A study of the theories of kinetogenesis

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A STUDY OF THE THEORIES OF KINETOGENESIS.

A Thesis
Submitted to the Faculty of the Graduate
College of the State University of Iowa,
in Partial Fulfillment of the Require-
ments for the Degree of Master of Science.

By
Beulah Hayden.

Iowa City, Iowa.
1912.
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INTRODUCTION.

The purpose of this work is to make a study of the theories of kinetogenesis and an application of those theories to the foot structures of mammals. As the field is so broad it was found necessary to restrict the study to the feet of the carnivores and ungulates. The material used was obtained from the State University of Iowa Museum. It should be kept in mind that, while only the feet are considered and compared, the conclusions drawn are not based solely on that evidence, but very often upon teeth and skull structures as well. This is especially true in all the work done on phylogeny.

Kinetogenesis is the theory of the development by motion. It is an attempt to explain structures as we find them today, by the mechanical environment to which the animals of the past were subjected. Since Professor Cope was the first man to propose the theory of kinetogenesis with reference to foot structure, his theories will be carefully studied. They were modified by the work of Professor Osborn, which must also be considered. Finally, after many years of work upon the material of the museums of this country, and in comparison of the results reached by other
workers, Mr. W. K. Gregory has arrived at conclusions which differ decidedly from those reached by either Professor Cope or Professor Osborn.

The classification used, is that given by Osborn in his "Age of Mammals" 1910. It is used because it is conservative, making only those changes necessitated by new material and careful study of forms already known.

Since Cope based his theories of kinetogenesis upon the phylogenetic series which he built up, it has been necessary to go as far as possible into the phylogenies of the groups studied. Material which has come to light since the work of Professor Cope, makes it impossible to accept his classification or the phylogenies based upon it. In the lines of descent of the horse and the camel, the phylogenies used here, are those given by Professor W. B. Scott in his class in "Vertebrate Palaeontology" for this year, and are based on Osborn's classification.

A short discussion of a typical mammalian manus and pes will be inserted here in order that the descriptions of the forms studied may be as condensed as possible.

The manus, or the third segment of the anterior limb, is made up of the carpus, and metacarpus, and phalanges. The typical
carpus is made up of two rows of small, rounded or cube-like bones, articulating with each other by flat articulations. The proximal row, from within outwards, consists of scaphoid, lunar and cuneiform; the distal row, of trapezium, trapezoid, magnum and unciform. Between the two rows in the primitive carpus, was a centrale but in most mammals it is now fused with other bones. Sesamoid bones are developed in the tendons passing over the carpus. The pisiform, on the ulnar side, is the largest of these bones and, since it is not a true carpal element, will not be considered. Distally the carpal elements articulate with the metacarpals, the trapezium with the first metacarpal, the trapezoid with the second, the magnum with the third and the unciform with the fourth and the fifth. The carpal elements may become fused or may be suppressed.

The metacarpals are usually five, named from within outward and articulating with the carpals by almost immovable joints: the distal articulations with the phalanges are freely movable.

The digits are usually five in number, each, excepting the first, made up of three phalanges, freely movable upon each other. The first digit has two segments. The ungual phalanges are usually modified to form hoofs or claws.

The pes is the terminal segment of the posterior limb and,
also, consists of three parts, tarsus, metatarsus and phalanges.

The tarsus is composed of seven roughly cubical elements arranged in two rows. The proximal row contains the astragalus and calcaneum. The astragalus is dorsal and enters into the tibiotarsal articulation; the calcaneum is plantar and projects back to form the heel bone. On the inner side the navicular is interposed between the two rows; on the outer side they are in contact. Named from within outward the distal row is made up of the internal, middle, external cuneiforms and cuboid. They articulate with the first, second, third, and fourth and fifth metatarsals respectively. The metatarsals and phalanges are very similar to those of the manus.

The joints of the manus and pes are all movable but differ greatly in the amount of mobility. As a rule, the joints between the elements of the carpus and tarsus and between the carpus and metacarpus, and tarsus and metatarsus, are gliding joints, with but little motion. It is greatest between the astragalus and calcaneum when it allows inversion of the foot. The ankle joint is a hinge joint; the wrist may have a condyloid or hinged articulation.
Order CARNIVORA.

The phylogeny of the Carnivores is especially unsatisfactory because the remains preserved are essentially scattered and few. It is always true that the carnivorous population at any time is far less than the herbivorous. In the geologic record this is accentuated by the fact, that, since as a rule carnivores are solitary, there was still less chance for the remains to be preserved in any numbers. Most of the remains found, which would give light on relationship, are known only by the skulls or teeth. So in this order no direct line of descent will be attempted and only well-known relationships will be mentioned.

The flesh eaters of the Eocene were the Creodonta, described by Cope as pentadactyl; plantigrade; astragalus usually ungrooved; long tailed; with larger heads; smaller brains, and shorter legs than modern carnivores. Their origin is not definitely known.

The relationship between the true creodons and the true carnivores or Fissipedia is still a matter of discussion. Cope thought the connection a very close one but, as Professor Osborn says, Science (2) 7. p. 145, "The actual links between the Creodonta and the Carnivora (Fissipedia) are unknown! The latest work, however, seems to show that the Fissipedia were derived from an off shoot of the Creodonta thru the family Miacidae which
presents divergent lines of development and seems to directly foreshadow the modern families. The question of the exact phylogeny of the Fissipedia can not be settled until new material gives more light on obscure points. But it is well known that the creodonts are found only in the Eocene and that the true carnivores appear in the Upper Eocene.

The origin of the Pinnipedia is also unsettled. Wortman (1902) attempts to show that they were derived from the Oxyaenid Creodonts. Weber (1907) by a careful study of comparative anatomy, seems to be able to prove that there is a closer relationship between the Arctoid Fissipeds. Both theories are open to criticism.

**Typical Creodont Manus and Pes.**

No manus or pes is known from the Creodont of the Basal Eocene but both are described for *Dissacus, Dromocyon, Oxyaena, Patriofelis* of the Lower and Middle Eocene. From these remains we are able to construct a typical form. The manus was pentadactyl, plantigrade; scaphoid and lunar distinct, and articulating with the radius; centrale present; trapezium relatively large; pollex somewhat divergent; trapezoid and magnum small; lunar resting almost equally on centrale, magnum and unciform. The metacarpals from II to V over ride each other.
The pes was, also, pentadactyl; plantigrade; astragalus with an ungrooved superior surface; fibular articulation more sharply angled downward than the tibial; head flattened antero-posteriorly but convex transversely, and extending beyond the calcaneum to articulate with both cuboid and navicular; cuboid elongate.

Family URSIDAE.

The family first appears in the Middle Miocene as Hyænarctus, Nicholson and Lydekker; but the genus Ursus is not found until the Pliocene.

Ursus americanus Pallas.

Manus; pentadactyl; almost plantigrade; short and broad.

Carpus; broad and loosely put together.

Scapholunar large, rectangular; articulating proximally with the radius by broad, rounded, ovate facet; radial protuberance separated from facet by groove; distal articulations four, the inner for trapezium, the second for trapezoid; the third, deeply grooved, for the magnum, and the outer, saddle shaped, for the unciform. The cuneiform, wedge shaped, articulating proximally with ulnar, and distally with unciform. The trapezium relatively large.

The trapezoid, the smallest bone.
Magnum small, roughly triangular in cross section.

Unciform pyramidal, with extensive distal facet for metacarpals IV and V.

Metacarpals, five, short and stout; rounded; overriding at base; distal articulations rounded and keeled below; formula 3-4-5-2-1.

Pes: pentadactyl, plantigrade, short and broad.

Tarsus: more compact than manus.

Astragalus: trochlear surface broad and slightly grooved, the outer keel being longer and higher than the inner, grooved near inner border; fibular articulation large and triangular; neck short and broad; head convex and elongated transversely; extending beyond the calcaneum and with a cuboid contact; calcaneal facets two, rounded, the sustentacular convex, the ectal concave.

Calcaneum: large and stout; tuber pronounced; sustentaculam continued to distal end of bone; cuboidal contact broad.

Navicular: lunar, proximal facet deeply concave, distal facets for cuneiforms continuous, separated by slight ridges; cuboidal contact throughout inner surface.

Cuboid: cubical; elongate; distally articulating with metatarsals IV and V.

Cuneiforms: all wedge-shaped and subequal.
Metatarsals five; short, stout; rounded; distal articulation rounded and keeled below; formula 4-3/5-2-1.

Phalanges of both manus and pes normal; the distal phalanx developed into a claw.

SUMMARY.

1. Both manus and pes pentadactyl and plantigrade; not compact.

2. Radial articulation condyloid.

3. Trapezium relatively large; trapezoid and magnum small.

4. Metacarpals stout; in contact only at base; distal articulations rounded and keeled below.

5. Astragalus moderately grooved; contact with cuboid retained.

6. Cuneiforms sub-equal.

7. Metatarsals very similar to metacarpals.

Family CANIDÆ.

According to Wortman and Matthew, Ancestry of Canidae, Am. Mus. Nat. Hist. Vol. 12; p. 118; the phylum began in the Upper Eocene with *Vulpanus* which is known only by the jaw. *Vulpanus* is clearly ancestral to *Procynodictus* and in this genus the feet are known. The manus is shorter than in modern Canidae. The scaphoid, lunar
and centrale have already fused into the scapho-lunar. The pes is pentadactyl, short and heavy but with a tendency to become elongate. The tarsus is very much as in the descending genus *Cynodictus*. *Cynodictus* is undoubtedly ancestral to *Canis*. Well preserved material shows that the manus is short and spreading, but the pes is becoming clearly elongate. It is pentadactyl, the first metatarsal very slender, the distal articulations rounded and not cylindrical as in *Canis*; upper part of shaft compressed, distal part expanded. The excavation on the second phalanx indicates a claw more retractile than in modern forms.

The genus *Canis* dates from the Upper Miocene.

*Canis familiaris* Linn.

Manus: digitigrade; first digit rudimentary; long, slender and compact.

Carpus: laterally compressed, very compact; forming about one fourth of the whole length.

Scapho-lunar: large, irregular; radial facet continued on to radial protuberance forming saddle-shaped articulations; distal articulations four, a very small one for trapezium, oval one for trapezoid, trough-like one for magnum, large one for unciform.

Cuneiform: proximally, convex facet for radius, concave one for styloid process of ulna; distally, concave articulation for
unciform.

Trapezium: very small and flattened.

Trapezoid and magnum subequal.

Unciform: wedge-shaped; truncated with articulation with scapho-lunar; outer surface very convex for cuneiform.

Metacarpals: compressed and arched proximally; expanded and less arched distally; first, rudimentary; others slender, nearly uniform in diameter; flattened; distal articulations cylindrical, keeled below; formula 3-4-2/5 #1.

Pes: digitigrade; longer and relatively more slender than manus.

Tarsus: long; very slender, forming one half length of foot; elements compact.

Astragalus: with narrow trochlea, deeply grooved, outer keel longer and higher than inner, grooved nearest inner side; triangular articular surface for tibia in extreme flexion anterior to trochlea; neck long and slightly constricted; head oval, convex, articulating only with navicular.

Calcaneum: long and slender; tuber bifid; sustentaculum not extending to distal end; distal facet for cuboid, triangular.

Navicular: closely applied to astragalus; lunar in form; distal facets for internal and middle cuneiforms flat.
Cuboid: longer than wide; calcaneal articulation oblique.

Cuneiforms: external, large and cubical; middle, about one fourth of external in size; internal, rudimentary.

Metatarsals: first, rudimentary; others long, slender and flattened; diameter uniform. Metatarsus compressed and arched proximally, slightly expanded distally. Distal articulations of third and fourth cylindrical; that of second and fifth more rounded; all keeled below; formula 4-3-5-2 #1.

Phalanges in both manus and pes normal. Ungual phalanges modified into non-retractile claws.

SUMMARY.

1. Manus and pes compact; digitigrade; first digit rudimentary in both, more so in pes than in manus.

2. Radial articulation saddle-shaped.

3. Trapezium very small; trapezoid and magnum small.

4. Metacarpus compressed, proximally, arched; slightly expanded distally. Distal articulations cylindrical, keeled below.

5. Astragalus deeply grooved, narrow, neck long, no cuboid contact.

6. Internal cuneiform rudimentary.

7. Metacarpals similar to metatarsals in general.
Family HYAENIDAE.

The family was probably derived from the Viverridae during the Middle Miocene. The genus Hyaena is first found in Lower Pliocene and is very abundant in the Upper Pliocene and Pleistocene but is known largely from the teeth.

_Hyaena striata_ Linn.

Manus: digitigrade; tetradactyl; long and slender.

carpus: arched; compact; about one fourth the length of manus.

Scapho-lunar: relatively very large; radial articulation more saddle-shaped than in _Canis_; cuneiform articulations extensive; distal facets elongated.

Cuneiform: Wedge-shaped; articulates only with ulna above; distal unciform facet flat.

Trapezoid: wedge-shaped; larger than magnum.

Unciform: a truncated wedge, with a convex cuneiform contact.

