A brief note on the human visceral skeleton - An evolutionary perspective

Une note brève sur le squelette viscéral dans une perspective évolutive

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AN EVOLUTIONARY PERSPECTIVE

UNE NOTE BRÈVE SUR LE SQUELETTE VISCÉRAL
DANS UNE PERSPECTIVE ÉVOLUTIVE

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ABSTRACT

A review of the visceral skeleton whose origin is in the branchial arches is reported here. It refers to bones, muscles and ligaments of relevant anatomical areas (ear ossicles, basicranium and mandible). The phylogenetic role of visceral skeleton components in the classification of prehistoric human remains has been analyzed by many scholars. It seems that the large morphological variation of these components among human groups makes their taxonomic significance questionable.

Keywords: Middle ear ossicle, hyoid bone, mandibular foramen, hominine.

RÉSUMÉ

Cette contribution porte sur le squelette viscéral qui, trouvant son origine dans les arcs branchiaux, concerne os, muscles et ligaments de différentes régions anatomiques (osselets de l'oreille moyenne, basicranium et mandibule). Le rôle phylogénétique de ces différents composants dans la classification des fossiles humains a été analysé par plusieurs auteurs. La grande variation morphologique qui affecte ces composants interpelle quant à leur utilisation à des fins d'analyse taxinomique.

Mots-clés : *osselet de l'oreille moyenne, os hyoïde, foramen mandibulaire, Homininé.*

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INTRODUCTION

The human skull, as that of all mammals, is formed by bones of different embryonic origin. The neurocranium develops from membranous bones in the vault and enchondral bones in the basicranium. The bones of the splanchnocranium or face are mainly of membranous origin. Some of the components of the skull, especially in the ear (ear ossicles), basicranium (styloid process), and mandible (mandibular ligaments) are of visceral origin and link between membranous and enchondral elements of the skull. The visceral skeleton is basically formed by structures of the branchial arches. The human embryo has six pairs of branchial arches. The first three, the mandibular, the hyoid, and the thyro-hyoid arches are related to the ontogenetic development of ear and hyoid organs. The last arches are not named and are related to the formation of laryngeal and pharyngeal structures.

The mandible is dermal or membranous in its origin and not related to the cartilage of Meckel which belongs to the first branchial arch. This cartilage contributes to the formation of two of the middle ear ossicles: the malleus and the incus. The anterior ligament of the malleus, and the spheno-mandibular ligament are also a part of the first mandibular arch as well as the muscles of mastication.

The second arch and its Reichert's cartilage are responsible for the development of the third middle ear ossicle, the stapes, the styloid process, the lesser cornu of the hyoid and the superior part of the body of this bone. It also contributes to the formation of the stylohyoid ligament and muscles of facial expression.

The greater cornu of the hyoid bone and the lower part of its body as well as some pharyngeal muscles are issue of the third arch. Finally, as just mentioned, the last three arches are related to the development of the laryngeal cartilages and laryngo-pharyngeal muscles (Moore 1973).

In view of the diversity in the embryonic origin and development of the cranio-facial bones among modern humans it is not surprising that a large individual and group variation can be observed in this part of the body. Physiological and functional aspects related to mastication, sense organs, respiration as well as the unique position of the human head due to the erect posture make the evolutionary study of the visceral skeleton of the head in this group as highly complicate. Environmental and cultural factors that influence the general morphology of the skull (*e.g.* climatic conditions, nutritional changes related to the use of fire and its influence in the choice of food, working positions) only add more difficulties to the general understanding of the evolutionary development of the cranio-facial skeleton.

PALEOANTHROPOLOGICAL DATA

From the fossil hominid record some of the anatomical structures of the branchial skeleton can be distinguished. Thus, the styloid process has been mentioned several times in the pertinent literature (*e.g.* McCown, Keith 1939; Heim 1989).

