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STANCE.AND GAIT IN THEROPOD DINOSAURS

The stance and gait of theropod dinosaurs are interpreted within the framework and constraints of functional morphology and biomechanics. The morphology of theropods is compared to known functional locomotory systems in extant lizards, crocodilians and birds. From these comparisons it was determined that muscle scars found on the bones of theropods represented a muscle pattern more similar to crocodilians than to the other two taxa. This conclusion allows the determination of the most likely posture of the many proposed for theropod dinosaurs. The traditional, almost erect stance, as well as the modern "avian like" stance are rejected because they are biomechanically unsound. The running stance arrived at in this study is one in which the presacral vertebral column is held approximately 20 degrees above the horizontal. The tails of theropods probably were well off the ground and were likely pivoted from side to side in synchrony with the movements of the legs.

INTRODUCTION

Restorations of theropod dinosaurs have been presented by various authors (Marsh 1893; Osborn 1917; Ostrom 1969; Russell 1972; Tarsitano, Ph.D. thesis). These restorations have resulted in basically three different postures for theropod dinosaurs. Relying upon their interpretation of dinosaur osteology, Marsh (1893) and Osborn (1906, 1917) reconstructed theropods in an upright position with the presacral vertebrae forming an angle of about 50 degrees above the horizontal. Ostrom (1969), Newman (1970) and Russell (1972) restored theropods with a horizontal vertebral column based upon osteology and hip joint morphology. Russell (1972) also restored the pelvic musculature of coelurosaurs based on his interpretation of the pelvic musculature of theropods. Russell's theropod restoration was derived from comparisons of theropod muscle scar

evidence with the pelvic muscles of crocodilians, birds and mammals. Tarsitano's (Ph.D. thesis) theropod restoration was based on an investigation of lizard, crocodilian and avian pelvic and hindlimb musculature, and the comparison of this musculature with muscle scar evidence from the pelvis and hindlimb of theropods. This work, in addition to a study of the osteology and hip joint morphology (based on the work of Hotton 1980, and pers. comm.) and a functional analysis of the locomotory systems of crocodilians and theropods led to his positioning the vertebral column of theropods at approximately 20 degrees above the horizontal.

    In order to restore the stance of theropods, it is first necessary to identify and interpret in functional terms the salient features of the locomotory morphology in theropod dinosaurs, the hallmark of which is bipedal locomotion. This has been achieved through a modification of the pelvic and hindlimb morphology and the expansion of certain muscles from the thecodontian plan. Thus it is important to first understand the thecodontian system of locomotion before attempting to restore a bipedal theropod. By doing so the changes in morphology and function in the transition from thecodont to theropod can be determined.

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THECODONTIAN LOCOMOTION

    Although progress has been made in understanding the phylogeny of thecodonts (Charig and Reig 1970; Bonaparte 1975; Sill 1974), they are still largely represented by grades instead of clades. This is due to the poor fossil record of thecodonts and the incomplete preservation of those specimens which are known. This is certainly true of the small upland and/or arboreal forms that must have existed, as evidenced by *Longisquama*. The present paper uses the term Pseudosuchia as, at least, the ancestors of theropods (Broom 1913; Huene 1921; Walker 1964). This relationship is based on the synapomorphies of the skull, tarsus and ischia (Broom 1913; Walker 1964; Tarsitano, Ph.D. thesis). Ancestors of other dinosaurian groups as well as birds may also be relegated to the Pseudosuchia as they become known (Heilmann 1926). It should be understood however, that the avian ancestor would not belong to the same group of pseudosuchians which were ancestral to any dinosaur taxon (Tarsitano and Hecht 1980).

    The locomotory morphology of pseudosuchian thecodonts is essentially crocodilian in nature (Krebs 1963; Ostrom 1976). Both crocodilians and pseudosuchians are mainly quadrupedal. This type of locomotion is correlated to, or a consequence of, a sprawling gait and is tied to the structure of the tarsus, overlapping metatarsals, femur, hip joint and pelvic and hindlimb musculature (Schaeffer 1941; Brinkman 1980a,

1980b; Tarsitano, Ph.D. thesis; Hecht and Tarsitano, in press). Crocodilians and pseudosuchians have a crocodilian tarsus (Krebs 1963) or a variation of this ankle type termed the "crocodilian reversed tarsus" (Cruickshank 1979; Thulborn 1980). In the crocodilian and pseudosuchian tarsus the proximal tarsal elements play a key role in locomotion (fig. 1a). The astragalus is bound to the tibia while the calcaneum moves with the pes (Schaeffer 1941). Thus there exists an intratarsal joint of a complex nature between the two proximal tarsals. The important features of this joint will be described here for convenience. A comprehensive description can be found in Hecht and Tarsitano (in press). The medial element, the astragalus, bears a peg-like structure on its lateral surface which articulates with a socket on the medial surface of the calcaneum. This articulation comprises the primary joint between the calcaneum and astragalus. The secondary joint occurs between the astragalar trochlear found on the posterior surface of the astragalus and the tongue of the calcaneum (fig. 1b). The tongue process lies directly posterior to the calcaneal socket and projects medially to glide over the trochlea of the astragalus. The calcaneum (fig. 1a, b, c) is also moveable against the fibula. The calcaneum bears proximally a condyle (fibular condyle) which is free to rotate under a ventrally cupshaped cartilage ventral to the fibula (fig. 1c). The weight of the fibula is born by the fibula facet of the astragalus. The calcaneum bears posteriolaterally a tuber which serves to change the direction of pull of the foot extensors and tendons of the *M. flexor tibialis externus* and *M. ambiens* as they make their way to metatarsal V (Schaeffer 1941; Gadow 1882; Brinkman 1980b; Tarsitano, Ph.D. thesis). The femur of pseudosuchians and crocodilians is also very similar. The head of the femur is not medially extended to form a roller surface (Hotton 1980, and pers. comm.). Instead, the head is anterioposteriorly directed. There is also a lateral torsion in the femur so that the shaft of the bone does not lie in the same plane as the head. In this regard, the lateral femoral condyle is larger than its medial counterpart. Finally, although the acetabulum may be perforate, an overhanging shelf forming the dorsal boundary of the acetabulum which is essential to a hip roller joint and upright stance does not exist in pseudosuchians.

