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Late Upper Pleistocene human peopling of the Far East: multivariate analysis and geographic patterns of variation

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Abstract

This research deals with the History of the human peopling of Far East Asia during the Late Upper Pleistocene. It brings some new answers to the question of modern human migrations in the Far East. This study is based on morphometric analysis of 45 fossil *crania*. The results of the multivariate analyses, combined with the recognition of geographic patterns of variation, separate the fossils into three morphological classes. These three clusters enable us to propose a likely scenario for the human peopling of the Far East from about 67 000 years ago. ***To cite this article: F. Demeter et al., C. R. Palevol 2 (2003).***

Résumé

Peuplement humain de l'Asie extrême-orientale au Pléistocène supérieur récent : analyses multivariées et structuration spatiale. Cette recherche traite de l'Histoire du peuplement humain de l'Asie extrême-orientale depuis le Pléistocène supérieur récent. Elle apporte de nouvelles réponses à la question du premier peuplement humain moderne de l'Extrême Orient. Cette étude s'appuie sur l'analyse morphométrique de 45 crânes fossiles. Les résultats des analyses multivariées, complétées d'une détection de structuration spatiale, divisent le groupe fossile en trois classes morphologiques. Ces trois classes nous permettent de proposer un scénario probable du peuplement humain de l'Asie extrême-orientale depuis environ 67 000 ans. ***Pour citer cet article : F. Demeter et al., C. R. Palevol 2 (2003).***

Keywords: Far East Asia; Prehistory; *Homo sapiens*; Late Upper Pleistocene; multivariate analysis; geographic pattern variation

Mots clés : Asie extrême-orientale ; préhistoire ; *Homo sapiens* ; Pléistocène supérieur récent ; analyses multivariées ; structuration spatiale

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1. Introduction

Palaeogeographical studies show the constant evolution of the environment, especially during the Pleistocene [4,10–12,16,17,20,30,33,38] and emphasize the important repercussions of these climatic variations on the development and adaptation of the flora and of the fauna.

The last Great glaciation of the Pleistocene had several successive peaks, simplifying: once about 60 000 BP, one more about 30 000 BP and another one about 18 000 BP. During these great cold periods, a fall of at least 125 m from the present sea level occurred [20,31,33,38]. This fall in sea level had, as a consequence, the potential discovery by humans of new lands, notably those of the Sunda shelf in South-East Asia (Fig. 1). During such glaciation, the Japan archipelago, island of Taiwan, and the islands of South-East Asia, Malaysia, a part of the Philippines and the Sonde archipelago, were connected to Eurasia [4,6,11,33,38]. It was then possible to reach Indonesia from Japan on foot. These new, uncovered lands were the result of a climate that became colder, leading to the production and accumulation of ice at the North and South poles. Furthermore, such climatic changes had very strong effects on the flora. Indeed palynological analyses [13,14,20,33,37] show that falls of temperature were accompanied by the replacement of species by other species, better adapted to cold and aridity.

The temperature drop was progressive and can be considered as a determining element in the history of modern human colonisations. Indeed, the cold probably led humans, living in Northern lands, to move southwards following the seashore [6] where the climate was less severe. The proximity of the sea would have presented two advantages since: (i) the seashore could have been a landmark for human groups in their movements; and (ii) it would have favoured those populations whose subsistence economy was mainly based on marine resources. As a consequence, this made their southward migration possible towards the Sonde archipelago, and particularly to Java. Fast as it might have been, their progress was of course dependent on eustatic variations (change in sea level). Actually, to cover the distance between Japan and Indonesia in less than 10 000 years, each human generation would only have to move 50 km southwards in its subsistence area [1].

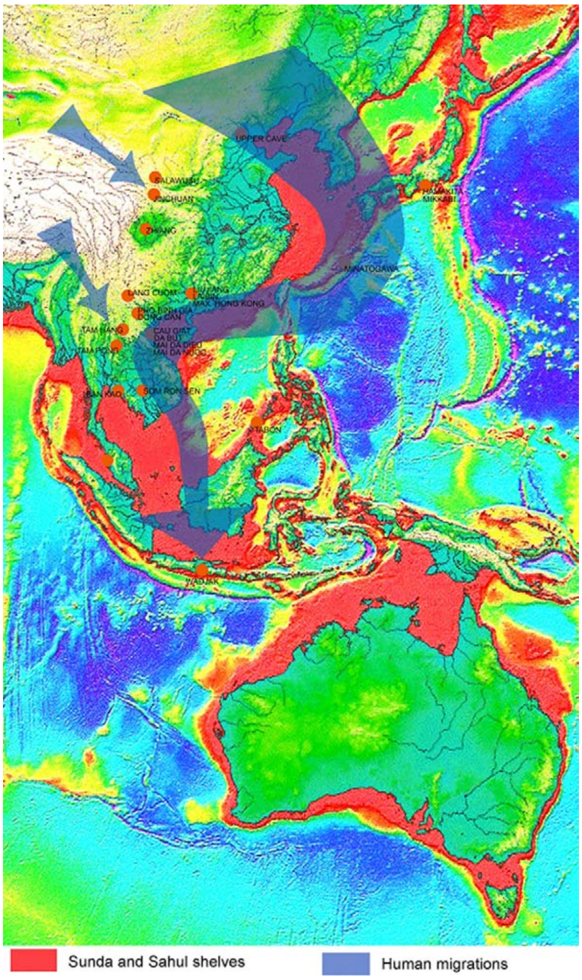

Fig. 1. Far East Asia and Australasia bathymetric chart, showing Sunda and Sahul shelves, the fossils sites location and the human migrations directions suggested in this work.

Fig. 1. Carte bathymétrique de l'Asie extrême-orientale et de l'Australasie, représentant les plateaux continentaux de Sunda et de Sahul, les sites fossilifères et les routes migratoires humaines suggérées dans cette étude.

Concerning the modern human peopling of the world, nowadays two main theories co-exist: the multi-regional evolution hypothesis and the single, recent origin hypothesis based on fossil and genetic data. The first theory follows the Franz Weidenreich [41] polycentric theory of human origin: it is a gradual and continuous evolution process which would have allowed the evolution of modern humans from archaic *Homo sapiens*, themselves coming from *Homo erectus*, in each region of the ancient world. At the beginning, this theory, called 'multi-regional hypothesis' was suggesting that the gene exchanges between several groups were restricted. Nowadays, some authors like Alan Thorne and Milford Wolpoff [42,43] have readapted Franz Weidenreich's theory. They stressed the importance of the gene exchanges between populations and called their theory 'multi-regional evolution hypothesis'. Concerning the human peopling of the Far East, this theory is supported by several palaeoanthropologists among whom Wu Xin Zhi [44]. His conclusions bring the idea of the co-existence of two modern human groups, one in China and the other in Indonesia, directly coming from *Homo erectus* forms, originated from these two regions.

