

41. On the External Characters and Classification of the Mustelidæ. By R. I. Pocock, F.R.S., F.Z.S.

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(Text-figures 27-39.)

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Introduction.

In 1869 Gray (Cat. Carnivorous etc. Mammals Brit. Mus. pp. 79-142) relegated the genera which by all modern zoologists are referred to the family Mustelidæ to two families, Mustelidæ and Melinidæ. The Mustelidæ were divided into the following tribes:—(1) Mustelina for *Martes*, *Mustela*, *Putorius*, *Gulo*, *Galera*, *Grison*; (2) Lutrina for *Lutra* and other genera of typical otters; (3) Enhydrina for *Enhydra*. The Melinidæ were similarly divided into the tribes:—(1) Melina for *Arctonyx*, *Meles*, *Taxidea*, *Mydaus*; (2) Mellivorina for *Mellivora*; (3) Mephitina for *Mephitis*, *Conepatus*, *Spilogale*; (4) Zorillina for *Zorilla* [= *Ictonyx*]; (5) Helictidina for *Helictis*.

From my present standpoint the interest of Gray's classification lies in its influence upon Gill, who in 1872 (Smiths. Misc. Coll. xi. pp. 64-65) followed Flower (P. Z. S. 1869, pp. 11-15) in fusing the Melinidæ and Mustelidæ into one family, for which the latter name was retained, and elevated all Gray's tribes to the rank of subfamilies—Mustelinæ, Melinæ, Zorillinæ, Mephitinæ, etc. As will appear in the sequel, this classification in my opinion better expresses the affinities of the genera dealt with than any that followed it*.

In 1883 Flower (Encycl. Brit., Mammalia, pp. 439-440) divided the Mustelidæ into the following subfamilies:—

- (1) Melinæ for *Mephitis*, *Arctonyx*, *Meles*, *Mydaus*, *Taxidea*, *Mellivora*, *Helictis*, *Ictonyx*.
- (2) Mustelinæ for *Galictis* [*Tayra* + *Grison*], *Mustela* [= *Martes*], *Putorius* [= *Mustela*], *Gulo*.
- (3) Lutrinnæ for *Lutra*, *Aonyx*, *Enhydra* [= *Latax*].

This arrangement, based mainly on the structure of the feet,

* I have intentionally ignored such family names as Mellivoridæ, Zorillidæ, etc., proposed by Rochebrune and Mephitidæ proposed by Rhoads, because no attempt was made to define the families thus casually designated and no reasons were given for assigning that rank to the groups.

was adopted by Mivart (P. Z. S. 1885, pp. 393–395); and with the addition of *Pæcilogale* and *Lyncodon* to the Mustelinæ was repeated by Flower and Lydekker in 1891 ('Mammalia,' pp. 567–591). It was also accepted by Sedgwick ('Students' Text-Book of Zoology,' ii. p. 624, 1905).

In 1902 de Winton ('Zoology of Egypt, Mammalia,' p. 245), trusting apparently to the structure of the teeth, modified Flower's system by transferring *Mephitis*, *Conepatus*, *Mellivora*, and *Ictonyx* from the Melinæ to the Mustelinæ. Max Weber in 1904 (Die Säug. pp. 536–538) followed de Winton with respect to the allocation of *Mellivora*, but otherwise agreed with Flower. And in the same year Trouessart (Cat. Mamm., Suppl. pp. 187–215) also followed Flower, but put *Pæcilogale* into the Melinæ. He further subdivided Mustelinæ into two tribes:—Guloneæ for *Gulo*, *Galictis* [= *Tayra* + *Grison*], and *Lyncodon*, and Musteleæ for *Mustela* [= *Martes*] and *Putorius* [= *Mustela*], with subgenera *Lutreola* and *Arctogale* [= *Mustela*].

In 1912 Miller (Cat. Mamm. Western Europe, pp. 340–341) divided the Mustelidæ into four subfamilies:—(1) Melinæ containing "about a dozen genera," of which only *Meles* is quoted and dealt with; (2) Lutrinnæ containing "four genera," *Lutra* alone being discussed; (3) Guloninæ containing *Gulo* and probably *Mellivora*; (4) Mustelinæ restricted to the genera *Martes*, *Mustela* (with its subgenera *Putorius* and *Lutreola* and *Mustela*), and *Vormela* *.

Although Miller, like de Winton, seems to have relied mainly on the teeth, it seems clear that a large number of the genera placed by de Winton in the Mustelinæ were left by Miller in the Melinæ, where Flower placed them. Another point to be noticed in connection with Miller's classification is his severance of *Gulo* from the Mustelinæ as the type of a special subfamily †, with the guess that *Mellivora* is a related genus.

Setting aside for the moment the classifications of Gray and Gill, two conclusions come out from this brief review:—(1) There is complete agreement amongst recent writers with regard to the status of the Lutrinnæ; (2) Although Flower's subdivisions have held the field until the present day, there is a great variety of opinion as to the constitution of the Melinæ and Mustelinæ. It is admitted by all that *Meles*, *Arctonyx*, *Taxidea*, *Mydaus*, and *Helictis* are Melinæ; and that *Martes*, *Mustela* (with related generic or subgeneric forms, such as *Vormela*, *Putorius*, *Lutreola*), as well as *Tayra*, *Grison*, and *Lyncodon* are Mustelinæ. But *Mephitis*, *Spilogale*, *Conepatus*, *Mellivora*, *Ictonyx*, and *Pæcilogale*

* In 1911 Satunin (Mitt. Kauk.-Museums, v. p. 267) defined the genera *Vormela* and *Putorius*, admitting the following subgenera of the latter, *Putorius* (s.s.), *Lutreola*, *Ictis*, and *Kolonokus*. The genus *Putorius* is equivalent to *Mustela* as understood by Miller, *Ictis* (=subgenus *Mustela*) being employed for the stoats and weasels. Miller was perhaps not acquainted with this paper when he wrote his 'Catalogue of the Mammals of Western Europe.'

† This was originally done by Gray in 1825 (Ann. Phil. xxvi. p. 339); but in his latest classification he abandoned the group named Guloninæ.

have been placed according to the fancy of authors in either subfamily. It is quite clear therefore that there is something wrong with the classification, and that the characters used for defining the two subfamilies are insufficient for the purpose.

In 1920 (Proc. Zool. Soc. pp. 179-187 and pp. 424-436) I attempted to show that Miller's guess as to the kinship between *Gulo* and *Mellivora* was untenable; and that there is practically no evidence of sufficiently close relationship between *Meles* and *Taxidea* to justify their retention in the same subfamily. *Gulo* was affiliated with *Martes*; Gill's subfamily Mellivorinæ was resuscitated for *Mellivora*; Taxidiinæ was proposed as a new subfamily group for *Taxidea*; and *Meles* and *Arctonyx* were provisionally left as the sole representatives of the Melinæ.

Subsequently (Proc. Zool. Soc. 1921, pp. 473-486 and pp. 535-546) a study of the auditory bullæ in the Mustelidæ supplied additional characters for the definition of the subfamilies; and reasons for the admission of several genera of Lutrinæ were brought forward.

In the following pages the external characters of all available genera, apart from *Gulo*, *Mellivora*, *Meles*, *Taxidea*, and the genera of Lutrinæ, which I dealt with in the papers just mentioned, are described in detail; and a summary of the results setting forth my views on the classification of the Mustelidæ is given at the end.

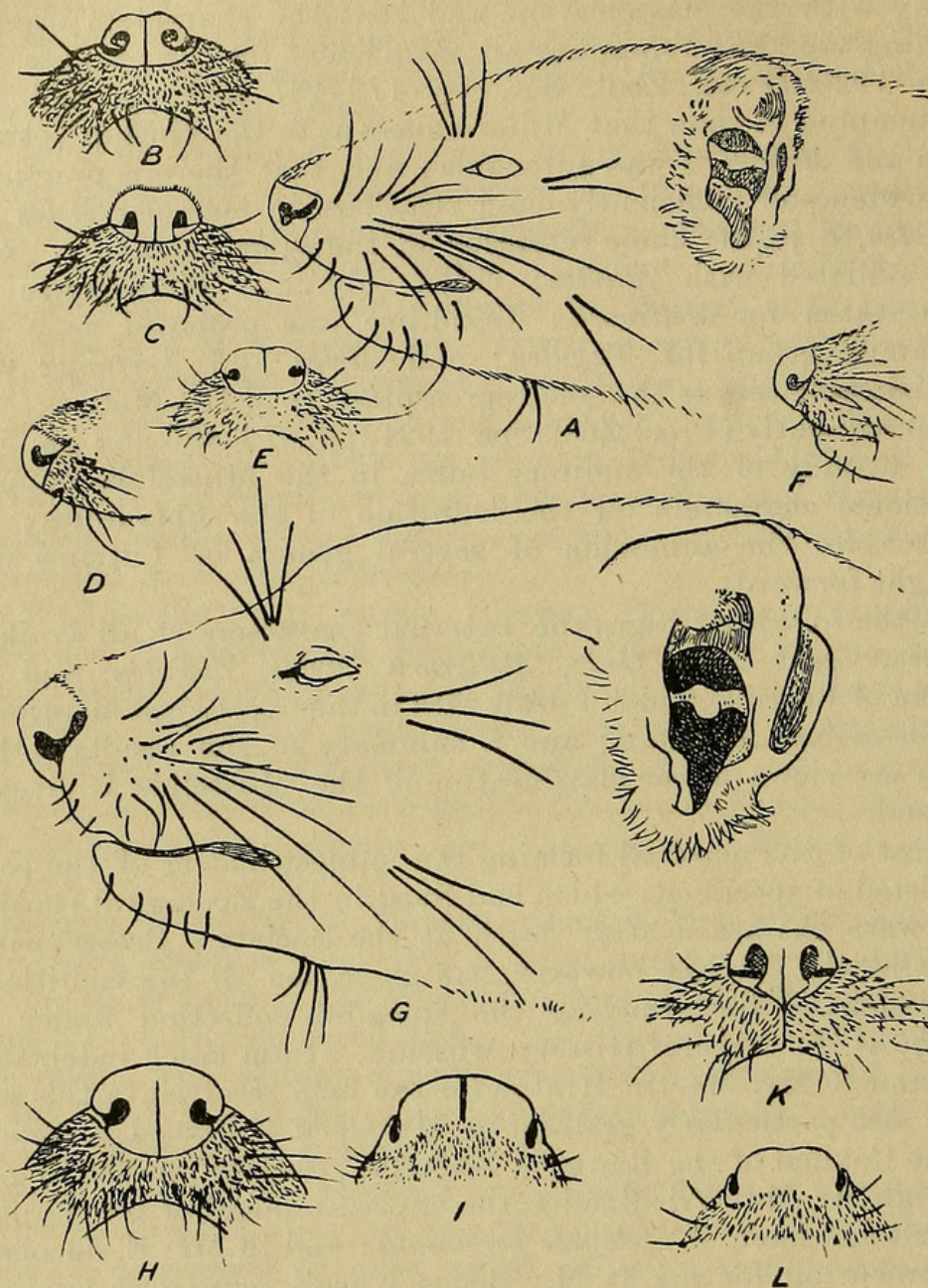
Most of the material forming the subject-matter of the paper consisted of specimens which had lived in the Zoological Gardens and were examined after death at the Society's Prosectorium. Mr. Oldfield Thomas, however, has given me all the facilities at his command for studying the splendid collection under his charge at the Natural History Museum. I am much indebted to him and to Mr. Martin Hinton for the help received in this way. I am also particularly grateful to Mr. Cyril Hopwood, a member of the Council of the Rangoon Zoological Society, for sending me through Mr. Max Friedlander, the Superintendent of the Gardens, a spirit-specimen of *Melogale personata*; and to Mr. E. Jacobson, for procuring for me at Mr. Boden Kloss's request, a similarly preserved example of *Plesiogale nudipes* * from Fort de Kock on the west coast of Sumatra.

The Rhinarium.

The most primitive type of rhinarium is found in *Martes* and *Gulo*. It is naked above, the lateral slits of the nostrils extend nearly to its posterior margin, the infranarial portions are shallow or moderately deep, the inferior edge is convex or angled, but it is not, strictly speaking, continued over the upper lip—that is to say, the gutter which cleaves the lip consists of smooth skin differentiated by its texture from the rhinarium above. This

* Gray referred this species, with others, to his genus *Gymnopus* (see *infra*, p. 818). That name, however, is preoccupied. Hence I propose *Plesiogale* as a substitute.

Text-figure 27.



- A. Side view of head of *Putorius putorius*.
 B. Front view of rhinarium of the same.
 C. The same of *Gale nivalis*.
 D. Side view of rhinarium of the same.
 E. Front view of rhinarium of *Plesiogale gymnopus*.
 F. Side view of rhinarium of the same.
 G. Side view of head of *Charronia flavigula*.
 H. Front view of rhinarium of the same.
 I. Upper view of rhinarium of the same.
 K. Front view of rhinarium of *Martes foina*.
 L. Upper view of rhinarium of the same.

$\times \frac{1}{3}$.

gutter is continued as a groove up the middle line of the rhinarium between the nostrils. (Text-fig. 27, K, L.)

