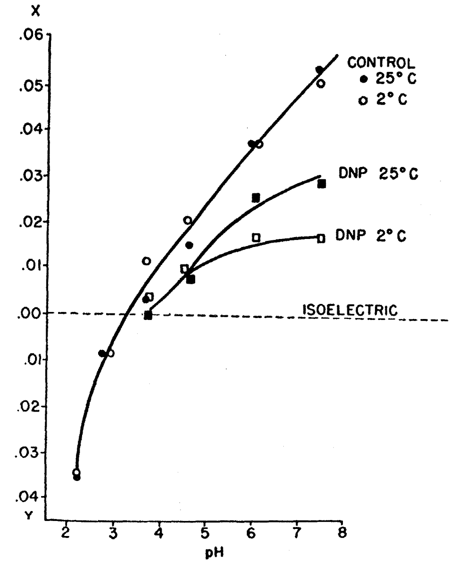

Fig. 1. Titration curves of frog muscle surface. Ordinate, density of colloidal charge in equivalents; abscissa, *p*H. Control curves at 2°C and 25°C are compared with curves observed with 0.001*M* 2-4-dinitrophenol.

sue or wool surfaces (*2*). Similar effects are shown by the other anions (Table 1). In titration curves of wool and connective tissues, many anions combine with protein to displace the curves in the same way.

Certain properties of the muscle surface studied in vivo may be compared with those determined in vitro. The negative charge density at *p*H 7.4 (0.053 equivalents; see Table 1) is lower than that of the isolated muscle proteins (0.100 equivalents) (*7*), but is consonant with that value when bound calcium, magnesium, and amines are taken into account. The fact that anions lower the negative colloidal charge has been discussed elsewhere (*2*). By forming salt linkages with positively charged groups, an anion *A* may increase the negative charge of the colloid *P*. For example,

$$P^- + A^- = (AP)^{--}$$

If this leads to the simultaneous binding of more than one hydrogen ion, the negative colloidal charge is decreased:

$$(AP)^{--} + 2H^+ = (APH_2)$$

In the general case *P* would be polyvalent with numerous negative charges. The negative charge would be lowered by the simultaneous binding of anions and hydrogen ions to form the complex (APH_2). In the case of 2-4-dinitrophenol, the anionic O^- group would form a salt linkage with a positively charged amino group of the colloid. The two NO_2 groups would form hydrogen bonds simultaneously. In the process the Donnan ratio is changed, sodium is displaced, and chloride is simultaneously taken up by the surface (*2*). Other anions with strongly electronegative groups (NO_2, I, CN, CHOH) likewise coordinate by means of hydrogen bonds with conjugate electronegative groups (CONH, COO^-, SH, and so forth) of the colloid. In all cases a rearrangement of hydrogen and electrostatic bonds of the colloid would shift the titration curve. Because of the low bond energies which are involved, high labilities would be expected for anion-cation exchange reactions (*2*).

A direct relationship between ion distribution and the energy derived from cellular respiration has frequently been postulated, and appears under various guises as active transport of ions. The above experiments show that redistribution of anions and cations is produced by combination of respiratory inhibitors with extra- and intracellular charged colloidal aggregates. Anionic metabolites and inhibitors similarly alter the titration curves (and ion distributions) of connective tissues, as well as those of metabolically inert wool fibers and other colloids including ion-exchange resins. Lowering of respiration in poikilotherms by temperature reduction leads to no significant effect on colloidal charge or electrolyte distribution, although energy production is greatly diminished.

From this point of view, respiratory changes without simultaneous changes in colloidal state need not affect ion distribution. Inhibitors, which by definition decrease respiration, are bound to the colloidal matrix, and thereby produce redistributions of all other anions and cations (*8*).

