THE SMALL CARNIVORS OF THE MIOCENE.

F. B. LOOMIS.

During the summer of 1931 the Amherst College Expedition found a nearly complete skeleton of the little known genus Oligobunis in the Lower Rosebud formation of South Dakota. This with other small carnivors previously found in the Miocene has led to a study of this group, known mostly from jaws and small fragments. Aside from adding to the number of species known to have lived in America during the Miocene, the study of the above-mentioned skeleton has led the writer to the belief that Oligobunis and a number of other related genera are not to be thought of as early mustelids, but rather as civets of the Herpestes or mongoose type. For the sake of clarity the new material is first described, and then the relationships of the various genera are considered.

Oligobunis Cope.

The genus was established by Cope[1] on an imperfect skull and jaws of *O. crassivultus* from the John Day beds of Oregon. Matthew[2] added the species *O. lepidus* from the Upper Rosebud beds of South Dakota, the species being based on a muzzle with both the upper and lower dentitions. Lastly Thorpe[3] described a large skull and jaws from the Lower Harrison beds of northwestern Nebraska. To the above this paper adds two more species, one based on a practically complete skeleton, and the other a skull and jaws. The genus, *Oligobunis,* is characterized by an elongate skull, the facial region being short, while the brain case is unusually long. There are prominent postorbital processes. The sagittal crest is barely indicated toward the rear, and the occipital crest is very low. The auditory bullae are moderately inflated, elongated and there is a suggestion of division into anterior and posterior chambers. The dental formula is $i\frac{3}{3}c\frac{1}{1}p\frac{4}{4}m\frac{2}{2}$. In some cases upper premolar 1 is lacking and in all it is greatly reduced. The character of the teeth is very like that of *Cynodictis* on the one side, from which it

[1] Amer. Nat., p. 497, 1881; and Report U. S. Geol. Surv. of the Territories, **3**, 939, 1884.
[2] Bul. Amer. Museum Nat. Hist., **23**, 194, 1907.
[3] This Journal, **1**, 480, 1921.

differs in having one less lower molar. On the other side the dentition approaches that of *Herpestes* quite closely. Skeletal characters will be added in the description of the next species and the phyletic position discussed in the light of all the known facts at the end of the paper. The range of the genus is from the John Day to the Upper Rosebud.

The various species may be distinguished as follows:

	Length of the skull incisors to occiputal condyle	Length of upper premolar-molar dentition	
O. crassivultus		40 mm.	John Day
O. gemmarosae	86 mm.	27 mm.	Lower Rosebud
O. vantasselensis	75 mm.	24 mm.	Lower Harrison
O. darbyi	97 mm.	33 mm.	Lower Harrison
O. lepidus		30 mm.	Upper Rosebud

Oligobunis gemmarosae sp. nov.

(Figs. 1-4.)

Holotype, catalogue number 31-33, Amherst College Museum, a nearly complete skeleton from Porcupine Creek, six miles west of the postoffice, in Lower Rosebud beds of South Dakota.

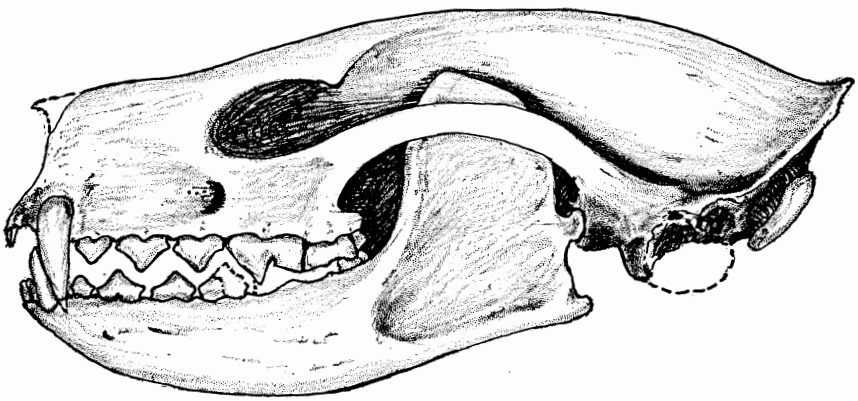

Fig. 1. *Oligobunis gemmarosae*, the skull from the left side; ⅔ nat. size.

