Locomotion in derived dicynodonts (Synapsida, Anomodontia): a functional analysis of the pelvic girdle and hind limb of *Tetragonias njalilus*

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Abstract: A general locomotor model for derived dicynodont anomodonts is proposed on the basis of a functional analysis of the pelvic girdle and entire hind limb of the medium-sized Middle Triassic dicynodont *Tetragonias njalilus*. The joint mobility of the hind limb is examined, and a hind limb step cycle is reconstructed. The data provided in this case study indicate that *Tetragonias* adopted a highly adducted (upright) hind limb posture during stance and most of its stride. Nevertheless, lateral undulation of the vertebral column must also have contributed to the locomotion of dicynodonts. Character optimization of the traits associated with an upright posture of the hind limb shows a gradual evolution of dicynodont locomotion. The evolution of an upright hind limb posture has occurred several times independently in a number of amniote clades. Within synapsids, the Anomodontia, Dinocephalia, and Theriodontia acquired a parasagittal hind limb gait already as early as the late Paleozoic and early Mesozoic, prior to its evolution in mammals. This phenomenon has previously been explained as being related to an increase in body size as a response to increased biomechanical stress on the limb. This scenario appears plausible with respect to dicynodonts because of the occurrence of megaherbivore-sized taxa in the Triassic, but this study shows that a parasagittal gait had already evolved in the medium-sized basal kannemeyeriiform *Tetragonias*. Therefore, the vertical support of the body by the hind limbs in medium-sized dicynodonts could have allowed the evolution of the large Triassic taxa in the first place.

Résumé : Un modèle général de locomotion pour les anomodontes dicynodontes est proposé à la lumière d'une analyse fonctionnelle de la ceinture pelvienne et du membre postérieur entier du dicynodonte de taille moyenne *Tetragonias njalilus*, du Trias moyen. La mobilité des articulations du membre postérieur est examinée et le cycle de pas de ce membre est reconstitué. Les données découlant de la présente étude de cas indiquent que *Tetragonias* adoptait une posture du membre postérieur très adductée (verticale) en position debout et durant la majeure partie de sa foulée. Ceci dit, l'ondulation latérale de la colonne vertébrale participait également à la locomotion des dicynodontes. L'optimisation des caractères associés à une posture verticale du membre postérieur démontre une évolution graduelle de la locomotion chez les dicynodontes. L'évolution d'une posture verticale des membres postérieurs a eu lieu à plusieurs reprises de façon indépendante chez différents clades amniotes. Parmi les synapsides, les Anomodontes, les Dinocéphales et les Thériodontes avaient acquis une démarche parasagittale des membres postérieurs dès le Paléozoïque tardif et le Mésozoïque précoce, préalablement à leur évolution mammifère. Ce phénomène a déjà été expliqué comme étant relié à une augmentation de la taille du corps en réponse à l'augmentation des contraintes biomécaniques agissant sur les membres. Si ce scénario semble plausible en ce qui concerne les dicynodontes, étant donné l'existence de taxons de la taille de mégaherbivores durant le Trias, la présente étude démontre que le kannamyeriiforme basal de taille moyenne *Tetragonias* avait déjà acquis une démarche parasagittale à cette époque. Ainsi, le support vertical du corps par les membres postérieurs chez les dicynodontes de taille moyenne pourrait, à l'origine, avoir rendu possible l'évolution des grands taxons triasiques.

[Traduit par la Rédaction]

Introduction

The Dicynodontia, the most diverse subgroup within the Anomodontia, are an extinct group of non-mammalian synapsids from the Permo-Triassic that were the dominant terrestrial herbivores and achieved a worldwide distribution. At the end of the Permian, the diversity of dicynodonts declined to a few genera, but the Dicynodontia had a second radiation during the Triassic. This radiation of Triassic dicynodonts consisted primarily of members of a single clade, the Kannemeyeriiformes, except for the genera *Kombuisia* (Fröbisch and Reisz 2004; Fröbisch 2006), *Myosaurus* (King 1988; Angielczyk 2001; Angielczyk and Kurkin 2003), and *Lystrosaurus* (Keyser and Cruickshank

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Fig. 1. Phylogenetic relationships of higher taxonomic groups with the Dicynodontia. The topologies from the Permian and the Triassic taxa are taken from and simplified after Fröbisch (2006) and Maisch (2001), respectively. The evolution of the main characters associated with an upright posture of the hind limb is plotted on the cladogram, emphasizing a gradual evolution of the change in hind limb motion. The phylogenetic position of *Tetragonias njalilus* is within the basalmost clade of the kannemeyeriiform dicynodonts, the Shansiodontidae. *Tetragonias* possesses all characters associated with an upright hind limb posture and thus represents an ideal model for the locomotion of derived dicynodonts.
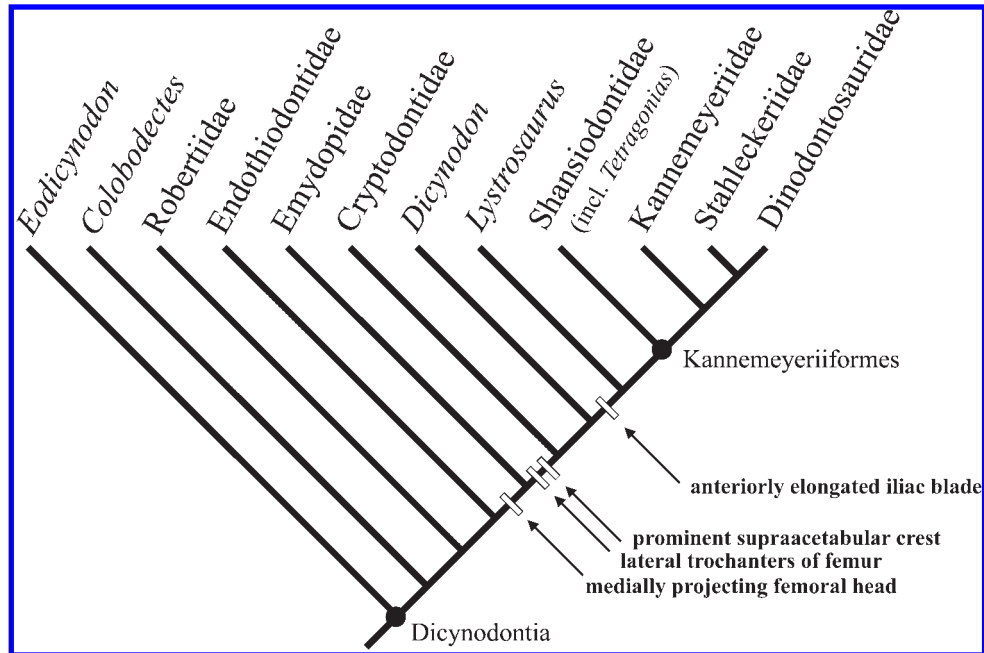
1979; Maisch 2001, 2002), whereas the Permian radiation consisted of several clades.