The second hypothesis is more recent. Recommended by Louis Leakey [21] in 1960s, this hypothesis suggests an unique origin of modern humans, certainly coming from Africa. By the end of the Middle Pleistocene, modern humans or *Homo sapiens* would have evolved directly from archaic *Homo sapiens* on the African continent. Archaic *Homo sapiens* would have adventured in Eurasia, as suggested by Chris Stringer [34], first replacing those human groups (*Homo erectus*) already settled in the area and subsequently colonizing the rest of the World thousands of years later.

Concerning the Far East, some authors [23], propose that these modern humans would have reached first the northern part of the Far East, which included, at that time, the Japanese archipelago, before moving towards southern lands. Our research takes place within this hypothetical framework, underlining that the oldest representative of our fossil sample studied here precisely comes from Northern Far East Asia (Liujiang, Northern China). We tried to bring some answers to the question of the modern human peopling of Far-East Asia, since the Late Upper Pleistocene, about 67 000 years ago (age of Liujiang, the oldest modern human ever found in this region) [44]. Our conclusions, based on multivariate and geographic analyses of morphometric measures of the *cranium*, offer new perspectives on the prehistoric modern human settlement in this far part of Eurasia.

2. Material and methods

2.1. The reference sample

In statistical anthropology, when a human 'fossil sample' needs to be considered within the general framework of the human evolution, the comparison between this population and another, called the 'reference sample' is necessary. Concerning our study, we decided to limit the reference sample to modern specimens coming from Far-East Asia, the same region where our fossil sample comes from. This arbitrary choice gives the maximum chance of finding in the reference sample the same, or at least close morphological characters, as those shown by the fossil sample. The reference sample is supposed to have a biological meaning because the corresponding specimens are likely to be the descendants of the ancient populations that lived in the same area. Our reference sample consists of 100 specimens whose origins are known, represented by calvariums and mandibles. 118 metrical measurements were doubled checked and taken on each on these 100 *crania*. These 100 individuals come from Japan, China, Vietnam, Laos, Thailand, Cambodia, Philippines and Indonesia: six individuals from Japan (Hiogo-Kobé, Steenackers Collection registered in 1886), nine individuals from China (Soller Collection registered in 1886), forty-seven individuals from Vietnam (Canoville Collection registered in 1884), twenty-three individuals from Laos (Noël Bernard Collection registered in 1920), ten individuals from Thailand (Bel Collection registered in 1896), one individual from Cambodia (Pannetier Collection registered in 1920), one individual from Philippines (Eugène Salomon Collection registered in 1897), three individuals from Indonesia (Dumoutier Collection registered in 1874).

2.2. The fossil sample

The fossil sample consists of 86 *crania* of fossil modern humans discovered in Far-East Asia from Japan to Indonesia (Fig.1) [6]. We would like to emphasize that all the measurements were taken on originals with the exception of the Chinese samples. These casts account for the Upper Cave (3 of them) samples at Zhoukoudian, since the originals disappeared in the 1940s, and the Hong Kong fossil [19] housed in the Senckenberg Museum in Frankfort. All *crania* are presently housed in different laboratories throughout the world with the exception of the fossils coming from Cambodia, Laos, together with some Vietnamese ones, which are stored in France. The Japanese Minatogawa, Hamakita and Mikkabi fossils are housed in the University of Tokyo. The other Chinese fossils, Liujiang, Mapa and Salawusu are stored in the Institute of Vertebrate Palaeontology and Palaeoanthropology of Beijing (IVPP). The Vietnamese fossils, Mai Da Dieu, Mai Da Nuoc and Dong Can are housed in the Institute of Archaeology of Hanoi. The Indonesian fossils are housed in the National Museum of Natural History of Leiden in The Netherlands. Fossils coming from Cambodia, Laos, and Vietnam were brought back to France at the beginning of the last century and in the 1930s by researchers working for the *École Française d'Extrême Orient*, the National Museum of Natural History of Paris or even for the Indochina Geological Service. All of them are nowadays housed in the Biological Anthropology Laboratory of the National Museum of Natural History in Paris (*Musée de l'Homme*). The conditions in which some of these ex-Indochinese fossils were re-discovered have to be mentioned: while one of us (F.D.) was doing his PhD research in 1998, he was making an inventory of all the South-East Asians fossils in the Biological Anthropology Laboratory collections, with the help of Ph. Mennecier and M. Chech. Fortunately the fossils discovered 70 years ago in Cambodia (Samrong Sen) [9], in Vietnam (Cau Giat, [5,8], Pho Binh Gia [21]) and from Laos (Tam Hang) [15] were identified. Such fossils had never been, or were incompletely described, in publications and some of them were in very fragmentary condition. Nevertheless, they were all gathered in several wooden boxes and then stocked in a room. This happened when the old Ethnographic Museum was replaced in 1936 by the Palais de Chaillot, where the Musée de l'Homme is at present located. This accounts for the fact that these boxes and all the material they contained were forgotten by the scientific community during more than 70 years.

With the support of the Collège de France, the Prehistory Laboratory of the Human Palaeontology Institute of Paris (IPH) and the Biological Anthropology Laboratory of the National Museum of Natural History in Paris (Biological Anthropology Laboratory, Musée de l'Homme), a ^{14}C dating program on some of these fossils was started [7]. The absolute dating results make the fossils older than their discoverers thought in the 1930s; moreover, it is interesting to note that, according to the correspondence between researchers and notably that of M. Colani, more South-East Asian archaeological sites were known in the 1930s than those that have been described in the literature up until now. Concerning Vietnam, we can mention in Hoa Binh Province the sites of Lang Kay, Da Phuc, Lang Gam, Lang Tanh, Lang Tieng, Lang Mi; in Quang Binh Province, the sites of Kim Bang, Bat Môt, Duc Thi, Xom Tham, Yên Lac sites; in Than Hoa Province, the Lang Bong site; in Ha Nam Province, the Dong Noi and Hang Oa sites; in Thai Nguyen Province, the Na Ca site; and in Ninh Binh Province, the Phu Té site.

2.3. Morphological measurements

Concerning the statistical aspect of this study, as a first step, we performed a bivariate quantitative analysis on the fossil *cranium* of the 86 individuals. The fragmentary aspect of 41 fossils led us to withdraw them from the statistical analysis. On the remaining 45 well-preserved fossils, we were able to take 118 measurements. For our methodology, we followed that developed by E. Peyre and C. Menin [26,29]. We highlighted the morphological characteristics using sigmoid profiles upon 13 variables whose presence was constant. Sigmoid profiles show morphological features of an individual considering the fossil variable compared to the reference sample in terms of sigma. This term gave the name to the graphic [27]. The ordinate axis or sigmoid scale is divided into standard deviation or σ. Only the standard deviation for each character is used as a reference. The reference sample is then represented by a base-line on the ordinate axis at the zero points (0). Starting from this point, we compare the individuals or group of individuals with this base-line. If the mean value of some characters in the selected sample is *m1* and the corresponding mean value in some other sample is *m2*, then the quantity is represented by means of a graph: $\left(\frac{m1-m2}{\sigma}\right)$ where σ is the standard deviation of the sample, *m1* the mean value.

