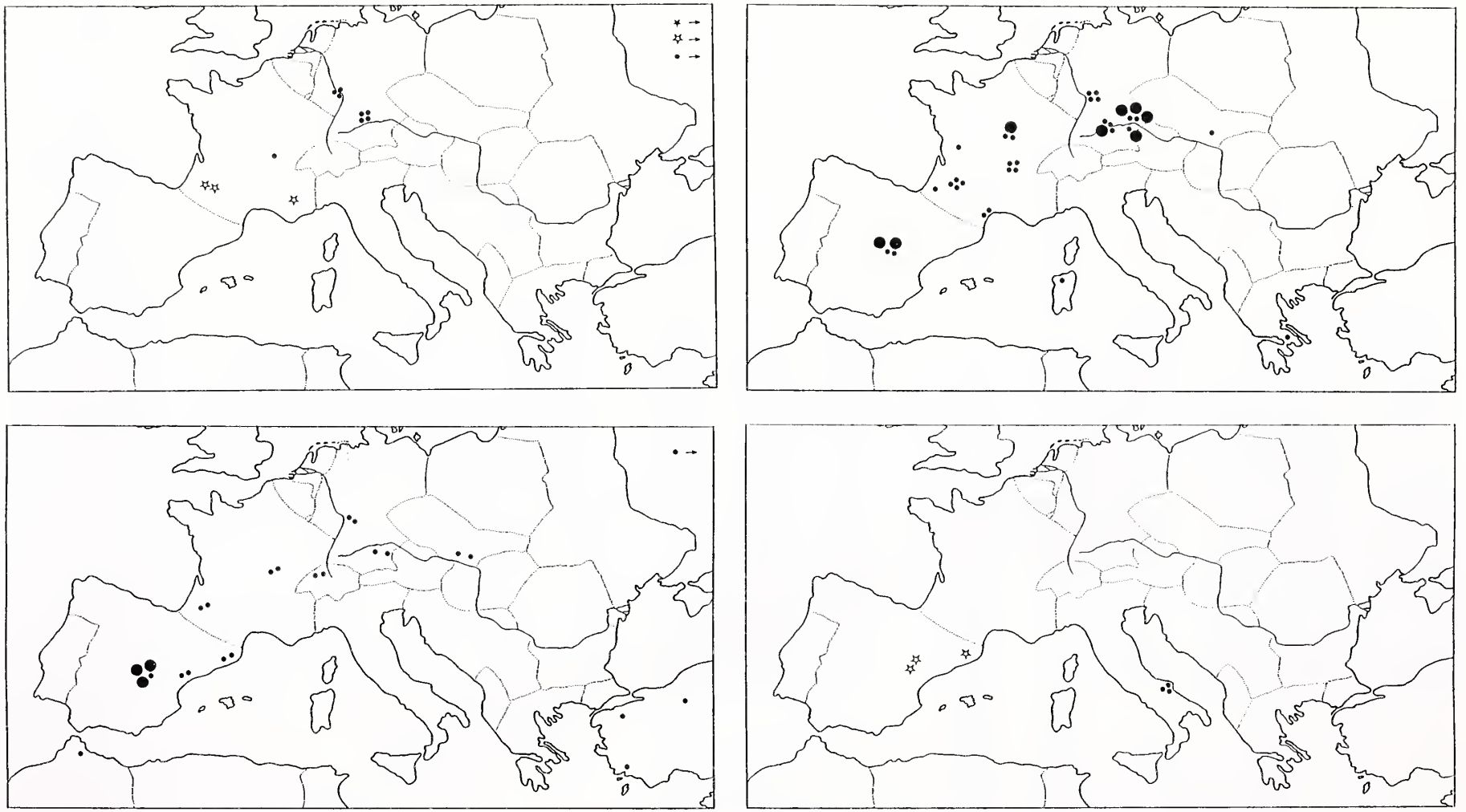

Fig. 2–5: Fig. 2.—Map of Europe showing Oligocene records of Crocidosoricinae, including three records from Asia. Closed star: early Oligocene; open stars: middle Oligocene; dots: late Oligocene. Fig. 3.—Map of Europe showing early Miocene records of Crocidosoricinae. Small dots: one record; large dots: five records. Fig. 4.—Map of Europe showing middle Miocene records of Crocidosoricinae, including one record from China. Small dots: one record; large dots: five records. Fig. 5.—Map of Europe showing late Miocene and Pliocene records of Crocidosoricinae. Stars: late Miocene; dots: Pliocene.

A PRELIMINARY ANALYSIS OF BIOGEOGRAPHY AND PHYLOGENY OF *CROCIDURA* FROM THE PHILIPPINES

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ABSTRACT

White-toothed shrews of the genus *Crocidura* from the Philippine Islands were compared with species from mainland Southeast Asia and the continental shelf islands of the Sunda Shelf. External and cranial variation indicate that three groups of taxa are present in the Philippines: a population of *C. attenuata* from the Batanes Islands; a group of medium-sized species including the named taxa *C. beatus*, *C. grayi*, *C. halconus*; and a group of large species, including *C. grandis*, *C. mindorus*, *C. negrina*, and *C. palawanensis*. One external and three dental synapomorphies are shared by *C. beatus*, *C. grayi*, and *C. halconus*, and at least one cranial synapomorphy is shared by this group and *C. mindorus*, *C. negrina*, and *C. grandis*, indicating that all six may form a monophyletic group restricted to the Philippines. Four synapomorphies unite all of these species with the *C. fuliginosa* group of continental Southeast Asia, rather than with the *C. attenuata* group. Analysis of allozyme variation in three Philippine populations (*C. beatus*, *C. grayi*, and *C. mindorus* from Sibuyan) and three reference populations from the Malay Peninsula revealed close relationships between Philippine populations and one member of the widespread Asian *C. fuliginosa* group (provisionally referred to *C.* cf. *malayana*). Sister-taxon relationship between *C. beatus* and *C. grayi* was supported by genetic distance data and cladistic analysis of allelic characters. Results of genetic analyses were strongly concordant with those of morphological analyses. *Crocidura* occur on virtually every Philippine island, including geologically Recent oceanic islands, indicating that they colonize well. The distribution of individual species corresponds strongly to the extent of land areas during the late Pleistocene when sea level was 120 m lower than at present. Current patterns of diversity of shrews in the Philippines have probably resulted from three or four separate colonizations from Asia and subsequent speciation which involved both vicariance and colonization events. Sympatry is restricted to members of different species groups.

INTRODUCTION

The Philippine Islands support a mammal fauna that is remarkable for its diversity and level of endemism; of the roughly 170 species, over 100 species (59%) are endemic (Heaney et al., 1987). These figures exceed even Madagascar, where about 80 mammal species are endemic (Jenkins, 1987:63). This exceptional degree of diversity is the result of both colonization from outside sources and phylogenetic diversification within the archipelago (Heaney, 1986, 1991; Heaney and Rickart, 1990). However, the number of individual cases is small in which there is documentation of the origin of the Philippine fauna and of its subsequent history within the archipelago. Moreover, statements about distributional patterns and levels of endemism depend on accurate information concerning taxonomic and geographic limits of species. When taxonomic status is arbitrary (that is, when actual species are not recognized or minor geographic variants are mistakenly recognized as species), patterns of endemism may easily be misinterpreted. In the Philippines, many species and genera have been reviewed recently (see references in Heaney et al., 1987), so that general patterns are discernable. However, several genera have never been reviewed in a systematic fashion, and these may influence current interpretations of the origin and evolution of the Philippine mammalian fauna. Equally importantly, phylogenies have been proposed for only a few groups, limiting our ability to interpret patterns of speciation and diversification.

Foremost among these diverse but unstudied groups are the shrews of the genus *Crocidura*. The purposes of this paper are: 1) to determine if any Philippine *Crocidura* are conspecific with those on the adjacent Asian continent, 2) to define taxonomic and geographic limits of species in the archipelago, 3) to analyze information concerning phylogenetic relations of the species, and 4) to discuss the evolutionary biogeography of the Philippine shrew fauna.

Unfortunately, only small samples of conventional specimens (i.e., skins and skulls) are available from most taxa considered in this study. Compounding this problem is a paucity of postcranial skeletons and fluid-preserved specimens and of frozen tissue for biochemical studies, making it especially difficult to define species limits and determine the phylogenetic relationships of these species. In this paper, we summarize all available information as a means of clarifying some past points of uncertainty, and of developing hypotheses for further study.

METHODS

All twelve cranial measurements were taken by Heaney with dial calipers graduated to 0.05 mm or digital calipers graduated to 0.01 mm. Cranial measurements were defined in Heaney and Timm (1983). External measurements were taken from specimen labels, and so are likely to include substantial interobserver variation. Terminology for morphology of the P^4 follows Jenkins (1984), and for foot pads follows Brown and Yalden (1973). Principal components analyses were conducted based on both correlation and variance-covariance matrices of base-10 logarithm-transformed cranial measurements, using SAS Version 6.03 (SAS Institute Inc., 1988). Results of the two analyses were nearly identical, and so only the results of the correlation matrix analysis are reported here. Cladistic analysis of morphological characters was conducted using PAUP (version 3.0; Swofford, 1990), using methods described in the text.

Photographs were taken in an Amray Model 1810 scanning

electron microscope using untreated specimens. Micrographs were prepared of all Philippine taxa except *C. grandis*, which is known only from the holotype.

Tissues of 11 freshly-trapped individuals from three populations were frozen in liquid nitrogen and later transferred to a freezer for storage at −80°C. Biochemical analyses of allozyme variation using starch-gel electrophoresis was conducted by Ruedi for 32 loci using procedures described by Pasteur et al. (1987). These were compared to two Malaysian species of the *C. fuliginosa* complex recently analyzed by Ruedi et al. (1991). The first (*C.* cf. *fuliginosa*) is characterized by a relatively low fundamental number of chromosome arms, and is represented by one population from the Cameron Highlands of the Malay Peninsula (designated "CH" in figures; $n = 8$). The second (*C.* cf. *malayana*), characterized by a higher fundamental number of chromosomes, is represented by a population from the mainland of the Malay Peninsula (designated "UG" in figures; $n = 4$) and by one from nearby Tioman Island (designated "TI" in figures; $n = 6$). We used *Crocidura russula* ($n = 10$) from Switzerland (Maddalena, 1990) as an outgroup.

Nei's genetic distance (Nei, 1978) was calculated from allele frequencies in each population. Nei's genetic distances were used to estimate a phylogenetic tree using the Fitch-Margoliash algorithm (Fitch and Margoliash, 1967) as implemented on the FITCH program of PHYLIP (Felsenstein, 1989), and tested for robustness to choice of taxa using the jackknife approach of Lanyon (1985). Phylogenetic relationships also were assessed by parsimony analysis of allozyme distribution, considering each allele as a binary character (Buth, 1984; Dowling and Brown, 1989). The most parsimonious tree was found by the branch-and-bound algorithm using Wagner parsimony (PENNY program of the PHYLIP 3.2 system; Felsenstein, 1989). Each branching point was tested for significance by bootstrapping characters (Felsenstein, 1985), giving the proportion of 100 replicated trees based on resampled data sets possessing the node in question.

Results

We approached the goals of this study through a series of steps that allowed us to test successive hypotheses regarding Philippine populations of *Crocidura*. As the first step, we used cranial morphometric variation to test the null hypothesis that Philippine shrews are not distinguishable from mainland or continental shelf populations of shrews, i.e., that they are conspecific. As the second step, we reexamined populations for which we could not reject the null hypothesis, investigating nonmetric variation in cranial, dental, and external characters. In the third step, we developed a hypothesis of phylogenetic relationships using morphological characters; and in a final step, we examined genetic variation in several populations as an independent test of our hypothesis of relationships.

Cranial Morphometric Variation

Sixty individuals from the Philippines with complete crania, along with 75 individuals of six Asian species from 11 localities, were included in a principal components analysis to assess overall mensural similarity and geographic variation. Cranial measurements and sample sizes for Philippine taxa are given in Table 1. The results (Fig. 1, Table 2) indicate that most variation (89%) is explained by a single axis. All measurements contribute approximately equally on this axis, indicating that it represents size variation. The second axis is weighted heavily by the breadth of the palate between M^3s; this is the most direct measure of palatal width. Rostral length, rostral width, and condyle-to-glenoid length also contribute to this axis, although less strongly. Examination of the third and fourth axes yielded no interpretable pattern and explained little variation, and so they were not considered further.

Inspection of Fig. 1 shows that most of the species included in this analysis fall into three groups readily defined by size. *Crocidura horsfieldi*, *C. maxi*, *C. monticola*, and *C. suaveolens* (G–K in Fig. 1) form a group of small species (low loadings on the first axis) that are unlike any populations in the Philippines. Sample sizes are small, but the magnitude of the differences suggests a high level of distinctiveness. We therefore reject conspecificity between these species and those in the Philippines.

A second group (A–B, M–S, X in Fig. 1) includes populations of intermediate size. These are *C. attenuata* from Taiwan and Vietnam and shrews from the main body of the Philippines (falling within current definitions of *C. beatus*, *C. grayi*, and *C. halconus*), plus a population from the Batanes Islands, which lie midway between Luzon and Taiwan. Within this group, two clusters are apparent. *Crocidura attenuata* (A, B) scores higher on axis II than do the other species; in other words, *C. attenuata* has a broad palate and short rostrum. Only one specimen of *C. beatus* overlaps *C. attenuata*. The population of unknowns from Batan Island (X) lies closest to the cluster of *C. attenuata*, with some overlap. The second cluster (M–S) appears to be internally identical on the second axis but shows variation along the first axis, with individuals from Mindoro tending to be smallest, from Mindanao larger, from Luzon still larger, and from Bohol, Leyte, and Maripipi the largest. On this basis, we reject conspecificity of *C. beatus/grayi/halconus* (hereafter referred to as the "*C. grayi* group") with any reference taxa, but fail to reject the hypothesis that the Batan population is conspecific with *C. attenuata*.

The third group (C–F, T–W, Y–Z in Fig. 1) is made up of individuals of largest size. It consists of the *C. fuliginosa* group from Borneo and mainland Asia (C–F), and the named Philippine taxa *C. grandis*, *C. mindorus*, *C. negrina*, *C. palawanensis*, and an individual of unknown species from Sibuyan Island (T–W, Y–Z). Sample sizes are small for all Philippine taxa in this group, restricting the strength of the interpretations. Within the group, *C. negrina* (U) tends to be smaller than *C. fuliginosa* (C–F), whereas *C. palawanensis* (V) tends to score higher on the second axis than do most specimens of *C. fuliginosa* (F). *Crocidura mindorus* (T) and the unknown from Sibuyan (Y) fall near each other, but are indistinguishable from *C. fuliginosa* on these axes; *C. grandis* (Z) is also in the midst of this cluster. On this basis, we are unable to reject the null hypothesis of conspecificity of these large shrews with the *C. fuliginosa* group, although some differences are present in

two cases (*C. negrina* and *C. palawanensis*).

Qualitative Variation

Examination of specimens indicated that four suites of features varied substantially between the populations under study: interorbital breadth, posterior palatal breadth, shape of P^4, and size and position of the pads of the hind feet.

Interorbital Breadth.—*Crocidura grandis*, *C. mindorus*, and the unknown from Sibuyan all have exceptionally broad interorbital regions (Table 1); *C. grandis* is the most extreme. *Crocidura negrina* and members of the *C. grayi* group have moderately broad interorbital regions, and *C. palawanensis*, *C. fuliginosa*, and *C. attenuata* progressively less so.

Posterior Palatal Breadth.—As noted in the cranial morphometric analysis, there is substantial variation in the shape of the posterior portion of the palate. In *Crocidura attenuata* from the mainland and Taiwan and the unknowns from the Batanes Islands, the portion of the palate that supports the molars is much broader, and progressively increases in breadth posteriorly, in comparison to specimens of similar size from the main body of the Philippines (the *C. grayi* group). This is readily visible in Fig. 2, and is apparent in measurements of the labial width across M^2s and palatal width between M^3s (Table 1). In *C. fuliginosa*, *C. palawanensis*, and the *C. mindorus* group the molar-bearing portion of the palate is most similar to that of the *C. grayi* group (Fig. 2); the palate is narrow relative to the size of the molars, as in the *C. grayi* group, rather than broad as in *C. attenuata*. Moreover, the line defined by the lingual margins of the upper molars is at a small angle to the midline, rather than substantially diverging posteriorly as in *C. attenuata*.

Shape of P^4.—As noted by prior authors (e.g., Jenkins, 1976, 1982, 1984; Heaney and Timm, 1983), the shape of P^4 often varies substantially between species. Taxa included in this study vary in size and shape of the talonid heel, the degree of concavity of the posterior margin of the tooth, prominence of the parastyle, and in the degree of development of the lingual cingulum (Fig. 3, 4).

Crocidura attenuata has the most distinctive P^4 of the taxa studied (Fig. 3, 4). The posterior margin of the tooth is highly concave and the talonid heel well-developed, so that a wide space is left between the P^4 and M^1 except where they touch at the labial edge. The lingual cingulum is typically low and moderately narrow. The population from Batan Island has a P^4 similar in shape, except that the posterior edge is slightly less concave. Additionally, the lingual cingulum is slightly broader but does not project as far anteriorly. Thus the tooth has low but conspicuous points at both the protocone and the anterior tip of the cingulum, rather than being nearly smoothly curved as is typical. The parastyle forms a moderately high and prominent cusp. *Crocidura attenuata* and the Batanes specimens have narrower molars (in the anterior-posterior axis) than all other populations in the study.

At the opposite extreme in these respects are the shrews of the *C. grayi* group. The P^4 of *C. grayi* (Fig. 3, 4) has a very broad, smoothly curving talonid heel that leaves a narrow gap between it and the M^1. Most of this expansive talonid is rimmed by the lingual cingulum. The angle formed by the talonid and the shearing edge of the paracone and distostyle (defined by Jenkins, 1984:66) is fairly abrupt (Fig. 3). The parastyle is low, forming only a small, rounded projection. Eight specimens from Mount Isarog in southern Luzon and four from Haights-in-the-Oaks in northern Luzon are very similar to the specimen shown in Fig. 3. One specimen shows slightly more expansion of the talonid and two slightly less. In one, the cingulum terminates just posterior to the protocone so that the protocone forms a more sharply defined angle in the edge of the tooth. Little if any of this variation is due to age, since the basal outline of the tooth is modified only in very old animals. *Crocidura beatus* and *C. halconus* are very similar to *C. grayi*. The latter differs only in being slightly smaller; the former has a slightly broader tooth in the labiolingual plane, and in particular has a slightly broader talonid region.

The P^4 of *C. fuliginosa* (Fig. 3, 4) is most similar to that of the *C. grayi* group. It differs in being larger, in having the entire lingual portion of the tooth broader, and in having the talonid slightly broader and more strongly expanded posterolingually. However, the parastyle is moderately large and distinct, much like that of *C. attenuata*. A series of 15 specimens of *C. fuliginosa foetida* from Mount Kinabalu, Sabah, exhibits little variation from the example in Fig. 3. A few have less of an anterolingual expansion, there is slight variation in the degree of concavity of the posterior edge, and the lingual edge is slightly convex in one specimen, rather than flattened or slightly concave.

In comparison with *C. fuliginosa*, *C. palawanensis* has slightly less concavity to both the anterior and posterior edges of P^4, and the protocone is placed slightly more anterolingually. The specimen of *C. palawanensis* shown in Fig. 3 has a narrower talonid than other specimens from Palawan and Balabac; in the others, the talonid is greater in area and more rounded, and less elongate on the labiolingual axis. The P^4 of the single specimen of *C. grandis* is indistinguishable from the series of *C. fuliginosa foetida*. None of the *C. fuliginosa*, *C. palawanensis*, or other members of the *C. mindorus* group has a P^4 as small as that of *C. negrina*, and it appears that the parastyle is smaller in *C. negrina* than in other populations with the exception of the *C. grayi* group. The lingual edge of the P^4 of *C. mindorus* is convex in both known specimens (unlike the typical state in *C. fuliginosa*). Additionally, the talonid of the holotype of *C. mindorus* is greatly enlarged (Fig. 3) and is virtually identical to that of the unknown from Sibuyan. The paratype of *C. mindorus* has the talonid less enlarged, roughly equal to that of typical *C. fuliginosa foetida*. The P^4 of *C. grandis* is indistinguishable from that of *C. fuliginosa foetida*.

On this basis, we are again unable to reject the hypothesis that the animals from the Batanes Islands are conspecific with *C. attenuata*. The members of the *C. grayi* group are distinct from both *C. attenuata* and the *C. mindorus* group. Within the *C. grayi* group, *C. halconus* does not differ from *C. grayi*, but *C. beatus* differs slightly. Within the *C. mindorus* group, although there are few specimens with which to assess variation, *C. negrina* is apparently distinct on the basis of small differences. *Crocidura mindorus* and the unknown from Sibuyan

are very similar to each other, but slightly different from all others. *Crocidura fuliginosa* and *C. palawanensis* differ subtly, and are most similar to the *C. mindorus* group.

Hind Foot Pads.—Comparisons were made using all taxa for which fluid-preserved specimens are available: *C. attenuata* (from Taiwan), *C. beatus*, *C. fuliginosa foetida* (from Borneo), *C. grayi*, *C. negrina*, and the unknowns from Batan and Sibuyan. Several morphotypes are present. The first includes only *C. attenuata* from Taiwan and the unknowns from the Batanes. These have very short, broad feet with small, rounded plantar pads (Fig. 5). Pigmentation is relatively light, and the "granulae" (the small, often pigmented fleshy bumps) on the ventral surface of the foot are relatively inconspicuous. Hairs on the dorsal surface of the feet are short and comparatively small in diameter (i.e., fine rather than coarse). Animals from the Batanes tend to have plantar pads slightly smaller and closer together, but are otherwise identical to those from Taiwan.

The second morphotype is represented by *C. beatus* and *C. grayi* (Fig. 5). Their hind feet are longer but of the same width as those of *C. attenuata*, so that they are proportionately narrower. They have heavily pigmented ventral surfaces, and the granulae are prominent. The plantar pads are of moderate size, with a tendency to be slightly elongate and flattened proximally. Specimens from Leyte, Maripipi, and Luzon are nearly identical. The distinctiveness of the foot morphology of this species group again causes us to reject its conspecificity with any other taxa.

The third type is shown by *C. fuliginosa foetida*, *C. negrina*, and the Sibuyan shrew (Fig. 5). They are generally similar in having hind feet that are long but varying in width. The soles are moderately pigmented, and granulae are prominent. The plantar pads are more elongate than in the *C. beatus* type, but proximal flattening is equivalent. Within this group, *C. fuliginosa* has broad, heavy hind feet, and the unknown from Sibuyan has the narrowest, least heavy feet, with *C. negrina* intermediate. The thenar and hypothenar pads of the Sibuyan shrew are closest to the interdigital pads, so that the central area of the palm is smallest, and the thenar tends to be more elongate than in the other two species. We tentatively conclude that *C. negrina* and the Sibuyan animal differ from Bornean *C. fuliginosa*.

Phylogenetic Analysis of Morphological Data

Analysis of the above characters is limited by lack of a phylogenetic framework for Southeast Asian *Crocidura* as a whole. In particular, determination of the polarity of characters is complicated by uncertainty about the most appropriate outgroup. For consistency with genetic analyses (for which tissues samples are scarce), we selected *C. russula* from Switzerland as an outgroup for determining polarity of the characters listed in Table 3. Jenkins (1976) considered *C. russula* to be morphometrically "central" in an analysis of Eurasian shrews, unlike *C. fuliginosa* which was found to be distinctive. Phylogenetic analyses by Maddalena (1990) and Maddalena and Ruedi (1994), based on allozymes and karyotypes, respectively, have shown *C. russula* to be an early derivative of the clade of Palearctic shrews that also includes the *C. fuliginosa* group.

The cladistic analysis of data in Table 3 found the shortest tree to be of 14 steps; there were 14 trees of this length. The large number of trees is associated with missing data for several characters and with a few unstable nodes, and the consistency index for the 14 trees is high (0.86). Fig. 6A shows a "semi-strict" consensus tree for the 14 shortest trees. That is, it includes those nodes that are not contradicted by alternative arrangements, and indicates the percentage of the 14 trees that supported a given node. The Batanes shrews are the sister group to Taiwan *C. attenuata*, with no characters that distinguish them. These two species are distantly related to all other taxa. *Crocidura palawanensis*, *C. fuliginosa*, and *C. negrina* form progressive sister taxa to the clade including other Philippine taxa. This clade is made up of an unresolved quadrichotomy, one branch of which is made up of the *C. grayi* group.

A second perspective on the cladistic analysis is presented in Fig. 6B. This is a 50% majority-rule consensus of the 14 shortest trees. This analysis accepts nodes that are supported by 50% or more of the 14 trees, and indicates the percent of the trees that support a given node. It is very similar to the prior tree (Fig. 6A), except that *C. palawanensis* and *C. fuliginosa* are now part of an unresolved trichotomy. The quadrichotomy involving the *C. grandis* and *C. grayi* groups has been partially resolved, with the *C. grayi* group as the sister taxon to *C. mindorus* and the Sibuyan shrew, with *C. grandis* and *C. negrina* as successive outgroups.

Table 3 shows that there are two synapomorphies that unite *C. attenuata* and the population from the Batanes Islands, but no derived characters shared by these two and any of the other taxa. Four synapomorphies (one dental and three from the hind foot pads) unite *C. fuliginosa* and *C. palawanensis* with the shrews from the Philippines.

Within the remaining Philippine shrews, three synapomorphies (3b, 4b, and 7c) are shared by the *C. grayi* group, but there are no synapomorphies within the group. One character (5c; low degree of concavity of the posterior edge of P^4) is either a synapomorphy for all Philippine shrews but reversed to 5b in *C. negrina* and *C. grandis*, or was developed independently in the *C. grayi* group and in *C. mindorus* and the unknown from Sibuyan. *Crocidura grandis*, *C. mindorus*, and the shrew from Sibuyan share one synapomorphy (exceptionally broad interorbital region), but there are no synapomorphies that unite these with *C. negrina* unless 5c is a true synapomorphy.

Genetic Analyses

The frequencies of alleles at 32 loci are presented in Table 4. The matrix of genetic distances and associated standard errors (Nei, 1978) derived from these data is presented in Table 5. Sample sizes are small, and all of the genetic analyses should be regarded as provisional, to be refined and expanded when more specimens are available.

A Fitch-Margoliash analysis of the genetic distance matrix (Fig. 7A; see Methods) indicates that *C. beatus* and *C. grayi* are sister taxa, the Sibuyan shrew is their sister taxon, and the two populations of *C.* cf. *malayana* are their collective sister

taxon. *Crocidura* cf. *fuliginosa* was the sister taxon to all of these.

Coding of these data for the presence or absence of each allele in Table 3 produced 63 binary characters, of which 21 are informative about ingroup relationships. A cladistic analysis of these data using boot strapping for 100 repetitions produced nearly the same relationships (Fig. 7B). The only difference was a shift of the Sibuyan shrew to a position as sister taxon to the two populations of *C.* cf. *malayana* rather than the *C. grayi* group. However, in both cases the genetic distance is small and the nodes are not strongly supported, so that we view these results as indicating an unresolved trichotomy between the Sibuyan shrew, the two populations Of *C.* cf. *malayana*, and the *C. grayi* group.

These results suggest that the Philippine shrews and *C.* cf. *malayana* share a common ancestor which invaded the Philippines relatively recently. The other Malayan shrew (*C.* cf. *fuliginosa*) is apparently more distantly related to this clade, and apparently did not colonize the Philippines.

The results of these analyses of allozyme characters (Fig. 7) are strongly concordant with those of morphological characters (Fig. 6). One important difference regards definition of members of the *C. fuliginosa* species group. In the genetic analysis (Fig. 7), it is apparent that one particular member of this group, *C.* cf. *malayana*, is most closely related to the Philippine shrews, whereas *C.* cf. *fuliginosa* is more distant. There is currently no documented morphological difference between *C. malayana* and *C. fuliginosa*, and they have been considered synonyms (Jenkins, 1984). Until species limits and relationships within the species group are resolved, we can make no further comment on this problem.

In both genetically-based analyses, *C. beatus* and *C. grayi* are sister taxa, differing by several characters from the Sibuyan shrew and representatives of the *C. fuliginosa* group. The placement of the Sibuyan shrew is unresolved in the genetic analysis, but weakly defined as the sister taxon to the *C. grayi* group in morphological analyses. More specimens of nearly all taxa are needed to further resolve relationships.

Species Limits

The lack of characters that distinguish the population in the Batanes Islands from *C. attenuata* lead us to recommend that these be considered conspecific. Similarly, the number of synapomorphies and the absence of more than very slight differences between *C. mindorus* and the shrew from Sibuyan lead us to consider them to be conspecific, but we urge continued study of these shrews.

Of the previously-named taxa in the *C. mindorus* group, we suggest no changes. The three species appear to be closely related, but differences in size, degree of pilosity of the tail, and shape of the P^4 (see species accounts) indicate separate evolutionary histories.

We recommend that *C. grayi* and *C. halconus* be considered conspecific, as noted previously by Heaney et al. (1987). Although there are slight differences in size and shape of P^4, these are trivial and seem to represent only minor geographic variation. We do not suggest use of a trinomial because this would give a false impression of the precision of current knowledge.

In spite of the close relationship between *C. grayi* and *C. beatus*, we do not recommend treating these as conspecific at this time. The differences in external, dental, and cranial morphology and in gene frequencies make it apparent that the sometimes subtle variation is consistent in indicating evolutionary independence. It is possible that more extensive data will show that they would best be recognized as subspecies, but we currently lack the information to make such fine distinctions.

Synopsis of Relationships

As a means of formalizing interpretation of the above results, we present Fig. 8 as our current hypothesis of relations for the Philippine shrews. All data indicate sister-group relationship for *C. beatus* and *C. grayi*. The morphological data show strong support (Fig. 6A, B) for the *C. mindorus* group as the sister taxon to the *C. grayi* group. One of the genetic analyses (Fitch-Margoliash; Fig. 7A) supports this, and the other is uninformative in this respect. Relationships within the *C. mindorus* group are generally unresolved by the analyses. We thus place the *C. mindorus* group plus the *C. grayi* group as an unresolved quadrichotomy in Fig. 8 as a means of indicating both general relationships and the node that is most in need of further investigation.

Crocidura palawanensis is so similar to members of the *C. fuliginosa* group that we can distinguish it only with difficulty (see species accounts), and so we place it as the sister taxon of *C. fuliginosa* (sensu lato). These two taxa are consistently identified in morphological and genetic analyses as the outgroup to the shrews from the main body of the Philippines (Fig. 6, 7), and we include them in that position in Fig. 8. *Crocidura attenuata* is unambiguously identified by morphological analyses as the most distant branch in phylogenetic analyses, and we show it so in Fig. 8.

Discussion and Conclusions

Biogeography

The five endemic and two widespread species here recognized from the Philippine Islands occur throughout the archipelago (Fig. 9), on landbridge (Palawan and Balabac), old oceanic (Luzon, Mindanao, and associated smaller islands), and young oceanic islands (Batan, Negros, and Sibuyan). They have been found on every island on which they have been sought.

Three endemic species are each confined to single large Pleistocene islands. *Crocidura beatus*, known from Biliran, Bohol, Leyte, Maripipi, and Mindanao, and *C. grandis*, known only from Mindanao, are restricted to the Pleistocene island of Greater Mindanao; *C. negrina* occurs on the Pleistocene island of Greater Negros-Panay; and *C. palawanensis* is known only from Palawan and Balabac, which were united as part of Greater Palawan during the late Pleistocene.

Additionally, *C. attenuata* is known in the Philippines only from one island in the Batanes group; these were isolated from other islands during the Pleistocene. The Batanes Islands lie midway between Luzon and Taiwan. This represents the first

evidence of colonization of the northern Philippines from Taiwan (Heaney, 1986).

Other species are more widespread. *Crocidura mindorus* is now known from Mindoro, which remained separate from other islands during the Pleistocene, and the nearby small oceanic island of Sibuyan. *Crocidura grayi* occurs on Luzon and Catanduanes, which were joined as Greater Luzon, and on the adjacent island of Mindoro.

Diversification Within the Philippines

With seven species, *Crocidura* is the second most speciose genus of nonvolant mammal in the Philippines; only the endemic forest mice of the genus *Apomys* are more speciose (Musser, 1982; Heaney, 1986). This large number of endemic species is atypical of nonendemic genera in the Philippines. Of 15 nonendemic genera, only two (*Crocidura* and *Rattus*; 13%) have more than one species in the Philippines, whereas 53% of the endemic genera have more than one species. This difference implies that *Crocidura* and *Rattus* have unusually good colonizing ability, and this is supported by the presence of both genera on isolated oceanic islands within the Philippines and in the oceanic portions of the Indo-Australian archipelago to the south.

Our conclusions regarding phylogenetic relationships and species limits (Fig. 8) carry implications regarding the likely historical processes of diversification within the Philippines. It appears that there have been three or four separate colonizations of the Philippines from the Asian mainland. Perhaps the most recent of these was the arrival of *C. attenuata* in the Batanes Islands, presumably from the nearby island of Taiwan. The deep water surrounding the Batanes and lack of evidence of dryland connection to Asia implies overwater colonization.

Another recent colonization was that which produced *C. palawanensis*, a species only slightly different from *C. fuliginosa*. This occurrence is strongly concordant with the Pleistocene history of Palawan. The fauna of the Palawan island group shares very little with the main body of the Philippines. Instead, 96% of the genera and about 60% of the species of nonvolant mammals are shared with Borneo and the rest of the continental shelf islands. This pattern is due to the probable presence of a land bridge between Palawan and Borneo during the middle Pleistocene (ca. 160,000 years ago), when sea level dropped to about 160 m below the present level. Water between Palawan and Borneo is about 140 m deep (Heaney, 1986). Sea level dropped only to 120 m below current sea level during the late Pleistocene, thereby keeping Palawan isolated, so that the two species probably have been disjunct for about 160,000 years.

The three species of the *C. mindorus* group probably represent a third colonization. Although they might have originated from a common ancestor with *C. palawanensis*, it is more likely that they are derived from the common ancestor of *C. fuliginosa* and *C. palawanensis*, since they share no characters with *C. palawanensis* that are not also shared with *C. fuliginosa*. This group has apparently diversified along the western rim of the Philippines, with each species now on a separate island. There is no evidence that these islands were ever connected as a single land mass (Heaney, 1986, 1991), so overwater colonization on three occasions is implied.

Finally, the *C. grayi* group might have originated from the *C. mindorus* group within the Philippines, or from the common ancestor of *C. fuliginosa*, *C. palawanensis*, and the *C. mindorus* group. Portrayal of the relevant nodes on Fig. 8 indicates that the latter possibility is more likely, but the weakness of the relevant node does not allow firm conclusions. Once in the Philippines, they speciated between Greater Luzon and Greater Mindanao. Overwater colonization across the narrow San Bernardino Straits is the most likely mechanism, although the possibility of a land bridge across the straits cannot be entirely discounted (Heaney, 1986). Colonization from Luzon to Mindoro by *C. grayi* is likely, since current evidence does not indicate past dryland connection between these two islands (Heaney, 1986, 1991).

We conclude that shrews of the genus *Crocidura* have entered the Philippines on three or four occasions, once from the north reaching only the Batanes Islands, and two or three times from the south. Having entered the Philippines from the south, they have repeatedly crossed narrow sea channels. In one case (*C. palawanensis*) speciation followed vicariance due to a rise in sea level. In three cases (*C. negrina*, *C. grandis*, and *C. mindorus*) it seems certain and in one case (*C. beatus* and *C. grayi*) likely that speciation followed overwater colonization. In two cases (*C. attenuata* in the Batanes and *C. grayi* on Mindoro), overwater colonization has not resulted in recognized speciation. Sympatry of *Crocidura* in the Philippines involves two cases in which members of the *C. mindorus* group and the *C. grayi* group occur sympatrically, but never members of a single species group. The biogeographic history of the genus *Crocidura* in the Philippines is one of both colonization and diversification, with the latter taking place through both vicariance and dispersal, and with current patterns of species richness the result of both speciation and direct colonization.

Taxonomic Accounts of Philippine Species

Crocidura attenuata

1872. *Crocidura attenuata* Milne-Edwards, Rech. Mamm., p. 263. Type locality, Moupin, Szechwan, China.

Remarks.—In comparison with *C. attenuata* from Taiwan and with *C. grayi* from Luzon, specimens from Batan Island have a short tail (ca. 42 mm) like shrews from Taiwan, rather than moderately long as on Luzon (ca. 60 mm). Bristle hairs are present on the proximal three-fourths of the tail of all three taxa, but are longer on shrews from Taiwan and Batan than from Luzon (10 vs. 6 mm, respectively). The shorter hairs that are closely appressed to the tail are short in Batan and Taiwan shrews, giving the tail the appearance of being nearly naked, whereas shrews from Luzon have longer hairs so that their tails look moderately hairy and have inconspicuous scales. The feet are pale brown on specimens from Batan and Taiwan, and dark brown on those from Luzon. The pelage of shrews from Batan and Taiwan is moderately dense but short, whereas shrews from Luzon have denser and longer pelage.

Specimens from Batan are unlike all others in having P^4 with a more strongly developed protocone which is placed more anterolingually than in other species, giving the tooth a

distinctive shape (Fig. 3).

Specimens examined.—Batan Island. Batanes Prov.: Basco Airstrip (2 USNM); Itbud (1 USNM); no specific locality (2 USNM).

Crocidura beatus

1910. *Crocidura beatus* Miller, Proc. U. S. Natl. Mus., 38:392. Type locality, Mt. Bliss, Mindanao, elev. 5750 ft. Holotype, USNM 144647.

1934. *Crocidura parvacauda* Taylor, Monogr. Bur. Sci. (Manila), 30:83. Type locality, Saub, Cotabato Prov., Mindanao, sea level. Holotype, UIMNH 33390.

Remarks.—A small shrew, condyloincisive length 20.0–21.5 mm. Relative to *C. grayi*, there are usually only a few vibrissae-like hairs on the basal one-half of the tail, and these tend to be fine and short (rather than many coarse hairs over most of the length of the tail). The claws on fore and hind feet are slightly shorter and less robust. The cranium is slightly more elongate and narrow, and the braincase is slightly more inflated. In side view of the cranium, the anterior tip of the nasal aperture has walls that come to an acute anterodorsal point, nearly forming a right angle between anterior edge and dorsal edge, rather than being lower and more rounded. The upper P^4 and molars are slightly broader and the toothrow is slightly longer (Fig. 2).

Relative to *C. attenuata*, the braincase is more inflated, the interorbital region is broader, the molars are proportionately larger, and the posterior margins of P^4 and upper molars are very slightly concave, rather than strongly so (Fig. 3). The tail is longer, and all hairs are longer giving the tail a hairier appearance. The pelage is longer and denser, and the feet more darkly pigmented. Relative to *C. negrina*, the cranium is smaller and has a markedly shorter postpalatal region, and the ascending ramus of the mandible is lower; dental proportions are similar. Other taxa differ substantially in morphometric traits (Fig. 1, discussion above).

Crocidura parvacauda is known only from the holotype. The skin label now has the note, "skin made up from alcohol specimen, skull not found Feb. 1956, carcass in alcohol." A search of the UIMNH collection by Heaney in 1983 failed to produce the skull. The skin does not differ in any conspicuous way from *C. beatus*. Only the tail differs in being shorter (35 mm vs. 52–60 mm for those we have examined), which was noted by Taylor as the prime distinguishing feature. All of the measurements of the skull given by Taylor (1934:84) fall within the range of those for a series from Mindanao. Given the absence of any difference other than tail length, and the frequency of tail damage in small mammals, we recommend that *C. parvacauda* be considered a synonym of *C. beatus* until additional short-tailed specimens may be found.

Specimens examined.—Biliran. 5 km N, 10 km E Naval, elev. 850 m (1 USNM). Bohol. 1 km S, 1 km E Bilar, 320 m (1 USNM). Leyte. Leyte Prov., Mt. Lobi Range: Tampas, Burauen, 2300 ft (2 DMNH); Mt. Pangasugan, 8.5 km N, 2.5 km E Baybay, 500 m (2 USNM); Mt. Pangasugan, 10 km N, 4.5 km E Baybay, 950 m (6 USNM). Maripipi. Leyte Prov.: 1 km N, 1.5 km W Maripipi town, 400 m (2 UMMZ). Mindanao. Agusan Prov.: Mt. Hilong-Hilong, Siwod, 3500 ft (3 DMNH). Bukidnon Prov.: Mt. Katanglad, Malaybalay, 5200 ft (2 DMNH); Mt. Katanglad (1 SMF). Cotabato Prov.: Saub, sea level (1 UIMNH). Zamboanga Prov.: Dabiak, Labao (1 FMNH); summit of Mt. Bliss, 5750 ft (1 USNM); Mt. Malindang, Duminigat, 5200 ft (1 FMNH).

Crocidura grandis

1910. *Crocidura grandis* Miller, Proc. U. S. Natl. Mus., 38:393. Type locality, Grand Malindang Mt., Mindanao, 6100 ft. Holotype, USNM 144648.

Remarks.—A large shrew, condyloincisive length 23.6 mm. Relative to *C. mindorus*, the tail is thicker with fewer long vibrissae-like hairs, hind feet longer and apparently less heavily pigmented; cranium more elongate, braincase slightly less globose, interorbital region broader, molars slightly larger. Relative to *C. fuliginosa*, quite similar, interorbital region broader, braincase slightly more inflated. Relative to *C. negrina*, generally larger; cranium proportionately more elongate, interorbital region broader, postpalatal region longer, unicuspids slightly broader. All other Philippine taxa are substantially smaller.

Specimens examined.—Mindanao. Grand Malindang Mt., 6100 ft (1 USNM).

Crocidura grayi

1890. *Crocidura grayi* Dobson, Ann. and Mag. Nat. Hist., ser. 6, 6:494. Type locality, Philippine Islands; precise locality unknown. Holotype, BMNH 55.12.24.421.

1910. *Crocidura halconus* Miller, Proc. U. S. Natl. Mus. 38:391. Type locality, spur of main ridge of Mount Halcon, Mindoro, 6300 ft. Holotype, USNM 144652.

Remarks.—A small shrew (condyloincisive length 18.8–20.7 mm) with a narrow rostrum and proportionately narrow molar teeth. Differs from *C. beatus* and *C. attenuata* as discussed above. Other Philippine taxa are appreciably larger (Table 1).

Specimens examined.—Catanduanes. 4 km E Summit, 250 m (1 USNM). Luzon. Benguet Prov.: Haights-in-the-Oaks (near Barrio Sayangan, Atok, ca. 2400 m) (4 USNM). Camarines Sur Prov.: Mt. Isarog, 475 m (1 PNM), 900 m (2 USNM), 1125 m (25 USNM), 1350 m (3 USNM), 1550 m (2 USNM), 1750 m (6 USNM). Mountain Prov.: Mt. Data (1 BMNH). Rizal Prov.: "probably Manila" (1 AMNH). No specific locality (2 BMNH). Mindoro. Bulalacao (1 USNM). Main ridge of Mt. Halcon, 4500 ft (3 USNM); spur of main ridge of Mt. Halcon, 6300 ft (1 USNM). Occidental Mindoro Prov.: Mt. Iglit Station (2 MMNH); 1 mi W Mt. Iglit Station (1 MMNH); 0.5 mi NE Mt. Iglit Station (1 MMNH); 3.5 mi NE Mt. Iglit Station (12 MMNH); 4 mi NE Mt. Iglit Station (6 MMNH); 5 mi NE Mt. Iglit Station (2 MMNH).

Other records.—Luzon. Abra Prov.: Lagangilang (Lawrence, 1939).

Crocidura mindorus

1910. *Crocidura mindorus* Miller, Proc. U. S. Natl. Mus., 38:392. Type locality, summit of main ridge of Mt. Halcon, 6300 ft. Holotype, USNM 144654.

Remarks.—A moderately large *Crocidura* with a well-expanded, relatively globose braincase. Relative to *C. fuliginosa*, cranium generally less elongate; braincase proportionately shorter, more globose; molars laterally narrower; toothrow shorter. Posterior margins of upper molariform teeth less concave. Lower incisors less robust, lower molars with lower crowns, coronoid process lower, less robust. Relative to *C. grandis*, the tail is thinner with fewer long hairs on proximal half, hind feet shorter and heavily pigmented; cranium less elongate, interorbital region slightly narrower. Relative to *C. negrina*, braincase more globose, interorbital region broader, slightly narrower upper molars, lower coronoid process. Other taxa appreciably smaller.

Specimens examined.—Mindoro. Main ridge of Mt. Halcon, 6300 ft (2 USNM). Sibuyan Island. Romblon Prov.: NW slope Mt. Guitinguitin, 4.5 km S, 4 km E Magdiwang, 325 m (1 FMNH).

Crocidura negrina

1952. *Crocidura negrina* Rabor, Nat. Hist. Misc., Chicago Acad. Sci., 96:6. Type locality, Dayungan, elev. 4500 ft, Cuernos de Negros (= Mt. Talinis), Negros Island. Holotype, FMNH 78445.

Remarks.—A medium-sized shrew, condyloincisive length 22–23 mm. Relative to *C. beatus*, larger, proportionately longer rostrum, shorter postpalatal region, lower coronoid process on ascending ramus. Relative to *C. grayi*, larger, wider rostrum, broader molars, and longer toothrow. Relative to *C. fuliginosa*, shorter postpalatal region, broader interorbital region, posterior margin of upper molariform teeth much less concave. Relative to *C. mindorus* braincase less globose, narrower interorbital region, slightly broader upper molars, higher coronoid process on ascending ramus.

Specimens examined.—Negros. Negros Oriental Prov.: Dayungan, Cuernos de Negros, 4500 ft (1 FMNH); Camp Lookout, Valencia, 500 m (1 SU); Naguro, Siaton, 700 m (1 DMNH); Lake Balinsasayao, 3 km N, 14 km W Dumaguete, 830 m (1 UMMZ), 1000 m (1 UMMZ), 1200 m (1 UMMZ).

Crocidura palawanensis

1934. *Crocidura palawanensis* Taylor, Monogr. Bur. Sci., Manila. Type locality, Brooke's Point, Palawan Island, Philippines. Holotype, AMNH 241679.

Remarks.—A relatively large *Crocidura*, condyloincisive length 21.7–24.7 mm, cranium relatively elongate, interorbital region narrow, posterior margin of upper molariform teeth moderately concave. Relative to *C. grandis*, interorbital region narrower and braincase slightly broader and shorter, posterior margin of molariform teeth less concave. Relative to *C. mindorus* cranium more elongate; braincase less globose; interorbital region narrower; molar teeth laterally broader, posterior margins more highly concave. Lower incisors more robust; lower molars with higher crowns; coronoid process higher, more robust. Relative to *C. negrina*, longer postpalatal region, narrower unicuspids, posterior margins of molariform teeth more concave. Other Philippine taxa substantially smaller, differing in quantitative traits (Fig. 1, discussion above). Relative to *C. fuliginosa*, specimens from Palawan and Balabac are slightly larger than those from Borneo, have narrower palates, and have P^4s that have less concave posterior edges. External differences are not consistent. Specimens from Palawan have longer tails and longer pelage than specimens from Borneo and Balabac. Balabac specimens have tails of equal length but shorter pelage than those from Borneo. The differences between *C. palawanensis* and the Sunda Shelf shrews are weak, and the Palawan shrews may eventually be synonymized with a species from the Sunda Shelf. We do not take such action here both because of the uncertainty regarding species limits of shrews on the Sunda Shelf, and in order to keep attention focused on the differences that are present.

Specimens examined.—Balabac. Palawan Prov.: Dalawan Bay, Minagas Point (2 USNM). Palawan. Palawan Prov.: Mt. Mantalingajan, 3600–4350 ft (1 USNM); Babuyan, Puerto Princesa, sea level (1 FMNH); Brooke's Point (1 AMNH).

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APPENDIX

Crocidura edwardsiana from "Ile Soulou" (= Jolo Island, Sulu Archipelago), is currently misidentified in systematic literature. Trouessart (1880) named this species at a time when *Pachyura* (= *Suncus*) was considered a subgenus of *Crocidura*. Although the original description made no subgeneric designation, it stated that there are 28 teeth, and only four teeth are mentioned anterior to the molariform teeth, making it fit the current definition of *Crocidura*. However, Trouessart (1897) listed *edwardsiana* as a variety of *Crocidura* (*Pachyura*) *caerulea*, which is now considered a synonym of *Suncus murinus*. Hollister (1912) listed *edwardsiana* as a species of *Pachyura* on the basis of Trouessart's (1897) description of four upper unicuspids, the erucial diagnostic character of *Suncus*. However, Taylor (1934) listed *edwardsiana* as a species of *Crocidura*, apparently on the basis of the original description of the unicuspids. Subsequent authors have followed Taylor uncritically (e.g., Honacki et al., 1982; Musser and Heaney, 1985).

The original description was based on two specimens; no others have been obtained subsequently. The paratype was not found by F. Petter in 1986 (Petter, personal communication) and is presumed lost. The holotype of *C. edwardsiana* (MNHNP 1881–3895) was examined by R. Hutterer on 29 January 1987 (Hutterer, personal communication). He found it possessed all of the characteristics of a juvenile of one to two weeks age: pelage hairs short and gray, skull not fully calcified, basisphenoid suture open, and teeth unworn. The right side of the palate was still eovered by flesh, but the left side had been cleaned and the fourth upper unicuspid was visible. Cranial measurements (as defined by Heaney and Timm, 1983) were: CIL 25.0; UTR 11.8; MB 8.9; GW 10.5; PL 11.6; IO 5.5; RL 8.2; PPD 5.1; RB 3.6; PPL 10.4; CGL 8.8; P4M3 6.3; M2M2 8.7; PWM3 4.1; COR 6.4; LTR 11.2. He concluded that the holotype is a juvenile *Suncus murinus* of "caravanning age." The presence of four unicuspids, with the measurements given here, and identification of the holotype as a juvenile, make identification of this taxon as *Suncus murinus* unambiguous, in keeping with Trouessart's (1897) assessment.