In *Charronia* the gutter is obliterated, except close to the convex lower margin of the rhinarium, which is grooved above, and the upper lip is scantily hairy in the middle line. (Text-fig. 27, G-I.)

In *Gale*, *Mustela*, and *Putorius* it is also obliterated or nearly so, and the infranarial portions of the rhinarium are shallower. In *Gale nivalis* the hair of the muzzle encroaches on the upper surface. (Text-fig. 27, A-D.)

In *Plesiogale nudipes* the rhinarium is large, with a median groove, deep infranarial portions, and naked above back to the posterior ends of the nostril slits. (Text-fig. 27, E, F.)

In *Ictonyx*, as in *Putorius*, the rhinarium is lightly biconvex above and mesially grooved in front, with the inferior edge horizontal in the middle, convex at the sides where it curves backwards; but the infranarial portions are deeper than in *Gale*, *Mustela*, or *Putorius*, and this area of the rhinarium is wider than the upper portion. There is no trace of gutter and the continuously hairy upper lip is about as deep as the height of the rhinarium. (Text-fig. 29, A-B.)

In an example of *Grison furax*, or an allied species, from Brazil, the upper surface of the rhinarium is evenly rounded from side to side, the groove is on the lower half of the front surface, and the nostrils are wide apart. The infranarial portion is deep in the middle, but quite narrow laterally, where it passes beneath the slit of the nostril; and this narrowed piece is defined from the median piece by an oblique groove. There is no trace of gutter and the depth of the lip is less than that of the rhinarium. Two or three specimens of *Grisonella* (sp. ?) from Cordova in the Argentine show individual variation in the rhinarium. In one the upper surface is lightly biconvex, the median groove is distinct, and there is no gutter, in the other the median groove is obsolete, the upper surface is uniformly convex as in *Grison*, and there is a very shallow gutter. In both the infranarial portion is tolerably deep and mesially angled below, but the lateral portions, which in *Grison* pass backwards beneath the nostril slits, are practically obsolete. (Text-fig. 28, A-C.)

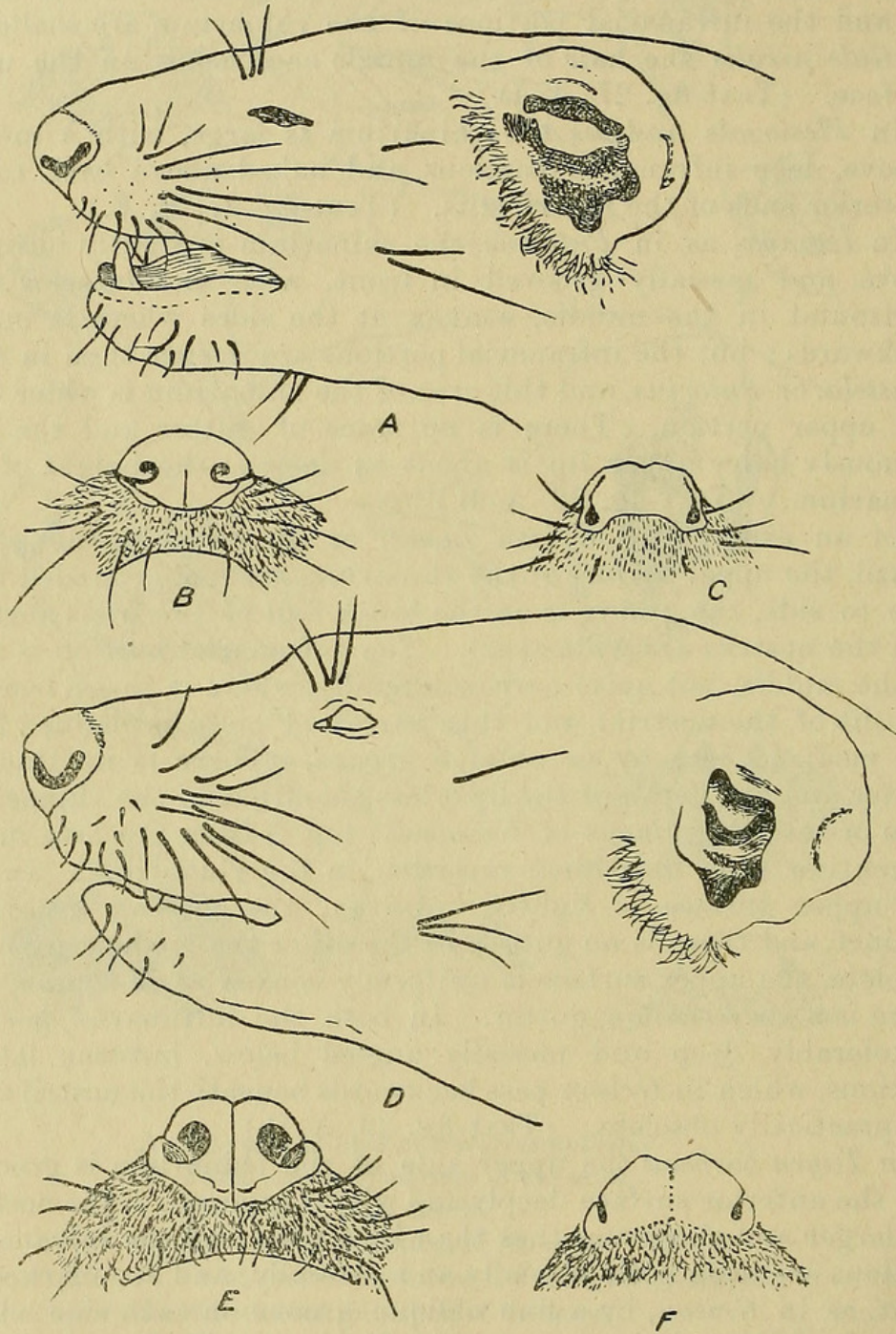
In *Tayra barbara* the upper side of the rhinarium is grooved and the anterior surface deeply and widely grooved. The nostrils are larger and closer together than in *Grison* and the infranarial portions are deep both mesially and laterally, and are marked in front, as in *Grison*, by a fine oblique groove on each side which meets its fellow of the opposite side in the middle line above the inferior angle of the rhinarium in front. The rhinarium is about twice as deep as the upper lip, which has no gutter. (Text-fig. 28, D-F.)

The rhinarium of *Taxidea* recalls that of *Gale*, *Mustela*, and *Putorius* in the shallowness of the infranarial portions and the presence of the median groove. It is, however, relatively wider,

has the nostrils a little closer together, and the upper surface overgrown with hair nearly to the anterior margin. The lip has no gutter and is not so deep as the rhinarium.

In *Mellivora* the rhinarium is wide as in *Taxidea*, and the

Text-figure 28.



- A. Side view of head of *Grison furax* or a closely allied species.
- B. Front view of rhinarium of the same.
- C. Upper view of the same.
- D. Side view of head of *Tayra barbara*.
- E. Front view of rhinarium of the same.
- F. Upper view of the same.

$\times \frac{1}{3}$.

upper lip is shallow and without gutter; but the infranarial portions are somewhat deeper than in that genus; there is no median groove and the lateral slits of the nostrils are more abbreviated, and the upper surface is quite naked.

In *Meles* the rhinarium is very large and naked, the infranarial portions being exceedingly deep and often convexly produced in the middle below. The nostrils are tolerably close together, but the lateral slits, although narrow, are long. There is no median groove, and the upper lip, shallower than the rhinarium, has no gutter.

In the Skunks the range in variation of the rhinarium is very instructive. In *Spilogale* it is very like that of *Martes*, having shallow infranarial portions defined by faint grooves from the median portion, a median groove in front in the lower part, an angled inferior border, and a complete gutter dividing the upper lip, which is not quite so deep as the rhinarium. (Text-fig. 29, C.)

In *Mephitis* the infranarial portions are always deep, wide, and well-defined laterally beneath the posterior slit of the nostrils as in *Meles*, and when the groove between the nostrils and the two defining the infranarial portions and the gutter on the lip are absent, the resemblance to that genus is particularly close. But in a specimen, said to have come from Manitoba, the rhinarium is lower and somewhat wider than in other examples, the lip is cleft by a shallow gutter continued on to the lower half of the rhinarium, and the lateral portions are defined by shallow grooves running from the nostrils to the middle line of the inferior edge. (Text-fig. 29, D, E.)

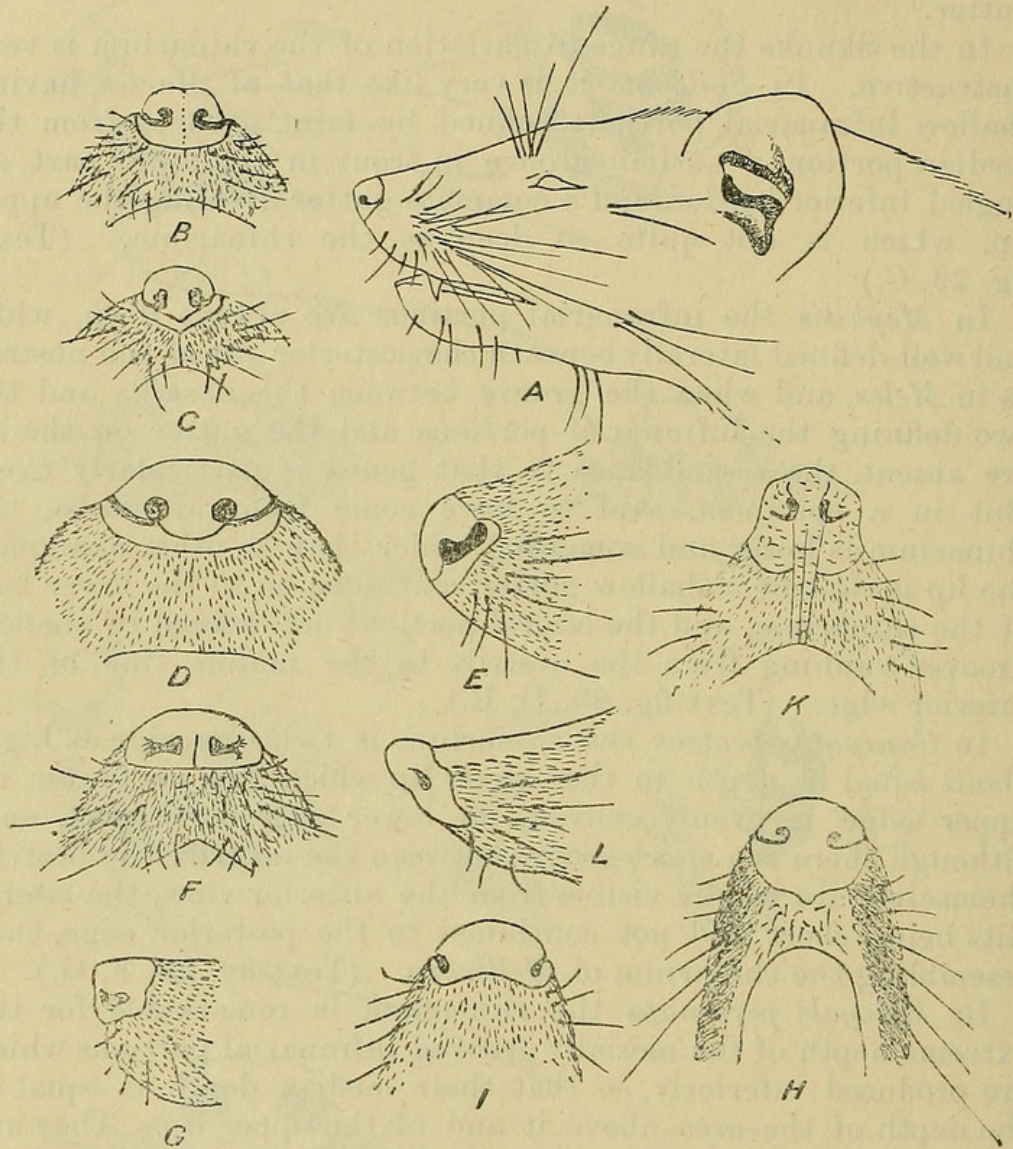
In *Conepatus proteus* the rhinarium is twice as wide as high, about equal in depth to the upper lip which has no gutter, its upper edge is evenly convex, its lower edge horizontal, and, although there is a short groove between the nostrils, the nostrils themselves are wholly visible from the anterior view, the lateral slits being short and not continued to the posterior edge, thus resembling the rhinarium of *Mellivora*. (Text-fig. 29, F, G.)

In *Melogale personata* the rhinarium is remarkable for the extreme depth of the mesially grooved infranarial portions which are produced inferiorly, so that their median depth is equal to the depth of the area above it and of the upper lip. They are also very deep laterally beneath the slits of the nostrils, which are continued to the posterior border of the rhinarium. The upper lip is ungrooved and is only sparsely hairy mesially and laterally as far back as the angle of the mouth. (Text-figs. 29, H, I; 30, G.)