Metacarpals: four; third and fourth long and slender; second and fifth shorter and stouter; distal articulations cylindrical, keeled below, formula 3/4-2/5.

Pes: digitigrade; relatively more slender than manus.

tarsus: elongate, about one third of length; compact.

Astragalus: trochlear surface rather narrow and deeply
grooved; outer keel longer and higher than inner; neck long and rather constricted; head convex, articulating only with navicular.

Calcaneum: long and slender, three fourths length of tarsus.

Navicular: markedly lunar in form; distal articulations separated by ridges.

Cuboid: roughly cubical.

Cuneiforms: external large and cuboidal; middle about half as large; internal fused with rudiment of first metatarsal.

Metatarsals: long; of uniform diameter; equally slender; distal articulations cylindrical, keeled below; formula 3-4-2/5. The metatarsus as a whole, compressed proximally and slightly expanded distally.

Phalanges very similar to those of Canis.

SUMMARY.

1. Manus and pes digitigrade; tetradactyl; compact.
2. Manus relatively stouter than pes.
4. Trapezium absent; trapezoid larger than magnum.
5. Metacarpus compressed proximally, expanded somewhat distally; distal articulations cylindrical and keeled below.
6. Astragalus not so narrow as in Canis; deeply grooved; neck long; no cuboid contact.
7. Internal cuneiform fused with rudimentary metatarsal.

8. Metatarsals all slender; distal articulations cylindrical and keeled below.

Family FELIDAE.

The family Felidae dates from the Middle Miocene. Representatives of the genus Felis are found in the Loup Fork Beds of the Miocene although the genus is not abundant until the Pliocene. The family was probably derived from the Creodonta thru the Miacidae.

*Felis concolor* Linn.

Manus: digitigrade, pentadactyl; broad; stout and loosely put together.

Carpus: short, broad and not compact.

Scapho-lunar; irregular; not so large proportionately as in *Hyæna* or *Canis*; the radial articulations slightly saddle-shaped, much less so than in preceding families.

Cuneiform: articulating with neither radius nor scapho-lunar but is between ulna and undiform.

Trapezium, trapezoid, and magnum subequal.

Unciform with rather narrow scapho-lunar contact.

Metacarpals: first, very short and stout and not articulating
with others; the rest long; rounded; well separated, except at base where all override; distal articulations except for first, rounded and head-like, keeled below; formula 3-4-2-5-1.

Pes: digitigrade, elongated, but broad and stout.

Tarsus forms about one third the length of foot; not compact.

Astragalus: trochlear surface deeply grooved; outer keel much the higher, wider, and longer; neck long; head rounded and articulating only with navicular.

Calcaneum: long, slender and expanded distally.

Navicular: deeply concave proximally.

Cuboid: very slight navicular and cuneiform articulations.

Cuneiforms: external, almost as large as cuboid; middle, one fourth the size of external; internal fused with rudimentary first metatarsal.

Metatarsals: four; first rudimentary and fused; third slightly stoutest; all slender, rounded; distinct, save at base where they override; distal articulations rounded, with that of third and fourth tending to be cylindrical; all keeled below; formula 3/4-2/5- #1.

Phalanges: normal; ungual phalanges modified into retractile claws with second phalanges excavated to receive them when retracted.
17.

SUMMARY.

1. Manus and pes digitigrade; manus pentadactyl; pes with first digit rudimentary; both rather loose.

2. Radial articulation slightly saddle-shaped.

3. Trapezium, trapezoid and magnum subequal.

4. Metacarpus not compressed but divergent; distal articulations rounded and keeled below.

5. Astragalus not so narrow as in Canis, grooved; no cuboid contact.

6. Internal cuneiform fused with rudimentary metatarsal.

7. Metatarsals divergent; distal articulations of third and fourth tend to become cylindrical; others rounded, keeled below.


SUMMARY OF FISSIPEDIA.

I. Characters constant through the suborder.

1. Scaphoid, lunar and centrale fused into scapho-lunar.

2. Digits never less than four.

3. Ungual phalanx developed into claws.

4. Scapho-lunar - unciform contact always present.

5. Head of astragalus always ovate and convex.

6. Calcaneum expanded distally and continuous.
II. Characters differing between plantigrade and digitigrade types.

<table>
<thead>
<tr>
<th>Character</th>
<th>Plantigrade</th>
<th>Digitigrade</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manus and pes</td>
<td>stout, broad</td>
<td>elongate</td>
</tr>
<tr>
<td>Digits</td>
<td>five</td>
<td>five or four</td>
</tr>
<tr>
<td>Radial articulation</td>
<td>condyloid</td>
<td>saddle-shaped</td>
</tr>
<tr>
<td>Trochlea of astragalus</td>
<td>slightly grooved</td>
<td>deeply grooved</td>
</tr>
<tr>
<td>Astragalo-cuboid contact</td>
<td>present</td>
<td>absent</td>
</tr>
<tr>
<td>Metapodial articulation</td>
<td>rounded</td>
<td>cylindrical or rounded</td>
</tr>
</tbody>
</table>

III. Marked similarities in Digitigrade Forms.

1. All forms are elongate in most parts, especially the metapodials.

2. In Canis and Hyaena both manus and pes are compact.

3. In Canis and Hyaena metacarpus and metatarsus are compressed proximally and expanded distally. The bones are flattened; diameters uniform; outline angular.

4. The distal articulations of the metapodials, especially the third and fourth of Canis and Hyaena, are cylindrical. The third and fourth metatarsal of Felis show a tendency to be cylindrical.

5. The astragalus in all the forms is deeply grooved, with the outer keel longer and higher than the inner.

6. The radial articulation of Hyaena is decidedly
saddle-shaped; That of Canis is slightly less so; and in Felis there is only a slight tendency in that direction.

7. There is a loss of the first digit of the pes in all the forms and the manus of Hyaena shows similar reduction. In Canis it is rudimentary and in Felis it is functional.

IV. Marked Dissimilarities.

1. The manus and pes of the Felis is not compact as in Canis and Hyaena, but loosely put together.

2. The metapodials of Felis are not compressed, flattened or angular, but are divergent and rounded.

3. The metapodials of Felis have, in general, rounded articulations, and not cylindrical ones as in Canis and Hyaena.

4. The claws are retractile in Felis and non-retractile in Canis and Hyaena.

V. Correlated Characters.

1. When first digit is functional trapezium and internal cuneiform are normal; if absent or rudimentary, they are suppressed or small.

2. When the third digit is larger than the second, the external cuneiform becomes enlarged.
Suborder PINNIPEDIA.

Family OTARIIDAE.

Fossil remains referable to the family have not been found in rocks earlier than the Pleistocene.

Eumetopias stelleri Lesson.

Manus: broad, paddle-like.

Carpus: short, broad, and massive.

Scapho-lunar: exceptionally large and massive; radial articulations condylar.

Cuneiform: not in contact with scapho-lunar but above and lateral in position articulating with shortened ulna, and sending processes down to fifth metacarpal.

Trapezium: larger than trapezoid or magnum.

Unciform: relatively small, articulates distally with fourth metacarpal only; facet for fifth on outer side.

Metacarpals: stout, cylindrical; fifth shortest and stoutest; distal articulations broad, convex, keeled below; formula, 1-2-3-4-5.

Phalanges: elongated, cylindrical; formula 1/2-3-4-5.

Pes: elongated, paddle-like; when extended, long axis continuous with that of leg, dorsal surface outward, plantar inward,
astragalus and calcaneum in same plane below; when flexed, at right angles to leg, astragalus tends to rise above calcaneum.

Tarsus: very massive and broad.

Astragalus: large, trochlear surface extended down over body, slightly grooved; fibular facet sloping gently; neck long, twisted; head elongate, convex from above downward; astragalo-cuboid contact retained; calcaneum facets on outer side and outer part of lower surface.

Calcaneum: very broad, massive; lies at outer side of astragalus; cuboid articulation concave.

Navicular: broad, lunar; distal facet flat.

Cuboid: longer than wide.

Cuneiforms: external and middle subequal; internal much larger.

Metatarsals: cylindrical, elongate; first stoutest; distal ends club-like, convex; formula, 1-5-2/4-3.

Phalanges: elongate-cylindrical, basal ones especially so; subequal; digits one and five stoutest.

SUMMARY.

1. Both manus and pes broad, elongate and paddle-like.

2. Radial articulation condyloid.
3. Trapezium larger than trapezoid or magnum or unciform which is unusually small. Metacarpal IV articulating distally; and V laterally with it.

4. Astragalus with trochlear surface slightly grooved; fibular surface gently angled; cuboid contact retained.

5. Internal cuneiform very large.

6. Metapodials elongate, cylindrical; convex heads distally.

7. Phalanges greatly elongated; cylindrical.

8. Foot capable of inversion, calcaneum at side of astragalus.

Family PHOCIDÆ.

Remains referred to this family are found in the Pliocene, and rarely in the Miocene of Europe.

Phoca vitulina Linn.

Manus: relatively small, broad, paddle-like.

Carpus: not compact.

Scapho-lunar: large; radial facet saddle-shaped; no contact with cuneiform.

Cuneiform: above scapho-lunar, articulating with ulna.

Trapezium: very large; trapezoid, magnum and unciform small; latter articulating with the fifth metacarpal, laterally.
Letacarpals: stout, not greatly elongate; formula, 1-2-3-4-5.

Phalanges: rounded; formula, 2-1-3-4-5.

Pes: relatively larger and broader than manus; always inverted with dorsal surface outward, plantar inward.

Tarsus: not compact.

Astragalus: on level with calcaneum; trochlear surface restricted to two convex, oval facets on upper part of body; fibular facet at gentle angle from these surfaces; neck long, slightly constricted; head flattened laterally and elongate from above downwards; calcaneal facets, on ental side of body and sustentacular on lower surface.

Calcaneum: short, not extending back of astragalus; cuboid contact quite concave.

Navicularr: almost cubical.

Cuboid: cubical, no astragalar contact.

Cuneiforms: external larger than middle, both smaller than internal.

Metatarsals: stout, and not unusually lengthened; formula, 1-5-2-4-3.

Digital formula, 1-2/3-4/5.
SUMMARY.

1. Both manus and pes paddle-like; pentadactyl.
2. Radial articulation saddle-shaped.
3. Trapezium large; trapezoid, magnum and unciform small; the latter articulating with metacarpal V laterally.
4. Trochlear surface of astragalus restricted to oval, convex facet; fibular surface, obliquely placed; no cubical contact.
5. Internal cuneiform larger than others.
6. Metapodials but moderately lengthened.
7. Phalanges elongate and cylindrical.
8. Foot permanently inverted; calcaneum lateral to astragalus and with no tuber.

Summary of PINHIPEDIA.

I. Characters common to both.

1. Both manus and pes broad, rather loosely put together, elongate and paddle-shaped.
2. Scaphoid, lunar and centrale fused into large scapholunar.
5. Scapholunar-unciform contact present; unciform small, articulating with fifth metacarpal laterally.
6. Cuneiform never articulating with scapho-lunar but above it.
7. Trapezium and intercal cuneiform large.

8. In manus, first or second digit longest and fifth shortest; in pes, first and fifth longest and stoutest and third shortest; digits, five.

II. Characters differing.

<table>
<thead>
<tr>
<th>Characters</th>
<th>E. stelleri</th>
<th>P. vitulina</th>
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<tbody>
<tr>
<td>Radial articulation</td>
<td>condyloid</td>
<td>saddle-shaped</td>
</tr>
<tr>
<td>Position of pes</td>
<td>inverted or normal</td>
<td>always inverted</td>
</tr>
<tr>
<td>Astragalar trochlea</td>
<td>broad, almost flat</td>
<td>restricted to oval, convex facets</td>
</tr>
<tr>
<td>Head of astragalus</td>
<td>flattened transversely</td>
<td>flattened laterally</td>
</tr>
<tr>
<td>Tuber of calcaneum</td>
<td>extending back of astragalus</td>
<td>even with astragalus</td>
</tr>
<tr>
<td>Calcaneo-cuboid facet</td>
<td>almost flat</td>
<td>deeply concave laterally</td>
</tr>
<tr>
<td>Metapodials</td>
<td>very elongate</td>
<td>not very elongate</td>
</tr>
<tr>
<td>Phalanges</td>
<td>cylindrical</td>
<td>less cylindrical</td>
</tr>
</tbody>
</table>
Cohort UNGULATA.

Order PERISSODACTYLA.

The origin of the Perissodactyla is still the source of much speculation; their relationship with other orders is an equally disputed subject. Osborn gives the order equal rank with the Artiodactyla under the cohort Ungulata; Cope gave the two equal rank under Diplarthra. Some recent writers would separate them and make them unequal in rank.

Cope believed that the Perissodactyla were derived from the Condylarthra through the Amblypoda. He considers Phemocodon as the form ancestral to all ungulates. It has been generally recognized for some time that the Amblypoda were an aberrant, specialized group leaving no descendants and so dropping at once from our consideration. There is no positive evidence that the Perissodactyla are derived from the Condylarthra. Matthew, 1897; Bull. Am. Mus. Nat. Hist. p. 309, and Osborn 1898; Ibid. p. 163; plainly show that Phemocodon and its much less specialized ancestor Ruprotogonia cannot be considered as ancestral to the Perissodactyla. It is highly probable, though, that they resemble the ancestral type.