Middle ear ossicles are known from *Australopithecus* (Rak, Clark 1979; Moggi-Cecchi, Collard 2002), European Middle Pleistocene specimens (Quam 2006), Middle and Upper Paleolithic hominids from Eurasia (Angel 1972; Arensburg, Nathan 1972; Heim 1982; Arensburg, Tillier 1983; Lisonek 1992; Arensburg *et al.* 1996; Ponce de Leone, Zollikoffer 1999; Spoor 2002; Rougier 2003; Quam 2006; Quam, Rak 2008) and Africa (Crèvecoeur 2007), Epipaleolithic and modern populations (*e.g.* Massali 1964; Arensburg *et al.* 1981; Sarrat *et al.* 1988).

The first fossil hyoid bone hitherto was recovered from the Middle Paleolithic layers of Kebara (Israel) and this discovery has thrown a new light on the question of the origins of the articulated language (Arensburg *et al.* 1989, 1990). Recently, the discovery of a child hyoid bone of *Australopithecus afarensis* (Alemseged *et al.* 2006) and that of two Middle Pleistocene hyoid bones from the Sima de los Huesos site in Spain (Martinez *et al.* 2008) were reported.

Soft tissues such as ligaments and muscles are obviously missing in skeletons but their attachment, (*e.g.* masticatory muscles, spheno-mandibular, pterygo-mandibular and stylo-mandibular ligaments) are of special importance and have given place to many studies (*e.g.* Kallay 1970; Rak *et al.* 1994; Stefan, Trinkaus 1998).

Middle ear ossicles

The ear bones in almost all Mammalia present a striking morphological similarity. Only few genera (*e.g.* Cetacea) present ear bones which differ substantially from those of other mammals. Such seems to be also the case for the incus of the *Australopithecus robustus* SK 848 from Swartkrans that, according to Rak and Clark (1979: 63) "is far beyond the range of normal variation characteristic of the incudes of modern man and the great apes". By contrast the study of the stapes of the

Australopithecus africanus Stw 151 in Sterkfontein and that of the oval window area of other individuals from the same site presented by Moggi-Cecchi and Collard (2002: 261), indicate "a marked difference in stapedial footplate size between *Australopithecus* and living great apes on one hand, and modern humans on the other".

These results obtained from two middle ear ossicles and observations on the oval window may be due to specific differences between the Genera of *Australopithecus*, or to the small number of individuals studied. They can also be related to some abnormality in the morphology of the structures described or to the sample size of modern hominids (N = 4) employed in the comparative analysis. Interestingly the data brought by Moggi-Cecchi and Collard (2002) on the oval window area suggest also that the *Homo habilis* specimen from Sterkfontein (Stw 53) should be considered as closer to Australopithecines and great apes than to other species of the genus *Homo*. Furthermore the stapedial footplate area in Sterkfontein 151 is so small that it falls outside the range of variation in chimpanzees.

The first reports on fossil middle ear bones, those from Darra-I-Kur from Afghanistan and Qafzeh 11 from Israel (Angel 1972; Arensburg, Nathan 1972) demonstrated that morphologically and metrically the incus and malleus of these Middle Paleolithic specimens were in the range of variation of Epipaleolithic, historic and modern populations. These observations were confirmed by the description of the incus from Qafzeh 21 (previously called Qafzeh 4a, Arensburg, Tillier 1983; Tillier 1999), and that of the stapes from Subalyuk 2 (Arensburg *et al*. 1996).

The Neanderthal bones from La Ferrassie 3 (France) appear also in the normal range of human variation, although Heim (1982) attributed to the crura of La Ferrassie stapes and to the angle between the processes of the incus a specific morphology. In the former he described a strong asymmetry between the anterior and posterior crura and in the later a close angle between the processes. It must be mentioned, however, that straight and arched crura are present in all human samples and are not characteristic of any particular group (Sarrat *et al*. 1988). In addition, given our assessment of photographs of the incus for La Ferrassie 3 [3], it is clear that the criteria employed by Heim for definition of the incudal angle

differ from those commonly employed in studies of fossil and recent incuses (Arensburg, Nathan 1972; Arensburg *et al*. 1981; Arensburg, Tillier 1983). When both incuses are measured in the same way the angle of La Ferrassie 3 (97°), as well as that of Qafzeh 11 (94°), fall within the modern range of variation.

