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Evolutionary anatomy of the plantar aponeurosis in primates, including humans

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Abstract

The plantar aponeurosis in the human foot has been extensively studied and thoroughly described, in part, because of the incidence of plantar fasciitis in humans. It is commonly assumed that the human plantar aponeurosis is a unique adaptation to bipedalism that evolved in concert with the longitudinal arch. However, the comparative anatomy of the plantar aponeurosis is poorly known in most mammals, even among non-human primates, hindering efforts to understand its function. Here, we review previous anatomical descriptions of 40 primate species and use phylogenetic comparative methods to reconstruct the evolution of the plantar aponeurosis and its relationship to the plantaris muscle in primates. Ancestral state reconstructions suggest that the overall organization of the human plantar aponeurosis is shared with chimpanzees and that a similar anatomical configuration evolved independently in different primate clades as an adaptation to terrestrial locomotion. The presence of a plantar aponeurosis with clearly developed lateral and central bands in the African apes suggests that this structure is not prohibitive to suspensory locomotion and that these species possess versatile feet adapted for both terrestrial and arboreal locomotion. This plantar aponeurosis configuration would have been advantageous in enhancing foot stiffness for bipedal locomotion in the earliest hominins, prior to the evolution of a longitudinal arch. Hominins may have subsequently evolved thicker and stiffer plantar aponeuroses alongside the arch to enable a windlass mechanism and elastic energy storage for bipedal walking and running, although this idea requires further testing.

KEYWORDS

human evolution, locomotor behaviour, non-human primates, plantar aponeurosis, plantaris muscle

1 | INTRODUCTION

The plantar aponeurosis is a connective tissue structure in the plantar region of the foot that has been most thoroughly characterized in humans, but is also present in numerous mammals. In humans, this structure, also called the plantar fascia, is a broad sheet of highly fibrous tissue in which collagen fibres are regularly orientated to span the entire plantar aspect of the foot from the heel to the toes (Standring and Gray, 2016). Its general anatomy in adults, illustrated in Figure 1, has been variously described

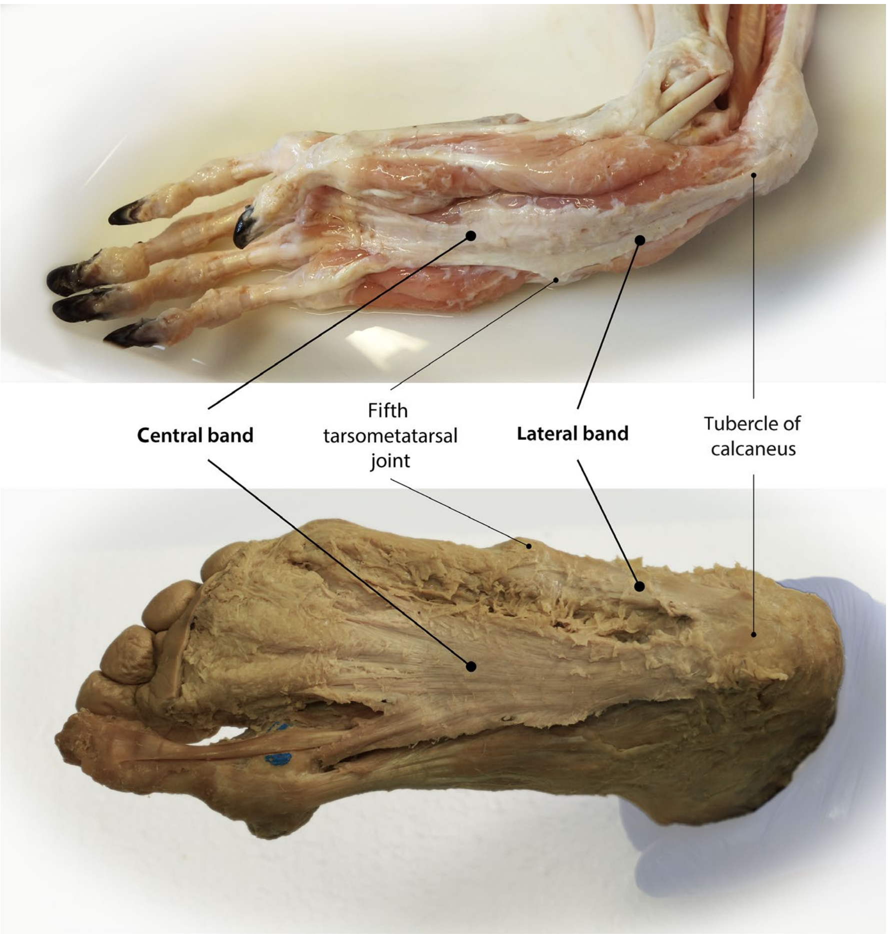


FIGURE 1 General anatomy of the plantar aponeurosis in baboons (*Papio anubis*) and humans. Both share a prominent central band and a lateral band that attaches proximally to the lateral tubercle of the calcaneus and distally to the joint capsule at the fifth tarsometatarsal joint. In baboons, the lateral band progresses further distal. The central band attaches proximally to the medial tubercle of the calcaneus and fans out distally to attach to the subcutaneous tissue and joint capsules of the first to the fifth metatarsophalangeal joints as well as the plantar bases of the corresponding proximal phalanges. The photos were provided with permission from Anthony Herrel (baboon) and Hanno Steinke (human).

(Sinnatamby and Last, 2011; Sarrafian, 2011; Abrahams, 2013; Moore *et al*. 2014; Netter, 2014; Standring and Gray, 2016), but embryonic development studies confirm that it usually consists of two distinct parts (Dylevský, 1991; Kalicharan *et al*. 2017). First, there is a prominent central band that attaches proximally to the medial tubercle of the calcaneus and fans out distally to attach to the subcutaneous tissue and joint capsules of the second through to the fifth metatarsophalangeal joints as well as the plantar bases of the corresponding proximal phalanges (Bojsen-Moller and Flagstad, 1976). Second, a lateral band that attaches proximally to the lateral tubercle of the calcaneus and distally to the joint capsule at the fifth tarsometatarsal joint is also usually present (Stecco *et al*. 2013). A third, medial band has also been described, but it is much thinner than the other two parts (Stecco *et al*. 2013) and is likely to be part of the fascial sheath of the abductor hallucis muscle (Kalicharan *et al*. 2017). Outside of humans, the comparative anatomical organization of the plantar aponeurosis is not widely known in most mammal species, even among non-human primates. This lack of comparative data hinders efforts to understand the functional purpose of the plantar aponeurosis in humans, despite its clinical and evolutionary importance.

Beyond being an anatomically interesting structure, the human plantar aponeurosis has received considerable clinical attention because of plantar fasciitis, a pathological inflammation of the connective tissue that can cause pain and immobility. Currently, about one in 10 Britons experiences plantar fasciitis at some point during his or her life (Garrow *et al*. 2004; Menz *et al*. 2010), and in the USA the condition accounts for an average of one million patient visits per year (Riddle and Schappert, 2004). Aetiologically, plantar fasciitis is recognized as an injury caused by excessive and repetitive loading of the foot's longitudinal arch (Wearing *et al*. 2006). The longitudinal arch is a structure unique to humans that is defined geometrically by the conformation of the tarsal and metatarsal bones and is maintained by soft tissue structures of the foot, including the plantar aponeurosis. Purported risk factors for plantar fasciitis include a tight Achilles tendon, weak intrinsic foot muscles, excessive foot pronation, overuse from too much running, obesity, prolonged standing and physical inactivity (Hill and Cutting, 1989; Kaya, 1996; Rome, 1997; Rome *et al*. 2001; Wearing *et al*. 2006). Despite the contradictory nature of some of these risk factors, all apparently interfere with what is thought to be the fundamental role of the plantar aponeurosis in humans: supporting the longitudinal arch during walking and running (Hicks, 1955).