MILTON B. ENGEL
HUBERT R. CATCHPOLE
NORMAN R. JOSEPH
Colleges of Dentistry, Medicine, and Pharmacy, University of Illinois, Chicago

References and Notes

1. E. J. Cohn, *Physiol. Revs.* **5**, 349 (1925); J. Steinhardt, *Ann. N. Y. Acad. Sci.* **41**, 287 (1941); J. Steinhardt and E. M. Zaiser, *J. Biol. Chem.* **183**, 789 (1950); I. M. Klotz and J. M. Urquhart, *J. Am. Chem. Soc.* **71**, 847 (1949).
2. N. R. Joseph, H. R. Catchpole, D. M. Laskin, M. B. Engel, *Arch. Biochem. Biophys.* **84**, 224 (1959); N. R. Joseph and M. B. Engel, *Arch. Biochem. Biophys.* **85**, 209 (1959); M. B. Engel, N. R. Joseph, *Arch. Biochem. Biophys.* **86**, 117 (1960).
3. D. E. Green and J. Jarnifelt, *Perspectives in Biol. and Med.* **2**, 163 (1959).
4. L. Michaelis and M. L. Menten, *Biochem. Z.* **49**, 333 (1913); R. A. Alberty and V. Massey, *Biochim. et Biophys. Acta* **13**, 347 (1954); M. London, H. McHugh, P. B. Hudson, *Arch. Biochem. Biophys.* **73**, 72 (1958).
5. Buffer solutions were prepared at six different *p*H levels: 7.4, 6.0, 4.6, 3.7, 2.9, and 2.2. The ionic strength in each case was approximately 0.15. At *p*H 6 and 7.4, phosphate buffers were used, while acetate–acetic acid mixtures were used at *p*H 3.7 and 4.6. Sodium was the only cation present, while chloride accounted for 90 percent or more of the total anion concentration. NaCl-HCl mixtures were used at *p*H 2.9 and 2.2.
6. Below *p*H 3 the values of E_a° depend on *p*H as well as on temperature. At 25°C the values of E_a° in millivolts are −11.8 (*p*H 3.7 to 7.4), −10.1 (*p*H 2.9), and −4.2 (*p*H 2.2). At 2°C the corresponding values are −10.9, −9.3 and −3.9 mv. The values of *k* are 197 (25°C) and 182 (2°C). Methods of calculating these constants have been given (*2*).
7. E. J. Conway, *Physiol. Revs.* **37**, 84 (1957).
8. This work was supported in part by grants from the U.S. Public Health Service (A-968-C2 and D-1147).

19 May 1960

Cranial Capacity of Oreopithecus bambolii

Abstract. From a plaster reconstruction of the skull of the August 1958 skeleton, the cranial capacity of *Oreopithecus bambolii* has been estimated as falling between 276 and 529 cubic centimeters, thus within the ranges of variation of both orang-utan and chimpanzee. In cranial capacity, therefore, and probably in body-brain ratio as well, *Oreopithecus* is a hominoid.

The taxonomic status of *Oreopithecus bambolii,* a fossil catarrhine primate from the Lower Pliocene of Italy, hence some 12 million years old, has been a matter of considerable controversy ever since the type specimen, a mandible with teeth, was described by Gervais in 1872 (*1*). In recent years, however, particularly following Hürzeler's discovery of a large number of additional specimens at Baccinello, Italy, it has become increasingly evident that *Oreopithecus* is a member of the superfamily Hominoidea, which comprises the families Pongidae (anthropoid apes) and Hominidae (man and his immediate forerunners) (*2*). This interpretation has been strengthened by studies of an adult skeleton discovered on 2 August 1958 (*3*). The precise allocation of *Oreopithecus* within the Hominoidea remains uncertain, however. The present communication deals only indirectly with this problem. Rather, it deals specifically with an attempt to estimate the cranial capacity of the 1958 skull, which is the only one sufficiently complete to justify such a procedure.

