Morphological Variation and Sexual Behavior in the Human Past

II. The Origin of East Asians and their Sexual Behavior

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SUMMARY

Sexual behavior is the crucial element of global migration and the population expansion of humans in the past. Based on the previous proposal that female pubic length is inversely correlated with the sexual activity of her male partner, the sexual activity of hominids in Palaeolithic Europe, Middle East and East Asia was assessed. A long pubic feature in the female pelvis of current East Asians can be seen in the Asian Palaeolithic hominid, i.e. the Jinniushan (around 200,000 years old), China. On the other hand, short pubises, characteristic of current Europeans, were seen in Pleistocene female hominins (except for Neanderthals) unearthed in Europe and Middle East. It was inferred from the previous proposal that their male partners could be sexually more active than East Asian male hominins. In addition to East Asian characteristic facial and dental morphology, close similarity in the sexual behavior of current East Asians to the Jinniushan can be satisfactorily explained by the model of the regional origin of the East Asian population.

Key Words: sexual activity, pelvic morphology, human origin, East Asian

INTRODUCTION

It has been generally accepted that the Homo lineage originally appeared in Africa, followed by its successful global expansion. There has been growing evidence that Asia has been a pivotal site in the migration of the Homo lineage, in particular H. erectus, and in evolution of both archaic and anatomically modern H. sapiens. Their migration and population expansion was the beginning of the global impact of human history. Such successful expansion would probably owe to the reproductive strategy which the Homo lineage has acquired in evolution.

It has been revealed that pelvis with the long pubis was most frequently seen in East Asian females, whose male partners had the small size of the erect penis and were sexually least active. Whereas a pelvis with the short pubis was often seen in the females of the other populations in which their male partners showed large penises and were sexually more active, suggesting an inverse correlation between the pubic length of female and the sexual activity of her male partner. The population-characteristic feature seems to correspond to the evolutionary history of each population. A few pubic fossils have been unearthed in Europe, Middle East and East Asia. An interesting observation is that the pubic length of the Jinniushan in China was as long as or longer than the mean of the current Asian’s pubis and much longer than those of current people, living in Europe and Africa. I shall describe these people as “East Asian/Asian”, “European” and “African” respectively in terms of specific people and also the
people of "population 1, 2 and 3" in general terms, respectively \(^4\). They originally came from the regions of geographically related indigenous populations, such as Northeast/East Asia, Europe (and Middle East) and Africa. In the present study, the pubic length of a few Palaeolithic hominins unearthed in East Asia, Middle East and Europe is compared with those of current people and then their sexual behaviors are inferred. This paper deals only with male sexual behavior unless otherwise mentioned, as more complex processes are involved in females and will be discussed separately.

Heated debates have been and still are being made on the origin of modern humans in relation to the global migration of hominins. There are at least two possibilities. Firstly, our direct ancestral \(H. sapiens\) was evolved locally in widespread regions of major continents, e.g. Africa, Asia and Europe, from the founding hominins after global expansion of what is called \(H. erectus\) from Africa—hereafter called the "first wave of migration" from Africa. Secondly, modern humans are derived of only one of the species arose in various regions: that is \(H. sapiens\) of an African origin. This particular hominin expanded by global migration to other continents and occupied in total replacement of other indigenous hominins—the "second wave of migration". The former view has been known as the "regional continuity" model \(^10,11\) and the latter as the "out-of-Africa" model \(^12,14\). In this paper, I will refer these models in order to argue which model can account for the observations, which will be described here, more favourably.

**Continuity of the pelvic trait in East Asian fossil records**

It has been pointed out that the females of each population have the unique mean length of pubises, which correspond to their specific pelvic shapes: longest in population 1, medium in population 2 and shortest in population 3 \(^4\). Most of females in population 1 showed the "gynaecoid" structure. Various surveys have repeatedly revealed that the pattern, in order of sexual activity, of population 1 < population 2 < population 3. This result was supported by the analyses of the "bio-available" testosterone level in blood, responsible for male sexual activity \(^5\). The next question arises as to how and when East Asians acquired the genetic basis for their pubic structure of females and the low sexual activity of males. A comprehensive review of continuity in Asian fossil records has already been reported \(^6\).

