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## ON THE OSTEOLOGY OF *MESOHIPPUS* AND *LEPTOMERYX*, WITH OBSERVATIONS ON THE MODES AND FACTORS OF EVO- LUTION IN THE MAMMALIA

W. B. SCOTT,

COLLEGE OF NEW JERSEY, PRINCETON.

THE genus *Mesohippus* stands about midway in the line of equine descent, so far as that line is known, and is itself, very probably, an actual ancestor of the modern horses, or at all events is so closely allied to such ancestor as to answer all the purposes of this study. Although the horse series is perhaps the most complete of any that have yet been made out among mammalian phylogenies, yet it is not my design to attempt a description of all the members of this series, as that would require a very extended and voluminous account, and is, besides, quite unnecessary for the main object in view. This object is to ascertain, so far as is yet possible, the mode or law of evolution in a mammalian phylum, and as the place of *Mesohippus* in the equine phylum seems to be fairly well established, a comparison with existing forms will yield instructive results.

The very number of well-preserved fossil equine genera is a source of embarrassment, and renders the systematic position of some of these forms a matter of grave doubt. Thus the relation of the European genera *Anchilophus*, *Anchitherium*, and *Hipparion* to their American contemporaries and to existing species, is very far from clear, and to assume, as has been done,

that the genus *Equus* has had a dual origin, on the one hand from *Hipparion*, and on the other from *Protohippus*, involves a degree of convergence which cannot be admitted in the present state of our knowledge. It follows, therefore, that results drawn from such a doubtful phylum can be of little service, and on that ground these genera of uncertain position will not be taken into consideration.

I have chosen *Mesohippus* as the subject of the following description for a twofold reason: in the first place, because its ancestral relation to the modern genus is extremely probable; and secondly, because its structure is the least fully known of almost any of the horse series, and we may thus avoid the repetition of well understood facts. The description is founded chiefly upon a series of specimens obtained by the Princeton expeditions of '82 and '90. I am also indebted to the kindness of Professor Cope for the loan of some of his beautiful material from Colorado.

The typical American species, *M. Bairdi*, was first described by Leidy as belonging to *Palæotherium*, (No. 32, p. 122), but shortly afterwards referred by him to *Anchitherium*, under which name it is described in all of Leidy's subsequent publications on the subject. In 1875, Marsh erected it into the type of a new genus, *Mesohippus*, with the following definition: "This genus presents characters intermediate between *Orohippus* Marsh, and *Anchitherium* von Meyer. The skull and teeth are very similar to those of the latter genus and the dental formula is the same. In the feet, however, the lateral digits are larger, the fifth metacarpal is represented by an elongated splint bone; and the second and third cuneiform bones of the pes are not co-ossified. The type of the genus is *Mesohippus Bairdi* — *Anchitherium Bairdi*, Leidy." (No. 34, p. 248.)

With regard to this description it may be noted that the fifth metacarpal is present in *Anchitherium*, as is demonstrated by the facet for it upon the unciform, but nothing is known as to its shape. The other distinctions are obviously not of generic, but only of specific value, and consequently the new genus has not been generally accepted as such. I have shown elsewhere, however, that the characters of the incisor teeth are sufficient to generically separate the European form from that of the American White River beds. (No. 49.) In the former they

have broad crowns with distinct pits or invaginations of the enamel, while in the latter the crowns are sharp and chisel-shaped, very much as in *Hyracotherium*, without any trace of such invagination. (Cf. Cope, No. 9, Pl. XLIX. *a*, Fig. 3; and Kowalevsky, No. 25, Pl. III., Fig. 57.)

There are, besides, not unimportant differences in the construction of the molars and of various parts of the skeleton, which show that *Mesohippus* is a more primitive form than *Anchitherium*, and indeed it may be doubted whether the European type is in the line of equine descent at all, but does not rather form a side-branch.

It is not necessary for our purpose to enter into the question whether the equines of the John Day Miocene should be referred to *Anchitherium* or not.

Though the White River species has so long been known, our knowledge has been chiefly confined to the structure of the skull and the dentition, which have been described and figured by Leidy. Cope has published some valuable notes on the skeleton (No. 11), as has also Marsh (No. 35), but these are too brief for the object of this paper. Kowalevsky's excellent memoir upon *Anchitherium* (No. 25) was never completed, and is to some extent vitiated by the supposition, now abandoned, that *Palæotherium* is the primitive horse-type.

## I. THE DENTITION.

The dentition has been so fully described by Leidy (No. 33), Osborn (No. 42, p. 88), and others, that a brief summary is all that is necessary here.

1. *Upper Jaw*. The superior incisors and canines are not preserved in any of the specimens which I have seen, but the alveoli for them show that they were present in un-reduced number, and that they were of small size. The first premolar is a small, compressed, and simple cone, with a rather strong cingulum developed on the inner side of the crown. The other premolars are almost exactly like the molars in construction, with very slight differences of detail; thus the posterior pillar is less developed and sometimes altogether absent; the posterior transverse crest is more completely divided from the postero-internal cusp. In other respects the transformation is complete. The second pre-

molar shows a beginning of the peculiar shape seen in the horse, not being quadrate in outline, but narrower in front than behind, and having a forward extension of the antero-external angle.

Although the premolars have thus entirely assumed the molar pattern, yet the development of them as presented by the Eocene genera, shows that, just as in the Artiodactyls, the functionally similar parts of the crown are not homologous in the two series.

The molars of *Anchitherium* differ very slightly from those of *Mesohippus*, the median ribs of the external lobes are less distinctly shown, the transverse crests, which in the American form do not quite reach the outer wall of the crown, are connate with the ectoloph; the median cusps, para- and metaconules, are relatively smaller, and the posterior pillar larger. In both genera the teeth are typically brachyodont.

2. *Lower Jaw.* The incisors of *Mesohippus* are small, with narrow crowns, and simple, sharp cutting edges, which are abruptly truncated. The canine is also small and erect. The first premolar is a minute compressed conical tooth, implanted by a single fang, and not separated by a diastema from the second. The second premolar is not quite molariform, the posterior crescent only being developed, the anterior portion of the tooth being compressed and somewhat trenchant. The third and fourth premolars and the true molars are composed of two crescents; the anterior pillar is well developed, forming with the metaconid the twin cusps (*aa* of Rüttimeyer); the posterior pillar which rises from the cingulum behind the entoconid is present, but less advanced. The third molar has quite a large fifth lobe or talon.

In the recent *Equidæ*, the most important change to be noticed is that the teeth have become very long and prismatic, and covered with cement. The incisors have deep pits of enamel, and the pattern of the molars has become very complex, through the sinuous folding of the enamel crests; nevertheless, this complicated hypsodont molar is plainly derived from the simple tooth of *Mesohippus*. "By tracing back the rise of the eleven elements which compose the upper *Equus* molar, we find that six belong to the primitive sextubercular bunodont crown. Two elements of the ectoloph, the anterior pillar and median pillar, rise from the simple primitive basal cingulum of the

*Hyracotherium* molar : the same mode of development, we have just seen, is true of the posterior pillar. The eleventh element, the fold of the postero-external angle of the crown, is not prominent until we reach *Equus*." (Osborn, No. 42, p. 89.)

Wide as appears to be the interval between the molar pattern of *Mesohippus* and that of the recent forms of *Equidæ*, it is completely bridged over by the teeth of such intermediate forms as *Merychippus*, *Protohippus*, etc.

## II. THE SKULL. (Pl. XXII., Figs. 1, 2 ; Pl. XXIII., Fig. 17.)

The skull of *Mesohippus* has been well described and figured by Leidy (No. 33), but his specimens were not very complete, and we need to examine this portion of the skeleton from a somewhat different point of view.

The cranium is long, narrow, and low, the face deeper, but short and tapering rapidly forward, the orbits are placed far forward, their anterior rim being over the first molar. The cranio-facial axis is straight and the occipital surface high and narrow.

The basi-occipital is broad, stout, and strongly convex, with a faintly marked median keel. The condyles are rather small, not strongly projecting, and in contact in the median line below ; the articular surfaces are continued forward some distance upon the inferior surface of the basi-occipital ; but these surfaces are narrow and nearly flat, not concave from before backward, and not having the elevated anterior borders which occur in the horse. The exoccipitals are rather low and broad, and form a very strong convex prominence in the median line, which lodges the large vermis of the cerebellum. This prominence is not thickened and diploëtic, as in *Equus*, but has very thin walls. The superior margin of the foramen magnum is notched in the median line, and on each side of the median line there is a small protuberance. The paroccipital processes are long, slender, and compressed. The supra-occipital is quite high and narrow, concave in the median line, and with acute margins, forming the lambdoid crest ; it extends but a little way upon the roof of the cranium. The occiput as a whole is proportionately higher and narrower than in the horse, and the surfaces for ligamentous and muscular attachment are much less prominent and rugose. The foramen magnum is narrower and more circular in outline.

The basi-sphenoid is shorter and more slender and tapering than the basi-occipital, but otherwise like it in shape. The pre-sphenoid is so covered by the expanded vomer that little of it can be seen. The alisphenoid is of peculiar shape; the ascending portion is divided by an angulation into two portions, of which the anterior is high, narrow, and nearly vertical; and the posterior forms a broad, flat, and nearly horizontal surface, rising gently to the glenoid cavity. The much more elevated position of the latter in the horse gives to this part of the alisphenoid a very different appearance. The orbito-sphenoid is high, but rather narrow, not forming nearly so much of the wall of the orbit as in the horse.

The periotic has a high, but very narrow mastoid portion, which is exposed between the squamosal and the exoccipital, and forms a large part of the wall of the cerebellar fossa, as is plain in a longitudinally bisected skull. The tympanic is not ankylosed with the periotic, and in most specimens has become detached and lost. It is very small and forms a minute bulla with an elongated tubular meatus, and ending in front in a short, sharp styloid process; it encircles and apparently is co-ossified with the tympanohyal. The periotic is in contact with the basi-occipital, so that the large lacerated foramina are not continuous, nor so extensive as in the horse.

The squamosal is large, forming much of the side walls of the cranium, but not rising so high relatively as in the horse; the zygomatic process is quite long and slender, and as in the horse, extends forward so as to form part of the inferior rim of the orbit. The peculiar and exceptional construction of the horse's orbit is thus already indicated. The glenoid cavity is likewise characteristically equine in structure; its articular portion is very narrow, slightly concave from side to side, and convex from before backward; its external portion is raised, and when viewed from the side forms a prominent tubercle, which, however, is not so broad, nor so conspicuous as in the horse. The post-glenoid process is quite high, massive, and rugose; between the post-glenoid process and the articular surface there is a broad, shallow depression. The post-tympanic process is short and inconspicuous, and is closely applied to the mastoid portion of the periotic. The deep notch between the post-tympanic and post-glenoid processes lodges the tubular auditory meatus.

The jugal is quite long and slender, its posterior portion reaching back nearly to the glenoid cavity: it extends, however, but little upon the face, very much less than in the horse, and the masseter surface is but feebly developed. As a whole, the zygomatic arch is decidedly different from that of *Equus*, being longer, much more slender and compressed. These differences are due in part to the changed position of the orbits, and in part to the increased relative importance of the masseter muscle in the modern species.

The parietals are long, but narrow; anteriorly they diverge strongly to receive the posterior projections of the frontals; the sagittal crest is short and inconspicuous, but longer and more prominent than in the horse; anteriorly the ridges diverge and form a narrow triangular area. Near the posterior portion of the suture with the squamosal, the parietal is perforated by a number of large venous foramina: in the horse these foramina are situated in the squamosal, are more scattered, and extend farther forward.

The frontals are very long, but rather narrow; their shape is much as in the horse, but the forehead is narrower and slightly concave. The frontal sinus is but little developed, and does not extend over the brain at all. The fronto-nasal suture is nearly straight, but in the median line the frontals send forward a narrow tongue, which is wedged in between the diverging nasals. The cranium is quite sharply constricted behind the orbits. The post-orbital processes are long and slender, with rugose edges; there is no trace of any corresponding process from the zygomatic arch. The superior rim of the orbit is more prominently projecting in some specimens than in others, and in the former there are two small supra-orbital foramina; in the latter the foramen is represented by a notch at the anterior base of the post-orbital process.

The lachrymal is quite large, and though smaller than in the existing genus, extends well up on the face and articulates superiorly with the nasal as well as the frontal; in front of the orbit there is a pit or depression, which is partly upon the lachrymal, but more extensively upon the maxillary. This pit is very much deeper in some specimens than in others, though this difference may be a sexual one, as I have reason to believe is the case in *Oreodon*. There is an obscure lachrymal spine:

upon the rim of the orbit, and the foramen is single and placed well within the orbit.

The nasals are very long and narrow, and in general appearance resemble those of the horse, but with some differences. Posteriorly they are quite broad, reaching nearly to the antero-superior margin of the orbit, and diverging so as to receive between them the short and sharp nasal processes of the frontals. In front of this expansion the nasals become very narrow, but their sides are bent down nearly at right angles to the horizontal portion, very much as in the horse. The free ends extend far beyond the suture with the premaxillaries, and taper much less rapidly than in *Equus*, their tips being rounded and blunt, not sharp points.

In correspondence with the small size of the incisor teeth, the alveolar portion of the premaxillaries in *Mesohippus* is but feebly developed and is conspicuously smaller transversely, and more especially in the vertical diameter than in *Equus*: the ascending ramus is much shorter and less obliquely directed than in the horse; it forms a thin and narrow plate and has a short contact with the nasal. The anterior nares are much lower and narrower than in the horse. The palatine plates of the premaxillaries are very small, and the spines much more slender and very much shorter than in the horse, as are also the anterior palatine foramina.

The maxillaries are chiefly remarkable for their small extent vertically, especially of the alveolar portion, which is very low, so that the inferior rim of the orbit is brought very near to the molars; but even the portion which is applied to the formation of the nasal chamber is much less extended vertically than in the existing species. There is a short diastema between the canine and the first premolar, and just in front of the latter the face is slightly constricted. The maxillary is also much shorter, proportionately, than in the modern forms, in correlation with the much smaller size of the molars. The alveolus is extended some distance behind the last molar, but less than in *Equus*, and there is a well marked notch between the palatine and this portion of the alveolus. The palatine processes of the maxillaries are narrow and quite short, which is brought about by the position of the posterior nares, which extend as far forward as the first molar, and thus have a much more anterior situation than in the

existing type. The masseter crest is very feebly developed, and does not extend at all in advance of the jugal suture.

The palatines form very little of the hard palate and are chiefly confined to enclosing the posterior nares laterally. This opening is decidedly horseshoe-shaped, broad and rounded in front, and much contracted behind. The palatines are in contact with the maxillaries throughout, the inner wall of the orbit being formed in its postero-inferior portion by the outer wall of the narial opening, giving to this region of the skull an entirely different appearance from that which occurs in the horse. The pterygoids are very small and inconspicuous, and do not form distinct hamular processes. The vomer, so far as it can be made out, agrees with that of *Equus*.

The inferior maxillary has a slender and compressed horizontal ramus, which tapers rapidly forward, and is very sharply constricted at the diastema, expanding again slightly to form the incisor alveolus. The two rami are firmly co-ossified, and the symphysis is quite long. The symphysial region is directed quite sharply upward and forward, thus forming an angle with the remainder of the horizontal ramus, while in *Equus* the symphysis is flattened, procumbent, and in the same straight line as the molar-bearing region. These differences are no doubt due to the changes in the character and especially the size of the incisor teeth. The angle is regularly rounded and has a thickened border; it is more extended antero-posteriorly than in the horse. The ascending ramus, on the other hand, is decidedly lower, and the condyle less elevated above the level of the molars. The coronoid process is regularly recurved and pointed, and resembles that of the ruminants rather than that of *Equus*. The condyle is extended transversely, but very narrow antero-posteriorly.

The cranial foramina of *Mesohippus* have attained very nearly the modern arrangement. The anterior palatine foramina are much shorter than in the horse, and the posterior palatine foramina are farther forward, opposite the first molar. The infra-orbital is over *pm.* 3, as in *Equus*, but much lower down than in that genus, and it is separated from the orbit by a much shorter interval. The supra-orbital foramen is sometimes present, sometimes indicated by a notch. The optic foramen is placed in front of the foramen lacerum anterius, and not above it. There is an

alisphenoid canal. The large space surrounding the small tympanic bone includes the Eustachian canal, foramen lacerum medium and posterius, and the carotid canal; in none of the fossils which I have seen can these foramina be distinguished.

The numerous venous foramina which perforate the parietal, are in the horse shifted to the squamosal. In the mandible there are three small mental foramina, extending from *pm.* 3 to the diastema.

When viewed in longitudinal section, the skull of *Mesohippus* (Pl. XXIII., Fig. 17) presents many important differences from that of *Equus*. Especially striking is the small size of the nasal chamber and the large size of the brain cavity, especially in the antero-posterior direction. The cerebellar fossa is decidedly larger in proportion, and is less overlapped by the cerebral fossa. There is very little thickening or diploëtic structure in the posterior parietal and supra-occipital regions, and the alisphenoids and orbito-sphenoids are excessively thin. The frontal sinus is exceedingly small, and does not extend over the hemispheres. The nasal chamber is low and narrow, and the maxillary sinus much smaller than in *Equus*. Unfortunately the specimen gives us no information as to the condition of the vomer or of the maxillo- and ethmoturbinals.

I have not been able to see a well-preserved skull of the European *Anchitherium*, nor, so far as I am aware, has any such specimen been figured. Kowalevsky's drawings (No. 25, Pl. III., Figs. 50-52, 56, and 57) show some differences from *Mesohippus*, especially in the increased thickness and width of the alveolar portion of the premaxillaries and of the *symphysis mandibuli*, corresponding to the development of the incisor teeth. *Anchitherium* appears to agree with *Mesohippus* in having a well-marked pre-orbital depression.

In the skull of *Equus* the principal changes are as follows: (1) The face has become greatly elongated and increased both in vertical and transverse diameters. (2) The alveolar portion of the maxillaries and premaxillaries has become very much higher, in correspondence with the development of prismatic teeth. (3) The anterior nares are much higher and wider, the nasals longer and tapering anteriorly to sharp points. (4) There is no pre-orbital depression. (5) The jugal and lachrymal are much more extended upon the face, and the masseter crest

has become very prominent, extending far forward upon the maxillary. (6) The maxillary alveolus extends farther behind the last molar. (7) The posterior nares are placed far back, and the posterior part of the palatines is not in contact with the alveoli. (8) The orbits are completely enclosed, much elevated in position, and pushed back of the molar series. This shifting causes important changes in the shape of the alisphenoids. (9) The zygomatic arch is shorter and more massive. (10) The cranial cavity is broader and more rounded, and the cerebral fossa overlaps the cerebellar. (11) The tympanic is ankylosed with the petrotic. (12) Large sinuses are developed in the frontals and diploëtic thickenings in the median line of the parietals and occipitals. (13) In the lower jaw the symphysis is broadened, procumbent, and in the same line with the rest of the horizontal ramus; the ascending ramus is higher and narrower, the coronoid straighter and less pointed, and the condyle higher above the level of the molars.

### III. THE BRAIN.

The brain of *Mesohippus* has been described and figured by Osborn (No. 42, p. 87), who says of it: "*Mesohippus* had a large and well-convoluted brain. The length and breadth indicate that it weighed about one-third as much as the brain of the recent horse, while if we estimate the body weights of the fossil and recent animals by the relative size of the humeri, the brain of the Miocene species was proportionally heavier. The cerebrum of the horse is, however, much more highly convoluted, and the frontal lobes are relatively broader. The *Mesohippus* brain is distinguished in a marked manner by the longitudinal direction of the parietal and occipital sulci, and by the deep transverse frontal sulci, from the oblique sulci of all recent ungulates. In fact, in this respect it bears a marked general resemblance to the brain type of recent Carnivora, and conforms with the higher Ungulata of the Eocene." To this may be added that the hemispheres are narrower and less capacious in the fossil, and as in all the lower members of the ungulate series, they taper much anteriorly. This brain shows in the parietal and occipital region very close agreement with the principal fissures of the equine brain as figured by Krueg (No. 27, Taf. XXIII.), but in the frontal region the agreement is much less close, owing to the transverse direction of the frontal sulci.

Another well-preserved specimen of a *Mesohippus* brain-cast was obtained by the Princeton Expedition of 1890, which presents some differences from the one figured by Osborn. This brain was of a larger animal (perhaps species), and is more modern in appearance, the frontal lobes being decidedly broader, and the convolutions richer and more sinuous. In the frontal region the sulci tend to become less exactly transverse, and in the parietal region a slight tendency to obliquity of the sulci is observable. The olfactory lobes are large, and the cerebellum is not overlapped by the hemispheres to the same degree as in the recent species.

#### IV. THE VERTEBRAL COLUMN.

1. *Cervical Vertebrae*. The atlas (Pl. XXII., Fig. 3) is rather long antero-posteriorly in proportion to its breadth. The anterior cotyli for the occipital condyles are deeply concave and are notched, sometimes more and sometimes less deeply, on their outer margins. Inferiorly they are almost in contact, but above are widely separated by a deep and broad notch of semi-circular outline. The neural arch is rather broad and low, and the neural spine is represented by a low rugose ridge; on each side of this there is another similar ridge which runs obliquely forward and outward, ending above the foramen for the first spinal nerve. The inferior arch is strongly convex, and constricted in the middle by the deep fossæ into which the vertebrarterial canals open; there is a small but very distinct hypapophysial tubercle. The posterior cotyli for the centrum of the axis are rather high and narrow, and face obliquely backward and inward; the articular surface for the odontoid process is in some cases separated from the cotyli by deep grooves, either partially or completely; in others the two are continuous. The transverse processes are very short, but extended from before backwards, with regularly curved and slightly thickened free margins. When viewed from the side, the process presents a slight sigmoid curvature, and runs obliquely downward and backward. At the anterior root of the transverse process there is a deep notch for the first spinal nerve which is not converted into a foramen. The posterior opening of the vertebrarterial canal is on the dorsal side of the transverse process. In advance of its anterior opening there is a small vascular opening, which enters but does not perforate

the side of the atlas. The characters of the atlas of *Mesohippus* are thus obviously equine.

The atlas of *Anchitherium* figured by Kowalevsky (No. 25, Pl. I., Fig. 40), so far as it is preserved, closely resembles that of *Mesohippus*. The notch which separates the anterior cotyli above is not so broad or deep; the posterior cotyli face more directly backward, and the foramina for the dorsal branches of the first pair of spinal nerves are continued forward as deep grooves. In other respects the two are alike.

In the modern *Equidæ* the atlas has become broader and more rugose and massive in construction; the transverse processes are extended forward, converting the notches at their bases into foramina, and the posterior openings of the vertebral arterial canals are considerably enlarged.

The axis (Pl. XXII., Figs. 5-9) of *Mesohippus* presents many more differences from the modern type than does the atlas, and is also subject to an unusual degree of individual variation. The centrum is long, very much depressed and quite broad in front, becoming narrower and deeper behind, ending in a nearly circular and deeply concave posterior face. On the posterior half there is a thin but prominent hypapophysial keel, terminating in a small tubercle. The articular surfaces for the atlas are usually high and narrow, rising far up on the sides of the neural canal, but their shape varies much in different individuals; ordinarily they are nearly flat, or very slightly concave from side to side, the medial margin standing somewhat in advance of the external, and slightly convex from above downward; but sometimes the medial margins are far in advance of the external, giving the surfaces a curiously warped appearance. Sometimes the surfaces project down below the general level of the centrum, producing a deep notch between the two; in other cases they do not so project, and there is no notch. The odontoid process varies much in shape, being in some specimens short, broad, and straight, with truncated free margin; in others longer, narrower, curved upward, and pointed; but in all cases it is peg-like, and either flat or convex on the dorsal side, very different from the broad spout-like odontoid of the horse. The facet upon its inferior surface is usually separated from the articular faces of the centrum, but is sometimes continuous with them, as is the case in the corresponding surfaces of the atlas.

