Evolution, Bipedalism, and Precision Throwing in Hominids

Pedro Juan Urbano Cardona

Abstract: The evolution of powerful and precise throwing developed a means of defense and attack that enabled hominins to colonize the savanna, occupy a new ecological niche, and become hunter-gatherers, essentially becoming humans. The first achievement occurred when the bipedalism and hand structure of Australopithecus allowed for throwing that was powerful and precise enough to defend against predators when venturing into open fields to exploit resources. Subsequently, the precision grip and more complex motor skills in H. habilis developed throwing as a means to compete, at least occasionally, for carrion with savanna predators, similar to how Hadza women use wooden digging sticks to drive off a leopard from its fresh kill. Finally, H. ergaster specialized in throwing, acquiring the most favorable anthropometry for maximum performance, with modifications in the glenohumeral joint, longer legs, shorter forearms, and optimal weight and height, which made it a hunter-gatherer of the savanna and its Homo descendants colonizers of all the Earth's emergent lands.

Introduction

The powerful one-handed throwing of relatively light objects reaches its pinnacle in athletic competitions, where we see burly men and women throwing javelins, hammers, discs, or shots to record distances unmatched by any other animal. This ability is unique to Homo sapiens, as no other animal can perform this action with such power. This capability must have played a crucial role in hominin adaptation concerning food acquisition, defense, and attack. Studies on modern hunter-gatherers show how accurate throwing of projectile weapons allows them to obtain meat from medium and large animals, either by scaring off predators when scavenging (O'Connell et al. 1988) or through spear hunting (Turnbull, 1965). A group of Mbuti in the northeastern Congo forest uses a hunting technique where women drive animals into nets tied together forming a wide semicircle about a meter high, so that men can spear them (Turnbull, 1965). This simple strategy may have been used, with some variation, since the adaptation to precision and powerful throwing appeared, having great survival value for hominins. Thus, although huntergatherers lack the strength, speed, and incisors and canines needed to obtain large animals in close combat, they have increased meat consumption in their diet compared to other primates (Turnbull, 1965), a trait possibly already present in Australopithecus africanus (Sponheimer, 1999) due to the higher presence of the isotope C13 in their teeth, although this increase could be due to the consumption of grains, nuts, and tubers from the savanna rather than animals from it. Some chimpanzees, Pan troglodytes, are also good throwers of stones, feces, and sticks. A Gombe chimpanzee in Tanzania was once observed throwing a large stone at an adult animal, hitting and driving it away enough for another chimpanzee to grab the guarded infant (Teliki, 1981). On two other occasions, they hunted baboon infants by throwing stones (Goodall, 1986). They even use clubs with devastating effects, as demonstrated when a group of chimpanzees destroyed a mechanical leopard, built to observe their response, using sticks placed nearby (Kortlandt, 1967), showing an offensive attitude towards a predator. Throwing objects during displays and games is a common behavior in all long-term studied chimpanzee populations (Whiten et al., 1999). Although they often lack the precision to hit the target, it has great value because it allows them to scare other animals (Goodall, 1986). All these facts suggest that throwing objects drove an evolutionary process in hominins, culminating in our refined ability to throw with great power and precision.

Throwing in Hominins before Homo ergaster

It is very likely that the common ancestor of hominins and the genus Pan could throw objects with as much precision and power as wild chimpanzees, and that Australopithecus further developed this ability with bipedalism (Kortlandt, 1980). This led to the necessary anatomical changes in bones, joints, and muscles (Aiello and Dean, 1990, Coppens and Picq, 2001), increasing the number of lumbar vertebrae, as seen in Lucy (A. L. 288-1), which enhanced the rotation, flexion, and extension angles of the lumbar spine and trunk, necessary for more powerful throwing by increasing the projectile's inertia. Moreover, bipedalism itself likely favored throwing by enabling quick preliminary steps and more coordinated speed transmission from the hip to the hand via the shoulder and elbow, essential for throwing by increasing inertia (Arbeit et al., 1988). The lead leg plays a crucial role in braking and stabilizing the body, with the quadriceps femoris fixing the knee joint almost fully