The earliest Perissodactyla show but little divergence into the three groups which later developed into the horse, the tapir
and the rhinoceros. Certain characters of the order, however, are perfectly distinct from their first appearance. Because they are so constant, and because so much material has been examined, we may state rather definitely certain characteristics of the ancestral forms of carpus and tarsus.

Both manus and pes had advanced beyond the condylarth stage; the first digit on the manus was lost and the first and fifth on the pes, giving a formula never more than IV-III. The third digit was longest; the foot was narrow. This type of foot may have come from the Condylarthra, but not from the Phendagodus; for the carpus of the earliest perissodactyla had a broader lunar-unciform contact. Since Euprotogonia, the ancestor of Phendagodus, was, also, characterized by an interlocking carpus, it is safe to say that the serial carpus of the latter is secondary, and Phendagodus could not have been in the perissodactyl line of descent.

Family EQUIDAE.

**Phylogeny.**

<table>
<thead>
<tr>
<th>Genus</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>Equus</td>
<td>Upper Pliocene, Pleistocene, Recent.</td>
</tr>
<tr>
<td>Pliohippus</td>
<td>Pliocene</td>
</tr>
<tr>
<td>Protohippus</td>
<td>Upper Miocene (Loup Fork)</td>
</tr>
<tr>
<td>Desmatippus</td>
<td>Middle Miocene (Deep River)</td>
</tr>
</tbody>
</table>
Professor Scott believes in a single phylogenetic line for the horse, in this country at least, and not, as some palaeontologists, in a polyphyletic origin.

The literature on the various genera in the line of descent of the horse is far from satisfactory; the different workers having used different names for the same forms. The following results were obtained by study and comparison of many references.

**Mesotherium** Marsh.

Syn. *Hyracotherium* Owen, of Cope and *Protorohippus* Wortman.

The genus first appears in the Wasatch; the members vary in size from a house cat to a fox, but all are typically perissodactyl; femur and humerus proportionately longer and feet shorter than in horse; bones of leg and forearm separate; foot formula, $IV^1$ $III^1$.

Manus: carpal elements normal and interlocking; first digit rudimentary; third longest; fifth shortest.

Pes: astragalus deeply grooved and horse-like, with a distinct
cuboid facet; fifth digit rudimentary; second and fourth sub-equal; third longest and stoutest.


**Protorohippus** Wortman.

Gedley does not recognize this as a good genus but places it with *Eohippus*. It is recognized by Scott, Wortman and Matthew. It first appeared in the Wind River; is slightly larger than *Eohippus*, resembles it in most respects but the rudimentary digits are completely lost leaving a formula IV· III.

**Orohippus** Marsh.

*Syn. Hyracotherium* by Cope and Wortman; *Pliolopus* by Osborn.

The genus appears in the Bridger.

Manus: trapezium proportionately smaller; fifth digit smaller but functional; third becoming very horse-like.

Pes: neck of astragalus elongated, with a distinct cuboid contact; fourth metatarsal stouter than second.

*Fig. Marsh, Am. Journ. Sci., 1892(3) vol. 43, p. 349.*

**Epihippus** Marsh.

*Epihippus* of the Uinta shows an increase in size; the lateral digits are smaller.
Mesohippus Harsh.

Mesohippus of the White River marks a great advance. Complete skeletons are known. The osteology has been carefully studied and compared with that of the horse by Professor Scott. Since the genus is almost central in the line of descent and the remains have been so perfectly preserved as to make detailed study possible a rather close comparison with the horse will be given in order that the similarities may be more readily seen and the course of development noted.

The size is about that of a Newfoundland dog.

Limbs: lengthening rapidly; ulna and fibula reduced, beginning to co-ossify; feet elongated.

Carpus: primitive but horse-like.

Scaphoid: narrow transversely; high antero-posteriorly; proximal facet greater in antero-posterior extent than either lunar or cuneiform; broad and convex anteriorly, narrow and concave posteriorly; distal facets three, one behind the other; anterior, largest, flat for magnum; internal, concave for trapezoid; postero-internal small for trapezium; no posterior facet for head of magnum. Scaphoid and lunar closer together than in horse; contact only at superior and inferior margins.

Lunar: high and narrow; proximal end broader than distal;
radial facet convex anteriorly and concave posteriorly; distal facet unevenly divided between magnum and unciform.

Cuneiform: narrow; greatest diameter antero-posteriorly; proximal surface small, concave, for ulna; distal, concave for unciform.

Trapezium: small, nodular; articulating with scaphoid proximally, and head of second metacarpal distally.

Trapezoid: low, narrow in front but broader posteriorly; distally articulating with second metacarpal only; having no facet for the third as in the horse; position more lateral than in horse.

Magnum: high; narrow; proximal facets equally divided between scaphoid and lunar; flat distal facet articulating only with third metacarpal; on radial side small facet for second metacarpal.

Unciform: narrow; compressed; high, projecting distally beyond magnum; proximally, a small lunar facet and large cuneiform articulation; distally, large facet for fourth and small one for fifth metacarpal.

Metacarpals: Second, third and fourth functional; fifth rudimentary. Second slender, compressed, with shaft flattened and applied to third; proximally articulating with magnum and
trapezium, extensively with trapezoid; distal trochlea compressed laterally, smaller than shaft; carina nearly median, below, only. Third, large but relatively more narrow than in horse. Fourth, more slender than third, head narrower. Fifth, head as large as head of fourth; tapering rapidly; no phalanges.

Phalanges: becoming horse-like; those of lateral digits narrower and less symmetrical.

Tarsus: more horse-like than manus.

Calcaneum: long, slender and compressed; tuber short and massive; fibular facet distinct; quite a distance between ecto-facet and distal end of bone; sustentaculum massive, with narrow astragalar facet; inferior astragalar facet narrow and limited; cuboidal facet narrow, concave, extending downwards and outwards. In the horse, calcaneum relatively shorter and stouter; ecto-facet divided and separated; cuboidal facet divided.

Astragalus: deep; narrow; trochlea obliquely set; internal crest longer, both below and above the external; neck long, extending beyond the crests; ecto-facet deeply concave and separated but slightly from long, narrow marginal sustentacular facet; head concave slightly from side to side; cuboid contact small. In the horse, trochlea wider, the crests wider; the neck shorter; head a straight line laterally.

Cuboid: higher and narrower than in the horse, extending
distally beyond the external cuneiform; no antero-superior navicular facet as in horse; distal end articulating with fourth and slightly with third metatarsal.

Navicular: relatively higher and narrower than in horse.

Internal and middle cuneiforms fused, as in horse, but separated distally, where the internal is larger and articulates with second metatarsal. External cuneiform high, narrow and articulating slightly with second metatarsal.

Metatarsals: second, third and fourth functional; second compressed, slender, articulating with cuneiforms; third long, slender, expanded distally; proximally, articulating with external cuneiform and slightly with cuboid; fourth, shaft larger than second.


Desmatippus Scott.

Syn. Parahippus Leidy.

While Scott retains the generic name Desmatippus, Gidley and Granger would reduce it to the genus Parahippus Leidy. It is found in the Deep River Beds and is transitional between the Oligocene and Loup Fork forms. It is slightly larger and with lateral digits more reduced.
Protohippus Leidy.

The carpus and tarsus are broader and not so high, approaching the equine appearance. Only the third digits are functional, the lateral ones being greatly reduced but retaining phalanges. In size Protohippus is about as large as a pony.

Pliohippus Marsh.

This genus is questioned and even the type specimen is so fractured that it cannot be definitely decided upon. The tendency seems to be to include it with Equus.

Equus Linn.

The genus appears first in the Upper Pliocene and is numerous in both numbers and species during Pliocene Pleistocene and Recent times. There has been, and still is, no little discussion as to the origin of the domestic horse Equus caballus Linn. J. C. Evart, of the University of Edinburgh, 1909: Science, (n.s.) Vol. 30, p. 219, believes that he has evidence of the origin of the domestic races of horses from at least six species of the Pleistocene horses, and is inclined to believe that these species arose by different lines of descent from common Miocene ancestors. Evart bases this theory on the comparative breadth of face, deflection of the facial angle and length of molar. If this be true Equus caballus is a composite species.
Equus caballus Linn.

Manus: very elongate; monodactyl; axis of support thru the median line of third digit; gait unguligrade.

Carpus: compact; elements more or less cubical; no centrale; bones of proximal row subequal.

Scaphoid: rather narrow; proximal facet concave anteriorly and convex posteriorly; entire distal surface articular, the anterior facet being the larger; flat for magnum, the lateral facet small, concave for trapezoid; lunar facets small and dorsal.

Lunar: wedgeshaped; broader above than below; proximal facet convex above, concave below; distal facet unequally divided between magnum and unciform, the facet for the former being long, rectangular and twice as broad as the latter facet, dorsally, while the unciform articulation is shorter and triangular.

Cuneiform: slightly narrower than scaphoid and lunar; proximally, a long, concave radial facet; distally, a sinuous concave unciform contact.

Trapezoid: small and entirely below lateral part of magnum; proximally, a convex facet for scaphoid; distally, an almost flat facet for second metacarpal.

Magnum: low, broad, roughly triangular, wider above than below; proximally, articulating with scaphoid and lunar; distally,
has a large facet for third metacarpal and a small one for the second.

Unciform: narrower than the magnum, but higher, extending beyond it distally; lateral in position; proximally, with small, flat lunar facet and long sinuous convex articulation for cuneiform; distally, with an inner facet for third metacarpal and a small outer one for fourth.

Metacarpals: second and fourth small, tapering and splint-like; often fused with the third. The third large, expanded at both extremities; proximally articulating with magnum and unciform; distal trochlea extending well on to dorsal surface; carina almost median and as extensive as the articulation.

Phalanges: first, longest proximal surface grooved mesially for carina of trochlea, distal surface grooved centrally and convex laterally; second phalanx shorter than first; the ungual phalanx modified to form a symmetrical hoof.

Pes; elongate; monodactyl, axis of support thru median line of third digit; gait unguligrade.

Tarsus: elevated; elements compact; relatively high; lateral elements rotated posteriorly.

Astragalus: trochlea deeply grooved, with the groove a little nearer the outer side; keels nearly equal in height, obliquely placed, slanting outward and forward; inner keel extending farther
posteriorly, and the outer one further anteriorly; neck suppressed, not extending beyond trochlear keels; head straight laterally, gently convex from above downward; navicular facet long, narrow, and extending the length of dorsal part of head, down on inner side and on the inner part of the plantar portion, the upper and lower portions of the articular surface being separated by a distinct fossa; cuboid contact small, flat, triangular, on outer plantar portion of head; sustentacular facet oval, twice as long as wide; continued back from lower navicular articulation; ecto-facet in two planes; the one, oval, in plane of sustentacular facet, forming a reversed angle with it; the other, sickle-shaped, on the outer portion of the outer keel; inferior astragalar facet continuous with navicular-cuboid facet.

Calcaneum: somewhat stout, with enlarged tuberosity; sustentaculum broad as long, ovoid facet on outer portion; ecto-facet in two planes; inferior facet small and distal; cuboid articulation long, narrow, directed downward and inward, and continuous with the inferior facet above.

Navicular: wide and flat; astragalar articulation straight, concave from above downward; distal articulation with cuneiforms almost flat.

Cuboid: small; postero-lateral in position; articulating
proximally with astragalus and calcaneum; laterally with navicular and external cuneiform; distally with fourth metatarsal and slightly with the third.

External cuneiform: wide and flat; very like the navicular; articulating distally with third metatarsal.

Internal and middle cuneiform: fused; postero-lateral in position; articulating distally with the second metatarsal.

Metatarsals: second and fourth small and splint-like, fused with third; third very long, broadened at extremities, proximal facet slightly concave; distal trochlea with well marked keel continuous into dorsal surface.

Phalanges: very similar to those of manus.

SUMMARY OF SERIES.

I. The general evolution through the whole line we may say is:

1. The lengthening of manus and pes with increase in size of the whole body.

2. A reduction of lateral digits.

3. Development of monodactyl type of foot.

4. Rotation posteriorly of lateral elements, especially in pes.

5. Broadening of elements supporting third digit as well as the elements of the digit.
6. Change of astragalar head from convex to straight, laterally.


II. Characters persistent through the series.

1. Deep grooving and obliquity of trochlea.

2. Lunar-unciform contact always present.

3. Astragalo-cuboid contact always present but small.

4. Sustentacular facet oval, near the outer margin and tending to form a reversed angle with ectal facet. Inferior and sustentacular facet well separated.

Order ARTIODACTYLA.

Whatever the relationship of the Artiodactyla to the Perissodactyla, it is generally acknowledged that in North America, at least, they develop much later in point of time. There is but one genus in the Wasatch which may be referred to this order. Genera are more numerous in the Bridger and Uinta and very numerous in the Miocene. The Tylopoda is the only group in this country whose phylogeny is known with any degree of certainty. There are lines present in the Miocene closely related to the Suidae and Cervidae, but not ancestral to them. Modern artiodactyl families do not appear in North America until in the Pleistocene indicating
migration from other sources.

