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THE ORIGIN OF A MAMMALIAN ORDINAL CHARACTER

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INTRODUCTION

By studying the evolutionary trends of organisms paleontologists have become aware of the peculiar circumstances surrounding the origin of higher categories. Most orders, classes and phyla of invertebrates and vertebrates appear abruptly in the geological record with one or more character complexes well differentiated but without any indication of transitional stages. Several theories have been postulated to explain this phenomenon but there have been few detailed discussions of particular examples. This paper represents an attempt to analyze the evolutionary trend culminating in the appearance of an order of mammals, the even-toed ungulates or Artiodactyla.

Of the twenty-six currently recognized orders of eutherian mammals, about fifteen probably had a Paleocene origin. The identification of the earliest members of an order is dependent upon the possibility of identifying one or more definitive ordinal character complexes, which are usually present in an otherwise still relatively primitive stock. The determination of the ancestral group from which a mammalian order such as the Artiodactyla originated is, by necessity, largely based on inference. Usually but a few heritage characters are available that indicate definite affinity and thus tend to bridge, however incompletely, the structural, if not the chronological hiatus.

The first known members of the Artiodactyla are possibly unique among the mammals in that they can be identified positively only on the basis of a single character complex, in the foot, which practically reached its definitive form before other skeletal characters were in more

than an incipient stage of phylogenetic development. The intermediate steps in the evolution of this complex, which represents the highly specialized form of the tarsus, are unknown. The primitive generalized (or relatively unspecialized) type from which it evolved can be recognized, however, and the time interval during which the transformation took place can be estimated with reasonable accuracy. It is possible, therefore, to consider the magnitude of the morphological change during this period as well as the associated functional alternations. In discussing these problems here it will also be of interest to consider possible factors that favored an initial emphasis on the evolution of this particular character complex. A more detailed study of the origin and function of the artiodactyl tarsus has been published elsewhere (Schaeffer, 1947), and only such details of morphology and function as are necessary for the understanding of the problem will be repeated.

The erection of the Cohort Ferungulata (Simpson, 1945) to include the various orders of extinct and Recent carnivores and ungulates (fig. 1) is based on the fact that these greatly diversified groups had a common late Cretaceous origin. The paleontological data suggest that the most primitive ferungulates, the arctocyoniid creodonts, reached their definitive status before the beginning of the Paleocene. Likewise the earliest ungulates, the condylarths, were differentiated by the early Paleocene.

Until recently, the ancestral stock of the Artiodactyla was essentially unrecognized although the condylarths as a group were considered to be structurally antecedent. Simpson (1937) has pointed

