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Weights of bones and tissues at maturity and growth of the skeleton of rhesus (*Macaca mulatta*) and cynomolgus (*Macaca fascicularis*) monkeys.[a,b]

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[b]These experiments were begun in 1954 under the auspices of the U.S. Atomic Energy Commission and were supported until 1980 by the USAEC and its successor agencies, the U.S. Energy Research and Development Administration and the U.S. Department of Energy. Support was provided from 1981 to 1987 by the U.S. Nuclear Regulatory Commission, and the project was reinstated by the USDOE from 1988 to 1991.
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ABSTRACT

Between 1954 and 1983, two species of Macaques (cynomolgus and rhesus, both sexes, mainly adults) were used in investigations of the metabolism of ^{90}Sr, ^{238}Pu, and ^{241}Am at the Ernest Orlando Lawrence Berkeley National Laboratory, Berkeley, CA, and at the University of Rochester Medical School, Rochester, NY (study population later moved to the Delta Primate Center, Covington, LA), and in studies of reproductive physiology at the Yale University School of Medicine, New Haven, CN. In the course of those investigations, data gradually accumulated for the weights of the healthy whole body, all of the bones (fresh and ashed), and in some cases also of soft tissues. The study population ultimately comprised 86 female rhesus monkeys (58 adult, 28 immature), 34 male rhesus monkeys (16 adult, 18 immature), 39 female cynomolgus monkeys (33 adult, 6 immature), and 13 male cynomolgus monkeys (9 adult, 4 immature). All of the data have been compiled, and this report summarizes the body, tissue, and bone weights of healthy adults of the four species and sex groups and provides empirical descriptions of the growth of the body, the skeleton, and the major skeletal units of male and female Macaques.

The body proportions (fractions of body weight contributed by individual organs and tissues) are similar for the four Macaque species-sex groups (cynomolgus and rhesus, female and male). Data from the most suitable of these four species-sex groups can be used to estimate tissue and organ weights of other Macaque species through their body weight ratios. The overall proportions (whole skeleton fresh and ashed weight fractions contributed by individual bones or skeletal units) of the four groups of skeletons are similar but not identical. There are minor species- and sex-related differences (not all statistically significant). Within species (same species, female compared to male) the differences are fewer and smaller (rarely significant) than they are between species (same sex, different species). The most pronounced differences (significant) in the skeletal proportions of these two Macaques are the proportionally larger heads of the cynomolgus monkeys (both sexes) and their proportionally smaller lower limbs and pelvis compared with rhesus monkeys (both sexes). The skeletal data set for the most appropriate

species-sex group (taking account of sex, body type, and size) can be used to make reasonable estimates of he weights of the skeleton, bones, and major skeletal units of other Macaque species through their body weight ratio.

For females (males) of both species, growth rates of the body, skeleton, and major skeletal units are similar, when weight during growth is expressed as a fraction of weight at maturity. Growth of the body, skeleton, and skeletal units can be described by pairs of discontinuous exponentials (females 0 to 0.7 and 0.7 to 5 years of age; males, 0 to 1.1 and 1.1 to 7 years of age). The parameters of those expressions can be used to estimate the mass of the growing female or male Macaque skeleton and its major units from its known age or body weight.

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INTRODUCTION

Between 1954 and 1983, a monkey colony was maintained at the Ernest Orlando Lawrence Berkeley National Laboratory (LBNL) to conduct biokinetic studies of trace amounts of several important hazardous radionuclides—^{90}Sr, ^{241}Am, ^{238}Pu, ^{237}Np, and ^{233}U. During those years, wild-caught rhesus monkeys (adult and immature) and wild-caught cynomolgus monkeys (mainly adults) were injected with a radionuclide and killed at times from 1 day to 20 years after injection to measure radionuclide distribution, retention, and excretion.

Between 1954 and 1963, the toxicity, kinetics, and maternal transfer of fed or injected ^{90}Sr were investigated at the University of Rochester Medical School Atomic Energy Project (UR) using wild-caught rhesus monkeys (adult and immature). In 1963, the UR project was moved to the Delta Primate Center, Covington, LA, and in 1968 when the UR-Delta project was terminated, eight live monkeys and all project materials were transferred to LBNL. The ^{90}Sr dosages and experimental protocols of the UR-Delta project were sufficiently similar to those used at LBNL that the results of the two ^{90}Sr studies could be combined.

Body weights were monitored regularly in both colonies to assess general health. Autopsies were conducted to obtain bone and tissue weights for the purpose of calculating radiation doses to the tissues from internally deposited radionuclides, particularly the skeleton, to monitor skeleton and tissues for the presence of neoplasms, and to identify any radiation related tissue or bone changes. The rhesus monkeys in the ^{90}Sr studies at LBNL and UR-Delta provided whole body and bone weight data and some tissue weight data (age at death, 2.4 to 28 years). In the course of the studies of maternal transfer to ^{90}Sr, offspring were born to some ^{90}Sr-bearing mothers, and several of these young rhesus monkeys (newborn to 4.8 years) were eventually autopsied to obtain ^{90}Sr distribution and bone weight data. The cynomolgus monkeys in the actinide studies at LBNL provided whole body and bone weight and, in most cases, soft tissue weight data (age at death, 2.5 to >16 years).

Between 1959 and 1973, LBNL received eviscerated carcasses of some adult wild-caught female rhesus monkeys and of captive-born immature male and female rhesus monkeys from a breeding colony at the Yale University School of Medicine. In addition, skeleton material became available from a few young monkeys that died at LBNL soon after birth or died of infectious diseases shortly after arrival but before assignment to an experiment.

During the 10 years following closing of the LBNL monkey colony and completion of the associated laboratory work, the radionuclide and bone and soft tissue weight data that had been accumulating for nearly 30 years were systematically recalculated and entered on standardized coding forms and into a computer-based electronic archive.[1] Calculation methods were developed to account for missing skeletal parts and to partition the weights and radionuclide content of bones that had been managed as groups among the individual bones or bone types comprising the groups. [For example, apportioning the total weight of the combined bones of the upper spine between cervical and thoracic vertebrae and apportioning the total weight of the lumbar vertebrae between arches and bodies.]

In early 1991, the existence of this large and unique, but still unreported, file of detailed data for weights of tissues and bones of two Macaque species came to the attention of investigators at Health Canada, who were conducting a study of toxicity, kinetics, and maternal transfer of lead in female cynomolgus monkeys. The study protocol included measurements of body weight, blood lead, and lead in bone biopsy samples, but there were no measurements of total skeletal mass or total skeletal lead. In order to construct a physiologically and anatomically appropriate kinetic model of lead in individual monkeys, it was necessary to be able to (a) estimate total skeleton and skeletal mineral weights and total skeletal lead from the recorded mature body weight and the lead concentration in the biopsy specimens, and (b) to relate retained bone lead to skeletal growth for those monkeys that were placed on the high-lead diet before skeletal maturity.

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[1]The electronic archives of all the original data for each monkey, organized by radionuclide and animal accession number (Du90a;90b;93), are on file at the International Radiobiology Archives of Long-term Animal Studies, Richland, WA.

This report was prepared to assist the investigators in the Health Canada lead study in the analysis of their data. Both male and female monkeys were included in the LBNL and UR-Delta radionuclide studies and the skeletal materials obtained from the Yale colony. However, nearly three-fourths of the animals in those combined populations were females and the Canadian lead study included mainly females. For those reasons this compilation emphasizes the data for females. The results are presented in a general format and in sufficient detail to make the data useful to other investigators.

ANIMALS

The genus *Macaca* includes 12 species ranging in body size from 3.5 kg (female, *M. fascicularis*) to 18 kg (male, *M. arctoides*). The differences among the species are largely body size and external appearance, their comparative anatomy is similar, and they are genetically compatible (Na67; Be74). Although most of the work done by us and others on composition, morphometry, and aging of monkey bone (Go64;Va58;Be78;Sm79) has been with material from rhesus monkeys, gross and microscopic skeletal anatomy and temporal and spatial of patterns skeletal maturation appear to be similar for *M. fascicularis* (cynomolgus) and *M. mulatta* (rhesus). Most of the monkeys included in this compilation were purchased from animal importers; they were captured in the wild at 1 to 3 y of age. A few adults in the LBNL studies were obtained from other monkey colonies (retired breeders, excess stock, colony liquidation). More than one-half of the monkeys that were immature at death were born in the LBNL, UR-Delta, or Yale colonies. Chronologic age at injection or death was determined from laboratory records, purchasing records, skeletal roentgenograms (Va58), and dentition (Hu61).

1. Americium-injected monkeys

The kinetic studies of Americium (Am) in monkeys, were begun in 1960, because there were no metabolic data for this important nuclear by-product in animals larger or longer-lived than rodents (Du73). Between 1960 and 1981, 28 cynomolgus monkeys, (24 adult, three immature female; one adult male) and one adult male rhesus monkey were each given one intravenous

(i.v.) or intramuscular (i.m.) injection of ^{241}Am citrate at dosages from 3.7 to 32 $kBq.kg^{-1}$ (Du 90a). Dosages were selected based on our ability as of the date of the injection to detect the alpha activity, or after 1970 to detect the 59.5 keV photons, in blood samples, small tissues, and excreta collected at times after injection longer than 30 days. Blood or plasma was sampled periodically, and excreta were collected continuously. The Am-injected monkeys were serially sacrificed, except for one female euthanized after development of an osteosarcoma, at times from 1 to 2199 days after injection. Soft tissues were weighed, and all bones were weighed wet and ashed. All samples were radioanalysed. For monkeys scheduled to be killed at times longer than 30 days after injection, dosages were 16 ± 9 $kBq.kg^{-1}$, on average.

2. Plutonium-injected monkeys

The plutonium (Pu) studies in monkeys were begun in 1973, because the data for Pu metabolism in human beings were incomplete and unsatisfactory. In the interval 1973 to 1985, 25 monkeys [cynomolgus (nine adult and one immature female, five adult male); rhesus (four adult and two immature female, two adult and two immature male)] were given one i.v. or i.m. injection of $^{238}Pu(IV)$ in 0.08 M sodium citrate, pH 3.5. For monkeys scheduled to be killed at times longer than 30 days, dosages were 12 ± 0.8 $kBq.kg^{-1}$, on average. Four monkeys scheduled to be killed within a few days after injection received larger amounts. Blood or plasma were sampled periodically and all excreta were collected continuously. The animals were serially sacrificed at times from 2 hours to 1100 days after injection, except for one female that died in an anesthesia accident and one female that died from causes not determined, but apparently unrelated to the internal Pu irradiation. All soft tissues were weighed, and all bones and bone parts were weighed wet and ashed. All samples were radioanalysed.

3. Other actinides

Three male cynomolgus monkeys were used in 1985 in exploratory studies of other actinide elements: $^{237}NpO_2Cl$ was injected i.m. into two adults at dosages of 1.1 and 0.8 $kBq.kg^{-1}$, and they were killed at 4 and 757 days, respectively; $^{233}UO_2Cl_2$ was injected i.m. into one immature

animal (5 years old) at a dosage of 6.3 kBq.kg^{-1}, and he was killed at 3 days. Procedures were the same as those used in the Pu studies.

4. Strontium-injected monkeys

a. LBNL. The ^{90}Sr studies at LBNL were begun in early 1954 because of concerns about the health hazards of ^{90}Sr in worldwide fallout. They were designed to provide metabolic and dosimetric data in a species as closely related as possible to man. Between 1954 and 1981, 36 wild-caught immature and adult male and female rhesus monkeys, and one adult male cynomolgus monkey were injected with ^{90}Sr. Dosages in monkeys held for more than 1 year were, on average, 444 ± 187 kBq.kg^{-1} (range 220 to 904 kBq.kg^{-1}). Bone weight data were also available from three immature offspring of ^{90}Sr-injected mothers (two female, one male) and two males and two females chronically fed low dosages of ^{90}Sr (Du93).

The LBNL monkeys were killed or died at times from 1 day to 19.6 years after exposure. Causes of death were, as follows: serial sacrifice (29), infection or parasitism (7), accidents (4), euthanasia because of severe debilitation (3—endometriosis, uterine neoplasm, strangulated bowel). At death, 21 females and six males were adults, and 10 females and one male were immature. At autopsy, four of the males killed in adulthood showed signs of incipient "cage paralysis," a slow rarefaction of the lower limb bones and pelvis caused by restrictive caging in adolescence. The fresh and ashed weights of their bones and whole skeletons were within the ranges for other adult male rhesus monkeys, and their bone data were included in this compilation.

In all, detailed bone data are available from 43 monkeys in the LBNL ^{90}Sr studies: 27 adults (21 female rhesus, five male rhesus, one male cynomolgus) and 15 immature rhesus (12 female, three male).

b. University of Rochester. Between 1954 and 1963, at the University of Rochester Medical School (UR), ^{90}Sr was administered to 24 wild-caught rhesus monkeys that eventually provided bone data: 11 females and 11 males had been injected i.v. at dosages from 410 to 590 kBq.kg^{-1}. Six females and one male had been fed ^{90}Sr (dosages discussed below). In addition, bone data

were available from seven immature animals that had acquired ^{90}Sr by placental and/or milk transfer (Ca61,62;Gök62). In 1963, the live monkeys and all study records were moved to the Delta Primate Center, Covington, LA (Delta). When that program was terminated in 1968, five adult male and three nulliparous adult female ^{90}Sr-injected monkeys were shipped alive to Berkeley for inclusion in the ongoing LBNL study. In addition to skeletal roentgenograms and medical records of live and dead monkeys, LBNL received all the accumulated results of *in vivo* measurements of ^{90}Sr retention, bone weight and radioanalytical data, some bones fixed in 80% ethanol, and four complete dry skeletons (Du93). The UR-Delta monkeys were killed or died at times from 7 days to 16 years after their ^{90}Sr exposure. Causes of death were, as follows: serial sacrifice (14), infection or parasitism (8), accident (2), neoplasia (4—two radiation-related bone neoplasms, one gingival carcinoma, one laryngeal tumor), euthanasia because of severe debilitation (3—two inguinal hernias, one endometriosis), failure to survive delivery or birth (4—one mother, three newborns), unknown causes (2).

In all, bone data are available from 36 rhesus monkeys in the UR-Delta ^{90}Sr studies: 23 adults (15 female, eight male) and 13 immature (seven female, six male).

5. Uninjected monkeys

In collaboration with the late Dr. G. Van Wagenen of Yale University School of Medicine, we obtained whole skeletons of 18 wild-caught adult female rhesus monkeys ranging in age from 6.7 to 26 years and skeletons from six immature rhesus monkeys born in captivity (three male and three female, newborn to 4.8 years old). Details of caging, diet, and care in the Yale colony have been published (Va50).

Bone weight weight data were obtained from eight immature monkeys (newborn to 5 years) that died of infections or parasitism in the LBNL colony before radionuclide administration: rhesus, five female and one male; cynomolgus, one male and one female.

6. Complete study population

All bone data from the radionuclide studies and the uninjected monkeys were combined and sorted by species, sex, and age at death, yielding usable data for the following populations: rhesus female (58 adult, 24 immature); cynomolgus female (33 adult, five immature); rhesus male (16 adult, 16 immature); cynomolgus male (nine adult, three immature). The numbers of adult monkeys of each species and sex group furnishing soft tissue weight data are given in Tables 1 and 2. The numbers of immature monkeys for whom soft tissues were weighed are too small and their ages at death are too scattered to be useful, and those small data sets all not included in this compilation.

METHODS

1. Cages

a. LBNL. All animals in the LBNL colony lived continuously after arrival in separate cage units. From 1960 to 1970, monkeys injected with Am were kept in metabolic cages (0.53 m tall, floor area 0.20 m^2) constructed of sheet iron and screen coated with heavy-duty heat-cured paint. From 1954 to 1970, uninjected monkeys and the ^{90}Sr-injected animals were kept in the individual units of four-unit, galvanized metal cages 0.61 m high, with a floor area of 0.75 m^2 for large males, and 0.37 m^2 for all other animals. After 1970, all monkeys at LBNL were housed according to body size in stainless steel metabolic cages equipped with a squeeze mechanism: cage dimensions ranged from 0.7 to 0.9 m high with floor areas from 0.37 to 0.65 m^2.

b. UR. The monkey colony of the University of Rochester Atomic Energy Project, Radiation Toxicology Section, was located in an air-conditioned room, and the monkeys were kept in cages $0.9 \times 0.9 \times 1.2$ m, two or three to a cage.

c. Delta Center: All animals were housed individually in large sheltered outdoor cages furnished with a hutch for sleeping.