Although this skull is considerably crushed, its fragments fortunately remained closely associated within its lignite matrix. Its condition, however, precludes direct measurement of the cranial capacity. Some indirect method therefore must be employed. While we were in Basel in August, 1959, Dr. Hürzeler generously permitted us to study his plaster reconstruction of the skull and to take the basic measurement necessary for an estimation of its cranial capacity (*4*). This consists of an estimation of the volume of the braincase by immersion in water and measurement of the consequent displacement of the liquid. Braincase volume in itself is of course no direct clue to cranial capacity. It is true that Jørgensen and Quaade (*5*) reported a close correlation between external cranial volume (representing the water displaced by that part of the skull above the horizontal glabella-inion plane) and cranial capacity in modern man, but their method is not applicable to all primates because of generic differences in skull form. If there were a relatively constant ratio between internal and external cranial volumes, determination of the cranial capacity of our fossil would be a simple matter. The ratio varies considerably, however, chiefly because of differences in relative thickness of the calvaria and cranial base. Therefore, in order to provide a basis for determining the probable limits of the cranial capacity of *Oreopithecus*, the ratio between cranial capacity and braincase volume has been calculated in a series of 21 adult catarrhine primates (*6*). Multiplying the braincase volume of the *Oreopithecus* plaster reconstruction by the extreme ratios of this series provides maximum and minimum estimates of the cranial capacity in this particular fossil.

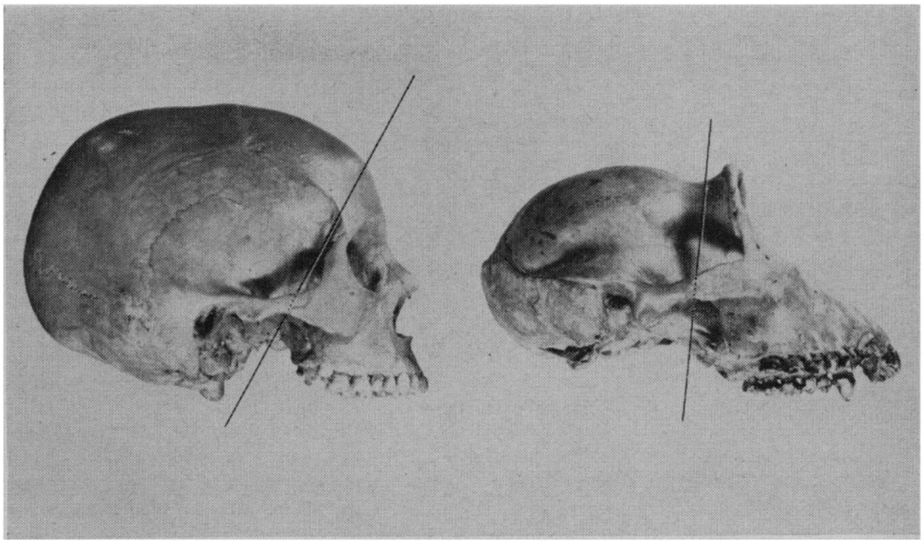

Fig. 1 Skulls of adult female Negro (left) and adult male chimpanzee (right), showing the line of demarcation between facial skeleton and braincase used in this study. The braincase, as herein defined, is that part of the cranium posterior to a plane passing from immediately behind the supraorbital ridges, above, through the lateral pterygoid plates, below.

The braincase, as defined in the present study, is that part of the cranium posterior to a plane passing from immediately behind the supraorbital ridges above through the lateral pterygoid plates below, as shown in Fig. 1. The volume of the *Oreopithecus* braincase, as thus measured from water-displacement of the plaster reconstruction, is 565 cc. This particular reconstruction, while excellent, naturally cannot be considered precise. Dr. Hürzeler himself did not regard it as entirely satisfactory in all details. Notwithstanding, we are of the opinion that, at least in so far as the size of the braincase is concerned, it cannot be greatly in error. On the assumption, however, that the reconstructed braincase may be either slightly too small or slightly too large, a correction factor of ± 75 cc seems in order. This allows for an error of reconstruction of approximately ± 0.5 cm in all dimensions. The volume of the braincase thus can be regarded as lying anywhere between 490 and 640 cc. Hence, both of these limits have been used in estimating the cranial capacity of *Oreopithecus* (see Table 1) (*7*). The smallest cranial-capacity/braincase-volume ratio in the series of primates measured by us is that of an orang-utan, 0.564; the largest is that of a gibbon, 0.826 (Table 1, column *a*/*b*). By applying these, respectively, to the minimum (Table 1, column 490 × *a*/*b*) and maximum (Table 1, column 640 × *a*/*b*) braincase volumes estimated for the *Oreopithecus* skull, limits of 276 and 529 cc are obtained. The cranial capacity of the August 1958 specimen thus can reasonably be regarded as anywhere between 276 and 529 cc.