One important observation on ancient and modern incuses is the presence of a notch in the inferior surface of the short process (Arensburg, Nathan 1971; Winerman *et al*. 1980). This notch is present in Qafzeh 21 and 11 (early modern humans from Israel), Le Moustier 1 (Neanderthal from France, Ponce de Leon, Zollikofer 1999: 487) and probably other human fossils as well as in approximately half of all modern populations. It is absent in all non human primates and seems to be a specific human adaptation that regulate incudal vibrations. Its presence in ancient and modern populations suggests that "the ontogeny of the incus is similar in Neanderthals and modern humans (Ponce de Leon, Zollikofer 1999: 487). The preservation of the stapes among prehistoric human remains is extremely rare. Indeed, only four specimens have been found and described till present (Sterkfontein Stw 151, Darra-i-Kurr, Subalyuk 2 and La Ferrassie 3). By contrast, the temporal bone is better preserved and some of its structures, including the oval window, may be easily measured. The strait anatomical relationship between the shape and areas of the stapes footplate and those of the oval window makes these two structures almost identical in size. The difference in size between footplate and oval window areas in two individuals studied here varies from 0.011 to 0.014 mm^2. Then, the measurements of the oval window may give a genuine idea of the size of the functional part of the stapes, its footplate.

The oval window areas measured on four Levantine Middle Paleolithic specimens were compared to the stapedial footplate area of the Neanderthal La Ferrassie 3 child. The range of distribution documented by this Middle Paleolithic sample (N = 5) overlaps with the stapedial footplate area of a recent sample (N = 20). Furthermore two of the Sterkfontein specimens fall within this range of distribution.

A recent study conducted by Quam (2006) has enlarged the Qafzeh sample with four new ear ossicles (two incus and two malleus) and brought additional data with the Amud 7 incus. Their analysis gives important new information on these bones (Quam, Rak 2008). The Qafzeh Mousterian sample (now represented by 4 incus and 3 malleus coming from 4 individuals) accurately documents for the first time individual variation within one

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3. During the preparation of this note, the bone was not available for revision.

prehistoric site. The authors mention (p. 431) that "there are clear anatomical differences between the ear ossicles in the Neandertal and *H. sapiens* evolutionary lineages… although all of the anatomical variants considered in the present study can also be found in living humans". For example, the Qafzeh 11 incus "resembles Neandertals" and "is both metrically and morphologically very similar to that of Amud 7". Undoubtedly these observations open a large field of research for future analyses and conclusions dealing with the role of the ear bones in the understanding of human evolution.

Several middle ear ossicles and oval windows of Paleolithic hominids (*e.g.* Neanderthals from Le Moustier 2, France and others) are still unpublished. The complete description certainly will clarify many aspects of this important part of the human visceral skeleton related to the perception of sounds (*e.g.* size proportions between the bony processes, size of the stapes footplate, bilateral asymmetry) and therefore to communication.

The hyoid bone

The idea of a limited Neanderthal articulated speech capability was originally supported by observations done on their skull. The presence of superior geni processes in the mandibular symphysis, because of their attached tongue muscles (genioglossus), was considered as an indicator of a linguistic capability (Zaborowski 1898; Thomson 1915; Vallois 1962). Accordingly, most of the human fossil specimens that instead of a process presented a geni fossa remainded beyond the possibilities of a speech capability. The angle of the styloid processes, an adduced basicranial flatness in Neanderthals, especially in La Chapelle-aux- Saints, the shortness of the neck, the antero-posterior distance between the cervical vertebral column and the mandible, etc. were some of the features adduced for the incompatibility of Neanderthals to speak. Furthermore, the larynx in this Paleolithic population was considered to be in a high position, similar to that of non human primates or that of small human children before the age of full vocalization (Lieberman, Crelin 1973; Laitman *et al.* 1979). According to these authors, in Neanderthals the space between the base of the cranium and the larynx was too small to permit a normal resonance box and therefore limited their linguistic capability.