In size this is one of the smaller of the known species, its skull being but 86 mm. long. It appears very like *O. darbyi* and *O. lepidus*. It, however, differs from the former both in size and in having four instead of three upper premolars.

From *O. lepidus* it differs in size and in being slender and lightly built.

As in this type we have the only known skeleton of any of these small carnivors, a description of this skeleton will aid in placing the position of the genus. In broad outline the skeleton resembles that of *Cynodictis,* and is a little larger. Matthew[4] made a restoration of *Cynodictis,* using as a model the skeleton of a genet and modifying it where necessary. The skeleton here at Amherst looks for all the world like this restoration, except as to the feet, which seem compact and the claws non-retractile, as Scott says those of *Cynodictis* are also.

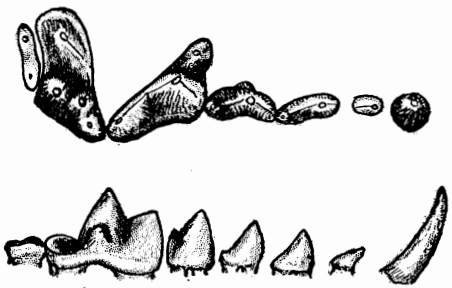

Fig. 2. *Oligobunis gemmarosae,* the upper dentition of the left side; and below the lower dentition of the same side seen from the inner side. Both nat. size.

It is a long bodied form similar to civets, with a long tail, and with the front limbs very much shorter than the hind limbs.

The vertebral column (complete in our skeleton) has 7 cervicals, 13 dorsals, 7 lumbars, 3 sacrals, and we have six elongated tail vertebrae. Such a formula is characteristic of civets and dogs, differs from mustelids in having one less dorsal and one more lumbar. The ribs are very slender and the sternum ossified.

The scapula is peculiar in shape, being short and extremely wide, the pre-fossa being considerably wider than the post-fossa, and the acromion process very long. This is similar to both *Cynodictis* and *Herpestes.* The humerus is slender with stubby tuberosities, very like that of *Cynodictis.* In this form the deltoid ridge is barely outlined. On the

[4] Mem. Amer. Museum of Nat. Hist., 1, 380, Pl. 37, 1901.

expanded lower end there is a good sized entepicondylar foramen, a character of civets but lacking in dogs. The olecranon process of the ulna is short and rounded. The radius is like

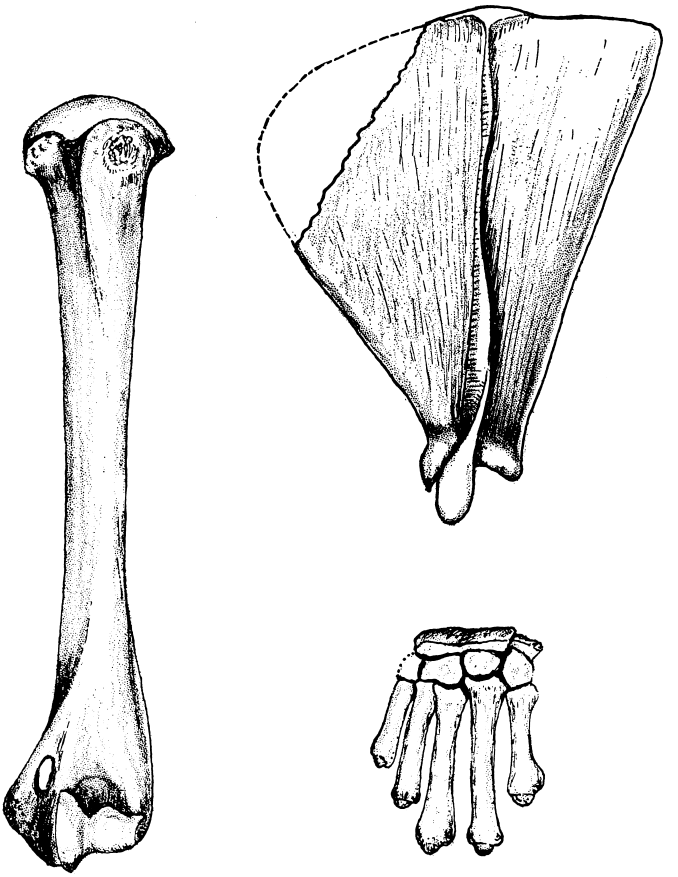

Fig. 3. *Oligobunis gemmarosae,* the humerus, scapula and front foot of the left side; ⅔ nat. size.

