Moult Topography of Microtinae, other Rodents and Lagomorphs

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The signs of moulting have been long used to solve some taxonomical problems. Moulting of rodents, however, has been studied but very little. Besides there still exist some controversies. Thus it became necessary to summarize the literature data. The author has been able to supply some new facts to solve this problem with the help of his own materials as well as by studying collections of the Zoological Museum of the Moscow University and of the Zoological Institute of the U.S.S.R. Academy of Sciences.

Methods

The flayed stretched skins have been thoroughly studied. It has been noticed that the color of a hair at the root in most rodents was dark, while its tip was lighter. When the skin of a moulting animal is bent crosswise, one can notice in the thick of the fur light stripes composed by the tips of the new hairs. By this and by a dark pattern on the skin it is easy enough to see the sequence of growth of the new hair during moulting.

1. *Lagurus lagurus* Pall.

The juvenile moulting proceeds by the sublateral type. The growth of the new hair begins from the lower parts of the sides and the head, and spreads on the belly and the upper parts of both sides. When the belly is covered with the new fur, the growth of the new hair spreads towards the back. The moulting terminates on the head or on the rump. According to the smaller details there can be discerned four varieties of moulting, which do not disturb the whole plan (Fig. 1).

The autumnal moulting of adult and semiadult voles proceeds also by the sublateral type (Fig. 2). The first three varieties of this moulting resemble the ones of the juvenile moulting. However in the fourth variety the moulting of the middle of the back occurs the last.

The spring moulting has the same order of sequence. It has three kinds of varieties (Fig. 3). The second variety, however, is somewhat set apart and proceeds only in spring. The other two resemble the above mentioned varieties.

Spring and autumnal moultings in the old animals are irregular (a diffused type of moulting).

2. *Microtus gregalis* Pall.

The juvenile and seasonal moultings of these voles proceed by four varieties of the sublateral type (Fig. 4). The old animal moult diffusely.

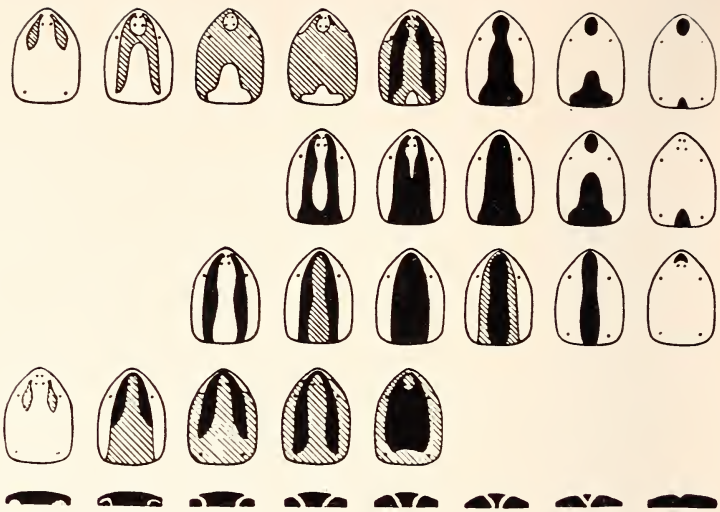

Fig. 1. Scheme of juvenile moulting in *L. lagurus* Pall. Below — cross section of fur

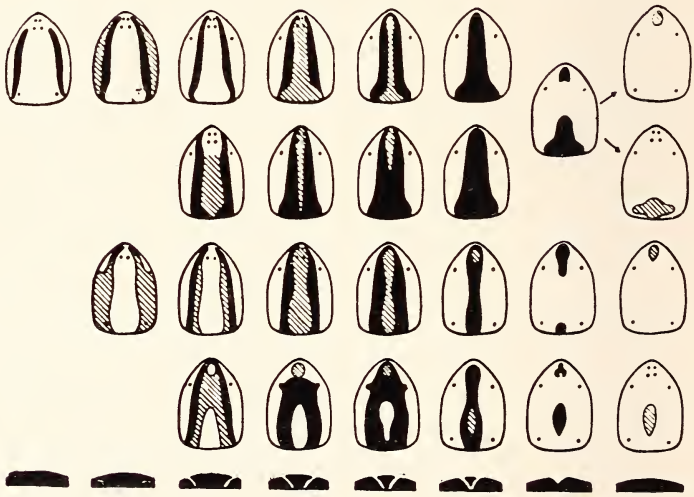

Fig. 2. Scheme of autumnal moulting in *L. lagurus* Pall.

3. *Microtus oeconomus* Pall.

These voles moult by the sublateral type (Fig. 5). The phases of moulting are usually well expressed. Those skins with darkish bellies and backs are registered often.

4. Moulting of Other Representatives of the Genera *Microtus* and *Alticola*

The sublateral type of moulting has been registered in the following species: *Microtus arvalis* Pall., *M. mongolicus* Radde, *M. transcaspicus* Satun., *M. middendorffi* Poljak., *M. hyperboreus* Vinogr., *M. ungurensis* Kastsch., *M. fortis* Büchn., *M. agrestis* L., *M.*

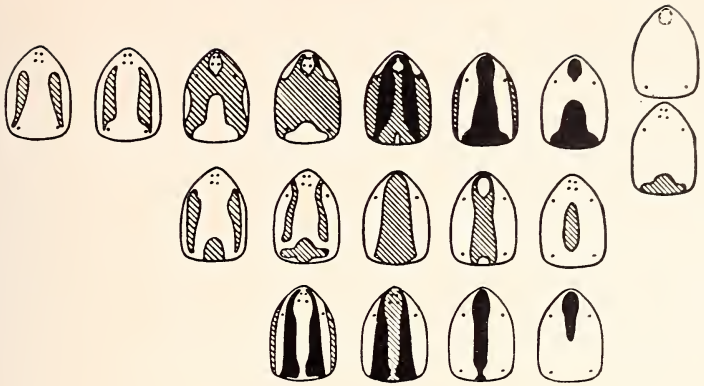

Fig. 3. Scheme of spring moulting in *L. lagurus* Pall.