In other words, we measure each *m2* from *m1* and divide it by the standard deviation (σ) of the reference sample.

As a second step, we used a cluster analysis to characterize the fossil sample. We wanted to check whether the database was structured and whether the individuals could be gathered by similar morphology. Consequently, we chose to use the Hierarchical Cluster

Analysis (HCA). As exposed by Williams Howells [18], this method shows by the mean of a graphic, the dendrogram, the different main clusters according to an aggregation criterion. We choose the Ward criterion [40] that gathers individuals with the smallest loss of information.

In order to get rid of the 'size' factor and to keep only the 'shape' of the *crania*, we had to normalize our database upon Williams Howells recommendations [18]. First of all, the specimens raw measurements were rendered into standard form called *Z*-scores. The deviation of each score from the general mean is divided by the general standard deviation (Table 1). Then the mean of each individual's *Z*-scores was calculated. It was called 'Pensize'. Pensize = $(Z1+Z2+\cdots+Zg)/G$, where G is the number of measurements. Then, the *Z*-scored were centered once again by subtracting from each of them that individual's Pensize (table not shown), so that the sum of these deviated scores is zero. These newly centered figures are called C-scores (table not shown).

Once the C-score database matrix is calculated, the HCA is used to study the relations among individuals. This method, which only considers the cases rather than the variables, is also called 'Q-mode analysis'. The results of the Hierarchical Cluster Analysis, according to the Ward criterion [43], is represented by the dendrogram of Fig. 1. The meaning of the different branches is as follows: the individuals gathered on the same side have a close morphology. This hierarchy is indexed, meaning that each cut corresponds to a numeric value indicating at what level clustering happens. This index, called the aggregation level, shows the distance between clusters. The higher this aggregation level is, the less similar the morphology is.

2.4. Multidimensional scaling analysis and the distance matrices

Multidimensional scaling analysis (MDS) [32,35] was applied to the data to graphically identify possible patterns of spatial variation. This multivariate method takes a set of dissimilarities (as in a distance matrix) and returns a set of points such that distances among the points in the plot are approximately equal to the dissimilarities. MDS is not so much an exact procedure as rather a way to 'rearrange' objects in an efficient manner, so as to arrive at a configuration that best approximates the observed distances.

It actually moves objects around in the space defined by the requested number of dimensions, and checks how well the distances between objects can be reproduced by the new configuration. In more technical terms, it uses a function minimization algorithm that evaluates different configurations with the goal of maximizing the goodness-of-fit (or minimizing 'lack of fit').

The most common measure that is used to evaluate how well (or poorly) a particular configuration reproduces the observed distance matrix is the stress measure. The raw stress value Phi of a configuration is defined by:

$$Phi = \Sigma[d_{ij} - \mathrm{f}(\delta_{ij})]^2$$

In this formula, d_{ij} stands for the reproduced distances, given the respective number of dimensions, and δ_{ij} (*delta*$_{ij}$) stands for the input data (i.e., observed distances). The expression $f(\delta_{\mathrm{ij}})$ indicates a *nonmetric*, monotone transformation of the observed input data (distances). Thus, it will attempt to reproduce the general rank-ordering of distances between the objects in the analysis. The MDS analysis (Figs. 3 and 4), as well as the dendrogram (Fig. 2), were computed by means of the software *Statistica version 5.0* by StatSoft Inc on the same Ward [42] matrix.

2.5. Geographic pattern variation analysis

2.5.1. Monmonier's maximum difference algorithm

Since human morphometrical differences may show correspondences with geography, general methods of geographic analysis can be successfully applied to anthropology. This is what the present study is confirming. We aimed at visualizing the data contained in distance matrices on a geographic map. This implies the computation of neighbouring problems (computational geometry). Delaunay triangulation [2] is the fastest triangulation method to connect a set of points (localities) on a plane (map) by a set of triangles (see dotted lines in Fig. 5E). Such triangles satisfy the 'empty circle' property: the circumcircle of each triangle does not contain any of the points. It is the most direct way to connect (triangulate) adjacent points on a map. It must be noted that the Delaunay triangulation is the dual structure of the Voronoi diagram [39] (solid lines in Fig. 5E) and one can be derived from the other.

Once a network connecting all the localities is obtained, each edge of the network is associated with the