2. Diet

a. LBNL. From 1954 to about 1958, the monkey diet consisted of fresh fruit and vegetables, reconstituted dry milk fortified with protein, iron and vitamins, and "Chim biscuits" (supplier not known) (Du56b). Purina Monkey Chow (Ralston Purina Co., St. Louis, MO) was introduced as the dry food in about 1958; it was greasy and friable, and because it was rejected by many of the monkeys, a great deal of waste fell into the excreta collection pans hampering both collection and chemical processing. From 1961 to about 1970, infant teething biscuits and enriched bread were used as the dry food. In about 1970, the Purina Monkey Chow (Purina #5038, Ralston Purina Co., St. Louis, MO) was reformulated. It was cohesive and accepted by the animals, so there was little waste, and the calcium and protein contents had been increased so there was no longer a need for the milk supplement. Thereafter, the diet consisted of Purina Monkey Chow, fresh fruit and vegetables, and vitamin and iron supplements (Du85a). These individually cages monkeys were fed individualized diets, with quantities adjusted to maintain a steady growth rate, or in the case of adults, to maintain a reasonably constant weight and suppress obesity.

b. UR. Monkeys were fed a diet generally described as "an enriched high protein diet" (Gök62), and water *ad lib.*

c. Delta Center: Animals were fed Purina Monkey Chow and water *ad lib.* In addition to the food, an iron and vitamin C supplement and 50 mg of isonicotinic acid were given on 1/4 slice of orange 5 days per week.

3. Health care and colony management

Before 1963, monkeys caught in the wild were imported into the U.S. in large groups and delivered to buyers without quarantine. Monkeys brought to LBNL were initially housed in a separate room and treated for intestinal worms with oral vermifuges. Dehydration, fever, diarrhea, and vomiting were treated—not always successfully—with fluids, penicillin, and terramycin. Stool samples were examined for protozoa; all incoming animals were assumed to carry dysentery organisms and were given both oral and parenteral antiamoebic drugs until three negative stool samples were obtained.

After 1963, monkeys were imported into the U.S. in smaller groups and quarantined for several weeks by the importers. The monkeys that arrived at LBNL were generally in good health and free of life-threatening infectious GI tract organisms. However, as a precaution (later, an accreditation requirement) new animals were placed in an LBNL quarantine facility, where they were tested and treated until demonstrated to be free of tuberculosis, intestinal worms, and intestinal protozoa.

The long tails of cynomolgus monkeys were docked to about 10 cm length, and the upper canine teeth were removed from all male monkeys at about 5 years of age. All animals in the colony were examined two to four times a year. Physical examinations included the following: body weight, hemogram, TB test, inspection of eyes, ears, skin, teeth and genitalia, palpation for abdominal lumps, and evaluation of breathing and chest sounds.

Standards of housing, care, and cleanliness improved over the years, and the animal colony at LBNL was eventually accredited by the American Association for Accreditation of Laboratory Animal Care and is a Registered Research Facility (USDA Animal and Plant Health Inspection Service, license No. 93-210).

4. Anesthesia

Macaques of both species are physically strong and intractable unless physically restrained or sedated. Anesthetics and tranquilizing drugs and the periods of their use were, as follows: 1954 to 1966, barbiturates, mainly "Nembutal," occasionally supplemented by ethyl ether gas; 1960-1973, "Sernylan," a long-acting tranquilizer (phencyclidine hydrochloride, Parke-Davis or Bioceutic Labs.); 1973-1983, "Ketelar," (Ketamine hydrochloride, Parke-Davis); atropine sulfate (Hart-Delta labs.) was used to suppress salivation; Acepromazine (acepromazine maleate, Ayerst Labs., New York, NY 10017) was used as a muscle relaxant).

Before 1966, surgical procedures (tail docking, tooth extraction, repair of wounds), physical examinations, nuclide injections, and blood sampling were performed under barbiturate anesthesia. From 1966 to 1974, all of the above procedures and external measurements of

photon emissions were performed under Sernylan and Acepromazine tranquilization. After 1974, all procedures that required removing an animal from its cage for several hours were performed under repeated Ketelar tranquilization, except that Sernylan and Acepromazine continued to be used for specialized *in vivo* counting procedures that required complete immobilization. Blood samples taken many hours or days apart and intramuscular injections of nuclides were performed without sedation using only physical restraint or the squeeze-up apparatus of the cages. Records of anesthesia use at UR and Delta were fragmentary.

At UR, 30 $mg.kg^{-1}$ of pentobarbital (Nembutal) was apparently used when anesthesia was deemed necessary. At Delta, Sernylan was used for *in vivo* counting, marrow biopsies, and roentgenography.

5. Health records

Each animal was given a colony accession number (tattooed on the chest), and a medical history file was established. Those chronologic records, which were later incorporated into each animal's experimental file, include body weights, results of hemograms and TB tests, details of accidents, roentgenograms, surgical procedures, and treatment of infections or parasitism. No detailed accounts were available concerning management and animal health care at the UR and Delta Center monkey colonies, however, in-house veterinary care was available at both. Chronologic records from Delta (1964 to 1968) contain reports of regular physical examinations, which included TB test results, body weights, and hemograms. The health status of each monkey was evaluated at UR and verified at Delta at the time the colony was moved to the Delta Center, and the veterinary service at Delta evaluated, and we verified at LBNL, the good health of the monkeys sent to LBNL in 1968.

AUTOPSY PROCEDURES

General autopsy procedures were similar in the three Laboratories. Deviations from the LBNL procedures described below are noted in the appropriate sections.

1. Dissection

Under an overdose of Nembutal, Sernylan and Diabutal, or Ketelar and Diabutal the abdomen was opened, and as much blood as could be withdrawn was taken through a catheter set in the inferior vena cava into large heparinized syringes. The thoracic and abdominal organs were removed *en bloc*, examined, dissected cleanly, weighed, and placed in Pyrex beakers of appropriate size for drying and ashing. Samples of tissues taken for histology or autoradiography were weighed to account for the loss of their radioactivity from subsequent radioanalysis and fixed in 80% ethanol (specimens for autoradiography) or neutral formalin (for histology only). The contents of the gastrointestinal tract was removed, and the tissues were rinsed, blotted, and weighed. The carcass was skinned, and the pelt, along the subcutaneous fat, the ears, and the ischeal calluses, was placed in a tared beaker. All soft tissue removed in the skeletal dissection (muscle, fat, connective tissue) was placed in tared beakers, and weighed.

It was not always possible to deflesh a monkey carcass immediately after the animal was autopsied. In those cases, the bone samples to be used for autoradiography and their nuclide content control samples were removed; the remainder of the carcass with the pelt as intact as possible was stuffed with wet towels and wrapped in several layers of plastic and frozen in a sealed thick plastic bag. Frozen carcasses were thawed at room temperature before dissection.

2. Bones

The skeleton was disarticulated and defleshed with sharp blades; all parts were weighed wet. A standard set of defleshed, weighed bone samples was preserved in 80% ethanol for preparation of autoradiographs. The reserved bones included: right half of calvarium, right humerus, right 5th rib, first (later on also third) lumbar vertebrae, and after 1974 two central sternebrae. The left half of the calvarium, left humerus, left 5th rib, second lumbar vertebra (all remaining separated lumbar vertebrae), and the remainder of the sternum were weighed wet and ashed and radioanalyzed to account for the parts removed for autoradiography (see Appendix Calculations). Defleshing the bones of a monkey was a painstaking procedure usually requiring the effort of two technicians for two to three working days. Bones were weighed immediately

after defleshing; drying was suppressed by wrapping parts of the skinned eviscerated carcass remaining to be defleshed in wet towels and refrigerating them in tightly closed plastic bags. Defleshed bones that were to be divided were collected, wrapped in wet towels and refrigerated in plastic bags, until near the end of each work day, when all bone sawing was done at one time. Bones were divided with a Stryker bone saw behind a thick plastic shield in a fume hood lined with waxed paper. When sawing of bones was completed, the bonedust was wiped from the shield and the hood floor with damp tissues, which were collected in a beaker. When defleshing of a whole skeleton was complete; all the collected bonedust was ashed.

The wrists and hands (hand bones), ankles and feet (foot bones) and the cervical, thoracic, and caudal vertebrae (tail) are groups of small bones that are difficult to deflesh completely; in most cases they were roughly cleaned without disarticulation. Their fresh weights were estimated from their measured ash weights and the ash fractions of those bone assemblages determined for several monkey skeletons that were defleshed with special care. The teeth were removed from skull and mandible after ashing; their fresh weights were estimated from the average ash fraction of extracted fresh monkey teeth (see Appendix Calculations).

The degree of subdivision of bones into structurally distinct parts (e.g, compact bone, cancellous bone in red marrow, cancellous bone in fatty marrow) evolved as knowledge was gained about the relationships between bone structure and physiology and radionuclide behavior, and as radioactivity detection devices were improved and radioanalytical procedures were refined to obtain accurate analyses with less labor. (i) Bones formerly analyzed intact, were physically divided into anatomically distinct parts (see Fig. 1). (ii) Bones of similar structure, initially analyzed as groups (e.g., lumbar, sacral, and caudal vertebrae all combined), were analyzed as separate samples, and still later, arches and bodies of individual vertebrae were divided and analyzed separately. (iii) The early practice of combining the costal cartilages with the sternum was stopped, when it was realized that the variably mineralized cartilages cores contributed a significant fraction of the ash weight but only a small and variable fraction of the nuclide content of the combined sample.

a. Original bone protocol, 1954. Most of the bones of the six cynomolgus and 19 rhesus monkeys dissected at either LBNL or UR before 1963 were weighed and radioanalyzed undivided and in groups. The following bones were grouped into seven samples: (i) costal cartilages and sternum (cc + st). (ii) all bones of wrists, hands, ankles, and feet (h + f), (iii) cervical and thoracic vertebrae (CV + TV), (iv) last five lumbar vertebrae, sacrum, and tail (LV (3-7) + sacrum + tail), (v) ends of all long bones except humerus and clavicles, (vi) shafts of all long bones except humeri and clavicles, (vii) intact left humerus.

b. Changes in bone protocol, 1963. Skeletal dissection was improved to include separation of the variable number of caudal vertebrae from the combined lower lumbar vertebrae and sacrum, and in early 1964 to include division of the humerus, and most other long bones, into ends and shafts. Eighteen cynomolgus and 69 rhesus monkeys were dissected between 1963 and 1973.

c. Changes in bone protocol, 1974. Major refinements in the skeletal sampling protocol were introduced to obtain more detailed data on the non-uniform nuclide distributions in the different skeletal structures. The new procedures were as follows: (i) sternum and costal cartilages were separated; (ii) cervical and thoracic vertebrae were separated; (iii) sacrum was separated from the lower lumbar vertebrae, (iv) each of the four lower lumbar vertebrae was divided by sawing into body and arch (see Fig. 1). (v) The proximal and distal ends of each pair of long bones (previously combined and analyzed as "ends" samples) were analyzed separately; (vi) bones of the wrists and hands were weighed and analyzed separately from the bones of the ankles and feet. Fifteen cynomolgus and 24 rhesus monkey skeletons were dissected and radioanalyzed between 1974 and 1981.

d. Changes in bone protocol, 1981. In late 1981, data from more extensively subdivided monkey skeletons were needed to aid interpretation of radiochemical analysis of a thoroughly subdivided human skeleton (Br85) . Ten cynomolgus and six rhesus monkey skeletons were dissected after 1981 according to a sampling protocol with the following additional refinements: (a) The cervical and thoracic vertebrae (except for CV1, atlas, which was analyzed intact) were

divided into arch and body as shown for LV2 in Fig. 1, and the arches and bodies of adjacent pairs of vertebrae were analyzed together (e.g., CV2 plus CV3 arches; TV1 plus TV2 bodies. (b) The assemblages of small bones of the wrists and hands and of the ankles and feet (previously analyzed as two samples, hands and feet) were disarticulated, cleanly defleshed and grouped for analysis into six sets of similar bones—carpals, metacarpals, hand phalanges, tarsals, metatarsals, and foot phalanges: (c) The clavicles were divided into sternal and acromial ends and shaft in the manner used for the large long bones (Fig. 1). (d) Scapulae and pelvis were divided as shown in Fig. 1. (e) The cranium, from which the calvarium had routinely been separated, was further divided by straight saw cuts into three samples with somewhat different ash fractions and cancellous bone contents—(i) zygomatic processes, (ii) facial bones and frontal bone posterior to the superciliary ridge, and (iii) the bones that constitute the base of the cranium, occipital bone and the temporal bones posterior to the zygomatic process and the attachment of the temporal muscles.

3. Salvage of vertebral samples

Early analysis of the nuclide data emphasized deposition and retention in the whole skeleton. As entry of the detailed bone distribution data on standardized summary forms proceeded and the first sets of autoradiographs were developed, it became plain that dosimetrically important details of intraskeletal distribution of radionuclides had been missed in the dissections and radioanalyses completed before 1974. Twenty-two nuclide-injected cynomolgus and 49 rhesus monkeys had been dissected using bone protocols which yielded no measurement of nuclide concentration in nearly homogenous cancellous bone (e.g., sternum or separated thoracic or lumbar vertebral bodies). To correct that omission, at least in part, all unused whole vertebrae (LV3) or remnants of cut vertebrae (LV1) were salvaged from the bone sets that had been fixed and stored in ethanol for autoradiography. Vertebral body and arch were divided, dried, ashed, weighed, and analyzed for radionuclide, providing at least one measurement of ash content and concentration in a specimen of LV arch and/or LV body for all but 11 of the nuclide-injected monkeys.

4. Drying and ashing

Tissue and bone samples were dried at 100°C. Beakers containing dried muscle, skin, or the mesentery were weighed, liquid fat was decanted, and the beakers were reweighed to obtain the weight of the discarded fat. The dried samples were ashed in a furnace at 550°C as long as necessary to reduce them to a grey ash. Ash weights of the bones were recorded.

CALCULATIONS

1. Presentation of data

All measurements (weights of whole body, tissues, and fresh and ashed bones) and calculated relationships (fractions of body weight, ash fractions of bones, and weight fractions whole fresh and ashed skeleton) are presented as mean ± SD, where $SD = [\sum dev^2(n-1)^{-1}]^{1/2}$. Significant is used throughout in the statistical sense (*t*-test, $p \leq 0.01$) (Fi54). All values shown in the Tables of data are rounded to two significant figures, however, statistical tests used the original unrounded values. Discrepancies in sums are due to rounding.

2. Accounting for missing skeletal parts and partitioning weights of bone groups

It was necessary to account for the ash weights of the skeletal parts that had been reserved for autoradiography, and to estimate realistic wet weights for the bone samples or bone groups that were not weighed wet (teeth), not disarticulated or incompletely defleshed (hands, feet, portions of spinal column). Many of the bones from monkeys in the early radionuclide studies were grouped for weighing and radioanalysis. It was necessary to partition (by calculation) the total weight of the grouped bones among their components in order to be able to include their bone data in the present analysis.

The calculations are based on anatomical principles and observed relationships among the fresh and ashed bone weights in bones of cynomolgus (16 female, nine male) and rhesus (19 female, 11 male) adults that were completely disarticulated, defleshed, and well subdivided, as follows: i) There is left-right symmetry. ii) Each bone or distinctive part of a bone contributes a nearly constant fraction of the total wet and ashed weights of a specific group of bones and of the

whole skeleton. iii) In the absence of disease or trauma, the individual bones and their distinctive anatomical parts have nearly constant ash and soft tissue fractions.

Potentially useful relationships among the weights of the components of bone groups and the whole bone group or other skeletal parts were tabulated for cynomolgus and rhesus females and males. Mean ± SD were computed for each group separately, and group means were tested to determine if differences were statistically significant. Where no significant species differences existed, data for all monkeys were combined. There were some species-related differences in the weight and structural parameters of the lumbar vertebrae. Data from the well subdivided Macaque skeletons were used for the calculations that account for missing vertebrae, partition combined samples of lower lumbar spine-plus-sacrum (in some cases also -plus-tail) into their components, and partition the lumbar vertebrae into arch and body fractions (see Appendix).