The outstanding success of anomodonts as terrestrial herbivores is generally ascribed to their highly efficient masticatory apparatus (Crompton and Hotton 1967; Rybczynski and Reisz 2001; Angielczyk 2004), but their locomotor capabilities also need to be considered. Previous functional analyses of the postcranium in dicynodont anomodonts include Permian (Watson 1960; Cox 1972; Cluver 1978; King 1981*a*, 1981*b*, 1985; Ray and Chinsamy 2003) and Triassic taxa (Pearson 1924; Walter 1986). The locomotion of basal, non-dicynodont anomodonts has as yet not been investigated. Presumably, these animals were sprawlers with both pairs of limbs, which certainly represents the plesiomorphic gait for amniotes (Sumida and Modesto 2001; Holmes 2003) and is also suggested for basal dicynodonts (King 1981*b*; Rubidge et al. 1994). The Triassic Kannemeyeriiformes include the largest dicynodont taxa and have among the most derived postcranial skeletons of any dicynodonts (Walter 1985). In addition to the Kannemeyeriiformes, other highly derived taxa, i.e., *Kingoria* (King 1985), and specialized forms, e.g., the fossorial *Cistecephalus* (Cluver 1978), *Kawingasaurus* (Cox 1972), and *Diictodon* (Ray and Chinsamy 2003), had already evolved in the Permian.

Although some of these studies are thorough, a complete hind limb step cycle, with special consideration of the possible range of mobility, has not yet been reconstructed. The aim of this study is to test existing hypotheses for the locomotion of late dicynodonts by means of a detailed case study of the hind limb step cycle of the Middle Triassic dicynodont *Tetragonias*. Within the kannemeyeriiform dicynodonts, the Shansiodontidae form a basal clade of medium-sized

dicynodonts (Fig. 1) (Maisch 2001; Vega-Dias et al. 2004), of which *Tetragonias* is known from one species, *T. njalilus* from the Manda Formation (Anisian) of the Ruhuhu Valley, Tanzania. The basal phylogenetic position of *Tetragonias* within derived dicynodonts, as well as its medium size, makes this taxon an ideal model to assess the evolution of an upright hind limb posture in kannemeyeriiforms. Previous studies of dicynodont postcrania mainly considered the motion on the stylopodium, often disregarding the zeugopodium and autopodium. The morphology of the ankle joint, however, is essential for the reconstruction of the locomotor abilities of an animal (Kemp 1982). This study represents the first description of a dicynodont step cycle of the entire hind limb. The reconstructed options of locomotion are proposed to represent a model for the locomotor abilities of derived dicynodonts in general.

Material and methods

The interpretation of locomotor abilities of extinct tetrapods is usually difficult because important features such as articulation surfaces and sites of muscle attachments are often incompletely preserved. In addition, exhaustive studies of extant forms show clearly that there is significant variation in limb movements even among the individuals of one taxonomic group. It is generally possible, however, to determine the typical stance and gait of a certain taxon.

The material of *Tetragonias* used in this study is part of the collections of fossil vertebrates from the Manda Formation (southwestern Tanzania) which are housed in the Institut und Museum für Geologie und Paläontologie in Tübingen (GPIT), Germany, and in the University Museum of Zoology Cam-

bridge (UMZC), England. The material comprises cranial and postcranial elements of several individuals in different ontogenetic stages. Most anatomical information was gained from the holotype (GPIT 292) and specimen UMZC T.754. Compared to other fossil vertebrates from these deposits, the type specimen of *T. njalilus* is exceptionally well preserved. It includes a complete right hind limb, which constitutes the crucial part of the biomechanical analysis presented here. Additional information, especially about pelvic girdle and pes, was gained from specimen UMZC T.754. Based on its size and ossification patterns, e.g., unfused pelvic bones, the latter specimen is considered to be subadult, in contrast to the interpretation by Cruickshank (1967) that this specimen is an adult female. The type specimen is slightly larger in size and shows co-ossification of the pelvic bones, and is therefore interpreted to represent an adult individual.

The basis for the mobility reconstruction of the skeletal elements is a revised osteological description of the pelvic girdle and hind limb of *Tetragonias* and a reconstruction of the associated myology, which is presented elsewhere (Fröbisch 2003; J. Fröbisch, in preparation[2]). In contrast to the generally used orientations within dicynodont postcrania for anatomical description (King 1988; Ray and Chinsamy 2003), it is considered to be appropriate to describe pelvis and hind limb orientations referring to an anatomically neutral position, which is the stance phase of the step cycle.

The reconstruction of arthrology and mobility is based on bone adjustment experiments referring to the mismatches of the articular surface and biometry. Plaster replicas were taken from all elements of the right pelvis and hind limb of the holotype of *T. njalilus* to avoid damage to the original bones. The replicas were mounted with a system of mobile clamps, which allowed the bones to be rearranged for each stage of the step cycle (Fig. 2). This methodology was used in a number previous case studies (e.g., Galton 1971; Gishlick 2001; Senter and Robins 2005) and represents only an approximation of the full motion range and sequence of the living animal. The mismatch of the articular surfaces yielded the hints to reconstruct the thickness of articular cartilage, estimated to range between 2 and 10 mm, which compares well with extant taxa (Holliday et al. 2001). The freedom of movement was restricted by the reconstruction of the best estimate of the main load of the bones during the entire step cycle. The vectors of these main loads were concluded from the shape of the bone and the epiphyseal surfaces, respectively. The dimensions of the articular surfaces at each joint were presumed to represent the limits of the possible motion range, which when in articulation are referred to as "bone lock" in the following. The step cycle positions were digitally photographed in orthal views and transferred to sketches. Still, all statements concerning the hind limb mobility of *Tetragonias* have an estimated error range of about 5%–10% due to a lack of direct extant analogs. Critical elements of a step cycle such as timing of events cannot be observed or inferred from osteology alone, so the results need to be taken as approximation.

Tetrapod locomotion is generally considered to comprise complex movements and a wide spectrum of limb postures.

Fig. 2. Experimental apparatus for reconstruction of the hind limb mobility and step cycle of *Tetragonias njalilus*.

As shown by Hutchinson and Gatesy (2000), the potential range of femoral mobility forms a hemisphere centred at the acetabulum, with a radius equal to the length of the femur and an equator orientation parallel to the sacrum. To express femoral movement within this hemisphere, three degrees of freedom are important for description (Gatesy 1991; Hutchinson and Gatesy 2000). These are retraction, abduction, and long-axis rotation (Fig. 3).

Results

Posture of the pelvic girdle

The stance is considered to be the proper arrangement for description of the pelvic and hind limb elements. The iliac blade forms the major vertical component, whereas the ischium and pubis describe a distinct angle of about 60° to the vertical plane, pointing ventromedially (Fig. 4). This angle is best preserved and observable in the pelves of the holotype, where all pelvic bones are fused in the acetabulum. Such a direct observation of this angle could not be made in the only complete pelvis of *Tetragonias*, which is part of the immature specimen UMZC T.754, since the pelvic bones of this individual are still unfused due to its early ontogenetic stage. But here as well, the shape of the medial bone surface of the

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[2]Fröbisch, J. A revision of the hind limb anatomy with a myology reconstruction of *Tetragonias njalilus* (Synapsida, Dicynodontia). In Preparation.

