

Energy Consumption of European and African Shrews

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Is the extremely high oxygen consumption of shrews due to an unusually high basal metabolism? In an attempt to answer this long-standing question, we have measured the oxygen consumption of 13 species of shrews of different origin: from Europe — *Sorex araneus*, *S. minutus*, *Neomys fodiens*, *Crocidura russula*, and *Suncus etruscus*; from Africa — *Crocidura bottegi*, *C. bicolor*, *C. juvenetae*, *C. poensis*, *C. theresae*, *C. wimmeri*, *C. flavescens*, and *C. giffardi*. The measurements, taken over a period of 20—30 minutes, were made in small, closed-system chambers at 25°C. The metabolic rate of our shrews of the subfamily *Soricinae* lies between the mean and minimum values of the *Soricini* ($M = 126.2 W^{0.52}$ cal/h and $M = 32.6 W^{0.53}$ cal/h, respectively), as recorded in the literature. The average for the African *Crocidurinae* is much lower ($M = 43.6 W^{0.67}$). The metabolic rate of the European *Crocidura russula* agrees with that of the African species. Thus, the *Crocidurinae* are characterized by a relatively low metabolic rate; the *Soricinae*, and in particular the tribe of the *Soricini*, by an extremely high metabolic rate. The tribes *Neomyini* and *Blarinini* occupy an intermediate position. These differences are also to be found at the level of the basal metabolism. This main difference between the two subfamilies can most likely be explained by evolution in geographical isolation under differential climatic conditions: the *Crocidurinae* having evolved in tropical Africa and the *Soricinae* in temperate Eurasia. [Centre Suisse de Recherches Scientifiques en Côte d'Ivoire (CSRS) and Institut de zoologie et d'écologie animale, 19, place du Tunnel, CH-1005 Lausanne, Switzerland].

I. INTRODUCTION

The conspicuous voracity of shrews, which suggests a special type of metabolism, has already been described by Brehm (1868). Morrison & Pearson (1946) conducted the first respirometric measurements and demonstrated an energy consumption far above that of rodents having a comparable body size. The authors thus postulated that the *Soricidae* might assume a special physiological status among the mammals (Pearson, 1948). Since that time, numerous contributions to the subject have appeared, mainly from the USA, England and Poland (— detailed literature register in Gębczyński, 1965, 1971). Although

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the results in these latter publications are basically the same and the relatively high values were consistently confirmed, the respective interpretations are diametrically opposed to each other.

Crucial is the question whether the basal metabolism (M_b) of shrews corresponds to that of the other warm-blooded organisms — which is calculated according to the formula of Kleiber (1967) $M_b = 3 W^{0.75}$ (heat production M_b per hour in kcal; body weight W in kg). The basic difficulty lies in the fact that direct measurements of basal metabolism in shrews cannot be made because the requisite conditions of postabsorptive state and tranquil behaviour are mutually exclusive. A shrew with an empty stomach seeks food in an extremely active manner, for without nourishment death rapidly ensues.

Thus, in order to calculate the basal metabolism, the gross results of respiratory measurements must be corrected — whereby the specifically dynamic action of the protein-rich food must be taken into consideration. While Morrison, Ryser & Dawe (1959), by means of their corrections, arrived at completely normal basal metabolism values accepted by other authors (Hawkins, Jewell & Tomlinson, 1960; Buckner, 1964), Gębczyński (1965, 1971) points to the questionable nature of these corrections, and adheres to the contention that the *Soricidae* represent a special situation.

A new aspect of this situation was revealed by the work of Dryden *et al.* (1969) concerning the thyroid activity of the Indian house shrew *Suncus murinus*. These results show a totally normal energy metabolism, comparable to that of rodents, which might be due to the conditions of laboratory confinement, but more probably results from the tropical origin of the experimental animals. The latter explanation is supported by the investigation of Hunkeler & Hunkeler (1970). These authors examined the food consumption of 4 species of African shrews, which turned out to be considerably less than that of European and American shrews.

