their specific membrane properties would then give rise to the motor pattern.

A model of how the known synaptic interactions of lamprey spinal premotor interneurons could generate rhythmic activity is presented in Fig. 2D. The segmental interconnections among the neurons that have been established by paired recordings (*6*) are shown by solid lines. These neurons are phasically active during fictive locomotion (*18, 19*), as indicated beside the circuit diagram. As the excitability level of the neurons is raised by descending or sensory input or by bath application of an excitatory amino acid, a cycle begins on the more excitable side of the cord. The EINs of that side then excite all of the ipsilateral neurons of the network. The CCINs in their turn inhibit all contralateral neurons, and, as long as the CCINs are active, the contralateral side remains inhibited. The CCINs turn off earlier than other ipsilateral neurons (*4, 6, 19*), and, after doing so, all neurons on the contralateral side become disinhibited. Because of the high background excitability, the EINs and the other neurons become active, and the CCINs in turn inhibit the previously active side.

It is critical that the CCINs are turned off; otherwise, activity becomes locked on one side. The turn-off mechanism could be provided by the ipsilateral inhibition from lateral interneurons. These cells are depolarized in phase with the MNs, and they spike during the depolarizing phase. Thus, their activity would tend to turn off ipsilateral CCINs early. The lateral interneurons would then assume the important role of indirectly turning off all ipsilateral activity. A summation of the action potential afterhyperpolarization, particularly in the CCINs, may also contribute.

In a qualitative fashion this circuit can thus be expected to produce rhythmic alternating activity at the segmental level. To achieve an insight concerning the presumed operation of the network, the model must be based on available quantitative data on the membrane properties of the neurons and the different types of synaptic interactions. Further details of the spinal circuitry will undoubtedly be revealed (*20*), but the connections established thus far may be sufficient to explain the basic pattern of alternation in a segment, and they will in any case be important in forming the output of the spinal locomotor circuitry.

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9. The latency consists of the conduction time in the EIN axon and the synaptic delay. Conduction time could be estimated in four cases where conduction velocity could be measured (0.4 to 1.1 m/sec). By assuming a constant conduction velocity along the axon and by subtracting the estimated conduction time from the EIN to the MN, we found that the synaptic delays were 2.6, 2.7, 3.3, and 4.8 msec. These values are similar to previous reports of presumed direct chemical synaptic delays in the lamprey (*7*) [C. M. Rovainen, *J. Comp. Neurol.* **154**, 207 (1974)].
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20. Not included in the model are two other known classes of premotor interneurons: the excitatory CCINS and ipsilateral inhibitory interneurons. These cells display only weak activity during fictive swimming (*7*; J. T. Buchanan and S. Grillner, unpublished observations). Some of the neurons of the model may exhibit bistable membrane properties resulting in plateau potentials and a pacemaker tendency (*16*). After administration of strychnine to the in vitro preparation, both bilateral synchronous bursting [A. H. Cohen and R. M. Harris-Warrick, *Brain Res.* **293**, 164 (1984)] and unilateral bursting (*2*) can occur. It is not known if the strychnine bursting reflects activity in the locomotor network.
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Climbing Adaptations in the Early Eocene Mammal *Chriacus* and the Origin of Artiodactyla

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A virtually complete articulated skeleton of the arctocyonid *Chriacus*, recently found in northern Wyoming, is one of the most intact early Eocene mammal skeletons ever found. It exhibits numerous adaptations characteristic of mammals that climb, including strong bony crests and processes (reflecting powerful musculature), ability for considerable forearm supination, a highly mobile ankle joint, plantigrade feet, curved and transversely compressed claws, and a long, possibly semiprehensile tail. These features contrast sharply with those of the oldest artiodactyls and indicate that *Chriacus* or a similar arctocyonid was not ancestral to the Artiodactyla, as has been proposed.

EARLY EOCENE MAMMALIAN FAUNAS are important because they include the first known representatives of many modern orders coexisting with archaic types. Our knowledge of these mammals has been based primarily on teeth, jaws, and fragmentary skeletal remains because good skeletons are rare. Recent work in the Willwood Formation, Bighorn Basin, Wyoming, has yielded a virtually complete, articulated skeleton of the rare arctocyonid *Chriacus* (USGS 2353) (Fig. 1B) (*1*), of which only jaws and a few skeletal elements have previously been described (*2*). Despite its rarity, *Chriacus* is important because of its proposed proximity to the origin of the mammalian order Artiodactyla, a hypothesis based principally on dental morphology (*3*). The postcranial anatomy of *Chriacus* is now better known (and its adaptations can be more confidently inferred) than in most contemporaneous mammals. Thus comparison of its skeleton with those of the most ancient artiodactyls (*4, 5*) affords significant new evidence by which to assess the status of *Chriacus* as the ancestor of Artiodactyla.

