Morphofunctional Evolution of the Pelvic Girdle and Hindlimb of Dinosauromorpha on the Lineage to Sauropoda

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Nothing in Biology Makes Sense Except in the Light of Evolution

(Theodosius Dobzhansky)

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The Road Not Taken

Two roads diverged in a yellow wood,
And sorry I could not travel both
And be one traveller, long I stood
And looked down one as far as I could
To where it bent in the undergrowth;

Then took the other, as just as fair,
And having perhaps the better claim,
Because it was grassy and wanted wear;
Though as for that the passing there
Had worn them really about the same,

And both that morning equally lay
In leaves no step had trodden black.
Oh, I kept the first for another day!
Yet knowing how way leads on to way,
I doubted if I should ever come back.

I shall be telling this with a sigh
Somewhere ages and ages hence:
Two roads diverged in a wood, and I -
I took the one less travelled by,
And that has made all the difference.

(Robert Frost)

Chapter 1

General Introduction: Sauropoda
Overview and Goals

1.1 INTRODUCTION

Sauropods are characterized by a small skull in relation to their body size, a long neck and tail, columnar limbs and a barrel-shaped trunk. More than 100 valid sauropod genera are known to date, discovered in the terrestrial sediments on all continents. Sauropods first occurred in the Norian/Rhaetian and were extinct at the Cretaceous/Tertiary boundary (see Upchurch et al. 2004, Smith and Pol 2007). The most outstanding feature of sauropods is their exceptionally large body size. Sauropods are by far the largest animals that ever lived on earth. The largest sauropod known from a reasonably complete skeleton is the sauropod *Brachiosaurus brancai* from the Upper Jurassic of East Africa. With a length of 25 m and a height of about 13 m, the body mass estimated for *Brachiosaurus* ranges between 25 and 87 tons (see Anderson et al. 1985, Henderson 2006). The widely ranging results are related to different methods applied, but also demonstrate the difficulty in calculating the mass of extinct animals, in which the body bauplan differs significantly in body size and shape from that of extant animals. Alexander (1998) argued that an average mass of 45 to 50 tons appears to be adequate for *Brachiosaurus*. Incomplete skeletons indicate that some sauropods were even larger than *Brachiosaurus*. *Argentinosaurus huinculensis* from the Lower Cretaceous of South America and *Supersaurus* sp. from the Upper Jurassic of North America have been estimated with a body mass of 100 tons (Hokkanen 1986, Benton 1989), and *Amphicoelias altus* from the Upper Jurassic of North America has been estimated with 150 tons (Paul 1998). Nevertheless, the incompleteness of the specimens appears to be inadequate to support these claims and Alexander

(1998) argued that the heaviest sauropods might have been between 50 and 80 tons. In fact, more recent body mass estimates calculated a body mass of around 70 tons for *Argentinosaurus* (Mazzetta et al. 2004). With a body mass of at least 50 tons, sauropods are by the order of a magnitude heavier than other – extinct or extant – terrestrial vertebrates. The upper body size boundary for theropods is found to be around 10 tons (Carrano 2005, 2006). The largest theropod known from a complete skeleton is *Tyrannosaurus rex* from the Upper Cretaceous of North America with an estimated mass of 7 tons (Anderson et al. 1985, Alexander 1989, Farlow et al. 1995). With an estimated body mass of 13 to 14 tons, the incomplete skeletons of *Carcharodontosaurus saharicus* (Stromer 1931) from the Upper Cretaceous of Africa and *Giganotosaurus carolinii* (Coria and Salgado 1995) from the "middle" Cretaceous of South America indicate that some theropods might have been heavier than *Tyrannosaurus* (Therrien and Henderson 2007). The largest ornithischian known from a reasonably complete skeleton is *Shantungosaurus giganteus* from the Upper Cretaceous of China (Hu 1973). Seebacher (1999) estimated the body mass of *Shantungosaurus* with 22 tons. This is considerably more than the estimated mass of other large ornithischians, which ranges between 1 to 4 tons (see e.g. Peczkis 1994). With an estimated body mass of around 11 tons (Fortelius and Kappelman 1993), the mammalian *Indricotherium transouralicum* (Rhinocerotidae) from the Oligocene of Asia reaches the body mass of the largest theropods and ornithischians. However, the herbivorous *Indricotherium* is by far the largest terrestrial mammal known. Other mammals, extinct or extant, are considerably smaller than *Indricotherium*. The largest known extant herbivorous mammals are the African elephant with 5,5 tons (Laws 1966), the white rhinoceros with 2,2 tons, the hippopotamus with 1,5 tons and the giraffe with 1,2 tons (Owen-Smith 1988). Carnivorous mammals are considerably smaller. The largest extant carnivores, bears, have a body mass of up to 800 kg (Burness et al. 2001) and the body mass of the largest extinct carnivorous mammals has been estimated with up to 900 kg (see Savage 1973, Burness et al. 2001). Carrano (2006) argued that the reduction of body size in several marcronarian lineages indicates that sauropods probably reached their upper body size boundary. It was often argued that sauropods reached the upper body size boundary for terrestrial tetrapods (e.g. Upchurch et al. 2004). This body upper size boundary was thereby regarded to be mechanical: larger tetrapods were not able to support their body mass on land. Hokkanen (1986), however, calculated that terrestrial quadrupeds were capable to support a body mass of up to 100 tons.

Although there is no direct evidence for the diet of sauropods, the exceptionally large body size and features in the skull and teeth are suggestive for an obligate herbivorous diet (e.g. Bakker 1971, Coombs 1975, Upchurch and Barrett 2000, Barrett and Upchurch 2007). Independent from the metabolic rate assumed, the large body size of sauropods required a large amount of plant material. It has been shown that sauropods had powerful shearing bites and were capable of a relatively precise occlusion. Nonetheless, the lack of fleshy cheeks has prevented extensive mastication (Barrett and Upchurch 1995, 2007, Barrett 2000). It was commonly assumed that sauropods possessed a gastric mill, which assisted the mechanical breakdown of the plant material in the gut (Calvo 1994, Christiansen 1996). Recent studies (Wings and Sander 2007), however, showed that there are good reasons to doubt that a gastric mill was present in the gut of sauropods. Anyhow, the elongated trunk of sauropods provided space for an elongated gut with a long passage time. A long passage time allowed thorough microbial fermentation to take place. Furthermore, the large body size of sauropods results in a decrease in the mass-specific metabolic rate, which allowed subsidence on poor-quality, high-fiber vegetation (Farlow 1987, Barrett and Upchurch 2007). The function of the long necks in sauropods is a subject of ongoing discussion. Whereas some authors argued for a subhorizontal neck position (e.g. Martin 1987, Martin et al. 1998, Stevens and Parrish 1999), other authors reconstructed a subvertical neck position (e.g. Christian and Heinrich 1998). The position of the neck is supposed to have an impact on the feeding strategy of sauropods in terms of the question if they were high browsers or low browsers. Regardless of the impact of the neck posture on the feeding strategy, Upchurch and Barrett (2000) argued that variations in the length of the cervical ribs and neural spines indicate that neck function might have varied between sauropod taxa. In the past, non-sauropodan sauropodomorphs have been regarded as predatory, scavengers, omnivores, and herbivores (Galton 1985, Barrett 2000). However, features in the skull, dentition, and the overall body shape are suggestive for a herbivorous or omnivorous diet in the majority of these taxa (Barrett 2000, Galton and Upchurch 2004, 2007, Barrett and Upchurch 2007). The tendency towards obligate herbivorous diet in sauropodomorphs is intimately associated with increasing body size (Barrett and Upchurch 2007). The tendency to elongate the trunk and the neck can be observed early in sauropodomorph evolution (Parrish 1998, Rauhut et al. in prep.). In fact, the combination of an elongated neck and large body size in some basal sauropodomorphs has led to the assumption that basal sauropodomorphs were the earliest high-browsing herbivores (Bakker 1978, Parrish 1998). The basal saurischian *Eoraptor lunensis* lacks clear herbivorous or carnivorous adaptations. Based on the heterodont dentition, an omnivorous diet is assumed. Other basal saurischians, such as *Herrerasaurus ischigualastensis* were assumed to be obligatory carnivorous, indicated by the serrated and caudally curved teeth and supported by a manus, which permitted grasping and raking (see Langer 2004). Until recently, little was known about the diet of non-dinosaurian dinosauromorphs. The lack of material belonging to the skull – only a poorly preserved and fragmentary maxilla assigned to *Marasuchus lilloensis* PVL 3871 is known (Bonaparte 1975, Sereno and Arcucci 1994) – and manus hampered the reconstruction of their diet. Nonetheless, mainly based on their small body size, basal dinosauromorphs are often regarded as omnivorous (e.g. Rauhut 2003). Most recently, the almost complete skeleton of *Silesaurus opolensis* allowed new insights into the diet of non-dinosaurian dinosauriform. The presence of a beak and denticulate teeth are suggestive for an obligate herbivorous diet at least in this taxon (Dzik 2003).

Ever since the first description of sauropods the biomechanical challenge of the load-carrying girdles and limbs has been of great interest to scientists. Owen (1841) was the first scientist to examine the remains of a sauropod, which he named *Cetiosaurus* or the "whale-lizard". Owen nested the remains of *Cetiosaurus* within the Crocodylia and assumed a strictly aquatic or even marine habitat for the sauropod. The reconstruction of an aquatic habitat was mainly based on the spongy texture of the bones normally recognized in marine animals. Although this line of evidence was later rejected by Hatcher (1903), the idea of an aquatic habitat of sauropods had a great impact on later studies. In the following 130 years, almost all paleontologists assumed sauropods to be more or less aquatic (e.g. Phillips 1871, Marsh 1883, 1884, Cope 1884, Hatcher 1901, Matthew 1903, Huene 1922, 1929, Wiman 1929). Amongst others, the extensive cartilaginous caps on the limb bones, indicated by the roughened articular surface not seen in extant terrestrial megaherbivores, were interpreted as being not suitable for supporting the body mass of sauropods on land (e.g. Osborn 1898, Hatcher 1901, Hay 1910, Lull 1915). As a consequence, it was assumed that sauropods had to use the buoyancy of water for support and assistance during locomotion (Osborn 1898, 1899a, 1899b, 1904, 1905, Hatcher 1901, Matthew 1910, Osborn and Mook 1919, 1921). Using the acetabulum and the development of the femoral head, Philips (1871) reconstructed a sprawling limb posture, a reconstruction later followed by others (e.g. Hay 1910). Although some authors considered a terrestrial habitat for at least some sauropods (e.g. Hatcher 1903, Gregory 1920), nobody considered a fully terrestrial habitat for sauropods apart from Riggs (1901, 1903), until Bakker (1971) and later Coombs (1975) published their influential papers on the habit and habitats of sauropods. Both Bakker and Coombs used comparative anatomy to demonstrate that features formerly interpreted as indicative for an aquatic habitat were actually consistent with a terrestrial habitat. Alexander (1985) was able to demonstrate that, despite of the cartilage caps, the appendicular skeleton of sauropods was in fact strong enough to support their body mass on land, later supported by the calculations of Hokkanen (see above). Most striking, however, were the evidences from the trackway record, which clearly show that sauropods walked on land (e.g. Thulborn 1990, Lockley et al. 1994, Wright 2005). To date, the fully terrestrial habit of sauropods is no longer questioned. Sauropods are commonly regarded as obligate quadrupeds (but see Barrett and Upchurch 2007) with a graviportal locomotor habit (e.g. Coombs 1978, Carrano 1999, 2005). The graviportal locomotor habit of sauropods represents adaptations for resisting extreme loading, which is reflected in the osteology: i) columnar limbs, ii) relative elongation of femur or relatively reduction of length of distal limb, iii) increased limb bone robusticity, iv) increased eccentricity cross-section of femoral shaft, v) reduction of muscle insertion sites, vi) broad metatarsus, vii) reduction of phalanges, viii) entaxonic pes, and ix) relatively elongated forelimbs (Coombs 1978, Carrano 1999, 2001, Wilson and Carrano 1999, Yates 2004). Measurements based on trackways assigned to sauropodan trackmakers indicate that their trackmakers were restricted to slow walking with estimated speeds of 3 – 6 km/hr (Alexander 1976, 1985), and sometimes 12 km/hr (Russell 1980). Froude numbers and bone strength indicators, however, show that top speeds of around 25km/hr might have been – at least theoretically – possible (Alexander 1991). Christiansen (1997) argued that the modest muscle scars on the limb bones of sauropods are indicative for a moderate musculature. Christiansen further noted that sauropods relied on propodial retraction, with M. caudofemoralis longus being the main femoral retractor (Gatesy 1990), contrary to the epipodal progression in most mammals. Non-sauropodan sauropodomorphs are commonly regarded as facultative bipeds with small-sized and lightly build taxa, such as *Anchisaurus polyzelus*, being more bipedal than others. *Thecodontosaurus antiquus* is often regarded as obligate biped. On the other hand, large-sized and heavy-build taxa, such as *Riojasaurus incertus*, are often regarded as more quadrupedal or even obligate quadruped (e.g. Galton 1990, Barrett and Upchurch 2007). Small-sized and obligate bipedal taxa were often assumed to be placed at the basis of the Sauropodomorpha (e.g. Gauthier 1986, Galton 1990), so that Sauropodomorpha has to be regarded as initially obligate bipeds (but also see Barrett and Upchurch 2007). Thus, obligate bipedal locomotion of Sauropodomorpha was assumed to be retained from their ancestors, the basal saurischians. The locomotor posture of basal saurischians, but also that of basal dinosauromorphs, is inferred mainly from the disparity of the limbs (e.g. Romer 1971a, Coombs 1978). Based on the relatively elongated forelimbs, an obligate quadrupedal locomotor posture is assumed for *Silesaurus* (Dzik 2003).

As early as 1883, Dollo presented the first restoration of soft-tissues in dinosaurs when reconstructing the muscles attaching to the fourth trochanter in *Iguanodon*. Since this first attempt, the myology of both the cranium and postcranium has been reconstructed in numerous studies. Relating to its assumed functional importance, the restoration of the myology of the pelvic girdle and hindlimb has always been of special interest to comparative anatomists. Traditionally, either crocodiles or birds have been used as extant models for the reconstruction of soft-tissues in dinosaurs (e.g. Huene 1907-1908, Gregory and Camp 1918, Gregory 1919, 1920, Romer 1923a,c, 1927b, Russell 1972, Borsuk-Bialynicka 1977, Norman 1986). Basing the soft-tissue reconstruction of an extinct animal on a single extant taxon, however, does not allow tracing the nature of evolution of the myology (e.g. Bryant and Russell 1992, Witmer 1995). The Extant Phylogenetic Bracket approach acknowledged this problem. By reconstructing soft-tissues of an extinct taxon in an explicit phylogenetic framework, the evolution of osteological correlates of soft-tissues from outgroup to ingroup taxa can be traced and their modifications interpreted in the light of evolution of the soft-tissues. To date, the Extant Phylogenetic Bracket approach is well established and its great potential has been demonstrated when applied to the reconstruction of the myology of the pelvic girdle of theropods (Gatesy 1990, Hutchinson 2001a,b, Carrano and Hutchinson 2002, Hutchinson and Garcia 2002, Hutchinson et al. 2005) and the ornithischian *Maiasaura peeblesorum* (Dilkes 2000).

As mentioned above, sauropod remains were classified as crocodilians, when first described by Owen (1841). In 1878, Marsh established the term Sauropoda for a new suborder of dinosaurs. Later, Huene established the terms Prosauropoda (1920) and Sauropodomorpha (1932), the latter containing prosauropods and sauropods. The Prosauropoda were subdivided in three families, Thecodontosauridae, Plateosauridae, and Melanorosauridae (Romer 1956). The idea that sauropods are descendants from initially small-sized bipedal taxa and that increasing body size and the tendency to obligate quadrupedal locomotion is reflected in the assumed systematic of sauropodomorphs. Thus, melanorosaurids are commonly regarded as transitional to sauropods (e.g. Romer 1956). Charig et al. (1965) advocated for an alternative scenario. Based on the development of the hand and foot skeleton, Charig et al. (1965) argued that it has to be ruled out that sauropods are the descendants from obligate bipedal sauropodomorphs. Alternatively, Charig et al. (1965) favored heavy-build and quadrupedal basal archosaurs ("thecodonts") as ancestors of sauropods, an idea later revived by Heerden (1997). Cladistic analyses of the interrelationships of sauropodomorphs, however, demonstrated that sauropods were descendants from non-sauropodan sauropodomorphs. The interrelationships of non-sauropodan sauropodomorphs and their relationship to sauropods, however, are a subject of ongoing discussion. Gauthier (1986) was the first who included sauropodomorphs in a cladistic analysis. Because Gauthier focused on the origin of Aves, the interrelationships of sauropodomorphs were not described in detail. The phylogenetic hypothesis of Sereno (1989), which showed that non-sauropodan sauropodomorphs ("prosauropods") are monophyletic, was very influential for later cladistic analyses (e.g. Benton et al. 2000) and had also impact on the reconstruction of the interrelationships of sauropods (e.g. Wilson and Sereno 1998, Wilson 2002, Upchurch et al. 2004). New finds of sauropodomorphs from Europe, South America, China, and India (e.g. *Saturnalia tupiniquim* [Langer et al. 1999], *Pantydrayo caducus* [Yates 2003a], *Unaysaurus tolentinoi* [Leal et al. 2004], *Lamplughsaura dharmaramensis* [Kutty et al. 2007], *Antetonitrus ingenipes* [Yates and Kitching 2003], *Lessemsaurus sauropoides* [Pol and Powell 2007], *Gongxianosaurus shibeiensis* [He et al. 1999], *Isanosaurus attavopachi* [Buffetaut et al. 2000], *Tazoudasaurus naimi* [Allain et al. 2004]), and the re-examination of known material have led to new hypotheses on the interrelationships of sauropodomorphs in recent years. Most importantly, the new phylogenetic hypotheses have demonstrated that basal sauropodomorphs have to be regarded as paraphyletic with respect to sauropods. However, the phylogenetic hypotheses differ with respect to the taxa, which constitute a monophyletic Prosauropoda (compare Yates 2003a,b, 2004, 2007, Yates and Kitching 2003, Galton and Upchurch 2004, Upchurch and Barrett 2007).

1.2 OVERVIEW AND GOALS

Body size is one of the most significant determinants affecting all aspects of the form and function of an organism (e.g. Schmidt-Nielson 1984, Biewener 2003). The exceptionally large body size that is not surpassed by any other group of terrestrial tetrapods and the unique bauplan of sauropods, with the small skull, long neck, trunk and tail, make them an interesting group to study the impact of body size on their morphofunctional evolution. In fact, the biomechanical challenge to support their enormous body mass on land, and the physiological and ecological reasons for the evolution of the sauropod bauplan have always been of great interest to scientist. Explained by the assumed functional importance, a special focus was drawn on the pelvic girdle and hindlimb. Although it is widely agreed that increasing body size has an impact on the evolution of the osteology and myology of the pelvic girdle and hindlimb, as well as locomotor function of the hindlimbs, the morphofunctional evolution of the pelvic girdle of sauropods has not been studied in detail yet. In the past, studying the morphofunctional evolution of the pelvic girdle and hindlimb was hampered by the lack of a material assigned to basal sauropodomorphs and basal sauropods, as well as the lack of a robust phylogenetic hypothesis of interrelationships of sauropodomorphs. In recent years, numerous new finds and new phylogenetic hypotheses have considerably improved our understanding of the evolution of sauropodomorphs.

The thesis presented here deals with the morphofunctional evolution of the pelvic girdle and hindlimb of dinosauromorphs on the lineage to sauropods, using an integrative approach combining osteology, myology, ichnofossils, and biomechanics. The goals of this work are:

1) studying the evolution of the osteology and myology of the pelvic girdle and hindlimb of dinosauromorphs on the lineage to sauropods;

2) studying the evolution of the hindlimb posture and locomotor posture of dinosauromorphs on the lineage to sauropods;

3) studying the impact of body size on the morphofunctional evolution of the pelvic girdle and hindlimb of dinosauromorphs on the lineage to sauropods.

An improved understanding of the morphofunctional evolution of the pelvic girdle and hindlimb will help to improve our understanding of the biology of sauropods and provides the basis for further studies on biomechanical aspect of the postcranium of sauropods as well as their physiology and ecology.

Chapter 2

Material and Methods

2.1 MATERIAL

The osteology of a wide range of extinct archosauriformes was studied in order to collect data of the pelvic girdle and hindlimb. Qualitative observations were made to study the presence and absence of potential muscle attachment sites. Measurements were taken with a digital caliper or measuring-tape, and documented with photographs and drawings. When direct access to specimens was not possible, supplementary data and measurements were taken from the literature (see Table 2-1 for source of data).

The myology of *Caiman crocodilus* (spectacled caiman) and *Gallus gallus* (chicken) were dissected in order to gain insights into the myology of the pelvic girdle and hindlimb of extant archosaurs. Thus, the nature of attachment of muscles on the bone surface or soft-tissues was studied.

2.2 METHODS

The Extant Phylogenetic Bracket approach (*sensu* Witmer 1995) is an important part of this thesis, and both soft-tissues and functional morphology were reconstructed in an explicit phylogenetic framework. The interrelationships used here are mainly based on Ezcurra (2006) for basal dinosauromorphs and basal saurischians. The interrelationships of sauropodomorphs are based on Yates (2007). In contrast to Ezcurra (2006) and Yates (2007), *Eoraptor lunensis* and the herrerasaurids

Table 2-1. Source of data (literature and specimens) for archosauriforms used in this study. Accession numbers denote specimens examined by the author first hand; other data were obtained from the literature.

Material	Source
Archosauriformes	
Erythrosuchus africanus	BMNH R3592:
Euparkeria capensis	SAM 6047, SAM 6049; Ewer 1965;
Ornithodira	
Scleromochlus taylori	BMNH R3146, R3556, R3557, R 4323/4; Woodward 1907, Huene 1914, Benton 1999;
Dinosauromorpha	
Dromomeron romeri	Irmis et al. 2007a;
Lagerpeton chanarensis	UPLR 06, PVL 4619, 4625; Romer 1971a, 1972b, Bonaparte 1984, Arcucci 1986, Sereno and Arcucci 1993;
PVL 3870	PVL 3870; Bonaparte 1975, Sereno and Arcucci 1994;
Dinosauriformes	
Lewisuchus admixtus	UPLR 01;
Agnosphytys cromhallensis	Fraser et al. 2002;
Eucoelophysis baldwini	Ezcurra 2006;
Marasuchus lilloensis	PVL 3871; Romer 1971a, 1972b, Bonaparte 1975, Sereno and Arcucci 1994, Fechner and Rauhut 2006;
Pseudolagosuchus major	PVL 4629, UPLR 53; Arcucci 1987, Novas 1989;
Sacisaurus agudoensis	Ferigolo and Langer 2006;
Silesaurus opolensis	Dzik 2003, Dzik and Suljei 2007;
Ornithischia	
Heterodontosaurus tucki	Santa Luca 1980;
Lesothosaurus diagnosticus	BMNH RUB 17;
Pisanosaurus mertii	Casamiquela 1967, Bonaparte 1976;
Scelidosaurus harrisonii	BMNH R1111, R6704;
Saurischia	
Chindesaurus bryansmalli	Long and Murry 1995;
Eoraptor lunensis	PVSJ 512; Sereno et al. 1993;
Guaibasaurus candelariensis	MCN-PV 2355, 2356; Bonaparte et al. 1999, 2007, Langer and Benton 2006;
Herrerasaurus ischigualastensis	PVL 2566, 373, PVSJ 104, 464; Reig 1963, Novas 1992, 1993, Sereno and Novas 1993;
Staurikosaurus pricei	MCZ 1669; Colbert 1970, Galton 1977, 2000;
Streptospondylus altdorfensis	MNHN 8605, 8607-8609, 9645;
Theropoda	
Ceratosaurus nasicorni	YPM 4681;
Coelophysis bauri	UCMP 129618, AMNH 7223, 7224, 7228 - 7230, 7232; Colbert 1989;
Dilophosaurus wetherilli	UCMP 37302; Welles 1984;
Elaphrosaurus bambergi	MB Gr.S. 38-40;
Liliensternus liliensterni	MB.R.2175.7;
Segisaurus halli	UCMP 32101;
Sinraptor dongi	IVPP 10600; Currie and Zao 1993;
Syntarsus rhodiensis	BMNH R 10071, R9584 (cast);
Sauropodomorpha	
Anchisaurus polyzelus	YPM 208, 209, 1883; Galton 1976, Yates 2004;
Antetonitrus ingenipes	BP/1/4952; Yates and Kitching 2003;
Barapasaurus tagorei	ISI R 50; Jain et al. 1977
Blikanasaurus cromptoni	SAM K403; Galton and Heerden 1985, 1998;
Camelotia borealis	BMNH R2870-2872c, R2874b-c, R2878a; Galton 1985, 1998;
Cetiosaurus oxoniensis	Upchurch and Martin 2002, 2003;
Coloradisaurus brevis	Bonaparte 1978;
Efraasia minor	SMNS 12667, 12668; Huene 1907-08, Galton 1973;
Eucnemesaurus fortis	Van Hoepen 1920, Heerden 1979, Yates 2006;
Euskelosaurus brownii	Haughton 1924, Heerden 1979;
Gongxianosaurus shibeiensis	He et al. 1998;
"Gyposaurus" sinensis	IVPP V.26; Young 1941b;
Isanosaurus attavipachi	Buffetaut et al. 2000;
Jingshanosaurus xinwaensis	Zhang and Yang 1994
Klamelisaurus gobiensis	IVPP V.9492
Kotasaurus yamanpalliensis	21/SR/PAL; Yadagiri 1988, 2001;
Lamplughsaura dharmaramensis	Kutty et al. 2007;
Lessemsaurus sauroides	Pol and Powell 2007;
Lufengosaurus huenei	IVPP V15; Young 1941a;
Mamenchisaurus hochuanensis	GCC V 20401; Young and Chao 1972, Russell and Zheng 1993,;
Massospondylus carinatus	SAM 5135; Van Hoepen 1920, Cooper 1981;
Melanorosaurus readi	NM QR1551, SAM-PK-3449, 3450; Haughton 1924; Heerden and Galton 1997, Galton et al. 2005;

Table 2-1. continued

Mussaurus patagonicus	PVL 4068; Bonaparte and Vince 1979;
Pantydraco caducus	Kermack 1984, Yates 2003b, Galton and Yates 2007;
Patagosaurus farisi	PVL 4170; Bonaparte 1986;
Plateosauravus cullingworthi	SAM 3340, 3341, 3343, 3349, 3603; Haughton 1924, Heerden 1979;
Plateosaurus engelhardti	SMNS 13200, GPIT 1; Huene 1926;
Plateosaurus gracilis	Huene 1907-08, 1915, Yates 2003b;
Plateosaurus ingens	Galton 1986;
Riojasaurus incertus	PVL 3808, ULPR 56; Bonaparte 1972;
Ruehleia bedheimensis	MB RvL 1; Galton 2001;
Saturnalia tupiniquim	MCP 3844-PV, MCP 3845-PV; Langer et al. 1999, Langer 2003, Langer and Benton 2006;
Shunosaurus lii	IVPP T5401; Dong et al. 1983, Zhang 1988;
Tazoudasaurus naimi	Allain et al. 2004, Allain and Aquesbi 2008;
Thecodontosaurus antiquus	BMNH R1539-1545, R1547-1549, R1552, R15389, R49984, R49984; YPM 2192, 2193; Huene 1907-08, Benton et al. 2000;
Unaysarus tolentinoi	UFSM 11069; Leal et al. 2004;
Volkheimeria chubutiensis	PVL 4077; Bonaparte 1979;
Vulcanodon karibaensis	Raath 1972, Cooper 1984;
Yunnanosaurus huangi	Young 1942;

are regarded here as basal saurischians, with the herrerasaurids being more derived than *Eoraptor*. Fechner and Rauhut (2006) noted that PVL 3870, formerly assigned to *Marasuchus lilloensis* (Sereno and Arcucci 1994), has to be regarded as a non-dinosauriform dinosauromorph and is placed here between *Lagerpeton chanarensis* and *Dromomerom romeri* (Irmis et al. 2007a) (Fig. 2-1).

Dinosauromorphs are bracketed by Crocodylia (outgroup) and Aves (ingroup) (Fig. 2-2). The soft-tissues of the pelvic girdle and limb of Dinosauromorpha were reconstructed using crocodiles and birds as phylogenetic framework (see above). Additional information on the pelvic girdle and limb of crocodiles was taken from Gadow (1882), Romer (1923b), Ribbing (1938), Kriegler (1961), Tarsitano (1981), and Cong et al. (1998). Hudson et al. (1959), McGowan (1979), Mellet (1985), Nickel et al. (2003), and Gangl et al. (2004) were chosen as additional source of information on the myology of the pelvic girdle and limb of Aves. In order to trace the nature of character evolution of the osteological correlates of muscles and to identify causal association between soft-tissues and osteological correlates, basal Sauria were included (Fig. 2-3). Information on the myology of the pelvic girdle and hindlimb of lepidosaurs was taken from Fürbringer (1870), Gadow (1882), Osawa (1898), Byerly (1925), Ribbing (1938), and Kriegler (1961). The nomenclature of the myology of the pelvic girdle and hindlimb of non-avian Sauria follows Romer (1922, 1923b). The nomenclature of the myology of the pelvic girdle and hindlimb of Aves follows the Nomina Anatomica Avium (Vanden Berge and Zweers 1993).

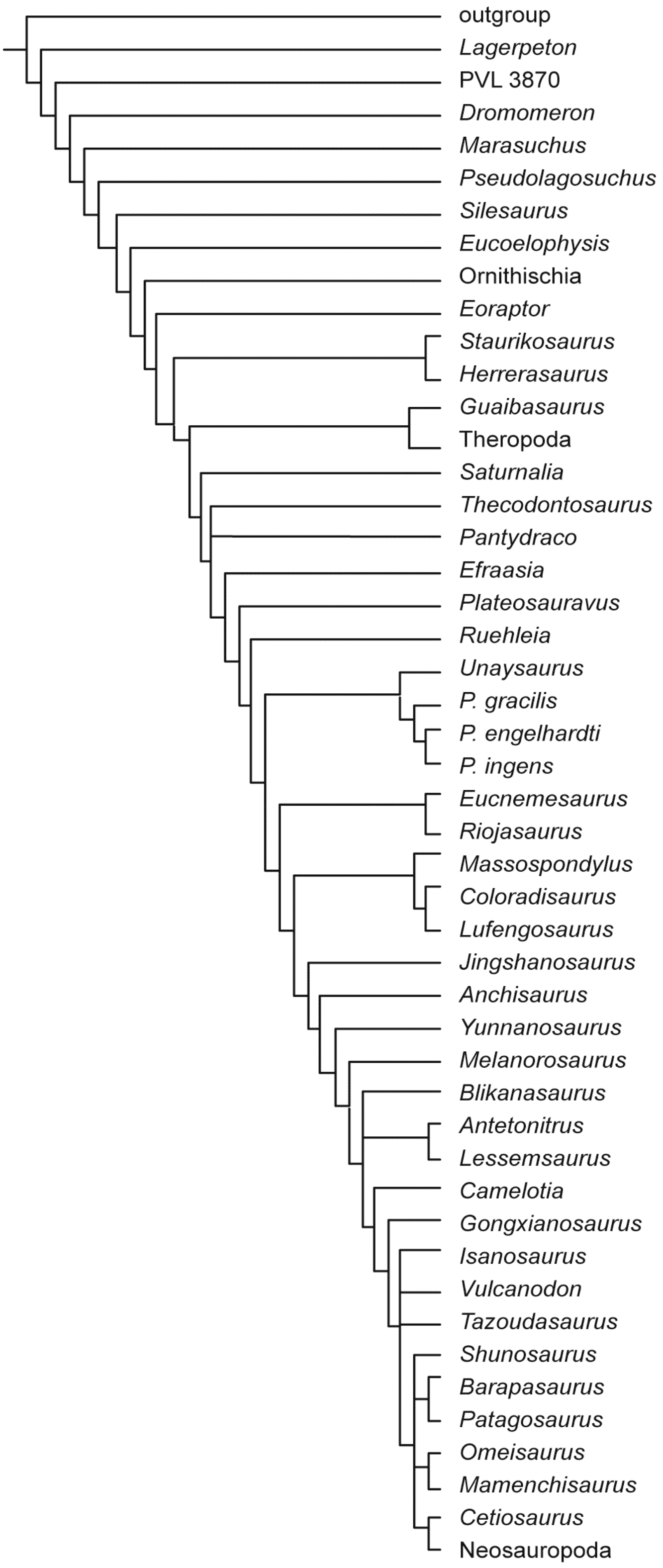


Figure 2-1. Phylogenetic framework of dinosauromorphs on the lineage to sauropods used in this study; mainly based on Ezcurra (2006) for basal dinosauromorphs and on Yates (2007) for sauropodomorphs.

Most questions concerning the homology of the muscles of the pelvic girdle and hindlimb of Sauria are solved to date. The homology of the "deep dorsal thigh" muscles and of the "flexor cruris group", however, is still under discussion (compare the hypotheses of homology provided by Romer 1923b, Walker 1977, Hutchinson 2002). Nonetheless, the hypothesis of homology of Romer (1923b, 1927a, 1942), Rowe (1986) and Carrano and Hutchinson (2002) is applied here (Fig. 2-2). The level of speculation required for reconstructing the musculature of dinosauromorphs follows the levels of inference established by Witmer (1995). If soft tissue data from extant bracket taxa unequivocally support the reconstruction of an unpreserved feature of the extinct taxon (both bracketing taxa have the feature), the reconstruction is a level I inference. Equivocal support from extant taxa (one bracketing taxon lacks the feature) is a level II inference. The unequivocal absence of support from extant taxa (both bracketing taxa lack the feature) is a level III inference. Tubercles, crests, grooves, pits, ridges, and scars are regarded as clear osteological correlates of muscles. Some muscles, however, cannot be correlated to a clear osteological correlate (McGowan 1979, Bryant and Seymour 1990, Bryant and Russell 1992). In cases, in which inferences lack conclusive data from osteological correlates, they are referred to as level I', II', and III' (Witmer 1995). A level I' inference is less robust than a level I inference but better supported than a level II inference (Witmer 1995). In this study, a level III and III' inference is not reconstructed.

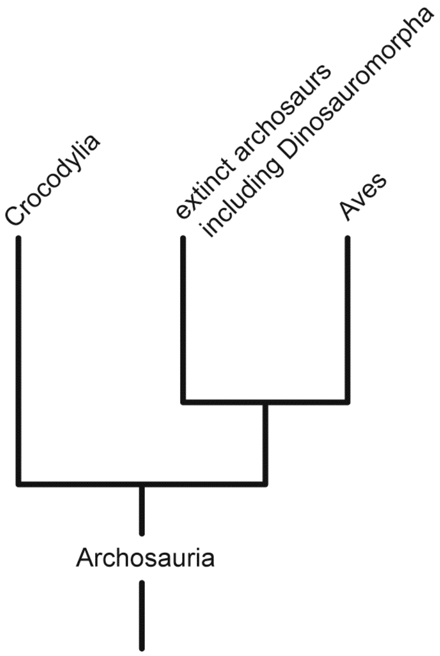


Figure 2-2. Phylogenetic framework of extinct archosaurs and its immediate extant sister-groups.

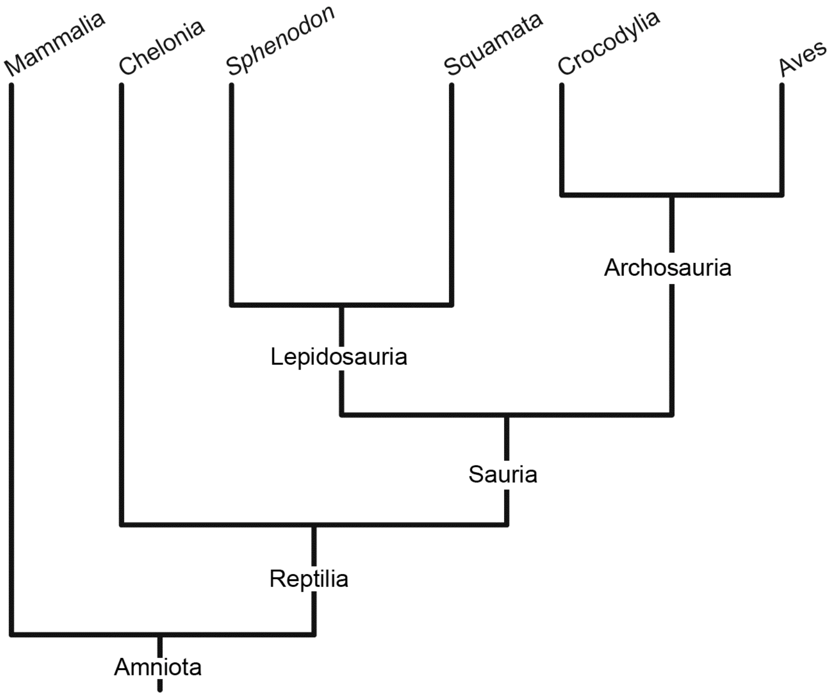


Figure 2-3. Phylogenetic framework of Amniota used in this study; based on Gauthier et al. (1988).

Functional morphology represents the examination of the form – function relationships of an organism or group with the aim to establish a causal relationship of form and function. The approach followed here is the so-called empirical – analytical approach, which consists ideally of four steps: i) examination of morphological and functional findings, ii) statistical evaluation of the results, iii) formulating a descriptive theory, and iv) extrapolation and generalization. Information on the hindlimb posture and locomotion was gained from the literature, with Schaeffer (1941), Cott (1960), Brinkman (1980), Webb and Gans (1982), Gatesy (1990, 1991b, 1995, 1997), Blob (2001), Reilly and Elias (1998), Reilly and Blob (2003), and Reilly et al. (2005) as source of information on crocodiles and Gatesy (1991b, 1995, 1997) on Aves. Additionally, literature on the locomotor function of basal reptiles was studied (Snyder 1952, 1954, 1962, Rewcastle 1980, 1981, Reilly 1994, Christian 1995, 2007, Christian and Garland 1996, Reilly and Delancey 1997a,b, Irschick and Jayne 1999, Blob 2001). Information on the hindlimb posture and locomotion of extinct non-dinosaurian archosaurs was gained from Charig (1972) and Parrish (1986). The work of Gatesy, Carrano and Hutchinson and co-workers was consulted for information on hindlimb posture and locomotion of theropods (Hutchinson and Gatesy 2000).

Table 2-2. Terminology and homology of the muscles of the pelvic girdle and hindlimb of Sauria. The terminology of the muscles of the pelvic girdle and hindlimb of Sauria is based on Gadow (1882), Romer (1923b). The homology of the muscles of the pelvic girdle and hindlimb of Sauria is based on Romer (1923b, 1927a, 1942) and Rowe (1986).

Muscles in Crocodylia	*Sphenodon*	Squamata	Crocodilia	Aves	Muscles in Aves
M. iliotibialis	IT	IT	IT1	IA	M. iliotibialis anterior
	—	—	IT2	IP	M. iliotibialis posterior p. preacetabuaris
	—	—	IT3	IP	M. iliotibialis posterior p. postacetabularis
M. ambiens 1	AMB	AMB	AMB1	AMB	M. ambiens
M. ambiens 2	—	—	AMB2	—	
M. femorotibialis externus	FMT	FMT	FMTE	FMTL	M. femorotibialis lateralis
M. femorotibialis internus	—	—	FMTI	FMTIM	M. femorotibialis intermedius
	—	—	—	FMTM	M. femorotibialis medius
M. iliofibularis	ILFIB	ILFIB	ILFIB	ILFIB	M. iliofibularis
M. iliofemoralis	IF	IF	IF	IFE	M. iliofemoralis externus
	—	—	—	ITC	M. iliotrochantericus caudalis
M. puboischiofemoralis internus 1	PIFI1-+2	PIFI1	PIFI1	IFI	M. ischiofemoralis internus
M. puboischiofemoralis internus 2	—	PIFI2	PIFI2	ITCR	M. iliotrochantericus cranialis
	—	PIFI3	—	ITM	M. iliotrochantericus medius
M. pubotibialis	PIT	PIT1	PIT	—	
	—	PIT2		—	
M. flexor tibialis internus 2	—	PIT3	FTI2	—	
M. flexor tibialis internus 1	FTI1	FTI1	FTI1	—	
M. flexor tibialis internus 3	FTI2	FTI2	FTI3	FCM	M. flexor cruris medius
M. flexor tibialis internus 4	—	—	FTI4	—	
M. flexor tibialis externus	FTE	FTE	FTE	FCLP	M. flexor cruris lateralis p. posterior
	—	—	—	FCLA	M. flexor cruris pars anterior
M. adductor femoris 1	ADD	ADD	ADD1	PIFM	M. puboischiofemoralis medius
M. adductor femoris 2	—	—	ADD2	PIFL	M. puboischiofemoalis lateralis
M. puboischiofemoralis externus 1	PIFE	PIFE	PIFE1	OL	M. obturatorius lateralis
M. puboischiofemoralis externus 2	—	—	PIFE2	OM	M. obturatorius medialis
M. puboischiofemoralis externus 3	—	—	PIFE3	—	
M. ischiotrochantericus	ISTR	ISTR	ISTR	ISF	M. ischiofemoralis
M. caudofemoralis longus	CFL	CFL	CFL	CFC	M. caudofemoralis pars caudlis
M. caudofemoralis brevis	CFB	CFB	CFB	CFP	M. caudofemoralis pars pelvica
M. gastrocnemius lateralis	GL	GL	GL	GL	M. gastrocnemius longus
	—	—	—	GIM	M. gastrocnemius intermedius
M. gastrocnemius medialis	GM	GM	GM	GM	M. gastrocnemius medius
M. flexor digitalis longus	FDL	FDL	FDL	FDL	M. flexor digitorium longus
M. flexor digitalis brevis	FDB	FDB	FDB	FDB	M. flexor digitorium brevis
M. flexor hallucis longus	FHL	FHL	FHL	FHL	M. flexor hallucis longus
M. tibialis anterior	TA	TA	TA	TC	M. tibialis cranialis
M. extensor digitorium longus	EDL	EDL	EDL	EDL	M. extensor digitorium longus
M. extensor digitorium brevis	EDB	EDB	EDB	—	
M. extensor hallucis longus	EHL	EHL	EHL	EHL	M. extensor hallucis longus
M. fibularis longus	FL	FL	FL	FL	M. fibularis longus
M. fibularis brevis	FB	FB	FB	FB	M. fibularis brevis
M. pronator profundus	PP	PP	PP	—	
M. popliteus	POP	POP	POP	POP	M. popliteus
M. interosseus cruris	IC	IC	IC	—	

Information on the locomotion of sauropodomorphs was gained from Christian and Preuschoft (1996), Christiansen (1997) and Carrano (2005). Information on biomechanics and locomotor biomechanics was gained from Wolff (1892; "Wolff's law" predicts that every change in the form and function of bones lead to changes in its internal architecture and external form), Pauwels (1965; "Pauwels principle of the causal morphogenesis" predicts that the form and structure of bones are the results of mechanical determinates, such as external forces [weight forces, ground reaction force, inertia] and internal forces [muscle forces] acting on the body), Kummer (1959, 2005), Biewener (1989, 1990, 2003, 2005), and Hildebrandt and Goslow (2004). An important part of a functional morphological study is the usage of ratios. Here, ratios are used which are assumed to be of functional significance. These ratios are the hindlimb to trunk ratio (trunk = gleno-acetabular distance), the forelimb to hindlimb ratio, and the distal limb (tibia + metatarsal III/IV) to femur ratio.

Ichnofossils provide insights into the functional morphology of an extinct animal that are not apparent from the osteology alone (Farlow and Pianka 2000). The potential of ichnofossils as an additional source of information on the locomotion of extinct tetrapods rests on the identification of the potential trackmaker. Unfortunately, there is currently no consensus to what taxonomic level ichnofossils can be correlated to osteological taxa with confidence. Nevertheless, most authors agree that a correlation to family or genus level appears reasonable (e.g. Baird 1980, Sarjeant 1990, Olsen et al. 2002, Thulborn 2006). In the past, the assignment of ichnofossils to osteological taxa was mainly based on overall similarities of the hand and foot skeleton of osteological taxa known with a comparable stratigraphically and biogeographically distribution (Haubold and Klein 2002). In recent years, the synapomorphy-based approach was established (Olsen and Baird 1986, Olsen et al. 1998, Wilson and Carrano 1999, Haubold and Klein 2000, 2002, Wilson 2005, Wright 2005). By using synapomorphies and autapomorphies of the hand and foot skeleton, as well as overall proportions of the limbs and trunk, the circle of potential trackmaker is considerably constraint. The synapomorphy-based approach further provides the possibility to attribute tracks and traces to osteological taxa independent from their biogeographical distribution. Information on ichnofossils was gained from the literature (e.g. Peabody 1948, Haubold 1969, 1971a,b, 1999, Haubold and Klein 2000, 2002, Rainforth 2003, Wright 2005, Milàn et al. 2008).

Chapter 3

Locomotor capabilities of the basal dinosauromorph *Lagerpeton chanarensis* and its implications for the early evolution of dinosaurs

3.1 INTRODUCTION

At the end of the Triassic, long-established tetrapod groups, such as basal archosaurs (e.g. Phytosauridae, Ornithosuchidae, Aetosauria), temnospondyl amphibians, prolacerticforms, procolophonids, became extinct and were replaced by mammals, turtles, lepidosaurs, crocodilians, pterosaurs, and dinosaurs. When dinosaurs first appeared in Carnian strata, they were rare components of their fauna. Nonetheless, after their first radiation in the Norian, dinosaurs became the dominating clade in the terrestrial ecosystems of the Mesozoic. The dominance of dinosaurs has been argued to be related to their superior adaptations, such as endothermy, intelligence, and locomotion. Dinosaurs were assumed to be initially obligate bipeds with an erect hindlimb posture and able to attain and sustain high maximum running speed (see Benton 1997, 2004). Obligate bipedality and high maximum running speed associated with a manus modified for grasping and raking in basal saurischians and theropods are commonly regarded as adaptations to a carnivorous habit (or at least an omnivorous habit) (e.g. Sereno 1993, Langer and Benton 2006). In basal ornithischians, the modified manus is interpreted as an adaptation to digging and tearing (Norman et al. 2004).

It is widely accepted that dinosaurs retained the cursorial bipedal locomotion of their ancestors, the basal Dinosauromorpha, which are commonly regarded as omnivores (e.g. Rauhut 2003). However, little is known about the anatomy, function or ecology of basal dinosauromorphs. In the past, *Lagerpeton chanarensis* (Romer 1971, 1972a, Arcucci 1986, Sereno and Arcucci 1993), *Marasuchus lilloensis* (Romer 1971, 1972a, Bonaparte 1975, Sereno and Arcucci 1994), and

Pseudolagosuchus major (Arcucci 1987), all known from the Ladinian Los Chañares Formation of Argentina, were the only unquestionable non-dinosaurian dinosauromorphs. In recent years, new finds and re-evaluation of known material improved our knowledge on the diversity of this group. Fechner and Rauhut (2006) noted that the taxon *Marasuchus* actually consists of two taxa, a basal dinosauriform (PVL 3871 = *Marasuchus*) and a non-dinosauriform dinosauromorph (PVL 3870 = unnamed taxon). Most recently, Irmis et al. (2007a) described the remains of the non-dinosauriform dinosauromorph *Dromomeron romeri* from the Norian of North America. *Silesaurus opolensis* (Dzik 2003) from the Norian of Poland and *Eucoelophysis baldwini* (Ezcurra 2006) were identified as dinosauriforms closely related to basal dinosaurs. Basal dinosauromorphs are mainly known from material of the pelvic girdle and hindlimb (Table 3-1). Solely *Silesaurus* is known from an almost complete skeleton lacking only parts of the skull, the manus and the distal caudal vertebral column (Dzik 2003). Most interestingly, *Silesaurus* shows specializations in the cranial and postcranial skeleton, which contradict the traditional idea of non-dinosaurian dinosauromorphs. *Silesaurus* has a beak and denticulate teeth, features commonly argued to be suggestive for an obligately herbivorous diet. The relatively elongated forelimbs in *Silesaurus* served as an indicator for obligate quadrupedal locomotion. Thus, *Silesaurus* does not serve as a model for the origin of dinosaur locomotion. However, a good understanding of their locomotor capacities is required to understand the early evolution of dinosauromorphs and its implications for the origin of dinosaurs. For this purpose, the locomotor function of the basalmost known dinosauromorph, *Lagerpeton*, was studied, using an integrative approach combining data from osteology, myology, biomechanical considerations, and ichnofossils applied on an explicit phylogenetic framework. The new interpretation of the functional morphology of *Lagerpeton* and the evaluation of supposed adaptations allows new insights into the early evolution of dinosaurs.

3.2 MATERIAL AND METHODS

The osteology of *Lagerpeton* has been described previously by Romer (1971, 1972a), Bonaparte (1984), Arcucci (1986), and most recently by Sereno and Arcucci (1993). *Lagerpeton* is known from several incomplete skeletons comprising material of the pelvic girdle and hindlimb and posterior dorsal vertebrae (Table 3-1). The following reconstruction is based on the most complete skeleton PVL 4619 consisting of a pelvis preserved in three dimensions and an articulated and complete right and left hindlimb. Additional information, especially on the morphology of the tarsus and pes, is gained from the holotype material UPLR 06. In order to trace the nature of character evolution of the pelvic girdle and hindlimb and its implications for the evolution of the locomotor function and ecology on the lineage to dinosaurs, *Lagerpeton* was compared to other non-dinosaurian dinosauromorphs. The phylogenetic hypothesis of Ezcurra (2006) served as phylogenetic framework. As with *Lagerpeton*, the material of *Marasuchus*, PVL 3870, and *Pseudolagosuchus* was studied first hand. Information on the skeleton of *Dromomeron*, *Silesaurus* and *Eucoelophysis* was gained from the literature (Dzik 2003, Ezcurra 2006, Irmis et al. 2007; also see Table 3-1). PVL 3870 is assumed here to be a non-dinosauriform dinosauromorph more derived than *Lagerpeton*. *Dromomeron* (Irmis et al. 2007a) is assumed here to be a non-dinosauriform dinosauromorph more derived than PVL 3870 (Fig. 3-1). Measurements were taken from the pelvic girdle and hindlimb of *Lagerpeton*, PVL 3870, *Marasuchus,* and *Pseudolagosuchus* and their morphology was documented with photographs and drawings.

The Extant Phylogenetic Bracket approach (*sensu* Witmer 1995) was used to reconstruct both soft-tissues and functional morphology. Crocodilia and Aves are the extant bracketing taxa to dinosauromorphs. In order to gain insights into the myology of crocodiles and birds *Caiman crocodilus* and *Gallus gallus* were dissected, with special emphasis on the myology of the pelvic girdle and hindlimb. As additional source of information on myology of crocodiles, Gadow (1882) and Romer (1923b) were used. For neognaths, the literature of Vanden Berge and Zweers (1993) and Nickel et al. (2003) was studied. The nomenclature of the muscles follows the traditional terminology for non-avian reptiles (e.g. Romer 1922, 1923b, 1942, Rowe 1986) and the Nomina Anatomica Avium for birds (Vanden Berge and Zweers 1993). The assumption of homology of the muscles of extant archosaurs follows Romer (1923b, 1927a, 1942) and Rowe (1986). Osteological correlates of muscles (e.g. tubercles, scars, rugosities) were used to identify the origin and insertion of a muscle. In those instances, in which muscles leave no visible traces on the bone, they were inferred according to the phylogenetic framework and their relationships with other muscles in the extant bracketing taxa.

To avoid unsubstantiated functional analogical assumptions, form-function relationships should be reconstructed in an explicit phylogenetic framework (Bryant and Russell 1992). However, for two reasons the extant phylogenetic bracket is widened here to include extant lizards in this study: 1) Crown-group crocodiles move using a sprawling locomotor posture, in which the femur is abducted to 55° from the parasagittal plane (Reilly and Elias 1998) and a more erect posture, in which the femoral abduction ranges between 30° – 20° (Gatesy 1991a, Reilly and Elias 1998). The origin of crown-group crocodiles from fully terrestrial and even cursorial crocodylomorphs is well established (Charig 1972, Parrish 1987) and the intermediate locomotor posture is considered to be the result of the secondary adaptation to a semi-aquatic lifestyle (Parrish 1987). According to the findings of Reilly and Elias (1998), the locomotion of crown-group crocodiles differs from that of other recent animals. 2) Studies of Christian (1995, 2007), Christian and Garland (1996), Biewener (1990, 2003, 2005), Blob and Biewener (1999), and Blob (2001) have shown the affect of body size and mass on the locomotor posture of terrestrial animals. Even small adult crocodilian taxa are by far larger and heavier than basal dinosauromorphs. In addition to their fully terrestrial locomotion, most extant lizards are subequal in body size and mass to basal dinosauromorphs. Finally, their relatively close phylogenetic relationship to dinosauromorphs justifies using lizards as functional analogues (Bryant and Seymour 1990).

