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Continuity and discontinuity in the postcranial remains of *Homo erectus* +

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Abstract

The earliest record of the postcranial remains of *Homo erectus* was provided by Dubois who recovered a femur from Trinil in Java. Dubois believed this Trinil femur was associated with the Trinil calotte now attributed also to *Homo erectus*. Doubts about the attribution of this femur to *Homo erectus* have echoed the findings of anatomists, over many years, who could not distinguish the Trinil femur from that of *Homo sapiens* on anatomical grounds. Weidenreich in 1941 described the Zhoukoudian femora as distinct in their morphology and Olduvai Hominid 28 was shown to share features with these remains. Later work on the Koobi Fora hominids has shown similar results. Pelvic remains of *Homo erectus* are now known from Olduvai, Koobi Fora and Arago.

The new skeleton of *Homo erectus* (WT 15,000) from West Turkana, North Kenya, shows similar femoro-pelvic features but they are less well expressed owing to the juvenility of the specimen.

Key words: Java, Trinil, femur, microanalysis, *Homo erectus*

The history of the discovery of postcranial bones attributed to *Homo erectus* is itself a story of continuity and discontinuity as well as one of controversy. The earliest record of a limb bone attributed to a Middle Pleistocene hominid is the femur from Trinil in Java. This femur was recovered by E. Dubois in 1892 from the sediments of the Solo river close to the find-site of the Trinil calotte (Dubois 1894). The calotte and the femur were attributed to *Pithecanthropus erectus*, later *Homo erectus*, and bipedal gait was claimed for the creature on the grounds of femoral morphology. Indeed this claim was uncontested by anatomists since their assessment of the femur was that it differed little, if at all, from that of *Homo sapiens*. (Manouvrier 1895; Hepburn 1897; Weinert 1928; Weidenreich 1941; Lamy 1984). Doubts about the attribution of the Trinil femur to *Homo erectus* were expressed by Day & Molleson (1973) on anatomical grounds as well as from the viewpoint of dating; we were unable to confirm or deny the Middle Pleistocene antiquity of the Trinil femur.

New investigations of the composition of the Trinil remains were prompted by the remarkable work of Bartstra (1982) who discovered that the Kabuh deposits in Java that contained the Trinil fauna are overlaid by younger Terrace deposits (0.01 m.y. BP). This discovery now provides a plausible explanation for the anatomical confusion that has existed over the Trinil femur since the turn of the century. It seems plain that Dubois did not recognise that the younger Terrace deposits overlaid the Middle Pleistocene layer at Trinil and therefore attributed a *Homo sapiens* femur from the overlying layer to his *Pithecanthropus erectus*. It was this femur that Dubois depended upon for his contention that this *Pithecanthropus erectus* was upright and bipedal, an irony since it seems likely to belong to *Homo sapiens*.

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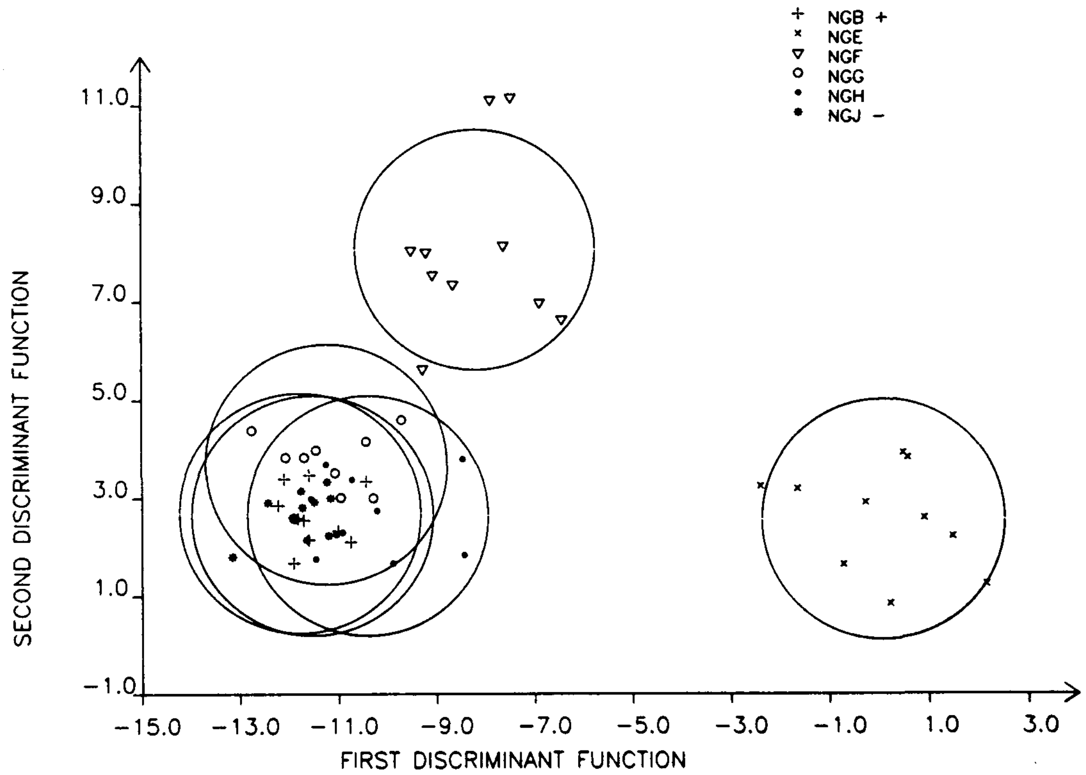

