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Endocranial Volumes of Early African Hominids, and the Role of the Brain in Human Mosaic Evolution

Volumetric data are presented for 16 of the early hominids from both South and East Africa. Although the sample sizes are small, the statistical data support the conclusion that at least three taxa are represented; *Australopithecus africanus*, *A. robustus*, and *Homo habilis*. These data, plus certain morphological attributes, indicate that the brains of early hominids were reorganized to a human pattern, regardless of their small endocranial capacities. Some speculative suggestions are made regarding the possible relationship between brain and body weights, as well as Stephan's (1972) "progression indices". If the speculations are correct, they provide additional support for the idea that brain reorganization occurred early in human evolution, and that concepts which regard the brain as having a more terminal role in human mosaic evolution are incorrect, as all of the fossil encephalization or "progression indices" are in the range of modern *Homo sapiens*.

1. Introduction

This paper is written in honour and recognition of Prof. R. A. Dart's outstanding contributions to our knowledge of human evolution. It is a pleasure for me to admit that Dart's (1956) paper, "The relation of brain size and brain pattern to human status", has always had a most important role in influencing my own view of the evolution of the human brain, a paper which he cheerfully and kindly sent me when I was a beginning graduate student in Anthropology, working under the late Prof. T. McCown. The idea of reorganization of the brain early in hominid evolution was certainly not an original suggestion of mine, but merely a theme early proposed by G. E. Smith (1924), demonstrated by Dart in his famous *Nature* paper of 1925 for the Taung specimen, and again enunciated in his 1956 article. I have merely elaborated on that theme in my earlier papers (Holloway, 1966, 1967, 1968, 1970).

Through the kind invitation of Prof. P. V. Tobias, I have been able to study all of the endocast remains of the South African australopithecines, a project enthusiastically begun and published earlier by Schepers (1946, 1950). With the kind permission and support of the Leakeys, I have also been able to study the remains of the current East African hominids. In this paper I will report on some results from these recent studies. As the analyses of morphological differences are still underway, I will limit myself to the determinations of endocranial capacities, and attempt to evaluate some of these findings in relation to some current ideas about human mosaic evolution.

2. Materials and Methods

The following fossils have been the subject of my research:

South African—Taung, STS60, STS71, STS19/58, STS5, SK1585, MLD37/38, MLD1.

East African—Olduvai Hominids 5, 7, 9, 12, 13, and 24; East Lake Rudolf specimens 406,732, and the Chesowanja specimen from Baringo district.

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Table 1

Specimen	Region	Taxon	Capacity (cc)	Method	Evaluation
Taung	South Africa	*A. africanus*	440	A	1
STS 60	South Africa	*A. africanus*	428	A	1
STS 71	South Africa	*A. africanus*	428	C	2–3
STS 19/58	South Africa	*A. africanus*	436	B	2
STS 5	South Africa	*A. africanus*	485	A	1
MLD 37/38	South Africa	*A. africanus*	435	D	2
MLD 1	South Africa	?	500 ± 20	B	3
SK 1585	South Africa	*A. robustus*	530	A	1
O. H. 5	East Africa	*A. robustus*	530	A	1
O. H. 7	East Africa	*H. habilis*	687	—	2
O. H. 13	East Africa	*H. habilis*	650	C	2
O. H. 24	East Africa	*H. habilis*	590	A	2
O. H. 9	East Africa	*H. erectus*	1067	A	1
O. H. 12	East Africa	*H. erectus*	727	C	3
E. R. 406	East Africa	*A. robustus*	510 ± 10	D	2
E. R. 732	East Africa	*A. robustus*	500	A	1

These represent only those specimens complete enough for reasonable estimation of volume. While other specimens, such as types 2 and 3 (Schepers, 1946), STS 25, STS 17, are being studied, I am not including them here, since they do not yield volumetric data of the same degree of confidence as the others listed above, and require much further study. Similarly, I am not including the 338-s specimen discovered by Prof. F. C. Howell from the Omo, Ethiopia region, pending his own description of that piece. Table 1 lists these specimens, their major taxon, endocranial capacities, and an evaluative description of the methods employed and confidence in determining these values, which is described below.

