Skeleton of *Diacodexis*, Oldest Known Artiodactyl

Abstract. *A nearly complete skeleton of early Eocene* Diacodexis, *the oldest known member of the mammalian order Artiodactyla, is described. Its slender, elongate limb elements indicate that* Diacodexis *was highly cursorial and closer in postcranial adaptations to tragulids and other primitive ruminants than to living or extinct nonruminant artiodactyls. Its skeletal specializations call into question the widespread notion that* Diacodexis *was the ancestor of all later artiodactyls.*

The mammalian order Artiodactyla is the most successful group of ungulates and, apart from rodents, the most diverse and abundant group of mammalian herbivores. The Eocene Dichobunidae of North America, Europe, and Asia are the oldest known artiodactyls and are widely regarded as the most primitive members of the order (*1–5*). The oldest dichobunid is early Eocene *Diacodexis*, whose teeth and jaws are well known from North American deposits (*6–11*) and have also been reported from Europe (*12, 13*). Because of its antiquity and generalized dentition, *Diacodexis* has been portrayed as the basal artiodactyl (*3, 14, 15*). Knowledge of its skeleton, however, has been restricted to a few fragmentary hind limb elements described a century ago (*16*). A substantial part of a skeleton, discovered in 1979 in Wyoming, displays a suite of specialized cursorial adaptations surpassing those in any other mammal of comparable antiquity and even those of many later nonruminant artiodactyls. These specializations foreshadow those of neoselenodont artiodactyls (camels and ruminants) (*17*).

The most ancient skeletal specimen of an artiodactyl is a representative of *Diacodexis* and consists of the tarsus, fragments of the femur, tibia, and innominate, and a lumbar vertebra (*16*). Isolated astragali of *Diacodexis* have also been reported (*7, 13*). The only other early Eocene remains belong to the somewhat younger and larger *Bunophorus*, also known from a tarsus and fragmentary tibiae and metatarsals (*4*). Middle Eocene and later dichobunids are better known. Marsh (*18, 19*) reported a skeleton of *Homacodon* from Wyoming (but illustrated only its astragalus). The foot skeleton of *Dichobune* from Europe has long been known (*20*), and Franzen (*21*) has described a nearly complete skeleton of *Messelobunodon* from the middle Eocene of Germany.

The new skeleton of *Diacodexis metsiacus* (USGS 2352), collected from the Lower Eocene Willwood Formation (Wasatchian) of the Bighorn Basin, Wyoming (Yale Peabody Museum locality 55), has both dentaries, part of the palate and skull, much of the vertebral column, ribs, parts of the scapulae and forelimbs, most of the pelvis, and, on one side or the other, nearly complete hind limbs (Fig. 1 and Table 1). These elements indicate that *Diacodexis* was about the size of a rabbit (*Sylvilagus*).

The skeleton, though artiodactyl-like, is primitive compared with many, but not all, later artiodactyls in that the ulna is moderately strong and separate from the radius, the fibula evidently complete, the cuboid and navicular unfused, and the metapodials separate. The lateral metapodials are relatively less reduced than in many other artiodactyls. Although the manus is not preserved in this specimen, it was probably pentadactyl, as in *Hypertragulus* (*22*). There were five metatarsals (I, presumably vestigial, is indicated by a facet on II)—in contrast to all other artiodactyls. The femur bears a small third trochanter (for insertion of the superficial gluteal muscle), a feature also found in archaic ungulates such as phenacodontids and arctocyonids but lost in all other artiodactyls. The tail is longer than in most other artiodactyls. Finally, as is well known, the teeth of *Diacodexis* are very primitive, showing no tendency toward selenodonty; rather they are bunodont and the upper molars are tritubercular. Most of these primitive traits distinguish *Diacodexis* pri-