Table 1
Z scores
Tableau 1
Les mesures Z

	REF.	ZLMX	ZLNB	ZWMX	ZWFS	ZWFI	ZHBB	ZMZG	ZMZD	ZLFT	ZWBO	ZWIO	ZWBZ	ZHFS
PBGia 1	18 504	1.226	1.954	0.617	1.089	0.261	2.298	–0.199	–0.381	0.495	0.031	–0.185	0.621	–0.001
Dthuoc	19 424	1.135	1.793	–0.662	–0.317	–0.321	0.339	–0.548	–0.730	0.455	0.818	–1.757	0.283	0.436
CGiat II	24 961	0.909	1.393	–0.546	0.152	1.010	0.271	–0.378	–0.446	0.356	0.231	–0.425	–0.012	0.304
CGiat I	26 832	0.863	1.312	–0.313	0.933	0.844	0.257	–0.369	–0.438	0.337	0.287	0.444	1.184	0.278
Dong Can	/	0.863	3.168	1.431	1.558	3.173	–1.310	1.195	1.017	–0.137	1.606	0.915	0.846	1.152
L Cuom 4	19 411	0.863	1.312	–0.894	–0.629	–1.818	0.257	–1.245	–1.429	0.337	0.147	–1.128	–0.244	0.278
Cau Giat	23 105	0.682	–0.222	1.663	0.933	0.677	–1.052	0.498	0.318	0.317	0.031	–0.499	1.296	0.709
L Cuom 5	19 412	0.591	0.831	0.268	–0.473	–0.820	0.175	–1.768	–1.954	0.218	0.427	0.444	0.531	0.120
L Cuom 1	19 408	0.500	0.327	–1.417	–1.723	–0.155	–0.279	–0.199	–0.381	0.179	0.021	–0.499	–1.856	0.067
MDa Nuoc	/	0.410	0.511	–0.720	–0.005	–0.155	1.010	–0.304	1.017	1.353	0.134	–1.442	0.306	–0.302
L Cuom 8	19 415	0.319	0.350	–0.894	–0.317	0.677	0.094	–0.264	–0.344	0.100	0.147	–0.814	–0.244	–0.039
LCuom 10	19 417	0.228	0.190	–0.429	–0.317	–0.321	0.066	–1.419	–1.604	0.061	0.259	–0.391	1.747	–0.092
THS 10	20 539	0.228	–0.039	0.733	0.620	–0.487	1.010	1.282	1.104	–0.081	0.504	0.758	1.071	1.773
THoa DB	19 454	0.137	–1.414	–1.243	–0.005	–0.487	–0.408	–0.548	–0.730	–0.878	–0.362	0.601	–0.167	–1.420
L Cuom 9	19 416	–0.135	–0.222	–0.894	–0.161	0.012	0.365	1.021	0.842	–0.001	0.663	0.130	0.396	0.177
THS 14	20 538	–0.135	–0.956	1.779	1.245	0.511	0.365	1.544	1.367	–0.440	0.198	0.412	1.240	1.241
THS 11	20 540	–0.135	–1.322	–0.313	–0.161	0.345	–0.408	0.498	0.318	–0.957	–0.362	0.287	–0.730	–0.356
PBGia 3	23 097	–0.225	–0.612	0.384	–0.317	–0.654	–0.070	–1.071	–1.255	–0.137	0.455	–0.499	0.846	–0.355
L Cuom 11	19 418	–0.316	–0.314	0.384	0.152	0.511	0.108	1.195	1.017	–0.121	0.504	0.130	0.171	–0.710
MDa Dieu	/	–0.498	–1.139	–1.301	–2.348	–1.319	–0.794	–0.060	–0.206	–0.081	–0.339	–0.814	–1.371	–1.420
LCuom 13	19 420	–0.498	–0.589	–0.546	–0.005	–0.487	0.752	–0.548	–0.730	–0.479	0.231	–0.499	–1.405	0.886
TP 1	20 541	–0.498	–0.039	–0.081	–1.098	–0.071	–0.150	0.581	1.017	0.477	1.291	0.444	–0.280	1.063
THS 3	20 537	–0.588	–0.864	–0.081	–0.161	–0.321	–0.408	0.062	–0.031	–1.037	–0.362	0.444	–0.730	–0.622
TH TTA	20 543	–0.679	–1.139	0.268	0.620	–0.321	0.365	–0.896	–1.080	–1.037	–0.362	0.528	–0.505	0.531
THS 4	20 542	–1.042	–0.589	0.501	–0.317	–0.570	–0.279	1.718	1.367	–0.440	0.031	2.645	–0.392	–0.356
THS 22	20 550	–1.405	–0.956	–2.057	–2.504	–1.818	–2.211	–0.373	–0.027	–0.918	–1.071	–1.128	–2.081	–1.597
THN 3	20 533	–1.677	–1.322	–1.011	–1.879	–1.402	–1.567	–0.199	–0.381	–0.639	–0.362	–0.185	–1.405	–0.444
THS 13	20 534	–1.949	–1.322	0.966	0.464	–0.654	–0.279	–0.373	–0.556	–0.559	0.031	0.130	–0.505	0.975
THS 2	20 535	–2.403	–1.780	–0.313	–0.161	1.176	–0.923	–0.373	–0.381	–0.815	–0.170	0.250	–0.748	–0.817
BKI.BVII	/	0.500	–0.131	0.849	1.401	0.261	1.010	0.446	0.318	0.532	0.031	1.387	0.396	–0.356
BKI.BXV	/	–0.271	0.052	0.501	0.620	0.677	1.267	1.892	1.716	–1.276	0.346	0.130	1.409	2.305
BKI.Inconnu	/	–1.586	0.365	1.082	–0.317	–1.652	1.707	–0.722	–0.905	–4.361	0.031	2.225	0.621	0.886
Minat I	/	0.047	–0.314	1.256	–0.348	–0.554	–0.343	–0.461	0.143	0.317	0.763	–1.882	1.263	–0.178
Minat IV	/	–0.498	–0.406	–0.081	–0.801	–1.253	–1.503	–0.784	1.751	–0.041	–0.087	–1.379	–1.236	–1.242
Minat II	/	–1.858	–0.635	–0.778	–0.473	–1.086	–1.825	–1.594	–1.604	0.078	–0.047	–1.537	–1.293	–3.193
U Cave I	/	1.770	0.419	0.675	1.089	1.842	–0.408	0.672	0.493	0.477	0.504	0.444	1.184	1.596
UCaveIII	/	1.226	0.298	–0.662	–0.786	1.010	0.326	0.847	0.668	0.414	0.031	0.287	–1.068	0.177
Liujiang	/	0.682	–0.131	0.268	0.933	0.012	–0.408	–0.722	–0.643	0.118	–0.047	0.633	–0.955	–0.586
UCave II	/	0.047	0.236	–0.894	0.464	0.844	0.881	–1.245	–1.429	1.125	0.346	0.130	0.508	–0.001
Jinchuan	/	–0.044	1.152	–2.057	0.464	0.677	2.556	0.190	1.978	1.180	–3.182	–0.952	–1.279	–0.621
Zhiyang	/	–1.133	0.765	–0.778	–1.567	–0.920	–1.825	1.282	–0.032	2.070	–4.850	–1.128	–0.899	–1.644
SRon Sen	20 849	–0.062	–0.323	1.163	0.089	0.511	–0.012	–0.188	–0.262	–0.067	0.641	–0.656	1.131	0.975
Wadjak 1	/	1.589	0.327	1.663	1.401	0.261	0.108	–0.505	–0.563	0.636	0.378	1.230	0.801	0.088
Wadjak 2	/	1.589	0.327	1.663	1.401	1.176	0.108	–0.505	0.458	0.636	0.378	1.387	0.801	0.088

Legend: The measurements defined by Martin[25] are LMX : 1, LNB :5, WMX :8, WFS : 10, WFI : 9, HBB : 17, HFS : 48, HSA 48(1), WIO : 50, WBZ : 45, The measurements defined by Twiesselmann [36] are LFT : 12; also, the mastoid height MZ according to Broca [3].