Fig. 3. The three degrees of freedom of the femur: (A) retraction; (B) abduction; (C) long-axis rotation (A and B redrawn from Hutchinson and Gatesy 2000).
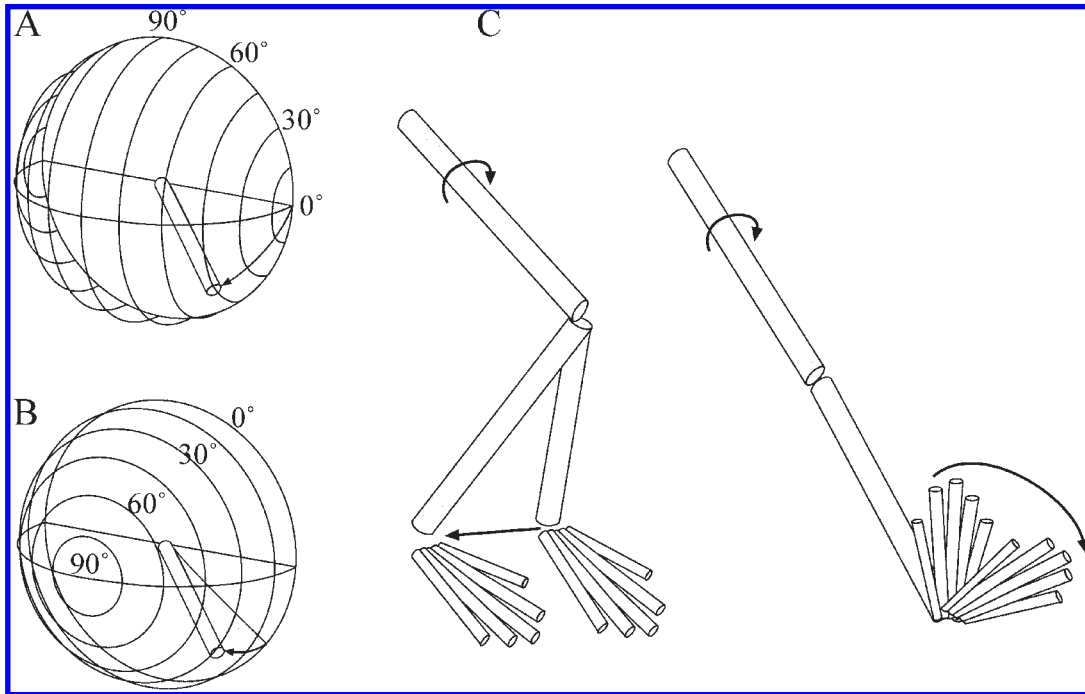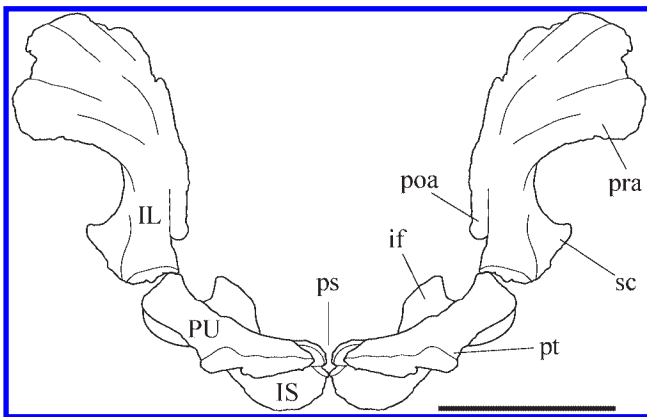

Fig. 4. Reconstruction of pelvic girdle (specimen UMZC T.754) in anterior view. if, ischial flange; IL, ilium; IS, ischium; poa, postacetabular part of ilium; pra, preacetabular part of ilium; ps, pelvic symphysis; pt, pubic tubercle; PU, pubis; sc, superacetabular crest. Scale bar = 10 cm.


pelvic girdle supports a distinct angle between the dorsal and ventral pelvic elements. As a result of this curvature in the pelvis of *Tetragonias*, the pubis and ischium extend far medially, and they are here reconstructed to meet with the corresponding part of the other side in a weak symphysis along the body midline (Fig. 4). This interpretation contrasts with the description of Cruickshank (1967, p. 194), who stated that it "is hard to see how the two halves of the pelvis of *Tetragonias* could have met in life, unless there was a considerable amount of cartilage between the ventral extremities." This discrepancy is clearly a misinterpretation, which results from Cruickshank's incorrect expectation that the orientation of the whole pelvis was essentially vertical.

The nature of the pubic or puboischiadic symphysis in dicynodonts has been debated extensively (King 1988). After reviewing this topic, Cox (1959) concluded that the absence of a sutured or fused bony symphysis was the usual condition in the Dicynodontia and that there is little evidence as to whether a cartilaginous or ligamentous connection was commonly present. The absence of a sutured symphysis has been suggested for *Kannemeyeria* (Pearson 1924), *Oudenodon* (= *Dicynodon andrewsi* (Broom 1925); = *Dicynodon kolbei* (von Huene 1931)), *Stahleckeria potens* (von Huene 1935), *Kingoria* (Cox 1959; King 1985), and "*Dicynodon*" *trigonocephalus* (King 1981a). In contrast, sutured or at least cartilaginous and ligamentous connections have been reported for *Lystrosaurus* (Watson 1912) and *Diictodon* (= *Dicynodon sollasi* (Broom 1925); Ray and Chinsamy 2003). In *Tetragonias*, the relatively straight medial margins of the puboischiadic plates suggest a contact that was certainly supported by ligaments or cartilage, but there is no evidence for a suture or fusion along the midline. A reduction of the bony pelvic symphysis in dicynodonts in contrast to a powerful and well-ossified ventral connection in "pelycosaurs" has been observed in all cases. Different functional interpretations of this significant feature have been suggested, ranging from reproductive adaptations for laying bigger eggs (Watson 1960) or even for viviparity (King 1981a, 1988) to the reduction of postural and locomotor stresses at the ventral midline (Hotton 1986).

Another point is that, although all hip bones are isolated in specimen UMZC T.754, Cruickshank (1967) postulated that the pubis and ischium were fused in life, whereas they remained mobile against the ilium. In contrast to this, all pelvic bones in the holotype of *T. njalilus* at the left and also at the right side of the pelvic girdle are completely fused. Thus, it is apparent that movement between the pelvic bones of one body side was impossible in the mature animal.

