直立人及其在人类演化上的位置
——纪念中国科学院古脊椎动物与古人类研究所建所 65 周年

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导　言

在第二次世界大战之前，直立人 (*Homo erectus*) 标本只产自亚洲，即爪哇和中国。后来，在非洲发现了直立人化石。有人把欧洲的最古老的人类化石，诸如出自德国的莫埃尔 (Mauer) 和比尔青斯勒本 (Bilzingsleben)、法国的托塔维尔 (Tautavel) 和希腊的佩特拉洛纳 (Petralona) 的人类化石，认为是直立人的成员。在本文我只分析亚洲和非洲的化石。

历 史 回 顾

荷兰医生和古生物学家杜步哇 (Eugene Dubois)于 1890—1892 年在爪哇特里尼尔 (Trinil)首次找到人猿超科的遗骸，起初他认为这些遗骸是属于黑猩猩，定其名为人猿 (*Anthropopithecus*)。1892 年 8 月，在特里尼尔找到了很直的左股骨，杜步哇推测其与原先的发现同属一个个体并定了种名：人猿属直立种(*Anthropopithecus erectus*)。到 1893 年，他改变了想法，起用了猿人(*Pithecanthropus*)这个名字。这样，猿人属直立种 (*Pithecanthropus erectus*)这个名称在 1893—1894 年开始出现在人类古生物学的出版物上。

1910 年，英国的 A.C.哈登 (A.C.Haddon) 想把这种生物从人科中分出去，定了个独立的科，叫作猿人科 (Pithecanthropidae)；它介于猿科 (Simiidae) 与人科 (Hominidae) 之间。

在中国，裴文中发现的北京人迎来了另一个属名：中国猿人属 (*Sinanthropus*) (Black，1927)。21 年之后，在南非斯瓦特克朗 (Swartkrans) 发现了类似的化石类型，被命名为远人 (*Telanthropus*) (Broom and Robinson，1949)；在阿尔及利亚突尼芬 (Ternifine) 发现的则被称为阿特拉人 (*Atlanthropus*) (Arambourg，1954)。

在古人类学历史上，这是主张"多分"的时代。后来，终于认识到如此众多的属名使得这些早期人类的生物学上的亲缘关系混淆不清起来。一种相反的趋势始于 1939 年魏敦瑞与孔尼华在中国的历史性会见。他们把中国猿人属 (*Sinanthropus*) 合并入猿人属 (*Pithecanthropus*)，在同一属内有两个种，即猿人属直立种 (*P.erectus*) 和猿人属北京种

(*P.pekinensis*).

到了 1950 年，迈耶（Ernst Mayr）提出了所有的直立种和像直立种的类型并不归于不同的属，而是归于人属（*Homo*），都归于人属直立种（*Homo erectus*）名下。不久，罗宾逊（Robinson, 1961）把近人并入人属直立种。在克拉克（Clark）的"人类进化的化石证据"一书的第二版（1964），去掉了"猿人"（*Pithecanthropus*）这个词，代之以"直立人"（*H.erectus*）。1960 年，一个完整的直立人头骨在坦桑尼亚由刘易斯·李基（Louis Leakey, 1961）发现，其直立人样的特征马上被识别出来。

因而，自 60 年代早期以来，承认了人属直立种（*H.erectus*）曾生活在南非、北非和东非的许多地方。特别是在肯尼亚北部的库彼福勒（Koobi Fora）于 1975 年和 1976 年发现了被认为是直立人的早期成员的两具头骨。近来，在特卡纳（Turkana）湖西的纳里奥科托姆（Nariokotome）发现了直立人年青个体的骨架（Leakey and Walker, 1985）。非洲的直立人化石还出自摩洛哥的托马斯采石场（Thomas Quarries）（1969、1972）、埃塞俄比亚的梅尔卡·孔图尔（Melka Kunture）（1973）以及肯尼亚的莱纳穆克（Lainyamok）（1976、1984）等地。

直立人化石的系统地位

自 60 年代以来，大多数古人类学家同意人属直立种是一多型种（polytypic species），其起源可追到更新世之初。这一物种的遗骸至少在亚洲和非洲都有发现。欧洲的最早的人科遗骸是否可被划分到这一物种中去，议论颇多。我本人同意德·卢姆雷（H.de Lumley）等人的主张：某些最早的欧洲人科成员也是直立人成员。

这一概念难被古人类学界认同，因为它受到了两种截然相反的理论的挑战。一种观点认为某些非洲遗骸应从人属直立种（*H.erectus*）改名为新的种名：人属匠人种（*H.ergaster*）（Groves and Mazak, 1975）。这一提议多年无人置理（Meikle and Parker, 1994）。在 90 年代，人属匠人种这一名字复活了，被用来划分库彼福勒的以前被置于人属直立人名下的一些头骨（KNM-ER 3733 和 KNM-ER 3883）（参阅 Wood, 1991、1992）。