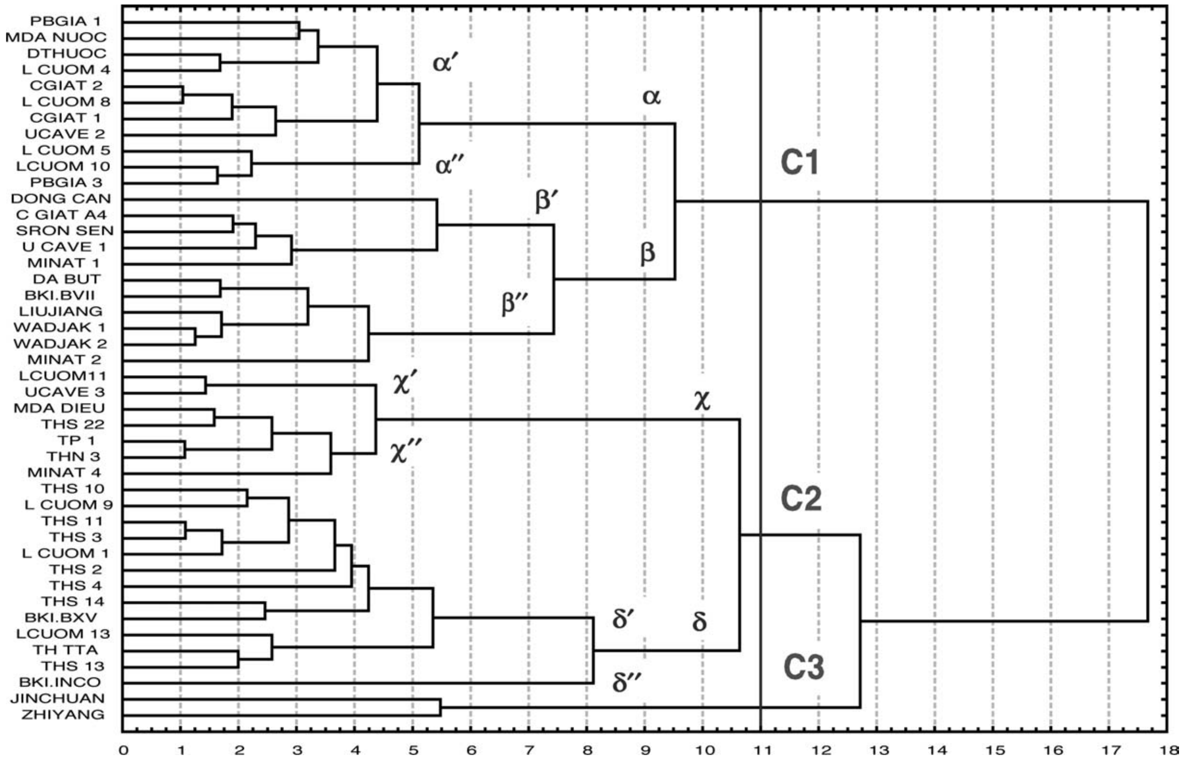

Fig. 2. Dendrogram drawn upon 16 variables of the *calvarium* according the Ward aggregation criterion [40].

Fig. 2. Dendrogramme dessiné d'après 16 variables du *calvarium* en utilisant le critère d'agrégation de Ward lors du calcul de la matrice de distance [40].

estimated value of distance from the Ward [43] matrix. Monmonier's maximum-difference algorithm [28] was used to identify boundaries, namely the geographic areas where morphological differences between pairs of samples were the largest ones. The first boundary is traced perpendicular to the edges of the network. Starting from the edge where the distance value is maximum and proceeding across adjacent edges, we continued the procedure until the forming boundary reaches either the limits of the triangulation (map) or closes on itself by forming a loop around a sample. In case of multiple barriers they can stop on a pre-existing boundary. Note that, when two edges have the same value, the shorter edge is included in the boundary; the rationale for this choice was that, when the same distance value is observed between two pairs of localities at different spatial distances, the obstacle to gene-flow was probably stronger between localities, which were geographically closer to each other.

The Monmonier's algorithm, based on a Delaunay triangulation, allows one to identify directions where the variation of a given parameter is higher, suggesting the presence of a boundary. Boundaries were obtained with a software developed by E. Guerard and F. Manni that will be soon released.

To provide evidence of the inter-variability of the different measures, we analysed them in four different groups concerning the length, width and height, of *crania* as well as the mastoid height and computed 4 different distance matrices. We applied separately the Monmonier's maximum difference algorithm on each of them (respectively Figs. 5 A, B, C, D).

2.5.2. Mantel randomisation test

The Mantel test [24] measures the association between the elements in two matrices by a suitable statistic, and determines the significance by comparison with the distribution of the statistic found by randomly reallocating the order of the elements in one of the matrices. This test was meant to indicate the association between morphologic distances and their corre-

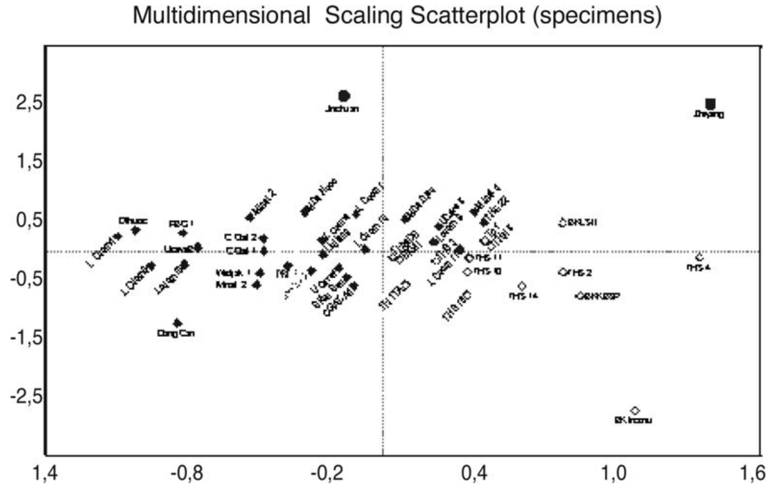

Fig. 3. Multidimensional scaling of the fossils considered in this study. The plot was computed on a distance matrix between all the 45 specimens that accounts for 13 measures of length, width, height and mastoid height of the *crania*. Stress: 0.16. • = Chinese samples; ◇ = Coastal and insular specimens; ◇ = inner land specimens.

Fig. 3. Analyse multidimensionnelle des fossiles retenus dans cette étude. La projection des points est réalisée d'après une matrice de distance calculée sur 45 individus. Sur le crâne ont été retenues, 13 mesures de hauteur, de longueur, de largeur, ainsi que de hauteur des mastoïdes. Stress: 0,16. • = Groupe chinois; ◇ = Individus côtiers et insulaires; ◇ = Individus continentaux.

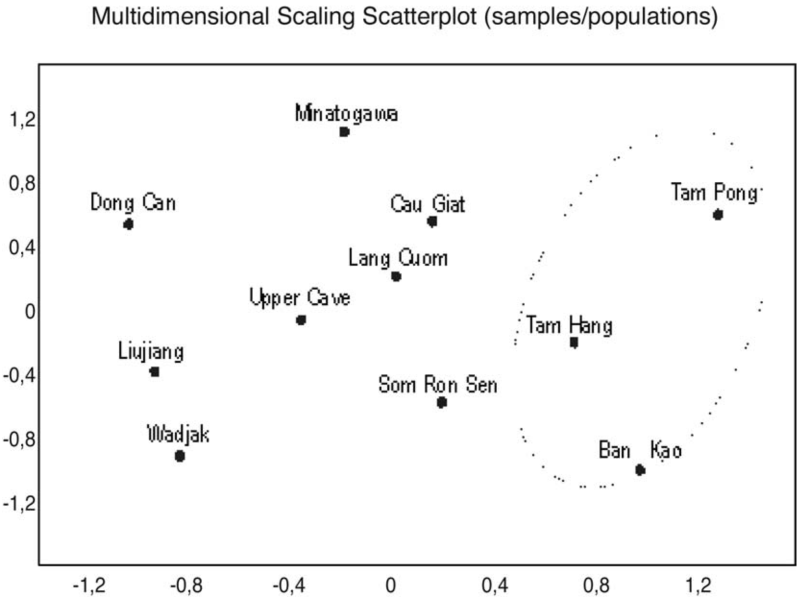

Fig. 4. Multidimensional scaling of the fossils considered in this study grouped in samples (populations). The plot was computed on a distance matrix between 11 samples where the Chinese fossils of Jinchuan and Zhiyang were withdrawn since outliers. Stress: 0.14. Inner land samples are enclosed by a dotted circle.

