

若干有争议的直立人头骨特征在周口店 和东非人科成员中的出现情况

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摘 要

多年来,直立人被看作是一个公认的物种;它曾分布于亚洲和非洲,也可能还曾分布于欧洲。这个物种包括了从距今180万年至距今大约20万年的人科成员。直立人标本彼此之间有着许许多多的相似之处,因此,归属于同一个物种已为众所认可(Howells 1980, Rightmire 1984)。

然而,这一观点好几年来受到一些研究者的质疑(Andrews 1984, Stringer 1984, Wood 1984)。这些研究者使用的是分支系统学方法。使用这种方法是试图复原出演化谱系中分裂出新种和其它分类单元的过程。该方法并不涉及全部相似之点,而是着重于单一的形态性状状态及其变化和分裂情况。依据这一方法,共有的衍生特征或独有的衍生特征对复原物种之间的关系才是有用的。亚洲的与非洲的直立人之间的许多共有性状常只被当作在其它分类单元里也存在的原始性状而已。

根据分支系统学方法,一些研究者(Stringer 1984, Wood 1984)强调:若干独有的衍生性状状态或特化性仅存在于东亚的直立人之中。Andrews (1984)对原始特征作了进一步地剔除,表列出东亚直立人具有的7个近裔自性:额矢状嵴、顶矢状嵴、厚的颅盖骨、顶骨的角圆枕、枕外隆突点远离枕内隆突点、乳突裂、以及孟内突与鼓板之间的隐窝。

Andrews (1984)根据这些特征提出了一个假说,认为“人类的演化绕过了亚洲的直立人,其演变顺序是从能人依次经由 ER3733 人、ER3883 人、OH9 人和 OH12 人而导至中更新世的早期智人…”。

最近几年里,这个想法受到了重视也受到了批判。但是,对于所开列的这7个特征在非洲是否出现,仍然难以确定且令人困惑。

本文将介绍对这些特征进行逐项重新研究的初步结果。我们检查了东非早期人属和直立人的几乎全部的原件标本,此外,也检查了北京人的整套模型和出自北非和印度尼西亚的原件材料。

结果可简述如下。

额矢状嵴(其两侧兼有沿嵴的矢向扁平区)普遍地出现在北京头骨上、出现在和县头骨上(Wu Rukang 1982),也出现在某些印度尼西亚人科成员头骨上。在东非的直立人中,这样的矢状嵴出现在180万年前的 ER-3733 头骨上。此外,在 OH12 头骨上出现

轻微的矢状嵴。诸如 Bodo、Omo2、Broken Hill 和 Eliye Springs 之类远古智人,也有矢状嵴 (Braüer and Leakey 1986); 在欧洲,在 Arago 以及其它的远古标本中也有。看来,这个特征似乎是在非洲最早出现,因而未必是东亚直立人的近裔自性。

东亚直立人的顶矢状嵴在位置上、长度上以及显著性上均有很大的变异。ER-3733 头骨的前凶区已破碎,但该头骨强烈的额矢状嵴十分可能导致前凶区有所隆起。早期直立人 ER-3883 在其顶骨的前半部也显示出微弱的矢状嵴。此外,微弱的矢状嵴还呈现在阿尔及利亚的 Ternifine4 标本上。在远古智人中,例如 Omo2、Eliye Springs 和 Petralona 标本,呈现出中矢隆起或者矢状嵴。

颅盖骨厚度在前凶点处和顶结节处已作过测量。表 1 表明东亚直立人的平均值与东非直立人的平均值在前凶点处的几乎相同,在顶结节处的仅稍有差别。虽然差别显而易见是无意义的,但应该提到的是,在测量技术上还有不牢靠之处,对已发表的数据作一番核对就可知道这一点。

角圆枕在所有周口店顶骨上都发育,但强壮程度不一。在印度尼西亚人科成员中,该性状变异更大。在非洲,角圆枕较少见但并非没有。在 OH12 标本上,其乳突角处显得有些肿胀。在 Ternifine4 标本上也有稍微发育的角圆枕。还有一些标本具有角圆枕,例如 Bodo、Broken Hill 和 Arago 标本。

