

## Homoplasy and the evolution of dinosaur locomotion

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*Abstract.*—In this paper, I survey hindlimb and pelvic anatomy across non-avian dinosaurs and analyze these within a cladistic framework to quantify patterns of change within the locomotor apparatus. Specifically, I attempt to identify where homoplasy constitutes parallelism and may thereby be used to infer similar selective pressures on hindlimb function. Traditional methods of discrete character optimization are used along with two methods for evaluating changes in continuous characters in a phylogenetic context (squared-change parsimony and clade rank correlation). Resultant patterns are evaluated in light of the biomechanics of locomotion and the relationship between form and function in extant terrestrial vertebrates.

Although non-avian dinosaurian locomotor morphology is strikingly uniform, these analyses reveal the repeated derivations of several morphological features that have potential relevance for hindlimb locomotor function. Anterior and posterior iliac expansion, a medially oriented femoral head, and an elevated femoral lesser trochanter each evolved independently multiple times within Dinosauria. These changes probably reflect enlargement of several hindlimb muscles as well as a general switch in their predominant function from abduction-adduction (characteristic of “sprawling” limb postures) to protraction-retraction (characteristic of parasagittal, or “erect,” limb postures). Several “avian” characteristics are shared with more basal theropods, and many were acquired convergently in other dinosaurian lineages. The evolution of the avian hindlimb therefore represents a cumulative acquisition of characters, many of which were quite far removed in time and function from the origin of flight.

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### Introduction

The evolution of non-avian dinosaurs presents a promising system for the study of terrestrial locomotor evolution for several reasons. First, although non-avian dinosaurs spanned at least four orders of body size (Peczis 1994), they were constrained to a predominantly parasagittal (i.e., “erect”) limb posture from their origin (Sereno 1991a; Novas 1996). Second, their general pelvic and hindlimb morphology is markedly uniform (Charig 1972; Walker 1977; Carrano 1999), showing little evidence for deviations that would imply development of more specialized forms of locomotion (e.g., fossoriality, arboreality). This apparent evolutionary stability makes the locomotor transition from non-avian theropods to birds even more remarkable.

This transition involved modifications of the entire musculoskeletal system, not simply the structures directly associated with flight. As more detailed phylogenetic studies have focused on theropod dinosaurs and the origin of birds (e.g., Holtz 1994, in press; Norrell and

Makovicky 1997; Forster et al. 1998), it has become clear that many features formerly thought to typify birds are characteristic of much more inclusive clades. In fact, many of the changes involved in the evolution of birds occurred within non-avian ornithodirans, and therefore it is impossible to understand or evaluate these changes without an examination of non-avian dinosaur evolution. In particular, bipedalism was modified significantly throughout non-avian dinosaur evolution, despite the fact that its origination from the quadrupedal posture of basal archosauromorphs remains obscure (Sereno 1991a; Novas 1996). The bipedalism inherited by birds was not identical to that of basal ornithodirans, nor was it strictly identical to that of basal theropods or even basal tetanurans (Carrano 1998a,b). Numerous osteological changes support hypotheses of change in muscle anatomy, arrangement, and function throughout the origin of birds (Gatesy 1990, 1995).

Unfortunately, it is not possible to test hypotheses of locomotor function in fossil taxa directly. The extant phylogenetic bracket (e.g.,

Witmer 1995) provided by crocodylians and birds can use bone and muscle homologies to constrain such hypotheses, but its power is compromised here by the profound differences between these two living groups (Romer 1923b, 1927a; Gatesy 1990, 1995). Furthermore, although extant crocodylians are appealing analogues for primitive (quadrupedal, "sprawling") archosaurs, they are likely to exhibit derived locomotor features as well. Therefore, the transition to the parasagittal posture of dinosaurs and birds cannot simply be equated to a transition between the crocodylian and avian conditions. It is necessary to include information from intermediate, and in this case entirely extinct, taxa. What kind of information may be added, and how may it be used to resolve or clarify aspects of this evolutionary transition?

In addition to inferences about homology acquired through the extant phylogenetic bracket, the mechanical importance of structural changes can also be inferred from homoplasy. Homoplasy often acts as "background noise" with regard to phylogenetic reconstruction. In many instances, homoplasy may simply be due to the increased probability of repeated states in a character given sufficient evolutionary time, but in others it may represent the effects of some external constraint (mechanical, developmental, ecological) on a biological system. In these cases, homoplasy can provide a focal point for further investigation into such constraints and help reveal underlying selective pressures affecting the evolution of a lineage (Brooks and McLennan 1991; Brooks 1996). The assumption is that homoplasy reflects similar responses on the part of different lineages to common, fundamentally similar selective pressures. Among different types of homoplasy, parallelism—the acquisition of similar derived states by closely related lineages that share a common primitive state—may be particularly useful because it reflects similar modifications of a (presumably) identical original system.

In this paper, I identify and quantify instances of parallelism in hindlimb and pelvic osteology within Dinosauria. Because dinosaur evolution involved a radiation into sev-

eral diverse clades, similar evolutionary trends in these lineages can be used as independent indicators of constraint. I evaluate these patterns in the context of terrestrial locomotor biomechanics because of the strong form-function correlations observed in extant taxa, which are additionally bolstered by considerable theoretical support (e.g., Carter 1987; Currey 1987; Biewener 1989; Bertram and Biewener 1990). These same biomechanical principles can also allow hindlimb and pelvic morphology to be used to assess general locomotor habit (*sensu* Carrano 1999) in individual dinosaur taxa and, where appropriate, larger clades. Nevertheless, other biological factors, such as developmental constraints (e.g., Wake 1991), may be at work and cannot be excluded as possible explanations for parallel evolution for the simple reason that developmental data are unavailable for extinct taxa.

Finally, I investigate the implications of these patterns and their corresponding functional explanations for three aspects of dinosaur evolution: (1) the changes likely to have occurred during the origin of ornithomimid bipedalism; (2) the subsequent modifications of this ancestral condition up to and including the evolution of various "avian" locomotor features within non-avian theropods; and (3) the parallel evolution of several key locomotor features in different dinosaur clades.

### Materials and Methods

*Data Collection.*—Locomotor morphology was evaluated both qualitatively and quantitatively. I examined 1460 dinosaur specimens, representing 335 species from all major dinosaur clades, as well as four basal dinosauromorphs (Appendix 1 in Carrano 1998b, supplemented with additional data), a subset of which was used in quantitative analyses.

I measured the following: femoral length (FL), distance between the lesser (or "anterior") trochanter and the proximal end of the femur (LT), angle of the femoral head relative to the mediolateral plane (HA), and the lengths of the iliac pre- and postacetabular blades (AL, PL) (Fig. 1). These features were chosen because they represent the origination and insertion points for several hindlimb muscles, as

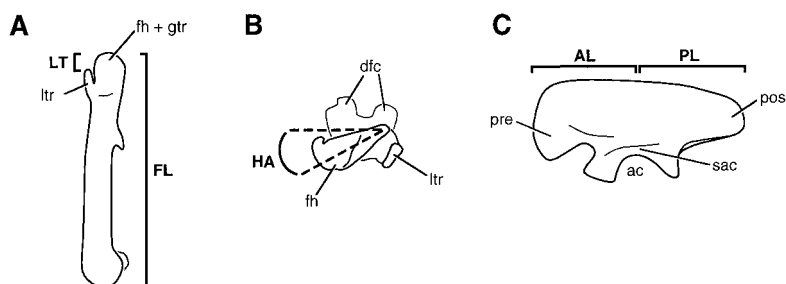


FIGURE 1. Measurements used in this study. A, left femur in lateral view, with proximal toward the top. B, Left femur in proximal view, with lateral toward the right. C, Left ilium in lateral view, with dorsal toward the top. Measurements: AL = preacetabulum length, FL = femur length, HA = angle between femoral head long axis and mediolateral plane, LT = distance from lesser trochanter to proximal end of femur, PL = postacetabulum length. Morphological features: ac = acetabulum, dfc = distal femoral condyles, fh = femoral head, gtr = greater trochanter, ltr = lesser trochanter, post = postacetabular process, pre = preacetabular process, sac = supra-acetabular crest.

well as the out-levers for muscle activity. Data were taken with Mitutoyo dial calipers (<200 mm) or measuring tape (>200 mm) and documented with photographs. When direct access to specimens was not possible, measured data were supplemented with data from the literature and measurements taken from photographs.

In addition, I made qualitative observations on these and other morphological structures, noting particularly the presence/absence, size, and shape of possible muscle attachment sites. I made similar observations on the hindlimb and pelvic osteology and musculature of extant archosaurs (*Alligator*, *Meleagris*, and *Gallus*) and combined them with those made by previous authors on these and other extant archosaurian taxa (e.g., Shufeldt 1909; Romer 1927a, 1942; Raikow 1985; Gatesy 1994, 1997, 1999a,b; Patak and Baldwin 1998). These ultimately provided a set of qualitative data that was used to help interpret the quantitative patterns observed in the measurement data set. For consistency with the modern literature, I employ common-use spellings of several muscles instead of Romer's (1923a).

I used the direct measurements of femoral head orientation in the data analyses, but calculated three indices from the remaining measurements that would specifically reflect mechanical changes in the dinosaurian pelvic and hindlimb skeleton. The protractors and retractors of the hindlimb originate on the anterior and posterior blades of the ilium, respectively. Increases in the anterior or poste-

rior extent of these blades would increase both the cross-sectional area of these muscles and the anteroposterior components of their lines of action. Relative anterior (RA) and posterior (RP) expansions of the ilium were calculated as percentages of femur length:

$$RA = AL/FL \quad (1)$$

$$RP = PL/FL \quad (2)$$

where AL and PL are measures of the in-levers, and FL the out-lever, of muscle action. Note that these indices *increase* as the ilium becomes more anteroposteriorly elongate.

Derivatives of the primitive *M. iliofemoralis* insert on or near the femoral lesser trochanter, a proximally projecting bump or lamina on the anterolateral edge of the femur (Romer 1923a,b, 1927b). These derivatives function as femoral protractors and rotators in extant birds (the only extant archosaurs with a parasagittal gait) (Gatesy 1999b). Modifications in the position of the proximal end of this trochanter would alter the moment arms of the attached muscles with respect to the out-lever of activity, the distal end of the femur. Therefore, the relative distance of the lesser trochanter from the proximal end of the femur (RLT) was calculated relative to total femur length:

$$RLT = (LT / FL) * 100 \quad (3)$$

where multiplication by 100 simply produces a percentage. Note that RLT *decreases* as the lesser trochanter approaches the proximal end of the femur.

*Data Analysis.*—I analyzed the measurement data in a phylogenetic context to identify instances of parallelism and quantify patterns of change. This involved both discrete and continuous data, and as such required the use of several different techniques. Not surprisingly, optimizations of discretely coded data tend to produce less ambiguous results, but often at the expense of data resolution. In other words, discrete coding of continuous data can acquire clarity through oversimplification. The converse, however, is also true. Continuous data are inherently difficult to analyze in a discrete context. Even when a technique is available to map these data onto a phylogeny, changes between successive taxa (or putative ancestors and descendants) are likely to be very small in any well-sampled lineage. Thus, stepwise changes across the tree are minimized relative to the total differences between distant endpoints, as these differences are distributed (usually as evenly as possible) across the branches of the tree. One possible solution is to compare the terminal taxa in a clade only with their most recent common ancestor, but one problem is that more basal ancestral nodes are also more likely to have associated higher error values.

Femoral head orientation exhibits only two states—45° anteromedial and fully medial—and these were coded discretely. Homoplasies were identified when independent occurrences of the derived state (fully medial) occurred, and were interpreted as unambiguous when both accelerated and delayed transformations produced identical reconstructions (e.g., Swofford 1993; Schultz et al. 1996). The three indices were also coded discretely, but in these cases such coding represents a simplification of their original continuous distributions. AL and PL were each given two states: (1) unexpanded and (2) expanded. AT was given three states: (1) not raised above the femoral shaft, (2) intermediate in height between the shaft surface and the proximal end of the bone, and (3) flush with the proximal end. These states were mapped onto the phylogeny, optimized, and analyzed in the same manner as femoral head orientation.

