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A review of the distal femur in *Australopithecus*

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Abstract

In 1938, the first distal femur of a fossil *Australopithecus* was discovered at Sterkfontein, South Africa. A decade later, another distal femur was discovered at the same locality. These two fossil femora were the subject of a foundational paper authored by Kingsbury Heiple and Owen Lovejoy in 1971. In this paper, the authors discussed functionally relevant anatomies of these two fossil femora and noted their strong affinity to the modern human condition. Here, we update this work by including eight more fossil *Australopithecus* distal femora, an expanded comparative dataset, as well as additional linear measurements. Just as Heiple and Lovejoy reported a half-century ago, we find strong overlap between modern humans and cercopithecoids, except for inferiorly flattened condyles and a high bicondylar angle, both of which characterize modern humans and *Australopithecus* and are directly related to striding bipedalism. All other measured aspects of the femora are by-products of these key morphological traits. Additional fossil material from the early Pliocene will help to inform the evolution of the hominin distal femur and its condition in the *Pan*-*Homo* common ancestor that preceded bipedal locomotion.

KEYWORDS

Australopithecus, bipedalism, hominin

1 | INTRODUCTION

Over 50 years ago, Case Western University anatomist Kingsbury Heiple and Kent State University paleoanthropologist C. Owen Lovejoy teamed up to write a foundational paper on the functional anatomy of the *Australopithecus* distal femur.[1] At the time, only two fossil femora (TM 1513 and Sts 34) were known for this genus, both assigned to the species *Australopithecus africanus*.[2,3] The authors aimed to resolve debates surrounding the supposed ape-like affinities of these fossils by examining several relevant features of the distal femur. These included the bicondylar angle, shaft robusticity, patellar surface, intercondylar notch, and shape of the articular surface. They concluded that these fossils were distinctly hominin and displayed the necessary suite of morphologies that characterize a habitually striding biped.[1] Here, we update that work with new fossils and an expanded comparative dataset to revisit this key area of the body for understanding bipedal evolution in early hominins.

In 1938, Robert Broom described the first distal femur of a Plio-Pleistocene hominin.[4] Discovered at Sterkfontein cave in South Africa, this fossil (TM 1513) was assigned to *Plesianthropus transvaalensis*, a taxon that would later be subsumed under *A. africanus*. In his discussions of the TM 1513 femur, Broom consistently remarked that it had characteristics of a biped.[4,5] He stated, “One thing is, I think quite certain, the femur is that of an animal that walked, as does man, entirely or almost entirely on its hind feet” (p. 73).[5]

A decade later, a second distal femur of *A. africanus* from Sterkfontein (Sts 34) was introduced to the world by Broom and Robinson.[6] In their description of the fossil, the authors noted that it showed similar characteristics to the TM 1513 femur. They also noted unique features of both femora, including a tall intercondylar notch.[6] Despite these observations, the authors concluded that both fossil hominin femora share strong affinities with modern humans and thus belonged to bipedal hominins.[6] A half-century ago, the first

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hominin fossils discovered at the paleoanthropological site of Hadar, Ethiopia were a distal femur and proximal tibia (A.L. 129). Discovered in 1973, Johanson et al.[7] used the bipedal characteristics outlined by Heiple and Lovejoy[1] to classify the individual as a hominin. Thus, the relevance of the distal femur to interpretations of hominin locomotion has long been investigated.

As the superior part of the joint, the distal femur can provide insight into the function of the knee, which is a critical anatomy in upright walking. The hominin knee has evolved from a joint shaped for mobility in a primarily arboreal environment, to one adapted for stability in an extended-legged biped.[8,9] And with this evolutionary change in function came a suite of changes in femoral morphology, including flattened femoral condyles and a pronounced bicondylar angle, two features claimed to reflect an extended, bipedal posture.[1,8,9] Thus, even in isolation, a distal femur can provide direct insight into an individual's locomotor behavior and a species' evolutionary history. However, the question remains, how reliable are these features to interpretations of bipedal locomotion?

Since Heiple and Lovejoy's 1971 review, eight additional *Australopithecus* (the fossil distal femora used in this review do not include any *Paranthropus* individuals as it is difficult to discern whether isolated femora belong to *Paranthropus* or *Homo* given overlap at many African localities) distal femora, complete enough to be included in this study, have been discovered. These fossils represent multiple hominin taxa including *A. prometheus*, *A. afarensis*, *A. africanus*, and *A. sediba* and span a geologic age of ~3.6–1.98 million years ago (Ma). These new fossil discoveries have brought about new methods and measurements that have aided in our collective understanding of the evolution of the hominin knee. But while studies have focused on one or more of these hominin femora,[1,9–16] none have incorporated all existing *Australopithecus* distal femora.

The current study is an updated and expanded review of the known sample of *Australopithecus* distal femora inspired by Heiple and Lovejoy[1] (Figure 1). While it is now commonplace to use three-dimensional shape analyses to interpret hominin fossils, this methodology will be reserved for future studies. This review will focus instead on linear and angular measurements of the distal femur employed by Heiple and Lovejoy[1] and subsequent studies[16] (Table 1).

This review will focus only on those linear measurements considered to be functionally salient. That is, the measurements discussed here have been suggested to provide direct insight into the functioning of the knee joint (Table 1).

It is well established that *Australopithecus* utilized bipedal locomotion.[24–26] However, the nature of this locomotor behavior in *Australopithecus* remains contentious. For instance, some have argued that the bipedal gait of these hominins was equivalent to modern humans,[9,27] but additional fossil material and kinematic analyses have pointed to variation in hominin bipedal gait.[28–30] Other discussions have focused on the frequency of bipedalism in *Australopithecus* with some arguing for continued use of arboreal behaviors[31] and others suggesting full commitment to terrestrial bipedalism.[32] In this review, results will be evaluated within the context of modern human bipedalism. If the *Australopithecus* knee functioned during bipedal gait as it does in modern humans, then these fossils should have distal femoral anatomies within the range of variation of modern humans. While the current dataset includes only a sample of modern human femora, we still expect the *Australopithecus* fossils to fall close to, if not within, this sample range if the previous hypothesis is to be accepted.

2 | BICONDYLAR ANGLE

The bicondylar angle is formed by the long axis of the femur and the line perpendicular to the plane of the inferior aspect of the condyles.[8,17] This angle, also called knee valgus or a carrying angle, helps position the knees and feet beneath the center of mass during bipedal travel.[8,9] This angle measures approximately 8°–11° in modern humans,[17,33,34] and is significantly lower in chimpanzees (1°–4.2°), gorillas (−2.5° to 2°), and orangutans (3°–5°).[17,19,35] Interestingly, a recent study by Hunt et al.[35] found this angle to be slightly higher in some chimpanzees, with forest habitat individuals possessing a mean angle of −0.33° while the dry habitat individuals have a mean of 4.2°.[35] While the savanna chimpanzees in this study show a higher bicondylar angle, the lowest angle of the modern human range is still two times higher than the highest value for chimpanzees. This in turn will have different effects on the transmission of forces through the knee joint in these groups. Furthermore, Drummond-Clark et al.[36] have shown that bipedal posture in chimpanzees occurs more frequently in forest conditions than in the savanna making it unclear what the relationship is between bipedalism and bicondylar angle expression in chimpanzees.

Ontogenetic studies have shown that the development of the bicondylar angle in humans is directly related to habitual use of a bipedal gait. Tardieu and Trinkaus[37] found that humans are born without a bicondylar angle, then exhibit a steady increase in this angle throughout the juvenile period and into adulthood. Shefelbine et al.[17] modeled the loads incurred by the human femur during bipedal gait finding that the applied stresses stimulate greater bone growth on the medial side of the femur than the lateral thus creating the bicondylar angle.

The bicondylar angle can be reliably measured in seven *Australopithecus* fossils. Five of these have values above the range for modern humans somewhere between 12° and 15°.[17] Two (A.L. 333-4 and U.W. 88-63) are within the lower end of the range for modern humans (Table 2). The large angle characterizing the majority of the fossils is likely the result of a shorter femur and wider interacetabular distance in these hominins.[1,9,38]

The adoption of a high bicondylar angle is associated with a suite of morphological changes in the distal femur. These morphologies include the depth of the patellar surface, height of the lateral patellar lip, and mediolateral widths of the condyles. Each of these will be discussed in more detail.