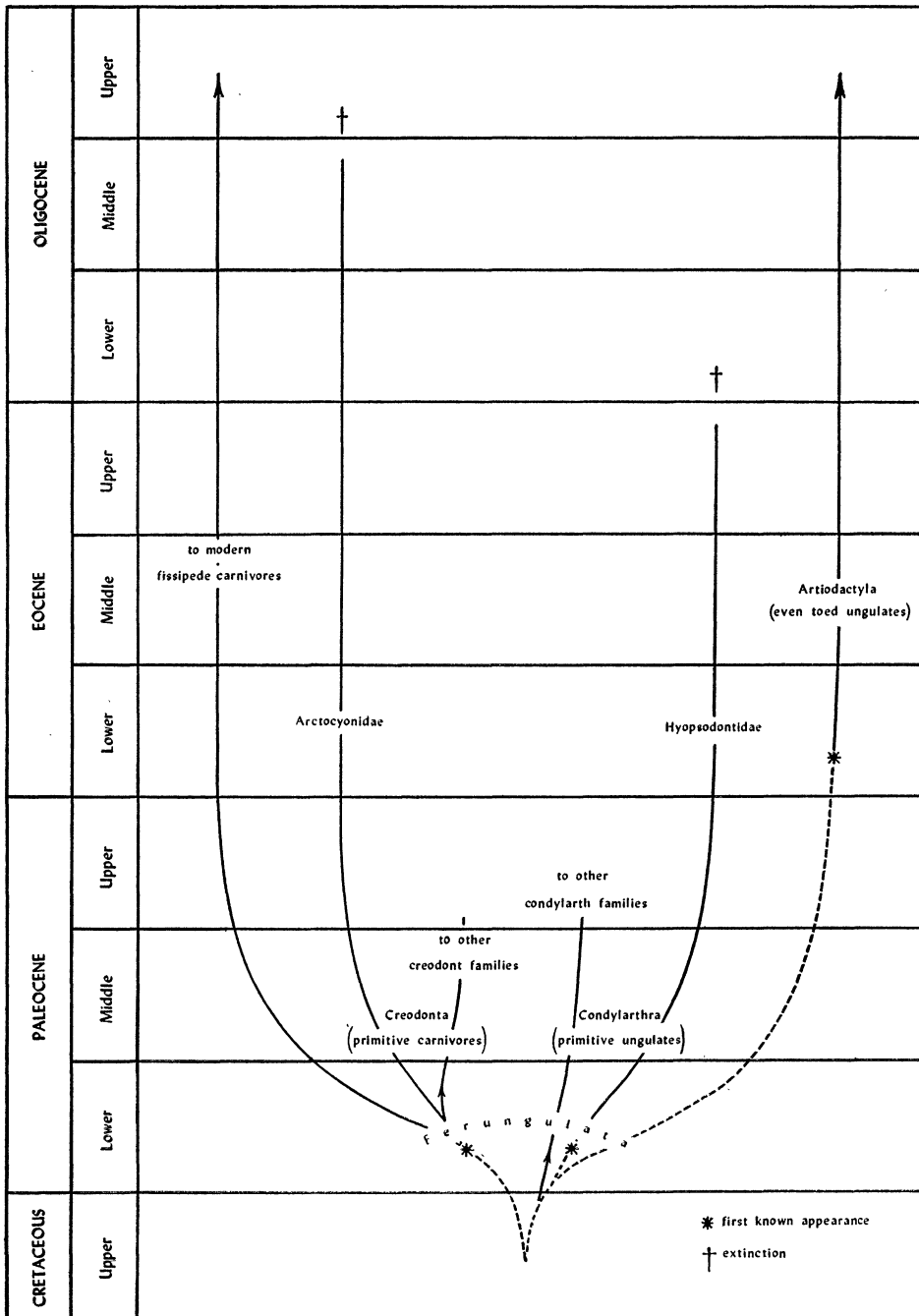


FIG. 1. Simplified phylogeny indicating the relationship of the Artiodactyla to the other ferungulate groups mentioned in the text.

out, however, that the dentition of the earliest and most primitive family of condylarths, the Hyopsodontidae, is almost indistinguishable from that of the earliest artiodactyls such as the Lower Eocene genus *Diacodexis*. This resemblance, Simpson states, is much too great in the significant details of tooth form to be ascribed to convergence. In fact, one genus now placed in the Hyopsodontidae was at first considered to be a true Paleocene artiodactyl on the basis of tooth form. The available fossil evidence, therefore, leads to the almost inescapable conclusion that the evolutionary trend which culminated in the Order Artiodactyla was initiated no earlier than sometime in the Lower Paleocene.

PALEONTOLOGICAL EVIDENCE

The skeleton of a hyopsodontid condylarth is similar in many respects to that of a generalized placental mammal, possessing primitive characters that are, in fact, common to the earliest representa-

tives of several orders. Because of this basic resemblance, various hyopsodontids have previously been assigned to the Artiodactyla, the Primates and the Insectivora. Recent studies, particularly on the dentition, indicate affinity with the Condylarthra (as well as relationship with the Artiodactyla). It might be pointed out here that tooth characters are used extensively in paleomammalogy, not only to determine the relationships of higher categories, but also to separate taxonomic groups at generic and specific levels. Although there are examples of parallelism and convergence in tooth form among mammals, the chances of close duplication of a complicated tooth pattern are so exceedingly remote in distantly or unrelated groups that the dentition, in most cases, offers a more exact indication of relationship than almost any other part of the skeleton.

In contrast to the dentition, the hyopsodontid foot (fig. 2), as preserved in the genus *Choeroclaenus*, is structurally un-