Ichnofossils have proved to be a valuable source of information on the limb posture and locomotor performance of fossil archosaurs (Wilson and Carrano 1999, Carrano and Wilson 2001, Haubold and Klein 2002). Therefore, the results from the functional morphological analysis were compared to the ichnofossil record of tracks and trackways assigned to basal dinosauromorphs. The potential of ichnofossils as an additional source of information on the functional morphology of extinct animals is strongly dependent on the reliability of the identification of the trackmaker. Unfortunately, there is only little consensus to what taxonomic level ichnofossils can be correlated to body fossils with confidence, although most authors agree that a correlation to family or genus level appears to be reasonable (e.g. Baird 1980, Sarjeant 1990, Olsen et al. 2002, Thulborn 2006). In the past, the assignment of ichnofossils to osteological taxa was mainly based on

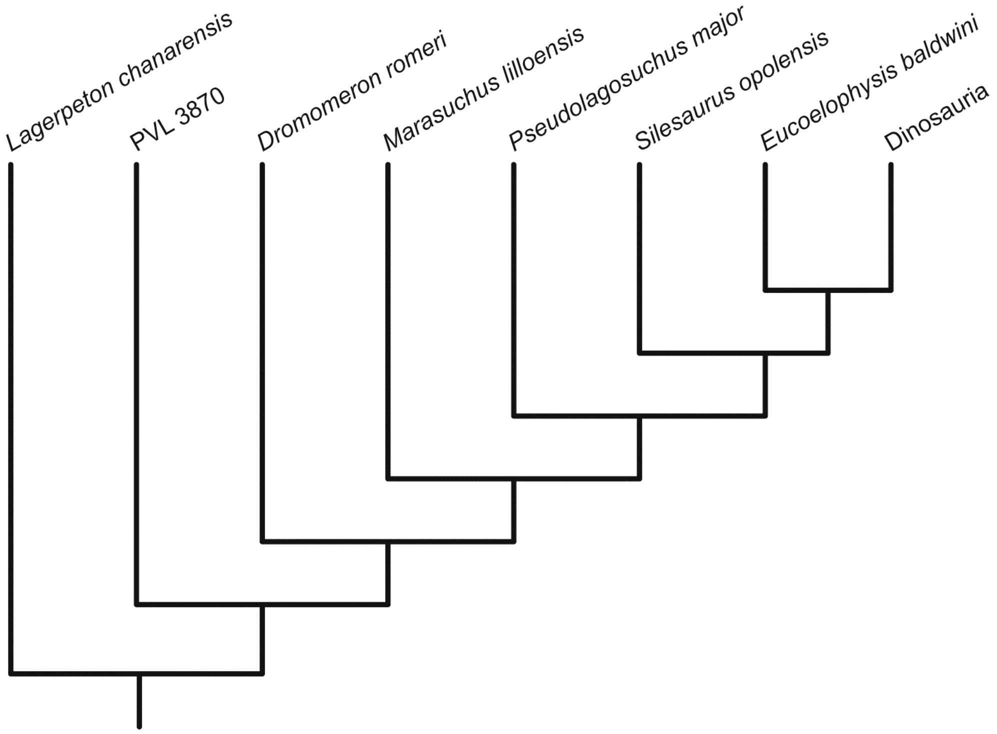


Figure 3-1. Phylogenetic framework of Dinosauromorphs used in this study, mainly based on the phylogenetic hypothesis of Ezcurra (2006). Systematic placement of PVL 3870 after Fechner and Rauhut (2006) and of *Dromomeron romeri* after Irmis et al. (2007a).

overall similarities of the hand and foot skeleton of osteological taxa known with a comparable stratigraphically and biogeographically distribution (Haubold and Klein 2002). In recent years, however, the synapomorphy-based approach was established (Olsen and Baird 1986, Olsen et al. 1998, Haubold and Klein 2000, 2002, Wilson and Carrano 1999, Wilson 2005). By using synapomorphies and autapomorphies of the hand and foot skeleton, as well as overall proportions of the hindlimbs and trunk, the circle of potential trackmaker is considerably constrained. The synapomorphy-based approach further provides the possibility to attribute tracks and traces to osteological taxa independent from their biogeographical distribution. The information on basal dinosauromorph trackways is mainly based on the studies of Peabody (1948), Haubold (1967, 1971a, 1999), Haubold and Klein (2002), and Klein and Haubold (2007).

Institutional abbreviations: **GR**, Ghost Ranch Hull Museum of Paleontology, New Mexico; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge; **NHM**, Natural History Museum, London; **NMMNH**, New Mexico Museum of Natural History, Albuquerque; **PVL**, Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán; **UPLR**, Museo de Paleontología, Universidad Provincial de La Rioja, La Rioja;

3.3 RESULTS

3.3.1 Osteology of the pelvic girdle and hindlimb of *Lagerpeton chanarensis*

The pelvic girdle of *Lagerpeton* is broader transversely than tall (Fig. 3-2a,b,c), resulting in an interacetabular value (anteroposterior extent of the dorsal iliac blade / interacetabular distance) of 1.2. In basal Dinosauromorpha, both the preacetabular process and postacetabular process are strongly developed, but the postacetabular process is much more prominent. The acetabulum of *Lagerpeton* is closed and of moderate depth, with its outline posterodorsally inclined. The supraacetabular crest of *Lagerpeton* is developed as a shallow lip on the anterodorsal rim of the acetabulum (Arcucci 1986, Sereno and Arcucci 1993). Compared to the femoral head, the acetabulum of *Lagerpeton* is relatively large (Sereno and Arcucci 1993, Fig. 3-2a,d). The pubis of *Lagerpeton* measures 33% of the femoral length. The pubic apron is very broad transversely, with its mediolateral extent exceeding its proximodistal extent (Sereno and Arcucci 1993) (Fig. 3-2a). The pubis of *Lagerpeton* is angled at 40° from the horizontal plane (Fig. 3-2c). The ischium of *Lagerpeton* is subequal to the pubis in length (Fig. 3-2c). The prominent puboischiadic plate, with a large ventral extension characterizes the pelvis of *Lagerpeton* (Arcucci 1986, Sereno and Arcucci 1993). The femur of *Lagerpeton* is sigmoidally curved in anterior (Fig. 3-2d) and lateral view. The femoral head is not well offset from the femoral shaft and directed anteromedially (Romer 1971, Arcucci 1986, Sereno and Arcucci 1993). In *Lagerpeton*, the femoral head is angled at 70° from the transverse plane (PVL 4916) (Fig. 3-2e). The fourth trochanter of *Lagerpeton* is located on the proximoposterior shaft of the femur (Romer 1971, Arcucci 1986, Sereno and Arcucci 1993). As noted by Sereno and Arcucci (1993) the fourth trochanter is visible in anterior view (Fig. 3-2d). Sereno and Arcucci (1993) further argued that the proximodistal extent of the fourth trochanter, which spans over the proximal third of the femur, is unique to *Lagerpeton* within dinosauromorphs. The distal end of the femur of *Lagerpeton* is relatively broad transversely, if compared to the cross-section of the femoral mid-shaft. The lateral femoral condyle of *Lagerpeton* projects further distally and posteriorly, resulting in an oblique distal articulation surface of the femur (Fig. 3-2d). The crus of *Lagerpeton* is notably longer than the femur (Fig. 3-2d,f), with a tibia to femur ratio of 1.2. The crus of *Lagerpeton* is closely appressed and the tibia and fibula are very slender (Fig. 3-2f). The proximal end of the tibia is strongly, and the distal end of the tibia moderately mediolaterally flattened. The mid-shaft of the tibia of *Lagerpeton* is anteroposteriorly flattened. A fibular flange is developed on the proximoanterior fibula of *Lagerpeton*. The distal articulation facet of the tibia and fibula of *Lagerpeton* is beveled (Fig. 3-2f,g), with the medial surface of the tibia and the lateral surface of the fibula projecting further distally. The proximal tarsus of *Lagerpeton* is preserved in PVL 4619 and in UPLR 06, and in both cases the astragalus and calcaneum are preserved in articulation (Fig. 3-2i,g,h). The preservation of the proximal tarsus in articulation is fairly poor. In *Lagerpeton* only a faint suture is present, which suggests that the proximal tarsus of *Lagerpeton* is co-ossified to form an astragalocalcaneum (Romer 1971, Sereno and Arcucci 1993). The astragalocalcaneum of *Lagerpeton* is very robust and dorsoventrally relatively high (Fig. 3-2g). The ascending process is located on the lateral astragalus, providing only little space for the articulation with the fibula (Fig. 3-2i,g) (Novas 1989, Sereno and Arcucci 1993). Contrary to the observation of Arcucci (1986) and Sereno and Arcucci (1993), only the distal tarsal 4 is preserved in *Lagerpeton* (Fig. 3-2j) (PVL 4619, UPLR 06). The distal tarsal 4 of *Lagerpeton* is anteroposteriorly elongated, waisted, with an anterior plate and a posterior heel. The distal tarsal 4 covers the proximal end of metatarsal 4 and is set at a marked angle from the transverse plane (Sereno and Arcucci 1993, Fig. 3-2j). *Lagerpeton* is characterized by an ectaxonic pes, with digit IV>digit III>digit II (Fig. 3-2k) (Romer 1971, Arcucci 1986, Sereno and Arcucci 1993). The metatarsus of *Lagerpeton* is bundled, with slender and considerably elongated metatarsals. Metatarsal IV is the longest element of the metatarsus and metatarsal V is reduced to a bone splint. The phalangeal series is subequal to the metatarsus in length, with a phalangeal series of 2-3-4-5-0 (Romer 1971, Arcucci 1986, Sereno and Arcucci 1993). The metatarsus of *Lagerpeton* equals 53% of the tibia in PVL 4619 (metatarsal IV x 100 / tibia).

3.3.2 Locomotion of *Lagerpeton chanarensis*

Table 3-1. Material and source of data of non-dinosaurian dinosauromorphs. Boldface indicates material belonging to the pelvic girdle and hindlimb.

Taxon		Source	Material
Lagerpeton chanarensis Romer 1971	PVL 4619	Bonaparte 1984; Arcucci 1986; Sereno and Arcucci 1993;	**pelvic girdle articulated with partial right and almost complete left hindlimb lacking only distal phalanges and unguals**;
	UPLR 06	Romer 1971, 1972a; Arcucci 1986; Sereno and Arcucci 1993;	**articulated right hindlimb**;
	PVL 4625	Bonaparte 1984; Arcucci 1986; Sereno and Arcucci 1993;	articulated vertebral column including posterior dorsal, sacral, and anterior caudal vertebrae;
	PVL 5000	Bonaparte 1984; Sereno and Arcucci 1993;	**proximal left femur**;
	MCZ 4121	Romer 1972a;	**partial left and right femora**;
Dromomeron romeri Irmis et al. 2007a	GR 218 – 223, 234 , NMMNH P-35379	Irmis et al. 2007a;	**left and right femur, nearly complete right femur, partial left femur, left tibia, two complete astragalocalcaneum;**
unnamed non-dinosauriform dinosauromorph	PVL 3870	Bonaparte 1975; Novas 1989; Sereno and Arcucci 1994;	partial skeleton including the maxilla and braincase, complete presacral vertebral column, anterior caudal vertebrae, **pelvic girdle, almost complete articulated left and right hindlimbs lacking only distal phalanges and unguals;**
Marasuchus lilloensis Sereno and Arcucci 1994	PVL 3871	Romer 1972a; Bonaparte 1975; Sereno and Arcucci 1994;	partial articulated skeleton including posterior dorsal vertebrae, almost complete caudal vertebral column, left scapulacoracoid, humerus, radius, ulna, **pelvic girdle lacking the ischium, almost complete articulate left and right hindlimbs lacking only distal phalanges and unguals**;
Pseudolagosuchus major Arcucci 1987	PVL 4629	Arcucci 1987, Novas 1989;	partial articulated skeleton including rib fragments, posterior dorsal vertebrae, **articulated left and right pubis, articulated left hindlimb lacking distal tarsus and pes**;
	UPLR 53	Arcucci 1987;	**left femur, tibia and fibula**;
Silesaurus opolensis Dzik 2003	various numbers	Dzik 2003; Dzik and Sulej 2007	several articulated skeletons and several hundreds of isolated bones including the **complete pelvic girdle and hindlimbs**:
Eucoelophysis baldwini Sullivan and Lucas 1999	NMMNH P-22298	Sullivan and Lucas 1999, Ezcurra 2006	incomplete postcranial material consisting of two dorsal and four incomplete caudal vertebrae, **nearly complete right pubis, partial right ischium, ilium fragment, partial femora, partial left tibia, incomplete right metatarsal II and IV, and complete metatarsal III, phalanges,** ?incomplete scapulacoracoid

3.3.2.1 Reconstruction of the hindlimb posture of *Lagerpeton chanarensis*

Crown-group crocodiles move using a sprawling locomotor posture and a more erect hindlimb posture or high walk (Cott 1960, Brinkman 1980, Webb and Gans 1982), with a femoral abduction ranging from 55° from the parasagittal plane in sprawling gait (Reilly and Elias 1998) to 30° – 20° in

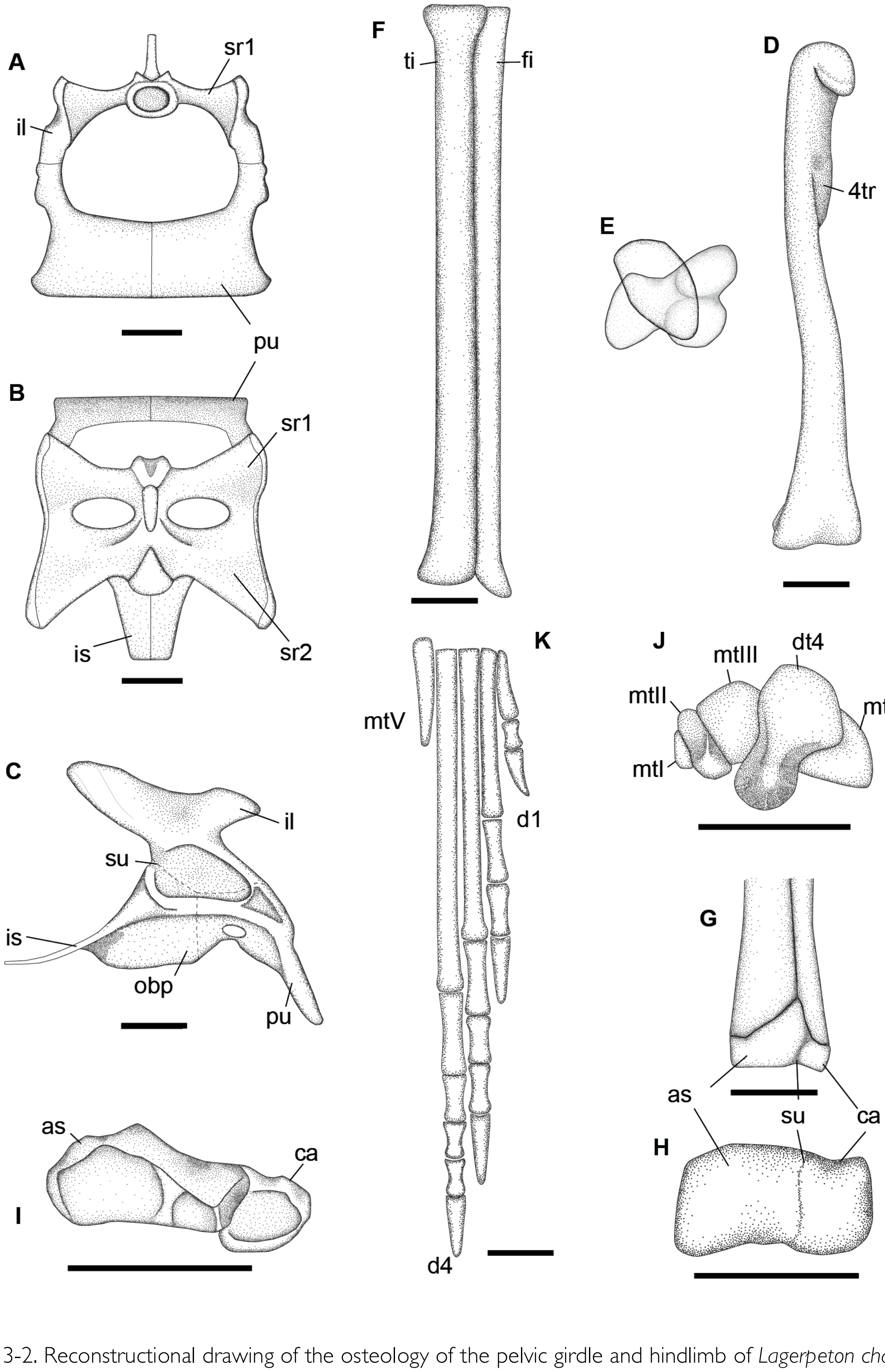


Figure 3-2. Reconstructional drawing of the osteology of the pelvic girdle and hindlimb of *Lagerpeton chanarensis* (PVL 4619, UPLR 06). Pelvis (PVL 4619) in A, anterior view, B, dorsal view, and C, lateral view. D, left femur (PVL 4619) in anterior view. E, depicting the torsion of femoral head against the distal femoral condyles. F, tibia and fibula in anterior view (PVL 4619). G, depicting the contact of tibia and fibula with astragalus and calcaneum in UPLR 06. H, astragalus and calcaneum (UPLR 06) in ventral view. J, dorsal view on dt IV and metatarsus of UPLR 06. K, reconstructional drawing of the pes of *Lagerpeton* based on PVL 4619 and UPLR 06 in plantar view. 4tr: fourth trochanter, as: astragalus; ca: calcaneum; d1, 2: digit 1, 2; dt I-IV: distal tarsal I-IV; fi: fibula; il: ilium; is: ischium; mtI-V: metatarsal I-V; obp: obturator plate; pu: pubis; sr 1-2: sacral ribs 1-2; su: suture; ti: tibia. Scale bar equals 1 cm.

the more erect gait or high walk (Gatesy 1991b, Reilly and Elias 1998). Based on the abducted femur during high walk, the locomotor posture of crown-group crocodiles is referred to as semi-erect or intermediate. The origin of crown-group crocodiles from fully terrestrial and even cursorial crocodylomorphs with an erect hindlimb posture is well established (e.g. Charig 1972, Parrish 1987) and the evolution of the intermediate hindlimb posture is considered to reflect a secondary adaptation to the semi-aquatic lifestyle (Parrish 1987). However, in spite of their evolutionary (and functional) history, Hutchinson and Gatesy (2000) showed that the locomotor apparatus of crown-group crocodiles resemble the ancestral archosaurian condition regarding its osteology and myology. In crown-group crocodiles, the closed acetabulum indicates a laterally held femur, in which the medially directed resulting joint forces of the femoral head cause the medial acetabular wall to ossify (Charig 1972, Christian 1995). The large and shallow acetabulum permits a large range of femoral protraction and retraction, adduction and abduction (Parrish 1986, Hutchinson and Gatesy 2000), as well as medial rotation (Hutchinson and Gatesy 2000). Crown-group crocodiles are characterized by an adductor-based postural support which is ancestral for archosaurs (Hutchinson and Gatesy 2000). The adductor-based postural support of basal archosaurs is the result of a laterally held femur, so that the pes is placed lateral to the hip joint. With the pes placed laterally to the hip joint, the vector of the ground reaction force, which is directed roughly vertically in the transverse plane (Blob 2001) develops an abductor moment on the hip joint. In order to control the limb posture, powerful adductor muscles originating from the pelvis ventral to the acetabulum and inserting on the femur and proximal tibia are required (Fig. 3-4). Mm. adductor femoris 1 and 2, M. puboischiotibialis, and M. puboischiofemoralis externus 3 were identified as femoral adductors in crown-group crocodiles (Gatesy 1997, Reilly and Elias 1998, Hutchinson and Gatesy 2000, Reilly and Blob 2003, Reilly et al. 2005). M. puboischiofemoralis externus 3 arises from the ischial obturator blade, posteroventrally to the acetabulum and between the origins of Mm. adductor femoris 1 and 2. M. puboischiofemoralis externus 3 inserts on the posterolateral aspect of the femur and Mm. adductor femoris 1 and 2 insert on the posterior aspect of the femoral shaft, distal to the fourth trochanter. M. puboischiotibialis also originates from the obturator blade, between the origins of Mm. puboischiofemoralis externus 3 and adductor femoris 2, and inserts on the proximal tibia (Gadow 1882, Romer 1923a, Cong et al. 1998). The main abductor of the femur, M. iliofemoralis, is developed as a single muscle in crown-group crocodiles, originating from the lateral iliac blade, dorsal to the acetabulum, and inserting on the greater part of the lateral femoral shaft (Gadow 1882, Romer 1923a, Gatesy 1997, Cong et al. 1998, Hutchinson and Gatesy 2000).

On the lineage to Aves, M. iliofemoralis is separated into at least two muscles, Mm. iliofemoralis externus and iliotrochantericus caudalis (Rowe 1986). The origin of M. iliotrochantericus caudalis occupies a large area of the preacetabular iliac blade and inserts on the anterolateral rim of the trochanteric crest of the proximal femur. M. iliofemoralis externus originates from the preacetabular iliac blade anterodorsally to the acetabulum and inserts distally to insertion of M. iliotrochantericus caudalis on the femoral shaft (Fig. 3-4). The separation of M. iliofemoralis into Mm. iliofemoralis externus and iliotrochantericus caudalis marks the development of an abductor-controlled postural support (Hutchinson and Gatesy 2000). The abductor-controlled postural support is an adaptation to an erect hindlimb posture and is often regarded to be associated with obligate bipedality. Here, the pes is placed medially to the hip joint and the adductor moment developed at the hip joint by the ground reaction force has to be controlled by powerful abductor muscles. The establishment of the abductor-controlled postural support is associated with the reduction or the loss of femoral adductors (Mm. puboischiotibialis and puboischiofemoralis externus 3) or the modification of the position of their origin and insertion (Mm. puboischiofemoralis medialis and lateralis) and therewith also their function on the lineage to Aves. The abductor-controlled postural support in Aves is associated with a perforated and deep acetabulum. In combination with a well-developed femoral head, femoral motion regarding adduction and abduction is greatly restricted (Hutchinson and Gatesy 2000), which is in accordance with the parasagittally operating limb of Aves.

The insertion points of the M. iliofemoralis externus and M. iliotrochantericus caudalis of birds are homologous with the lesser trochanter and trochanteric shelf of dinosauriforms (Rowe 1986). The absence of a lesser trochanter and trochanteric shelf in non-dinosauriform dinosauromorphs shows that an adductor-controlled postural support has to be reconstructed in *Lagerpeton*. According to the Extant Phylogenetic Bracket, M. iliofemoralis of *Lagerpeton* arises from the lateral iliac blade dorsal to the acetabulum and inserts on the greater part of the lateral femoral shaft (Fig. 3-4). The prominent ischial obturator blade serves as the origin site of the femoral adductors Mm. adductor femoris 1 and 2 and M. puboischiofemoralis externus in *Lagerpeton*. Mm. adductor femoris 1 and 2 insert on the

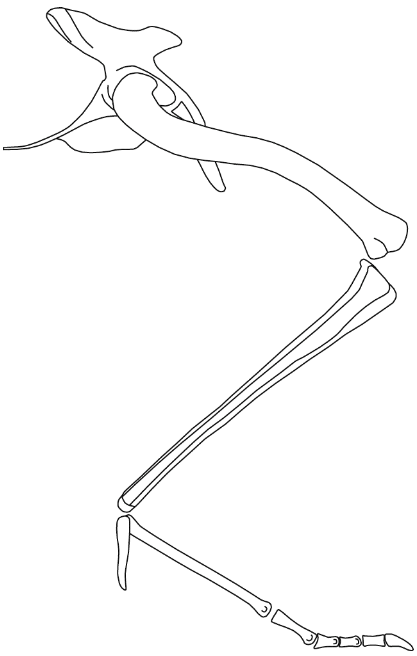


Figure 3-3. Reconstructional drawing the pelvic girdle and hindlimb of *Lagerpeton chanarensis* in lateral view; based on PVL 4916 and UPLR 06. Not to scale.

posterior femoral shaft, distal to the fourth trochanter. The insertion of M. puboischiofemoralis externus is on the posterolateral aspect of the proximal femur. Although the presence of M. puboischiotibialis is equivocal in *Lagerpeton*, its adductor-controlled postural support might be suggestive for the reconstruction of the femoral adductor (Hutchinson 2002a, Chapter 5). In *Lagerpeton*, the ancestral adductor-controlled postural support is associated with a relatively large and shallow acetabulum (Fig. 3-2c), indicating a large range of femoral motion. The closed acetabulum indicates that the resultant joint forces of the femoral head are directed mainly medially rather than dorsally. Brinkman (1980) noted that femoral long-axis rotation is a key-component in a sprawling locomotor posture. The medial rotation of the femur is translated into the parasagittal excursion of the crus (Parrish 1986) and prevents the perpendicularly oriented distal femoral articulation facet to be laterally rotated during retraction of the limb (Gatesy 1991b). Accordingly, the development of the distal articulation facet of the femur provides an indicator for inferring the range of femoral abduction (Jenkins 1971b, Parrish 1986). The distal articulation facet of the femur of tetrapods, which have a marked femoral abduction, is very broad transversely and oriented in the same plane as the long-axis of the femur (Blob 2001), or at least set at a marked angle to the femoral long-axis (Parrish

1986). With decreasing femoral abduction, the distal femoral articulation facet becomes less broad transversely and migrates from the ventral aspect of the femoral shaft to its distal end. The distal femoral articulation facet of *Lagerpeton* is set at a small angle to the femoral shaft and is relatively narrow transversely if compared to typical sprawling tetrapods (Fig. 3-2d) (Jenkins 1971b, Parrish 1986). The crus and tarsus of *Lagerpeton* form a functional unit (Fig. 3-2g). The co-ossified astragalus and calcaneum (Fig. 3-2i,g,h) greatly restricts the independent movement of tibia and fibula, which allows the lateral rotation of the crus required when rotation at the knee is involved (Haines 1942, Brinkman 1980). Moreover, the functional unit of crus and proximal tarsus implies that the ankle joint is of mesotarsal position, located between the proximal and distal tarsus (Schaeffer 1941, Rewcastle 1980). The function of the mesotarsal joint is very complex, allowing extension and flexion of the metatarsus as well as rotation of the crus against the metatarsus (Rewcastle 1980). In extant lizards, the major distal articulation element of the mesotarsal joint is the distal tarsal IV. Although the distal tarsus of *Lagerpeton* is not completely preserved, the comparison with extant lizards indicates a functional similarity of the mesotarsal joint in non-dinosauriform dinosauromorphs and extant lizards. The dorsoventrally relatively high distal tarsal IV of *Lagerpeton* (Fig. 3-2j) suggests that it serves as the major distal articulation element as in extant lizards. The aligned orientation of the distal tarsal IV in association with the relatively high heel indicate that the movement of the pes was not restricted to simple extension and flexion, but adapted to allow some rotation of the pes against the crus. Lateral rotation of the pes is indicated by the ectaxonic pes of *Lagerpeton* (Fig. 3-2k), which represents an adaptation for the resistance against lateral rotation (Rewcastle 1980).

The pelvic girdle and hindlimb of *Lagerpeton* differs significantly from the osteology and myology of birds as outlined above. *Lagerpeton* shares with ancestral archosaurs and crown-group crocodiles the adductor-controlled postural support and the joint morphology, which allows a wide range of femoral motion and long-axis rotation. The adductor-controlled postural support, the wide range of femoral motion and the long-axis rotation are suggestive for a sprawling hindlimb posture as characteristic for basal archosaurs. Crocodiles and *Lagerpeton* differ from typical sprawlers with respect to their ability of laterally rotate of the distal limb segments. In crocodiles, the lateral rotation of the distal limb is mainly allowed by joints between the metatarsals, which is considered to be an adaptation to the secondary sprawling limb posture of crown-group crocodiles and unique to those

(Brinkman 1980). In *Lagerpeton*, the tightly appressed elements of the crus (Fig. 3-2f), the mesotarsal joint, and the bundled metatarsus indicate that an intermediate hindlimb posture rather than a sprawling hindlimb posture was developed, probably comparable to the high walk in crown-group crocodilians.

3.3.2.2 Reconstruction of the locomotor capacities of *Lagerpeton chanarensis*

As far as inferable from the remains of *Lagerpeton*, the hindlimb is relatively elongated compared to the pelvic girdle (Fig. 3-3). The femur is shorter than the distal limb (tibia + metatarsus) with a distal limb to femur ratio of 1.79. A short femur associated with a considerably elongated distal hindlimb is suggestive for a cursorial locomotor habit (Coombs 1978). Cursorial tetrapods tend to maximize the out-velocities by increasing the rotational speed at the joint (Hildebrand and Goslow 2004). An increased rotational speed at the acetabulum is achieved by short lever arms of muscles arising from the pelvis. Because most muscles arising from the pelvis insert on the distal femur or proximal tibia, a short femur is required to achieve short lever arms of femoral extensors and flexors, as well as femoral rotators. With the elongation of the distal limb, the ankle extensors are elongated. In crown-group crocodiles and Aves, Mm. gastrocnemii are ankle extensors, originating from the distal femur and proximal tibia in crown-group crocodiles and Aves and inserting on the metatarsus and pes in crown-group crocodiles and on the tarsometatarus in Aves (Gadow 1882, Nickel et al. 2003). According to the Extant Phylogenetic Bracket, Mm. gastrocnemii of *Lagerpeton* arose from the distal femur and proximal tibia and insert on the metatarsus and pes. The relative length of the ankle extensors is a good indicator for the running capabilities of archosaurs (Hutchinson et al. 2005): the longer the ankle extensors the higher the maximum running speed. In *Lagerpeton*, the elongation of the distal limb is most marked in the metatarsus, which equals more than 50% of the length of the tibia. Thus, the ankle extensors are considerably elongated, indicating the ability for high maximum running speed. The relatively elongated hindlimbs allow increasing speed without the necessity to increase the energy-consuming stride frequency.

Obligate bipedality requires that the body can be statically balanced on one limb. Such static balance can however only be achieved with the pes placed close to the sagittal plane. In fact,

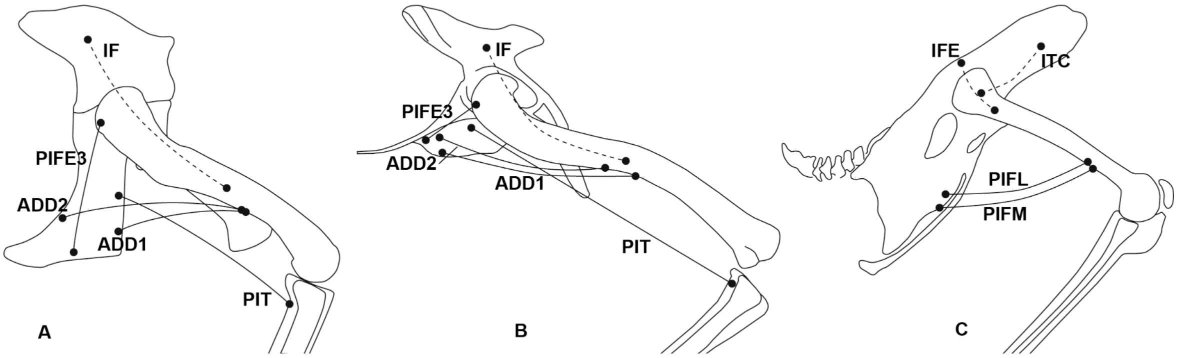


Figure 3-4. Comparison of the adductor and abductor musculature of the pelvic girdle and hindlimb of extant archosaurs and *Lagerpeton* in lateral view. In A, *Alligator* and B. *Lagerpeton*, the femoral adductor musculature consists of M. iliofemoralis (IF) and the femoral abductors M. adductor femoris 1 + 2 (ADD1 + 2), M. puboischiotibialis (PIT), and M. puboischiofemoralis externus 3 (PIFE3). In C, *Gallus*, the femoral adductors are M. iliotrochantericus caudalis (ITC) and M. iliofemoralis externus (IFE). The femoral adductors consist of Mm. puboischiofemoralis lateralis (PIFL) + medialis (PIFM). Not to scale.

trackways assigned to obligate bipedal dinosaurs show that their trackmakers placed their pedes close to the trackway midline (e.g. Thulborn 1990). With the pes being placed close to the sagittal plane, the pes is also placed medially to the hip joint. Consequently, an adductor moment is exerted on the femur so that an abductor-controlled postural support is required to control the limb posture in obligate bipeds. A transversely narrow pelvis thereby reduces the lever arm of the ground reaction force (Christian and Preuschoft 1996). In fact, obligate bipedal dinosaurs are not only characterized by an abductor-controlled postural support, but also by a transversely narrow pelvis. *Tyrannosaurus rex*, a definite obligate bipedal dinosaur, is characterized by an interacetabular distance (interacetabular width / anterposterior expansion of ilium) of 0.3, with iliac blades, which almost abut dorsally (Osborn 1916: Fig. 20). In *Lagerpeton*, the interacetabular distance is 1.2, which indicates that the pelvis of *Lagerpeton* is broader transversely than long anteroposteriorly. The transversely broad pelvis, the adductor-controlled postural support and especially the intermediate hindlimb posture clearly indicate that obligate bipedal locomotion has to be ruled out for *Lagerpeton*.

Thus, features commonly used to reconstruct an obligate bipedal locomotor posture in *Lagerpeton* (the assumed disparity of the limbs with elongated hindlimbs which is most marked in the distal limb), are actually indicative for a cursorial locomotor habit.

3.3.3 Tracks and trackways of non-dinosauriform dinosauromorphs trackmakers: *Rotodactylus*

The ichnogenus *Rotodactylus* is known from the Late Olenekian to Early Ladinian (Peabody 1948, Haubold 1967, 1999, Haubold and Klein 2002, Klein and Haubold 2007). First described from North America (Peabody 1948), the ichnogenus has subsequently been described in Europe (Haubold 1967, Demathieu 1970, Demathieu and Gand 1973, 1974, Demathieu and Leitz 1982, Demathieu 1984) and Northern Africa (Kotanski et al. 2004). The manus prints of *Rotodactylus* are pentadactyl, but functionally tridactyl, with external digit imprints reduced in length. The manus prints further show that the manus of the trackmaker was digitigrade, with a bundled metacarpus (Fig. 3-5). The pes prints are ectaxonic with digit IV>digit III>digit II. Digits I and digit V are reduced to dot-like imprints. The imprint of digit V is set proximal to digit IV, separated from the latter by a gap (Fig. 3-5). The length of the pes prints varies between 34 mm and 80 mm (Peabody 1948, Haubold 1971a). Compared to the manus prints, the pes prints are placed with a relatively large distance from the trackway midline (Fig. 3-5b,c,d). Relative to the trackway midline, the long-axis of the pes prints is rotated laterally. The cross-axis of the pes prints is aligned anteromedially to posterolaterally relative to the trackway midline (Fig. 3-5a). The pes prints always overstep the manus prints (Peabody 1948, Haubold 1967, 1971a, 1999, Haubold and Klein 2002). Peabody (1948) noticed that with increasing stride length the pes prints are placed closer to the trackway midline (Fig. 3-5d). Manus prints are lacking in some trackways (Peabody 1948, Haubold 1967, Haubold and Klein 2002).

Ever since its first description, the *Rotodactylus* trackmaker was considered to be closely related to the origin of dinosaurs (Peabody 1948, Huene 1956, Haubold 1967). When providing a phantom reconstruction of the potential trackmaker, Haubold (1967) recognized the correspondence in the overall proportions of his reconstruction and the basal ornithodiran *Scleromochlus* according the restoration presented by Huene (1914). In fact, *Rotodactylus* shares with *Scleromochlus* a digitigrade pes with bundled and slender metatarsus and the length of the metatarsus being 50% or more that of the tibia (Haubold and Klein 2002). With the description of the vertebrate fauna of the Middle Triassic Los Chañares Formation new potential trackmakers, the non-dinosauriform dinosauromorphs, came into the picture. *Rotodactylus* shares with non-dinosauriform dinosauromorphs a pentadactyl but functionally tridactyl ectaxonic pes with digit IV longer than digit

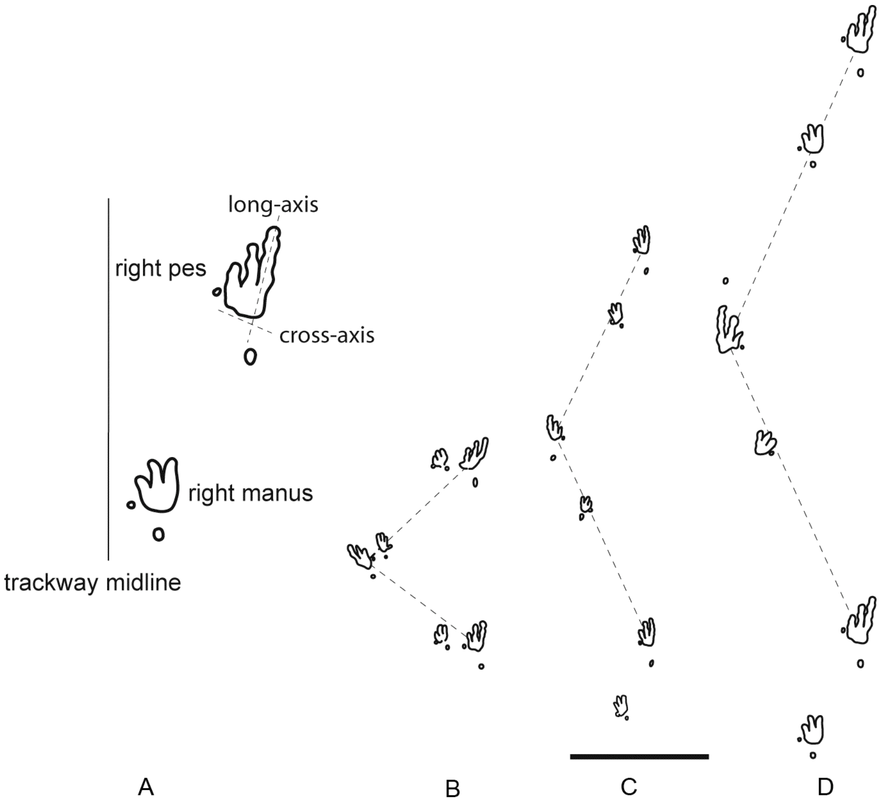


Figure 3-5. *Rotodactylus matthesi* trackways. A, depicting the overstepping of the pes prints by the manus prints and the variation of gauge and stride length. In B, the gauge is very broad with a short stride length. In C, and D, the gauge is narrower with increasing stride length. The manus prints always overstep the pes prints. Modified from Haubold (1971b). Scale bar equals 5 cm.

III (Haubold 1999, Haubold and Klein 2002). The ichnogenus *Rotodactylus* is known from the Late Olenekian to Early Ladinian (Peabody 1948, Haubold 1967, 1971a, 1999, Haubold and Klein 2002, Klein and Haubold 2007), whereas the non-dinosauriform dinosauromorph body fossils are only known from the Ladinian (Stipanicic 1983) and Norian (Irmis et al. 2007a). Nevertheless, due to the synapomorphy-based approach, the assignment of *Rotodactylus* to non-dinosauriform dinosauromorph trackmakers is well supported (Haubold 1999). Dinosauroid tracks and traces are characterized by a digitigrade pes posture, with impression of the heel being absent or small. The pes prints indicate a mesaxonic and functionally tridactyl pes, with the cross-axis of the pes orthogonal or aligned obliquely from anteromedial to posterolateral relative to the trackway midline. Dinosauroid traces are further characterized by a narrow trackway, with high values of pace angulation and for the ratio of stride length to trackway width (see Thulborn 2006).

The manus prints in the *Rotodactylus* trackways show that the trackmaker moved using a quadrupedal locomotor posture (Peabody 1948, Haubold 1967, 1971a, 1999, Haubold and Klein 2002). As indicated by the narrow gauge of the manus prints, the forelimbs of the *Rotodactylus* trackmaker operated in the parasagittal plane (Peabody 1948, Haubold 1967, 1971a, 1999, Haubold and Klein 2002). The pes prints are, however, always placed with a considerably greater distance from the trackway midline compared to the manus prints (Peabody 1948, Haubold 1967, 1971a, 1999), demonstrating the intermediate hindlimb posture of the trackmaker. Regarding the orientation of the pes prints in relation to the trackway midline, the trackways of basal Archosauriformes and dinosaurs differ significantly from each other. With the long-axis of the pes prints set at a marked angle from the trackway midline and the cross-axis being aligned posteromedially to anterolaterally from it, the pes prints of basal Archosauriformes are supposed to reflect their crurotarsal ankle joint. The long-axis of the pes prints of trackways assigned to dinosauroid trackmakers is set parallel to the trackway midline and the cross-axis is set orthogonal to the trackway midline or aligned anteromedially to posterolaterally relative to it, indicating an ankle joint of a mesotarsal position (e.g. Lockley and Meyer 2000, Thulborn 2006). The trackways of non-dinosaurian dinosauriform trackmakers resemble the dinosauroid trackways regarding the narrow gauge of the trackmaker and the orientation of the long-axis and cross-axis relative to the trackway midline (Fig. 3-5a) (Haubold and Klein 2000, 2002). The long-axis of the pes prints rotated slightly laterally in relation to the trackway midline and the cross-axis being aligned obliquely from anteromedially to posterolaterally relative to the trackway midline indicates that the ankle joint of the *Rotodactylus* trackmaker was functionally different to that of Dinosauriformes.

Peabody (1948) and Haubold (1967) argued that the overstepping of the manus prints by the pes prints, even during slow locomotion, demonstrates the highly cursorial morphology of the trackmaker, with markedly elongated hindlimbs and relatively short forelimbs, possibly associated with a short trunk. This results in a small coupling value (gleno-acetabular distance / forelimb length + hindlimb length) (Fig. 3-6). As shown above, a small coupling value is characteristic for basal ornithodirans. Haubold (1971a) measured a coupling value of 0.27 for *Scleromochlus*. In fact, Haubold (1967) ruled out *Scleromochlus* as a potential trackmaker for the *Rotodactylus* trackways based on the very small coupling value. The coupling value of the *Rotodactylus* trackmaker ranges from 0.3 to 0.5.

Haubold (1999) stated that *Rotodactylus* is characterized by a unique pattern of acceleration unseen in any other trackway assigned to Triassic archosaurs. The acceleration of the trackmaker is reflected in the varying position of the pes prints relative to the manus prints. With increasing stride length, the pes prints are placed at a greater distance anterior to the manus prints. Furthermore, with increasing stride length the pes prints are placed relatively closer to the trackway midline (Peabody 1948, Haubold 1967, 1999). Increased stride length is related to increased speed. With increasing speed, the transition from quadrupedal to bipedal locomotion is observed, indicated by the absence of manus prints (Peabody 1948, Haubold 1967). Haubold and Klein (2002) were able to demonstrate that the absence of manus prints is not a preservational artifact, but reflects the facultative bipedal locomotion of their trackmakers. The capability to facultative bipedality is differently well developed in the ichnogenus. Whereas the oldest known ichnotaxon assigned to *Rotodactylus*, *R. matthesi* (Haubold 1967, 1999) appears to be the product of an obligate quadrupedal trackmaker, the bipedal locomotor capacities of *R. cursorius* appears to be very well developed (Peabody 1948).

3.3.4 The bauplan and locomotor function of Dinosauromorpha

3.3.4.1 Reconstruction of the bauplan of basal Dinosauromorpha

The *Rotodactylus* trackmaker is characterized by a marked disparity of the limbs, with relatively elongated hindlimbs and / or a short trunk (Fig. 3-6) (Peabody 1948, Haubold 1967, 1999). Haubold (1999) inferred from the pes prints that the metatarsus of the trackmaker equals 50% of the tibia or more. The reconstruction of the bauplan of non-dinosaurian dinosauromorphs based on the evidences gained from *Rotodactylus* corresponds to the information on the bauplan gained from osteological remains and the phylogenetic framework. Osteological remains of non-dinosauriform dinosauromorphs are known from *Lagerpeton*, PVL 3870 and *Dromomeron*. The remains of *Dromomeron* are found disarticulated. Thus, it is not possible to gain insights into the proportions of the limb. PVL 3870 is known from a complete hindlimb found in articulation and an incomplete presacral vertebral column. Although the total length of the gleno-acetabular distance cannot be

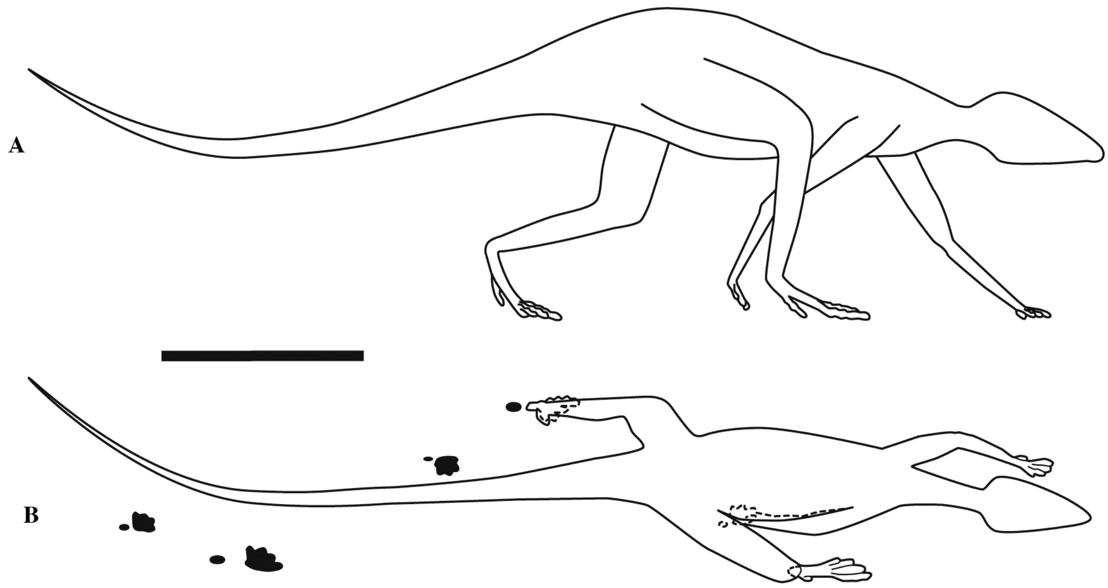


Figure 3-6. Reconstructional drawing of the *Rotodactylus* trackmaker in A, lateral and B, dorsal view. Modified from Haubold (1967). Scale bar equals 5 cm.

reconstructed from these remains, the restoration of Sereno and Arcucci (1994) indicates that PVL 3870 was characterized by a relatively short trunk. The hindlimbs of PVL 3870 are comparable to *Lagerpeton* regarding their overall proportions. The relatively elongated hindlimb of PVL 3870 is most marked in the distal limb, with the femur being shorter than the tibia. In PVL 3870, the metatarsus equals 56% of the length of the tibia. The phylogenetic framework formed by the basal ornithodiran *Scleromochlus taylori* (Benton 1999) and basal dinosaurs, such as *Eoraptor lunensis* (PVL 512), *Herrerasaurus ischigualastensis* (Novas 1993, Sereno 1993), and *Heterodontosaurus tucki* (Santa Luca 1980) confirms the information on the bauplan gained from *Rotodactylus* and the sparse osteological remains of non-dinosauriform dinosauromorphs. The phylogenetic framework shows that basal Dinosauromorpha are characterized by a marked disparity of the limbs with a short trunk.

3.3.4.2 Reconstruction of the locomotor capacities of non-dinosauriform Dinosauromorpha

The trackways of *Rotodactylus* show that the quadrupedal locomotion with the intermediate hindlimb posture is not unique to *Lagerpeton* but probably characteristic for all non-dinosauriform dinosauromorphs. However, *Rotodactylus* further shows that their non-dinosauriform dinosauromorph trackmakers were able to run bipedally at least at high speed. The trackways of *Rotodactylus* also show that their trackmaker were able to frequent acceleration (Peabody 1948, Haubold 1967, 1999). Frequent acceleration is also reflected in the bauplan of non-dinosauriform dinosauromorphs. The marked disparity of the limbs, with relatively short forelimbs and elongated hindlimbs, are interpreted as an adaptation to frequent acceleration and high maximum running speed (Christian and Garland 1996). As reflected in the trackways of *Rotodactylus*, non-dinosauriform dinosauromorphs tend to run with a more erect hindlimb posture with increased speed (Peabody 1948, Haubold 1967). With a more erect hindlimb posture, the effective stride length is increased.

3.3.5 Evolution of the pelvic girdle and limb of Dinosauromorpha on the lineage to basal dinosaurs – implications for the evolution of locomotion

Lagerpeton shares most aspects of the functional morphology of the pelvic girdle and limb with basal archosaurs (Fig. 3-7). Features of the functional morphology of *Lagerpeton* shared with basal archosaurs are commonly regarded as reflecting a sprawling or at best an intermediate hindlimb posture (see above). The functional morphology of the pelvic girdle and limb of *Lagerpeton* differs from most basal archosaurs with respect to the digitigrade pes posture and the bundled and elongated metatarsus, as well as the marked disparity of the limb. These features are shared with basal Ornithodira and are commonly regarded as adaptations to an erect hindlimb posture (e.g. Charig 1972). However, this study has shown that these features are also found in association with an intermediate hindlimb posture and rather reflect adaptations to cursoriality than to an erect hindlimb posture. The development of a perforated acetabulum with a laterally projecting supraacetabular crest, a well-developed femoral head oriented in the transverse plane, a straight femoral shaft in anterior view, oblique joint surfaces, and a mesaxonic pes, as well as the acquisition of the abductor-controlled postural support are also commonly regarded as adaptations to an erect hindlimb posture in archosaurs (e.g. Charig 1972, Parrish 1986, Hutchinson and Gatesy 2000). With exception of the perforated acetabulum, all these features were developed on the lineage to dinosaurs. Furthermore, the development of the cnemial crest, the lesser trochanter and trochanteric shelf and the brevis

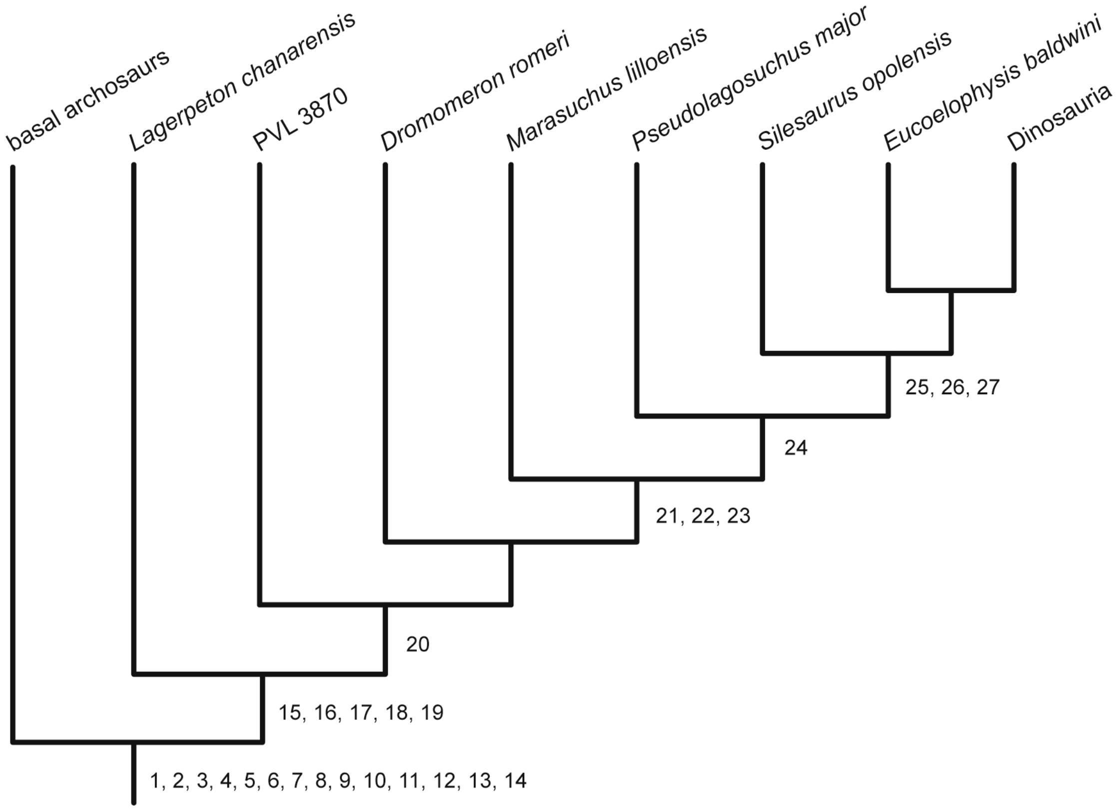


Figure 3-7. Morphofunctional evolution of the pelvic girdle and hindlimb of non-dinosaurian dinosauromorphs mapped on the phylogenetic framework. 1, acetabulum closed, shallow and of moderate depth; 2, femoral head weakly offset from proximal shaft; 3, femoral head only slightly inturned; 4, pubis and ischium short; 5, femur horizontally; 6, femoral shaft sigmoid in anterior view; 7, distal articulation facet oblique with lateral condyle projecting further distally; 8, primitive mesotarsal joint; 9, adductor-controlled postural support; 10, plantigrade; 11, quadrupedality; 12, femur longer than tibia; 13, ectaxonic pes; 14 primitive mesotarsal joint; 15, femur shorter than tibia; 16, advanced mesotarsal joint; 17, digitigrade pes posture; 18, intermediate hindlimb posture; 19, facultative bipedality; 20, more bilateral symmetric pes; 21, cnemial crest; 22, abductor-controlled postural support; 23, elongated pubis; 24, mesaxonic pes; 25, distal articulation facet of femur plane; 26, acetabulum deep; 27, lateral projecting supraacetabular crest.

fossa reflect the modification of the myology of the pelvic girdle and limb. This certainly indicates a change in the hindlimb posture. The mosaic-like pattern of the acquisition of the osteomyological features and its meaning for the evolution of the hindlimb posture of Dinosauromorpha has yet to be studied in detail. Nevertheless, this shows that the pelvic girdle and limb of *Lagerpeton* shows a unique character combination of ancestral and derived features.

3.4 DISCUSSION

3.4.1 Previous studies on the locomotor function of *Lagerpeton chanarensis*

The reconstruction of *Lagerpeton* with a quadrupedal locomotion and an intermediate hindlimb posture contrasts the traditional idea of the locomotion of *Lagerpeton* in particular and non-dinosauriform dinosauromorphs in general. When Romer (1971) first described the remains of *Lagerpeton*, he regarded the basal dinosauromorph as a cursorial biped. Romer inferred the cursorial locomotor habit from the proportions of the hindlimb of *Lagerpeton*, with the tibia being longer than the femur. The erect hindlimb posture was inferred from the "…sharply inturned head of the femur…" (Romer 1971:8). According to the understanding of Romer, both the cursorial locomotor habit and the erect hindlimb posture are suggestive for obligate bipedality, without citing any features in support of this view. However, Romer noted that the suggestion of obligate bipedal locomotion in *Lagerpeton* "…is increased by the shortness of the front legs of "*Lagosuchus*" [=*Marasuchus*]" (Romer 1971:8).

