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Major Transformations in the Evolution of Primate Locomotion

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Introduction

Compared to other mammalian orders, Primates use an extraordinary diversity of locomotor behaviors, which are made possible by a complementary diversity of musculoskeletal adaptations. Primate locomotor repertoires include various kinds of suspension, bipedalism, leaping, and quadrupedalism using multiple pronograde and orthograde postures and employing numerous gaits such as walking, trotting, galloping, and brachiation. In addition to using different locomotor modes, primates regularly climb, leap, run, swing, and more in extremely diverse ways. As one might expect, the expansion of the field of primatology in the 1960s stimulated efforts to make sense of this diversity by classifying the locomotor behavior of living primates and identifying major evolutionary trends in primate locomotion. The most notable and enduring of these efforts were by the British physician and comparative anatomist John Napier (e.g., Napier 1963, 1967b; Napier and Napier 1967; Napier and Walker 1967). Napier's seminal 1967 paper, "Evolutionary Aspects of Primate Locomotion," drew on the work of earlier comparative anatomists such as LeGros Clark, Wood Jones, Straus, and Washburn. By synthesizing the anatomy and behavior of extant primates with the primate fossil record, Napier argued that

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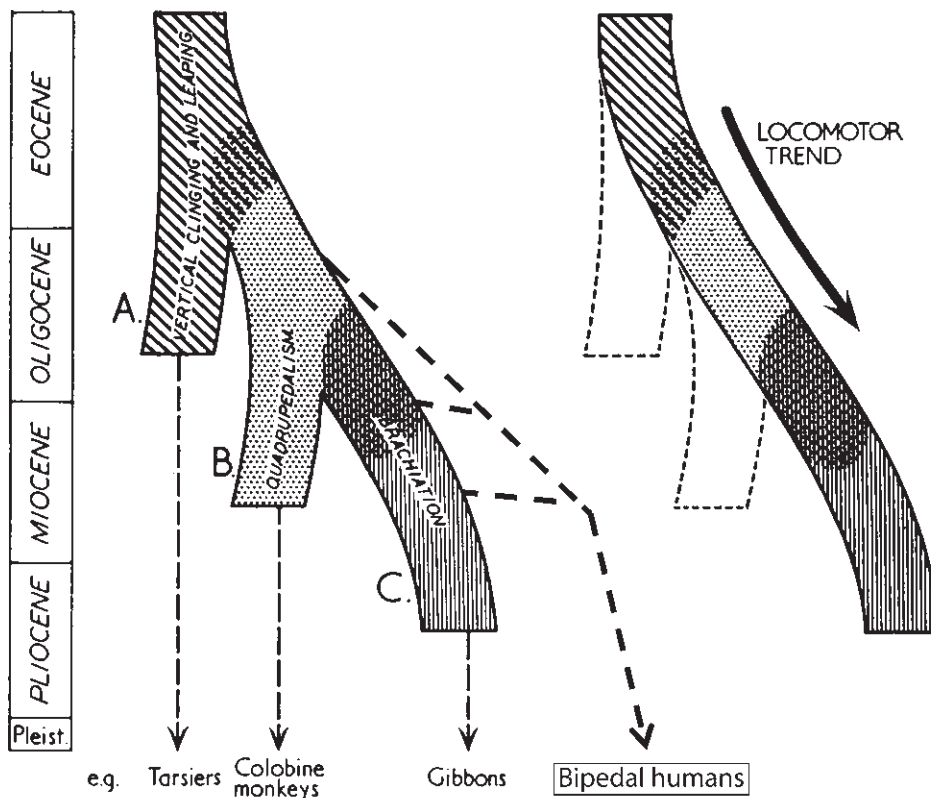† Department of Human Evolutionary Biology, Harvard University

FIG. 15.1 Trends in the evolution of primate locomotion. Napier portrayed the evolution of primate locomotion as a progression or trend. Vertical clinging and leaping was the initial locomotor behavior for Primates in the Eocene, and gave rise to quadrupedalism in the Oligocene, which, in turn gave rise to brachiation in the Miocene. Each of these stages is still present among living taxa. It is unclear which form of locomotion gave rise to human bipedalism. Modified from Napier (1967b).

the evolution of primate locomotion could be characterized by a series of distinct locomotor stages (fig. 15.1). According to this scheme, the earliest primates were *vertical clingers and leapers*, similar to living galagos, tarsiers, and indriid lemuroids; vertical clingers and leapers subsequently gave rise to *arboreal quadrupeds* similar to living Old World monkeys; and arboreal quadrupeds gave rise to brachiators or *suspensory* primates, like the living apes. Last but not least, *bipedal* humans evolved from these suspensory apes (Napier 1967a).

Napier's scheme has influenced, directly and indirectly, much thinking about the evolution of primate locomotion, but it is based on the assumption that the behaviors and morphologies of extant primates are sufficient to characterize the kinds of locomotor behavior, hence morphological adaptations, found in fossil primates. But is this assumption warranted? Can present day diversity usefully predict the ancient diversity that gave rise to the patterns we observe today? How

can the fossil record help reevaluate Napier's scheme? In this contribution, we examine major transitions in primate evolution to consider what the primate fossil record tells us about the evolution of primate locomotor diversity, drawing especially upon insights derived from Farish A. Jenkins Jr.'s research. Jenkins repeatedly showed that the locomotor behavior of primates and other vertebrates is closely related to details of the joint surfaces involved in specific movements. Jenkins's meticulous research on the mechanics and kinematics of virtually all joints, including the elbow (Jenkins 1973), wrist (Jenkins and Fleagle 1975; Jenkins 1981), hip (Jenkins 1972; Jenkins and Camazine 1977), and ankle (Jenkins and McLearn 1984) provide a fundamental basis for inferring the locomotor behavior of fossil primates and for thinking about the evolution of extant primates. Using this perspective, we focus on four major transitions: (1) the origins of vertical clinging and leaping; (2) the evolution of terrestrial quadrupedalism; (3) the

origin and evolution of suspensory locomotion; and (4) the origin and evolution of bipedalism in humans. Our unsurprising, but often unappreciated, conclusion is that locomotor diversity among primates was much greater in the past than it is today, and that many morphological features used to infer locomotor adaptations appear in past species in different combinations than are found today (e.g., Jungers et al. 2002; Fleagle 2013). Put differently, many locomotor adaptations evolved independently, in different combinations, and in different ways. One could not possibly reconstruct the evolution of primate locomotion correctly without an integrated approach that includes studying the fossil record, laboratory studies of the locomotor biomechanics, and careful comparative analyses of morphology with a special focus on joint function.

Vertical Clinging and Leaping, and Primate Origins

In 1967, Napier and Walker named and described a distinctive type of locomotion among living primates, "vertical clinging and leaping." Their designation of this behavior notes, "The animals concerned are arboreal, have a vertical clinging posture at rest and are well adapted to a leaping mode of progression during which the hind limbs, used together, provide the propulsive force" (Napier and Walker 1967, 204) for leaping between vertical supports. As examples, they identified *Tarsius*; the indriids *Indri, Propithecus,* and *Avahi*; lemurids such as *Lepilemur* and *Hapalemur*; and the lorisoids *Galago* and *Euoticus*. In addition to describing and drawing locomotor behaviors, they identified a collection of bony features in the skeleton that were found in various living leapers and seemed associated with the behavior. In addition, they suggested, "The special interest of this locomotor group of Vertical Clinging and Leaping is that it appears in a preliminary study to constitute the only known locomotor adaptation of Eocene primates; possibly it is to be regarded as the earliest locomotor specialization of primates and therefore preadaptive to some or possibly all of the later patterns of primate locomotion" (Napier and Walker 1967, 204).

The vertical clinging and leaping (VCL) hypothesis has received much criticism (e.g., Cartmill 1972; Martin 1972; Szalay 1972; Stern and Oxnard 1973; Anemone 1990; Martin 1990). Many critics argued that this "locomotor group" actually contains animals with very

different morphological features; others argued that it wasn't sufficiently inclusive because there are vertical clingers among other groups of primates, especially New World monkeys (e.g., Kinzey et al. 1975). Perhaps most damning was Szalay's (1972, 33) claim that "the osteological characters that might be *invariably* associated with vertical clinging and leaping have not been deduced as yet, if such clear-cut features exist at all." In a later review of the topic, Anemone (1990) found that many musculoskeletal features shared by vertical clingers and leapers are also found in related primates that do not engage in VCL. Most critics of the VCL hypothesis also noted that leaping among primates is not a single type of locomotion with a single set of anatomical correlates. Primate leapers have evolved in many different clades, each with different initial morphologies. In addition, leaping may be combined with many other types of movements, leading to morphological compromises. Finally, primates may show adaptations for leaping to and from substrates with very different orientations and sizes.

