The functional origin of dinosaur bipedalism: Cumulative evidence from bipedally inclined reptiles and disinclined mammals

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Abstract

Bipedalism is a trait basal to, and widespread among, dinosaurs. It has been previously argued that bipedalism arose in the ancestors of dinosaurs for the function of freeing the forelimbs to serve as predatory weapons. However, this argument does not explain why bipedalism was retained among numerous herbivorous groups of dinosaurs. We argue that bipedalism arose in the dinosaur line for the purpose of enhanced cursoriality. Modern facultatively bipedal lizards offer an analog for the first stages in the evolution of dinosaurian bipedalism. Many extant lizards assume a bipedal stance while attempting to flee predators at maximum speed. Bipedalism, when combined with a caudofemoralis musculature, has cursorial advantages because the caudofemoralis provides a greater source of propulsion to the hindlimbs than is generally available to the forelimbs. That cursorial advantage explains the relative abundance of cursorial facultative bipeds and obligate bipeds among fossil diapsids and the relative scarcity of either among mammals. Having lost their caudofemoralis in the Permian, perhaps in the context of adapting to a fossorial lifestyle, the mammalian line has been disinclined towards bipedalism, but, having never lost the caudofemoralis of their ancestors, cursorial avemetatarsalians (bird-line archosaurs) were naturally inclined towards bipedalism.

1. Introduction

A historical anecdote credits Plato with once responding to the question “What is man, and what separates him from all other beasts?” with the succinct, if philosophically unsatisfying, answer: “Man is unique; he is a featherless biped” (El Murr, 2010; Ferg, 1976). By modern standards, Plato’s zoological knowledge was limited, but his historic witticism remains anatomically astute. Putting aside salutary and racochetal locomotors (such as members of the Dipodidae, Dipodomyinae, Macropodidae, and Pedetidae) and facultative bipeds (which assume a bipedal stance only under exceptional circumstances), Homo sapiens is arguably the only extant obligate biped, outside of the Aves (although possible exceptions to Plato’s characterisation are Smutsia temminckii, the ground pangolin, which frequently stands and walks bipedally (Pietersen et al., 2014), and a handful of other primates that amble bipedally in the rare instances when they leave their arboreal homes (Aerts et al., 2000; Hewes, 1961)).

Because human bipedalism is so unusual amongst mammals, great effort has been spent tracking the origin of bipedalism within hominids and theorizing functional explanations for its evolution. Many such explanations have been offered. Three of the most enduring and widely considered theories are thermoregulation, enhanced vision, and freeing hands. The thermoregulatory theory suggests that a bipedal stance is beneficial because, during midday, it leaves relatively less surface area exposed to the overhead sun and, therefore, permits greater heat tolerance (Rodman and McHenry, 1980; Wheeler, 1984, 1985). The enhanced vision theory maintains that, because rearing back onto only the hindlimbs raises the head, bipedalism grants a constant vantage point from which distant resources and predators can be better detected (Ravey, 1978). In the case of hominids, both the thermoregulatory and enhanced vision theories have fallen out of general favor for two main reasons. First, many early bipedal hominids are known to have inhabited densely forested environments, where vegetation would have obscured overhead sunlight and obstructed long-distance vision (Lovejoy, 1981; White et al., 1995, 2009; Rayner et al., 1993; Pickford and Senut, 2001). Second, the bipedal benefits afforded in both theoretical scenarios are unrelated to any unique aspect of primate anatomy or behavior and, therefore, should be applicable to a range of other tetrapods. Thus, neither of the two theories do anything to explain the uniqueness of hominid bipedalism.

The hands-freeing theory argues that bipedalism evolved in the context of a switch from an arboreal to a more terrestrial lifestyle. By evolving full locomotive reliance on only the hind limbs, the forelimbs were freed to serve other tasks, such as carrying resources and wielding...
wepons (Hews, 1961; Fifer, 1987). This theory was first proposed by Darwin in The Descent of Man (Darwin, 2003), and numerous subsequent researchers have offered variants on the theory that place greater significance on the specific function(s) that the freed hands could have performed, such as transporting offspring (Leakey, 1976) or collecting resources as gifts for potential mates (Lovejoy, 1981; Parker, 1987). The hands-freeing explanation is dependent on the unusual grasping and dexterous hands of primates, and, unlike the thermo-regulatory and enhanced vision theories, satisfactorily explains why no similar selective pressures led to the development of bipedalism in other extant lineages.