Fig. 5. Orientation of the pelvis of *Tetragonias njalilus* (specimen UMZC T.754) in lateral (A) and medial (B) view. Gray lines indicate the direction of load transmission (arrow) from the vertebral column to the pelvis and the angle between the vertebral column and the horizontal plane. Scale bar = 10 cm.
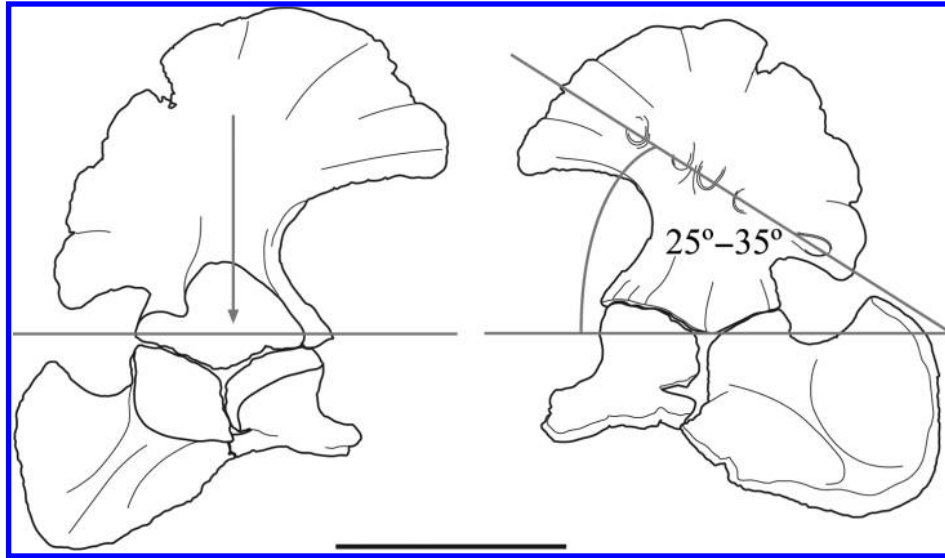
In addition to the separation of the pelvis into a vertically and a more horizontally oriented part, its orientation also needs to be defined concerning a possible gradient to the horizontal, a consequence of an upward-arched backbone of the animal. This topic has already been discussed by Cruickshank (1967), who proposed a strong curvature in the vertebral column in all dicynodonts. In his analysis, he calculated an angle between the anterior and posterior parts of the vertebral column of 87° for *Tetragonias*, assuming an average ventral taper of 3° per vertebral centrum and a number of 29 precaudal vertebrae, excluding atlas and axis, which were thought to be held horizontally. This would result in an angle of about 45° between the sacrum and the horizontal plane.

The present work reveals new information on the structure of the pelvis of *Tetragonias* that indicates a different and less distinct angle of the sacrum to the horizontal (Fig. 5) compared with that proposed by Cruickshank (1967). The sacral rib articulation facets on the medial surface of the ilium indicate that the area of the heaviest load transfer from the vertebral column to the pelvis and hind limb is via the two most prominent facets, numbers two and three. They are situated in the centre of the medial side of the iliac blade, right above the prominent supraacetabular crest laterally. This location supports a backward rotation of the entire pelvic girdle because the load transmission obviously must occur perpendicular to the horizontal and where the bone is thickest, represented by the peduncle of the ilium. With this pillar oriented vertically, the row of sacral rib facets shows an angle ranging from 25° to 35° to the horizontal plane, suggesting a distinctive but less pronounced curvature of the backbone than that proposed by Cruickshank.

In this orientation of the pelvic girdle, the supraacetabular crest is strongly overhanging the acetabulum, forming a well-developed dorsal roof to the laterally pointing articulation surface. This feature emphasizes a direct transmission of the body load from the pelvis to the femur, resulting in a more adducted position of the hind limb.

Hip joint mobility

In the stance, the stylopodium is almost in a parasagittal position, with its major orientation pointing anteroventrally (Fig. 6B). This femoral arrangement in stance, but also its flexibility during motion, is on the one hand determined by the acetabular–femoral articulation, and on the other hand strongly dependent on its distal articulation with the zeugopodials.

The proximal joint is defined by the interactions between the acetabular articulation facet and the femoral head. The latter is situated far medially and anteriorly from the long axis of the bone (Fig. 6H), suggesting an adducted position of the femur. Although there is no evidence of a neck, the ball-and-socket joint allows the femur a great amount of flexibility as a function of the three degrees of freedom.

As mentioned previously, the potential range of femoral mobility forms a hemisphere centred at the acetabulum, with a radius equal to the length of the femur and an equatorial orientation parallel to the sacrum (Fig. 3A). In contrast to this potential flexibility, the most reasonable range of femoral mobility within this hemisphere covers a much smaller area. For *Tetragonias* this has been determined by bone lock and was used to reconstruct the hind limb step cycle.

The maximal parasagittal rotation option of the femur includes an angle of about 160° (Fig. 7A). This value is very high because it is measured between the maximal protraction in a resting pose of the animal (Fig. 8) and the maximal retraction phase during the step cycle. It is evident that this value does not represent the definite excursion angle during the stride. In a fast-walking animal this angle probably varied between 90° and 110° and is likely to have been smaller during slow locomotion.

The femoral abduction mobility is much more restricted by bone lock, caused by the prominent proximal trochanters of the femoral head and the shape and size of the acetabulum, including the strongly overhanging supraacetabular crest. This limits femoral abduction to about 45°–50°. If soft tissues like cartilage, muscles, and ligaments are taken into

