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Gommery, Dominique

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SUPERIOR CERVICAL VERTEBRAE OF A MIOCENE HOMINOID AND A PLIO-PLEISTOCENE HOMINID FROM SOUTHERN AFRICA

by

Dominique Gommery

UPR 2147 du CNRS, 44 rue de l'Amiral Mouchez, 75014 Paris, France.

ABSTRACT

The Miocene hominoid and Plio-Pleistocene hominid vertebral record is poor. In 1994, a complete atlas of a hominoid was found in breccia at Berg Aukas in Namibia. Its age was estimated to be middle Miocene (13 myr) on the basis of microfauna. This locality yielded the holotype of *Otavipithecus namibiensis* and the atlas could belong to the same genus. The specimen exhibits clear hominoid traits such as a weakly salient retroglenoid tubercle at the superior articular facet of the lateral mass, and a horizontal transverse process. This morphology of the transverse process is close to that of pygmy chimpanzees, gibbons and African colobines, suggesting that *Otavipithecus* was arboreal. This confirms the conclusions drawn from other parts of the skeleton. From the size of the atlas, a body weight of 15-20 kg is estimated for the Berg Aukas hominoid, which accords with previous estimates based on its teeth.

The second fossil considered in this paper is an axis from Swartkrans, SK 854, dated to nearly 1,8 myr. This axis is compared with another Plio-Pleistocene axis from Ethiopia, AL 333.101. SK 854 shows a morphology different from that of humans and AL 333.101, and also of apes. The South African axis was attributed to *Paranthropus* by Robinson (1972), and its morphology is probably typical of bipedalism associated with climbing.

KEYWORDS: Cervical vertebrae, hominoid, hominid, Miocene, Plio-Pleistocene, Namibia, South Africa.

INTRODUCTION

Man differs from other primates by his orthograde posture and his permanent bipedal locomotion. All non-human hominoids also show these two characteristics, but only occasionally. Postcranial elements, especially the vertebral column, have tended to be neglected in the reconstruction of hominid and hominoid phylogeny. Nevertheless, several studies on the vertebral column of extant primates point to functional and systematic differences between apes and humans (Ankel 1967 & 1972; Gommery 1993, 1994, 1995, 1996, 1998b; Schultz 1961; Shapiro 1993). Some observations have been made on fossil hominoids and hominids (Benade 1990; Conroy *et al.*, 1996; Gommery 1995, 1996 & 1997; Harrison 1991; Johanson 1982; Köhler & Moyà-Solà 1997; Sanders & Bodenbender 1994; Senut & Gommery 1997; Ward 1990, 1993 ; Ward *et al.* 1993; Leutenegger 1977; Sanders1998; Schmid 1983 & 1991).