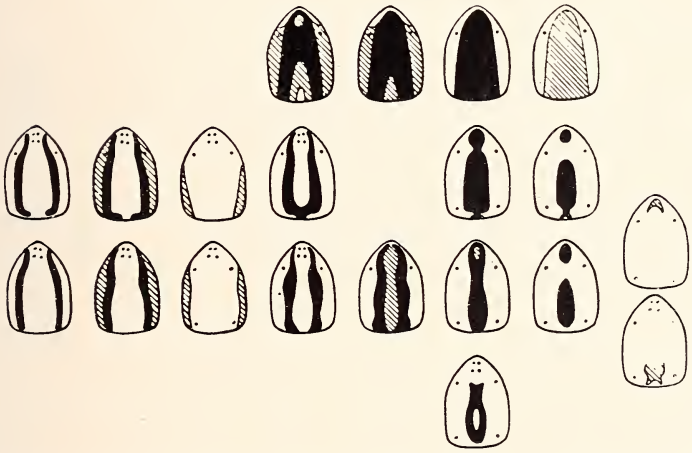

Fig. 4. Scheme of juvenile and seasonal moultings in *M. gregalis* Pall.

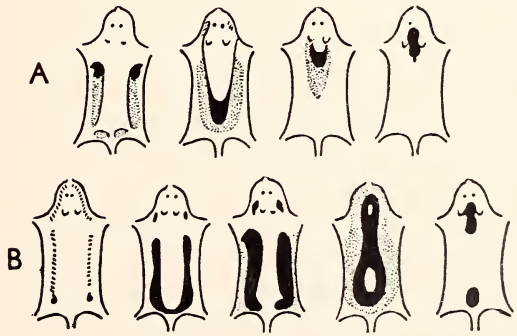

Fig. 5. Scheme of juvenile (A) and seasonal (B) moultings in *M. oeconomus* Pall. (By BAUER)

socialis Pall., *M. brandti* Radde, *M. vinogradovi* Fet., *M. carruthersi* Thomas, *M. blythei* Blanford, *M. gud* Satun., *M. nivalis* Mart., *M. roberti* Thomas, *M. majori* Thomas, *M. limnophilus* Büchn., *Alticola lemminus* Mill., *A. argentatus* Severtz., *A. strelzovi* Kastsch. It was described for *M. subterraneus* Sel. (Langenstein-Issel, 1950) and *M. californicus* Peale (Ecke & Kinney, 1956) as well.

Thus, the general plan of moulting in different Microtinae appears to be exceptionally stable. It is the same both for arctic and for desert animals, for the inhabitants of meadow lands and of forests, and also for the inhabitants of semidesert. Is it possible that it depends on the mode of life of the animals? To answer this question it would be interesting to note moulting in the aquatic animals — *Arvicola terrestris* L. and *Ondatra zibethica* L., and also in the representatives of the Genus *Ellobius,* which almost never appear on the land surface.

5. *Arvicola terrestris* L.

According to Ognev's data (1950), these animals also have the sublateral type of moulting. This can be seen on Fig. 6. Their juvenile and autumnal moultings closely resemble the above type of moulting even in its minute details.

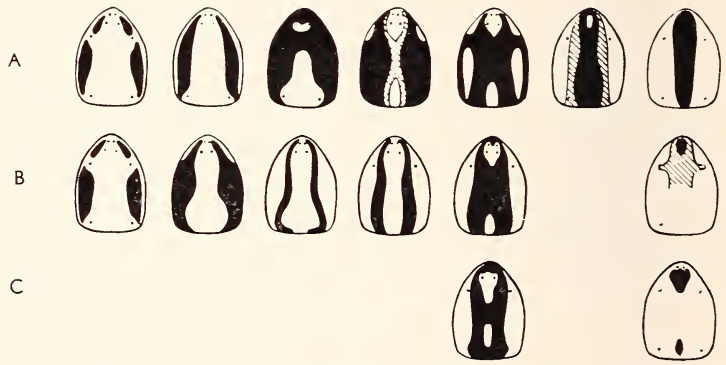

Fig. 6. Scheme of moulting in *A. terrestris* L. (A — juvenile, B and C — autumnal)

6. *Ondatra zibethica* L.

As can be noticed on Fig. 7, in the autumn the growth of the new hair in these animals begins also from lower parts of sides. The first phases of moult however are not isolated, but are simultaneous with other phases of this process. E. g., the growth of

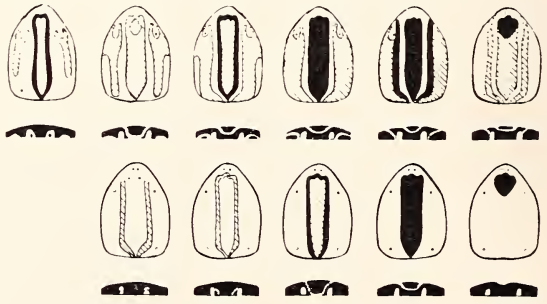

Fig. 7. Scheme of moulting in O. *zibethica* L.

the hair on the sides begins simultaneously with the growth of the hair on the lower margin of the back; the broadening of these zones of moult spreads almost on the whole of the skin, leaving only a narrow light stripe between the back and the sides. It is easy to see that in this case there are combined the last phases of the juvenile and the first phases of the autumnal moultings. It can be explained by the heavy growth of a fur coat and by the slow growth of the hair.

The above mentioned features do not disturb the general plan of the sublateral type of moulting.

7. *Ellobius talpinus* Pall.

In the fall 40% of animals had clear picture of the sublateral type of moulting (Fig. 8A). 10% of them simultaneously had signs of the primary and terminal phases of moulting, as it had been registered in O. *zibethica* L. (Fig. 8B). The remaining 60% had a similar picture, but with the presence of the compensating moult (Fig. 8C). The old animals moulted diffusely (Fig. 8D).

