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## PALAEOGALE AND ALLIED EARLY MUSTELIDS

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### INTRODUCTION

The European Oligocene and, to some extent, late Eocene and early Miocene are characterized by an abundance of small carnivores varied and often confusing in structure and affinities. They seem to include intermediate or transitional types between canids, mustelids, viverrids, and felids (groups that are sharply distinct in the recent fauna), to such a degree that the distribution of these genera among established families is not satisfactory at present and may in part be quite arbitrary. Among these genera there are, nevertheless, some that can be placed without serious question, and this is particularly true of a few in which the dentition, cranial foramina, and other characters appear to be unmistakably mustelid. This is notably true of the genera *Palaeogale*, *Plesiogale* (hitherto confused with *Palaeogale*), and *Plesictis*. These genera are of peculiar interest not only because they include the earliest definitely recognizable mustelids, but also because at least two of them are remarkably widespread and have an interesting bearing on intercontinental migrations and correlations. It will be shown in the present paper that *Palaeogale*, although hitherto reported as a European genus, also occurs in Asia and in North America and that a relatively primitive form of *Plesictis* (possibly generically or subgenerically separable from the later and more typical species) is common to Europe and North America, at least.

This brief study had its origin in attempts to identify a skull and jaws found by Albert Thomson in the Big Badlands in 1937. In labeling that year's collection I noted that this specimen resembles *Bunaelurus* but lacks  $M^2$  and therefore labeled it as *Palaeogale* sp., in accordance

with Matthew's statements (see below) that *Bunaelurus* is distinguished from *Palaeogale* only by the presence of  $M^2$ . I called the importance of this find to the attention of the late Dr. Walter Granger, who was particularly interested in this subject because it also bears on some of his Mongolian discoveries and researches. He proposed that we should make the necessary wider comparisons in connection with the Asiatic faunas, and the specimen was put away for future study. His death and my absence in military service caused the specimen to be temporarily forgotten, but it came to light again after my return as I checked several such projects left unfinished by Dr. Granger. The present note is an attempt to carry out the study planned by him.

The results of this study, given in more detail and with the necessary evidence on later pages, were surprising. It was found that the specimen in question belongs both to *Bunaelurus* and to *Palaeogale*, in other words that these names are synonymous. Their previous separation has been due in part to inadequate knowledge of the variation of the dental formula in these animals and in part to comparison not with *Palaeogale*, strictly speaking, but with a group of European species that now appears to be generically separable. For this group the name *Plesiogale* is available, and the distinction of *Plesiogale* from *Palaeogale*, with which it has long been considered synonymous, is a second unexpected result of this study. Mongolian specimens referred in publication to *Bunaelurus* and later in manuscript to *Palaeogale* are also briefly reviewed and are found to be true *Palaeogale*, completing the link between Europe and North America as

regards these Oligocene mustelids. A comment on *Mustelavus* is appended, suggesting that this genus is perhaps a synonym of *Plesictis*, or perhaps a separable genus but, if so, one that probably should include some European *Plesictis*. In either case, this genus also exemplifies the Oligocene faunal interchange between the Old World and the New. Wider problems involved in this interchange, for instance the apparent failure of the more viverroid associates of these mustelids to

accompany them on their travels, are not discussed in this short contribution. New definitions of *Palaeogale*, *Plesiogale*, and *Plesictis* are given, but discussion of their broader affinities is deferred for a more general study of the family.

Besides finding the specimen out of which this study grew, Mr. Thomson prepared it. Mr. John C. Germann prepared the accompanying illustrations. Dr. G. L. Jepsen kindly lent the fine Princeton specimen of "*Bunaelurus*."

#### EUROPEAN PALAEOGALE AND PLESIOGALE

The nomenclatural and general taxonomic situation regarding the European mid-Tertiary mustelids is quite confused and will be discussed here only as far as necessary to clarify the status and relationships of American and Asiatic forms. For comparison with *Bunaelurus*, only the European forms now customarily referred to *Palaeogale* are closely pertinent. The genus *Palaeogale* was established by H. von Meyer in 1846. His definition was brief and vague, but it clearly suffices to establish the name as of that date under the International Rules. Two species were named, *P. pulchella* and *P. fecunda*, but these were not distinguished. Gervais (1848-1852) later described a related (if not identical) species as *Mustela minuta*. Schlosser (1887) considered *M. minuta* the same as *P. pulchella* and called the species *P. minuta*. He listed *P. fecunda* as a separate species. More recent European students (e.g., Viret, 1929) consider that all three of these species, and probably one or two others, are synonyms and continue to prefer *P. minuta* as the valid name. Both *P. pulchella* and *P. fecunda* are prior in publication date, but it is possible to argue that they were not really defined until after *P. minuta*. The name to be used is of secondary importance, and I shall tentatively use *P. minuta* in conformity with the European students. The essential point is that the type of *Palaeogale* must be *P. pulchella* or *P. fecunda* and that if both these names are synonyms of *P. minuta*, as agreed by the competent recent workers, then the species currently called *P. minuta*

is type of *Palaeogale*. It is true that Helbing (1917, p. 440) explicitly designated *P. angustifrons* as "Typusspecies" of *Palaeogale*, but this is necessarily invalid because that species was unknown to the author when he defined *Palaeogale*.

In 1847 Pomel proposed the genus *Plesiogale* with the sole species *P. angustifrons*. Various other species, or supposed species, have from time to time been placed in *Plesiogale*, but *P. angustifrons* is the type of the genus. (And, as noted above, it is not available as type of *Palaeogale*.)