Fig. 1. The elemental content of samples B, E, F, G, H, J taken from the bones recovered from these layers of the High Terrace sediments of the Solo River at Ngandong in Java discriminated by means of canonical variate analysis. Sample E differs markedly from the other samples.

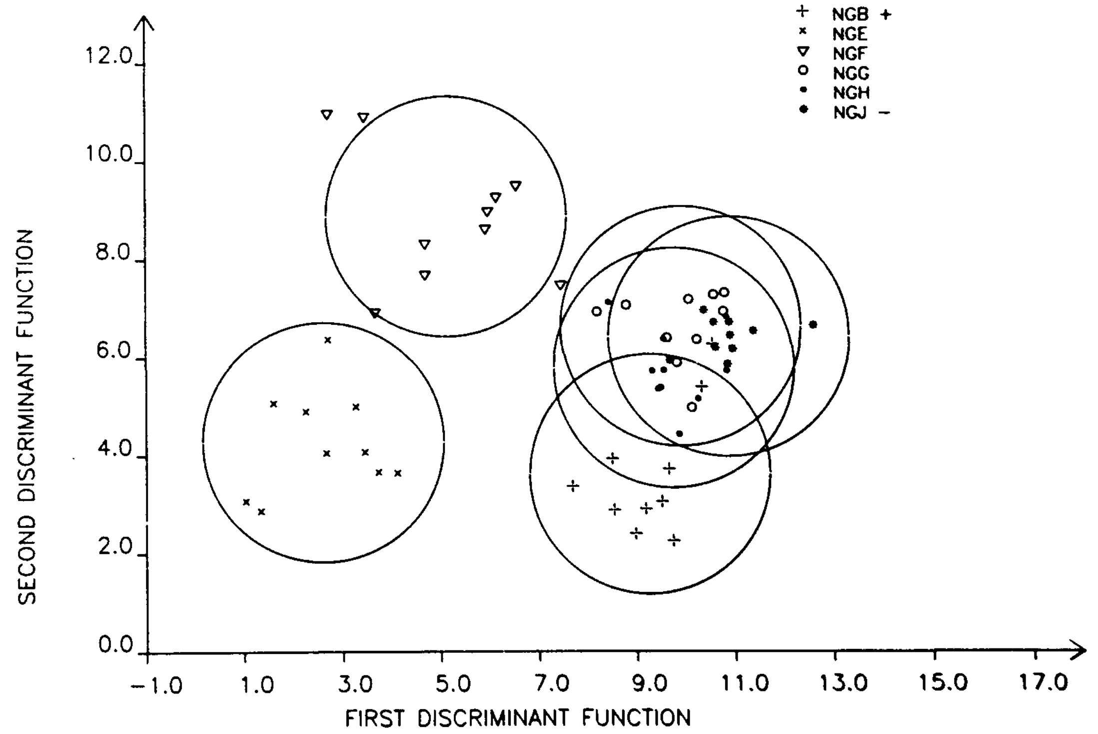

Fig. 2. The elemental content of samples B, E, F, G, H, J discriminated as before but with the removal of Silicon from the discrimination. The effect is to reduce the discrimination between the samples, in particular sample E.