关于枕外隆突点与枕内隆突点的距离,在测量方法上以及在这个功能复杂的特征的适用性上尚有许多问题。与大多数文献 (Turner and Chamberlain 1989) 所说的相反,这个距离其实是能够在许多非洲直立人和早期人属化石上确定的。我们发现枕外隆突点与枕内隆突点的距离 (按 Martin 氏的定义) 在 10 件标本中有 3 件是超过 18 毫米的 (ER-3733 标本、OH9 标本、ER-1805 标本)。这些测量值全在东亚直立人的变异范围之内。

与文献 (Stringer 1984、Rightmire 1986) 所述的相反,乳突裂在东非的早期人属、直立人以及远古智人中也是存在的。例如在 ER-1813、OH12 和 ER-3884 标本上,鼓板的岩嵴并不与乳突融合 (Braüer et al. 待发表)。然而,这个特征却定义拙劣且变异很大。

最后一个特征是介于隆起的孟内突与鼓板之间的隐窝,如周口店 III 号标本左侧所呈现的那样 (在该个体的右侧,则形态大为不同)。该特征并不像上述那些特征的那样有争议,因为大家都一致认为这种裂口状的形态不仅在亚洲的直立人里出现,而且也在非洲的直立人里出现 (例如 ER-3883 标本)。

综合分析,在这 7 个特征里我很难看出特化的东亚直立人特征。它们全在非洲的直立人之中出现,有的甚至在早期的人属里出现。因此,这些特征大多可被认为是原始特征而不是东亚的近裔自性。本研究表明,尚无令人信服的依据可把东亚直立人假设为高度特化的物种、假设为人类演化的旁枝。而且,有明确的证据表明,这些特征大多也存在于东亚远古智人之中 (Wu Xinzhi and Wu Maolin 1985)。

此外,我认为分支系统学方法有着许多理论上的难题,在此我只能提及其中几个难题:

这类性状的变化与生殖隔离的起源或物种的形成并无直接的关系。在任一物种的存

在期内,特征更有可能起变化;

这7个特征中的大多数十分可能是与骨质增加有关的。因此,所列举的特征数目还得减少;

演化趋势的逆向也是有可能的,骨厚的变弱就是一个例子。因而,较厚的颅盖骨未必相当于特化的“死胡同”特征。

分支系统学方法虽然有较多的难题,但可能是有用的手段,不过,这只是有用手段中的一种而已。为更好地理解这些人科成员样本中的变异性在系统发育中的实质作用,对那些已经提出的亚洲近裔自性还需要作全面而详尽的分析和比较(Bräuer and Mbua, 在研究中),对其它许多特征也需要如此。

(张银运译)

THE OCCURRENCE OF SOME CONTROVERSIAL *HOMO ERECTUS* CRANIAL FEATURES IN THE ZHOUKOU- DIAN AND EAST AFRICAN HOMINIDS

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Abstract

On the basis of cladistic analyses, some authors have recently questioned the widely-held view that *Homo erectus* is a single species which existed in Asia, Africa, and Europe. It has been argued that the Asian sample is characterized by a unique set of derived features (autapomorphies) not present in the African specimens, and may thus represent a side branch of human evolution.

More precise morphological descriptions and comparisons of these suggested autapomorphic features in hominid samples from various geographic region may help shed light upon this controversy. This paper will show the presence and variability of some critical features in the Zhoukoudian and in the *erectus* and *habilis* samples from East Turkana and Olduvai.

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For many years *Homo erectus* has been thought to be a well established species which inhabited Asia, Africa, and probably Europe (see papers in Sigmon and Cybulski 1981). Any *Homo* fossil which could not be classified as either *Homo habilis* or *Homo sapiens* was generally specified as *Homo erectus* including the more than 1.5 million year old fossils from Kenya as well as the much younger Peking Man. All *erectus* crania exhibit basic similarities such as strongly developed and projecting supraorbital tori, low frontal profiles, sharply angulated occipitals, and a cranial vault which becomes narrower upwards. These and many other similarities have lead to the widespread assumption that all these specimens belong to one species (Howells 1980, Rightmire 1984).

However, for several years this view has been questioned by some researchers using the so-called cladistic method (Andrews 1984, Stringer 1984, Wood 1984). This approach attempts to reconstruct the splitting of evolutionary lineages into species and other taxa. In contrast to the phenetic approach, this method is not concerned with the many overall similarities between the various hominid samples. Instead, it focuses on single morphological characters or character states, and their change and splitting. Two basic kinds of similarities are differentiated: similarities in ancestral or primitive features which are inherited from a common ancestor, and similarities in derived or advanced character states which are transformations of ancestral states (Delson et al. 1977).

