

COMPETITIVE EXCLUSION AMONG LOWER PLEISTOCENE HOMINIDS: THE SINGLE SPECIES HYPOTHESIS

MILFORD H. WOLPOFF

University of Michigan

As early as 1950, Ernst Mayr suggested applying the competitive exclusion principle to early hominid evolution. As a result, the single species hypothesis emerged. Other authors, such as Schwalbe (1899; 1913), Weinert (1951), and Weidenreich (1943), interpreted hominid evolution within the framework of (what we would now describe as) a single evolving polytypic lineage, based purely on morphological considerations. Mayr, however, was the first to give this interpretation a theoretical basis in the synthetic theory.

The single species hypothesis rests on the nature of the primary hominid adaptation: culture (structured learned behaviour). Because of cultural adaptation, all hominid species occupy the same, extremely broad, adaptive niche. For this reason, allopatric hominid species would become sympatric. Thus the competitive exclusion principle can be legitimately applied. The most likely outcome is the continued survival of only one hominid lineage.

The origin of bipedal locomotion

As Mayr originally claimed and as Washburn has often stressed (1951; 1960; 1963), one of the primary hominid morphological adaptations centres about bipedal locomotion. Other distinctive hominid characteristics not related to diet either arise from this adaptation, or form secondary adaptations.

What selective pressures lead to bipedalism? What selective advantages did bipedalism confer on very early hominids? Many answers to these questions have been proposed. For instance, Hewes (1961) suggests food transport across the savanna as the primary adaptive advantage of bipedal locomotion, and L. S. B. Leakey points to the ability to see over tall grass (personal communication). While these suggestions obviously form part of an adaptive explanation, by themselves they simply do not explain the presence of an adaptive advantage strong enough to compensate for the loss of quadrupedal mobility (Washburn 1951: 69; Pfeiffer 1969: 43-53; Oakley 1959: 443); nor do they take sufficient account of the concomitant dangers due to predators in a savanna existence (Bramblett 1967). As Brace (1962: 607) put it: 'It would seem that a weaponless biped trudging over the savanna with a load of ripe meat would be an exceedingly poor bet for survival'.

Thus the use of tools as a means of defence appears to be critical. A dependence upon tools both in offensive and defensive behaviour explains the selective advantage of bipedal locomotion: the hands are freed during locomotion so that a tool or

weapon is available at all times. The question of availability at all times is crucial, for the great apes can both produce and carry tools (Goodall 1964). However, tool use in chimpanzees differs from human tool use in one important respect: chimpanzees do not regularly use their tools as weapons, nor do they depend upon tools as a means of defence (Goodall 1964). Still, the established use of tools by these pongids as part of their normal way of life makes it likely that the ancestors of the earliest hominids were also capable of this behaviour.

Since the ability to make and use tools as a learned and ecologically important type of behaviour is not restricted to hominids, the unique hominid *dependence* upon tools for defence is all the more revealing. Faced with a predator, a hominid who knew how to use a club for defence but did not have one available was just as dead as one to whom the notion never occurred. The advantage of carrying weapons continuously probably provided the greatest impetus to the morphological changes transforming bipedal locomotion from a possibility to an efficient form of movement.

All the relevant australopithecine skeletal material known indicates a completely bipedal stance (Lovejoy *et al.* in press). Of most importance is the presence of a greater sciatic notch in pelvises from Swartkrans, Sterkfontein, Makapansgat and Kromdraai. This brings the action of gluteus maximus posterior to the acetabulum, causing it to act as an extensor. It has been suggested that the femoral attachment for gluteus maximus appears somewhat more lateral than modern man in the Swartkrans and Olduvai femora. However, in the only complete and relatively undistorted australopithecine *os innominatum*, STS 14 from Sterkfontein, the orientation of the acetabulum is also somewhat more lateral than the more anterior-lateral orientation often found in modern man. Articulation of either Swartkrans femur in the Sterkfontein acetabulum shows a *posterior* attachment of gluteus maximus on the femur, when the femur shaft is placed in the plane of the iliac pillar. Thus the 'human' condition is achieved in the total morphological pattern. Actually, the position of this muscle attachment and the lesser trochanter in australopithecine femora is consistent with moderate anteversion (Heiple & Lovejoy 1971). There is no reason to believe the morphology of the (undiscovered) pelvises actually associated with the Swartkrans femora would be any different. In addition, Day (1969) infers a lateral acetabulum for robust australopithecine pelvises from the posterior position of the lesser trochanter of the femur. Moreover, the acetabulum orientation is not outside the range of *Homo sapiens* variation (Lovejoy & Heiple in press).