因而，第一种挑战就是主张"多分"的挑战。它主张非洲的像直立种的标本中有某些标本而不是全部标本属于匠人种而不属于根据中国和爪哇材料定义的直立种。

对直立人系统地位的第二种挑战就是主张"合并"。这是魏敦瑞的老主张的复活。魏敦瑞认为人属直立种与人属智人种（*H.sapiens*）应是同一个物种。这个物种的名字应是智人种，因为这一种名在 18 世纪时就建立了，而直立种是很晚才命名的（Wolpoff *et al.*, 994）。

总之，关于直立人的地位目前至少有三种相互较量的观点。

一个学派是把人属直立种看作为一个合适的多型种，这个种从大约 1.8 百万年前至 4—0.5 百万年前期间分布到旧大陆的大部分地区（例如，Rightmire, 1990; Kramer, '93）。

第二个学派是严格的分支系统学者，将人属直立种这一几乎是世界范围的种代之以二

个甚至三个不同的种,即人属直立种、人属匠人种以及人属海德堡种
(*H.heidelbergensis*)。

另有一些学者,即第三个学派,有根有据地要把人属直立种并入人属智人种 (例如,
Wolpoff *et al.*, 1994)。

零假设测验

假设亚洲组的由直立人化石标本或像直立人化石标本所代表的人群与非洲组的之间并
无物种上的差别,即假设这两个组属于同一个物种。测验这一假设的一种手段就是检查这
两组的同源性的测量性特征和分析合并样本组的变异性。如果用变异系数 (CV) 来衡量
变异的程度,则我们可以讲:若零假设成立,则合并样本组中的某一测量性特征的 CV 将
不会过份高于单一人群中或单一物种中各有关样本的那个特征的 CV 之变动范围。换言
之,该合并样本的 CV 应低于由已知两个或两个以上有关的种所组成的某一样本的 CV
(参阅 Kramer, 1993)。

我曾提出颅外表的测量性特征不是同源性的特征。在此,我赞同采用颅容量;各对比
标本的颅容量可看作是同源的。

表 1 和表 2 显示出在许多现生的和远古的人猿超科成员的样本中,CV 值都超过 10%
这个值。

现在来看看直立人样本。周口店样本和爪哇样本各自的 CV 值都高于 10%,其上界
几乎达到 13%。如此高的值在其它人猿超科成员中并非异常。中国与爪哇合并组的 CV
值为 12.4%,与南方古猿鲍氏种的、人属能人种的、周口店样本的以及好几个现生人猿
超科成员组的并无多大差别。东非直立人的值高达 15.4%,但与现代人群中的最高值
14.9% 相近,而被尼人样本的值 16.9% 超过。若把北非萨莱 (Sale) 头骨的颅容量值加到
组成东非直立人样本的肯尼亚和坦桑尼亚的 5 个头骨中去,则 CV 值降到 13.6%。如果把
中国、爪哇、坦桑尼亚、肯尼亚以及摩洛哥的直立人标本合并在一起,则得到该合并样本
的例数为 22 例、CV 值为 13.2%。

颅容量的变异性不支持把非洲的像直立人的化石中的某些或全部与亚洲的化石分开而
另成一物种的理论。另外,托拜厄斯 (Tobias, 1971; 1975) 和米勒 (Miller, 1991) 获
得的结果表明,有许多因素会影响 CV 且使化石样本的 CV 的含意混淆不清。这些因素包
括例数太少、样本偏态、两性差异程度的不同、样本的性别组成不同、种内地理性变异、
种内时序性变异乃至颅容量的测量技术等。

因而,用颅容量的 CV 将很难解答第二个问题:在一个合并现代智人与直立人的样本
里,其 CV 值是否会在人猿超科的合理的范围之内抑或非常之高以至可以认为直立人当该
与智人分开而另成一个物种?

赞同人属直立种并入人属智人种

我本人在不久之前曾一直倾向于人属直立种是一个确实无误的多型种这一概念。我并

不信服用分支系统学方法把人属直立种分成多个物种这一作法。我觉得沃尔波夫等 (Wolpoff et al., 1994) 的论证的许多方面是很有说服力的，即人属直立种应并人高度多型的人属智人种中去。长期来我坚信更新世人属进化的标志是脑量增大、语言技巧增强以及文化生活的日趋丰富和文化从属性的日趋深化。脑量、语言和文化这些因素很可能是结合成一个整体，在更新世人属演化中这对多型化有利而并不对物种形成有利。如果我们把这些生物文化演化趋势看作是从人属能人种之后的人属的近裔性状，则在生物文化的和脑量的连续而深入演变的情况下，就很难设想在直立人与智人之间会有物种形成事件。在前述的三种解释中，沃尔波夫等 (Wolpoff et al., 1994) 的解释是最有可能的。

