ART. XXIV.—*Osteology and Affinities of the Genus Stenomylus*; by FREDERIC B. LOOMIS.

DURING the summer of 1907 the Amherst College field party while prospecting in the sandstones of the Lower Harrison levels some five miles to the southeast of the Agate Spring postoffice, Sioux Co., Nebraska, found fragments of a Stenomylus smaller than the *S. gracilis* then known. During that season a few badly shattered remains were collected, after which work was continued in other sections of the field. On returning the next season, however, the same levels were further excavated, on which it developed that there was a veritable quarry of these skeletons at this locality; for no less than eighteen skulls, together with enough disarticulated bones to represent the complete skeletons, were collected from one pocket, and in an adjacent portion of the hill three complete skeletons were found. Following this the Yale University party collected three skeletons, the American Museum party five or six skeletons, and the Carnegie Museum party five or six. During the season of 1909 the Carnegie Museum again collected in this quarry, obtaining a large number of skeletons. Thus already not less than forty skeletons, and I should estimate many more, have been taken out, and as the specimens are found along over 150 feet of the face of the hill, I see no reason why as many more complete skeletons should not be obtained from the same source. With this wonderful and well-distributed material there is every reason that a complete description should be made both for identification, osteological study, and comparison.

The quarry.—The Stenomylus quarry is located some five miles due southeast of Agate Spring postoffice, and about one and a half miles up the "draw" south of the upper Harris place, and about the same distance a little east of south from the famous Agate Springs quarry of the Carnegie Museum. The horizon is in the Lower Harrison beds about 75 feet from their upper boundary. The matrix is a fine, homogeneous, well-bedded, soft sandstone, which differs materially from the much coarser and more irregularly bedded sandstone typical of these beds. These fine sands are about 100 feet in thickness and seem to have a limited extension, being traced only about three-fourths of a mile to the south and thinning out very soon in the other directions. To the east the Upper Harrison beds directly overlie these fine sandstones. The Stenomylus remains occur in two levels; the one about four feet above the other, and both some 70 feet below the top. In the lower of the two levels the skeletons are pretty much disassociated, while in the upper level, when a specimen is found, it is usually a more or less complete skeleton. Above these levels there is nothing approaching a bone bed, but occasionally Stenomylus remains are, however, found throughout the whole thickness of the fine sandstones. The even sorting and bedding of these sands indicate deposition in comparatively quiet water; and as the Lower Harrison beds seem to be flood-plain deposits, it would appear that these finer sandstones were laid down in some more sheltered area behind a barrier, which barrier must have been of considerable extent and height to account for the deposition of about 100 feet of uniform material. The Stenomylus remains presumably floated to their final resting place, and each of the two bone-bearing levels represents the destruction of scores of individuals. The simplest reconstruction of conditions would picture a herd of the unfortunate creatures during the distress of a great flood taking refuge on the highest available point of land; which, however, proved too low, and after surrounding them the rising waters drowned and carried off the whole herd, males and females, young and old. The carcasses then floated down stream and were accumulated in the backwater, where they were then buried in the accumulating sands. This was apparently a relatively rapid accumulation, for the carcasses, especially in the upper level, are not pulled to pieces by carnivores. The position of the head in the type (fig. 1) is characteristic of a good many of the skeletons, and I believe is common among drowned animals. Presumably the same point of land in two seasons proved to be a fatal trap for herds of these delicate creatures, and afterward it was only occasionally that an individual carcass was washed into the area where these sands were accumulating. Remains of other animals are very scarce in these sandstones, but a few isolated bones, the Diceratherium, and the major part of a skeleton of *Daphœnodon superbus* Peterson, and a few bird bones do occur with the Stenomylus bones, and confirm the stratigraphic determination of Lower Harrison.

Plan.—In considering the material it seems best to give a detailed osteological description of this species, followed by the distinctive comparisons of the three known species, and finally to consider the affinities and phylogenetic position of the genus.

Stenomylus hitchcocki sp. nov.

Type.—The type is a complete skeleton, all the bones articulated and in place, No. 2059 of the Amherst College collection. With this are used six skulls and a dozen upper and lower jaws, together with some four disarticulated skeletons and iso-

FIG. 1.

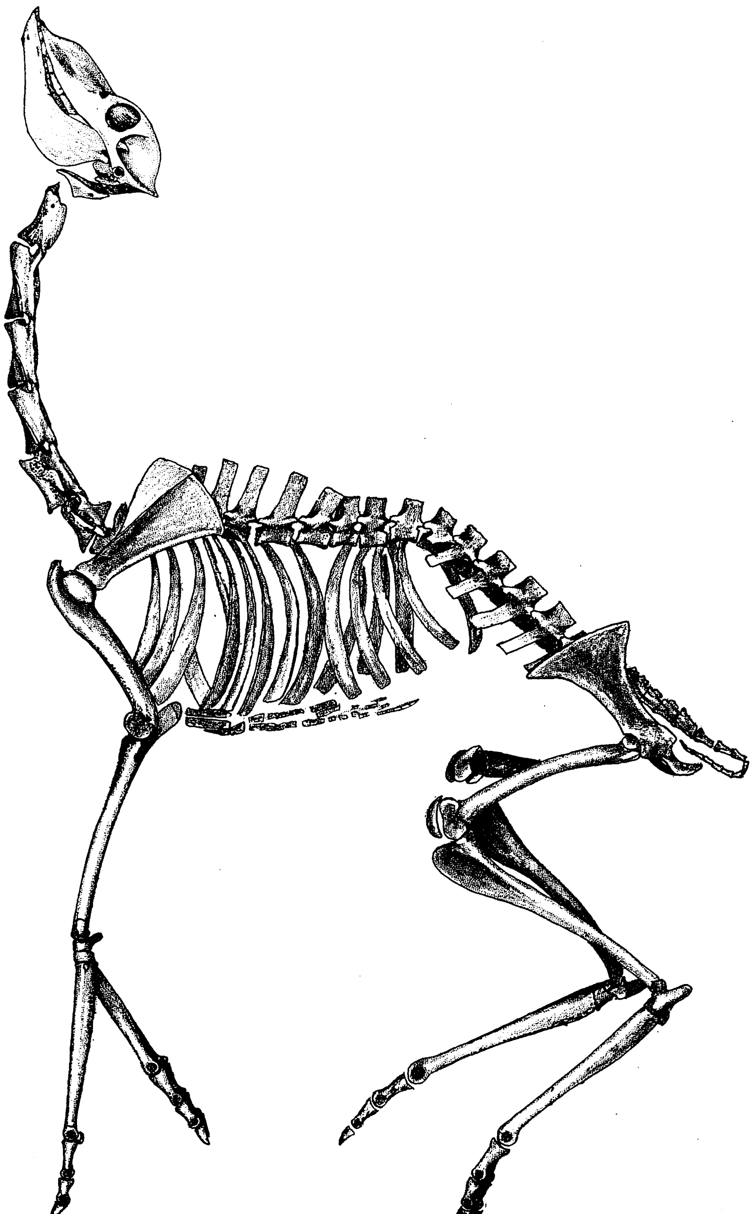


FIG. 1. *Stenomylus hitchcocki*, type specimen as seen lying in the original matrix. ×1/6.

lated bones, and the four complete skeletons of the American Museum. In the series are individuals which are interpreted as male and female, and a number of young having but their milk dentition. The species is named after Dr. Edward Hitchcock, whose work in comparative anatomy and paleontology was the stimulus for the expedition and the work of the writer. The individual used for the type is one which has just reached maturity as shown by having all the molars worn, but that is all, for the epiphyses of several of the limb bones are still free from their shafts. The position of the type specimen is that of an animal which has just laid down with legs outstretched and head thrown back, or probably better, of an animal which has been drowned, but is natural enough so that we can readily get measurements of the whole animal.