The rhinarium of *Mydaus* is even more aberrant and recalls that of the Suidæ in the sense that it consists of a somewhat rounded disc with two subcircular nostrils on its anterior surface, the slits of the nostrils being very narrow and short. The infranarial portions are much deeper than the upper portion of the rhinarium and are everywhere of equal depth. They are

defined by a vertical groove running downwards from the nostril, and each of these grooves is continuous with the outer edge of a long, narrow, parallel-sided philtrum, of the same texture as the rhinarium, which extends to the edge of the upper lip and is marked by a groove passing upwards on to the rhinarium. In front of the rhinarium above them is a naked strip of skin on the muzzle. (Text-fig. 29, K, L.)

Text-figure 29.



- A. Side view of head of *Ictonyx capensis*.
- B. Front view of rhinarium of the same.
- C. The same of *Spilogale putorius*.
- D. The same of *Mephitis mephitis*.
- E. Side view of the same.
- F. Front view of rhinarium of *Conepatus proteus*.
- G. Side view of the same.
- H. Front view of rhinarium of *Melogale personata*.
- I. Side view of the same.
- K. Front view of rhinarium of *Mydaus meliceps* (from dried skin).
- L. Side view of the same.

$\times \frac{1}{3}$.

The genera may be grouped as follows by the rhinarium :—

- a. No complete and true philtrum resembling the rest of the rhinarium in texture dividing the upper lip, which is at most grooved.
- b. Upper lip divided by a complete groove of smooth naked skin, giving mobility to the right and left halves *Gulo, Martes.*
- b'. Groove on upper lip obliterated or nearly so, the two halves of the lip not separately movable, or only slightly so.
- c. Infranasal portion of rhinarium much shallower beneath lateral slits of nostrils than above them.
- d. Infranasal portion laterally very narrow *Mustela, Gale, Putorius, Charronia, Grison, Taxidea.*
- d'. Infranasal portion laterally moderately deep... *Tayra, Ictonyx, Spilogale, Mephitis, Conepatus.*
- c'. Infranasal portion very deep beneath lateral slits, approximately as deep as portion above them *Meles, Melogale.*
- a'. A long narrow philtrum, resembling the rest of the rhinarium, dividing the upper lip; infranasal portions everywhere very deep *Mydaus.*

The Facial Vibrissæ.

The number of tufts of facial vibrissæ characteristic of the Carnivora is typically present in the Mustelidæ; but the vibrissæ themselves are longer and more numerous in predatory forms (like *Martes*, *Mustela*, and *Ictonyx*) than in fossorial forms (like *Mellivora*, *Meles*, and *Mephitis*). They are especially well developed in the matter of rigidity and number in the truly semi-aquatic genera like *Lutra* and *Amblonyx*; but in the tropical West-African Otter, *Paraonyx*, Hinton records the complete absence of the superciliary and upper genal tufts. In other genera, like *Meles*, the upper genal tuft is sometimes apparently absent; but a noticeable point about this tuft in all genera, when it is present, is its high position on the cheek, only a little below and behind the posterior corner of the eye. In the one fresh example of *Tayra barbara* examined, I could find no trace of the interramal tuft. (Text-figs. 27-29.)

In *Melogale personata* the vibrissæ are all long and numerous as in predatory forms, the submentals being unusually well developed on the area of nearly naked skin which runs along the lower lip as far as the angle of the mouth, corresponding to that of the upper lip. (Text-fig. 30, G.)

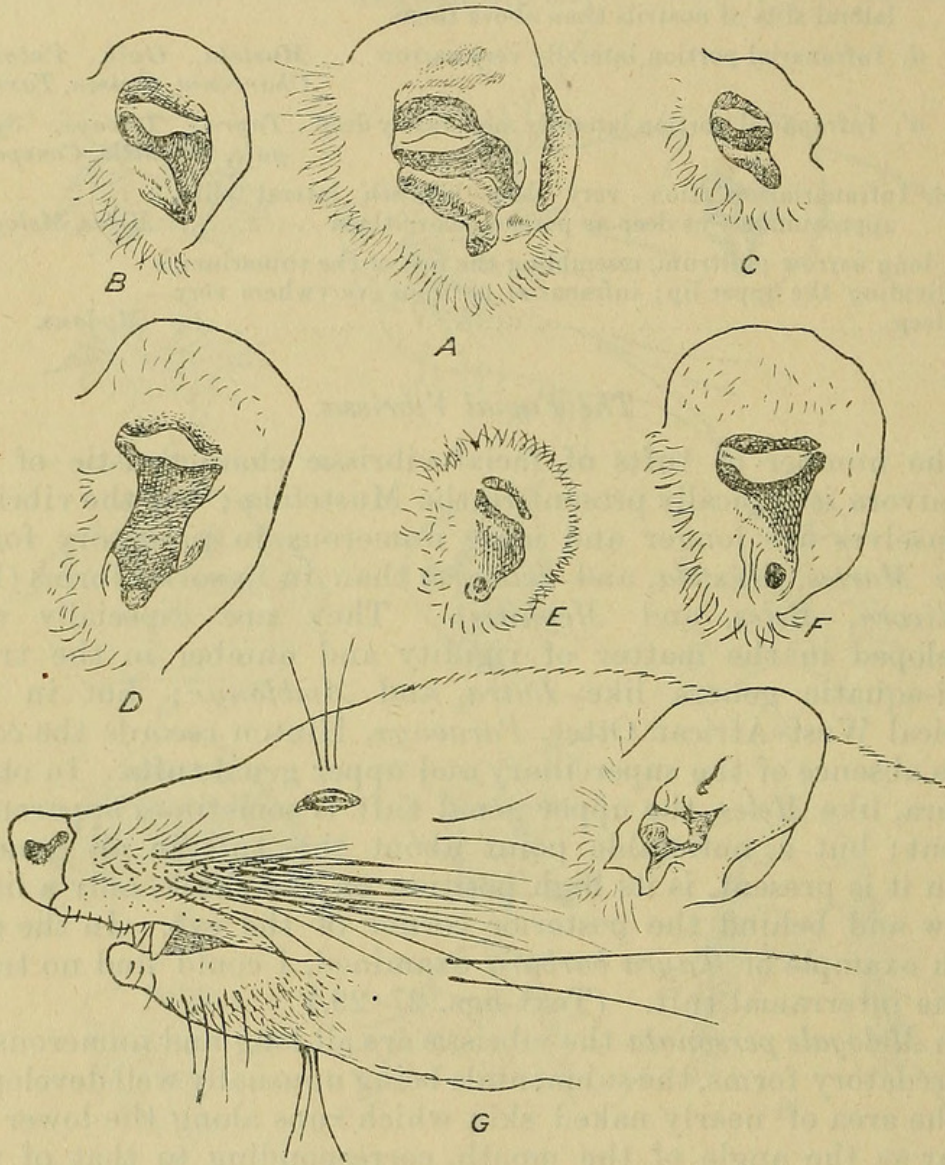
The External Ear.

The external ear shows every grade between high specialisation, the primitive condition, and almost complete degeneration. In its highest types, as exemplified by *Martes** and *Charronia*, it is of tolerably large size and is provided with a well-developed bursa, the posterior flap of which is large, has a strongly convex margin, and is attached above behind the straight-edged portion of the

* See my paper on the Pine and Beech-Martens (P. Z. S. 1914, pp. 1062-1068).

posterior border of the ear which constitutes the anterior flap. The supratragus has a simple subglobular thickening. The tragus and supratragus are well defined and separated by a distinct notch, and the antero-internal and postero-internal thickenings descend behind or within the tragal and antitragal prominences respectively. (Text-fig. 27, G.)

Text-figure 30.



- A. Ear of *Gale nivalis*.
 B. „ *Pæcilogale albinucha* (from dried skin).
 C. „ *Lyncodon patagonicus* („ „).
 D. „ *Mephitis mephitis*.
 E. „ *Conepatus proteus*.
 F. „ *Spilogale putorius*.
 G. Side view of head of *Melogale personata*.

D, E, F, G, $\times \frac{1}{3}$.

In *Mustela*, *Gale*, *Plesiogale*, and *Putorius* the ear is relatively smaller and rounder than in *Martes*, and further differs in that

the thickening of the supratragus is larger and valvular, and the edge of the cavity has a small soft membranous flap just above the supratragus, which is especially well developed in *Plesiogale*. Moreover, the antero-internal thickening curves sharply beneath the supratragus posteriorly. In *Gale*, *Mustela*, and *Plesiogale* the bursa is almost or quite as well developed as in *Martes*, but in *Putorius* it is reduced to a marginal slit, owing to the reduction in size of the posterior flap, the edge of which is nearly straight. (Text-figs. 27, A ; 30, A.)

Gulo has the pinna like that of *Martes*, but relatively smaller and provided with a smaller bursa ; and the pinna of *Melogale* is very like that of *Mustela* and *Gale*, the bursa, tragus, and antitragus being well developed, but the supratragus is less valvular, the antero-internal ridge descends more vertically, and there is a little pouch above the hollow. (Text-fig. 30, G.)

Tayra and *Grison* also resemble *Mustela* and *Gale* in the presence of the upper membranous flap, the valvular supratragus, the posterior curvature of the antero-internal ridge beneath the supratragus ; but differ in the reduction of the bursa to an even greater extent than is seen in *Putorius*. The posterior flap is continuous above and below with the margin of the pinna, and the anterior flap is represented by a very shallow ridge of integument a little in front of it, so that the pouch is reduced to a minimum. In *Grison* and *Grisónella* the valvular supratragus and the flap above it are larger than in *Tayra* ; and in *Grisónella* the anterior ridge of the bursa is shorter than in *Grison*. (Text-fig. 28, A, D.)

In *Ictonyx*, and also in *Pæciliotis* and *Pæcilogale*, judging from dried skins, the pinna differs essentially from that of *Mustela*, *Gale*, and *Putorius* in the total absence of all trace of the bursa and of the membranous flap above the supratragus. Otherwise it is similar. (Text-figs. 29, A ; 30, B.)

In *Meles* and *Taxidea* the pinna is smaller than in *Ictonyx*, and the supratragus has a simple subglobular thickening as in *Martes*. Otherwise they are tolerably similar ; the pinna is less salient in *Taxidea* than in *Meles*.

In *Lutra* the pinna, although much reduced, is of the same simple type as in *Meles*. In *Hydriotes* it is simplified by the almost complete suppression of the tragus and antitragus and of the supratragus apart from the subglobular thickening.

In *Spilogale*, *Mephitis*, and *Conepatus* a noticeable peculiarity in the pinna is the entire absence of the tragal thickening, so that the external orifice of the ear is exposed and not hidden in a cup-like hollow ; and the cavity of the pinna has no definite anterior rim. The low antero-internal ridge curves posteriorly beneath the valvular supratragus, which appears to be set higher in the ear than in other genera. The pinna is of comparatively large size in *Spilogale* ; but in *Conepatus*—at all events, in *C. proteus*—it is much reduced and scarcely stands away from the head. There is no trace of the bursa. (Text-fig. 30, D-F.)

In *Lyncodon* also the pinna is as much reduced as in *Conepatus*, standing away from the head as a shallow short ridge, the lower end of which does not reach nearly to the *aditus inferior*. There is no bursa, but the structure of the ridges could not be determined on dried skins. (Text-fig. 30, C.)

The pinna of *Mellivora* surpasses even that of *Conepatus* and *Lyncodon* in reduction in size. It is represented merely by a thickening of the integument, without any free edge, round the small cavity; and, judging from the descriptions, the pinna of *Mydaus* is very similar to that of *Mellivora*, but I am unable to say whether the orifice is exposed as in *Mephitis*, *Spilogale*, and *Conepatus* or concealed by a tragal thickening.