Section TYLOPODA.

Family CAMELIDAE.

The line of the Artiodactyla which is most complete and in which the stages are known as well as in the equine series, is the line of descent of the camels. This line was developed in this country and modern species are in their present habitat because of extensive migrations during the Pleistocene.

Phylogeny.

<table>
<thead>
<tr>
<th>Auchenia</th>
<th>Camelus</th>
<th>Pleistocene and Recent.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Procamelus</td>
<td>Miocene</td>
<td>(Loup Fork)</td>
</tr>
<tr>
<td>Protolabis</td>
<td>Miocene</td>
<td>(Deep River)</td>
</tr>
<tr>
<td>Pseudolabis</td>
<td>Oligocene</td>
<td>(Rose Bud)</td>
</tr>
<tr>
<td>Poebrotherarium</td>
<td>Oligocene</td>
<td>(John Day)</td>
</tr>
<tr>
<td>Eotylopus</td>
<td>Oligocene</td>
<td>(M. &amp; U. White R)</td>
</tr>
<tr>
<td>Prottylopus</td>
<td>Oligocene</td>
<td>(L. White River)</td>
</tr>
<tr>
<td>?Monocodon</td>
<td>Eocene</td>
<td>(Uinta)</td>
</tr>
<tr>
<td>?Trigoneelastes</td>
<td>Eocene</td>
<td>(Bridger)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(Wasatch)</td>
</tr>
</tbody>
</table>

There are, undoubtedly, forms between Procamelus and Auchenia and Camelus but it is hard to say just which of the
numerous forms of the Pleistocene should be given the position. There is still a question as to the Wasatch and Bridger representatives; Trigoneleastes and Homocodon. The former is a tiny, very primitive, pentadactyl artiodactyl; the latter is also small, with toes IV-V, and probably ancestral to many groups.

**Protylopus** Wortman.

Protylopus is a camel beyond doubt, though still very small. The ulna is complete and separate. In the manus the third and fourth digits are largest, but the second and fifth are functional. In the pes the lateral digits are slender and rudimentary. There are no cannon bones as yet, but the metapodials are flattened in their upper portion and rounded below. The medullary cavities are large as in the camel.


**Poebrotherium** Leidy.

Complete skeletons of this camel are well known and have been carefully studied and compared with the llama by Professor Scott.

Manus: gait unguligrade.

Carpus: as a whole, broad and low.

Scaphoid: narrow and deep; posteriorly extending well up on to the radius; distally, three facets; small postero-internal one
for trapezium, a relatively small, concave one for trapezoid; large, nearly flat for the magnum.

Lunar: higher and broader than scaphoid, but not so deep; proximal surface convex, almost quadrate; inner surface straight and more closely applied to scaphoid than in llama; posteriorly, a bifid process; distally, the beak is long, the magnum facet longer and more oblique than that of unciform, the two meeting at an acute angle, while in the llama the surfaces are equal and meet at a right angle.

Cuneiform: high, narrow and deep; proximal surface very like that of scaphoid; the distal surface entirely concave, but narrow, for unciform.

Trapezium: small, nodular; attached to scaphoid, trapezoid, and a rudimentary second metacarpal.

Trapezoid: relatively smaller than in llama; slightly concave proximally for the scaphoid; distally, two facets, the one for the second metacarpal and the other for a process from the third; they meet in an open angle.

Magnum: low and broad; not more than one half as high as unciform; proximally, flattened front for the scaphoid, and convex posteriorly for both lunar and scaphoid; distally, a large, flat, triangular facet for third metacarpal.
Unciform: high and narrow; lunar facet small; that of cuneiform large, transverse, convex and curved; distally the articulation is largely with fourth metacarpal, but with a small facet for third and a still smaller one for fifth.

Metacarpals: third and fourth functional, second and fifth scale-like rudiments; all free; second, short and blunt headed, tapering rapidly, placed in excavation on third; third elongate, but relatively shorter than in modern forms, shaft slender, flattened where applied to fourth but rounded below, diverging distally; trochlea narrow, convex from before backward, carina almost mesial but on lower surface only; fourth, very similar but slender; fifth smaller and flatter than second and in excavation on side of fourth.

Phalanges: differs somewhat decidedly from modern forms. First phalanx slender, long, but relatively shorter than in the llama, and with extremities less expanded, distal articular surface not extending on to dorsal surface; second phalanx, short and compressed, distal articular surface extending on dorsal surface; ungual phalanx similar to that of deer, long, high, pointed, rounded on the outer and flat on the inner side as in any artiodactyl; no indication of a pad. Toes not so divergent as in modern forms.
Pes: gait unguligrade.

Tarsus: higher and narrower than in llama.

Astragalus: narrow, with a narrower groove than in llama; neck long, but not compressed; cuboid contact narrow; that for navicular, hour-glass shaped.

Calcaneum: longer and more slender than in llama; sustentaculum not so prominent and not grooved above.

Navicular: high, narrow; no posterior hook; entirely free from cuboid; astragalar facet concave from before backward, saddle-shaped from side to side, emarginate mesially by fossa from fibular side; distal facet, anteriorly large, flat, for middle and external cuneiform, small one posteriorly for internal cuneiform.

Cuboid: higher and narrower than in llama; calcaneal facet broader than the navicular, just the reverse from the modern conditions; the distal facet for the fourth metatarsal not emarginate as in the camel; laterally there is a small facet for the fifth.

External and middle cuneiform fused, high and narrow; no contact with second metatarsal.

Metatarsals: third and fourth functional; second and third scale-like; second articulates with internal cuneiform, tapers
rapidly and may be coalesced with the third; the third and fourth
are similar to but longer than the corresponding metacarpals,
closely applied, diverging distally; fifth small but never coalesced with fourth.

Phalanges much as in manus.

Fig. Journ. Morph. Vol. V; p. 44.

**Pseudolabis.**

This genus is largely transitional between *Poebrotherium* and *Procamelus.***

**Protolabis** Cope.

In this genus the greatest change has been in the formation of the cannon bones by the fusing of the metapodials. The fusion is not complete, however, and the distal extremities diverge somewhat. The beginning of the elastic pad probably dates from this time. In size *Protolabis* is smaller than the llama.

**Procamelus** Cope.

This genus is very modern; the size is about that of the llama but more slender. A comparison of the manus with *Poebrotherium* shows that the scaphoid is broader and more massive; the lunar narrower, the unciform and magnum facets more nearly equal and the angle less acute; the cuneiform, heavier and wider;
trapezium not present; trapezoid larger; magnum higher in proportion to the breadth; the unciform reduced in height projecting distally but little below the magnum. The metacarpals are fused but deeply cleft distally. The most marked change is in the phalanges, for in the Procamelus the distal end of the first phalanx, as well as the second, has the articular surface extending well dorsally; the ungual phalanx is reduced and flattened, the elastic pad was undoubtedly formed.

Figured Jour. Morph. Vol. XV Pl. III, fig. 52, p. 79.

Thyes is also very modern. The astragalus is broader in proportion to its height; calcaneum compressed and deep, with a prominent sustentaculum, and a long, narrow cuboid facet, the distal end extending a little beyond that of astragalus; navicular low; fossa in astragalus facet larger and deeper.

Fig. Journ. Morph. Vol. V Pl. III, fig. 53; p. 79.

It is from Procamelus that the modern genera are derived.

Auchenia guanaca (Molina).

Manus: long and slender; gait digitigrade.

Carpus: high and narrow; not extremely compact.

Scaphoid: high; narrow; deep; wider posteriorly than anteriorly; proximally, long, concave facet for radius; distally, flat articulation for magnum, and a larger posterior concave one.
for trapezoid.

Lunar: from dorsal view equal to scaphoid in width and height but not so deep; much narrower posteriorly; magnum and lunar facets equal in extent dorsally, and meeting at a right angle.

Cuneiform: larger than lunar and as deep as scaphoid; radial facet broad and concave; distal unciform articular surface long and concave.

Trapezoid: small, latero-posterior in position; articulating distally with third metacarpal.

Magnum: wide; low; triangular; broader in front than behind; scaphoid and lunar facets oblique to each other; articulation for third metacarpal flat.

Unciform: very similar to magnum, but not quite so broad.

Metacarpals: third and fourth, only, present, fused into cannon bone proximally but diverging distally; cannon bone long and slender, expanding distally; trochlea with carina only on lower surface.

Phalanges: first, long, expanded proximally, narrow distally; distal articulation trochlear, extending well dorsally; second phalanx shorter and stouter, distal surface trochlear; ungual phalanx reduced, small, flat; dorsal keel tending to become mesial, with both borders rounded. Toes diverge decidedly and ungual
phalanges widely separated.

Pes: elongate; narrow; gait digitigrade.

Tarsus: typically artiodactyl.

Astragalus: deeply grooved; trochlear surface parallel to long axis of bone; crest high and wide; groove pinched in both above and below with a deep fossa anteriorly; neck short and not constricted; distal surface trochlear articulating in outer one third with cuboid and in inner two thirds with navicular; sustentacular facet long; rectangular and taking up almost entire lower surface of body; ecto-facet small, on outer side of body.

Calcaneum: rather long and slender; sustentaculum short and extending only a short distance forward; facet small and oval, covering not more than half of astragalar surface, leaving the rest exposed to view posteriorly; bone deeply notched and incomplete distally; ecto-facet small and on outer side of notch; cuboid facet long and narrow, restricted by a fossa in the lower part.

Cuboid: deeply notched proximally and higher internally than externally to the notch; calcaneal facet long, saddle-shaped dorsally, notched below; astragalar articulation equal in width but shorter, concave; distal facet for fourth metatarsal large.

Navicular: compressed, as wide as cuboid but not so high;
hook suppressed.

Internal cuneiform very small.

Middle and external cuneiform fused, large, compressed; supporting third metatarsal.

Metatarsals: fused to form cannon bone similar to that of manus and about equal in length.

Phalanges much as in manus.

SUMMARY OF SERIES.

I. In a summary of the series as a whole we may say evolution has been along the line of:

1. Elongation of manus and pes associated with increase in size of body.

2. Suppression of lateral digits. In Protylopus formula, IV - II 2; Poebrotherium II 2 - II 2; Procamelus II - II.

3. In fusing of metapodials; in Protylopus and in Poebrotherium there was no fusing, in Procamelus it had begun, and is more complete in modern forms.

4. In formation of pad, no evidence of it in Poebrotherium, beginning in Protolabis and formed in Procamelus.

5. In change from unguligrade to digitigrade gait, from Protylopus to Protolabis, the phalanges are typically artiodactyl, unguligrade; from Protolabis on to modern genera the phalanges are
typically digitigrade. This change was undoubtedly associated with development of the pad.

II. Characters persistent thru series.

1. Astragalus deeply grooved, trochlea parallel to axis of body.

2. Lunar-unciform contact always present.

3. Astragalo-cuboid contact large.

4. Sustentaculum short, facet small and oval; bone notched anteriorly.

Auchenia has been taken as a typical artiodactyl and its phylogeny closely traced. Artiodactyls of other families will be briefly considered and compared and no phylogeny attempted. Conclusions can then be drawn from the group as a whole.

Section SUINA.

Family SUIDAE.

Sus scrofa Linn.

Manus: broad, stout; not greatly elongate.

Carpus:

Scaphoid: cubical; radial facet concave above, convex below; magnum articulation flat; facet for trapezoid postero-lateral in
position, and concave.

Lunar: stout and cubical; radial articulation saddle-shaped; distal facet irregularly concave, divided almost equally between magnum and unciform; lateral articulations with scaphoid and cuneiform extensive.

Cuneiform: about equal in size to scaphoid, and to lunar.

Trapezoid: small; almost nodose; posterolateral in position; articulating with second metacarpal distally.

Magnum: wide, rather flattened; narrowed below; proximal facet almost equally divided between scaphoid and lunar; distal articulation with third metacarpal.

Unciform: as wide as, and higher than magnum; distally, articulating broadly with fourth metacarpal, and slightly with fifth and third.

Metacarpals: second and fifth slender, with small proximal, and much larger distal extremities; nearly as long as the median metacarpals; third and fourth stouter and larger, diameter of shaft nearly uniform; closely applied but free; trochlea narrower than shaft; carina sharp, ridge-like, continued dorsally, and nearer the inner side.

Phalanges: of lateral digits smaller and weaker than of mesial digits. First phalanx stout; about half the length of
metacarpal; axis of distal articulation obliquely placed; articulation not extending on to dorsal surface. Second phalanx stout, compressed, no longer than wide; axis of both articulations obliquely placed. Ungual phalanx longer than second; flat below; pointed, straight on inner and rounded on outer margin.

The lateral digits are not functional under ordinary conditions; the functional digits do not diverge greatly.

Pes: rather stout and not greatly elongate.

Tarsus:

Astragalus: deeply grooved, crests parallel to long axis of body, grooved near inner side; distal articulation trochlear and extending well on to dorsal surface, separated from upper trochlea by a fossa; navicular articulations on the inner two thirds, cuboid on outer one third; lower part of body taken up by broad calcaneal facet.

