Recent Discoveries and Perspectives in Human Evolution

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Table of Contents

2.

AUSTRALOPITHECINE SHOULDERS: NEW REMAINS FOR OLD DEBATE

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Abstract: *Since the discovery of three well preserved australopithecine skeletons, viz., Malapa (*Australopithecus sediba*), Woranso-Mille (*Australopithecus afarensis*) and Dikika (juvenile* Australopithecus afarensis*) the debate about their putative arboreal locomotion is still not closed although their upper limbs, and in peculiar their shoulder girdles, are well preserved. Upper arms movements depend directly on shoulder architecture such that this complex is the key system for knowing the arboreal part of any primate behaviour. Notwithstanding within these three newcomers the shoulder remains are well preserved, the studies on them have lead to opposite conclusions. In present work I discuss why these three newcomers have not sold out the debate about australopithecine arboreal behaviour. There are a number of reasons for the divergent inferences, such as the conservation state as well as the hominoid species used for comparisons, being the major ones. The out shoulder morphology of these three newcomers lead me to draw a scheme of australopithecines shoulder which is close to the first* Homo *species and extant apes but not similar to any of them.*

Keywords: *Scapula; Clavicle; Humerus; Locomotion;* Australopithecus afarensis; Australopithecus sediba

INTRODUCTION

Shoulder is an important joint complex because it links the upper limb to the axial skeleton and allows, due to the clavicle, upper limb movements outside the parasagital plane. This allows climbing and manipulating habits within Theria – five orders still possess a complete clavicle, viz., Primates, Chiroptera, Insectivora (except Potamogale), Dermoptera, and Tubilidentata (Lessertisseur and Saban 1967). Although, shoulder complex is very important to understand extinct hominin behaviour, very little work has been done on it (Oxnard 1968a, b; Vallois 1976, 1977; Vrba 1979; Senut 1981; Voisin 2001a, 2004a, 2010) because shoulder remains are very scarce and fragmentary, especially for older species like australopithecines. Thereby, we knew very little about australopithecine shoulder before 2006. But, since 2006, three newcomers, Woranso-Milles (*Australopithecus afarensis*), Dikika (juvenil *Australopithecus afarensis*) and Malapa (*Australopithecus sediba*) have fundamentally enhanced our knowledge about australopithecines shoulder. However, studies on their shoulders lead to opposite conclusions, which apparently make no sense and compel a review.

This paper attempt a comparative analysis of the shoulder studies of these three newcomers (Alemseged et al. 2006; Berger et al. 2010; Haile-Selassie et al. 2010; Green and Alemseged 2012; Churchill et al. 2013) and try to explain the contradictions among conclusions arrived at by various studies. Nevertheless, this work would not classify publications from the worst to the best but just make a reflection about palaeoanthropological studies and give my point of view about australopithecines arboreal behaviour.

I will start with a summary of the characteristics of the shoulders of these three new australopithecines and I would try to highlight the weaknesses of these studies and complete, when possible, analysis made by authors. I will then draw an architectural scheme of the australopithecines shoulder.

AUSTRALOPITHECINES

Australopithecus sediba (Malapa)

The two Malapa fossils are not the most complete australopithecine remains, but they are exceptional for the shoulder study. In particular, MH2 individual displays a nearly complete clavicle and a very well preserved scapula and humerus. These three bones belong to the same side (Berger et al. 2010; Churchill et al. 2013).

The dorsal view morphology of the Malapa clavicles (UW88-38 & UW88-1) is described as closer to the chimpanzee than to modern human (Churchill et al. 2013) which is coherent with the Fig. 2 of their paper, especially for the complete clavicle UV88-38 (MH2 individual).

If *Australopithecus sediba* clavicles are morphologically closer to the chimpanzee than to modern humans thus Malapa clavicles would display two curvatures in dorsal view (Fig. 2.1), but picture from Churchill and colleagues does not allow to determinate any curvatures in dorsal view. These two curvatures are associated to a scapula

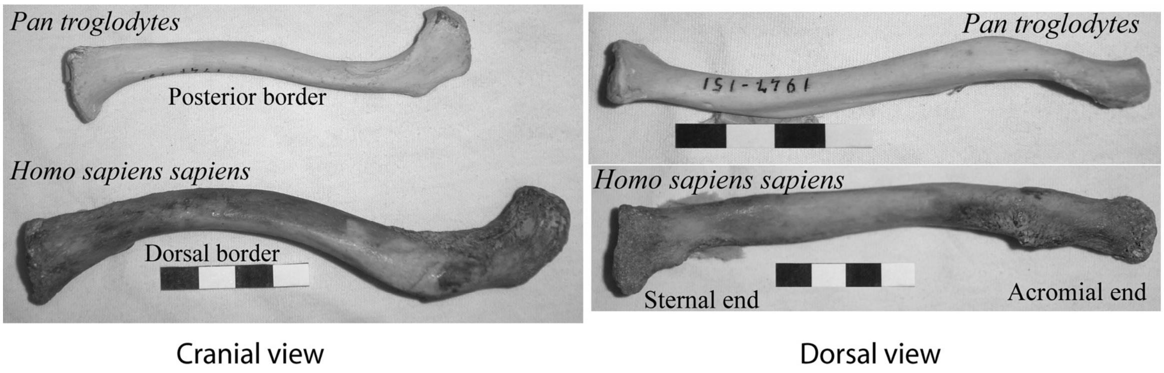

Fig. 2.1. Chimpanzee and human clavicles in superior (left) and in dorsal (right) view