Fig. 4. Analyse multidimensionnelle des fossiles étudiés regroupés en populations. La projection des points est réalisée d'après une matrice de distance calculée sur 11 groupes d'individus en excluant les fossiles chinois de Jinchaun et Zhiyang qui sont extrêmes. Stress: 0,14. Les groupes continentaux sont encerclés en pointillé.

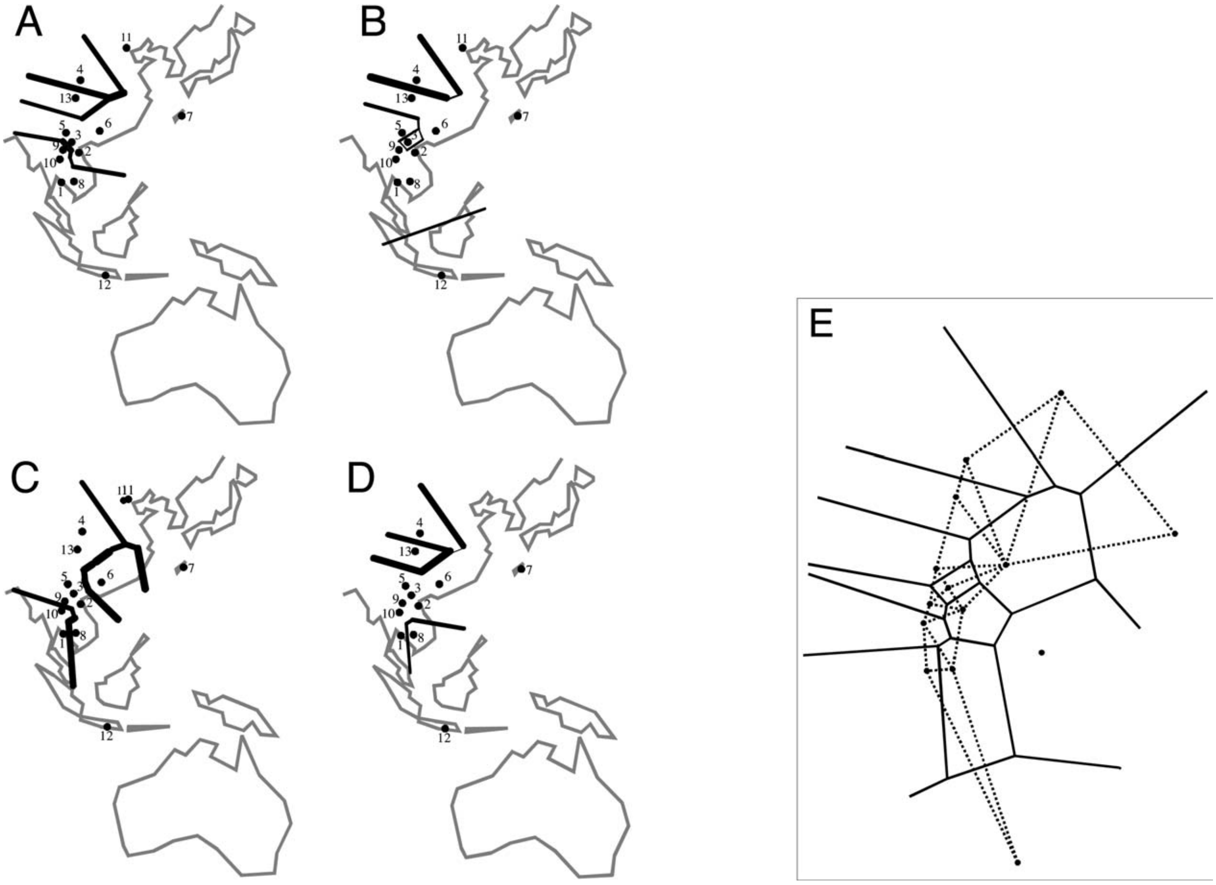

Fig. 5. Analysis of geographic patterns of morphologic variation by Monmonier's algorithm [28]. The analysis was performed separately on four matrices accounting for length (A), width (B), height (C), and the mastoid height (D) of *crania*. The thickness of the edges of the barriers are proportional to their significance, computed as the inverse ratio between the higher distance measure associated to the triangulation and the distance associated to each crossed edge. In (E) the Delaunay triangulation (dotted lines) [2] and the Voronoi tessellation (solid lines) [39] among samples are shown. In (A); (B); (C) and (D) samples are numbered according to the following key: 1) Ban Kao; 2) Cau Giat; 3) Dong Can; 4) Jinchuan; 5) Lang Cuom; 6) Liujiang; 7) Minatogawa; 8) Samron Sen; 9) Tam Hang; 10) Tam Pong; 11) Upper Cave; 12) Wadjak; 13) Zhiyang.

Fig. 5. Analyse de structuration spatiale de variation morphologique du crâne humain selon l'algorithme de Monmonier [28]. L'analyse a été réalisée séparément, d'après quatre matrices calculées d'après les longueurs (A), les largeurs (B), les hauteurs (C) et les hauteurs des mastoïdes (D). Les épaisseurs des bordures des frontières sont proportionnelles à leurs significations et ont été calculées selon le *ratio* inverse de la plus grande distance associée à une triangulation, puis ces distances ont elles-mêmes été associées à chaque bordure rencontrée. En (E), la triangulation de Delaunay (lignes en pointillés) [2] et la tessellation de Voronoi (lignes en trait fort) [39] entre les groupes d'individus sont représentées. En (A) , (B) ; (C) et (D), les groupes d'individus sont numérotés selon le code suivant: 1) Ban Kao; 2) Cau Giat; 3) Dong Can; 4) Jinchuan; 5) Lang Cuom; 6) Liujiang; 7) Minatogawa; 8) Samron Sen; 9) Tam Hang; 10) Tam Pong; 11) Upper Cave; 12) Wadjak; 13) Zhiyang.

sponding geographic ones. A correlation coefficient, R_0, is calculated for the original matrices. After a random permutation process between the rows and columns within one of the matrices a new correlation index, $R_{i,}$ is recalculated. The randomisation procedure was repeated 1000 times. If the original matrices were correlated, the disruption caused by the permutations should reduce the correlation coefficient. The measure of significance is the number of times that the original correlation coefficient (R_0) was exceeded by the permutated values R_i with $1<i<1000$. Conversely, if the matrices were uncorrelated there is no reason to assume that the permutations would decrease the correlation coefficient and they may indeed increase it. Significant levels are measured by the Z statistic [22]. The computation was performed using the Microsoft® Excel® *macro* Mantel.xla version 1.2 compiled by Dr. R.A. Briers (r.briers@shef.ac.uk).

