Sivatherium (Giraffidae, Mammalia) of the Latest Pliocene of Ahl al Oughlam (Casablanca, Morocco) and the Evolution of the Genus in Africa.*

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Introduction

The deposit at Ahl al Oughlam, discovered by J. P. Raynal and J. P. Texier in 1985, has been collected since 1989 by the National Institute of the Archaeological Sciences and Heritage of the Kingdom of Morocco and the French Prehistoric and Paleontological Mission as part of the "Casablanca Program." It has yielded the richest fauna known from the end of the North African Cenozoic (Raynal et al., 1990; Geraads 1993, 1995), biochronologically dated approximately 2.5 Ma.

All the giraffid elements presenting diagnostic characters can be assigned unambiguously to *Sivatherium maurusium* so the absence of *Giraffa*, a genus that arose in the Early Pliocene in eastern and southern Africa (Harris 1976a, b, 1991; Geraads, 1986:474), is unquestionable. *S. maurusium* is represented by more than one hundred specimens, none of which are cranial fragments - only some teeth. Still, it is the most important collection of postcranial remains of this species and the only significant set of remains of giraffids from the Plio-Pleistocene of Africa. It consists of about twenty astragali, as many tarsals and carpals, and about 35 metapodials, of which about twenty are near-complete. The longer bones of the skeleton are rare and the conditions of the deposit make their extraction very difficult. This set offers the first point of solid comparison with that of *Sivatherium hendeyi* of the Early Pliocene of Langebaanweg (Harris, 1976a) and allows the interpretation of a distinctly unique path in the skeletal evolution of this genus in Africa

All the material is housed in the collections of the National Institute of the Archaeological Sciences and Heritage, Rabat.

Description and comparisons

The dentition of *S. maurusium* is well-known (Pomel, 1893; Arambourg, 1961, 1979; Singer and Bone, 1960; Harris 1976a, b, 1991; Geraads, 1987) but the material from Ahl al Oughlam offers supplementary benefit. First of all, it is quite clear that after examining the most complete maxillaries, Aa0-274 (fig. 1g), Aa0-3013, and the isolated teeth, that the Moroccan specimens are of relatively small size in relation to those of the Early Pleistocene of eastern Africa and to those of the Early Pliocene of Langebaanweg.

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A single specimen from Laetoli remains smaller than those from Morocco (Table 1). The teeth from the end of the Pliocene, wherever their geographic origin, are therefore smaller than both the older and younger ones.

Although none of the lower premolars, the most diagnostic teeth, have been found, the dentition appears advanced in the molarization of Dp3, of which the anterior lobe is almost closed in the two specimens and the median valley is almost filled in by the anterior development of the metaconid in Aa0-3176 (fig. 1e, f); the older Dp3's from Makapansat and the Garaet Ichkeul, on the other hand, possess an open anterior lobe (Singer and Bone, 1960; pl. 32 a-c; Arambourg 1979; pl. 29, fig. 1).

Most of the limb bones are represented at Ahl al Oughlam. However, more common, and therefore more useful because they allow the determination of the effect of individual variability, are the astragalus and metapodial. These bones underwent the most notable modifications in proportions.

The metacarpals are of a consistent morphology with in particular an open synovial fossa on the palmar face of the proximal extremity. The metacarpal of the Early Pleistocene of Ain Hanech bears in contrast a closed synovial fossa, although it is near the same length. This character does not seem directly linked to the lengthening of the bone as thought by Bohlin (1926:171). The proportions of the metacarpals at Ahl al Oughlam are somewhat variable. Most of them (7 specimens) form a homogeneous group of small size, of which two larger specimens clearly distinguish themselves (Fig. 1 a-c, Fig. 2). The histogram of the measurement that perhaps increases the most, the distal transverse dimension visually confirms this distinction of the two groups quite well, although the sample (N = 19) is not sufficient for the K-S test to show a significant difference in a normal distribution. As a specific distinction is improbable, it is undoubtedly necessary to recognize a sexual dimorphism here that exists in the skeleton of the modern giraffe but which has never been observed in a fossil giraffid.

In the older deposits (Wadi Natrun in Egypt and Langebaanweg) as well as among *S. giganteum* of the Upper Siwaliks, the metacarpals are larger but of similar proportions. On the other hand, one Late Pliocene specimen from Koobi Fora (Harris, 1991) is a little smaller than those from Morocco. In the more recent African deposits (Ain Hanech, Olduvai, and Elandsfontein) they are hardly shorter than those of presumed females from Ahl al Oughlam, but more robust.

Fig. 1. *Sivatherium maurusium*, Ahl al Oughlam – a, metacarpal Aa0-3204 (male?); b, metacarpal Aa02894; c, metacarpal Aa0-112 (female?); d, metatarsal Aa0-2896; e-f, lower milk tooth set right Dp2-Dp4, e, occlusal view, f, lingual view, Aa0-3176; g, upper tooth set Aa0-274 - a-d, x5/18; e-f x5/6; g, x1/2.

