therefore explains why there is approximately an equal distribution of "visible" and "invisible" tails in the STM images while all the head groups appear the same.

If one takes a simple contour over the vertical component of the hydrogen states in the molecules (Fig. 4c), one obtains a striking agreement with the STM contour in Fig. 4b. Both the 2.5 Å spacing in the alkyl tail and the 3.8 Å spacing in the head group are reproduced. This suggests that the STM is sensitive to the hydrogen orbitals of the molecules. One interpretation is that the contrast in these STM images is due mainly to topography rather than to differences in work function or density of states (*5*); that is, the phenyl groups are "brighter" than the alkyl tails because their hydrogen orbitals are higher above the substrate and have a larger component normal to the substrate. However, it is also possible that the contrast is caused by the perturbation of the graphite wave functions by their interaction with the molecular orbitals. The mixing of the molecular states with the graphite may create new states within 1 V of the fermi energy. Simple (*10*) and extended (*1, 2*) Hückel calculations have been applied quite successfully to STM studies of molecular systems. Such calculations would show more precisely the positions of the empty and filled electronic states of the cyanobiphenyl-graphite system and would help verify the structural model we have proposed.

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Scaling Body Support in Mammals: Limb Posture and Muscle Mechanics

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The scaling of bone and muscle geometry in mammals suggests that peak stresses (ratio of force to cross-sectional area) acting in these two support elements increase with increasing body size. Observations of stresses acting in the limb bones of different sized mammals during strenuous activity, however, indicate that peak bone stress is independent of size (maintaining a safety factor of between 2 and 4). It appears that similar peak bone stresses and muscle stresses in large and small mammals are achieved primarily by a size-dependent change in locomotor limb posture: small animals run with crouched postures, whereas larger species run more upright. By adopting an upright posture, large animals align their limbs more closely with the ground reaction force, substantially reducing the forces that their muscles must exert (proportional to body mass$^{0.74}$) and hence, the forces that their bones must resist, to counteract joint moments. This change in limb posture to maintain locomotor stresses within safe limits, however, likely limits the maneuverability and accelerative capability of large animals.

BODY SIZE IS ONE OF THE MAJOR factors that affects the form and function of an organism. Because area-dependent functions increase less rapidly than volume-dependent requirements of the organism, severe scaling constraints on functional capacity may result as organisms evolve to larger size (*1*). It has long been recognized that body size is also a critical factor influencing the mechanical support of animals (*2*). Specifically, the ability of muscles to generate force or bones to resist force depends on tissue cross-sectional area, which decreases in proportion to an animal's weight with increased size. Accordingly, considerable emphasis has focused on hypothesized size-dependent changes in the shape of mammalian limb bones (skeletal allometry) (*3*). Yet mammalian limb bones scale surprisingly close to isometry (maintaining similar relative proportions) when considered over nearly the entire size range of the class (*4*). This unexpected finding indicates that stresses acting in the skeleton should increase with increased size. As the material strength of bone does not vary significantly within mammals (*5*), increased locomotor stress would suggest that large animals may operate near to the limit of the strength of their skeletons (a low safety factor). Empirical determinations of skeletal stress in different sized mammals during conditions of strenuous activity (high-speed running or jumping), however, indicate that peak skeletal stresses are fairly uniform for mammals ranging from 0.1 to 300 kg in body mass (*6*), maintaining a safety factor (fracture stress/peak locomotor stress) of between 2 and 4.