Calcaneum: rather stout; sustentaculum short, with flattened, rounded facet almost transverse to axis of bone; on outer portion is knob-like malleolar facet and a small astragalar contact.

Navicular: somewhat compressed; deeply concave for astragalar articulation; hook long and plantar in position.

Cuboid: as high as both navicular and cuneiform; astragalar facet as wide as calcaneal.
Internal cuneiform small and nodular. Middle and external cuneiforms fused, flattened, compressed.

Metatarsals: proportionately longer than metacarpals. Second and fifth smaller proximally and expanded distally; shorter than mesial ones; similar to those of metacarpus. Third and fourth longer and stouter; distal trochleae very similar to those of manus.

Phalanges similar to those of manus.

SUMMARY.

1. Elongation of manus and pes not marked.
2. Lateral digits but partly reduced.
3. But little co-ossification; no cannon bones; carpal and tarsal elements free.
4. Transverse axis of phalangeal articulations oblique to the transverse axis of the bone.
5. Articulation at distal end of first phalanx not continued on to dorsal surface.
6. Trochlea of astragalus parallel to axis of body; the distal surface markedly trochlear and articulating broadly with cuboid; sustentacular surface broadly ovate and taking up most of lower surface of body.
7. Calcaneum with small sustentaculum; interrupted distally.
Section PECORA.

Family CERVIDÆ.

Alce alces (Linn.)

Manus: elongated; relatively slender.

Carpus:

Scaphoid and cuneiform slightly higher than lunar; both markedly convex proximally; lunar concave radially; distally, with obliquely placed, subequal facets for magnum and unciform; trapezium small and nodular; trapezoid fused with magnum into wide, flat bone; unciform not as wide as, and higher than, magnum.

Metacarpus: second and fifth metacarpals present as loose splints distally; third and fourth metacarpals fused completely into cannon bones, widely expanded distally, less so proximally, trochlea closely placed, carina extending on to dorsal surface.

Phalanges: lateral phalanges smaller and shorter than functional ones, extending down only to the distal end of first phalanx, very similar in form to functional one. First phalanx longest and stoutest, distal articular surface extended slightly on to dorsal surface; second phalanx shorter and articulation distally on dorsal surface, marked; ungual phalanx as long as second, pointed, high, keeled, flat below, straight on inner and curved on outer side.
Functional digits spread but little.

Pes: longer and relatively more slender than manus.

Astragalus: short, massive; trochlea deeply grooved, with keels parallel to body axis; neck short; distal trochlear surface massive; sustentacular articular surface broad and mesial in position.

Calcaneum: long; fairly slender; with short, stout sustentaculum; and narrow cuboid surface.

Cuboid and navicular fused into stout, irregular bone. Cuneiforms also fused and may even fuse with cuboid-navicular.

Metatarsals: three and four, only, present, fused in a cannon bone, very similar to that of manus but proportionately longer.

Phalanges: slightly longer than those of manus; distal facet of first phalanx more markedly continued onto the dorsal surface. Phalanges of digits two and five also present but not articulating with the other bones. They are small and not so long as in manus.

SUMMARY.

1. Manus and pes elongated and relatively slender.

2. Lateral digits not wholly suppressed; phalanges, only
present in pes, and metacarpals and phalanges in manus. Suppression began at proximal end of metapodials and lateral digits did not articulate with rest of foot.

3. Cannon bones fully fused; trapezoid and magnum, cuboid and navicular, and cuneiforms, fused.

4. Distal articulation of first phalanx in manus and more markedly in pes, appears on dorsal surface.

5. Astragalus deeply grooved, trochlea parallel to body distal articulation trochlear; cuboid contact broad.

6. Calcaneum with short, stout sustentaculum; interrupted distally.

Family BOVIDAE.

Ovis aries Linn.

Manus: elongate, slender.

Carpus: high, narrow; bones of proximal row subequal in width and height; magnum facet of lunar almost equal to unciform, both flat and obliquely placed; cuneiform distinctly notched, fitting over unciform; trapezoid fused with magnum into a broad, flat bone; unciform not as wide as, but higher than magnum.

Only third and fourth metacarpals present, fused into a cannon bone; distal trochlea narrow, carina sharp, on mesial side, extending well dorsally.
Phalanges: first, longest, with no dorsal, distal, articular surface; second, shorter, with distal articulation extending well dorsally; ungual phalanx long, high, pointed, straight on inner and rounded on outer surface. Digits diverge slightly.

Pes: also elongate and slender.

Astragalus: trochlea short and deeply grooved, sides parallel to body; neck suppressed; distal trochlea very convex.

Calcaneum: long; with short sustentaculum; interrupted distally; cuboid facet narrow.

Navicular and cuboid fused and articulating continuously with astragalus.

Middle and external cuneiforms fused; inner one small and nodular.

Cannon bone longer than in manus, otherwise very similar. Phalanges correspond to those of manus.

**SUMMARY.**

1. Manus and pes elongate and slender.

2. Laterally digits entirely suppressed.

3. Cannon bones fully fused; trapezoid and magnum, and cuboid and navicular, fused.

4. No evidences of articulations on dorsal surface of first phalanx.
5. Astragalus with trochlea deeply keeled and parallel to long axis of body; distal surface trochlear; lower facet large and mesial.

6. Calcaneum with short sustentaculum; interrupted distally.

_Bubalus kerabau_

Manus: massive, broad, stout.

Carpus:

Scaphoid; lunar and cuneiform cubical, subequal; in dorsal view magnum and lunar facets are as 2 : 1; cuneiform with deep, long, radial facets; trapezoid fused with magnum into low, broad, bone; unciform almost as broad but higher.

Metacarpals: rudimentary nodes appear as the second and fifth metacarpals; third and fourth completely fused into a cannon bone, expanded above and below, stout; distal trochlea closely placed, carina broadly rounded and extending on to the dorsal surface.

Phalanges: first, broad and stout, no distal articulation dorsally; second, shorter and stouter with distal dorsal articulation; ungual phalanx broad, flat below, very rounded on outer side.

Digits do not diverge markedly.

Pes: longer than manus but stout and massive.
Tarsus:
Astragalus: short; trochlea massive and deeply notched, keels parallel to body axis; articulation separated from distal facet by deep fossa; distal facet trochlear.
Calcaneum: tuber short; sustentaculum short, stout; facet rounded; cuboid facet narrow and elongate.
Navicular and cuboid fused and articulating continuously with astragalus and calcaneum.
External and middle cuneiform fused; low and broad; inner one small and nodular.
Metatarsals: cannon bone only present; longer than in manus but similar. Phalanges very similar to those of manus.

SUMMARY.
1. Manus and pes moderately lengthened but stout.
2. Lateral digits entirely suppressed in pes and only nodules in manus.
3. Cannon bones fully fused; trapezoid and magnum, navicular and cuboid, fused.
4. No evidence of distal dorsal articulation on first phalanx.
5. Astragalus with deeply keeled trochlea, parallel to axis of body; distal facet trochlear; lower facet broad and mesial.
6. Calcaneum with stout, short sustentaculum; interrupted distally; narrow cuboid contact.

SUMMARY OF ARTIODACTYLA.

As a whole we may say:

1. There has been a lengthening of manus and pes, most marked in A. alces, A. guanaca and O. aries; less so in B. kerabau and least of all in S. scrofa.

2. There has been a loss of lateral digits, complete in A. guanaca and O. aries, rudimentary metacarpals in B. kerabau, rudimentary distal end of metacarpal and phalanges of manus and phalanges only of pes in A. alces; only first digit lost in S. scrofa.

3. In A. guanaca the gait is digitigrade but unguligrade in the line of descent, the distal end of first phalanx is facetted on dorsal surface; A. alces is partly, tho less, digitigrade showing less facetting; the other forms are all unguligrade and the first phalanx is not articular on dorsal, distal surface.

4. Metapodials are not fused in S. scrofa; partly fused with distal ends divergent in A. guanaca; fusion complete in the other forms but the line of fusion evident in A. alces and B kerabau, almost obsolete in O. aries. In S. scrofa and A. guanaca
the cuneiforms are fused and the other tarsal elements are free; in all the other species the trapezoid and magnum, cuboid and navicular, are fused as well.

5. In every case the keels of the astragalus are deep and parallel to the long axis of the bone; the neck is suppressed; and the distal surface trochlear forming a hinge joint in the tarsus. The sustentacular facet is large, ovate, mesial in position, on the lower side of the body; cuboid contact broad.

6. The sustentaculum in every case is short and with a rounded facet transverse to the long axis of the bone. The calcaneum is deeply notched or interrupted distally and the cuboid contact narrow.

7. In every case there has been a broad lunar-unciform contact.
THEORIES RELATING TO KINETOGENESIS.

Plasticity of the Skeleton.

The skeleton is not an unyielding, fixed structure; it is plastic, readily moulded by the soft parts with which it comes in contact. The long bones of a skeleton show deep grooves, formed by tendons; and muscle scars whose prominence depends upon the size and activities of the muscle attached. The parietal is grooved on its inner surface by the middle meningeal artery. It is well known that an aneurism or a tumor will quickly cause absorption of the osseous tissue coming in contact with it. The changes in the jaw during the development of the teeth, are due to the pressure of the soft parts below.

External pressure may also affect bone structure. Cope cites a case in which, under abnormal conditions, a joint was produced. He says: "In the first case, that of the human elbow; the cubitus was luxated posteriorly so that the humeral condyles articulated with the ulna anterior to the coronoid process. The head of the radius is in contact with the external epicondyle on its posteroinferior face. The results are as follows: a new coronoid was developed in front of the abnormal position of the humeral condyle to an elevation above the shaft of the ulna exceeding that of the normal coronoid. Between it and the normal coronoid was
developed a perfectly functional cotylus which embraces the humeral condyle like the normal cotylus. The latter has its articular surface buried under osseous deposits so as to be no longer visible. The region of contact between the head of the radius and the external epicondyle has developed in the latter, a large cotylus which permits of both rotary and vertical movement of the former. The articular surface of the humeral condyle, except where in articulation with the ulna, is roughened and partially overgrown with exostoses, so as to alter the form to a great extent. The opportunity of examining this specimen I owe to Provost Pepper of the University of Pennsylvania, in whose museum it is preserved." Primary Factors of Organic Evolution, Chap. 6: p. 277.

Based upon his own observations of the effects of abnormal stresses and strains upon articulation, as well as on the works Hütter and other German investigators, Cope gives the following generalizations:

1. "Continued excessive friction removes osseous tissue from the points of contact until complete adaptation is accomplished and the friction is reduced to a normal minimum. Then a normal articular surface is produced.

2. "When the normal friction is wanting, and an inflammatory
condition is maintained by a pulling strain on the investing synovial membrane, excess of osseous deposit is produced.

3. "Stress on the articular tendons and ligaments stimulates osseous deposits at their insertion, which deposit may be continued into their substance. This is a pulling stress."

The above only goes to show that osseous tissue is not fixed, that it is plastic and will, during the life of an individual, accommodate itself to various mechanical stresses and strains. It is not at all unreasonable then, to think that continued mechanical influences applied through geologic ages would show an effect upon the skeletons of animals and furthermore, that this effect would be noticeable in the bones of the feet which are affected by mechanical conditions.

Moulding of Articulations.

Since osseous material is plastic, and abnormal articulations can be produced by purely mechanical forces, it is not unreasonable to suppose that the normal articulations are modified by the mechanical forces acting upon them. Cope's theory is built upon this basis. In a general way it is as follows:

A good illustration of the influence of mechanical environment upon the moulding of articulations, is to be found in the
ankle and wrist joints of ungulates. The ankle joint of a modern ungulate is a treble keeled joint, two keels of the astragalus fitting into two grooves on the tibia and a middle keel from the tibia fitting into a median groove in the astragalus. Such a joint may be broken but can not be displaced. Since all modern mammals are derived from primitive Tertiary forms with an ungrooved unkeeled astragalus, it ought to be possible to trace various stages in the development of modern forms in a palaeontological series. Cope found such a series, and from it concluded that the mechanical forces were operative in producing results. He explained it as follows: "The outer walls of the bones were dense while the inner portions were more spongy. The astragalus, being narrower laterally than the tibia, presented the denser, outer wall, within the outer wall of the tibia, to a relatively less dense portion of the bone. Continued impact in locomotion caused the astragalus to press upward and cause bone absorption of the softer tissue, hence allowing the outer wall of the tibia to pass down over that of the astragalus. The central keel of the tibia was formed by the downward pressure of the soft tissue of the tibia, due to gravity, upon the soft tissue of the astragalus, again causing bone absorption and the formation of the groove in the astragalus."
The same thing applies to the wrist joint. In primitive forms it was uniformly concave. Here the surface of the radius has been hollowed out by the upward pressure of the carpal bones against the broad extremity of the radius. The keels were formed by the bones between the carpal elements not subjected to the pressure from below and influenced by the pull of gravity.

