A multivariate examination of the Hexian calvaria

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Abstract The Homo erectus calvaria from Hexian, Anhui province, China is an important component of the fossil sample from East Asia. This specimen is the most complete Chinese H. erectus cranium found outside Zhoukoudian. Previous work has shown that the fossil crania from Zhoukoudian exhibit a unique metric pattern not seen in specimens from Africa or Indonesia. Multivariate statistics that assess the statistical significance of distances have not been used to compare the Hexian cranium to other relevant fossils, and this has hampered our appreciation of the pattern and magnitude of variation in the Chinese fossil record. This study involves the use of Mahalanobis distances to examine the variation present in a large sample of Homo erectus crania. Two separate examinations utilizing up to 7 measurements on 15 crania were performed to maximize the number of available specimens. Random expectation statistics were then used to test for significance between these fossils. Our results highlight clear metric dissimilarities between the Hexian calvaria and the fossils from Zhoukoudian. These metric patterns also separate Hexian from Zhoukoudian V, a skull with which it shares some more modern non-metric features. Our results indicate a greater degree of variation in the human fossil sample from China than has previously been recognized.

Key words: Homo erectus, Zhoukoudian, China, variation, Pleistocene

Introduction

Longtandong cave (31° N, 118° E) was unearthed in 1973 during construction of an irrigation canal. After mammalian fossils were discovered, the Institute of Vertebrate Paleontology and Palaeoanthropology conducted a number of excavations at the site in 1980 and 1981. This work yielded a number of fossilized human remains, including a nearly complete skullcap, additional cranial fragments, a fragmentary left mandibular body with attached M2 and M3, and several isolated teeth (Wu and Dong, 1985; Wu and Poirier, 1995). The most complete specimen, PA 830, is only minimally distorted and retains a nearly complete frontal and left parietal, a slightly damaged right parietal, an almost complete left temporal, a partial right temporal, the upper portion of the greater wing of the left sphenoid, and the occipital squama (Wu and Poirier, 1995). Based on the lack of internal or external sutural obliteration, the specimen is believed to represent a young adult male (Wu, 1985; Etler, 1994; Wu and Poirier, 1995).

The Hexian skullcap has been allocated to Homo erectus by a number of researchers (Wu, 1985; Wu and Dong, 1985; Etler, 1990, 1994, 1996; Etler and Li, 1994; Wu and Poirier, 1995; Brown, 2001) due to the low cranial vault outline, scarcity of the greater wing of the left sphenoid, and the occipital squama (Wu and Poirier, 1995). Based on the lack of internal or external sutural obliteration, the specimen is believed to represent a young adult male (Wu, 1985; Etler, 1994; Wu and Poirier, 1995).

The Hexian skullcap has been allocated to Homo erectus by a number of researchers (Wu, 1985; Wu and Dong, 1985; Etler, 1990, 1994, 1996; Etler and Li, 1994; Wu and Poirier, 1995; Brown, 2001) due to the low cranial vault outline, position of maximum breadth at the supramastoid crests, thick cranial vault bone, coincidence of inion and opisthocranion, and the presence of the cranial buttressing system commonly found in Asian members of this taxon. An early study of the cranium by Huang and colleagues (1982) suggested that Hexian showed similarities to both Chinese and Javan specimens of H. erectus. Dong (1989) felt that the cranial contours of Hexian bore a strong similarity to the Javan material and were quite unlike those of other Chinese fossils. Later studies, however, have often allied Hexian with the collection of specimens from Zhoukoudian (39° N, 115° E). Etler (1990, 1994, 1996) as well as others (Wu, 1985; Wolpoff, 1999) have pointed out a number of similarities between Hexian and the later Skull V specimen from the upper part of Locality 1 (the Lower Cave). These similarities include a number of more modern features not found in the earlier Zhoukoudian sample, however, including the high curvature of the temporal squama, reduced ectocranial buttressing, decreased distance between inion and endinion, a relatively broad frontal bone, and shallower supratoral sulcus (Wu, 1985; Etler and Li, 1994; Etler, 1996; Wolpoff, 1999). In other details, such as its greatly reduced postorbital constriction and the maximum cranial breadth, Hexian appears more advanced than even Zhoukoudian V (Etler, 1994; Etler and Li, 1994; Wolpoff, 1999). The presence of these more progressive features, in conjunction with several dates that suggest a more recent age for both Skull V and Hexian (discussed in Etler, 1990), is viewed by some as evidence for regional continuity in the Chinese fossil record (Wu and Dong, 1985; Etler, 1990, 1994, 1996; Wolpoff, 1999).