It is impossible here to describe in detail the methods used to reconstruct the total endocast volumes for each of the specimens, since each required its own unique treatment. The methods used on the South African fossils, aside from MLD 1, have already been discussed elsewhere (Holloway, 1970*a*,*b*), and SK 1585 has been described extensively in Holloway (1972*a*). Still, some short comments are necessary. In Table 1, Method A refers to direct water displacement of either a full or hemiendocast with minimal plasticine reconstruction. Method B refers to an ascertainment based on the partial endocast method as described by Tobias (1967, 1971). Method C uses extensive plasticine reconstruction involving close to half of the total endocast, and Method D refers to the use of a formula

$$V = f[\tfrac{1}{2}(LWB + LWH)]$$

as described by Mackinnon, Kennedy & Davies (1956), where f is determined from other complete endocasts of the same taxon, or those most closely related. In addition, I have weighted each reconstruction by a crude scale of 1–4 with reference to confidence or surety of the final volume, based on the methods used, and which takes into consideration the amount and condition of the original specimen. Evaluation 1 is the highest or best rank. Admittedly, this is a subjective scale, but in lieu of extensive description, it is better than nothing.

The statistical results were achieved using standard deviations for small samples, by assuming a coefficient of variation, (c.v.) $= \dfrac{\text{S.D.} \times 100}{\text{mean}} = 10\,\%$, and by using the "student"

t-test for significant differences on small, uncorrelated samples (Table 2) (Simpson, Roe & Lewontin, 1960: 176).

Included in this paper are some thoughts on the relationship between brain and body weights, and how these fossils are placed with regard to Stephan & Andy's (1969) determination of "progression indices" within the Primate Order (see also Stephan, 1972).

3. Results

Table 1 gives the resulting cranial capacities for each of the fossils investigated, as determined by either water displacement, partial endocasts, or formula methods, and Table 2 presents the statistical analyses. There has been considerable controversy about the significance of these statistical data, and of course, the small sample sizes make any statements suspect.* Nevertheless, taken in conjunction with all other lines of anatomical data, and the temporal and spatial distribution of the various fossils, I believe three taxa are indicated by these data, aside from Olduvai hominids 9 and 12, which are presumably *Homo erectus* types. It is the explicit opinion of this author that indeed there are three

Table 2

Comparison	t	p	
Gracile vs. robust	2·69	<0·05	>0·02
Gracile vs. *H. habilis*	5·76	<0·001	
Robust vs. *H. habilis*	2·91 n.b.	<0·02	>0·05
Gracile and robust vs. *H. habilis*	5·38	<0·001	

Gracile average ($n = 7$) = 442 cc; robust average ($n = 4$) = 517 cc
Homo habilis average ($n = 4$, incl. O.H. 16 at 650 cc) = 637 cc

Standard deviations obtained from assuming coefficient of variation at 10%, where $\text{c.v.} = \dfrac{\text{s.d.} \times 100}{\text{mean}}$.

All P values from two-sided tables,

$$t = \frac{(x - y)\sqrt{\dfrac{N_1 N_2}{N_1 + N_2}}}{\sqrt{\dfrac{(N_1 - 1)\,\text{s.d.}_x^2 + (N_2 - 1)\,\text{s.d.}_y^2}{N_1 + N_2 - 2}}}.$$

s.d. gracile = 44 cc; s.d. robust = 52 cc; s.d. *H. habilis* = 64 cc.
n.b. with $n = 6$ for both groups, $t = 3{\cdot}56$, $p < 0{\cdot}01 > 0{\cdot}001$

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* I have purposely used larger standard deviations for the "student" t-test than the data at hand give, since the samples are small in number and a bias is built into the methods which utilize data from one endocast to gain data for another (see Holloway, 1970*a*,*b* for further discussion). At the same time, I have used the actual sample sizes. This combination of procedures makes the t-test an extremely rigorous one, as is particularly evident in the small t-value between the gracile and robust australopithecines in Table 2. Increasing the sample size by two or three makes a considerable difference in the possible t-values, as can be seen when $N = 6$ for the robust and habiline groups, instead of $N = 4$. The co-efficient of variation of 10% is about the same as in extant pongids and modern *Homo sapiens*. The formula for t is from Simpson, Roe & Lewontin (1960).