Fig. 6. Hypothetical step cycle for *Tetragonias njalilus* as reconstructed from the holotype material in lateral (A–F) and anterior (G–L) view (foot shown schematically): (A, F, G, L) maximal protraction phase; (B, H) stance phase; (C, I) retraction phase; (D, J) maximal retraction phase; (E, K) protraction phase. Sine curve reflects vertical undulation of the vertebral column during the stride.
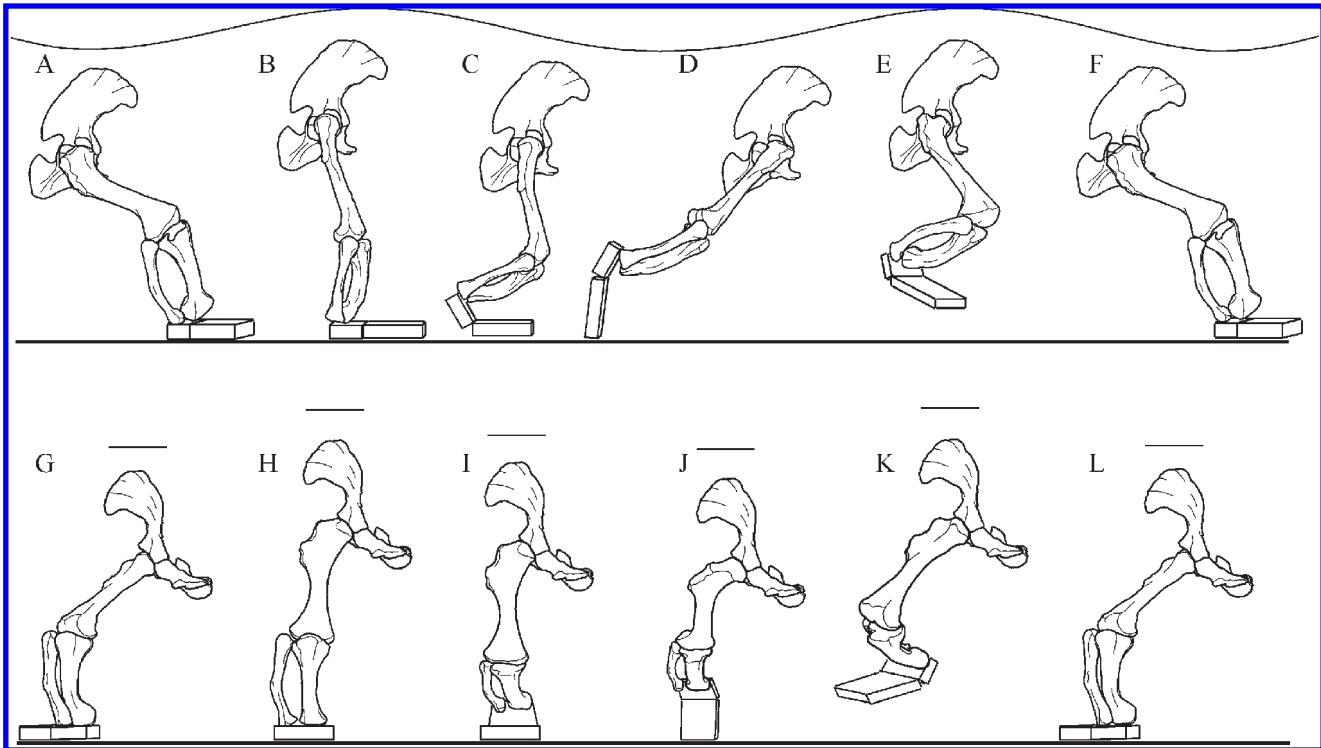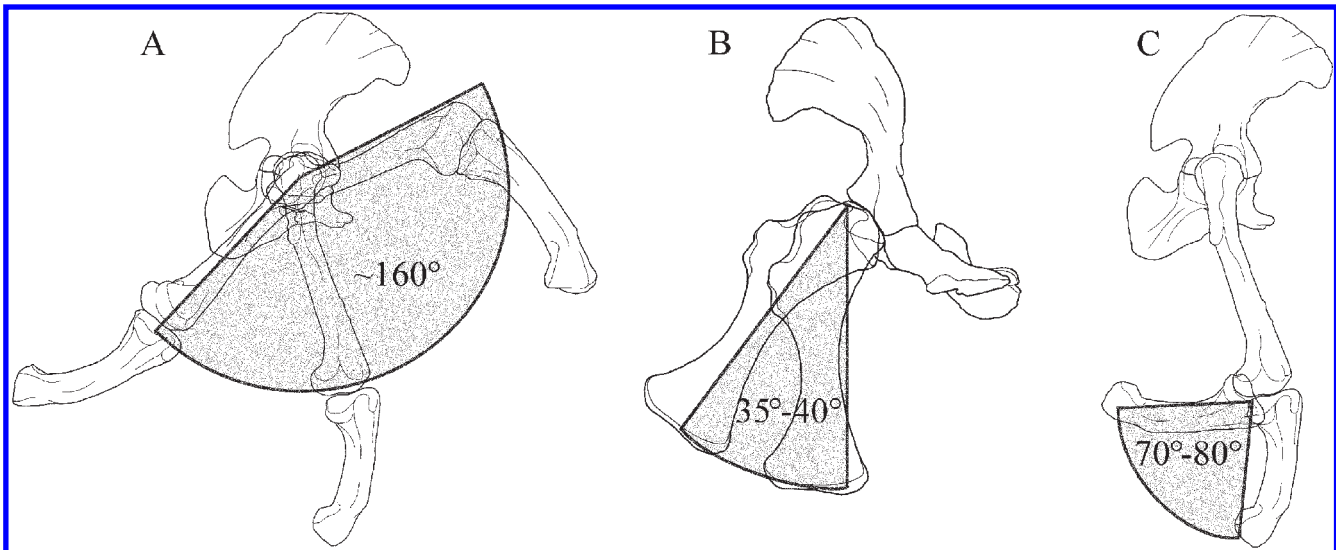

Fig. 7. Flexibility of the femur in protraction–retraction (A) and abduction (B); flexibility of the knee joint (C).


account, the abduction was probably limited to 35°–40° (Fig. 7B). The greatest abduction values were measured for two postures with little or no load on the whole leg. These postures are the resting pose (Fig. 8) and the protraction phase during the stride (Fig. 6G) to lift the pes off the ground. In contrast to this, the smallest abduction angles of just a few degrees are significant for postures and phases during the stride, which are correlated with the maximal body load on the leg (Fig. 6H).

The third degree of freedom of the femur is rotation about its long axis. The use of lateral and medial long-axis rotation

as relative terms for movement is considered to be more practical than absolute data. The femoral orientation during stance with its transverse axis perpendicular to the sagittal plane is considered to be the neutral position. Hutchinson and Gatesy (2000) showed that long-axis rotation of the femur does not change its position within the hemisphere. Such movements rather affect the zeugopodium and autopodium, being strongly dependent on flexion or extension in the knee joint (Fig. 3C). In a fully extended knee, long-axis rotation causes a spin of the foot, "toeing out" in lateral rotation and "toeing in" in medial rotation. In contrast to this,

Fig. 8. Resting pose of *Tetragonias njalilus* as reconstructed from the holotype material in right lateral (A) and anterior (B) view. Scale bars = 10 cm.

Fig. 9. Right hind foot of *Tetragonias njalilus* (specimen UMZC T.754) in dorsal view. Scale bar = 5 cm.
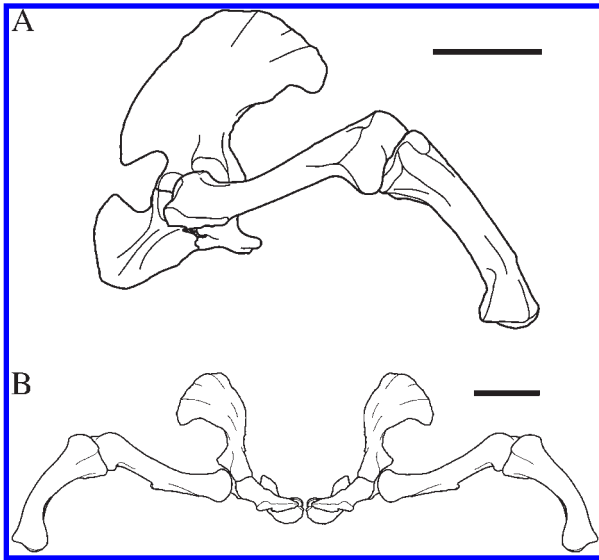

medial rotation with a flexed knee results in abduction of the zeugopodium, whereas lateral rotation causes adduction. In *Tetragonias*, the greatest long-axis rotation angles of the femur could be obtained in the resting posture and protraction phases of the stride. Thereby, the femur is rotated laterally about a few degrees in relation to the neutral position. During the stride, the femur continuously rotates medially, finishing the maximal retraction phase approximately in neutral orientation or with a slight medial rotation.

Knee joint mobility

The distal femoral articulation is characterized by a hinge-like joint, only allowing flexion and extension as major movements of the crus. In the stance, the orientations of the tibia and fibula are considered to be essentially vertical. Their proximal and distal articulation surfaces dip slightly posteriorly, towards the middle of the shaft. This is a result of the curvature of the tibia. The possible movement in the knee joint is dependent on a number of factors. Extension is mainly restricted by the cnemial crest, the intersulcal ridge, and the limited separation of the femoral condyles distally. The bone lock suggests a maximal knee extension with an angle of about 25°–30° to the long axis of the femur. Therefore, a straight orientation of the knee in full extension, as was suggested for *Placerias* (Camp and Welles 1956), was not possible in *Tetragonias*. During knee flexion, the movement was likely restricted by knee ligaments and the maximal angle between the distal femoral condyles and the proximal tibial sulci. For maximal flexion of the knee, the bone lock suggests an angle of about 100°–105° to the femoral long axis. Therefore, the knee could be flexed only slightly above 90°. Thus, the maximal excursion angle of the knee joint varied between 70° and 80° (Fig. 7C).