extended. In Australopithecus afarensis (Lucy, A. L. 288-1), there is a strong insertion on the anterior inferior iliac spine for the rectus femoris muscle of the quadriceps (Coppens and Picq, 2001), similar to H. sapiens, channeling muscular energy appropriately onto the lead leg during throwing. This would make bipedal hominins more forceful in offensive behaviors than chimpanzees. Additionally, as hands were no longer used for quadrupedal locomotion, the precision grip in Paranthropos robustus (Susman, 1994), with a thumb metacarpal morphology in SKX 5016 compatible with a developed muscular system like ours, and possibly in Australopithecus afarensis (Aiello, 1994), with thumbs of similar length to the other fingers and proper finger positioning to allow thumb opposition when grasping a spherical object, likely contributed to precision throwing of objects fitting in one hand, allowing them to direct the projectile's trajectory better. Furthermore, the first Oldowan toolmakers would have initiated the neuromotor development necessary for more refined throwing, as striking one stone with another to extract a flake and obtain a cutting edge involves forcefully and precisely throwing the forearm to impact a specific point. Kanzi, a pygmy chimpanzee (Pan paniscus), performs this operation rudimentarily, as when taught to produce cutting edges this way, he only obtains small flakes (Toth et al., 1993). Bonobos understand the utility of a percussion created lithic tool to cut a rope tying a box hiding a reward (Toth et al., 1993), but cannot systematically produce it, preparing the tool beforehand as hominins making protobifaces did (Roche et al. 1999).

Throwing in Homo ergaster/erectus

In Homo ergaster, with complete adaptations to arboreal life gone, the glenoid cavity oriented laterally (Bramble and Lieberman, 2004) and probably decreased muscular connections between the shoulder girdle and the cervical spine and skull (with the muscle rhomboid origin varying and the atlantoclavicular muscle disappearing), shifting the shoulders sideways, increasing shoulder and arm movement range, and thus throwing speed, making it more powerful (Arbeit, 1988). These adaptations, along with adopting anthropometric measures similar to current high-competition javelin throwers, with a height and weight surpassing 1.80 m and 85 kg respectively (http://www2.webpark.cz/booboo/Athletics.htm.), likely made H. ergaster/erectus true throwing specialists, acquiring the optimal size and shape to perform this activity most effectively. These morphometric values have been present since Homo ergaster, both in height (Walker and Leakey, 1993) and weight, considering the KNM-ER 3228 hip bone is part of a broad pelvis (with width directly related to total weight in modern humans, Ruff et al., 1997), similar to the Pelvis 1 of Homo heidelbergensis from Sima de los Huesos (Arsuaga et al., 1999), unlike the narrower pelvis of H. sapiens, previously reconstructed from very incomplete and fragmentary KNM-WT 15000 pelvis remains, which estimated a weight of about 60 kg (Walker and Leakey, 1993). Moreover, KNM-WT 15000 has upper (humerus) and lower limb (femur) proportions, and arm and forearm bone ratios similar to Homo sapiens (Walker and Leakey, 1993), allowing maximum muscular force and segmental speed efficiency in throwing because:

1. In the lower limbs and pelvis, the muscular force required for throwing increases as the action moves away from the ground due to the increase in torque (Zanon, 1987), especially if preceded by an explosive run. This favors longer lower limbs to transition from long muscles (with less force and high contraction speed in the limbs) to muscles that stabilize the pelvis, using shorter, stronger muscles with lower contraction speeds to stabilize the hip.
2. In the trunk and upper limbs, due to the motor freedom of the shoulder, elbow, and wrist, the torque generated by these muscles must be timed appropriately (Zanon, 1987). This means transitioning from short, strong, slower contracting muscles in the trunk to longer muscles with higher contraction speeds that use stored elastic potential energy during the pre-contraction stretch phase to develop more power, especially in the arm muscles that move the shoulder and elbow joints, which are crucial for throwing. This requires the upper limbs to avoid atrophy and be relatively longer than the trunk compared to most mammals to allow for broad movements.
3. The forearm is shorter relative to the arm than in Australopithecus and Homo habilis (OH 62) (Coppens and Picq, 2001), and less heavy than that of the chimpanzee in relation to total body mass (Aiello and Dean, 1990), which allows for increased speed and, therefore, throwing power by offering less resistance.