The anatomical relationship between the plantar aponeurosis and the longitudinal arch has been used to define two biomechanical mechanisms for human foot function. First, in the windlass mechanism proposed by Hicks (1954), the plantar aponeurosis is described as wrapping around the metatarsal heads like a cable wrapping around a drum to insert onto the proximal phalanges of

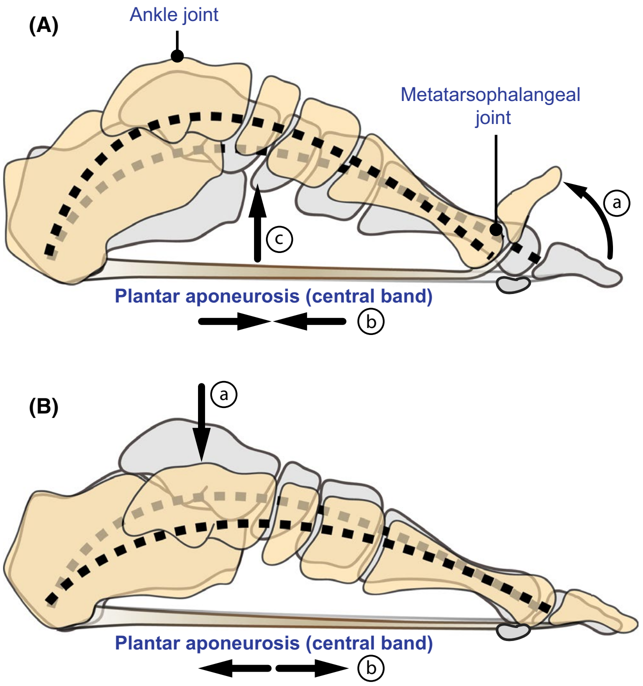


FIGURE 2 Biomechanics of the human foot involving the plantar aponeurosis. (A) In the windlass mechanism, the plantar aponeurosis is described as wrapping around the metatarsal heads like a cable wrapping around a drum to insert onto the proximal phalanges of the toes (a). Dorsiflexion of the toes creates tension in the plantar aponeurosis (b) that exerts a linear force that pulls the calcaneus forward and effectively raises the longitudinal arch (c). This makes the foot a stiff lever for effective power transmission from the ankle joint. (B) When the foot is loaded in stance phase (a), the longitudinal arch is compressed and the foot elongates, causing the plantar aponeurosis to stretch like a rubber band and store elastic energy (b). The plantar aponeurosis then recoils as it is unloaded, returning most of this elastic energy to the foot to aid in push-off and reduce the metabolic energy required for running

the toes (Figure 2A). Thus, dorsiflexion of the toes creates tension in the plantar aponeurosis that tends to pull the calcaneus towards the metatarsal heads. This motion creates an upward force in the longitudinal arch that effectively counters compressive forces from above and stiffens the foot. The windlass mechanism is believed to be activated during push-off in walking and running when the toes are dorsiflexed following heel lift. The plantar aponeurosis has also been shown to behave like an energy-storing spring during bipedal running (Ker *et al.* 1987; McDonald *et al.* 2016; Stearne *et al.* 2016; Wager and Challis, 2016; Figure 2B). When the foot is loaded in stance phase, the longitudinal arch is compressed, and the foot elongates, causing the plantar aponeurosis to stretch like a rubber band and store elastic energy. The plantar aponeurosis then recoils as it is unloaded, returning most of this elastic energy to the foot to aid in push-off and reduce the metabolic energy required for running.

Because of these special functions, it is commonly assumed that the human form of the plantar aponeurosis is an adaptation to bipedalism unique to humans that evolved in concert with the longitudinal arch (e.g. Aiello and Dean, 1990; Griffin *et al.* 2015). However, numerous studies have reported and/or described plantar aponeuroses or similar structures in the feet of other mammals, including some non-human primates such as our closest living relatives, the great apes (Lewis, 1962; Swindler and Wood, 1982; Bennett *et al.* 1989; Vereecke *et al.* 2005; Wareing, 2016). While these reports demonstrate that the plantar aponeurosis is not a uniquely human structure, the degree to which it differs in humans from those of other animals, and particularly other primates, remains unclear. Lovejoy *et al.* (2009) argued that the human plantar aponeurosis more closely resembles those of distantly related cercopithecoid monkey species than those of closely related great apes. They suggested that the ‘thick and dense’ plantar aponeurosis in cercopithecoids is related to adaptations for propulsive behaviours such as above-branch running and leaping, whereas the ‘minimal’ plantar aponeurosis in great apes allows midtarsal laxity for suspensory postures such as pedal grasping and vertical climbing. They argued further that humans inherited a thick plantar aponeurosis from their last common ancestor (LCA) with chimpanzees, and that extant great ape species independently experienced evolutionary reduction in their plantar aponeuroses as adaptations to suspensory locomotion. Based on this argument, one might predict that primates with adaptations for ‘propulsive’ foot postures possess more human-like plantar aponeuroses, whereas those with adaptations for more ‘suspensory’ foot postures do not. However, although all great apes sometimes use their feet in suspensory postures, most locomotion in the African apes (*Pan* and *Gorilla*) is terrestrial (Doran, 1997), which benefits from a relatively stiff foot for enhanced propulsion (Holowka *et al.* 2017). Thus, an alternative hypothesis would be that more terrestrial primates, including the African apes, have human-like plantar aponeurosis organization, whereas more arboreal primates do not.

Lovejoy *et al.* (2009) raised this issue in their description of the remains of *Ardipithecus ramidus*, a 4.4-million-year-old fossil hominin from Ethiopia for which much of the postcranial skeleton has been recovered. Based on these remains, as well as variations in plantar soft tissue anatomy among extant catarrhines, Lovejoy *et al.* (2009) argued that the LCA of humans and chimpanzees had feet more like those of Old World monkeys in some respects than those of great apes and that this hominin would, therefore, have used different locomotor behaviours than great apes. Subsequent studies (e.g. Bates *et al.* 2013; White *et al.* 2015; Aerts *et al.* 2018; Simpson *et al.* 2019) have echoed this sentiment, and hence the notion of a non-great ape-like foot in the earliest hominins has gained some acceptance. However, the characterization of plantar aponeurosis anatomy in primates by Lovejoy *et al.* (2009) is based on a single source (Hartman *et al.*, 1933) that includes only a vague, passing mention of the structure in rhesus macaques (*Macaca mulatta*). Thus, uncertainty about comparative plantar aponeurosis anatomy among primates persists and has major ramifications for our understanding of the evolution of human bipedalism.

To shed light on these issues, this study reviews previous anatomical descriptions and uses phylogenetic comparative methods to reconstruct the evolution of the plantar aponeurosis in primates. We focus on the comprehensive analysis by Loth (1908), who dissected and illustrated 126 primate feet, but whose descriptions have been generally overlooked, probably because they were published in German over 100 years ago. Importantly, Loth recognized the considerable variation among primates in specific aspects of plantar aponeurosis attachments and their relationship to the plantaris muscle, a plantarflexor of the ankle that is often categorized as belonging to the triceps surae muscles (Daseler and Anson, 1943; Langdon, 1990; Vereecke *et al.* 2005; Hanna and Schmitt, 2011). In various mammalian taxa, the plantaris muscle is primitively continuous with the plantar aponeurosis (Lewis, 1962). It usually originates from the femur just above the lateral condyle under cover of the lateral head of the gastrocnemius muscle and gives rise to a tendon which emerges medial to the Achilles tendon. In its primitive mammalian form, its distal portion presents a fibrous cap as it passes smoothly over the posterior end of the calcaneal bone to enter the plantar sole and blend with the plantar aponeurosis (Daseler and Anson, 1943; Lewis, 1962; Figure 3). Based on that primitive insertion, Lovejoy *et al.* (2009) argued that plantaris presence is developmentally related to the presence of other soft tissue structures in the foot, including the plantar aponeurosis.

In light of the uncertainty about comparative plantar aponeurosis anatomy, and its relation to the plantaris muscle, the aim of the present study was to clarify variation and evolution of the plantar aponeurosis among primates and especially in humans by synthesizing previous anatomical descriptions and applying comparative phylogenetic methods to test four evolutionary hypotheses. First, we test the hypothesis that primates with a plantaris muscle also possess a plantar aponeurosis, whereas those that do not will lack both structures. Additionally, we test the hypothesis, following Lovejoy *et al.* (2009), that primates that use their feet in 'propulsive' postures (including frequent running and/or leaping) possess plantar aponeuroses with more human-like configurations, including clear lateral and central bands. Conversely, primates that use their feet mainly in 'suspensory' postures (pedal grasping and vertical climbing) will lack features of the plantar aponeurosis found in humans. We also test an alternative hypothesis, that primates that engage in substantial terrestrial locomotion possess human-like plantar aponeuroses, whereas those that are primarily arboreal do not. Finally, we test the more general hypothesis that humans possess a unique form of the plantar aponeurosis. By this, we refer to the qualitative presence or absence