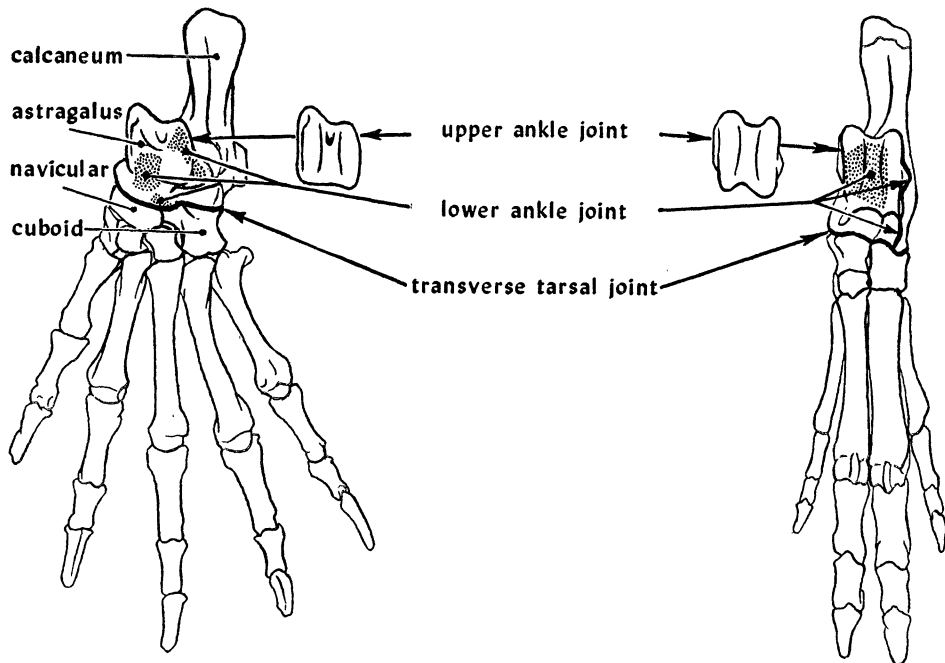


FIG. 2. Comparison of the left hind foot of a primitive ferungulate (*Clanodon*) and an artiodactyl (*Sus*) showing the location of the three main tarsal joints. The stippled areas represent the articulations between the astragalus and the calcaneum.

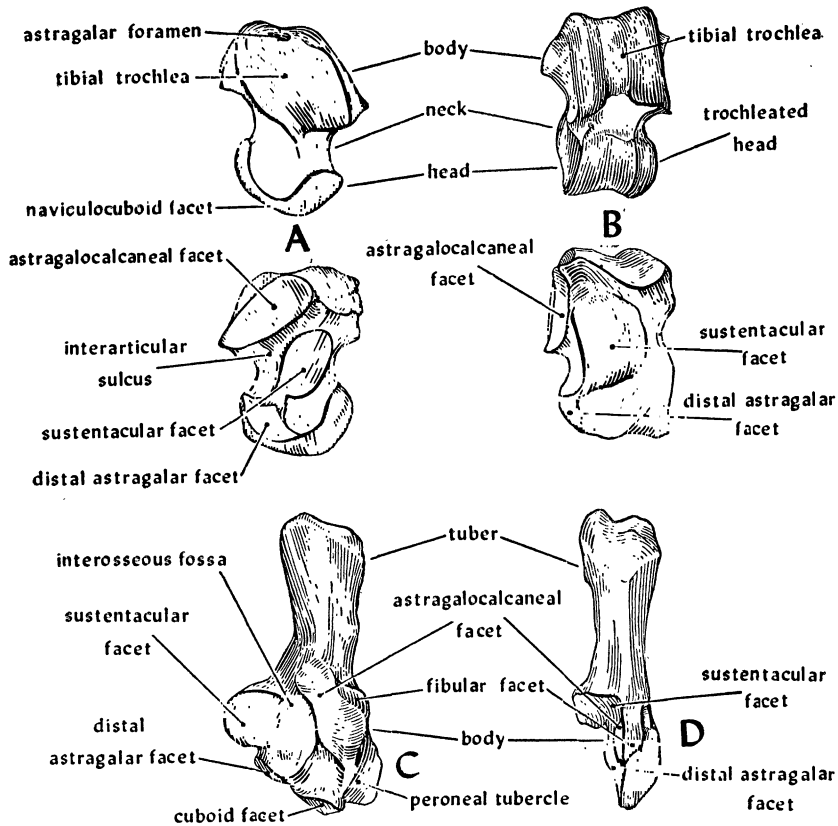


FIG. 3. Dorsal and ventral views of the astragalus of the hyposodontid *Choeroclaenus* (A) and the artiodactyl *Diacodexis* (B) and dorsal views of the calcaneum of arctocyonic creodont *Claenodon* (C) and the artiodactyl *Merycochoerus* (D).

changed from that of the arctocyonic creodonts, including the presence of claws rather than hoofs (hoofs are present in all other condylarth families). Among the bones of the foot, the astragalus and calcaneum, which are the proximal elements of the tarsus proper, most readily demonstrate different types of locomotor adaptation. Matthew (1909 and 1937) considered the mammalian astragalus to be of almost as great diagnostic value as the dentition, although others have demonstrated that it must be used with caution (Simpson, 1937).