It seems that throwing objects first co-evolved with the emergence of bipedalism in early hominins, utilizing both the musculature of the lower limbs and trunk, as well as the upper limbs more effectively than chimpanzees due to bipedalism adaptation. Later, it determined the body pattern in size, weight, and proportions in the genus Homo, making it a specialized thrower by expanding movements of all limbs, thereby increasing the speed and power of throwing.

With H. ergaster, throwing precision likely improved as well, given the increase in cranial capacity, over 800cc in KNM-ER 3883 and 3733 (Leakey and Walker, 1976), and the greater complexity in making Acheulean tools, which can be associated with H. ergaster bone remains (Asfaw et al., 1992). This suggests that there was a development in the motor areas of the brain and corticospinal projection pathways that directly control the motoneurons innervating the upper limb muscles in this hominin. This evolution of the nervous system would facilitate an increase in motor coordination compared to earlier hominins, with an extra number of neurons for finer, more synchronized, and effective control over the kinetic chain involved in tool making and throwing (Calvin, 1983). Additionally, the emergence of hand laterality, at least from KNM-WT 15000, which shows greater development of the right deltoid muscle's clavicular insertion and a longer right ulna (Walker and Leakey, 1993) than their respective left counterparts, would imply an improvement in throwing efficiency and likely a hemispheric specialization of the brain for better programming of throws (Corbalis, 1991; Wilkins, 1995).

Throwing versus Endurance Running

Bramble and Lieberman (Bramble & Lieberman, 2004) argue that the anatomical modifications previously described in the locomotor apparatus, along with other changes in Homo compared to chimpanzees, such as the expansion of the area of origin of the gluteus maximus muscle and the erector spinae muscles, the greater separation between the thorax and pelvis (Aiello & Dean, 1990; Bramble & Lieberman, 2004), and the longer lengths of the Achilles tendon, iliotibial tract, and peroneus longus muscle (Swindler & Wood, 1973) are a result of adaptation to long-distance endurance running that uses aerobic metabolism as an energy source. This is because these modifications involve a more pronounced trunk rotation relative to the head or hips, facilitating balance while running, greater stabilization of the trunk or head, a reduction in stress during the action, and lower energy consumption. However, considering that the hominin attributed with the adaptation to endurance running, H. ergaster, weighed more than 85 kg, the energy expenditure required for such efforts would not be efficient compared to current elite longdistance runners who weigh less than 70 kg (http://www2.webpark.cz/booboo/Athletics.htm). These runners, being lighter than a javelin thrower, conserve energy, an essential factor for maintaining effort over a long time (Zintl, 1991). Furthermore, if the biacetabular and bi-iliac crest distances of the pelvis of H. ergaster are similar to those of H. heidelbergensis (Arsuaga et al., 1999), the biomechanical efficiency in endurance running would be less than in our species, as the lengths of the resistance arms of the levers formed by the muscles that stabilize the pelvis increase, implying greater energy expenditure. However, this could be advantageous for throwing by increasing the insertion surface for stronger muscles and by expanding the pelvic rotation movement by advancing the hip on the side carrying the projectile, increasing its speed in the throw, leading to a more powerful throw (Arbeit, 1988). Therefore, H. ergaster would not be specialized in long-distance endurance running.