Schlosser (1887) placed *angustifrons* doubtfully in *Palaeogale*. He considered *Palaeogale* and *Plesiogale* as synonyms and selected the former name for use on the grounds that *Plesiogale* had also been used for species of *Stenogale*. This argument has no bearing under the International Rules, but *Palaeogale* is the prior name as noted above. Recent students, especially Helbing (1917, 1930) and Viret (1929), have referred *angustifrons* to *Palaeogale* without question and have thus treated *Plesiogale* as a synonym of *Palaeogale*. It has, however, been noted, especially by Viret, that there are (at least) two groups of species in *Palaeogale* as thus defined, a group of small species including *P. minuta*, *P. felina* (a Phosphorites species, older than others referred to the genus), and various possible synonyms, varieties or allies, and a second group of larger animals represented mainly by *P. angustifrons*, with a considerable number of close allies or synonyms.

It may now be emphasized that these two species groups represent the two proposed genera *Palaeogale*, type *minuta*, and *Plesiogale*, type *angustifrons*. It will appear from the following discussion that these groups do almost certainly represent distinct, valid genera. Unfortunately, *angustifrons*, the best-known species, has been used almost exclusively in defining *Palaeogale* and in comparing that genus with others, especially by Helbing. Thus the characters usually ascribed to *Palaeogale* in the literature are really those of *Plesiogale* and belong to *Palaeogale* only when they happen to be shared by the two genera. The clear contrast between "*Bunaelurus*" and "*Palaeogale*" drawn by Helbing (1917) is in reality a contrast between *Palaeogale* (with which *Bunaelurus* is now found to be synonymous) and *Plesiogale* (to which Helbing's well-preserved "*Palaeogale*" specimen really belonged)—a confusion engendered by Helbing's using *angustifrons* as if it were typical of *Palaeogale*, instead of the less well-known *minuta*.

*Palaeogale minuta* (or the *P. minuta* group) is represented chiefly by lower jaws, in which the distinction between *Palaeogale* and *Plesiogale* is very slight. In 1879, however, Filhol figured two skull fragments as "*Mustela mustelina*," a species that belongs to the *Palaeogale minuta* group and is probably the same as that species. Between them, these two specimens show almost the whole structure of the skull, although  $M^1$ , a crucial tooth for generic definition, is lacking. Helbing (1917), however, denied that these belong to *Palaeogale* and suggested that the rostral fragment, at least, is *Stenogale*. At the same time Helbing described and figured an upper dentition referred to *Palaeogale minuta*, again lacking  $M^1$ . Viret (1929) maintained that Filhol's specimens do belong to *Palaeogale minuta* and pointed out that their differences from *P. angustifrons* merely show that "*P. minuta* Gerv. appartient à un rameau bien particulier

de *Palaeogale*. . . ." Viret also described and figured, unfortunately not very clearly, another upper jaw of *P. minuta* in which  $M^1$  is shown for the first time.

The fallacy in Helbing's treatment of this problem is, again, that he considers differences from *P. angustifrons* as *ipso facto* differences from *Palaeogale* and does not consider the alternative, which turns out to be correct beyond much doubt, that *angustifrons*, itself, does not belong in *Palaeogale*. The characters taken as excluding the skull parts in question from *Palaeogale* now seem, in fact, to be generic characters of *Palaeogale* excluding *angustifrons* from that genus. Thus Viret's "rameau bien particulier" is simply true *Palaeogale*, and the *angustifrons* branch is generically distinct as *Plesiogale*.

This important conclusion is strongly suggested by the published data on the European forms, summarized above. It receives its strongest support, however, from American specimens hitherto placed in *Bunaelurus*. As will be shown on the following pages, these specimens demonstrate the association in single individuals of lower jaws generically inseparable from *Palaeogale* (and markedly distinct from *Stenogale*) with upper dentitions and skulls of the type ascribed by Filhol and by Viret to *Palaeogale minuta* and shown by Helbing to be generically different from "*Palaeogale*" (properly *Plesiogale*) *angustifrons* but considered by him as belonging, in part, to *Stenogale*. This evidence leaves no serious doubt as to the conclusion that *Palaeogale* and *Plesiogale* are distinct genera and that the cranial and some of the dental characters ascribed to *Palaeogale* by Helbing are in reality characteristic of *Plesiogale*, while characters ascribed by him to *Bunaelurus* and, in part, to *Stenogale* are characteristic of *Palaeogale*.

The principal differences between *Palaeogale* and *Plesiogale* will be brought out in connection with the review of "*Bunaelurus*," which is considered synonymous with *Palaeogale*.

## AMERICAN "BUNAEURUS" = PALAEOGALE

## HISTORY

In 1873, Cope described the then new genus and species *Bunaelurus lagophagus* and in the same work he named a "*Canis osorum*." In his definitive study of the White River fauna (1884) Cope noted that "*Canis osorum*" might be a synonym of *Bunaelurus lagophagus* or a second species of *Bunaelurus*. No distinction between the two possible species was given. *Bunaelurus* was distinguished from European *Plesiogale* (including *Palaegale* as now defined) and from *Gulo* (from which Cope thought *Plesiogale* inadequately distinguished) by the crested, non-tubercular nature of  $M_2$ . In fact  $M_2$  is very closely similar in some specimens, at least, of *Palaegale*, and Cope's definition did not distinguish *Bunaelurus* from *Palaegale*, nor do his specimens show any clear-cut difference between those two supposed genera. Schlosser (1887) was justified in saying that *Bunaelurus* "gehört wohl zu *Palaegale*."

In 1902 Matthew described a mustelid skull, without lower jaws, which he referred to *Bunaelurus lagophagus*, although it could not be directly compared with the type or any other known specimens previously referred to the genus, all lower jaw fragments. In epigrammatic style, Matthew called *Bunaelurus* "*Palaegale* with a minute second [upper] molar still retained." He noted no other contrast between the genera. In 1903 Matthew described (without an illustration) *Bunaelurus infelix*, not very satisfactorily distinguished from *B. lagophagus* but said to have  $P_4$  perhaps stockier and longer, the protocone of  $M_1$  more rounded and transverse. The characters of the genus were not further discussed.