that of *Cynodictis.* The front foot is less than half the length of the hind foot. There are five metacarpals and they are slender and fairly spreading, again like *Cynodictis* and *Herpestes.*

The pelvis has a rather long post-acetabular portion, again civet like. There is a long slender penis bone, slightly curved and lightly grooved on the sides. The femur is slender and

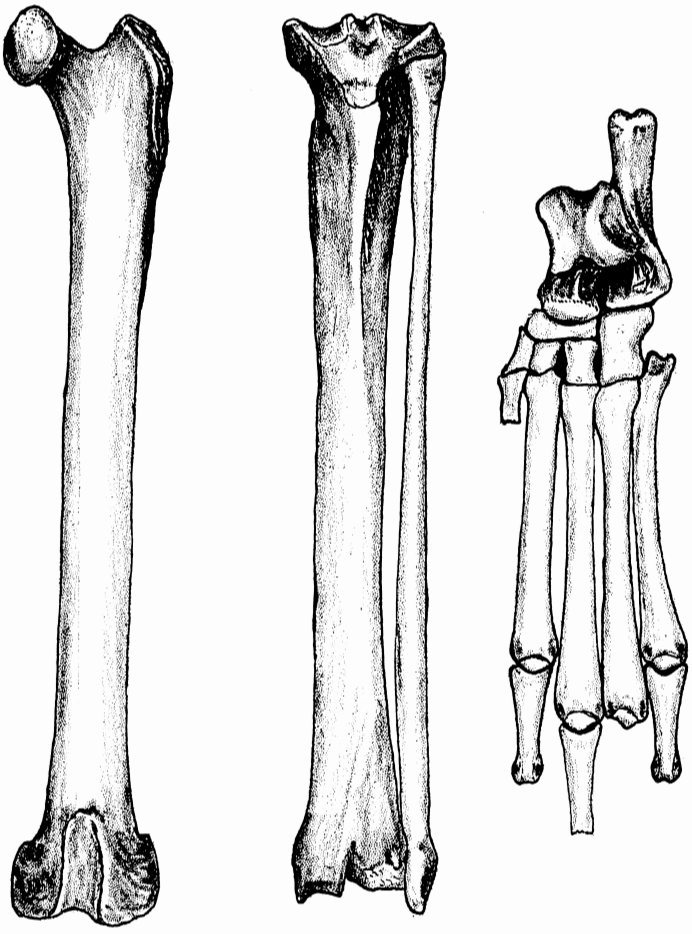

Fig. 4. *Oligobunis gemmarosae,* the left hind limb; ⅔ nat. size.

long, the greater trochanter rising scarcely as high as the head, and there is no lesser trochanter. The tibia and fibula are slightly shorter than the femur. The foot is also very elongated, the metatarsals being compactly grouped and the toes

being slender. Unfortunately neither front or hind foot has preserved an ungual phalanx.

The following measurements will give specific character to the specimen.

Measurements.

Length, snout to the base of the tail	435 mm.
Scapula, height	46 mm.
width	48 mm.
Humerus, length	73 mm.
Radius, length	59 mm.
Metacarpus III, length	16 mm.
Pelvis, length	70 mm.
Femur, length	92 mm.
Tibia, length	86 mm.
Metatarsus III, length	36 mm.

Oligobunis vantasselensis sp. nov.

(Fig. 5.)

Holotype, catalogue number 20-99, Amherst College Museum, a skull and jaws from Van Tassel, Wyo., Lower Harrison Beds.

