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INVITED REVIEW ARTICLE

StW 573 **Australopithecus prometheus:** *its significance for an australopith bauplan*

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Short title: StW 573 and the australopith bauplan

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13, 741 words

Abstract

300 Words

The StW 573 skeleton of *Australopithecus prometheus* from Sterkfontein Member 2 is some 93% complete and thus by far the most complete member of that genus yet found. Firmly dated at 3.67 Ma, it is one of the earliest specimens of its genus. A crucial aspect of interpretation of locomotor behaviour from fossil remains is an understanding of the palaeoenvironment in which the individual lived and the manner in which it would have used it. While the value of this ecomorphological approach is largely accepted, it has not been widely used as a stable framework on which to build evolutionary biomechanical interpretations. Here, we collate the available evidence on StW 573's anatomy in order to reconstruct what might have been this individual's realised and potential niche. We explore the concept of a common *Australopithecus bauplan* by comparing the morphology and ecological context of StW 573 to that of paenocontemporaneous australopiths including *Au. anamensis* and KSD-VP-1/1 *Au. afarensis*. Each was probably substantially arboreal and woodland-dwelling, relying substantially on arboreal resources. We use an hypothesis-driven approach, tested by: virtual experiments, in the case of extinct species; biomechanical analyses of the locomotor behaviour of living great ape species; and analogical experiments with human subjects. From these, we conclude that the habitual locomotor mode of all australopiths was upright bipedalism, whether on the ground or on branches. Some later australopiths such as *Au. sediba* undoubtedly became more terrestrial, allowing sacrifice of arboreal stability in favour of manual dexterity. Indeed, modern humans retain arboreal climbing skills but have further sacrificed arboreal effectiveness for enhanced ability to sustain striding terrestrial bipedalism over much greater distances. We compare StW573's locomotor adaptations to those of living great apes and protohominins, and agree with those earlier observers who suggest that the common panin-hominin Last Common Ancestor was postcranially more like *Gorilla* than *Pan*.

1.1 Introduction:

The fossil record is nearly always a partial record of the dental and bony morphology of individuals, and occasionally an imprint of their activities that may leave a preservable trace (known as ichnofossils, and including footprints). To reconstruct complex behaviour of single individuals on the basis of bony morphology, let alone species-typical behaviour, is extremely challenging. Moreover, physical interaction with the outside world is dominated by the hands and feet These alone make up half the bones in the whole body, while contribituing very little to its total mass or volume. It follows that hand and foot bones have very complex interactions with each other, and, via tendons, receive very complex external forces which constitute the step-by-step, grasp-by-grasp estimates made by the brain's motor control system of required action, based on external feedback from the

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extremities themselves, and the vestibulocochlear, visual and auditory senses. They must be, to a greater or lesser extent, randomized best-guesses based on motor learning. This mechanism is widely known as 'degeneracy' (S. Latash et al. [2002], Whitaker and Bender (2010), Seifert et al., 2016), where many different structures can serve one function, and which operates down to the level of the gene. Degeneracy in systems such as human hands and feet, interacts with ecological dynamics to foster evolvability and robusticity (Whitaker and Bender, 2010; Seifert et al., 2016). By extension, this applies to the great apes, which, evolving in the mid to late Miocene in a period of intense ecological change, have thus been able to respond to climate instability by plasticity, which is particularly evidenced at the muscle fibre level (Neufuss et al., 2014). However, this 'degeneracy' renders the hands and feet, perhaps counter-intuitively, relatively uninformative on locomotor adaptation.

Prior to discovery of StW 573, our most complete evidence of locomotor adaptation of early hominins was the one-third complete AL-288-1 skeleton (*Australopithecus afarensis*). Otherwise, our best evidence came from partial skeletons covering the spectrum of lesser completeness: lacking gnathocranium (such as Sts 14 and StW 431); substantially partial *Australopithecus* skeletons (such as KSD-VP-1/1 ~3.6 Ma., Haile-Selassie et al., 2010); juvenile material such as Dikika ~3.3 Ma (Alemseged et al., 2005); or the much younger and now seemingly highly derived Malapa *Australopithecus sediba* partial skeletons, MH-1 and MH-2, ~1.977 Ma (Berger et al., 2010, and see Churchill et al*.,* 2013).

Over two decades, an over 90% complete skeleton has been excavated from Member 2 at Sterkfontein, South Africa. StW 573, dated firmly at ~3.67 Ma (Granger et al., [2015]; see Bruxelles et al. [2019] for stratigraphy and Clarke [2019a] for taphonomy). This skeleton is the first discovered for which limb lengths can be directly measured, not estimated, and is roughly contemporaneous with the Laetoli footprint trail, so will be highly informative on gait of early australopiths such as the trail makers (reviewed in eg. Crompton and McClymont, 2021). This specimen, StW 573 is an adult female *Australopithecus prometheus* (Clarke, 2019a), and includes partially deformed cranium, full dentition, hands and a partial left foot, almost complete upper and lower limbs, clavicles, scapulae, pelvis, ribs and vertebrae. MicroCT has revealed details on a well preserved endocast and internal ear (Beaudet et al., 2019a,b). Together these provide unique opportunities to advance our understanding of *Australopithecus* skeletal morphology and function. This skeleton was found in an underground karst cave immediately below the habitat in which it lived. Combining this fact with with associated palaeoenvironmental data means that we are uniquely positioned to analyse the ecomorphological niche of this single individual of this species. This may in turn inform us on the overall *bauplan* of australopiths. The foot bones of StW 573, have been reported elsewhere (Clarke and Tobias, 1995; Deloison 2003, 2004), with full descriptions of the hands to be presented by Jashashvili, et al. (under review). Given this, and their degeneracy, hand and foot function is not extensively discussed herein.

Our interpretations of niche should ideally be made within an ecological formulation that is hypothesis- and experiment-driven. We find this in Wainwright's (1991) 'Ecomorphology: Experimental Functional Anatomy for Ecological Problems'. It updates Bock and von Wahlert (1965) in its focus on *performance,* and specifically *performance of the individual.* This approach is vital because it is the reproductive success of the individual that drives adaptation at population and species levels. Wainwright's experimental approach, which he applied for example to cichlid fishes, obviously cannot be applied directly to extinct animals, but with appropriate circumspection, analogy to experiments on individuals of closely related species, and increasingly now,

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biomechanical simulation using skeletal model of the individual under study, do provide a way forward to analyse their performance capabilities.

In Wainwright's (1991) formulation, ecomorphology may be examined at three, partially overlapping levels. Level *(a)* is the ***realised niche*** – that behaviour adopted by an individual or population in a given environment at a given time. With reference to locomotor behaviour, this would include knuckle-walking quadrupedalism in open country by *Pan troglodytes*. Realised niche of extinct species is most obviously reflected in the skeletal elements of individuals, which, reflect lifetime responses to imposed load. Level *(b)* is the ***potential niche*** - that which could be adopted given a change in environmental circumstances, either *in situ* through climate change, or, by movement of the individual to another region. Thus, crudely put, a human might work in flat fields one year, but engage in arboriculture the next: upright terrestrial walking might then be replaced substantially by climbing. Level *(c)* is the ***fundamental niche***. This is the equivalent of potential niche, applied to the performance capabilities of a higher taxon, assessed, for example, by differential statistical characteristics of postcrania compared to other taxa. It is perhaps yet more a theoretical concept than *(a)* and *(b)*, but not dissimilar to a *bauplan.*

Herein, we attempt to use the ecomorphology framework to partially reconstruct the locomotor ecomorphology of StW 573 and elucidate her locomotor capabilities *(1)*. A full interpretation of her performance capabilities must
await publication of current virtual tendon travel simulations and alternative muscle arrangements. We thus present information provided by analogy to experiments on humans and published modelling work. Following Wainwright's (1991) formulation we *(2)* review the published paleoenvironmental data for Sterkfontein Members 2 and 4 (Bruxelles et al. 2019; Clarke, 2019a) that informs on the likely floral and faunal environment and possible dietary habits. *(3)* We present the StW 573 skeleton in a qualitative discussion of long bone joint shape, which is not fully addressed in Heaton et al. (2019) and present limited metrics *(3.1)*, in comparison with data from the literature, to indicate to what extent StW573 can be regarded as a 'typical' australopith. By extension these may help to inform on a likely fundamental niche of *Australopithecus. (4)* We review the functional morphology of the those features *(4.1)* the pectoral girdle (Carlson et al., 2021) and *(4.2)* long limb bones (Heaton et al., 2019) that we consider to be most informative of realised niche. We use metrics from these, from the australopith literature and limited original metrics to plot StW 573's position within the australopith range of variation. *(5)* We discuss this evidence for a common australopith bauplan and conceivable fundamental niche and present our argument for plasticity *(5.1)* at intraspecific and higher taxonomic levels and discuss the palaeoecology of StW 573 in relation to *Au. anamensis* and Laetoli *Au. afarensis (5.2). (6)* We review the literature on extinct protohominin locomotion, including in particular *Orrorin* and *Ardipithecus ramidus*, and relate this to our hand-assisted bipedality hypothesis for the arboreal origins of bipedality. *(7)* We review relevant biomechanical performance data for extant great apes and experimentation on humans and finally *(8)* We review literature for computer simulation experiments that may inform StW 573's likely performance capabilities and those of other contemporaneous and later australopiths.

We emphasise that until the dentition is available for dietary analysis, and virtual models of StW573 are completed (Crompton et al., [*in prep.*]), we must rely primarily on available palaeonvironmental data to reconstruct her likely locomotor ecomorphology. This includes palaeoenvironmental data from Member 4, as we (see Clarke and Kuman, 2019) regard StW431, coming from Member 4, as most likely a male *Australopithecus prometheus*.

1.2. Background:
From the 1960s and the discovery of the close genetic relationship of *Pan* and *Homo*, the dominant paradigm for the origins of human bipedalism was based on arguments for a terrestrial, 'knuckle-

walking' ancestry (see especially Washburn, 1967; and reviewed in Richmond et al., 2001). However, Senut (1982) noted that no hominin olecranon fossa bears the strong lateral crest seen in all quadrupedal monkeys, *Pan, Gorilla* and *Pongo* (but curiously not apparent in *Hylobates,* perhaps reflecting the requirements of specialized armswinging locomotion). Susman (1983) noted that the metacarpophalangeal joint aspect of the metacarpals of AL 288-, lacks the transverse dorsal ridges and expanded dorsal articular surfaces associated with knuckle-walking in living African apes. Clarke (1998, 2002), later pointed out that the hand morphology and the limb ratios of StW 573 bear no anatomical evidence that it was a knuckle-walker. Nevertheless, Richmond et al. (2001) returned to a knuckle-walking model, although Dainton and Macho (1999) and Dainton (2001) were already questioning whether 'knuckle-walking' was ontogenetically and behaviourally a unitary phenomenon in the African apes. Kivell and Schmitt (2009) provided clear evidence, that it was not.

In fact, the idea of an arboreal origin for bipedality is far older. (Lamarck (1809, page 170) says:

"As a matter of fact, if some race of quadrumanous animals, especially one of the most perfect of them, were to lose, by force of circumstances or some other cause, the habit of climbing trees and grasping the branches with its feet in the same way as with its hands, in order to hold on to them; and if the individuals of this race were forced for a series of generations to use their feet only for walking, and to give up using their hands like feet ; there is no doubt, according to the observations detailed in the preceding chapter, that these quadrumanous animals would at length be transformed into bimanous, and that the thumbs on their feet would cease to be separated from the other digits, when they only used their feet for walking"

Darwin (1859) also endorsed an arboreal origin for bipedality, while in 1934, Keith postulated that in the human ancestor legs would have played a "more important part than the arms in orthograde life in the trees" (Keith, 1934, p. 15). He concludes: "It was on the trees, not on the ground, that man came by the initial stages of his posture and carriage" (Keith, 1934, p. 15). By 1946, Hooton had dismissed the 'knuckle-walking' element of African ape locomotion as most likely a secondary consequence of high upper body mass associated with arboreal climbing.

More recently, Senut in particular has championed an arboreal origin of human erect bipedality, based on morphological data. In 1980 and 1981, she noted that stabilisation of the elbow for knuckle-walking was absent in australopiths, while the supracondylar crest of the humerus was strongly marked, suggesting an important element of climbing in their locomotor repertoire. She therefore rejected *Pan* as a good model for the locomotion of the last common ancestor with humans. Following discovery of *Orrorin tugenensis*, Senut's group (Pickford et al. 2005; Galik et al. 2004) argued that in addition to internal features, the proximal femur bears features indicating habitual hip extension, such as the groove for *obturator externus* on the back of the femoral neck (Day, 1969; Lovejoy et al., 2002).Together with evidence from the distal thumb phalanx for precision gripping (Gommery and Senut 2005) these features indicated that this species was fully bipedal and yet partially arboreal.

These morphological observations suggesting arboreal bipedality were supported, and extended by detailed field observations of orang-utans (*Pongo pygmaeus borneanus*) (Thorpe et al., 2007) which identified a large component of hand-assisted arboreal bipedality. Orang-utans are too distantly related to humans to be very informative on the origins of human bipedality. Crompton et al. (2010) noted that is clearly frequently enough used by lowland Western gorillas to have been recorded for wildlife programmes, and quantification of this and other locomotion is currently underway in Gabon under the supervision of Thorpe and Sellers, although there do not seem to have been

reports of it in *Pan*. Hence they proposed hand-assisted arboreal bipedality as the likely origin of human bipedalism.

There is no universal agreement as to whether the separation of humans and their kin from other great apes and their kin should be recognised at Family level (Hominidae), Subfamily (Homininae), Tribe level (Hominini) or Sub-Tribe level (Hominina). The first author (RHC) does not accept a contrast between 'apes' and 'humans' as endorsed by Andrews (2020): considering that humans are typical African apes, and despite the general view that humans are most closely related to chimpanzees, this does not imply that the postcrania of the common human/chimpanzee ancestor resembled that of modern chimpanzees, as we shall argue below. The first author adopts separation at the level of the Tribe. Thus, for the purposes of this paper, chimpanzees fall into tribe Panini and gorillas into tribe Gorillini; then both, together with tribe Hominini, fall into subfamily Homininae. Orang-utans fall into subfamily Ponginae, and all of these subfamilies fall into family Hominidae.

2. Palaeoenvironment

Reconstruction of the ecomorphology of StW 573 is greatly facilitated by the rare circumstances of its burial and fossilization. We know that StW 573 died from a fall into a vertical shaft directly below its native habitat in the Blaaubank river valley (Clarke, 2019a). The 'death trap' nature of the deposition of the Sterkfontein Member 2 fauna, of which StW 573 is part, may skew palaeoenvironmental interpretations because primates and felids are over-represented and time-averaging probably occurred (Pickering et al., 2004). Nonetheless, the environment around the cave is cautiously reconstructed as rocky hills covered in brush and scrub, and potentially also a valley bottom with riverine forest, swamp and standing water (Pickering et al., 2004). Although living representatives of all or nearly all of the fossil species found in Member 2 show a strong terrestrial component to their locomotor repertoires, they were probably comfortable exploiting mixed habitats (Elton, 2001), which suggests that the environment was not completely open. The presence of substantial open areas has also been noted at other southern and eastern African Pliocene sites dated to 3-4 Ma, in contrast to some earlier sites that appear more closed (Pickering et al., 2004). Although there is little evidence that Member 2 was dominated by dense woodland or forest (ibid.), the presence of colobines certainly suggests that the environment was not completely open, as these monkeys are ecologically dependent on trees (Elton et al., 2016). Member 2 contains *Makapania* among the rare bovid fossils. *Makapania* is a takin-like bovid, and takins today are woodland-dwelling. Bruxelles et al. (2019) note that the Member 2 talus sediments contain evidence of well-developed lateritic soils on the surface, which indicates a stable landscape around the cave entrance, and thus established vegetation in the immediate locality, probably including large trees. The younger Member 4 breccia also contains *Makapania,* as well as large cercopithecoids (Pickering et al., 2004), and there are numerous fossil fragments of forest vines that would have required large trees (Bamford, 1999). The species of vine identified (*Dichapetalum mombuttense*) is today known exclusively from central and western African tropical forest. In Member 2, following a dry period when StW 573 was mummified, there was a change to much wetter conditions that resulted in the formation of flowstones and calcified breccias (Clarke, 2019a). Whether such conditions were episodic or longer-term is unknown, but there is good evidence for moister environments in both Members 2 and 4.

3. The StW 573 skeleton

The above provides information on the palaeoenvironment which StW 573 inhabited, and from which she fell to her death in a solution fissure. We can now attempt, as far as currently possible, to interpret the the skeletal anatomy of this specimen Here, we integrate the functional anatomy of

the StW 573 skeleton as interpreted from the primary regional anatomical descriptions published in a special online issue of *Journal of Human Evolution* guest-edited by Stratford and Crompton (10.1016/j.jhevol.2021.103008). In addition to information therein provided on taphonomy by Clarke (2019a) and stratigraphy by Bruxelles et al. (2019), a detailed inventory of the StW 573 partial skeleton was presented by Clarke (2019a), and a full description of the skull by Clarke and Kuman (2019). The endocast and inner ear are reported by Beaudet et al. (2019a,b), and the atlas was described in in a paper published elsewhere by Beaudet et al. (2020). The long limb bones have been reported in Heaton et al. (2019) and the pectoral girdle in Carlson et al. (2021). Jashashvili et al. (under review) will report on hand and wrist morphology. The foot bones were reported earlier, by Clarke and Tobias (1995) and Deloison (2004) and have been extensively discussed more recently by Jashashvili et al. (2020) and Zipfel and Wunderlich (2020).

In summary, StW 573 has: a complete cranium and mandible; many vertebrae and ribs; a partial pelvis with ischiopubic ramus; femora (broken but with overlapping morphology allowing confident length reconstruction); one intact and one slightly damaged but measurable tibia; partial left and right fibulae that overlap sufficiently to be sure of length and morphology; a partial left foot (consisting of calcaneum, talus, navicular, all three cuneiforms, and proximal halves of first and second metatarsals) and a partial lateral cuneiform from the right foot (see Deloison, 2003, 2004); two scapulae (the right being articulated with the humerus); both claviculae; both humeri (one partially crushed); both radii and ulnae, the left side near-intact and the right side crushed by rock pressure but in articulation with the humerus; and finally one partial and one virtually complete hand (the latter missing only one distal phalanx). The complete skeleton and, in more detail, the limb bones of StW 573 are presented in Fig. 1. The pelvis, crushed and deformed on the left side, requires virtual reconstruction before its traits and functional morphology can be fully interpreted with confidence.