In this article, I shall briefly cite the representative cases which are relevant to further discussions.

There are a few significant fossil records, showing continuity in East Asian traits and incremental modernization, in particular in cranial morphology, of the people of population 1 from \(H. erectus\) during the middle-late Pleistocene transition. These specimens have already been reported as crucial fossil remains for the regional continuity model of human evolution in East Asia.

The Dali cranium, 230–180KY old \(^5\), was discovered in Shaanxi Province, China \(^6\). The observed features of the skull show a mosaic of some characters of \(H. erectus\) and late \(H. sapiens\). Some of them are within the range of the variation of the Zoukodian \(H. erectus\) skull and significantly other features fall within the values of current East Chinese population \(^16\). The observation that the Dali skull possessed Inca bones as discovered in skulls from Zoukodian \(^6\), suggests continuity in the developmental trait of Inca bone formation. The Dali cranium displays the traits characteristic of gracile—anatomically modern —\(H. sapiens\) found in China, but not in Europe and Africa \(^8,16\).

The Jinniushan—anatomically modern—\(H. sapiens\) specimens (200KY or somewhat older, 280KY), most relevant to this paper, were unearthed at Jinniushan, located in Southern Yingkou County, China, together with a nearly complete cranium, a well preserved left innominate and others \(^6\). It has been suggested that all of the cranial and other remains belong to one adult individual \(^6,9,16\). The Jinniushan was previously assumed to be male \(^16\). However, the careful examination showed that the Jinniushan was in fact female \(^7\). The Jinniushan also retains some of features similar to \(H. erectus\) pekinensis as well as the trait in facial morphology of \(H. sapiens\), in particular those of East Asian population \(^6,16\).

Etler \(^16\) mentioned that the overall morphological patterns of the Jinniushan skull is definitely along the lines of modernization and fits in well with the regional continuity model of modernization of East Asian population from \(H. erectus\). Therefore, the fact that the
unique facial features are not special to the Dali, but are also seen in the Jinniushan would suggest that these features were actually widely spread among the archaic *H. sapiens* inhabited in China. The Liupjiang specimens (111 – 139KY old or alternatively older than 153KY) were discovered in Liupjiang county, Guangxi Zhuang Autonomous Region in Southern China.  

Etler described that the Liupjiang seems to have slightly archaic features, but share certain characters particularly in facial morphology, with current Asians, e.g. a short and wide face, and a broad and low nasal region. The traits of the Liupjiang which are shared with those of current East Asians are also seen in the pelvic morphology of the right innominate, discovered together with the cranium. Importantly, it showed gracile features. For example, the sciatic notch index fell within the range of current East Chinese population. Recent investigations of the hominin remains in the lower reaches of the Yangtze River have shown that the gracile—anatomically modern—*H. sapiens* was widely present along the River at around 100KY ago (see later description).

Although shovel-shaped upper incisors are sometime seen in Europeans and Africans, most of them are in the "trace" or "minor" shoveling category. More than 50% of these populations have no shovel-shaped incisors, whereas the incidence of well shaped shoveling in current Chinese is more than 67%. Thus such a high incidence suggests that typical incisor shoveling is also one of the features, characteristic of East Asians. It has been reported that all Pleistocene upper incisors from China, e.g. Jinniushan and Liupjiang, were shovel-shaped as current Chinese incisors. Once again, there is clear continuity in the dental trait, characteristic of East Asians.