The keels on the metapodials of ungulates were caused by pressure upon the end of the bone during locomotion, of the sesamoid bones in the flexor tendons. The bone in the median line between the tendons was not subject to the pressure and formed the keel. It always appeared first on the lower surface of the metapodial. In many animals such as the carnivors and the camel, it never extended on to the dorsal part of the articulation, but in the horse and most artiodactyls it became continuous. The Muybridge photographs of animals in motion show that at the last moment of rest on the ground, the phalanges in the horse are flexed anteriorly at right angles to the metapodials. The motion is too rapid to be observed by the eye, but it aids in accounting for the keel or carina on the dorsal surface beyond the influence of the sesamoid bones. It was formed, in all probability, to fit the groove in the upper surface of the first phalanx which was moulded to fit the keel on the lower part of the metapodial.
The keel was not complete dorsally in the ancestors of the horse; neither is it found complete in animals whose feet are padded.

In the Artiodactyla, the inner and outer sides of the distal trochlea of the metapodials are not the same, the outer one being more deeply impressed. This may be due to the fact, that, since the digits diverge, the impact has been unequally transmitted, the line of pressure passing through the outer portion.

The forces which have entered largely into the moulding of articulation are impact, torsion and flexure. The effect of the impact alone is to be found in the facetting of the distal end of the radius, the grooving of the distal end of the tibia, and the grooving of the proximal end of the astragalus. Torsion only, has affected the alternation of the carpals in man. Torsion and impact without flexure, have caused the alternation of carpals and tarsals in ungulates. Torsion, flexure in one plane and impact have caused tongue and groove joints.

This theory is supported by the fact that the most perfectly interlocking joints have been produced in those animals who have lived upon the dry land, and have developed great speed and a high degree of digitigradation. All these factors would tend to make the impact greater and the effect upon the joints would be more noticeable.
Digital Reduction.

Digital reduction is supposed to be due to the elongation of those digits receiving the most impact and strain in rapid locomotion; and to the lack of growth in the other digits due to a complementary loss of growth material and nutrition. In the primitive, pentadactyl, plantigrade mammal, the distribution of strain and impact was very general and there was no reduction. Animals which are aquatic or arboreal, have remained pentadactyl because the distribution of strain has remained equal. If the distribution became unequal, those digits receiving the most impact and strain, that is, those digits reaching the ground first in plantation, and leaving it last in recovery, became elongated. The position of these digits depended upon the angle of the foot upon the leg in locomotion. The middle digit was developed if the foot was directed straight forward; the outer digits, if inward; the inner digits, if outward. Examples of these forms of development may be seen in man where the axis of support passes through the first digit; in the horse where it passes through the third; and in the kangaroo where it passes through the fourth. The fact that the greatest reduction is to be found in animals living on the dry uplands and developing great speed, and that there is almost none in animals with padded
feet is a strong argument for the mechanical theory of digital reduction.

This theory has been worked out by John A. Ryder, Am. Nat., Vol. 11; p. 603, and was accepted and heartily endorsed by Cope. Mr. Ryder pointed out, that where the distribution of strain had been unequal in either pair of limbs and generalized in the other, digital reduction has taken place in one pair only. In the marsupials, the fore limbs are not specialized but the hind limbs, used in locomotion, are highly modified. Fossorial animals usually have the fore limbs most changed. Where digital reduction began in, or has proceeded farther in the hind feet, it is to be noted that locomotion is by leaping, as in the kangaroo; or that in running the push forward is given by the hind feet, as in carnivores. He concluded:

1. "That the mechanical force used in locomotion during the struggle for existence has determined the digits which are now performing the pedal function, in such groups as have undergone digital reduction.

2. "That where the distribution of mechanical strain has been alike on all the digits of the manus, or pes, or both, they have remained in a state of approximate uniformity of development."
Evolution of Carpus and Tarsus.

Cope believed that all ungulates with alternating carpus and tarsus arose from a taxopodous or linear seried stage, and passed through an amblypodous stage intermediate between the two. When Dr. Schlosser expressed the opinion that the Diplarthra arose directly from the Taxopoda without the intervention of the Amblypoda, Cope disagreed with him and replied as follows: Am. Nat., 1887, p. 935.

"The conversion of a taxopod into a diplarthrous ungulate has been accomplished by the rotation outward of the lower leg with the first row of the carpus and tarsus on the second row, or by the rotation inward of the second row on the first in both the fore and hind feet. This rotation has resulted sooner or later in the loss of the internal digits (thumb and great toe) from both extremities. In the history of the sliding outwards of the first row, the outside element of the row has always preceded, in time, the inside element. The Amblypoda show this clearly. The lunar bone has extended outward so as to rest on the outside bone of the second row, (unciform) in part, as well as the one upon which it properly rests (magnum). But the scaphoid has not slipped outward so as to rest on the magnum of the second row. That continues to rest on its proper successors below, the trapezoid
and trapezium, the latter taking half the burden. This structure is absolutely intermediate between that of the Taxeopoda and that of the Diplarthra and I imagine that all ungulates in passing from the taxeopodons to the diplarthrous stages, traversed the amblypodous. The only other conceivable path would have been thru a type in which the scaphoid has extended over the magnum while the lunar did not pass outward beyond the limits of the magnum. No such type has been found. On the other hand I have shown that the Oreodontidae have pushed the transposition of the bones of the first carpal row to such an extent that the magnum has gotten entirely under the scaphoid, while the unciform supports the lunar completely. Thus the alternating position, with its useful mechanical consequences, has been lost to this group, the effect produced being exactly that seen in the Amblypoda. This may have something to do with the extinction of the Oreodontidae.

"The cause of this rotation of the first on the second row of carpals and tarsals may be now referred to. Mammals, except those which are completely plantigrade, turn the toes out in walking. In the Ungulata the toes of the posterior foot are more strongly turned outward than those of the anterior foot. In the digitigrade Carnivora, which represent the highest type of Ungulata, the movement is reversed, the anterior toes being turned
outward more than the posterior. As the foot is descending toward the ground, it is, with the distal part of the leg, rotated from within outward. The rotation of the foot is promptly arrested at the moment of its contact with the ground, and the effect of this arrest is to produce a torsion of the leg and a pressure from within outward of the proximal or moving element of each articulation against the distal or fixed element. Thus a constant torsion strain from within outward has been exerted by the first row of carpal and tarsal bones, on the second row, and thus has arisen, as I believe, the gradual transition from the linear arrangement of these bones of the Condylarthra to their alternation seen in the Diplarthra. The advance of diplarthrism is in direct ratio to the advance of digitigradism, for the greater the length of the foot, the greater is the elasticity of the leg and the greater is the torsion. This is especially true of the posterior leg with its prominent heel; and thus is explained the fact that diplarthrism appears in that foot before it does in the fore-foot, as in Proboscidia.

"This reasoning, when applied to the Ungiculata series, is modified by other circumstances. In the Carnivora the weight of the body does not rest on the ungues as in the Ungulata, but on
the pads of connective tissue beneath the digits. Consequently, on the application of the foot to the ground the distal bones in the carpal and tarsal articulations, do not present the rigid resistance seen in the Ungulata, but yield more or less to the torsion. Hence no alternation of these bones takes place in the hind foot of the Carnivora, where the eversion of the digits is moderate. In the case of the fore-foot, the eversion and consequent torsion are so great that the alternation is produced. In the manus of the plantigrade bear the alternation is almost nil.

To summarize we may say: All primitive mammals had a carpus and tarsus whose elements were in a linear series. It is still retained to a great extent in the Ungiculata. In the Ungulata where a strong ankle and wrist joint was an advantage, the carpus and tarsus became interlocking. It could be developed by the outward rotation of the first row, or the inward rotation of the second; Cope explains it on the basis of the outward rotation of the first row. All ungulates have passed from the taxeopodous, through the amblypodous, to the diplarthrous stage. The degree of interlocking is proportional to the digitigradism. In the Carnivora the elastic pad reduced the concussion and the mechanical effect.

In Primary Factors of Organic Evolution, 1896, Cope expresses
the same theory in a different way. This time he explained it on the basis of inward rotation of the second row. He says:

"It has been already pointed out in the chapter on phylogeny that the taxeopodous type of foot preceded the diplarthrous in time. Beside the alternation mentioned, it is quite general in both types for the metapodial bones to possess a facet for contact with that element of the carpus or tarsus next exterior to the one to which they have their principal articulation. From these facts it is evident that the bones of the second carpal and tarsal rows have, in the process of evolution, assumed a position interior to their primitive position with reference to the first row proximal to them and the metapodials distal to them. The cause of this shifting of position is to be found in the movements of the limbs in progression and especially in rapid progression.

"If we observe the movements of the limbs of a diplarthrous ungulate, we shall see that, as the foot is planted on the ground, the prominent flexures of the limbs, the elbow and gambril joints are turned inward, so that the limb, were it free from the ground, would be twisted or rotated on its long axis from within outwards. As the foot rests on the ground, the limb experiences a torsion strain in the directions mentioned. This throws the weight on the interior bones of the lower leg, radius and tibia. Thus
these bones have acquired a great superiority in dimensions over the external elements (ulna and fibula) in all Diplarthra. The bones of the inner side of the first carpal and tarsal rows have thus transmitted an ever increasing share of impact, as the radius and tibia have developed, and have grown with their growth at the expense of the external elements, the cuneiform of the carpus and the calcaneum in the tarsus which have become very narrow elements in the higher Diplarthra. As the pressure has been obliquely from within outwards, the growth of the proximal elements, the scaphoid and lunar in front, and the astragalus behind, has been in the same direction. It has been shown by Dr. H. Allen that just before the recovery of the foot, the latter is directed outward from a line parallel with the axis of the body, so that the weight falls on the inner part of the sole of the former. This naturally causes the bones of the foot to press inwards on the heads of the metapodials, so that the latter tend to grow outwards on the second tarsal row. In this way were produced the facets on the external side of the heads of the metapodials. Thus is accounted for, on simple mechanical principles, the phenomenon of carpal and tarsal displacement exhibited in its highest development by the Diplarthra."

In either formulation of the theory, the cause of the inter-
locking condition is torsion and impact on the leg and foot during locomotion. In the first case the force acts downward and outward, in the second, it acts upward and inward; the two are, of necessity, equal. The later expression of the theory explains the enlargement of the inner elements of leg and fore-arm and the proximal row of carpus and tarsus, and the external facetting of the metapodials.

Cope advanced the hypothesis to explain the development of the Ungulata in two series; the one retaining a single digit for support, the Perissodactyla; the other retaining two digits, the Artiodactyla. He supposed that the Perissodactyla or their ancestors, took to the dry uplands at an early date. There, impact on the solid ground would tend to elongate the digit which was already the longest, the third. The Artiodactyla, however, developed from swamp-living ancestors and remained in this habitat for a long time. Walking in the mud, especially after the elevation of the foot began, would tend to spread the digits on either side of the median line. Impact on the third and fourth would be about equal, and they would develop equally. At the same time, drawing the foot out of the mud would cause a transverse strain which would tend to make some joints more mobile. The ones affected were between the two rows of tarsal elements. Thus two typically
SUMMARY.

1. The primitive mammalian foot was pentadactyl, plantigrade, serial in arrangement, astragalus ungrooved.

2. Modern articulations such as the wrist and ankle joints have been produced by mechanical forces, torsion, impact and flexure, acting upon a plastic skeleton. Stages in the development of such joints are shown in paleontological series.

3. The carinae on the metapodials have been caused by the pressure of the sesamoid bones during locomotion. It is not continued dorsally in animals with padded feet because the pad reduced the impact.

4. Displacement has been caused by the torsion of the foot and leg during locomotion and has increased with digitigradism. Both carpal and metacarpal displacement can be explained by the rotation inward of the distal row of carpal bones. Displacement is not so marked in Ungulate orders because the pad on the foot has lessened torsion.

5. Reduction has been due, first to displacement, second to unequal distribution of strain upon the digits.

6. Those elements which have received the most impact and
transmitted the most pressure, have grown the most rapidly.

7. Impact and strain have stimulated osseous deposit, and where elements have been closely applied, has caused fusion as in the formation of the cannon bone and fusion of podial elements in Artiodactyla. The cannon bone of the camel has not fused entirely because of the formation of the pad.

8. Perissodactyla and Artiodactyla have descended from common ancestors, for similarities of foot structure indicate close relationship.

Evolution of the Ungulate Foot.