A new reconstruction of the La Chapelle-aux-Saints skull placed the basicranial angulation of this neanderthal close to that of modern humans (Heim 1989). The angle of the styloid process to the basicranium was obviously "modernized". This angle, contrary to former views, has no relevance to the position of the mandible, the hyoid, the pharynx or the laryngeal cartilages. the styloid process is related to these organs through ligaments (stylohyoid and stylomandibular) and muscles (styloglossus, stylopharyngeus and stylohyoideus) of branchial origin whose flexibility make irrelevant the original direction of the process to its underlying structures.

The discovery of the hyoid bone associated to the Kebara 2 skeleton strongly impacted our knowledge on the biological and social status of Middle Paleolithic hominids (Arensburg *et al.* 1989, 1990). The interpretation of this discovery provoked bitter disagreement between scholars that postulated, on one hand, that Middle Paleolithic Hominids were limited in their speech capabilities (Lieberman, Crelin 1973; Laitman *et al.* 1990) and others that accepted for this group a full linguistic faculty (Arensburg *et al.* 1990; Schepartz 1993). Furthermore the Kebara 2 hominid skeleton allowed the reconstruction of the vocal tract with certitude. The hyoid bone was found to be, metrically and morphologically, in the range of variation of all modern humans (Arensburg *et al.* 1990). The muscular imprints indicative of the position of the hyoid with respect to the mandible (*e.g.* mylohyoid, digastric muscles) permitted to place these bones of Kebara 2 in their normal, physiological position, that is, the inferior border of the mandible and the body of the hyoid at the level of the fourth cervical vertebra. The height of the mandibular ramii and that of all the cervical vertebral bodies in Kebara 2 together with a normal cervical lordosis corroborated the low position of the laryngeal vocal tract in this specimen. These observations have been reevaluated and confirmed by recent works (Lieberman, McCarthy 1999). According to Martinez *et al.* (2008), the modern hyoid morphology was present in the fossil record by at least 530 kyrs at Sima de Los Huesos.

Shape of the mandibular foramen

The inner ear and mandible are two parts of the skull that do not develop from the visceral skeleton but are of ectodermal origin. Both, however, are so straightly related in their function to branchial structures that they must be included here. The spheno-mandibular ligament of the first branchial arch is attached around the mandibular foramen that permits the passage of the inferior alveolar

nerve and vessels through the body of the mandible. The shape of this foramen is related to the attachment of the spheno-mandibular ligament and individual variation among recent humans is well documented (see Rouas 2007). However this feature has been considered as having a taxonomic relevance in ancient human remains (Kallay 1970).

Among Neanderthals its superior border has been described as horizontal (0-H shape) while in *Homo sapiens* it is currently in angle (V shaped). In modern populations the ligament gives many intermediate forms to the foramen, with a U shape, large or narrow modern V shape, "Neanderthal" O-H shape, largely open inferior alveolar canal, etc. (Stefan, Trinkaus 1998). The O-H shape occurs in 41.7% of adult European Neanderthals (Stefan, Trinkaus 1998), 44.4% of Early Upper Paleolithic mandibles and 5.3% of Late Upper Paleolithic remains (Frayer 1992), making its taxonomic value highly questionable. Such a configuration of the mandibular foramen is lacking on non-adult Neanderthals (Tillier 1995).

As mentioned before, the muscles of mastication whose origin is in the first branchial arch are attached to different parts of the mandible. These visceral muscles are then extremely important in the development and shape of the mandible. Indeed, as in many other parts of the skeleton (*e.g.* nuchal area of the skull, deltoid tuberosity of the humerus, linea aspera of the femur), the biomechanic forces applied by the muscles basically contribute to the final skeletal morphology. In the specific case of the mandible, the visceral muscles of mastication are strongly responsible for the shape of the condyle (lateral pterygoid *vs.* levator muscles), the extro/introversion of the gonion (*e.g.* masseter *vs.* medial pterygoid), the rugged shape of the medial surface of the ramus (medial pterygoid), the shape and position of the coronoid process (*temporalis*) and the curvature of the mandibular (sigmoid or semilunar) notch (lateral pterygoid *vs. temporalis*).