### Pelvic variation: comparison of the pubic length of Palaeolithic and current East Asians with the specimens in Europe and Middle East

The preservation of a whole pelvic structure in fossil records has been very rare except for the Pelvis 1, SH. However, the pubic length of some fossil specimens has been measured. The Jinniushan inominate specimen shows gracile features around the iliac butress and ischial tuberosity. The superior pubic ramus is quite thin in cross-section and seems to be elongated mediolaterally. The value of pubic (acetabulosymphysial) length reported by Rosenberg was 87.4 mm. The average female values of the pubic length (measured from the point at which ischium and pubis meet in the acetalabulum) of current human populations are as follows: Europeans 77.9 ± 4.4 mm, n: 100; Japanese 82.9 ± 4.1 mm, n: 115; Eskimo 80.1 ± 5.1 mm, n: 95. Since pubic length measured in this way is longer than pubic (acetabulosymphysial) length used by Rosenberg, the pubis of the Jinniushan was actually much longer than the average of current human populations (Fig. 1). Neanderthal specimens, e.g. the Kebara, the Pelvis 1, SH, the Krapina 208, the La Ferrassie 1 etc., discovered in Europe exhibited the pubic rami as long as that of the Jinniushan. Neanderthal female values were calculated.

![Fig. 1 Correlation between the pubic length of a female and the erect penis size of her partner.](image-url)
Fig. 2 Variation in the pubic length of current and archaic humans.

Data were taken from the figure (acetabullosynpheseal length versus femoral head diameter squared in current and fossil specimens) of Rosenberg. The length of each specimen below (−) or above (+) the least-squares-regression-line shown in the figure was estimated and re-plotted in the histogram. Since Rosenberg has shown that sexual dimorphism can be extended into pelvic morphology and the past, female values were calculated from the values of male archaic specimens using pubic dimorphism index, 105.4, which is the average of the results observed by refs. 20, 63 and 64. White and black bars represent the distribution of current and fossil specimens, respectively. Ca: Barma del Caviglione, CM: Cro-Magnon, P: Pomedost, Pa: Paviland, Q: Qafzeh and S: Skhul.

under the assumption that the dimorphism of Neanderthals was the same as that of current humans (see Fig. 1). The Jinniushan was estimated to be 68.78 ± 4.30 cm tall, based on the length of ulna. Even if their body sizes were taken into consideration, the pubic rami of the Jinniushan (female) and the Kebra (male, 88 mm in acetabullosynpheseal length, but the calculated female value was 95 mm long) and the Pelvis 1, SH (male, 82 mm in acetabullosynpheseal length, but 86 mm in calculated female length) were obviously long. It has reported that pubic length is “body-size” dependent. However, such a dependency cannot be seen in some cases. For example, as already discussed, current Japanese females are obviously smaller in body size (in terms of body weight and height) than Europeans and Africans, living in America. Yet, their pubises are actually longer than those of latter people (Fig. 1). I would not totally rule out the possible dependence of pubic length on body size, but I feel strongly that the length of female pubis depends upon the shape of her pelvic cavity as well. Therefore, it seems more likely that the long pubic rami of the Jinniushan and Neanderthals were due to their pelvic shape-plantypeloid-and cavity. In fact, Rosenberg et al. mentioned that the pelvic inlet shape of the Jinniushan was quite platypeloid. On the other hand, the pubis of anatomically modern H. sapiens (with an exception of the Skhul 9) discovered in Europe and Middle East was much shorter than that of the Jinniushan. In order to emphasize this view, Rosenberg’s results was modified to the histogram, in which variations in the pubic (acetabullosynpheseal) length of current and archaic humans were estimated from the result shown in Fig. 3 and plotted (Fig. 2). It is clear that all of 10 fossil specimens (with the exception of the Skhul 9) of anatomically modern H. sapiens from Europe and Middle East fell only within the lower range of current humans or were on the outside of the lower end of the ranges. This implies that the pubises of anatomically modern H. sapiens (except for the Skhul 9) in Europe and Middle East regions were shorter or much shorter than those of “average” current humans. Trinkaus also mentioned that the Jinniushan specimen had in fact a long pubis, compared with more other fossil specimens of anatomically modern H. sapiens. It should be noted, however, that such a trait was only observed when bones were fully grown up at the neonatal stage, as their pubises showed a unique developmental growth curve. All of these observations show that the Jinniushan displayed her pubis much longer than those of anatomically modern H. sapiens found in Europe and Middle East regions, and those of the current population 3 people in America. On the other hand, the pubic length of the Jinniushan is rather closer to those of current East Asians than Palaeolithic and current non-Asians. Therefore, it may be inferred from the hypothesis previously proposed that anatomically modern H. sapiens found in Europe and Middle East regions were sexually more active than current East Asians and much more than the Jinniushan. The Skhul 9 is one of the most peculiar specimens found in the Skhul cave. The femur is massive, its head having a diameter of 48 mm. The skull has unmistakable male characters. Yet the anatomical features of the pelvis are simi-
lar to those of a female. All of the Skhul pelvises tend to show "modern" forms and differ from the Neanderthal 15. However, the Skhul 9 differs from other Skhul specimens. Although the Skhul 9 could be a hybrid between the Neanderthal and the anatomically modern *H. sapiens* in Europe, it can not be ruled out the possibility that the feature of the Skhul 9 was in part derived from the hominin inhabited in Pleistocene East China, e.g. a descendant from the Jinniushan. Further vigorous examinations are required to confirm this possibility.