Fig. 1 about here

Metrics: data from these sources and the literature are the primary source of the Tables and Figures in this contribution, but we (Elton) made supplementary ts made for the right clavicle of StW 573. Given the delicate state of the StW 573 fossils, these were taken with digital calipers on a high-quality first-generation epoxy resin cast prepared by Clarke. We estimated stature for StW 573 (see below and Fig. 2) using maximum femoral length (335 mm [Heaton et al., 2019]) and the classical and reduced major axis (RMA) equations provided in Hens et al. (2000) based on small-stature human ('pygmy') populations. We estimated body mass of StW 573 (see also below and Fig. 2) using the femoral head superoinferior (SI) and distal tibia mediolateral (ML) equations given in Grabowski et al. (2015). Femoral head SI width is only an estimate for StW 573, but it was used to calculate body mass, because it was the best performing univariate estimator for other early hominins (Grabowski et al., 2015). Given that size is itself biologically and evolutionarily meaningful (Dobzhansky, 1973), particularly in the biomechanics of bipedality (Wang and Crompton, 2003), linear dimensions are generally plotted with no adjustment for size, but we include some plots of ratios and indices.

Fig.2 about here
3.1 Affinities, proportions, stature, body mass, age and sex
Based on its craniodental morphology, StW 573 is referred to *Australopithecus prometheus,* discussed at length in Clarke and Kuman (2019). It is elderly, as judged by cranial sutural fusion, and female, as judged from sciatic notch shape. The taxon *Australopithecus prometheus,* named originally for the parieto-occipital fossil MLD 1, has been shown by Clarke (2019b) to be valid and therefore not a *nomen nudum*, as incorrectly proposed by Berger and Hawkes (2019). StW 431,

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found in Sterkfontein's Member 4 (Toussaint et al., 2003), is considered by Clarke and Kuman, (2019) to be a male of the same species.

Although (Clarke, 1988, 1994, 2013) and Clarke and Kuman (2019) presented cranial and dental data to suggest the existence of a second *Australopithecus* species in South Africa, there has been ongoing general reticence to accept this interpretation. With reference to specimens other than StW 573, studies on multiple skeletal elements have already pointed to different postcranial morphs at Sterkfontein (Deloison, 2003, 2004; Partridge et al., 2003; Zipfel and Berger, 2009; De Silva et al., 2013; Clarke, 2013; Su and Carlson, 2017; Fornai et al., 2018). Most recently, Georgiou et al. (2020) have confirmed the existence of different functional morphs at Sterkfontein based on femoral head trabecular architecture and related them to frequency of climbing behaviour.

Moreover, Clarke and Kuman (2019) argue for taxonomic distinction of the morph represented by the partial skeleton of StW 431 and the near-complete StW 573 skeleton, attributed to *Au. prometheus*, versus the form represented by the partial skeleton Sts 14. Macho et al. (2020) reject the association of StW 573 and StW 431. They argue, for example, that parts of the StW 573 iliac margin and iliac spines appear to them to resemble those areas in the chimpanzee in being thinner, thus differing with StW 431 and Sts 14. Although some researchers have noted that it is challenging to interpret the variability present in *Australopithecus* material from the Plio-Pleistocene of southern Africa (e.g., DeSilva et al., 2013), there is no indication that the different craniodental morphs at Sterkfontein are explained wholly by sexual dimorphism (Clarke, 1994, 2013; Lockwood and Tobias, 2002; Clarke and Kuman, 2019). Ecologically and taphonomically, the presence of one hominin species at a given location does not rule out the occurrence of a second, just as a number of adaptively similar large-bodied monkeys co-occur, some probably sympatrically, at southern African Plio-Pleistocene sites (Elton, 2007, 2012). Sympatry is not uncommon in large-bodied extant primates, including gorillas and chimpanzees. Even if hominin species could not live sympatrically, time-averaging in the Sterkfontein deposits could also conceal regional dispersals and local extinctions of multiple hominin species, a phenomenon that has been argued to play a major role in the apparent speciosity of large-bodied carnivorans in the Witwatersrand craton(O'Regan and Reynolds, 2009). Given the distinguishing features of the StW 573 skull (Clarke and Kuman, 2019), it is thus highly likely that different species are sampled at Sterkfontein within the postcrania as well.

As reported by Heaton et al. (2019), StW 573 is the first *Australopithecus* for which intermembral limb indices can be stated with confidence. These are outside and above the human range as reported by Schultz (1937), but below the range that he reports for *Gorilla* at 110-125, and for *Pongo* at 135-150.9. Heaton et al. (2019) report an intermembral index of 85.5, compared to mean values of 115.8 in *Gorilla gorilla*, 105.6 in *Pan troglodytes* and 103.4 in *Pan paniscus*, versus 67.9 for Khoisan, and 68.4 for other *Homo sapiens*. The classical and RMA equations yielded stature estimates for StW 573 of 123 cm and 125 cm respectively. Body mass of StW 573 estimated using the femoral head superoinferior (SI) and tibial distal end mediolateral (ML) equations yielded values of 33.2 kg and 27.4 kg respectively. Although stature estimation for Plio-Pleistocene hominins has limitations, not least because of body proportion differences between them and extant comparative taxa (see Hens et al. [2000] for a review), Fig. 2 shows that StW 573 falls within the estimated range of other early hominins. The same is true for body mass, the accurate reconstruction of which is also challenging (see Ruff and Niskanen [2018] for a recent overview). It has been stated that there is high variability in stature and body mass in Pliocene and Early Pleistocene hominins (Will et al., 2017), something that is also evident from the Laetoli footprints (Leakey, 1987; Masao et al., 2016). However, the extreme rarity of associated cranial and postcranial remains makes estimation of stature and body mass for known *Australopithecus* species hazardous. Small sample sizes and uncertain taxonomic attributions make both intra- and interspecific comparisons challenging, and the evidence for taxonomically structured variation in body size (stature and mass) among

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Australopithecus species is equivocal (Will et al., 2017). The estimated body mass of StW 573 is 27-32 kg, depending on means of calculation. It does little to illuminate taxonomic patterns, falling as it does (Fig. 2) within the (overlapping) ranges of *Au. afarensis* (AL 288-1 being particularly small at 26 kg, the largest being some 42 kg) and South African *Australopithecus* as a whole at ~23-34 kg.

Lipping of the margins of the lumbar vertebral bodies (see Fig. 3) and very heavy toothwear (Clarke and Kuman, 2019), as well as the fusion of cranial sutures noted above (unpublished data) indicate that StW 573 was an old adult.

Fig. 3 about here

As noted above, StW 573 is the only *Australopithecus* in Member 2 of the Silberberg Grotto, (Pickering et al., 2004; Clarke, 2019a). Perspective is, however, provided by analysis of other South African early hominin fossils. Sts 5, from Sterkfontein Member 4, was diagnosed by Broom et al. (1950) as a mature female, which has now been supported by Villmoare et al. (2013), and hominin adults in the older age classes comprise ~17% of mandibular and maxillary specimens at Drimolen and 23% at Swartkrans (Riga et al., 2018). Thus, even given taphonomic differences between South African cave sites, it is not unusual for older adults to be sampled. Attribution of StW 573 to sex is challenging, given the paucity of early hominin pelves and differences in pelvic form between *Australopithecus* and modern humans (reviewed in Haeusler and Schmid [1995] and Claxton et al. [2016]). However, based on the method described in Simpson et al. (2008), the greater sciatic notch morphology (see Fig. 3) is distinctively female (more details below). Craniodentally, the canines and incisors are small compared to StW 252 (a young *Au. prometheus* specimen) and the base of the cranium is narrow (Clarke and Kuman, 2019). Endocranial volume is small compared to other, albeit later, *Australopithecus* (Beaudet et al., 2019a). These features, alongside general postcranial dimensions (see Heaton et al., 2019), also suggest that StW 573 is female.

4. Functional morphology of the fore- and hindlimb

4.1: Functional morphology of the forelimb:
Pectoral girdle: The scapular blade of StW 573 has been subject to reconstruction prior to full interpretation (Carlson et al., 2021). It features a large supraspinous fossa, indicating power in early stage abduction of the glenohumeral joint, and strong medial buttressing, both recalling the scapulae of nonhuman great apes. However, the complete right clavicle (see Fig. 4), described and figured more fully in Carlson et al. (2021), is broadly humanlike in form, with a strong sigmoid shape in superior view, although the superior and inferior curvatures resemble those of *Pan* and *Gorilla* more than those of *Homo* when viewed from a parasagittal perspective.

Fig. 4 about here

The claviculohumeral ratio (100 x clavicle length / maximum humerus length) of StW 573 is 49, within the range of orang-utans (Larson, 2007), modern humans, early modern *Homo* and Neandertals, but above the ratios of the Dmanisi sample at ~44 – 47, KNM-WT 15000 at ~41 (see Churchill et al. [2013] for comment on preservation) and, MH2 at 40 (Churchill et al., 2013; Roach and Richmond, 2015). If shoulder position can be inferred from claviculohumeral ratio (see Roach and Richmond, 2015, for a critique), the relatively long StW 573 clavicle suggests that it was not anteriorly positioned (as has been argued for KNM-WT 15000 [Larson, 2007]), and instead it may be positioned more laterally like that of modern humans, but somewhat more elevated distally than in the latter. Here, the more *Pan*- and *Gorilla*-like superior and inferior curvatures need to be borne in mind. However, craniad elevation of the distal clavicle is nothing like that reported for

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Au. sediba, the clavicular form of which has been regarded as indicating a shoulder position considerably higher than that seen in modern humans (Churchill et al., 2013; and see Melillo et al. 2019). Rein et al., (2017) interpret this degree of elevation as indicating a secondarily derived suspensory locomotion. However, this need not be the case: it might indicate a ground based adaptation for feeding on bushes, as proposed (for the origins of bipedalism) by Hunt (1994). A somewhat distally elevated posture of the clavicle in StW 573 is indicated by a rather more cranially oriented glenoid fossa than seen in humans. The supraspinous fossa is large and non-human ape-like, and the axillary side of the scapula is reinforced by a stout ventral bar, as in living non-human apes. The middle third of the StW 573 clavicle is craniocaudally flat with no evidence of inferomedial inflection. Its dimensions are summarized and compared to other relevant taxa in Table 1.

Table 1 about here

In the scapula, the StW 573 spine was most similar to that of *P. pygmaeus* in axillary border/spine angle, and slightly more similar to *P. pygmaeus* than to *Gorilla gorilla* in medial border/spine angle (Carlson et al., 2021). An 18-variable canonical variates analysis of the scapula by Carlson et al. (2021) plots StW 573 on the edge of the *G. gorilla* cluster (but near a *Pan troglodytes* individual at the extreme of the *Pan* cluster), and further from all other extant taxa. StW 573, DIK-1-1 (R), DIK-1-1 (L), and MH 2 fell close to the means of CV 1 and CV 2, and outside clusters of extant taxa, except that StW 573 fell within the variation of extant gorillas. In an 11 variable CVA, StW 573 and MH 2 fell near one another in the area of overlap between *G. gorilla* and *P. pygmaeus.* As in the 18-variable CVA, StW 573 again fell closer to *G. gorilla* than other taxa except for MH. Thus, overall, Carlson et al. (2021) found that StW 573 probably agreed with non-human African apes in scapular form to a greater degree than other *Australopithecus* scapulae (KSD-VP-1/1, MH 2, and both DIK-1-1 scapulae). They conclude that a high glenohumeral joint, a dorsally-positioned scapula and relatively more nonhuman ape-like cranial orientation of the glenoid fossa may have offered selected advantages in below branch arboreal positional behaviours. However, when synchronous lower limb action is taken into consideration, these would support hand-assisted bipedalism (cf. Thorpe et al., 2007).

Humerus: The left proximal humerus of StW 573 is distorted although the head remains largely complete (Heaton et al., 2019). Anteroposterior humeral head diameter is estimated as 31 mm, within the range of other early hominins, including *Au. afarensis,* but slightly smaller than some other South African *Australopithecus* (Fig. 5).

Fig. 5 about here

Humeral torsion, at 120˚, falls within the range of orang-utans (Larson, 2007) and other early hominins, being lower than that of AL 288-1 and Sts 7, but slightly higher than MH 2 (Heaton et al., 2019), and considerably higher than ARA-VP-7/2 (112˚; Lovejoy et al., 2009b). Modern humans, chimpanzees and gorillas have similar degrees of humeral torsion (Larson, 2015), unlikely to be accounted for by functional convergence, with high torsion in chimpanzees and gorillas likely to be related to their (distinct forms of) 'knuckle-walking' quadrupedalism and high torsion in humans related to their frequent manipulation and throwing. Since orang-utans do not knuckle-walk or engage in throwing, and manipulation is no commoner than in gorillas and chimpanzees, it follows that the moderate torsion in orang-utans and early hominins may reflect the primitive condition (and see Rose, 1989, Moya-Sola and Kohler, 1996, and pers. comms. from D. Pilbeam to RHC). At 290 mm (Heaton et al., 2019), the left humerus of StW 573 has a longer maximum length than the very few other early hominin specimens available for comparison (Fig. 6).

Its humerofemoral (86.6) and intermembral (85.5) indices, however, are quite similar to those of AL 288-1 (84.3 and 85.6 respectively) and ARA-VP-6/500 (89.1 and 89-91 respectively) (Heaton et al., 2019). StW 573 falls within the range for humeral head diameter of *Au. afarensis* but below that of other South African *Australopithecus* for which data is available (see Fig. 6). Humeral length of StW 573 is greater than the other available specimens, which sample the smaller body mass range of many early hominins.

Fig. 6 about here

However, for distal humerus dimensions (Fig. 7a-d: mediolateral trochlear width, anteroposterior trochlear width, mediolateral distal articular surface width, and biepicondylar width in early hominins), StW 573 falls within the range for *Au. afarensis.* However, the dimensions are lower than those for *Au. anamensis,* except for anterioposterior trochlear width, and lower than the probable male *Au. prometheus* StW 431, except for mediolateral distal articular surface width.

Figs. 7a-d about here

Physical data for other specimens are too incomplete to form any consistent pattern, and in our view, the only reasonable conclusion is that, where sample size is sufficient, StW573 appears typical of early *Australopithecus* morphology. Indeed, distal humerus morphology is very variable in humans (Hill and Ward, 1988). McHenry and Brown (2008) note that it is also heterogeneous in early hominins, and they suggest that morphological variability within early hominins indicates exploitation of different ecological niches. StW 573's lateral supracondylar crest (origin of brachioradialis) is intact and substantial, implying power in pronation and elbow flexion. This is argued to be important for climbing, perhaps specifically vertical climbing (Hunt, 1991). StW 573 has a salient lateral margin for the trochlear articulation, which may imply ulnar stability through reducing axial rocking, although this distinction may not be sufficiently major to imply active selection (*sensu* Lovejoy et al., 2016). On the whole, therefore, the distal humerus morphology of StW 573 is consistent with a substantial degree of arboreality, as is more strongly evidenced by scapular morphology.

Radius, ulna, and hand: At 240-250 mm maximum length (Heaton et al., 2019), the StW 573 radius plots within the range of estimated radial lengths for other early East African and South African hominins (Fig. 8).

Fig. 8 about here

The StW 573 brachial index is very similar to that of *Gorilla* and *Au. sediba* (one of the few other hominins where the index can be calculated with a degree of certainty (Heaton et al*.,* 2019). This lends weight to the argument that *Au. prometheus* incorporated climbing behaviour into its locomotor repertoire, especially in combination with the relatively powerful *m. brachioradialis* noted above. Like the *Au. anamensis* specimen KNM-ER 20419 (Heinrich et al., 1993), StW 573 has a "distinct anteromedial bevel" to its radial head, resulting in "eccentric placement of the capitular fossa" (Heaton et al., 2019, p. 173). This morphology may indicate the importance of stabilising the elbow when the arm is semi-pronated and hence when there is greatest advantage for *m. brachioradialis* (Clemente, 1985; Heinrich et al., 1993), adding to the evidence for climbing behaviour which is strongly expressed. The ulnar keeling in StW 573, described by Heaton et al. (2019), may (as they imply) help resist forces generated across the elbow when brachioradialis contracts (see Drapeau, 2008). Alongside this, both the left radius and ulna in StW 573 have strong curvature (laterally in the radius, dorsally in the ulna (Heaton et al., 2019). Forelimb curvature is variable in early hominins (Drapeau et al., 2005), but its presence is consistent with arboreality. The

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left and right ulnae display asymmetry, with the left being strongly dorsally curved but mediolaterally straight; while again appearing mediolaterally straight, is less dorsally curved. At present, there is no conclusive evidence whether the asymmetry reflects healed premortem injury to the left arm (as suggested by Heile et al., 2018), or remodelling on the basis of handedness *in vivo*, a phenomenon far less common in non-human great apes (Schultz, 1937). Indeed, the endocast shows that a left occipital petalia, an expansion of the occipital lobe into right side of the cortex and a feature associated in living humans with handedness, was present (Beaudet et al, 2019a).

Table 2 about here

A radial neck that is long compared to the overall length of the bone (Table 2) is often associated with arboreality, as it indicates an increased moment arm of the elbow flexor *m. biceps brachii* (Napier and Davis, 1959; Conroy, 1976; Harrison, 1989). However, allometry may confound the signal (Reno et al., 2000), and we also note the variation among hominoid taxa reported by Heinrich et al. (1993), who also noted that *Au. anamensis* had an *m. biceps brachii* moment arm more similar to *Pan* than *Homo.* The neck length index of StW 573 is very similar to that of KNM-ER 20419*.* It is possible that the similarity in neck length index between *Pan*, *Homo* and the two species of *Australopithecus* examined here has a phylogenetic basis. Nonetheless, the medially orientated radial tuberosity of StW 573 (Heaton et al., 2019) is consistent with high power in supination of *m. biceps brachii*, a feature more in common with non-human apes than modern humans (Aiello and Dean, 1993), given other features of the forelimb which indicate a considerable degree of arboreality. Unfortunately, the epiphysis of the StW 573 distal radius is too damaged to make inferences about the adaptations of the wrist joint, which could have provided important evidence about range of motion and locomotion.

