

A new approach to evaluate the cursorial ability of the giant theropod *Giganotosaurus carolinii*

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Blanco, R.E. & Mazzetta, G.V. 2001. A new approach to evaluate the cursorial ability of the giant theropod *Giganotosaurus carolinii*. — *Acta Palaeontologica Polonica* **46**, 2, 193–202.

The cursorial capability of the South American giant theropod *Giganotosaurus carolinii* should have been quite limited taking into account the strength indicator of its femur (approximately 7 GPa^{-1}) as well as the risk of experiencing grave or even lethal injuries involved in the falling of this multitonne animal on a run. However, even at low speeds a fall would have caused serious injuries. Thus, in accordance to the approach developed in this study, the maximum speed of *Giganotosaurus* should be not that which will implicate corporal lesions with minimum probability of lethality. Instead, its maximum speed should be that which would permit the recovery of body equilibrium as each step is taken. Taking into consideration this approach, an indicator of stability is defined for bipedal, cursorial animals. This indicator is determined by the relationship between the time available for the movement of hip joint during the retraction of a hindlimb and the time needed to move the opposite hindlimb by an angle (in function of the speed) of sufficient magnitude as to facilitate the recovery of body equilibrium. This indicator was used to estimate the maximum speed of locomotion of *Giganotosaurus* (about 14 m s^{-1}) at which, from a kinematic point of view, the danger of falling does not exist.

Key words: Dinosauria, Theropoda, *Giganotosaurus*, cursorial gait, Cretaceous, South America.

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Introduction

Different approaches have been used to assess the locomotor capabilities of dinosaurs (see for example, Alexander 1976, 1985; Coombs 1978; Bakker 1986, 1987; Farlow *et al.* 1995) and consequently several attempts have been made to estimate the maximum speed attained by giant bipedal dinosaurs (Thulborn 1981, 1982; Bakker 1986; Farlow

et al. 1995). The South American mid-Cretaceous (Albian–Cenomanian) carnivorous dinosaur *Giganotosaurus carolinii* (Coria & Salgado 1995) is one of the largest known theropods and, with a length of more than 12 metres, might have been even larger than the notorious Late Cretaceous *Tyrannosaurus rex*.

Up to the present, biomechanical studies of the locomotion of South American dinosaurs are very scarce (Alonso & Marquillas 1986; Mazzetta 1999; Mazzetta *et al.* 2000; Mazzetta & Blanco this volume). In this study, we present a new approach to estimate the locomotor ability of bipedal dinosaurs, and provide an estimate of the speed of *Giganotosaurus* for the first time.

Material and methods

Farlow *et al.* (1995) pointed out that the risk of falling limits the maximum speed of a cursorial biped. On the basis of this argument, they hypothesise that the cursorial capacity of *Tyrannosaurus rex* would have been limited, moving at speeds which did not entail a great risk of falling. This gigantic and massive theropod did not have forelimbs sufficiently well developed to impede or cushion a fall, so if a fall did occur, it might have caused serious or lethal injury. However, the argument of Farlow *et al.* (1995) does not explain the behaviour of certain extant species that choose to move at high speeds, even at the risk of suffering significant or lethal injuries (Alexander 1996). For example, the gibbon (*Hylobates syndactylus*) moves rapidly between the high branches of trees using brachiation, and the ostrich (*Struthio camelus*), the largest living cursorial biped, achieves considerable running speeds (Alexander *et al.* 1979; Alexander 1996) in spite of lacking forelimbs sufficiently adequate to impede or cushion a fall. It should be mentioned that the possibility of injury is size related – as bigger animals have relatively less surface area with respect to their mass, on falling each unit of surface area will have to cushion a proportionally greater amount of the animals mass. This is why mice do not hurt themselves if they are dropped from around 4 metres, but a person will be injured or killed. This problem is out of the scope of this paper, and we will focus on whether the animal will fall or not, assuming that falling will represent a real danger.