According to the cladistic approach, shared derived or uniquely derived traits are useful for the reconstruction of the relationships between groups or species. From this perspective, the many shared characteristics between Asian and African *erectus* are regarded to be only primitive characters, which are also present in other taxa and are therefore not so relevant for phylogenetic analysis.

Based on the cladistic approach, some researchers emphasized that there is a number of uniquely derived character states or specializations (autapomorphies) only present in East Asian *Homo erectus* (Stringer 1984, Wood 1984). Reassessing and summarizing these results by further eliminating primitive features, Andrews (1984) arrives at a list of seven autapomorphies which he believes to be present only in East Asian *erectus* but not in African specimens generally attributed to *erectus* (or *Homo sapiens* with only very few exceptions which are thought to have evolved in parallel):

- Frontal keel
- Parietal keel
- Thick cranial vault bones
- Angular torus on parietal
- Inion well separated from endinion
- Mastoid fissure
- Recess between entoglenoid and tympanic plate

Based on the assumption that these features occur only in East Asian *erectus*, Andrews (1984: 172) proposed the hypothesis "that human evolution bypassed *erectus* in Asia, with a sequence of changes from *habilis* through ER 3733 and 3883 and OH 9 and 12, giving rise to a middle Pleistocene early *sapiens*..." During the last years this idea has received attention and criticism (e. g. Bilsbrough and Wood 1986, Hublin 1986, Rightmire 1986, Tattersall 1986, Turner and Chamberlain 1989). Although various authors expressed doubts that some of these suggested characters are really autapomorphies of East Asian *Homo erectus*, there are still unclarities and problems.

This paper presents some results of a new study of the respective features, and thus new evidence with regard to the basis of this hypothesis. May these seven features be restricted to East Asia which would favour the idea that Asian *Homo erectus* represents a specialized side-branch of hominid evolution, or are they also present outside this area which would imply that both Asian and African *erectus* belong to the same species?

For this study we examined nearly all original specimens of East African early *Homo* and *Homo erectus* with regard to these features. Not only did we record the presence or absence of the respective features, but also tried to describe the expression of the features as exactly as possible. I also studied a complete cast collection of Peking Man and original ma-

terial from Northern Africa and Indonesia.

Occurrence of features

Frontal keel

A frontal keel accompanied by parasagittal flattening on either side is generally present on the Peking skulls and on some but not all of the Indonesian hominids.

Among East African early *Homo* and *Homo erectus* (this region could be examined on 8 specimens), a well developed frontal keel accompanied by parasagittal flattening is present on the 1.8 million year old cranium ER-3733 from Lake Turkana/Kenya (Plate I-1). There is also a slight keeling on the frontal fragment of Olduvai H12 (approx. 700,000 years old). More frontal keelings on African specimens appear in early and late archaic *Homo sapiens*, as on Bodo and Omo 2 from Ethiopia, on Broken Hill/Kabwe from Zambia (Plate I-2), and on Eliye Springs from Kenya (Bräuer and Leakey 1986).

In Europe, there is a frontal keel on Arago and on other archaic specimens. This feature is quite variable in size, shape, and prominence. According to the presently available fossil samples, the occurrence of a frontal keel is found most frequently in East Asia. It also being present on the advanced *erectus* cranium from Hexian (Wu Rukang 1982). However, because it occurs first in Africa, it is unlikely for the frontal keel to be an East Asian *erectus* autapomorphy.

Parietal keel

The mid-sagittal keeling on the parietals is also highly variable among East Asian *erectus* in its position along the suture and its length and prominence. In Zhoukoudian Skull XII e. g., it is well developed along the anterior half of the sagittal suture, in others it is more restricted to the bregmatic area (e.g. in Zhoukoudian X and Sangiran 2).

What about African early *Homo* and *Homo erectus*? Andrews (1984: 174) stated that a parietal keel does not appear to be present on any of the African specimens.