Can it be more than mere coincidence that these calculated extremes, 276 and 529 cc, not only are almost identical with the measured limits of variation, 276 and 523 cc, in the combined series of 194 adult orang-utan skulls studied by Gaul and by Schultz (*8*) but also agree closely with the 290 and 500 cc limits in the combined series of 94 adult chimpanzee skulls measured by Zuckerman and by Schultz (*9*)? Whatever this may signify, the cranial capacity of this *Oreopithecus* skull almost certainly falls within the ranges of variation of these two great apes. The cranial capacity of the adult gorilla

Table 1. Cranial capacities in cubic centimeters (column *a*), braincase volumes in cubic centimeters (column *b*), and the ratio between cranial capacity and braincase volume (column *a*/*b*) in 17 extant and 4 fossil adult catarrhine primates; and possible cranial capacities, in cubic centimeters, of *Oreopithecus*, secured by multiplying its estimated braincase volumes by the various values of ratio *a*/*b* (columns 490 × *a*/*b*, 565 × *a*/*b*, 640 × *a*/*b*).

Primate	*a*	*b*	*a*/*b*	490 ×*a*/*b*	565 ×*a*/*b*	640 ×*a*/*b*
Macaca mulatta ♂	99	133	0.744	365	420	476
Macaca mulatta ♀	87	115	.756	370	427	484
Papio sphinx ♀	148	187	.791	388	447	506
Presbytis melalophus ♂	66	91	.725	355	410	464
Hylobates agilis ♂	95	115	.826	405	467	*529*
Symphalangus syndactylus ♂	127	179	.709	347	401	454
Orang-utan ♀	417	717	.581	285	328	372
Orang-utan ♀	353	625	.564	*276*	319	361
Chimpanzee ♂	430	692	.621	304	351	397
Chimpanzee ♀	378	563	.671	329	379	429
Gorilla ♂	593	978	.606	297	342	388
Gorilla ♀	463	788	.587	288	332	376
Gorilla ♀	478	833	.573	281	324	367
Australopithecus (Sterkfontein No. 5)	480(*14*)	782	.613	300	346	392
Neanderthal (La Chapelle-aux-Saints)	1626(*15*)	2168	.750	368	424	480
Neanderthal (Gibraltar No. 1)	1250(*16*)	1665	.750	368	424	480
Rhodesian Man	1280(*17*)	1890	.677	332	383	433
Negro ♂	1280	1775	.721	353	407	461
Negro ♂	1627	2025	.803	393	454	514
Negro ♀	1133	1478	.766	375	433	490
Negro ♀	1323	1765	.749	367	423	479

is somewhat greater, extending from 420 to 685 cc (*10*). Even so, if its larger calculated possibilities prove to be valid, the cranial capacity of the Italian fossil also lies within the range of the giant African great ape. In any event, the cranial capacity of *Oreopithecus* is that of a hominoid. Its lowest estimated capacity, 276 cc, is much larger than that recorded for any Old World monkey; the capacities of even large adult baboons fall short of 200 cc (*11*).