I also analyzed the indices as continuous characters. Continuous characters present

problems for reconstructing their distribution and patterns of change across the discrete topology of a cladistic phylogeny, and there is no consensus on how best to treat such data in a phylogenetic context. Therefore, I analyzed these indices using two methods: squared-change parsimony (SCP) and Spearman-rank correlation (SRC).

First, all three indices were mapped onto the phylogeny and optimized using the squared-change parsimony option in MacClade 3.01 (Maddison and Maddison 1992). Squared-change parsimony reconstructs ancestral (nodal) values by using the values of terminal taxa, but unlike independent contrasts (Felsenstein 1985) it attempts to minimize the sum of squared changes across all branches of the phylogeny (Huey and Bennett 1987; Maddison 1991; Maddison and Maddison 1992; Polly 1999). I analyzed patterns of change by calculating paired comparisons between each ancestral and descendant state (EACH) (Harvey and Pagel 1991: pp. 162–165) and between the most recent common ancestor of a clade and all its descendants (MRCA). Mean values of the descendant states were compared with calculated ancestral values and deemed significantly different if they exceeded the ancestral value by more than one standard deviation. Mean and median differences, the number of increases versus decreases (analyzed with a one-sample sign test), and the sum change for various clades were used to indicate directionality of trends within various clades and for Dinosauria as a whole. I considered the mean differences to be significant if they were more than one standard deviation away from zero.

Unfortunately, squared-change parsimony has several statistical pitfalls, perhaps the most serious being that it has the highest probability of accurately reconstructing ancestral states when changes across the tree are random, i.e., they proceed under a Brownian-motion model (Martins 1999). If, as is the case here, considerable directionality is suspected, the accuracy of ancestral-state reconstructions must also be questioned (Garland et al. 1999; Martins 1999). This does not mean that these reconstructions are necessarily inaccurate, only less probably accurate. Furthermore, be-

cause the method attempts to minimize the sum of squared changes across the tree, resultant ancestor-descendant changes can be quite small. Results from this method are therefore interpreted cautiously.

Second, I analyzed these indices without reconstructing ancestral states, but instead by examining the correlation of terminal values with clade rank. I used the nonparametric Spearman-rank correlation (Sokal and Rohlf 1995) to test for congruence in rank order between two variables (here, a taxon's index value and its clade rank). Strong, significant correlations (a strongly positive or negative rho associated with a significant *p*-value) would be evidence of a trend within in a data set or lineage. Parallelism would appear as multiple lineages exhibiting similar, independent trends in a particular direction. In other words, more highly nested taxa of different lineages would share similarly higher (or lower) index values relative to more basal taxa. Because examination of a large, more symmetrical cladogram can obscure trends within individual lineages by overlapping several discordant patterns (as has been noted in age rank-clade rank correlation studies [Norrell and Novacek 1992]), I examined several in-group dinosaur clades separately from Dinosauria.

The phylogeny used here included 107 terminal taxa and represents an amalgamation of several recent studies (Fig. 2) (Holtz 1994, in press; Novas 1996; Wilson and Sereno 1998; Forster et al. 1998; Sereno 1999). The number of terminal taxa included in a specific analysis depended on which taxa could be coded for that particular variable; therefore, the phylogenies for each variable differ with respect to the presence or absence of certain taxa but all are mutually congruent. All terminal taxa are represented either by individual specimens or averages of several adult individuals.

### Results

*Orientation of the Femoral Head.*—The femoral head is primitively anteromedial, as exhibited by basal dinosauromorphs, prosauropods, herrerasaurids and *Eoraptor*, and basal ornithischians. It is shifted into a fully medial orientation at the nodes Neornithischia, Sauropoda, and Neotetanurae (Figs. 3, 4). These

transitions occurred independently, but intermediate forms are absent in each instance: the femoral head is oriented at 40–45° anteromedial in primitive forms, and nearly plumb with the mediolateral axis in derived forms. Using the present cladistic hypothesis of relationships, these changes are never followed by reversals in any subsequent lineages (Fig. 4).

*Anterior and Posterior Expansions of the Ilium.*—When coded discretely, character-state optimization indicates that elongation of the preacetabular process unambiguously occurs three times independently early in dinosaur evolution (Fig. 5): at the nodes Ornithischia, Sauropoda, and Neotheropoda. Dinosauromorphs, basal theropods (*Eoraptor* and herrerasaurids), and prosauropods share an unexpanded anterior ilium (RA < 0.3 [=30% of femur length]) (Table 1, Fig. 5); thus, this condition is inferred to be primitive for both Saurischia and Dinosauria. Elongation occurs to varying degrees in derived lineages, with RA occasionally exceeding 0.5 (e.g., Ceratopsidae, Stegosauria, Ankylosauria; Table 1).

Patterns of change in RA are generally consistent with the discrete pattern when it is treated as a continuous character. Using squared-change parsimony, most lineages of dinosaurs show nonsignificant trends toward lengthening the preacetabular process (increasing RA) (Table 1, Fig. 6). Mean RA values are larger than ancestral values for nine groups, three of which exceed their ancestral values by more than one standard deviation (Dinosauroomorpha, Theropoda, and Thyreophora). Five groups (particularly Prosauropoda) show relatively smaller mean values of RA, with one (Prosauropoda) smaller by more than one standard deviation.

Trends are more ambiguous when ancestor-descendant changes are calculated. The mean, median, sum, and number of changes indicate more trends toward increasing RA than toward decreasing it, but several decreases are apparent (Table 2). MRCA generally achieves more significant results than EACH, and the various statistics produce more congruent results. The only consistently negative changes (i.e., negative in all statistics under both EACH and MRCA) occur in Prosauropoda and Stegosauria, but in each case both the magnitude



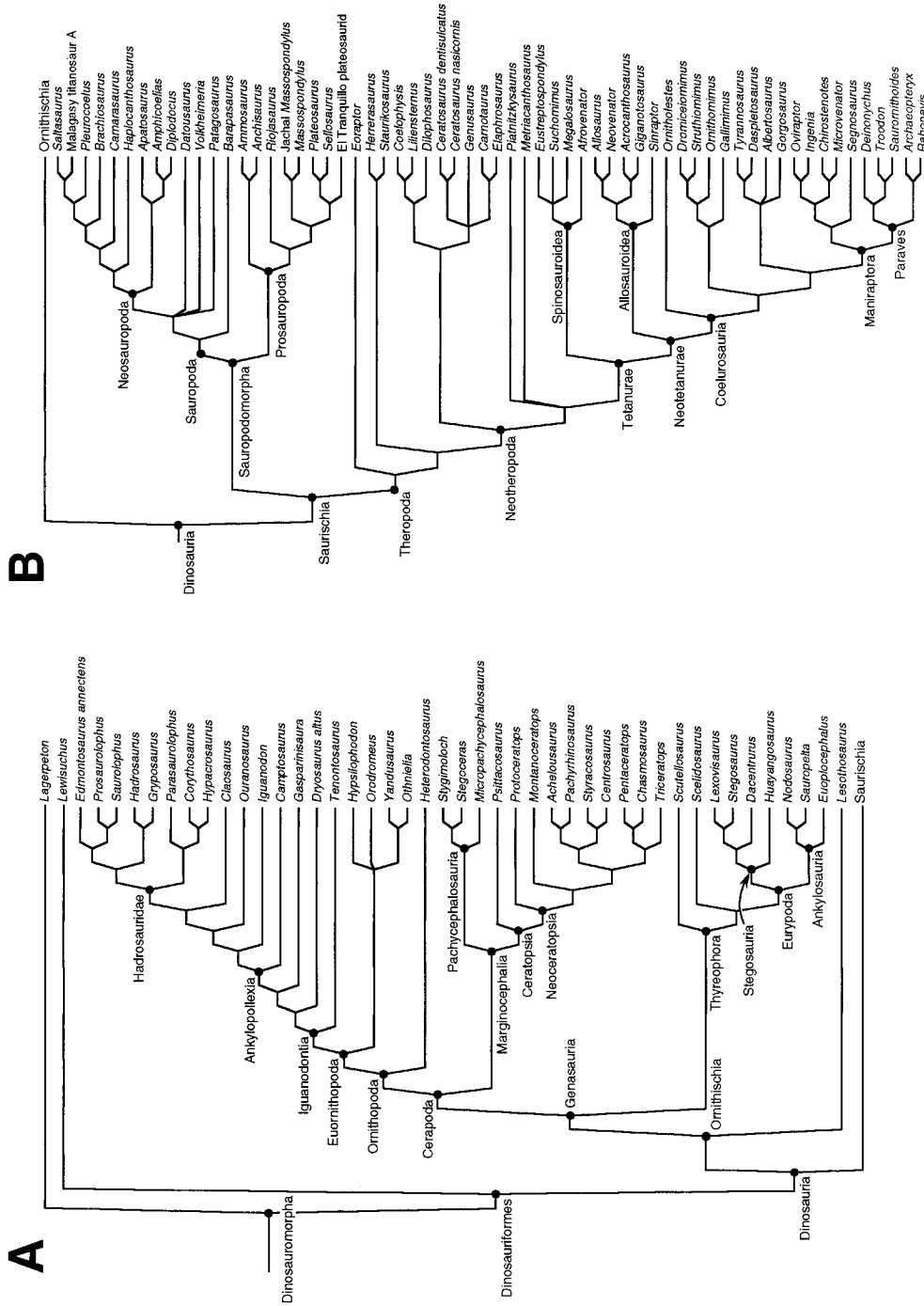


FIGURE 2. Phylogeny of 107 taxa used for character-state reconstruction in this study. A, Ornithischia and basal Dinosauriformes, modified from Novas 1996; Sereno 1986, 1999; and Sereno and Arcucci 1993, 1994. B, Saurischia, modified from Gauthier 1986; Holtz 1994, in press; Sues 1997; Forster et al. 1998; Wilson and Sereno 1998; and Sereno 1999. Several additional taxa were examined qualitatively but were not included in the quantitative analyses because the necessary measurements could not be taken.

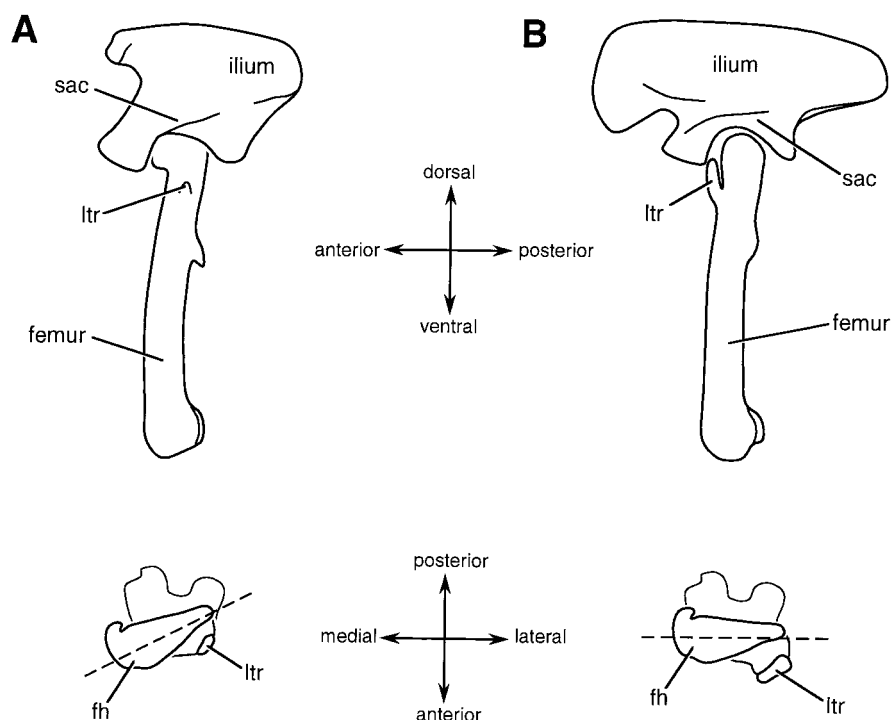


FIGURE 3. Changes in femoral head orientation within Dinosauria. A, In primitive taxa (e.g., *Herrerasaurus*), the femoral head is oriented anteromedially and articulates beneath the supra-acetabular crest of the ilium at an angle with the mediolateral axis. B, In derived forms (e.g., *Gorgosaurus*), the femoral head is fully medially oriented and the supra-acetabular crest is reduced. In each diagram, the top illustration is a lateral view of the left femur and ilium in articulation, and the bottom illustration is a proximal view of the same femur. Abbreviations as in Figure 1. Dashed line = long axis of femoral head.

and significance are quite low. Similar, but less ambiguous, results are apparent when Spearman-rank correlation is used. In most lineages, derived taxa tend to have higher RA values, significantly so in Dinosauromorpha, Dinosauria, Saurischia, and Theropoda (Table 3). Several ornithischian clades show decreases in RA with increasing clade rank, although most also exhibit very small sample sizes.