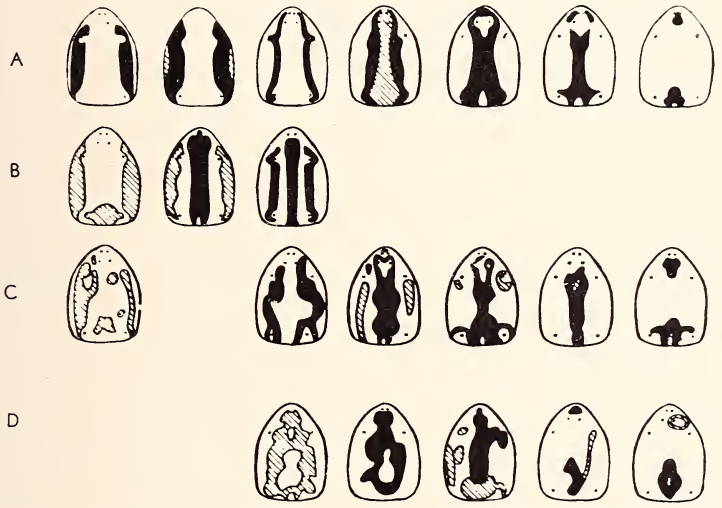

Fig. 8. Scheme of autumnal moulting in *E. talpinus* Pall. (A, B, C — subadultus and adultus, D — senex)

The autumnal and spring moultings in *E. fuscocapillus* Blyth proceeded also sublaterally.

It is evident that moult topography does not depend on the animals' mode of life. Is it possible that moulting in genetically more ancient rodents is different? It will be interesting to observe moulting in lemmings and bank voles.

8. Lemmings

In accordance with Ognev's data (1948) the autumnal moulting in *Dicrostonyx torquatus* Pall. proceeds sublaterally, however, in *Lemmus lemmus* L. it appears to proceed in a reverse sequence. Examination of skins proved that *Myopus schisticolor* Lill. (Fig. 9A), *L. lemmus* (Figs. 9B, C) and *L. obensis* Brants (Fig. 9D) moult sublaterally. But a few skins had a V-shaped dark pattern proceeding from the root of the tail (Fig. 9C, extreme right). It proves that there must be the sacral subtype of the cephalo-sacral type of moulting, the detailed description of which is given below.

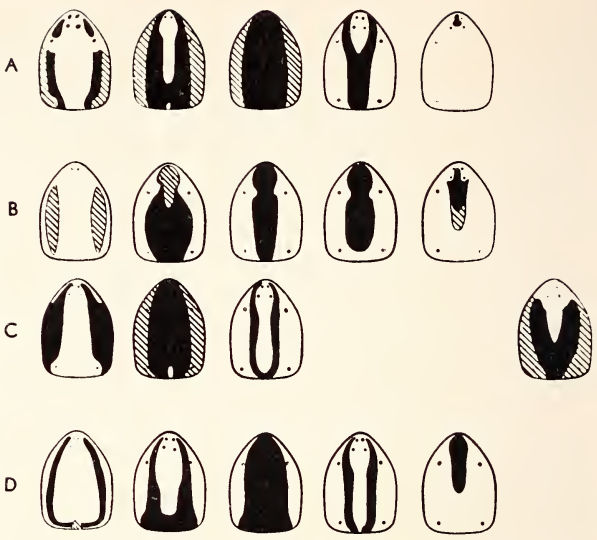

Fig. 9. Scheme of seasonal moulting in lemmings (explanation in the text)

9. *Clethrionomys*

The seasonal and juvenile moultings of *C. glareolus* Schreb. proceed by so well expressed sublateral type that it is very easy to discern some individual varieties typical, for example, of *L. lagurus* Pall. (Fig. 10A–C). About 5 % of the skins had signs of the cephalo-sacral type of moulting (Fig. 10D).

The seasonal and juvenile moultings of *C. rufocanus* Sund. proceed by the sublateral type of moulting too (Fig. 11).

The juvenile moulting of *C. rutilus* Pall. proceeds by the sublateral type (Fig. 12A, B). In spring the adult animals moult by the same type (Fig. 12 C, D), however the growth of the new hair on the rump is retarded, thus on the dark pattern of the skin there appears a very characteristic light spot. In the fall the adult animals moult by the

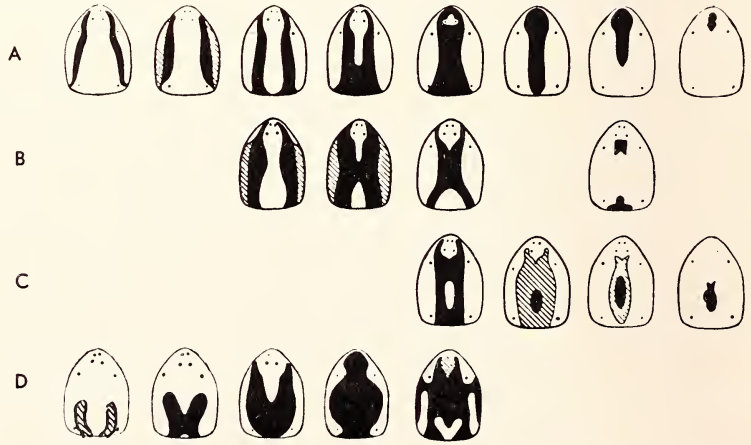

Fig. 10. Scheme of moulting in *C. glareolus* Schreb. (explanation in the text)

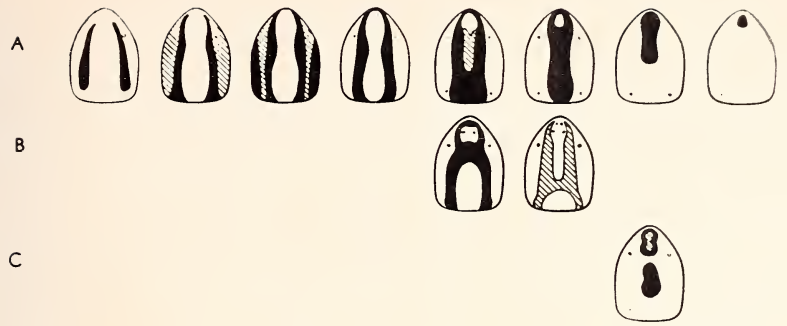

Fig. 11. Scheme of moulting *in C. rufocanus* Sund.