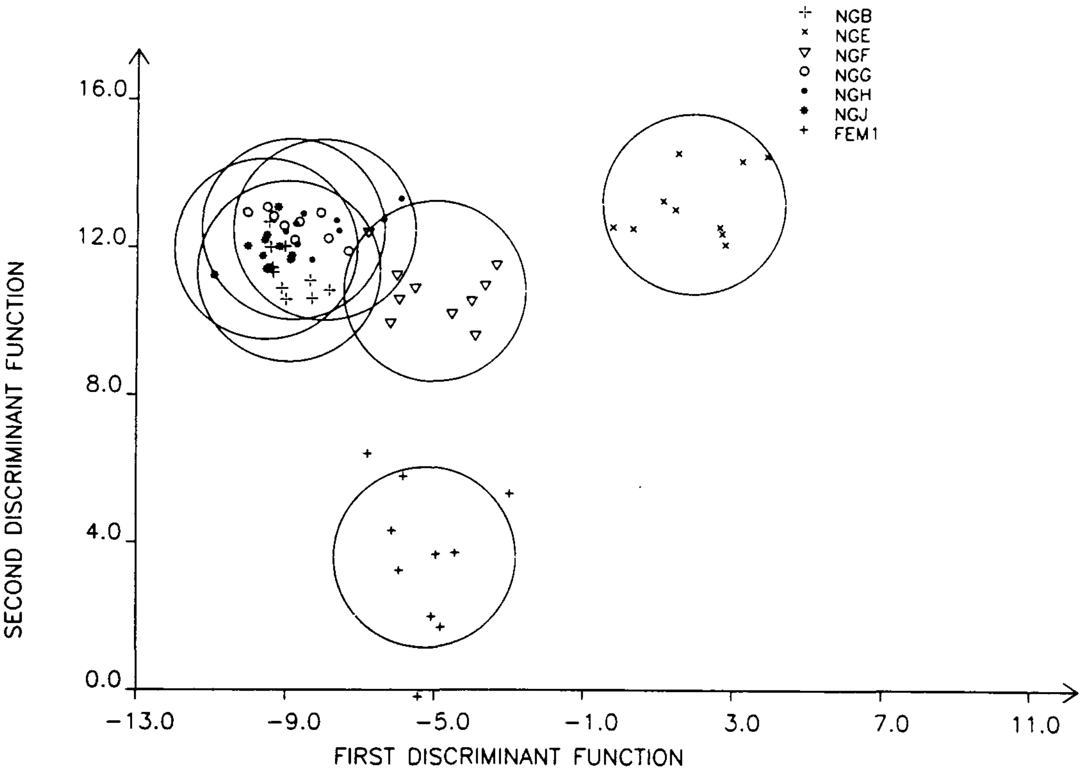

Fig. 3. The elemental content of the samples from the High Terrace sediments compared with that of Trinil Femur I. This shows that Femur I is separated from the Ngandong sample.

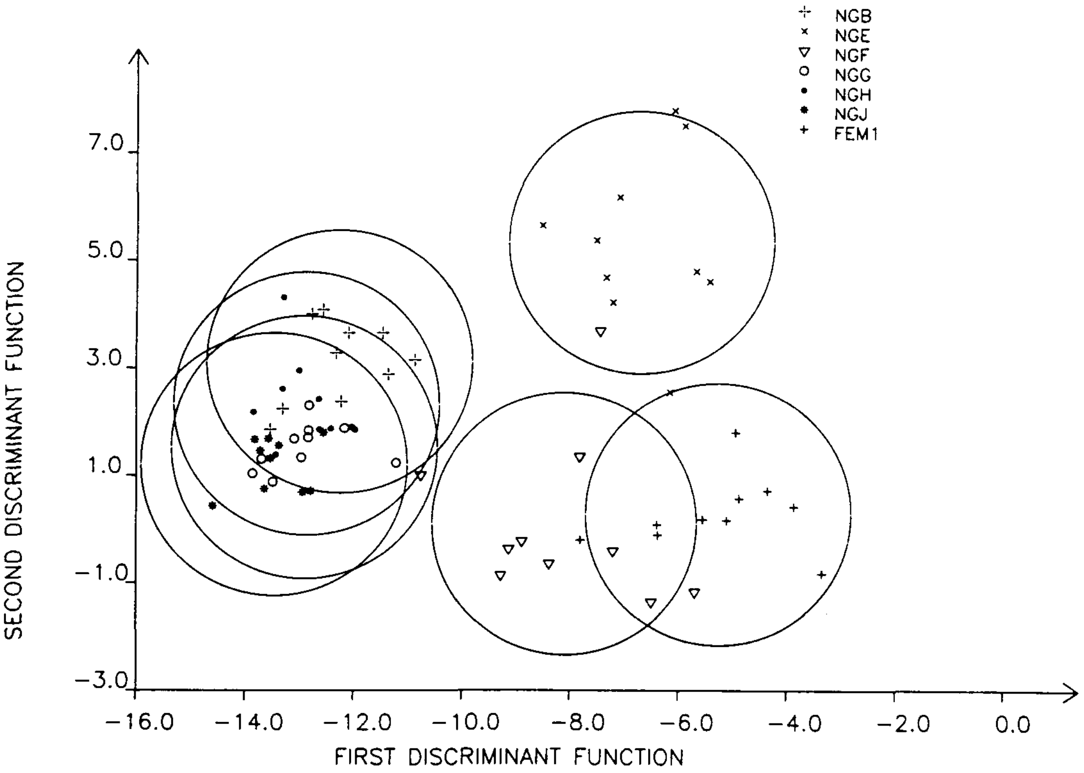

Fig. 4. The same analysis as in Fig. 3 but with the removal of Silicon from the discrimination. This again reduces the discrimination and shows the Trinil Femur I to be similar in composition to the comparative samples from the High Terrace deposits.

