Fig. 1. Type one pulses. These show "spontaneous" activity. In response to a stimulus the pulses are produced at higher frequency with far more regular spacing. Voltages in Figs. 1 and 2 were measured from peak to trough. Scale, 10 μv; 25 msec.

Fig. 2. Type two pulse. This pulse was not produced in response to type one activity, which would normally be superimposed upon it. Scale, 20 μv; 50 msec.

A colonial retraction of zooids is evoked by a single, above-threshold, mechanical or electrical stimulus to the surface membrane of an individual. Stimuli applied to the extended tentacles of a single animal in a colony produce a retraction response in that animal only. During a colonial response, all extended lophophores within a few centimeters of the zooid stimulated are involved in an almost simultaneous withdrawal. Those nearest the point of stimulation retract for a longer period than those on the edge of the retracting area. Second and third stimuli applied a few seconds after the first one may produce small increases in the area of spread, but the response can never be made to spread over the entire colony. The response to subsequent stimuli shows marked habituation (measured by the response area). Retractions and extensions of one or more lophophores were monitored with a narrow light beam and a photodiode (Texas Instruments, type H-38 NPN photoduodiode) connected to an oscilloscope and pen recorder. This apparatus was also used to measure the delays between stimulus and response at varying distances from the point of stimulation. The response spreads at a velocity of about 100 cm sec⁻¹. The protective lophophore withdrawal response takes place very rapidly (60 to 80 msec) and corresponds to a peak contraction rate (the greatest velocity reached by the muscle during a single contraction) of more than 20 muscle lengths per second in the lophophore retractor muscle, which is probably the fastest contracting muscle known [compare other extremely fast muscles—locust flight muscle, 13 lengths per second (9); rat diaphragm, 11 lengths (10); and frog sartorius, 10 lengths (11)]. In view of this, the muscle might be expected to show interesting ultrastructural adaptations to contractions at great velocity.

Electrophysiological recordings, in which extracellular suction electrodes were used (12), showed two distinct types of electrical pulses within the colony. "Type one" pulses (Fig. 1) are of about 2 msec duration and up to 10 μv in amplitude. They are conducted between zooids at a velocity of about 100 cm sec⁻¹. These data indicate probably nervous (or possibly neuroid) origin. As no other suitable nervous or neuroid pathway has been described, the pulses may emanate from the tiny neurites in the colonial nervous system described by

Lutaud (6). If so, their conduction velocity is surprisingly rapid. A single above-threshold stimulus causes a burst of type one activity, the size of the response depending upon the magnitude of the stimulus. These pulses show three features of particular interest. (i) They are very regularly spaced, which suggests pacemaker control. (ii) Their peak frequency during a burst is often extremely high (more than 200 sec⁻¹), and they often continue to fire at high frequency for long periods of time. (iii) A single burst may contain more than 1000 pulses in the first 10 seconds. This probably unique property suggests that the nerves involved may have a most unusual degree of tolerance to changes in internal ionic concentration. The threshold, conduction velocity, and habituation of the type one response correspond with those of the colonial withdrawal of polypides.

Type two pulses (Fig. 2) are not conducted between zooids but occur whenever the lophophore retractor muscle of an animal contracts beneath the recording electrode; they are of two parts. The first is of large amplitude (up to 200 μv) and short duration (10 msec); this is followed by a much longer duration component probably related to the muscular activity. The first part could be nervous activity in a giant axon system innervating the muscle and possibly coming from the main ganglion of the zooid. There is a frequency-dependent relation between type one and type two pulses, although type two pulses can be recorded without type ones (see Fig. 2). In this case they are probably not the result of colonial activity.

The nonlinear increases in the size of the colonial retraction response following repetitive stimulation closely resemble the behavior of certain coral polyps (13).

Since, however, the type one pulses can be shown to travel outside the immediate area covered by the colonial response, Horridge's theoretical explanation of coral behavior in terms of the density of active neurites in a nerve net will not explain the observed results in the Bryozoa.

These results represent the first electrophysiological evidence for a functional colonial nervous system in gymnolaemate Bryozoa. The nerve plexus is anatomically simple (7), but allows versatility in the control of colonial behavior.

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Allometry and Early Hominids

We applaud the use of allometry which allows Pilbeam and Gould (1) to treat the welter of early hominid finds in an orderly and integrated manner. In passing, we note that the same approach could profitably be applied to testing possible male-female dimorphism at early hominid sites (2).

