

# EIGHTEEN PRINCIPLES OF ADAPTATION IN ALLOIOMETRONS AND ARISTOGENES.<sup>1)</sup>

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With 12 figures.

(Eingelangt am 8. April 1935.)

We must ever draw a very sharp distinction between the CAUSES of the origins and adaptations of biocharacters which may remain partly or wholly mysterious, and the MODES of adaptation which the various branches of zoology and palaeontology are now revealing with surprising fullness.

It is a great pleasure to contribute to the Festschrift of a palaeontologist who, through his scientific and popular writings during the past two decades has surpassed all others in setting forth in twelve popular volumes of synthetic description the remarkable discoveries in vertebrate palaeontology of the last half century. In OTHENIO ABEL's voluminous and graphic style the life of all periods of the Mesozoic and Cenozoic is philosophically described. In sympathy with the new subdivision of the biological sciences which he terms Palaeobiologie, may I, in the present contribution, supplement his effort to conjoin the spirit of the science of the past (Palaeontology) and the spirit of the science of the present (Zoology)

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<sup>1)</sup> This is the fourteenth contribution by the author on the "Origin of Species" and the principles of biomechanical evolution as demonstrated in palaeontology, the series beginning in the year 1925. See OSBORN's "Fifty-Two Years of Research, Observation and Publication", New York, 1930.

which are too often separated. This contribution is in part an epitome of my own biological generalizations drawn from the observations of the Titanotheres and Proboscidea Monographs during the years 1900—1935<sup>2</sup>).

In the "origin of species" as defined by the modes of origin of biomechanical characters, the outstanding biological generalizations are:

**Alloiometrans**, similar new adaptations of proportion in the older elements of the skull and skeleton, arise as convergences in phyla of diverse phylogenetic stocks. Such evolution is rapid and temporal.

**Aristogenes**, similar origins of new adaptive biomechanical characters, arise as parallelisms in phyla of similar phylogenetic stocks, however remote in geologic time. Such evolution is slow and secular.

### **Biology Retarded by Exklusive Specialization in Palaeontology and Zoology.**

The divorce, from palaeontological discovery and from palaeontological generalization, of anatomy and physiology, of zoology, of heredity including genetics seriously retards our understanding of the all-embracing Biology or science of life as a whole. Through whatever portal we enter the mysterious temple of living nature, we soon become absorbed in the phenomena immediately around us to the exclusion of all other phenomena. Anatomists, zoologists and palaeontologists, who are making marvelous discoveries in the biomechanical modes of adaptation, rarely concern themselves with principles of physiology and heredity including genetics, or with the great discoveries now being made in biochemistry and biophysics which underlie the functional adaptive actions, reactions and interactions resulting in the evolution of different organs. Palaeontology has long since remade and remoulded the speculative phylogenies based on embryology and zoology. Palaeontology is now

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<sup>2</sup>) HENRY FAIRFIELD OSBORN: "The Titanotheres of Ancient Wyoming, Dakota and Nebraska", U. S. Government Printing Office, Washington, D. C. 1929. Chapter XI, "Causes of the Evolution and Extinction of the Titanotheres" (OSBORN Bibliography number 1929 800.) "Proboscidea, a Monograph of the Discovery, Evolution, Migration and Extinction of the Mastodons and Elephants of the World." Volume I, New York 1936.

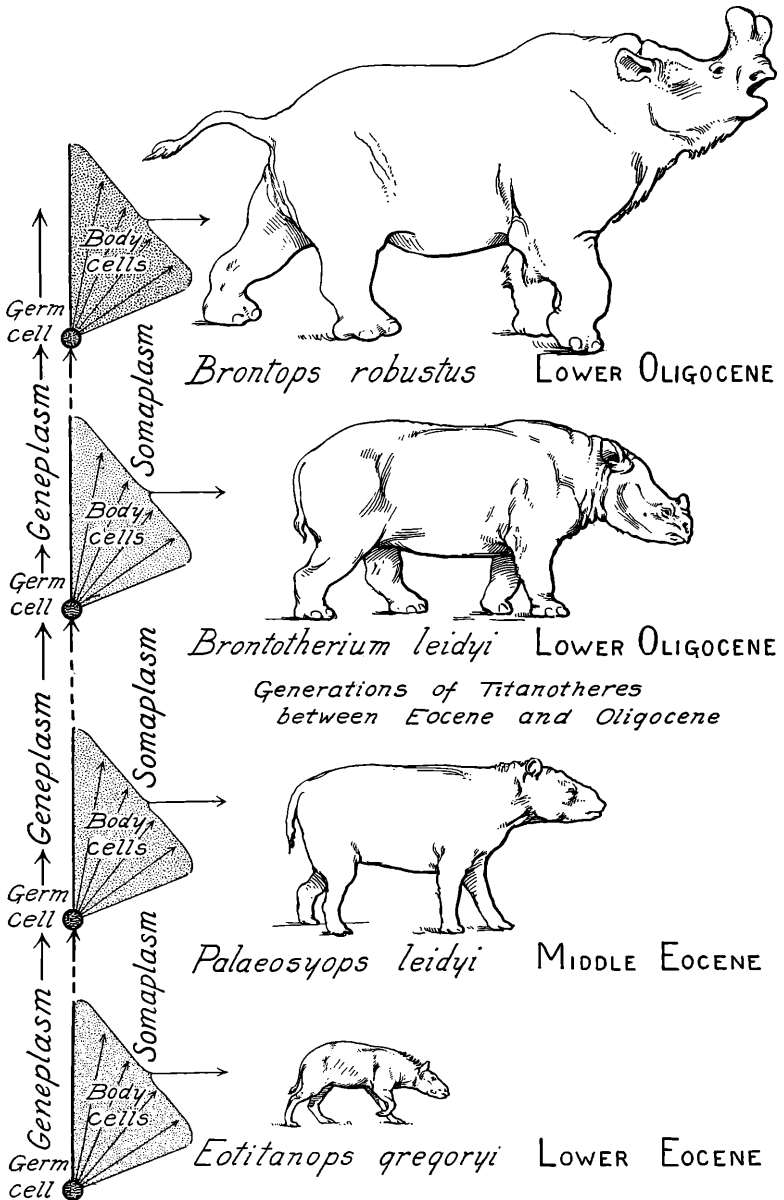


Figure 1. Continuous Geneplasm (germ cells) and Discontinuous Somaplastm (body cells): Twenty Million Year Evolution from *Eotitanops gregoryi* of the Lower Eocene to *Brontops robustus* of the Lower Oligocene.

After OSBORN, Titanotheres Monograph, Vol. II (1929:800).

Aristogenes in the continuous geneplasm of the horns and in the relatively few new cones and conlets of the grinding teeth.

Alloimetrans in the somaplastm of the feet, body and cranium transforming the slender digits of the primitive sub-cursorial *Eotitanops* with light body and equal facial and cranial region into the massive graviportal *Brontops* with heavy body, abbreviated facial and elongated cranial region.

destined to remake and remould the five classic hypotheses<sup>3)</sup> of evolution based on zoology and comparative anatomy.

On the other hand geneticists and experimentalists, while contributing brilliantly to the structural and functional principles of heredity, tend to adhere to ancient biological hypotheses insecurely based solely on the phenomena which they are observing, and to

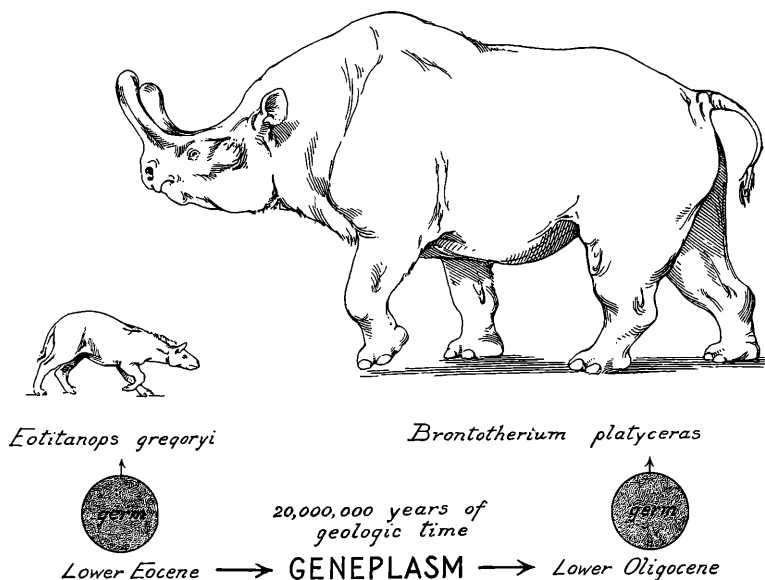


Figure 2. Continuous Geneplasm in 100,000 Generations of Titanotheres Succeeding each other through 20,000,000 Years of Geologic Time.

After OSBORN, Titanotheres Monograph, Vol. II (1929:800).

The geneplasm of the Lower Eocene *Eotitanops gregoryi*, enriched by relatively few Aristogenes in the horns and new cusps on the grinding teeth and very numerous Alloiometrans, evolves into the geneplasm of the giant flat-horned *Brontotherium platyceras* of the Lower Oligocene.

ignore the modes of adaptation actually observed and recorded by zoologists and palaeontologists. Thus widely divorced from Palaeontology in their separate fields of observation, the majority of biologists of the world are congregating in schools and unconsciously adopting evolutionary creeds which not only seriously retard our understanding but postpone the day when Biology may rank with Physics, Chemistry, Astronomy on a solid foundation of well-determined and universal principles of adaptation. These principles

<sup>3)</sup> The classic hypotheses are those of ARISTOTLE, BUFFON, LAMARCK, DARWIN-WEISMANN, and DE VRIES.