Reconstruction of RP as a discrete character indicates that a short postacetabular process is primitive for Dinosauria, as observed in basal dinosauromorphs, basal theropods, and basal ornithischians. It was expanded several times within the group, although not synchronously with the preacetabulum (Fig. 5). Again, this occurred three times independently, at the nodes Cerapoda, Neotheropoda, and Sauropodomorpha. Primitively, RP is only 1.0–1.4, but derived lineages may extend the postacetabulum such that RP is as high as 5.6 (Table 1).

Optimization of a continuous RP using squared-change parsimony reveals that increases again characterize most lineages, generally with low significance levels (Table 4). Statistical trends indicate a tendency toward increasing RP, with slightly positive mean, median, and sum changes, as well as more positive than negative changes (Table 4). EACH and MRCA achieve similar results, with the latter tending toward higher significance levels. The only consistent decrease occurs in Stegosauria, whereas consistent increases are present in most other groups. Spearman-rank correlation demonstrates that derived taxa tend to have higher RP values, with 12 positive correlations (five significant) and three negative correlations (one significant). Correlations are generally high and more significant than those for RA (Table 5, Fig. 7).

*Morphology of the Lesser Trochanter.*—Primitively, the lesser trochanter is small and no

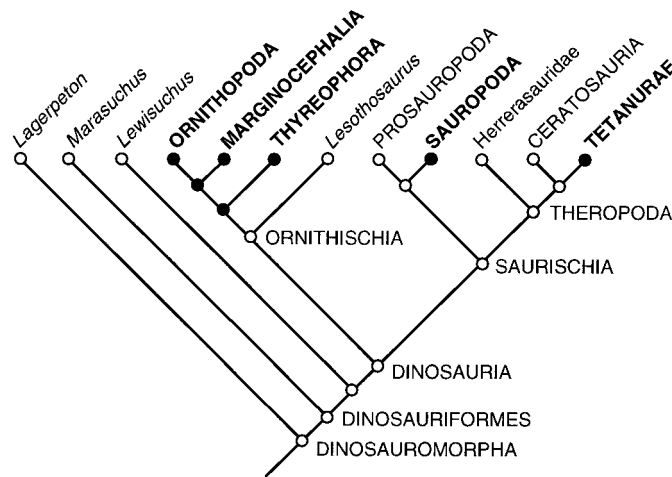


FIGURE 4. Changes in femoral-head orientation within Dinosauria. Note that optimizations produce unambiguous ancestral-state reconstructions, and that acquisition of a medial femoral head is never followed by reversal to the primitive state. Open circles/plain text = anteromedial femoral head, filled circles/bold text = fully medial femoral head (angle with mediolateral plane = 0°).

larger than a rugose bump on the femoral shaft (the “not raised” state). This condition is evident in basal dinosauromorphs, basal theropods, Prosauropoda, and Sauropoda. Under discrete coding, there are three independent

acquisitions of the “intermediate” derived state (Ornithischia, Ceratosauroidea, and Tetanurae; Fig. 8), although phylogenetic revisions of Theropoda (Forster 1999; Carrano and Sampson 1999) would reduce the latter two in-

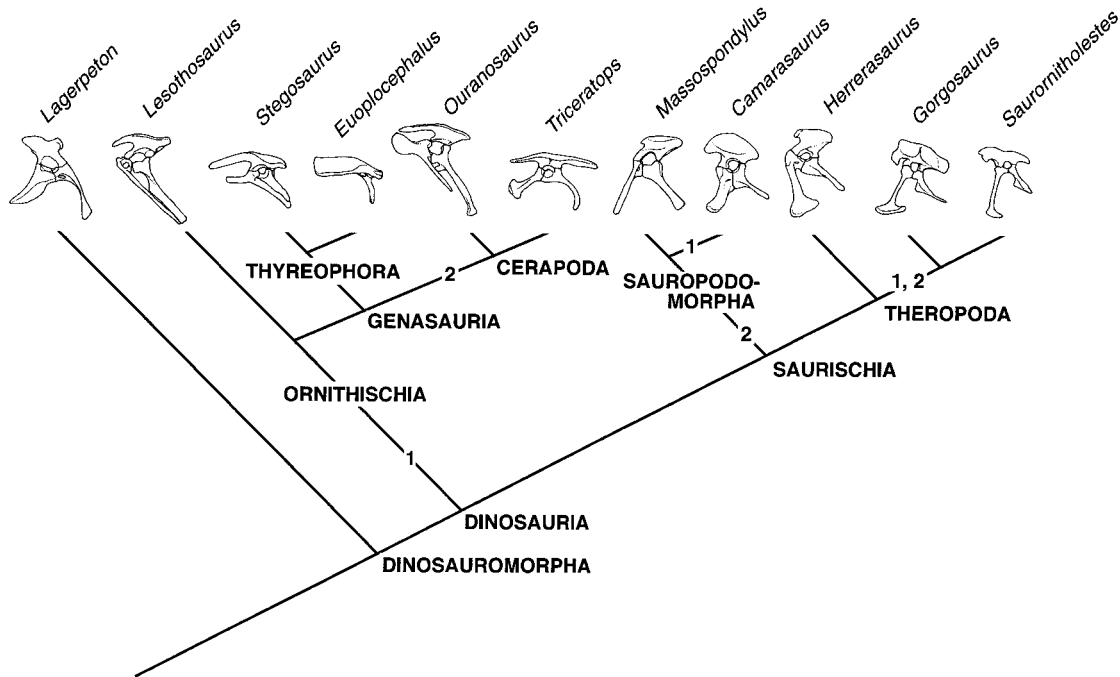


FIGURE 5. Changes in ilium morphology within Dinosauria. Primitively (e.g., *Lagerpeton*), the ilium has short pre- and postacetabular processes. These processes are expanded independently and asynchronously in different lineages within both Saurischia and Ornithischia. 1 = expansion of preacetabulum, 2 = expansion of postacetabulum. All illustrations are of the left pelvis in lateral view, with anterior to the left (the ilium is the uppermost bone here).



TABLE 1. Mean (RA, RP, RLT) values (not mean changes) and ancestral (RA\*, RP\*, RLT\*) values of the three indices, the latter reconstructed using squared-change parsimony. Note that ancestral values tend to be lower than the mean values for RA and RP and higher than the mean value for RLT.

| Clade               | RA          | RA*  | RP          | RP*  | RLT          | RLT*  |
|---------------------|-------------|------|-------------|------|--------------|-------|
| Dinosauromorpha     | 0.43 ± 0.14 | 0.23 | 0.43 ± 0.12 | 0.17 | 7.98 ± 5.27  | 12.15 |
| <b>Dinosauria</b>   | 0.43 ± 0.14 | 0.32 | 0.44 ± 0.12 | 0.29 | 9.69 ± 5.65  | 8.72  |
| <b>Saurischia</b>   | 0.37 ± 0.09 | 0.31 | 0.40 ± 0.08 | 0.32 | 9.67 ± 5.69  | 10.77 |
| Theropoda           | 0.38 ± 0.09 | 0.26 | 0.42 ± 0.09 | 0.32 | 7.68 ± 5.39  | 11.81 |
| Sauropodomorpha     | 0.34 ± 0.08 | 0.34 | 0.37 ± 0.07 | 0.34 | 13.86 ± 3.73 | 10.77 |
| Prosauropoda        | 0.26 ± 0.07 | 0.34 | 0.41 ± 0.06 | 0.35 | 15.76 ± 1.61 | 14.17 |
| Sauropoda           | 0.39 ± 0.04 | 0.37 | 0.34 ± 0.07 | 0.36 | 12.51 ± 3.21 | 10.43 |
| <b>Ornithischia</b> | 0.52 ± 0.14 | 0.43 | 0.48 ± 0.13 | 0.34 | 5.87 ± 5.06  | 6.42  |
| Ornithopoda         | 0.44 ± 0.07 | 0.46 | 0.43 ± 0.07 | 0.41 | 3.50 ± 1.69  | 3.97  |
| Marginocephalia     | 0.52 ± 0.05 | 0.48 | 0.61 ± 0.13 | 0.46 | 4.65 ± 2.01  | 4.33  |
| Pachycephalosauria  | 0.47 ± 0.04 | 0.48 | 0.40 ± 0.05 | 0.40 | 4.79 ± 1.00  | 4.67  |
| Ceratopsia          | 0.54 ± 0.05 | 0.50 | 0.67 ± 0.07 | 0.54 | 4.61 ± 2.17  | 3.77  |
| Thyreophora         | 0.71 ± 0.18 | 0.57 | 0.42 ± 0.11 | 0.43 | 13.80 ± 6.81 | 5.06  |
| Stegosauria         | 0.63 ± 0.11 | 0.73 | 0.35 ± 0.12 | 0.45 | 12.30 ± 1.18 | 12.32 |
| Ankylosauria        | 0.88 ± 0.23 | 0.93 | 0.49 ± 0.12 | 0.46 | 19.47 ± 4.65 | 15.58 |

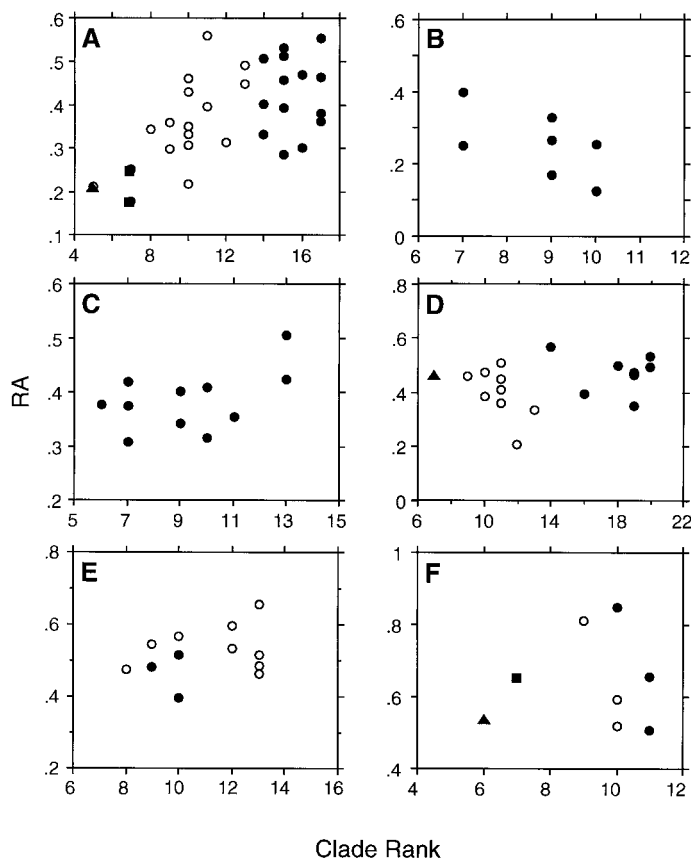


FIGURE 6. Correlations between terminal values for RA and clade rank. Note that there is a generally positive (though not significant) correlation between these two values in most groups (see Table 3). A, Theropoda; triangle = *Eoraptor*, squares = Herrerasauridae, open circles = basal neotheropods, filled circles = Coelurosauria. B, Prosauropoda. C, Sauropoda. D, Ornithopoda; triangle = *Heterodontosaurus*, closed circles = basal euornithopods, filled circles—Hadrosauridae E, Marginocephalia; filled circles = Pachycephalosauria, open circles = Ceratopsia. F, Thyreophora; triangle = *Scutellosaurus*, square = *Scelidosaurus*, open circles = Stegosauria, closed circles = Ankylosauria.

