

Actes du XIVème Congrès UISPP, Université de Liège, Belgique, 2-8 septembre 2001

Acts of the XIVth UISPP Congress, University of Liège, Belgium, 2-8 September 2001



SECTION 1: THÉORIES ET MÉTHODES / THEORY AND METHOD

Colloque / Symposium 1.7

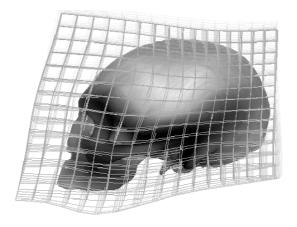
Three-Dimensional Imaging in Paleoanthropology and Prehistoric Archaeology

Edited by

Bertrand Mafart Hervé Delingette

With the collaboration of

Gérard Subsol



BAR International Series 1049 2002

3-D IMAGING AND TRADITIONAL MORPHOMETRIC ANALYSIS OF THE ADOLESCENT NEANDERTAL FROM LE MOUSTIER

Jennifer L. THOMPSON, Andrew J. NELSON, Bernhard ILLERHAUS

Résumé: Les auteurs se proposent de montrer l'étendue des informations qui peuvent être utilisées par les paléoanthropologues pour décrire les hominidés fossiles, analyser leurs variations de dimensions et de proportions et interpréter ces données grâce aux nouvelles techniques d'imageries tridimensionnelles associées aux méthodes d'analyses plus conventionnelles. En prenant comme exemple le crâne de l'adolescent néandertalien Le Moustier I, les auteurs montrent l'intérêt de l'association de ces deux méthodologies pour l'étude et la description du crâne, l'étude de la denture et du squelette post-crânien de ce fossile. Les résultats obtenues sont ensuite remplacés dans une plus large perspective en démontrant leurs intérêt pour l'étude de la croissance et du développement et l'analyse phylogénique.

Abstract: The purpose of this paper is to outline information that can be used by paleoanthropologists to describe fossil hominid morphology, to document size and shape variables, as well as to interpret those data within a broader context using 3-D imaging techniques as well as traditional analytical methods. Using the Le Moustier 1 adolescent Neandertal as an example, this paper will demonstrate the benefits of both types of techniques for the analysis of fossil hominid specimens. It will outline how these techniques were used to describe the skull, dentition, and postcranial skeleton, to identify species specific features, and to determine the age and sex of the Le Moustier 1 specimen. It will then place these data into a broader analytical context to address both growth & development issues and phylogenetic implications of the findings.

INTRODUCTION

With the discovery of any new fossil hominid specimen, the task of the paleoanthropologist is to undertake a description of the specimen and its state of preservation, describe the specimen's anatomy, compare that anatomy to other fossils of similar antiquity, to determine shared species characteristics, the chronological age of the specimen, its sex, and any unique features of the individual. This information is then used to place the individual into a broader phylogenetic, and, if appropriate, ontogenetic context. To achieve these goals, paleoanthropologists have, until recently, relied solely on traditional morphometric measurements to measure size and shape of skeletal elements, including the skull, teeth, and postcrania. They have also relied on non-metric traits to examine features such as muscle development or the presence/ absence of shared, shared derived, or derived, species specific characteristics. While these techniques have produced a rich body of research, paleoanatomists' efforts have been hampered in two ways. First of all, not all fossils are complete. Second, valuable information about internal morphology of skeletal elements is often missed, due to the difficulty of undertaking radiographic analysis and/or the difficulty of interpreting two-dimensional (2-D) plane film radiographs.

The field of paleoanthropology has been revolutionized by the addition of computed, or computerized tomography to our battery of analytical tools. Computerized tomography (CT) images have contributed to our knowledge of the internal morphology and to our ability to study overall dimensions of incomplete or fragmentary fossil skulls (Tate & Cann 1982; Conroy & Vannier 1984, 1986; Wind 1984; Zonneveld & Wind 1985; Zonneveld *et al.* 1989; Conroy *et al.* 1990; Spoor

et al. 1993; Spoor & Zonneveld 1994, 1995; Spoor et al. 1994; Hublin et al. 1996; Thompson & Illerhaus 1998, 2000, in press). This technique can be used to produce 2-D "slices" through a fossil, or to produce three-dimensional (3-D) images. The latter ability allows one to make virtual reconstructions of skulls from their various fragments without damaging the original specimen (Kalvin et al. 1992; Thompson & Illerhaus 1998, 2000, in press; Zollikofer et al. 1995, 1998). CT imaging has also been used to investigate internal structures of the skull such as the labyrinth of the inner ear and the frontal sinus as well as the dentition of fossil hominids (e.g. Spoor & Zonneveld 1995: Spoor et al. 1993; Hublin et al. 1996; Seidler et al. 1997; Thompson & Illerhaus 1998, 2000, in press).