In 1890 Henry F. Osborn published in the Trans. Am. Philos. Soc. n. s. Vol. 16, his theories of the evolution of the ungulate foot, which differ in many respects from those advanced by Cope three years before. It is very probable that the criticism of Cope's theory brought forward by Osborn, accounts for the re-statement of that theory in 1896, for while no mention is made of Osborn's work, the modifications are such as to answer his objections. Osborn's theory may be stated in brief as follows: the primitive ungulate foot may be known from a study of Phendcodus. It was pentadactyl, plantigrade; the first and fifth digits shortest; the podial elements serially arranged; the only interlocking
joints being beneath the scaphoid and unciform of the manus, and the navicular and cuboid of the pes, as in all mammals. In the pes the tibia and fibula both rested on the astragalus, the trochlear surface was almost flat, facing upward; the neck was short; the head articulated with the navicular and often slightly with the cuboid; there were but two calcanear facets. The calcaneum rested on the ground. In the manus there was a centrale; the distal row of carpals was broader than the proximal. This primitive structure is essentially preserved in the Hyrax. Secondary articulations are, then, an adaptation to digitigradism which results in the elevation of the wrist and ankle joints, and a displacement of the podials and metapodials. The change from the serial stage to the interlocking is an advantage against lateral strain. It should be noted that the displacement of the metapodials upon the podials takes place before the displacement between the two rows of podial elements. In the manus the second and third metacarpals always acquire facets on the ectal sides with the magnum and unciform. The lunar, then, either by growth, or by the growth of the unciform, spreads over the latter, in all groups save in the Proboscidea. The growth of the scaphoid over the magnum may proceed at the same time. In the pes the flexor tendon and with it the astragalar foramen disappears; the trochlear groove
deeps; the navicular facet becomes saddle-shaped and then flat; the inferior calcaneal facet is formed by a division of the sustentacular; the astragalo-cuboid facet is formed by growth from both directions. This course of development is found in all forms excepting the Proboscidea and the monodactyl horse. The metatarsal displacement is much less constant than the metacarpal although as a rule it is toward the ectal side.

The evolution of the manus and pes of ungulates involves the following processes and probably in the following order:

1. Elevation from plantigrade to digitigrade position.
2. Growth of certain elements and the reduction of others.
3. Displacement of elements from a serial to an interlocking arrangement.
4. Coalescence of parts primitively distinct.

These processes all interact upon each other and affect the growth of the parts in question. The influences at work are many and varied and each has its definite place.

In the manus the evolution is more complex and also more constant than in the pes. It may be discussed under the following headings:

1. Relations of Growth, Reduction and Displacement.

If displacement changes the vertical position and relations
of the podial elements, there must be an increased growth on the part of others. Displacement itself is due not only to growth but involves an actual rotation although not so much as Cope thought necessary. Growth is accelerated by vertical pressure and displacement by lateral strain as well. Displacement may be arrested in cases where the weight is transmitted thru the median toe. Growth will then, through pressure, tend to make up for previous displacement. There is every reason to think that reduction is largely due to the elevation of the foot.

2. Theories of Modification.

Ryder points out that reduction is the result of unequal stress and strain on the digits.

Cope formulated the first theory of displacement. His theory does not explain the shifting of the metapodials which, excepting in the Proboscidea, takes place in the same direction as the displacement of the proximal row of podials. If the torsion strain experienced by the foot acts, as interpreted by Cope, it would be felt first at the podial-metapodial articulation and would tend to displace the metapodials toward the ental instead of the ectal side.

3. Relation of size of Ulna and Radius to Displacement.

In general it may be said that while the direction of dis-
metapodials begins with the elevation of the wrist joint and precedes the intercarpal displacement."


With displacement and reduction, the third metapodial as well as the fourth and fifth is in contact with the unciform. As the fifth persists longer than the first, for a time, weight is transmitted from without inward thru three digits to the unciform which thus receives the maximum of vertical and lateral strain on the ectal side of the distal row. From the proximal row, weight is usually transmitted thru the radius and so is received by the ental side on the scaphoid and lunar. So the marked displacement of the lunar on the unciform and the scaphoid on the magnum may be explained in part at least by the growth toward the mesial line of the scaphoid and unciform.

7. Reduction and Displacement.

Ryder has pointed out the relationship between reduction and distribution of strain. Cope would have displacement as the cause of, or preceding reduction. This can not be true for there is reduction without displacement.

If the various types of reduction and displacement are studied without regard to phylogeny, they may be arranged into groups as:
placement to the ectal or ental side is determined by the weight being borne on the ental or ectal side, the amount of displacement is independent of the amount of weight transmitted on that side.

4. Growth and Reduction.

Growth and reduction are due to hypertrophy or atrophy of certain elements with use or disuse, or change in nutrition. Since both lateral and vertical pressure are active, those elements with the maximum resultant of the two forces will grow most.

5. Metapodial Displacement.

A study of the instantaneous photographs of animals in motion, shows that, as the fore foot descends it strikes the ground under the trunk. The outer border of the foot comes in contact with the earth first, the inner border leaves last, so that the weight of the body is borne from without inward, and the torsion of the body, in so far as transmitted to the foot, from without inward. In the manus the metacarpal displacement is practically constant throughout ungulates, the second and third metacarpals having facets on the ectal side for the magnum and unciform respectively. The only variation is in the adaptively reduced Artiodactyla. " This disposition of the facets is perfectly adapted to resist the strain upon the metapodials as the foot swings inward in descent. Thus the ectal displacement of the
1. Forms with no displacement or reduction, purely theoretical.

2. Amblypoda in which the lunar only is displaced and there is no median axis.

3. Proboscidea in which the lunar only is displaced but toward the ental side.

4. Tetradactyl Perissodactyla and all Artiodactyla with the third and fourth toe on either side of a mes-axial line. Displacement seems arrested.

5. All tridactyl forms with the axis through the third digit.

6. Monodactyl forms where the displacement is compensated for by growth.

In the Amblypoda and Proboscidea the diverging toes transmit strain from all sides; the lunar has been enlarged; there has been no reduction. In the forms that have been highly reduced except in case 6, there is an equality between the scapho-magnum and lunar-unciform facets. From comparison, it would seem that reduction, in changing the digital strain, affects these facets. In the Artiodactyla, where the strain between the third and fourth metapodials has been uniform since Eocene time, there has been no change in displacement. Displacement seems to be the result of an attempt to maintain the axis of support which has been disturbed by reduction. So Prof. Cope, in saying that displacement
causes reduction, has put the effect before the cause.

In the tarsus the same principles cause displacements, but, since the hind foot is used for propulsion rather than for support, as in the fore foot, the metatarsals are displaced according to differences in lateral strain in either direction. The growth of the astragalus toward the cuboid and the cuboid toward the astragalus are concomitant; both are toward the mes-axial line just as is the growth of the scaphoid and unciform.

In conclusion, Osborn says: "The laws of adaptation of the serial plantigrade foot to digitigradism may be summarized as follows:

1. "Displacement is effected by growth, arrested growth or reduction of different elements and takes place in the direction of the greatest lateral strain, being most rapid in the elements which are subjected to the maximum vertical impact and lateral strain.

2. "The direction and degree of intercarpal displacements are adapted to the gradual alterations of the major axes in the bones of the forearm and metapodium respectively, as brought about by reduction, and tend to maintain these proximal and distal axes in the same vertical line.

3. "The initial displacement, however, preceding and inde-
pendent of reduction, is the ectal movement of the metapodials, adapting these elements to resist the strain of the "stroke" upon the outer border as the foot extends downward and inward.

4. "In the unreduced isodactyl types, the strain of the spreading metapodials converges to the center of the carpus, without a definite median distal axis, and the lunar spreads to the ectal or ental side according as the respective growth of the radius or ulna alters the major axis of the forearm.

5. "In the Diplarthra, the major axis of the forearm passes through the radius and thru the third digit (Mesaxonia) or between the third and fourth digits (Paraxonia). The outward displacement of the entire upper upon the entire lower row of carpals, is apparent, not real; the magnum and lunar are arrested in growth, and the lunar remains almost directly in the mes-axial line; what actually takes place is the ental growth of the unciform and the ectal growth of the scaphoid toward the mes-axial line, thrusting the magnum and lunar apart.

6. "This growth is affected by the reduction of the lateral digits in so far as this alters their relation to the major axis of the metapodium. When reductions leave the major axis between the third and fourth digits, this growth is arrested; when it leaves it directly thru the third digit it is extreme; when the
third digit alone transmits the main impact, the displacement is neutralized by the growth of the elements which directly support this digit, i.e. magnum and cuneiform."

Evolution of Manus and Pes.

W. K. Gregory, in Bull. Am. Mus. Nat. Hist. Vol. 27; 1910, gathers together all of the work done on the evolution of the manus and pes in the past few years. He says in the introduction: "The very important researches of Broom (1904) on the structure of the feet in the Permian and Triassic mammal-like reptiles and of Emery (1901) on the embryonic manus and pes in Echidna and Didelphys, when compared with the description of the feet of Eocene mammals by Cope, Osborn, Matthew and others and also with the feet of all the existing unguiculate orders, together furnish a fairly adequate basis for a review of the evolution of the carpus and tarsus in mammals."

It is now generally admitted that the amphibians are far removed from the direct line of descent of the mammals. The view held by Owen, and later worked out by Osborn and Broom, placing the ancestors of the Mammalia in or near the reptilian order Cynodontia, is quite widely accepted. These reptiles were Triassic in age and are found in South Africa. While they show unmistakable
reptilian characters, the Cynodontia foreshadow the mammals in many respects; in vertebrae, in shoulder girdle, in pelvic girdle and in skull. Unfortunately the carpus and tarsus are but imperfectly known. We may obtain a good idea of the prototype of the mammalian carpus and pes from the study of closely related orders, Anomodontia and Therocephalia.

The Carpus.

The manus of *Oidenodon*, an Anomodont, is more or less paddle-like. There are present two carpal elements not found in mammals, centrale 2 and the fifth distal carpal. The radiale is below the radius, the ulnare below the ulna, the intermedium is between the two. They foreshadow the scaphoid, cuneiform and lunar respectively. The centrale 1 is distal to the radiale; centrale 2 has the position usually taken by the centrale in modern mammals. The distal row is made up of five small carpal elements, the first four foreshadowing the trapezium, trapezoid, magnum and unciform; the fifth is fused or lost in Mammals. It is figured in *Bull. Am. Mus. Nat. Hist.* Vol. 27; p. 440, fig. 2.

In *Opisthoctenodon* also an Anomodont, carpale 5 has disappeared; centrale 2 is very small; centrale 1 is assuming the position retained among mammals. Figured *Ibid*, fig. 3.

In *Theriodesmus* a Therocephalian, the carpus is much more
mammalian in character. Centrale 2 is minute; centrale 1 has the same position as in mammals; carpale 5 is absent; carpale 4 is enlarged and articulates with two metacarpals; the trapezium is larger than the trapezoid. If centrale 2 were absorbed or fused, the intermedium (lunar) would rest directly on carpale 4 (unciform), thus producing the so-called interlocking type of carpus which we see distinctly foreshadowed here in the Triassic reptiles. Figured, Ibid, fig. 5.

The study of the foetal manus of *Echidna* shows some remarkable resemblances to those of *Ondenodon* and *Theirodesmus*. The whole hand is paddle-like and outspread as in the former. The fused scapho-lunar-centrale might have been derived from the radiale, intermedium, and centrale. Centrale 2 might have fused with the unciform. Figured, Ibid, fig. 8.

The manus of *Didelphys* is more mammalian but still shows marked resemblances to the reptilian forms studied. The lunar-unciform contact is broad. Figured, Ibid, fig. 9.

No mammalian manus is known before the Basal Eocene although mammals must have existed before that time, with a pentadactyl manus; divergent pollex; large trapezium; free centrale; small magnum; and probably a broad lunar-unciform contact. Our reason for assuming this is because these characters are found in the
earliest mammals. The lunar-unciform contact may have begun in the Triassic; it has persisted in the Marsupials, Edentates, Rodents, Insectivores, Creodonts, Fissipeds, Tellodonts, Primates, Condylarthrs (Euprotogonia), Amblypoda (Pantolambda), Perissodactylys, Artiodactyls, Cetacea and Sirenia. The presence of the lunar-unciform contact and free centrale give the interlocking carpus which is a primary and not a secondary condition. The secondary condition is found rather in those forms which have lost this contact as in Tubulidentata, Hyracoidea, Embrithopoda and Proboscidea. In reviewing the manus of the various orders we find evidence of the primitive nature of the interlocking carpus.

Order INSECTIVORA.

The Insectivora is a primitive order in many ways. In the majority of modern forms the free centrale and lunar-unciform contact are preserved. In fossil forms, so far as the manus is known, there is a free centrale and a lunar unciform contact that may vary from broad to narrow but is always present.

Order RODENTIA.

In forms with wide spreading digits, such as Castor, the lunar-unciform contact is broad; in swiftly running forms it is narrow. A free centrale is usually found.
Order TILLODONTIA.

On the whole, these forms closely resemble the Creodonta.

Suborder CREODONTA.

The manus is well known from many Creodonts and in all there is a free centrale and a lunar which rests equally on the centrale, magnum and unciform.

Suborder FISSIPEDIA.

The manus is essentially like that of the Creodonta with the scaphoid, lunar and centrale fused. The unciform contact is broad.

Order CONDYLARTHRA.

The well known Phenacodus is now generally regarded as descended from the ancestral Euprotogonia which, according to Matthew, is intermediate between Phenacodus and Creodonts. In Euprotogonia there is a distinct lunar-unciform contact and probably a centrale. While Phenacodus is usually regarded as serial, it too, often shows a slight lunar-unciform contact.

Order AMBLYPODA.

With the increase in weight the carpus became broad; the lunar widened and increased the lunar-unciform contact.

Order HYRACOIDEA.

The carpal facets tend to become horizontal; the magnum is
large; the lunar partly overspreads the trapezoid and centrale; the lunar-unciform contact is variable but is usually evident from the palmar view.

Order EMBRITHOPODA.

Carpus very similar to Elephas.