TABLE 2. Squared-change parsimony results for RA. Mean, sum, and median of ancestor-descendant changes, with numbers of increases and decreases; *p*-value refers to results of a one-sample sign test. A, Analyzed using all ancestor-descendant comparisons within the specified clade (*EACH*). B, Analyzed using comparisons only between most recent common ancestor and descendant taxa of specified clade (*MRCA*). Asterisks indicate significant correlations.

| Clade               | Mean           | Sum    | Median | +  | -  | <i>p</i> | <i>n</i> |
|---------------------|----------------|--------|--------|----|----|----------|----------|
| A. <i>EACH</i>      |                |        |        |    |    |          |          |
| Dinosauromorpha     | 0.003 ± 0.058  | 0.512  | -0.002 | 85 | 90 | 0.7624   | 175      |
| <b>Dinosauria</b>   | 0.004 ± 0.057  | 0.623  | -0.002 | 84 | 88 | 0.8191   | 172      |
| <b>Saurischia</b>   | 0.003 ± 0.047  | 0.269  | -0.001 | 44 | 45 | >0.9999  | 99       |
| Theropoda           | 0.003 ± 0.050  | 0.189  | 0.001  | 29 | 28 | >0.9999  | 57       |
| Sauropodomorpha     | 0.000 ± 0.040  | -0.012 | -0.004 | 14 | 16 | 0.8555   | 30       |
| Prosauropoda        | -0.010 ± 0.050 | -0.134 | -0.016 | 5  | 8  | 0.5811   | 13       |
| Sauropoda           | 0.005 ± 0.031  | 0.093  | 0.000  | 8  | 8  | >0.9999  | 16       |
| <b>Ornithischia</b> | 0.003 ± 0.067  | 0.262  | -0.002 | 39 | 43 | 0.7407   | 82       |
| Ornithopoda         | -0.002 ± 0.047 | -0.080 | -0.003 | 15 | 22 | 0.3240   | 37       |
| Marginocephalia     | 0.002 ± 0.033  | 0.060  | 0.005  | 14 | 11 | 0.6900   | 25       |
| Ceratopsia          | 0.005 ± 0.032  | 0.087  | 0.005  | 11 | 8  | 0.6476   | 19       |
| Pachycephalosauria  | -0.006 ± 0.043 | -0.030 | -0.008 | 2  | 3  | >0.9999  | 5        |
| Thyreophora         | 0.011 ± 0.124  | 0.186  | -0.014 | 8  | 9  | >0.9999  | 17       |
| Stegosauria         | -0.033 ± 0.077 | -0.230 | -0.044 | 2  | 5  | 0.4531   | 7        |
| Ankylosauria        | 0.034 ± 0.206  | 0.170  | 0.055  | 3  | 2  | >0.9999  | 5        |
| B. <i>MRCA</i>      |                |        |        |    |    |          |          |
| Dinosauromorpha     | 0.000 ± 0.000  | 28.768 | 0.000  | 89 | 7  | <0.0001* | 96       |
| <b>Dinosauria</b>   | 0.000 ± 0.000  | 39.528 | 0.000  | 76 | 18 | <0.0001* | 94       |
| <b>Saurischia</b>   | 0.058 ± 0.101  | 2.896  | 0.061  | 37 | 13 | 0.0009*  | 50       |
| Theropoda           | 0.121 ± 0.101  | 3.860  | 0.124  | 28 | 4  | <0.0001* | 32       |
| Sauropodomorpha     | -0.004 ± 0.095 | -0.064 | 0.010  | 10 | 8  | 0.8145   | 18       |
| Prosauropoda        | -0.084 ± 0.091 | -0.589 | -0.086 | 1  | 6  | 0.1250   | 7        |
| Sauropoda           | 0.018 ± 0.056  | 0.203  | 0.010  | 7  | 4  | 0.5488   | 11       |
| <b>Ornithischia</b> | 0.086 ± 0.160  | 3.764  | 0.063  | 35 | 9  | <0.0001* | 44       |
| Ornithopoda         | -0.029 ± 0.087 | -0.606 | 0.001  | 11 | 10 | >0.9999  | 21       |
| Marginocephalia     | 0.040 ± 0.067  | 0.520  | 0.032  | 9  | 4  | 0.2668   | 13       |
| Ceratopsia          | 0.045 ± 0.060  | 0.451  | 0.042  | 7  | 3  | 0.3438   | 10       |
| Pachycephalosauria  | -0.012 ± 0.061 | -0.036 | 0.006  | 2  | 1  | >0.9999  | 3        |
| Thyreophora         | 0.140 ± 0.232  | 1.260  | 0.085  | 6  | 3  | 0.5078   | 9        |
| Stegosauria         | -0.112 ± 0.143 | -0.447 | -0.148 | 1  | 3  | 0.6250   | 4        |
| Ankylosauria        | -0.043 ± 0.322 | -0.128 | -0.087 | 1  | 2  | >0.9999  | 3        |

TABLE 3. Spearman-rank correlation results for RA. Asterisks indicate significant correlations.

| Clade               | rho    | Z      | <i>p</i> | <i>n</i> |
|---------------------|--------|--------|----------|----------|
| Dinosauromorpha     | 0.274  | 2.631  | 0.0085*  | 93       |
| <b>Dinosauria</b>   | 0.229  | 2.175  | 0.0296*  | 91       |
| <b>Saurischia</b>   | 0.510  | 3.532  | 0.0004*  | 49       |
| Theropoda           | 0.532  | 2.915  | 0.0036*  | 31       |
| Sauropodomorpha     | 0.155  | 0.640  | 0.5219   | 18       |
| Prosauropoda        | -0.393 | -0.962 | 0.3359   | 7        |
| Sauropoda           | 0.393  | 1.243  | 0.2137   | 11       |
| <b>Ornithischia</b> | -0.201 | -1.286 | 0.1985   | 42       |
| Ornithopoda         | 0.368  | 1.604  | 0.1087   | 20       |
| Marginocephalia     | 0.231  | 0.765  | 0.4440   | 12       |
| Ceratopsia          | -0.021 | -0.059 | 0.9530   | 9        |
| Pachycephalosauria  | 0.125  | 0.177  | 0.8597   | 3        |
| Thyreophora         | -0.183 | -0.519 | 0.6041   | 9        |
| Stegosauria         | -0.550 | -0.953 | 0.3408   | 4        |
| Ankylosauria        | -0.625 | -0.884 | 0.3768   | 3        |

TABLE 4. Squared-change parsimony results for RP. Mean, sum, and median of ancestor-descendant changes, with numbers of increases and decreases;  $p$ -value refers to results of a one-sample sign test. A, Analyzed using all ancestor-descendant comparisons within the specified clade (*EACH*). B, Analyzed using comparisons only between most recent common ancestor and descendant taxa of specified clade (*MRCA*). Asterisks indicate significant correlations.

| Clade               | Mean           | Sum    | Median | +   | -  | $p$      | $n$ |
|---------------------|----------------|--------|--------|-----|----|----------|-----|
| A. <i>EACH</i>      |                |        |        |     |    |          |     |
| Dinosauromorpha     | 0.004 ± 0.049  | 0.756  | 0.006  | 100 | 75 | 0.0696*  | 175 |
| <b>Dinosauria</b>   | 0.005 ± 0.049  | 0.794  | 0.007  | 98  | 74 | 0.0795*  | 172 |
| <b>Saurischia</b>   | 0.005 ± 0.043  | 0.454  | 0.008  | 55  | 35 | 0.0446*  | 90  |
| Theropoda           | 0.004 ± 0.047  | 0.200  | 0.008  | 33  | 23 | 0.2288   | 56  |
| Sauropodomorpha     | 0.005 ± 0.038  | 0.174  | 0.007  | 20  | 12 | 0.2153   | 32  |
| Prosauropoda        | 0.009 ± 0.039  | 0.115  | 0.012  | 8   | 5  | 0.5811   | 13  |
| Sauropoda           | 0.002 ± 0.039  | 0.031  | 0.002  | 11  | 7  | 0.4807   | 18  |
| <b>Ornithischia</b> | 0.003 ± 0.055  | 0.261  | 0.001  | 42  | 39 | 0.8243   | 81  |
| Ornithopoda         | -0.001 ± 0.053 | -0.042 | -0.008 | 16  | 21 | 0.5114   | 37  |
| Marginocephalia     | 0.011 ± 0.048  | 0.264  | 0.014  | 15  | 9  | 0.3075   | 24  |
| Ceratopsia          | 0.017 ± 0.048  | 0.316  | 0.014  | 12  | 6  | 0.2379   | 18  |
| Pachycephalosauria  | -0.017 ± 0.049 | -0.084 | -0.006 | 2   | 3  | >0.9999  | 5   |
| Thyreophora         | -0.002 ± 0.072 | -0.039 | 0.001  | 9   | 8  | >0.9999  | 17  |
| Stegosauria         | -0.025 ± 0.062 | -0.173 | -0.033 | 2   | 5  | 0.4531   | 7   |
| Ankylosauria        | 0.014 ± 0.115  | 0.068  | 0.015  | 3   | 2  | >0.9999  | 5   |
| B. <i>MRCA</i>      |                |        |        |     |    |          |     |
| Dinosauromorpha     | 0.150 ± 0.129  | 14.068 | 0.133  | 84  | 10 | <0.0001* | 94  |
| <b>Dinosauria</b>   | 0.264 ± 0.134  | 25.310 | 0.252  | 95  | 1  | <0.0001* | 96  |
| <b>Saurischia</b>   | 0.086 ± 0.098  | 4.305  | 0.092  | 40  | 10 | <0.0001* | 50  |
| Theropoda           | 0.105 ± 0.102  | 3.356  | 0.114  | 26  | 6  | 0.0005*  | 32  |
| Sauropodomorpha     | 0.026 ± 0.085  | 0.463  | 0.026  | 14  | 4  | 0.0309*  | 18  |
| Prosauropoda        | 0.060 ± 0.071  | 0.419  | 0.036  | 5   | 2  | 0.4531   | 7   |
| Sauropoda           | -0.020 ± 0.082 | -0.217 | -0.011 | 5   | 6  | >0.9999  | 11  |
| <b>Ornithischia</b> | 0.138 ± 0.147  | 6.075  | 0.102  | 36  | 8  | <0.0001* | 44  |
| Ornithopoda         | 0.013 ± 0.088  | 0.281  | -0.000 | 11  | 10 | >0.9999  | 21  |
| Marginocephalia     | 0.159 ± 0.146  | 2.061  | 0.220  | 11  | 2  | 0.0225*  | 13  |
| Ceratopsia          | 0.320 ± 0.085  | 3.201  | 0.334  | 10  | 0  | 0.0020*  | 10  |
| Pachycephalosauria  | -0.001 ± 0.070 | -0.004 | 0.019  | 2   | 1  | >0.9999  | 3   |
| Thyreophora         | -0.017 ± 0.143 | -0.155 | -0.013 | 4   | 5  | >0.9999  | 9   |
| Stegosauria         | -0.110 ± 0.145 | -0.440 | -0.153 | 1   | 3  | 0.6250   | 4   |
| Ankylosauria        | 0.031 ± 0.167  | 0.092  | -0.024 | 1   | 2  | >0.9999  | 3   |