The following table shows briefly the principal modifications in the external ear:—

- | | |
|---|--|
| a. Bursa retained. | |
| b. Bursa marginal, upper end of its posterior flap hidden by that of anterior flap | <i>Mustela</i> , <i>Gale</i> , <i>Plesiogale</i> ,
<i>Putorius</i> , <i>Martes</i> , <i>Charronia</i> , <i>Gulo</i> , <i>Melogale</i> . |
| b'. Bursa remote from margin, shallow, its posterior flap in no way concealed by anterior flap..... | <i>Tayra</i> , <i>Grison</i> , <i>Grisonella</i> . |
| a'. Bursa absent. | |
| c. Auditory orifice concealed, usually by tragal thickening. | |
| d. Pinna laminate, standing away from head. | |
| e. Supratragus a well-developed valvular flap | <i>Ictonyx</i> , <i>Pæciliotis</i> ,
<i>Pæcilogale</i> . |
| e'. Supratragus at most a ridge with rounded thickening. | |
| f. Pinna moderately large | <i>Meles</i> , <i>Taxidea</i> . |
| f'. Pinna much reduced | <i>Lutra</i> , <i>Amblonyx</i> , etc. |
| d'. Pinna a thickened rim of integument | <i>Mellivora</i> . |
| c'. Auditory orifice exposed, not concealed by tragal thickening | <i>Spilogale</i> , <i>Mephitis</i> , <i>Conepatus</i> . |

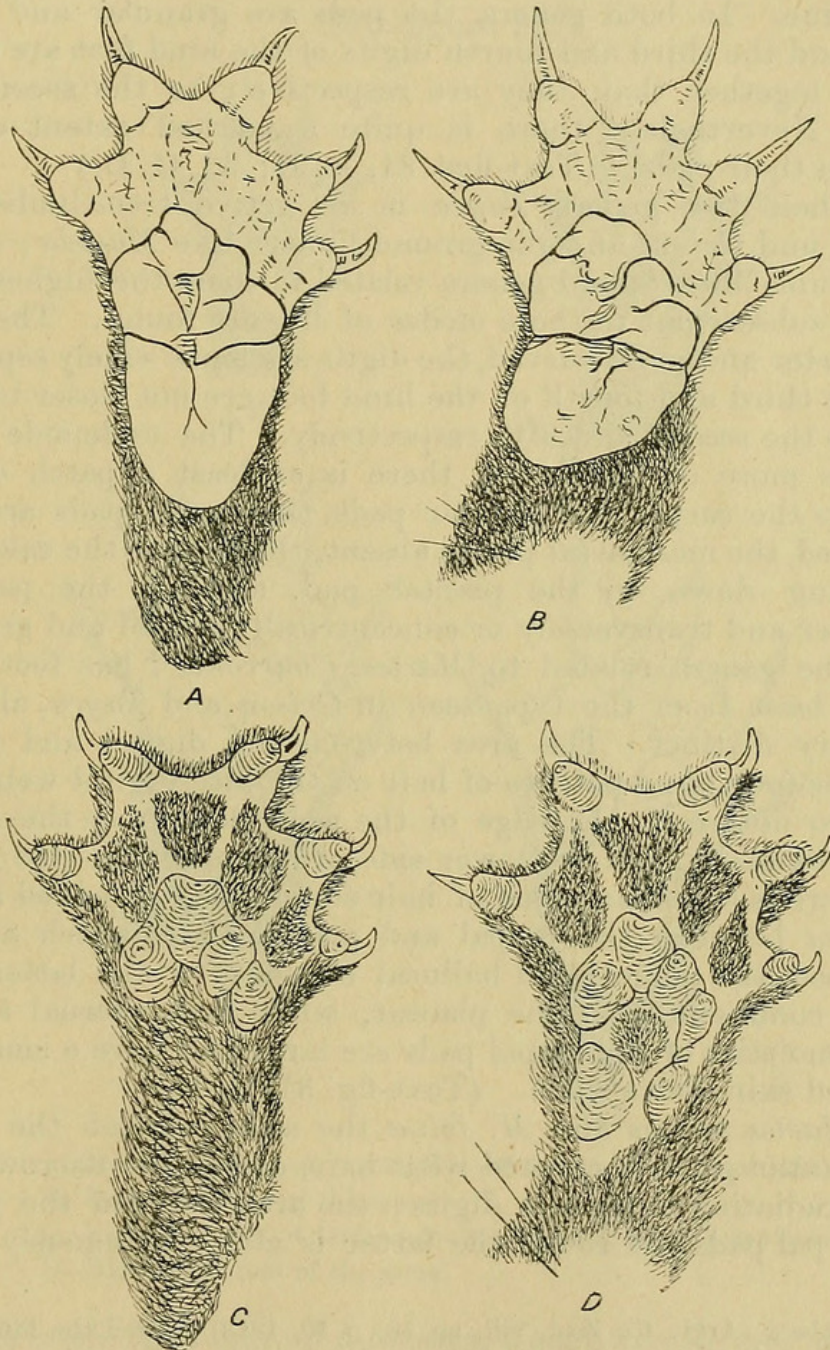
The Feet.

In describing the feet of the Mustelidæ I start with two assumptions. First, that the primitive feet were adapted for running or climbing, or both combined, and not for digging or swimming, which hamper, if they do not prevent, the first-mentioned activities. Second, that the feet were naked below, provided with short curved claws, interdigital webbing up to the proximal end of the pads, large 4-lobed plantar pads, double carpal and metatarsal pads, and a hairy heel; and that the digits were unequal in length, the first being the shortest, the second and fifth next and approximately equal in length, and the third and fourth the longest and also approximately equal, so that the digital pads, when not spread, formed a strongly curved line round the anterior margin of the plantar pad. And possibly in the hind foot the third and fourth digits were more closely tied together than to the second and fifth respectively.

The genera whose feet most nearly approach these hypothetical feet are *Tayra* and *Grison*. It is therefore needless to describe them in detail. From the material examined I have not been

able to satisfy myself that there is any fundamental difference between the feet of the two, unless it be that in *Grison* the plantar pads are defined from the carpal and metatarsal pads by a deeper and wider groove. In *Tayra* these pads are confluent throughout their width, there is only a very slight trace of division between the two moieties of the carpal pad and none in

Text-figure 31.



- A. Right hind foot of *Tayra barbara*.
 B. Right fore foot of the same.
 C. Right hind foot of *Charronia flavigula*.
 D. Right fore foot of the same.

$\times \frac{1}{2}$.

the case of the metatarsal pad *. In an example of *Grison furax* or an allied form, from Brazil, there is a comparatively large area between the plantar and carpal pads, the latter are well defined but mesially in contact, and there is some naked skin above the large external pad. Similarly, in the hind foot there is some naked skin above the somewhat rounded metatarsal pad, which except internally is distinctly separated from the plantar pad. These differences from the feet of *Tayra* are, however, not so well defined in examples of *Grisonella* from Cordova in the Argentine. In both genera the pads are granular and tessellated, and the third and fourth digits of the hind foot are a little nearer together than they are respectively to the second and fifth. Nevertheless, there is quite a marked extent of web between their pads. (Text-figs. 31, A, B; 32, C, D.)

Of these two genera *Tayra* is an active tree-climber like *Martes*, and *Grison* an agile ground-hunter like *Mustela*; and in *Martes* and *Mustela* and genera related to them the highest type of feet subservient to those modes of life are found. The claws are shorter and more curved, the digits are more widely separable, and the third and fourth of the hind foot are not closer together than to the second and fifth respectively. The underside of the webs is more or less hairy, there is at least a patch of hair between the carpal and plantar pads, the carpal pads are quite separated, the metatarsal pad is absent, the hair of the calcaneum extending down to the plantar pad, and all the pads are narrower and transversely or concentrically ridged and grooved.

Of the genera related to *Martes*, *Charronia* † has feet which depart least from the type seen in *Grison* and *Tayra*, although still very distinct. The area between the digital and plantar pads has four large patches of hair on the interdigital webs; but these do not reach the edge of the webs distally or the plantar pads proximally, and the lower side of the digits is also naked; and there is a similar patch of hair surrounded by naked skin on the area between the carpal and plantar pads, which are well developed, the pollical and hallucal elements of the latter being widely confluent with the plantar, while the internal and external moieties of the carpal pads are large and have a small area of naked skin above them. (Text-fig. 31, C, D.)

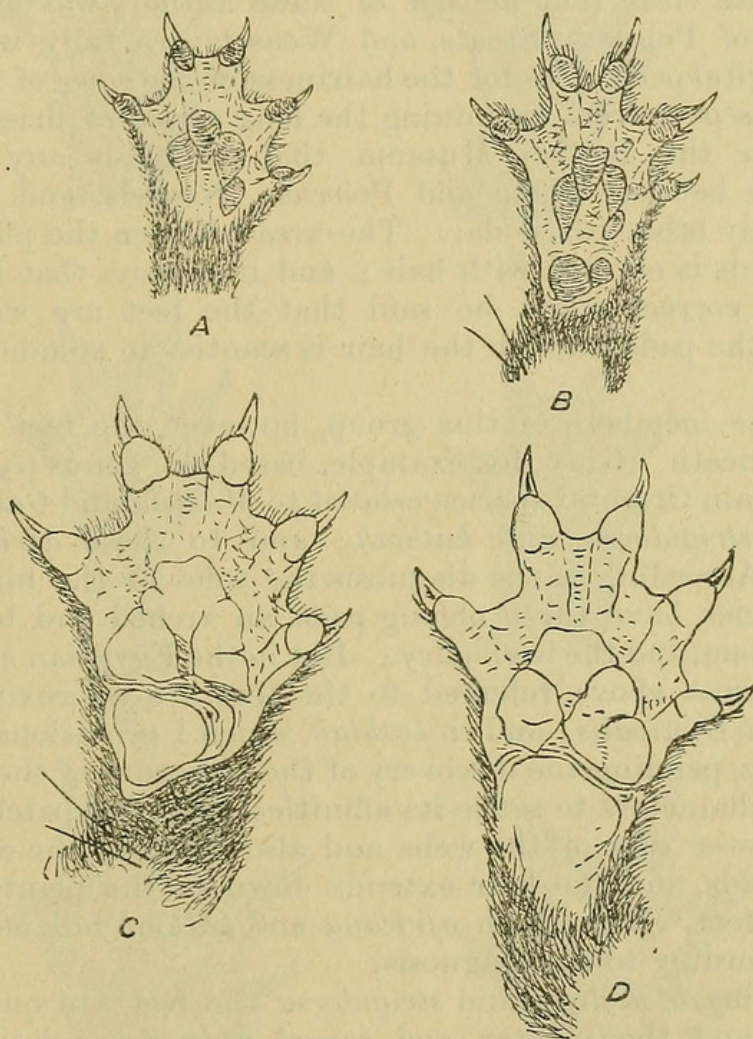
In *Martes martes* and *M. foina* the area between the digital and plantar pads is covered with hair, except for narrow naked strips radiating along the digits; the area between the plantar and carpal pads and round the latter is also continuously hairy;

* Lönnberg (Arkiv för Zool. viii. no. 16, p. 10, 1913) figured the hind feet of two forms of *Tayra* from different altitudes and localities in Ecuador, to show that the combined plantar and metatarsal pad—there being no line of demarcation between them—is longer in the race from the lowlands. Defects in the drawings of these feet may be attributed to their being taken from skins softened in water after being dried.

† In 1918 I resuscitated this genus of Gray's, based upon *Martes flavigula*, when I found that the baculum differs greatly from that of *Martes martes* and *M. foina* (Ann. & Mag. Nat. Hist. (9) i. pp. 308-310).

the plantar pads are smaller, more subdivided, their pollical and hallucal elements are connected by a narrow strip with the main pad, and the carpal pads are much reduced and separated by a longer space from the plantar pad. *M. foina*, however, has much larger digital, plantar, and carpal pads than *M. martes**, and thus more nearly approaches *Charronia*. In *M. martes* the digital pads are narrowly ovate, the plantar pads are broken up into four areas connected by narrow naked strips, and the carpals are quite small.

Text-figure 32.



- A. Right hind foot of *Pæcilogale albinucha* (from dried skin).
- B. Right fore foot of the same.
- C. Right fore foot of *Grisonella* sp. from Cordova, Argentine.
- D. Right hind foot of the same.

In *Mustela erminea* and *hibernica*, *Gale* † *nivalis* and *africana*, *Putorius putorius*, *furo*, and *nigripes* the feet, except that they are relatively shorter and stouter, generally resemble those of

* For figures illustrating these differences, subsequently verified on other specimens, see my paper on these species of *Martes* (Proc. Zcol. Soc. 1914, pp. 1062-1068).

† Distinguishable from *Mustela* by the shape of the baculum.

Martes in hairiness and pad development. But in *G. africana* alone have I found the plantar pad broken up into four elements to the same extent as in *M. martes*; and only in *G. africana* could I find the inner moiety of the carpal pad; but, judging from its minute size in this species, it may have been overlooked in the others. (Text-fig. 33, C-F.)

Writing of the Minks (*Lutreola*), Flower and Lydekker ('Mammals, Living and Extinct,' p. 586), said that they differ from the Polecats, Stoats, and Weasels "by the toes being partially webbed and by the absence of hair in the intervals between the naked pads of the soles of the feet." From this statement it seems quite clear that neither of these authors was aware that the toes of Polecats, Stoats, and Weasels are fully webbed up to the digital pads. As for the hairiness of the soles of the feet, I cannot discover from examining the long series of dried skins of Minks in the British Museum that there is any essential difference between them and Polecats, Weasels, and Stoats in that or any other particular. The area between the plantar and digital pads is covered with hair; and it appears that Baird was perfectly correct when he said that the feet are well furred between the pads, though the hair is scantier in summer than in winter.

In some members of this group, however, the feet are quite naked beneath. Gray, for example, based the genus *Gymnopus** upon certain Oriental species related to *Mustela* and *Gale*, namely *nudipes*, *strigidorsa*, and *kathiah*; and to these *africana* was added. According to the diagnosis the soles of the hind feet in these species have three oblong pads, an arched and bald space behind them, and the heel hairy. But in the Egyptian example of *Gale africana* above referred to the feet are approximately as hairy as in *G. nivalis*; and in *kathiah*, which I provisionally retain in *Mustela*, pending the discovery of the structure of the baculum or other characters to settle its affinities, there is a patch of hairs on the lower side of the webs and also between the carpal and plantar pads, and the hair extends down to the plantar pad on the hind foot. Thus both *africana* and *kathiah* fall outside the genus according to the diagnosis.