The skeleton of *Chriacus* is essentially primitive and generally similar (in the few comparable parts) to the skeletons of small early Paleocene arctocyonids (*6*). It is unmistakably that of a scansorial (climbing)

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animal that was as adept in the trees as on the ground, and anatomical traits reflecting such habits pervade the skeleton. Among extant mammals, the closest analogues in postcranial anatomy and, by inference, locomotor habits, are the most arboreal members of the carnivoran families Procyonidae [*Potos* (kinkajou), *Nasua* (coati), *Ailurus* (lesser panda)] and Viverridae [*Paguma* and *Paradoxurus* (palm civets), and *Arctictis* (binturong)]. *Chriacus* was a medium-sized Paleogene mammal (~5 to 10 kg), slightly larger than *Nasua*.

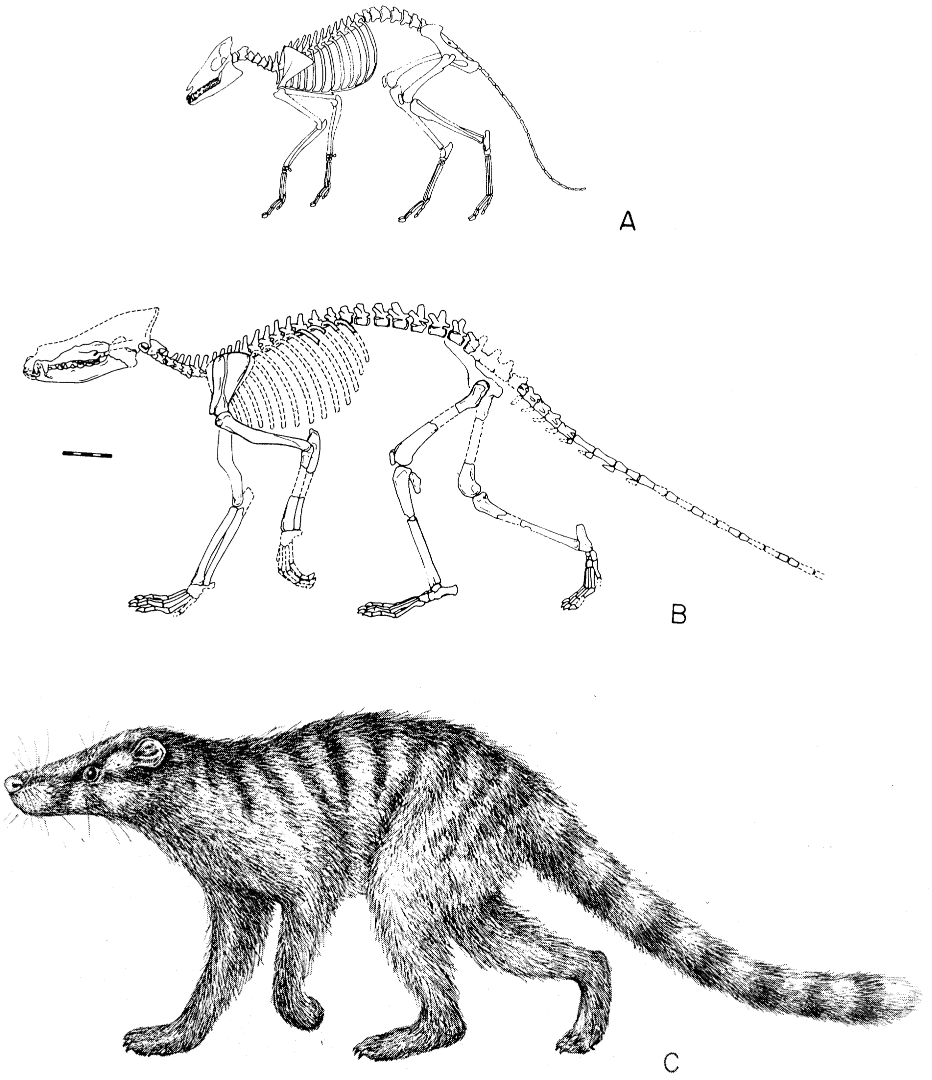

Fig. 1. (**A**) Skeletal reconstruction of *Diacodexis*, oldest known artiodactyl, after (*4*). (**B**) Skeletal reconstruction of *Chriacus* based on USGS 2353; dashed elements are missing or obscured by the matrix in this specimen. (**C**) Life restoration of *Chriacus*. Scale bar, 5 cm, applies to all three figures.