In 1917 Helbing pointed out various cranial and dental distinctions between "*Bunaelurus*" *lagophagus* (on the basis of the skull described by Matthew) and "*Palaegale*" *angustifrons*. These characters, along with others now considered as distinguishing *Palaegale* from *Plesiogale*, are listed on a later page.

In their White River monograph, Scott

and Jepsen (1936) figured a fine new specimen referred to *Bunaelurus lagophagus*, skull and lower jaw, but they did not describe or comment on this specimen, and their discussion of the genus is simply a quotation from Matthew, 1902. Clark (1937) remarked that *Bunaelurus* occupies an isolated position among known American mustelids, but he did not compare it with the Old World mustelids. (He was concerned rather with *Mustelavus* and *Plesictis* than with *Palaegale* or *Bunaelurus* and mentioned the latter only in passing.)

## MATERIAL

The materials here reviewed include all those previously mentioned in the literature and one good additional specimen.

1. A.M.N.H. No. 6812, part of right lower jaw with  $P_{3-4}$  (in crypts and imperfectly visible),  $dm_4$ , and  $M_{1-2}$ . From the Orellan of Cedar Creek, Colorado. Type of *B. lagophagus*.

2. A.M.N.H. No. 6813, fragment of the left lower jaw with  $M_1$ . From the Orellan of Cedar Creek, Colorado. Figured by Cope (1884, pl. 67a, fig. 14) and referred to *B. lagophagus*. (As figured, another fragment with  $P_3$  was included, but Cope noted in the legend that this was an erroneous association.)

3. A.M.N.H. No. 6814, fragment of left lower jaw with  $P_3$ , fragments of  $P_2$  and  $P_4$ , and alveoli for C and  $P_1$ . Orellan of Cedar Creek, Colorado. Type of "*Canis*" *osorum*.

4. A.M.N.H. No. 9311, fairly complete skull with left  $P^2-M^2$ , right  $P^4-M^2$  and alveoli for other teeth except the incisors. From the upper Orellan of East Pawnee Butte, Colorado. Collected by Albert Thomson in 1901. Referred to *B. lagophagus* and figured and described by Matthew (1902).

5. A.M.N.H. No. 9620, fragment of left lower jaw with  $P_4-M_1$  (both broken) and a fragment of  $M_2$ . Chadronian of Pipestone Springs, Montana. Type of *B. infelix*.

6. Princeton Museum No. 13588, nearly complete skull with right  $P^3-M^1$  and frag-

ments or alveoli of the rest of the dentition, and part of left lower jaw with  $P_2$  and  $P_4-M_2$  and alveoli for C and  $P_3$ . Basal Orellan, Indian Creek Basin, west of Sheep Mountain, South Dakota. Collected by John Clark in 1932. Referred to *B. lagophagus* by Scott and Jepsen (1936) and figured but not described by them.

7. A.M.N.H. No. 38825, skull, nearly complete but severely crushed, with left  $P^2-M^1$  and canine alveolus, and most of right lower jaw with  $P_1$ ,  $P_4-M_2$ , and alveoli for C and  $P_2-3$ . Lower Orellan, 6 miles south of Scenic, South Dakota. Collected by Albert Thomson in 1937. Not hitherto figured or described.

#### DENTITION

American students, especially, have tended to stress the generic value of differences in the dental formula. The presence of  $M^2$  was the only character given by Matthew (1902) to distinguish *Bunaelurus* from *Palaegale*, and the same character is given by Clark (1937) to distinguish *Mustelurus* from *Plesictis*. The present study emphasizes again (see, e.g., Simpson, 1943) that no character should be assigned generic value *a priori*. The same character may at times be generic, at times specific, and at times individual within a species or subspecies. It is a valid and not a humorous statement to say that a generic character can best be defined as simply a character diagnostic of a genus. The presence or absence of a given tooth is sometimes typical or universal in a genus, and is then a generic character. At other times it varies within one population and is then not a generic (or specific) character. Among many examples, variation of the incisor and molar formula in man is familiar. *Palaegale* proves to be another example.

In A.M.N.H. No. 9311, the skull described by Matthew, the upper cheek tooth formula is  $P^4M^2$ .  $P^1$  was vestigial, represented on the specimen only by a single, minute alveolus.  $M^2$  has the crown preserved, but this is tiny and this tooth is also clearly vestigial and virtually functionless. In Princeton Museum No. 13588, the specimen figured by Scott and Jepsen,

the formula also appears to have been  $P^4M^2$ , but  $M^2$  is represented only by remains of alveoli so small and even partly obliterated that this tooth may well have been lost in life and, again, can hardly have been functional. A.M.N.H. No. 38825, our new specimen, is in all other respects so like A.M.N.H. No. 9311 that I see no suggestion of specific distinction, but its formula is  $P^4M^1$ . There is no

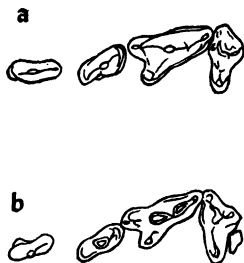


Fig. 1. *Palaegale lagophaga* (Cope). Crown views of left  $P^2-M^1$  or  $M^2$ . a, A.M.N.H. No. 38825,  $M^2$  absent. b, A.M.N.H. No. 9311,  $M^2$  present.  $\times 2$ .

trace of  $M^2$  or its alveoli, and this tooth was either congenitally lacking or lost very early in life with subsequent complete resorption of the alveoli. The only reasonable interpretation is, in my opinion, that  $M^2$  was being lost in this line of evolution and that these specimens are from the particular stage (Orellan in the American sequence) when there was intra-population variation between the presence and the absence of vestigial  $M^2$ .