The astragalus of *Choeroclaenus* (fig. 3A) has a wide, shallow trochlea for articulation with the tibia. The head of the astragalus, which contacts distally both the navicular and the cuboid bones, is

mediolaterally rounded. The neck between the tibial trochlea and the head is constricted. The plantar surface of the astragalus has an elongated, ovoid astragalocalcaneal facet which is separated from an oval sustentacular facet by a deep interarticular sulcus. A small, poorly defined articular surface, which may be called the distal astragalus facet, is situated adjacent to the naviculocuboid facet.

The calcaneum of *Choeroclaenus* (fig. 3C) has a strongly developed heel process or tuber. The astragalocalcaneal facet of this bone is located at the proximal end of the tuber, with a similarly shaped fibular facet adjacent to its medial border. There is a well-developed shelf or sustentaculum on the lateral side of the calcaneum, on the dorsal surface of which is situated the

sustentacular facet which articulates with its counterpart on the astragalus. The rhomboidal cuboid facet makes up almost the entire distal surface of the calcaneum.

This brief description of the two proximal elements of the eutherian tarsus could apply to the primitive members of a number of mammalian orders as well as to many more specialized descendants. It would fit the astragalus and calcaneum of such diverse forms as the less specialized insectivores, many of the primates including man, some rodents and most terrestrial carnivores. With relatively minor differences, which Matthew nevertheless considered of importance, this basic pattern has been very persistent in spite of adaptive trends affecting other parts of the skeleton. The greatest alteration, as might be expected, has occurred among the terrestrial mammals in the cursorial and saltorial types. It is basically associated with two interrelated mechanical factors, increase in leverage, increase in speed, or both.

The artiodactyl tarsus (fig. 2) reached its definitive form, except for minor refinements, in the early Eocene. The highly characteristic astragalus (fig. 3B) has a deepened tibial trochlea with sharp medial and lateral crests. A distinct neck region is no longer evident. The portion of the head articulating with the cuboid and navicular bones has been transformed into an anteroposteriorly rounded trochlea with flattened medial and lateral surfaces. The plantar surface of the astragalus is dominated by the sustentacular facet which is elongated parallel to the long axis of the entire bone. The astragalocalcaneal facet has been reoriented in the same manner. The distal astragalal facet on the lateral surface of the trochlea is more clearly defined and is of greater functional significance.

The artiodactyl calcaneum (fig. 3D) has a relatively less robust tuber and a greatly modified body. The sustentaculum has been altered so that its facet is directed more distally than dorsally, while the astragalocalcaneal and fibular facets,

in their astragalal counterparts, have their long axes oriented essentially parallel to the long axis of the entire bone.

The change in the form of the distal end of the astragalus was associated with an increase in the articular contact of this bone with the cuboid and a marked decrease in the area of the calcaneocuboid articulation. The proximal surfaces of both the navicular and cuboid are markedly concave to accommodate the distal astragalal trochlea.

FUNCTIONAL INTERPRETATION

A more dynamic picture of the differences between the hyposodontid and artiodactyl tarsi may be obtained through a comparison of the orientation and function of the three major tarsal joints. For practical reasons, the positions of these axes were determined for the tarsi of the arctocyonid creodont *Claenodon* and the sheep, *Ovis*. The three joints (figs. 2 and 4) in question are (a) the upper ankle joint between the tibia and fibula on one side and the astragalus and calcaneum on the other, (b) the lower ankle joint between the astragalus and calcaneum and (c) the transverse tarsal joint between the astragalus plus the calcaneum and the cuboid plus the navicular.

In mammals generally, the upper ankle joint has probably had a more conservative history than either the lower ankle or transverse tarsal joints. The orientation of the axis is roughly at right angles to the long axis of the tibia and runs in a mediolateral direction. Motion at this joint is always restricted to an anteroposterior movement (dorsi- and plantar flexion) of the foot on the lower leg. In the transition from hyposodontid to artiodactyl, the axis remained in about the same position. Further restriction of movement and greater joint stability was obtained in the latter through deepening of the tibial trochlea and further elaboration of the external and internal flanges on the distal end of the tibia. These flanges, the lateral one representing the last remnant of the well-developed hyp-