Like most extant climbing mammals, *Chriacus* was characterized by powerful limb musculature, very mobile joints, and flexible, plantigrade feet with claws—features that facilitate ascent, descent, and a firm hold on the substrate (Fig. 2) (*7–10*). Indicative of well-developed musculature in the forelimb of *Chriacus* are the large, projecting acromion process on the scapula (origin of the acromiodeltoid muscle which abducts the humerus) and the long, elevated deltopectoral ridge extending beyond midshaft on the humerus. The humerus is broad distally, as in *Nasua*, with a large medial epicondyle (origin of carpal and digital flexors) and well-developed lateral supracondylar ridge (origin of extensors and brachioradialis, a powerful elbow flexor when the manus is in midprone position). At the elbow, the ovoid radial head and cylindrical capitulum permitted substantial forearm supination, reflected also at the distal radioulnar articulation. The olecranon process in *Chriacus*, as in climbing carnivores (*7, 10*), is prominent and directed slightly anteriorly relative to the long axis of the ulna, indicating a normally flexed elbow. A well-developed pronator quadratus muscle, important in climbers, is demonstrated by a sharp crest on the mediodistal surface of the ulna, as in *Nasua*, *Ailurus*, and *Paradoxurus*. The manus is pentadactyl and plantigrade (*7, 10–12*), with digits terminated by curved, laterally compressed unguals reminiscent of those of *Potos*. Many of these forelimb attributes also typify digging mammals, and it is probable that *Chriacus* (like *Nasua* and some other climbers) was capable of this behavior as well.

Scansorial habits are equally apparent in the hind limb of *Chriacus*. The form and extent of the articular surface of the femoral head (especially its anterior margin, which forms an angle of 55° to 60° with the femoral shaft) and the relatively proximal position of the fovea indicate that the femur was normally abducted at least as much as in recent climbing carnivores (*13*). As in the latter (*7*), the lesser trochanter is directed medially rather than posteriorly, and the ventral border of the ilium is expanded, reflecting a powerful iliopsoas muscle (femoral flexor). Distally the femoral condyles show little posterior projection and the patellar groove is comparatively broad and shallow, as in climbers generally (*7*) and *Nasua* in particular. The extremities of the fibula (the only parts preserved) indicate that this bone was robust.

Climbing adaptations often are more manifest in the hind foot than elsewhere in the skeleton (*8*). The foot of *Chriacus*, like the manus, was pentadactyl and plantigrade (*14*). These traits, together with its slightly divergent hallux and claw-bearing unguals (similar to those of the manus), are typical of climbers. More significantly, the talocrural, subtalar, and midtarsal joints were modified to permit an extraordinary range of motion comparable to that in scansorial procyonids such as *Nasua*, *Ailurus*, and *Potos* (*9*). Although plantarflexion was more limited than in the latter (by the less curved talar trochlea and relatively high astragalar foramen), the shallow, broad articular surfaces of the distal tibia and talar trochlea, as well as the extensive, rounded talofibular articulation, resulted in a very flexible talocrural joint. The subtalar joint allowed medial rotation and anterior translation of the calcaneus, resulting in substantial pedal inversion. Supination was promoted at the transverse tarsal joint by a mechanism similar to that in *Potos* or *Nasua* (*15*). Hence the structure of the tarsal joints in *Chriacus* indicates a very flexible foot with a range of excursion approximating or exceeding that in *Nasua* (which cannot fully reverse its foot) but probably less extreme than in *Potos* (which employs full hind foot reversal) (*9*). This degree of mobility is characteristic of scansorial mammals that descend tree trunks headfirst (*8, 9*).