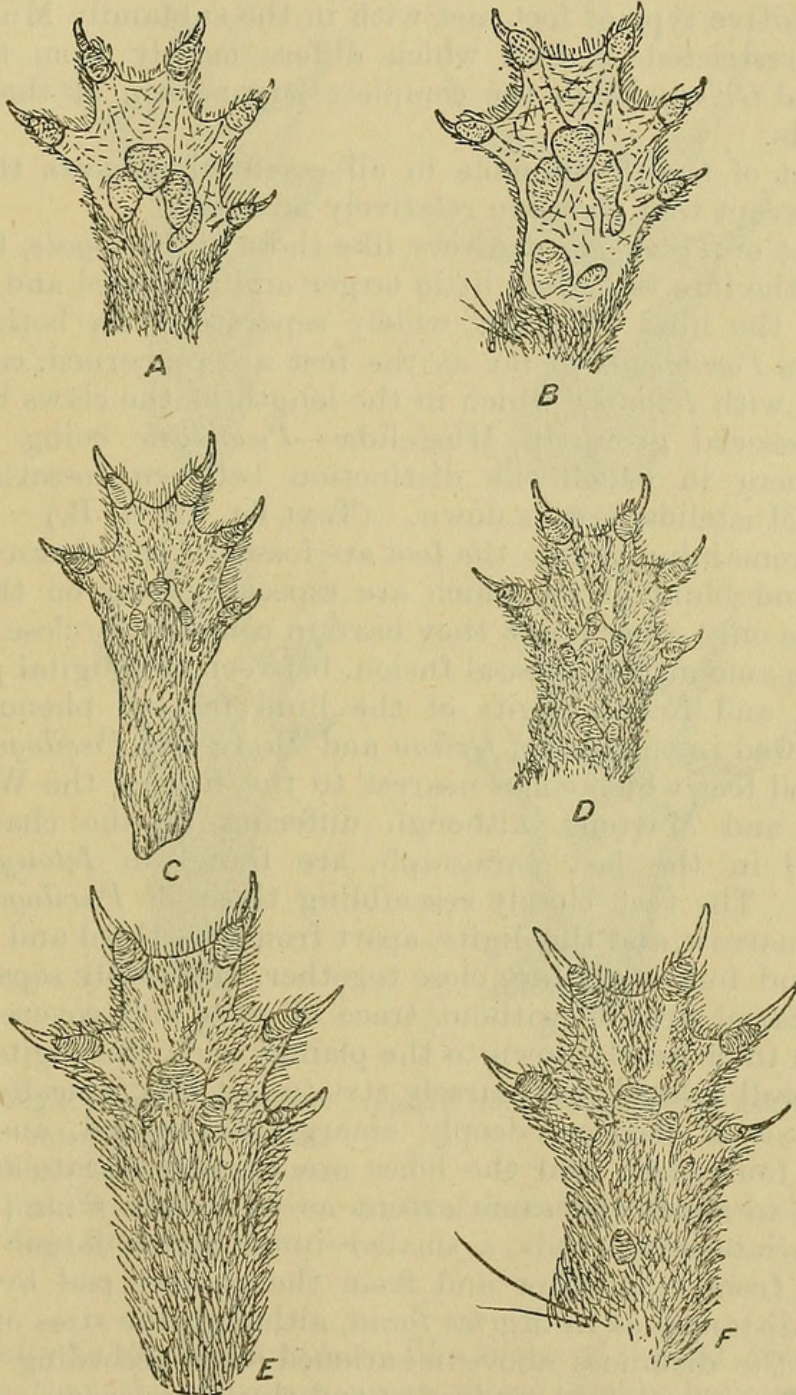
In *Plesiogale nudipes* and *strigidorsa* the feet are quite naked beneath, and the plantar and carpal pads are relatively considerably larger than in *Mustela*, *Gale*, and *Putorius*, and apparently less coarsely striated. The plantar pads are very distinctly four-lobed, the three main lobes being widely in contact, while the pollical and hallucal lobes are attached to the posterior end of the inner of the three main lobes. The two carpal pads are well developed and almost in contact. Just above them there is a narrow naked space, and there is a corresponding space, which, however, seems to vary individually

* Quoted in this paper as *Plesiogale* (see above p. 805), of which *nudipes* is the type-species. I premise that the group is at least as much worth nominal recognition as *Lutreola* or *Kolonokus*.

in *P. nudipes*, and lies behind the plantar pad of the hind foot. (Text-fig. 33, A, B.)

The feet of these two species are of great interest. It might be claimed that their nakedness is a secondarily acquired character, correlated with life in warmer latitudes than those

Text-figure 33.



- A. Right hind foot of *Plesiogale nudipes*.
- B. Right fore foot of the same.
- C. Right hind foot of *Gale nivalis*.
- D. Right fore foot of the same.
- E. Right hind foot of *Putorius putorius*.
- F. Right fore foot of the same.

frequented by typical Stoats, Weasels, and Polecats. If *nudipes*, which ranges from the Malay Peninsula to Borneo, were alone concerned, that view would be more defensible than, in my opinion, it is. But *strigidorsa* occurs much farther to the north, in Sikhim. Again, it must be remembered that the tropical American species *brasiliensis*, which may be taken as the type of Gray's genus *Neogale*, if it be resuscitated, has hairy feet. I incline, therefore, to the opinion that in *Plesiogale* we have the most primitive type of foot met with in the subfamily Mustelinæ as here restricted—a foot which differs mainly from that of *Grisson* and *Grissonella* in the complete suppression of the metatarsal pads.

The feet of *Gulo** resemble in all essential respects those of *Martes*, except that they are relatively broader.

The feet of *Pæcilogale* are very like those of *Plesiogale*, but the claws of the fore feet are a little larger and the third and fourth digits of the hind foot less widely separated. In both these particulars *Pæcilogale*, so far as the feet are concerned, connects *Plesiogale* with *Ictonyx*, which in the length of the claws belongs to the fossorial group of Mustelidæ—*Pæcilogale* being one of those genera in which the distinction between fossorial and cursorial Mustelidæ breaks down. (Text-fig. 32, A, B.)

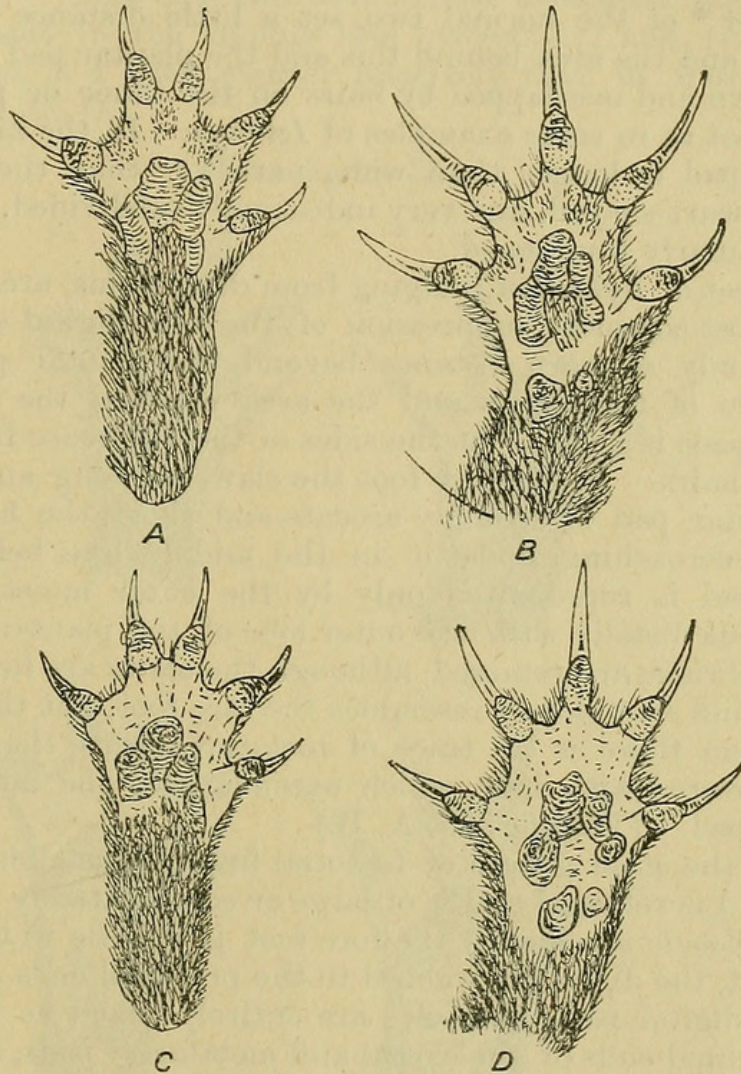
In the remaining genera the feet are fossorial and characterised by long and blunt claws, which are especially long on the fore feet. The only other point they have in common is close union, sometimes amounting to basal fusion, between the digital pads of the third and fourth digits of the hind feet—a phenomenon foreshadowed in the feet of *Grisson* and *Tayra* and *Pæcilogale*.

Fossorial feet which come nearest to the feet of the Weasels, Polecats, and Martens, although differing in the characters mentioned in the last paragraph, are found in *Ictonyx* and *Pæciliotis*. The feet, closely resembling those of *Pæcilogale*, are tolerably narrow, and the digits, apart from the third and fourth of the hind foot which are close together, are widely separable; the metatarsal area is without trace of pads and covered with hair down to or nearly down to the plantar pad; the digital pads are oval, well defined, and coarsely striate—at least apically; the plantar pad is narrow, deeply emarginate behind, and very distinctly four-lobed, and the lobes are coarsely striate and are in contact to about the same extent as in *Martes foina*; there are two striate carpal pads, a smaller inner and a larger outer, separated from each other and from the plantar pad by about the same distances as in *Martes foina*, although the sizes of these pads and the distances above mentioned vary according to the species. The carpal pads are largest and the distances in question smallest in the species in which the area round them and the area between the plantar and digital pads are naked. In other

* See my paper on the external characters of this genus (Proc. Zool. Soc. 1920, pp. 179-187).

species the hair of the carpus extends to the carpal pads, overlaps the inner and spreads into the posterior emargination of the plantar pad; and there is a scanty patch of hair upon the lower side of the interdigital integument*. (Text-fig. 34, A-D.)

Text-figure 34.



- A. Right fore foot of *Ictonyx capensis*, from S. Africa, with hair on interdigital integument.
 B. Right fore foot of the same.
 C. Right hind foot of *Ictonyx* sp., from the Sudan, with naked soles.
 D. Right fore foot of the same.

× $\frac{1}{3}$.

In *Pæciliotis* the feet are more like those of typical *Mustela*, in the sense that the soles are much more thickly hairy and the plantar pad is smaller and more subdivided, no doubt in conformity with the sandy habitat of the animal.

The feet of *Taxidea* resemble those of *Ictonyx* in the absence

* Thus Thomas's statement that *Ictonyx* may be distinguished from *Pæciliotis* by the nakedness of the soles of the feet does not hold good.

of the metatarsal pad, but in most respects they are very different. The digits are shorter, closer together, with the pads larger, less well defined, and the interdigital webs (although narrower) extend further up the pads, especially on the fore foot. The plantar pad of the broad fore foot, although wider than long, is narrower than the foot itself, indistinctly lobate, and much less deeply emarginate behind; there is a single small carpal pad, representing the outer * of the normal two, set a little distance behind the plantar, and the area behind this and the plantar pad is partially overgrown and overlapped by hairs on the inner or pollical side of the foot as in some examples of *Ictonyx*. In the hind foot the plantar pad is longer than wide, narrower than the foot, irregularly heart-shaped, and very indistinctly subdivided. The pads are granularly roughened.

The feet of *Lyncodon*, judging from dried skins, are peculiar in the almost complete suppression of the interdigital webs, which extend only a short distance beyond the plantar pads. The underside of the digits and the area between the digital and plantar pads is naked, but the sides of the digits are fringed with longish hairs. In the fore foot the claws are long and fossorial, the plantar pad is strongly arcuate and short, the hairs of the carpus encroaching upon it in the middle line behind. The carpal pad is represented only by the outer moiety, which is continuous distally with the outer lobe of the plantar pad. The carpal vibrissæ are retained, although the claws are fossorial.

The hind foot closely resembles the fore foot, but the claws are short; and there is no trace of metatarsal pads, the metatarsus being covered with hair, which extends over the middle of the plantar pad. (Text-fig. 35, A, B.)

In all the other genera of fossorial footed Mustelidæ the metatarsal pad is retained and is of large or comparatively large size.