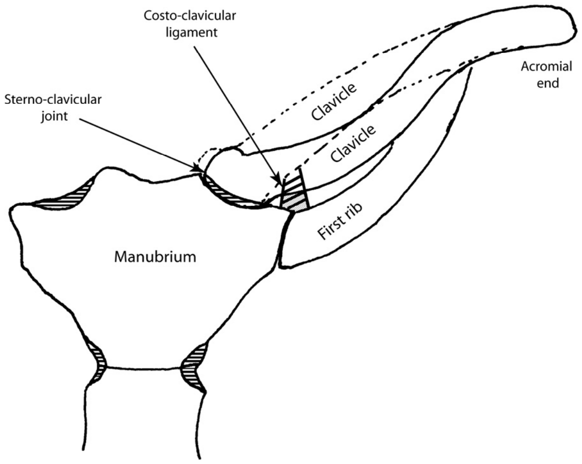

Fig. 2.2. Clavicles associated with a high scapula in regard to the thorax. Dotted line: clavicle with a unique inferior curvature (human morphology); full line: clavicle with two curvatures in dorsal view (great apes morphology). Note the high difference in regard to the manubrium between the two clavicular morphologies (after Voisin 2006)

which is higher in regard to the thorax than in modern human. The sternoclavicular joint is supported by the costoclavicular ligament (the Fig. 2 of Churchill and colleagues paper shows a clear costoclavicular imprint on the sternal end of the clavicle), which exists only in apes and humans (Cave 1961) and limits horizontal and vertical clavicle movements (Voisin, 2006). In this case, a costoclavicular ligament elongation increases the mobility and weakness of the sternoclavicular joint and involves greater muscular control, exerted by the subclavius muscle. In apes, an important superior curvature permits us to associate a high and dorsal scapula with respect to the thorax and a clavicle with its medial end nearly parallel to the manubrium (Fig. 2.2). This condition avoids the elongation of the costo-clavicular ligament (Voisin 2006). Hence, the scapula of *Australopithecus sediba* would be dorsal and higher in regard to the thorax than in modern human. Thereby, the shoulder architecture of this species might be closer to the great apes architecture than to modern human one, as Churchill and colleagues already proposed it.

Malapa clavicles are described as very short by Churchill et al. (2013) as they are shorter than other australopithecines clavicles (Tab. 2.1). However, there are only two australopithecine clavicles which are sufficiently well preserved to estimate correctly their absolute length: the Kadanuumuu one (but see below) and the AL333x-6/9 one. On the other hand, the absolute length of the Malapa clavicle fits with the lowest chimpanzee values (Tab. 2.1). To avoid size effect, the claviculo-humeral index (*clavicle maximum length/humerus maximum length * 100*) has been used. This ratio is the more appropriate method because there is a common isometric scaling relationship between clavicular and humeral length across all non human primates (Larson 2007, 2013). This ratio has not been calculated before Malapa discovery because no individual displayed complete clavicle and humerus from the same side. The value for *Australopithecus sediba* claviculo-humeral index is very low, outside the range of variation of modern human (Tab. 2.1), but inside the gibbon and chimpanzee range of variation (Voisin 2000). In other words, clavicles of Malapa australopithecine are relatively short and humerus is relatively long, which is an arboreal character.

The shortness of the Malapa clavicles implies a scapula, although dorsal, which is more lateral in regard to the thorax than in modern human, even more lateral than Kadanuumuu scapula (but see below). This more laterally position of the scapula corresponds to great apes shoulder architecture and close to what existed in oldest *Homo* species (Voisin 2010). Hence, the Malapa shoulder is characterized by a scapula which is higher and less dorsal in regard to the thorax than in modern human. This architecture is close to that of great apes (Schultz 1961; Sakka 1985; Voisin 2010) and hence might be associated to a funnel chest like in extant great apes.

Churchill and colleagues emphasize the great conoid tubercle which exists on the two clavicles remains UW88-38 (MH2) and UW88-1 (MH1). Following Vbra (1979) these authors consider that this character is associated to arboreal behavior. However, there is a great variation about the size of this tubercle, especially on australopithecines clavicles and its function is still unclear (Larson 2013).

Concerning the humerus, Churchill and his colleagues emphasize the humeral torsion, whereas they give numerous metrics data on the two humeral remains in

*Tab. 2.1. Absolute and relative clavicular length in apes, modern humans and some australopithecine clavicles. M: mean (in mm); SD: standard deviation; (L): left; (R): right; §: fossils and Primates not included in Haile-Selassie et al. (2010) and in Churchill et al. (2013); *: data calculated with the complete humeral length estimated. **: Data calculated with the humerus and clavicle length estimated; –: No data available (after table S8 of Haile-Selassie et al., 2010 and after table S1 of Churchill et al. 2013)*

Taxon	Sample	Clavicle Length	Claviculo-humeral index	Authors
§Hylobates	§22	§M: 93.9 SD: 7.7	§M: 41.2 SD: 4.6	Voisin (2000)
§Pongo pygmaeus	§24	§M: 163.4 SD: 22.3	§M: 49,1 SD: 2.35	Voisin (2000)
Pan troglodytes	25	M: 128.7 SD: 8.8	M: 43,8 SD: 2.6	Churchill et al. (2013)
§Pan paniscus	§19	§M: 104.2 SD: 2.9	§M: 37.1 SD: 1.6	Voisin (2000)
Gorilla gorilla	25-18	M: 151.2 SD: 20.6	M: 36.3 SD: 2.0	Haile-Selassie et al. (2010)
Homo sapiens	25-59	M: 148.7 SD: 11.3	M: 45.4 SD: 2.7	Haile-Selassie et al. (2010)
§West Neandertals	§5	§M: 157.9 SD: 16.9	–	Voisin (2011)
§Homo ergaster	§KNM-WT 15000 (R)	§129.0	§44.5 (41.7)*	Voisin (2000)
	§KNM-WT 15000 (L)	§127.0	–	Voisin (2000)
§Homo sp	§Narmada clavicle (R)	§ 90.0	–	Sankhyan (1997)
	§Narmada clavicle (L)	§~90.0	–	Sankhyan (2005)
§Homo habilis	§OH48 (L)	§129.5	–	Voisin (2000)
Australopithecus sediba	UW88-38 (R)	107.5	40.0	Churchill et al. (2013)
Australopithecus afarensis	§AL333x-6/9 (R)	97.9	–	Lovejoy et al. (1982)
	KSD-VP-1/1f (L)	156.4	§32.5**	Haile-Selassie et al. (2010)