Some of the described anatomical modifications would indeed provide greater trunk rotation, better stabilization of the trunk and head, stress reduction, and adequate energy utilization, but for the powerful throwing of objects that generates large torque (Zanon, 1987) (the rest of the modifications directly involve the throwing action, as previously indicated), and also for sprinting that uses anaerobic metabolism, in the same sense understood for endurance running. H. ergaster would be a magnificent thrower capable of wounding animals with thrown weapons and running short to medium distances at sufficient speed to hunt them down.

The Archaeological Record

The great value of object throwing for the survival of hominins is related to their ability to create throwing weapons that could wound and kill prey and potential predators. The oldest and most reliable evidence of throwing weapons is a set of several wooden spears or javelins, between 1.80 and 2.30 meters in length and 3 to 5 centimeters in diameter, perfectly sharpened and designed to be thrown, as demonstrated by ballistic studies. These were found in Schöningen, Germany, and date back to around 400,000 years ago (Thieme, 1997). One of them was found in close association with an equid skull that had a hole produced by a pointed weapon. This weaponry, along with other pointed wooden tools (Thieme, 1997), which due to their morphology and shorter dimensions seem intended for close-range actions, would make the Homo who made them a true apex predator, capable of taking down large game.

Although there are no older archaeological wooden remains than those mentioned above, due to the preservation issues of this material, the study of the wear on the cutting edges of lithic tools indicates that wood was worked on very early (Keeley & Toth, 1981). Therefore, it can be assumed that from the appearance of Homo, throwing weapons for defense and attack were made using this material.

APPENDIX
Adaptations in Throwing Athletes: Comparisons with the Fossil Record and Evolutionary

Implications

Specific motor activity patterns, such as throwing objects with the dominant hand, when repeated intensely and over long periods from childhood, produce specific anatomical, biomechanical, and functional adaptations in the postcranial skeleton. This has been demonstrated by various studies on athletes from several disciplines where throwing forms the basis of the motor actions performed in competitions and training. The results of these studies allow us to compare them with data obtained from the analysis of the paleoanthropological record and, therefore, draw some conclusions about the activities that the fossilized individuals might have engaged in (Rhodes, 2006; Rhodes & Knüsel, 2005).

In professional handball players who started competing before the age of ten, it has been observed that the difference in the humeral torsion angle (the angle formed between the axis of the humeral head and the axis of the elbow) in the dominant arm compared to the non-dominant arm, an average asymmetry of 14.39° (49.08° in the dominant side and 34.68° in the non-dominant side), is greater than in the control group, which only has an average asymmetry of 1.76° (41.46° versus 39.70°) (Pieper, 1998). The same is true for pitchers who play baseball, with an average difference of 17° between the two limbs, 40° and 23°, while in the control group the asymmetry is –1° on average, 18° and 19°, with significant differences also in the external rotation of the humerus at 90° of abduction, an average of 9° in professionals (128° in the dominant arm and 119° in the non-dominant arm) compared to 1° in the control group (113° and 112°, respectively) (Crocket et al., 2002; Osbahr et al., 2002; Reagan, 2002).

These humeral torsion data are compatible with those obtained in KNM-WT 15000 (Walker & Leakey, 1993). Additionally, the right clavicular insertion of the deltoid muscle would be more developed as an adaptation to more vigorous physical work of the right upper limb, very possibly for throwing. The humeral torsion characteristic of throwers is also compatible with that of Australopithecus sp. (Bramble & Lieberman, 2004), which differs from that of chimpanzees and untrained H. sapiens (Larson, 2007), suggesting an adaptation that increases the external rotation of the shoulder and the elastic energy of the accelerator muscles in throwing (Boach et al., 2013).