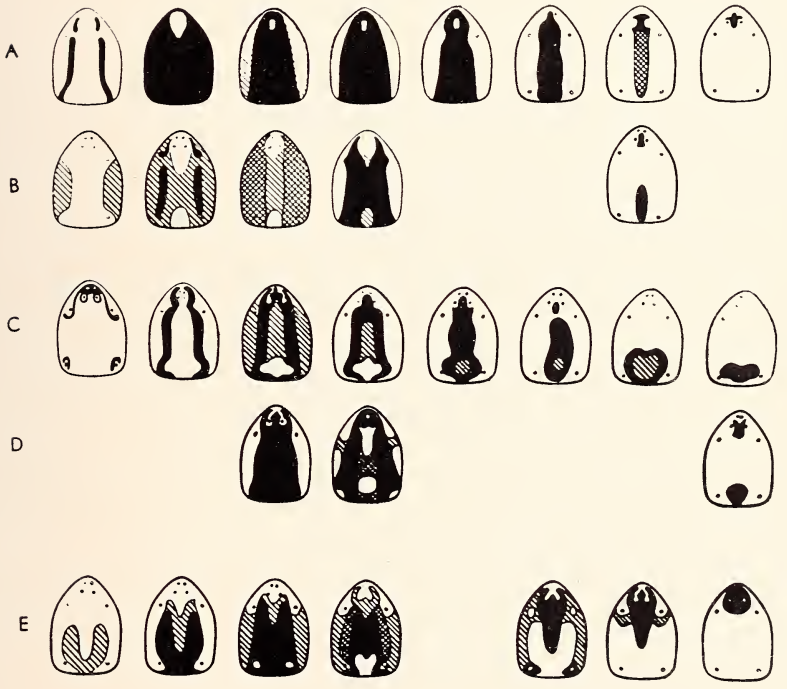

Fig. 12. Scheme of moulting in *C. rutilus* Pall. (A, B — juvenile, C. D — spring, E — autumnal)

sacral subtype. In this case the growth of the new hair begins on the rump and forms the V-shaped spot (Fig. 12E). Both branches of this spot spread to the forelegs, first the spot extends on the whole of the back and then spreads to the neck. Later the growth of the hair begins on the belly, sides of the head (below the ears and eyes) and on the back of the head.

The old animals moult diffusely.

Thus in phylogenetically more ancient Microtinae there is one more type of moulting, which is best demonstrated in a more primitive representative of the Genus, *C. rutilus.*

10. Gerbillinae

The juvenile and autumnal moultings of *Meriones meridianus* Pall. (Fig. 13A) and *M. tamariscinus* Pall. (Fig. 13B) proceed by the sublateral type. The old animals moult diffusely. The same sequence of moulting can be traced also in *M. erythrourus* Gray, *M. unguiculatus* A. M.-Edw., *Rhombomys opimus* Licht.

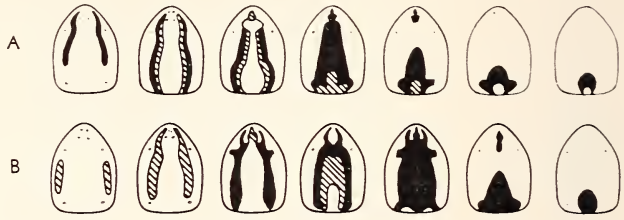

Fig. 13. Scheme of moulting in Gerbillinae (explanation in the text)

11. Cricetinae

The juvenile, autumnal and spring moultings of *Cricetus eversmanni* Brandt (Fig. 14) proceed by both varieties of the sublateral type, i. e. the growth of the new hair begins from the lower parts of the sides and extends to the belly and back. The sea-

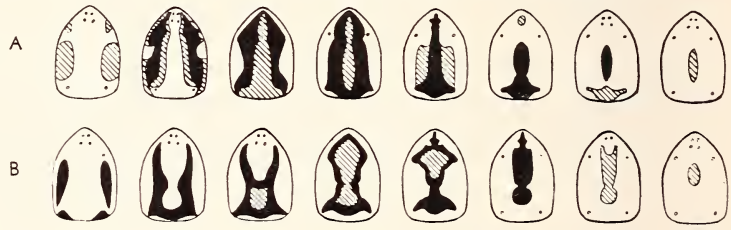

Fig. 14. Scheme of juvenile (A) and seasonal (B) moultings in *Cricetus eversmanni* Brandt

sonal moulting of *Cricetulus barabensis* Pall., *C. migratorius Pall.* and *C. triton* Wint. does not differ from the one in Microtinae even in its minute details.

The juvenile, spring, autumnal and winter moultings of *Phodopus sungorus* Pall. proceed by quite a different plan (Fig. 15). The growth of the new hair begins with

Fig. 15. Scheme of juvenile and seasonal moultings in *Pho. sungorus* Pall. A — spring, summer, B — winter

two spots which are on both sides of the spine in the posterior part of the back. Soon these spots blend, and there are formed two more spots, which first join together and later become one with the first one on the back. Then the space of the growing hair spreads to other parts of the back, to the head, sides and belly.

Thus these animals have a new type of moulting. However, the fauna of Cricetinae being not very numerous it is difficult to observe its whole picture.

12. Muridae

The seasonal and juvenile moultings in *Nesokia* indica Gray, *Rattus norvegicus* Berkenh. and *R. rattus* L. proceed by the sublateral type. It is still better demonstrated in mice (Fig. 16). In the latter it is even possible to discern the variety of moulting identical to that in Microtinae. The old animals moult diffusely.

The analogous sequence of moulting in mice and rats was described by Haddow and his colleagues (1945) and Fraser & Nay (1953).