their table S9. The humeral torsion of the two *Australopithecus sediba* humerus is very low but similar to other australopithecines values and inferior to extant apes as well as modern humans (Churchill et al., 2013, Table 2). This result confirms Larson (1996) affirmation suggesting that the similar high degree of torsion found in the latter two groups evolved independently and thus is derived trait.

Although, the Figure 1 from Churchill and colleagues displays an hominoid like overall morphology for the MH2 proximal humerus, they only give data about the antero-posterior diameter of the head which is close to that of modern human and chimpanzee. However, the humeral head morphology is not exactly similar between apes and modern humans. The former have a spherical humeral head or slightly broader than tall while the latter is characterized by an humeral head which is slightly taller than wide (Larson 2007, 2013). Thus a precise study of the proximal humerus has to be done. The morphology and size of the two tubercles are not similar between extant hominoids and are linked to function (Voisin 2000; Larson 2007). Hence, Malapa humerus would give us new insight about australopithecines locomotion pattern in the future with new studies. Indeed, Ciochon and Corrucini (1976) have shown the proximal part of the Sts7 humerus is peculiar in the size of the great tubercle and does not fit either with modern human morphology or of the apes.

Moreover, Churchill and colleagues do not take into account the relative position of the deltoid tuberosity even if they give the absolute position of this tuberosity in their table S9 (Table 2.3). If this position is calculated as a ratio (*deltoid position/Humeral maximum length * 100*) it might be possible to compare it between hominoids (Voisin 2004b). Voisin (2004b) has demonstrated that the lowest values are associated with the most arboreal apes such as Orangutan and Gibbon. The higher values are associated to knuckle walker and biped primates (Chimpanzee, Gorilla and human). As shown in table 2.3, *Australopithecus sediba* tuberosity position index is similar to that of *Pongo* and *Hylobates*. In other words, the insertion of the deltoid muscle on the humerus shaft of *Australopithecus sediba*, revealed by the deltoid tuberosity position, is characteristic of a well-developed arboreal behavior.

The scapula of the individual MH2 (UW88-56) is very well preserved (see figure 3 in Churchill and colleagues paper) and its overall morphology cluster it easily with great apes ones (Churchill et al. 2013). It possesses a cranially oriented glenoid fossa, a markedly cranially directed spine, a convex vertebral border, an acromion process (UW88-103[1]) which is long and curved with a large attachment area for supraspinatus muscle. All those traits are characteristic of apes (Vallois 1932) even if

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[1] This remains comes from a left scapula.

*Tab. 2.2. Humeral torsion angles in extinct hominins and extant hominoids after table S8 of Churchill et al. (2013). M: Mean; SD: Standard deviation; n: Sample size; *: May be not* A. africanus *even not australopithecine (see Howell & Coppens (1976) and McHenry (1994); §: Fossils not included in Churchill et al. (2013) paper. According to picture S26 (Haile-Selassie et al., 2010) length of the humerus KSDP-VP-1/1f has been estimated to 235 mm. As this remains represent 60% of its real size, thus the real size is estimated to 480 mm*

Species	**Individual**	**Adult**	**Subadult**	**Author**
Australopithecus sediba	UW88-57, (MH2)	117.0°	–	Churchill et al. (2013)
	UW88-34, 42, 88 (MH1)	112.0°	–	Churchill et al. (2013)
Australopithecus afarensis	A.L.288-1 (Lucy)	124.0°	–	Churchill et al. (2013)
Australopithecus africanus	§Omo 119-73-2718*	130.0°	–	(Larson 1996)
	§Sts 7	127.0°	–	(Larson 1996)
Homo erectus	D4167	110.0°	–	Churchill et al. (2013)
	KNM-WT 15000	–	111.5°	Churchill et al. (2013)
	D2680	–	104.0°	Churchill et al. (2013)
Homo floresiensis	B1/50	115.0°	–	Churchill et al. (2013)
Homo sapiens		M: 165.0° SD: 6.9°, n: 27	M: 168.0° SD: 4.5°, n: 4	Churchill et al. (2013)
Gorilla gorilla		M: 159.9° SD: 5.1°, n: 17	M: 162.3° SD: 4.5°, n: 6	Churchill et al. (2013)
Pan troglodytes		M: 153.4° SD: 6.5°, n: 4	M: 155.8° SD: 2.0°, n: 2	Churchill et al. (2013)
Pongo pygmaeus/abelii		M: 135.0° SD: 6.5°, n: 5	M: 138.4° SD: 7.5°, n: 9	Churchill et al. (2013)
Hylobates lar		M: 116.6° SD: 8.1°, n: 11	M: 118.0° SD: 6.9°, n: 10	Churchill et al. (2013)

Tab. 2.3. Metric characteristics of A. sediba *proximal humerus (After table S9 of Churchill et al. 2013); §: Data not included in Churchill et al. (2013). M: Mean; SD: Standard deviation; n: Sample size*