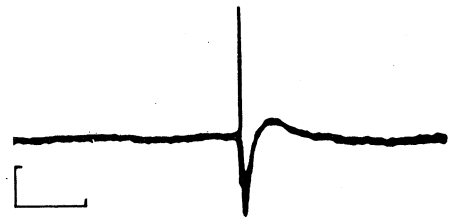Our purpose here, however, is not to question the treatment of the australopithecines per se, but to question the validity of the taxon which Pilbeam and Gould place as the first recognized member of the lineage leading to Homo sapiens. The very existence of the taxon "Homo habilis" owes more to an extraordinarily wide press, such as that to which Pilbeam and Gould correctly attributed the enshrinement of the killer ape image, than to actual data (3).

Homo habilis was one of the last crea-

tions of the late L. S. B. Leakey (4), whom one of the authors has described as "a lavish splitter in an age of lumpers" (5). And just as this predilection damaged his paleontology, we suggest that in following and extending his example they have reduced the credibility of their interpretations.

The problems involved in the *Homo habilis* concept are nowhere better outlined than in the difficulties in deciding what specimens to include in it. When their article was written, Pilbeam and Gould used neither Olduvai Hominid (OH) 13 nor OH 24 (6), although the first was a paratype of the taxon (4) and the second was attributed to it as the most complete cranium (7). On the other hand, the small Rudolf mandibles such as ER 992 and ER 730 were included, although Pilbeam now agrees with us in believing that the dental variation in the australopithecines is so great that jaws and teeth alone are of no use in distinguishing taxa (6), a conclusion recently emphasized by the discovery of a Rudolf cranium with a 500-cm³ brain and very small teeth (ER 1813) (8).

The sample which Pilbeam (6) is now willing to attribute to *Homo habilis* consists of only four specimens: OH 7, the putative type specimen (mandible, parietals, and hand), OH 16 (very fragmentary cranium and teeth from both jaws), ER 1470 (complete cranium and roots or sockets of most teeth), and ER 1590 (skull cap and upper teeth). The OH 7 parietals were found crushed flat, and both the curvature of the bones and their fit on the sagittal suture were reconstructed. The cranial capacity is, and has been, anybody's guess (3), but the close correspondence of the parietal arc dimensions with those of other specimens of known capacity suggest that a value significantly in excess of 500 cm³ is unlikely. The hand is very small. Specimen OH 16, unfortunately fragmented by a herd of cattle, has been reconstructed three times, and in all cases there is no continuous bone surface in any direction. The present reconstruction is known to be inaccurate, since a gap between the supraorbitals at glabella is far too small for the bone fragment now known to fit into this position. Neither the actual shape nor the size of this cranium can as yet be determined, and at present, there is no possibility of determining the cranial capacity. Specimens ER 1470 and 1590 are both larger crania, and 1470 is the only specimen of the group with known capacity (775 cm³). The 1470 face is extremely large (second only to OH 5) and has the anterior masseteric attachment known for all large australopithecines, as well as a very large posterior dentition, as shown by the size of the roots of 1470 and the size of the actual teeth of 1590. Features of the face and posterior teeth, including size and relative breadth of the postcanine teeth, size of the face, and curvature of the occipital, do not fit the diagnosis of *Homo habilis* (4). In sum, there is no specimen with both known brain size and known tooth size, although the indication is that ER 1470 and 1590 have large brains and large teeth, while OH 7 has a smaller brain and smaller teeth. Body size is unknown for any specimen, excepting the indication that OH 7 might have been small since the hand is small. As for tooth size, the new mandibular sample (OH 7 and OH 16 only) has a posterior area sum more than 100 mm² greater than reported (1). These facts make it difficult to place the sample on a regression of tooth size and body size, or cranial capacity and body size, without guessing at two of the three parameters for the taxon *Homo habilis*.

Anyone may make such guesses, but they should not then form the basis for an evolutionary scheme dependent on the pattern of allometric change. Perhaps ER 1470 and 1590 are simply large australopithecine specimens. Pilbeam and Gould's data show that if ER 1470 weighed 200 pounds (90.6 kg), it would fall on the australopithecine power function regression and not on that of *Homo*.

Is it unreasonable to expect that ER 1470 was a large specimen? The 314-mm Omo ulna and the "Broomstick" femur (ER 736) show that individuals approaching if not exceeding 6 feet (~ 1.8 m) occurred (9) and would most certainly have possessed substantial bulk (10). The largest femurs from East Rudolf have been attributed to *Homo* (ER 736, 737, 803, 1472, and 1481) (11), and if these are thought of as *Homo habilis*, as Pilbeam and Gould seem to have done, one could conclude that this instead of "*Australopithecus boisei*" was the largest of the lower Pleistocene hominid taxa.