The muscles operating on the mandible are directly related to the constraints of mastication and then to physiological (masticatory strength), environmental (kind of food available) and cultural (choice of food, use of teeth as working tool) aspects. It is not exceptional, then, to find that Neanderthals and Inuits present "similar morphological specializations related to an increasing efficiency of the force production on the anterior dentition" all this related to similar diets and environment (Spencer, Demes 1993: 17). Obviously, the taxonomic value of the anterior dental attrition in both groups is nil as well as many of the morphological variations observed in ancient

and modern human groups (*e.g.* lateral projection of the condylar process, medial pterygoid tubercle, shape of the *sulcus mandibularis*, development of the coronoid process, etc. (for a whole description of these variations see Schultz 1933).

DISCUSSION

The membranous labyrinth, ectodermal (neuroecto-dermal) in its origin and the bony labyrinth that develops from mesenchymal cartilage, are closely related in their topography and function to the middle ear organs of branchial origin. Vibrations that permit the perception of sounds are transmitted from the external ear to the cochlea of the internal ear by the auditory ossicles through the oval window.

Sensory organs in three membranous semicircular canals and vestibular sacs (utricle and saccule) are responsible of equilibrator reflexes, position of the eyes and movements of the head, as well as static and kinetic balance (Eckhardt, Hildebrand 1998). These structures are related to the posture of the body and, among Hominids, to the erect posture. There is a broad consensus among paleoanthropologists that bipedalism is one of the first, if not the first acquisition in the course of hominization. Therefore, the neurological mechanism that has permitted this adaptation certainly developed at the same time in order to allow equilibrium and head movements in the new erect posture.

Adduced differences in the inner ear between early hominids, Neanderthals, modern humans and non-human primates that place Neanderthals outside the morphological range of the hominid and even primate variation seem to be bizarre (Hublin *et al*. 1996). It must be emphasized that the three semicircular canals considered to have a taxonomic value are, indeed, tilted, the lateral is sometimes found in the superior position, or less frequently, in a lower position. Furthermore, "one third of the canals were found to be asymmetric in both, their orientation and their position" in modern humans (Caix, Outrequin 1979: 261).

New studies of these structures have shown that classic Neanderthals such as Le Moustier are, indeed, in the normal range of variation displayed by *Homo erectus* and *Homo sapiens*, and "the taxonomic value of otic characteristics has to be reconsidered" (Ponce de Leon, Zollikofer 1999: 487). Spoor and Zonneveld (1998: 248)

also compart this view: "labyrinthine traits should be used with care in phylogenetic analysis because of possible homoplasies following from the functional association with vestibular function".

From this short review it appears controversial to employ morphological features of components derived from the visceral skeleton in taxonomic and phylogenetic studies. As documented by the fossil record it is clear that a series of functional structures related to sense organs and speech capabilities have not changed from hundred thousands years.

BIBLIOGRAPHY

ALEMSEGED (Z.), SPOOR (F.), KIMBEL (W.H.), BOBE (R.), GERAADS (D.), REED (D.), WYNN (J.-G.) 2006, A juvenile early hominin skeleton from Dikika, Ethiopia, *Nature* 443: 296-301.

ANGEL (L.) 1972, A Middle Palaeolithic temporal bone from Darra-I-Kur, Afghanistan, *Transactions of the American Philosophical Society* 62: 54-56.

ARENSBURG (B.), NATHAN (H.) 1971, Observations on a notch in the short (superior or posterior) process of the incus, *Acta Anatomica* 78: 84-90.

ARENSBURG (B.), NATHAN (H.) 1972, À propos de deux osselets de l'oreille moyenne d'un Néanderthaloïde trouvés à Qafzeh (Israël), *L'Anthropologie* 76 : 301-307.

ARENSBURG (B.), HARELL (M.), NATHAN (H.) 1981, The human middle ear ossicles: morphometry and taxonomic implications, *Journal of Human Evolution* 10: 199-205.

ARENSBURG (B.), TILLIER (A.-M.) 1983, A new Mousterial child from Qafzeh (Israel): Qafzeh 4a, *Bulletins et Mémoires de la Société d'Anthropologie de Paris*, n.s., 10, 13: 61-69.

ARENSBURG (B.), TILLIER (A.-M.), VANDERMEERSCH (B.), DUDAY (H.), SCHEPARTZ (L.A.), RAK (Y.) 1989, A Middle Palaeolithic human hyoid bone, *Nature* 338: 758-760.