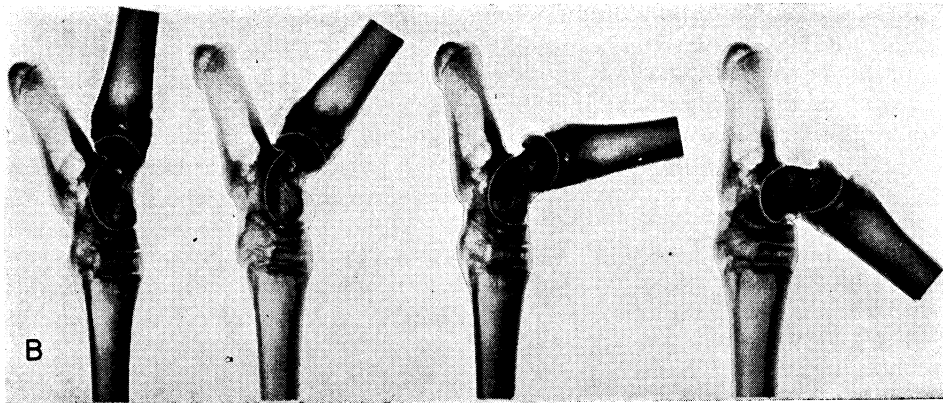


FIG. 4. Roentgenogram of the tarsal area of a living goat showing the rotation of the astragalus.

sodontid fibula, articulate with the tibia in a sort of tongue-and-groove relationship.

In contrast to the upper ankle joint, the lower ankle joint was subjected to a very radical change in orientation and function during the hyposodontid-artiodactyl transition. In the generalized mammalian foot, including the hyposodontid, the axis of rotation of the lower ankle joint has a very characteristic oblique orientation running in general from the dorsal surface of the neck of the astragalus to the lateral side of the heel process of the calcaneum. Movement is largely restricted to an inversion-eversion rotation of that portion of the foot below the astragalus, with the latter functionally united with the tibia by the presence of the tibial flanges and associated ligaments. In the artiodactyls, on the other hand, the change in the form of the astragalus and calcaneum previously discussed caused a shift in the orientation of the axis of the lower ankle joint to a position essentially parallel in all aspects to that of the upper ankle joint. There was during the hyposodontid-artiodactyl transition, a change in joint motion from inversion-eversion of the foot to one involving only fore and aft rotation of the astragalus. This rotation occurs only during extension and flexion of the foot and cannot occur independently of movement at the transverse tarsal joint.

Motion at the transverse tarsal joint in

the hyposodontids involves two differently formed and rather complex articular surfaces. For the purposes of this discussion, however, the movement may be considered as essentially flexion and extension. The axis of this joint is almost parallel to that of the upper ankle joint. During the transition phase there was a simplification and structural convergence of the two articular surfaces (astragalus articulating with both the cuboid and navicular) with movement at the artiodactyl stage increased but practically limited to flexion and extension (fig. 4). The position of the axis suffered some reorientation which is of no particular significance in this discussion.

It is thus evident that the structural modifications in the tarsus during the transition period finally resulted in a unique arthroal condition in which the axes of the three main tarsal joints have an essentially parallel orientation. This situation permitted, by the Lower Eocene, a freedom of movement on the part of the astragalus not present in any other order of mammals. A tendency in this direction did develop in some of the rodents, in the lagomorphs, and in certain of the extinct, neotropical, cursorial types such as the litopterns; the tarsus of these forms suggests resemblance to an intermediate stage in the hyposodontid-artiodactyl transition.

The biomechanical significance of the artiodactyl tarsus, as in the case of any portion of the vertebral skeleton, is difficult to evaluate without extensive experimental evidence which, in turn, may reasonably be employed as a basis for functional studies on fossil forms. The analysis of tarsal joint action provides certain tentative conclusions regarding the biomechanics of the artiodactyl foot. The double-trochleated astragalus may be compared to a cam-like structure that rotates in a socket formed by the tibia, calcaneum, navicular and cuboid. The eccentric location of the cam axis, here the axis of the transverse tarsal joint, permits a greater degree of rotation at its proximal than at its distal end and has suggested to Kripp (1935) that the artiodactyl astragalus is, in effect, a velocity mechanism which increased the speed of rotation of the foot during flexion and extension. This is an adaptation of some significance in the cursorial artiodactyls as it must accelerate locomotion and, as part of this same effect, amplify the momentum imparted to the hind feet during the characteristic leaping stride.

The typical mammalian foot, including the hyposodontid, when in contact with the ground, may be considered as a lever of the first class (Gregory, 1912), with the fulcrum located at the upper ankle joint, the power applied by the crural flexor muscles at the heel process and the resistance provided by the foot pressing against the ground. The leverage of the artiodactyl foot is complicated by the nature of the astragalus (fig. 5), which might be considered as an additional movable segment in the hind limb. With antero-posterior motion of the foot occurring at both the upper ankle joint and the transverse tarsal joints, it is possible to postulate the presence of two interrelated lever systems with separate fulcra, one at each of these joints.