Other pelvic features indicate erect posture. The acetabulum in both Swartkrans and Sterkfontein specimens is very large, compared with the total size of the pelvis (Schultz 1969*b*). This indicates that the full weight of the upper part of the body passes through the joint. Schultz showed that the australopithecine ratios of acetabulum to pelvis size fall within the human and outside the ape range of variation. All the specimens have an iliopectoral groove. Indeed, all the australopithecine pelvises are similar, except for size, in every feature not obviously altered by post mortem distortion. It is particularly significant that this similarity includes features in which both gracile and robust pelvises differ from what is normal for *Homo sapiens* (although within the range of variation), such as the horizontal orientation and more marked distance between margins of the ischial tuberosity relative to the

position of the acetabulum, the presence of an *anterior* iliac pillar, the more lateral orientation of the acetabulum, and so on.

A number of authors have pointed to details of femoral morphology indicating erect posture in the australopithecines (Le Gros Clark 1947; Strauss 1962; Day 1969; Lovejoy & Heiple 1970). All femora have an obturator externus groove (Day 1969). The heads of australopithecine femora from Swartkrans, Sterkfontein (reconstructed), and East Rudolf are large, relative to the size of the bone.

The Olduvai foot is completely human in form, indicating both effective weight transmission and a striding gait (Day & Napier 1964). The Olduvai talus, the object of a separate study, also shows features suggesting bipedalism as does the talus from Kromdraai (Day & Wood 1968). Even the single terminal phalanx from Olduvai, hominid 10, shows evidence of bipedality (Day & Napier 1966). The Sterkfontein vertebral column suggests the presence of curvature in the lumbar area (Robinson 1956). The low position of the nuchal line in all specimens (Le Gros Clark 1967) indicates a long lever arm for the nuchal musculature, and a vertical orientation of the vertebral column.

Since the living African apes are capable of prolonged bipedal locomotion *without* all these morphological adaptations, the presence of such a total morphological pattern in the australopithecines most likely indicates habitual bipedalism in the same sense that modern man is habitually bipedal, although not necessarily in the same detailed way.

The pre-australopithecine hominids could be described as primates with the morphological and behavioural capabilities of living apes, using these capabilities in order to adapt to a way of life similar to that of baboons. The australopithecines themselves show the morphological consequences of this adaptation. The special fracturing of the battered baboon skeletal material at australopithecine-bearing sites such as Taung and Makapansgat suggests competition between these ecologically similar primate species.

The meaning of reduced canines

According to this hypothesis, the reduced canines found in even the earliest australopithecines indicate a replacement of the canine defensive function (Washburn & Avis 1958: 425) by regularly employing implements as a means of defence, as Darwin suggested a century ago.

In this regard, it is important to establish that both gracile and robust australopithecines have reduced canines. Specifically, the canines of both australopithecine types are not significantly different in size from each other, or from those of *Homo erectus*. Table 1 gives mandibular and maxillary canine area (L*B) data for the three groups. Area is used as a measure of canine size, combining maximum length and breadth. Because maximum breadth occurs at the base, and maximum length is usually not too far above it, only the most extreme wear invalidates area as a size measure. Sources for the *Homo erectus* material are given in another publication (Wolpoff 1970a). The australopithecine data were measured by C. L. Brace in South Africa and at Olduvai. Additional specimens from east Africa were published by Howell (1969), Walker (1971), Coppens (1970), and R. E. F. Leakey (1971). The three Java mandibles were described by Marks (1953) and Tobias &

TABLE I. Canine area averages (mm²).

	\bar{x}	(Range)	CV	N	\bar{x}	(Range)	CV	N
<i>Mandibular</i>								
Australopithecines								
Gracile	87	(73-104)	12	13	93	(73-127)	18	8
Robust	81	(66-96)	11	18	88	(86-111)	14	19
<i>Homo erectus</i>	77	(62-98)	15	16	97	(83-113)	11	10
<i>Homo sapiens</i>	58	(37-81)	15	311	72	(41-120)	15	283
Australian aborigines	71	(64-80)	8	15	90	(58-120)	20	15
New Britain	59	(50-74)	10	44	73	(59-92)	11	43
European	56	(37-77)	17	42	68	(53-98)	16	42
Malay	52	(44-72)	14	12	71	(64-85)	17	3

von Koenigswald (1964). Table I shows an extensive similarity among canine areas. Living groups of man show far greater differences in average areas (Wolpoff 1970a: tables 22 and 27). Extant population averages for mandibular canines range 52 mm² to 71 mm². The corresponding range for maxillary canine averages is from 68 mm² to 90 mm².