Despite these criticisms, VCL behaviors are still widely attributed to fossil primates, especially early primates. Following Jenkins's approach, it is useful to evaluate the skeletal indicators of VCL by focusing on the appropriate joints and the specific behaviors that take place at those joints: clinging, which involves the forelimb as well as hands and feet; and leaping from vertical supports, which involves the hind limb, especially the hip. In 1980, Szalay and Dagosto published an important review of the evolution of the elbow in early primates. Among their observations they noted the presence in extant indriids (*Propithecus*) of a "secondary" articulation, termed a "clinging facet," above the humeral trochlea that seems to be the result of habitual use of clinging postures. Importantly, this "clinging facet" is commonly found in other primates that have been identified as "vertical clingers," including tarsiers, some galagos, pygmy marmosets, and white-faced sakis (Fleagle and Meldrum 1988), and it is not found in habitually quadrupedal primates.

Almost all primates can leap to some degree, but habitual leapers are usually characterized by a set of musculo-skeletal adaptations that enable them to rapidly extend their hind limbs for propulsion (e.g., Stern 1971; Fleagle 1977a, 1977b; Anemone 1990). As a rule, leapers have a long ischium for increasing the moment

FIG. 15.2 Leaping from a vertical support, as illustrated by the sifaka on the left, involves a different excursion of the femur relative to the axis of the trunk and pelvis, and a different orientation of the ischium, than either quadrupedal walking or leaping from a horizontal support, as illustrated by the lemur on the right. Modified from Fleagle and Anapol (1992.)

arm of hip extensors (Smith and Savage 1956). They also tend to have a deep knee joint to increase leverage of the quadriceps via the patella. In addition, leapers usually have a very proximal attachment for the hamstrings on the tibia so that hip extension is not accompanied by knee flexion, as it is in quadrupeds (e.g., Haxton 1947; Stern 1971; Fleagle 1977a, 1977b). However, as shown in figure 15.2, the mechanics of leaping from vertical supports are considerably different from the mechanics of leaping from a horizontal support (Fleagle and Anapol 1992). In quadrupedal walking or leaping from a horizontal support, the excursion of the femur is approximately perpendicular to the axis of the trunk, and the hamstrings achieve maximum leverage by extension of the ischium distally along the axis of the trunk or the blade of the ilium. However, during leaping from a vertical support with a vertical (or orthograde) body position, maximum extension of the hind limb brings the femur in line with the axis of the trunk or the blade of the ilium. For this kind of movement, distal extension of the ischium is not only unhelpful

but also makes contraction of the hamstrings impossible because it greatly shortens the distance between their origin and insertion. Thus, primates that leap from a vertical posture have a dorsally rather than distally elongated ischium.

Oddly, Napier and Walker (1967) and other authors (Zuckerman et al. 1973; Walker 1974; McArdle 1981) noted that VCL primates are unusual among mammalian leapers in having a distally short ischium, but the mechanical significance of this feature was not appreciated. Dorsal rather than distal elongation of the ischium in primates leaping from a vertical or orthograde posture evolved for the same mechanical reason that upright, bipedal humans also have an ischium that extends dorsally rather than distally (fig. 15.3; e.g., Robinson 1972). The distally extended ischium of chimpanzees explains why, even when you force a chimpanzee to walk bipedally with its trunk in an orthograde posture, its femur remains nearly perpendicular to the axis of its trunk, as Jenkins (1972) elegantly documented using cineradiography. A broad comparison of primate

pelves (fig. 15.4; also other figures in Fleagle and Anapol 1992) shows that habitual vertical clingers from many different families are characterized by an ischium that extends dorsally rather than distally, whereas quadrupeds and primates that normally leap from horizontal supports have a distally extended ischium (Fleagle and Anapol 1992). Confirmation for this observation comes from primates (*Lepilemur*, *Hapalemur*, and *Eulemur rubriventor*) that have a more mixed locomotor repertoire—sometimes running and leaping from horizontal supports, sometimes clinging and leaping from vertical supports. In these species, the ischium tends to be extended both distally and dorsally.

We can therefore conclude that, contra Szalay's (1972) pessimistic conclusion 40 years ago, there are at least two anatomical features that distinguish habitual vertical clingers and leapers from primates that rely more extensively on other modes of locomotion: clinging facets and dorsally extended ischia. If we apply these features to the available skeletal material of Eocene primates from North America and Europe, we find no early primates with the distinctive short, dorsally extended ischium of habitual vertical clingers and leapers (fig. 15.4) and none show a clinging facet on the humerus. However, there are several early Eocene primates (*Notharctus*, *Smilodectes*, and *Omomys*) in which

the ischium is extended both distally as well as dorsally, suggesting that these species were probably capable of leaping from either horizontal or vertical supports (Fleagle and Anapol 1992). In addition, evidence of the hamstring attachments on the tibia suggest that none of the notharctines (*Notharctus*, *Smilodectes*, or *Cantius*)—regularly described as vertical clingers and leapers on the basis of limb proportions—had a proximal attachment for the hamstrings in the tibia. Instead, they display a distal insertion more characteristic of arboreal quadrupeds. Other early Eocene taxa, notably *Shoshonius* (see Dagosto et al. 1999), also seem to have been primarily arboreal quadrupeds. It should be noted that many early primates are thought to have been leapers of some kind based on their ankle morphology. However, as numerous workers have noted (Gebo et al. 2012; Ni et al. 2013), there is no indication from ankle morphology that these taxa were as committed to VCL as are extant indriids, tarsiers, and some galagos. Moreover, the presence of elongated tarsals in cheirogaleids indicates that tarsal elongation does not necessarily imply leaping behavior.

Almost 50 years after its initial proposal, we can draw several conclusions about the VCL hypothesis. First, vertical clinging and leaping is just one of many different types of leaping locomotion used by living primates, many of which have a wide range of musculoskeletal
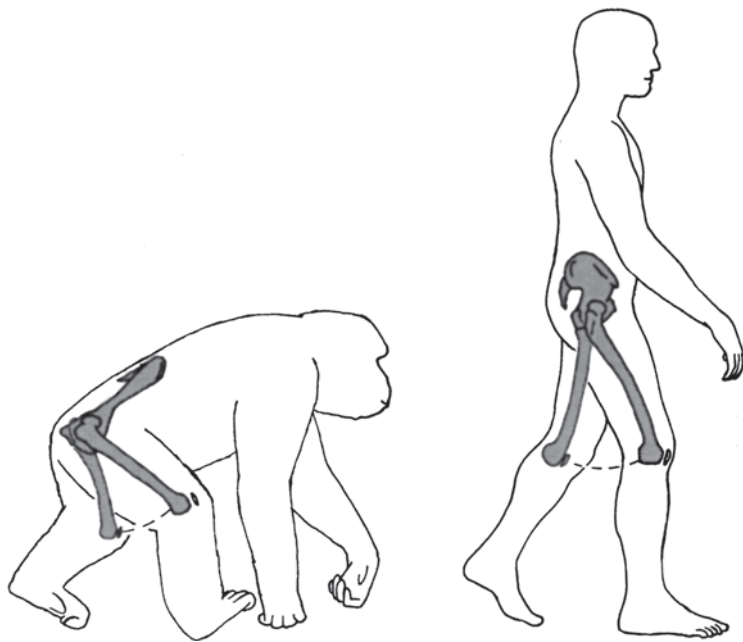