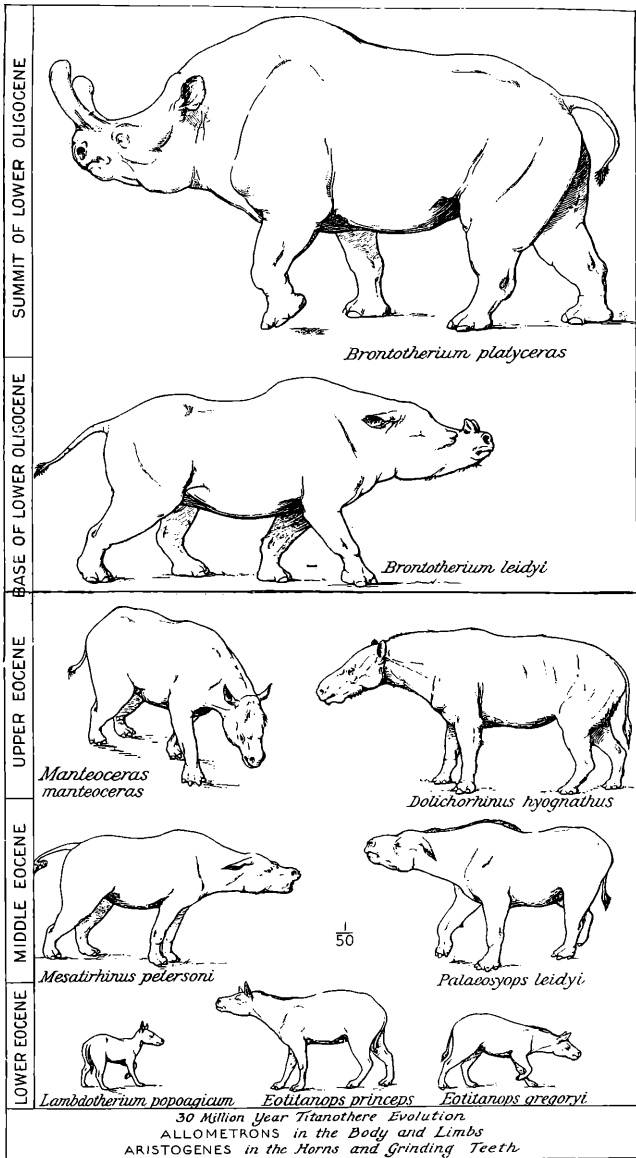


Figure 3. Adaptive Radiation of Fifteen Phyla of Titanotheres from Lower Eocene to Lower Oligocene Time: 20,000,000 Years.

After Osborn, Titanotheres Monograph, Vol. II (1929: 800).

- 1) Lambdotheres: Lambdotherium popoagicum of the Lower Eocene.
- 2) Palaeosyopines: Eotitanops gregoryi, most primitive true Titanotheres.
- 4) Metarhines: Mesatirhinus petersoni, first rudiment of Horn.
- 2) Palaeosyopines: Palaeosyops leidy, entirely lacking Horn rudiment.
- 8) Manteoceratines: Manteoceras manteoceras, prophetic Horn rudiments.
- 9) Dolichorhines: Dolichorhinus hyognathus, prominent Horn rudiments.
- 11) Brontotherines: Brontotherium leidy, small flattened Horns, large flattened Horns.
- 11) Brontotherines: Brontotherium platyceras, extremely large flattened Horn.

of adaptation afford fixed points of observation and measurement upon which we may advance toward the eternally mysterious problem of the causes of adaptation.

### Applications to Palaeontology of WEISMANN'S Distinction between Somaplasm and Geneplasm.

Recalling the illogical neo-Lamarckism of my great predecessor Professor COPE, which for a while I shared, we palaeontologists must express our debt to AUGUST WEISMANN for first demonstrating the sharp distinction between bodily characters and germinal characters (Figures 1, 2). It is the evolution of the geneplasm which governs the modes of adaptation. The important geneplasmic adaptations (= Heritage — GREGORY) which are extremely slow and secular in their progress are often masked by the relatively temporary somaplasmic adaptations (= Habitus — GREGORY) which are so conspicuous that they divert our attention from the more profound heritage. Let us express the distinctions between these adaptive processes in five Greek terms:

**Somatogenesis** (Greek  $\sigma\omega\mu\alpha$ , body of a man), somatogenes bodily in origin, reactional modifications which temporally adapt the individual to new conditions.

**Skesisgenesis** (Greek  $\sigma\chi\acute{\epsilon}\sigma\iota\varsigma$ , a state, condition, habit of body which is alterable) heritable somatogenic modification, resulting from change of habit, habitudinal adaptation. Basis of Lamarckian and neo-Lamarckian hypotheses, origins of acquired adaptations from theoretic inherited effects of habit.

**Tychogenesis** (Greek  $\tau\acute{\upsilon}\chi\eta$ , by chance) heritable chance geneplasmic variations of DARWIN. D. mutants of DE VRIES, adaptive or inadaptive, subject to Natural Selection. Basis of Darwinian, Weismannian and neo-Darwinian hypotheses of the origin of D. mutations, subspecies and species.

**Aristogenesis** (Greek  $\acute{\alpha}\rho\iota\sigma\tau\omicron\varsigma$ , best born, born of the best, of best or fittest origin), in part W. mutations of WAAGEN (1869), "rectigradations" of OSBORN (1889), "aristogenes" of OSBORN (1931). Basis of Osbornian theories of the origin of new characters<sup>4</sup>).

<sup>4</sup>) HENRY FAIRFIELD OSBORN: "Aristogenesis, the Creative Principle in the Origin of Species", *The American Naturalist*, Vol. LXVIII, No. 716, pp. 193—235. "The Dual Principles of Evolution", *Science*, December 28, 1934, Vol. 80, No. 2087, pp. 601—605.

**Tetrakinesis** (Greek τέτρα four, and κίνησις, signifying to move or set in motion), the four energetic factors of (a) physico-chemical environment, (b) biotic environment, (c) somatogenetic adaptation of habit and function, (d) geneplasmic adaptation or heritage. The "tetraplasy" and "tetrakinesis" of OSBORN. Adaptive reactions subject to organic or coincident selection (BALDWIN, LLOYD MORGAN, OSBORN).

### Distinctions between "Mutations" of WAAGEN and "Mutants" of DE VRIES.

The D. "mutant" of DE VRIES, like the W. "mutation" of WAAGEN, is a systematic or taxonomic term of the lowest known order. Whereas the term W. "mutation" expresses a gradual stage in the appearance and continuous evolution of one or more characters, the term D. "mutant" expresses the sudden and discontinuous appearance of one or more characters from the geneplasm. For example, among the Mollusca a right-handed bivalve is a "mutant" from the normal left-handed bivalve.

Each of these authors, WAAGEN and DE VRIES, sensible of the enormous prestige of the Linnaean term "species" felt it necessary to convince his readers that he had discovered a new systematic stage

#### W. mutation.

This new geologic or "time" stage WAAGEN called "mutation". We may distinguish it as a "W. mutation" WAAGEN'S observations of 1869 were upon the ascending mutations of *Ammonites subradiatus*; they relate both to secular changes of proportion and to secular origins of new sculptural and biomechanical characters.

Observed and strongly supported by invertebrate and vertebrate palaeontology.

#### D. mutation.

This new geographic or "space" stage DE VRIES called a "mutant". We may distinguish it as a "D. mutant". From DE VRIES observations (1895 to 1908) upon the evening primroses *Oenothera Lamarckiana*) sprang the Mutation Hypotheses of DE VRIES, and the Mutation Theory of the sudden origin of new characters and of new subspecies and species in plants and animals.

Not observed or supported by invertebrate or vertebrate palaeontology.

## Distinctions between the Alloimetrons and Aristogenes of OSBORN.

In the course of thirty-four years' intensive research on the evolution of two widely distinct kinds of quadrupeds — the Titanotheres and the Proboscidea — with the cooperation of WILLIAM K. GREGORY I have concentrated research upon biomechanical adaptations of two kinds, namely: (1) the biomechanical principles governing changes of proportion in the cranium and in the limbs, technically known as "alloimetrons"; (2) the principles governing the origins of new characters, technically known first as "rectigradations" (OSBORN, 1881), later as "aristogenes" (OSBORN, 1931).

Alloimetric and aristogenic biocharacters form the basis not only of phylogeny but of all the grades of taxonomy or classification; they are the basis of origin of ascending mutations, subspecies, species, genera, subfamilies, families and orders (see Figures 4 and 8). It is important to establish very clearly the differences between them.

The aristogene as a single new biocharacter is readily distinguishable from the W. mutation time stage of WAAGEN or the geographic D. mutant of DE VRIES; it is of secular origin and its evolution may take an enormous period of time. For example (Figure 9), in the evolution of the third inferior molars in the Longirostrine Mastodont phylum *Trilophodon*, one aristogene, a new conical element, appears on the average in the course of a million years; thirty aristogenes in thirty million years.