In true European *Palaegale* (excluding *Plesiogale*) the presence or absence of  $M^2$  can be determined in only two published specimens, as far as I know, and it is said to be absent in both. The evidence does not demonstrate that  $M^2$  never occurred, but it would not be surprising if it had been completely absent by that time. These specimens are of late Oligocene or early Miocene age, and are thus later than the middle Oligocene American skulls. This character is not known in *P. felina*, the early or middle Oligocene European species. One might hazard a guess that  $M^2$  will be found present or variable in this form. In any case, it is clear that this

character, in itself, does not suffice to distinguish *Bunaelurus* from *Palaeogale*.

In the lower jaws, American and European alike,  $M_2$  is always present, as far as known. Although much reduced in size, this tooth has not become quite functionless but forms part of the shear against  $M^1$ . There is, however, evidence that  $P_1$  is functionless and variable in the American forms and that its history parallels that of  $M^2$ . Of the three American specimens that include this region, A.M.N.H. Nos. 6814 and 38825 have a vestigial, one-rooted  $P_1$ , but this tooth was probably absent in Princeton Museum No. 13588. In the later European *Palaeogale* this tooth is usually, perhaps always, absent, while in *P. felina* it appears to be normally present. As for  $M^2$ , the evidence is that  $P_1$  was usually present in early *Palaeogale*, became variable in about the mid-Oligocene, and was eliminated by late Oligocene or early Miocene.

It would, of course, be a possible taxonomic procedure to distinguish an earlier genus with  $P_1^4M_2^2$  from a later genus with  $P_3^4M_2^2$ , but then the American Middle Oligocene forms that show the transitional stages could be classified only in the most arbitrary way. A.M.N.H. No. 38825, with the formula  $P_1^4M_2^2$ , could be placed in either genus, or neither, and yet it does not seem to be specifically distinct from A.M.N.H. No. 9311, with  $P_4^4M_2^2$ , and, at most, not generically distinct from Princeton Museum No. 13588 with still a fourth formula,  $P_3^4M_2^2$ . Nor can I see any other characters to support any groupings that could be based on these various dental formulas. It seems necessary to recognize that *Palaeogale* (including *Bunaelurus*) has the variable formula  $P_4^4M_2^2$ .

As shown especially by Viret and Helbing, there are slight but probably significant differences between  $P^4$  of *Palaeogale minuta* and of *Plesiogale angustifrons* (also referred to *Palaeogale* by them). *Pa. minuta* has a stronger parastyle, has the main external cusp (parametacone) strong and inclined posteriorly with a deep sharp cleft between its blade and the metastylar blade, and has the small protocone pointed somewhat anteriorly, with a strongly

concave embayment between it and the parastyle. In *Pl. angustifrons* the parastyle is small, the main cusp is less inclined backward and is followed by a broad notch rather than a cleft, and the protocone extends more medially, with a less concave embayment between it and the parastyle. In the American specimens, the parastyle is about intermediate in size, and the other characters are about as in *Pa. minuta*, definitely resembling that species in the characters by which it differs from *Pl. angustifrons*.  $M^1$  in true European *Palaeogale* is known to me only in the rather vague figure and brief description by Viret (1929) of a specimen referred to *Palaeogale minuta*. He emphasizes that this tooth is quite unlike  $M^1$  of *Plesiogale angustifrons*, in which the structure of  $M^1$  has been fully and clearly published. In *Pa. minuta*, according to Viret, this tooth is strongly triangular, with a straight anterior face and a sharp antero-external parastyle. His figure seems to show, even though not so clearly as might be desired, that the protocone is relatively sharp, not expanded into a talon, and not surrounded by a cingulum. In *Pl. angustifrons*, on the other hand, the tooth is composed of two rather irregular, expanded lobes, one external, with a bulbous and not sharply produced parastyle, and the other internal, composed of an expanded protocone surrounded by a cingulum—an early form of the familiar expansion of this region in many later mustelids.

Here, again, the specimens hitherto called *Bunaelurus* agree in every essential with *Palaeogale minuta*, that is, with true *Palaeogale*, and differ markedly from *P. angustifrons*, that is, from *Plesiogale*. The marked difference in the protocone was noted by Helbing (1917) who, however, considered this a difference between *Bunaelurus* and *Palaeogale*. (No  $M^1$  of true *Palaeogale* was known to him.) The only suggested difference between American and European *Palaeogale* (or "*Bunaelurus*" and *Palaeogale minuta*) in this tooth is that Viret says that the paracone and metacone of *P. minuta* are of almost equal size, while in our specimens the metacone is distinctly

smaller. The difference seems, however, to be slight, and it may be only in the manner of speaking.

The lower jaws and dentitions of *Palaeogale minuta* and *Plesiogale angustifrons*, both well known and illustrated by a number of specimens, are very much alike except in size. There are, however, at least two fairly definite distinctions. In *Pa. minuta* P<sub>2</sub> is a rather long but simple,

of *Pa. minuta*, if anything in exaggerated form. In *Pa. minuta* M<sub>2</sub> has a somewhat elongate or ovoid crown, longitudinally crested but generally with three vague but distinguishable cusps. In *Pl. angustifrons* this tooth is still more reduced, generally nearly circular in outline, without a really distinct longitudinal crest and with only one readily distinguishable cusp. In this respect, also, the American specimens,