FIG. 15.3 Human bipedalism, shown on the right, involves a different excursion of the femur than quadrupedal walking in a chimpanzee, shown on the left. The femoral excursion in bipedal walking is similar to that used in leaping from a vertical support (fig. 15.2) and is made possible by a dorsal, rather than a distal, extension of the ischium. Modified from Fleagle and Anapol (1992).
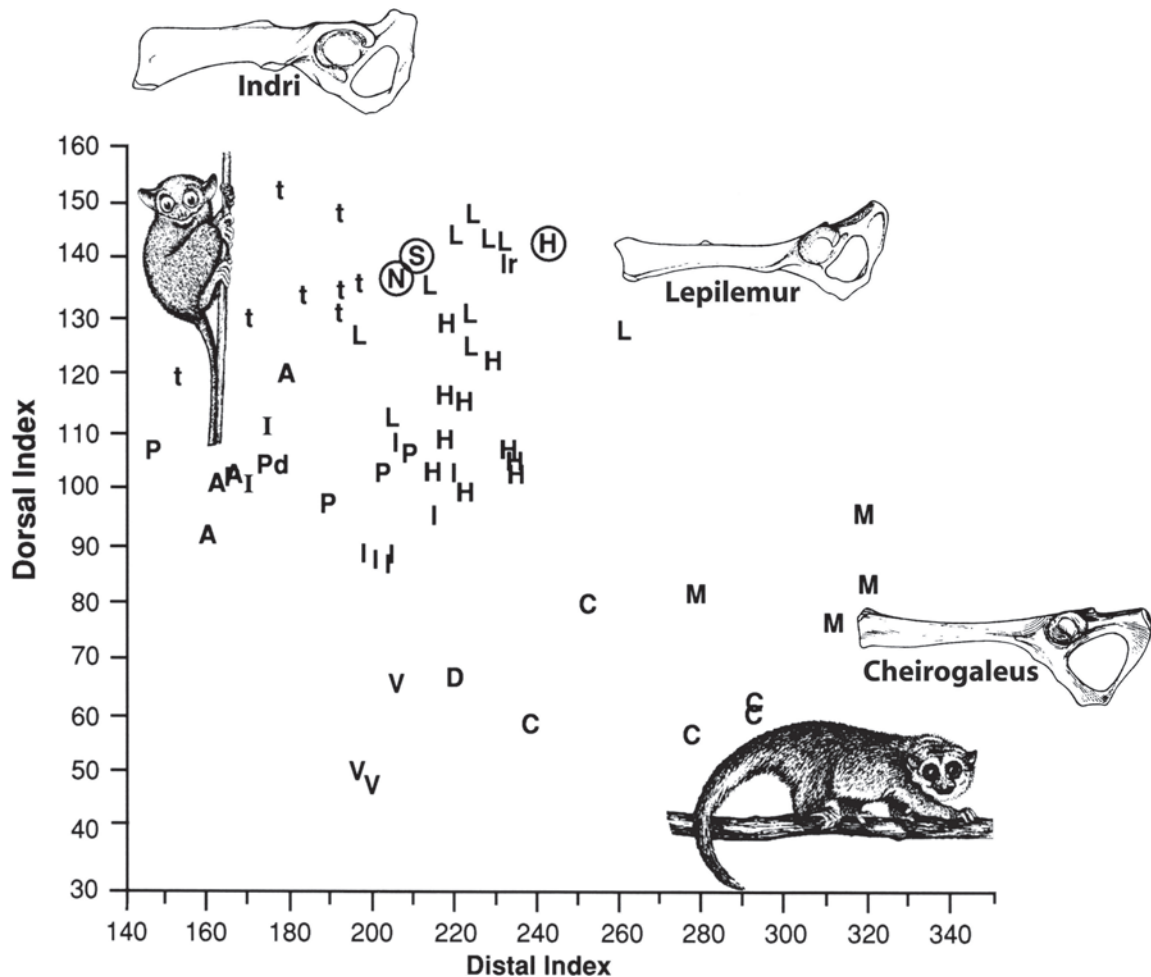
FIG. 15.4 A plot of the relative distal projection of the ischium and the relative dorsal projection of the ischium separates taxa that habitually leap from vertical supports such as tarsiers (t, upper left) from more quadrupedal taxa such as dwarf lemurs (C, lower right). Some taxa, such as *Lepilemur* (L) *or Hapalemur* (H), have an ischium that is elongated in both directions, and both taxa have been reported to be adept at leaping from both vertical and horizontal supports. The pelves of Eocene primates (circled letters) all plot near these "all purpose leapers" rather than with habitual vertical clingers and leapers. Pelves of Eocene fossils: N = *Notharctus*; H = *Hemiacodon*, S = *Smilodectes*. For other taxa see Fleagle and Anapol (1992). Redrawn from Fleagle and Anapol (1992).

features. Second, VCL behaviors evolved independently several times in the Order Primates, each time slightly differently. Third, there is no indication that habitual VCL as practiced by extant indriids, tarsiers, or galagos was the primitive locomotor behavior for the earliest primates or was practiced by any known Eocene primates, including the basal haplorhine *Archicebus*, known from a nearly complete skeleton (Ni et al. 2013). The mosaic combinations of features evident in Eocene primates are not found in any single living primate taxon. This suggests that early primates tended to have a highly generalized locomotor anatomy capable of a wide range of locomotor behaviors including some vertical leaping, but they did not show the morphology or behaviors seen in the specialized extant taxa as envisioned by Napier and Walker (1967).

The Evolution of Terrestrial Quadrupedal Locomotion

It is paradoxical to discuss quadrupedal locomotion in primates in the context of transformations because, as discussed above, it seems most likely that the earliest primates were some type of arboreal quadruped or quadrupedal leaper (Jenkins 1974; Kirk et al. 2008). Similarly, the earliest platyrrhines, the earliest catarrhines, the earliest hominoids, and perhaps even the earliest hominins were arboreal quadrupeds (see below). Put

differently, arboreal quadrupedalism is probably the baseline from which other locomotor modes evolved in primates.

That said, one key locomotor transformation in primate evolution is from arboreal to terrestrial quadrupedalism. As Jenkins noted in 1974, the difference between being an arboreal and terrestrial quadruped is less clear for smaller animals than for larger ones for two reasons. For a small animal, the ground in a forested environment is not a uniform substrate because small irregularities in terrain and vegetation pose greater hurdles for a small animal than a larger one. Similarly, in an arboreal environment, small animals would more likely encounter branches and boughs much larger than their body that could be traversed without grasping. For larger primates, however, the main functional challenges posed by an arboreal environment are balance and grasping on relatively smaller supports (e.g., Napier 1967a; Fleagle and Mittermeier 1980). Consequently, primates who are much larger than the supports upon which they are walking or running maintain their balance by lowering their center of gravity with flexed and abducted limbs (Grand 1968; Schmitt 2003b), by using their tail as a counterbalance, and by maintaining a firm grasp on several supports throughout each step cycle, which likely involves some degree of hyperpronation at the wrist (Jenkins and Fleagle 1975; Jenkins 1981).

These size-related challenges change on the ground. For terrestrial primates, the problem of balance and the associated need for digital grasping are relaxed, making possible selection for other performance tasks. This shift is reflected in many aspects of the anatomy of terrestrial quadrupeds such as the frequent reduction or loss of the tail, and the evolution of longer, subequal fore- and hind limbs. In addition, several well-documented features of the forelimb are likely adaptations for terrestrial quadrupedalism (Jenkins 1973; Jolly 1967; Bown et al. 1982; Fleagle 1999). In these primates, the greater tubercle of the humerus extends well above the relatively narrow humeral head, and the olecranon process tends to extend dorsally rather than proximally because the action of the triceps normally takes place with the elbow extended rather than flexed as in arboreal quadrupeds. Adaptations for terrestrial quadrupedalism in the elbow are particularly well documented and understood (Jenkins 1973). The muscles involved in wrist and digit flexion used during locomotion arise largely from the medial epicondyle of the humerus. During terrestrial quadrupedalism, the forearm is normally pronated, and contraction of the wrist and digit flexors generates a supinating torque around the humero-ulnar joint (Jenkins 1973). Because the ulna, unlike the radius, is not free to rotate, many terrestrial quadrupeds counteract these torques with two osseous adaptations. First, the medial epicondyle tends to project dorsally rather than medially, directing the action of the muscles more in line with the pronated forearm. Second, there is a prominent medial lip on the trochlea of the humerus (and also on the lateral side of the olecranon fossa) that helps keep the ulna in the joint. Because weight bearing is likely more important than mobility in the midcarpal joint of terrestrial quadrupeds, the proximal surface of the hamate usually faces more proximally (Jenkins and Fleagle 1975).

As one might expect, the suite of forelimb adaptations for terrestrial quadrupedalism outlined above apparently evolved independently at least three times in primates. Among catarrhines, these adaptations are most prominent in terrestrial Old World monkeys such as baboons, macaques, mandrills, and geladas, plus numerous extinct monkeys, including *Victoriapithecus* (Harrison 1989) and *Dolichopithecus* (Szalay and Delson 1979). These adaptations are also present in some of the stem hominoids in the Miocene of Africa such as *Proconsul nyanzae* (Fleagle 1999). Among the Malagasy lemurs, the archeolemurine indriids, *Archaeolemur* and *Hadropithecus*, are very similar to baboons and macaques in their elbow anatomy (Jouffroy 1963; Walker 1974; Jungers et al. 2002). Finally, the most terrestrial of the extant apes, gorillas and chimpanzees, show a mosaic of features related to a combination of arboreal and terrestrial quadrupedal locomotion. Like other terrestrial primates, they have fore- and hind limbs that are more similar in length than those of other apes, and the midcarpal joints of their wrists are more suitable for bearing weight than those of gibbons or orangutans (Jenkins and Fleagle 1975; Richmond et al. 2001). However, all apes have a distinctive elbow joint that provides both stability and mobility in all types of locomotion (Jenkins 1973). Thus, as with VCL, terrestrial quadrupedalism has evolved in many different lineages of primates, all of which share common features related to the uniform mechanics of the behavior, but the similarities are often mixed with clade-specific differences.