The elements of the locomotory system of crocodilians and pseudosuchian thecodonts correspond to a mainly quadrupedal level of organization. Their hindlimb morphology can now be explained in functional terms. In order for the intratarsal joint to function, the calcaneum must be free to rotate. This means that the pes must first be lifted from the lateral side. The foot extensors, the *M. gastrocnemius* (tibial and fibular heads), *M. peroneus*, *M. flexor tibialis externus*, *M. ambiens* and *M. caudofemoralis* (by way of the *M. gastrocnemius*) all are directed to the lateral side of the foot (figs. 2, 3) in particular to the fifth metatarsal (Brinkman 1980b; Schaeffer 1941; Tarsitano, Ph.D. thesis). Thus the muscular func-
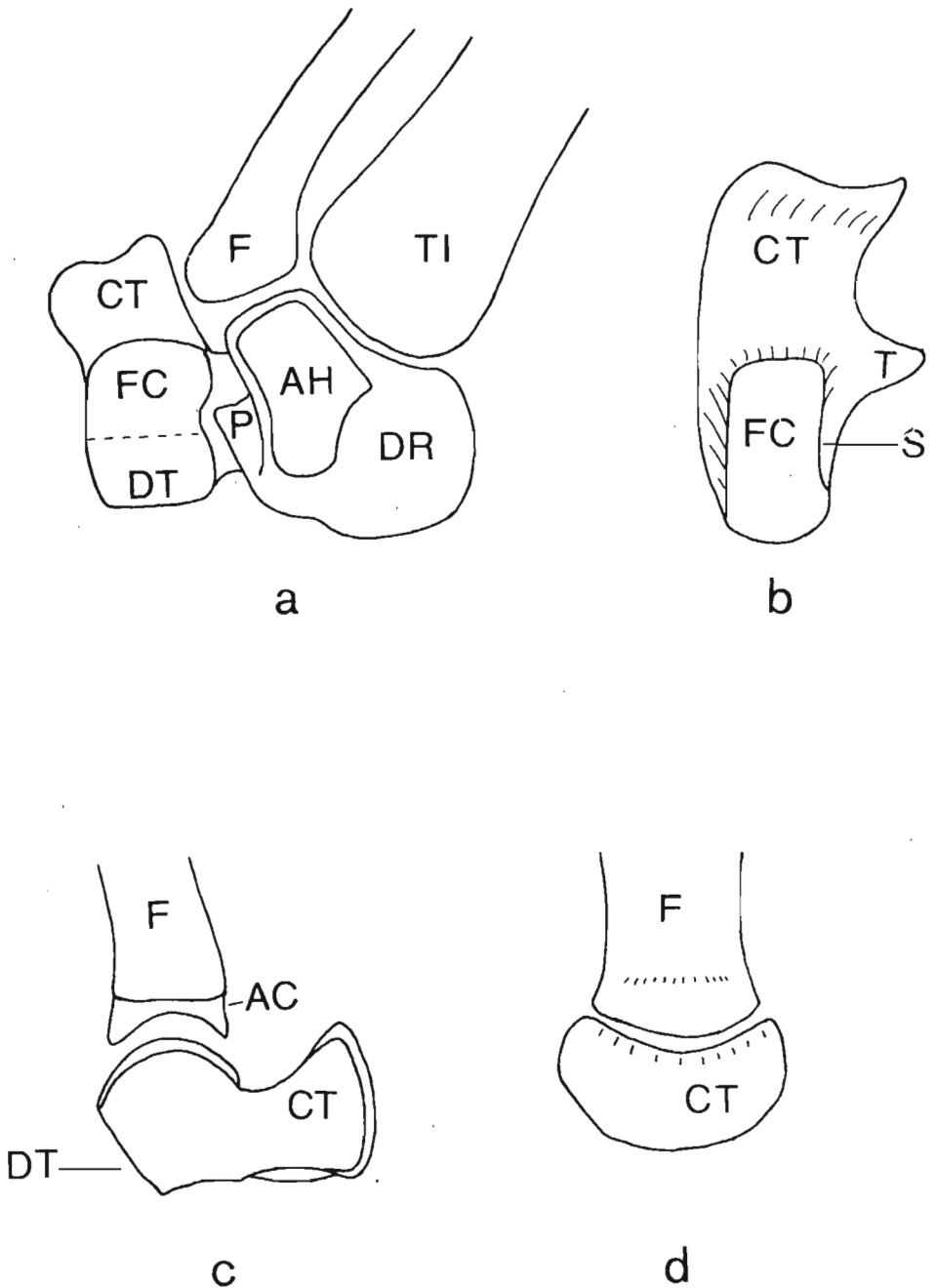
Fig. 1. Various tarsal elements of archosaurs: *a* distal view of the right tarsus of a eusuchian crocodilian; *b* proximal view of the right calcaneum of the pseudosuchian *Prestosuchus*; *c* lateral view of the left calcaneum of a eusuchian crocodilian; *d* lateral view of the left calcaneum of a theropod dinosaur AC articular