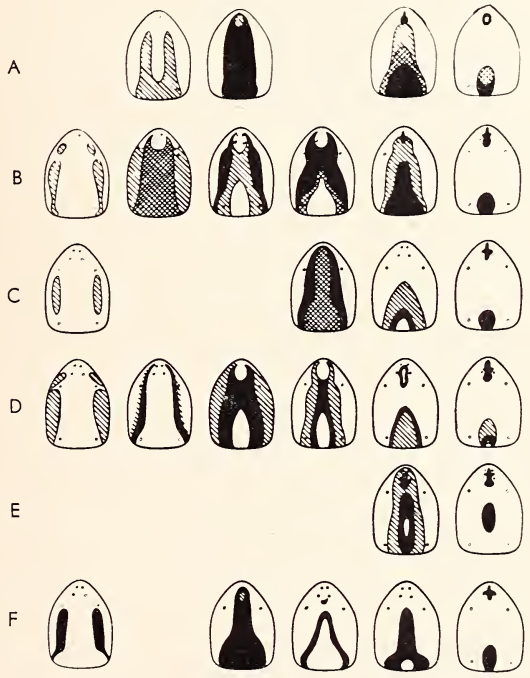

Fig. 16. Scheme of moulting in Muridae. A — autumnal moulting in *Mus musculus* L., B — autumnal and juvenile moultings in *Apodemus agrarius* Pall., C — seasonal moulting in *A. speciosus* Temm., D and E — juvenile and seasonal moultings in *A. sylvaticus* L., F — juvenile and autumnal moultings in *A. flavicollis* Melch.

13. Spalacidae and *Myospalax*

These specialized groups of rodents have a great semblance and sometimes are placed into one family (Ognev, 1947).

In the seasonal moulting the growth of the new hair in the adult Spalacidae *(Spalax microphthalmus* Güld., *S. giganteus* Nehr., *S. leucodon* Nordm.) begins from the head and spreads to the back (Fig. 17A). Sometimes in the middle of the back there

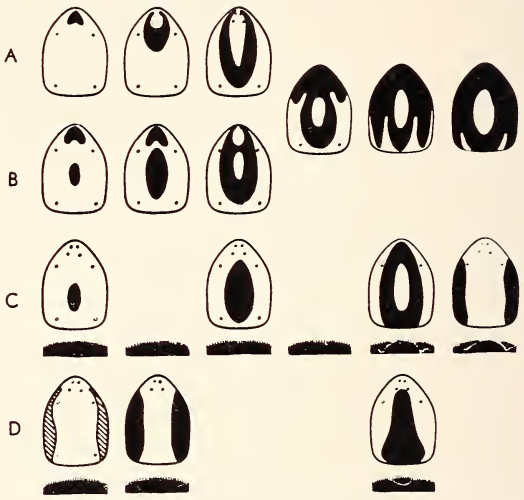

Fig. 17. Scheme of seasonal (A, B, C) and juvenile (D) moultings in Spalacidae

appears an independent site of moulting, which later on blends with the former one (Fig. 17B), and then extends almost over the whole upper part of the body, excluding the posterior part of the back. Then the hair grows on the chest and sides and still later, on the rest of the skin. This sequence is characteristic of the cephalic subtype

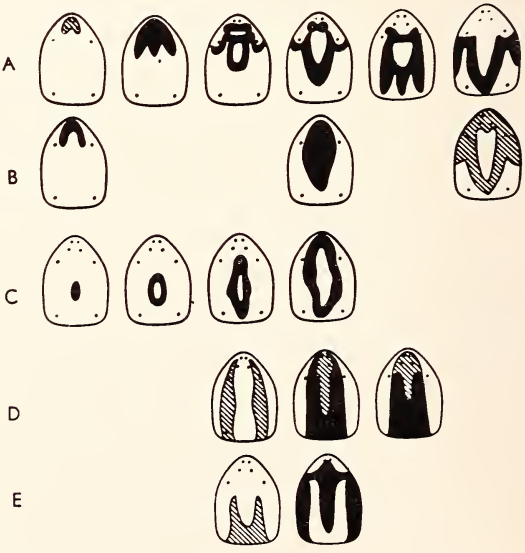

Fig. 18. Scheme of moulting in *Myospalax* (A, B, C, — seasonal, D, E — juvenile, see the text)

of the cephalo-sacral type of moulting. Only sometimes moulting begins from the middle of the back, and from there it extends evenly on the whole skin (Fig. 17C).

Judging by very few skins available, the young animals moult by the sublateral type (Fig. 17D).

The seasonal moulting in the adult *Myospalax (M. myospalax* Laxm., *M. psilurus* A. M.-Edw., *M. dybowskii* Tschersky) (Fig. 18A, B, C) is analogous with that in Spalacidae. But their juvenile moulting (Fig. 18D) proceeds by the sublateral type, and it is even possible to discern the varieties identical with those in Microtinae. But it appears that there is also a sacral subtype of moulting (Fig. 18F).

14. Dipodidae

Sicista subtilis Pall. moults by a special variety of the sublateral type (Fig. 19A). The growth of the hair begins from the lower parts of the sides and terminates in the middle of the back.

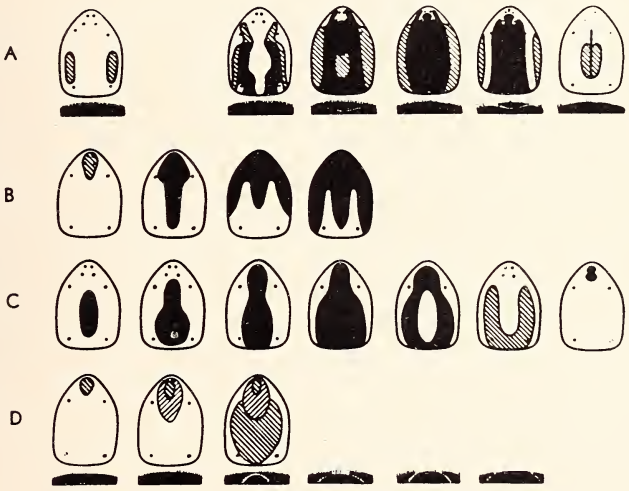

Fig. 19. Scheme of moulting in Dipodidae. A — Sicistinae, B, C — *Allactaga* and *Scirtopoda*

The seasonal moulting in *Allactaga jaculus* Pall., *A. elater* Licht., *Scritopoda telum* Licht. is analogous with that in Spalacidae and *Myospalax* (Fig. 19B, C), i. e., it proceeds by the cephalic subtype of the cephalo-sacral type.