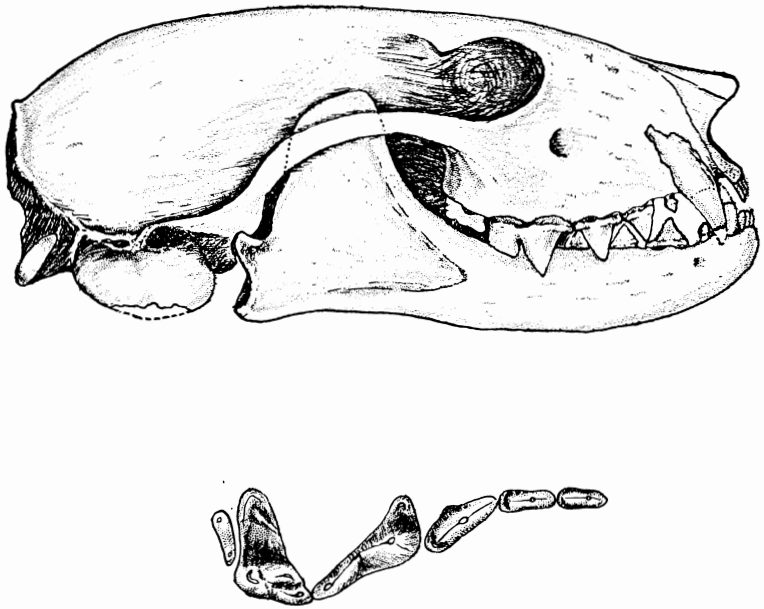

Fig. 5. *Oligobunis vantasselensis,* the skull ⅔ nat. size; and below the upper dentition nat. size.

This is the smallest of the species yet found, and but 4/5 as large as *O. darbyi* from the same beds. It may be the female of that species; for there is no way of deciding this point; but it differs in several important ways.. It has a small upper premolar 1, which is lacking in *O. darbyi,* and the second upper molar is less reduced, as is also lower premolar 1. On this skull the bullae are well preserved and there is at least a partial partition between the anterior and posterior chambers.

Measurements.

Total length of the skull	75 mm.
Total length of the upper dentition	24 mm.
Total length of the lower dentition	26 mm.

Paroligobunis.

This genus was established by Peterson[5] for the lower jaw and parts of the skeleton of a form which appears much like *Oligobunis,* but has a much heavier build and more crowded teeth. Then also lower molar 2 is less reduced. So far as it is known Peterson is correct in placing the genus close to *Oligobunis* for the foot remains and the parts of the hind limb known do resemble *Oligobunis.* The teeth, however, are blunter and show a wear which in one case has ground off at least a third of each crown, and would indicate quite a different habit for these animals.

Paroligobunis petersoni sp. nov.

(Fig. 6.)

Holotype, catalogue number 2011, of the Amherst College Museum, a left jaw from three miles southeast of Van Tassel, Wyoming, in beds of Upper Harrison age. Named for O. A. Peterson, who extensively explored this region.

This species is about 2/3 as large as the type species, *P. simplicidens.* The jaw is heavily built, with a wide, heavy ascending ramus. The canine, while heavy, is relatively smaller than in Peterson's species. Lower molar 1 has a small trenchant heel, i. e., the hypoconid is well developed and the endoconid lacking, a feature in which it differs from *Cynodictis* and *Oligobunis,* the latter having a hypoconid and a reduced endoconid. A second specimen shows the same characters but has the tops of the teeth badly worn off.

[5] Mem. Carnegie Museum, **4**, 269, 1910.

Measurements.

Length of the jaw, incisor to the condyle	63 mm.
Length of the dentition	41 mm.
Length of molar I	10 mm.

Plionictis.

The genus was established by Matthew[6] for a skull and jaws which he had originally attributed to *Mustella.* It represents a group of small carnivors with a dental formula of $i\frac{3}{3}\,c\frac{1}{1}\,p\frac{4}{3}\,m\frac{1}{2}$ and with large sharp-pointed teeth. Upper molar 1 is very peculiar (see Fig. 10) in that the three

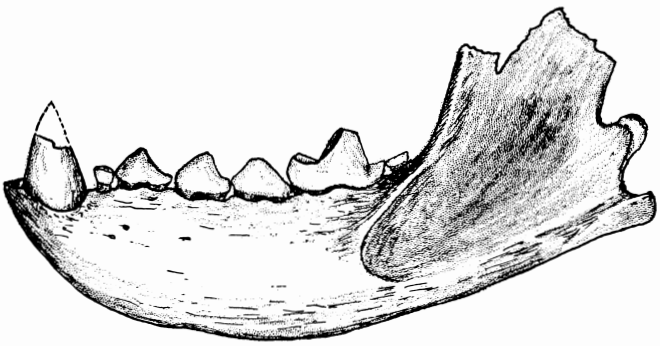

Fig. 6. The left lower jaw of *Paroligobunis petersoni*; ⅔ nat. size.

outer cusps, parastyle, paracone, and metacone, are closely crowded together and make a cluster on an upper level, while the lingual portion of the tooth is reduced to a narrow process at a lower level. The peculiar upper molar is almost identical with the corresponding tooth in *Bunaelurus,* which, however, has a vestigal molar 2. The European genus *Stenoplesictis* also has this peculiar tooth and on the basis of the known material the two genera, *Plionictis* and *Stenoplesictis* can not be distinguished. Until more complete material is known it may be well to allow both genera to be used for the skeleton is unknown in both places.