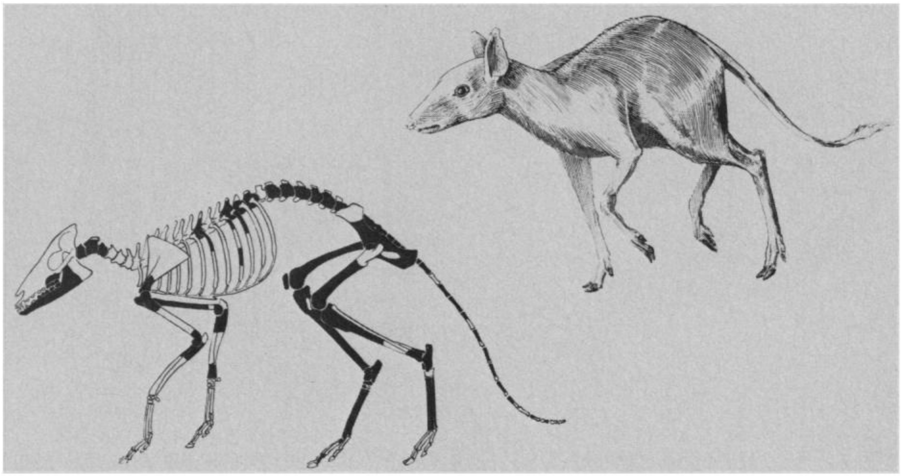

Fig. 1. Reconstruction of the skeleton and artistic restoration of *Diacodexis* based on USGS 2352. Preserved elements of skeleton are darkened.

Table 1. Selected skeletal measurements of *Diacodexis metsiacus*, USGS 2352. The length of humerus was estimated from an incomplete element. Abbreviations: R, right; L, left.

Bone	Dimension	Measurement (mm)
Humerus	Length	~ 62 (probable range, 60 to 65)
	Breadth, distal end	8.2 R, ~ 7.5 L
Radius	Breadth, proximal end	4.9 R, 5.1 L
Femur	Length	70.8 R
	Breadth, distal end	11.8 R
	Depth, distal end	15.4 R
Patella	Length	10.9
	Breadth	5.3
Tibia	Length	82.6 R
	Breadth, proximal end	12.1 R, 12.1 L
	Maximum diameter, midshaft	5.2 R
Calcaneus	Length	20.5 R, 20.3 L
Astragalus	Length	10.2 R
Metatarsals		
III and IV	Length	45.0 L
III	Maximum diameter, midshaft	3.3 R
II and V	Length	~ 40.5
Vertebrae		
Lumbar 5	Length	10.3
Lumbar 6	Length	8.8
Proximal lumbars	Length	11.2, 12.0
Thoracic (?proximal)	Length	7.8, 8.2
Caudals (proximal)	Length	7.5, 8.5, 11.3
Caudals (middle)	Length	14.0, 15.2, 15.5

marily from neoselenodont artiodactyls.

Associated with these decidedly primitive characters are numerous cursorial specializations that are strikingly progressive for a mammal of such antiquity. Most salient among them are the marked elongation and slenderness of the limb elements (Fig. 2). The hind limbs are larger and much longer than the forelimbs, and the distal segments of the hind limbs are relatively long. The distal end of the femur is narrow and deep, as is the patellar groove. The cnemial crest of the tibia, though prominent, is comparatively short, extending distally only about 25 percent of the tibial length, as in *Tragulus*. The fibula is thin and splintlike, presumably continuous (most of the shaft is not preserved), and free from the tibia proximally but synostosed with it distally. As has been noted (*16, 23*), the astragalus displays the double-pulley structure that is diagnostic of artiodactyls. The foot is paraxonic, with four long gracile metatarsals (and a vestigial metatarsal I); the lateral metatarsals (II and V) are somewhat reduced in girth and length relative to the central ones. The metatarsals are arranged in an arch, the lateral ones posterolateral (relative to the median axis of the foot) to the central ones. A single, possibly a middle, phalanx is preserved. Its distal articular surface extends well onto its dorsal aspect, indicating substantial parasagittal mobility and suggesting that *Diacodexis* was unguligrade. Cursorial features of the forelimb include the narrow distal humerus, perforated olecranon fossa, and broad radial head, which articulates with both the intercondyloid ridge (capitulum) and the trochlea of the humerus.