To explain these divergent observations, I propose that similar stresses are achieved in the mammalian skeleton by a size-dependent change in locomotor limb posture, shifting from the crouched postures of small animals to the more upright postures of larger species (*7*). Though originally recognized by

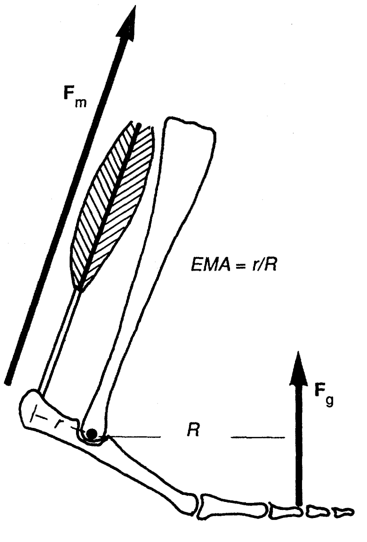

Fig. 1. Schematic illustration of effective mechanical advantage (*EMA*) defined for the extensor muscles acting about the ankle joint. $\mathbf{F}_g$ is the ground reaction force vector (measured with use of a force platform), and *R* is its mechanical advantage acting about the ankle. $\mathbf{F}_m$ is the force exerted by the ankle extensor muscle group about the ankle with a mechanical advantage of *r* to counteract the moment exerted by $\mathbf{F}_g$. When muscles had differing mechanical advantages at a joint, a weighted mean mechanical advantage $\bar{r}$ was calculated for the group as a whole (*11*).

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Table 1. Least-squares regression statistics for muscle effective mechanical advantage (*EMA*) of the forelimb and hindlimb as a function of speed.

Animal	*n*	Mass (kg)		Slope (±95% CI)	*y*-intercept	SE
Chipmunk (*Tamias striatus*)	2	0.092	fore	0.010 (±0.020)	0.072	0.009
			hind	−0.003 (±0.027)	0.087	0.012
Ground squirrel (*Spermophilus tridecemlineatus*)	3	0.137	fore	0.007 (±0.023)	0.131	0.011
			hind	−0.005 (±0.014)	0.157	0.007
Goat (*Capra hircus*)	3	27.3	fore	−0.015 (±0.026)	0.897	0.090
			hind	−0.053 (±0.114)	1.027	0.055
Dog (*Canis familiarris*)	2	38.1	fore	0.009 (±0.029)	0.328	0.014
			hind	0.004 (±0.035)	0.479	0.017
Horse (*Equus callabus*)	3	275	fore	−0.020 (±0.035)	0.969	0.014
			hind	−0.029 (±0.052)	1.159	0.025

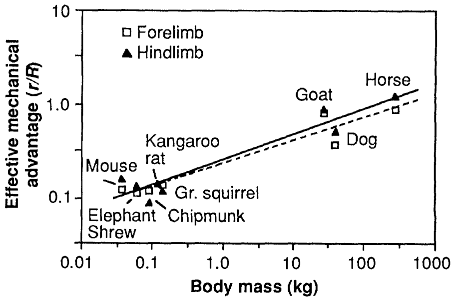

Fig. 3. Graphs of forelimb effective mechanical advantage (*EMA*) (dashed line) and hindlimb *EMA* (solid line) measured at the trot-gallop transition speed of each species plotted as a function of body mass on logarithmic coordinates. Significant and similar increases in *EMA* were observed for both the forelimb and hindlimb muscle extensor groups with increasing body size. This overall increase in *EMA* for a limb is consistent with the interspecific scaling of *EMA* for individual joints of the limb (Table 2). The observed increase in *EMA* indicates that, when normalized for body weight, limb muscles exert proportionately lower forces in larger animals.

Gray (*8*), the mechanical significance of a size-dependent variation in locomotor limb posture in terms of the scaling of muscle and bone stress has largely been overlooked. As Gray noted, a shift to an upright posture aligns the segments and joints of the limb more closely with the ground reaction force vector ($\mathbf{F}_g$) exerted at the foot (Fig. 1). This not only reduces the relative bending to which a bone is subjected, but more importantly decreases the moments exerted about the joints of the limb (*8, 9*). This reduction in joint moments decreases the forces that the muscles must exert to support the animal (and hence, the compressive force that the bone must resist). In effect, closer alignment of the limb to $\mathbf{F}_g$ increases a muscle's "effective mechanical advantage" (*EMA*) at the joint. *EMA* is defined as the ratio of the extensor muscle moment arm (*r*) to the moment arm of the ground reaction force (*R*) acting about the joint and is used as an index of this effect. A size-dependent increase in the *EMA* of limb muscles, acting to diminish mass-specific muscle force in larger animals, could explain how peak stresses of similar magnitude act in the bones and muscles of small and large mammalian species.