The capture and breeding of European shrews between 1965 — 1969 at the Institute of Zoology in Basel enabled me to make observations which suggest a greater complexity in this problem. A comparison of the native common shrew (*Sorex araneus*) with the almost equally heavy common European white-toothed shrew (*Crocidura russula*) of the same geographic origin revealed marked differences respecting survival time in traps, food consumption, and potential life span — all suggestive of a differential energy consumption (Vogel, 1972). As all the high consumption measurements (with one insignificant exception) were recorded with representatives of the red-toothed shrews, I am led to suspect differences at the level of the two subfamilies. The *Soricinae*

would then be characterized by an elevated, the *Crocidurinae* possibly by a relatively »normal« level of metabolism.

A three-year stay at the »Centre Suisse de Recherches Scientifiques« (CSRS) in the Ivory Coast enabled me to become familiar with those species which Hunkeler & Hunkeler (1970) had already examined respecting food consumption. During a subsequent stay in Europe, it was then possible to compare the oxygen consumption of European representatives with that of several African shrews.

II. MATERIAL AND METHODS

In June 1972, 13 representatives of 7 African species¹ were available for respirometric measurements: from Upper Volta 2 *Crocidura giffardi* de Winton, 1898 (Nobéré 11° 31' N/1° 13' W and Bobo-Dioulasso 11° 13' N/4° 18' W); from the Ivory Coast 1 *Crocidura bicolor* Bocage, 1889 (Ouango-Fitini 9° 34' N/4° 1' W), 1 *Crocidura juvenetae* Heim de Balsac, 1958, 1 *C. theresae* Heim de Balsac, 1968, 4 *C. poensis* (Fraser, 1843), 2 *C. wimmeri* Heim de Balsac & Aellen, 1958, and 2 *C. flavescens* (I. Geoffroy, 1827), all originating in Adiopodoumé 5° 20' N/4° 8' W, near Abidjan. One *Crocidura bottegi* Thomas, 1898, likewise from Adiopodoumé, was delayed and arrived in Bern for measurement at a later date.

For purposes of comparison, 4 species of Swiss origin were available: 4 *Crocidura russula* (Hermann, 1780), 1 *Sorex araneus* Linné, 1758 (juvenile), 2 *Sorex minutus* Linné, 1766 (juvenile), and 2 *Neomys fodiens* (Pennant, 1771).

For additional material, the original data obtained at an earlier time employing the same methods with *Suncus etruscus* (Weibel, Burri & Claassen, 1971) were made available to me. This animal originated from the Basel captive colony (Vogel, 1970).

At the time the experiments began, all the shrews had been in captivity for at least a week and were thus accustomed to the new conditions.

A comparison of the literature reveals that respirometric measurements over 24 hours are preferable to short-time measurements. Nevertheless, because this type of measurement demands that the experimental animals be maintained under the most natural conditions possible, and because this precondition was not realizable at the time, we were compelled to conduct short-time measurements.

Oxygen consumption was measured in a closed system with automatic oxygen renewal; details can be found by Burri, Gehr, Mueller & Weibel (1975). Before the measurements began, the animals were placed into the experimental cage for 10 minutes — which was usually sufficient for calming the animals down. The experiments lasted 20 — 30 minutes. An observational protocol of animal activity served to facilitate critical evaluation of extreme results. With few exceptions, activity in the small cage is greatly reduced.

The experimental chamber was maintained at a temperature of 25°C. by circulating water; for the European species, this lies surely in the zone of neutral temperature. For the African species, whose thermoneutral zone lies presumably

¹ All nomenclature is according to Heim de Balsac (1966, 1968) and Heim de Balsac & Aellen (1958).

(1965) — which were obtained during 24-hour measurements with a large experimental group — supplemented with the reliable data of Buckner (1964).

The means of *Sorex* and *Microsorex* vary around the regression line $\log M = 2.10 + 0.52 \log W$ (M = total consumption in cal/h, W = weight in g), with a correlation coefficient of $r = 0.95$. Representatives of the genera *Neomys* and *Blarina*, on the other hand, lie clearly below this line; their metabolism is, in spite of their body weight, remarkably low. The exceptional situation of *Blarina* has been referred to by Martinsen (1969).

The minimal values from Buckner (1964) and Pearson (1948) serve well as further points for comparison, and lie on a regression line parallel to that of the above-mentioned means: $\log M = 1.92 + 0.53 \log W$, with a correlation coefficient of $r = 0.87$. Our *Sorex* measurements lie between the minimal and mean values of these authors. On the other hand, the average of *Neomys fodiens* lies too high — this being caused by the extreme activity of one single experimental animal. This possibility must further be taken into consideration by the evaluation of other extremely high values.

