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Bakker's (1971) recent article in this journal, hypothesizing the presence of homeothermy in dinosaurs, has revived speculation on a subject of considerable paleontological and physiological interest: the evolution of homeothermy in the vertebrates. However, his article contains numerous factual errors, contradictions, and logical faults. We wish to summarize several objections to his arguments and conclusions.

Bakker fails to demonstrate a logical connection between fully erect posture and homeothermy. The essence of his argument is that since the only vertebrates now possessing a fully erect gait are homeothermic and since dinosaurs are hypothesized to have possessed an upright posture, dinosaurs must have been homeothermic. Such a statement is neither logically nor biologically sound. If there is a causal connection (implication) between these factors, what is its physiological basis? If no causal linkage can be demonstrated, then the two components of the conjunction must approximate full correlation for the argument to be compelling. We will examine the correlation between these factors.

Doubtless high thermal inertia was characteristic of the massive reptiles in the past, as it is today: Galapagos tortoises undergo very little thermal perturbation during the course of a day (Mackay, 1964). However, thermal stability is not a sufficient criterion for homeothermy (consider bathypelagic fishes). Using metabolic data from contemporary reptiles, Bartholomew and Tucker (1964) have calculated that an increase in bulk *per se* is insufficient to establish significant homeothermy within any dinosaur of reasonable size (Colbert, 1962; Van Valen, 1969). The essential feature of homeothermic organisms is their possession of an internal source of heat production which frees them from dependence on external thermal sources; this difference is emphasized by the terminology "ectothermy" and "endothermy" (Cowles, 1962). This internal source of heat is provided by a metabolic rate in mammals and birds which is much greater than in reptiles of a similar size at comparable body temperatures. This metabolic differential is seven-fold in 10 kg. mammals and lizards during rest (Templeton, 1970) and is much greater during activity. The central problem in the evolution of homeothermy is the explanation, both in selective and physiological terms, for this increased metabolism and the large energetic demands which it entails.

Bakker believes that the dinosaurs possessed high metabolic rates (p. 646), but his only evidence is their postulated erect posture. Only if the maintenance of an erect posture requires more energy than that required for a sprawling posture can a physiological connection be established between posture and homeothermy. Bakker believes this stance is less energetically expensive than the sprawling posture (p. 646); therefore, it must produce less, not more, metabolic heat. A less energetically expensive stance does not somehow provide more energy for thermoregulation: all bodily processes ultimately produce heat anyway. If dinosaurs did indeed have higher metabolic rates, these must be the result of some other metabolic process than muscular activity, and Bakker does not propose an alternative mechanism. The energetic demands of standing erect appear to be low in any event. The metabolic rate of sheep, cows, and humans is only 9% greater when standing than when lying down; no metabolic increment occurs in horses (Brody, 1945).

We may examine metabolic data from contemporary organisms to determine whether limb suspension and standard metabolic rate are indeed correlated phylogenetically. Modern lizards, according to Bakker (p. 640), show a gradation in limb length from short-limbed, slow-moving forms to longer-limbed active animals. Summaries of metabolic data for these animals (Dawson, 1967; Bennett and Dawson, 1971) fail to reveal any correlation between limb length and metabolic rate: at equal body temperatures, standard metabolic rate is solely a function of body size. Although aerobic scope (the differential between rates of oxygen consumption during rest and maximal activity) is high in *Varanus*, its standard metabolic rate is no higher than that of other lizards of the same size (Bennett, 1971, 1972). Alligators possess a semi-erect stance and have four-chambered hearts, diaphragms, and elaborate lungs, but their metabolic rates are indistinguishable from those of other reptiles (Huggins et al., 1971). Metabolic rates have not been determined for another reptilian group with a semi-erect posture, the chameleons, but it is doubtful that these sluggish animals possess singular metabolic powers. Thus, in spite of the variety of activity patterns and limb forms in modern reptiles, metabolic rate is conservative and shows no trend with activity or posture.

The implications of the low metabolic rates of primitive mammals are misrepresented in Bakker's examination (p. 655). Low body temperatures and metabolic rates in these animals are not necessarily primitive characters: this approach has been criticized elsewhere (Schmidt-Nielsen et al., 1966). Low metabolism can equally well be correlated with other factors, such as low environmental productivity or feeding habits. Monotremes and marsupials have low metabolic rates because of their low body temperatures. At body temperatures equal to those of eutherians, the metabolic rates of these animals are calculated to be equivalent to those of placentals (Schmidt-Nielsen et al., 1966; Dawson and Hulbert, 1970). These facts suggest that the biochemical adjustment to the metabolic increment demanded by homeothermy were made very early, and that the diversity apparent in modern mammals involves subsequent evolution away from that primitive pattern, either by alteration of body temperature or reduction of enzymatic activity.