This condition represents a high degree of flexibility within the knee joint of *Tetragonias*. This interpretation is supported by the presence of a well-developed popliteal fossa at the posterior side of the distal part of the femur. This fossa indicates the presence of cruciate ligaments inside the knee
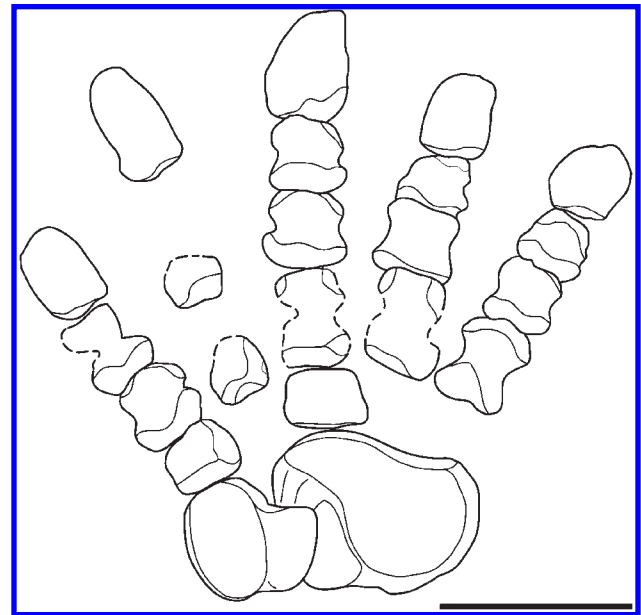
joint and might also be correlated with the existence of menisci.

Ankle joint mobility

The ankle joint is of particular importance for the determination of an animal's locomotor abilities (Kemp 1982) and provides information on potential adaptations for flexion, extension, and rotation of the foot. In *Tetragonias*, the articulation between zeugopodium and autopodium shows a relatively simple organization. The tarsus and pes form a plantigrade foot with the digits directed anteriorly (Fig. 9). There is a small amount of rotational flexibility compared to the tight, hinge-like knee joint. This is expressed by a less restricted but still definite articulation between the zeugopodium and the autopodium. The rotational component within the ankle joint is only of marginal significance, however. The main movements of the ankle joint are flexion and extension.

The tibia represents the main weight-supporting element of the zeugopodium. The distal articulation with its domed, further distally projecting, medial side clearly fits onto a facet on the medial side of the dorsal astragalar surface. This facet of the astragalus is anteroposteriorly elongated and is relatively larger than the connecting distal part of the tibia. Such an extension emphasizes the mobility of the ankle joint, being mainly operational for flexion and extension. Thereby, the higher lateral part of the distal tibial articulation is supported by the lateral side of the astragalus, which is elevated dorsally. This is a result of the mediolateral arching of the tarsus (Fig. 10).

The lateral part of the ankle is supported by the fibula. Its distal articulation surface clearly projects ventrally, and its orientation is not significantly affected by the distinctively curved shaft. This articulation facet connects with the dorsal surface of the calcaneum, where a broad, concave facet enables slightly more flexibility within this part of the ankle joint.

This configuration of the ankle joint strongly implies a

Fig. 10. Right proximal tarsus of *Tetragonias njalilus* (specimen UMZC T.754) in posterior view. afc, articular facet of calcaneum; cpa, channel for perforating artery; ma, medial articular facet of astragalus; olp, overhanging later process of astragalus; pp, pyramidical process of calcaneum. Gray curve illustrates the arch formed by the proximal tarsus.
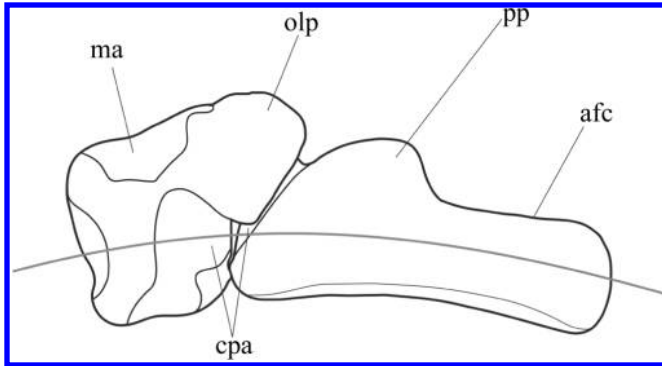
plantigrade posture of the foot in *Tetragonias*. This requires an additional joint within the foot to enable a more effective propulsion and dorsiflexion of the foot. The exact position of this intertarsal joint cannot be reconstructed because of the fragmentary preservation of the distal tarsal elements. It may have been situated between the distal tarsals and the metatarsals, however, because the latter elements are phalangiform. Additional flexibility during the stride might also have existed between all other elements of the foot.

The primary axis of dorsiflexion while rolling off the foot also cannot be reconstructed with certainty. Cruickshank (1967) figured and mentioned a distinct asymmetry within the foot of specimen UMZC T.754. This is thought to be primarily expressed in an opposing twist of the terminal phalanges of the first two digits (preaxial) in relation to digits three to five (postaxial). Personal examination of the material corroborates this observation only with respect to the terminal phalanx of digit three, which shows a distinct twist to the lateral side. It is more likely that this condition is pathological, however, as it has briefly been noticed by Cruickshank. This is also supported by a well-preserved foot of a juvenile specimen of *Tetragonias* in the Tübingen collection, which does not show the described asymmetry in the pes. Therefore, it is most likely that the axis of dorsiflexion while rolling off the foot runs through the third digit in *Tetragonias*, which is the longest and most robust element of the pes in dicynodonts. This would guarantee the longest contact with the ground for an efficient force-transmission system.

Step cycle

A hypothetical stride for the hind limb of *Tetragonias* was reconstructed based on its known anatomy (Fröbisch 2003) and its locomotor abilities (this study). The resulting step cycle is expressed in a sketch, showing the right pelvis and hind limb during locomotion in lateral and anterior views (Fig. 6). The continuous motion of the hind limb is expressed in a few representative phases that show significant changes during action. The cycle begins and ends with the phase of maximal protraction, with the rest of the stride being divided into four additional stages, namely stance phase, retraction phase, maximal retraction phase, and protraction phase.

Maximal protraction phase (Figs. 6A, 6F, 6G, 6L)

In the maximal protraction phase the hind limb reaches its anteriormost position during the stride, and little load is put on the leg during the first ground contact. The femur is retracted at an angle of about $50°–60°$ to the sacral equator, and its angle of abduction is relatively high at about $15°–25°$. In addition, the femur is rotated laterally a few degrees and the knee is not fully, but highly extended ($\sim35°$ towards the femoral long axis). This causes a slight adduction of the zeugopodium, resulting in a position of the foot that is slightly closer to the body midline than the knee. The entire plantar surface of the foot contacts the ground, and it shows a slight angle to the sagittal plane, pointing anterolaterally.