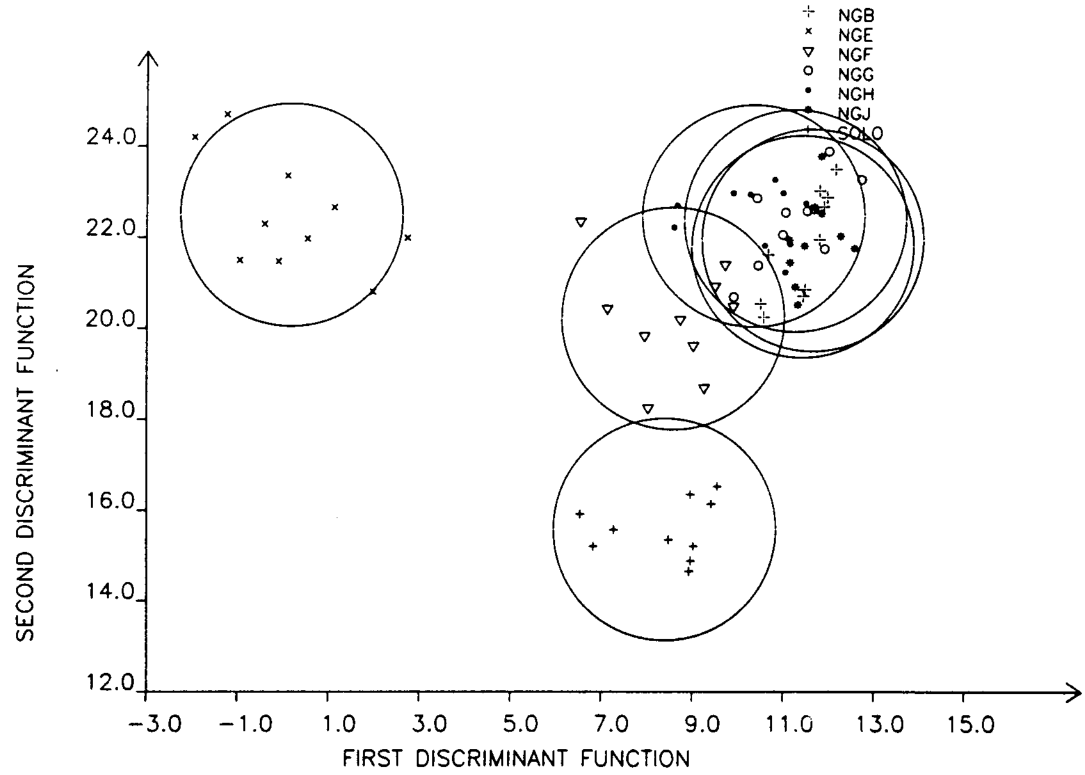

Fig. 5. A comparison of the Ngandong samples with a sample taken from the Solo skulls that are known to come from these deposits shows some discrimination.