Height at the shoulders ...	684^{mm} (27 in.)
Length of head	175^{mm} (7 in.)
Length of neck	380^{mm} ($13\frac{1}{2}$ in.)
Length of body	433^{mm} (17 in.)
Length of tail	155^{mm} ($6\frac{1}{4}$ in.)

This individual is slightly smaller and lighter in build than some of the others, and I have interpreted it as a female. In comparing the measurements with those of other Tylopoda it will be apparent that the body is unusually short; the limbs, therefore, appear long, though when compared with the length of the humerus, they are but little longer relatively than those of Pöebrotherium. The neck in conjunction with the increase of limb is also a little longer than that of the Oligocene tylopod.

Skull.—The relatively small skull has a wide cranium but a narrow compressed muzzle. The basicranial axis is only slightly bent. In conformity to the lateral compression of the muzzle the nasals are slender splints which diverge when they reach the wedge-shaped anterior end of the frontals. These latter bones are very wide, overhanging the orbits which stand out from either side of the skull. The two parietals are fused medianly and make a bone of considerable extent, on the posterior half of which is situated a low sagittal crest, which unites with the strong lambdoidal crest. This latter crest is high and projects strongly backward, overhanging the occiput. The premaxillæ rise rapidly on the high muzzle, expanding somewhat at the upper end. It is the maxilla which makes up the greater part of the side of the snout and in this bone are two deep pits on either side, the first a preorbital pit, a little in front of the orbit and high up on the muzzle; the second a subnasal pit, considerably in front of the former and much lower on the muzzle. The preorbital pit, situated some 20^{mm}

in front of the orbit, is an oval depression some 25^{mm} long by 12^{mm} high, and so deep that between the two sides there is but 9^{mm}, which must nearly close the olfactory space within the muzzle. In like manner the subnasal pit is well down on the side of the snout, and extends from over premolar 1 to over premolar 4, being about the same size as is the preorbital pit. In the latter case the depth of the pits is, however, such that

FIG. 2.

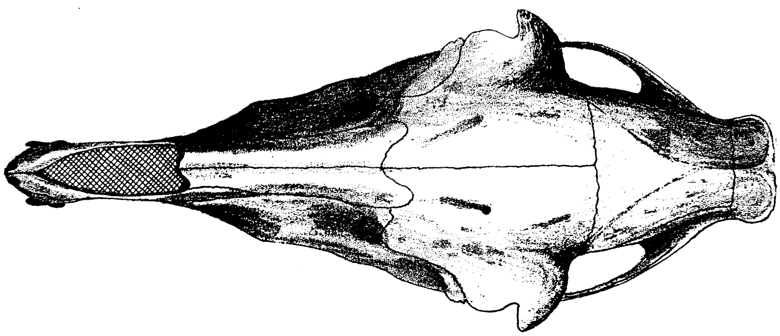


FIG. 2. *Stenomylus hitchcocki*, skull seen from above. × 1/2.

there is but six millimeters between the two sides of the skull opposite the bottom of the pits, so they must practically close the internal olfactory passage in that vicinity. Similar, though less developed, pits occur in other primitive genera among the Tylopoda: and the preorbital pit is also characteristic of several species of horses of the Oligocene genus, Mesohippus. The pits were probably occupied by glandular structures, but pits of such extent are not known to the writer among recent genera. The pit occupied by odor-secreting glands among certain artiodactyls may be cited as a counterpart, but it is hard to believe that odor glands in any species became as large as those pits would indicate.

As is usual for members of the tylopod-phylum, there is an orbital vacuity of some extent at the juncture of the maxilla, nasal and lacrymal bones. The lacrymal bone itself is relatively large, extending considerably in front of the orbit. The margin of the orbit is sharply outlined and smooth except that on the lacrymal there are two deep and characteristic notches. The lacrymal foramen is well within the border of the orbit. The jugal bone bounds the front and lower part of the orbit, meeting in the rear the broad postorbital process of the frontal. The squamosum is of moderate dimensions, and carries a slender zygomatic process. On the lower surface the glenoid articular surface can scarcely be described as a cavity, making as it does rather a wide convex rectangular area which must have allowed very free movement to the lower jaw, both laterally and vertically. The postglenoid facet is practically vertical and closely appressed to the bulla, the two facets (glenoid and postglenoid) being separated by a gap, as is the case in modern camels. The tympanic bone is fused to the squamosum, the external auditory meatus being a closed slightly pro-

FIG. 3.

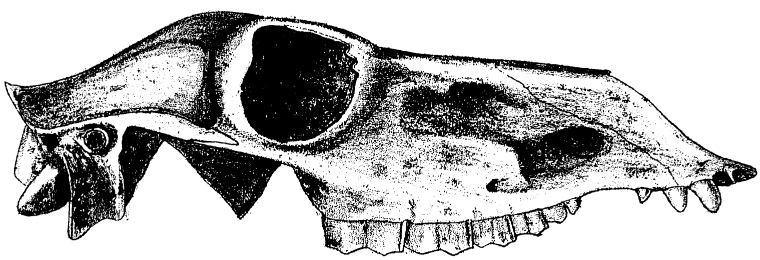


FIG. 3. *Stenomylus hitchcocki*, side view of the skull. × 1/2.

jecting ring; while the greatly inflated bulla is filled with cancellous bone, as is the case in Tylopoda generally. The bulla is also fused to the paroccipital process for most of its length. The occipital bones are all fused, and the occiput is narrow and small. The two condyles are sessile, and do not project behind the plane of the occiput. Below, their facets do not quite meet, being separated by a narrow groove of about a millimeter, the groove being, however, much wider in youthful specimens. The pterygoids unite with the palatines to make deep plates projecting below the base of the skull. The posterior nares open between the palatines so far forward as to make a very short hard palate. The front of the naral opening is opposite the front of the second molar, which in general is very far forward for this opening. However, in the Tylopoda generally it is characteristic to have the posterior nares open well forward: so that this genus simply shows a somewhat higher specialization in this feature. I feel that the compression of the muzzle by the preorbital and subnasal pits tends to cause the posterior opening of the respiratory passage to emerge into the mouth as far forward as possible.

The mandible is decidedly deep for so slender a creature, but the reason for this is readily seen in the extreme hypsodont condition of the teeth, which in a recently mature individual extend nearly to the bottom of the jaw. The symphysis is of moderate length and spout-like in form. The angle of the mandible is not produced into the upward hook-like process so common among the tylopods but shows simply a slight projection (see fig. 6) at that point. The coronoid process is short and slender, being slightly recurved. The articular condyle is broad and slightly concave, the postglenoid facet being large and resembling that of the llama.