We don't know about ER-3733, because of its fragmentary condition in the bregmatic region. However, it appears likely that the strong frontal keel led to some bregmatic eminence. Moreover, the early *erectus* ER-3883 from Lake Turkana (ca. 1.6 million years old) exhibits a slight keeling in the anterior half of the parietals accompanied by some parasagittal flattening (Plate I-3). A slight keeling in the central part of the sagittal suture appears also to be present on the 700,000 year old Ternifine fossil from Algeria (Plate I-4). Among the more recent East African archaic *sapiens* material, mid-sagittal prominences or keelings are present, e.g. on Omo 2 and Eliye Springs, and in Europe on the Petralona cranium. The situation concerning this feature appears as complex as that of the frontal keel (Bräuer and Mbua, in preparation).

Thickness of vault bones

As one would expect, this feature exhibits great variability within and between geographic regions. Moreover, measurements taken by different authors are rarely identical as a review with published data showed. There are more or less great deviations due to uncertainties with regard to technique and the finding of reproducible points. Table 1 shows the mean values of East Asian and East African samples with regard to thicknesses at bregma and parietal eminence. At bregma the average thicknesses are approximately the same for the three geogra-

phic samples of *Homo erectus* (8.7 to 8.9 mm). Lying 1.6 mm above that of East African *erectus*, the Zhoukoudian material shows the greatest mean value for the parietal eminence.

This, however, is due especially to one individual value of 16 mm given by Weidenreich (1943). Among the African remains there are also some thick vault fragments, the parietal eminences of which are missing. Due to this, the differences between East Asian and African *erectus* would become even lesser than indicated by Table 1. In addition, thick parietals with values close to or even above the Zhoukoudian means are also present among East African and European archaic *Homo sapiens*.

Table 1 Thickness of the parietal bone in East Asian and East African hominids

		Bregma	Parietal eminence
<i>EAST ASIA</i>			
Zhoukoudian ^{1,2,3}	\bar{x}	8.8(n = 6)	10.4(n = 9)
	min-max	7.0-9.9	(5.0)-16.0
Sangiran ³ /Trinil	\bar{x}	8.9(n = 6)	9.9(n = 8)
	min-max	7.5-11.0	8.0-11.0
<i>EAST AFRICA</i>			
Early <i>Homo</i>	\bar{x}	6.1(n = 5)	7.3(n = 4)
	min-max	4.0-7.5	4.0-10.0
<i>Homo erectus</i>	\bar{x}	8.7(n = 5)	8.8(n = 8)
	min-max	6.0-11.0	7.0-11.0

1) data from Weidenreich (1943); 2) personal study of the 1966 cranium;

3) some data from Jacob (1966, 1973) and Grimaud-Hervé and Jacob (1983).

Angular torus

Such a tuber-like swelling at the mastoid angle is more or less strongly developed on all Zhoukoudian parietals. Among the Indonesian hominids, this character exhibits much more variability ranging from absence (e.g. Sangiran 2 and 10), and very slight swellings (e.g. Sangiran 4), to strong tori (Sangiran 31) (Rightmire 1984, Sartono and Grimaud-Hervé 1983)

In Africa, this feature occurs more rarely, but with great variability as well. On early *Homo* or *Homo habilis* known so far there appear to be no angular tori. On the *Homo erectus* cranium Olduvai H9, the area is markedly raised as is the entire area of the squama bordered by the temporal lines. Thus, it is not the typical angular torus as found in East Asia. There however, may exist functional relationships. But on Olduvai H12 a part of the mastoid angle is flared outward indicating that some swelling in this area was developed (Plate 1-5).

A slight plateau-like swelling restricted to the mastoid angle is also present on the *Homo erectus* parietal from Ternifine (Algeria), and a clear angular torus is developed on the Bodo parietal from Ethiopia (Asfaw 1983). Broken Hill exhibits a prominent swelling in this area as well.

In Europe, the feature is especially well developed on the Arago parietal. Although an angular torus appears to be more frequent in East Asian *erectus*, it is by no means restricted to this species or this part of the world.

Inion separated from Endinion

Considerable problems concerning this character, with regard to the method of measuring, should not be underestimated. Should the distance be measured directly, as Weidenreich probably did, in this case the measurement being affected by the thickness of the bone, or should it be determined as difference between inion-opisthion and endinion-opisthion? Moreover, should the inion be placed on the centre of the torus (Weidenreich 1943) or, following Martin's definition, on the point where the superior nuchal lines meet (Martin-Saller 1957)?