TABLE 1

AMERICAN " <i>Bunaelurus</i> " = <i>Palaeogale</i>	FILHOL'S SPECIMENS REFERRED TO " <i>Mustela mustelina</i> " = <i>Palaeogale</i> <i>minuta</i>	<i>Plesiogale angustifrons</i>
No postorbital processes <sup>a</sup>	"On peut dire qu'il n'existe pas d'apophyses postorbitaires"	Small but distinct post-orbital processes
Porus acusticus without ossified meatus <sup>a</sup>	"L'orifice externe du conduit auditif ne correspond pas à un canal osseux"	Short, distinct ossified meatus
Palate short, rim of choanae on a level with protocone of M <sup>1</sup> <sup>a</sup>	"L'orifice postérieur des fosses nasales correspondait . . . à l'extrémité interne de la tuberculeuse"	Palate long, choanae well posterior to M <sup>1</sup>
Pterygoid crests narrowing posteriorly and closely approximated at their ends	"Le canal guttural se rétrécissait rapidement. . ." Figure shows structure almost exactly as in " <i>Bunaelurus</i> "	Pterygoid crests parallel and well separated posteriorly
Cerebellar region long and separated externally from cerebral region by a distinct groove	Closely similar if not exactly the same structure as " <i>Bunaelurus</i> " visible in Filhol's figure	Cerebellar region short and not clearly distinguished externally from the cerebral
In connection with the last character, the lambdoid crests and the general aspect of the whole posterior part of skull quite distinctive	Like " <i>Bunaelurus</i> " as far as known from published data	Quite distinct from " <i>Bunaelurus</i> " or true <i>Palaeogale</i>
Stylomastoid foramen more lateral, near porus acusticus and in same plane	Not clear in figure, but Filhol's statement that the "orifice du canal stylomastoïdien" is above the "extrémité postérieure" of the porus suggests structure as in " <i>Bunaelurus</i> "	Stylomastoid more posteromedial
Foramen ovale relatively caudal, posterior to level of postglenoid processes, and at posterior end of pterygoid crests	Anterior to the foramen lacerum medius "on trouve le trou ovale correspondant au point d'origine des apophyses ptérygoïdes"	Foramen ovale slightly more anterior in position

<sup>a</sup> These are the skull characters noted by Helbing.

two-rooted tooth with a decidedly procumbent anterior cusp followed by a long, longitudinally crested heel. In *Pl. angustifrons* P<sub>2</sub> is less procumbent and has a relatively shorter heel—it is, indeed, essentially like P<sub>3</sub> except for being smaller and simpler. Among the American specimens, only Princeton Museum No. 13588 shows this tooth. It is different from that of *Pl. engustifrons* and has the characters

three of which include this tooth, agree with *Palaeogale minuta*. This character is also known in *Palaeogale felina* of the Phosphorites (see Teilhard, 1914–1915), a poorly known species but one probably more nearly than *P. minuta* in the same stage of evolution as the American forms.

In summary, the dentition of American "*Bunaelurus*" in no way distinguishes it from *Palaeogale* but is distinct in several

respects from that of *Plesiogale*, hitherto confused with *Palaeogale*.

#### SKULL

As noted above, the only true or typical European *Palaeogale* skull parts known are the two described by Filhol and said by Helbing not to belong to that genus. Helbing's comparison of *Bunaelurus* with *Palaeogale* is a comparison with "*Palaeogale*" *angustifrons*, i.e., with *Plesiogale*. Comparison of our "*Bunaelurus*" = *Palaeogale* skulls with Filhol's specimens shows that they are essentially alike and confirms Filhol's assignment of the latter to *Palaeogale* and Viret's refutation of

and the separation of *Plesiogale angustifrons* as generically distinct.

In view of the interest attaching to the cranial foramina in mustelids (see, e.g., Pocock, 1921) a figure is given to show these in *Palaeogale*, evidently representing the most primitive mustelid type, along with *Plesictis* (cranial foramina well figured by Helbing, 1928)<sup>1</sup> and *Plesiogale* (foramina mostly visible but not identified in Helbing, 1930).

#### AMERICAN SPECIES OF *Palaeogale*

Although only seven specimens of American *Palaeogale* are known to me, these vary so much that they seem, at first sight and

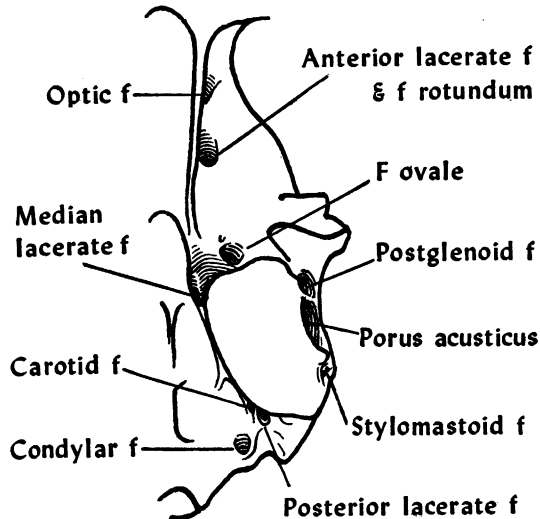


Fig. 2. *Palaeogale lagophaga*. Ventral view of left basicranium, showing arrangement of cranial foramina. F = foramen. Based on A.M.N.H. No. 9311, in comparison with A.M.N.H. No. 38825 and Princeton Mus. No. 13588.  $\times 2$ .

Helbing. The most important characters involved may be given in tabular form (see table 1).

Doubtless other differences in the skulls may be found, but the available data suggest that the three groups are essentially alike in other respects. The preceding comparison shows very clearly that the American specimens, inseparable from *Palaeogale* by the dentition, are also inseparable from Filhol's specimens in skull structure. This in turn confirms the assignment of those specimens to *Palaeogale*

<sup>1</sup> Helbing's identifications of the two distinct foramina in the orbital region of *Plesictis* are, however, erroneous or confusingly designated. He calls the anterior of these "foramen sphenoidale" and the posterior "foramen rotundum." Comparison with *Palaeogale* and with a series of recent mustelids leaves no doubt that the anterior of these two foramina is the optic foramen and the posterior the common external opening of the anterior lacerate foramen and the foramen rotundum. A true sphenoidal foramen does occur in recent mustelids, but it is always a considerable distance anterodorsal to the optic foramen and smaller than the latter. It cannot be Helbing's "foramen sphenoidale," and no true sphenoidal foramen is seen in Helbing's figure or in our specimens of *Palaeogale*. If present in these Oligocene forms, it must be minute and obscure. I am indebted to Dr. D. Dwight Davis, of the Chicago Natural History Museum, for advice regarding identifications of foramina in this region in mustelids.

according to the usual criteria, to represent at least four and perhaps five species. Beside the differences in dental formula, noted above, and minor differences of shape and proportions difficult to evaluate in the imperfect materials, the size range is very considerable, several dimensions showing a range of 30 per cent or more in a sample of only four or five measurements.