In this predictive kinematic model of the cursorial capacity of bipedal animals we assert that the principle limitation for cursorial capacity is the maximum speed at which the biped is capable of recovering body equilibrium. Accordingly, the different gaits utilised by a cursorial biped may be understood as activities used to impede falling or to maintain equilibrium. Independent of its speed of locomotion, as a cursorial biped moves a limb to take a step, it loses its equilibrium momentarily until it is restored by the excursion (forward movement) of the other limb. When a cursorial biped moves at high speeds over the supporting limb, less time is available for the animal to move the other limb forward in order to regain equilibrium. To estimate the maximum speed of locomotion of a cursorial biped, an indicator of stability (*I.S.*) is constructed and is defined by the following equation:

$$I.S. = \frac{t_A}{t_N} \quad (1)$$

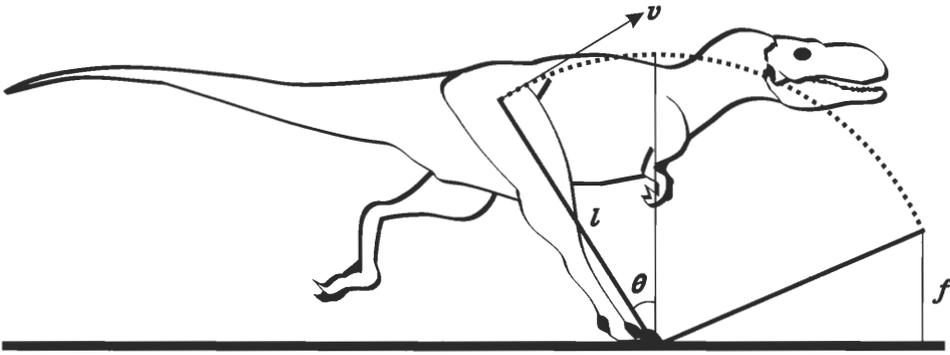


Fig. 1. Rotation of the coxofemoral joint in a biped. The joint rotates in a parasagittal plane with radius l around an axis at the foot contact point. It begins when one of the feet rests on the ground, and the corresponding limb carries out a circular movement with constant tangential speed v . The femur length (f) is the minimum height of the coxofemoral joint above the ground that is necessary to allow the forward movement of that limb in the next step.

where t_A is the time available for the movement of the hip joint, between the instant a limb is at rest on the ground and the instant the hip joint reaches its minimum height with respect to the ground, and t_N is the time necessary to move the non-supporting limb a certain angle (as a function of the speed) sufficient to make possible the recovery of equilibrium.

Some assumptions were made in order to obtain a rough estimation of t_A and t_N . In a biped, moving at any speed, the progression (in the parasagittal plane) of the coxofemoral joint could be considered as a rotation movement around an axis situated at the point of contact of the foot with the ground. Such a rotation begins the instant one of the feet rests on the ground (Fig. 1). This movement has a radius of rotation of length l (where l is the limb length) and carries out a circular movement with constant tangential speed v . If the acceleration of this circular movement is greater than the gravity acceleration as, for instance, in fast running, this movement is dynamically impossible, but in any case it provides a good kinematical estimation of t_A during the ground phase of the run. More realistic assumptions for fast running, like the one considering the hip joint moving in a straight line, give nearly the same results. The length of the femur (f) is considered as the minimum height, with respect to the ground, of the coxofemoral joint during any stage in the locomotory cycle that is necessary to allow the forward movement of that limb in the next step. In other words, the maximum extent possible for the circular movement of the coxofemoral joint that permits the continuation of the animal progression (avoiding a fall) is produced when the coxofemoral joint attains a height equivalent to the length of the femur. If, during the progression of the animal, the coxofemoral joint dropped to a height less than the length of the femur, there would not be sufficient distance between the hip and the ground to permit the interposition of the hindlimb in order to achieve the recovery of body equilibrium. Nonetheless, such a theoretical situation was considered in order to find out the top speed given for the limiting case.

In a walking gait, t_A is the duration of the aforementioned circular movement of the coxofemoral joint. In a running gait, it becomes necessary to consider, in addition, a

suspended stage. In this situation a fraction of the available time (t_A) becomes the duration of the suspended phase. If we consider that, for a running speed, the time involved in the suspended phase is equal to the corresponding time in the supported phase (as observed in films of modern cursorial bipeds running near to the top speed), t_A is given by the following expression:

$$t_A = 2 \frac{l}{v} \left[\arccos \left(\frac{f}{l} \right) + \theta \right] \quad (2)$$

where θ is the angle (expressed in radians) between the vertical and the line defined by the point of contact of the foot and the coxofemoral joint (as shown in Fig. 1). In the previous expression, the speed v is inversely proportional to t_A : that is to say that when the speed of the animal increases, less time is available for the retraction of the supporting limb and thus for the recovery of body equilibrium.