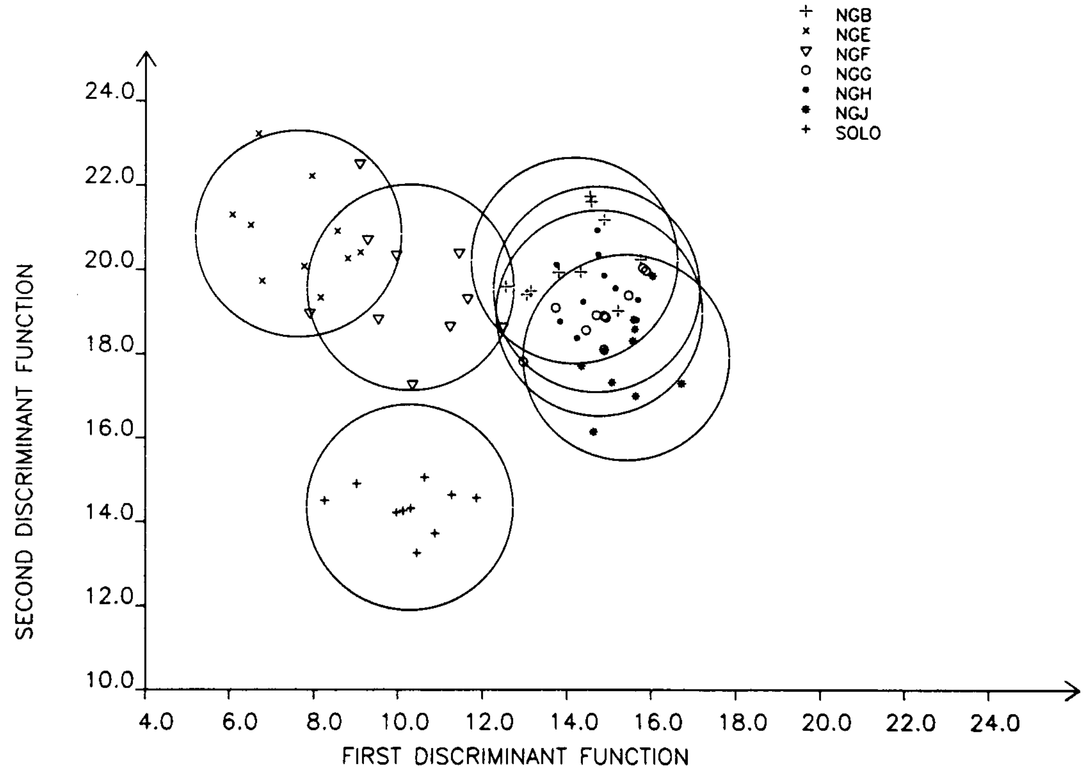

Fig. 6. Removal of Silicon from the analysis reduces the discrimination of sample E but has little effect on the Solo sample that is known to come from this layer.

Javan analytical results

The new stratigraphic evidence coupled with the advent of a new method of analytical investigation, energy dispersive X-ray microanalysis, allowed a reappraisal of the samples taken from the Trinil material. The results of this reappraisal showed that the Trinil Femur I was significantly different in its composition from all of the other material from the site that was examined (Day 1984).

One of the reasons for this could be that the Trinil Femur I had been in the deposits for much less time than the other fossils; in other words it was intrusive into the Kabuh layer from the overlying High Terrace sediments. Samples of bone taken from a series of levels within the High Terrace deposits at Ngandong have been dated by the uranium series disequilibrium technique and dates between 31-101 Kyears have been recorded for specimens taken from layers B C D E F G H (Bartstra et al. 1988). Drillings from specimens from layers B E F G H J have been investigated recently by X-ray microanalysis and the results compared with those obtained for Trinil Femur I and for the Solo skulls by means of multivariate statistical analysis. The Solo skulls are known to derive from the High Terrace sediments at Ngandong.

Initially samples B E F G H and J were analysed and the relative amounts of heavy elements in each sample compared by means of canonical variate analysis (Fig. 1). The results indicate that all of the samples are similar in their elemental make up exept for sample E. The low levels of calcium and phosphorus in the sample raised doubts as to whether it was indeed fossil bone. The level of silicon in the samples (particularly sample E) suggested contamination by sand so the specimen was "cleaned" by removing silicon from the calculations. The effect of this was to reduce the discrimination between the samples, in particular sample E (Fig. 2). The next step was to include Trinil Femur I with the Ngandong High Terrace samples (Fig. 3). This showed Trinil Femur I separated from the Ngandong samples by almost as much as the maverick sample E, but removal of the silicon contamination (Fig. 4) again markedly reduced the discrimination and showed Trinil Femur I to be similar in composition to the comparative samples from the High Terrace deposits. Finally the comparison of the Ngandong samples with a sample from the Solo skulls shows some discrimination (Fig. 5) but removal of the contamination changes the position of sample E but has little effect on Solo (Fig. 6) which is known to come from the High Terrace deposit.

These results obtained in 1986 did not provide conclusive proof that Trinil Femur I is derived from the younger High Terrace deposits now known to overlie the Kabuh at Trinil but the similarity of the composition of Trinil Femur I with samples known to come from the High Terrace deposit (including the Solo skulls) as well as its differences from the other Trinil femora (Day 1984), strengthens the case for the view that Trinil Femur I is intrusive and belongs to *Homo sapiens* from the Upper Pleistocene.

Recently new investigations of the elemental content of the Trinil remains, the Solo IV (Ngandong V) skull, some faunal remains from the Trinil and Jetis Beds of Sangiran, as well as the samples B, E., F, G, H, J & K provide by G.-J. Bartstra, have focussed on calcium to phosphorus ratios. The results confirm the previous findings and suggest most strongly that the Trinil I Femur derives from a more recent stratum above the "fossil layer" (Hauptknochenschicht, HK) in which the Trinil calotte was found. It is concluded that the Trinil Femur I belongs to *Homo sapiens*. A reappraisal of the published stratigraphic information suggests how the confusion may have arisen (Bartsiokas & Day 1993).