The following measurements give the proportions of the skull:

Specimen	Length incisor to occ. condyle	Length premolar 2-molar 3	Orbit weight by width	Width across orbits	Width across molars 2	Age	Sex
S. hitchcocki type	166	60.5	27 × 26·5			barely mature	♀
S. hitchcocki 2019	179	58	24 × 28	67	37	old	♀
S. hitchcocki 1090	191	67	28 × 29	68		mature	♂
S. hitchcocki 2009		33 ρ^{2-4}				milk	
S. crassipes	211	78				mature	
S. gracilis		80	27 × 26	95	57	mature	

Age.—The series of adult skulls fall into two classes irrespective of the amount of wear of the teeth, namely smaller, lighter ones, which I should interpret as female; and larger, heavier ones, which would be males. Aside from these characters of relative proportion I have found no distinctive sex characters. As all the associated skeletons must have been accumulated at one time, and births presumably took place in the spring, such individuals as show differences in age must have been a year apart. On this basis, the youngest, which have the entire milk dentition and the first molar just showing, would be one year old; while the next set, in which the third molar is just up, would be two years old, at which time they have reached nearly full size, as shown by such a specimen as the type. How long they lived would be difficult to estimate, but every indication points to very rapid wear of the teeth; so that five or six years seem to me to represent the probable length of life of the older individuals studied.

Dentition.—The dental formula is $i.\frac{3}{3}c.\frac{1}{1}p.\frac{4}{4}m.\frac{3}{3} = \frac{22}{22} = 44$, which is the full and primitive set. The upper incisors are simple chisel-shaped teeth, entirely unreduced and crowded into a full series. The upper canine is laterally compressed, making it into a subincisiform tooth, which stands a little apart from the incisors, however. Behind the canine there is a moderate diastema which precedes the reduced two-rooted first premolar, while behind this tooth a much greater diastema occurs, separating it widely from the second premolar, which, like its predecessor, is reduced and two-rooted. The third premolar follows without any diastema, and is a narrow elongated tooth, but with none of the specializations of the teeth which follow it. The fourth premolar has acquired the selenodont character, though but single-lobed, its inner and outer cusps having developed into high crescentric ridges, with a deep pit between. The three molars are all extremely hypsodont,

FIG. 4.

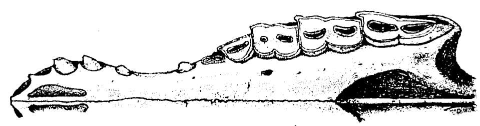


FIG. 4. *Stenomylus hitchcocki*, upper dentition and palate. × 1/2.

which is one of the most marked features of the genus. Each tooth is very simple, consisting of two lobes, each with a deep pit in it. There is no cement in the valleys. Each tooth is nearly flat on the outer side, there being but a slight convexity outside the paracone and metacone, and no column except that the anterior border of each molar is developed into a parastyle. The widest portion of the series is at the second lobe of the first molar. The crown of each molar is greatly developed in height, as is seen in the section of a second molar (fig. 5), the top being slightly narrower than the base, so that as they wear the teeth appear relatively wider. A slightly worn second upper molar of *S. hitchcocki* has a crown 23^{mm} high which contained a pit 19^{mm} deep, these pits in the upper molars being materially deeper than in the lower molars. The successive molars seem to come up slowly or else the wear is very rapid, for when molar 3 is but slightly worn the first molar is down to the bottom of the pit. In addition to the considerable height of the crown the upper part of the pulp cavity fills in with dentine, so that some time after the bottom of the pit is reached the tooth still has a solid center, in the middle of which is a small discolored "mark." Inasmuch as the wear seems to continue considerably below the base of

FIG. 5.

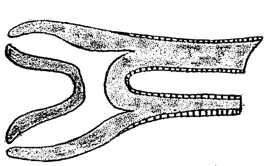


FIG. 5. *Stenomylus hitchcocki*, section of upper second molar, to show depth of pit. ×1/1.

the pit, the tooth in addition to its great height must increase still more by growth at the base during life.

The lower dentition.—The lower incisors are flattened and expanded at the top so that each successive incisor slightly overlaps the preceding one. The laterally compressed canine is grouped with the incisors and has assumed the incisiform character completely. Even the first premolar is semi-incisiform and stands close behind the canine, being thus in the incisor group. Behind this there is a considerable gap in front of the second premolar, which, though two-rooted, is considerably reduced. Behind this in turn occurs a wide diastema followed by the small but sharp third molar. It is only

FIG. 6.

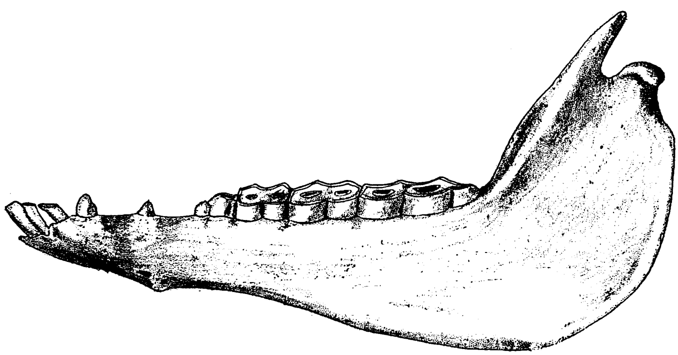


FIG. 6. *Stenomylus hitchcocki*, mandible with lower dentition. × 1 / 2.

the fourth premolar which is to any degree functional as a grinding tooth, and this is a short, narrow, single-cusped tooth without any pit, of molariform adaptation. The three molars, however, are developed into deep hypsodont and compressed teeth, each with its deep pits. The first molar is the smallest of the three, consisting of two lobes, which like the others have a straight face on the inner side, there being no columns except the parastyle on the front margin of each molar. This tooth cuts the gum apparently at about the end of the first year and wears very rapidly, for when the third molar appears this tooth has worn below the base of the pit; but it is to be remembered that in the lower teeth the pits are not nearly as deep as in the upper molars. While the second lower molar is somewhat larger, it is otherwise like the first. But the third molar has three lobes, the last one being only a little smaller than the two preceding it. The extreme depth of this tooth is shown by the illustration (fig. 7), which is a typical young specimen of *S. hitchcocki*, and shows that in a crown 34^{mm} high the pit is but 9^{mm} deep. However, the tooth is available for much greater wear than the depth of the pit; for as age increases the pulp cavity fills with dentine and makes some 18^{mm} more available. The great height of these teeth is the cause of the great depth of the lower jaw noticed in the description of the mandible.

Milk dentition.—Young jaws are found in surprisingly large numbers, practically all of them being of about the same age, and showing the full milk dentition, together with the unworn first molar. These skulls are entirely disarticulated, and I have seen no incisor or canines of the upper jaw, though they were doubtless there. The first upper premolar is situated near the canine and behind it is a considerable diastema, between it and the second small pointed premolar. It is on

FIG. 7.

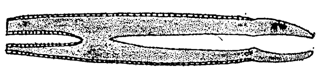


FIG. 8.

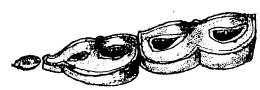


FIG. 7. *Stenomylus hitchcocki*, section of third lower molar to show depth of pit. ×1/1.
FIG. 8. Upper premolars of the milk dentition. ×1/2.

the third and fourth of this series that the burden of grinding is thrown. Like adult molars, they are strongly hypsodont with high crescentric crests and deep pits. They differ, however, in having the outer face more convex over the paracone and metacone, and in having a well-developed mesostyle as well as a parastyle; from which it may be concluded that these features were also present on the teeth of the ancestral

FIG. 9.