Table 1.—*Selected measurements of* Crocidura *from the Philippine Islands.* [a]*Estimated by LRH from dried skin.*

Locality	*n*	Condyloincisive Length	Braincase Width	Interorbital Width	Rostral Length	Postpalatal Depth	Rostral Width	Postpalatal Length	Condyle to Glenoid	Upper Toothrow	P^4 to M^3	M^2 to M^2 (Labial)	Palatal Width	Total Length	Tail Length	Hind Foot
Crocidura beatus																
Biliran	1	—	9.5	—	—	3.7	—	9.8	8.7	—	5.3	6.3	2.3	144	56	16
Bohol	1	21.2	9.1	4.6	8.6	3.8	2.9	9.7	8.4	9.4	5.3	6.5	2.4	143	59	16
Leyte	6	21.30±0.40	9.56±0.23	4.72±0.25	8.47±0.19	3.92±0.13	2.75±0.23	9.50±0.18	8.37±0.18	9.33±0.23	5.27±0.12	6.38±0.04	2.50±0.14	153.8±10.1	65.3±9.2	15.6±0.9
		(20.6–21.7)	(9.3–9.8)	(4.3–5.0)	(8.3–8.7)	(3.7–4.1)	(2.5–3.0)	(9.3–9.8)	(8.1–8.6)	(9.0–9.6)	(5.1–5.4)	(6.3–6.4)	(2.3–2.7)	(145–163)	(53–75)	(14–16)
Maripipi	2	21.05	9.35	4.85	8.5	3.7	2.65	9.5	8.25	9.3	5.35	6.5	2.7	149.5	68.5	16.0
		(20.6–21.5)	(9.2–9.5)	(4.8–4.9)	(8.5)	(3.7)	(2.6–2.7)	(9.3–9.7)	(8.0–8.5)	(9.1–9.3)	(5.2–5.5)	(6.4–6.6)	(2.6–2.8)	(146–153)	(68–69)	(15–17)
Mindanao	9	20.38±0.47	9.20±0.26	4.54±0.18	8.14±0.25	3.76±0.15	2.60±0.17	9.20±0.07	8.13±0.10	8.81±0.37	5.09±0.24	6.01±0.21	2.38±0.10	136.8±6.1	56.7±2.9	14.8±1.5
		(20.0–21.1)	(8.8–9.5)	(4.3–4.8)	(7.7–8.4)	(3.5–3.9)	(2.3–2.9)	(9.1–9.3)	(8.0–8.3)	(8.3–9.3)	(4.8–5.5)	(5.6–6.2)	(2.2–2.5)	(127–142)	(52–60)	(12–16)
Crocidura palawanensis																
Balabac	2	22.25	9.5	4.7	9.25	4.0	2.9	9.75	8.95	9.9	5.8	6.9	2.6	150	63	15
		(21.7–22.8)	(9.3–9.7)	(4.7)	(8.4–10.1)	(3.9–4.1)	(2.8–3.0)	(9.5–10.0)	(8.6–9.3)	(9.6–10.2)	(5.6–6.0)	(6.7–7.1)	(2.6)	(143–157)	(56–70)	(14–16)
Palawan	3	23.97±0.64	9.8	4.87±0.12	9.60±0.36	4.20±0.20	2.90	10.77±0.35	9.37±0.21	10.53±0.23	5.83±0.06	7.00±0.36	2.60±0.17	171	85	17.0
		(23.0–24.7)	(9.6–10.0)	(4.8–5.0)	(9.2–9.9)	(4.0–4.4)	(2.9)	(10.4–11.1)	(9.2–9.6)	(10.4–10.8)	(5.8–5.9)	(6.7–7.4)	(2.5–2.8)	(161–181)	(68–90)	(16–18)
Crocidura grayi																
S. Luzon	10	20.58±0.47	9.63±0.23	4.65±0.14	8.44±0.18	3.89±0.11	2.59±0.16	8.99±0.31	8.11±0.23	9.19±0.24	5.27±0.14	6.11±0.16	2.41±0.57	142.6±5.4	59.6±2.6	15.7±0.7
		(19.8–21.04)	(9.2–10.0)	(4.4–4.8)	(8.2–8.8)	(3.7–4.0)	(2.4–2.9)	(8.5–9.4)	(7.7–8.5)	(8.9–9.7)	(5.1–5.6)	(5.8–6.3)	(2.3–2.5)	(133–149)	(57–64)	(15–17)
N. Luzon	8	20.13±0.57	9.37±0.20	4.59±0.25	7.99±0.24	3.67±0.08	2.53±0.13	8.90±0.22	7.96±0.24	8.89±0.24	5.10±0.17	6.05±0.24	2.48±0.11	—	52.0	13.7
		(19.3–20.9)	(9.1–9.7)	(4.2–4.9)	(7.6–8.4)	(3.6–3.8)	(2.4–2.8)	(8.6–9.2)	(7.6–8.2)	(8.5–9.3)	(4.9–5.4)	(5.7–6.5)	(2.4–2.7)		(49–59)	(13–14)
Crocidura halconus																
Mindoro	31	19.50±0.38	9.10±0.20	4.43±0.13	7.85±0.24	3.60±0.12	2.50±0.11	8.62±0.26	7.82±0.15	8.58±0.29	4.87±0.18	5.86±0.13	2.34±0.13	128.9±5.1	55.2±3.3	14.0±0.7
		(18.8–20.2)	(8.5–9.5)	(4.2–4.7)	(7.5–8.2)	(3.4–3.9)	(2.3–2.8)	(8.1–9.1)	(7.6–8.1)	(7.8–9.0)	(4.4–5.1)	(5.5–6.1)	(2.2–2.5)	(118–139)	(48–60)	(13–16)
Crocidura grandis																
Mindanao	1	23.6	10.3	5.4	9.5	4.2	2.7	10.9	9.1	10.1	5.7	6.9	2.9	157	58[a]	19
Crocidura mindorus																
Mindoro	2	22.45	10.3	5.15	9.10	4.1	2.75	9.85	8.85	9.85	5.55	6.6	2.65	167	75.5	17.5
		(22.3–22.6)	(10.1–10.5)	(5.1–5.2)	(9.1)	(4.1)	(2.7–2.8)	(9.5–10.2)	(8.8–8.9)	(9.8–9.9)	(5.5–5.6)	(6.6–6.7)	(2.6–2.7)	(160–174)	(73–78)	(17–18)
Crocidura negrina																
Negros	5	22.25	10.15	4.90	9.07±0.35	4.00	2.70	9.80	8.70	9.97	5.50	6.87	2.70	158.3	71.6	17.7
		(22.0–22.5)	(10.0–10.3)	(4.7–5.1)	(8.7–9.4)	(3.9–4.1)	(2.5–2.8)	(9.5–10.1)	(8.7)	(9.7–10.3)	(5.3–5.8)	(6.7–7.0)	(2.6–2.8)	(155–167)	(68–73)	(17–18)
Crocidura sp.																
Batan	4	19.97±0.67	9.10±0.18	4.45±0.06	7.93±0.15	3.70–0.08	2.43±0.05	8.73±0.42	7.73±0.25	9.03±0.31	5.15±0.17	6.23±0.25	2.60±0.12	—	—	—
		(19.4–20.7)	(8.9–9.3)	(4.4–4.5)	(7.8–8.1)	(3.6–3.8)	(2.4–2.5)	(8.4–9.2)	(7.5–8.0)	(8.6–9.3)	(4.9–5.3)	(5.9–6.5)	(2.5–2.7)			
Sibuyan	1	23.4	10.2	5.1	9.8	4.0	2.9	10.0	8.7	10.7	6.1	7.1	2.7	172	75	17

Table 2.—*Results of a principal components analysis of log-transformed cranial measurements of* Crocidura *from the Philippines and adjacent areas. Axes I and II are graphed in Fig. 1.*

Variable	Axis I	Axis II
Condyloincisive length	0.30	−0.05
Braincase width	0.29	−0.02
Interorbital width	0.28	−0.12
Rostral length	0.30	−0.15
Postpalatal depth	0.29	0.04
Rostral width	0.27	−0.27
Postpalatal length	0.29	−0.10
Condyle to glenoid	0.29	−0.23
I^1 to M^3	0.30	−0.03
P^4 to M^3	0.29	−0.04
M^2 to M^2 (labial)	0.30	0.12
Palatal width at M^3	0.26	0.90
Cumulative % variance	89.5	92.0
Eigenvalue	10.7	0.29

Table 3.—*List of qualitative characters discussed in the text, giving the character state for each of the populations from the Philippines and from three reference populations. Character numbers and state codes are those used in Fig. 6.*

Species	1 Interorbit	2 Posterior Palate	3 Parastyle of P^4	4 Lingual Exposure of P^4	5 Concavity of P^4	6 Thenar and Hypothenar	7 Pigmentation of Feet	8 Plantar Granulae
Crocidura attenuata	narrow	broad	prominent	low	great	small and rounded	slight	inconspicuous
Crocidura sp. (Batanes)	narrow	broad	prominent	low	great	small and rounded	slight	inconspicuous
C. beatus	moderate	narrow	low	moderate	low	elongate and flattened	heavy	prominent
C. grayi	moderate	narrow	low	moderate	low	elongate and flattened	heavy	prominent
C. halconus	moderate	narrow	low	moderate	low	elongate and flattened	heavy	prominent
C. fuliginosa	narrow	narrow	prominent	high	moderate	elongate and flattened	moderate	prominent
C. grandis	broad	narrow	prominent	high	moderate	elongate and flattened	—	—
C. mindorus	broad	narrow	prominent	high	low	elongate and flattened	—	—
C. negrina	moderate	narrow	prominent	high	moderate	elongate and flattened	moderate	prominent
C. palawanensis	narrow	narrow	prominent	high	moderate	elongate and flattened	—	—
Crocidura sp. (Sibuyan)	broad	narrow	prominent	high	low	elongate and flattened	moderate	prominent
C. russula	narrow	narrow	prominent	high	great	small and rounded	slight	inconspicuous

Table 4.—*Frequency of allozymes in seven populations of* Crocidura. *Dashes indicate values of zero.*

Locus	Relative Speed	*C. grayi* $n = 9$	*C. beatus* $n = 1$	*Crocidura* sp. (Sibuyan) $n = 1$	*C. fuliginosa* (CH) $n = 8$	*C. malayana* (UG) $n = 4$	*C. malayana* (TI) $n = 6$	*C. russula* $n = 10$
ADA	+155	—	—	—	—	—	0.08	—
	+140	—	—	—	0.25	—	0.84	—
	+120	0.75	—	—	0.75	0.50	0.08	—
	+100	0.25	1.0	1.0	—	0.50	—	1.0
ADH	−100	1.0	1.0	1.0	1.0	1.0	1.0	1.0
AK-1	+112	—	—	—	0.13	—	—	—
	+100	1.0	1.0	1.0	0.87	1.0	1.0	1.0
ALB	+95	0.05	—	1.0	1.0	0.50	1.0	—
	+91	0.28	—	—	—	0.50	—	1.0
	+84	0.67	1.0	—	—	—	—	—
CK-1	+100	1.0	1.0	1.0	1.0	1.0	1.0	1.0
CK-2	+100	—	—	—	1.0	1.0	—	1.0
	+71	1.0	1.0	1.0	—	—	1.0	—
EST-1	+135	—	—	—	—	—	—	1.0
	+106	1.0	1.0	1.0	—	1.0	1.0	—
	+87	—	—	—	1.0	—	—	—
GOT-1	+200	—	—	—	1.0	—	—	—
	+100	1.0	1.0	1.0	—	1.0	1.0	1.0
GOT-2	−100	1.0	1.0	1.0	1.0	1.0	1.0	1.0
a-GPD	+153	—	—	—	0.13	—	—	—
	+100	1.0	1.0	1.0	0.87	—	—	1.0
	+67	—	—	—	—	1.0	1.0	—
G-6-PD	+120	—	—	—	1.0	—	—	—
	+115	1.0	1.0	1.0	—	1.0	1.0	—
	+107	—	—	—	—	—	—	1.0
HBB	−100	1.0	1.0	1.0	—	1.0	1.0	1.0
	−82	—	—	—	1.0	—	—	—
HK-1	+163	—	—	—	0.13	—	—	—
	+110	0.11	—	—	—	—	0.33	—
	+100	0.89	1.0	1.0	0.87	1.0	0.67	1.0
HK-2	−100	1.0	1.0	1.0	—	0.50	0.83	1.0
	−81	—	—	—	—	0.25	—	—
	−76	—	—	—	1.0	0.25	0.17	—
GDH	+118	1.0	1.0	1.0	—	1.0	1.0	—
	+100	—	—	—	1.0	—	—	—
	+0	—	—	—	—	—	—	1.0
IDH-1	+155	1.0	1.0	1.0	1.0	1.0	1.0	1.0
IDH-2	−100	1.0	—	1.0	1.0	1.0	1.0	—
	−75	—	—	—	—	—	—	1.0
	−45	—	1.0	—	—	—	—	—
SOD-1	+102	—	—	—	0.06	—	—	—
	+100	—	—	—	0.88	0.25	—	—
	+94	—	—	—	0.06	0.38	1.0	—
	+84	0.06	—	1.0	—	0.25	—	1.0
	+79	0.55	1.0	—	—	0.12	—	—
	+65	0.39	—	—	—	—	—	—
SOD-2	−100	1.0	1.0	1.0	1.0	1.0	1.0	—
	−60	—	—	—	—	—	—	1.0
SOD-3	−100	1.0	1.0	1.0	1.0	1.0	1.0	—
	−85	—	—	—	—	—	—	1.0
LAP	+100	1.0	1.0	1.0	1.0	1.0	1.0	1.0
LDH-1	+100	1.0	1.0	1.0	1.0	1.0	1.0	1.0

Table 4 (cont.)

LDH-2	−110	1.0	1.0	1.0	1.0	1.0	1.0	1.0
MDH-1	+100	1.0	1.0	1.0	1.0	1.0	1.0	1.0
MDH-2	−100	1.0	1.0	1.0	1.0	1.0	1.0	1.0
MOD	−125	—	—	—	—	—	—	1.0
	−115	—	—	—	1.0	—	—	—
	−105	1.0	1.0	1.0	—	1.0	1.0	—
MPI	+137	—	—	0.50	0.87	0.88	0.42	0.80
	+100	1.0	1.0	0.50	0.13	0.12	0.58	0.20
PA	+80	1.0	1.0	1.0	1.0	1.0	1.0	1.0
6-PGD	+180	—	—	1.0	—	0.50	0.48	—
	+140	1.0	1.0	—	—	0.50	0.52	1.0
	+100	—	—	—	1.0	—	—	—
PGI	−200	—	—	—	—	—	—	1.0
	−100	1.0	1.0	1.0	1.0	1.0	1.0	—
PGM	+150	—	—	—	0.19	—	—	—
	+120	0.28	1.0	1.0	0.81	1.0	1.0	—
	+100	—	—	—	—	—	—	1.0
	+75	0.72	—	—	—	—	—	—
PROT-A	+100	1.0	1.0	1.0	1.0	1.0	1.0	1.0

Table 5.—*Matrix of Nei's genetic distances (and standard errors) for Southeast Asian* Crocidura, *calculated from data in Table 4. Abbreviations for taxa as in Table 4.*

	C. fuliginosa (CH)	*C. malayana* (UG)	*C. malayana* (TI)	*C. grayi*	*C. beatus*	*Crocidura* sp. Sibuyan
C. mal. (UG)	0.34689 (0.11285)					
C. mal. (TI)	0.49254 (0.13896)	0.11089 (0.05430)				
C. grayi	0.53944 (0.15011)	0.19448 (0.07679)	0.21593 (0.08019)			
C. beatus	0.51422 (0.14610)	0.15998 (0.06685)	0.18357 (0.07675)	0.07695 (0.04265)		
C. sp. Sibuyan	0.42709 (0.13264)	0.10561 (0.05382)	0.13397 (0.06788)	0.15663 (0.06724)	0.09996 (0.05872)	
C. russula	0.54250 (0.15099)	0.44351 (0.12827)	0.56945 (0.15528)	0.50845 (0.14121)	0.46134 (0.13624)	0.36350 (0.11989)

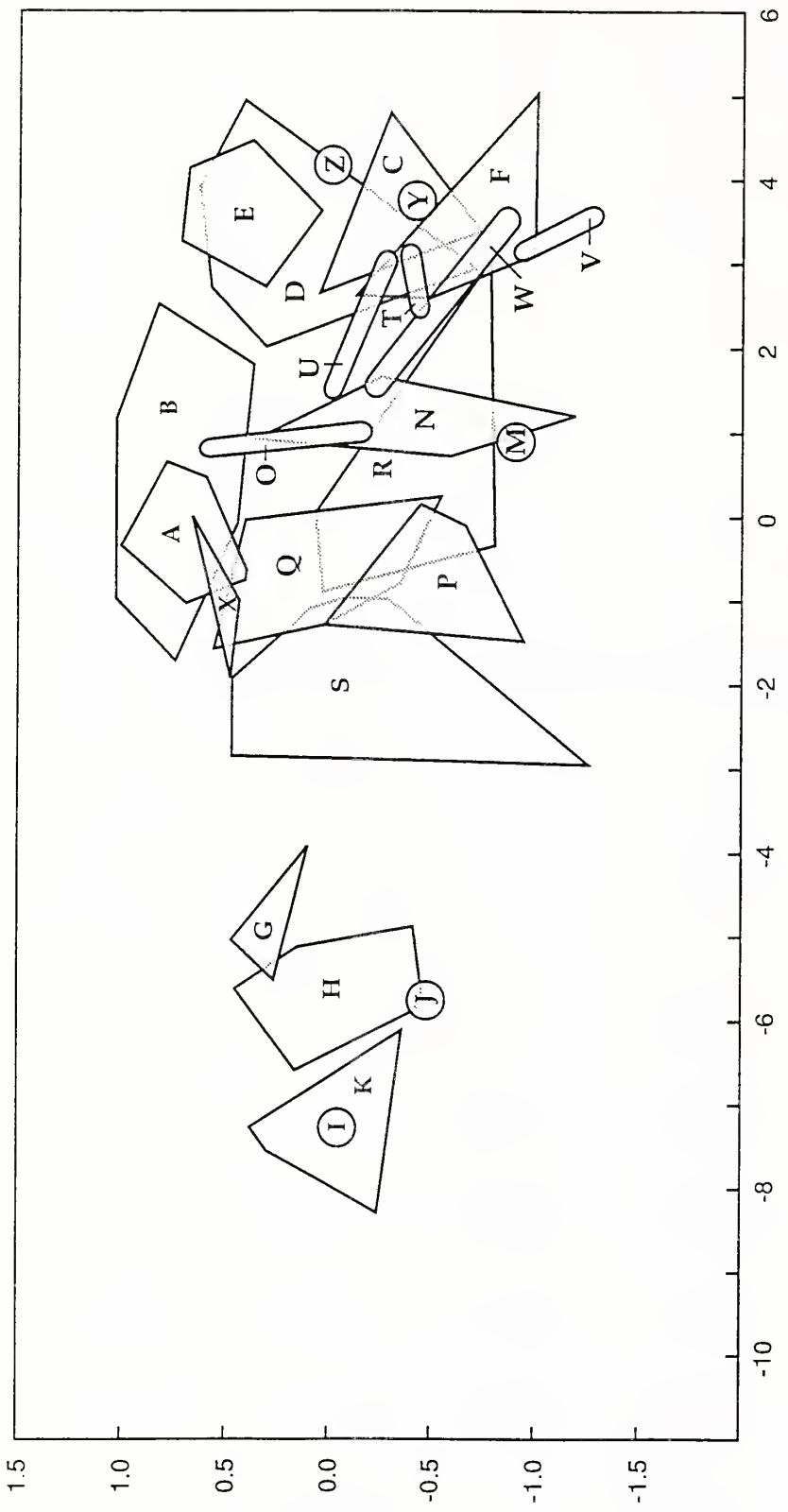

Fig. 1.—Results of principal components analysis of cranial measurements of *Crocidura* from the Philippines and adjacent areas. A: *C. attenuata* from Taiwan. B: *C. attenuata* from Vietnam. C: *C. fuliginosa foetida* from Sarawak. D: *C. fuliginosa foetida* from Sabah. E: *C. fuliginosa* from Vietnam. F: *C. fuliginosa malayana* from peninsular Malaysia. G: *C. horsfieldi indochinensis* from Vietnam. H: *C. horsfieldi indochinensis* from Burma. I: *C. monticola* from Borneo. J: *C. maxi* from Java. K: *C. suaveolens phaeopus* from China. L: *C. beatus* from Biliran. M: *C. beatus* from Bohol. N: *C. beatus* from Leyte. O: *C. beatus* from Maripipi. P: *C. beatus* from Mindanao. Q: *C. grayi* from northern Luzon. R: *C. grayi* from southern Luzon. S: *C. grayi* from Mindoro. T: *C. mindorus* from Mindoro. U: *C. negrina* from Negros. V: *C. palawanensis* from Palawan. W: *C. palawanensis* from Balabac. X: unknowns from Batanes Islands. Y: unknown from Sibuyan Island. Z: *C. grandis* from Mindanao.

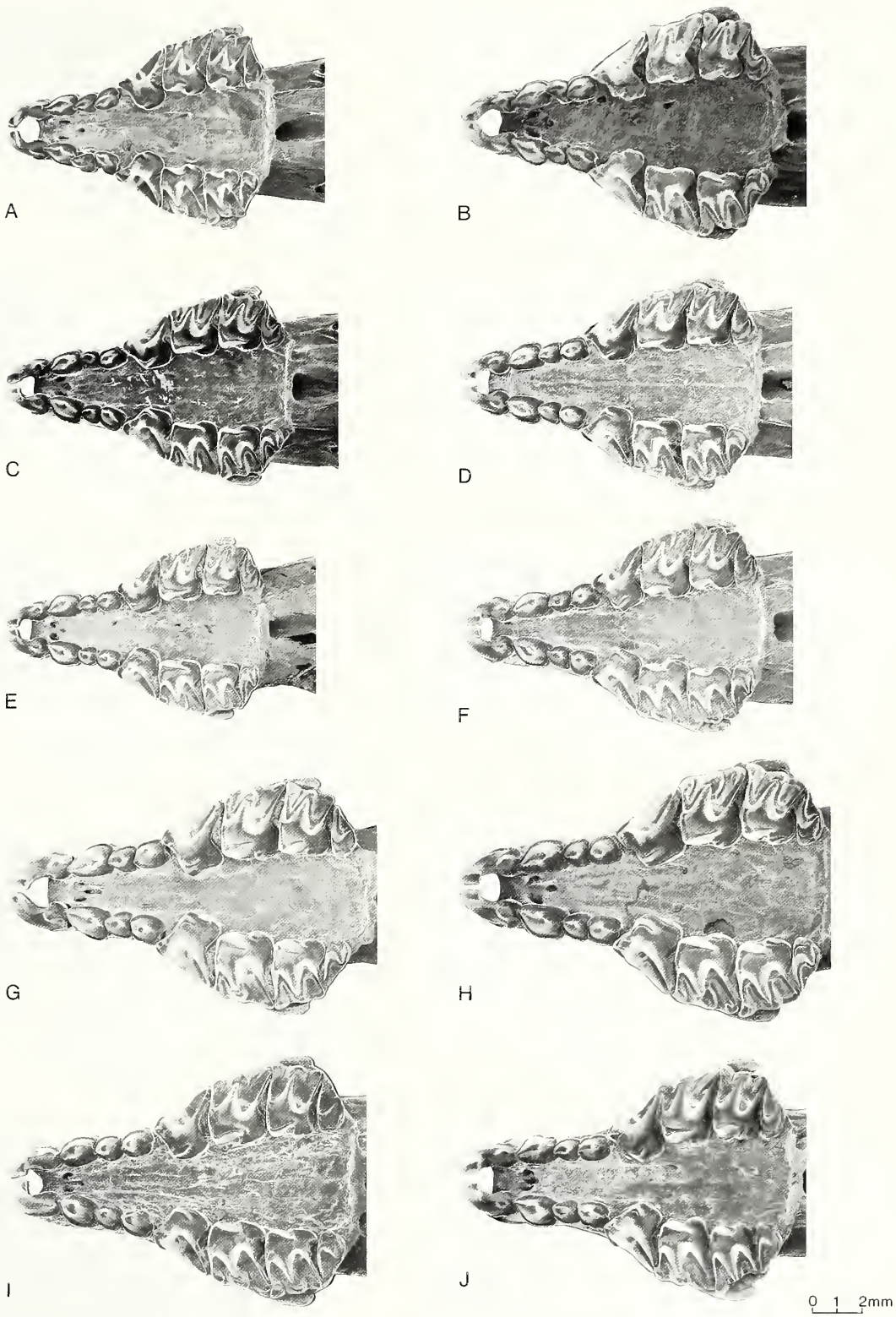

Fig. 2.—Scanning electron micrographs of the upper toothrows and palates of A: *C. attenuata* from Vietnam (FMNH 46641); B: *Crocidura* sp. from Batan Island (USNM 463794); C: *C. grayi* from Luzon (USNM 573365); D: *C. beatus* from Maripipi Island (UMMZ 160372); E: *C. halconus* from Mindoro (FMNH 87388); F: *C. negrina* from Negros Island (UMMZ 158881); G: *C. fuliginosa* from Borneo (FMNH 33055); H: *Crocidura* sp. from Sibuyan Island (FMNH 137022); I: *C. mindorus* from Mindoro (USNM 144653); J: *C. palawanensis* from Palawan Island (FMNH 63022).

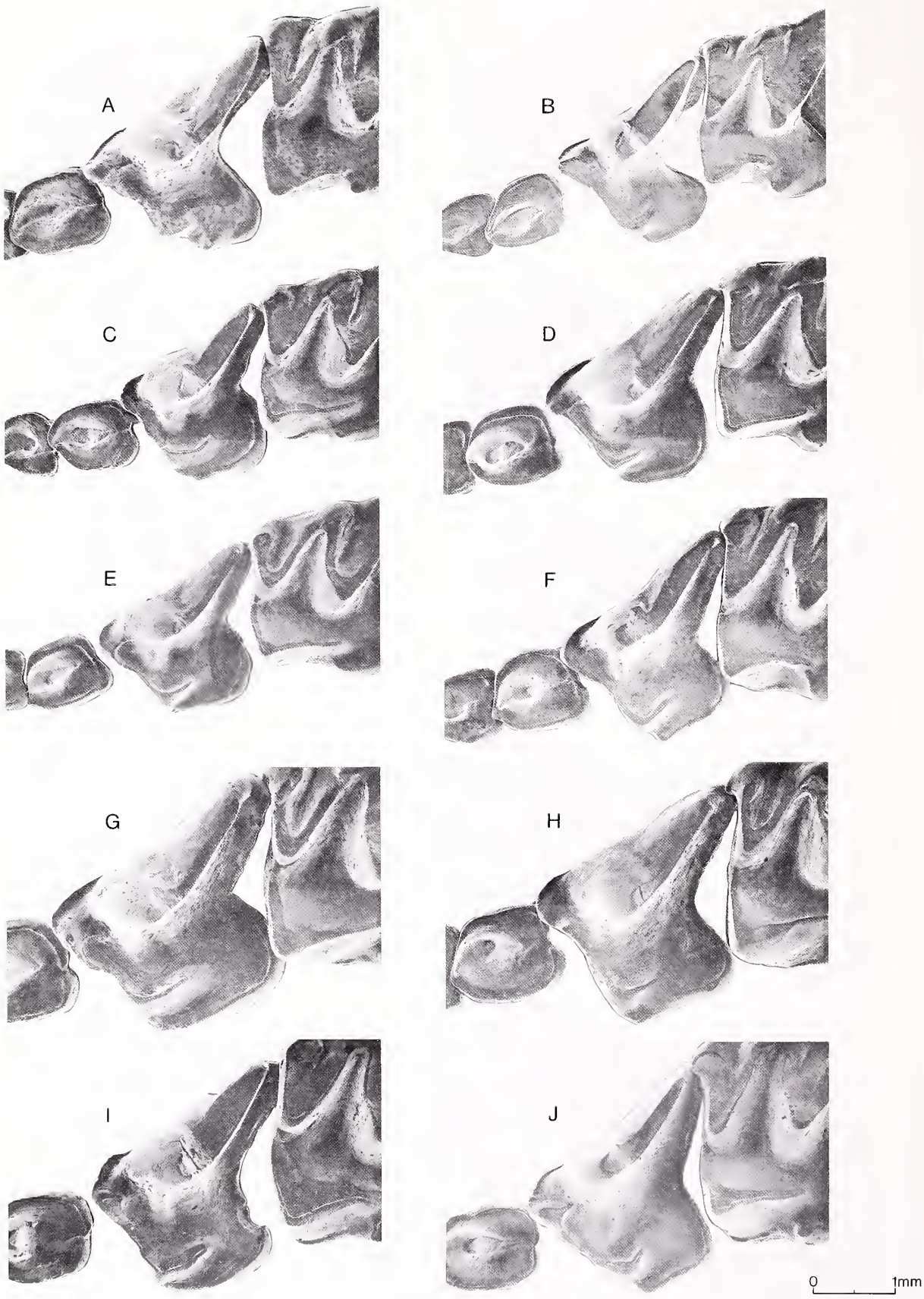

Fig. 3.—Scanning electron micrographs of the P^4s of *Crocidura*; all labels as in Fig. 2.

Fig. 4.—Scanning electron micrographs of the upper left toothrows of *Crocidura*; all labels as in Fig. 2.

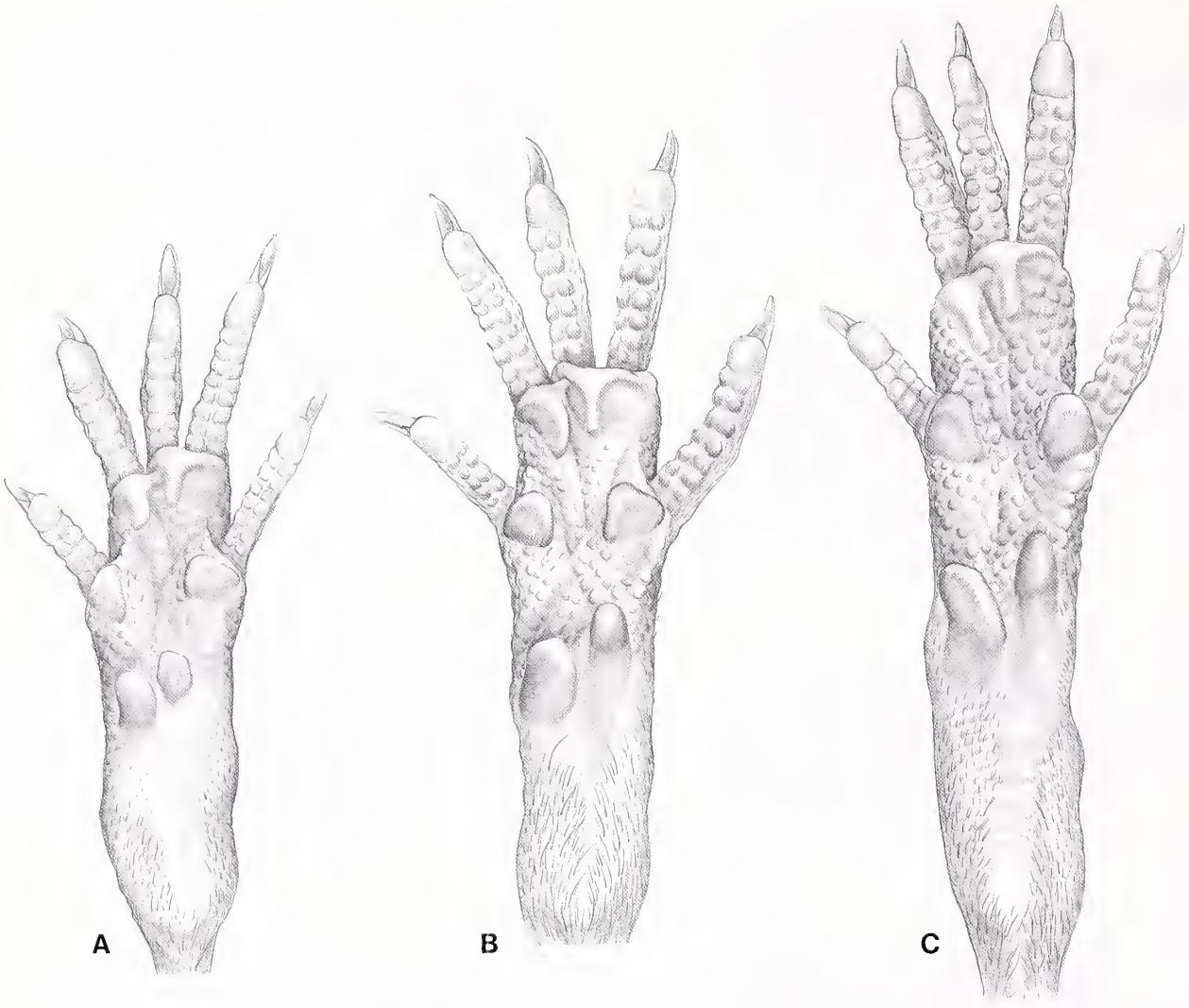

Fig. 5.—Hind feet of *C. attenuata* from Batan Island (left); *C. grayi* from Mt. Isarog, Luzon (center); and *C. mindorus* from Sibuyan Island (right).

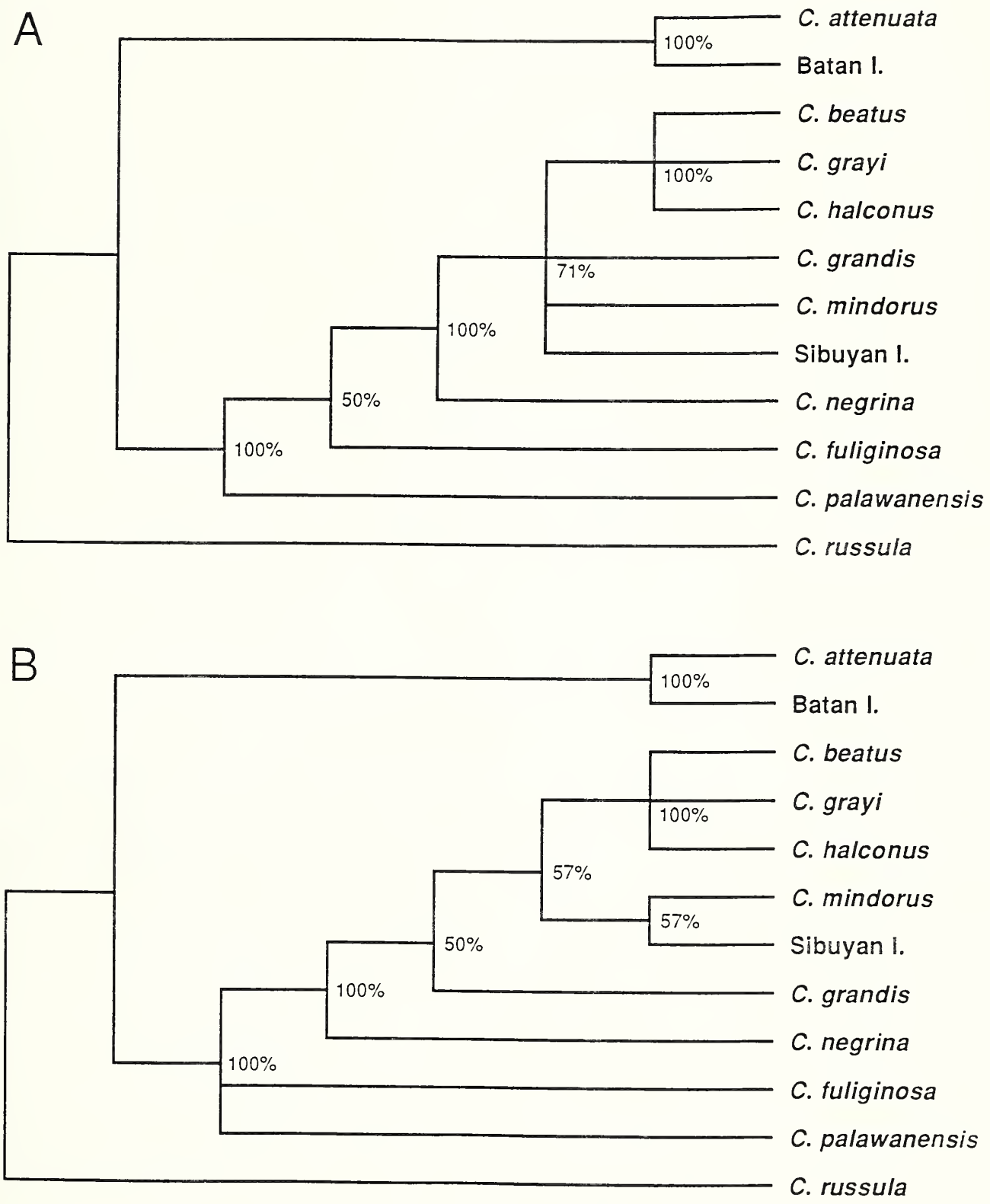

Fig. 6.—Results of cladistic analysis of morphological characters in Table 3. A: "Semistrict" consensus of 14 shortest trees. B: "Majority-rule" consensus of 14 shortest trees (see text for definitions). Index of consistency = 0.86.

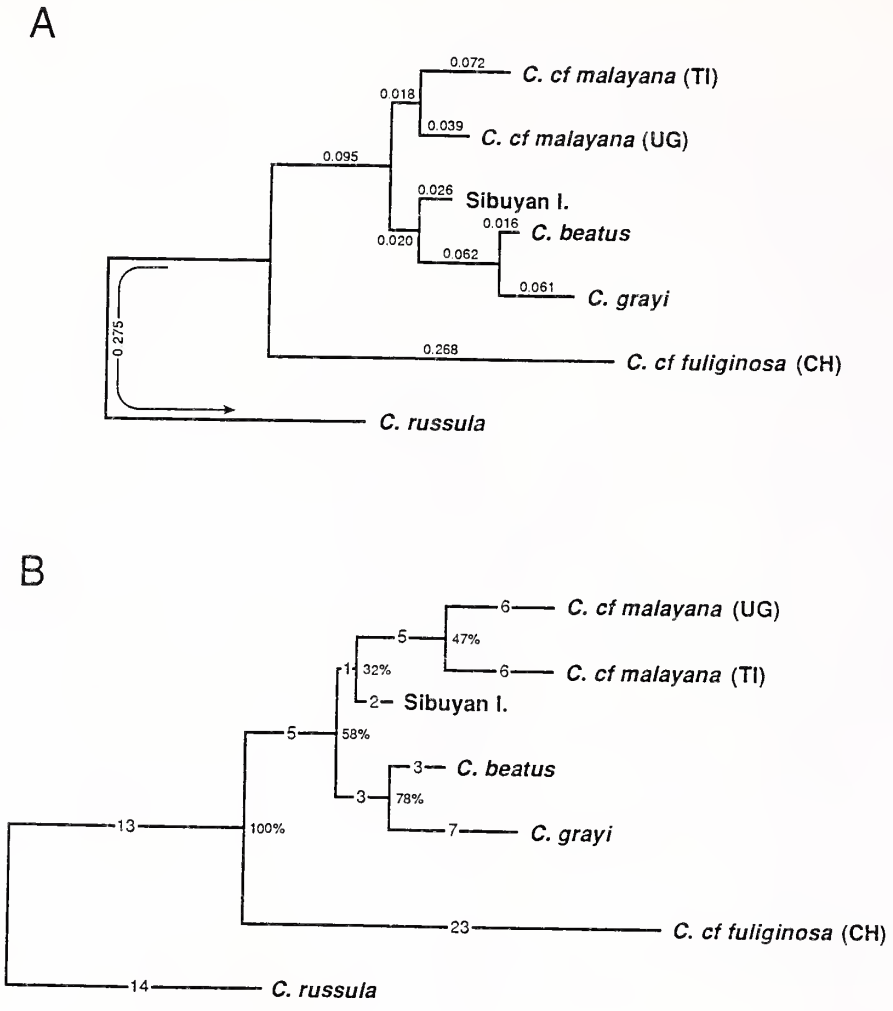

Fig. 7.—A: Results of Fitch-Margoliash analysis of Nei's genetic distances based on allozyme frequencies presented in Table 2. Estimated branch lengths are proportional to those shown in the figure. Black circles indicate nodes that are robust to a jackknife manipulation of taxa. B: Results of cladistic parsimony analysis of data in Table 2 (see Methods and text).

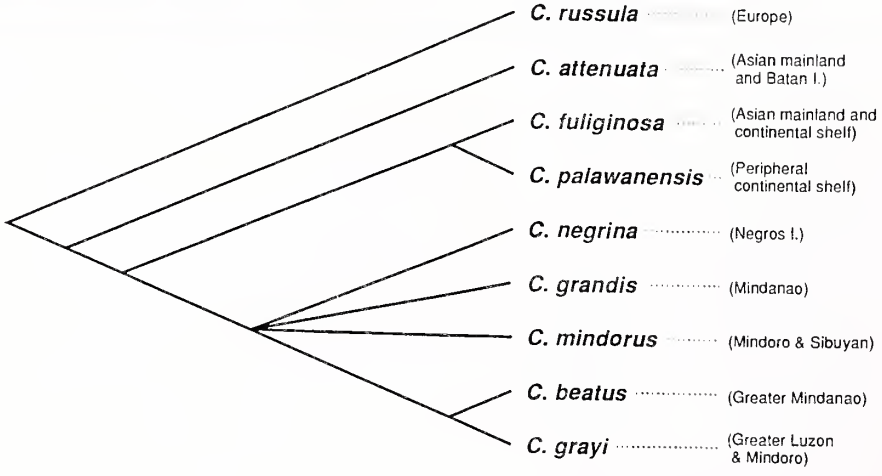

Fig. 8.—Final hypothesis of phylogenetic relationships; distributions indicated in parentheses.

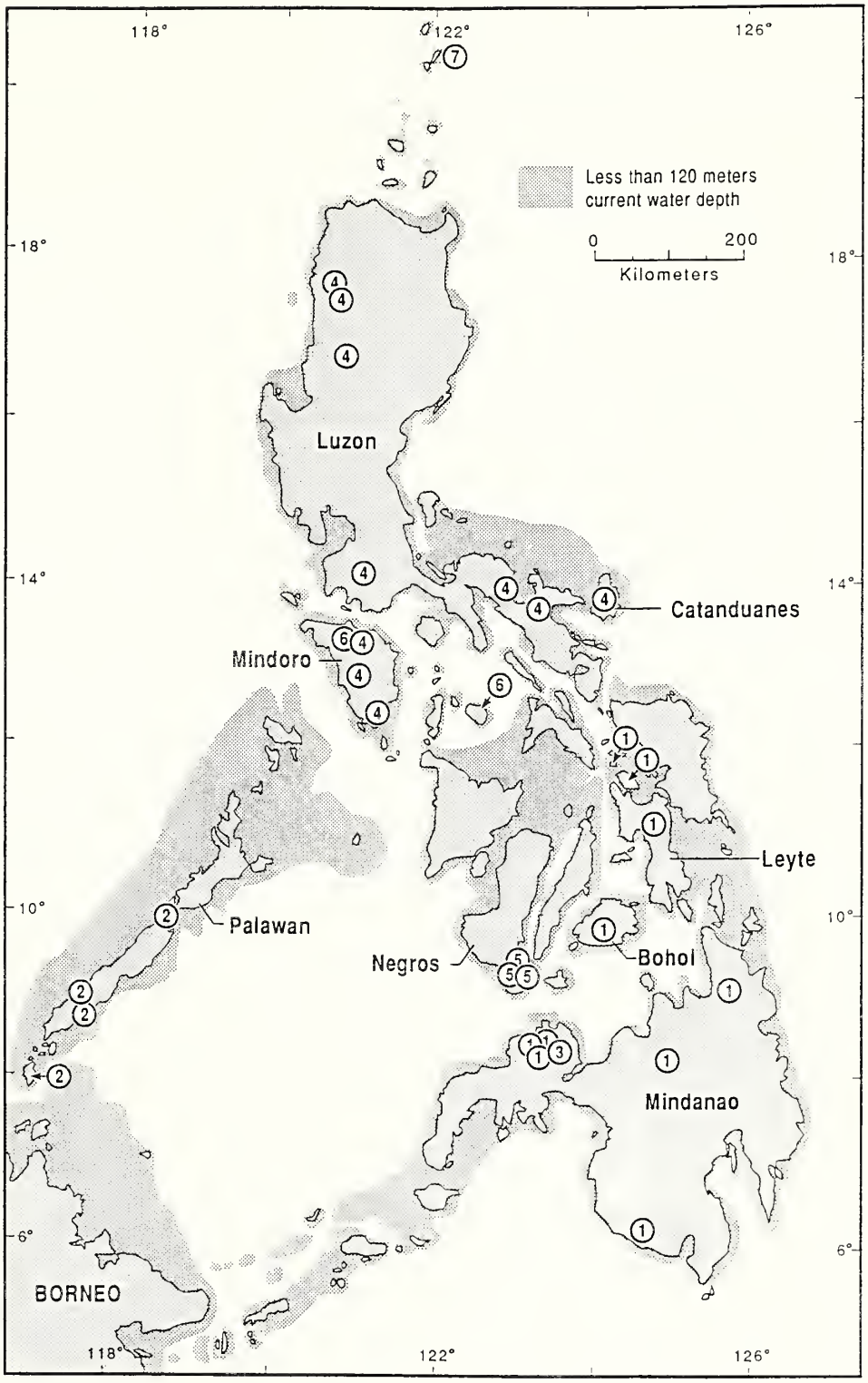

Fig. 9.—Map of the Philippine Islands showing the extent of islands during the late Pleistocene period of low sea level when water dropped 120 m, and the localities from which *Crocidura* have been taken. 1 = *C. beatus*, 2 = *C. palawanensis*, 3 = *C. grandis*, 4 = *C. grayi*, 5 = *C. negrina*, 6 = *C. mindorus*, 7 = *C. attenuata*.

EVOLUTION AND PHYLOGENETIC AFFINITIES OF THE AFRICAN SPECIES OF *CROCIDURA*, *SUNCUS*, and *SYLVISOREX* (INSECTIVORA: SORICIDAE)

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ABSTRACT

Members of the shrew genus *Crocidura* are Old World in distribution, with 96 of the 151 described species occurring in Africa. The fossil record is meager and consequently it is necessary to rely on comparative studies of Recent species for reconstruction of phylogeny. Attempts to elucidate the systematics of African *Crocidura* have resulted in the recognition of species groups that share a few general characteristics without rigorous consideration of their phylogenetic affinities. A set of 42 discrete morphological characters was used to evaluate phylogenetic relationships within the genus *Crocidura*, and among *Crocidura*, *Suncus*, and *Sylvisorex*. *Myosorex* was used as the out-group. Parsimony and cluster analyses of external and cranial features of African crocidurine shrews were used to examine phenetic affinities, determine phylogenetic relationships, and to infer possible speciation events based on biogeographic patterns.

African species of *Crocidura*, *Suncus*, and *Sylvisorex* do not represent monophyletic lineages. The generic level distinctions among *Crocidura*, *Suncus*, and *Sylvisorex* based on tooth number are not maintained when additional characteristics are included in parsimony or cluster analyses. Further, the *Crocidura* species groups that have previously been defined vary according to which characters are included in the analysis. A high degree of homoplasy in cranial and external morphology warrants the use of additional characters such as soft tissue anatomy, anatomy karyotypes, and biochemical data to derive testable phylogenetic hypotheses.

Most of the crocidurine shrews examined in this study occur throughout the lowland forests and savannas of east and west Africa, and in the highlands of Ethiopia, Kenya, Tanzania, Uganda, and Zaire in presumed refugia of arid phases in east and west Africa. Past climatic changes have undoubtedly been a major mechanism in the speciation of crocidurine shrews in Africa.

INTRODUCTION

The soricid genus *Crocidura* is the largest and one of the least understood genera of mammals. Species range in weight from 2.5 to 100 g, and are characterized by lack of pigment on the incisors, relatively long tails that are usually covered with a mixture of long and short bristly hairs, paired lateral musk glands between the front and hind legs, and 28 teeth. Members of this Old World genus occur in Africa, southern Europe, and Asia, as well as Indonesia and the Philippine Islands. Of the 151 recognized species, 96 occur in Africa, 22 in southern Europe and Asia, and 31 in Indonesia and the Philippine Islands (Honacki et al., 1982). Throughout their geographic range, members of *Crocidura* inhabit damp and dry forests, grasslands, deserts, and areas of human habitation (Smithers, 1983; Nowak, 1991). Phylogenetic affinities among African species of *Crocidura*, *Suncus*, and *Sylvisorex*, all members of the subfamily Crocidurinae, are unclear. Crocidurinae is characterized by the retention of primitive characters. Modern forms differ from those of the late Miocene and from one another by the loss of one, two, or three upper and lower antemolars; reduction in the talonid of the lower third molar; and a greater emargination of the posterior basal outline of the upper premolar and upper first molar. The generic boundaries are, however, based on very few characters. *Suncus* differs from *Crocidura* by the retention of a fourth upper antemolar. *Sylvisorex* differs from both *Suncus* and *Crocidura* by a lack of tail bristles, but further differs from *Crocidura* by the retention of a fourth upper antemolar.

Heim de Balsac and Lamotte (1956, 1957) examined phylogenetic affinities among the African shrew genera within the subfamily Crocidurinae, and associated evolutionary advancement with increases in body size, pilosity of the tail, size of the rostral portion of the skull, a flattening of the braincase, and a decrease in the complexity of the dentition. *Myosorex* is considered the most ancient of the living genera because it has the largest number of teeth (n = 32), and *Suncus*, *Sylvisorex*, and *Scutisorex* are viewed as descendants of this stock because these genera have one less lower antemolar (Fig. 1). *Crocidura* and *Paracrocidura* have the most reduced dentitions (n =28), having lost one upper and one lower antemolar. *Paracrocidura* is described as a distinct radiation derived from an ancestor common to *Sylvisorex* and *Crocidura*. *Crocidura* is considered the most advanced of the genera. However, the relationship between *Crocidura* and its two closest sister groups, *Suncus* and *Sylvisorex*, was unresolved. Heim de Balsac and Lamotte (1956) considered that *Crocidura* might be diphyletic, originating from both *Sylvisorex* and *Suncus* by loss of an upper antemolar.

Dippenaar and Meester (1989) examined the cladistic relationships among species of the *C. luna-fumosa* complex using morphological data. *Sylvisorex* and *Myosorex* were used as out-groups. Their conclusions about plesiomorphic and apomorphic character-states in *Crocidura* are consistent with the findings of Heim de Balsac and Lamotte (1956, 1957). The resulting cladogram was unresolved in that no apomorphy defined the *C. luna-fumosa* complex. The species complex was established on phenetic grounds, so one or more of the species may be more closely related to members of other species complexes. The extent to which these phenetically defined species complexes reflect phylogenetic affinities remains to be tested.

Butler et al. (1989) examined relationships among African crocidurine shrews based on multivariate analysis of mandibular

data (Fig. 2). Two groups of *Sylvisorex* are noted: the lunaris group (*S. morio*, *S. lunaris*, *S. ollula*) and the *granti* group (*S. granti*, *S. megalura*, *S. howelli*, *S. johnstoni*, *S. olduvaiensis*). The *lunaris* group is considered primitive in most characters, whereas the *granti* group is judged more advanced because of a decrease in dental complexity. *Suncus* forms a single group that is similar to the *Sylvisorex granti* group, with the exception of *S. murinus*. *Crocidura suaveolens* shares characters with *Crocidura fuscomurina*. The *fumosa* group of *Crocidura* (*maurisca*, *dolichura*, *fumosa*, *mariquensis*, *pitmani*) is assumed to have a common origin with the *Sylvisorex granti* and *lunaris* groups. Given the prevalence of parallelism, monophyly is viewed as unlikely. Because five groups of *Crocidura* are confined to Africa, they probably originated there (Butler et al., 1989). Most species of *Suncus* are from the Oriental region; thus, they may have arisen from a *Sylvisorex*-like form from Asia, such as *Feroculus*, that subsequently extended its range to Africa (Butler et al., 1989). Finally, a diphyletic origin for *Crocidura* was again suggested (Butler et al., 1989).

Maddalena (1989) examined systematic relationships among 21 European and African species of *Crocidura* using allozyme data. *Sylvisorex* spp. were used as out-groups. Palearctic and Afrotropical species were separated into two major groups using phenetic and cladistic analyses of 25 loci (Fig. 3). Within the Palearctic group, *C. russula* forms the sister taxon to the remaining species. Branch 2 of the cladogram contains Afrotropical species of *Crocidura* with the exception of *C. luna* and *C. bottegi*. *Crocidura luna* is in a clade by itself and is the primitive sister-group to the other species of *Crocidura* examined. The large-sized shrews *C. flavescens*, *C. lamottei*, *C. olivieri*, and *C. viaria* form a monophyletic group. The remaining species of branch 2 form a sister-group to the giant shrews. These *Crocidura* species form nine monophyletic groups, but the relationships among these groups remain unresolved.

Past studies of the systematics of African *Crocidura*, without rigorous consideration of the phylogenetic affinities with *Sylvisorex* and *Suncus*, have resulted in the recognition of species groups that share some general characteristics. The objectives of this study were to identify additional morphological characters useful in evaluating phylogenetic affinities, provide a detailed description and analysis of each potential character, examine relationships among Afrotropical *Crocidura* and out-group taxa using phenetic and parsimony methods, compare results derived from different methods, and consider the evolution and biogeography of African crocidurine shrews.

Materials and Methods

I examined 18 African species and subspecies of *Crocidura*, five species of *Myosorex*, three species of *Suncus*, and four species of *Sylvisorex*. Only those *Crocidura* species that possess primitive dental characteristics were included in this study, under the assumption that evolutionary advancement is associated with a reduction in the complexity of the dentition. The species of *Crocidura* included in this study are medium-sized, with the second upper antemolar equal in size to the third (rather than smaller), and having a hypocone on the fourth upper premolar, or a complex talonid on the third lower molar, or both. All specimens of *Myosorex*, *Sylvisorex*, *Crocidura*, and *Suncus* from Africa available at the National Museum of Natural History were examined.