Respecting the tropical *Crocidurinae*, 6 of the 8 means of these African species lie beneath the minimal values of the *Soricinae*. With exclusion of the *Crocidura bottegi*, which completely deviates from the experimental series, the measurements vary about the regression line $\log M = 1.64 + 0.67 \log W$, with a correlation coefficient of $r = 0.98$. Only one value, that for *Crocidura wimmeri* lies too high; nevertheless, this is accounted for as in the previous case of *Neomys fodiens*, i.e. by the extreme activity of the experimental animals. Only after a period of adjustment exceeding 30 minutes was one such animal sufficiently calmed down in the experimental chamber; thereafter his energy consumption decreased to the typical African rate (— the lowest of the four values in Figure 1).

Our African *Crocidura bottegi* deviates in an unexpected manner from these otherwise homogenous results, lying in the midst of the higher values of the *Soricinae*. This is all the more surprising inasmuch as Hunkeler & Hunkeler (1970) had recorded a distinct difference in reference to their holarctic comparison species respecting food consumption. Still and all, these authors also pointed to a tendency toward increased food consumption, and related this to the extreme sensitivity of this species in captivity. *C. bottegi* also proved itself to be highly sensitive in our work — so that the possibility that an abnormal state existed in our single experimental animal can not be excluded. For this reason, I have omitted this species in the calculation of the regression line.

The most decisive point in our comparison concerns the energy consumption of the European *Crocidura russula*. As Fig. 2 shows, the mean value of the 4 measured animals lies beneath the regression line of the

Table 1

Energy consumption of *Soricidae* according to various authors plus personal mean values.

W=body weight, g; M= consumption per hour, cal/g; $M/W^{0.75}$ =consumption per metabolic body size.

No.	Species	W	M	M/W	$M/W^{0.75}$	Author
(a) Means						
SORICINI						
1	<i>Sorex cinereus</i>	3.6	253	70.4	96.8	Buckner, 1964
2	<i>Sorex arcticus</i>	5.4	289	53.5	81.5	Buckner, 1964
3	<i>Microsorex hoyi</i>	3.5	277	79.4	108.1	Buckner, 1964
4	<i>Sorex araneus</i> juv.	7.7	368	47.5	79.4	Gębczyński, 1965
5	<i>Sorex araneus</i> ad.	11.6	462	39.7	73.4	Gębczyński, 1965
6	<i>Sorex minutus</i> juv.	2.9	207	71.4	92.8	Gębczyński, 1971
7	<i>Sorex minutus</i> ad.	4.6	249	53.9	78.8	Gębczyński, 1971
NEOMYINI & BLARININI						
8	<i>Blarina brevicauda</i>	20.1	403	20.0	42.4	Buckner, 1964
9	<i>Cryptotis parva</i>	5.7	342	60.0	92.6	Pfeiffer & Gass, 1961
10	<i>Neomys anomalus</i>	13.6	428	31.5	60.4	Gębczyńska & Gębczyński, 1965
11	<i>Neomys fodiens</i> juv.	14.7	446	30.3	59.3	Gębczyńska & Gębczyński, 1965
12	<i>Neomys fodiens</i> ad.	16.9	394	23.3	47.2	Gębczyńska & Gębczyński, 1965
(b) Minimum						
SORICINI						
13	<i>Sorex cinereus</i>	3.6	129	35.8	49.3	Buckner, 1964
14	<i>Sorex arcticus</i>	5.4	195	36.2	55.0	Buckner, 1964
15	<i>Microsorex hoyi</i>	3.5	187	53.5	71.3	Buckner, 1964
16	<i>Sorex cinereus</i>	3.5	176	50.4	68.7	Pearson, 1948
17	<i>Sorex vagrans</i>	5.0	190	38.1	56.8	Pearson, 1948
18	<i>Sorex trowbridgii</i>	6.7	231	34.5	55.5	Pearson, 1948
19	<i>Sorex pacificus</i>	10.4	289	27.8	49.8	Pearson, 1948
(c) Personal means						
CROCIDURINAE						
20	<i>Crocidura bicolor</i>	5.6	142	25.6	39.2	this publication
21	<i>Crocidura jouvenetae</i>	8.0	172	21.6	36.3	"
22	<i>Crocidura poensis</i>	16.7	249	14.9	30.2	"
23	<i>Crocidura theresae</i>	17.6	284	16.1	33.0	"
24	<i>Crocidura wimmeri</i>	23.5	460	19.6	43.1	"
25	<i>Crocidura flavescens</i>	38.0	492	12.9	32.1	"
26	<i>Crocidura giffardi</i>	99.0	934	9.4	29.8	"
27	<i>Crocidura bottegi</i>	3.5	213	61.4	83.9	"
28	<i>Crocidura russula</i>	12.0	205	17.1	31.9	"
29	<i>Suncus etruscus</i>	2.9	185	63.7	83.0	"
SORICINAE						
30	<i>Sorex minutus</i>	3.2	173	54.1	72.3	"
31	<i>Sorex araneus</i>	7.3	290	39.5	65.0	"
32	<i>Neomys fodiens</i>	16.8	536	31.9	64.7	"