Perhaps the most difficult evidence to reconcile concerning the presumptive connection between homeothermy and limb suspension is cited by Bakker himself. He states that "the similarity of echidna thermoregulation to that of therians suggests that homothermy was already well-developed in the first mammals of the Triassic" (p. 655) and that "the shift to Semierect and Fully Erect posture had not occurred in most mammals by the Late Jurassic" (p. 654). What is the supposed causal connection between limb suspension, metabolism, and homeothermy if mammals with a sprawling gait were homeothermic and no association between these factors can be demonstrated in contemporary organisms?

Bakker asserts that homeothermy in mammals was an adaptation to nocturnality (p. 655) and implies that the reptilian ancestors of this line had a low thermal preferendum. Although the habits of these reptiles are unknown, it is doubtful that all the cotylosaur and therapsid ancestors of the mammals remained swamp-dwelling forms with a low body temperature, since they were among the largest and most active terrestrial forms of their time. Homeothermy more likely evolved in heliothermic forms, which would have maintained higher levels of activity. The sensory evidence which Bakker cites for nocturnality in Jurassic mammals (p. 656) is irrelevant since their ancestors were presumably homeothermic in the Triassic (p. 665).

To further complicate matters, even Bakker's biomechanical analysis is questionable, since it is based on lack of understanding of mammalian locomotion. He assumes that fully erect posture is characteristic of the majority of mammals and birds (p. 637). As he describes the fully erect posture, this statement is simply not true. The posture which he describes is characteristic of

some large forms such as elephants, humans, *Diprotodon*, ground sloths, and some bears. Typical mammalian and avian limb postures differ from those of reptiles principally in the medial rotation of the elbow (in mammals) and knee so that the limb elements tend to be flexed in a parasagittal rather than a transverse plane. Medial rotation is *not* necessarily correlated with a straightening of the joints to produce the columnar stance. Neither complete medial rotation nor columnar stance are characteristic of the great majority of mammals (see Jenkins, 1971). Mammals that are swift and enduring runners are characterized by the retention of the flexed elbow and knee; this flexion is especially obvious in forms such as horses.

The support of an animal at rest is largely a function of the skeleton. Even when the limbs are flexed, ligamentary, tendonal, and joint surface adaptations facilitate the fixation of the limb by passive (non-muscular) mechanisms. It is the presence of structures of this nature which allow horses to sleep while standing and to expend little metabolic energy in support. It is important to note that the problem of skeletal and ligamentary resistance to the force of gravity is a passive structural property and that no expenditure of muscular energy will improve or detract from the ability of bone to resist compression or shear in a static system. A stance that is mechanically inefficient but structurally adequate to resist the shear and compressional effects of gravity in a static system does not necessarily require more muscular energy than a mechanically optimal structure. The sprawling stance of modern reptiles, although structurally weak, need not involve more active muscular stabilization than the typical stance of modern mammals. In both mammals and reptiles, there is at least one major flexed joint in each limb. Passive fixation of these joints would not require the expenditure of muscular energy in either case.

The sprawling posture is non-adaptive in large vertebrates, independent of the energetic cost of maintaining flexed joints by muscular means. With increasing body size, the ability of the skeleton to resist shear and compression increases as the two-thirds power of body mass; that is, the skeleton of larger animals is relatively weaker than that of smaller ones. In an animal standing in a sprawling posture, even with the joints passively fixed, a large shear component acts on the non-vertical elements of the skeleton. Since the ability of bone to resist shear is lower than its ability to resist compression (Evans, 1957), adaptations reducing shear, even at the expense of increased compression, are to be expected in large animals. Such an adaptation is the repositioning of the limbs into a columnar stance beneath the body. Even if the animal is not particularly active, one would predict the evolu-