Given the focus of this symposium it seemed appropriate to discuss the application of 3-D imaging in paleoanthropology by demonstrating the use of both traditional morphometric methods as well as CT methods using Le Moustier 1 as a case study. This individual is an adolescent Neandertal, discovered in 1908 at the site of Le Moustier in the Dordogne of France (Hauser 1909). It was described briefly when first discovered (Klaatsch 1909a, b, c, d; Klaatsch & Hauser 1909) but, by comparison to today's standards was, until recently, relatively unstudied (Bilsborough & Thompson in press a). Work on this specimen began again in 1992 and, since then one of us (JT) along with various co-authors undertook a description and analysis of the skull, dentition and postcranial skeleton, as well as a CT or virtual reconstruction of the skull. The intent of this paper is to summarize some of these results, highlighting the contribution of both traditional and CT methods to our interpretation of the morphology of this specimen.

DESCRIPTION OF SPECIMEN & SPECIES SPECIFIC CHARACTERISTICS - SKULL

Weinert's (1925) original reconstruction of the Le Moustier 1 cranium was dismantled during the late 1960's and Figure 1 illustrates the current disassembled state of the skull and dentition. With Alan Bilsborough of Durham University, UK, JT undertook a detailed anatomical description of the specimen using traditional methods (Thompson & Bilsborough 1997, 1998a, b, in press; Thompson in press). In these papers, we used conventional morphometric techniques to describe typical Neandertal features such as cranial size and shape (long, low skull), the state of particular anatomical traits (e.g. occipital bun, iniac fossa, mastoid tubercle, shape of the orbits) and so on. We noted that some Neandertal features are not fully developed, due to the immaturity of the specimen. These features include the lack of a retromolar space, the gracile supraorbital torus, and the lack of mid-facial prognathism. We also identified unique features such as the asymmetry of the entoglenoid processes of the cranial base and the misshapen left mandibular condyle - likely broken and healed while the individual was still living.

Early in 1994, JT and BI were invited to undertake a virtual CT reconstruction of the skull by the director of the Museum fur Vor- und Fruhgeschicte, Berlin where the specimen is housed. This provided us with the opportunity to further our analysis of the morphology of the specimen (Hoffmann 1997; Hoffmann *et al.* 1994). A full description of the reconstruction process, using microcomputed tomography data, is outlined elsewhere (Thompson & Illerhaus 1998). The microcomputed tomography data were collected for this analysis using the 3-D micro-tomograph housed at Bundesanstalt für Materialforschung und -Prüfung (BAM), Berlin using methods developed at BAM (e.g. Illerhaus *et al.* 1994; Illerhaus *et al.* 1997 a, b).

Figure 2 illustrates several views of the virtual reconstruction of the Le Moustier 1 skull. This figure illustrates that the overall shape of the skull is typical of adult Neandertals — the long, low skull, and occipital bun are evident, as is the youthful features mentioned above — the lack of retromolar space, undeveloped mid-facial prognathism, etc.

Aside from the reconstruction, two additional objectives were successfully achieved using the CT data: 1) we were able to differentiate between real fossilized bone and reconstructed material (plaster etc.) and 2) we were able to examine internal structures of the skull. Analysis revealed that much of the palate was composed of reconstructed material, as were several cranial pieces (see Thompson & Illerhaus 1998 for details). Access to the CT data allowed us to examine the frontal sinuses in virtual space. Neandertal sinuses usually spread to mid-orbit but do not extend up onto the frontal bone (Heim 1978; Tillier 1974; Trinkaus 1983; Vlcek 1967, 1969). This individual's sinuses are not likely to have been fully grown, explaining why they do not extend to mid-orbit. CT data also allowed us to isolate the labyrinth of the inner ear. Analysis reveals that Le Moustier 1 follows the Neanderthal pattern of having an inferiorly positioned posterior semicircular canal relative to the plane of the lateral canal (Thompson & Illerhaus 1998, 2000, in press).

DESCRIPTION OF SPECIMEN & SPECIES SPECIFIC CHARACTERISTICS - DENTITION

A detailed description and analysis of the dentition has also been undertaken using traditional methods (Bilsborough & Thompson in press b). In that paper, we discussed the preservation of the dentition, development of marginal ridges, accessory cusps, dental wear, dental metrics. The paper also



Figure 1 - Le Moustier I skull and dentition Image reproduced with permission from Thompson & Illerhaus, 1998, *J Hum Evol* 35, 647-665.