TABLE 5. Spearman-rank correlation results for RP. Asterisks indicate significant correlations.

| Clade               | rho    | Z      | $p$     | $n$ |
|---------------------|--------|--------|---------|-----|
| Dinosauromorpha     | 0.301  | 2.885  | 0.0039* | 93  |
| <b>Dinosauria</b>   | 0.254  | 2.406  | 0.0161* | 91  |
| <b>Saurischia</b>   | 0.415  | 2.874  | 0.0040* | 49  |
| Theropoda           | 0.349  | 1.914  | 0.0557* | 31  |
| Sauropodomorpha     | 0.054  | 0.223  | 0.8232  | 18  |
| Prosauropoda        | 0.500  | 1.225  | 0.2207  | 7   |
| Sauropoda           | -0.061 | -0.194 | 0.8461  | 15  |
| <b>Ornithischia</b> | 0.080  | 0.511  | 0.6093  | 42  |
| Ornithopoda         | 0.031  | 0.136  | 0.8918  | 20  |
| Marginocephalia     | 0.587  | 1.948  | 0.0514* | 12  |
| Ceratopsia          | 0.412  | 1.167  | 0.2433  | 9   |
| Pachycephalosauria  | 0.875  | 1.237  | 0.2159  | 3   |
| Thyreophora         | -0.600 | -1.697 | 0.0897* | 9   |
| Stegosauria         | -0.850 | -1.472 | 0.1410  | 4   |
| Ankylosauria        | 0.125  | 0.177  | 0.8597  | 3   |

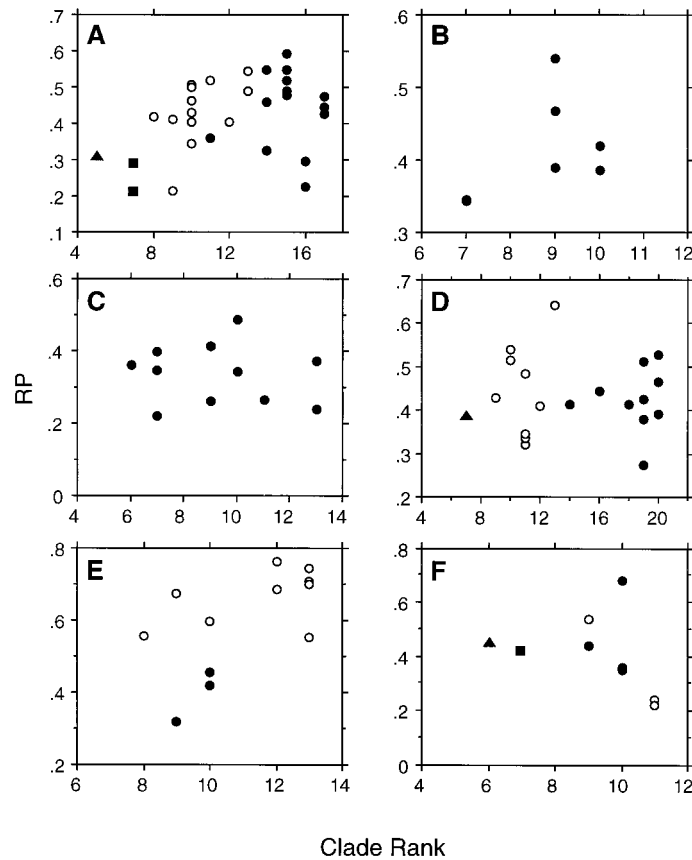


FIGURE 7. Correlations between terminal values for RP and clade rank. As with RA, most correlations are weakly positive (see Table 5). A, Theropoda; triangle = *Eoraptor*, squares = Herrerasauridae, open circles = basal neotheropods, filled circles = Coelurosauria. B, Prosauropoda. C, Sauropoda. D, Ornithopoda; triangle = *Heterodontosaurus*, closed circles = basal euornithopods, filled circles = Hadrosauridae. E, Marginocephalia; filled circles = Pachycephalosauria, open circles = Ceratopsia. F, Thyreophora; triangle = *Scutellosaurus*, square = *Scelidosaurus*, open circles = Stegosauria, closed circles = Ankylosauria.

stances to a single occurrence. There are five acquisitions of the “flush” derived state (Euornithopoda, Pachycephalosauria, Neoceratopsia, Eurypoda, and Neotetanurae; Fig. 8), although the exact condition in pachycephalosaurs is subject to some debate (Maryanska 1990). This pattern is entirely congruent with ordered evolution of this character, as the “intermediate” condition always appears before the “flush” condition. Primitive values of RLT range from 10.0 to 15.0 (eurypodans, sauropodomorphs, basal theropods), and derived values may be reduced to 3.0–7.0 (most ceratopsids, coelurosaurians) (Table 1). At  $RLT \leq 7.0$ , the proximal end of the lesser trochanter is located at or above the rotational axis of the femur.

Using squared-change parsimony, EACH

and MRCA produce somewhat different results. Under EACH, nearly all groups have a negative mean, median, and sum change, as well as greater number of decreases, supporting a general trend toward reducing RLT (Table 6). MRCA shows seven groups with positive trends and six with negative, often contradicting the results from EACH. However, Dinosauromorpha, Dinosauria, Ornithischia, and Ornithopoda show consistently negative trends, whereas no group shows a consistently positive trend. Spearman-rank correlation reveals largely similar results (Table 7, Fig. 9). Although there are many positive trends in addition to negative ones, only the negative trends are significant, and these include the most major clades (Dinosauromorpha, Dinosauria, Saurischia, Ornithischia, Theropoda).

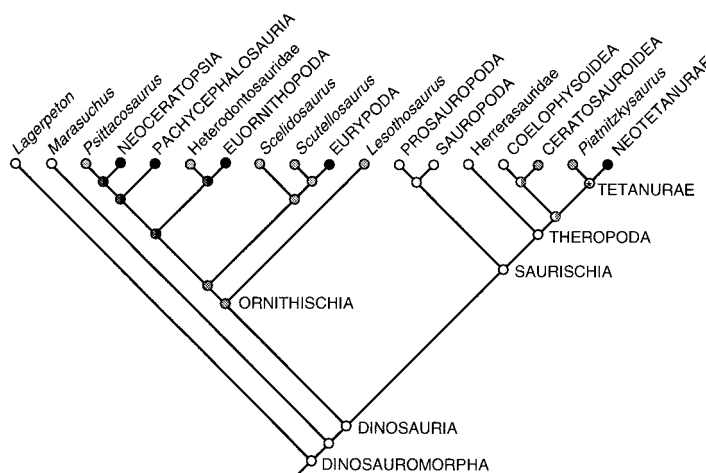


FIGURE 8. Changes in lesser trochanter morphology within Dinosauria. Note that, although the character states at several nodes cannot be reconstructed unambiguously, transformations in this character occur in a regular sequence. The “not raised” state (open circles) generally precedes the “intermediate” state (gray circles), which in turn generally precedes the “flush” state (filled circles). Ambiguous state assignments are indicated by dual-colored circles (the asterisk at Tetanurae reflects ambiguity between all three states).

Most increases are associated with small sample sizes, and characterize groups that are more clustered rather than linearly arranged.

### Discussion

*Orientation of the Femoral Head.*—All primitive dinosauromorph femora are characterized by an anteromedially oriented head (Galton 1990, Sereno 1991b, Sereno and Arcucci 1993, 1994), a condition shared with many other basal archosaurs (Parrish 1986). This orientation is best observed when the femur is examined in proximal view: when the distal femoral condyles are aligned in a mediolateral plane, the femoral head has an orientation of 40–45° anterior to it (Fig. 3A). Prosauropods, basal theropods, and basal ornithischians also exhibit the primitive condition. In these taxa, the femoral head apparently articulated beneath the pendant iliac supra-acetabular crest such that the latter rested on the sinuous dorsal surface of the greater trochanter (Fig. 3B) (Cooper 1984; Padian and Olsen 1989; Sereno and Arcucci 1994). This crest creates a shelf that may have assisted in restricting femoral abduction by abutting against the anterolateral edge of the greater trochanter and may have helped to guide and restrict femoral long-axis rotation. Examination of femora and acetabula in primitive taxa (*Marasuchus*, *Lag-*

*erpeton*, *Prosauropoda*, *Herrerasauridae*, *Coelophysoidea*, *Lesothosaurus*, *Heterodontosaurus*) demonstrates a congruence between the dorsal surface of the greater trochanter and the ventral surface of the supra-acetabular shelf that supports this inference.

In derived taxa, the femoral head is fully medial and articulates at a right angle to the plane of the acetabulum. Concomitantly, the dorsal surface of the greater trochanter has lost the curved ridge characteristic of more primitive forms, and as a result it no longer conforms to the ventral surface of the supra-acetabular shelf, which is reduced and no longer pendant. With a medially oriented femoral head, the anterolateral proximal femoral muscles (particularly *Mm. puboischiofemoralis internus* and *M. iliofemoralis externus*) would have been located more anteriorly (rather than laterally), reducing the rotational or abduction components of their actions and allowing them to serve primarily as femoral protractors (Fig. 10). *Mm. puboischiofemoralis internus* acts as a protractor in extant crocodylians, with little abduction or rotation (Gatesy 1997), and its actions would have remained little changed. Abduction and rotation by *M. iliofemoralis externus*, however, would have become unnecessary, suggesting the potential for change in this muscle's function. In fact,

TABLE 6. Squared-change parsimony results for RLT. Mean, sum, and median of ancestor-descendant changes, with numbers of increases and decreases; *p*-value refers to results of a one-sample sign test. A, Analyzed using all ancestor-descendant comparisons within the specified clade (*EACH*). B, Analyzed using comparisons only between most recent common ancestor and descendant taxa of specified clade (*MRCA*). Asterisks indicate significant correlations.