The neural arch is not very high, and is much broader in some specimens than in others; the pedicels are perforated near the anterior edge for the passage of the second pair of spinal nerves. The neural spine is very peculiar, being a long, high, hatchet-shaped, thin, and very much compressed plate, which terminates behind in an obtuse point, projecting considerably beyond the postzygapophyses and raised much above them; altogether very different in shape and appearance from the structure seen in the horse. The postzygapophyses are large and very prominent; in some specimens they are directed nearly straight outward, in others more obliquely outward and backward. Sometimes they are quite concave from side to side, but again they are as strongly convex. Transverse processes are not preserved in any of the specimens which I have seen.

The axis of *Anchitherium*, so far as known, is, according to Kowalevsky (No. 25, p. 69, Pl. I., Fig. 46), entirely like that of the horse; it differs from the axis of *Mesohippus* in the much greater outward projection of the anterior part of the centrum with the atlanteal facets. A more important difference is in the shape of the odontoid, which, though still relatively short, is completely spout-like in shape.

In the horse the anterior articular surfaces project outward and also downward, as in some specimens of *Mesohippus*; the odontoid process is spout-shaped, though not so deeply concave as in the ruminants; its facet for the atlas is continuous with those on the anterior face of the centrum, the medial margins of which stand far in advance of the external. The neural spine is relatively low but very massive, and with a thickened rugose margin, which posteriorly bifurcates into two ridges, one of which passes into and dies away upon the postzygapophyses; the latter form, therefore, the hindermost projection of the vertebra. The neural canal is proportionately low and narrow. The centrum is very strongly opisthocœlous, and the posterior face is obliquely placed, slanting upward and forward.

It will be observed that the numerous individual variations of the axis of *Mesohippus* consist chiefly in approximations to the condition found in the horse, now in one respect, now in another.

The third, fourth, and fifth cervical vertebræ of *Mesohippus* (Pl. XXII., Fig. 10) are very much alike; they all have elongate

centra, which are strongly keeled inferiorly, and have faces set obliquely to the long axis; the anterior face is hemispherical, and the posterior deeply concave. In these three vertebræ the centra are of nearly equal length. The neural arches are low and very broad on top; the zygapophyses are large, strongly projecting, and present nearly vertically. The neural spine is represented by a faint ridge on the third, which becomes a small tubercle on the fourth, and a distinct spine on the fifth. The transverse processes have considerable antero-posterior extension and become successively shorter and stouter as we pass backward; at the same time the inferior lamella, which is rudimentary on the third, steadily enlarges on the succeeding vertebræ.

The sixth cervical (Pl. XXII., Figs. 11 and 12) is shorter than the preceding ones, and has no hypapophysial keel or tubercle; instead, the lower edge of the posterior face is emarginated in the median line. The neural spine is quite high and inclined strongly forward. The transverse process is a short, stout hook, curved upward at the extremity, and the inferior lamella has greatly increased in size, attached to the centrum throughout its length, and projecting considerably both in front and behind it.

The seventh cervical is still shorter than the sixth; it has a broad, flat, and depressed centrum, which, in advance of the transverse processes, is somewhat suddenly constricted to form the small, nearly hemispherical, and obliquely placed head; the posterior face is quite broad, and displays on each side of the rounded pit for the head of the first dorsal a facet for the head of the first rib. The transverse processes are quite stout and simple, and are not perforated by the vertebrarterial canal. The prezygapophyses are nearly flat, very prominent, and obliquely set, facing more inward than upward; the postzygapophyses are less conspicuous, as they do not project behind the neural spine. The latter is stout, strongly inclined backward, and occupies the whole antero-posterior extent of the neural arch, but unfortunately none of the specimens is sufficiently complete to enable us to estimate its height.

Comparing the posterior five cervical vertebræ of the horse with those of *Mesohippus*, we find many important differences. The centra have been much elongated, so that the neck as a whole is much longer than in the Miocene genus; all of the

processes for muscular and ligamentous attachments are much more prominent and massive, in correlation with the increased size and power of the animal. The faces of the centra are more decidedly concave behind and convex in front, and are set more obliquely to the long axis of the vertebræ, so that the neck exhibits a more decided sigmoid curvature, as well as being longer. Neural spines have disappeared from all but the seventh, where the spine is much lower proportionately than in *Mesohippus*. In *Equus asinus*, however, there is a very short spine on the sixth also, and the inferior lamella on this vertebra is less developed than in the Miocene form.

The number of dorsal vertebræ which *Mesohippus* (Pl. XXII., Figs. 13-15) possessed is uncertain, though it can hardly have been less than eighteen. The first vertebra of the series has a centrum very similar in character to that of the seventh cervical, but shorter, and less strongly opisthocœlous. The transverse processes are quite long, and have very large, crescent-shaped and deeply excavated facets for the tubercles of the first pair of ribs. The prezygapophyses are very large and prominent, the postzygapophyses much smaller, but projecting strongly behind and to the sides of the neural spine; the latter is stout, especially on the posterior edge. The succeeding dorsals gradually lose these characters, the centra becoming less opisthocœlous, the transverse processes shorter and with more flattened facets; the zygapophyses on the third dorsal are developed on the anterior and posterior faces of the neural arch. Metapophyses appear quite early in the series and on the ninth (?) vertebra they are very prominent. In the middle region the transverse processes are very short and are placed above the centrum. The spines are long, but very thin and much compressed; in the anterior region they have expanded tips. The posterior dorsals become longer and have trihedral, sharply keeled, and slightly opisthocœlous centra, with faces set obliquely to the long axis. The spines are quite high, but very thin and inclined forward; the zygapophyses are more lateral in position and slightly concave and convex respectively, thus being of a somewhat interlocking character.

The anterior lumbar vertebræ have elongate trihedral and sharply keeled centra, which are slightly opisthocœlous and have oblique faces; in these vertebræ the transverse diameter

but little exceeds the vertical; posteriorly the centra become much broader and more depressed. The spines appear to be thin and compressed, the transverse processes quite stout and with considerable antero-posterior extent; on the last (Pl. XXII., Fig. 16) and penultimate vertebræ the transverse processes have articular surfaces for contact with those of the succeeding vertebræ. The zygapophyses are interlocking in a moderate degree. The obliquity of the faces of the dorsal and lumbar vertebræ show that the back was decidedly arched.

In the horse the back is nearly straight and the dorso-lumbar vertebræ vary less in length in the different regions; the lumbar vertebræ in particular are shorter in proportion than those of *Mesohippus*. The spines are much more massive and more nearly straight, and the zygapophyses of the posterior dorsal and lumbar regions are much more decidedly of the interlocking type.

The first sacral vertebræ of *Mesohippus* has a very much depressed centrum; the pleurapophyses are greatly expanded and form the large iliac surfaces, the second vertebræ not contributing to their formation. On the anterior edge of the pleurapophysis is a very large convex facet for the transverse process of the last lumbar.

No caudal vertebræ are preserved in the specimens.

Nothing is known of the sternum, and the few fragments preserved indicate that the ribs were more slender in proportion than are those of the recent horses.

## V. THE FORE LIMB.

The *scapula* is not well preserved in any of the specimens, but enough remains to indicate its chief characters. The glenoid cavity is nearly circular and quite shallow, and is slightly notched at its antero-internal border by the synovial incision. The coracoid process is very large, both in the vertical and antero-posterior directions, but is thin and plate-like, and is not recurved at the free end. The neck is very narrow and long; the spine rises somewhat nearer to the glenoid cavity than in the horse, and is not median in position, but nearer to the coracoid border, thus making the postscapular fossa larger than the prescapular. None of the specimens has a sufficiently well-

preserved spine to show whether a metacromion was present. The glenoid border is much thickened, and the coracoid border, so far as preserved, is quite thin and sharp. The course of the former indicates that the blade of the scapula was proportionately broader than in the horse, and the neck is much more contracted.

The fragment of *Anchitherium* scapula which Kowalevsky figures (Pl. I., Fig. 37), agrees very closely with that of *Mesohippus*, the only observable difference being that the coracoid is somewhat more massive. "La *spina scapulæ* commence plus loin du bord glénoïdale que dans les Paléothériums et monte presque perpendiculairement, avec une légère inclinaison en dehors ou en arrière; cette inclinaison de la *spina scapulæ* en dehors est très caractéristique pour tous les imparidigités, elle s'explique par le fait que cette portion de l'omoplate sert d'insertion aux grands muscles qui aide à tourner le bras (*M. cucullaris*, ce muscle est insignifiant chez le cheval). Chez les rhinocéros cette partie de la *spina* donne encore un processus en arrière pour augmenter la superficie de l'insertion musculaire. Avec la réduction des mouvements latéraux ce caractère commence à se perdre, et chez le cheval tous les mouvements latéraux des extrémités sont réduits à leur minimum, la *spina scapulæ* perd les caractères périssodactyles et fait un pas vers les ruminants; elle s'incline dans sa partie antérieure en dedans" (No. 25, p. 5).

It is of interest to observe that the scapula of *E. caballus* differs from that of *E. asinus* in very much the same way as does the scapula of the camel from that of the llama.

The humerus (Pl. XXIII., Figs. 19-22) of *Mesohippus* is relatively short; the head is flattened and projects very strongly backward; when the bone is placed in the vertical position, the head presents more posteriorly than superiorly. The external tuberosity is very large, extending across nearly the entire anterior face of the bone and ending in a stout, blunt hook, which overhangs the bicipital groove. This tuberosity is divided into two portions, a smaller external one with smooth surface, and a larger rugose internal one. The inner tuberosity is well developed, and incloses, with the outer, a very deep and narrow bicipital groove, which is situated at the antero-internal angle of the head. In none of the specimens which I have examined is

there any indication of the bicipital tubercle at the bottom of the groove. The shaft is slender and slightly curved in a sigmoid shape; in the middle it is of nearly circular section, below this transversely oval, and proximally it is also oval, with the long axis directed from before backward. The deltoid ridge is prominent and rugose and runs far down on the shaft, forming, however, no projecting hook; the supinator ridge is distinctly marked, but short. The anconeal fossa is very small, but deep, and penetrates the shaft to form the supra-trochlear foramen. The distal end is but little expanded transversely, and the trochlea is set obliquely to the long axis of the shaft; it is also of considerably greater vertical height internally than externally. The inner condyle is broad on the anterior face, but becomes much narrower on the distal and posterior sides; the intercondylar ridge forms a broad and thick rounded prominence. The external condyle is almost confined to the anterior face, hardly descending at all upon the distal surface; its outer portion projects laterally and is flared in a peculiar manner, forming with the corresponding surface on the radius a joint which allows an extraordinary degree of flexion. The obliquity of the trochlea has the effect of throwing the radius outward during flexion; otherwise the arrangement of facets is such that the two bones could be brought into contact through almost their whole length without dislocation.

The epicondyles are but feebly developed, the external one being hardly indicated, the internal one somewhat larger and more prominent. The inner side of the distal end has a considerably greater antero-posterior depth than the outer, so that when the bone is viewed from the side the internal margin of the anconeal fossa is seen to project behind the outer margin, but much less decidedly than in *Equus*.

The humerus of *Anchitherium* is very similar to that of *Mesohippus*, but more equine in construction. The shaft is rather stouter, and the deltoid ridge more prominent, an incipient hook being plainly indicated. The external tuberosity is considerably reduced in size, not extending so far toward the medial line. The internal tuberosity is also smaller, and the bicipital groove much wider and shallower, and has moved toward the outer side; the beginning of the bicipital tubercle is likewise clearly shown. The distal end is, according to Kowalevsky, thoroughly hippoid in character, and so far as can be judged from his

figure, it has not the peculiar flaring external condyle which is so characteristic of *Mesohippus*.

In the horse, the shaft has become much stouter and straighter, as well as longer than in the Miocene genus, and the ridges for muscular attachment, especially the deltoid hook, much better developed. The external tuberosity is little, if any, larger than the internal, and does not project over the bicipital groove, which, in its turn, has become very broad, and is divided into two portions by the large bicipital tubercle. The latter is now as prominent as either of the tuberosities. The distal trochlea is broad, set nearly at right angles with the long axis of the shaft, and of uniform height. The inner condyle is proportionately more extended than in *Mesohippus*, and the intercondylar ridge more thickened. The external condyle has not the peculiar facet above described, and there is no supratrochlear foramen. The inner margin of the anconeal fossa projects far behind the outer.

The humerus of *Mesohippus* is in many ways like that of *Pæbrotherium*, while that of *Equus* is very similar to that of the camel, especially in the construction of the proximal end.

The ulna (Pl. XXIII., Fig. 23) of *Mesohippus*, though much reduced, is usually distinct from the radius throughout; in some specimens, however, the distal ends of the two bones are co-ossified for a short distance. The olecranon is quite high, but thin and compressed, with a thick end and abruptly truncated superior margin; it is continued upward in a vertical line with the shaft, hardly projecting at all backward. The sigmoid notch is shallow, and the articular facets for the humerus are confined to its superior and anterior faces, and are obliquely placed with reference to the long axis of the shaft. The radial facets are two, of which the outer one is decidedly the larger and more prominent. The shaft is very slender and compressed, but not interrupted, and the distal end is but slightly expanded and bears a small saddle-shaped facet for the cuneiform.

The radius (Pl. XXIII., Figs. 23-25) is short and has a shaft which is arched forward and quite slender, though in the latter respect there is considerable variation, some specimens being decidedly stouter than others. The shaft is much flattened antero-posteriorly, and is of transversely oval section and nearly uniform diameter, except at the extremities. The proximal end

is quite broad, the increase being chiefly upon the external side. There are three clearly demarcated facets for the humerus, of which the internal is the broadest, and is separated from the external by the broad and deep intercondylar notch, which, however, emarginates the anterior edge but slightly. The external facet projects strongly beyond the line of the shaft; it is nearly flat and descends steeply from behind forward, somewhat as in *Oreodon*. The very unusual amount of flexion which this arrangement permits has been already mentioned. Distally the radius is thickened, but not much expanded transversely; the anterior face has broad, not very deep sulci for the extensor tendons, and on the external side there is a deep groove for the distal end of the ulna. There are two carpal facets, for the scaphoid and the lunar; the former is concave in front, and behind forms a stout convex projection which extends much posteriorly to the lunar facet and is reflected up upon the hinder face of the bone. The surface for the lunar is simply oval and concave; its greatest diameter is transverse, in which dimension it somewhat exceeds the scaphoid, but is much less extended antero-posteriorly. The tubercle for the insertion of the biceps and brachialis internus muscles is on the inner side of the proximal end. The ulna and radius of *Anchitherium* present no important differences from those of the American genus.

In *Equus* the ulna and radius have completely coalesced and the shaft of the former is interrupted. The olecranon is longer and projects more strongly backward than in *Mesohippus*, and its free end is more regularly rounded. The shaft of the radius is much stouter and more expanded at the extremities; the facet for the internal humeral condyle is decidedly broader in proportion, and the intercondylar groove notches the anterior margin quite deeply. The rugosity for the biceps and brachialis internus is on the anterior face.

The carpus of *Mesohippus* (Pl. XXIII., Figs. 26-28) is in general appearance and construction very much like that of the horse, but with many differences of detail, and on the whole decidedly more primitive. The carpus of *Anchitherium* is distinctly nearer to the modern condition, which is partly due to its greater size, partly to the more pronounced enlargement of the median digit, and reduction of the lateral ones.

The scaphoid is rather narrow transversely, but high and of

considerable antero-posterior depth. The internal side is rugose and marked by a deep oblique groove, which, however, does not appear to be a tendinal sulcus; the posterior face is also rugose, but less transversely extended than in the horse, where this face forms a hook projecting toward the ulnar side. The proximal facet for the radius has a greater antero-posterior extent than that of the lunar or cuneiform; it is broader and slightly convex in front, narrower and concave behind. On the ulnar side of the scaphoid there are two facets for the lunar, of which the inferior is less distinct than in the horse, and the interval between the scaphoid and lunar not so large as in that animal. The distal surface of the scaphoid exhibits three articular facets, arranged one behind the other; of these the anterior and largest one is for the magnum, which is nearly plane; behind and slightly internal to it is the concave facet for the trapezoid, and on the postero-internal angle a minute facet for the trapezium. There is no posterior facet for the head of the magnum. The scaphoid of *Anchitherium* is very similar to that of *Mesohippus*, but is relatively lower and broader and more cubical in shape, and the trapezoid facet more entirely posterior to that for the magnum. Both of these features are exaggerated in the horse, and the palmar face of the scaphoid much widened and inflected towards the ulnar side. Usually there is no facet for the trapezium in *Equus*, but according to Kowalevsky it very often is present (No. 25, p. 20).

The lunar is high and narrow, with the proximal end considerably broader than the distal. The radial facet is slightly convex in front, concave behind, and on the internal side descends somewhat upon the anterior face of the bone. The lunar is in contact with the scaphoid only at the superior and inferior borders, being elsewhere separated by a considerable interval, but it is closely applied to the cuneiform throughout. The distal end, when seen from the front, is unevenly divided between the magnum and unciform, the former surface being usually much the wider; in one specimen the proportion is  $1 : 1\frac{1}{2}$ ; in another, the magnum facet is but slightly broader than that for the unciform. The latter facet has a smaller antero-posterior extent than the former, the projection from the palmar side covering only the magnum.

The cuneiform is very narrow transversely, its principal diameter being the antero-posterior, caused by a prominent and

massive projection from the palmar face. The proximal surface is small, slightly concave, and occupied by the ulna; there is a small facet also for the radius, but this is not apparent in all specimens. Distally there is a concave facet for the unciform, which is broader behind than in front. The pisiform facet is narrow, but long, and but little oblique in position, presenting nearly directly upwards. The cuneiform of the horse is relatively broader and more massive, but lower; the posterior projection is much less prominent, and the pisiform facet is nearly vertical, presenting backward, and but very slightly upward.

The pisiform is of entirely different shape from that seen in the horse; it is quite long and compressed, with a somewhat contracted neck and expanded free end, which is slightly inflected at the tip. The cuneiform facet is long and narrow and entirely on the inferior surface, forming nearly a right angle with the ulnar facet, with which it is continuous (though in some specimens it is separated from it by a short interval); the latter is of triangular shape, and slightly concave. In the horse, the pisiform has a much greater vertical diameter and no neck; the ulnar and cuneiform facets are both on the proximal end, on nearly the same plane, and separated from each other by a deep notch.

The trapezium is a very small nodular bone, with its vertical diameter the principal one; proximally it has a minute contact with the scaphoid, and distally it presents an oblique facet for the posterior side of the head of the second metacarpal, projecting below the level of the distal face of the trapezoid.

The trapezoid is rather low, and very narrow in front, broader behind. Its position is rather more lateral than in the horse, and more of it is visible when the manus is viewed from the front. The proximal surface is somewhat convex, the distal nearly plane, and there is a small posterior facet for the trapezium. The trapezoid supports only metacarpal II., and there is no separate posterior facet for the magnum such as occurs in the horse.

The magnum is relatively high and narrow, in correlation with the moderate degree of expansion which the median digit has undergone. The proximal surface is in front divided, nearly equally, between the facets for the scaphoid and the lunar, the former slightly the broader, the latter more oblique in position, and the two meeting in an open angle, and forming a sharp ridge. Posteriorly the magnum is covered only by the lunar,

into a concave facet of which the narrow, elevated "head" of the magnum fits. The distal surface of the magnum is nearly plane, broad in front and narrow behind, and is occupied entirely by the third metacarpal, but on the radial side is a small facet for metacarpal II. The magnum of *Anchitherium*, as figured by Kowalevsky (No. 25, Pl. II., Fig. 1), is very different from that of *Mesohippus*, being low and very broad, and the lunar facet is relatively very wide; on the ulnar face there is in front but a single facet for the unciform, which occupies the whole height of the magnum, while in the horse this facet is divided into superior and inferior portions. Some specimens of *Mesohippus* agree with *Anchitherium* in this respect, others with *Equus*. In the latter genus, the magnum has become extremely broad and low, which especially affects the radial side, so that the scaphoidal facet is now much broader than the lunar. In particular, the posterior portion of the magnum, which is very narrow in *Anchitherium*, and still more so in *Mesohippus*, has become very wide in the horse.

The unciform is narrow and compressed, but very high, having nearly twice the vertical diameter of the magnum, and in consequence projecting far below the distal face of the latter. The proximal end exhibits a small facet for the lunar, and a much larger one for the cuneiform, which is reflected well down upon the postero-external face. Distally there is a large facet for metacarpal IV. and a much smaller one for metacarpal V. The facet for metacarpal III. is vertical and entirely lateral in position, being placed upon the radial side of the bone, and not at all distal. In *Anchitherium* (Kowalevsky, Pl. II., Figs. 1 and 9), the unciform is lower, and the distal portion much more produced posteriorly; the facet for metacarpal III. is very oblique in position. The unciform of the horse is very different from that of the Miocene genera; it is much lower, hardly projecting at all below the level of the magnum, which it exceeds but little in height; the lunar facet has become somewhat broader, and the facet for metacarpal III. almost entirely distal in position, forming a gently curved outline with the facet for metacarpal IV.; of course, there is no facet for a fifth digit; posteriorly the unciform is seen to rest upon the third metacarpal: in *Mesohippus* this is not the case.

The *metacarpus* (Pl. XXIII., Figs. 26-28, 30) consists of three

functional members, the second, third, and fourth, and one rudimentary, the fifth. Metacarpal II. is very slender, compressed, and elongated, with a much flattened shaft which is closely applied to that of the median digit, and which is arched forward. The proximal end is somewhat thickened antero-posteriorly, but very little wider than the shaft; it exhibits three well-marked facets, — a small one on the posterior or radial edge, for the trapezium; a larger, slightly concave, and truly proximal one for the trapezoid; and on the ulnar side a small facet for the magnum. The distal trochlea is very much compressed laterally and narrower than the inferior end of the shaft; the carina is very nearly median in position, not at all prominent, and entirely confined to the palmar side.

Metacarpal III. is by far the largest of the series, though it is relatively much narrower and more slender than in the later genera of the equine phylum. The shaft is flattened antero-posteriorly, and of transversely oval section; it is narrowest and deepest above, becoming broader and shallower distally. The proximal surface is nearly plane, but is not placed so nearly at a right angle with the long axis of the shaft as in the horse, rising gently toward the ulnar side. This facet for the magnum is broader in front than behind, — a difference which is more marked than in *Equus*, and is suddenly constricted in the middle. The proximal surface displays no facets for the trapezoid or unciform. The unciform facet is on the ulnar side of the head and presents altogether laterally; this facet is divided by a deep groove into anterior and posterior portions. The distal end is expanded laterally just above the trochlea, which is narrower; the carina is much stouter and more prominent than in the lateral digits, and extends farther upon the anterior face, but not so far as in *Anchitherium*.

Metacarpal IV. is more slender than No. III. and has a narrower and less thickened head. The unciform facet is nearly plane and of triangular shape, with the apex directed posteriorly. Upon the radial side there is a small facet for the overlapping projection of metacarpal III., and on the ulnar side another for the head of No. V.

The fifth metacarpal is represented by a rudiment which carries no phalanges. The head is as large as in No. IV., but the shaft is very slender and tapers rapidly to a point. The

unciform facet is narrow and slightly concave from side to side, the ulnar border rising somewhat higher than the radial.

The metacarpus of *Anchitherium* exhibits no very important differences from that of *Mesohippus*. The median digit is much broader relatively and appears also to be longer in proportion; the unciform facet is more obliquely placed, so as to present upward as well as laterally; the carina of the distal trochlea is somewhat more prominent, and continued farther up upon the anterior face of the bone. The second and fourth metacarpals are very much as in the American genus, but judging from the facet upon the unciform, metacarpal V. is still further reduced, and must have been concealed from view by No. IV., when seen from the front; in *Mesohippus* it is plainly visible in the anterior aspect. The carpo-metacarpal articulations have undergone no important modification from the condition found in the latter.

The metacarpus of the horse (see Fig. B, p. 336), on the other hand, presents some very important changes. The fifth digit has entirely disappeared, the second and fourth reduced to mere splint bones without phalanges. The median metacarpal has greatly increased in breadth and thickness, especially toward the radial side, and the distal carina has become very stout and encircles the entire trochlea, dorsal as well as palmar. The anterior unciform facet has become almost entirely proximal instead of lateral in position. Seen from the front, the carpo-metacarpal articulations seem to have undergone little change, but the great increase in breadth of the posterior portion of the head has brought the median metacarpal into contact with the trapezoid and unciform, thus supporting it on all of the distal carpals.