人属直立种并入人属智人种后的分类情况

目前，在人属直立种这一多型种之内可识别出许多地理亚种，开列如下：

人属直立种 (*Homo erectus*)
　　亚种 (Subspecies)：

直立亚种 (*erectus*)	毛里坦亚种 (*mauritanicus*)
古爪哇亚种(*palaeojavanicus*)	匠人亚种 (*ergaster*)
北京亚种 (*pekinensis*)	奥杜威亚种 (*olduvaiensis*)
蓝田亚种 (*lantianensis*)	开普亚种 (*capensis*)
海德堡亚种(*heidelbergensis*)	

如果大家同意把人属直立种并入人属智人种，则人科系统要作一个大的改动。对更新世的人科成员似可采用四名制，例如：

Homo sapiens erectus erectus	*Homo sapiens erectus mauritanicus*
Homo sapiens erectus pekinensis	*Homo sapiens erectus ergaster*
Homo sapiens erectus lantianensis	*Homo sapiens erectus olduvaiensis*
Homo sapiens erectus heidelbergensis	*Homo sapiens erectus capensis*

这样的四名制命名法既罗嗦又繁杂，会被认为是不适宜的。我们或许可简单地称其为直立亚种中国族 (race) 或中国变种 (variety)、直立亚种坦桑尼亚族等等。

对智人亚种作级别上的进一步细分，也将会出现同样的难题。

因为四名制太麻烦，较非正式的解决方法可能会受欢迎。如果把这些分类学上纠缠不清的东西当作论据以反对把人属直立种并入人属智人种，那就错了。若因此而有碍这两物种的合并则不是我的本意。

结　　论

亚洲和非洲的直立人标本颅容量的变异性不支持某些非洲直立人应另成一新种的这一主张。直立人的系统地位仍有两种概念：(1) 直立人是一合适的多型种；(2) 直立人与智

人是同一个物种，应并入智人种。作者从前曾支持第一种概念，但根据新近的古生物学证据和分子证据，现日益向第二种概念靠近。

<div align="right">（张银运　摘译）</div>

THOUGHTS ON *HOMO ERECTUS* AND
ITS PLACE IN HUMAN EVOLUTION

65th Anniversary of the Institute of Vertebrate Paleontology and Paleoanthropology
Academia Sinica, Beijing, China

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AVANT-PROPOS

On its 65th birthday, I bring greeting to the world—renowned I.V.P.P. and its predecessor, the Cenozoic Research Laboratory of the Geological Survey of China, on behalf of the International Association of Human Biologists and of the Palaeo—anthropology Research Unit at the University of the Witwatersrand, Johannesburg, South Africa. Congratulations are due also to the Academia Sinica on the 65th anniversary of the discovery of the first complete calvaria at the famous Peking Man site of Zhoukoudian. There are two more reasons for celebration, as far as I am concerned: first my presence here in Beijing marks the beginning of a close scientific link between the New South Africa and the People's Republic of China, and between two major research organisations: the I.V.P.P. of the Academia Sinica and the Palaeo—anthropology Research Unit of the University of the Witwatersrand. From the sub—tropical zone of the Southern Hemisphere to the sub—tropical zone of the Northern Hemisphere, *Australopithecus* greets Peking Man. On this, my first visit to Beijing, I am happy and excited to meet old and new Chinese friends, to see Zhoukoudian and some of the fossil jewels in your collection. I pause to remember the tragic loss, during the Sino—Japanese War just over 50 years ago, of all the fossil hominid materials recovered during the first 20 years of the existence of this Institute. My Chinese colleagues deserve the highest praise for the remarkable and courageous way in which, twelve years after the suspension of excavation at Zhoukoudian and in the very year of the establishment of the People's Government in Beijing 45 years ago, they resumed work at Zhoukoudian. It was a happy portent that, on the third day, 29th September 1949, the first

tooth was found in the new excavation (Jia Lanpo and Huang Weiwen 1990). This marked the beginnings of a new collection, which has made the I.V.P.P. one of the seven leading world repositories of fossil hominids.

Introduction

Until World War II , specimens of *Homo erectus* had been identified solely from Asia, namely Java and China. In much the same way, accidents of discovery dictated, in the first half of the 20th century, that members of the Australopithecinae were known only from South Africa. In the second half of the century, australopithecine fossils were found in East Africa, namely in Tanzania, then in Kenya and Ethiopia. So it came to be seen that *Australopithecus* was a pan-African genus whose remains extended from southern Africa, up the eastern flank of Africa practically as far north as the Red Sea. Similarly, the pre-war view that pithecanthropine remains(including *Sinanthropus*) were confined to eastern and south-eastern Asia changed when remains attributable to *Homo erectus* came to light in Africa. There discoveries led to the realisation that *Homo erectus* was an Old World phenomenon. Moreoever, some regard the oldest remains from Europe — such as those from Mauer and Bilzingsleben in Germany, Tautavel in France and Petralona in Greece — as members of *H. erectus*. In this analysis, I confine my remarks to the Asian and African fossils.