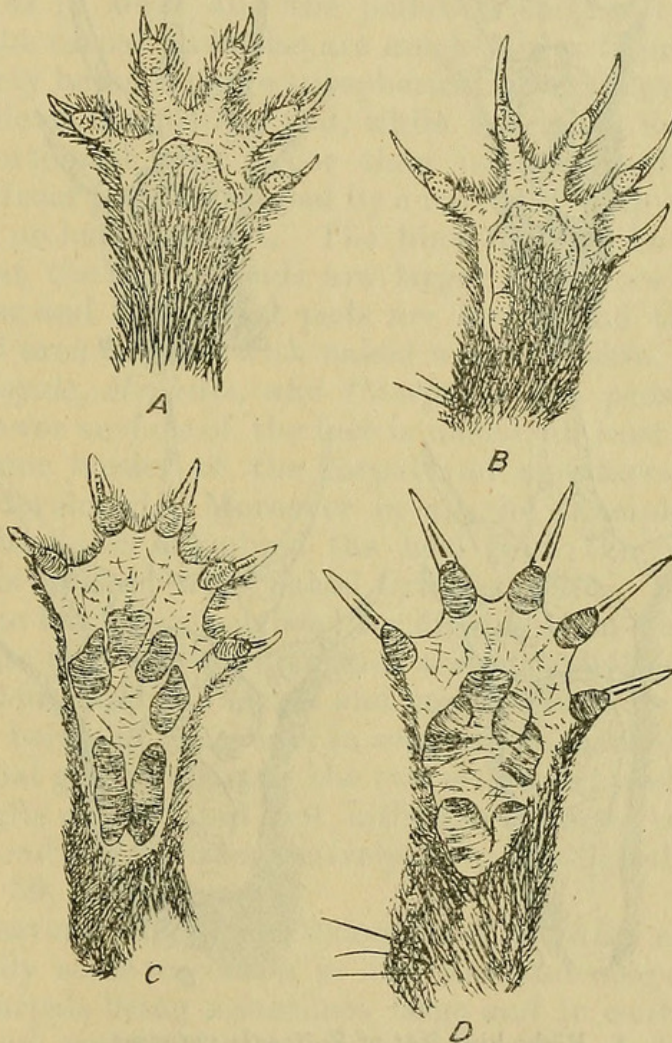
In *Melogale personata* † the fore foot is a little wider than the hind foot, the digits are webbed to the proximal ends of the well-defined digital pads, the soles are entirely naked as far back as the proximal ends of the carpal and metatarsal pads, and all the pads are tolerably coarsely striated, although less coarsely than in *Mustela*, *Martes*, *Gulo*, and *Ictonyx*. The fore foot otherwise tolerably closely resembles that of *Meles*, but the digits are rather more separable, the digital pads are better defined, the plantar pad is relatively narrower, more distinctly four-lobed, with its anterior and posterior margins more curved, the two elements of the carpal pad are in contact or very nearly so in the middle line, and the carpal vibrissæ are well developed. In the hind foot the digits are markedly more widely separable than in *Meles*, there

* In my paper on *Taxidea* and *Meles* (Proc. Zool. Soc. 1920, p. 428) I inadvertently described the carpal pad as representing the inner or radial carpal of *Meles*.

† Hodgson figured the hind foot of this species, but wrongly labelled it *Urva cancrivora* (Journ. As. Soc. Bengal, xvi. pl. ii.). A figure of the fore foot is in his unpublished drawings.

being quite a distinct space between the third and fourth, although the space is narrower than that between the second and third or fourth and fifth. As in the fore foot the digital pads are better defined, the plantar pad is narrower, much more strongly curved, and very distinctly four-lobed, the hallucal lobe, like the pollical lobe of the fore foot, being as large as the others individually. There are two well-defined elongated metatarsal pads, confluent in the middle line proximally, and the hairy calcaneal area is a little shorter relatively than in *Meles meles*. (Text-fig. 35, C, D.)

Text-figure 35.



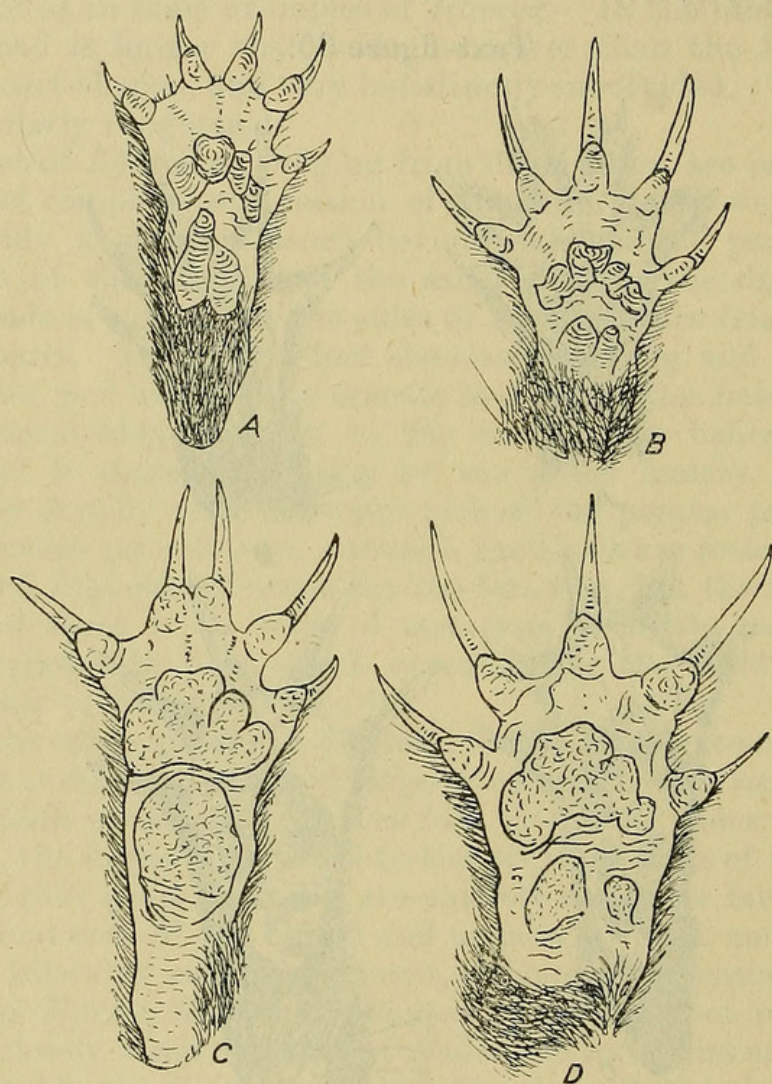
- A. Right hind foot of *Lynxodon patagonicus* (from dried skin).
- B. Right fore foot of the same.
- C. Right hind foot of *Melogale personata*.
- D. Right fore foot of the same.

C, D, $\times \frac{1}{3}$.

The feet of *Meles meles* I have already described and figured (Proc. Zool. Soc. 1920, pp. 426-428, fig. 20, A, B). In addition to the differences mentioned above, it may be added that they are of a more decidedly fossorial type than in *Melogale*, the hind

foot being narrower as compared with the fore foot, with the pads of the third and fourth digits confluent. In both the fore and hind foot the plantar pads are very wide, the carpal pads of the fore foot are separated, and there is a patch of hair on the area behind the plantar pad. In the hind foot the metatarsal pads are shorter and more confluent, and closer to the plantar pad than in *Melogale*, and all the pads are granular or papillate, not striated.

Text-figure 36.



- A. Right hind foot of *Spilogale putorius*.
 B. Right fore foot of the same.
 C. Right hind foot of *Mephitis mephitis*.
 D. Right fore foot of the same.

$\times \frac{1}{3}$.

Judging from dried skins and from Hodgson's unpublished drawings referred to in my paper quoted above, the feet of *Arctonyx* seem to resemble those of *Meles* in all essential particulars. The soles of the feet are quite naked. The large naked area above the plantar pad of the hind foot has two elongated

thickenings representing metatarsal pads; the plantar pad of the hind foot is about as wide as long and markedly three-lobed (Hodgson probably accidentally omitted the hallucal element) and narrower than the foot; the digital pads of both feet are oval and well defined. In the fore foot the plantar pad is markedly four-lobed and wider than long, and separated from it by a considerable space are the two rather large carpal pads, which are together about as wide as the plantar pad. The pads are coarsely granular and tessellated.

The fore foot of *Mellivora* resembles that of *Taxidea* rather than that of *Meles* in the large size of the digital pads and the extension of the webbing along their edges, but the plantar pad is as wide as in *Meles*, and the pollex is shorter than in either genus. The carpal pads also are much larger than in either, the outer moiety being a large subspherical mass at least as long and half as wide as the plantar pad, while the much smaller, smooth pollical portion is also larger than in *Meles*, and the two are separated from the plantar pad by a narrower strip of integument, which has no hairs upon it. The hind foot is like that of *Meles*, except that the digital pads are larger and more fully webbed, the plantar and metatarsal pads are larger, and the rest of the metatarsal area covered with naked wrinkled skin.

In *Spilogale*, *Mephitis*, and *Conepatus* the pads are granular and the lower surface of the feet is naked, at least as far back as the posterior border of the carpal and metatarsal pads, which are well developed. Moreover in all the examples of *Mephitis* and of *Conepatus* examined the heel from the metatarsal pad upwards is covered with naked wrinkled skin. *Spilogale* seems to have the feet less specialised for digging than the other genera, in the sense that the plantar pads are more distinctly broken up into four lobes and the carpal and metatarsal pads more reduced, the latter being, at all events in some cases, marked by a distinct longitudinal groove defining the two elements; and the third and fourth digits of the hind foot, although closer to each other than to the second and fifth respectively, have the digital pads unfused. (Text-fig. 36, A, B.)

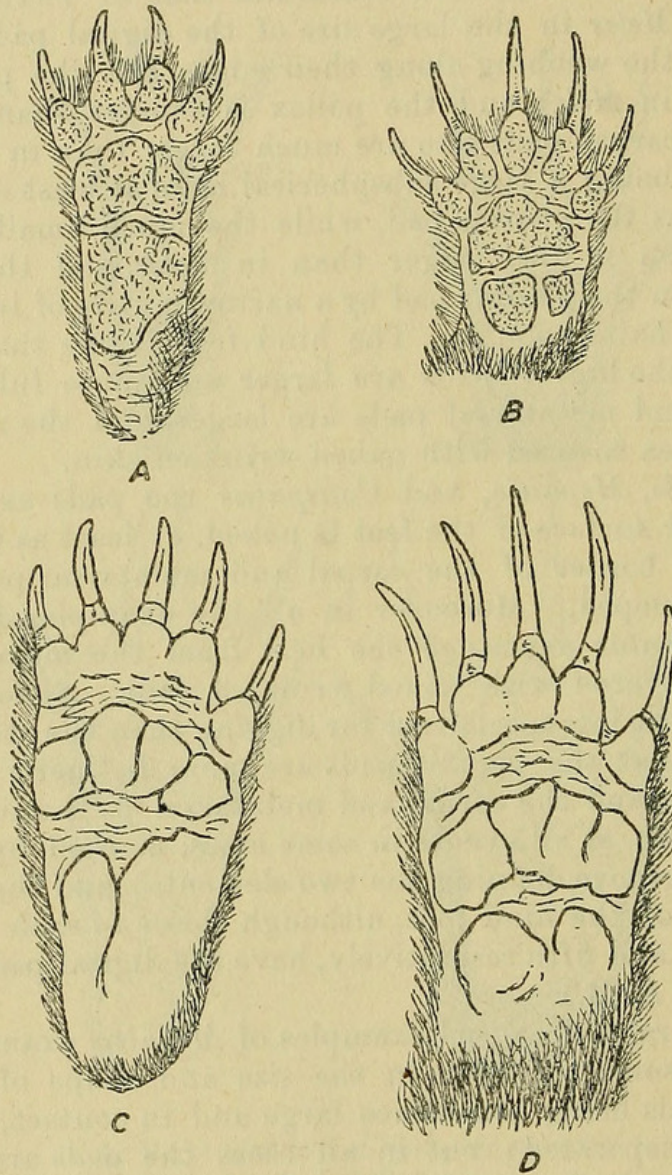
In the several unlocalised examples of *Mephitis* examined there is naturally some variation in the size and shape of the pads, the two carpals being sometimes large and in contact, sometimes smaller and separated; but in all cases the pads are relatively larger than in *Spilogale* and less subdivided, and the digits are shorter and more fully webbed, the pads of the third and fourth of the hind foot being fused in the middle line. (Text-fig. 36, C, D.)

A further stage of specialisation is seen in *Conepatus proteus*, where the plantar, carpal, and metatarsal pads are as well developed as in any example of *Mephitis*; but the digital pads are larger and are united by webbing almost up to their proximal ends. (Text-fig. 37, A, B.)

The most highly specialised type of fossorial foot is perhaps

found in *Mydaus*. The pads of the second, third, fourth, and fifth digits are fused together, except quite at their distal ends, as completely as the pads of the third and fourth digits of the hind foot are sometimes fused in *Meles*. The pads of the pollex and hallux, however, are independently movable, although attached by shallow webbing to the pad of the second digit. The soles are quite naked. The plantar pads are as wide as the

Text-figure 37.



- A. Right hind foot of *Conepatus proteus*.
- B. Right fore foot of the same.
- C. Right hind foot of *Mydaus meliceps*.
- D. Right fore foot of the same.

$\times \frac{1}{3}$.

feet, much wider than long, lightly arcuate, and four-lobed, the pollical and hallucal elements being large. There are two well-developed, slightly separated carpal pads, the inner being much the smaller of the two. Conjointly they are almost as wide as

the plantar pad, from which they are separated by a short space, and there is an area of naked skin above them. In the hind foot the metatarsal area is naked to the heel and is provided with two long pads as wide as the foot, the inner being the wider of the two. (Text-fig. 37, C, D.)