cartilage; AH anterior hollow of the astragulus; CT calcaneal tuber; DR distal roller of the astragulus; DT distal tarsal four facet of the calcaneum; F fibula; FC fibular condyle of the calcaneum; P peg of the astragalus; S socket of the calcaneum; T tongue of the calcaneum; TI tibia.
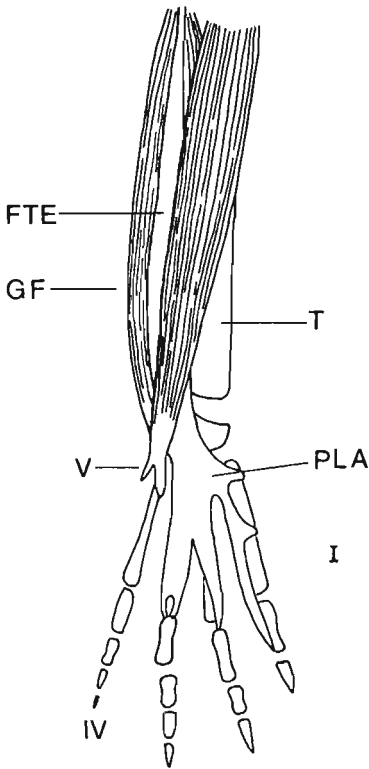
Fig. 2. Superficial shank muscles of a eusuchian crocodilian. FTE tendon of the *M. flexor tibialis externus*; GF fibular head of the *M. gastrocnemius*; PLA plantar aponeurosis; T tibia.
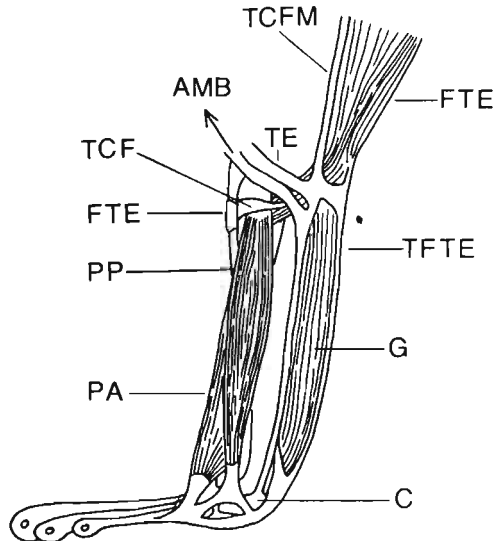
Fig. 3. Lateral view of the left shank and pes of a eusuchian crocodilian. AMB *M. ambiens*; C ɾalcaneum; FTE *M. flexor tibialis externus*; G *M. gastrocnemius*, fibular head; PA *M. peroneus anterior*; PP *peroneus posterior*; TCF tendon of the *M. caudofemoralis* attaching to the fibula; TCFM tendon of the *M. caudofemoralis*, forming the main origin for the fibular head of the *M. gastrocnemius*; TE tendon of the *M. caudofemoralis* to the extensor tendon of the knee; TFTE tendon of the *M. flexor tibialis externus* to the fifth metatarsus.