The StW 573 left ulna has a maximum length of 259 mm (Heaton et al., 2019), in comparison to the 278 mm of AL 438-1, *Au. afarensis* (Drapeau et al., 2005). The StW 573 brachial index of 82.8 is very similar to that of *Gorilla gorilla*, 80.6 (n= 22), lending weight to the argument that *Au. prometheus* incorporated substantial climbing behaviour into its locomotor repertoire. The StW 573 ulnar trochlear notch faces anteriorly, with a trochlear notch orientation index of 82.1 (using the index as defined in Churchill et al. [2013]) and an angle of 8° (Heaton et al., 2019). This morphology, derived compared to extant apes, is entirely consistent with that of other *Australopithecus* (Drapeau et al., 2005; Churchill et al., 2013). It may reflect increased loading of the flexed elbow (Drapeau et al., 2005). The function of the elbow flexors appears, however, to vary among *Australopithecus*. In StW 573, the mechanical advantage of *m. brachialis* (as defined in Churchill et al. [2013]) is 0.139. This groups reasonably closely with those *Australopithecus* (0.145 ± 0.009) in Churchill and colleagues' (2013) sample, but it is higher than *Au. sediba* (0.127), which is thought by those authors to have "relatively poor mechanical advantage for the elbow flexors" (Churchill et al., 2013, p. 4). The *m. triceps brachii* mechanical advantage (again as defined in Churchill et al. [2013]) of StW 573 is 0.068, closer to the modern human mean (0.065±0.007) than to *Au. sediba* (0.075) or the *Australopithecus* mean (0.081±0.003). This implies less power in elbow extension in *Au. prometheus* compared to the other *Australopithecus.* However, the longer humerus length must be taken into consideration, and more extensive future analyses will shed further light on the forelimb biomechanics of *Au. prometheus*. With respect to locomotor signals in the proximal ulna of *Au. afarensis* and other *Australopithecus*, Drapeau (2008, p. 99) commented that it was "difficult to resolve issues about the specifics." The addition of *Au. prometheus* does little to help this, suggesting that *Australopithecus* show quite noisy variations on a common theme that incorporates a degree of arboreality (possibly employing different modes in different species) alongside terrestrial bipedalism.

As reported in Clarke (1998, 2002), the relative proportions of the thumb and fingers of StW 573 are modern-human-like, as with the AL 333/333w *Au. afarensis* hand (Alba et al., 2003). This suggests that modern human-like hand proportions, as well as grasping capacities (Clarke, 1998, 2002) had

their origins in arboreal behaviour before they were exploited in more terrestrial hominins for tool-use.

The StW 573 trapezium (Fig. 9) bears a salient apical ridge, a feature commonly present and marked in living gorillas. Trapezium morphology is highly variable in primates (Napier and Davis, 1959), so care must be taken in interpretation, but it is likely that the apical ridge, absent in humans, might help brace the thumb and its ulnar and radial carpometacarpal and metacarpophalangeal collateral ligaments against forced abduction (Glickel et al., 1999). In gorillas, the apical ridge might therefore stabilize the pollex in abducted pinch grips during climbing, and we suggest that this would be similar in StW 573: in both cases, this would particularly benefit climbing on smaller diameter supports. Jashashvili et al. (under review) note that the hand is also characterized by midcarpal joint form favouring stability rather than mobility.

Fig. 9 about here

4.2. Functional morphology of the hindlimb
Pelvis: The StW 573 pelvis (see Fig. 3) requires retrodeformation prior to full analysis and comparison, as it is highly distorted and fragmentary on the left, with the dorsal surface largely comprised of matrix supporting paper-thin bone. For that reason, it is not described in the special issue of *Journal of Human Evolution* on the StW 573 skeleton. However, on the right, the StW 573 pelvis is considerably less deformed, although some distortion exists in the lateral third of the iliac blade. Unlike the case in StW 431, the greater sciatic notch is open and symmetrical, and based on the method described in Simpson et al. (2008), it exhibits a female-like morphology, as the chord between the deepest inflection and the opening of the greater sciatic notch lies at the halfway point. The iliac pillar (Fig. 10) is evident in CT scans for three quarters of the height of the ilium, but it does not reach the iliac crest; the iliac pillar, as with other *Australopithecus*, lies closer to the anterior superior iliac spine than in modern *Homo*. It is strongly marked, indicating substantial craniocaudal loading.

Fig. 10 about here

. The acetabular margin is complete and undistorted dorsally. The internal superoinferior diameter of the acetabulum is 41.3 mm, compared to 34.7 mm in AL 288-1 (Johanson et al., 1982). That of the acetabulum of StW 431 is difficult to assess accurately as the inferior rim of the acetabulum is missing, but it is ca. 40 mm. and thus the femoral head of StW 573 is a close match for the acetabulum of StW 431. The Sts 14 os coxae and that of AL 288-1 are small, with small acetabulae, but come from much smaller individuals. Macho et al. (2020) claim that in visual comparison some features of the StW573 ilium are more 'chimpanzee-like' than that of StW 431. However, casts of the prepared StW 573 pelvis and attached vertebrae and the reconstructed StW 431 pelvis (Fig. 3) may be compared to ventral views of *Pan, Pongo* and *Gorilla* pelves taken from 3D models constructed from CT of specimens we dissected for tendon length studies (see Fig. 11).

Fig. 11 about here

A relatively greater similarity of the StW 573 pelvis to that of *Pan* is not apparent. A recently discovered and reconstructed (but as-yet undescribed) ischiopubic element of StW 573 is a close match also to the StW431 os coxa. As can be seen in Fig.11 there is no indication in either of these fossils of the long and narrow ilium seen in both *Pan* and *Pongo*, and a better match is to *Gorilla* among extant great apes. Schultz (1930) provides the indices for *Homo sapiens* of ilium length/ischium length as 139.0 and ilium width/ilium length as 89.2. The corresponding indices for *Pan* (species indeterminate) are 199.4 and 62.2, for *Pongo pygmaeus* 199.9 and 77.4, and for *G.*

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gorilla gorilla 185.1 and 89.7. The values were 195.5 and 86.0 in *G.g. beringei*, although he notes sample size was small. Schultz (1949, p. 414) thus remarked that "generally speaking, the pelvic topography of the gorilla is least removed from that of man, though there is still a very significant gap."

It is worth noting also that Hooton (1931) illustrates this similarity between gorilla and human. He states that the gorilla, because of its his great bulk, "has very broad iliac blades curving around the pelvic inlet in a fashion recalling that of man" (Hooton, 1946, p. 110 and see his Fig. 9). Importantly, Fornai et al. (2021) have demonstrated that the probabilities of sampling sacral morphologies as distinct as those of Sts 14 and StW 431 from a single species are as low as 1.3 to 2.5% (based on a human sample) or 0.0 to 4.5% (for a sample of other great apes). There does thus now seem to be clear postcranial evidence that Member 4 *Australopithecus* samples more than one species, supporting the craniodental evidence presented by Clarke and Kuman (2019). It is thus more parsimonious to accept the likelihood that StW 573 and StW 431 do indeed belong to a single second species, *Au. prometheus*, and thus that the postcrania are more closely comparable to each other than either is to *Au africanus* Sts 14, than to posit a third species.

Kozma and colleagues (2018) calculated 'Dimensionless Mechanical Advantage' in the hip musculature of some early hominins, focussing in particular on the hamstrings in non-human great apes and monkeys. However, they make their contrasts primarily between 'apes' and hominins, which rather obscures the shorter and broader ilium of *Gorilla* than *Pan* and *Pongo*, and the consequences, for example, for the extensor moment of the glutei.
Virtual tendon travel studies are an ideal way of assessing 3D moment arms about joints, as Goh et al. (2017, 2019) did for the hip, knee, ankle and foot of western lowland gorillas. Contrary to earlier studies which used dissection approaches, they found that these gorillas have very effective hip extensors even in extended hip postures, despite the high frequency of vertical climbing behaviour in this species.

Fig. 12 about here

Femur: The StW 573 femur shows very clear evidence of bipedalism, but equally, in most aspects, it falls well within the range of other *Australopithecus*. In femoral head diameter (Fig. 12), StW 573 has an estimated mean very similar to that of the *Au. afarensis* specimens in the comparative sample, with the exception of AL 288-1, but it is somewhat higher than the South African *Australopithecus* mean (data from DeSilva et al., 2013). It has a human-like bicondylar angle of 11° (Heaton et al., 2019). Only a small portion an intertrochanteric crest has been preserved (Heaton et al., 2019), but its presence is evidence of a strong iliofemoral ligament which would help maintain upright posture. The StW 573 platymeric index (AP/ML shaft diameter immediately below lesser trochanter x 100, which indicates the degree of anteroposterior flattening) is 77.9 (Heaton et al., 2019). That of StW 573 falls slightly below the range for South African *Australopithecus* but above the range for *Au. afarensis* (Fig. 13).

Fig. 13 about here

Platymeric indices in *Pan* and *Gorilla* (DeSilva et al., 2013) show a tendency towards a more rounded proximal femoral shaft. Ruff and Hayes (1983a,b) noted that the proximal femur of modern human Puerto Rican females is more platymeric than that of males, presumably as a response to relatively higher mediolateral forces. Westcott (2006) observed that the human femur becomes flatter anteroposteriorly during ontogeny, attributed to the greater mediolateral loads on the femur that occur with mature bipedal gaits. The pattern of platymeria in modern humans can of course not be

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assumed to apply to earlier hominins, especially more arboreal hominins. While the subtrochanteric shaft is more rounded in *Orrorin tugenensis*, StW 573 falls within the range of variation of adult modern humans and *Australopithecus* and is very similar to *Au. sediba* (Marchi et al., 2017; see Fig. 13). This would of course be consistent with a high degree of terrestriality. StW 598 has a more rounded shaft than StW 573 but StW 99 a more flattened one, probably because according to R.J.C. it is most likely a *Paranthropus* from Member 5 (not Member 4) (Pickering et al., 2019). Most *Au. afarensis* specimens are anteroposteriorly flatter (data from DeSilva et al., 2013)

Fig. 14 about here

Relative neck length and neck shape again fall within the range of variation of other *Australopithecus* (Heaton et al., 2019). Given the preservation of the proximal femur (see Fig. 14), biomechanical neck length in StW 573 is cautiously estimated here as ~55 mm, below the South African *Australopithecus* mean (see Fig. 15); comparative data from DeSilva et al. [2013]).

Fig. 15 about here

It is well within the range of variation of early hominins as a whole and occupies an intermediate position between modern humans/gorillas and chimpanzees. Biomechanical neck length is a proxy for moment arm of the hip abductors *m. gluteus minimus* and *medius* (Rein, 2020), and the similarity in biomechanical neck length in StW 573 and other *Australopithecus* indicates that the *Au. prometheus* hip was similarly stabilised during bipedal walking.

Fig. 16 about here

In the distal femur (Fig. 16), the lateral femoral condyle of StW 573 is posteriorly 'elliptical', as is also reported for KSD-VP-1/1 *Au. afarensis* (Lovejoy et al., 2016). Similar to the human lateral femoral condyle, StW 573 has a relatively rounded posterior/dorsal section and flat anterior/ventral section. StW 573 has a deep patellar groove and shows a high lateral wall for patellar retention (Heaton et al., 2019), as is also the case, for example, in KSD-VP-1/1 (Lovejoy et al., 2016) and *Au. sediba* (DeSilva et al., 2013). That StW 573 was an habitual biped is also reinforced by the evidence of a strong marking for *m. popliteus* (Heaton et al., 2019), a muscle that in humans helps 'unlock' the knee from its posture in upright bipedal standing to permit recommencement of walking (see below).

It is worth noting that while the relative geometry of the lateral and medial femoral condyles in at least some *Pan* is very similar (Fig 16) the asymmetry seen in StW 573 is to some extent echoed by those of some lowland gorilla individuals. This would itself increase knee stability in full extension and would be consistent with the finding of Goh et al. (2017) that hip extensors in *Gorilla* retain high extensor moments even near full extension, enabling effective bipedal standing and quite likely propulsion.

Tibia and fibula: StW 573 has an anteriopposteriorly longer, concave medial tibial condyle and a shorter, less concave lateral condyle, matched by an anteriopposteriorly long, convexly rounded section on the medial femoral condyle but an (again anteriopposteriorly) anteriorly flatter lateral condyle (Fig. 17).

Fig. 17 about here

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The StW 573 intercondylar eminences (height: medial ~7.5 mm, lateral ~6 mm) are marked, as in modern humans. There is a similar relationship between relative lengths of the tibial condyles to other *Australopithecus* (Fig. 18). The shape of the StW 573 tibial condyles (Fig. 19) is similar overall to those of *Au. anamensis*, but *Au. afarensis* is more divergent, possibly related to its high valgus angle.

Figs. 18 and 19 about here

This notwithstanding, Organ and Ward (2006) found no difference in lateral tibial condyle geometry between StW 514a (not included in our dataset because the medial condyle is incomplete anteroposteriorly) and *Au. afarensis*. The difference in lengths between the two condyles is the bony basis of the 'locking' mechanism of the knee (see, e.g., Dye, 1987 and Lovejoy, 2007). In this mechanism, the condyles and cruciate ligaments form a four-bar linkage. In knee extension, because of the flatter condylar morphology of the ventral part of the lateral condyles, the lateral condyle ceases sagittal rotation before the medial condyle. 'Rollback' ensues, compressing the lateral meniscus and further immobilizing the lateral condyle. Thus, a passive coronal rotation of the knee results, spiralizing fibres in the cruciate ligaments and stabilizing the knee. This allows standing with minimal expenditure of muscular energy for balance, but a strong *m. popliteus* is required to reverse the rotation and 'unlock' the knee.

The StW 573 tibial diaphysis is laterally flattened, with a platycnemic index (mediolateral diaphyseal width at nutrient foramen / anteroposterior diaphyseal width at nutrient foramen x 100) of 64.5 (Heaton et al., 2019), compared to the *Australopithecus* index range of 64.7 – 68.4, a modern human index of 64.8 – 84.7, a gorilla index of 58.1 – 81.1 and a chimpanzee index of 55.7 to 73.0 (data from Marchi et al., 2017). Distal tibial shape (maximum anteroposterior depth of the distal tibia / maximum mediolateral width of the distal tibia x 100) for StW 573 falls within the range of other *Australopithecus* (Fig. 20).

Fig. 20 about here

Some non-human great ape (NHGA) -like traits have already been noted in the StW 573 tibia and fibula, relating to the tibial interosseous border, attachment of m. *soleus* on the fibula and shape of the tibiotalar joint (Heaton et al., 2019). On the fibula, the StW 573 fibulotalar articulation is orientated inferiorly (Heaton et al., 2019). An "ape-like downward orientation" is noted for the fibulotalar articular facets of *Au. afarensis* from Hadar, interpreted as evidence for high ankle joint mobility (Marchi, 2015, p.146), an interpretation that can be extended to StW 573. Tibiotalar joint geometry for *Australopithecus* other than StW 573 is discussed by Carlson et al. (2020) and is not reviewed extensively here. The StW 573 tibiotalar articular surface shows some fracturing and exfoliation, so confidence in measurements cannot be high, but shape (mediolateral anterior width / mediolateral posterior width) seems relatively high (ratio of 1.5), suggesting a mediolaterally wider anterior surface than other South African *Australopithecus*. Some doubt exists as to the appropriate comparative sample (see Carlson et al., 2020), but if correct, this might have given relatively free medial-lateral deviation of the foot on the crus, which would serve arboreal bipedalism better than terrestrial.

The morphology of the available footbones has been discussed by Clarke and Tobias (1995) and Deloison (2003), and the metrics reported at length by Deloison (2004). As noted above, since both hands and feet have very high degrees of freedom, with multiple joints crossed by many active and passive soft tissues, they are now regarded as characterised by neurobiological degeneracy and joints may be recruited by motor control systems in different combinations, step-to-step, grasp-to-grasp (see, e.g., Latash et al., 2002, Seifert et al., 2016). Functional interpretation is thus highly complex and outside the remit of this review. Significance of degeneracy in the hands and feet for

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hominins will be discussed in McClymont et al. (unpublished data.). Whether any morphological differences from modern human footbones such as those reported by Deloison (2004) offered significant advantage in arboreal climbing remains to be determined, but this would require analysis of a sample which includes human climbers such as the Twa (more below). Fig. 21 shows that modern human indigenous climbers can certainly use the hallux to grasp small vines powerfully enough to support vertical climbing.

Fig. 21` about here

5. Au. prometheus: evidence for a common Australopithecus bauplan and fundamental niche

Throughout this contribution, we have observed that, for most of the metric traits examined, StW 573 falls within the range of variation (non-size-adjusted) for early hominins, and specifically *Australopithecus*, as a whole. These skeletal similarities suggest a common *Australopithecus* locomotor *bauplan*, reflecting a similar fundamental niche, suggesting that *Australopithecus* of different species had similar potential niches, incorporating competent terrestrial and arboreal bipedalism, to greater or lesser degrees. We agree with McHenry and Brown (2008) to the extent that morphological variability between individual early hominin fossil skeletons, or skeletal elements, may indicate exploitation by those individuals of different realized niches, but fundamental niche appears to be similar.

The postcranial evidence reported in Heaton et al. (2019) and Carlson et al. (2020) and reviewed and examined further here, suggests that *Au. prometheus* was competent arboreally, a conclusion reinforced by the inner-ear mechanism and atlas cranial facet orientation of StW 573 (Beaudet et al., 2019, 2020). The lateral semicircular canal is mediolaterally large, as in nonhuman great apes but not *Homo*, although the apical part of the cochlea has loose turns, resembling the case in humans. The superior articular facets of the atlas are more concave than in *Homo*, and the inferior articular facets are more vertically inclined, which would have been likely to constrain motion of the head in the transverse plane. The small cross-section of the transverse foramina and left carotid canal suggest relatively low blood perfusion of the brain. All these together suggest that the ability to make the fine adjustments of unsupported bipedal gait required for long-distance terrestrial walking (striding) may have been limited (and see Pontzer 2017). This interpretation is in agreement with the conservative relative proportions of limb segments stressed by Heaton et al. (2019) and Carlson et al. (2019), despite the unequivocally human-like functional anatomy of the knee, which is clearly adapted for stability in extended postures, whether static or mobile. This is further evidence that australopiths, at the time of formation of the Laetoli footprint trails, used extended rather than flexed postures of the lower limb during bipedal walking.

Ward et al. (2001) suggest, largely on the basis of a parasagittal set of the talocrural articulation, that the eastern African *Au. anamensis,* slightly older than StW 573, was predominantly a terrestrial biped, but they acknowledge it may have included substantial arboreality in its locomotor and postural repertoire. Contemporaneous with StW 573, *Au. afarensis* clearly retained traits associated with arboreality (Stern and Susman, 1983). If directional selection was operating to remove 'anachronistic' arboreal adaptations from the *Australopithecus* form (see Ward 2002, 2013), or even if they remained selectively neutral, it might be considered unlikely to persist in different species across a period of one million years. Further, this might be thought to suggest that retention of forelimb adaptations suitable for climbingwere retained by stabilising selection because they allowed a large fundamental niche to be occupied, characterised by effective arboreal, as well as terrestrial, foraging. This would again be consistent with expectations from neurobiological degeneracy theory (Seifert et al., 2016).