A *t* test was used to test for significance of difference, using the data in table I. In the mandible as well as the maxilla, both gracile and robust australopithecines are *not significantly different* from *Homo erectus* even at the 5 per cent. level. In fact, they are not significantly different from each other at the 5 per cent. level! Apparently, australopithecine canines were already reduced to Mid-Pleistocene hominid size.

Australopithecines were small to moderate-sized creatures. The most recent body size estimation for STS 14 (one of the smallest specimens) is 42-43 inches, weighing between 40 and 50 pounds (Lovejoy & Heiple 1970). The Olduvai tibia suggests a height of 56 inches (Coon 1963: 285). No estimates for the robust australopithecines have exceeded 200 pounds, and the small size of the femur heads of SK 82 and 97 (Napier 1964) suggests considerably less for at least some. Others were larger, as a comparison of Swartkrans mandibles shows (Wolpoff 1971b, fig. 1); the size range at this site alone was extensive. A similar size range occurs for postcranial material from East Rudolf (R. E. F. Leakey 1971).

Graciles and robusts overlapped considerably. Robinson indicates that male gracile and female robust australopithecines were approximately equal in robustness and stature (1970: 1219). A small body weight for many of the specimens is suggested by the size of the bones and joint surfaces. All the joints through which the weight of the body passes are very small: often smaller, in fact, than the joints in very small *Homo sapiens* (Broek 1938). The Swartkrans femur heads are as small as those of chimpanzees, although the full weight of the upper body does not usually pass through this joint in chimpanzees. The size of the neck, shaft, and reconstructed head in the Sterkfontein femur is even smaller. The sacral articular area of the Sterkfontein pelvis is considerably smaller than that of a comparably sized bushman pelvis.

There is every indication that early Pleistocene savanna primates of this size range would not lack natural predators, and would thus require a means of defence. The robust australopithecines have been compared to gorillas. Gorilla males,

however, weigh between 300 and 400 pounds (Napier & Napier 1967) and do not live on savanna. The necessity of maintaining an adequate means of defence for a savanna-dwelling lower Pleistocene primate in the australopithecine size range is suggested by the fact that savanna-dwelling baboons of this time period were characterised by large projecting canines coupled with a body size sometimes exceeding that of male gorillas (R. E. F. Leakey 1969; Freedman 1957; von Koenigswald 1969; L. S. B. Leakey & Whitworth 1958).

The evidence for tool use

Chimpanzees have been observed both walking erect and using tools. This indeed is part of their normal repertoire. The common ancestors of pongids and hominids were probably also capable of such behaviour. In view of the complex morphological and neurological prerequisites of primate tool use, and its transmission, and the very different adaptive patterns of the living hominid and pongid species now capable of such activity, it is unlikely that tool use arose in parallel after the lineages separated.

Given this reconstruction of pre-divergence behavioural capability, we must ask why the lineage separation occurred. The single species hypothesis rests on the *assumption* that the *dependence* upon tools as a means of defence allowed the savanna-forest niche divergence to occur, and thus formed the basis for this split. The resulting adaptation allowed effective hominid utilisation of savanna resources: first seeds and roots (Jolly 1970), and later scavenged game (Dart 1957; 1964; M. D. Leakey 1967). Pongids, on the other hand, became better adapted to a forest niche than their dryopithecine ancestors.

What were australopithecine tools like? The earliest dated implements, at this time, come from deposits on the east side of Lake Rudolf (M. D. Leakey 1970b), Kenya. These deposits are associated with a date of at least 2.6 million years (Fitch & Miller 1970). On the other hand, I believe, the earliest direct evidence of hunting activity, as opposed to scavenging or single kill sites (of possibly already incapacitated animals) derives from sites near the top of Bed I in Olduvai Gorge, *at least 1.5 million years later*. If tools were invented by 'killer ape' ancestors as a means for gathering animal protein (Ardrey 1961), archaeology indicates that these early hominids were not very good at it, because most early tools are simple cutting edges and digging implements (L. S. B. Leakey 1960): there are no hunting tools. Such implements could be interpreted as part of a dietary adaptation based on scavenging and gathering roots (unobtainable for baboons). Thus, Jolly's seed-eater hypothesis seems supported. *Homo erectus* is apparently the earliest hominid to show the dental reduction commensurate with significant meat-eating.