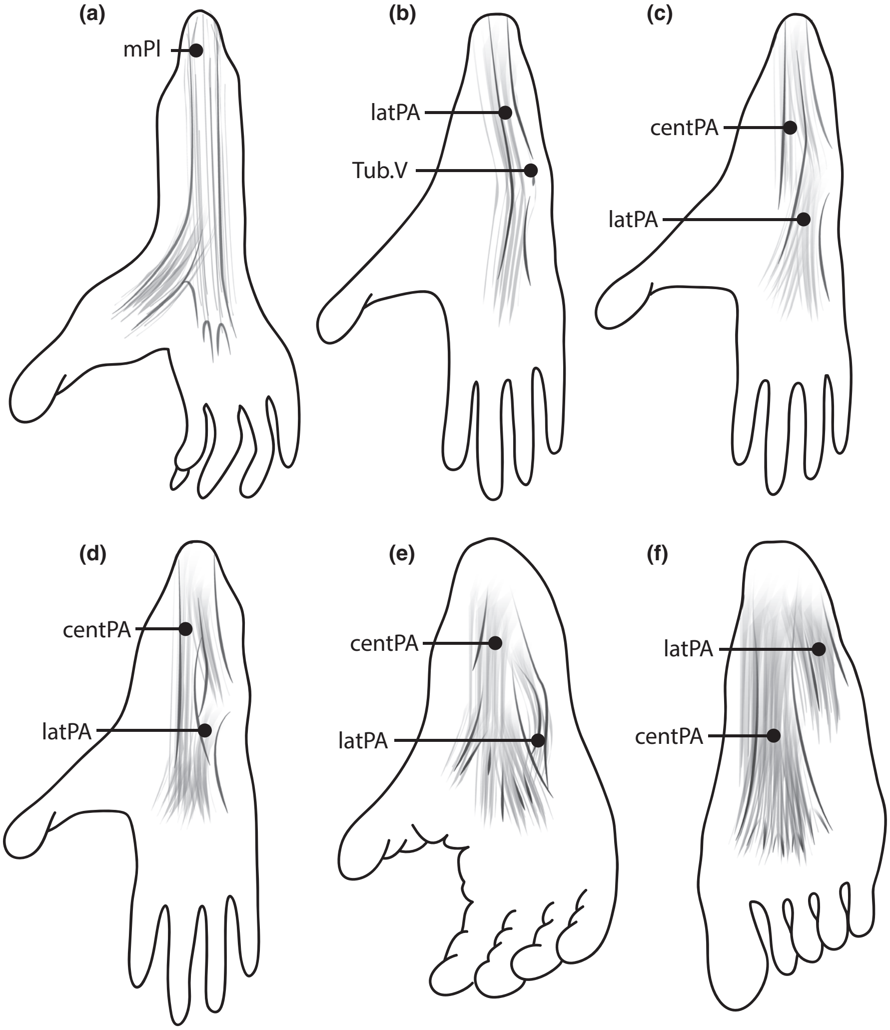


FIGURE 3 Illustrations of the anatomical variation of the plantar aponeurosis among primates. (a) The plantar aponeurosis is primitively continuous with the plantaris muscle (mPl). This form is described, for example, in black-and-white ruffed lemurs (*Varecia variegate*). (b) The plantar aponeurosis forms a lateral band (latPA) that attaches proximally to the lateral tubercle of the calcaneus and distally to the joint capsule at the fifth tarsometatarsal joint Tub.V), as described, for example, in Venezuelan red howlers (*Alouatta seniculus*). (c–f) Various formations of the plantar aponeurosis, with a lateral and a central band (centPA). While the lateral band appears prominent in olive baboons [*Papio anubis* (c)] and guinea baboons [*Papio papio* (d)], the central band is more prominent in chimpanzees [*Pan troglodytes* (e)] and humans [*Homo sapiens* (f)].

in other primates of the lateral and central bands comprising the human plantar aponeurosis, although we lack the data to test whether human plantar aponeuroses are thicker, stiffer or tougher than those of other primates.

2 | METHODS

2.1 | Included primate species

To compare the variation of plantar aponeurosis form among humans and other primates and clarify its relation to the plantaris muscle, we reviewed the existing literature on primate foot descriptions. As noted above, our data are primarily drawn from Loth (1908), but we also reviewed more recent reports of primate foot dissections to expand this dataset and test Loth's descriptions (Murie and Mivart, 1869; Keith, 1894; Straus, 1930; Hartman *et al.* 1933; Raven, 1936; Stilwell, 1957; Swindler and Wood, 1982; Langdon, 1990; Sarmiento, 1994; Aerts, 1998; Thorpe *et al.* 1999; Gebo, 2005; Vereecke *et al.* 2005; Carlson, 2006; Payne *et al.* 2006; Channon *et al.* 2009; Hirasaki and Kumakura, 2010; Diogo *et al.* 2013a; Sefczek and Dunham, 2014; Wareing, 2016; Table 1). We restricted our analysis to studies that contained detailed information in the form of text on the presence or absence of three prominent key characters: (1) a plantaris muscle; (2) a central band of the plantar aponeurosis; and (3) a lateral band of the plantar aponeurosis.

In total, we were able to include 40 primate species and one outgroup species in the analysis (Table 1). Of these, all three characters of five species were described in sufficient detail in other studies to compare with Loth's description: *Gorilla gorilla* (Straus, 1930; Diogo, 2011; Wareing, 2016), *Homo sapiens* (Daseler and Anson, 1943; Stecco *et al.* 2013), *Pan troglodytes* (Diogo, 2013b; Wareing, 2016), *Pongo pygmaeus* (Langdon, 1990; Diogo *et al.* 2013a; Wareing, 2016), and *Chlorocebus sabaeus* (Keith, 1894). Further, single characters of 10 species were described in sufficient detail in other studies to compare with Loth's description (Table 1). In addition, personal communications confirmed the plantar aponeurosis anatomy described by Loth (1908) in *Papio anubis* (G. Berillon, pers. comm.; A. Herrel, pers. comm.), *Papio papio* and *Macaca mulatta* (A. Herrel, pers. comm.).

2.2 | Coding of anatomical plantar aponeurosis descriptions

Descriptions of plantar aponeurosis anatomy were considered for code assignment when they indicated presence or absence of regular, parallel-oriented fibres, and descriptions of plantaris anatomy had to state whether the tendon passed smoothly over the calcaneus or adhered to it (Figure 3). To permit quantitative comparisons and reconstruct ancestral states, all character descriptions were coded into discrete character states. The plantaris muscle was coded into three states: 0 = plantaris muscle absent; 1 = plantaris muscle present, smoothly passing beneath the calcaneal bone to blend with the plantar aponeurosis (primitive insertion); 2 = plantaris muscle present, but with little or no control of tension in the plantar aponeurosis. State 2 covers various descriptions. At one extreme, it includes a plantaris muscle with a tendon that passes beneath the calcaneal bone to blend with the plantar aponeurosis but, in contrast to state 1, transverse ligamentous fibres bind its tendon strongly to the surrounding periosteal tissue. At the other extreme, it includes a plantaris muscle that inserts into the calcaneal bone with no further connection to the plantar aponeurosis. All descriptions have in common that the plantaris muscle cannot produce tension in the plantar aponeurosis. The central and lateral bands of the plantar aponeurosis were coded into two states: 0 = well-defined, parallel-oriented fibres absent; 1 = well-defined, parallel-oriented fibres present. For state 1, these structures were described as discreetly differentiated from other soft tissue structures in the foot, and consisting of fibres predominantly aligned with the long axis of the foot. Unfortunately, this coding scheme did not allow us to consider reported within-species variation or conflicting descriptions of plantaris or plantar aponeurosis anatomy, so in select cases where such inconsistencies existed, we ran the analyses using alternate coding schemes.

2.3 | Classification of primate locomotor behaviour

To test the relationship between plantar aponeurosis form and locomotor behaviour among primates, we used two classificatory schemes to compare alternative hypotheses. First, to test the hypothesis that plantar aponeurosis anatomy is related to suspensory or propulsive foot postures, we categorized species as ‘suspensory’ or ‘propulsive’ based on analyses that describe them using their feet in 'suspensory' postures in Rowe *et al.* (1999) and Fleagle (2013; Table 1; Figure 4). The suspensory category includes regular use of the foot to hang from branches or grasp branches with the hallux in opposition to the other digits during vertical climbing and clambering. Primates who do not use these behaviours were considered to have feet adapted primarily for ‘propulsive’ postures, such as running and leaping. To test the second hypothesis, that plantar aponeurosis anatomy is related to terrestrial locomotion, we categorized species as ‘terrestrial’ if they spent at least 16% of their locomotion time on the ground, and arboreal if they did not, following Gosselin-Ildari (2013). If the necessary data for that categorization were not available, we based our categorizations on descriptions in Fleagle (2013) and Rowe *et al.* (1999).

2.4 | Ancestral state reconstruction

To reconstruct the evolution of plantar aponeurosis form, phylogenetic data of all included primate species were downloaded from the 10k Tree website (Arnold *et al.* 2010). This phylogeny is based on genetic data, with branch lengths obtained from a Bayesian

TABLE 1 Summary of descriptions for the characterization of the plantaris muscle and plantar aponeurosis as well as classification of locomotor behaviour among primates.