Unfortunately, the dating of the Hexian cranium as well as the specimens from Zhoukoudian has been problematic, and
this has muddied attempts to understand the variation present within and between these populations. Grün and colleagues (1997) and others (Huang, 1993, 1995, cited in Grün et al., 1997) correlated layers 3 and 4 at Zhoukoudian to oxygen isotope stages 8 and 9 with an age range of 245–330 ka. Zhoukoudian V was excavated from layer 3 (locus H) (Weidenreich, 1943; Grün et al., 1997). The Hexian skull was initially dated biostratigraphically to the middle Pleistocene (Huang et al., 1982), and the faunal elements were found to be similar to the upper layers at Zhoukoudian at oxygen isotope stage 8, or an age range of 240–280 ka (Xu and You, 1984, cited in Wu, 1985). Uranium series dates at Hexian produced somewhat younger ages, dating animal teeth associated with the human remains to between 150 and 190 ka (Chen and Yuan, 1988). Finally, Grün and colleagues (1998) conducted further U-series and ESR dating on rhinoceros teeth obtained from the same stratigraphic level as the hominin fossils and arrived at a date of 412 ± 25 ka. This most recently reported date would make Hexian contemporaneous with the earlier, more primitive specimens from the lower layers of Zhoukoudian, skulls X, XI, and XII (Grün et al., 1997, 1998). Clearly, this would be irreconcilable with the notion that Hexian and Skull V from Zhoukoudian represented a later population that was more derived and would instead suggest a high degree of temporal and morphological variation in the Chinese assemblage. More recent dates have again reorganized this sequence, however. Shen and colleagues (2001) performed new U-series dates at Zhoukoudian that place Zhoukoudian V at between 400 and 500 ka and the earlier crania at > 600 ka. If confirmed, this new set of dates could make Zhoukoudian V and Hexian geologically contemporaneous and thus potentially representative of a more derived population of H. erectus.

Recent studies have found that the Zhoukoudian crania exhibit a metric pattern that is apparently unique among specimens attributed to H. erectus (Kidder, 1998; Kidder and Durband, 2000; Antón, 2001a, 2002). The posterior and inferior cranial vault in the Zhoukoudian sample is significantly narrower than the vaults found in the African or Indonesian specimens, which share similarly broad posterior cranial vaults (Kidder, 1998; Kidder and Durband, 2000; Antón, 2001a, 2002). These results suggest that the Zhoukoudian crania exhibit a derived metric pattern that is not found in the highly diachronic samples from Africa or Indonesia.

Hexian is the best-preserved cranium of Chinese H. erectus to be found outside of Zhoukoudian, and thus it can provide information on the variation seen in the Far East during the Pleistocene. While a number of researchers have compared the Hexian skullcap to the Zhoukoudian crania using morphological characters or univariate methods (Wu and Dong, 1985; Etler, 1990, 1994, 1996; Etler and Li, 1994; Wu and Poirier, 1995), there have been few attempts to use multivariate statistics to compare these specimens. While univariate comparisons are certainly useful, only limited conclusions can be drawn from them because they are restricted to only one or two cranial measurements at a time. Multivariate statistics allow a more comprehensive examination to be undertaken because they test several measurements simultaneously to examine patterns of variation.