Arcucci (1986, 1989) and Sereno and Arcucci (1993) argued that *Lagerpeton* might have been a saltator. The anterior inclination of the neural spines of the posteriormost dorsal vertebrae, the small size of the pelvis compared to the hindlimb, and the reduction of the lateral digits of the pes were cited to justify the reconstruction of a saltatorial locomotion. Saltatorial locomotion in dinosaurs has been discussed before. Raath (1972) described pes prints of a small theropod dinosaur from the Early Jurassic of Zimbabwe. The pes prints were preserved side by side and Raath argued that this has to be regarded as the trackway of a saltatorial biped. Later, Bernier et al. (1984) described a trackway of a saltatorial theropod from the Upper Jurassic of France. However, the re-examination of these trackways has shown that they represent resting positions or the trackway of a turtle rather than dinosaurs with a saltatorial locomotion. Likewise, the characters chosen by Arcucci (1986, 1989) and Sereno and Arcucci (1993) for justifying saltatorial locomotion in *Lagerpeton* are not convincing. In mammals, the adaptations of the vertebral column to saltatorial locomotion are more far-reaching than reported by Arcucci (1986, 1989) and Sereno and Arcucci (1993). Saltatorial locomotion is especially reflected in the pelvic girdle. These modifications include the fusion of the vertebrae of the sacrum and the reduction of the neural spines (Howell 1932, Herkner 1989). This is not the case in *Lagerpeton*. In fact, the robustness and size of the pelvic girdle compared to the hindlimb, and the development of the neural spines, are comparable to other basal Ornithodira (e.g.

Arcucci 1987, Sereno and Arcucci 1994, Benton 1999, Dzik 2003). The relatively small pelvic girdle (or relatively elongated hindlimbs!) and the reduction of the lateral digits in *Lagerpeton* have to be regarded as cursorial adaptations, as proposed by Romer (1971), rather than saltatorial adaptations.

3.4.2 Biomechanical reasons for facultative bipedal locomotion

The velocity of terrestrial tetrapods depends on stride length and stride frequency. Above a critical velocity, stride frequency cannot be increased, so that increasing velocity can only be achieved by increasing the stride length (Christian et al. 1994, Christian 1995). Due to the disparity of the limbs, the maximum stride length of the hindlimbs is considerably larger than that of the relatively shorter forelimbs in lizards. To keep up with the elongated hindlimbs, the angle velocity and the excursion of the forelimbs has to be increased, or they have to be accelerated faster than the hindlimbs. However, muscle forces limit both the increase of the angle velocity with greater excursion and the faster acceleration of the forelimbs (Christian et al. 1994). The maximum vertical component of the ground reaction force is larger for the stronger hindlimbs, so that they contribute more to the body support (Christian et al. 1994). The support of the forelimbs during locomotion is further reduced by increasing the effective stride length of the hindlimbs, for example by shifting from a plantigrade pes posture to a digitigrade pes posture (Irschick and Jayne 1999) and / or by moving the hindlimbs in a more parasagittal plane, or by increasing the angle of the trunk relative to the horizontal plane (Irschick and Jayne 1999). By lifting the forelimbs off the ground, the stride length of the hindlimbs is no longer limited by the shorter forelimbs.

Christian (1995) distinguished between two groups of recent lizards, according to their locomotor capabilities. The first group consists of mainly small taxa with relatively short hindlimbs and a tail that equals or slightly exceeds the head-trunk distance. These lizards are often good climbers, but relatively slow. Lizards assigned to the second group are generally larger than those assigned to the first group and are characterized by a marked disparity between the limbs, with considerably elongated hindlimbs. The tail of these lizards is elongate, notably exceeding the head-trunk distance. Members of the second group are often very fast runners, with a well-developed ability to bipedal locomotion, which has been reported in an increasing number of taxa (Christian et al. 1994). Snyder

(1962) proposed that in recent lizards the stride of the hindlimbs is increased up to three times by shifting to a bipedal locomotor posture. According to these considerations, the disparity of the limbs and the requirement to rely on fast running speed cause the bipedal locomotor posture (Christian and Garland 1996, Christian 2007). Nonetheless, Christian (1995) noted that the maximum running speed increases only little with the bipedal locomotor posture and Irschick and Jayne (1999) noted no increase of the running speed of bipedal lizards at all. However, Urban (1956), Sukhanov (1974), Christian (1995), and Irschick and Jayne (1999) observed that lizards stumble frequently over their forelimbs at least at high speeds. It appears that fast running lizards lift the forelimbs off the ground to avoid co-ordination problems.

Snyder (1952, 1954, 1962) provided a detailed study on the musculoskeletal adaptations in facultative bipedal recent lizards. According to Snyder (1952, 1954, 1962), musculoskeletal adaptations to facultative bipedality involve the vertebral column, the forelimbs, and the pelvic girdle and hindlimb. Nevertheless, adaptations to facultative bipedal locomotion appear to involve the pelvic girdle and hindlimb to a much greater extent than the forelimbs. Compared to obligate quadrupedal lizards, facultative bipedal lizards are characterized by a transversely relatively narrow pelvis, resulting in a narrow interacetabular width. Facultative bipedal lizards tend to have an anteroposteriorly expanded ilium, which is most marked in the cranial elongation of the preacetabular process. The disparity of the limbs, with the hindlimbs longer than the forelimbs, is far more marked in facultative bipedal lizards when compared to obligate quadrupedal lizards. Whereas the elongation of the hindlimb appears to involve all segments of the limb, the elongation appears to be most marked in the proximal segments, such as the femur and tibia. Adaptations to bipedal locomotion in lizards further involve the shortening of the presacral vertebral column and the development of a long and relatively heavy tail.

Snyder (1952, 1954, 1962) noted that the most pronounced difference between the myology of obligate quadrupedal and facultative bipedal lizards is of quantitative nature, so that the arrangement of the myology of facultatively bipedal lizards can be distinguished from that of obligate quadrupedal lizards mainly in the allocation of the muscle bulk. Thus, facultative bipedal lizards concentrate the muscles on the proximal limb and tendons for insertion are correspondingly lengthened. The cranial elongation of the preacetabular process indicates a cranial shift of the corresponding muscles originating on the preacetabular process or inserting on the preacetabular process.

The osteological adaptations in the pelvic girdle and hindlimb associated with facultative bipedality in extant lizards are generally consistent with osteological characteristics of the pelvic girdle and hindlimb of *Lagerpeton*. *Lagerpeton* shares with facultative bipedal lizards the marked disparity of the limbs and the relatively short trunk. Nonetheless, some of the osteological characteristics in the osteology of the pelvic girdle and hindlimb associated with facultative bipedal locomotion in extant lizards appear to contradict the assumed osteological adaptations to facultative bipedal locomotion in the pelvic girdle and hindlimb of *Lagerpeton*. As mentioned above, the pelvis of *Lagerpeton* is relatively broad transversely with a relatively short preacetabular process, whereas facultative bipedal lizards are characterized by a narrow pelvis, with a relatively elongated preacetabular process. These conflicting adaptations, however, are inconsistent only at first glance and relate to the fact that lizards move using a sprawling locomotor posture and that facultative bipedal lizards were compared to obligate quadrupedal lizards, whereas *Lagerpeton* was characterized by an intermediate hindlimb posture and was compared to obligate bipedal dinosaurs with an erect hindlimb posture. If compared to basal archosaurs with an obligate quadrupedal locomotor posture and a sprawling hindlimb posture, the pelvis of *Lagerpeton* is relatively narrow and the preacetabular process is relatively well developed. The observation that the elongation of the hindlimb is most marked in the proximal limb of cursorial facultative bipedal lizards is relatively elongated compared obligate quadrupedal lizards is contrary to observations made in mammals (e.g. Snyder 1954, Carrano 1999) and Ornithodira in general (Coombs 1978, Gauthier 1986, Benton 1999) and *Lagerpeton* in particular, in which the elongation of the hindlimb of cursorial taxa is most marked in the distal limb segments, such as the tibia and pes. This also relates to the fact that lizards move using a sprawling hindlimb posture, whereas mammals and Ornithodira move or moved using an intermediate or erect hindlimb posture. In tetrapods with a sprawling hindlimb posture, the femur is always longer than the tibia (e.g. Ewer 1965). When elongation of the hindlimb length is required, the femur has to be elongated likewise. In tetrapods with an erect (or intermediate) hindlimb posture, the femur is relatively reduced in length with increasing body size as adaptation to a cursorial locomotor habit (e.g. Coombs 1978, Carrano 1999). Thus, the conflicting adaptations in the osteology of the pelvic girdle and hindlimb of facultative bipedal lizards and *Lagerpeton* are due to the different hindlimb posture rather than being actually inconsistent.

The trackmakers of *Rotodactylus* were able to run very fast using a quadrupedal locomotory posture (pers. com. Haubold). This might indicate that non-dinosauriform dinosauromorphs used bipedal locomotion not to increase their maximum running speed but, comparable to extant lizards, in order to avoid co-ordination problems resulting from their bauplan. In fact, with increasing speed, the amount to which the pedes oversteps the manus increases. The trackways of *Rotodactylus* further show that their trackmaker change from an intermediate hindlimb posture to a more erect hindlimb posture with increasing speed. The erect hindlimb posture is probably achieved in order to increase the effective stride length of the trackmaker. When a more erect and more upright hindlimb posture is associated with an increasing trunk angle, the forelimbs will lose the contact to the ground. As in extant lizards, ultimately the bauplan of non-dinosauriform dinosauromorphs is the reason for the facultative bipedal locomotion.

3.5 CONCLUSIONS

The integrative approach applied here, combining osteology, myology, biomechanical considerations, and trace fossils contributes significantly to our knowledge on the locomotion of non-dinosauriform dinosauromorphs. *Lagerpeton* was reconstructed with an adductor-controlled postural support and moved using an intermediate hindlimb posture. Based on the transversely broad pelvis, the adductor-controlled postural support and the intermediate hindlimb posture, a quadrupedal locomotor posture is assumed for *Lagerpeton*. Both the adductor-controlled postural support with the intermediate hindlimb posture and the quadrupedal locomotor posture of *Lagerpeton* resemble ancestral archosaurs rather than dinosaurs, which have an abductor-controlled postural support with the erect hindlimb posture and an obligate bipedality. The ichnogenus *Rotodactylus*, which is assigned to non-dinosauriform dinosauromorph trackmakers, demonstrates that quadrupedal locomotion associated with an intermediate hindlimb posture is not unique to *Lagerpeton* but probably characteristic for non-dinosauriform dinosauromorphs. *Rotodactylus* further shows that non-dinosauriform dinosauromorphs were facultative bipeds. Bipedal locomotion in non-dinosauriform dinosauromorphs is interpreted to reflect the requirement to rely on fast running speed and their bauplan. The bauplan of non-dinosauriform dinosauromorphs is reconstructed with considerably elongated hindlimbs associated with relatively short forelimbs and / or a short trunk. Bipedal locomotor posture might have been achieved in order to avoid co-ordination problems of the elongated hindlimbs and the short forelimbs. However, it cannot be ruled out that an obligate bipedal locomotor posture led to an increase in maximum running speed, which is otherwise limited by the relatively short forelimbs. The modification of the osteology and myology of the pelvic girdle and limbs might indicate an improvement of the locomotor capacities within dinosauriforms.

Chapter 4

Does size matter? Effects of body size on the evolution of locomotion

4.1 INTRODUCTION

Locomotion is of fundamental importance for all aspects of the biology of terrestrial vertebrates, which require movement. The ability to actively forage for food sources is just as pertinent to locomotion as the ability to prey capture or escape, migration, and social interactions (Carrier 1987, Biewener 2003). This explains why reconstructing the locomotor capabilities of extinct organisms provide a powerful tool to get insights into the biology of extinct vertebrates beyond their anatomy and evolution. This holds also true for dinosaurs, as for any other group. The fossil record of basal dinosaurs is very scattered and fragmentary. The oldest records of material that is unquestionably dinosaurian, comprising both saurischians and ornithischians, are reported from Carnian strata of South America. The remains from the Ischigualastian Formation have dominated our picture of basal dinosaur anatomy, evolution, and ecology. The skeletal remains from the Argentinean Ischigualasto Formation (*Eoraptor lunensis* [Sereno et al. 1993], *Herrerasaurus ischigualastensis* [Reig 1963, Sereno and Novas 1992, 1993, Novas 1993, Sereno 1993], *Pisanosaurus mertii* [Casamiquela 1967]), from the Brazilian Santa Maria Formation (*Staurikosaurus pricei* [Colbert 1970] and *Saturnalia tupiniquim* [Langer et al. 1999, 2007, Langer 2003]), and from the Brazilian Caturrita Formation (*Guaibasaurus candelariensis* [Bonaparte et al. 1999, 2007]) are generally relatively complete and often found in articulation. The marked disparity of the limbs, with elongated hindlimbs and relative short forelimbs, the remarkably elongation of the distal hindlimb elements, and the large hindlimb to trunk ratio, as in *Eoraptor*, *Herrerasaurus*, and *Staurikosaurus*, have often been considered to indicate obligate bipedality in dinosaurs (Galton 1970, Coombs 1978). Adaptations in the skull (sliding intramandibular joint, serrated an mediolaterally compressed teeth) and the manus (relatively elongated metacarpus, penultimate phalanges, distal phalanges relatively elongated, trenchant unguals) are supposed to demonstrate the carnivorous habit of basal saurischians (Sereno 1993, Langer 2004, Langer and Benton 2006). The obligate bipedal locomotor posture of dinosaurs is considered to have been inherited from their predecessors, the dinosauromorphs (e.g. Benton 1997, Padian 1997). Both the obligate bipedal locomotor posture and the carnivorous habit are retained in theropods. The locomotor posture of basal Sauropodomorpha has remained controversial. They have been considered by various authors to represent obligate bipedal, facultative bipedal and sometimes obligate quadrupedal (Barrett and Upchurch 2007), and are further supposed to be herbivorous or omnivorous (Barrett 2000).

Our picture of the locomotor capacities of basal dinosauromorphs and early evolution of dinosaurs was challenged with the finding of *Silesaurus opolensis* and the new reconstruction of the locomotor apparatus of *Lagerpeton* (see Chapter 3). Considered to be a non-dinosaurian dinosauriform (Ezcurra 2006, Langer and Benton 2006), the relatively elongated forelimbs indicate that *Silesaurus* was an obligate quadruped, whereas its beak and denticulate teeth are interpreted as herbivorous adaptations (Dzik 2003). Most recently, Fechner (2005, 2006a,b, 2007, Chapter 3) reconstructed the locomotor posture of non-dinosauriform dinosauromorphs as quadrupedal with an intermediate hindlimb posture. The quadrupedal locomotor posture with an intermediate hindlimb posture of non-dinosauriform dinosauromorphs is consistent with the reported ichnofossil record (Peabody 1948, Haubold 1967, 1971a, 1999, Haubold and Klein 2000, 2002, Chapter 3). Moreover, the ichnofossil record shows that dinosauriform trackmakers also moved using a quadrupedal locomotor posture and that obligate bipedality on the lineage to saurischians had not evolved prior to the Norian (Olsen et al. 1998, Haubold and Klein 2000, 2002, Klein and Haubold 2007). As a result, the erect hindlimb posture and obligate bipedality are commonly regarded as key-innovations in dinosaur evolution (e.g. Bakker 1971, 1986, Charig 1972, 1984, Bonaparte 1982, Benton 1997) and often considered to be accompanied by other superior adaptations, such as the ability to attain and sustain high running speed, endothermy, and, not at least, intelligence (Bakker 1971, Benton 1997). These superior adaptations are supposed to constitute a competitive advantage and explain the success of dinosaurs after the faunal changeover at the end of the Carnian (Benton 1997). The body fossil record of basal dinosauromorphs and basal saurischians, however, is too fragmentary to reconstruct the evolution of the locomotor posture solely based on osteological remains. In order to reconstruct both the evolution of the erect hindlimb posture and the obligate bipedality on the lineage to saurischians, an integrative approach combining osteology, myology and biomechanical considerations is used. The results of the functional morphological study are compared with the ichnofossil record assigned to dinosauromorphs and do not only provide the basis for interpreting the ecology of Dinosauromorpha and its evolution on the lineage to basal saurischians, but also provide the basis for reconstructing the locomotor posture of basal Sauropodomorpha.

4.2 ORIGIN AND INTERRELATIONSHIPS OF BASAL SAURISCHIANS

In field campaigns in the 1960s, A.S. Romer and during subsequent fieldwork J.F. Bonaparte and others discovered a diverse fauna of small-sized archosaurs from the Argentinean Los Chañares Formation, some of which being closely related to the origin of dinosaurs (Romer 1971, 1972a,b, Bonaparte 1975, Arcucci 1986, 1987). In 1971, Romer described the remains of two new "thecodonts", *Lagerpeton chanarensis* and *Lagosuchus talampayensis*. Although relatively incomplete, Romer recognized the exceptional morphology of the hindlimb, distinguishing both *Lagerpeton* and *Lagosuchus* from all other Archosauriformes previously described from the Los Chañares Formation. At the time, the incompleteness of the material and the unusual composition of ancestral and advanced character states of the pelvic limb did not allow Romer to establish a phylogenetic placement beyond Pseudosuchia for *Lagerpeton* and *Lagosuchus*. Although convinced of the close relationship of *Lagerpeton* and *Lagosuchus* to the radiation of Archosauriformes leading to dinosaurs, Romer doubted that both *Lagerpeton* and *Lagosuchus* could be regarded as lying on the direct lineage of the origin of dinosaurs. Together with new material and new insights into basal dinosaur anatomy and systematics, the phylogenetic relationship of *Lagerpeton* and *Lagosuchus* to each other and their placement regarding the origin of dinosaurs initiated controversial discussion in subsequent years. In 1972a, Romer erected a new species within the genus *Lagosuchus*, *Lagosuchus lilloensis*, distinguishing it from *L. talampayensis* solely by its smaller size. When Bonaparte (1975) reviewed the material of

Lagosuchus, he considered *L. lilloensis* a junior synonym of *L. talampayensis*. Furthermore, Bonaparte assumed that *Lagosuchus* was a part of the "thecodont" radiation, which gave rise to saurischians and ornithischians. Unable to assign *Lagosuchus* to a known "thecodontian" family, Bonaparte further erected a new family, the Lagosuchidae. In 1986, Arcucci reviewed the material of *Lagerpeton* and added new material to this taxon. According to her findings, the unusual morphology of the pelvic girdle and hindlimb of *Lagerpeton* solely reflected its advanced locomotor capabilities and similarities in the morphology of the pelvic girdle and hindlimb of *Lagerpeton* and the lagosuchids were rather due to adaptive convergences than reflecting a close phylogenetic relationship. Later, Arcucci (1987) described a new member of the Archosauriformes from the Los Chañares Formation, *Pseudolagosuchus major*, which she assigned to Lagosuchidae mainly due to the similarities in the proximal tarsus. Arcucci further pointed out the similarities between the tarsus of Lagosuchidae and basal saurischians. More recently, Sereno and Arcucci (1994) reviewed the material of *Lagosuchus* and revealed that the type material of *L. talampayensis* is not diagnostic and that therefore the genus *Lagosuchus* has to be considered a nomen dubium. Sereno and Arcucci (1994) thereupon erected a new genus, *Marasuchus*, and referred most of the material previously referred to *L. lilloensis* to *Marasuchus lilloensis*. Sereno and Arcucci (1994) assumed that *Lagerpeton* and *Marasuchus* share a more recent common ancestry with dinosaurs than with pterosaurs. Furthermore, Sereno and Arcucci (1993, 1994) argued that *Marasuchus* (or lagosuchids) were more closely related to dinosaurs than *Lagerpeton*, but that they were not able to reveal the relationship between *Lagerpeton* and the lagosuchids. The close association of the lagosuchids *Marasuchus* and *Pseudolagosuchus* to the origin of dinosaurs was supported in cladistic analyses carried out by Gauthier (1986), Novas (1996), Benton (1999), and Ezcurra (2006).

For a long time, *Lagerpeton*, *Marasuchus,* and *Pseudolagosuchus* from the Los Chañares Formation were the only recorded unquestionable non-dinosaurian dinosauromorphs. New finds and the re-evaluation of known material in recent years are now bringing new forms into the picture. Most recently, Irmis et al. (2007a) described a new non-dinosauriform dinosauromorph, *Dromomeron romeri*, from the Norian of North America. When Dzik (2003) described the material of *Silesaurus opolensis* from the Carnian of Poland, he assumed three possible phylogenetic positions for this taxon. According to his findings, *Silesaurus* either represents an early member of the ornithischian lineage, or belongs to a lineage leading to both ornithischians and sauropodomorphs, or represents a non-dinosaurian Dinosauriformes more advanced than the Dinosauriformes of the Los Chañares Formation. Langer and Benton (2006) and Ezcurra (2006) advocated for nesting *Silesaurus* within Dinosauriformes outside Dinosauria. Langer and Benton (2006) pointed out the lack of affinities of *Silesaurus* to ornithischians, noting that the support is not compelling. Until recently, *Eucoelophysis baldwini* from the Norian of North America was considered a coelophysoid dinosaur (Sullivan and Lucas 1999). The re-evaluation of the material of *Eucoelophysis* revealed that this taxon is lacking synapomorphies linking *Eucoelophysis* with theropods or even dinosaurs and has to be placed outside Dinosauria as the immediate sister taxon to dinosaurs (Ezcurra 2006). In the same work, Ezcurra pointed out the striking similarities between *Eucoelophysis* and *Silesaurus*.

The phylogenetic placement of *Herrerasaurus ischigualastensis* (Reig 1963, Sereno and Novas 1992, 1993, Novas 1993, Sereno 1993), *Eoraptor lunensis* (Sereno et al. 1993), and *Staurikosaurus pricei* (Colbert 1970, Galton 1977) from the Carnian of South America within dinosaurs and their relationship to each other was widely discussed. At present, the monophyly of *Herrerasaurus* and *Staurikosaurus*, forming the Herrerasauridae, is well supported (e.g. Benedetto 1973, Novas 1989, 1992, Langer 2004, Langer and Benton 2006, Ezcurra 2006). However, at times *Herrerasaurus* and *Staurikosaurus* were considered more distantly related basal dinosaurs, with *Herrerasaurus* being more derived than *Staurikosaurus* (Colbert 1970, Galton 1977, Brinkman and Sues 1987, Benton 1990, Sues 1990). In the ongoing discussion on their phylogenetic placement, herrerasaurids were considered an outgroup to the Ornithischia – Saurischia dichotomy (Gauthier 1986, Novas 1989, 1992, Benton 1990), as Saurischia *incertae sedis* (Benedetto 1973, Galton 1977, Langer 2004, Langer and Benton 2006, Ezcurra 2006), as sauropodomorphs (Colbert 1970, Cooper 1981), or basal theropods (Bonaparte 1978, Galton 1985, Sereno and Novas 1992, 1993, Novas 1993, Rauhut 2003, Sereno 1993). Fraser et al. (2002) advocated for nesting *Herrerasaurus* outside Dinosauria within Dinosauriformes. *Eoraptor* is regarded as basalmost theropod (Sereno et al. 1993, Rauhut 2003, Ezcurra 2006, Ezcurra and Novas 2006), or a Saurischia *incertae sedis* more derived than the herrerasaurids (Langer 2004, Langer and Benton 2006, Yates 2006, 2007). In the late 1990ies, new material of two basal dinosaurs from South America was discovered. When first described, *Guaibasaurus candelariensis* from the Carnian of Brazil was considered a basal saurischian (Bonaparte et al. 1999). In the cladistic analysis of Langer (2004) and Langer and Benton (2006), *Guaibasaurus* came out as the immediate sister taxon to theropods, whereas Yates (2006, 2007) nested *Guaibasaurus* within theropods. Most recently, Bonaparte et al. (2007) advocated for placing *Guaibasaurus* close to the origin of sauropodomorphs based on new material. *Saturnalia tupiniquim* is a small-sized basal dinosaur from the Carnian of Brazil (Langer et al. 1999, Langer 2003, Langer et al. 2007). *Saturnalia* was considered either to represent the basalmost known sauropodomorph (Langer et al. 1999, Yates 2003, 2007, Yates and Kitching 2003, Langer et al. 2007, Upchurch et al. 2007) or its immediate sister taxon (Langer 2004, Langer and Benton 2006), depending on the definition of this clade. Upchurch and Galton (2004), however, considered *Saturnalia* a basal sauropodomorph more derived than *Thecodontosaurus*. Most recently, Ferigolo and Langer (2006) described the remains of *Sacisaurus agudoensis* from the Carnian to Norian of Brazil. Ferigolo and Langer (2006) pointed out the close phylogenetic affinity to *Silesaurus*. However, a phylogenetic analysis of the placement of *Sacisaurus* has not, to date, been published.

4.3 MATERIAL AND METHODS

The osteology of dinosauromorphs, including basal saurischian dinosaurs, was studied in order to collect data of the pelvic girdle and hindlimbs. Furthermore, the osteology of the pelvic girdle and hindlimb of a wide range of specimens of basal archosauriforms, basal ornithischians, basal theropods, and basal sauropodomorphs were studied for comparison. Measurements were taken with digital calipers or measuring-tape, and documented with photographs and drawings. When direct access to specimens was not possible, supplementary data and measurements were taken from literature (see Table 4-1 for source of data).

The functional morphology and evolution within Dinosauromorpha on the lineage to basal Saurischia were studied from two aspects, ichnofossils and body fossils. Ichnofossils provide an additional source of information on functional aspects of the locomotor apparatus not evident from morphology alone, especially when the body fossil record is scarce and fragmentary. Therefore, the Triassic dinosauroid ichnofossil record was reviewed based mainly on the studies of Peabody (1948), Haubold (1967, 1971a, 1999), King and Benton (1996), Haubold and Klein (2000, 2002), and

Table 4-1. Source of data (literature and specimens) for Dinosauromorpha used in this study. Accession numbers denote specimens examined by the author first hand.

Taxon	Source
Dinosauromorpha	
Lagerpeton chanarensis	UPLR 06, PVL 4619, 4625; Romer 1971, 1972b, Bonaparte 1984, Arcucci 1986, Sereno and Arcucci 1993;
PVL 3870	PVL 3870; Bonaparte 1975, Sereno and Arcucci 1994;
Dromomeron romeri	Irmis et al. 2007;
Dinosauriformes	
Marasuchus lilloensis	PVL 3871; Romer 1971, 1972b; Bonaparte 1975; Sereno and Arcucci 1994; Fechner and Rauhut 2006;
Pseudolagosuchus major	PVL 4629, UPLR 53; Arcucci 1987; Novas 1989;
Silesaurus opolensis	Dzik 2003;
Eucoelophysis baldwini	Ezcurra 2006;
Saurischia	
Eoraptor lunensis	PVL 512; Sereno et al. 1993;
Herrerasaurus ischigualastensis	PVL 2655, 373, PVSJ 104, 464; Reig 1963, Novas 1992, 1993, Sereno and Novas 1993;
Staurikosaurus pricei	MCZ 1669; Colbert 1970; Galton 1977, Galton 2000;
Guaibasaurus candelariensis	MCN-PV 2355, 2356; Bonaparte et al. 1999, 2007, Langer and Benton 2006;

Thulborn (2006) and compared to the results of the functional morphological study. A robust phylogenetic hypothesis is essential for tracing the nature of character evolution of the pelvic girdle and hindlimb and to provide a frame for the functional evolution of the locomotor posture. The phylogeny of dinosauromorphs used here (Fig. 4-1) is based on the hypotheses of Novas (1996), Langer (2004), Ezcurra (2006), and Langer and Benton (2006). Regarding the phylogenetic placement of *Eoraptor*, a position as basalmost saurischian is assumed here (pers. com. O.W.M. Rauhut). The putative dinosauriformes *Agnostiphys cromhalliensis* (Fraser et al. 2002) and *Saltopus elingensis* (Huene 1910) are not included in this study due to their uncertain phylogenetic placement. *Sacisaurus agudoensis* (Ferigolo and Langer 2006) is also excluded for the same reason. Due to its very fragmentary preservation (see Sullivan and Lucas 1999, Ezcurra 2006), *Eucoelophysis* is not included in this study. The re-examination of the material of *Marasuchus* within this study has revealed significant differences between the holotype PVL 3871 and PVL 3870 (Fechner and Rauhut 2006). According to these findings, only the material of PVL 3871 is considered here the dinosauriform *Marasuchus*. PVL 3870 is considered here a non-dinosauriform dinosauromorph placed between *Lagerpeton* and *Dromomeron* (Irmis et al. 2007a, see also Chapter 3). Concerning

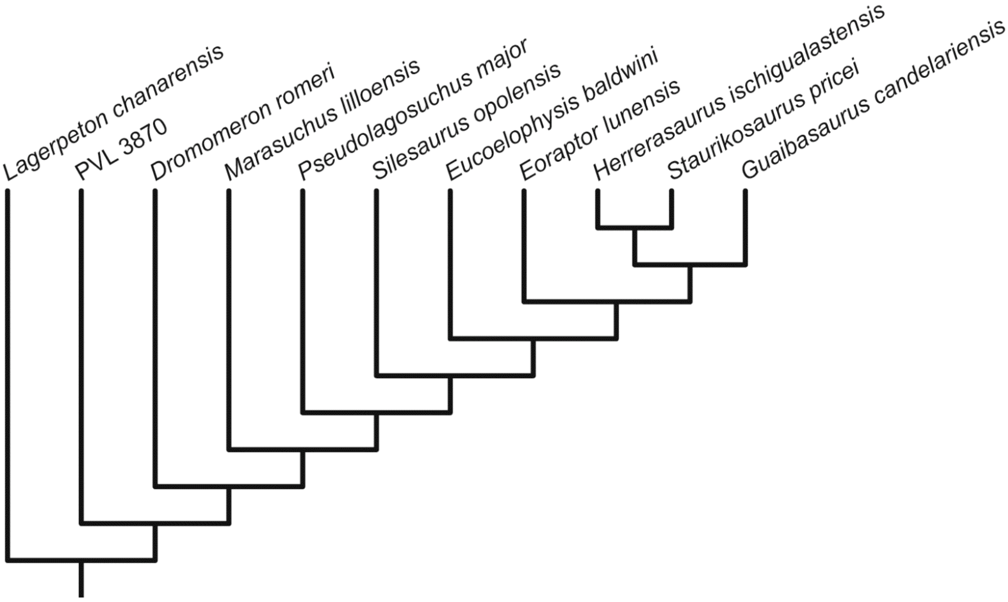


Figure 4-1. Phylogenetic framework used to map the morphofunctional evolution of the pelvic girdle and hindlimbs of Dinosauromorpha; mainly based on the phylogenetic hypotheses of Novas (1996) and Ezcurra (2006).

Pseudolagosuchus and *Lewisuchus admixtus* (Romer 1972b), it is currently under discussion whether *Pseudolagosuchus* has to be regarded as a synonym for *Lewisuchus* (see Arcucci 2005), therefore the material of *Lewisuchus* is not included in this study. Other putative basal saurischians, such as *Chindesaurus bryansmalli* (Long and Murry 1995), *Spondylosoma absconditum* (Huene 1942), *Alwalkeria maleriensis* (Chatterjee 1987), and *Caseosaurus crosbyensis* (Hunt et al. 1998) are not included in this study due to their fragmentary or poor preservation and / or uncertain phylogenetic placement. The reconstruction of the hindlimb posture of Dinosauromorpha on the lineage to basal Saurischia is mainly based on osteological features identified to reflect different locomotor posture and is based on studies of Jenkins (1971b), Charig (1972), Parrish (1986) and Fechner (Chapter 3). The reconstruction of the locomotor posture is inferred from the development of the manus, the disparity of the limbs and the hindlimb to trunk proportions.

Institutional abbreviations: **MCN**, Museu de Ciências Naturais, Fundacão Zoobotânica, Porto Alegre; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge; **NHM**, British Museum of Natural History, London; **NMMNH**, New Mexico Museum of Natural History, Albuquerque; **PVL**, Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán; **PVSJ**, Museo de Ciencas Naturales, Universidad Nacional de San Juan, San Juan; **UPLR**, Museo de Paleontología, Universidad Provincial de La Rioja, La Rioja.

4.4 RESULTS

4.4.1 Evolution of the locomotion of saurischians – evidence from the ichnofossil record

In early dinosaurs and their predecessors, the improvement of the locomotor apparatus is supposed to play an important role in their evolution. Novas (1996) noted that about 70% of the characters diagnosing the Dinosauromorpha are located in the pelvic girdle and hindlimb. The dominance of the characters located in the pelvic girdle and hindlimbs certainly reflects the improvement of the locomotor performance, but also relates to the fact that pelvic girdle and hindlimbs are the best represented elements in the current sample. According to the considerations outlined above, the adaptations in the locomotor apparatus should be reflected in the dinosauroid ichnofossil record. Dinosauroid tracks and traces are characterized by following criteria: manus prints absent or small compared to pes prints; digitigrade pes posture, with impression of heel absent or small; mesaxonic pes; cross-axis of pes orthogonal or aligned obliquely from anteromedial to posterolateral; functionally tridactyl pes; narrow trackway, with high values of pace angulation and for the ratio of stride length to trackway width (Nopcsa 1923, Demathieu and Haubold 1978, Haubold 1983, summarized in Thulborn 2006). According to our present understanding of basal dinosaur anatomy and systematics, the characters chosen for defining dinosauroid ichnofossils certainly cover the tracks and trackways of dinosaurs. By definition, dinosauroid ichnofossils do not include ichnofossils of non-dinosauriform dinosauromorph trackmakers (Haubold 1999, Haubold and Klein 2002, Chapter 3). Fechner (2005, 2006a,b, 2007, Chapter 3), however, has shown that major changes in the locomotor posture have taken place in basal dinosauromorph evolution, so that ichnofossils attributed to non-dinosaurian dinosauromorphs are included in this study in order to cover this important stage for our understanding of the origin and evolution of early dinosaur locomotion. Ichnofossils of non-dinosaurian dinosauromorph trackmakers and dinosauroid ichnofossils are very abundant in the track-bearing layers of the Triassic. However, on critically reviewing the ichnofossil record, recent studies revealed that the Triassic dinosauroid ichnofossil record is less diverse than previously suggested (King and Benton 1996, Weems 1987, 1992, Olsen et al. 1998, Haubold and Klein 2000, 2003, Thulborn 2006). According to these studies, the following ichnogenera are considered to represent the activities of putative dinosauroid trackmakers and tracks of non-dinosaurian dinosauromorphs and are valid (in chronological order): *Rotodactylus* (Peabody 1948, Haubold 1967, Demathieu 1970, Demathieu and Gand 1973, 1974, Demathieu and Leitz 1982, Demathieu 1984, Kotanski et al. 2004) from the Lower to Middle Triassic of North America, Europe, and Northern Africa; *Sphingopus* (Demathieu 1966, Haubold and Klein 2002) from the Middle Triassic of Europe; *Parachirotherium* from the Middle Triassic of Europe (Rehnelt 1950, Kuhn 1958, Haubold 1971, Haubold and Klein 2002); *Atreipus* from Upper Triassic of Europe and North America (Bock 1952, Olsen and Baird 1986, Haubold and Klein 2000, 2002, Klein and Haubold 2007); *Grallator* from Upper Triassic to the Lower Jurassic of Europe, North America, and Africa (e.g. Hitchcock 1847, Olsen et al. 1998, Klein and Haubold 2007); *Eubrontes* from the Upper Triassic to Lower Jurassic of North America (Hitchcock 1836, Olsen et al. 1998, Klein and Haubold 2007).

Ichnofossils as an additional source of information are of particular importance when the body fossil record is scarce and fragmentary (Lockley et al. 1994, Wilson and Carrano 1999, Carrano and Wilson 2001, Wilson 2005, Chapter 3). In addition to providing information on the spatiotemporal distribution of taxa, the great potential of ichnofossils rests on the fact that they present the only source to study the motion of extinct animals directly (Henderson 2003) and therefore reveal aspects of the functional morphology not apparent from the osteology alone (Farlow and Pianka 2000).

In the past, minor changes in the overall shape of the prints, the number of digits, especially the presence or absence of lateral digits, the presences or absence of manus prints, and the variation in the trackway pattern, were used to establish new ichnospecies or -genera (e.g. Haubold 1971b, Thulborn 1990). Only few attempts have been made to set tracks and traces into an evolutionary context (e.g. Lockley and Meyer 2000). In their outstanding study on the Triassic ichnofossil record of Germany, Haubold and Klein (2000, 2002) noticed that a single trackway can comprise pes prints with pentadactyl to tridactyl impressions, as well as the transition from quadrupedal to bipedal locomotor posture. On the one hand, this shows the problematic of ichnotaxonomy. On the other hand, it shows the great potential of ichnofossils as additional source of information on the locomotion of body fossils.

4.4.1.1 Evolution of the dinosauroid pes

The characteristic mesaxonic and functionally tridactyl pes (digit III>IV>II) of dinosaurs evolved from the ectaxonic pes and functionally tridactyl pes (digit IV>III>II) of non-dinosauriform dinosauromorphs. Associated with the development of the mesaxonic pes is the development of the parallel orientation of the long-axis of the pes relative to the trackway line and the functionally tridactyl pes of the dinosauroid-type (see Haubold and Klein 2000, 2002). As mentioned above, the functionally tridactyl pes of all Dinosauriformes shows more or less regular impressions of external digits. According to Haubold and Klein (2000, 2002), the tridactyl pes evolved by forming a central digit group II – IV and the isolation of the external digits I and V (Fig. 4-2). In basal dinosauroid pes prints, such as *Sphingopus* and *Parachirotherium*, imprints of digits I and V are regularly present. Regarding the development of the tridactyl pes, *Parachirotherium* appears to be more derived than *Sphingopus*, in which the isolation of digit I is less progressed (Haubold and Klein 2000, 2002). In *Atreipus*, *Grallator*, and *Eubrontes* the development of the tridactyl pes is more advanced. The impressions of external digits are very rare, if present at all (e.g. Olsen and Baird 1986, Olsen et al. 1998, Haubold and Klein 2000, 2002).

4.4.1.2 Evolution of the dinosaur body bauplan

The pes print of the *Rotodactylus* trackmaker always oversteps the manus print (Fig. 4-2), indicating that the hindlimb of the trackmaker is considerably elongated, most likely associated with a short gleno-acetabular distance, resulting in a coupling value (gleno-acetabular distance / forelimb length + hindlimb length) of <0,50 (Peabody 1948, Haubold 1967, 1971a,b). The trackway record assigned to Dinosauriformes reveals that the length of the hindlimb is relatively reduced compared to non-dinosauriform Dinosauromorpha. In *Sphingopus*, the manus print is placed directly laterally to or in front of the pes print, separated from the latter by a gap (Demathieu 1970, Haubold and Klein 2002).

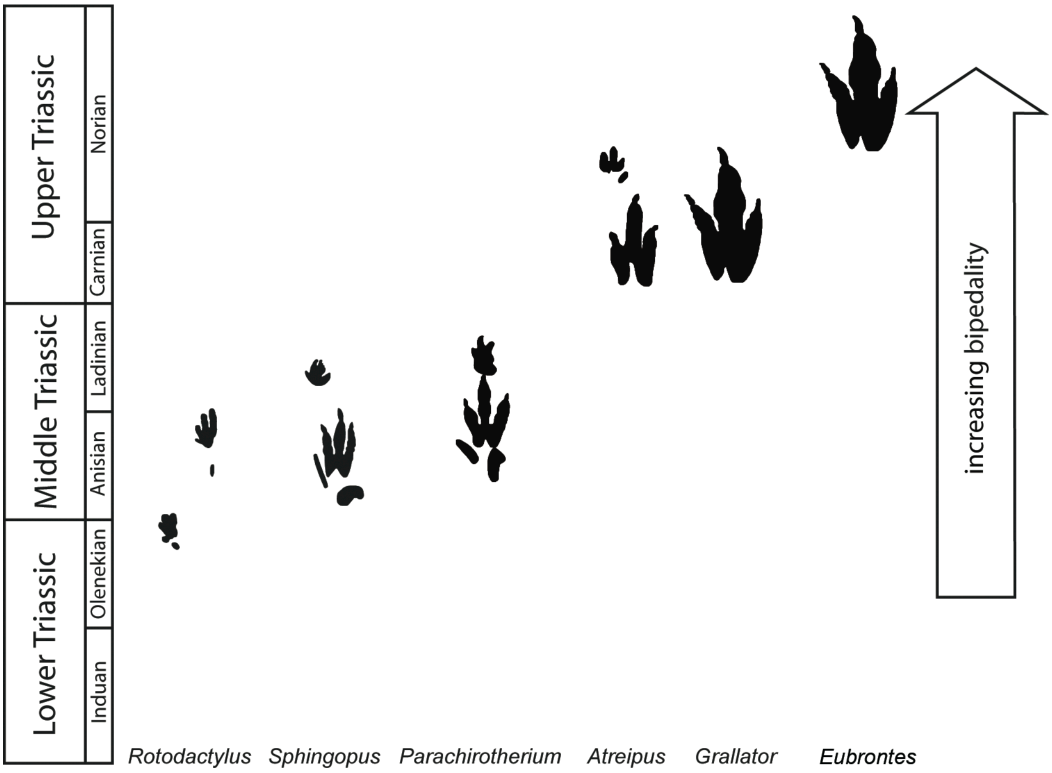


Figure 4-2. Diagram of tracks and trackways assigned to dinosauromorph trackmakers showing the increasing tendency towards bipedal locomotion through time. *Parachirotherium* is the trackway of an obligate quadrupedal trackmaker. Based on Haubold and Klein (2000, 2002) and Klein and Haubold (2007). Not to scale.

The manus print of *Parachirotherium* is placed in front of the pes print without a gap (Haubold and Klein 2000, 2002). The position of the manus print relative to the pes print varies in *Atreipus* from laterally to the pes print to in front of the pes print, separated by the latter with a gap (Olsen and Baird 1986, Haubold and Klein 2000, 2002). Thus, the coupling value of more derived Dinosauriformes varies between 0.7 – 1.0, indicating a relative reduction of the hindlimb length and / or a relative elongation of the gleno-acetabular distance (Haubold 1971b).

4.4.1.3 Evolution of the locomotor posture

The locomotor posture of dinosauromorphs as inferred from the ichnofossil record differs from the locomotor posture reconstructed from the body fossils. The ichnogenus *Rotodactylus* nicely

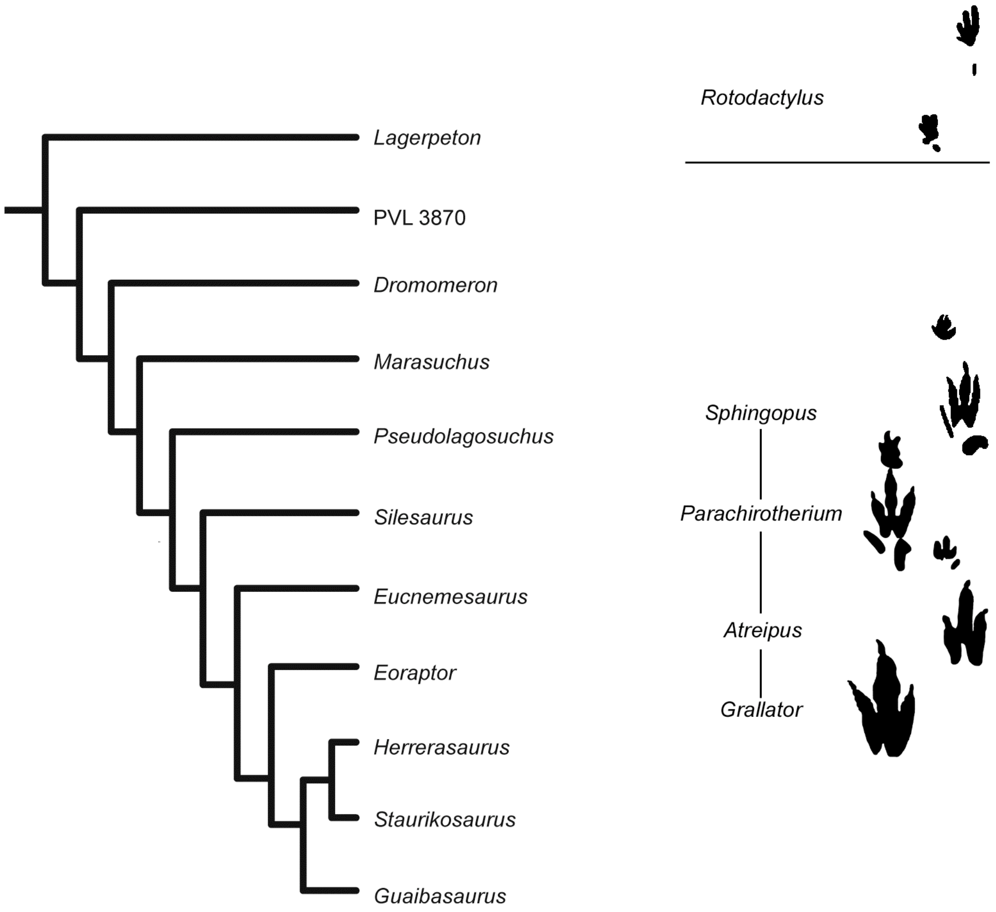


Figure 4-3. Hypothesis of systematic placement of dinosauromorph ichnogenera based on Haubold and Klein (2002) and Klein and Haubold (2007) using a phylogenetic framework based on the hypotheses of Novas (1996) and Ezcurra (2006).

demonstrates the locomotor posture of non-dinosauriform dinosauromorphs. The pes is placed with a relatively large distance from the midline, indicating an intermediate hindlimb posture of the trackmaker (Chapter 3). The quadrupedality of non-dinosauriform dinosauromorphs is demonstrated by the presence of manus prints. However, the absence of manus prints in some ichnotaxa reveal that the *Rotodactylus* trackmaker was a facultative biped (Peabody 1948, Haubold 1967, Haubold 1971a, 1999). As reflected in the trackway record, Dinosauriformes moved using an erect hindlimb posture. The evolution of the erect hindlimb posture in Dinosauriformes is associated with the evolution of the mesaxonic pes and the orientation of the long-axis of the pes parallel to the trackway line (e.g. Olsen and Baird 1986, Olsen et al. 1998, Haubold and Klein 2000, 2002), both of which reflect the evolution of the mesotarsal joint of dinosaurs (e.g. Lockley and Meyer 2000). With exception of *Parachirotherium, Grallator*, and *Eubrontes*, the presence of pes only trackways shows that dinosauriform trackmakers were facultative bipeds (see Olsen and Baird 1986, Haubold and Klein 2000, 2002, Klein and Haubold 2007). According to the available evidence, the trackmaker of *Parachirotherium* appears to be an obligate quadruped (Haubold and Klein 2000), whereas the obligate bipedal locomotor posture of the *Grallator* and *Eubrontes* trackmaker was never seriously questioned (e.g. Olsen et al. 1998). Haubold and Klein (2000, 2002) and Klein and Haubold (2007) showed that an increasing ability for bipedal locomotion is reflected in the track-bearing layers from the Lower to Upper Triassic, inferred from the decreasing presence of manus prints in the facultative bipedal trackways of *Rotodactylus* – *Sphingopus* – *Atreipus* (Fig. 4-2). The first records of obligate bipedal dinosauriform trackmakers, such as *Grallator* and *Eubrontes*, occur in the Norian.

4.4.2 Evolution of the locomotion of basal saurischian dinosaurs – evidence from the body fossil record

4.4.2.1 Evolution of the dinosauroid pes and the assignment of dinosauromorph ichnotaxa to body fossils

Lagerpeton is characterized by an ectaxonic pes with digit IV>III>II (Fig. 4-6). Digit I is considerably reduced in length and metatarsal V is reduced to a bone splint. The metatarsus is bundled, with slender, elongated metatarsals. The phalangeal series of *Lagerpeton* is 2-3-4-5-(?)0. The phalangeal series of the pes equals the metatarsus in length (Romer 1971, Arcucci 1986, Sereno and Arcucci 1993). The pedes of PVL 3870 and *Marasuchus* equal the pes of *Lagerpeton* with respect to the bundled, slender and elongated metatarsals and the phalangeal series. However, in PVL 3870 digit II–IV are of subequal length, and the pes of *Marasuchus* is mesaxonic with digit III>IV>II (Bonaparte 1975, Sereno and Arcucci 1994). The pedes of Dinosauriformes more derived than *Marasuchus* retain the mesaxonic form, but differ from that of *Marasuchus* with respect to the relatively shorter metatarsus. The phalangeal formula of Dinosauriformes is 2-3-4-5-(?)0 and 2-3-4-5-1 in *Herrerasaurus* (Fig. 4-6, Reig 1963, Novas 1993, Sereno and Arcucci 1994,Bonaparte et al. 1999, 2007, Dzik 2003,

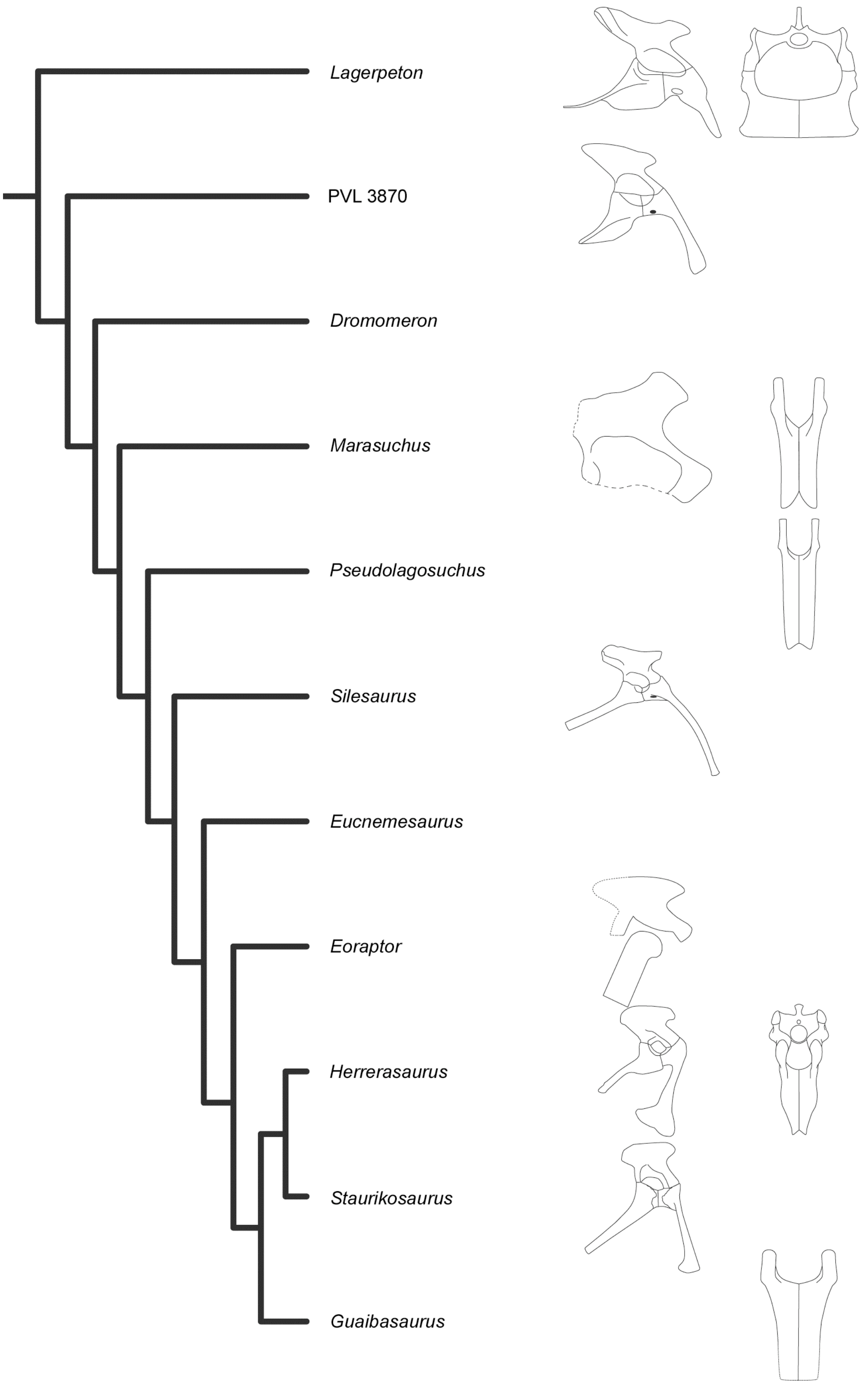


Figure 4-4. Evolution of the pelvis of dinosauromorphs included in this study. Pelvis of *Silesaurus* re-drawn from Dzik (2003). Not to scale.

Langer 2003). The overall proportions of the pes are relatively similar in more derived Dinosauriformes and basal saurischians. The tendency to reduce the external digits, as shown in the trackway record, is not reflected in the body fossil record. The metatarsal V equals less (*Silesaurus* [Dzik 2003], *Guaibasaurus* [Bonaparte et al. 1999, 2007]) or more than 50% of metatarsal III (*Herrerasaurus* [Reig 1963, Novas 1993]).

Based on the evolution of the pedes in Dinosauromorpha as outlined above, Haubold and Klein (2002) were able to assign dinosauroid ichnofossils to dinosauromorph body fossils (Fig. 4-3). The assignment of *Rotodactylus* to non-dinosauriform dinosauromorphs is based the pentadactyl but functionally tridactyl pes and the ectaxonic pes with digit IV longer than digit III (Haubold 1999, Haubold and Klein 2002, Chapter 3). Based on the synapomorphy-based approach *Sphingopus*, *Parachirotherium*, *Atreipus*, *Grallator* and *Eubrontes* can be assigned to the dinosauriform body fossil with confidence (Fig. 4-3). However, as Haubold and Klein (2002) showed, it is difficult to distinguish between derived Dinosauriformes and basal Saurischia.

4.4.2.2 Evolution of the dinosaur body bauplan

As demonstrated in Chapter 3, non-dinosauriform dinosauromorphs are characterized by a marked disparity of the limbs, with considerably elongated hindlimbs, relatively short forelimbs and / or a short trunk. This bauplan is also characteristic for basal Dinosauriformes, such as *Marasuchus* (PVL 3871, Sereno and Arcucci 1994). The body fossil record of more derived Dinosauriformes and basal saurischians shows that the hindlimb length is in fact relatively reduced. Compared to *Scleromochlus*, the hindlimbs of *Eoraptor* (Sereno et al 1993), *Herrerasaurus* (Reig 1963, Sereno and Novas 1992, Novas 1993), *Guaibasaurus* (Bonaparte et al, 1999, 2007), and especially of *Silesaurus* (Dzik 2003) are reduced in length relatively to the forelimbs, resulting in a forelimb to hindlimb ratio (humerus + radius + metacarpal III / femur + tibia + metatarsal III) of 0.49 in *Eoraptor*, 0.47 in *Herrerasaurus* (Sereno 1993) and 0.53 of *Guaibasaurus* (Bonaparte et al. 2007). The hindlimb to trunk ratio appears to vary in Dinosauriformes. According to the reconstruction of Dzik (2003), *Silesaurus* had a hindlimb to trunk ratio of 0.7 - 08. *Eoraptor* is characterized by a hindlimb to trunk ratio of about 1.0 – 1.1. The hindlimb to trunk ratio of *Staurikosaurus* is estimated at 1.6 – 1.8. Both the evolution of the

Table 4-2. Osteological characters used to distinguish the sprawling, intermediate, and erect hindlimb posture in archosaurs. Based on Charig (1972), Parrish (1986) and Fechner (Chapter 3).