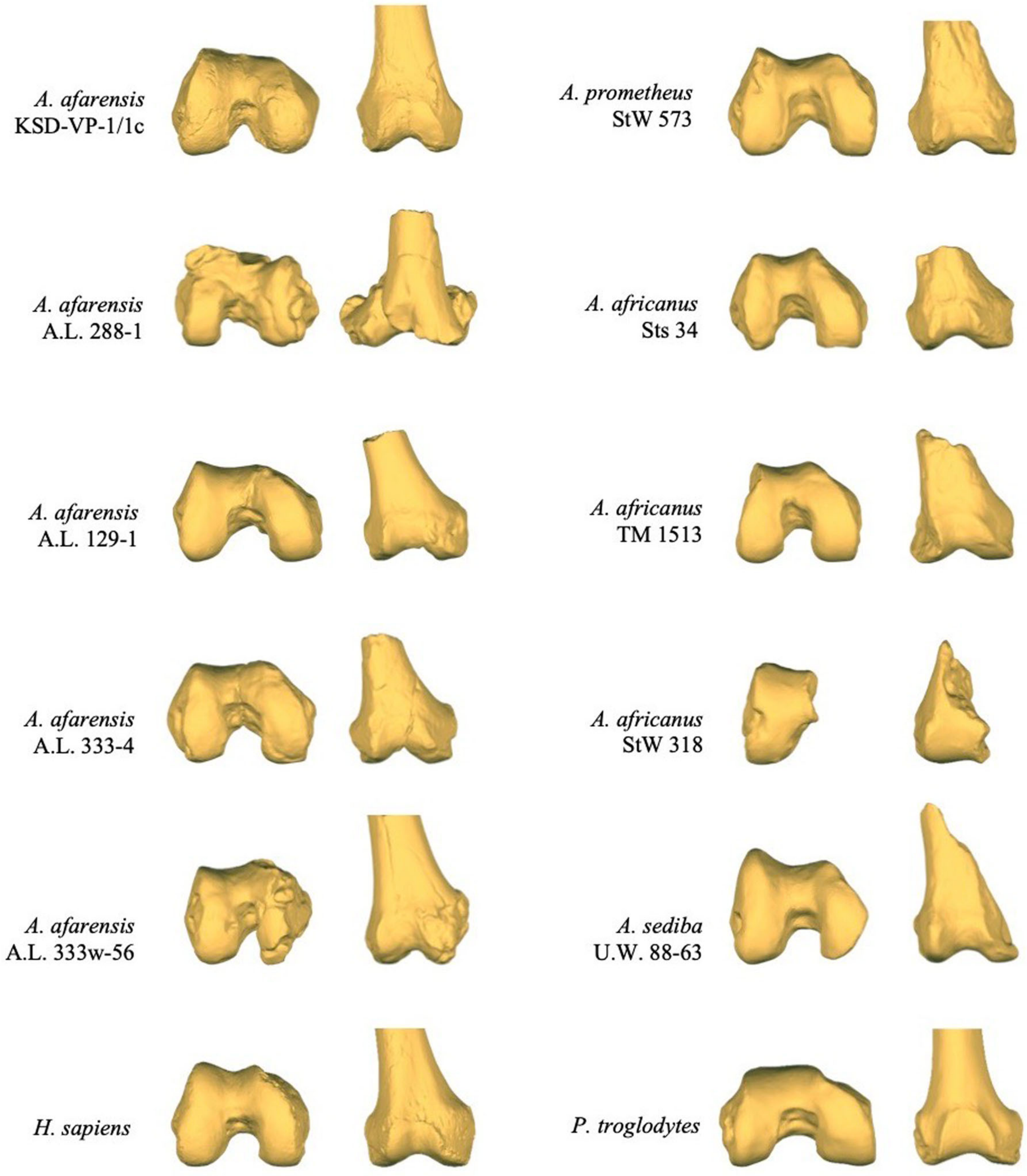

FIGURE 1 Inferior (left) and anterior (right) views of the existing sample of fossil *Australopithecus* distal femora as well as a modern human and chimpanzee for comparison. Eight additional fossil femora have been discovered since Heiple and Lovejoy.[1] A.L. 288-1, KSD-VP-1/1c, and TM 1513 are mirrored so that all images are of the right femora. Images scaled to roughly the same size.

2.1 | Patellar surface depth

The patellar surface is the anterior region of the femur that articulates with the posterior aspect of the patella. Tardieu[16] noted a gradual flattening of the patellar surface in mammals from the unguligrade condition to the plantigrade. In an unguligrade animal (e.g., horse), a deep patellar surface permits a tightly fitting patella that is guided through strong, parasagittal movements of flexion and extension.[16] In a plantigrade animal (e.g., bear), the flattened patellar surface permits greater movement of the patella, which allows the knee joint to engage in rotation as well as flexion and extension.[16]

This latter form of the patellar surface characterizes the distal femora of modern apes.[1,8,44] Their flattened surfaces allow greater mobility at the knee, which complements a largely arboreal lifestyle. Although plantigrade, modern humans diverge from the typical plantigrade condition of this feature and instead have a deep patellar surface. This morphology has been associated with a habitual bipedal gait as it promotes stability at the joint.[1,2,8,10,13,16]

TABLE 1 Functional hypotheses for the distal femur in modern humans, primates, and *Australopithecus*.

Feature	Hypothesized function
Bicondylar angle	A bicondylar, or valgus, angle forms in bipeds to position the feet directly under the center of mass for stability and efficiency.[8,9] This angle is present in modern humans measuring at least one standard deviation above the largest angle seen among extant primates (5.3° in *Macaca*). This angle is greater on average in *Australopithecus* than humans. It is absent or much lower in modern apes and cercopithecoids.[17]
Patellar surface depth	A deepened patellar surface provides greater stability of the patella to prevent dislocation in both bipeds and cercopithecoids.[16] Patellar dislocation in bipeds is the result of the bicondylar angle which exerts a lateral force at the joint.[1,2,8,10,13,16] Cercopithecoids utilize strong movements of extension at the knee, which also necessitates a deeper surface.[1] In apes the patellar surface is flattened to promote greater knee mobility.[8,16]
Lateral patellar lip height	Modern humans have elevated lateral patellar lips to help prevent patellar dislocation in a valgus knee.[9,13–16] Apes do not have a pronounced lateral lip as they do not possess a bicondylar angle and thus do not exhibit lateral forces for dislocation. Cercopithecoids possess some degree of a lateral patellar lip as a consequence of the deepened patellar surface.
Mediolateral widths of condyles	Modern humans have equal mediolateral widths of the condyles reflecting a more equal distribution of load through the knee joint in bipeds. Apes have unequal widths of the condyles with the medial condyle being wider.[18,19] This is either the result of greater rotation at the knee joint or the varus position of the knee directing greater load through the medial compartment.[13,16,18,20–22]
Anteroposterior elongation of condyles	Modern humans have condyles that are elongated both anteriorly and posteriorly. Anterior elongation increases the patellar moment arm for greater efficiency during a bipedal gait while posterior elongation maximizes the area of contact in the knee joint helping with load dissipation.[9] Cercopithecoids also have some elongation in the condyles due to their deep patellar surfaces.[23] Modern apes do not exhibit any elongation in the condyles as their knees are adapted for mobility rather than load dissipation.
Relative intercondylar notch height	This measurement was performed in Heiple and Lovejoy[1] given the observation of an accessory intercondylar notch in TM 1513. However, no functional hypothesis was provided for this anatomy. Here, we hypothesize that this feature is related to the anteroposterior elongation of the condyles. Posterior expansion without anterior elongation of the condyles, as seen in many *Australopithecus* individuals, creates a high notch index while equal elongation or no elongation in either direction results in a lower notch index.
Distal epiphyseal proportions	The distal epiphysis in modern humans and cercopithecoids has a square profile reflecting a narrower posterior width and lengthened condyles.[16] This shape limits mobility thus promoting a more stable knee. Apes have a rectangular-shaped epiphysis due to their wider posterior widths and shortened condyles reflecting a more mobile knee joint.[16]

Although they did not perform any quantitative analyses, Heiple and Lovejoy[1] argue that the deep patellar surface of modern humans is a corollary of the bicondylar angle.[37] As the quadriceps muscle contracts to extend the knee, the line of force exerted by this pull is angled due to the valgus position of the femur, imposing a lateral force on the patella. In fact, it has been shown that patellar dislocations are more frequent among modern human females who typically possess higher bicondylar angles.[45] It follows, then, that the patellar surface in modern humans is deeper to secure the patella and help prevent patellar subluxation.[1]

This argument was complicated by Wanner[46] who analyzed a sample of modern humans and found no direct correlation between bicondylar angle and depth of the patellar surface. Expanding on this finding, Stern and Susman[47] suggested that the deep patellar surface was indeed a protection against patellar dislocation in a bicondylar femur, but specifically when the knee is in positions of flexion.

This idea is supported by the characterization of the human knee as tibial dominant.[9] Because the posterior surface of the human patella is not uniform (i.e., it exhibits two separate facets with a thickened interfacet ridge), contact between the patella and distal femur is reduced as the joint flexes, which increases the risk of patellar dislocation.[9] While a direct correlation may not exist between the bicondylar angle and patellar surface depth across modern humans, the latter is likely a response to a valgus femur and ultimately associated with a bipedal gait.

The depth of the patellar surface differs markedly between modern humans and apes, however, the deep patellar surface in cercopithecoids can complicate functional interpretations of this anatomy.[48] In fact, Heiple and Lovejoy[1] noted that the leaping behaviors utilized by some cercopithecoid species require strong extension at the knee joint that may result in a deep patellar surface for greater stability. Therefore, they hypothesized that leaping species like *Nasalis* should show deepened patellar surfaces.[1]

There is a clear separation between primate taxa in the depth of the patellar surface that appears to align with locomotor behavior (Figure 2). Those genera with the flattest surfaces include *Pongo*, *Hylobates*, and *Symphalangus*, all of which are highly arboreal and would thus benefit from a more mobile knee joint with a flattened

TABLE 2 *Australopithecus* distal femora.

Specimen	Taxon	Age (Ma)	Bicondylar angle (°)	Depth of patellar surface	Relative intercondylar notch height (NH/PH ×100)	Distal epiphyseal proportions (PW/LL)	Mediolateral width ratio of condyles (MW/LW)	Lateral patellar lip height (LL-PH)
StW 573	*A. prometheus*	3.67(?)	11[a]	129.5	64.4	1.36	1.06[a]	7.6
KSD-VP-1/1c	*A. afarensis*	3.6	–	157.8	50.6	1.3	0.96	–
A.L. 129-1	*A. afarensis*	3.4–3.0	15[b]	149.2	64.5	1.41	1.01	6.4
A.L. 333-4	*A. afarensis*	3.4–3.0	9[b]	149.5	60.4	1.29	–	5.1
A.L. 333w-56	*A. afarensis*	3.4–3.0	10.5	–	73.6	–	–	–
A.L. 288-1	*A. afarensis*	3.2	12[c]	–	–	–	–	–
TM 1513	*A. africanus*	3.4(?)–2.0	14[d]	144.4	52.3	1.26[e]	1.03[e]	5.3
Sts 34	*A. africanus*	3.4(?)–2.0	15[d]	142.3	60.0	1.25	1.13[e]	6.2
StW 318	*A. africanus*	3.4(?)–2.0	–	–	–	–	–	6
U.W. 88-63	*A. sediba*	1.98	9[f]	135.1	53.8	1.15[f]	0.97	10.5
	H. sapiens	–	8–11	140.8 (6.3)	56 (3.3)	1.2 (0.05)	1.0 (0.09)	4.2 (1.5)
	P. troglodytes	–	1–4.2[b,g,h]	163.4 (6.7)	63.1 (3.5)	1.5 (0.1)	1.3 (0.1)	1.8 (1.4)
	P. paniscus	–	~1[g,h]	161.3 (9)	57.6 (1.1)	1.4 (0.06)	1.1 (0.02)	0.7 (1.1)
	G. gorilla	–	−0.7 to 2[g,h]	160.2 (8.1)	62.4 (2.9)	1.6 (0.1)	1.3 (0.1)	1.1 (1.7)
	G. beringei	–	−2.5 to 2[g,h]	157.1 (4.4)	65.7 (3.5)	1.5 (0.06)	1.5 (0.1)	1.2 (1.8)
	P. pygmaeus	–	3–5[g,h]	171.4 (8.5)	64.8 (6.3)	1.5 (0.16)	1.2 (0.1)	0.6 (1.5)
	H. lar	–	–	169.1 (6.4)	60.6 (5.3)	1.4 (0.05)	1.3 (0.09)	1.4 (0.7)
	S. syndactylus	–	–	167.3 (8)	61.5 (7)	1.4 (0.06)	1.3 (0.1)	1.0 (0.9)
	P. anubis	–	3[i]	148.5 (7.5)	61.6 (2.8)	1.2 (0.06)	1.2 (0.08)	3.3 (1.2)
	M. fascicularis	–	5.3[i]	154.7 (8)	55.3 (4.9)	1.2 (0.08)	1.1 (0.1)	1.1 (0.5)

Note: All measurements without a superscript were taken by the current study. Standard deviation in parentheses.