RESULTS

1. Suitability of tissue and bone weights

Three-fourths of the Macaques (both species, both sexes, all ages) that provided the tissue and bone weight data presented here were injected with a radionuclide. It is prudent to question whether those weights are within normal limits for uninjected monkeys of the same origins, species, sex, and age. The radionuclide studies using these monkeys were designed to quantify normal mineral biokinetics, and the radionuclide dosages used at LBNL were kept as low as possible to avoid altering the normal rates of tissue renewal (cell death and replacement) and of ion exchange, growth, and maintenance remodeling in the skeleton.

a. Radiation effects in other species. Large amounts of retained, internally deposited, alpha-emitting radionuclides (^{226}Ra, ^{239}Pu, ^{241}Am) eventually deliver damaging radiation doses to the skeleton and/or liver. Cumulative, clinically detectable, radiation dose related skeletal and liver damage has been observed in dogs at 2 to 5 years after injection of large dosages of those radionuclides. Skeletal damage is seen at 5 years after > 2 kBq.kg^{-1} of ^{226}Ra, and skeletal and liver damage are seen at 2 to 5 years after injection of > 33 kBq.kg^{-1} of ^{241}Am or > 11 kBq.kg^{-1} of

^{239}Pu (Ta72a, 72b). Skeletal damage was not observed in dogs followed for up to 13 years after injection of dosages of ^{90}Sr ranging from 19 to 3700 kBq.kg^{-1} (LI70).

Whole body retention of radionuclides that emit externally detectable photons was followed by *in vivo* whole body counting of several groups of dogs injected at dosages from 1.5 to 370 kBq.kg^{-1} of ^{226}Ra, 0.07 to 166 kBq.kg^{-1} of ^{241}Am, or 0.02 to 11 MBq.kg^{-1} of ^{90}Sr. Only at the highest dosage of ^{226}Ra was bone damage severe enough to suppress normal mineral turnover and prolong radionuclide retention in the skeleton (LI70). Skeletal changes related to severe radiation damage by the highest dosages of ^{226}Ra or ^{239}Pu include accelerated loss of teeth, loss of mandibular aveolar bone, fractures of the ribs and vertebral processes, and plugged Haversian canals in cortical bone (Je62; Ta72a). Very large dosages of bone-seeking radionuclides in growing rats and mice severely retard and stunt skeletal growth: > 107 MBq.kg^{-1} of ^{89}Sr, >74 kBq.kg^{-1} of ^{226}Ra, > 296 kBq.kg^{-1}of ^{239}Pu (He48).

b. Americium-injected monkeys. One monkey that received 13 kBq.kg^{-1} of Am developed an osteogenic sarcoma at 1037 days. Some evidence was found of mild transient cellular damage in those livers that still contained more than a few percent of the injected Am at times longer than 6 months after injection. No other changes in soft tissue or bone were seen that were unequivocally related to internal radiation.

c. Plutonium-injected monkeys. No monkeys developed a neoplasm or blood dysacrasia during the short course of this study. Some evidence was found of mild transient cellular damage in those livers that still contained more than a few percent of the injected Pu at times longer than 6 mo after injection. Decalcified sections of bone from the four longest held Pu-injected monkeys (1.5 to 3 years) revealed no unequivocal radiation damage.

d. Strontium-injected monkeys. (i). *LBNL Studies:* The largest dosage of ^{90}Sr administered to a monkey in the LBNL studies was 650 kBq.kg^{-1}, about one-half of the smallest dosage shown to induce bone tumors (osteosarcoma) in dogs within 10 to 14 years after injection (Wr83). No bone tumors were seen in these ^{90}Sr-injected monkeys (mean dosage 433 $\pm$ 130 kBq.kg^{-1}; mean observation time 9.1 $\pm$ 5.3 years, range 1.2 to 19.6 years). Blood dyscrasias associated

with radiation (pancytopenia, leukemia) were not observed in the semi-annual hemograms obtained from the LBNL animals. Before 1960, several monkeys died from anemia caused by *E. histolytica*; active red marrow was found in the usual sites at death. In 1960, quarantine of new animals was instituted, stool examinations became routine, suitable drugs became available to eliminate intestinal protozoans, and deaths associated with anemia ceased. Three males injected with ^{90}Sr as adults and observed for more than 10 years developed corneal opacities, but without data from uninjected monkeys of the same ages, it is not possible to discriminate between a radiation effect and normal aging. About 5.6 years after injection of 650 $kBq.kg^{-1}$ of ^{90}Sr, one male injected in adulthood developed a squamous cell carcinoma of the gingiva that could have been induced by the radioactivity in the underlying bone.

(ii) *UR Studies:* During the time that adult rhesus monkeys injected with ^{90}Sr at UR were housed at the Delta Primate Center (1964 to 1968), radiation-related effects were sought, as follows: roentgenographic studies were made of the long bones to look for sites of altered bone structure; polymorphonuclear leucocyte lobulation was investigated; bone marrow cytology was studied; peripheral lymphocytes and bone marrow cells were cultured to look for chromosome aberrations. Roentgenographically, no significant differences in the structure of long bones were found between ^{90}Sr-injected monkeys and controls (Tu67a). Polymorphonuclear leucocyte lobulation and numbers of aberrant lymphocyte or bone marrow chromosomes were within control ranges. Bone marrow cytology deviated slightly from controls but was not considered significant (Pa68).

e. Strontium-fed monkeys at UR. Among 10 monkeys fed ^{90}Sr, two were adults (mean body weight 6.8 kg) and eight were immature (mean body weight 4.1 $\pm$ 0.7 kg). No measurements were made of the fraction of fed ^{90}Sr absorbed from the GI tract. If it is assumed that GI absorption by the monkeys was 30% (adults) to 40% (immature) of the amount fed (within the ranges for absorption of Ca and Sr in mature and growing human beings, ICRP74), the systemic uptake of ^{90}Sr would have been as follows: for the growing monkeys fed 18.5 to 37 $MBq.kg^{-1}$, absorbed dosages would have been from 2600 to 4100 $kBq.kg^{-1}$; for the adults fed 2.7 to

4.8 MBq.kg–1, estimated absorbed dosages would have been 810 to 1440 kBq.kg^{-1}. One growing monkey with an estimated absorbed dosage of 4100 kBq.kg^{-1} died of marrow aplasia at 131 days, and two growing monkeys with estimated absorbed dosages of 3570 kBq.kg^{-1} developed bone tumors at about 1200 days (Tu60;Ca61,62). The absorbed dosages estimated for the immature monkeys are all greater than the minimum injected ^{90}Sr dosage that induced marrow aplasia and/or bone tumors in young adult dogs (1300 kBq.kg^{-1}, Wr83).

f. Summary of findings in injected monkeys. The largest dosages of injected radionuclides in monkeys held for more than one year in the LBNL and UR-Delta studies (30, 11, and 580 kBq.kg^{-1} of ^{241}Am, ^{238}Pu, or ^{90}Sr, respectively) were at or below the thresholds for alteration of bone structure observed at comparable post-injection intervals in dogs. The monkeys possess a biliary excretion pathway for both Am and Pu, consequently, damaging amounts of those radionuclides were not retained in their livers; mild damage seen within weeks after injection was repaired, and there was no permanent atrophy or reduction of liver weight (Du73,85).

The dosages of ^{90}Sr in the long-held rhesus monkeys were all $\leq$ 950 kBq.kg^{-1} taken into blood; no measurable structural changes or damage were seen in the bones of dogs observed up to 13 years after injection of ^{90}Sr in that dosage range (LI70). Terminal radiographs of the skeletons of many of the Sr-injected rhesus monkeys observed for times as long as 20 years after injection revealed no rarefactions of skull or long bones, nor was there evidence of recent or repaired fractures of ribs or vertebral processes, the most prominent skeletal changes seen in human beings with long-standing burdens of ^{226}Ra (Lo54).

The total fresh and ashed weights of the whole skeleton and the major skeletal units were compared for two groups of adult female cynomolgus monkeys injected with an alpha-emitting radionuclide: those killed at post-injections times less than 1 year (when radiation damage in dogs given the highest dosages of ^{226}Ra begins to be evident), and those kept for longer times after radionuclide injection. In nearly all cases, the mean weights of the total skeleton and major skeletal units were the same for the monkeys killed early (accumulated radiation doses to the skeleton still small) and those killed at longer times after radionuclide injection (greater accumulated radiation

doses to the skeleton). Only one male cynomolgus monkey was held longer than 1 year after injection of an alpha-emitting nuclide, so no direct comparison was possible between animals with greater or lesser radiation doses. It was assumed that the results obtained for the females (no significant effect of their internal irradiation doses on bone or tissue weights) also applied to the males. Soft tissue, bone, and skeletal weights of the injected cynomolgus monkeys are considered to be within normal limits, and data for all of these animals (killed early or at longer times after an actinide injection) were combined into four appropriate sex-age groups.

A comparison was made of the skeletons of 35 wild-caught adult female rhesus monkeys injected with ^{90}Sr and held for more than one year in the LBNL or UR-Delta colonies (Appendix Table 1) and the skeletons of 16 wild-caught uninjected adult female rhesus monkeys housed for the duration of life at Yale (Appendix Table 2). There were no significant differences between the skeletal parameters of the two groups, even though the mean body weight of the Yale group (8.3 ± 1.4 kg) is significantly greater than that of the LBNL-UR group (6.4 ± 1.5 kg). It appeared that the housing and diet conditions at LBNL-UR were less conducive to post-maturity accumulation of body fat than those at the Yale colony, but more importantly, the cumulative radiation doses from the retained ^{90}Sr were not large enough either to diminish or increase the mass of the individual bones or the whole skeleton. Grand means were therefore calculated for the parameters of the whole skeleton, the major skeletal segments, and individual bones for a total of 58 wild-caught adult female rhesus monkeys housed for duration of life in the three colonies. When account is taken of the considerable differences in caging at the three colonies, the tabulated bone data presented here can be considered to be representative of female rhesus monkeys caught in the wild at 1 to 3 years of age and held thereafter in captivity.

Bone and tissue weight data are available only from nuclide-injected, wild-caught adult male rhesus monkeys. Within that group of 16 animals, only five were killed at times less than 1 year after nuclide injection, too few to define a low radiation dose sub-group that would serve as a substitute for uninjected controls. Based on (a) the equivalent bone weights of injected and uninjected wild-caught adult female rhesus monkeys, (b) the equivalent bone weights of the two

sub-groups of wild-caught adult female cynomolgus monkeys (smaller vs. larger radiation dose), and (c) the absence of changes in skeletal reotgenograms, it was assumed that the internal radiation doses in the adult rhesus males (13 of 16 received the beta emitter, ^{90}Sr) had no discernible effect on the weights or degree of mineralization of their bones.

2. Body composition of adult Macaques

a. Management of data. (i) *Weight of whole body*: Monkeys at LBNL were weighed twice yearly at the time of their physical examination and at the UR-Delta colony just before *in vivo* measurement of ^{90}Sr retention. Body weight, which was regarded as a general indicator of health status, was also used to adjust dosages of tranquilizers and radionuclides, and at LBNL, to adjust food intake. In addition, animals were weighed on arrival in the colonies, just before a radionuclide injection, and at autopsy. The number of measurements of body weight of individual monkeys varied widely, from only a few for monkeys injected with a radionuclide immediately after release from quarantine and used in a short-term study to numerous for animals whose radionuclide retention was followed for many years. Each monkey provided one set of bone weight data. To insure that the body weight data set conformed with the set of skeletal measurements and to avoid overrepresentation by the long held animals, the weight data for each adult monkey was reduced to a single value: The mean body weight in good health was computed for each adult, from 4.5 years of age to death for females and from 6.5 years of age to death for males. Measurements made during and for 6 months after a pregnancy, rapid weight gains (gradually reduced by limiting food intake), and rapid weight losses before death or euthanasia due to illness were excluded. All of the body weight data for each growing monkey were plotted against age. In animals other than those killed serially, the healthy body weight was extrapolated from its growth curve to insure that weight at death reflected the expected upward trend.

Monkeys in the Yale rhesus colony were weighed frequently (Va56), but only one value of body weight in good health was provided for the animals whose carcasses were received at

LBNL, and those reported weights apparently did not exclude unusually high values caused by obesity or pregnancy or low values caused by illness.

The body weights reported here (Tables 7 and 9) for mature wild-caught female and male rhesus monkeys are within the ranges reported for wild-caught monkeys of this species (Na67). They are within the ranges reported at maturity for female and male rhesus monkeys born and raised in captivity (many formula fed), but are about one SD below those reported means (differences not significant) (Va56).

(ii) *Soft tissues*: The monkeys included in Tables 1 and 2 provided fresh weights for at least five of the following organs (liver, kidneys, heart, lungs, spleen, brain, gonads), the pelt and/or empty GI tract, and the whole body and fresh skeleton plus teeth and tail. "Other soft tissue" (which includes muscle, fat, connective tissue, blood, blood vessels, nervous tissue) was estimated as the difference between the healthy body weight and the summed organ weights. A default value was calculated for each unweighed organ based on the animal's body weight and the measured proportional weight of that tissue in other monkeys of the same species-sex group.

(iii) *Teeth*: Most of the adult monkeys included in this compilation were subjects in metabolic studies with radioactive metal ions. Only a small fraction of an injected foreign metal ion becomes associated with mature erupted teeth, and then only on the dentinal surfaces of the pulp cavity and the cemental surfaces of the roots (Du73). Although the teeth experience wear, they are not subject to structural maintenance remodeling as are the bones, and for the purpose of characterizing the metabolism of a metal ion, the teeth should not be considered part of the skeleton. The large upper canine teeth were routinely extracted from males before they reached maturity, and there was age-related tooth wear and some random tooth loss in older animals. Consequently, few monkeys that died or were killed at ages > 10 years possessed their full complement of adult teeth. The weight of the monkey teeth was not closely coupled to skeleton weight, and it ranged from 1.7 to 3.0% of skeleton weight, respectively, in rhesus males and cynomolgus females. For all of those reasons, the weights and radionuclide content of the teeth were managed separately from the skeleton.

(iv) *Tail*: The Macaque tail is a species characteristic. The rhesus tail is short and stubby, while that of the cynomolgus monkeys is long and curling. The metabolism studies required all monkeys to be housed individually in cages that allowed quantitative collection of excreta, in some cases continuously for several years. For reasons of hygiene and to improve excreta collections, the tails of the cynomolgus monkeys were docked to a short, but variable length. The weight of the tail ranged from 1.8% of skeleton weight in the rhesus monkeys to 4.3% in the female cynomolgus monkeys. The metabolic data obtained in the monkeys was intended for use in constructing metabolic models of the study radionuclides suitable for application to human beings. Because human beings have no tail, and because the size of the tail (weight and mineral content) varied, a decision was made early in the metabolic studies not to include the weight or radionuclide content of the tail as part of the skeleton.

For completeness, the data for the fresh weights of the teeth and tail are included in Tables 1 and 2, and the mean fresh and ashed weights of the teeth and tail are given in the footnotes to Tables 3, 5, 7, and 9 for each species-sex group.

b. Cynomolgus monkeys. All 33 female and nine male cynomolgus adults were completely dissected, their major soft tissues and all bones were weighed, and their body compositions could be reasonably well described. However, the brain and gonads and the empty GI tract were weighed for only about one-half of the animals. The weights of the major soft tissues and mineralized tissues and the individual tissue fractions of total body weight are compiled in Table 1 (females) and Table 2 (males). The mean healthy body weights of these monkeys were used with their bone data (Tables 3 and 5) to calculate the body weight fractions of their major skeletal units (Tables 4 and 6).

c. Rhesus monkeys. Among the adult rhesus monkeys that were eventually skeletonized, 21 of 58 females and nine of 16 males were dissected sufficiently completely to provide a reasonable description of body composition. The weights of major soft tissues and mineralized tissues and the individual tissue weight fractions of body weight are compiled in Table 1 (females) and Table 2 (males).

Most of the adult rhesus monkeys had been used in ^{90}Sr metabolism studies, in which the skeleton is the only significant organ of nuclide deposition. The viscera and the soft tissue removed in the skeletal dissection (pelt, muscle, connective tissue, etc.) of 19 females and seven males had been pooled for radioanalysis, but not weighed. The carcasses of 18 wild-caught adult female rhesus monkeys received from the Yale colony had been eviscerated and stored frozen for varying periods of time before defleshing the skeleton; the variably dried soft tissue was not weighed. The healthy weights of those incompletely dissected monkeys (37 female and seven male) and their bone data were combined with the body weight and bone data from the completely dissected animals. Tables 7 and 9 present the data for bone weights, and Tables 8 and 10 present the body weight fractions of the major skeletal units.