The phalanges of *Mesohippus* are very like those of *Anchitherium*. Those of the lateral digits are short, slender, and much compressed laterally; the unguals narrow and pointed. Those of the median digit are longer, very much broader, and more symmetrical in shape. The proximal one is relatively much shorter than in the horse; the groove for the metacarpal carina is confined to the palmar half, and the distal articular surface does not extend so far upon the dorsal side. The ungual phalanx is long, broad, flattened from above downwards, and pointed. It is not so much elongated as in *Anchitherium*, but very different in shape from the characteristic ungual of the existing *Equidæ*.

## VI. THE HIND LIMB.

The pelvis (Pl. XXIII., Fig. 31) of *Mesohippus* is very like that of the horse, with some differences of detail. The neck of the ilium is much longer and more slender, when viewed from the side, but rather broader when viewed from below, owing to the prominence of the pubic border, upon which a small rugose spine is developed. The plate is too much injured in the only specimen at my disposal to allow an accurate determination of its shape, but it is plain that it expands much less abruptly than in *Equus*, and apparently it is relatively much smaller than in that genus. The acetabulum is deep, with prominent edges, and the pit for the round ligament is smaller and more median in position than in the modern forms.

The ischium is long and quite straight; for most of its length it is much more slender and rod-like, and less curved upward than in *Equus*. The posterior portion is expanded and depressed, sending off from its outer side a long and sharp but low tuberosity. Above the acetabulum the border of the ischium is very slightly elevated into a crest, which terminates behind in a shallow groove for the internal obturator tendon. The obturator foramen is very much larger proportionately than in the living forms, and consequently the posterior expansion of the ischium much smaller.

Kowalevsky states that in *Anchitherium* the crest of the ischium is more rounded and thickened than in the horses, and that the sulcus for the internal obturator tendon, which is wanting in the horses, is profound (p. 15).

The femur of *Mesohippus* (Fig. A) is characteristically equine in appearance. The shaft is quite long and stout, in comparison with the other long bones, but slender as compared with the modern type. When viewed from the side, it presents a decided sigmoid curve. The head is small and nearly sessile, but rises somewhat above the bridge connecting it with the great trochanter: the pit for the round ligament is deep, but narrow and

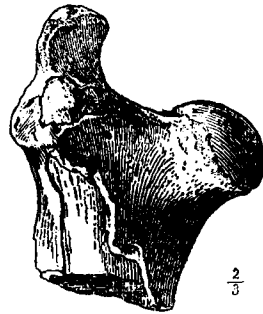


FIG. A. — Right femur of *Mesohippus*; anterior view.  $\times \frac{2}{3}$ .

short. The great trochanter is low, massive, and rugose in front, behind it rises into a high, stout hook, which projects far above the head; the digital fossa does not invade the shaft, but is formed by the recurved edge of the trochanter. The second trochanter is a long, rugose, and prominent ridge, and the third is moderately developed. The distal condyles, of which the outer is considerably the larger, are rather small and do not project strongly backward; the groove separating them is wide but shallow. The rotular trochlea is broad and shallow, with edges which are sharp and of nearly equal height. A long depression runs up the shaft above the trochlea. Above the external condyle, on the posterior side of the shaft, there is a deep pit for the plantaris muscle. In *Anchitherium* (de Blainville, *Palæotherium*, Pl. VII.) the femur is very like that of the American genus, but is somewhat stouter and straighter, and more equine in the details of construction.

In the horse, the femur has become very much stouter, and all the processes for muscular attachment more massive. The head is sessile, and the great trochanter approaches nearer to it, and the pit for the round ligament is much larger. These changes, as Kowalevsky has pointed out, involve to a considerable degree the loss of rotatory movements, and the confining of the motion of the femur to the vertical plane. The condyles are much more massive and prominent; the trochlea is oblique to the long axis of the shaft, and its inner border greatly elevated and enormously thickened.

The tibia (Pl. XXIII., Figs. 32, 33) of *Mesohippus* is long and very slender, and the shaft has a slight sigmoid curvature. The femoral facets are slightly concave and are placed obliquely to the long axis of the bone, inclining downward and backward. The cnemial crest is long and massive, and has the usual deep tendinal sulcus on its outer edge. The distal end is quite narrow, and the astragalar facets are deep and very oblique in position, with a high intercondylar ridge, which is more prominent behind than in front; the inner malleolus is only moderately developed.

The proximal end of the *fibula* is not preserved in any of the specimens; the distal end is sometimes co-ossified with the tibia, as is also a considerable portion of the shaft; in other specimens it is free. This end is expanded to form a stout

external malleolus, which exhibits two facets, — an internal one for the astragalus, and on the posterior side of the distal surface a small one for the calcaneum.

In *Anchitherium*, the tibia and fibula are very much as in the American form, but the former is straighter and decidedly more massive.

In the horse, the tibia has become nearly straight and very heavy; the femoral facets are nearly at right angles to the long axis of the shaft; the cnemial crest is very massive, but does not extend so far down the shaft as in *Mesohippus*; the distal end of the fibula is indistinguishably fused with the tibia, but preserves its facet for the calcaneum, at least in some cases.

The tarsus of *Mesohippus* (Pl. XXIII., Figs. 34, 36–38) is very equine in appearance and construction. The calcaneum is rather long and quite slender and compressed, the dorso-plantar diameter being conspicuously small; the two borders are straight and nearly parallel. This is true also of *Equus*, but in this genus the short, massive, and deep tuber has a very different appearance. The distance from the superior or “ectal” astragalar facet to the distal end is very considerable; this facet forms a high crest, descending obliquely toward the tibial side, and on its posterior aspect there is, as Osborn has pointed out (No. 41, p. 546), a very distinct fibular facet. This ectal astragalar facet is slightly prolonged at its infero-external angle. The sustentaculum is very prominent and massive, but has only a proportionately narrow facet for the astragalus. The inferior astragalar facet is narrow and of limited antero-posterior extent. The cuboidal facet is narrow, slightly concave, and obliquely placed with reference to the long axis of the bone, descending downwards and forwards. Posteriorly it is very little recurved or inflected toward the tibial side.

The calcaneum of *Anchitherium* is more equine in shape, as is especially marked in the increased dorso-plantar diameter of the tuber calcis and the more pronounced beginning of the “facette surnuméraire” by a prolongation of the infero-external angle of the ectal astragalar facet. The inferior astragalar facet, on the other hand, is less equine, being much more extended antero-posteriorly than in *Mesohippus*. The sustentaculum is more prominent and massive than in the latter genus, and the cuboidal facet but little recurved posteriorly.

In *Equus* the calcaneum has become relatively shorter and stouter, the dorso-plantar diameter being especially increased; the sustentaculum is very prominent and enlarged both transversely and from above downwards. There are two ectal astragalar surfaces, the supernumerary facet being completely separated from the principal one. The cuboidal facet is divided into two portions by a ridge, the smaller anterior one running from before backwards, and the larger posterior one directed nearly transversely. This curvature and transverse extension of the distal end, together with the enlarged sustentaculum, give to the posterior aspect of the horse's calcaneum a very different appearance from that seen in *Mesohippus*, though an indication of the modern arrangement is clearly apparent in the older genus.

The astragalus of *Mesohippus* has a narrow, deeply incised, and obliquely directed trochlea, the condyles running downward and outward. The internal condyle is longer than the external, extending beyond it both above and below, and inferiorly reaching to the navicular facet, while the external condyle is separated from this facet by a considerable interval. The surface for the external malleolus is narrow and in some specimens quite strongly everted as a distinct process at its lower end; the facet for the internal malleolus is very much broader, and terminates inferiorly in a pit, into which the tip of the malleolus fits in extreme flexion. Internal to this is a prominent tubercle for the attachment of the astragalo-metatarsal ligament. On the plantar side of the astragalus three calcaneal facets are visible; the ectal is very deeply concave, and at its infero-external angle there is a small, plane facet, the beginning of the supernumerary facet. The ectal facet is separated by only a narrow interval from the sustentacular, and in some specimens, notably those of the larger animals, the two are in contact. The sustentacular facet is long, narrow, and nearly flat; distally it forms a projection of the posterior margin of the navicular surface. The inferior calcaneal facet is very small and elongate oval in shape. The distal surface for articulation with the navicular is relatively narrow, and of irregular shape. It is slightly concave from side to side, and the external margin projects strongly downward; a similar projection is formed on the posterior margin. As Osborn has pointed out (No. 41, p. 546), the fossa in the navicular surface

varies much in depth and distinctness. The cuboidal surface is very small, and abruptly truncates the projection of the external margin already mentioned.

The astragalus of *Anchitherium* is very much like that of *Mesohippus*, but is relatively broader, especially the distal end, and the neck is shorter, so that the external condyle projects downwards as far as the navicular surface. The projection of the external margin of the latter surface is less pronounced than in *Mesohippus*; that from the plantar margin rather more so. According to Kowalevsky, there is no fossa in the navicular facet: "J'ai examiné plus de quarante astragales de l'*Anchithérium* sans pouvoir trouver un seul qui présenterait cette échancrure caractéristique, toute la surface tarsienne est invariablement d'un poli uniforme. Sur deux astragales seulement j'ai pu remarquer à l'endroit où se trouve l'échancrure chez les chevaux une légère rugosité" (No. 25, p. 39).

The astragalus of the horse has become decidedly broader, the trochlea more widely open, and the condyles thicker; the neck is shorter, and the condyles overhang so far as to project below the navicular surface. The supernumerary calcaneal facet is quite widely separated from the ectal. The surface for the external malleolus is broader. The anterior margin of the navicular facet forms a nearly straight line, there being no projection of the outer edge, but the posterior projection is very strongly developed. The fossa of the navicular facet is very distinct. The cuboidal facet is more completely distal than in the earlier forms.

The cuboid of *Mesohippus* is high and narrow, but deep antero-posteriorly, and with a short but broad and rugose posterior hook. The proximal surface is somewhat oblique to the vertical axis of the bone, descending anteriorly; it is obscurely divided into two portions, of which the anterior is the broader, but there is no such difference as in *Anchitherium*; the two are in the same antero-posterior line. The astragalar facet is very small and placed on the tibial side of the cuboid. There is no antero-superior facet for the navicular, the two bones being separated at this point by the downward projection of the astragalus, but there is a well-marked antero-inferior facet. Posteriorly there is a small projecting process, which carries two facets, a superior one for the navicular and

an inferior one for the ectocuneiform. The distal surface is much smaller than the proximal and bears a slightly convex, rounded facet for the fourth metatarsal; on the tibial side there is a very small, entirely lateral facet for the third metatarsal, which is enabled to touch the cuboid laterally, because the latter projects below the ectocuneiform, having a height greater than that bone and the navicular combined.

In the cuboid of *Anchitherium* the calcaneal facet is more distinctly divided into anterior and posterior portions, the latter being very much narrower and somewhat recurved. The facet for metatarsal III. is of very different shape, being broader in front and narrower behind, and that for metatarsal IV. is more oblique in position, presenting downward as well as inward. The whole bone is more massive and thickened, and the posterior projection longer and more rugose.

In the horse, the cuboid has become very different. The calcaneal facet is now very distinctly divided into anterior and posterior portions, though the two are still continuous, and the latter is strongly incurved. There is a large antero-superior facet for the navicular, the astragalus no longer intervening between the two; the posterior facet for the navicular and ectocuneiform is much more prominent than in *Mesohippus*. The distal surface also exhibits important changes. The facet for metatarsal III. is very much larger and altogether distal in position, while that for metatarsal IV. has become very oblique and rather more lateral than distal; an additional facet for this metatarsal appears on the postero-internal angle. The cuboid does not descend below the ectocuneiform.

The navicular of *Mesohippus* is low and broad, though relatively higher and narrower than in the existing genus. The proximal surface is concave and the posterior margin considerably elevated at its inner and outer angles; between the two is the wide depression for the corresponding process from the astragalus. There is a small triangular space in the navicular facet, which extends toward, but does not reach, the fibular margin; this represents the fossa which occurs in the horse and is more clearly shown than the corresponding structure on the astragalus. There is no anterior facet for the cuboid: when the two bones are placed in position, they divaricate anteriorly; the posterior cuboidal facet is quite large and is continuous

with that of the ectocuneiform. The distal surface has two facets, for the ectocuneiform and the coalesced meso- and entocuneiforms respectively. The former is broad, and sends out a narrow posterior prolongation. The latter is much smaller and regularly convex from before backwards, and does not show any definite separation into facets for the two elements of the compound cuneiform.

The navicular of *Anchitherium* is broader and lower, and the antero-external angle is very much produced, encircling the cuboid in a curious way (Kowalevsky, Pl. III., Fig. 17). The posterior prolongation of the facet for the ectocuneiform is curved sharply toward the fibular side, and the facet for the first and second cuneiforms are in contact, though their limits are defined by a ridge. There is no fossa in the astragalar surface.

In *Equus* the navicular is still broader and lower; it has quite a large anterior facet for the cuboid, and the posterior facet has become more prominent. The elevations of the posterior proximal margins and the depression between them are hardly more marked than in *Mesohippus*, but have become decidedly more massive and rugose. The fossa in the astragalar surface is deep and conspicuous and continuous over the fibular margin. The facet for the coalesced cuneiforms, especially for the entocuneiform portion, has become decidedly larger; but the principal increase in the breadth of the navicular is, as Kowalevsky has suggested, in that portion of it which supports the ectocuneiform.

In *Mesohippus*, the ento- and mesocuneiforms have coalesced. The disposition of the equine tarsus to become reduced in breadth, but increased in depth, and to close behind so as to form a circle, has been pointed out by Rütimeyer (No. 46, p. 17), and is already very apparent in the White River genus. The entocuneiform is high and compressed, and sharply everted so as to be in contact with the cuboid; it greatly exceeds the mesocuneiform in vertical height, rising much above it on the navicular and descending much below it distally. The navicular facets of the two elements are confluent, but the distal facets are very distinctly separated; of the latter there are two only, one on the distal surface of the mesocuneiform for the head of the second metatarsal, and one on the anterior face of the entocuneiform for the hinder edge of the same metatarsal. There

is no connection with the median digit. The ectocuneiform is high and narrow proportionately; its proximal and distal surfaces are D-shaped, with the curve directed anteriorly, and a short, narrow tongue directed posteriorly from the hinder edge. The navicular surface is emarginated by a small fossa on the fibular edge; the distal facet also shows a very shallow oval fossa, but the articular surface of the tongue, or posterior prolongation, is continuous with that of the body of the bone, nor is its free end transversely extended. There is a small and sessile antero-inferior facet for the cuboid, and a larger postero-superior one. There is also on the tibial side of the posterior prolongation a small facet for the second metatarsal.

In *Anchitherium*, the ecto- and mesocuneiforms are co-ossified, and the entocuneiform is free. The former is broader and lower than in the American genus, and of very different shape, as is especially shown in the fact that the posterior tongue or beak is directed toward the fibular side, instead of backward (cf. Pl. XXIII., Fig. 36, with Kowalevsky, Pl. II., Fig. 23). There is on this beak no facet for the second metatarsal.

In the horse, the ento- and mesocuneiforms are co-ossified, as in *Mesohippus*, though in some specimens all three of the bones are distinct, and Forsyth Major states that, as a rare exception, the ecto- and mesocuneiforms unite (No. 18, p. 62). The ectocuneiform is greatly increased in breadth and is very low; the beak is very much wider, and bears at its posterior end a distinct broad facet for metatarsal III., which is separated by a wide fossa from the anterior one; the latter is reduced in antero-posterior extent, as compared with that of *Mesohippus*. There is normally no facet on cu. 3 for the second metatarsal; but Kowalevsky reports finding it rarely, and then associated with a reduction in width of the facet for metatarsal III. upon the beak (No 25, p. 45). The mesocuneiform presents two distal facets, for the second and third metatarsals respectively. As a whole, the tarsus of *Equus*, compared with that of *Mesohippus*, has decreased in height and increased in breadth and depth, and is especially modified by the connection of the median metatarsal with all three of the distal tarsal elements.

The metatarsus of *Mesohippus* (Pl. XXIII., Fig. 39) consists of the second, third, and fourth metatarsals, the fifth having completely disappeared. Metatarsal II. is very much compressed

laterally, and has a long, very slender shaft. The head is expanded antero-posteriorly and bears two facets, one proximal for the mesocuneiform, the other oblique and posterior for the entocuneiform: there is also a small lateral facet for the tongue of the ectocuneiform, but there appears to be no anterior contact with the latter in some specimens, though there clearly is in others. Connection with the median metatarsal is by means of ill-defined facets. The distal end is much compressed and slightly recurved, with a sharp keel on the plantar side of the trochlea; the portion of the trochlea medial to the keel is decidedly more prominent than the external portion.

The third metatarsal is very long and slender; proximally it is narrow and deep, distally it becomes broader and flattened antero-posteriorly. The head bears a facet for the ectocuneiform, which is broad, with a rounded anterior margin and a narrow posterior tongue or beak. The articular surface is continuous over the proximal end, being only slightly interrupted by a small fossa. The facet for the cuboid is small and somewhat oblique, but more lateral than proximal in position. There are two small facets for the fourth metatarsal, which are placed very near together. The distal end of the shaft is quite broad and has two lateral tubercles for ligamentous attachments; the trochlea is narrower and is terminated above by a deep pit. The carina is more prominent than on the median metacarpal, and there is a very obscure indication of it upon the anterior face. The proportions of this digit vary considerably in the different specimens, being decidedly stouter in some than in others.

The second metatarsal rises higher than the third, and the third higher than the fourth. The latter is slightly stouter than the second and has a more thickened and rugose head; it bears a single facet for the cuboid, but there is in some individuals a posterior prolongation of this, which may be regarded as the beginning of a second one.

In the metatarsus of *Anchitherium* the median digit is decidedly larger proportionately than in the American form, and in particular the head is transversely extended; its articulations are also different, in that the cuboidal facet shows a stronger tendency to become proximal, and a small connection with the mesocuneiform is established. Distally the shaft is still broader

than the trochlea, but there is no pit above the latter. The head of metatarsal IV. is decidedly more massive, and the difference in the shape and size of the shaft between this and metatarsal II. much more marked (see Kowalevsky, No. 25, Pl. II., Fig. 28).

In *Equus* there are very important changes aside from the great development of the median digit, and the reduction of the lateral ones to splint bones, accompanied by the loss of their phalanges. The head of metatarsal II. now has the facet for the entocuneiform proximal, and that for the mesocuneiform oblique and anterior.

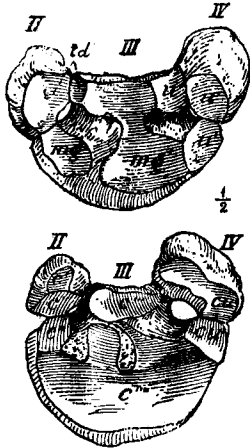


FIG. B. — *Equus Burchelli*. Proximal end of left metacarpus and metatarsus (after Kowalevsky).  $\times \frac{1}{2}$ . *td'*, facet for the trapezoid; *mg'*, for the magnum; *u'*, for the unciform; *c'*, for the ento-; *c''*, for the meso- and *c'''*, for the ectocuneiform; *cu'*, for the cuboid.

The head of metatarsal III. has four distinct facets, three anterior for the meso- and ectocuneiforms and cuboid respectively, the latter altogether proximal in position; the fourth facet is posterior and for the beak of the ectocuneiform, and is separated by a large fossa from the anterior surface for that bone. The transverse breadth of the posterior facet is very striking as compared with the same structure in *Mesohippus*. The head of metatarsal IV. is provided with two distinct facets for the cuboid. The distal end of the shaft of the median metatarsal is not produced laterally beyond the trochlea, and there is no pit above the latter.

The phalanges of the pes in *Mesohippus* appear to be somewhat more massive than those of the manus; whether they are shorter the available material does not enable me to decide.

## VII. RESTORATION OF MESOHIPPIUS (Fig. C).

The successive genera of the horse series show for the most part a steady increase in size from the tiny *Hyracotherium* of the Wasatch Eocene to the great animals of Post-Pliocene times. *Mesohippus*, however, has not reached a large stature, advancing

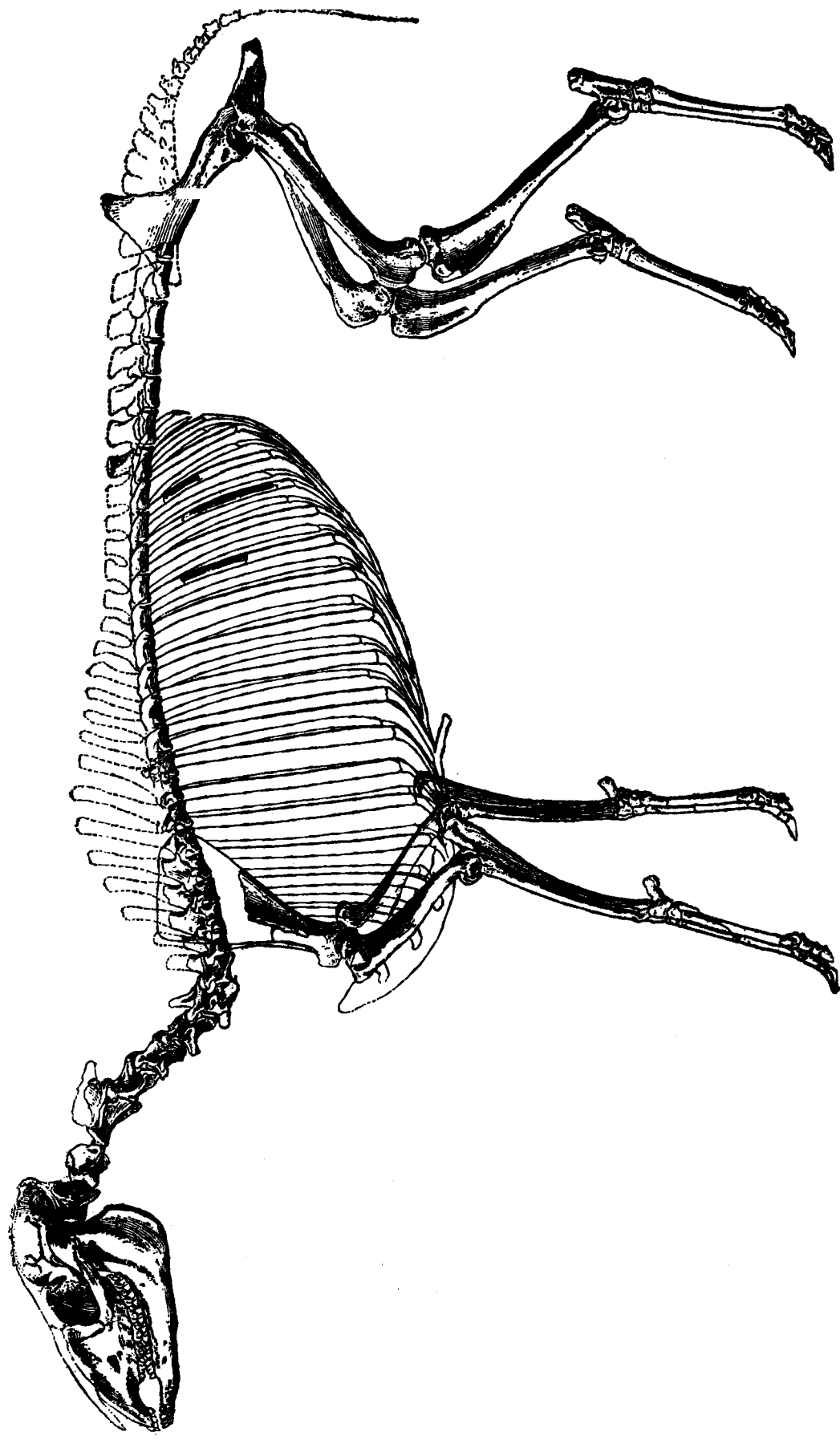


FIG. C. — Restoration of *Mesohippus Bairdi*; about two-ninths natural size.

beyond its Bridger predecessor, *Pachynolophus*, much less in regard to size than in morphological differentiation; the larger species of the Bridger genus are but little inferior in this respect to the smaller species of the White River form. In spite of its comparatively high degree of differentiation, *Mesohippus* was a very small animal compared with the recent horses, about the size of a Newfoundland dog. The skeleton is essentially like that of existing *Equidæ* in character and appearance, but presents many striking points of difference.