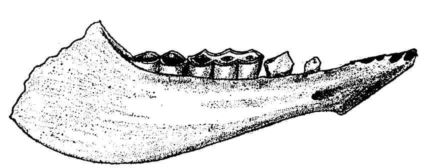


FIG. 9. *Stenomylus hitchcocki*, mandible with the milk dentition. ×1/2.

form. The third and fourth deciduous premolars are each two-lobed and in general resemble the permanent molars.

Lower jaws are usually the better preserved, the alveoli for the three incisors and the canine being present on several specimens. The canine is grouped with the incisors as in the adult. The first premolar is represented by a tiny alveolus scarcely larger than a pin hole, from which I judge that the tooth was vestigial. The second premolar stands isolated with a considerable diastema on either side of it, and like the third premolar is still a single-cusped tooth. The grinding tooth of the lower jaw is the fourth premolar, and this is developed as a large three-lobed, molariform tooth, with high crescentic cusps, and deep pits in each lobe. In all the specimens this tooth is well worn as though it had been used for grinding grass some time, which is the reason that I have assigned the age of one year to the individuals with this and the first molar just showing, as is uniformly the case.

Cervical vertebræ.—The neck as a whole is long and slender, each constituent vertebra being markedly elongated, as is usual among Tylopoda. The atlas is relatively long and narrow, the anterior cotyli being deeply excavated to make the articulation for the occipital condyles. In the lower side the two articular facets are separated by a groove in *S. hitchcocki* (confluent in *S. crassipes*), while on the upper side the two cotyli are separated by a wide notch. The posterior ends of the transverse processes are prolonged backward to make short horn-like projections, which extend behind the facets for the axis much as in Pöebrotherium. The posterior facet for the axis is high and inflexed along the upper border, for the under side of the odontoid process. The edges of the transverse processes make a nearly straight line, in contrast to the sinuous one commonly found. The vertebrarterial canal enters the

FIG. 10.

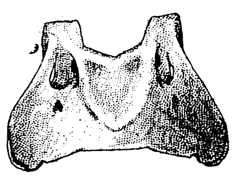


FIG. 11.

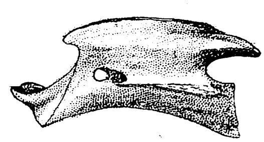


FIG. 10. *Stenomylus hitchcocki*, atlas seen from the dorsal side. × 1/2.
FIG. 11. Axis seen from the side. × 1/2.

neural pedicle just to one side of the axial facet and passing through the arch comes out again about the middle of the centrum. The first spinal nerve had its exit adjacent to the anterior opening of the vertebrarterial canal.

The axis is also a long and slender bone, with a long, low spinous process ending to the rear in two small tubercles, a feature very characteristic of the camels. The transverse processes begin just in front of the middle of the centrum and make moderately expanded wings to either side, their outer edges being slightly flexed downward. The anterior facet for the atlas is a wide concave face extending in a trifle over half a circle, and dying out on the neural arches. The odontoid process is short and thick with a tubercle on its upper surface. In this the genus differs from the early tylopods, which have a semicylindrical odontoid, while that of the modern genera is spout-like. The vertebrarterial canal is confluent with the neural canal through the posterior third of the vertebra, then enters the pedicle of the neural arch, passing obliquely through and coming out about a third of the way from the front of the centrum. Just in front of the vertebrarterial foramen there is a wide opening for the exit of the second spinal nerve.

The third, fourth and fifth cervicals are so similar that they may be treated together. They are all long and slender, having only the smallest vestiges of a spinous process, in which feature they resemble the modern camels, even having the characteristic to a more marked degree than any of the other genera in the family. The transverse processes, expanding wing-like on either side, extend the whole length of the centrum, and then are prolonged into slender projections as seen in fig. 12. These transverse processes do not have the anterior portion of the wing prolonged into a distinct lobe, as is the case in the modern Tylopoda; but rather have the lobe barely indicated, as is the case in Pöebrotherium and Oxydactylus. A ventral keel develops on the posterior third of the centrum, expanding to the rear until it is very prominent. In none of these three vertebræ is the vertebrarterial canal visible externally. On cervicals 3–7 the anterior of the centrum is moderately convex, the posterior end concave.

The sixth cervical is markedly different from the others. First its dorsal spine is vestigial, which is well developed in the modern camels and in Pöebrotherium: then the transverse process is a short thin plate the distal end of which is bent backward. The interior lamellæ are developed into wide plates which extend the whole length of the centrum and project downward. These are not, however, divided into an anterior and posterior lobes as in the modern tylopods, but have a straight lower border as is the case in Pöebrotherium. The vertebrarterial canal enters the base of the neural pedicle at the rear and penetrates the entire length, leaving just under the prezygaphysis.

Fig. 12.

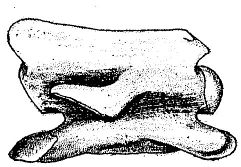


Fig. 12. *Stenomylus hitchcocki*, sixth cervical seen from the side. ×1/2.

The seventh cervical is much shorter than the others, and has a moderate neural spine. The transverse processes are developed as wings to either side and about half the length of the centrum, the outer margin being prolonged fore and aft and thickened. The wide posterior facet is placed obliquely to the length of the centrum, indicating a marked upward bend to the neck, so it is fair to conclude that the head was carried high. On the rear there are facets for the first ribs.

From the foregoing it is clear that this genus in such deep-seated characters as the position of the vertebrarterial canal, the reduction of the neural spines, and the characters of the transverse processes, relates itself closely to the Tylopoda, having especial affinity to the primitive genus Pöebrotherium.

The following measurements give the relative sizes of the various vertebræ in the three known species and in Pöebrotherium.

Length of Centrum × Width of Vertebra.

	1st.	2d.	3rd.	4th.	5th.	6th.	7th.
S. hitchcocki	33 long / 39 wide	54 / 29	68 / 41	58 / 37	54 / 37	49 / 37	35 / 40
S. crassipes	35 / 51	62 / 33	67 / 35	54 / —	— / 38	48 / 45	
S. gracilis					75 / —	72 / —	
P. wilsoni	36 / —	66 / —	63 / —	58 / —	56 / —	45 / —	36 / —

Dorsal vertebræ.—The dorsal series consists of twelve vertebræ, measuring 242^{mm}. The neural spines are all wide thin plates, so closely set in front as to leave almost no intervals between vertebræ, and reaching a maximum in height on the fifth dorsal, from which point on they are lower with increasing intervals between successive spines. The anticlinal vertebra is the eleventh dorsal. Metapophyses appear first on the eighth dorsal and occur on each successive centrum, situated each time a little higher and further forward, until on the eleventh the metapophysis unites with the prezygapophysis and together they make a concave facet which incloses the cylindrical postzygapophysis.

FIG. 13.

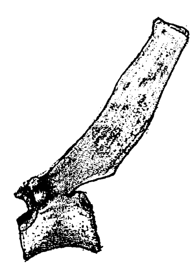


FIG. 13. *Stenomylus hitchcocki*, sixth dorsal seen from the side. ×1/2.

Lumbar vertebræ—The lumbar series consists of seven vertebræ, which total 190^{mm} in length. Each one is characterized by having the above described interlocking series of concave prezygapophyses and cylindrical postzygapophyses as is typical of Tylopoda generally. While the neural spines only rise to moderate heights, they are wide, thin plates, considerably expanded above. The transverse processes extend, attaining the (for so small a form as *S. hitchcocki*) considerable length of 34^{mm}.