The population sub-group of adult female rhesus monkeys that contributed both soft tissue and bone weight data (Table 1) includes only animals that had been housed in the LBNL colony, where body weights were stabilized by individually adjusting food intake (mean body weight, 6.0 ± 1.6 kg). Consequently, the sub-group in Table 1 does not include soft tissue or mineralized tissue data from any of the heavier (fatter) *ad lib* fed, wild-caught animals kept for duration of life at the Yale, UR, or Delta colonies. The heavier animals are included in the grand mean body weight for all 58 wild-caught adult female rhesus monkeys (grand mean body weight, 7.0 ± 1.7 kg), and their bone data are included in the compilations of Tables 7 and 8.

d. Comparison of species. (i) *Female*: The mean body weight of the adult cynomolgus females is 58% of that for rhesus females (Table 1). The ratios of the weights of most tissues are within ± 10% of the female species ratio of body weight (cynomolgus/rhesus). Weights of kidneys and heart of the cynomolgus females are about 30% greater and those of the spleen and ovaries, three and two times greater, respectively, than is predicted by the species body weight ratio. The overall agreement of the body weight fractions of the individual tissues of adult females of these two Macaque species (significantly different only for spleen) suggests that errors will be small, if data for females of one species are used to estimate tissue weights of females of the other species through their species body weight ratio.

(ii) *Male*: The mean body weight of the adult cynomolgus males is 68% of that for adult rhesus males (Table 2). The ratios of the weights of only one-half of the individual tissues are within ± 10% of the male species ratio of body weight (cynomolgus/rhesus). Weights of heart and lungs of the cynomolgus males are about 35% less and those of the spleen, pelt, and testes are 30 to 60% greater than is predicted by the species body weight ratio. The body weight fractions of most tissues of adult males of the two Macaque species are similar (significantly different only for heart, lungs, and pelt) suggesting that data for males of one species can be used to estimate tissue weights of males of the other species through their species body weight ratio, but the errors of such estimates will be larger than those for females.

e. Comparison of sexes. (i) *Cynomolgus monkeys*: The mean body weight of the adult female cynomolgus monkey is 55% of that for adult cynomolgus males (Tables 1 and 2). The ratios of the weights of the large tissues (pelt, other soft tissue, mineralized tissues) are within ± 20% of the cynomolgus sex ratio of body weight (female/male). The weights of all of the female organs are 25% (liver) to 55% (brain, kidneys) greater than is predicted by the body weight ratio. The body weight fractions of the organs and mineralized tissues of the females are 30 to 70% greater than in the males (significant for heart, lungs, spleen, and brain), because, compared with the males, cynomolgus females are less muscular and tend to accumulate less body fat.

(ii) *Rhesus monkeys*: The mean body weight of the adult female rhesus monkeys is 64% of that for the adult rhesus males (Tables 1 and 2). The ratios of the weights of most of the tissues are within ± 20% of the rhesus sex ratio of body weight (female/male). The weight of the female heart is 30% smaller and the weights of the kidneys, brain, and teeth of the females are 30 to 40% greater than is predicted by the body weight ratio. The body weight fractions of the rhesus female organs and mineralized tissues are generally similar to those of the males, and only the proportional contribution of the female brain is significantly larger. As is the case for the cynomolgus monkeys, the body weight fraction of other soft tissue of the female rhesus monkeys is less than that of the more muscular males.

3. Composition of the adult Macaque skeleton

Weights of the whole fresh bones include periosteum, articular cartilages, and marrow. Individual bones (e.g., pelvis, sternum), paired bones (e.g., humeri, scapulae), and groups of structurally similar bones (e.g., ribs, bones of hands and wrists) are referred to hereinafter simply as bones or groups of bones. All of the bones were weighed, except as noted below, immediately after dissection (fresh weight) and after ashing (ashed weight). Total skeletal dissections were completed for 33 adult female (Table 3) and nine adult male (Table 5) cynomolgus monkeys caught in the wild at various ages and housed thereafter in the LBNL colony and 58 adult female (Table 7) and 16 adult male (Table 9) rhesus monkeys caught in the wild, usually before maturity, and housed thereafter in the LBNL, UR, Delta, or Yale colonies.

It should be re-emphasized that only the ashed weights of the vertebrae and hand-wrist and foot-ankle bones were measured for every monkey skeleton. Those groups of small structurally complex bones are especially difficult and time consuming to dissect cleanly, and that extra effort was made only for a few representative monkey skeletons of each sex and species. The fresh weights of those bone groups in all other monkey skeletons were estimated from their measured ashed weights and the mean ash fractions of each bone group obtained from the smaller sub-populations (11 cynomolgus and 11 rhesus monkeys, male and female, see Appendix).

Three skeletal parameters (shown in Tables 3, 5, 7, and 9) were calculated for each bone and bone group describing the degree of mineralization and the skeletal proportions: Ash fraction: ash weight bone (g)/ fresh weight bone (g), expressed as percent mineral in whole fresh bone; fraction of fresh skeleton weight: fresh weight bone (g)/ fresh weight skeleton (g), expressed as percent of total fresh skeleton weight; fraction of ashed skeleton weight: ashed weight bone (g)/ ashed weight skeleton (g), expressed as percent of total skeleton ash. The ash fractions of the four species-sex groups (Tables 3, 5, 7, and 9) can be used to estimate unmeasured wet or ashed bone weights; the fresh and ashed weights of bones can be used to estimate total skeleton weights; total skeleton weights can be used to estimate weights of individual bones.

a. Variability within species and sex groups. Within-group variability was examined by calculating the coefficient of variation (V) (eqn. 1) of the body weight and the fresh and ashed weights of the whole skeleton of each species-sex group,

$$V = 100 \times SD.\bar{x}^{-1} \quad (1)$$

where $\bar{x}$ is the mean of the variable of interest, and SD is its standard deviation. Within each of those four groups, the average coefficient of variation ($\bar{V}$) was calculated for the five measures of size, mineralization, and skeletal proportions of its set of individual bones or groups of structurally similar small bones (20 bones or bone groups, costal cartilages excluded).

The body weights of the larger groups of adult Macaque females are more variable [V is 24% (rhesus) and 26% (cynomolgus)] than those of the smaller groups of males of the same species (V is 17 and 19%, respectively). However, the variabilities of the skeleton weights are nearly the same for the four species-sex groups. The fresh and ashed weights of the whole skeletons of the four species-sex groups are remarkably consistent (V ranges from 14 to 20%), considering the ranges in age, internal radiation history, and residence times in four colonies with differing diets and housing arrangements.

Overall, the variability of bone size and mineralization shown for the individual bones in Tables 3, 5, 7, and 9 was the least for the large long bones, pelvis, mandible, and scapulae, which have well defined and easily cleaned exterior surfaces and undergo little change after maturity. Variability was greatest for four small bones or groups of bones that are difficult to dissect cleanly (patellae, cervical and thoracic vertebrae) or that undergo variably increasing mineralization with age (sternum, costal cartilages).

Within each species-sex group, the average variation of the fresh and ashed weights of the sets of bones are all somewhat greater ($\bar{V}$ ranges from 19 to 24%) than those of their respective whole skeletons. Within each group, the variations of the weights of individual bones and the average variability of the bone sets includes, in addition to the major variable of skeletal size, a smaller amount of individual variation. For example, the mean fresh weight of the humerii of the group of nine adult cynomolgus males is 48.3 ± 9.5 g, and V is 19.7%. If the measured individual

humerii weights are normalized to the mean skeleton weight for the group, the resulting mean fresh weight of the humerii is 48.3 ± 3.1 g, and V is reduced to 6.4%. For that bone pair, 68% of the variability in the fresh weight is related to skeletal size, and 32% is due to individual variation.

Within the four species-sex groups, variability in the degree of mineralization of the individual bones (ash fractions) is small ($\bar{V}$ ranges from 9 to 15%), attesting to the absence of significant radiation effects on the skeletons (either hypermineralization or rarefaction) and to minimal age-related skeletal changes within the age range investigated (7 to 26 y).

The skeletal proportions of all four species-sex groups are highly conserved, as is demonstrated by the small variability of the fractions of skeletal fresh and ashed weights contributed by the individual bones ($\bar{V}$ ranges from 10 to 14%).

b. Comparison of species. (i) *Females:* The fresh weight of the adult female cynomolgus skeleton is 61% as large as that of the adult female rhesus skeleton. Omitting the costal cartilages, in which both size and mineralization are not as closely controlled as in the bones, the mean species ratio (cynomolgus/rhesus) of fresh weight of the 20 bones and bone groups is 0.61 ± 0.07, with a range from 0.53 (cervical vertebrae) to 0.75 (sacrum). The female cynomolgus cranium, mandible, ribs, and sacrum (Table 3) are significantly larger fractions of skeletal fresh weight than those of the rhesus females (Table 7), and the cynomolgus femora, tibiae, and foot-ankle bones are significantly smaller fractions.

The ash fraction of the female cynomolgus skeleton is 8% less than that of the female rhesus skeleton (significant). The ash fractions of 12 of the 15 bones and bone groups, for which there are independent measurements of wet bone weight, are slightly, but significantly, smaller in the cynomolgus than in the rhesus females. The cynomolgus female mandible, thoracic and lumbar vertebrae, sacrum, and hand-wrist bones are significantly greater fractions of skeletal ashed weight than those of the rhesus females, and the cynomolgus scapulae, pelvis, ulnae, femora, and tibiae are significantly smaller fractions.

(ii) *Males*: The fresh weight of the male cynomolgus skeleton is 57% of that for the male rhesus skeleton. The mean species ratio (cynomolgus/rhesus) of fresh weights of the 20 bones

and bone groups is 0.58 ± 0.09, with a range from 0.46 (patellae) to 0.82 (mandible). The male cynomolgus cranium and mandible (Table 5) are significantly larger fractions of skeletal fresh weight than those of the rhesus males (Table 9), and the cynomolgus femora, tibiae, and pelvis are significantly smaller fractions.

The ashed weight of the male cynomolgus skeleton is 61% of that for the rhesus males, greater than the fresh weight ratio. The mean ratio (cynomolgus/rhesus) of the ashed weights of the 20 bones and bone groups is 0.60 ± 0.12, with a range from 0.45 (patellae) to 0.83 (cranium). The ash fraction of the male cynomolgus skeleton is 6% greater than that of the male rhesus skeleton (not significant). The ash fractions of 12 of the 15 male cynomolgus bones and bone groups, for which fresh weight was measured are slightly, but not significantly, greater than those of the male rhesus bones. The cynomolgus cranium and mandible are significantly greater fractions of the skeletal ashed weight than those of the rhesus males, and the cynomolgus ulnae, pelvis, femora, and tibiae are significantly smaller fractions.

c. Comparison of sexes. (i) *Cynomolgus*: The fresh weight of the adult female cynomolgus monkey skeleton is 63% as large as that of the adult males. The mean sex ratio (female/male) of fresh weights of the 20 bones and bone groups is 0.61 ± 0.07, with a range from 0.51 (cervical vertebrae) to 0.76 (patellae). The female pelvis is a significantly larger fraction of skeletal fresh weight than that of the males, and the female radii are a significantly smaller fraction.

The ashed weight of the female cynomolgus skeleton is 59% of that for the male skeleton, somewhat less than the fresh weight ratio. The mean ratio (female/male) of ashed weights of the 20 bones and bone groups is 0.60 ± 0.06, with a range from 0.50 (clavicles) to 0.78 (sacrum). The ash fraction of the female skeleton is 6% less than that of the male skeleton (not significant). The ash fractions of 14 of the 15 bones and bone groups, for which wet weight was measured, were slightly, but not significantly, smaller than those of the males. The female lumbar vertebrae and sacrum are significantly greater fractions of skeletal ashed weight than those of the males, and the female scapulae are a significantly smaller fraction.

(ii) *Rhesus*: The fresh weight of the adult female rhesus monkey skeleton is 59% as large as that of the adult males. The mean sex ratio (female/male) of the fresh weights of the 20 bones and bone groups is 0.60 ± 0.05, with a range from 0.48 (patellae) to 0.74 (cranium). The female cranium and sacrum are significantly larger fractions of skeletal fresh weight than those of the males, and only the female ulnae are a significantly smaller fraction.

The ashed weight of the adult female rhesus monkey skeleton is 64% of that for the males, greater than the fresh weight ratio. The mean ratio (female/male) of ashed weights of the 20 bones and bone groups is 0.62 ± 0.06, with a range from 0.53 (sternum) to 0.80 (cranium). The ash fraction of the female skeleton is 9% greater than that of the male skeleton (significant). The ash fractions of the female cranium, pelvis, humerii, ulnae, tibiae, and fibulae are significantly greater than those of the male bones, and none are significantly smaller. The female cranium is a significantly greater fraction of skeletal ashed weight than that of the males, and the female scapulae, ulnae, and femora are significantly smaller fractions.

d. Summary of results. The data for the weights and skeletal proportions of individual bones shown in Tables 3 and 5 (cynomolgus monkeys) and Tables 7 and 9 (rhesus monkeys) were recompiled to describe the major skeletal units (Tables 4, 6, 8, and 10). By combining data for individual bones into those larger groups, subtle differences in the proportions and compositions of the skeletons of the four Macaque species-sex groups could be magnified and their similarities and differences examined more closely.

Comparisons of the within- and between-species ratios of the fractions of total fresh weight contributed by the major skeletal units provide better evidence of the relative proportions of their skeletons than the individual bones. Comparisons of the ash fractions of the major skeletal segments within and between species provide estimates of the relative amounts of soft tissue (mainly marrow) contained in those groups of bones. The ash fractions (ashed weight/fresh weight) are subject to technical errors (some compensating), particularly drying of bones before and during defleshing and incomplete removal of all but the most closely adhering soft tissue. The fractions of the total ashed weight contributed by major skeletal units involve only the well defined

ashed weights, and they generally confirm the small, but in some cases significant, differences in the distribution of mineral in the skeletons of the four Macaque species-sex groups.

The fresh and ashed weights of the lumbar vertebral bodies and long bone ends (Tables 3, 5, 7, and 9) provide additional information about the relative abundance of marrow in skeletal parts composed mainly of trabecular bone, and in the case of the long bone shafts, about the relative amounts of marrow and bone. Relative volumes of marrow and bone tissue were estimated assuming that native bone tissue is approximately 60% ash by weight and that the average densities of bone tissue and mixed marrow are approximately 2.0 and 1.0 g/cm^3, respectively (Go64):

Bone tissue mass = 1.667 × ashed weight (g),

Bone tissue volume = 0.5 × bone tissue mass (cm^3)

Relative volume (marrow/bone tissue) =

(fresh weight – 1.667 × ashed weight)(0.5 × 1.667 × ashed weight)$^{-1}$ (cm^3/cm^3) (2)

(i) *Between species. Females*: Adult female rhesus monkeys are about twice as large and their skeletons are about 65% larger than adult cynomolgus females. In spite of those large differences in size, their skeletal proportions are similar (Tables 4 and 8). In the females, the pelvis and spinal column contribute similar proportions to the total fresh skeleton weight. However, the head and thorax of cynomolgus females are proportionately somewhat larger, and the limbs somewhat smaller, than in the rhesus females (differences small but significant). The significantly smaller ash fractions of the skeletal segments of the cynomolgus females indicate less mineralization and relatively more marrow space than in the rhesus female bones. (The spinal column was not considered because wet weights of vertebrae were estimated for so many monkeys.) Comparison of the total ashed weight fractions confirm the larger proportion of skeletal mineral in the female cynomolgus monkey spinal column and the larger proportion of skeletal mineral in the lower limbs and pelvis of the rhesus females. The relative volumes of marrow and bone tissue in the lumbar vertebral bodies of the females of the two species (Tables 3 and 7,

eqn. 2) are nearly the same, suggesting that other parts of the female cynomolgus spinal column (cervical vertebrae, vertebral arches) are relatively more mineralized. The bones of the lower limbs of the cynomolgus females are proportionately smaller than those of the rhesus females and less well mineralized: The relative marrow volumes of the ends and shafts of the cynomolgus long bones are 17 and 21% greater, respectively, than those of the rhesus females.

(ii) *Males*: The whole body and skeleton of male rhesus monkeys are, respectively, 56 and 75% larger than male cynomolgus monkeys. The proportional contributions to total fresh skeleton weight of the male cynomolgus and rhesus upper limbs, spinal column, and thorax are similar (Tables 6 and 10), but the male cynomolgus head is proportionally larger and the lower limb bones and pelvis are proportionally smaller than in rhesus males (differences significant). The ash fractions of the skeletal segments of the cynomolgus males are generally larger than those of the rhesus males (significant for whole skeleton). The male cynomolgus head and the male rhesus lower limbs and pelvis are comparatively larger fractions of the total ashed weight, in agreement with the relative sizes of these skeletal units indicated by their fresh weight proportions. The spinal column of the cynomolgus males is more mineralized, but the relative marrow volumes in the lumbar vertebral bodies (Tables 5 and 9, eqn. 2) are the same for both species, suggesting that, like the cynomolgus females compared with rhesus females, the relative amounts of bone in other parts of the spine are greater in the cynomolgus than in the rhesus males. The lower limb bones of the male rhesus monkeys are not only proportionally larger than those of the cynomolgus males, but their gross compositions differ. The relative marrow volumes in the rhesus male long bone ends and shafts are 15 and 40% larger, respectively, than in the cynomolgus males.