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5.1 Plasticity at intraspecific and higher taxonomic levels

The variation evident in the tribe Hominini, with large metric ranges in even single species, points to considerable intraspecific plasticity, alongside sexual dimorphism. Examining and understanding this plasticity is vital to considering the realised, rather than simply fundamental, niche. Inevitably, when interpreting the hominin fossil record, attention is focused on locomotor and postural evidence garnished from bone morphology, as it is usually impossible to consider soft tissue, thoroughly. Yet soft tissue has the potential to be more plastic and hence responsive to environmental subtleties. Fossil studies that reveal the bone architecture of fossil specimens that supported the soft tissue force application throughout life, are very valuable (Kivell, 2016; Chirchir 2019). Further valuable to the understanding of a realised niche in fossil specimens, are studies of soft tissue architecture in extant great apes. A good example of this comes from the ankle, a region which we stated above provides essential information about arboreality. DeSilva (2009) argued that the human ankle joint was incapable of dorsiflexion to the extent required for 'chimpanzee-like' vertical climbing, a view that has gained traction (e.g., Lovejoy et al., 2016). This is despite other research (Kraft et al., 2013) that showed that modern Twa hunter-gatherers, with typical human values for the talar facet of the tibia, can nevertheless achieve high ankle dorsiflexion and engage in vertical climbing since they tend to have longer fibres in the gastrocnemius muscle than neighbouring, non-climbing agricultural communities. Further, Holowka et al. (2017) have argued that DeSilva's (2009) estimates of ankle dorsiflexion in chimpanzee vertical climbing were probably erroneously high and an artefact of his method. They observe that chimpanzee quadrupedal walking is characterized by higher ankle dorsiflexion angles than typical of human bipedal walking. Thus, the linkage of talar facet morphology in chimpanzees with vertical climbing argued by DeSilva (2009) may now be largely unsustained.

Care must be taken in interpreting trabecular architecture, as Tsegai et al. (2018) found that differences in the trabecular bone volume fraction differences between forelimb and hindlimb in humans and chimpanzees did not clearly reflect locomotor loading. However, they noted that degree of anisotropy was more likely to reflect locomotor loading than species. Thus, we might speculate that internal femoral head architecture in hominins might also respond to activity characteristics, giving findings similar to those recorded at Sterkfontein by Georgiou et al. (2020), and confirmed in the metatarsals of hominins (Patel et al. 2018). Thus, arboreal foraging of some kind remains within the human fundamental niche (Kraft et al. 2019). This demonstrates the importance of plasticity -- the ability to adapt musculoskeletal anatomy during development to enhance function in the realized niche -- to all great apes, including humans, which is a useful tool when evaluating the locomotor performance of fossil hominins. Indeed, long ago, Keith (1934) viewed plasticity as crucial in great ape evolution:

"The presence of big-bodied primates in the Miocene indicates that a branch of the higher primates had then entered a period of evolutionary plasticity and was undergoing profound functional and structural changes. It was in this plastic period that I suppose the human line to have separated from that of the great anthropoids." (Keith, 1934, p. 20)

Here Keith (1934) refers to evolutionary, rather than ontogenetic plasticity. Whitaker and Bender (2010) and Seifert et al., (2016) show how increased evolvability driven by neurobiological degeneracy at gene level allows taxa to respond quickly to climate and environmental change.

Thus, paleoanthropological interpretations could be enhanced by greater acknowledgment that fundamental and realized niches of species and higher taxa are not identical, and that realized niches change according to environmental contexts. Those of us who study fossils can rarely carry out "laboratory experiments on the effect of morphological variation on behavioural performance"

(Wainwright, 1991, p. 680), except by analogy to closely related species amenable to experiment, such as ourselves (see below). However, we can do so *in silico*, as we will again discuss below.

5.2 Palaeoecology of StW 573 in relation to Au. anamensis *and Laetoli* Au. afarensis

The taphonomic evidence (Clarke, 2019a) is clear that StW 573 was found immediately below its habitat, most likely hilly, rocky shrubland / bushland, with areas of denser woodland or forest in the valley bottom (Pickering et al., 2004), associated with the Blaaubank water course, which would have been much larger than the stream that exists today. This is thus the realised habitat niche of StW 573. More work is required to reconstruct its dietary niche fully – important when considering posture alongside locomotion -- but the toothwear in StW 573, with particularly heavy wear on the lingual aspect of the anterior dentition closely resembles that in available *Au. anamensis* dentitions (Clarke and Kuman, 2019). In living primates, such wear has been associated by Koyabu and Endo (2010) with eating fruits with hard pericarp. The realised dietary niche of StW 573 is thus likely to have incorporated foraging for arboreal resources. Early studies by Beaudet et al. (2021) using the Diamond synchrotron suggest that StW 573 suffered two bouts of severe dietary stress in childhood, again consistent with (but not necessarily due to) reliance on low quality, seasonally deficient food resources.

The fundamental niche of Pliocene *Australopithecus* seems generally to have comprised a mix of C3 and C4 resources in a 'mosaic' habitat. A C3-dominated diet or a diet with a small C4 component has been inferred for both *Au. anamensis* and *Ar. ramidus*, with *Au anamensis* associated primarily with woodland/bushland/shrubland with a smaller local component of forest (Cerling et al., 2013). More recently, Manthi et al. (2020) found Kanapoi *Au. anamensis* to have similar δ13C values to extant 'savanna' *Pan* populations. They inferred that the hominins at the Kanapoi *Au. anamensis* location was feeding on C3 foods such as fruit and leaves from trees within a grassy woodland/bushland/shrubland with a non-continuous canopy. Our understanding of the palaeoenvironment at Laetoli at the time of formation of the footprint trails and the date of the type specimen of *Au. afarensis* is still in flux, but Su and Harrison (2007, p. 303) summarise it thus: "a mosaic habitat comprising of open woodland, grassland and shrubland, as well as closed woodland along seasonal water courses." Eruptions of the Sadiman volcano, and the consequent ashfall, in which the Laetoli footprint trails were made, seem to have caused only short-term disruptions of this environment. Although Rift Valley hominin habitats have a distinctly different physical geography from the Witwatersrand craton, the palaeoenvironment at Laetoli at the time of the Upper Laetolil beds and that of the Kanapoi *Au. anamensis* may not have been very different from that at either Sterkfontein in Member 2 times, except that watercourses were likely permanent and associated closed forest likely present at Sterkfontein. Neverthertheless, *Au. anamensis*, *Au. afarensis* and *Au. prometheus* were all likely effective in exploiting arboreal, open woodland forest and forest resources, but less effective in open grassland.

6. Extinct protohominin locomotion

Here, we discuss interpretations of likely locomotion in protohominins including Danuvius, Sahelanthropus, Orrorin and Ardipithecus, which have been mooted as illuminating the precursors of hominin bipedalism.

There is continued disagreement over whether the hominoid *Danuvius* was an arboreal biped at 11.62 Ma (Williams et al., 2019, but see Böhme et al., 2019b). There is also continued disagreement over the bipedality of *Sahelanthropus* (ca. 7 Ma) due to the lack of postcranial evidence. A femur thought by some to belong to *Sahelanthropus* has been described by others as lacking any external or fracture-exposed evidence for bipedality (Macchiarelli et al., 2020. MicroCT by Guy et al. (preprint, 2020) of this specimen revealed a prominent femoral calcar (robusticity proximomedial to the lesser trochanter), which is also present in the proximal femur of *Orrorin* (Kuperavage and Eckhardt, 2009; Kuperavage et al., 2018). In humans, experimental cadaveric studies similarly make a

strong link between the calcar femorale and stress distribution in the proximal femur of humans (Zhang et al., 2009). Presence of a femoral calcar does not, however imply that a fossil is a hominin, as some *Gorilla* specimens at least also exhibit a calcar femorale (e.g., KUPRI 1492 on the Kyoto University Digital Morphology Museum site [pers. comm. to RHC from Adam Kuperavage]).

More broadly, we must consider body mass as a very significant influence on the ability to stabilize the body above branches during arboreal locomotion. The description (see e.g., White et al., 2015) of the arboreal locomotor behaviour of *Ardipithecus ramidus* (4.4 Ma), as apparently dominated by 'cautious climbing' and plantigrade quadrupedalism despite occasional orthograde bipedalism, is somewhat difficult to interpret *in toto*. While humans can and do display all of these in arboreal contexts
[see, e.g., Kraft et al,. 2014]). The high initial body weight estimate of 51 kg for ARA-VP -6/500 (Lovejoy et al. 2009a) as pointed out by Crompton et al. (2010), would be nearly twice the weight of males of the largest cercopithecine *Mandrillus sphinx* (~32 kg [Smith and Jungers, 1997]) and much heavier than those of the largest colobines, *Rhinopithecus roxellana* and *Nasalis larvatus* (male masses ~20 kg [Smith and Jungers, 1997]). With no tail, and thick plantar tissue (Lovejoy et al., 2009c) which would have reduced gripping effectiveness, it is difficult to understand how it coped with inevitably high destabilizing torques in plantigrade quadrupedalism, or with (apparently) unsupported bipedalism in an arboreal context, as suggested by White et al. (2015). It seems quite likely therefore that the lower estimate of ca. 32 kg by Grabowski et al. (2015) is more accurate Apparently rejecting White's interpretations of Ardipithecus arboreal locopmotion,Prang et al. (2021) attempted to resurrect a knuckle-walking/suspensory model of hominin origins based on morphometric analysis of the *Ardipithecus ramidus* hand bones. It might be thought somewhat obtuse to model locomotion of the whole body entirely from one of the functionally most variable and least determinate parts of the body, and, although suspensory locomotion is evidenced in all living hominoids, including ourselves, knucklewalking is not and appears to have been independently derived in *Pan* and *Gorilla* (Kivell and Schmidt, 2009).

It remains the case that at ~3.67 Ma, only 0.73 Ma after the date of *Ardipithecus ramidus*, *Australopithecus prometheus* StW 573 was a capable upright terrestrial biped able to traverse over short to medium distances. Yet it continued to engage extensively in arboreal activity, likely using a mix of (sometimes) hand-assisted bipedality and quadrumanous climbing. Its lower limb was very similar to our own, as far as joint shape was concerned, although long- bone length was primitively short, which may have limited endurance in terrestrial walking, and as noted above, the semicircular canals (Beaudet et al., 2019b) and joints in the atlas (Beaudet et al., 2020) appear to be better adapted for mobility in a three- dimensionally complex arboreal environment. Also, the effectiveness of blood perfusion of the brain, as witnessed by the small cross-section of the carotid foraminae of the atlas (Beaudet et al., 2020), does not appear to be adapted for extended activity in open country.

StW 573 may have engaged in some suspension, but then so do humans, as discussed below. There is no evidence whatsoever in the StW 573 hands of knucklewalking, nor in those of *Au. afarensis.* Its upper limb, however, retained an ability greater than our own to use supports above shoulder level. Variability in *Australopithecus* postcrania is very high, but StW 573 falls within that range of variation in nearly all characteristics. Postcranial features seem to be built on proportions that are primitive for living great apes as a whole, not derived as those of *Pan* seem to be. If *Pan* and *Homo* separated between 4-8 Ma, as Wood and Grabowski (2015) conclude, that is very close to, or after, the dates for *Sahelanthropus*, *Orrorin*, and possibly even *Ardipithecus ramidus,* which all display some features at least of upright bipedalism.

7. Biomechanical performance data for extant great apes

If we accept the argument of Böhme et al. (2019; but see Williams et al., 2019), some European late Miocene apes, such as *Danuvius*, did sometimes walk bipedally, with extended knees, in an arboreal context (as does *Pongo* today, see Thorpe et al. 2007). However, Böhme et al. (2019) reject our 'hand-assisted bipedalism' model (see e.g., Thorpe et al., 2007 and Crompton et al., 2010). They erected their own new locomotor category for *Danuvius*, 'extended limb clambering' on the grounds that lower limb forces in orang-utan bipedalism are insufficient to exert hip and knee forces of the scale that would require the bony buttressing they claim to have observed. They do not present evidence to support this assertion. Crompton et al. (2010) argued that as torques (tending to flex joints and destabilize the body above a supporting branch) will increase as the cube of linear dimensions, but muscle power to resist them only as the square of linear dimensions (see, e.g., Alexander, 2003) orthogrady, permitting the hands to exert much larger balancing moments about the feet than in quadrupedal posture, is increasingly beneficial with increased size. Further, Johanssen et al. (2017) demonstrated that exposing human subjects to a movie of swaying branches while they stood on a branch-like bouncy springboard destabilized them as much as wearing a blindfold when on the same support. Light fingertip support significantly enhanced balance and reduced thigh muscle activity by up to a third. Thus, the origins of hominin bipedalism in arboreal bipedalism with extended joints may have been driven substantially by increased body size in apes.

It is evident from Heaton et al. (2019) that upper limb lengths were short in StW 573 compared to the living non-human great apes. This suggests less ability to embrace large supports with the upper limb, and particularly, shorter reach, which we hypothesise reduces the energetic efficiency of arboreal locomotion. Unusually, perhaps, an analogy to human performance capacities can be used to provide some test of this hypothesis. Halsey et al. (2017) measured the impact of variation in morphology and locomotor behaviour on the rate of oxygen consumption of 19 elite male parkour athletes as they repeatedly traversed an arboreal-like assault course of 103 m horizontal length, including arm swinging/brachiation. The course consisted of a range of generic gymnasium apparatus such as vaulting horses, raised blocks, high bars, wall bars, and areas filled with loose foam blocks to emulate the range of mechanical conditions present in an arboreal pathway, rather than the exact structure of the forest canopy. Thus, parts of the course incorporated support compliance, irregularity and discontinuity to reflect the conditions experienced during gap crossing between tree crowns. Others were rigid and predicated to reflect the phases between bouts of gap crossing when even large-bodied apes may walk into and out of the core of a tree along thick boughs. Halsey et al. (2017) found that familiarity with the course had a substantial effect on reducing energetic costs, but there was no evidence to suggest that the locomotor behaviour profile of each individual (or the combination of locomotor behaviours that they selected between first and last trials) influenced their ability to attenuate costs. We must, therefore, presume more subtle mechanical adjustments are being made to attenuate locomotor challenges. Importantly, athletes with longer arm spans and shorter legs were particularly able to achieve energetic economies. Thus, our hypothesis that shorter reach would reduce the efficiency of arboreal locomotion is confirmed for one hominin at least, namely *Homo sapiens*. Therefore, based on this analogy, we conclude that the limb proportions of StW 573 would indeed likely have reduced her energetic efficiency in arboreal climbing compared to non-human great apes, but given her high humeral length, reach and thus efficiency would have been higher than in *Homo*, suggesting that StW 573 was under active selection to balance terrestrial and arboreal effectiveness.

Crompton et al. (2003) rejected both the knucklewalking quadrupedalism model (Gebo, 1992) and the vertical climbing model of Fleagle et al. (1981) for the origins of bipedality, on kinematic

grounds, since both normally-raised *Pan troglodytes* and *P. paniscus* do not sustain voluntary bipedalism for more than a couple of seconds. They also do not attain hip and knee extension ranges close to those in human bipedal walking. Orang-utans, however, can sustain hip and knee extension ranges in voluntary bipedal walking very close to those that we sustain. Instead, they proposed arboreal orthograde scrambling like that of orang-utans, including an element of hand-assisted bipedality as the likely forerunners of bipedal walking.

With respect to the origins of orthogrady itself, we suggest that increased body weight, and thus increased lateral torques about the thorax tending to rotate the body around the branch, decreases stability (see Crompton et al. 2010). It is noteworthy that it is females, not males, which appear to be the most often arboreal in *Mandrillus*, *Rhinopithecus* and *Nasalis* (RHC, pers. obs.). Orthogrady, evident in hominoids from *Morotopithecus* (circa 18-20 Ma) onwardsn, either avoids this issue by facilitating forelimb suspension, or, in compressive orthogrady, by enabling the hands to exert much higher leverage about the feet by lateral reach branch contact at around shoulder height, than the destabilizing torques exerted by gravity about the feet. Monkeys appear to lack the thoracolumbar adaptations allowing sustained orthogrady seen in all apes.

Watson et al. (2009) investigated kinematics during load carrying in humans, and zoo populations of common chimpanzees, bonobos, lowland gorillas and Bornean orang-utans found that in quadrupedal locomotion load carriage led to a more upright trunk and a change in shoulder motion. These changes were exacerbated progressively in tripedal and bipedal gaits when carrying more awkward loads. Thus, load carrying may have contributed to erect truncal posture and changes in the shoulder.

Thus, we suggest that StW 573 was an effective arboreal biped and climber that had sacrificed some arboreal effectiveness in favour of enhanced energetic efficiency in walking medium distances on the ground. Her locomotor posture was competent upright bipedalism, whether on the ground or on branches, and she was able to stand upright without much muscular activity because of a 'locking' or 'screw-home' mechanism in the knee. Such a feature does not seem to have been present in *Ar. ramidus,* suggesting that it was unlikely to have engaged extensively in terrestrial bipedalism. The two other early *Australopithecus*, *Au. anamensis* and *Au. afarensis* KSD-VP-1/1 however probably shared a similar niche to StW 573, since a locking mechanism is also present in the knee of *Au. afarensis* at least in *Danuvius* (but again see contra Williams et al. [2019]). The mean of vertical force peaks in orang-utan bipedalism measured by forceplate, is actually not small compared to those in *Homo*: between 0.84 (Payne, 2001) and 0.95 (Kimura, 1985) times body weight (bw) according to individual, versus 1.23 bw in *Homo sapiens* (Kimura, 1985). Neither do Böhme et al. (2019) consider the experimental evidence of Johannsen et al. (2017) who showed that light fingertip contacts (light touch) can dramatically stabilize bipedal walking on supports in simulated arboreal environments, reducing required hip muscle forces by some 30%. In other words, orang-utan bipedalism is, like our own, compressive orthogrady (Thorpe and Crompton, 2007), where the superincumbent weight is borne by the legs. Thus, the creation of another locomotor category by Böhme et al. (2019) is most likely unwarranted. Hand-assisted bipedality is the appropriate descriptor for the locomotion that likely gave rise to hominin bipedality. Thorpe and Crompton's (2007) discussion of locomotion in orang-utans was based on the standard descriptors in Hunt et al. (1996) and we endorse their plea that new locomotor categories should not be generated without due consideration, especially where a single fossil specimen, the locomotion of which cannot be observed, is under discussion.

8. Virtual models and their impact on the origins of bipedalism

Locomotor anatomy of *Pan* is commonly regarded as derived with respect to the last common ancestor with *Homo* (see, e.g., Isler et al. 2006; Drapeau and Ward, 2007; White et al. 2015; Young et al. 2015). Chimpanzees have a remarkably narrow range of intermembral indices. Isler et al. (2006) demonstrate that this narrow range optimises swing symmetry between fore- and hindlimbs, which is a basis for effectiveness in terrestrial quadrupedal gait. Chimpanzee intermembral index is high, and it is suggestive that manuports used by chimpanzees as hammer-stones in cracking *Panda oleosa* nuts in the Taï forest are carried no more than 10-15 m (Profitt et al., 2018). Inverse dynamic modelling by Wang and Crompton (2004a and b) based on limb proportions showed that chimpanzees cannot carry loads without incurring dramatically higher mechanical energy costs. AL-288-1 would have incurred considerably smaller cost increases but primarily when walking upright, and KNM-WT 15000 would have been able to shoulder-carry loads of 10-15% of body mass with no greater mechanical cost than AL-288-1 would incur walking upright but unloaded.