African species. As mentioned above though, we cannot exclude a small metabolic increase in the case of the African animals due to the experimental temperature. Hildwein (1972), who was able to measure 3 *Crocidura occidentalis* in Gabun, did indeed obtain lower values than ours². In conclusion, the metabolism of European *Crocidura* coincides roughly with that of African *Crocidurinae*.

Most important of all is the indisputably large difference between the values of the European *Crocidura russula* in comparison to that of *Sori-*

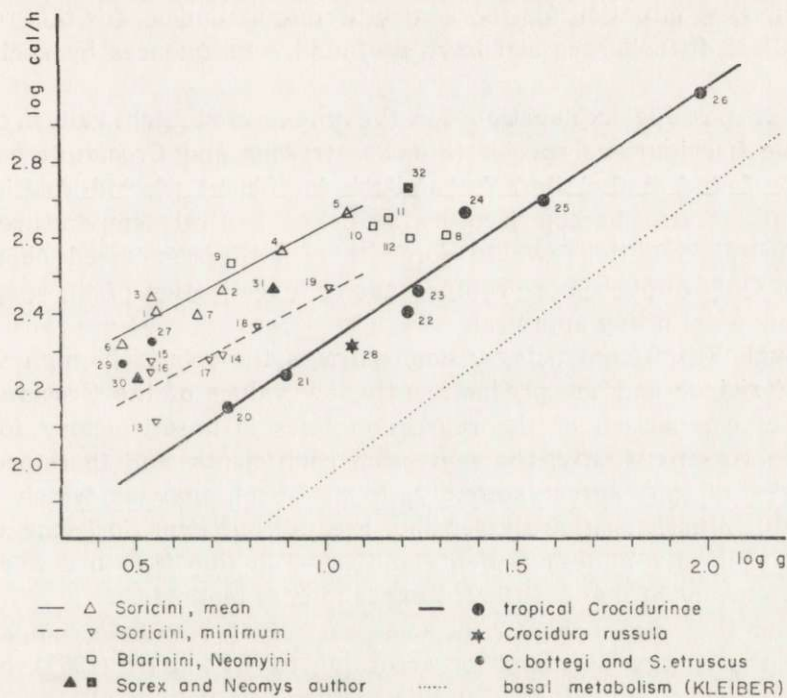


Fig. 2. Energy consumption of *Soricinae* and *Crocidurinae*: Graphic representation of Table 1.

Solid symbols=personal mean values. Regression lines: Mean values of *Soricini* $M=126 W^{0.52}$; Minimal values of *Soricini* $M=82.6 W^{0.53}$; Mean values of *Crocidurinae* $M=43.6 W^{0.67}$; Basal metabolism according to Kleiber $M_b=16.2 W^{0.75}$ cal/h.

cinae, especially of *Sorex araneus* (of equal weight). Thus, these respirometric experiments confirm the concept of differential metabolic consumption as previously postulated on the basis of various indices (Vogel, 1972).

² After completion of this manuscript, Dryden, Gębczyński & Douglas (1974) published measurements of oxygen consumption of the tropical *Suncus murinus* (*Crocidurinae*). The values for adult animals of a long-existing laboratory colony are also somewhat below the values of our African shrews.