		Character state							Plantar aponeurosis general descriptions[c]	Locomotor behaviour[d]	
		Plantaris muscle[a]			Lateral part[b]		Central part[b]				
Species	***n***	**0**	**1**	**2**	**0**	**1**	**0**	**1**		**S-P**	**T-A**
Hominidae											
Gorilla gorilla gorilla[e]	6	Loth (1908), Straus (1930), Diogo, (2011), Wareing (2016), Payne *et al.* (2006)	Loth (1908), Wareing (2016), Straus (1930)				Loth (1908), Wareing (2016), Straus (1930)		Raven (1936), Sarmiento (1994)	Suspensory Fleagle (2013)	Terrestrial
Homo sapiens[e]	50			Loth (1908), Langdon (1990)		Loth (1908), Stecco *et al.* (2013)		Loth (1908), Stecco *et al.* (2013)		Propulsive Fleagle (2013)	Terrestrial
Pan troglodytes troglodytes[e]	11	Loth (1908)[f], Wareing (2016), Diogo (2013b), Thorpe *et al.* (1999), Carlson (2006)		Loth (1908)[f], Wareing (2016), Thorpe *et al.* (1999), Carlson (2006)		Loth (1908), Wareing (2016)		Loth (1908), Wareing (2016)	Raven (1936)	Suspensory Gosselin-Ildari (2013), Fleagle (2013)	Terrestrial
Pan paniscus	4			Wareing (2016), Payne *et al.* (2006), Vereecke *et al.* (2005)		Wareing (2016), Vereecke *et al.* (2005)		Wareing (2016), Vereecke *et al.* (2005)		Suspensory Gosselin-Ildari (2013), Fleagle (2013)	Terrestrial
Pongo pygmaeus[e]	4	Loth (1908)[g], Payne *et al.* (2006)		Loth (1908)[g], Diogo etal.(2013a), Langdon (1990)	Loth (1908), Wareing (2016), Sarmiento (1994)		Loth (1908), Wareing (2016), Sarmiento (1994)			Suspensory Gosselin-Ildari (2013), Fleagle (2013)	Arboreal
Hylobatidae											

(Continues)

TABLE 1 (Continued)

		Character state							Plantar aponeurosis general descriptions[c]	Locomotor behaviour[d]	
		Plantaris muscle[a]			Lateral part[b]		Central part[b]				
Species	*n*	0	1	2	0	1	0	1		S-P	T-A
Hylobates muelleri	3	Loth (1908)			Loth (1908)		Loth (1908)		Hirasaki and Kumakura (2010)	Suspensory Fleagle (2013)	Arboreal
Hylobates lar	2			Vereecke *et al.* (2005), Payne *et al.* (2006)		Vereecke *et al.* (2005)		Vereecke *et al.* (2005)		Suspensory Fleagle (2013)	Arboreal
Symphalangus syndactylus	11	Loth (1908), Langdon (1990), Channon *et al.* (2009)			Loth (1908)		Loth (1908)			Suspensory Fleagle (2013)	Arboreal
Nomascus leucogenys	1			Vereecke *et al.* (2005)		Vereecke *et al.* (2005)		Vereecke *et al.* (2005)		Suspensory Fleagle (2013)	Arboreal
Cercopithecidae											
Cercocebus torquatus atys	3			Loth (1908)		Loth (1908)		Loth (1908)		Propulsive Gosselin-Ildari (2013)	Terrestrial
Chlorocebus pygerythrus	3			Loth (1908)		Loth (1908)		Loth (1908)		Propulsive Gosselin-Ildari (2013)	Terrestrial
Chlorocebus sabaeus[e]	4			Loth (1908), Keith (1894)		Loth (1908), Keith (1894)		Loth (1908), Keith (1894)		Propulsive Gosselin-Ildari (2013)	Terrestrial
Colobus vellerosus	1		Loth (1908)		Loth (1908)		Loth (1908)			Propulsive Gosselin-Ildari (2013)	Terrestrial
Erythrocebus patas	4			Loth (1908)		Loth (1908)		Loth (1908)		Propulsive Gosselin-Ildari (2013)	Terrestrial

(Continues)

TABLE 1 (Continued)

		Character state							Plantar aponeurosis general descriptions[c]	Locomotor behaviour[d]	
		Plantaris muscle[a]			Lateral part[b]		Central part[b]				
Species	*n*	0	1	2	0	1	0	1		S-P	T-A
Macaca arctoides	1			Loth (1908)		Loth (1908)		Loth (1908)		Propulsive Gosselin-Ildari (2013)	Terrestrial
Macaca fascicularis	6			Loth (1908), Langdon (1990), Sefczek and Dunham (2014)		Loth (1908)	Loth (1908)		Sefczek and Dunham (2014)	Propulsive Gosselin-Ildari (2013)	Arboreal
Macaca maura	3			Loth (1908)		Loth (1908)	Loth (1908)			Propulsive Gosselin-Ildari (2013)	Arboreal
Macaca mulatta	4			Loth (1908)		Loth (1908), Stilwell (1957), Herrel (2019)$^{p.c.}$		Loth (1908), Stilwell (1957), Herrel 2019$^{p.c.}$	Hartman *et al.* (1933)	Propulsive Gosselin-Ildari (2013)	Terrestrial
Macaca nemestrina	6			Loth (1908)		Loth (1908)		Loth (1908)		Propulsive Gosselin-Ildari (2013)	Terrestrial
Macaca sinica	4			Loth (1908)		Loth (1908)		Loth (1908)		Propulsive Gosselin-Ildari (2013)	Arboreal
Mandrillus sphinx	4			Loth (1908)		Loth (1908)		Loth (1908)		Propulsive Gosselin-Ildari (2013)	Terrestrial
Papio anubis	5			Loth (1908)		Loth (1908), Herrel (2019)$^{p.c.}$, Berillon (2019)$^{p.c.}$		Loth (1908), Herrel (2019)$^{p.c.}$, Berillon (2019)$^{p.c.}$		Propulsive Gosselin-Ildari (2013)	Terrestrial
Papio cynocephalus	2			Loth (1908)		Loth (1908)		Loth (1908)	Swindler & Wood (1973)	Propulsive Gosselin-Ildari (2013)	Terrestrial

(Continues)

TABLE 1 (Continued)

		Character state									
		Plantaris muscle[a]			Lateral part[b]		Central part[b]		Plantar aponeurosis general descriptions[c]	Locomotor behaviour[d]	
Species	***n***	**0**	**1**	**2**	**0**	**1**	**0**	**1**		**S-P**	**T-A**
Papio hamadryas	5			Loth (1908)		Loth (1908)		Loth (1908)		Propulsive Rowe *et al.* (1999)	Terrestrial
Papio papio	7			Loth (1908)		Loth (1908), Herrel (2019)$^{\text{p.c.}}$		Loth (1908), Herrel (2019)$^{\text{p.c.}}$		Propulsive Fleagle (2013)	Terrestrial
Presbytis melalophos	3		Loth (1908)		Loth (1908)		Loth (1908)			Propulsive Gosselin-Ildari (2013)	Arboreal
Semnopithecus entellus	4		Loth (1908)		Loth (1908)		Loth (1908)			Propulsive Gosselin-Ildari (2013)	Terrestrial
Trachypithecus cristatus	2		Loth (1908)		Loth (1908)		Loth (1908)			Propulsive Gosselin-Ildari (2013)	Arboreal
Cebidae											
Cebus albifrons	2			Loth (1908)	Loth (1908)		Loth (1908)			Propulsive Rowe *et al.* (1999)	Arboreal
Sapajus apella	1			Loth (1908), Langdon (1990)	Loth (1908)		Loth (1908)			Propulsive Gosselin-Ildari (2013)	Arboreal
Cebus capucinus	1			Loth (1908)	Loth (1908)		Loth (1908)			Propulsive Rowe *et al.* (1999)	Arboreal
Callithrix jacchus	7		Loth (1908)	Langdon (1990)	Loth (1908)		Loth (1908)			Propulsive Fleagle (2013)	Arboreal

(Continues)

TABLE 1 (Continued)

		Character state									
		Plantaris muscle[a]			Lateral part[b]		Central part[b]		Plantar aponeurosis general descriptions[c]	Locomotor behaviour[d]	
Species	*n*	0	1	2	0	1	0	1		S-P	T-A
Atelidae											
Alouatta seniculus	1			Loth (1908), Langdon (1990), Sarmiento (1983)		Loth (1908)	Loth (1908)			Suspensory Fleagle (2013)	Arboreal
Ateles paniscus	2	Loth (1908), Langdon (1990)			Loth (1908)		Loth (1908)			Suspensory Fleagle (2013)	Arboreal
Lemuridae											
Eulemur fulvus fulvus	1		Loth (1908), Murie and Mivart (1869)		Loth (1908)		Loth (1908)		Gebo (2005)	Propulsive Rowe *et al.* (1999)	Arboreal
Eulemur macaco macaco	1		Loth (1908), Murie and Mivart (1869)		Loth (1908)		Loth (1908)		Gebo (2005)	Suspensory Rowe *et al.* (1999)	Arboreal
Eulemur mongoz	1		Loth (1908), Murie and Mivart (1869)		Loth (1908)		Loth (1908)		Gebo (2005)	Propulsive Rowe *et al.* (1999)	Arboreal
Varecia variegata variegata	2			Loth (1908)		Loth (1908)	Loth (1908)			Suspensory Rowe *et al.* (1999)	Arboreal

(Continues)

TABLE 1 (Continued)

		Character state									
		Plantaris muscle[a]			Lateral part[b]		Central part[b]		Plantar aponeurosis general descriptions[c]	Locomotor behaviour[d]	
Species	***n***	**0**	**1**	**2**	**0**	**1**	**0**	**1**		**S-P**	**T-A**
Galagidae											
Galago gallarum	2		Loth (1908)		Loth (1908)		Loth (1908)		Aerts (1998)	Propulsive Fleagle (2013)	Arboreal
Lorisidae											
Loris tardigradus	5			Loth (1908)	Loth (1908)		Loth (1908)			Suspensory Fleagle (2013)	Arboreal

In total, 40 primate species of eight primate families were included into the analysis.