15. Myoxidae

The moulting in *Glis glis* L., *Muscardinus avellanarius* L. and *Dyromys nitedula* Pall. proceeds by the sublateral type, and phases of moulting may be strongly pronounced (Fig. 20A), or the growth of the hair spreads nearly all over the whole skin very quickly (Fig. 20B), this is very typical of the younger animals. The old animals moult diffusely.

An analogous type of moulting in *G. glis* L. was registered by Donaurov, Popova and Chonjakina (1938).

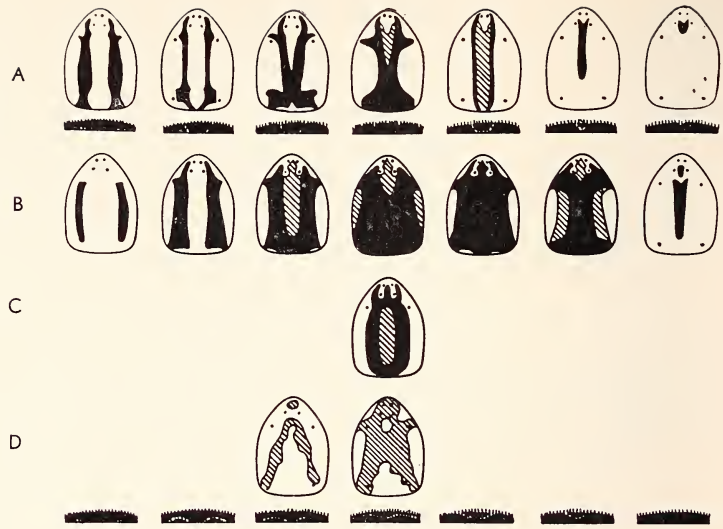

Fig. 20. Scheme of moulting in Myoxidae. A, B, C — adultus and juvenis, D — senex

16. Sciuridae

The moulting in *Sciurus vulgaris* L. was described by Naumov (1934). In the spring the growth of the hair in adult animals begins around the eyes, then it proceeds to the upper and lateral parts of the head, down the shoulders and along the middle of the back. Then the hair begins to grow on both sides, on the belly and finally on the upper and lower extremities, this being the cephalic subtype of the cephalo-sacral type of moulting.

The moulting on the tail proceeds independently from the rest of the body once a year, and it begins from the middle.

The autumnal moulting proceeds in a reverse sequence by the sacral subtype of the cephalo-sacral type of moult. It begins on the rump with a V-shaped spot, the spot gradually increases in size, extends to the hind legs and simultaneously to the head with two stripes on both sides along the back. Then the moult proceeds on the back, and the growth of the new hair spreads to the head and lower parts of the sides, belly and forelegs (Fig. 21A). The young animals moult in the same way.

The cephalo-sacral type of moulting was described for *Spermophilopsis leptodactylus* Licht. (Lavrov & Naumov, 1934) and for *Tamiasciurus hudsonicus loquax* Bangs (Layne, 1954).

In accordance with the researches carried out by Hansen (1953–1954), the northern and mountain representatives of *Citellus* and *Cynomys*, which hibernate about seven months a year, moult diffusely. The representatives of *Ammospermophilus*, *Ictidomys* and *Xerospermophilus*, which dwell in the South and almost never hibernate, have two sequences of moulting as do most of Sciuridae. The representatives of *Callospermophilus*, *Otospermophilus* and *Poliocitellus* occupy an intermediate position in the geographical distribution and in the period of winter hibernation, they moult only once a year, beginning from the head.

According to the literature data various representatives of *Marmota* moult once a year and the growth of the hair begins from the rump.

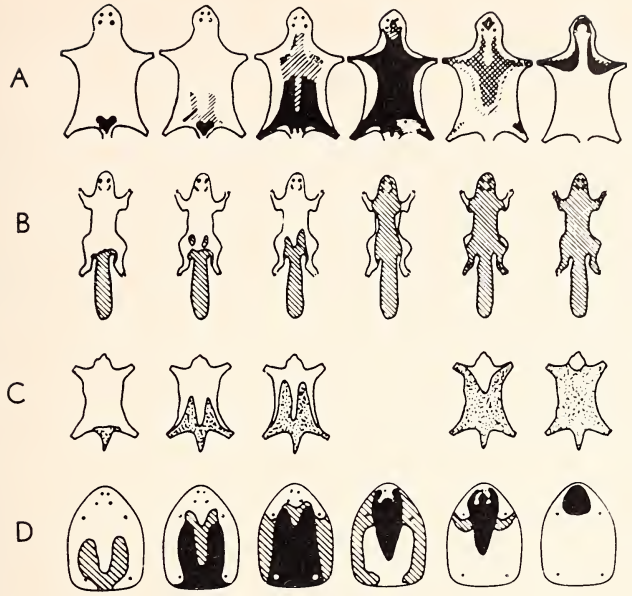

Fig. 21. Scheme of moulting in Sciuridae. A — *Sciurus vulgaris* L., B — *Tamiasciurus hudsonicus loquax* Bangs, C — *Spermophilopsis leptodactylus* Licht., D — *Clethrionomys rutilus* Pall., for the sake of comparison

17. *Ochotona*

The juvenile moulting in O. *pricei* Thomas, O. *daurica* Pall., O. *alpina* Pall. and O. *pusilla* Pall. (Fig. 22B, C, D) proceeds by the sublateral type. It is so much the same as that in Microtinae, that it is easy to discern the identity for these varieties.