But what of those bipeds with feathers? Until the 1980’s, the explanation for avian bipedalism seemed so obvious that it did not merit intense consideration: birds walked on only their hind limbs because their forelimbs were wings (Du Brul, 1962). Of course, the modern recognition that birds are derived from dinosaurs has revealed that the bipedalism of birds was already present in their dinosauromorph ancestors, long before the evolution of wings. Why dinosauromorph bipedalism first evolved has remained a relatively ignored and unsatisfactorily addressed question. We propose that bipedalism arose in the dinosaur line for the purpose of enhanced cursoriality.

2. Bipedalism at the origin of Dinosauria

At present, all known theropod dinosaurs are obligate bipeds (although quadrupedalism has been occasionally suggested in the case of the single species Spinosaurus aegyptiacus (Ibrahim et al., 2014; Bailey, 1997)). Obligate bipedalism is also universal among heterodontosauurs and pachycephalosaurs, and it is widespread among ornithopods, although many advanced iguanodontian ornithopods are generally considered only facultative bipeds. Obligate or facultative bipedalism is a shared trait of the earliest and most primitive ceratopsians, thyreophorans, and sauropodomorphs. Thus, bipedalism, to at least some degree, is a basal trait of all major dinosaur groups. Moreover, the oldest known dinosaurs (including the ornithischians Staurikosaurus, Herrerasaurus, and Pisanosaurus, and the saurischians Eoraptor, Herrerasaurus, and Steaurikosaurus) are all obligate bipeds, and, as such, confirm that bipedalism is basal to the Dinosauria as a whole (Fig. 1).

Thus dinosaur bipedalism appears to have had a single origin, with quadrupedalism evolving independently in multiple lineages. These multiple instances of secondary quadrupedalism coincide with the attainment of great body size, in the context of herbivory. Four limbs are naturally better at supporting large body weights, and herbivory generally favors enlargement of the digestive tract to accommodate the gastronomically more challenging act of breaking down cellulose. This digestive requirement leads to the enlargement of the abdominal cavity and thus a disproportionate increase in mass anterior to the hips and hindlimbs. Such a front-end-heavy body plan favors the attainment of a quadrupedal stance. Additionally, the attainment of quadrupedalism also coincided with disproportionate increases in absolute body masses that resulted from the evolution of heavy body-armor, within thyreophorans, and with the anteriorly displaced center of body mass that resulted from the evolution of cranial armor and horns, within the ceratopsians and hyper-elongate necks in the sauropodomorphs.

Numerous synapomorphies of Dinosauria appear to have been adaptations to facilitate enhanced bipedalism (see discussion in following sections). The oldest dinosauromorph fossils are footprints left by quadrupedal track makers about 250 million years ago (Brusatte et al., 2011); however, many later dinosauromorphs and dinosauromorphs have been recognized as bipeds (Brusatte et al., 2011). Thus, the bipedalism observed at the base of the dinosaur tree appears to have first arisen just outside it. In considering the origin of bipedalism within the dinosauromorphs and its subsequent retention and enhancement within Dinosauria proper, it is first worth evaluating the application of the multiple theoretical explanations derived to explain bipedalism in hominids.

Neither the thermoregulatory nor the vision-enhancing theory seem good fits, given that bipedal dinosaurs are now recognized as having horizontal body positions (Paul, 2005); therefore, bipedalism results in no substantial elevation of the head or reduction in exposed dorsal surface area. In contrast, the hands-freeing theory has been considered by multiple authors to be a valid and probable explanation (Sullivan, 2015; Hutchinson and Gatesy, 2001). Early dinosaurs and their ancestors were not arboreal and did not possess the highly dexterous hands or large brains of primates. Adopting bipedalism would certainly not have allowed dinosaurs to effectively use their forelimbs in transporting resources or performing complex manipulations. Instead, proponents of the hands-freeing theory have suggested that assuming a bipedal stance allowed dinosaurs to make better use of their clawed forelimbs in capturing and subduing prey (Sullivan, 2015; Hutchinson and Gatesy, 2001). This explanation is supported by the predatory nature of early dinosaurs and their immediate ancestors, and by the fused clavicles and grasping hands of early theropod dinosaurs, which may have enhanced their ability to grapple prey with their forelimbs (Hopson, 2001; Sereno, 1994; Farlow and Holtz, 2002).