Morphological continuity

If it is accepted that the Trinil Femur I does not represent *Homo erectus* then the Zhoukoudian postcranial remains gain importance since they were found in clear association with *Homo erectus* skulls and teeth at the Zhoukoudian site. Their description by Weidenreich (1941) makes clear that the femora have a series of features not matched *as a group* from samples of *Homo sapiens* remains despite the fact that many of the features that Weidenreich described may be found individually in such comparative samples. The recovery of the Olduvai Hominid 28 femur from Bed IV Olduvai Gorge, with the same suite of features as the Zhoukoudian femora, was of great significance since it provided a link between Asia and Africa in terms of femoral morphology and a link with pelvic anatomy since the Olduvai Hominid 28 femur was closely associated in the deposit with a hip bone. The hip bone also was shown to have a unique suite of morphological features including some that are unmatched in any comparative series (Day 1971). Further femoral finds from Koobi Fora (KNM-ER 737, 1472, 1481) (Day 1978; Kennedy 1983), as well as KNM-ER 1808, have confirmed the morphological pattern of this bone while the recovery of KNM-ER 3228 from Koobi Fora has confirmed that pattern of morphology first described for Olduvai Hominid 28 (Rose 1984). The chain of morphological continuity that stretches from China to Tanzania and then to Kenya was to be extended to Europe by the recovery of the Arago remains from southern France including femora (Arago XLVIII, LI, and LII) and a hip bone (Arago XLIV) that show similarities to the patterns previously recognised in the African and Asian material (Day 1982; Sigmon 1982).

The last link in this chain is the "Turkana Boy" (KNM-WT 15,000) from Nariokotome,

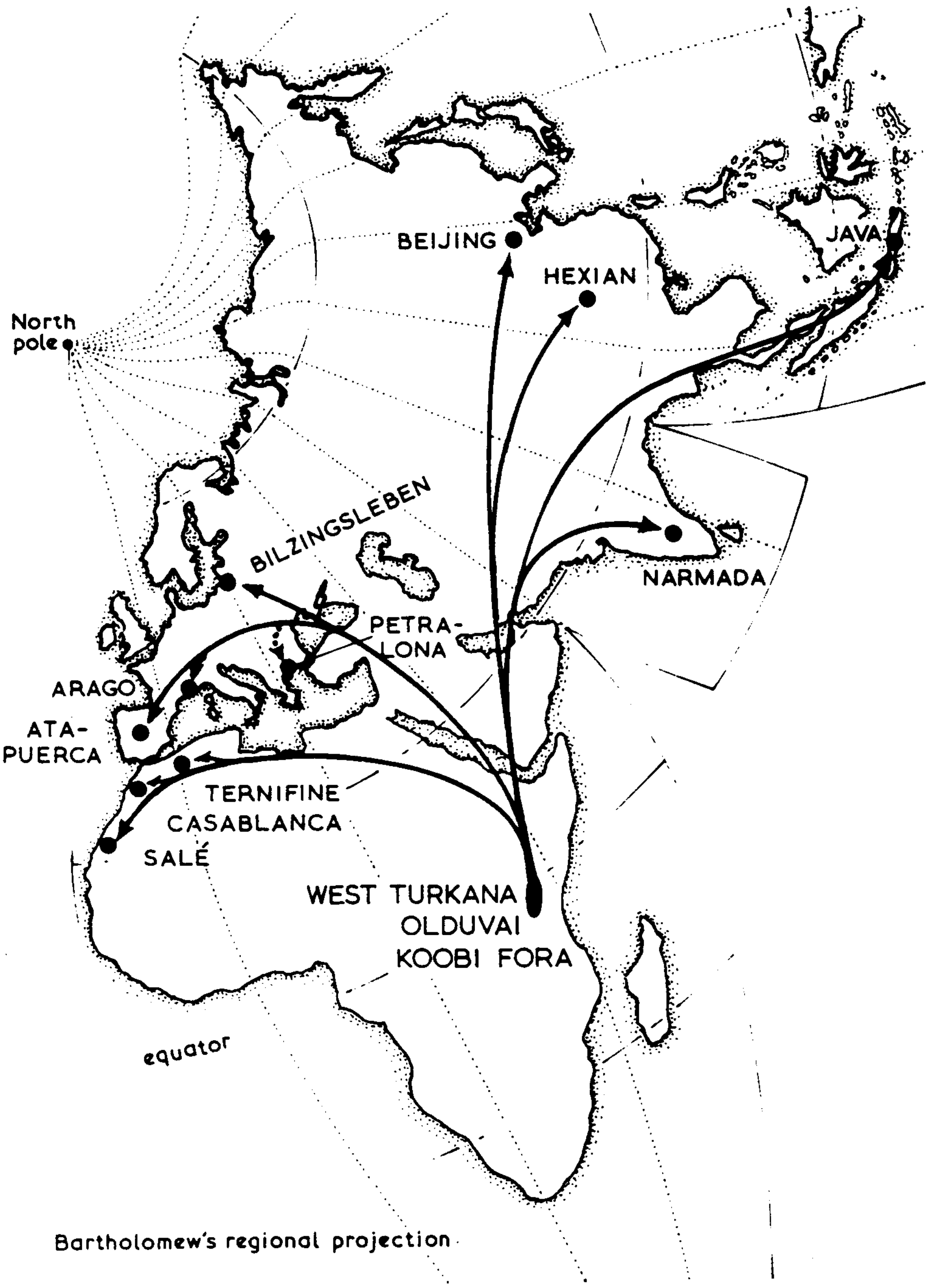

Fig. 7. The possible origin and dispersal of *Homo erectus* within the Old World.

west of Lake Turkana, north Kenya; an almost complete skeleton attributed to *Homo erectus* that has both femora virtually intact as well as an almost complete pelvis. Examination of the femora and pelvis has shown that not all of the features described for *Homo erectus* (Weidenreich 1941; Day 1971) are present perhaps because of the specimen is too immature for the full development of the femoro-pelvic complex. However, the pronounced subtrochanteric platymeria, the narrow medullary cavity, the lack of A/P bowing and the thick shaft have been identified. As Walker & Leakey (1993) suggest , "... others may have appeared had the youth lived to maturity."