In this compound lever system the force and resistance are still applied at the heel process and foot respectively. When the foot first touches the ground at the begin-

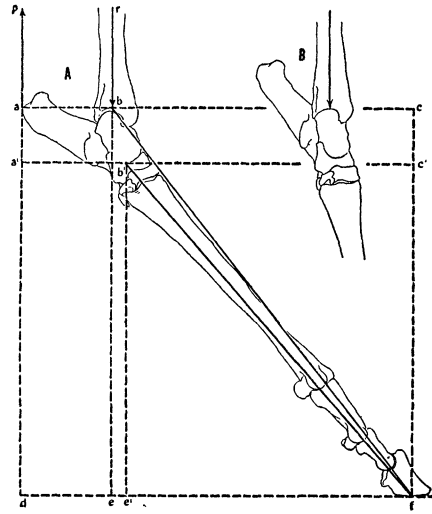


FIG. 5. A. Composition of forces in the artiodactyl hind foot oriented in the position assumed at the beginning of the propulsive stride. B. Position at the end of the stride.

ning of the propulsive phase, there is still some movement possible at the transverse tarsal joint although most of the extensor motion at this joint occurs prior to the contact. Observable motion at the upper ankle joint is initiated at this time. A lever analysis of this situation (fig. 6) indicates that at the onset of propulsion when maximum power is required the power arm ($a'b'$) of the more distal lever is longer than that (ab) of the proximal lever and the resistance arm of the former ($b'c'$) shorter than that of the latter (bc). There is thus a very slight but real mechanical advantage over the typical mammalian condition. Manter (1938), investigating locomotion in the cat, found that at the beginning of the propulsive phase of the hind limb a horizontal, longitudinal force produced by the resistance between the foot and the ground caused an actual retarding effect which was quickly overcome. That such an initial retarding effect is common to all tetrapods appears evident (Barclay, 1946) when the position of the entire hind limb in relation to the acetabulum is considered. The rapid and efficient overcoming of this negative action must be of prime importance in a

cursorial mammal and the double lever effect in the artiodactyls may serve an important function in this regard.

The functional significance of any cursorial specialization is directly related to the ability of the animal to move at an initial and sustained speed great enough to permit escape from an enemy. In this connection it is interesting to note that the limb ratios (for example, length of third metatarsal to length of femur) of most of the more generalized artiodactyls of the Tertiary and Recent fall within the range of the larger predatory carnivores. This overlap in ratios would place a high premium on the functional efficiency of the early artiodactyl tarsus, and its specialization prior to any marked increase in limb ratio clearly suggests its importance in this connection.

EVOLUTIONARY IMPLICATIONS

As pointed out earlier, ungulates, that may be identified as artiodactyls, apparently reached an ordinal status by the beginning of the Eocene. The primitive hypsodontid condylarths, from which the even-toed ungulates were derived are first known from Lower Paleocene deposits. The transitional stage between hypsodontid and artiodactyl, therefore, probably had a maximum duration of not over 15 million years according to the most recent opinions on the length of the Paleocene.

The time interval available for this transformation in tarsal design is brief according to paleontological standards and the rate of evolutionary change may be regarded as relatively rapid. The failure to discover any of the intermediate forms between the initiation and completion of the transition represents a situation that is common to the origin of nearly all the orders of mammals. Invariably the earliest representatives of a given order appear abruptly with one or more ordinal characters fully differentiated and there is good evidence for the belief that the preceding transitional period was tachytelic (Simpson, 1944).

Intensive collecting in deposits where transitional forms should occur but are actually absent suggests, although it does not necessarily prove, that these forms had a restricted geographical distribution throughout most of the transitional period. The taxonomic group involved in the transition was also undoubtedly limited, possibly to the specific level. There is slight reason for believing that intermediate forms may exist unrecognized in collections as all the known Paleocene faunas have been thoroughly studied and evaluated.

In order to explain this anomalous situation Simpson (1944), in a further extension and application of Wright's theories, has suggested as a hypothesis that mega-evolution usually occurs in small (in the Wrightian sense) populations subject to genetic drift. According to his concept, quantum evolution may account for the relatively rapid origin of higher categories such as families and orders. The non-adaptive change resulting from genetic drift that is characteristic of small isolated populations and usually brings about their extinction may, in very rare instances, actually be preadaptive for a different adaptive zone. The presence of preadaptation, which is a primary requirement, may thus permit the survival of the population and initiate its subsequent expansion at a new adaptive level. Quantum evolution is, as Simpson states, an all-or-none reaction; if the isolated population is unable to attain a new adaptive zone it will suffer extinction.

This concept of mega-evolution provides a possible explanation for two established facts in paleontology, the rapid and often radical transformation involved in the origin of many higher categories and the usual absence of specimens representing any level of the transitional stage. If the trend occurred in a small isolated, or probably even a small semi-isolated population, the chances of obtaining a sample by any available collecting technique are very remote (assuming that

some individuals in the population were preserved).