The Carpal Vibrissæ.—The occurrence of these tactile hairs in many different orders of Mammals suggests that they are a primitive mammalian character. I have not mentioned them under the separate generic headings because they are present in most of the forms discussed. They are especially well developed in the active predaceous forms like *Mustela*, *Martes*, *Tayra*, *Grison*, and the *Lutrinæ*. In the fossorial forms they appear to be of less importance, judging from the frequent difficulty there is in distinguishing them amongst the long hairs of the leg. They are present, however, in *Lyncodon* and in *Ictonyx*. In the latter they are not always to be detected with certainty, and the tuft may be reduced to one bristle. But the sense of touch locates their position by the perception of a small wart-like swelling on the skin, where, as pointed out by Beddard, the nerve supplying the vibrissæ ends. This swelling is present in such highly specialised diggers as *Mellivora* and *Taxidea*, although I failed to differentiate the vibrissæ themselves. In *Meles*, *Mephitis*, and *Conepatus* I could find neither swelling nor vibrissæ.

The Anus and External Genitalia.

So far as is known, the normal pair of anal glands is present in all genera of the family, but they vary greatly in development. In many cases, *i. e.* in *Martes*, *Gulo*, *Tayra*, *Lutra*, *Taxidea**, *Meles*, the glands are not enlarged and the secretion is not particularly offensive in scent to Man, and is not apparently used by the animal itself for defensive purposes. But in other genera, like *Mellivora*, *Grison*, *Ictonyx*, *Mephitis*, *Conepatus*, the glands are enlarged, the secretion is copious, and is ejected at an enemy in case of attack or when two individuals of the same species fight together. And these genera are unusually coloured, being either grey above and black below or striped with white along the dorsal area†. *Putorius* also is accredited with the same habit, although the scent of the secretion is not so pungent and lasting as in the other genera mentioned. Nor is the coloration so striking; but the underfur is creamy white when the coat is lifted and this pallid hue often pervades nearly the whole body‡.

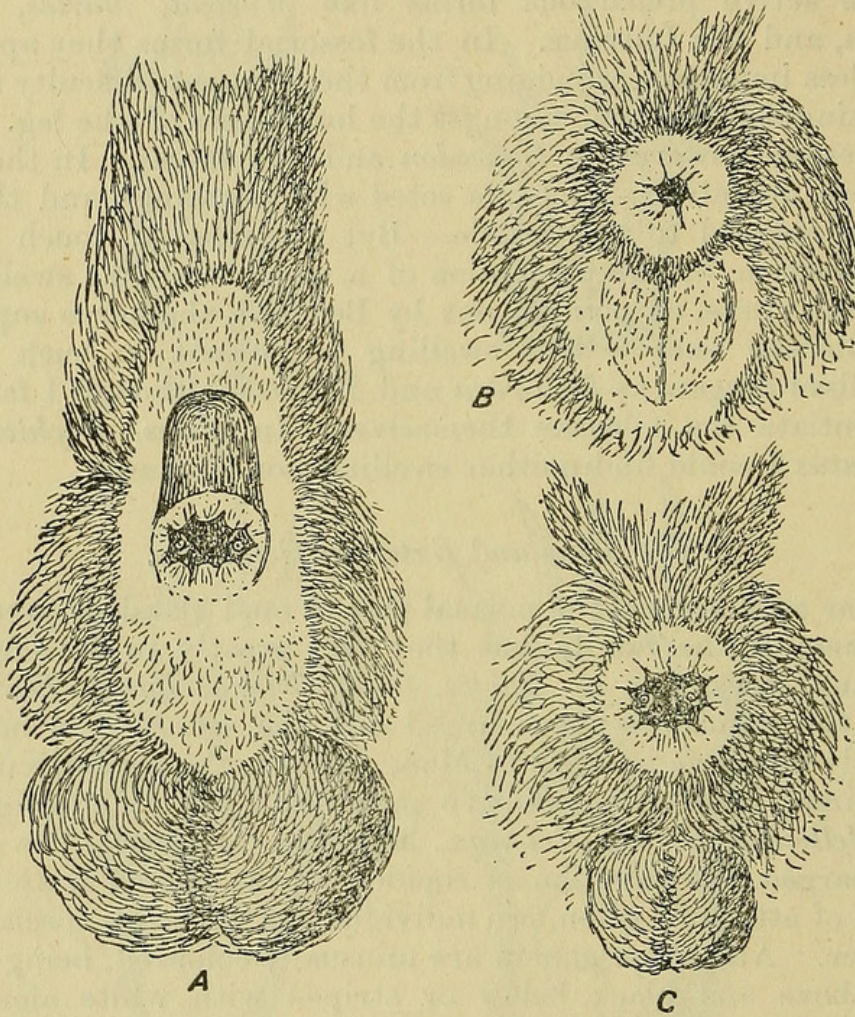
* At least in the single female example I examined.

† See my paper, "The Warning Characters of Musteline Carnivora" (Proc. Zool. Soc. 1908, p. 955). In this paper I threw out the suggestion that the similarity in colour between *Tayra* and the Canine genus *Speothos* might be an instance of mimicry, on the supposition that the secretion of the anal glands in *Tayra* might turn out to be offensive as it is in *Grison*. Since subsequent observation has shown this not the case, the suggestion must be withdrawn. It does not seem likely that *Speothos* is the offensive model mimicked by *Tayra*.

‡ See my paper on the warning coloration of *P. nigripes* (Proc. Zool. Soc. 1911, pp. 559-560).

The anus itself is typically exposed as a button-shaped convex disc, everywhere surrounded by hair as in *Martes*, *Mustela*, *Gulo*, *Lutra*, *Ictonyx*, and others; but in some cases, as in *Mellivora*, it is sunk in a circular thickening of corrugated integument, whereas in *Meles* there is a more definite thinner-walled pouch round it. In *Tayra*, again, there is above the anus a shallow depressed area, bounded on each side and posteriorly towards the

Text-figure 38.



- A. Anal region of *Tayra barbara* ♂, showing the naked skin around the anus and the depression above it.
 B. The same of *Melogale personata* ♂, showing the scrotum close beneath the anus.
 C. The same of *Grisonella* sp. from Cordova, Argentine.

× $\frac{1}{3}$.

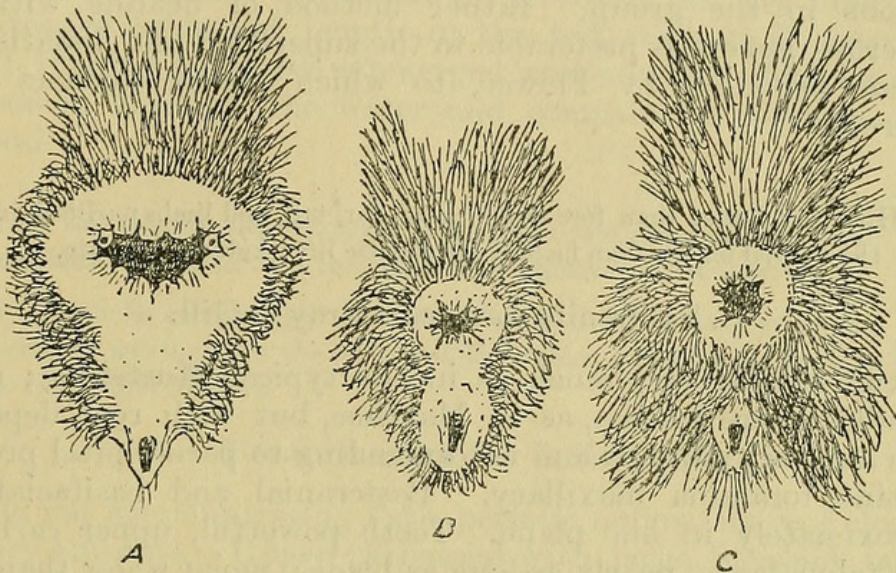
root of the tail by a low ridge of skin. Possibly some modification similar to this was the origin of the deep subcaudal glandular pouch present in *Meles* and, according to accounts, in *Arctonyx*. (Text-fig. 38, A-C.)

The perineal region between the anus and vulva or scrotum is thickly overgrown with hair in *Gulo*, *Martes*, *Mustela*, *Ictonyx*,

and *Lutra*. It is similarly hairy in a male *Grisonella*, but in a female of the same species it is naked or scantily hairy. It is also scantily hairy in *Mellivora*, *Tayra*, *Taxidea*, *Meles*, *Mephitis*, and *Conepatus*.

In all cases examined the vulva is a fusiform excrescence with a vertical slit-like orifice, bounded on each side by two labia enclosing the clitoris and the urinary and genital orifices. (Text-fig. 39, A-C.)

Text-figure 39.



- A. Anus and vulva of *Conepatus proteus*.
 B. The same of *Grisonella* sp. from Cordova, Argentine.
 C. The same of *Plesiogale nudipes*.

The penis is very variable in shape, in accordance with the shape of the *baculum*; but the prepuce is always situated well in advance of the scrotum, as in the Canidæ, Procyonidæ, and Ursidæ.

The Classification of the Mustelidæ.

In the classification which follows I have adopted the method employed by Gray of combining analytical headings, which give prominence to particular characters, with the definitions ordinarily found in the text-books, where the characters are set forth as if of equal value. For the interpretation of the table it is necessary to remember that contrasted headings are marked by the same letter—e. g., *a-a'*, *b-b'*, and so on. I have adopted all the sub-families originally proposed and defined by Gray and Gill, and consistency in treatment has compelled the addition of several new groups of that rank. It is not claimed that they are all of equal value. The Guloninæ, for instance, have been admitted rather as a concession to the opinion of a distinguished contemporary than as a mark of my conviction that the characters deserve the rank assigned to them. Systematists of the old

school will probably criticise the classification on the grounds that most of the subfamilies are monotypical. That objection is, however, in my opinion, illogically hollow. Differentiating characters and degrees of affinity are in danger of being completely lost sight of, if structural variations are disregarded because of their restriction to an isolated genus represented by two or three, or even a single species. And I can see no logical halting-place between some such amplification of Gill's classification as that here proposed and the classification of Turner (Proc. Zool. Soc. 1848, p. 86), who admitted no names for subordinate sections in the group. Either method of dealing with the numerous genera is preferable to the superficial and dissatisfying system proposed by Flower, to which recent authors have adhered.

- a.* Hind feet larger than fore feet*; head, fur, tail, and limbs modified in the normal mammalian fashion for aquatic life; kidneys lobulate.

Subfamily LUTRINÆ Gray & Gill.

Skull shaped very much as in the typical Mustelinæ; cavity of bulla, where known, as in Martiniæ, but with roof depressed upon auditory annulus and not extending to paroccipital process; palatine foramina maxillary. Basicranial and basifacial axes approximately in one plane. Teeth powerful, upper carnassial with talon large, nearly as long as blade; molar wider than long, but about as large as carnassial; lower carnassial with long wide heel and large metaconid. Hind feet with normally proportioned digits, the second and fifth much shorter than third and fourth. Tail long.

Genera *Lutra*, *Hydricis*, *Lutrogale*, *Amblonyx*, *Aonyx*, *Paraonyx*, and possibly others.

In my paper on "The External Characters of some Species of Otters" (Proc. Zool. Soc. 1921, pp. 535-546), reasons were given for regarding the Otters as modified descendants of the Musteline-Martine stock of the Mustelidæ rather than of the Meline stock as suggested by Miller.

Subfamily LATAXINÆ, nom. nov.

(= *Enhydrinæ* Gray & Gill.)

Differing from the Lutrinæ in having the hind feet very large and paddle-like, with digits subequal, but the fifth slightly longer than the third or fourth; the tail short, the basicranial axis depressed at an angle upon basifacial axis; the angular of the

* Flower's frequently copied statement that the feet in the Lutrinæ are "short and rounded" is unintelligible. The feet of the Melinæ, on the contrary, he described as "elongated."

mandible remote from the condyle ; the teeth with rounded cusps, and the median lower incisor suppressed.

Genus *Latax*.

No one can doubt that *Latax* is a Lutrine profoundly modified in adaptation to marine life. The change in its method of feeding, from the capture of swift-swimming fish to the picking up and crushing of sessile molluscs or slow-moving crustaceans, has modified the teeth and skull in the way indicated ; and the increase in size and alteration in structure of the hind feet, accompanied by loss of length in the tail, suggests the need for skilful turning amongst submerged rocks, rather than for swift progression through the water and comparative activity upon the land.

- a'*. Hind feet usually smaller, never larger than fore feet ; no structural modifications subservient to aquatic life ; kidneys not lobulate.
- b*. Cavity of bulla completely divided into two subequal chambers by oblique partition passing from the stylo-mastoid foramen forwards and inwards to the carotid foramen.

HELICTIDINÆ Gray & Gill.

Bulla not communicating with periotic hollow, its roof close to auditory annulus. Upper carnassial with large bicuspid talon ; molar wider than long, smaller than carnassial ; lower carnassial with moderate heel and large metaconid. Rhinarium very deep below nostrils, lateral slit of nostrils long and complete ; no philtrum or groove on upper lip. Ear with well-developed bursa. Feet fossorial, naked below, but narrow, with webbing only extending to proximal end of digital pads, which are widely separable ; all the pads coarsely striate ; two long metatarsal pads. No anal pouches.

Genera *Helictis* and *Melogale*.