[a] The plantaris muscle was coded into three states: plantaris muscle absent (0), plantaris muscle present, smoothly passing beneath the calcaneal bone to blend with the plantar aponeurosis (1) and plantaris muscle present, being bound to or inserting into the calcaneal bone with little to no further connection to the plantar aponeurosis (2).

[b] The lateral and central band of the plantar aponeurosis were coded into two states: well-defined, parallel-oriented fibres absent (0) and present (1).

[c] Character state reported, but details as provided by Loth (1908) are not given.

[d] Locomotor behaviour was characterized by the two categories ‘suspensory’ or ‘propulsive’ (S-P) and ‘terrestrial’ or ‘arboreal’.

[e] Complete confirmation (all characters) of descriptions provided by Loth (1908).

[f] Presence of the plantaris muscle in chimpanzee is quite variable: 54.3% present (Loth, 1908).

[g] Presence of the plantaris muscle in orangutan is quite variable: 3.7% present (Loth, 1908).

[p.c.], personal communication.

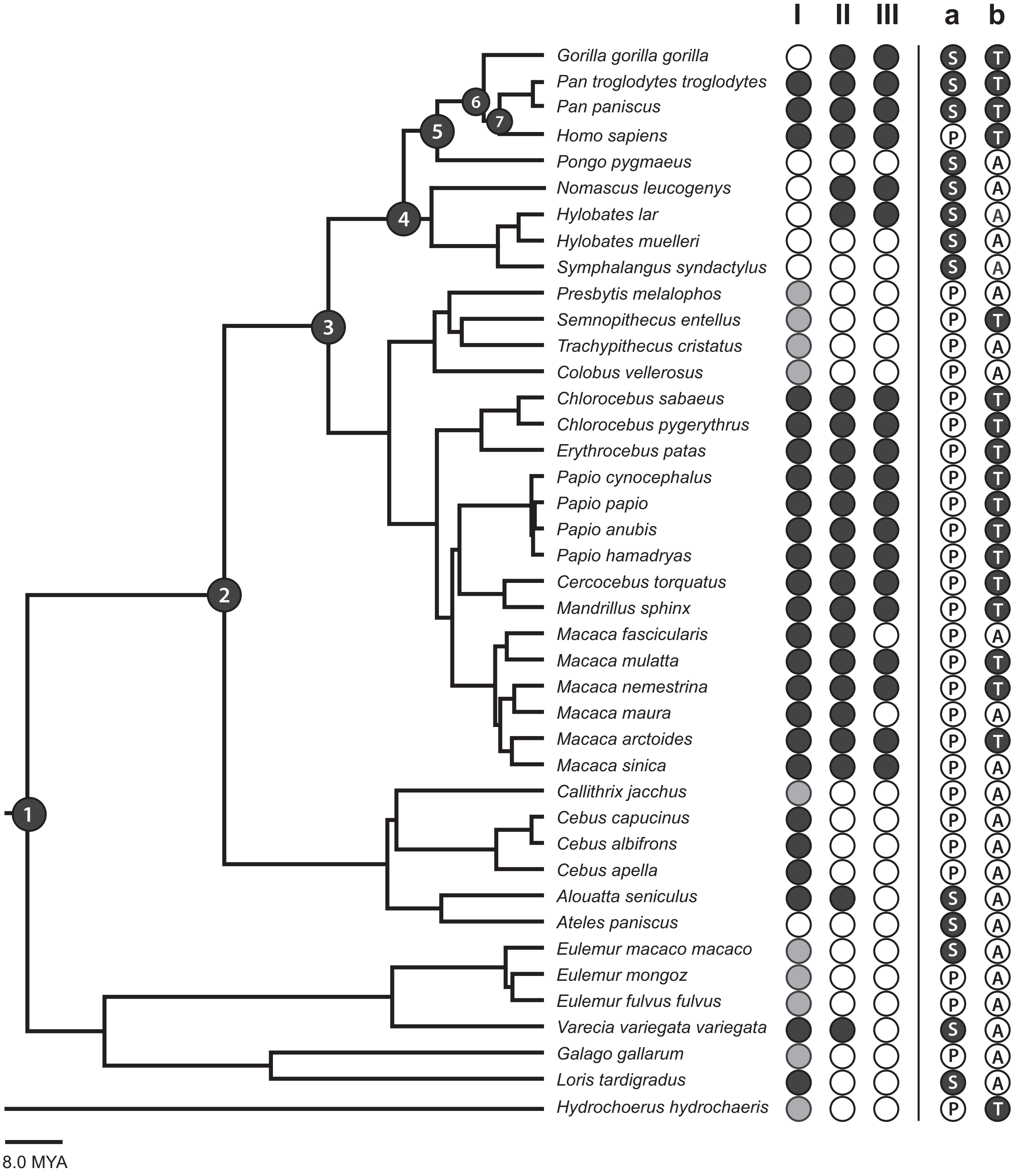


FIGURE 4 Documentation of the variation of plantar aponeurosis form among humans and other primates and classification of primate locomotor behaviour. The absence (white dot) or presence (black or grey dot) of three key characters was documented: plantaris muscle (I) as well as lateral (II) and central (III) band of a plantar aponeurosis. Two categories were used to classify primates' locomotor behaviour. The first category indicates primates that have feet primarily adapted for suspensory (black dot with S), vs. propulsive (white dot with P). The second category indicates primates that spend significant amounts of time in terrestrial (black dot with T) vs. arboreal locomotion (white dot with A). To understand the evolutionary pattern that preceded humans the plantar aponeurosis form was analysed at each of the following major nodes (black numbered dots), representing last common ancestors of: all primates (1), all haplorhines (2), all catarrhines (3), all apes (4), great apes (5), African apes (6), and *Pan*/*Homo* (7).

phylogenetic analysis (for more details see Arnold *et al.* 2010). The phylogeny was then imported into Mesquite reconstruction software (Mesquite version 3.40, www.mesquiteproject.org; Maddison and Maddison, 2006, 2018) to build a character matrix defining the state of the three documented key characters for each species (Figure 5). The capybara (*Hydrochoerus hydrochaeris*), the largest living rodent, which is comparable to primates in height and weight, was added to the character matrix as an outgroup species (García-Esponda and Candela, 2016). To find the ancestral states for each of the three key characters, we used a likelihood reconstruction. For each ancestral node, this reconstruction finds the state assignment that maximizes the probability of arriving at the observed states in the terminal taxa. For our likelihood calculation, we applied the Mk1 model ('Markov k-state 1 parameter model'). The single parameter in this model is the rate of change with any change, either a character gain or lost (from state 0 to 1 or state 1 to 0 for the central band, for example), being equally probable. Details on the statistics underlying Mk1 reconstructions are provided elsewhere (Pagel, 1994; Schluter *et al.* 1997). To reconstruct the evolutionary pattern that preceded humans, we analysed the plantar aponeurosis form at the nodes representing LCAs of all primates, all haplorhines, all catarrhines, all apes, great apes, African apes, and *Pan*/*Homo*. To test the two hypotheses about the relationship between plantar aponeurosis anatomy and locomotor behaviour, we mapped the above described behavioural categorizations onto the phylogeny and compared them to the distribution of coded anatomical features among the extant primate taxa.

3 | RESULTS

3.1 | Plantaris muscle

As summarized in Figure 4, the plantaris muscle was absent in five species. In nine species the plantaris muscle was present in a primitive state, smoothly passing beneath the calcaneal bone to blend with the plantar aponeurosis. It was present but bound to or inserted into the calcaneal bone with limited or no further connection to the plantar aponeurosis in 26 species. *Pan troglodytes* was unusual in having an inconsistent presence of the plantaris muscle. In three of the nine described specimens (Loth, 1908; Wareing, 2016) it was absent or only unilaterally present (Diogo, 2013b; Wareing, 2016).

The presence or absence of the plantaris muscle was also analysed in relation to the presence or absence of a plantar aponeurosis (Figure 4). In nine species the plantaris was primitively continuous with the plantar aponeurosis. In 22 species the plantaris muscle and the plantar aponeurosis were both present, but not smoothly connected without plantaris adhesion or attachment to the calcaneus. In four species the plantaris muscle was present and inserted onto the calcaneus but the plantar aponeurosis was absent, and in one species the plantar aponeurosis was present while the plantaris muscle was absent. Both anatomical features were absent in four species.