Species	**Humeral maximum length (1)**	**Humeral head antero-posterior diameter (2)**	**Deltoid tuberosity position (3)**	**Deltoid tuberosity position index (3)/(1)**
Au. sediba	269 n: 1	32.3 n: 1	134 n: 1	§49.8 n: 1
australopithecines	M: 263.6 SD: 47.1; n: 3	M: 34.9 SD: 5.9; n: 7	117 n: 1	–
early/archaic *Homo*	M: 307.0 SD: 17.0; n: 2	–	151 n: 1	–
modern *Homo*	M: 305.7 SD: 21.3; n: 67	M: 37.9 SD: 3.7; n: 67	M: 155.0 SD: 12.8; n: 67	§M: 54.5 SD: 2.7; n: 25
Gorilla	M: 420.5 SD: 41.2; n: 20	M: 57.2 SD: 7.8; n: 20	M: 232.5 SD: 30.9; n: 20	§M: 58.8 SD: 3.1; n: 37
Pan troglodytes	M: 283.5 SD: 14.7; n: 23	M: 39.5 SD: 2.5; n: 23	M: 153.8 SD: 13.1; n: 23	§M: 55.3 SD: 3.3; n: 33
§Pongo pygmaeus	§M: 324.2 SD: 29.1; n: 20	§M: 36.8 SD: 5.3; n: 20	§M: 158.7 SD: 14.0; n: 20	§M: 49.0 SD: 2.4; n: 20
§Hylobates sp.	§M: 228,9 SD: 12.7; n: 17	§M: 15.7 SD: 1.4; n: 17	§M: 112.1 SD: 13.7; n: 14	§M: 49,5 SD: 4.6; n: 31

their functional role is not always clear. According to Churchill and colleagues, the glenoid fossa of UW88-56 (MH2) is narrow relative to its height, with proportions most similar to orangutans and gorillas. However, the value these authors give for the glenoid fossa index is lower than any extant Hominoid (Tab. 2.4). Thus, this value may be an typographic error. Moreover, between Gorilla, Chimpanzee and Human there are no significant differences concerning the glenoid fossa index (Vallois 1932; Senut 1981; Voisin 2000), Table 2.4). Anyway, data available for australopithecines are included in extant hominoid variation (Tab. 2.4) and there are no obvious differences between Hominoid, except Gibbon (Voisin 2000).

According to Churchill et al. (2013) principal component analysis (PCA) the MH2 scapula is morphologically more similar to *Pongo* scapula than other Hominoids (see

Tab. 2.4. Metric characteristics of MH2 scapula and other hominoids (After tables S3 & S4 in Churchill et al. 2013). M: Mean; SD: Standard deviation, n: sample size

	Glenoid-Axillary Angle		**Glenoid Index**		**Supra and Infra Scapular Fossa Ratio**			
Species	***Value***	***Authors***	***Value***	***Authors***	***SFB***	***IFB***	***(1)/(2)***	***Authors***
Au. Sediba (MH2)	123.4°	Churchill et al. (2013)	55.6	Churchill et al. (2013)	49.4	89.2	0.55	Churchill et al. (2013)
A. afarensis (AL. 288 1L)	132° 115° 130° 132.2°	Voisin (2000) Senut (1981) Stern & Susman (1983) Green & Alemseged (2012)	67.5 78.5	Senut (1981) Voisin (2000)	–	–	–	–
A. afarenis (DIK-1-1)	Right: 128.6° Left: 129.2°	Green & Alemseged (2012)	–	–	–	–	Right: 0.75 Left: 0.68	Green & Alemseged (2012)
A. africanus (Sts 7)	120° 116° 128°	Vrba (1979) Senut (1981) Green & Alemseged (2012)	60,6 60,6 51,4 58,5	Vrba (1979) Vallois (1977) Robinson et al. (1950) Senut (1981)	–	–	–	–
A. africanus (Stw 162)	124.3°	Green & Alemseged (2012)	–	–	–	–	–	–
Modern *Homo*	M: 137.8° SD: 4.6; n: 47	Churchill et al. 2013	68.3 5.2	Churchill et al. (2013)	7.2 6.4	108.3 8.24	M: 0.44 SD: 0.05; n: 47	Churchill et al. (2013)
Pan troglodytes	M: 119.0° SD: 4.9; n: 14	Churchill et al. (2013)	71.2 4.7	Churchill et al. (2013)	74.5 6.6	78.5 6.8	M: 0.96 SD: 0.12; n: 14	Churchill et al. (2013)
Gorilla	M: 122.4° SD: 4.3; n: 20	Churchill et al. (2013)	69.4 4.5	Churchill et al. (2013)	111.3 18.9	121.4 19.2	M: 0.91 SD: 0.08; n: 20	Churchill et al. (2013)
Pongo	M: 124.1° SD: 3.5; n: 8	Churchill et al. (2013)	62.1 4.3	Churchill et al. (2013)	39.1 9.6	102.3 7.4	M: 0.38 SD: 0.07; n: 8	Churchill et al. (2013)
Hylobates	M: 115.3° SD: 5.2; n: 33	Churchill et al. (2013)	77.8 7.5	Churchill et al. (2013)	44.6 3.6	20.2 3.2	M: 2.27 SD: 0.46; n: 33	Churchill et al. (2013)

SFB= Supraspinatus fossa breadth, IFB= infraspinatus fossa breadth

figure S2 in Churchill and colleagues paper). However, the inferior axillary border has a prominent flange at the origin of teres major, indicating hypertrophy of this adductor and medial rotator of the humerus like in most human (Vallois 1932). For some traits also, like the glenoid fossa orientation, Malapa values are closer to *Gorilla* than *Pongo* (Churchill et al. 2013). This latter remark is interesting because the overall morphology of Dikika scapula is closer to *Gorilla* one than to any other apes (see below). The differences could be explained by locomotion differences between this two species as well as age differences (see below). Moreover, *Australopithecus sediba* scapula shape, as measured by the scapular index, is most similar to that seen in *Homo* and *Pan* than in *Pongo* (Table 2.4). All these remarks explain why *Australopithecus sediba* scapula is also close to the human cloud in Churchill et al. (2013) PCA (see figure S2 in Churchill and colleagues paper). Therefore Churchill and colleagues works reach the first description of *Australopithecus africanus* scapula by Broom et al. (1950). These latter authors noticed that *Australopithecus africanus* scapula share most characters with *Pongo* and few with other Hominoids, especially humans.