The index of relative brain size, an expression of the cranial capacity (in cubic centimeters) as a percentage of body weight (in grams), is of considerable interest. Schultz (*12*) has reasonably argued that the body weight of the 1958 specimen of *Oreopithecus* must have been about 40 kg, which approximates the weight of the average chimpanzee or female orang-utan. With this figure, the body-brain index of the fossil could be as little as 0.69 or as much as 1.32. The minimum index, 0.69, lies well within the adult range of variation for the three great apes (*11*). The maximum index, 1.32, while considerably above that recorded for any adult gorilla, is but slightly larger than the adult maxima of both the orang-utan and chimpanzee; it is slightly smaller, however, than the minimum index for adult man (*11*). Both of these estimated *Oreopithecus* indices are paralleled among Old World monkeys. However, this index of relative brain size tends to be inversely proportional to body weight in primates (*11*). Consequently, if its larger index, 1.32, is valid, *Oreopithecus* can be regarded as somewhat advanced in relative cranial capacity and hence in relative size of brain, for it undoubtedly was a much bigger animal than any Old World monkey of comparable body-brain index. Indeed, this index falls below 1.0 in all Old World monkeys weighing more than 10 kg (*11*).

Its encephalic magnitude, both absolute and relative, confirms the assignment of *Oreopithecus* to the Hominoidea. It is not permissible, however, from this character alone, to allocate that fossil more precisely. Although the degree of its encephalic development is equivalent to that found in existing great apes, it does not of necessity follow that *Oreopithecus* belongs in the family of the great apes, the Pongidae. For one thing, we lack the truly requisite comparative data, since we are quite ignorant of the cranial capacities of the undoubted Lower Pliocene ancestors of the great anthropoids; hence we do not know whether the pongid brain of that time had as yet attained its present size. Nor does its relatively moderate cranial capacity necessarily exclude *Oreopithecus* from the family Hominidae; for a Lower Pliocene hominid would scarcely be expected to possess a brain as large as those of undoubted men, since it now is quite evident that the brain lagged behind the rest of the body during hominid phylogeny (*13*). Hence, despite brains that were of great-ape dimensions, the early Pleistocene "man-apes" of South Africa, the australopithecines, have not been denied admission to the Hominidae. Size of brain per se therefore would not debar *Oreopithecus*; for not only is its cranial capacity within the great-ape range, but it may well be as large, both absolutely and relatively, as those of some australopithecines (for example, *Australopithecus* [Sterkfontein No. 5]; see Table 1, column *a*). Thus, although the cranial capacity definitely identifies *Oreopithecus* as a member of the Hominoidea, it is of no aid in deciding whether this creature belongs in the Pongidae, the Hominidae, or a family of its own.

WILLIAM L. STRAUS, JR.
MIGUEL A. SCHÖN
*Department of Anatomy,
Johns Hopkins University,
Baltimore, Maryland*