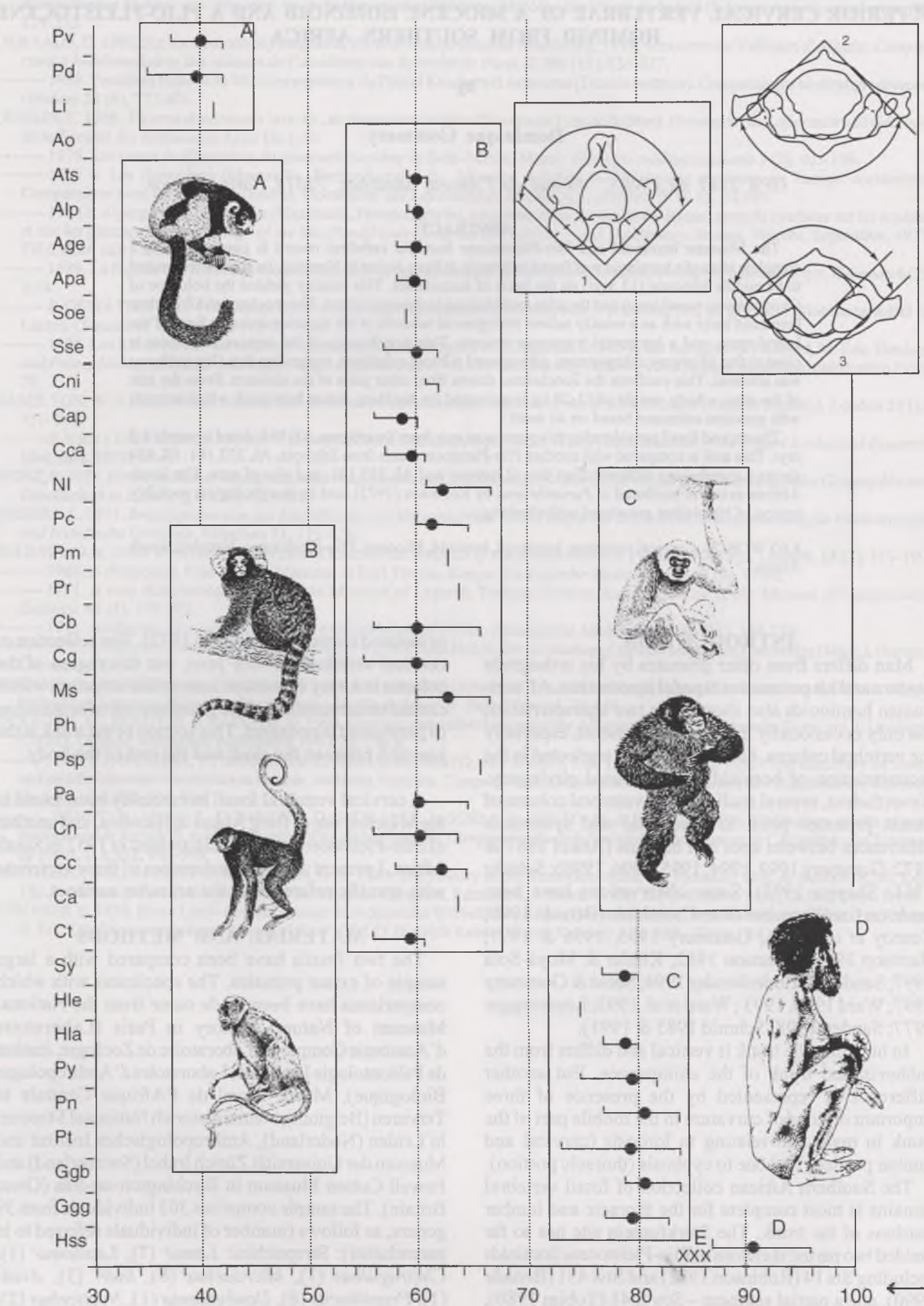
In humans, the trunk is vertical and differs from the subhorizontal trunk of the chimpanzee. But another difference is represented by the presence of three important regions of curvature in the mobile part of the trunk in man, two relating to lordosis (cervical and lumbar portion) and one to cyphosis (thoracic portion).

The Southern African collection of fossil vertebral remains is most complete for the thoracic and lumbar portions of the trunk. The Sterkfontein site has so far yielded two partial skeletons of Plio-Pleistocene hominids including Sts 14 (Robinson 1972) and Stw 431 (Benade 1990), and a partial segment – Stw 8/41 (Tobias 1980), or isolated elements (Robinson 1972). The collection of cervical vertebrae is very poor, but this region of the column is a very important anatomical structure which can aid understanding of the phenomenon of acquisition of permanent bipedalism. This section of the trunk is the junction between the skull and the rest of the body.

A cervical vertebral fossil has recently been found in the Miocene site of Berg Aukas in Namibia, and another of Plio-Pleistocene age was discovered in 1952 in South Africa. I present some characteristics of these vertebrae with specific reference to the articular surfaces.

MATERIAL AND METHODS

The two fossils have been compared with a large sample of extant primates. The specimens with which comparisons have been made come from the National Museum of Natural History in Paris (Laboratoire d'Anatomie Comparée, Laboratoire de Zoologie, Institut de Paléontologie Humaine, Laboratoire d'Anthropologie Biologique), Musée Royal de l'Afrique Centrale in Tervuren (Belgium), Natuurhistorich Nationaal Museum in Leiden (Nederland), Anthropologisches Institut und Museum der Universität Zürich Irchel (Switzerland) and Powell Cotton Museum in Birchington-on-Sea (Great Britain). The sample comprises 303 individuals from 39 genera, as follows (number of individuals referred to in parentheses): Strepsirhini: *Lemur* (7), *Lepilemur* (1), *Cheirogaleus* (1), *Microcebus* (8), *Indri* (3), *Avahi* (1), *Propithecus* (8), *Daubentonia* (1), *Nycticebus* (2),