| Clade               | Mean           | Sum      | Median | +  | -  | <i>p</i> | <i>n</i> |
|---------------------|----------------|----------|--------|----|----|----------|----------|
| <b>A. EACH</b>      |                |          |        |    |    |          |          |
| Dinosauromorpha     | -0.111 ± 1.817 | -20.723  | -0.050 | 89 | 98 | 0.5585   | 187      |
| <b>Dinosauria</b>   | -0.138 ± 1.801 | -25.118  | -0.053 | 86 | 96 | 0.5047   | 182      |
| <b>Saurischia</b>   | -0.078 ± 2.035 | -8.154   | 0.158  | 53 | 51 | 0.9219   | 104      |
| Theropoda           | 0.028 ± 1.966  | 1.854    | 0.345  | 37 | 30 | 0.4638   | 67       |
| Sauropodomorpha     | -0.293 ± 2.165 | -10.247  | -0.184 | 15 | 20 | 0.4996   | 35       |
| Prosauropoda        | -0.516 ± 1.105 | -7.742   | -0.465 | 6  | 9  | 0.6072   | 15       |
| Sauropoda           | -0.078 ± 2.790 | -1.480   | -0.130 | 9  | 10 | >0.9999  | 19       |
| <b>Ornithischia</b> | -0.224 ± 1.449 | -17.220  | -0.081 | 32 | 45 | 0.1711   | 77       |
| Ornithopoda         | -0.005 ± 0.999 | -0.169   | -0.080 | 15 | 22 | 0.3240   | 37       |
| Marginocephalia     | -0.089 ± 1.221 | -2.051   | -0.158 | 8  | 15 | 0.2100   | 23       |
| Ceratopsia          | -0.083 ± 1.306 | -1.581   | -0.158 | 6  | 13 | 0.1671   | 19       |
| Pachycephalosauria  | -0.229 ± 0.996 | -0.688   | -0.344 | 1  | 2  | >0.9999  | 3        |
| Thyreophora         | -1.293 ± 2.286 | -18.098  | -0.893 | 6  | 8  | 0.7905   | 14       |
| Stegosauria         | 0.004 ± 1.345  | 0.017    | -0.046 | 2  | 2  | >0.9999  | 4        |
| Ankylosauria        | -2.447 ± 2.755 | -12.237  | -3.454 | 1  | 4  | 0.3750   | 5        |
| <b>B. MRCA</b>      |                |          |        |    |    |          |          |
| Dinosauromorpha     | -4.078 ± 5.709 | -0.001   | -5.748 | 42 | 62 | 0.0624   | 104      |
| <b>Dinosauria</b>   | -0.694 ± 5.719 | -72.173  | -2.316 | 28 | 78 | <0.0001* | 106      |
| <b>Saurischia</b>   | -1.095 ± 5.686 | -64.602  | -0.423 | 28 | 31 | 0.7948   | 59       |
| Theropoda           | -4.129 ± 5.388 | -165.174 | -3.957 | 11 | 29 | 0.0064*  | 40       |
| Sauropodomorpha     | 2.070 ± 3.731  | 39.337   | 1.948  | 12 | 7  | 0.3593   | 19       |
| Prosauropoda        | 1.727 ± 1.953  | 13.816   | 2.301  | 6  | 2  | 0.2891   | 8        |
| Sauropoda           | 1.952 ± 4.084  | 21.473   | 0.680  | 7  | 4  | 0.5488   | 11       |
| <b>Ornithischia</b> | -0.549 ± 5.057 | -24.726  | -1.858 | 10 | 35 | 0.0002*  | 45       |
| Ornithopoda         | -0.474 ± 1.693 | -10.895  | -0.650 | 8  | 15 | 0.2100   | 23       |
| Marginocephalia     | 0.316 ± 2.007  | 3.789    | 0.781  | 7  | 5  | 0.7744   | 12       |
| Ceratopsia          | 0.838 ± 2.166  | 8.377    | 1.343  | 7  | 3  | 0.3438   | 10       |
| Pachycephalosauria  | 0.172 ± 1.402  | 0.344    | 0.172  | 1  | 1  | >0.9999  | 2        |
| Thyreophora         | 8.745 ± 6.812  | 69.959   | 8.108  | 7  | 1  | 0.0703*  | 8        |
| Stegosauria         | -0.006 ± 1.661 | -0.018   | 0.309  | 2  | 1  | >0.9999  | 3        |
| Ankylosauria        | 4.705 ± 5.798  | 14.114   | 6.937  | 2  | 1  | >0.9999  | 3        |

TABLE 7. Spearman-rank correlation results for RLT. Asterisks indicate significant correlations.

| Clade               | rho    | Z      | <i>p</i> | <i>n</i> |
|---------------------|--------|--------|----------|----------|
| Dinosauromorpha     | -0.524 | -5.321 | <0.0001* | 100      |
| <b>Dinosauria</b>   | -0.505 | -5.078 | <0.0001* | 98       |
| <b>Saurischia</b>   | -0.582 | -4.398 | <0.0001* | 58       |
| Theropoda           | -0.705 | -4.346 | <0.0001* | 39       |
| Sauropodomorpha     | 0.139  | 0.588  | 0.5565   | 19       |
| Prosauropoda        | -0.125 | -0.331 | 0.7409   | 8        |
| Sauropoda           | 0.484  | 1.531  | 0.1258   | 11       |
| <b>Ornithischia</b> | -0.295 | -1.932 | 0.0534   | 40       |
| Ornithopoda         | -0.141 | -0.647 | 0.5177   | 20       |
| Marginocephalia     | 0.484  | 1.606  | 0.1082   | 11       |
| Ceratopsia          | 0.512  | 1.536  | 0.1244   | 9        |
| Pachycephalosauria  | 0.500  | 0.500  | 0.6171   | 2        |
| Thyreophora         | 0.601  | 1.591  | 0.1117   | 8        |
| Stegosauria         | 0.125  | 0.177  | 0.8597   | 3        |
| Ankylosauria        | 0.875  | 1.237  | 0.2159   | 3        |



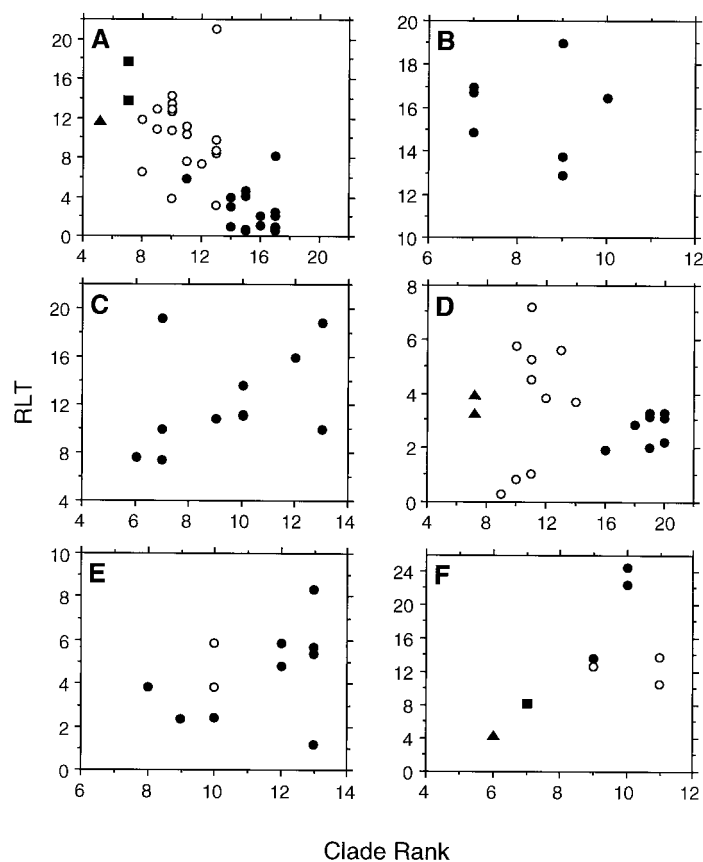


FIGURE 9. Correlations between terminal values for RLT and clade rank. Both positive and negative correlations are evident, but only the negative trends are significant (see Table 7). A, Theropoda; triangle = *Eoraptor*, squares = Herrerasauridae, open circles = basal neotheropods, filled circles = Coelurosauria. B, Prosauropoda. C, Sauropoda. D, Ornithopoda; triangle = Heterodontosauridae, closed circles = basal euornithopods, filled circles = Hadrosauridae. E, Marginocephalia; open circles = Pachycephalosauria, filled circles = Ceratopsia. F, Thyreophora; triangle = *Scutellosaurus*, square = *Scelidosaurus*, open circles = Stegosauria, closed circles = Ankylosauria.

the protracting abilities of the *M. iliofemoralis* would have been further enhanced by femoral head reorientation when associated with the expanded preacetabular ilium. Additionally, the greater relative mediolateral breadth of the medially oriented femoral head acts to resist femoral abduction by abutting against the acetabular rim. Among other archosaurs, the femoral head is nearly medial in poposaurids, rauisuchids, and *Ornithosuchus* (Parrish 1986), taxa that, like dinosaurs, appear to have had a fully erect limb posture (Bonaparte 1984; Parrish 1986, Sereno 1991a).

*Anterior and Posterior Iliac Expansion.*—In the primitive dinosauriform pelvis, the ilium is approximately as tall dorsoventrally as it is long anteroposteriorly, and has a slender, sub-triangular preacetabular process counterpoint

to a larger, blunt postacetabular process (Fig. 5). There is little surface texturing to indicate the bounds of individual muscle masses on the lateral surface. The acetabulum is closed medially and its dorsal rim is extended ventrally and laterally to form a supra-acetabular crest that overhangs the acetabular opening. This general condition is apparent in *Lagosuchus*, *Lagerpeton*, *Marasuchus*, *Lewisuchus*, *Lesothosaurus*, several “fabrosaur” specimens (Santa Luca 1984), *Eoraptor*, Herrerasauridae, and Prosauropoda, although the condition in *Pisanosaurus* (the most primitive ornithischian) is not determinable from the preserved mold of the pelvis (Bonaparte 1976; Sereno 1991b). A small, blunt postacetabular process is also present in basal thyreophorans (*Scutellosaurus* and *Scelidosaurus*), but these taxa have an ex-

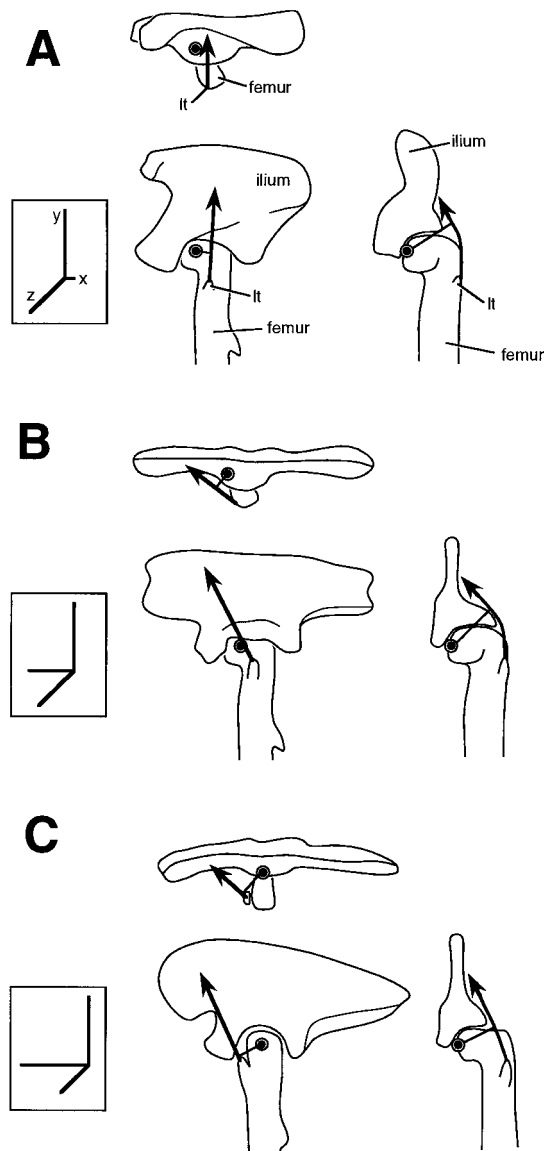


FIGURE 10. Effects of changes in femoral head orientation on *M. iliofemoralis* function. In each diagram, the proximal left femur is shown articulated with the left ilium in three views: dorsal (top left), lateral (bottom left), and anterior (in cross-section; right). Arrows indicate the lines of action for the *M. iliofemoralis*, with a perpendicular line representing the moment arm around the point of rotation (circle). The inset diagrams show the relative three-dimensional components of the line of action as proportional lines. Note that as the z-axis shortens, abduction is diminished; as the x-axis is lengthened, protraction is enhanced. A, In the basal theropod *Herrerasaurus*, the femoral head is anteromedially oriented. The *M. iliofemoralis* originates on the unexpanded lateral iliac surface and inserts on the lesser trochanter (lt), confining its role largely to femoral abduction. B, In the ceratosaurian theropod *Carnotaurus*, the lesser trochanter is elevated and the preacetabular ilium is elongated.

panded anterior iliac blade. Anterior expansion occurs in Sauropoda, Neotheropoda, and Ornithischia, while posterior expansion occurs in Sauropoda, Neotheropoda, Eurypoda, and Cerapoda. The derived, extended postacetabulum may be long and slender (ornithopods), flat and mediolaterally wide (thyrophorans), or dorsoventrally tall (sauropods and neotheropods).