Historical review

When the Dutch physician and palaeontologist, Eugene Dubois, first found hominoid remains at Trinil in Java between 1890 and 1892, he at first thought they belonged to a chimpanzee, and he named it *Anthropopithecus*. This was De Blainville's(1893) name for the chimpanzee genus. It may seem far-fetched today to speak of a Javanese chimpanzee. Yet only 15 years earlier, Richard Lydekker(1876), of the Geological Survey of India, had claimed he could identify *Anthropopithecus* from the Siwaliks of northern India. Dubois did not under-estimate its importance, even as a chimpanzee, because it would have been the first Javanese chimpanzee and it was more man-like than any of the living anthropoid apes. When the very straight left femur of Trinil was found in August 1892, Dubois assumed it belonged to tne same individual and applied the species name, *Anthropopithecus erectus*. By 1893, he had changed his mind about its systematic status, probably because of its large endocranial capacity, which he estimated at 1000 cm^3. He viewed it as a common ancestor of apes and humans. With a nice historical sense, he resurrected the name *Pithecanthropus*, which Ernst Haeckel had proposed in 1867 to name a creature of his scientific imagination. Haeckel envisaged a hypothetical stage in evolution, which must have bridged the gap between apes and the human family. It was precisely such a creature that Dubois thought he had found. This is testified to by the title of Dubois's 1894 paper, "*Pithecanthropus erectus:* eine Menschenahnliche Ubergangsform aus Java" [a man-like transitional form from Java]. So the name *Pithecanthropus erectus* entered into the published

lore of human palaeontology in 1893—1894.

In 1910, A.C. Haddon of England was inclined to separate this creature from the hominids and he assigned it to a separate family, Pithecanthropidae, between the "Simiidae" and the Hominidae. [As an interesting parallel, 15 years later, R.A. Dart(1925) was to do the same with *Australopithecus*. Unable to reconcile its features with membership of either the Hominidae or the Pongidae, he proposed to place it in a separate family, Homo—simiadae.]

The finding in China of an allied form, Peking Man, by Pei Wenzhong ushered in another generic name, *Sinanthropus* (Black, 1927). Twenty—one years later, from Swartkrans, South Africa, a similar form was named *Telanthropus* (Broom and Robinson, 1949), while from Ternifine in Algeria, *Atlanthropus* was named (Arambourg, 1954).

It was an era of "splitting" in the history of palaeo—anthropology. Later, it came to be realised that the multitude of generic names was obscuring the biological affinities of these early humans. A reverse trend started with the historic meeting in China between Franz Weidenreich and Ralph von Koenigswald in 1939. Their joint article appeared in *Nature* under the title "The relationship between *Pithecanthropus* and *Sinanthropus*" (1939). They concluded that the differences between the two sets of remains were no more than one might find between two races of modern man. Accordingly, they "lumped" the genus *Sinanthropus* into *Pithecanthropus* which had been named earlier. They left two species in the united genus, namely *P. erectus* and *P. pekinensis*.

By 1950 Ernst Mayr could propose that all *erectus* and *erectus*—like forms belonged, not to a separate genus, but to *Homo*, under the specific name *Homo erectus*. This proposal was not immediately adopted. For instance, in the first edition of Clark's book, "*The Fossil Evidence for Human Evolution*" (1955), he used the nomen *Pithecanthropus*. So did Simonetta (1957) in his classification: he, however, "lumped" *Telanthropus* into *Pithecanthropus*. Soon afterwards Robinson (1961) proposed that *Telanthropus* be lumped into *H. erectus*. The second edition of Clark's book (1964) eliminated the term *Pithecanthropus* and replaced it with *H. erectus*.

The first signs of an African *H. erectus* were the remains of "*Telanthropus*" found at Swartkrans in 1949. As noted above, its *erectus* affinities were not recognised at the time. When the hominids of Ternifine in Algeria(1954—1955) and of Sidi Abderrahman in Morocco (1955) were discovered, their close resemblance to Peking Man was recognised. The Algerian finds were made the type of *Atlanthropus mauritanicus* by Arambourg and Hoffstetter (1954), but later that, too, was "lumped" into *H. erectus*. One of the completest crania of *H. erectus* was found in 1960 at Olduvai in Tanzania by Louis Leakey (1961). Its *erectus*—like features were immediately apparent.