The presence/absence of the plantaris muscle was further analysed with regards to the species locomotor behaviour. For the first hypothesis (propulsive vs. suspensory), it was absent in most suspensory species (state 0:5 of 13 species). In contrast, all propulsive species possess either a plantaris that is bound to or inserts into the calcaneus, with limited connection to the plantar aponeurosis (state 2, 19 of 27 species) or a primitive plantaris morphology with a tendon that smoothly blends into the plantar aponeurosis (state 1, eight of 27 species). For the second hypothesis, most arboreal species (52%) either lacked a plantaris muscle (state 0; three of 23 species) or possessed the primitive plantaris morphology (state 1; nine of 23 species). Conversely, almost all terrestrial species (88%) possessed plantaris muscles that are bound to or insert into the calcaneus (state 2). The only exceptions were *Gorilla* (state 0) and *Semnopithecus* (state 1).

The likelihood reconstruction (Figure 5a) for the plantaris muscle unambiguously predicts that the LCA of all primates most likely had a plantaris that blended with the plantar aponeurosis (state 1:94.0%). The likelihood of this anatomy dropped to 31.2% in the LCA of haplorhines, with the presence of a plantaris that was bound to or inserted into the calcaneal bone being more likely (56.9%). The plantaris was most likely to insert into the calcaneus (state 2) for the catarrhine LCA (75.3%), the LCA of all apes (88.3%), great apes (79.7%), and African apes (83.1%). Finally, the LCA of *Pan* and *Homo* probably had a plantaris that inserted into the calcaneus (state 2:98.0%). All probabilities described above use a state 2 coding for *Pan troglodytes*, but, as described earlier, the plantaris is not always present in *Pan troglodytes* specimens. Therefore, we performed ancestral state reconstructions coding the plantaris as absent in *Pan*. The results for most nodes showed no major change, and the LCA reconstruction of *Pan* and *Homo* decreased to a likelihood that the plantaris was present and inserted into the calcaneus of 86.0%.

3.2 | Plantar aponeurosis: lateral band

As shown in Figure 4, a lateral band of the plantar aponeurosis with well-defined, parallel fibres was absent in 17 species and present in 23 species. In the first locomotor behaviour hypothesis, the lateral band was present in 54% suspensory species and 60% of propulsive species. In the second locomotor behaviour hypothesis, the lateral band was present in all terrestrial species except *Semnopithecus*, and absent in most (70%) arboreal species.

Based on the ancestral state reconstructions (Figure 5b), the lateral band was most likely to have been absent in the LCA of all primates (97.0%), and haplorhines (65.3%). In contrast, the lateral band was likely to have been present in the LCA of catarrhines (64.4%), apes (87.6%), great apes (85.9%), African apes (99.0%) and the LCA of *Pan* and *Homo* (99.8%).

3.3 | Plantar aponeurosis: central band

A central band of the plantar aponeurosis with well-defined, parallel fibres was absent in 20 species and present in 20 species (Figure 4). There was some ambiguity in reports of this feature

FIGURE 5 Ancestral state reconstruction to find the ancestral states for plantaris muscle (a), lateral band (b) and central band (c) of the planar aponeurosis. The absence (white dot) or presence (black or grey dot) of three key characters was documented for each taxon. For each ancestral node (pie chart) the reconstruction finds the state assignment that maximizes the probability of arriving at the observed states in the terminal taxa. Black numbered dots represent last common ancestors of: all primates (1), all haplorhines (2), all catarrhines (3), all apes (4), great apes (5), African apes (6), and *Pan/Homo* (7).

among two species. In the case of orangutans (*P. pygmaeus*), we found detailed descriptions from Loth (1908) and Wareing (2016). While Wareing (2016) characterizes orangutans as possessing a plantar aponeurosis, she describes the structure similarly to Loth (1908): a plantar sheet of fibrous tissue appears to be present, but it is very thin, mainly oblique or meshed, and with no discerning division into a lateral and central band. We therefore coded the plantar aponeurosis—the lateral and central band—as absent (state 0). In the case of chimpanzees (*Pan troglodytes*), the relative thickness of the central band varies between individuals, according to Loth (1908) and Wareing (2016), but both describe it as possessing clearly defined, parallel fibres regardless. Loth suggests that thicker plantar aponeuroses are related to the presence of a plantaris muscle, although his argument is based on the single specimen with a plantaris that he dissected.

In the first locomotor behaviour hypothesis, a central band was present in only 38% of suspensory species and was present in only 51% of propulsive species. In the second locomotor behaviour hypothesis, the central band was present in all terrestrial species except *Semnopithecus entellus* and was absent in all arboreal species except *Nomascus leucogenys*, *Hylobates lar* and *Macaca sinica*.

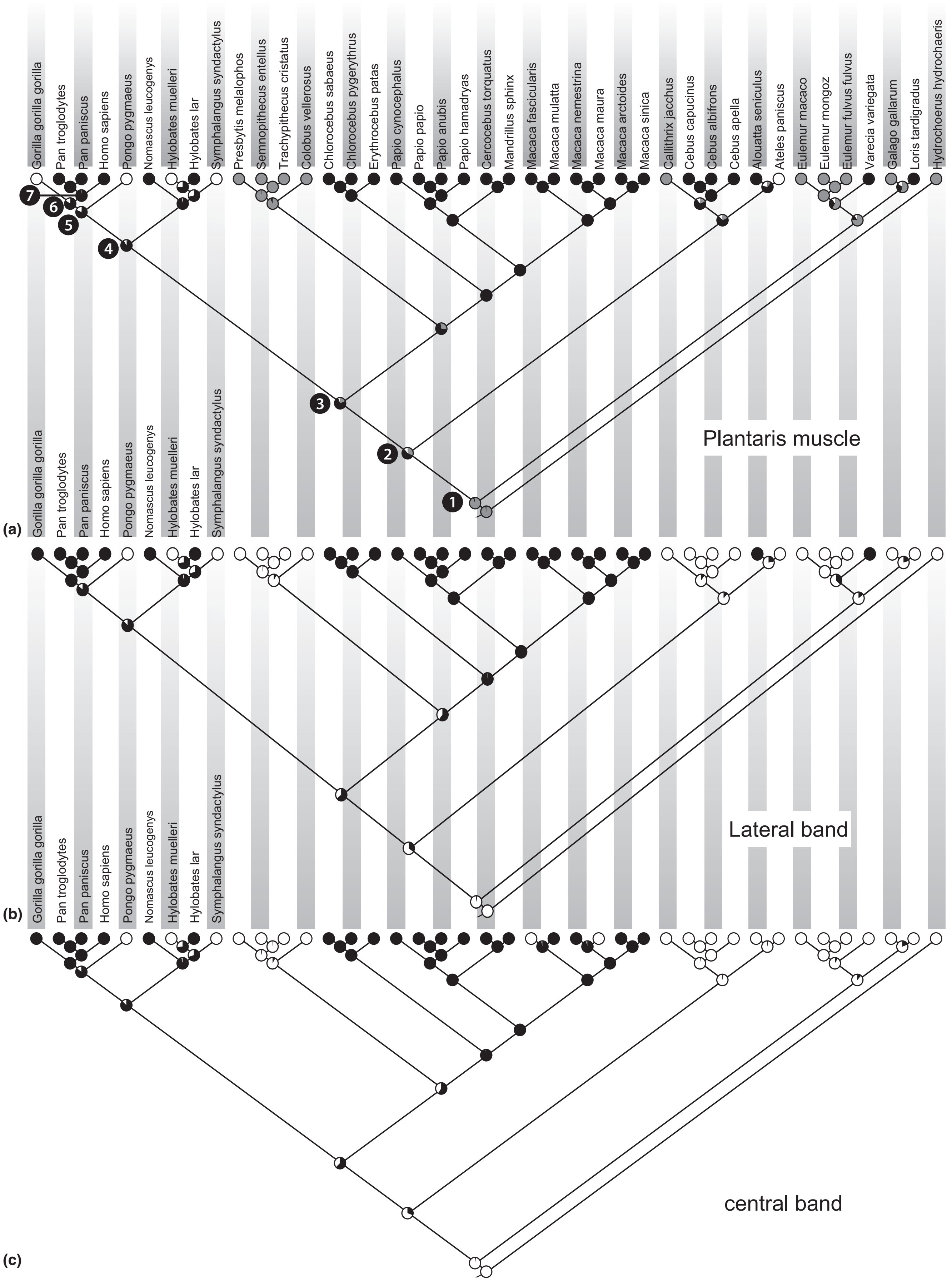
Based on the ancestral state reconstructions (Figure 5c), the central band was most likely to have been absent in the LCA of all primates (97.5%), and haplorhines (69.2%). In contrast, the central band was likely to have been present in the LCA of catarrhines (62.7%), apes (87.1%), great apes (85.5%), African apes (99.0%) and the LCA of *Pan* and *Homo* (99.8%).

4 | DISCUSSION

This study reviewed published anatomical descriptions of the plantar aponeurosis among extant primates and used phylogenetic comparative methods to test evolutionary hypotheses. First, we tested the general hypothesis that humans possess a unique form of the plantar aponeurosis. Our results do not support this hypothesis as we found that 19 species had plantar aponeuroses with human-like anatomy. Further, we tested two evolutionary hypotheses relating plantar aponeurosis anatomy to locomotor behaviour: first, that plantar aponeurosis anatomy reflects use of the foot in suspensory vs. propulsive locomotor postures (Lovejoy *et al.* 2009), or alternatively, that it reflects the proportion of time species engage in terrestrial locomotion. The latter hypothesis was strongly supported by our results, while the former was not. Finally, we tested the hypothesis that the plantaris muscle and plantar aponeurosis are integrated during development, and thus primates that possess a plantaris should also possess a plantar aponeurosis (Lovejoy *et al.* 2009). This hypothesis was rejected.