The apparently unique metric pattern seen in the Zhoukoudian sample suggests a level of differentiation from other H. erectus populations that is unmatched in Africa or Indonesia (Kidder and Durband, 2000; Antón 2001a, 2002). On the other hand, the apparent mosaic of more primitive and derived features seen in Hexian, as well as the numerous similarities and differences the specimen has with the Zhoukoudian population, may indicate an evolutionary transition in the direction of modern humans (Wu and Dong, 1985; Etler, 1994, 1996; Wolpoff, 1999). Hexian could potentially join Zhoukoudian Skull V as representatives of a more derived H. erectus population, if we find that it shares the Zhoukoudian metric pattern, or it could help illuminate a pattern of variation in the Chinese fossil record that has yet to be fully explored. Clearly, a multivariate comparison of the Hexian cranium to other H. erectus specimens from China as well as Africa and Indonesia would be of considerable value.

Materials

The cranial sample utilized in this study is shown in Table 1. The comparative fossil sample includes 21 of the most complete hominids commonly described in the literature as H. erectus (Rightmire, 1990; Wu and Poirier, 1995; Antón, 2002). This is an extremely diachronic sample ranging from approximately 1.8 Ma for the older range of the African sample to possibly as recent as 50 ka for the Ngandong material (Swisher et al., 1996, 1997). These specimens were chosen for their completeness in an effort to maximize the number of measurements available for study. The Howells modern human data set, comprised of 2354 individuals representing various modern human populations (Howells, 1973, 1989, 1995), was used to estimate the covariance structure.

For the purposes of this study, Zhoukoudian Skull III is

<table>
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<th>Table 1. Hominid specimens used in this study</th>
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<tr>
<td>Hexian*</td>
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<td>Zhoukoudian III*</td>
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<td>Zhoukoudian V*</td>
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<td>Zhoukoudian X*</td>
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<td>Zhoukoudian XI*</td>
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<td>Zhoukoudian XII*</td>
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<td>OH 9</td>
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<tr>
<td>KNM-ER 3733*</td>
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<tr>
<td>KNM-ER 3883*</td>
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<td>Sangumbangan 1*</td>
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<td>Sangumbangan 3*</td>
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<td>Sangumbangan 4*</td>
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<td>Sangirian 10*</td>
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<tr>
<td>Sangirian 12*</td>
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<td>Sangirian 17*</td>
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* Denotes use in multivariate tests.
considered a young adult specimen. While Black (1929) initially identified this skull as an adolescent, he later modified this diagnosis to that of an early adolescent male approximately equivalent to 12 years of age (Black, 1930). Weidenreich (1943) essentially agreed with Black but gave the specimen a slightly younger age of 8–9 years. Mann (1981) disagrees with these assessments, and instead takes the position that this specimen is a young adult based on the development of muscle markings and the overall size of the cranium. Antón (2001b) concurs, and places Zhoukoudian III at an older adolescent/young adult developmental age. Due to the work of Mann (1981) and Antón (2001b), the decision was made to include Zhoukoudian III in the current analysis. While such a controversial specimen would normally be removed from consideration, the Hexian calvaria is also considered to be that of a young adult. Therefore, the inclusion of Skull III would serve to increase the likelihood of similarities between the Chinese fossils. In addition, these tests may further elucidate the relationships of both of these crania to the rest of the sample. KNM-WT 15000, conversely, was eliminated from this study due to its adolescent status (see Walker and Leuky, 1993). This specimen, unlike the two Chinese fossils, is clearly that of a young adolescent approximately 11 years of age in dental development (Smith, 1993), and was deemed too young for consideration in this sample.