Finally, the best dental correlate with body size in the species *Homo sapiens* is the size of the anterior teeth (12). These are quite large in ER 1470 and 1590. Thus, there is some reason to expect that these specimens were very large, and consequently "fit" the australopithecine regression. We believe that our interpretation is as justified as that of Pilbeam and Gould. The point is that no evolutionary scheme should be hinged on evidence with this degree of uncertainty.

We have been at some pains to discuss the nature of the data that underlie the establishment of what we feel is an unwarranted unit in an otherwise worthwhile analysis. It is not out of line, however, to make brief mention of the skimpy state of the data that underlie the other points, even if we accept the validity of the samples used. (i) There is not a single lower Pleistocene hominid cranium with a known cranial capacity that is associated with any postcranial material useful for determining body size. (ii) This is also true of *Homo erectus*. (iii) Only one published australopithecine allows the determination of both the summed posterior area and cranial capacity, and even in this case (OH 5), we have reason to believe that the capacity is too small. (iv) The correlation between femur length and body weight in *Homo sapiens* is not significant (13) so that even if there were crania with posterior dentitions, determinable cranial capacities, and associated limbs, it is doubtful that limb length would be an adequate estimator of body weight, the basis of these allometric comparisons.

Fitting curves to sets of three data points, and drawing conclusions from them, is a risky procedure at best. In this case the problems are far more serious, since in five out of six of the data points used, at least one of the variables is an unverifiable guess, and in some cases both are either complete guesses or based on sample sizes where $N = 1$.

We have been aware of these difficulties for some time, which is why earlier suggestions of an allometric relation between the various australopithecine forms (14) have never been followed with a quantified demonstration. However satisfactory the idea seems, we simply don't believe there are sufficient or appropriate data to quantify it.

If there is more than one lineage to be found among the lower Pleistocene hominids, we believe they overlap so greatly that fairly complete specimens cannot be distinguished by any set of consistent criteria. The present evidence shows that this overlap occurs no matter how many lineages there might have been, and this itself is an important datum. As extremely closely related mammals, hominid species constantly found together would unquestionably be in competition, which would be expected to result in extinction, population dislocation, or niche divergence. The length of the East African sequence and the persistent recovery of various hominid morphotypes together at all levels shows that neither extinction nor population displacement occurred. If there was niche divergence, we can find no morphological evidence of differing adaptive patterns under the very circumstances where we would most expect such evidence. The alternative interpretation is that there are no competing species because there is only one lineage of "the 'same' animal represented over a wide range of size" (1). We welcome any attempt to determine within an evolutionary framework consistent criteria for a

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second lower Pleistocene hominid lineage, but the point remains that this use of *Homo habilis* neither included a definition of the taxon, nor met the criteria of the original definition. This has not been done so far, and the varied use of the taxon has created nothing but confusion. Hence we reiterate the previous suggestion (*3*) that " '*Homo habilis*' be formally sunk."

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16 December 1974

Pilbeam and Gould (*1*) ask "Could large animals require larger teeth than their smaller ancestors just to maintain functional equivalence?" Their query is related to the fact that metabolic rates in mammals increase by the 0.75 power of body mass. If tooth surfaces increased by the 0.75 power of body mass, they might be considered metabolically scaled. On the other hand, simple geometric scaling would result in an increase in tooth surfaces by the 0.67 power of body mass. Although the exponents of the regression equations relating tooth surfaces to body mass in their table 4 are not significantly positively allometric, Pilbeam and Gould suggest that the postcanine dentitions of primates and other mammals may nevertheless be metabolically scaled. Gould (*2*, p. 24) has concluded, apparently on theoretical grounds, that because of metabolic changes, "invariably, ... larger animals have relatively larger teeth—not because they eat different foods, but simply because they are larger." However Kay (*3*) has shown that when dietary influences are removed, tooth surfaces in mammals are usually geometrically scaled. Several instances are given where large species actually have relatively smaller tooth surfaces than their smaller relatives. No in-

Table 1. Scaling of second molar crushing surfaces and postcanine tooth areas in selected mammalian groups. The slopes listed are the exponents of the power functions relating body mass and tooth surfaces. All measurements were converted to logarithms. Abbreviations: A, crushing surfaces of second lower molars; B, total surface of postcanine teeth; *N*, sample size (number of taxa). The 95 percent confidence intervals of the slope are indicated.