To test this hypothesis, different sized mammals were made to run over a force platform and filmed in lateral view (*10*) to determine the mechanical advantage (*R*) of the ground reaction force in relation to the corresponding moments exerted about the joints of the limb. A weighted mean mechanical advantage $\bar{r}$ of extensor muscle groups was determined from radiographs or anatomic dissection, and adjusted for observed angular displacements at the joint (*11*). The *EMA* of extensor muscle groups was calculated for joints of the forelimb and hindlimb over the period of contact of the limb with the ground (support phase). Generally, for a given species each extensor muscle group acting about a joint in the limb had a consistent *EMA* during the middle third of the support phase; the variation in *EMA* being lowest in the two distal joints and highest in the two proximal joints of either limb (*12*). A mean *EMA* was determined for each limb joint during the middle third of the support period over a range of speed and gait for each species. As the ground reaction force, and the moment exerted at a joint, typically pass through a maximum near the middle of the support phase, the *EMA* of the limb muscles at this time determines the maximal force that the muscle group must exert. Further, no significant change in *EMA* was observed with increased speed and change of gait within any of the species (Fig. 2 and Table 1), indicating that each species maintains a characteristic limb posture over its range of gait and speed. The trot-gallop transition speed of each species (all quadrupeds) was used to compare changes in *EMA* as a function of body size. As no significant correlation between *EMA* and speed or gait was found, selection of the trot-gallop transition speed does not bias the results presented here. The trot-gallop transition speed moreover has been argued to represent a functionally equivalent speed, at which similar bone and muscle stresses act in different species, and being easily defined, represents a reliable basis for comparing interspecific data (*13*).

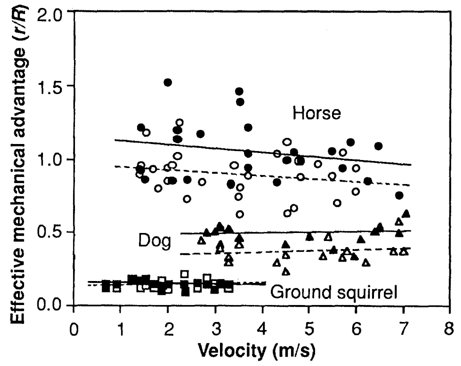

Fig. 2. Graphs of effective mechanical advantage (*EMA*) for joints of the forelimb (open symbols and dashed lines) and hindlimb (solid symbols and solid lines) of the horse, dog, and ground squirrel, showing that *EMA* does not vary significantly with change of speed and gait, but does increase with increased body size. The lines were determined by the method of least-squares regression (see Table 1).

The effective mechanical advantage of both forelimb and hindlimb extensor muscle groups increases significantly with increased body mass (Fig. 3). This increase is essentially the same for forelimb and hindlimb muscle groups, with the overall scaling of *EMA* proportional to body mass $M^{0.258}$ (±0.048 95% confidence interval; regression of data for both limbs combined, $n = 15$). Though less robust than the pooled data for the hindlimb and forelimb as a whole, a significant increase in *EMA* was found at each joint with increased body size (Table 2). The observed increase in extensor muscle *EMA* indicates a significant reduction in mass-specific force that these muscles must exert as body size increases. Given that ground reaction forces generally vary in direct proportion to an animal's weight (*6, 14*), the scaling of *EMA* indicates that extensor muscle force scales proportional to $M^{0.74}$, and hence, mass-specific muscle force (Newton per kilogram) scales proportional to $M^{-0.26}$. When normalized for differences in body weight, this scaling relation means that the mass-specific force exerted by the muscles of a 300-kg horse is only 17% of the mass-specific force exerted by the muscles of a 0.3-kg squirrel when each species moves at its trot-gallop transition speed. This reduction in the force accounts for 80 to 85% of the decrease in total force transmitted to the bone needed to counteract joint moments and maintain peak bone stresses similar to those of the smaller species (*9*).