Sacrum.—The sacrum consists of four fused vertebræ having a total length of 59^{mm} and a width of 62^{mm}. The first of the component vertebræ sends out a stout and much expanded pleurapophysis to receive the ilium. To this is added the smaller but still stout pleurapophysis of the second sacral vertebra. These two sacrals are heavy, but the two posterior vertebræ having only to support the tail are reduced and have become very slender.

Caudal vertebræ.—The tail is supported by 14 vertebræ, of which the proximal ones are short and wide with well-marked transverse processes. Beginning with the seventh, however, the vertebræ are without transverse processes, and become approximately cylindrical rods, the last one being but 5^{mm} long and but 1^{mm} in diameter. The whole series measures 170^{mm}, indicating a tail of moderate length.

Ribs.—The first of the ribs is short and stocky, while the succeeding eleven are thin and wide (though not so wide as in the living camels), the interval between succeeding ribs being about half the width of the rib itself. A typical rib measures 175^{mm} long by 18 wide. Each rib has two heads rather close together, followed by a narrow abruptly curving neck, and then expands and stretches in a gentle curve toward the sternum. The uncrushed ribs show the body to have been decidedly narrow and moderately deep. The first five ribs were attached directly to the sternum by short calcified costal cartilages; the sixth and seventh by longer calcified cartilages; and the succeeding three are connected by long costal cartilages to each other and indirectly to the sternum; while the eleventh and twelfth are free ribs.

Sternum.—The sternum consists of a slender presternum of 22^{mm} length, followed by five wide sternal segments fused to each other. Opposite the point of union of each two segments the margin is expanded and offers an attachment for the costal cartilages. The sixth joint receives the two longer costal cartilages. Finally there is the xiphisternum, a thin expanded lamella of bone extending some 42^{mm} behind the rest of the sternum.

Fore limb.—The scapula is relatively long and narrow, the anterior margin extending upward in a decidedly concave curve, while the posterior margin is bounded by a like though less concave curve. The high spinous crest divides the blade into a smaller prescapular and a larger postscapular fossa, the latter being bounded on the outside by a raised ridge running along the posterior margin. Along the upper edge, the spine of the scapula is thickened and rugose for muscular attachments. Proximally it extends forward, making a slender acromian

FIG. 14.

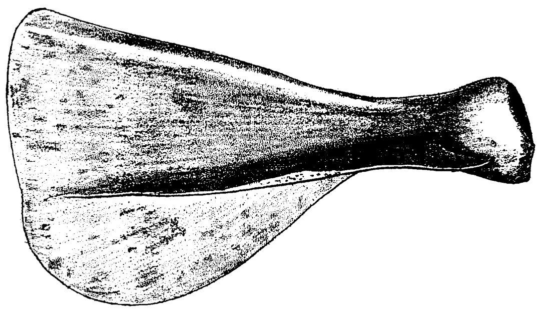


FIG. 14. *Stenomylus hitchcocki*, scapula seen from the dorsal side. x 1/2.

process which does not extend quite to the level of the glenoid fossa. The coracoid process is of but moderate dimensions and rolled inward, making a hook-like process. The shallow glenoid fossa is wider than high in the ratio of 4 to 3.

The humerus is slender and moderately long, the shaft having a well-marked sigmoid curvature. Corresponding to the shallow glenoid, the sessile head is but moderately convex. The greater tuberosity spreads along fully half of the width of the head, rising high above it, and overhanging the narrow bicipital groove; while the low lesser tuberosity of only half the width of its neighbor bounds the groove on the inner side. The bicipital groove when viewed from the front is seen to lie

FIG. 15.

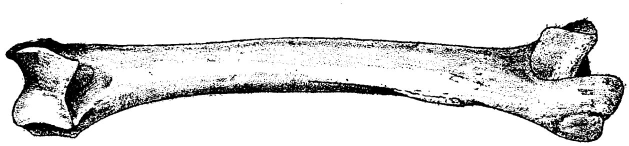


FIG. 15. *Stenomylus hitchcocki*, humerus, seen from the dorsal side. x 1/2.

just to the inner side of the median line; and while narrow at the bottom, it expands up onto the lesser tuberosity, so that its width is about equal to that of the tuberosity. There is no trace of the bicipital tubercle dividing the groove into two parts as in modern camels. The deltoid ridge is well-marked, rising just under the head and reaching down to about the middle of the shaft. The supinator ridge is barely visible. The trochlea stands at almost right angle to the length of the shaft, is a little higher on its inner than on its outer margin, and has the intertrochlear ridge but feebly developed and situated near the middle of the ulnar side. The anconeal fossa is low and deep, but does not perforate the shaft.

The radius and ulna are completely fused throughout their entire length, thus making a long, slender curved shaft. Using the length of the humerus as a unit, the length of the ulnar-radius would be 1·38, which is relatively longer than is the case in Pöebrotherium (1·15) or the modern camel (1·25), but does not compare with the length of Oxydactylus. At both the upper and lower ends of the radius occurs a groove indicat-

FIG. 16.

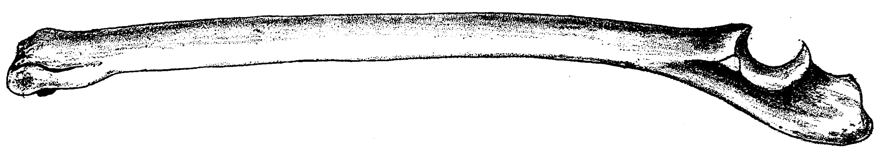


FIG. 16. *Stenomylus hitchcocki*, fused radius and ulna outer aspect. × 1/2.

ing the original boundaries of the ulna, the lower end of the groove penetrating so as to make a complete foramen. The compressed olecranon process is moderately high and wide, the upper anterior edge having in it a wide groove for the extensor tendon.* The humeral facets on the ulna are confined to the superior border of the sigmoid notch and are not confluent with the facets on the inferior border on either the inner or outer side. To this statement I found in ten cases but one exception, in which case the upper facet was confluent with the lower along the inner side of the sigmoid notch. It is a peculiarity of Pöebrotherium and the Tylopoda generally that the humeral facet on the upper border of the sigmoid notch is confluent with the facets on the lower border only along the inner side. This typical tylopod condition is characteristic of the species *S. gracilis*† and *S. crassipes* also. On the distal end of the radius there are three facets for articulation with the carpal bones, that for the scaphoid being the largest and rectangular in outline; that for the lunate being narrow and

* This groove is characteristic of Pöebrotherium and Oxydactylus but not found in modern Tylopoda. Peterson does not find the groove in *S. gracilis*. Ann. Carnegie Museum, vol. iv, p. 292.

† Last cit. p. 455.

obliquely placed; while that for the cuneiform is triangular in outline and about half of it carried on the lower end of the ulna.

The carpus is compact and relatively high, the upper row of bones being the scaphoid, lunate and cuneiform as is typical for Tylopoda, their only peculiarity being that the lunate is relatively high and narrow. In the distal row the unciform is considerably deeper than the magnum; magnum and trapezoid are distinct, as is characteristic of tylopods; and the trapezium is represented by a tiny ossicle found also in Pöebrotherium. The pisiform is light and slender in its outlines.

FIG. 17.