	Sprawling	Intermediate	Erect
Pelvis			
number of sacral vertebrae	generally 2	2, occasionally 3	3–11
preacetabular process	absent	generally weakly developed	generally strongly developed
supraacetabular crest	absent	weak	strong
acetabulum	imperforate large, of moderate depth	imperforate large, of moderate depth	perforated small and deep
pubis and ischium	plate-like	somewhat elongated	very elongated
Femur			
femur position	horizontally	oblique when moving fast	vertically at all times
femoral head	not very distinct; very slightly inturned (70 - 30°)	very distinct; very slightly inturned (70 - 30° / 45 - 30°)	distinct; strongly inturned (45 - 0° or minimal)
femoral shaft	gently sigmoid	gently sigmoid	fairly straight
distal articulation facet of femur	parallel or set at a marked angle to femoral shaft; broad transversely	slightly oblique in terms that lateral condyle projects further distally	plane or slightly oblique in terms that the medial condyle projects further distally
fourth trochanter	absent	weakly developed	often strongly developed
Crus			
cnemial crest	absent	absent	present
lesser trochanter and trochanteric shelf	absent	absent	present
tibia	not twisted	not twisted	twisted
Tarsus			
tarsus form	simple	crocodiloid	simple
ankle joint	crurotarsal	mesotarsal	mesotarsal
calcaneum tuber	absent	present	absent
Pes			
pes posture	plantigrade	plantigrade	digitigrade
phalangeal series	much longer than metatarsals	the same as or slightly shorter than metatarsals	the same as or slightly longer than metatarsals
trend towards bilateral symmetry	none	slight	strong, very strong in bipeds
longest digit	IV	III	III
reduced digits	none	IV slightly reduced; V strongly reduced	I reduced or absent in bipeds; IV slightly reduced; may be absent in bipeds

dinosauroid pes and the evolution of the bauplan show that information gained from the ichnofossil record generally correspond to the evolution of the body fossil record. Thus, information on the functional morphology gained from the ichnofossil record can be used as an additional source of information on the functional morphology and its evolution of Dinosauromorpha on the lineage to basal Saurischia.

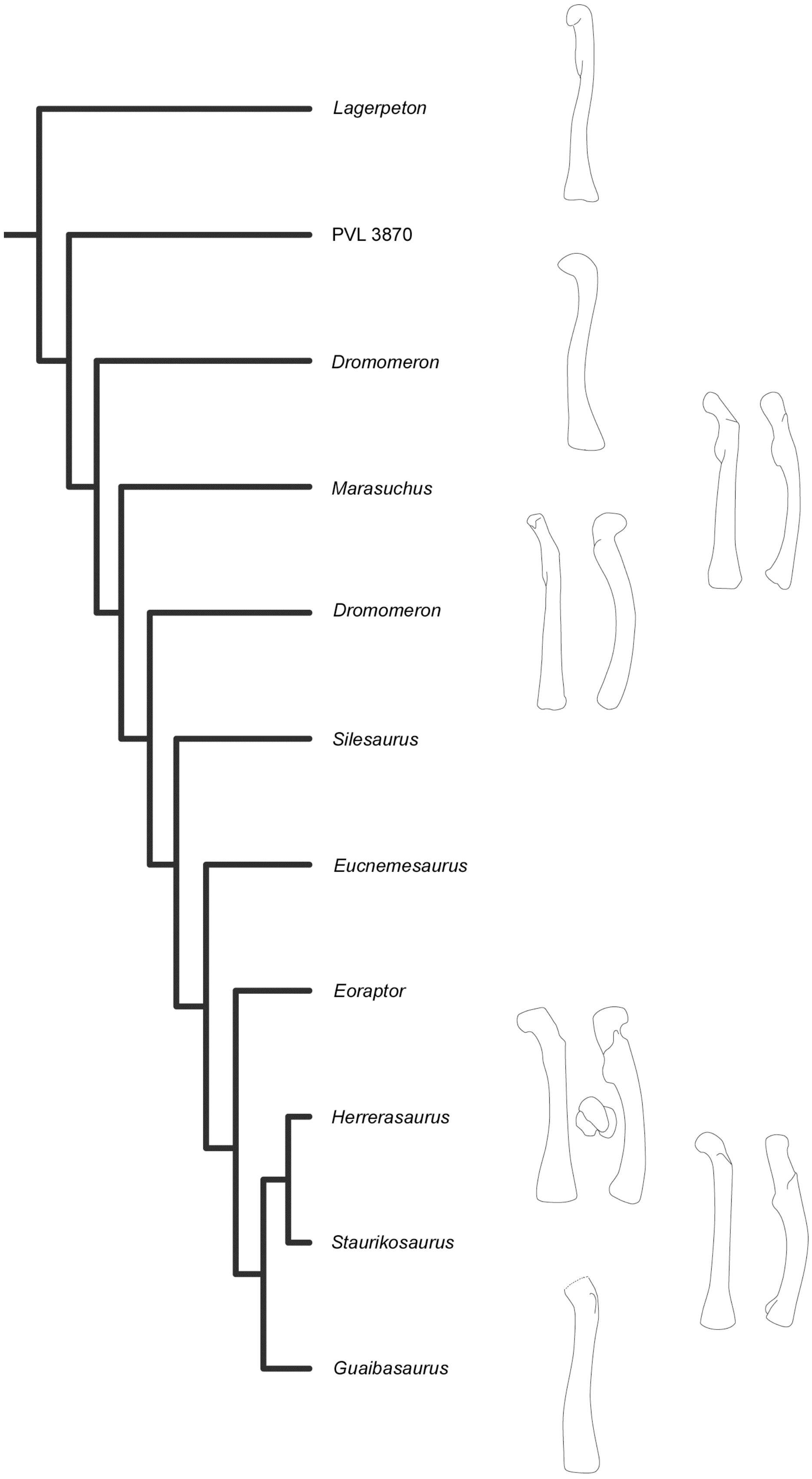


Figure 4-5. Evolution of the femur of dinosauromorphs included in the study. Not to scale.

4.4.2.3 Evolution of the hindlimb posture

Traditionally, the hindlimb posture of recent tetrapods is subdivided into three major categories: sprawling, intermediate (also often called semi-sprawling or semi-improved), and erect gait (Bakker 1971, Charig 1972, Parrish 1986) (Fig. 4-7). The subdivision into three categories is based on postural mechanics, which is, on the other hand, supposed to be reflected in the osteology of the pelvic girdle and limb (Table 4-2). The reconstruction of the hindlimb posture rests on the development of the acetabulum, knee joint, and ankle joint (Jenkins 1971b, Parrish 1986). As a result, the acetabulum was shown to be the most reliable single character for determining the hindlimb posture (Jenkins 1971b, Charig 1972, Parrish 1986). In a sprawling hindlimb posture, the acetabulum is closed, shallow and relatively large compared to the femoral head. In a laterally held femur the medially directed resulting joint forces of the femoral head cause the acetabulum wall to ossify (Charig 1972, Christian 1995). A shallow acetabulum allows a wide range of femoral protraction – retraction, adduction – abduction, as well as femoral rotation (Charig 1972, Parrish 1986, Hutchinson and Gatesy 2000). Femoral long-axis rotation is a key-component in a sprawling locomotor posture (Charig 1972, Brinkman 1980, Parrish 1986). The femoral head is weakly offset from the proximal femoral shaft and angled from the transverse plane to 30 – 70° (Parrish 1986). In association with the large and shallow acetabulum, this allows a large range of femoral long-axis rotation during retraction of the limb. The sigmoid curvature of the femoral shaft in anterior and lateral view of sprawling archosaurs indicates an enhanced resistance against torsion. The medial rotation of the femur is translated into the parasagittal excursion of the crus (Parrish 1986), facilitated by the oblique distal articulation facet of the femur (Parrish 1986, Gatesy 1991). Accordingly, the development of the distal articulation facet of the femur provides an indicator for inferring the range of femoral abduction (Jenkins 1971a, Parrish 1986, Blob 2001). The distal articulation facet of the femur of archosaurs with a marked femoral abduction is very broad transversely and oriented in the same plane as the long-axis of the femur (Blob 2001) or at least set to a marked angle to the femoral long-axis (Parrish 1986). Independent movement of the elements of crus is required when rotation at the knee is involved (Haines 1942, Brinkman 1980). During retraction of the limb, the pes is rotated laterally. The ankle joint of sprawling archosaurs is oblique to the long-axis of the tibia and allows rotation between crus and metatarsus. The metatarsus

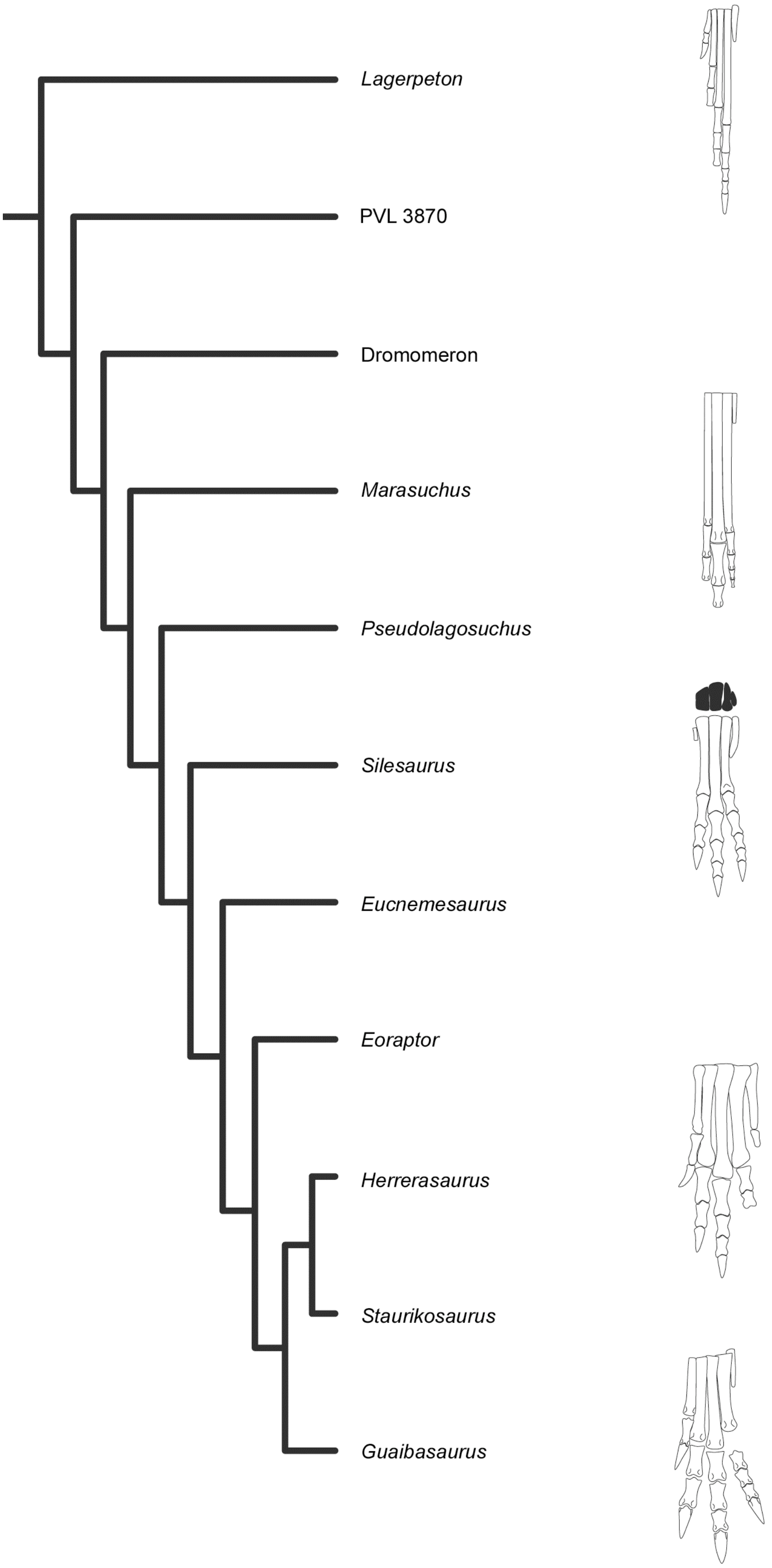


Figure 4-6. Evolution of the pes of dinosauromorphs included in this study. Pes of *Silesaurus* re-drawn from Dzik (2003). Not to scale.

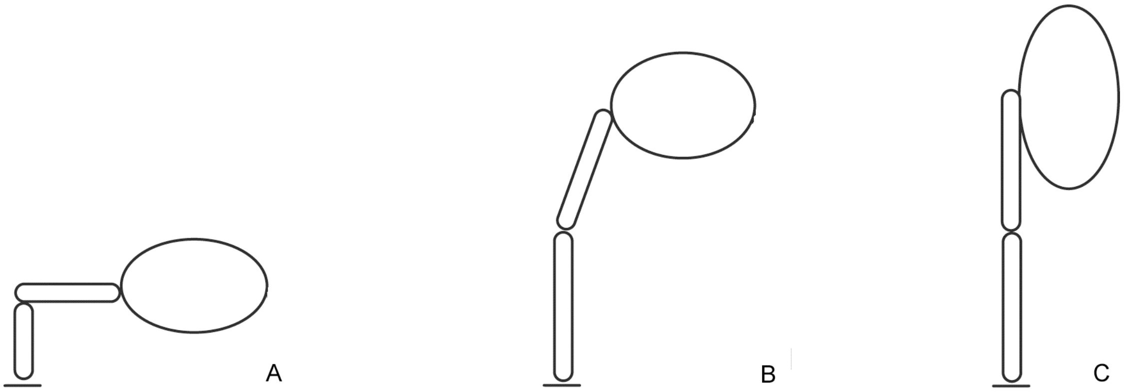


Figure 4-7. Diagrammatic representation of stance-phase postural support in archosaurs; based on Charig (1972). A, sprawling limb posture, B, intermediate limb posture and C, erect limb posture.

is short and broad. The phalangeal series is longer than the tarsus. The pes has a plantigrade posture and is ectaxonic. Characteristic for sprawling archosaurs is the adductor-controlled postural support (Hutchinson and Gatesy 2000).

An erect hindlimb posture is characterized by limb segments, which mainly operate in the parasagittal plane. Long-axis rotation is greatly reduced although it plays an important role in fine scale postural adjustment (Parrish 1986). In archosaurs with a vertically held femur, the resultant joint forces of the femoral head are directed dorsally rather than medially. With the resultant joint forces being directed mainly dorsally, a laterally projecting supraacetabular crest is developed to cover the femoral head and the acetabulum fails to ossify (Charig 1972, Parrish 1986, Christian 1995). The acetabulum is deep and relatively small compared to the femoral head. Associated with the well-developed femoral head, which is angled at 45° from the transverse plane or lies in the transverse plane, the femoral adduction and abduction, as well as long-axis rotation of the femur is reduced. The femoral shaft is straight in anterior view, indicating that torsional forces are reduced and that resistance against mediolateral bending is enhanced. Both knee joint and ankle joint are hinge-like to allow extension and flexion of the limb segments (Charig 1972, Parrish 1986). The metatarsus is bundled and relatively short, with a phalangeal series that equals the metatarsus in length (Charig 1972). The pes is mesaxonic and has a digitigrade posture. Characteristic for an erect hindlimb posture in archosaurs is the acquisition of the abductor-controlled postural support (Hutchinson and Gatesy 2000).

The intermediate hindlimb posture falls between the extremes of the sprawling gait and the erect gait, but beyond this remains ambiguously defined. Intermediate locomotion is known from crown-group crocodiles (Brinkman 1981, Gatesy 1991, Reilly and Elias 1998, Reilly and Blob 2003, Reilly et al. 2005). Crown-group crocodiles move using a sprawling posture and a more erect posture, the high walk (Cott 1961, Brinkman 1980, Webb and Gans 1982), with a femoral abduction ranging from 55° (from the parasagittal plane) in the sprawling gait (Reilly and Elias 1998) and 30° – 20° in the high walk (Gatesy 1991, Reilly and Elias 1998). Based on the more adducted femur during high walk, the locomotor posture of crown-group crocodiles is referred to as intermediate. The origin of crown-group crocodiles from fully terrestrial and even cursorial and fully erect crocodylomorphs is well established (Charig 1972, Parrish 1987) and the intermediate locomotor posture is considered to be the result of the secondary adaptation to a semi-aquatic lifestyle (Parrish 1987). The intermediate hindlimb posture requires osteological adaptations, which permit flexibility of the movement of the joints of the limb. Thus, the osteology of the pelvic girdle and limb of archosaurs with an intermediate hindlimb posture resembles in most aspects osteological adaptations found in sprawling archosaurs (Table 4-2). However, a few modifications in the osteology are found in the pelvic girdle and proximal limb. These modifications reflect that femoral abduction and long-axis rotation is reduced. Major functional modifications, however, are expected in the distal limb segments. In crocodiles, the distal limb operates as a functional unit, and lateral rotation of the distal limb is restricted.

None of the dinosauromorphs included in this study shows features, which are indicative exclusively for a sprawling hindlimb posture (Table 4-3). In *Lagerpeton*, the development of the acetabulum, the femoral head and the sigmoidally curved femoral shaft in anterior view and the ectaxonic pes are indicative for a sprawling gait (Fig. 4-4, 4-5, 4-6). However, the distal articulation facet of the femur, the tightly appressed tibia and fibula, as well as the bundled metatarsus, however, show that the lateral rotation of the distal limbs was greatly restricted, which is indicative for an

	Lagerpeton	PVL 3870	*Dromomeron*	*Marasuchus*	*Pseudolagosuchus*	*Silesaurus*	*Eoraptor*	*Herrerasaurus*	*Staurikosaurus*	*Guaibasaurus*
Pelvis										
number of sacral vertebrae	2	–	–	2	–	3	3	3	3	3
preacetabular process	weakly developed	weakly developed	–	weakly developed	–	weakly developed	weakly developed	weakly developed	weakly developed	weakly developed
supraacetabular crest	weak	weak	–	weak	–	strong	strong	strong	strong	strong
acetabulum	imperfoate	imperfoate	–	imperfoate	–	imperfoate	perforated	perforated	perforated	perforated; partially
	large, of moderate depth	large, of moderate depth	–	large, of moderate depth	–	relatively smaller and deeper	relatively smaller and deeper	relatively smaller and deeper	relatively smaller and deeper	relatively smaller and deeper
pubis and ischium	somewhat elongated	somewhat elongated	–	strongly elongated	stronlgy elongated	stronlgy elongated	stronlgy elongated	stronlgy elongated	stronlgy elongated	stronlgy elongated
Femur										
femoral head	not very distinct; angled at 70°	not very distinct; angled at <60°	not very distinct, slightly inturned	not very distinct; angled at 50 - 70°	not very distinct,; angled at 70°	not very distinct;	distinct	distinct; angled at 60°	distinct	not very distinct;
femoral shaft	gently sigmoid in anterior and lateral view	gently sigmoid in anterior and lateral view	gently sigmoid in anterior and lateral view	gently sigmoid in anterior and lateral view	gently sigmoid in lateral view, sigmoid in lateral view	gently sigmoid in lateral view, sigmoid in lateral view	gently sigmoid in lateral view, sigmoid in lateral view	gently sigmoid in lateral view, sigmoid in lateral view	gently sigmoid in lateral view, sigmoid in lateral view	gently sigmoid in lateral view, sigmoid in lateral view
distal articulation facet of femur	slightly oblique in terms that lateral condyle projects further distally	slightly oblique in terms that lateral condyle projects further distally	slightly oblique in terms that lateral condyle projects further distally	slightly oblique in terms that lateral condyle projects further distally	plane; narrow transversel	plane; narrow transversely	–	plane; narrow transversely	oblique in terms that the medial condyle projects further distally; narrow transversely	plane, narrow transversely
fourth trochanter	weakly developed	weakly developed	weakly developed	weakly developed	weakly developed	weakly developed	–	strongly developed	strongly developed	strongly developed
Crus										
cnemial crest	absent	present	present	present	present	present	present	present	present	present
lesser trochanter and trochanteric shelf	absent	absent	absent	present	present	present	present	present	present	lesser trochanter reduced; trochanteric shelf present
tibia	not twisted	not twisted	not twisted	not twistd	not twisted	not twisted	twisted	twisted	not twisted	twisted
Tarsus										
tarsus articulation	mesotarsal joint	mesotarsal joint	mesotarsal joint	mesotarsal joint	mesotarsal joint	mesotarsal joint	mesotarsal joint	mesotarsal joint	–	mesotarsal joint
calcaneum tuber	absent	absent	absent	absent	absent	absent	absent	absent	–	absent
Pes										
pes posture	digitgrade	digitgrade	–	digitgrade	–	digitgrade	digitgrade	digitgrade	–	digitgrade
phalangeal series	the same length as metatarsals	the same length as metatarsals	–	the same length as metatarsals	–	the same length as metatarsals	the same length as metatarsals	the same length as metatarsals	–	the same length as metatarsals
tendency towards bilateral symmetry	slight	slight	–	strong	–	strong	strong	strong	–	strong
longest digit	IV	III– IV	–	III	–	III	III	III	–	III
reduced digits	I and V sligthly reduced	I and V slightly reduced	–	I and V sligthly reduced	–	I and V strongly reduced	I and V strongly reduced	I and V strongly reduced	–	I and V strongly reduced
hindlimb posutre	intermediate	intermediate	intermediate	intermediate - erect	erect?	erect	erect	erect	erect	erect

intermediate hindlimb posture. The reconstruction of an adductor-controlled postural support supports a non-erect hindlimb posture (Chapter 3). The pelvic girdle and hindlimb of PVL 3870 resembles in most aspects the condition seen in *Lagerpeton*. Only the development of the pes of PVL 3870 differs from that of *Lagerpeton*. The pes of PVL 3870 shows a clear tendency towards a bilateral symmetric or mesaxonic pes. The remains of *Dromomeron* are relatively incomplete, so that it is difficult to trace the modifications in the pelvic girdle and hindlimb. Nonetheless, in *Dromomeron* the cnemial crest first occurs. The cnemial crest is a site of attachment for femoral extensors as well as ankle flexors. The occurrence of the cnemial crest thus indicates modifications of the limb kinematics. The modifications in the distal limb of PVL 3870 and *Dromomeron* are only minor, and the presence of an adductor-controlled postural support in association with the development of the acetabulum, femur and crus are indicative for an intermediate hindlimb posture in these taxa (Table 4-3). The pelvic girdle and hindlimb of *Marasuchus* is of particular interest. In *Marasuchus*, an abductor-controlled postural support is present, a feature commonly associated with an erect hindlimb posture in archosaurs. In *Marasuchus*, however, the abductor-controlled postural support is associated with an acetabulum and features in the femur, which indicate in non-dinosauriform dinosauromorphs an intermediate hindlimb posture. The result of this character combination is difficult to interpret. Was *Marasuchus* able to move using an erect hindlimb posture despite of the development of the acetabulum or was the intermediate hindlimb posture retained despite of the abductor-controlled postural support? Unfortunately, there are no trackways which could solve this problem. Considering the small size of *Marasuchus* (discussed below), it is assumed here that *Marasuchus* was able to move using an intermediate and erect hindlimb posture. With exception of the open acetabulum, *Silesaurus* shows all features commonly assumed to reflect an erect hindlimb posture. An open acetabulum first occurs in basal saurischians. Therewith, all hallmarks reflecting an erect hindlimb posture, such as opened acetabulum with an overhanging supraacetabular crest, well developed femoral head, femoral shaft straight in anterior view, oblique articulation facets or hinge-like joints, mesaxonic pes, and an abductor-controlled postural support, are present in basal saurischians (Table 4-3, Fig. 4-4, 4-5, 4-6).

Table 4-3. Osteological characters of the pelvic girdle and hindlimbs used to reconstruct the hindlimb posture of Dinosauromorpha. Characters taken from Table 4-2.

The evolution of the pelvic girdle and limb of Dinosauromorpha shows that the evolution of an erect hindlimb posture is gradual and the classical categories sprawling – intermediate – erect are artificial and that the evolution of different locomotor postures forms a continuum (Table 4-3), as assumed by Gatesy (1991).

4.4.2.4 Evolution of the locomotor posture

The evolution of obligate bipedality is closely linked with the acquisition of an erect hindlimb posture. Obligate bipedal locomotion requires that the body can be statically balanced on one limb. Statical balance, however, is only achieved with the pes placed close to the midline. Consequently, the erect hindlimb posture is a requirement for obligate bipeds and obligate bipedal locomotion has to be ruled out in archosaurs with a sprawling or intermediate hindlimb posture. Based on these considerations, a quadrupedal locomotor posture was reconstructed for *Lagerpeton*. However, trackways showed that a facultative bipedal locomotion was characteristic for non-dinosauriform dinosauromorphs (Chapter 3). Trackways assigned to dinosauriform trackmakers show that their trackmaker had a narrow gauge. In most cases, however, the narrow gauge is associated with a facultative bipedal locomotion (*Sphingopus*, *Atreipus*) or obligate quadrupedal locomotion (*Parachirotherium*). Obligate bipedal locomotion is only observed in more derived dinosauriform trackmakers (*Grallator*, *Eubrontes*). The trackway record shows that the evolution of obligate bipedal locomotion is associated with increasing size of the trackmaker. Pes prints of facultative bipedal Dinosauriformes trackmakers on the lineage to basal saurischians do not exceed 140 mm in length (Olsen and Baird 1986). Pes prints of obligate bipedal dinosauriform trackmakers, however, are larger. *Grallator* is the product of a relatively small trackmaker with pes prints measuring up to 150 mm in length (Haubold and Klein 2002). Other obligate bipedal ichnofossils assigned to basal theropods are by far larger, with pes prints of *Anchisauripus* measuring 150 – 250 mm and of *Eubrontes* measuring more than 250 mm in length (Olsen et al. 1998, Haubold and Klein 2000). Within facultative bipedal Dinosauromorpha, Haubold and Klein (2000, 2002) noted an increasing ability for bipedal locomotion (*Rotodactylus* – *Sphingopus* – *Atreipus*). This increasing ability for bipedal locomotion is associated with increasing size (*Rotodactylus*; 34 – 80 mm; *Sphingopus*, 110 mm; *Atreipus* 140 mm).

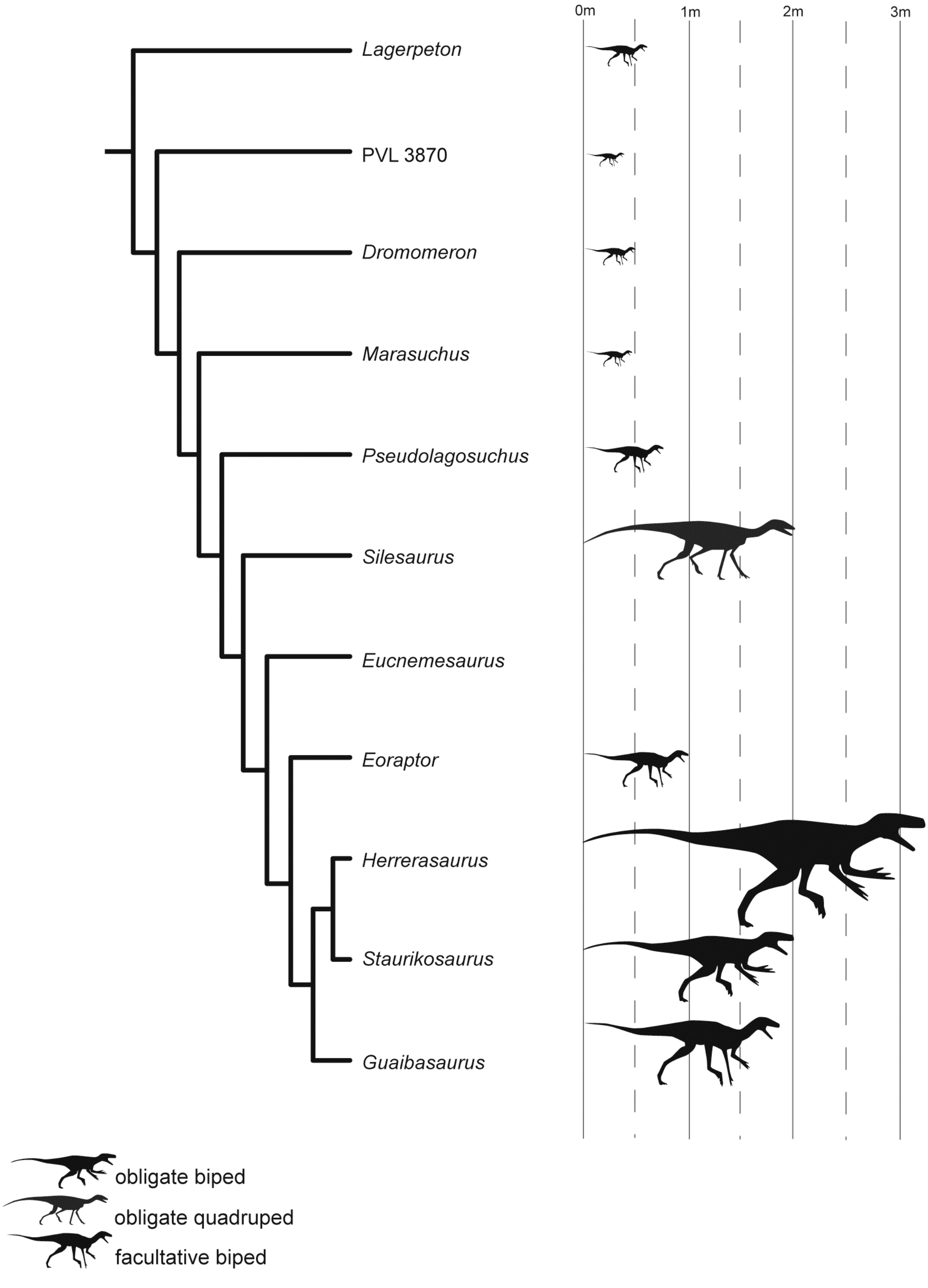


Figure. 4-8. Diagram depicting the correlation of body size and locomotor posture.

Haubold and Klein (2000) noted that imprints of a theropod-like manus are not recorded in the dinosauroid ichnofossil record. Thus, the occurrence of functionally modified manus appears to indicate the transition from facultative bipedal locomotion to obligate bipedal locomotion. Unfortunately, among dinosauromorphs including basal saurischians, the manus is only preserved in *Herrerasaurus* (Sereno 1993), *Guaibasaurus* (Bonaparte et al. 2007) and *Eoraptor* (PVSJ 512). The manus of *Herrerasaurus* is relatively long compared to the total length of the forelimb. The metacarpals are relatively slender and the distal phalanges are considerably elongated. The unguals are pointed and trenchant. Metacarpals I – IV are preserved in the manus of *Herrerasaurus*. Digit III appears to be slightly longer than digit II and only a rudimentary phalanx is preserved on metacarpal IV. The distal articulation facet on metacarpal I shows that *Herrerasaurus* was able to oppose digit I. Deep extensor pits on the phalanges are considered to indicate the hyperextension of the manus (Sereno 1993). Compared to *Herrerasaurus*, the manus of *Eoraptor* and *Guaibasaurus* appear to be relatively short in relation to the total length of the forelimb (Bonaparte et al. 2007). Both metacarpals and phalanges are relatively robust in *Eoraptor* and *Guaibasaurus* and an elongation of distal phalanges is not observed. The unguals are relatively blunt and dorsoventrally flattened. Metacarpals I – V are preserved in the manus of *Eoraptor*, with no phalanges preserved on metacarpal IV and V. Digit II appears to be slightly longer than digit III. The distal articulation surface of metacarpal I is modified as in *Herrerasaurus* and suggests that *Eoraptor* was able to oppose digit I. Metacarpals I – IV are preserved in *Guaibasaurus*. Digit II is longer than digit III. There are no phalanges preserved on metacarpal IV. Bonaparte et al. (2007) reconstructed digit I of *Guaibasaurus* as very robust and without a modified distal articulation facet of metacarpal I. The manus of *Herrerasaurus* resembles the manus known from theropods and the modification of its manus compared to *Eoraptor* and *Guaibasaurus* is considered to reflect an adaptation to grasping and raking (Sereno 1993). The manus of *Eoraptor* and *Guaibasaurus* are well suited for being used as support during locomotion and share the following characters with manus prints assigned to dinosauriformes: the short phalangeal series; digit II>III>I; the tendency to reduce digits IV and V. With an estimated length of 3 – 5 m (Langer 2004), *Herrerasaurus* is considerably larger than any other basal dinosauromorph or even most basal theropods. With a length of about 1 m, *Eoraptor* is considerably smaller than *Herrerasaurus* (Sereno et al. 1993). With increasing size, the joints of the limb have to be aligned closer to the vector of the ground reaction force in order to increase the effective mechanical advantage (Biewener 1990, 2005). According to these considerations, the hindlimbs of *Herrerasaurus* have to be aligned closer to the vector of the ground reaction force in order to increase the effective mechanical advantage than it would be the case in *Eoraptor*. Although *Herrerasaurus* and *Eoraptor* have almost the same forelimb to hindlimb ratio, 0.47 and 0.49 respectively, the relatively more upright hindlimb posture of *Herrerasaurus* does not allow placing the hands on the ground during locomotion. The relatively small size of *Eoraptor*, however, allows moving with a more flexed hindlimb posture, so that the hands can be used as support during locomotion. A facultative bipedal locomotion in *Eoraptor* is supported by the hindlimb to trunk ratio of 1.0 – 1.1 (Galton 1970). The length of *Guaibasaurus* ranges with 1,70 m between the body size of *Eoraptor* and *Herrerasaurus* (Langer 2004). The hands of *Guaibasaurus* demonstrate that the immediate sister-taxon of theropods was a facultative biped. The length of *Staurikosaurus* is estimated at about 2 m (Paul 1988), ranging between the length of the facultative bipedal *Guaibasaurus* and the obligate bipedal *Herrerasaurus*. Unfortunately, no hands are preserved to infer the locomotor posture in *Staurikosaurus*. However, the relatively large hindlimb to trunk ratio of 1.6 – 1.8 indicates that *Staurikosaurus* was an obligate biped (Galton 1970). As mentioned above, basal theropods are considered to be obligate bipeds, an assumption supported by the functionally modified manus. Basal theropods, such as *Coelophysis bauri* (Cope 1887), *Liliensternus liliensterni* (Huene 1934), and *Syntarsus rhodiensis* (Raath 1969) are approximately 2 m long (see Paul 1988). It appears that a length of about 2 m presents the critical size above which obligately bipedal locomotion is required for Dinosauromorpha. All non-ornithischian basal dinosauromorphs on the lineage to basal saurischians smaller than 2 m are characterized by a facultatively bipedal locomotion (Fig. 4-8). The obligate bipedal locomotor posture of small-sized (<2 m) coelurosaurian theropods has to be regarded as derived relative to the locomotion of basal saurischians and basal theropods. Dzik (2003) argued that the relatively elongated forelimbs in *Silesaurus* indicate an obligate quadrupedal locomotion. In fact, the estimated forelimb to hindlimb ratio is 0.95 in *Silesaurus* (Chapter 6). The reconstruction of an obligate quadrupedal locomotion in *Silesaurus* corresponds with the hindlimb to trunk ratio of 0.7 – 0.8 (Dzik 2003). The obligate quadrupedal locomotion of *Silesaurus* appears to be a unique and represents an independent development.

4.5 DISCUSSION

4.5.1 Does size matter?

Size is often argued to be a key-variable affecting form and function of an organism (e.g. Bakker 1971, Schmidt-Nielson 1984, Biewener 2003). Functional consequences resulting from the change of mechanical but also physiological properties have to be overcome with increasing size during the ontogenetic and evolutionary history of an organism. This holds also true for the locomotion of terrestrial tetrapods. The ground reaction force is the main determinant of the moments developed at the joints of the limb (Biewener 1990, 2003). The ground reaction force is equal in magnitude and opposite in direction to the force that the limb exerts on the supporting substrate (Biewener 1990). In order to control the limb posture, muscle forces have to oppose the moments of the ground reaction force developed at the joints of the limb. Because the ground reaction force is weight-related, muscle forces required to control the limb posture increase with body size and mass (Biewener 1990, 2005). An increase of the muscle mass, however, negatively affects the locomotor performance by increasing the total body mass and the inertia, which has to be overcome by acceleration of the body (Christian and Garland 1996). With the joints aligned closer to the vector of the ground reaction force, the magnitude of muscle forces required to control limb posture is reduced and the effective mechanical advantage is increased (Biewener 1990, 2005). The increasing effective mechanical advantage allows retaining the locomotor capabilities in spite of increasing size. This is consistent with the observation that larger animals tend to run with a more upright limb posture (Biewener 2003, 2005). Above a critical body size, however, the effective mechanical advantage cannot be increased, so that the locomotor capabilities are reduced. In mammals, this critical size ranges between 300 – 500 kg (Biewener 1990, 2003, 2005). In small mammals, the muscle forces required to control the limb posture are relatively small. In contrast to larger mammals, which are limited to a relatively small functional diversity, small mammals are characterized by a wide functional spectrum of their locomotor apparatus. They often move using a more flexed limb posture (e.g. Biewener 2003, 2005) and are even not restricted to a fully erect hindlimb posture (e.g. Jenkins 1971a, Rewcastle 1981).

The ground reaction force also affects the postural support of animals, which move using a sprawling locomotor posture. Christian (1995, 2007, Christian and Garland 1996) studied the biomechanics of the sprawling limb posture of extant lizards. Recent lizards are the most common representatives of sprawling tetrapods (Rewcastle 1981). Although often proposed (see e.g. Bakker 1971, Charig 1972, Dodsen 1974, Parrish 1986), sprawling limb posture is not necessarily inferior to the erect hindlimb posture. Small lizards are as fast as or even faster than mammals of the same size. However, this is only true for small lizards. With increasing size, lizards become slower than mammals of the same size (e.g. McMahon and Bonner 1983, Christian 1995). Christian (1995) noted that the hindlimbs of lizards scale with negative allometry, which means that with increasing size the hindlimb length is reduced with respect to the trunk length. As in tetrapods with an erect gait, the joints of sprawling tetrapods are affected by the ground reaction force, so that opposing muscle forces have to control the limb posture. In contrast to mammals with an erect hindlimb posture, the magnitude of muscle forces required to control the limb posture can only slightly be reduced by aligning the joints closer to the vector of the ground reaction force. Christian and Garland (1996) and Christian (2007) noted that the muscle forces acting on the limb joints are mainly reduced by reducing the length of the limbs in recent lizards. Since limb length is positively linked with speed (Snyder 1952, Irschick and Jayne 1999), the reduction of the limb length negatively affects the locomotor performance of sprawling tetrapods. Christian (2007) rightly reasoned “it is not possible to be a sprawler, large, and fast at the same time”. Thus, sprawling tetrapods, which have to rely on high speed, have to remain small or have to change their limb posture from sprawling to erect. Christian (1995, 2007) estimates the critical body size in which a postural change is required with about 30 cm trunk length or a body mass ranging between several hundred grams to a few kilograms.

Osteological features reflecting biomechanical adaptations to an intermediate hindlimb posture are only found in very small Dinosauromorpha, such as *Lagerpeton*, PVL 3870, and *Marasuchus*. These basal Dinosauromorpha have a trunk length of less than 30 cm and a body mass of several hundred grams. The fact that *Marasuchus* is smaller than *Lagerpeton* but shows greater adaptation towards an erect hindlimb posture than the latter might indicate that the material assigned to *Marasuchus* represents a not fully-grown specimen. With increasing body size, osteological features indicating biomechanical adaptations to an erect gait dominate over adaptations for a sprawling gait.

Osteological features indicating a fully erect hindlimb posture had not evolved prior the occurrence of derived Dinosauriformes/basal Saurischia, which have a body mass of around 4 – 10 kg (Chapter 6). Most interesting, the evolution of the postural grades show that the rigid system established by Bakker (1971) or Charig (1972) is not applicable in Dinosauromorpha. Adaptations to a more erect gait first occur in the distal limb segments, such as pes and tarsus. Crus and femur reflect adaptations to a more erect gait next and the pelvis retains the ancestral condition the longest as noted by Novas (1996).

4.5.2 Biomechanical reasons for bipedal locomotion in archosaurs

Sagittal bending of the presacral vertebral column is a key-component in the locomotion of mammals, allowing them to achieve high running speed by considerably increasing the stride length (Rewcastle 1981, Hildebrand and Goslow 2004). In dinosauromorphs, however, trapezoid dorsal neural spines, horizontal zygapophyses, and the hyposphene-hypantrum articulation are indicators for the rigidity of the presacral vertebral column (Rewcastle 1981, Hildebrand and Goslow 2004). Trapezoid dorsal neural spines and horizontal zygapophyses are characteristic for all basal dinosauromorphs (Novas 1993, Sereno and Arcucci 1993, Dzik 2003, Bonaparte et al. 2007) and present in basal theropods (e.g. Colbert 1989, Huene 1934, Welles 1984) as well as in basal sauropodomorphs (e.g. Huene 1907-1908, 1926). The hyposphene-hypantrum articulation of the trunk is supposed to be characteristic for Saurischia, and found in basal theropods (e.g. Huene 1934, Welles 1984, Bonaparte 1986, Colbert 1989, Madsen and Welles 2000) and sauropodomorphs (e.g. Huene 1926, Bonaparte 1972, Van Heerden 1979, Cooper 1981, Benton et al. 2000), with exception of Rebbachisauridae and Titanosauridae (e.g. Apesteguia 2005). The hyposphene-hypantrum articulation is also known in basal saurischians (Novas 1993, Bonaparte et al. 1999, Langer and Benton 2006,). The presence of the hyposphene-hypantrum articulation is considered to be ambiguous in *Eoraptor* (pers. com. O.W.M. Rauhut, *contra* Sereno et al. 1993) and in *Staurikosaurus* (Bittencourt 2004, contrary to Novas 1993). The limited ability of sagittal bending in Dinosauromorpha negatively affects their locomotor performance regarding the ability to achieve high maximum running speed with a quadrupedal locomotor posture. In order to compensate for the limited sagittal bending of the vertebral column, a highly cursorial morphology is developed. The great disparity of the limbs, on the other hand, enforces a facultative bipedal locomotor posture (Chapter 3). As noted above, facultative bipedality in Dinosauromorpha is only possible up to a critical size. Above this critical size, an obligate bipedal locomotor posture is required when the animal has to rely on fast running speed. In other words: it is not possible to be quadrupedal, large, and fast at the same time.

4.5.3 Implications for the locomotor posture of basal Sauropodomorpha

Basal Sauropodomorpha, such as *Saturnalia* (Langer et al. 1999, Langer 2003), are relatively small animals, with a length of around 1.5 m. This small size of basal Sauropodomorpha was often used as an indicator of obligate bipedal locomotion. The idea of bipedality was based on the assumption that basal Sauropodomorpha retained the obligate bipedal locomotor posture from their ancestors, the basal saurischians. On the lineage to Sauropoda, Sauropodomorpha evolved a quadrupedal locomotor posture. The evolution of the quadrupedal locomotor posture was always considered as being correlated to increasing size and the evolution of an elongated trunk due to the evolution of a herbivorous diet. Therefore, medium-sized Sauropodomorpha are considered to be facultatively bipedal (see Upchurch and Barrett 2007). This study, however, has shown that obligate bipedal locomotion is not ancestral for Sauropodomorpha and that obligate bipedality is a consequence of the necessity to couple fast running speed with increasing size. Herrerasaurids and theropods, obligate bipedal saurischians, show clear cursorial adaptations in the hindlimb, such as a bundled metatarsus with reduction of the lateral digits, and their manus are modified for grasping, not locomotion. Sauropodomorpha do not show these adaptations in the hindlimb, with a generalized pes, and the manus show adaptations to both grasping and load-bearing (see Barrett and Upchurch 2007). This, and the fact that basal sauropodomorphs are smaller than the critical size above which saurischians appear to have moved using an obligate bipedal locomotor posture, suggests that basal Sauropodomorpha were at best facultative bipedal. Based on the development of the manus, Charig et al. (1965) already doubted that obligate quadrupedal sauropods were descendents from obligate bipedal Dinosauromorpha.

4.5.3 Ecological implications

Little is known about the ecology of basal saurischians and their predecessors. Based on the carnivorous morphology of their skulls and manus, basal saurischians and later theropods are considered be medium- to large-sized hunters. The carnivorous habit is supposed to have evolved from agile and omnivorous Dinosauriformes (Rauhut 2003). On the lineage leading to sauropods, a quadrupedal locomotor posture evolved, related to the increasing size of sauropodomorphs and the evolution of a herbivorous diet. Thus, basal sauropodomorphs are supposed to be bipedal and possibly omnivorous and medium-sized sauropodomorph dinosaurs being facultative bipeds. The results of this study provide new insights in the evolutionary ecology of basal saurischian dinosaurs and their predecessors.

If the intermediate hindlimb posture of non-dinosauriform dinosauromorphs indicates that they evolved from sprawling archosaurs or if the intermediate hindlimb posture is associated with the miniaturization of the clade Ornithodira (see Hutchinson 2006), can only be solved by studying the hindlimb posture and its evolution in basal archosaurs. Nonetheless, the remarkable disparity of the limbs of non-dinosauriform dinosauromorphs and *Marasuchus* indicates that basal dinosauromorphs had to rely on fast acceleration, not being able to sustain high running speed (Herkner 1989, Christian and Garland 1996). This enables basal dinosauromorphs to fast escape, but is also characteristic for ambush-predators, as seen in extant squamates. The necessity to rely on fast running speed associated with increasing size forced Dinosauriformes to evolve an erect hindlimb posture. With increasing size, however, the relative length of the hindlimbs is reduced related to the trunk length. This implies that the ability to rapidly accelerate is relatively reduced. On the other hand, an erect hindlimb posture indicates long-time activity of Dinosauriformes, most likely associated with the ability to achieve and sustain high running speed (Herkner 1989, Carrier 1987). According to the available evidence, obligate bipedality evolved independently from the evolution of the erect hindlimb posture and features in the skull and hand skeleton interpreted as carnivorous morphology evolved before the obligate bipedal locomotor posture evolved. The obligate quadrupedality of *Silesaurus*, the *Parachirotherium* trackmaker and possibly basal sauropodomorphs and their herbivorous diet indicates that they realized a different ecological niche.

4.6 SUMMARY

Body size and body mass have proved to be the dominant factors for both the evolution of the erect gait and the obligate bipedal locomotion. The ground reaction force is equal in magnitude and opposite in direction to the force that the limb exerts on the supporting substrate. Consequently, the relatively low body mass of small animals requires only little muscle force to control the limb posture. Accordingly, the sprawling locomotor posture does not negatively affect the running capabilities of small animals. With increasing body size, the muscle forces required to control the limb posture negatively affect the locomotor performance. For animals that have to rely on fast running speed, a transition of the locomotor posture from sprawling to erect limb posture is required. The body size and mass range, which requires a change of the posture in order to increase the effective mechanical advantage, spans between several 100 g to a few kg or a trunk length of about 30 cm. In animals with an erect gait, the small body size allows running with a more flexed limb posture. Moreover, small animals are even not restricted to an obligate erect limb posture. With increasing body size, the joints of the limb have to be aligned closer to the vector of the ground reaction force in order to reduce the muscle force required to control the limb posture and to increase the effective mechanical advantage. In contrast to small animals, animals above a critical size are restricted to an erect hindlimb posture and have to run with a more upright limb posture. These biomechanical considerations are reflected in the fossil record. *Lagerpeton,* PVL 3870, *Dromomeron* and *Marasuchus* are by far the smallest dinosauromorphs included in this study. Supported by the ichnofossil record assigned to non-dinosauriform dinosauromorphs, the musculoskeletal reconstruction revealed that *Lagerpeton*, PVL 3870 and probably *Dromomeron* moved using an intermediate hindlimb posture. The development of the pelvic girdle and limb of *Marasuchus* combines both characters, reflecting a more sprawling limb posture and adaptations to an erect hindlimb posture. The musculoskeletal reconstruction and the trackway record shows that all larger dinosauromorphs moved with an obligate erect hindlimb posture. The trackway record further shows that dinosauromorphs moved using a facultative bipedal locomotor posture. Facultative bipedal locomotion in dinosauromorphs results from their bauplan with the markedly forelimb – hindlimb disparity and the rigidity of the presacral vertebral column. However, both relatively short forelimbs and limited ventral flexion and extension of the vertebral column negatively affect the ability to achieve high running speed. The bipedal locomotor posture is attained to overcome these negative affects of quadrupedal locomotion. Facultative bipedality in saurischian was used from the Anisian to the Late Norian. *Herrerasaurus* and *Staurikosaurus* are the only dinosauromorphs included in the study, which are shown to move using an obligate bipedal locomotor posture.

According to the available evidence, the more upright limb posture due to larger size and the necessity to rely on fast running speed forced them to change from facultative bipedal to obligate bipedal locomotor posture. Because *Guaibasaurus*, the immediate sister taxon to theropods, is reconstructed as a facultative biped, obligate bipedality on the lineage to theropods evolved at least twice independently. The occurrence of obligate bipedal ichnofossil faunas in the Norian matches with the first occurrence of theropods. Obligate quadrupedality in Dinosauriformes evolved in taxa, which did not to rely on fast running speed. This did not evolve *in spite* of their small body size, as commonly suggested, but *because* of their small size. The reconstructed variability of locomotor options of dinosauromorphs indicates an early functional and ecological diversity of dinosauromorphs not previously recognized.

Chapter 5

The myology of the pelvic girdle and hindlimb of *Plateosaurus engelhardti* (Dinosauria: Sauropodomorpha) with comments on the reliability of muscle reconstructions in sauropod dinosaurs

5.1 INTRODUCTION

The reconstruction of soft-tissues of dinosaurs has always been of great interest to scientists. In addition to give shape to scaled dinosaur models used for calculations of their body mass (e.g. Colbert 1962), soft-tissue reconstructions serve as additional source of information on the functional morphology of dinosaurs, as well as behavior and ecology (e.g. Bakker 1986, 1987, Carpenter and Smith 2001, Carpenter 2002, Hutchinson and Gatesy 2000, Hutchinson et al. 2005). Relating to the assumed functional importance for the locomotion of dinosaurs, a special focus has always been on reconstructing the myology of the pelvic girdle and hindlimb (e.g. Gregory and Camp 1918, Romer 1923b, 1927b, Galton 1969, Russell 1972, Walker 1977, Tarsitano 1981, Perle 1985, Gatesy 1990, Carrano and Hutchinson 2002). In the past, owing to the fact that soft-tissue reconstructions were strongly dependent on the rationales of the author due to the lack of an explicit methodology, they were often looked at with caution or even with mistrust. Although authors recognized the phylogenetic relationships of dinosaurs and used crocodiles or birds and sometimes both as extant models for reconstructing soft-tissues, they did not provide rationals for their assumptions and / or a detailed discussion for the muscles reconstructed, including presence or absence of muscles as well as their arrangement. In recent years, a new approach, using an explicit methodological basis for reconstructing soft-tissue was established, the Extant Phylogenetic Bracket (*sensu* Witmer 1995). By studying the myology of the bracketing extant taxa and the correlation of soft-tissues to osteological correlates, as well as the homology of these osteological correlates and their evolution on the lineage from the outgroup to the ingroup, allows to reconstruct the myology of fossil taxa. Gatesy (1990) Dilkes (2000) and later Hutchinson and co-authors (Hutchinson and Gatesy 2000, Hutchinson 2001a,b, 2002, Carrano and Hutchinson 2002, Hutchinson and Garcia 2002, Hutchinson 2004a, b, Hutchinson et al. 2005, Hutchinson and Gatesy 2006) showed the great potential of the Extant Phylogenetic Bracket approach, applying it to the pelvic girdle and hindlimb of both theropods and ornithischians. Only few attempts have been made to reconstruct the myology of the pelvic girdle and hindlimb of sauropodomorphs (Huene 1907-1908, Gregory and Camp 1918, Romer 1923a, Borsuk-Bialynicka 1977, Cooper 1981) and the Extant Phylogenetic Bracket approach was only used by Langer (2003) and Otero and Vizcaíno (2008).

Reconstructing the myology of the pelvic girdle and hindlimb of sauropods is complicated by two major problems: 1) the pelvic girdle and hindlimb of sauropodomorphs are characterized by the reduction of muscles insertion sites (Yates 2004) and 2) sauropodomorphs have no living descendants. Both the reduction of the muscle insertion sites (= osteological correlates) and the lack of living descendants do not allow to trace the nature of the evolution of the myology. However, a good knowledge of the myology of sauropodomorphs helps to improve our understanding of their function and thus biology.

I offer here the reconstruction of the myology of the pelvic girdle and hindlimb of the non-sauropodan sauropodomorph *Plateosaurus engelhardti*. The osteology of the pelvic girdle and limb of *Plateosaurus* resembles in most aspects the plesiomorphical saurischian condition (see Rauhut et al. in press). Thus, osteological correlates identified in the extant bracketing taxa can be homologized with features found in *Plateosaurus* and guarantee a reliable reconstruction of soft-tissues. On the other hand, *Plateosaurus* shows adaptations found in the pelvic girdle and hindlimb of sauropods, such as increasing robustness and reduction of osteological correlates. The myology of the pelvic girdle and limb of *Plateosaurus* is reconstructed using the Extant Phylogenetic Bracket. In addition to improving our knowledge of the myology of the pelvic girdle and hindlimb of non-sauropodan sauropodomorphs, this reconstruction will allow evaluating the reliability of the reconstruction of the myology of the pelvic girdle and hindlimb of sauropods.

5.2 MATERIAL AND METHODS

The restoration of the myology of *Plateosaurus* is based on the material of specimen SMNS 13200, an almost completely preserved skeleton lacking only parts of the left forelimb and distal caudal vertebrae. SMNS 13200 has been described in detail by Huene (1926). Measurements were taken with a measuring tape and the study of the material was documented with digital photographs and drawings.