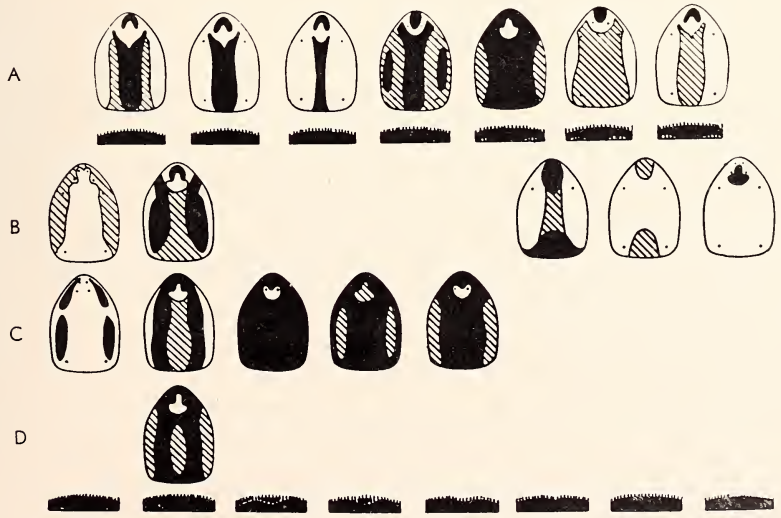

Fig. 22. Scheme of juvenile moulting in *Ochotona* (explanation in the text)

In the youngest animals the first phases of the juvenile moulting begin when the growth of the juvenile hair on the back can still be observed. The moulting very quickly spreads all over the skin of the animal. In this case the dark pattern on the skin is more complicated (Fig. 22A).

The autumnal moulting in *O. pricei* Thomas proceeds by the subdorsal subtype of the ventrosubdorsal type. It starts with two spots on the lower parts of the back. The spots gradually increase in size, and blend in the middle of the back, finally the single spot spreads all over the back and the higher parts of the sides (Fig. 23A). Then moulting extends to the rump, sides and neck, and finally to the belly and head. The moulting terminates on the legs of the animal. *O. daurica* Pall. moults exactly the same way (Fig. 23B).

The spring moulting in both these species appears to begin from the legs and then proceeds to the belly and sides, i. e., it is quite reverse to the way of the autumnal moulting (Fig. 23C). But usually these animals moult diffusely.

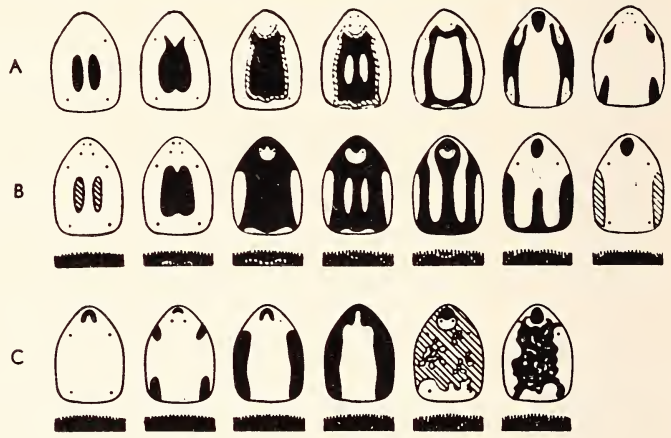

Fig. 23. Scheme of autumnal (A, B) and spring (C) moultings in *Ochotona*

18. *Lepus timidus* L.

The autumnal moulting in *L. timidus* was described by Aspisov (1936). White winter fur at first appears on the tail, then on the hind and fore legs, and on the lower part of the body. Later it appears on the head, sides and back. The summer fur holds out the longest on the sides of the back as one or more pairs of spots. (Fig. 24). In the laboratory conditions moulting in hares proceeded in the same way (Afonskaja, 1949). Thus, in this case there also has been observed the ventrosubdorsal type of moulting, though the autumnal moulting in hares proceeds in the sequence of the spring moulting in *Ochotona*.

The spring moulting in a hare proceeds very quickly. The fur is shedding in flocks. The spots of the summer gray fur appear diffusely, and it is difficult to discern the reverse way of moulting.

Discussions

It has been observed that in different representatives of the orders Rodentia and Lagomorpha there are only four types of moulting, i. e., sublateral, cephalo-sacral, ventrosubdorsal and diffused. There is no doubt that in the future there will be observed

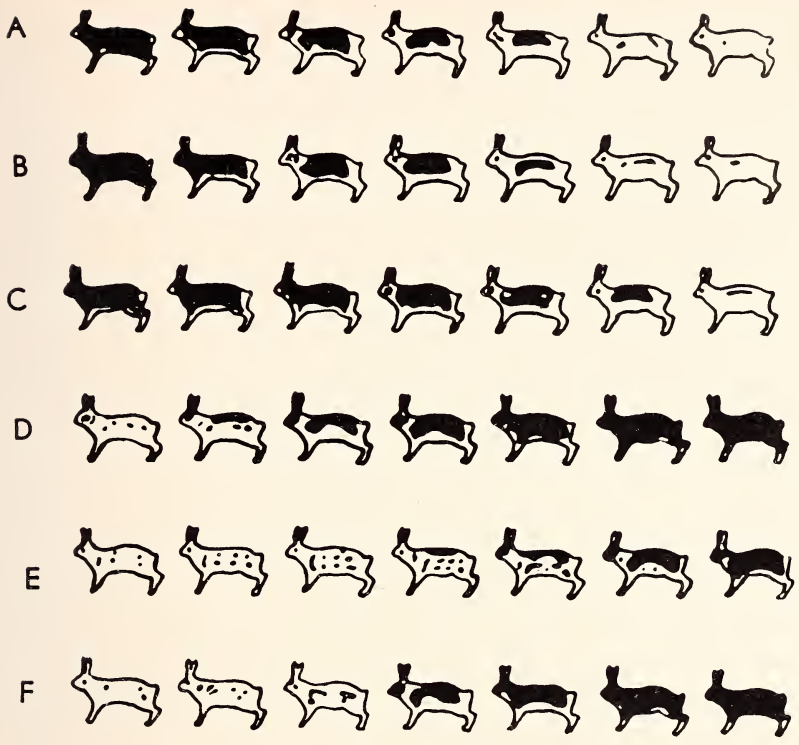

Fig. 24. Scheme of autumnal (A, B, C) and spring (D, E, F) moultings in *Lepus timidus* L., (by Aspisov)

other types of moulting, e. g., in *Phodopus sungorus* Pall. Possibly the cephalo-sacral type is a compound type composed of two types. And yet moultings in rodents are identical, e. g., in Cricetidae, Muridae and Myoxidae, they resemble even in minute details.