It is assumed that the excursion of the non-supporting limb has a uniform angular acceleration; thus the time necessary to complete the excursion is obtained by the following expression:

$$t_N = \sqrt{\frac{2 \left[\arccos \left(\frac{f}{l} \right) + \theta \right]}{\alpha}} \quad (3)$$

where α is the angular acceleration of the suspended limb of the animal, which in turn is given by the following expression:

$$\alpha = \frac{\tau}{I} \quad (4)$$

This angular acceleration depends on the sum of the moments (τ) produced about the coxofemoral joint by the muscles utilised in the excursion of the limb. Each of these muscles exerts a force F , whose line of action is situated perpendicular to a distance x (known as the lever arm) with respect to the coxofemoral joint; each moment Fx contributes to the forward rotation of the thigh around this joint. The angular acceleration also depends on the moment of inertia (I) of the limb, which is given by $\Sigma(mr^2)$, where m is the mass of the limb and r is the radius of rotation of every segment of the limb (for a more detailed explanation of the calculation of the moment of inertia of body parts, see Alexander 1983: p. 28). The moment of inertia varies with the distribution of the mass in the limb (Hildebrand 1985). It is low when the weight is more proximal and high when the weight is more distal. In this way, the moment of inertia is reduced when the limb mass is concentrated proximally to the rest of the body.

This situation is found in the limbs of cursorial vertebrates. The masses of the most important appendicular muscles are concentrated very close to the body and the actions of these muscles are transmitted by tendons to the distal parts of the limbs. This arrangement has been interpreted as a strategy to reduce the moment of inertia of the limbs and thus the energetic costs of locomotion (McGowan 1991). As previously mentioned, we made the assumption that angular acceleration is constant during the movement of the hip joint and that hence there is no deceleration. The latter could be achieved at the expense of the ground reaction force during the footfall. In fact, force moments and moments of inertia change their values during limb movement, but the

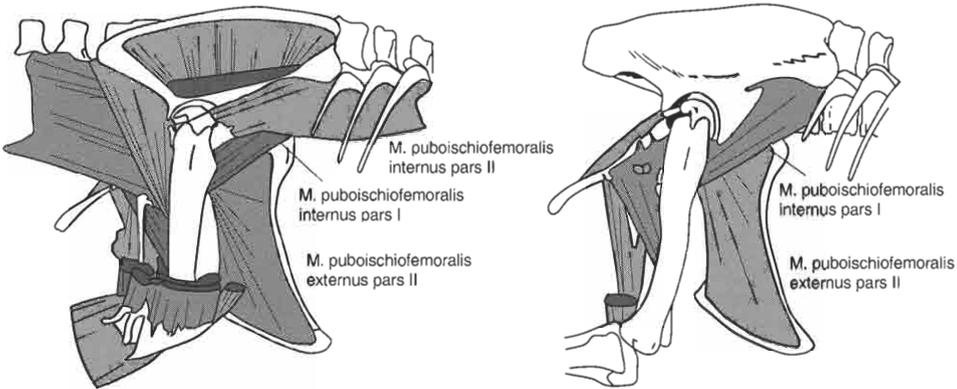


Fig. 2. Restoration of the pelvic musculature of a theropod. Muscles involved in the excursion of the limb are detailed (m. puboischiofemoralis externus, pars I is hidden beneath the internal surface of the pubis). M. puboischiofemoralis internus is considered the principal femoral protractor (modified from Romer 1923).

effects of these changes are negligible in comparison with the ones based on other unavoidable sources of uncertainty (mainly the uncertainties derived from the muscular reconstruction of extinct species), and consequently they were not considered in the model.

In this kinematic model, the moment of inertia is taken (for the calculation of angular acceleration) as the average value between the moment of inertia corresponding to the total flexion of the limb at the level of the knee (0°) and the limb extended 90° at the same level.

In the proposed kinematic model, when t_A is less than t_N , a cursorial biped would be moving at a speed so great that there would not be sufficient time to move the non-supporting limb forward in order to recover body equilibrium, and the biped would fall. Therefore, an indicator of stability equal to one (when $t_A = t_N$) corresponds to the maximum speed that a cursorial biped is capable of attaining.