While the evolution of bipedalism did potentially free theropod forelimbs to adapt concomitantly towards a stricter role as weapons, there are reasons to be skeptical that such forelimb function was itself the driving selective force behind the evolution of dinosaurian bipedalism. The inclination to prescribe great adaptive significance to the freed hands of dinosaurs and their early relatives may be a human bias. Bipedalism for the sake of enhanced predation is not observed in other lines of predators, and many modern predators, such as varanids and felines, make good use of their forelimbs when subduing prey, despite being obligate quadrupeds. Moreover, the immediate outgroups to Dinosauria (Lagerpetidae and Silesauridae) have forepaws that show no signs of being especially adapted for grasping or predation. While the earliest dinosaurs and obligately bipedal dinosauromorphs have relatively long forelimbs (as would be expected, given the only recent loss of the forelimbs’ locomotive function) (Sereno, 1994), the forelimbs of most later forms are greatly reduced in their maximum anterior reach. In many Triassic and Jurassic theropods, the forelimbs are so short that it is difficult to envision them grappling with any prey that could not have already been seized by the jaws. In the case of numerous Triassic theropods, such as Coelophysus, the maximum reach of the arms barely stretched half the length of the neck (Fig. 2). That reduction in forelimb length, seen even in many early theropods, suggests that the forelimbs did not play a vital role in predatory success (but see Carpenter (Carpenter, 2002) for a different interpretation). Similarly, although the ornithischian and theropod lineages split early in the history of dinosaurs, bipedalism was retained in multiple lineages of advanced small and medium-sized ornithischians, which were herbivorous and, therefore, not advantaged by prey-capturing forelimbs. This retention of bipedalism among smaller herbivorous dinosaurs is all the more curious, given the apparent ease with which there was a reversion to quadrupedalism in multiple instances among larger herbivorous dinosaurs. We offer the alternative (thou not intrinsically mutually exclusive) suggestion that the driving force behind dinosaurian bipedalism was in the hindlimbs and tail.

3. Facultative bipeds and the caudofemoralis complex

Whatever selective pressures led to dinosauromorph bipedalism, it is reasonable to assume that the formerly obligate-quadrupedal dinosauromorph ancestors did not spontaneously evolve obligate bipedalism in full. Rather, the eventual evolution of obligate bipedalism was likely preceded by gradational facultively-bipedal stages. As such, modern facultative bipeds may provide analogues to these stages and offer insights into their functional origin. Although extant non-avian obligate bipedalism is rare, facultative bipedalism is conspicuously widespread within one extant clade – Squamata – where it has evolved indepen-
Examples of facultative bipedalism can be found among members of the Agamidae, Crotaphytidae, Corytophanidae, Iguanidae, and Phrynosomatidae. In all of these lizards, bipedalism is adopted, not when the forelimbs are needed for predatory or other specialized functions, but when running at maximum speed (usually, when fleeing a perceived threat) (Aerts et al., 2003; Irschick and Jayne, 1999a; Clemente et al., 2008; Snyder, 1962, 1952). The phenomenon of facultative-bipedal running in lizards has been well studied, and its biomechanics, associated anatomical adaptations, and ecological role are well understood (Christian et al., 1994).