The Evolution of Suspensory Locomotion

Brachiation, hanging, or more broadly, suspensory locomotion, in which animals regularly suspend themselves by their arms (and usually other appendages as well) has long been a prominent topic in discussions of primate evolution as a whole, but especially for the evolution of apes and humans. The transition from quadrupedalism to brachiation was the second event in Napier's scheme, and followed on Sir Arthur Keith's observations of the behavior and anatomy of gibbons in Southeast Asia, which led him to suggest that many of the anatomical specializations shared by living apes and humans in the trunk, viscera, and other parts of the musculoskeletal system were adaptations to forelimb suspension and orthograde postures (e.g., Keith 1891, 1923; Washburn 1968). As a group, the living apes (Hominoidea) including the gibbons (Hylobatidae) and the great apes (orangutans, gorillas, chimpanzees, and humans) share many anatomical features of their limbs and trunk that have been related to suspensory behavior. These features include loss of the tail; derived lumbar vertebrae with transverse processes coming off the arch rather than the vertebral body (in siamangs but not small gibbons); long forelimbs relative to hind limb and trunk length; a spherical humeral head; a reduced ulnar styloid process, which prevents the ulna from articulating with the carpus; relatively long, curved, manual and pedal phalanges (except in humans); a femur whose head extends above the greater trochanter; broad, shallow femoral condyles (except in humans); a talus with a low shallow trochlea; and a calcaneus with a broad sustentaculum. Finally, the elbow joint of all living apes is also distinctive. Unlike other primates, the distal articulation of the ape humerus has a relatively deep and narrow trochlea with prominent borders on both the medial and lateral side, clearly demarcating the trochlea from the capitulum, which is normally rounded or spherical with a distinct *zona conoidea* medially. The olecranon fossa on the joint's posterior aspect tends to be relatively deep. The complementary features on the antebrachium include an ulna sigmoid cavity that is often keeled to match the deep trochlea on the humerus along with a very short olecranon process that fits into the olecranon fossa to permit full extension at the elbow. The ape radius has a rounded head that permits extensive rotation with the rounded capitulum (Rose 1988). As suggested by Jenkins (1973; also Washburn 1968), this morphology provides apes with a stable elbow with extensive rotational capability at all positions of flexion and extension, an important adaptation for an animal that spends most of its day supporting and moving its body using its forelimb.

Although it is generally assumed that the above described anatomical features related to suspension in hominoids are shared derived features of the superfamily Hominoidea, there are numerous variations in the distribution of these features and their expression among extant apes, leading some authors to suggest that many may be parallelisms (Larson 1998; but see Young 2003). Moreover, the fossil record of ape evolution samples much more locomotor diversity than we can observe among extant taxa. These differences among extant apes, together with a consideration of the fossil record, call for a reinterpretation of the evolution of suspensory locomotion in hominoids, a group that first appeared in Africa and initially diverged from Old World monkeys in the late Oligocene, approximately 25 million years ago. In fact, evidence of suspensory behavior in ape evolution is remarkably rare in the Miocene of Africa despite an abundance of fossil anthropoids that are certainly not Old World monkeys and which most authorities believe are apes, perhaps even great apes. Only three or four of the ape features commonly related to suspensory behavior have been reported in the fossil apes from the African Miocene. Loss of the tail is known for one late Miocene taxon (*Nacholapithecus*) and is likely for several early Miocene species of *Proconsul*, although clear evidence in the form of a sacrum is missing. The much-discussed functional significance of tail loss in suspensory hominoids most likely results from the lack of any positive selection for a long tail as a balancing organ combined with the re-use of tail musculature (e.g., the levator ani) into the pelvic diaphragm of species that were perhaps more orthograde and less strictly quadrupedal.

Other early indications of some suspensory behavior in African fossil apes are found in *Morotopithecus* from the early Miocene of Uganda (e.g. Gebo et al. 1997; MacLatchy et al. 2000; MacLatchy 2004). This taxon is unique among fossil apes from the Miocene of Africa in having lumbar vertebrae that resemble those of extant apes in many features, including transverse processes that emerge from the pedicle rather than from the ver-

tebral body (Sanders and Bodenbender 1994). This dorsal repositioning of the transverse process presumably facilitates stability of the lower back in suspensory behavior. It is also found in the extinct sloth lemurs of Madagascar, another lineage of suspensory primates (Shapiro et al. 2005). *Morotopithecus* has also been argued to be unique among large African Miocene apes in having an ape-like glenoid process of the scapula that is rounded, rather than pear-shaped as in most monkeys. A rounded glenoid is associated with a mobile glenohumeral joint. Although the larger apes from the Miocene of Africa appear to have been mostly arboreal and terrestrial quadrupeds, the smaller proconsuloids such as *Dendropithecus* and *Simiolus* have features including long slender limbs, an *Ateles*-like wrist morphology, and long manual phalanges that suggest some suspensory behavior (e.g., Fleagle 1983; Rossie et al. 2012). However, beyond these hints, the Miocene record of ape evolution in Africa, especially among the larger taxa, seems to document predominantly quadrupedal animals throughout the epoch. The middle and late Miocene fossil record of hominoids in Europe is strikingly different and indicates a wider, more mosaic range of suspensory abilities. *Pierolapithecus*, a late Miocene hominoid from Spain, has many ape-like features missing in *Proconsul* including a broad shallow thorax, lumbar vertebrae with the transverse processes coming off the base of the pedicle, and absence of an articulation between the ulna and the wrist (Moyà-Solà et al. 2004). However, the hands of *Pierolapithecus* may be less elongated and less curved than those of extant Asian apes (Alba 2012; but see Deane and Begun 2010). *Hispanopithecus* and *Rudapithecus* also show similarities to suspensory extant apes in aspects of their digital length and curvature, but unlike extant apes, have short metacarpals. Moreover, in none of these taxa is the olecranon process of the ulna as reduced as in extant hominoids. *Oreopithecus* from the latest Miocene of Italy shows the most extensive skeletal similarities to extant apes in features indicative of suspensory behavior, but is widely considered the most distant in its likely phylogenetic relationships (e.g., Begun et al. 2012). Thus while the middle and late Miocene hominoids of Europe show more evidence of suspensory behavior than those from the early Miocene of Africa, they are nevertheless different from any modern apes in many features. Rather, they show a mosaic of features not found in any extant apes or monkeys.

The hominoid fossil record in Asia is even less similar to what one observes among extant apes. In fact, while gibbons and siamangs (Hylobatidae) and orangutans (Ponginae) of Southeast Asia are the most suspensory of the apes, and also of all living primates, there is little evidence for suspensory behavior in any Asian fossil primates. Although *Sivapithecus*, from the late Miocene of Indo-Pakistan, appears to have an elbow region similar to that of extant great apes in the shape of the distal humerus, most aspects of the postcranial anatomy of *Sivapithecus*, and also *Ankarapithecus* from the late Miocene of Turkey (Kappelman et al. 2003), suggest arboreal quadrupedal behavior. While the overall morphology of the postcranial remains of *Sivapithecus* is clearly similar to that of extant apes, *Sivapithecus* shows a mosaic of hominoid features but no specific similarities to any one extant taxon and no indications of suspension as seen in extant orangutans (e.g., Madar et al. 2002). The contrast between the striking similarities in facial anatomy shared by *Sivapithecus* and *Pongo* (e.g., Pilbeam 1982), and the apparent differences in their postcranial anatomy (e.g., Pilbeam et al. 1990; Mader et al. 2002), has been called the "*Sivapithecus* Dilemma" (Pilbeam and Young 2001), and there are alternate views on how *Sivapithecus* and other Asian fossil hominoids are related to living apes.

Regardless of how one reconstructs phylogenetic relationships among fossil and living apes, there has been considerable homoplasy in the evolution of suspensory behavior within Hominoidea, and postcranial evidence for habitual suspensory locomotion, which is characteristic of all living apes, is not found in most fossil representatives of the clade. Only in the middle-late Miocene of Europe are there indications of significant suspensory behavior. Living apes are thus poor referential models for interpreting much of the locomotor history of hominoids as they are known from the fossil record.