tion coincides with that of the ankle. Since the pes is first lifted laterally, the metatarsals must overlap to brace the inside digits of the pes which supply the support and convey the applied force of the foot extensors to the ground. Furthermore, since the pes must be lifted from the lateral side, the femur cannot be brought under the body and must be held at an angle to the vertical, hence the femoral torsion. All of the above stated morphology is part of one functional complex and is a level of organization and not a clade. It is apparent that all saurischian dinosaurs have evolved from a pseudosuchian ancestry since the remmants of the crocodilian tarsus is to be seen in theropods, sauropods and prosauropods. The ischia and pubes of pseudosuchians are decidedly saurischian and not crocodilian. While episodes of bipedalism are not unknown in crocodilians, the normal mode of locomotion is quadrupedal. A bipedal posture is possible when enough momentum has been attained in order that the presacral region may be lifted (the vertebral column extended). Thus it is likely that pseudosuchians were also able to run bipedally in such

fashion but this type of bipedalism should not be confused with that of theropods. The primitive method of balance in thecodontian and croco- dilian bipedal progression is that of a cantilever system. In this system the downward torque of the presacral region is balanced by the down- ward torque in the opposite direction produced by the tail. This system of balance is also used by bipedal lizards (Snyder 1949, 1952, 1954) and bipedal dinosaurs (Tarsitano, Ph.D. thesis). Birds have adopted another system of bipedalism. The tail is not used as a counterbalance but is instead reduced for aerodynamic reasons. With the reduction of the tail in birds (including *Archaeopteryx*) the pubes had to grow posteriorly in order that the viscera could be shifted under the pelvis thereby reducing the presacral downward torque. This adaptation would shift the center of gravity posteriorly. The shortening of the femur and the elongation of the tibiotarsus coincided with the posterior shift of the center of gravity under the pelvis. The result of these modifications of the pelvis and hindlimb in birds is that the tibiotarsus bone-muscle complex is the primary system of locomotion. In thecodonts, crocodilians and dinosaurs it is the tail-femoral-bone-muscle complex which is most important in locomotion. Thus, in order to interpret the osteology and muscle scars of theropods, it is better to compare theropods to crocodilians which have the same morphology as the pseudosuchian predecessors of theropods. I have found that of the muscles which leave scars on the pelvis and femur (Tarsitano, Ph.D. thesis), there is a one-to-one correspondence between crocodilian muscle scars and the muscle scars found in well preserved theropods. In contrast, the avian pelvis and system of balance has been so modified as to be unreliable in the interpretation of theropod morphology.

THEROPÔD LOCOMOTION

The morphology of theropod locomotion can be derived from that of pseudosuchians. The change from a facultative biped (thecodont) to an obligate theropod biped is understandable in terms of efficiency. Bipedal locomotion is more energy efficient than is a reptilian method of quad- rupedal locomotion (Hotton 1980). The change to obligate bipedalism necessitates an overhaul in pseudosuchian morphology. The legs had to be brought under the body in theropods in order to support the weight of the body at less energy cost to the musculature. This change in stance brings the movement at all joints in the hindlimb in the same plane of motion. The result is an increase in torque to the joints and an increase in stride length (Hildebrand 1974). In order to achieve this posture the crocodilian ankle joint must be modified. What apparently has occured

is that the fibular condyle of the calcaneum has been reduced and the fibula has shifted back onto the dorsal surface of the calcaneal tuber (Tarsitano, in prep.). This condition is seen at least in the theropods, prosauropods and ornithopods. Through this modification the calcaneum ceases to move and the mesotarsal joint is established (fig. 1d). The change in function of the calcaneal tuber also changes its effect on the foot extensors thereby allowing the more medial placement of these muscles on the foot. With the development of the mesotarsal joint, the metatarsals would no longer need to overlap and the functionally symmetrical "tridactyl" foot could be evolved. As the legs were brought under the body the torsion of the femur disappeared and the femoral head expanded inward to form a roller. These adaptations lead to a more fore-aft swinging of the limb and a natural bipedal posture.

To understand the positioning of the vertebral column one must first understand the musculature of the crocodilian hindlimb. For the sake of brevity I will only refer to the crocodilian muscles which play key roles in locomotion. Full descriptions can be found in Gadow (1882), Romer (1923), Tarsitano (Ph.D. thesis) and Brinkman (1980b). Of the protractors, the *M. puboischiofemoralis internus* parts 1 and 2 and the anteriormost portions of the *M. iliotibialis* are most important. The *M. puboischiofemoralis internus* part 1 originates in all crocodilians on the first sacral vertebra and the corresponding internal surface of the ilium (fig. 4). The insertion is on the anterior surface of the fourth trochanter. The second part of this muscle originates from the last five presacral vertebrae.
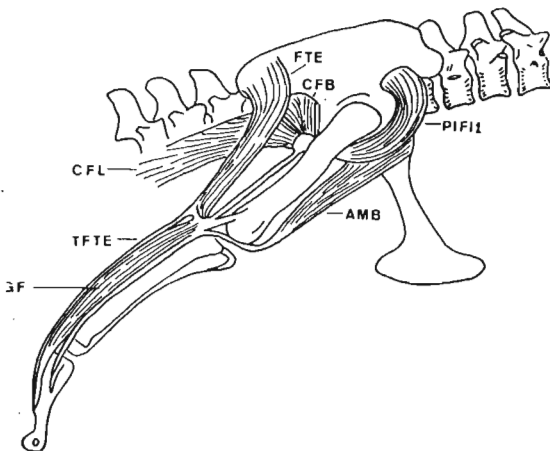