Stance phase (Figs. 6B, 6H)

In the stance stage the hind limb is in neutral position with maximal body load on the leg. The femur is retracted at an angle of about $95°$ relative to the sacral equator, which results in an orientation with the distal end of this element pointing slightly anteroventrally ($\sim20°$ to the vertical). It shows a slight abduction angle of approximately $5°$, and it is not significantly rotated about its long axis, being in the neutral orientation. The knee joint is in full extension ($\sim25°$ to femoral long axis), which results in an almost vertical orientation of the tibia. The whole plantar surface of the foot is still on the ground, but its orientation has twisted medially since the maximal protraction phase, with the digits pointing anteriorly now. In contrast to the previous stage, the astragalus is also rotated anteriorly. Thereby, the tibia slid anteriorly over the dorsal articulation surface of the astragalus, while the fibula still articulates with the lateral side of the calcaneum.

Retraction phase (Figs. 6C, 6I)

The retraction phase provides propulsion. The femur did not move significantly since the stance phase. Femoral retraction has increased slightly to an angle of about $105°$, so the femur is mainly oriented ventrally ($\sim10°$ to the vertical). In this posture, the femur is fully adducted and still in neutral orientation, not showing any long-axis rotation. The most striking difference from the stance position is expressed in the position of the zeugopodium and autopodium. The knee joint is flexed at an angle of $30°–40°$ ($60°–70°$ to femoral long axis). In this position, only the pes is still on the ground, being flexed towards the tarsus.

Maximal retraction phase (Figs. 6D, 6J)

The maximal retraction phase is the last stage of the propulsive phase right before the pes leaves the ground for protraction. The femur is maximally retracted, to about $150°–160°$ to the sacral equator ($35°–45°$ beyond the vertical). It shows a very slight abduction angle, so the femur is mainly oriented posteroventrally. In addition, the femur is rotated medially along its long axis at a very small angle. This results only in a negligible twist of the foot, however, because the knee joint is in maximal extension ($25°–30°$ to femoral long axis) and the foot only contacts the ground with the tip of the third terminal phalanx.

Protraction phase (Figs. 6E, 6K)

The protraction phase represents the recovery stroke. The femur is retracted only about $70°–80°$ in relation to the

sacral equator, but it shows the highest abduction angle during the stride (25°–35°). The knee joint reaches maximal flexion with an angle of about 100°–105° to the femoral long axis. This causes a strong adduction of the lower leg, with the foot being rotated laterally and situated close to the body. This prevents the foot from being dragged along the ground during protraction.

In summary, the propulsive phase of the stride of *Tetragonias* primarily takes place in a highly adducted posture of the entire hind limb, only reaching abduction angles of a few degrees. During protraction, the femur shows the greatest abduction angle, and it is slightly rotated laterally, which results in a relative adduction of the lower leg and an orientation of the foot directed anterolaterally rather than straight anteriorly. This orientation remains until the foot is placed on the ground again and starts the next retraction phase. Thus, the largest abduction angle in a stage with at least some body load on the leg is achieved at the beginning of the stride (15°–25°). This is interpreted to indicate the presence of a lateral undulation of the vertebral column that causes a swinging movement of the hip. In addition, the hip is thought to undulate in a dorsoventral direction in the form of a sine curve as illustrated in Fig. 6.

Discussion

For dicynodont anomodonts, a relatively high number of functional analyses of the locomotor apparatus have been attempted. Specialized forms and general locomotor types have previously been examined. All taxa show a strongly abducted (sprawling) forelimb step cycle, whereas the hind limb seems to develop from a primitively abducted posture (e.g., in *Robertia* (King 1981*b*)) to a more adducted one in derived taxa (e.g., *Kingoria* and the Kannemeyeriiformes (King 1985; Walter 1985, 1986)).

Two general models for the hind limb locomotion of derived dicynodonts have been proposed. The first one was introduced by King (1981*a*, 1988, 1990), who considered *D. trigonocephalus* to possess a locomotor apparatus typical of dicynodonts. She proposed a complex hind limb movement, combining a sprawling phase and an upright phase within the same step cycle. In contrast, Kemp (1982) argued in the second model that the locomotion of dicynodonts may have functioned according to his dual-gait hypothesis, which he proposed for therapsids in general. He investigated the stance and gait in a therocephalian and observed a remarkable specialization in the ankle, with a newly evolved mobile joint, allowing rotation as well as flexion and extension, not present in "pelycosaur"-grade synapsids, but actually analogous to the intertarsal joint of modern crocodiles (Kemp 1978). This condition is thought to be functionally intermediate between a primitive sprawling gait and an erect gait and would result in a speed-dependent gait similar to that of extant crocodilians. More than any other single feature, the modification of the ankle joint lends support to this hypothesis of a dual gait in therapsids. Recently, the assumption of Kemp (1982) that a speed-dependent multipurpose gait could have been ancestral to the mammalian parasagittal gait was tested statistically and appeared biomechanically plausible (Blob 2001).

King (1985) also examined the locomotor abilities of

Kingoria, a highly derived Permian form, which possesses a strongly adducted hind limb step cycle but is not on the lineage to the Triassic kannemeyeriiform dicynodonts, belonging instead to the Emydopidae (see Fig. 1). Her investigation of the ankle joint, being so far the only one on dicynodonts, does not support a dual gait in this taxon, but *Kingoria* seems to be adapted for adducted locomotion to a greater degree than any other known dicynodont. Some features of this form show a derived condition even beyond that of the Kannemeyeriiformes. For example, the pelvis is highly modified towards the mammalian condition (e.g., very slender and elongate anterior process of ilium, reduction of dorsal expansion of iliac blade, and complete reduction of pubic tubercle), and there is evidence for a patella and a small tuber calcanei.

The present study of the basal kannemeyeriiform *Tetragonias* provides data about its ankle joint which demonstrate unequivocally that this form and probably all kannemeyeriiform dicynodonts were not capable of using a highly abducted (sprawling) movement during any phase of the stride, neither permanently nor on a speed-dependent basis. Instead, a number of characteristics imply an upright posture and highly adducted gait throughout most of the step cycle of derived dicynodonts such as *Tetragonias*. These characteristics include the anteriorly elongated iliac blade of the pelvis, the strongly overhanging supraacetabular crest, the medially projecting femoral head, the presence of prominent and laterally projecting trochanters at the proximal end of the femur, the almost symmetrical condyles at the distal end of the femur, and the structure of the ankle joint, which restricts its flexibility primarily to flexion and extension and inhibits extensive rotational movements. When plotted in a dicynodont phylogeny (Fig. 1), the characters are distributed over multiple nodes in a step-like fashion, which suggests a gradual evolution of the upright posture within dicynodonts.