Temporal continuity

It seems, therefore, that it is possible to identify a femoro-pelvic complex of anatomical features (Day 1971) that taken together, may be distinctive of *Homo erectus* or at the least typical of a segment of a palaeospecies of that name. It also indicates that a group of hominids appear to have solved some of the problems of bipedal locomotion by the same means resulting in morphological continuity over a long period of time. The oldest of all the specimens mentioned must be KNM-ER 3228 that is derived from the Lower Member of the Koobi Fora Formation, below the KBS Tuff, and is dated at 1.9 m.y. BP. KNM-ER 1808 was recovered from the Upper Member of the Koobi Fora Formation below the Okote Tuff Complex and is dated at 1.8 m.y. BP. KNM-ER 737 is derived from the base of the Koobi Fora Tuff in the Upper Member of the Koobi Fora Formation and is dated at 1.6 m.y. BP. The KNM-WT 15000 specimens was recovered from lake sediments that immediately overlie a tuff identified as a component ash of the Okote Tuff Complex of the Koobi Fora Formation whose date has been given as 1.65 m.y. BP (McDougall et al. 1985). The remains from Trinil in Java are derived from the Kabuh Beds at about 0.5-0.75 m.y. old (Pope & Cronin 1984). The Olduvai Hominid 28 remains derive from Bed IV which is dated at 0.8-0.6 m.y. BP (Hay 1976) and finally the Arago site perhaps dated as early as 0.4 m.y. BP or as late as 0.2 m.y. BP. If the published dates of the material cited above are taken as the best estimates that are available then the morphological complexes associated with the femora and the pelves must have persisted for about 1.5 million years.

Geographical continuity

With a limited number of sites and a small sample of postcranial material it is hazardous to attempt to propose a pattern of spread of *Homo erectus* throughout the Old World, however if the find sites that have produced cranial material are also taken into consideration it may be more profitable.The oldest sites are in East Africa and therefore it seems inescapable that at present this region must be seen as that in which *Homo erectus* first appeared (Fig. 7). Spread from there to other parts of Africa, Europe and Asia as well as India could have occured in the way depicted and at varying rates. In no sense is deliberate migration proposed here, merely the spread of a successful form into areas that were congenial and could support an expanding population. In addition some of the sites shown may not prove eventually to have yielded *Homo erectus* remains since interpretations vary, particularly when finds are limited, and evolution will have taken place during the course of a dispersal that lasted about 1.5 million years.

Evolutionary continuity

Description of *Homo erectus* have been given by many authors who have attempted to define the species using phenetic characters (Weidenreich 1943; Le Gros Clark 1964; Howell 1978; Howells 1980; Day & Stringer 1982, 1991; Rightmire 1984; Stringer 1984). Others have attempted to identify autapomorphic features in relation to the taxon *Homo erectus* but with little success (Wood 1984; Andrews 1984; Hublin 1986; Bilsborough & Wood 1986). The apparent occurrence, in the Asian examples rather than those from Africa, of the few autapomorphic features proposed for *Homo erectus* led to the suggestion that *Homo erectus* is a solely Asian species (Andrews 1984). The weakness of this suggestion stems from the small number and poor quality of the autapomorphies upon which it was based; indeed some of those proposed are dubiously autapomorphic. Further criticism of the proposal that *Homo erectus* is a solely Asian species has been made on the grounds that only characters that relate to the "specific mate recognition system" (SMRS) will necessarily change at speciation and that the autapomorphies suggested for *Homo erectus* do not come into this category (Turner & Chamber lain 1989). A more widely held view sees *Homo erectus* as a palaeospecies that shows evidence of evolution through time from a more primitive ancestor, such as *Homo habilis*, to a more advanced successor such as *Homo sapiens* (Le Gros Clark 1964; Campbell 1972; Wolpoff 1980, 1984; Howells 1981; Day 1984). A viewpoint that may be characterised by a phylogenetic diagram of simple, if not simplistic, type (Fig. 8).