The variables used are shown in Table 2. Due to the extremely fragmentary nature of the fossil material, variables were chosen based on their presence on Hexian as well as their use in the Howells data set. Measurements for the Hexian calvaria were taken from those available in Etler and Li (1994) and these were compared against other published measurement sets for the specimen (i.e. Wu and Dong, 1982; Wu and Poirier, 1995). This comparison did not reveal any inconsistencies in the reported dimensions for Hexian. For the remaining fossils, measurements were conducted on original specimens of the Ngandong fossils and Sangiran 12 and 17 by one of the authors (A.D.). All other data were taken from Weidenreich (1943, 1951), Rightmire (1990), Wu and Poirier (1995), Wolpoff (1999), Delson et al. (2001), and Baba et al. (2003) and checked on available cast specimens when possible.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition</th>
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<tr>
<td>GOL</td>
<td>Maximum cranial length (1, 2)</td>
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<tr>
<td>XCB</td>
<td>Maximum cranial breadth (1, 2)</td>
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<tr>
<td>XFB</td>
<td>Maximum frontal breadth (2)</td>
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<tr>
<td>AUB</td>
<td>Biauricular breadth (1, 2)</td>
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<tr>
<td>ASB</td>
<td>Biasterionic breadth (1, 2)</td>
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<tr>
<td>FRC</td>
<td>Frontal chord (1)</td>
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<tr>
<td>PAC</td>
<td>Parietal chord (1)</td>
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<tr>
<td>OCC</td>
<td>Occipital chord (1)</td>
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Measurements are defined in Howells (1973). Number in parentheses denotes inclusion in a particular multivariate test.

Methods

It is well known that fossil specimens present a number of problems for multivariate statistical analyses. To minimize these, the data set from Howells (1973, 1989, 1995) is used to estimate a within-group covariance matrix. While under ideal circumstances the covariance matrix should reflect variation similar to that of the subjects under examination, this is clearly impossible in the case of fossil crania. The Howells data set is the best alternative currently available, providing a pooled covariance matrix from 28 samples of modern humans.

Mahalanobis distances are computed for the fossil samples after Jantz and Owsley (2001). Two analyses are performed utilizing either five or seven variables. These two tests allow us to maximize either the number of fossil specimens or the number of measurements analyzed. The variables are transformed using the Darroch and Mosimann (1985) shape adjustment technique. While Hawks and colleagues (2000) have recently criticized the use of size adjustment techniques in craniometric studies of this nature, other workers have found ample justification for their use (e.g. Mosimann and James, 1979; Darroch and Mosimann, 1985; Simmons et al., 1991; Corruccini, 1992). When employing this methodology, each variable for each individual (row in the data matrix) is divided by the geometric mean for all variables. This results in a dimensionless shape variable. The practical effect of this technique is to remove isometric size.

Measurements are limited to those quantifying aspects of vault length and breadth. Although the measurements in their raw form may be moderately to highly correlated, the approach used here insures that only the independent information of each variable contributes to the Mahalanobis distance, at least to the extent that the modern covariance matrix applies to the fossil crania. Consequently, the Mahalanobis distances quantify shape variation in sagittal and coronal planes of the vault.

Once the Mahalanobis distances have been calculated, the fossil crania can be compared to one another by the use of random expectation statistics. Through this method, the distance between pairs of individuals randomly selected from a population will be distributed as $\sqrt{(2p - 1)}$ with a variance of 1, where $p$ is one minus the number of dimensions (number of independent variables) (DeFries-Gussenhoven, 1967). This random expectation statistic can be used to determine whether the distance between the fossils exceeds that expected between individuals drawn from a single population in the Howells data set (Jantz and Owsley, 2001). Furthermore, any distance greater than 1.96 standard deviations above the random expectation value reflects statistical significance by a two-tailed test.

Results

Test 1: seven measurements on 11 crania

Table 3 presents the matrix of distances between each of the fossil crania. In this test, the random expectation is 3.316, and any distance exceeding 5.276 can be considered significant. Figure 1 depicts the canonical variate plot
reflecting these differences. The first axis accounts for 54.65% of the variance in this analysis. The separation between the crania is primarily influenced by high positive loadings on maximum frontal breadth and biasterionic breadth and a high negative loading on biauricular breadth. The second axis accounts for a further 26.13% of the variation among the fossils. This separation is driven by a high negative loading on frontal chord and a high positive loading on biasterionic breadth. These analyses, then, primarily separate the crania based on the breadths of the midvault and occipital as well as both length and breadth of the frontal bone.