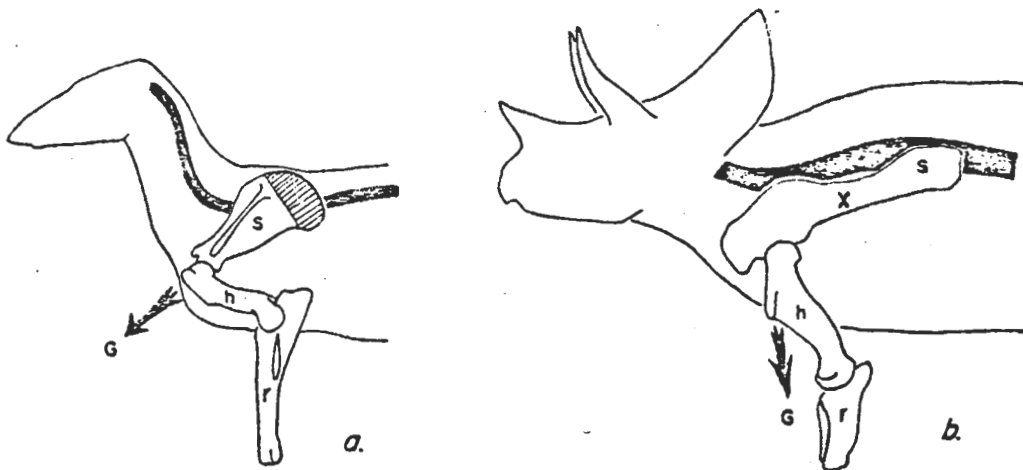


FIG. 1. Diagram of scapula(s), humerus(s), and radius -ulna(r) in an animal standing at rest. A. a cursorial mammal, B. (after Bakker) *Triceratops*. Note that the mammalian humerus is flexed in relation to the scapula when the animal stands at rest. Protraction results in the extension of the humerus on the scapula and in the rotation of the scapula on the body wall. In the dinosaur the humerus appears to be incapable of further extension in relation to the scapula. Further protraction of the forelimb can occur only through flexion of the radius -ulna on the humerus or rotation of the scapula on the body wall. The arrow, G, indicates the direction in which the glenoid cavity is facing. Note that it faces *anteriorly* in the mammal.

tion of columnar limbs in very large forms, since these physical considerations apply even to animals at rest. These factors are certainly responsible for the columnar stance of elephants and apparently also explain that of dinosaurs.

Bakker asserts that dinosaurs were rapidly moving forms, capable of attaining high speeds (p. 648). The possession of elongate limbs by these animals is not *de facto* evidence of the capacity for rapid locomotion. As Smith (1968) pointed out, absolute speed does not increase with body size due to the complex non-linear relation between mass, velocity, and endurance. Additionally, the ability to displace the center of gravity vertically, a factor involved in rapid gaits such as leaping or galloping, is severely curtailed by large size. Bakker's arguments that large dinosaurs could gallop rest upon analogies of joint angulations in mammals. The analogy between the dynamic functioning of the mammalian and dinosaur shoulders is false because the freedom permitted during protraction in the former is not possible in the latter. In running mammals, the scapula is protracted through approximately sixty degrees. The remainder of the forelimb protraction is due to the extension of the humerus on the scapula (Dalzell, 1970). In contrast to mammals, the position of the dinosaur scapula in relation to the vertical humerus is also the maximally protracted position for the scapulo-humeral complex (see Fig. 1). Further protraction

of the glenoid would result in anatomically impossible positions for either the coracoid or the vertebral border of the scapula or both (see Fig. 2). Further reach in a vertebrate with a fully protracted scapula can only be accomplished by the flexion of the forelimb at the elbow. For a large, heavy animal such as a dinosaur, this would create high shear forces in the elbow. While such forces may not be limiting at slow gaits, they increase in a non-linear fashion with increased acceleration, and it is doubtful that high velocities could be attained by such an anatomical system. Structural properties of muscle and bone are not linear in relation to body size: small animals are rarely stressed by mechanical limitation, but large animals almost certainly are. Bakker's analysis does not take into account the biomechanical constraints on movement in large animals.

Dinosaurs may well have been homeothermic, but Bakker fails to construct a convincing case. This failure rests on an inadequate analysis of the biomechanics of fossil and contemporary vertebrates and on the inability to establish a physiological connection between homeothermy, metabolism, and posture. We urge caution in the acceptance of his conclusions. A proper analysis of this problem should include a rigorous examination of the physiology of thermoregulation and locomotion in contemporary vertebrates. It should also be based on considerations of the