Simpson also points out that mega-evolution may occur in a less radical manner and actually intergrade with other modes of evolution, particularly phyletic. An evolutionary pattern possibly of significance in connection with the origin of the artiodactyls involves the appearance of preadaptation in a transitional population without the possible deleterious effect of genetic drift. Radical change in either member of the organism-environment equilibrium may ultimately produce a situation bringing about the extinction of the population or, in very rare instances, result in the quantum evolution effect. If the equilibrium changes without being lost, however, it indicates that the population has responded adaptively to environmental change. Thus a modification in the nature of the selection pressure can, under these circumstances, favor a new evolutionary trend with the critical transitional period between two adaptive zones being one of more or less continuous adaptation. Such a transition is more phyletic than quantum in its mode but may nevertheless approach the latter in rate and magnitude of change.

Certain features of the hyposodontid-artiodactyl transition may reasonably be inferred on the basis of the known facts. In the early Paleocene a fairly large population of preartiodactyls, here considered to be primitive hyposodontids, occupied a warm, moist, forested environment. The adaptive zone was relatively stable and the population was presumably subjected to only mild selection pressure. As must characterize all generalized ancestral stocks which give rise to higher categories, this one possessed a high degree of genetic plasticity with a potentiality for entering a variety of different adaptive zones. Sometime during the first half of the Paleocene some changing feature or features of the environment affected a particular segment of this hyposodontid population. The nature of this change is unknown, but it is very

reasonable to suppose that it was associated directly or indirectly with the evolution of the earliest carnivores, the creodonts. Although the Lower Paleocene creodonts and condylarths share many features in common, by the Middle Paleocene the creodonts were more specialized in a typically carnivore direction and became more efficient predators. This increase in the efficiency of the carnivores was, of course, intimately associated with the development of ungulate specialization and possibly both were related to some modification in the physical environment such as a tendency toward a more open plains habitat (there is actually no direct evidence of such change in the Paleocene) or to an expansion of the ungulates and carnivores into such an already existing habitat.

These generalized herbivorous hyposodontids reacted to the increased predator pressure in a manner common to most ungulate groups by evolving a mechanism for faster locomotion. Why the tarsus was affected in this connection prior to any significant change in limb ratios or to reduction in the number of digits is an intriguing but at present unanswerable problem. As pointed out in the functional analysis, the tarsal modification increased the propulsive force exerted by the foot as well as accelerated the protraction and retraction phases of hind limb. This obviously had some initial selective advantage over those cursorial adaptations that were emphasized later in the Tertiary.

The evolution of the tarsus during the hyposodontid-artiodactyl transition must have been essentially rectilinear and continuously adaptive. It seems reasonable to suppose that the effect of selection pressure on the new trend almost from the time of its inception was great enough to channel variation. The complexity of the tarsal joints and their intimate functional relationship certainly would not permit more than slight deviation in any portion of the complex without loss of efficiency, not to mention actual malfunction.

The evolution of the artiodactyl tarsus did not involve, in a broad sense, a complete change of function but rather a trend toward specialization and restriction of function. While it is true that the reorientation of the axis of the lower ankle joint did produce a marked modification in the function of the astragalus, there was no radical, basic change in the action of the foot as a whole in relation to its role in locomotion. It is therefore difficult or impossible to determine at what point in the transition the tarsus was preadaptive for a specialized cursorial function and, in fact, such a point probably did not exist. Along with the continuous adaptation of the tarsal complex for the precursorial environment there was a progressive preadaptation for the artiodactyl or cursorial one.

As the artiodactyl tarsus almost reached its biomechanical limit of specialization by the beginning of the lower Eocene, there was relatively little postadaptive change. The significance of the biomechanical limit has recently been discussed by Huxley (1942, p. 494). It represents that stage in an adaptive trend at which the greatest possible degree of mechanical efficiency is attained and beyond which further change can only be essentially nonadaptive. (It is, of course, not possible to prove that an actual biomechanical limit has been reached in a particular case although the weight of evidence may make it extremely probable.) If the limit is reached at a generalized level, however, as in the case of the primitive reptiles with their horizontally oriented proximal limb segments, it is possible to approach another and different limit by entering a new adaptive zone. In advanced mammal-like reptiles the entire limb assumed an almost vertical position permitting motion in a parasagittal plane. The biomechanical potentialities of this limb reorientation were so great that a number of different limits were now possible and were finally attained only in the many different groups of mammals ultimately derived from the therapsids.