The skull is much smaller, and in particular the facial region is shorter, shallower, and more tapering. The orbit is relatively very large, not enclosed behind, and situated very far forward and low down in the face. This position of the orbit brings about other noticeable differences in the character of the skull, as for example the great elongation of the zygomatic arch, and especially of the malar or jugal portion of it. The arch is also quite slender and the masseteric crest is but slightly developed and does not extend forward upon the maxillary. The short-crowned molars render the alveolar portion of the maxillary very low and contracted, in sharp contrast to the alveolus in those genera which have prismatic teeth, and owing to the very small size of the canine and incisor teeth, the premaxillaries and the symphysis of the lower jaw are short and slender, which in its turn modifies the shape and size of the anterior narial opening. The ascending ramus of the mandible is relatively low and of quite a different shape from that seen in *Equus*, and the condyle is not placed nearly so far above the level of the molars.

The neck is quite long, but the vertebræ are much less massive, not so decidedly opisthocœlous, and with less strongly developed processes than in *Equus*. The neural spine and odontoid process of the axis are of entirely different shape in the two genera, and in the Miocene form the spines on the fifth and sixth vertebræ are much higher. The back is long, and, as appears from the faces of the posterior dorsal and lumbar vertebræ, much more arched than in the horse; the spines, so far as they are preserved, are more slender and compressed. If we may judge from the comparatively few fragments which have been preserved, the ribs were more slender, rounded, and less flattened than in the horse, — a peculiarity which is common to nearly all of the earlier ungulates.

The limbs would appear to be quite as long as in the horse, or even somewhat longer, in proportion to the size of the body ; but the relative lengths of the constituent parts are quite different in the two genera. The scapula seems to have been rather broad, somewhat as in *E. asinus*, and has but a small coracoid process. The humerus is rather long, but with a slender shaft, and with the tuberosities and deltoid ridge and hook not strongly developed. The conformation of the proximal end of the humerus is entirely different from that which occurs in the true *Equidæ*, and is closely similar to that of the White River camel, *Pæbrotherium*. The ulna and radius are likewise rather long and slender ; the shaft of the former is complete and uninterrupted, though much reduced in diameter ; the two bones are only slightly co-ossified at the distal end. The carpus is decidedly higher, but narrower than in the recent forms, and the arrangement of its component parts quite different, in correlation with the greater number of functional digits. I have seen no complete specimens of the metacarpals, and so their length is conjectural. In width and antero-posterior depth, the third metacarpal is much inferior to that of *Equus*, and its carpal articulations quite different. On the other hand, the splint bones of the horse are represented by the second and fourth functional digits in *Mesohippus*, while the fifth digit of the latter is a splint bone. The phalanges are much shorter and very much less massive, and in particular the ungual phalanx of the third digit is very small when compared with the massive bone of recent forms, though its shape is very suggestive of equine affinities.

The pelvis is in general very like that of the horse, but with some marked differences ; the sacral plate of the ilium is somewhat more expanded vertically and less everted horizontally ; the crest above the acetabulum is more prominent ; the ischium is somewhat shorter and nearly straight, the posterior end curving upward very much less. The femur has a stout shaft, as compared with that of the humerus, but very slender in proportion to the horse's femur ; it is quite long relatively to that of the latter animal ; the trochanters are much less massive, and the condyles smaller and project backward less strongly ; the rotular trochlea is wider, shallower, and less prominent, and has its two margins of nearly equal height,

while in the recent type the trochlea is massive, very prominent, and obliquely directed, the inner margin being much higher than the outer. The tibia is long, but very slender, except in the upper portion, which is deepened antero-posteriorly by the large cnemial crest. The fibula may have been complete; at all events, the distal end is quite large, and in several of the specimens a considerable length of the very slender shaft is attached to it. In some individuals the distal ends of the tibia and fibula are co-ossified, in others they are separate, and this does not appear to be altogether a matter of age, but rather of individual variability. The tarsus is relatively higher and narrower, and of less antero-posterior extent than in the recent forms; the calcaneum longer and less massive. The metatarsus is of nearly the same length proportionately as in the horse, but the third digit is very much less enlarged, while the second and fourth, as in the manus, are functional and of nearly the same length as the third. The enlargement of the median metatarsal has proceeded somewhat farther than in the case of the corresponding metacarpal.

As the restoration is drawn from several individual specimens, reduced to a common average standard, it is impossible to give the relative dimensions of the parts with any great accuracy, but, on looking over a large number of specimens, it is clear that the hind limbs are decidedly longer, in proportion to the fore limbs, than in the recent species. In the figure this is compensated by the degree of flexion given to the posterior extremities, though very possibly the hind quarters were much more elevated, in somewhat the same fashion as in the tragulines, though of course in a less marked degree.

There are thus many points of difference, as regards the proportionate development of the various parts of the skeleton, between *Mesohippus* and *Equus*, and these divergences, more especially the smaller and differently shaped head and the very slender tridactyl feet, give to the older type quite another physiognomy than that of the recent representatives of the group, even without taking into consideration its very much smaller size. Nevertheless, no one can examine the skeleton of the Miocene genus without being struck by its essentially equine nature; in the teeth alone is the fundamental similarity of plan not apparent at the first glance, though even here a careful

examination reveals the connection very clearly. This similarity extends also to the earlier members of the equine series, for *Hyracotherium* from the lower Eocene belongs as unmistakably to this line as do any of the later genera. Indeed, one of the most striking features of this phylum is the way in which its essential features, and even many apparently insignificant details, are, as it were, sketched out in very early times and then gradually elaborated, without deviation and without retrogression, until the final term of the series is reached.

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#### THE OSTEOLOGY OF *LEPTOMERYX EVANSI* LEIDY.

This problematical little selenodont is very abundantly represented in the White River beds by fragments of jaws and teeth; but owing to their small size and extreme fragility, well preserved skulls and parts of the skeleton are very rare. However, by combining the material contained in the Princeton Museum with that in the Academy of Sciences in Philadelphia, and some beautifully preserved specimens which Professor Cope has most kindly placed at my disposal, I am enabled to give a fairly complete account of the structure of this genus.

#### I. THE DENTITION.

1. *Upper Jaw.* The skulls of all the specimens which I have examined are broken away anteriorly, so that the premaxillary region is lost, and it is therefore impossible to say whether *Leptomeryx* had any remains of upper incisors, but from the character of the lower incisors it seems probable that the superior set had vanished. From the analogy of *Amphitragulus* and the tragulines, it might seem likely that the upper canine, at least in the males, was a long, recurved blade. But, on the other hand, no such tooth has ever been found associated with *Leptomeryx* remains. None of the specimens shows any trace of the first upper premolar, and if present at all, it must have been separated by a considerable diastema from the second. *Pm.* 2 is a sharp, compressed, cutting blade, which seen from the outside has a considerable resemblance to the corresponding tooth of

*Tragulus*, but the median ridge is much more pronounced and the depressions in front of and behind it much deeper. A more important difference is in the large internal cusp (deuterocone) which in *Tragulus* is a mere rudiment. *Pm.* 3 is similar, but the deuterocone is still larger, and from its anterior edge there passes a ridge to the outer wall of the crown enclosing a small valley. In some specimens, however, which agree exactly with the typical *Leptomeryx* in size and in the construction of the upper molars, the premolars are quite as simple as in the tragulines. *Pm.* 4 is of the typical ruminant pattern, consisting of an internal and an external crescent; the horns of the inner crescent are separated from the outer wall and are connected with it only at an advanced stage of wear.

The outer side of the tooth resembles that of the preceding premolars.

The molars are composed of four crescents and closely resemble those of the smaller deer. They differ from the molars of *Tragulus* in the greater thinness and compression of the crescents, and in the presence of well-developed basal pillars between the internal lobes; the median and anterior external pillars are also very prominent, while in *Tragulus* the anterior one is but feebly developed, and the median one is absent. In *Dorcatherium* (*Hyæmoschus*), on the other hand, the external pillars are very well marked, but here there is no internal pillar and the lobes of the tooth are more massive and conical, less completely crescentoid than in *Leptomeryx*. In the latter the internal crescents are separated from each other in the unworn tooth by a considerable interval. The valleys are perfectly simple, and not complicated by any projections from the walls. The inner side of the crown is covered with a very finely wrinkled enamel, but the external side is smooth and polished. The cingulum is confined to the anterior and posterior faces of the crown.

2. *Lower Jaw.* The incisors are somewhat peculiar and not at all traguline in character. The median incisor is procumbent, long, straight, and narrow; in shape it is more like that of *Moschus* than that of the deer or chevrotains, but is very much narrower, more elongate, and very different from the corresponding tooth in *Tragulus*. The second and third incisors are shorter, somewhat more spatulate, and are curved toward

the outer side of the jaw. They are less procumbent than the median, and project slightly upward. They are much like the corresponding teeth in *Coassus*. The third is somewhat shorter and broader than the second. The crown of the canine is not preserved in any of the specimens, but its fang shows that it had taken on the functions of an incisor, and that it was slightly larger than the external member of that series.

The first premolar is a very small tooth, which is separated by a considerable diastema from the canine, and by a shorter one from the second premolar. The crown is a perfectly simple, erect, and compressed cone, and were it not for its position in the jaw, might easily be taken for a small canine. This tooth is inserted by a single fang.

The succeeding premolars increase successively in size and complexity from the second to the fourth. When looked at from the external side, they are all very much alike except in size, and are composed of a high, compressed, and very acute cone, with sharp-pointed anterior and posterior basal cusps, except that in *pm.* 2 the anterior cusp is wanting. On the inner side, however, there are more important differences. In *pm.* 4, there is a thin crest which runs back from the median apex of the tooth parallel to its external wall and enclosing a deep valley with the latter; an indication of this same structure, but not nearly so marked, is visible on *pm.* 3. Compared with the premolars of *Tragulus*, those of *Leptomeryx*, both upper and lower, are in most specimens very much more complicated.

The inferior molars are at first sight much like those of *Tragulus*, but there are some important differences. Schlosser has pointed out a peculiarity which occurs in all tragulines: "Die unteren Molaren sind ausserordentlich charakteristisch. Sie haben in der vorderen Hälfte auf jedem Monde eine starke, von der Spitze nach hinten zu herablaufende kammförmige Leiste" (No. 47, p. 73). These characteristic crests are usually, but not invariably, present in *Leptomeryx*, and often occur on the posterior crescents as well. In this genus also the valleys are wider and deeper than in *Tragulus*, and the talon of the last molar decidedly larger; it consists of two distinct cusps, of which the external one is the larger, and is separated from its fellow by a deep cleft. There are no basal pillars on the lower molars. All of the inferior molars and premolars

are covered with a finely wrinkled and minutely tuberculated enamel.

The milk dentition is decidedly traguline in character.  $\underline{D}^4$  is molariform, but very small, and the median internal and external pillars feebly marked;  $\underline{d}^3$  consists of three external cusps, of which the anterior is very long, compressed, and trenchant, which is much larger than in *Tragulus*, and a small postero-internal crescent, from which a faint ridge runs forward; this ridge is also better developed than in *Tragulus*.  $\overline{D}^4$  is composed of three pairs of crescents, of which the anterior pair are quite small and much like the talon of  $\overline{m}^3$ .  $\overline{D}^3$  is much like the premolar which succeeds it in the permanent set.

The dentition of *Leptomeryx* is on the whole most like that of the tragulines, especially in the construction of the molars and the milk dentition; on the other hand, the incisors are very different, and the premolars much more complex, though less so than in the *Cervidæ*.

## II. THE SKULL.

The skull of *Leptomeryx* is peculiar in several respects, and with many points of resemblance to that of the chevrotains, presents almost as many differences. As in the primitive ungulates generally, the cranium is long, narrow, and low, the eye very far forward in the face. The occiput is low, and the upper contour of the skull curves regularly upward and forward to a point just behind the orbits and thence downward to the face. The orbits are rather smaller than in *Tragulus*, are situated higher in the face, and project somewhat more strongly outward. As in that genus, they are very deep and are posteriorly separated only by a thin interorbital septum, so that the optic foramina are nearly or quite confluent—a peculiarity which is shared by some of the small antelopes and by *Pæbrotherium*.

There appear to be two types of skull represented among the specimens: in one, that figured by Leidy (No. 33, Pl. XIV.), the occiput is low and rather broad, and the sagittal crest is very short, hardly longer than in *Tragulus*. The second type, which perhaps belongs to a species as yet unnamed, has a higher, narrower occiput, and a much longer sagittal crest with narrower forehead and less abruptly diverging supraciliary ridges.

In other respects it is not necessary to distinguish between the two.

Examining the skull more in detail, the following structures present themselves. The basi-occipital is broader and flatter than in *Tragulus* and tapers more regularly forward; in the chevrotains the enormous size of the tympanic bullæ reduces the basi-occipital and basi-sphenoid to a mere rod, which is keeled in the median line. In *Leptomeryx* this keel is not present, but we find a pair of small surfaces for muscular attachments, much as in the deer. The condyles are small, sessile, and less widely separated than in the tragulines. The exoccipitals are low and rather narrow, and are flat or even concave from side to side, in sharp contrast to the very convex surface of the smaller tragulines. The supra-occipital is, in one type of *Leptomeryx* skull, quite high; in the other much lower; in both it extends well over upon the sides of the cranial cavity and is terminated by a projection which is the hindermost part of the skull, whereas in *Tragulus* the upper margin of the foramen magnum projects further back. The lambdoidal crest is much more prominent than in the tragulines. The foramen magnum is also higher and somewhat narrower than in the latter. The paroccipital processes are small, but are relatively longer, stouter, and less compressed than in *Tragulus*; they stand but very little in advance of the condyles, from which they are separated by deep but narrow fossæ.

The basi-sphenoid is broader than in *Tragulus*, but does not extend so far forward between the pterygoids. The alisphenoid is directed nearly horizontally, but there is a curious angulation or ridge in it, from which a portion of the bone passes upward, bounding the anterior edge of the temporo-sphenoidal lobe of the cerebrum; the pterygoid plates of the alisphenoids are, unfortunately, broken away in all of the specimens. The horizontal portion is much longer than in the tragulines and much more distinctly separated from the glenoid cavity. The orbito-sphenoids are much as in the tragulines, and form a thin and fragile interorbital septum.

The tympanic bullæ differ from those of the tragulines in a very important and characteristic way; they are very much smaller in every dimension, but especially in the vertical direction; they are not filled with cancellated tissue, but are hollow,

and the walls are composed of very dense, flinty-looking bone. The meatus auditorius is a long tube, with relatively very large diameter, which extends more decidedly backward and less upward than in the tragulines. The postero-external angle of the bulla shows a rather wide and shallow styloid groove. So far as I can interpret the sutures, there appears to be a broad surface of the petiotic exposed between the squamosal and the occipital ; but if so, it lies entirely in the occipital plane and not on the side.

The parietals are very long and form almost the entire roof of the cranium ; they are much longer and narrower than in *Tragulus*. This narrowing is partly due to the fact that the brain itself is narrower, and partly that the squamosals encroach much more upon them. In front of the latter, the parietals send down descending processes to the sphenoids. The sagittal crest varies in length, but is always longer than in the tragulines. Anteriorly the parietals diverge somewhat to receive the frontals and are thus rather longer on the sides than in the median line.

The squamosals are very long and high proportionately, and form most of the side walls of the cranial cavity. The root of the zygomatic process is stouter, but less extended antero-posteriorly, and the process itself is longer and heavier than in *Tragulus* ; the zygoma rises slightly forward, whereas in the recent genus it descends anteriorly. The glenoid cavity is very different in the two forms ; in the existing type, it is a broad, flat surface, with nothing deserving the name of a post-glenoid process ; in *Leptomeryx* "its fore part is nearly straight transversely, and inclines slightly outward from its inner extremity, and slopes convexly backward and outward into a comparatively deep concavity, bounded behind by a post-glenoid tubercle proportionately stronger than in the deer" (Leidy). The post-tympanic process is also more distinctly developed than in *Tragulus*. The jugal has a nearly straight course, and is relatively a very large bone, with much greater vertical diameter than in *Tragulus* ; the masseteric crest occupies nearly the same position as in that genus, but is not nearly so well developed. There is quite a long post-orbital process, but it is shorter than in the existing genus, and does not quite reach the corresponding process of the frontal. The lachrymal, on the

other hand, is distinctly smaller than in the tragulines, and has no pit ; it articulates with the frontal, maxillary, and jugal, but is separated from the nasal by a small vacuity which is developed at this point, as in the deer and many other ruminants. There is a single large lachrymal foramen placed within the rim of the orbit. The frontals are shorter and broader than in the tragulines. They extend farther behind the orbits, but not so far in front of them as in those animals, and thus are concerned more in roofing the cranial cavity and less in covering the nasal cavity. Except for their smaller size and greater elevation in the face, the orbits have very much the same position that they occupy in *Tragulus*, their anterior rim being over the first molar.

The nasals are not preserved in any of the specimens which I have seen. The maxillaries are long and low, especially the alveolar part, which, however, is higher than in *Tragulus*, and the facial portion which forms the side of the nasal cavity is also higher than in that genus. The palatine processes of the maxillaries are narrow and slightly concave from side to side. The molars are arranged in gently curved lines, which give the hard palate its greatest width at about the first true molar.

Unfortunately the premaxillaries are broken away in all of the available specimens, so that those very characteristic parts of the skull cannot be described. The posterior nares are situated far back, and the roof is formed by the palatines for some distance behind the last molar, as in the tragulines, but the lateral palatal notches are shallower and wider than in those animals, and the palatines are continued farther forward in the roof of the mouth ; the pterygoids do not extend so far back and are more widely separated from the tympanic bullæ.

The lower jaw is very peculiar, especially for the great breadth of the ascending ramus ; the angle is strongly prominent, giving to this region of the jaw a very different appearance from that of *Tragulus*, and somewhat like *Cainotherium*, but differing from the latter in being regularly curved and not notched ; its margin is also somewhat inflected. The masseteric fossa is deep and placed high up, as in *Pæbrotherium*. The coronoid process is stout and apparently vertical in position. The condyle is shaped very much as in the chevrotains, but

risks much higher above the level of the teeth and projects more directly vertically and less posteriorly. The horizontal ramus is slender and shallow, with a nearly straight inferior border. The symphysis is quite long and differs from that of *Tragulus* in being much less sharply compressed inferiorly, and in having its superior margins erect, not flaring and everted.

The *foramina* of the skull of *Leptomeryx* are, on the whole, most like those of the tragulines, but not without some important differences. The optic foramina are confluent and situated far forward; the foramen lacerum anterius is relatively small; the foramen rotundum has not coalesced with the foramen lacerum anterius, as it has in *Tragulus*, but is situated close to the foramen ovale. Owing to the small size of the auditory bulla, the foramina in this region are very different from those of the chevrotains, the foramina lacerum medius and posterius being large, and the carotid canal not grooving the side of the bulla. Post-glenoid, stylo-mastoid, and condylar foramina are present. At least one large venous foramen pierces the parietal near the sagittal crest. The infra-orbital foramen is placed very low down, just above *p.* 2. The foramina in the anterior part of the orbit are very characteristic in the tragulines, and are thus described by Rüttimeyer: "Von einer Fossa sphenomaxillaris, wie sie sonst den Wiederkäuern zukommt, ist eigentlich bei Tragulina nicht zu reden, da der Alveolartheil des Oberkiefers so niedrig ist, dass er nur als Boden der Augenhöhle dient, ohne dieselbe zu verengen. Nur der trichterförmige Eingang des Infraorbitalcanals bleibt als Rest einer Fossa sphenomaxillaris übrig, während das Foramen sphenopalatinum, und zwar von rundlicher Form, vollkommen frei an der Innenwand der Augenhöhle liegt. Unter ihm führt das For. palatinum superius nach abwärts, um sich in das auffallend weite und ungefähr in der Mitte der Gaumenbeine liegende Gaumenloch zu öffnen" (No. 45, p. 19). This description applies almost exactly to *Leptomeryx*, except that the opening of the infra-orbital canal is divided into two parts, as it shows a tendency to be in *Tragulus*; the lachrymal foramen is placed much higher up than in that genus, and the supra-orbital canal has the same position and relative size, but the groove which runs forward from it is shorter and less distinctly marked.

## III. THE BRAIN.

The museum of the Academy of Natural Sciences in Philadelphia contains a brain-cast which appears to belong to *Leptomeryx*, although it is smaller than the skull figured by Leidy (No. 33, Pl. XIV.). In shape and in the character of the convolutions this specimen is very like the intracranial cast of *Tragulus* figured by Milne-Edwards (No. 37, Pl. VI., Fig. 2). The olfactory lobes are decidedly larger than in the modern form, the hemispheres narrower, and the cerebellum and cerebrum not in contact, so that the corpora quadrigemina were probably partly uncovered. The hemispheres are very narrow anteriorly; the constriction is more sudden than in *Tragulus* and the portion in front of it much smaller. The splenial fissure does not appear to show upon the dorsal surface, as it does in the chevrotains and the small deer, though this is not quite certain. The lateral fissure is longer and better marked than in *Tragulus*; the suprasylvian fissure follows very much the same course as in that genus, but the coronal sulcus, with which it is continuous, is more oblique and approaches nearer to the median line. The occipital lobes are broad and the temporo-sphenoidal lobes deep.

The cerebellum is large, with very prominent and convoluted vermis; the posterior surface of the latter is strongly projecting, is vertically placed, and forms nearly a right angle with the dorsal surface. The top of the cerebellum is nearly in the same plane as the top of the cerebrum, agreeing in this respect with *Cainotherium* rather than with *Tragulus*. The lateral lobes of the cerebellum are apparently smooth and the flocculi are small. The medulla oblongata is very thick.

## IV. THE VERTEBRÆ.

Of the spinal column we have preserved the neck and first two dorsal vertebræ of one specimen, and several scattered dorsal and lumbar vertebral centra of other individuals. The cervicals are very much indeed like those of *Tragulus*. The atlas is short and broad, with transverse processes of only moderate extent, very different from those of the Pecora. The axis has

a broad, much depressed, and opisthocœlous centrum; the condyles for the atlas rise higher upon the sides of the neural canal than in the modern genus. The odontoid process is short and peg-shaped, not in the least like the spout which occurs among the true ruminants. In the Cope collection, however, there is a small axis with a broad depressed odontoid, much as in *Oreodon*, but this may belong to *Hypisodus*. The transverse processes of the axis are short and slender and perforated by the vertebrarterial canal. The neural spine is developed into a great hatchet-shaped plate; the upper margin of this spine is nearly straight and the posterior edge almost vertical, while the anterior one curves gently downward and forward. In spite of its great size, the spine overhangs the third vertebra hardly at all. This spine differs strongly from the corresponding ones of *Cainotherium* and *Tragulus*. The third cervical has a rather long opisthocœlous centrum with a slight keel; the spine is a low ridge. The fourth vertebra is somewhat shorter than the third, but has a more distinct keel, ending posteriorly in a stout tubercle; the neural spine is short, slender, and inclined distinctly forward. The fifth vertebra is like the fourth, except that it has no keel on the centrum and that the neural spine is considerably higher. On the sixth the spine is still higher, much better developed, indeed, than in *Tragulus*, and as in that genus, the transverse process has a large pleurapophysial plate. The seventh cervical is decidedly the shortest vertebra of the series, but has the same depressed, opisthocœlous shape as the others; the spine is very much stouter than that of the preceding vertebræ and much heavier than in the modern genus.

The anterior dorsals are very small; they have short and simple transverse processes, terminating in concave facets for the tubercles of the ribs. The spines are proportionately stouter than in *Tragulus*, and incline strongly backward.

The lumbar vertebræ are relatively shorter than in the tragulines and indicate a less strongly arched back, which is also borne out by the fact that the disproportion between the length of the fore and hind limbs is not so great as in *Tragulus*.

The rib fragments which are preserved indicate a thorax similar to that of the modern genus. Nothing is known of the sternum.

## V. THE FORE LIMB.

The scapula is very similar to that of the tragulines. The glenoid cavity is small and rounded. The coracoid process small, slender, and strongly recurved. The neck is very slender and contracted, and continues for some distance upward; the coracoid border curves gently forward for most of its length,

while the glenoid border is nearly straight. The spine does not arise so near to the glenoid cavity as in *Tragulus*, but rises higher. The acromion is more prominent, and projects more strongly downward than in that genus. As in most of the ruminants, the spine is placed much nearer to the coracoid than to the glenoid border, thus making the post-scapular fossa very much larger than the prescapular, which, indeed, is extremely narrow.