### Alloimetrons.

#### Adaptations of Proportion.

1. Alloimetron (Greek ἀλλοίος "of another sort or kind, different" and μέτρον, "to measure in any way") signifies biocharacters arising from changes of proportion or intensity which may be expressed in measurements and indices, for example, the quantitative proportional changes of the head (Figure 5) expressed in the Greek terms

### Aristogenes.

#### Adaptations of Origin.

1. Aristogene (Attic Greek ἄριστος, signifying "best in its kind". The Greek "genesis" (γένεσις) from the Aryan base meaning "to produce, bring into being" means "origin, source, birth, descent; mode of formation or production" Unlike alloimetrons and somatogenes, aristogenes add biocharacters entirely new to the



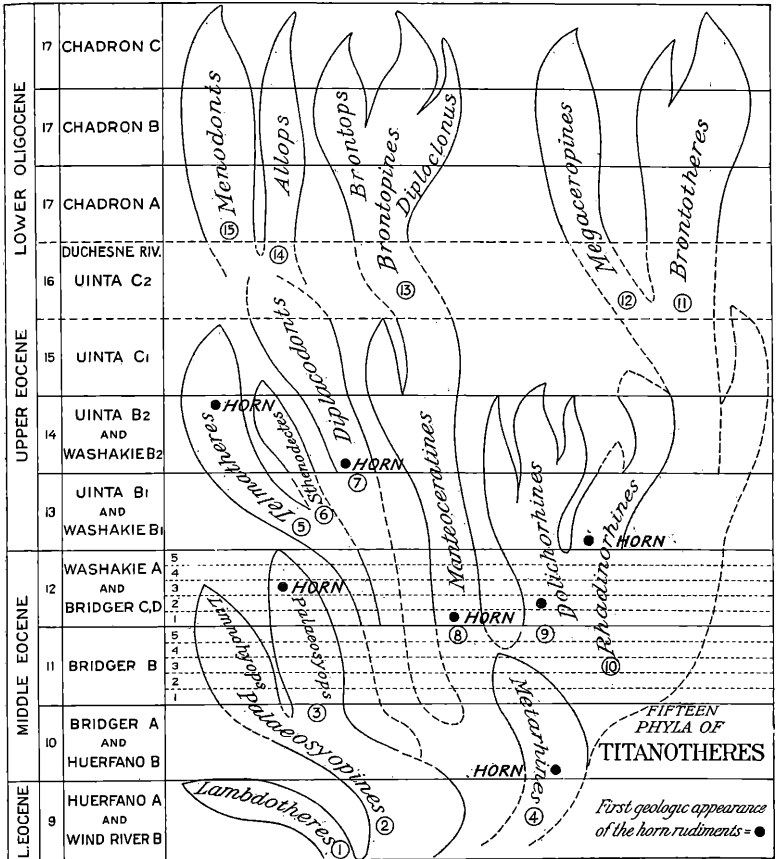


Figure 4. Aristogenesis of the Bony Horns, Originating in Titanotheres Adaptively Radiating from Lower Eocene to Lower Oligocene Time.

After Osborn, Titanotheres Monograph, Vol. II (1929:800).

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|----------------------------|--|
| 1. Lambdotheres            | 9. Dolichorhines                       |
| 2. Palaeosyopines          | 10. Rhadinorhines                      |
| 3. Palaeosyops, Limnohyops | 11. Brontotheres                       |
| 4. Metarhines              | 12. Megaceropines                      |
| 5. Telmatheres             | 13. Brontopines, Brontops, Diploclonus |
| 6. Sthenodectes            | 14. Allops                             |
| 7. Diplacodonts            | 15. Menodonts                          |
| 8. Manteoceratines         |  |

Independent aristogenesis of Horn rudiments in widely separated intervals of geologic time as discovered in the researches for the Titanotheres Monograph in the Eocene to Oligocene of North America.

In Central Asia was discovered a sixteenth branch of Titanotheres, Embolotherium in which there is no trace of the horn rudiment above the eyes; by a change of function the naso-frontal bones are elongated and upturned adaptively taking the function of the gigantic flat horns of Brontotherium platyceras.

brachycephaly (broad headed), dolichocephaly (long headed), brachyopy (short faced), dolichopy (long faced), bathycephaly (deep skulled) hypsicephaly (high skulled), etc., or in the limb proportions (Figures 6, 7) brachydactyly (broad fingered), dolichodactyly (long fingered), leptodactyly (slender fingered), dolichopody (long footed), brachiopody (short footed), dolichomely (long limbed), brachymely (short limbed), etc., or in tooth proportions (Figures 9, 10) brachyodonty (short toothed), hypsodonty (long toothed), etc.

2. The origin of alloiometrons is contemporaneous with changes of habit or function; certain new alloiometrons are anticipated by habit or function.

3. Alloiometrons are not governed or predetermined by germinal potentiality within certain phyla of racial, specific, generic, family and ordinal descent. On the contrary, within species and even within races diverse alloiometrons or more or less profound changes of proportion, are independently arising.

4. Alloiometrons are relatively rapid in development, or temporal.

organism; they arise directly from the geneplasm; they demonstrate genetic potentiality; they arise through genetic predetermination; like W. mutations they slowly and continuously progress in an adaptive direction; they are coordinated with the eighteen principles of biomechanical adaptation; they reveal in the geneplasm an originative or creative principle altogether new to Biology.

2. The origin of aristogenes anticipates habits and functions; new biocharacters thus arise long before they come into use.

3. Aristogenes are governed or predetermined by germinal potentiality within certain phyla or racial, specific, generic, family and ordinal descent. This is demonstrated (Figures 4, 5) in the independent origin of horns in many separate lines of Titanotheres, also in the independent origin of similar aristogenes in the grinding teeth of the many separate lines of Proboscideans.

4. Aristogenes are relatively slow in development, or secular.

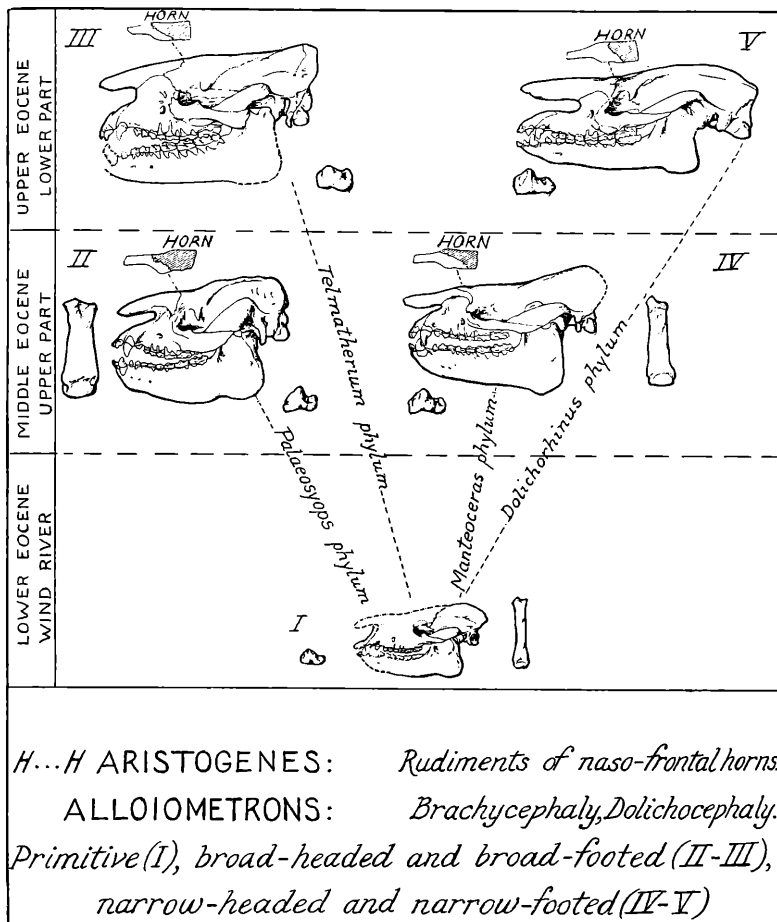


Figure 5. Aristogenes in Paired Horn Rudiments and in Dental Cusps. Alloiometrons in Cranial and Metapodial Proportions. Lower to Upper Eocene Titanotheres.

After Освожн, Titanotheres Monograph, Vol. II (1929:800).

Phylum 2. Lower Eocene Eotitanops. No Horn rudiment, face and cranium equal, leptodactyl.

Phylum 2. Middle Eocene Palaeosyops. Inconspicuous Horn rudiment, brachycephalic, brachydaetyl.

Phylum 8. Middle Eocene Manteoceras. Prominent Horn rudiment, mesaticephalic, mesodaetyl.

Phylum 5. Upper Eocene Telmatherium. Inconspicuous Horn rudiment, mesaticephalic.

Phylum 9. Upper Eocene Dolichorhinus. Conspicuous Horn rudiment, dolichocephalic, brachydaetyl.

## Convergent Alloiometrans in the Cranium and Limbs of Ungulates and Dinosaurs.

See Figures 1—6.

The evolution of adaptively divergent and convergent proportions necessitated a new branch of biomechanics termed "Alloimetrics". It occurred to OSBORN to measure the skeletal limb segments of all the ungulates in the hope of establishing certain uniform principles in the proportional evolution of the limb segments. With the aid of GREGORY this hope was brilliantly realized and the underlying principles of limb segment adaptation were not only established in the ungulate mammals but were found to be identical in graviportal mammals like the elephants (Figure 6) with those in the graviportal dinosaurs like *Camarasaurus* as shown in the accompany Tables I—III. These important biomechanical principles of alloimetry form the subject of Chapter X of the Titanotheres Monograph.

**Primitive Symmetry.** In the Titanotheres Monograph the proportions of the face and cranium in the primitive Perissodactyle (*e. g.*, *Eohippus*) were found to be very similar to these in the primitive Coudylarthra (*e. g.*, *Euprotogonia*), that is, face and cranium about equal in length. Similarly the three fore and hind limb segments: (a) femur-humerus, (b) tibia-radius, (c) pes-manus, were also found to be equal in length (see also symmetry in limbs of embryonic *Equus*, Figure 7).