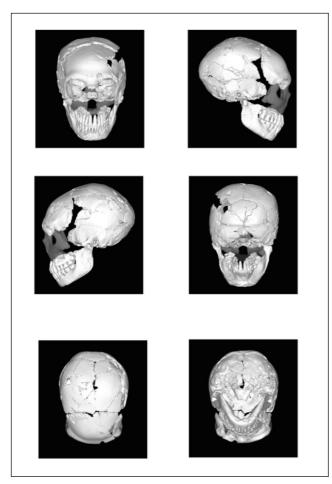


Figure 2 - Virtual reconstruction of the Le Moustier 1 skull Images reproduced with permission from Thompson & Illerhaus, 1998, *J Hum Evol* 35, 647-665.

examined features like the extent of shoveling on the upper central incisors, the presence of deep lingual pits on the upper lateral incisors, and the presence of extra cusps (e.g. Carabelli's cusp on the upper first molars and a tuberculum intermedium or metaconulid on the lower third molars). The extent of dental wear was documented. For example, the lower incisors show labial wear indicating an overbite, there is asymmetrical wear when comparing left and right dental arcades, and there is evidence of dental probing between the teeth. The presence and degree of enamel hypoplasia was also noted.

Thompson and Illerhaus (in press) used CT data to enhance the description of gross morphology by allowing us to "slice" the teeth in several planes. This analysis revealed that the upper premolars both have double roots. In the genus *Homo* it is typical for the first upper premolar to have two roots, but the second premolar to have a single root (Hillson 1996). The second upper premolars of Le Moustier 1 are fully two-rooted teeth with a larger buccal and smaller lingual root which expands our knowledge of the variation and/or presence of this trait in Neandertals. We were also able to document at the extent of taurodontism (the expanded pulp cavities of the specimen), a trait characteristic of Neandertals. We were also able to fully visualize an impacted canine which had fully formed, but never erupted. Finally, the CT analysis of the dentition played an important

role in the determination of the age of this individual (see below).

DESCRIPTION OF SPECIMEN & SPECIES SPECIFIC CHARACTERISTICS - POSTCRANIA

Thompson & Nelson (in press b) provide a detailed description and metric analysis of the postcranial skeleton of Le Moustier 1, using casts and what remains of the original specimen. Unfortunately, the postcranial bones were badly damaged by fire at the end of WWII. The original material that survived the fire suffered shrinkage and some distortion from the heat (Hermann, 1977), but we were still able to determine a great deal about this individual by examining the anatomy in a comparative perspective.

The Le Moustier 1 postcranial skeleton possesses a number of typical adult Neandertal features. For example, a cast of a rib fragment is thick and triangular in cross-section, but whether the rib cage was barrel-shaped as in adult Neandertals is unknown. In fact, given the youthful age of the Le Moustier 1 individual, it is unlikely that the chest had reached its adult proportions, since those are achieved at the end of the adolescent period (Tanner 1962). According to Klaatsch (1909c, d), the Le Moustier 1 clavicle is relatively long and slender as seen in adult Neanderthals though a cast indicates that it is missing its epiphyses. According to Thompson & Nelson (in press b) the chest of Le Moustier 1 is deep. The arm bones indicate that the radial tuberosity is placed medially, the radius is strongly curved, the humerus is robust with a strongly marked deltoid tuberosity typical of adult specimens (Klaatsch & Hauser 1909), there is a prominent M. pronator quadratus crest on the ulna, and an anterior orientation of the trochlear notch of the ulna. Despite his youth, we can see from the well developed muscle attachment areas on the arms that the capability for strong rotation and supination of the forearm was already present in this youth. This observation has important behavioural implications (see Thompson in press; Thompson et al. in press, for discussion of these features).

Comparisons between the limb dimensions of this individual with those of adult Neandertals, demonstrates that in several features, such as femoral head size, Le Moustier 1 was a scaled version of the adult form (Thompson & Nelson, in press b). Le Moustier 1 was also a scaled version of the adult form in having shortened distal limbs. The arm bones show a similar pattern. Like adult Neandertals, the diaphysis of the Le Moustier 1 femur is robust, cylindrical, lacks a pilaster, has thick cortical bone and a relatively narrow marrow cavity.

The postcranial elements were not examined by CT methods as they were damaged and distorted by fire, although they were examined using plane film radiography (Hermann 1977). However, in a less damaged specimen, CT analysis would certainly be of use in accurately measuring things such as thickness and distribution of cortical bone, and the distribution and orientation of trabecular bone.

SEX DETERMINATION

From the time of its discovery in 1908, Le Moustier 1 was assumed by many researchers to be male based on its size and robusticity. However, since all Neandertals are robust compared to living modern humans, this conclusion must be approached with caution. The determination of sex also has relevance to the determination of age, as females mature earlier than males. In assessing the sex of this specimen using traditional methods, Thompson & Nelson (in press a, b) examined the size of the dentition (the teeth are large compared to both early and late Neandertals) the form of the mandibular ramus flexure and the absolute and relative size of the femoral head. These features indicate that this individual was a male.