This kinematic model was used to estimate the maximum speeds of living cursorial bipeds (human and ostrich) and of the giant theropod *Giganotosaurus carolinii*. For the dinosaur, a restoration was made of the musculature responsible for the limb excursion based on studies of the pelvic musculature of theropod dinosaurs developed by Gregory & Camp (1918), Romer (1923), and Tarsitano (1983). It is assumed that the muscles involved in the limb protraction were parallel-fibred and exerted a tension (force per unit area of transverse section) σ of $1 \times 10^5 \text{ N m}^{-2}$, equivalent to that achieved by the skeletal muscles of living vertebrates at their maximum power (for the value of σ , see Weis-Fogh & Alexander 1977). In this way, the force F produced by each one of these muscles may be calculated by the equation $F = \sigma A$, where A is the estimated area of each muscle's transverse section.

Fig. 2 shows the restoration of the pelvic musculature of a theropod, in which the muscles involved in the excursion of the limb are detailed. The muscles involved in the protraction of the femur are (in accordance with the nomenclature of the muscles of the pelvic region used by Romer 1923) the m. puboischiofemoralis internus, parts I and II (designated here in as p.i.f.i. I and p.i.f.i. II) and the m. puboischiofemoralis externus,

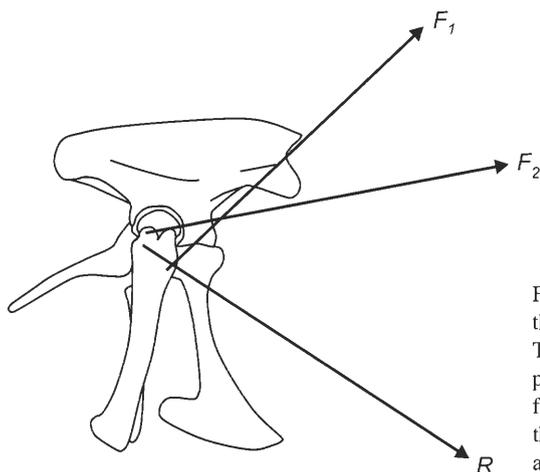


Fig. 3. Lines of action of the forces produced by the muscles involved in the limb protraction. The forces F_1 and F_2 are exerted by the muscles p.i.f.i. I and p.i.f.i. II, respectively, while the force R is the resultant of the forces exerted by the muscles p.i.f.e. I and p.i.f.e. II (see text for abbreviations).

parts I and II (from now on, p.i.f.e. I and p.i.f.e. II). Of these, the p.i.f.i. is considered the principal femoral protractor (Tarsitano 1983).

The p.i.f.i. I originates from the first sacral vertebrae and from the corresponding internal surface of the ilium, and it inserts on the proximal portion of femur, over the anterior surface of the fourth trochanter. The p.i.f.i. II originates from the internal surface of the transverse process of the lumbar vertebrae (the last five presacral vertebrae) and it inserts on the lateral surface of the femur, close to the greater trochanter. The p.i.f.e. I originates from the internal surface of the pubis, emerging (unlike the p.i.f.i.) from below the m. ambiens, where it joins the p.i.f.e. II (of which it is a derivative) and it inserts posteriorly (together with the p.i.f.e. II) on the proximal part of the femur in its medial surface close to the fourth trochanter. In its turn, the p.i.f.e. II originates from the external surface of the pubis. Fig. 3 details the lines of action of the forces produced by the aforementioned limb muscles. The insertion point is the point of application and the corresponding longitudinal axis of the muscle is its direction.

The moments of inertia of the limb of the bipedal dinosaurs studied were calculated by first estimating its mass by volumetric approximation, assuming a density of 1060 kg m^{-3} for the muscle (as observed for the striated muscle of mammals by Méndez & Keys 1960) and of 2000 kg m^{-3} for the bones (see Spector 1956).

The model presented here relies upon several assumptions. Nonetheless, it takes into account the influence of maximum speed on many of the anatomical adaptations considered characteristic of cursorial animals (see Hildebrand 1985). Accordingly, the length of the hindlimb, the relative femur length, the mass distribution in the hindlimb (moment of inertia), the muscle mass involved in the movement of the hindlimb, and the maximum angle of excursion of the hindlimb were the set of anatomical features considered in the formulation of the indicator of stability. These arguments suggest that this approach is quite reliable for comparisons of maximum speeds among different bipedal species, but that it is not so useful in estimating absolute values of maximum speed. The model was also applied to extant bipeds (*Struthio camelus* and *Homo sapiens*) in order to assess its consistency.