[6] Bul. Amer. Museum Nat. Hist., **50**, 135, 1924.

Plionictis sanguinarius sp. nov.

(Fig. 7.)

Holotype, catalogue number 2012, Amherst College Museum, a skull and jaws, 7 cervicals and the scapula, from the south rim of Goshen Hole three miles west of the Nebraska-Wyoming line, in beds of Lower Rosebud age.

This skull has the typical short muzzle and long brain case of a herpestid civet, but has the molars reduced to but one,

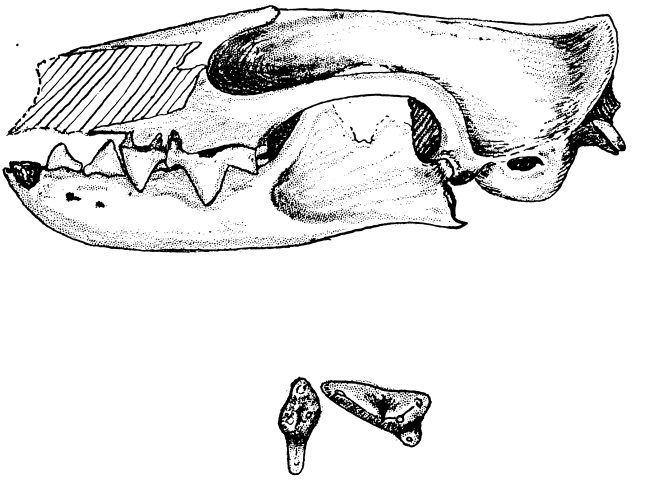

Fig. 7. The skull of *Plionictis sanguinarius* from the left side; ⅔ nat. size. Below the right upper premolar 4 and molar 1; nat. size.

and that even reduced as described above. This species is a little smaller than *P. ogygia* from the Pawnee Creek beds, and has much higher sagittal and occipital crests. It, however, resembles Matthew's species in having lost the first lower premolar, making the dental formula $i\frac{3}{3}c\frac{1}{1}p\frac{4}{3}m\frac{2}{1}$, which seems to be typical for the genus. All the teeth are long-crowned and sharp. The cervicals show nothing at variance with those of *Oligobunis,* and the scapula is like that of *Oligobunis* also, having its prefossa twice as wide as the postfossa, which is typically herpestid.

Measurements.

Length of the skull, incisors to back of the occipital crest	68 mm.
Length of the upper dentition, incisors to molar 1	30 mm.
Length of upper premolar 4	9 mm.
Length of upper molar 1	2 mm.

Pachycynodon Schlosser.

This genus was formed for tiny European carnivors of the late Oligocene. They have the dental formula of the dogs, $i\frac{3}{3}c\frac{1}{1}p\frac{4}{4}m\frac{2}{3}$, and this genus along with *Cynodon* is usually credited as a subfamily (Cynodontinae) of the dogs. They resemble *Cynidictis* in the dental formula, and in having both the hypoconid and the entoconid developed on the lower carnassial, making a basined heel: but they differ in that the upper carnassial has a very oblique shear and has an unusually large tritocone. The molars are quite dog-like. The whole build is very slender. These may well represent a side line of earliest dogs, but seem rather to a true viverroid. It has not previously been recorded in America, but seems to be one of the migrants which arrived here in middle or late Oligocene along with *Cynodictis, Plionictis* (*Stenoplesictis*) and *Stenicthis* (the American equivalent of *Stenogale*).

Pachycynodon delicatus sp. nov.

(Fig. 8.)

Holotype, catalogue number 31-102, of the Amherst College Museum, a lower jaw, from Porcupine Creek, So. Dakota, in the Lower Rosebud beds.