Using CT methods Thompson & Illerhaus (2000, in press) made a virtual endocast of the specimen. The cranial capacity is $1540 \, \mathrm{cm^3} \, (\pm \, 7.7 \mathrm{ml})$. Details of this work have already been published (e.g. Illerhaus & Thompson 1999). This estimate of cranial capacity of Le Moustier 1 falls within 1 standard deviation of the male adult Neandertal mean and well above the Neandertal female mean (Thompson & Nelson in press a) — again indicating that this individual was male. Thus we concur with the original assessment that this is indeed a male individual.

AGE DETERMINATION - TEETH

Early papers published photographs of some of the teeth out of their sockets, but not all details were clear. The specimen, in its current state, shows all the dentition fully erupted, except for the impacted left permanent canine and the third molars. In its current state, the distal parts of the lower third molar crowns are obscured by matrix and all 4 molars are positioned as if they were erupting. This observation is important because, in the initial publications, Hans Klaatch, an anatomist, said that all 4 wisdom teeth were totally encased within the jaws. However, subsequently, at least twice, the teeth were removed from the jaws for study. The position of the molar teeth has an impact on one's estimate of age, so this point is rather important as we will see below. If the molars are erupting, this would indicate, by human standards, an age of 16 or more. However, if the molars were unerupted, the age at death estimate would be younger, depending upon the state of development of the crown and root of each tooth.

The 3-dimensional capabilities of the CT analysis allowed us to "cut and paste" the third molars into their crypts, demonstrating that there was ample space for them within the alveolus, suggesting that they were unerupted. Furthermore, we were also able to clearly visualize the developing roots of the molars (see Ponce de Leòn et al. 2000 for an alternative approach). The roots were only approximately 25% complete, indicating a dental age of 15.5 years, using modern human standards (see Thompson & Nelson 2000, in press a, for explanation). At this stage, this individual had achieved roughly 85% of adult dental maturity.

The ability to clearly visualize the roots is quite important, as tooth formation is generally thought to yield the most accurate estimate of an individual's age, as eruption times can vary greatly

AGE DETERMINATION - SKELETON

Work by Nelson & Thompson (2000, 2002, in press) reveals that, according to the length of his femur, the Le Moustier 1 specimen is equivalent to a 10.5 year old modern human boy. An examination of the original specimen (Thompson & Nelson in press a) revealed that the rami of the ischium and pubis were not fully fused, but had begun to unite. The fact that they are not fully united in this specimen would suggest that he is 9 years of age or less, skeletally, according to modern human standards. Expressing his estimated stature as a percentage of adult height, Le Moustier 1 matches a 12 year old modern human body who has achieved 85% of his adult stature (Nelson & Thompson 2000). Recall that the dental estimate for this individual was 15.5 year of age. A typical 15 year old modern human boy would have achieved approximately 95% of his adult stature (Nelson & Thompson 1999). Thus, it is clear that age estimates based on dental development and on postcranial growth are not in accord for this individual.

GROWTH & DEVELOPMENT ISSUES

This lack of concordance between dental and skeletal age led to an investigation of growth and developmental issues from a broader perspective (Thompson & Nelson 2000). Work by Thompson & Nelson (2000) indicated that *Homo erectus* is similar to apes in having relatively fast skeletal growth relative to dental growth. Upper Paleolithic modern humans apparently followed the recent modern human pattern. Neandertals appear to have delayed postcranial growth relative to their dental growth (or to have had fast dental growth relative to postcranial growth).

Nelson & Thompson (2001, in prep.) applied the same technique to explore the rate of growth of the skull relative to the dentition. They found that in some dimensions, such as facial height, both Neandertals and Upper Paleolithic modern humans both demonstrate a delay of cranial growth relative to dental growth. While this is superficially consistent with the delay in relative growth of the postcranium, the fact that the Neandertals demonstrate both delays, while the Upper Paleolithic sample delays facial height and not linear growth is really quite striking.

Using 3-D imaging, Thompson & Illerhaus (1998, 2000) took several metric measurements of the virtual reconstruction. These dimensions were compared between Le Moustier 1 who is dentally 15.5 years of age against another Neandertal specimen (Teshik Tash) that is about 10 years of age (as well as younger specimens), since comparison with a younger individual allows us to narrow down the timing of the

attainment of adult morphologies. We note that mid-facial prognathism is not fully developed in either individual and therefore Le Moustier 1 would have likely grown a more typical Neandertal face, including a retromolar space, had he growth to full maturity. Facial prognathism would likely have increased had Le Moustier 1 lived to adulthood, by lengthening of the jaws to accommodate the eruption of the third molars, but at present his upper facial height measurement differs little from that of Teshik Tash indicating that this feature likely develops late in Neandertal ontogeny.