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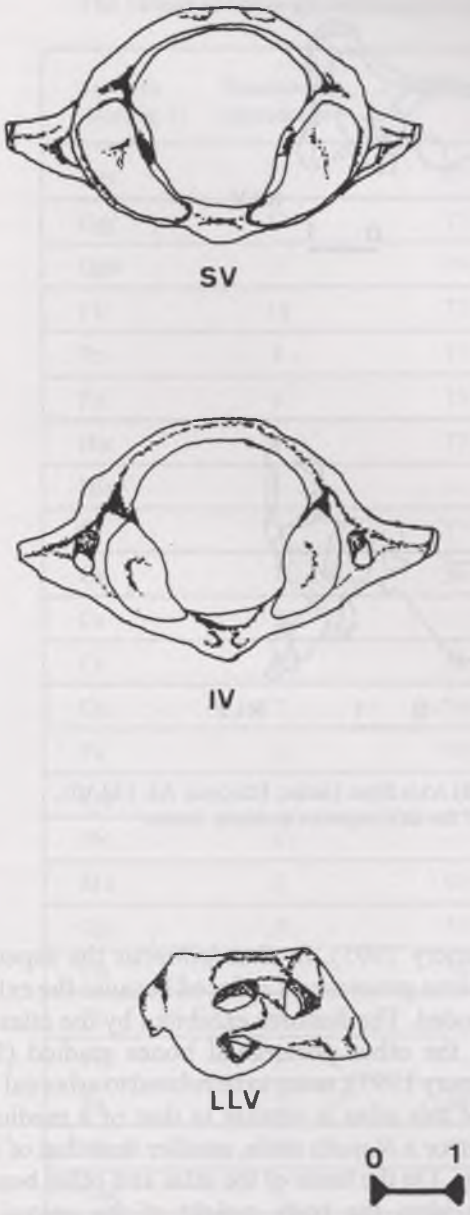


Figure 2. Atlas from Berg Aukas, Namibia. BA 104'91. SV: superior view; IV: inferior view; LLV: left lateral view.

Perodicticus (2), *Galago* (4); Tarsiers: *Tarsius* (1); Platyrrhini: *Callithrix* (1), *Leontopithecus* (1), *Aotus* (2), *Callicebus* (1), *Pithecia* (2), *Cacajao* (1), *Cebus* (16), *Saimiri* (6), *Ateles* (13), *Lagothrix* (2), *Alouatta* (11); Cercopithecoidea: *Cercopithecus* (24), *Cercocebus* (9), *Erythrocebus* (2), *Macaca* (9), *Papio* (9), *Mandrillus* (6), *Theropithecus* (2), *Nasalis* (4), *Colobus* (17), *Presbytis* (7); Hominoidea: *Hylobates* (15), *Symphalangus* (3), *Pongo* (6), *Pan* (35), *Gorilla* (29), *Homo* (37). This list includes an important sample of wild animals but the Strepsirhini listed include some zoo animals. The observations have been extended to other mammals such as rabbit, dog, cat, horse, cow, bear, lion, etc...

ANATOMICAL DIFFERENCES (Figure 1)

In previous studies (Gommery 1995 & 1997), I observed specific anatomical parts on the superior articular facet (*fovea articulares superiores atlantis*): the retro-glenoid tubercle. The distinction is based on the orientation of curvature of this part. The curvature is more or less cranial. The morphology permits one to distinguish four groups of extants primates: 1) Strepsirhini and *Tarsius*; 2) Platyrrhini and Cercopithecoidea; 3) apes and 4) humans. We observe the same morphological difference on the posterior part of the inferior atlas articular facet (*fovea articulares inferior atlantis*) and the superior axis articular facet (*facies articularis anterior*). We call these parts the homologous part of the atlas retro-glenoid tubercle (Gommery 1995, 1998a, 1999).

In this study we model three angles in different extant primates describing the orientation of the retro-glenoid tubercle and the homologous part on the atlas and axis (Figure 1 & Table 1). We have taken these measurements directly on the bones and also from X-Ray to confirm the data. The same four groups of extant primates show specific mean values: 1) 40° for Strepsirhini (range: 35° - 42°), 2) 60° for Platyrrhini (range : 55° - 67°) and Cercopithecoidea (range : 56° - 67°), 3) 80° for apes (range : 73° - 84°) and 4) 90° for humans (range : 87° - 96°).These angles represent different functional models: one, represented by Strepsirhini (e.g. Malagasy lemur),