In professional tennis players, compared to the control group, a greater external surface and a smaller internal surface have been observed in the cortical bone of the humerus of the dominant limb (Jones et al., 1977), especially if they began practicing the sport at a very early age. This implies a difference in robustness and stiffness (which depends on the diameter of the bone's cross-section) of 45% and 62%, respectively (Trinkaus et al., 1994). These differences are similar to those obtained in Neanderthals and modern humans from ten thousand to thirty thousand years ago, which can be interpreted as an adaptation to throwing by these populations (Schmitt & Churchill, 2003).

Besides the anatomical and biomechanical adaptations described in the locomotor skeletons of handball and baseball players, variations have also been recorded in the electromyogram (EMG) of javelin throwers compared to a control group in throws with the dominant hand (Illyés & Kiss, 2005). Both javelin throwers and the control group showed a high level of activity, above 75%, in the EMG of the pectoralis major, anterior deltoid, middle deltoid, posterior deltoid, supraspinatus, infraspinatus, biceps brachii, and triceps brachii muscles. However, the activity level of these muscles in javelin throwers is significantly higher than in the control group, except for the biceps brachii, which has a slightly higher activity level in the control group (Illyés & Kiss, 2005).

It is also noteworthy that the muscles with the lowest and highest activity levels among those mentioned do not match exactly between the two groups. In javelin throwers, the muscles with the lowest activity level are the anterior deltoid and biceps brachii, while in the control group they are the anterior, posterior, and middle deltoid. Regarding the highest activity level, in the control group, it is the triceps brachii (96.87%), while in javelin throwers, it is the triceps brachii (99.80%) and the posterior deltoid (100%) (Illyés & Kiss, 2005). The contrast in the activity level of the posterior deltoid between javelin throwers and the control group (which activates among the lowest, at 81.27%) is particularly striking (Illyés & Kiss, 2005). Let's examine the possible evolutionary implications that can be drawn from these records.

The triceps brachii is an agonist, accelerator muscle in single-hand throws, similar to the gesture performed by handball players, pitchers, or javelin throwers in their respective sports. Its maximum activity level is achieved in this type of throw because the long head of the muscle, being a biarticular bundle, only fully accomplishes its elbow extensor effect of the throwing limb when this limb is in abduction and external rotation of the glenohumeral joint, adopting the appropriate joint angle for optimal pre-tension of the muscle to subsequently allow its maximum performance (Fidelius, 1971).

The posterior deltoid is the agonist muscle in horizontal abduction (moving the arm from a 90° abduction position), the starting position for handball, javelin, etc., acting more actively in this throw (Gowan et al., 1987; Kelly et al., 2002) (in addition to stabilizing) during the preparation phase, the stretch phase of the motor muscles to allow them to reach their maximum performance, and especially during the braking phase of the glenohumeral joint, which is crucial to adequately transmit acceleration to the elbow joint (Arbeit et al., 1988). The participation of this bundle is essential in throwers since it activates maximally as we have described (Illyés & Kiss, 2005).

Of the other muscles mentioned, the pectoralis major and subscapularis are agonist, accelerator muscles, while the infraspinatus, supraspinatus, biceps brachii, and the anterior and middle deltoid are stabilizer and decelerator muscles (Gowan et al., 1987; Kelly et al., 2002). All these muscles perform a specific function depending on their line of action, which is determined by the direction between their origin and insertion. When comparing the line of action of shoulder muscles in our species and members of the genus Pan, it is observed that they differ mainly due to two morphological variations of the scapula. In chimpanzees, the glenoid cavity adopts a more cranial orientation than in H. sapiens (Aiello & Dean, 1990; Coppens & Picq, 2001; Alemseged et al., 2006) and the scapular spine is more inclined (Alemseged et al., 2006).