FIG. D. — Left humerus and radius of *Leptomeryx Evansi*; natural size. Cope collection.

The humerus is a stouter bone than that of *Tragulus*, though constructed very much like it; the head is somewhat larger and heavier, the external tuberosity higher and more massive, but less hook-like and overhanging the bicipital groove less; the internal tuberosity is heavier but less compressed and prominent, and consequently the bicipital groove is

not so deep. The shaft is slender, but of greater antero-posterior diameter, and relatively longer. The distal end is very much alike in the two genera, the trochlea oblique to the long axis of the shaft, with large internal and small external condyle, separated by the prominent intercondylar ridge.

The radius and ulna are entirely separate throughout their length, and show no tendency to co-ossification. The former is decidedly longer than in *Tragulus* and proportionately more slender. The proximal end is very much alike in the two genera, except that the groove for the intercondylar ridge of the

humerus is not so deep in *Leptomeryx*. The shaft is flattened and nearly straight. The distal end is much less expanded than in *Tragululus*. The ulna is much reduced and has a very slender shaft; the olecranon is higher than in the modern genus, but of less antero-posterior diameter.

The manus, which has been described by Cope (No. 10), is very traguline in character, both in general appearance and in details of structure. The scaphoid is not preserved in any of the specimens, nor is the trapezium; not improbably the latter was altogether wanting. The proximal end of the lunar is shaped very much as in the Pecora, but the distal end is very different, in that the lunar rests almost wholly upon the unciform and has only a lateral contact with the magnum—a traguline character upon which Cope has laid much stress. The cuneiform is very small, and is not in contact with the radius; its ulnar surface is saddle-shaped and extends well down upon the external surface of the bone. The trapezoid and magnum have coalesced; the compound bone is low, rising slightly behind; it is supported almost exclusively by the scaphoid. Distally it presents facets for the second and third metacarpals. The unciform is the largest bone in the carpus, but is not so high proportionately as in *Tragululus*.



FIG. E.—Left manus of *Leptomeryx Evansi*; natural size. Cope collection.

The metacarpus consists of four digits, none of which shows any tendency to coalesce with another. The lateral digits are very slender, though not so much so as in the chevrotains; the median digits are of about the same relative length, but decidedly more slender. Metacarpal II. articulates with a downward projection from the trapezoid element of the trapezo-magnum. Metacarpal III. articulates medially with the side of this same projection, proximally with the magnum, and laterally with the unciform, sending out a process which overlaps the head of No. IV. Metacarpals IV. and V. articulate only with the unciform. The manus is thus of the "adaptive type." The carinæ of the metacarpals are entirely confined to the palmar surface.

The phalanges of the manus do not differ appreciably from those of *Tragululus*.

## VI. THE HIND LIMB.

Of the pelvis, only the ilium is preserved, but this is very different from the ilium of *Tragulus*; the neck is much shorter, less compressed, and more trihedral in shape; the plate is broader, more everted, and more suddenly expanded; the crest above the acetabulum is higher and thicker. What is preserved of the pelvis, therefore, rather resembles that of the true ruminants than of the tragulines.



FIG. F. — Left pes of *Leptomeryx Evansi*; natural size. Cope collection.

The proximal end of the femur is also very different from that of *Tragulus*; the neck is much longer and more constricted, and the head relatively smaller; the great trochanter is higher and more massive, and the bridge connecting this process with the head is more constricted, the digital fossa is much deeper, and the second trochanter more massive and prominent. The shaft appears to be rather more slender. The distal end is very much like that of the modern genus. The rotular trochlea is broad and shallow, with margins of nearly equal height; it is very long vertically, and but little arched antero-posteriorly. The condyles have but a small fore and aft diameter; they are of nearly equal size and quite widely separated. Above the external condyle there is sometimes a pit, sometimes a rugosity, for the plantaris muscle.

The patella is long, narrow, and pointed, resembling that of *Tragulus*, except for the much diminished thickness of its proximal portion.

The tibia is of about the same relative length as in the modern type, but the cnemial crest is more prominent; the outer condyle projects considerably beyond the line of the shaft. The astragalar surface is not very deeply grooved and the internal malleolus of only moderate length. The fibula is completely

reduced ; its proximal end forms a short, sharp spine, co-ossified with the tibia ; the distal end is generally free, and in this case forms a nodule wedged in between the distal end of the tibia and the calcaneum. In one specimen, however, which may possibly belong to a different but closely allied form, the distal end of the fibula is co-ossified with the tibia, forming an external malleolus, just as in the chevrotains. A similar variability in the fibula is to be found in *Dorcathe-rium* (Flower, No. 17, p. 180).

The pes, as Cope has shown, is more like that of the Pecora than of the Tragulina. The astragalus is higher and narrower than in *Tragulus* ; the calcaneum is rather shorter. The cuboid and navicular have coalesced, as have also the meso- and ecto-cuneiforms. Cope states that "the ecto- and meso-cuneiforms are distinct, and there is no ento-cuneiform" (No. 10, p. 405), but this is a mistake. The ento-cuneiform is present, and the other two are co-ossified, just as in the ordinary ruminants.

The third and fourth metatarsals have coalesced into a cannon-bone, which is extremely like that of *Tragulus* in appearance and relative length, but is decidedly more slender, and as in that genus the carinæ appear only on the plantar side. The lateral digits, however, are very different, as only the proximal ends are preserved, and these have coalesced with the cannon-bone, just as in the true ruminants. The limits of metatarsals II. and V. are still plainly visible in the compound bone. Except for the position of the distal carinæ of the cannon-bone, therefore, the tarsus and metatarsus of *Leptomeryx* show all the characteristics of the Pecora. The contrast between the condition of the manus and that of the pes in this genus is, as Cope has remarked, quite unparalleled.

The phalanges resemble those of the fore foot, but, as in *Tragulus*, they are considerably larger than the latter.



FIG. G. — Right cannon-bone of *Leptomeryx Evansi* ; showing the rudimentary mt. II : natural size. Cope collection.



FIG. H. — Proximal and ungual phalanges of the pes of *Leptomeryx Evansi* ; natural size. Cope collection.

## VII. RESTORATION.

With many differences of detail, the skeleton of *Leptomeryx* is exceedingly like that of *Tragulus* in general character and appearance. If we compare the restoration (Fig. I) with the skeleton of *T. stanleyanus*, the following differences are apparent. The head is rather smaller and, with its long cranium, small open orbit, and curiously formed lower jaw, is strikingly different from that of the modern genus. The neck is rather longer, the lumbar region shorter, and the back much less strongly arched, owing to the greater relative length of the fore limb. Except for this increased length, the less reduction of the lateral digits, the smaller size and separation of the median digits, the fore limb of *Leptomeryx* is almost a reproduction of that of *Tragulus*.

Although the disproportionate length of the posterior limbs, as compared with the anterior ones, is less in *Leptomeryx* than in the existing genus, it is still very great and striking, and the appearance of the hind limbs in the two genera is very similar. Such differences as do occur — and, as we have seen, there are some very important ones — are hardly apparent in a general glance at the skeleton. The entire absence of the lateral digits in the pes, and the shorter and differently shaped pelvis, are the only divergences which call for mention.

## VIII. THE SYSTEMATIC POSITION OF LEPTOMERYX.

Very different opinions have been expressed by various writers upon the position of this remarkable genus. Leidy (No. 33) placed it among the *Moschidæ* (in which family he appears to have included the chevrotains) and considered that it combined characters of the tragulines and the deer. Schlosser has adopted substantially the same view. "Näher kommt den Traguliden die Gattung *Leptomeryx* aus dem Miocän von Nebraska . . . *Leptomeryx* selbst ist auf jeden Fall nur der Überrest gewisser Mittelformen zwischen den Traguliden und Cerviden" (No. 47, p. 75).

Rütimeyer takes a very different view of the matter. "Die Merkmale des Schädels mit Einschluss namentlich des Unterkiefers scheinen weit eher auf eine nahe Beziehung von *Lepto-*

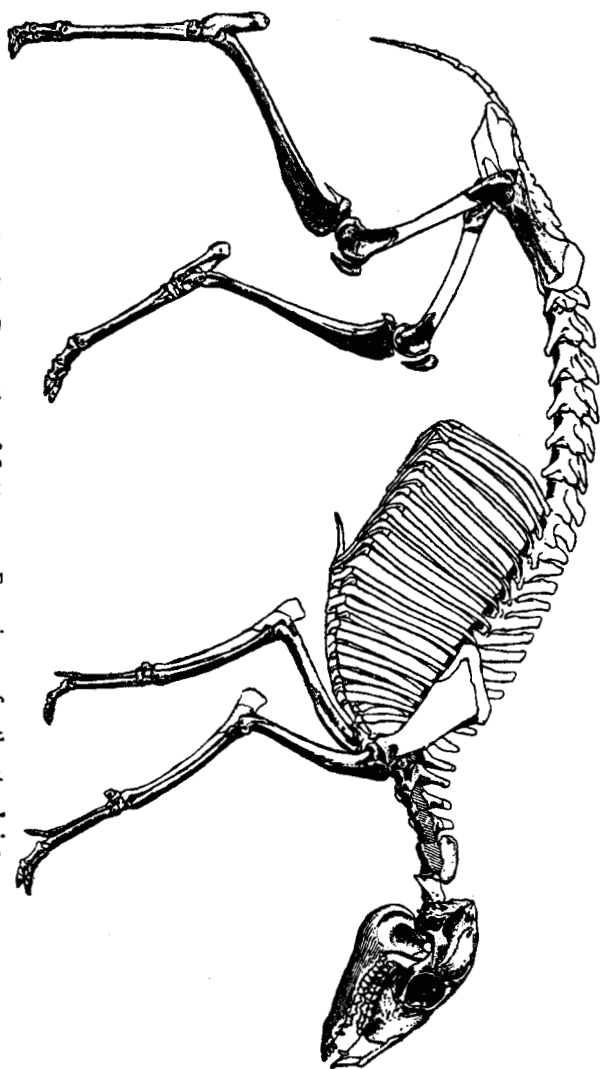


FIG. 1.—Restoration of *Leptomeryx Evansi*; one-fourth natural size.

*meryx* zu den in Nordamerika so stark vertretenen Vorläufern der Camelina (*Oreodon*, *Procamelus*, *Leptauchenia*, etc.) hinzu-  
deuten und denjenigen von *Tragulina* und *Cervina* sehr fern zu  
stehen. Zu demselben Schluss scheint mir das fast vollständig  
erhaltene Gebiss zu führen. Von vorn herein ist es bemerklich  
durch die den Kameelen so eigenthümliche Unregelmässigkeit  
der Ausführung des selenodonten Baues von obern und untern  
Molaren, aber auch die Praemolaren stehen vor allem denjenigen  
von *Tragulina* sehr fern; eher liessen sie sich — mindestens für  
diejenigen des Unterkiefers — in dem stark abgetragenen Zu-  
stand, den die Abbildung darstellt, mit solchen von *Coassina*  
vergleichen. Aber weit näher scheinen sich wieder denjenigen  
von *Procamelus* und ähnlichen kleinen *Prodromal*-Formen anzu-  
schliessen. Nach jeder Richtung scheint mir also *Leptomeryx*  
den hornlosen Wiederkäuern des europäischen Miocens sehr  
ferne zu stehen" (No. 45, pp. 98, 99).

Though we now know pretty nearly all parts of the skeleton  
of *Leptomeryx*, the proper reference of the genus is by no means  
easy. As a preliminary to the discussion of this problem, it  
may be useful to point out some of the peculiarities which sepa-  
rate the Pecora from the *Tragulina*. It will not be necessary  
to consider the *Tylopoda* in this connection, for it must be  
obvious from the foregoing description that *Leptomeryx* can  
have nothing to do with this group, such resemblances as do  
occur being merely primitive characters common to all the early  
selenodonts, which the *Tylopoda* have retained.

The salient characters of the traguline skull are, according to  
Rütimeyer the following: (1) Very small size. (2) The cranio-  
facial axis is straight. (3) The orbits are very large, median in  
position, and separated by a thin septum, but they do not pro-  
ject much beyond the sides of the skull; the optic foramina are  
confluent. (4) The cranium is long, narrow, and low, and the  
parietal zone is correspondingly long. (5) The occipital surface  
is unusually high, narrow, and convex, and the supra-occipital  
is extended upon the side walls of the cranium. (6) The alæ  
orbitales are extraordinarily extended, reaching to the roof of the  
skull. (7) A short sagittal crest is formed. (8) The frontal  
zone is limited to the roof of the orbits and nasal cavity. To  
these should be added (9) the large size of the auditory bullæ,  
which are filled with cancellous tissue.

In the dentition the characteristic points are: (10) the peculiar spatulate form of the lower incisors; (11) the great simplicity of the premolars; (12) the presence of crests upon the anterior crescents of the lower molars (this Schlosser regards as the most important character of all); (13) the character of the milk molars.

'In the vertebral column we observe: (14) the shape of the atlas; (15) the peg-like odontoid process of the axis; (16) well-developed neural spines on the cervical vertebræ; (17) the long, curved, dorso-lumbar region.

In the limbs we have: (18) the great length of the hind limbs as compared with the fore limbs; (19) the ulna and radius are not coalesced; (20) the lunar rests almost entirely upon the scaphoid; (21) the median metacarpals may coalesce into a cannon-bone or not; (22) the lateral metacarpals are complete; (23) the lower end of the fibula fuses with the tibia, except sometimes in *Dorcatherium*; (24) the cuboid, navicular, and cuneiforms fuse into one compound bone; (25) the median metatarsals form a cannon-bone; (26) the lateral metatarsals are complete, though very slender; (27) the keels on the distal ends of the metapodials are confined to the palmar and plantar side.

It is obvious that *Leptomeryx* agrees with the tragulines as regards much the greater number of these characters. The skull is that of the chevrotains with most of the primitive features emphasized. To this statement two exceptions must be made: (1) the occiput is flattened or even concave, and (2) the auditory bullæ are small and not filled with cancellous tissue.

In the dentition, we see that *Leptomeryx* agrees with the tragulines in the characters 12 and 13, and differs from them as to numbers 10 and 11. Some specimens, however, have premolars as simple as those of *Tragulus*, which shows that this character is not a constant one. We may add here that the brain is also very traguline, but little weight can be given to this fact, as there is the same resemblance between *Moschus* and *Tragulus*. "In other respects, the brain of *Tragulus*, as far as its surface markings are concerned, is a simplified miniature of that of the *Cervidæ*" (Flower, No. 17, p. 176). All the traguline characters in the vertebral column recur in that of *Leptomeryx*.

In the fore limb there are no important differences between *Leptomeryx* and the tragulines, even in matters of such detail as the mutual relations of the carpal bones. In the hind limb, the differences are more important. The lower end of the fibula appears usually to remain free, though sometimes it fuses with the tibia; the cuneiforms do not coalesce with the cubo-navicular, and only the proximal ends of the second and fifth metatarsals are preserved, and they coalesce with the cannon-bone. But even in the pes, the distal keels occur only on the plantar side of the metatarsals. Thus in the twenty-seven characters enumerated above as distinguishing the tragulines, *Leptomeryx* agrees with that group more or less completely in twenty-one.

On the other hand, there are the following points of agreement with the Pecora: (1) The character of the occiput; (2) of the auditory bulla; (3) the form of the lower incisors; (4) the complexity of the premolars; (5) the character of the tarsus, and (6) of the metatarsus, except for the shape of the distal end. If the more primitive extinct members of the Pecora be included in the comparison, the number of correspondences with *Leptomeryx* would be much increased.

To those who accept the position of Boas, that the tragulines are a group of simplified ruminants which have been derived from typical members of that series, and not to be regarded as a primitive group (No. 3, p. 522), the apparently intermediate character of *Leptomeryx* would be just what we should expect, and this genus would then be considered as one of the direct ancestors of the tragulines. For reasons into which the limitations of space forbid my entering here, I cannot agree with this view, and therefore cannot adopt such an explanation of the position of the genus before us.

It seems clear to me that the probable interpretation of the problem is this. *Leptomeryx* is a side branch of the traguline stem, given off before the extreme concentration of the tarsus characteristic of existing members of that stem had been acquired, and which has paralleled more or less exactly the characters of the Pecora in certain particulars; e.g. the condition of the auditory bullæ and the constitution of the posterior cannon-bone. There is every reason to suppose that the character of the tarsus in *Leptomeryx* is nearly what it was in the ancestral tragulines. Such a conclusion may seem highly

improbable, and yet when the list of unmistakable parallelisms to be given in the next section is examined, it will appear less unlikely. Nor will the difficulty be diminished by assuming that the resemblances to the Pecora are due to genetic affinity, because then we should have to account for an even greater number of resemblances to the tragulines, which could not have occurred in the ancestor common to this group and the Pecora. If we agree with Rüttimeyer, and refer *Leptomeryx* to the fore-runners of the camels, then the difficulties become all the greater.

Obviously, the final solution of the question can only be reached when we have learned more of the selenodonts of the Uinta formation, and are enabled to trace the ancestry of *Leptomeryx* back to the Eocene forms. From the evidence at present available, I cannot doubt that the genus has a real relationship to the tragulines, with certain independently acquired resemblances to the Pecora, resemblances which appear to be carried even further in the curious little genus *Hypisodus*, with its prismatic molars and highly specialized inferior incisor series.

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#### ON THE MODE OF EVOLUTION IN THE MAMMALIA.

We may now attempt to apply the results gained from the history of the fossil mammals, discussed in this and the preceding paper, to the problems which were stated in the paper on the Tylopoda (No. 52, pp. 2-9). In the discussion which follows I shall not undertake to go over the whole vast field which these questions open up, but shall confine myself as far as possible to the mammals, using other groups of organisms only occasionally as a means of comparison and illustration. To do more than this would require a volume.

1) The first question propounded, viz. that as to the single or multiple origin of genera, is at bottom rather a question about words than about things, and the answer which we make to it will to a great extent depend upon the view taken as to the definition of the word *genus*. If we make classification an expression of real relationship, and not of mere similarity of structure, as should certainly be the end proposed, then it is obvious that all the species of a genus must be more nearly allied

to each other than they are to those of any other genus, recent or extinct. But as genera are at present employed and in the existing state of knowledge, such an exact expression of relationship is impracticable, as that would necessitate a minute knowledge of the phylogeny of each species, such as we are very far from possessing. In the current usage, a genus is a group of nearly allied species agreeing among themselves and differing from all others in the possession of some common character. But if the various species of the ancestral genus may acquire the new character independently of each other (parallelism), or if the species of widely different genera may gradually assume a common likeness (convergence), then it is plain that such a genus is an artificial assemblage of forms of polyphyletic origin. That such parallelism of development does occur, we shall see in the next section, and there are good reasons for believing that convergence is not so rare a phenomenon as it is generally assumed to be; from which it follows with great probability that many generic groups are not real expressions of relationship, but artificial assemblages of similar forms.

While it is easy to make these distinctions theoretically, in practice it is a matter of extreme difficulty, even under the most favorable circumstances, at least so far as cases of parallel development are concerned. Many of the known cases of convergence show that this process is more apparent than real, and may generally be unmasked upon careful examination, though even here the cases of the Ammonites, presently to be mentioned, show the need of extreme caution. The mutual relationships of the various species of two successive genera are usually very obscure. In a given case each of the five species of genus *A* may seem to have been derived from a different species of genus *B*, and yet the assumption of such a mode of derivation may prove to be altogether erroneous, because of the tendency so frequently to be observed for each member of a descending series to develop a similar cycle of variations. Neumayr (No. 40, p. 61) has observed this among invertebrates: "Ein anderer bisweilen beobachteter Fall von grosser Wichtigkeit ist der, dass die verschiedenen Glieder einer Reihe Variationen derselben Art zeigen; während also ein Theil die Merkmale gleichmässig nach einer Richtung im Laufe der Zeit mutirt, zeigen andere Charaktere regellose Abänderungen und

jede Mutation entwickelt denselben Varietätenkreis." In spite of this source of difficulty, many of the facts of palæontology render it extremely probable that many genera, *as now constructed*, are of multiple origin, as was long ago suggested by Cope (No. 5), but our present knowledge is insufficient to enable us to point out the particular cases. Mivart goes so far as to argue that genetic relationship should have but a subordinate place in deciding questions of classification. "Real genetic affinity must exist, and when it can be securely detected must be most important. But the response of organization to need being such as it is (structure and function manifesting themselves so simultaneously), the discrimination between genetic and adaptive families must long, if not ever, continue a work of extreme delicacy and difficulty. . . . On this view, the classification of existing and extinct animals can never, at any future time, be constructed on a purely genetic basis; but surely it need not therefore be a purely arbitrary and artificial system" (No. 38, p. 510).

2) The problems of parallelism and convergence, of which that as to the origin of genera is merely a special case, open up a discussion of far-reaching extent and importance, which can only be briefly touched upon here, though the facts of palæontology are perhaps the most instructive in this connection. The distinction between the two classes of phenomena is obviously one of degree rather than of kind, and it will therefore be convenient to consider them together. What we may call negatively parallel development, *i.e.* the independent suppression of similar parts in different phyletic series, is a very well-recognized phenomenon. Thus, nearly all the known mammals from the Puerco Eocene agree in having an entepicondylar foramen in the humerus, the third trochanter on the femur, a perforated astragalus, an alisphenoid canal, and, probably, interlocking cylindrical zygapophyses on the posterior dorsal and lumbar vertebræ. In existing groups of mammals these characters are scattered and combined in the most heterogeneous fashion, suppression or retention of one or more of them being carried out in widely separated orders. The edentates of the Old and New Worlds are for the most part united by merely negative characters and very probably represent a polyphyletic group. In the same manner, reduction in the number of digits, of teeth,

of vertebræ and ribs, may be similarly brought about in very different groups.

When we come to examine positive differentiation, the same parallelism is abundantly proven. The prismatic, cement-covered molar, has been independently developed in many forms; *e.g.* several of the ruminants, certain pigs, the horses, one of the rhinoceroses (*Elasmotherium*), the elephants, many rodents, etc. The resemblance of the molar of *Elasmotherium* to that of the horse is very striking, but its fundamental plan is rhinocerotid and not equine. The scalpriform incisor, growing from a persistent pulp, is repeated in many very different orders of mammals. Within narrower limits, the selenodont molar-pattern has been several times independently evolved: 1) in the true ruminants; 2) in the camels; 3) in the oreodonts, not to mention the somewhat aberrant types of dentition exhibited by *Anoplotherium*, *Xiphodon*, *Cainotherium*, and the like. The rhinoceros form of molar has been independently acquired at least twice; namely, in the rhinoceros and hyracodont lines. In a great many different series of perissodactyls, as well as in *Hyrax*, the premolars have become molariform; the dentition of certain creodonts has become extremely cat-like, and that in forms which can have no direct connection with the true cats. There is a wonderful similarity in the mode of development of cerebral convolutions in many different lines of ungulates, a similarity which the fossil series show to have been independently acquired, and which are plainly the necessary outcome of mechanical principles. In the same way we find that the milk dentition of all the primitive selenodonts agrees in character, as does that of all existing members of the group, except the tragulines, which still retain the ancient structure, but the history of the various ruminant lines proves that the modern type has been independently acquired at least three times, in the Pecora, the Tylopoda, and the later *Oreodontidæ*, such as *Merychys* (No. 51, p. 370). The spout-shaped odontoid process of the axis has arisen in the true ruminants, the horses, the camels, and, to a certain degree, in the later oreodonts, such as *Merychys*. The proximal end of the humerus in the modern Tylopoda is extremely like that of the horse, and the lower Miocene representatives of these two series, *Pæbrotherium* and *Mesohippus*, also agree almost exactly as to the structure of the

humerus, but in this case the bone is of a more primitive type, with single bicipital groove and no bicipital tubercle, or only a very rudimentary one.