Order PROBOSCIDEA.

The lunar becomes very broad, overspreads the trapezoid and causes a reduction of the scaphoid.

Order ARTIODACTYLA.

In the earliest forms there is a distinct lunar-unciform and scapho-centrale contact. It was probably less than in modern forms.

Order PERISSODACTYLA.

In the ancestral Perissodactyls the carpus was narrower and less interlocking than in modern types but even in the most primitive forms known, the lunar rested on the magnum and unciform on the posterior aspect. The development of the interlocking type is secondary then, only in broadening the contact.

Order SIRENIA.

The centrale is not present but the lunar and unciform are in contact.
The lunar - unciform contact is retained.


1." The structural prototype of the mammalian carpus is realized in the Permian and Triassic Therapsida in which the carpus differs from that of mammals chiefly in retaining two elements which afterwards disappear as primitive mammalian characters.

2." The essential feature of the inter-locking type, namely, the scapho-centrale-magnum and the lunar - unciform contacts are present in many Ungulate orders and are probably a primitive mammalian character.

3." In the Ungulates the retention of the grasping function and of the diverging pollex, favors the development of oblique facets and of a strongly interlocking carpus.

4." Loss of a divergent pollex and the development of either ambulatory and cursorial habits or of great weight, often favors the flattening of the carpal facets in horizontal planes and the development of the serial carpus (e.g., certain Insectivores, Rodents, Proboscidea etc.).

5." The Perissodactyl and Artiodactyl manus have been derived
from different varieties of the incipiently interlocking types. In both also the interlocking features became emphasized, the serial features more or less suppressed.

6. "The observed and inferred modes of evolution of the carpus in mammals suggests first the complexity of the factors that have contributed to the results and second, the apparent inadequacy of the explanations which take into account only natural selection on the one hand and adaptive fitness on the other.

7. "In different orders different elements seem to be dominant factors and to have as it were, greater growth vigor to crowd and modify their fellows."

Tarsus.

In the pes of Ondenodon the astragalus and calcaneum are protypal, not differentiated into head, neck and trochlea or sustentaculum and tuber; the intermedium is present; other elements are homologous with those of mammals. It is figured, Bul. Am. Mus. Nat. Hist. Vol. 27, p. 440, Fig. 28,2.

In the Echidna the tarsus is strangely modified. The calcaneum is smaller than the astragalus; the tuberosity points downward. The astragalus has a large convex postero-external condyle bearing the fibula and most of the tibia.
The distinctive characters of the Marsupial astragalus appears to be its oblique position at the side of the calcaneum; broad trochlea with poorly defined crests; short neck; continuity of sustentacular and navicular facets; and the absence of a cuboid contact.

Among placental mammals the most primitive astragalus probably had a broad trochlea, short neck, and convex head. In the Rodentia and Edentata the astragalus has a wide, low-keeled trochlea; and a short, oblique neck; a very convex head; ectal and sustentacular facets are parallel, oblique and separated by a groove which may end in an astragalar foramen. The cuboid contact is variable but usually absent.

Order INSECTIVORA.

The astragalus is usually long and slender, with a wide trochlea whose ridges may be developed to a varying extent.

Suborder CREODONTA.

The trochlear crests are variable. The astragalo-cuboid contact appears to be primitive in this group.

Suborder FISSIPEDIA.

The trochlea is very narrow and the keels are rounded. The astragalo-cuboid contact is retained to a slight extent.
Order CONDYLA 

The astragalus is very similar to that of the Creodont type although the astragalocuboid contact is lost.

Order ARTIODACTYLA.

The Artiodactyla were probably derived from a type similar to the primitive Creodonts with an astragalocuboid contact. The sustentacular facet is very broad and flattened on the back.

Order PERISSODACTYLA.

The order arose from a type in which the astragalocuboid contact may not have been present at first and is absent or very narrow in Eocene Perissodactyls. Later it widened progressively but never has been as broad as in the Artiodactyla. The sustentacular facet forms a reversed L.

From this study and comparison of mammals of many orders and of primitive forms we are in a position to conclude, that since the lunar-unciform and scaphoid-centrale-magnum contacts are retained by so many orders and since they were foreshadowed in the Triassic Reptilia, the interlocking carpus is a primary and not a secondary condition and was inherited by the mammalian stem from the reptilian ancestry. These orders in which the serial carpus predominates are secondary rather than primary and a study
of their phylogeny will show that they are derived from interlocking ancestors as is the case with Phenacodus, the typical example.

Relation of Perissodactyla and Artiodactyla.

As mentioned before, Cope gave the Perissodactyla and Artiodactyla equal rank under the order Diplarthra. He believed that both were descended from the Condylarthra thru Phenacodus, and considered that the similarities of foot structure in the two groups indicated a close relationship. Osborn, in his latest classification, ranks the two as orders under the Cohort Ungulata for the same reason.

Basing his theory on the work done by Wortman, Matthew and others as well as upon his own comparisons of the material in the National Museum, Gregory has arrived at the conclusion that the Ungulata vera or Diplarthra is an unnatural group; the similarities between the two groups in foot structure is due to convergence and a possible inheritance from the far removed protungulate ancestors, and not to any close relationship. The similarities upon which relationship has always been based are largely characters of foot structure. In the earliest known Artiodactyl manus, Ancodus, the carpal elements are the same and
arranged in the same way as in the oldest Perissodactyls; alternating in type; centrale fused with scaphoid; lunar contact with unciform broad; third digit longer than others. But in spite of such resemblances, the trend of all evidence indicates a fundamental difference between the two groups.

With respect to the carpus and tarsus these differences are:

1. In the first known Perissodactyla, the third digit is longest and digits two and four tend to be subequal; in the earliest Artiodactyla, while the third digit is longer than the fourth, it is digits two and five which tend to be subequal.

2. In the pes, the primitive Perissodactyl is tridactyl and mesaxonic; the primitive Artiodactyl is tetradactyl and paraxonic.

3. In the Lower Eocene Perissodactyls, the astragalo-cuboid facet is small and limited; in the corresponding Artiodactyls it is broad.

4. The early Perissodactyls present a gently curving navicular facet; the early Artiodactyls, a sharply convex and trochlear navicular articulation.

5. The sustentacular facet of early Perissodactyls is always narrow and on the inner posterior border; in the Artiodactyls the facet is broad, ovate and central in position. These
characteristics were well established by (Bridger) Middle Eocene times.

So it seems that the Perissodactyla and Artiodactyla are widely separated rather than closely related. For this reason Gregory would separate them and rank them unequally. His proposed scheme of classification is:

Superorder PARAXONIA Marsh.

Order ARTIODACTYLA Owen.

Superorder UNGULATA (Linn.).

Order MESAXONIA (Marsh).

Suborder PERISSODACTYLA Owen.
CONCLUSIONS.

Cope and Osborn agree that the primitive mammalian foot was pentadactyl, plantigrade and serial. They disagree as to the cause of displacement; Cope would explain it by mechanical forces, only; Osborn believes that beside the mechanical forces, the podial elements grew or had their growth arrested in such a way as to maintain the major axis of the limb in a straight line. He points out that metapodial displacement precedes podial displacement which can not be explained by Cope's theory. Cope's theory is weakened by the fact that in stating it twice he used the same force acting in the same way to produce different results.

Gregory shows that a serial condition of the primitive carpus and tarsus is false. The interlocking carpus was foreshadowed in the Triassic reptiles, was characteristic of primitive mammals and has been retained in most orders. The serial arrangement, when found, can be traced back to ancestors with interlocking form just as Phenacodus has been traced to Euprotopsogonia. There is then no need of any theory to account for the interlocking or so called displaced carpus and tarsus only in as much as the facets in contact have been increased or decreased.
from the ancestral type. Considering the many factors that must have entered into the evolution of manus and pes, it is impossible to ascribe the outcome to any one cause. While the same mechanical forces may have been acting upon different groups, differences in heredity and incipient power of development, would cause unlike results. A good illustration of this is found in the Perissodactyla and Artiodactyla. Similarity in habit and mechanical environment produced, through convergence, an apparent likeness in structure; but beneath the apparent likenesses are deep-seated differences which can be explained only by descent from different ancestors.

For instance, Cope explained that the obliquity of the astragalar trochlea of the horse, a Perissodactyl character distinctly marked from early Eocene, was due to the torsion upon the foot. The torsion on the feet of Artiodactyla must have been as great but they have been characterized from their first appearance by a trochlea whose keels were parallel to the long axis of the bone. The same force applied in the two cases has apparently produced different results. The only explanation lies, as Gregory indicates, in a widely separated line of descent for the two groups.

In conclusion we may say that kinetogenesis has been a great, but not the only factor, in the evolution of the feet of mammals.
The theories offered by Cope of the plasticity of the skeleton, the moulding of articulations and digital reduction, in so far as concerned with unequal distribution of strain, may be retained. The theory of displacement of carpus and tarsus is based upon a false assumption, the serial type as primitive, and seeks to explain evolution in all groups of mammals by purely mechanical causes.

Osborn's theory of carpal and tarsal evolution is based upon the same assumption but may still be of some value in giving an idea of the cause of secondary widening or narrowing of the primitive interlocking type.

Gregory points out that the primitive tarsus was interlocking in type and makes clear the fact that the factors of evolution are complex and complicated, and no one set of factors, no matter how important, can hope to explain the results of evolution in all cases.

Application of Theories to Material Studied.

To be able to determine exactly how much kinetogenesis has had to do with the evolution of the feet of any mammal as we find it today, it would be necessary to know the structure and habits of
all the forms in the line of descent of that mammal, as well as the modern specimen. Without such a knowledge, which, in most cases, is impossible, the explanation must be more or less incomplete. A summary of each form studied has been given. Conclusions will be drawn from it without restatement.

_Ursus americanus._

Both manus and pes are primitive, indicating an animal whose feet have been specialized very little in any one direction. At the same time, the manus is relatively stouter and shorter as well as broader. This modification is probably due to the habit of digging which characterizes this hyaena.

_Canis familiaris._

Manus and pes by their compactness, elongation and digitigradism indicate the greatest amount of modification among carnivores for speed. The saddle-shaped radial articulation is less easily displaced; the angulation of the metapodials is due to their compactness; the distal cylindrical articulations allow great freedom of movement in running but no lateral motion; all adaptations are for speed.

_Hyaena striata._

The pes is very similar to that of Canis in modification for speed. The manus is relatively stouter and shorter as well as broader. This modification is probably due to the habit of digging which characterizes this hyaena.
Felis concolor.

With the development of retractile claws as weapons, speed was less of an advantage than ability to use the claws; so the feet are not compact but loose; the metapodials diverge; their distal articulations are rounded; the radial articulation is very slightly saddle-shaped; all modifications allow spreading of the digits in grasping prey.

Eumetopias stelleri.

Both manus and pes are modified for swimming in being paddle-shaped. Inversion of the pes, while of direct advantage in swimming, is not yet fixed and the foot may be used in walking. Elongation of the digits and the lengthening and increased diameter of the outer ones, are probably due to the pressure of the water.

Phoca vitulina.

Inversion in the pes has become complete. Cope suggested that it was at first voluntary and later fixed because flexion and extension were lost through disuse.

Equus caballus.

The feet of the horse have been adapted for speed. The lines of evolution have been pointed out. Every modification along the line of elongation, suppression of lateral digits, development of
the unguligrade gait, has been for greater speed. The broadening
of the elements has been to give a broad enough basis of support
for a monodactyl type of foot.

*Auchenia guanaca.*

Elongation again indicates speed. The metapodials are but
partially fused and the distal extremities diverge. Cope suggested
that the fusion was not complete because the development of the
pad, late in geologic time, lessened the impact but the distinct
divergence of the distal ends of the metapodials, a characteristic
of the family, began long before the bones began to fuse. The
differences between the cannon bone of this family and other
Artiodactyl families probably indicates remote relationship, a
supposition of which we are fairly sure from paleontological
evidence. We have but little grounds for speculation as to why
the gait of the family changed from unguligrade to digitigrade
but it was probably connected with the formation of the connective
tissue pad.

*Sus scrofa.*

Elongation is so moderate, suppression of digits is so
slight and fusion of elements so entirely lacking that there is
no hesitation in believing that the feet are very primitive in
type and have not been highly modified for speed on hard ground.
**Alce alces.**

Modification here has also been for speed as can be seen in the elongation, reduction and fusion of elements. Why the lateral digits should be reduced first at the proximal extremity is not known. No mechanical reason has been suggested though the same order of reduction is followed throughout most of the family. The explanation must be found elsewhere.

**Ovis aries.**

Modification for speed has become almost complete, for elongation is marked; reduction is complete and fusion of elements is far advanced.

**Bubalus kerabau.**

Elongation is not so great and the elements are all stouter, reduction is practically complete and fusion is well advanced. The feet seem, however, to be adapted to support a heavy animal as well as so highly modified a foot can be.

In looking over material studied it is found that it might be possible to explain many structures by kinetogenesis, although it is not safe to say that mechanical forces alone produce the results, and until the phylogenies of many more families are known it will be impossible to tell just how much is due to kinetogenesis and how much is due to other factors.
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