A set of 42 characteristics was selected for parsimony and cluster analyses of *Sylvisorex*, *Suncus*, and *Crocidura*. These characters are discrete (present or absent), or form a series of states that represent modifications or alternative forms of a homologous structure. A detailed description of each character follows. Character states were coded from primitive to advanced indicating likely directional trends (i.e., polarity) over evolutionary time using the out-group method (Watrous and Wheeler, 1981). *Suncus* and *Sylvisorex* are sister-groups of *Crocidura*. *Myosorex*, the most primitive member of the subfamily Crocidurinae, was used in out-group analysis of *Crocidura*, *Suncus*, and *Sylvisorex*.

Survey of the Characters

The 42 characters selected for cladistic analysis are grouped by anatomical region. Characters of the teeth (T1–15), naso-maxillary region (N1–6), palatal region (P1–3), brain case (C1–4), orbito-temporal region (O1–3), basicrania (B1–6), and external features (E1–5) were examined (Table 1). The letters A through D refer to character states as listed in Table 1.

Character T1. Posterior Cusp of I^1 Bicuspid.—A, absent; B, present. This character is unique to *Crocidura*, and thus is treated as the derived condition.

Character T2. Proximal Width (Lateral View) of I^1.—A, weak (< ½ rostral depth); B, robust (≥ ½ rostral depth). The character state T2 is a measurement of the width of I^1 relative to the rostral depth (rostral depth is measured from the superior border of the nasals to the superior I^1 alveolus). The robust condition is treated as the derived condition. It is weak in *Sylvisorex*, but robust or weak in *Suncus* and *Crocidura*. The robust condition is noted most often in the savanna species. Enlargement of the incisors may allow consumption of larger and tougher prey items, and may be adaptive in areas where a large proportion of hard-bodied prey items is available (Hutterer, 1986).

Character T3. Cusp-Like Posterior Lingual Cingulum of I^1.—A, absent; B, present. This trait appears to be produced by the crowding of the first upper antemolar and I^1. The occurrence of a cusp-like cingulum on I^1 is a character whose polarity is difficult to determine from the occurrence within out-groups. *Crocidura* as well as the out-groups show both conditions.

Character T4. Relative Size of the Second and Third Upper Antemolars.—A, second upper antemolar smaller than third (length or width); B, second upper antemolar equal in size to third. The second upper antemolar may be smaller than or equal in size to the third. Heim de Balsac and Lamotte (1956) concluded that a decrease in the size of the third upper antemolar represented the derived condition. The distribution of this character within out-groups generally supports this assumption.

Character T5. P^4, Hypocone.—A, absent; B, present.

Retention of the P^4 hypocone is considered primitive by Heim de Balsac and Lamotte (1956). The polarity of this character is difficult to determine based on the occurrence within out-groups. The presence and absence of a P^4 hypocone are seen in *Crocidura*, *Suncus*, and *Sylvisorex*, but the presence is far less frequent in *Crocidura* than in the other species, suggesting that parallel losses have occurred in *Suncus* and *Sylvisorex*. Tooth wear may obscure reliable observation of this character.

Character T6. P^4, Parastyle Height (Lateral View).—A, less than third antemolar; B, equal to or greater than third antemolar. A tall P^4 parastyle relative to the height of the third antemolar appears to be the primitive condition based on the pattern seen within out-groups. This feature may be produced in one of several ways: the P^4 parastyle may be proportionately large, the third antemolar may be proportionately small, or differences in the size or shape of the maxilla may alter the positional relationship between the teeth.

Character T7. M^3 Size Relative to M^2 Size (Anterior-Posterior).—A, small (length $<$ ½ that of M^2); B, large (length $\geq$ ½ that of M^2). The M^3 of *Crocidura* ranges in size and shape from broad and square to long and narrow. Heim de Balsac and Lamotte (1956) concluded that the M^3 decreases in size with evolutionary advancement. Out-group analysis confirmed these conclusions.

Character T8. Fourth Upper Antemolar.—A, absent; B, present. This tooth is present in some *Myosorex*, and all *Suncus* and *Sylvisorex* species, but absent in *Crocidura*. It has traditionally formed the basis for the distinction between *Crocidura* and its two closest sister genera *Suncus* and *Sylvisorex*. A reduction in the number of teeth has been associated with evolutionary advancement in crocidurine shrews (Heim de Balsac and Lamotte, 1957).

Character T9. I_1, Cutting Surface with Accessory Cusps or Denticulations.—A, absent; B, single; C, double; D, triple. The presence of accessory cusps on the I_1 is considered primitive by a number of authors (Heim de Balsac and Lamotte, 1957; Butler and Greenwood, 1979). This character is well-developed in several species of *Sylvisorex*; most have two denticulations. *Sylvisorex lunaris* has three denticulations, and the third may be an autapomorph of that species (Butler et al., 1989). The cutting surface of the I_1 is slightly serrated (one or two accessory cusps) to smooth in species of *Suncus* and *Crocidura*. It is not clear whether the presence of a single accessory cusp on the I_1 is due to a reduction in the number of cusps or an independently derived character.

Character T10. I_1, Upwardly Curved (Distally).—A, absent; B, present. The distal end of the I_1 is straight in certain species of *Myosorex*, *Sylvisorex*, and *Crocidura*. *Suncus* and most *Crocidura* species have an upwardly curved I_1. The upturned condition is considered the derived condition by Heim de Balsac and Lamotte (1956). A straight lower incisor is the derived condition, based on the occurrence within out-groups.

Character T11. I_1 Lingual Groove.—A, low; B, elevated. The medial side of the lower incisor has a groove that curves above the notch of the basal border in *Myosorex*, *Suncus*, and some *Sylvisorex* (*lunaris* and *ollula*), and below the notch in other *Sylvisorex* (*granti* and *megalura*) and *Crocidura*. An elevated groove is considered the plesiomorphic condition.

Character T12. M_3, Complex Talonid with a Fovea and Entoconid.—A, absent; B, present. The loss of the M_3 entoconid and reduction of the talonid to a single cusp is seen in species of *Suncus*, *Sylvisorex*, *Scutisorex*, *Crocidura*, and in some soricines (e.g., *Cryptotis*). Members of Crocidurinae with a well-developed talonid basin of the M_3 often retain the distinctiveness of the entoconid and hypoconid. Loss of the M_3 entoconid may have a history of frequent parallelism within Soricidae. Heim de Balsac and Lamotte (1957) concluded that evolutionary advancement in crocidurines is associated with simplification of the M_3 talonid. A fovea occurs only in species with a complex M_3 talonid. The presence of an M_3 fovea is most likely primitive, based on the distribution pattern of this character within out-groups. This trait occurs in *Myosorex*, but has been lost in some species of *Suncus*, *Sylvisorex*, and *Crocidura*.

Character T13. P_4 Metaconid.—A, absent; B, present. The P_4 metaconid is common in *Sylvisorex* and *Myosorex*, but often absent in *Suncus* and *Crocidura*. The metaconid is lost with evolutionary advancement.

Character T14. First Lower Antemolar.—A, tricuspid; B, bicuspid; C, unicuspid. The most primitive living crocidurines (*Myosorex* spp.) and extinct crocidurines have a tricuspid first lower antemolar, whereas *Suncus* and *Crocidura* have a unicuspid first lower antemolar. Therefore, the loss of cusps on the first lower antemolar is the advanced condition.

Character T15. Mental Foramen Position Relative to the P_4.—A, under; B, posterior. The mental foramen occurred below the P_4 in Miocene crocidurines, while in Pliocene to Recent forms, it occurs below the anterior root of the M_1 (Butler and Greenwood, 1979). The anterior position is considered the primitive condition.

Character N1. Rostrum Length Relative to Width.—A, short broad ($\geq$50%); B, intermediate ($<$50%, $>$45%); C, long narrow ($\leq$45%). The rostral width just anterior to the interorbital foramen multiplied by 100 and divided by the distance between the posterior margin of the lateral wall of the interorbital foramen and the anterior edge of the I^1 alveolus was used to describe rostrum shape. Heim de Balsac and Lamotte (1957) concluded that evolutionary advancement is associated with an increase in the size of the rostral portion of the skull. Rostral shape is a character whose polarity is difficult to determine based on the occurrence of this trait within out-groups. *Crocidura* as well as *Suncus* and *Sylvisorex* have rostra that vary from short and broad to long and narrow.

Character N2. Maxilla, Zygomatic Process.—A, absent; B, present. The zygomatic process of the maxilla is the site of origin for the external pterygoid muscle. A prominent zygomatic process may occur in species that eat food requiring lateral grinding motions. A prominent zygomatic process is present in *Myosorex* and *Sylvisorex*, absent in *Suncus*, and either present or absent in *Crocidura*. The presence of the zygomatic process is the primitive condition.

Character N3. Maxilla, Lateral Wall of Infraorbital Foramen.—A, broad (width $\geq$ length); B, narrow (width $<$ length). The lateral wall of the maxilla may be broad or

narrow, independent of specimen size. A broad lateral wall of the infraorbital foramina is the primitive condition seen in *Myosorex*. *Crocidura* as well as the out-groups show both conditions.

Character N4. Maxilla, Bimaxillary Width Relative to Breadth Between Infraorbital Foramina.—A, narrow (≥60%); B, intermediate (51–59); C, wide (≤50%). The breadth between infraorbital foramina multiplied by 100 is divided by the greatest width across the maxillary region to measure bimaxillary width. Bimaxillary width is either intermediate or wide in *Myosorex*, *Sylvisorex*, and *Suncus*, suggesting that a narrow bimaxillary width is the derived condition in *Crocidura*.

Character N5. Lacrimal, Tubercle.—A, absent; B, present. This trait is a projection on the lacrimal just exterior to the lacrimal foramen on the anterior border of the lateral wall of the infraorbital foramen. A lacrimal tubercle is lacking in *Myosorex* and either present or absent in *Sylvisorex*, *Suncus*, and *Crocidura*. The presence of a lacrimal tubercle is the derived condition.

Character N6. Nasals, Lateral Margins.—A, straight, with a gradual medial curve posteriorly; B, convex, with an anterior and a posterior constriction. A convex lateral margin on the nasal bone, seen only in *Crocidura*, is considered the derived condition.

Character P1. Posterior Accessory Incisive Foramen.—A, absent; B, 1; C, 2; D, 3. One to three accessory foramina may be present posterior to the incisive foramina. The incisive foramina transmit the palatine branch of the trigeminal nerve from the maxillary branch (nasopalatine nerves). The function of the accessory foramina, however, is unknown. The plesiomorphic state is the lack of accessory incisive foramina or one accessory incisive foramen, while the occurrence of two or three posterior incisive foramina is the apomorphic state.

Character P2. Diastema Between Third or Fourth Upper Antemolar and P^4.—A, absent (teeth touching); B, weak (obscured by P^4 parastyle in ventral view of skull); C, well-developed (not obscured by P^4 parastyle in ventral view of skull). The absence of a diastema between the third upper antemolar and P^4 is the apomorphic state in *Crocidura*. *Suncus* and *Sylvisorex* have a weak to well-developed diastema between the fourth upper antemolar and P^4. An even larger diastema can be obtained with the loss of the fourth upper antemolar. The loss of this diastema may be accomplished either by a shortening of the rostrum or an increase in the robustness of the dentition.

Character P3. Diastema, Between M^1 and M^2 (Lingual).—A, absent (teeth touching); B, weak (obscured by protocone of M^2 in ventral view of skull); C, well-developed (not obscured by protocone of M^2 in ventral view of skull). The absence of a diastema between M^1 and M^2 is the apomorphic state in *Crocidura*. *Suncus* and *Sylvisorex* have a well-developed diastema between M^1 and M^2. The loss of this diastema may result from an increase in the robustness of the dentition.

Character C1. Cranial Shape (Dorsal View).—A, short, broad (width ≥ length); B, long, narrow (width ≤ length). Cranial shape is calculated by dividing cranial length (distance between the glenoid fossa and the occipital condyle) by the greatest width of braincase. Heim de Balsac and Lamotte (1957) concluded that evolutionary advancement in crocidurine shrews is associated with elongation of the cranium. *Myosorex* and *Sylvisorex* have short, broad crania whereas *Suncus* and some *Crocidura* species have elongated braincases; thus, the short, broad braincase is most likely the plesiomorphic state.

Character C2. Cranial Depth (Lateral View).—A, bulbous (braincase depth >55% width); B, flattened (braincase depth ≤55% width). Cranial depth is measured as the distance between the basioccipital and the highest point on the dorsal surface of the braincase divided by braincase width. Heim de Balsac and Lamotte (1957) concluded that evolutionary advancement is associated with a flattening of the cranium. Out-group analysis does not generally support this hypothesis. *Sylvisorex*, one *Suncus*, and two *Myosorex* species have bulbous braincases. Two *Suncus* species have flattened crania, but both the inflated and the flattened braincases occur in species of *Crocidura*. Thus, the inflated state is most likely the plesiomorphic state.

Character C3. Temporalis Muscle Origin.—A, small (meets sagittal crest at union with lambdoidal crest); B, large (meets sagittal crest anterior to union with lambdoidal crest). This muscle scar is produced by the origin of the temporalis muscle. *Myosorex* has a small muscle scar, as does the *lunaris* group of *Sylvisorex*. *Suncus*, some *Crocidura*, and the *granti* group of *Sylvisorex* have large temporalis muscle scars. The polarity is difficult to determine based on the pattern of occurrence within out-groups. Although this character may reflect dietary differences among species, a lack of data prevents confirmation of this idea.

Character C4. Interparietal.—A, absent; B, present. An interparietal is present in *Myosorex* and *Scutisorex*, but lacking in *Suncus* and most *Sylvisorex* and *Crocidura*. The presence of an interparietal is the plesiomorphic state for this character.

Character O1. Incomplete Fusion Between Temporalis and Squamosal.—A, absent; B, present. When present, incomplete fusion between the temporalis and squamosal persists in adults. This character, absent in *Sylvisorex* but present in some *Suncus*, *Crocidura*, and *Myosorex*, suggests that incomplete fusion between temporalis and squamosal may have a history of parallelism within Crocidurinae.

Character O2. Squamosal, Shape of Glenoid Fossa, Dorsal View.—A, rounded; B, angular. The shape of the glenoid fossa may be influenced by the size of the external pterygoid muscle. One of its heads originates on the anterior edge of the superior articular facet of the mandibular fossa. The polarity of this character is difficult to determine based on the study of out-groups. *Myosorex* has an angular glenoid fossa, whereas *Suncus*, *Sylvisorex*, and *Crocidura* show both conditions. The shape of the glenoid fossa may reflect dietary differences among taxa.

Character O3. Infraorbital Constriction.—A, wide (≥55% of braincase width); B, intermediate (51–54% of base width); C, narrow (≤50% of braincase width). This character is a ratio between the least infraorbital width to the greatest width of the braincase. The polarity of this character is difficult to determine based on the occurrence within out-groups. A wide to

intermediate infraorbital constriction is seen in *Myosorex* species, whereas all three conditions are seen in *Sylvisorex*, *Suncus*, and *Crocidura*. However, because a narrow infraorbital constriction is rare in all three genera, a narrow infraorbital constriction may be the apomorphic condition.

Character B1. Basioccipital, Lateral Grooves Extending Anteriorly to the Basisphenoid.—A, absent; B, present. The rectus capitus muscles, used to flex the head, insert on the basioccipital producing lateral grooves. Polarity of this character is difficult to determine. Lateral grooves are present in *Sylvisorex*, but both conditions are present in *Myosorex*, *Suncus*, and *Crocidura*. The absence of the basioccipital lateral grooves may be due to a reduction in the size of the rectus capitus muscle or a shift in the insertion.

Character B2. Basioccipital and Basisphenoid, Medial Groove.—A, absent; B, present. The longus capitus muscle inserts on the basioccipital and basisphenoid producing the medial groove. This muscle is also used to flex and support the head. The absence of the medial groove may be due to a reduction in the size of the longus capitus. This medial groove is lacking in *Myosorex*, *Sylvisorex*, and most *Crocidura* species, but is common in *Suncus*. Therefore, this character is a synapomorphy of *Suncus* and *Crocidura*.

Character B3. Basioccipital and Basisphenoid, Shape of Raised Portion.—A, V-shaped; B, hourglass-shaped; C, Y-shaped. The basioccipital and basisphenoid have raised areas that may appear V-shaped, hourglass-shaped, or Y-shaped. The polarity of this character cannot be determined based on the occurrence within out-groups.

Character B4. Petrosal, Medial Process.—A, runs lateral to the basioccipital grooves; B, interrupts the basioccipital grooves. The medial process of the petrosal either runs lateral to the basioccipital grooves or interrupts them. There is a positive correlation between the medial process interrupting the basioccipital grooves and a reduction of the basioccipital grooves. The medial process of the petrosal running lateral to the basioccipital grooves is the plesiomorphic state, seen in *Myosorex* and *Sylvisorex*. Both character states are seen in *Suncus* and *Crocidura* species.

Character B5. Alisphenoid Bone, Position of Vidian Foramen.—A, medial to pyriform fenestra; B, anterior to or parallel with the anterior border of the pyriform fenestra. The vidian foramen carries the vidian nerve. Evolutionary advancement in this character is associated with the vidian foramen which occurs posterior to the anterior edge of the pyriform fenestra. The vidian foramen occurs anterior to or parallel with the pyriform fenestra in *Myosorex* and most *Sylvisorex* species, whereas both conditions occur in *Suncus* and *Crocidura*. The anterior position is the primitive condition.

Character B6. Alisphenoid Bone, Vascular Foramen Size.—A, absent; B, small (similar in size to vidian foramen); C, large (much larger than vidian foramen). The function of this foramen is not known. There are no blood vessels passing through this foramen in *C. russula* and it begins to ossify with age in some species. Evolutionary advancement is associated with a decrease in size of this foramen. The vascular foramina are large in *Myosorex*, medium to large in *Suncus*, and absent to large in *Sylvisorex* and *Crocidura*.

Character E1. Tail, Proportion Covered by Bristles.—A, none; B, proximal ⅓; C, proximal ⅔; D, all. A bristled tail is a synapomorphy of *Crocidura* and *Suncus*, not seen in *Sylvisorex* and *Myosorex*. Heim de Balsac and Lamotte (1956) concluded that an increase in pilosity of the tail is associated with evolutionary advancement. A transformation series for this character is difficult to determine. Species of *Suncus* either have a tail that is fully bristled, or one that is two-thirds bristled. Pilosity of tail in *Crocidura* varies from species with no tail bristles to those with fully bristled tails. This suggests that tail bristles have been gained and secondarily lost in *Crocidura*, or that *Crocidura* is paraphyletic arising from *Suncus* and *Sylvisorex*.

Character E2. Tail Length Relative to Head and Body Length.—A, short (< ½ HB); B, medium (> ½ HB, <HB); C, long (>HB). *Myosorex* species have short tails except for *M. longicaudatus*, *Suncus* have medium tails, *Sylvisorex* have medium to long tails, and *Crocidura* species have a full range of tail lengths. A long tail is the derived condition. However, the presence of a long tail relative to the body length is a character that may have a history of parallelism. Climbing species of *Sylvisorex*, *Suncus*, and *Crocidura* have long tails. The adaptive advantage of having a long tail for balance in climbing species of mammals is well-documented (Hutterer, 1985).

Character E3. Body Size (Head-Body Length).—A, small (<80 mm); B, medium (80–110 mm); C, large (>110 mm). An increase in body size has been associated with evolutionary advancement by Heim de Balsac and Lamotte (1957). *Myosorex* and *Sylvisorex* are small to medium in body size, where as *Suncus* and *Crocidura* range in size from small to large. A large body size is the derived condition. However, the plesiomorphic condition may be either small or medium.

Character E4. Foot Length Relative to Head and Body Length.—A, small (≤15%); B, medium (16–19%); C, large (≥20%). *Suncus* species have medium-sized hind feet, but species of *Myosorex*, *Sylvisorex*, and *Crocidura* may have small, medium, or large hind feet. The plesiomorphic state for this character is a medium-sized foot relative to body length. A large hind foot may be associated with climbing ability; *Crocidura dolichura* and *Sylvisorex megalura* are known climbers having both long tails and large hind feet.

Character E5. Pelage Color, Ventral.—A, same as dorsal pelage; B, slightly lighter than dorsal pelage; C, distinctly lighter. The plesiomorphic state for this character is a ventral pelage slightly lighter than dorsal pelage. *Sylvisorex*, *Suncus*, and nonburrowing *Myosorex* species have the plesiomorphic state. Burrowing species of *Myosorex* and one species of *Crocidura* examined do not have a lighter ventral pelage. A distinctly lighter ventral pelage is an apomorphy of *Crocidura*.

Statistical Methods

PAUP (Phylogenetic Analysis Using Parsimony, version 2.4; Swofford, 1985) was used to examine phylogenetic affinities among *Crocidura* (n = 19), *Suncus* (n = 3), and *Sylvisorex* (n = 4) taxa. The Outgroup method of PAUP was used to root the

tree. Four species of *Myosorex* were examined and a hypothetical ancestor was used as the out-group. The polarity of ten characters could not be determined, so they were treated as unordered. These include: T3, T10, N1, N2, N3, O1, O2, B1, B3, and E1. The FARRIS method with alternate branch swapping, MULPARS, and CONTREE of PAUP were used. Character states assigned to each species are listed in Table 1. CLUSTER, a clustering program of SYSTAT (The System for Statistics, Evanston, Illinois: SYSTAT, Inc., 1986), was used to examine phenetic affinities among species using the same character-state data subjected to parsimony analysis. The Euclidean distance and average linkage methods were used.

Results and Discussion

Phylogenetic and Phenetic Relationships

The maximum of 50 trees was produced by PAUP with a length of 218 and a consistency index of 25%. A consensus tree was produced using CONTREE, a consensus tree program of PAUP (Fig. 4). Beginning at the top of the consensus tree, *Suncus murinus* from northeast Africa, *S. varilla* from southern Africa, and *C. lamottei* from west Africa form a monophyletic group. The relationships within this first group are unresolved. Both species of *Suncus* had to gain an upper antemolar for this set of relationships to be valid. Teeth are generally lost rather than acquired in mammalian evolution. The next monophyletic group consists of *C. luna luna* from the highlands of Kenya, *C. l. selina* from the highlands of Uganda, *C. l. schistacea* from the highlands of Kenya and Tanzania, *C. fumosa* from the highlands of east Africa, and *C. batsei* from west and central Africa. *Crocidura l. luna* and *C. l. selina* share a close affinity to one another, while *C. l. schistacea* shows a closer affinity to *C. fumosa* and *C. batsei*. This grouping corresponds to the *C. luna-fumosa* group described by Dippenaar and Meester (1989), with the exception of *C. batsei*. The third monophyletic group includes *C. glassi* from the Ethiopian highlands, *C. z. zaodon* and *C. z. tarella* both from central and east Africa, and *C. littoralis* from central Africa. Relationships within this third group are unresolved. *Crocidura nigeriae* from west Africa and *C. tephra* from Sudan form the fourth monophyletic group. The fifth group includes *C. mariquensis* subspecies from southern Africa and *C. poensis* from west Africa. *Crocidura lanosa* and *C. congobelgica*, both from central Africa, form the sixth monophyletic group. The seventh monophyletic group consists of *Suncus lixus* from southern Africa; *Sylvisorex granti* from central Africa; *Sylvisorex megalura* from east, central, and west Africa; and *C. dolichura* from central Africa. The relationship between *Sylvisorex* species and *C. dolichura* within this group remains unresolved. Finally, *C. nilotica* from central Africa, *Sylvisorex lunaris* from central Africa, and *Sylvisorex ollula* from west central Africa are monophyletic species.

The results of cluster analysis show a close phenetic affinity among the hypothetical ancestor, *Sylvisorex lunaris* and *Sylvisorex ollula* (Fig. 5). In the second cluster, *Suncus murinus*, *C. lamottei*, and *Suncus varilla* form a group. *Crocidura lamottei* has a close phenetic affinity to *Suncus* and belongs to the subgenus *Afrosorex* (Hutterer, 1986). Members of the subgenus *Afrosorex* are savanna species that share several derived characteristics (Hutterer, 1986). *Crocidura congobelgica* and *C. dolichura* show a close phenetic affinity to the members of the *Sylvisorex granti* group (*Sylvisorex megalura* and *Sylvisorex granti*) in the third cluster. *Crocidura batsei*, *C. fumosa*, and *C. l. schistacea* form the fourth cluster. The fifth cluster includes *C. l. selina*, *C. l. luna*, *C. tephra*, *C. nigeriae*, and *C. nilotica*. The sixth cluster includes *C. m. shortridgei*, *C. m. mariauensis*, *C. poensis*, and *C. littoralis*. *Crocidura glassi*, *C. z. tarella*, and *C. z. zaodon* form the seventh cluster. The last group, at the bottom of the phenogram, includes *Suncus lixus* and *C. lanosa*.

Parsimony analyses suggest a close relationship between the three *C. luna* subspecies and *C. fumosa*, whereas cluster analysis does not show a close phenetic affinity. This association noted in parsimony analysis corresponds to the *luna-fumosa* group of Dippenaar and Meester (1989), which is based on cranial and dental features. However, Butler et al. (1989) placed *C. fumosa* in the *fumosa* group (along with *C. maurisca*, *C. dolichura*, and *mariquensis*), and *C. luna* in the *C. turba* group (along with *C. monax* and *C. foxi*). *Suncus* does not form a monophyletic group. *Suncus murinus* and *S. varilla* form a monophyletic group along with *C. lamottei*, whereas *Suncus lixus* shows a close affinity to the *Sylvisorex granti* group. *Crocidura dolichura* is more closely related to the *Sylvisorex granti* group than to the other species of *Crocidura* examined. Based on these associations, monophyly in *Crocidura*, *Suncus*, and *Sylvisorex* seems unlikely. The two *Sylvisorex* species groups, *granti* and *lunaris*, are distinctive enough to be considered separate subgenera based on the study of only four of seven species. Thirteen characteristics separate *Sylvisorex granti* and *Sylvisorex megalura* from *Sylvisorex lunaris* and *Sylvisorex ollula* (Table 2). The remaining species of *Sylvisorex* must be studied before it can be determined whether subgeneric boundaries should be defined.

The relationships of *Sylvisorex*, *Suncus*, and *Crocidura* are unclear. The results of this study suggest that *Suncus varilla*, *S. lixus*, *S. murinus*, and the *Sylvisorex granti* group have evolved from *Crocidura* through the acquisition of an upper antemolar. However, teeth are lost more often than gained in mammals over evolutionary time. An alternative explanation is that a long history of co-occurrence in Africa (12 million years) may have led to many parallel and convergent evolutionary trends in morphology, and through extinction, *Suncus* and *Sylvisorex* may have lost many primitive members, leaving behind a few primitive and some relatively advanced species.

Historical Biogeography and Speciation

The concept that animal speciation in Africa has been strongly influenced by cycles of arid and moist climatic phases is well-established (Moreau, 1952). These fluctuations in climate apparently isolated some animal species and led to the distribution expansions of others. During the Pleistocene, montane biomes extended from the highlands of Cameroon to the Ethiopian highlands and to southern Africa (Grubb, 1978; Moreau, 1952, 1962). Following the Pleistocene, the forest areas decreased in size, resulting in the fragmentation of west

and central African lowland forests, and the isolation of numerous islands of montane forest at higher elevations which have become refugia (Fig. 6; Grubb, 1978; Robbins, 1978). The pattern of fragmentation, however, is not clear. Few African mammal taxa have a sufficiently large geographic distribution and adequate geographic variation to recognize centers of dispersal or refugia. *Crocidura*, however, is an excellent model for studies of African and Old World biogeography: it is speciose; has low vagility; and occurs throughout Europe, Africa, Asia, Indonesia, and the Philippine Islands.

The African montane species of *Crocidura* possessing primitive dental characteristics might represent fragmented relics of formerly widespread species that have subsequently diverged within these isolated areas. Examples of this pattern are seen in *C. luna* and *C. fumosa* from the highlands of Kenya, Uganda, and Tanzania, and in *C. glassi* from the highlands of Ethiopia. Species adapted to drier and more open habitats, such as *C. lamottei*, appear to be phylogenetically advanced and probably evolved in Recent times with the expansion of the Sahara Desert and the retreat of the central forest region, as suggested by Hutterer (1986).

Conclusions

Crocidura, *Suncus*, and *Sylvisorex* do not represent monophyletic lineages. The generic distinctions among *Crocidura*, *Suncus*, and *Sylvisorex*, based on tooth number, are not maintained when additional characteristics are included in parsimony or cluster analyses. Similarly, the species groups that have been defined vary according to which characters are included in the analysis. A lack of fossil data and a high degree of homoplasy in cranial and external morphology warrants the use of additional characters such as soft tissue anatomy, karyotypes, and biochemical data to derive testable hypotheses. More evolutionary data clearly are needed both for testing these hypotheses and for developing more rigorous models of speciation.

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Table 1.—*Character states for species included in parsimony and cluster analysis. Character abbreviations refer to anatomical regions as follows: tooth characters (T1–15), naso-maxillary region (N1–6), palatal region (P1–3), braincase (C1–4), orbito-temporal region (O1–3), basicrania (B1–6), external features (E1–5). For a more detailed description of each character, see survey of the characters in Materials and Methods.*

Species	Character State TTTTTTTTTTTTTTTNNNNNNPPPCCCCOOOBBBBBBEEEEE 123456789012345123456123123412312345612345
Ancestor	AABABBBBBABBBAACBABAAAACABAABBBAACABCAABBB
S. murinus	ABBABABBABBAACABABCAABCCBBBABBCBBBBBBDBBBA
S. lixus	AAAAABBBABAABCAAAABAA?CCBBBAABABBBABBCBA??
S. varilla	ABBBAAABABAAACBAABCBAABCBBBABBAAAABACDAABB
Sy. lunaris	AABABABBDABBBBBBAABBAABCAAAAABCBAAABAABBBB
Sy. granti	AAAAABBBCAABBBBAAAABAACCBABAAAABABAABACACB
Sy. ollula	AABBBABBBABABAACBBBBABBCAAAAABBBBBBABAABBBB
Sy. megalura	AAAAAABBBBABBCAABAAAAACCBABBAAABACABCACACB
C. l. luna	ABBABABAABBBBCBAAABAABCCAABABBABACBACCBBBB
C. l. selina	ABBAAABAABBBBCBAAABAABCCAABABBABACBABBBBBB
C. l. schistacea	ABAAAABAABBABCBABABAABBBAABABBABAAAABCBBBB
C. fumosa	AAAAAABABABABCAABAAAABBBAAAABAAAAABACCBBBB
C. m. mariquensis	AABBBABABBBBACBCAACAABCCBABAAAABBBAAABBACB
C. m. shortridgei	AABBAABABBBBACBCABBAABCCBABABAABACAABBBBCB
C. glassi	AAABABBAAABAACACABBBBBBBBABAAAABABBAABBBBB
C. lamottei	BBBBBAAAABBAACBBAACBABBBBBBABBBBAABABDABAA
C. poensis	AAABAABABBBAACBBAABBABCCBBBABAABABABBCBBCB
C. batsei	ABAAAABABBBBBCBBAABBABABABBABBABAABBBBBBBB
C. nigeriae	AAAAAAAAAABABCBBABBBABCCBBBABBABACAACBBBBB
C. z. zaodon	AAABABBABABBACBBAABBBBBBBABABBBBACAABDBBBB
C. z. tarella	AAABABBAAABBACBBAABBBBCBBABABBABACAAACBBBB
C. littoralis	AAABAABABBBBACBBABBBABBCBAAABBABACAAAABBBB
C. lamosa	AABBAABABBBABCACABBAA?CCAABBBBAAAABAAABBCB
C. dolichura	AAAAABBABBBBACAAAAABA?CCBABBAABAABBAAACACB
C. congobelgica	AAABAABABBBAACAAAABBABCBBABBBBBAABBACABABB
C. tephra	ABABAABAABBAACBBABBBABCCAABABBBBACBABCBBBB
C. nilotica	ABABABBABABABCBCAABBABCCAABAABBBABABCCBBBB

Table 2.—*Diagnostic features observed in the* Sylvisorex granti *and* lunaris *groups.*

Character	*granti* Group (*megalura*)	*lunaris* Group (*lunaris*)
Cusp-like posterior lingual cingula on the upper incisor	absent	present
P^4 hypocone	absent	present
Height of lingual groove on the lower incisor	low	high
Rostrum length	short	long
Bimaxillary width	narrow	wide
Size of diastema between the third upper antemolar and P^4	large	small
Braincase shape	long	short
Size of temporalis muscle scar	large	small
Interorbital constriction width	wide	narrow
Vascular foramen	present	absent
Tail length relative to head and body length	equal to or longer	shorter
Body size	small	large
Hind foot size	large	small to medium

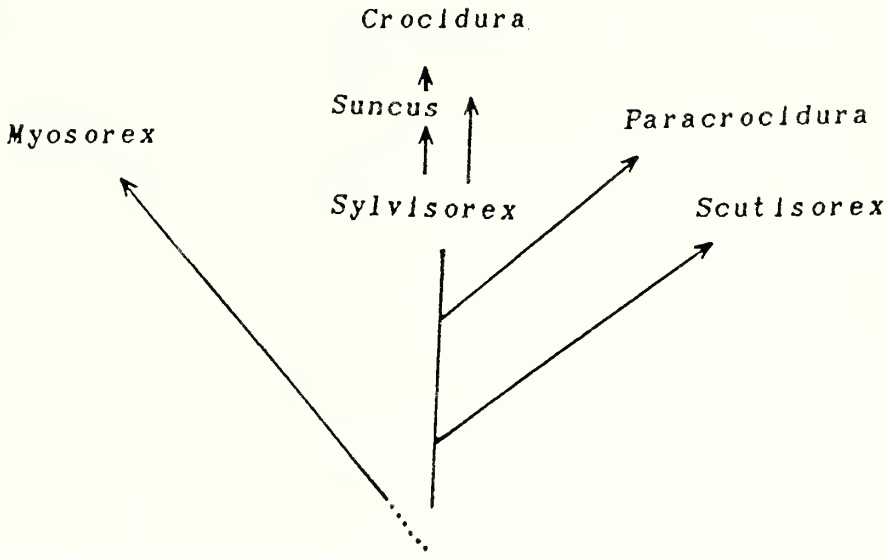

Fig. 1.—Phylogenetic affinities among African crocidurine shrews based on cranial and dental morphology from Heim de Balsac and Lamotte (1957).

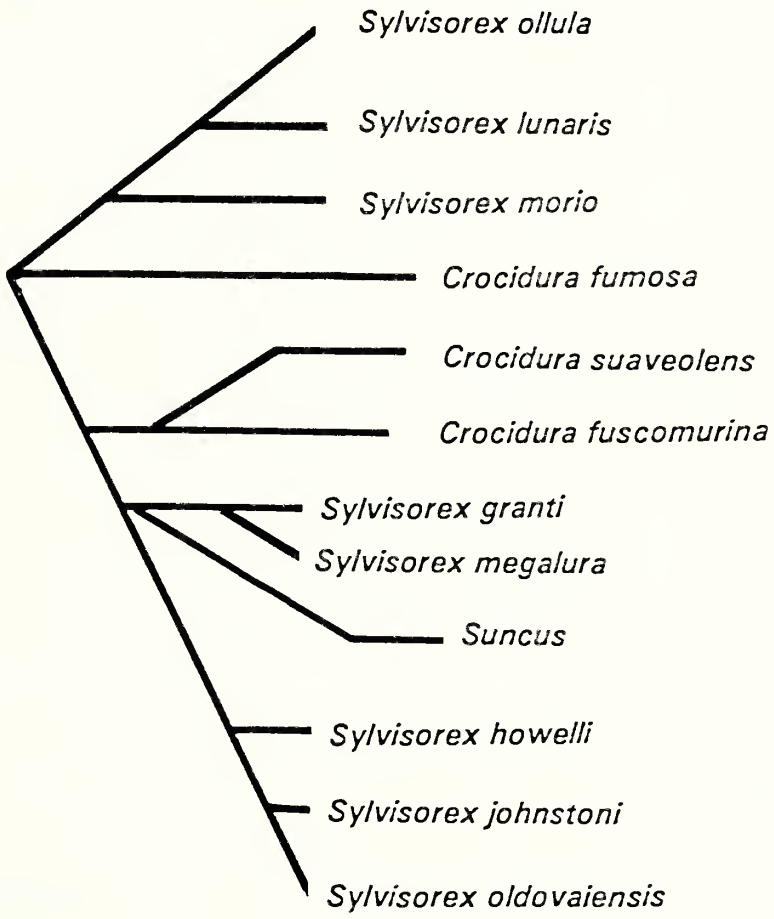

Fig. 2.—Phylogenetic affinities among species of *Sylvisorex*, with possible branching points of *Suncus*, and *Crocidura* based on multivariate analysis of mandibular morphology following Butler et al. (1989).

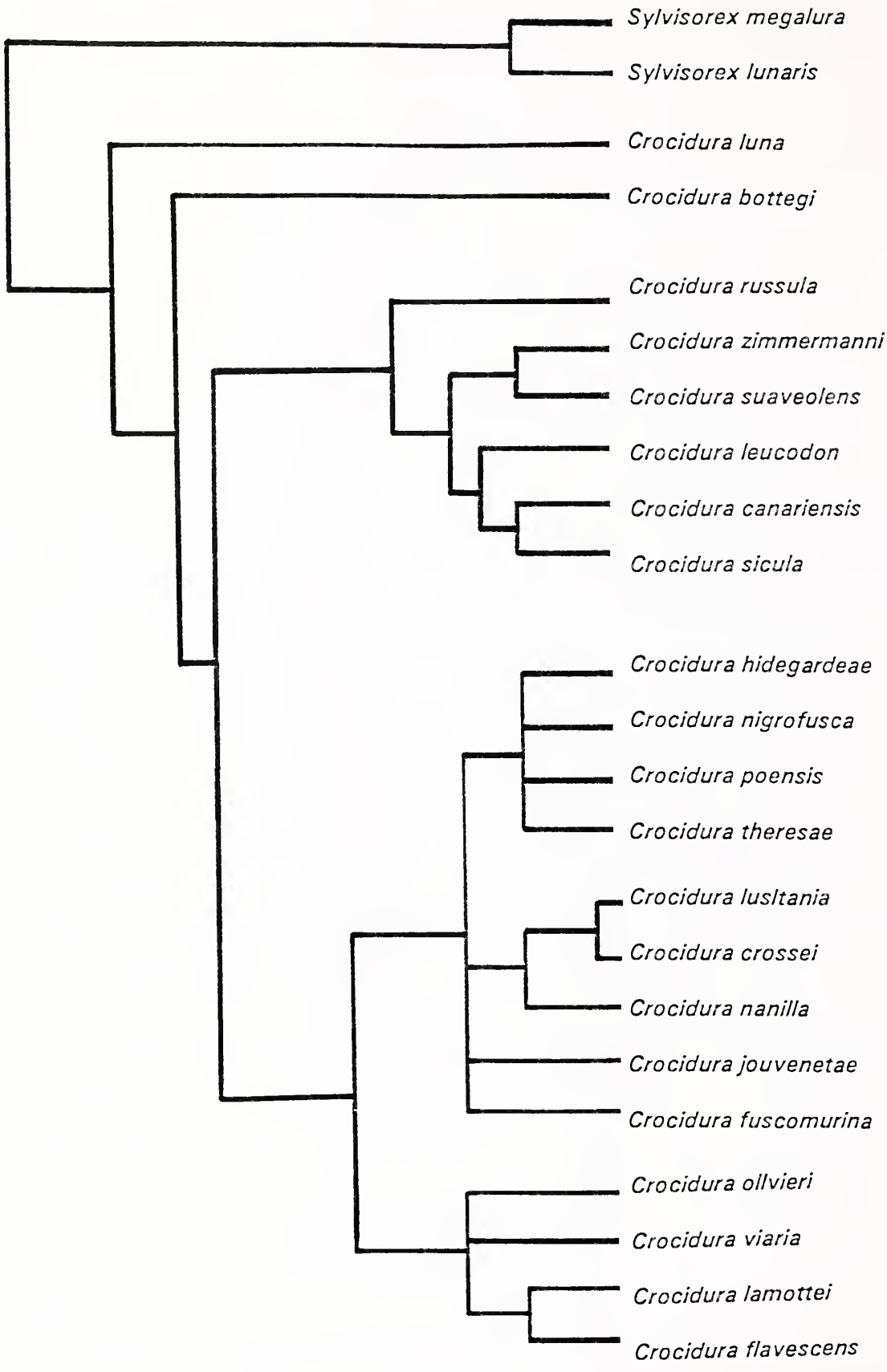

Fig. 3.—Cladistic relationships among 21 *Crocidura* species based on 25 polymorphic loci from Maddalena (1989).

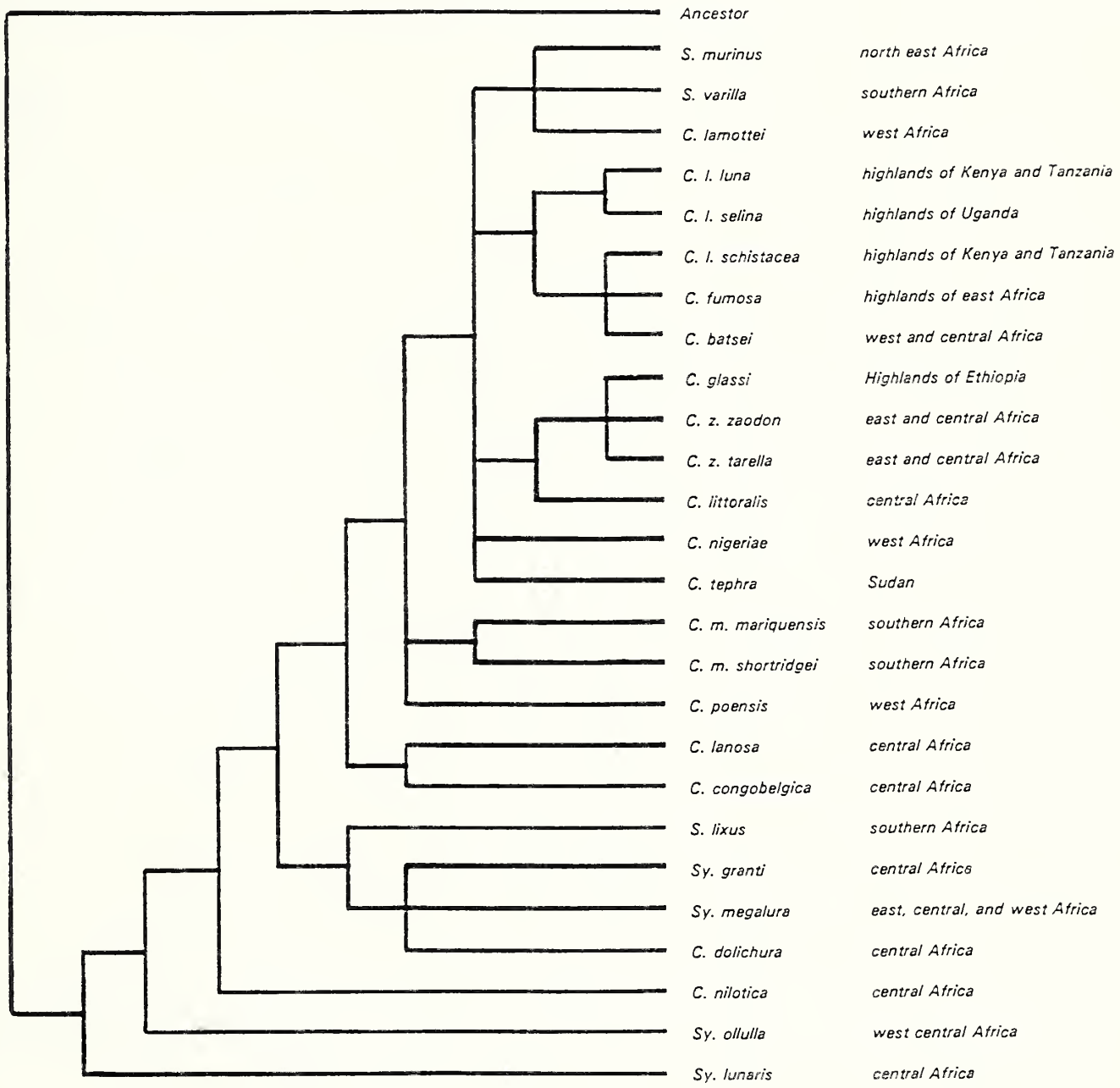

Fig. 4.—Phylogenetic relationships among *Suncus*, *Sylvisorex*, and *Crocidura* based on parsimony analysis of 42 morphological characters. The geographic distribution of each species is listed to the right.

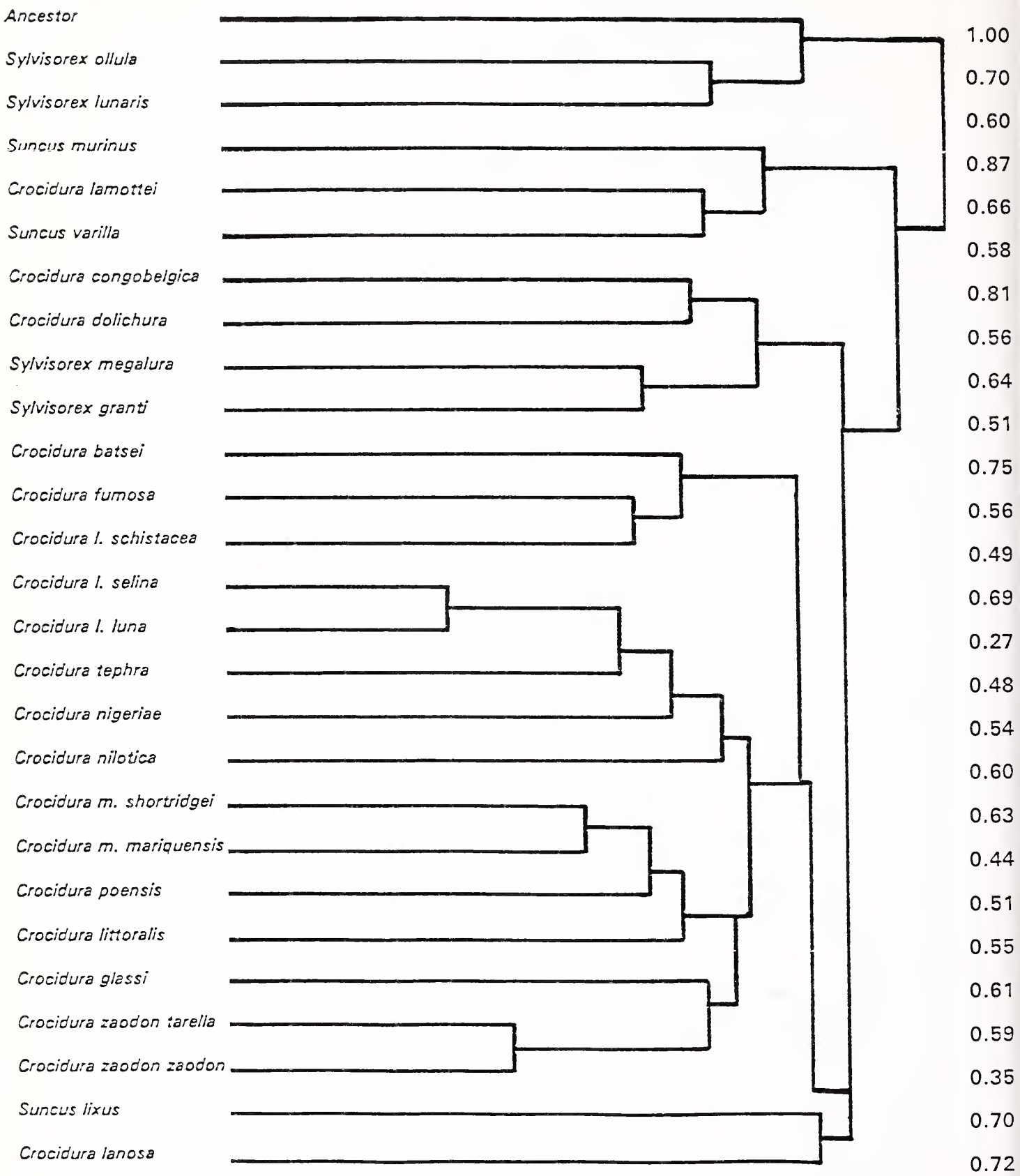

Fig. 5.—Phenetic affinities among *Suncus*, *Sylvisorex*, and *Crocidura* based on cluster analysis of 42 morphological features using the Euclidean distance and the average linkage method of SYSTAT (System for Statistics, 1986). Distance values between groups are listed on the right side.

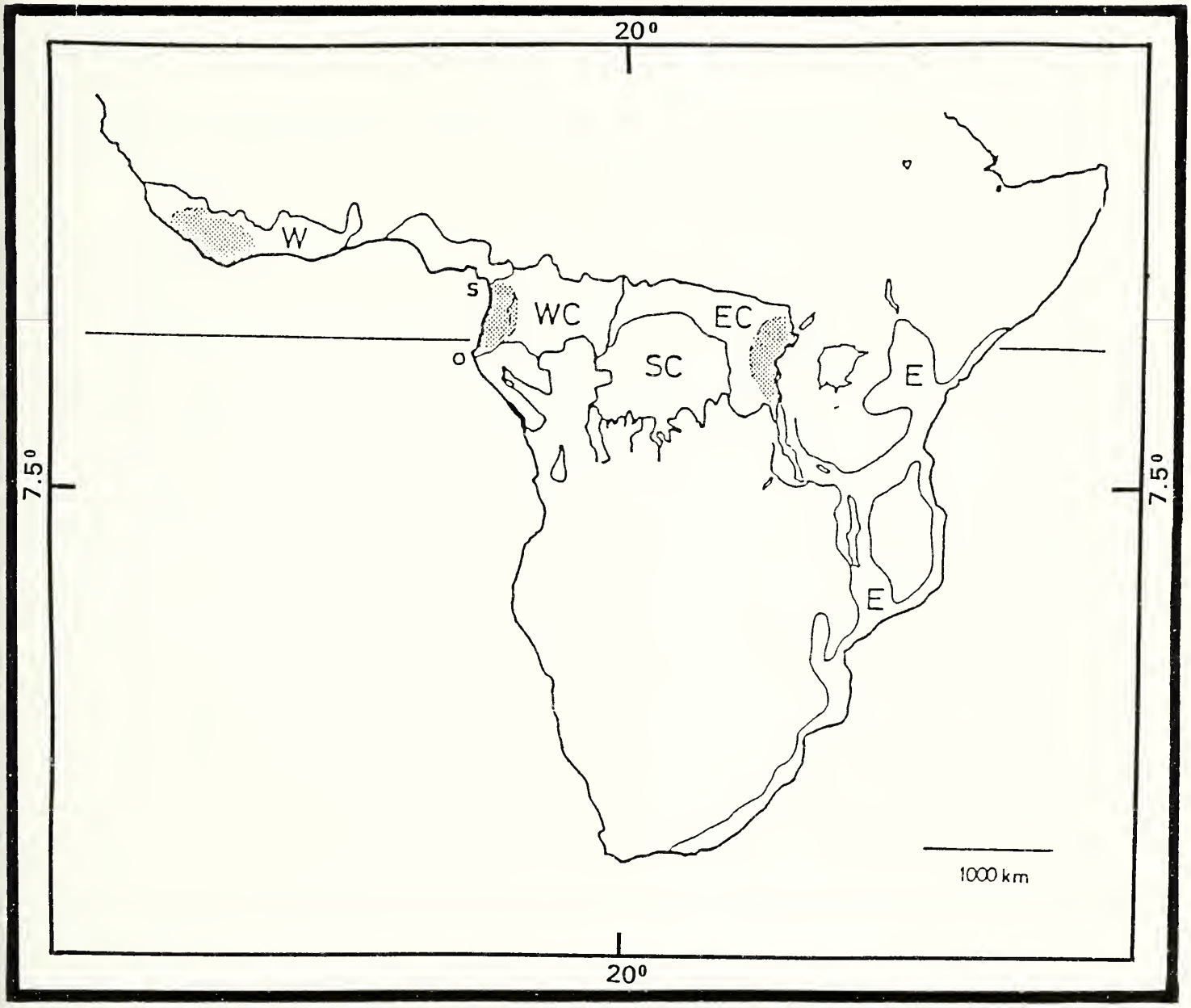

Fig. 6.—Faunistic divisions of the forest biome in Africa, with presumed major refugia of extreme arid phases stippled and more Recent refugia of less extreme arid phases in intervening zones. W, western region, Dahomey Gap on the eastern boundary; WC, west-central region, bounded by the Oubangui-Congo rivers, Sanaga River (S), and Ogoue River (O); EC, east-central region, bounded by the Congo River; SC, south-central region; E, eastern region, the forest is restricted to small mountains and coastal forest Islands. Taken from Grubb (1978).