The steps of modernization which may be observed in following out the history of many different groups of mammals are, seen to keep curiously parallel, as may be noticed, for example, in the series of skulls figured by Kowalevsky (No. 26, Pl. IX.), where we find similar changes occurring in such families as the pigs, deer, antelopes, horses, elephants, etc. Indeed, one may speak with propriety of a Puerco, or Wasatch, or White River type of skull, which will be found exemplified in widely separated orders. Of course there are exceptions, some types being in advance of, and others lagging behind, the standard of their age, and others, again, attaining great peculiarities of structure which will not be perpetuated; but, on the whole, the type of skull or limbs keeps strikingly true to the standard. These facts emphasize the truth of the proposition laid down by Cope: "From these and many analogous cases, the general law may be deduced, that identical modifications of structure, constituting evolution of types, have supervened on distinct lines of descent" (No. 8, p. 343). Of similar import are the simultaneous and similar variations of different orders, according to geographical location, such as the characters of the Lepidoptera in the different Malay islands, to which Wallace has directed attention (No. 56), and which is exhibited in such a striking way by the coloring of Arctic and desert animals, and very many other well-known phenomena. All this but illustrates anew the conclusion long since universally accepted, that no natural system of classification can be founded upon the presence or absence of a single character.

Parallelism may, however, extend much further than this, and embrace, not single characters only, but whole series of them. It is this fact which renders the proper reference of such forms as *Leptomeryx* so very difficult. If the interpretation of the tylopodan phylogeny which was given in my former paper be correct, then the camels and the true ruminants have no common ancestor nearer than the *Dichobunida*, animals with quinquetuberculate upper molars, complete dentition, short limbs, unreduced ulna and fibula, and tetradactyl feet, all the digits being free. The two series have independently acquired tetra-selen-

odont molars ; have lost all or nearly all of the superior incisors ; have developed types of skull which, with all their differences, have many features in common ; in both the limbs and especially the metapodials have greatly elongated ; the ulna and fibula are very much reduced and in precisely the same fashion ; the cannon-bones in both series are composed of just the same elements ; in both episphenial processes have been independently developed upon the zygapophyses of the lumbar vertebræ, and in both the odontoid process of the axis, which was originally peg-like, has become spout-shaped. The stomach of the camel resembles that of the typical ruminants in a way that we cannot suppose to be due to a common inheritance from the *Dichobunidæ*. In both series the final result is strikingly alike, though the parallelism is by no means complete, and as we have already noticed, the keen insight of Rüttimeyer detected the true relationship from a comparison of the modern forms alone. In one respect, however, I must venture to differ from his interpretation of the facts. Rüttimeyer regards the llama as less aberrant than the camel ; a better statement would perhaps be that its parallelism to the Pecora is more complete.

The resemblance between the creodonts and the carnivorous marsupials has been much dwelt upon, but I think that it may be shown that the relationship between the two groups is a very remote one and that the points of likeness are due partly to parallel development and partly to the retention in both series of certain primitive characteristics.

The group of reptiles presents very similar phenomena ; on the one hand there are the Dinosauria, which have developed so many ornithic peculiarities in the hind limb, while, on the other hand, the Pterosauria possess equally striking avian features in the skull, cervical vertebræ, sternum, and shoulder girdle. To assume, as has been done, that the birds are diphyletic, is to admit the principle of convergence in almost its extreme form, while if this be denied, then the bird-like structures of either the pterosaurs or the dinosaurs, or both, must be due to parallelism.

Among the invertebrates the same problems confront us. Thus Würtenberger finds well marked convergences among the ammonites. "Aus den Betrachtungen welche wir bisher über die Stammesgeschichte der Ammoniten angestellt haben, dürfte

wohl ohne weiteres schon hervorgehen, dass der Ursprung der meisten der hier berücksichtigten Gruppen sich als monophyletisch zu erkennen gibt; denn fast immer sehen wir eine bestimmte Form oder enger begrenzte Formengruppe nur als das Glied einer einzigen Entwicklungsreihe auftreten; nur einzelne wenige Fälle machten sich bemerklich, wo aus verschiedenen Formenreihen einander sehr ähnliche Endglieder hervorgingen. Es sei z. B. an die *Mutabilis*-Gruppe erinnert; hier wurden diese Endglieder einander selbst so ähnlich, dass sogar schon mehrere derselben zu einer einzigen Art vereinigt worden, und wir demnach hier sogar von einem polyphyletischen Ursprunge der *Species* sprechen könnten. Wenn nun aber die äusseren Umgänge solcher *Mutabilis*-formen einander noch so ähnlich werden, so sind dann die inneren Windungen um so verschiedener und verrathen den verschiedenartigen Ursprung der allenfalls zu einer *Species* zusammengefassten Individuen nur zu deutlich, so dass eine solche polyphyletische *Species* dann eben bloß noch als eine naturwidrige Zusammenstellung verschiedenartiger Dinge erscheint. . . . Solche Fälle wie bei der *Mutabilis*-Gruppe, wo zu verschiedenen Zeiten verschiedene Formen, ähnlichen Existenzbedingungen sich anpassend, derart sich abänderten, dass sie einander sehr ähnlich wurden, trifft man bei den Ammoniten noch mehrfach" (No. 61, pp. 106, 107).

Hyatt fully confirms these results, and adds others to them: "The evidence is very strong that *Baculites*, *Scaphites*, etc., of the Cretaceous are not necessarily species of the same genus, but probably always polyphyletic in origin. The *Baculites* of North America have so close resemblance to those of Europe that they are usually considered as allied species; but there are indications, in the peculiar nodular markings and great size of many species, which lead us to think that they originated from American stocks" (No. 23, p. 31).

Haeckel believes that the *Siphonophora* are of diphyletic origin, part of them being derived from trachomedusoid ancestors, and part from anthomedusoid (No. 22, p. 40).

Similar examples, drawn from a very wide range of animal groups, might be multiplied almost indefinitely, but those here given are sufficient to prove what probably few morphologists doubt, namely, that parallelism and convergence of development are very real phenomena. Much more difficult to

decide is the question as to how far these processes may be carried. In all of the cases cited, the final result is not identity, but similarity, and there is in all of them some fundamental discrepancy which exposes the deceptive character of the process. I have already quoted Rüttimeyer's opinion as to the relationship between the camels and the typical ruminants. Semper found that while the shells of certain genera of land mollusca exhibit a remarkable degree of convergence, the structure of the soft parts was sufficient to correct the improper association of these forms. Other instances might be cited to show that a careful use of the comparative method is often able to avoid these obstacles. On the other hand, one cannot doubt that great numbers of such cases have escaped detection, as the instructive instance of the *Mutabilis* group of ammonites plainly renders probable; for if the embryological stages of these shells were not preserved in the inner whorls, no palæontologist would hesitate to class them together as closely allied, or even as members of the same species. In the construction of the larger taxonomic groups, which embrace so many and such various forms, the difficulties arising from parallelism, both positive and negative, become greatly increased, and only complete and unbroken phyletic series will enable us to overcome them entirely. It is, therefore, quite impossible to determine, from our present knowledge, to what extent these processes may be carried, though probably few morphologists will follow Mivart in the extreme position which he has taken upon this question. The fixity of direction of the lines of development, which is so strikingly exemplified in nearly all well-defined series of descending forms, seems to offer some assurance that these interrelations of various groups will not prove to be so inextricably confused as to defy any attempt to unravel them.

The supposed dual origin of the horse in the Old World and the New does not offer such insuperable difficulties as one might at first imagine. In both hemispheres occur almost unbroken series, from the Eocene *Hyracotherium* to the existing *Equidæ*, and were only one of these series known, probably no one would hesitate to regard it as the true ancestral line. But several of the genera, such as *Hyracotherium*, *Pachynolophus*, *Hippotherium*, occur both in Europe and in America, and there can be little doubt that these genera originated in one continent

and reached the other by immigration. Other genera form abortive side branches which lead to no permanent results, and thus it seems altogether probable that there is only one series, at least as late as the Pliocene. That some species of *Equus* should be derived from *Protohippus* and others from *Hippotherium*, as Cope has suggested, it is by no means impossible, but cannot be admitted until the ancestral history of these species has been followed out step by step.

These considerations show how profoundly important it is that in all phylogenetic discussions the possible effects of parallelism and convergence should never be lost sight of. One of the commonest fallacies to which neglect of these factors leads is the assumption that because two allied groups possess a certain character, their common ancestor must also have possessed it. This may or may not be true in any given case. For example, it has been shown that the spout-like, odontoid process of the axis has been independently developed several times, yet Boas concludes that the ancestor common to all ungulates must have possessed it: "Auch beim Pferd, beim *Anchitherium* (nach Kowalevsky) und (nach Flower) beim Tapir verhält sich der Proc. odont. ähnlich wie bei den typischen Wiederkäuern, und es ist somit wahrscheinlich dass die gemeinsamen Vorfahren *aller Ungulaten* diesen Charakter besaßen und dass auch die konische Form, etc., desselben beim Schwein sekundär erworben ist" (No. 3, p. 518). But even this conclusion involves the admission of a parallel development of the peg-like odontoid in the pigs, tragulines, rhinoceroses, etc. Flower's view is more consonant with the facts of palæontology. "The form of the odontoid process in the Tylopoda might lead to the idea that they were segregated from the ruminant stock after the Tragulina had been given off; but as it is also found in the horse, it is probably adaptive, as are the hypsodont molars" (No. 17, p. 190).

It is further evident that Huxley's dictum to the effect that in forming natural groups "it is more important that similarities should not be neglected than that differences should be overlooked," cannot be maintained. On the contrary, it is only a due consideration of the differences that enables us to distinguish artificial from natural groups. It is likewise clear, if these conclusions be sound, that no general rules can be laid

down for determining the taxonomic value of any particular structure, whether it is adaptive or inherited, positive or negative. In this respect every group must be considered by itself, neglecting nothing. Fürbringer has reached very similar results in his great work on the birds: "Unter diesen Umständen muss die Beurtheilung dieser heterogenen Kennzeichen und die Auslese unter ihnen *für jede Gruppe von Anfang an* unter den bereits angegebenen Cautelen getroffen werden und nirgends darf man vergessen dass dieses oder jenes Merkmal, das sich bei 10 Familien als ein constantes bewährte, bei einer 11<sup>ten</sup> eine ganz überraschende, seine taxonomische Anwendbarkeit sehr beeinträchtigende Flüssigkeit darbieten kann" (No. 19, p. 1134).

4. Palæontology is not well adapted to solve the fourth problem, as to whether lost structures may be regained, because we never can be sure that any case which might seem to require such an interpretation is not really due to an imperfection of the geological record. The apparent reacquisition of a digit, for example, might be due to the fact that the ancestor of the polydactyl form had not been preserved. There is, however, one case which is of interest as indicating possibilities in this direction. One of the most characteristic features of the *Oreodontidae* is the fact that the first inferior premolar has assumed the form and function of the canine, while the latter is functionally one of the incisors. This condition is obviously a secondary one and implies a change from the ordinary relations of these teeth. On the other hand, in *Pithecistes*, one of the later and more aberrant members of the family, the caniniform premolar has disappeared and the canine has again taken on its normal functions. This is, of course, not exactly a case in point, as the canine was not lost and reacquired, but it would seem to indicate that such reacquisition is not impossible. If Weissman's interpretation of the relations of *Siredon* to *Amblystoma* be correct, then this is a clear case of a lost organ being reacquired; *e.g.* the gills, although these organs are normally present and functional in the larval state of *Amblystoma* (No. 58). At all events, such reacquisition, among the higher animals at least, would certainly seem to be unusual, and should not be assumed in any given case, except upon the clearest evidence.

5. So far as the series of fossil mammals which we have been considering are concerned, the developmental history appears to

be very direct, and subject to comparatively little fluctuation, advancing steadily in a definite direction, though with slight deviations. Thus in the cameline series, the size and position of the orbit, the shape and character of the posterior nares appear to change first in one direction and then in another, so that in some respects the skull of *Pæbrotherium* is more modernized and ruminant-like than that of the camel. But these fluctuations are slight and of no great importance. On the whole we are impressed by the steady march of differentiation; thus, in the equine series the premolars one by one become molariform, the molar pattern more complex, the face elongated, the digits are continually reduced in number, the median digit becomes more and more enlarged, and the carpal and tarsal bones adjusted to the new character of the strains, the limbs become more and more elongated, and the stature of the whole animal increased. In many genera the cycle of variation appears to be a singularly small one, and as Neumayr has observed in the Mollusca, the same or a very similar cycle appears in successive genera. Thus in the genera *Palæosyops*, *Diplacodon*, and *Titanotherium*, of the Bridger, Uinta, and White River formations respectively, there are curious similarities in the specific variations, which are repeated in each of the successive formations. The same thing is true of the Oreodons of the White River, and Eporeodons of the John Day, though perhaps these cases are in part to be explained as belonging to genera of multiple origin, where several species of the older genus have similarly and simultaneously taken on the character of the new. Indeed, the limited plasticity of the mammals, except along certain definite lines, is very marked. In every formation the majority of species appear to die out without leaving any successors behind them, and too early a specialization would seem to be fatal to the perpetuation of a group. With rare exceptions the progenitors of permanent lines seem to be those forms which have not strayed too far in any direction from the safe middle course; every formation contains numerous examples of what from one point of view may be called premature differentiations, advantageous, no doubt, to their possessors, but not sufficiently plastic to adapt themselves readily to new conditions.

These facts are opposed to the assumption that in the evolution of a *mammalian* phylum frequent alternations of advance

and retrogression have occurred. Of course, a mammal may advance to a certain degree and then degenerate, but that is not the point under consideration. Nor is it meant that the direction of advance is something absolutely fixed; on the contrary, this direction may be followed for a certain length of time, and then changed. A very instructive example of this is given by the history of the Pecora. The lower miocene representatives of this series, which are hornless, *Amphitragulus*, *Palæomeryx*, etc., show a continually increasing size of the upper canines, which are still retained in the hornless deer, *Moschus*, *Hydropotes*, etc., as well as in the small-antlered muntjaks, while in the typical *Cervidæ* and in the *Bovidæ* the antler and the horn have been gradually substituted as weapons, and the upper canines have dwindled to mere rudiments or entirely disappeared. *Chalicotherium* is doubtless an example of the change of direction of specialization.

Obviously, this conclusion is far from certain, and may well be modified or even disproved by more extensive and complete material. Nor can we extend this result to the lower groups of animals. The facts which have been brought out with regard to the Axolotl, the experiments of Schmankeiwitsch (No. 48) on *Artemia*, and many other facts, render it inapplicable to these forms. But it appears to be the fact that, just as the power of regeneration of lost parts diminishes as we ascend in the scale of animal life, so plasticity of organization and capacity for differentiation of structure in widely different directions diminishes also.

6. As a general rule, it certainly appears to be the case that among mammals differentiation is by reduction in the number of parts, but there are some facts which go to show that this rule is not without exceptions. Thus in the toothed whales and in certain edentates the number of the teeth has surely been increased, as has the number of the phalanges in the Cetacea and the Sirenia. Probably no one will be inclined to believe that the primitive antelopes had four horns and that *Tetraceros* is the only living form which has retained this peculiarity. On the contrary, it seems certain that in this genus an additional pair of horns has been developed, just as in certain monstrous domestic breeds of sheep. In certain breeds of dogs a double hallux has been rendered constant. Indeed, reduplication of

parts is a very common teratological occurrence, and there is no *a priori* reason to assume that such reduplication might not occasionally be selected and perpetuated. The fourth molar of *Otocyon* appears to me to be probably either a case of this sort, or of permanent reversion, as any other assumption with regard to it seems very unlikely. *a*) That all the known fossil cynoids have no direct connection with the existing dogs, can hardly be believed by any one who has examined the material, and yet all of these, with occasional individual exceptions (which still occur among the recent *Canidæ*, see Filhol, No. 16), have but three molars at most. *b*) That the *Canidæ* are of dual origin, one line through *Miacis*, *Daphænus*, *Cynodictis*, etc., to *Canis*, and the other through unknown ancestors to *Otocyon*, involves a degree of convergence which known facts do not justify us in assuming. Between the third and fourth hypotheses, that the additional molar is atavistic, or that it has been added *de novo*, it is very difficult to decide; for in the fairly complete mammalian series which we have been considering in the present and preceding papers, neither process can be shown to have taken place. Yet both are conceivable and do take place in individual cases; and if so, they might, under favorable circumstances, and provided they recurred frequently enough, be rendered permanent. In *Otocyon* the dentition is much more primitive (aside from the number of the molars) than in any other known member of the family, recent or fossil. Judging from the state of development of the skull and skeleton, this condition almost certainly implies retrogression, which may possibly have stimulated atavistic tendencies. The problem can be definitely solved, however, only by a much more complete phyletic series than we can at present command. At all events, this reacquisition or addition *de novo* can only be very exceptional in the history of the higher mammals.

7. In large groups of mammals the method which is followed in the reduction of parts is generally a very uniform one. Thus Owen's laws of the reduction of digits hold good for all artiodactyls and perissodactyls. Great uniformity is also exhibited in the order of disappearance of the teeth, but this is not without exceptions; *e.g.* in artiodactyls the first premolar is usually the first one to disappear, but in the camel this tooth is retained, while the second is lost. The Creodonta and Carnivora follow another law, but in these groups there is less uniformity, and

other exceptions might be cited. With regard to the mode of reduction of the vertebral column, fossils are not well adapted to throw light upon the question, because specimens in which the vertebral column is at all completely preserved are very rarely found. So far as the evidence goes, however, it appears to favor Fürbringer's position, that reduction is from behind forward, and that the changing numbers of the dorso-lumbar vertebræ are due to a shifting of the limb-girdles. The early forms of mammals in which the number of trunk-vertebræ is known, have, for the most part, a larger number than have their modern representatives, and a very general characteristic of these ancient forms is their very long, stout, and well-developed tails. This evidence is, however, too imperfect to be at all conclusive, and whatever may be true of the mammals, Parker's results seem to show that in the turtles, suppression of vertebræ may take place in the cervical region without affecting the position of the limb-girdles or the number of the dorso-lumbar-sacra. Baur has recently published (No. 2) the results of his studies upon the spinal columns of certain lizards, crocodiles, and serpents, in which he comes to the conclusion that intercalation does occur. "My opinion is that in the increase of the number of segments, not only in vertebrates, but also in invertebrates, intercalation has played a much greater rôle than is generally admitted" (p. 335). The evidence adduced is not, however, altogether conclusive.

8. Increased size and weight of body of course entail increased thickness and massiveness of the bones, with much more prominent and rugose processes for the attachment of muscles and ligaments; but the effect upon the skeleton is much more profound and far-reaching than this, as will appear from a comparison of the Proboscidea, the Dinocerata, and the equally huge perissodactyl, *Titanotherium*, which are about as widely separated from one another as three ungulate lines well can be. Little is known about the phylogeny of the elephants, but so far as the other two series are concerned, their earlier members are in many respects less alike than the later ones, while in the final members of all three lines we find many and striking resemblances. The neck is shortened, the trunk very long, and the anterior dorsal vertebræ rendered very heavy, with much elongated spines to support the massive head, which is greatly en-

larged, but lightened by large sinuses or air-cells. The ribs are very long, and strongly arched, to carry the great mass of viscera. The scapula is triangular in shape, and in the *Dinocerata* extremely like that of the elephant, with greatly elongated suprascapular border and very large post-scapular fossa, prominent and massive acromion. The humerus also is much alike in these two groups, but that of *Titanotherium* is more rhinoceros-like. In all, the ulna is unreduced or even enlarged, and the carpus is composed of massive cubical blocks. The ilium is in all greatly everted and immensely broadened in the transverse direction. The femur is long and massive; that of *Uintatherium* is almost an exact copy of that of the elephant, having neither third trochanter nor pit for the round ligament, both of which are preserved in the earlier members of the Amblypoda, e.g. *Coryphodon*. In all, the tibia is short, and the fibula complete; the astragalus extends far over on the cuboid, though separated from it in the elephant by the navicular, and is little or not at all grooved, so that the maximum of motion is at the knee-joint. The tarsus of *Uintatherium* is in general character very much like that of the elephant, while that of *Titanotherium* does not lose its perissodactyl structure.

The metapodials are short and massive, especially so in the *Dinocerata* and *Proboscidea*, and the ungual phalanges are reduced and nodular in shape, showing that in all the foot was enveloped in a pad. It seems probable that great size and weight of body stops in most cases the process of digital reduction. In *Titanotherium* the number is, it is true, only IV. in the manus and III. in the pes; but then this degree of reduction is already reached in the Bridger genus, *Palæosyops*, which is of moderate size. The other two series are pentadactyl,<sup>1</sup> and in all the foot is nearly isodactyl; i.e. the digits are all of approximately the same length and thickness, though in *Titanotherium* there is more inequality than in the others. In all three groups there are no medullary cavities in the long bones, the interior of which is filled with cancellous tissue.

<sup>1</sup> To this statement one exception must be made. The specimens of naviculars of *Dinotherium giganteum*, from Pikermi, preserved in the Paris museum, show only a very small facet for the first cuneiform, while in the *D. Bavaricum* of the Vienna museum there is no facet for that bone. This points to a great reduction or loss of the hallux. The same statement will apply to a rather small, *Uintatherium*-like navicular in the Princeton museum.

The comparison might be extended to the larger rhinoceroses and hippopotamuses, and would show much the same state of things in a less pronounced degree. It is thus apparent that mere increase in size and body-weight may produce many remarkable convergencies in skeletal structure in animals which are but distantly related to one another. Indeed, so many and so close are the approximations of the *Dinocerata* to the elephants, that Cope, at one time, proposed to place them among the Proboscidea (No. 6).

The materials for determining the effects of great diminution of stature among the ungulates are much less complete and satisfactory, though probably the many points of resemblance between the tragulines and *Cainotherium*, and perhaps also *Leptomeryx*, as also between the tragulines and dwarf antelopes, are largely due to this factor.

Fürbringer has reached very similar results with regard to the influence of stature in the birds: "Im speciellen Theile dieser Arbeit konnte an zahlreichen Stellen gezeigt werden, dass bei der Ausbildung der Knochen und Muskeln die Körpergrösse der verschiedenen Vögel keinen gleichgiltigen Factor spielt, sondern vielmehr in sehr bestimmter Weise mit charakteristischen Differenzirungen des Vogelkörpers coincidirt. Luftarmuth bis Luftleere des Skeletes verbindet sich bei den kleineren Vögeln mit relativ mächtiger Entwicklung der Flugmuskulatur, während andererseits ein höherer Grad von Pneumaticität bei den grösseren Fliegern mit einer grossen Ersparniss an Muskelementen Hand in Hand geht. . . . Aber auch sonst konnten nach der Körpergrösse variirende Verhältnisse nachgewiesen werden. Mit zunehmender Grösse wächst im Allgemeinen, doch nicht ohne Ausnahmen, der Intercoracoidalwinkel, die Spannung der Clavicula, die Zahl der Halswirbel, die sternale Krümmung, etc., während andererseits die Configuration des Xiphosternum in sehr vielen Fällen eine Vereinfachung, die Crista sterni und die Crista lateralis humeri eine Verminderung ihrer Höhe darbietet. Die Configuration der Gelenke zeigen mit zunehmender Grösse auch im Ganzen eine Zunahme der Differenzirung. . . . Welche specielleren Correlationen hierbei in Frage kommen entzieht sich zunächst unseren Blicken; aber auf Grund der bisherigen Beobachtungen dürfen wir mit dem Factum rechnen, dass im Grossen und Ganzen bei

den ziemlich grossen und mässig grossen Vögeln die einfacheren und primitiveren Verhältnisse vorwiegen, während die grossen, wie auch die kleinsten Formen eine einseitige Entwicklung und eine grössere Abweichung von den als ursprüngliche zu beurtheilenden Bildungen darbieten. . . . Wie mir scheint sind es aber nicht allein die Vögel, deren grösste und sehr grösse Formen eine höhere Differenzirung und eine grössere Abweichung von primitiven Zuständen darbieten. Vielmehr scheint diese Regel eine recht weite Verbreitung zu besitzen. Ich erinnere u. A. an das Verhalten der Wirbelsäule, die z. B. bei den kleineren und primitiveren Formen der Plesiosaurier eine viel geringerer Zahl von Halswirbeln besitzt als bei den grösseren und mehr typischen Verwandten, ferner an den Brustgürtel der bei den kleineren Insectivora und Rodentia verschiedene an ursprünglichere Bildungen erinnernde Verhältnisse darbietet, welche den grösseren Thieren fehlen, dann an Carpus und Tarsus, wo ebenfalls bei den genannten Abtheilungen der Säugethiere durch Albrecht, Bardeleben, Baur und Leboucq eine im Ganzen recht primitive Anordnung nachgewiesen werden konnte" (No. 19, pp. 991-3).