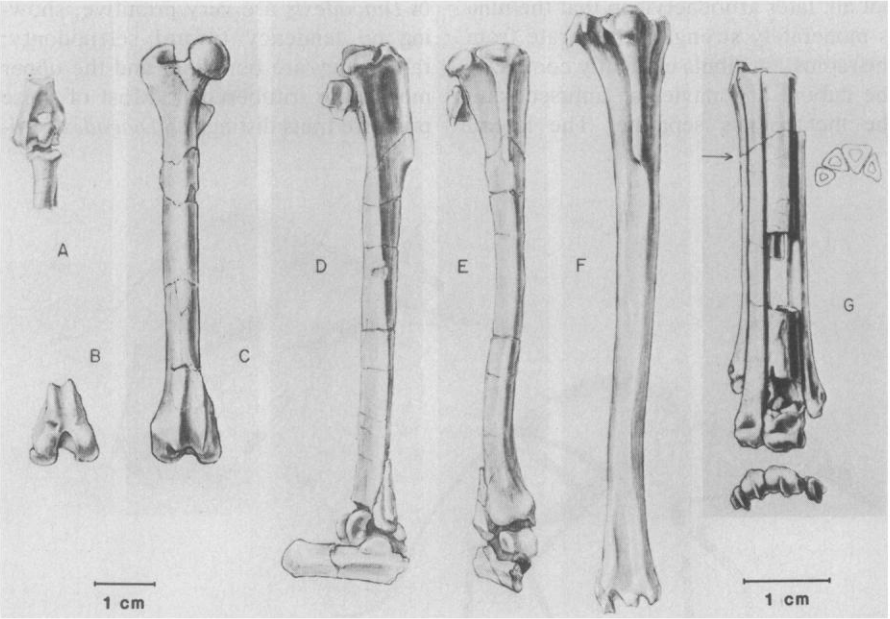

Fig. 2. Limb elements of *Diacodexis* (USGS 2352): (A) left distal humerus and proximal radius; (B) right distal femur, from below; (C) right femur; (D and E) right tibia, proximal and distal fibula, and calcaneus and astragalus, in lateral view (D) and anterior view (E); (F) anterior view of right tibia of *Tragulus*; and (G) left metatarsals. Scale bar for (A) to (F) is on the left and for (G) on right.

These features, many of which would enhance the length and rate of stride (*24*), indicate that *Diacodexis* had cursorial capabilities probably exceeding those of any of its mammalian contemporaries, as well as those of non-neoselenodont artiodactyls (for example, Suina and oreodonts). This can be illustrated by comparing its limb proportions with those of other ungulates (Table 2). The limb elements of *Diacodexis* are much more gracile and the relative lengths of the tibia and metatarsals (indicated by crural and femorometatarsal indices) much greater than in the condylarth *Phenacodus*, a generalized quadruped with only incipient cursorial adaptations (*25*). The hind limb indices are also higher than in *Hyracotherium* [femorometatarsal index = 50 (*25*) and crural index about 100 or less (*16*)], the oldest perissodactyl, contemporary with *Diacodexis*, and one of the most proficient cursors of its time. Among artiodactyls, *Diacodexis* is most similar in limb proportions to other dichobunids, such as *Messelobunodon*, and to the primitive Oligocene ruminant *Hypertragulus*; however, the metatarsals of *Diacodexis* are relatively somewhat longer than in either of them. There is also a close resemblance to the primitive ruminants *Archaeomeryx* (late Eocene) (*26*) and *Tragulus* (Recent) and to *Cainotherium* (*27*), a nonruminant from the Oligocene of Europe. Although these three genera are more progressive than *Diacodexis*, in that the relative size of their forelimbs is further reduced, all three have a slightly lower crural index than the early Eocene genus. Moreover, only in *Tragulus* are the metatarsals relatively longer than in *Diacodexis*; in *Cainotherium*, for example, they are decidedly shorter. The limb elements in Suina (represented by recent *Sus* and Oligocene *Archaeotherium* in Table 2) and oreodonts (*28*) are not markedly elongat-

Table 2. Indices and relative dimensions of some limb elements in *Diacodexis* (USGS 2352) and other ungulates. Artiodactyls: *Messelobunodon*, middle Eocene dichobunid from Germany (*21*); *Hypertragulus*, Oligocene hypertragulid from North America (*22*); *Archaeomeryx*, late Eocene leptomerycid of Mongolia (*26*); *Tragulus*, recent tragulid of Asia (USNM 317286); *Hyemoschus*, recent tragulid of Africa (AMNH 53617); *Cainotherium*, Oligocene cainotheriid of Europe (*27*); *Archaeotherium*, Oligocene entelodont of North America (*22*); *Sus*, recent suid (USNM 49953); and *Phenacodus*, Paleocene and Eocene condylarth of North America (*16, 25*).

Taxon	Index*		Relative length†		
	Crural	Femoro-metatarsal	Femur	Tibia	Metatarsal III or IV
Diacodexis	117	64	114 (109 to 118)‡	133 (127 to 138)‡	73 (69 to 75)‡
Messelobunodon	109	57	117	128	67
Hypertragulus	116	55	115	134	63
Archaeomeryx	112	61	125	140	76
Tragulus	110	78	123	136	96
Hyemoschus	98	49	138	136	68
Cainotherium	104	~ 46	124	131	~ 55
Archaeotherium	78	48	106	82	51
Sus	90	37	110	99	40
Phenacodus	95	35	128	121	

*Crural index = (tibia length/femur length) × 100; femorometatarsal index = (metatarsal III or IV length/femur length) × 100. †Relative lengths of femur, tibia, and metatarsal III or IV (whichever is longer) are based on a standardized humeral length of 100. Humerus in USGS 2352 is nearly complete, and its original length is estimated at 62 mm. ‡Ranges of elements for humeral length of 60 to 65 mm.

ed, the tibia is typically shorter than the femur (crural index <100), and the metapodials are relatively short (femorometatarsal index <50). They appear considerably more generalized than *Diacodexis*.