IDENTIFICATION OF THE CAROLINIAN SHREWS OF BACHMAN 1837

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ABSTRACT

In his 1837 monograph of North American shrews, Bachman named seven new species and redescribed six of other authors. These 13 names represent seven currently recognized taxa. Of particular interest are the species with which Bachman was most familiar, *Sorex carolinensis* (=*Blarina carolinensis*), *S. cinereus* (=*Cryptotis parva*), and *S. longirostris*, which Baehman described from the vicinity of Charleston, South Carolina. Topotypical material had been too meager to be useful, but by means of formalin-charged pitfalls, we obtained near-topotypical series of all three species. We have used these specimens to redefine Bachman's taxa. The names *Sorex carolinensis* and *S. longirostris* are correctly applied in current nomenclature, but *S. cinereus* is not a synonym of *Cryptotis parva parva* Say as previously thought.

INTRODUCTION

Three species of shrews (*Sorex longirostris*, *Blarina carolinensis*, and *Cryptotis parva*) are common and widespread in the lowlands of the southeastern United States. All three were discovered by John Bachman in the vicinity of Charleston, South Carolina. He described and named them in 1837 in a monograph of the shrews of North America. Bachman's monograph contained descriptions of 13 species of shrews in North America north of Mexico. These represent seven species in today's nomenclature. Bachman stated that shrews were the least studied and most poorly collected group of North American mammals. He believed that more species would be found. The most recent checklist for the same area (Jones et al., 1986) listed 31 species of shrews.

As a taxonomist Bachman was ahead of his time. His descriptions are easily interpreted, and they are thorough without being cluttered with minutia. His species accounts consist of a brief diagnosis ("Characters"), dental formula, dentition, form, color, measurements, comparisons, distribution, and habits. He recognized that species are variable and perceived the need for collecting series of specimens.

Some of Bachman's specimens still exist in the Academy of Natural Sciences of Philadelphia (ANSP) and in the National Museum of Natural History, Smithsonian Institution (USNM). However, they are in poor condition and difficult to interpret in the absence of good supporting material. Until recently, topotypical specimens have not been available, and it has been necessary to use specimens from northeastern Georgia and central North Carolina to represent Bachman's species (Miller, 1895:40; Jackson, 1928:86). Consequently, application of Bachman's names at the level of subspecies has been clouded with doubt. In current nomenclature Bachman's *Sorex longirostris* and *Sorex carolinensis* are the nominate subspecies *S. l. longirostris* and *Blarina c. carolinensis*. *Sorex cinereus* is thought to be a synonym of *Cryptotis parva parva*.

A major objective of this project was to collect series of shrews in coastal South Carolina, near Charleston, where Bachman obtained his specimens. We were spurred by questions on several fronts to obtain fresh series of Bachman's shrews. For example, we wondered whether the federally threatened *Sorex longirostris fisheri* Merriam might be widespread in coastal Virginia and the Carolinas, rather than restricted to the Dismal Swamp. Could it be the same as Bachman's *Sorex longirostris*? Also we were suspicious, after studying his description, that Bachman did not have a specimen of *Cryptotis parva parva* in hand when he described *Sorex cinereus*.

BACHMAN'S SHREWS

From literature Bachman knew six species of North American shrews, described from the northern United States and Canada prior to 1837. We list them here with page numbers in Bachman (1837), in order of their current nomenclatorial status. Note that in Bachman's day all shrews were included in the Linnaean genus *Sorex*.

Sorex personatus I. Geoffroy Saint-Hilaire 1827
Page 398; a synonym of *Sorex cinereus* Kerr (see Jackson, 1925:55).

Sorex forsteri Richardson 1828
Page 386; a synonym of *Sorex cinereus* Kerr (see Miller, 1895:40).

Sorex palustris Richardson 1828
Page 396; *Sorex palustris* Richardson.

Sorex brevicaudus Say 1823
Page 381; *Blarina brevicauda* Say.

Sorex talpoides Gapper 1830
Page 397; *Blarina brevicauda talpoides* Gapper.

Sorex parvus Say 1823
Page 394; *Cryptotis parva* Say.

In addition to these six established taxa of North American shrews, which Bachman treated briefly in his 1837 monograph, he described seven more as new species. Three of the new species, the Carolinian shrews which were based on his own material, Bachman described in considerable detail. They are the subject of this paper. The other four new species, based on references in literature and on specimens supplied by correspondents, received more cursory treatment by Bachman. We list the new species here, with page numbers in Bachman (1837), in order of their current nomenclatorial status; the Carolinian shrews are indicated with an asterisk.

Sorex richardsoni Bachman
Page 383; a synonym of *Sorex arcticus* Kerr (see Jackson, 1925:55 and Miller, 1895:38).

Sorex cooperi Bachman
Page 388; a synonym of *Sorex cinereus* Kerr (see Miller,

1895:41).

**Sorex longirostris* Bachman

Page 370; *Sorex longirostris* Bachman (see Miller, 1895:40, 52–53, 56).

Sorex dekayi Bachman

Page 377; a synonym of *Blarina brevicauda talpoides* Gapper (see Bangs, 1902:75 and Merriam, 1895:10).

**Sorex carolinensis* Bachman

Page 366; *Blarina carolinensis* Bachman. Regarded as a subspecies of *Blarina brevicauda* Say by Merriam (1895:14) and subsequent authors until restored to the status of a species by Handley (1971:300). See also Tate et al. (1980).

**Sorex cinereus* Bachman

Page 373; *Cryptotis parva floridana* Merriam. A homonym of *Sorex cinereus* Kerr. Long thought by all authors to be a synonym of *Cryptotis parva parva* Say; shown in this paper to be a synonym of *Cryptotis parva floridana* Merriam.

Sorex fimbripes Bachman

Page 391. Enigmatic; unidentified. Most authors (e.g., Hall, 1981:28) have disregarded the details of Bachman's description and have regarded *Sorex fimbripes* as a synonym of *Sorex cinereus cinereus* Kerr. However, there is no reason to believe that Bachman did not describe *Sorex fimbripes* exactly as he saw it in his hand. Hollister (1911:381) was correct in rejecting the assignment of *Sorex fimbripes* to the synonymy of *Sorex cinereus* and in his assessment, "The description of *Sorex fimbripes* differs so widely from any known American shrew that the name is probably unidentifiable." We venture that it is only unidentifiable because the holotype is lost (Hollister, 1911) and the animal has never been collected again. In form and pelage, but not in size, coloration, or dentition, this shrew is reminiscent of *Nectogale elegans* of the eastern Himalayas. Otherwise it is unlike any known shrew. *Sorex fimbripes* Bachman is the type species of *Hydrogale* Pomel, 1848, a name preoccupied by *Hydrogale* Kaup, 1829.

Study Area and Methods

We collected within a few kilometers of the coast, in and near Francis Marion National Forest, 40–60 km northeast of Charleston, Charleston County, South Carolina. Collecting localities are listed in the species accounts. For *Sorex longirostris* we sought early to midsuccession mixed forest with herbaceous ground cover on damp organic soil, such as is occasionally found on swamp edges (Rose and Padgett, 1991). For *Cryptotis parva* we initially sought grassy ditch and dike banks in *Spartina* salt marsh. Eventually we settled for dense, not recently cut, grass hayfields. We expected to catch *Blarina carolinensis* wherever we set traps, except in salt marsh. We used Museum Special snap traps to catch specimens to be prepared as dry study skins. We used pitfalls for specimens to be stored in alcohol after extracting skulls.

We used six topless 2-liter plastic bottles (11 cm diameter × 20 cm deep) and a 1-gal metal can (15 cm diameter × 17.5 cm deep) in arrays of seven pitfalls each. The pitfalls were arranged in a three-leaf clover pattern (120° between arms), with the gallon can at the center and 2-liter bottles on either side, near the distal end of each arm (drift fence). The drift fences, made of aluminum siding, 1.2 m long by 30 cm high, met at the central can. An array fit into a triangle a little less than 2.5 m from corner to corner.

From July 1989 to September 1990 we had 154 pitfall traps distributed in 22 arrays of seven pitfalls each in three transects on swamp edges. In addition, from January to September 1990 we had 45 pitfalls, without drift fences, at 10-m intervals in two transects on shrub-bordered ditch banks in sandy weed fields. Because of ants and crabs, snap trapping proved infeasible during warm seasons. In January and February 1990 we used Museum Special snap traps baited with rolled oats or mouse parts (attached to trap treadles with twist-ties) in 100-trap transects in hayfields and weed fields to capture *Cryptotis parva* and *Blarina carolinensis*.

On 21 September 1989 Hurricane Hugo devastated coastal South Carolina with a tidal surge up to 5.9 m (19.5 ft) above normal high tide that inundated the salt marshes and adjacent coasts, and winds of 217 km/h (135 mph) that leveled the forests. In our study area more than 80% of the trees were uprooted or broken off. The storm eliminated any chance of catching *Cryptotis parva* in marshes, but it dramatically improved habitat for *Sorex longirostris* on the swamp margins. What had been dark, closed canopy forest with patchy herbaceous ground cover became open and sunny, with scattered trees and dense, continuous herbaceous ground cover. Within six months we were catching more *Sorex longirostris*, as well as open country mammals such as *Cryptotis parva* and *Reithrodontomys humulis*, where there had been forest.

Measurements.—Only specimens judged to be adult by tooth wear—molariform teeth showing little to moderate wear (subadult and adult of Choate, 1970)—were measured. Individuals with unworn teeth (young) or excessively worn teeth (old adult) were not measured. External measurements, assumed to have been taken in the conventional manner, are from specimen labels. Shrews immersed in liquid in pitfalls shrink or stiffen and yield an erroneously small total length. Thus, total length of shrews from fluid-charged pitfalls is not comparable to total length of shrews measured fresh from snap traps or live traps, so it is not included in the tables. Lengths of tail, hind foot, and ear do not change appreciably in liquid and were used in our tables of measurements. Cranial measurements were made with dial calipers and a binocular microscope as described by Jackson (1928), Choate (1970), and Junge and Hoffmann (1981). Abbreviations of measurements in the tables are as follows: condylobasal length (CBL), palatal length (PAL), maxillary breadth (MAB), interorbital breadth (IOB), maxillary toothrow length (MTR), cranial breadth (CRB), total length (TL), tail vertebrae (TA), hind foot (HF), and ear from notch (EA).

Results and Discussion

Sorex longirostris Bachman 1837

?*Sorex personatus* I. Geoffroy Saint-Hilaire, 1827:122.
Sorex longirostris Bachman, 1837:370.
O[tisorex] longirostris: DeKay, 1842:23.
Corsira forsteri: Lesson, 1842:89 = ?*Sorex longirostris* Bachman.
Musar[aneus] (Croc[idura]) bachmani Pomel, 1848:249.
Sorex personatus: Baird, 1857:30.
Sorex wagneri Fitzinger, 1868:512.

Type locality.—Swamps of the Santee, Hume Plantation, Cat Island, Georgetown County, South Carolina. Cat Island is on the north side of the mouth of the Santee River.

Holotype.—Academy of Natural Sciences of Philadelphia ANSP 479, "Mounted skin, skull inside except for rostrum which has been extracted" (Koopman, 1976). Collected by Alexander Hume.

Description.—*Sorex longirostris* of coastal South Carolina is a small long-tailed shrew; total length usually less than 90 mm; tail a little more than one-third of the total length (mean 31 mm); tail, forefeet and hindfeet small and delicate; tail naked in reproducing old adults of both sexes; ears hairy and relatively large, protruding conspicuously through fur; eyes minute but visible; vibrissae long, conspicuous, reaching ear when laid back. Coloration of upper parts uniformly brown, except flanks slightly paler, and vibrissal area black ("masked"); underparts pale orange-brown, not sharply defined from color of flanks; tail fuscous on dorsal surface and on distal third of ventral surface, buff on proximal two-thirds; forefeet and hindfeet pale buffy brown. Rostrum unusually short and broad for a *Sorex* (palate averages 39.9% of the condylobasal length and maxillary breadth 29.7% of the condylobasal length); postmandibular foramen absent (n = 22); tooth formula I 1/1, U 5/2, P 1/0, M 3/3 = 10/6 × 2 = 32; medial tine of upper incisor (where upper incisors touch one another) pigmented and within the pigmented area of the main cusp (9 of 16 cases), pigmented and contiguous with pigmented area of main cusp (5 of 16 cases), and unpigmented and separated from the pigmented area of the main cusp (2 of 16 cases); upper unicuspid row not particularly crowded; U^3 usually smaller than U^4 (16 of 22 cases), subequal in six cases (27%); U^5 fully visible in lateral view in 21 of 22 cases, partly hidden in one; only the tips of the upper unicuspids pigmented and all (n = 21) lack a pigmented ridge extending down to the cingulum on the lingual faces of the teeth.

Measurements.--See Table 1.

Comparisons.—*Sorex longirostris* from Charleston County, South Carolina, is medium-sized for the species and has a relatively long tail, short rostrum, and broad skull. Shrews with these characteristics are found in the Coastal Plain and Piedmont south and southwestward from coastal South Carolina to Georgia, Florida, Alabama, and Mississippi. Shrews are slightly smaller in the Ohio and Mississippi valleys, north Georgia, and in the interior of the Carolinas, Virginia, and Maryland (Table 1). *Sorex longirostris fisheri* Merriam from the Dismal Swamp, southeastern Virginia and adjacent North Carolina is larger and has a relatively longer tail and longer, narrower rostrum. South Carolinian shrews do not resemble *S. l. fisheri*. They do, however, resemble *S. l. eionis* Davis of the Gulf Coast of Florida more than do specimens of *S. l. longirostris* from the interior. Compared with coastal *S. longirostris*, *S. l. eionis* has a longer head and body, relatively shorter tail, and cranial measurements averaging slightly larger (Davis, 1957).

Nomenclature.—*Sorex personatus* I. Geoffroy Saint-Hilaire (1827) may be the oldest name for the southeastern shrew. Beginning with Baird (1857), *S. personatus* was used as the name for the southeastern shrew. In naming *S. personatus* Geoffroy Saint-Hilaire cited only the United States as its type locality. However, Baird (1857:31) believed that "The original specimen [of *S. personatus*] was collected in some one of the Atlantic States by Milbert, probably somewhere in the south...," i.e., within the range of *S. longirostris*. Baird went on to say, "It is with much pleasure that I am enabled to identify the hitherto obscure *Sorex personatus* of Geoffroy. A comparison of the specimen before me [USNM 637/1788 from Washington, D.C.] not only with the description, but with the beautiful figure given in Guerin's Magazin de Zoologie, 1833, shows a much more than usual agreement between the two in color, shape, dimensions, etc." On the basis of this comparison, Baird lodged *S. longirostris* in the synonymy of *S. personatus*. Incidentally he was correct in his identification of USNM 637/1788 as a southeastern shrew. Baird described the skin and teeth of that specimen in such detail that together with his table of measurements it is certain that, in spite of a fragmentary skull, the individual now labeled USNM 637/1788 is the specimen Baird described.

Miller (1895:40) called attention to Baird (1857:31) and raised the possibility that the reference pertained to *Sorex longirostris* Bachman. Miller examined USNM 637/1788, then without a skull, and pronounced it "wholly unidentifiable." He included the Baird reference with question in the synonymy of *S. personatus* I. Geoffroy Saint-Hilaire. Of *S. personatus* he said "...the original specimen was collected by Milbert in the United States, possibly in New York (Milbert collected the type of *Rhinichthys cataractae* Cuv. and Val. at Niagara Falls, N.Y.). The description is sufficiently accurate to show that the animal was the smaller common Long-tailed Shrew of the eastern United States [*S. personatus* = *S. cinereus*]."

Another perspective on *S. personatus* came from Merriam (1895:62): "Respecting the pertinence of the name *personatus* for this Shrew [the common small *Sorex* of eastern North America], Dr. G. E. Dobson wrote me from Netley, England, under date of October 5, 1885, as follows: 'I have lately returned from Paris, where I have been studying the Soricidae in the Museum of the Jardin des Plantes. I have found there the type of *Sorex personatus* Geoff., which is certainly = *S. cooperi*, the latter name becoming therefore, a synonym.'" Of *S. cooperi*, Miller (1895:41) said: "The *Sorex cooperi* which Bachman named in 1837 is without doubt the present species (*S. personatus*)."

Thus, authority for identification of *Sorex personatus* I. Geoffroy Saint-Hilaire as the common eastern North American masked shrew rests not with Baird, Miller, or Merriam, but

with Dobson as quoted by Merriam (1895). Dobson was the only one of the four who actually examined the holotype of *S. personatus*. We do not know whether the holotype still exists. Miller did not mention it in his manuscript notebooks describing types in European museums. Neither did Rode (1943) in his catalog of types of Insectivora in the Muséum National d'Histoire Naturelle, Paris. We do not believe that any of these determinations (Baird, Dobson, Miller, or Merriam) can be taken seriously, since Dobson did not know what all the possibilities were and could not have made pertinent comparisons, and neither Baird, Miller, nor Merriam had more than nondefinitive descriptions to go by. Without a holotype or a definite type locality we believe *Sorex personatus* I. Geoffroy Saint-Hilaire is unidentifiable. Miller (1895) associated the name *S. personatus* with the northern masked shrew, and Jackson (1925) synonymyzed it with *S. cinereus* Kerr.

Sorex longirostris Bachman (1837) is the earliest name that pertains unequivocally to the long-tailed shrew of the southeastern United States. Recognition of this fact dates from Miller's (1895:52) redescription of the species. *Musaraneus bachmani* Pomel (1848) and *Sorex wagneri* Fitzinger (1868) are renamings of *Sorex longirostris* Bachman.

Specimens examined.—All in the National Museum of Natural History unless otherwise noted. *S. l. eionis*: Florida: Wakulla County: St. Marks National Wildlife Refuge, St. Marks Unit, 1 skin and skull. *S. l. fisheri*: All localities are in the Great Dismal Swamp National Wildlife Refuge. North Carolina: Gates County: Cross Canal, 3 mi SW Corapeake, 4 skulls; Weyerhauser Ditch, 1.6 mi N North Carolina Highway 158, 5 skulls. Virginia: City of Chesapeake (= Norfolk County): East Ditch, 6 skulls; Feeder Ditch, 3 skulls; Portsmouth Ditch, 1 skull; 4.7 mi NNE Wallaceton, 1 skin and skull. City of Suffolk (= Nansemond County): Badger Ditch, 2 skulls; Jericho Ditch, 6 skulls; Lake Drummond, 7 skins and skulls (including holotype of *S. l. fisheri*), 2 alcoholics and skulls; Railroad Ditch, 1 mi E Desert Road, 5 skulls; West Ditch, 1 skull. *S. l. longirostris*: Alabama: Chambers County: 2 mi N Gold Hill, 12 skins and skulls. Arkansas: Benton County: 3 mi N War Eagle, 1 alcoholic and skull (University of Arkansas, Department of Zoology). Indiana: Tippecanoe County: 10 mi W Lafayette, 6 skins and skulls. Mississippi: Noxubee County: Macon, 1 skull. North Carolina: Wake County: Raleigh, 3 skins and skulls. South Carolina: Charleston County: Iron Swamp, 4.0 km SW Awendaw, 7 alcoholics and skulls, 2 alcoholics; Head of Mill Branch Swamp, 3.3 km NW McClellanville, 15 alcoholics and skulls, 27 alcoholics Virginia: Amelia County: Amelia Court House, 3 skins and skulls, 1 skin. Brunswick County: Seward Forest, near Triplett, 2 skins and skulls. Chesterfield County-Powhatan County line: Keswick Farm, 4 mi N Midlothian, 1 skin and skull. Hanover County: 1.2 mi S Montpelier, 1 skull. Montgomery County: Blacksburg, 2000 ft, 5 alcoholics and skulls (Virginia Commonwealth University).

Sorex carolinensis Bachman

Sorex carolinensis Bachman,1837:366.
Blarina brevicaudata: Lesson, 1842:89 = ?*Sorex carolinensis* Bachman.
Sorex (Anotus) carolinensis: Wagner, 1855:550 (*part.*).
Blarina carolinensis: Baird, 1857:45.
Blarina brevicauda: Allen, 1869:221.
Blarina brevicauda carolinensis: Merriam, 1895:13.

Type locality.—Bachman (1837:368) specified "South Carolina", "...both in the upper and maritime districts." The only specific area Bachman mentioned was Abbeville District in western South Carolina. Merriam (1895:13) restricted the type locality to "Eastern South Carolina". We further restrict the type locality to Charleston County, South Carolina, because Bachman lived in Charleston and was most familiar with the local fauna. He specified that *S. carolinensis* had been known to him for "nearly twenty years." He also mentioned seeing burrows of this shrew in plowed ground and ditch banks. Furthermore, the species that Bachman (1837:366) described, total length 3⅝ inches (108 mm), was unusually large for *Blarina carolinensis*. We believe the largest shrews are found near the coast.

Neotype.—None of Bachman's type material is known to exist. Since *Blarina carolinensis* is geographically variable and additional subspecies are likely to be named, we designate as neotype USNM 574157, adult male with moderately worn teeth, skin and skull, collected 27 July 1989, by Charles Handley and Merrill Varn, beside Awendaw Creek, 3.2 km E Awendaw Post Office, Charleston County, South Carolina, in a thicket at the edge of a salt marsh. Field number COH 15236.

Description.—This species can be recognized as a *Blarina* by its medium size (for a soricid), stout body, short tail (about as long as the head), blackish coloration, slit-like ear hidden in fur, tiny eye, and 32 teeth tipped with reddish pigment. Dorsal coloration in fresh pelage blackish with a slight brownish tint flecked with gray where hair bases show through; underparts paler, washed with brown, not sharply defined from dorsum, pallor not invading flanks; summer pelage slightly paler; vibrissae whitish, extending beyond the eye but not as far as the ear when laid back; forefeet buffy; hindfeet pale fuscous; tail blackish above, slightly paler beneath. Pelage becoming progressively browner in museum storage. Cranium moderately angular; tooth formula I 1/1, U 5/2, P 1/0, M 3/3 = 10/6 × 2 = 32; U^1 and U^2 large and subequal, U^3 and U^4 small and subequal, U^5 tiny but usually visible in lateral view; toothrows relatively uncrowded; maxillary process extends behind M^2; ascending ramus of mandible in lateral view bends up well behind posterior molar; posterior edge of P^4, M^1, and M^2 concave.

Measurements.—The neotype, in mm (additional measurements in Table 2): Total length 105, tail vertebrae 21, hind foot 12, condylobasal length 19.4, palatal length 8.7, maxillary breadth 6.8, interorbital breadth 5.2, maxillary toothrow length 7.3, cranial breadth 10.7.

Comparisons.—Shrews of coastal populations in South Carolina and North Carolina have a slightly longer rostrum than shrews of inland (Piedmont) populations in South Carolina and Virginia (Table 2). This variation is seen in means of condylobasal length (19.0 and 18.9 vs 18.6 and 18.6), palatal length (8.5 and 8.5 vs 8.1 and 8.2), and maxillary toothrow

length (7.3 and 7.3 vs 6.8 and 7.1). Other cranial and external measurements differ little, if any, between coastal and Piedmont populations.

Nomenclature.—*Sorex carolinensis* DeKay (1842:21), based on specimens from New York, is not the same as *S. carolinensis* Bachman. It is a synonym of *Blarina brevicauda* Say. On the other hand, *Sorex (Anotus) carolinensis* Wagner (1855:550) is a composite, based partly on *S. carolinensis* Bachman and partly on *S. carolinensis* DeKay. However, *S. carolinensis* DeKay alone is the type species of *Anotus*, which Wagner used tentatively as a subgeneric name for a species he mistakenly believed had 36 teeth and no external ear. *Talposorex* Pomel (1848) was also based on *S. carolinensis* DeKay. Baird (1855:47) noted the anomalous description of *S. carolinensis* DeKay and did not include DeKay's name in the synonymy of *S. carolinensis* Bachman.

Merriam (1895) indecisively referred to *S. carolinensis* Bachman as a species, *Blarina carolinensis*, or a subspecies, *Blarina brevicauda carolinensis*. Merriam thought it remarkable that *S. carolinensis* Bachman had remained free of synonyms. For 75 years following Merriam (1895), all authors used the name combination *Blarina brevicauda carolinensis*. Handley (1971), on geographic grounds, and Genoways and Choate (1972) and many subsequent authors on genetic grounds, have regarded *Blarina carolinensis* as a distinct species.

Specimens examined.—All in the National Museum of Natural History unless otherwise noted: North Carolina: Currituck County: Knotts Island, 5 skins and skulls (Norfolk [Virginia] Museum). South Carolina: Charleston County: Awendaw Creek, 3.2 km E Awendaw Post Office, 1 skin and skull; Iron Swamp, 4.0 km SW Awendaw Post Office, 4 alcoholics and skulls, 9 alcoholics; 3.4 km NE McClellanville, 2 skins and skulls; Head of Mill Branch Swamp, 3.3 km NW McClellanville, 3 alcoholics and skulls, 14 alcoholics. Darlington County: Society Hill, 1 skull. Dorchester County: 12.9 km SE St. George, 1 skin and skull. Georgetown County: Georgetown, 1 skin and skull; Plantersville, 2 skins and skulls. Richland County: Columbia, 4 skins and skulls, 1 skin. Williamsburg County: Lanes, 1 skin and skull. Virginia: Amelia County: Amelia, 25 skins and skulls.

Sorex cinereus Bachman

Sorex cinereus Bachman, 1837:373 (preoccupied by *Sorex arcticus cinereus* Kerr, 1792).
Corsira (Blarina) cinerea: Gray, 1838:124.
Blarina brevicaudata: Lesson, 1842:89 = ?*Sorex cinereus* Bachman.
M[usaraneus] (Cryptotis) cinereus: Pomel, 1848:249.
S(orex) carolinensis: Bachman, in Audubon and Bachman, 1854:344 (*part.*) = *Sorex cinereus* Bachman.
Blarina cinerea: Baird, 1857:48.
Blarina brevicauda: Allen, 1869:221 (*part.*).
[Blarina] (Soriciscus) [cinereus]: Coues, 1877:649.
Blarina (Cryptotis) parva: Merriam, 1895:17.
Cryptotis parva: Miller, 1912:24.
Blarina (Cryptotis) floridana Merriam, 1895:19.
Cryptotis parva floridana: Harper, 1927:270.

Type locality.—"Goose Creek about twenty-two miles from Charleston..." (Bachman, 1837:374). This must be road mileage because the town of Goose Creek, in Berkeley County, South Carolina, is 16 mi NNW of Charleston, measured from the Battery at the tip of the Charleston Peninsula (the point in Charleston most distant from Goose Creek). "They [the type specimens] were ploughed up from time to time from an old field which had laid in an uncultivated state for some years and was partially overgrown with weeds and bushes" (Bachman, 1837).

Syntypes.—Bachman (1837) based his description of *Sorex cinereus* on six specimens from Goose Creek that had been given to him by Mr. W. Wesner. Bachman wrote that he had "...received about twenty other specimens from various parts of the low country of Carolina—all of the size and colour of the above." At least three of Bachman's specimens of *Sorex cinereus* still exist. Two are in the Academy of Natural Sciences of Philadelphia, ANSP 477 and ANSP 478. They are labeled, "Bachman, Blarina cinerea, N.A." They are badly discolored skins with skulls inside. The third specimen is USNM 94 [skin]/1771 [skull] in the National Museum of Natural History, received as an exchange from the Academy of Natural Sciences, and cataloged on 26 April 1852. It is labeled "Dr. Bachman, Carolina, *Sorex cinereus*." All that remains of this specimen in the National Museum is a fragmentary rostrum of the skull (1771). The skin was transferred to the University of Michigan 1 April 1859 and was cataloged there. However, Handley could not find it at the University of Michigan on 31 May 1954.

Presumably these three specimens were among the six syntypes from Goose Creek rather than among the 20 other specimens mentioned by Bachman. Probably there is no way to be certain. In any case, we do not select one of them as lectotype.

Description.—*Sorex cinereus* Bachman is a small, short-tailed shrew with a slender tail about one-third of the head and body length (one-fourth of total length), delicate forefeet and hindfeet, slit-like ear wholly concealed in fur, acute snout, and tiny eyes. Coloration clear blackish gray above and grayish white below, fairly sharply divided on flanks; dorsal hairs tricolored, with wide blue-gray basal band, narrow whitish subterminal band, and short blackish tip imparting a "salt and pepper" appearance to dorsum; hairs of underparts bicolored, with wide blue-gray basal band and short whitish tip; vibrissae white, short, reaching back about halfway between eye and ear; forefeet and hindfeet whitish to grayish; tail bicolored, whitish below, blackish above. Skull narrow and slender; braincase rounded, not angular; auditory ring relatively large, much wider than basisphenoid between rings. Tooth formula I 1/1, U 4/2, P 1/0, M 3/3 = 9/6 × 2 = 30 teeth; maxillary teeth relatively small and posterior concavities on these teeth relatively shallow; U^4 usually visible in lateral view; distribution and sometimes intensity of chestnut pigmentation on teeth usually reduced.

Measurements.—See Table 3.

Comparisons.—To evaluate geographic variation in *Cryptotis parva floridana*, we selected four samples from the National Museum of Natural History to study in detail: southern Florida (Brevard County, representing typical *C. p. floridana*), northern

Florida (St. Marks area, Franklin and Wakulla counties), coastal South Carolina (Charleston County, representing typical *S. cinereus*), and coastal North Carolina (Dare, Hyde, and Cartaret counties). For comparison we used a series from Raleigh, North Carolina, to represent the local *C. p. parva* (typical *C. p. parva* from Blair, Nebraska, averages slightly larger).

The sample from southern Florida averages slightly, but not significantly, larger than the series from northern Florida in cranial dimensions (Table 3). External measurements of the southern series are significantly larger in total length with little overlap, but the specimens from northern Florida have a relatively longer tail (26% of total length vs 24%). There is broad overlap between the northern Florida and South Carolina samples, with the South Carolina specimens averaging slightly smaller. Between South Carolina and coastal North Carolina samples there is little difference in skull measurements (the same or slightly larger in South Carolina), but coastal North Carolina specimens average a little larger in external dimensions. The tail, however, averages slightly longer in South Carolina specimens (25% of total length vs 24%). In summary, with few exceptions there is a gradual change from larger in the South to smaller in the North in coastal *Cryptotis*. In the North there is an abrupt change to much smaller size in the interior at Raleigh, with little overlap in most measurements. This is shown dramatically in total length (declines only 10.2% between southern Florida and coastal North Carolina, but 12.3% between coastal North Carolina and Raleigh), and condylobasal length (declines 7.8% between southern Florida and coastal North Carolina, and 7.0% between the coast and Raleigh). Tail length, a characteristic that distinguishes *C. p. floridana* from *C. p. parva*, averages about 25% of total length along the coast from Florida to North Carolina. It averages 21% at Raleigh (also 21% at Blair, Nebraska).

Clinal diminution in size of *Cryptotis* along the coast from Florida to North Carolina is illustrated very well in the ratio of condylobasal length to maxillary breadth (Fig. 1, 2). The location of each score in the plot represents the position of each specimen along the axis defined by the discriminant function for that population. Both plots indicate that specimens from coastal South Carolina are similar to both *C. p. floridana* from Florida and specimens from coastal North Carolina previously reported as *C. p. parva*. All of these populations are well differentiated from *C. p. parva* of inland North Carolina.

In fresh pelage *C. p. floridana* is clear gray without a hint of brown, whereas *C. p. parva* is clear brown without a hint of gray. Summer and winter pelages vary in shade from pale to dark, but not in hue. However, in some instances old worn pelage of *C. p. floridana* may take on a brownish tinge in the field.

Postmortem changes in coloration can be dramatic in *Cryptotis*. Take for example a specimen (USNM 314998) that Handley noted in about 1960 to be "...in fresh, clean, winter pelage...almost clear gray dorsally, with hardly a hint of brown...indistinguishable from Florida *C. floridana*, but...strikingly distinct from topotypes of *C. parva* in similar pelage." In 1990 this doesn't look like the same specimen. Now it is brown dorsally, with hardly a hint of gray. It is similar to topotypes of *C. parva*. In 30 years this specimen changed from resembling one subspecies, *C. p. floridana*, to resembling another, *C. p. parva*!

Fortunately, not all postmortem changes in the museum are so dramatic. For example, consider the series from St. Marks National Wildlife Refuge, Florida, and that from McClellanville, South Carolina, used in this study. Sample size is the same in each. The skins are well-made, collected at exactly the same season (January–February), 12 years apart (1978 and 1990). Each series varies similarly from pale to dark, and when arranged by shade the two series are almost indistinguishable dorsally. Eleven months after they were collected the new specimens were still gray or gray with the slightest hint of brown; the old specimens were still gray but now slightly brownish dorsally. On the other hand, ventrally, the 1990 McClellanville specimens are easily recognized. Their whitish underparts contrast with the yellowish of the St. Marks specimens.

We suspect coloration of the McClellanville and St. Marks series would be identical if the collections had been made in the same year. We interpret the yellow-brown cast in the St. Marks series to be postmortem foxing. Such changes may be related to peculiarities in specimen preparation as well as conditions of storage. Foxing in *Cryptotis* was noted also by Choate (1970:204). This phenomenon must be taken into account in any color comparisons involving museum specimens of *Cryptotis*.

The dorsal coloration of specimens from coastal North Carolina, collected in 1939, is brown, not gray. These specimens are dark, rich brown; in some cases blackish-brown. They are darker than Raleigh specimens and differ from them also in the "salt and pepper" effect that characterizes *C. p. floridana*.

In addition to size of body and coloration of pelage, Merriam (1895) used several dental characters to distinguish *C. floridana* from *C. parva*. Measurements show that some of Merriam's characters (Table 4) are useful, some not. Shallowness of the posterior concavity on P^4 and M^1 and reduction in crowding of unicuspids (U^4 visible in lateral view) group specimens from Florida and coastal South Carolina together and distinguish them from Raleigh, North Carolina, specimens. Specimens from coastal North Carolina are intermediate. The amount of color on the teeth and the depth of the anterolingual notch on P^4 are variable and not diagnostic. Tooth color is often, but not always, paler in coastal and southern specimens.

Nomenclature.—During much of the 19th century *Sorex cinereus* Bachman had a curious history of cyclically hiding in the synonymy of *Blarina brevicauda* and being elevated to the position of type species of new subgenera. Lesson (1842:89) included Bachman's *Sorex cinereus* as a probable synonym of *Blarina brevicauda*. Similarly, Allen (1869) regarded all of the American short-tailed shrews as subspecies or synonyms of *Blarina brevicauda*. He thought the smallest short-tailed shrews, such as *Cryptotis cinerea* and *C. parva*, were merely young of *Blarina brevicauda*.

On the other hand, Pomel (1848:249), contrary to Lesson (1842), withdrew *Sorex cinereus* Bachman (= *Sorex parvus* Say) from synonymy and set it apart as the type species of a new subgenus, *Cryptotis*. Three decades later, Coues (1877) refuted the opinions of Allen (1869), restored the distinction between large and small short-tailed shrews, and described a new subgenus, *Soriciscus*, once again using "*Sorex parvus* Say or *S. cinereus* Bachm." as the type species. Oddly, Coues placed *Cryptotes* [sic] Pomel in the synonymy of *Blarina brevicauda*.

Baird (1857) had a third opinion. He did not recognize subgenera in *Blarina*, but he did recognize several species within the 30-toothed section of *Blarina* (= *Cryptotis*). Although he noticed that the Florida shrew was generally larger and longer-tailed, Baird was the first author to perceive a relationship between *Cryptotis* of Florida and coastal South Carolina. He referred a specimen (USNM 2155/3110) from Indian River, Florida, (near the type locality of the later named *Blarina floridana*) to *Blarina cinerea*. Furthermore, Baird (1857:62) distinguished between *Cryptotis floridana* (= *Blarina cinerea*) and *C. parva* (= *Blarina exilipes*). Baird's specimens of *C. floridana* were from Florida and coastal Georgia and South Carolina (also one from Pennsylvania on the basis of tail length). His specimens of *C. parva* were from Mississippi, Missouri, Tennessee, Illinois, and Virginia. Thus, the geographic ranges of Baird's two forms were very similar to the ranges we ascribe to *C. p. floridana* and *C. p. parva* in this paper.

Like Baird, Merriam (1895) recognized 32-tooth (subgenus *Blarina*) and 30-tooth (subgenus *Cryptotis*) divisions of *Blarina*. Also like Baird, Merriam recognized two forms of *Cryptotis* in the southeastern United States: the widespread *Cryptotis parva* and a new species, *C. floridana*, in Florida. Merriam (1895:18) noted that specimens from the coastal region of South Carolina and Georgia (the same specimens that Baird had referred to *Sorex cinereus* Bachman) are "somewhat larger than the typical form [*C. parva*]...appreciably [larger] than those from Raleigh, N.C." However, in spite of their larger size and gray rather than brown coloration, to Merriam's eye these specimens showed no approach to *C. floridana* in dental characteristics. Thus, he synonymyzed *Sorex cinereus* Bachman with *Cryptotis parva* Say, and he has been followed by all authors to the present day.

As we have shown in our comparisons, Merriam's (1895) synonymy is incorrect. Actually, *Sorex cinereus* Bachman is a prior name for *Blarina floridana* Merriam. However, since *Sorex cinereus* Bachman is a primary homonym of *Sorex cinereus* Kerr, it is unavailable and falls into the synonymy of *Blarina floridana* Merriam. Thus, Merriam's *B. floridana* is the first available name for the homonym *Sorex cinereus* Bachman. Its holotype is USNM 16510/23937, Chester Shoals, Florida.

Specimens examined.—All in the National Museum of Natural History unless otherwise noted. *Cryptotis parva floridana*: Florida: Brevard County: Chester Shoals, 11 mi N Cape Canaveral, 2 alcoholics and skulls (including holotype of *Blarina floridana*); Micco, 1 alcoholic and skull; Oak Lodge (East Peninsula, opposite Micco), 13 skins and skulls (Museum of Comparative Zoology, Harvard), 1 skin (Museum of Comparative Zoology, Harvard), 1 skull (Museum of Comparative Zoology, Harvard). Franklin County: Alligator Point, 8 mi SSE Panacea, 2 skins and skulls. Wakulla County: St. Marks National Wildlife Refuge, Panacea Unit, 2 skins and skulls, 1 skin, 3 skulls, 1 alcoholic; St. Marks National Wildlife Refuge, St. Marks Unit, 8 skins and skulls, 2 skulls, 12 alcoholics. North Carolina: Carteret County: 6 mi NE Beaufort, 2 skins and skulls; Bogue Island, near Morehead City, 2 skins and skulls. Dare County: Buxton, 1 skin and skull (North Carolina State Museum); Hatteras, 1 skin (American Museum of Natural History); 8–10 mi SW Stumpy Point, 5 skins and skulls, 1 skull. Hyde County: 10 mi N Englehard, 2 skins and skulls; 3 mi W Lake Landing, 7 skins and skulls, 1 alcoholic. South Carolina: Berkeley County: "Carolina" [= Goose Creek?], 1 skull; "North America" [= Goose Creek?], 2 skins with skull inside (Academy of Natural Sciences, Philadelphia). Charleston County: McClellanville, 4 skulls, 2 alcoholics and skull, 2 alcoholics; 3.4 km NE McClellanville, 8 skins and skulls; Mt. Pleasant, 1 skin and skull (Museum of Comparative Zoology, Harvard), 1 skin and skull. Georgetown County: Georgetown, 1 skin and skull. *Cryptotis parva parva*: Nebraska: Washington County: Blair, 11 skins and skulls (topotypes of *C. p. parva*). North Carolina: Wake County: Raleigh, 5 skins and skulls (Museum of Comparative Zoology, Harvard), 22 skins and skulls.

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Table 1.—*Cranial and external measurements of* Sorex longirostris *from localities in the southeastern United States. Historic and recent samples of* Sorex longirostris fisheri *are from areas now included in the Great Dismal Swamp National Wildlife Refuge. Abbreviations are defined in the section on methods.*

	CBC	PAL	MAB	IOB	MTR	CRB	TL	TA	HF	EA
					Sorex longirostris longirostris, Chambers County, Alabama					
$\bar{x}$ ± 2SE	14.6 ± 0.12	5.9 ± 0.08	4.4 ± 0.08	2.9 ± 0.08	5.4 ± 0.07	7.5 ± 0.06	82.5 ± 2.58	29.6 ± 0.62	10.1 ± 0.33	
Range	14.2–14.9	5.7–6.1	4.2–4.6	2.7–3.1	5.2–5.6	7.4–7.8	76.0–91.0	28.0–31.0	0.9–11.0	
n	11	11	11	11	11	11	11	11	11	
					Sorex longirostris longirostris, Charleston County, South Carolina					
$\bar{x}$ ± 2SE	14.8 ± 0.12	5.9 ± 0.08	4.4 ± 0.06	3.0 ± 0.03	5.4 ± 0.05	7.5 ± 0.06		30.8 ± 0.61	11.1 ± 0.13	7.8 ± 0.33
Range	14.4–15.5	5.7–6.3	4.1–4.6	2.8–3.1	5.2–5.6	7.2–7.8		27.0–34.0	11.0–12.0	6.0–9.0
n	21	22	19	22	22	21		21	21	21
					Sorex longirostris longirostris, central Virginia (Amelia, Brunswick, Chesterfield, and Hanover counties)					
$\bar{x}$ ± 2SE	14.3 ± 0.21	5.6 ± 0.10	4.3 ± 0.07	2.8 ± 0.09	5.2 ± 0.10	7.2 ± 0.12	83.4 ± 2.17	30.0 ± 1.90	10.9 ± 0.52	
Range	14.0–14.6	5.8–5.9	4.2–4.3	2.6–2.9	5.1–5.4	7.1–7.4	76.0–90.0	25.0–33.0	10.0–12.0	
n	6	7	3	7	7	4	7	7	7	
					Sorex longirostris fisheri, Dismal Swamp, 1980–1988					
$\bar{x}$ ± 2SE	15.4 ± 0.20	6.2 ± 0.09	4.4 ± 0.09	3.0 ± 0.05	5.6 ± 0.05	7.8 ± 0.15		36.2 ± 1.00	11.4 ± 0.31	7.3 ± 0.72
Range	14.6–16.1	5.8–6.5	4.2–4.7	2.8–3.2	5.4–5.7	7.5–8.4		33.0–39.0	10.0–12.0	6.0–9.0
n	14	16	10	17	17	12		17	16	7
					Sorex longirostris fisheri, Dismal Swamp, 1895–1905					
$\bar{x}$ ± 2SE	15.7 ± 0.36	6.2 ± 0.11	4.5 ± 0.1O	3.0 ± 0.08	5.7 ± 0.18	7.8 ± 0.17	98.4 ± 4.70	36.6 ± 2.08	12.1 ± 0.40	10.0
Range	15.1–16.3	6.0–6.5	4.3–4.7	2.9–3.2	5.4–6.1	7.6–8.1	90.0–108.0	31.0–40.0	11.0–13.0	10.0
n	7	8	8	8	9	5	7	9	9	1

Table 2.—*Cranial and external measurements of* Blarina carolinensis *from coastal (Charleston and Currituck counties) and Piedmont (Richland and Amelia counties) localities in the Carolinas and Virginia. Abbreviations are defined in the section on methods.*

	CBC	PAL	MAB	IOB	MTR	CRB	TL	TA	HF	EA
					Blarina carolinensis, Charleston County, South Carolina					
$\bar{x} \pm 2SE$	19.0 ± 0.2	18.5 ± 0.12	6.6 ± 0.13	5.1 ± 0.07	7.3 ± 0.14	10.4 ± 0.16	102.0 ± 6.0	20.0 ± 1.73	12.4 ± 0.37	7.0 ± 0.98
Range	18.5–19.4	8.2–8.7	6.4–6.8	5.0–5.2	7.0–7.6	10.1–10.7	99.0–105.0	15.0–23.0	12.0–13.0	5.0–9.0
n	7	8	6	7	8	7	2	8	8	7
					Blarina carolinensis, Currituck County, North Carolina					
$\bar{x} \pm 2SE$	18.9 ± 0.46	8.5 ± 0.25	6.7 ± 0.28	5.1 ± 0.17	7.3 ± 0.16	10.4 ± 0.17	97.2 ± 3.06	18.4 ± 1.20	12.2 ± 0.40	
Range	18.3–19.4	8.2–8.8	6.4–7.0	4.9–5.3	7.0–7.5	10.2–10.6	93.0–100.0	17.0–20.0	12.0–13.0	
n	4	4	4	4	5	4	5	5	5	
					Blarina carolinensis, Columbia, Richland County, South Carolina					
$\bar{x} \pm 2SE$	18.6 ± 0.10	8.1 ± 0.27	6.6 ± 0.47	4.9 ± 0.13	6.8 ± 0.13	10.2 ± 0.30	99.0 ± 3.06	21.0 ± 0.00	12.7 ± 0.67	
Range	18.6–18.7	7.8–8.2	6.2–7.0	4.8–5.0	6.7–6.8	10.0–10.3	96.0–101.0	21.0–21.0	12.0–13.0	
n	2	3	3	3	3	2	3	3	3	
					Blarina carolinensis, Amelia County, Virginia					
$\bar{x} \pm 2SE$	18.6 ± 0.15	8.2 ± 0.12	6.6 ± 0.10	5.1 ± 0.90	7.1 ± 0.11	10.3 ± 0.09	93.2 ± 1.76	19.5 ± 0.64	12.2 ± 0.50	
Range	18.1–19.3	7.7–8.8	6.3–7.0	4.8–5.7	6.6–7.5	10.0–10.5	86.0–102.0	18.0–22.0	11.0–14.0	
n	17	19	18	19	17	14	17	15	13	

Table 3.—*Cranial and external measurements of* Cryptotis parva *from coastal and interior (Raleigh, North Carolina) localities in the southeastern United States. Abbreviations are defined in the section on methods.*

	CBC	PAL	MAB	IOB	MTR	CRB	TL	TA	HF	EA
					Cryptotis parva floridana, southern Florida					
$\bar{x}$ ± 2SE	17.2 ± 0.13	7.1 ± 0.12	5.4 ± 0.10	3.8 ± 0.11	6.2 ± 0.72	8.2 ± 0.18	94.9 ± 4.0	23.0 ± 1.51	11.7 ± 0.33	
Range	16.0–17.5	6.7–7.4	5.2–5.8	3.4–4.1	5.8–6.5	7.9–8.5	88.0–104.0	20.0–26.0	11.0–12.0	
n	8	12	12	11	12	6	8	8	9	
					Cryptotis parva floridana, northern Florida					
$\bar{x}$ ± 2SE	16.6 ± 0.24	6.9 ± 0.10	5.5 ± 0.12	3.6 ± 0.07	6.1 ± 0.12	8.1 ± 0.08	84.9 ± 2.30	22.0 ± 1.33	12.4 ± 0.56	
Range	16.1–17.5	6.6–7.3	5.2–5.8	3.3–3.9	5.7–6.5	7.9–8.3	77.0–90.0	18.0–25.0	11.0–14.0	
n	13	14	12	14	14	13	12	12	11	
					Cryptotis parva floridana, Charleston County, South Carolina					
$\bar{x}$ ± 2SE	16.1 ± 0.23	6.7 ± 0.10	5.3 ± 0.09	3.6 ± 0.07	5.9 ± 0.12	8.0 ± 0.07	82.4 ± 1.95	20.2 ± 0.72	10.6 ± 0.29	7.3 ± 0.37
Range	15.2–16.9	6.4–7.1	5.0–5.8	3.4–4.0	5.5–6.3	7.8–8.3	77.0–85.0	17.0–23.0	10.0–12.0	6.0–9.0
n	15	17	17	17	17	14	9	17	17	12
					Cryptotis parva floridana, coastal North Carolina					
$\bar{x}$ ± 2SE	15.9 ± 0.19	6.5 ± 0.14	5.2 ± 0.11	3.6 ± 0.04	5.9 ± 0.14	7.8 ± 0.12	85.2 ± 3.19	20.1 ± 1.05	11.0 ± 0.30	
Range	15.3–16.2	6.0–6.9	4.9–5.6	3.5–3.7	5.6–6.5	7.7–8.1	77.0–93.0	17.0–22.0	10.0–12.0	
n	10	12	12	12	12	7	10	10	10	
					Cryptotis parva parva, Raleigh, Wake County, North Carolina					
$\bar{x}$ ± 2SE	14.8 ± 0.13	6.1 ± 0.08	4.9 ± 0.05	3.4 ± 0.05	5.4 ± 0.05	7.6 ± 0.11	74.8 ± 1.4	16.0 ± 0.69	10.2 ± 0.33	
Range	14.3–15.4	5.8–6.6	4.7–5.1	3.2–3.7	5.2–5.6	7.2–7.9	70.0–82.0	13.0–19.0	10.0–11.0	
n	22	23	22	23	23	16	21	22	6	

Table 4.—*Dental characteristics of* Cryptotis parva *from the southeastern United States. Mean lengths and depths in mm, measured with an ocular micrometer.* [a]*Percentage (in parentheses) of* M^1 *length.*

Locality	*n*	Depth of Posterior Concavity[a]			M^1 Length	M^1 Length/ Condylobasal Length	U^4 Visible from Side	Tooth Color Reduced	P^4 Anterolingual Notch Enlarged
		P^4	M^1	M^2					
South Florida	11	0.230 (16.5)	0.230 (16.5)	0.201 (14.4)	1.397	8.1%	91%	45%	100%
North Florida	13	0.267 (19.2)	0.225 (16.2)	0.164 (11.8)	1.389	8.4%	77%	92%	69%
Coastal South Carolina	14	0.253 (19.2)	0.214 (15.8)	0.147 (10.8)	1.358	8.4%	79%	86%	36%
Coastal North Carolina	18	0.285 (21.6)	0.237 (18.0)	0.177 (13.4)	1.318	8.3%	56%	61%	67%
Raleigh, North Carolina	23	0.295 (23.5)	0.0261 (20.8)	0.182 (14.5)	1.255	8.5%	61%	35%	48%

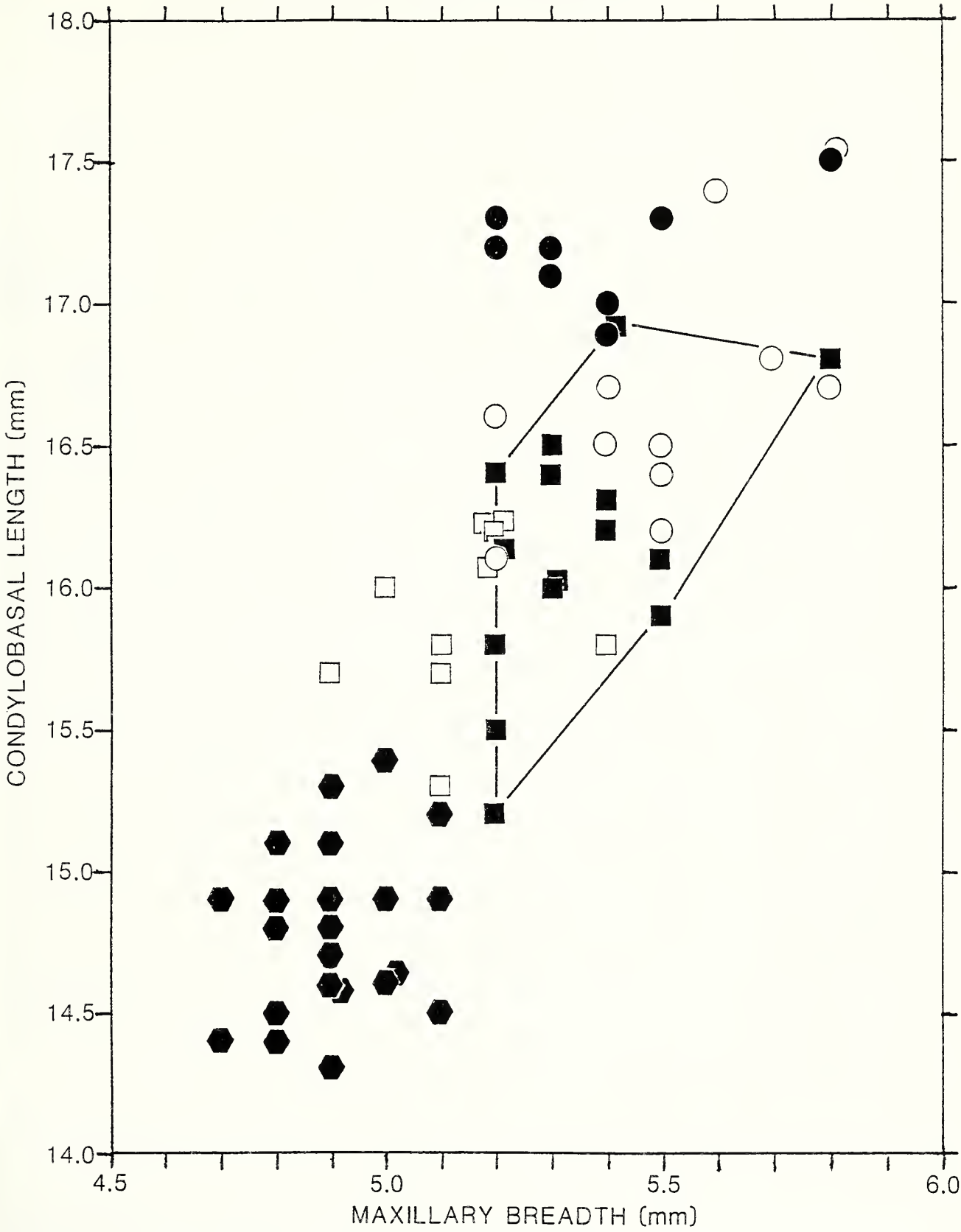

Fig. 1.—Bivariate scattergram of the ratio of measurements of condylobasal length and maxillary breadth from populations of *Cryptotis parva* summarized in Table 3. Symbols: *Cryptotis parva floridana*—southern Florida (solid dots), northern Florida (open dots), coastal South Carolina (solid squares), and coastal North Carolina (open squares); *Cryptotis parva parva*—Raleigh, North Carolina (hexagons).