References and Notes

1. P. Gervais, *Compt. rend.* **74**, 1217 (1872).
2. J. Hürzeler, *Verhandl. naturforsch. Ges. Basel* **65**, 88 (1954); **69**, 1 (1958); J. Kälin, *Experientia* **11**, 1 (1955); J. Piveteau, *Traité de Paléontologie, VII: Primates; Paléontologie Humaine* (Masson, Paris, 1957); W. L. Straus, Jr., *Science* **126**, 345 (1957); *Anat. Record* **132**, 511 (1958); G. Heberer, *Cold Spring Harbor Symposia Quant. Biol.* **24**, 235 (1959).
3. A. H. Schultz, *Z. Morphol. Anthropol.* **50**, 136 (1960); W. L. Straus, Jr., unpublished data.
4. We are greatly indebted, respectively, to the Wenner-Gren Foundation for Anthropological Research, New York (W. L. S., Jr.) and the Fundación Creole, Caracas, Venezuela (M. A. S.) for grants which made our trips to Basel and this study possible. We also are grateful to Dr. Johannes Hürzeler for the opportunity to study the actual skull of *Oreopithecus* and its plaster reconstruction.
5. J. B. Jørgensen and F. Quaade, *Am. J. Phys. Anthropol.* **n.s. 14**, 661 (1956).
6. The 21 skulls measured include representatives of all major groups of catarrhine primates: 4 Old World monkeys (2 macaques, *Macaca*; 1 baboon, *Papio*; 1 langur, *Presbytis*); 9 anthropoid apes (1 gibbon, *Hylobates*; 1 siamang, *Symphalangus*; 2 orang-utans; 2 chimpanzees; 3 gorillas); 1 australopithecine (*Australopithecus*: Sterkfontein No. 5); 3 fossil men (La Chapelle-aux-Saints and Gibraltar No. 1 Neanderthals, Rhodesian); and 4 modern men.
7. Each of the braincase volumes in Table 1 (column *b*) represents an average of three separate measurements. The volumes of the 4 fossil hominids were measured from standard plaster casts. Forty cubic centimeters have been subtracted from the measured *Australopithecus* volume because the infratemporal fossae are filled by foreign material, and 40 cc have been added to the measured La Chapelle-aux-Saints volume to account for defects in the skull. To prevent water from entering the cranial cavities of the actual skulls, all relevant foramina were first plugged with raw cotton and then sealed, together with any open sutures, with paraffin. In each instance, the volume measurement has been corrected to account for the paraffin and cotton. Corrections also have been made for prominent nuchal and sagittal crests; wherever feasible, these have been reconstructed in modeling clay (Plastolene), and the water displacement has been measured. The cranial capacities of the 4 fossil hominids have been taken from the literature. Those of all other skulls were measured by us, using small dried peas; each figure in Table 1 (column *a*) is an average of three separate measurements.
8. G. Gaul, *Z. Morphol. Anthropol.* **31**, 362 (1933); A. H. Schultz, *Contrib. Embryol. Carnegie Inst. Wash. No. 182* (1941), p. 57.
9. S. Zuckerman, *Proc. Zool. Soc. London* (1928), p. 1; A. H. Schultz, *Contrib. Embryol. Carnegie Inst. Wash. No. 170* (1940), p. 1.
10. A. H. Schultz, *The Anatomy of the Gorilla* (Columbia Univ. Press, New York, 1950), pt. V, p. 227.
11. A. H. Schultz, *Am. J. Phys. Anthropol.* **28**, 273 (194[illegible] *Proc. Am. Phil. Soc.* **94**, 428 (1950); *Irish J. Med. Sci.* (1957), p. 341.
12. A. H. Schultz, *Z. Morphol. Anthropol.* **50**, 136 (1960).
13. T. Edinger, *Confinia Neurol.* **9**, 5 (1949); *Year Book Am. Phil. Soc.* (1955), p. 119; W. E. Le Gros Clark, *The Antecedents of Man* (Quadrangle Books, Chicago, 1960); W. L. Straus, Jr., *Science* **119**, 265 (1954); S. L. Washburn, *Cold Spring Harbor Symposia Quant. Biol.* **15**, 67 (1950).
14. J. T. Robinson, *Transvaal Museum (Pretoria) Mem. No. 9* (1956), p. 1.
15. M. Boule, *Ann. Paléontol.* **7**, 85 (1912).
16. W. J. Sollas, *Ancient Hunters* (Macmillan, New York, ed. 3, 1924).
17. G. Elliot Smith, *Rhodesian Man and Associated Remains* (British Museum [Natural History], London, 1928), p. 52.

1 August 1960

Differential Sensitivity of Peripheral Retina to Intermittent White Light

Abstract. The ability of the eye to detect differences in the interruption rate of white light was investigated for various rates and for several locations on the temporal periphery of the right eye. The complex relationship previously reported was again found, but only for stimulation of the fovea. The results from the peripheral regions indicate that differential sensitivity is a decreasing function of the rate of intermittence.

Within recent years the differential sensitivity of the fovea to intermittent white light has been investigated several times, always with the same result (*1, 2*). Simply stated, the differential sensitivity appears to be a complex function of the rate of intermittence, decreasing as the rate of intermittence increases to 22.5 cy/sec, after which it increases sharply to the neighborhood of 35 cy/sec and then decreases again as the fusion point is approached. The luminance of the flickering source was such that fusion occurred in the neighborhood of 40 cy/sec for all observers. This effect has been found for numerous observers with different psychophysical methods and different on-