This scapular morphology in chimpanzees is associated with an arboreal lifestyle (Coppens & Picq, 2001), where keeping the arms above the head is essential. Thanks to the two mentioned characteristics, the line of action of the shoulder muscles is favored for this activity. H. sapiens, having a glenoid cavity with a lateral orientation and a much less inclined scapular spine (Alemseged et al., 2006) (with a relative increase in the surface area of the infraspinous fossa), changes the direction of the shoulder muscle fibers originating in these areas (posterior deltoid, long head of the triceps, infraspinatus, supraspinatus, subscapularis, and long head of the biceps) compared to chimpanzees. This change allows these muscles to perform their action more effectively in an anterolateral plane, which is ideal for throwing with horizontal abduction-adduction and external-internal rotation of the glenohumeral joint, rather than in a parasagittal plane as in the case of the genus Pan (Dufour & Pillu, 2006). This enables the triceps brachii and posterior deltoid to achieve maximum activity levels.

Fossil scapulae, if they preserve the glenoid cavity and spine, can indicate whether the specimens they belong to were adapted to an arboreal lifestyle or to throwing when compared to the scapulae of chimpanzees and humans, depending on whether they more closely resemble one or the other. The scapula of DIK-1-1, an A. afarensis, shows a morphology and orientation of the glenoid cavity similar to that of Gorilla gorilla (Alemseged et al., 2006), suggesting a partial arboreal adaptation. However, the scapular spine is inclined in an intermediate position between that of this gorilla species and humans (Alemseged et al., 2006), increasing the relative surface area of the infraspinous fossa and decreasing that of the supraspinous fossa. These characteristics can be interpreted as adaptive trends towards powerful one-handed throwing.

It is possible that DIK-1-1, Lucy, and their species were no longer arboreal (Lovejoy, 1981; Lovejoy, 1988) because the biomechanics imposed by the orientation of the scapular spine did not favor it, although they still retained many characteristics of their ancestors in the upper limbs, which might lead to some doubt (Stern & Susman, 1983).

The scapulae of KNM-WT 15000 (Carretero et al., 1997), the Homo specimens from the Sima de los Huesos in Atapuerca (Carretero et al., 1997), and the Neanderthals (Trinkaus, 1983) present an axilloglenoid angle (which measures the orientation of the glenoid cavity) that falls within the range of variation of the averages obtained from several populations of modern humans, namely, 119.5°-140.1° (Vallois, 1946). However, those from the Sima de los Huesos (140° and 144° for the two specimens where the measurement could be taken) and the Neanderthals (140.6° on average for European fossils) are at the upper end (Carretero et al., 1997), indicating that the orientation of the glenoid cavity was very lateralized.

It seems, therefore, that at least since H. ergaster, the scapula had already adopted characteristics conducive to allowing the shoulder muscles to perform an effective and powerful throwing action with the dominant hand.

Bibliography

[1]. Aiello, L.: "Thumbs Up for Our Early Ancestors". Science. 265, 1540-1541. 1994.
[2]. Aiello, L. et Dean, M.: "An introduction to Human Evolutionary Anatomy". Academic. London. 1990.
[3]. Alemseged, Z., Spoor, F., Kimbel, W. et al.: "A juvenile early homonin skeleton from Dikika, Ethiopia". Nature, 443,296-301. 2006.
[4]. Arbeit, E., Bartonietz, K., Borner, P. et al.: "The view of the DVFg of the GDR on talent selection technique and main training contents from beginner to top level athletes". New Studies in Athletics, 8, 57-74. 1988.