Figure 1. The retro-glenoid angle (1) with the two homologous angles on the atlas (2) and axis (3).
Graph legend : Horizontal axis: values of angles in degrees; vertical axis: species of primates. For each species, the range is represented by the horizontal line, with the minimum data marked by the up-turned tick and the maximum data by the down-turned tick; the dot represents the mean.
Key to abbreviations: A) Strepsirhini: *Propithecus verreauxi* (Pv), *Propithecus diadema* (Pd), *Indri indri* (Ii). B) Platyrrhini: *Aotus trivirgatus* (Ao), *Alouatta seniculus* (Ats), *Alouatta palliata* (Alp), *Ateles geoffroyi* (Age), *Ateles paniscus* (Apa), *Saimiri oerstoedii* (Soe), *Saimiri sciureus* (Sse), *Cebus nigrivittatus* (Cni), *Cebus apella* (Cap), *Cebus capucinus* (Cca). - Cercopithecoidea: *Nasalis larvatus* (Nl), *Presbytis cristata* (Pc), *Presbytis melalophos* (Pm), *Presbytis rubicundra* (Pr), *Colobus badius* (Cb), *Colobus guereza* (Cg), *Mandrillus sphinx* (Ms), *Papio hamadryas* (Ph), *Papio sp.* (Psp), *Papio anubis* (Pa), *Cercopithecus nictitans* (Cn), *Cercopithecus cephus* (Cc), *Cercopithecus ascanius schmidti* (Ca), *Cercocebus torquatis* (Ct). C) Non-human Hominoidea: *Symphalangus syndactylus* (Sy), *Hylobates leuciscus* (Hle), *Hylobates lar lar* (Hla), *Pongo pygmaeus* (Py), *Pan paniscus* (Pn), *Pan troglodytes* (Pt), *Gorilla gorilla beringei* (Ggb), *Gorilla gorilla gorilla* (Ggg). D) Human: *Homo sapiens sapiens* (Hss). E) *Paranthropus*: SK 854
Measurement legends : 1 – angle of retroglenoid tubercule on atlas : dorsal angle corresponding to the lateral borders of retroglenoid tubercles. 2 – homologous angle of the inferior articular facets on atlas : ventral angle corresponding to lateral borders or inside borders on the posterior parts (homologous parts of retroglenoid tubercles) of inferior articular facets. 3 - homologous angle of the superior articular facets on axis : ventral angle corresponding to the lateral border or to the median axis on the posterior parts (homologous parts of retro-glenoid tubercles) of the superior articular facets.

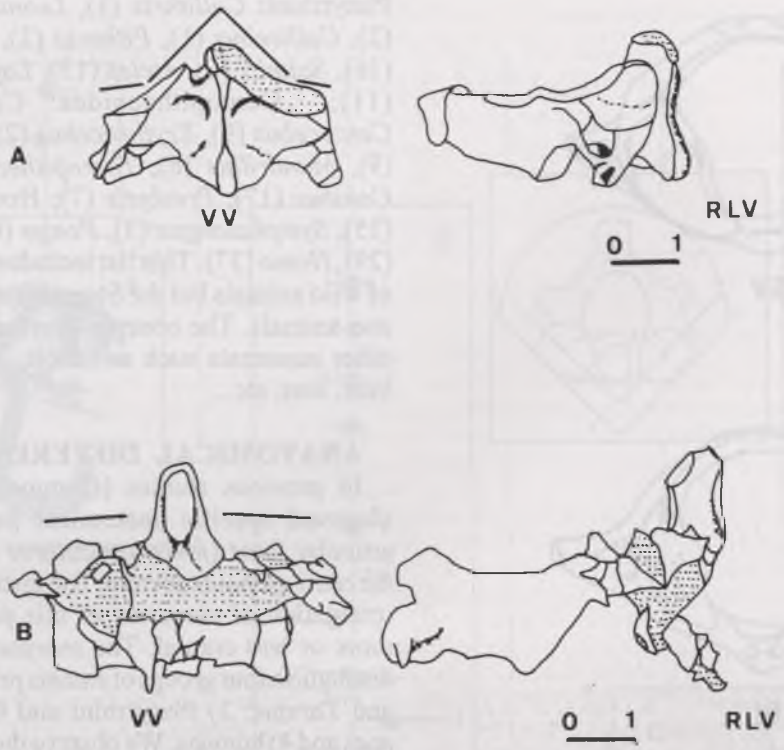


Figure 3. (A) Axis from Swartkrans, South Africa, SK 854; (B) Axis from Hadar, Ethiopia, AL 333.101. The line represent the transverse section of the different parts of the axis superior articular facets.
Abbreviations: VV, ventral view; RLV, right lateral view
Scale bar = 1 cm.

has low values and reveals a great capacity for flexion and extension movements; at the opposite extreme, the values for humans are high, and reveal a lesser capacity for flexion-extension movements.