Table 3

Specimen	Capacity (cc)	Body weight (lbs)	"Progression index"
Taung	440	45	19·8 (average for taxon)
STS 60	428	43·5	19·6
STS 71	428	43·5	19·6
STS 19/58	436	44	19·8
STS 5	485	49	20·6
MLD 37/38	435	44	—
MLD 1	500	50·9	19·8
SK 1585	530	54	20·8
O. H. 5	530	54	21·2
O. H. 7	687	69·9	21·2
O. H. 13	650	66·1	23·4
O. H. 24	590	60	22·9
O. H. 9	1067	108	22·1
O. H. 12	727	74	27·6
E. R. 406	510	52	23·9
E. R. 732	500	50·9	20·9
			20·8

$X = cY^b$ and $\log_e X = \log_e c + b \log_e Y$, where $b = 1$, and $c = 0{\cdot}02165$, or $\log_e X = -3{\cdot}83255 + \log_e Y$, where $X =$ brain weight, and $Y =$ body weight.

Basal insectivore line is Stephan (1972) $\log_{10} h = 1{\cdot}632 + 0{\cdot}63 \log_{10} k$

species represented by *Australopithecus africanus*, *Australopithecus robustus* (with two subspecies representing South and East African forms), and *Homo habilis*, exclusive of *Homo erectus*, which might be represented by Olduvai hominids 9 and 12, and by SK 15, 45, 63, 80 & 856e specimens described by Robinson (1956), Tobias (1967) and Clarke, Howell & Brain (1970). No value is given for the Chesowanja specimen from Baringo since I do not believe enough of the specimen is available for any kind of confident reconstruction. However, my measurements on the dimensions of the temporal fossa, and frontal rostrum suggest that the value is very similar to that of either STS 5 or O. H. 5, and I do not see any reason to give it any higher values. These opinions are reinforced by the clear differences in shape among these taxa, for the endocranial casts which have been made so far (see Holloway, 1972*b*, for further comments).

Table 3 presents some hypothetical body-weights for these different hominid forms, derived from the following formula for allometric relationship between brain and body weight: $X = kY^b$, where $X =$ brain weight, and $Y =$ body weight, and where $\log X = \log k + b \log Y$. These formulae derive from the original work of Snell (1891), Dubois (1897) and von Bonin (1937), and have been most thoroughly discussed and criticised by Count (1947). Kinsey (1972) has suggested that the evolution of the hominid brain has followed an allometric growth pattern based on selection for body size, such that the exponent b in the above equations is equal to 1·0. I have arrived independently at a figure which agrees with his, namely that the exponent is probably 1, or very close to it, but by a different method. At the Burg-Wartenstein Conference in 1970, I used Lovejoy & Heiple's (1970) estimate of australopithecine body weight as between 40 and 50 lbs, with my derived mean of 442 cc for new endocast volumes from my 1969 research. I found a brain: body-weight ratio of 1:46, as in modern man. By using this ratio, and a mean weight of 45 pounds, it was possible to estimate the body weights of other gracile australopithecines, and to solve simultaneously for k and b. The result was that the exponent $b = 1$, and this was checked further by using Tobias's (1971) figures for modern man. Using the common exponent value of $b = 0{\cdot}66$, as used by von Bonin (1937), gives some very improbable body weights for both modern man (277 lbs!) and *Homo erectus* from China (177 lbs!). Kinsey (1972) apparently interprets his results as proof of the existence of selection pressures for increased body size during hominid evolution, perhaps related to hunting proficiency. While the body weights generated by the above formula in Table 3 seem very reasonable, it does not prove that this need be the correct interpretation. Of course, without actual body weights, one cannot really check this formula as being the empirical description of hominid evolution in brain and body weights. Furthermore, it cannot tell us about the possible rates of change through time between various hominid lines as posed in my 1972*b* paper. It also ignores any question as to where in the brain the major growth is occurring. Perhaps one could even invert the question and ask if such a relationship might not mean that natural selection favoured an increase in brain size related to post-natal duration of dependence and growth, and that body weight followed along, constrained by the size of the female pelvis, and by genetic strategies which remained incredibly conservative.

Table 3 presents also the "progression indices" for the hominids using Stephan & Andy's (1969) and Stephan's (1972) basal insectivore equation, where the hominid body weight is substituted in the insectivore equation, and the resulting brain weight is divided into the actual brain weight of the hominid. The resulting ratio is the "progression index". This procedure gives very different "indices" for the hominids as compared to those derived by Stephan (1972: 161), all being within the range of modern man! This is to be expected, of course, since the body weights are based on the prior assumption that the coefficient k and exponent b remained constant in hominid evolution. I hope, then, that this exercise will not be accepted without extreme caution and scepticism, and that its presentation might encourage some more needed research into these relationships.