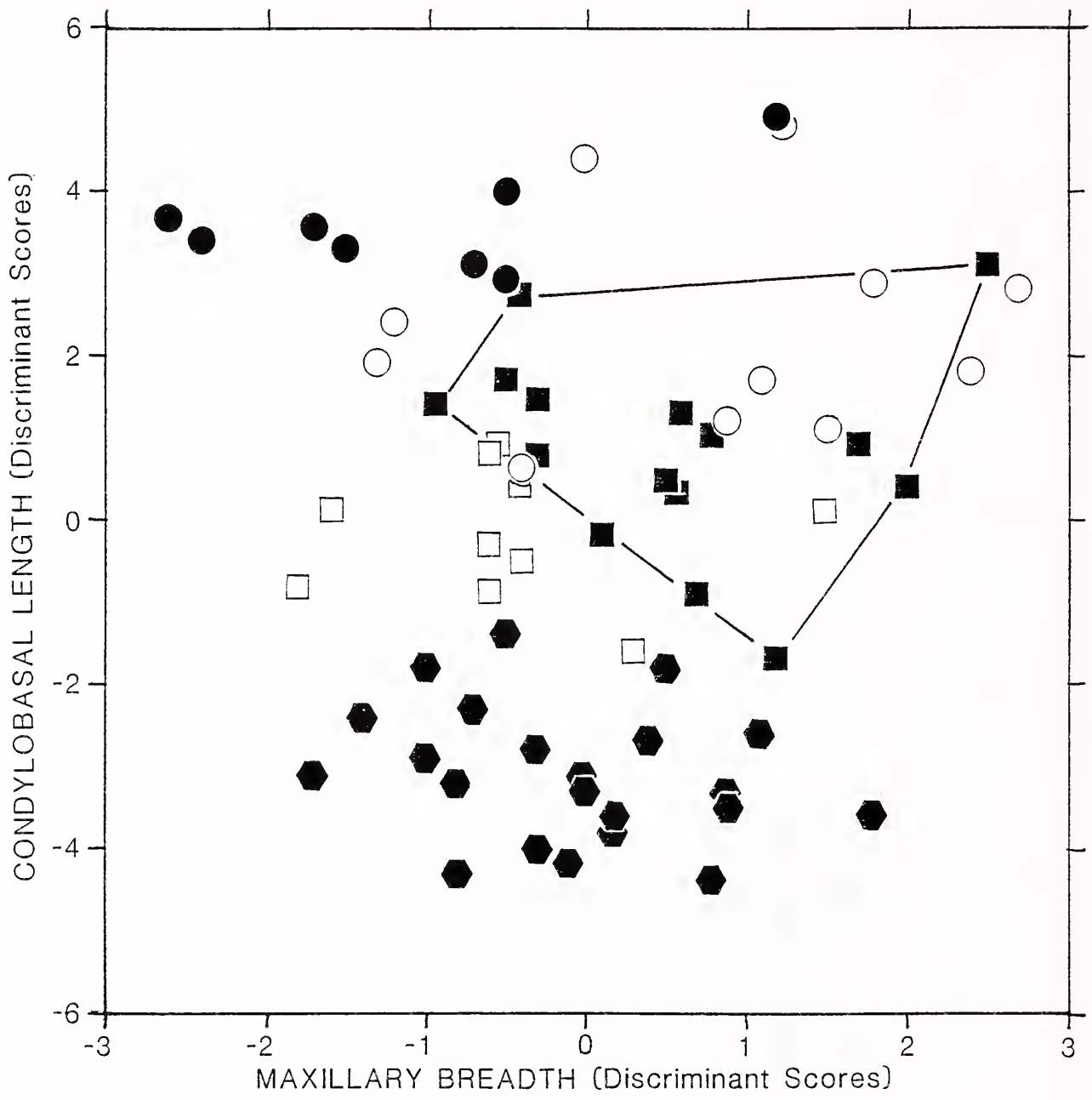

Fig. 2.—Scattergram of ratio of discriminant scores for condylobasal length and maxillary breadth of individuals from populations of *Cryptotis parva* summarized in Table 3. Symbols as in Fig. 1.

SHREWS OF ANCIENT EGYPT: BIOGEOGRAPHICAL INTERPRETATION OF A NEW SPECIES

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ABSTRACT

Mummified shrews found in ceremonial animal tombs of Akhmim near Thebes, Egypt, date from the 27th dynasty (2400 yr B.P.) and represent six species, one of which is described as new to science. The new species is probably now extinct. Its nearest living relatives are known from high forest areas of tropical Africa. The extant shrews of Egypt are briefly reviewed and nomenclatural changes are proposed, including the recognition of *C. whitakeri* instead of the previously listed *C. suaveolens*.

INTRODUCTION

Shrews and other vertebrates had an important place in the religion of the ancient Egyptians (Fig. 1), particularly in the late dynasties (Lurker, 1974). Together with nightjars, mongooses, snakes, toads, and beetles they formed the terrestrial animals "coming from the dark," whereas falcons and swifts formed the animals of the light (Kessler, 1989). In the view of Brunner-Traut (1965), shrews and mongooses may have represented two sides (night and day, dark and light) of the same deity. Along the Nile the Egyptians built many animal cemeteries, for which they used the term "restingplaces of the God Osiris-animal" (Kessler, 1989). Shrews and other animals were embalmed and mummified principally in the same manner as human bodies, although sometimes several individuals and several species were placed together.

In addition to their historical interest, animals preserved in the ceremonial tombs now kept in museum collections provide a unique record of animal life in ancient Egypt (Boessneck, 1988), allowing us to recognize changes in the distributions of animals in this area during the past five millennia.

Shrews are well-represented in the embalmed fauna. Lesson (1827) and Geoffroy Saint-Hilaire (1827) were the first to analyze mummified specimens from Egypt, followed by Lortet and Gaillard (1903) and Heim de Balsac and Mein (1971). The latter authors recorded six species of shrews from ancient Egypt, one of which they could not identify with certainty. Since then much information on African shrews has accumulated, and it is now possible to give a more precise identification of the material examined by them.

MATERIALS AND METHODS

The mummified shrews described in this paper are housed in the Musée Guimet d'Histoire naturelle, Lyon, and the collections of the Centre de Paléontologie, Université Claude Bernard, Lyon. A few voucher specimens, found in the research materials of the late Henri Heim de Balsac, are now deposited in the Muséum national d'Histoire naturelle, Paris. Comparative material of African Soricidae was studied in most European collections, the Smithsonian Institution, Washington, D.C., and the Field Museum of Natural History, Chicago. Measurements are given in mm. They were taken with an electronic caliper and include condyloincisive length (CIL), length of palate (PAL), greatest skull width (GW), height of cranial capsule (HCC), postglenoid width (PGL), maxillary breadth (MB), interorbital width (IO), upper toothrow length (UTR), coronoid length of mandible, distance from anterior border of first molar to posterior border of third molar (M^1–M^3), and length × width of upper (M^1, M^2, M^3) and lower (M_1, M_2, M_3) molars. The nomenclature of dental structures is the same as that figured by Jenkins (1984).

RESULTS AND DISCUSSION

The Past and Present Shrew Fauna of Egypt

The collection of mummified shrews preserved in the Musée Guimet represents six species, as stated by Heim de Balsac and Mein (1971). Table 1 gives a list of embalmed and extant species recorded from the territory of Egypt. Of the six embalmed species, five still live in Africa, but one species appears to be extinct. It is named and described below. Today *Crocidura religiosa* and *C. floweri* are confined to the upper Nile valley (Osborn and Helmy, 1980). However, *C. floweri* has recently been recorded from the Wadi el Natrun in the Western Desert (Goodman, 1988), and may therefore have a wider distribution. *Crocidura olivieri* belongs to a complex of African giant shrews which is widely distributed in tropical Africa (Heim de Balsac and Barloy, 1966). *Crocidura fulvastra* does not occur presently in Egypt. It is a species typical of the Sudan savanna, and has its northern distributional limit at Khartoum, Sudan (Hutterer, 1984). Four of the extant species and the extinct new species are related to sub-Saharan African shrews. *Crocidura whitakeri* is a North African species, and the two species of *Suncus* listed have Palearctic or Oriental affinities. *Crocidura whitakeri* (see comment in Table 1) is known from a single specimen which was described as *C. suaveolens matruhensis* Setzer, 1960, and which has since been cited as *C. suaveolens* (Osborn and Helmy, 1980; Hutterer and Harrison, 1988). The record of this species from Egypt makes it probable that *C. whitakeri* occurs in suitable habitats all along the northern coast of Africa eastward to Egypt, although the species is presently known in northwest Africa only from Morocco, Algeria, and Tunisia. The commensal *Suncus murinus* was imported to Suez by ships (Hutterer and Harrison, 1988).

Crocidura balsamifera new species

1971. *Crocidura* sp. groupe *dolichura*, Heim de Balsac and Mein, Mammalia, 35:230–238, figs. 6, 7, 9b, 10.

Material Examined.—Holotype: A fairly complete skull and right mandible, extracted from a bundle of embalmed shrews found in the archaeological complex of Akhmim (=Achmim or Akhmin), Thebes, Egypt. The radiocarbon age of this material is 2400 ± 140 yr B.P. (Heim de Balsac and Mein, 1971:238). Paratype: Frontal part of a skull with both mandibles; same data as holotype. The type material is deposited in the Musée Guimet d'Histoire naturelle de Lyon (holotype) and the Centre de Paléontologie, Université Claude Bernard, Lyon (paratype). It does not bear catalogue numbers. The third specimen mentioned by Heim de Balsac and Mein (1971) could not be traced.

Etymology.—The species epithet combines the Latin "balsamum," balm, with "fera," animal, thus meaning "embalmed animal."

Diagnosis.—Skull with characters of the *Crocidura dolichura* species group (sensu Dollman, 1916), including inflated braincase, slender and laterally depressed rostrum, weak dentition, and denticulated lower incisor, but differing from other members of the species group by large size (condyloincisive length 22.1 mm in holotype) and the presence of additional crests connecting the protocone, hypocone, and metacone of the first and second upper molars.

Measurements of the Holotype.—Condyloincisive length, 22.1; length of palate, 9.1; greatest skull width, 9.8; maxillary breadth, 6.4; interorbital width, 4.5; height of cranial capsule, 5.6; postglenoid width, 6.4; upper toothrow length, 9.6; M^3–M^3, 3.62; M^1–M^1, 5.79; M^1, 1.56 × 2.34; M^2, 1.38 × 1.98; M^3, 0.72 × 1.35; coronoid height of mandible, 5.0; M_1–M_3, 4.19; M_1, 1.65 × 1.08; M_2, 1.56 × 0.96; M_3, 1.26 × 0.72. Some measurements of the paratype are given in Table 2.

Description.—The bodies of the holotype and paratype were presumably destroyed during the process of unwrapping the drapery and dissolving the resin and are no longer available for study. However, Heim de Balsac and Mein (1971) stated that "one of the specimens showed a tail which we were able to clean from its covering resin and which did not show any vibrissae" (translation from French original). Therefore, it is likely that the species had a "naked" tail. The skull of *C. balsamifera* is large with a long frontal part and an inflated, rounded braincase (Fig. 2) which is smooth and lacks pronounced superior articular facets. The snout gradually tapers to the tip; in dorsal view it is narrow. The ramus of the mandible is weak, the coronoid process low and narrow at its top, and the posterior surface of the condylar process is higher than wide and not angled. The teeth are small in relation to the skull. The first upper incisor is relatively short, and its anterior cusp is about twice as long as the posterior cusp. The three unicuspids are large and have well-developed cingula. The anteriormost unicuspid is the largest, its anterior tip is aligned with the tip of the fourth premolar. The second is smaller than the third, but both surpass in height the parastyle of the fourth premolar. The parastyle is small and closely attached to the body of the fourth upper premolar. The first upper molar is remarkable for two characters. First, a subsidiary cusp or crest is present in the valley between mesostyle, metacone, and metastyle on the labial side (Fig. 3). Secondly, ridges connect the protocone, hypocone, and metacone, a condition also found in the second upper molar. This condition was observed by Heim de Balsac and Mein (1971) who termed this connection "metalophe." The third upper molar is large and stout. In the lower jaw, the first lower incisor is remarkable for the clear presence of two denticulations on the cutting edge of the tooth. The second lower incisor and the fourth lower premolar are large. The lower molars are low-crowned and robust. The third lower molar has a pronounced entoconid basin.

Comparisons.—Some of the dental characters of *C. balsamifera* are rarely present in *Crocidura* species. Subsidiary cusps on the first upper molars have been observed only in *C. yankariensis*, a small shrew inhabiting the northern savannas of Africa (Hutterer and Jenkins, 1980). A crest running from the protocone to the base of the metacone of the first and second upper molars is not frequent but does occur in some other species. Heim de Balsac and Mein (1971) recorded it in *C. floweri* and *C. maurisca*, and I observed it occasionally in *C. latona* (Hollister, 1916), and regularly in *C. manengubae* (Hutterer, 1982). It is also found in fossil shrews such as *Srinitium marteli*, from the Oligocene of France (Hugueney, 1976). No other species of *Crocidura* is known to me wherein these crests are so strongly developed and the protocone and hypocone are connected as in *C. balsamifera*. However, some Heterosoricinae show this pattern (Engesser, 1975). The lower incisor of *C. balsamifera* is also unusual with its two pronounced denticulations. In the genus *Crocidura*, this condition also occurs in *C. crenata* and *C. harenna* (Brosset et al., 1965*a*; Hutterer and Yalden, 1990). Otherwise this denticulation is a typical character of the genus *Sylvisorex*, suggesting that it may be a plesiomorphic character.

The tail lacking long bristles and the rounded skull with inflated braincase groups *C. balsamifera* with Dollman's (1916) "*dolichura* group" with type species *C. dolichura* Peters, 1876. This is a small shrew with a very long, naked tail and a rounded, laterally depressed, and dorsally inflated skull with weak dentition. Similar characters were reason enough for Heller (1910) to erect a new genus, *Heliosorex*, for what is now *C. roosevelti*. Other species with at least some of these characters are *C. muricauda*, *C. niobe*, *C. crenata*, *C. ludia*, *C. latona*, *C. polia*, *C. grassei*, and possibly *C. maurisca* and *C. kivuana*. Measurements of the type specimens of these species are given in Table 2. It is evident that *C. balsamifera* is in the upper size range and is exceeded only by *C. grassei*. However, the skull of *C. grassei* is more robust, has a flatter dorsal profile, possesses slightly heavier teeth, and has no denticulations on the first lower incisor (Brosset et al., 1965*b*, figs. 9–11). Differences with *C. maurisca* can be seen in a comparison with the figures given in Heim de Balsac and Mein (1971). *Crocidura kivuana* has a broader maxillary region and very different teeth (Heim de Balsac, 1968). The same applies to *C. congobelgica*, which may belong to this species group but has a very wide maxillary region (Hollister, 1916).

There exists some fossil evidence which indicates a rather old age for this species group. Wesselman (1984) referred a mandibular fragment from upper Pliocene sediments (dated as 3.03 ± 0.07 my B.P.) of the Omo valley, Ethiopia, to *C.* aff. *dolichura*. Two teeth from Plio-Pleistocene sediments east of Lake Turkana, Kenya, were also identified with this species by Black and Krishtalka (1986). Both localities are outside the present range of the species group.

The limits of the *C. dolichura* species group are not clear. Dieterlen and Heim de Balsac (1979), Dippenaar (1980), and Hutterer (1981, 1982, 1986) discussed various aspects of this group and their conclusions are not fully congruent. One problem is the possible inclusion in this group of species such as *C. littoralis*, *C. monax*, *C. oritis*, *C. ultima*, *C. lanosa*, *C. stenocephala*, *C. usambarae*, *C. manengubae*, *C. tansaniana*, and *C. telfordi*. These are medium to large blackish shrews which have a more or less naked tail of medium length. The skull is generally less inflated, the braincase hexagonal rather than rounded, the maxillary region broad and the dentition often heavy. Although there are certainly relationships between this assemblage and the *C. dolichura* species group, I prefer to treat them as separate groups. *Crocidura balsamifera* resembles only one of these species, *C. manengubae*. They are similar in size, but the proportions and shapes of the upper and lower teeth are different and *C. manengubae* has a hexagonal braincase.

After evaluation of all morphological characters, I assign *C. balsamifera* to the *C. dolichura* group, in the narrow sense defined above. The extant species of this group all occur in the high forest zone of Africa (Fig. 4). They are not abundant in numbers in a population, but up to three species of this group may occur together at one locality (Brosset, 1988). Only one species, *C. roosevelti*, occurs not within, but along the outer edge of the forest zone (Hutterer, 1981). From the known habitat preferences and morphology of these related species it may be deduced that *C. balsamifera* was a "forest shrew" with similar ecological requirements.

Changing Environments and Faunas

The presence of an extinct forest species in the embalmed fauna of ancient Egypt raises questions about the landscape in Egypt 2400 years ago. Of the 68 shrews unwrapped by Heim de Balsac and Mein (1971), 27 were *Crocidura religiosa*, 26 *C. olivieri*, 7 *Suncus etruscus*, 3 *C. floweri*, 3 *C. balsamifera* (including the lost specimen), and 2 *C. fulvastra*. The most abundant species, the small *C. religiosa*, is rarely found now in the upper Nile valley, as is *C. floweri* (Osborn and Helmy, 1980), suggesting that conditions for shrews are now less favorable. Both of these species have been identified in fossil material from middle Paleolithic lake deposits of southwestern Egypt (Kowalski et al., 1989). The fauna of Bir Tarfawi, which is about 135,000 yr B.P. in age, shows that there were lakes with dense vegetation including trees in southwestern Egypt at that time. Farther south at Oyo, northwestern Sudan, Ritchie et al. (1985) found pollen evidence for a humid phase supporting savanna and grassland between 8490 and 4920 yr B.P. Climatic changes in the Nile valley have been studied by Adamson et al. (1980) and Paulissen and Vermeersch (1987*a*, 1987*b*) Their results indicate alternating humid and arid periods since the Pleistocene, including severe flooding of the Nile in Egypt about 13,000–12,000 yr B.P. due to an overflow from Lake Victoria. The last major wet period in upper Egypt occurred during the early Holocene between 11,000 and 6,000 yr B.P. We may therefore hypothesize that during certain periods, swamps or gallery forests along the Nile were of sufficient size to support tropical shrews and allow them to extend their ranges. It is also possible that during heavy floods, small mammals were shifted northward on floating mats of vegetation and tree trunks. The ancestor of *C. balsamifera* could have reached Egypt that way. Although the aridity of the climate increased after 6,000 yr B.P. in upper Egypt, remnants of gallery forest could have remained until destroyed, either from natural causes or as a result of human exploitation.

The present shrew fauna of Africa provides examples which indicate that some "forest shrews" inhabit marshes or gallery forests adjacent to forest borders. For example, Heim de Balsac and Verschuren (1968) found *C. littoralis* to occur in considerable numbers in marshes in the Guinea savanna of the Garamba National Park, northeastern Zaire. This could possibly serve as a model for the habitat of *C. balsamifera* in ancient Egypt.

Acknowledgments

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Table 1.—*Synopsis of the past and present shrew fauna of Egypt.* [a]*The name* C. religiosa *is used in accordance with Corbet (1978) who selected a neotype. The application of the name* C. nana *Dobson, 1890, (type locality: Dollo, Somaliland) for this species by Heim de Balsac and Mein (1971) and Osborn and Helmy (1980) is not followed, based on an examination of the holotype of* nana *and the neotype of* religiosa *and comparisons with material from Egypt, Ethiopia, and Somalia.* C. religiosa *does not seem to occur outside Egypt.* [b]*The use of* C. olivieri *instead of* C. flavescens deltae *Heim de Balsac and Barloy, 1966, follows Corbet (1978) and Maddalena et al. (1987).* [c]C. fulvastra *has priority over* C. sericea *(Hutterer, 1984).* [d]*A recent examination of the holotype of* C. suaveolens matruhensis *Setzer, 1960, in the Field Museum of Natural History, Chicago, has shown that it bears all characters of* C. whitakeri. *The specimen constitutes the first and only record of this species from Egypt.* [e]*The species has not been collected in Egypt since 1832 (Hutterer and Tranier, 1990).*

Species	Known from Egypt		Conspecifics or Close Relatives in		
	Ancient	Present	Africa	Palearctic	Orient
Crocidura religiosa[a] (I. Geoffroy Saint-Hilaire, 1827)	x	x	x	—	—
Crocidura floweri Dollman, 1915	x	x	x	—	—
Crocidura olivieri[b] (Lesson, 1827)	x	x	x	—	—
Crocidura fulvastra[c] (Sundevall, 1843)	x	—	x	—	—
Crocidura balsamifera n. sp.	x	—	x	—	—
Crocidura whitakeri[d] de Winton, 1897	—	x	x	—	—
Suncus etruscus (Savi, 1822)	x	x	—	x	x
Suncus murinus[e] (Linnaeus, 1766)	—	(x)	—	—	x

Table 2.—*Cranial measurements of the type specimens of species assigned to the* C. dolichura *species group. Abbreviations as explained in Materials and Methods. Holotypes marked with an asterisk were measured by the author, other measurements were taken from original description. Sources: 1, American Museum of Natural History, New York (Hollister, 1916); 2, National Museum of Natural History, Washington, D.C.; 3, Muséum national d'Histoire naturelle, Paris; 4, Zoologisches Museum der Humboldt-Universität, Berlin; 5, The Natural History Museum, London; 6, Naturhistorisches Museum Basel (holotype skull lost; topotype skull measured from the Stuttgart Museum, SMNS 13413); 7, Musée Guimet d'Histoire naturelle, Lyon; 8, Centre de Paléontologie, Université Claude Bernard, Lyon; 9, unlabeled skull from Heim de Balsac's collection, now in the Muséum national d'Histoire naturelle, Paris (MNHNP 1981-1090).*

Species	CIL	UTR	PAL	GW	HCC	PGL	MB	IO	Notes, Source
C. polia	18.2	7.8	—	8.2	—	—	5.2	3.8	holotype 1
C. ludia	18.2	7.8	—	8.2	—	—	5.4	5.0	holotype 1
C. muricauda	18.4	8.1	7.8	8.1	4.9	4.8	5.0	3.8	holotype* 2
C. crenata	—	8.1	7.8	—	—	—	5.0	—	paratype* 3
C. dolichura	19.2	8.1	7.4	8.2	4.8	5.7	5.5	4.2	holotype* 4
C. niobe	19.6	8.2	7.8	9.1	5.3	6.1	6.1	4.5	holotype* 5
C. latona	19.8	8.7	—	8.9	—	—	6.1	—	holotype 1
C. maurisca	20.4	8.9	—	9.3	5.5	6.0	5.9	4.1	holotype* 5
C. roosevelti	—	8.6	8.5	8.4	—	5.7	5.9	4.6	holotype* 2
C. kivuana	20.8	9.2	—	9.6	5.9	6.2	6.6	4.8	topotype* 6
C. balsamifera	22.1	9.6	9.1	9.8	5.6	6.4	6.4	4.5	holotype* 7
C. balsamifera	—	9.9	9.8	—	—	—	6.4	4.6	paratype* 8
C. grassei	23.1	10.1	—	8.9	5.2	—	6.7	4.8	holotype?* 9

Fig. 1.—Examples of the role of shrews in ancient Egypt: Left, a small bronze dedicated to the winged god Horus; Right, transcription of hieroglyphics from the Kahun papyrus (both figures reproduced from Brunner-Traut, 1965, with permission).

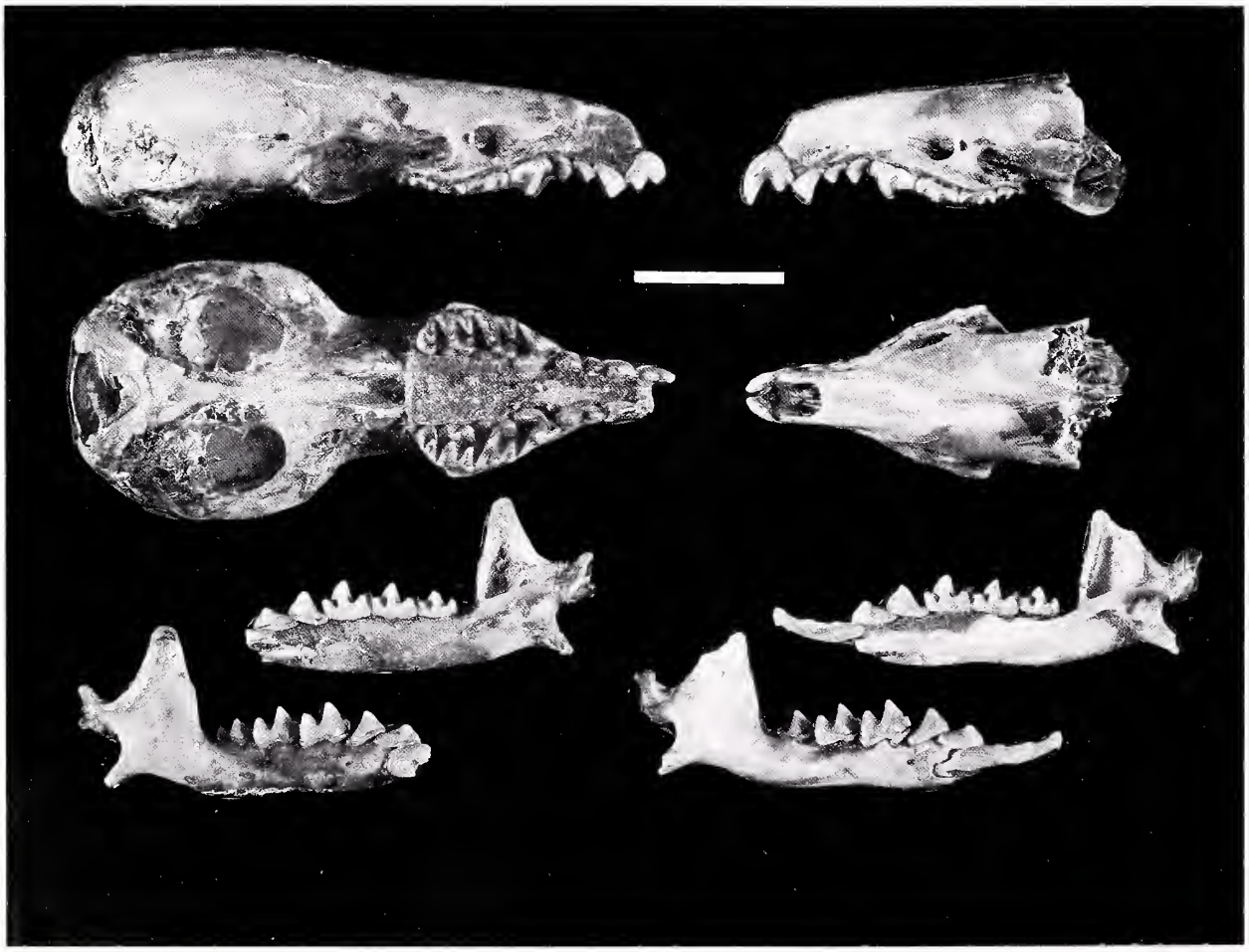

Fig. 2.—Skulls and mandibles of *Crocidura balsamifera* n. sp., holotype on left, paratype on right side of figure. Scale is 5 mm.

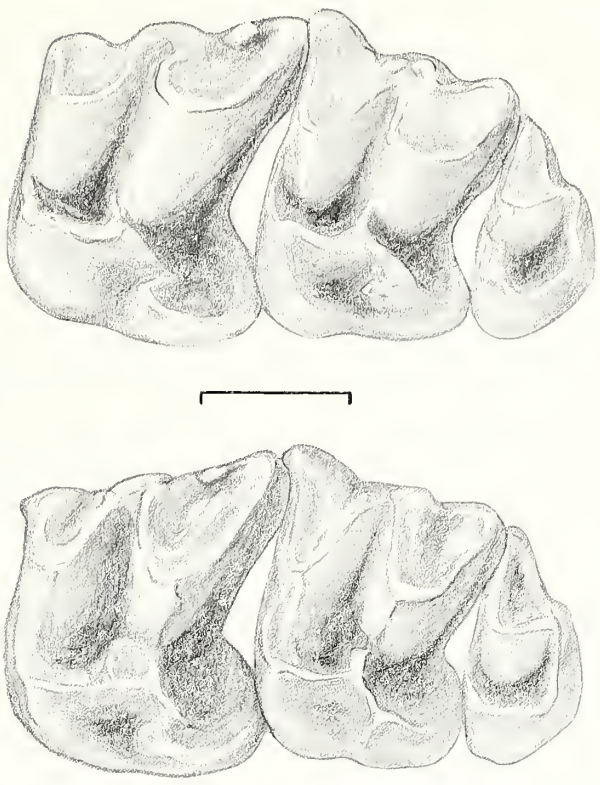

Fig. 3.—Occlusal view of M^1–M^3 of the holotype (upper figure) and paratype (below) of *Crocidura balsamifera* n. sp. Scale is 1 mm.

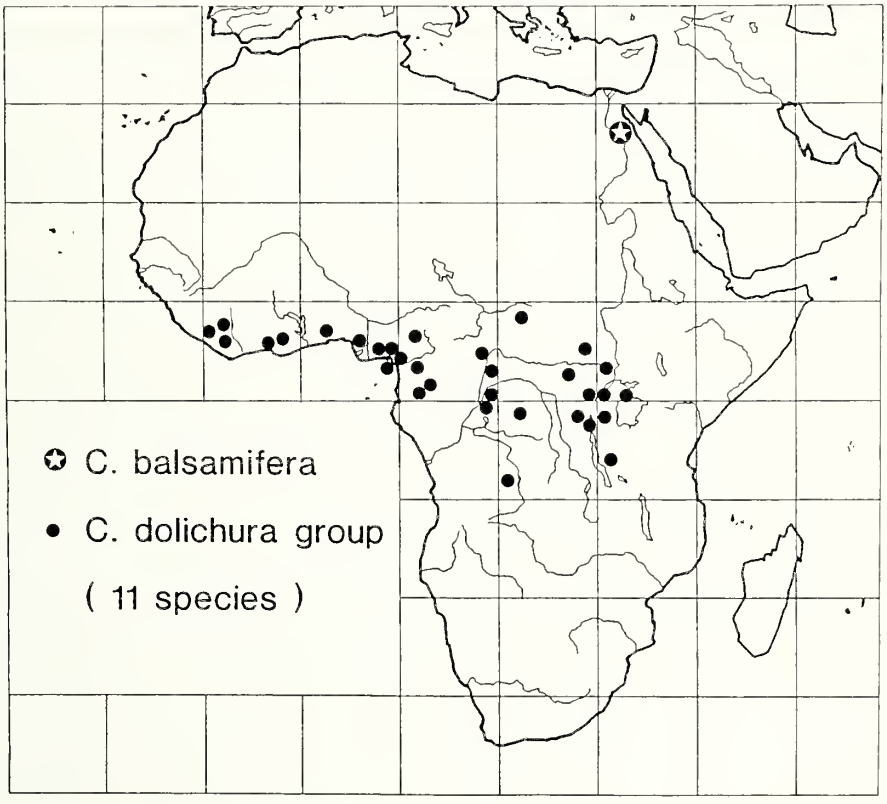

Fig. 4.—A comparison of the distribution of the *Crocidura dolichura* species group (11 species as listed in Table 2) and the new species from Egypt. Records are based on literature and author's unpublished data.

PROGESTERONE (P_4) AND ESTRADIOL (E_2) SECRETION BY *SUNCUS MURINUS* OVARIES AND ADRENALS IN VITRO

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ABSTRACT

Early studies of captive musk shrews (*Suncus murinus*) here and in Japan questioned the role of ovarian steroids in reproductive behavior and function and suggested adrenal involvement. Later studies documented "normal" plasma estradiol (E_2) concentrations and populations of uterine E_2 receptors but steroid production by explanted shrew ovaries and adrenals have not been reported. We determined relative in vitro secretions of P_4 and E_2 by these organs in both hCG-pretreated shrews and in organs supplemented with hCG in vitro. Paired whole ovaries from pretreated shrews released five times more P_4 than control ovaries but less than twice that of ovaries in medium supplemented with hCG. Ovarian E_2 output was variably elevated by hCG pretreatment. P_4 secretion by sliced adrenals was depressed by hCG in vivo and in vitro whereas E_2 output was unaffected by hCG. These results suggest that the ovary is an important source of P_4 and E_2 in this species. Perhaps the ovaries of this shrew produce other active steroids; alternatively, this shrew has poor E_2 utilization, or it uses P_4 "unconventionally."

INTRODUCTION

The hormonal functions of musk shrew (*Suncus murinus*) ovaries and adrenals are poorly understood. Especially enigmatic are concentrations of E_2 in blood and the role of this hormone in reproduction. Hasler (1973) was unable to measure serum E_2 by radioimmunoassay but more sensitive techniques indicated plasma E_2 concentrations of approximately 0.03 ng/ml in intact adult shrews (Rissman and Crews, 1988). Uteri bind tritiated E_2 (Dryden and Anderson, 1977; Keefer and Dryden, 1982) but the hormone fails to elicit the classic uterotropic response in this species (Dryden and Anderson, 1977; Rissman and Bronson, 1987). Females exhibit no behavioral estrus cyclicity (Dryden, 1969; Rissman et al., 1988). Some ovariectomized shrews copulate (Dryden and Anderson, 1977) but most do not (Rissman and Bronson, 1987). Early suggestions that the adrenal gland might supply steroids in support of sexual behavior (Dryden and Anderson, 1977) have been confirmed by adrenalectomy and ovariectomy experiments. Ovariectomy abolishes sexual behavior only slightly more than does adrenalectomy (Rissman and Bronson, 1987). Furthermore, studies by Furumura et al. (personal communication) strongly suggest adrenal and/or placental contributions of steroids toward implantation as well as pregnancy maintenance. Likewise, Rissman and Bronson (1987) suggested that adrenal-ovarian interaction drives sexual behavior and uterine development, perhaps separately or synergistically. They moreover raised the possibility that steroids other than E_2 are important modulators of reproductive functions in this species (Rissman and Bronson, 1987).

Ovaries of intact musk shrews respond to injected human chorionic gonadotropin (hCG) or luteinizing hormone (LH) by ovulating and producing morphologically normal corpora lutea (Dryden, 1985). It was therefore of interest to determine directly if secretion of sex steroids by ovaries and adrenals is under gonadotropin control. There are no published data on the secretion of E_2 or P_4 by *Suncus* ovaries and adrenals maintained in culture. This study was therefore undertaken to determine in vitro secretion of these hormones by preovulatory ovaries and by adrenals from animals treated with hCG.

MATERIALS AND METHODS

Treatment Groups

Sixteen multiparous shrews three to five months old were divided into three groups: 1) ovaries and adrenals of five shrews were controls; 2) five animals were injected with 50 IU of hCG (Sigma, Stock No. CG-2), and ten hours after injection (about five hours prior to expected time of ovulation), ovaries and adrenals were removed; 3) ovaries and adrenals were removed from six untreated animals and hCG (10 IU/culture well) was added to the culture medium in which the tissue was maintained.

Culture of Ovaries and Adrenals

All ovaries and adrenals were aseptically removed, cleaned of adjoining tissue under the stereomicroscope, and placed in culture wells, each containing 1 ml of culture medium. Culture was performed using multi-well plates (Corning) according to Fainstatt (1972).

Tissue was distributed in the following way: both ovaries and one adrenal from each shrew were placed in culture plate wells but the other adrenal was saved for perifusion. Since the diameter of shrew ovaries did not exceed 1 mm, they were cultured in toto. Adrenals were incised in the middle to facilitate penetration of culture medium in the perifusion apparatus.

Culture medium was α MEM (GIBCO) supplemented with 10% calf serum (GIBCO) and with penicillin, streptomycin, and mystatin in doses routinely used in tissue culture. Cultures were kept in a humid incubator at 37°C for 24 h in 95% O_2 atmosphere. After 24 hr in culture, media were collected and frozen for steroid analysis, and ovaries were frozen for protein assay.

Because only one adrenal from each animal was used in the tissue culture, the other adrenal from control and hCG-injected shrews was placed in a perifusion system, one per column. Tissue was perifused with α MEM for 6 hr (flow rate = 1 ml/90 min) at 37°C. Perifusion media were frozen for steroid analysis.

Radioimmunoassays were run using very specific antibodies obtained from Drs. O. D. Sherwood and G. D. Niswender. Intra-assay and interassay variations, both between 5% and 8%, were used as general averages in this study.

Steroids were measured according to the procedure previously reported by Bahr et al. (1980). Tissues were extracted with petroleum ether for progesterone (P_4) assay. Samples were extracted first for E_2 with anesthesia-grade ether. After evaporation of the ether, the residue was extracted again with a mixture of 1 ml hexane and 1 ml 75% methanol. The hexane phase was removed and the methanol evaporated. Samples were then assayed as previously described. Double extraction and antibody specificity obviated chromatographic separation for E_2 measurements. Culture media and perifusion effluents were assayed for E_2 and P_4 content according to the method of Bahr et al. (1980).

Several glands were fixed in Bouin's solution for histology. Perifusion data were analyzed by ANOVA for repeated measures using SAS program 5.16.

Results

Ovarian Morphology

Histologic appearances of follicles and interstitia of ovaries in control and treated groups conformed to previous descriptions (Dryden, 1969). Ovaries of untreated shrews contained many atretic and unenlarged follicles whereas ovaries of shrews treated with hCG underwent preluteinization hypertrophy and vascular/lymphatic distention similar to that observed in mated shrews. One ovary exposed in vitro to hCG contained an old corpus luteum unquestionably from a previous pregnancy. Interstitial hypertrophy was most extensive in ovaries of shrews pretreated with hCG and less so in those from control (uninjected) animals.

Ovarian P_4 Secretion

Control ovaries secreted 0.28 ± 0.07 ng P_4/pair/24 hr of culture. The amount of P_4 released by ovaries from hCG-injected shrews was approximately five times greater than the amount of P_4 produced by ovaries of control shrews (1.38 ± 0.10 ng/pair/24 hr; $P < 0.001$; Fig. 1). Conversely, levels of P_4 in medium containing ovaries treated with hCG in vitro were only 0.45 ± 0.05 ng. This concentration is statistically similar ($P = 0.09$) to that released from ovaries of shrews pretreated with hCG and with values for control ovaries.

Ovarian E_2 Secretion

The estradiol concentrations secreted into the culture medium by ovaries of different shrews were highly variable. Mean control E_2 secretion was 44.05 ± 20.98 pg/pair/24 hr. Ovaries from hCG-injected animals were steroidogenically more active, releasing 266.31 ± 128.12 pg/pair/24 hr. Although this output was five times greater than that of control ovaries, the difference was not significant ($P = 0.09$), presumably a function of group size and variability ($n = 5$, coefficient of variation = 107.28%, Fig. 1). Ovaries cultured in hCG-supplemented medium secreted 92.64 ± 19.99 pg E_2/pair/24 hr, which was not significantly different from control concentrations.

Adrenal Morphology

Tissue arrangements and appearances were similar between groups. Adrenals from all treatment groups were similarly compact. Cortical zonation or cellular hypertrophy did not differ. The deep zona fasciculata of all adrenals appeared steroidogenically active.

Adrenal P_4 Secretion

Each control adrenal released 57.19 ± 15.66 ng P_4/24 hr, whereas the adrenals of hCG-pretreated shrews and adrenals of shrews treated with hCG in vitro produced 38.99 ± 7.73 ng/24 hr and 45.23 ± 8.05 ng/24 hr, respectively. All values were statistically identical (Fig. 2). A similar but more pronounced "suppressing" effect of hCG on P_4 secretion was observed in perifused adrenals (control = 5.92 ± 2.40 ng/gland/24 hr; hCG-injected shrews were statistically significant by 4.5 hr ($P < 0.05$) with increased significance at 6 hr (from 5.59 ± 1.05 to 2.84 ± 0.62 ng/gland/24 hr; $P < 0.01$, Fig. 3).

Adrenal E_2 Secretion

Control adrenals released 4.35 ± 0.69 pg E_2/gland/24 hr. There was no significant difference in E_2 amounts secreted by adrenals obtained from hCG-injected shrews or by adrenals treated with hCG in vitro (Fig. 2). This lack of response by adrenals to hCG was also observed for adrenals in the perifusion system.

Discussion

Previous studies of *Suncus murinus* have shown that animals injected with hCG ovulate the same number of oocytes (Dryden and Pucek, 1976) at the same time (Singh and Dominic, 1982) as mated shrews. Ovaries of hCG-injected shrews also form corpora lutea of pseudopregnancy which are anatomically similar to those following sterile mating (Dryden, 1985). The present results extend these parallel responses to the ability of cultured ovaries to respond to hCG administered systemically or in vitro. This study also reports ovarian and adrenal P_4 and E_2 secretory responses under these two conditions.

Estradiol secretion by cultured, whole *Suncus* ovaries was extremely variable and low but could be enhanced five-fold by hCG-pretreatment of the donor shrew. Presumably more convincing enhancement of E_2 production by ovaries following pretreatment with hCG could be obtained by varying the gonadotropin dosage, time of assay after treatment, and by employing larger numbers of animals.

The weak response of shrew ovaries to hCG in vitro is puzzling. Cultured ovaries obtained from immature and mature mice secrete greater amounts of P_4 and E_2 under similar treatment (Neal and Baker, 1974; Ryle et al.,1975). In rats, the timing of hormone secretory response to ovarian receptor proliferation seems precisely timed (Szoltys, 1976, 1981; Szoltys et al, 1982; Madej, 1986). We have no such insight into the ovarian response of any shrew. Intervals of hormonal

sensitivity to stimulation may be transitory. Also, the shrew ovary in vitro may have a longer latent period than that of the mouse before becoming responsive to hCG. Clearly, more rigorous testing of *S. murinus* ovarian responses to varied hCG and treatment times needs to be done now that this species is firmly established in several research laboratories.

The role of the adrenal in the regulation of reproduction in *Suncus* is gaining support. Plasma and adrenal P_4 concentrations are significantly higher in receptive vs nonreceptive females (Hasler, 1973). Highest levels of adrenal P_4 occur in females 15 hr after copulation (Hasler and Nalbandov, 1980). Some ovariectomized shrews sustain pregnancy, mammary development, and high plasma P_4 concentrations (Furumura et al., 1983). Administered E_2 fails to enhance sexual behavior of ovariectomized females but socially interacting, intact females do experience elevated plasma P_4 levels (Rissman and Crews, 1988). These observations, along with the apparent dissociation of central and peripheral effects of steroids (Rissman and Bronson, 1987), strongly suggest adrenal involvement in the reproductive coordination of this species. This interpretation is supported by the ovariectomy/adrenalectomy manipulations of Furumura et al. (personal communication), who hypothesize the participation of both adrenals and ovaries in pregnancy maintenance. Ovariectomy followed by steroid replacement has also demonstrated that female scent-marking behavior of musk shrews, unlike that of the male musk shrew, is not gonadally controlled (Tennant et al., 1987). That study indicated the necessity of adrenal steroid support for some but not all of a female's reproductive behavioral repertoire. The brains as well as uteri of female musk shrews concentrate radiolabelled testosterone and estradiol in similar compartments; moreover, their vaginal epithelia bind higher concentrations of testosterone than of estradiol (Keefer and Dryden, 1985).

We cannot currently make much of hCG-induced "suppression" of P_4 production by perifused adrenals. They may not be responsive to hCG and physiologically deteriorate in culture, thus producing an illusory secretory depression over the time course monitored in this study.

Could the adrenals of female *Suncus* secrete testosterone under gonadotropic stimulation, as do those of marsupials (Vinson and Renfree, 1975)? Rissman et al. (1990) have shown that testosterone administered to ovariectomized *S. murinus* restores sexual behavior, also raising the issue of a possible role of androgen aromatization in female musk shrews.

The present results from unweighed cultured organs provide only hints about relative ovary and adrenal functions under endogenous gonadotropic influence in intact musk shrews. But, along with results of other studies discussed here, they certainly suggest the presence of intriguing endocrine mechanisms controlling reproduction which remain to be elucidated.

Acknowledgments

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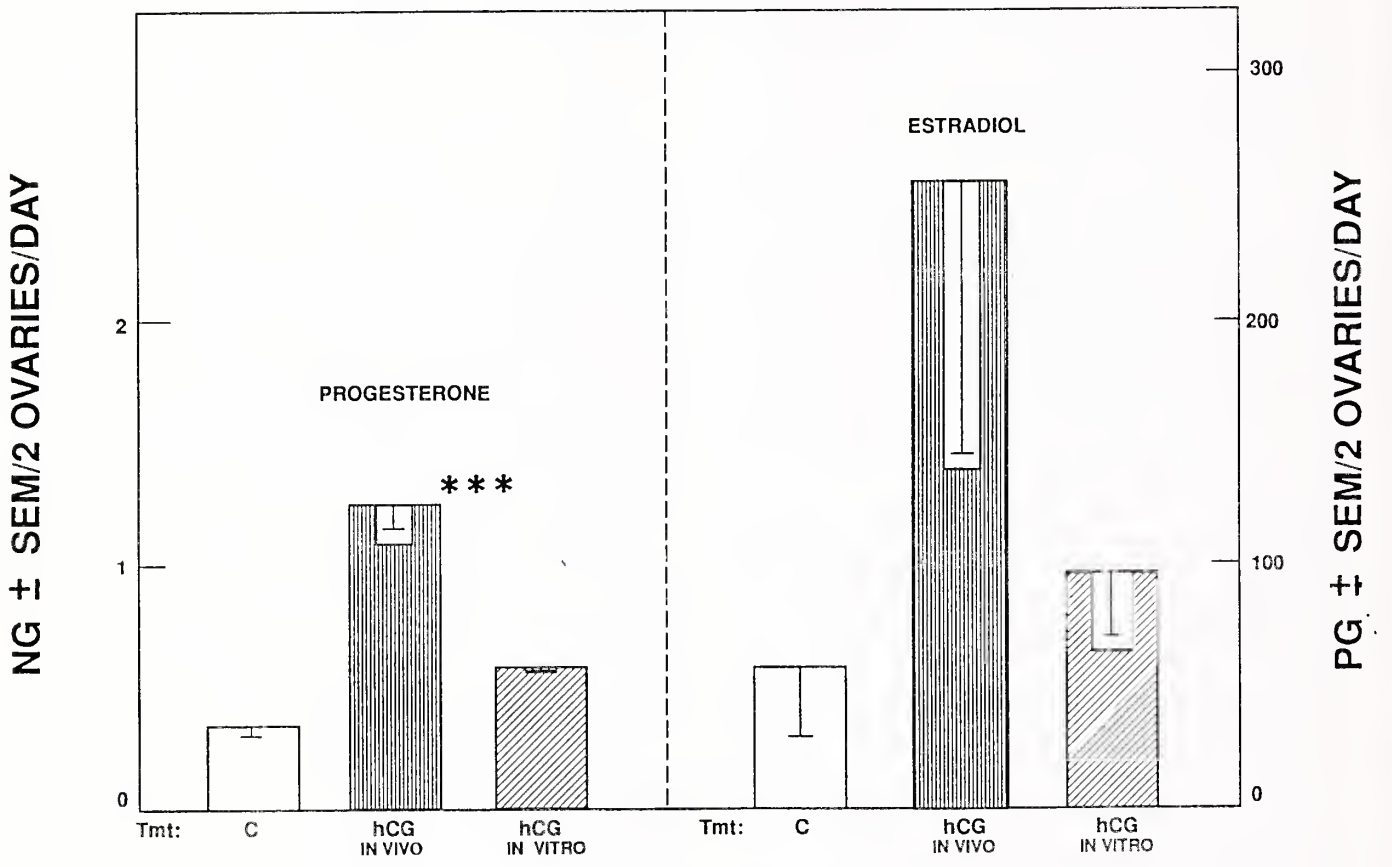

Fig. 1.—Progesterone and estradiol secretion by cultured shrew ovaries (2 ovaries/24 hr). C, control cultures: in vivo, ovaries from shrews injected with 50 IU hCG 10 hr before removal from the shrew; in vitro, 10 IU hCG/ml culture medium; ***, $P < 0.001$.