Although much attention is paid to the evolution of suspensory locomotion and orthograde posture and locomotion in hominoids, largely because of its relevance to the origins of human bipedalism (see below), suspensory behavior has evolved several times in other primate radiations. Pliopithecids, a widespread radiation of Old World anthropoids from the Miocene of Asia and Europe (and maybe Africa), were once thought to be related to gibbons, but are now usually considered

stem catarrhines. However, in many aspects of their postcranial anatomy, including a relatively short olecranon, a high brachial index, and a very mobile hip joint, they are very similar to the New World atelides such as *Alouatta*, *Lagothrix*, and *Ateles*, suggesting some suspensory behavior (e.g., Fleagle 1984a). The New World platyrrhine monkeys have been separated from the Old World catarrhines for over 30 million years. Among the platyrrhines, the largest taxa, the atelids, are all characterized by suspensory behavior. As initially documented by Erikson (1963) half a century ago and documented in much more detail since, the New World monkeys *Alouatta*, *Lagothrix*, *Brachyteles*, and *Ateles* show a cline in both suspensory behavior and morphology, with limb proportions and aspects of forelimb anatomy that often resemble the Old World apes. In addition, two related fossil taxa, *Protopithecus* (= *Cartelles*) and *Caipora*, are twice as large as any living New World monkeys and also show similar adaptations for suspensory behavior (Cartelle and Hartwig 1996; Hartwig and Cartelle 1996; Halenar 2011).

Suspensory behavior also evolved independently in the lemurs of Madagascar, another radiation of geographically isolated primates. Although the extant fauna of Malagasy primates are all less than 10 kg and are almost all primarily arboreal quadrupeds or leapers, many much larger extinct taxa are known from the fossil record from the last 26,000 years, and some of these species probably went extinct only in the last few hundred years. Among the most unusual of these extinct giant lemurs are the sloth lemurs of the subfamily Palaeopropithecinae (Godfrey and Jungers 2003). These lemurs ranged in size from about 10 kg for *Mesopropithecus*, the smallest, to about 200 kg for *Archaeoindris*, the largest. *Babakotia* (17 kg) and *Palaeopropithecus* (~40 kg) are intermediate in size. Sloth lemurs are the sister taxa of the living indriids. Although they are best known for their VCL behaviors in trees and bipedal hopping on the ground, the larger living indriids, *Propithecus* and *Indri*, frequently engage in suspensory behavior when they hang upside down by all four limbs or suspend themselves using only their feet. On the basis of limb proportions and many aspects of their skeletal anatomy, it seems that *Mesopropithecus* was a loris-like quadruped that also had some suspensory abilities, while *Babakotia* and *Palaeopropithecus* were dedicated arboreal suspensory folivores like living sloths (e.g., Jungers et al.

1997). The postcranial anatomy of the giant *Archaeoindris* is known from a single femur that resembles that of a ground sloth (Vuillaume-Randriamanantena 1988); at 200 kg it was probably largely terrestrial. *Babakotia* and *Palaeopropithecus* share many anatomical features with extant apes, including reduction or loss of a tail; a high intermembral index; an extremely short ulnar olecranon process; lumbar vertebrae with transverse processes arising from the arch; very long, curved phalanges; reduction or loss of the thumb; and a femur with the head literally on top of the shaft.

Thus, suspensory locomotion evolved many times in primates, often in anatomically similar ways involving long forelimbs, extreme mobility of joints, and enhanced grasping abilities. However, there are also unique differences in the nature of the suspensory behavior and associated anatomical structures in each primate radiation. In apes, the evolution of suspensory behavior has been associated with development of a mobile, but extremely stable elbow morphology that enables apes to support their weight in many different positions or in some cases to propel themselves between arboreal supports using only their arms. In addition, suspensory behavior in hominoids has involved major changes in the structure of the vertebrae, the loss of the tail, as well as rearrangements of the shape of the thorax and the suspension of the abdominal viscera. In contrast, suspensory platyrrhines all have a prehensile tail, which is an extra grasping organ. Like the platyrrhines, the sloth lemurs evolved a range of suspensory adaptations from more quadrupedal taxa to others resembling extant tree sloths that were probably incapable of any type of locomotion other than suspension. Thus the evolution of suspensory adaptations in primates has been very clade specific. As discussed below, it is difficult to determine the extent to which these different adaptations reflect phylogenetic contingencies, environmental differences under which the suspensory adaptations evolved, or compromises with selection for other behaviors.

Evolution of Human Bipedalism

Perhaps no locomotor transition in primate evolution is more contentious than the origin of bipedalism. And, as with the other transformations, major theories about hominin locomotor evolution have mostly used extant primate species—especially brachiating gibbons,

knuckle-walking African apes, and, of course, striding bipedal humans—as models for reconstructing ancestral locomotor behaviors. To some extent, these analogies have been necessitated by the deficiencies of the fossil record, but they have also been influenced by two strong preconceptions. First, bipedalism has long been posited as a driving force for many aspects of hominin evolutionary change. In Darwin's words: "If it be an advantage to man to stand firmly on his feet and to have his arms free . . . then I can see no reason why it should not have been advantageous to the progenitors of man to have become more erect or bipedal" (Darwin 1871, 141). Since then, efforts to explain human uniqueness often project modern human-like bipedalism back into the fossil record. Fossils that are neither ape-like nor human-like have tended to be interpreted, sometimes wrongly, as simply intermediate. Second, ever since Darwin, researchers who study human evolution have held strong views about the nature of the last common ancestor (LCA) of humans and apes, often based on assumptions about how and why hominin bipedalism evolved. Not surprisingly, preconceived notions about the LCA have then influenced interpretations of the fossil evidence.

The actual fossil evidence for the evolution of hominin bipedalism, however, challenges this way of thinking. In particular, analyses of early hominin functional morphology suggest that locomotor diversity in hominin evolution was considerably greater than has often been hypothesized. In the last two decades, new discoveries have led to the recognition of more than 19 putative hominin species (fig. 15.5), eight of which were unknown prior to 1994. These species are diverse not only cranially but also postcranially, indicating a variety of locomotor behaviors, many of which were unique, not necessarily ancestral to *H. sapiens*, and difficult to classify as intermediate between the LCA and modern humans. We explore this diversity in the context of two issues: the locomotor adaptations of the LCA of humans and chimps, and locomotor diversity within the hominin lineage.

The Origin of Hominin Bipedalism

Hypotheses about the origin of hominin bipedalism have largely been based on speculation necessitated by the absence of direct fossil evidence. Molecular analyses indicate that the chimpanzee and human lineages probably diverged between 5 and 8 Ma (Kumar et al. 2005; Patterson et al. 2006), but prior to 1994 there were almost no hominin fossils older than 4 Ma. In the absence of fossils from the first few million years of hominin evolution, species from the genus *Australopithecus* were typically considered representative of all early hominins, even though the genus mostly dates to between 4 and 2 Ma. The absence of fossils from the first several million years of hominin evolution was, and still is, compounded by a nearly complete absence of any fossils attributed to *Gorilla* and *Pan* (but see McBrearty and Jablonski 2005; Suwa et al. 2007). As a result, reconstructions of the locomotor behavior of the LCA relied very heavily on models and inferences from extant apes. For a long time, the dominant model was that the LCA was gibbon-like: orthograde and suspensory (e.g., Keith 1923; Napier 1964). This idea is still favored by some (e.g., Crompton et al. 2010). An alternative view, first strongly advocated by Washburn (1968, 1973) and his students, is that the LCA was like an African great ape: a terrestrial quadruped as well as a suspensory climber. This reconstruction was bolstered by molecular evidence that chimpanzees and humans are monophyletic (Ruvolo 1997), and by scaling studies that have found that chimp and gorilla skulls are largely scaled versions of each other (Shea 1985; Berge and Penin 2004; Guy et al. 2005). Such scaling is less conserved in the postcranium (Jungers and Hartman 1988), but unless the many similarities between chimps and gorillas evolved independently, then the LCA of humans and chimpanzees must have been somewhat chimp- or gorilla-like. If so, the LCA was probably a knuckle-walker that also engaged in suspensory, orthograde climbing.