(iii) *Within species. Cynomolgus*: The body weight of the male cynomolgus monkeys is 80% larger that that of the females, and the skeleton is 58% larger. Even so, the proportions of the male and female cynomolgus skeletons are more alike than those of the females or the males of the two species. Differences in the overall skeletal proportions are minor (Tables 4 and 6). The female head is proportionately somewhat smaller, and the thorax and pelvis are somewhat

larger, than in the males (differences small but significant). The slightly, but not significantly, smaller ash fractions of the female bones (except spinal column) suggest less mineralization and larger relative marrow volumes in the female cynomolgus bones. The relative marrow volumes of the lumbar vertebral bodies and long bone ends, both trabecular bone sites (Tables 3 and 5, eqn. 2), are the same in the male and female cynomolgus monkeys. However, the relative marrow space in the female long bone shafts is 42% larger, an indication of the greater delicacy of the female long bones.

(iv) *Rhesus*: The body of male rhesus monkeys is about 45% larger than that of females, and the male skeleton is about 70% larger. There are only minor differences in the proportions of their skeletons (Tables 8 and 10). The female head is proportionally larger (significant), and the lower limbs are somewhat smaller than in the males (not significant). The significantly larger ash fractions of the female skeleton and its major units (except for thorax) reflect a generally greater mineralization of the female bones, that is, more bone tissue volume relative to marrow space. The proportional distributions of mineral in the male and female skeletons are similar, except for the slightly greater fraction of skeletal mineral in the female head. The relative marrow volumes of the lumbar vertebral bodies (Tables 7 and 9, eqn. 2) are nearly the same for both sexes, but the relative marrow volumes in the male long bone ends and shafts are 30 and 20% greater, respectively, than in the female long bones.

(v) *General comments*. The female cynomolgus monkeys are the smallest Macaque, and the male rhesus is one of the largest. Within species, the Macaques exhibit marked sexual dimorphism. In spite of the great differences in body sizes and organ and tissue weights both within and between species, the proportions of their whole bodies, and particularly the proportions of their skeletons, are much alike. The proportional contributions of the skeleton to whole body weight (fresh skeleton weight/body weight) are the same for three of the four species-sex groups: rhesus males (16), $12 \pm 1.9\%$; rhesus females (58), $11 \pm 2.8\%$; cynomolgus males (9), $11 \pm 1.4\%$. The skeletal proportions of body weight of all three of those groups are significantly smaller than that of the cynomolgus females [(33), $14 \pm 2.7\%$]. A sub-

group of the 10 largest cynomolgus females (body weight ≥ 3.9 kg) was examined separately. The mean body weight was 4.5 ± 1.1 kg (at the lower end of the body weight ranges of cynomolgus males and rhesus females), and the fresh skeleton was 11 ± 0.2% of body weight, the same as for the other three species-sex groups. The combined evidence strongly suggests that the fresh skeleton of the cynomolgus females is proportionally larger, because these animals are less muscular and tend to acquire less body fat than the other three species-sex groups.

In general, the skeletal proportions of the females and males within each species are more alike than the proportions of the skeletons of the females or males of the two species (greater number of statistically significant differences). The mean within-species ratios (female/male) for the fresh and ashed weights of the 20 bones and bone groups (Tables 3, 5, 7, and 9) have coefficients of variation ranging from 8.5 to 10%, while those for the mean between-species ratios (cynomolgus/rhesus) range from 11 to 15%.

e. Compact and cancellous bone. The bones are composed of two structurally distinct types of bone tissue—compact (cortical) and cancellous (trabecular) bone—in proportions characteristic of the individual bones. Compact bone is dense and poorly vascularized; in adult rhesus monkeys, the surface-to-volume ratio is about 35 cm^2/cm^3 (ICRP79;Sm79). Cancellous bone is composed of spicules or thin plates surrounded by marrow; in adult rhesus monkeys the surface-to-volume ratio ranges from 250 cm^2/cm^3 for the finest trabeculae contained in active red marrow to about 50 cm^2/cm^3 for the coarsest trabeculae and plates contained in fatty marrow (Be76,78;ICRP74,79; Sm79).

The anatomical surfaces of cancellous and cortical bone are the initial sites of all mineral deposition in the skeleton. Some minerals eventually penetrate the bone volume (calcium and other alkaline earth elements, and to some degree chemically related elements like lead and uranium). Other minerals remain on the bone surfaces where they were originally deposited until those surfaces are removed by growth or structural remodeling or are covered by new bone (multicharged metals like the lanthanides and actinides) (Du62,73,85;ICRP79).

Data from adult cynomolgus monkeys (female, Table 3; male, Table 5) and adult rhesus monkeys (female, Table 7; male, Table 9) are available for the fresh and ashed weights and ash fractions of nearly homogeneous cortical and cancellous bone tissue. Compact bone (including its contained fatty marrow) is represented by the combined shafts of the six long bones—humerii, radii, ulnae, femora, tibiae, fibulae. Typical fine cancellous bone (including its red marrow) is represented by the bodies of the seven combined lumbar vertebrae. Tables 3, 5, 7 and 9 also contain data for the sternum and sacrum, which are composed mainly of fine trabeculae in red marrow. Coarser cancellous bone (mixtures of fine to course trabeculae and plates surrounded by mainly fatty marrow) is represented by the combined ends of the six long bones.

The distinguishing feature of each of these differing anatomical types bone is its ash fraction. The ash fraction of the long bone shafts (with their included marrow) is 48 to 50% for the two monkey species, which is substantially larger than the ash fraction of any whole bone. The ash fraction of the LV bodies, 23% for both species, is substantially less than the ash fractions of the whole lumbar vertebrae and nearly the same as that for the sacrum, but larger than that for the sternum (which has a thinner outer shell and contains no bony plates). The ash fractions of the combined long bone ends, 31 to 34% for adult cynomolgus and rhesus males and females, are similar to those of their whole skeletons, and in both species, also about the same as those of the clavicles, hands, feet, and pelvis.

4. Growth of the cynomolgus and rhesus monkey body and skeleton

a. Mathematical description of growth. One of the purposes of this report was to provide analytical descriptions of body and skeletal growth for use in converting measurements of lead (or other contaminants) in biopsy samples to total retention in growing and adult cynomolgus monkeys. A method was needed to estimate total skeleton weight and bone mineral mass of experimental animals from age or measured body weights.

Only six female and four male cynomolgus monkeys used in radionuclide biokinetic studies at LBNL were immature at the time of death. However, there are detailed bone data for 25 female

rhesus monkeys ranging in age from newborn to 5 years and 18 male rhesus monkeys ranging in age from newborn to 7 years. More than one-half of these immature rhesus monkeys were killed within a few weeks after a radionuclide injection; 10 were infants born to Sr-burdened mothers; eight were uninjected monkeys that died at the Yale colony or at LBNL before entry into a radionuclide study. The growth of female (male) cynomolgus monkeys can be estimated using the following assumptions: (a) the skeletal proportions and growth patterns of the females (males) of the two Macaque species are similar; (b) size (mass) is the only important difference between the growing, as well as, the mature skeletons of the females (males) of the two species; (c) body weights or weights of the growing bones of female (male) rhesus and cynomolgus monkeys can be combined, if they are expressed as fractions of their respective mature weights.

Mammalian growth from birth to maturity is well represented analytically as a Gompertz function (La65a,65b). However, accurate definition of Gompertzian growth requires frequent measurements of a large population of growing animals, particularly during the first growth quartile (De72). Skeleton and bone weights, which can be measured only once in each animal, are available for too few immature female and male monkeys, particularly during the first 1.5 years of life to define the parameters of Gompertzian growth functions. A simplified empirical approach was developed, which allows the weight of the skeleton and the major skeletal units of growing female or male Macaques to be estimated from age or body weight.

All of the data for body weights and fresh and ashed weights of the skeleton and the major skeletal units of growing Macaques were converted to fractions of their respective species- and sex-specific weights at maturity. The mathematical expression selected to represent body and skeletal growth is a pair of discontinuous exponential line segments, defined within limits of the independent variable, age (t), as follows:

R_1 (0 to t_1) years:

$$\text{Fraction of mature weight} = A_1 e^{0.693t/T_1}, \tag{3a}$$

R_2 (t_1 to t_2) years:

$$\text{Fraction of mature weight} = A_2 e^{0.693t/T_2}, \tag{3b}$$

where A_1 and A_2 are the intercepts on the ordinate (fraction of mature weight) at t = 0 years, T_1 and T_2 are the respective half-times in years of age, the age ranges are R_1 = 0 to t_1 (years) and $R_2 = t_1$ to t_2 (years), and t_2 is 5 and 7 years for females, and males, respectively.

The parameters of each line segment (intercept at t(0), A; half-time, T; and t_1, the age at which the two line segments intersect) were determined by log-linear regression analysis. The age-related trends after 1.5 years of age are sufficiently robust and the scatter within each data set whole body, skeleton and skeletal unit weights is sufficiently small that, in spite of the modest number of growing monkeys, the correlation coefficients of 24 of those 30 log-linear regression lines were greater than 0.81, and none was less than 0.71.

b. Growth from birth to 1.5 years. Few monkeys obtained from animal importers by the LBNL or UR-Delta colonies were younger than 1.5 years on arrival. The radionuclide studies did not include infant monkeys (birth to 1.5 years old), except for those born to or nursed by ^{90}Sr-burdened mothers to measure maternal transfer of ^{90}Sr. The survival rate at the Yale breeding colony was excellent, and LBNL received the carcasses of only two newborn rhesus males. Consequently, complete data sets (healthy body weight at age of death and fresh and ashed weights of all bones) were available for only nine female and six male infant monkeys (rhesus, except two cynomolgus newborns, one male and one female). Within that small group of infant monkeys for whom bone data were available, ages at death of 13 of 15 were equally divided between newborn (seven) and 1.2 to 1.3 years old (six); only two had died during the first year of life (one female and one male, each at about 6 months old). Those body and bone weight data alone were not sufficient to define the slope of the initial rapid component of the skeletal growth curve with any degree of confidence.

The growth patterns of the body and skeleton are not identical, for example, the Macaque skeleton is a larger fraction of body weight at birth (about 20%) than at maturity (11 to 14%). Even so, body growth is similar enough to skeletal growth to provide guidance about the growth

rate of the skeleton, particularly about the slope of the first rapid component. Several rhesus infants born to ^{90}Sr-burdened mothers at LBNL and UR-Delta had been weighed frequently from birth to about 1.5 years of age (three females, 11 measurements; nine males, 32 measurements). Those live weights (shown as monthly averages, designated by the open-square in Figs. 2a and 3a) established that the very rapid phase of body growth (and presumably also of skeletal growth) persisted for about only 0.7 year in female Macaques and about 1 year in males before the onset of the long period of slow growth to maturity.

Additional evidence that the very rapid initial growth rate of the Macaque body lasts for only about 9 months, is provided by the detailed body weight curves of laboratory-raised, formula-fed female and male rhesus monkeys (Va56). Their mature body weights and skeleton weights (based on measurements at LBNL of the skeletons of a few of these animals) are larger (not significantly) than those of nursed monkeys or those of the wild-caught monkeys whose skeletal growth is described here. Growth in body size of the formula-fed monkeys was recalculated and expressed as fraction of the mature weight measured at the Yale colony (Va56). Body growth of the Yale colony females agreed with the female growth curve (Fig. 2a) at all ages from birth to maturity. Growth of the Yale colony males agreed with the male growth curve (Fig. 3a) during the first year of life.

In accord with the evidence from the body weight data for rhesus monkeys [this study and published (Va56)] that the rate of body weight increase shifts at about 9 months of age from the very rapid initial rate to the slower prolonged growth rate, the initial segments of the growth curves for the fresh and ashed skeleton weights [Fig. 2b,c (females); Fig. 3b,c (males)] and of the major skeletal units (not shown graphically) were fitted using the mean weight of the newborns and the single weight values at 0.43 years (male) and 0.5 years (female). The slopes of those exponential line segments are uncertain, because of the small numbers of animals, but they are included in Tables 12 and 13 and as dashed lines in Figs. 2 and 3 for completeness, because they describe the available data.

c. Body and skeletal growth. (i) *Females*: The mean body weight of young adult female cynomolgus monkeys (26 monkeys, 5 to 10 y old) is 3.4 ± 0.6 kg, and that of older animals (7 monkeys, 10 to 16 y old) is 4.2 ± 1.6 kg. The body weight of the older animals is not significantly greater, and the grand mean body weight of all 33 adult female cynomolgus monkeys (Table 4) was used to represent mature weight in this species. The mean body weight of 18 wild-caught young adult female rhesus monkeys (5 to 10 y old) is 5.8 ± 1.7 kg, and that of 40 older animals (10 to 26 y old) is 7.4 ± 1.6 kg. The older rhesus females are significantly heavier, and body weight gain apparently continues after maturity and after cessation of skeletal growth in females of this Macaque species (Va56,58). For the purposes of this analysis, the body weight of the young adult rhesus sub-group was considered to be more representative of the weight of rhesus females at maturity and before accumulation of excess body fat.

The fraction of mature body weight of growing female cynomolgus monkeys is BW(t)/3350, where BW(t) is body weight in grams at age t in years, and similarly for growing female rhesus monkeys, the fraction of mature body weight is BW(t)/5850. The skeleton and major skeletal unit weights used for mature female cynomolgus and rhesus monkeys are those shown in Tables 4 and 8, respectively, for the whole study populations of 33 mature female cynomolgus monkeys (5 to 16 years old) and 58 wild-caught mature female rhesus monkeys (5 to 26 years old).

Plots of the fractional growth of the whole body and skeleton of females of both Macaque species combined are shown in Fig. 2a (whole body), 2b (fresh skeleton), and 2c (skeletal mineral). The six data points shown in each figure for the growing cynomolgus monkeys (filled circles) lie within the envelope of the measurements for the growing female rhesus monkeys, demonstrating the suitability of combining the data for both species. The growth patterns of the fresh and ashed weights of the major skeletal units of the females of the two species also agree (plots not shown).

(ii) *Males*: The relevant mature weights of the body, skeleton, and major skeletal units used for the males are those given in Tables 6 and 10, respectively, for the whole study populations of nine mature male cynomolgus monkeys (7 to 16 y old) and 16 wild-caught mature male rhesus

monkeys (7 to 28 y old). The group of adult male cynomolgus monkeys was too small to test for long-term body weight gain after maturity. The mean body weight of younger adult rhesus males (8 monkeys, 7 to 15 y old) is 10.1 ± 1.3 kg, and that of the older animals (8 monkeys, 15 to 28 y old) is 10.6 ± 2.2 kg. The weight of the older animals is not significantly greater, and the grand mean body weight of all 16 adult male rhesus monkeys (Table 10) was considered to be representative of their weight at maturity.

Plots of the fractional growth of the whole body and skeleton of males of the two Macaque species combined are shown in Fig. 3a (whole body), 3b (fresh skeleton), and 3c (skeletal mineral). The four data points shown in each figure for the growing cynomolgus monkeys (filled circles) lie within the envelope of the measurements for the growing male rhesus monkeys. The growth patterns of the fresh and ashed weights of the major skeletal units of the males of the two species also agree (plots not shown).

d. Comparison of body and skeleton growth in female and male Macaques. The overall patterns of body and skeletal growth are similar in female and male Macaques, but there are some important differences:

At birth, the weights of the male body and skeleton are smaller fractions of their mature weights than is the case for females: For example, the fractions of mature skeleton fresh weight in newborn males and females are 14 and 6.5%, respectively.

When growth is expressed as fraction of mature weight vs. age, the male growth curves are displaced below those of the curves for the females. (Compare Figs. 2 and 3.)

Growth of the Macaque body and skeleton matches the temporal pattern of epiphyseal closure and attainment of maximum crown-rump length. In the females, all epiphyses are united and increase in body length ceases between 4.5 and 5 years of age, while epiphyseal union and cessation of growth in body length occur at 6 to 7 years in the males (Va56, 58).