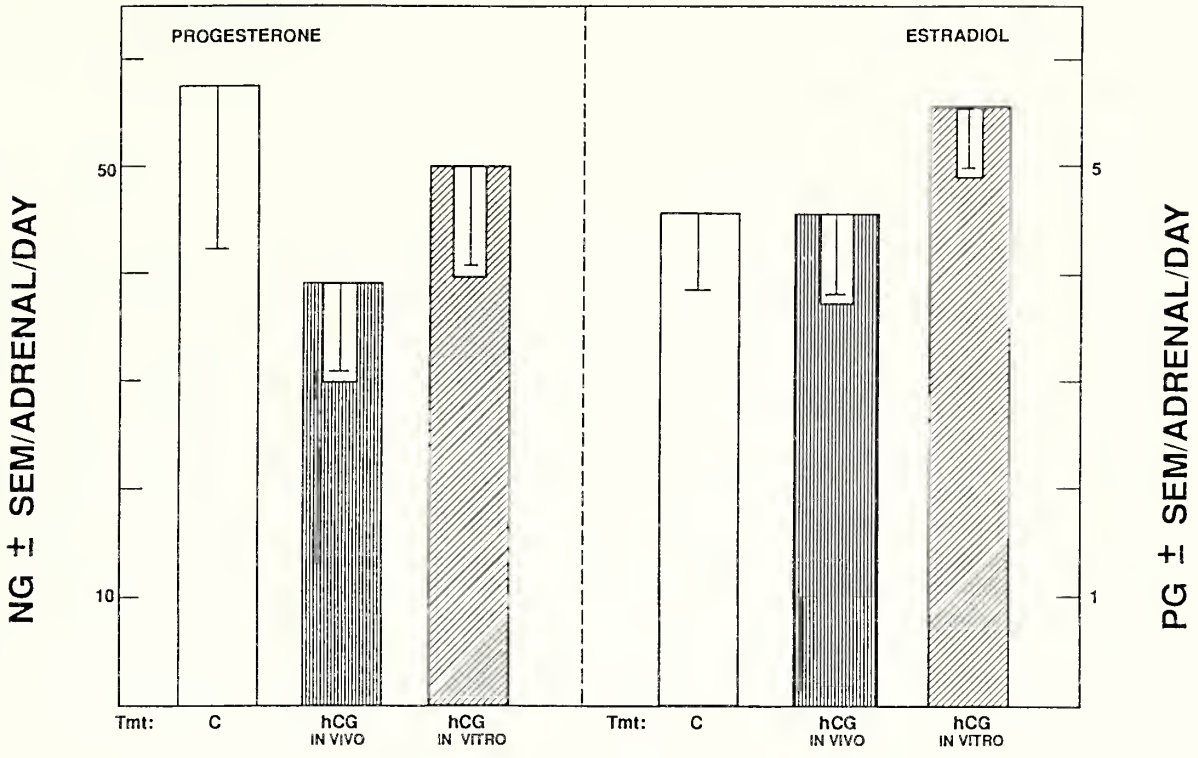

Fig. 2.—Progesterone (P_4) and estradiol (E_2) secretion by cultured shrew adrenals (1 adrenal/24 hr). Treatment groups as defined in Fig. 1. No significant differences among groups.

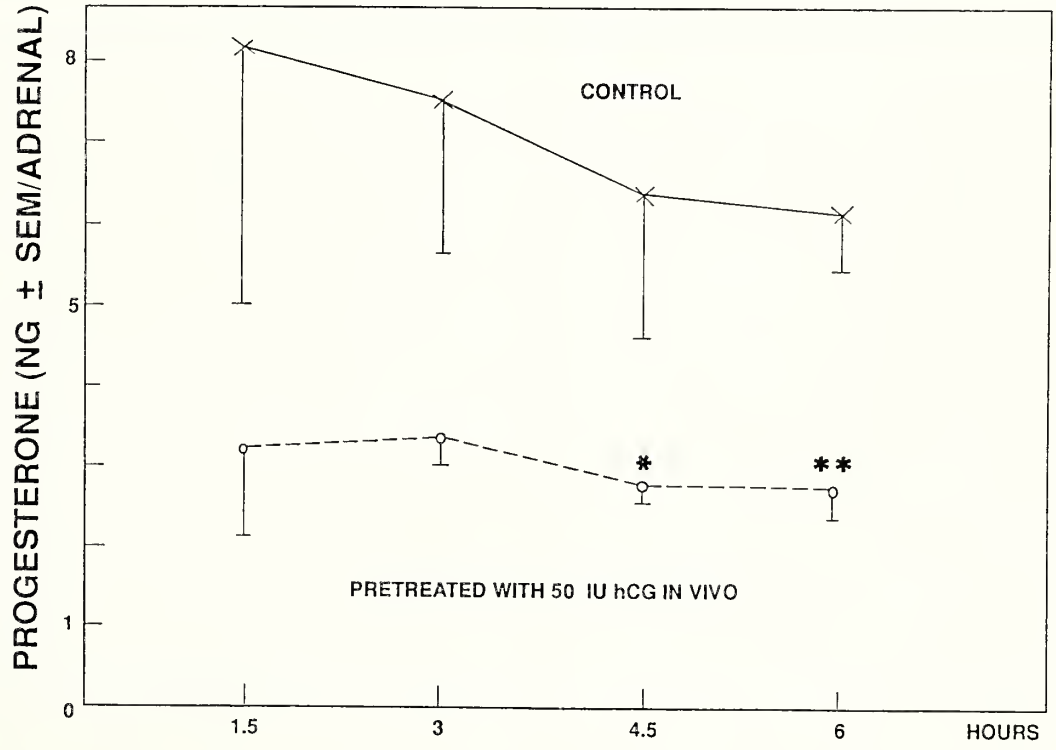

Fig. 3.—Progesterone secretion by perifused shrew adrenals; *, $P < 0.05$; **, $P < 0.01$. See text for experimental conditions.

METABOLIC RATES AND REGULATION OF CARDIAC AND RESPIRATORY FUNCTION IN EUROPEAN SHREWS

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ABSTRACT

As measures for metabolic rate, the cardiac and respiratory activity, oxygen consumption, heart rate, and respiratory rate were measured at different ambient temperatures in the white-toothed shrew *Crocidura russula* and the red-toothed shrews *Sorex araneus* and *Sorex minutus* to investigate systematic differences and thermoregulatory adaptations to specific habitats. The thermal neutral zone (TNZ) in such small mammals is very narrow and appears around 30°C in *C. russula*, but around 20°C and 25°C in *S. araneus* and *S. minutus*, respectively. Basal oxygen consumption in *C. russula* is 12% above the expected value predicted by the Kleiber curve and increases by 420% at 0°C. Basal respiratory rate increases 3.8 times, and basal heart rate to 1.7 times basal value at 0°C. Oxygen consumption per breath at 0°C is only 15% above the value in TNZ, whereas basal oxygen pulse increases to 255% at 0°C. Minimal oxygen consumption in *S. araneus* and *S. minutus* is 267% and 322% higher than predicted and increases only to 1.7 times basal value at 0°C. In both species, basal respiratory rate amounts to 435 min^{-1}. Consumed oxygen per breath amounts to 2.7 μl and 1.5 μl with an increase at 0°C of only 30% and 40% in *S. araneus* and *S. minutus*, respectively. Basal heart rates are 528 min^{-1} (*S. araneus*) and 786 min^{-1} (*S. minutus*); the values at 0°C are 20% higher. Oxygen pulse, which depends on heart mass, is 2.3 μl and 0.85 μl with an increase of up to 120% and 150% at 0°C in *S. araneus* and *S. minutus*, respectively.

The two main possibilities to deliver higher amounts of oxygen in the organism are to increase frequencies of respiration and heart activity, or to increase oxygen intake per breath and oxygen transport per heart beat. While in both *Sorex* species, the contribution of frequency regulation of respiration equals that of the volume regulation (50% each), *C. russula* shows a pure frequency regulation (95%), which is an exception among mammals. Regarding heart activity, frequency regulation accounts for only 33% and 25% of increased cardiac output in *C. russula* and *S. minutus*, respectively, whereas the volume and frequency regulation portions are almost equal (50%) in *S. araneus*.

INTRODUCTION

All small homeothermic animals show high mass-specific metabolic rates because of a disadvantageous relationship between body mass and body surface (Kleiber, 1967). In red-toothed shrews (Soricinae) especially, these metabolic rates are even higher than in other small mammals of the same body size (Pearson, 1947; Morrison, 1948; Tomasi, 1984; Nagel, 1985). In white-toothed shrews (Crocidurinae), mean body temperature is comparatively lower than in other mammals of the same size, and their metabolic rates are almost as low as in "standard" mammals (Vogel, 1976; Nagel, 1985; Mover et al., 1986). Little is known about adaptations concerning respiration or regulation of cardiac and respiratory function in shrews, information which would be required to support the elevated metabolic rates. Therefore oxygen consumption, respiratory rate, heart rate, and body temperature were investigated in the common shrew (*Sorex araneus*), the lesser shrew (*S. minutus*), and the common European white-toothed shrew *Crocidura russula* in order to investigate the physiological aspects of thermoregulation in small endotherms in general and to investigate systematic differences combined with geographic distribution and thermoregulatory adaptations to specific habitats.

MATERIALS AND METHODS

Seven specimens of *Crocidura russula* ($\bar{x}$ = 11.4 g), 11 *Sorex araneus* ($\bar{x}$ = 8.0 g), and six *Sorex minutus* ($\bar{x}$ = 3.4 g) were kept outdoors under seminatural conditions in large cages and fed alternately with commercial dog food and meal worms. Oxygen consumption ($\dot{V}_{O2}$) was measured in an open system (Servomex, type OA 184). A measurement chamber, described in Nagel (1986), was used to determine $\dot{V}_{O2}$, heart rate (HR), and respiratory rate (RR) in undisturbed shrews. The air flow through the measurement chamber was 15 L × h^{-1} (STPD). Oxygen consumption measurements lasted from one hour, at extreme ambient temperatures (Ta), to 24 hours at Ta to which the shrews were normally accustomed. The animals fasted for at least two hours before and during the experiments. The measurements were taken in a temperature-controlled cabinet regulated to ±1°C. Body temperature (Tb) was measured rectally at the end of each experiment by a calibrated electronic thermometer (Ahlborn Meß- und Regeltechnik, Therm 2245); the thermistor was inserted about 18 mm into the rectum in *C. russula* and 10 mm in *S. araneus* and *S. minutus*. Respiratory rate was measured by means of the whole body plethysmography (Drorbaugh and Fenn, 1955; Malan, 1973; Epstein and Epstein, 1978) with a micropressure transducer (Furness Controls Limited; type FC 011, measuring range ±2 millibar). To get sufficiently high signals, the air flow had to be adjusted to a pressure difference of −0.1 millibar between the inside and outside of the measurement chamber. To diminish the influences of the membrane pump, a thin capillary was inserted between measurement chamber and membrane pump. The electronic signals were registered either with a recorder (Goerz Metrawatt, type SE 120, Hewlett Packard, type 7702 B) or were analyzed with a storage oscilloscope (Tectronics, type 654). Heart rate was registered by foot electrodes (Nagel, 1986). Signals were recorded and analyzed parallel to measurements of RR with the same equipment. Oxygen consumption, RR, and HR were analyzed in normothermic shrews only, during the last 15–30 min of each experiment.

Data are presented as the mean ±SD. Statistical comparisons were made using a 2-sample Student's t-test (Bortz, 1979).

Differences were considered significant for $P < 0.05$. The theorem of Bienaymé-Tschebychev (Schaich, 1977) was used to compare basal metabolic rate with the mass-predicted value (Kleiber, 1967). The regression analysis was based on the least squares method.

Results

Body Temperature

The first parameter to determine the accuracy of temperature regulation is to measure Tb at different Ta. The range of Ta in which Tb is rather constant is the animal's state of normothermia. At lower Ta, Tb drops and the animals become hypothermic. At the upper end of normothermic Ta, Tb increases and the animals become hyperthermic. Tb at different Ta is shown in Fig. 1. The highest mean Tb at all Ta, shown by *S. minutus*, ranged from 37.6 ± 0.9°C to 37.9 ± 0.3°C at Ta of 20°C and below, but increased to 39.4 ± 0.3°C and 39.2 ± 0.2°C at 25 and 30°C, respectively. In *S. araneus*, Tb was always slightly lower than in *S. minutus* (Ta < 20°C, mean Tb = 37.2 ± 0.6–37.7 ± 0.9°C) but was also relatively constant. At Ta above 20°C in *S. minutus*, and 25°C in *S. araneus*, Tb increased to 39.2 ± 0.2°C and 38.3 ± 0.9°C, respectively. At higher Ta, the shrews were not able to relax and died within half an hour due to heat stress.

The response of Tb to changing Ta was remarkably different in *C. russula*. In the range of normothermia (Ta < 30°C), this species showed a wide variation of Tb with low mean values between 35.7 ± 1.1°C (Ta = 0°C) and 34.2 ± 0.8°C (Ta = 25°C). At Ta above 30°C, the animals lost normothermia and their Tb increased up to 37.9 ± 1.1°C (Ta = 37°C). The experiments had to be interrupted above 37°C, because *C. russula* did not relax and no values during rest could be measured. In no single case could Tb be regulated below Ta. Nevertheless, *C. russula* tolerated higher Ta than *S. araneus* and *S. minutus*.

Oxygen Consumption

The energetic expenditure of temperature regulation in normothermic animals is expressed by oxygen consumption (Fig. 2) at different Ta compared to the basal values. Because of the small size of *S. minutus*, its $\dot{V}_{O_2}$ was very high. The range of Ta in which $\dot{V}_{O_2}$ was lowest is denoted as the thermal neutral zone (TNZ) which appeared around 20°C in *S. araneus* and 25°C in *S. minutus*. The thermal neutral zone could not be determined more precisely because all measurements were made in 5°C Ta intervals. Ambient temperatures below and above TNZ at which $\dot{V}_{O_2}$ is increased is the lower critical temperature (Tlc) or the upper critical temperature (Tuc), respectively. The basal $\dot{V}_{O_2}$ in *S. minutus*, 12.0 ± 2.2 ml $O_2 \times g^{-1} \times h^{-1}$ was 3.2 times higher than predicted (Kleiber, 1967); (log M = 1.87 + 0.739 log W ± 0.03, M = basal metabolism [kcal × day^{-1}], W = body mass [kg], 1 ml O_2 = 4.8 cal). Oxygen consumption increased at Ta below 25°C. This increase can be described by the calculated regression equation: $\dot{V}_{O_2}$ [ml × g^{-1} × h^{-1}] = −0.288 × Ta + 19.6, n = 42, r = −0.635. The slope of this regression line is handled as the minimal thermal conductance. It was −0.288 ml $O_2 \times g^{-1} \times h^{-1} \times °C^{-1}$. The actual value lies 48% below the mass-predicted value (Herreid and Kessel, 1967).

Minimal $\dot{V}_{O_2}$ in *S. araneus* was 8.3 ± 1.6 ml $O_2 \times g^{-1} \times h^{-1}$ at 20°C. As in *S. minutus*, this value is 267% higher than the mass-predicted value. Oxygen consumption increased with decreasing Ta following the equation: $\dot{V}_{O_2}$ [ml × g^{-1} × h^{-1}] = −0.302 × Ta + 14.7, n = 128, r = −0.677. Minimal thermal conductance in *S. araneus*, −0.302 ml × g^{-1} × h^{-1} × $°C^{-1}$, was 15% below the predicted value. At 0°C the temperature-regulating response of $\dot{V}_{O_2}$ was 1.7 times the basal value in both *Sorex* species.

In normothermic *C. russula*, mean $\dot{V}_{O_2}$ at different Ta was lowest at 30°C. The mean value of basal $\dot{V}_{O_2}$, 2.32 ± 0.42 ml × g^{-1} × h^{-1}, was only 12% above the expected value and did not differ significantly from it. In spite of the relatively low Tb in the TNZ (Tb = 35.4 ± 0.7°C, Fig. 1), $\dot{V}_{O_2}$ was still higher than in other mammals of the same size. Below Ta of 30°C, $\dot{V}_{O_2}$ increased steadily to 9.76 ± 1.55 ml × g^{-1} × h^{-1} at the Ta of 0°C, which is 4.2 times higher than in TNZ. The temperature-dependent increase of $\dot{V}_{O_2}$ is described by the linear equation: $\dot{V}_{O_2}$ [ml × g^{-1} × h^{-1}] = −0.253 × Ta + 9.49, n = 108, r = −0.893. Thermal conductance (0.298 ml × g^{-1} × h^{-1} × $°C^{-1}$ was about 15% lower than the expected value.

In normothermic and torpid *C. russula*, $\dot{V}_{O_2}$ strongly depends on the level of regulated Tb which is shown in Fig. 3. At a Tb of 18°C (Ta = 15°C), $\dot{V}_{O_2}$ is even lower than 1 ml × g^{-1} × h^{-1}. At higher Tb $\dot{V}_{O_2}$ increases steadily with increasing Tb to a value of 7.5 ml × g^{-1} × h^{-1} at a Tb of 37°C. At high Tb, $\dot{V}_{O_2}$ in *C. russula* is almost as high as in *S. araneus* with the same Tb. Hence, the main difference in $\dot{V}_{O_2}$ between the species was the different level of regulated Tb. The remaining differences in $\dot{V}_{O_2}$ can be explained by the smaller body mass of *S. araneus*.

Respiratory Rate

Mean respiratory rate (RR) in relation to Ta was similar in *S. minutus* and *S. araneus* (Fig. 4). Basal RR was also almost identical (437 ± 86 min^{-1} in *S. minutus* and 433 ± 81 min^{-1} in *S. araneus*) and were 86% and 130% above the mass-predicted value (Stahl, 1967). At 0°C, RR increased due to the increased $\dot{V}_{O_2}$ to 598 ± 113 min^{-1} and to 557 ± 103 min^{-1} which were 1.4 and 1.3 times the basal values, in *S. araneus* and *S. minutus*, respectively. Respiratory rate remained nearly constant at Ta above the upper critical Ta. The mean basal value of RR in *C. russula* was much lower (40% below the mass-predicted value) than for both *Sorex* species and amounted to only 103 ± 19.8 min^{-1} within the TNZ. By Tb of 0°C, RR had increased to 393 ± 80.1 min^{-1}, which was a 3.8-fold increase over the basal value. This increase corresponds approximately to the 4.2-fold increase in $\dot{V}_{O_2}$. In contrast to *S. araneus* and *S. minutus*, RR in *C. russula* increased at Ta above the upper critical temperature. Highest respiratory rates could be found during sniffing. For short periods values of 800 min^{-1} could be reached.

Oxygen Consumed per Breath

The calculated amount of oxygen per breath, treated as the amount of oxygen absorption per breath, is the main parameter of the depth of breathing. Because of the different size of the shrews, which limits respiratory volume, the calculated oxygen consumed per breath was different among the species (Fig. 5). The basal value was 1.5 ± 0.1 μl in *S. minutus*, and 2.7 ± 0.5 μl in *S. araneus*. At 0°C, oxygen consumed per breath was elevated to 2.0 ± 0.5 μl and 3.4 ± 0.7 μl, which is a 1.3-fold increase in basal value for both species. Due to the constant RR at Ta above the upper critical Ta (Tuc), alterations in oxygen consumed per breath were negligible. In *C. russula*, volumes of oxygen consumed per breath increased from a mean of 4.3 ± 0.7 μl (Ta = 30°C) to 4.9 ± 0.5 μl (Ta = 0°C) which was only 15% above the value in TNZ. Above Tuc the volume of oxygen consumed per breath decreased slightly to a mean of 4.1 ± 1.1 (Ta = 35°C) and 3.8 ± 1.0 μl (Ta = 37°C).

The two main possibilities to satisfy higher oxygen demands in the body are: 1) to increase frequency of respiration, or (2) to increase oxygen intake per breath. In both *Sorex* species, frequency regulation accounted for 52% and volume regulation for 48% of the increase in respiratory performance calculated according to Bartholomew and Tucker (1963). In contrast, *C. russula* showed a pure frequency regulation (95%).

Heart Rate

High metabolic rates in shrews should be combined with high heart rate (HR) to guarantee the supply of oxygen to the body. In fact, HR was lower than expected (Fig. 6). Basal HR in *S. minutus* was lowest at Ta of 15°C whereas the lower critical Ta (Tlc) was near 25°C; it amounted to 774 ± 22 min^{-1} and was only 29% above the expected value (600 min^{-1}, Wang and Hudson, 1971). Heart rate was raised to 922 ± 105 min^{-1} at 0°C.

In *S. araneus*, minimal heart rate (528 ± 55 min^{-1}) occurred in the TNZ and was only 9% above the expected value. It increased to only 638 ± 119 min^{-1} at 0°C. In both *Sorex* species, HR increased 1.2 times the basal value at Ta of 0°C.

In *C. russula*, mean basal HR was 444 ± 37 min^{-1} at Ta of 30°C. This value corresponds exactly to the expected value. Lowering Ta to 0°C led to an increase of HR to 779 ± 108 min^{-1}. The relative increase of HR in *C. russula* was 75%.

Corresponding to $\dot{V}_{O_2}$, heart rate of *C. russula* also depends on the Tb (Fig. 7) of the animal. At a Ta of 15°C, the lowest measured heart rate during torpor (Tb = 18°C) was 81 min^{-1}. At higher Tb, heart rate increased to about 700 min^{-1} at a Tb of 36°C.

Oxygen Pulse

The calculated $\dot{V}_{O_2}$ per heart beat, the oxygen pulse, is given in Fig. 8. In *S. minutus*, basal oxygen pulse was 0.85 ± 0.1 μl. It increased to 1.3 ± 0.3 μl at 0°C, which is 50% higher than the basal value. In *S. araneus*, basal oxygen pulse amounts to 2.3 ± 0.5 μl. The increase at 0°C was to 2.8 ± 0.5 μl, or 1.2 times the basal value. In *C. russula*, the basal value was 0.98 ± 0.2 μl; oxygen pulse increased with increasing $\dot{V}_{O_2}$ (Ta = 0°C) about 255% to a mean value of 2.5 ± 0.4 μl. Above Tuc oxygen pulse increased to 1.3 ± 0.2 μl (Ta = 37°C) in *C. russula*, yet it remained almost constant in *S. minutus* and *S. araneus*.

In contrast to $\dot{V}_{O_2}$ and HR, oxygen pulse does not depend on Tb during torpor or normothermia in *C. russula* (Fig. 9); most of the values lie between 1–2 μl at Tb of 18–37°C.

In all cases, oxygen pulse of *S. araneus* was higher than the corresponding values of *C. russula* although heart mass and HR were lower and $\dot{V}_{O_2}$ higher than in the white-toothed shrew. This effect can be explained by a higher mass-specific oxygen-transporting capacity of the heart of *S. araneus* (Table 1), which generally was higher in the red-toothed shrews. Only at Ta of 0°C did *C. russula* have a higher value than *S. minutus*, which is three times smaller and has only half the heart mass.

The frequency regulation portion accounted for 33% and 25% of heart activity in *C. russula* and *S. minutus*, respectively, using the formula of Bartholomew and Tucker (1963). In *S. araneus*, the volume and frequency regulation portions were almost identical (51% and 49%, respectively).

Discussion

Body Temperature

The present investigation has shown that *C. russula* had a lower and less constant mean Tb than *S. araneus* and *S. minutus* (Fig. 1). Low Tb, also known in *Crocidura leucodon*, *Crocidura suaveolens*, *Suncus etruscus* (Nagel, 1977, 1985; Frey, 1979; Mover et al., 1986), and *Suncus murinus* (Balakrishnan et al., 1974; Hasler and Nalbandov, 1974), thus seems typical for white-toothed shrews in general. In contrast, *S. minutus* and *S. araneus* had high and constant Tb, also confirmed by Gebczynski (1977) and Sparti and Genoud (1989), in *Neomys fodiens* (Nagel, 1985), in *Sorex coronatus* (Sparti and Genoud, 1989), in *Blarina brevicauda* (Doremus, 1965; Platt, 1974; Merritt, 1986), in *Cryptotis parva* (Layne and Redmond, 1959), and in *Sorex cinereus* (Morrison et al., 1959). Above Tuc no real regulation of Tb took place; Tb fluctuated only with Ta. Comparing the species, the minimal difference between Ta and Tb depends on basal metabolic rate and is a sign for heat tolerance. The smaller this difference, the greater is the heat tolerance of the animal. Thus red-toothed shrews (Soricinae) show symptoms of severe heat stress even at a Ta of 30°C, a Ta at which *C. russula* is in thermoneutrality. The Soricinae are, like other small mammals with high Tb, typically adapted to a cold environment, a result also confirmed by Irving (1972) but not by Scholander et al. (1950), Precht et al. (1955), and Cossin and Bowler (1987). Thus, the regulation of high Tb obviously is no adaptation to high Ta, but the tolerance of a high Tb without regulatory response on it is favorable to endure high Ta.

There is no doubt that white-toothed shrews (Crocidurinae) have a more flexible temperature regulation, particularly due to their ability to enter torpor either spontaneously (Frey and Vogel, 1979; Genoud, 1985) or during periods of starvation (Wahlström, 1929; Kusnetzov, 1972; Vogel, 1974; Nagel,

1977, 1985; Frey, 1979). During torpor, Tb can drop passively to 18°C (Nagel, 1985). This low Tb in torpor always was higher than Ta (range 26–18°C), but does not depend otherwise on Ta; the shrews do not react as poikilotherms do. There are no obvious explanations about the level of Tb in torpor, but shrews regulate the certain Tb in torpor very well by alterations of $\dot{V}_{O2}$. The arousal from torpor, which takes place spontaneously or after a gentle disturbance of the animal, is followed by an increase in Tb at the rate of 0.5–0.9°C × min^{-1} (Nagel, 1985). Even during severe food deprivation (Martinsen, 1969; Gebczynski, 1971*a*), red-toothed shrews are not capable of torpor. Lindstedt (1980*a*), however, observed shallow hypothermia in the red-toothed shrew *Notiosorex crawfordi*, a desert-dwelling shrew from the southwestern USA. White-toothed shrews develop torpor by the fourth day of life (Nagel, 1989), when the young are still blind and naked. In young shrews torpor is only expressed if the animals are able to form groups of at least two animals. In field studies Vogel et al. (1984) observed groups of nesting *C. russula* only during winter, when food supply was reduced. Perhaps these animals formed "torpor groups" as described in the marsupial *Sminthopis crassicaudata* and the house mouse *Mus musculus* (Morton, 1978).

Oxygen Consumption

Both *Sorex* species in this study had high basal metabolic rates which were approximately 100% above the expected value (Kleiber, 1967). In white-toothed shrews, however, the relationship of metabolic rate to body mass corresponds approximately to the Kleiber curve. The exceedingly high basal metabolic rates in several species of Soricinae have been reported by many investigators (Morrison and Pearson, 1946; Pearson, 1947, 1948; Morrison, 1948; Morrison et al., 1952, 1953, 1959; Hawkins et al., 1960; Pfeiffer and Gass, 1962; Buckner, 1964; Doremus, 1965; Gebczynska and Gebzynski, 1965; Gebczynski, 1965, 1971*a*, 1971*b*; Martinsen, 1969; Neal and Lustick, 1974; Platt, 1974; Vogel, 1976; Lindstedt, 1980*b*; Tomasi, 1984). In contrast, the basal metabolic rate of *C. russula* was only a few percent higher than the expected Kleiber value, which is typical for all European Crocidurinae (Fons and Sicart, 1976; Vogel, 1976; Nagel, 1977, 1985; Frey, 1979) as well as for *Suncus murinus* (Dryden et al., 1974), *Crocidura occidentalis* (Hildwein, 1972) and *Crocidura russula monacha* (Mover et al., 1986). Although mean Tb was comparatively low in white-toothed shrews, basal metabolic rate was higher than the predicted value in all cases. The influence of regulated Tb on metabolic rate (Fig. 3) is expressed by a very strong correlation between $\dot{V}_{O2}$ and Tb in *C. russula*. The values are compared with the corresponding values in *S. araneus* at a Ta below Tlc of both species (Ta = 15°C). The main conclusion is: An individual of *C. russula* at a given high Tb has the same $\dot{V}_{O2}$ as an individual of *S. araneus* with the same Tb. Consequently, below Tlc in both species, differences in mean Tb are the principle explanation for the differences between both species. The role of lowered Tb and of actually lowered metabolic rate on the differences between *C. russula* and *S. araneus* is explained by Fig. 10, which shows that the role of different Tb is greater than that of actual different basal metabolic rates. Comparing the actual values of the Crocidurinae and Soricinae (Fig. 11) with those expected from the Kleiber curve, basal metabolic rates of the Soricinae seem to lose the dependence on body mass, whereas the Crocidurinae have reconfirmed Kleiber's correlation of basal metabolic rate and body mass by the loss of a constant and high Tb.

At low ambient temperatures (Ta = 0°C), $\dot{V}_{O2}$ in *C. russula* increased to a value 4.2 times the value at TNZ (Fig. 2). Because a similar increase in $\dot{V}_{O2}$ can be found in all other European Crocidurinae (Nagel, 1985), these white-toothed shrews must be regarded as adapted to high Ta. In contrast, $\dot{V}_{O2}$ in *S. minutus* and *S. araneus* increased only to 1.5 times the basal value. This relatively small response is a result of the high basal metabolic rate which has been interpreted as an adaptation to cold climatic conditions (Scholander et al., 1950; Irving, 1972; Weathers, 1979).

The slope of increasing $\dot{V}_{O2}$ at decreasing Ta (thermal conductance; Fig. 2) shows the supplementary $\dot{V}_{O2=}$ needed to maintain constant Tb at Ta below Tlc by an increase in heat production. This temperature-regulatory reaction of metabolism shows the total effect of Ta on $\dot{V}_{O2}$ of a homeothermic animal, neglecting the relationship to several parameters on which it depends. Thermal conductance, which depends on insulation, heat production, heat loss, and body temperature, shows a very similar pattern in all three species, varying between 0.288 ml $O_2 \times g^{-1} \times h^{-1} \times °C^{-1}$ (*S. minutus*), 0.302 ml $O_2 \times g^{-1} \times h^{-1} \times °C^{-1}$ (*S. araneus*), and 0.298 ml $O_2 \times g^{-1} \times h^{-1} \times °C^{-1}$ (*C. russula*). These values are about 15% in *S. araneus* and *C. russula* and in *S. minutus* about 48% below their mass-predicted values (Herreid and Kessel, 1967). There is no real difference in the reaction to cold between *S. araneus* and *C. russula* in spite of different levels of Tb and of different basal metabolic rates. In contrast, in other shrew species, thermal conductance depends indirectly on body mass (Nagel, 1977, 1985). The Tb correction of thermal conductance (Bradley and Deavers, 1980; McNab, 1980) leads to a more differentiated result of 0.21 ml $O_2 \times g^{-1} \times h^{-1} \times x\ °C^{-1}$ in *C. russula* and 0.17 ml $O_2 \times g^{-1} \times h^{-1} \times °C^{-1}$ in *S. araneus*, respectively. The lower thermal conductance in *S. araneus* can be explained by a better insulation, due to longer hair and a thicker fur. Nevertheless, the real effect of low Ta was the same in the two almost equal-sized species *S. araneus* and *C. russula*.

Respiratory Rate

Corresponding to their high metabolic rates, mean basal respiratory rate (RR) in *S. minutus* and *S. araneus* are also very high, at 86% and 130% respectively above the mass-predicted value (Stahl, 1967). In contrast, mean basal RR is 40% below the predicted value in *C. russula*. The two main possibilities to satisfy higher oxygen demands in the body are to increase frequency of respiration or to increase oxygen intake per breath. At low Ta in both Soricinae, RR and consumed oxygen per breath increased in the same way and the regulation of oxygen absorption was achieved not only by alteration of RR but also by changing tidal volume or oxygen extraction rate, or both. In both *Sorex* species, frequency regulation accounted for 52% and

volume regulation for 44% of increase in respiratory performance (Bartholomew and Tucker, 1963). This form of regulation is typical for most mammals and birds (Casey et al., 1979; Withers et al., 1979; Müller and Rost, 1983; Blake and Banchero, 1985; Müller, 1985; Prinzinger, 1988). In *C. russula*, $\dot{V}_{O2}$ is frequency regulated. Because of the small changes in volume of oxygen consumed per breath and the almost identical increase of $\dot{V}_{O2}$ (4.2-fold) and RR (3.8-fold) in *C. russula*, it can be assumed that respiratory depth and oxygen extraction rate are nearly constant. This statement must be preliminary, because no suitable methods are available to do these measurements in such small mammals. A similar situation was also found in the North American white-footed mice (Withers, 1977; Chappel, 1985), in hummingbirds (Prinzinger and Schuchmann, 1985; Prinzinger and Jackel, 1986) and even in the bat *Leptonycteris sanborni* (Carpenter and Graham, 1967), and seems to be typical for small animals with high metabolic rates and high RR. At Ta above Tuc, high Tb leads to a decrease of consumed oxygen per breath. It is assumed that respiration becomes more and more shallow, possibly due to increasing rates of evaporative heat loss. Real panting with very low volumes of consumed oxygen per breath was not observed, either in *C. russula* or in the *Sorex* species, although it is developed in birds of similar size (Prinzinger and Schuchmann, 1985; Prinzinger and Jackel, 1986). Heat dissipation by evaporation of water would probably be insufficient in this species, because normally no free water is available in the habitat of *C. russula*.

Heart Rate

Basal heart rate (HR) in both *Sorex* species is only 10–30% higher than predicted, whereas it corresponds exactly to the mass specific value in *C. russula* (Wang and Hudson, 1971), ($HR = 816 \times W^{-0.25}$, W = body mass [g]), (Fig. 12). Compared with the formula reported by Stahl and Gummerson (1967), ($HR = 241 \times W^{-0.25}$, W = body mass [kg]), basal HR is 26–62% lower. All data of basal HR in nonshrew mammals, for example of *Mus minutoides* (Goethel and Nagel, 1990) studied in my laboratory are much lower than the predicted value calculated after Stahl and Gummerson (1967) but fit quite well to the formula of Wang and Hudson (1971). In my opinion, the formula of Stahl and Gummerson (1967) is not suitable for mammalian allometry, especially at small body mass, and therefore is not considered further here. Dryden et al. (1971) reported a HR of 563–604 min^{-1} and Balakrishnan et al. (1974) a mean HR of 550 min^{-1} in the relatively large *Suncus murinus*. Heart rate is about 750 min^{-1} in the North American species *Blarina brevicauda* (Doremus, 1965), and it ranges from 600 min^{-1} in the masked shrew *Sorex cinereus* (Morrison et al., 1959). Weibel et al. (1971) and Bartels et al. (1979) investigated the smallest known mammal, *Suncus etruscus*, and found HR of 1000 min^{-1} and 700–1400 min^{-1} respectively. A comparison of the data from these investigations with the mass-expected and the reported values leads to the conclusion that the reported results are much too high and artificially distorted due to inappropriate methods. Measurement of HR by foot electrodes (Nagel, 1986) is an efficient and, therefore, favorable method for measuring heart frequency during rest, because the animals are not disturbed by handling and the results are not influenced by narcosis or other factors. The relatively low HR compared both to metabolic rates and to mass-predicted values in shrews can be explained by a particularly large heart (Stahl, 1965), which involves greater stroke volumes combined with a greater oxygen transport per heart beat. In European shrews, relative heart mass is 70–110% higher than in other small mammals (Bartels et al., 1979; Nagel, 1980, 1985), and must be regarded as a general adaptation to their high metabolic rates. Due to this adaptation, heart rate values that were 25–33% below the expected value (Nagel, 1980, 1985, 1991) are capable of delivering the oxygen to sustain their high metabolic rates.

Another adaptation to high metabolic rates is the reduction in body mass, called Dehnel's phenomenon (Buchalczyk, 1961; Mezhzerin, 1964; Pucek, 1965, 1970; Hyvärinen, 1969). Only heart mass remains constant and leads to a higher relative heart mass, probably to avoid too high HR during the strong metabolic efforts during winter. *S. araneus* reduces its body size during winter, but Dehnel's phenomenon could not be found in any white-toothed shrew.

The relative increase of HR in *S. minutus* and *S. araneus* was only 20% whereas that of *C. russula* was 75%. Compared with $\dot{V}_{O2}$, HR increased only moderately in all three species; the increased oxygen demands in tissues at lower Ta can be satisfied mainly by an increase in the transported oxygen amount per heart beat or an increase of the oxygen utilization in the blood. The amount of transported oxygen per heart beat cannot be estimated, but the effectively used amount of oxygen per heart beat can be calculated as $\dot{V}_{O2}$ per heart beat, i.e., as the oxygen pulse.

In comparison with the pure frequency-dependent regulation of ventilation in *C. russula* for regulation of heart function, frequency regulation as well as volume regulation were pronounced in all three species. In heart function regulation, the regulatory role of oxygen pulse was two times higher than heart frequency in *S. minutus* and *C. russula* (Bartholomew and Tucker, 1963). Only in *S. araneus* were frequency regulation and volume regulation equivalent.

Heart rate of the Crocidurinae during torpor depends very strongly on the Tb of the animal (Fig. 7). The lowest measured value was 60 min^{-1} in *Crocidura leucodon* (Tb = 18°C, Nagel, 1980). In spite of strong decreases in heart rate and $\dot{V}_{O2}$, oxygen pulse remains constant at a certain ambient temperature (Fig. 9; Nagel, 1980), which points out that torpor is a well-regulated state, because heart excitability depends on Tb (Nagel, 1986) and probably also on the contraction of the heart, but not $\dot{V}_{O2}$ per heart beat. Oxygen pulse itself can be influenced only by alterations in ambient temperature.

In spite of this strong increase of oxygen pulse, in no single case did mean values reach those in *S. araneus*, a species which is considerably smaller. This is astonishing because *C. russula* had a higher HR than *S. araneus* (Ta = 0°C) in spite of its greater body mass, lower Tb, lower metabolic rate, and lower basal HR. The mass-specific effect of oxygen transport per heart beat was considerably higher in *S. araneus* than for the

other two species (Table 2). No explanation for this fact can be given because no differences in the blood parameters are known between the species (Bartels et al., 1969; Wolk, 1974). Perhaps differences in arteriovenous oxygen levels, in the structure of the heart or heart activity regulation must be taken into account.

Conclusions

Comparing the distribution of the Soricinae and the Crocidurinae in the Old World, the red-toothed shrews are found from the temperate zone, to the subarctic and arctic regions. In contrast, the Crocidurinae are found in the tropical and subtropical regions, with few species in the cooler temperate zones. Their comparable low $\dot{V}_{O2}$ and low Tb, combined with a great tolerance to high Ta, point to their tropical origin (Table 2). As a group, the Crocidurinae have a good tolerance against heat, their TNZ is high (approximately 30°C) and their average basal metabolic rate is much lower than in the Soricinae. The stable climatic conditions of the warm regions, especially in the tropics, favor this economical energy budget. Several small and middle-sized subtropical and tropical mammals, such as rodents, insectivores, and primates, show the same adaptations in temperature regulation (Hildwein, 1972; Müller, 1975, 1979; Müller and Kulzer, 1977). The Crocidurinae have adopted another strategy, entering torpor, which also serves to save energy, especially in response to lack of food. However, torpor occurs at Ta between 10–25°C and cannot be equated with hibernation. The northern boundary of their distribution shows that, in spite of the ability to enter torpor, the Crocidurinae are not adapted to the climatic conditions of subarctic and arctic regions.

Red-toothed shrews have adapted a completely different strategy. Their well-regulated Tb, low TNZ and high basal metabolic rates enable them to endure the lowest temperature conditions, comparable to lemmings (Hart and Heroux, 1955), snow voles (Bienkowski and Marszalek, 1974), and weasels (Iversen, 1972; Casey and Casey, 1979).

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Table 1.—*Oxygen pulse (µl) per 100 mg heart mass in* S. minutus, S. araneus, *and* C. russula, *determined by actual values of oxygen pulse and of mean values of heart mass in the different species.* S. minutus *(46.6 ± 4.4 mg,* n = *3);* S. araneus *(72.2 ± 14.3 mg,* n = *17);)* C. russula *(89.0 ± 19.6 mg,* n = *20).*

Species	Ambient Temperature (°C)								
	0	5	10	15	20	25	30	35	37
S. minutus	2.55	2.75	2.34	2.45	2.49	2.27	2.14		
S. araneus	3.88	3.72	3.54	3.32	3.13	3.09	3.05		
C. russula	2.82	2.47	1.90	1.74	1.59	1.29	1.10	1.42	1.46

Table 2.—*Comparison of physiological features in* S. araneus *and in* Crocidura russula *as typical representatives of the subfamily Soricinae and Crocidurinae, respectively, in comparison to "standard" mammals.*

	Species	
	Sorex araneus	*Crocidura russula*
Body temperature	standard	low
Basal oxygen consumption	very high	standard
Metabolic adaptation	heat production	torpor
Respiratory rate	very high	low
Heart rate	standard	standard
Ecological adaptation	to cold	to heat
Distribution	temperate, subarctic, and arctic zone	temperate, subtropical, and tropical zone

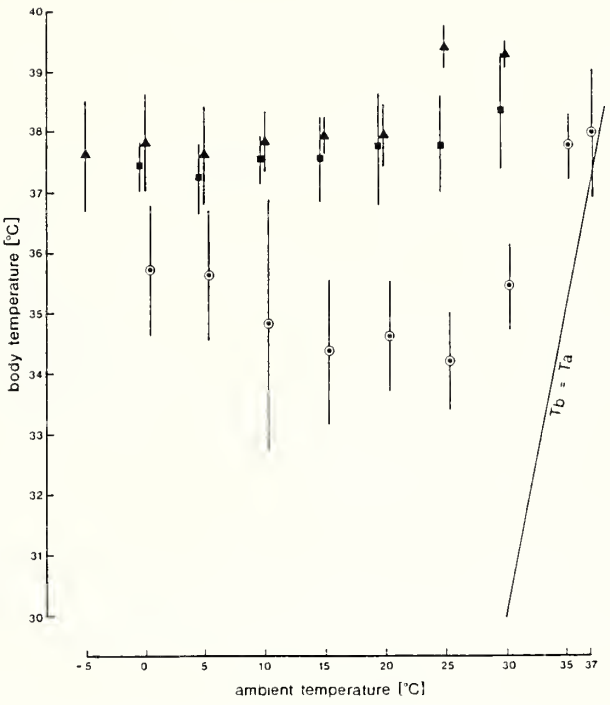

Fig. 1.—Mean body temperature (±SD) at different ambient temperatures in *Sorex minutus* (triangle), *Sorex araneus* (square), and *Crocidura russula* (circle).

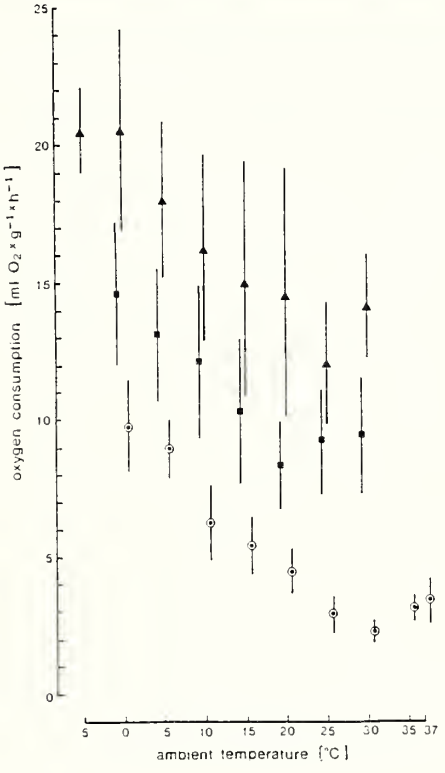

Fig. 2.—Mean oxygen consumption (±SD) at different ambient temperatures in *Sorex minutus* (triangle), *Sorex araneus* (square), and *Crocidura russula* (circle).

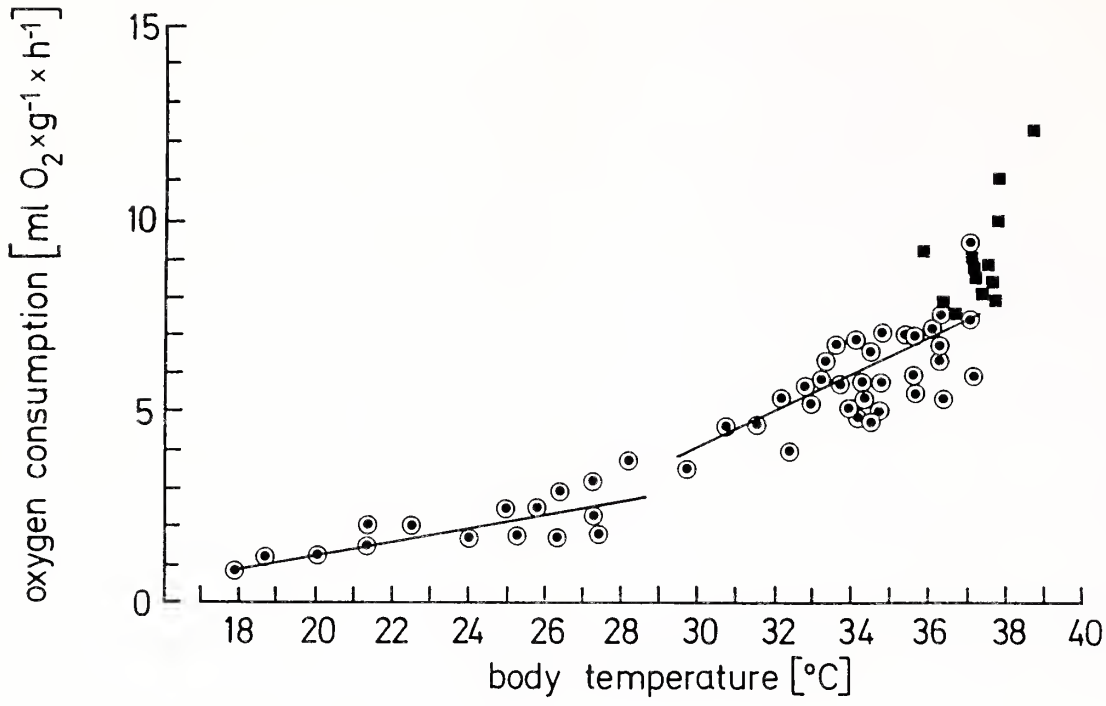

Fig. 3.—Oxygen consumption (single measurements) of torpid (Tb < 30°C) and normothermic (Tb > 30°C) *Crocidura russula* (circles) and *Sorex araneus* (squares) in relation to body temperature at ambient temperature of 15°C. Values from Nagel (1985) are included.

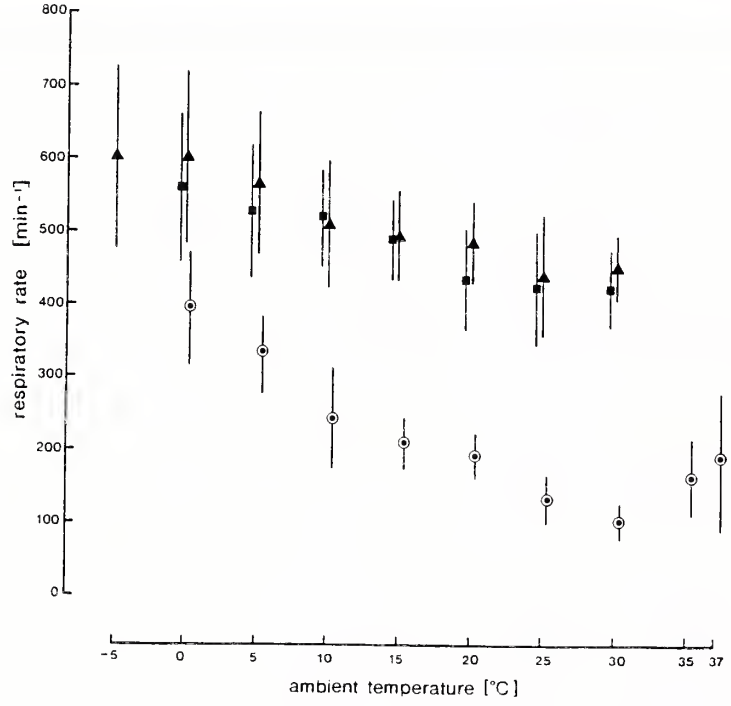

Fig. 4.—Mean respiratory rate (±SD) at different ambient temperatures in *Sorex minutus* (triangle), *Sorex araneus* (square), and *Crocidura russula* (circle).

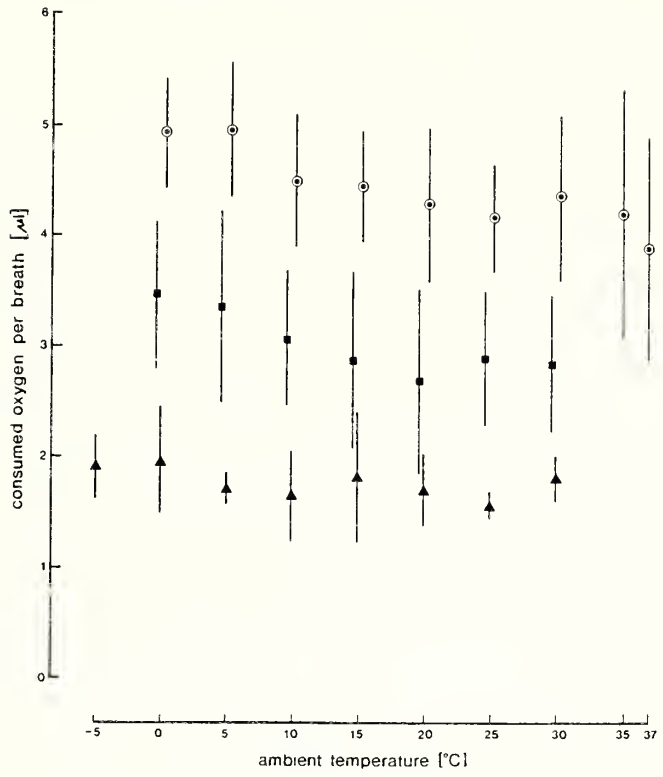

Fig. 5.—Mean oxygen consumption per breath (±SD) at different ambient temperatures in *Sorex minutus* (triangle), *Sorex araneus* (square), and *Crocidura russula* (circle).

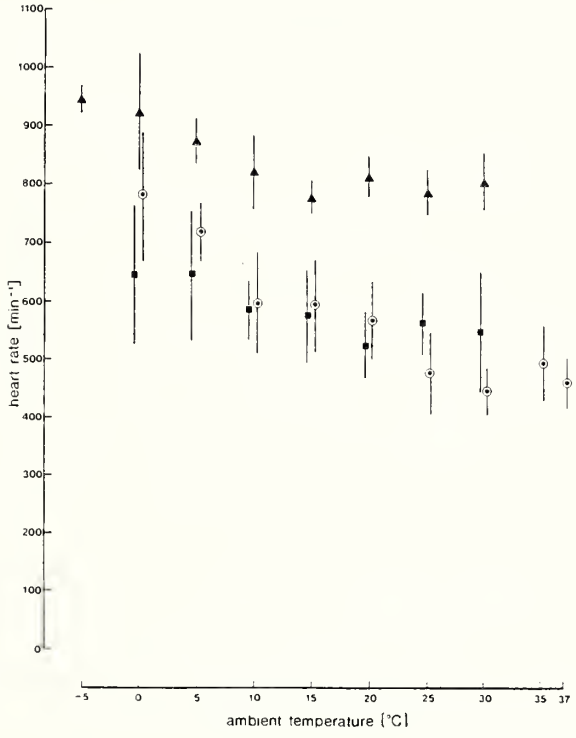

Fig. 6.—Mean heart rate (±SD) at different ambient temperatures in *Sorex minutus* (triangle), *Sorex araneus* (square), and *Crocidura russula* (circle).