However, Churchill et al. (2013) do not lent any attention to the coracoid process, maybe because it seems to very badly preserved according to their figure 3, but this process might be one of the australopithecines scapula part which is the best studied, at least for Sts 7 remains[2] (Broom et al. 1950; Oxnard 1968a; Ciochon and Corruccini 1976; Vallois 1976, 1977; Vrba 1979). Sts 7 coracoid process has been described as characteristic of brachiating habits but according to Vrba (1979) this may be due to a misinterpretation of the remains. Hence a description of a new remains would have helped to clear the situation because the coracoid process orientation is very peculiar in strictly bipedal primates (Voisin, 2000b).

Churchill et al. (2013) study about the shoulder shows an important arboreal behavior for australopithecines, at least for *Australopithecus sediba*. However, the UW88-56 (MH2 scapula) does not correspond exactly with any extant Hominoid species. This arboreal locomotion is associated to a usual bipedalism (Fleagle 1998; de Bonis, 1999; Cartmill and Smith 2009; Chevalier, 2013) which means when not climbing on trees, upper limb was in a pendant position like in humans. Hence, this mixed of arboreal and bipedalism behavior should explain the peculiar morphology of *Au. sediba* shoulder. In short, there are numerous traits in *Australopithecus sediba* shoulder morphology and some of them are relevant with

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[2] Sts 7 Scapula might be one of australopithecine shoulder remains which have been the most studied.

arboreal displacement, especially: (i) the clavicle morphology in dorsal view; (ii) the orientation of the scapula spine as well as its glenoid fossa; (iii) the position of the deltoid tuberosity on humeral shaft and (iv) the humeral torsion. However, some traits are closer to modern human: (i) prominent flange at the origin of teres major and (ii) the dimension of the infra (and supra spinatus fossa.

Australopithecus afarensis (Kadanuumuu or Woranso-Mille)

The skeleton of Woranso-Milles is very well preserved (Haile-Selassie et al., 2010), even if this specimen is not beautiful as Malapa one concerning the shoulder girdle. Only the left clavicle (KSD-VP-1/1f) and the right scapula (KSD-VP-1/1g) are preserved. The right humerus (KSD-VP-1/1b) is also preserved but lacks the proximal epiphysis. Haile-Selassie and colleagues present the clavicle as being long without giving any value of the current length of the remains. However, authors estimate the real length of this clavicle to 156[3] mm which is very long, corresponding to the mean length of gorilla or western neandertal (Voisin 2011), which are known to be longer than modern human clavicles (Tab. 2.1). This value corresponds also to the upper part of modern human variations and to the lower part of the orangutan variations (Tab. 2.1). It is interesting to note that Haile-Selassie and colleagues do not have taken into account Asian apes and forgot also *Pan pansicus*. The close phylogenetic relationship between hominins and the African apes makes the latter the most relevant comparative group and the first we think to use. However, it is also useful to take into account Asian apes to examine the morphological diversity among all extant apes to identify traits that are primitive for hominoids and to understand the functional role of some of them (Larson 2013).

Haile-Selassie and colleagues use only relative lengths for comparing clavicles, but absolute length is also interesting by itself because it is correlated to the scapula position in regard to the thorax, the morphology of the chest and make evolutionary comparison available (Voisin 2006, 2010). AL333x-6/9 is the most complete australopithecine clavicle discovered before KSD-VP-1/1f and attributed to *Australopithecus afarensis*. AL333x-6/9 is nearly complete but, according to Lovejoy et al. (1982) its real length cannot be estimated because of the great variation of these traits within hominoid. However, according to its preserved morphology and comparison with chimpanzee clavicles, AL33x-6/9 clavicle would not exceed a length of 140 mm (Tab. 2.1). The *Homo habilis* one (OH 48), like AL333x-6/9, is nearly complete while bone loss might be greater than in AL333x-6/9 clavicle and its real length would not have exceed 140 mm too (Voisin 2000). Turkana boy skeleton (KNM-WT 15000) has two nearly complete clavicles which are also short with low bone loss at their extremities (Tab. 2.1). Bone loss might be explained by the young age of this individual, around 12 years old (Brown et al. 1985; Walker and Leakey 1993; Schwartz and Tattersall 2003) and the real length would not have exceed 140 mm too (Voisin, 2000). This length would not have change so much until adult age because juvenile stage would not have been as long as modern human (Schwartz and Tattersall 2003) and also because the maximum clavicle growth has already been done. Even the two Narmada clavicles, which are much younger, display a shorter length than the Woranso-Mille clavicle (Sankhyan, 1997, 2005).[4] In other words, the great clavicle length of Woranso-Mille clavicle is not consistent with all Australopithecines and old *Homo* species clavicle morphology. Concerning the relative length the more appropriate method is the claviculo-humeral index (see above). There are two specimens within early hominins where this ratio can be determined: Malapa skeleton (which is the first claviculo-humeral index calculated for australopithecines) and Turkana boy. Malapa claviculo-humeral index is very low (see above) and KNM-WT 15000 (which is more recent) get also a relatively low one (Tab. 2.1). Within extant hominoids, orangutan and modern human display the higher claviculo-humeral ratio which mean these two species posses a long clavicle in regard to their size contrary to other apes, *Homo ergaster* and *Australopithecus sediba*. In other words, the short clavicle is a primitive trait and it becomes longer during human evolution to reach its greatest relative and absolute length with *Homo antecessor*, anatomically modern human and neanderthal (Voisin 2010). Using the estimation length for the Woraso-Mille humerus and clavicle given by Haile-Selassie et al. (2010) it is possible to calculate the claviculo-humeral ratio which is extremely low, much lower than Malapa value (Table 1). In other words, the Woranso-Mille clavicle would be relatively short and its humerus very long. These remarks are not human like at all, and Woranso-Mille individual looks more as a "super" apes, at least for the shoulder contrary to Halie-Selassie et al. (2010) affirmation. As the humerus is not complete and does not come from the same clavicle side, these authors have used some other technique to estimate the relative clavicle length. However, this relative length may be not comparable between species because it might be no isometric scaling between the different bone lengths they used.