Hence, from the early 1960s onwards, it was accepted that *H. erectus* had lived in various parts of South, East and North Africa. Later finds of *H erectus* have come especially from Koobi Fora, northern Kenya. This yielded two crania in 1975 and 1976 which were accepted as early members of *H. erectus*. More recently, the outstanding skeleton of an *H. erectus* youth came from Nariokotome west of Lake Turkana (Leakey and Walker, 1985). Other African finds

of *H. erectus* stemmed from the Thomas Quarries in Morocco (1969, 1972), Melka Kunturé in Ethiopia (1973) and Lainyamok in Kenya (1976, 1984).

The systematic status of the *erectus* group of fossils

From the 1960s onwards, most palaeo–anthropologists were agreed that *H. erectus* was a polytypic species whose origins, it was later shown, went back very nearly to the beginning of the Pleistocene era. The remains of the species were to be found in, at least, Asia and Africa. There was much discussion on whether the earliest hominid remains from Europe were to be classified in the same species. Personally, I was inclined to accept the claims, such as those of H. de Lumley, that some of the earliest European hominids, also, were members of *H. erectus* (Tobias, 1995).

This concept had scarcely been assimilated into the thinking of palaeo–anthropology, when it was challenged by two diametrically opposed theories. One view questioned whether some of the African specimens attributed to *H. erectus* were correctly assigned to that species. Upholders of this view suggested that some of the African remains should be removed from *H. erectus* and placed in a new species *H. ergaster* ("ergaster" is the Greek word for "workman" and refers to stone tools found on the same level as the type specimen)(Groves and Mazak, 1975). The creators of this supposed new species based their original diagnosis and hypodigm mainly on teeth and jaws from Koobi Fora. For a number of years, this proposal was largely ignored (Meikle and Parker, 1994). In the 1990's the name *H. ergaster* was revived (c.f.Wood, 1991, 1992) to classify some crania from Koobi Fora, KNM–ER 3733 and KNM–ER 3883, which had previously been placed in *H. erectus*. So the first challenge was a "splitting" one which suggested that some but not all African *erectus*–like specimens did not belong in *H. erectus* as defined from China and Java, but in a separate species *H. ergaster*.

This challenge has been based essentially on one or other of two lines of thinking. The first states that the combined sample of Asian and early African *erectus*–like fossils shows "an unusually large amount of variation". The same line of thinking ha sought to divide *H. habilis* into two species, *H. habilis* and *H. rudolfensis* (Wood, 1992), and to split *A. africanus* from Sterkfontein Member 4 into *A. africanus* and another species supposedly ancestral to *A. robustus* (Clarke, 1994). It is appropriate to ask whether any of the claimants has shown convincingly that the variability of the respective combined samples is appreciably higher than would be expected if they were members of the same species. The second line of thinking recognises "uniquely derived character states" or autapomorphies for East Asian *H. erectus* which are said to be absent from African *H. erectus* (Andrews, 1984; Stringer, 1984; Wood, 1984). As Bräuer (1994) has pointed out, this has led to the proposal that Asian *H. erectus* is a specialised evolutionary dead–end. Although both lines of thinking have been challenged and strong counter–evidence has been produced (c.f. Turner and Chamberlain, 1989; Rightmire, 1990; Kennedy, 1985; Bräuer and Mbua, 1992; Kramer, 1993; Bräuer, 1994), the view that some African *erectus*–like spec-

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imens should be assigned to another species, *H. ergaster*, is cited in a few text—books and articles.

The second major challenge to the systematic status of H. erectus is a "lumping" proposal. This revives Weidenreich's old suggestion that *H. erectus* and *H. sapiens* should be regarded as conspecific. The name of this species should be *H. sapiens* since that was established in the 18th century, whereas *H. erectus* was named much later (Wolpoff *et al.* 1994). At the Trinil Centenary Meeting at Frankfurt—am—Main, Germany, in 1991, these four scholars declared, "100 years of *Pithecanthropus* is enough!". They propose that a cladogenetic event about 1.8 million years ago separated *H. sapiens* from *H. habilis*. Orthodox cladists hold that two new species must be assumed to arise each time such a cladogenetic split occurred. However, Wolpoff *et al.* (1994) do not accept this tenet of cladistic procedure: they infer that, at the 1.8 Myr event, one new species arose, namely *H. sapiens* (including *H. erectus*), whilst the other branch comprised late—surviving, synchronic *H. habilis*. On their view, Pleistocene humanity has consisted of only a single species, *H. sapiens*, save for the co—existence of late *H. habilis* for the first few hundred thousand years of the Pleistocene.

In sum, at present there are at least three competing views on the status of *H. erectus*.

One school recognises *H. erectus* as a good polytypic species, spread through much of the Old World, spanning the period from about 1.8 to about 0.4—0.5 Myr (e.g. Rightmire, 1990; Kramer, 1993).

Secondly, strict cladists would replace a nearly worldwide species, *H. erectus*, by two or even three different species, namely *H. erectus, H. ergaster* and *H. heidelbergensis*.