The surprisingly high mean value of our *Suncus etruscus*, which cannot be explained by either unusual activity or by an abnormal state, merits a special commentary. On the basis of the mediterranean distribution of this species, which has also been found south of the Sahara (Heim de Balsac, 1958), one would theoretically expect a relatively low metabolism. Its ability to undergo reversible hypothermia (Vogel, 1974), extraordinary for a member of the *Soricidae*, points in the same direction. Nevertheless, its average weight of 1.9 g places *Suncus etruscus* in a borderline situation for the homeothermic mammals; for this reason, the smallest disturbances can have profound consequences by such tiny shrews.

Another possible explanation for the unexpected high values of the two little *Crocidurinae* species (*Suncus etruscus* and *Crocidura bottegi*) might be found in the short fur and the inefficient thermo-isolation: If these species are characterized by a higher neutral temperature, our experimental conditions would force them into pronounced chemoregulation. Only a much more comprehensive investigation of these species will allow a definitive appraisal.

Although Fig. 2 convincingly demonstrates the relatively high values of the *Soricinae* and the predominantly low values of the *Crocidurinae*, the direct comparison of the regression lines is unsatisfactory for the following reasons: firstly, the regression coefficients, and therefore also the slopes do not agree; secondly, a statistical analysis which could clarify the situation is hardly sensible because our own *Soricinae* values are based on only 7 measurements and those in the literature were obtained by means of many different experimental methods.

In order to arrive, however, at some sort of approximate comparison, we base the energy consumption, according to Kleiber (1967), on the »metabolic body size, $W^{0.75}$ «. By this method, employing all the values in Table 1, we arrive at a mean value of 69.1 ± 3.8 cal/h for the *Soricinae*, and 44.2 ± 6.6 cal/h for the *Crocidurinae*; the basal metabolism computed according to Kleiber results in 16 cal/h. Still and all, even this rough estimation demonstrates the difference between the two subfamilies. In spite of the inclusion of several questionable values, the Student's t — test yields a statistically highly significant difference ($P < 0.5\%$).

IV. DISCUSSION

Up until several years ago, there was general adherence to Kleiber's formula as the fundamental description of the basal metabolism of all homeotherms; deviating results were brought into agreement by means of corrective calculations. Poczopko (1971) then demonstrated that at least 4 levels of metabolism can be differentiated: in progressive

order the *Metatheria*, the *Eutheria*, the non-passerine birds and, at the summit, the *Passeriformes* (passerine birds). The same author also called attention to the disputed values for the small insectivores, (which surpass even those of the passerine birds), without nevertheless suggesting an appropriate classification.

A correct evaluation of the shrews has been hitherto impossible because previous investigations always compared them with rodents. Owing to the dissimilar nourishment and activity of these two animal groups, each set of results has been open to a wide variety of differential interpretations. Weighty physiological indices, such as tissue metabolism *in vitro* (Malzahn, 1974) and hematological criteria (Wólk, 1974) though, support once again an exceptional position for the family of the *Soricidae*. Our oxygen consumption studies, performed under identical conditions on 13 representatives of this family demonstrate differences between the two subfamilies which cannot be explained in terms of the specifically dynamic action of the food, and therefore imply a differential basal metabolism.

Pearson's (1948) and Gębczyński's (1965) conception of an especially high metabolism in shrews is thus confirmed by our results. Nevertheless this conclusion is valid only for the subfamily of the *Soricinae*, leaving out the problematical value for *Suncus etruscus*. On the other hand, compared with the red-toothed shrews, the subfamily *Crocidurinae* is characterized by a relatively low metabolism. These fundamental differences within the same family were already suspected by Dehnel (1950), based on Tupikova's (1949) investigation of the nourishment and activity of East-European shrews (*Crocidura suaveolens*, among others).

As far as the hitherto published data on energy consumption permit a conclusion, the *Soricinae* can also be sub-divided into extreme and more moderate forms. Here we see a clear correlation with Repenning's (1967) systematic classification into 3 tribes: the *Soricini* is characterized by the most extreme energy consumption; the *Neomyini* (e.g. *Neomys*) and the *Blarinini* (*Blarina* and *Cryptotis*) assume a more moderate position.