The lower jaws, six specimens, seem to fall into three groups as regards size of the teeth. The type of *Palaeogale lagophaga*, the type of "*Canis*" *osorum*, and A.M.N.H. No. 38825 form an intermediate group with  $M_1$  (lacking in "*C.*" *osorum*) 5.1–5.2 mm. in length and about 2.3 mm. in width. The types of *P. infelix* and A.M.N.H. No. 6813 (referred to "*Bunaelurus*" *lagophagus* by Cope and not since reclassified) have  $M_1$  5.8–5.9 mm. in length and again about 2.3 mm. in width, thus relatively longer and narrower. In the Princeton specimen  $M_1$  measures 4.5 by 2.0 mm. and is thus distinctly smaller than in the first group but has about the same proportions. Among the skulls, A.M.N.H. Nos. 38825 and 9311, with  $P^4$  5.5–5.7 mm. in length and 3.0–3.2 mm. in width, represent the first or middle-sized group, and Princeton Museum No. 13588, with  $P^4$  measuring 4.9 by 2.5 mm., is again noticeably smaller, as it is in all its dimensions, cranial as well as dental.

Many species of recent mustelids are characterized by great range in size and especially by strong sexual dimorphism. In some cases the *mean* for males is over 30 per cent larger than for females, and a large male may easily be 50 per cent larger than a small female. The difference between male and female of one species is commonly greater than between corresponding sexes of two different species.

If the situation was at all similar among the fossil mustelids—and some of the larger European collections strongly sug-

gest that it was—then a reliable specific arrangement of the American specimens is quite impossible at present. The three groups suggested by the specimens now in hand (far too few to show that these groups are real, in any event) obviously cannot represent the two sexes. Perhaps they represent large males, small males, and one female (the Princeton specimen), or a small female, large females, and males, although neither is probable on the hypothesis that males and females should tend to be equally common in collections. On the other hand, this hypothesis is not necessarily true, and yet there is no good reason why several distinct species might not be represented in these materials of rather heterogeneous origin.

For the present it may be best to continue to call the Orellan specimens, at least, *Palaeogale lagophaga*, pending discovery of larger samples that may permit a statistical solution of the problem, the only type of solution that is likely to be satisfactory.

The status of *Palaeogale infelix* (Matthew, 1903) is wholly dubious. Reading between the lines, it seems evident that Matthew saw no really clear distinction from *P. lagophaga* but separated *P. infelix* mainly because the age is different, Chadronian. Sinclair and Jepsen (1936) accepted the species frankly on this difference in age rather than on any morphological basis. Even the size difference between the types becomes of no importance in view of the fact that A.M.N.H. No. 6813, an Orellan specimen, is of almost exactly the same size and structure as the Chadronian type of *P. infelix*. It would, indeed, be unusual for one species to range so far, and perhaps later discoveries will validate *P. infelix*, but it must be admitted that no objective and valid diagnosis of that supposed species has been given.

#### CENTRAL ASIATIC PALAEOGALE

In a preliminary note, Matthew and Granger (1924) named and diagnosed *Bunaelurus ulysses* and *B. parvulus* from the Oligocene Hsanda Gol formation in the

Tsagan Nor Basin near Loh, Mongolia. The species were diagnosed on the basis of size only. (The morphological characters cited under "*B.*" *ulysses* occur in all species

of *Palaeogale* and "*Bunaelurus*," except for the variable presence of  $P_1$ .) Regarding the generic assignment, the authors said, "We have referred these species to the American genus *Bunaelurus*, which is separable from *Palaeogale* by retention of a minute  $M^2$  in the upper jaw. As the upper dentition of the Mongolian species is unknown, they might be referred to *Palaeogale*, but the reduction of  $M_2$  is relatively greater than in *P. felina*, conforming somewhat better with *Bunaelurus*." It is now known, apart from other considerations, that the distinction noted is not valid, typical *Palaeogale* rather than *P. felina*, probably the most primitive species of the genus, showing a reduction of  $M_2$  essentially as in the American and Mongolian specimens.

A later collection, made in 1925 (the first specimens were collected in 1922), included A.M.N.H. No. 21632, a skull fragment with incisors, canines, and all the cheek teeth of the left side and an associated right lower jaw with  $M_{1-2}$  and alveoli of C- $P_4$ , representing the smaller species, "*B.*" *parvulus*.  $M^2$  was absent in life, and on this account Matthew and Granger had all the specimens recatalogued as *Palaeogale ulysses* and *P. parvula*, but apparently did not publish this change of generic assignment.

The total collections of the two years, 1922 and 1925, included 21 partial lower jaws of *P. ulysses* and five partial lower jaws and associated lower jaw and skull fragment of *P. parvula*, as well as three specimens similar to *P. ulysses* but not certainly referable to that group.

The Mongolian specimens are fully characteristic of *Palaeogale*, and of course the present reduction of *Bunaelurus* to synonymy with *Palaeogale* removes the doubts as to which of these two supposed genera is represented. The original reference to *Bunaelurus* was correct in the sense that these specimens do not belong to *Plesiogale*, which was then usually taken to represent the European *Palaeogale*. As far as one can judge from inadequate data, the Mongolian specimens may be a little closer to American *Palaeogale*. For instance, in the one known upper dentition

(*P. parvula*) the parastyle of  $P^4$  is small and the metacone of  $M^1$  is reduced, as in *P. lagophaga*. In fact, if the Mongolian specimens had been found in the White River series they would probably have been referred to *P. lagophaga* without much question. This repeated occurrence on a third continent, again with a *P. minuta*-like lower jaw associated with a "*B.*" *lagophagus*-like upper jaw, confirms the revised conception of *Palaeogale* expounded in this paper.