Thirdly, other scholars find evidence to subsume *H. erectus* within *H. sapiens* (e.g. Wolpoff *et al.*, 1994).

It is proposed here to test the hypothesis that the Asian and African fossils belong to the same species, by reference to the endocranial capacities.

Testing the null hypothesis

Suppose that the null hypothesis posits that there are not species differences between the populations represented by Asian and African groups of *H. erectus* or *erectus*—like fossil specimens,that is to say, that the two groups belong to the same species. One means of testing this hypothesis would be to examine homologous metrical characters of the two groups and to analyse the variability of the combined sample. For any specific variable trait, it would be reasonable to deduce from the null hypothesis that the combined sample would show a degree of variation for that trait which is not appreciably higher than the variation shown by each one of a series of samples, each of which is known to stem from a single population or a single species. If we use the coefficient of variability (CV) as the measure of the degree of variation, we might say that, if the null hypothesis is true, the CV for a measurable trait in the combined sample which is being tested should not be appreciably higher than the range of CV's for that trait in a series of

related one—population or one—species samples. Alternatively, the CV for the combined sample should be lower than for a sample consciously compounded of data for two or more related species (c.f. Kramer, 1993).

The metrical traits should be "homologous" in the various samples. It is essential that we compare comparable traits. Several studies have used external cranial measurements (e.g. Kramer, 1993; Bräuer, 1994), and have failed to refute the null hypothesis. I have preferred not to include external cranial measurements as homologous, because in the hominids and, especially, in the erectus—like crania, there tends to be great variation in cranial thickness (Kennedy, 1985; Tobias, 1994) and in ectocranial superstructures (c.f. Tobias, 1967). There is also much variation in endocranial capacity. A simple external measure such as maximum cranial breadth may, in amy cranium, be enlarged for any one of three or more possible reasons: the calvarial thickness may be elevated; the endocranial capacity may be great; the cranium may be broader or less dolichocranial; or any two or all three factors may be causally related to increased cranial breadth. Clearly, over a range of hominid crania, cranial breadth would not necessarily be biologically equivalent from specimen to specimen. A fortiori, maximum cranial length may be enlarged if cranial thickness is great, if endocranial capacity is elevated, if the calvaria is more dolichocranial, if the supraorbital torus is well—developed, or if the occipital torus is appreciable, or for any two, three, four, or all five of these reasons. Maximum cranial length may not be homologous from hominid cranium to cranium.

For these reasons, I here favour endocranial capacity which may be regarded as homologous from specimen to specimen. A further reason for the use of endocranial capacity is that, as Miller (1991) has pointed out, the variability of endocranial capacity has been considered by both Wood (1985) and Stringer (1986) to support the hypothesis that more than one species is represented in the hypodigm attributed to *H. habilis*. These authors have used a cut—off point of 10% as the CV value beyond which a sample should be considered to be comprised of members drawn from two species. However, Miller's (1991) analysis has shown convincingly that there is no adequate basis for the acceptance of so arbitrary a cut—off point. His rigorous examination of the CV for endocranial capacity does not support the hypothesis of multiple species in *H. habilis*. In the same way, we here apply the data to test whether the Asian and African specimens of *H. erectus* are so highly variable as to have sampled more than one species.

Table 1 and 2 show that, in a number of samples of living and ancient hominoids, CV's exceed 10%. Of extant hominoids, sample values range higher than 11% in all the species listed except for *Hylobates lar*, *Hylobates agilis* and the bonobo (*P. paniscus*), and higher than 13% in siamang, gorilla and *H. sapiens*. If we compare the values for *H. habilis* (10.9—12.9%) with these data, there is no reason to consider the sample of *H. habilis* exceptionally variable.

Table 2 shows that the values of CV for small samples of fossil hominids are comparable in maximum estimates of CV with those of extant hominoids. For example, as Miller (1991) showed, the value for the pooled sample of *H. habilis* (12.9% in this study, 12.75% in Miller's

study) gives us no reason to consider the sample of *H. habilis* exceptionally variable. The value for the sample of *A. africanus* (5.3% as corrected) is among the smallest of all the hominoid values. On the reasoning of Wood and Stringer, this low value would certainly not support the contention that more than one species has been included in the *A. africanus* sample.

When we turn to the sample of *H. erectus*, we see that the Zhoukoudian and Java samples, considered separately, have CV's that are above 10%, ranging up to nearly 13%: such values are not extraordinary among other hominoid values. The value for the combined Chinese and Javanese samples —12.4%— is little different from values in *A. boisei*, the combined sample of *H. habilis*, Zhoukoudian alone, and several extant hominoid series. The value for *H. erectus* of East Africa is high, namely 15.4%, but it is close to the highest value in the modern human populations reviewed here, namely 14.9%, and is exceeded by one of the Neandertal samples assembled by Miller (1991) with a value of 16.9%. It is exceeded also by the corrected value of ? 20.2% for three crania assigned to *A. afarensis*, but the latter value on so inadequate a sample should be treated with the utmost caution. Thus, even the high value of the chronologically stretched out sample of East African *H. erectus* is not so marked as to deny conspecificity to this sample, by the standards of other hominoids. When the capacity of the North African Salé cranium is added to the five Kenyan and Tanzanian crania that comprise the East African sample of *H. erectus*, the corrected CV drops to 13.6% (n = 6) according to Miller's calculations.