Group	N	Slope
Cercopithecoidea (A)	81	0.62 ± 0.08*
Noncercopithecoid primates (A)	42	0.65 ± 0.06*
Noncercopithecoid primates (B)	10	0.59 ± 0.07*
Primate frugivores (A)	22	0.68 ± 0.08
Primate folivores (A)	15	0.71 ± 0.08
Primate insectivores (A)	5	0.47 ± 1.03
Bovid artiodactyls (B)	10	0.52 ± 0.06*

*Significantly less than 0.75.

stances of metabolic scaling were observed.

Two factors have been recognized (*3, 4*) which contribute to tooth size changes within lineages or in collections of closely related living species; tooth size increases with changes in body size, and tooth size differs in animals of different diet. The former simply means that larger animals usually have absolutely larger teeth than their relatives of smaller size. However, in determining the exponent of the power function describing this change it is necessary to eliminate the effects of diet. For example, for noncercopithecoid primates at a particular body size, frugivorous species have smaller teeth than do their insectivorous or folivorous relatives (*3*). Thus, for any group for which this holds, regression equations would appear to be positively allometric if the group's smallest members were frugivorous and its large members folivorous. Pilbeam and Gould do not mention that frugivores and folivores have different-sized teeth, but attribute differences in diet to differences in body size alone (*1*, p. 897). They calculate a regression for lemuroids, of which the smallest, *Microcebus*, is probably largely frugivorous (*5*) and the largest, *Indri*, takes higher percentages of leaves in its diet (*6*). Similarly, for ceboids, the smallest genus, *Cebuella*, may be fairly frugivorous; the largest genus, *Alouatta*, has a very high percentage of leaves in its diet (*7*). The slope of the power function relating postcanine tooth size to body size for hominoids (*1*, table 3) is quite large, although it is based on only four species and confidence intervals are not given. Again, this relation is probably accounted for by the fact that *Pan* takes much more fruit in its diet than does its larger relative *Gorilla* (*1*).

The information presented in Table 1 shows that when species groups are sam-

pled which have fairly uniform diets, or when frugivorous or folivorous species are distributed at all sizes, the exponents of the power functions relating body size to postcanine tooth areas or second molar areas are not significantly greater than 0.67. In several cases they are significantly less than 0.67. Thus, eliminating the effects of diet, postcanine tooth surfaces tend to follow simple geometric scaling with increased body size, or in some cases are relatively smaller in large species than in their small relatives. Relative increases in tooth surface expected for metabolic scaling are by no means a general phenomenon among mammals.

Recent unpublished work by Kay shows that although phalangeroid marsupials have significantly lower metabolic rates at a given body mass than placental mammals, their second molars do not differ significantly in size from cercopithecoid primates of the same body masses.

A reinterpretation of Pilbeam and Gould's data suggests that if their body size estimates for australopithecines are correct, then the larger species probably had more fiber in its diet than the smaller species; this supports rather than contradicts Robinson's (*8*) dietary hypothesis. However, their estimate of 47.5 kg for the body mass of the robust species is considerably lower than other estimates in the literature. Kay (*9*) reports estimates of between 60 and 90 kg. McHenry (*10*) suggests that some specimens may have been as large as 113 kg. If a higher figure were used, the exponent of the power function relating body mass and tooth surface would be strongly negatively allometric and might indicate more fiber in the diet of the gracile species than in that of the robust species, the reverse of Robinson's contention. Whichever option is chosen, the large size of the postcanines of all three species compared with the great apes suggests that all *Australopithecus* species may have had diets higher in fiber and grit content.

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Kay's data on the scaling of tooth size seem, at first, to contradict our own quite strongly. His table 1 shows the exponents of power functions representing seven groups of data; all but two of the exponents are below the geometric 0.66 (two significantly below) and none are significantly above. Yet, of these seven exponents, five are for functions relating only the area of the second molar to body size, not the entire postcanine row as in our analysis. We are not surprised that this single molar does not scale with positive allometry: our first subjective impressions led us to suspect that if positive allometry exists at all, the primary input to it arises from a relative increase in third molar size and a relative increase in premolar area due to molarization—that is, to "squaring" of teeth that are more triangular in smaller relatives. The first and second molars seem on visual inspection to change rather little in relative size from small to large species within a group; we accept Kay's confirmation gladly. Kay's table therefore contains only two entries (bovid artiodactyls and noncercopithecoid primates) calculated according to our criteria and therefore contradictory to our findings. We must simply maintain that there are, at present, more data supporting our position. For both of Kay's samples N is 10. We had six samples, all but one larger than this. Moreover, it is not true (as Kay asserts) that our exponents were not significantly positive in their allometry. Our best and largest sample (hystricomorph rodents, $N = 34$) has a slope significantly in excess of the value for geometric scaling; all our other slopes were positive and their lack of significance need reflect no more than the small size of our samples.