Abbreviations: LL, lateral condyle length; LW, lateral condyle width; MW, medial condyle width; NH, intercondylar notch height; PH, patellar height; PW, posterior width.

[a] Heaton et al.[39]

[b] Hunt et al.[35]

[c] Tardieu and Preuschoft[38] (the Macaca species used in this study is *Macaca sylvanus* not *Macaca fascicularis*). Anteroposterior distortion of the KSD-VP-1/1c femur likely obscures an accurate measurement of bicondylar angle in this specimen.[40] The *Australopithecus africanus* individual StW 129 is not included in this table as no accurate measurements were able to be taken from this fossil.

[d] Heiple and Lovejoy.[1]

[e] DeSilva and Grabowski.[41]

[f] DeSilva et al.[42]

[g] Ruff.[19]

[h] Shefelbine et al.[17]

[i] Pallas et al.[43]

patellar surface. *Pan* and *Gorilla* show surfaces that are slightly deeper than the Asian apes, but still relatively flat.

The deepest patellar surfaces belong to *Homo sapiens* and *Australopithecus*, supporting the claim that a bipedal gait requires a mechanism for patellar retention as outlined above. Cercopithecoids exhibit deeper patellar surfaces than the apes, and there is some overlap in the range of variation between *Papio* and *Australopithecus*. No significant difference was found between patellar depths for *Australopithecus* and *Papio anubis* ($p = 0.29$), nor for *Australopithecus* and *H. sapiens* ($p = 0.46$) suggesting it may be difficult to discern functional behavior from patellar depth alone.

All fossil femora are within the range for modern humans. *A. prometheus* (StW 573) and *A. sediba* (U.W. 88-63) are positioned only within the range for modern humans and do not overlap with any other taxa. The two *A. africanus* fossils (TM 1513 and Sts 34) are similar to one another in their patellar depths and are found in the

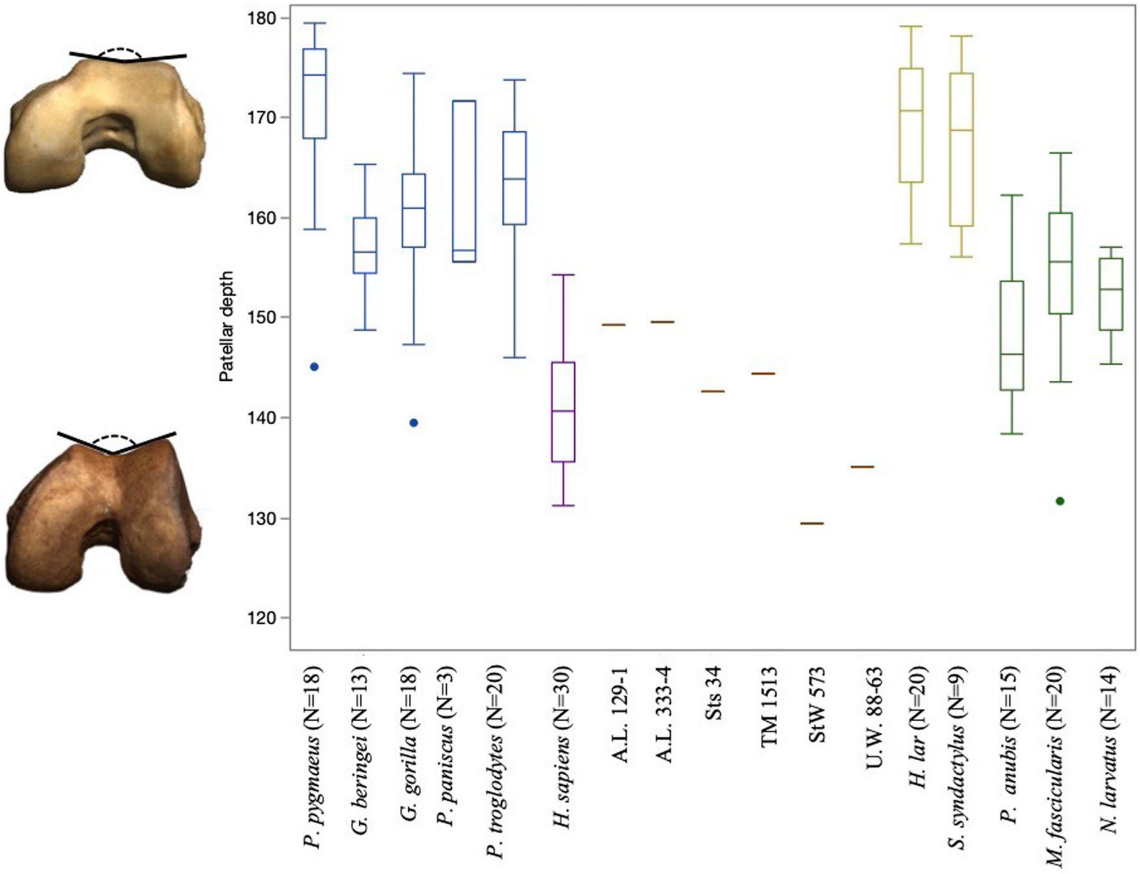

FIGURE 2 Box plot of the patellar depths for the sample of modern humans, primates, and *Australopithecus*. The primate sample specifically includes Nasalis as this taxon was hypothesized by Heiple and Lovejoy[1] to exhibit a deep patellar surface due to its use of leaping behavior. A.L. 288-1, A.L 333w-56, KSD-VP-1/1c, and StW 318 do not preserve the appropriate anatomy for accurate measurement and therefore were not included in this analysis. Images on the left depict two of the conditions for patellar surface depth. At the top is the inferior view of the distal femur of a chimpanzee with a shallow patellar surface depth. On the bottom is the distal femur of a modern human, which exhibits a notably deeper patellar surface. Depth was measured on three-dimensional scans of the distal femur for each specimen using the program Geomagic Control and reported as an angle with larger angles corresponding to shallower patellar surfaces and smaller angles corresponding to deeper ones.

overlapping range of modern humans and *P. anubis*. The other *A. afarensis* individuals (A.L. 129-1 and A.L. 333-4) have almost identical patellar depths which are shallower than all other *Australopithecus* fossils aligning closer to the range for *P. anubis* than modern humans.

The results here support the conclusion that patellar depth relates to patellar stability. The range for *Australopithecus* strongly aligns with *H. sapiens*; however, overlap between some fossil *Australopithecus* and *P. anubis* suggests that this trait should not be used in isolation given the different locomotor behaviors of these two groups.

2.2 | Lateral lip height

The anteroposterior elongation of the condyles and deepening of the patellar surface in the modern human femora creates lips, or bony extensions, on the medial and lateral edges of the patellar surface (Figure 3). As previously discussed, the valgus position of the femoral shaft creates a lateral force on the patella that increases the risk of dislocation. In positions at or near full extension, patellar retention is primarily accomplished by soft tissues like the *m. vastus medialis*.[9,46] However, in positions of knee flexion, the risk of patellar dislocation increases, necessitating additional preventative mechanisms like the deep patellar surface. This has resulted in the greater projection via the lateral patellar lip.[9,13–16]

Though functionally related in a biped, these two features do not covary. It has previously been found that the bicondylar angle and the extent of the lateral lip are not correlated in human knees. In fact, while the bicondylar angle is developmentally plastic, the patellar lip is present at birth.[49] Nonetheless, because it is the direct result of the forces produced by a bicondylar femur, the lateral patellar lip is regarded as a definitively bipedal trait.

On average, modern humans exhibit higher lateral patellar lips than other taxa though there is some overlap with *Pan troglodytes*, *Gorilla*, and especially *P. anubis* (Figure 3). In fact, there is no statistical difference ($p = 0.15$) between *H. sapiens* and *P. anubis*.