**Progressive Alloimetry.** From this equal length of face and cranium there diverged in *Titanotherium* a very short face (brachyopy) and very elongated cranium (dolichochny). *Equus*, in contrast, evolved a very long face (dolichopy) and abbreviated cranium (brachycrany). Similarly again, from the equal limb segments of *Euprotogonia* and *Eohippus* there evolved the extremely unequal limb segments of the cursorial or high speed *Equus* (Figures 6 and 7). The speed of each species of the Equidae family is determined by alloimetry.

From the standpoint of philosophical anatomy or Palaeobiology the first important induction or generalization from this new science of alloimetry is the following:

**First Principle:** Irrespective of remote ancestry and of remote phylogenetic affinity closely similar adaptive changes of proportion

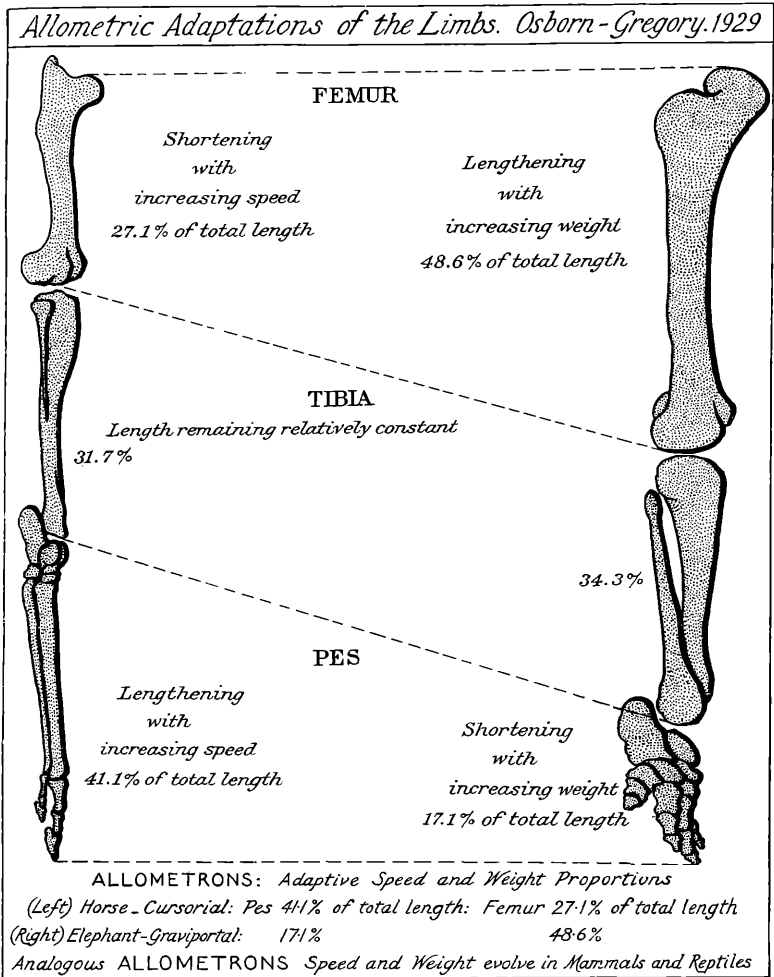


Figure 6. (Left) Equus: Alloimetroons of Speed; (Right) Elephas: Alloimetroons of Weight.

After OSBORN, Titanotheres Monograph, Vol. II (1929:800).

Abbreviating femur of the horse 27,1% of total length.

Elongating femur of the elephant 48,6% of total length.

Tibia of the horse relatively constant, 31,7% of total length.

Tibia of the elephant relatively constant, 34,3% of total length.

Elongating pes of the horse 41,1% of total length.

Abbreviating pes of the elephant 17,1% of total length.

Similar cursorial alloimetroons evolve in all quadrupeds attaining speed, irrespective of phyletic relationship. Similar graviportal alloimetroons evolve in quadrupeds irrespective of mammalian (Proboscidea) or reptilian (Sauropoda) affinity.

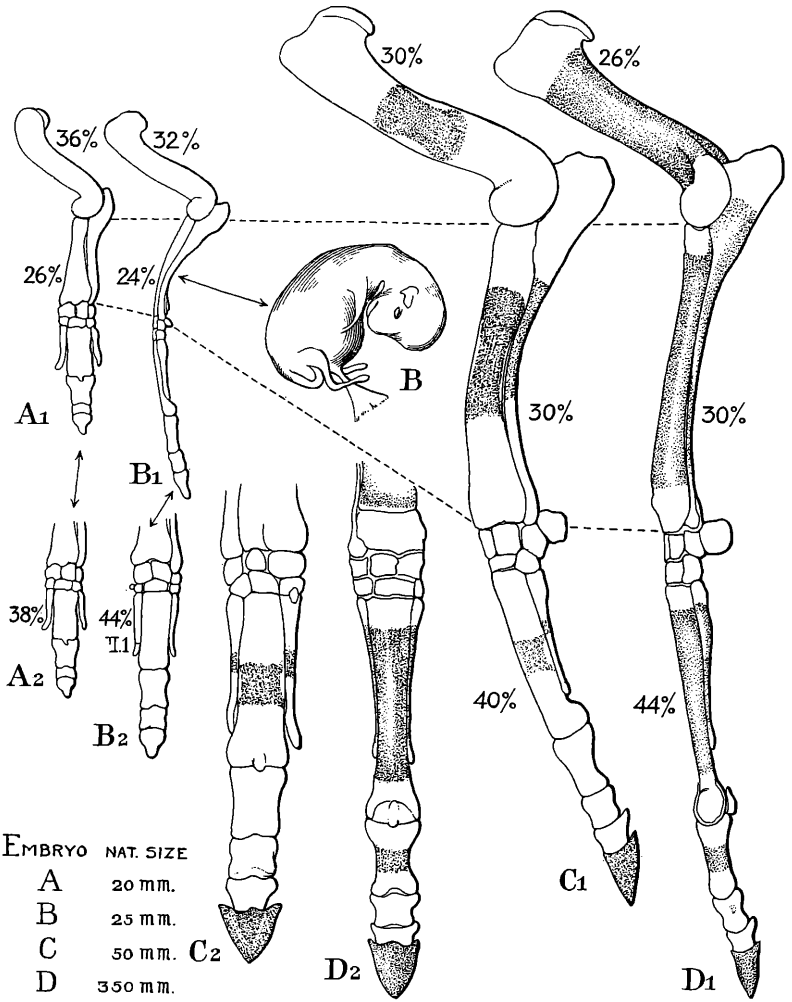


Figure 7. Ontogenetic Acceleration of Cursorial Alloiometrons in the Fore Limb of Equus, After OSBORN, Titanothera Monograph, Vol. II (1929: 800).

In embryo A (20 mm.), humerus, radio-ulna and manus are of equal or balanced length as in all primitive ungulates. In successive stages of embryo B (25 mm.) and embryo C (30 mm.) the humerus abbreviates and the radio-ulna and the manus rapidly elongate. Shortly before birth the limb proportions of embryo D (350 mm.) approach the alloiometrons of Equus. Immediately at birth the colt gallops alongside the mare. These speed alloiometrons have a high selective value.

	A <sub>1</sub>	B <sub>1</sub>	C <sub>1</sub>	D <sub>1</sub>
Total length	100	100	100	100
Humerus, % of length	36	32	30	26
Radius, % of length	26	24	30	30
Manus, % of length	38	44	40	44
Radio-humeral ratio	68	80	99	113
Metacarpo-humeral ratio	40	59	60	91

Articular lengths in every case Foot extended.

in the cranium and in the segments of the limbs arise in different lines of mammalian and reptilian descent.

Alloiometrans, whether in the cranium or limbs, are distinctively convergent processes in which motion, function and habit, resulting from adaptive radiation, play an important part. For example, irrespective of divergent ancestry of class rank, a graviportal dinosaur (*Camarasaurus*) exhibits exactly the same limb segment proportions as a graviportal elephant. The convergence is astonishingly close. Observe in the measurements below:

I. Primitive. In the primitive ancestral and foetal stages of the horse and all other Perissodactyls the tibia and femur are of equal length, the tibio-femoral ratio being 96—100. The metatarsus is half the length of the femur, the ratio being 43—52.

II. Cursorial. In cursorial adaptation the femur is invariably shortened (37—22 % of total limb length); the tibia is slightly lengthened (33—28 % of total length). The metatarsus is greatly lengthened in proportion to the tibia, rising from 31 % in *Phenacodus* to 42 % in *Antilocapra*, and 50 % in *Gazella ruficollis*.

III. Graviportal. In graviportal adaptation the femur is lengthened to 48,5 % of the entire limb; the tibia is shortened to 35,2—27 % of the entire limb; the pes is shortened to 25—16 % of the entire limb. The following Tables I—III present a striking synopsis of convergence in ancestral cursorial and graviportal adaptations.

Table I.

Balanced Segmental Lengths in Primitive Ungulates.