**The origin of East Asians**

The out-of-Africa model has claimed that during the period of 200KY – 100KY ago, global migration in terms of gene flow by African *H. sapiens* began. In fact, the early *H. sapiens* fossils, dating from 160KY to 154KY ago, have recently been discovered in Ethiopia, and claimed that this hominin would perhaps be responsible for the second wave of global migration and the total replacement of indigenous inhabitants in East Asia 14,25. If they really migrated via Middle East or Indo–Pacific coastline to East Asia from Africa, the trait of the short pubis acquired by East Asian females must have rapidly evolved during the extremely short period, as their long migration journey from Africa to East Asia would have taken years and years (probably not the order of 10–20KY, but very much longer). Since very few late Palaeolithic sites in China exhibited Mousterian technique 6, it is most likely that their own culture was apparently not influenced by other cultures. These observations, together with similarity in cranial and dental morphology, once again suggest that the observed similarity in the pubic trait of the Jinniushan to current East Asians can be most nicely explained by the regional continuity model. In other words, the sexual activity of current East Asians is more likely to be inherited from East Asian archaic *H. sapiens* dating back to the Jinniushan era. Since the Jinniushan is the sole Palaeolithic pubic remain so far discovered in East Asia, the question arises as to whether the Jinniushan was an individual, representative of the majority, minority or rare group in the relevant population. The Jinniushan was a fully grown adult of the child-producing age and thus was likely to have produced her fertile offspring. Therefore, whatev-

**Fig. 3** Distribution of Neanderthals and related hominins in Europe and Middle East, and widely spread Palaeolithic *H. sapiens* in East China.

D: the Dale and J: the Jinniushan.

...er the case was, her representation of the group could simply mean the number of generations after splitting to a new specific lineage. For example, assuming the random discovery of specimens, the majority case could be often seen at the near final/final or plateau stage of population expansion, whereas the other cases would correspond to the initial or just after initial stage of the lineage formation. Thus, similarity in cranial, dental and pubic morphology and their sexual behaviors can be well explained by the regional continuity model. The matter of a sole specimen would not necessarily jeopardise the above view. There is no doubt that more specimens are required for further confirmation.

Cann 36 thought that modern human populations expanded from an effective population size of around 10,000 individuals. At the time 230–180KY ago and around 150–100KY ago which, according to her claim, were before or just the beginning of global expansion from Africa, the "East Asian" hominins, e.g. the Dali, the Jinniushan and the Liujiang, who displayed the continuity in the specific traits of current East Asians, already thrived in East Asia. The fact that early and late *H. sapiens* fossil remains have been discovered at more than 47 sites in East China (Fig. 3) 6 suggests the possibility that a substantial proportion of global Pleistocene hominins had already inhabited the wide regions of East Asia, even though their sexual activity was considered to be low.
Possibility of "one-way-flow" of African genes to Palaeolithic East Asians