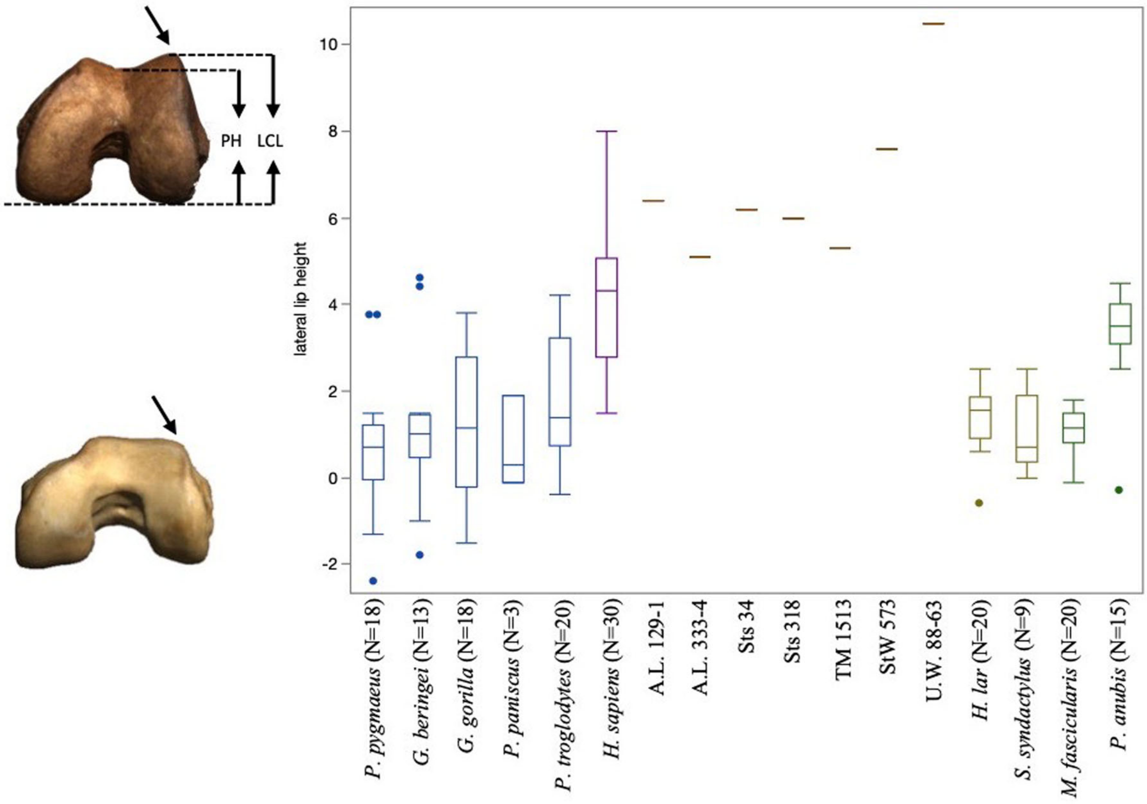

FIGURE 3 Box plot of the height of the lateral patellar lip in the sample of modern humans, primates, and *Australopithecus*. A.L. 288-1, A.L. 333w-56, and KSD-VP-1/1c do not preserve the appropriate anatomy for accurate measurement and therefore were not included in this analysis. Modern humans and *Australopithecus* exhibit the largest lateral lip heights with *Australopithecus sediba* (U.W. 88-63) significantly higher than all other taxa and *Australopithecus* individuals. *Papio anubis* is found within the range for modern humans indicating that lateral patellar lip height cannot be used in isolation to distinguish locomotor behavior. Lateral lip height measured as length of the LCL–PH. This measurement can be seen on the modern human femur found at the top left of the figure. The left femur of a chimpanzee is seen at the bottom left of the figure. Black arrows indicate the location of the lateral patellar lip. Measurements taken on three-dimensional scans for each individual using the program VXelements. LCL, lateral condyle; PH, patellar height.

Nevertheless, *Australopithecus* has the highest values for lateral lip height, overlapping almost exclusively with the higher end of the modern human range. Only *A. sediba* (U.W. 88-63) is outside the range for modern humans exhibiting the highest lateral lip of the current sample.[29]

While an increased lateral patellar lip height is very likely the result of a high bicondylar angle in habitually bipedal individuals, the complete overlap in the range of values for this trait between modern humans and *P. anubis* indicates that this trait cannot be used in isolation when making locomotor inferences.

2.3 | Mediolateral dimensions of the femoral condyles

The mediolateral widths of the femoral condyles differ between apes and humans (Figure 4). Modern apes have wider medial condyles than lateral while humans show more equal proportions.[18,19] However, the functional significance of this anatomy is somewhat unclear (see discussion in MacLatchy et al.[50]). Some have argued that asymmetry in the condyles of apes enhances internal/external rotation at the knee joint.[16,18] Others have proposed that this asymmetry is due to the varus angle of the femur in apes which directs greater load through the medial compartment of the knee.[20,21] In humans, loading is relatively equal through the knee joint during bipedal locomotion, which would promote greater condylar symmetry.[13,20,22]

Apes possess a wider medial condyle (Figure 4), which aligns with previous observations of condylar asymmetry.[50] In contrast, modern humans and *Australopithecus* have symmetrical condyles with ratios very close to 1, consistent with an even distribution of load through the knee joint during bipedalism. There is a statistically significant difference between modern humans and all ape taxa ($p < 0.001$) as well as between modern humans and *P. pygmaeus* ($p = 0.0002$) despite the lower values for the latter. However, there is considerable overlap with quadrupedal monkeys.

Interestingly, *P. pygmaeus* has more symmetrical condyles than the African apes. Additionally, ratios for *Gorilla beringei* are noticeably higher than those for *G. gorilla*. Given the greater terrestriality of *G. beringei*, the hypothesis that a wider medial condyle reflects greater

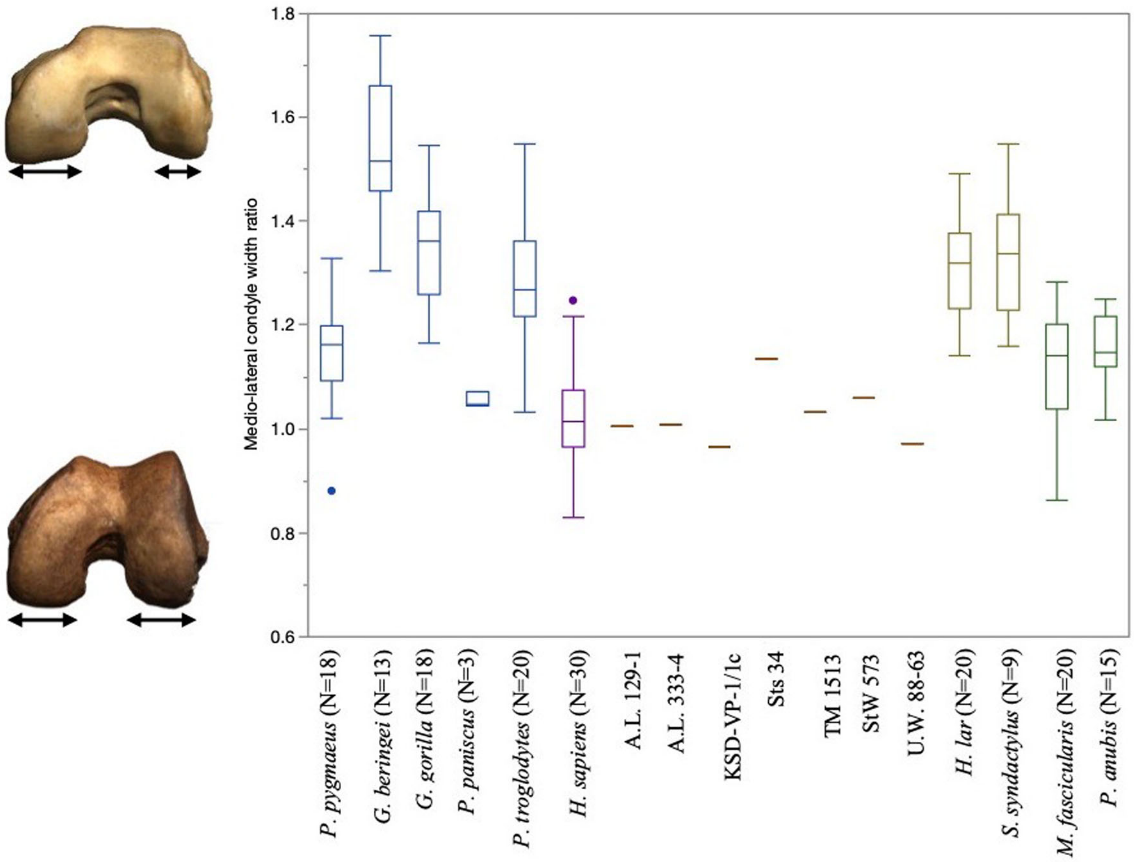

FIGURE 4 Boxplot of mediolateral condylar width ratio in the current sample of extant primates, modern humans, and *Australopithecus*. A.L. 288-1, A.L. 333w-56, and StW 318 do not preserve the appropriate anatomy for accurate measurement and therefore were not included in this analysis. Widths of the condyles were taken from three-dimensional scans for all distal femora using the program VXelements. The ratio is calculated as medial condyle width/lateral condyle width. Images on the left of the graph show the inferior view of a left chimpanzee femur (top) and the left modern human femur (bottom). The chimpanzee femur has a wider medial condyle than lateral while the modern human femur has equally sized condylar widths.

rotation of the knee joint during arboreal climbing is challenged by these data.

A plausible explanation for these results is the degree of varus/valgus in these taxa. Ruff[19] calculated the degree of inclination of the femur in a sample of extant gorillas, chimpanzees, and orangutans and found that the greatest amount of varus, or bow-leggedness, was seen in *G. beringei* (−2.5) with slightly less varus in *G. gorilla* (−0.7). Orangutans on the other hand showed the greatest degree of valgus (+3.8). These data align with the pattern of condylar asymmetry suggesting that symmetry of the condyles may be impacted by knee varus/valgus—that is the bicondylar angle creates differential patterns of loading through the knee joint.

Australopithecus distal femora have symmetrical condyles like modern humans, consistent with bipedal gait. However, overlap between the ranges for modern humans, *Australopithecus*, and cercopithecoids suggests that the mediolateral condyle width ratio cannot be used in isolation to discern locomotor behavior and cannot be solely related to knee varus/valgus.

3 | CONTOUR OF FEMORAL CONDYLES

3.1 | Condylar elongation

Like the bicondylar angle, the contour of the femoral condyles has been argued to be one of the strongest indicators of a human-like bipedal gait.[8,9,12,13,15,16] In modern humans, the condyles are anteroposteriorly elongated and inferiorly flattened to maximize cartilage contact between the tibia and femur in an extended position.[9,14] In apes, the condyles are rounded and not expanded to facilitate greater mobility between the femur and tibia.[8]

Increased contact with the tibial plateau is the result of elongation specifically in the posterior portion of the condyle.[9] Anterior elongation is argued to be an adaptation to increase the mechanical advantage of the quadriceps muscle near full extension by lengthening the patellar moment arm.[9] Therefore, the human condyle exists in two parts, a posterior portion, and an anterior portion, both with distinct functional roles related to extended-limb, bipedal locomotion (Figure 5a,b).[9] To quantify the elliptical profile of the femoral condyle, Lovejoy[9] proposed a measurement that calculates the extent of posterior elongation (Figure 5a).