Alloiometric Ancestral and Foetal Balance of Equal Segment Lengths in Primitive Equines, Camels, Tapirs. Tibia and Femur of Equal Length. Metatarsus one-half to one-third Length of Femur.	<i>Euprotogonia</i> (condylarth)	<i>Eohippus</i> (primitive equine)	<i>Eotylopus</i> (primitive camel)	<i>Heptodon</i> (primitive tapir)
Hind limb, total length of .	100	100	100	100
Femur, length of 31 — 34 % .	31	33	32	34
Tibia, length of 31 — 34 % .	32	32	31	34
Pes, length of 32 — 37 % .	37	35	37	22
Tibiofemoral ratio, 96 — 101 % .	101	100	96	100
Metatarsofemoral ratio, 43 — 52 % .	43	50	52	43

Table II.  
Cursorial Ungulates. Speed Convergence.

Alloimetric Convergence of Cursorial Limb Ratios in Condylarths, Equidae, Bovidae, Antilocapridae. Femur Shortening, Tibia and Metatarsals Lengthening.	<i>Phenacodus</i>	<i>Euprotogonia</i> (condylarth)	<i>Eohippus</i> (Equidae)	<i>Mesohippus bairdii</i>	<i>Mesohippus</i> ? sp.	<i>Neohipparton whitneyi</i>	<i>Equus kiang</i>	<i>Antelope cervicapra</i>	<i>Antilocapra americana</i>	<i>Gazella dorcas</i>	<i>Gazella ruficollis</i>
Hind limb, total length .	100	100	100	100	100	100	100	100	100	100	100
Femur, length of 37 — 22% — decrement	37	31	33	33	—	27,1	28	25	27	23	22
Tibia, length of 33 — 28% — balance .	32	32	32	33	—	31,7	28	31	31	32	28
Pes, length of 31 — 50% — increment .	31	37	35	34	—	41,1	44	44	42	45	50
Tibiofemoral ratio, 84 — 126% — increment	84	101	100	100	108	117	94	121	123	125	126
Metatarsofemoral ratio, 31 — 117% — increment	31	43	50	57	68	101	68	100	103	81	117

Table III.  
Graviportal Quadrupeds. Weight Convergence.

Alloimetric Convergence of Graviportal Limb Ratios in Dinosaurs, Elephants, Amblypods, and Titanotheres. Femur Lengthening, Tibia and Metatarsals Shortening.	<i>Brontosaurus</i> (graviportal)	<i>Diplodocus</i> (light-limbed)	<i>Camarasaurus</i> (heavy-graviportal)	<i>Elephas</i> (graviportal)	<i>Uintatherium</i>	<i>Coryphodon</i>	<i>Brontops robustus</i>
Hind limb, total length	100	100	100	100	100	100	100
Femur, length of 48 — 55% — increment	48,5	48,5	48,6	48,6	55	48	48
Tibia, length of 35,2 — 27% — decrement	32	35,2	33,7	34,3	28	29	27
Pes, length of 25 — 16% — decrement .	19,5	16,3	17,7	17	17	23	25
Tibiofemoral ratio, 72 — 53% — decrement .	66	72	69	60	53	61	55
Metatarsofemoral ratio, 26 — 10% — decrement	12	24	13	13	10	14	26

### Particulate and Coordinate Alloimetric Convergence.

Every bony segment in the fore and hind limbs (pelvis-scapula, femur-humerus, tibia-radius, manus-pes) undergoes coordinated or



correlated convergence. Thus in the Perissodactyla we observe convergent cursorial forms of the scapula and ilium, convergent mediportal forms of the scapula and ilium, convergent graviportal forms of the scapula and ilium. These convergencies are in what may be called harmonic locomotor convergence to mediportal, cursorial and graviportal habits. An exception is the giant *Baluchitherium grangeri* skeleton recently reconstructed by GREGORY in which the limb skeleton is simply a harmonic enlargement of the limb skeleton of the *Aceratherium incisivum* type. Not only the main segments of the fore and hind limbs but each component bony element of the carpus and tarsus displays similar alloiometric convergence and adaptation to cursorial, mediportal or graviportal modes of locomotion.

**Particulate Alloiometrans.** Each bone and each dental element in each organ of every mammal adaptively reacts to its own particular local and highly specialized mechanical problem. Of two immediately contiguous bones, one may lengthen, the other may shorten; one may broaden, the other may become narrower. Of two immediately contiguous cusps (Figure 12) each reacts independently of the other.

**Particulate Aristogenes.** This separate, independent and particulate biomechanical alloiometry in the higher ungulates of each of the 280 bones composing the primitive ambulatory quadruped (*Phenacodus*) is precisely concordant with the particulate aristogenesis and separate, independent response of the four main enamel cones of the lower ungulate grinding teeth and of the six enamel cones of the upper ungulate grinders. The Titanotheres are restricted in adaptive radiation of their grinding teeth by the bunoselenodont or cone-and-crescent pattern, whereas the adaptive aristogenesis in the grinding teeth of the Proboscidea is the most extreme which has been discovered in any division of the mammalia.

**Secular Adaptive Reaction.** Alloiometrans, including changes of proportion in the limbs, in the skull, and in the grinding teeth, the organs intensively investigated in the Titanotheres and Proboscideans, follow rather than precede change of habitat and change of function. Proboscideans (Figure 8) such as the relatively primitive phylum leading to the forest-living *Mastodon americanus*, exhibit an arrested development of the grinding teeth nearly to the end of Pleistocene time attributable to their continuous forest-living habits. This is analogous to the arrested development both of the

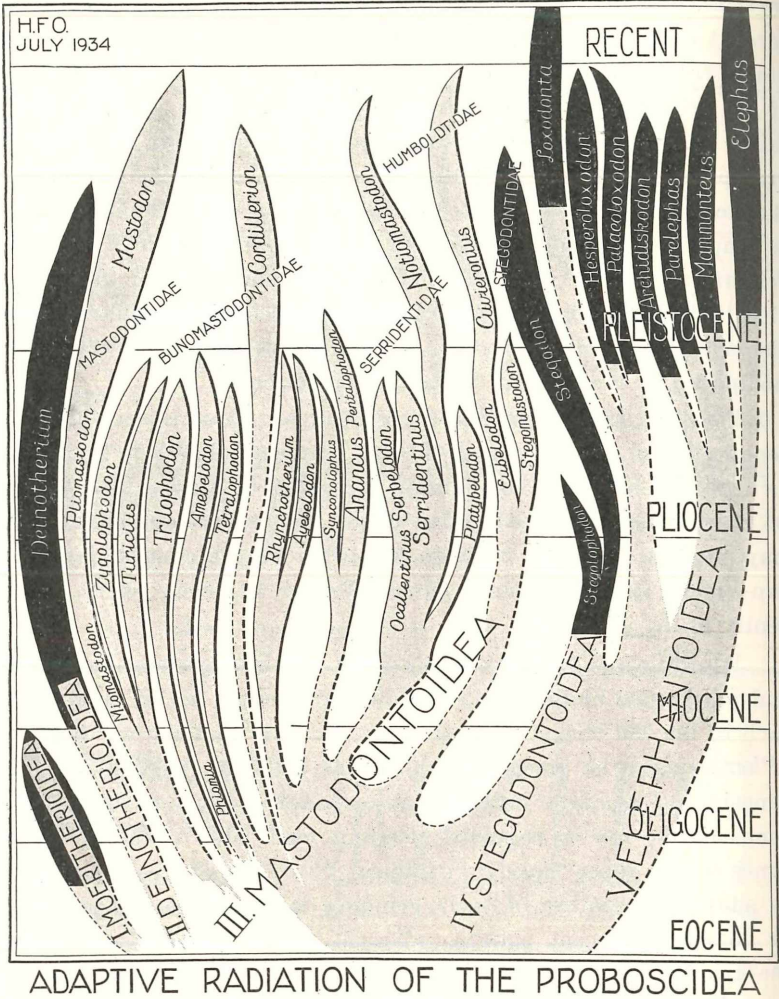


Figure 8. Polyphyletic Adaptive Radiation of the Probosceida. Twenty-eight Lines of Descent. See OSBORN'S Probosceida Memoir Vol. I.

This phylogenetic chart (July 1934) displays the twenty-eight more or less widely distinct lines of descent in adaptive radiation observed in the five great Probosceidan suborders: I. Moeritherioidea, II. Deinotherioidea, III. Mastodontoidea, IV. Stegodontoidea, and V. Elephantoida. For example, the genus *Mastodon*, as known to Darwin, breaks up into eighteen widely distinct genera; the genus *Elephas* breaks up into eight widely distinct genera.

Each of these phyla is clearly distinguished by the divergent fundamental ground plan of the grinding teeth, also by the divergent adaptive functions of the superior and inferior incisive tusks. From this new world of Probosceidan adaptation may be selected three outstanding examples of adaptive radiation, all of which are new to the science of palaeontology, as illustrated in Figures 9, 10 and 11.