Among lizards, bipedalism is associated with those forms with the highest maximum sprint speeds and the most elongated hindlimbs (Aerts et al., 2003; Irschick and Jayne, 1999a; Snyder, 1952; Christian et al., 1994). That bipedalism is associated with greater cursorial ability is intrinsically counterintuitive. Why should employing one fewer set of limbs result in improved running performance? In general, if both limb sets are roughly equivalent in length and musculature, a quadrupedal posture should outperform a bipedal one (Hutchinson and Gatesy, 2001; Coombs, 1978). Moreover, in the specific case of lizards, when cursorily-less specialized facultative bipedal runners have been compared with closely-related obligate quadrupedal runners, the facultative bipedal runners have been found to have no significant advantage in either maximum attainable speed or in locomotor efficiency (Clemente et al., 2008) — although such comparisons have found facultative bipedal runners to have naturally greater acceleration (Clemente et al., 2008) and less rotational inertia (Aerts et al., 2003) (the latter because assuming a bipedal stance shifts the center of mass closer to the hips and, thus, closer to the active axis of rotation, although the importance of this may be minimal, given that facultative bipedal lizards are generally observed to flee in a roughly linear path (Irschick and Jayne, 1999b)).

Key to resolving the apparent contradiction between bipedalism and cursoriality is recognizing that, in lizards, the forelimbs and hindlimbs are intrinsically unequal in terms of musculature. The power strokes of the lizard hindlimbs are driven primarily by the caudofemoralis muscle complex. The m. caudofemoralis (composed of the m. caudofemoralis longissimus and the m. caudofemoralis brevis) is anchored to the anterior tail vertebrae and chevrons, immediately posterior to the ilium, and it inserts onto the fourth trochanter of the femur and, via an accessory tendon, onto the proximal ventral surface of the tibia (just below the knee joint) (Snyder, 1962; Persons and

Fig. 1. Bipedalism throughout the dinosaur lineage. Obligate bipedal taxa in green, facultative bipedal taxa in blue, and quadrupedal taxa in purple. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 2. The theropod Coelophysis, which, despite being an early predatory dinosaur, had short arms with a reach well-short of its jaws.
Currie, 2011a). In most cases, the caudofemoral muscles exceed the forelimb retractors in size (Aerts et al., 2003; Snyder, 1962; Persons and Currie, 2011a). Additionally, because the caudofemoral muscles are uniquely positioned along the tail, they can increase in posterior extent and lateral girth with little restriction, and exceptionally long and large caudofemoral muscles characterize the highly cursorial and facultative bipedal forms (Snyder, 1962, 1952; Persons and Currie, 2011a). Thus, the hindlimbs of lizards are naturally disposed to become more powerful relative to the forelimbs.

This discrepancy in locomotive power resulting from the caudofemoral musculature has several implications. First, it means that, at the same stride frequency, the hindquarters of a quadrupedal lizard generate greater propulsion and thus undergo greater acceleration (Aerts et al., 2003). Second, it means that investment in lengthened hindlimb proportions have a greater net cursorial benefit than would an equivalent investment in lengthened forelimb proportions. Thus, cursorial lizards are prone to disproportionate elongation hindlimbs, to out-of-phase forelimb/hindlimb strides, and to effectively “pop-a-wheelie” onto their more powerful hindlimbs. (A similar phenomenon is observed in the “bipedal run” of some cockroaches, when the running insects rear back onto only their more powerful third sets of legs (Herreid et al., 1981).) A third implication is the rear shift in the center of mass that an enlarged caudofemoralis creates and the tendency for this shift to increase the cantilevering effect of the tail on the body, thereby making it easier for the torso and forelimbs to be raised, when bipedalism is assumed (Irsich and Jayne, 1999a). Finally, the combination of proportionately more elongate hindlimbs and a discordant forelimb/hindlimb stride leads to the threat of stride overlap and front and hindlimbs becoming awkwardly entangled. This is not a strictly theoretical concern, Irsich and Jayne (Irsich and Jayne, 1999a) preformed trials on bipedal and quadrupedal running lizards and observed that high-speed quadrupedal runners frequently tripped over their own feet, while facultative bipedal runners were freed from this hazard. These trips did substantively affect the lizards overall performance (Irsich and Jayne, 1999a). It is also entirely reasonable to regard such forelimb-hindlimb interference as a non-trivial concern, given that lizards generally engage in facultatively bipedal running when fleeing danger and that a safeguard against stumbling has the potential to be a life-or-death difference.