Nelson & Thompson (2000, 2002, in press) have examined various aspects of long bone growth including length and robusticity. Ontogenetic data sequences were collected from juvenile and adult archaeological samples of "cold adapted" Inuit and "warm adapted" Khoi San. The results demonstrate statistically significantly different slope between the juvenile and the adult individuals from both samples. Also of interest, the growth trajectories "flex" about the time of adolescence, when linear growth ceases, but somatic growth continues. When Neandertal and early Upper Paleolithic modern humans were contrasted with the extant modern human samples, Neandertals follow a "cold adapted" pattern similar to the Inuit, while the Upper Paleolithic modern humans follow a "warm adapted" pattern.

Given that the Le Moustier specimen had achieved 85% of his adult dental and skeletal growth, this allows us to say something about growth patterns in Neandertals in general. Assuming Le Moustier 1 to be typical of juvenile Neandertals, we can deduce that prior to 85% adult growth, limb proportions, tibial robusticity, and many typical adult Neandertal features were already established. This means that had Le Moustier 1 lived to adulthood, his jaws would have lengthened to increase the extent of mid-facial prognathism, to allow the creation of a retromolar space, and allow the eruption of the third molars as their roots finished forming. As the size and robusticity of the supraorbital torus increased in size, so too would have the size and lateral extent of the frontal sinuses. The size of the Le Moustier 1 femur had yet to reach adult proportions, but presumably this would have occurred by the time of achievement of full adult stature when the long bone epiphyses had completed fusion.

PHYLOGENETIC IMPLICATIONS

Le Moustier 1 is a late Neandertal, dating to approximately 40,000 years or younger (Mellars, 1986; Mellars & Grün, 1991; Valladas et al., 1986) which is about when Upper Paleolithic modern humans appear in Europe. Despite this late date, this individual exhibits features found in specimens from the early part of the Neandertal time range and thus do not suggest any evidence of interbreeding between Neandertals and early modern populations.

Work by JT and AN on aspects of growth and development has shown interesting contrasts in patterns of growth between ancient modern humans and Neandertals:

- Neandertals experienced a delay in postcranial growth relative to dental growth compared to both ancient and modern humans.
- Both Neandertals and Upper Paleolithic modern humans experienced a delay in some cranial measurements relative to dental growth, but only Neandertals exhibit a relative delay in both cranial and postcranial growth.
- Neandertals appear have followed a "cold adapted growth trajectory" while Upper Paleolithic modern humans followed a "warm adapted growth trajectory";
- Both Neandertals and Upper Paleolithic modern humans exhibited an adolescent growth spurt in some skeletal dimensions;

These studies all demonstrate significant contrasts between Neandertals and Upper Paleolithic modern humans suggesting that they followed separate evolutionary pathways.

CONCLUSIONS

The use of the Le Moustier 1 specimen as a case study has allowed us to demonstrate the complementary nature of computerized tomography and traditional morphometric methods. Each technique has unique strengths, allowing us to access particular kinds of data. Furthermore, these methods produce similar results in areas where the techniques overlap (independently confirming each technique). However, the use of CT data and 3-D imagery allows scientists to move into new realms, such as being able to examine the morphology and dimensions of the labyrinth of the inner ear. The other advantages of CT analysis are that it is non-destructive and, using the appropriate software, it allows researchers to view external and internal structures in both 2 and 3- dimensions, to take measurements of those structures, allows the differentiation of real fossilized bone from reconstruction material, and the virtual reconstruction of fragmentary crania. The complementary nature of these techniques is certain to expand our knowledge or basic fossil morphology. These data are critical in the addressing of ontogenetic and phylogenetic research questions.

Acknowledgements

The authors would like to thank Dr Bertrand Mafart and Herve Delingette for the invitation to participate in this special symposium. We would also like to thank Professor W. Menghin, Director of the Museum für Vor- und Frühgeschichte, Berlin for permission to undertake this new reconstruction of the Le Moustier 1 skull and Mrs. A. Hoffmann for her assistance at each stage of this project. Special thanks should go to Professor H. Czichos, the President of the Bundesanstalt für Materialforschung und-prüfung (BAM), for use of their 3-D Microtomograph and software. We are grateful to Dr. J. Goebbels, T. Wolk, and D. Meinel, for their expertise and support throughout the course of this project. Particular thanks should go to Dr. Fred Spoor for his advice and expertise in measuring the labyrinths of the Le Moustier 1 specimen and to Nathan Jeffery for technical

assistance. J. L. Thompson is grateful to Dr. Chris Stringer, British Museum of Natural History, for permission to measure comparative cast material and to Mr. R. Kruszynski for his assistance during each of her visits. A. J. Nelson would like to acknowledge the Department of Anthropology, University of Western Ontario.