Table 1. Dimensions of the upper teeth (length x width) of African *Sivatherium*
[eleven lines of measurements – see table in original publication]

*: isolated teeth

Lengths P2-M3: Aa0-274: ~215; Peninj: ~235 KNM-ER 797: 244.

Fig. 2. Length of the metacarpal of *Sivatherium* according to its proximal transverse dimension. Measurements (in millimeters) according to Harris (1976a; 1991), Singer and Bone (1960). The dimensions of the largest Mc of Aa0 are approximate.

The metatarsal, rarer than the metacarpal, bears, as always in *Sivatherium*, only a single articular surface for the cubo-navicular. The distal extremity Aa0-957 is interesting in the covering of part of the vascular canal of the anterior face – a convergence with the cervids. There too, the Pliocene specimens from Langebaanweg (Harris, 1976a) and the Garaet Ichkeul (Arambourg, 1979), and of *S. giganteum* are larger.

As for the astragalus, the depth of the depressions for the tendons of the cubo-navicular is quite variable but they are always very much offset (the tendons are of unequal heights). The distribution of the dimensions (16 measurable pieces) suggests no sexual dimorphism in this bone. All the older astragali from Langebaanweg (Harris, 1976a) and Laetoli (Harris, 1987) are clearly larger than those from Ahl al Oughlam (and much thicker than those of *Giraffa*). Only one Langebaanweg specimen (No. 1242; Harris, 1976a) is similar to those from Morocco but just as for certain, more recent deposits, it seems difficult to exclude the possibility of confusion with *Giraffa*. In the Pleistocene the astragalus from Anabo Koma (Geraads, 1985), where *Giraffa* is unknown, just as those from Olduvai and Lake Turkana, are however larger than those from Ahl al Oughlam.

Figure 3. Length of the metatarsal of *Sivatherium* according to its distal transverse dimension. Measurements (in millimeters) according to Harris (1976a; 1991), Singer and Bone (1960), Arambourg (1979).

Evolution of *Sivatherium* in Africa

The Pan-African distribution of *Sivatherium* across the Pliocene and Early Pleistocene strongly suggests that its evolution there is anagenetic, yet the evolution of its skeleton is more complex than considered by Harris (1976a), who saw only a shortening of the metapodials. In reality it is quite clear that the limb bones from the older deposits (Langebaanweg, Laetoli, Garaet Ichkeul, Wadi Natrun), wherever their geographic setting in Africa, are generally larger than those from Ahl al Oughlam, or than those from the Late Pliocene of Kenya. Subject to confirmation from other Late Pliocene deposits, this evolution seems therefore a Pan-African phenomenon. Although the sample is insufficient to verify that the process is exactly isometric, no modification of the robustness of the bones is apparent. Therefore, it is a simple decrease in size, observable in the dentition as well, yet without a change in proportions, which marks the skeletal evolution of *Sivatherium* in Africa during the first phase of the evolution of the genus in the Pliocene in contrast to *S. giganteum* of the Siwaliks, which maintained a large size.

Later, during the second phase, the dentition and the astragalus show minor increases in size but they are accompanied by a slight shortening and clear thickening of the metacarpals.

Fig. 4. Medial height of the astragalus of *Sivatherium* according to its distal transverse dimension. Measurements (in millimeters) after Harris (1976a, 1987, 1991).

If the changes in metapodial proportions between the Late Pliocene and the Early Pleistocene can be easily interpreted as resulting from an increase in size and therefore of body weight, the decrease of the latter across the Pliocene is more unusual and not as easy to explain. Indeed, if the question of body size and weight frequently keeps the attention of paleontologists and ecologists (e.g. LaBarbera, 1990), one must first underscore the calculated relationships within physiological parameters and second, the practical utility. The strict application of Dollo's law even allows for the refinement of the dating of the deposits (Legendre and Bachelet, 1994). On the other hand, the research on the size modifications outside of the extreme case of dwarfism restricts itself more often to very general considerations with its reduction being attributable to decreases of available resources or variations in temperature. Dayan et al. (1991) showed, however, that at least among the Carnivora, Bergmann's law suffers from so many exceptions that it hardly deserves its status as a scientific term. In this case the Pan-African extension of the phenomenon and the consistent reduction in temperature throughout the Pliocene (Miller and Fairbanks, 1985) renders climatic explanations as improbable. The direction of evolution in *Sivatherium* seems to be clearly in conflict with that seen in another large mammal with perhaps a comparable lifestyle (Geraads, 1985), the rhinoceros *Ceratotherium*. According to Guerin (1979) the change in proportions indeed takes place in this lineage across the Pliocene with *C. praecox* having more gracile bones than the succeeding *C. simum*. Perhaps, it could be precisely that the competition between these two genera is related to their evolution, but the sample is still insufficient for an eventual character displacement to be invoked.

Be that as it may, the variations in size and proportions of the metapodials of *Sivatherium* are sufficiently clear to be of biochronological interest, applicable throughout Africa.

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