This analysis indicates a clear separation between the Hexian calvaria and the fossils from Zhoukoudian. In fact, Hexian is significantly different from every other specimen in the analysis with the exception of KNM-ER 3883. The three Zhoukoudian crania group only with themselves, and show statistically significant shape differences from all but two of the African and Indonesian crania. The only exceptions are the distance between Zhoukoudian III and KNM-ER 3883, and the distances between Ngandong 12 and Zhoukoudian III and XI. These scores do not reach the value required for statistical significance.

The African and Indonesian specimens generally show a high degree of shape similarity to one another. None of the Indonesian specimens differed significantly in terms of their shape from another specimen from that region. Within the African sample, the KNM-ER 3883 cranium is significantly separated from only Zhoukoudian XI and XII. The only exception to the overall homogeneity of shape in this group is the KNM-ER 3733 cranium, which is significantly different from every other specimen except for KNM-ER 3883 and Ngandong 12.

Test 2: five measurements on 15 crania
Table 4 shows the matrix of distances from the second test. Here the random expectation is 2.645, and any distance that exceeds 4.605 is considered significant. Figure 2 depicts the canonical variates plot of these data. The first axis accounts for 66.89% of the variance in the second analysis. The separation between the crania is primarily influenced by high negative loadings on biauricular breadth and maximum cranial length and high positive loadings on biasterionic breadth and maximum frontal breadth. The second axis accounts for 15.49% of the variance and is primarily driven by a high negative loading on maximum cranial breadth. Therefore, this analysis tends to group crania that have relatively narrower maximum breadths with broad occipital and frontal dimensions (the African and Indonesian samples and Hexian) versus those that have a broad maximum breadth and narrow occipital and frontal bones (the Zhoukoudian sample).

The results of this analysis generally agree with those obtained from the first trial. Again, we see a significant separation between the fossils from Zhoukoudian and the rest of the sample. Hexian is closer to the African and Indonesian fossils in this test, and is significantly different from the entire Zhoukoudian sample. As in the first test, the Zhoukoudian crania form a cluster that is widely separated from the African and Indonesian specimens, and Hexian groups much more comfortably with the latter assemblage. Of the Zhoukoudian skulls, X and XII were significantly different from every specimen in the African and Indonesian sample, XI was significantly different from all except KNM-ER 3883, and Skulls III and V showed a similar pattern of significant differences to all but Ngandong 12, Sambungmacan 1, and KNM-ER 3883.
As in the first test, the African and Indonesian specimens examined exhibit a high degree of similarity. Only Sangiran 2 showed any significant differences compared to other crania, and this skull was separated from only Sangiran 17 and KNM-ER 3733. In the African sample we find that KNM-ER 3733 does not show as many significant separations from the rest of the sample as it did in the first test, and fails to group with only the aforementioned Sangiran 2 and the five Zhoukoudian crania. KNM-ER 3883, on the other hand, closely followed its pattern from the first test, differing significantly from only two crania, Zhoukoudian X and XII.

The results of the present study closely parallel work previously reported by Kidder (1998) and Kidder and Durband (2000) demonstrating that the Zhoukoudian crania are characterized by broad biauricular and narrow biasterionic measurements. Conversely, the African and Indonesian specimens exhibit broad biauricular and biasterionic measurements. Figure 3 illustrates the two differing patterns seen in the fossil sample. This figure depicts a simple plot of biauricular breadth on the x-axis and biasterionic breadth on the y-axis, and includes all the specimens included in this study as well as some additional specimens that were not utilized in the multivariate tests. Once these specimens were plotted, simple regression lines were obtained for both the Zhoukoudian sample and the combined sample of African and Indonesian specimens, and the location of the Hexian fossil.

### Discussion

These analyses reveal an interesting pattern of variation in the Chinese specimens under consideration. The Hexian calvaria consistently plots away from the Zhoukoudian fossils and shows a cranial shape that is more similar to the African and Indonesian specimens. In addition, Hexian is always sta-
tistically significantly separated from the Zhoukoudian crania. Hexian does not exhibit the Zhoukoudian pattern of a broad midvault and narrow occipital, and instead shows an extremely broad midvault as well as a broad occipital. This study supports earlier work done by Kidder (1998), Kidder and Durband (2000), and Antón (2001a, 2002) that revealed a unique metric pattern in the Zhoukoudian crania. The analyses conducted demonstrate that the Zhoukoudian fossils exhibit a narrowing of the posterior vault in conjunction with a broad midvault, and this combination is not repeated in other H. erectus fossils outside of this sample.