Gene flow had occurred through interbreeding among the local communities widely spread in the continent. If some of the sexually active male hominins arrived at East Asia and met the local residents who already occupied the East Asian continent, intensive gene flow should have occurred. In fact, it has been suggested that around 80% of nuclear loci of current humans assimilated genetic material from non-African archaic humans. According to the re-assessment by Templeton of the mitochondrial DNA data, which Cann et al. argued for their claim of the out-of-Africa model, their data were consistent with a view of recurrent gene flow. As already mentioned, the newly arrived male migrants were considered to be sexually very active and the local hominins were least active. Under such a situation, it would be a natural consequence that gene flow took place predominantly in "one way" from the migrant males to the local females. The transferred Y chromosome of African origin appeared to be spread within the East Asian population. During a long period in evolution, the Y chromosome of local origin would eventually be completely replaced by the Y chromosome of African origin. There were significant differences in stability and effective population sizes between Y chromosome and X chromosome/autosome. Considering the possibility that the dilution out and/or selective sweep of African male X chromosomal and autosomal genes might have occurred, the X chromosome/autosomes of East Asian origin would tend to be preserved more often and were thus maintained as a major component in the East Asian population. The different patterns of migration for females and males and the possible polygamous society can not fully explain the observed disparity. Ke et al. have observed that all of the Asians examined (total 163 different sub-populations in Asia) carried a mutation at three sites (YAP, M89 and M130) on the Y chromosome. These three mutations have coalesced to another mutation (M168T), which was claimed to be originated in Africa about 35KY to 89KY ago. On the other hand, the age estimated with the use of autosomal/X chromosomal genes ranges from 535KY to 1,860KY ago. These age estimations under a variety of assumptions were not with great accuracy.

However, if we accept the estimated ages merely as a gross order of the time of events, the above age actually corresponded to the era of H. erectus in East Asia. Namely, genes on the X chromosomes/autosomes could be basically of local origin from H. erectus in East Asia and the Y chromosome could be of the African origin. Thus, the between-populational difference of sexual behaviors could well account for the huge disparity in age estimation by X and Y chromosomal genes. The proposition of the "one-way-flow" of male genetic components is also supported by the studies of nested cladistic analyses of paternal (Y chromosomal) and maternal (mitochondrial) DNA data. This is in good accordance with the view that males played a specific role in intercontinental, e.g. Africa to East Asia, population expansion and females contributed to population structure (recurrent gene flow).

A DNA analysis of Neanderthals has shown that Neanderthals went extinct without contributing at mitochondrial DNA to modern humans. As already described, the pubic length of Neanderthals was as long as the Jinniushan. Therefore, the sexual activity of Neanderthals was considered to be as low as the Jinniushan's activity. Furthermore, it appears likely that Neanderthals occupied limited regions in Europe. A low sexual activity and possibly the limited population size of Neanderthals in these regions could well account for complete disappearance of their population when coexisting with sexually dominated "modern Europeans". The view of possible gene flow from sexually active "modern Europeans" would be supported by the recent discovery of two human remains, a mandible (34–36KY) in Romania and an almost whole skeleton (24–25KY) in Portugal. These hominins were characteristic of a mosaic of archaic, early modern human and Neanderthal morphological features. A single cause of Neanderthal's extinction appears to be unlikely. However, both low sexual activity and small population size together with other crucial factors could lead to eventual dilution out of Neanderthal's DNA and/or to the severe disturbance in their own breeding within the Neanderthal's society.

The female pubis of the current Bantu population, living under the hot environment, is as short (73.2 ± 4.1 mm) as that of population 3 people in America. Whereas the pubic length of female Eskimo (80.1 ± 5.1
strongly suggest that great caution is required in assigning East Asian and western Pacific prehistoric human remains to a particular period on the basis of morphology alone as Endo and Baba concluded. Recent excavation of the Akashi site has revealed that the clod which was originally attached to the innominate remain at the time of discovery was in fact from the Nishiyagi IV layer and thus that the Akashi was most likely to have come from the stratigraphic layer of the Nishiyagi IV deposit. It seems possible, therefore that the Akashi is one of the valuable hominid remains showing the gracility of the H. sapiens populations that were widely and contemporaneously distributed in East Asian and Pacific regions. Pubic rami were unfortunately missing from all of these specimens.