FIG. 17. *Stenomylus hitchcocki*, carpus from the anterior side. × 1/2.

The metacarpus consists of the functional digits III and IV, together with tiny nodules representing the upper ends of digits II and V. Metacarpus II is a nodule some 10^{mm} in length, occupies a pit on the outer side of the third metacarpal, and carries two tiny artificial facets, one for the trapezium, the other for the trapezoid. Metacarpals III and IV are relatively long, almost equaling the humerus in this dimension, and separate from each other throughout their entire length. Along the upper two-thirds they are closely appressed and flattened, but through the distal third they spread apart and each metacarpal bone has a circular cross section. At the proximal end metacarpal III rises slightly above mc. IV and has on the end a larger facet for the magnum and a smaller one for the trapezoid, behind which is a tiny facet for the trapezium, while on the lateral border there is a smoothed surface for the vestigial mc. II. The proximal end of the fourth metacarpal has almost the entire

FIG. 18.

FIG. 18. *Stenomylus hitchcocki*, metacarpus from the anterior side. × 1/2.

upper surface given up to a large facet for the unciform, only a small spur rising behind and presenting facets to the magnum and trapezoid. On the ulna side there is a small excavation for a tiny nodule some $5–7^{mm}$ long and representing the fifth metacarpal. The distal ends of the third and fourth metacarpals carry the enlarged trochlea for the phalanges, each with a high carina, which is, however, confined to the plantar side.

The two first phalanges are long and slender, with the distal ends expanded in true tylopod manner. The upper articular surface is a shallow concavity, a notch in the lower margin being the only indication of the carina of the metapodial. The distal phalanges are a trifle over half the length of the proximal ones, and like them are considerably expanded, though not to the extent found in modern camels. The upper articular face is a shallow groove, while that on the lower end extends from on the upper clear around on to the plantar surface. The ungual phalanges are high, long pointed, rounded on the outer side and nearly vertical on the inner face. They are typical for a distinctly digitigrade artiodactyl.

FIG. 19.

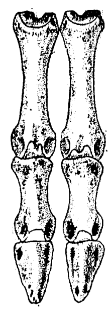


FIG. 19. *Stenomylus hitchcocki*, phalanges from the upper side. × 1/2.

The following figures give the measurements for the various front limb bones in the three known species:

	Scapula			Humerus			Ulnar-radius*		Metacarpus		Phalanges		
	length	width	width of fossa	length	diameter of head	diameter of trochlea	length	thickness	length	thickness	length 1	2	3
S. hitchcocki	138	78	22	168	26	27·5	225(191)	10·5	158·5	11·25	35	20	17
S. crassipes				194	32	28·57	229(194)	13	166	13 5	41		
S. gracilis				195	37	33	254(225)		184		44		

FIG. 20.

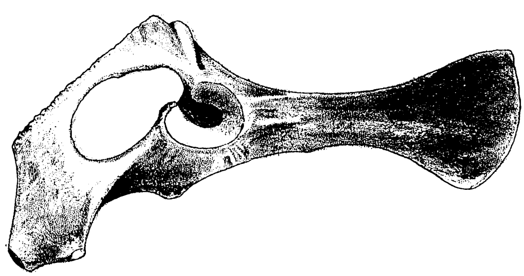


FIG. 20. *Stenomylus hitchcocki*, os innominatum seen from the lateral aspect. × 1/2.

Hind limb.—While in general the innominate bone is of the tylopod type, it is longer and relatively less expanded,

* In parenthesis is given the length of the radius.

especially in the iliac region. The upper end of the ilium is widely expanded and has a large area for the attachment on the sacrum. The neck of peduncle is longer and slenderer than usual. In the neighborhood of the acetabulum this bone is marked by several transverse ridges for the attachment of muscles quite as in the modern camels. The ischium is stout and expanded behind, a high slender process with its tuberosity rising on the superior ridge, and a second, the ischial tuberosity, being well developed at the posterior angle. The pubis is short and stocky, being expanded along the wide symphysis until it meets the ischium. In general conformity to the elongation of the pelvis the thyroid foramen is oval. The acetabulum is deep with a wide notch below.

The short femur has a marked curvature, being generally tylopod in character. Its head is small and rounded, with the pit for the round ligament well to the posterior side. The bridge between the head and the greater trochanter is both short and high, as is common to the camels generally; and the greater trochanter rises high above it, making a wide notch, as

FIG. 21.

FIG. 21*a*.

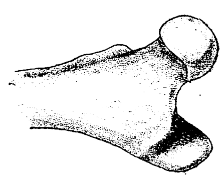


FIG. 21. *Stenomylus hitchcocki*, femur seen from the inner side. × 1/2.
FIG. 21*a*. Head of femur from the posterior side.

is also found in Pöebrotherium. The bridge is compressed antero-posteriorly, so that the digital fossa makes a deep pit, the bottom of which is about on a level with the lesser trochanter. This latter is situated high on the shaft, and from it runs a long ridge for muscular attachments. The rotular trochlea is broad and shallow and does not extend far up on the shaft. The external condyle is larger than the inner, which stands obliquely to the transverse axis of the shaft.

The patella is broadly oval and simple in outline, having nothing of the prolonged process common to later Tylopoda.

The slender tibia is about a fourth longer than the humerus, which, when compared with other tylopoda, is not long. The facets for the femoral condyles are wide and nearly flat, being separated by a bifid tubercle. The cnemidial crest is extremely prominent, and extends about a third of the way down the bone. In the regions of the crest the cross section is triangular, but below the section is transversely oval. The distal end of the bone is expanded and the inner astragular facet much wider and shallower than the outer, the two being separated by a prominent septum. Both these facets and that on the septum are interrupted in the middle by a shallow depression, which extends from near the inner margin of the inner facet all but to the outer margin of the outer facet. This is a very marked characteristic of the modern camels, and begins as far back as in Pöebrotherium at least. The fibular facet is divided by the groove for the fibula shaft into anterior and posterior portions.

FIG. 22.

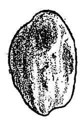


FIG. 22. Patella. ×1/2.

The .proximal end of the fibula is reduced to a tiny spine fused to the fibula; the distal end to a nodular bone wedged

FIG. 23.

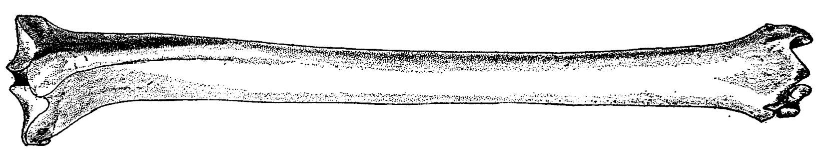


FIG. 23. *Stenomylus hitchcocki*, tibia and fibula from the anterior side. ×1/2.

in between the tibia and the calcaneum. It presents a tiny spur above, vestige of the original shaft, which fits into the groove on the tibia; and has a long continuous facet for articulation on the tibia. On the inner surface is a crescentic grooved facet for the astragulus, and on the lower surface a concave face for the calcaneum.

In conformity to the slender build the tarsus is narrow and high. The astragulus is narrow, with the external condyle somewhat higher than the internal. On the distal trochlea the facet for the cuboid is relatively narrow, while that for the navicular is proportionally wide. The plantar facet is comparatively narrow and small. In general, however, the astragulus would be recognized as tylopod. The calcaneum is of moderate length, being distinguished only by the considerable antero-posterior diameter of its shaft, this depth being especially great near the facet for articulation on the cuboid.