ARENSBURG (B.), SCHEPARTZ (L.A.), TILLIER (A.-M.), VANDERMEERSCH (B.), RAK (Y.) 1990, A reappraisal of the anatomical basis for speech in Middle Palaeolothic hominids, *American Journal of Physical Anthropology* 83: 137-146.

ARENSBURG (B.), PAP (I.), TILLIER (A.-M.), CHECH (M.) 1996, The Subalyuk 2 middle ear stapes, *International Journal of Osteoarchaeology* 6: 185-188.

CAIX (M.), OUTREQUIN (G.) 1979, Variability of the bony semicircular canals, *Anatomia Clinica* 1: 259-265.

CRÈVECOEUR (I.) 2007, New discovery of an Upper paleolithic auditory ossicle: the right malleus of Nazlet Khater 2, *Journal of Human Evolution* 52: 341-345.

ECKHARDT (R.B.), HILDEBRAND (A.H.) 1998, Semicircular canal size and upright stance: a comparative perspective, *American Journal of Physical Anthropology*, suppl. 26, Annual Meeting 74.

FRAYER (D.) 1992, The persistence of Neanderthal features in post-Neanderthal Europeans, *in* G. Brauer, F.H. Smith (eds), *Continuity or complete replacement: controversies in Homo sapiens evolution*, A.A. Balkema, Rotterdam, p. 171-180.

HEIM (J.L.) 1982, Les enfants Néandertaliens de La Ferrassie Masson Éd., Paris.

HEIM (J.L.) 1989 La nouvelle reconstitution du crâne Néanderthalien de La Chapelle-aux-Saints, méthodes et résultats, *Bulletins et Mémoires de la Société d'Anthropologie de Paris*, n.s., 1 : 95-118.

HUBLIN (J.J.), SPOOR (F.), BRAUN (M.), ZONNEVELD (F.), CONDEMI (S.) 1996, A late Neanderthal associated with Upper Paleolithic artifacts, *Nature* 381: 224-226.

KALLAY (M.) 1970, Komparative naponeme o celjustima Krapinsikth Praljudi s obzirom na polozaj mectu Hominidima, *in* M. Malez (ed.), *Krapina 1891-1969*, Jugoslavenka Akademija Znanosti i Umjetnosti, Zagreb, p. 153-164.

LAITMAN (J.T.), HEIMBUCH (R.C.), CRELIN (E.S.) 1979, The basicranium of fossil hominids as an indicator of their respiratory system, *American Journal of Physical Anthropology* 51: 15-34.

LAITMAN (J.T.) REIDENBERG (J.S.), GANNON (PJ.), JOHANSSON (B.), LANDAHL (K.), LIEBERMAN (P.) 1990, The Kebara hyoid: what can it tell us about the evolution of the hominid vocal tract? *American Journal of Physical Anthropology* 8l: 254.

LIEBERMAN (P.), CRELIN (E.S.) 1973, On the speech of Neanderthal man, *Linguistic Inquires* 1: 203-223.

LIEBERMAN (D.E.), MCCARTHY (R.C.) 1999, The ontogeny of the cranial base angulation in humans and chimpanzees and its Implication for reconstructing pharyngeal dimensions, *Journal of Human Evolution* 36: 487-517.

LISONEK (P.) 1992, Ossicula auditus mladopaleolitickych lovcu mamutu z Dolnich Vestonic, *Acta Musei Nationalis Pragae* XLVIII: 65-68.

Massali (M.) 1964, Dati sulla variabilita morphometrica e *Italiano di Anatomia edi Embriologia* 69: 435-446.

Martinez (I.), Arsuaga (J.L.), Quam (R.), Carretero (J.M.), Gracia (A.), Rodriguez (L.) 2008, Human hyoid bones from the Middle Pleistocene site of Sima de Los Huesos (Sierra Atapuerca, Spain), *Journal of Human Evolution* 54: 118-124.

McCown (T.D.), Keith (A.) 1939, *The Stone Age of Mount Carmel: The fossil human remains from the Levalloiso-Mousterian*, Vol. 2, Oxford, Clarendon Press.