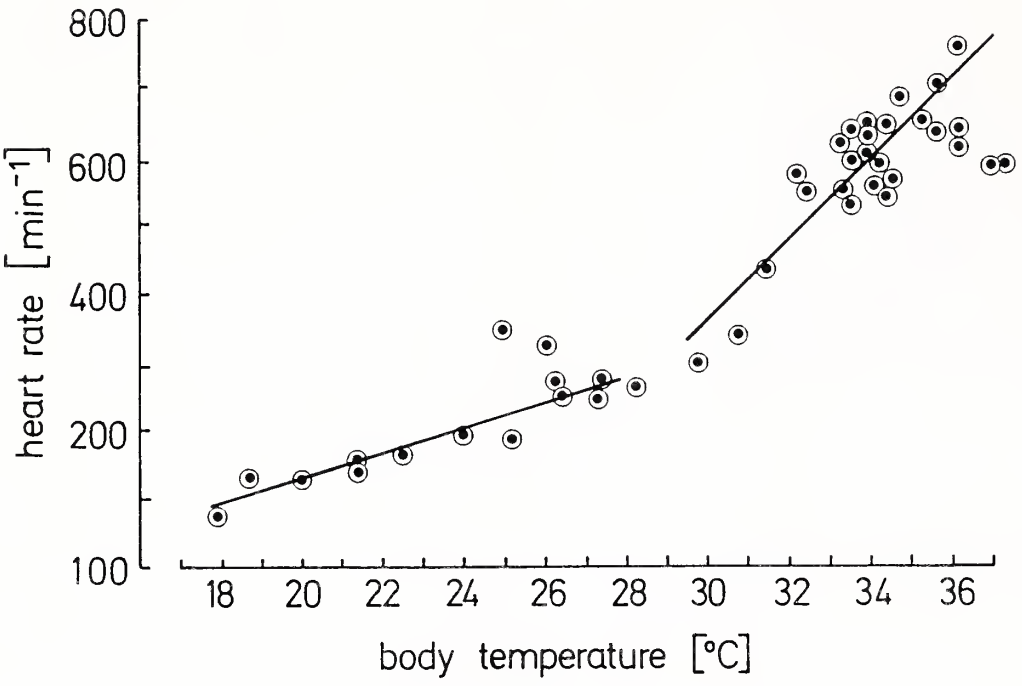

Fig. 7.—Heart rate (single measurements) of torpid (Tb < 30°C) and normothermic (Tb > 30°C) *Crocidura russula* (circles) in relation to body temperature at ambient temperature of 15°C. Values from Nagel (1985) are included.

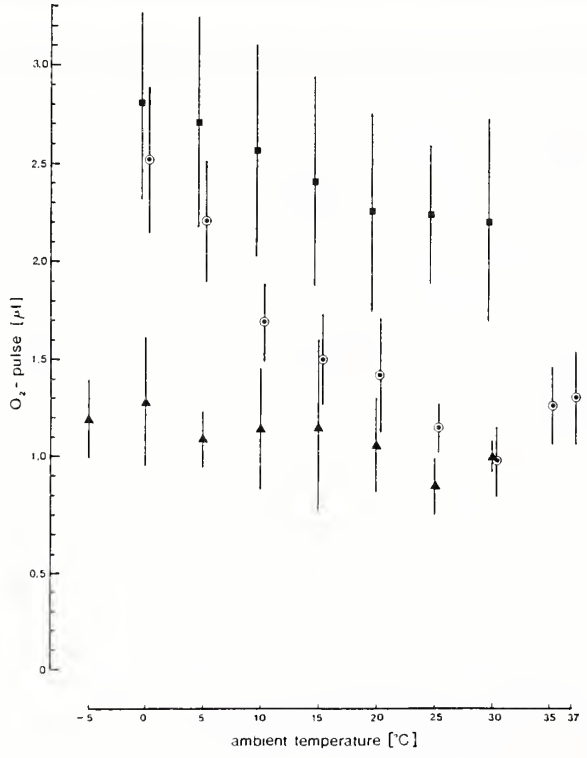

Fig. 8.—Mean oxygen pulse (±SD) at different ambient temperatures in *Sorex minutus* (triangle), *Sorex araneus* (square), and *Crocidura russula* (circle).

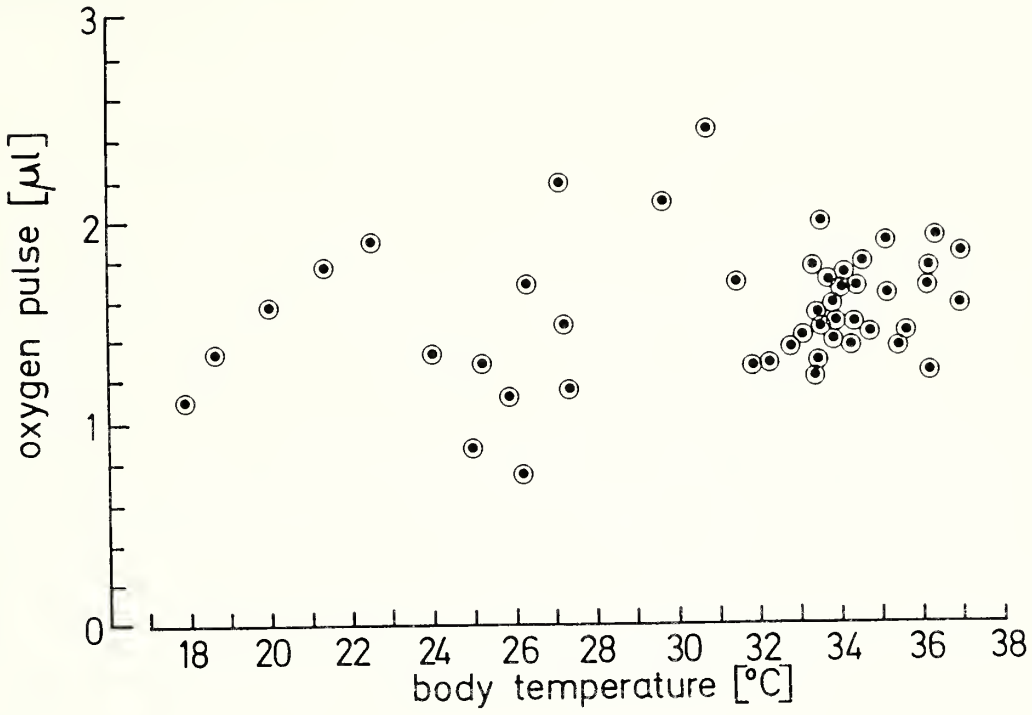

Fig. 9.—Oxygen pulse (single measurements) of torpid (Tb < 30°C) and normothermic (Tb > 30°C) *Crocidura russula* in relation to body temperature at ambient temperature of 15°C. Values from Nagel (1985) are included.

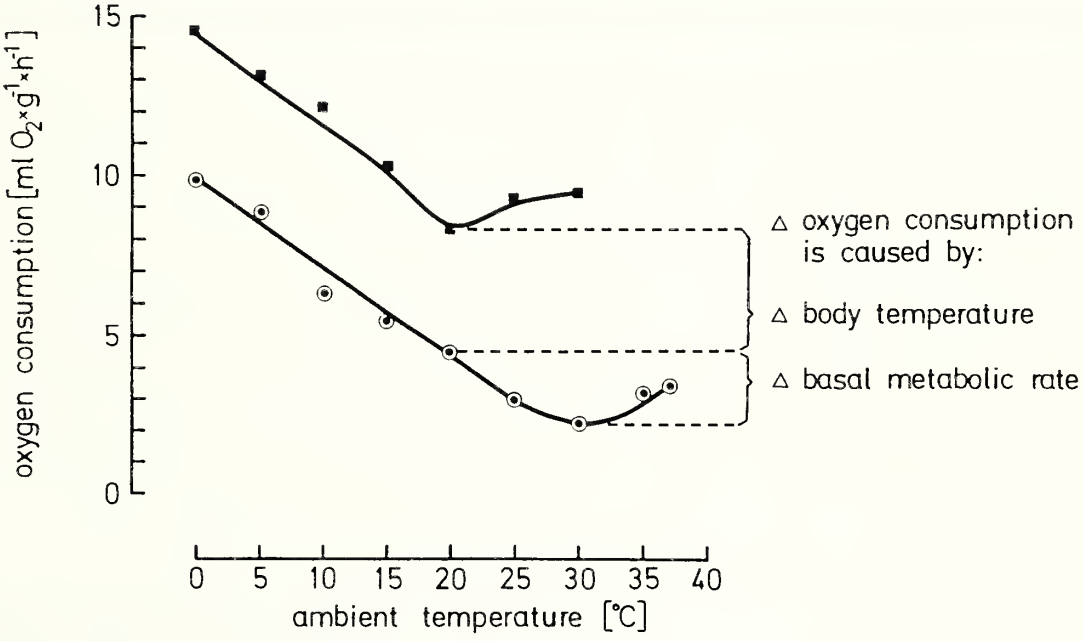

Fig. 10.—Influence of body temperature and different basal metabolic rates in *Crocidura russula* (circles) and *Sorex araneus* (squares) on oxygen consumption.

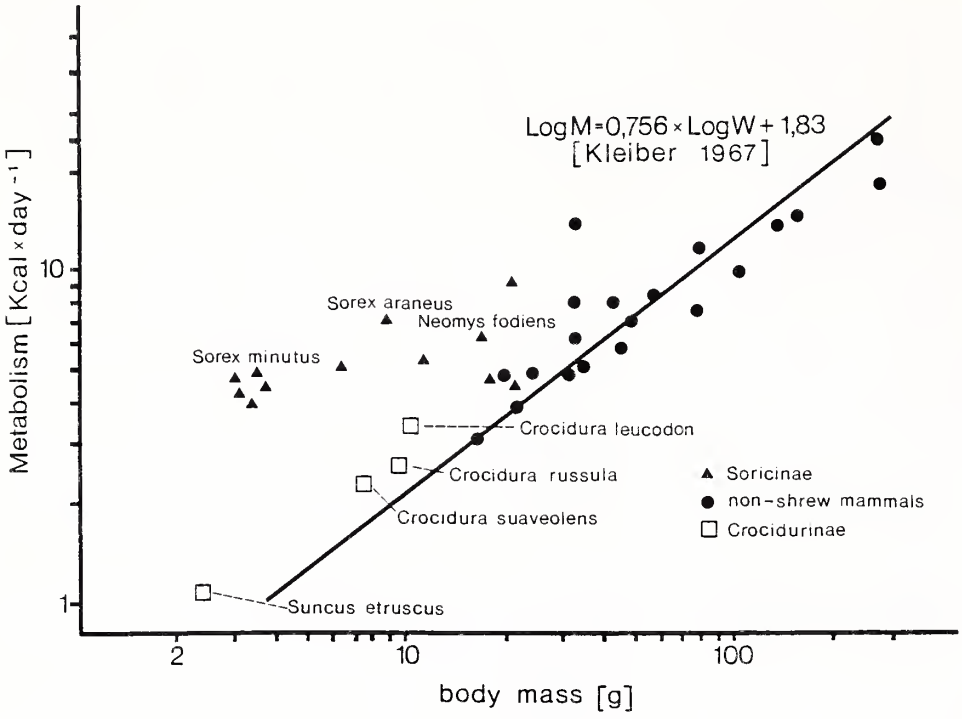

Fig. 11.—Metabolism of red-toothed shrews (Soricinae) and white-toothed shrews (Crocidurinae) compared with other mammals.

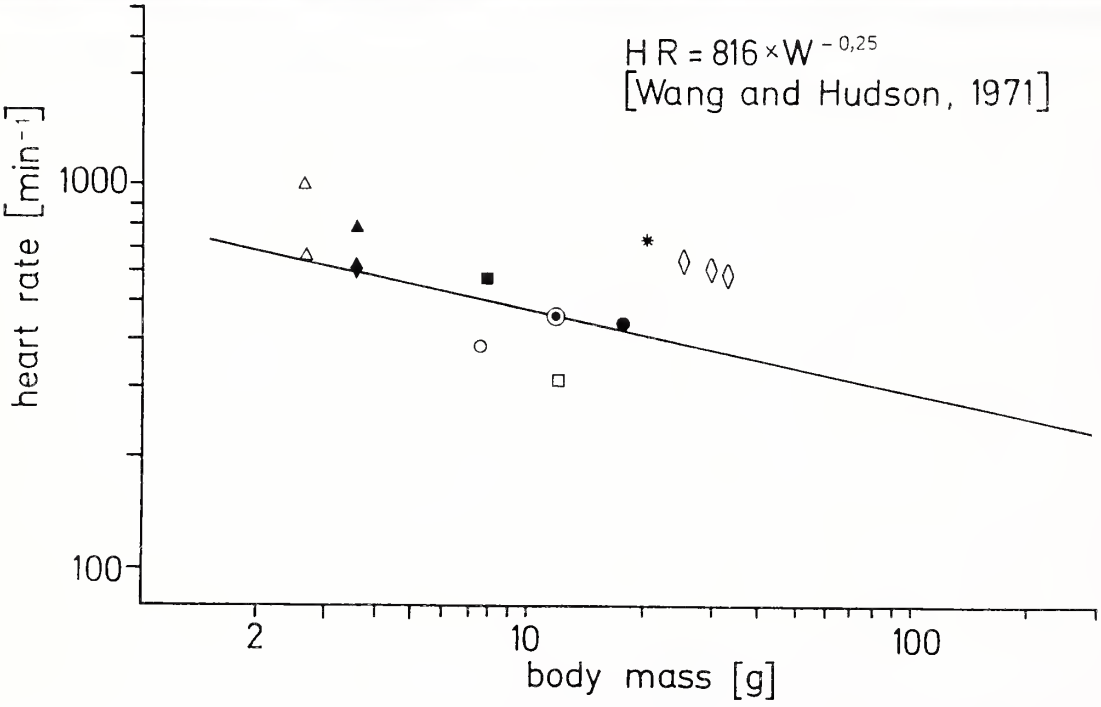

Fig. 12.—Basal heart rates in relation to body mass (double log sclaes) in *S. minutus* (closed triangles), *S. araneus* (closed squares), and *C. russula* (bull's eye) compared with the mass-predicted values (Wang and Hudson, 1971) and with data from the literature: *Neomys fodiens* (closed circle), *Crocidura suaveolens* (open circle), *Crocidura leucodon* (open square) (Nagel, 1980); *Suncus murinus* (open diamond) (Dryden et al., 1971; Balakrishnan et al., 1974); *Blarina brevicauda* (asterisk) (Doremus, 1965); *Sorex cinereus* (closed diamond) (Morrison et al., 1959); *Suncus etruscus* (open triangle) (Weibel et al., 1971; Bartels et al., 1979).

THE WHITE-TOOTHED SHREW *CROCIDURA RUSSULA MONACHA*: HOW DOES ITS PHYSIOLOGY FIT MAMMALIAN ALLOMETRY?

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ABSTRACT

By comparing physiological and reproductive parameters of the crocidurine shrew *Crocidura russula monacha* to interspecific eutherian mammalian allometric equations, deviations from common mammalian patterns are revealed. These include higher-than-predicted basal metabolic rate, heat transfer constant, heart mass, ventilation and gestation time, and lower-than-predicted lung mass and heart rate. Physiological limits, ecological adaptations, and inherited trends are thought to explain these deviations.

INTRODUCTION

Allometry provides a practical tool for analyzing the physiological consequences of body mass (Gould, 1966). Although body mass contributes a major fraction to the variability of many physiological parameters among mammals (Schmidt-Nielsen, 1984), significant deviations from a general allometric prediction occur and may reflect special cases, such as ecological adaptations (McNab, 1986), life history and reproductive patterns (Read and Harvey, 1989), or phylogenetic inherited characteristics (Gittleman, 1986; Calder, 1987; Elgar and Harvey, 1987).

When plotted allometrically, values of shrew variables occupy the extreme left side of mammalian allometric curves, raising the questions of a possible limit to mammalian size on one hand, and of mammalian physiological potential on the other. A high basal metabolic rate (BMR) (at rest, postabsorptive state, and in thermoneutrality) is characteristic of shrews.

The white-toothed shrew *Crocidura russula monacha* Thomas, 1906, cf. *Crocidura suaveolens* Pallas, 1811 (Catzeflis et al., 1985) has a body mass of 7–9 g. Its specific oxygen consumption rate at BMR is 26% higher than expected from body mass allometry (Mover et al., 1986). Thus, high cardiac output, respiratory ventilation, and food intake are also expected. Reproductive parameters such as gestation period and postnatal growth rate are also known to be related to maternal rate of energy expenditure (McNab, 1986).

The purpose of this study is to examine if circulatory, respiratory, and reproductive variables measured in *C. r. monacha* fit the expected values obtained from interspecific allometric relationships, i.e., that they may be explained by body mass considerations alone, and thus if possible deviations may be related to physiological limitations, special ecological adaptations, or inherited characters.

MATERIAL AND METHODS

Animals.—Nonreproductive female shrews were kept long enough in separate cages (40 × 30 × 5 cm) at 29°C and 14L:10D conditions to be considered summer-acclimated. Live fly larvae and minced meat mixed with milk powder were supplied once a day. Water was supplied ad libitum. Resting oxygen consumption rates, respiratory frequencies, tidal volumes, and heart rates were measured simultaneously. Six females were used in this experiment. The female gender was chosen to provide a base line for comparisons with reproductive parameters. All measurements were performed in a constant temperature cabinet at 31°C, which is within the thermoneutral zone of these shrews (28–36°C; Mover et al., 1986).

Heart and Lung Masses.—Hearts and lungs were removed from 15 nonreproductive females. The lungs including tracheae were weighed immediately after removal. Blood in the ventricles and atria was rinsed with saline, the fluids were absorbed, and the empty hearts were immediately weighed (Mettler BA28; ±0.01 mg).

Ventilation and Oxygen Consumption.—A measuring chamber consisting of two small cylindrical, horizontal plastic tubes (internal diameter [ID] = 4 cm) separated into head (3 cm long) and body (7 cm long) compartments by an elastic latex membrane was constructed from the finger of a surgeon's glove. The membrane had a hole in its center which was lubricated with silicon grease and fitted to be gas-tight around the shrew's neck, separating head from body compartment, without apparent interference of the normal respiratory rate. This was confirmed by comparing the respiration rate to that of an unrestrained animal in the same chamber. The body compartment tube was perforated to allow free air movement due to volume changes during respiration. In order to measure accurately the rate of oxygen consumption, dry, CO_2-free air was drawn through the head compartment which served as an "open" metabolic chamber, at a constant rate (75–90 ml/min) by an air pump. The same air was also used to calibrate the O_2 analyzer (±0.005%). Oxygen consumption was calculated using the redried CO_2-free outgoing flow rate (±0.5 ml) and the O_2 concentration in it as: O_2 consumption rate = outgoing gas flow rate times O_2 fraction difference between incoming and outgoing gas divided by (1 − O_2 fraction of incoming gas) (Depocas and Hart, 1957) where the O_2 uptake and the flow rate are given in ml dry gas at 0°C, pressure of 760 Torr, per hour, STPD. An Applied Electrochemistry O_2 Analyzer, model S-3A, was used to measure oxygen concentrations, and 16 × 0.7 cm ID columns of 20-mesh "Drierite" and "Ascarite" were inserted in the flow paths in series to absorb water and CO_2 from the gas before entering and after leaving the head compartment. The changes in air-flow rates caused by inspiration and expiration in the head compartment were

measured across a fixed resistance portion of the outflow tubing as pressure differences (range: ±1 mm H_2O) by a Valedyne DP15TL pressure transducer, and used for calculating respiratory rate. Calibration of tidal volume was performed by producing artificial tidal volumes (10–70 μl) at frequencies of 150–450 min^{-1}. This was done by moving mercury in a vertical graduated glass tube like a piston, using a variable speed motor, and inspecting the mercury deflections. The glass tube was connected to the head compartment for calibration through a metal tube of the same dimensions as the trachea of a shrew (10 mm long × 0.9 mm ID). Respiratory flow oscillations produced both artificially and by animals were recorded on a Gould recorder (model 2660), digitized off-line (Hipad Tablet Digitizer), and fed to a computer (PDP 11/23) where time integrations of the respiratory flow cycles around the mean flow were made to produce water vapor saturated tidal volume values expressed in μl at experimental temperature and pressure.

Heart Rate.—The floor of the body compartment contained two rows of three electrically separated, copper-conducting square sheets (each 2 × 1 cm). A lead from each copper sheet was connected to oscilloscope (Tetronix 502) inputs through a selection switchbox. For ECG inspection, pairs of leads from these sheets, which were spread with electrically conductive paste in contact with the legs, were selected. The amplified ECG was recorded simultaneously with ventilatory parameters.

Animals were allowed to reach steady-state values before the experiments began. Each female was measured once. Each measurement included O_2 consumption and 5–15 sequences of at least ten respiratory cycles and the simultaneously-measured heart rate.

The reproduction and thermoregulation parameters were taken from Mover et al. (1986, 1988). The expected values were calculated from relevant allometric equations using the mean body mass of 7.9 g.

Results

Table 1 summarizes a comparison of mass specific oxygen consumption rate in BMR conditions between *C. r. monacha* (O_2 consumption of 2.56 ml [STPD]/[g·h] ±0.56 SD) and allometric predictions, and some values from the literature.

Table 2 describes the BMR and heat transfer constant of *C. r. monacha* recalculated in energy units assuming a respiratory coefficient of 0.88 (Mover et al., 1986), and its ventilatory and circulatory parameters at BMR conditions. The results are compared with available interspecific allometric predictions from the literature.

In Table 3 we have compared measured values of gestation time, litter mass, neonatal brain mass, and averaged embryonic growth rate of *C. r. monacha* (newborn mass divided by gestation time) taken from Mover et al. (1988) with values predicted using allometric equations.

Discussion

Nonreproductive State.—Unlike the soricine shrews, the values of the oxygen consumption rate at rest of crocidurine shrews tend to approach those that are expected from their body masses (Vogel, 1976). However, in the white-toothed shrew *Crocidura russula monacha*, the values obtained were generally higher than those predicted for a typical eutherian mammal (Table 1). Our measurements were made on summer-acclimated animals during the resting phase of the circadian cycle (daytime), at complete rest, and only mean minimal values were taken into account (see Mover et al., 1986, for details). Summer-acclimated *C. russula* are also known to have an elevated oxygen consumption in low ambient temperatures (Lardet, 1989). Nevertheless, this oxygen consumption is much lower than expected within its systematic group due to the much elevated BMR of the Soricinae (Table 1; Nagel, 1994). The elevated value of oxygen consumption of *C. r. monacha* compared with mammals in general could result in a relatively high body temperature as was found in the soricine shrews (Sparti and Genoud, 1989). However, because it is accompanied by a proportionately elevated heat-transfer constant (Table 2), body temperature (32–37°C: Mover et al., 1986) varies on the low side of the normal mammalian range (Schmidt-Nielsen, 1984). Why such a strategy of high energy expenditure and heat loss has evolved in this species is not clear. The values given by Nagel (1985) and Sparti (1990) are 31 and 37% lower for the European *C. russula*, but Sparti (1990) reports a value similar to ours for *C. suaveolens*. Our summer-acclimated animals may be adapted primarily to withstand heat-stress conditions where a high thermal conductance is advantageous in preventing overheating. Lardet (1989) found for the European *C. russula* a heat transfer constant in winter which was 41% lower than in our shrews, and in summer, a constant which was only 32% lower. The potential for high heat production helps to overcome the low heat capacity, which is a function of small size. The nocturnal mode of activity, when ambient temperatures in the field are relatively low, can now be associated with increased energy expenditure and heat production during this activity. Conflicting demands due to fluctuations in ambient temperatures between day and night, especially in winter, at the ground level, and in the near-arid zones where *C. r. monacha* are found in Israel may also explain the presence of a significant capacity for nonshivering thermogenesis (NST) found in our summer-acclimated shrews (4.4 ml [STPD]/(g·h); unpublished data).

How are the higher-than-expected oxygen demands of *C. r. monacha* met by the circulatory and respiratory systems? Table 2 shows that the changes from the expected, which occur in the heart and lungs of this shrew, deviate in opposite directions: the heart is relatively large and slow in rate, while the lungs are relatively small and respiratory frequency is high. This leads to an unusual ratio of heart rate to respiration frequency of 2.1 in *C. r. monacha*, compared with the ratio of 4.3 as predicted from mammalian allometry (Stahl, 1967). A relatively large heart may lead to efficient heart work since it enables a high stroke volume resulting in only a minor increase in the heart's oxygen consumption, while an increase in heart rate notably increases the heart's metabolic needs (Roth, 1976). A smaller heart with a higher beat frequency could reach the limit of contraction-relaxation time of the heart muscle, especially

during activity (Schmidt-Nielsen, 1984). The large density of mitochondria needed to activate a small, fast-beating heart may impair its mechanical activity (Weibel, 1984) and thus a larger heart may have a favorable mitochondrial fraction. In addition, as in athletes, a relatively large heart may increase the scope of its performance during activity.

Ventilation is more than proportionately elevated compared with the oxygen demands. The higher-than-expected ventilation is achieved by increasing respiration frequency while tidal volume is kept near expected values (Table 2). Because the small size of the shrew makes its CO_2 capacity low, in the face of a very high specific CO_2 production rate, the high ventilation rate may be necessary to regulate both CO_2 stores and blood pH more precisely. It will be interesting to test this idea in other small mammals. From the measured data and assuming a dead space of one-third tidal volume (Dejours, 1981), we calculated an alveolar O_2 pressure of about 110 Torr for *C. r. monacha*, which is very high compared with the 88 Torr predicted according to Weibel (1984). This "hyperventilation" maintains a high oxygen head pressure in the alveoli which facilitates oxygen diffusion to the blood. Since both lung mass (Table 2) and lung diffusion capacity of the shrew correspond to body mass and not to its higher-than-expected energy metabolism (Weibel et al., 1981), relative hyperventilation may provide a mechanism for overcoming O_2 diffusion difficulties through the alveolar-blood barrier. It may also provide an important avenue for evaporative heat loss since the specific ventilation of about 1.5 ml/(g·min) is very high (in man it is about 0.1 ml/[g·min]), but in order to evaluate it quantitatively, expired air temperature has to be measured.

Reproductive State.—In eutherian mammals, high metabolic rates will tend to correlate with a short gestation period for a given maternal size (McNab, 1980, 1986). Martin (1981) contends that maternal metabolic rate during gestation determines the neonatal brain mass, and Hofman (1983) found a strong correlation between maternal metabolism, litter birth mass, and neonatal brain mass. For *C. r. monacha* these relationships do not hold; although BMR exceeds the expected value, the gestation period is far longer than expected (Table 3). According to the above correlations, the combination of such a long gestation period and high BMR should have resulted in a rapid intrauterine growth and a large neonate brain mass. However, neonatal brain mass, embryonic growth rate, and litter body mass in *C. r. monacha* fit rather precisely the allometrically expected values (Table 3). In fact, crocidurines are similar to soricine shrews in their growth rate (Vogel, 1972) despite their longer gestation period. This may indicate that the newborn of *C. r. monacha* are relatively more advanced in their development at birth as indicated for Crocidurinae in general (Vogel, 1981).

While it seems that maternal body mass explains some of the reproductive variables in *C. r. monacha*, the long gestation, relative precociality, and short postnatal development period (Hellwing, 1971) are better explained as phylogenetically inherited characters. As in the metatherian pattern (Lillegraven et al., 1987), no correlation between body mass, metabolic rate, and gestation period can be detected. The long gestation period in *C. r. monacha* may serve to partition in time the maternal energy investment during simultaneous lactation and pregnancy (Mover et al., 1989). Females conceive on the day of delivery. During the first seven days of gestation, the embryonic litter mass is almost nil. It reaches a total mass of 0.08 g only at the end of the tenth day (Mover et al., 1988), while during these ten days energy intake for milk production is rising to a value which is 4.8 times that needed to sustain the nonpregnant, nonlactating female shrew (Mover et al., 1989). Omitting these first ten days brings the gestation time of 28 days closer to the predicted value (Table 3).

In conclusion, many characteristics of the white-toothed shrew *C. r. monacha* fit the general predictions for mammalian values expected for such a body mass. However, there are deviations due to three main constraints: 1) physiological performance limitations, such as a lower-than-expected heart rate apparently to avoid approaching the upper frequency and efficiency limits; 2) ecological adaptations where the low body capacity limitations challenge homeostasis, e.g., thermoregulation, as demonstrated by the high intensity of metabolism and the high heat-transfer coefficient that nevertheless result in a "normal" body temperature, and the relative hyperventilation which enables both higher-than-expected oxygen delivery and fast regulation of CO_2 and pH levels; and 3) an inherited reproductive strategy in which body mass and the high BMR have no visible correlation with the neonatal development rate. Instead, the longer-than-predicted gestation period helps to partition the energy intake demands of the simultaneously lactating and pregnant female.

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Table 1.—*A comparison of mass-specific oxygen consumption rate at rest, thermoneutrality, and post-absorptive state, between* Crocidura russula monacha, *selected allometrically predicted values, and observed values. The upper part compares* C. r. monacha *with general mammalian pattern; the middle part, within a limited systematic group which includes soricid values; the lower part, with other measurements of populations of the same species. Positive values represent an increase of* C. r. monacha *above predicted or observed; negative values, below predicted or observed.*

Type of Comparison	Deviation (%)	Authority
Eutherian mammals, full range	+16	Brody, 1945
" " " "	+26	Kleiber, 1961
" " " "	+8	Hayssen & Lacey, 1985
" " up to 450 g	+22 to +35	McNab, 1988
Rodents and insectivores up to 100 g	+11	Bartels, 1980
Insectivores	−83	Hayssen & Lacey, 1985
Soricomorpha	−100	McNab, 1988
C. russula	−4	Nagel, 1985
C. russula	+11	Nagel, 1994
C. russula	−14	Sparti, 1990
C. suaveolens	+10	Nagel, 1985
C. suaveolens	−13	Sparti, 1990

Table 2.—*Measured and expected heat transfer coefficients, ventilatory, and circulatory parameters of the white-toothed shrew* Crocidura russula monacha. *[1]Kleiber, 1961; [2]Bradley and Deavers, 1980; [3]Stahl, 1967.*

Variable	Oxygen Consumption (mW/g)	Heat Transfer Coefficient (mW/g °C)	Respiration Frequency (1/min)	Tidal Volume (μl)	Ventilation (BTPS) (ml/min)	Lung Mass (mg)	Heart Mass (mg)	Heart Rate (1/min)
Measured	14.28	2.29	273	47	11.7	81.4	68.2	566
±SD	3.1	0.01	68	12	2.3	9.51	8.15	71.7
Predicted	11.38[1]	1.75[2]	188[3]	50[3]	7.88[3]	93.7[3]	50.5[3]	808[3]
Measured/predicted	1.26	1.31	1.45	0.94	1.48	0.87	1.36	0.70

Table 3.—*Measured and expected reproduction parameters of the white-toothed shrew* Crocidura russula monacha. *[1]Mover et al., 1988; [2]Hofman, 1983; [3]Rahn, 1980; [4]Calder, 1982.*

Variable	Gestation Time (d)	Litter Body Mass (g)	Neonatal Brain Mass (mg)	Embryonic Growth Rate (g/d)
Measured[1]	28	2.79	61.91	0.032
±SD	1	0.14	6.95	0.002
Predicted	17[2]	2.61[3]	63.03[2]	0.034[4]
Measured/predicted	1.65	1.06	0.98	0.94

THE STRUCTURE AND ADAPTIVE PECULIARITIES OF PELAGE IN SORICINE SHREWS

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ABSTRACT

The fur structure of four soricine shrews, *Sorex araneus*, *S. caecutiens*, *S. minutus*, and *Neomys fodiens*, was investigated in animals collected at different seasons in extreme western Russia. Hairs of shrews can be classified into four categories based on structure and function: monotrich, Type I guard, Type II guard, and woolly. All except monotrichs are tapered with longitudinal bands, have three to seven segments, and grow singly and perpendicularly from the skin surface. Guard and especially woolly hairs are short and thin with well-marked distal segments, whereas monotrichs are long and thick. Winter hairs are thinner and longer than summer hairs, due mainly to an increase in the number of segments from three to four to six to seven. Also, the density of the pelage increases by 20–30 percent as winter approaches. Three distinct concentric regions (core, cortical, and cuticular) were revealed in the microstructure of the hair shaft. A shrew hair is characterized by the presence of two longitudinal furrows near the tips of guard hairs, smooth margins of cuticular scales, an interrupted pattern of the cortical layer of the shaft, and zonal coloration of the shaft. The insulative property (coefficient of heat conductivity) of shrew pelage also was examined. Physical thermoregulation is important in the maintenance of temperature homeostasis during the molt period.

INTRODUCTION

Soricine shrews have extremely high levels of metabolism (McNab, 1991; Nagel, 1994) yet must survive the low winter temperatures of the temperate and subarctic locations where they occur. Their small size precludes use of long, dense hairs or fatty layers for insulation, and consequently they lose much heat by thermal conductance. To minimize heat loss and maintain a favorable energy balance, these shrews have acquired a complex of ecological and morphological adaptations for surviving the energy costs of thermoregulation. The objective of this study was to investigate the role of the fur, including the microstructure of different hairs and peculiarities of the molt, as adaptations for physical thermoregulation.

MATERIALS AND METHODS

The skins of 157 shrews of four species (*Sorex araneus*, *S. caecutiens*, *S. minutus*, and *Neomys fodiens*) were examined. For comparison, representatives of other families of Insectivora and Rodentia were studied as well, including *Talpa europaea* (n = 37), *Sicista betulina* (n = 18), *Clethrionomys glareolus* (n = 42), and *Microtus oeconomus* (n = 14). Investigations of hair distribution on the skin, structure of a single hair shaft, density and length of hair, and topography of the hair cover were conducted according to traditional methods (Williams, 1938; Borowski, 1952; Sokolov, 1973). The microstructure of hair shafts was observed using a microscope at 600–1350× magnification (immersion lens). Imprints of the cuticular layer were made on slides coated with clear nail polish. The insulative properties of skins were determined (by the coefficient of thermoconductivity method) with the use of a special apparatus, IT-3, from the Institute of Technical Thermophysics of the Ukraine Academy of Sciences in Kiev. This instrument measures heat loss from a constant source through a dried, flat skin.

RESULTS

General Characteristics of the Fur

The pelage of soricine shrews is distinctive. The fur is short, velvety, soft, perpendicular to the skin surface, and does not form the so-called "hair flow" which is common in most mammalian pelage. Because of their segmental structure, the hairs lie easily in any direction, do not rumple, and retain air. Shrew hairs are thin and consist of slightly thickened or widened segments interrupted by occasional constrictions where the shaft bends at an obtuse angle (Fig. 1, 2). This feature makes the fur elastic and gives a layered effect to the surface regardless of the direction the hair tips point. All four species of shrews examined had dark, predominantly brown hairs on the dorsal side, and light, dirty-white hairs on the venter. Most had a well-pronounced transitional color zone on each flank, but this feature was absent in one specimen of *Neomys fodiens*.

The color of fur is determined by the presence and concentration of melanin and lipochrome, the black and brown pigments. The major tone of coloration is determined by the concentration of lipochrome in the distal segments of the guard hairs. Other segments of all hairs contain melanin. Pigments are absent in the upper parts of the distal segments, which have no coloration. However, the light-reflecting scales add a specific silver luster to the fur. Newly molted fur looks more vivid, shiny, and lustrous compared to old, dull fur with frayed ends.

Differentiation of the Hairs

Shrew hairs are classified into four categories: monotrich, Type I guard, Type II guard, and woolly (Fig. 1, 2). The monotrich is thick, long, and elastic. The shaft is nearly straight and spindle-shaped but round in cross section. Its base is not twisted, and segments and constrictions are absent. The shaft gradually narrows at the tip, becoming filiform and nearly colorless. The thickness of the shaft also narrows at the root.

Monotrichs are outnumbered 150–200:1 by the other hair types. Although not adding significantly to the fur cover, monotrichs fulfill an important sensory function. Compared to other hair types, the sacs of monotrichs lie in deeper layers of the dermis where the nerve ganglia are more developed.

The guard hair is shorter and thicker than the monotrich, and is distinctly segmented. The distal lancet-shaped segment of the guard hair is most pronounced, being longer and wider than other segments and comprising 25–50 percent of the length of the shaft. The longitudinal bends of the shaft allow the guard hair to lie in any direction.

There are two types of guard hairs. The Type I guard hair is widest and longest in segments among the segmented hairs, and is longer in winter having six segments than in summer with 3–4 segments present. Whether in summer or winter pelage, the distal segment constitutes up to 50 percent of the length of the shaft. The distinctive feature of the guard hair is the presence of longitudinal grooves on the sides of the distal segments, creating an H-shaped profile in cross section (Fig. 2). These grooves are closed in the constriction and tip of the guard hair, a feature that is distinctive and diagnostic for the Soricinae. Species-specific features are less pronounced. A distinctive feature in *N. fodiens* but in other soricines is the "internal bar," which is formed by a diagonal slat on the bottom of the groove (Fig. 2).

The Type II guard hair is slightly shorter and thinner than Type I. Its terminal segment comprises up to 25 percent of the shaft length. In both winter and summer, Type II hairs have one segment more than Type I guard hairs; i.e., Type II hairs have seven segments in winter and 4–5 segments in summer (Tables 1–3).

The guard hairs have zonal coloration, a character which varies in different parts of the pelage. On the abdomen, the end segments of guard hairs are white, but on the back and flanks they are dark brown but colorless at the very tips. Other segments of the guard hairs of all parts of the body are intensely black. The highest concentration of melanin occurs in the core of widened parts of segments, but in narrow areas the melanin is diffusely distributed, producing lighter coloration. Large inter- and intracellular air cavities refract the light, producing a lustrous sheen to the hair in appropriate lighting. Together with the zonation of coloration, the combination of dark and light segments determines the variety of fur shades in different parts of the pelage.

The main functions of guard hairs are to protect the more delicate woolly hairs from mechanical damage and rumpling, and provide the structure or matrix for the other hairs of the pelage. Besides bending to cover the woolly layer, the thickened terminal segments of guard hairs promote the formation of the insulative air layer and enhance thermoregulation.

Woolly hairs, although thinnest and shortest, have the same number of segments as Type II guard hairs. The terminal lancet-shaped segment is less developed than the other segments. The density of woolly hairs is greater than that of other types, and can make up 40–60% of all hairs. Their main function is to provide insulation and reduce thermal conductance.

These characteristics of the four main types of hair are extremely heterogeneous within each type. Yet, in comparison with other mammals, hair differentiation in shrews is much less variable. This is explained by their ancient origin, their fossorial adaptations, and the presumed adaptive value for each hair type and the specific combination of types (Ivanter et al., 1985). Each hair type participates equally in mechanical and thermal protection of the body, but the presence of multiple types of hair permits the specialization of some types to enhance thermoregulation and others to improve the mechanical and protective qualities without an increase in length, density, or mass of the fur. Such an increase would impede the active movements of small mammals.

Hair Shaft Structure

Two distinctly delimited concentric layers (cortical and cuticular) surrounding a core region were revealed in the microstructure of the hair shaft (Fig. 3). The cuticula, forming the external covering of the shaft, consists of one layer of horned, nonconcentric scale cells with the open side directed toward the tip of the shaft. These unpigmented, semitransparent cuticular scales differ in form and size in different regions of the shaft. In both the preroot zone and constricted sections, cuticular scales are elongated with smooth, round borders and do not fit tightly with one another. (In rodents, the scale borders in such places are toothed.) This loose fit in shrews provides the necessary flexibility of the shaft. Where the shaft widens, particularly in the distal segment, the cuticular scales become short, wide, and toothed on the borders (Fig. 4, Sa, Sc, Sm, Sb). This design keeps the hair shaft rigid. In rodents, by contrast, scale cells of cuticula look like narrow, twisting ribbons that cling to the shaft, giving each a characteristic appearance (Fig. 4, Cg and Mo).

The characteristics of winter and summer hair cuticula varied only slightly in each species of shrew. Age variation was also minor. There were few differences in form and size of scales, and the general morphology was conservative. Compared to hair cuticula from other systematic groups inhabiting similar environments, no common features were noted. However, closely related species from different habitats had similar cuticular structures. For example, the cuticula of shrews in the genus *Sorex* differed more from *Clethrionomys* from the same habitats than from the cuticula of other insectivores, such as *Talpa*, a fossorial mammal, or *Neomys*, a semiaquatic mammal. Overall, hair characteristics are determined more by taxonomic affiliation than by ecological factors.

The moderately thick cortical layer, which lies between the cuticular layer and the core, consists of the spindle-shaped and highly keratinized cells which provide the tensile strength of the shaft. The cortical layer is well-formed along the entire length of the shaft, and forms the cover of the central channel. The cortical layer has no pigment, but in the Rodentia it contains melanin granules and, together with the core, determines the coloration of the hair. In rodents, the cortical layer is thinner and more evenly distributed along the shaft.

The coloration and thickness of the hair depend on the development and structure of the core, especially the size and position of the lens-shaped cells, the presence of pigment, and

intra- and intercellular air-filled cavities. The diameter of the core changes in the growing hair, and varies in different parts of the hair shaft. The end segment of the core is most highly developed, where numerous pigment granules, lying like loosely stacked coins, determine the hair coloration. In the widest part of the segment, core cells are arranged in three rows (4–6 rows in rodents), whereas at the base and tip of the shaft and near constrictions, the core becomes two-rowed. In thin, bent areas of the hair, such as between segments and in the preroot section of the growing hair, the core is very narrow, thread-like, sometimes interrupted, and has a diffuse distribution of pigment. In these places, the hair is covered with the longest scales. In the preroot section and tip of the fully grown hair, both core and pigment are practically absent. In contrast, the core region is well-developed and pigmented in the root of the growing hair shaft, especially in the initial period of growth when hairs are located inside the skin. As a hair grows, the most recently produced section at the base of hair shaft is filiform. The gradually widening channel initially does not have a pronounced cellular structure and is characterized by a scattering of pigment. Later this changes to a strict alternation of air cavities and pigmented cells, reaching maximum development in the terminal segment of the hair shaft.

Within the general microstructural features of the hair shaft are found numerous variations and deviations, depending on the type of hair, grade of maturation, location on the skin, season of the year, and species of mammal. The core region is most variable. For example, the core of each monotrich and guard hair has 1–2 rows of core cells in its thinnest parts but many rows in the segments of the thicker part. In contrast, in woolly hairs, the core is either almost nonexistent or interrupted, has only one row of core cells along the entire shaft, and contains numerous air chambers. The relationship between the core and cortical regions differs among hair types. The cortical layer is best developed in monotrichs, less in guard hairs, and least in woolly hairs, whereas the core is best developed in the shafts of woolly hairs. The seasonal changes are more apparent. As a rule, the shaft of a winter hair has a thicker core but a thinner cortical layer. The winter increase in core thickness is due mainly to the enlargement of the air cavities, thus improving the insulative qualities of the fur.

Fur Density

Hair density is one of the most variable indices of the fur structure. Both intra- and interspecific differences were found (Table 4). The fur of shrews is denser than that of rodents in both winter and summer. Among the Insectivora, the densest fur belongs to *Talpa europaea* with hair density 1.5 times greater than that of *Sorex minutus*, the smallest shrew examined. Between these extremes of density lie, in order, *Neomys fodiens*, *Sorex araneus*, and *S. caecutiens*. *Clethrionomys glareolus* has the least dense hairs of all, but *Sicista betulina*, with 100–150 hairs per mm^2, has the densest fur in its summer pelage.

Although the body appears fully furred, hair density varies at different locations (Table 4). In most of the eight species examined, the thickest fur occurred on the back. The topography of fur density depends on the animal's ecology as well as its habitat. The hair density of *Talpa europaea* is thinnest on the sides, while hair density in shrews is thinnest on the abdomen. However, the hair density of *Neomys fodiens* is uniform across the sides and abdomen, but is still thickest on the back.

Seasonal changes in hair density are more obvious. The winter pelage is 1.2–1.4 times thicker than in summer, due to increased numbers of woolly hairs rather than guard or directing hairs, whose numbers remain constant. The highest density was observed in the fur of molting animals, when "old" hairs remain among intensively growing "new" hairs. The hair density also depends on the age of the animal, confirmed by the negative relationship between hair density and body size.

Thickness of the Hair Shaft

Shafts of different types of hair vary in thickness (Table 5). Woolly hairs not only are thinner than guard hairs and monotrichs, but are more uniform in thickness. The width of the lancet-shaped terminal segment of a woolly shaft from *Sorex araneus* varies from 4.5–5.0 μ, with a coefficient of variation (CV) of 3.9%. In the Type II guard hair, the diameter varies from 26.0–28.7 μ, with a CV of 13.6%. The shaft thickness also changes with season. The winter hairs of all types are thinner, softer, and lighter in color than summer hairs. The relative thickness of the core channel increases from summer to winter, from comprising 50–65% of the total diameter in summer to 60–85% in winter (Table 5). Therefore, although the total thickness of the hair shaft increases in summer, the core narrows. In winter, the shaft narrows and the thickness of the cortical region increases.

Among the majority of species investigated, in cross section the hairs are thickest on the back and thinnest on the abdomen. *Neomys fodiens* and *Talpa europaea* are exceptions, with abdominal hair slightly thicker than that of the sides and back. This is due to the animals' specific life habits. As previously mentioned, the hair shafts with greatest diameter are those of monotrichs; guard hairs are slightly thinner, and woolly hairs the thinnest. However, an opposite relationship holds for the proportion of the core in cross section. The core is large in woolly hairs, intermediate in guard hairs, and small in monotrichs. Therefore, the thinner the shaft, the greater the contribution of the core and the smaller the contribution of the cortical layer.

Length of the Hairs

Three or four zones based on the length of hairs were identified in the pelage of eight species of small mammals (Fig. 5). Among *Sorex*, the sacrum (stippled pattern, Fig. 5) had the longest and densest fur. A second zone, with hairs 0.5–0.7 mm shorter, covered nearly all of the remaining back and sides. A third zone surrounded the second like a narrow ribbon; and a fourth zone covered the venter, where the hairs are shortest. According to the nomenclature of Tserevitnov (1958), such pelage topography is called the "sacral-equal type." The "equilateral type" of fur, characteristic of *Neomys fodiens*, had

hair of moderate length on the back, long hair on the sacrum and flanks, and short hair on the venter. The "equal type" of fur on *Talpa europaea* consists of a relatively constant length of fur over the entire body.

The pelage of shrews caught in summer was much shorter than that of winter shrews (Table 6). The summer fur was formed by three-segmented Type I guard and four-segmented woolly and Type II guard hairs, whereas the winter fur had six-segmented (Type I) and seven-segmented (Type II) guard hairs and woolly hairs. The summer guard hairs of *Sorex araneus* averaged 4.2 mm, with the terminal segments comprising 2.6 mm of this length. In the winter, the guard hairs averaged 7.5 mm and the terminal segments were 2.8 mm. Thus, the winter guard hairs were 1.6–1.8 times longer than in summer, an increase seen also for other categories of hair (Table 6). Overall, all categories of hairs from winter-caught *S. araneus* were longer than in summer. Among the monotrichs, winter fur covering different parts of the four species of soricine shrews was 0.9–3.8 mm ($\bar{X}$ = 2.3 mm), or 30% greater than summer values. Among the guard hairs, this range was 1.6–3.7 mm ($\bar{X}$ = 2.7 mm, 42%), and among woolly hairs, the range was 0.7–3.8 mm ($\bar{X}$ = 2.00 mm, 37%). Thus, from summer to winter the hair length increased an average of 30–40%.

Insulative Properties of the Pelage

The insulative properties of the pelage depend in part on the "inert" air in the core region but more importantly on the thickness of the "stable" air that reduces the convection current which moves heat from the skin surface through the pelage to the surface of the fur. These features combine to provide an effective thermal insulation (Scholander et al., 1950; Hammel, 1955; Irving and Krog, 1955; Sokolov, 1973; Schmidt-Nielsen, 1975; Ivanter et al., 1985). A pelage of densely packed thick, long hairs intermixed with thin hairs provides a stable air layer, and consequently heat is better conserved compared to other pelage. Thermoconductivity also depends on the amount of air in the core of hair shafts (and thus is greater when the core has little air) and on the pores of the skin surface and, in turn, on the density and thickness of the skin. Hair structure also affects thermoconductivity based on the presence of longitudinal grooves on the shaft, the number of segments, and the manner in which the hairs lay in the pelage.

The pattern of heat conductivity from dry prepared skins of animals collected at different seasons confirmed that the combination of changes in hair density and quality combined to affect the insulative properties of the pelage (Table 7). The thermoconductivity of the fur showed well-pronounced taxonomic and seasonal variations, as determined by the structural peculiarities of the pelage. The longer, thinner and more numerous the hair shafts and the thicker the skin, the lower the thermoconductive coefficient and, consequently, the better the insulation. Each species demonstrated a pronounced seasonal variability, and this suggested a correlation between the thermoconductive coefficient and hair length, thickness, and numbers.

The coefficient of heat conductivity (CHC) of summer skins was greater than that of winter skins (Table 7); in *Sorex araneus* this difference was 27.3%; in *S. caecutiens*, 34.6%; in *S. minutus*, 26.8%; in *Talpa europaea*, 30.2%; in *Clethrionomys glareolus*, 21.5%; in *Microtus oeconomus*, 30.9%; and in *Neomys fodiens*, 7.3%. These values corresponded to the seasonal changes in the length and thickness of the fur. The rank correlation index of Spearman (r_s) between hair length and specific thermoconductivity of the skin was statistically significant ($r_s = -0.41$, $t = 2.3$, $P < 0.05$). The correlation between CHC and density of the fur was higher and more significant ($r_s = -0.66$, $t = 3.6$, $P < 0.01$). When hair length and hair density were combined and correlated with CHC, the correlation was still greater ($r_s = 0.90$, $P < 0.001$). In brief, the rate of heat loss was inversely proportional to the density of the pelage.

The fur of shrews was shorter and denser than that of voles. In addition, the segmentary structure of hair prevents rumpling and allows the fur to lie easily in any direction. This keeps the "stable" or trapped air within the fur, and improves its insulative properties. *Neomys fodiens* and *Talpa europaea*, which have the longest and densest pelage of the insectivores examined, have insulative properties nearly twice that of any of the three *Sorex* species.

The insulative properties of mammal skins at the peak of molting were better those of winter skins (Table 7). As mentioned, thermoconductivity is reduced by the thickening of the skin and increase in fur density due to the combination of old hairs and newly emerging ones. Thus, the efficiency of thermoregulation in shrews during the molting period is increased during this transition. Energy demands are increased by 20–30% during the molting period. Because molt may occur during seasons when the abundance and quality of food is changing, energy savings resulting from pelage would be highly adaptive during the molt.

Discussion

Among the four insectivores in this study are representatives of three adaptive types, i.e., semiterrestrial (*Sorex* sp.), fossorial (*Talpa*), and semiaquatic (*Neomys*). This division allowed the identification of the most typical and obviously adaptive features of hair structure for each species and assessment of these features from an ecological perspective.

By life habits, environment, and fur structure, shrews combine many features that are characteristic of terrestrial and fossorial mammals. They inhabit temperate and cold climates where conditions of constant thermal deficit prevail. Thus, these insectivores must have fur which is light and suitable for easy movement, but with high insulative properties. The fur is characterized by moderate density and length of the hair, an uneven density and length of cover over different parts of the body, the mace-shaped form of the terminal segment, the slight twisting of the shaft at the base of the hair, and a relatively well-developed core in the center of the hair shaft.

It is well-known that solid hair shafts are not good insulators because of the relatively high thermoconductivity of the keratin. The principal role in thermoprotection, besides the "inert" air in air chambers of the shaft, belongs to the so-called "stable" air formed in the pelage as a result of maximum reduction of

convection currents. In shrews, the structure of the fur promotes the maintenance of this insulative layer of air. Hair shafts are located singly and perpendicular to the skin surface, are segmented and twisted, and differentiated into categories. Guard and monotrichs grow among and protect the woolly hairs, not only protecting the fur from rumpling but also reducing the escape of air and its heat. By having a relatively less developed hair core as compared with rodents, but with much higher hair durability by the thickened cortical layer, shrews compensate for the deficit of "inert" air in the core of individual hairs by an increased content of "stable" air in the fur. As a result, the thermoconductivity coefficient of shrew fur is less than that of rodents (Table 7). However, the lower insulative properties of the fur of voles is not maladaptive. Voles compensate by obtaining other mechanisms to maintain a favorable energy balance; e.g., they have better chemical thermoregulation, occupy microhabitats possessing burrows with constant temperatures, and construct nests to aid in reducing thermal conductance.