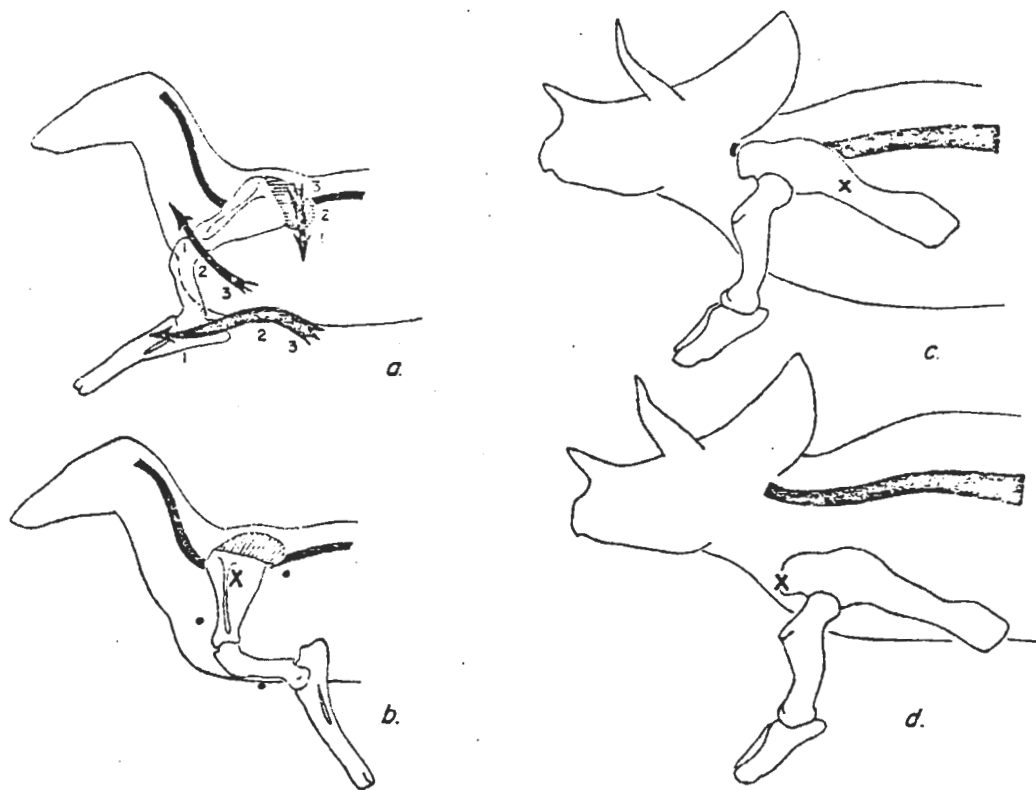


FIG. 2. A. Position of the forelimb in a cursorial mammal during protraction. The arrows indicate the paths of the limb segments. X is the center of rotation of the forelimb on the body wall. B. The forelimb in a cursorial mammal in the retracted position. The dots indicate the relative position of the forelimb when the animal is standing at rest. Hypothetical positions of scapula in *Triceratops* allowing protraction of humerus in parasagittal plane anterior to the position of the humerus in Figure 1. C. Protracted forelimb in *Triceratops*, assuming that rotation occurs, as in mammals, around a point near the vertebral end of the blade of the scapula. D. Protracted forelimb in *Triceratops*, assuming that the coracoid is anchored to a midline element. Neither C nor D is anatomically possible. In C the medially curving edge of the coracoid would interfere with the trachea and carotid canal. In D the scapular blade is carried too far ventrally on the animal.

dynamics, as well as the statics, of the locomotory system. The latter should include an analysis of all the skeletal elements and not just selected ones. It is especially important to use direct mechanical models of the organisms under study rather than relying on argument by analogy from other organisms.

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Our argument (Bennett and Dalzell, 1973) with Bakker has never concerned the possession of endothermy by dinosaurs. It rather deals with the logical methods employed on biomechanical data in his previous paper (Bakker, 1971). This original paper postulated endothermy in dinosaurs on the basis of convoluted arguments involving postural adjustments, metabolism, and homeothermy. We pointed out the logical difficulties with these assertions, principally concerning the inability to correlate these factors. Bakker (1974) now maintains his original argument only related erect posture to high continuous levels of activity necessary for support of the high energy budgets associated with endothermy and that no other metabolic associations with posture were intended. I can only conclude that if this assertion is the sole basis of the original article, then Bakker's previous paper was without major substance. What sort of necessary connection is postulated between erect

posture and high levels of food consumption? Are there not other possible selective pressures for altered limb support? Is not one of these support of a massive body? How is this postural adjustment supposed to prove greater activity or food consumption? I submit that until direct and causal connections can be demonstrated between these factors that conclusions based on these tenuous assumptions be disallowed.

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