As discussed earlier, the anterior ilium represents the origination site for a knee extensor (*M. iliotibialis*) and several femoral protractors and abductors (derivatives of *M. iliofemoralis* and *Mm. puboischiofemoralis internus*). Thus, anterior expansion of the ilium would have increased the anteroposterior extent of both knee extensors and femoral protractors and abductors (Fig. 11A) (Parrish 1986). The morphology of the dorsal iliac border in many dinosaurs suggests that the expanded *M. iliotibialis* may have had a distinct anterior head ("sartorius" sensu Romer 1923b, 1927b) as well as additional subdivisions. Although the lateral iliac blade often bears a median dorsoventral ridge (particularly in saurischians), this is not clearly linked to partitioning of *M. iliofemoralis* (contra Russell 1972; Walker 1977). Nevertheless, the expanded anterior ilium may have supported multiple derivatives of this muscle, particularly considering that the lateral femur bears some evidence of partitioning at the insertion points (trochanteric shelf, accessory trochanter, lesser trochanter, etc.). Additionally, *Mm. puboischiofemoralis internus medialis*, which originates on the medial surface of the anterior ilium, may have also been expanded anteriorly with the preacetabulum.

An increase in knee extensor mass and length would have increased the contribution these muscles could have made to stride length. In contrast, crocodylian knee extensors contribute less to stride length (Gatesy 1997),

←

The expanded *M. iliofemoralis* occupies part of the lateral ilium anterior to the acetabulum, and thus can protract as well as abduct. C, In the tetanuran theropod *Eustreptospondylus*, the femoral head is fully medial. This reduces the abductor role of *M. iliofemoralis*, which is now a major femoral protractor.

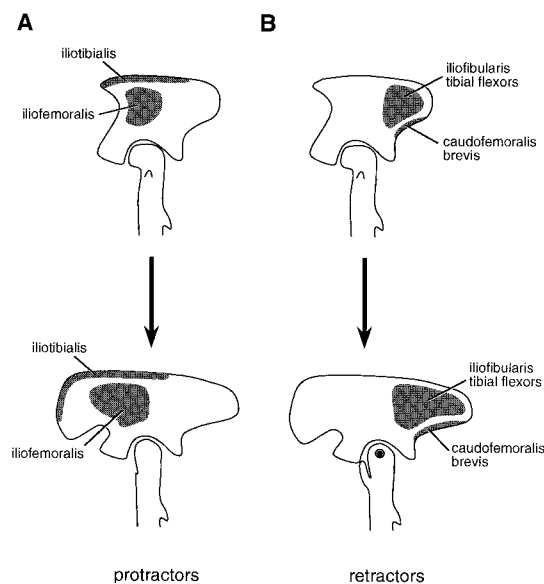


FIGURE 11. Evolution of the hindlimb protractors and retractors. Left lateral views of the left ilium and proximal femur articulated in the acetabulum, with the primitive condition illustrated by *Herrerasaurus* (top) and the derived condition by *Gorgosaurus* (bottom). A, The protractors (hip flexors and knee extensors) originate dorsal and anterior to the acetabulum, *M. iliobialis* from the dorsal border of the ilium, and *M. iliofemoralis* from the lateral surface. As the preacetabulum expands, *M. iliobialis* is enlarged greatly along the dorsal border, eventually extending to nearly twice its primitive size. B, The retractors (hip extensors and knee flexors) originate entirely posterior to the acetabulum, *M. iliofibularis* and *Mm. flexores tibiales* from the lateral iliac surface, and *M. caudofemoralis brevis* from within the brevis fossa. As the postacetabulum expands, these muscles are enlarged and extended more posteriorly, enhancing their retractor roles.

particularly when the leg is abducted. By increasing the anterior position of these muscles, a greater amount of limb protraction could occur for a given amount of muscle shortening than would have previously. Thus, the total muscle mass dedicated to hip flexion and knee extension was increased in dinosaurs with anteriorly expanded ilia, with the additional transformation of one of the former limb abductors (*M. iliofemoralis*) into a protractor in the process. This pattern has been observed and similarly explained in other archosaurs (e.g., rauisuchians) (Parrish 1986). Increased use of knee extension in Dinosauria was accompanied by the development of an anteriorly extended cnemial crest on the proximal tibia. This structure would have dis-

placed the line of action of the knee extensors away from the joint, acting to increase their moment arms around the knee much as a patella does in mammals and certain birds (Alexander and Dimery 1985).

The lateral aspect of the postacetabular process is the origination site for several knee flexors (*M. iliofibularis* and *Mm. flexores tibiales*), and a hip flexor (*M. caudofemoralis brevis*) originates on the ventral iliac border and within the brevis fossa (Romer 1923b, 1927a). Lengthening of this portion of the ilium probably affected limb retraction by increasing the posterior action of these muscles, thereby lengthening the posterior range of the femur and lower limb during the support phase (Fig. 11B). In doing so, these muscles could act to retract the limb a greater distance for a given contraction than they would have previously. In particular, *M. caudofemoralis brevis* is probably one of the primary femoral retractors (along with *M. caudofemoralis longus*); thus, alterations in its origination site would profoundly affect hindlimb retraction.

Anteroposterior iliac expansion suggests that, with the exception of basal saurischians and basal ornithischians, most dinosaurs would have possessed increased hindlimb protraction and retraction relative to primitive archosaurs (Perle 1985; Novas 1996). Some muscles may have undergone an increase in muscle cross-sectional area (entailing an increase in muscular force), but more generally the total potential anterior and posterior range of limb motion would certainly have been increased by these iliac expansions. Although other archosaurs appear to have expanded the anterior ilium independently (Parrish 1986), there are comparatively few instances of posterior expansion, implying that dinosaurs were unusual in the degree to which femoral retraction (and knee flexion) was developed.

*Morphology of the Lesser Trochanter.*—Primarily, the lesser trochanter is located along the anterolateral edge of the femoral shaft somewhat below the proximal end and is contiguous (or nearly so) with the more laterally located trochanteric shelf. The lesser trochanter is a low knob or ridge in basal dinosauromorphs and is located approximately 15–20%

of femoral length from the proximal end. This primitive condition is evident in prosauropods and basal theropods, both of which retain a distinct trochanteric shelf.

The surface of the lesser trochanter was the insertion site for *M. iliofemoralis* (Romer 1923b, 1927b) and was primitively located ventral and lateral to the point of rotation for the femoral head (Fig. 10A). Because *M. iliofemoralis* originated on the lateral iliac surface dorsal to the point of femoral rotation, it would have acted primarily to abduct the femur, as it does in extant crocodylians (Gatesy 1994, 1997). Its line of action passed around and above the point of femoral rotation as the muscle passed over the greater trochanter between its origination and insertion (Fig. 10A). Given that the basal archosaurian condition was similar to that seen in extant lepidosaurs and crocodylians, the position and function of the lesser trochanter appears to have been little modified in primitive non-avian dinosaurs (Romer 1923a; Gatesy 1997).

In crocodylians, femoral protraction is accomplished by the *Mm. puboischiofemoralis internus* and *externus* (Gatesy 1994, 1997), and these muscles may have served a similar purpose in primitive ornithomirans. However, the need for substantial abduction (presumably from *M. iliofemoralis*) was probably obviated to some extent by a parasagittal limb posture in dinosaurs. *M. iliofemoralis* may have acquired a role in protraction at this point, and at least some of its avian derivatives retain this function (Gatesy 1994, 1999b). It is notable that elevation of the lesser trochanter occurs simultaneously with, or slightly after, expansion of the preacetabular ilium (and is therefore accompanied by further enhancement of the protractor functions of the *M. iliofemoralis*). This transition occurs independently in ornithomirans and saurischians.

In more derived dinosaurs, the lesser trochanter becomes enlarged and its proximal end is elevated above the femoral shaft (Fig. 10C). This would have brought the insertion point of *M. iliofemoralis* closer to the point of greatest mechanical advantage, increasing its effectiveness and allowing it to generate the same torque with less expenditure of force (Biewener 1989). This arrangement would be

advantageous for rapid protraction of the femur during the swing phase, when substantial force would not have been employed. Protraction is further enhanced by medial reorientation of the femoral head in derived taxa, which brings the lesser trochanter into a fully anterior position and reduces the mediolateral component of action (see above; Fig. 10B).

In certain lineages (particularly derived Coelurosauria), the lesser trochanter is appressed to the femoral shaft alongside the greater trochanter. Invariably this occurs in lineages where the lesser trochanter had long achieved a fully proximal elevation, and thus the relative position of the muscle insertion would have remained largely unchanged. It is unclear what effects such an arrangement would have had, although a more direct attachment of the *M. iliofemoralis externus* to the femoral shaft may have provided an advantage in medial rotation. At least one avian derivative of *M. iliofemoralis* acts as a medial rotator (Gatesy 1999b), and perhaps this differentiation occurred along with the development of an appressed lesser trochanter.

#### Implications for Dinosaur Locomotor Evolution

These results demonstrate that homoplasy is rampant in the evolution of the dinosaurian locomotor apparatus. Because several lineages independently acquired very similar (or identical) derived states from the same primitive state, these homoplasies are interpreted as parallelisms. Many modifications involved structures that served as attachment sites for hindlimb muscles, thereby effecting significant alterations in musculature and locomotor function. The mechanical implications of these osteological changes clarify several evolutionary transitions within Dinosauria.

*Origins of Parasagittal Posture and Bipedalism.*—Basal Archosauriformes tend to be both quadrupedal and “sprawling,” (although the primitive condition of Archosauria is ambiguous [Seren 1991a]), indicating that both bipedalism and parasagittal posture are derived within this clade (Charig 1972; Parrish 1986; Seren 1991a). Unfortunately, the potentially informative transitional series between these “sprawling” quadrupeds and bipedal, para-

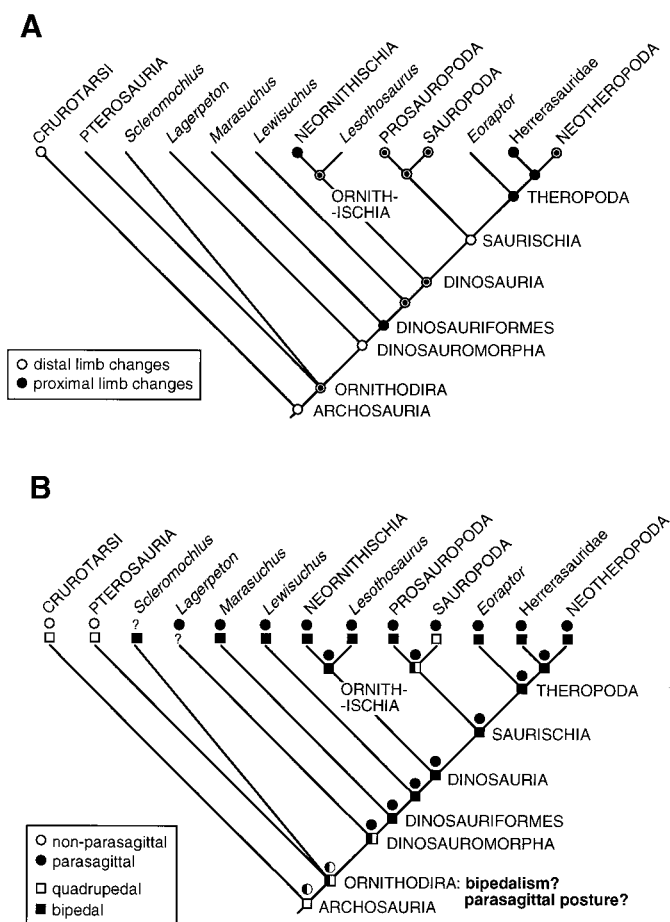


FIGURE 12. Evolution of posture and hindlimb features within Dinosauria. A, Postural evolution, showing development of parasagittal posture (filled squares) from “sprawling” posture (open squares, and bipedalism (filled circles) from quadrupedalism (open circles). Half-filled symbols indicate ambiguous character-state optimizations. Note that bipedalism appears to be primitive for at least Dinosauriformes, and parasagittal posture for at least Dinosauromorpha. B, Evolution of hindlimb features. Changes in the distal limb joints (open circles) tend to be concentrated at lower nodes in the cladogram, whereas changes in proximal joints (filled circles) are more prevalent at highly nested nodes. Many nodes are characterized by changes throughout the limb (filled circle within open circle). Data from Novas 1996 and Sereno 1999.

sagittal basal dinosauromorphs is incomplete, and therefore the origins of these characteristic postures are ambiguous, unfortunately so because they have evolved only rarely in vertebrate history. Optimization of these two postural conditions on a phylogeny of Archosauria reveals that a parasagittal posture can be unambiguously reconstructed at Dinosauromorpha, but that bipedalism can only be unambiguously reconstructed at Dinosauriformes (Fig. 12A). This ambiguity is due to the incomplete nature of *Lagerpeton*, for which no forelimb materials are known. In addition, controversy surrounding the possible hin-

dlimb postures of pterosaurs and the basal ornithodiran *Scleromochlus* (Padian 1983; Sereno 1991a; Bennett 1997; Clark et al. 1998; Benton 1999) renders reconstructions of the ornithodiran condition dubious as well. The earliest known dinosauromorphs may have been bipedal saltators (Sereno and Arcucci 1993) or striders, but it seems likely that parasagittal limbs preceded permanent bipedalism for simple reasons of support and stability (Chargin 1972; Gatesy and Biewener 1991).