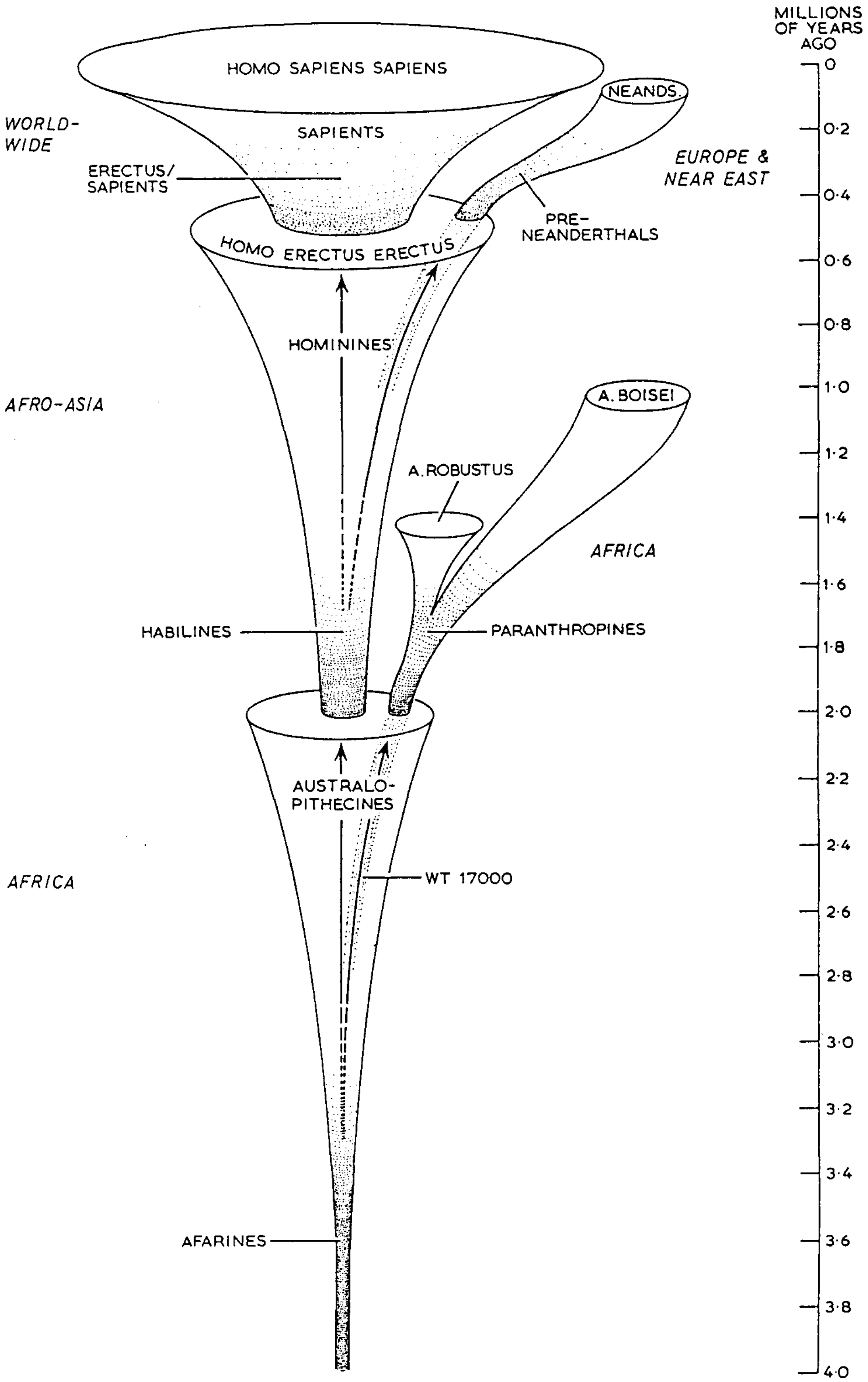

Fig. 8. A phylogenetic representation that indicates the continuity of *Homo erectus* with those from whom he arose and those to whom he gave rise.

Consideration of the postcranial bones attributed to *Homo erectus* discloses that there seems to be a set of features of the anatomy of the femur and the pelvis (the femoro-pelvic complex) that can be identified in examples from Asia, Europe and Africa over a time span of as much as 1.5 million years. This degree of morphological, geographical and temporal continuity demands explanation. Setting aside suggestions such as disease or nutritional disorder there seems to be three main possibilities that must be considered:
(1) That the femoro-pelvic complex is a series of unconnected morphological characters that appear by chance to be a group in the small number of examples that we have from the fossil record.
(2) That the femoro-pelvic complex is a set of characters species-specific to *Homo erectus*.
(3) That the femoro-pelvic complex is a response to the needs of evolving bipedalism in a hominine line that is increasing its body size, its geographical range and the complexity of its behaviour.

Of the three possibilities the third seems to be the most likely to be correct. In terms of continuity and discontinuity it seems that *Homo erectus* shows evolutionary continuity in the postcranial parts that are known and relate to upright posture and bipedal gait.

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