Given the proportions of StW 573, with a high intermembral index, outside the human range and higher than the index of KNM-WT 15000, we may hypothesize that StW 573 would not perform as well in load carrying as would KNM-WT 15000. However, we may further hypothesize that the somewhat longer legs and shorter arms of StW 573 would have given increased distance-specific effectiveness in unloaded bipedalism, compared to NHGAs, but not when load carrying.

Feix et al (2015) use an interesting modelling approach to assess the relative importance of thumb length and joint mobility in high precision manipulation and find that both are prerequisites for the manipulation potential required for stone tool manufacture: both appear to have been present in *Au afarensis*, but despite the long thumb, the apical ridge on the trapezium of StW 573 thus suggests that prehension was less important to this individual at least than stable grasps on arboreal supports, There is no evidence of tool manufacture in Sterkfontein Member 2. Performance assessments of manipulative skills by humans, gorillas and orang-utans (Bardo et al 2017) interestingly rated gorillas higher than orang-utans, which they suggest may reflect the greater terrestriality of the former. Bardo et al. (2018) went on to use modelling approaches to assess biomechanical potential for tool-related behaviours, and again orang-utans perform poorly, requiring higher muscle forces for a similar range of motion. The hand of *Au. sediba* however would have had the potential for stone tool use and perhaps manufacture, and these contributions together might suggest that prehensive capability had become more important to these individuals than stable grasping of larger vines and branches, consistent with the suggestion of Bardo et al. 2017).

Lowland gorillas have the most human-like foot proportions among the great apes (Schultz, 1963), having, for example, a long tarsus and short lateral phalanges (Schultz, 1963): the phalanges of the third digit are about 33% of foot length versus 43% in *Pongo* and 35% in *Pan troglodytes*. In a static analysis, gorillas have a power arm to load arm ratio equal to that of humans, better than either chimpanzee or orang-utan, albeit at the cost of large normal forces at the ankle (Wang and Crompton, 2004b). Further, Wang et al. (2014) found that in simulations of human-like bipedal walking, it is gorillas which most resembled humans in terms of mean joint force and mean joint torque in the joints of the foot. As they do perform both hand-assisted bipedality and some terrestrial bipedality in the wild, gorillas seem to be the most useful living comparator among the African apes (reviewed in Crompton, 2016). Together with Goh et al. (2017, 2019), these data strongly suggest that a postcranially relatively gorilla-like Last Common Ancestor for humans and chimpanzees is most likely. Indeed, this idea is not new, being suggested by Elliot Smith in 1924. However, there remains the question of what ecological advantage accrues to gorillas from their own locomotor configuration that does not accrue to hominins in the same habitat. This advantage might revolve round gorillas' greater ability to climb large cross-section tree-trunks, for which modern humans require technological aids. Forwards dynamic modelling of musculoskeletal

performance (see, e.g., Sellers et al., 2005, 2010) in vertical climbing in lowland gorillas, and in StW 573 once the trunk is reconstructed, should prove highly informative. It should, however, be combined with field studies of indigenous populations of humans living in sympatry with western lowland gorillas, most likely in the Congo basin, to differentiate arboreal zone access capabilities in humans and gorillas.

Conclusions

Following Wainwright's (1991) formulation of ecomorphology, we suggest that the potential niche of StW 573 was exploitation of both arboreal and terrestrial contexts, facilitated by locomotor plasticity. Under the assumption of such plasticity, arboreality probably remains part of the potential niche of *Homo sapiens.* Our species can and does engage in cautious climbing and even plantigrady, as well as orthograde, and often, just like StW 573, hand-assisted bipedality in arboreal contexts. These remain part of our potential niche, expressed in some living populations (Kraft et al., 2014).

It seems likely that StW 573 was, in her realized niche in the Blaaubank valley environment, an effective arboreal biped and climber that had sacrificed some arboreal effectiveness in favour of enhanced energetic efficiency in walking medium distances on the ground. Her habitual locomotor posture was upright bipedalism, whether on the ground or on branches, and she was able to stand upright without much muscular activity because of a 'locking' or 'screw-home' mechanism in the knee which does not seem to have been present in *Ar. ramidus.* A niche similar to that of StW 573 was probably shared by *Au. anamensis* (Bobe et al. 2020) and KSD-VP-1/1 *A. afarensis* (Su, 2016). Thus, *Pan* can no longer be seen as the most suitable locomotor comparator for early hominins, while *Pongo* remains very largely but not exclusively arboreal. Despite an earlier separation date from Hominini than that of Panini, *Gorilla* species are probably more informative as an extant species for locomotor comparisons.

Regarding an australopith *bauplan*, comparisons with other available australopith skeletal materials suggest broadly similar adaptations and ecomorphology, towards arboreal and terrestrial exploitation of woodland, and terrestrial exploitation of grassland in the immediate vicinity within the constraints of palaeoenvironmental differences. Wood and Boyle (2016) noted that taxonomic diversity is high in hominins and protohominins from 4 MYA, but this diversity was assessed primarily from considerations of cranial morphology. However, there are indications that some, but by no means all, later *Australopithecus,* such as *Au. sediba* were more terrestrial than early australopiths. Finally, and most importantly, since the great apes (including humans) have responded to climate instability specifically by retaining and enhancing plasticity (see, e.g., Neufuss et al., 2014), we should expect variability in great ape evolution and base our interpretation of fossil taxa on that expectation.

Statements

Conflict of Interest Statement

The authors have no competing interests to declare.

Author Contributions

Crompton, McClymont, Elton and Thorpe conceived and wrote most of the text; Sellers, Pataky and Goh contributed ideas on in-silico experimentation; Heaton, Pickering, Carlson, Jashashvili, Beaudet and Bruxelles commented on sections within their particular expertise. Kuman helped tremendously with editing and provision of images. Clarke led the excavation and preparation team over the two decades since discovery of the first foot bones and provided discussion and comments on the text.

Dedication

RHC and JMC dedicate their contribution to the memory of their close friend and colleague, Russ Savage.

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Figure captions

Figure 1: Left (a): The long limb bones of StW 573 from Clarke, 2019 (original specimen, reused with permission: license 4942050211741). Right: (b) The full StW 573 skeleton as of 2019, original specimen (photo courtesy Paul Myburgh)

Figure 2: Estimated stature plotted against estimated body mass for early hominins. *Australopithecus prometheus* (StW 573) stature estimated from maximum femoral length using the reduced major axis equation from Hens et al. (2000) for small stature populations. *Australopithecus prometheus* (StW 573) body mass estimated from femoral head superoinferior ('femur') and tibial distal end mediolateral ('tibia') equations given in Grabowski et al. (2015). Comparable estimated statures and body masses for comparative specimens (South African *Australopithecus* sp. [Sts 14, StW 25, StW 443, StW 392], *Au. afarensis* [AL 288-1, AL 333-3, KSD-VP 1/1], *A. ramidus* [ARA-VP 6/500]) as reported in Will et al. (2017). StW 573 falls within the range of other early hominins for both estimated stature and body mass. Note that estimates are also provided in Will et al. (2017) for StW 99 but are not included here because the specimen may be *Paranthropus* (Partridge et al., 2003).

Figure 3. Above: associated pelvic elements and lumbar vertebrae of StW 573. Ischiopubic elements found separately are not included as they are heavily fragmented although in a unit, and await publication. Note the apparent lipping of the vertebral bodies. Centre: Reconstructed pelvis of StW 431. Below, lateral views of left: StW 573, right, StW 431 to show similarities in acetabulae. Photos from first-generation casts, courtesy Ronald Clarke.

Figure 4. Superior aspect of the right clavicle, photo by RHC from a first generation cast. Note the strong sigmoid curvature.

Figure 5: Anteroposterior humeral head diameters in early hominins. StW 573 falls within the range of other early hominins. *Australopithecus afarensis* comprises AL 288-1, AL 333-107, and southern African (SA) *Australopithecus* sp. comprises Sts 7, Sts 328. Circles represent means and bars maximum and minimum values. Data from Johanson et al. (1982), McHenry (1992), Haile-Selassie et al. (2010), Churchill et al. (2013), Heaton et al. (2019).

Figure 6. Maximum humerus length in early hominins. That of StW 573 is longer than the other specimens, which sample the smaller body mass range of early hominins. Data from Johanson et al. (1982), Asfaw et al. (1999), Haile-Selassie et al. (2010), Churchill et al. (2013), Heaton et al. (2019).

Figure 7 a-d. Distal humerus dimensions in early hominins. (a) Mediolateral trochlear width; (b) anteroposterior trochlear width; (c) mediolateral distal articular surface width; (d) biepicondylar width. StW 573 (*Au. prometheus*) falls within the range of other *Australopithecus* (*Au. afarensis* comprises AL 288-1, AL 137-48a and AL 322-1 plus KSD-VP-1/1b for all dimensions apart from anteroposterior trochlear width). StW 431 likely to be a male *Au. prometheus*. Circles represent means and bars maximum and minimum values. Data from Johanson et al. (1982), McHenry (1992), Haile-Selassie et al. (2010), Churchill et al. (2013), Heaton et al. (2019).

Figure 8: Maximum radius length estimated for StW 573 and other early hominin specimens. All are estimates, although the radius of StW 573 is virtually complete (Heaton et al., 2019). The StW 573 value is for the well-preserved left radius, estimated because of minor damage. Comparative data from Grine and Susman (1991), Heinrich et al. (1993), Asfaw et al. (1999), Lovejoy et al. (2009).

Figure 9. The trapezium of StW 573 (right) compared to that of a human (left),
Note the apical ridge (red arrows) in StW 573, which is more salient than it is in humans.
Image courtesy Ronald Clarke.

Figure 10. Right, horizontal CT sections of the right ilium of the original fossil to show the extent of the iliac pillar. CT performed by Kristian Carlson. Approximate position of the pillar is marked as 'IP'. In 3 and 4, the iliac pillar appears to be displaced dorsally, and approximate position is marked as 'IP?' Left, the positions of these sections on a photo of a first generation cast, by RHC.

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Figure 11: Top Left, pelvis of a *Pan troglodytes.* Top Right, pelvis of a *Pongo pygmaeus*, Middle left, pelvis of a male *Gorilla gorilla.* In each case these are taken from CT meshes of the subjects dissected for our studies of tendon length and were zoo specimens. Middle right, a commercial cast of a female gorilla. Bottom: pelves of StW 573 (above, unreconstructed) and StW 431 (below, reconstructed), courtesy of Ronald Clarke. The particular similarity of the pelvis of *Gorilla* to that of humans was noted by Schultz (1930, 1949).

Figure 12: Superoinferior femoral head diameters in early hominins. StW 573 value estimated (Heaton et al., 2019). Circles represent means and bars maximum and minimum values. Comparative data as reported in DeSilva et al.et al. (2013). Comparative data as reported in DeSilva et al.et al. (2013). Southern African *Australopithecus* sp. comprises MLD 46, StW 25, StW 392, StW 403, StW 501, StW 522, StW 527, StW 598. Note that a value is also provided in DeSilva et al. (2013) for StW 99 but is not included here because the specimen may be *Paranthropus* (Partridge et al., 2003)

Figure 13: Platymeric index of the femur in early hominins. *Australopithecus prometheus* (StW 573) value from Heaton et al. (2019). Circles represent means and bars maximum and minimum values. Comparative data as reported in DeSilva et al.et al. (2013) and Pickering et al. (in review). *Australopithecus afarensis* comprises AL 288-1, AL 333-3, AL 211-1, MAK-VP 1/1 (DeSilva et al., 2013). Southern African *Australopithecus* sp. comprises StW 522 (as reported in DeSilva et al. [2013]) and StW 598 (as reported in Pickering et al. [in review]). Note that an estimate is also provided in DeSilva et al. (2013) for StW 99 but is not included here because the specimen may be *Paranthropus* (Partridge et al., 2003).

Figure 14: Femoral neck and head of StW 573. Taken by RHC from a first generation cast

Figure 15: Biomechanical femoral neck lengths in early hominins. StW 573 value estimated. Circles represent means and bars maximum and minimum values. Comparative data as reported in DeSilva et al. (2013). *Australopithecus afarensis* comprises AL 288-1, AL 333-3. Southern African *Australopithecus* sp. comprises MLD 46, Sts 14, StW 522 (estimated), StW 598. Note that a value is also provided in DeSilva et al. (2013) for StW 99 but is not included here because the specimen may be *Paranthropus* (Partridge et al., 2003).

Figure 16: Lateral (left) and Medial (right) femoral condyle shape. Top: StW 573; Middle: a *Gorilla gorilla* individual; Bottom: *a Pan troglodytes* individual. Images of StW 573 made by RHC from a first-generation cast. Others originals in the Liverpool University collection, courtesy of Kristiaan D'Août.

Figure 17: Tibial condyles of StW 573: Top, from above (first-generation cast, by RHC)
Bottom: medial, lateral and frontal views (original, courtesy of Ronald Clarke) .

Figure 18: Relative lengths of the tibial condyles. These are similar among *Australopithecuss* (Spearman's correlation r = 0.94, *p* = 0.005). StW 573 data from Heaton et al. (2019). Comparative data as reported in DeSilva et al. (2018). *Australopithecus afarensis* comprises AL 129-1, AL 288-1, AL 333x-26, AL 330-6.

Figure 19: Tibial condyle shape (mediolateral width / anteroposterior width x 100 for each condyle). The shape of the StW 573 tibial condyles is similar overall to those of *Au. anamensis*, but *Au. afarensis* is more divergent, especially in medial condyle shape. StW 573 data from Heaton et al. (2019). Comparative data as reported in DeSilva et al. (2018). *Australopithecus afarensis* comprises AL 129-1, AL 288-1, AL 333x-26, AL 330-6.

Figure 20: Distal tibial shape. StW 573 falls within the range of other *Australopithecus*. StW 573 data from Heaton et al. (2019). Comparative data as reported in DeSilva et al. (2018). Southern African (SA) *Australopithecus* sp. comprises StW 358, StW 567. *Australopithecus sediba* comprises MH2, MH4.