As noted earlier, the Hexian skullcap has suffered some postdepositional deformation to the cranial vault (e.g. Etler and Li, 1994; Brown, 2001). However, the authors are confident that this distortion has not influenced the results of this examination to any appreciable degree. Brown (2001) noted that this deformation is limited to the anterior third of the parietal bones in Hexian. While such deformation could have slightly increased the breadth measurements of the specimen, such minor alterations would not have markedly affected cranial measurements. In addition, our craniometric study has primarily highlighted differences seen between Hexian and the Zhoukoudian specimens in the relative breadths of the occipital and midvault. Based on the published descriptions of the slight deformation suffered by Hexian, it is unlikely that these breadths could have been differentially affected in a way that would negate these findings.

The position of Zhoukoudian III in these examinations is worthy of note. While some workers have deemed it a subadult (Black, 1929, 1930; Weidenreich, 1943), our tests placed it very closely to the other, clearly adult, specimens from this site. These results would seem to indicate that Zhoukoudian III is probably a young adult nearing the completion of growth, following the conclusions of Mann (1981) and Antón (2001b). Its clear separation from Hexian, also identified as a young adult, is significant for the interpretation of these results. If these two specimens were derived from a similar population one would expect greater shape similarity between them due to their comparable age. Our findings do not support this conclusion, and instead suggest significant variation between Hexian and the entire Zhoukoudian sample.

These metric examinations indicate a remarkable degree of stasis in the cranial architecture of the Zhoukoudian hominids. Layer 11, from which Zhoukoudian III was excavated, has been correlated to oxygen isotope stage 14 with an age range of 520–555 ka (Grün et al., 1997) and could be older than 800 ka (Shen et al., 2001). As mentioned earlier, the Zhoukoudian V specimen has been given a much more recent date of 245–330 ka (Grün et al., 1997) though this cranium may be as old as 400–500 ka (Shen et al., 2001). While only one test could be used to compare both of these crania due to the fragmentary condition of Skull V, the two specimens were very similar to one another. In fact, the Mahalanobis distance between Zhoukoudian III and V was shorter than any other inter-Zhoukoudian distance. Thus, it would appear that the metric pattern seen in the Zhoukoudian hominids remained essentially unchanged over a long period of time. This finding is particularly interesting in light of the apparently more modern non-metric features in Zhoukoudian V (Wu, 1985; Etler and Li, 1994; Etler, 1996; Wolpoff, 1999), and requires more detailed study.

These results suggest that the Chinese H. erectus sample is characterized by a greater degree of variation than is currently appreciated, and support similar claims by Etler (1990, 1994) after his own surveys of the Chinese fossil record. In particular, dental variation in the sample is very high, “with some teeth from Yunxian and Hexian far outstripping Zhoukoudian teeth in all metric parameters” (Etler, 1994: p. 109). The differences in cranial architecture found in this study are particularly interesting considering the more progressive features shared by Hexian and Zhoukoudian V. While it would be most parsimonious to assume that the occurrence of more modern features—such as a high, rounded temporal squama, reduced postorbital constriction, and reduced supraboral sulcus on the frontal bone (Etler, 1990, 1994, 1996; Wolpoff, 1999)—in both of these specimens is due to shared ancestry, their clear metric dissimilarity presents a problem with this assumption.