In the last two decades, three new genera of hominins from the late Miocene and early Pliocene have been discovered. *Sahelanthropus tchadensis*, which is from Chad and dated to between 6 and 7.2 Ma, is so far known only from cranial material (Brunet et al. 2002, 2005), although undescribed postcranial remains exist (Beauvillian and Watté 2009). The one *Sahelanthropus* cranium, however, is sufficiently complete to indicate that when the species was locomoting with its orbital plane perpendicular to earth horizontal (as primates usually do), its foramen magnum was oriented inferiorly (Zollikofer et al. 2005). Because the long axis of the upper cervical vertebral column in great apes and
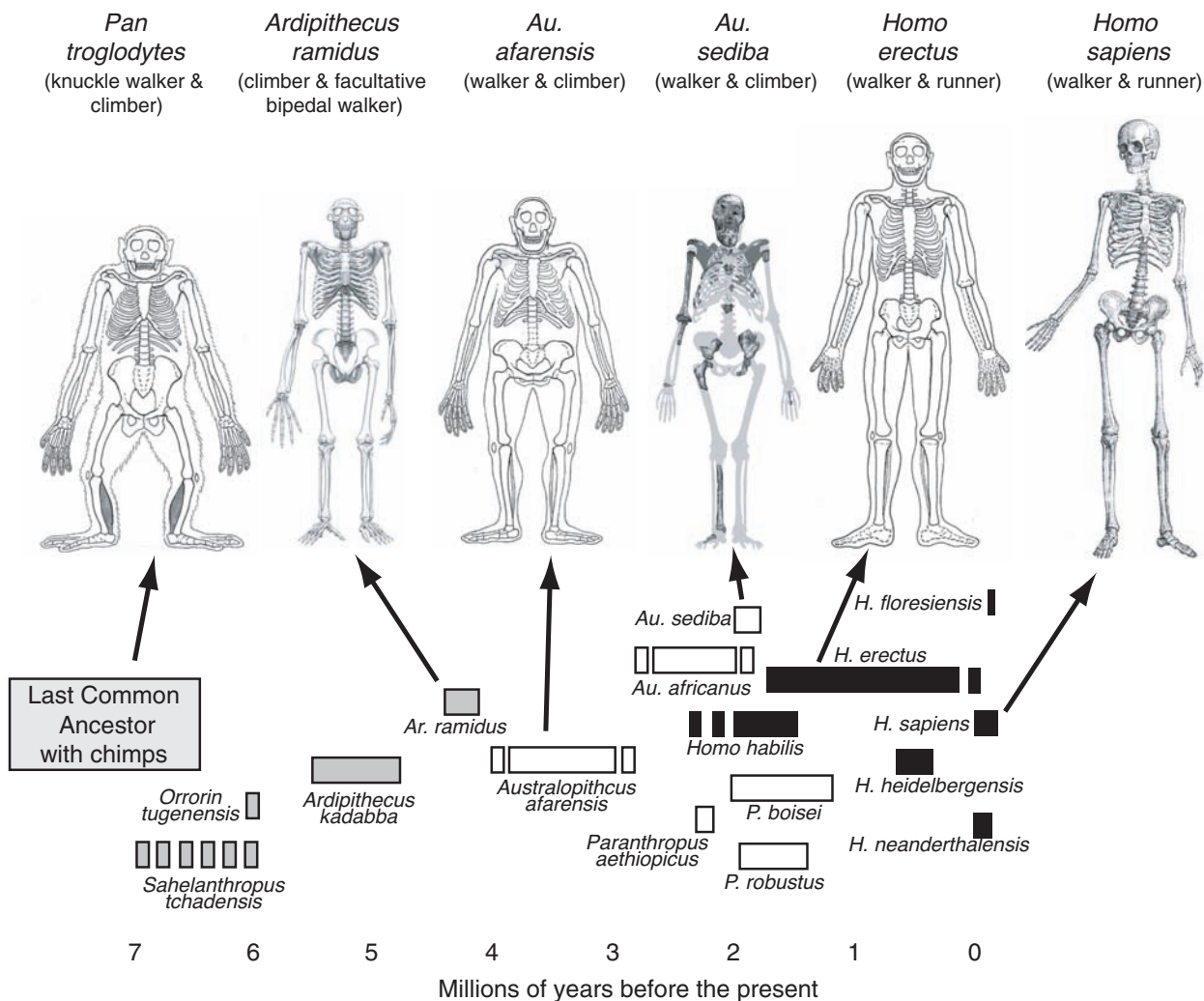
FIG. 15.5 Major hominin species and approximate ages (bottom) divided into three general grades: early hominins (gray), australopiths (white), and the genus *Homo* (black). Shown above are reconstructions of the skeleton for four fossil hominin species: *Ardipithecus ramidus*, a facultative biped and climber; *Australopithecus afarensis*, a habitual biped and climber; *Australopithecus sediba*, also a habitual biped and climber; *Homo erectus*, a walker and runner. Also shown are *Pan troglodytes,* a knuckle-walker climber; and *Homo sapiens,* a walker and runner. Reconstructions of *P. troglodytes, Au. afarensis*, and *H. erectus* are from Bramble and Lieberman (2004); reconstruction of *Au. sediba* courtesy of Lee Berger; reconstruction of *Ar. ramidus* courtesy of Tim White.

humans is always within 10° of perpendicular to the foramen magnum, this is indirect evidence for some form of bipedalism (Lieberman 2011). *Orrorin tugenensis*, which is from Kenya and is dated to approximately 6 Ma (Pickford and Senut 2001), includes a femur that has a number of features (a relatively large femoral head, a long femoral neck, and a transversely broad upper femoral shaft) that align it with later hominins rather than any ape, suggesting some form of bipedal locomotion (Richmond and Jungers 2008; but see Almécija et al. 2013). Finally, *Ardipithecus* is known from two Ethiopian

species: *Ar. kadabba*, dated to 5.2–5.8 Ma, and *Ar. ramidus*, dated to 4.3–4.4 Ma. *Ar. ramidus* is the best known of these species, and includes a partial skeleton, ARA-VP-6/500, which has a suite of pelvic and hind limb features that suggest bipedalism, the most compelling being a superoinferiorly short ilium (see below).

Although *Sahelanthropus, Orrorin*, and *Ardipithecus* likely support the hypothesis that bipedalism is a key derived early feature of the hominin lineage, these three genera have sparked considerable debate regarding the LCA and the nature of early hominin bipedalism. Most

arguments center on interpretations of the *Ardipithecus* skeleton. White, Lovejoy, and colleagues have proposed that *Ardipithecus* was a "facultative" biped that lacks features typical of *Pan* and *Gorilla* (White et al. 2009; Lovejoy, Suwa, Simpson, et al. 2009; Lovejoy, Latimer, et al. 2009; Lovejoy, Suwa, Spurlock, et al., 2009; Lovejoy, Simpson, et al., 2009). In particular, the skeleton is purported to have equally long fore- and hind limbs (based on the radius-tibia ratio), relatively short metacarpals, proximal metacarpal joints capable of substantial dorsiflexion at the metacarpophalangeal joints, and no adaptations for knuckle-walking. These observations along with other inferences led to the interpretation of the LCA as a non-suspensory, pronograde, above-branch quadruped—more like reconstructions of *Proconsul* than any extant great ape. This interpretation, if correct, requires considerable levels of homoplasy in recent hominoid evolution, including most of the features shared between chimps and gorillas, as well as others shared between chimps, gorillas, and orangutans. Moreover, Lovejoy and colleagues' reconstruction of *Ardipithecus* is based on many inferences from anatomical features that are not preserved (e.g., a long, flexible lumbar column) or difficult to estimate reliably from the available evidence (e.g., body mass and limb proportions), and it disregards those features that *Ardipithecus* shares with *Pan* and *Gorilla* in the cranium, foot, and upper limb. Ongoing analyses may lead to substantial reinterpretations of the species' anatomy and locomotor adaptations. One possibility is that *Ardipithecus* retains many similarities to chimpanzees and gorillas with adaptations for both orthograde suspensory and bipedal locomotion. An alternative hypothesis is that *Ardipithecus*, *Sahelanthropus*, and *Orrorin* are not hominins at all (Wood and Harrison 2011). Homoplasy is extremely common in all phylogenetic reconstructions (e.g., Lockwood and Fleagle 1999), and just as it is difficult to sort out the first fossil mammals (Cartmill 2012; Luo, this volume), it may also prove to be a challenge to distinguish reliably the earliest hominins from closely related late Miocene hominoid taxa. Further, if these proposed early hominins are more closely related to chimps or gorillas or members of extinct clades, then bipedalism evolved more than once in the Hominoidea.