The myology of the pelvic girdle and limb of *Plateosaurus* was reconstructed according to the Extant Phylogenetic Bracket approach *sensu* Witmer (1995), with crocodiles and birds as phylogenetic framework. In order to gain information on the myology of crocodiles and birds, *Caiman crocodilus* and *Gallus gallus* were dissected, with special emphasis on the myology of the pelvic girdle and limb. Additional information on the pelvic girdle and limb of crocodiles was taken from Gadow (1882), Romer (1923b), Kriegler (1961), Tarsitano (1981), and Cong et al. (1998). Hudson et al. (1959), McGowan (1979), Nickel et al. (2003), Gangl et al. (2004) were chosen as additional source of information on the myology of the pelvic girdle and limb of Aves. In order to trace the nature of character evolution of the osteological correlates of muscles and to identify causal association between soft-tissues and osteological correlates, basal Sauria were included in this study. Information on the myology of the pelvic girdle and hindlimb of lepidosaurs came from Gadow (1882), Osawa (1898), Byerly (1925), and Kriegler (1961). The nomenclature of the myology of Sauria followed Romer (1922, 1923b, 1942), Rowe (1986), and Carrano and Hutchinson (2002). The nomenclature of the myology of birds followed the Nomina Anatomica Avium (Vanden Berge and Zweers 1993). The homology of the muscles of the pelvic girdle and limb of extant archosaurs is based on Romer (1922, 1923b, 1927a, 1942, Rowe 1986).

The level of speculation required for reconstructing the musculature in *Plateosaurus* followed the level of inferences established by Witmer (1995). If soft tissue data from extant bracket taxa unequivocally support the reconstruction of an unpreserved feature of the extinct taxon (both bracketing taxa have the feature), the reconstruction is a level I inference. Equivocal support from extant taxa (one bracketing taxon lacks the feature) is a level II inference. The unequivocal absence of

Table 5-1. Terminology and homology of the muscles of the pelvic girdle and hindlimb of Sauria. The terminology of the muscles of the pelvic girdle and hindlimb of Sauria is based on Gadow (1882), Romer (1923b). The homology of the muscles of the pelvic girdle and hindlimb of Sauria is based on Romer (1923b, 1927a, 1942) and Rowe (1986).

Muscles: Crocodilia	*Sphenodon*	Squamata	Crocodilia	Aves	Muscles: Aves
M. iliotibialis	IT	IT	IT1	IA	M. iliotibialis anterior
	—	—	IT2	IP	M. iliotibialis posterior p. preacetabuaris
	—	—	IT3	IP	M. iliotibialis posterior p. postacetabularis
M. ambiens 1	AMB	AMB	AMB1	AMB	M. ambiens
M. ambiens 2	—	—	AMB2	—	
M. femorotibialis externus	FMT	FMT	FMTE	FMTL	M. femorotibialis lateralis
M. femorotibialis internus	—	—	FMTI	FMTIM	M. femorotibialis intermedius
	—	—	—	FMTM	M. femorotibialis medius
M. iliofibularis	ILFIB	ILFIB	ILFIB	ILFIB	M. iliofibularis
M. iliofemoralis	IF	IF	IF	IFE	M. iliofemoralis externus
	—	—	—	ITC	M. iliotrochantericus caudalis
M. puboischiofemoralis internus 1	PIFI1-+2	PIFI1	PIFI1	IFI	M. ischiofemoralis internus
M. puboischiofemoralis internus 2	—	PIFI2	PIFI2	ITCR	M. iliotrochantericus cranialis
	—	PIFI3	—	ITM	M. iliotrochantericus medius
M. pubotibialis	PIT	PIT1	PIT	—	
	—	PIT2		—	
M. flexor tibialis internus 2	—	PIT3	FTI2	—	
M. flexor tibialis internus 1	FTI1	FTI1	FTI1	—	
M. flexor tibialis internus 3	FTI2	FTI2	FTI3	FCM	M. flexor cruris medius
M. flexor tibialis internus 4	—	—	FTI4	—	
M. flexor tibialis externus	FTE	FTE	FTE	FCLP	M. flexor cruris lateralis pars posterior
	—	—	—	FCLA	M. flexor cruris lateralis pars anterior
M. adductor femoris 1	ADD	ADD	ADD1	PIFM	M. puboischiofemoralis medius
M. adductor femoris 2	—	—	ADD2	PIFL	M. puboischiofemoalis lateralis
M. puboischiofemoralis externus 1	PIFE	PIFE	PIFE1	OL	M. obturatorius lateralis
M. puboischiofemoralis externus 2	—	—	PIFE2	OM	M. obturatorius medialis
M. puboischiofemoralis externus 3	—	—	PIFE3	—	
M. ischiotrochantericus	ISTR	ISTR	ISTR	ISF	M. ischiofemoralis
M. caudofemoralis longus	CFL	CFL	CFL	CFC	M. caudofemoralis pars caudalis
M. caudofemoralis brevis	CFB	CFB	CFB	CFP	M. caudofemoralis pars pelvica
M. gastrocnemius lateralis	GL	GL	GL	GL	M. gastrocnemius longus
	—	—	—	GIM	M. gastrocnemius intermedius
M. gastrocnemius medialis	GM	GM	GM	GM	M. gastrocnemius medius
M. flexor digitalis longus	FDL	FDL	FDL	FDL	M. flexor digitorium longus
M. flexor digitalis brevis	FDB	FDB	FDB	FDB	M. flexor digitorium brevis
M. flexor hallucis longus	FHL	FHL	FHL	FHL	M. flexor hallucis longus
M. tibialis anterior	TA	TA	TA	TC	M. tibialis cranialis
M. extensor digitorium longus	EDL	EDL	EDL	EDL	M. extensor digitorium longus
M. extensor digitorium brevis	EDB	EDB	EDB	—	
M. extensor hallucis longus	EHL	EHL	EHL	EHL	M. extensor hallucis longus
M. fibularis longus	FL	FL	FL	FL	M. fibularis longus
M. fibularis brevis	FB	FB	FB	FB	M. fibularis brevis
M. pronator profundus	PP	PP	PP	—	
M. popliteus	POP	POP	POP	POP	M. popliteus
M. interosseus cruris	IC	IC	IC	—	

support from extant taxa (both bracketing taxa lack the feature) is a level III inference. Tubercles, crests, grooves, pits, ridges, and scars are regarded as clear osteological correlates of muscles. Some muscles, however, cannot be correlated to a clear osteological correlate (McGowan 1979, Bryant and Russell 1992, Bryant and Seymour 1990). In cases, in which inferences lack conclusive data from osteological correlates, they are referred to as level I', II', and III' (Witmer 1995). A level I' inference is less robust than a level I inference but more supportive than a level II inference (Witmer 1995). In this study, a level III and III' inference is not reconstructed.

Basal Sauria and crocodiles move using a sprawling locomotor posture, with the femur being held laterally and more or less horizontally, and a plantigrade pes posture. The hindlimb of Aves operates in the parasagittal plane, with the femur being held anteriorly and more or less horizontally and a digitigrade pes posture. In *Plateosaurus*, the hindlimb operates in the parasagittal plane with a femur being held anteriorly and more or less vertically and a digitigrade pes posture (Fig. 5-4). The differing limb posture results in a differing orientation of the bone surfaces. For a better comparison, all bone surfaces are oriented as it is supposed to be in *Plateosaurus*.

Muscle function in extinct animals (but also in extant animals!) is often inferred from its topology or architecture (origin and insertion of a muscle and the relationship to each other). Gatesy (1995) was able to show that in fact muscle function often correlates to its topology. However, Gatesy (1995) also demonstrated that muscle function can change during evolution without the change of the topology. In addition, it has been demonstrated that it is not possible to draw conclusions from the area of attachment to the size or functional significance of a muscle (e.g. Davis 1964, Stevens 1966, Rose 1987). According to this, reconstructing muscle function in an extinct animal requires more than the simple reconstruction of the muscle architecture. Based on these considerations, muscle function was not reconstructed here.

Institutional abbreviation: **FMNH**, Field Museum of Natural History, Chicago; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart.

5.3 RESULTS

5.3.1 Comparative myology of the pelvic girdle and hindlimb in the phylogenetic bracket

Musculus iliotibialis (IT)

M. iliotibialis of *Sphenodon* arises with a single muscle tendinous anteriorly to the origin of M. iliofemoralis and anteroventrally to the origin of M. iliofibularis (Gadow 1882, Osawa 1898, Byerly 1925, Dilkes 2000). In squamates, M. iliotibialis consists of two heads originating tendinously from a narrow area, extending from the anterior margin to the posterior margin of the iliac blade (Gadow 1882, Dilkes 2000). In extant archosaurs, M. iliotibialis arises with three parts from the dorsal margin of the lateral iliac blade, forming the superficial layer to other thigh muscles (Fig. 5-1a,b). In crocodiles, M. iliotibialis 1 is the anteriormost of those and takes origin from the Spina anterior, posteroventrally to M. iliocostalis and anterodorsally to M. iliotibialis 2. M. iliotibialis 2 originates dorsally to the origin of M. iliofemoralis (Gadow 1882, Romer 1923b, Tarsitano 1981). The posteriormost part, M. iliotibialis 3, arises from the dorsal margin of the postacetabular iliac blade, posterodorsally to the origin of M. iliofibularis and anterodorsally to the origin M. flexor tibialis internus 2 (Romer 1923b, Tarsitano 1981). The end-tendon of Mm. iliotibiales fuses with that of Mm. femorotibialis and ambiens to form a common extensor tendon inserting on the anterior aspect of the proximal tibia (Fig. 5-2a; Gadow 1882, Romer 1923b, Tarsitano 1981). The end-tendon of M. iliotibialis 3 has an additional insertion on the end-tendon of M. ambiens (Romer 1923b). In Aves, M. iliotibialis is separated into Mm. tibialis cranialis and lateralis (Vanden Berge and Zweers 1993). M. iliotibialis cranialis takes origin from the lateral aspect of the anterodorsal Ala preacetabularis ilii, dorsally to the origin of M. iliotrochantericus caudalis. M. iliotibialis lateralis arises with two heads from the dorsal margin of the lateral iliac blade, with M. iliotibialis lateralis pars preacetabularis taking origin on the Crista dorsalis of the Ala preacetabularis ilii, dorsally to the origin of M. iliofemoralis externus, and M. iliotibialis lateralis pars postacetabularis arising aponeurotic along the Crista dorsolateralis, dorsally to the origin of M. iliofibularis. Both parts of M. iliotibialis insert with a common tendon on the anterior aspect of the tibiotarsus (Fig. 5-2c), next to the insertion of M. femorotibialis (Hudson et al. 1959, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculus femorotibialis (FMT)

In Sauria, the origin of M. femorotibialis occupies the greater part of the femoral shaft, with a varying number of parts. In lepidosaurs, M. femorotibialis consists of a single muscle. In *Sphenodon*, M. femorotibialis originates from the greater part of the anterior aspect of the femoral shaft (Osawa 1898). In squamates, M. femorotibialis originates from the greater part of the femoral shaft, separated on the posterior aspect of the femur by the insertion of Mm. adductor femoris 1 and 2 (Dilkes 2000). In basal Sauria, M. femorotibialis inserts on the anteroproximal tibia (Gadow 1882, Osawa 1898, Dilkes 2000). M. femorotibialis of crocodiles consists of two muscles (Fig. 5-2a, 5-3a). M. femorotibialis internus arises from the anterior, lateral, posterior, and medial aspect of the femoral shaft. M. femorotibialis externus arises from the posterolateral aspect of the femur (Gadow 1882, Romer 1923b). M. femorotibialis inserts with the common extensor tendon on the anterior aspect of the proximal tibia (Gadow 1882, Romer 1923b). In Aves, M. femorotibialis consists of three parts (Fig. 5-2c, 5-3c). M. femorotibialis lateralis arises from the anterolateral aspect of the femoral shaft. M. femorotibialis medius arises medioposterior aspect of the femoral shaft. M. femorotibialis intermedius arises from the greater part of the anteromedial aspect of the femur. Mm. femorotibiales of Aves inserts in common on the lateral aspect of the Crista cnemialis (Hudson et al. 1959, Nickel et al. 2003, Gangl et al. 2004).

Musculus ambiens (AMB)

In basal Sauria, M. ambiens consists of a single muscle, arising from the Tuberculum pubis on the lateral or anterolateral aspect of the proximal pubis and inserting on the anteroproximal tibia (Gadow 1882, Osawa 1898, Romer 1923bb, Byerly 1925, Rabl 1915-16, Kriegler 1961). In crocodiles, M. ambiens consists of two parts, Mm. ambiens 1 and 2 (Fig. 5-1a, 5-3a). M. ambiens 1 arises from a marked rugosity on the anterolateral aspect of the proximal pubis (Gadow 1882, Romer 1923b). The tendon of insertion of M. ambiens 1 is subdivided into two crura, with one crus fusing with the common extensor tendon and the second crus inserting on the Caput lateralis m. gastrocnemius (Romer 1923b, Tarsitano 1981, Hutchinson 2002). M. ambiens 2 takes origin from the medial aspect of the proximal pubis, posterodorsally to the origin of M. puboischiofemoralis externus, and fuses with M. iliotibialis at the middle of the thigh (Gadow 1882, Romer 1923b). In Aves, M. ambiens consists of a single muscle (Fig. 5-1c; Vanden Berge and Zweers 1993). M. ambiens of Aves arises

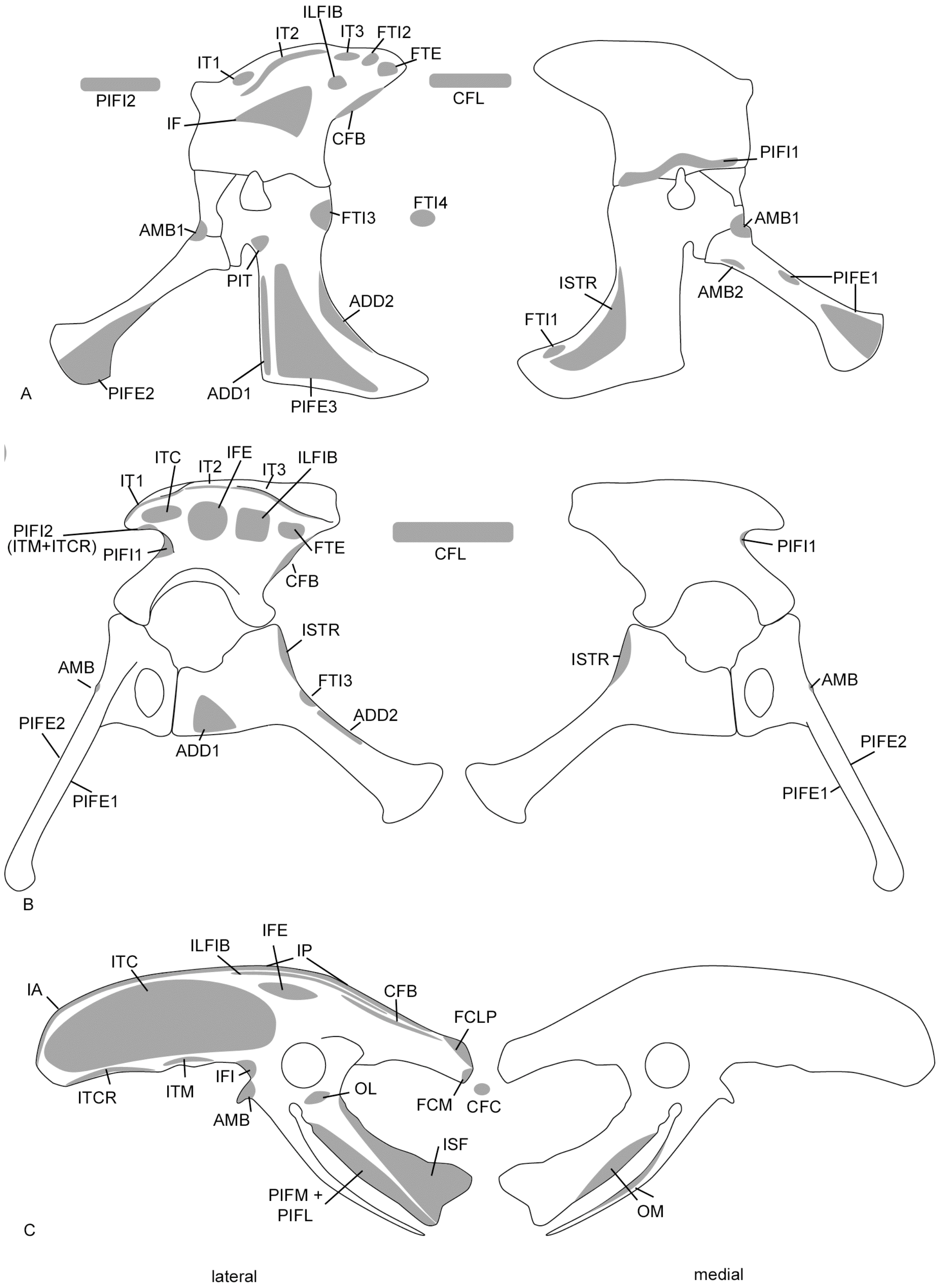


Figure 5-1. Musculature of the pelvis in A, *Alligator*, B, *Plateosaurus,* and C, *Apteryx*. *Alligator* redrawn from Romer (1923b) and *Apteryx* from McGowan (1979). Abbreviations of muscles taken from Table 5-1. Dark grey indicates the site of origin of a muscles. Not to scale.

from the Tuberculum preacetabularis of the ilium and inserts on the aponeurosis of Mm. flexores perforati digiti II, III, and/or IV (Hudson et al. 1959, McGowan 1979, Nickel et al. 2003).

Musculus iliofibularis (ILFIB)

In *Sphenodon*, M. iliofibularis arises from the lateral iliac blade posterodorsally to the origin of M. iliotibialis and dorsally to the origin of M. iliofemoralis (Gadow 1882, Osawa 1898, Dilkes 2000). In squamates, M. iliofibularis originates from the lateral iliac blade, ventrally to the origin of M. iliotibialis and posteriorly to the origin of M. iliofemoralis (Gadow 1882, Dilkes 2000). M. iliofibularis of crocodiles arises from the posterodorsal aspect of the lateral blade, posterodorsally to M. iliofemoralis (Fig. 5-1a). In basal Sauria and crocodiles, M. iliofibularis inserts proximal on the lateral fibula shaft, with an additional insertion on the Caput laterale m. gastrocnemius in crocodiles (Fig. 5-3a; Gadow 1882, Osawa 1898, Romer 1923b, Tarsitano 1981, Dilkes 2000). In Aves, M. iliofibularis takes origin along the Crista iliac dorsolateralis of the dorsolateral ilium and inserts on the Tuberculum m. iliofibularis fibulae (Fig. 5-1c, 5-3c; Hudson et al. 1959, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculus iliofemoralis (IF)

M. iliofemoralis is a single muscle in basal Sauria and crocodiles (Fig. 5-1a, 5-2a). In *Sphenodon*, M. iliofemoralis arises from the lateral iliac blade, posteriorly to the origin of M. iliotibialis and ventrally to the origin of M. iliofibularis. It attaches to the greater part of the lateral aspect of the femur, between the origin of Mm. femorotibialis and adductor femoris (Osawa 1898, Byerly 1925). M. iliofemoralis of squamates arises from lateroposterior ilium, ventrally to the origin of M. iliotibialis and anteriorly to the origin of M. iliofibularis. It inserts on the lateroposterior aspect of the proximal femur, between the insertion of Mm. adductor femoris and puboischiofemoralis externus (Gadow 1882, Dilkes 2000). In crocodiles, M. iliofemoralis arises fleshy from the lateral iliac blade, dorsally to the acetabulum (Gadow 1882, Romer 1923b, Tarsitano 1981) and anteroventrally to the origin of M. iliofibularis and posteroventrally to the origin of M. iliotibialis 2 (Romer 1923b, Tarsitano 1981). M. iliofemoralis inserts on the greater part of the lateroposterior aspect of the femur, separating the origin of Mm. femorotibialis externus and internus (Romer 1923b). In Aves, M. iliofemoralis externus arises from the lateral ilium, dorsally to the acetabulum and posteriorly to the origin of M. iliotrochantericus caudalis. It inserts by tendon distally to the Trochanter femoris on the lateral aspect of the proximal femur. M. iliotrochantericus caudalis takes origin from the greater part of the lateral Ala preacetabularis ilii and inserts by tendon anterolaterally on the Trochanter femoris (Fig. 5-1c, 5-2c; Hudson 1959, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculus puboischiofemoralis internus (PIFI)

M. puboischiofemoralis internus of basal Sauria and crocodiles has two parts, Mm. puboischiofemoralis internus 1 and 2 (Fig. 5-1a, 5-2a). In lepidosaurs, Mm. puboischiofemoralis internus 1 and 2 arise from the medial aspect of the puboischiadic plate. M. puboischiofemoralis internus inserts on the anterior aspect of the proximal femur, dorsally to the origin of M. femorotibialis (Gadow 1882, Dilkes 2000). In crocodiles, M. puboischiofemoralis internus 1 arises from the medial aspect of the ilium and the ventral aspect of the sacral rips. The muscle passes the pelvis anteriorly to insert fleshy on the medial aspect of the proximal femur, anterior to the insertion of M. caudofemoralis longus. M. puboischiofemoralis internus 2 arises from the bodies and ventral aspect of the transverse processes of the posterior lumbar vertebrae and inserts with two tendons on the anterolateral aspect of the proximal femur, dorsally to the origin of M. femorotibialis internus (Gadow 1882, Romer 1923b, Tarsitano 1981). In Aves, M. iliofemoralis internus arises from the ventral margin of the lateral iliac blade and inserts posteromedial aspect of the proximal femur, ventrally to the tendon of insertion of M. obturatorius medialis. M. iliotrochantericus cranialis arises from the anteroventral margin of the Ala preacetabularis of the ilium and inserts on the anterolateral aspect of the femoral shaft, ventrally to the insertion of M. iliotrochantericus caudalis. M. iliotrochantericus medialis arises from the ventral margin of the Ala preacetabularis ilii and inserts by tendon distally to the Trochanter femoris (Fig. 5-1c, 5-2c; Hudson et al. 1959, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculus puboischiotibialis (PIT)

M. puboischiotibialis of lepidosaurs arises with two, sometimes with three parts, from the Ligamentum puboischiadicum and from the Processus lateralis pubis in squamates (Gadow 1882, Romer 1942, Kriegler 1961, Dilkes 2000) and in common with M. ambiens from the Ligamentum puboischiadicum, the anteroproximal pubis and from the Symphysis ischiopubica in *Sphenodon* (Gadow 1882, Osawa 1898, Byerly 1925, Kriegler 1961, Dilkes 2000). It inserts on the medioproximal or lateroproximal tibial, dorsally to the origin of M. gastrocnemius and anteriorly to the insertion of Mm. flexor tibialis internus and externus (Dilkes 2000). In crocodiles, M. puboischiotibialis arises from anterodorsal obturator plate of the ischium, dorsally to the acetabulum and between the origin of Mm. adductor femoris 2 and puboischiofemoralis externus 3 (Romer 1923b). Distally, M. puboischiotibialis joins Mm. puboischiofemoralis externus 3 and adductor femoris 1 to insert on the posterolateral aspect of the proximal tibia (Fig. 5-1a, 5-3a; Romer 1923b, Tarsitano 1981). M. puboischiotibialis is absent in Aves (Vanden Berge and Zweers 1993).

Musculus flexor tibialis internus (FTI)

In *Sphenodon*, M. flexor tibialis internus consists of three parts originating on the proximal caudal vertebrae and posterolateral ischium, posteriorly to the origin of M. puboischiofemoralis externus (Dilkes 2000). M. flexor tibialis internus of squamates consists of three parts, arising primarily from the Ligamentum ilioischiadicum, with a small part arising from the posterolateral ischium, posteriorly to the origin of M. puboischiofemoralis externus (Dilkes 2000). In crocodiles, M. flexor tibialis internus consists of four parts (Fig. 5-1a, 5-3a). M. flexor tibialis internus 1 arises from the posterior margin of the medial aspect of the pubis, posteriorly to M. ischiotrochantericus (Romer 1923b). M. flexor tibialis internus 2 takes origin from the lateral aspect of the posterodorsal iliac blade, posteriorly to M. flexor tibialis externus (Romer 1923b). M. flexor tibialis internus 3 arises from the ischial tuberosity on the lateral aspect of the proximoposterior ischium, proximally to M. adductor femoris 2 (Romer 1923b). M. flexor tibialis 4 takes origin from the ilioischiadic fascia (Carrano and Hutchinson 2002, *non* Tarsitano 1981). Mm. flexor tibiales internii insert in common on the posteromedial and posterolateral aspect of the proximal tibia (Tarsitano 1981). In Aves, M. flexor cruris medialis is a single muscle (Fig. 5-1c, 5-3c). M. flexor cruris medialis arises from the lateral aspect of the posterodistal ischium. It inserts in common with M. flexor cruris lateralis on the proximoposterior or proximolateral aspect of the tibiotarsus (Hudson et al. 1965, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculus flexor tibialis externus (FTE)

In *Sphenodon*, M. flexor tibialis externus arises from the Tuber ischii and from the ventral aspect of the Processus transverses of the anterior caudal vertebrae (Gadow 1882). In squamates, M. flexor tibialis externus arises from the Ligamentum ilioischiadicum and from the posterodorsal edge of the lateral iliac blade (Gadow 1882). M. flexor tibialis externus of lepidosaurs inserts on the posteromedial aspect of the proximal fibula, with an additional tendon inserting on the Caput medius m. gastrocnemius (Gadow 1882). In crocodiles, M. flexor tibialis externus arises by tendon from the posterodorsal margin of the lateral iliac blade, posteroventrally to M. iliotibialis 3 and anterodorsally to M. flexor tibialis internus 2 (Gadow 1882, Romer 1923b). M. flexor tibialis externus inserts by tendon shared with M. flexor tibialis internus 3 on the medial aspect of the proximal tibia next to the origin of M. gastrocnemius medialis (Fig. 5-1a, 5-3a; Romer 1923b). In Aves, M. flexor cruris lateralis pars pelvica arises fleshy from the Processus terminalis ilii and fleshy-aponeurotically from the proximal caudal vertebrae. M. flexor cruris lateralis pars accessoria arises fleshy from the posterolateral aspect of the femur, proximal to the Condylus lateralis femoris. It inserts tendinous in common with Pars pelvica m. flexor cruris lateralis on the proximomedial aspect of the tibiotarsus, next to the origin of M. gastrocnemius medialis (Fig. 5-1c, 5-3c; Hudson et al. 1959, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculus adductor femoris (ADD)

In lepidosaurs, the origin of M. adductor femoris is restricted to the Ligamentum puboischiadicum. It inserts on the posterolateral femoral shaft, between the origin of M. femorotibialis and the insertion of M. iliofemoralis (Gadow 1882, Dilkes 2000). M. adductor femoris consists oft two muscles in crocodiles, Mm. adductor femoris 1 and 2 (Fig. 5-1a, 5-2a). M. adductor femoris 1 arises fleshy from the greater part of the anterior margin of the lateral ischium (Gadow 1882, Romer 1923b, Tarsitano 1981) and inserts by fleshy tendon on the adductor ridge of the posterior aspect of the femur, distally to the fourth trochanter (Gadow 1882, Tarsitano 1981). M. adductor femoris 2 arises fleshy from the distal part of the posterior margin of the ischium (Gadow 1882, Romer 1923b, Tarsitano 1981). The

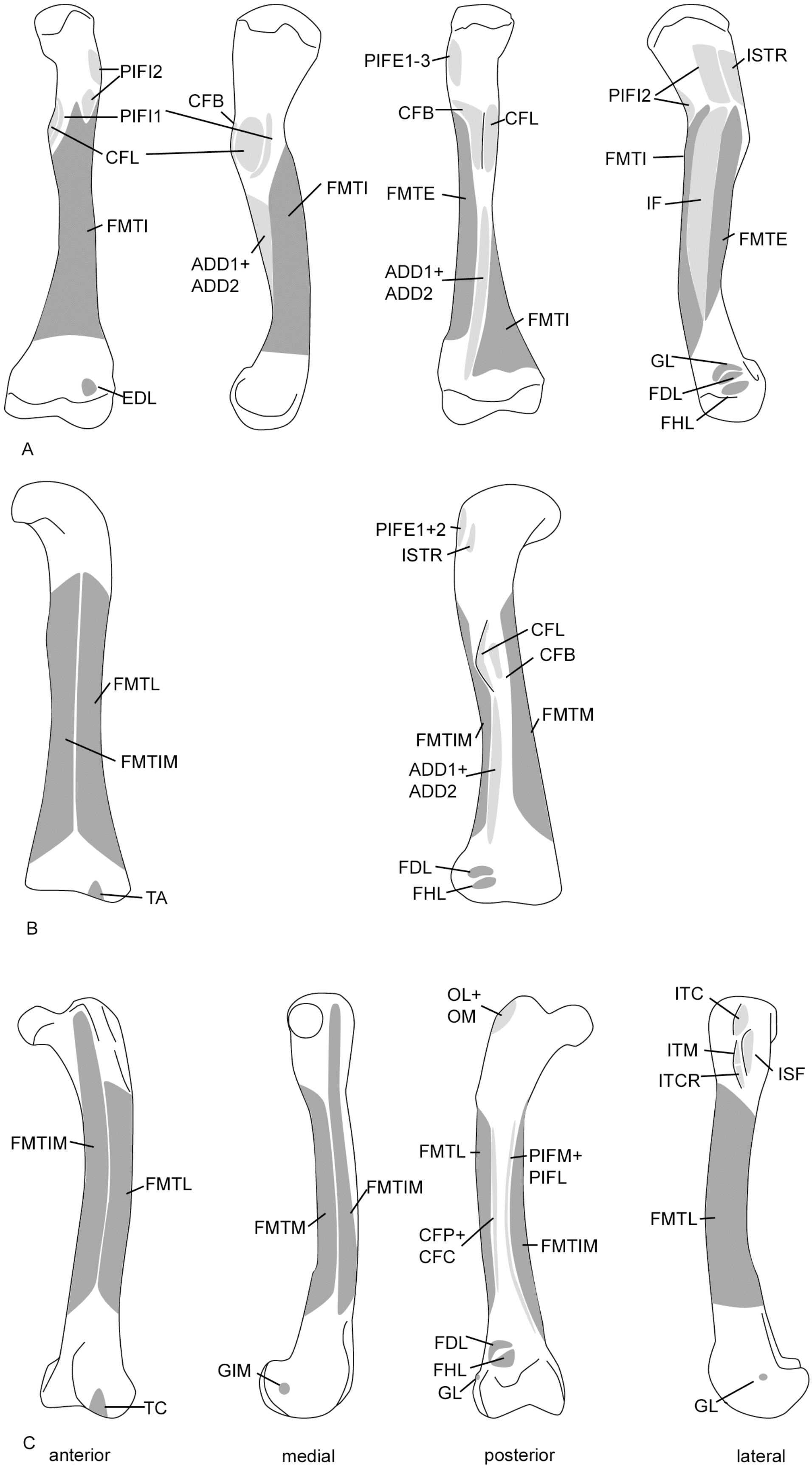


Figure 5-2. Musculature of the femur in A, *Alligator*, B, *Plateosaurus,* and C, *Apteryx*. *Alligator* redrawn from Romer (1923b) and *Apteryx* from McGowan (1979). Abbreviations of muscles taken from Table 5-1. Dark grey indicates the site of origin of a muscle, light grey the site of insertion of a muscle. Not to scale.

tendinous insertion of the M. adductor femoris 2 is on the posterior aspect of the femur, dorsally to the insertion of M. adductor femoris 2, extending from the fourth trochanter to the Condylus lateralis femoris (Gadow 1882, Romer 1923b, Tarsitano 1981). In Aves, Mm. puboischiofemoralis pars lateralis and pars medialis arise from the lateral aspect of the ventral ischium and inserts on the Linea intermuscularis caudalis on the posterior femoral shaft (Fig. 5-1c, 5-2c; Hudson et al. 1959, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculi puboischiofemorales externi (PIFE)

In *Sphenodon*, M. puboischiofemoralis externus arises from the lateral aspect of the posterodistal pubis and from the anterior margin of the lateral aspect of the distal ischium (Gadow 1882). It inserts on the Trochanter major femoris on the posterior aspect of the proximal femur (Gadow 1882), dorsally to the insertion of M. iliofemoralis (Dilkes 2000). M. puboischiofemoralis externus of squamates arises from the lateral aspect of the ischium (Gadow 1882) and from the medial aspect of the posterodistal part of the pubis (Dilkes 2000). It inserts on the Trochanter major femoris on the posterior aspect of the proximal femur, dorsally to the insertion of M. iliofemoralis (Dilkes 2000). In crocodiles, M. puboischiofemoralis externus is subdivided into Mm. puboischiofemoralis externus 1, 2, and 3 (Fig. 5-1a, 5-2a; Gadow 1882, Romer 1923b, Tarsitano 1981). M. puboischiofemoralis externus 1 takes origin with two heads from the medial aspect of the pubic plate, one of which originating on the middle part of the blade, and the second head on the distal pubis and prepubic cartilage. An additional site of origin is on the last abdominal rib (Romer 1923b, Tarsitano 1981). M. puboischiofemoralis externus 2 arises from the greater part of the lateral aspect of the distal pubic plate (Gadow 1882, Romer 1923b). M. puboischiofemoralis externus 3 originates from the greater part of the lateral aspect of the distal ischium, between the origin of the two heads of M. adductor femoris and ventrally to Mm. puboischiotibialis and flexor tibialis internus 1 (Gadow 1882, Romer 1923b). Mm. puboischiotibialis externus 1, 2, and 3 insert in common on the lateral aspect of the proximal femur (Gadow 1882, Romer 1923b). In Aves, M. obturatorius lateralis pars dorsalis arises from the posteroventral margin of the Foramen obturatum and inserts on the Trochanter femoris. Pars ventralis m. obturatorius lateralis originates from the Incisura obturatoria and inserts on the Impressio obturatoria, on the posterolateral proximal femur. M. obturatorium medialis fills the

Fenestra ischiopubica and the caudal aspect of the Foramen ilioischiadicum, passes laterally through the Foramen obturatum and inserts distally to the tendon of M. iliofemoralis externus on the Trochanter femoris (Fig. 5-1c, 5-2c; Hudson et al. 1959, Nickel et al. 2003, Gangl et al. 2004).

Musculus ischiotrochantericus (ISTR)

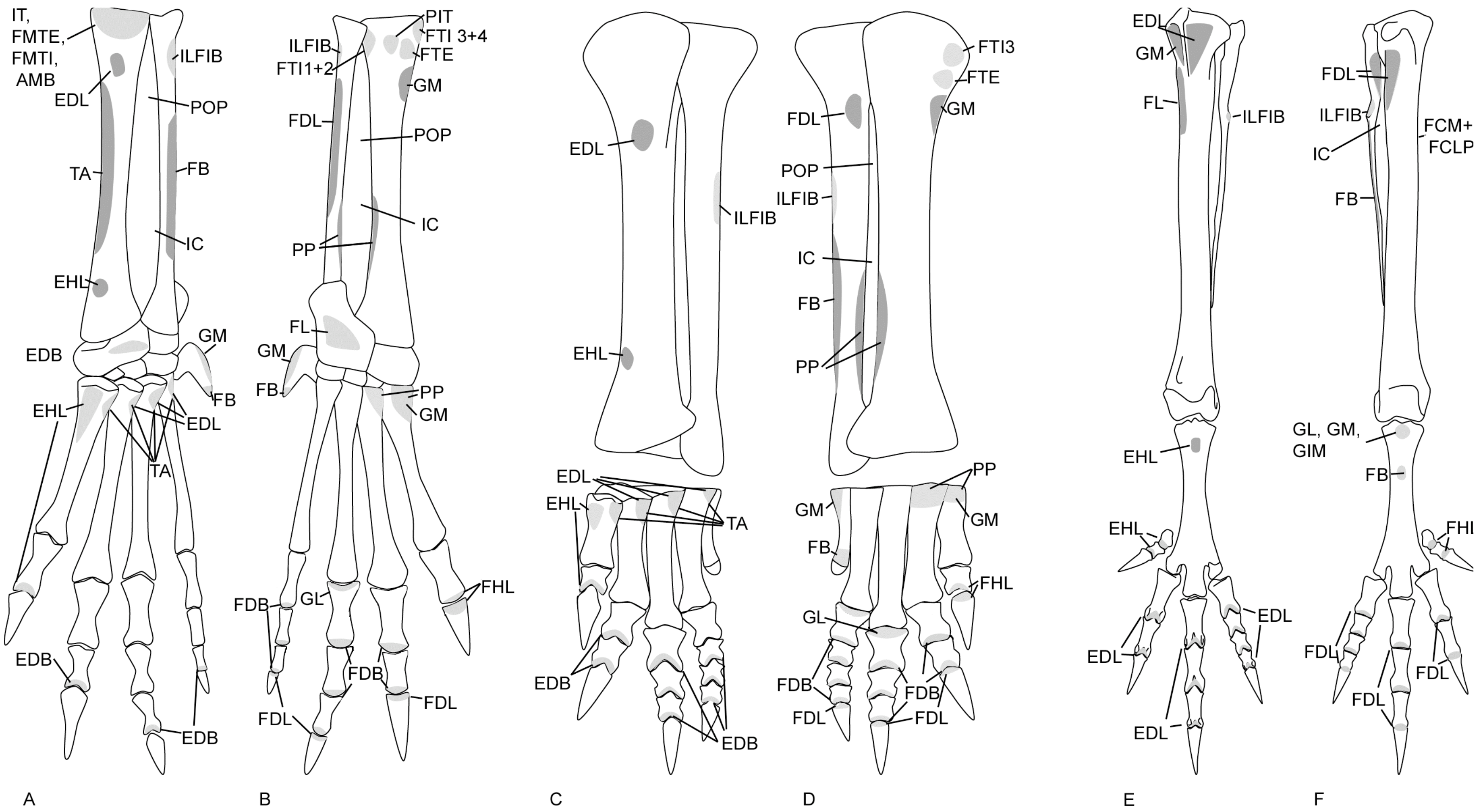
In lepidosaurs, M. ischiotrochantericus arises from the posterior margin of the ischium, in *Sphenodon* from the lateral ischium and in squamates from the medial ischium posterior of the origin of M. puboischiofemoralis internus (Dilkes 2000). It inserts on the posterior aspect of the proximal femur in *Sphenodon*, dorsally to the origin of M. femorotibialis, and on the anterior aspect of the proximal femur in squamates, dorsally to the insertion of M. puboischiofemoralis internus (Gadow 1882, Dilkes 2000). M. ischiotrochantericus of crocodiles takes its fleshy origin from the posterior part of the medial aspect of the ischium and inserts by tendon on the proximolateral aspect of the femur (Fig. 5-1a, 5-2a; Gadow 1882, Romer 1923b, Tarsitano 1981). In Aves, M. ischiofemoralis arises from the posterior margin of the Foramen ilioischiadicum to the posterior margin of the ischium and inserts by tendon distally to the Trochanter femoris on the posterolateral aspect of the femur, between the insertion of Mm. iliotrochantericus cranialis and medius (Fig. 5-1c, 5-2c; Hudson et al. 1959, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculi caudofemoralis longus (CFL) et brevis (CFB)

M. caudofemoralis longus of lepidosaurs takes origin from the bodies and ventral aspects of the transverse processes, as well as hemapophysis of a varying number of caudal vertebrae. M. caudofemoralis brevis arises from the medial aspect of the posterior iliac blade. Mm. caudofemoralis longus and brevis insert on the posterior aspect of the proximal femur. In crocodiles, M. caudofemoralis consists of two parts (Fig. 5-1a, 5-2a). M. caudofemoralis longus takes origin from the bodies and ventral aspect of the transverse processes of the third to thirteenth/fifteenth caudal vertebrae and their hemapophysis, sometimes additionally on the last sacral vertebrae (Gadow 1882, Romer 1923b, Tarsitano 1981). It inserts by tendon on the fourth trochanter and medially to it. A secondary tendon leads to the knee, contributing to the origin of Pars lateralis m. gastrocnemius (Romer 1923b, Tarsitano 1981, Hutchinson 2002). M. caudofemoralis brevis originates from the bodies and the ventral aspect of the transverse processes of the second sacral vertebra and the first caudal vertebra, as well as from the medial aspect of the posterior margin of the ilium. M. caudofemoralis brevis inserts fleshy on the medial aspect of the fourth trochanter, dorsally to the insertion of M. caudofemoralis longus (Gadow 1882, Romer 1923b, Tarsitano 1981). In Aves, M. caudofemoralis pars caudalis arises tendinous ventral from the pygostyle and inserts on the posterolateral aspect of the femur, ventrally to the insertion of M. caudofemoralis pars pelvica. M. caudofemoralis pars pelvica originates fleshy, partly tendinous from the Crista iliaca dorsolateralis and Margo caudalis ilii (Fig. 5-1c, 5-2c; Hudson et al. 1959, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculus gastrocnemius (GA)

Two parts of M. gastrocnemius, Pars lateralis m. gastrocnemius and Pars medialis m. gastrocnemius, are plesiomorphical for Sauria (Fig. 5-2a, 5-3a,). M. gastrocnemius lateralis arises from the posterolateral aspect of the Condylus lateralis femoris, ventrally to the origin of M. flexor digitorium longus. In lepidosaurs and M. gastrocnemius medialis arises from the lateral or posterolateral aspect of the proximal tibia, between the origin of M. tibialis anterior and the insertion of M. puboischiotibialis, with an additional site of insertion ventrally to the insertion of M. pubotibialis in *Sphenodon* (Gadow 1882, Osawa 1898, Byerly 1925, Dilkes 2000). In lepidosaurs, two heads of M. gastrocnemius medialis are present, with a second head arising from the end-tendon of M. puboischiotibialis (Gadow 1882, Osawa 1898). Both parts of M. gastrocnemius form distally the Fascia plantaris inserting on the ventrolateral aspect metatarsal V and on the ventrolateral aspect of each non-ungual phalanx of digit II-V in *Sphenodon* and digits III-IV in squamates (Dilkes 2000). M. gastrocnemius of crocodiles also has two muscles. M. gastrocnemius lateralis arises by a short tendon from the lateroposterior aspect of the Condylus lateralis femoris and inserts on the basis of phalanx I of digit III. M. gastrocnemius medialis arises fleshy from the medial aspect of the proximal tibia. M. gastrocnemius medialis inserts on the basis of metatarsus I and on the lateral aspect of digit V (Gadow 1882). In Aves, M. gastrocnemius consists of three heads (Fig. 5-2c, 5-3c). Pars lateralis m. gastrocnemius arises by tendon from the posterolateral basis of the Condylus lateralis femoris and from the Tuberculum m. gastrocnemius lateralis. The Pars medialis m. gastrocnemius takes origin from the proximal patellae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and from the Ligamentum patellae and from the Crista cnemialis cranialis as well as from the Fascies gastrocnemialis. The Pars intermedia m. gastrocnemius arises from the Condylus medialis femoris. The end-tendon of the M. gastrocnemius inserts on the hypotarsus (Hudson et al. 1959, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculus flexor digitorium longus (FDL)

In basal Sauria, M. flexor digitorium longus consists of two heads, one of which arising from the lateral aspect of the Condylus lateralis, dorsally to the origin of M. gastrocnemius lateralis. The second head arises from the posterior aspect of the distal fibula and calcaneum in *Sphenodon* (Dilkes 2000), and from the posterior aspect of the posteroproximal fibula and the calcaneum in squamates (Dilkes 2000). It inserts on the ventral aspect of the ungual of each digit (Dilkes 2000). In crocodiles, M. flexor digitorium longus comprises two heads (Fig. 5-2a, 5-3a). M. flexor digitorium longus caput femorale arises by tendon from the lateral aspect of the Condylus lateralis femoris. M. flexor digitorium longus caput fibulae takes origin from the posterior aspect of the fibula. Both heads fuse to form a fascia, which is subdivided into three tendons inserting on the ventral aspect of the unguals of digit II – IV, with additional tendons inserting on each interphalangeal joint (Kriegler 1961, Tarsitano 1981, Dilkes 2000). In Aves, M. flexor digitorium longus has two heads (Fig. 5-2c, 5-3c). Caput tibiale m. flexor digitorium longus takes origin on the proximal tibia and Caput fibulare m. flexor digitorium longus arises from the posterior shaft of the fibula. The end-tendon of M. flexor digitorium longus is subdivided in three crura inserting on the Tuberculum flexorium of the terminal phalanges of digits II – IV. Additional tendons insert on each interphalangeal joint (Hudson et al. 1959, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Figure 5-3. Musculature of the distal limb in *Alligator*, *Plateosaurus,* and *Apteryx*. A, *Alligator* in anterior and B, posterior view, C, *Plateosaurus* in anterior and D, posterior view, E, *Apteryx* in anterior and F posterior view. *Alligator* redrawn from Reese (1915) and *Apteryx* from McGowan (1979). Muscle abbreviations taken from Table 5-1. Colors as in Fig. 5-2. Not to scale.

Musculus flexor digitorium brevis (FDB)

M. flexor digitorium brevis of basal Sauria takes origin from the Fascia plantaris. Distally, M. flexor digitorium brevis is subdivided into several tendons inserting on the basis of the proximal phalanges of digit I – IV in *Sphenodon* (Osawa 1898) and on digit I – V in squamates (Gadow 1882, Kriegler 1961). In crocodiles, M. flexor digitorium brevis arises from the Fascia plantaris and is subdivided into four tendons inserting on the basis of the ventral aspects of the proximal phalanges of each digit (Fig. 5-3a; Tarsitano 1981). M. flexor digitorium brevis is absent in birds (Vanden Berge and Zweers 1993, Dilkes 2000).

Musculus flexor hallucis longus (FHL)

In Sauria and extant archosaurs, M. flexor hallucis longus arises from the lateral aspect the lateral Condylus femoris and inserts on the ventral aspect of the phalanges of digit I (Fig. 5-2a, 5-2c, 5-3a, 5-3c; Carrano and Hutchison 2002).

Musculus extensor digitorium longus (EDL)

M. extensor digitorium longus of basal Sauria arises from the anterior or lateral aspect of the proximal tibia, ventrally to the insertion of the extensor tendon and inserts by on the basis of the dorsal aspect of metatarsal I (Gadow 1882, Osawa 1898, Byerly 1925). In crocodiles, M. extensor digitorium longus arises by tendon from the anterior Condylus lateralis femoris and fuses with M. tibialis anterior. Distally, M. extensor digitorium longus is subdivided into four tendons inserting on the laterodorsal aspect of the basis of metatarsals I – IV (Fig. 5-2a, 5-3a; Gadow 1882, Tarsitano 1981). In Aves, M. extensor digitorium longus arises from the lateral aspect of the Crista cnemialis cranialis, on the Sulcus intercristalis, medially on the Crista cnemialis lateralis, with an additional origin on the proximal two third of the anterior aspect of the tibiotarsus. It has a tendinous insertion on the phalanges of the digits II, III and IV (Fig. 5-3c; Hudson et al. 1959, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculus extensor digitorium brevis (EDB)

In basal Sauria, M. extensor digitorium brevis arises from the anterolateral aspect of the calcaneum and inserts on the Tuberculum extensorium on the dorsal aspect of the phalanges of digit II – V in *Sphenodon* (Gadow 1882, Kriegler 1961, Dilkes 2000) and squamates (Dilkes 2000). In crocodiles, M. extensor digitorium brevis arises from the anterior aspect of the astragalus. The muscle is subdivided into several crura inserting on the Tuberculum extensorium of the terminal phalanx of digit II – IV (Fig. 5-3a; Gadow 1882, Dilkes 2000). M. extensor digitorium brevis is absent in birds (see Vanden Berge and Zweers 1993, Carrano and Hutchinson 2002).

Musculus extensor hallucis longus (EHL)

M. extensor hallucis longus of basal Sauria originates from the anterior aspect of the distal fibula and inserts on metatarsal I (Gadow 1882). In crocodiles, M. extensor hallucis longus is a small muscle arising tendinous from the anterior aspect of the distal fibula. It muscle inserts fleshy onto the dorsal aspect of the proximal half of metatarsal I and on the phalanges of digit I (Fig. 5-3a; Gadow 1882). In Aves, M. extensor hallucis longus arises from the Sulcus extensorius of the tarsometatarsus and inserts on the Tuberculum extensorium of the ungual of digit I (Fig. 5-3c; McGowan 1979, Nickel et al. 2003).

Musculus tibialis anterior (TA)

Lepidosaurs and crocodiles share a similar origin of M. tibialis anterior from the anterior aspect of the tibia (Dilkes 2000, Gadow 1882). In basal Sauria, M. tibialis anterior inserts on the basis of metatarsal I (Dilkes 2000) and in crocodiles on metatarsals I – III (Fig. 5-3a; Dilkes 2000). In Aves, Caput tibiale m. tibialis cranialis arises lateral on the Crista cnemialis cranialis, on the Crista patellaris, and on the Crista cnemialis lateralis. Caput femorale m. tibialis cranialis arises from the Condylus lateralis femoris. Both heads insert in common on the Tuberositas m. tibialis cranialis on the anterior aspect of the tarsometatarsus (Fig. 5-2c, 5-3c; Hudson et al. 1959, McGowan 1979, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculi fibularis longus (FL) et brevis (FB)

In *Sphenodon*, M. fibularis consists of a single muscle, arising from the anterolateral aspect of the greater part of the fibula and attaches to the lateral aspect of the calcaneum and on the basis of metatarsal V, with additional fascicles inserting on the basis of metatarsal IV (Gadow 1882, Osawa 1898, Byerly 1925). In squamates, M. fibularis longus arises from the anterior aspect of the fibula and inserts by tendon on the calcaneum, with an additional insertion on the dorsal aspect of metatarsal V. M. fibularis brevis originates on the entire posterolateral aspect of the fibula and inserts by tendon on metatarsal V, with fascicles inserting on the basis of metatarsal IV and digit V (Rabl 1915-16, Kriegler 1961). In crocodiles, M. fibularis longus arises from the lateral aspect of the fibula, proximoposteriorly to the origin of M. fibularis brevis, and inserts on the ventral aspect of the calcaneum. M. fibularis brevis arises from the lateral aspect of the fibula. The end-tendon contributes to the Tendon achillis and inserts on the lateral margin of the distal end of metatarsal V (Fig. 5-3a; Gadow 1882, Kriegler 1961). In Aves, M. fibularis longus arises distally on the Crista cnemialis lateralis and aponeurotic on the Crista patellaris, on the Crista cranialis and on the Linea extensoria of the tibiotarsus. M. fibularis longus is fused with the M. flexor perforans et perforatus digiti II and the Pars medialis m. gastrocnemius. Its end-tendon, which is separated into a Tendo caudalis inserting on the Cartilago tibialis and a Tendo lateralis inserting in the end-tendon of the M. flexor perforatus digiti III. M. fibularis brevis originates on the lateral aspect of the fibula and inserts on the Tuberositas m. fibularis brevis on the shaft of the tibiotarsus (Fig. 5-3c; Hudson et al. 1959, McGowan 1979, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculus pronator profundus (PP)

In *Sphenodon*, M. pronator profundus arises from the greater part of the posterior aspect of the fibula and on the proximal part of the Membrana interosseus. The tendon inserts on the plantar aspect of the basis of metatarsal I – III (Gadow 1882, Osawa 1898, Byerly 1925). In squamates, M. pronator profundus arises from the greater part of the posterior aspect of the fibula and sometimes from the tibia. It inserts by tendon on the astragalus (Gadow 1882) or on the basis of metatarsal I, with additional fascicles inserting the basis of the metatarsals II and III. In crocodiles, M. pronator profundus originates fleshy from the posteromedial aspect of the fibula and posterolateral aspect of tibia, posterior to the attachment of Mm. interosseus cruris and popliteus (Gadow 1882, Tarsitano 1981).

Its proximal part is fused with M. flexor digitalis longus (Gadow 1882). It inserts by tendon on the basis of the ventromedial aspect of the metatarsals I and II (Fig. 5-3a; Gadow 1882, Kriegler 1961, Tarsitano 1981). M. pronator profundus is absent in Aves (see Vanden Berge and Zweers 1993, Carrano and Hutchinson 2002).

Musculus popliteus (POP)

In basal Sauria and crocodiles, M. popliteus originates from the facing aspects of the proximal tibia and fibula, dorsally to M. interosseus cruris. The distal extend of M. popliteus varies in basal Sauria and crocodiles (Fig. 5-3a; Osawa 1898, Romer 1922). In Aves, M. popliteus arises on the proximal fibula and inserts on the Fossa poplitea (Fig. 5-3c; Hudson at al. 1959, McGowan 1979, Nickel et al. 2003, Gangl et al. 2004).

Musculus interosseus cruris (IC)

M. interosseus cruris of lepidosaurs attaches to the facing aspects of the distal tibia and fibula, distally to the origin and insertion of M. popliteus (Gadow 1882) and crocodiles (Fig. 5-3a; Gadow 1882, Kriegler 1961, Cong et al. 1998). In Aves, M. interosseus cruris is absent (see Vanden Berge and Zweers 1993, Carrano and Hutchinson 2002).

5.4 DISCUSSION

5.4.1 Reconstruction of the myology of the pelvic girdle and limb in *Plateosaurus engelhardti*

Musculi iliotibialis 1, 2 et 3

The reconstruction of three parts as well as the origin and insertion of M. iliotibialis is unequivocal in *Plateosaurus* (Fig. 5-1b, 5-3c, 5-4a). In extant archosaurs M. iliotibialis consists of three parts arising from the dorsal margin of the lateral ilium and forming the dorsal layer to other thigh muscles. In basal Sauria, M. iliotibialis is a single muscle having a varying site of origin on the lateral ilium. The dorsal shift of the origin and the separation into three parts is related to the anteroposterior expansion of the ilium on the lineage to archosaurs. In *Plateosaurus*, the origin of M. iliotibialis 1 – 3 is indicated by a marked rugosity on the dorsal margin of the ilium (level I inference). M. iliotibialis 1 arises dorsally or anterodorsally to the origin of M. iliotrochantericus caudalis. M. iliotibialis 2 arises dorsally to the origin of M. iliofemoralis externus and M. iliotibialis 3 takes origin dorsally to the origin of Mm. iliofibularis and flexor tibialis externus. In basal Sauria and extant archosaurs, M. iliotibialis inserts in common on the anterior aspect of the proximal tibia. In Aves, M. iliotibialis inserts on the lateral aspect of the cnemial crest. The presence of a cnemial crest indicates that M. iliotibialis of *Plateosaurus* attaches to the lateral aspect of the cnemial crest (level I' inference).