Atlas BA 104'91 (Figure 2)

In northern Namibia, the fossiliferous breccia at Berg Aukas, near Grootfontein, dated by microfauna to the Middle Miocene (13 -12 myr), has yielded a hominoid, *Otavipithecus namibiensis* (Conroy & *et al.* 1992). The first remains, discovered in 1991 by a French-American team, consisted of a right partial mandible. In 1994, during acid preparation of a breccia block from this locality, Martin Pickford discovered a hominoid atlas BA 104'91 (Figure 2) (Conroy *et al.* 1996; Senut & Gommery 1997). On the atlas, the cranio-dorsal orientation of the glenoid cavities, especially the retroglenoid tubercles, suggest that movements of flexion-extension were powerful at the joint for the occipital condyles. The angle of the retroglenoid tubercle is 81°; the observed range for apes is 73° to 84° with a mean of 80° (Figure 1 & Table 1). The narrowed and elongated morphology of the transverse processes, close to that seen in *Pan paniscus* (the pygmy chimpanzee, or bonobo) and gibbons, would be related to a more extended lateral inclination of the head on the trunk. The aspect of the transverse processes is a long triangle in Bonobo, gibbons and African colobines and is different from the trapezoid transverse processes in terrestrial African cercopithecids (Gommery 1995). In *Otavipithecus* the aspect of the transverse processes is reduced because the extremities are eroded. The features exhibited by the atlas, as well as by the other postcranial bones studied (Senut & Gommery 1997), seem to be related to arboreal life. The size of this atlas is similar to that of a medium-sized baboon or a *Nasalis* male, smaller than that of a female bonobo. On the basis of the atlas and other bones, such as the ulna, the body weight of the animal can be estimated, compared with the same proportions of atlas and ulna of a medium size baboon and a *Nasalis* male, at roughly 15-20 kg (Jungers 1985). The same weight has been estimated based on the size of the molar on the mandible (Conroy *et al.* 1992).

Axis SK 854: Figures 3 & 4

The South African axis, SK 854 (Figure 3), was discovered at Swartkrans in Member 1, and its age is estimated at 1,8 million years (Robinson 1972; Brain 1993). We compare this axis with an Ethiopian axis AL 333-101 (Figure 3), dated to approximately 3,3 myr (from the DD2 and DD3 level of the Denen Dora Member of the Hadar locality AL 333 (Lovejoy *et al.* 1982; Walter 1994). These two axis specimens are the only ones known from the African Plio-Pleistocene hominid collection. The two specimens differ in the orientation of the superior articular facet which resembles a platform in the Ethiopian axis and is cone shaped near the odontoid process, and which describes a platform

TABLE 1.
The values of retro-glenoid angle with the homologous angles on the atlas and axis.

Species (See Fig. 1)	Number of specimens	Minimum	Maximum	Mean	Standard deviation
Hss	37	87	96	90.58	2.64
Ggg	12	77	83	79.67	1.92
Ggb	5	79	84	81.2	1.92
Pt	14	73	84	79.57	3.71
Pn	8	77	84	81	2.27
Py	6	75	82	78.83	2.79
Hla	5	77	80	78.6	1.34
Hle	1	—	—	75	—
Sy	5	77	80	78.6	1.34
Ct	7	56	61	59.28	1.8
Ca	1	—	—	64	—
Cc	7	58	65	61	2.94
Cn	7	56	64	60.14	2.54
Pa	3	60	65	62.67	2.52
Psp	1	—	—	66	—
Ph	1	—	—	62	—
Ms	2	60	67	63.5	4.95
Cg	5	55	63	60	3.39
Cb	7	56	66	60.43	3.41
Pr	1	—	—	64	—
Pm	1	—	—	63	—
Pc	2	60	65	62.5	3.53
Ni	3	61	67	63.67	3.05
Cca	5	57	61	59.2	1.48
Cap	2	56	60	58	2.83
Cni	3	61	62	61.33	0.58
Sse	3	57	62	60.33	1.53
Soe	1	—	—	59	—
Apa	2	58	61	59.5	2.12
Age	4	58	61	59.75	1.26
Alp	2	59	60	59.5	0.71
Ats	5	59	61	60.8	1.3
Ao	1	—	—	62	—
Ii	1	—	—	41	—
Pd	2	35	42	38.5	4.95
Pv	2	37	42	39.5	3.53