Figure 21: Top: Archival image of an indigenous arboreal forager climbing a thin vine using flexed elbow postures and hallucal grasp (courtesy of Kirk Endicott) Bottom: An indigenous Batek arboreal forager demonstrating his hallucal grasp for climbing a small vine (video frame, courtesy of Vivek Venkataraman)
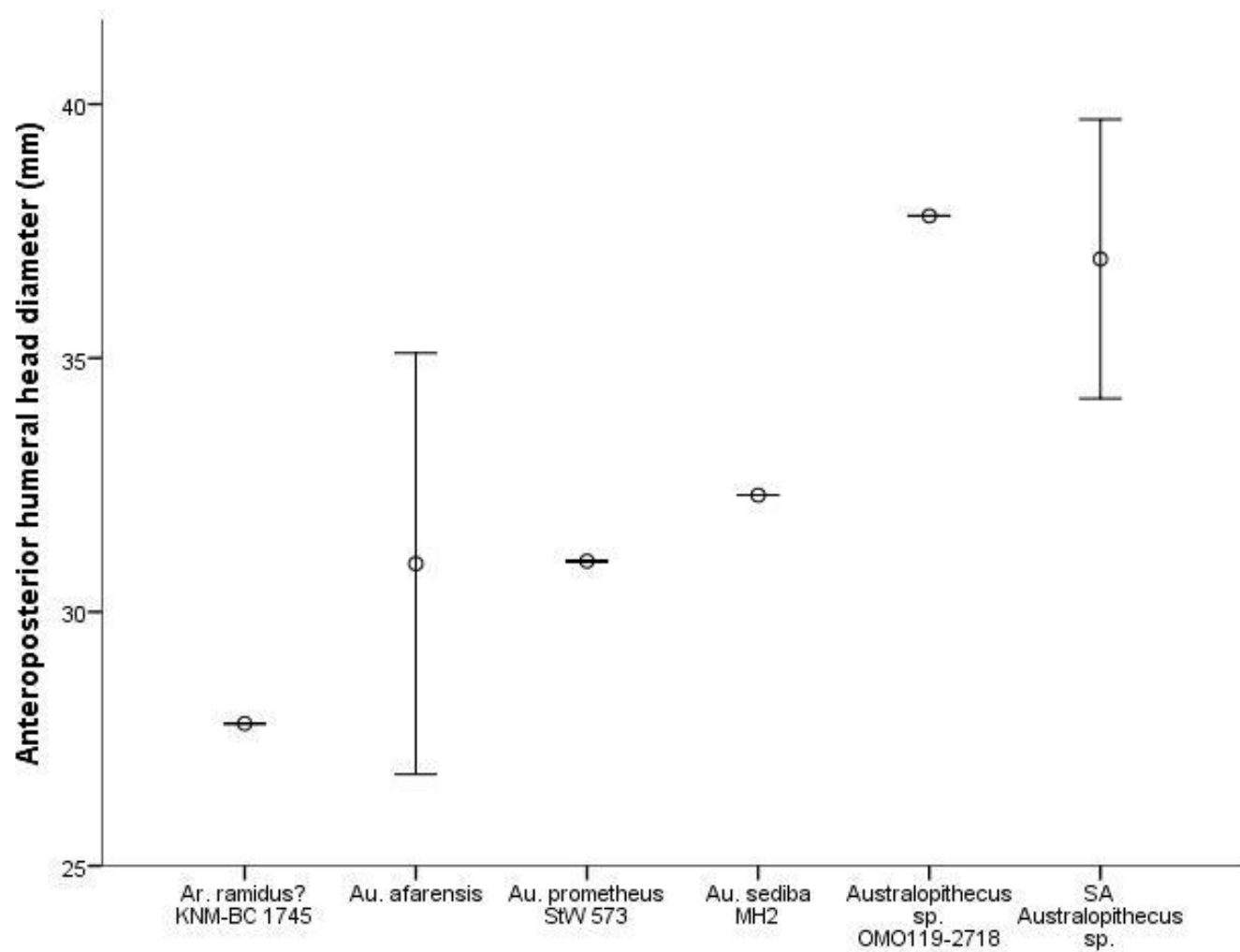