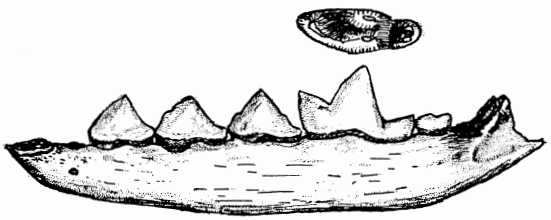

Fig. 8. *Pachycynodon delicatus,* the left lower jaw; nat. size.

This tiny lower jaw is almost identical in size with *P. tenuis* of the Phosphorites of Quercy, differing only in that the teeth are slightly longer. Each of the premolars of this species has

a slight bulge on the anterior margin, suggestive of an incipient cusp, but it can not be said to actually develop as one on any of the teeth. On the carnassial the protoconid is very high, and the metaconid is ⅔ as high and sharply separated from it. Both the hypoconid and the entoconid are well developed making a basin in the heel. From premolar 1 to molar 3 the length is 26 mm.

Pachycynodon harlowi sp. nov.

(Fig. 9.)

Holotype, catalogue number 31-34, of the Amherst College Museum, both lower jaws, from 3 miles southeast of Van Tassel, Wyoming, in the Upper Harrison beds. The name is for J. W. Harlow, who found the type.

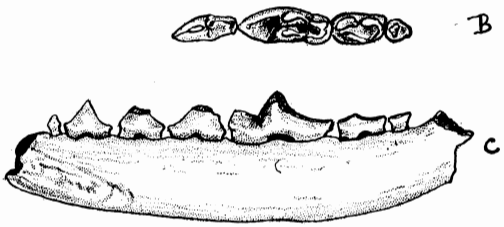

Fig. 9. *Pachycynodon harlowi,* the right lower jaw; nat. size.

This species has a lower jaw almost identical in size with that of *P. delicatus* of the Lower Rosebud, but differs in that molars 2 and 3 are larger, while the premolars make a slightly shorter series. The characteristics of the teeth are as above described, but in this individual there is considerable wear on the crowns. The length from premolar 1 to molar 3 is 26 mm.

In all of the foregoing it is impressed on the writer that viverrine characters are very abundant, especially those associated with the *Herpestes* division. To take up first the place of *Oligobunis.* It resembles *Cynidictis* unquestionably, and it also resembles *Herpestes.* From *Cynodictis* it differs in the bulla being more elongate, slightly constricted into an anterior and posterior chamber, and in having a much smaller opening for the auditory canal. From *Herpestes* this genus differs in a lesser development of the postorbital processes, the having of the protocone on upper molar 1, and in an even

greater reduction of molar 2. In all its specialized characters it approaches *Herpestes*; so I should put *Oligobunis* in the

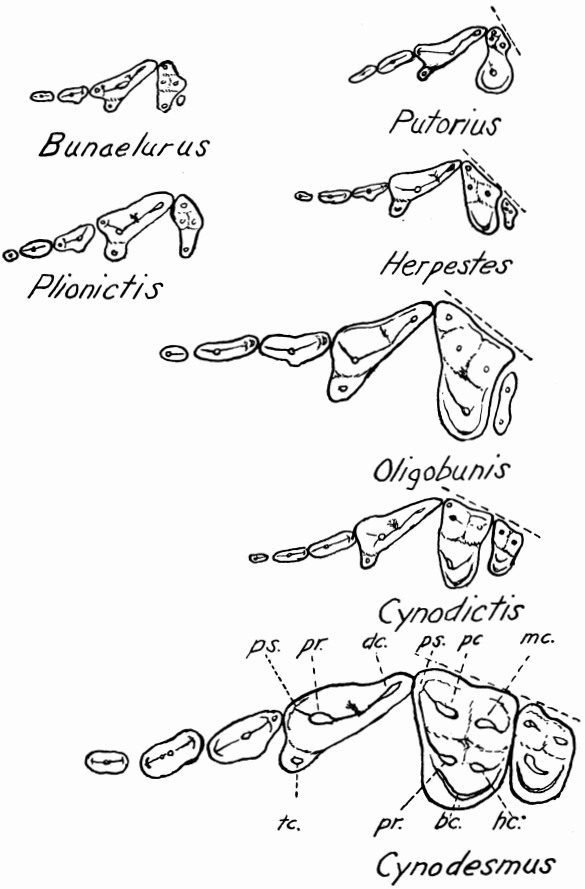

Fig. 10. The upper dentitions of various genera to show the progressive reduction of the upper molars and changes in their character. On the left two aberrant genera. All ⅔ nat. size. bc. basal cingulum, dc. deuterocone, hc. hypocone, mc. metacone, pc. paracone, pr. protocone, ps. parastyle, tc. tritocone.

herpestine group of civets. The fact that it is related so closely to *Cynodictis* raised the question as to viverrine relationships of *Cynodictis*, which has so long figured as the basal representative of the dogs.