Since there is only one upper jaw, we do not know whether  $M^2$  was regularly absent or whether it was variable. Among the lower jaws, seven show the region of  $P_1$ . In six of these (four of *P. ulysses* and two of *P. parvula*),  $P_1$  was surely present. In

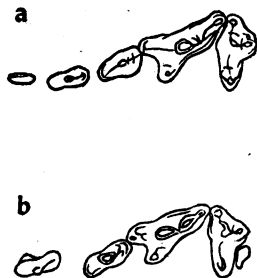


Fig. 3. *Palaeogale* from Asia and from North America. Crown views of left upper cheek teeth. a, *P. parvula*, Mongolia, A.M.N.H. No. 21632,  $P^1$ - $M^1$  ( $M^2$  absent). b, *P. lagophaga*, Colorado, A.M.N.H. No. 9311,  $P^2$ - $M^2$ .  $\times 2$ .

one (*P. ulysses*), it may have been absent, but this is highly dubious. If not constant in the Mongolian forms, the presence of this tooth was at least usual in them, a distinction from *P. minuta* and a resemblance to *P. lagophaga* (in which, however,  $P_1$  may sometimes be absent) and to *P. felina*. This would agree with the probability that the Hsanda Gol is older than the European occurrences of *P. minuta*, although the absence of  $M^2$  in the one Mongolian upper jaw makes for some apparent, but probably not real, inconsistency in this particular line of evidence. The Hsanda Gol may be nearly Orellan in age, and, as has been seen,  $M^2$  may be absent in Orellan *Palaeogale*.

The occurrence together of two groups of *Palaeogale* distinguished only by dif-

ference in size suggests the possibility that these are the two sexes of one species. The length of  $M_1$  in the type of *P. parvula*, apparently about average for that group, is 4.6 mm. In *P. ulysses* the range in well-identifiable specimens is 5.4–6.3 (there are two still larger specimens, but these may not belong here), the mean of 13 specimens is 5.8, and the type measures 6.0. Considerable as the size difference is, it can be equaled in the sex groups in some single species of living mustelids. It is also improbable, but not impossible, that two such similar species of one genus of mustelids lived together. On the other hand, the

larger group (males?) is relatively more abundant than would be expected if the two sexes were equally numerous and equally likely to be collected as fossils (a possible assumption but by no means a necessary one). It must also be remembered that among mustelids of this general type, taxonomic distinctions are usually clearer in the upper than in the lower jaws and that the upper jaw of *P. ulysses* is unknown. Thus there are arguments both ways, but on present evidence it does seem rather likely to me that *P. ulysses* is the male and *P. parvula* the female of the same species.

#### A NOTE ON *MUSTELAVUS* AND *PLESICTIS*

*Mustelavus* Clark, 1937, was based on associated skull and jaws from the upper Chadronian of South Dakota. Clark (1937) stated that, "Resemblance to *Plesictis pygmaeus* is so close that it is almost impossible to find ground for a specific distinction in the lower jaws. Comparison of the skull with Filhol's figures of *Plesictis* reveals one sharp difference—retention of  $M^2$  in *Mustelavus* and its absence in *Plesictis*. Also, the parietal crests of *Plesictis* are more strongly developed than are those of *Mustelavus*. Otherwise the two are extremely similar in dentition, in skull configuration, and in basicranial anatomy."

Analogy with *Palaegale*, in which (if my interpretation is correct)  $M^2$  may be present or absent within the limits of a single species, casts considerable doubt on the use of this character to distinguish early mustelid genera when all other characters are so nearly the same. In *Plesictis*, as in *Palaegale*, the early Miocene specimens, with which Clark compared his *Mustelavus*, lack  $M^2$ , but this is present in the early forms more nearly contemporary with *Mustelavus* (see Teilhard, 1914–1915). The evidence of the parietal crests is even more equivocal. These

seem to be virtually lacking in a Phosphorites representative of the *Plesictis* line (Teilhard, 1914–1915) and extremely variable in the later forms (compare, for instance, the very dissimilar crests of two skulls placed by a careful student in a single species, Viret, 1929, pl. 15, figs. 8c and 9).

These facts raise serious doubts as to whether *Mustelavus* can be clearly and naturally separated from *Plesictis*. It is possible that more extensive comparison will show that the earlier forms of this line can usefully be separated from the later. In that case, it may well be that *Mustelavus* characterizes the earlier Oligocene both in Europe (Phosphorites *Plesictis*) and in America (Chadronian), while the Stampian to Aquitanian and associated late forms in Europe are *Plesictis*, *sensu stricto*. It cannot, however, be reasonably maintained that *Mustelavus* is distinct from *Plesictis* as that genus has been used in the recent literature. Retention of *Mustelavus*, if this proves to be valid, will require redefinition of *Plesictis*. (The type of *Plesictis* is *P. genettoides*, an advanced species, so that the name will go with the more specialized group if such a generic separation proves feasible.)

REDEFINITION OF *PALAEOGALE*, *PLESIOGALE*, AND *PLESICTIS*

By way of clarification and summary, the more essential characters that distinguish *Palaeogale*, *Plesiogale*, and *Plesictis* from other mustelids and from each other are here given in formal diagnoses.

**PALAEOGALE VON MEYER, 1846**

TYPE: *Palaeogale minuta* (= *P. pulchella* = *P. fecunda*).

SYNONYM: *Bumaelurus* Cope, 1873; type, *B. lagophagus*.

KNOWN DISTRIBUTION: Early or middle Oligocene to early Miocene, Europe. Early and Middle Oligocene, North America. Middle Oligocene, Mongolia.