[5]. Arsuaga, J.L., Lorenzo, C., Carretero, J.M. et al.: "A complete human pelvis from the Middle Pleistocene of Spain". Nature, 399, 255-258. 1999.
[6]. Asfaw, B. et al: "The earliest Acheulan from Konso-Gardula". Nature, 360, 732-735. 1992.
[7]. Bramble, D. et Lieberman, D.: "Endurance running and the evolution of Homo". Nature, 432, 345-352. 2004.
[8]. Calvin, W.: "A stone's throw and its launch window: timing precision and its implications for language and hominid brains". Journal of Theoretical Biology, 104, 121-135. 1983.
[9]. Carretero, J.M., Arsuaga, J.L. et Lorenzo, C.: "Clavicles, scapulae and humeri from the Sima de los Huesos site (Sierra de Atapuerca, Spain)". J hum Evol 33,357-408. 1997.
[10]. Coppens, Y. et Picq, P.: "Aux Origines de l'humanité. De l'apparition de la vie à l'homme moderne". Fayard. 2001.
[11]. Corballis, M.: "The Lopsided Ape". New York. Oxford University Press.1991.
[12]. Crockett, H., Gross, L., Wilk, K. et al.: "Osseous adaptation and range of motion at the glenohumeral joint in professional baseball pitchers". Am J Sports Med 30, 20-26. 2002.
[13]. Dufour, M. et Pillu, M.: "Biomecánica funcional. Cabeza, tronco. Extremidades." MASSON. ELSEVIER. Barcelona. 2006.
[14]. Fidelius, K.: "Biomechanische Parameter der oberen Extremitäten". Varsovia. 1971.
[15]. Goodall, J.: "The Chimpanzees of Gombe: Patterns of Behavior". Cambridge. Harvard University Press. 1986.
[16]. Gowan, I., Jobe, F., Tibone, J. et al.: "A comparative electromyographic analysis of the shoulder during pitching". Am J Sports Med 15,586-590. 1987. http://www2.webpark.cz/booboo/Athletics.htm
[17]. Illyés, A. et Kiss, R.: "Shoulder muscle activity during pushing, pulling, elevation and overhead throw". J Electromyogr Kinesiol 15,282-289. 2005.
[18]. Jones, H., Priest, J., Hayes, C. et al: "Humeral hypertrophy in response to exercise". Journal of Bone and Joint Surgery 59A:204-208. 1977.
[19]. Keeley, L. et Toth, N.: "Microwear polishes on early stone tools from Koobi Fora, Kenya". Nature, 293, 464-466. 1981.
[20]. Kelly, B., Backus, S., Warren, R. et al.: "Electromyographic analysis and phase definition of the overhead football throw". Am J Sports Med 30,837-847. 2002.
[21]. Kortlandt, A.: "Experimentation with chimpanzees in the wild". En D. Starck, R. Schneider et H. Kuhns: Progress in primatology, 119-139. New York. Plenum Prees. 1967.
[22]. Kortlandt, A.: "How might hominids have defended themselves against predators and foodcompetitors?". Journal of Human Evolution, 9, 79-112. 1980.
[23]. Larson, S.: "Evolutionary transformation of the hominin shoulder". Evol. Anthropol. 16, 172-187. 2007.
[24]. Leakey, R. et Walker, A.: "Australopithecus, Homo erectus and the Single Species Hypothesis". Nature, 261, 572-574. 1976.
[25]. Lovejoy, C.: "The origin of man". Science 211,341-350. 1981.
[26]. Lovejoy, C.: "Evolution of human walking". Sci Am 259,118-125.1988.
[27]. O'Connell, J. F., Hawkes, K. et Jones, N. B.: "Hadza Scavenging: Implications for Plio/Pleistocene Hominid Subsistence". Current Anthropology, 29: 356-363. 1988.
[28]. Osbahr, D., Cannon, D. et Speer, K.: "Retroversion of the humerus in the throwing shoulder of college baseball pitchers". Am J Sports Med 30,347-353. 2002.
[29]. Pieper, H.: "Humeral torsion in the throwing arm of handball players". Am J Sports Med 26,247-253. 1998.
[30]. Reagan, K., Meister, K., Horodyski, M. et al.: "Humeral retroversion and its relationship to glenohumeral rotation in the shoulder of college baseball players". Am J Sports Med 30,354-360. 2002.
[31]. Rhodes, J.: "Adaptations to Humeral Torsion in Medieval Britain". Am J Phys Anthropol 130:160-166. 2006.
[32]. Rhodes, J. et Knüsel, C.: "Activity-related skeletal change in medieval humeri: Crosssectional and architectural alterations". Am J Phys Anthropol 128:536-546. 2005.
[33]. Roach, N., Venkadesan, M., Rainbow, M. et al.: "Elastic energy storage in the shoulder and the evolution of high-speed throwing in Homo". Nature 498, 483-487. 2013.
[34]. Roche, H. et al.: "Early hominid stone tool production and technical skill 2.34 Myr ago in West Turkana, Kenya". Nature, 399, 57-60. 1999.
[35]. Ruff, C., Trinkaus, E. et Holliday, T.: "Body mass and encephalization in Pleistocene Homo". Nature, 387, 173-176. 1997.