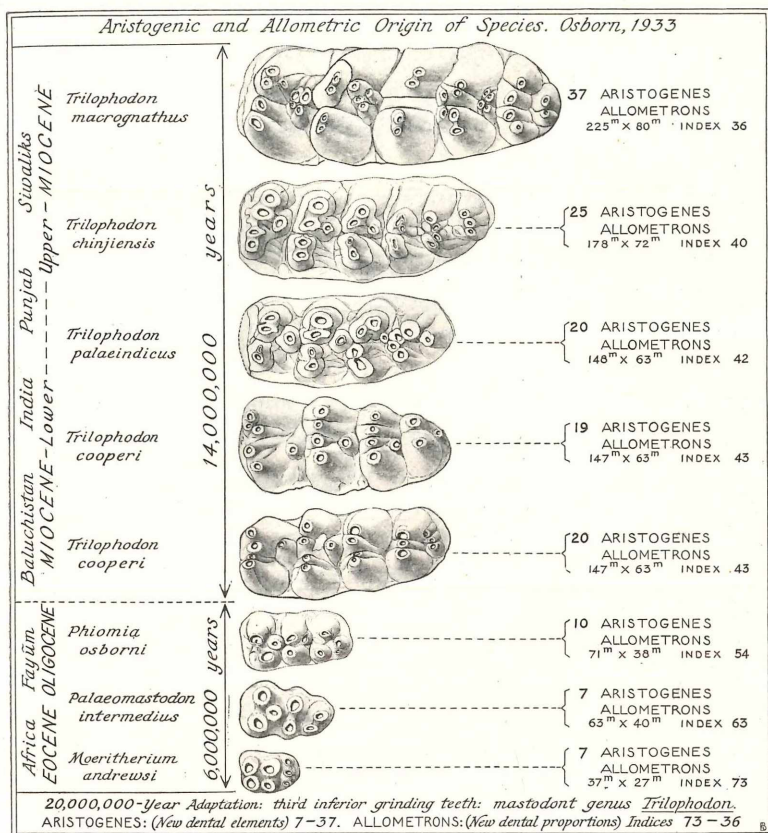


Figure 9. Aristogenesis in the Third Inferior Grinding Teeth of the Mastodont Phylum *Trilophodon*.

See OSBORN'S Proboscidea Memoir, Vol. I.

*Trilophodon* originated in Oligocene Africa; entered Eurasia at the opening of the Miocene; early appeared in Baluchistan and India; evolved through the Siwaliks; migrated widely in North America; everywhere distinguished by central conules in the valleys.

Observe that the evolution of alloiometrans (e. g., new dental breadth-length proportional indices) is wholly independent of the evolution of the 7-37 aristogenes (new dental cusps).

	Aristogenes New dental cusps	Alloiometrans Breadth-length indices
Collateral ancestry:		
African Eocene <i>Moeritherium andrewsi</i>	7	73
African Oligocene <i>Palaeomastodon intermedius</i>	7	65
African Oligocene <i>Phiomia osborni</i>	10	54
Direct ancestry:		
Baluchistan Miocene <i>Trilophodon cooperi</i>	20	43
India Lower Siwaliks <i>Trilophodon cooperi</i>	19	43
India Lower Siwaliks <i>Trilophodon palaeindicus</i>	20	42
India Upper Siwaliks <i>Trilophodon chinjiensis</i>	25	40
India Upper Siwaliks <i>Trilophodon macrognathus</i>	37	36

tridactyl feet and simple lophodont grinding teeth of the forest-living horses belonging to the genus *Hypohippus*. On the contrary, the change of feeding habit which may necessitate a change in locomotion is followed by alloiometric and aristogenic response in every part of the organism.

The generalization appears to be inevitable that while there is not an immediate adaptive biomechanical reaction there is a secular adaptive reaction. This is not in the immediate manner imagined by LAMARCK because it is observed in the grinding teeth which are destroyed by use and disuse as well as in the limbs which are greatly improved by use and disuse. We have every reason to believe that while there is no immediate alloiometric reaction to new habits, new functions and new environment in the sense of LAMARCK and BUFFON, there is a secular adaptive reaction taking place over long periods of geologic time. This enables us to formulate a second distinctive evolutionary alloiometric principle:

**Second Principle.** Convergent alloiometrons in the limbs, cranium and grinding teeth arise as relatively rapid secular changes following adaptive radiation in habit and function. They are most strongly convergent where there are the most intense similarities in the geographic and geologic environment.

**Tetraplasy and Tetrakinesis.** The relative proportions of different parts of the fore and hind limbs of the cranium, and of the grinding teeth are the resultants of Tetrakinesis, the four-fold action, reaction and interaction of (a) the physical environment, (b) the living environment, (c) the more or less energetic habit or function, and (d) the greater or less response of the hereditary geneplasm in its powers of predetermination or potentiality. Tetrakinesis is essentially the interaction of four complexes of energy subject to constant action of the Darwinian principle of Selection or survival of the fittest.

**Summary.** Alloiometrons, in the biomechanical evolution of ungulates, arise subsequent to changes of environment and habit. (1) Theoretically they arise as secular adaptive reactions, in long periods of geologic time, to changes in the physical and living environment. (2) They are not limited by the hereditary predeterminations in the geneplasm. (3) In the case of the skeleton they often appear as soma-

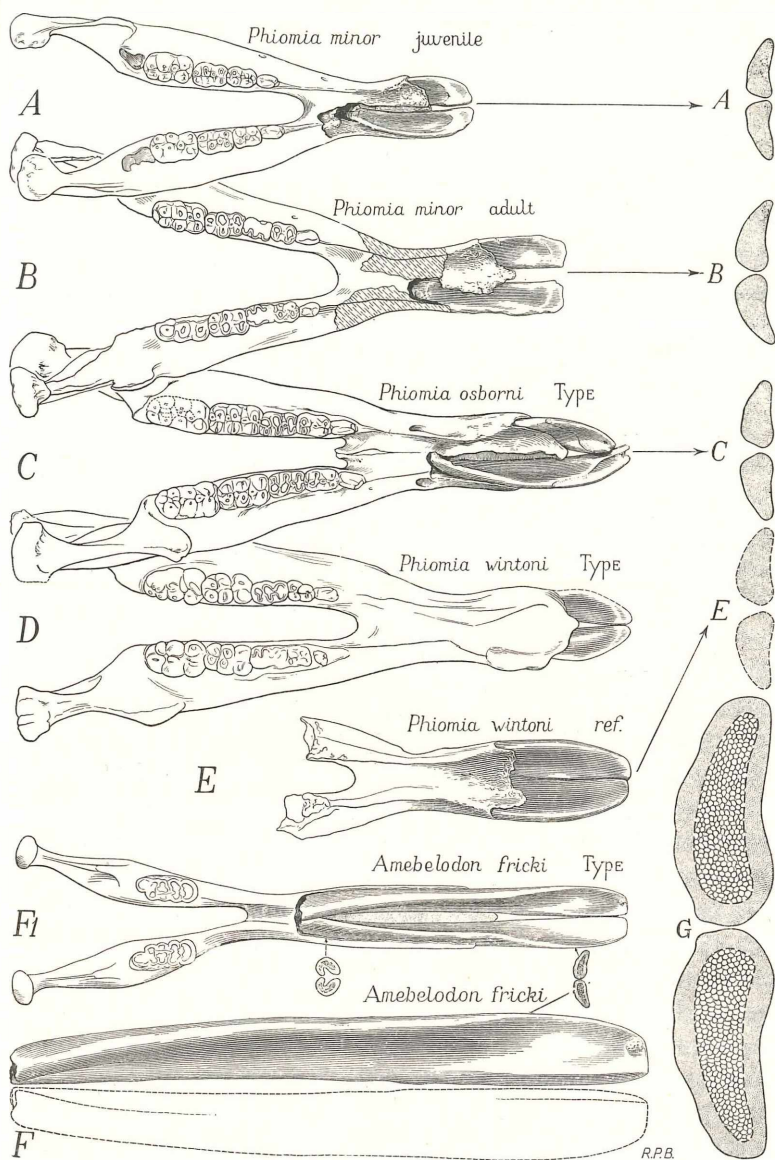


Figure 10. Amebelodonts or Shovel Tuskers, Thirty Million Years Evolution of *Phiomia minor* of North Africa into *Amebelodon fricki* of Nebraska.

See Proboscidea Memoir, Vol. I, Plate V, pp. 235-236. Alloimetric increment and decrement in relative lengths of (a) mandible, (b) incisive teeth and (c) grinding teeth.

- A, 1/9th nat. size: *Phiomia minor*, juvenile, Oligocene, N. Africa.  
 B, " " " *Phiomia minor*, adult, Oligocene, N. Africa.  
 C, " " " *Phiomia osborni* type, Oligocene, N. Africa.  
 D, " " " *Phiomia wintoni* type, Oligocene, N. Africa.  
 E, " " " *Phiomia wintoni* ref., Oligocene, N. Africa.  
 F<sub>1</sub>, 1/27th " " *Amebelodon fricki* type, Pliocene, Nebraska.  
 F, 1/13th " " *Amebelodon fricki* type tusks; Pliocene, Nebraska.  
 G, 1/3rd " " *Amebelodon fricki* ref., tusks in section. Pliocene, Texas.<sup>5)</sup>

<sup>5)</sup> Dr. BARBOUR does not believe that dentinal tubules such as indicated in G occur in the tusks of F, type of *Amebelodon fricki*.

plasmic adaptations before they become hereditary. (4) Alloiometrans, as convergent phenomena relatively rapid in evolution, are in wide contrast to aristogenes which are of creative origin, relatively slow in the course of geologic time, and antecedent to habit and function. (5) Whereas alloiometrans are essentially convergent as between unrelated groups producing an apparent or superficial similarity (*Habitus* — GREGORY), aristogenes are essentially genoplasmic (*Heritage* — GREGORY) in origin and invariably divergent as between unrelated groups, *e. g.*, divergence in the eighteen phyla of Proboscidea.

### Alloimetric Increment and Decrement in Relative Lengths of (A) Mandible, (B) Incisive Tusks, and (C) Grinding Teeth.

(See Figure 10.)