Musculi femorotibialis medius, lateralis et intermedius

In basal Sauria, M. femorotibialis is a single muscle arising from the greater part of the femoral shaft. In extant archosaurs, the number of parts is increases to two in crocodiles and three in Aves. Extant archosaurs have Mm. femorotibialis medialis (lateralis of Aves) and internus (medius of Aves) in common. The presence of the third part, M. femorotibialis intermedius is suggested to be a recent novelty in Aves (see Dilkes 2000, Hutchinson 2001, 2002, Carrano and Hutchinson 2002) and indicated by the development of a dorsoventrally running Linea intermuscularis cranialis on the anterior aspect of the femur (e.g. Carrano and Hutchinson 2002, Hutchinson 2002). Although there is no evidence of a Linea intermuscularis cranialis on the anterior aspect of the femur in *Plateosaurus*, Langer (2003) described the presence of a Linea intermuscularis cranialis in *Saturnalia tupiniquim* and most recently, Otero and Vizcaíno (2008) identified a Linea intermuscularis cranialis in the titanosauriform *Neuquensaurus australis.* In both cases the Linea intermuscularis cranialis runs from the proximal to the distal end of the femoral shaft. Langer (2003) reconstructed three parts of M. femorotibialis in *Saturnalia,* as in Aves. Otero and Vizcaìno (2008) reconstructed two parts of M. femorotibialis, as in crocodiles. A proximodistally running Linea intermuscularis, however, clearly indicates the presence of three parts of M. femorotibialis. Moreover, the presence of a Linea intermuscularis cranialis in the basal sauropodomorph *Saturnalia* suggests that M. femorotibialis is separated into three parts at the basis of sauropodomorphs, and *Neuquensaurus* shows that the separation into Mm. femorotibialis lateralis, medius and intermedius is retained in sauropods. In *Plateosaurus*, M. femorotibialis lateralis arises from the greater part of the anterolateral aspect of the femur (level I' inference), M. femorotibialis medius from the posteromedial aspect of the femur (level

Table 5-2. Muscles inferred as present in *Plateosaurus engelhartdti*. ? = unresolved at present. Muscle abbreviations as in Table 5-1.

Muscle	Origin	Level of inference	Insertion	Level of inference
IT1	dorsal margin of anterolateral iliumn	I	lateral cnemial crest	I'
IT2	dorsal margin of lateral ilium	I	lateral cnemial crest	I'
IT3	dorsal margin of posterior ilium	I	lateral cnemial crest	I'
FMTL	anterolateral femur	I'	lateral cnemial crest	I'
FMTIM	anteromedial femur	II'	lateral cnemial crest	II'
FMTM	medioposterior femur	I'	lateral cnemial crest	I'
AMB	pubic tubercle on proximolateral pubis	I	lateral cnemial crest	I'
			additional insertion on M. gastrocnemius or digital flexor	I'
ILFIB	posterolateral ilium	I'	Trochanter m. iliofibularis fibulae	I
IFE	lateral ilium, anterodorsally to acetabulum	I'	lesser trochanter	II
ITC	lateral ilium, anterodorsally to dorsally to acetabulum	I'	proximolateral femur, posterodistally to lesser trochanter	II
PIFI1	preacetabular fossa	II'	medioproximal femur	I'
PIFI2	ventral aspect of preacetabular process	II'	lateroproximal femur	I'
PIT	*? (obturator blade of lateral ischium)*	II'	*? (posteroproximal tibia)*	II'
FTI1	*? (lateral posterodorsal ilium)*	II'	*? (lateroproximal tibia)*	II'
FTI2	*? (lateral posterodorsal ilium)*	II'	*? (lateroproximal tibia)*	II'
FTI3	dorsoproximal ischial shaft	I	medioproximal tibia	I'
FTE	posterodorsal part of lateral ilium	I'	medioproximal tibia	I'
ADD1	obturator blade of lateral ischium	I'	posterior distal femur	I'
ADD2	lateral ischial shaft	I'	posterior distal femur	I'
PIFE1	anterior pubic apron	I'	greater trochanter	I
PIFE2	posterior pubic apron	I'	greater trochanter	I
PIFE3	*? (lateral aspect of obturator process)*	II'	*? (greater trochanter)*	II
ISTR	medial ischium	I'	posterolateral aspect of proximal femur	I'
CFL	bodies and ventral aspect of transverse processes and hemapohyses of caudal vertebrae 1-30	I	fourth trochanter	I
CFB	brevis fossa	II	medial to fourth trochanter	I
GL	posterolateral aspect of Condylus lateralis femoris	I'	ventral aspect of basis of phalanx I of digit III	II'
GM	medioproximal tibia	I'	ventral aspect of basis of mt I and lateral aspect of digit V	II'
GIM	?		?	
FDL	lateral aspect of Condylus lateralis femoris and posteroproximal fibula	I'	ventral aspect of ungual of each digit	I
FDB	plantar aponeurosis	II'	Tuberculum flexorium of non-ungual phalanges of each digit	II'
FHL	lateral aspect of Condylus lateralis femoris	I'	ventral phalanges and unguals of digit I	I'
TA	cnemial crest of tibia	I'	basis of anterior aspect of mt I - III	I'
EDL	anterior aspect of distal femur and proximal tibia	I'	laterodorsal aspect of the basis of mt I-V	II'
EDB	anterior proximal tarsus		Tuberculum extensorium of the terminal phalanx of each digit	
EHL	anterodistal fibula	II'	basis of metatarsal I	I'
FL	lateral fibula	I'	posterior calcaneum	I'
FB	lateral fibula	I'	distal metatarsal V	I'
PP	posterior tibia and fibula	II'	basis of metatarsals I - II/III	II'
POP	fossa on the proximomedial tibia	I	medial aspect of proximal fibula	I'
IC	lateral aspect of distal tibia	II'	medial aspect of distal fibula	II'

I' inference), and M. femorotibialis intermedius from anteromedial aspect of the femur (level II' inference). The origin of Mm. femorotibialis lateralis and medius is separated by the insertion of M.

adductor femoris 1 and 2 (Fig. 5-2b, 5-4a,b). The insertion of M. femorotibialis is unequivocal. In basal Sauria and extant archosaurs, M. femorotibialis inserts in common on the anterior aspect of the proximal tibia. As in Aves, M. femorotibialis inserts on the lateral aspect of the cnemial crest in *Plateosaurus* (level I' inference of Mm. femorotibialis lateralis and medius and level II' inference for M. femorotibialis intermedius).

Musculus ambiens

M. ambiens consists of a single muscle in basal Sauria and Aves. The presence of a second muscle, M. ambiens 2, is unique to crocodiles. The reconstruction of the presence of M. ambiens 2 in *Plateosaurus* is equivocal (level II' inference). M. ambiens of basal Sauria originates from a prominent Tuberculum pubis on the anterior or anterolateral aspect of the proximal pubis. The Tuberculum pubis of basal Sauria gives not only to M. ambiens, but provides also insertion to M. abdominus obliquus and the pelvic ligaments (Hutchinson 2001b). With the shift of the insertion of M. abdominus obliquus and the reduction of the pelvic ligaments within Archosauriformes (Hutchinson 2002), the prominent Tuberculum pubis is reduced. In crocodiles, the marked rugosity on the anterior aspect of the proximal pubis, which gave rise to M. ambiens 1, is homolog to the prominent Tuberculum pubis of basal Sauria and the Tuberculum pubis of dinosaurs. With the retroversion of the pubis on the lineage to Aves, the origin of M. ambiens moved to the anteroventral ilium, the Tuberculum preacetabularis (Hutchinson 2001b). In *Plateosaurus*, the presence of Tuberculum pubis on the anteroventrally projecting pubis indicates the origin of M. ambiens (level I inference). The insertion of M. ambiens in *Plateosaurus* is equivocal (level II' inference). M. ambiens of *Plateosaurus* inserts either on the anterior aspect of the proximal tibia, as in basal Sauria and crocodiles, or on a digital flexor as in Aves (Fig. 5-1b, 5-2c, 5-4a).

Musculus iliofibularis

M. iliofibularis is a very conservative in basal Sauria and extant archosaurs. The site of origin is on the lateral aspect of the ilium, posteriorly or posterodorsally to the origin of M. iliofemoralis or M. iliofemoralis externus, respectively. M. iliofibularis inserts on the lateral or anterolateral aspect of the fibula. In crocodiles, the insertion of M. iliofibularis is marked by a rugosity, which is considered to be

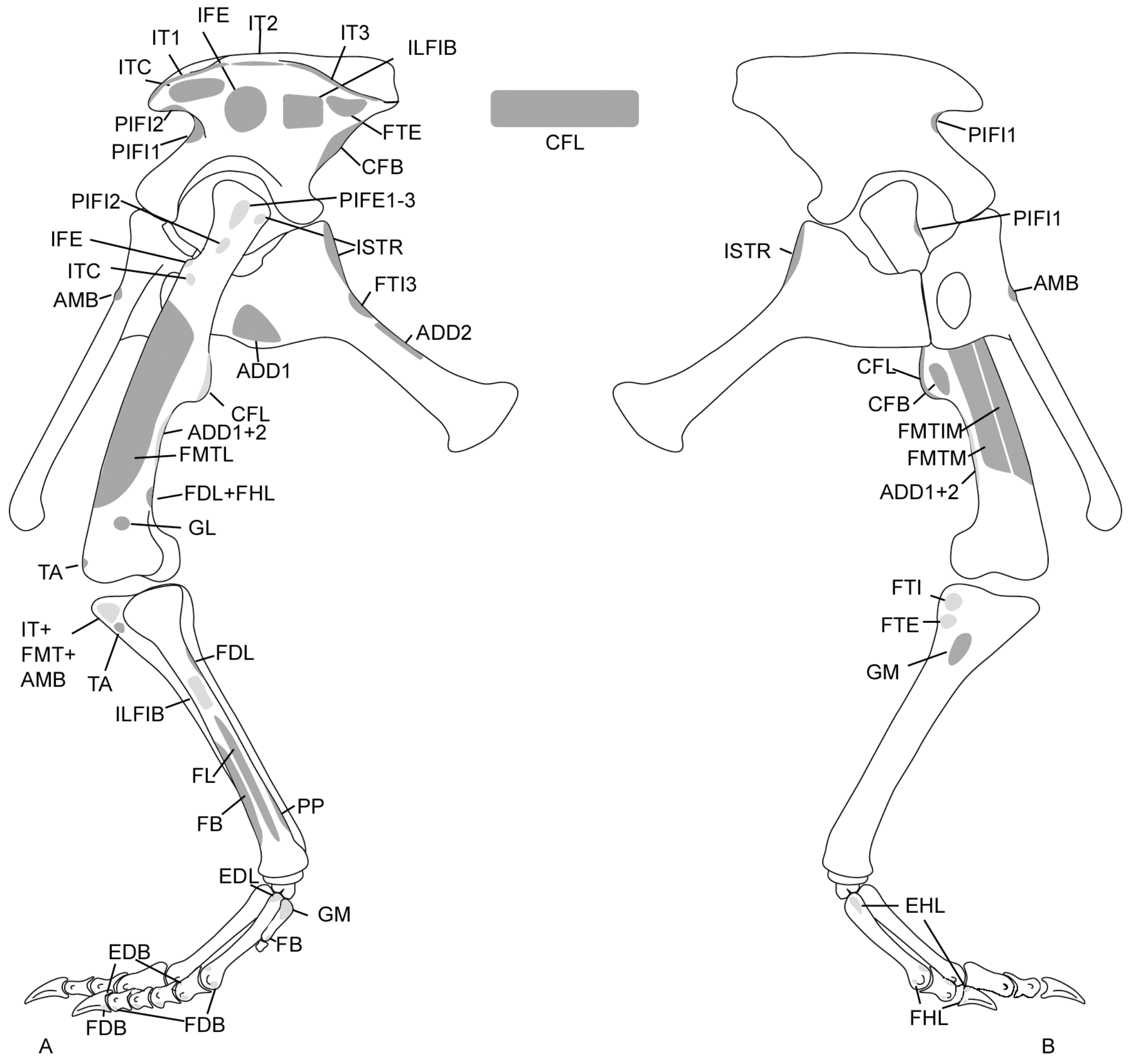

Figure 5-4. Muscles of the pelvic girdle and hindlimb of *Plateosaurus* in A, lateral and B, medial view. Abbreviations of muscles as in Table 5-1. Colors as in Fig. 5-2. Not to scale.

homolog to the Tuberculum m. iliofibularis fibulae, the site of insertion of M. iliofibularis in Aves (Romer 1922). In *Plateosaurus*, M. iliofibularis arises from the lateral aspect of the posterior ilium (level I' inference), between the origin of Mm. iliofemoralis externus and flexor tibialis externus. It inserts on the Tuberculum m. iliofibularis fibulae (level I inference) (Fig. 5-1b, 5-3c, 5-4a).

Musculi iliofemoralis externus and iliotrochanericus caudalis

In basal Sauria and crocodiles, M. iliofemoralis is a single muscle originating from the lateral ilium dorsally to the acetabulum. It inserts on varying sites on the femur. On the lineage to Aves, M.

iliofemoralis is separated into two muscles, Mm. iliofemoralis externus and iliotrochantericus caudalis. According to Rowe (1986), the separation of M. iliofemoralis is indicated by the presence of the lesser trochanter and trochanteric shelf on the anterolateral aspect of the proximal femur in Dinosauriformes. The lesser trochanter of Dinosauriformes marks the insertion of the tendon of M. iliotrochantericus caudalis and the trochanteric shelf marks the insertion of the tendon of M. iliofemoralis externus. On the lineage to Aves, the trochanteric shelf is reduced and M. iliofemoralis externus inserts on the femoral shaft on a site, which is homolog to the trochanteric shelf of Dinosauriformes. M. iliotrochantericus caudalis inserts on the Crista femoris, which is homolog to the lesser trochanter (Rowe 1986). In *Plateosaurus*, a lesser trochanter is present on the anterolateral aspect of proximal femur (Huene 1926). The trochanteric shelf is present in basal sauropodomorphs, such as *Saturnalia* (Langer 2003), but reduced in more derived sauropodomorphs (see Yates 2007). A marked rugosity on the femoral shaft posterodistally to the reduced trochanteric shelf indicates the insertion and thus presence of M. iliofemoralis externus. Hence, Mm. iliofemoralis externus and iliotrochantericus caudalis are present in sauropodomorphs, as in Aves (Fig. 5-1b, 5-2b, 5-4a). In *Plateosaurus*, M. iliofemoralis externus arises from the lateral ilium, dorsally to the acetabulum (level I' inference). M. iliotrochantericus caudalis arises anteriorly to the origin of M. iliofemoralis externus (level I' inference). M. iliofemoralis externus inserts on the lesser trochanter (level I inference) and M. iliotrochantericus caudalis inserts on the femoral shaft posterodistally to the lesser trochanter, marked by a rugosity (level II inference).

Musculi puboischiofemoralis internus 1 et 2

In basal Sauria, Mm. puboischiofemoralis internus 1 and 2 arise from the medial aspect of the ilium. Crocodiles share the origin of M. puboischiofemoralis internus 2 on the medial aspect of the ilium, whereas the origin of M. puboischiofemoralis internus 2 of crocodiles moved to the bodies and ventral aspect of the transverse processes of the posterior dorsal vertebrae. As the ventral pelvis was reduced on the lineage to birds (Hutchinson 2001), the origin of M. puboischiofemoralis internus 1 moved to the ventrolateral aspect ilium. With the reduction of the fossa in basal birds, the origin of M. puboischiofemoralis internus 1 moved further laterally to attach to the lateral iliac blade (Norell et al. 2001) and is referred to as M. iliofemoralis internus. The origin of M. puboischiofemoralis internus

2 moved to the lateroventral aspect of the ilium on the lineage to Aves and is separated into Mm. iliotrochantericus cranialis and medialis. The timing of the separation of M. puboischiofemoralis 2 into Mm. iliotrochantericus cranialis and medialis is uncertain, but probably close to the origin of the Ornithurae. The shift of M. puboischiofemoralis internus 2 from the posterior dorsal vertebrae might be correlated to the cranial extension of the preacetabular iliac blade on the lineage to Aves. In *Plateosaurus*, M. puboischiofemoralis internus 1 arises from the fossa on the anteroventral aspect of the ilium (level II' inference). The origin of M. puboischiofemoralis internus 2 in *Plateosaurus* is equivocal and therewith the presence of a single muscle (M. puboischiofemoralis internus 2) or two (Mm. iliotrochantericus cranialis and medialis) is equivocal (level II' inference). M. puboischiofemoralis internus 2 could have attached to the posterior dorsal vertebrae as in crocodiles or to the lateroventral aspect of the anterior ilium as in Aves. The insertion of M. puboischiofemoralis internus 1 in basal Sauria and extant archosaurs is on the medial aspect of the proximal femur. This insertion is retained in *Plateosaurus* (level I' inference). As in extant archosaurs, M. puboischiofemoralis internus 2 / Mm. iliotrochantericus cranialis and medialis of *Plateosaurus* inserts on the lateral aspect of the proximal (level I' inference) (Fig. 5-1b, 5-4a,b).

Musculus puboischiotibialis

The reconstruction of M. puboischiotibialis in *Plateosaurus* is equivocal. M. puboischiotibialis is present in basal Sauria and crocodiles. Being an important flexor of the thigh in basal Sauria (Walker 1973), M. puboischiotibialis is reduced in crocodiles and lost on the lineage to Aves. The reduction of this muscle is not reflected in the fossil record (see Dilkes 2000, Hutchinson 2002, Carrano and Hutchinson 2002). If present, M. puboischiotibialis of *Plateosaurus* arises from the lateral aspect of the obturator plate of the ischium and inserts on the posterior aspect of the proximal tibia (both origin and insertion level II' inference).

Musculus flexor tibialis internus 3

The number of parts of M. flexor tibialis internus varies in Sauria and extant archosaurs. From two parts in lepidosaurs, the number increases to four in crocodiles. On the lineage to Aves, M. flexor tibialis internus 1, 2, and 4 are lost. The reduction of these muscles, however, is not reflected in the fossil record (see Dilkes 2000, Carrano and Hutchinson 2002). The reconstruction of M. flexor tibialis internus 3 in *Plateosaurus* is unequivocal. Phylogenetic inference indicates that M. flexor tibialis internus 3 of *Plateosaurus* arises from the dorsal margin of the proximal ischium (level I inference), between the origin of Mm. ischiotrochantericus and adductor femoris 2 and inserts on the medioposterior aspect of the proximal tibia (level I' inference), next to the insertion of M. flexor tibialis externus and the origin of M. gastrocnemius medialis (Fig. 5-1b, 5-3b, 5-4a,b). The presence of Mm. flexor tibialis internus 1, 2, and 4 is equivocal (level II' inference). If present, Mm. flexor tibialis internus 1 and 2 originate on lateral aspect of the posterodorsal ilium and insertion on the posteroproximal tibia. M. flexor tibialis internus 4 is regarded here as an autopmorphy of crocodiles (see Table 5-1).

Musculus flexor tibialis externus

The presence of M. flexor tibialis externus is unequivocal in *Plateosaurus*. In crocodiles and Aves, M. flexor tibialis externus (M. flexor cruris lateralis pars pelvica) originates from the lateral aspect of the posterior ilium, posteriorly or posterodorsorally to the origin of M. iliofibularis. In *Plateosaurus*, the origin of M. flexor tibialis externus is reconstructed on the lateral aspect of the posterior ilium, posteriorly to the origin of M. iliofibularis (level I' inference). The insertion of M. flexor tibialis externus in *Plateosaurus* is on the medioposterior aspect of the proximal tibia (level I' insertion) (Fig. 5-1b, 5-3b, 5-4a,b) and is considered to be homologous to the insertion of this muscle crocodiles and Aves. The presence of M. flexor cruris lateralis pars accessoria in *Plateosaurus* is equivocal. The development of this muscle is not reflected in the fossil record or indicated by osteological correlates in *Plateosaurus* (level II' inference).

Musculus adductor femoris 1 et 2

In basal Sauria, M. adductor femoris consists of a single muscle arising from the Ligamentum puboischiadicum. With the reduction of the pelvic ligaments on the lineage to archosaurs (Hutchinson 2001b), the origin of M. adductor femoris moved to the adjacent ischium surface and was separated into two parts. The origin of M. adductor femoris 1 and 2, separated by the origin of M. puboischiofemoralis externus 3. With the retroversion of the pubis and the reduction of the obturator plate on the lineage to Aves, the origin of Mm. adductor femoris 1 and 2 moved posteriorly relatively to the acetabulum and are referred to as Mm. puboischiofemoralis pars lateralis and pars medialis. In *Plateosaurus*, the origin of M. adductor femoris is reconstructed on the lateral aspect of the obturator plate (level I' inference), probably separated by the origin of M. puboischiofemoralis externus 3. The insertion of M. adductor femoris in basal Sauria and extant archosaurs is on posterior aspect of the femur. In *Plateosaurus* Mm. adductor femoris 1 and 2 inserts on the posterior aspect of the femur (level I inference), separating the origin of M. femorotibialis medius and lateralis (Fig. 5-1b, 5-2b, 5-4a,b).

Musculi puboischiofemorales externii 1 et 2

M. puboischiofemoralis externus of basal Sauria consists of a single muscle. With the reduction of the pelvic ligaments on the lineage to archosaurs, M. puboischiofemoralis externus is separated into three parts. With the retroversion of the pubis and the reduction of the obturator blade on the lineage to Aves, M. puboischiofemoralis externus 3 is lost and the site of origin of M. puboischiofemoralis externus 1 and 2 moved posteriorly compared to crocodiles. The reduction of M. puboischiofemoralis externus is not reflected in the fossil record (see Dilkes 2000, Carrano and Hutchison 2002). The insertion of Mm. puboischiofemorales externii on the proximal femur of basal Sauria is retained in extant archosaurs. Indicated by the plesiomorphic condition of the pelvis of *Plateosaurus*, three parts of M. puboischiofemoralis externus is reconstructed (Fig. 5-1b, 5-3b, 5-4a). The origin of M. puboischiofemoralis externus 1 is reconstructed on the medial aspect of the pubis and M. puboischiofemoralis externus 2 arises from the lateral aspect of the pubis (level II' inference), as in crocodiles. M. puboischiofemoralis externus 3 arises on the lateral aspect of the ischial obturator plate (level II' inference), separating the origin of Mm. adductor femoris 1 and 2. Mm. puboischiofemorales externii insert on the greater trochanter (level I inference and level of II inference for PIFE3).

Musculus ischiotrochantericus

M. ischiotrochantericus (M. ischiofemoralis of Aves) is a very conservative muscle in extant archosaurs. It originates on the posterior margin of the ischium and inserts on the lateroposterior aspect of the proximal femur. According to the phylogenetic inference, M. ischiotrochantericus of *Plateosaurus* originates on posterior margin of the ischium (level I' inference) and inserts on lateroposterior margin of the proximal femur (level I' inference) (Fig. 5-1b, 5-2b, 5-4a,b).

Musculi caudofemoralis longus and brevis

In Sauria, M. caudofemoralis consists of two parts, Mm. caudofemoralis longus and brevis. M. caudofemoralis longus of basal Sauria and crocodiles arises from the bodies and ventral aspect of a varying number of caudal vertebrae. M. caudofemoralis longus inserts on the posterior aspect of the femur, on the fourth trochanter in crocodiles. M. caudofemoralis longus is the longest muscle in basal Sauria and crocodiles. With the reduction of the postsacral vertebral column on the lineage to Aves, the muscle is reduced. Gatesy (1990) noted that the transition of caudal vertebrates with fully developed neural spines and reduced neural spines marks the extension of M. caudofemoralis longus in extant and extinct archosaurs. According to this, M. caudofemoralis longus of *Plateosaurus* arises from the bodies and ventral aspect of the first 25 caudal vertebrae (level I inference). It inserts on the fourth trochanter (level I inference) (Fig. 5-1b, 5-2b). M. caudofemoralis brevis of basal Sauria and crocodiles arises from the posterior margin of the ilium. On the lineage to Aves, the origin of M. caudofemoralis brevis moved to the lateral aspect of the ilium. This transition is supposed to be marked by the presence of the brevis fossa (Romer 1923b, Gauthier 1986, Novas 1996), which first occurs in Dinosauriformes. M. caudofemoralis brevis arises from the brevis fossa on the posterior margin of the ilium (level II inference). Its insertion is on the medial depression of the fourth trochanter, medially to the insertion of M. caudofemoralis longus (level I inference) (Fig. 5-1b, 5-2b, 5-4a, b).

Musculus gastrocnemius lateralis et medialis

M. gastrocnemius of basal Sauria and crocodiles consists of two muscles, M. gastrocnemius lateralis and medialis. On the lineage to Aves, a third part of M. gastrocnemius, Pars intermedius m. gastrocnemius, evolved. M. gastrocnemius intermedius is probably a derivate of M. gastrocnemius pars medialis (Hutchinson 2002). The occurrence of M. gastrocnemius intermedius is, however, not reflected in the fossil record. In basal Sauria and extant archosaurs, M. gastrocnemius arises from the distal femur and proximal tibia. In basal Sauria and crocodiles, M. gastrocnemius forms the Fascia plantaris, which attaches to the calcaneum tuber, metatarsal V and on digit III or V. The presence of M. gastrocnemius intermedius in *Plateosaurus* is equivocal (level II' inference). M. gastrocnemius lateralis of *Plateosaurus* arises from the posterolateral aspect of the Condylus lateralis femoris, next to the origin of M. flexor digitorium longus (level I' inference), and M. gastrocnemius medialis arises from the posterolateral aspect of the proximal tibia, next to the insertion of M. flexor tibialis internus 3 and flexor tibialis externus (level I' inference). M. gastrocnemius of *Plateosaurus* inserts on the ventral aspect of the basis of metatarsal V and the basis of phalanx I of digits I – III/IV (level II' inference) (Fig. 5-2b, 5-3b, 5-4a,b).

Musculus flexor digitorium longus

M. flexor digitorium longus of basal Sauria and crocodiles consists of two heads, one arising from the lateral aspect of the Condylus lateralis femoris and the second head arising from the proximoposterior aspect of the proximal fibula. On the lineage to Aves, the site of origin of M. flexor tibialis longus moved from the femur to the tibia. The site of origin of the second head originates from the posterior fibula. The shift of M. flexor digitorium longus from the femur to the tibia probably relates to the re-orientation of the femur on the lineage to Aves. In *Plateosaurus*, the orientation of the femur suggests that the origin of M. flexor digitorium longus resembles basal Sauria and crocodiles (level I' inference). In basal Sauria and extant archosaurs, M. flexor digitorium longus inserts by tendon on the Tuberculum flexorium of the ungual of digits II – III/V and II – IV in Aves. In *Plateosaurus*, M. flexor digitorium longus inserts on the Tuberculum flexorium of the ungual of digits II – V (level I inference) (Fig. 5-2b, 5-3b, 5-4a).

Musculus flexor digitorium brevis

In basal Sauria and crocodiles, M. flexor digitorium brevis takes origin from the Fascia plantaris and inserts on the plantar aspect of the proximal phalanges of digits II – IV/V. With the reduction the of the Fascia plantaris on the lineage to Aves, M. flexor digitorium brevis is reduced. The reduction of the Fascia plantaris is marked by the reduction of the calcaneum tuber, metatarsal V and distal phalanges. The plesiomorphic condition of the pes of *Plateosaurus* suggest the presence of M. flexor digitorium brevis arising from the Fascia plantaris and inserting on the plantar aspect of the Tuberculum flexorium of the phalanges of digits II – V (level II' inference) (Fig. 5-3b).

Musculus flexor hallucis longus

In extant archosaurs, M. flexor hallucis longus arises from the posterodistal femur and inserts on the ventral aspect of the phalanges and ungual of digit I. In *Plateosaurus*, both origin and insertion retain the condition seen in extant archosaurs (level I' inference) (Fig. 5-3b, 5-4a).

Musculus extensor digitorium longus

In basal Sauria and crocodiles, M. extensor digitorium longus arises from the anterolateral aspect of the distal femur and from the anterior aspect of proximal tibia in Aves. In basal Sauria and crocodiles, M. extensor digitorium longus inserts on the basis of the dorsolateral aspect of a varying number of metatarsals. In Aves, M. extensor digitorium longus inserts on the unguals of digits II – IV. Phylogenetic inference indicates that M. extensor digitorium arises either of the anterolateral aspect of the femur as in basal Sauria or crocodiles or on the anterior aspect of the femur as in Aves (level I' inference). The insertion of M. extensor digitorium in *Plateosaurus* is equivocal (level II' inference) and depends on the assumption of the presence of M. extensor digitorium longus in *Plateosaurus* (see below). Considering the presence of M. digitorium brevis, M. extensor digitorium longus inserts on the base of the metatarsals II – IV. If M. extensor digitorium brevis is absent, M. extensor digitorium longus inserts on the dorsal aspect of the unguals digit II – IV. However, a conservative reconstruction with M. extensor digitorium brevis being present is preferred here (Fig. 5-2b, 5-3b, 5-4a).

Musculus extensor digitorium brevis

In basal Sauria and crocodiles, M. extensor digitorium brevis arises from the proximal tarsus and inserts on the extensor pits of the unguals of digit II – V (Gadow 1882, Kriegler 1961, Dilkes 2000). M. extensor digitorium brevis is absent in Aves. It is commonly assumed that M. extensor digitorium brevis is reduced on the lineage to Aves. The reduction, however, is not revealed in the fossil record. Dilkes (2000) argued that M. extensor digitorium brevis became fused with M. digitorium longus on the lineage to Aves. This corresponds to the shift of the insertion of M. extensor digitorium longus.

The reconstruction of M. extensor digitorium brevis in *Plateosaurus* requires a level II' inference. If present, M. extensor digitorium brevis arises from the anterior aspect of the proximal tarsus and inserts on the dorsal aspect of the ungual of digits II – V (Fig. 5-3b, 5-4a).

Musculus extensor hallucis longus

In basal Sauria and crocodiles, the origin of M. extensor hallucis longus is on the anterolateral aspect of the distal fibula and the insertion on the dorsal aspects of the phalanges of digit I (Gadow 1882). With the retroversion of digit I on the lineage to Aves, the origin of M. extensor hallucis longus moved to the anteromedial aspect of the proximal tarsometatarsus and the insertion moved posteriorly (Carrano and Hutchinson 2002). In *Plateosaurus*, M. extensor hallucis longus arises from the distal fibula (level II' inference) and inserts on the proximal metatarsal I (level I' inference), as indicated by the plesiomorphical condition of the pes (Fig. 5-3b).

Musculus tibialis anterior

The reconstruction of the origin of M. tibialis anterior in *Plateosaurus* is unequivocal. As in basal Sauria and extant archosaurs, M. tibialis anterior originates on the anterior aspect of the proximal tibia (level I' inference). An additional site of origin, as in Aves, is equivocal. In basal Sauria and extant archosaurs, M. tibialis anterior inserts in the dorsal aspect of the basis of a varying number of metatarsals or on the anterior aspect of the tarsometatarsus, respectively. In *Plateosaurus*, M. tibialis anterior inserts on the dorsal aspect of the basis of metatarsals I –II/III (level I' inference) (Fig. 5-3b, 5-4a).

Musculus pronator profundus

Based on phylogenetic inference alone, the presence of M. pronator profundus in *Plateosaurus* is equivocal. In basal Sauria and crocodiles, M. pronator profundus arises from the greater part of the posterior or medial aspect of the fibula, with an additional attachment on the tibia in squamates and crocodiles, and inserts on the plantar aspect of a varying number of metatarsals, sometimes with an additional insertion on the astragalus. On the lineage to Aves, M. pronator profundus is reduced. Hutchinson (2002) proposed that the reduction of this muscle correlates to the reduction of the distal fibula. The plesiomorphical condition of the crus of *Plateosaurus* suggests the presence of M.

pronator profundus (Fig. 5-3b, 5-4a). In *Plateosaurus*, M. pronator profundus originates on the posterior or posteromedial aspect of the fibula and lateral tibia (level II' inference) and inserts on the basis of the dorsal aspect of the metatarsals I – II/III (level II' inference).

Musculi fibularis longus et brevis

With exception of *Sphenodon*, M. fibularis of Sauria consists of two muscles. In squamates and crocodiles, M. fibularis longus arises from the anterior aspect of the fibula and inserts on calcaneum. M. fibularis brevis arises from the lateral aspect of the tibia and inserts of metatarsal V. On the lineage to Aves, the origin of M. fibularis longus moved to proximal tibia and its end-tendon fused with a digital flexor. M. fibularis brevis of Aves arises from the fibula and inserts on the tarsometatarsus. The site of origin of M. fibularis longus in *Plateosaurus* is either on the tibia or fibula (level I' inference) and inserts on the calcaneum (level I' inference). M. fibularis brevis of *Plateosaurus* attaches to the lateral fibula (level I' inference) and inserts on metatarsal V (level I' inference) (Fig. 5-3b).

Musculus popliteus

In basal Sauria and extant archosaurs, M. popliteus attaches to the facing aspects of the proximal tibia and fibula. In Aves, the attachment of M. popliteus on the tibia is correlated to the Fossa poplitea. The reconstruction of M. popliteus in *Plateosaurus* is unequivocal, with attachment to the facing aspects of the proximal tibia and fibula (Fig. 5-3b). The attachment of M. popliteus on the tibia is marked by a depression homolog to the Fossa poplitea in Aves (level I inference). The attachment on the fibula is a level I' inference.

Musculus interosseus cruris

The reconstruction of M. interosseus cruris in *Plateosaurus* is equivocal and cannot be solved by phylogenetic inference alone. In basal Sauria and crocodiles, M. interosseus cruris attaches to the facing aspects of the distal tibia and fibula (Gadow 1882, Kriegler 1961). With the reduction of the distal fibula on the lineage to Aves, M. interosseus cruris is reduced (Carrano and Hutchinson 2002, Hutchinson 2002). Considering the plesiomorphical condition of the crus in *Plateosaurus*, the presence of M. interosseus cruris attaching to the facing aspect of the distal tibia and fibula is reconstructed here (level II' inference) (Fig. 5-3b).

5.4.2 Reliability of muscle reconstructions in sauropods

Only few studies tried to quantify the correlation of soft-tissues and osteological features in terrestrial vertebrates. Bryant and Seymour (1990) noted that up to 80% of the soft-tissues of subrecent carnivores (*Ursidae* and *Canidae*) were associated with an osteological correlate. Not quantifying their observations, Nicholls and Russell (1985) noted that in the pectoral girdle and forelimb of extant archosaurs (*Alligator* and *Struthio*) only few muscles were correlated to an osteological feature. This observation is consistent with the findings of McGowan (1979, 1982, 1986), who noted that only 30% or even less of the appendicular muscles of birds (*Apteryx* and *Gallirallus*) are correlated to osteological features. Based on these findings, McGowan (1979) concluded that the myology of archosaurs cannot be reconstructed solely based on osteological features. Similarily, Jasinoski et al. (2006) noted that the correlation of muscles to osteological features in extant archosaurs is relatively low. According to the observation of Jasinoski et al. (2006), around 40% of the muscles attaching to the scapulacoracoid of birds are correlated to an osteological feature. The marked difference in the correlation of soft-tissues to osteological features in mammals and archosaurs was explained by a differing nature of attachment (see Bryant and Seymour 1990). This assumption, however, is mainly based on the statement of Romer (1927b), who argued that a tendinous attachment is commonly associated with a clear osteological correlate, whereas a fleshy attachment often leaves no marks on the bone surface. Bryant and Seymour (1990), however, noted that no correlation between tendinous or fleshy attachment and osteological correlates could be found. Bryant and Seymour (1990) suggested that there might be a correlation between carnivores and herbivores and the frequency of the presence of osteological correlates, with the soft-tissue – osteological feature correlation being higher in carnivores than in herbivores.

When reconstructing the myology of the pelvic girdle and hindlimb of *Tyrannosaurus rex* with the Extant Phylogenetic Bracket approach, Carrano and Hutchinson (2002) were able to correlate 74% of the reconstructed muscles to osteological features. This correlation is higher than in extant archosaurs and close to the correlation found in mammals. In the pelvic girdle and hindlimb of *Plateosaurus*, 39 muscles were reconstructed. 35% of the muscles of the pelvic girdle and hindlimb of *Plateosaurus* are correlated to an osteological feature. The remaining 65% of the muscles have no osteological correlate and were reconstructed solely based on phylogenetic inference. With a ratio of 35%, correlation in *Plateosaurus* equals that of other extant archosaurs, but is markedly lower than in *Tyrannosaurus*. Following the argument of Bryant and Seymour (1990), the difference in the correlation might be related to the fact that *Plateosaurus* is a herbivore (or omnivore?), whereas *Tyrannosaurus* is a carnivore. Unfortunately, Bryant and Seymour (1990) were not able to test their hypothesis: why is a higher correlation found in carnivores? The *Tyrannosaurus* material used by Carrano and Hutchinson (2002), FMNH PR 2801, is of exceptionally good preservation, whereas the material of *Plateosaurus* used here, SMNS 13200, is less well preservation. Before the correlation of soft-tissues and osteological correlates can be discussed in extinct archosaurs, a detailed discussion of the correlation has to be carried out for extant archosaurs and other terrestrial tetrapods.

Sauropods are characterized by the reduction of osteological correlates. This reduction is expressed in form of the reduction of "soft"-correlates, such as rugosities, pits, and in form of the reduction of prominent structures. The trochanteric shelf is reduced in basal non-sauropodan sauropodomorphs, the lesser trochanter and the brevis fossa are reduced in basal sauropods (see Yates 2007). Coombs (1978) noted that the reduction of osteological correlates of muscles is found in all large-sized animals and has to be regarded as an adaptation to a graviportal locomotor habit. The reason, however, remains unclear. Pauwels (1956) showed how the development of the attachment of the muscle on the bone surface influences the stress pattern developed in the bone: the presence of a tubercle on the bone surface modifies the stress pattern and increases the high peak forces. In order to reduce high peak forces applied on the bone, prominent structures have to be reduced and the attachment area of the muscle on the bone has to be enlarged.

With the reduction of the osteological correlates, the direct identification of muscles decreases and the number of muscles, which have to be reconstructed solely based on phylogenetic inference increases. This fact is problematic for one reason: sauropods have no living descendants. In contrast to theropods, in which osteological adaptations and the associated soft-tissue arrangement (reduction, development or modification of muscles) can be traced on the lineage to Aves, osteological adaptations and the associated soft-tissue arrangement cannot be traced likewise, because of the lack of an extant ascendant. The attempt to reconstruct the muscles of the flexor cruris group and adductor muscles in *Plateosaurus* has revealed these difficulties. Whereas the timing of the reduction of these muscle groups is not reflected in the fossil record on the lineage to Aves, the absence of these muscles in extant birds allows to discuss potential evolutionary scenarios. The evolution of certain groups of muscles on the lineage to sauropods is highly speculative: the presence, absence or modification has to be discussed.

The exceptionally large body size of sauropods suggests special adaptations in the pelvic girdle and hindlimb to resist the enormous body mass. The dorsoanterior elongation of the iliac blade (*Kotasaurus* and more derived sauropods; Yadagiri 2001), the reduction of the lesser trochanter (*Thecodontosaurus* and more derived sauropodomorphs; e.g. Yates 2007) and trochanteric shelf (in sauropodomorphs more derived than *Saturnalia*; e.g. Yates 2007) and the columnar limb posture (*Isanosaurus* and more derived sauropods; see Chapter 6) as well as the semi-plantigrade pes posture (*Vulcanodon* and more derived sauropods; e.g. Wright 2005) are, amongst others, indicative of the modification of the muscle architecture and lever arms of the muscles. The reduction of the laterodistal phalanges of the pes (in *Shunosaurus* and more derived sauropods; e.g. Allain and Aquesbi 2008) is correlated with the reduction of the associated muscles in order to reduce the relative mass of the distal limb (Chapter 6). Christiansen (1997) noted that the locomotion of sauropods resembles in most aspects the locomotion of large-sized mammals, such as elephants; the specific details of the locomotion of sauropods, however, were unlike any extant tetrapod. Due to the lack of osteological correlates, tracing the nature of the changes in the myology of sauropods associated with the modifications in the functional morphology provides difficulties and increases the degree of speculation.

5.5 CONCLUSIONS

Presented here is the first complete reconstruction of the myology of the pelvic girdle and limb of a sauropodomorph, using the Extant Phylogenetic Bracket approach. It has been shown that usage of the Extant Phylogenetic Bracket approach considerably decreases the level of speculation concerning the presence of absence of muscles and provides information on the arrangement of the muscles of the pelvic girdle and hindlimb of *Plateosaurus*. In total, 39 muscles were reconstructed. Of these, 35% were correlated to osteological features, such as tubercles, pits, ridges, or rugosities. The reconstruction of 65% of the muscles is solely based on phylogenetic inference. 51% of the muscles of the pelvic girdle and limb of *Plateosaurus* are reconstructed with a level I or I' inference. In other words, these muscles share the same attachment in the extant outgroup (crocodiles), extant ingroup (birds) and *Plateosaurus*. 41% of the muscles of the pelvic girdle and limb of archosaurs underwent a transformation from the outgroup to the ingroup, which required a level II of II' inference. Major modifications in the myology of the pelvic girdle and hindlimb of archosaurs are related to the retroversion of the pubis and the development of a slender ischium on the lineage to Aves, which is reflected in the shift or loss of muscles originally attaching to these elements. The development of the tibiotarsus on the lineage to Aves in association with the reduction of the distal fibula, and the development of the tarsometatarus on the lineage to Aves are related to the modification of the origin and insertion of the muscles attaching to these elements. These changes in the muscle architecture probably reflect functional changes from the semi-erect hindlimb posture of the obligate quadrupedal crocodiles to the obligate bipedal and striding birds and the associated changes in the posture of the limb elements and of the biokinematics in the hindlimb. Both the modification of the pelvis and the modification of the distal limb occur close to recent birds and associated modifications in the myology are most probably not reflected in the myology of sauropodomorph dinosaurs.

The reliability of soft-tissue reconstructions is dependent on the correlation of soft-tissues to osteological features. With a ratio of 35% soft-tissue – osteological feature correlation in *Plateosaurus*, the non-sauropodan sauropodomorph lies within the range of extant archosaurs. On the lineage to sauropods, however, these osteological correlates are reduced, so that fewer muscles can be reconstructed with confidence. The reliability of the soft-tissue reconstructions in sauropods based in phylogenetic inference alone is relatively low. This is problematic, because novelties in the arrangement of the pelvic girdle and hindlimb of sauropods as adaptation to larger body size have to be expected. The nature of this evolution cannot be traced with confidence inferring the muscles solely based on phylogenetic inference. An extrapolatory approach based on biomechanics has to be applied to improve our knowledge on the myology of sauropods and potential adaptations to large size.

Chapter 6

Evolution of the graviportal locomotor habit in sauropod dinosaurs

6.1 INTRODUCTION

Ever since their first description, the exceptional large body size of sauropods and the related biomechanical challenges to support this enormous body size on land have been of great interest to scientists. Amongst others, the extensive cartilaginous caps on the limb bones indicated by roughened articular surfaces not seen in extant terrestrial megaherbivores were thought as being not suitable for supporting a sauropod's body mass on land (Osborn 1898, Hatcher 1901, Hay 1910, Lull 1915), so that an aquatic or amphibious lifestyle was reconstructed for them (e.g. Phillips 1871, Marsh 1883, 1884, Cope 1884, Hatcher 1901, Matthew 1903, Huene 1922, 1929, Wiman 1929). Evidence that sauropods were able to support their body mass on land comes from different sources. Bird (1941) and later other authors (e.g. Thulborn 1990, Farlow 1992, Lockley et al. 1994, Wright 2005) were able to assign tracks and trackways to sauropods that clearly demonstrate that their trackmaker walked on land. Sauropod tracks and trackways further show that their trackmakers were obligate quadrupeds and restricted to slow walking (Thulborn 1982), achieving speeds of 3 – 6 km/hr (Alexander 1976, 1985). Additionally, sauropodan ichnofossils reveal that their trackmakers had a pad on the heel as seen in extant elephants (e.g. Coombs 1975, Wright 2005). Furthermore, Bakker (1971) and Coombs (1975) demonstrated that osteological, physiological, and geological evidences are indicative for a terrestrial habitat of sauropods, and Alexander (1971) and Hokkanen (1986) calculated that the limb bones and the musculature were well suited to support a sauropod's body mass on land.

Being the largest tetrapods that ever lived on land, sauropods had to evolve a graviportal locomotor habit with numerous osteological adaptations in the postcranium to resist their enormous body mass. The graviportal locomotor habit in sauropods includes: i) columnar limbs, ii) relatively elongated femur, iii) increased limb bone robusticity, iv) increased eccentricity of the femoral midshaft, v) reduced muscle insertion sites, vi) broad metatarsus, vii) reduced pedal phalanges, viii) entaxonic pes, and ix) relatively elongated forelimbs (Coombs 1978, Carrano 1999, 2001, Wilson and Carrano 1999, Yates 2004). The graviportal locomotor habit is not only reflected in the osteology of sauropods, but also in the locomotor function. It is commonly thought that the obligate quadrupedal locomotor posture of sauropods is a result of their large size. This holds also true for the reduced limb flexion (see Carrano 2005). Christiansen (1997) argued that sauropods share with other large terrestrial tetrapods the propodial retraction of the hindlimb. The concentration of the adaptations of the graviportal locomotor habit in the pelvic girdle and hindlimbs reflects their great functional importance. The pelvic girdle is connected to the vertebral column via sacral ribs, and serves as an anchor point for the hindlimbs to transmit the body mass (Rasskin-Gutman and Buscalioni 2001). In quadrupedal dinosaurs, up to 80% of the body mass has to be supported by the pelvic girdle and hindlimbs (Alexander 1985).

Regardless of the great functional importance of the pelvic girdle and hindlimbs in sauropods in general and of the graviportal locomotor habit in particular, the morphofunctional evolution of their pelvic girdle and hindlimb has not been studied yet. This is of particular interest, because sauropods are descendants from the only clade of miniaturized archosaurs (Hutchinson 2006), the Dinosauromorpha, and studying the morphofunctional evolution of the pelvic girdle and hindlimb of dinosauromorphs on the lineage to sauropods will considerably improve our understanding of the biology of those. For this purpose, I offer here the first study of the evolution of the graviportal locomotor habit of dinosauromorphs on the lineage to sauropods in order to gain insights into i) the pattern of the evolution of the adaptations to the graviportal locomotor habit, ii) the correlation of the evolution of the graviportal locomotor habit and body size and iii) the biomechanical reasons which require the evolution of the graviportal locomotor habit.

Table 6-1. Source of data (literature and specimens) for archosauriforms used in this study. Accession numbers denote specimens examined by the author first hand; other data were obtained from the literature.

Material	Source
Archosauriformes	
Erythrosuchus africanus	BMNH R3592:
Euparkeria capensis	SAM 6047, SAM 6049; Ewer 1965;
Ornithodira	
Scleromochlus taylori	BMNH R3146, R3556, R3557, R 4323/4; Woodward 1907, Huene 1914, Benton 1999;
Dinosauromorpha	
Dromomeron romeri	Irmis et al. 2007a;
Lagerpeton chanarensis	UPLR 06, PVL 4619, 4625; Romer 1971, 1972b, Bonaparte 1984, Arcucci 1986, Sereno and Arcucci 1993;
PVL 3870	PVL 3870; Bonaparte 1975, Sereno and Arcucci 1994;
Dinosauriformes	
Lewisuchus admixtus	UPLR 01;
Agnosphytys cromhallensis	Fraser et al. 2002;
Eucoelophysis baldwini	Ezcurra 2006;
Marasuchus lilloensis	PVL 3871; Romer 1971a, 1972b, Bonaparte 1975, Sereno and Arcucci 1994, Fechner and Rauhut 2006;
Pseudolagosuchus major	PVL 4629, UPLR 53; Arcucci 1987, Novas 1989;
Sacisaurus agudoensis	Ferigolo and Langer 2006;
Silesaurus opolensis	Dzik 2003, Dzik and Suljei 2007;
Ornithischia	
Heterodontosaurus tucki	Santa Luca 1980;
Lesothosaurus diagnosticus	BMNH RUB 17;
Pisanosaurus mertii	Casamiquela 1967, Bonaparte 1976;
Scelidosaurus harrisonii	BMNH R1111, R6704;
Saurischia	
Chindesaurus bryansmalli	Long and Murry 1995;
Eoraptor lunensis	PVSJ 512; Sereno et al. 1993;
Guaibasaurus candelariensis	MCN-PV 2355, 2356; Bonaparte et al. 1999, 2007, Langer and Benton 2006;
Herrerasaurus ischigualastensis	PVL 2566, 373, PVSJ 104, 464; Reig 1963, Novas 1992, 1993, Sereno and Novas 1993;
Staurikosaurus pricei	MCZ 1669; Colbert 1970, Galton 1977, 2000;
Streptospondylus altdorfensis	MNHN 8605, 8607-8609, 9645;
Theropoda	
Ceratosaurus nasicorni	YPM 4681;
Coelophysis bauri	UCMP 129618, AMNH 7223, 7224, 7228 - 7230, 7232; Colbert 1989;
Dilophosaurus wetherilli	UCMP 37302; Welles 1984;
Elaphrosaurus bambergi	MB Gr.S. 38-40;
Liliensternus liliensterni	MB.R.2175.7;
Segisaurus halli	UCMP 32101;
Sinraptor dongi	IVPP 10600; Currie and Zao 1993;
Syntarsus rhodiensis	BMNH R 10071, R9584 (cast);
Sauropodomorpha	
Anchisaurus polyzelus	YPM 208, 209, 1883; Galton 1976, Yates 2004;
Antetonitrus ingenipes	BP/1/4952; Yates and Kitching 2003;
Barapasaurus tagorei	ISI R 50; Jain et al. 1977
Blikanasaurus cromptoni	SAM K403; Galton and Heerden 1985, 1998;
Camelotia borealis	BMNH R2870-2872c, R2874b-c, R2878a; Galton 1985, 1998;
Cetiosaurus oxoniensis	Upchurch and Martin 2002, 2003;
Coloradisaurus brevis	Bonaparte 1978;
Efraasia minor	SMNS 12667, 12668; Huene 1907-1908, Galton 1973;
Eucnemesaurus fortis	Van Hoepen 1920, Heerden 1979, Yates 2006;
Euskelosaurus brownii	Haughton 1924, Heerden 1979;
Gongxianosaurus shibeiensis	He et al. 1998;
"Gyposaurus" sinensis	IVPP V.26; Young 1941b;
Isanosaurus attavipachi	Buffetaut et al. 2000;
Jingshanosaurus xinwaensis	Zhang and Yang 1994
Klamelisaurus gobiensis	IVPP V.9492
Kotasaurus yamanpalliensis	21/SR/PAL; Yadagiri 1988, 2001;
Lamplughsaura dharmaramensis	Kutty et al. 2007;
Lessemsaurus sauroides	Pol and Powell 2007;
Lufengosaurus huenei	IVPP V15; Young 1941a;
Mamenchisaurus hochuanensis	GCC V 20401; Young and Chao 1972, Russell and Zheng 1993;
Massospondylus carinatus	SAM 5135; Van Hoepen 1920, Cooper 1981;
Melanorosaurus readi	NM QR1551, SAM-PK-3449, 3450; Haughton 1924; Heerden and Galton 1997, Galton et al. 2005;

Table 2-1. continued

Mussaurus patagonicus	PVL 4068; Bonaparte and Vince 1979;
Pantydraco caducus	Kermack 1984, Yates 2003b, Galton and Yates 2007;
Patagosaurus farisi	PVL 4170; Bonaparte 1986;
Plateosauravus cullingworthi	SAM 3340, 3341, 3343, 3349, 3603; Haughton 1924, Heerden 1979;
Plateosaurus engelhardti	SMNS 13200, GPIT 1; Huene 1926;
Plateosaurus gracilis	Huene 1907-08, 1915, Yates 2003b;
Plateosaurus ingens	Galton 1986;
Riojasaurus incertus	PVL 3808, ULPR 56; Bonaparte 1972;
Ruehleia bedheimensis	MB RvL 1; Galton 2001;
Saturnalia tupiniquim	MCP 3844-PV, MCP 3845-PV; Langer et al. 1999, Langer 2003, Langer and Benton 2006;
Shunosaurus lii	IVPP T5401; Dong et al. 1983, Zhang 1988;
Tazoudasaurus naimi	Allain et al. 2004, Allain and Aquesbi 2008;
Thecodontosaurus antiquus	BMNH R1539-1545, R1547-1549, R1552, R15389, R49984, R49984; YPM 2192, 2193; Huene 1907-1908, Benton et al. 2000;
Unaysarus tolentinoi	UFSM 11069; Leal et al. 2004;
Volkheimeria chubutiensis	PVL 4077; Bonaparte 1979;
Vulcanodon karibaensis	Raath 1972, Cooper 1984;
Yunnanosaurus huangi	Young 1942;

6.2 MATERIAL AND METHODS

A wide range of material has been examined in order to study the osteology of the pelvic limb of Dinosauromorpha on the lineage to Sauropoda. Measurements were taken with a digital caliper or measuring-tape and documented with photographs and drawings. When direct access to specimens was not possible, supplement data and measurements were taken from literature (see Table 6-1 for source of data).

The phylogenetic hypotheses of Ezcurra (2006) for the interrelationships of dinosauromorphs and basal saurischians and Yates (2007) for the interrelationships for sauropodomorphs were adopted as an evolutionary framework for this study. *Eoraptor lunensis* and the herrerasaurids are regarded here as basal saurischians with *Eoraptor* being placed basal to the herrerasaurids. *Dromomeron romeri* is a non-dinosauriform dinosauromorph more derived than *Lagerpeton chanarensis* (Irmis et al. 2007a). Fechner and Rauhut (2006) have shown that *Marasuchus lilloensis* consists of two taxa, with PVL 3871 being *Marasuchus* and PVL 3870 being a non-dinosauriform dinosauromorph nested between *Lagerpeton* and *Dromomeron* (Fig. 6-1).