Fig. 4. Reconstructed pelvic and hindlimb muscles of the theropod dinosaur *Tyrannosaurus rex*. AMB *M. ambiens*; CFB *M. caudofemoralis brevis*; CFL *M. caudofemoralis longus*; FTE *M. flexor tibialis externus*; GF *M. gastrocnemius*, fibular head; PIFI1 *M. puboischiofemoralis internus* part one; TFTE tendon of the *M. flexor tibialis externus*.
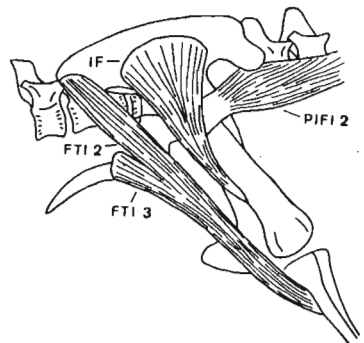
Fig. 5. Reconstructed pelvic and hindlimb muscles of the theropod dinosaur, *Tyrannosaurus rex*. FTI2 *M. flexor tibialis internus* part two; FTI3 *M. flexor tibialis internus* part three; IF *M. iliofemoralis*; PIFI2 *M. puboischiofemoralis internus* part two.
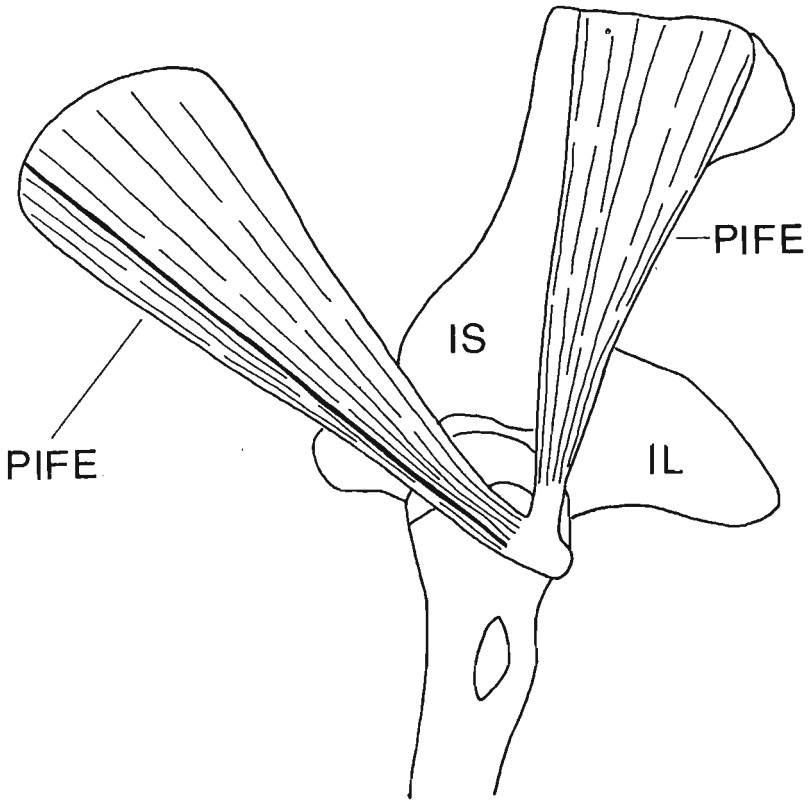
Fig. 6. Ventral view of the right side of a eusuchian crocodilian pelvis and hindlimb. IL ilium; IS ischium; PIFE1,2,3 *M. puboischiofemoralis externus* parts one, two and three.

The insertion lies on the lateral surface of the femur just distal to the femoral head (fig. 5). Thus, the *M. puboischiofemoralis internus* is primarily responsible for protracting and lifting the femur. The *M. puboischiofemoralis externus* parts 1 and 2 originate on the broad surface of the pubis. They converge on the upper medial surface of the femur to insert with the third part of this muscle on the back of the femur below its head (fig. 6). The major action of this muscle is to rotate the femur outward, solving the femur's "knocking on pubes" problem (Charig 1972). This rotation of the femur is concordant with the movement of the hip roller joint of theropods as proposed by Hotton (1980). The *M. puboischiofemoralis externus* parts 1 and 2 also serves to protract the femur. The *M. ambiens* (fig. 4) originates at the junction of the ilium and pubis. Only part 1 of this muscle is significant for the present discussion. It crosses laterally over the knee joint between the layers of the extensor tendon formed by the *M. femorotibialis* ventrally and the *M. iliotibialis* dorsally (Tarsitano, Ph.D. thesis), to run down the shank in the fascia of the *M. gastrocnemius* to insert on the calcaneal tuber and fifth metatarsus (fig. 3).

The *M. ambiens* protracts the femur and stabilizes the outward rotation of the femur; it is also a shank flexor and pedal extensor. Finally, the *M. iliotibialis* originates on the dorsal rim of the ilium and inserts onto the proximal anterior surface of the tibia, forming part of the extensor tendon of the knee. This muscle can act to lift and sligthly protract the thigh. The retractors of the femur are mainly the *M. caudofemoralis longus* and *brevis* (*M. coccygeofemoralis*). The *longus* originates from the third to the thirteenth caudal vertebrae (Romer 1923). It inserts into the fourth trochanter and sends a long tendon to the *M. gastrocnemius* (figs. 3, 4). The *brevis* originates from the internal surface of the postacetabular ilium and the last sacral vertebra. It also inserts into the fourth trochanter. The *M. iliofemoralis* may also aid in the retraction of the femur due to its insertion of the postero-lateral surface of the femur (fig. 5).