Unfortunately, the implements first used for defence were probably simple clubs of wood and bone. Their use is only occasionally, and often indirectly, shown (Dart 1957). To ask which came first, defensive implements or tools for cutting while scavenging and digging while gathering, is a 'chicken and egg' type of question. They are both part of the same adaptive complex: the hominid ecological equivalent of savanna-adapted baboons.

The early dependence on implements as a means of defence allowed an effective savanna adaptation, and consequently led to the differentiation of the hominid

stock, necessitating bipedal locomotion and consequently providing its selective advantage. Culture, in this context, can be viewed as an adaptation to insure the effective transmission of tool use from generation to generation. Selection acted to modify the hominid morphology in the direction of producing a more efficient culture-bearing animal, allowing both the structuring and the transmission of survival-oriented kinds of learned behaviour.

Any bipedal small-canined hominid population should not only have been culture-bearing, but indeed should have been dependent upon culture for its survival. African archaeology offers support for the first part of this contention, for tools have been associated with all the earliest known bipedal hominids. At Olduvai implements are directly associated with both gracile and robust australopithecines on a series of living floors in Bed I (M. D. Leakey 1966; 1967). In the Koobi Fora area of Lake Rudolf, an Oldowan industry and numerous australopithecines derive from the same deposits (M. D. Leakey 1970*b*; R. E. F. Leakey 1970*a*; 1970*b*; 1971). At Makapansgat, australopithecines are found both within and between breccia strata with pebble tools (Dart 1955*b*; 1962*a*; 1962*b*). The well-described industry at Sterkfontein (Robinson 1957; Mason 1962: 472-5) derives from the middle breccia. Recent investigations indicate that STS 5 also comes from this breccia (Tobias & Hughes 1969). In fact it has been suggested that all Sterkfontein australopithecines come from the middle breccia (Tobias & Hughes 1969: 164) rather than from the lower breccia as originally claimed. An industry characterised as Acheulean derives from the deposit which yielded the Natron mandible (Isaac 1965; 1967). Definite stone tools occur at Swartkrans (Brain 1958; 1967; 1970; M. D. Leakey 1970*a*), and at least one convincing artefact came from Kromdraai (Brain 1958). Indeed, some of the australopithecine industries are surprisingly advanced. In addition to Natron, the Sterkfontein assemblage has been called early Acheulean (Mason 1962: 472-5), and the Swartkrans collection likened to Olduvai Bed II sites such as BK II (M. D. Leakey 1970*a*).

In numerous cases the evidence directly associates *both* gracile and robust australopithecines with the use and manufacture of stone tools. More often than not, most of these seem associated with scavenging activity. Australopithecine scavenging has been adequately demonstrated from the body part distribution at both Makapansgat (Dart 1957) and Olduvai Bed I (M. D. Leakey 1967).

Culture and competitive exclusion

Man has adapted *culturally* to the physical environment, and has adapted *morphologically* to effectively bearing culture. Thus culture, rather than any particular morphological configuration, is man's primary means of adaptation. His morphological evolution has been consistently directed by selection for a more effective culture-bearing creature. Culture plays the dual role of man's primary means of adaptation, as well as the niche to which man has morphologically adapted. In this sense, all hominids occupy the same adaptive niche.

The fact that culture is an integral part of man's adaptive pattern suggests that cultural evidence is as important as osteological evidence in reconstructing hominid evolutionary history.

Although culture may have arisen as a defensive survival mechanism, once present, it opened up a whole new range of environmental resources. Culture acts to

multiply, rather than to restrict, the number of usable environmental resources. Because of this hominid adaptive characteristic implemented by culture it is unlikely that different hominid species could have been maintained. Mayr (1950) originally applied Gauss's principle (1934) of competitive exclusion to the understanding of hominid evolution. As he interprets the principle:

the logical consequence of competition is that the potential coexistence of two ecologically similar species allows three alternatives: (1) the two species are sufficiently similar in their needs and their ability to fulfil these needs so that one of the two species becomes extinct, either (a) because it is 'competitively inferior' or has a smaller capacity to increase or (b) because it has an initial numerical disadvantage; (2) there is a sufficiently large zone of ecological nonoverlap (area of reduced or absent competition) to permit the two species to coexist indefinitely (1950: 68).