Australopithecines chest is usually described as "funnel-shaped", more or less similar to that of extant apes, which implies a scapula less dorsal than in modern human associated to a shorter clavicle (Voisin 2006, 2010). This kind of architecture with a less dorsal scapula is also found in the first *Homo* species (Larson 2007; Voisin 2010). Hence, the very long clavicle attributed to *Australopithecus afarensis* by Haile-Selassie and colleagues means a scapula located dorsally as in modern human associated to very broad thorax. It is thus difficult

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[3] More precisely Haile-Selassie *et al*. (2010) propose a length comprises between 140 and 170 mm with the most probable value at 156 mm.

[4] The Narmada right clavicle is complete and 90 mm in length (Sankhyan, 2005) though on first reporting (Sankhyan, 1997) it was thought incomplete and estimated to be 100 mm long. But, the left clavicle is incomplete and appears to be of a similar short length.

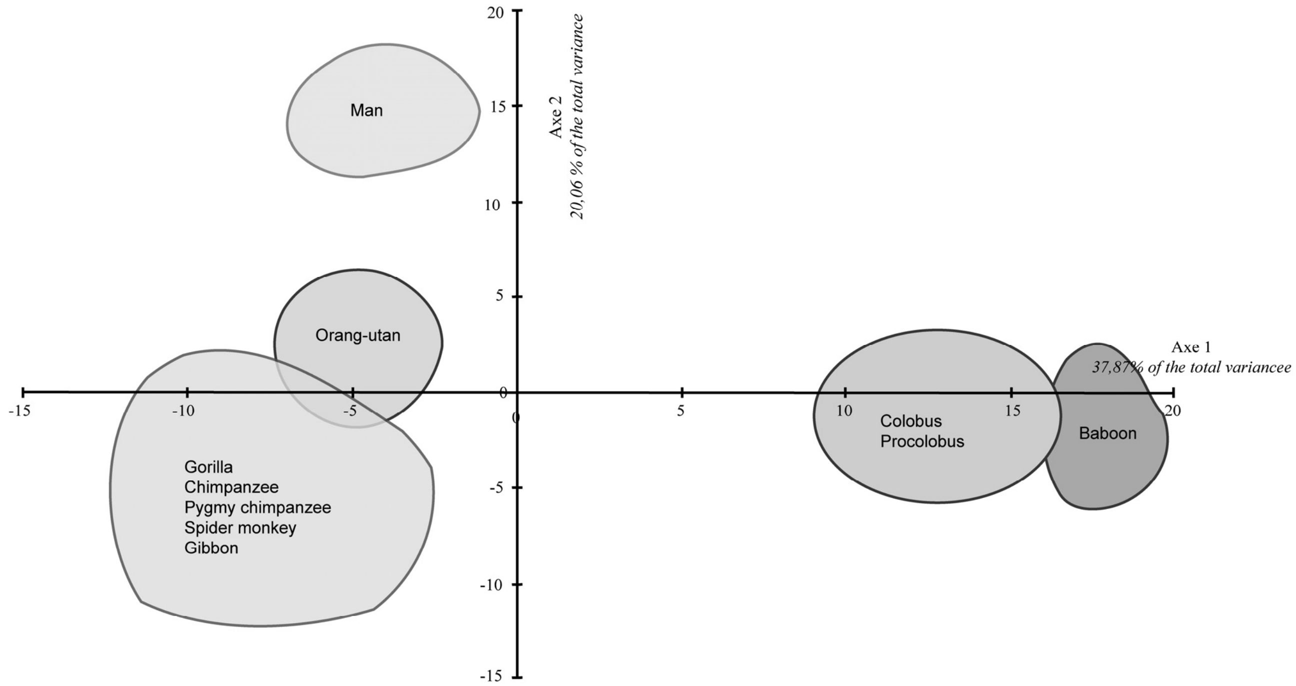

Fig. 2.3. PCA of shoulder data (clavicle, scapula and humerus) showing primates shoulder architecture (after Voisin 2000)

to conceive that, at least in *Australopithecus afarensis*, the clavicle becomes very long, associated to a broad thorax, to reduce in length after (associated again with a tight chest), with the appearance of genus *Homo*. Haile-Selassie and colleagues describe the chest morphology of Woranso-Mille skeleton as nearest to modern human than to other australopithecines.

In other words, this clavicle and the chest morphology associated to, do not fit with australopithecine morphology even if a great sexual morphology would have characterized *Australopithecus afarensis* (Cartmill and Smith 2009 for a review). Moreover, Larson (2013) in her review about australopithecine shoulder morphology does not take into account this clavicle while she includes the scapula, meaning thus the trouble it creates.