The extremely important question as to whether development is always by the accumulation of minute gradations, or whether it may not, sometimes at least, be *per saltum*, is one which can never receive a conclusive answer from palæontology, because we can never be sure that what appears to be *per saltum* development is not merely due to the loss of certain links in the chain. There are, however, some facts which seem to point to the conclusion that evolution does not always proceed at a uniform rate, but that there are periods when this rate is much accelerated, and widespread changes and readjustments are carried out. While it is perfectly true that frequently the successive forms in a series of beds point "rather to substitution through migration than to transmutation," yet this is often not the case, as in those series where we may follow out the transmutation step by step. Yet even in these series it is generally found to be the case that the amount of structural change is greater in any phylum in passing from one formation to another than between the top and bottom of the same formation. To assume that the rate of development is always constant would involve the further assumption that the unrecorded gaps between

the successive horizons represent a longer time than do the formations themselves. So far, at least, as the fresh-water Tertiaries of North America are concerned, this assumption receives little support from geology, and we may fairly infer that the geographical changes which brought about the drying up of the great lakes in one region and their appearance in another were accompanied by an accelerated rate of change in the organic world.

The conclusions as to the mode or laws of evolution which thus seem to follow from the study of series of fossil mammals can make no pretensions to novelty, as they have all been repeatedly suggested before. Nor can they be regarded as entirely conclusive, for some of them, as we have already seen, may be fairly interpreted in several ways; it is not even possible, in the present state of knowledge, to entirely avoid all pre-suppositions in the construction of the phyletic series. But inasmuch as there is so little agreement upon these points, I have thought that it would be of service to clearly state just what the problems are and how the known facts seem to be related to them. On some of the questions the evidence speaks with no uncertain sound; thus, for example, arrange the phyletic series how we may, the occurrence of parallelism and convergence in development is clear. This conclusion can only be avoided by the assumption of complex cross and reticulated relationships, such as no one has ever ventured explicitly to defend. I venture to hope that morphologists may test and extend these tentative results by applying to them other and wider classes of facts than those from which they have been drawn.

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#### ON SOME OF THE FACTORS IN THE EVOLUTION OF THE MAMMALIA.

The question of evolutionary philosophy as to which there is at present the most dispute is undoubtedly that with regard to the causes of variation, together with the problems of heredity, which are inseparably connected with it. The brilliant essays of Weismann have done great service in calling renewed attention to these fundamental questions, for there can be no doubt that most speculations upon the subject had been taking

too much for granted, and that the foundations of one essential part of current evolutionary belief were insecurely laid. The whole subject needs, therefore, to be exhaustively re-examined and tested from every side.

For the purposes of this paper it is not necessary for me to enter into the reasons of my dissent from Weismann's theory of the continuity of the germ-plasm, nor to explain why, in my opinion, so far from rendering the phenomena of heredity more intelligible, it tends to confuse them still further and to end logically in a system very like the old preformationism. As Lloyd Morgan has very pithily put it, "I cannot but regard Weismann's doctrine of the continuity of germ-plasm as a distinctly retrograde step. His germ-plasm is an unknowable, invisible, hypothetical entity. Material though it be, it is of no more practical value than a mysterious and mythical germinal principle. By a little skilful manipulation it may be made to account for anything and everything. The fundamental assumption that whereas germ-plasm can give rise to body-plasm to any extent, body-plasm can under no circumstances give rise to germ-plasm, introduces an unnecessary mystery. Biological science should set its face against such mysteries" (No. 39, pp. 141 and 142). But into this subject we need not enter, because so far as the mammals are concerned, the difficulty of comprehending how somatic changes can affect the germ in appropriate fashion so as to reproduce these changes in the offspring, is in no way diminished by a denial, or even a complete refutation of the continuity theory. Weismann states the difficulty thus: "It is perfectly right to defer all explanation, and to hesitate before we declare a supposed phenomenon impossible, because we are unable to refer it to any of the known forces. No one can believe that we are acquainted with all the forces of nature. But, on the other hand, we must use the greatest caution in dealing with unknown forces, and clear and indubitable facts must be brought forward to prove that the supposed phenomena have a real existence, and that their acceptance is unavoidable" (No. 57, pp. 80 and 81). But does the assumption that acquired characters are transmissible involve, as a matter of fact, an appeal to unknown forces? Rather, I should say, to the as yet not well understood operation of known forces. In another connection, Weismann has himself well defended this principle, when, in

arguing against the idea of a vital force, he says: "The latter, [*i.e.* the ontogenetic vital force] is no longer admitted by anybody, now that we have turned from mere speculation to the investigation of nature's processes; nevertheless its non-existence has not been demonstrated, nor are we yet in a position to prove that all the phenomena of life must be traced to purely physico-chemical processes, to say nothing of our actually being able to so trace them" (No. 58, p. 643).

In his later papers, Weismann admits that the germ-plasm may be modified in various ways. "It must be admitted that there are cases, such as the climatic varieties of certain butterflies, which raise some difficulties against this explanation. I, myself, some years ago, experimentally investigated one such case, and even now I cannot explain the facts otherwise than by supposing the passive acquisition of characters, produced by the direct influence of climate" (No. 57, p. 99). "I am at present inclined to believe that Professor Vines is correct in questioning whether sexual reproduction is the *only* factor which maintains Metazoa and Metaphyta in a state of variability" (No. 60, p. 322). We have, indeed, abundant evidence that food, temperature, moisture, salt, and the like may have a profound influence upon the germ-plasm, and though we can form no conception of the way in which the amount of salt in the water will change *Artemia* into *Branchipus*, or the quantity of food will determine the proportion of the sexes in tadpoles, or how the change of food-plant metamorphosed the Texan species of *Saturnia* into something very different (see Moritz Wagner, No. 55, pp. 307-310), yet we are not impelled to take refuge in an appeal to unknown forces. Nor can the well-known influence of the germ-glands upon the body be explained in the sense of determining just how and why the effect is produced. If the presence of the germ-glands can so profoundly affect the soma, why should the converse influence appear so incredible? Still more mysterious is the influence exerted upon the maternal organism by the spermatozoa (or perhaps the foetus), so that the offspring by later sires often show characters of previous sires. Virchow pronounced the stigmata of Louise Lateau to be "either fraud or miracle," but the recent investigations in hypnotism show that the case may be explained without accepting either horn of the dilemma. Whether acquired characters be transmitted or not, it is cer-

tainly inadmissible to speak of such transmission as inconceivable or as involving the operation of unknown forces.

It is extremely difficult to obtain any satisfactory evidence of the transmission of acquired characters, and this for two reasons. In the first place, it is generally well-nigh impossible to determine in any given instance whether a character is acquired or congenital (employing the latter term to designate characters due to changes in the germ-plasm itself). As a rule, it is taken for granted that those structural features with which an animal is born or hatched are altogether congenital, but nothing can be more improbable; for we know that embryos are very sensitive to changed conditions, and are easily modified, but to determine what characters are due to changes in the ovum and what to modifications in the embryo, is a difficult matter. For my own part, I am not inclined to attach much importance to the supposed cases of transmitted mutilations, as from an *a priori* standpoint they are improbable, and more especially because the long-continued mutilations practised by many savage races appear to be without result in this respect. Nevertheless, such facts as those stated by Eimer (No. 15, p. 191) and DeCandolle (No. 14, p. 94), from their own knowledge, and the experiments of Obersteiner upon guinea-pigs, are not to be dismissed with a sneer. Arbuthnot Lane has come to the conclusion "that a force which produces no obvious change in the skeleton of the antecedents, but only a tendency to change, can, acting as a developmental factor, cause the apparently spontaneous development of that change in the offspring" (No. 29, p. 215). It is also well worthy of inquiry how far the extraordinary skill and deftness of Japanese and other Oriental workmen is due to the fact that handicrafts have long been hereditary in the same families.

Dall's position is an eminently reasonable one: "The contention of Weismann, that 'not a single fact hitherto brought forward can be accepted as proof' of the transmission of acquired characters, demands attention. This reminds one of the familiar statement of twenty years ago, that the Darwinians had not brought forward a single instance of the conversion of one species into another species. If the Dynamic Evolutionist brings forward an hypothesis which explains the facts of nature without violence to sound reasoning, that hypothesis is entitled

to respect and consideration until some better one is proposed or some vitiating error detected in it" (No. 12, p. 7). When we remember that evolution is a slow process, it is hardly to be expected that dynamic influences should be immediately apparent, though the experiments on *Artemia* and on feeding caterpillars point to a different conclusion. The question must be decided, if at all, by the inductive method, by determining how the observed facts can best be interpreted.

When we turn to the hypotheses which Weismann proposes in place of what Dall calls the dynamic theory, we might naturally require the same rigid demonstration which he demands of his opponents, but of such demonstration we find little, but rather ingenious speculation. Although he has abandoned the view that sexual reproduction is the *only* factor in inducing variability, he still appears to maintain that it is by far the most important. "I am still of the opinion that the origin of sexual reproduction depends upon the advantage which it affords to the operation of natural selection; nay, I am completely convinced that only through its introduction was the higher development of the organic world possible. . . . Even if, however, from our present knowledge it is probable that sexual reproduction is not the sole radical cause of variability in the Metazoa, still no one will dispute that it is a most effective means of heightening variations, and of mingling them in favorable proportions. I believe that the important part which this method of reproduction has played in calling out the existing processes of selection, is hardly diminished, even if one grants that direct influences upon the idioplasm call forth a portion of individual variability" (No. 60, p. 323). Weismann still maintains that somatogenic characters, the effects of use and disuse, and the like, cannot be transmitted, and attempts "to elucidate the phenomena without the aid of this principle."

But as Lloyd Morgan has pointed out, "by sexual admixture alone, there can be no increase or decrease, beyond the mean of the two parental forms. If, then, the union of sperm and ovum be the source of new or more favorable variations, other than or stronger than those of either parent, this must be due to the fact that the hereditary tendencies not merely commingle, but, under favorable conditions, combine, in some way different indeed from, but perhaps analogous to, that exemplified in chem-

ical combination" (No. 39, p. 151); of course such organic combination is not vouched for by a particle of evidence.

Again, on the theory of heredity propounded by Weismann, such variations are necessarily single, and there is no probability that the same variation will arise twice, even in the same litter. Now it has never been shown that such variations can be perpetuated in spite of the swamping effects of free intercrossing, nor that such minimal differences as a slight shifting of the carpal and tarsal elements, or the presence of a tiny incipient cusp upon a tooth, can be of decisive effect in the struggle for existence. This difficulty has long been felt, and many attempts have been made to meet or to evade it. Weismann has stated the case thus: "Such calculations as those quoted by Darwin from the article in the *North British Review* of March, 1867, are extremely deceptive, since we have no means of measuring the amount of protection afforded, and we can therefore hardly compute with any certainty, in how great a percentage of individuals a change must contemporaneously occur in order to have a chance of becoming transferred to the following generation. . . .

*Variations which occur singly have but little chance of becoming predominant characters*, and this is obviously what Darwin concedes; but this is by no means equivalent to the assumption that only those variations which from the first occur in numerous individuals, have a chance of being perpetuated" (No. 58, pp. 658 and 659). But it is difficult to see, on Weismann's principles, how variations can occur other than singly (*i.e.* excluding those cases of the influence of the environment upon the germ-plasm, by which many individuals are simultaneously affected), except in the direct line in which the change first appeared, for by hypothesis every fertilized ovum is different in important respects from every other, and on the doctrine of chances there is only an infinitesimal probability that it can ever be duplicated. The argument that variations do occur in nature sufficient to give the necessary material for the operation of natural selection, does not touch the real difficulty, which is what *causes* these variations? It is taking a great deal for granted to assume that they are solely or even mainly due to sexual reproduction.

The relatively fixed direction taken by variations, which has been insisted upon by so many observers, — *e.g.* Askenasy (No. 1), Eimer, Geddes and Thompson (No. 21), Osborn (No. 43), —

comes out most clearly in the series of fossil mammals. Granting that unlimited variation is no necessary part of the selection theory, it seems strange that new facets on the bones and new cusps on the teeth should appear only in such definite ways, and that there should not be many tentative attempts and false starts before the proper development is hit upon. In the structure of the carpus and tarsus we find that in any given phylum very definite lines of evolution are early established and closely adhered to, and the changes are just those called for by the operation of dynamical influences. If Weismann's position were correct, we ought to find much greater latitude of variation.

It is thus difficult to understand how even a single variation can be established by the unaided operation of sexual reproduction and natural selection, but the difficulty is greatly increased when we take into account the phenomena of parallelism and convergence. We have seen that the selenodont type of molar tooth has been independently acquired in at least three lines, and probably in many more. The molariform premolars which occur in so many perissodactyls, in some artiodactyls, and in other groups, though copying more or less exactly the pattern of the molars, are composed of parts which are not homologous with those occupying similar positions in the molar crowns. These changes can be followed step by step and accounted for, if we admit the action of mechanical influences, but are very puzzling on the hypothesis of all round variation. The spout-shaped odontoid process of the axis occurs in the camels, the true ruminants, the horses, and other groups, and it has been shown that this structure is not due to inheritance from a common ancestor, but has been separately acquired. Still more striking is the case cited by Kowalevsky (No. 26), of the sudden and simultaneous appearance (using these terms in their geological sense) in so many different groups of the prismatic or rootless molar, with very complex enamel foldings, and the valleys filled with cement. Kowalevsky believes that the occasion of this remarkable revolution, as it may be fairly called, was the great extension of the grassy plains, and the consequent change on the part of most herbivorous animals from a diet of soft plants and leaves, to the siliceous grasses. Now what is the probability that such a series of changes in horses, rhinoceroses, pigs, ruminants, elephants, and other families, should be

due primarily to the mingling of different hereditary tendencies, especially when it is remembered that none of the ancestors of these groups possessed any such teeth? Or can it be reasonably contended that such parallel variations are due to the direct action of the climatic or other environment upon the germ-plasm? The tendency to the formation of prismatic molars appears even in the early Tertiary times, as is seen in *Paloplotherium* and *Hypisodus*, but these were premature attempts, and led to nothing. Cope has shown how clearly the skeletal peculiarities of the feet of the Tylopoda may be deduced from the mechanical effects of the cushion or pad upon which the foot rests, and I may add that the steps of the enlargement of this pad may be inferred, in the extinct forms, from the successive changes in the phalanges. The similarities between the elephants, on the one hand, and *Uintatherium*, on the other, are just those which must accompany greatly increased height and bulk, though the latter is the more important factor.

Furthermore, the facts of pathology and surgery bring clearly before us the way in which the skeleton is moulded by the pressures and strains to which it is subjected. The tendinal sulci are formed by the pressure of the tendons, and if these tendons are dislocated, the old grooves are gradually filled up and new ones formed. "After dislocations the old articular cavities will be filled up and disappear, while at the new point where the head of the bone is actually placed, a fresh articulation is formed, to which nothing will be wanting in the course of a few months, neither articular cartilages, synovial fluid, nor the ligaments which retain the bone in place" (Marey, No. 36, pp. 88, 89). The arrangement of the trabeculæ in the interior of the bones is in the direction of the line of the greatest pressure and strain, giving great strength with a minimum of material. When, by a fracture and reunion, the relation of the bone to the line of strain is changed, the direction of the trabeculæ will be correspondingly altered. The papers of Arbuthnot Lane (Nos. 28 and 30) give an admirable account of the way in which long-continued routine labor will modify the shapes and articulations of the bones. It would, however, be a mistake to suppose that the bone-structure is entirely due to influences exerted in the lifetime of the individual, for the facts of development show that these structures appear in the foetus before such influences are exercised.

We have seen that the proximal end of the humerus is very similar in the White River representatives of the horses and camels (*Mesohippus* and *Pæbrotherium*), having the bicipital groove single, narrow, and placed at the antero-internal angle of the head, while the external tuberosity is very large, and extends across nearly the entire anterior face of the bone. In the modern forms the bicipital groove is double, being divided by the large bicipital tubercle, and the external tuberosity is reduced to the size of the internal one. If all of these changes, which are carried out in such exact accord with the mechanical exigencies of each case, are not somatogenic, how can they be accounted for? What chance is there of such occurrences repeatedly taking place in widely separated groups of animals as the result of sexual reproduction, or of changes in the germ-plasm which stand in no other causal connection with the mechanical needs of the body, than that those variations which happen to be favorable are preserved? The improbability of such an explanation is still further increased by the fact that the numerous non-mechanical variations, which on this theory ought to occur, are not to be found in the fossil series except very rarely, and then as the manifest results of disease or accident. Why should there be such a profound difference between the method in which useful changes are brought about in the individual and those which modify the species? and how can we explain the mysterious pre-established harmony between the two classes of phenomena? It seems very wonderful that an "ever-vigilant natural selection," which introduced sexuality for the very purpose of producing and combining variations, should have failed to seize and make use of somatogenic changes. This class of phenomena is by no means confined to the vertebrate skeleton. Dall has shown how the characters of the hinge and shell of the bivalve mollusks have been evolved in accordance with mechanical principles (No. 12, p. 445). He has also shown "how the initiation and development of the columellar plaits in *Voluta*, *Mitra*, and other Gasteropods, is the necessary mechanical result of certain comparatively simple physical conditions; and that the variations and peculiarities connected with those plaits perfectly harmonize with the results which follow with inorganic material subjected to analogous stresses" (No. 13, p. 9). Neumayr, in describing the transition

of *Paludina Neumayri* into *P. Hærnesi*, says: "Wenn man ein Thonmodell von *Pal. Neumayri* hätte und dasselbe auf die einfachste und kürzeste Weise in *Pal. Hærnesi* umformen wollte, man könnte es kaum anders machen als die Natur vorgegangen ist" (No. 40, p. 61). Jackson has reached very similar results in the same department of investigation (No. 24).

It must not be inferred from what has been said above, that there is no individual variation among fossil mammals; on the contrary, there is a great deal of such variation, so that it is often a matter of extreme difficulty to distinguish the species even of the same horizon from one another, and the larger the number of specimens compared, the greater does the difficulty become. Nevertheless, these variations are to a great extent those which dynamical necessities demand, besides others for which, as yet, no explanation can be given. Indeed, there is some reason to question whether individual variations, in the ordinary sense of that term, form in all cases the material with which natural selection has to operate. Neumayr has called especial attention to the distinction between "mutations" and variations, using the former phrase, which was adopted from Von Waagen, to designate the successive members of a series in geological time, while the latter is employed for contemporaneous alterations in the same horizon. "Noch andere Eigenthümlichkeiten stellen sich ein, welche die Mutationen als etwas von den Varietäten Verschiedenes bezeichnen; so in erster Linie, dass in der Regel eine bestimmte Mutationsrichtung in jeder Reihe vorhanden ist, indem durch eine längere Aufeinanderfolge von Schichten hindurch immer dieselben Charaktere in demselben Sinne von einander abweichen. Wenn man die beiden hier abgebildeten Reihen genauer betrachtet, so sieht man, dass dieselben von einem Gliede zum anderen ohne wesentliche Schwankungen und Abwege in geradester Linie sich der Endform nähern. . . . Ein anderer bisweilen beobachteter Fall von grosser Wichtigkeit ist der, dass die verschiedenen Glieder einer Reihe Variationen derselben Art zeigen; während also ein Theil die Merkmale gleichmässig nach einer Richtung im Laufe der Zeit mutirt, zeigen andere Charaktere regellose Abänderungen und jede Mutation entwickelt denselben Varietätenkreis" (No. 40, pp. 60-61). Similar facts are clearly marked in several of the mammalian series, as in the various

species of the successive genera *Palæosyops*, *Diplacodon*, and *Titanotherium*, of *Oreodon* and *Eporeodon*, and many others. On the other hand, it is by no means always the case that those genera which exhibit the greatest amount of variability at any given time, are those which in the long run have undergone the most extensive "mutation"; on the contrary, such genera frequently exist for very long periods substantially unchanged, but showing great variability at every stage in their history.

These facts at least suggest the possibility that individual variations are not incipient species, but that the causes of transformation lie deeper, and act with more or less uniformity upon large numbers of individuals. It may, perhaps, be the outcome of future investigations, that while variations are generally due to the union of changing hereditary tendencies, mutations are the effect of dynamical agencies operating long in a uniform way, and the results controlled by natural selection. While this *may* be true, a great many facts must be gathered in its support, before it can be regarded as more than a suggestion.

In particular, it is difficult to see how a new character can arise from the crossing of two forms, neither of which possess that character. Some facts are, it is true, recorded, which seem to show that new characters may thus arise, as for example in certain hybrid plants which exhibit features present in neither of the parent species. But, for the present, such facts must be received with great reserve, for the analogy of domesticated breeds shows that crossing favors reversion, and in every case the supposed new characters may be atavistic. At least, no conclusion can be safely drawn from such facts, until it is shown that reversion is excluded. To avoid this difficulty as to the production of new characters, Weismann assumes that all variations are quantitative and not qualitative. This is equivalent to saying that there are no qualitative differences in the organic world. No summation of quantitative differences can bring about chemical changes; for example, the first appearance of muscle, cartilage, and the various tissues cannot thus be accounted for, and if the principle be abandoned for these cases, its importance is at once destroyed. The only escape from this difficulty is the suggestion of Lloyd Morgan, already quoted, that impregnation represents not a mere commingling, but a combination analogous to chemical union; but for this there is no evidence, and Morgan himself is

not inclined to accept it. Many authorities attribute just the opposite influence to sexual reproduction to that which Weismann postulates. Strasburger regards it as the means of removing injurious modifications, and of keeping the species constant to its type, and a very similar position is taken by Hatschek and others. But in view of the many observations collected by Darwin upon the subject of cross and self-fertilization, and of the physiological importance of crossing to the individual, both Weismann's position, on the one hand, and Strasburger's, on the other, appear to be but a very partial and incomplete view of the matter. At all events, we are entitled to demand much fuller and more satisfactory evidence before attributing to sexual reproduction such a pre-eminent place as a factor in evolution.

In the course of development the reduction and loss of structures plays quite as important a part as differentiation and the acquisition of new organs. No one can study any large group of vertebrates without being struck by the way in which the two processes accompany and balance each other. In any advancing group of organisms the course of differentiation does not affect all organs alike; some are stationary, others are progressing towards a higher state of efficiency, and others again are retrograding and even disappearing. It is this fact which makes the natural arrangement of any group of organisms such a very difficult and puzzling problem. It is obvious, therefore, that any system of evolutionary philosophy must include an explanation of the way in which organs are reduced and suppressed, as well as the mode in which they are acquired. The current view of the matter is that the loss of organs is due to atrophy from disuse, but this view is of necessity entirely rejected by Weismann, who has examined the problem with much care in his very interesting essay, "*Ueber den Rückschritt in der Natur*" (No. 59). According to him the efficient cause of reduction is cessation of selection or panmixia, by which useless parts, being no longer selected, tend gradually to disappear, and a free intercrossing, as regards those particular structures, is no longer prevented. This view, however, presupposes that selection is the only power which originates and maintains structures,—a thesis which is very far from being proved, if it can even be regarded as probable. Indeed, the

whole theory of panmixia is highly problematical, supported by very few observed facts, and the very cases which Weismann cites show how unsatisfactory is his explanation. Let us examine a few of these cases. "Ein Beispiel ganz anderer Art geben uns diejenigen Thiere an die Hand, welche einen Theil ihres Körpers in Gehäusen verbergen. So stecken die Einsiedlerkrebse ihren Hinterleib in leere Schneckenschalen, die Larven der im Wasser lebenden Köcherfliegen verfertigen sich Gehäuse in denen sie ihren langgestreckten vielgliedrigen Hinterleib verbergen und dasselbe thun die Raupen gewisser kleiner Schmetterlinge aus der Gruppe der Spinner. Bei allen diesen Thieren finden wir nun, dass die Haut der durch Gehäuse geschützten Körpertheile weich ist und weisslich, d. h. ohne besonderen Farben, während die aus der Schale hervorragenden Theile den gewöhnlichen harten Hautpanzer der Gliederthiere und verschiedentliche, meist lebhaftere Farben besitzen. Nun kann man ja in einem gewissen und etwas uneigentlichen Sinn sagen, der Hautpanzer der Krebse und Insekten habe die 'Funktion' die inneren weichen Theile des Thiers vor äusseren Verletzungen zu schützen, aber im wahren Sinn ist das eben keine Funktion, weil keine Thätigkeit damit verbunden ist; die Leistung des Panzers beruht einfach auf seiner gänzlich passiven Anwesenheit. Ob das Thier durch ihn gegen Stiche oder Bisse, oder ob solche Bedrohungen gar nicht bis an ihn gelangen, das ist für den Panzer selbst und sein Gedeihen völlig gleichgültig; er verliert und gewinnt dabei nichts und am allerwenigsten hängt sein Wohlbefinden davon ab, möglichst häufig von Stichen oder Bissen getroffen zu werden. Er kann unmöglich dadurch direkt zur Rückbildung veranlasst werden, dass er durch das Gehäuse solchen Angriffen ganz entzogen ist. Wenn also der Panzer in allen den drei angeführten Fällen, sich genau so weit zurückbildet, als der Körper von dem schützenden Gehäuse bedeckt ist, so kann dies wiederum nur dadurch erklärt werden, dass für die von dem Gehäuse bedeckten Körperstellen der Panzer überflüssig und bedeutungslos wurde und dass Naturzüchtung sich desshalb nicht mehr mit seiner Erhaltung befassen konnte" (No. 59, p. 19).