Estimating the body size of extinct animals always provides difficulties. This holds particularly true for extinct animals in which the bauplan differs significantly from that of extant animals. With their markedly elongated necks and tails, the body size of sauropodomorphs is difficult to

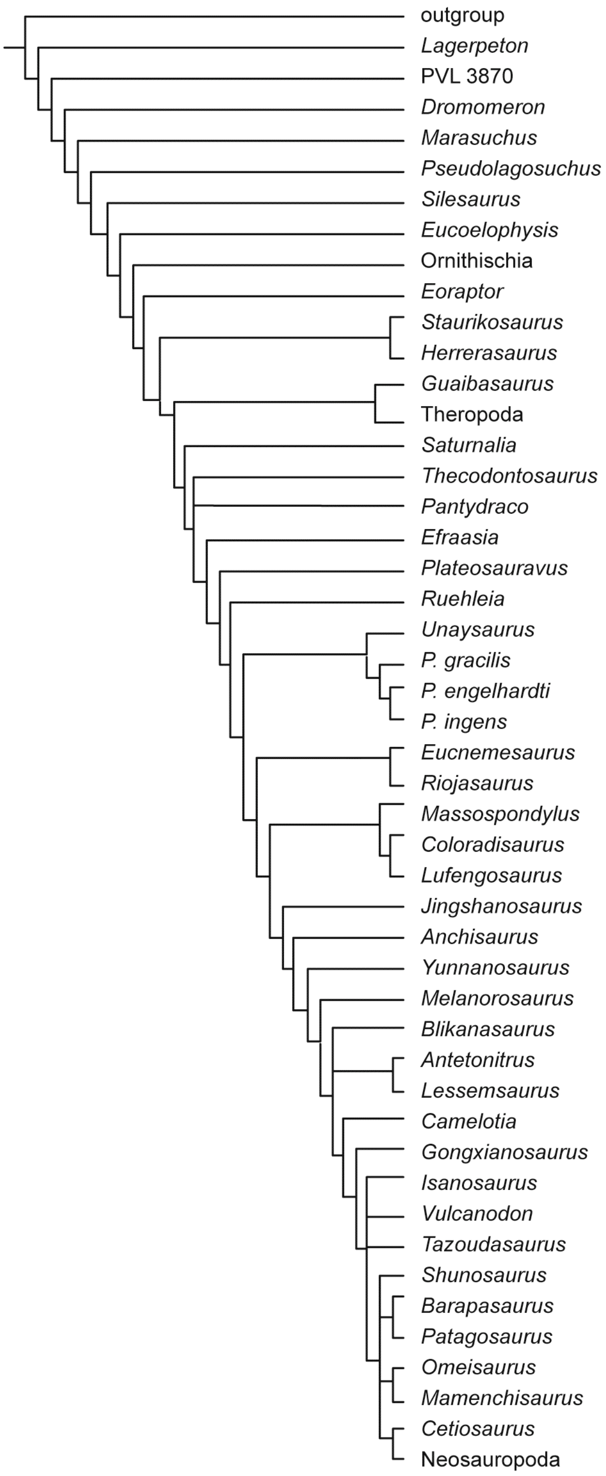

Figure 6-1. Phylogenetic framework of Dinosauromorpha on the lineage to Sauropoda used in this study; mainly based on Ezcurra (2006) and Yates (2007).

measure and to compare with other taxa. Thus, the body mass is used here as a proxy for the evolution of the body size. Body mass estimations differ greatly in different studies dealing with this

Table 6-2. Terminology and homology of the muscles of the pelvic girdle and hindlimb of extinct archosaurs. The terminology of the muscles of the pelvic girdle and hindlimb of extinct archosaurs is based on Gadow (1882), Romer (1923b). The homology of the muscles of the pelvic girdle and hindlimb of extinct archosaurs is based on Romer (1923b, 1927a, 1942) and Rowe (1986).

Muscles	Crocodylia	Aves	Muscles
M. iliotibialis 1	IT1	IA	M. iliotibialis anterior
M. iliotibialis 2	IT2	IP	M. iliotibialis posterior pars preacetabuaris
M. iliotibialis 3	IT3	IP	M. iliotibialis posterior pars postacetabularis
M. ambiens 1	AMB1	AMB	M. ambiens
M. ambiens 2	AMB2	—	—
M. femorotibialis externus	FMTE	FMTL	M. femorotibialis lateralis
M. femorotibialis internus	FMTI	FMTIM	M. femorotibialis intermedius
—	—	FMTM	M. femorotibialis medius
M. iliofibularis	ILFIB	ILFIB	M. iliofibularis
M. iliofemoralis	IF	IFE	M. iliofemoralis externus
—	—	ITC	M. iliotrochantericus caudalis
M. puboischiofemoralis internus 1	PIFI1	IFI	M. ischiofemoralis internus
M. puboischiofemoralis internus 2	PIFI2	ITCR	M. iliotrochantericus cranialis
—	—	ITM	M. iliotrochantericus medius
M. puboischiotibialis	PIT	—	—
M. flexor tibialis internus 2	FTI2	—	—
M. flexor tibialis internus 1	FTI1	—	—
M. flexor tibialis internus 3	FTI3	FCM	M. flexor cruris medius
M. flexor tibialis internus 4	FTI4	—	—
M. flexor tibialis externus	FTE	FCLP	M. flexor cruris lateralis p. posterior
—	—	FCLA	M. flexor cruris pars anterior
M. adductor femoris 1	ADD1	PIFM	M. puboischiofemoralis medius
M. adductor femoris 2	ADD2	PIFL	M. puboischiofemoalis lateralis
M. puboischiofemoralis externus 1	PIFE1	OL	M. obturatorius lateralis
M. puboischiofemoralis externus 2	PIFE2	OM	M. obturatorius medialis
M. puboischiofemoralis externus 3	PIFE3	—	—
M. ischiotrochantericus	ISTR	ISF	M. ischiofemoralis
M. caudofemoralis longus	CFL	CFC	M. caudofemoralis pars caudalis
M. caudofemoralis brevis	CFB	CFP	M. caudofemoralis pars pelvica
M. gastrocnemius lateralis	GL	GL	M. gastrocnemius longus
—	—	GIM	M. gastrocnemius intermedius
M. gastrocnemius medialis	GM	GM	M. gastrocnemius medius
M. flexor digitalis longus	FDL	FDL	M. flexor digitorium longus
M. flexor digitalis brevis	FDB	FDB	M. flexor digitorium brevis
M. flexor hallucis longus	FHL	FHL	M. flexor hallucis longus
M. tibialis anterior	TA	TC	M. tibialis cranialis
M. extensor digitorium longus	EDL	EDL	M. extensor digitorium longus
M. extensor digitorium brevis	EDB	—	—
M. extensor hallucis longus	EHL	EHL	M. extensor hallucis longus
M. fibularis longus	FL	FL	M. fibularis longus
M. fibularis brevis	FB	FB	M. fibularis brevis
M. pronator profundus	PP	—	—
M. popliteus	POP	POP	M. popliteus
M. interosseus cruris	IC	—	—

topic. This does not only relate to the problems concerning estimates of body mass of extinct animals with a unique bauplan differing from all extant animals, but is also due to differing methods applied. In order to analyze the evolution of the body size, not specific values were used – because of the differing body mass estimates – but dinosauromorphs were categorized in logarithmic size classes 0 – 10 kg; 10 – 100 kg; 100 – 1000 kg; 1000 – 10 000 kg; >10 0000 kg, each of which subdivided into thirds (1= 0 – 4 kg; 2= 4 – 7 kg; 3= 7 – 10 kg; 4= 10 – 40 kg; 5= 40 – 70 kg; 6= 70 – 100kg; 7= 100 – 400 kg; 8= 400 – 700 kg; 9= 700 – 1000 kg; 10= 10000 – 4000 kg; 11= 4000 – 7000 kg; 12= 7000 – 10 000 kg; 13= 10 000 – 40 000). Body mass estimates for dinosaurs used here were mainly based on Peczkis (1994) and Seebacher (2001). Paul (1988) served as source of information on body mass estimates of non-dinosaurian dinosauromorphs. The body mass of taxa not included in the studies listed above was estimated by comparison of the femoral length and femoral robusticity. The femoral robusticity is inferred from the mediolateral diameter of the femoral midshaft – femoral length ratio (FML/F).

The myology of the pelvic girdle and hindlimb was reconstructed according to the Extant Phylogenetic Bracket approach *sensu* Witmer (1995). Dinosauromorpha are bracketed by crocodiles (outgroup) and birds (ingroup). In order to gain information on the myology of the pelvic girdle and hindlimb, crocodiles and birds were dissected with focus on the myology of the pelvic girdle and hindlimb. Additional information on the myology of the pelvic girdle and hindlimb of crocodiles and birds were gained from Gadow (1882), Romer (1923b), McGowan (1979), Nickel et al. (2003) and Gangl et al. (2004). The hypothesis of homology of the myology of archosaurs follows Romer (1923b, 1927a, 1942), Rowe (1986), and Carrano and Hutchinson (2002). The nomenclature of the myology of the pelvic girdle and hindlimb follows Romer (1922, 1923b) for non-aves Sauria and Vanden Berge and Zweers (1993) for Aves (Table 6-2). The discussion of the presence – absence and arrangement of the muscles of the pelvic girdle and hindlimb of dinosauromorphs follows Fechner (Chapter 5).

Longitudinal bone curvature is defined to represent the moment arm of the axial component of force acting on a bone, which causes this force to exert a bending moment about the bone's midshaft. Longitudinal bone curvature is considered to be a function of body size: with increasing body size, the femoral curvature is supposed to decrease. The femoral curvature is used here as an indicator for the hindlimb posture (e.g. Biewener 1983). Bone curvature (ς) is measured as the moment arm (X) against chord length ($2L$) (Fig. 6-2)

$$\varsigma = X/2L \times 100$$

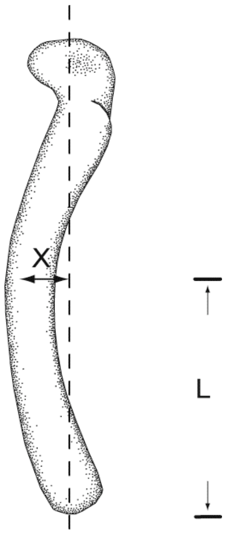

Figure 6-2. Diagrammatic representation of the method for determining the femoral curvature, ς. Bone curvature was calculated as X/2L x 100 to compare the curvature of bones of different size dinosauromorphs.

Ratios of the forelimb length to hindlimb length (FL/HL) and hindlimb length to trunk length (HL/T) are commonly used to reconstruct the locomotor posture. A short trunk and relatively short forelimbs are regarded as an indicator for obligate bipedal locomotion (e.g. Galton 1970), whereas the elongation of the trunk and the elongation of the forelimbs are regarded as an adaptation to obligate quadrupedal locomotion in sauropods (e.g. Barrett and Upchurch 2007). Although no explicit ratios have been articulated to reconstruct the locomotor posture from the FL/HL ratio, a FL/HL ratio of 0.5 or less is regarded here as adaptation to an obligate bipedal locomotor posture. A FL/HL ratio of 0.65 or more is regarded as an adaptation to an obligate quadrupedal locomotion. Facultative bipedal locomotion is poorly defined. However, facultative bipedal locomotion is commonly regarded as intermediate between the extremes of obligate bipedal and obligate quadrupedal locomotion and thus characterized by a FL/HL ratio of 0.5 to 0.65. According to Galton (1970), a HL/T ratio of 0.69 to 0.9 indicates an obligate quadrupedal locomotor posture. A HL/T ratio of 0.95 to 1.15 indicates an adaptation to a facultative bipedal locomotor posture and a HL/T ratio of 1.22 to 1.9 is indicative for an obligate quadrupedal locomotor posture. Dinosauromorphs on the lineage to sauropods often lack material of the manus. In order to generate the forelimb to hindlimb ratio, the length of the manus has to be estimated. In completely known forelimbs of dinosauromorphs on the lineage to sauropods, the length of the metacarpal II equals 20 – 30 % of the length of the ulna. Additional information on the locomotor posture is gained from the development of the manus and the ichnofossil record.

Institutional abbreviations: **AMNH**, American Museum of Natural History, New York; **BMNH**, British Museum of Natural History, London; **BPI**, Bernard Price Insitute for Palaeontological Research, Johannesburg; **GCC**, Geological College of Chengdu, Chengdu; **GPIT**, Institut für Geologie und Paläontologie, Tübingen; **ISI**, Indian Statistical Institute, Calcutta; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; **MACN**, Museo Argentina de Ciencas Naturales 'Bernardino Rivadavia', Buenos Aires; **MB**, Museum für Naturkunde, Berlin; **MCN**, Museu de Ciências Naturais, Fundacão Zoobotãnica, Porto Alegre; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge; **MNHN**, Muséum National d'Histoire Naturelle, Paris; **NM**, National Museum, Bloemfontein; **PVL**, Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán; **PVSJ**, Museo de Ciencas Naturales, Universidad Nacional de San Juan, San Juan; **SAM,** South African Museum, Cape Town; **SR**, Geological Survey of India, Hyderabad; **UCMP**, University California Museum of Paleontology, Berkeley; **UPLR**, Museo de Paleontología, Universidad Provincial de La Rioja, La Rioja; **YPM**, Yale Peabody Museum, New Haven.

6.3 RESULTS

6.3.1 Evolution of body size

Basal dinosauromorphs, such as *Lagerpeton*, PVL 3870, *Dromomeron*, and *Marasuchus* are exceptionally small, not only if compared to dinosaurs, but generally for archosaurs (Hutchinson 2006). The limb bones are very slender and the femoral length is 77 mm or less. The body mass of those taxa has been estimated with a few hundred g (Paul 1988; see Table 6-3). No formal body mass estimates have been provided for more derived non-dinosaurian dinosauromorphs, such as *Pseudolagosuchus* and *Silesaurus*. By comparing the body size of *Pseudolagosuchus* (F= 113 mm) and *Silesaurus* (F=129.3) with basal dinosauromorphs and basal saurischians, a body mass of 4 – 7 kg is suggested. With a femoral length of 158 mm and an estimated body mass of 7 – 10 kg, *Eoraptor* is the smallest known basal saurischian. The femoral length of *Guaibasaurus* is 215 mm and the femoral length of *Staurikosaurus* is 228 mm and both have an estimated body mass of 10 – 40 kg. *Herrerasaurus* is exceptionally large for a basal saurischian (F= 345 mm). This is also reflected in its body mass, which was estimated with 100 – 400 kg. With a femoral length of 157 mm, the basal sauropodomorph *Saturnalia* is relatively small. Due to its body size, which is similar to *Eoraptor*, a body mass of 7 – 10 kg is estimated, although the FML/F of 9.9 indicates that *Saturnalia* was more robust than *Eoraptor* with an FML/F of 8.2. In sauropodomorphs more derived than *Saturnalia*, the body size increased rapidly. Whereas *Thecodontosaurus* is characterized by a femoral length of 255 mm and a body mass of 70 – 100 kg, the body mass of *Efraasia* is estimated with 400 – 700 kg and a femoral length of 492 mm. With few exceptions, non-sauropodan sauropodomorphs more derived than *Efraasia* had a body mass of 1000 – 4000 kg and the femoral length ranges between 560 – 680 mm (Table 6-3). *Massospondylus*, *Anchisaurus*, and *Yunnanosaurus* are of smaller body size. *Massospondylus* has a femoral length of 355 mm and an estimated body mass of 100 – 400 kg. *Anchisaurus* is of exceptionally body size for a sauropodomorph, with a femoral length of 218 mm. The body mass of *Anchisaurus* was estimated with 10 – 40 kg. With a femoral length of 540 mm, the body mass of *Yunnanosaurus* is estimated with 700 – 1000 kg. No formal body mass estimates of basal sauropods (*sensu* Yates 2007) have been generated so far. Dependent on the femoral length assumed (F=544 – 578 mm), the basalmost sauropod *Blikanasaurus* is estimated with a body mass of 700 – 1000 kg or 1000 to 4000 kg. *Antetonitrus* and *Lessemsaurus* are estimated with a body mass of 1000 – 4000 kg. Peczkis (1994) estimated the body mass of *Camelotia* with 1000 – 4000kg. The overall comparison of *Camelotia* with other sauropodomorphs (Table 6-3) suggests that a body mass of 4000 – 7000 kg has to be estimated. With exception of *Isanosaurus*, all basal sauropods more derived than *Camelotia* are characterized by a body mass of 10 000 – 40 000 kg. *Isanosaurus* is relatively small for a basal sauropod with an estimated body mass of 1000 – 4000 kg.

Looking at Table 6-3 shows that the body size of dinosauromorphs on the lineage to sauropods evolved more or less gradually. Based on the phylogenetic hypotheses used here, the body mass of *Massospondylus*, *Anchisaurus*, *Yunnanosaurus*, and *Isanosaurus* was reduced secondarily.

Table 6-3. Body mass estimates of dinosauromorphs used in this study; based on Paul (1988), Peczkis (1994), and Seebacher (1999). Data taken from sources in Table 6-1. F= femoral length, FML/F= femoral mediolateral midshaft diameter/femoral length. FML/F was used as indicator for the femoral robusticity.

Taxon	F	FML/F	Peczkis 1994	Seebacher 1999	Paul 1988	this study
Lagerpeton	76,7 mm	7,6	–	–	0.45 kg	0-4 kg
PVL 3870	42,2 mm	7,9	–	–	0.091 kg	0-4 kg
Dromomeron	64,3 mm	13,3	–	–	–	0-4 kg
Marasuchus	55,1 mm	9,1	–	–	0.18 kg	0-4 kg
Pseudolagosuchus	113 mm	8,1	–	–	–	4-7 kg
Silesaurus	129,3 mm	9,6	–	–	–	4-7 kg
Eoraptor	157,8 mm	8,2	7-10 kg	–	–	7-10 kg
Herrerasaurus	345 mm	8,5	100-400 kg	–	–	100-400 kg
Staurikosaurus	228 mm	–	10-40 kg	–	–	10-40 kg
Guaibasaurus	214 mm	8,9	–	–	–	10-40 kg
Saturnalia	157 mm	9,9	–	–	–	7-10 kg
Thecodontosaurus	255 mm	–	70-100 kg	–	–	70-100 kg
Efraasia	495 mm	–	–	–	–	400-700 kg
Plateosauravus	760 mm	9,3	1000-4000 kg	–	–	1000-4000 kg
P. engelhardti	680 mm	13,7	1000-4000 kg	–	–	1000-4000 kg
Riojasaurus	625 mm	17,5	1000-4000 kg	–	–	1000-4000 kg
Massospondylus	355 mm	12,6	100-400 kg	–	–	100-400 kg
Lufengosaurus	577 mm	–	1000-4000 kg	–	–	1000-4000 kg
Anchisaurus	218 mm	11,6	10-40 kg	–	–	10-40 kg
Yunnanosaurus	540 mm	–	700-1000 kg	–	–	700-1000 kg
Melanorosaurus	560 mm	–	1000-4000 kg	–	–	1000-4000 kg
Blikanasaurus	544-578 mm [e]	–	–	–	–	700-4000 kg
Antetonitrus	794 mm	18,5	–	–	–	1000-4000 kg
Lessemsaurus	776 mm	–	–	–	–	1000-4000 kg
Camelotia	1040 mm	13,5	1000-4000 kg	–	–	4000-7000 kg
Gongxianosaurus	1164 mm	23,2	–	–	–	10 000-40 000 kg
Isanosaurus	760 mm	16	–	–	–	1000-4000 kg
Vulcanodon	1100 mm	14,6	10 000-40 000 kg	–	–	10 000-40 000 kg
Tazoudasaurus	1230 mm*	16,2	–	–	–	10 000-40 000 kg
Shunosaurus	1200 mm	14,1	10 000-40 000 kg	4 793,5 kg	–	10 000-40 000 kg
Patagosaurus	1530 mm	–	10 000-40 000 kg	–	–	10 000-40 000 kg
Cetiosaurus	1615 mm	–	10 000-40 000 kg	–	–	10 000-40 000 kg
Mamenchisaurus	–	–	10 000-40 000 kg	18 169,7 kg	–	10 000-40 000 kg
Omeisaurus	1310 mm	–	10 000- 40 000 kg	11 796 kg	–	10 000-40 000 kg
Neosauropoda	–	–	10 000-40 000 kg	–	–	10 000-40 000 kg

[e] femoral length estimated using the length of the distal limb (tibia + mt III).

* femoral length as estimated by Allain and Aquesbi (2008).

6.3.2 Osteological evolution of the pelvic girdle and hindlimb

With the exception of PVL 3870, *Marasuchus* (PVL 3871) and *Herrerasaurus* (PVL 2655, but also see PVSJ 461), the ilium of dinosauromorphs and basal saurischian is anteroposteriorly longer than high dorsoventrally. The preacetabular process is of subtriangular shape and small. The postacetabular process is also small, but more robust than the preacetabular process. The iliac blade retains this form in non-sauropodan sauropodomorph dinosaurs. In basal sauropods, the preacetabular process is modified. First, it is anteriorly expanded in basal sauropods, such as *Kotasaurus* (21/SR/PAL; Yadagiri 2001) and *Shunosaurus* (IVPP V.9065; Dong et al. 1983), and then dorsally expanded to form a lobe-shaped ilium in neosauropods. This development goes along with the reduction of the postacetabular process.

The acetabulum of *Lagerpeton* (PVL 4619; Sereno and Arcucci 1993) and *Marasuchus* (PVL 3871) is closed and of moderate depth, with its oval outline posterodorsally inclined. Compared to the femoral head, the acetabulum of both *Lagerpeton* (Sereno and Arcucci 1993) and *Marasuchus* is relatively large. In both *Lagerpeton* and *Marasuchus* the supraacetabular crest on its anterodorsal margin is poorly developed. Sereno and Arcucci (1994) argued for a "semi-perforated" acetabulum in *Marasuchus*. However, their reconstruction is mainly based on the pelvis of PVL 3870, in which the medial wall of the acetabulum is fragmented, as noted before by Bonaparte (1975). The left acetabulum is articulated with the femur, so that only the medial aspect of the acetabulum is visible. Furthermore, the elements of the left site of the pelvis of PVL 3871 are anteroposteriorly deformed (compare Fig. 5a and 5b in Sereno and Arcucci 1994). Most likely, the acetabulum of *Marasuchus* PVL 3871 is not originally "semi-perforated", but this impression is due to the anteroposterior compression of the pelvis. The acetabulum of *Silesaurus* remains closed. However, additionally to its smaller size relatively to the femoral head, it appears to be considerably deeper than the acetabulum of basal dinosauromorphs (Dzik 2003). Also, the supraacetabular crest on the anterodorsal margin of the acetabulum of *Silesaurus* is developed as a prominent laterally projecting crest (Dzik 2003). In the herrerasaurids, the acetabulum is fully open, whereas the acetabulum of *Guaibasaurus* (MCN-PV 2355; Bonaparte et al. 1999, 2007) is only semi-perforated. A prominent supraacetabular crest overhangs the acetabulum of basal saurischian dinosaurs anterodorsally. A semi-perforated acetabulum is also known in *Saturnalia* (MCN 3844-PV, MCN 3845-PV; Langer 2003). In all sauropodomorphs more derived than *Saturnalia*, the acetabulum is fully open. The perforation of the acetabulum is associated with the elongation of the pubic and ischial peduncle. Whereas the ischial peduncle remains small in sauropodomorph dinosaurs and is even reduced in sauropods to a knob-like structure, a consistent trend to elongate the pubis peduncle is observed towards sauropod dinosaurs. The supraacetabular crest is reduced in sauropodomorphs and lost in sauropods.

However, in basal sauropods, such as *Lessemsaurus* (Pol and Powell 2007), the supraacetabular crest is still present. A brevis fossa first occurs in Dinosauriformes, namely *Silesaurus* (Dzik 2003). Whereas the brevis fossa is present in the eusaurischian *Guaibasaurus* (MCN-PV 2355; Bonaparte et al. 1999, 2007) and *Saturnalia* (MCN 3844-PV, MCN 3845-PV; Langer 2003), it appears to be absent in *Eoraptor* (PVL 512) and the herrerasaurids (PVL 2566, MCZ 1669; Colbert 1970, Novas 1993). The development of a brevis shelf in the herrerasaurids has been discussed controversially. Novas (1993) noted a furrow on the posterior iliac blade of *Herrerasaurus* (PVL 2655), which is sometimes identified as the brevis shelf (e.g. Langer 2004). This furrow, however, appears to be a preservational artifact rather than representing an osteological structure. When Colbert (1970) first described the remains of *Staurikosaurus*, he missed that a bone fragment is attached to the medial aspect of the posterior blade of the left ilium and reconstructed the posterior shelf of the iliac blade with a convex outline (see Colbert 1970, Langer 2004). The brevis shelf of *Staurikosaurus* is originally slightly concave, as shown in the right ilium (Galton 2000). The brevis fossa is present in *Guaibasaurus* (MCN-PV 2355; Bonaparte et al. 1999, 2007) and retained in all non-sauropodan sauropodomorphs including basal sauropods *sensu* Yates (2007), but is lost in sauropod dinosaurs more derived than *Vulcanodon* (Raath 1972, Cooper 1984).

The pubis of dinosauromorphs and basal saurischians is variable in orientation and length. In *Lagerpeton* (PVL 4619) and *Silesaurus* (Dzik 2003), the pubis is directed anteroventrally, corresponding to a propubic condition. In most dinosauromorphs and basal saurischians, however, the pubis has a mesopubic orientation, with the pubis directed ventrally. In *Saturnalia* (MCN 3844-PV, MCN 3845-PV; Langer 2003) and sauropodomorphs, the pubis is of a propubic condition. The propubic condition is retained in most sauropods. The pubis of basal dinosauriforms and basal saurischians forms a broad pubic apron, which is oriented in the transverse plane. In eusauropods, the shaft is less apron-like, twisted to face more posteromedially and has an enlarged pubic foramen proximally.

The ischium of dinosauromorphs is a conservative element, which can roughly be subdivided into an obturator plate anteroproximally and a stab-like ischial shaft. The obturator blade is prominent in *Lagerpeton* (PVL 4619), *Eoraptor* (PVSJ 512) and *Herrerasaurus* (PVL 2655; Novas

1993). Towards sauropods, the obturator plate is reduced and the ischial shaft becomes more robust.

With exception of the basal dinosauromorphs *Lagerpeton* (PVL 4619), *Dromomeron* (Irmis et al. 2007a), PVL 3870, and *Marasuchus* (PVL 3871), the femur is straight in anterior and sigmoidally curved in lateral view. In basal dinosauromorphs, the femoral shaft is also sigmoidally curved in anterior view. The femoral shaft of basal dinosauromorphs and basal saurischians is subrounded to subtriangular in cross section (e.g. *Lagerpeton* PVL 4619; *Herrerasaurus* PVL 2655). In the lineage to sauropods, the femoral shaft is anteroposteriorly flattened to form an eccentric circumference in *Isanosaurus* (Buffetaut et al. 2000) and more derived sauropods. The femoral head is deflected from the transverse plane to 50 – 70° in anterior direction in dinosauromorphs and basal saurischians. Towards sauropods, the deflection from the transverse plane is reduced to around 45° in anterior direction in basal non-sauropodan sauropodomorphs to the orientation in the transverse plane in more derived forms, such as *Lufengosaurus* (IVPP V.15; Young 1941a) and sauropods. Towards sauropods a consistent trend to increase the robustness of the femur and to reduce the sigmoid curvature in lateral view is observed. In *Gongxianosaurus* (He et al. 1993) and more derived sauropods, the femur is completely straight in lateral view. A prominent lesser trochanter and a trochanteric shelf are present anterolaterally on the proximal femoral shaft of Dinosauriformes (Novas 1996). The exception is *Guaibasaurus*, in which the trochanteric shelf is reduced (MCN-PV 2355; Bonaparte et al. 1999, 2007). The trochanteric shelf is present in *Saturnalia* (MCN 3844-PV, MCN 3845-PV; Langer 2003) but absent in all more derived sauropodomorph dinosaurs (Yates 2007). The lesser trochanter is reduced to a low ridge, but present in all "prosauropods" and basal sauropods, with the exception of *Gongxianosaurus* (He et al. 1998) and *Isanosaurus* (Buffetaut et al. 2000). In *Shunosaurus* (IVPP V.9065; Dong et al. 1983, Zhang 1988) and more derived sauropods, the lesser trochanter is lost. A fourth trochanter on the posteromedial side of the femoral shaft is plesiomorphically present in dinosauromorphs. In basal representatives of this clade, the fourth trochanter is located at the proximal end of the femoral shaft. Towards sauropods, the fourth trochanter moves to a more distal position on the posterior femoral shaft. In most eusauropods, the fourth trochanter is located at approximately the mid-shaft of the femur. Furthermore, the trochanter is developed as a stout flange in basal sauropodomorphs, but reduced to a stout, but low ridge in sauropods. In the latter, a prominent groove is usually present medial to the trochanter on the medial side of the femoral shaft.

Tibia and fibula of dinosauromorphs and basal saurischians are slender elements of subequal length. The anterior aspect of the proximal tibia of Dinosauriformes displays an anterior projecting process, the cnemial crest (Novas 1996). The cnemial crest becomes more prominent, but also more slender towards sauropod dinosaurs. In *Shunosaurus* (IVPP V.9065; Dong et al. 1983, Zhang 1988) and more derived eusauropods, the cnemial crest projects anterolaterally. In mamenchisaurids, the orientation of the cnemial crest is almost entirely laterally (GCC V 20401; Young and Chao 1972, Allain and Aquesbi 2008). The distal end of the tibia in saurischian dinosaurs is of rectangular (*Herrerasaurus* PVL 2566), oval (*Staurikosaurus* MCZ 1669), or subtriangular (*Guaibasaurus* MCN-PV 2355) shape. A groove on the laterodistal aspect of the tibia accommodates the ascending process of the astragalus. In sauropodomorph dinosaurs, the distal end of the tibia is subtriangular in outline. Towards sauropods the tibia becomes more robust and somewhat flattened anteroposteriorly. The fibula is a strap-like bone with expanded proximal and distal ends. A prominent Tuberculum m. iliofiubularis fibulae is present on the anterolateral or lateral side of the fibula in all saurischians, and this character is retained in sauropodomorphs. As in the case of the tibia, the fibula becomes more robust on the lineage towards sauropods. With the reduction of the calcaneum within eusauropod dinosaurs, the fibula becomes slightly elongated compared to the tibia and the distal end is expanded medially to articulated with the astragalus.

The proximal tarsus of *Lagerpeton* and *Marasuchus* is robust and dorsoventrally relatively high. In *Lagerpeton*, the proximal tarsus is co-ossified to form an astragalocalcaneum (PVL 4619, UPLR 06; Romer 1971a, Sereno and Arcucci 1993, Chapter 3). In *Marasuchus* (PVL 3871), the proximal tarsus appears not to be co-ossified. As in *Lagerpeton* (UPLR 06), the astragalus overlaps the calcaneum dorsally in *Dromomeron* (Irmis et al. 2007a). The ascending process on the astragalus of *Lagerpeton* (Sereno and Arcucci 1993), *Dromomeron* (Irmis et al. 2007a), and *Marasuchus* (PVL 3871) is placed on the lateral surface, providing little space for the articulation with the fibula. The first occurrence of the typical peg-and-socket articulation between the astragalus and calcaneum of Dinosauriformes, including the basal saurischians, is recorded in *Pseudolagosuchus* (PVL 4629; Arcucci 1987). The medially developed peg of the subtriangular-shaped calcaneum articulates with a facet on the lateroventral astragalus. On the posterior surface of the calcaneum of *Pseudolagosuchus* and more derived dinosauriformes a posterolateral process is developed (Arcucci 1987, Novas 1989, 1993, Dzik 2003, Langer 2003). The astragalus of basal saurischians is robust and of rectangular shape. The ascending process is located at the medial half of its dorsal aspect. The calcaneum of basal saurischian dinosaurs is a flat disc of subtriangular shape in medial view. A keel on the medial aspect of the calcaneum slides into a groove of the dorsolateral aspect of the astragalus to form a keel-and-groove articulation. Both astragalus and calcaneum retain their form and function in non-sauropodan sauropodomorphs and sauropods. In eusauropods the form of the astragalus becomes wedge-shaped.

Elements of the distal tarsus are rarely preserved in dinosauromorphs. Only distal tarsal 4 is known in *Lagerpeton* (Chapter 3, *contra* Arcucci 1986, Sereno and Arcucci 1993). The distal tarsal 4 of *Lagerpeton* (PVL 4619) is anteroposteriorly elongated, waisted, and subdivided in an anterior plate and a posterior heel. In *Herrerasaurus* (PVSJ 373), distal tarsal 3 and 4 are preserved. Distal tarsal 3, or the medial distal tarsal, is of oval shape and dorsoventrally flattened. The distal tarsal 3 covers the metatarsals III and parts of metatarsal II. Distal tarsal 4, or the lateral distal tarsal, of *Herrerasaurus* resembles roughly the distal tarsal 4 of *Lagerpeton*. It is anteroposterior elongated, although less pronounced than in *Lagerpeton*. The waisted shape is adumbrated. The posterior heel is present, but less developed than in *Lagerpeton*. The distal tarsus of basal saurischian dinosaurs consists of two disc-like elements, distal tarsal III and IV. Distal tarsals III is capping the proximal end of metatarsal III and distal tarsal IV is capping the proximal end of metatarsal IV. With exception of basal sauropod dinosaurs, both distal tarsal III and IV are reduced or lack ossification in sauropods.

The pedes of *Lagerpeton* (PVL 4619, UPLR 06; Romer 1971, Arcucci 1986, Sereno and Arcucci 1993) and *Marasuchus* (PVL 3871) are, despite of significant differences, relatively similar. The metatarsus of *Lagerpeton* and *Marasuchus* is considerably elongated and subequal in length to the phalangeal series. The metatarsus is bundled and the metatarsals are slender. The pes of *Lagerpeton* is ectaxonic, with digits IV>III>II. The phalangeal series of *Lagerpeton* is 2-3-4-5-0. The proximal metatarsals are relatively to each other parallel. The pes of *Marasuchus* shows that it is incipient

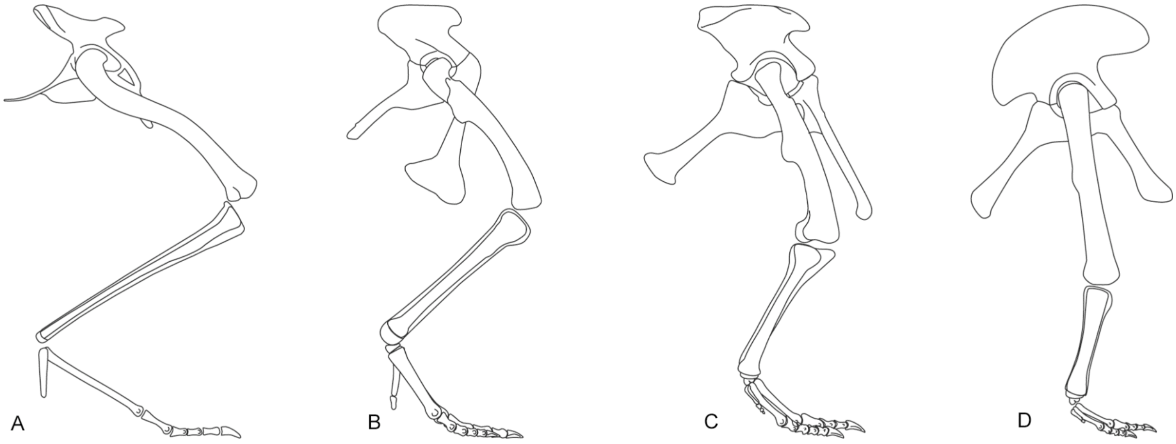

Figure 6-3. Diagram showing the hindlimb proportions of A, *Lagerpeton*, B, *Herrerasaurus*, C, *Plateosaurus* and D, *Shunosaurus*. All in right lateral view. Not to scale.

mesaxonic, with digit III being slightly longer than digit II and digit IV. The phalangeal series is ?-?(2preserved)-?(2 preserved)-?(4 preserved)-0. In *Silesaurus* (Dzik 2003) and basal saurischians (Reig 1963, Novas 1993, Bonaparte et al. 1999, 2007, Langer 2003), the pes is mesaxonic, with digit III being considerably longer than digit II and digit IV. The phalangeal series is slightly shorter than the metatarsus in *Silesaurus* according to Dzik (2003) ?-3-4-5-0. The pes of basal saurischians is mesaxonic with a bundled metatarsus. Metatarsal III is the longest element of the metatarsus and metatarsals II and IV are subequal in length. Metatarsal I is considerably reduced in length and less robust compared to metatarsals II-IV, and metatarsal V is reduced to a bone splint. In *Herrerasaurus*, a rudimentary phalanx is preserved. The phalangeal formula of basal saurischians is 2-3-4-5-0 (Langer 2004) and in *Herrerasaurus* 2-3-4-5-1 (PVL 2655; Novas 1993). Towards sauropods, the metatarsals and phalanges increase in robustness. The relative length of metatarsal III and IV is reduced so that metatarsals I-V iare subequal in length. With exception of basal eusauropods, such as *Shunosaurus* (IVPP V. 9065; Dong et al. 1983, Zhang 1988), the mesaxonic pes is modified to an ectaxonic pes, with metatarsus II being the longest element of the metatarsus. The phalanges of the lateral digits are reduced so that the phalangeal formula of basal sauropods is 2-3-4-2-1. In some basal sauropods, such as *Shunosaurus* and *Mamenchisaurus* (GCC V 20401; Young and Chao 1972), the phalangeal formula is 2-3-4-3-1. The metatarsus of sauropod dinosaurs is not bundled but broad and spreading.

Table 6-4. Hindlimb proportions of Dinosauromorpha. Data taken from sources in Table 6-1. F, femur; mt III, metatarsal III, FL, femoral length, HL, hindlimb length; T, trunk.

taxon	tibia / F	tibia + mt III (IV) / F	mt III(IV) / F	FL / HL	HL / T	femoral curvature
Lagerpeton	1.17	1.79	0.62	–	–	6.3
PVL 3870	1.18	1.85	0.66	–	–	4.2
Marasuchus	1.27	2	0.73	~0.50†	–	5.2
Pseudolagosuchus	1.11	–	–	–	–	8.4
Silesaurus	0.89	1.38	0.38	~ 0.95†	0.7-0.8	4.9
Eoraptor	1.02	1.5	0.49	0.47	1.0-1.1	–
Herrerasaurus	0.91	1.39	0.48	0.49	–	9.4
Staurikosaurus	1.08	–	–	–	1.6-1.8	10.3
Guaibasaurus	0.99	1.43	0.44	0.53	–	11.1
Saturnalia	1.01	1.54	0.53	041-0.42†	1.1	13.4
Pantydraco#	0.97	1.46	0.48	–	–	–
Efraasia	0.88	1.3	0.42	0.55	0.8-0.9	16.1
P. engelhardti	0.73	1.08	0.35	0.56	0.9-1.0	8.6
Riojasaurus	0.77	1.13	0.36	0.6	0.82	8.2
Massospondylus	0.84	1.24	0.40	0.53	1.2	8.2
Lufengosaurus	0.69	1.07	0.39	0.46	–	–
Anchisaurus	0.66	1.11	0.45	0.63	0.8-0.9	5.6
Yunnanosaurus	0.83	1.2	0.37	0.48	–	–
Melanorosaurus	0.73	1.13	0.26	0.57-0.59†	–	–
Blikanasaurus	0.65-0.69 e	0.9-1.0	–	–	–	–
Antetonitrus	0.64	0.89	0.25	0.84	–	4.9
Gongxianosaurus	–	–	–	0.70-0.75*	–	0
Vulcanodon	0.57	0.79	0.22	0.75-0.77†	0.9-1.0	0
Shunosaurus	0.57	0.71	0.15	0.68	1.0-1.1	0
Cetiosaurus	0.58	–	–	–	–	0

[e] Femoral length estimated using the length of the distal limb
† Forelimb length estimated on the basis of the length fof the ulna
*based on Barrett and Upchurch (2007)
[#] juvenile

The limb bones of basal dinosauromorphs, such as *Lagerpeton*, PVL 3870, *Dromomeron* and *Marasuchus* are very slender, as indicated by the FML/F (Table 6-3). With increasing body size, the robusticity of the limb bones increased. In sauropods, all elements of the limb bones – femur, crus, and metatarsals – are very robust.

6.3.3 Hindlimb proportions

Basal dinosauromorphs, such as *Lagerpeton* (Fig. 6-3a), PVL 3870, and *Marasuchus* are characterized by a short femur and an elongated distal limb (tibia + metatarsal III). In *Lagerpeton*, the distal limb to femur ratio is 1.79, in PVL 3870 1.85 and in *Marasuchus* 2.0. The elongation of the distal limb is thus most marked in the metatarsus, which equals more than 45% of the length of the tibia (Table 6-4).

	Lagerpeton		*Herrerasaurus*		*Plateosaurus*		*Shunosaurus*	
	origin	insertion	origin	insertion	origin	insertion	origin	insertion
IT1	dorsal margin of preacetbular process, anterior to IT2	anteroproximal tibia	dorsal margin of lateral ilium, anterior to IT2, dorsally to ITC	lateral cnemial crest	dorsal margin of lateral preactabular process, anterior to IT2, dorsally to ITC	lateral cnemial crest	dorsal and anterior margin of of lateral ilium, anterior to IT2, dorsally to ITC PIFI1-2?	lateral (or anterior) cnemial
IT2	dorsal margin of lateral ilium, between IT1 and IT3, dorsally to IF	anteroproximal tibia	dorsal margin of lateral ilium, between IT1 and IT3, dorsally to IFE	lateral cnemial crest	dorsal margin of lateral ilium, between IT1 and IT3, dorsally to IFE	lateral cnemial crest	dorsal margin of lateral ilium, between IT 1 and IT3, dorsally to IFE	lateral (or anterior) cnemial
IT3	dorsal margin of lateral ilium, between IT3 and IFE, dorsally to ILFIB	anteroproximal tibia	dorsal margin of lateral ilium, between IT2 and FTE, dorsally to ILFIB	lateral cnemial crest	dorsal margin of lateral ilium, between IT2 and FTE, dorsally to ILFIB	lateral cnemial crest	dorsal margin of lateral ilium. between IT2 and FTE, dorsally to ILFIB	lateral (or anterior) cnemial
AMB	pubic tubercle	anteroproximal tibia	pubic tubercle	lateral cnemial crest	pubic tubercle	lateral cnemial crest	anteroproximal pubis	lateral (or anterior) cnemial
ILFIB	posterolateral ilium, posterior to FTE, posterodorsally to IF	Tuberculum m. Iliofibularis fibulae	posterolateral ilium, posterior to FTE, posterior to posterodorsally to IFE	Tuberculum m. Iliofibularis fibulae	posterolateral ilium, posterior to FTE, posterior to posterodorsally to IFE	Tuberculum m. Iliofibularis fibulae	posterolateral ilium, between FTE and IFE	Tuberculum m. Iliofibularis fibulae
IF/IFE	lateral ilium, dorsally to acetabulum, ventrally to IT2	lateral femur	lateral ilium, between ITC and ILFIB	lesser trochanter	lateral ilium, between ITC and ILFIB	lesser trochanter	lateral ilium, between ITC and ILFIB	anterolateral proximal shaft
ITC	–	–	lateral iliac blade, ventraly to IT1, anterior to IFE	trochanteric shelf	lateral iliac blade, ventrally to IT1, between PIFI1-2 and IFE	anterolateral proximal shaft, distally to IFE	lateral iliac blade, ventrally to IT1, between PIFI1-2 and IFE	anterolateral proximal shaft, distally to IFE
PIFI1	preacetabular fossa	proximomedial femur	preacetabular fossa	proximomedial femur	preacetabular fossa	proximomedial femur	preacetabular fossa	proximomedial femur
PIFI2	preacetabular fossa	proximomedial femur	preacetabular fossa	proximomedial femur	preacetabular fossa	proximomedial femur	preacetabular fossa	proximomedial femur
FMTE	anterior femoral shaft	proximoanterior tiba	anterior femoral shaft	lateral cnemial crest	anterolateral femoral shaft	lateral cnemial crest	anterlateral femoral shaft	lateral (or anterior) cnemial
FMTIM	–	–			anteromedial femoral shaft	lateral cnemial crest		lateral (or anterior) cnemial
FMTI	posterior femoral shaft	proximoanterior tiba	posterior femoral shaft	lateral cnemial crest	posterior femoral shaft	lateral cnemial crest		lateral (or anterior) cnemial
PIT	obturator blade of lateral ischium	proximposterior tibia	–	–	–	–	–	–
FTI3	ischial tuberosity	proximposterior tibia	ischial tuberostiy	proximposterior tibia	ischial tuberosity	proximposterior tibia	ischial tuberosity	proximoposterior tibia
FTE	posterodorsal ischium	proximal tibia	posterodorsal ischium	proximal tibia	posterodorsal ischium	proximal tibia	posterodorsal ischium	proximal tibia
ADD1	obturator blade of lateral ischium	posterodistal femur	obturator blade of lateral ischium	posterodistal femur	obturator blade of lateral ischium	posterodistal femur	obturator blade of lateral ischium	posterodistal femur
ADD2	lateral ischial shaft	posterodistal femur	lateral ischial shaft	posterodistal femur	lateral ischial shaft	posterodistal femur	lateral ischial shaft	posterodistal femur
PIFE1	anteroposterior pubic apron	greater trochanter	anteroposterior pubic apron	greater trochanter	anteroposterior pubic apron	greater trochanter	anteroposterior pubic apron	greater trochanter
PIFE2	anteroposterior pubic apron	greater trochanter	anteroposterior pubic apron	greater trochanter	anteroposterior pubic apron	greater trochanter	anteroposterior pubic apron	greater trochanter
PIFE3	obturator blade of lateral ischium	greater trochanter						
ISTR	medial ischium	posterolateral aspect on proximal femur	medial ischium	posterolateral aspect on proximal femur	medial ischium	posterolateral aspect on proximal femur	medial ischium	posterolateral aspect on proximal femur
CFL	bodies and ventral aspect of transverse processes and hemapohyses of ? caudal vertebrae	medial to fourth trochanter	bodies and ventral aspect of transverse processes and hemapohyses of ? caudal vertebrae	medial to fourth trochanter	bodies and ventral aspect of transverse processes and hemapohyses of the first 35 caudal vertebrae	medial to fourth trochanter	bodies and ventral aspect of transverse processes and hemapohyses of ? caudal vertebrae	medial to fourth trochanter
CFB	posterior ilium	medial to fourth trochanter, distally to insertion of M. caudofemoralis longus	brevis fossa	medial to fourth trochanter, distally to insertion of M. caudofemoralis longus	brevis fossa	medial to fourth trochanter, distally to insertion of M. caudofemoralis longus	posterolateral ilium	medial to fourth trochanter, distally to insertion of M. caudofemoralis longus
GL	posterolateral aspect of Condylus lateralis femoris	metatarsal V, basis of phalanx of digits I-IV	posterolateral aspect of Condylus lateralis femoris	metatarsal V, basis of phalanx of digits I-IV	posterolateral aspect of Condylus lateralis femoris	metatarsal V, basis of phalanx of digits I-IV	posterolateral aspect of Condylus lateralis femoris	metatarsal V, basis of phalanx of digits I-IV
GM	posterolateral tibia	metatarsal V, basis of phalanx of digits I-IV	posterolateral tibia	metatarsal V, basis of phalanx of digits I-IV	posterolateral tibia	metatarsal V, basis of phalanx of digits I-IV	posterolateral tibia	metatarsal V, basis of phalanx of digits I-IV
FDL	Condylus lateral femoris	terminal phalanx of each digit	Condylus lateral femoris	terminal phalanx of each digit	Condylus lateral femoris	terminal phalanx of each digit	Condylus lateral femoris	terminal phalanx of each digit
FHL	posterodistal femur	plantar aspect of phalanges and ungual of digit I	posterodistal femur	plantar aspect of phalanges and ungual of digit I	posterodistal femur	plantar aspect of phalanges and ungual of digit I	posterodistal femur	plantar aspect of phalanges and ungual of digit I
FDB	plantar aponeurosis	plantar aspect of each digit	plantar aponeurosis	plantar aspect of each digit	plantar aponeurosis	plantar aspect of each digit	plantar aponeurosis	plantar aspect of each digit
EDB	anterodistal fibula	proximodorsal phalanx of each digit	anterodistal fibula	proximodorsal phalanx of each digit	anterodistal fibula	proximodorsal phalanx of each digit	anterodistal fibula	proximodorsal phalanx of each digit
EHL	distal fibula	base of metatarsal I	distal fibula	base of metatarsal I	distal fibula	base of metatarsal I	distal fibula	base of metatarsal I
EDL	posterolateral aspect of distal femur and proximal tibia	lateral aspect of basis of metatarsals I-V	posterolateral aspect of distal femur and proximal tibia	lateral aspect of basis of metatarsals I-V	posterolateral aspect of distal femur and proximal tibia	lateral aspect of basis of metatarsals I-V	posterolateral aspect of distal femur and proximal tibia	lateral aspect of basis of metatarsals I-V
TA	cnemial crest	dorsal metatarsal I	cnemial crest	dorsal metatarsal I	cnemial crest	dorsal metatarsal I	cnemial crest	dorsal metatarsal I
PP	posterior or posteriomedial tibia	basis of metatarsals I-II/III	posterior or posteriomedial tibia	basis of metatarsals I-II/III	posterior or posteriomedial tibia	basis of metatarsals I-II/III	posterior or posteriomedial tibia	basis of metatarsals I-II/III
POP	fossa and proximomedial tibia	proximomedial fibula	fossa and proximomedial tibia	proximomedial fibula	fossa and proximomedial tibia	proximomedial fibula	fossa and proximomedial tibia	proximomedial fibula
IC	laterodistal tibia	medial fibula	laterodistal tibia	medial fibula	laterodistal tibia	medial fibula	laterodistal tibia	medial fibula
FL	tibia	dorsal aspect of metatarsal V	tibia	dorsal aspect of metatarsal V	tibia	dorsal aspect of metatarsal V	tibia	dorsal aspect of metatarsal V
FB	tiba	dorsal aspect of metatarsal V	tibia	dorsal aspect of metatarsal V	tibia	dorsal aspect of metatarsal V	tibia	dorsal aspect of metatarsal V

With increasing body size, the length of the distal limb is relatively reduced. Thus, the relative reduction of the distal limb is most marked by the reduction of the relative length of the metatarsus. In *Pseudolagosuchus* and *Staurikosaurus*, the femur is still shorter than the tibia, with a tibia to femur ratio of 1.12 in *Pseudolagosuchus* and 1.08 in *Staurikosaurus*. In *Silesaurus* and *Herrerasaurus*, the femur, however, is considerably longer than the tibia, with a ratio of 0.89 in *Silesaurus* and 0.91 in *Herrerasaurus* (Fig. 6-3b). In *Eoraptor*, *Guaibasaurus* and *Saturnalia*, femur and tibia are approximately of the same length. In all sauropodomorphs more derived than *Saturnalia* the femur is longer than the tibia (Table 6-4). The distal limb to femur ratio dinosauromorphs more derived than *Marasuchus* and basal saurischians ranges between 1.38 in *Silesaurus* and 1.5 in *Eoraptor*. In the basal most sauropodomorph, the distal limb to femur ratio is 1.54. Towards sauropods, the distal limb to femur ratio is reduced to 1.3 in *Efraasia*, 1.08 in *Plateosaurus* (Fig. 6-3c) and 1.13 in *Melanorosaurus*. In sauropods, the distal limb is shorter than the femur, resulting in a ratio of 0.89 in *Antetonitrus* or 0.71 in *Shunosaurus* (Fig. 6-3d).

6.3.4 Myology of the pelvic girdle and hindlimb

The myology of the pelvic girdle and hindlimb of Sauria is relatively conservative (Table 6-5). Most of the changes in the myology of the pelvic girdle and hindlimb of dinosauromorphs on the lineage to sauropods are related to changing biokinematic requirements, as indicated by the development or reduction of osteological correlates. Basal dinosauromorphs, such as *Lagerpeton* (Table 6-5), PVL 3870, and *Dromomeron* share with basal archosaurs the adductor-controlled postural support (Hutchinson and Gatesy 2000, Chapter 3, 4). The adductor-controlled postural support of archosaurs is characterized by a single femoral abductor, M. iliofemoralis. The occurrence of the lesser trochanter and trochanteric shelf in Dinosauriformes (Novas 1989) marks the separation of M. iliofemoralis into Mm. iliofemoralis externus and iliotrochantericus caudalis (Rowe 1986) and thus the establishment of

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Table 6-5. Muscles of the pelvic girdle and hindlimb inferred as present in *Lagerpeton*, *Herrerasaurus*, *Plateosaurus* and *Shunosaurus*. Muscle abbreviations as in Table 6-2.

an abductor-controlled postural support (Hutchinson and Gatesy 2000). The reduction of the trochanteric shelf in basal sauropodomorphs and of the lesser trochanter in basal sauropods does not imply that the both Mm. iliofemoralis externus and iliotrochantericus caudalis are reduced (see also Chapter 5). It is considered here that both muscles attach to the femoral shaft with reduction of the correlated osteological structures. However, the establishment of the abductor-controlled postural support is associated with the reduction of the femoral adductor M. puboischiofemoralis externus 3 (see Hutchinson and Gatesy 2000, Chapter 4). With the occurrence of the cnemial crest on the anterior aspect of the proximal tibia in Dinosauriformes, the insertion of Mm. iliotibiales, ambiens, and femorotibialis externus et internus, and the origin of Mm. tibialis anterior moved from the anterior aspect of the proximal tibial shaft to the lateral aspect of the cnemial crest. With the development of a lateral projecting cnemial crest in mamenschisaurids and more derived sauropods, the attachment of the correlated muscles moved from the lateral aspect of the tibia to the anterior aspect of the tibia. The occurrence of the brevis fossa marks the shift of M. caudofemoralis brevis from the posterior margin of the ilium to the lateral aspect of the posterior ilium (Romer 1923c, Novas 1996; Table 6-5). As in basal archosaurs, M. femorotibialis of basal dinosauromorphs consists of two parts, Mm. femorotibialis internus and externus (Table 6-5). In basal sauropodomorphs, M. femorotibialis is separated into three muscles, with M. femorotibialis intermedius being a derivate of M. femorotibialis internus. The development of M. femorotibialis intermedius is indicated by the occurrence of a Linea intermuscularis on the anterior aspect of the femur (Chapter 5). With the reduction of the distal phalanges of the lateral digits in basal sauropods, the correlated muscles, such as Mm. gastrocnemius medius, flexor digitalis longus, and fibularis brevis, are reduced, but not lost.

Not all changes in the myology of the pelvic girdle and hindlimb are indicated by changes in the osteology. The reduction of Mm. flexor tibialis internus 1, 2, 4 on the lineage to Aves cannot be timed (Carrano and Hutchinson 2002, Hutchinson 2002, Chapter 5). The presence or absence of the muscles of the flexor cruris group in sauropodomorphs cannot be reconstructed using the Extant Phylogenetic Bracket approach alone.