The positioning of the vertebral column can now be understood in functional terms. If the vertebral column is oriented at about 50 degrees above the horizontal, the *M. puboischiofemoralis internus* will bring the femur upwards and not forward. The result is a high, inefficient "marching-in-place" gait. In order to stand with the vertebral column at such an angle the *M. caudofemoralis* would have to be almost fully contracted. Thus at such a high angle, the vertebral column makes bipedal locomotion impossible. If the vertebral column is held horizontally there are also problems in locomotion. The *M. puboischiofemoralis internus* may bring the femur only partially forward but can hardly lift the femur. The postures giving theropods a horizontal vertebral column and having the femur protracted to the level of the vertebral column are biomechanically and physiologically impossible since the femur would be dislocated from the hip (tearing the *ligamentum teres*) and the protractor muscles would have to contract more (by as much as three times) than is physiologically possible. When crocodilians run bipedally, the presacral region is lifted in order that the *M. puboischiofemoralis internus* can lift as well as protract the thigh. A horizontal vertebral column limits the protraction and retraction of the femur. This would allow theropods to walk but inhibit their ability to run. This may be explainable in terms of length tension curves of muscle contraction (Ramsey 1960; Abbott and Wilkie 1953; Gans and Bock 1965). The lifting of the presacral region acts to stretch the protractor muscles loaded by the weight of the hindlimb. According to Wilson (1979), this would permit a faster shortening velocity of these muscles and would allow them to produce more work. If the vertebral column of theropods were held horizontally then both protractors and retractors would be either short (reducing the excursion of their insertion points) or their contraction would produce less tension (due to the slackness of the muscles). For these reasons, extension of the vertebral column is essential to reptilian bipedal locomotion. The same is true for
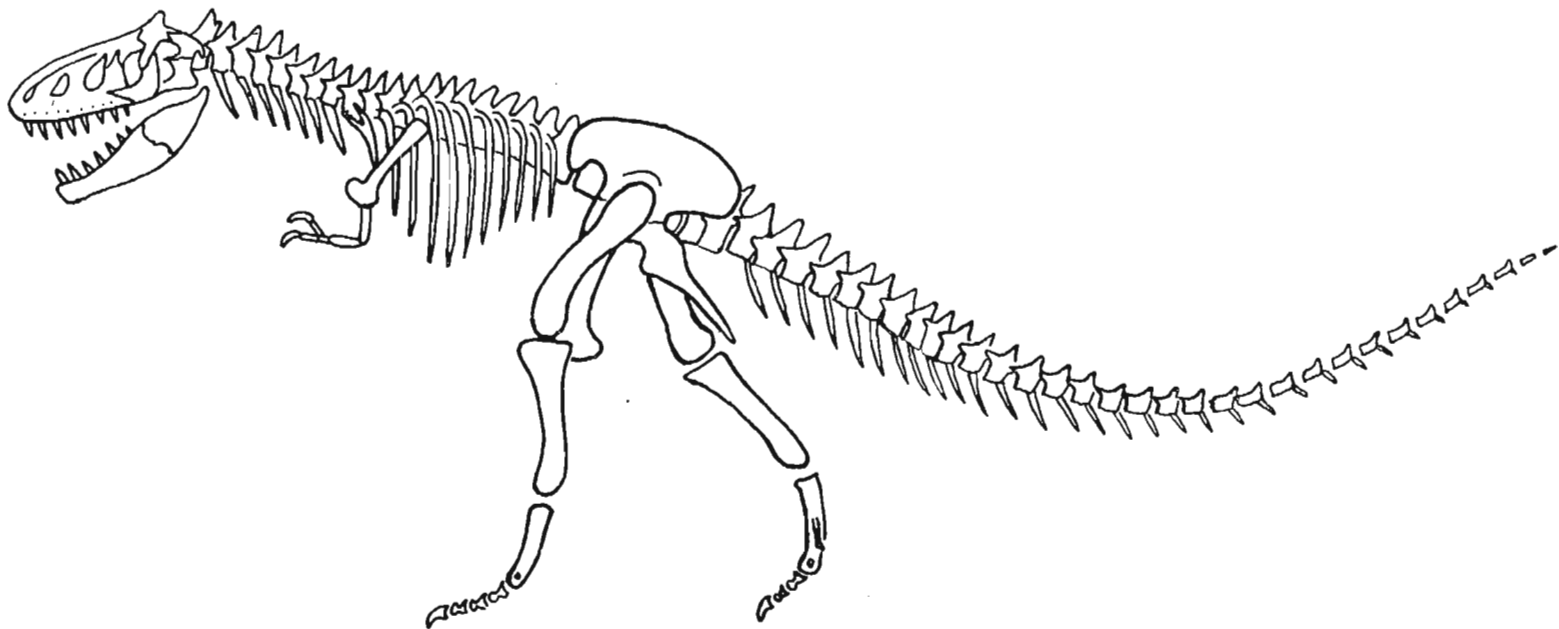
Fig. 7. Diagrammatic representation of the theropod dinosaur, *Tyrannosaurus rex*, during a walking gait.

the retractor function of the *caudofemoralis*. Extension of the tail renders the same benefits to the retractor musculature. The first few caudal vertebrae of theropods never have elongated ossified postzygopophyses for this reason. Thus the vertebral column in theropods should have been held at an angle of about 20 degrees above the horizontal (fig. 7). Attempts at giving theropods ratite avian postures can do so only by neglecting the large differences in osteology and musculature, as well as method of balance and locomotion that clearly exists between theropod dinosaurs and birds.