The findings of our study challenge the assumption that humans possess a unique form of the plantar aponeurosis that is primarily tied to its fundamental role in supporting the longitudinal arch during walking and running (Griffin *et al.* 2015). The human plantar aponeurosis is characterized as a broad sheet of highly fibrous tissue that can be separated into two distinct bands: a prominent central band and a smaller lateral band (Dylevský, 1991; Kalicharan *et al.* 2017). Surprisingly, a generally similar configuration of the plantar aponeurosis can be found in many primate taxa, including cercopithecines and our closest living relatives, the African apes. These findings are independently verified in multiple studies that report anatomical descriptions of the plantar aponeurosis in great apes, vervets, macaques and baboons (Keith, 1894; Loth, 1908; Straus, 1930; Swindler and Wood, 1982; Wareing, 2016; G. Berillon, pers. comm., A. Herrel, pers. comm.). Based on our ancestral state reconstruction, a human-like plantar aponeurosis configuration was most likely to have been present in the LCA of apes, great apes and African apes, as well as in the LCA of *Pan* and *Homo*. It is therefore most probable that humans inherited the present form of the plantar aponeurosis from our LCA with chimpanzees. Alternatively, the present form could have evolved independently in extant hominids. While this possibility is considerably less parsimonious, there are other examples of homoplasy regarding the plantar aponeurosis within the animal kingdom. For instance, the plantar aponeurosis of the Tasmanian Devil (*Sarcophilus harrisi*), another predominantly terrestrial mammal (Owen and Pemberton, 2011), resembles that of primates in presenting clear lateral and central bands (Lewis, 1962).

The presence of a human-like plantar aponeurosis configuration among non-human primates and other mammals that lack longitudinal arches leads us to question inferences that these structures are evolutionarily related. Although it is unlikely that the appearance of the plantar aponeurosis corresponded with evolution of a longitudinal arch, humans may have re-purposed the central band for arch-related functions, namely enhancing the stiffness of the foot under loading. Limited data about the mechanical behaviour of the plantar aponeurosis in humans and African apes indicate that the stiffness of the central band in humans (Wright and Rennels, 1964; Guo *et al.* 2018) is about twice as high as in gorillas and chimpanzees (Wareing, 2016). This difference could be related to an assumed thickening of the plantar aponeurosis in humans (e.g. Susman, 1983), although we currently lack comparative quantitative data to verify this. Thus, future research should be directed at collecting more quantitative data on plantar aponeurosis material properties in a wide range of primates. We hypothesize that humans have evolved thicker, stiffer plantar aponeuroses relative to those of other primates to help facilitate the


Gorilla gorilla gorilla
Pan troglodytes
Pan paniscus
Homo sapiens
Pongo pygmaeus
Nomascus leucogenys
Hylobates muelleri
Hylobates lar
Symphalangus syndactylus
Presbytis melalophos
Semnopithecus entellus
Trachypithecus cristatus
Colobus vellerosus
Chlorocebus sabaeus
Chlorocebus pygerythrus
Erythrocebus patas
Papio cynocephalus
Papio papio
Papio anubis
Papio hamadryas
Cercocebus torquatus
Mandrillus sphinx
Macaca fascicularis
Macaca mulatta
Macaca nemestrina
Macaca maura
Macaca arctoides
Macaca sinica
Callithrix jacchus
Cebus capucinus
Cebus albifrons
Cebus apella
Alouatta seniculus
Ateles paniscus
Eulemur macaco
Eulemur mongoz
Eulemur fulvus fulvus
Varecia variegata
Galago gallarum
Loris tardigradus
Hydrochoerus hydrochaeris
7
6
5
4
3
2
1
Plantaris muscle
(a)
Lateral band
(b)
central band
(c)

special adaptive functions of the human longitudinal arch (Holowka and Lieberman, 2018). Specifically, these changes may have enabled the human plantar aponeurosis to act as a more effective truss under loading (Lapidus, 1963), or helped facilitate the function of the windlass mechanism during push-off in walking (Hicks, 1954; Caravaggi *et al.* 2009). However, it is likely that the plantar aponeuroses of other primates can effectively stiffen the midfoot to some extent, even in the absence of a longitudinal arch (Bennett *et al.* 1989; Wareing, 2016).

Another function of the plantar aponeurosis that might have been re-purposed in humans with the evolution of a longitudinal arch is its spring-like behaviour (Ker *et al.* 1987). During running, the longitudinal arch lengthens and lowers in early stance, which allows mechanical energy to be stored in the stretched plantar aponeurosis and consequently reduces the energetic cost of running through elastic recoil (Ker *et al.* 1987; McDonald *et al.* 2016; Stearne *et al.* 2016). Interestingly, Bennett *et al.* (1989) demonstrated a similar energy-saving spring function of the plantar aponeurosis in cadaveric feet from pig-tailed macaques (*Macaca nemestrina*) and vervet monkeys (*Chlorocebus aethiops*), which lack arches but possess human-like plantar aponeuroses (Loth, 1908). Unlike the energy-storing mechanism in humans, the feet of these monkeys bend to form a convex plantar surface when subjected to high loads, stretching the plantar aponeurosis and storing strain energy, which can be returned in the subsequent elastic recoil (Bennett *et al.* 1989). These findings indicate that the energy-storing capacity of the plantar aponeurosis can be used by primates without longitudinal arches (Bennett *et al.* 1989). However, the estimated energy storage in human feet (17%, Ker *et al.* 1987) is greater than in monkey feet (12%, Bennett *et al.* 1989), potentially indicating an adaptation for improved endurance running performance in humans (Bramble and Lieberman, 2004).

Interestingly, Vereecke and Aerts (2008) discuss the possibility of a monkey-like energy-saving mechanism in the plantar aponeuroses and digital flexor tendons of gibbons during bipedalism, although they do not provide estimates of energy savings. In this regard, our analysis revealed potential variation among hylobatids in plantar aponeurosis anatomy. While Loth (1908) described two hylobatid species, *Symphalangus syndactylus* and *Hylobates muelleri*, as lacking a plantar aponeurosis with well-defined, parallel-oriented fibres, Vereecke *et al.* (2005) described the presence of a plantar aponeurosis consisting of a lateral and central band in two hylobatid species (*Hylobates lar* and *Nomascus leucogenys*). Future research should investigate the possibility of plantar aponeurosis variation among hylobatids, and its implications for the relationship between plantar aponeurosis anatomy and locomotor behaviour among primates.

Our findings do not support the argument put forward by Lovejoy *et al.* (2009) that plantar aponeurosis anatomy reflects use of the foot in propulsive vs. suspensory locomotor postures, as highlighted by differences in plantar aponeurosis anatomy among extant non-human great apes. All these species use their feet to grasp arboreal supports during suspensory behaviours (such as vertical climbing), yet the African apes have human-like plantar aponeurosis organization while orangutans (and some hylobatids) do not. This difference is probably related to substrate use: whereas orangutans are primarily arboreal (Fleagle, 2013), a significant component of African ape locomotion occurs on the ground (Doran, 1993, 1997). In another revealing comparison, spider monkeys (*Ateles paniscus*) also lack a plantar aponeurosis (Loth, 1908; Langdon, 1990). Spider monkeys and other atelines have been argued to converge on non-human apes in many respects related to their use of suspensory locomotor behaviours (Fleagle *et al.* 1981), but like the orangutans, they are mainly restricted to arboreal travel (Fleagle, 2013). Thus, the presence of a well-defined plantar aponeurosis among the African apes appears to be closely related to frequent use of terrestrial substrates during locomotion.

The terrestrial underpinnings of a well-defined plantar aponeurosis are highlighted by the nearly universal presence of both central and lateral bands of the plantar aponeurosis among primate species with a significant terrestrial component in their locomotor behaviour. This includes most of the cercopithecine taxa in our sample, which were mostly categorized as terrestrial. Of the three arboreal cercopithecines included in this study, two lacked a central band, further supporting the notion that plantar aponeurosis anatomy is strongly related to substrate use. Based on ancestral state reconstructions, it is likely that central and lateral bands of the plantar aponeurosis evolved in the earliest cercopithecines, and were maintained in all taxa that continued to engage in significant terrestrial locomotion. Bennett *et al.* (1989) found that the plantar aponeurosis confers considerable stiffness in the feet of two of the monkey species (*Chlorocebus* sp. and *Macaca nemestrina*) coded as terrestrial in our analysis. Thus, it is likely that this added stiffness is advantageous during locomotion on the ground, but that it is unimportant to locomotion on arboreal substrates.