	Absolute Increment of mandible and tusks	Relative increment of incisive tusks and mandible	Relative decrement of grinding teeth and mandibular length	Relative increment of $M_3$ and mandi- bular length
A	100	29%	46%	Unerupted
B	120	31%	34%	10%
C	130	33%	38%	11%
D	135	35%	34%	10,5%
F <sub>1</sub>	395	54%	13%	12,5%

In the alloimetric evolution of the Amebelodonts, the paired shovel tusks dominate the mandible, increasing from 29 % to 54 % of the entire mandibular length; the increase in relative mass is now being determined. The grinding surface of the molar teeth is correspondingly decreased from 46—13 % of the mandibular length. While the mandible as a whole increases four-fold, namely from 100 to 395, the grinding surface of the third inferior molar increases from only 10—12,5 % of the entire mandibular length. This is an outstanding example of alloimetric adaptation. While the third inferior grinding tooth is relatively constant in size and in its aristogenes and performs a relatively unimportant function, the incisive tusks not only increase enormously in length and in mass, but the aristogenic dentinal tubules strengthen the tusks and prolong their abrasive action.

### Eighteen Principles of Aristogenesis Observed in Zoology and Palaeontology.

In OSBORN'S "Evolution of Mammalian Molar Teeth" (1907: 301, p. 228) aristogenes are first clearly defined as "rectigradations":

“By rectigradations I refer to the origin of new cusps or cuspules which appear determinately, definitely, orthogenetically in both the upper and lower teeth — quite independently in different orders of mammals, and separated perhaps by vast intervals of time.

There is some law of predisposition operating here. If it were not for this law the cusps of the teeth of mammals would present an infinite variety of origin, whereas they actually present a singular uniformity of origin except in the multituberculates and other possible exceptions noted in the preceding chapters. It is the modelling of the cusps after they appear which gives the infinite variety.

We do not know what conditions this ‘law of predisposition’; we only see evidence of the influence of community of origin or hereditary kinship.”

Aristogenes. (Figures 9, 10 und 12) agree with the W. mutations of WAAGEN in arising inconspicuously and directly from the geneplasm always in an adaptive direction. As WAAGEN observed in 1869, W mutations are so inconspicuous in origin that we would not note them except for their reappearance in more conspicuous form in later generalizations. This observation, based on the shells of invertebrates, is exactly in accord with the origin of the numerous single components of the dental crowns of mammalia. Although extremely inconspicuous at the start they become more conspicuous in geologic time and finally may become single organs of extreme dominance. Take, for instance, a single component, termed the hypococone, of the crown of the molar teeth (Figure 12) in two primitive horses, *Hyracotherium* and *Merychippus*. In its Paleocene origin this hypococone is extremely inconspicuous, barely visible; in fact, it is a typical aristogene. Never before in the history of palaeontology has there been such an opportunity for the observation of aristogenesis in single organs, such as the six or more components of the molar crowns of ungulates (Figure 12), as is afforded in the world wide collections of grinding teeth and other single organs of fossil mammals which have risen from about thirty specimens in the Hayden Meek Collection of 1862 to approximately 30,000 specimens in the year 1935.

In comparing the adaptations of the six major elements of the molar crowns (Figure 12), namely the proto-, meta-, para-, and hypococone, also the proto- and metaconules, in the higher ungulates we observe that each of these six aristogenes has its own independent geologic history as well as its own adaptive biomechanical evolution. In horses, rhinoceroses, tapirs, mastodonts and elephants, we may

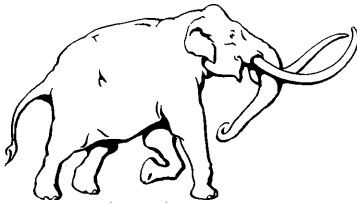
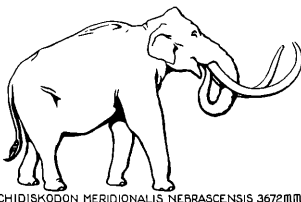
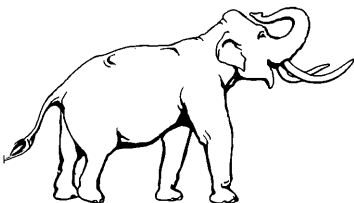
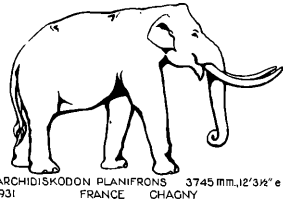
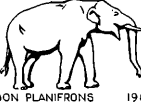


PLEISTOCENE OF AMERICA	 <p>ARCHIDISKODON (IMPERATOR) MAIBENI 1931 NEBRASKA</p>	<p>NEBRASKA UPPER PLEISTOCENE <i>High-crowned giant Archidiskodon</i> 18 lofty ridge-plates. Enamel length = mm.</p>
	 <p>ARCHIDISKODON MERIDIONALIS NEBRASCENSIS 3672mm. 12' 2 1/2" 1933 S. NEBRASKA</p>	<p>NEBRASKA LOWER PLEISTOCENE <i>Medium-crowned Archidiskodon</i> 14 ridge-plates. Enamel length = mm.</p>
LOWER PLEISTOCENE OF FRANCE	 <p>ARCHIDISKODON MERIDIONALIS 3721mm. 12' 2 1/2" 1931 S. FRANCE DURFORT</p>	<p>FRANCE LOWER PLEISTOCENE <i>Medium-crowned elephant molars</i> 13-14 ridge-plates. Enamel length = 2824 mm.</p>
	 <p>ARCHIDISKODON PLANIFRONS 3745mm. 12' 3 1/2" e 1931 FRANCE CHAGNY</p>	<p>FRANCE LOWER PLEISTOCENE <i>Low-crowned elephant molars</i> 13 ridge-plates. Enamel length = mm.</p>
PLIOCENE. AFRICA. INDIA	 <p>TYPE ARCHIDISKODON PLANIFRONS 1980mm. 6'6" e 1931 INDIA SIWALIKS</p>	<p>INDIA. UPPER PLIOCENE <i>Molars of primitive elephant type</i> 10-12 ridge-plates. Enamel length = 1515 mm.</p>
	 <p>TYPE ARCHIDISKODON SUBPLANIFRONS 1400mm. 4'7" e SOUTH AFRICA</p>	<p>SOUTH AFRICA. MIDDLE PLIOCENE <i>Molars transitional from mastodon to elephant</i> 6 ridge-plates. Enamel length = 650 mm.</p>
	 <p>TYPE ARCHIDISKODON PROPLANIFRONS SOUTH AFRICA</p>	<p>SOUTH AFRICA. MIDDLE PLIOCENE <i>Mastodon-like molars</i> 5 1/2 ridge-plates. Enamel length = 690 mm.</p>
<p>ARCHIDISKODON: THREE-MILLION-YEAR EVOLUTION AND MIGRATION SOUTH AFRICA TO AMERICA AND MEXICO H.F.O. 1935</p>		

Figure 11. Origin, Evolution and Migration of the Genus *Archidiskodon* from the Upper Pliocene of Africa to the Middle Pleistocene of Nebraska and Mexico.

See Osborn's Proboscidea Memoir, Vol. II.

This great phylum of the Elephantoides has been traced in the twenty-seven years of research on the Proboscidea from its primitive progenitors (*Archidiskodon proplanifrons* and *A. subplanifrons*) in South Africa to the gigantic *Archidiskodon maibeni* of Nebraska, Texas and north Mexico, apparently a single phylum.



demonstrate one of the most important inductions or generalizations in modern palaeontology, namely:

Every single aristogene obeys the eighteen principles of biomechanical adaptation, namely, it has its own individual and particulate adaptive history it is coordinated with the functions and adaptations of the organism as a whole; its survival and relative strength or its reduction and elimination is determined by its degrees of service.

We may now apply to the single components of organs like the hypocone of the molar teeth the eighteen chief biomechanical principles which have been observed by zoologists, anatomists and embryologists from the times of Aristotle to those of GOETHE and DARWIN and of the present day. These are:

1. Genetic-progression or development, as in the median digits of the Equidae to the sacrifice of the lateral digits (Figure 7).
2. Genetic-retrogression or degeneration, as in the lateral digits of the Equidae which are sacrificed for the median digit (Figure 7).
3. Genetic-acceleration or hurrying forward in time of appearance, as in the precociously elongated limbs of young ungulates and birds which must run to escape enemies immediately at birth (Figure 7).
4. Genetic-retardation or slowing down in time of appearance, as in the limbs of birds and ungulates which are helpless of motion at the time of birth.
5. Genetic-compensation, as in Aristotle's example of nature taking the powers of defense from the teeth and adding it to the horns (*e. g.*, Cervidae) or vice versa. The defense of the horns substitutes the defense by teeth. (Figures 1—5). In certain Titanotheres the acceleration of the horns is compensated by the retardation of the tusks and grinding teeth (*Brontotherium*, Figure 2). Conversely in the short-horned Titanotheres *Menodus* the acceleration of the tusks and grinding teeth is compensated for by the retardation of the horns.
6. Genetic-balance (Figure 10), the equilibrium between the development and degeneration of parts so that a functional and anatomical balance is always maintained.
7. Genetic-economy, adjustment to service. The total of the

intake of energy remaining the same, the whole organism is in a state of adaptive equilibrium (Figure 10).

8. Genetic-alloiometry or change of proportion, as in the limbs of all ungulates in which the proportions of each segment of the limb are profoundly altered in adaption to cursorial (*Equus*), mediportal (*Tapirus*) and graviportal (*Elephas*) habit (Figures 6 and 7).

9. Genetic-coadaptation in function and structure, as in the coadaptation of the entire body of: a) *Cervus megaceros* to carrying the giant horns (see HERBERT SPENCER), b) *Loxodonta*, the African elephant, to the giant uprooting tusks, *Brontotherium* a Titanotheres, to the giant horns (Figures 1 and 2).