The lower ratios of *H. sapiens* indicate that the horizontal tangent is much longer than the vertical in these individuals reflecting an elongated posterior portion. In *P. troglodytes*, this ratio is much higher indicating more equal lengths of these tangents and thus a more circular profile to the condyle (Figure 5c).

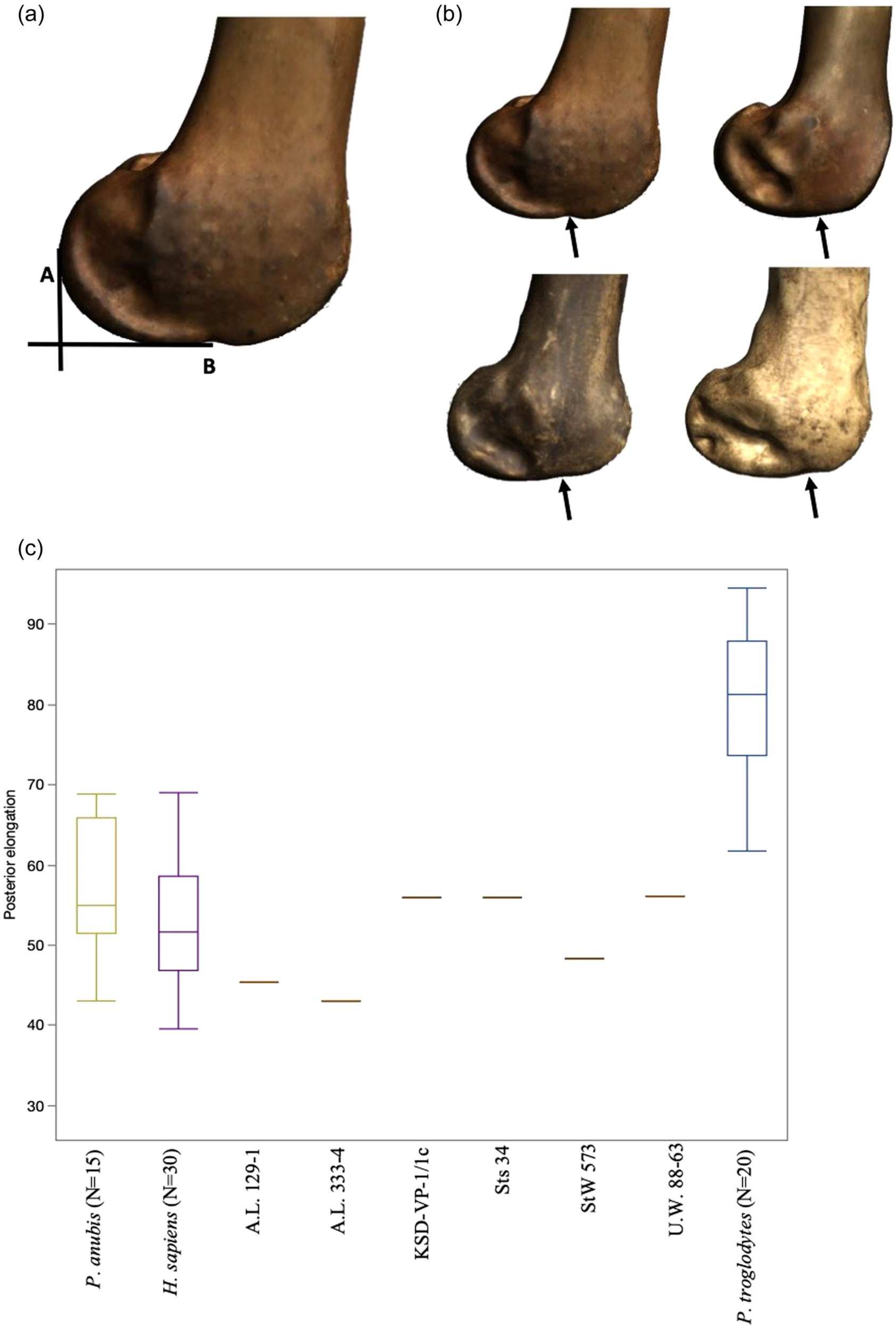

FIGURE 5 (See caption on next page).

FIGURE 6 Lateral view of the femur of (left) *Papio anubis*, (middle) a modern human, and (right) *Australopithecus afarensis* A.L. 129-1. While all three individuals exhibit some degree of anteroposterior condylar elongation, *P. anubis* has a rounded inferior surface while the modern human and *Australopithecus* have flattened surfaces. This flattening increases the surface area contact between the femur and tibia for greater load dissipation in a bipedal gait.

Australopithecus femora are all well within the range for modern humans. In fact, *A. afarensis* (A.L. 129-1 and A.L. 333-4) possess even lower ratios than most modern humans, indicating greater posterior elongation. These data support the assertion that a bipedal gait is associated with elongation of the femoral condyle in the posterior compartment, resulting in an elliptical profile. These data indicate that posteriorly expanded femoral condyles are key to load dissipation in an extended position and thus an essential anatomy for habitual bipedalism in early *Australopithecus*. However, some caution is warranted in interpreting these data in isolation since there is an overlap in posterior condylar expansion with *Papio*.

While anterior expansion is not directly quantified here, Lovejoy[9] notes a lack of this expansion in *A. afarensis*, which can also be seen in Figure 5b. Anterior expansion and a resulting increased moment arm for the quadriceps evolved in *Homo*.[9,29]

3.2 | Inferior condylar surface

The condyles of cercopithecoids are also slightly elongated like modern humans, but they are not inferiorly flattened, which is an important distinction (Figure 6).[23] Heiple and Lovejoy[1] discuss the importance of this flattening in modern humans and *Australopithecus* and its role in load dissipation in a bipedal gait. Inferior flattening of the femoral condyles maximizes articular contact of the joint near full extension, which occurs following the swing phase and just preceding heel strike during the human gait cycle.[1,51] The condylar curvature in the cercopithecoid femora aligns with a more flexed knee posture during quadrupedal gait and rotational capabilities during climbing.[1,23]

3.3 | Intercondylar notch

Much like the bicondylar angle is related to patellar depth, lateral lip height, and relative condylar width, anterior expansion of the femoral condyles appears to be the driver for two other femoral anatomies: the relative intercondylar notch height and proportions of the distal epiphysis.

The intercondylar notch is the space between the femoral condyles that houses the tibial spines during articulation. Importantly, this area encloses the major ligaments of the knee joint including the

FIGURE 5 (a) Measurement for quantification of lateral condylar shape as established by Lovejoy.[9] A.L. 288-1, A.L. 333w-56, TM 1513, and StW 318 do not preserve the appropriate anatomy for accurate measurement and therefore were not included in this analysis. Comparative primate taxa are limited to modern humans, chimpanzees, and *Papio* to directly replicate the analysis by Lovejoy,[9] and evaluate the similarities with cercopithecoids. Femora were aligned so that the view was perpendicular to the anteroposterior axis of the lateral condyle. Alignment was also compared to the figures provided in Lovejoy.[9] A vertical tangent (A) and a horizontal tangent (B) are placed on the bone in a lateral view. The vertical length (A) is measured from the intersection with the meniscal groove to its intersection with (B) while the horizontal length (B) is measured from its point on the lateral meniscal groove to its intersection with (A). This measurement was performed on three-dimensional scans of the distal femora using the program ImageJ. (b) Profile view of the lateral condyle in top left: modern human, top right: modern chimpanzee, bottom left: *Australopithecus afarensis* A.L. 333-4, bottom right: *A. afarensis* A.L. 129. The arrows mark the location of the lateral meniscal notch which separates the anterior and posterior portions of the articular surface of the lateral condyle. Note the circular shape to the chimpanzee condyle compared to the elongated elliptical shape of the human condyle. All *Australopithecus* fossils exhibit an elongated elliptical condyle. Note the anterior expansion of the condyle in the modern human. This anterior expansion is absent in the chimpanzee and weak in both the *A. afarensis* individuals. Images not to scale. Figure adapted from Lovejoy.[9] (c) Boxplot of the quantification for posterior elongation in a sample of modern humans, *Papio anubis*, *P. troglodytes*, and *Australopithecus*. Significant overlap exists between modern humans, *P. anubis*, and *Australopithecus* indicating posterior condylar elongation while *P. troglodytes* has values that indicate little to no posterior elongation.

anterior and posterior cruciate ligaments and the anterior and posterior meniscofemoral ligaments.[8,52] In modern humans, these ligaments are important for bipedalism as they prevent hyperextension and hyperflexion and help to limit mediolateral rotation, guiding the femur over the tibia throughout the range of movement.[8,9] In modern chimpanzees, these ligaments are in slightly different positions to accommodate greater medial rotation and sliding of the femur on the tibia.[8]

Attachment sites for the cruciate ligaments can be identified on bone, which can help interpret knee function in fossil hominin femora. Evidence of a human-like arrangement of the ligaments could reflect a knee adapted for loading and stability in extension. A modern human arrangement of cruciate ligaments has been found in *A. sediba*, *A. africanus* (TM 1513 and Sts 34), *A. prometheus*, and *A. afarensis* (A.L. 333-4).[39,41,42,53]

Early interpretations of the *A. africanus* TM 1513 femur by Clark[2] noted an additional indentation on the lateral side of the intercondylar notch thought to represent a secondary attachment point for the anterior cruciate ligament. The presence and location of this indentation were interpreted as evidence for a taut anterior cruciate ligament in full knee extension supporting a human-like bipedal gait in this fossil.[2] However, it was later found that this secondary attachment point had been observed in some monkeys and apes and therefore was not a reliable indicator of human-like knee extension.[48]