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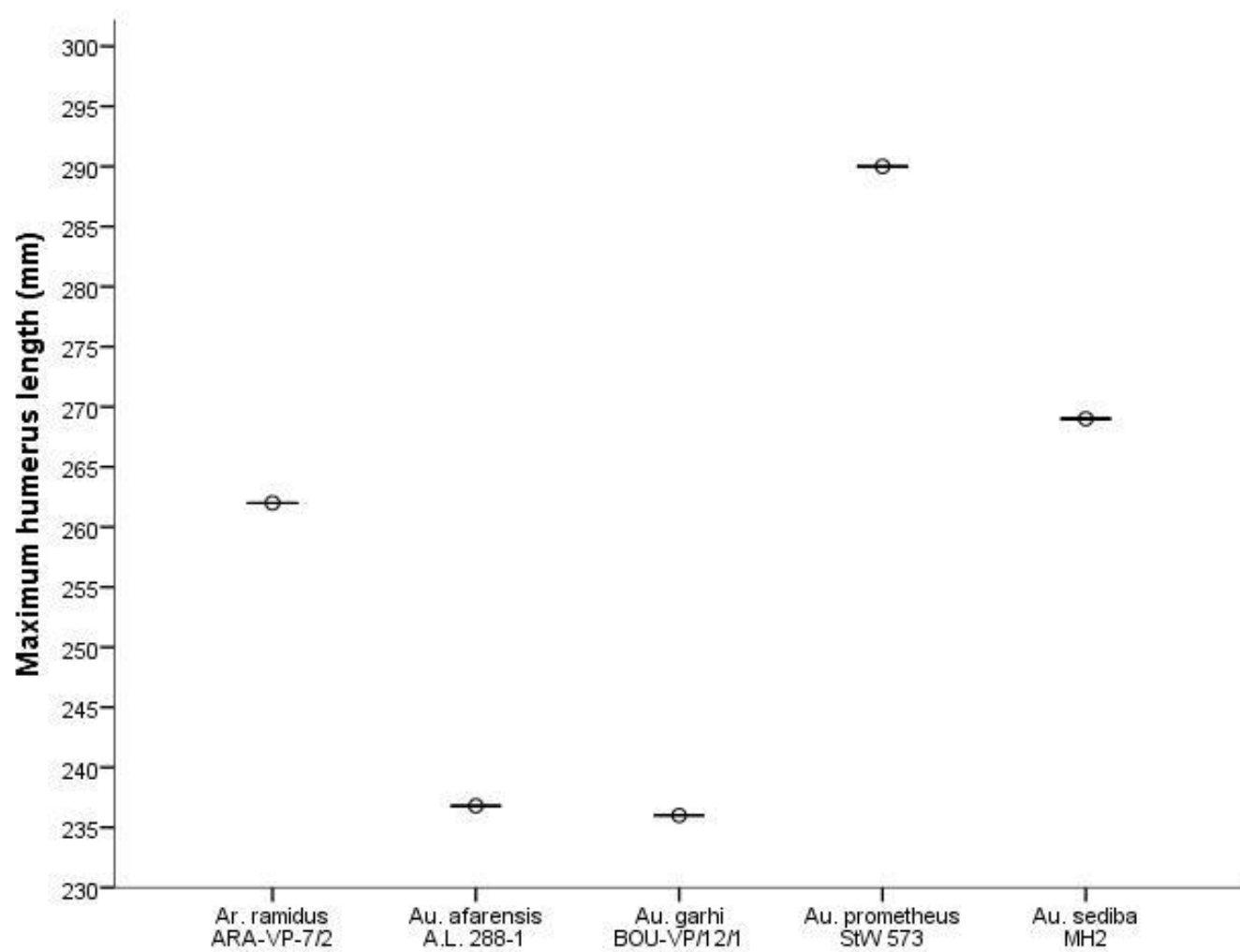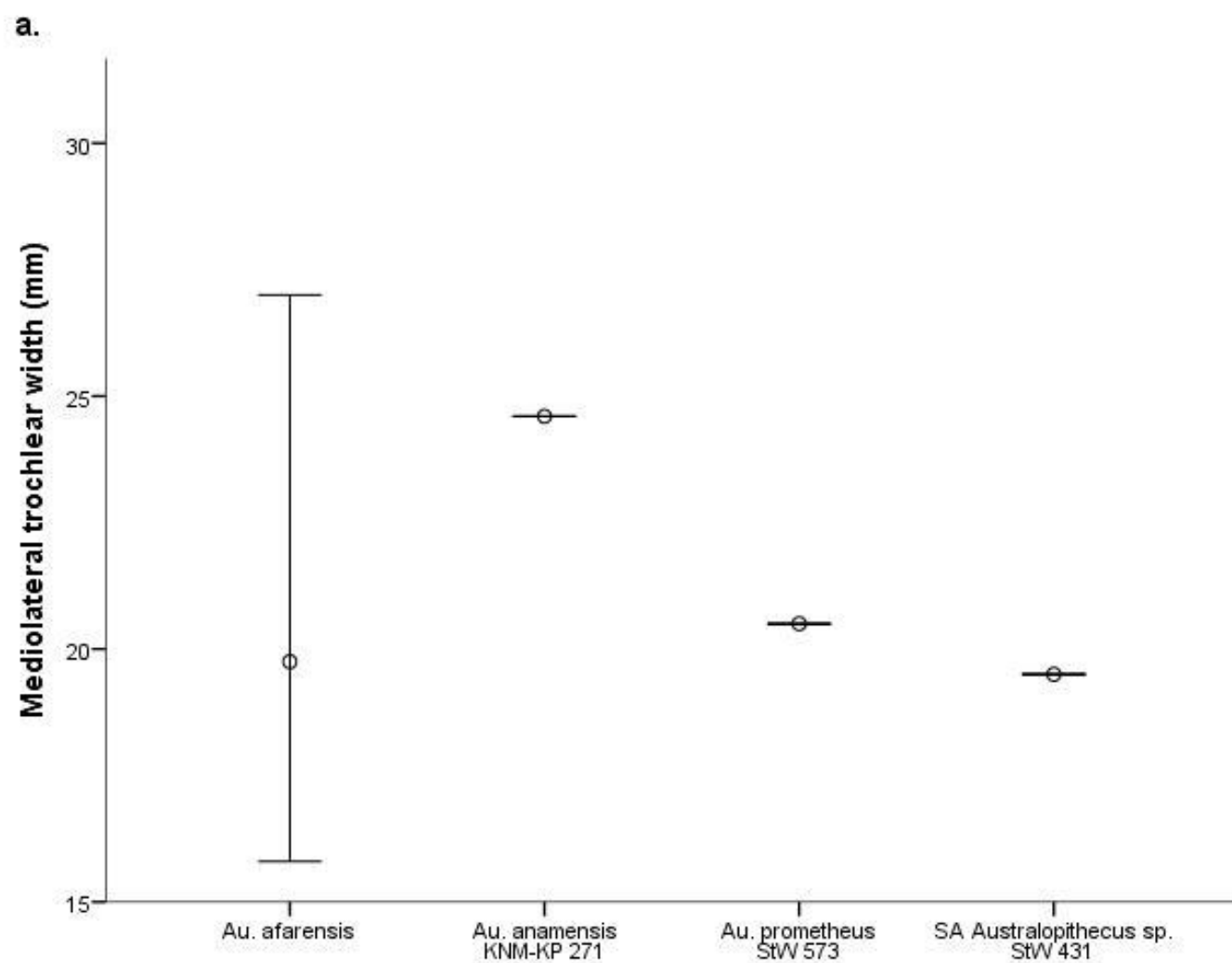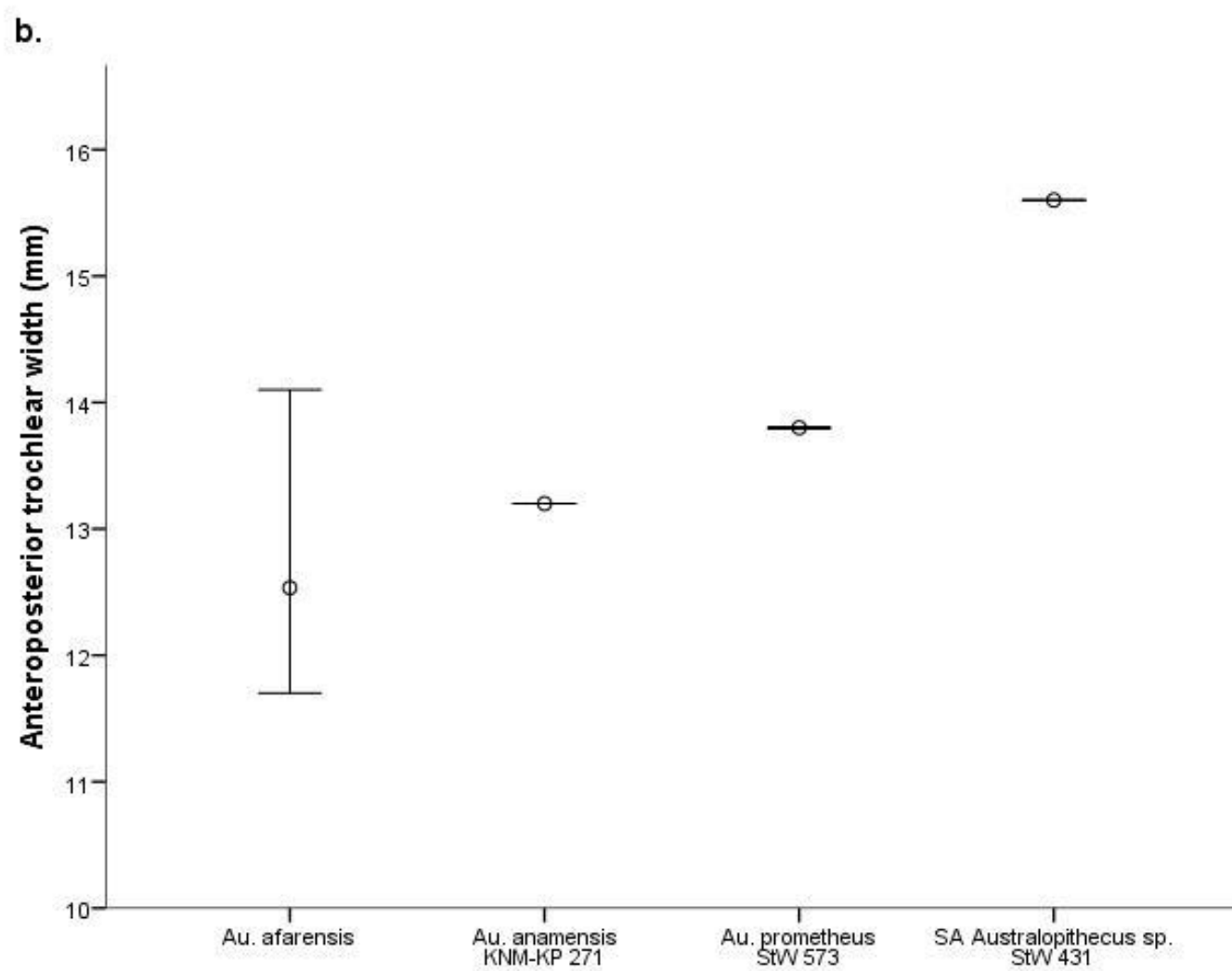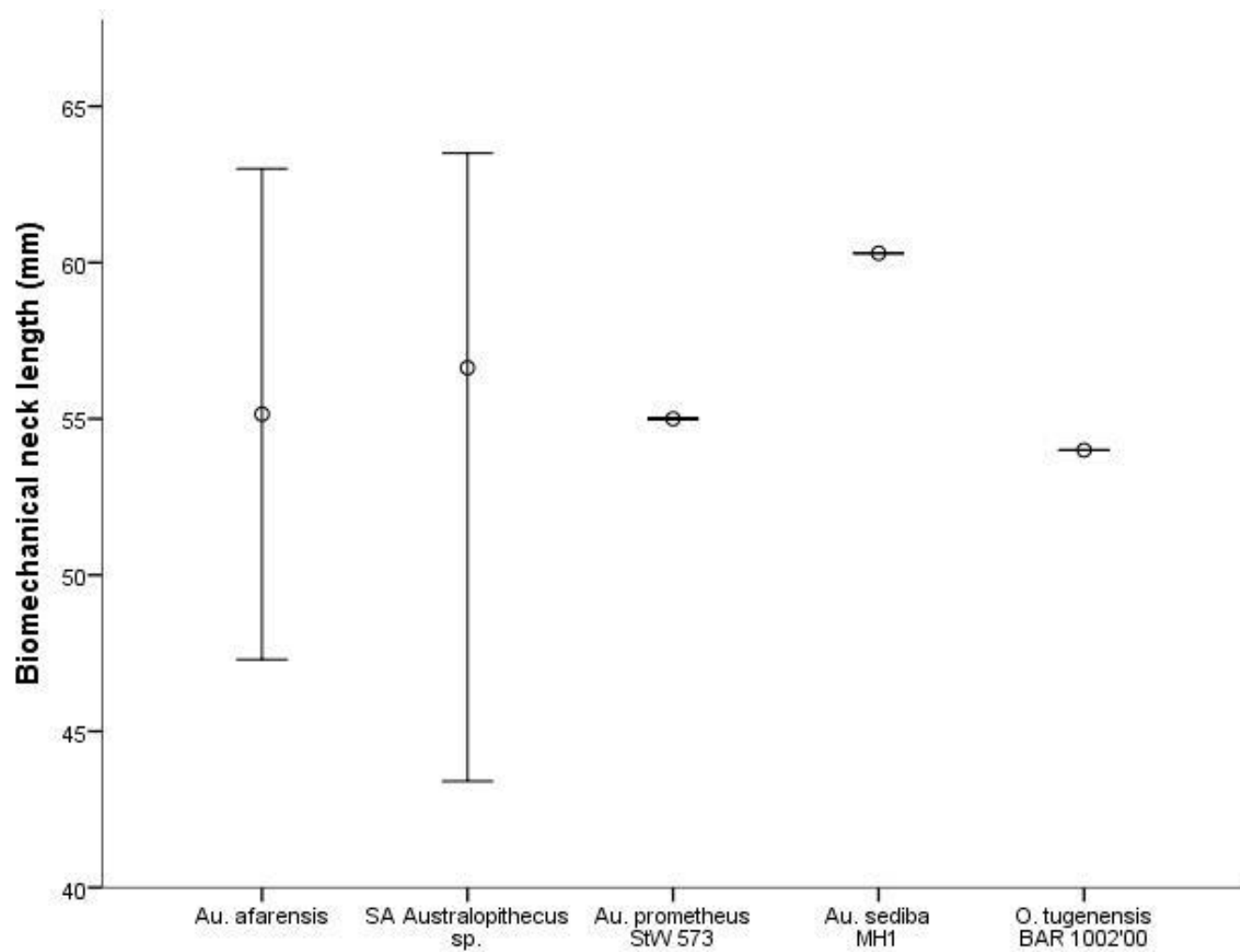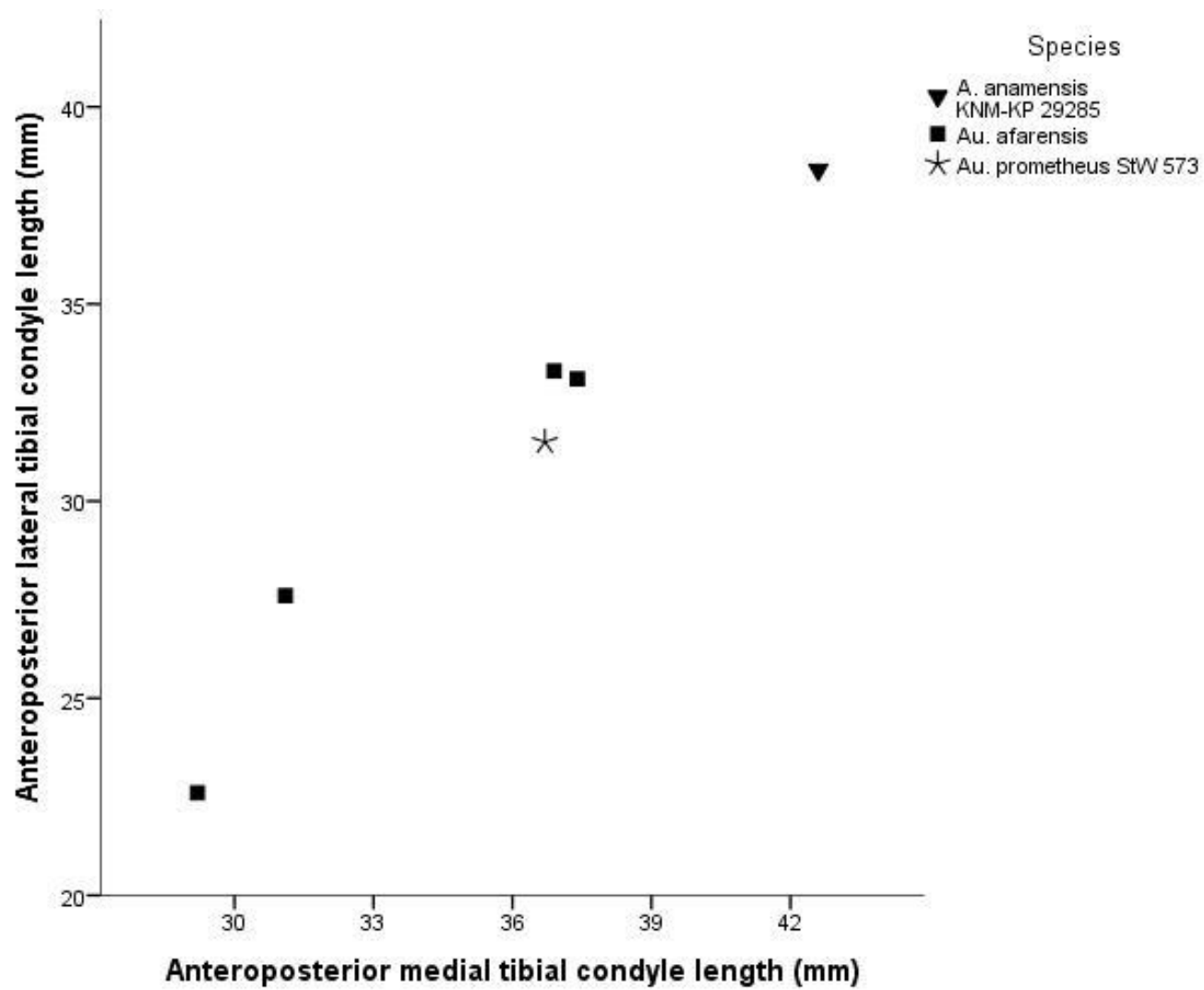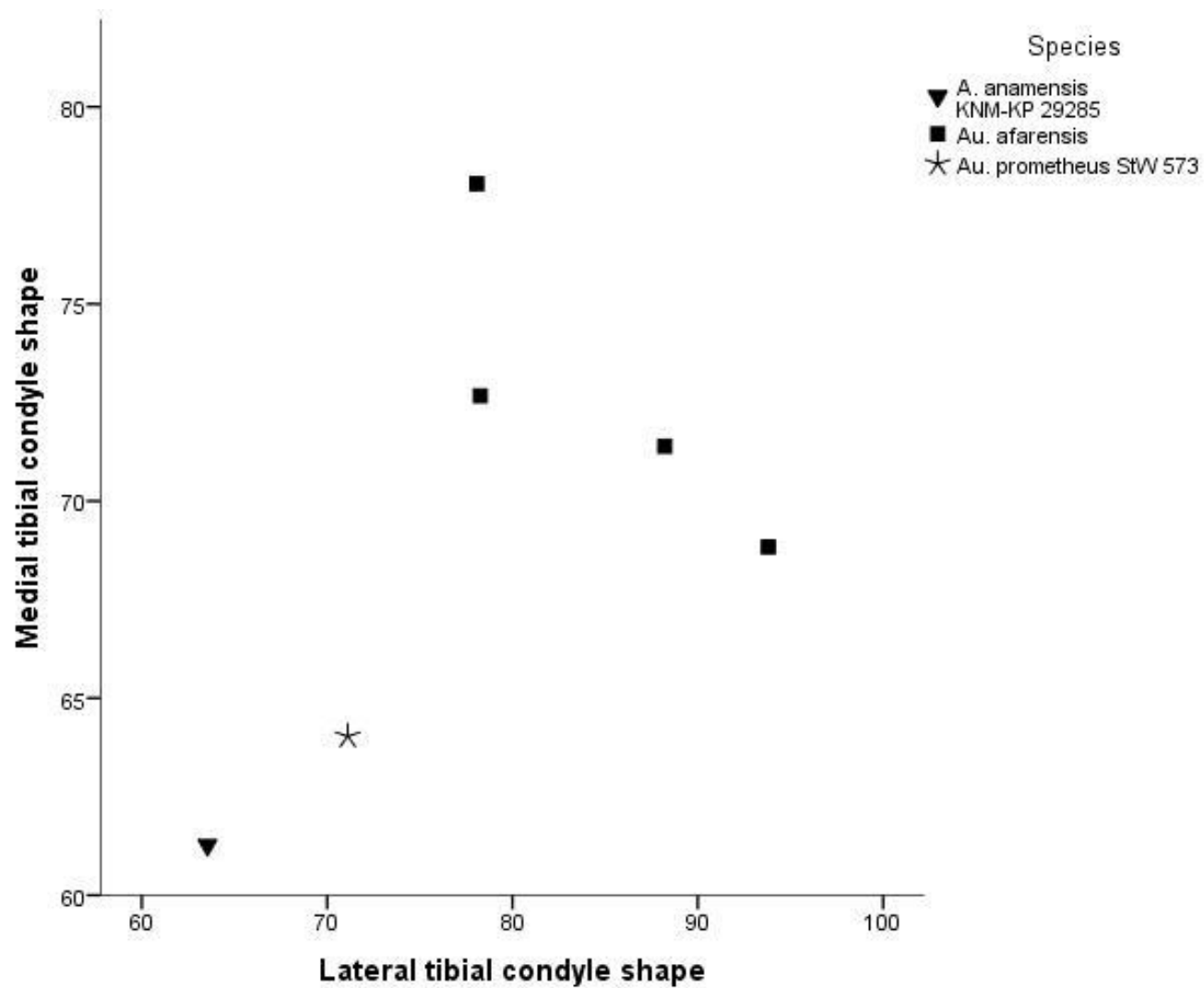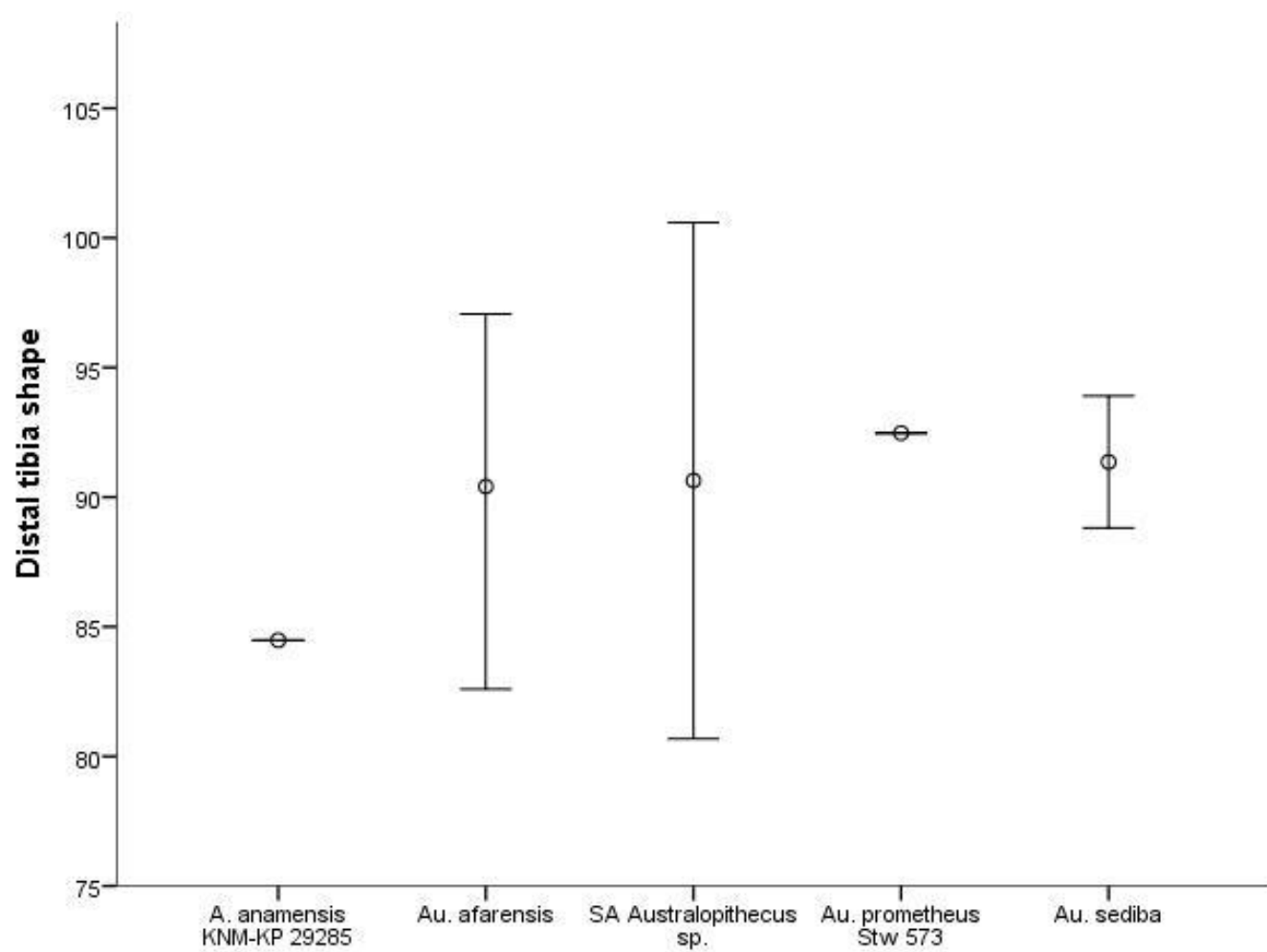**a.**