In the early growth phase, the growth rate of the body of both sexes exceeds the growth rate of the skeleton. Male body weight increases about 15% faster than that of the females. Initial growth of the male skeleton (fresh weight) is about 70% as fast and skeletal mineralization is

about 75% as fast as in the females, but the early rapid growth of the male skeleton continues for an additional 5 months.

In the later growth phase, the rate of increase of male body weight is about 25% faster than that of females, while rates of increase of fresh and ashed skeleton weights are nearly the same for both sexes. Slow growth persists for 1.5 to 2 years longer in the males.

e. Differential growth of major skeletal units. The skeletal proportions of newborn and mature Macaques are not the same. In both sexes at birth, the head, spinal column, and thorax are larger fractions of the fresh and ashed skeletal weight, while the appendages and pelvis are smaller fractions than they are at maturity. Early growth of the major skeletal units is qualitatively similar in both sexes: The head, spinal column, and thorax (larger fractions of mature weight at birth) grow about 70% as fast as the limbs and pelvis (smaller fractions of mature weight at birth).

In the later growth phase in both sexes, the early growth pattern is reversed and the bones of the head, spinal column, and thorax grow about 20% faster than those of the limbs and pelvis. The sex differences in the rates of late growth of the major skeletal units are smaller than during early growth.

f. Skeletal growth relative to body weight. The slope of the linear regression line of the fresh skeleton fraction of body weight is negative from birth to 5 years (females) and birth to 7 years (males). Although the fresh skeleton comprises about 20% of birth weight, more rapid and greater relative growth of other body parts result in mature skeleton fractions of only about 13 and 11% of body weight in females and males, respectively. The equations of the linear regression curves of the fresh skeletal fraction of the body from birth to 5 years (female) and birth to 7 years (male) are, where t is age in years:

$$\text{Fresh skeletal fraction of whole body} = -14t + 190 \ (g.kg^{-1}) \qquad \text{female,} \qquad (4a)$$

$$= -12t + 190 \ (g.kg^{-1}) \qquad \text{male .} \qquad (4b)$$

The skeleton of the immature Macaque is less well mineralized than the mature skeleton, and the slopes of the linear regression lines of both the skeletal ash fraction (ash weight/fresh weight)

and ashed skeleton fraction of the whole body are positive. Skeletal mineralization in both female and male Macaques increases from only about 20% (20g ash per 100g skeleton) at birth to mature levels of 33 to 36%. The technical difficulties in obtaining accurate fresh weights of some bones (discussed earlier) are more pronounced in skeletonizing the small less well mineralized bones of growing skeletons. The following expressions, birth to 5 years (female), and birth to 7 years (male), are approximate; they underestimate the mature ash fraction of the females and overestimate that of the males.

$$\text{Ash fraction of skeleton} = 1.7t + 21 \ (g.100g^{-1}) \quad \text{female,} \quad (5a)$$

$$= 2.2t + 20 \ (g.100g^{-1}) \quad \text{male.} \quad (5b)$$

Skeletal mineralization is coupled to the growth of the skeleton in size, and the ashed skeleton fraction of the whole body increases very slowly from about 37g ash per kilogram of body weight at birth to mature levels of about 45g ash per kilogram of body weight at 5 years in females and 7 years in males. The linear regression equations of the ashed skeleton fraction of the whole body from birth to 5 years (female) and birth to 7 years (male) are,

$$\text{Ashed skeleton fraction of whole body} = 1.4t + 38 \ (g.kg^{-1}) \quad \text{female,} \quad (6a)$$

$$= 1.0t + 36 \ (g.100g^{-1}) \quad \text{male.} \quad (6b)$$

g. Estimation of skeletal mass in growing Macaques. The fraction of mature weight of the skeleton and its major units can be estimated for a growing female or male cynomolgus or rhesus monkey by entering its known age (t in years) in equations (3a) or (3b) along with the appropriate parameters given in Tables 12 and 13. The numerical solution (fraction of mature weight at age t years) is then multiplied by the appropriate mature weight for the skeletal part (fresh or ashed) of the species to obtain the weight of the skeleton or a major skeletal unit.

In a reversal of the above procedure, equations (3a) and (3b) and the parameters of the growth of body weight given in Tables 12 and 13 can be used to estimate the ages of growing monkeys from their measured body weights.

h. Errors of estimate. It must be emphasized that ages were imprecisely known for many of the growing monkeys. Only a few birth dates were known. The ages of the monkeys in the LBNL studies were obtained from skeletal roentgenograms, which are more accurate for monkeys less than 2 years old (±1.5 months) than for monkeys between 2 and 5 years old (female) and 2 and 6.5 years old (male) (± 4 to 6 months) (Va58).

The ages of some of the monkeys used in the UR studies are even more uncertain, because they were estimated from colony records and body weight charts. The influence of those errors in age determination are unknown, but because ages were as likely to be under- as over-estimated, they are expected to contribute more to the overall variability than to the numerical values of the curve parameters of Tables 12 and 13.

Based on the mean ± SD of the ratios (measured/calculated) computed for each variable for each of the 34 female and 22 male monkeys contributing growth data, estimates of body weight of the female Macaques of known age appear to be reliable to within ±35%, and those for males, to within ±18%. Estimates of the weights of the fresh or ashed skeleton and its major units appear reliable to within ±20%.

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Table 1. Tissue weights and body weight fractions of adult female cynomolgus (5 to 16 y) and rhesus monkeys (5 to 26 y)[a]

	Tissue weight (g)				Fraction of body weight (% BW)	
	Cynomolgus		Rhesus		Cynomolgus	Rhesus
	n[b]	mean ± SD	n[b]	mean ± SD	mean ± SD	mean ± SD
Liver	33	80 ± 29	21	130 ± 31	2.3 ± 0.6	2.2 ± 0.5
Kidneys	33	17 ± 5.4	21	21 ± 3.4	0.5 ± 0.2[f]	0.4 ± 0.1
Heart	29	16 ± 4.6	19	22 ± 4.9	0.5 ± 0.2[f]	0.4 ± 0.1
Lungs	29	21 ± 5.7	18	38 ± 9.6	0.6 ± 0.2	0.7 ± 0.2
Spleen	32	6.0 ± 3.1	20	5.0 ± 2.2	0.2 ± 0.1[f,g]	0.1 ± 0.04
Brain	14	61 ± 4.6	13	86 ± 9.9	1.7 ± 0.3[f]	1.4 ± 0.2[h]
Ovaries	17	0.5 ± 0.2	17	0.5 ± 0.2	0.01 ± 0.001	0.01 ± 0.004
GI tract[c]	14	99 ± 28	5	150 ± 35	2.6 ± 0.8	2.6 ± 0.7[h]
Pelt[d]	30	540 ± 240	18	780 ± 310	15 ± 4.3	12 ± 4.4
Other soft tissue[e]	33	2200 ± 720	21	4000 ± 1500	62 ± 4.4	66 ± 7.1
Skeleton	33	460 ± 63	21	700 ± 112	14 ± 2.7	12 ± 2.4
Teeth	33	14 ± 2.6	21	17 ± 3.1	0.4 ± 0.1	0.3 ± 0.08
Tail	33	20 ± 8.6	21	13 ± 2.8	0.6 ± 0.2	0.2 ± 0.06
Total body	33	3500 ± 900	21	6000 ± 1600		

[a]Sexually mature (regular menstrual cycles) and skeletally mature (all epiphyses united). [b]Number of measurements (n); not all listed tissues were weighed for some monkeys; n for body fraction same as for tissue weight. [c]Gastrointestinal tract tissue freed from mesentery and cleaned of contents. [d]Includes adhering subcutaneous fat. [e]Body weight in good health minus sum of measured tissues and organs: includes muscle, fat, connective tissue, residual blood, blood vessels, nervous tissue. [f]Significantly greater than male cynomolgus monkeys. [g]Significantly greater than female rhesus monkeys. [h]Significantly greater than male rhesus monkeys.

Table 2. Tissue weights and body weight fractions of adult male cynomolgus (7 to 14 y) and rhesus monkeys (7 to 28 y)[a]

	Tissue weight (g)				Fraction of body weight (% BW)	
	Cynomolgus		Rhesus		Cynomolgus	Rhesus
	n[b]	mean ± SD	n[b]	mean ± SD	mean ± SD	mean ± SD
Liver	9	120 ± 29	8	180 ± 30	1.8 ± 0.3	2.0 ± 0.3
Kidneys	9	20 ± 4.1	8	28 ± 5.1	0.3 ± 0.1[f]	0.3 ± 0.07
Heart	8	21 ± 4.1	8	50 ± 16	0.3 ± 0.04[f,h]	0.5 ± 0.2
Lungs	8	27 ± 12	7	60 ± 15	0.4 ± 0.2[h]	0.7 ± 0.2
Spleen	9	7.5 ± 1.9	8	6.8 ± 2.8	0.1 ± 0.06[f]	0.07 ± 0.03
Brain	8	72 ± 9	5	95 ± 8.2	1.1 ± 0.1[f]	1.0 ± 0.1[g]
Testes	9	40 ± 18	7	46 ± 6.7	0.6 ± 0.2	0.5 ± 0.08
GI tract[c]	8	130 ± 40	3	160 ± 48	2.0 ± 0.3	1.7 ± 0.6[g]
Pelt[d]	9	1000 ± 240	6	1100 ± 280	16 ± 3.2[i]	11 ± 2.6
Other soft tissue[e]	9	4200 ± 920	8	6500 ± 960	65 ± 4.4	69 ± 3.7
Skeleton	9	730 ± 144	8	1200 ± 250	11 ± 2.6	12 ± 2.3
Teeth	9	17 ± 3.5	8	20 ± 3.8	0.3 ± 0.06	0.2 ± 0.04
Tail	9	28 ± 14	8	22 ± 4.2	0.4 ± 0.2	0.2 ± 0.06
Total body	9	6400 ± 1200	8	9400 ± 1100		

[a]Sexually mature (testes descended) and skeletally mature (all epiphyses united). [b]Number of measurements (n); not all listed tissues were weighed for some monkeys; n for body fraction same as for tissue weight. [c]Gastrointestinal tract tissue freed from mesentery and cleaned of contents. [d]Includes adhering subcutaneous fat. [e]Body weight in good health minus sum of measured tissues and organs: includes muscle, fat, connective tissue, residual blood, blood vessels, nervous tissue. [f]Significantly less than female Cynomolgus monkeys. [g]Significantly less than female rhesus monkeys. [h]Significantly less than male rhesus monkeys. [i]Significantly greater than male rhesus monkeys.

Table 3. Weights and skeletal fractions of bones of adult female cynomolgus monkeys (≥ 5 y, 3.5 ± 0.9 kg, n=33)

	Wet weight (g)[a]	Ash weight (g)	Ash fraction (a/w, %)	Bone/skeleton (%)	Bone ash/skeleton ash (%)
	mean ± SD	mean ± SD	mean ± SD	mean ± SD	mean ± SD
Cranium[b]	76 ± 11	26 ± 5.1	33 ± 4.5[f]	17 ± 1.6[g]	17 ± 1.7
Mandible[b]	21 ± 3.4	9.1 ± 1.7	43 ± 5.5[f]	4.7 ± 0.7[g]	6.0 ± 0.7[g]
Scapulae	15 ± 2.5	5.0 ± 1.0	33 ± 6.2[f]	3.3 ± 0.3	3.3 ± 0.3[f,h]
Clavicles	2.8 ± 0.6	0.9 ± 0.2	33 ± 5.3	0.6 ± 0.1	0.6 ± 0.1
Ribs	24 ± 4.3	7.3 ± 1.3	30 ± 4.4[f]	5.3 ± 0.5[g]	4.8 ± 0.4
Sternum	4.6 ± 1.7	0.6 ± 0.2	13 ± 2.4	1.0 ± 0.1	0.4 ± 0.1
Costal cartilages	6.6 ± 1.4	0.9 ± 0.3	14 ± 4.7[g]	1.4 ± 0.4	0.6 ± 0.2[g]
Cervical vertebrae[c]	10 ± 2.5	2.9 ± 0.6	*28*	2.3 ± 0.4	1.9 ± 0.2
Thoracic vertebrae[c]	27 ± 5.8	7.7 ± 1.6	*28*	6.0 ± 0.9	5.0 ± 0.7[g]
Lumbar vertebrae[c]	46 ± 7.8	13 ± 2.4	*28*	10 ± 0.9	8.8 ± 0.7[g,i]
LV bodies[d]	*21 ± 4.0*	*4.8 ± 1.1*	*23 ± 2.7*		
Sacrum	13 ± 2.5	3.2 ± 0.6	25 ± 2.1	2.8 ± 0.4[g]	2.1 ± 0.3[g,i]
Pelvis	41 ± 7.7	12 ± 2.3	31 ± 5.3[f]	8.9 ± 0.9[i]	8.2 ± 0.7[f]
Humeri	30 ± 4.5	12 ± 2.2	39 ± 4.6[f]	6.4 ± 0.4	7.6 ± 0.6
Radii	12 ± 1.8	5.0 ± 0.9	43 ± 4.0[f]	2.5 ± 0.2[h]	3.3 ± 0.2
Ulnae	13 ± 2.0	5.8 ± 1.0	44 ± 3.9[f]	2.9 ± 0.2	3.8 ± 0.4[f]
Hands[c]	15 ± 2.8	4.7 ± 0.8	*30*	3.3 ± 0.4	3.1 ± 0.3[g]
Femora	40 ± 6.1	15 ± 2.6	39 ± 3.5[f]	8.6 ± 0.5[f]	10 ± 0.6[f]
Tibiae	25 ± 3.4	9.3 ± 1.7	37 ± 3.4[f]	5.4 ± 0.3[f]	6.1 ± 0.4[f]
Fibulae	5.5 ± 0.9	2.4 ± 0.4	43 ± 4.4[f]	1.2 ± 0.1	1.6 ± 0.4
Patellae	3.2 ± 1.0	0.6 ± 0.1	19 ± 6.5[f,h]	0.7 ± 0.2	0.4 ± 0.1
Feet[c]	28 ± 5.3	8.7 ± 1.6	*32*	6.1 ± 0.6[f]	5.7 ± 0.5
Long bone ends[d]	*53 ± 7.0*	*17 ± 2.9*	*32 ± 3.1*		
Long bone shafts[d]	*69 ± 12*	*33 ± 6.5*	*48 ± 4.1*		
Total skeleton[e]	460 ± 63	150 ± 25	33 ± 2.8[f]		

[a]Intact bones include marrrow, periosteum, and articular cartilages. [b]Excludes teeth. [c]Fresh weights calculated for 22 of 33 monkeys using grand mean ash fractions of vertebrae (0.28 ± 0.05, 140 measurements), hand bones (0.30 ± 0.03, 22 measurements), and foot bones (0.32 ± 0.03, 22 measurements) of cleanly dissected adult Macaques of both sexes and species. [d]Data for LV bodies (33 monkeys); long bone ends and shafts (21 monkeys). These partial bone values (shown in italics) are included in the totals for whole bones and the complete skeleton. [e]Excludes teeth (14 ± 2.6 g fresh; 9.3 ± 1.8 g ash) and tail (20 ± 8.6 g fresh; 5.7 ± 2.4 g ash). [f]Significantly less than female rhesus monkeys. [g]Significantly greater than female rhesus monkeys. [h]Significantly less than male cynomolgus monkeys. [i]Significantly greater than male cynomolgus monkeys.

Table 4. Weights of major skeletal units of adult female cynomolgus monkeys (≥5 y, 3.5 ± 0.9 kg, n=33).

	Wet weight (g)	Ash weight (g)	Ash fraction a/w (%)	Bone/skeleton (%)	Bone ash/skeleton ash (%)
	mean ± SD	mean ± SD	mean ± SD	mean ± SD	mean ± SD
Head[a]	98 ± 15	35 ± 6.6	35 ± 4.4[e]	21 ± 2.1[f,g]	23 ± 2.2
Upper limbs	70 ± 10	27 ± 4.7	39 ± 3[e]	15 ± 0.8	18 ± 1.0
Lower limbs	100 ± 16	36 ± 6.2	36 ± 2.3[e]	22 ± 1.2[e]	24 ± 1.2[e]
Spine[b]	98 ± 16	27 ± 4.7	28 ± 2.1	21 ± 1.9	18 ± 1.4[f,h]
Thorax[c]	54 ± 7.7	15 ± 2.4	28 ± 4.0[e]	12 ± 0.8[f,h]	9.7 ± 0.6
Pelvis	41 ± 7.6	12 ± 2.3	31 ± 5.2[e]	8.9 ± 0.9[h]	8.2 ± 0.7[e]
Skeleton	460 ± 63	150 ± 25	33 ± 2.8[e]	*14 ± 2.7*[d,f,h]	*4.5 ± 0.8*[d]

[a]Excludes teeth. [b]Excludes tail. [c]Includes costal cartilages. [d]Skeleton weight/body weight (%) (shown in italics). [e]Significantly less than female rhesus monkeys. [f]Significantly greater than female rhesus monkeys. [g]Significantly less than male cynomolgus monkeys. [h]Significantly greater than male cynomolgus monkeys.