Novas (1996) noted that several features of basal ornithodiran pelvic and femoral morphology suggest that the transition to biped-



alism involved preferential changes at the knee and ankle joints, rather than the hip. For example, the morphologies of the dinosauriform knee and ankle restrict these joints to motions in the parasagittal plane (precluding extensive abduction-adduction) (Serenó and Arcucci 1990; Sereno 1991a; Novas 1996). Associated changes in hip morphology include the development of a femoral lesser trochanter and an iliac brevis shelf, suggesting some enlargement of femoral protractor and retractor musculature (Gauthier 1986; Novas 1996). Many other pelvic features were not dramatically altered during the subsequent origin of Dinosauria, suggesting fewer changes in pelvic muscle orientation (Novas 1996). Likewise, femoral head orientation, iliac morphology, and the triradiate pelvis were little altered until within Dinosauria.

This basic pattern appears to hold, although the sequence of changes is somewhat complex (Fig. 12B), with many clades characterized by changes throughout the hindlimb. In general, however, distal (knee and ankle) changes are more prevalent at basal nodes and more highly nested nodes tend to be characterized by proximal (hip) changes (Novas 1996). Such a sequence would be expected in association with acquisition of parasagittal posture given the arrangement of musculature in the amniote hindlimb. The hip joint is endowed with considerable musculature that can assist in mediolateral stabilization; many modern mammals are capable of sustained locomotion even when (surgically) lacking a femoral head (e.g., Squire et al. 1991; Remedios et al. 1994). Distal hindlimb joints have little stabilizing musculature and instead possess slender flexion-extension muscles combined with stiffening retinacula. Osteological modifications might therefore be necessary at more distal joints if a stable change in posture is to be effected.

The femoral and pelvic morphology of basal ornithodirans suggests that *M. iliofemoralis* and *Mm. puboischiofemoralis internus* were located in positions similar to those in crocodylians and lepidosaurs. In crocodylians, these muscles serve to lift the limb clear of the substrate and draw it forward during the swing phase (Gatesy 1997). The ornithodiran femur

is parasagittal and therefore requires less extensive abduction during swing (in fact the tendency for the limbs to abduct during support must be countered by the adductors and limb-joint morphology). Thus the abductor role of *M. iliofemoralis* would be expected to decrease. Basal ornithodiran iliac morphology exhibits a more pronounced preacetabular process, which presumably served as the origination site for *M. iliotibialis* (Romer 1927a). This would have placed this muscle more anteriorly and allowed it to serve as a knee extensor (Gatesy 1997) as well as a lower-limb abductor. Again, the adoption of a parasagittal limb posture would have encouraged transformation of the original role of this muscle. Primitively, the iliac postacetabulum was short as it is in crocodylians, indicating that hip flexors (originating on the tail) remained dominant over knee flexors (originating on the posterior ilium).

Once parasagittal posture had been evolved, bipedalism may have originated in a group of quadrupedal basal ornithodirans as a behavioral adaptation. Occasional bipedalism would have been possible following changes in knee and ankle morphology that restricted hindlimb motion to the parasagittal plane (Serenó 1991a; Novas 1996). More proximal modifications occurred later, including elaboration of the protractor-retractor roles of the pelvic muscles (Novas 1996) at the expense of abduction-adduction.

*Evolution of the Avian Hindlimb.*—Dinosaurs exhibit a series of modifications that indicate increased specialization of a permanently bipedal and upright hindlimb posture. Some of these are related to the reduced abduction and adduction associated with a predominately parasagittal hindlimb posture. Medial orientation of the femoral head, elevation of the lesser trochanter, and elongation of the pre- and postacetabular processes of the ilium all increase the effectiveness of protraction and retraction at the expense of abduction for several major pelvic muscles (Figs. 10, 11). Such increases could occur without any other alterations in hindlimb musculature. In addition, enlargement and functional elaboration occurred as well, resulting in four distinct *Mm. ilioprotractores* on the lateral ilium of extant



birds. The evolution of these muscles is clouded, however, by controversies surrounding the homologies and functions of several deep dorsal muscles. Specifically, it is not clear whether the avian *Mm. iliotrochanterici* were derived entirely from the primitive *M. iliofemoralis* (Romer 1923a,b, 1942) or from both the *M. iliofemoralis* and the *M. puboischiofemoralis internus* (Romer 1927a; Rowe 1986).

In crocodylians, *M. iliofemoralis* and *M. puboischiofemoralis internus* are active during the swing phase, the former as a femoral abductor and the latter as a femoral protractor (Gatesy 1994, 1997). In birds, however, the various *Mm. iliotrochanterici* act at different times during the stride and have different roles. The avian *Mm. iliofemoralis externus* and *iliotrochantericus cranialis* are involved in femoral protraction during early swing, whereas *Mm. iliotrochanterici medius* and *caudalis* function as femoral rotators and retractors during stance (Gatesy 1994, 1999b).

Muscle function has two basic components: (1) line of action, which changes if the origin and/or insertion of a muscle is altered, and (2) timing of activity, which changes when the neural input is altered. Action is therefore linked to muscle morphology and can potentially be grossly inferred from living and fossil taxa. However, timing can be compared only in living taxa, and this may significantly alter the perceived function of a muscle as inferred from morphology alone. More importantly, examining these two components as static, separate elements represents a highly simplified view of muscle function, and one which undoubtedly misrepresents actual function to some degree (Gatesy 1994).

Regardless of which hypothesis of homology is correct, the muscles derived from the deep dorsal mass clearly underwent significant functional changes during the evolution of birds. Both hypotheses of homology imply that the *Mm. iliofemoralis externus* and *iliotrochantericus cranialis* of birds have been only slightly differentiated relative to the original function (action + timing) of *M. iliofemoralis*, whereas *Mm. iliotrochanterici medius* and *caudalis* have acquired significantly new roles. Both hypotheses are also similar in terms of numbers of changes (if timing and ac-

tion are both included, and provided that single-step changes are assumed for several major alterations in muscle timing and location), suggesting that neither is, strictly, more "parsimonious" than the other.

However, non-avian dinosaur morphology helps to constrain the timing of some of these changes, removing them from the origin of flight. Non-avian theropod iliac and femoral morphology suggests some subdivision of *M. iliofemoralis externus* and *Mm. puboischiofemoralis internus* over the crocodylian and lacertilian conditions, and at least some of the *Mm. iliotrochanterici* must have been present primitively in Neornithes. Thus, subdivision of the primitive archosaurian pelvic musculature was already underway within non-avian theropods, and this process cannot be ascribed solely to the selective pressures involved in the origin of flight. If, as suggested, the functional changes between the crocodylian *M. iliofemoralis*/*Mm. puboischiofemoralis* (abduction/protraction) and the avian *Mm. iliotrochanterici* (rotation/protraction) are related to the acquisition of a parasagittal posture and bipedalism, then they should be expected to have occurred much more basally within Theropoda. Parallel changes of this nature occurred in other dinosaur groups as well.

*Parallel Modifications of Hindlimb Function.*—The three major changes in the dinosaurian hindlimb apparatus are described here—(1) femoral head orientation, (2) lesser trochanter height, and (3) anteroposterior expansion of the ilium—all show parallelism within Dinosauria. All three changes occur in two groups (theropods and ornithischians) and two changes occur in one (1 and 3 in sauropods); all are independent occurrences (Figs. 4, 5, 8). Whether mechanical or developmental (or other) constraints were directly involved in creating this evolutionary pattern is unknown, but these changes would have had similar mechanical effects regardless of where and when they arose. Similar adaptations may therefore be inferred for these different dinosaur clades. As discussed, these changes generally reflect the eventual dominance of protraction/retraction over abduction/adduction for several hindlimb muscles, a transition associated with

the development of a parasagittal hindlimb posture. Although all dinosaurs were descended from an ancestor with this posture, these similar modifications were acquired subsequently and independently.

However, not all clades of dinosaurs may have possessed the derived *M. iliofemoralis* and *Mm. puboischiofemoralis internus* inferred for some non-avian theropods. It is possible that changes in these muscles had occurred early in dinosaurian evolution, resulting in a wider inherited distribution for the derived condition. Both sauropods and ornithischians differ significantly from theropods in hip morphology, suggesting that some differences in musculature were likely. For example, the ornithischian preacetabular ilium is markedly narrow dorsoventrally, whereas the pubis often exhibits a long, neomorphic prepubic process. These two features have been associated with a variety of pelvic muscles (e.g., Romer 1942; Galton 1969; Coombs 1979), underscoring the difficulty in identifying soft-tissue correlates for novel structures (Witmer 1995).

In the ornithischian pelvis, the elevated lesser trochanter is associated with the elongated preacetabular ilium, suggesting that *M. iliofemoralis* was expanded in this clade, although independently from theropods and sauropods. Unlike theropods, there is less clear evidence on the proximal femur for subdivisions of this muscle, and the presence of any *Mm. iliotrochanterici* is unclear (although suggested in Romer 1942, Galton 1969). Expansions of the *M. iliotibialis*, *Mm. flexores tibiales*, and *M. iliofibularis* were also substantial components of the expanded iliac musculature.

In sauropods, the lesser trochanter remains low but the preacetabular ilium is considerably enlarged. Some expansion of *M. iliofemoralis* likely accompanied this iliac enlargement, but as with ornithischians evidence is ambiguous regarding the presence of subdivisions of this muscle. The small lesser trochanter may indicate a modest *M. iliofemoralis*, but it may also be a result of the general reduction in the prominence of muscular insertions throughout Sauropoda.

Further, more detailed investigations of pelvic and hindlimb morphology in these clades

are required before these subtle distinctions are clarified. Regardless, the same changes toward increased protraction and retraction (with associated reductions in abduction) are clear in both ornithischians and sauropods, paralleling the condition seen in theropods.

### Conclusions

This paper combines qualitative and quantitative morphologic data with a systematic survey of dinosaur taxa to draw conclusions about the evolution of locomotion in this group. Optimization of both discrete and continuous characters reveals the parallel evolution of several hindlimb and pelvic features in different dinosaurian lineages. In this context, parallelism provides an insight into the possible mechanical advantages of such innovations. Furthermore, parallelism can enlighten evolutionary transitions in extinct taxa by illustrating the similar results of repeated "experiments" on a particular ancestral condition. On a wider scale, convergences may also be useful in understanding evolutionary transitions by providing examples of similar derived conditions achieved from quite different ancestral conditions.

The independent acquisitions of expanded iliac pre- and postacetabular processes, a medially oriented femoral head, and an elevated lesser trochanter occur several times in non-avian dinosaur evolution. Associated modifications of hip and femur morphology resulted in dominance of protraction and retraction over abduction and adduction for several proximal hip muscles. Many of these changes may be related to the permanent acquisition of a parasagittal hindlimb posture, the evolution of bipedalism, and subsequent diversification within this mechanical context. Specific changes in muscle morphology and function are inferred to have occurred within non-avian theropods, many not associated with the origin of flight. Their parallel occurrence in dinosaurian lineages more distantly related to birds (ornithischians and sauropods) supports this interpretation.

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