The absence of a well-defined plantar aponeurosis in orangutans, potentially gibbons, colobines, and platyrrhines, suggests that a human-like organization of the plantar aponeurosis evolved convergently in cercopithecines and African apes, likely as an adaptation to terrestrial locomotion. This scenario supports the argument that the LCA of humans and chimpanzees frequently engaged in terrestrial quadrupedalism (Gebo, 1992; Richmond *et al.* 2001; Wrangham and Pilbeam, 2002; Pilbeam and Lieberman, 2017). Some researchers favour the alternative, less parsimonious inference that chimpanzees and gorillas could have evolved human-like plantar aponeurosis anatomy along with other adaptations for terrestrial knuckle-walking convergently (Kivell and Schmitt, 2009), while humans evolved their plantar aponeurosis anatomy independently for bipedal locomotion. Regardless of these different evolutionary scenarios, our results do not support the argument that the LCA of humans and chimpanzees had a foot that was poorly adapted for suspensory locomotion (Lovejoy *et al.* 2009). Even if this species possessed human-like plantar aponeurosis anatomy, this should not have had a major effect on its suspensory locomotor capabilities. Similarly, our results run counter to the argument that the feet of African apes are adapted for extreme pliability to the detriment of their use as stiff levers during terrestrial locomotion (Lovejoy *et al.* 2009). Unfortunately, we were not able to assess the relative thickness or mechanical properties of the plantar aponeurosis across species but, based on previous descriptions, it is probable that the plantar aponeuroses of the African apes cannot confer the same stiffness to the foot as in humans (Susman, 1983; Wareing, 2016). Nevertheless, the retention or independent evolution of lateral and central bands in humans and African apes conforms to the notion that this structure was selected to provide some degree of foot stiffness (Bennett *et al.* 1989), and thus likely contributes to the versatility that makes the feet of chimpanzees and other African apes well adapted for both terrestrial and arboreal locomotor behaviours (Holowka *et al.* 2017). The ability to stiffen the foot might also be attributed to a change in the developmental relationship between the plantaris muscle and the plantar aponeurosis.

Our phylogenetic reconstruction shows that the LCA of all primates most likely had a plantaris muscle that was primitively continuous with the plantar aponeurosis. This primitive feature is shared by many mammals (Lewis, 1962; Anapol and Barry, 1996; Perry, 2004; McClearn, 22005; Warburton *et al.* 2012; García-Esponda and Candela, 2016), including most of the strepsirrhines in our study. However, among most extant catarrhines, the tendon of the plantaris is strongly bound to the periosteal tissue of the calcaneus, and therefore the plantaris loses its ability to directly increase tension in the plantar aponeurosis. This transition may reflect a developmental de-coupling of these structures, as our data indicate that within species the plantaris and plantar aponeurosis are not necessarily both present or absent. For example, in gorillas and in some chimpanzees and humans, a plantar aponeurosis is present while the plantaris is missing (Loth, 1908; Langdon, 1990; Diogo, 2011; 2013b; Wareing, 2016). In contrast, capuchin monkeys (*Cebus capucinus*, *Cebus albifrons and Cebus apella*) and the red slender loris (*Loris tardigradus*) have a plantaris that inserts into the calcaneal bone, but a plantar aponeurosis is absent (Loth, 1908). Another example that may reflect the gradual de-coupling of the plantaris muscle and the plantar aponeurosis is the anatomical condition in chimpanzees. Both Loth (1908) and Wareing (2016) observed well-defined fibre bundles forming lateral and central bands, but they varied somewhat in qualitative thickness between individuals. Loth (1908) relates this variation to the presence of a plantaris muscle, based on his observation that the plantar aponeurosis was thickest in the one specimen he dissected with a plantaris muscle present. Although this argument is based on only one specimen and therefore requires further investigation, it supports a primitive developmental link between these structures. Conversely, his observations also highlight the developmental de-coupling, as we observe the presence of a central and lateral band independent of the presence or absence of a plantaris muscle. This condition contrasts with cercopithecines, where the central and lateral band are continuous with a regularly present plantaris muscle, although the muscle's tendon adheres strongly to the calcaneus (Keith, 1894; Loth, 1908). Therefore, the plantar aponeurosis and its relation to the plantaris muscle in African apes most closely resembles the condition described in humans (Loth, 1908). In humans, the plantar aponeurosis is always present while the plantaris is missing in about 10% of humans (Daseler and Anson, 1943; Langdon, 1990). We therefore reject the hypothesis that the plantaris has a strong developmental relationship to the plantar aponeurosis in all primates (Lovejoy *et al.* 2009). In its most primitive form, the plantar aponeurosis is essentially a continuation of the plantaris (Loth, 1908). Selection may have favoured the separation and de-coupling of these structures in some primates to allow the plantar aponeurosis to stiffen the midfoot passively without the necessity of activating the plantaris, which is an ankle plantarflexor. This may have been advantageous in more terrestrial primates that use plantigrade or semi-plantigrade foot postures (Schmitt and Larson, 1995), where greater foot stiffness could enhance propulsive power production during locomotion.

It is crucial to bear in mind that the functional implications of this study are restricted to anatomical descriptions of the plantar aponeurosis. Unfortunately, comparative data of the thickness and mechanical properties are missing on a large scale. While the human pattern of the plantar aponeurosis may not be unique among primates, it may well be derived in terms of thickness and material properties, highlighting the need to develop a full picture of the anatomical and mechanical variability of the plantar aponeurosis among primates and its relation to locomotor function. A further limitation of this study was that we had to rely on a few published descriptions of plantar aponeurosis anatomy in determining our classification scheme. Because a clear, thorough description including specific information about the central and lateral bands was necessary to code species for this study, we relied primarily on Loth (1908). While we were able to independently verify the descriptions in Loth for several of the species in this study, there were partly conflicting descriptions for plantar aponeurosis anatomy in orangutans (*P. pygmaeus*) in Wareing (2016). We coded the plantar aponeurosis as absent in this species because, without the description of consistent longitudinal organization or clearly defined central and lateral bands, the plantar aponeurosis cannot be clearly distinguished from the epimysium overlying the flexor digitorum brevis. Similarly, we coded the plantar aponeurosis as absent in Müeller's gibbon (*Hylobates muelleri*) and siamangs (*Symphalangus syndactylus*). Nevertheless, if these species do possess clearly defined plantar aponeuroses, several of our major findings would have to be adjusted. First, our argument that plantar aponeurosis presence is related to terrestrial locomotion would be weakened, but so would the argument that suspensory locomotion selected against a plantar aponeurosis (Lovejoy *et al.* 2009). Second, this finding would bolster the idea that hominins inherited a functional plantar aponeurosis from their LCA with chimpanzees, and re-purposed this structure for bipedal locomotion. Further study of plantar aponeurosis anatomy in these and other primate species could help provide further clarity to these possibilities.

Finally, higher sample sizes and independent observations could shed more light on within-species variation in plantaris and plantar aponeurosis anatomy. The variation described for species such as chimpanzees and orangutans (Loth, 1908; Wareing, 2016) is fascinating and begs further investigation. While our study used a simplistic coding scheme to categorize these structures, this approach may mask real species-level variation that could be functionally relevant, as well as indicative of the directionality of selective forces. Besides inheritance and selection, variation is an essential ingredient of adaptive evolution. Some of the conflicting anatomical descriptions we encountered in our study may be attributable to heritable variation within species. Since our ancestral state reconstruction did not allow the consideration of within-species variation, more complex evolutionary models that take such variation into account (e.g. Goolsby, 2017) could provide greater insight into the evolution of plantar aponeurosis and plantaris anatomy. Perhaps more importantly, future investigation of these structures using continuous morphological measurements will greatly enhance our understanding of their adaptive significance with regard to primate locomotion, including human bipedalism.

In conclusion, the present review of plantar aponeurosis anatomy and variation in non-human primates reveals that the overall anatomical configuration of this structure is not unique to humans. Furthermore, our ancestral state reconstructions suggest that humans probably inherited this configuration from their LCA with chimpanzees and that a similar anatomical configuration evolved independently in different primate clades as an adaptation to terrestrial locomotion. The presence of a well-developed plantar aponeurosis with lateral and central bands in the African apes suggests that this structure is not prohibitive to suspensory locomotion and that these species possess versatile feet adapted for both terrestrial and arboreal locomotion. Whether independently acquired or not, this plantar aponeurosis anatomy would have been advantageous in enhancing foot stiffness for bipedal locomotion in the earliest hominins, prior to the evolution of a longitudinal arch. However, it is likely that hominins evolved thicker and stiffer plantar aponeuroses alongside the arch to enable a windlass mechanism and elastic energy storage for bipedal walking and running. In the future, more work is needed to determine the adaptive functions as well as within-species variation of the plantar aponeurosis and plantaris muscle in non-human primates and other mammals. Nevertheless, our findings shed light on the evolutionary origins of the human plantar aponeurosis and the specialized function of this structure in the human foot.

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CONFLICTS OF INTEREST

None declared.

DATA AVAILABILITY STATEMENT

All data generated or analysed during this study are included in this published article.

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