4. Caudofemoral implications

Thus, although bipedalism does not result in greater cursorial ability senso stricto, when cursorial ability is being selected for in the presence of a well-developed caudofemoralis complex, a number of factors conspire to favor and foster it. The caudofemoral musculature is, by no means, unique to lizards. It is the basal condition of Tetrapoda (Romer, 1956). Squamata simply represent the only extant group that manifests the caudofemoral/bipedal relationship, because all other large groups of tetrapods have either lost or greatly reduced the caudofemoral complex (as in mammals, ground birds, and anurans) or have retained the caudofemoral complex but are non-terrestrial and/or non-cursorial (as in crocodilians, salamanders, and turtles). Although the caudofemoralis was reduced in the avian lineage (Persons and Currie, 2012; Gerty, 1990, 2002; Gerty and Thomasom, 1995), the muscle complex was large and was the predominant hindlimb retractor in dinosaurs and in non-avian dinosauromorphs (Persons and Currie, 2011a, 2012, 2011b, 2014; Persons et al., 2013). Many of the anatomical traits that typify early dinosaurs, including some frequently regarded as synapomorphic, relate to facilitating an enhanced caudofemoral complex. These included the presence of dorsally raised caudal ribs (Persons and Currie, 2011a), which allowed for expanded caudofemoral musculature, and the prominence and asymmetrical form of the femoral fourth trochanter (Nesbitt, 2011; Brusatte, 2012).

It should be pointed out that previous authors have argued that the presence of long and robust tails was an influential factor in the evolution of bipedal locomotion within saurians (and, similarly, that the absence of long robust tails may have limited the evolution of bipedalism within mammals) (Hutchinson and Gatesy, 2001; Snyder, 1967; Tarsitano, 1983). These arguments have usually focused on the effect large tails had on the center of mass and the greater weight that the hindlimbs naturally bore, making it easier to achieve reliance on only the hindlimbs. Similar arguments can also be made based on the larger size and greater rigidity of the pelvic, as compared to the pectoral, girdle. However, while such arguments help to explain why bipedalism has been more widespread and successful in tetrapod groups with large tails than in groups, such as mammals, that have relatively lightweight tails, they fail to explain the more fundamental question of why quadrupedalism would be abandoned in favor of bipedalism.

We therefore suggest a cursorial explanation for dinosaurian bipedalism and propose the following adaptive scenario, with the hopes that its various aspects will be considered, scrutinized, and quantitatively investigated by future inquires. First, early dinosauromorphs are recognized as having been small bodied carnivores living alongside a slew of larger predators (most prominently a diverse array of curotarsans) (Brusatte et al., 2008; Benton et al., 1997). Such a niche favored speed and agility, for the purpose of both fleeing predators and pursuing small agile prey. Possessing a large caudofemoralis, the same factors inferred to have repeatedly led to the evolution of facultative bipedalism in extant lizards led dinosaurian ancestors to develop facultative bipedalism. However, unlike lizards, whose cursorial performance is generally limited to short bursts of speed, dinosaurian ancestors were intrinsically more active (perhaps endothermic to some degree) and benefited from sustaining longer and longer periods of high cursorial performance. To facilitate this, the hindlimbs and associated pelvic and caudal anatomy became increasingly adept at maintaining a bipedal stance. Simultaneously, a reduction in forelimb length and mass was favored, because the forelimbs were used decreasingly in locomotion and because reduction in forward mass facilitated easier passive balance on the hindlimbs. Eventually, the hindlimbs were adequately adapted to support locomotion at all speeds and gaits, and the forelimbs were reduced to the point that they were wholly inadequate for locomotion, resulting in a highly cursorial and fully obligate bipedal dinosauromorph that stood well-balanced on only the hindlimbs and possessed an enhanced caudofemoral complex. That bipedalism evolved to facilitate cursoriality explains why the trait was retained in many lineages of small fleet-footed herbivorous dinosaurs but was abandoned in larger and heavily armored forms.