Table 1　CV Endocranial capacity of extant hominoid samples[*]

Sample	Reange of CV values for varied samples	Sample	Reaoge of CV values for varied samples
Hylobates lar	7.51—7.81	*Gorilla gorilla* ♂	7.41—13.30
Hylobates agilis	10.32	*Gorilla gorilla* ♀	7.46—10.34
Symphalangus syndactylus	12.95—13.09	*Pongo pygmaeus* ♂	7.70—11.72
Pan troglodytes ♂	7.94—11.63	*Pongo pygmaeus* ♀	9.31—10.24
Pan troglodytes ♀	8.24— 9.24	*Homo sapiens*	6.1—14.87
Pan paniscus	5.22—10.83		

* Data based on the extensive series of values assembled by Tobias (1971) and on some additional values gleaned from Stringer (1986) and Miller (1991).

Table 2　CV Endocranial capacity of fossil hominids (corrected for small sample size)[*]

Sample	Range of CV values for varied samples (%)	Sample	Range of CV values for varied samples (%)
H. erectus pekinensis of Zhoukoudian	11.3—12.7	*H. habilis*	10.9—12.9
H. erectus erectus of Java	10.1—10.8	*A. afarensis*	?20.2
H. erectus of China + Java	12.4	*A. africanus*	5.3
H. erectus of East Africa	15.4	*A. boisei*	12.0
H. erectus of Africa	13.6	*H. sapiens neanderthalensis*	3.8—16.9 (mean 12.2)
H. erectus of Asia + Africa	13.2—14.7	*H. sapiens soloensis*	7.2—9.1

* The values in the Table are based on data of Holloway (1975, 1980, 1981, 1983), Tobias (1971, 1987, 1991, 1994), Wood (1991) and Miller (1991) and other studies summarised by them. All values have been corrected for small sample size as recommended by Sokal and Braumann (1980) and as applied by Miller (1991).

Thus, we have values for the Asian *H. erectus* of 12.4% (n = 16) and for the African *H. erectus* of 13.6% (n = 6). When we treat them as a combined sample of Chinese, Javanese, Tanzanian, Kenyan and Moroccan *H.erectus* specimens, we obtain a CV of 13.2% for 22 specimens. [This value supersedes my 1987 estimate of 14.5% corrected to 14.7%, for a total of 15 Asian and African specimens of *H. erectus*.] The value for the combined Asian+African *H. erectus* series (13.2%) is slightly less than that for the African series alone (13.6%), and only slightly more than the value for Zhoukoudian alone (12.7%). It is similar to the upper estimate for *H. habilis* (12.9%) and it lies within the ranges of CV's for modern humans and gorillas.

It is concluded that the variability of endocranial capacity provides no support for the theory that some or all African *erectus*—like fossils should be placed in a separate species from that which accommodates the Asian fossils. Moreover, the results obtained by Tobias (1971, 1975) and Miller (1991) show that many factors may influence the CV and may confound the interpretation of CV's for fossil samples. Those factors include small sample sizes, skewed samples, varying degrees of sexual dimorphism, varying sexual composition of the sample, geographic intraspecific variation, temporal intraspecific variation and even techniques for the measurement of endocranial capacity. For example, with small samples, Miller has shown that there are broad confidence limits to estimates of CV's, often so broad that they make CV's useless as measures of relative variability (c.f. Andrews 1978).

It will therefore be extremely difficult for the CV's of endocranial capacity to be used to answer the second question. In a combined sample of modern *H. sapiens* and of *H. erectus*, would values for the CV be within reasonable hominoid limits, or would they be so exaggeratedly high as to support the view that *H. erectus* must be regarded as a separate species from *H. sapiens?* We may be obliged to resort to other approaches to test the hypothesis that *H. erectus* and *H. sapiens* may be accommodated within a single species.