[36]. Schmitt, D. et Churchill, S.: "Experimental evidence concerning spear use in Neanderthals and early modern humans". J Archaeol Sci 30:103-114. 2003.

[37]. Sponheimer, M. et Lee-Thorp, J. A.: "Isotopic Evidence for the Diet of an Early Hominid, Australopithecus africanus". Science, 283: 368-370. 1999.

[38]. Stern, J. et Susman, R.: "The locomotor anatomy of Australopithecus afarensis". Am J Phys Anthropol 60,279-317. 1983.

[39]. Susman, R.: "Fossil evidence for early hominid tool use". Science, 265, 1570-1573. 1994.

[40]. Swindler, D. et Wood, C.: "An Atlas of Primate Gross Anatomy: Baboon, Chimpanzee and Man". Univ. Washington Press. Seattle. 1973.

[41]. Teliki, G.: "The omnivorous diet and eclectic feeding habits of chimpanzees in Gombe National Park, Tanzania". En G. Teliki et S. O. Harding: Omnivorous primates: gathering and hunting in human evolution, 305-343. New York. Columbia University Press. 1981.

[42]. Thieme, H.: "Lower Palaeolithic hunting spears from Germany". Nature, 385, 807-810. 1997.

[43]. Toth, N., Schick, K., Savage-Rumbaugh, E. et al.: "Pan the Tool-maker: Investigations Into the Stone Tool-making and Tool-using Capabilities of a Bonobo (Pan paniscus)". Journal of Archaeological Science, 20(2), 81-91. 1993.

[44]. Trinkaus, E., Churchill, S. et Ruff, C.: "Postcranial robusticity in Homo. ll: Humeral bilateral asymmetry and bone plasticity". Am J Phys Anthropol 93, 1-34. 1994.

[45]. Trinkaus, E.: "Neandertal postcrania and the adaptive shift to modern humans". In E. Trinkaus (ed.): The Mousterian Legacy: Human Biocultural Change in The Upper Pleistocene. B.A.R. Int ser 164,165-200. 1983.

[46]. Turnbull, C. M.: "Wayward Servants: The Two Worlds of the African Pygmies". Natural History Press. New York. 1965.

[47]. Vallois, H.: "L'omoplate humaine: Étude anatomique et anthropologique". Bull Mém Soc Anthropol Paris Série 7, 9,129-168; 10,110-191; Série 8, 3,3-153; Série 9 7,16-100. 1928-1946.

[48]. Walker, A. et Leakey, R.E.F.: "The Nariokotome Homo erectus skeleton". Berlín. Springer Verlag. 1993.

[49]. Whiten, A., Goodall, J., McGrew, W. et al.: "Chimpanzee Cultures". Nature, 399, 682-685. 1999.

[50]. Wilkins, W. et Wakefield, J.: "Brain evolution and neurolinguistic preconditions". Behavioral and Brain Sciences, 18, 161-226. 1995.

[51]. Zanon, S.: "Hipótesis biomecánica fundamental para el lanzamiento de jabalina". En R.F.E.A. (ed.): Cuadernos de Atletismo nº 6, Jabalina y peso. Pila Teleña. Madrid. 1987.

[52]. Zintl, F.: "Entrenamiento de la resistencia: Fundamentos, métodos y dirección del entrenamiento". Martínez Roca. Barcelona. 1991.