There are two conditions that must be met for closely related species to coexist sympatrically: (1) they must be able to tolerate the hazards occurring in the area of overlap; (2) they must differ from each other in such a manner that they do not enter into a 'struggle for existence' in which one succeeds at the expense of the other.

In culture-bearing hominids, it is particularly difficult to meet these conditions. For the separation of two species, a fortuitous isolation of part of the parent species must occur over sufficient time for genetic isolating mechanisms to become established. If this separation were to have occurred before the hominid differentiation, then culture presumably arose independently in each lineage, as shown by both the archaeological evidence and by the same morphological evidence for bipedalism found in both gracile and robust australopithecines. On the other hand, a separation after the hominid differentiation is questionable for exactly the same reasons that sympatry itself is questionable (Mayr 1963: 66).

Even if two separate hominid lineages could have arisen, how could they have been maintained for an appreciable length of time? One of the advantages afforded by culture is the great ecological diversity in the utilisation of a broad ecological base which it allows. In consequence, hominids tend to spread over a broad range, occupying areas where only *some* resources are available at a given time. That is, hominids can utilise more resources than are ever available at one place. Thus, the australopithecines spread over the Old World tropics and semi-tropics from South Africa to Java, occupying a large variety of climatic habitats and living sites. Synchronic culture-bearing hominid species could not help but become sympatric (Cain 1953) in a number of different areas. Related species are more likely to be found in similar habitats than are unrelated ones (Williams 1947; Bagenal 1959). The sympatric hominid species would then be in competition for *different* resources in *different* areas of overlap. For the total range of each species, the overlapping resource base would necessarily be extensive.

With competition occurring in different areas for different resources between species each able to utilise a broad ecological base, subsequent adaptation *could not reduce competition*. New adaptations would have to be learned. Rather than narrowing the range of utilised environmental resources for each species, such further adaptation would probably broaden this range by increasing the capacity to learn how to utilise additional resources, and thus *increase* the amount of real competition for the whole species. That is, competition would most likely cause each hominid

species to develop the ability to utilise a wider range of resources and thus increase the amount of competition. One surely must succeed at the expense of the other.

Application to the Lower Pleistocene

Most authors now apply the results of competitive exclusion in interpreting Mid-Pleistocene and more recent hominids, recognising only one synchronic hominid species. The single species hypothesis is primarily applied here to hominid origins, predicting the valid application of competitive exclusion in interpreting earlier hominid remains.

There are excellent reasons to believe that culture played a crucial role in australopithecine survival, in and apart from the logic dictated by the single species hypothesis. Mann (1968), for instance, has been able to demonstrate that the rate of australopithecine development and maturation was delayed, as in modern man, rather than accelerated as in modern chimpanzees. Based on molar eruption timing, Mann showed that australopithecine children took as long to mature as do our own. If selection for increased learning capacity, associated with cultural behaviour, resulted in delayed maturation in Lower Pleistocene hominids, it must have been operative *before* the Pleistocene.

Similarly, McKinley (1971) demonstrated that australopithecines (graciles and robusts) followed a 'human' model of short birth spacing. In baboons, gorillas and chimpanzees, successive births are spaced apart by the length of child dependency. Thus in slow maturing chimpanzees, he calculated an average birth interval of 4.6 years from data given in Goodall (1967), the only available source. In man the maturation timing is about half as fast, so the corresponding period of child dependency is close to eight years. Human births, however, are not spaced by this period, but rather can be as close together as one to two years. This seems primarily due to the influence of complex social factors on the effect of child dependency. The result is highly adaptive to rapid population expansion. Australopithecines follow the human model of delayed maturation timing. The corresponding birth spacing, following the chimpanzee model but based on the delayed maturation rate, is close to eight years. However, the average time between births calculated by McKinley (1971), three to four years in the robusts and four to five years in the graciles, is less. Social behaviour, far more complex than that evinced by baboons, acted to *shorten* the effects of child dependence in australopithecines, although Mann's work shows that this period of dependence was *longer* for them than it is in modern pongids. In both cases, the evidence clearly indicates extensive australopithecine adaptation to social-cultural behaviour. This suggests that such behaviour was adaptively important prior to the Lower Pleistocene.