Table 5. Weights and skeletal fractions of bones of adult male cynomolgus monkeys (≥ 7 y, 6.4 ± 1.2 kg, n=9).

	Wet weight (g)[a]	Ash weight (g)	Ash fraction (a/w, %)	Bone/skeleton (%)	Bone ash/skeleton ash (%)
	mean ± SD	mean ± SD	mean ± SD	mean ± SD	mean ± SD
Cranium[b]	130 ± 28	46 ± 11	36 ± 2.7	17 ± 1.0[g]	18 ± 1.3[g]
Mandible[b]	38 ± 8.7	17 ± 3.6	45 ± 2.7	5.3 ± 0.2[g]	6.7 ± 0.3[g]
Scapulae	27 ± 6.5	9.5 ± 1.8	38 ± 2.9	3.5 ± 0.2	3.7 ± 0.1[f,i]
Clavicles	5.1 ± 1.5	1.8 ± 0.4	35 ± 4.4	0.7 ± 0.1	0.7 ± 0.1
Ribs	35 ± 6.9	12 ± 2.9	33 ± 4.2	4.8 ± 0.2	4.6 ± 0.6
Sternum	6.8 ± 2.1	1.0 ± 0.6	14 ± 3.2	0.9 ± 0.2	0.4 ± 0.2
Costal cartilages	9.8 ± 2.7	1.6 ± 0.5	17 ± 3.5[g]	1.4 ± 0.2	0.6 ± 0.2
Cervical vertebrae[c]	20 ± 7.7	4.8 ± 1.3	*28*	2.6 ± 0.6	1.8 ± 0.2
Thoracic vertebrae[c]	46 ± 13	12 ± 3.0	*28*	6.2 ± 0.7	4.7 ± 0.6
Lumbar vertebrae[c]	71 ± 14	20 ± 4.1	*28*	9.8 ± 0.5	7.9 ± 0.4[h]
LV bodies[d]	*34 ± 6.0*	*7.5 ± 1.4*	*22 ± 1.0*		
Sacrum	17 ± 3.4	4.1 ± 1.0	24 ± 2.0	2.3 ± 0.3	1.6 ± 0.2[h]
Pelvis	58 ± 13	20 ± 4.4	34 ± 2.0	8.0 ± 0.5[f,h]	7.7 ± 0.6[f]
Humeri	48 ± 9.5	21 ± 3.8	43 ± 1.7	6.6 ± 0.4	8.1 ± 0.5
Radii	20 ± 3.8	9.1 ± 1.7	45 ± 1.7	2.8 ± 0.2[i]	3.6 ± 0.2
Ulnae	22 ± 3.6	10 ± 1.7	46 ± 2.8	3.0 ± 0.2	4.0 ± 0.3[f]
Hands[c]	25 ± 3.4	7.6 ± 1.3	*30*	3.5 ± 0.4	3.0 ± 0.2
Femora	61 ± 12	25 ± 4.9	41 ± 2.1	8.3 ± 0.4[f]	9.8 ± 0.5[f]
Tibiae	38 ± 7.2	15 ± 3.2	40 ± 3.1[g]	5.2 ± 0.4[f]	6.0 ± 0.5[f]
Fibulae	8.4 ± 1.5	3.7 ± 0.7	45 ± 3.0	1.2 ± 0.02	1.5 ± 0.1
Patellae	4.1 ± 0.4	1.0 ± 0.3	26 ± 4.1[i]	0.6 ± 0.1	0.4 ± 0.1
Feet[c]	43 ± 10	13 ± 3.4	*32*	5.9 ± 1.0	5.2 ± 0.8
Long bone ends[d]	*86 ± 18*	*28 ± 6.2*	*32 ± 2.3*		
Long bone shafts[d]	*110 ± 20*	*57 ± 9.9*	*50 ± 2.4*		
Total skeleton[e]	730 ± 140	260 ± 51	35 ± 1.5[g]		

[a]Intact bones include marrrow, periosteum, and articular cartilages. [b]Excludes teeth. [c]Fresh weights calculated for 5 of 9 monkeys using grand mean ash fractions of whole vertebrae (0.28 ± 0.05, 140 measurements), hand bones (0.30 ± 0.03, 22 measurements), and foot bones (0.32 ± 0.03, 22 measurements) of cleanly dissected adult Macaques of both sexes and species. [d]These partial bone values for 9 monkeys (shown in italics) are included in the totals for whole bones and the complete skeleton. [e]Excludes teeth (17 ± 3.5 g fresh; 11 ± 2.4 g ash) and tail (28 ± 14 g fresh; 7.8 ± 3.8 g ash). [f]Significantly less than male rhesus monkeys. [g]Significantly greater than male rhesus monkeys. [h]Significantly less than female cynomolgus monkeys. [i]Significantly greater than female cynomolgus monkeys.

Table 6. Weights of major skeletal units of adult male cynomolgus monkeys (≥7 y, 6.4 ± 1.2 kg, n=9).

	Wet weight (g)	Ash weight (g)	Ash fraction a/w (%)	Bone/skeleton (%)	Bone ash/skeleton ash (%)
	mean ± SD	mean ± SD	mean ± SD	mean ± SD	mean ± SD
Head[a]	170 ± 35	68 ± 14	38 ± 2.5	23 ± 1.0[f,h]	24 ± 1.6[f]
Upper limbs	120 ± 20	48 ± 8.3	41 ± 1.4	16 ± 1.0	19 ± 1.0
Lower limbs	150 ± 29	58 ± 12	38 ± 1.6	21 ± 1.4[e]	23 ± 1.3[e]
Spine[b]	150 ± 37	41 ± 9.1	27 ± 1.5	21 ± 1.4	16 ± 0.9[g]
Thorax[c]	83 ± 17	26 ± 5.7	31 ± 2.5	11 ± 0.5[g]	10 ± 0.8
Pelvis	58 ± 13	20 ± 4.4	34 ± 2.1	8.0 ± 0.5[e,g]	7.7 ± 0.6[e]
Skeleton	730 ± 140	260 ± 51	35 ± 1.5[f]	*11 ± 1.4*[d,g]	*4.0 ± 0.5*[d]

[a]Excludes teeth. [b]Excludes tail. [c]Includes costal cartilages. [d]Skeleton weight/body weight (%) (shown in italics). [e]Significantly less than male rhesus monkeys. [f]Significantly greater than male rhesus monkeys. [g]Significantly less than female cynomolgus monkeys. [h]Significantly greater than female cynomolgus monkeys.

Table 7. Weights and skeletal fractions of bones of adult female rhesus monkeys caught in the wild and housed at LBNL, UR, or Yale (≥5 y, 6.9 ± 1.8 kg, n=58).

	Wet weight (g)[a]	Ash weight (g)	Ash fraction (a/w, %)	Bone/skeleton (%)	Bone ash/skeleton ash (%)
	mean ± SD	mean ± SD	mean ± SD	mean ± SD	mean ± SD
Cranium[b]	120 ± 23	45 ± 8.4	39 ± 3.8[g,i]	15 ± 1.8[f,i]	16 ± 1.9[i]
Mandible[b]	29 ± 4.8	14 ± 2.3	47 ± 4.5[g]	3.8 ± 0.5[f]	5.0 ± 1.0[f]
Scapulae	25 ± 4.8	10 ± 2.2	40 ± 5.2[g]	3.4 ± 0.3	3.7 ± 0.3[g,h]
Clavicles	5.0 ± 1.3	1.7 ± 0.4	35 ± 5.9	0.7 ± 0.1	0.6 ± 0.1
Ribs	37 ± 12	12 ± 2.9	34 ± 5.5[g]	4.8 ± 1.0[f]	4.6 ± 0.6
Sternum	8.0 ± 2.2	1.0 ± 0.3	13 ± 2.8	1.1 ± 0.2	0.4 ± 0.1
Costal cartilages	9.6 ± 2.8	1.0 ± 0.4	10 ± 3.4[f]	1.3 ± 0.3	0.4 ± 0.1[f]
Cervical vertebrae[c]	20 ± 5.9	5.3 ± 1.3	*28*	2.6 ± 0.6	2.0 ± 0.2
Thoracic vertebrae[c]	50 ± 13	12 ± 3.0	*28*	6.5 ± 1.0	4.5 ± 0.6[f]
Lumbar vertebrae[c]	73 ± 17	20 ± 5.1	*28*	9.7 ± 1.0	7.4 ± 0.7[f]
LV bodies[d]	*38 ± 8.6*	*8.6 ± 2.1*	*23 ± 3.3*		
Sacrum	17 ± 4.0	4.1 ± 1.0	25 ± 2.6	2.3 ± 0.2[f,i]	1.5 ± 0.1[f]
Pelvis	67 ± 5.0	24 ± 5.4	36 ± 4.1[g,i]	8.8 ± 0.9	8.9 ± 0.9[g]
Humeri	48 ± 9.3	22 ± 5.4	45 ± 5.1[g,i]	6.4 ± 0.4	8.0 ± 0.8
Radii	20 ± 4.4	9.0 ± 2.1	46 ± 4.1[g]	2.6 ± 0.2	3.3 ± 0.3
Ulnae	24 ± 4.9	11 ± 2.4	48 ± 4.4[g,i]	3.1 ± 0.3[h]	4.2 ± 0.3[h]
Hands[c]	26 ± 6.2	7.6 ± 1.9	*30*	3.4 ± 0.6	2.8 ± 0.3[f]
Femora	72 ± 14	30 ± 6.9	42 ± 3.8[g]	9.5 ± 0.6[g]	11 ± 0.8[g,h]
Tibiae	47 ± 10	19 ± 4.7	41 ± 4.3[g,i]	6.2 ± 0.5[g]	7.0 ± 0.6[g]
Fibulae	9.5 ± 2.0	4.5 ± 1.0	47 ± 4.4[g,i]	1.3 ± 0.1	1.7 ± 0.3
Patellae	4.3 ± 1.2	1.2 ± 0.4	28 ± 9.0	0.6 ± 0.1	0.4 ± 0.1
Feet[c]	50 ± 10	16 ± 3.5	*32*	6.7 ± 0.8[g]	5.9 ± 0.5
Long bone ends[d]	*96 ± 20*	*33 ± 12*	*34 ± 5.6*		
Long bone shafts[d]	*120 ± 23*	*59 ± 12*	*50 ± 4.7*		
Total skeleton[e]	760 ± 140	270 ± 53	36 ± 2.5[g,i]		

[a]Intact bones include marrow, periosteum, and articular cartilages. [b]Excludes teeth. [c]Fresh weights calculated for 40 of 50 monkeys using grand mean ash fractions of vertebrae (0.28 ± 0.05, 140 measurements), hand bones (0.30 ± 0.03, 22 measurements), and foot bones (0.32 ± 0.03, 22 measurements) of cleanly dissected adult Macaques of both sexes and species. [d]Data for 31 monkeys. These partial bone values (shown in italics) are included in the totals for whole bones and the complete skeleton. [e]Excludes teeth (17 ± 2.7 g fresh; 12 ± 1.9 g ash) and tail (16 ± 6.3 g fresh; 4.6 ± 1.8 g ash). [f]Significantly less than female cynomolgus monkeys. [g]Significantly greater than female cynomolgus monkeys. [h]Significantly less than male rhesus monkeys. [i]Significantly greater than male rhesus monkeys.

Table 8. Weights of major skeletal units of wild-caught adult female rhesus monkeys housed at LBNL, UR-Delta, or Yale (≥5 y, 6.9 ± 1.8 kg, n=58)

	Wet weight (g)	Ash weight (g)	Ash fraction (a/w) (%)	Bone/skeleton (%)	Bone ash/skeleton ash (%)
	mean ± SD	mean ± SD	mean ± SD	mean ± SD	mean ± SD
Head[a]	140 ± 25	58 ± 10	40 ± 3.4[f,g]	19 ± 2.1[e,g]	22 ± 2.5[g]
Upper limbs	120 ± 23	50 ± 11	42 ± 3.2[f,g]	16 ± 1.1[f]	18 ± 1.2
Lower limbs	180 ± 34	71 ± 15	38 ± 2.8[f,g]	24 ± 1.4[f]	26 ± 1.4[f]
Spine[b]	160 ± 36	41 ± 9.7	26 ± 3.3	21 ± 2.2	15 ± 1.4[e]
Thorax[c]	84 ± 20	25 ± 6.4	31 ± 3.6[f]	11 ± 1.3[e]	9.6 ± 0.9
Pelvis	67 ± 15	24 ± 5.5	36 ± 3.7[f,g]	8.8 ± 1.0	8.9 ± 0.8[f]
Skeleton	760 ± 140	270 ± 53	36 ± 2.5[f,g]	*11 ± 2.6*[e]	*4.1 ± 0.9*[d]

[a]Excludes teeth. [b]Excludes tail. [c]Includes costal cartilages. [d]Skeleton weight/body weight (%) (shown in italics). [e]Significantly less than female cynomolgus monkeys. [f]Significantly greater than female cynomolgus monkeys. [g]Significantly greater than male rhesus monkeys.

Table 9. Weights and skeletal fractions of bones of adult male rhesus monkeys caught in the wild and housed at LBNL or UR-Delta (≥7 y, 10 ± 1.7 kg, n=16).

	Wet weight (g)[a]	Ash weight (g)	Ash fraction (a/w, %)	Bone/skeleton (%)	Bone ash/skeletal ash (%)
	mean ± SD	mean ± SD	mean ± SD	mean ± SD	mean ± SD
Cranium[b]	160 ± 32	56 ± 11	35 ± 2.9[h]	13 ± 2.0[f,h]	14 ± 2.1[f,h]
Mandible[b]	48 ± 9.5	21 ± 3.8	46 ± 4.2	3.8 ± 0.6[f]	5.1 ± 0.8[f]
Scapulae	44 ± 8.0	17 ± 3.0	38 ± 4.3	3.6 ± 0.4	4.1 ± 0.3[g]
Clavicles	8.9 ± 2.1	3.0 ± 1.0	32 ± 4.1	4.8 ± 0.7	4.6 ± 0.4
Ribs	60 ± 14	20 ± 4.4	31 ± 4.1	4.8 ± 0.7	4.6 ± 0.4
Sternum	14 ± 2.5	1.9 ± 0.6	14 ± 3.3	1.0 ± 0.2	0.4 ± 0.1
Costal cartilages	17 ± 3.8	1.7 ± 0.7	11 ± 2.6[f,h]	1.3 ± 0.3	0.4 ± 0.2
Cervical vertebrae[c]	36 ± 10	8.9 ± 2.5	*28*	2.9 ± 0.6	2.1 ± 0.4
Thoracic vertebrae[c]	84 ± 19	20 ± 4.9	*28*	6.7 ± 0.8	4.6 ± 0.6
Lumbar vertebrae[c]	130 ± 27	32 ± 7.6	*28*	10 ± 0.9	7.6 ± 0.7
LV bodies[d]	*63 ± 17*	*14 ± 3.9*	*21 ± 2.7*		
Sacrum	26 ± 5.7	6.4 ± 1.5	25 ± 3.2	2.0 ± 0.2[h]	1.5 ± 0.1
Pelvis	120 ± 30	40 ± 9.4	31 ± 3.2[h]	9.4 ± 1.3[g]	8.9 ± 0.7[g]
Humeri	84 ± 13	35 ± 6.1	41 ± 4.3[h]	6.6 ± 0.4	8.3 ± 0.7
Radii	33 ± 5.5	15 ± 3.1	43 ± 4.6	2.7 ± 0.2	3.6 ± 0.4
Ulnae	43 ± 7.0	19 ± 3.6	44 ± 4.5[h]	3.4 ± 0.3[i]	4.5 ± 0.4[g,i]
Hands[c]	44 ± 12	12 ± 2.3	*30*	3.5 ± 0.8	2.9 ± 0.4
Femora	130 ± 28	50 ± 11	40 ± 4.6	9.8 ± 1.3[g]	12 ± 1.4[g,i]
Tibiae	81 ± 16	30 ± 7.1	36 ± 3.5[f,h]	6.3 ± 0.9[g]	7.1 ± 0.9[g]
Fibulae	15 ± 2.6	6.8 ± 1.6	43 ± 5.8[h]	1.2 ± 0.2	1.6 ± 0.2
Patellae	8.6 ± 2.8	2.2 ± 0.6	24 ± 6.5	0.7 ± 0.2	0.5 ± 0.1
Feet[c]	84 ± 16	26 ± 4.8	*32*	6.8 ± 0.9	6.1 ± 0.6
Long bone ends[d]	*170 ± 30*	*52 ± 14*	*31 ± 3.6*		
Long bone shafts[d]	*200 ± 36*	*98 ± 15*	*48 ± 4.2*		
Total skeleton[e]	1300 ± 240	420 ± 75	33 ± 2.0[f,h]		

[a]Intact bones include marrow, periosteum, and articular cartilages. [b]Excludes teeth. [c]Fresh weights calculated for 10 of 16 monkeys using grand mean ash fractions of whole vertebrae (0.28 ± 0.05, 140 measurements), hand bones (0.30 ± 0.03, 22 measurements), and foot bones (0.32 ± 0.03, 22 measurements) of cleanly dissected adult Macaques of both sexes and species. [d]Data for 11 monkeys. These partial bone values (shown in italics) are included in the totals for whole bones and the complete skeleton. [e]Excludes teeth (21 ± 4.0 g fresh; 15 ± 2.7 g ash) and tail (25 ± 7.3 g fresh; 7.1 ± 2.0 g ash). [f]Significantly less than male cynomolgus monkeys. [g]Significantly greater than male cynomolgus monkeys. [h]Significantly less than female rhesus monkeys. [i]Significantly greater than female rhesus monkeys.