50

b.

c.

d.

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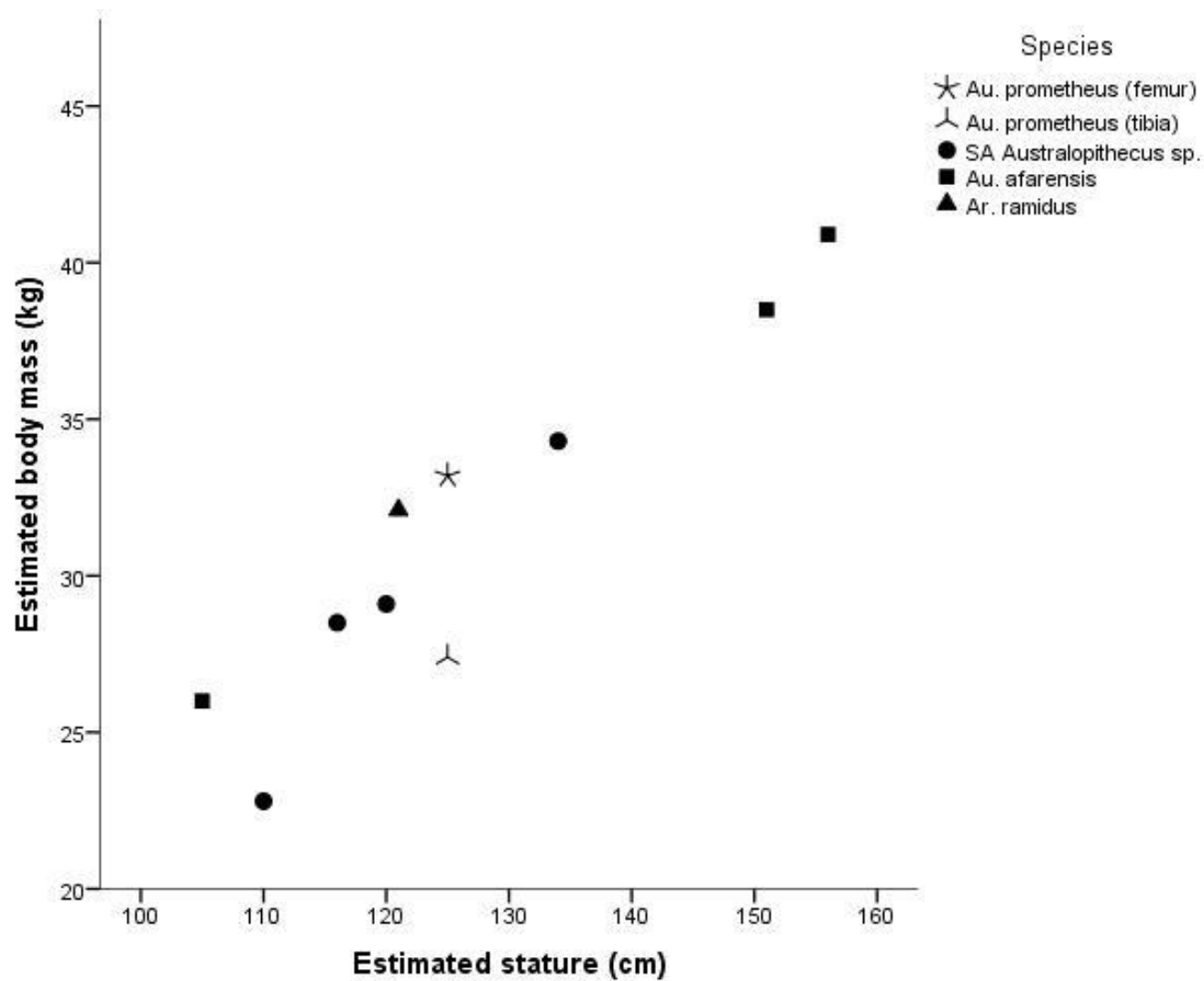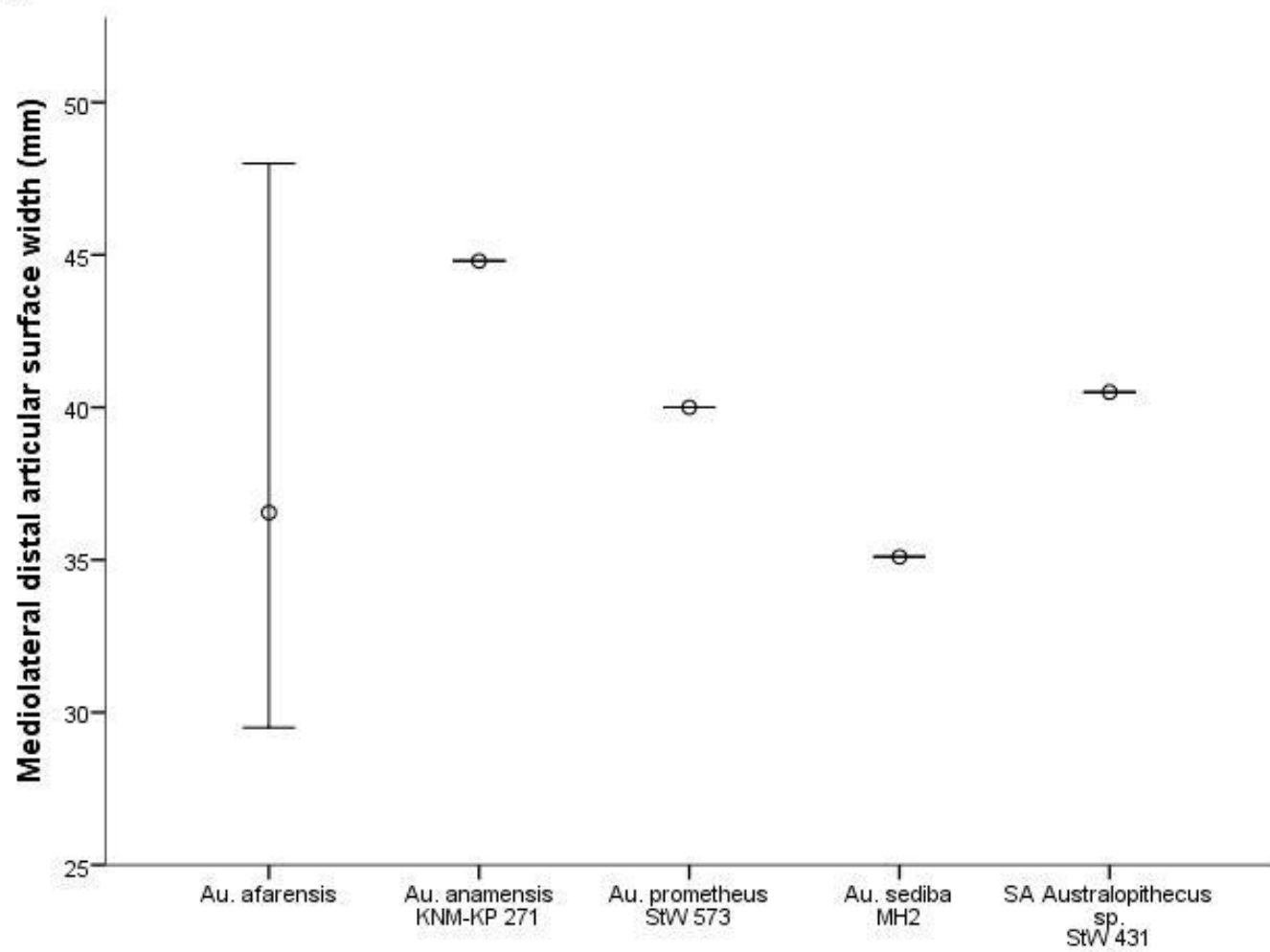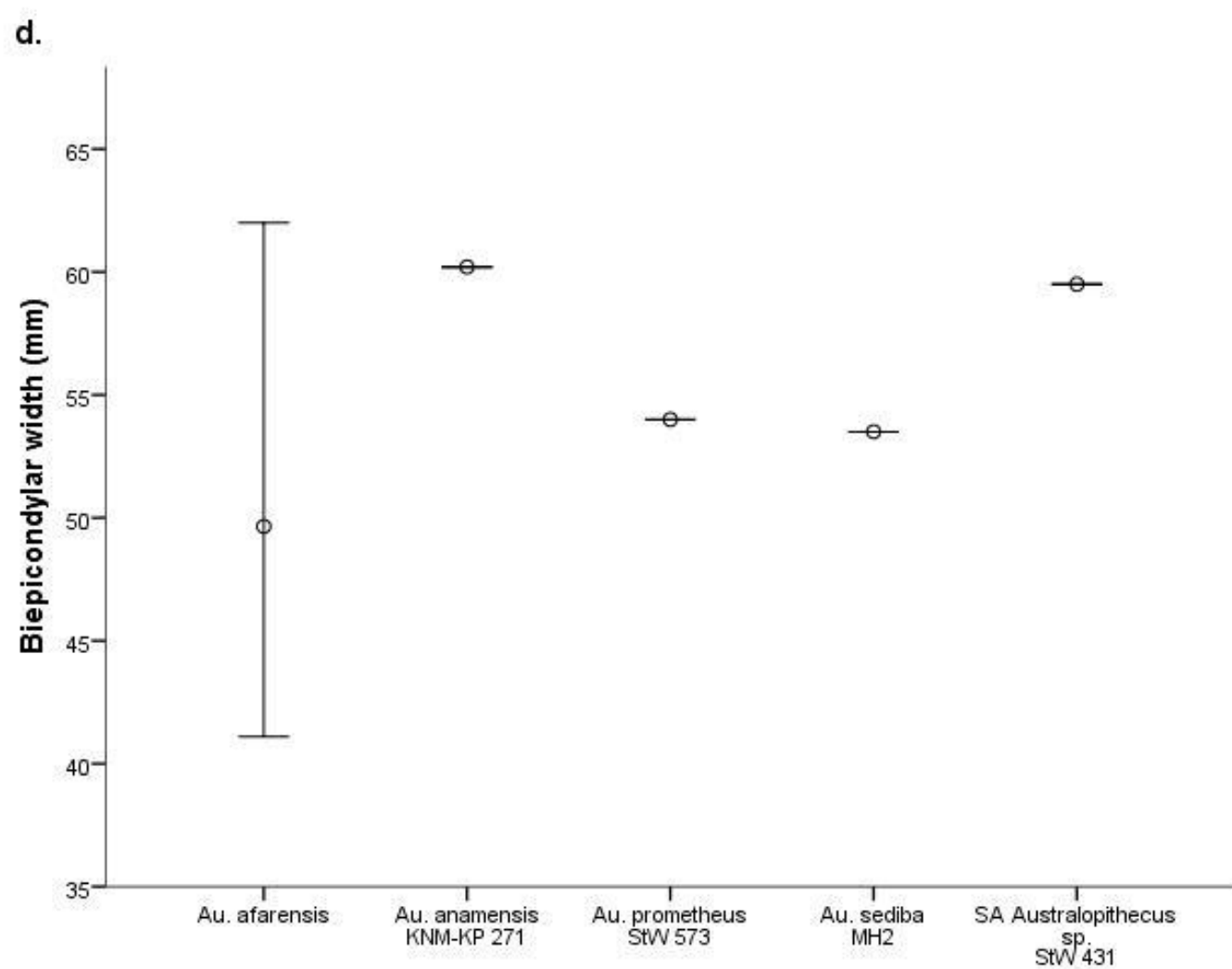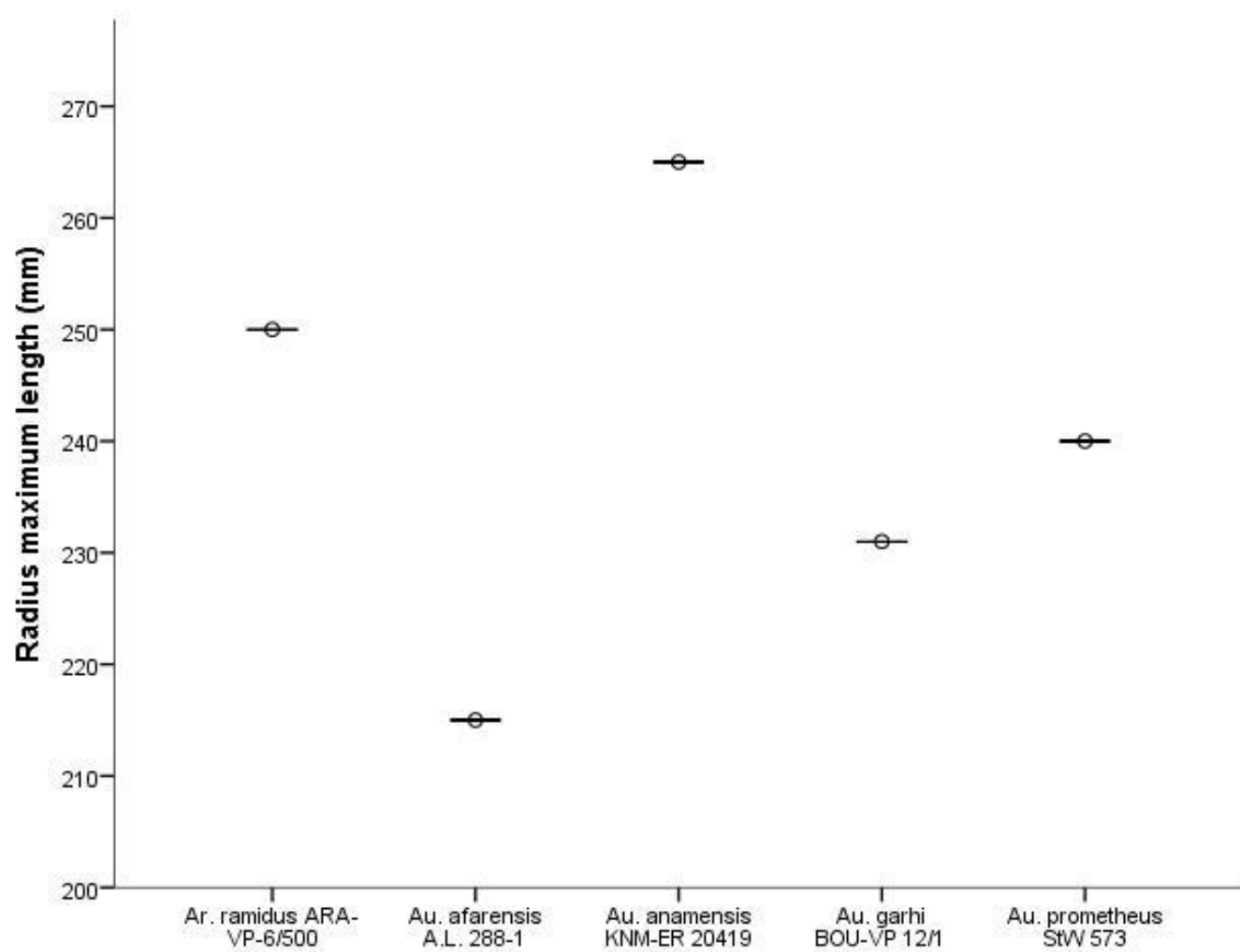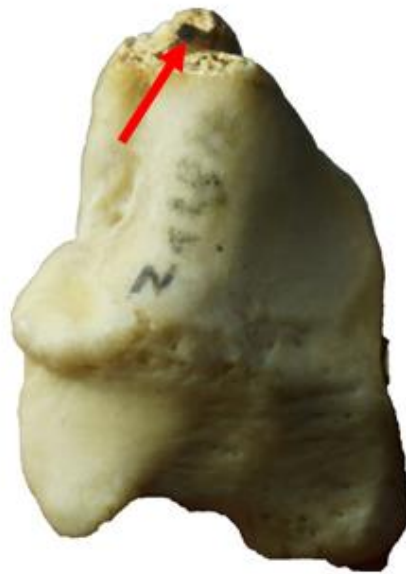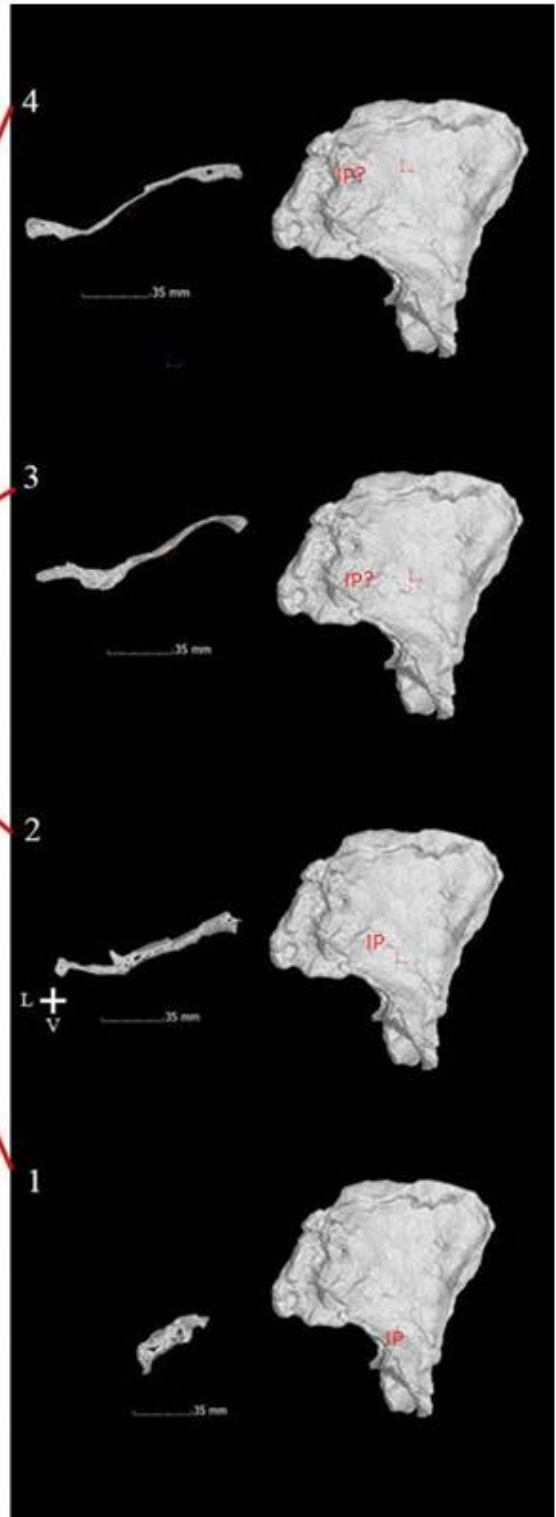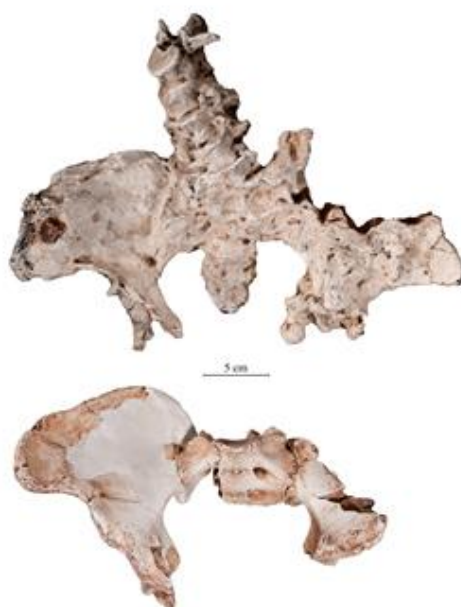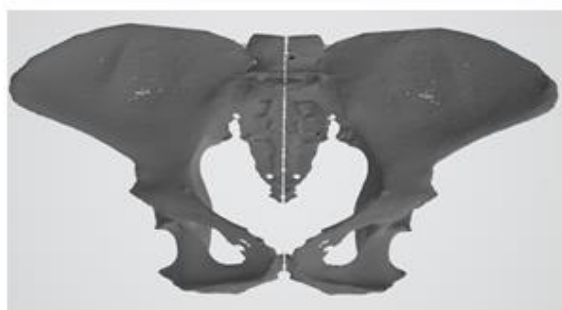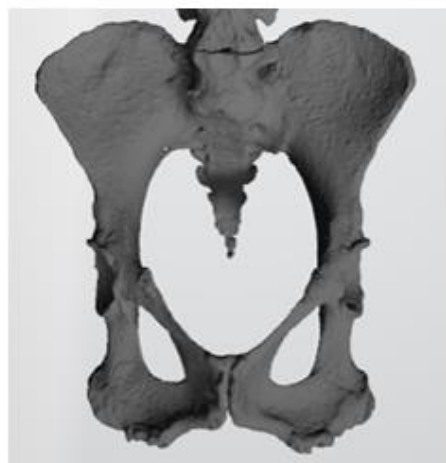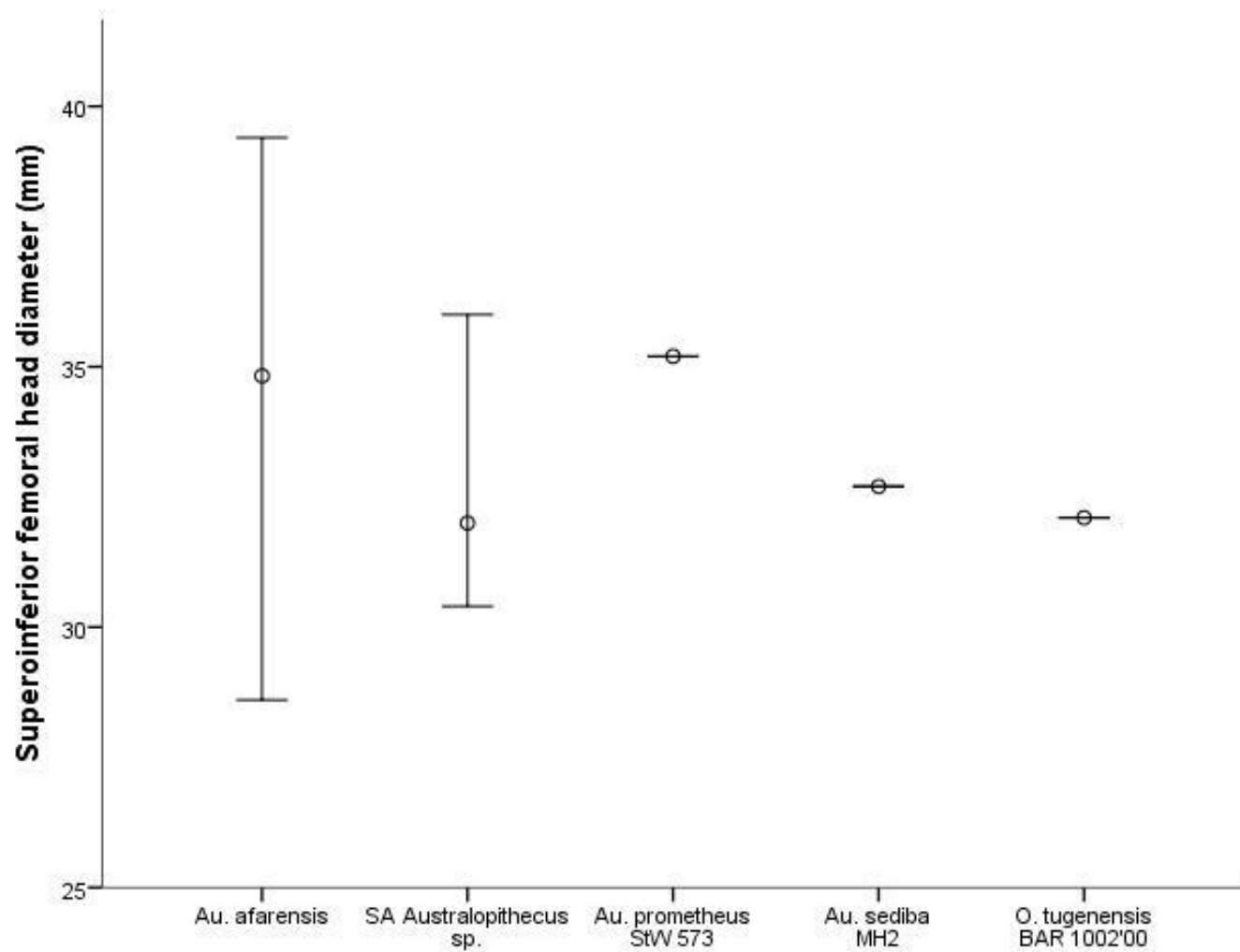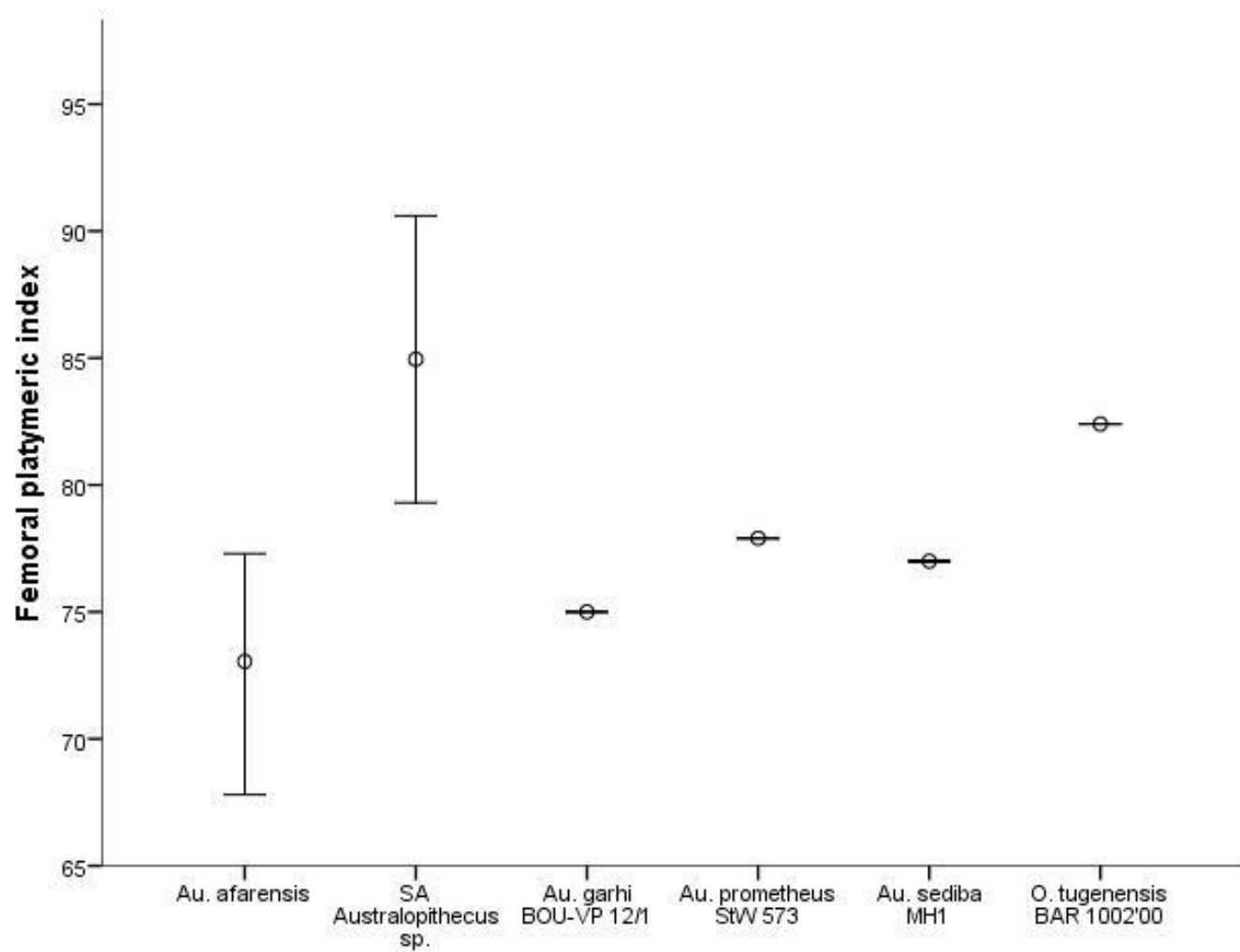
Table 1: Clavicle metrics of StW 573 compared to other hominins[a] and NHGAs*

Specimen	Maximum length (mm)	Anterioposterior-diameter at conoid (mm)	Circumference at midshaft (mm)	SuperioInferior diameter at conoid (mm)	
StW 573 [*a]	142.9	14.3	38	11.6	
KSD-VP-1	~156	--	46	--	
A.L. 438-1	--	16.3		12.9	
A.L. 333x-6/9	--	12.4		9.3	
MH2	~108	--	27	--	
	~131	--	Mean 35 (sample also includes OH-48, ATD 6-50 and D-41610)	--	
Modern humans [*c]	148.7 ± 11.3	--	Mean 39.2 N=25	--	
Pan[*c] (species unknown)	Mean 117, N=9	--	Mean 35.8 N=25	--	
Gorilla gorilla[*c]	Mean 151, N=15	--	Mean 43.2 N=25 (species unknown)	--	
*Gorilla beringei**	Mean 163 (N=6)	--	--	--	
*Pongo pygmaeus**	Mean 159 (N=43, 36 adults)	--	--	--	

Table 2: radial neck metrics of StW 573 and comparative sample.[a]

Specimen/taxon	Relative radial neck thickness ([anteroposterior neck diameter / anteroposterior head diameter] x 100)	Radial neck length (mm; from the middle of the proximal surface of the radial head to the centre of the radial tuberosity)	Relative radial neck length ([neck length / maximum length] x 100)
StW 573	69.9	34	14.2
A.L. 288-1	~63		
KNM-ER 20419	~64	39	~14.7
Homo sapiens (mean)	~64		14.1
Pan (mean)	~ 55		15.6
Gorilla (mean)	~51		18.4
Pongo (mean)	~58		12

[a] Left radius of StW 573 from Heaton et al. (2019); radius metrics for *Pan*, *Homo sapiens*, A.L. 288-1 and the Allia Bay radius KNM-ER 20419 from Heinrich et al. (1993) (~ = estimated from plot).