This feature in TM 1513 has been described as an "accessory notch" and can be seen as a small extension of the intercondylar notch (Figure 7). Despite its lack of relation to the anterior cruciate ligament, Heiple and Lovejoy[1] sought to quantify the extent of this anterior expansion in TM 1513. The authors calculated two relative notch heights: one using the accessory notch and another using the anterior-most extent of the medial side of the notch.[1] They compared these measurements to the relative notch height of the other *A. africanus* femur Sts 34, and a sample of modern humans, African apes, and orangutans. When the accessory notch was included, TM 1513 had a much higher index than all other taxa, including the other *A. africanus* Sts 34, and was above two standard deviations for the modern human mean. When the accessory notch was not included, TM 1513 was within one standard deviation of modern humans, similar to their position for Sts 34.[1]

The authors noted that this accessory notch is not uncommon in the distal femora of humans and African apes, however, they did not propose a functional relevance for this anterior expansion, nor of the relative notch height in general. Here, the measurement for relative notch height used by Heiple and Lovejoy[1] following Kern

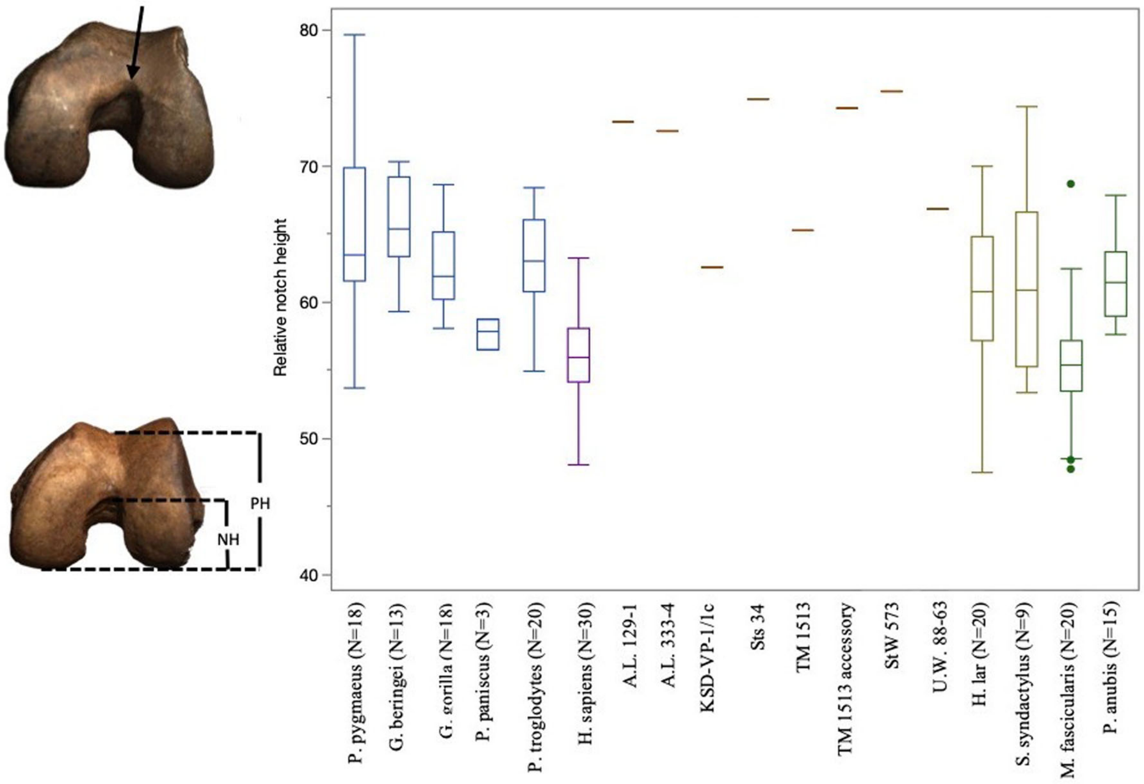

FIGURE 7 Boxplot of the range of values for relative intercondylar notch height among extant primates, humans, and *Australopithecus*. A.L. 288-1, A.L. 333w-56, and StW 318 do not preserve the appropriate anatomy for accurate measurement and therefore were not included in this analysis. There is significant overlap between all taxa, but the range for *Australopithecus* is noticeably higher than all other species. The image on the top left shows an inferior view of *Australopithecus africanus* TM 1513 with an arrow pointing to the accessory notch. The image on the bottom left shows the measurement for relative notch height. This is NH/PH × 100. NH, notch height; PH, patellar height.

et al.[48] is replicated using an expanded sample of modern humans, extant primates, and *Australopithecus* (Figure 7). Additionally, TM 1513 is included twice (labeled "TM 1513" and "TM 1513 accessory") to assess the effect of the accessory notch on this index and its relationship to the other fossil hominins.

The relative intercondylar notch height overlaps in many different primate taxa suggesting that this metric is not associated with specific locomotor behavior (Figure 7). However, *Australopithecus* generally has larger notch indexes, as Heiple and Lovejoy[1] also found. We regard this as the logical result of a distal femur that has evolved posterior condylar expansion without accompanying anterior patellar elongation. As previously noted (i.e., Figure 6), the *Australopithecus* sample exhibits posterior elongation of the condyle, but weak anterior elongation, a unique combination amongst primates that results in a higher notch index.

The value of relative notch height is calculated as a ratio of intercondylar notch height to patellar height (Figure 7) both of which would be affected by anteroposterior elongation of the condyle. However, elongation in both the anterior and posterior directions would result in a notch height index similar to those that exhibit no elongation in either direction. This would explain the large degree of overlap between modern humans and cercopithecoids with greater anteroposterior condylar elongation, and the ape sample with no condylar elongation.

Relative intercondylar notch height may therefore reflect anteroposterior expansion of the condyles and the high values for *Australopithecus* suggest that these hominins had not yet evolved an increased patellar moment arm which first evolves in femora assigned to early *Homo*.[9,29]

3.4 | Proportions of the distal epiphysis

The proportions of the distal femoral epiphysis have been hypothesized to relate to knee mobility in primates.[16] The elongated and elliptically shaped condyles in modern humans give the distal epiphysis a square shape in inferior view, while the reduced condylar length and wide posterior width of the distal epiphysis in modern apes give it a rectangular shape (Figure 8).[16]

The functional argument follows that a more squared distal epiphysis tightens the articulation between the tibial spines and the intercondylar notch, limiting mobility at the joint.[16] Conversely, the wider posterior width in the ape femur provides more room for the tibial spines, allowing greater external and internal rotation at the joint.[16]

To analyze these shape differences, Tardieu[16] measured the proportions of the distal femur in a sample of modern humans, fossil hominins, and extant primates by calculating the ratio of lateral condyle length to posterior width. She concluded that all primates, including modern humans and fossil hominins, have a posterior width that is greater than the lateral condyle length and that this index falls into three different groups: (1) The human and monkey condition in which the lateral condyle length is slightly shorter than the posterior width and promotes knee stability. (2) The great ape state in which the posterior width is 1.5–2 times the length of the lateral condyle and is mobile. (3) The hylobatid state, which is intermediate between the previous two.

The pattern outlined by Tardieu[16] can be seen in Figure 8. All taxa have ratios larger than one, suggesting that the posterior width is greater than the lateral condyle length in all primate species. Ranges for the great apes are higher than all other taxa with average values near 1.5, indicating a more rectangular profile as proposed by Tardieu. The lowest ratios, and thus more square epiphyseal shape, belong to modern humans and cercopithecoids with values around 1.2, again supporting the categorization put forth by Tardieu.[16]

These results align with the variation in knee stability employed by these groups. That is, the rectangular proportions that characterize the great apes would permit more mobility. The square proportions of humans and cercopithecoids support the knee stability required for terrestrial parasagittal flexion-extension utilized by these groups, respectively.

Overall, the range for *Australopithecus* is positioned slightly higher than modern humans with an average near 1.3, and shows equal overlap between modern humans and the hylobatids. This finding aligns with the general pattern for *Australopithecus* in which posterior condylar elongation exists without anterior elongation. This unequal elongation would affect the shape of the distal epiphysis resulting in a more rectangular outline compared to modern humans.

Individual placement of the fossil femora is generally at the higher end of the range for modern humans, if not above it, though *A. sediba* is securely within the range for modern humans. This result aligns with the results of relative notch height for this taxon, which suggested greater anterior expansion and a more favorable moment arm for the quadriceps compared with other species of *Australopithecus*.

Previous debates about sexual dimorphism in *A. afarensis* used this measure of distal proportions to differentiate A.L. 129-1 and A.L. 333-4[16,18,54] and led, in part, to suggestions of dinichism.[47] Results from Tardieu's[16] study placed the A.L. 129-1 femur in the range for *Pan* and the A.L. 333-4 femur within the range for *H. sapiens*, with no overlap between the two groups. With a larger comparative dataset and a broader evolutionary context, the differences between A.L. 129-1 and A.L. 333-4 are not as stark and are best interpreted as fitting within the normal range of variation for a genus that has a more rectangular distal femur than modern humans owing to a shorter anterior patellar surface.

The current results support the pattern of distal epiphyseal shape outlined by Tardieu[16] and suggest that this index can reliably differentiate primate taxa in a manner that seems to reflect knee stability/mobility. However, the overlap between modern humans and cercopithecoids suggests that this trait cannot be used to directly infer bipedal locomotion.