A decision in favour of "lumping" *H. erectus* into *H. sapiens*

Until recently, my personal leanings have been towards the concept that *H. erectus* constituted a distinct, polytypic species. For reasons that I have developed elsewhere (Tobias, 1995), I have remained unconvinced by the mode of use of cladistic methods which leads to multiple species in place of *H. erectus*. I have found many aspects of the argument of Wolpoff et al. (1994) most persuasive, that is, the view that would combine *H. erectus* into a highly polytypic *H. sapiens*. My long—held conviction has been that the evolution of Pleistocene *Homo* was marked by progressive encephalisation (with numerous effects on cranial form), increasing linguistic skills and ever—growing richness of cultural life and intensity of cultural dependence. It is probable that encephalisation, language and culture were the integrating factors that favoured polytypy rather than speciation in the Pleistocene evolution of *Homo*. If we see these biocultural evolutionary tendencies as apomorphous features of *Homo* after *H. habilis*, a speciation event between *erectus* and *sapiens* would be most difficult to conceive, given the continuity and inten-

sity of the biocultural and encephalic trends. When this scenario is added to the lines of evidence assembled by Wolpoff et al. (1994), I am led to conclude that their interpretation is the most probable of the three that have been listed.

Taxonomic consequences of "lumping" *H. erectus* into *H. sapiens*

At present, a number of geographical subspecies are recognised within the polytypic species, *H. erectus*. In Asia, at least four subspecies have been recognised: *H.e. erectus* and *H.e. palaeojavanicus* in Java, and *H.e.pekinensis* and *H.e.lantianensis* in China. In Africa, several subspecies have been recognised: *H.e. mauritanicus* in north—west Africa, and the Olduvai, Koobi Fora and Swartkrans variants. The Swartkrans form was originally designated *Telanthropus capensis* and so the nomen *H.e. capensis* would be appropriate for it. The Olduvai form (OH 9) was the subject of an unauthorised nomenclatural take—over. After L.S.B. Leakey discovered Olduvai hominid 9, and before the person to whom he had allocated it for study and description had completed his examination, G. Heberer was permitted to examine but not to publish on the specimen. He forthwith did publish an account of it (1963) and stated that, if he had been permitted to name the new specimen, he would have called it *"Homo leakeyi"*. As this was a conditional naming, it was not valid, since conditional names are not recognised in the International Code of Zoological Nomenclature. Subsequently Heberer spoke of it in print as *H. erectus leakeyi*, but since the original naming had been invalid, this reassignment of the taxon was equally unacceptable. Tobias proposed to call the subspecies by a geographical nomen, *H. erectus olduvaiensis*. The Koobi Fora crania, jaws and teeth were originally called *H.erectus*, and then, for a few workers, *H. ergaster:* if that proposed taxon is "lumped" back into *H. erectus*, it would be appropriate for it to be designated *H. erectus ergaster*. Those who have accepted the Mauer mandible as representing a subspecies of *H. erectus* have long used the name *H.e.heidelbergensis*.

The subspecies of *H. erectus* may thus be listed as follows:

Homo erectus

Subspecies: *erectus*

palaeo javanicus	*mauritanicus*
pekinensis	*ergaster*
lantianensis	*olduvaiensis*
heidelbergensis	*capensis*

A major revision of hominid systematics would be necessitated if it were generally agreed that *H. erectus* be subsumed within *H. sapiens*. First, the nomen *erectus* would be relegated to tertiary status: for the current hypodigm of *H. erectus* would become members of a subspecies, *Homo sapiens erectus*. How would the present subspecies of *H. erectus* then be designated? Two possible taxonomic devices would be available: as is often done in avian and other systematics, a quadrinomial system might have to be resorted to in respect of the Pleistocene hominids. For

example, we should find ourselves using such terms as:

Homo sapiens erectus erectus　　　　　　*Homo sapiens erectus mauritanicus*

Homo sapiens erectus pekinensis　　　　　*Homo sapiens erectus ergaster*

Homo sapiens erectus lantianensis　　　　*Homo sapiens erectus olduvaiensis*

Homo sapiens erectus heidelbergensis　　　*Homo sapiens erectus capensis*

Such quadrinomial nomina are both unwieldy and inelegant and would probably be deemed unsuitable. We could then simply speak of *Homo sapiens erectus*, north Chinese race or variety, *Homo sapiens erectus*, Tanzanian race, and so on.

The same set of problems would arise in regard to the classification of subdivisions of *Homo sapiens sapiens*.

Since the quadrinomial system is cumbersome, it is probable that the less formal solution would find favour. It would be wrong to regard these taxonomic implications as arguments against the subsumption of *H. erectus* into *H. sapiens*. It is not my intention to raise this as a deterrent to the acceptance of conspecificity. However, it would be as well to face these implications of the proposed change before they are used as counter-arguments to the adoption of conspecificity.

Conclusion

The evidence of the variability of endocranial capacity of Asian and African specimens which have been assigned to *H. erectus* does not support the claim that some African *H. erectus* specimens should be re-assigned to a new, separate species. The two remaining concepts on the systematic status of *H. erectus* are: (1) that it is a good, polytypic species, or (2) that it is conspecific with *H. sapiens* into which it should be subsumed. The author formerly supported (1) but is increasingly drawn to (2), in the light of newer palaeontological and molecular evidence.

Acknowledgments

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