3. Results

3.1. Inter-sample and inter-specimen variability

Geological ages of the fossils were not considered to constitute 'same age' groups of specimens. Although the time period covering the fossil sample age, about 67 000 (Liujiang, China upon ^{14}C dating on the associated fauna) [44] to 1200 BP (Cambodia, Samrong Sen, upon direct ^{14}C dating) [6] is quite large at an individual scale, it seems to have a small impact regarding the evolutionary process of modern man. This assumption is confirmed by the result in this study of the multivariate analyses, which do not isolate the Liujiuang specimen (the oldest of the fossil samples). Indeed, both dendrogram and the multidimensional scaling plot groups Liujiang with the Wadjak specimens which are known to be 9000 years old. Considering this result, one can assume that a same morphology could persist over generations and then at the same time concerning the methodology, the pertinence of grouping specimens by same age is flawed.

The dendrogram (Fig. 2) shows three main clusters of specimens or groups we called C1, C2 and C3. The first group ('C1', Fig. 2) consists, by construction, of specimens characterized by a high *cranium*, long and broad *cranial* vault (*calva*) with a high, long and fairly broad face. The second group ('C2', Fig. 2) consists, by construction, of specimens themselves divided into two other distinct sub-groups ('χ' et 'δ'). The first sub-group 'χ' consists of specimens with a relatively high *cranium*, short, with a narrow *calva*. The face is low, long and very broad at the orbit level and with a narrow frontal. The second sub-group 'δ' consists of specimens with a rather short *cranium*, a narrow *calva* and frontal, a quite broad face and a very broad interorbital section. The third group ('C3', Fig. 5) is represented by two specimens. They show the same morphological characteristics of the previous sub-group 'δ' but with a very long face.

It is well known that environmental factors (mainly related to the diet), at least at an individual level, can increase the morphological variability of the skull, whose range of variation is genetically coded. To overcome the confounding effects of this source of variation it is advisable to study morphological differences by grouping several specimens in samples that are then compared. The rationale is that inter-specimen differences play a minor role and samples trends become recognizable. On the other hand, this choice may obscure some information because of a sort of 'averaging process' that underlies the computation of any distance matrix from a set of variables.

MDS analysis of inter-specimen differences and inter-sample differences are shown in Figs. 3 and 4, respectively. Both analyses show a clear differentiation between sea-border and inner-land excavated sites. At an individual level (Fig. 3) the two groups can be distinguished, roughly on each side of the *y* axis, as follows. *The first group* (Fig. 3), composed of specimen from Lang Cuom ('Lcuom 4/5/10/13/1/8'), Dong Thuoc ('Dthuoc'), Pho Binh Gia ('PBG1', 'PBG2'), Mai Da Nuoc ('MDN'), Minatogawa ('Minat 1', 'Minat 2'), Liujiang, Wadjak ('Wadjak 1', 'Wadjak 2'), Upper Cave ('Ucave 1', 'Ucave 2'), Samrong Sen ('SronSen'), Cau Giat ('Cgiat 1/2/A4'), and Dong Can. All these individuals come from coastal sites previously described by the 'C1' morphology (Fig. 2). *The second group* is composed of specimen from Tam Hang ('THS3', 'THS13', 'THS11', 'THS10', 'THS14', 'THS4', 'THS22', 'THS2', 'THN3', 'THTTA'), Than Hoa ('THOA DB'), Tam Pong ('TP1'), Ban Kao ('BKVII', 'BKLSII', 'BKKBSP', 'BKInconnu'), Mai Da Dieu ('MDD'), Lang Cuom ('Lcuom C9', 'Lcuom 11'), Upper Cave ('UC3') and Minatogawa ('Minat4'). Besides the individuals belonging to Jinchuan and Zhiyang, that clearly appear to be outlier, the absence of clusters of specimens (Fig. 3) or samples (Fig. 4) was observed. Except the five individuals ('Mai Da Dieu', 'UC3', 'Minat4', 'Lcuom9' and 'LCuom11'), all the other individuals come from inner-land sites described by the 'C2' morphology.

3.2. Geographic patterns of differentiation

The Multidimensional Scaling (MDS) scatterplot shows (Figs. 3 and 4) a continuous range of variation that is not related to geographic distances. The absolute lack of association between biometrical differences and geography was assessed by the Mantel test [24]. Cross correlations between pairs of specimen, or pairs of samples, and their associated geographic distance is neither correlated nor significant. This result suggests the presence of discontinuities in the pattern of variation between samples that may be visualized as boundaries. To visualize barriers that separate samples, we applied the Monmonier's maximum difference algorithm [28] on four distance matrices corresponding to the length (Fig. 5A), height (Fig. 5B), width (Fig. 5C), and mastoid height (Fig. 5D) of the studied fossil skulls. The rationale for this choice is to provide a more reliable analysis of the fossils studied in this paper.

This approach raises a question on the informative power of each of the different biometrical measures taken on skulls. If, in a given set of different measurements only a few are shown to be variable (among specimen or samples), then the distance matrix computed from all these measures will actually reflect the variability of this single variable measure and can be defined as being not robust. The separate analysis (Fig. 5 A/B/C/D) shows that strong boundaries encompass specimen of Jinchuan and Wadjak that, as in the MDS analysis (Figs. 3 and 4), show the most significant differences compared with other samples. With the exception of matrix 4 (Fig. 5D), a boundary isolates Jinchuan and Wadjak that are shown to be very different one from each other. The other barriers differ in their patterns, even though a certain longitudinal differentiation between coastal (sea-border) and innerland samples appears. In Fig. 5A it can be seen that samples of Tam Hang (9) and Tam Pong (10) are on the left side of a boundary that splits them from costal samples as Cau Giat (2), Dong Can (3). In this respect Lang Cuom (5) seems to be more isolated from these two groups (Fig. 5B). Likewise, Liujiang (6) is put apart from neighbouring samples even though this datum is supported only by data characterizing *cranium* width (Fig. 5C). Concluding, even the individual of Samrong Sen (8) is set apart from different boundaries (Fig. 5D and, partially, 5C) thus indicating its biometrical difference from neighbouring samples.

4. Discussion

In this section, we present the interpretations of the two multivariate analyses (Hierarchical Cluster Analysis and the Multidimensional scaling) combined with the results of the analysis of geographical patterns of variation, which highlight a morphological structure within the fossil sample split up into 3 morphological clusters (C1, C2, C3).