OTHER MORPHOLOGICAL CONSIDERATIONS

Other misconceptions of theropod morphology include the positioning of the hallux and neck region. Traditionally, the hallux of theropods has been thought to ·be reflexed as in birds (Osborn 1899). This idea has been challanged by Hecht (1976), Tarsitano and Hecht (1980), Hecht and Tarsitano (1983) and Tarsitano (Ph.D. thesis). It will also be challanged here. Most paleontologists place the hallux in a reflexed position when the foot is not found in articulation. When the foot is found in articulation, the hallux is found preserved parallel to digit 2. Preserved unreflexed halluces are found in *Coelophysis, Velociraptor, Saurornithoides* (Osborn 1924) and *Compsognathus* (Tarsitano and Hecht 1980). When the hallux is not found in articulation it is usually conveniently placed into the muscle scar of the M. *gastrocnemius* (tibial head)! The position of the hallux on metatarsal II and its morphology preclude the halluces of theropods from being opposable. In preserved (*in situ*) theropod feet the hallux is found midway down the length of metatarsal II. The ungual of the hallux is reduced to about one-half the size of the unguals of the other digits. Thus, the hallux of theropods is a reduction character, associated with a cursorial habit (see Hecht and Tarsitano 1983). That the hallux of theropods is so high up on metatarsal II and so small precludes its ability to oppose the other digits. This condition is found in theropods that are contemporaneus with *Archaeopteryx* as well as in theropods that are found much later in the Cretaceous. Theropods which predate *Archaeopteryx* have a hallux parallel to metatarsal II. The conclusion is that the character state of the hallux of theropods and that of the *Urvogel, Archaeopteryx,* are not morphologically, functionally or phylogenetically related to one another.

The cervical region of theropods has also been subject to the whims of paleontologists disregarding the constraints of cervical morphology. In restorations of theropods with horizontal vertebral columns, the cervical region is angled upward at nearly 90 degrees where the cervical vertebrae

meet the dorsal vertebrae. (Ostrom 1969). In order that the head be held level, another bend is needed just distal to the axis. How these large bends over just a few (or two) vertebrae are accomplished is never explained nor clearly illustrated. The fact is, in both morphological and functional terms these bends cannot be explained and would have no doubt contributed significantly to the demise of the dinosaurs! If such large bends were to occur then they would occur only by dislocation of the vertebral centra and their pre- and postzygapophyses from each other. Theropod necks with their amphicoelous vertebrae and unknown cervical musculature cannot make such bends. Their comparisons with avian necks composed of heterocoelous vertebrae are dubious. Osteological and muscular specializations would have to be described before such angling in theropod necks would be acceptable.

CONCLUSION

Functional morphology plays an important role in the interpretation of the morphology of fossil vertebrates. Character analysis against a functional framework acts as a check on the restorations of fossils and the establishment of synapomorphies. Furthermore, functional analysis prevents the counting of the same functional complex more than is prudent (Hecht and Edwards 1977). Morphologies described for fossils must be able to perform their intended function. The interpretation that the hallux of theropods is opposable is a case in point. A morphological and functional analysis of this character in theropods better fits the picture of reduction corresponding to the lessening of the limb inertia in a cursorial animal than its interpretation as a bird-like hallux. Functional analysis prevents the positioning or interpretation of bones or other organ systems by preconceived notions. Finally, the use of functional morphology based on known extant organ systems enables the morphological interpretations of fossils to become testable. Only through knowledge gained from the living can we hope to interpret the past.

REFERENCES

ABBOTT, B. C. and WILKIE, D. R. 1953. The relation between velocity of shortening and the tension length curve of skeletal muscle. — *J. Physiol.*, **120**, 214.

BONAPARTE, J. F. 1975. Nuevos materiales de *Lagosuchus talampayensis* Romer (Thecodontia-Pseudosuchia) y su significado en el origen de los Saurischia. Chañarense Inferior, Triásico Medio de Argentina. — *Acta Geol. Lilloana*, **13**, 5—90.

BRINKMAN, D. 1980*a*. Structural correlates of tarsal and metatarsal functioning in *Iguana* (Lacertilia, Iguanidae) and other lizards. — *Can. J. Zool.*, **58**(2), 277—289.

—   1980*b*. The hindlimb step cycle of *Caiman sclerops* and the mechanics of the crocodilian tarsus and metatarsus. — *Ibidem*, **58**(12), 2187—2200.

BROOM, R. 1913. On the South African pseudosuchian *Euparkeria* and allied genera. — *Proc. Zool. Soc. London*, **1913**, 619—633.

CHARIG, A. J. 1972. The evolution of the archosaur pelvis and hindlimb: an explanation in functional terms. *In*: K. A. Joysey and T. S. Kemp (eds), Studies in Vertebrate Evolution, 121—155. Oliver and Boyd, Edinburgh.

—   and REIG, O. A. 1970. The classification of the Proterosuchia. — *Biol. J. Linn. Soc.*, **22**, 121—171.

CHATTERJEE, S. 1978. A primitive parasuchid (Phytosaur) reptile from the Upper Triassic Maleri formation of India. — *Palaeontology*, **21**(1), 83—127.

CRUICKSHANK, A. R. I. 1979. The ankle joint in some early archosaurs. — *S. Afr. J. Sci.*, **75**, 168—178.

GADOW, H. 1882. Beiträge zur Myologie der hintern Extremität der Reptilien. — *Morphol. Jb.*, **7**, 329—466.

GANS, C. and BOCK, W. 1965. The functional significance of muscle architecture: A theoretical analysis. — *Ergeb. Anat. Entwicklungsges.*, **38**, 115—142.