Scott[7] long ago pointed out the many viverrine characteristics of *Cynodictis*; the short muzzle associated with an elongated brain case, the elongated body with the front limbs extremely shortened, the scapula with the prefossa wider than the postfossa, the entepicondylar foramen of the humerus, the astragulus with the elongated neck and shallow groove on the roller surface, the reduction of the upper molars, and the emphasis on the basal cingulum instead of on the proto- and hypocones. On the other side the resemblance to dogs is mainly the dental formula and the basin in the heel of the lower carnassial. Civets and dogs have in common the vertebral formula, the dental formula, and the unreduced feet.

To the matter of the presence of a basin in the heel of the lower carnassial I can not attribute as much emphasis as has been given, for it is due to the relative development of the entoconid. When it is well developed there is a basin, when less or not developed the tooth is referred to as having a trenchant heel, and on this the whole dog family is divided. It seems to me a character dependent on the use made of the carnassials, and so is variable, the trenchant character being more than once developed, though the basin structure is primitive.

While dogs and the herpestid civets presumably came from the same stock, *Cynodictis* seems to me to have already progressed too far toward the herpestids by Oligocene times to be considered a dog. I can not see how such truly canid forms as *Cynodesmus, Temnocyon* or *Tephrocyon* can be derived from *Cynodictis,* a form with so many distinctly herpestid characters that would have to be lost again to make it a canid. Doubtless *Cynodictis* and *Cynodesmus* came from a common stock; but by the Oligocene the one line had already shortened the muzzle, elongated the body and shortened the front limbs, while the other was elongating the muzzle, shortening the body and elongating the front legs.

Viverridae early acquired the long body, short front legs, and short muzzle. This shortening of the muzzle is peculiar in that it involves reducing the molar series. Early in its history the viverrine and herpestine sections of the family separated, the former group retaining the retractile claws, the latter having non-retractile claws. The canid and mustellid lines are derivatives of the group with non-retractile claws.

[7] Trans. Amer. Phil. Soc., **19**, 364-401, 1898.

Before the loss of any molar teeth the Daphaenus group of dogs separated off from the herpestine line. About the same time the Cynodesmus group of dogs arose, and it seems to me that this was before middle Oligocene time. *Cynodictis* shows the first reduction of molars having but ⅔. Two other features of this shortening of the molar region appear in figure 10. First the angle between the premolar series of teeth and the molar series becomes progressively more acute as the molar reduction goes on. Second in the herpestine group the parastyle on the upper molars becomes a more and more important cusp, and on the inner portion of these teeth the protocone becomes less and less important, the basal cingulum furnishing the inner cusps, or ridge. The canids, on the other hand, do not reduce the upper molars any further than the loss of the third one, and from Oligocene time on they generally enlarged the two molars and elongated the muzzle. They also tend to develop the protocone and hypocone to a greater and greater extent, the parastyle disappearing. From these considerations *Cynodictis*, with some emphasis on the parastyle, no hypocone, the protocone small, a high basal cingulum, and molar 2 reduced, would seem to be an early representative of the *Herpestes* line. *Oligobunis* is a much more advanced representative, even more in its teeth than *Herpestes* itself, though in some other characters it is not so far along.

Bunaelurus and *Plionictis* are representatives of a highly specialized side line which is not represented to-day by any living form. Another line of deviation is represented by forms which expanded the lingual side of molar 1 at the same time as the outer side of this tooth was being compressed. This line led to *Mustella* and *Putorius*, the typical mustellids. *Mephitis*, *Taxidea*, and *Lutra* seem to me to represent a group which came off this line independently somewhere in the Miocene.

AMHERST COLLEGE,
AMHERST, MASS.