DIAGNOSIS: An early mustelid with cheek tooth formula  $P_{4-3}M_{2-1}^1$ .  $P_1$  and  $M^2$  vestigial or absent.  $P^4$  with small protocone, directed forward, large, somewhat recumbent main blade separated by a deep cleft from the strong metastylar blade.  $M^1$  strongly transverse, short and wide, triangular, with sharply projecting parastyle, small, simple protocone, not expanded anteroposteriorly and without cingulum.  $P_2$  procumbent, with long, shearing heel.  $M_1$  compressed, without metaconid, heel unbasined, with longitudinal shearing crest.  $M_2$  small but functional, elongate oval in outline, with weak longitudinal crest, without metaconid or basined talonid but with three vague cusps in series. No postorbital processes. No ossified auditory meatus. Palate ending at level of  $M^1$ . Pterygoid crests converging posteriorly. Cerebellar region long and bounded externally by a distinct groove posterior to the cerebral region. Stylomastoid foramen lateral, near porus. Foramen ovale posterior to level of postglenoid processes. Carotid foramen small and nearly confluent with posterior lacerate foramen. Sagittal crest single throughout. Paroccipital process free, small.

**PLESIOGALE POMEL, 1847**

TYPE: *Plesiogale angustifrons*.

KNOWN DISTRIBUTION: Late Oligocene and early Miocene, Europe.

DIAGNOSIS: An early mustelid with cheek tooth formula (usually)  $P_3^1M_2^1$ .  $P^4$

with protocone directed medially, parametacone and metastyle blades separated by large, open notch.  $M^1$  bilobed or pyriform, with rounded parastyle, protocone lobe small relative to most later mustelids but expanded relative to *Palaeogale*, surrounded by cingulum.  $P_2$  erect,

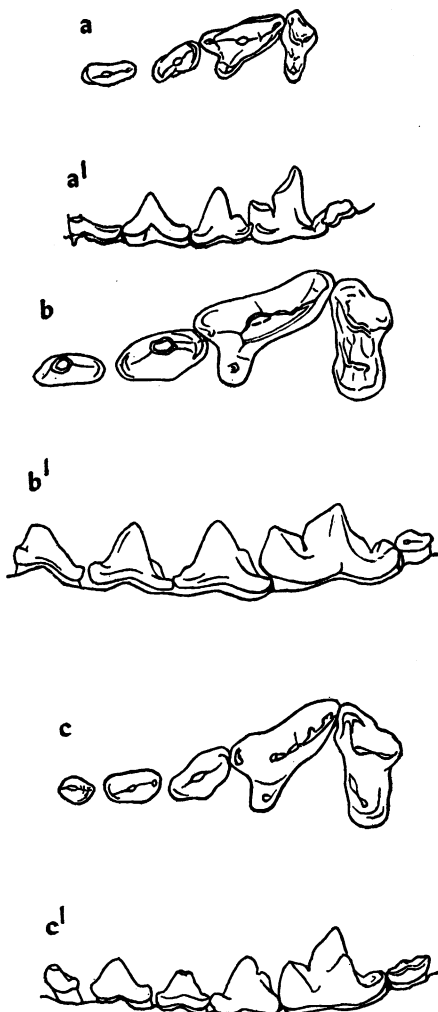


FIG. 4. Three genera of Oligocene mustelids. Crown views of left upper and internal views of right lower cheek teeth. a, a', *Palaeogale* (composite, from American specimens referred to *P. lagophaga*),  $P^2-M^1$  and  $P_2-M_2$ . b, b', *Plesiogale* (European, *P. angustifrons*, redrawn after Helbing),  $P^2-M^1$  and  $P_2-M_2$ . c, c', *Plesictis* (European, *P. genettoides*, from A.M.N.H. No. 11001),  $P^1-M^1$  and  $P_1-M_2$ . All  $\times 2$ .

with short heel.  $M_1$  as in *Palaegale*, without metaconid, heel unbasined, with longitudinal shearing crest.  $M_2$  vestigial, crown nearly circular, without definite crest and usually with only one distinct cusp. Small postorbital processes. Short ossified auditory meatus. Palate relatively long, extending definitely posterior to  $M^1$ . Pterygoid crests parallel, well separated. Cerebellar region short and not distinguished from cerebral region externally. Stylomastoid foramen well separated from and posteromedial to foramen ovale more anterior than in *Palaegale*. Sagittal crest single throughout.

#### PLESICTIS POMEL, 1846

TYPE: *Plesictis genetoides*.

PROBABLE SYNONYM<sup>1</sup>: *Mustelavus* Clark, 1937; type, *M. priscus*.

KNOWN DISTRIBUTION: Early Oligocene to early Miocene, Europe. Early Oligocene, North America.

DIAGNOSIS: An early mustelid with cheek tooth formula  $P_4^1M_2^{2-1}$ .  $M^2$  vestigial or absent, other teeth functional.  $P^4$

resembling *Palaegale* but of heavier general build.  $M^1$  similar to *Plesiogale*, with somewhat expanded protocone and internal cingulum, but tending to retain more triangular contour.  $P_2$  essentially like  $P_3$ , erect with short heel.  $P_4$  rather plump, with postero-external accessory cuspule.  $M_1$  canid-like, plump, with large metaconid nearly equal to paraconid, heel small but distinctly basined.  $M_2$  small but with basined talonid and distinct trigonid with protoconid and metaconid and sometimes also definable paraconid. Moderate postorbital processes. Partly ossified auditory meatus, cleft ventrally. Palate and pterygoid crests about as in *Plesiogale*. Cerebellar region short and not distinguishable externally (cf. *Plesiogale*) and stylomastoid foramen and foramen ovale also about as in *Plesiogale*. Carotid foramen somewhat larger and farther rostral than in *Palaegale*, well separated from posterior lacerate foramen. Sagittal crest double posteriorly and usually throughout (except in most primitive forms?). Paroccipital process free, larger than in *Palaegale*.

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<sup>1</sup> *Mustelavus* is a synonym under the present diagnosis of *Plesictis*. Its distinction, if feasible, would involve another, narrower definition of *Plesictis*.

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