FIG. 24.

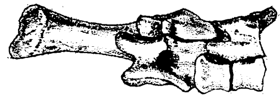


FIG. 24. *Stenomylus hitchcocki*, tarsus. × 1/2.

The cuboid is compressed transversely, developed in the antero-posterior diameter, and carries a heavy plantar hook in the rear. The navicular is moderately developed, having a large concave face for the astragulus, which facet is notched on the inner margin. The lower side has a large facet for the ecto-meso-cuneiform and a smaller one for the ento-cuneiform, beside the lateral articulations where it rubs against the cuboid. The ecto-meso-cuneiform is free from the navicular, rectangular in

FIG. 25.

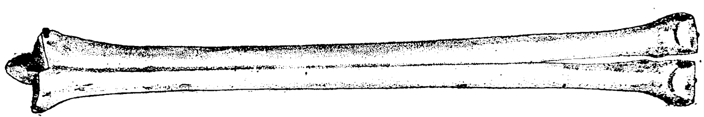


FIG. 25. *Stenomylus hitchcocki*, metatarsus from the anterior side. × 1/2.

form, and carries a single facet above for the navicular, a second below for the third metatarsal, and a third laterally for the ento-cuneiform. This last bone is a small nodule, with facets for the navicular, the ecto-meso-cuneiform and for the plantar process of the cuboid.

FIG. 26

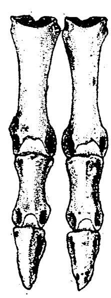


FIG. 26. *Stenomylus hitchcocki*, phalanges of the hind foot, from the upper side. × 1/2.

The metacarpus consists of the functional digits III and IV, fused for a little more than the upper half of their length, a tiny nodule representing mt. II, and a still smaller nodule representing mt. V. In length the metatarsus is a trifle longer than the metacarpus. The vestige of the second metatarsal is 8^{mm} long by 6^{mm} wide and carries a tiny facet for articulation on the ento-cuneiform. The vestige of mt. V is but 3^{mm} long and 5^{mm} wide and has no facets. The upper end of the third metatarsal is occupied by the facet for the ecto-meso-cuneiform, that of mt. IV by the facet for the cuboid; then each contributes a strong process from the plantar side, on the inner side of which is a facet for the ento-cuneiform. The distal ends of the two metapodials spread in a characteristic manner and each carries a broad trochlea for phalangeal articulation, and on each of these there is a prominent carina, which, however, is confined to the lower side and is not as prominent as the corresponding ones on the front metacarpals.

The proximal phalanges are a trifle shorter than those of the front foot, but otherwise similar in form. The distal and ungual phalanges are also very like those of the front foot.

The following figures give the comparative measurements of the three species of Stenomylus.

	Femur			Tibia		Metatarsus		Phalanges		
	length	diameter of head	diameter of trochlea	length	diameter of upper end	length	thickness	1	2	3
S. hitchcocki	176	18	31	210	32·5	166	11	36	20	17
S. gracilis	205	19	34	248	38	198		44		
S. crassipes	212	20	38·5	213	39	185	12·5			

Classification.

Stenomylus Peterson

Ann. Carnegie Museum, vol. iv, 1906, p. 41.
" " " vol. iv, 1908, p. 286.

The type species is *S. gracilis*, found by Peterson in the Lower Harrison beds of Sioux Co., Neb. The genus may be defined as follows: Stenomylus is a slender member of the Tylopoda, adapted to an upland life, with an extreme hypsodont dentition of i.$\frac{3}{3}$c.$\frac{1}{1}$p.$\frac{4}{4}$m.$\frac{3}{3}$=$\frac{22}{22}$=44; the upper canines partly and the lower canines wholly inciform, the first lower premolar tending the same way; vertebral formula c.7d.12-l.7c.14; an elongated neck; limbs didactyl and digitigrade: magnum and trapezoid free; and navicular and ecto-meso-cuneiform free. Horizon, Lower Harrison.

At present three species are distinguished as follows:

Stenomylus gracilis Peterson

Ann. Carnegie Museum, vol. iv, 1906, p. 41.
" " " vol. iv, 1908, p. 286.

Distinguished by larger size, narrower upper molars, lower canine less incisiform, diastema between lower premolar 1 and 2 shorter, lower jaw narrower, metacarpals coössified a part of their length, and in details the most specialized of the three species.

Stenomylus hitchcocki sp. nov.

See preceding description of osteology for details. The species is distinguished by its small size, relatively narrow molars, lower canine completely caniniform, diastema between lower premolar 1 and 2 relatively long, premolar 2 greatly reduced, lower jaw deep, metacarpals separate their entire length. In general the species is the least specialized of the three.

Stenomylus crassipes sp. nov.

The species is distinguished in that while the size of the skull is approximately that of *S. gracilis*, the neck and limbs are markedly shorter and heavier; the premolars are much more reduced; and the lower canine is completely incisiform.

To this the following details may be added as a description of the species. The type is number 2150 in the Amherst College collection, and was found seven miles northeast of

FIG. 27.

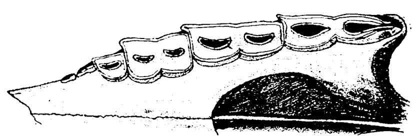


FIG. 27. *Stenomylus crassipes*, upper dentition and palate. × 1/2.

Agate, Sioux Co., Neb., in the uppermost sandstones of the Lower Harrison beds. The type consists of the skull (lacking premaxillæ) and lower jaws, together with 6 cervical, and 3 dorsal vertebræ, scapula, humerus, ulno-radius, carpals, metacarpals, and phalanges. With this has been used specimen 14220 of the American Museum of Natural History, consisting

FIG. 28.

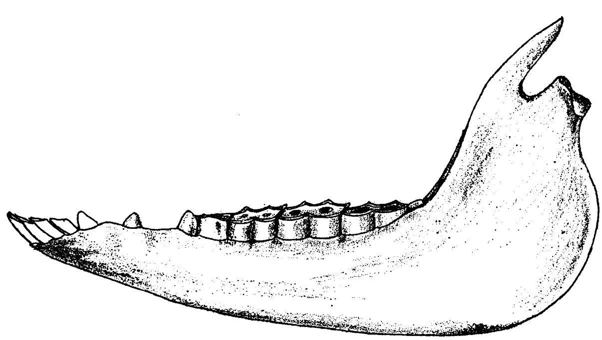


FIG. 28. *Stenomylus crassipes*, mandible and lower dentition for the outer side. × 1/2.

of nearly all parts of the skeleton; but the find is composed of the bones of more than one individual.

As is characteristic of the skeleton, the skull is heavily built, the cranial region being short, and the frontals wide. The premaxillæ and premolar regions are shortened over the corresponding regions of *S. gracilis*, but the back of the skull is about the same size. In dentition the upper incisors are the usual well-developed chisel-shaped teeth crowded together; the canine is reduced and separated from the incisors by a diastema of 4^{mm}, being a like distance from the tiny first

FIG. 29.