Addresses of the authors:

- J. L. THOMPSON, Department of Anthropology, University of Nevada, Las Vegas, 4505 Maryland Parkway, Box 455012, Las Vegas, Nevada, 89154-5003, USA. thompsoj@unlv.edu
- A. J. NELSON, Department of Anthropology, University of Western Ontario, London, ON, Canada, N6A 5C2.
- B. ILLERHAUS, Bundesanstalt für Materialforschung und prüfung, Unter den Eichen 87, D-12205 Berlin, Germany.

BIBLIOGRAPHY

- BILSBOROUGH, A. & THOMPSON, J. L., In Press a, The Changing Context and Significance of the Le Moustier 1 Neandertal. In *Die Sammlungen von Otto Hauser Staatliche Museen zu Berlin Preußischer Kulturbesiz.* edited by A. Hoffmann.
- BILSBOROUGH, A. & THOMPSON, J. L., In Press b, Dentition of the Le Moustier 1 Neanderthal. In *The Neandertal Adolescent Le Moustier 1 New Aspects, New Results*, edited by H. Ullrich. Staatliche Museen zu Berlin Preußischer Kulturbesiz.
- CONROY, G. C. & VANNIER, M. W., 1984, Noninvasive three dimensional computer imaging of matrix filled fossil skulls by high resolution computed tomography. *Science* 226, p. 457-458.
- CONROY, G. C. & VANNIER, M. W., 1986, Three-dimensional computer imaging: some anthropological applications. In *Primate Evolution*, edited by J. G. Else & P. C. Lee. Cambridge: Cambridge University Press, p. 211-222.
- CONROY, G. C., VANNIER, M. W., & TOBIAS, P. V., 1990, Endocranial features of Australopithecus africanus revealed by 2- and 3-D computed tomography. *Science* 247, p. 838-841.
- HAUSER, O., 1909, Découverte d'un squelette du type du Neandertal sous l'abri infériur du Moustier. *L'Homme Préhistorique* 7, p. 1-9.
- HEIM, J-L., 1978, Contribution du massif facial à la morphogenése du crâne Néanderthalien. In Les Origines Humaines et les Époques de l'Intelligence, Paris: Masson et Cie, p. 183-215.
- HERMANN, B., 1977, Über die reste des poskranialen skelettes des Neandertalers con Le Moustier. *Z. Morph. Anthrop.* 68, p. 129-149.
- HILLSON, S., 1996, Dental Anthropology. Cambridge, Cambridge University Press.
- HOFFMANN, A., 1997, Zur Geschichte des Fundes von Le Moustier. *Acta Praehistorica et Archaeologica* 29, p. 7-16.
- HOFFMANN, A., GOEBBELS, J. & ILLERHAUS, B., 1994, Virtual reconstruction of the skull of Le Moustier - project proposal. Berichtsband 45, Teil 1. Deutsche Gesellschaft für Zerstörungsfreie Prüfung e.V. 4th Int. Conf. NDT of works of Art
- HUBLIN, J-J., SPOOR, F., BRAUN, M., ZONNEVELD, F., & CONDEMI, S., 1996, A late Neanderthal associated with Upper Palaeolithic artefacts. *Nature* 381, p. 224-226.