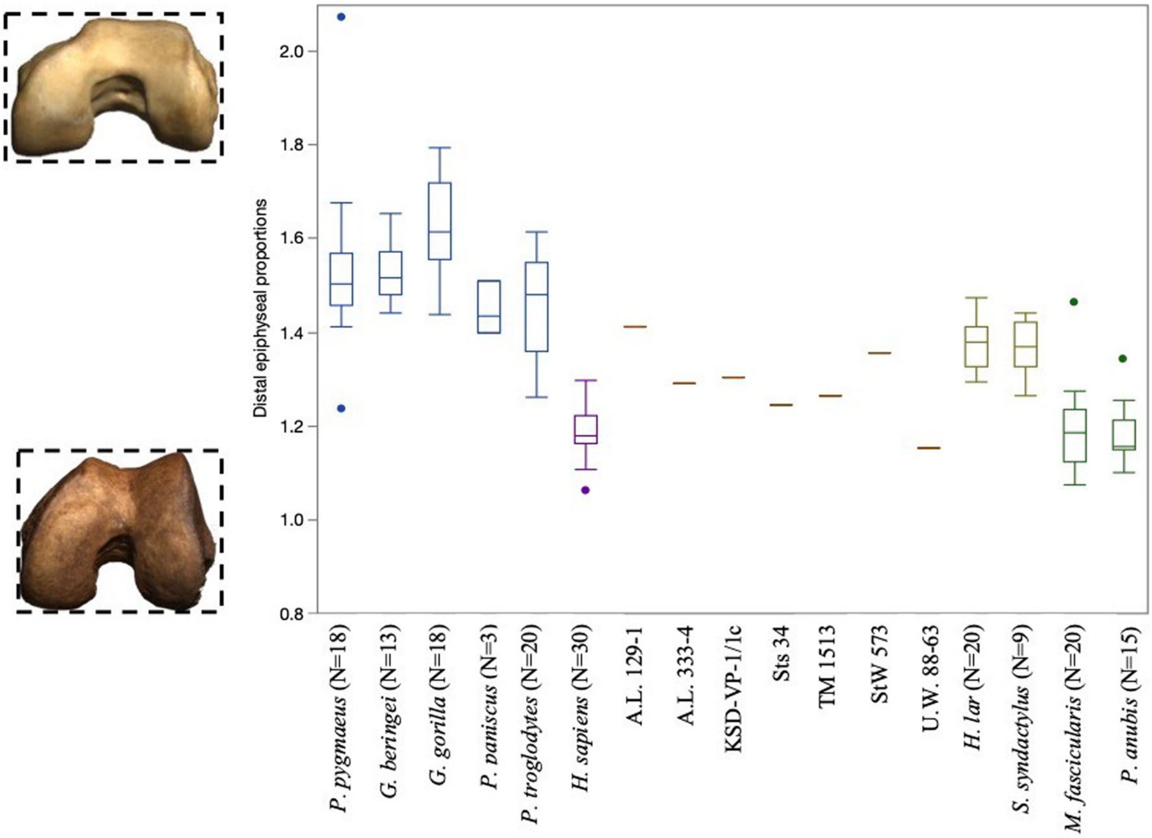

FIGURE 8 Boxplot of distal femoral proportions for a sample of modern humans, extant primates, and *Australopithecus*. A.L. 288-1, A.L. 333w-56, and StW 318 do not preserve the appropriate anatomy for accurate measurement and therefore were not included in this analysis. Images on the left are the inferior view of a left distal femur for (top) a chimpanzee and (bottom) a modern human. The dotted outline emphasizes the shape of the distal epiphysis which is rectangular in apes and square in humans. Measurement for epiphyseal shape was calculated as PW/LCL. All measurements were taken on three-dimensional scans for each specimen in the program VXelements. LCL, lateral condyle length; PW, posterior width.

4 | DISCUSSION

4.1 | Anatomical complexes

While there has been a tendency to atomize the knee, this study finds that the morphologies that constitute the distal femur fall into two anatomical complexes, each the product of different forces acting on the joint.

The first complex is driven by forces that influence joint stability and includes the depth of the patellar surface, the height of the lateral patellar lip, and the widths of the femoral condyles. In modern humans and *Australopithecus*, destabilizing, laterally oriented forces generated by the bicondylar angle increase the risk of patellar dislocation. To minimize this risk, the human and *Australopithecus* distal femur has evolved a deep patellar surface and high lateral patellar lip to keep the patella in place.

A deep patellar surface and high lateral patellar lip also characterize the cercopithecoid distal femur. Paradoxically, however, these species do not possess a bicondylar angle nor do they practice habitual bipedalism. Instead, these groups utilize terrestrial and arboreal quadrupedalism in which the hind limb habitually moves from strong states of flexion to extension.[55] This movement is mostly restricted to the parasagittal plane and requires patellar retention throughout the gait cycle thus resulting in a deep patellar surface and heightened patellar lips.

For both patellar surface depth and lateral lip height, ape taxa are noticeably distinct from modern humans and cercopithecoids. Apes tend to move their hind limbs in a variety of positions including internal and external rotation. Therefore, they have a shallow patellar surface and lower lateral lip to allow for increased movement at the joint.

Variation in these two femoral anatomies is in line with previous analyses of primate patellae. Compared to modern apes, human and cercopithecoid patellae are anteroposteriorly thicker, which increases the mechanical advantage of the quadriceps muscle.[55] This in turn increases the efficiency of the hind limb as it moves from states of flexion to extension as is characteristic of both striding bipedalism and cercopithecoid quadrupedalism.[55] Having a deep patellar surface and heightened patellar lip can help retain a thicker patella and ensure both an efficient and stable knee joint. Modern apes have shorter and thinner patellae that are capable of much greater movement about the joint including internal and external rotation, motions that are less expressed in the modern human and cercopithecoid repertoires.

Finally, the shared condylar symmetry in the knees of hominins and cercopithecoids reflects even, stereotypical loading of the joint. Apes, conversely, have greater condylar asymmetry perhaps to enhance rotation in an arboreal context. This observation was previously discussed as the result of knee varus/valgus with greater valgus associated with greater condylar symmetry. However, this explanation is complicated by the symmetrical condyles of cercopithecoids, which do not have a valgus femur. The functional explanation for this pattern of condylar asymmetry (see summary in MacLatchy et al.[50]) requires further kinematic analyses that are beyond the scope of this study.

The shared morphologies between modern humans and cercopithecoids in this first complex of anatomies raises an interesting yet complicated issue given the vastly different nature of their locomotor repertoires. While both taxa require a stable knee joint for their respective locomotor behaviors, further kinematic analyses are needed to fully understand the extent of these shared morphologies. Captive studies of non-human primates, particularly macaques, have found that cercopithecoids are able to adopt human-like gait kinematics when trained for bipedal walking.[56] These kinematics were the result of greater extension of the hind limb, though it is unclear exactly how the overlapping morphologies of the knee allow trained macaques to adopt human-like bipedal gait. Additionally, the current study includes only measurements hypothesized to relate to bipedal locomotion. This raises the likely possibility that other morphologies of the distal femur differ between hominins and cercopithecoids.

For instance, while not measured in the current study, there is an observable difference in the heights of the medial and lateral lips between modern humans and cercopithecoid femora. Because the bicondylar angle of modern humans results in strong lateral forces, the femur exhibits a heightened lateral patellar lip, but only a moderate medial lip. In cercopithecoids, however, the lateral and medial lips are of relatively equal height, which keeps the patella in place throughout the flexion-extension movements that characterize quadrupedal locomotion in the absence of additional strong lateral forces.

The second complex that characterizes the distal femur is a result of the anteroposterior femoral condylar expansion. This expansion influences the relative intercondylar notch height, proportions of the distal epiphysis, and inferior flattening of the condyles.

The presence of both anterior and posterior elongation in the femoral condyles of modern humans and cercopithecoids results in a low relative notch index. Elongation in the posterior compartment accommodates greater surface area contact between the femur and tibia which helps to dissipate forces in an extended position. For modern humans, this position is habitually occupied by the joint in a striding bipedal gait. In cercopithecoid quadrupedalism, the knee joint consistently moves from a state of strong flexion to extension, necessitating increased contact between the femoral condyles and tibial plateau. Anterior elongation of the condyles increases the moment arm of the quadriceps. A more efficient quadriceps muscle is highly beneficial for a knee joint that is in habitual extension like modern humans and a knee joint that is constantly moving from states of flexion to extension like cercopithecoids. Therefore, both groups exhibit anteroposterior elongation of the condyles.

Because of how the notch index is measured, the lack of any elongation in the ape femoral condyles also results in a similarly low relative notch index. *Australopithecus* is the only taxonomic group to exhibit a noticeably high notch index reflecting the presence of posterior elongation to dissipate the high forces generated at the knee during bipedal gait, but not anterior elongation, in their condyles. Anteriorly elongated condyles characterize the distal femur of early fossil *Homo*.[9,29]

The condylar expansion also impacts the proportions of the distal epiphysis. Expansion of the condyles results in a square-shaped distal epiphysis in modern humans and cercopithecoids. The shortened condyles of modern apes paired with their greater posterior widths create a more rectangular shape to the epiphysis. *Australopithecus* finds itself somewhere in the middle of these states due to the unequal expansion of the condyles and is thus intermediate between a square and rectangular-shaped epiphysis.

Lastly, inferior flattening of the condyles, as seen in modern humans and *Australopithecus*, is the product of an increased load through the knee joint. This inferior flattening is absent in all quadrupedal taxa including apes and cercopithecoids, which can distribute loads through four limbs, reducing the relative force through each individual limb. As bipeds, modern humans and *Australopithecus* distribute this load through only two limbs. Inferior flattening of the condyles in these taxa helps to increase surface area contact at the joint, which can accommodate greater forces incurred during bipedal walking and running.

These two complexes shed light on the interrelatedness of the locomotor anatomies that make up the knee joint and caution against treating any one of these morphologies in isolation.

4.2 | Shared morphologies between humans and cercopithecoids

In a larger evolutionary context, two possibilities exist to explain the pattern of shared morphology between modern humans and cercopithecoids. The first is that these morphologies were inherited from a common ancestor, consistent with the hypothesis that the last common ancestor of *Pan* and *Homo* had a body form that was more pronograde and monkey-like.[57–60] The second possibility is that these morphologies evolved in parallel in modern humans and cercopithecoids. This interpretation would suggest that the need for knee stability evolved multiple times and with similar anatomical solutions. If the modern human knee evolved from a cercopithecoid-like state, this would necessitate the reduction of the medial patellar lip, which would be difficult to explain functionally. If, however, the human knee evolved from an ape-like form, this would necessitate a heightening of the lateral patellar lip as a result of the forces imposed by the bicondylar angle.