**GENERAL DISCUSSION**

Assuming that the Jinniushan was the representative of the relevant population or subgroup, the low sexual activity of archaic H. sapiens in East Asia would suggest that their testes were small in size, implying that Pleistocene H. sapiens in East Asia had a small capacity of sperm production and thus lived in the less sperm-competitive societies. They probably formed small living groups that made them less severe in sperm-competition as seen in Neanderthal's societies, e.g. the Combe Grenal rock shelter in France. It has been observed that various biological functions, including human behaviors, are "population-density" dependent. It is plausible, that small living groups and communities would have been spread out across a wide range of the East Asian continent with a certain defined density.

Taken all of the observations into consideration, it is highly likely that the low sexual activity of current East Asians did not result from the second wave of migration, nor was derived from Europe, but of an East Asian origin. The later stage of Homo evolution, in particular archaic and anatomically modern H. sapiens, was confined to three major continents, i.e. Africa, Europe and East Asia. Fossil records together with archaeological evidence have shown that during the period of this stage many of the major events in human evolution had occurred in East Asia rather than in Europe. In fact, the environment in East China at the
middle Pleistocene was really favorable for hominin occupation and propagation. For example, 26 mammalian taxa were found at the discovery site (Locality A and C) of the Jinniushan. These include Equus sanmeniensis, Dicerorhinus merki, Macaca robustus and some avian species, e.g. Trogonthium 6,30. Based on the faunal evidence at Jinniushan, it can be deduced that the environment was mosaic with dense forest, a thick bushland, a beautiful grassland and a broad wetland 30. Plants and animal life would have thrived in the region. Such a good and rich environment in East China at the middle Pleistocene would no doubt have made it possible for successful hominin propagation. It would be conceivable, therefore, that prior to the second wave of migration, if it really happened, the East Asian continent would have been widely occupied by successfully propagated H. sapiens of an East Asian origin (Fig. 3) and that their population in East Asia would have already reached a significant proportion of the global population. This view is supported by the results of nuclear DNA analysis of the current human populations. In fact, the genetic analyses of β-globin (autosomal) and pyruvate dehydrogenase E1α subunit (X chromosomal) gene sequences have suggested that the ancestral hominin population was located in Asia, as well as in Africa, older than or about 200 KY ago and that they were widely dispersed at this time 21,30.

Mitochondrial genome replacement without serious changes in nuclear genomes has been widely observed in the two sibling species of various organisms, including mammals (see ref. 60). It appears highly likely that, like the above cases, the mitochondrial genomes of Asian H. sapiens residents, who were sexually least active, were replaced with those of sexually active African migrants during the period of the second wave of migration. This implies that the only mitochondrial genomes of their descendents, such as current Asians, have actually their origin in Africa and that current Asians do not represent the pure descendents of African migrants at all.

CONCLUSION

Based on the previous proposal that female pubic length is inversely correlated with the sexual activity of the male partner, the sexual activity of the Jinnie

Acknowledgements. I thank Drs. A. Thorne (Australian National University), I. Yoshioka (Nagoya). D. Shaw (Australian National University). K. Sorimachi (Dokkyo Medical University) and K. Rosenberg (University of Delaware) for their critical reading of the manuscript at the early stage, for reference collection and also for valuable conversations and suggestions. I am particularly indebted to late Dr. K. Kasai (Kyoto), who suddenly deceased in 2001, for providing me with his valuable information. I also thank Mrs. C. Stuart-Moore, Mr. D. Buckle and Ms. J. Olsen (Australian National University) for their advice on an earlier draft of this manuscript.

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