Moore (K.L.) 1973, *The Developing Human, Clinically Oriented Embryology* W.B. Saunders Co. Philadelphia.

Moggi-Cecchi (J.), Collard (M.) 2002, A fossil stapes from Sterkfontein, South Africa, and the hearing capabilities of early hominids, *Journal of Human Evolution* 42: 259-265.

Ponce De Leon (M.S.), Zollikofer (C.P.E.) 1999, New evidence from Le Moustier 1: Computer-assisted reconstruction and Morphometry of the skull, *The Anatomical Record* 254: 474-489.

Quam (R.) 2006, *Temporal bone anatomy and the evolution of the acoustic capacities in fossil humans*, PhD., Binghamtom University, NY.

Quam (R.), Rak (Y.) 2008, Auditory ossicles from southwest Asia Mousterian sites, *Journal of Human Evolution* 54: 414-433.

Rak (Y.), Clark (R.J.) 1979, Ear ossicle of *Australopithecus robustus*, *Nature* 279: 62-63.

Rak (Y.), Kimbel (W.), Hovers (E.) 1994, A Neandertal Infant from Amud Cave, Israel, *Journal of Human Evolution* 26: 313-324.

Rouas (P.) 2007, *Les foramens de passage de la branche mandibulaire du nerf trijumeau (V3), Positions relatives, repères cranio-faciaux, implications anthropologiques*, Thèse de l'Université Bordeaux 1, spécialité Anthropologie Biologique (Unpublished).

Rougier (H.) 2003, *Étude descriptive et comparative de Biache-Saint Vaast 1 (Biache-Saint Vaast, Pas-de-Calais, France)*, Thèse de l'Université Bordeaux 1, spécialité Anthropologie Biologique (Unpublished).

Sarrat (R.), Garcia Guzman (A.), Torres (A.) 1988, Morphological Variations of Human Ossicula Tympani, *Acta Anatomica* 131: 146-149.

Schepartz (L.A.) 1993, Language and modern human origins, *Yearbook of Physical Anthropology* 36 : 91-126.

Schultz (H.E.) 1933, Ein beitrag zur rassen morphologie des unterkiefers, *Zeitschrift fur Morphologie und Anthropologie* 32: 275-366.

Spencer (M.A.), Demes (B.) 1993, Biomechanical analysis of the masticatory system configuration in Neanderthals and Inuits, *American Journal of Physical Anthropology* 91: 1-20.

Spoor (F.) 2002, The auditory ossicles, *in* J. Zilhao, E. Trinkaus (eds), *Portrait of the Artist as a Child, the Gravettian Human Skeleton from the Abrigo do Lagar Velho and Its Archeological **Context**,* Instituto Portugués de Arqueologia, Lisbon, p. 293-296.

Spoor (F.), Zonneveld (F.) 1998, Comparative review of the human bony labyrinth, *Yearbook of Physical Anthropology* 41: 211-251.

Stefan (V.H.), Trinkaus (E.) 1998, Discrete trait and dental morphometric affinities of the Tabun 2 mandible, *Journal of Human Evolution* 34: 443-468.

Thomson (A.) 1915, On the presence of genial tubercles on the mandible of man, and their suggested association with the faculty of Speech, *Journal of Anatomy and Physiology* 50: 39-74.

Tillier (A.-M.) 1995, Neanderthal ontogeny: a new source for critical analysis, *Anthropologie* XXXIII, 1-2: 63-68.

Tillier (A.-M.) 1999, *Les Enfants Moustériens de Qafzeh, Interprétation Phylogénétique et Paléoauxologique*, Cahiers de Paléoanthropologie, CNRS Éditions, Paris.

Vallois (H.V.) 1962, Langage articulé et squelette, *Homo* 13 : 114-121.

Winerman (I.), Nathan (H.), Arensburg (B.) 1980, Posterior Ligament of the Incus: Variations in its Components *Ear, Nose and Throat Journal* 59: 227-231.

Zaborowski (S.) 1898, *L'Homme préhistorique*, 5e édition, C. Reinwald, Paris.