This simple, posture-based mechanism also suggests a means by which peak stresses

Table 2. Interspecific scaling of *EMA* as a function of body size for individual joints based on mean values for each species. The following number of individuals of each species were studied: mouse, $n = 2$; elephant shrew, $n = 2$; kangaroo rat, $n = 3$; chipmunk, $n = 2$; ground squirrel, $n = 3$; goat, $n = 3$; dog, $n = 2$; and horse, $n = 3$. Only data for the hindlimb joints of the kangaroo rat (a bipedal hopping rodent) were included in the analysis. Allometric equations, of the form $y = bx^a$, were calculated by least-squares regression of log-transformed data.

Joint	b	a (±95% CI)	SE
Forelimb ($n = 7$)			
Wrist	0.244	0.186 (±0.089)	0.034
Elbow	0.263	0.264 (±0.134)	0.052
Shoulder	0.160	0.266 (±0.086)	0.035
Overall*	0.233	0.246 (±0.087)	0.034
Hindlimb ($n = 8$)			
Ankle	0.275	0.169 (±0.046)	0.019
Knee	0.243	0.345 (±0.109)	0.045
Hip	0.215	0.301 (±0.116)	0.047
Overall*	0.256	0.271 (±0.079)	0.032

**EMA* at the metacarpophalangeal joint was not included in the interspecific comparisons as the data for the smallest species were considered unreliable.

in the muscle are maintained at a fairly constant level over a range of body size. With previously published values (*15*) for the scaling of muscle fiber length (proportional to $M^{0.23}$) and muscle mass (proportional to $M^{1.03}$) for extensor muscle groups in mammals, the scaling of muscle fiber cross-sectional area can be derived as, A_m is proportional to $M^{0.80}$ (A_m = muscle mass/fiber length). Because verebrate striated muscle exerts nearly a constant force in proportion to its fiber cross-sectional area (*16*), the scaling of A_m, though indicative of increased fiber pinnation to augment force generation (positive allometry), suggests a decreased ability of muscles to generate force relative to their size in larger animals. This decrease in force-generating ability however matches closely the observed decrease in force required to support the limb of larger animals, owing to increased *EMA* of their muscles as limb posture becomes more upright. Combining the results of muscle fiber area scaling, with the scaling of muscle force reported here, suggests that muscle stress scales nearly independent of body size (proportional to $M^{0.06}$), consistent with the uniform force generating ability of vertebrate striated muscle.

A size-dependent reduction in mass-specific muscle force, correlated with a relative decrease in muscle fiber length (*15*), indicates further that the mass-specific volume of muscle fibers activated to generate force during locomotion is similar in both large and small animals. As energy use during locomotion is principally determined by the breakdown of adenosine triphosphate (ATP) in skeletal muscles of the limbs and trunk, the forces that these muscles must exert is likely a key factor in determining the amount of ATP consumed. These observations are supported by data showing that the mass-specific energy expended by an animal during each stride is the same at the trot-gallop transition speeds of different sized mammals (*18*).

Although both locomotor specialization and phylogeny are important factors influencing the organization of muscular, tendinous, and bony elements in the skeleton of an animal (*19*), the fundamental requirement of these elements to provide effective mechanical support of the body must not be jeopardized. It would appear that when the skeletal support elements of related taxa share similar material properties, the form, organization, and function of these elements will be constrained to maintain similar levels of peak stress. Over much of their size range, mammals achieve similar stresses largely by changes in the overall organization of these elements in the limb, and only to a lesser extent by alterations in the shape and relative proportions of the elements. The extent to which a taxon can maintain a characteristic shape and patterning of limb movements over a range of body size, and the consequences of doing so, remains largely unknown. Whereas the data presented here are for constant speed locomotion, under natural conditions animals must perform over a much broader range of activity. It seems clear that large ungulate species (>200 kg), in part because of having a more upright posture, sacrifice maneuverability and range of locomotor performance for being large (*8, 9*). Because accidental loading events (falls, and so on) are those which produce the highest stresses, even if rare in occurrence, selection for a skeletal system that is strong enough to withstand accidental loading seems likely. Behaviorial modifications of large mammalian species to decrease the probability of such accidents, therefore, may be equally important in maintaining similar stresses, despite isometric scaling of the skeleton.