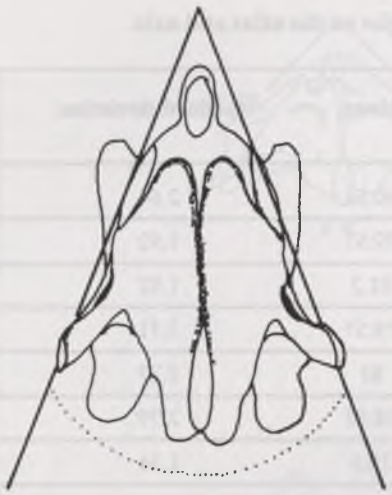


Figure 4:. Axis cone-shape (after Delattre 1924).
The superior articular facets are contained on a virtual cone-shape where the movements are localised in the articulation between atlas and axis. The cone shape axis is symbolized by the axis of the odontoid process

near the border in the South African axis. Another significant difference is the presence of a well-developed and sharp ventral crest on the vertebral body (*crista ventralis*) in the South African fossil. This crest ends in a prominent tubercle (*tuberculum anterius*). The ventral face on the vertebral body is very similar to the morphology in the bonobo, but unlike the Ethiopian fossil. The Ethiopian axis is more human in form.

Delattre (1924) described a cone-shaped superior articular surface of the axis in many mammals, especially primates, but with two isolated superior articular facets (Figure 4). The association of the superior articular facet with the odontoid process makes a functional plan of rotation but also an angulation with the vertebral body of the axis. The angulation of the odontoid is responsible for one component of the lordosis curvature of the spinal column. In the Ethiopian axis, the odontoid process is straight, whereas in the Swartkrans specimen, just the beginning of angulation of the odontoid process is observed. It seems that the odontoid process described a slight angulation.

The homologous angle of the superior articular facets of axis SK854 is 85° (Figure 1). This falls just between the apes (73° - 84°) and humans (87° - 96°). By comparison, the axis AL 333.101 has a homologous angle of 90°, the same value as the human mean.

The morphology of the vertebral body and superior articular surface of the axis reveal certain biomechanical constraints. The platform axis, as in AL 333.101, corresponds with compression forces typical of upright posture and permanent bipedy, as is the case in humans. The cone shaped axis corresponds with tensional forces associated with flexion-extension movements and the degree of opening depends on the particular systematic group. In extant hominoids, we consider two groups, one corresponding to man characteristed by permanent bipedy and the second group corresponding to apes, especially the great apes which are quadrupedal, have a semi-erect posture, practise knuckle-walking, climbing and very occasional bipedy. The Swartkrans specimen presents mixed characters, and suggests the presence of more flexion-extension movement than in humans and less than in great apes. This axis is perhaps more typical of bipedalism associated with climbing in the same way as some other Plio-Pleistocene hominid postcranial bones (Senut 1978, Senut & Tardieu 1985 & Tardieu 1979). The specimen was attributed to *Paranthropus* by Robinson (1972). In addition other Plio-Pleistocene superior cervical vertebrae confirms the presence of two locomotor groups in early hominids (Gommery 1995 & 1997).

CONCLUSION

The cervical vertebrae represent the junction between the head and the body. Understanding the evolution of the cervical trunk is very important for an understanding of the change from quadrupedalism to bipedalism. The only known African Miocene cervical vertebra is represented by BA 104'91 from Namibia. This atlas shows many characteristics found in arboreal hominoids and colobines. Some morphological characteristics resemble those seen in the pigmy chimpanzee, or bonobo. The conclusion, for the atlas accords with that based on other postcranial bones of *Otavipithecus* (Senut & Gommery 1997). In SK 854, a Plio-Pleistocene hominid, some characteristics are associated with one of the specific types of bipedalism of the first hominids. The South African axis presents the same locomotor characteristic as other East African Plio-Pleistocene superior cervical vertebrae. At the same time, another specimen presents the characteristics of permanent bipedalism as in humans. Although its systematic position is not clear, it may represent either *Homo* or *Praeanthropus* (Senut 1995 & 1996) or a specific Australopithecine lineage as *Australopithecus anamensis* (Coppens 1995).

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