According to Haile-Selassie et al. (2010), only the right scapula (KSD-VP-1/1g) is preserved. This bone preserves a nearly complete infraspinous fossa, the entire spine (post-mortem bent) and a complete glenoid cavity but acromion and coracoid are lacking. A small portion of the supraspinous fossa, including the scapular notch, is preserved but not sufficiently to determine the size of this fossa. The supraspinous fossa lack does not allow estimating the proportion of the two fossa. The ratio of the two fossa is important for determining the kind of upper limbs use (see below about Dikika).

Moreover, Haile-Selassie et al. (2010) just give two pictures of this scapula. The two are oriented ventrally with one where the scapula is very little in size and the second is a radiologic one. Hence, no morphological information could be seen on the images.

Woranso-Mille scapula displays ape traits, like a glenoid fossa cranially oriented as well as traits bringing it closer to human scapula, like its overall morphology. This mixture of traits is usual in the australopithecine upper limbs and as lead to two ways of thinking. The first one considers the ape-like morphology as an indication of keeping the ability to climb trees (i.e. Stern and Susman 1983; Stern 2000) and the second one suggests that these features are simply retention of an archaic condition (i.e. Latimer 1991; Ward 2002). Haile-Selassie et al. (2010) show in their PCA that traits like glenoid fossa orientation are not a powerful variable for separating primate scapula. As most australopithecine scapulas remains are limited to the glenoid fossa with short part of the axillary border, they use the “bar-glenoid” angle (Stern and Susman 1983) to estimate the glenoid fossa orientation. To explain why this angle is not powerful to separate species they use a visual observation between the AL.288 scapula remain and a fragmentary modern human scapula (figure S21 in their paper). However, a careful study of this picture shows clear differences between the “bar-glenoid” angles of these two scapulas.

Haile-Selassie and colleagues prefer using geometric relationships within the scapula infrastructure that they consider more powerful to differentiate primates scapula. However, a trait could be not powerful enough to differentiate individuals inside a group, but have a great functional interest. Haile-Selassie and colleagues thus perform a PCA with their own data and the Woranso-Mille scapula fit closer to human cloud than any other species (see figure 4 in Haile-Selassie et al. (2010) paper). However, they use only African apes for comparison and, as we have seen above it is necessary to include all non human hominoid. Chucrchill et al. (2013) showed that the position of a specimen relatively to the hominid clade depended on the choice of a variable. Besides, it also depends on the species used for such comparison. This latter remark could be explained by the fact that Hominoid shoulder architecture is highly variable within hominoid and functional groups can be easily recognized contrary to Cercopithecidae and Colobidae (Voisin 2000) (Fig. 2.3).

Within hominoid shoulder three kinds of architecture could be define: a group including only Orangutan, an another one including only modern human and a group including *Gorilla*, *Pan Hylobates* and even *Ateles* (Voisin 2000) (Fig. 2.3).

Australopithecus afarensis (Dikika)

Dikika is a presumed 3 years old female well preserved skeleton (Alemseged et al. 2006). Concerning the shoulder only the two scapulas are still present. However, the conservative stage is exceptional, especially for a young individual.

The glenoid fossa as well as the spine is oriented cranially, which corresponds to apes morphology and to other australopithecines remains (Tab. 2.4). The glenoid fossa orientation does not significantly change between childhood and adulthood in *Pongo*, *Pan* and *Gorilla* (Green & Alemseged, 2012) contrary to modern human where the glenoid fossa becomes more cranially, even if it still faces much more laterally than in apes (Green & Alemseged, 2012). Starting from DIK-1-1, a humanlike ontogenetic pattern would imply that adult *Australopithecus afarensis* individuals should have more cranially oriented shoulder joints than those displayed by other australopithecine remains. However, both juvenile and adult *Australopithecus afarensis* representatives have comparably oriented shoulder joints, suggesting that this trait remained relatively stable during ontogeny alike or very close to African apes growth trajectory.

The cranially oriented spine induces a greater supraspinatus fossa and a lesser infraspinatus fossa than in humans and similar to what it is found in the two other well preserved australopithecine scapulas (Malapa and Woranso-Mille) and extant apes (see above). These features are clearly seen from the figure 1 of Green & Alemseged (2012) where the two scapulas are shown from dorsal, ventral and lateral view. This spine orientation and the associated scapular fossa development provides a direct line of action for the supra spinatus muscle in preventing displacement of the humeral head during elevation of the humerus (Tuttle & Basmajian, 1978; Rouvière, 1982; Larson et al., 1986; Kapandji, 1994). Thus this muscle is more solicited in suspensory behaviors than in manipulating behaviors. Even if the infra spinatus acts also to prevent the elevation of the humeral head, its main action is to rotate laterally the humerus; which is less important during suspensory behaviors contrary to manipulating ones (Rouvière, 1982; Larson et al., 1986; Kapandji, 1994).

A first PCA analysis (Alemseged et al. 2006), and then confirmed by canonical variates analyses (CVA) performed by Green & Alemsegd (2012), shows that the overall morphology of the Dikika scapula is very close to that of juvenile *Gorilla*. As the multivariate analyzes not only use as much variables as possible but include also Asian apes which made the comparison more robust than the one made with Woranso-Mille scapula (see above). As seen above, Woranso-Mille scapula is close to human one according to Haile-Selassie et al. (2010), contrary to Dikika one although they belong to the same species. However, we have seen also that the human like shoulder of the Woranso-Mille specimen seem to be a misinterpretation, and that the *Australopithecus sediba* shoulder is closer to that of Dikika than to Woranso-Mille one.