The hypothesis of a dual-gaited locomotion in the Synapsida as an intermediate condition during the evolutionary transition from a sprawling to a parasagittal gait (Kemp 1982) has previously been tested and was considered to be biomechanically plausible (Blob 2001). A speed-dependent multipurpose gait is here rejected for derived dicynodonts because their ankle joint does not allow the extensive rotational movements necessary for a dual-gaited locomotor model. In fact, it is questionable whether Kemp's (1982) hypothesis of a dual-gait stage in postural evolution is at all applicable to dicynodonts. The presence of a dual gait in therocephalians (Kemp 1978) does not necessarily imply its presence in anomodonts as well, particularly when considering that both taxa represent distinct phylogenetic lineages that acquired an upright hind limb posture independently. This hypothesis can be tested in future analyses of more basal anomodonts, however, and might provide valuable insights into the evolution of upright posture in general. In any case, if the upright stance and gait of derived dicynodonts evolved according to Kemp's hypothesis, the dual-gait phase of this evolutionary scenario must have occurred earlier.

In summary, the step cycle of *Tetragonias* is characterized by a highly adducted posture of the entire hind limb during retraction, and in the protraction phase the femur shows maximal abduction and a distinct rotation angle in lateral direction. The latter causes relative adduction of the lower

leg and also a slight lateral rotation of the foot. Thus, the largest abduction angle with at least some body load on the leg is at the beginning of the stride and probably at the end of it. Similar hind limb orientations during the stride have been described for the prosauropod dinosaur *Plateosaurus* (Christian et al. 1996). Such a pattern, where the hip approaches the supporting foot, has also been reported for extant taxa (Christian 1995), such as recent monitor lizards and chickens, although they possess radically different gaits. This feature in hind limb locomotion seems to be related to an undulating movement of the vertebral column in lateral directions, however, causing a swinging movement of the hip. An additional movement of the hip is expressed as undulation in a dorsoventral direction as a result of the shifting body load from one leg to the other (Fig. 6).

Undulating horizontal movements of the longitudinal body axis appear to be a reasonable part of dicynodont locomotion and of prosauropod dinosaur locomotion, since lateral undulation is a plesiomorphic feature in tetrapod locomotion. Although both groups have strongly adducted (erect) hind limbs, their forelimbs move in an abducted (sprawling) pattern with a major rotational component within the horizontal plane to increase the step length of these relatively short extremities (King 1988; Christian et al. 1996) and to keep the foot pointing forward. Direct observations of this phenomenon are not part of this study, but for reasons of completeness such additional features are mentioned to provide an overall picture of the locomotor apparatus of *Tetragonias*. The possibility of a lateral undulation of the vertebral column in dicynodonts has previously been discussed by several authors. Cox (1959), Watson (1912, 1960), Cruickshank (1967), and Hotton (1986, 1991) stated that there was great flexibility, especially in the anterior dorsal part of the vertebral column. In contrast, King (1981*a*) reported a less flexible backbone in dicynodonts compared to that of "pelycosaur"-grade synapsids. This was later discussed by Hotton (1986), who recognized a flexibility reduction in the vertebral column only as a result of reduction in vertebral count. This study of *Tetragonias* clearly supports the hypothesis that lateral undulation is an important part in dicynodont locomotion. Nonetheless, future research on the locomotor apparatus of dicynodonts and especially the flexibility of the vertebral column is necessary to further test this new model.

Lastly, all the proposed models for locomotion in derived dicynodonts describe an evolutionary trend within anomodonts towards an upright posture of the hind limb, whereas the forelimb retains a sprawling posture. The independent acquisition of a parasagittal gait of the hind limb has been proposed for a number of amniote lineages, including anomodonts, dinocephalians, and theriodonts (Blob 2001) within the Synapsida, and ornithosuchids, rauisuchians, early crocodylomorphs, pterosaurs, and dinosauromorphs (Benton 2005, p. 143) within the Reptilia (sensu Modesto and Anderson 2004). It has been proposed that there is a causal relationship between the evolution of a parasagittal gait and an increase in body size (Biewener 1989, 1990; Blob 2001). This phenomenon can be explained as a response to increased biomechanical stress on the limb. The adoption of an upright posture reduces the otherwise increasing stress on the bones by aligning the limb closer to the vector of the ground reaction force (GRF), which is the force that the ground exerts on a limb in reac-

tion to the force being applied on the substrate by the limb during stance and gait. In animals with a primarily abducted (sprawling) limb posture, the GRF vector is lateral to the acetabulum and imparts an abduction moment about the hip joint. This force is opposed by strong ventral muscles, originating from the lateral surface of the puboischiadic plate and inserting on the shaft of the femur. In animals with a more adducted limb posture, the GRF vector is positioned closer to the body midline and rather creates an adduction moment about the hip joint. Therefore, this force needs to be opposed by dorsal muscles, originating from the lateral side of the ilium and inserting on the proximal femur. The expansion and differentiation of such a dorsal muscle, the M. iliofemoralis (Mm. glutei and M. tensor fasciae latae), in non-mammalian therapsids has been correlated with changes in limb posture from abducted (sprawling) to more adducted (erect) (Romer 1922).

An anteriorly and dorsally expanded iliac blade as origin and a proximally and laterally situated femoral insertion of the M. iliofemoralis are also present in *Tetragonias*, supporting this scenario. Moreover, it is suggested that the evolution of uprightness in the hind limb, although correlated with an increase in size, not only occurs in megaherbivores or other extremely large tetrapods, but also is already acquired in medium-sized taxa such as *Tetragonias*. Therefore, a parasagittal posture need not be accompanied by size increase; rather, body-size increase requires a more parasagittal posture.

Conclusion

The general model for hind limb locomotion in derived dicynodonts, as reconstructed here from a case study of the medium-sized Middle Triassic dicynodont *Tetragonias njalilus*, suggests the adoption of a highly adducted hind limb posture in the stance and during most of the stride. During retraction the step cycle is characterized by a highly adducted posture of the entire hind limb, and in the protraction phase the femur shows maximal abduction and a distinct rotation angle in the lateral direction. This rotation causes relative adduction of the lower leg and additionally a slight lateral rotation of the foot. Therefore, the largest abduction angles with some body load on the hind limb are at the beginning of the stride and at its end. This is interpreted as evidence for a sinusoidal movement of the vertebral column during dicynodont locomotion. In addition, the backbone describes a distinct curvature that is expressed in a gradient of the sacrum to the horizontal. Lastly, the pelvic girdle also performed positional changes in the vertical direction as a result of the shifting body load during the stride.

The proposed model for locomotion in derived dicynodonts describes an evolutionary trend within anomodonts towards an upright posture of the hind limb. In addition, independent acquisition of a parasagittal hind limb movement has been proposed for a number of amniote lineages, primarily on the basis of statistical approaches. The best way to test these hypotheses is by performing biomechanical case studies for these taxa, as done here for *Tetragonias*. This phenomenon of an independent evolution of uprightness in the hind limb of several amniote lineages prior to the origin of mammals has been associated with an increase in body size to reduce

the increasing biomechanical stress on the limb. For the Dicynodontia this scenario is plausible, considering the occurrence of large herbivorous taxa in the Triassic, but this study shows that a parasagittal gait already evolved in medium-sized basal members of the Kannemeyeriiformes, as exemplified by *Tetragonias*. Therefore, it is here suggested that a parasagittal posture was a prerequisite for body-size increase in tetrapods.

Acknowledgments

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