- ILLERHAUS, B. & THOMPSON J. L., 1999, Calculating CT data from matched geometries. DGZfP-Proceedings BB 67-CD, p. 189-191, (www.dgzfp.de/ctip.html).
- ILLERHAUS, B., GOEBBELS, J., & RIESEMEIER, H., 1997, Computerized tomography and synergism between technique and art. In Selected Contributions to the International Conference on New Technologies in the Humanities and Fourth International Conference on Optics Within Life Science OWLS IV, Münster, Germany, 9-13 July 1996, edited by D. Dirksen & G. von Bally. Heidelberg: Springer Verlag, p. 91-104.
- ILLERHAUS, B., GOEBBELS, J., RIESEMEIER, H., & STAIGER, H., 1997, Correction techniques for detector systems in 3D-CT. *Proceedings of SPIE* 3152, p. 101-106.
- ILLERHAUS, B., GOEBBELS, J., REIMERS, P., & RIESEMEIER, H., 1994, The principle of computerized tomography and its application in the reconstruction of hidden surfaces in objects of art. *4th Inter. Conf. NDT of works of Art DGZFP, Berichtsband* 45, p. 41-49.
- KALVIN, A. D., DEAN, D., HUBLIN, J-J., & BRAUN, M., 1992, Visualization in anthropology: Reconstruction of human fossils from multiple pieces. In *Proceedings of IEEE Visualization*, 92, edited by A. E. Kaufman & G. M. Nielson, p. 404-410.
- KLAATSCH, H., 1909a, Der primitive mensch der verganenheit und der gegenwart. In *Verhandlungen der Gesellschaft Deutscher Naturforscher und Ärzte*, edited by A. Wangerin. Leipzig: Verlag von F.C.W. Vogel, p. 95-108.
- KLAATSCH, H., 1909b, Die neueste ergebnisse der paläontologie der menschen und ihre bedentung für das abstammungs-problem. *Z. Ethnol.* 41, p. 537-584.
- KLAATSCH, H., 1909c, Die fortschritte der lehre von der Neandertalrasse (1903-1908). Ergebn. Anat. Entw.-gesch. 17, p. 431-462.
- KLAATSCH, H., 1909d, Preuves que *l'Homo mousteriensis hauseri* appartient au type du Néandertal. *L'Homme Préhistorique* 7, p. 10-16.
- KLAATSCH, H. & HAUSER, O., 1909, Homo mousteriensis hauseri. *Arch. fr. Anthrop.* 35, p. 287-289.
- MELLARS, P., 1986, A new chronology for the French Mousterian period. *Nature* 22, p. 410-411.
- MELLARS, P. & GRÜN, R., 1991, Comparison of the electron spin resonance and thermoluminescence dating methods: Results of ESR Dating at Le Moustier (France). *Cambridge Archaeological Journal* 1, p. 269-276.
- NELSON, A. J. & THOMPSON, J. L., 1999, Growth and Development in Neandertals and other Fossil Hominids: implications for hominid phylogeny and the evolution of hominid ontogeny. In *Growth in the Past: Studies from Bones and Teeth*, edited by R. D. Hoppa & C. M. FitzGerald. Cambridge Studies in Biological Anthropology. Cambridge: Cambridge University Press, p. 88-110.
- NELSON, A. J. & THOMPSON, J. L., 2002, Neanderthal Adolescent Postcranial Growth. In *Human Evolution Through Developmental Change*, edited by N. Minugh-Purvis & K. McNamara. Baltimore: John Hopkins University Press, p. 442-463.
- NELSON, A. J. & THOMPSON, J. L., In Press, Le Moustier 1 and the interpretation of stages in Neandertal growth and development. In *The Neandertal Adolescent Le Moustier 1 New Aspects, New Results*, edited by H. Ullrich. Staatliche Museen zu Berlin Preußischer Kulturbesiz.
- PONCE DE LEÓN, M. S., ZOLLIKOFER, C. P. E., MARTIN, R. D., & STRINGER, C. B., 2000, Investigation of Neanderthal morphology with computer-assisted methods. In *Neanderthals*

- on the Edge, edited by C. B. Stringer, R. N. E. Barton, & J. C. Finlayson, Oxford: Oxbow Press, p. 237-248.
- SEIDLER, H., FALK, D., STRINGER, C., WILFING, H., MÜLLER, G. B. ZUR NEDDEN, D, WEBER, G. W., REICHEIS, W. & ARSUAGA, J-L., 1997, A comparative study of stereolithographically modelled skulls of Petralona and Broken Hill: implications for future studies of middle Pleistocene hominid evolution. *Journal of Human Evolution* 33, p. 691-703.
- SPOOR, C. F. & ZONNEVELD, F.,1994, The bony labyrinth in <u>Homo erectus</u>; a preliminary report. *Courier Forschungs-Institut Senckenberg* 171, p. 251-256.
- SPOOR, C. F. & ZONNEVELD, F., 1995, Morphometry of the primate bony labyrinth: a new method based on high-resolution computed tomography. *Journal of Anatomy* 186, p. 271-286.
- SPOOR, C. F., WOOD, B., & ZONNEVELD, F., 1994, Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion. *Nature* 369, p. 645-648.
- SPOOR, C. F., ZONNEVELD, F. W., & MACHO, G. A., 1993, Linear measurements of cortical bone and dental enamel by computed tomography: applications and problems. *American Journal of Physical Anthropology* 91, p. 469-484.
- TANNER, J. M., 1962, *Growth at Adolescence*. 2nd edition. Oxford: Blackwell Scientific Publications.
- TATE, J. R. & CANN, C. E., 1982, High-resolution computed tomography for the comparative study of fossil and extant bone. *American Journal of Physical Anthropology* 58, p. 67-73.
- THOMPSON, J. L., In Press, Le Moustier 1 and its place among the Neandertals. In *The Neandertal Adolescent Le Moustier 1 New Aspects, New Results*, edited by H. Ullrich. Staatliche Museen zu Berlin Preußischer Kulturbesiz.
- THOMPSON, J. L. & BILSBOROUGH, A., 1997, The current state of the Le Moustier 1 skull. *Acta Praehistorica et Archaeologica* 29, p. 17-38.
- THOMPSON, J. L. & BILSBOROUGH, A., 1998a, Time for one of the last Neanderthals. In *Proceedings of the XIII Congress of the U.I.S.P.P.- Forlì (Italia, 8/14 September, 1996), volume 2*, edited by F. Facchini, A. Palma di Cesnola, M. Piperno, & C. Peretto. Forlì: Abaco, p.289-298.
- THOMPSON, J. L. & BILSBOROUGH, A., 1998b, Time for one of the last Neanderthals. *Mediterranean Prehistory Online* http://www.med.abaco-mac.it/.
- THOMPSON, J. L. & BILSBOROUGH, A., In Press, The skull of Le Moustier 1. In *The Neandertal Adolescent Le Moustier 1 New Aspects, New Results*, edited by H. Ullrich. Staatliche Museen zu Berlin Preußischer Kulturbesiz.
- THOMPSON, J. L. & ILLERHAUS, B., 1998, A new reconstruction of the Le Moustier 1 skull and investigation of internal structures using 3-D-mCT data. *Journal of Human Evolution* 35, p. 647-665
- THOMPSON, J. L. & ILLERHAUS, B., 2000, CT Reconstruction and analysis of the Le Moustier 1 Neanderthal. In Neanderthals on the Edge, edited by C. B. Stringer, R. N. E. Barton, & J. C. Finlayson, Oxford: Oxbow Press, p. 249-255.