4. Discussion

Before turning to any interpretation of these results, particularly with respect to current ideas about human mosaic evolution, a few comments are necessary. Most obvious, perhaps, is the need for further research on methods of reconstructing final endocranial volumes. The partial endocast method used by Tobias (1967, 1971) and myself, really requires much further testing and repetition. It is very encouraging, I believe, that my results, often based on different methods on the East African hominids, corroborate so closely the estimations given by Tobias (1971). Two trials with the MLD 1 occipital portion, however, did give fairly different results, and perhaps the method is best suited to fairly large pieces, or large percentages of the total volume. Surely, it could be used with confidence for other hominids, such as Swanscombe for example? Secondly, the brain:body-weight relationship shown here needs much further investigation. Our samples are extremely small, and all estimations of early hominid body weights are suspect until much more postcranial material is discovered and much further research is done on the question. The establishment of any relationship, particularly by the log-log method (which is really an engineer's device to get a straight line through a dispersion of points!), can provide only a meagre clue to the selective forces and thus the evolutionary dynamics operating in hominid evolution. In fact, there are not even good, reliable, extensive sampling data on the relationship for healthy, normal brain and body weights in any modern human population, as Tobias (1970) has already shown.

Finally, of course, these results do not tell us anything about other parameters of neural organization, such as possible differences between hominid grades in different masses of cortical tissue, e.g. parietal vs. temporal lobe surface areas, or gyral and sulcal changes in configuration.*

There are, however, at least between these hominids and extant apes, clear differences of gross cerebral morphology which indicate that the early hominids did possess brains reorganized along essentially human lines. For example, the placement of the lunate sulcus in the Taung specimen is clearly where Dart (1925) said it was, and as later corroborated by Schepers (1946) and Le Gros Clark (1947). This can only mean an expansion of the posterior parietal association cortex by the time of the australopithecines. It also appears in the SK 1585 endocast of the robust line (Holloway 1972*a*). The temporal and cerebellar lobes are very human in shape, and distinct from those of any of the apes. There is also an expansion of the third inferior frontal convolution, containing the so-called Broca's area for motor control of the speech apparatus. The problem remains as to how exactly, i.e. quantitatively, to demonstrate these changes unequivocally. These observations are currently being investigated and will be reported at a later date. In sum, the brains of these earliest hominids already show a number of reorganizational changes, as advanced by Dart (1956), regardless of their low cranial capacities. What does this mean for our understanding of mosaic human evolution?

Current concepts of mosaic evolution as applied to human evolution, e.g. Washburn & Avis (1958), Washburn & Howell (1960), Washburn & Shirek (1967), Washburn (1967), relegate a terminal role to the brain in human evolution. This view is based on the obvious fact that the great increase in cranial capacity follows other morphological changes in the hominid fossil record, such as the dentition, locomotor skeleton, and manual anatomy. The exposure of Piltdown Man as a fraudulent, contrived combination of ape jaw and human cranium had led many anthropologists to accept the oversimplified dictum that the brain was the last organ to evolve during human evolution. This unwarranted conclusion then leads to analyses of evolutionary dynamics which ignore the brain as a focus of natural selection for behaviour during the earliest hominid phases.

This paper has argued the converse: that the brain has always had a significant, if not primary, role in human evolution, and that current conceptions of mosaic evolution as applied to hominid evolution are too simplified and thus misleading. In other words, the morphological and archaeological evidence of the australopithecine and habiline remains, if not of the earlier *Ramapithecus* materials, indicates that evolution had already occurred in the brain, since natural selection had been favouring different behavioural patterns from those of apes.†

In the first place, as I have discussed elsewhere (Holloway 1966, 1967, 1968*a*,*b*, 1969), cranial capacity taken alone is an extremely poor indicator of behavioural ability, a fact

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* Some preliminary results from my laboratory on areal surface of various divisions of the cortex and cerebellum do not as yet suggest any significant differences from those already known for extant apes, microcephalics or normal humans [see Holloway (1968) for review of this material].