Is the conclusion that gracile and robust australopithecines are members of the same hominid lineage really so unlikely? Authors other than myself have demonstrated greater differences among groups of anatomically modern *Homo sapiens* (Bielicki 1966; Brace 1963*a*; 1963*b*; 1967*a*; 1967*b*; Buettner-Janusch 1966; Dart 1955*a*; LeGros Clark 1967; Oppenheimer 1964). Variation among all australopithecines appears on a par with variation in both gorillas and chimpanzees (Wolpoff 1970*b*; Remane 1959; Schultz 1937; 1954; 1963; 1968; 1969*a*). As Campbell has pointed out (1969), this interpretation fits the established pattern of both gracile and robust groups of people in Africa from the Lower Pleistocene to the present.

The synchronic occurrence of both gracile and robust australopithecines has been demonstrated in east Africa from terminal Pliocene well into the Lower Pleistocene (Arambourg & Coppens 1967; 1968; Coppens 1970; Arambourg *et al.* 1967; 1969; Howell 1968*a*; 1968*b*; 1969; Patterson & Howells 1967; R. E. F. Leakey 1970*a*; 1970*b*; 1971; L. S. B. Leakey 1960; Martyn Tobias 1967). The available evidence indicates that social and cultural behaviours acted as evolution-orienting factors over this time span.

If the graciles and the robusts truly are separate lineages, there can by definition have been no gene flow between them. Given the facts that 1) they were supposed to be adapting quite differently, and that 2) they were synchronic for at least two million years (Howell 1969), one would expect non-overlapping differences in adaptively differentiated features to have occurred. Conversely, if this expectation were not permissible it would be impossible to test the hypothesis suggesting that the gracile and robust australopithecines were two different lineages. At that point, the question of separate australopithecine species would become unanswerable, and hence phylogenetically meaningless.

The interpretation of separate australopithecine lineages yields two testable predictions: 1) One expects non-overlapping sets of differences between the two lineages which indicate different adaptations, and consequently separate total morphological patterns; 2) One expects these differences to become greater through time.

The first prediction is best approached by directly testing the dietary hypothesis (Robinson 1956; 1963*a*; 1963*b*). Do graciles and robusts evince different dietary adaptations? The robusts are supposed to be adapted to a far more vegetarian diet than the graciles. Consequently, the grinding area of their cheek teeth should be considerably greater. The predicted difference in grinding area is fundamental to the dietary hypothesis. Without it, the demonstrable differences between gracile and robusts can only be related to size. Actually, the size difference complicates comparison of the cheek teeth. The robusts should have larger teeth corresponding to their larger size (Robinson 1963*b*), and at the same time they should also have larger teeth because of their more vegetarian diet. In sum, they should have *much* larger cheek teeth than do the graciles.

Table 2 presents data to test this prediction. Sources for the australopithecine

TABLE 2. Averaged summed posterior areas (mm²).
Mandibular

	\bar{x}	(Range)	CV	N	\bar{x}	(Range)	CV	N
Australopithecines								
Gracile	901	(770-1006)	10	8	849	(788-946)	7	6
Robust	1010	(666-1883)	17	16	969	(781-1354)	16	12
<i>Homo erectus</i>	656	(557-731)	8	14	643	(529-858)	18	8
<i>Homo sapiens</i>	496	(353-649)	11	216	501	(307-710)	14	238
Australian aborigines	539				581			
American aborigines	498				493			
Europeans	464				464			
Japanese	449				449			
Lapps	391				388			
<i>Pan gorilla</i>					1011	(744-1481)	14	318

measurements have already been given. Sources for the remaining hominid data are given in another publication (Wolpoff 1970a). Data are given for the summed areas (length times breadth) of the posterior tooth rows (PM₃—M₃) of individual specimens. In both mandible and maxilla, the graciles are about 88 per cent. the size of robusts. Averages representing the range of modern populations are given for comparison. In the posterior dentition, Lapps are only 83 per cent. of the size of other Europeans and in the extreme case they are 73 per cent. the size of Australian aborigines in the mandible and 67 per cent. in the maxilla. In both absolute and percentage differences, gracile and robust australopithecines are considerably closer together than numerous modern populations, in some cases living side by side. While these data do not mean that the graciles and the robusts are identical to each other, they clearly indicate extensive similarity in an adaptive complex which is supposed to show significant difference.