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10. For the larger species (>1 kg in body mass), a Kistler (model 9203) force plate (0.4 by 0.6 m) was used to resolve vertical and horizontal (fore-aft) forces acting on the limb when it was in contact with the force platform. High-speed light cinefilms (60 to 200 frames per second, depending on animal size and speed) of the animals were taken in lateral view and synchronized with the force recordings by a camera shutter pulse. Data were either entered directly into a microcomputer (analog/digital sampling at 1 kHz) or recorded on an FM tape recorder and played out to the computer for analysis at a later time. For the smaller species, a much smaller force plate (0.1 by 0.2 m) [N. C. Heglund, *J. Exp. Biol.* **93**, 333 (1981)] was used to record vertical and horizontal components of the ground reaction force. High-speed x-ray cinefilms (150 to 200 frames per second, with Siemens Tridoros G equipment) were taken to obtain accurate kinematic information for joint position. These data were sampled, entered into a microcomputer and analyzed as described above. Following experimental recordings, morphological data were obtained from radiographs or dissection of the animals' limbs. Mean muscle moment arms were determined from measurements over the full range of motion observed from the films for the joint.
11. Because, in most cases, more than one muscle acts about a joint, a weighted mean moment arm $\bar{r}$ for the muscle group was calculated with the assumption that the individual muscles exerted force in proportion to their fiber cross-sectional area (A_m, that is, individual muscles develop equal stress). Although this oversimplifies the manner in which motor units within a muscle group are recruited [R. E. Burke, in *Handbook of Physiology* (American Physiological Society, Bethesda, MD; distributed by Williams & Wilkins, Baltimore, 1981), vol. 2, pp. 345–422. It enables a solution to an otherwise

indeterminant problem. A muscle group's weighted mean mechanical advantage at a joint was calculated as $\bar{r} = r_1 \times F_1 + r_2 \times F_2 + \ldots + r_n \times F_n$, where $F_1 = (A_1/A_{tot})F_{tot}$, $F_2 = (A_2/A_{tot})F_{tot}$, and $A_{tot} = A_1 + A_2 + \ldots + A_n$. F_{tot} represents the total muscular force required to balance the joint moment exerted by the ground reaction force, A_{tot} is the total fiber cross-sectional area of the muscle group, and *n* is the number of muscles acting about the joint. In this analysis inertial effects of limb segment movement during the support phase are ignored; however, these forces are small compared to the ground reaction force during steady speed locomotion.

12. The coefficient of variation (*CV*) for changes in *EMA* during the middle third of the support period of the stride ranged from 0.06 to 0.74 for all joints in all species (overall mean *CV*, 0.31 ± 0.22; *n* = 56, eight limb joints in each of seven species). *EMA* was most consistent at the distal limb joints (0.15 ± 0.08, *n* = 28) compared to the proximal limb joints (0.46 ± 0.19, *n* = 28).
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14. Available data, though limited, indicate that under conditions of steady speed locomotion, maximal ground reaction forces acting on a limb generally are between two and four times an animal's body weight, irrespective of an animal's body size [T. A. McMahon, in *Scale Effects in Animal Locomotion*, T. J. Pedley, Ed. (Cambridge Univ. Press, Cambridge, 1977), pp. 143–151; G. A. Cavagna, N. C. Heglund, C. R. Taylor, *Am. J. Physiol.* **223**, 244 (1977)]. R. McN. Alexander *et al.* [*J. Zool. Lond.* **183**, 135 (1979)] have argued, based on relative limb support time (duty factor) that, within ungulates, ground reaction forces likely decrease with increased size. However, no measurements of ground reaction forces for a broad range of these species have been made.
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Scale Invariance in Food Web Properties