† Neither Washburn and his students nor I are involved here in a "chicken-egg" controversy, and we surely agree that feedbacks of various kinds have been in operation between the brain and other functional adaptational patterns. I am simply placing more emphasis on the role of the brain than others, since this aspect of early human evolution has certainly been underestimated by most writers on human evolution.

well-known in physical anthropology. Cases of microcephaly [see also Lenneberg (1967) regarding the species-specific activities of the human brain] show conclusively that the *internal* organization of the human brain is responsible for the behavioural specifics not shared by pongids with equal or larger capacites. It is true that we remain ignorant about what these reorganizational changes might be. From a logical viewpoint, as Ashby (1960) has shown, it is possible to alter the internal parts, or quantitative relations between parts in a machine, and alter the total output, without adding "new parts".* Consequently, a single parameter such as cranial capacity is logically exempt as an indicator of behavioural specificity. The possibility is eminent, then, that when a morphological pattern as crude as cranial capacity is associated with other morphological (e.g. a bipedal pelvic and foot structure, a more advanced hand skeleton, a human dentition), and behavioural remains (stone tools made to a standard pattern), it camouflages a different internal organization of neural components and their relationships with the appropriate morphological matrix. This is only a logical extension of such evidence; the direct evidence from hominid brains can never be known.

According to Washburn & Hamberg (1965) (see also Washburn, 1967, and particularly Washburn & Shirek, 1967), behaviour precedes structure in evolution. Obviously, however, for any behavioural change to be evolutionary in significance, it must first rest upon an organic basis, underlain by a genetic change associated with the behaviour; otherwise, evolution is impossible. It is possible that this bias toward behaviour leads the above students into their particular view of the brain evolving last. There is no question that behaviour is extremely important in understanding evolution, but a piece of bone is not simply an isolated piece of matter separated from behaviour. A bone was imbedded in muscle, supplied with blood, and equally important, the functioning composite was supplied with nerves. Thus it was an extension, an integral part of, behaviour. Any item of locomotory action, such as in bipedalism, is behaviour, and must have an underlying neural basis, a controlling set of commands integrated within higher centres, which themselves are related to other behavioural processes such as proprioception, perception, and cognition. Bipedalism, tool-use and making, or hunting cannot be divorced from neural controls simply because cranial capacity is not large, or increased beyond that of other animals with similar behavioural patterns.

Moving from a logical to a more empirical level, the *direct* morphological evidence from the australopithecine and habiline remains indicates an animal with most of the following attributes when compared to any extant ape: (1) increased absolute brain size(habilines); (2) increased relative brain size (australopiths and habilines); (3) a pelvic, foot, and hand structure approaching modern humans. These indicate that selection pressures had been operating on behavioural patterns associated with locomotion and manipulation, resulting in structural changes with their underlying neural bases. The indirect evidence of these fossil remains from both South and East Africa (Robinson, 1956; Leakey, 1966, 1971; Tobias, 1967, 1971) suggests additional advances which must have had a different organic basis from that found in present day apes, although based on the same biological processes: (1) stone tools made to a standardized pattern (the "Oldowan"); (2) an incipient dependence on hunting for procuring protein-rich foods, shown by the faunal associations

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* Ashby (1960) also showed the converse, i.e. that it was possible to keep a constant output even when its components varied their interactions by interacting feedbacks which became self-setting in accordance with an overall programme.

and living sites; (3) a reduction in sexual dimorphism, at least in terms of the upper canines, and possibly the size of the body, which may have included features of epigamic morphology. In the first set of direct evidence, there are clear structural changes involving bone, and thus by anatomical extension, muscles and the nervous organizations supporting their functions. Each of these behavioural sets, such as bipedal walking, toolmaking, etc., must have been interconnected with other behaviours not directly related to the primary anatomical evidence, such as discussed in my 1970 paper, involving attention, hunting, sociality, etc. In the second set of indirect evidence, i.e. those of a more "psychic" behavioural quality, there is a combination of features suggesting a complex integration of *social* behavioural adaptations (e.g. hunting, division of labour, full-time sexual receptivity of the female, less aggressiveness within the group, planning, symbolization), which logically must have been served by different complexes of neural organization. Indeed, these must have been integrated with the first set based on direct evidence.