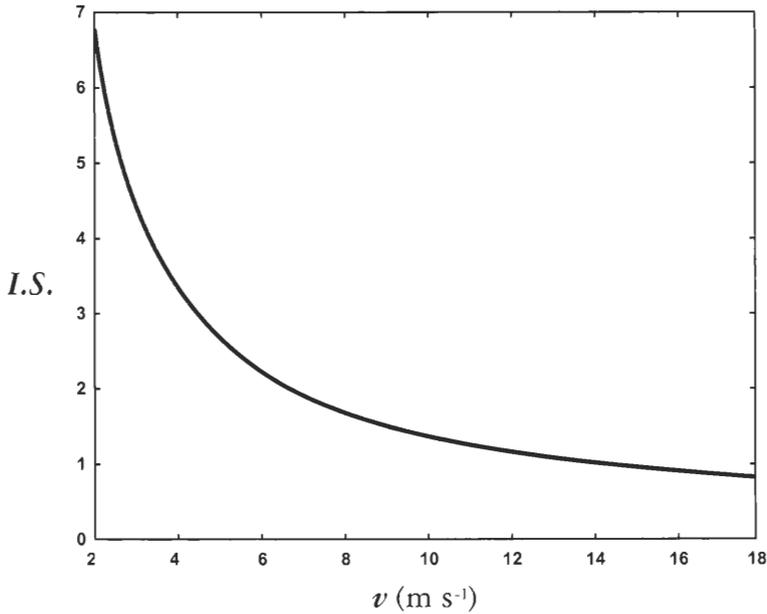


Fig. 4. Graph of the indicator of stability ($I.S.$) as a function of speed (v) for the Gondwanan theropod *Giganotosaurus carolinii*. See text for more explanations.

Results

Fig. 4 shows the graph of the indicator of stability ($I.S.$) as a function of speed (v) for the Gondwanan theropod *Giganotosaurus carolinii*. As expected, the stability of this bipedal tetrapod diminished with increasing speed of locomotion. As mentioned above, according to the proposed kinematic model, the maximum speed of a cursorial biped would be that when the indicator of stability is equal to one. Table 1 shows maximum speeds for *Giganotosaurus carolinii*, and for the two largest extant cursorial bipeds, the ostrich (*Struthio camelus*) and the human (*Homo sapiens*), estimated by means of the model and, for the extant species, observed maximum speeds. As shown, the estimated speeds for extant bipeds are similar to their observed maximum speeds. An Olympic athlete can easily sprint 100 m in 10 seconds, therefore averaging a speed of 10 m s^{-1} , with a peak speed of approximately 12 m s^{-1} (Alexander 1992), while an adult human without previous athletic training is capable of a maximum speed of close to 8 m s^{-1} . The ostrich was observed to achieve a maximum speed of 16 m s^{-1} (Alexander 1996).

The estimated maximum speed for *Giganotosaurus* would have permitted it to run at least as fast as small theropods, as judged from the estimated maximum speed of small theropods from their footprints. Farlow (1981) estimated that a relatively small theropod (with a hip height of about 1.4 m) from a dinosaur tracksite in Texas moved at 12.1 m s^{-1} , until now the greatest speed recorded for a dinosaur. The above interpretation is not compatible with the opinion of Colinvaux (1978), who suggests that large theropods were not fast-moving active predators but slow moving scavengers. How-

Table 1. Maximum speeds of cursorial tetrapods estimated from the proposed kinematic model. The maximum running speed of *Struthio camelus* was taken from Alexander (1996). Body mass of *Giganotosaurus carolinii* was taken from Mazzetta (1999).

Taxon	Body mass (kg)	Maximum speed (m s ⁻¹)	
		observed	estimated
<i>Giganotosaurus</i>	9 000	–	14
<i>Struthio</i>	120	16	18
<i>Homo</i>	70	8	9

ever, the fact that it exhibits a considerable cursorial capacity would not disqualify this gigantic theropod from scavenging occasionally; in fact, all modern carnivores, no matter how efficient they are as predators, also eat carrion.

Discussion

An analysis of the limb bone strength indicator in *Giganotosaurus* appeared to show that this giant bipedal carnivore was relatively slow moving. The strength indicator of its femur (approximately 7 GPa⁻¹, according to an estimate provided by Mazzetta 1999) is considerably lower than the corresponding value for the ostrich (44 GPa⁻¹, as calculated by Alexander 1985).