More fossils and more analyses will undoubtedly shed needed light on *Ardipithecus* as well as *Sahelanthropus* and *Orrorin*. Regardless of what we will eventually learn about these species, it seems likely that the LCA's postural repertoire included more than orthograde, and that its locomotor repertoire included suspensory hanging and climbing as well as quadrupedal and bipedal gaits—all of which one can observe in chimpanzees and gorillas. Even though there is no morphological evidence for knuckle-walking in early hominins, and despite arguments to the contrary (e.g., Kivell and Schmitt 2009; White et al. 2009), parsimony suggests that it is more likely than not that the LCA sometimes knuckle-walked (Richmond et al 2001), perhaps as an adaptation to allow a suspensory primate with relatively long forelimbs to engage in terrestrial quadrupedalism.

Locomotor Diversity among Hominins

For many decades, alternative theories about locomotor evolution within the hominin clade have focused on where the australopiths fall on a continuum between two endpoints. One endpoint is the hypothetical LCA, which must have been a partly arboreal ape with some adaptations for orthograde and pronograde locomotion (see above). The other, uncontested endpoint is *H. sapiens*. A common view is that australopith locomotion was intermediate between these two endpoints, and included habitual bipedal walking as well as tree climbing. How australopiths walked, however, remains unclear. Some scholars have proposed that australopiths did not walk with a completely modern gait with relatively extended hips and extended knees (EHEK), but instead with a bent-hip bent-knee (BHBK) gait, not unlike modern chimps when they walk bipedally, because they retained ancestral adaptations for arboreality that compromised bipedal performance (e.g., Susman et al. 1984; Schmitt 2003a). Others have argued that australopiths had a very modern human-like EHEK gait that might even have been more efficient than modern humans, whose performance has been compromised by adaptations for giving birth to large-brained infants (e.g., Lovejoy 1988; Ward 2002). Few question the inference that since *H. erectus*, the genus *Homo* has had an essentially, modern human-like style of locomotion (Wood and Collard 1999).

The fossil record requires us to recognize more diversity in hominin locomotion than these schemes hypothesize (fig. 15.5). A major cause of this reevaluation has been evidence for facultative bipedalism in

Ardipithecus. Although fossils ascribed to this genus have many adaptations for arboreality, such as a highly abducted and internally rotated, short hallux, that would have been effective at grasping, they also preserve several features that are likely adaptations for bipedal posture and locomotion. The *Ardipithecus* pelvis, albeit distorted, has a superoinferiorly short ilium that appears to have laterally oriented blades that would have allowed the gluteus medius and minimus to function as hip abductors during stance (Lovejoy, Suwa, Spurlock, et al., 2009). In addition, *Ardipithecus* feet have dorsally canted metatarsophalangeal joints capable of hyperextension at toe-off, and an apparently semirigid midtarsal region that would have helped permit powered toe-off, although more along the lateral column of the foot than in humans (Lovejoy, Latimer, et al. 2009; Haile-Selassie et al. 2012). If *Ardipithecus* is a hominin, it was probably not an obligate terrestrial biped but instead was often arboreal, and probably incorporated bipedalism only as part of a broader locomotor repertoire.

There is also new evidence for considerable locomotor diversity within *Australopithecus*. *Au. afarensis*, long the focus of attention, has some adaptations for arboreality as well as habitual bipedalism (see Aiello and Dean 1990; Stern 2000; Ward 2002), but the extent to which it or other australopiths had a BHBK or EHEK gait is unresolved. The need to counter the high hip and knee moments required by a BHBK explains most of the fourfold greater cost of transport in bipedal chimpanzees versus modern humans (Sockol et al. 2007), suggesting there would have been strong selection against BHBK gaits, which provide little performance benefit for an habitual biped (Sellers et al. 2005). Analyses of trabecular orientation of the distal tibia in *Au. africanus* strongly point to human-like ankle hence knee and hip orientations during peak loading (Barak et al. 2013), and analyses of the Laetoli footprints combined with estimates of effective leg length (Raichlen et al. 2008), limited ankle dorsiflexion (DeSilva 2009), evidence for a heel-strike during walking (Latimer and Lovejoy 1989), and a dorsally projecting ischium (Pontzer et al. 2009) are commensurate with an EHEK in *Au. afarensis*. Although some researchers have hypothesized that the relatively long toes of *Au. afarensis* would have compromised its ability to walk with a human-like gait (Susman et al. 1984), inverse dynamic analyses indicate that the

high moments generated around the metatarsophalangeal joints in *Au. afarensis* would have been a challenge during only running not walking (Rolian et al. 2009).

Au. afarensis, moreover, is not the sole representative of australopith locomotion as previously assumed. A 3.4 Ma foot from Burtele, Ethiopia has a short, abducted hallux and very long, curved phalanges, which indicate that hominins with *Ardipithecus*-like feet were contemporary with *Au. afarensis* (Haile-Selassie et al. 2012). Another interesting contrast is provided by two partial skeletons of *Au. sediba* from South Africa dated to approximately 2 Ma (Berger et al. 2010). This species has many adaptations for habitual bipedalism, including a *Homo*-like pelvis (Kibii et al. 2011), but it has an inverted subtalar joint and its tuber calcaneus is relatively small and chimp-like without a weight-bearing lateral plantar process (Zipfel et al. 2011). These and other pedal features, which are less derived than in *Au. afarensis*, suggest that *Au. sediba* walked with an inverted foot without a distinct heel strike and with less medial weight transfer during stance (DeSilva et al. 2013). *Au. sediba*'s upper limb is also primitive with a relatively high brachial index; long, curved manual phalanges; and a short clavicle with a cranially oriented glenoid joint indicative of a narrow ape-like shoulder adapted for suspensory climbing (Berger et al. 2010; Kivell et al. 2011; Churchill et al. 2013). Although there is much research to be done, and postcranial anatomy is poorly known for many species, it is reasonable to hypothesize that there was considerable locomotor diversity within the genus *Australopithecus*, with more than one kind of striding gait still sometimes associated with substantial arboreality.

Finally, it has become evident that locomotor diversity within the genus *Homo* is also greater than previously credited. Many scholars of the human fossil record have interpreted the postcranial differences between *Australopithecus* and *Homo* as a shift to more committed, effective walking (e.g., Aiello and Dean 1990), but an alternative hypothesis is that some of these shifts reflect selection for endurance running—a gait that has been largely ignored in theories about hominin locomotor evolution. Like other primates, apes gallop infrequently and for only short distances (Hunt 1992), but humans are unusual among mammals and unique among primates in being exceptional long distance runners (Carrier 1984; Bramble and Lieberman 2004). Bramble and Lieberman proposed that selection

for endurance running capabilities in the genus *Homo* explains many novel features (e.g., enlarged anterior and posterior semicircular canals, an expanded gluteus maximus proprius, shortened toes) that improve running performance, but have little effect on walking. Endurance running was probably crucial for early hunting before the comparatively recent (<500 Ka) invention of lithic projectile technology (Lieberman et al. 2008). These authors also proposed that trade-offs between adaptations for climbing and running, not climbing and walking, have resulted in humans being the only extant primate that is rarely arboreal. Adding to diversity, moreover, is evidence for variation within the genus *Homo*. For example, an early pelvis attributed to *H. erectus* is relatively wide (Simpson et al. 2008), and archaic *Homo* species such as *H. heidelbergensis* and *H. neanderthalensis* have relatively wider interacetabular distances and more laterally flared ilia than *H. sapiens* (Arsuaga et al. 1999; Bonmatí et al. 2010). The biomechanical consequences of these differences remain speculative.

Discussion and Conclusions

Napier's (1967) "locomotor trend" in primate evolution was just that: a sequence of proposed evolutionarily successive developments, with primates from the Eocene and Oligocene being primarily vertical clingers and leapers, then quadrupedal monkeys appearing in the Oligocene and Miocene, followed by the evolution of brachiators in the Miocene and Pliocene, and topped off by bipedal humans. Each of these locomotor types was based on living representatives, and his scheme made sense given the very limited record of fossil primates from Europe and Africa known at the time. Today, it is more accurate to describe the evolution of these different patterns of locomotion as major transformations that occurred at least three times independently in isolated radiations of primates: the haplorhines of Eurasia and Africa, the Malagasy strepsirrhines, and the platyrrhines of Central and South America (fig. 15.6). In each of these radiations we find leapers, arboreal quadrupeds, and suspensory species, and in one, we also find bipeds. Napier (and others such as Straus [1962]) also saw primate evolution as a progression toward forelimb suspension and increasing length of the forelimb relative to the hind limb. That unidirectional view is no longer tenable, especially when one considers locomo-

tor evolution within clades. As described above, within Old World haplorhines the earliest members were probably leapers, from which quadrupeds evolved, and then later gave rise to both suspensory and bipedal forms. Among Malagasy strepsirrhines, it is unclear whether the ancestral taxa were leapers or quadrupeds, and it is not totally clear whether the suspensory sloth lemurs evolved from more quadrupedal ancestors or from leapers. Among the New World platyrrhines, it is almost certain that both the specialized leapers and specialized suspensory taxa evolved from quadrupeds.