- THOMPSON, J. L. & ILLERHAUS, B., In Press, 3-D-μCT Endocast and cranial capacity of the Le Moustier 1 skull. In *The Neandertal Adolescent Le Moustier 1 New Aspects, New Results*, edited by H. Ullrich. Staatliche Museen zu Berlin Preußischer Kulturbesiz.
- THOMPSON, J. L. & NELSON, A. J., 2000, The Place of Neandertals in the Evolution of Hominid Patterns of Growth and Development. *Journal of Human Evolution* 38, p. 475-495.
- THOMPSON, J. L. & NELSON, A. J., 2001, Relative postcranial and cranial growth in Neandertals and modern humans. *American Journal of Physical Anthropology*. Special Supplement, p. 149.
- THOMPSON, J. L. & NELSON, A. J., In Press a, Estimated age at death and sex of Le Moustier 1. In *The Neandertal Adolescent Le Moustier 1 New Aspects, New Results*, edited by H. Ullrich. Staatliche Museen zu Berlin Preußischer Kulturbesiz.
- THOMPSON, J. L. & NELSON, A. J., In Press b, The Postcranial skeleton of Le Moustier 1. In *The Neandertal Adolescent Le Moustier 1 New Aspects, New Results*, edited by H. Ullrich. Staatliche Museen zu Berlin Preußischer Kulturbesiz.
- THOMPSON, J. L., NELSON, A. & B. ILLERHAUS, In press, A study of the Le Moustier 1 Neandertal summary of results. In Die Sammlungen von Otto Hauser: Staatliche Museen zu Berlin-Preußischer Kulturbesiz, edited by A. Hoffmann.
- TILLIER, A.-M., 1974, Contribution à l'étude des hommes fossiles Moustériens du Moyen Orient: La pheumatisation de la face. *Paléorient* 2, p. 63-468.
- TRINKAUS, E., 1993, *The Shanidar Neandertals*. New York: Academic Press.
- VALLADAS, H., GENESTE, J. M., JORON, J. L., & CHADELLE, J. P., 1986, Thermoluminescence dating of Le Moustier (Dordogne, France) *Nature* 322, p. 452-454.
- VLCEK, E., 1967, Die Sinus frontales bei europäischen Neandertalern. *Anthrop. Anz.* 30, p. 166-189.
- VLCEK, E., 1969, Neandertaler der Tschechoslowakei. Prag: Verlag der Tschechoslowakischen Akademie der Wissenschaften.
- WEINERT, H., 1925, Der Schädel des eiszeitlichen Menschen von Le Moustier in neuer Zusammensetzung. Berlin: Springer.
- WIND, J., 1984, Computerized X-ray tomography of fossil hominid skulls. *American Journal of Physical Anthropology* 63, p. 265.
- ZOLLIKOFER, C. P. E., PONCE DE LEÓN, M. S., & MARTIN, R. D., 1998, Computer-assisted paleoanthropology. *Evolutionary Anthropology* 6, p. 41-54.
- ZOLLIKOFER, C. P. E., PONCE DE LEÓN, M. S., MARTIN, R. D., & STUCKI, P., 1995, Neanderthal computer skulls. *Nature* 375, p. 283-285.
- ZONNEVELD, F. W. & WIND, J., 1985, High-resolution computed tomography of fossil hominid skulls: a new method and some results. In *Hominid Evolution: Past Present and Future*, edited by P. V. Tobias. New York: Alan R. Liss, p. 427-436.
- ZONNEVELD, F. W., SPOOR, C. F., & WIND, J., 1989, The use of CT in the study of the internal morphology of hominid fossils. *Medicamundi* 34, p. 117-128.