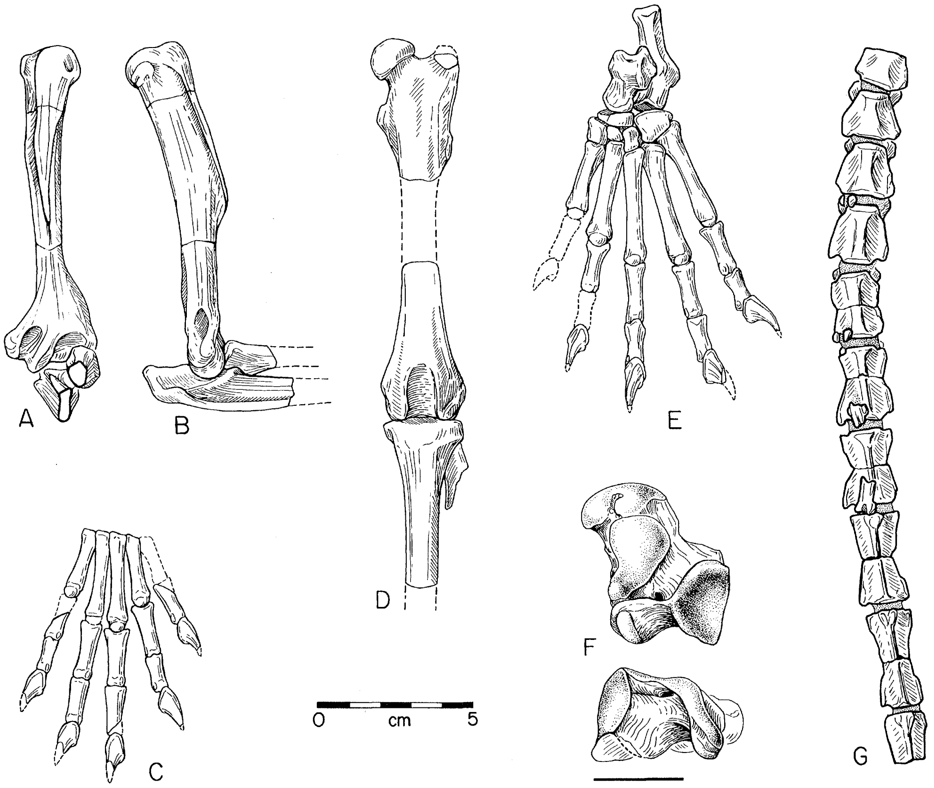

Fig. 2. Skeletal elements of *Chriacus* sp. (A to E and G) USGS 2353 (scale bar, 5 cm) and (F) USGS 15404 (scale bar, 1 cm). (**A**) Left humerus, anterior view. (**B**) Left humerus, proximal radius and ulna, medial view. (**C**) Right manus. (**D**) Left femur, proximal tibia and fibula, anterior view. (**E**) Left tarsus and pes. (**F**) Left talus, ventral (top) and posterior views. (**G**) Caudal vertebrae 4 through 13, ventral view (anterior at top).

Many climbing mammals have a long, robust tail used for balance or, in certain arboreal forms, as a prehensile organ (*2, 16, 17*). Osteological correlates of prehensility, while not definitive, include a long tail, hemal processes (especially distally), broad transverse processes, and broad mid-centra—all features associated with better developed caudal musculature (*16, 18*). The tail of *Chriacus* was long and massive. The 16 preserved caudals—the proximal two-thirds or so of the tail—are nearly as long as the precaudal spine, the entire tail having been perhaps 50 percent longer. All of these vertebrae have flaring transverse processes and broad mid-centra, comparing closely with the caudals of the prehensile-tailed *Arctictis* and *Didelphis* and the semiprehensile-tailed *Nasua* (*19*). Prominent hemal processes are preserved on caudals 7 through 11 and probably were present more distally. The tail of *Chriacus* clearly was well adapted for use in balancing and may have been at least semiprehensile, but conclusive evidence must await discovery of the most distal caudals.

Artiodactyla first appeared in the early Eocene, but their origin has long been obscure. It is widely held that they evolved from Paleocene arctocyonid or hyopsodontid condylarths, and dental evidence (in the absence of good skeletal remains) has suggested an arctocyonid near *Chriacus* as the most probable ancestor (*3*). Only recently have good skeletons of the oldest artiodactyls (Dichobunidae) become known (*4, 5*). The skeleton described here provides little support for a close relationship between *Chriacus* and early artiodactyls. Dichobunids were gracile animals, with elongate limbs modified for running and leaping (*4, 5*). Their metapodials were especially long and slender, the feet paraxonic, and the terminal phalanges more hoof-like than claw-like. Bony crests and processes were weakly expressed, reflecting muscular specialization for speed rather than power. Joint structure (elbow and tarsus in particular) prohibited forearm supination and restricted motion to a parasagittal plane, instead of enhancing mobility at these joints. To derive artiodactyls from a *Chriacus*-like ancestor would have required a considerable series of intermediate stages, as yet unknown (*20*). Moreover, the presence of a robust, possibly semiprehensile tail, and a specialized lower incisor tooth-comb used for grooming (*21*) further weaken the possibility that *Chriacus* or a similar arctocyonid was ancestral to artiodactyls. The origin of Artiodactyla remains elusive, perhaps to be found in some group not yet considered.

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20. Early Eocene *Chriacus* is contemporary with the oldest known artiodactyls and therefore cannot be in their ancestry, but the genus is known also from most of the Paleocene. There is no reason to suspect that the skeleton in Paleocene *Chriacus* differed significantly from this one.
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