It should be pointed out that, in a number of fundamental ways, the hindlimb anatomy and biomechanics of modern lizards and dinosauromorphs are far from analogous. Most notably, lizards have a sprawling stance and are largely plantigrade, while dinosauromorphs possessed a parasagittal gait and were digitigrade. However, these postural differences are not intrinsically discordant with our adaptive scenario or with any of the caudofemoralis-related factors favoring bipedalism. Indeed, in some regards, the opposite appears true. That early quadrupedal dinosauromorphs already possessed parasagittal limbs is confirmed by fossil trackways, which also show that the strides of the more elongated hindlimbs overlapped those of the forelimbs (Brusatte et al., 2011). This combination may have been particularly prone to the stumbling effect observed in modern lizards. Similarly, because a non-sprawling stance makes balancing on a single foot easier, particularly when moving at slower speeds, the parasagittal gait of dinosauromorphs may have made the transition from facultative bipedalism to obligate bipedalism substantially easier.

5. Bipedal bottlenecks

If it is true that a well-developed caudofemoralis complex creates an
evolutionary predisposition to adapt bipedalism alongside cursoriality, it follows that, given the former diversity of diapsid lineages with large caudofemoral musculature, other examples of bipeds should be found when similar selective conditions arose. The fossil record supports this prediction. Among archosaurs, bipedalism has evolved more than twice, with multiple presumed facultative and obligate bipedal Triassic cruritorsans (crocodile-line archosaurs) now known (Kubo and Kubo, 2012; Gauthier et al., 2011; Nesbitt and Norell, 2006; Schachner et al., 2011). In a statistical study of bipedalism and cursorial adaptations among Triassic archosaurs, Kubo and Kubo (Kubo and Kubo, 2012) found bipedalism to correlate positively with limb proportions indicative of high cursoriality, with obligate bipeds having consistently more extreme cursorial adaptations than quadrupeds, and with facultative bipeds being intermediate. Based on relatively lengthened hindlimbs, several non-archosaur fossil taxa have also been identified as facultative biped runners. These include the Permian holosaurid Eudibamus, which is also thought to have been digitigrade with a nearly vertical limb position while running (Berman et al., 2000), and the Triassic prolacertiformes Langobardisaurus (Renesto et al., 2002) and Macrocnemus (Rieppel, 1989).

The Triassic, in particular, seems to have been a heyday for lineages experimenting with bipedalism, with bipedal dinosauromorphs, prolacertiforms, and poposaurid crocrodilomorphs all evolving at this time. This abundance of bipeds may reflect the Triassic’s unusual ecological context where, in the wake of the Great Permian Extinction, tetrapod lineages had the opportunity to adapt to a slew of emptied terrestrial niches and where, potentially, the first evolutionary arms-races between endothermic lineages began (Bakker, 1971). This favored the evolution of new and more cursorial predators and new and more cursorial prey. Bipedalism is not the only cursorial trend recognizable among the terrestrial Triassic fauna (Sullivan, 2015; Bates and Schachner, 2011). It was also during this time that the ornithodirans (bird-line archosaurs) evolved more paragastral gaits and erect postures, and the “rauisuchians” and aetosaurs evolved more para-sagittal gaits through the functionally equivalent pillar-erect postures (Sullivan, 2015; Bates and Schachner, 2011). Dinosauromorphs and basal crocodilomorphs evolved digitigrade postures, and the ornithodirans evolved the mesotarsal ankle, which also provided cursorial benefits. Following the Triassic-Jurassic Extinction Event and during the ensuing age of dinosaur dominance, the various other bipedal lineages that had evolved during the Triassic became extinct. The Paleogene might well have seen a similar surge in diapsid bipeds, were it not for the rapid successes of mammalian and avian lineages at filling the niches left vacant by the extinction of non-avian dinosaurs.

The relative scarcity of obligate bipeds among mammals reflects the lack of the caudofemoralis complex within the lineage. However, its absence is curious, given that modern mammals are among the most cursorial of vertebrates, that therapsids were among the groups vying for dominance during the Triassic, and that synapsids share the same dinosaurian cursorial adaptations among Triassic archosaurs, Kubo and Kubo (Kubo and Kubo, 2012) found bipedalism to correlate positively with limb proportions indicative of high cursoriality, with obligate bipeds having consistently more extreme cursorial adaptations than quadrupeds, and with facultative bipeds being intermediate. Based on relatively lengthened hindlimbs, several non-archosaur fossil taxa have also been identified as facultative biped runners. These include the Permian holosaurid Eudibamus, which is also thought to have been digitigrade with a nearly vertical limb position while running (Berman et al., 2000), and the Triassic prolacertiformes Langobardisaurus (Renesto et al., 2002) and Macrocnemus (Rieppel, 1989).