In checking the various possibilities on the isolated occipital of Zhoukoudian XII for which Weidenreich (1943) gave a distance of 35 mm (the second greatest value within the Zhoukoudian sample) I could arrive at this figure by calculating the difference between the inner and outer measurements as well. By using Martin's definition of inion, I got 25 mm. Using this method, I received 18 mm for Sangiran 2 and 15 mm for Sangiran 4.

With regard to East African hominids, some authors claimed that there is no available data for this character (Stringer 1984, Andrews 1984, Turner and Chamberlain 1989).

It is in fact possible to analyse this feature on at least 10 specimens of East African early *Homo* and *Homo erectus*. These specimens show a great range in distance of up to 25 mm (using Martin's definition for inion and by calculating the difference). At least three individuals (ER-3733, OH-9, ER-1805) exhibit values greater than 18 mm and are thus completely within the range of East Asian *erectus* including the Zhoukoudian values.

Nevertheless, the inion/endinion distance is a quite complex feature. It is the result of interaction between at least two morphologies: the endocranial proportions and the nuchal musculature (Stringer 1984). More adequate approaches are necessary to evaluate the differences and similarities of this complex within and between geographic samples.

Mastoid fissure

This more or less deep fissure between the petrosal crest of the tympanic and the mastoid process occurs in the Zhoukoudian material and in other East Asian specimens. According to Stringer (1984) and Andrews (1984), this feature is found only in the Asian members of *Homo erectus*. Rightmire (1986: 825) also mentions that this trait doesn't seem to be present in Africa.

Our study comes to a different conclusion. The anatomical area concerned was rather well preserved in seven of the East African early *Homo* and *Homo erectus* remains studied. In at least 2 specimens, ER-1813 (ca. 1.9 million years old) and OH 12, the petrosal crest is not fused to the mastoid process (Plate I-6, I-7). Moreover, in OH-24 an individual type of mastoid fissure appears to be present.

It must be emphasized that this fissure varies considerably in medio-lateral shape, size and depth. The shape of the petrosal crest is also quite variable. A well developed fissure is also present on the ER-3884 archaic *Homo sapiens* from East Lake Turkana (Bräuer et al. in press).

Recess between entoglenoid and tympanic plate

The last feature is the recess between the convex entoglenoid process and the tympanic plate, as e.g. present on the left side of the Zhoukoudian Skull III. Interestingly, the morphology is quite different on the right side of the same specimen. These strong intra-individual differences have already been mentioned by Weidenreich (1943: 47).

Whatever this might indicate, this feature is not as controversial as the preceding ones as there is agreement in the current discussion that such a cleft-like morphology not only

occurs among Asian but also in African *erectus* (as e.g. in ER-3883 (Plate I-8). Although a clear assessment is not possible due to the somewhat fragmentary condition of the mandibular fossa, the morphology in ER-1813 does not appear to be much different.

Conclusions

Summarizing these analyses, it is hard for me to see specialized East Asian *erectus* features in these seven characters. Because all of them occur within African *Homo erectus* and some even in early *Homo*, most, if not all of these features, could be regarded as primitive rather than East Asian autapomorphies. This study shows that there is no convincing basis for the hypothesis that East Asian *Homo erectus* was a highly specialized species, a side-branch of human evolution. Moreover, there is clear evidence that most of these features are also present in East Asian archaic *Homo sapiens* (Wu Xinzhi and Wu Maolin 1985).

Even if there were to exist single derived features restricted to East Asian *erectus*, would this justify the conclusion that such a lineage might represent a different human species? I think there is a number of theoretical problems of which I can only mention a few here.

There is no direct relationship between the change of such morphological features and the origin of reproductive isolation or speciation (Tattersall 1986). Features are more likely to change throughout the time of existence of a species (Turner and Chamberlain 1989). Differences in geographic pattern might thus often represent intraspecific variability.

It is quite probable that most of the seven features are related to an increase in bone mass. This would mean that the list of features would have to be reduced. Reversals of evolutionary trends are also likely, as for example a reduction in bone hypertrophy (Hublin 1986). Thus, a thicker cranial vault need not represent a specialized "dead-end" feature.

The cladistic approach is faced by these and many other problems. It nevertheless can be a useful instrument, but only one among others. The analysis of the phylogenetic relevance of the various geographic lineages of *Homo erectus* requires complex approaches. Detailed analyses of the variability of, and comparisons between the seven features discussed here (Bräuer and Mbua, in preparation), and of many other characters, are necessary to attain better understanding of the variability within these hominid samples.

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