The inadequacy of this account of the function of the armor is too obvious to need comment; one might as well say that the bones of the vertebrate skeleton perform their functions

merely by their passive presence, and therefore could not be affected by disuse, which we know very well is not the case. Probably no one imagines that the armor of crustaceans and insects owes its origin to "Stiche und Bisse," or that its welfare in any way depends upon them, but muscular activity, contact with the water, light, etc., are essential. On the theory of panmixia what is the probability that the reduction should reach *exactly* as far as the tube or shell in which the animal lives? It is a matter of no consequence whether the armor extends a little way into the tube or not; why, then, such superfluous accuracy? Admitting that this might happen in the case of one species, it becomes more and more improbable with every case observed. On the other hand, if the presence of the tube or shell does have a direct effect, this exact correspondence is just what might be expected. Indeed, Weismann's explanation is contradicted by a dictum which he lays down in another part of the same essay, though it should be added that this proposition refers primarily to positive differentiation. "Die Organismenwelt beweist uns, dass dem so ist, denn bis ins Einzelste hinein, sehen wir jede lebende Art sich zweckmässig gestalten, als es unumgänglich nothwendig ist, um sie existenzfähig zu machen, *nicht um ein Minimum mehr*" (p. 30).

The case of the neuter insects does, however, offer a formidable difficulty to the doctrine of the inherited effects of disuse, as, indeed, it does to any explanation. It would lead too far from the main subject of this paper to give to this problem the full and extended discussion which it requires. I can, therefore, only refer the reader to Eimer's examination of this question (No. 15, p. 286 ff.), which it seems to me is quite as probable as Weismann's, to say the least; especially if one will carefully follow out the steps of the probable process by which, for example, the worker ants have lost their wings. But even if we admit Weismann's position in regard to the neuter insects, it would merely be saying that disuse is not the only factor in the suppression of organs, an assumption which few would be bold enough to make. At all events, Darwin, who first insisted upon the difficulty presented by these insects, did not regard it as militating in any way against the assumption of the effects of disuse in other cases.

The positive evidence in favor of the theory of panmixia is

extremely scanty, and indeed what direct evidence there is, tells against it. Thus Galton's researches have brought out the law of "regression to mediocrity," by virtue of which the succeeding generations of a population resemble each other. "In each generation, individuals are found to be tall and short, heavy and light, strong and weak, dark and pale; and the proportions of those who present these several characteristics in their various degrees, tend to be constant" (No. 20, p. 116). Galton's results, which are too long to quote and cannot very well be abridged, tell strongly against attributing any importance to panmixia as a factor in transformation. Lloyd Morgan, following the same line of reasoning, points out that panmixia "can only affect a reduction from the 'survival-mean' to the 'birth-mean'" (p. 191). "Unless, therefore, some cause be shown why the negative variations should be prepotent over the positive variations, we must, I think, allow that unaided panmixia cannot affect any great amount of reduction" (p. 193). Lankester does not admit that panmixia can explain the reduction of parts, unless assisted by the principle of economy of growth (No. 31, p. 559). But the importance of this principle may be easily overrated. In the admirably thorough investigations of Tornier (No. 54) upon the calcaneo-astragalar joint, it is shown how closely the development and reduction of facets follows the manner in which the foot is used, and the consequent mechanical necessities. Now, it is incredible that economy of growth should demand the reduction of these minute facets, when such rudiments as the splint-bones of the horse or the pelvis of the whale are allowed to persist in the organism. Nor is it easy to see how the principle of economy can apply to domesticated animals, and still more to internal parasites which have such a superabundance of nutriment, and yet the latter are precisely the forms in which reduction of parts has proceeded to the greatest extremes. Among domesticated animals and plants we find that those parts which are not subject to selection are (aside from the effects of correlation and the direct action of the environment, such as too much or too little of certain foods, water, etc.) remarkably constant, which by Weismann's theory they should not be.

Another class of facts, which are very difficult to explain from the standpoint of panmixia, is furnished by certain larvæ. In another paper (No. 50) I have examined the development of

the higher sense organs of *Petromyzon*, which are subject to a remarkable degree of retardation. Thus the eye, throughout the long larval life of the creature, is extremely small and deeply buried beneath opaque tissues of the head. Even at its first appearance the optic vesicles are extremely minute, and the lens is tiny. The retina remains in a rudimentary condition throughout larval life, and only when the larva is metamorphosed into the sexual animal does the eye reach its normal size and development. Similarly, the olfactory organ during the larval period is a simple epithelial sac, which at the time of metamorphosis becomes an exceedingly complicated structure. The ear alone attains in the larva a degree of development comparable to what it has in the adult. This retarded condition of the higher sense organs has an obvious connection with the habits of life; for the larva lies buried in the mud and sand of rivers, while the adult lives in clear and swift waters. The effects of the larval habits are shown even in the embryo before hatching; for the sense organs, and especially the eye, are proportionately much smaller than they are in other vertebrates, even in the earlier stages. These facts are easily enough explained, if we admit the direct action of the environment, at first arising in the larva, and then gradually transferred to the embryonic stages, just in the way in which Hyatt and Würtenberger have shown that new characters in the shells of ammonites arise first in the fully adult shell, and then are gradually transferred to earlier and earlier stages. But to refer this retardation in the development of the sense organs of *Petromyzon*, to what in this connection may fairly be called fortuitous changes in the germ-plasm, is merely to conceal our ignorance under the guise of an explanation.

When we turn to the series of fossils, and follow out the history of disappearing organs, we find little to support the theory of panmixia. The reduction is steady and sure, if slow, exhibiting of course a certain degree of individual variation, but not the fluctuations which we should naturally expect to find, were panmixia alone the cause of the reduction. As a matter of fact, when examining an extensive series of fossils reaching through many horizons, it is difficult to escape the suspicion that individual variations are not the material with which natural selection works, so steadily does the series advance toward what seems almost like a predetermined goal. This slowness and steadiness

of reduction, together with other facts already mentioned, render the question as to whether mutilations are or are not transmissible, a matter of relatively small importance; for only those direct effects of the environment which similarly modify many individuals and are long continued can be of real significance in the work of transformation. "On the whole, even taking into consideration the effects of panmixia, of reversed selection, and the principle of economy, the reduction of organs is difficult to explain, unless we call into play 'disuse' as a co-operating factor" (Lloyd Morgan, No. 39, p. 197).

Weismann's views upon the factors of evolution are, to a great extent, deductions from his theory of heredity. If established, they will render impossible any real insight into the mechanism of development in any given case, and we shall always leave unexplained the immense series of cases in which development follows just such a course, and no other, as it would do if somatogenic influences really shaped the result; the path being followed out with neither fluctuation nor important deviation, as is apparent whenever extensive phylogenetic series can be thoroughly studied. Of course, it is no argument against the truth of these theories that such should be their outcome, but it should be clearly recognized that progress does not consist in substituting a phrase or a formula for an explanation. This has been well expressed by Claus (No. 4, pp. 27, 28), who says:—

"Wollten wir auf die Verwerthung derselben [d. h. der functionellen Anpassungen] verzichten, so würden wir mit Nägeli und Weismann auf die geheimnisvollen Vorgänge im Innern des Idioplasma und der Keimzelle beschränkt sein, die wir uns zwar als moleculär-mechanische Veränderungen theoretisch vorstellen können, deren factischer Verlauf aber unbekannt und überdies seiner wahren Ursache nach im völligen Dunkel bleibt. Das ist das Gemeinsame an den Theorien Nägeli's und Weismann's und wird nicht etwa, wie letzterer meint, durch den Umstand widerlegt, dass er zur Begründung seiner Lehre eine einfache Thatsache verwerthe. Wenn es auch eine Thatsache ist, dass bei der Befruchtung die Vererbungstendenzen, welche in der Eizelle schlummern, sich mischen, und daraus ein neuer Organismus mit einem bisher noch nicht dagewesenen Gemenge individueller erblicher Charaktere hervorgeht, so ist doch damit das Geheimnissvolle des bezüglichen Vorganges nicht minder

behaben als das Dunkel, welches in Nägeli's Vervollkommnungstendenz liegt, für deren Bestehen auch thatsächliche Verhältnisse der im Sinne der Vervollkommnung fortschreitenden Entwicklung geltend gemacht werden. . . . Denn was ist diese in das Urkeimplasma hineingelegte Entwicklungsordnung Anderes als eine ihrem Wesen nach geheimnissvolle phyletische Kraft, über deren bewirkende Ursache wir ebensowenig durch Nägeli's zweckmässig eingerichtete Vorgänge der Molecularmechanik, wie durch Weismann's Vererbungs- und Entwicklungstendenzen auch nur eine entfernte Auskunft erhalten. Auch in den von Letzterem verwertheten Variationen wird man doch nur Bedingung oder Anlass zu der besonderen Structurgestaltung des Keimplasmas und diesen entsprechenden Bewegungsvorgängen der Molecülgruppen, nicht aber die bewirkende Ursache der Erscheinung selbst erkennen. . . . Weismann täuscht sich daher selbst wenn er Nägeli's Annahme eines völlig unbekannten Principis gegenüber die Umwandlungen der Organismen lediglich aus den *bekannten* Kräften und Erscheinungen ableiten zu können glaubt. In Wahrheit steht derselbe mit Nägeli auf wesentlich gleichem Boden, auf der Supposition eines inneren, treibenden Entwicklungsprincipis, wenn er auch die Annahme desselben nicht zugesteht und ohne dessen Hilfe auskommen zu können vermeint."

The great difficulty in the way of the "dynamic theory" of evolution (to use Dall's phrase) is the problem of heredity, of understanding how changes in the periphery can modify the germ-plasm in such a way as to reproduce the new characters in the offspring. But, admitting this difficulty to the fullest extent, it would certainly seem that the proper method of treatment is first to determine what are the facts of heredity, and then attempt an explanation of them, not to formulate an *a priori* view, and then ascertain whether the facts can be made to support it. I am not concerned to elaborate here a theory of heredity, being strongly of the opinion that, in the present state of knowledge, nothing better than provisional working-hypotheses can be devised, which, of course, may serve a most useful and valuable purpose, but which have little chance of final establishment.

To sum up the results of our examination of certain series of fossil mammals, one sees clearly that transformation, whether

in the way of the addition of new parts or the reduction of those already present, acts just *as if* the direct action of the environment and the habits of the animal were the efficient cause of the change, and any explanation which excludes the direct action of such agencies is confronted by the difficulty of an immense number of the most striking coincidences. We must all heartily agree with Weismann in saying that "we require, not a mere formal explanation of the origin of species of the most comfortable nature, but the real and rightful explanation." Whether his theories, profound and brilliant as they are, are to give us this real and rightful explanation, the future must decide.

GEOLOGICAL MUSEUM,  
PRINCETON, N.J., July 20, 1891.

P.S. — The preceding paper was all in type before I received Lloyd Morgan's very valuable and suggestive article on "The Nature and Origin of Variations" (Proceedings of the Bristol Naturalists' Society, Vol. VI., Part III.). I regret this the more because Professor Morgan seems to have somewhat misapprehended the character of the evidence to be derived from palæontology in favor of the dynamical view of evolution. "Those American zoölogists who have studied the evolution of mammalian teeth contend that the occurrence of new points and cusps is not indeterminate, but determinate. New elements of tooth-structure appear in definite positions. There is nothing to indicate selection from among indefinite variations. Other evidence of like implication is adduced by American evolutionists; but this of tooth-structure is put forward as the strongest case. I am inclined to think that the facts of palæontology, so far as they go, point in this direction. But I question whether they can be regarded as conclusive. In criticising the position, stress may be laid on the imperfection of the geological record; and it may be urged that the number of individuals in our palæontological collections is not sufficient to constitute a truly representative sample. Furthermore, on the hypothesis of selection, the individuals possessed of teeth with points and cusps in other than these adaptive positions must have been weeded out in the early stages of life. In view of these objections the evidence

cannot be said to be convincing, though in my opinion it affords some presumption in favor of determinate variation" (p. 5).

"We have seen that the American school of biologists contend that variations, for example in tooth-structure, are determinate and not indeterminate. They also contend that these variations are largely due to the inherited effects of use and disuse. They tell us that in a large percentage of cases the new elements of tooth-structure appear in regions of ancestral wear and abrasion. Granting the determinate variations, we may perhaps inquire whether the abrasion may not be due to the presence of incipient points rather than the development of points to increased abrasion. It is admitted that the new points do not always occur where there has been previous abrasion. Granting the determinate variations, therefore, it does not appear to be satisfactorily proved that they are due to the effects of inherited use and disuse. Seeing the nature of tooth-growth and development, one needs very cogent evidence of the production of new points or cusps at regions of marked ancestral abrasion. The development of certain elements of vertebrate limb-structure and concomitant dwindling of other elements may be adduced as more readily comprehensible effects of inherited use and disuse. But here we have not the same evidence of the determinate nature of the variations, and the theory of selection from among favorable indeterminate variations is not to the same extent, on the showing of the American school themselves, excluded. It seems, then, that where the evidence for determinate variations is strong, the theory of use-inheritance is difficult of acceptance, and where use-inheritance is more readily comprehensible there is less evidence that the variations are determinate" (pp. 14, 15).

For my own part, I wish to disclaim the idea of belonging to any "school" whatever. Those American observers who have especially devoted themselves to the morphology of extinct forms have independently reached certain conclusions, in which they agree; as to other results, they are by no means so concordant. It seems to me that the evidence points very strongly in certain directions, but new evidence may at any time altogether destroy the force of the old. So far as I can see, the theory of determinate variations and of "use-inheritance" is not antagonistic, but supplementary to natural selection, the

latter theory attempting no explanation of the *causes* of variation. Nor is it for a moment pretended that use and disuse are the sole or even the chief factors in variation. On the contrary, we know that many other and even more important factors enter into the process.

Turning now to Professor Morgan's criticisms of the palæontological evidence, we may say that the objection drawn from the imperfection of the geological record and from the small number of individuals contained in the museums, can be allowed little weight. So far as several of the mammalian phyla are concerned, the number of missing links must be very small, the wonderful series of American fresh-water Tertiaries being in this respect quite unrivalled in the known world. Of the better known species, the collections already contain hundreds and sometimes thousands of individuals available for study. If results obtained from such material point in one direction, it is surely most illogical to assume that specimens yet to be discovered will probably lead to opposite conclusions. The probabilities are all the other way. Professor Morgan seems also to suppose that individuals "in the early stages of life" are uncommon as fossils; but this is very far from being the case; they are abundantly represented in the collections and show no more tendency to indeterminate variation than do the adults. But even were the young stages unknown, before their absence could be allowed weight as an objection, it would be necessary to show that such very slight changes were of "elimination value."

I am unable to see why the evidence afforded by foot-structure is any less cogent in support of determinate variations than that derived from the teeth, except in so far that not nearly so many completely preserved feet are found. But where they do occur in numbers, the result is the same. The carpus and tarsus of the equine series from *Hyracotherium* to *Equus* form as striking an example of this as could be desired. The non-mechanical variations do not occur. The difficulty of comprehending how teeth can be modified by use, must be freely admitted. But it should be remembered that a completely formed tooth is not by any means a dead, inorganic mass. Its health depends upon use, and I have seen fossils which clearly demonstrate the ill-effects of disuse of teeth in the individual.

Further, the principle already quoted from Arbuthnot Lane with regard to the skeleton, will doubtless apply to the teeth; "that a force which produces no obvious change in the skeleton of the antecedents, but only a tendency to change, can, acting as a developmental factor, cause the apparently spontaneous development of that change in the offspring." The admission, quoted by Professor Morgan, that "the new points do not always occur where there has been previous abrasion," is due to the fact that freshly formed and unworn teeth were examined in that regard, overlooking later stages of wear. In all cases known to me, the new points appear in places where, at some stage, there is special abrasion. Of course, it would be folly to pretend that the mechanics of dental evolution have been completely worked out or that no difficulties exist. On the contrary, only a beginning has been made, but as a *working hypothesis* the assumption that the effects of use and disuse can be inherited, and that mechanical factors do have a part in the result, has already rendered such good service, that we feel justified in retaining it.

That the effects of use and disuse are not the only factors in producing variations in tooth-structure, we have clear evidence. Thus Nathusius has shown that in the swine defective nourishment may have a remarkable effect in modifying the character of the teeth. "Die Zähne des Versuchsthiers haben einen ausserordentlich dünnen Schmelzüberzug, so dünn, dass derselbe auf den Kauflächen von mol. 1 bereits vollständig, von mol. 2 beinah ganz abgenutzt ist, während bei dem gut genährten in Vergleich gezogenen Thier bei mol. 1 nur eine schwache Abnutzung stattgefunden hat und bei mol. 2 sogar nur die Haupthügel des vorderen Jochs oben so weit ihre Spitzen verloren haben, dass man in dem massiven Schmelzring einen kleinen Knochenkern erkennt.

"Dieser dünne Schmelzüberzug ist sehr wenig in Falten gelegt, es ist dies besonders auffallend an dem noch in der Höhle befindlichen mol. 3 dessen Haupthöcker beinahe ganz glatt sind. Alle Nebenhöcker und Warzen sind schwach entwickelt, an mol. 1 sogar kaum eine Spur davon vorhanden.

"So hat denn dieser Versuch in frappanter Art ergeben, in welchem Grade nicht nur die Stärke des Schmelzüberzuges, sondern auch das Zerfallen der Zahnkronen in zahlreiche und

crenellirte Nebenhöcker und Warzen abhängig ist von der Ernährung des Thieres" (Schweineschädel, pp. 102, 103).

I do not wish to be understood as in any way deprecating the extremely candid, fair, and open-minded criticism to which Professor Morgan has subjected the evidence drawn from the study of American fossils; but I cannot consent to be bound by the admissions of members of the "American school." While I freely grant that the evidence presented in the foregoing pages in favor of mechanical factors in evolution is not convincing or conclusive, I think it may fairly claim to afford something more than "a presumption in favor" of such factors.

PRINCETON, October 12, 1891.

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## EXPLANATION OF THE PLATES.

(Where not otherwise indicated, all the figures are of natural size.)

## PLATE XXII.

FIG. 1. *Mesohippus Bairdi*. Skull, from the side.  $\times \frac{3}{4}$ . This skull is drawn from a specimen in the Princeton Museum, with details added from specimens in the Academy of Natural Sciences, Philadelphia. *C.* canines; *Ty.* tympanic bulla; *par.* paroccipital process; *Ms.* mastoid portion of the periotic.

FIG. 2. *Mesohippus Bairdi*. Skull, base view of a somewhat larger specimen.  $\times \frac{3}{4}$ . *i.f.* incisive foramen; *c.* canine alveolus; *m. 1*, first molar; *ac.* alisphenoid canal; *Ty.* tympanic bulla; *par.* paroccipital process; *c.f.* condylar foramen.

FIG. 3. *Mesohippus Bairdi*. Atlas, dorsal view. Cope collection. *v.c.* vertebrarterial canal; *a.n.* atlanteal notch.

FIG. 4. *Equus caballus*. Atlas, ventral view.  $\times \frac{1}{3}$ . After de Blainville.

FIG. 5. *Mesohippus Bairdi*. Axis, from the side.

FIG. 6. " " Axis, postzygapophyses seen from above.

FIG. 7. " " The same, another specimen.

FIG. 8. " " Axis, seen from the front.

FIG. 9. " " The same, another specimen.

FIG. 10. " " Fifth cervical vertebra, from the side.

FIG. 11. " " Sixth cervical vertebra, from the front.

FIG. 12. " " The same, from the side.

FIG. 13. " " Second dorsal vertebra, from the side.

FIG. 14. " " The same, from the front.

FIG. 15. " " Last dorsal vertebra, from the side. Cope collection.

FIG. 16. " " Last lumbar vertebra, from behind.

## PLATE XXIII.

FIG. 17. *Mesohippus Bairdi*. Skull, longitudinal section. *o. c.* occipital condyle; *B. S.* basi-sphenoid (crushed out of place); *Cb. F.* cerebellar fossa; *C. F.* cerebral fossa; *F. S.* frontal sinus.

FIG. 18. *Equus caballus*. Skull, longitudinal section.  $\times \frac{1}{4}$ . After de Blainville.

FIG. 19. *Mesohippus Bairdi*. Left humerus, from the front.  $\times \frac{2}{3}$ . *e. t.* external tuberosity; *i. t.* internal tuberosity; *bc. g.* bicipital groove; *d. r.* deltoid ridge.

FIG. 20. The same, from the outer side.  $\times \frac{2}{3}$ .

FIG. 21. The same, proximal end.

FIG. 22. The same, distal end.

FIG. 23. *Mesohippus Bairdi*. Left ulna and radius, from the outer side. *R.* radius; *U.* ulna.

FIG. 24. *Mesohippus Bairdi*. Radius, proximal end, from the front.

FIG. 25. " " Radius, distal end. *s'*, scaphoidal facet; *l'*, lunar facet.

FIG. 26. *Mesohippus Bairdi*. Right manus, from the front. *S.* scaphoid; *L.* lunar; *C.* cuneiform; *Tm.* trapezium; *M.* magnum; *U.* unciform.

FIG. 27. *Mesohippus Bairdi*. The same, from the outer side.

FIG. 28. " " The same, proximal view.

FIG. 29. *Equus caballus*. Carpus, from the front.  $\times \frac{1}{4}$ . After de Blainville.

FIG. 30. *Mesohippus Bairdi*. Metacarpals II., III., and IV., proximal ends.

FIG. 31. *Mesohippus Bairdi*. Right innominate bone, from the side.  $\times \frac{2}{3}$ . *t. i.* tuberosity of the ischium. (Cope collection.)

FIG. 32. *Mesohippus Bairdi*. Left tibia, from the front. *T.* tibia; *F.* fibula.  $\times \frac{2}{3}$ .

FIG. 33. *Mesohippus Bairdi*. The same, distal end.

FIG. 34. " " Left tarsus, from the front. *cf.* fibular facet of calcaneum; *Cb.* cuboid; *N.* navicular; *C.<sup>s</sup>* ecto-cuneiform; *C. 1 + 2*, coalesced meso- and ento-cuneiforms.

FIG. 35. *Equus caballus*. Right tarsus, from the front.  $\times \frac{1}{4}$ . After de Blainville.

FIG. 36. *Mesohippus Bairdi*. Left tarsus, distal end.

FIG. 37. " " Left astragalus, plantar side. *c'*, *c''*, *c'''*, facets for the calcaneum; *cb.* for the cuboid.

FIG. 38. *Mesohippus Bairdi*. Left calcaneum, from the medial side. *a'*, *a''*, *a'''*, facets for the astragalus; *cf.* for the fibula.

FIG. 39. *Mesohippus Bairdi*. Right metatarsus.  $\times \frac{2}{3}$ .