The summed posterior areas for 318 gorilla maxillae are included: I measured some of these specimens at the American Museum of Natural History. Specimens from the Yale Peabody Museum and other sources were published by Pilbeam (1969), and those at the University of Wisconsin by Booth (1971). Most of the material was measured by Mr P. Mahler, of the University of Michigan, and myself, from the Hamann-Todd collection. Mandibles could not be used because of the lack of P₃ analogy. The averages for gorillas and robust australopithecines are within 5 per cent. of each other, although the smallest gorillas have at least double the maximum body mass estimated for robust australopithecines, and the larger specimens have three to four times the mass. The presence of a robust australopithecine-sized posterior grinding area in a species considerably larger, restricted to a primarily vegetarian diet, gives indication of the diet of the robusts. Jolly (1970) has argued that hominids arose from a savanna-based primate adapted to the intensive mastication involved in small object feeding. Given this tooth size comparison with the much larger gorillas, adapted to a forest foliage diet, the dietary part of Jolly's 'seed eaters' hypothesis seems substantiated.

According to Robinson's dietary hypothesis, gracile australopithecines are supposed to have reduced posterior dentitions because of their presumed more omnivorous diet. As table 2 indicates, the graciles have posterior summed grinding areas completely within the range of variation of gorillas, in spite of the likelihood that their body size was between one-quarter and one-eighth gorilla size. Most estimates give robusts about double the average weight of graciles. If even approximately true, the graciles have relatively *larger* posterior teeth. Is it really so likely that the graciles had a more omnivorous diet than the robusts? Or rather, in keeping with Jolly's hypothesis that early hominids appear to be dentally adapted to a heavily masticated diet, does it not appear more probable that *both* the smaller graciles and the larger robusts subsisted on a diet of scavenged game, small objects and roots.

The second prediction is also questionable. Robust specimens from Omo (for instance L7-125) and Olduvai are considerably *more* extreme than robusts from apparently younger sites such as Swartkrans and Kromdraai. I do not conclude that there is a trend from greater to lesser robustness in the robusts (although this is possible), both because the earlier sample size is too small and because the range of variation in the later specimens is almost great enough to include the earlier ones.

Certainly, however, there is no indication of the reverse tendency, as is predicted from the interpretation of separate lineages. This observation also directly contradicts the character displacement hypothesis suggested by Schaffer (1968).

With the increasing amount of data accumulated, numerous workers have come to recognise the intensive intergradation and overlap of gracile and robust australopithecines both in terms of individual specimens and in terms of entire sites such as Kromdraai and Makapansgat where 'intermediate' populations could be represented (Le Gros Clark 1967; Brace 1963*a*; 1963*b*; 1967*a*; Campbell 1969; Dart 1955*a*; 1964; Buettner-Janusch 1966; Simons 1968; Mann 1970; Wolpoff 1968; 1970*a*; 1970*b*; 1971*a*). Indeed, one of those most familiar with the actual specimens has recently concluded:

The distinction between these two lines should not be overstated: it is suggested that gene exchange between the two lines might have been possible. Such hybridizing effects might have aided the 'toning down' of the extremely robust earlier *A. boisei* into the later less robust *A. robustus*; and secondly, might account for a number of *A. robustus* features in the otherwise *A. africanus* forms of Makapansgat (Tobias 1969: 311-12).

This description can only refer to subspecies within the same species.

There are certainly differences between what I have referred to as gracile and robust australopithecines, just as there is a difference between Bushmen and Bantu, or Norwegians and Lapps, or Lowland and Mountain gorillas. These differences can be extensive. One would never confuse crania of Bushmen and Bantu with each other, whether a single cranium or a much larger sample was involved. Different *types*, however, are not necessarily different *species*. If a sampling of australopithecine mendelian populations were available, I believe that we would characterise some as gracile, some as robust, and still others as intermediate. Thus a plausible interpretation of australopithecine variation refers the differences between them to sub-species level. This interpretation fits the predictions of the single species hypothesis.

The single species hypothesis is concerned with consequences of the pongid-hominid lineage separation. As such, it presents a way of approaching early hominid interpretations which would otherwise be untestable. While Jolly's 'seed eaters' hypothesis deals with the consequences of how early hominids *subsisted* on the savanna, this hypothesis considers the consequences of how they *defended* themselves. The two views are not contradictory.

The single species hypothesis is grounded in the synthetic theory, and fits the available evidence. Those who believe it to be invalid must not only demonstrate the unequivocal value of their proposed refutations, but must also replace the hypothesis with one which fits the evidence better.

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