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The robustness of five common food web properties is examined by varying the resolution of the data through aggregation of trophic groupings. A surprising constancy in each of these properties is revealed as webs are collapsed down to approximately half their original size. This analysis of 60 invertebrate-dominated community food webs confirms the existence of all but one of these properties in such webs and addresses a common concern held by critics of food web theory that observed food web properties may be sensitive to trophic aggregation. The food web statistics (chain length; predator/prey ratio; fraction of top, intermediate, and bottom species; and rigid circuits) are scaling in the sense that they remain roughly invariant over a wide range of data resolution. As such, within present standards of reporting food web data, these statistics may be used to compare systems whose trophic data are resolved differently within a factor of 2.

OBSERVATIONS FROM LARGE COLLECTIONS of food webs extracted from the literature have produced a number of intriguing empirical generalizations about the structure of ecosystems (*1–16*). These simple patterns are regarded by some investigators (*4, 17, 18*) as law-like and fundamental to our understanding of ecosystem architecture. They include the following well-known properties: P1, food chains are typically short, normally consisting of five or fewer trophic levels (*1–3, 17, 19, 20*); P2, network connectance (the number of possible linkages as a fraction of all possible linkages in the web) declines predictably as species number increases, so that the product of species number and connectance (S·C) is roughly constant (*5–7, 18, 21, 22*); P3, the ratio of predator to prey species in a web is roughly constant, between 1 and 3, independent of total species number (*11, 23*); P4, the fraction of top predators (not preyed upon by any species in the web), basal species (pure autotrophs or detritus), and intermediate species is independent of total species number and, as such, is scale-invariant (*8, 9*); and P5, species trophic niches tend to be packed together closely, in that most if not all observed consumer overlap graphs (a food web diagram in which points represent consumer species and lines (not arrows) connect pairs of points to indicate when two consumers share one or more food resources in common) are rigid circuit graphs; that is, they are paved with triangles (*12–17*). Technically, a rigid circuit graph is one in which all circuitous paths through more than three points are shortened by a chord (*13*).

Each of these properties is based in part on an ever-expanding compendium of food webs collected from the literature that now includes more than 113 cases (*10, 12, 24, 25*). These include a wide variety of natural environments; 23 terrestrial, 32 freshwater, and 58 marine webs. Although the prospect of acquiring an understanding of ecosystems from such general properties is attractive, critics of food web theory have expressed concern over the quality of the data being used to derive them, specifically over the lack of uniformity exercised in choosing trophic categories (*4, 26–28*). For example, within certain webs of this collection one finds fish resolved to the species or ontogenetic level, whereas in other webs, studied by different investigators, they may be lumped together as a single category. Moreover, this lack of uniformity in aggregation and resolution exists even for taxonomic and trophic groupings within individual webs. These rather troubling concerns about the existing food web database have cast serious doubt on the validity of the hypothesized food web generalizations (*4, 21, 26–28*), although, to date, such criticisms have only been supported with anecdotal and hypothetical examples (*21*).

To evaluate these shortcomings in the existing database directly, as they affect the derived food web properties, would require that the original field investigators reassemble each web in a more comprehensive and uniform manner. The difficulty of this task for even one system is evidenced by the fact that there are no good examples of such comprehensive food web data published for large whole systems (*29*). As an alternative test, one can study how systematic lumping of trophic categories in existing data affects whether one observes the claimed food web properties. That is, are the above properties sensitive to the various levels of aggregation chosen or are they "scaling" in the sense that they remain relatively constant over a wide range of food-web data resolution (*30*)?

To answer this question, we have examined a newly compiled set of 60 inverte-

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