Although *Helictis* has been allowed by almost universal consent to retain a place in the Melinæ, where it was placed by Flower, recent examination has justified its separation from that subfamily, as I suggested last year, and its assignment to a special subfamily as proposed by Gray and Gill. The auditory bulla is quite peculiar, and the teeth are neither Meline nor Musteline ; the rhinarium may be described as Meline and the ear as Musteline ; the feet, although fossorial in the matter of the claws, are not so specialised for digging as those of *Meles* ; the tail, moreover, is long and there is no trace of the subcaudal pouch found in that genus. Apart from the auditory bulla *Helictis* is a less specialised form than *Meles*, and is a type intermediate between the "fossorial" and "non-fossorial" members of the Mustelidæ. Its trivial name Ferret-Badger is not inappropriate.

- b'. Cavity of bulla, when divided, separated into an anterior larger and a posterior smaller chamber by a transverse partition running from the stylomastoid to the foramen lacerum posticum.
- c. Walls of bulla everywhere thick and permeated with air-cells continuous with those of the mastoid, the cells of which may communicate with the cavity of the bulla.

Subfamily MUSTELINÆ, s. s.

Skull with long cranial and short facial portions. Teeth sectorial, talon of upper carnassial small, anterior; molar much wider than long; lower carnassial with cuspidate heel, metaconid retained or absent; *pm.* 1 lost above and below. Tympanic annulus in contact with roof of bulla. Palatine foramina maxillary. Rhinarium small. Bursa of ear marginal, large or moderately so. Feet cursorial, usually hairy below, no metatarsal pads; other pads moderate or small, coarsely striate, claws short and curved; digits webbed to proximal end of pads, the 2nd, 3rd, and 4th widely separable. Baculum with a narrow, long, deep groove in its distal third beneath, ending in a median rounded apex.

Genera *Mustela*, *Gale*, *Plesiogale*, *Putorius* (with such subgenera of one or the other as *Lutreola* and *Kolonokus*), *Vormela*.

The restriction of the term Mustelinæ to the Stoats, Weasels, and Polecats is justified by the number of characters by which they differ from other members of the Mustelidæ. The group contains a larger number of species than any other subfamily, and, apart from the Lutrinæ, is more widely distributed. When the tropical forms are better known, other genera may be added; but perhaps characters negating some statements in the description of the subfamily may come to light.

- c'. Walls of bulla thin, its cavity either closed behind or opening into a spacious periotic hollow.
- d. Cavity of bulla closed behind.
- e. Teeth sectorial, approximately as in Mustelinæ, the upper carnassial being longer than wide, with the talon anterior and narrow-necked, and the molar wider than long, etc., and the line of the upper incisors nearly straight. Feet scansorial and cursorial, with short sharp claws.

Subfamily MARTINÆ, s. s.

Two carpal pads separated by hairy space from narrow plantar pad, digital webs hairy below; no metatarsal pads. A well-developed marginal bursa on ear. No trace of pouch above anus. *Pm.* 1 retained above and below. Baculum with two or four branches.

Genera *Martes* and *Charronia*.

Although usually associated with the Stoats, Weasels, and

Polecats, which they generally resemble in the structure of the feet and teeth, the Martens differ from them principally in the structure of the auditory bullæ, but also in their longer jaws, less sectorial teeth, the retention of *pm.* 1, and the position of the posterior palatine foramina on the suture.

Subfamily GULONINÆ Gray & Miller.

Chiefly distinguishable from the Martinæ by having the pre-orbital foramen in front of the orbit, the bullæ small, the auditory tube long, the occipital region short, the mastoid large, the upper anterior premolars separated from the lower, and the metaconid of the lower carnassial suppressed.

Genus *Gulo*.

Subfamily TAYRINÆ, nov.

Distinguishable from the Martinæ and Guloninæ by having the two carpal pads fused into a large mass as large and as wide as the large plantar pad and in contact with it, by the presence of a large metatarsal pad and naked interdigital webs and a very shallow bursa remote from the posterior edge of the ear, by the loss of *pm.* 1 above and below, the presence of a shallow subcaudal pouch, and an apically unbranched baculum.

Genus *Tayra* (= *Galera*).

The Tayra was for quite unintelligible reasons formerly regarded as congeneric with the Grison, the two being quoted as *Galictis*. They are at least as different as the Polecat is from the Marten.

- e'*. Teeth not of the sectorial type, the upper carnassial about as wide as long, with the talon median and arising by a long base from the blade; the molar about three times the size of the carnassial, as long as wide; lower carnassial with a long wide heel, and the metaconid as large as the other cusps; the upper incisive line curved. Feet fossorial, with long powerful claws.

Subfamily MELINÆ, s. s.

Two carpal pads separated by a naked or hairy space from the wide plantar pad; interdigital webs naked below, narrow between the digital pads; third and fourth digits of hind foot in contact; a well-developed, partially divided metatarsal pad. No trace of bursa on ear. Rhinarium very deep beneath lateral slits of nostrils. A deep subcaudal glandular pouch.

Genera *Meles* and *Arctonyx*.

I have seen no fresh specimen of *Arctonyx*, but the external form is exceedingly Badger-like. The teeth, too, are very like those of *Meles*. The cranial differences between them are well known. In the extension of the mastoid below the auditory

orifice the two genera appear to be peculiar in the family, although this character is foreshadowed in *Gulo*.

- d'. Cavity of bulla opening into a large or very large hollow space in the mastoid portion of the periotic.
- f. Palate produced posteriorly, so that the mesopterygoid fossa is far behind the molar teeth; baculum, where known, a stout bone.
- g. Rhinarium a subcircular flattish disc, continued to the edge of the upper lip by a narrow long philtrum resembling it in texture; nostrils anterior, above middle of rhinarium; the lateral slits almost obliterated. Feet fossorial, with pads of 2nd, 3rd, 4th, and 5th digits united nearly to their apices.

Subfamily MYDAINÆ Gray.

Skull with muzzle and dentition much as in the Melinæ, but with frontal postorbital processes absent, zygomata and mandible slender, and mastoid not produced below auditory orifice. Cavity of bulla ceasing just behind petrous portion of periotic, and opening laterally into hollow of mastoid portion of periotic by a single orifice as in the Mephitinæ. Pinna of ear reduced to a simple rim. No subcaudal pouch.

Genus *Mydaus*.

I have seen no fresh specimen of this genus, and the structure of the baculum, if developed, is apparently unknown. The Teledu has well-marked peculiarities, especially in the structure of the rhinarium and feet. The rhinarium is unique; and the only genus which shows an approach to the fusion of the digital pads is *Conepatus*. The latter also has the pinna of the ear greatly reduced with the orifice exposed, and the bulla of *Mydaus* seems to resemble tolerably closely that of the Mephitinæ; but in other respects, particularly in the long jaws, the curved upper incisive line, the long posterior palate, the backward position of palatine foramina, the genus more nearly approaches the Melinæ. If Ferret-Badger is a good name for *Helictis*, perhaps Skunk-Badger would be a suitable appellation for *Mydaus*.

- g'. Rhinarium normal, nostrils much nearer its lower than its upper edge, the lateral slits long; no trace of philtrum and no groove on upper lip. Pads of 2nd, 3rd, 4th, and 5th digits free.
- h. Tympanic annulus projecting as a free ridge into bulla, not confluent with its roof, the posterior rafter arched high above petrous, leaving a large space between the chambers, of which the posterior is not multiloculate; bullæ encroaching on glenoid in front.
- i. Teeth sectorial, in a general way like those of Martinæ; occipital crest inclined backwards and inwards from mastoid, not semicircular from back view.

Subfamily MELLIVORINÆ Gray & Gill.

Periotic hollow, comparatively small, not extended to tip of mastoid, which, like the paroccipital, stands prominently away

from bulla, the latter rounded in front and remote from hamular; palatine foramina on suture. Lower carnassial without metaconid; last lower molar lost; upper molar with wide cingulum. Feet very broad, digits closely tied, with large carpal and metatarsal pads in contact with wide plantar pads. Pinna of ear reduced to an integumental thickening. A glandular pouch round anus.

Genus *Mellivora*.

Subfamily ICTONYCHINÆ.

(=*Zorillinae* Gray & Gill.)

Periotic hollow larger, extending to tip of mastoid, which, like the paroccipital, is close to the bulla; the latter pointed in front and fused with hamular; palatine foramina on maxilla. Lower carnassial with high acute metaconid; last lower molar retained; upper molar without wide cingulum. Feet narrow, but claws long, the digits widely separable; pads small, carpals separated from plantar pad; metatarsal absent. Ears with large pinna. Circumanal integument unmodified.

Genera *Ictonyx* (*Zorilla*) and *Pæciliotis*. (? *Pécilogale*.)

- i'. Teeth not sectorial; upper carnassial enormous, with very large bicuspid talon; molar a little smaller than carnassial, triangular, its inner and anterior borders subequal as in *Melinae*; lower carnassial with large cuspidate heel and large metaconid; occipital crest rising nearly vertically from mastoid, and nearly semicircular from posterior aspect.

Subfamily TAXIDINÆ Pocock.

Feet broad and fossorial with long claws as in *Mellivorinae*, but plantar pads narrower, a single small carpal pad remote from plantar pad, and no metatarsal pad. No glandular pouch associated with anus. Ear with pinna well developed.

Genus *Taxidea*.

- h'. Tympanic annulus confluent at its summit with roof of bulla; posterior rafter-like partition of the bulla close down upon the petrous, leaving a narrow passage between the two chambers, the posterior of which is markedly multilocular; bullæ remote from glenoid in front.

Subfamily GRISONINÆ, nov.

Teeth as in *Mustelinae*, but talon of upper carnassial much larger, occupying nearly half the inner surface of the tooth; palatine foramina maxillary. Feet not fossorial, almost as in *Tayrinae*, but with carpal pads farther from plantar pad. Pinna of ear well developed with bursa present, but small and in front of posterior margin. No subcaudal pouch.

Genera *Grison*, *Grisonella*.

Subfamily LYNCODONTINÆ, nov.

Differing from the Grisoninæ in cranial and more particularly in external characters. Bullæ inflated, not flattened externally towards auditory orifice, with anterior edge obliquely transverse, not emarginate; mesopterygoid fossa longer; *pm.* 2 lost above and below. Feet with long fossorial claws, but unique in the family; digits only webbed for a short distance beyond plantar pads; hairy laterally, mesially naked below, like the reduced webs. Carpal pads reduced to the external moiety which is in contact with the plantar pad, the rest of the carpal area covered with hair, which encroaches over the middle of the plantar pad; no trace of metatarsal pads; plantar pad of hind foot reduced like that of fore foot. Upper lip completely grooved. Ear greatly reduced, no trace of bursa or of valvular supratragus.

Genus *Lyncodon*.

I have seen no fresh examples of this small Patagonian genus, my observations having been made upon dried skins and skulls in the Natural History Museum. The coloration is very like that of *Grison*, with which *Lyncodon* was affiliated by Matschie, and I suggested that the likeness might be a case of Müllerian or genuine mimicry (Proc. Zool. Soc. 1908, p. 953). It cannot be claimed that the genus is closely related to *Grison*. Even the evidence that it is a very aberrant form of the *Grison*-group is not convincing, despite the resemblance between the two in the internal structure of the bulla suggested by my unavoidably imperfect examination of this portion of the skull in *Lyncodon*. The feet differ from those of *Grison* at least as profoundly as the feet of *Mustela* or *Martes* differ from those of *Meles* or *Mellivora*.

f. Palate not produced posteriorly, the mesopterygoid fossa reaching almost up to the line of the upper molar teeth. Baculum unossified or ossified as an exceedingly slender undifferentiated rod.

Subfamily MEPHITINÆ Gray & Gill.

Cavity of bulla simple, ceasing close behind petrous, communicating with large periotic hollow by means of a small circumscribed orifice set forwards in a line with the outer end of the petrous and in front of the stylomastoid foramen, which is set far in and narrowly separated from the foramen lacerum posticum. Bulla not nearly extending to paroccipital, but encroaching on glenoid in front. Muzzle massive, but zygomata and postorbital processes weak. Teeth resembling those of the Melinæ and Mydainæ, but the upper incisive row nearly straight, the upper molar not twice the size of the carnassial and wider than long; *pm.* 1 lost above and below; palatine foramina maxillary. Feet fossorial, with

soles naked, two carpal pads, and metatarsal pad ; pads of 3rd and 4th digits of hind foot basally united. Ear with orifice not concealed behind tragal ridge. No pouches associated with anus.

Genera *Spilogale*, *Mephitis*, *Conepatus*.

Although the Skunks constitute a well-developed subfamily, they seem to be linked in a measure with the Melinæ through *Mydaus*. The three genera show considerable range in structure, *Spilogale* being the least, and *Conepatus* the most, specialised form, the former standing nearest to the more typical members of the Mustelidæ, such as *Ictonyx*, and *Conepatus*, in its feet, ears, and rhinarium, foreshadowing the peculiarities of *Mydaus*.



Pocock, R. I. 1921. "41. On the External Characters and Classification of the Mustelidae." *Proceedings of the Zoological Society of London* 1921, 803–837.
<https://doi.org/10.1111/j.1096-3642.1921.tb03292.x>.

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