The uneven character of the hair cover on different zones of the body, a characteristic of semiterrestrial species, is an important additional component of physical thermoregulation. The zone in the middle of the back, which undergoes the most severe cooling, is covered by the longest and densest fur. The venter is least protected from the cold, because the hair cover is sparser and shorter. The usefulness of such topography is apparent when the shrew rolls into a ball during sleep. In this configuration, the ventral part of the body is covered, exposing a minimal area of surface for thermoradiation. Also, the exposed parts of the sleeping shrew are mostly well-furred.

The pelage also protects the shrew from mechanical damage by reducing the pressure of the surrounding substrate as shrews move in narrow burrows, leaf litter, bushes, and grasses. To some extent, the mechanical protection function is opposed to the insulative function. The most durable and protective hair shafts would have poorly developed cores, whereas thinning leads to a decrease in insulative properties. This contradiction is solved in several ways. One is the numerical increase in thin-cored shafts, a compromise that promotes both good mechanical and insulative properties. A second way is the differentiation of hair types, a sort of division-of-labor function where the guard and monotrichs offer mechanical protection and the woolly hairs provide good insulation. A third mechanism involves the irregularity of the structure of the hair shaft along its length. For protection, coreless ends of hair shafts are especially valuable, with their high mechanical properties provided by the well-developed cortical layer. Other narrowed parts of the hair shaft also contribute to high durability with their slightly developed or absent cores and thick tougher cortical layers. In such places the hair shaft is easily bent to any side without damage, providing elasticity and thereby preventing the shaft from being fractured or crushed.

In *Talpa europaea*, the categories of hair types are similar, producing fur that is relatively short, smooth, and dense with a slightly pronounced pile and little taper to the tail. Such specific structure of the fur allows the animal to move freely forward and backward in narrow burrows.

Microstructural peculiarities of mole hair have pronounced adaptive value. For example, the slight development of the core layer of the hair shaft and consequent greater cortical layer improve the mechanical qualities. That this applies only to directing and guard hairs and not to woolly hair, which has thicker cores than other hairs, improves the thermoresistance of the hair. The woolly hair, covered by the guard and directing hairs, experiences minimal mechanical disturbance, thereby reducing the need for mechanical properties and permitting a specialization toward greater insulative properties. As it has denser, longer fur and thicker skin than the shrew, the mole's external cover offers greater thermoresistant properties.

The structure of the hair cover of *Neomys fodiens* shares features common to both terrestrial shrews and moles. Its hairs, unlike those of other insectivorans, are longest on the flanks, a feature which may improve the hydrodynamics as it swims and dives. Other morphological peculiarities include the presence of longitudinal grooves of the flattened guard hairs of the flanks; the relatively slight development, compared with other Insectivora, of the core in grana of covering hairs; the thinning and lengthening of all types of hair, the latter by increase in segment number; and the higher density and thickness of the skin. These characters combine to provide an improved ability to retain heat in an air layer within the fur. Thus, the fur stays dry, making a more perfect insulative covering. The character of molting is also distinctive, for the changes occur gradually and molting is prolonged (Ivanter et al., 1984, 1985). Finally, *N. fodiens* has the countershading of the body that is typical of aquatic animals, with a dark back and light underside and no transitional zone at the flanks. According to Cott (1940), this is due to the optical effect, desirable for inhabitants of the upper layers of water, which obscures the body by masking the shadow.

Other characteristic features of the aquatic *N. fodiens* include the more pronounced differentiation of hairs into categories, and the uniform type of pelage topography. The monotrichs and guard hairs are typically wider and have more flattened terminal segments. These produce an overlapping, almost tile-shaped cover which, because of the surface tension of the water, retains the insulative air layer in the woolly hair (Gudkova-Aksenova, 1951; Sokolov, 1973). Entrapment of the air layer is enhanced by the density of woolly hairs, the twisting character of their shafts, and the comparatively better-developed core region (72–73% versus 49–50% in covering hairs). Typically, the guard hairs are straighter than in other shrews. Contacts between cuticular scales and the hair shaft, and between the scales themselves produce a sleek surface for the hair. In addition, close spacing of the rows of scales provides an effective protection from moistening.

This research also supports suggestions by a number of authors (Appelt, 1973; Hutterer and Hurter, 1981; Vogel and Köpchen, 1978) about the typical profile of the cross section of guard hairs from *N. fodiens*. Because of the numerous diagonal cuticular slats that cover the bottom of longitudinal grooves on the guard hairs on the flanks, the H-profile has 1.5–2.0 times more teeth than shrews in the genus *Sorex*. This peculiarity is also an adaptation to swimming, because additional teeth

contribute to trapping air within the fur.

In conclusion, shrews have four types of hair that differ in their contributions to protection and thermoregulation. The long, thick, and elastic monotrichs comprise only 0.5% of hairs, but serve an important sensory function. Wooly hairs are thin and short, but constitute 40% (summer) to 60% (winter) of the pelage density and are important in thermoregulation. The two types of guard hairs protect as well as insulate. Winter pelage is 20–40% thicker and hairs 30–40% longer than in summer. In winter, all hairs are thinner, softer, and lighter in color than in summer, and the hollow cores of the hairs increase substantially. Despite being thinner in diameter, winter hairs have larger hollow cores, comprising 60–85% of hair cross section. Insulation is due to the dead air space of the pelage that reduces heat convection from the body, and, to a lesser extent, to the hollow nature of hairs. Tests with dried skins showed that winter pelage was about 30% more effective at retaining heat than summer pelage. Overall, shrews are able to minimize thermal conductance during the winter months through a combination of changes in hair quality and hair density.

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Table 1.—*Characteristics of summer fur from three body regions in* Sorex araneus.

Type of Hair	*n*	Number of Hairs Per 4 mm^2	Length of Hair (mm)	Thickness of Hair (μ)	Number of Segments
		Back			
Monotrich	17	3.6 ± 0.2	5.1 ± 0.06	50.0 ± 0.3	1
Type I guard	25	114.0 ± 4.0	4.2 ± 0.01	50.0 ± 0.4	3
Type II guard	25	89.8 ± 5.7	4.0 ± 0.05	27.2 ± 0.4	4
Woolly	25	235.3 ± 7.1	3.6 ± 0.02	12.6 ± 0.1	4
		Side			
Monotrich	16	2.3 ± 0.1	4.7 ± 0.03	49.9 ± 0.5	1
Type I guard	24	94.6 ± 5.7	4.3 ± 0.04	49.7 ± 0.6	3
Type II guard	25	66.3 ± 6.5	4.1 ± 0.09	26.1 ± 0.4	4
Woolly	26	232.4 ± 5.7	3.4 ± 0.01	9.8 ± 0.2	4
		Abdomen			
Monotrich	18	2.0 ± 0.1	4.4 ± 0.04	49.8 ± 0.6	1
Type I guard	25	169.2 ± 6.7	4.1 ± 0.04	49.7 ± 0.4	3
Type II guard	24	83.6 ± 4.9	3.6 ± 0.03	28.0 ± 0.3	4
Woolly	23	224.6 ± 7.1	3.3 ± 0.01	10.2 ± 0.1	4

Table 2.—*Characteristics of winter fur from three body regions in* Sorex araneus.

Type of Hair	*n*	Number of Hairs Per 4 mm^2	Length of Hair (mm)	Thickness of Hair (μ)	Number of Segments
		Back			
Monotrich	16	4.1 ± 0.3	8.5 ± 0.09	30.2 ± 0.2	1
Type I guard	20	119.2 ± 3.1	7.5 ± 0.08	30.1 ± 0.6	6
Type II guard	20	135.6 ± 5.0	7.0 ± 0.08	25.4 ± 0.4	7
Woolly	24	264.2 ± 5.1	6.2 ± 0.03	7.2 ± 0.3	7
		Side			
Monotrich	15	3.0 ± 0.1	8.5 ± 0.06	30.1 ± 0.3	1
Type I guard	16	117.0 ± 4.2	7.1 ± 0.05	30.0 ± 0.5	6
Type II guard	18	104.2 ± 3.6	6.9 ± 0.03	25.2 ± 0.3	7
Woolly	21	205.4 ± 3.9	5.9 ± 0.02	7.2 ± 0.4	7
		Abdomen			
Monotrich	17	2.3 ± 0.1	7.9 ± 0.09	31.0 ± 0.4	1
Type I guard	24	122.3 ± 3.3	6.1 ± 0.07	30.2 ± 0.1	6
Type II guard	26	141.7 ± 5.1	5.6 ± 0.05	25.1 ± 0.8	7
Woolly	22	299.1 ± 5.0	4.6 ± 0.02	7.4 ± 0.6	7

Table 3.—*Characteristics of summer fur from three body regions in* Neomys fodiens.

Type of Hair	*n*	Number of Hairs Per 4 mm^2	Length of Hair (mm)	Thickness of Hair (μ)	Number of Segments
		Back			
Monotrich	17	3.5 ± 0.2	8.0 ± 0.02	50.0 ± 0.4	1
Type I guard	25	137.2 ± 5.1	6.5 ± 0.11	27.6 ± 0.5	4
Type II guard	16	108.1 ± 5.3	6.2 ± 0.01	23.0 ± 0.3	5
Woolly	18	218.6 ± 5.0	6.0 ± 0.02	9.8 ± 0.1	5
		Side			
Monotrich	16	2.9 ± 0.1	8.5 ± 0.08	50.0 ± 0.6	1
Type I guard	25	120.2 ± 3.4	7.0 ± 0.06	28.1 ± 0.5	4
Type II guard	21	106.9 ± 3.9	6.5 ± 0.09	21.3 ± 0.3	5
Woolly	24	120.9 ± 4.1	6.2 ± 0.03	10.0 ± 0.1	5
		Belly			
Monotrich	14	2.1 ± 0.1	7.5 ± 0.08	50.0 ± 0.7	1
Type I guard	18	128.3 ± 4.1	5.9 ± 0.07	37.1 ± 0.6	4
Type II guard	19	107.1 ± 4.0	5.6 ± 0.05	27.2 ± 0.2	5
Woolly	25	130.6 ± 3.9	5.3 ± 0.02	10.2 ± 0.1	5

Table 4.—*Seasonal difference in the density of hairs (number of hairs/4 mm^2) in five species of insectivores and three species of rodents from northwestern Russia.*

Species	Season	*n*	Back	Side	Abdomen
Sorex araneus	summer	25	442.7 ± 7.3	395.6 ± 7.9	479.8 ± 4.6
	winter	25	523.1 ± 7.2	429.6 ± 4.4	565.4 ± 9.0
Sorex caecutiens	summer	25	389.9 ± 6.8	376.3 ± 7.7	332.8 ± 7.6
	winter	25	538.5 ± 8.9	432.7 ± 8.7	460.9 ± 9.1
Sorex minutus	summer	14	364.0 ± 6.7	328.3 ± 6.0	266.4 ± 4.3
	winter	15	463.4 ± 5.3	413.1 ± 5.1	395.9 ± 4.7
Neomys fodiens	summer	18	467.4 ± 6.1	350.9 ± 5.3	368.1 ± 5.0
Talpa europaea	summer	16	521.1 ± 9.6	368.9 ± 9.2	457.9 ± 5.9
	winter	15	728.7 ± 9.8	538.1 ± 9.1	572.0 ± 9.2
Sicista betulina	summer	18	576.3 ± 8.3	495.7 ± 3.1	381.9 ± 7.0
Clethrionomys glareolus	summer	15	299.9 ± 3.0	288.8 ± 3.1	225.4 ± 1.8
	winter	13	422.5 ± 4.6	399.2 ± 4.1	284.7 ± 2.1
Microtus oeconomus	summer	15	334.0 ± 2.9	288.1 ± 1.9	317.6 ± 2.1
	winter	15	478.7 ± 6.1	453.6 ± 5.6	460.2 ± 5.8

Table 5.—*Thickness of hairs on the backs of five insectivores and three rodents from northwestern Russia. "Percent" refers to the thickness of the cortical layer as a percentage of the total thickness of the hair.*

Species	Season	Guard Hairs			Woolly Hairs		
		n	Thickness of Hair (μ)	Percent	*n*	Thickness of Hair (μ)	Percent
Sorex araneus	summer	25	40.0 ± 0.4	58.0	25	12.6 ± 0.1	63.0
	winter	20	30.1 ± 0.6	63.4	24	7.2 ± 0.3	77.0
Sorex caecutiens	summer	50	31.1 ± 0.6	64.3	28	11.0 ± 0.8	61.8
	winter	28	27.0 ± 0.4	61.5	26	7.9 ± 0.3	78.5
Sorex minutus	summer	25	27.6 ± 0.4	54.7	29	10.0 ± 0.3	61.0
	winter	24	23.8 ± 0.02	64.7	33	6.1 ± 0.3	80.3
Neomys fodiens	summer	16	27.6 ± 0.05	50.0	18	9.8 ± 0.1	72.1
Talpa europaea	summer	25	32.4 ± 0.3	50.9	19	10.9 ± 0.2	54.2
	winter	17	27.8 ± 0.5	66.1	25	9.7 ± 0.2	70.1
Sicista betulina	summer	20	17.4 ± 00.2	79.9	18	15.8 ± 0.2	81.0
Clethrionomys glareolus	summer	22	49.1 ± 0.3	79.5	20	28.1 ± 0.2	78.2
	winter	18	20.1 ± 0.2	71.3	18	11.9 ± 0.2	79.9
Microtus oeconomus	summer	10	49.1 ± 0.6	87.0	10	22.8 ± 0.7	54.3
	winter	9	48.6 ± 0.6	87.8	9	16.4 ± 0.3	81.6

Table 6.—*Length of hairs (mm) in five species of insectivores and three species of rodents. Sample sizes in parentheses.*

Species	Season	Back		Side		Abdomen	
				Guard Hairs			
Sorex araneus	summer	4.2 ± 0.01	(25)	4.3 ± 0.04	(24)	4.1 ± 0.04	(25)
	winter	7.5 ± 0.08	(20)	7.1 ± 0.05	(16)	6.1 ± 0.07	(24)
Sorex caecutiens	summer	4.0 ± 0.05	(50)	4.0 ± 0.04	(60)	3.7 ± 0.3	(50)
	winter	7.5 ± 0.07	(28)	7.7 ± 0.04	(29)	5.2 ± 0.5	(26)
Sorex minutus	summer	3.3 ± 0.01	(25)	3.2 ± 0.01	(25)	2.9 ± 0.01	(24)
	winter	5.2 ± 0.02	(24)	5.1 ± 0.01	(25)	4.7 ± 0.01	(25)
Neomys fodiens	summer	6.5 ± 0.11	(25)	7.0 ± 0.06	(25)	5.9 ± 0.07	(18)
Talpa europaea	summer	7.9 ± 0.02	(25)	7.7 ± 0.01	(18)	6.4 ± 0.04	(18)
	winter	11.2 ± 0.05	(19)	10.9 ± 0.04	(18)	10.0 ± 0.06	(19)
Sicista betulina	summer	8.1 ± 0.09	(25)	7.1 ± 0.09	(25)	6.7 ± 0.04	(25)
Clethrionomys glareolus	summer	8.4 ± 0.03	(22)	8.0 ± 0.03	(26)	7.5 ± 0.02	(28)
	winter	11.2 ± 0.03	(18)	9.9 ± 0.03	(22)	9.1 ± 0.03	(26)
Microtus oeconomus	summer	12.2 ± 0.05	(14)	11.9 ± 0.05	(11)	10.1 ± 0.06	(9)
	winter	15.1 ± 0.05	(9)	14.7 ± 0.05	(10)	13.8 ± 0.06	(16)
				Woolly Hairs			
Sorex araneus	summer	3.6 ± 0.02	(25)	3.4 ± 0.01	(26)	3.3 ± 0.01	(23)
	winter	6.2 ± 0.03	(24)	5.9 ± 0.02	(21)	4.6 ± 0.02	(22)
Sorex caecutiens	summer	3.5 ± 0.02	(25)	3.3 ± 0.01	(25)	3.1 ± 0.01	(40)
	winter	5.2 ± 0.03	(26)	5.0 ± 0.01	(25)	3.8 ± 0.02	(23)
Sorex minutus	summer	2.8 ± 0.04	(29)	2.8 ± 0.04	(27)	2.4 ± 0.01	(25)
	winter	4.2 ± 0.02	(33)	4.0 ± 0.04	(25)	3.6 ± 0.05	(27)
Neomys fodiens	summer	6.0 ± 0.02	(18)	6.2 ± 0.03	(24)	5.3 ± 0.02	(25)
Talpa europaea	summer	6.5 ± 0.02	(29)	6.4 ± 0.03	(25)	5.1 ± 0.01	(25)
	winter	10.1 ± 0.02	(25)	9.4 ± 0.01	(20)	8.9 ± 0.02	(25)
Sicista betulina	summer	7.5 ± 0.11	(27)	6.5 ± 0.08	(25)	5.7 ± 0.04	(24)
Clethrionomys glareolus	summer	7.3 ± 0.02	(20)	7.0 ± 0.04	(22)	6.6 ± 0.02	(32)
	winter	9.4 ± 0.03	(18)	9.1 ± 0.03	(28)	7.9 ± 0.02	(24)
Microtus oeconomus	summer	10.9 ± 0.04	(16)	10.0 ± 0.03	(15)	8.6 ± 0.06	(10)
	winter	12.3 ± 0.07	(9)	11.9 ± 0.05	(10)	11.0 ± 0.02	(14)

Table 7.—*Coefficient of heat conductivity (CHC = 10^{-3} w/m °K) of dry skins in seasonal samples of five insectivores and three rodents from northwestern Russia. Note: autumn specimens were molting.*

Species	Season	*n*	CHC	$\bar{X} \pm SE$
Sorex araneus	summer	16	38.2–50.0	47.6 ± 0.8
	winter	15	35.0–45.4	37.4 ± 0.6
	autumn	12	33.1–41.2	34.7 ± 0.5
Sorex caecutiens	summer	16	50.0–60.0	54.0 ± 1.2
	winter	15	38.3–42.6	40.1 ± 0.5
	autumn	13	37.1–44.8	39.4 ± 0.3
Sorex minutus	summer	15	49.0–59.2	53.5 ± 0.9
	winter	14	38.0–49.0	42.2 ± 0.5
	autumn	9	36.0–45.0	39.0 ± 0.4
Neomys fodiens	summer	18	30.0–42.1	32.5 ± 0.9
	autumn	14	28.0–39.0	30.3 ± 0.8
Talpa europaea	summer	9	24.2–30.0	26.7 ± 0.3
	winter	8	19.0–22.4	20.5 ± 0.3
	autumn	8	18.9–21.0	19.1 ± 0.3
Sicista betulina	summer	22	48.0–50.3	48.6 ± 0.3
	autumn	4	37.9–38.2	38.1 ± 0.4
Clethrionomys glareolus	summer	20	45.2–53.1	49.8 ± 0.9
	winter	16	37.0–50.0	41.0 ± 0.8
	autumn	14	36.1–42.1	38.7 ± 0.8
Microtus oeconomus	summer	11	46.7–53.2	47.8 ± 0.4
	winter	5	34.1–38.4	36.5 ± 0.4
	autumn	8	34.1–40.9	36.1 ± 0.6

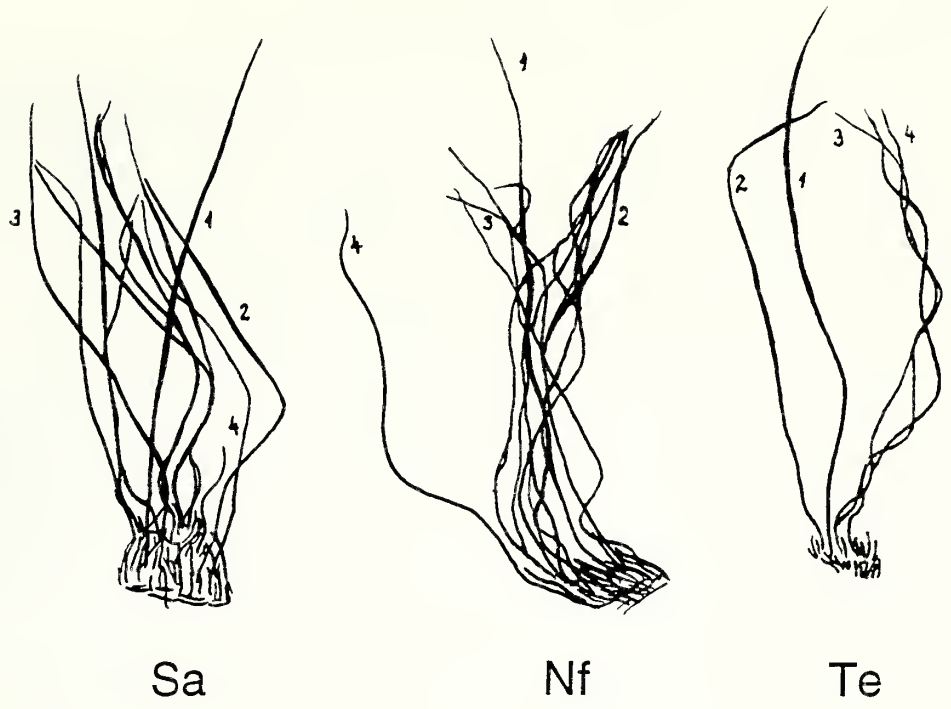

Fig. 1.—Summer hairs in *Sorex araneus* (Sa), *Neomys fodiens* (Nf), and *Talpa europaea* (Te). Numbers refer to: 1, monotrichs; 2, Type I guard hairs; 3, Type II guard hairs; 4, woolly hairs.

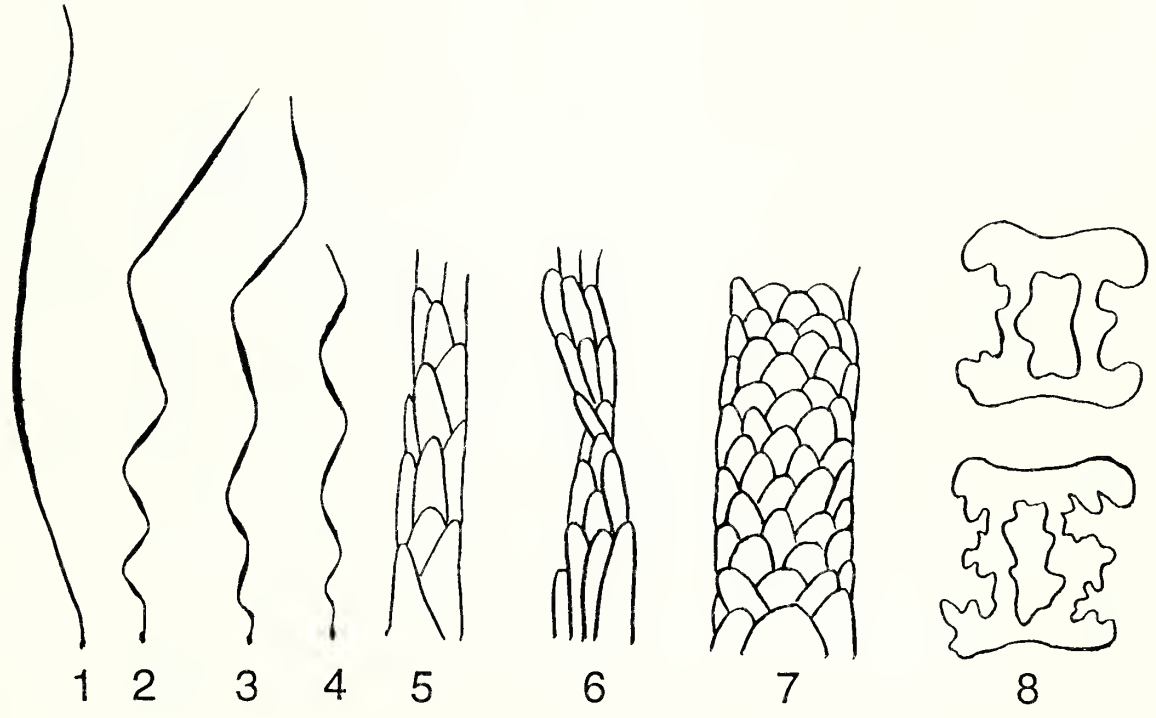

Fig. 2.—Structure of winter hairs in *Sorex araneus*. 1, monotrichs; 2, Type I guard hairs; 3, Type II guard hairs; 4, woolly hairs; 5–7, texture of the cuticular layer: 5, in lower zone of hair; 6, in zone of bending; 7, wide part of hair segment; 8, H-shaped profiles in cross section of guard hairs of *S. araneus* (upper) and *Neomys fodiens* (lower).

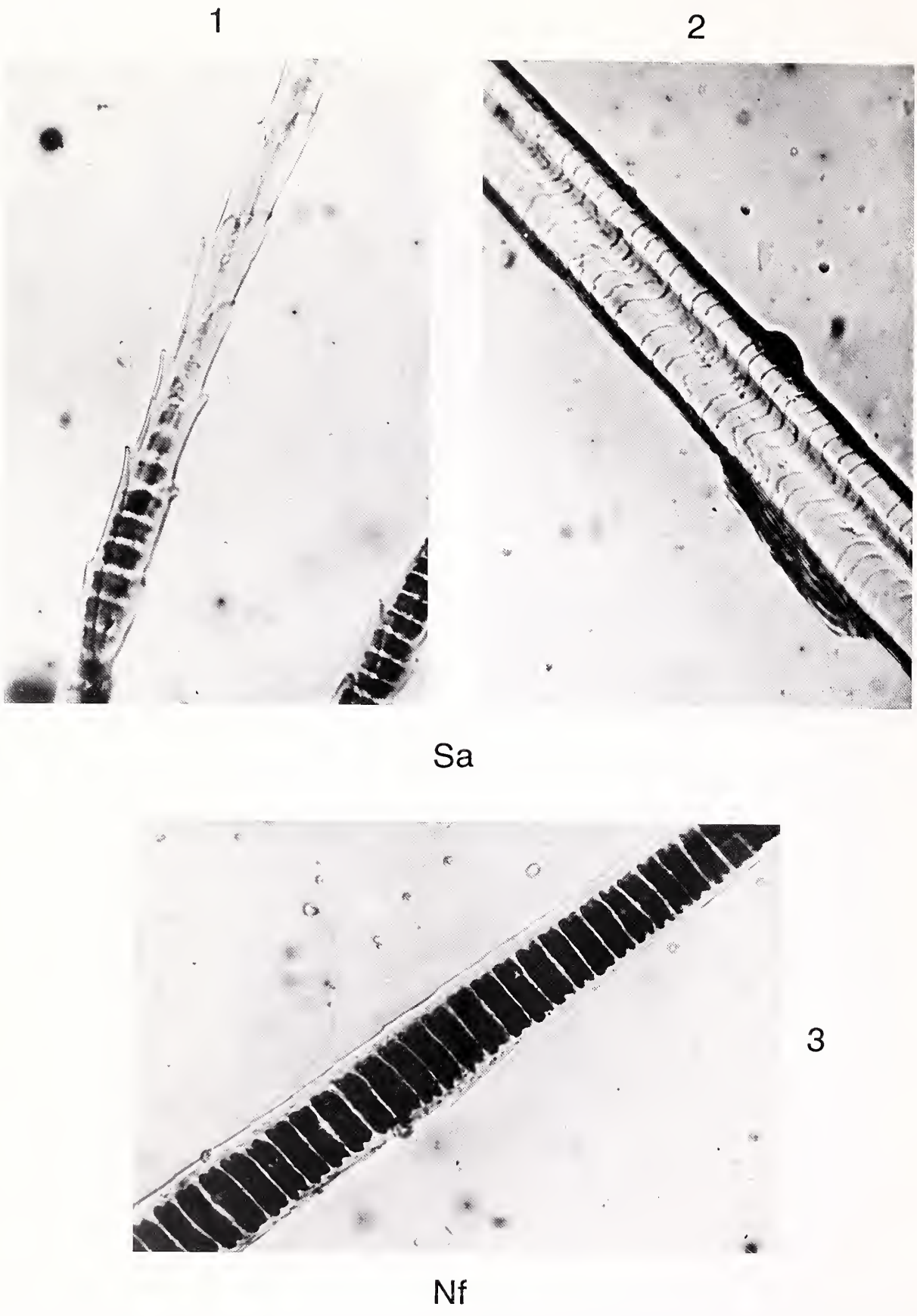

Fig. 3.—Microstructure between segments (1) and in the distal segments (2) of the guard hair shaft in *Sorex araneus* (Sa), and *Neomys fodiens* (Nf, 3).

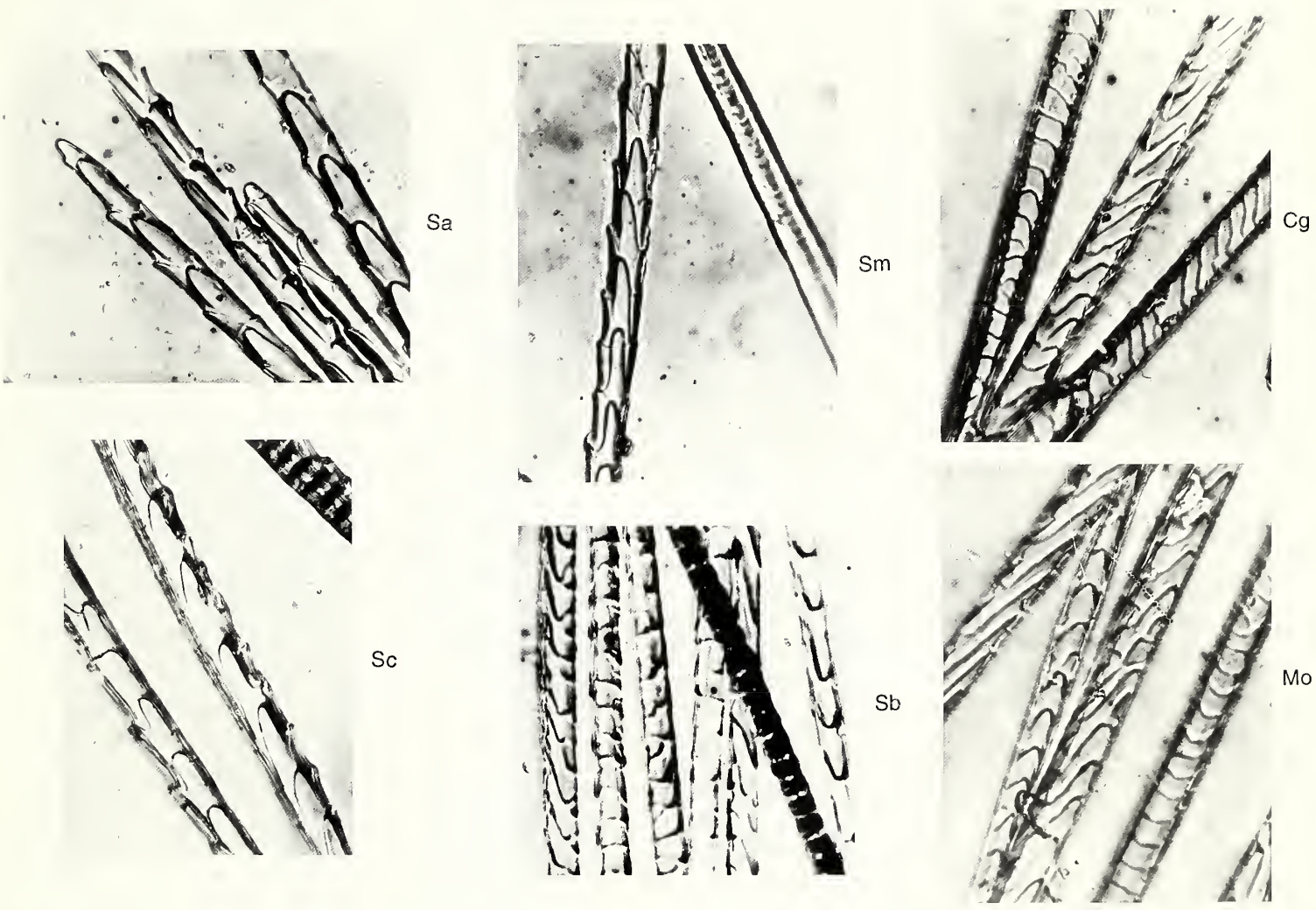

Fig. 4.—Structure of the cuticular layer in *Sorex araneus* (Sa), *S. cinereus* (Sc), *S. minutus* (Sm), *Sicista betulina* (Sb), *Clethrionomys glareolus* (Cg), and *Microtus oeconomus* (Mo).

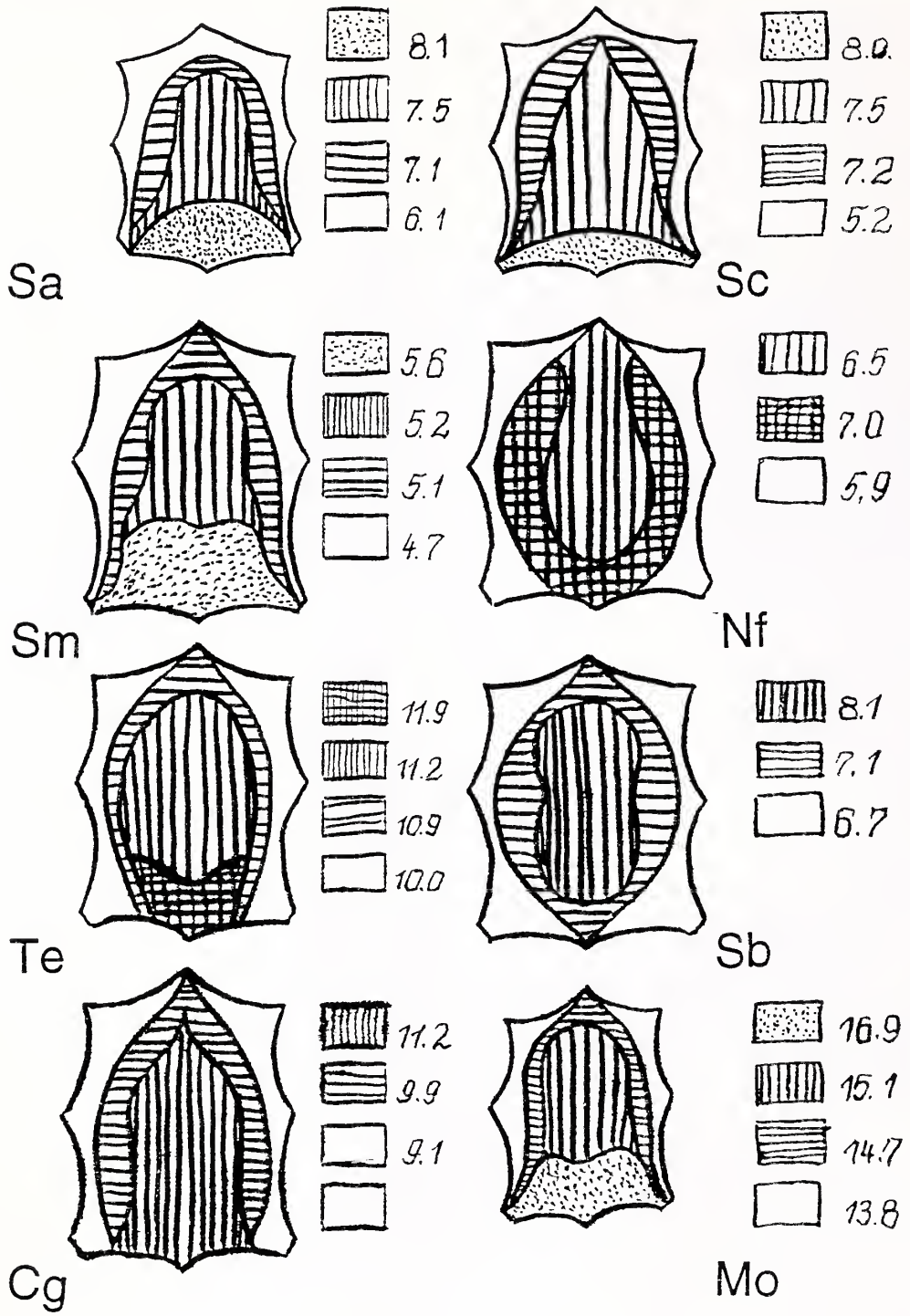

Fig. 5.—Topography of hair length (mm) in *Sorex araneus* (Sa), *S. cinereus* (Sc), *S. minutus* (Sm), *Neomys fodiens* (Nf), *Talpa europaea* (Te), *Sicista betulina* (Sb), *Clethrionomys glareolus* (Cg), and *Microtus oeconomus* (Mo). Each figure represents a dried skin and the patterns represent the areas of uniform hair lengths of the dimensions given next to the symbols in the boxes. The stippled pattern is found on the sacral region (rump).

SORICID BIOLOGY: A SUMMARY AND LOOK AHEAD

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The International Colloquium on the Biology of the Soricidae, which was held from 8 to 14 October 1990 at the Carnegie Museum of Natural History's Powdermill Biological Station, represents the first comprehensive international meeting devoted to the study of shrews. During the first half of this century, cricetid and murid rodents occupied center stage in research to understand the biology of mammals, and more recently research by bat biologists has yielded important insights into mammalian physiology, systematics, community structure, neural activity, and ecomorphology. Papers presented at the Powdermill colloquium and included in this volume revealed that shrews also have the potential for advancing our understanding in many areas of mammalian biology. In this chapter, I summarize the information and ideas presented by participants in the colloquium, while trying to identify areas of significant advances as well as potential areas for future research.

The family Soricidae (shrews) is the largest family in the order Insectivora, with 20 genera and 290 species. Among families of Recent mammals, only the Muridae (murid rodents, 1,122 species) and Vespertilionidae (common bats, 313 species) are larger. Shrews are widespread in the Nearctic, Palearctic, Oriental, and Ethiopian biogeographic regions, but barely extend into the northern Neotropical and are absent from the Australian region. Two suborders of shrews are recognized: Soricinae (red-toothed shrews) and Crocidurinae (white-toothed shrews). Soricine shrews, including such representative genera as *Sorex*, *Blarina*, *Cryptotis*, and *Neomys*, are largely Holarctic in distribution, with a few species in Central America and northwestern South America. They are most abundant and diverse in cool, moist boreal forest regions. In contrast, crocidurines are abundant and widespread in the Old World tropics and subtropics, especially Africa, the Indian and Indochinese subcontinents, and Malaysia. Limited geographic overlap between the distributions of soricine and crocidurine shrews occurs mainly in southern Europe and along the Palearctic-Oriental boundary.

With 185 species in such genera as *Crocidura*, *Suncus*, and *Myosorex*, crocidurine shrews are more diverse than soricines. They are also more diverse in body size and thermoregulatory ability, and are potentially more complex in patterns of distribution and ecology. We know considerably less about the biology of crocidurines than about soricine shrews because the distribution of the majority of mammalogists, who reside principally in Eurasia and North America, coincides with the distribution of soricines. Many crocidurine species, including some of the nearly 150 species of *Crocidura*, are known from relatively few specimens or localities. To illustrate the magnitude of the problems of studying crocidurines, Zaire, with 52 species of crocidurine shrews, has more shrew species than are found in the Americas.

Methodologies

Most information on the distribution, populations, and community structure of shrews has come from studies using kill traps, either snap or pitfall traps. In North America, knowledge of shrew distribution and abundance has been greatly advanced in the past two decades with the increasingly widespread use of pitfall traps; some species, such as *Sorex hoyi* and *S. longirostris*, can only be studied effectively with this method. However, methods or procedures for pitfall trapping differ widely for a variety of reasons, including the objectives of the study, the nature of the substrate, and the availability of materials and manpower. Results are most comparable to other studies when standardized methods for the shape of pitfall arrays or the spacing and length of pitfall transects (such as those presented in this volume) are used.

For some investigations, live trapping is clearly superior to kill trapping because the dynamic features of movement, lifespan, territory shifts, changes in body mass, and many others can be studied only by repeatedly observing an animal. Several papers in this volume report some of these details from mark-and-release studies. However, because many shrews do not survive well in live traps, it is difficult to secure long-term trapping records of individual shrews. Some shrews are so tiny that trap sensitivity can be a compounding problem. In addition, trapping throughout the winter poses further problems. Hawes' (1977) year-round study of two *Sorex* species in Canada remains a model for others to emulate.

Although radiotelemetry continues to hold promise in the study of shrews, the reductions in the size of radiotransmitters of the 1970s were not continued in the 1980s, consequently transmitters of the present generation are still too large for use with most species of shrews. Other electronic methods, such as tiny implants with holographic bar codes, are needed for the study of free-ranging shrews in the field or in seminatural enclosures. In sum, substantial challenges remain to secure shrews for study. Nevertheless, in many parts of the world great advances in understanding can be achieved by using the present methods.

Origin and Paleohistory

As with mammals in general, living shrews are a subset of past experiments in soricid evolution. Although shrews date from the mid-Tertiary, neither their small size nor their

distribution has changed much during their evolutionary history, although soricines apparently moved westward from Asia and later diversified in Europe. Soricines still dominate in the Holarctic, whereas crocidurines generally have tropical distributions, with relatively few species in temperate regions. Although many details are known about the fossil history of shrews in some regions, little or nothing is known elsewhere. With the increasing knowledge of the differences in physiologies and environmental tolerance between soricines and crocidurines, shrews are very important in understanding past environments.

Systematics and Evolution

The systematics and evolutionary relationships of many shrews remain uncertain. Because the cranial features important for identification have little phylogenetic value in some groups of shrews, it was not surprising to learn that cranial characters alone sometimes are not useful in phylogenetic studies. Some shrews show promise for yielding insight into how chromosomal evolution occurs, whether at the micro- or regional scale, because of their great variation in diploid numbers and chromosomal banding patterns. Furthermore, island populations of shrews are models to study the rate of evolutionary divergence between island and mainland populations, and how small mammals traverse water barriers and colonize offshore islands. The diversity, abundance, small size, and variability of shrews should contribute to their increased study and to substantial advances by systematic and evolutionary biologists during the coming decade.

Growth and Development

Because only a few species of shrews have been bred and raised successfully in the laboratory, the opportunities to study embryos of known age to determine developmental rates and to evaluate developmental processes have been limited. Soricine shrews have among the shortest gestation times of placental mammals. Young are born at an early stage of development (almost like that of newborn marsupials), and have a relatively long period of postnatal development. Whether altricial young affirms the primitive evolutionary status of shrews or represents a derived feature, such as in passerine birds and many rodents, is moot. Extremely small maternal body size and large litter size may be part of the explanation for the tiny size of altricial newborn shrews, but the high metabolic rates of shrews should hasten development, both before and after parturition (McNab, 1980). Of course, the efficiency of transfer in the placenta, enzyme kinetics, and the quality of milk are other factors that could account for the seemingly slow rate of development in at least some soricine shrews. For whatever reasons, there are notable differences in the developmental rates of shrews and mice (in which development has been thoroughly studied).

Postnatal development is also puzzling because shrews apparently differ from most small mammals in that young stay in the nest until virtually fully grown. By contrast, the young of most small mammals become semi-independent of the nest (and often are weaned) when only half or two-thirds grown. The most plausible explanation for the failure to catch juvenile or subadult shrews has been that young shrews are not exposed to traps because they remain nestbound during the 4–5 weeks of postnatal development. This is merely an assumption because almost nothing is known about rates or stages of postnatal growth in shrews, and even less about the behaviors associated with this period. Many such details could be learned in the laboratory using electronic devices and video cameras. Studies of development could also be important in understanding the evolutionary relationships of metatherian and eutherian mammals.

Anatomy and Morphology

Studies of shrew anatomy are potentially rewarding for several reasons. The shrew brain differs in appearance and proportions from the brains of most mammals, especially in the presence of exceptionally large olfactory bulbs. The brain of some soricid shrews physically shrinks more than the body during the winter months, a surprising revelation reported by Dehnel (1952). Dehnel's phenomenon, first reported for *Sorex araneus* in Poland and confirmed in other species of *Sorex*, remains in need of a plausible explanation. Other unusual anatomical modifications include the teeth, which in some soricines are highly modified to include red enamel (produced by iron pigments) and large procumbent incisors, which sometimes possess tines. In contrast, crocidurines are called "white-toothed shrews." The cheek teeth of shrews also are modified ("unicuspids") compared to those of most mammals, making the entire dentition, the jaw musculature, and masticatory mechanics a challenge for functional morphologists to study and understand. In some soricines, the hairs change in size and shape between seasons, as do the relative proportions of white and brown adipose tissues.

Although the eye of shrews has the basic eutherian components, the eyeball is small and many features are reduced. The ear likewise has the basic eutherian design but the small size of the head limits the auditory discrimation capacity of shrews. Although shrews were reported to navigate by echolocation more than 25 years ago, the link between hearing and behavior remains to be clarified. Much could be achieved by research on this topic. The olfactory system is well-developed and smell may surpass hearing as the most important sense in shrews. Species of *Blarina*, *Neomys*, and the solenodons have modified submaxillary (salivary) glands which produce toxins; these shrews and the duck-billed platypus, males of which have a spur associated with poison glands on the hind leg, are the only venomous mammals. The nature of the salivary toxin, its adaptive value, and whether the poison enables shrews to overpower and kill prey larger than themselves or to immobilize prey for later consumption are important issues in need of study. Finally, histological studies of gonads could be important in understanding the annual cycle of breeding in shrews. Soricine shrews are believed to be among the most reliable seasonal breeders of all small mammals, but the details of the annual cycle of the testis and ovary remain largely unknown.

Reproduction and Life-History Traits

Crocidurines differ from soricines in their life-history traits by being physically larger and having fewer and larger neonates after a longer gestation period. Weaning occurs sooner in *Crocidura* than in *Sorex*, and their young are weaned at a smaller mass measured as a percentage of adult body mass. If grams of young produced across pregnancy and lactation are considered in relation to maternal mass, *Sorex* allocates more than twice as much energy to reproduction as does *Crocidura*. The average *Sorex* female (6.5 g) produces 34.2 g of weaned young, or a mass of young equal to 526% of maternal mass, in 45.1 days. This value conforms to Pearson's (1944) observation that an 11-g *Blarina brevicauda* female supports a litter mass of 55 g near the end of lactation. By contrast, the average *Crocidura* female produces weaned young equal to 255% of maternal mass over 49.1 days, and for *Suncus murinus*, the largest crocidurine shrew, the value is 181% over 48.1 days.

Expressed as a percentage of maternal mass per day, the litter mass in these three genera accrued ten times faster during lactation than during pregnancy. For example, embryo mass of *Sorex* grew at a rate of 2.34% of maternal mass per day during pregnancy, but litter mass of neonates grew at a rate of 22.56% of maternal mass per day. For *Crocidura* these values are 1.06% per day during pregnancy and 11.19 % per day during lactation, and for *Suncus murinus* the values are 0.64% and 6.26% per day, respectively. Thus, although *Sorex* females seemingly allocate twice as much energy per gram of maternal mass to the production of a weaned litter compared to *Crocidura* or to *Suncus murinus*, the three genera are similar in the greatly increased cost of lactation over pregnancy. I agree with Bronson (1989) that the energetic costs of lactation in shrews can be enormous.

Physiology and Parasites/Disease

As the smallest mammals with the highest metabolic rates, shrews therefore have the highest energy demands on a mass-specific basis. Yet many soricine shrews live in extremely cold environments where they apparently must pay huge energy costs to survive. Because their small size precludes storing much fat or gaining much insulation value from winter pelage, shrews in winter would seem to need plentiful, energy-rich prey. Alternatively, they would need to modify dietary selection, build highly insulative subterranean nests, change solitary behavior to permit communal nesting, hibernate or enter torpor, or employ combinations of these to survive in cold environments. Soricine shrews probably avoid extremely low air temperatures by living underground and in the subnivean space between the ground and snow cover; nevertheless, they must confront temperatures near 0°C for many months of the winter. Although some soricines accumulate brown fat in autumn which is mobilized to produce heat by nonshivering thermogenesis as needed in the coldest months (Merritt, 1986), other strategies of shrews to survive winter conditions are poorly understood. Some shrews eat more vegetable matter and a few may aggregate during the winter months. Surprisingly *Crocidura* (not *Sorex*) has a relatively low body temperature and metabolic rate, and the ability to enter torpor, features that seemingly would be more adaptive in arctic rather than in tropical environments. Much can be learned in the coming years by relating physiology to ecology, such as by electronic monitoring for location and movements and changes in body temperature and heart rate. Dietary studies are badly needed, too, particularly throughout the year at locations with cold and snowy winters. Such studies could provide information on where shrews obtain the calories to maintain high body temperatures during cold months.

Shrews have not been much studied from the standpoint of diseases or parasites, in part because shrews generally are not economic pests although they sometimes are serious seed predators. Furthermore, shrews do not live as commensals to humans, thereby minimizing their potential role in disease transmission. However, a knowledge of the histopathological changes in populations may be important in understanding the dramatic year-to-year density changes that typify some populations of shrews.

Populations and Communities

Several papers in this volume substantially advance understanding of the ecology of soricine shrew populations and communities. Population density often fluctuates greatly from year to year in some species, but a long-term study of a *Blarina* population revealed mostly low-amplitude annual cycles and no relationship to the high-amplitude multiannual cycles of two syntopic microtine rodents. The causes of year-to-year differences in shrew population density are unknown but may be influenced by fluctuating amount and availability of food or by predator densities. Shrews apparently move modest distances, and the size and stability of territories are related to age and breeding activity. Shrews have fairly predictable breeding seasons, starting later in northern than in more southerly locations. Mortality rates are fairly constant throughout the year in some populations; mortality from autumn to spring may be as high as 75%, and the chance of surviving a second winter nil. Whether these patterns found in soricines also apply to crocidurines remains to be learned.

In the Holarctic biogeographic region, small mammal communities in most mesic, midlatitude sites are characterized by the presence of two or more soricine shrews. Shrew species tend to become proportionately more abundant in small mammal communities at higher latitudes. In North America the greatest diversities of shrews are found in the Oregon-Washington-British Columbia and northern Appalachian Mountain regions, whereas the greatest number of coexisting soricine shrew species apparently is in Siberia, where as many as nine species may be found in an area. Little is known about the diversity and role of crocidurine shrews in small mammal communities of Africa and Asia, but some localities surely have several species. Soricine shrews eat a variety of foods; however, each species usually specializes on a few species of common and abundant invertebrate prey. Prey size is not always related to the size of the shrew. If food of a particular size is abundant, the shrew species that optimally selects that food may become dominant in the shrew community. It is postulated in this volume that

large shrew species, which have twice the per capita food requirements of small shrews, exploit more productive habitats and have more stable local populations. By contrast, small species may exploit smaller and less productive habitat patches, and have transitory populations.

It is puzzling that the smallest soricine species seem to be the rarest and often have patchy distributions. Their low body masses and high metabolic rates, which result in short starvation times, tend to produce high extinction rates for small local populations. Their continued presence can be sustained, it seems, only by great fecundity and equally great dispersal capability. *Sorex minutissimus* in Eurasia and *Sorex hoyi* in North America, the smallest shrews, also seem to be the rarest. Perhaps this is due to a sampling problem, because in theory one of the best defenses against extinction of populations is large population size.

Most studies of shrews in North America, and to an extent elsewhere, have been conducted as adjuncts to studies of other species of small mammals, frequently microtine rodents. Although such studies are valuable, they rarely include experimentation or hypothesis testing for shrews, and mostly describe the dynamics and components of fitness of the population or composition of the small mammal community. Nevertheless, such information is badly needed for many shrew species, especially crocidurines, as a basis for formulating hypotheses and experiments for future studies. Relatively few studies have used live-trapping methods to mark and release shrews, while documenting the events of their lives. Fewer still have attempted to follow the daily lives of individual shrews via radiotelemetry or other electronic methods to evaluate physiological and behavioral changes within and among days and seasons. The studies reported here give a foretaste of what future investigations might reveal.

In conclusion, much remains to be learned about these fascinating small mammals, the smallest body masses of which are less than the theoretically smallest mass that can sustain metabolic rates (they haven't read the manual!), and which somehow survive the world's harshest winter environments despite the high energy costs associated with rapid heat loss, apparently low availability and quality of food, and inability to hibernate or enter torpor or even to form communal groups. Truly, the study of shrews will continue to be well repaid and to produce more results that will amaze us or continue to defy explanation.

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