One possible explanation for this variation has been suggested by Etler (1994) after consideration of some fragmentary material from the site of Nanjing (32° N, 119° E). This cave site has produced a fragmentary human cranium as well as numerous fossil fauna representing some 15 different taxa (Etler, 1994). These fauna represent a typical northern Chinese middle Pleistocene assemblage (Mu et al., 1993 as cited in Etler, 1994; Xu et al., 1993) and are similar to that recovered from Zhoukoudian locality 1. This faunal assemblage lacks typical southern Chinese taxa found at Hexian (Etler, 1994). Analysis of the fragmentary human remains from Nanjing suggests similarities with the Zhoukoudian fossils, rather than the much closer Hexian site (Etler, 1994; Antón, 2002). The fossil evidence from this cave site, including the human fossils, potentially depicts “a southern dispersal of Palaearctic elements during a cold, glacial phase or subphase of the middle Quaternary” (Xu et al., 1993 as cited in Etler, 1994). Etler (1994: p. 112a) suggests the possibility that H. erectus from Zhoukoudian represents a “cold-adapted racial variation within the population structure of middle Pleistocene east Asia.” Beals (1972) and Beals et al. (1983) have suggested that climate can influence the shape of the skull, and contend that data shows a trend toward brachycephaly in colder areas. Data collected from H. erectus crania are consistent with this conclusion (Beals et al., 1983). The hypothesis that the Zhoukoudian hominids potentially reflect a more cold-adapted morphology is worthy of future study [though see Antón (2002) for a more extensive discussion of this issue].

The effects of genetic drift might also have influenced the craniometric pattern seen at Zhoukoudian. Because of its position on the eastern periphery of the known range of H. erectus, it is probable that limited opportunities for gene flow would have been available in northern China during the Pleistocene. Thus, a variant skull form could have become fixed in this population. Thorne (1980) has noted that at the peripheries of a population, variation can be marked, particularly if environmental conditions vary widely. It is possible that colder environments at Zhoukoudian may have selected for changes in cranial shape, and this altered craniometric
form could then have become fixed in the population due to a lack of gene flow from outside the region. However, even in the absence of a climatic influence, a combination of founder effect and continued genetic drift due to low levels of gene flow could have led to the distinctive cranial shape seen in Zhoukoudian.

It is likely that a relatively broad occipital is a primitive trait for *H. erectus* (Antón, 2002). This would indicate that the craniometric pattern seen in Hexian is primitive while that found at Zhoukoudian is derived. As stated earlier, many of the non-metric features seen in Hexian are likewise derived from the conditions seen in the African, Indonesian, and most of the Zhoukoudian crania (Wu, 1985; Etler and Li, 1994; Etler, 1996; Wolpoff, 1999), but are shared with Zhoukoudian V. In addition, Hexian is less constricted postorbitally than any other *H. erectus* specimen, including Zhoukoudian V (Etler and Li, 1994). Finally, the extremely broad midvault measurement of Hexian separates that skull from the entirety of the *H. erectus* sample (Etler and Li, 1994), though it should again be noted that this breadth may have been slightly influenced by deformation (Brown, 2001).

From the current data it would appear that some level of homoplasy must be invoked to explain the pattern of morphologies present in the Chinese fossil sample. Hexian may represent a more northern migration of hominids similar to those found on Indonesia. This would be consistent with the evidence presented here on craniometric shape, but would suggest parallel development of the non-metric traits held in common with the Zhoukoudian V skull. Conversely, Hexian may represent a broader dispersal of hominids similar to Zhoukoudian V. This idea is not consistent with our findings on craniometric shape, however, and the exceptionally broad midvault and greatly reduced postorbital constriction seen in Hexian present further difficulties with this hypothesis. These conflicting data make it difficult to understand the potential relationships, if any, shared by these groups of fossils. It is hoped that further study might elucidate additional patterns in these data that might clarify these relationships. At present, however, the metric and non-metric data available for the Chinese fossil sample appear to provide somewhat contradictory results.

**Summary**

Our multivariate analysis of the Chinese *H. erectus* cranium from Hexian demonstrates a metric dissimilarity between that specimen and the Zhoukoudian fossils. While a broad midvault and narrow occipital region characterizes the Zhoukoudian crania, the Hexian specimen features an extremely broad midvault and similarly broad occipital. These metric patterns also separate Hexian from Zhoukoudian V, with whom it shares a number of more modern non-metric features. These results, in conjunction with previous studies by Etler (1990, 1994, 1996), suggest a greater degree of intraspecific variation in the human fossil sample from China than has previously been recognized.

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