Padian & Olsen (1989) concluded that, overall, the locomotory movements of non-avian theropods were more similar to extant birds (like ratites and galliformes) than to crocodiles or other living reptiles. However, non-avian theropods and birds did not use similar locomotory movements. Even though they use similar limb postures, there are differences between birds and non-avian theropods in limb orientation, kinematics and muscular mechanisms of movement of the hindlimb segments (Gatesy 1990).

The femur of birds is oriented almost horizontally during running, which increases the moments of flexion exerted upon it in comparison with the femora of other tetrapods. Thus the high value observed for the strength indicator of the femur of the ostrich may not be appropriate for comparison with the condition in other bipedal tetrapods. The femur of the ostrich would be expected to be relatively stronger than the femur of a comparable-sized theropod because of this difference in orientation.

In birds, the centre of mass is localised far forward of the hip joint. Thus birds need to maintain the femur relatively horizontally in order to place the foot below the centre of mass and so retain body equilibrium. This restriction excludes femoral retraction by the *caudi-femoralis longus* muscle as the main component to retract hindlimb, as observed in crocodiles and modern reptiles, and presumably also the condition in dinosaurs. Instead, birds primarily use the flexion of the knee to move the foot symmetrically under the centre of mass.

Unlike the condition in birds, the tail of non-avian theropods constitutes a substantial proportion of the total body weight, and thus the centre of mass is localised close to the hip joint (Alexander 1985). Consequently, the majority of non-avian theropods were not subject to the restrictions in orientation of the femur observed in living birds

where the tail has been lost. The horizontal femoral orientation and the flexion of the knee were not required in order to maintain the feet below the centre of mass, and consequently the entire locomotory limb would have been able to move under the acetabulum without any loss of balance (Gatesy 1990). According to this interpretation, the majority of the non-avian theropods did not need to use an avian pattern of movements of the limbs during the locomotion because the body was counterbalanced like a see-saw.

The locomotory pattern proposed for non-avian theropods implies that the stresses exerted on the femur of the theropods would not have been similar to those produced in the femur of the ostrich. Furthermore, as pointed out by Alexander (1985), the relative lengths of the appendicular bones of the theropod dinosaurs are different from those of the ostrich and from the corresponding bones of other extant tetrapods. Therefore, comparisons based on strength indicators of bones, that have been used to infer the cursorial capacities of *Giganotosaurus carolinii* with respect to those observed in the ostrich or in the human are of limited value.

Bakker (1986) and Paul (1988) argue, in contrary to more orthodox opinions (e.g., Coombs 1978), that the cursorial capacity of giant theropods like *Tyrannosaurus* was equivalent to that of much smaller theropods. Our estimation of the speed of *Giganotosaurus*, is in agreement with this opinion.

This kinematic model proves more suitable for the study of the locomotory capabilities of bipedal dinosaurs than the approach proposed by Alexander (1985), because the former does not presuppose a comparison with living bipeds. Moreover, the predictive capacity of the model used here was corroborated when applied to living bipeds.

Additionally, the best estimations of running velocity from theropod tracks made by Farlow (1981), if correct, suggest that the estimation of maximum speed obtained for *Giganotosaurus carolinii* by means of the kinematic model is a reasonable one.

Acknowledgements

The authors wish to express their gratitude to Paul M. Barrett for his useful comments on a draft of this paper, to Jimena Ballesteros for the drawings, and to Jessamyn S. Markley for most of its English translation. This research was supported in part by a grant from PEDECIBA to G.V. Mazzetta.

References

- Alexander, R. McN. 1976. Estimates of speeds of dinosaurs. — *Nature* **261**, 129–130.
- Alexander, R. McN. 1983. *Animal Mechanics* (2nd. ed.). 301 pp. Blackwell Scientific Publications, Oxford.
- Alexander, R. McN. 1985. Mechanics of posture and gait of some large dinosaurs. — *Zoological Journal of the Linnean Society* **83**, 1–25.
- Alexander, R. McN. 1992. *Exploring Biomechanics: Animals in Motion*. 247 pp. Scientific American Library, New York.
- Alexander, R. McN. 1996. *Tyrannosaurus* on the run. — *Nature* **379**, 121.
- Alexander, R. McN., Maloiy, G.M.O., Njau, R., & Jayes, A.S. 1979. Mechanics of running of the ostrich (*Struthio camelus*). — *Journal of Zoology, London* **187**, 169–178.
- Alonso, R.N. & Marquillas, R.A. 1986. Nueva localidad con huellas de dinosaurios y primer hallazgo de huellas de aves en la Formación Yacoraite (Maastrichtiano) del norte argentino. — *Actas del IV Congreso Argentino de Paleontología y Bioestratigrafía* **2**, 33–41.