Just as locomotor specializations evolved independently many times in different primate clades, there is also considerable diversity in the details of locomotor behavior and morphology both among and between the leapers, quadrupeds, and suspensors in different clades. It is not clear whether these clade-specific differences are the result of contingency caused by ancestry, effects of body size, selection for different behaviors and morphological compromises due to competition or habitat, or, most likely, some combination of these factors. For example, differences in the limb proportions and locomotor behaviors between leapers, quadrupeds, and suspensors are less extreme among platyrrhines than among catarrhines or strepsirrhines (Fleagle and Mittermeier 1980). Similarly, within the strepsirrhines, both quadrupeds and leapers tend to have relatively long hind limbs compared with their counterparts in other radiations.

The high degree of convergence and diversity among primates is phylogenetic "noise" to taxonomists but a boon to functional anatomists because these "natural experiments" allow us to use the comparative method to identify potential morphological correlates of specific behaviors and hopefully assess the relative contributions of phylogeny and function. As Jenkins repeatedly showed, however, such inferences still need to be tested experimentally in the lab by evaluating the biomechanical models that underlie hypotheses about how variations in anatomy affect performance. Such experiments are especially necessary to test functional interpretations of rare or unique combinations of features evident in fossils that are not represented by modern taxa. This problem is of special relevance to obligate bipedalism, which is present in just one extant taxon, *Homo sapiens*, limiting our abilities to interpret the behavior of fossil hominins that are generally similar to modern humans, but differ in details (Cartmill 1992). One cannot hope to explain the evolution

FIG. 15.6 Independent transformations have yielded similar locomotor diversity among major primate radiations. The primates of Eurasia and Africa (above) include leapers (*Tarsius* and *Galago*), both arboreal (*Cercopithecus*) and terrestrial (*Papio*) quadrupeds, and hangers or suspensory taxa (*Hylobates* and *Pongo*). Similarly, the endemic fauna of living and fossil lemurifroms from Madagascar includes a variety of leapers (illustrated by *Indri* and *Lepilemur*), arboreal (*Varecia*) and terrestrial (*Lemur* and *Hadropithecus*) quadrupeds, and suspensory "sloth lemurs" (*Palaeopropithecus* and *Babakotia*). Likewise, the radiation of platyrrhine monkeys in Central and South America includes leapers (*Cebuella* and *Pithecia*), arboreal quadrupeds (*Chiropotes*, *Saimiri*, and *Cebus*), and suspensory taxa (*Ateles* and *Brachyteles*). Drawings are not to scale. A cross indicates that the genus is extinct. Illustration by Stephen Nash.

of bipedalism simply by using modern species as simple referential models, and a better understanding of bipedal evolution will require new kinds of integration between laboratory and paleontological analyses.

Evidence that primates in many different clades independently evolved diverse locomotor specializations including different types of quadrupedalism, leaping, brachiation, and (in at least one case) bipedalism raises interesting questions about the selective forces and mechanisms that led to the evolution of this diversity. To address this question, we return to the three factors Napier identified in 1967: body size, habitat, and diet. Each of these has been addressed in subsequent research, and they are not totally independent.

Body size is unquestionably a major factor, but cannot be evaluated without also considering habitat. As outlined by Napier (1967; see also Fleagle and Mittermeier 1980; Fleagle 1984b, 1985) the relationship between body size and locomotion for arboreal creatures often concerns problems of balance, access to available supports, and gaps in the forest. For a quadrupedal and arboreal primate walking through a network on supports of variable size and flexibility, balance is major concern. In any given environment, small animals will find more supports that are relatively stable, but with increasing size, animals are less likely to find themselves in an environment that they can easily traverse quadrupedally. Suspensory postures, in which an animal hangs below supports, solve the problem of maintaining balance on relatively smaller mobile supports, which explains why larger primates tend to be suspensory. However, with increasing size, an individual needs to locate numerous strong supports, thus we find that larger species who use suspensory locomotion and postures are characterized by long forelimbs as well as mobile joints and grasping hands and feet enabling them to reach far and wide to locate sufficient supports. For small arboreal primates, the critical issue is not balance, but gaps in the canopy. Small primates are therefore more likely to be leapers. In addition, should they fall to the ground during a leap, a smaller animal will suffer less from the momentum of the fall (Cartmill and Milton 1977). In addition, leapers should be favored in habitats with more vertical supports, for example, those that frequent bamboo such a *Callimico* (Pook and Pook 1981) or *Hapalemur* (Tan 1999).

The effects of size on locomotion differ for more terrestrial primates, and probably for no clade more so than hominins, which includes the only primate that rarely uses trees, and does so clumsily: *H. sapiens*. Although large body mass can be a problem in trees because of balance and the need for larger supports, larger terrestrial quadrupeds are both faster and more economical (Alexander 1991), which may explain why there was a trend toward increasing body size, especially leg length, within hominins.

Finally, there is little evidence for any simple relationship between diet and locomotion. Napier (1967) argued that the locomotor differences between largely quadrupedal Old World monkeys and more suspensory apes related to a specialization for a diet of leaves in the former and fruits in the latter. However, both Old World monkeys and apes contain species that are predominately frugivorous and predominately folivorous with no clear relationship to locomotion. The same is true for Malagasy lemurs and platyrrhines. Indeed, Fleagle and Mittermeier (1980; also Fleagle 1984b) suggested that within specific faunas, species with similar diets tend use different locomotor and postural behaviors to access those foods in different parts of the habitat. Similarly, species with similar locomotor and postural abilities tend to differ in their diet. Thus, among frugivores, there are leaping, quadrupedal, and suspensory taxa. Conversely, among suspensory species there are frugivores and folivores. Nevertheless, there are certainly cases in which specific diets entail specialized locomotor or postural abilities. For example, gum-eating species need the ability to cling to tree trunks. Also animals feeding on terrestrial foods, need to have locomotor abilities for traveling on the ground.

The Tyranny of the Present

Regardless of whether one stands, hangs, or leaps back from the details, it is evident why our understanding of primate locomotor evolution, especially comparative and functional anatomy, is strongly rooted in our understanding of extant primates. These are the animals we can observe in the wild, study their muscles, and bring into the lab for experimental studies of their locomotor biomechanics and physiology. Fossil primates are, alas, mostly sampled from teeth and jaws; limb bones

are rare and often not associated with other body parts. Complete skeletons are exceptionally rare, and even then, just bones. Nevertheless, despite its limitations, the fossil record offers necessary insights into the history of primate locomotion that are not available from the study of extant taxa alone, and which suggest that, in many respects, extant primates offer a distorted view of the history of primate locomotion. Most significantly, the fossil record provides evidence of many locomotor morphologies and combinations of features that are not present in any extant species. This disparity between the present and the past is perhaps most extreme in Madagascar, where all extant taxa are small (<8 kg) leapers and arboreal quadrupeds. However, the fossil record from just the past few thousand years documents terrestrial quadrupeds, a whole radiation of large suspensory sloth lemurs, and some taxa such as the koala-like *Megaladapis* or *Archaeoindris*, a giant relative of the sloth lemurs with a femur that suggests it may have been most comparable to a ground sloth. Another source of extreme disparity are the hominoids, which used to include a wide variety of non-suspensory apes that are known only from the fossil record.

If we were to wander through a forest in the Eocene, Miocene, or Pliocene of Eurasia or Africa, we would see primates very different from those we observe today. Many of them would be quadrupedal, and we would see fewer leapers and suspensory primates, especially among the apes. We would see, however, a much greater range of intermediate morphologies and mosaic combinations. If any one clade might surprise us the most, it would probably be our own. We live in an unusual era in which just one species of hominin is present (and few of us have to locomote much anymore), but our unusual form of walking and running should not blind us to the greater diversity of bipedal and climbing behaviors that must have characterized our ancestors and cousins. In hindsight, the diversity of locomotor morphologies evident from the fossil record of primate evolution is a wonderful fortune. Paleontology would be very boring if the past were just like the present. However, ancient diversity poses substantial challenges, especially when trying to understand great transformations of the past, of which the extant species we observe today are just mere samples. The only effective approach to understanding the present is through an integrated research program that combines fieldwork, experimental studies of biomechanics, and detailed studies of morphology, especially the joint surfaces of bones that actually permit animals to move as they do.

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