The crural and femorometatarsal indices tend to be highest in running (cursorial) and jumping (saltatorial) mammals. The crural index for *Diacodexis* reflects such habits, falling in the middle of the range for living ruminants as well as that for rabbits (*29*). The femorometatarsal index is extraordinarily high for an early Eocene mammal and is comparable to that in many extant ruminants and higher than in rabbits (*29*). Thus *Diacodexis* may have been the most cursorial mammal of the early Eocene. Among small mammals, however, there may be no clear distinction between cursorial and saltatory habits; some species employ a combination of both locomotor modes. This is true of tragulids (*30, 31*), small forest ruminants of Asia and Africa, which are the closest living analogs of *Diacodexis*. The resemblance of *Diacodexis* to tragulids in limb proportions and body size suggests that it, too, was an adept leaper. It may have used its long tail for balance, as do several living saltatorial mammals (*24, 29*).

The notion that dichobunids are so primitive and short-limbed that, were it not for their characteristic astragalus, they might not be recognized as artiodactyls is prevalent (*3, 5, 32*). *Diacodexis* does not fit this image, however, nor do other dichobunids which, where known, are progressive and cursorially adapted like *Diacodexis*. The skeleton of *Diacodexis* appears to be slightly more specialized than that of *Messelobunodon* and nearly as specialized as those of *Hypertragulus*, *Archaeomeryx*, and *Tragulus*, which are considered to be the most primitive Ruminantia (Tragulina) (*17*). The only important postcranial features which are more primitive in *Diacodexis* than in tragulines are its free proximal fibula, retention of metatarsal I, and separate cuboid and navicular elements in the tarsus. This raises the question of whether *Diacodexis* is representative of the primitive artiodactyl skeletal condition, or whether it is too specialized to be ancestral to Suina and some extinct nonruminant groups. If *Diacodexis* is representative, we must revise our concept of the primitive artiodactyl skeleton and assume that reversal of cursorial trends (toward elongation and lightening of the limbs and reduction in size of some elements) must have occurred in various nonruminant lineages. While such reversals are possible (*33, 34*), it is equally probable, as judged from present evidence, that the basal artiodactyl was an unknown bunodont form with a much more generalized skeleton than that of *Diacodexis*.

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Upwelling of Hydrothermal Solutions Through Ridge Flank Sediments Shown by Pore Water Profiles

Abstract. *High calcium ion and low magnesium ion concentrations in sediment pore waters in cores from the Galápagos Mounds Hydrothermal Field on the flank of the Galápagos Spreading Center are believed to be due to a calcium-magnesium exchange reaction between circulating seawater and basement basalt. The nonlinearity of the calcium ion and magnesium ion gradients indicates that these discharging hydrothermal solutions on the ridge flank are upwelling at the rate of about 1 centimeter per year through the pelagic sediments of the Mounds Field and at about 20 centimeters per year through the hydrothermal mounds themselves.*

The recent discovery of hot springs on the Galápagos Ridge (*1*) and the East Pacific Rise (*2*) has provided the most spectacular evidence of ridge crest convection of seawater through hot basalt. The composition of these samples (*3*), together with earlier evidence (*4*), indicates that seawater-basalt exchange attending hydrothermal circulation is important in the marine mass balances of several elements; the process is a sink for seawater Mg^{2+} and a source of seawater Ca^{2+}. The intense convection of water at the center of spreading appears to cool the entire crust (*5*) but is of short duration, as reflected in the fact that the discharge of high-temperature hydrothermal solutions is limited to young crustal segments (*1*). Convection and associated hydrothermal processes continue at a much slower rate on the ridge flanks, for 5×10^6 to 7×10^7 years (*6*). This ridge flank convection process is reflected by a deficiency in conductive heat flow (*6*), increasing layer-2 velocity (velocity of basalt) (*7*), and nonlinear heat flow profiles indicating upwelling and downwelling of solutions through sediments (*6*). Sleep *et al.* (*8*) have argued that most of the global convective heat loss actually takes place on the ridge flanks.

The southern flank of the Galápagos Spreading Center is now the best understood example of a ridge flank convection system. Heat flow has been mapped in detail to a distance of 30 km south of the center of spreading (*5, 9*) (Fig. 1). The variations are believed to reflect the flow of water through the sediments to

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