To differentiate between these two possible explanations (shared ancestry vs. parallelism), it is essential to discover geologically older hominin distal femora. As of now, the oldest distal femur from this genus dates to approximately 3.6 million years (KSD-VP-1/1c and possibly StW 573). This leaves a >3-million-year gap between the *Pan* and *Homo* last common ancestor and the oldest hominin fossils, making the evolution of the hominin distal femur unclear. Therefore, fossil femora from this time will provide a great deal of insight into the evolution of the knee and the characterization of this joint in the body form of the *Pan*–*Homo* common ancestor that preceded hominin bipedalism. Until additional Pliocene fossils are recovered, a study of Miocene distal femora may also shed light on the pattern of knee evolution preceding *Australopithecus*.

4.3 | Bipedal traits

Despite the large degree of overlap between modern humans and cercopithecoids, two features of the distal femur separate these groups. These are the bicondylar angle and the inferiorly flattened condylar surface. In the conclusion of their 1971 review, Heiple and Lovejoy[1] specifically point out these two features and how they differentiate bipeds like modern humans and *Australopithecus* from quadrupedal primates. Modern humans have a marked bicondylar angle to position the feet under the center of gravity and flattened condyles to accentuate contact and increase load dissipation at the knee joint. These morphologies are distinctly related to striding bipedalism. Cercopithecoids lack a bicondylar angle and have rounded inferior condyles. More than 50 years after Heiple and Lovejoy[1] and with a broader sample of fossils and comparative specimens, we find similar results that the only traits associated with a bipedal gait in isolation are a marked bicondylar angle and inferiorly flattened femoral condyles.

This result informs earlier debates concerning "magic traits" versus the "total morphological pattern."[61–63] It would seem that modern humans and cercopithecoids generally share a total morphological pattern as regards their distal femora that reflects knee stability. However, the presence of a high bicondylar angle and inferiorly flattened femoral condyles in modern humans separate these taxa and are directly related to a striding bipedal gait, highlighting the functional importance of these two features alone.

4.4 | *Australopithecus* variation

For most of the studied traits, *Australopithecus* exhibits a human-like condition supporting their designation as habitually bipedal hominins. Two traits in which *Australopithecus* differs from modern humans are in the anterior elongation of the femoral condyles and the relative height of the intercondylar notch, which itself is a byproduct of posterior condylar expansion without anterior elongation. As found elsewhere,[9,29] anterior expansion of the patellar surface characterizes early *Homo* and likely improves bipedal efficiency during long-distance walking[64] or running.[65]

Furthermore, while most fossil femora are fairly clustered together for each trait, some display more diverse morphologies that may reflect variation in the bipedal gaits of *Australopithecus*. For instance, *A. prometheus* has a deeper patellar surface that lies outside the modern human range and a more rectangular distal epiphysis compared to other *Australopithecus* species. The deep patellar surface may indicate a knee that is more often in states of flexion that would require greater patellar stability while a rectangular profile may suggest more mobility as others have found,[66] although this hypothesis needs further testing considering the state of *Gorilla* as previously discussed.

A. sediba exhibits a significantly higher lateral patellar lip, lower, more human-like relative notch height, and square, more human-like distal epiphyseal shape. It has previously been hypothesized that the unique gait of *A. sediba* subjected the knee joint to a strong lateral force which prompted the heightened lateral patellar lip.[29] Data from the current study concerning the relative notch height and epiphyseal shape suggest that *A. sediba* had anteriorly expanded femoral condyles and thus a more developed patellar moment arm for greater efficiency of the quadriceps. These individual differences among *Australopithecus* point to the possibility of variation in the bipedal gait used by different species in this genus.

5 | CONCLUSION

The distal femur houses a suite of relevant anatomies that can provide insight into primate locomotor behavior including human-like bipedalism. Utilizing an expanded comparative dataset, the current study reassessed hypotheses about the locomotor relevance of several established knee morphologies as well as the human-like affinities of the *Australopithecus* distal femur, framed around a half-century-old classic paper in our discipline (Figure 9).[1]

Several important patterns have emerged from the results of this study. The first is that the distal femur can be understood in two functional complexes, each driven by various forces acting at the joint. The first complex is the result of lateral forces that impose a risk of patellar dislocation and includes depth of the patellar surface, height of the lateral patellar lip, and widths of the femoral condyles. The second complex is the result of high loads generated at the knee during gait. This complex includes the relative notch height, proportions of the distal epiphysis, and inferior flattening of the condyles. Different locomotor strategies, and the degree of knee stability required by these behaviors, have produced variation in the morphology of these anatomical complexes across different primate taxa.

The taxonomic variation of these complexes highlights a second important pattern drawn out by these data. In almost all measured traits, apes are distinctly separate from modern humans,

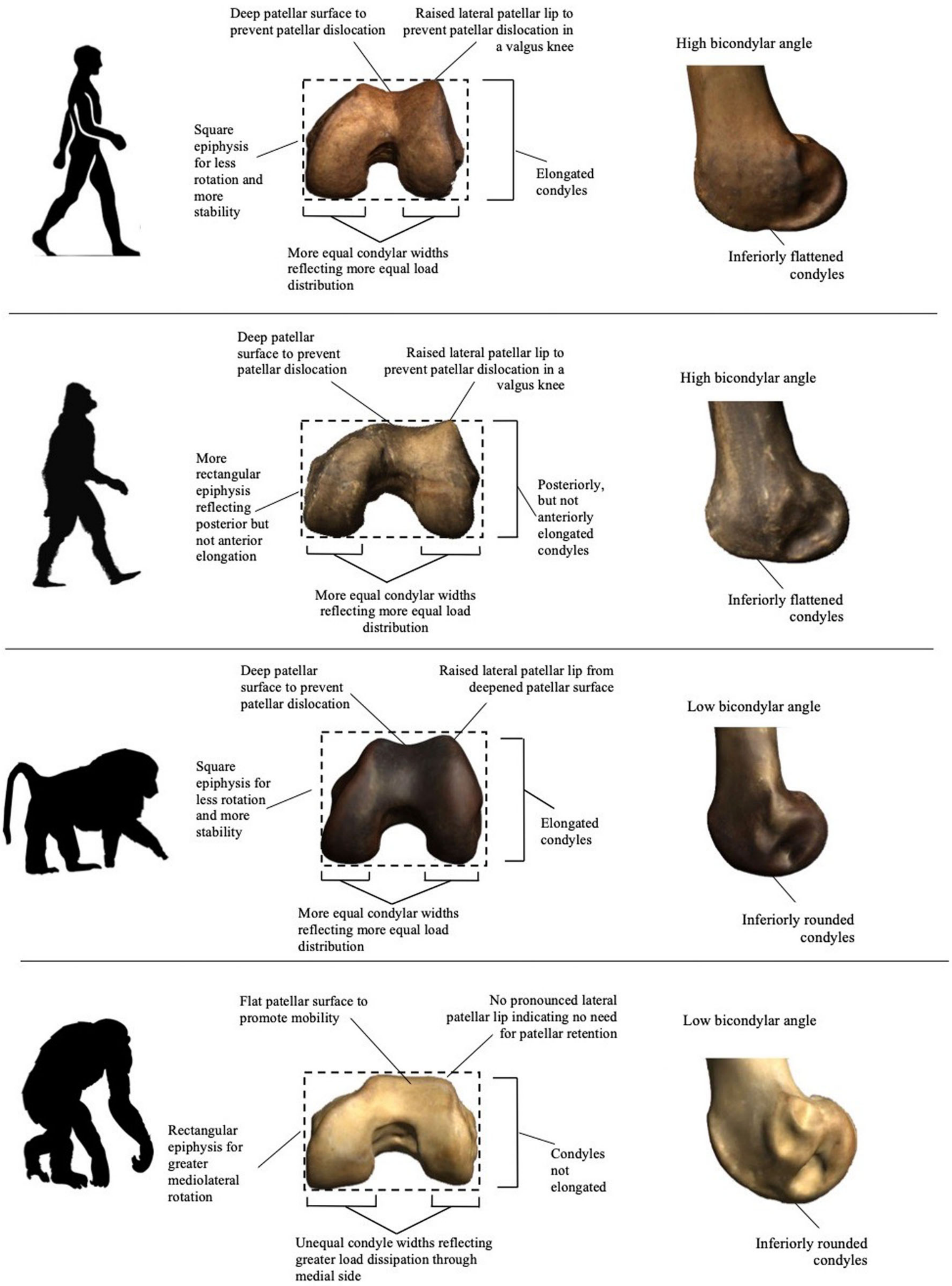

FIGURE 9 Image depicting the morphologies found for the traits discussed in the current study for a (top row) modern human, (second row) *Australopithecus*, (third row) cercopithecoid, (bottom row) chimpanzee. An inferior and lateral femoral view are shown for each with the anatomical descriptions labeled throughout. A.L. 129-1 was used as the example for *Australopithecus* and is mirrored in this image. While modern humans and cercopithecoids share many traits, those labeled on the images in lateral view (inferior surface of condyles and bicondylar angle) are directly associated with bipedal locomotion and separate modern humans and *Australopithecus* from all other taxa. Images on far left from PhyloPic.

but modern humans (and *Australopithecus*) overlap regularly with cercopithecoids. This similarity is likely the result of similar forces generated by different locomotor behaviors that each require stability of the knee.

Finally, in their 1971 review of the distal femoral anatomy of *Australopithecus*, Heiple and Lovejoy[1] concluded that the two *A. africanus* femora in their dataset (TM 1513 and Sts 34) clearly displayed hominin features that would indicate these individuals moved with a striding bipedal gait. With eight additional *Australopithecus* femora, the current study supports the conclusion drawn by these authors some 50 years prior. *Australopithecus* exhibits many modern human-like morphologies in the knee that reflect a habitual bipedal gait. However, variation among individual fossil taxa suggests that a variety of bipedal locomotor styles were employed during the Plio-Pleistocene. The future discovery of additional fossils will greatly enhance our understanding of the role of the knee joint in the evolution of bipedalism and the degree of variation in this gait among hominins.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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