The clear differentiation of the two Chinese fossils of Jinchuan and Zhiyang appears both from the multivariate analyses at specimen and sample level (Figs. 3 and 4). These fossils can be considered outliers belonging to two separate samples (since they considerably differ one from each other) that are distinct from the remaining samples of the region. Barrier analyses reinforce this conclusion. Separate analysis of different morphological traits such as the skull length, height, width of *crania* as well as the mastoid height, confirm the presence of strong barriers encompassing Jinchuan and Zhiyang fossils (Fig. 5 A, B, C, D). Remaining samples are more homogeneous and equally spaced on a Multidimensional-scaling plot (Figs. 3 and 4), suggesting the absence of clusters. This configuration does not mean that neighbouring samples on the plots are geographically close. The total lack of correlation between the distance matrices based on biometrical measures and on the corresponding geographic distances indicates the absence of any latitudinal cline in the pattern of morphological change and, therefore, a considerable variability between fossils that can be the result of different migration patterns in the early peopling of the area. The observation has to be related to strong differences of Chinese samples and to the differentiation between coastal samples and inner-land ones. This differentiation is suggested both: (i) by the analysis of fossils both at specimen (Fig. 3) and sample level (Fig. 4); and (ii) by barrier analysis (Fig. 5).

Concerning the first group (C1), the specimen coming from Liujiang is 67 000 ± 5 000 BP [44] and, therefore, its oldest member. The other specimens of this group are dated between 33 000 years BP (Upper Cave) [44] and 1200 years BP (Samrong Sen). The C1 group (Fig. 2) shows that the same morphological characteristics were present at least from 67 000 years (Liujiang) ago to at least 1200 years ago (Samrong Sen). These sites, corresponding to the fossils composing the C1 group, were found either in insular or in continental sites close to the sea (Fig. 1). Furthermore, such sites are distributed from the north to the south along the Eurasiatic coast. This very specific human presence close to the sea, with individuals sharing the same morphology, underlines a continuous coastal peopling.

Concerning the second group (C2) and the third group (C3), the geological age of the fossils is between 33 000 years BP (Upper Cave 3) and 6000 years BP (Ban Kao). The C3 group consists of two specimens

(Jinchuan et Zhiyang) exhumed from continental sites, far from the seashore. Within the C2 group, the specimens composing the sub-group δ are both coming from continental sites (Fig. 1) quite far from the seashore (Tam Hang, Tam Pong) and from continental sites close to the sea or from island sites (Lang Cuom 1, 9, 11, 13, BK.Inconnu and BKBXV, Minatogawa 4, Mai Da Dieu and Upper Cave 3). We note that subgroup δ is heterogeneous regarding the localisation of the exhumation sites from where fossils, with a close morphology, come from. The Lang Cuom site particularly attests this heterogeneity, compared with the other sites (see the spanning of corresponding specimens in the MDS plot of Fig. 3). Indeed, half of the fossils exhumed at Lang Cuom shows a morphology close to the one observed in C1, notably at the Liujiang site dated about 67 000 years BP. This C1 morphology can thus be interpreted as ancestral. The other half of the Lang Cuom fossils shows a morphology different from C1 and thus can be drawn to the morphology of C2 group. In other words, this second half can be gathered with Tam Hang, BK. Inconnu and BKBXV, Minatogawa 4, Mai Da Dieu and Upper Cave 3 are 33 000 years BP. We can conclude that the Lang Cuom fossils with the C1 morphology show an ancestral morphology inherited from their coastal ancestors.

During prehistoric times, one can suggest that social and economic constraints supported endogamy within human groups. Consequently, small populations would have had a stable gene pool until the arrival of immigrants. If this hypothesis is right, the morphological characters different from those seen in C1, that are also shared by a half of the Lang Cuom specimens, can be interpreted as: (i) a microevolution phenomenon leading to the emergence of new morphological characters in situ: or (ii) the result of the arrival of immigrants coming from mainland continental sites. The Tam Hang site demonstrates the presence of these immigrants on the way to the seashore sites as soon as 33 000 years BP (Upper Cave 3). We are more inclined to support such an interpretation because there are several sites, both insular or close to the seashore, that yielded individuals with a morphology close to C2 (Lang Cuom, Ban Kao, Mai Da Dieu, Upper Cave, Minatogawa). The main question of this study raises when noticing that specimens of the first main group 'C1' (Fig. 2) are confined to the Eurasiatic coast, and notably in insular sites or in continental sites close to the seashore. Although evidence of early modern human presence exists in Australia at least about 50 000 years ago [1], attesting navigation; this peculiar geographic distribution (C1 group) cannot be explained only by migrations across sea areas, since modification of the environment (drop of sea level and new lands emerging) 67 000 or even about 30 000 years ago would have offered humans easier colonisation paths.

5. Conclusions

The major objective of this work was to define the way in which the prehistoric modern human migrations occurred in Far East Asia during the Late Upper Pleistocene, about 67 000 years ago; in other words whether it was continuous or not [21] and from one or several regional centers [41–43]. A corollary task of this study consisted in analyzing the particular environmental conditions that humans met in this area. During the last great glaciation, the North of the Far East, the Japan archipelago, the Taiwan island, insular southern Far East, Malaysia, the Sonde archipelagos and a part of the Philippines were all connected with the Eurasiatic continent. It was then possible to go from Japan to Indonesia on foot. This climatic change had, moreover, some marked effects on the biotope. The progressive arrival of the cold can thus be considered as a determining element in the history of the human migrations. This migration, from the most northern areas of the Far East towards the south, was probably directed to those zones where the climate was less severe.

The terms 'Caucasoid and Mongoloid', often used in the morphological description of Far East populations, are too rigid to be used in our study. Indeed, this current analysis deals with modern human groups that could have had many opportunities of mixing with other human groups, making their morphological characterization difficult or even inappropriate with only one term. This is the reason why we choose to describe the three morphological groups by the set of traits that characterizes them.

We can summarize our results by proposing a scenario where there were at least 2 major regional centers from which human groups peopled Far East Asia during about 67 000 years. One group (C1 morphology, characterized by a high, long *cranium*, broad *calva* and very broad face, with a very thick *cranial* bone) was located in the North of the Far East, which included, during the sea withdrawals, the Japan archipelago. The study of Far East Asia environment changes during the Late Upper Pleistocene illustrates the geographical human migration context: islands were connected several times to the continent and these climatic changes had strong effects on the biotope. The progressive arrival of cold can also be considered as a determining element in the history of the human migrations as a phenomenon, which caused humans to move away from the most northern areas. This episode took place during the last glaciation, approximately 67 000 years ago. These humans (C1) would have then reached the Sunda shelf following the coast. Once arrived in the southern of the Far East, this same population underwent admixture, 30 000 year ago, with a second group of humans (C2 morphology, characterized by a rather short and fairly high *cranium*, with a broad *calva*, a narrow frontal bone, a rather broad face, and a very broad face between the orbit), originated from mainland South-East Asia. The 2 major morphologies (C1 and C2) described in this work illustrate the coexistence of at least 2 well characterized types of the first modern humans groups that colonized the Far East during the Late Upper Pleistocene, validating the multi-regional evolution hypothesis theory.

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