Seldom, however, in related groups of animals (e. g., in *Ochotona* and *Lepus)* the same seasonal moulting proceeds in a reverse sequence. An analogous phenomenon can be observed in related species of the Genus *Equus* (Mazak, 1962) and even in different individuals of the same species. Thus, Fraser & Nay (1953) registered reversion of moulting in naked mice *(Mus musculus* L.) under the influence of pregnancy.

The change of a fur coat in representatives of one family can proceed by several types of moulting. Thus, the juvenile moulting in Cricetidae proceeds by the sublateral type, the seasonal one either by the same or by the cephalo-sacral type, and old animals moult diffusely. The juvenile moulting in most examined rodents and lagomorphs proceeds by the sublateral type (Fig. 25). This type of moulting should be considered more ancient genetically. There have not been observed any signs of regulation of moulting plans from the primary diffused to a strictly definite one. Evidently the strict sequence of moulting had existed at the very dawn of the mammalian phylogenesis and had been very important for the temperature exchange process. With the development of a thermoregulation mechanism its significance has diminished and undergone reduction. This can be followed in the cases of ontogenesis (the old animals almost of every family moult diffusely), and of the phylogenesis (more ancient *Clethrionomys* have three types of moulting, and phylogenetically new representatives of Microtinae have only two types).

Theoretically the juvenile moulting in Sciuromorpha should proceed by the sublateral type, and the seasonal one by the cephalo-sacral type. In Sciuridae (*Sciurus vulgaris* L.), however the juvenile moulting has disappeared (Naumov, 1939), and sousliks can have only one moulting a year. They moult either by the cephalic subtype, or diffusely (Hansen, 1953–1954). Considering this phenomenon Hansen has come to the conclusion that the strict sequence of moulting had arisen from the primary diffuse type of moulting in ancrestal animals. This, however, has not been confirmed by the phylogenetic data, and it appears that *Citellus* and *Cynomys,* which moult diffusely, are undoubtedly younger genetically, and *Ammospermophilus* which moult twice a year, is more ancient (Bryant, 1945). An analogous unconfirmed conclusion about the phylogenesis of moult topography in Equinae was made by Mazak (1962). Both the seasonal and juvenile moultings are of the same cephalic subtype in Geomydae (Morejon & Howard, 1956), Thus this family should be placed in Sciuromorpha, as it had been done by Römer (1939) and Gregory (1951), but later some scientists (e. g., Wood, 1955) included it in Myomorpha.

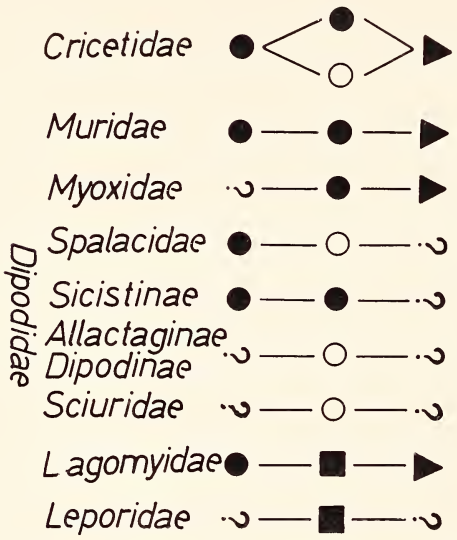

Fig. 25. Types of moulting in Rodentia and Lagomorpha

● = sublateral ○ = cephalo-sacral
▲ = diffuse ■ = subdorsal-ventral

Left: the juvenile moulting; middle: the seasonal moulting of adultes; right: seasonal moulting of old ones.

The representatives of Myomorpha have a tendency to lose the cephalo-sacral type of moulting. It is best demonstrated in Cricetidae, Muridae and Myoxidae. In these Families this type of moulting either does not exist at all, or occurs very seldom. At the same time more specialized families as Spalacidae and Dipodidae still retain this type of moulting.

In respect to Lagomorpha, their subdorsal-ventral type of moulting unknown in all investigated rodents gives a new confirmation to separate them as independent Order (Stohl, 1958). In accordance with the seasonal moulting these two Orders have some resemblance by the description of moultings in *Cervus elaphus* and *Ovis ammon* (Zalkjn, 1946; Antipin, 1947).

The cephalo-sacral type of moultings is found in Insectivora and Carnivora (Deparma, 1951; Crowcroft, 1955; Findley & Jones, 1956; Novikov, 1956). By the description of Petrov (1955) the autumnal moulting in *Mustela erminea* L. proceeds by the sublateral type. The study of moulting has just begun, so the data on hand are still very inadequate. Further researches may provide very interesting data for the study of phylogenesis of rodents and other mammals.

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Die Körperbedeckung der Stachelschweine[1]

Von Erna Mohr

Eingang des Ms. 1. 8. 1963

Die Körperbedeckung der Stachelschweine ist in den einzelnen Körperregionen ganz außerordentlich verschieden und wechselt vom feinsten Wollhaar bis zum zentimeterdicken starren Spieß. Stärke und Verteilung der verschiedenen Behaarungselemente sind gattungs-, ja zum Teil sogar artweise verschieden. Durch die vielfachen Übergänge ergeben sich einige Schwierigkeiten bei der Benennung der einzelnen Elemente.

Da eine zur Zeit in Europa am häufigsten gehaltene Art, das Weißschwanz-Stachelschwein, *Hystrix leucura* Sykes *(hirsutirostris* Brandt), von Lochte (1957) in bezug auf das Stachelkleid eingehend analysiert wurde, seien seine Befunde an dieser Art vorangestellt.

[1] Mit weitgehender und entscheidender Unterstützung der zoologischen Forschungsstelle der Deutschen Akademie der Wissenschaften im Berliner Tierpark.