HECHT, M. K. 1976. Phylogenetic inference and methodology as applied to the vertebrate record. Evolutionary Biology, **9**, 335—363. Plenum Press, New York and London.

—   and EDWARDS, J. L. 1977. The method of phylogenetic inference above the species level: *In*: M. K. Hecht, P. Goody and B. M. Hecht (eds), Major Patterns in Vertebrate Evolution, 3—51. Plenum Press, New York and London.

—   and TARSITANO, S. (in press). The tarsus and metatarsus of *Protosuchus* and its phyletic implications. Ernest Williams Festschrift, Cambridge.

—   and — 1983. *Archaeopteryx* and its paleoecology. *In*: Z. Kielan-Jaworowska and H. Osmólska (eds), Second Intern. Symp. Mesozoic Terrestrial Ecosystems, Jadwisin 1981. — *Acta Palaeont. Polonica*, **28**, 1—2, 133—136.

HEILMANN, G. 1926. Origin of the Birds. 208 pp. Witherby, London.

HILDEBRAND, M. 1974. Analysis of Vertebrate Structure. 710 pp. John Wiley and Sons, New York and London.

HOTTON, N. 1980. An alternative to dinosaur endothermy: The happy wanderers. *In*: R. D. K. Thomas and E. C. Olson (eds), A Cold Look at the Warm-Blooded Dinosaurs, AAAS Selected Symposium **28**, 311—350. Westview Press, Colorado.

HUENE, F. R. von. 1921. Neue Pseudosuchier und Coelurosaurier aus dem Württembergischen Keuper. — *Acta Zoologica*, **2**, 360—380.

KREBS, B. 1963. Bau und Funktion des Tarsus eines Pseudosuchiers aus der Trias des Monte San Giorgia (Kanton Tessin, Schweiz). — *Paläont. Z.*, **57**, 88—95.

MARSH, O. C. 1893. Restoration of *Anchisaurus*. — *Am. J. Sci.*, (3), **45**, 169—170.

NEWMAN, B. H. 1970. Stance and gait in the flesh-eating dinosaur *Tyrannosaurus*. — *Biol. J. Linn. Soc.*, **2**, 119—123.

OSBORN, H. F. 1899. Fore and hind limbs of carnivorous and herbivorous dinosaurs from the Jurassic of Wyoming. Dinosaur Contributions, No. 3. — *Bull. Am. Mus. Nat. Hist.*, **12**, 9, 161—172.

—   1906. *Tyrannosaurus*, Upper Cretaceous carnivorous dinosaurs. (Second communication). — *Ibidem*, **22**, 281—296.

—   1917. Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*. — *Ibidem*, **35**, 733—771.

—   1924. Three new Theropoda, *Protoceratops* zone, Central Mongolia. — *Am. Mus. Novit.*, **144**, 1—12.

OSTROM, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. — *Bull. Yale Peabody Mus. Nat. Hist.*, **30**, 1—165.

—   1976. *Archaeopteryx* and the origin of birds. — *Biol. J. Linn. Soc.*, **8**, 91—182.

RAMSEY, R. W. 1960. Some aspects of the biophysics of muscle. *In*: G. H. Bourne (ed.), The Structure and Function of Muscle, 303—358. Academic Press, New York.

ROMER, A. S. 1923a. Crocodilian pelvic muscles and their avian and reptilian homologues. — *Bull. Am. Mus. Nat. Hist.*, **48**, 533—552.

—   1923b. The pelvic musculature of saurischian dinosaurs. — *Ibidem*, **48**, 605—617.

RUSSELL, D. A. 1972. Ostrich dinosaurs from the late Cretaceous of Western Canada. — *Can. J. Earth Sci.*, **9**, 375—402.

SCHAEFFER, B. 1941. The morphological and functional evolution of the tarsus in amphibians and reptiles. — *Bull. Am. Mus. Nat. Hist.*, **78**, 395—472.

SILL, W. D. 1974. The anatomy of *Saurosuchus galilei* and the relationships of the rauisuchid thecodonts. — *Bull. Mus. Comp. Zool.*, **146**, 317—362.

SNYDER, R. C. 1949. Bipedal locomotion of the lizard *Basiliscus basiliscus*. — *Copeia*, **1949**, 129—137.

—   1952. Quadrupedal and bipedal locomotion in lizards. *Ibidem*, **1952**, 64—70.

—   1954. The anatomy and function of the pelvis girdle and hindlimb in lizard locomotion. — *Am. J. Anat.*, **95**, 1—46.

TARSITANO, S. 1981. Pelvic and hindlimb musculature in archosaurian reptiles. Ph. D. thesis, City University of New York.

—   and HECHT, M. K. 1980. A reconsideration of the reptilian relationships of *Archaeopteryx*. — *Zool. J. Linn. Soc.*, **69**(2), 149—182.

THULBORN, R. A. 1980. The ankle joints of archosaurs. — *Alcheringia*, **4**, 241—261.

WALKER, A. D. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. — *Phil. Trans. Roy. Soc.* (B), **248**, 53—134.

WILSON, J. A. 1979. Principles of Animal Physiology. Macmillan Publishing Co., Inc., New York.