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It is curious that such a major change in basic limb musculature should evolve twice in Neotherapsida and more curious still that the two lineages in which it evolved would be the only two therapsid clades to endure the Great Permian Extinction and persist into the Triassic. We speculate that the convergent loss of the caudofemoralis in dicynodonts and eutheriodonts relates to a shared trait of basal members of both groups: burrowing. Many dicynodonts and eutheriodonts have been recognized as fossorial, being frequently recovered in fossil burrow infills (Damiani et al., 2003; Ray and Chinsamy, 2003) and possessing both the robust, high-leverage limb and broad claw morphologies typical of burrowing animals. Burrowing habits may have favored the reduction and eventual loss of the caudofemoralis complex for a number of reasons. First, burrowing naturally emphasizes the musculature of the forelimbs in animals that excavate head first. This could result in the forelimb musculature overtaking the formerly advantaged hindlimb musculature and potentially in the eventual economical loss of hindlimb musculature. Second, a robust and long tail may be a significant hindrance when attempting to maneuver and change directions in the confines of a burrow. Finally, a robust and long tail diminishes the relative safety that fleeing into a burrow provides, because it makes the distance that a predator must reach in to snag the burrower that much shorter. Although there are exceptions, abnormally short tails are abundant in modern mammalian burrowers (badgers, lagomorphs, talpids, and vombatiforms) and also in several clades of fossorial squamates (helodontamid, Phrynosoma, Tiligu, and uromastyx). During the climatic disruptions of the
Great Permian Extinction, it may have been the ability of the dicynodonts and eutheriodonts to seek shelter in burrows that allowed them to survive, whereas other therapsids could not (Damiani et al., 2003). Having weathered the extinction, Triassic dicynodonts and eutheriodonts were free to emerge from their burrows and adapt to other niches. When they did, they lacked the caudofemoralis complex that would predispose them towards bipedalism and were, therefore, inclined to retain obligate quadrupedalism. This consequences has had lasting impact throughout mammalian evolution, and has, in turn, likely contributed to the evolution of other characteristically mammalian features that help to accommodate high acceleration and speed in obligate quadrupeds, including the vertebral lumbar region (which enhances dorsoventral vertebral flexibility and permits the forelimbs to contact the ground closer to the center of mass) and a more mobile shoulder girdle (which permits greater forelimb excursions) (Christian et al., 1994).

6. Conclusion

That dinosaurian bipedalism arose for the purpose of enhanced cursoriality, rather than as a means of freeing the hands for use in prey capture, is consistent with the functional origins of facultative bipedalism observed among modern squamates and inferred for multiple fossil diapsid taxa. It is also consistent with the relative infrequency of bipedalism observed in extant and fossil synapsids, which lost the caudofemoralis and, therefore, the impetus for cursorial bipedalism, early in their evolutionary history. Terrestrial mammals and dinosaurs share many similarities in terms of their ecology. Both have adapted to their own megafauna dynasties, and both have evolved numerous highly cursorial forms. The discrepancy between the high frequency of dinosaurian bipeds and the relative ubiquity of mammalian quadrupeds is a case of adaptive predetermination. In both groups, anatomy was destiny. Having never lost the caudofemoralis of their ancestors, cursorial synapsids could naturally inclined towards bipedalism, while, having lost the caudofemoralis in the Permain, the mammalian line has been disinclined towards bipedalism. Recognizing the cursorial origins of diapsid bipedalism reemphasizes the unusualness of hominid obligate bipedalism among mammals. It also shows that the current biped-impoverished world is the chance product of two evolutionary bottlenecks: the first being the disappearance during the Great Permian Extinction of those therapsid lines with a caudofemoralis complex, and the second being the more recent disappearance of the non-avian dinosaurs during the end Cretaceous Extinction.

References


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