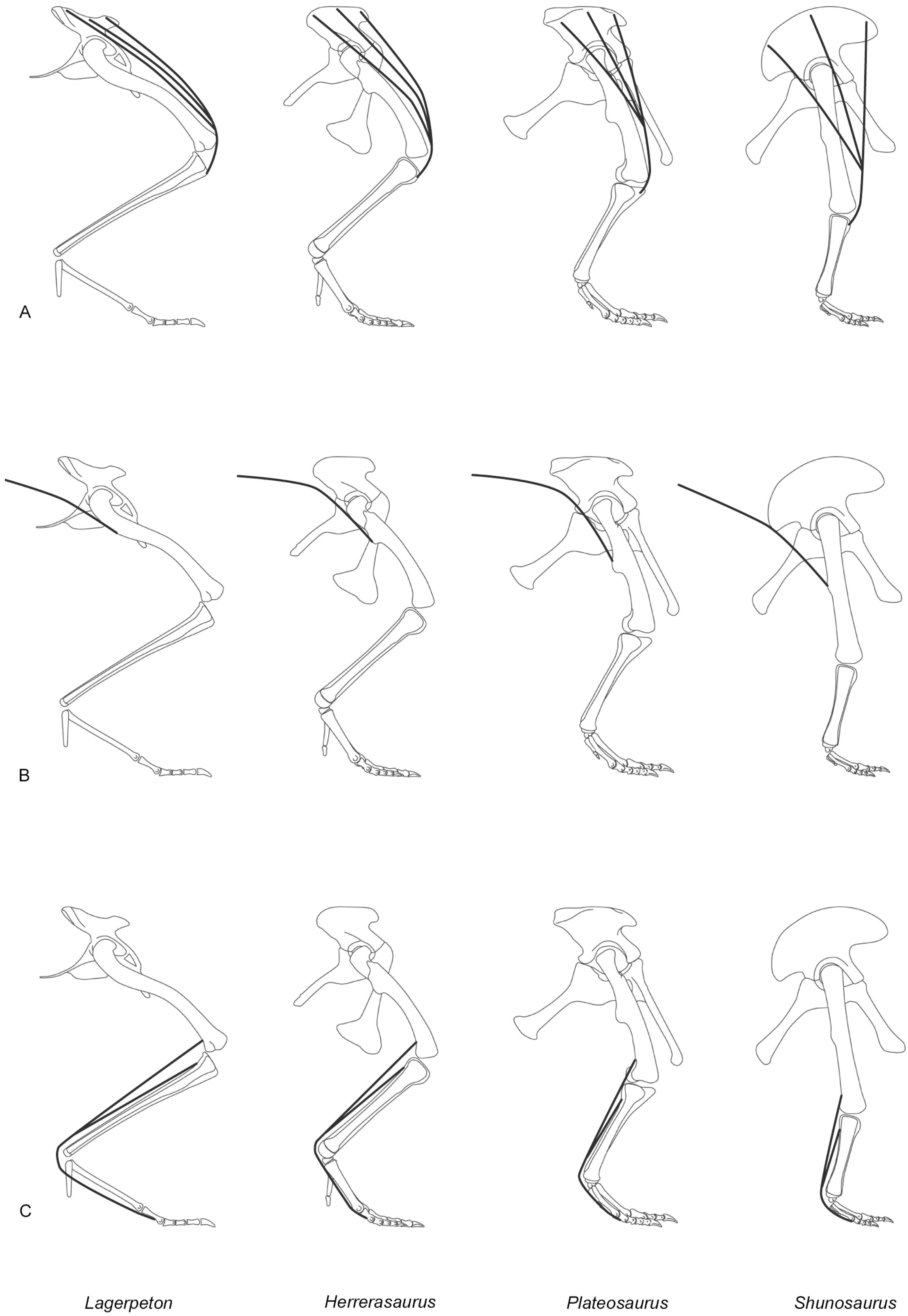

Figure 6-4. Diagram showing the affect of the modification of the hindlimb proportions on the associated muscles. A, shows the affect of the elongation of the femur on the muscles arising from the pelvis and attaching to the tibia (e.g. M. iliotibialis). B, shows the affect the distal shift of the insertion site of M. caudofemoralis longus and C, shows the affect of the relative shortening of the distal limb on the ankle extensors (M. gastrocnemius). All in right lateral view. Not to scale.

The most significant change in the myology of the pelvic girdle and hindlimb of dinosauromorphs on the lineage to sauropods is probably correlated to the change in the proportions of the hindlimbs (Fig. 6-4). Most muscles of the pelvic girdle and hindlimb of dinosauromorphs are one-joint or two-joint muscles. Thus, the length of the elements of the hindlimb is closely correlated to the length of the associated muscles. In basal dinosauromorphs with a short femur, muscles originating on the pelvic girdle and inserting on the proximal tibia are accordingly relatively short (Fig. 6-4a). Muscles originating on the distal femur or proximal tibia and inserting on the metatarsus and / or phalanges of the pes are relatively long in basal dinosauromorphs, because of the elongated distal limb (Fig. 6-4c). With the change of the proportions of the hindlimb on the lineage to sauropods, the proportions of the corresponding muscles are changed.

6.3.5 Hindlimb posture

Fechner (Chapter 3, 4) has shown that basal dinosauromorphs, such as *Lagerpeton*, PVL 3870, and *Dromomeron*, moved using an intermediate hindlimb posture. *Marasuchus* shows adaptations to both an intermediate and erect hindlimb posture. All more derived dinosauriformes were restricted to an erect hindlimb posture. The reconstruction of the hindlimb posture was based on osteological and myological features, with additional information gained from ichnofossils assigned to dinosauromorph trackmakers (see Chapter 4). It is more difficult to reconstruct if a taxon moved using a crouched or upright hindlimb posture (see Hutchinson and Gatesy 2006). The femoral curvature in lateral view is an often-used indicator (e.g. Biewener 1983). A marked curvature is considered to be indicative for a relatively crouched hindlimb posture, whereas a straight femur indicates an upright hindlimb posture. In basal dinosauromorphs, the femoral curvature is relatively low (Table 6-4), with 6.3 in *Lagerpeton*, 4.2 in PVL 3870 and 4.9 in *Silesaurus*. The femur of basal saurischians is characterized by a stronger curvature, ranging between 9.4 in *Herrerasaurus* and 11.1 in *Guaibasaurus*. In sauropodomorphs, a consistent trend to reduce the femoral curvature can be observed (Table 6-4). In non-sauropodan sauropodomorphs, the femoral curvature is reduced to 5.6 to 8.6. In *Saturnalia*, however, the femoral curvature is 13.4 and *Efraasia* is characterized by a femoral curvature of 16.1. In basal sauropods, the femoral curvature is greatly reduced to 4.9. A straight femur and therewith a fully upright hindlimb posture is present in *Gongxianosaurus* and all more derived sauropods.

6.3.6 Locomotor posture

Basal dinosauromorphs and basal saurischians are commonly regarded as obligate bipeds. The idea of obligate bipedality is based on the marked disparity of the limbs with relatively short forelimbs and the short trunk (Romer 1971, Coombs 1978, Arcucci 1986, Sereno 1993, Sereno and Arcucci 1993, 1994, Sereno et al. 1993). Non-sauropodan sauropodomorphs are commonly regarded as facultative bipeds. Light-bodied taxa, such as *Anchisaurus*, are considered to be more bipedal than others, whereas *Thecodontosaurus* is considered as obligate biped. On the other hand, heavy-bodied taxa, such as *Riojasaurus*, are often considered as obligate quadrupedal (e.g. Galton 1990). The obligate quadrupedal locomotion of sauropods evolved by elongation of the forelimbs and was associated by the elongation of the neck and trunk (e.g. Galton and Upchurch 2004, Barrett and Upchurch 2007).

In fact, with a relatively short trunk (see Chapter 3) and an FL/HL ratio of 0.5 (Table 6-4), the bauplan of non-dinosaurian dinosauromorphs is consistent with the proportions assumed to reflect obligate bipedal locomotion. Amongst non-dinosaurian dinosauromorphs, *Silesaurus* is an exception. Based on the reconstruction of Dzik (2003), *Silesaurus* is characterized by a FL/HL ratio of 0.95 and a HL/T ratio of 0.7 – 0.8. The bauplan of *Silesaurus* thus indicates obligate quadrupedal locomotion. The FL /HL ratios of basal saurischians range between 0.47 and 0.53 (Table 6-4), which is indicative for obligate bipedal locomotion. The HL/T ratio of 1.0 – 1.1, however, indicates facultative bipedal locomotion. Only *Staurikosaurus* with a HL/T ratio of 1.6 – 1.8 reflects an adaptation to obligate bipedal locomotion. Based on the ratios of the HL/T and FL/HL, the assumed facultative bipedal locomotion of non-sauropodan sauropodomorphs is only reflected in the bauplan of *Plateosaurus* with a FL/HL ratio of 0.56 and a HL/T ratio of 0.9 – 1.0. According to the FL/HL and HL/T ratios, *Anchisaurus* has to be regarded as an obligate quadruped (Table 6-4). All other non-sauropodan sauropodomorphs show a combination of FL/HL and HL/T ratio, which is indicative for obligate bipedal and facultative bipedal locomotion (e.g. *Saturnalia*) or facultative bipedal and obligate quadrupedal locomotion (e.g. *Efraasia*). Basal sauropods are characterized by a FL/HL ratio of 0.68 or higher, which is indicative of obligate quadrupedal locomotion. The HL/T ratio, however, ranges between 0.9 and 1.1, which is indicative for facultative bipedal locomotion.

Fechner (Chapter 4) already noted that both the FL/HL ratio and the HL/T ratio are not very suitable indicators for inferring the locomotor posture of dinosauromorphs. The FL/HL ratio only considers the total length of the long axis of the bones (humerus +ulna + metacarpal II / femur + tibia + metatarsal III). As outlined above, the hindlimbs of small-sized dinosauromorphs are strongly flexed. A more upright hindlimb posture evolves on the lineage to sauropods, but is not developed before *Gongxianosaurus* (Table 6-4). The forelimbs, however, are characterized by a fairly straight posture (see Haubold and Klein 2000, 2002, Chapter 3). Consequently, a FL/HL ratio of 0.5 in basal dinosauromorphs with a strongly flexed hindlimb posture and a fairly straight forelimb posture does not reflect the real disparity of the limbs. This is particularly true in taxa with a markedly elongated metatarsus. In taxa in which the flexed hindlimb posture and the elongated metatarsus is associated with a digitigrade pes posture, the metatarsus does not contribute much to the effective hindlimb length, because of the almost horizontal orientation of the metatarsus (Fig. 6-3a). In sauropods with a columnar hindlimb posture and a relatively short metatarsus, the effective hindlimb length equals more or less the total hindlimb length (Fig. 6-3d). Reconstructing the locomotor posture based on the FL/HL ratio should take into account considerations on the effective hindlimb length and not the total hindlimb length. Nonetheless, the hindlimb length was reduced relatively to the forelimb length in dinosauromorphs on the lineage to sauropods. The HL/T ratio of dinosauromorphs and the lineage to sauropods does not change markedly (Table 6-4). A constant HL/T is only achieved with both hindlimb length and trunk length being elongated likewise.

Fechner (Chapter 3, 4) showed that a relatively short trunk and a FL/HL ratio of 0.5 are associated with facultative bipedal locomotion in basal dinosauromorphs and basal saurischians. The facultative bipedal locomotor posture of basal dinosauromorphs and basal saurischians is consistent with the intermediate hindlimb posture of basal dinosauromorphs, such as *Lagerpeton*, PVL 3870, *Dromomeron* and probably *Marasuchus* (see above), and ichnofossils assigned to basal dinosauromorphs and basal saurischians (Chapter 3, 4). According to Fechner (Chapter 4), an obligate bipedal locomotor posture is only present in herrerasaurids among basal dinosauromorphs. The obligate bipedal locomotor posture of *Herrerasaurus* is indicated by the presence of a functionally modified manus, which reflects adaptations to grasping and raking (e.g. Sereno 1993). In *Staurikosaurus*, the reconstruction of the obligate bipedal locomotor posture is consistent with the HL/T ratio of 1.6 – 1.8. Haubold and Klein (2002) noted that a functionally modified manus as in herrerasaurids and theropods was not used as support during locomotion. The manus of non-sauropodan sauropodomorphs or "prosauropod"-like manus, however, was capable of grasping and load-bearing (Galton 1971, Cooper 1981, Barrett 2000, Galton and Upchurch 2004). A manus adapted to grasping and load-bearing is thus indicative for a facultative bipedal or quadrupedal locomotor posture (Barrett and Upchurch 2007). Bonnan and Senter (2007), however, challenged the assumption of facultative bipedal or quadrupedal locomotion in non-sauropodan sauropodomorphs by arguing that the limited range of motion of the forelimbs of *Plateosaurus* and *Massospondylus* prevented the effective pronation of the manus and thus quadrupedal locomotion. Nonetheless, Remes (2008) argued that at least some sauropodomorphs were able to pronate the manus and Christian and Preuschoft (1996) reconstructed a facultative bipedal locomotor for *Plateosaurus,* based on the bending moments along the presacral vertebral column. Carrano (2005) noted that the obligate quadrupedal locomotion of sauropods is indicated by the consolidation of the carpus and metacarpus in addition to the elongation of the forelimbs. The sauropod-like manus is considered to have lost the capability to grasping, so that it is solely to adapted to load-bearing (e.g. Yates 2004). Sauropods more derived than *Antetonitrus* are characterized by a sauropod-like manus, associated with relatively elongated forelimbs (FL/HL >0.68). The manus of *Antetonitrus* resembles a "prosauropod"-like manus more than a sauropod-like manus (Yates and Kitching 2003). The "prosauropod"-like manus of *Antetonitrus* is associated with a relatively elongated forelimb (FL/HL= 0.84). Based on the combination of "prosauropod"-like manus and elongated forelimbs, Yates and Kitching (2003) and later Carrano (2005) suggested that *Antetonitrus* marks the transition from the facultative bipedal locomotion of non-sauropodan sauropodomorphs to the obligate quadrupedal locomotion of sauropods, with *Antetonitrus* probably being a facultative biped. Following this consideration, the sauropod-like manus is assumed to reflect the acquisition of obligate quadrupedal locomotion, whereas the absence of a sauropod-like manus or the presence "prosauropod"-like manus is assumed to reflect facultative bipedal locomotion. In fact, the sauropod-like manus with the

Taxa	Body size			Osteology	HL			FL/HL	HL/T	Hindlimb posture				Locomotor posture	Locomotor habit	
	body mass	ζ				tibia + mt III/femur						femoral curvature				
Lagerpeton		7,6		acetabulum closed and shallow, weakly developed femoral head, femoral head inturned >45°, femur sigmoid curved in anterior view, distal articular facet oblique, ectaxonic pes, bundled metatarsus		1,79				intermediate		6,3		facultative bipedal		
PVL 3870	0-4 kg	7,9				1,85						4,2				
Dromomeron		13,3														
Marasuchus		9,1		lesser trochanter, trochanteric shelf, cnemial crest, mesaxonic pes		2		~0.5				5,2				
Pseudolagosuchus	4 -7 kg	8,1		distal articular facet plane, straight femur in anterior view						erect		8,4				
Silesaurus		9,6		deep acetabulum, prominent supraacetabular crest, brevis fossa		1,38		0.95	0.7 - 0.8					obligate quadrupedal		
Eucoelophysis		8,2												facultative bipedal		
Ornithischia	10 - 40 kg															
Eoraptor	7 -10 kg	8,2		open acetabulum		1,5		0.47	1.0 - 1.1							
Staurikosaurus	10 - 40 kg								1.6 - 1.8			10,3		obligate bipedal		
Herrerasaurus	100 - 400 kg	8,5	increased			1,38		0.48				9,4				
Guaibasaurus	10 - 40 kg	8,9				1,43		0.53				11,1		facultative bipedal		
Theropoda	100 - 400 kg													obligate bipedal		
Saturnalia	7 - 10 kg	9,9				1,54		0.41 - 0-42	1,1			13,4		facultative bipedal - obligate quadruepdal		
Thecodontosaurus	70 - 100 kg			reduction of trochanteric shelf												
Efraasia	400 - 700 kg					1,29		0.55	0.8-0.9			16,1				
Plateosauravus	1000 - 4000 kg	9,3														
Ruehleia																
Unaysaurus																
Plateosaurus	1000 - 4000 kg	13,7		femoral head inturned <45°		1,08		0.56	0.9-1.0			8,6				
Eucnemesaurus																
Riojasaurus	1000 - 4000 kg	17,5			distal limb	1,13	femur	0.6	0.82		crouched	8,2	upright		cursorial	graviportal
Massospondylus	100 - 400 kg	12,6	decreased			1,24		0.53	1,2			8,2				
Coloradisaurus																
Lufengosaurus	1000 - 4000 kg			femoral head inturned 0°		1,07		0.46								
Jingshanosaurus																
Anchisaurus	10 - 40 kg	11,6	decreased			1,11		0.63				5,6				
Yunnanosaurus	700 - 1000 kg					1,2		0.48	0.8-0,9							
Melanorosaurus	1000 - 4000 kg					0,91		0.57 - 0-59								
Blikanasaurus	700 - 4000 kg															
Antetonitrus	1000 - 4000 kg					0,89		0.84						obligate quadruepdal		
Lessemsaurus																
Camelotia	4000 - 7000 kg	13,5										4,9				
Gongxianosaurus	10 000 - 40 000 kg	23,2						0.70 - 0.75								
Isanosaurus	1000 - 4000 kg	16	decreased	femoral midshaft eccentric												
Vulcanodon		14,6		cranial expansion of preacetaublar ilium		0.79			0.9-1.0							
Tazoudasaurus		16,2		reduction of brevis fossa												
Shunosaurus	> 10 000 kg	14,1		loss of lesser trochanter, lateral projecting cnemial crest, reduction of phalanges, broad metatarsus, entaxonic pes		0.71		0.68	1.0-1.1			0				
Barapasaurus																
Patagosaurus																
Mamenchisaurus																
Neosauropoda				lobe-shaped preacetabular ilium												

consolidated carpus and metacarpus indicated an adaptation to resist enormous body mass. The presence of a sauropod-like manus hence only makes sense in obligate quadrupedal sauropods, in which the manus is exclusively used as support during locomotion. The presence of a "prosauropod"-like manus, however, does not necessarily indicate facultative bipedal locomotion. The "prosauropod"-like manus rather allows both facultative bipedal locomotion or obligate bipedal locomotion with other uses of the manus during rest. In fact, tracks and trackways assigned to non-sauropodan sauropodomorphs show that their trackmakers either moved using a facultative bipedal or a quadrupedal locomotor posture (Rainforth 2003, Milàn et al. 2008). According to this, the "prosauropod"-like manus of *Antetonitrus* does not rule out obligate quadrupedal locomotion. Moreover, the FL/HL of 0.84 (please note the relatively columnar hindlimb posture!) in *Antetonitrus* appears to be a good indicator for obligate quadrupedal locomotion. The FL/HL of *Riojasaurus* and *Anchisaurus* probably also indicates obligate quadrupedal locomotion, but facultative bipedal locomotion cannot be ruled out. Based on the available evidence (FL/HL ratio, HL/T ratio and the development of the manus), an obligate bipedal locomotor posture has to be ruled out for sauropodomorphs. Tracks and trackways assigned to sauropod trackmakers show that sauropods were obligate quadrupeds (e.g. Thulborn 1990, Lockley et al. 1994, Wright 2005).

6.3.7 Evolution of the graviportal locomotor habit in sauropods

Increasing body size is characteristic for the evolution of dinosauromorphs on the lineage to sauropods, and changes in the osteology and myology of the pelvic girdle and hindlimb, as well as changes in the hindlimb posture and locomotor posture are best viewed in the light of increasing body size (Fig. 6-5). Features commonly regarded as adaptation to a graviportal locomotor habit, such as i) columnar limbs, ii) relatively elongated femur, iii) increased limb bone robusticity iv) increased

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Figure 6-5. Diagram showing the evolution of the adaptations of the graviportal locomotor habit in sauropods mapped on body size.

eccentricity of the femoral midshaft, v) reduced muscle insertion sites on the limb bones, vi) broad metatarsus, viii) entaxonic pes, and ix) relatively elongated forelimbs (Coombs 1978, Carrano 1999, 2001 Wilson and Carrano 1999, Yates 2004), are present in sauropods with a body mass of 1000 – 4000 kg. Basal dinosauromorphs with a body mass of 0 – 4 kg are characterized by a cursorial locomotor habit (Fig. 6-5). The cursorial locomotor habit of dinosauromorphs includes adaptations such as i) crouched hindlimb posture, ii) short femur, iii) slender limb bones, iv) bundled metatarsus, v) ectaxonic pes, vi) great disparity of the limbs, and vii) short trunk (Coombs 1978, Carrano 1999, Chapter 3, 4). With increasing body size, the adaptations to a graviportal locomotor habit evolve in mosaic-like pattern (Fig. 6-5), so that the cursorial locomotor habit becomes less pronounced and the graviportal locomotor habit becomes more pronounced. The transition from cursorial to graviportal locomotor habit forms a continuum.

To understand the evolution of the graviportal locomotor habit, it is important to understand the impact of the ground reaction force on the limbs of a tetrapod. The ground reaction force is the main determinant of the moments developed at the joints of the limb (Biewener 1990, 2003) and is equal in magnitude and opposite in direction to the force that the limb exerts on the supporting substrate (Biewener 1990). In order to control the limb posture, muscle forces have to oppose the moments of the ground reaction force developed at the joints of the limb. Because the ground reaction force is weight-related, the muscle force required to control the limb posture increases with body size and mass (Biewener 1990, 2005). An increasing of muscle mass, however, negatively affects the locomotor performance by increasing the total body mass and the inertia, which has to be overcome by acceleration of the body (Christian and Garland 1996). With an alignment of the joints closer to the vector of the ground reaction force, the magnitude of muscle forces required to control limb posture is reduced and the effective mechanical advantage is increased (Biewener 1990, 2005). The increasing effective mechanical advantage allows retaining the locomotor abilities in spite of increasing body size. This is consistent with the observation that larger animals tend to run with a more upright limb posture (Biewener 2003, 2005). However, above a critical body size the effective mechanical advantage cannot be increased, so that the locomotor capabilities are reduced (Biewener 1990, 2003, 2005). In small terrestrial animals the muscle forces required to control the limb posture are relatively small. In contrast to larger animals, which are limited to a relatively small functional diversity, small animals are characterized by a wide functional spectrum of their locomotor apparatus. They often move using a more flexed limb posture (e.g. Biewener 2003, 2005) and are even not restricted to a fully erect hindlimb posture (e.g. Jenkins 1971b, Rewcastle 1981).

Cursorial dinosauromorphs with a body mass of 0 – 4 kg are characterized by an intermediate hindlimb posture (Fig. 6-5). The intermediate hindlimb posture of basal dinosauromorphs is associated with i) a closed and large acetabulum, ii) a shallow supraacetabular crest, iii) a weakly offset femoral head, iv) a sigmoid curvature of the femur in anterior view, v) an oblique distal articulation facet of the femur, and vi) an entaxonic pes (Chapter 3, 4). An erect hindlimb posture is present in dinosauromorphs with a body mass of >4 kg. The erect hindlimb posture of dinosauromorphs is characterized by the evolution of i) a perforated and relatively small acetabulum, ii) a prominent supraacetabular crest, iii) a well developed femoral head, iv) a straight femur in anterior view, v) a plane distal articulation facet of the femur, and vi) a mesaxonic pes (Chapter 4). Christian (1995, 2007) argued that an erect hindlimb posture is required in tetrapods, which have to rely on fast running speed despite of increasing body size. The erect hindlimb posture allows a positioning of the joints closer to the vector of the ground reaction force. The ability to align the joints of the limb in sprawling tetrapods is very limited, so that they have to increase the muscle forces to control the limb function. Relating to the over-proportional increase of limb segment diameters, sprawling tetrapods, which have to rely on fast running speed, are restricted to a relatively small body size (Christian 1995, Christian and Garland 1996). The evolution of the erect hindlimb posture in non-dinosaurian dinosauromorphs hence indicates that they had to rely on fast running speed (see also Chapter 5). A FL/HL ratio of 0.5 associated with a facultative bipedal locomotor posture requires a distinct crouched hindlimb posture. A distinct crouched hindlimb posture, however, is not reflected in the femoral curvature. The relatively low femoral curvature might be related to the intermediate hindlimb posture of basal dinosauromorphs, in which an enhanced resistance against torsion, not mediolateral bending, is required. The reduction of the femoral curvature in basal saurischians on the lineage to sauropods corresponds to the excepted evolution of a more upright hindlimb posture with increasing body size. A fully upright hindlimb posture, however, was first developed in sauropods with a body mass of 1000 – 4000 kg (Fig. 6-5). The evolution of the upright hindlimb posture was associated with a change of the proportions in the hindlimbs (Fig. 6-5).

In basal dinosauromorphs, the distal limb is markedly elongated. With a digitigrade pes posture, the joints of the limbs have therefore a relatively large distance to the vector of the ground reaction force. By reducing the relative length of the metatarsus on the lineage to sauropods, the joints of the limbs can be aligned closer to the vector of the ground reaction force (Fig. 6-3). The reduction of the relative length of the metatarsus is associated with the relative elongation of the femur on the lineage to sauropods (Fig. 6-3, 6-6). As shown above, a change of the limb bone proportions is associated with the changes of the proportions of the myology of the pelvic girdle and hindlimb. A change in the proportions of the myology has impact on the mechanical conditions. Lever function relies on the relationship between the fulcrum and the lever arm. Translated into a biological system, the fulcrum represents the joint and the lever arm is determined by the arrangement of the muscles along the limb bones. The relationship between the joint and muscle arrangement allows predictions on velocity and force (Hildebrandt and Goslow 2004). A limb designed to work at high velocity is characterized by a short femur and a relatively elongated distal limb. The short femur allows muscle to insert close to the joint (= short lever arms) and the relatively elongated distal limb increases the distance between the joint to the point of resistance (= long resistance arm). Both short lever arms and long resistance arm maximize the out velocities (Coombs 1978, Hildebrandt and Goslow 2004). Slender limb bones create less inertia, which has to be overcome with muscles forces. A limb designed to work at high force is characterized by long lever arms, reflected in the distal shift of muscle insertion sites and/or the elongation of the femur. The relative reduction of the distal limb results in the reduction of the associated muscles mass. Reduction of muscle mass is also achieved by the reduction of phalanges and thus of the reduction of the associated muscles. The reduction of muscle mass creates less inertia, which has to be overcome by retracting the limb. The hindlimb proportions of basal dinosauromorphs show that they are adapted to work at high velocity: the femur is short, the distal limb is markedly elongated and the limb bones are slender (Table 6-3). Muscles arising from the pelvis insert on the distal femur or proximal crus (Table 6-5; Fig. 6-3a). The short femur indicates that these muscles have short lever arms. The elongated distal limb indicates long resistance arms. Furthermore, basal dinosauromorphs have relatively long ankle extensors (M. gastrocnemius). M. gastrocnemius in dinosauromorphs arises from the distal femur and proximal tibia and inserts on the metatarsus (Table 6-5, Fig. 6-4c). Hutchinson et al. (2005) noted the relationship between the relative length of the ankle extensors (= M. gastrocnemius) and running speed: the longer the ankle extensors the faster the dinosaur. The short femur and the elongated distal limb of basal dinosauromorphs are associated with a proximal insertion of M. caudofemoralis longus on the femur (Table 6-5, Fig. 6-4b). M. caudofemoralis longus is the main retractor of the limb (Gatesy 1990). The proximal insertion of M. caudofemoralis longus allows moving the femur with a high angle velocity and a large excursion. The slender limb bones of basal dinosauromorphs decrease the inertia during retraction of the limb. With increasing body size, the hindlimb proportions show adaptations to work at more force but slower. With the relative elongation of the femur, the muscles inserting on the distal femur and/or proximal crus are elongated and thus the lever arms are elongated. The elongated of the femur is correlated with the distal shift of the insertion of the M. caudofemoralis longus. The distal insertion of M. caudofemoralis longus increases the force with which the femur is retracted and also the excursion of the femur is decreased. The relative reduction of the distal limb reduces the muscles mass and thus the inertia, which has to be overcome during retracting the limb.

Not all changes in the osteology and myology of the pelvic girdle and hindlimb regarded as adaptation to a graviportal locomotor habit are related to the ground reaction force. The increasing robusticity of the limb bones increases the resistance against body mass by increasing the diameter of the shaft. The increasing eccentricity of the femur, however, indicates the enhanced resistance against mediolateral bending (Wilson and Carrano 1999). The reduction of the muscle insertion sites might be related to the requirement to reduce the high peak forces exerted on the bone surface (Pauwels 1965, Chapter 5). In addition, the reduction of the lesser trochanter and trochanteric shelf modifies the moment arms of the associated muscles (Chapter 5). The entaxonic pes is the result of the reduction of the laterodistal phalanges, which were reduced, because the main axis of loading shifted from digit III, as in tetrapods with a mesaxonic pes, to digit I. The laterodistal phalanges are reduced in order to reduce the associated muscles and thus to reduce the relative mass of the distal limb (see also Chapter 5). The evolution of the entaxonic pes reflects a change in the biokinematics of the hindlimb, which is also reflected in the evolution of a lateral projecting cnemial crest. A lateral projecting cnemial crest results in the modification of the lever arms of the associated muscles (Table 6-5). The evolution of a broad metatarsus increases the area of support and therewith the locomotor performance.

In the past, it has been argued that the obligate quadrupedal locomotor posture of sauropods is the result of increasing body size and evolved from facultative bipedal non-sauropodan sauropodomorphs (e.g. Carrano 2005). The facultative bipedal locomotion of non-sauropodan sauropodomorphs, on the other hand, was thought to have evolved from obligate bipedal saurischians and basal dinosauromorphs (see Chapter 3, 4). Many modifications characterizing the evolution of sauropodomorphs have been used to serve as indicators for the transition from facultative bipedal locomotion to obligate quadrupedal locomotion (see Carrano 2005, 2006, Barrett and Upchurch 2007). Fechner (Chapter 3, 4) showed that basal dinosauromorphs including basal saurischians were initially facultative bipeds. The facultative bipedal locomotion of dinosauromorphs relates to the requirement to rely on fast locomotion. Fechner (Chapter 4) showed that running speed of quadrupedal dinosauromorphs is limited, because of the rigid vertebral column. Fast running speed in basal dinosauromorphs is achieved by the elongation of the hindlimb length. Elongation of the hindlimb length allows to increase the maximum running speed by increasing the stride length and by changing from the quadrupedal locomotor posture, which is used at slow speeds, to the bipedal locomotor posture used at high speeds. With increasing body size, however, retaining fast running speed is only allowed by changing to an obligate bipedal locomotor posture. In saurischians, the critical body size above which the change to obligate bipedal locomotion is required is 2 m. For reasons outlined above, a facultative bipedal or quadrupedal locomotion is assumed for sauropodomorphs. In contrast to the traditional idea, non-sauropodan sauropodomorphs show no tendency to a more frequent use of quadrupedal locomotion with increasing body size (Fig. 6-5). This might indicate that the locomotor performance of non-sauropodan sauropodomorphs was more diverse than previously suggested. The absence of obligate bipedal locomotion in sauropodomorphs with a body size of >2 m shows that sauropodomorphs had not – in contrast to theropods – relied on fast running speed.

The evolution of the graviportal locomotor habit of sauropods is traditionally considered to be an adaptation to resist enormous body mass. If so, the adaptations to the graviportal locomotor habit would be expected to occur very late in the evolution of sauropodomorphs. Most of the adaptations, however, occur very early in dinosauromorph evolution. The close relationship of most of the adaptations to the graviportal locomotor habit and the occurrence of these adaptations in small-sized taxa indicates that not resistance against enormous body mass, but retaining the locomotor performance despite increasing body size is the primary factor.

The evolution of the graviportal locomotor habit of sauropods follows strict biomechanical rules. These biomechanical rules do not only affect the morphofunctional evolution of sauropods, but also affect the morphofunctional evolution of other extant and extinct terrestrial tetrapods (Coombs 1978, Scott 1985, Carrano 1999). The close correlation of body size and form and function shows that body size is an important aspect in the evolution of terrestrial tetrapods. Because the adaptations to a graviportal locomotor posture follow strict biomechanical rules and are not systematically controlled, closely related taxa with differing body size have less characters in common than taxa being less closely related but being of similar body size. This is explained by the fact that similar sized taxa form an adaptive range (*sensu* Rewcastle 1981). Different sized taxa belong to different adaptive ranges and are thus characterized by different adaptations according to their body size.

Looking at Fig. 6-5 demonstrates that almost all taxa included in this study show exactly the combination of osteological and myological characteristics and function as predicted for their body size. Only two exceptions are found: *Silesaurus* and *Anchisaurus*. Being relatively small (4 – 7 kg), *Silesaurus* shows adaptations, which are characteristic for a larger taxon (1000 – 4000 kg). Very interesting, the exceptional bauplan of *Silesaurus* is associated with adaptations to a herbivorous diet (Dzik 2003). It is commonly regarded that dinosauromorphs are omnivorous and that obligate herbivory evolved later. The correlation of herbivorous diet or ecology and the bauplan of *Silesaurus* will have to be discussed. Based on its relatively small body size (10 – 40 kg), *Anchisaurus* was often regarded to be basal sauropodomorph. The proportions of the hindlimb of *Anchisaurus*, however, are characteristic for sauropodomorphs with body mass of 1000 – 4000 kg. Phylogenetic hypothesis generated recently (e.g. Yates 2006, 2007), place *Anchisaurus* within taxa, which have been estimated with a body mass of 1000 – 4000 kg. This and the proportions suggest that *Anchisaurus* is the descendent of larger taxa, which retained their proportions while decreasing body size.

6.4 DISCUSSION

The graviportal locomotor habit of sauropods is a biomechanical requirement to retain the locomotor performance with increasing body size and to resist large body size. The adaptations to a graviportal locomotor habit are not unique to sauropods, but are present in almost all large terrestrial tetrapods (e.g. Coombs 1978, Scott 1985, Carrano 1999).

The largest extant terrestrial tetrapods are the African elephant with a body mass of 3.9 – 5.5 tons (Laws 1966, Nowak 1999), the white rhinoceros with 2.2 tons, the hippopotamus with a body mass of 1.5 tons and the giraffe with 1.2 tons (Owen-Smith 1988). The largest extinct mammal is the Oligocene rhinocerothoid *Indricotherium transouralicum* with an estimated body mass ranging between 20 – 34 tons (Economos 1981, Alexander 1981). According to Fortelius and Kappelman (1993), however, a body mass of 11 to 15 tons has to be estimated for *Indricotherium*. The largest carnivorous mammals known are *Megistotherium osteothalestes*, a creodont from the African Miocene, with an estimated body mass of 880 kg (Savage 1973), and the mesonychid *Andrewsarchus mongoliensis* from the Oligocene of Asia with an estimated body mass of 600 – 900 kg. The largest extant Carnivora are bears and reach a body mass of up to 800 kg (Burness et al. 2001).

The upper size boundary of dinosaurs is much higher than that of mammals. The upper size boundary of non-sauropodan dinosaurs was estimated with around 10 tons (Carrano 2005). *Tyrannosaurus rex* is the largest theropod known from a complete skeleton. The body mass of *Tyrannosaurus* was estimated with up to 7 tons (Peczkis 1994). Therrien and Henderson (2007) argued that the upper size boundary of obligate bipedal theropods has to be estimated with 13 to 14 tons. The largest known ornithischian is *Shantungosaurus giganteus* from the Cretaceous of China (Hu 1973) with an estimated body mass of 22 tons (Seebacher 2001). The average body mass of other large ornithischians appears to be 4 tons with few exceptions reaching up to 7 tons (Peczkis 1994). *Argentinosaurus huinculensis* from the Lower Cretaceous of South America and *Supersaurus* sp. from the Upper Jurassic of North America have been estimated with a body mass of 100 tons (Hokkanen 1986, Benton 1989), and *Amphicoelias altus* from the Upper Jurassic of North America has been estimated with 150 tons (Paul 1998). Nevertheless, the incompleteness of the specimens appears to be inadequate to support these body mass estimates and Alexander (1998) argued that the heaviest sauropods might have been between 50 and 80 tons. With a body mass of at least 50 tons, sauropods are by the order of a magnitude heavier than other terrestrial vertebrates.

Burness et al. (2001) noted that body size is correlated to the land area occupied by the taxon. According to the results of Burness et al. (2001), dinosaurs are larger than predicted independently of the metabolic rate assumed. Burness et al. (2001) noted that the never-surpassed size of the largest dinosaurs remains unexplained. Blackburn and Gaston (2001) and other authors argued that physiological and ecological variables limit the theoretical maximum body size of a species. Janis and Carrano (1992), Farlow (1993) and Farlow et al. (1995) suggested that the body size is affected by many physiological and ecological variables, such as diet and intraspecific and/or interspecifiy competition for food, digestive processes, reproductive dynamics and intraspecific rivalry for breeding rights, thermoregualtion, and foraging strategies Farlow (1993) argued that it is not possible to identify one of these as the most important variable affecting body size. Nonetheless, the top herbivores of a land area are larger than the top carnivores due to the larger amount of food available to herbivores than to carnivores (Burness et al. 2001) and quadrupeds achieve larger body size than bipeds, because quadrupeds can support their body mass on four limbs, whereas bipeds have to support their body mass only on the hindlimbs (Hokkanen 1986, Therrien and Henderson 2006).

Hokkanen (1986) calculated that the theoretical maximum body size of terrestrial tetrapods was around 100 tons. With a body mass of up to 80 tons, sauropods came relatively close to the calculated theoretical maximum body mass for terrestrial tetrapods. Sauropods are not only unique to other terrestrial tetrapods with respect to their enormous body size, but also regarding their bauplan. Sauropods are characterized by a small skull, an elongated neck and trunk, an elongated tail and relatively long limbs (Upchurch et al. 2004). The unique bauplan of sauropods indicates that unique physiological and ecological adaptations have to be assumed. It appears that the bauplan or anatomy of sauropods enabled them to achieve their enormous body mass and the physiological and ecological variables affecting the theoretical maximum body size have only minor impact on their body size. In other terrestrial tetrapods, which are considerably smaller than the predicted theoretical maximum body size of 100 tons for terrestrial tetrapods, the anatomy or physiological and ecological variables or a combination of both, limits their upper body size boundary. The characters decreasing the theoretical maximum body size of tetrapods and the physiological and ecological variables having impact on the body size will have to be identified.

6.5 SUMMARY

The hindlimbs of dinosaurs are commonly regarded as very uniform. The study presented here has shown that the osteology, myology of the hindlimbs as well as function change considerably and that the changes are best viewed in the light of increasing body size.

Basal dinosauromorphs with a body size of <4 kg are characterized by a cursorial locomotor habit. The cursorial locomotor habit in basal dinosauromorphs includes a crouched hindlimb posture, a short femur, slender limb bones, a bundled metatarsus, an ectaxonic pes, a great disparity of the limbs, and a short trunk. With increasing body size, the cursorial locomotor habit becomes less pronounced whereas the impact of a graviportal locomotor habit increases. The graviportal locomotor habit is fully developed in sauropods with a body mass of >1000 kg and includes columnar limbs, a relatively elongated femur, an increased limb bone robusticity, an increased eccentricity of the femoral midshaft, reduced muscle insertion sites on the limb bones, a broad metatarsus, an entaxonic pes, and relatively elongated forelimbs. The transition from the cursorial locomotor habit to the graviportal locomotor habit forms a continuum and is due to biomechanical requirements. The evolution of the graviportal locomotor habit is primarily due to retaining the locomotor performance due to increasing body size and secondarily to resist enormous body size.

Cursorial dinosauromorphs moved using an intermediate hindlimb posture, characterized by a closed and relatively large acetabulum, a shallow supraacetabular crest, a weakly offset femoral head, a sigmoid curved femur in anterior view, oblique distal femoral articulation facet, and an ectaxonic pes. Dinosauromorphs with a body mass of >4 kg moved using an erect hindlimb posture. The erect hindlimb posture is correlated to an open acetabulum, prominent supraacetabular crest, well developed femoral head, straight femoral head in anterior view, plane distal articulation facet of the femur or oblique in terms that medial condyle projects further distally, mesaxonic pes and an abductor-based postural support. Basal dinosauromorphs including basal saurischians were facultative bipeds and were adapted to fast acceleration. Non-sauropodan sauropodomorphs were either facultative bipeds or obligate quadrupeds. There is no evidence indicating obligate bipedal locomotion. Sauropods were obligate quadrupeds.

Chapter 7

Summary, General Conclusions, and Future Perspectives

7.1 SUMMARY

Sauropods are unique among terrestrial vertebrates regarding their exceptionally large body size. Sauropods are the largest tetrapods that ever lived on land and, with an upper body size boundary of 50 to 80 tons, by the order of a magnitude larger than any other terrestrial tetrapod. Sauropods are descendants from the only known clade of miniaturized archosaurs, the dinosauromorphs. The body mass of basal dinosauromorphs was estimated with >4 kg, whereas the body mass of the basalmost sauropods was estimated with 1000 – 4000 kg. The body mass increase spans 5 orders of magnitude in a time range of 30 Ma.

Body size is an important – if not the most important – variable affecting all aspects of the biology of an organism. This holds also true for sauropods and the evolution of the form and function of their pelvic girdle and hindlimb. Up to 80% of a sauropod's body mass was carried by pelvic girdle and hindlimb. It is therefore not surprising that the pelvic girdle and hindlimb of sauropods show adaptations to resist enormous body mass. The adaptations to a so-called graviportal locomotor habit include i) columnar limbs, ii) relatively elongated femur, iii) increased limb bone robusticity, iv) increased eccentricity of the femoral midshaft, v) reduced muscle insertion sites, vi) broad metatarsus, vii) reduced pedal phalanges, viii) entaxonic pes, and ix) relatively elongated forelimbs. In contrast to the traditional idea, however, the graviportal locomotor habit in sauropods does not only reflect an adaptation to resist enormous body size, but primary reflects the requirement to retain an effective locomotor performance with increasing body size relative to the condition seen in basal dinosauromorphs.

To understand the evolution of the pelvic girdle and hindlimb as well as the evolution of the locomotor capacities, it is important to understand the impact of the ground reaction force on the hindlimb. The ground reaction force is the main determinant of the moments developed at the joints of the limb. The ground reaction force is equal in magnitude and opposite in direction to the force that the limb exerts on the supporting substrate. The limb posture is controlled by muscle force, which opposes the moments of the ground reaction force developed at the joints of the limbs. Because the ground reaction force is weight-related, muscle force required to control the limb posture increases with body size and mass. Increasing muscle mass, on the other hand, negatively affects the locomotor performance of an animal by increasing the total body mass and the inertia which has to be overcome by accelerating the body. With the joints aligned closer to the vector of the ground reaction force, the magnitude of muscle force required to control the limb posture are reduced and the effective mechanical advantage is increased. Increasing the effective mechanical advantage allows retaining the capabilities in spite of the increasing body size. This is consistent with the observation that larger animals tend to walk with a more upright limb posture. Above a critical body size the effective cannot be increased, so that the locomotor capabilities of these animals are reduced. On the other hand, small terrestrial animals, in which the muscle force required to control the limb posture, is relatively small, are able to use a wide functional spectrum. They often move using a very crouched limb posture and are not restricted to an erect hindlimb posture. In accordance to that, basal Dinosauromorpha with a body mass of <4 kg are characterized by a cursorial locomotor habit, sharing following features such as: i) crouched hindlimb posture, ii) short femur, iii) slender limb bones, iv) bundled metatarsus, v) ectaxonic pes, vi) marked disparity of the limbs, and vii) short trunk. The graviportal locomotor habit of sauropods evolved in a mosaic-like pattern: with increasing body size, the cursorial locomotor habit becomes less pronounced whereas the graviportal locomotor habit becomes more pronounced. The fully graviportal locomotor habit is established in sauropods with a body mass of 1000 to 4000 kg. In contrast to the traditional idea, cursorial dinosauromorphs were facultative bipeds, which moved using an intermediate hindlimb posture. Some basal dinosauromorph taxa were probably able to use both an intermediate and an erect hindlimb posture. The marked disparity of the limbs, with elongated hindlimbs and relatively short forelimbs of cursorial dinosauromorphs, reflects the adaptation to fast acceleration. The markedly elongated hindlimb allow to achieve high running speed by increasing the stride length without the necessity to increase the stride frequency. The elongated hindlimb compensate for the limited ability to sagittal bending of the vertebral column of dinosauromorphs. Dinosauromorphs with a body mass of >4 kg are characterized by an erect hindlimb posture. The erect hindlimb posture allows retaining fast running speed with increasing body size. Dinosauromorphs with a body size of <2 m moved using a facultative bipedal locomotion: they used a quadrupedal locomotor posture during slow locomotion and a bipedal locomotor posture during fast locomotion. The bipedal locomotor posture was either used to increase running speed or to avoid co-ordination problems between the short forelimb and the elongated hindlimb or both. Dinosauromorphs which do not have to rely on fast running speed were obligate quadrupeds. Dinosauromorphs on the lineage to saurischians which have to rely on fast running speed and have a body size of <2 m have to change to an obligate bipedal locomotor posture. Obligate quadrupedal dinosauromorphs with a body size of <2 m, such as *Silesaurus*, had not to rely on fast running speed. Non-sauropodan sauropodomorphs either retained the facultative bipedal locomotor posture or evolved an obligate quadrupedal locomotor posture. Sauropods were obligate quadrupeds.

The myology of the pelvic girdle and hindlimb of Dinosauromorpha on the lineage to Sauropoda is relatively conservative. Major changes relate to the change from the intermediate hindlimb posture (= adductor-controlled postural support) to the erect hindlimb posture (= abductor-controlled postural support) and to the change in the proportions of the limbs. A change in the proportions of the limbs/muscles is correlated with a change in the lever function. Lever function rely on the relationship between the fulcra (joint) and the lever arm (determined by arrangement of muscles). The relationship between the joint and the muscle arrangement allows prediction on velocity and force. A limb designed to work at high velocity is characterized by a short femur (= short lever arms) and a relatively elongated distal limb (= long resistance arms). A limb designed to work at high force is characterized by a long femur and a relatively short distal limb. Consequently, the hindlimb of cursorial basal dinosauromorphs were designed to work at high velocity. With increasing body size on the lineage leading to Sauropoda, the hindlimb shows adaptations to work at high force, which is consistent with increasing body mass.

Ichnofossils have been shown to be a valuable source of information on aspects of locomotion not apparent from osteology alone, providing direct evidence on the locomotion of dinosauromorphs. Thus, ichnofossils not only serve as a control of the results of a functional morphological study, but draw new light on the locomotion of dinosauromorphs to sauropods. The idea of initial facultative bipedal locomotion of dinosauromorphs was first gained from the ichnofossil record. In addition, ichnofossils usually serve as source of information on speed. Whereas as tracks and trackways assigned to basal dinosauromorphs show that there trackmakers were able to fast acceleration, sauropods were restricted to slow walking, achieving speeds of 3 – 6 km/hr.

Most interestingly, almost all taxa included in this study show features in the osteology (e.g. proportions, robusticity) and a locomotor habit as predicted for their body size. Only two taxa were found to be an exception: *Anchisaurus* and *Silesaurus*. *Anchisaurus* is exceptionally small for a non-sauropodan sauropodomorph. With a body mass of 10 – 40 kg, *Anchisaurus* is nested within sauropodomorphs with a body mass of 1000 – 4000 kg. Based on the small body size, *Anchisaurus* was often regarded as a basal sauropodomorph. However, the proportions of the hindlimb of *Anchisaurus* correspond with sauropodomorphs with a body mass of 1000 – 4000 kg. This indicates that *Anchisaurus* is the descendant of group a large sauropodomorphs and the proportions were retained despite of the decreased body size. In *Silesaurus*, the robusticity of the limb elements as well as the proportions of the hindlimb and the obligate quadrupedal locomotor posture resemble dinosauromorphs on the lineage to sauropods with a body mass of >1000 kg. The body mass of *Silesaurus,* however, was estimated with 4 – 7 kg. This relatively graviportal locomotor habit of *Silesaurus* might be explained with development of an obligate herbivorous diet.

7.2 GENERAL CONCLUSIONS

Using an integrative approach to study the evolution of the osteology and myology as well as the hindlimb posture and locomotor posture of dinosauromorphs on the lineage to sauropods considerably improved our understanding of the effect of increasing body size on the morphofunctional evolution of the locomotor apparatus.

Traditionally, comparative anatomy or functional morphology or a combination of both has been used to study the locomotion of dinosauromorphs. Integrating ichnofossils and biomechanics allowed to gain new insights into the locomotor function of dinosauromorphs on the lineage to sauropods and to question some of the traditional ideas on locomotion, which were considered well established and commonly not questioned. In the past, an erect gait of basal dinosauromorphs and the initial bipedal locomotion of dinosaurs were generally accepted. The idea that sauropodomorphs were initially obligate bipeds and that they evolved an obligate quadrupedal locomotor posture with increasing body size is based on the idea of initial obligate bipedal locomotion of dinosaurs. The study presented here has shown that the paradigm of initial obligate bipedal locomotion in dinosaurs is not highly questionable. In contrast, it was demonstrated that features commonly regarded as indicator for an obligate bipedal locomotion were indicators for quadrupedal locomotion. The paradigm shift allows new insights into the physiology and ecology of dinosauromorphs.

Biomechanics allows to generate rules on the locomotor function of a taxon. Testing these biomechanical rules using a large number of taxa enables to generate general rules on the locomotor function of dinosauromorphs and – applying it on an explicit phylogenetic framework – its evolution. Moreover, general biomechanical rules are independent from phylogenetic hypothesis and thus provide a valuable approach to test the phylogenetic independence of features associated with locomotion and thus to test phylogenetic hypothesis.

Ichnofossils are the only source of information representing direct evidence of locomotion of extinct tetrapods. With few exception, the potential of ichnofossils was not used in the past. The evaluation of the applicability of ichnofossils changed with the establishment of the synapomorphy-based approach. Nonetheless, most authors hesitate to assign ichnofossils to body fossils when the tracks and trackways do not agree with the assumed locomotor function of the body fossil. By doing so, ichnofossils only confirm the well-established ideas.

Both biomechanics and ichnofossils showed that body size is an important variable affecting the hindlimb posture and locomotor posture in dinosauromorphs. Different hindlimb postures (sprawling, intermediate, or erect), and locomotor postures (obligate quadrupedal or obligate bipedal), are reflected in features in the osteology and myology. The correlation of hindlimb posture and locomotor posture and therewith the correlation of osteological and myological characters to body size results in the constitution of adaptive ranges. The presence of adaptive ranges has impact on phylogenetic hypothesis: taxa of similar body size probably share more characters than more closely related taxa in which the body size differ significantly. Following this consideration, generating phylogenetic hypothesis should take into the impact of body size on anatomy.

Whereas the study presented here focused on the pelvic girdle and hindlimb, body size affects all parts of the cranial and postcranial skeleton. Thus, adaptive ranges exist for the skull, pectoral girdle and forelimbs, as well as for the axial skeleton. Furthermore, body size is only one variable affecting the form and function of an organism. In order to improve our understanding the function and the evolution of extinct tetrapods – not only dinosauromorphs – both the impact of body size on other parts of the cranial and postcranial skeletons and other variables affecting the form and function of an organism have to be studied.

7.3 FUTURE PERSPECITVES

One of the challenges in the study of sauropod locomotor function will be to create 3D musculoskeletal computer models to study muscle moment arms. Muscle moment arms are one of the major variables of skeletal muscle function and thus provide information on stance, gait and locomotor speed. The reconstruction of the evolutionary transition of the osteology and myology of the pelvic girdle and hindlimb, as well as new insights of the evolution of the hindlimb posture and locomotor posture gained in this study will provide the basis for such an approach.

The study presented here has shown that the evolutionary transitions of the osteology correlate to increasing body size. On the one hand, this might simply reflect that the evolution of sauropods is characterized by increasing body size. On the other hand, this could also indicate that phylogenetic hypotheses of dinosauromorphs on the lineage to sauropods are actually not reflecting osteological transitions based on a common evolutionary history but due to biomechanical requirements. This hypothesis can only tested by applying a phylogenetic independence approach, in which structural characteristic are tested for phylogenetic independence.

The effect of adaptive ranges and how physiological and ecological variables have impact on the bauplan / anatomy of an organism and thus on the theoretical maximum body size is one of the major challenges when enormous body size is studied.

Chapter 8

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03 – 04/2002	continental Upper Cretaceous of Esperaza, Southern France; continental Upper Jurassic of Portugal.
08 – 09/2001	continental Upper Cretaceous of Esperaza, Southern France.
3 – 04/2000	continental Upper Triassic and Lower Jurassic of the Little Karoo, Southern Africa.
08/1999	continental Upper Cretaceous of Esperaza, Southern France.
08/2000	continental Upper Cretaceous of Northern Spain and Southern France.

Professional Experience

03/2008 – 09/2008	Scientific assistant, Bayerischen Staatssammlung für Paläontologie und Geologie, München; reasearch project "Saurischian dinosaurs from the Elliot Formation of South Africa: anatomy, ecology, and evolution"; organization of the field campaign, field work, preparation, and research; project leader: Dr. O.W.M. Rauhut; international co-operation with Dr. A. Yates (WITS Johannisburg), Dr. P. Barrett (NHM London) and Dr. R. Butler (NHM London).

01/2005 – 04/2007	Scientific assistant, Bayerischen Staatssammlung für Paläontologie und Geologie, München; DFG project RA 1012/2.
05 – 12/2004	Scientific assistant, Museum für Naturkunde der Humboldt Universität, Berlin; DFG project RA 1012/2.
10/2002 – 09/2004	Student assistant, Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, Freie Universität Berlin; research project: "Phylogeny and paleobiogeography of terrestrial vertebrate of the Upper Jurassic of Kirghizia"; project leader: Prof. Martin; prepration of material.
10/1999 – 09/2001	Tutor, Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, Freie Universität Berlin; duties included tutoring and remedial teaching of undergraduates in paleontology and biology.

Teaching experience

WS 2004/2005	Paleontology for Biologists; Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, Freie Universität Berlin.
SS 2002	Osteology of the vertebrates; Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, Freie Universität Berlin.

Language abilities

german	(native)
English	(fluent)
french	(basic)

Grants and Awards

since 2007	Mentee of the Mentoring program of the LMUgeosciences (for excellent trainee reasearcher).
01/2006	Synthesys travel grant GB-TAF-1672, London.
10/2005	Doris O. and Samuel P. Welles Research Fund of the Paleontological Museum, University of California, Berkeley.
07/2004	Synthesys travel grant FR-TAF-933, Paris.

Membership in professional associations

since 2005	The Palaeontological Association
since 2001	Society of Vertebrate Paleontology
since 2000	Die Paläontologische Gesellschaft

Regina Fechner, 25. May 2009