The artiodactyl tarsus illustrates, on the other hand, the effect of extreme specialization in hastening the attainment of an apparently absolute limit. During the Tertiary, this order underwent a broad adaptive radiation which produced not only relatively conservative types but also extreme cursorial and graviportal forms. In all cases the tarsus remains amazingly similar. By way of postadaptive change there has been a relatively minor increase or decrease in the size of certain articular facets and a tendency toward fusion of the cuboid and navicular bones, probably refinements for somewhat greater mechanical efficiency and greater stability.

The pattern of evolution involved in the hyposodontid-artiodactyl trend is obviously complicated, with different character complexes evolving at different rates and in response to different factors of the environment. The evolutionary change which is directly related to the origin of the Order Artiodactyla, however, apparently involved originally only a single character complex, the tarsus. Even in this restricted sense the mode is more phyletic than quantum in nature although there are features that indicate some intergradation between the two.

The taxonomic category resulting from the trend is at the ordinal level, a high level being characteristic of quantum evolution. There is, however, no indication of abrupt transfer from one adaptive zone to another but rather of the change occurring in a single shifting adaptive zone as in phyletic evolution. Adaptation in the precursorial zone was essentially continuous and was intimately associated with preadaptation for the cursorial zone. Post-adaptation was restricted in the cursorial zone by an early approach to the biomechanical limit of specialization. Presumably there was no particular point in the trend that might be considered as a threshold in the sense employed by Simpson (1944, p. 209) since there was no one morphological or functional stage that the tarsus had to attain in order to

prevent the actual elimination of the trend.

With the diagnostic features of pure quantum evolution absent, it is reasonable to assume that the population segment involved in the transition was semi-isolated, with some migration and cross-breeding between it and adjacent populations. Wright (1941 and elsewhere) has pointed out that rapid evolution can occur under these circumstances even to the extent of evolving a new higher category. Following Simpson's interpretation, this mode is essentially phyletic and involves less radical change than pure quantum evolution. The magnitude of change resulting from any adaptive trend, however, must be evaluated on a relative basis. The tarsus of terrestrial mammals has been modified into a limited number of rather distinct types, with that occurring in the Artiodactyla probably representing the greatest departure from the arctocyonid level. In terms of tarsal evolution in terrestrial mammals it is, therefore, a radical change effecting the entire economy of the animal. In terms of tarsal evolution in the mammals as a whole (including extreme arboreal and aquatic forms) it is much less radical but still great enough to form the basis for a new order through the reaching of a new adaptive plateau.

It appears evident that the character complexes that define and delimit the higher categories of organisms have not evolved at the same rate or necessarily at the same time. They apparently reached their definitive form in a regular sequence which for some orders of mammals can be estimated with reasonable accuracy. In the case of the even-toed ungulates the tarsus was apparently the first complex to attain this goal. The change in the orientation of the longitudinal axis of the foot from a position essentially along the third toe to one between the third and fourth toes may have occurred coincidentally with the modification in the tarsus. This shift represents the appearance of another ordinal character. Its functional

significance was not fully realized, however, until digital reduction involving the loss of the first toe and relative decrease in the size of the second and fifth toes was initiated in the Eocene in the various artiodactyl groups. Changes occurring exclusively at subordinal and lower levels also were started during the Eocene with diversification of the dentition probably beginning before there was any great alteration in limb ratios.

SUMMARY

The character complexes of the various mammalian orders usually appear suddenly with no record of transitional stages from the presumed ancestral stock. The earliest members of the Artiodactyla are recognized positively on the basis of a single complex which is the highly specialized form of the tarsus. Basic similarity in the dentition of the Lower Eocene artiodactyls and a family of primitive Paleocene condylarths indicates that the latter represents the ancestral stock of the even-toed ungulates.

The transitional period from the primitive condylarths to the first true artiodactyls had a duration of not more than 15 million years. During this time there was a radical change in the form of tarsal elements and in the orientation of the axes of the three main tarsal joints. The resulting mechanism increased the speed of locomotion and probably reduced the retarding effect at the beginning of the propulsive stride.

According to paleontological standards the transition was rapid. It was also essentially rectilinear and continuously adaptive. Selection pressure, probably mostly predator pressure, channeled variation sharply during the entire trend. Preadaptation for the artiodactyl environment was a continuous process, occurring along with adaptation for the preartiodactyl one. The biomechanical limit of specialization for the tarsus was almost reached by the Lower Eocene, greatly reducing the possibility of modification in this complex during the Tertiary. The evolutionary

mode involved in the transition was essentially phyletic with some features attributed to quantum evolution.

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