As Dikika is a very young individual, a great part of the scapula is now lost because it was made of cartilage. The overall scapula morphology could change much when these cartilages are lost (see figure 1 of Hrdlička 1942). Moreover the overall morphology does change during juvenile growth in human (Hrdlička 1942) and especially among African apes (Green 2013). In other words, some conclusions must be taken with caution before another complete or near complete shoulder remains attributed to *Australopithecus afarensis* from different ages will be discovered. All these remarks could also explain differences between Dikika and Woranso-Mille differences. However, the adult shoulder of *Australopithecus sediba* is clearly adapted to arboreal locomotion and it seems strange that two very close species (*Australopithecus sediba* represented by Malapa and *Australopithecus afarensis* represented by Woranso-Mille) would have such important locomotion differences.

No clavicle and proximal humerus have been preserved with Dikika remains and thus conclusions have to be short concerning shoulder architecture concerning this individual. The clavicle, as shown above, allows to get much information as well concerning the shoulder architecture as the ability of arm rising. The humerus, especially the proximal part and the humeral torsion, give much information concerning the ability of arm rising too as well as brachiation capacity. In other words, clavicle and humerus would be useful not only to confirm the Dikika arborealism but also to precise it. Moreover, during growth there are some changes in scapula and clavicle morphology within modern humans and African great apes (Hrdlička 1942; Olivier and Capliez 1956; Green 2013) and thus some similar changes might also have existed in australopithecine shoulder during childhood.

DISCUSSION AND CONCLUSION

If we follow the line of thinking that the traits, like cranial orientation of the glenoid fossa, have no functional implications being merely archaic traits, then no relationship between bone morphology and function is implied. It is hard to consider so, otherwise most of the morphological studies on fossil remains would lose sense.

Tab. 2.5. Shoulder architectures within genus Homo. *Lateral: the scapula is more laterally placed than in modern human. Dorsal: the scapula is dorsally placed like in modern human (after Voisin, 2010)*

	Architecture 1	**Architecture 2**	**Architecture 3**
Clavicle curvatures (Dorsal view)	Two curvatures	Two curvatures	One curvature
Clavicle length	Short	Long	Long
Scapula position (in regard the thorax)	High	High	Low
	Lateral	Dorsal	Dorsal
Homo species	*Homo habilis,* *Homo ergaster*	Neanderthal *Homo antecessor*	Modern humans, Upper Paleolithic remains, Anatomically modern humans (i.e. Omo)

Anyway, Voisin (2010) has demonstrated there are three shoulder architectures within genus *Homo* (Table 2.5). The first architecture is characterized by a scapula which is high in regard to the thorax and less dorsal than in modern human and corresponds to the first *Homo* species (i.e. *Homo ergaster*). The second one is characterized by a scapula which is still high in regard to the thorax, but as dorsal as in modern human. This architecture corresponds to *Homo antecessor* and Neandertal. The last architecture is characterized by a scapula which is low in regard to the thorax and fully dorsal and corresponds to anatomically modern human (from Omo remains to living humans).

Furthermore, these architectures are linked to chest morphology. The shoulder architecture of the oldest *Homo* is associated to a "funnel shape" thorax, contrary to modern humans where the chest is more barrel like.

As Australopithecines *display* a short clavicle with two curvatures in dorsal view, at least for *Australopithecus sediba*, it is possible to conclude that their scapulas were more laterally placed and higher in regard to the thorax than in modern human. In this respect, their shoulder architecture was close to the oldest *Homo* species. However, they distinguished themselves by some arboreal traits like glenoid fossa orientation which do not exist in any *Homo* species. Australopithecine shoulder architecture is not identical to any apes too as Corrucini and Ciochon (1976) already propose it with their study on Sts 7 shoulder remains.

Some upper limbs movements would be possible or not (or not efficiency) depending shoulder architecture. Thereby, a more lateral scapula, as in australopithecines and old *Homo* species, would limit the gleno-humeral range of movement. With a more lateral scapula, flexion of the upper limbs will be easier than true abduction (Larson 2007). On the contrary, with a full dorsal scapula, the range of movements becomes larger and true abduction becomes possible (Larson, 2007).

Australopithecines shoulder is therefore more adapted to flexion than true abduction. This architecture associated to the scapula and humerus morphology, especially the humeral torsion, is characteristic of climbing ability.

Numerous factors explain the different conclusions obtained on australopithecines shoulder. First of all, interpretations of fossil remains depend on the preserved state of conservation, because it will impose traits we will use for studies. Moreover, to be sure to describe without any trouble any hominoid remains it is absolutely necessary to take into account all apes and not only the African ones. It is also important to have access to nearly all, if not all remains (at least good cast) of the species or relative species for comparison. It is also important to consider arboreal traits as functional ones and not as archaic features with any function, in peculiar for the shoulder. Indeed, bony structures of the scapula are not randomly arranged but depend on forces acting on the scapula (Roberts 1974; Preuschoft et al. 2012), which clearly shows there is a clear relationship between morphology and function for the shoulder. Moreover, the shoulder is a joint complex with more than 20 muscles (the exact muscles number depends on species). Such a complex system cannot function correctly in inappropriate way for a long time because of injuries (rotator cuff tear, tendinitis, etc.).

Australopithecine shoulder morphology is difficult to understand because it does fit exactly neither with the human one nor with the apes one. This is due to the fact that Australopithecines are totally biped when walking on the ground but still use also arboreal locomotion. These ubiquitous functions are also seen at least in *Australopithecus sediba* hand morphology (Kivell et al. 2011) as well as in foot morphology of *Australopithecus sediba* and *Australopithecus africanus* (Clarke & Tobias, 1995; Zipfel et al. 2011).

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