Finally, we must seek to unravel the meaning of these differences in basal metabolism. Contrary to the opinion of Scholander (1955), who excluded the possibility of a climatic adaptation through alteration of the basal metabolism, Hildwein (1972) demonstrated that animal groups typically native to the tropics (*Hyracoidea*, *Pholidota*, etc.) are characterized by a reduced basal metabolism. Nevo & Shkolnik (1974) have recently discovered differences in basal metabolism even between different chromosome races of *Spalax ehrenbergi* which correlate with the

respective mesoclimates. Thus, we arrive at an evolutionary explanation for certain differences in basal metabolism. When applied to our shrews, this explanation suffices for the low metabolism of the tropical *Crocidurinae*, but not for that of the Middle-European *Crocidura* species.

A possible solution, which at the present must remain a pure hypothesis, is forthcoming from the geographic distribution of the two contemporary subfamilies. The primary distribution area of the *Soricinae* is the holarctic region (excepting Mediterranean Africa), that of the *Crocidurinae* the palaeotropic region, nevertheless with a conspicuous tendency toward dissemination in Eurasian areas.

I consider it probable that from the ancestral *Soricidae*-stock, 2 groups became isolated under different climatic conditions: one, under tropical conditions in the Indo-African area, developed into the subfamily *Crocidurinae*; the other group, in a temperate climate, most likely Eurasia, evolved into the subfamily *Soricinae*. Repennig (1967), who likewise views a geographic isolation as the decisive factor in this subfamily development, places the separation in the Miocene Tethys seaway.

Due to secondary dissemination, the areas overlap in Eurasia. In Europe, the *Crocidurinae* are absent in the north as well as at higher altitudes, the *Soricinae* on the other hand in the low areas of the south. The area border of the sympatric zone of the subfamilies results thus from the combined effect of microclimate and energy consumption in interaction with the interspecific competition. In other words, by too cool a climate the *Crocidurinae* are no longer capable of competing, by too warm a climate, the *Soricinae*. Naturally, other factors, such as species-specific requirements, are also involved which cannot be discussed within the scope of this publication.

In the Americas, where competition from the originally tropically-adapted *Crocidurinae* is absent, the *Blarinini* have apparently developed within the *Soricinae*; the genus *Cryptotis*, for instance, has penetrated southwards into the insectivore vacuum of tropical Middle and South America. It is to be expected that these forms will also exhibit a secondarily climate-adapted lowered metabolism.

As a first step in the verification of this working hypothesis, the energy consumption and the ecological demands of European *Crocidurinae* should be examined on a wide basis.

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ZAPOTRZEBOWANIE ENERGETYCZNE EUROPEJSKICH I AFRYKAŃSKICH RYJÓWEK

Streszczenie

Próbując odpowiedzieć na pytanie czy poziom metabolizmu ryjówek jest rzeczywiście niezwykle wysoki, zmierzono zużycie tlenu u 13 różnych gatunków. Z gatunków europejskich były to: *Sorex araneus*, *S. minutus*, *Neomys fodiens*, *Crocidura russula* i *Suncus etruscus*; z afrykańskich — *Crocidura bottegi*, *C. bicolor*, *C. jouvenetae*, *C. poensis*, *C. theresae*, *C. wimmeri*, *C. flavescens* i *C. giffardi*. Pomiarów wykonywano przez 20—30 minut, w małym respirometrze typu zamkniętego, przy 25°C. Poziom metabolizmu ryjówek z podrodziny *Soricinae* mieści się pomiędzy średnią a minimalną wartością właściwą *Soricini* ($M=126,2 W^{0.52}$ cal/h i $M=82,6 W^{0.53}$ cal/h, odpowiednio), podawaną w literaturze (Tabela 1). Wartość średnia cechująca afrykańskie *Crocidurinae* jest znacznie niższa ($M=43,6 W^{0.67}$) (Ryc. 1).

Poziom metabolizmu europejskiej *Crocidura russula* jest taki jak u gatunków afrykańskich. Zatem *Crocidurinae* mają względnie niski metabolizm; *Soricinae*, a szczególnie tryb *Soricini* — bardzo wysoki. Tryby *Neomyini* i *Blarinini* zajmują pozycję pośrednią (Rys. 2). Różnice te dotyczą także metabolizmu podstawowego.

Ta wyraźna różnica pomiędzy oboma podrodzinaми może być zapewne tłumaczona tym, że ewolucja przebiegająca przy izolacji geograficznej, w różnych warunkach klimatycznych, dostosowała *Crocidurinae* do tropikalnej Afryki a *Soricinae* do klimatu umiarkowanego Eurazji.