10. Genetic-coordination or correlation of different structures and functions of the organism, as in Cetaceans, Sirenians, Titanotheres (Figures 1—4) and Proboscideans (Figure 11).

11. Autoadaptation including change of function or neo-adaptation, a process of somatogenesis and skesigenesis in which alterable parts may be profoundly modified by change of habit, as in upturned nasals of *Embolotherium* functioning as horns, no rudiments of the horn appearing on the fronto-nasal junction as in all other Titanotheres.

12. W. mutation of WAAGEN (1869), a stage defined by the slow origin and rise of new adaptive characters (alloiometrons and aristogenes). The W. mutation of WAAGEN expresses minute and inconspicuous stages of transformation in a definite direction, accumulating gradually and observable only after considerable passages of time; not the mere appearance of a single new character, hence not identical with the "rectigradation" or "aristogene" of OSBORN, hence also in contrast to the zoologic or botanic "variety"

"Although in minute characters, highly constant, surely recognizable." In this sense used by DEPÉRET, *e. g.*, "ascending mutations" transitional between species. Series of ascending mutations constitute the "Collectivart" or "collective species"

13. Mutationsrichtung of NEUMAYR, genetic trend of W. mutations, rectigradations or aristogenes increasing in orthogenetic directions, sometimes termed orthogenesis. This "Mutationsrichtung" trend or momentum is an exceedingly important element because it contains the principle of hereditary predetermination

found in OSBORN's "rectigradation" or „aristogenes“. (See Figure 9, aristogenesis or "aristogenes" in the *Trilophodon* molars.)

14. Genetic-continuity, as contrasted with the discontinuous (BATESON) or mutational (DEVRIES), the origin of new characters. The differences between successive ascending mutations become the

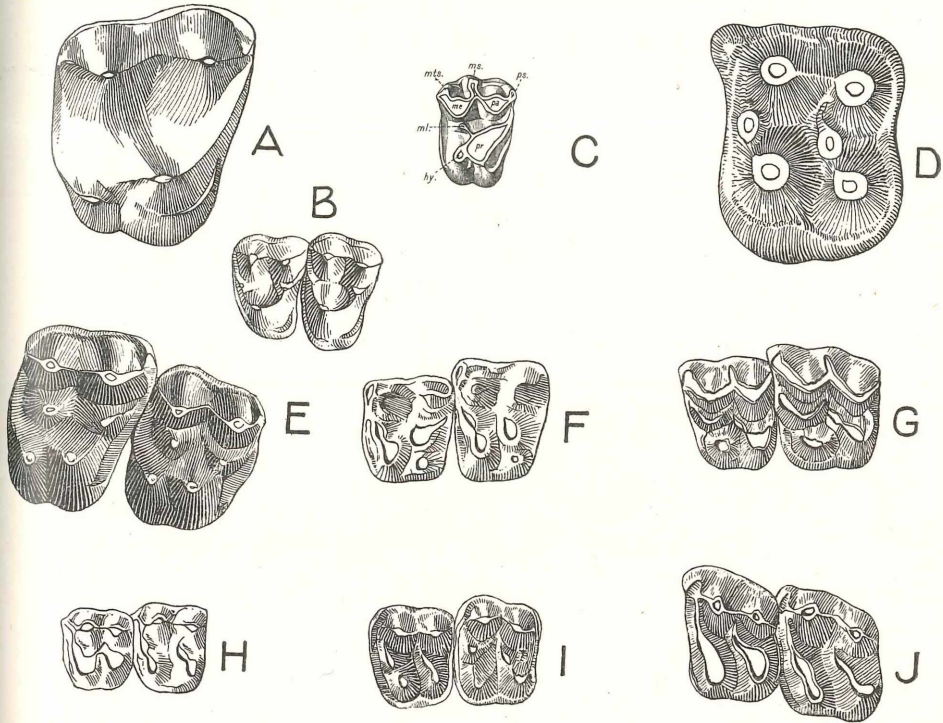


Figure 12. Aristogenesis in Molars of Different Orders, Families and Genera of Mammals. Cones, Conules, and Styles.

After OSBORN, GREGORY, MATTHEW, WORTMAN, and others.

Primates: Lemuroidea.

A — *Adapis magnus*, tritubercular, proto-, para-, meta- and hypocone.

B — *Omomy's*, tritubercular, addition of conules.

C — *Notharctus*, addition of para-, meso- and metastyle.

E — *Hyopsodus marshi*, addition of proto- and metaconule.

Perissodactyla: Equidae.

D — *Hyracotherium*, sextitubercular plus parastyle.

H — *Eohippus borealis*, sextitubercular plus parastyle.

I — *Protorohippus venticolus*, sextitubercular plus rudiment of hypostyle.

Perissodactyla: Tapiridae.

J — *Systemodon primeavus*, lophoid proto- and metaloph, also parastyle.

Artiodactyla: Dichobunidae.

F — *Homacodon vagans*, sextitubercular plus parastyle.

Condylarthra: Meniscotheriidae.

G — *Meniscotherium*, sextitubercular plus parastyle and mesostyle.

more minute in proportion as the strata from which the specimens come are more closely connected. DEPÉRET<sup>6)</sup> wrote: "The mutations have further this special characteristic, that they are always produced in the same direction, without oscillations or retrograde steps. But the slow and gradual variation of species remains none the less established by a complete series of certain proofs." (*E. g.*, series of *Anthrotherium*, of *Brachyodus*.) (See OSBORN, 1929:800, pp. 523, 524, *Menodus trigonoceras* evolves into *M. giganteus*).

15. Genetic-potentiality, the independent origin from similar ancestral stocks of similar aristogenes at different periods of geologic time, *e. g.*, bony horns of the Titanotheres (Figures 4 and 5) also aristogenic origin of dental cusps in Primates, Condylarths, Artiodactyls and Perissodactyls (Figure 12).

16. Genetic-predetermination, as in the origin of horned rudiments in Titanotheres of similar stock in successive periods of geologic time upon precisely the same fronto-nasal suture (Figure 4 und 5). An exception is *Embolotherium* in which no horned rudiment evolves.

17. Reciprocal-biomechanical reaction, as of the inferior grinding teeth in reversed mechanical reaction to every element in the superior grinding teeth, *e. g.*, convex curves in all parts of superior grinders are opposed to concave curves in all parts of the inferior grinders, and vice versa. See evolution of  $M_3^3$  especially in the Elephantoidea.

18. Genetic-rectigradations or aristogenes, the creative process of origin of new adaptive biomechanisms as in all the cusp components of the grinding teeth of mammals (Figure 9, evolution of molars in *Trilophodon*).

### Biological Generalizations from Thirty-four Years of Research on the Evolution of the Titanotheres and Proboscideans.

This contribution to the OTHENIO ABEL Festschrift is a condensed summary of two new and outstanding principles of biomechanical evolution which have been discovered by the most intensive researches on the origin, evolution, migration and extinction of one great family of Perissodactyls, the Titanotheres, and of the great order Proboscidea which is no known to embrace five sub-

<sup>6)</sup> CHARLES DEPÉRET, *The Transformations of the Animal World* (authorized translation), London, 1909, p. 69.

orders or superfamilies, eight families, seventeen subfamilies, thirty-nine genera and about three hundred species. The Titanothera Monograph occupied twenty years of exploration and intensive research and nine years in the press of the United States Geological Survey. The Proboscidea Monograph has occupied twenty-seven years of exploration and fourteen years of intensive research including nine years of passage through the American Museum press; this Monograph will be published in two volumes, it is hoped during the year 1935. All except one of the twelve illustrations in this article are reproduced, with some modifications for the sake of clarity, either from the Titanothera Monograph or from the Proboscidea Monograph. Never before has there been such an opportunity to study the Origin of Species.

The outstanding biological generalization is that in the bio-mechanical evolution of the vertebrates, that is, in the skeleton and in the teeth, two distinct processes of adaptation, due to distinct controlling causes, are simultaneously operating, as follows:

**Proportion.** First, the evolution of proportion, of degree, of the greater or less, of development or degeneration, known to the evolutionists of all time back to ARISTOTLE and his more or less well-known successors up to the time of BUFFON and LAMARCK and even DARWIN. Proportion is treated under the heading of alloiometry and of the alloiometrans including measurable degrees of proportionate change originating in different rates of development either in ontogeny or in phylogeny, in the contrasting processes of acceleration and retardation.

The causes of changes of proportion are partly known and largely unknown.

**Origin.** Second, evolution by the origins of new characters, which is treated under the head of aristogenesis. The discovery of this principle was partly adumbrated in the treatise by WAAGEN in the year 1869 under the head of what we shall call W. mutation, distinguished from the De Vriesian D. mutation of more recent date. These origins of new characters are due to a different set of causes than those operating on the alloiometrans. Origins lie entirely within the domain of heredity and the adaptive evolution of the geneplasm of which the aristogenes are the visible expression. Origins were actually discovered and first described in the dental evolution of

*Dromatherium* and *Microconodon*, supposed protodont mammals of Upper Triassic time, now placed among the primitive reptiles.

The causes of aristogenes are wholly unknown.

Ever since 1907 I have been working on the distinctions between alloiometrons and aristogenes with the results concisely summarized in the present paper, namely, that in the matter of antecedent causation aristogenes are distinctly originative and creative and in the last analysis all entirely new characters originate in this continuous and adaptive manner rather than through the survival of chance variation as in DARWIN'S theory of Natural Selection.

The American Museum of Natural History March 21, 1935.

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Autor(en)/Author(s): Osborn Henry Fairfield

Artikel/Article: [Eighteen principles of adaptation in Alloimetrans and Aristogenes. 273-302](#)