The latter evidence suggests, as others have pointed out (e.g. Etkin, 1954, 1963), that social behavioural adaptations were favoured by natural selection early in evolution, leading to more co-operative and less aggressive types of social existence than those found in most other terrestrial Primates, utilizing stone tools and hunting, and possibly based on sexual division of labour. These were probably present in the australopithecines, despite the small cranial capacities.

Both direct and indirect evidence mentioned above should lead to the conclusion that it is incorrect to view the brain as only following the rest of the anatomical changes. Instead, I see the social behavioural adaptations and the locomotor and manipulative changes as favoured through natural selection to effect an advance of brain evolution involving *both* its reorganization (Holloway, 1966, 1968*a*) and enlargement. The increasing use of proteins gained through hunting would surely have been adaptive in providing better nourishment for animals with a longer-growing brain. The possible feedback mechanisms between these variables and brain structure have been pointed out by Holloway (1967).

Increased absolute and relative brain size (see for example, Tobias's 1965 and 1971 figures for the australopithecines) must have meant different growth rates, or timing of physiological relations, dependent on endocrine interactions between target tissues and the complex effects of growth, androgen, and thyroid hormones, as well as ecological niche differentiation. Not only could these have affected growth rates of the brain; these would have been associated with increased dependency time of the offspring on the mother, involving more social nourishment and a higher quality of affective ties (Holloway, 1968*b*). The decrease in sexual dimorphism also suggests an endocrine reorganizaton, leading concomitantly to different growth rates and shifts to a more co-operatively-based social condition of the group. We cannot know, of course, whether full sexual receptivity of the female also came into being with this change during the australopithecine phase of human evolution, but such a change is not discordant with the changes suggested above.

The subsequent growth of the brain, from the australopithecines to modern man, was paralleled by an ever-increasing expansion of cultural complexity, reflected not only in the inventory and quality of stone tools, but also in the archaeological contexts, which show increased efficiency of hunting, utilization of more and larger animals, and possibly other cultural adaptations such as shelters, storage, and social structural adaptations. I have used the term "complexity management" (Holloway, 1967) to describe the positive feedback process of this continuing adaptation, and have tried to link the brain growth to features of neural organization such as increased neuron size, dendritic branching and glial/neural ratios, and decreased neural density. These, taken together, might account for much of the increase in cranial capacity, and might indeed be related to the allometric relationship between growth of the brain and body. At the same time, they are better correlated with behavioural efficiency than cranial capacity *per se* (see Holloway, 1966, 1967, and 1968 for details). This framework does not help with the peculiar reorganization changes internally, that led to the more species-specific attributes of human behaviour. The major difference between this framework and that of Washburn and his colleagues (*op. cit.*) is that I am attempting to relate the changes in behavioural complexity to neural parameters more meaningful than cranial capacity, and spell out in more detail the cybernetic processes operating. Another major difference is that I do not see stone tools or tool-making as primary causal factors in this subsequent neural enlargement. Rather, the stone tools are seen as but *clues* to behavioural processes that are more extensive in the adaptive sense than tool-making. In other words, natural selection was favouring social behavioural factors which enhanced co-operative adaptive strategies, particularly in hunting, involving both communication and stone tool-making, since the latter activities imply significant alterations in neural organization and cognitive behaviour.

5. Conclusion

The brain then, was certainly not *the* final adjustment in human mosaic evolution, but an essential component from the beginning. Thus Smith's (1924) and Dart's (1925) earliest conceptualizations are correct. In fact, many of the changes seen in the anatomical patterns must have been attended by changes in neural organization, and these were not necessarily reflected as changes in cranial capacity. Unless the anatomical and behavioural complexes are examined critically and *in depth*, the current use of the concept of mosaic evolution in human adaptation is likely to mask or hide the true complexities of the dynamics of human evolution. The usefulness of this concept exists at the gross descriptive level, and only more molecular levels of analysis will aid us in understanding the interplay of these dynamics.

Finally, the results of the endocranial studies discussed in this paper corroborate other morphological studies suggesting legitimate taxon separation between gracile and robust australopithecines, and *Homo habilis*. This should require us to examine more carefully the possibility of econiche differentiation within a basically savanna grassland environment.*

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* The main differentiating aspect of this differentiation would have been the amount of utilization of protein-rich resources as from scavenging, incipient small-game hunting, to a fuller dependence on large-game hunting.

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