- Bakker, R.T. 1986. *The Dinosaur Heresies: New Theories Unlocking the Mystery of the Dinosaurs and their Extinction*. 481 pp. William Morrow and Company, New York.
- Bakker, R.T. 1987. The return of the dancing dinosaurs. In: S.J. Czerkas & E.C. Olsen (eds.), *Dinosaurs Past and Present, Vol. 1*, 38–69. Natural History Museum of Los Angeles County, Los Angeles.
- Colinvaux, P. 1978. *Why Big Fierce Animals Are Rare: An Ecologists's Perspective*. 224 pp. Princeton University Press, Princeton.
- Coombs, W.P. Jr. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. — *Quarterly Review of Biology* **53**, 393–418.
- Coria, R.A. & Salgado, L. 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. — *Nature* **377**, 224–226.
- Farlow, J.O. 1981. Estimates of dinosaur speeds from a new trackway site in Texas. — *Nature* **294**, 747–748.
- Farlow, J.O., Smith, M.B., & Robinson, J.M. 1995. Body mass, bone 'strength indicator', and cursorial potential of *Tyrannosaurus rex*. — *Journal of Vertebrate Paleontology* **15**, 713–725.
- Gatesy, S.M. 1990. Caudofemoral musculature and the evolution of theropod locomotion. — *Paleobiology* **16**, 170–186.
- Gregory, W.K. & Camp, C.L. 1918. Studies in comparative myology and osteology. No. III. — *Bulletin of the American Museum of Natural History* **38**, 447–563.
- Hildebrand, M. 1985. Walking and running. In: M. Hildebrand, D.M. Bramble, K.F. Liem, & D.B. Wake (eds.), *Functional Vertebrate Morphology*, 38–57. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- Mazzetta, G.V. 1999. *Mecánica locomotora de dinosaurios saurisquios del Cretácico sudamericano*. 76 pp. M.Sc. thesis (unpublished). Facultad de Ciencias, Universidad de la República, Montevideo.
- Mazzetta, G.V. & Blanco, E.R. 2001. Speeds of dinosaurs from the Albian–Cenomanian of Patagonia and sauropod stance and gait. — *Acta Palaeontologica Polonica* **46**, 235–246.
- Mazzetta, G. V., Fariña, R. A., & Vizcaíno, S. F. 2000. On the palaeobiology of the South American horned theropod *Carnotaurus sastrei* Bonaparte. In: B. Pérez-Moreno, T.R. Holtz Jr., J.L. Sanz, & J.J. Moratalla (eds.), *Aspects of Theropod Paleobiology, Special Volume — Gaia* **15**, 185–192. Lisbon.
- McGowan, C. 1991. *Dinosaurs, Spitfires, and Sea Dragons*. 365 pp. Harvard University Press, Cambridge, Massachusetts.
- Méndez, J. & Keys, A. 1960. Density and composition of mammalian muscle. — *Metabolism* **9**, 284–288.
- Padian, K. & Olsen, P. E. 1989. Ratite footprints and the stance and gait of Mesozoic theropods. In: D.D. Gillette & M.G. Lockley (eds.), *Dinosaur Tracks and Traces*, 231–241. Cambridge University Press, Cambridge.
- Paul, G. S. 1988. *Predatory Dinosaurs of the World*. 464 pp. Simon & Schuster, New York.
- Romer, A. S. 1923. The pelvic musculature of saurischian dinosaurs. — *Bulletin American Museum of Natural History* **48**, 605–617.
- Spector, W. S. 1956. *Handbook of Biological Data*. 265 pp. W.B. Saunders, Philadelphia.
- Thulborn, R.A. 1981. Estimated speed of a giant bipedal dinosaur. — *Nature* **292**, 273.
- Thulborn, R.A. 1982. Speeds and gaits of dinosaurs. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **38**, 227–256.
- Tarsitano, S. 1983. Stance and gait in theropod dinosaurs. — *Acta Palaeontologica Polonica* **28**, 251–264.
- Weis-Fogh, T. & Alexander, R. McN. 1977. The sustained power output obtainable from striated muscle. In: T.J. Pedley (ed.), *Scale Effects in Animal Locomotion*, 511–525. Academic Press, London.