FIG. 29. *Stenomylus crassipes*, fused radius and ulna from the outer aspect. ×1/2.

premolar. The second premolar is also much reduced, as is the third and the fourth, this last being 2^{mm} shorter than its counterpart in *S. gracilis*. The molars, however, are relatively enlarged, corresponding in length and width with those of *S. gracilis*. The lower jaw is shortened in the regions in front of the molars, the lower canine being wholly incisiform, as is also the first premolar which is placed close to the canine, all five of these teeth being grouped in the incisor aggregation. The second premolar has a considerable diastema, both in front and behind it, both being, however, shorter than those of *S. gracilis*. The third and fourth premolars are also reduced, and the molars are enlarged corresponding to those in the upper jaw.

The cervical vertebræ resemble those of *S. hitchcocki* in character, but are thicker and shorter than in that of the *S. gracilis* species. From the table of measurements it will appear that the humerus is about the same length as that of *S. gracilis*, but the ulno-radius is some 30^{mm} shorter and at the same time much stockier. In the same way the metacarpus is materially shorter and heavier, mt. III and mt. IV being fused together for about half their length as in *S. gracilis*. The femur is relatively long, actually longer than that of *S. gracilis*, but as in the fore limb the tibia is extremely short, 35^{mm} shorter than that of *S. gracilis*. The metatarsus is also short and stocky, mt.

	Hypisodus	Stenomylus	Pöebrotherium
1	$i\frac{3}{3}c.\frac{1}{1}p.\frac{4}{4}m.\frac{3}{3}$	$i\frac{3}{3}c.\frac{1}{1}p.\frac{4}{4}m.\frac{3}{3}$	$i\frac{3}{3}c\frac{1}{1}p\frac{4}{4}m\frac{3}{3}$.
2	Dentition hypsodont	Dentition extremely hypsodont	Dentition brachydont.
3	Upper canine subincisiform	Upper canine subincisiform	Upper canine caniniform.
4	Lower canine incisiform	Lower canine incisiform	Lower canine caniniform.
5	Lower premolar 1 incisiform	Lower premolar 1 subincisiform	Premolar 1 normal.
6	Bulla large, hollow, fused to paroccipital process	Bulla large filled with canceolated tissue, fused to paroccipital process	Bulla large filled with canceolated bone, fused to paroccipital process.
7		Hard palate ends opposite front of second molar	Hard palate ends opposite back part of second molar.
8		Vertebral formula c.7d.12l.7s.4c.14.	Formula c.7d.12l.7s.4c.14.
9		Vertebrarterial canal passes through the pedicle of the neural arch	Vertebrarterial canal passes through pedicle of neural arch.
10		Cervical vertebræ elongated, neural spines on 2-6 vestigial	Cervical vertebræ elongated, neural spines on 2-6 greatly reduced.
11	Magnum and trapezoid fused	Magnum and trapezoid free	Magnum and trapezoid free.
12		Ulna facets on upper border of sigmoid notch interrupted on outer or both sides	Ulnar facets interrupted along the outer side.
13	4 functional digits on fore limb, upper and lower ends of mc. retained	2 functional digits retained on fore limb, upper ends only of vestigial digits retained	2 functional digits retained on fore limb, upper ends only of vestigial digits retained.
14	Navicular and cuboid fused	Navicular and cuboid free	Navicular and cuboid free.
15		Distal tibial facets interrupted	Distal tibial facets interrupted.
16	2 functional digits on hind foot, lateral mt. retain both upper and lower ends and digits	2 functional digits on hind foot, lateral mt. lose lower ends and digits	2 functional digits retained on hind foot. Lateral digits lose lower ends and digits.

III and mt. IV being fused rather more than half their length. From the foregoing it will appear that *S. crassipes* is a species closely resembling *S. gracilis*, but differentiated by the shortening of the limbs, especially below the elbow and knee, a heavier shorter-limbed type being thus evolved.

Affinities.—In his descriptions Peterson has placed the genus Stenomylus among the Tylopoda, near the long-limbed

FIG. 30.

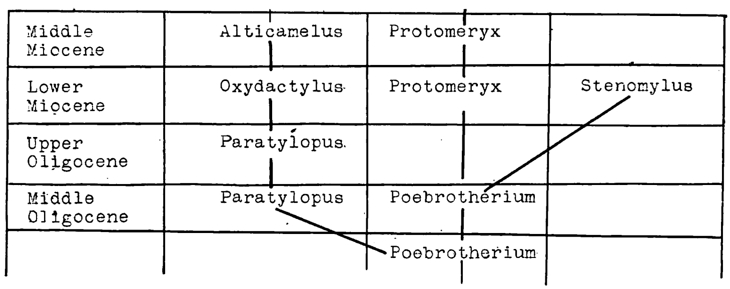
FIG. 30. *Stenomylus crassipes*, metatarsus and proximal phalanges. ×1/2.

type Oxydactylus; while Matthew* has associated the genus with Hypisodus among the Hypertragulidæ. In order to show concisely the points of likeness and difference to one or the other of these types, the characters of Stenomylus are in the above diagram arranged in parallel columns with those of Hypisodus on the one side and with Pöebrotherium on the other, the latter being used as illustrating a primitive tylopod.

From the foregoing table it is evident that in the matter of dentition (number 1-5) the genus Stenomylus approximates Hypisodus; but in the other skeletal features it is distinctly allied to the Tylopoda. This is especially marked in such deep-seated and fundamental characters as the cancellous bone in the bulla, the position of the vertebrarterial canal, the matter of the fusion of the magnum and trapezoid, the matter of fusion of the navicular and cuboid, and the manner in which the lateral digits have been reduced. These are characters less liable to modification on a change of habit, while the dentition is the first to respond to changes in the matter of food. I feel therefore that Stenomylus should be placed among the Tylopoda. Then as it is evident that the dentition is aberrant in its extreme hypsodont specialization, and presuming that this characteristic has been acquired in conjunction with a special feeding habit (which feeding habit would presumably be the same as characterizes Hypisodus, but a parallel adaptation), I feel that Stenomylus should be set off by itself. The habit, which is general to forms having this hypsodont dentition, is feeding on hard grasses, usually on the open prairies, the grass having in its stem considerable quantities of silica which causes extremely rapid wear of the teeth. I take it then that while

* Bull. Amer. Museum Nat. Hist., xxiv, 1908, p. 539.

the typical tylopod contemporaries of the Protomeryx type, fed on a generalized diet, and retained their brachydont dentition, and while the long-limbed Oxydactylus group were feeding on leaves and shrubbery, and likewise retained their brachydont dentition, that there arose another group of upland tylopods which took up the grazing habit, and these developed the hypsodont dentition. These then represent a separate branch of the Tylopoda, which must have had its beginning in the later part of the Oligocene, being derived from Pöebrotherium, which genus Stenomylus resembles in most of its characters. This group of tylopods seems to have flourished greatly during the lower Miocene, especially during the Lower Harrison, outside of which horizon it has not been found. I see no especial affinity to Oxydactylus other than that common to all Tylopoda. The affinities may be graphically indicated as follows:



The Lower Harrison beds then will show three types of Tylopoda, each presumably in a different type of habitat, the Stenomylus in the upland, the Protomeryx near or in the valleys where a considerable variety of vegetation flourished, and the Oxydactylus in the intermediate country and probably feeding on leaves and twigs of trees.

Collectors in the Lower and Upper Harrison beds can not but be greatly impressed by the great variety of tylopods which occur in these beds, there being beside the already known species certainly as many more indicated by the great variety of toe and isolated bones found. The Lower Miocene seems to be the period of especial luxuriant development for all types of camel-like forms.

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