In addition, we never claimed that the explanation for positive allometry lies in the 0.75 scaling of metabolism; we merely desired to assert an empirical regularity. The metabolic (physiological) explanation may well apply, but other ecological rationales are equally compelling (1). Rensberger (2), for example, on the basis of a general argument by Levins (3) about the perception of environmental grain, argues that small mammals can specialize in succulent food sources while large mammals must eat a range of items, some of necessarily less food value. Kay's correlation of frugivory with small teeth and folivory with large teeth may well hold, but could not this dietary preference be, in itself, related to body size on Rensberger's argument? In fact, Kay states that in three groups (prosimians, ceboids, and pongids) the smallest species we measured was a frugivore and the largest more folivorous.

Finally, we note Kay's agreement with

us that whatever the pattern of scaling within groups, the absolutely large size of postcanines in all australopithecines points to a fibrous and gritty diet—scarcely the stuff for a "killer ape."

We welcome Wolpoff's lengthy critique because it does summarize quite succinctly some of the inadequacies of the hominid record. Further, it demonstrates very clearly an approach in many ways diametrically opposed to ours. Although we disagree or take issue with many of Wolpoff's statements, we restrict ourselves to comments on only a fraction of them.

At a general level Wolpoff makes two major points: first, the hominid fossil record still leaves much to be desired; second, there are theoretical reasons for expecting these early hominids to come from only a single species lineage.

The first objection, of course, applies with equal force to all interpretations of early hominid evolution, Wolpoff's as well as ours. The second, "theoretical" objection is the one which puzzles us most. If it is indeed true that several hominid species could not coexist over any significant period of time, then no matter what the fossils look like they must belong to one species. The trouble with this argument is that the result (a single species), far from simplifying matters, considerably complicates explanation of what then becomes a unique and extraordinary intraspecies variability (4). Further, the premises strike us as being difficult to accept. Closely related species clearly can and do coexist. A good deal of empirical, experimental, and theoretical evidence demonstrates that species with partial niche overlap coexist quite happily, generally after some kind of character displacement (5). One way of explaining the Plio-Pleistocene hominid record in East Africa would be in terms of three species: two australopithecine species, adaptively similar, one small, the other approximately half again as heavy, which accords well with theoretical expectations and empirical observations; and a hominid species, adaptively different, having (at least) a larger brain and a differently organized dentition. Such a pattern violates no ecological "rules." The persistent recovery of several (discrete) morphotypes over a long segment of time in East Africa supports such an interpretation. Whatever the past problems with the diagnosis and hypodigm of *Homo habilis*, we feel that the OH 7 mandible, the type and name-bearer of *H. habilis*, and several other specimens, including OH 16 and KNM ER 1470 and 1590, most probably represent a nonaustralopithecine species, sufficiently distinct morphologically for us to infer (perhaps considerable) adaptive difference.

Now for some specific criticisms of Wolpoff's comments. Wolpoff suggests that 1470 is large-brained because it is a large australopithecine and mentions a figure of 200 pounds. However, an australopithecine with a brain volume of 775 cm^3 would weigh, not 200 pounds, but 360 pounds (163 kg)! This is clearly an unlikely alternative. Further, if 1470 is simply a large australopithecine, why is it not shaped like one? Wolpoff accepts our "qualitative" allometric arguments; qualitatively a 200-pound (or 360-pound) australopithecine would have cranial crests and superstructures better developed even than *Australopithicus boisei*, and an ultraflattened cranial profile. It would not look like 1470 qualitatively or quantitatively.

The relationship between anterior tooth size or femur length and body weight in *Homo sapiens* (intraspecies correlations) is irrelevant to a study of variation between species.

It clearly is going to be difficult to allocate some complete jaws and teeth to particular species, but let's not throw out the baby with the bath water; most workers would probably sort the present material into generally similar groupings, which is probably all we should hope for. And we certainly feel that we could sort *A. boisei* from *H. habilis*, at the least, on the basis of complete jaws and teeth.

Finally, we would like to avoid swear words like "lumper" and "splitter"; we split when we feel it is necessary, and lump for the same reason. Also, it is beginning to look as though L. S. B. Leakey was more often right than wrong on the subject of Plio-Pleistocene hominids. One of us has frequently criticized his work (6), but perhaps "following and extending his example" may not be such a bad idea after all!

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