Table 10. Weights of major skeletal units of wild-caught adult male rhesus monkeys housed at LBNL or UR-Delta (≥7 y, 10 ± 1.7 kg, n=16)

	Wet weight (g)	Ash weight (g)	Ash fraction (a/w) (%)	Bone/skeleton (%)	Bone ash/skeleton ash (%)
	mean ± SD	mean ± SD	mean ± SD	mean ± SD	mean ± SD
Head[a]	210 ± 41	78 ± 14	38 ± 2.2	16 ± 2.4[e,g]	19 ± 2.6[e,g]
Upper limbs	210 ± 37	81 ± 14	39 ± 3.8[g]	16 ± 1.1	19 ± 1.3
Lower limbs	320 ± 65	110 ± 24	36 ± 2.9[g]	25 ± 2.4[f]	27 ± 2.6[f]
Spine[b]	280 ± 66	67 ± 16	24 ± 1.5	22 ± 1.8	16 ± 1.6
Thorax[c]	140 ± 30	42 ± 8.8	31 ± 2.9	11 ± 1.4	10 ± 0.8
Pelvis	120 ± 30	38 ± 8.4	31 ± 3.0[g]	9.4 ± 1.2[f]	8.9 ± 0.7[f]
Skeleton	1300 ± 240	420 ± 75	33 ± 2.0[e,g]	*12 ± 1.9*[d]	*4.0 ± 0.6*[d]

[a]Excludes teeth. [b]Excludes tail. [c]Includes costal cartilages. [d]Skeleton weight/body weight (%) (shown in italics). [e]Significantly less than male cynomolgus monkeys. [f]Significantly greater than male cynomolgus monkeys. [g]Significantly less than female rhesus monkeys.

Table 11. Variability of individual bone and whole skeleton parameters of four Macaque species-sex groups.

	Coefficient of variation (V,%)[a]			
	Cynomolgus		Rhesus	
	Female (33)[b]	Male (9)[b]	Female (58)[b]	Male (16)[b]
Whole body	26	19	24	17
Whole skeleton				
fresh weight	14	18	18	19
ashed weight	16	19	20	18
Mean coefficient of variation ($\bar{V}$,%)[a,c]				
Individual bones (20)				
fresh weight	19	22	23	23
ashed weight	19	24	24	23
ash fraction (a/w)	15	9	13	13
Bone/skeleton	12	10	12	14
Bone ash/skeleton ash	13	11	13	13

[a]Coefficient of variation (V) calculated using eqn (1) and data from Tables 3, 5, 7, and 9. [b]Number of completely dissected skeletons. [c]Mean coefficients of variation ($\bar{V}$,%) for the 20 individual bones or bone groups (costal cartilages excluded) given for each species–sex group in Tables 3, 5, 7, and 9.

Table 12. Growth of the female Macaque skeleton expressed as pairs of discontinuous exponential straight-line segments relating fraction of mature weight to age in years.[a,b]

	Growth curve parameters[c]					
	Early phase			Late phase		
	R_1 (y)	A_1	T_1 (y)	R_2 (y)	A_2	T_2 (y)
Body weight	0–0.7	0.09	0.34	0.7–5.0	0.32	3.1
Skeleton-fresh	0–0.7	0.14	0.41	0.7–5.0	0.40	3.7
ashed	0–0.8	0.079	0.36	0.8–5.0	0.27	2.7
Skeletal units						
Head-fresh	0–0.6	0.20	0.47	0.6–5.0	0.45	4.4
ashed	0–0.6	0.12	0.34	0.6–5.0	0.32	3.2
Upper limbs-fresh	0–0.7	0.13	0.39	0.7–5.0	0.40	3.9
ashed	0–0.8	0.065	0.36	0.8–5.0	0.26	2.6
Lower limbs-fresh	0–0.6	0.11	0.28	0.6–5.0	0.43	4.1
ashed	0–0.7	0.055	0.27	0.7–5.0	0.27	2.6
Spine-fresh	0–0.8	0.15	0.58	0.8–5.0	0.32	3.0
ashed	0–1.1	0.081	0.56	1.1–5.0	0.23	2.4
Thorax-fresh	0–1.3	0.14	0.76	1.3–5.0	0.36	3.6
ashed	0–1.0	0.074	0.54	1.0–5.0	0.21	2.3
Pelvis-fresh	0–0.6	0.086	0.27	0.6–5.0	0.34	3.0
ashed	0–0.7	0.047	0.31	0.7–5.0	0.18	2.0

[a]Mature body weights used to evaluate growth curve parameters: cynomolgus females (33), 3500 ± 900 g, as shown in Table 4; rhesus females (18), 5800 ± 1700 g, a sub-group of young adults 5 to 10 y old. [b]Mature weights of whole skeleton and skeletal units (fresh and ashed) are those shown in Table 4 (33 cynomolgus females, 5 to 16 y old) and Table 8 (58 rhesus females, 5 to 26 y old. [c]A_1 and A_2 are the fractions of mature weights at t(0), T_1 and T_2 are the half-times in years, and R_1 and R_2 are the age ranges in years, respectively, of the early and late exponential growth curve segments, eqn (3a) and eqn (3b).

Table 13. Growth of the male Macaque skeleton expressed as pairs of discontinuous exponential straight-line segments relating fraction of mature weight to age in years.[a]

	Growth curve parameters[b]					
	Early phase			Late phase		
	R_1 (y)	A_1	T_1 (y)	R_2 (y)	A_2	T_2 (y)
Body weight	0–0.7	0.044	0.29	0.7–7.0	0.16	2.6
Skeleton-fresh	0–1.1	0.065	0.54	1.1–7.0	0.21	3.3
ashed	0–1.1	0.037	0.45	1.1–7.0	0.15	2.5
Skeletal units						
Head-fresh	0–1.2	0.12	0.63	1.2–7.0	0.40	5.9
ashed	0–1.0	0.069	0.44	1.0–7.0	0.28	4.0
Upper limbs-fresh	0–1.0	0.052	0.42	1.0–7.0	0.20	3.0
ashed	0–1.0	0.026	0.35	1.0–7.0	0.15	2.6
Lower limbs-fresh	0–1.2	0.054	0.51	1.2–7.0	0.22	3.3
ashed	0–1.2	0.027	0.38	1.2–7.0	0.18	2.8
Spine-fresh	0–1.0	0.056	0.54	1.0–7.0	0.19	3.3
ashed	0–1.5	0.035	0.53	1.5–7.0	0.17	3.0
Thorax-fresh	0–0.9	0.064	0.51	0.9–7.0	0.18	3.0
ashed	0–1.4	0.035	0.57	1.4–7.0	0.12	2.3
Pelvis-fresh	0–1.3	0.040	0.52	1.3–7.0	0.17	3.0
ashed	0–1.2	0.020	0.39	1.2–7.0	0.13	2.4

[a]Mature weights of whole body, skeleton, and skeletal units (fresh and ashed) are those shown in Table 6 (9 male cynomolgus monkeys ≥ 7 y old) and Table 10 (16 male rhesus monkeys ≥ 7 y old). [b]A_1 and A_2 are the fractions of mature weights at t(0), T_1 and T_2 are the half-times in years, and R_1 and R_2 are the age ranges in years, respectively, of the early and late exponential growth curve segments, eqn (3a) and eqn (3b).

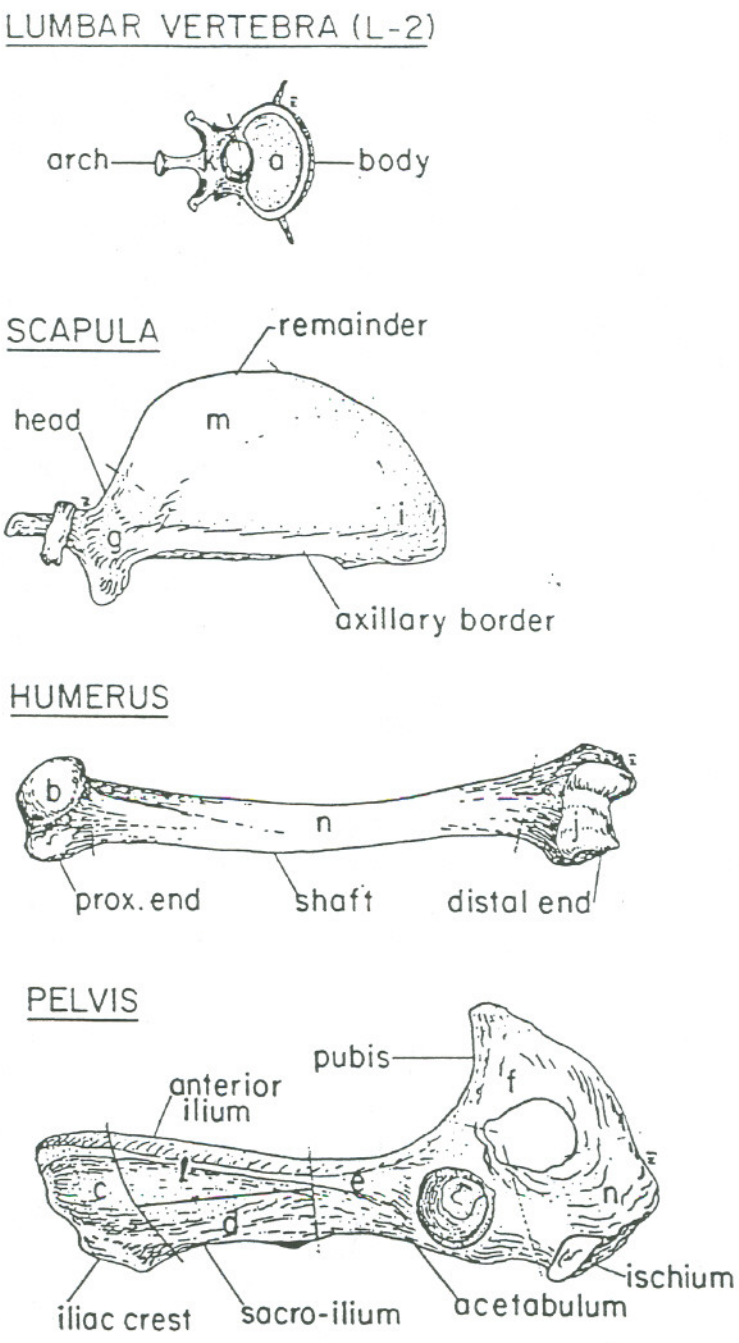

Figure 1. Division of some monkey bones into structurally distinctive parts. Long bones and clavicles were divided as shown for the humerus. Scapulae and pelvis were divided as shown. Vertebrae were divided as shown for LV2.

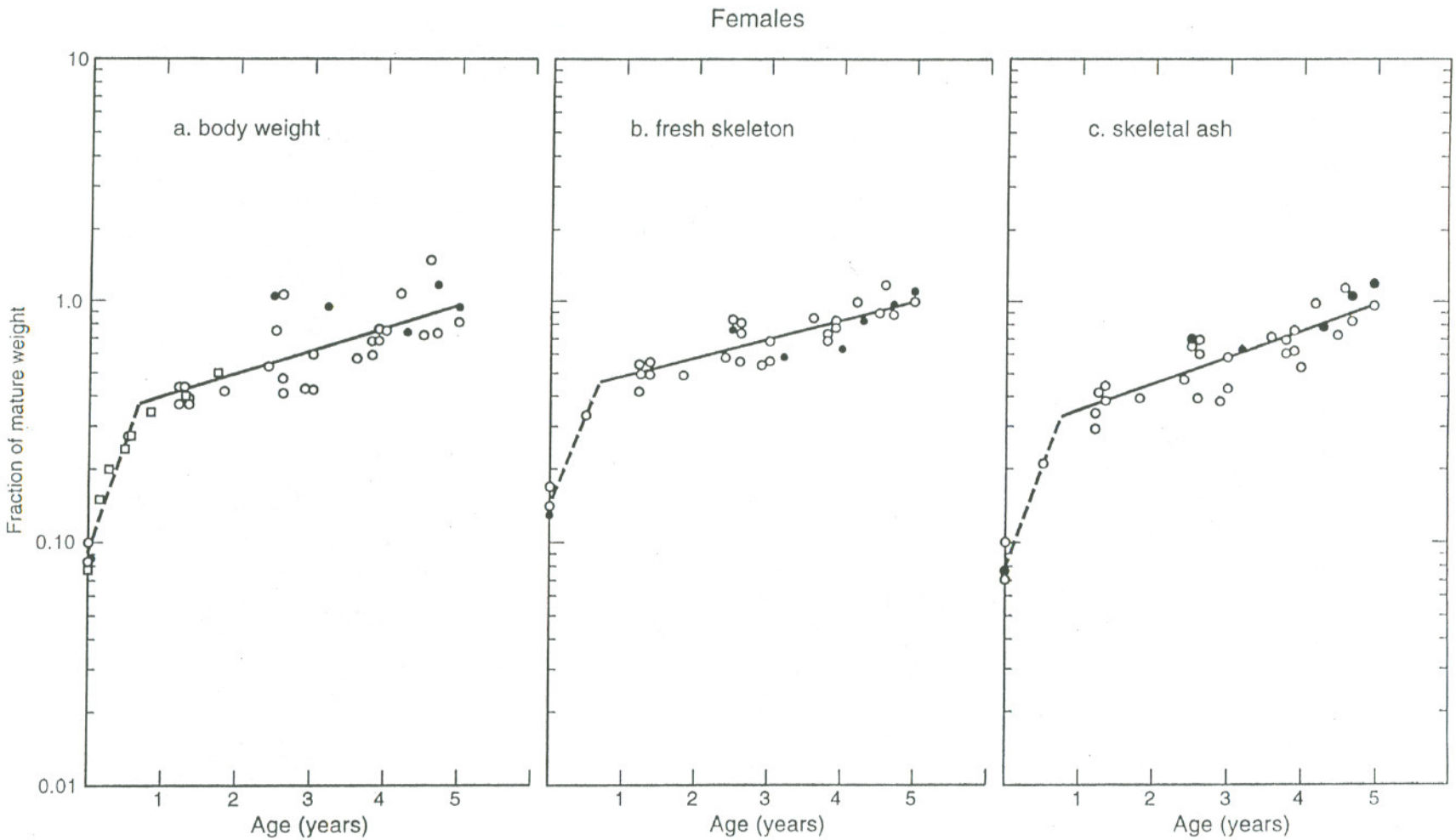

Figure 2. Females: Growth expressed as fraction of mature weight of (a) whole body, (b) fresh skeleton, (c) ashed skeleton. o-rhesus monkeys, ●-cynomolgus monkeys, □-sequential live weights of one or two rhesus monkeys. The paucity of data from very young monkeys makes the slopes of the rapid initial components of growth uncertain, and they are shown as dashed lines.

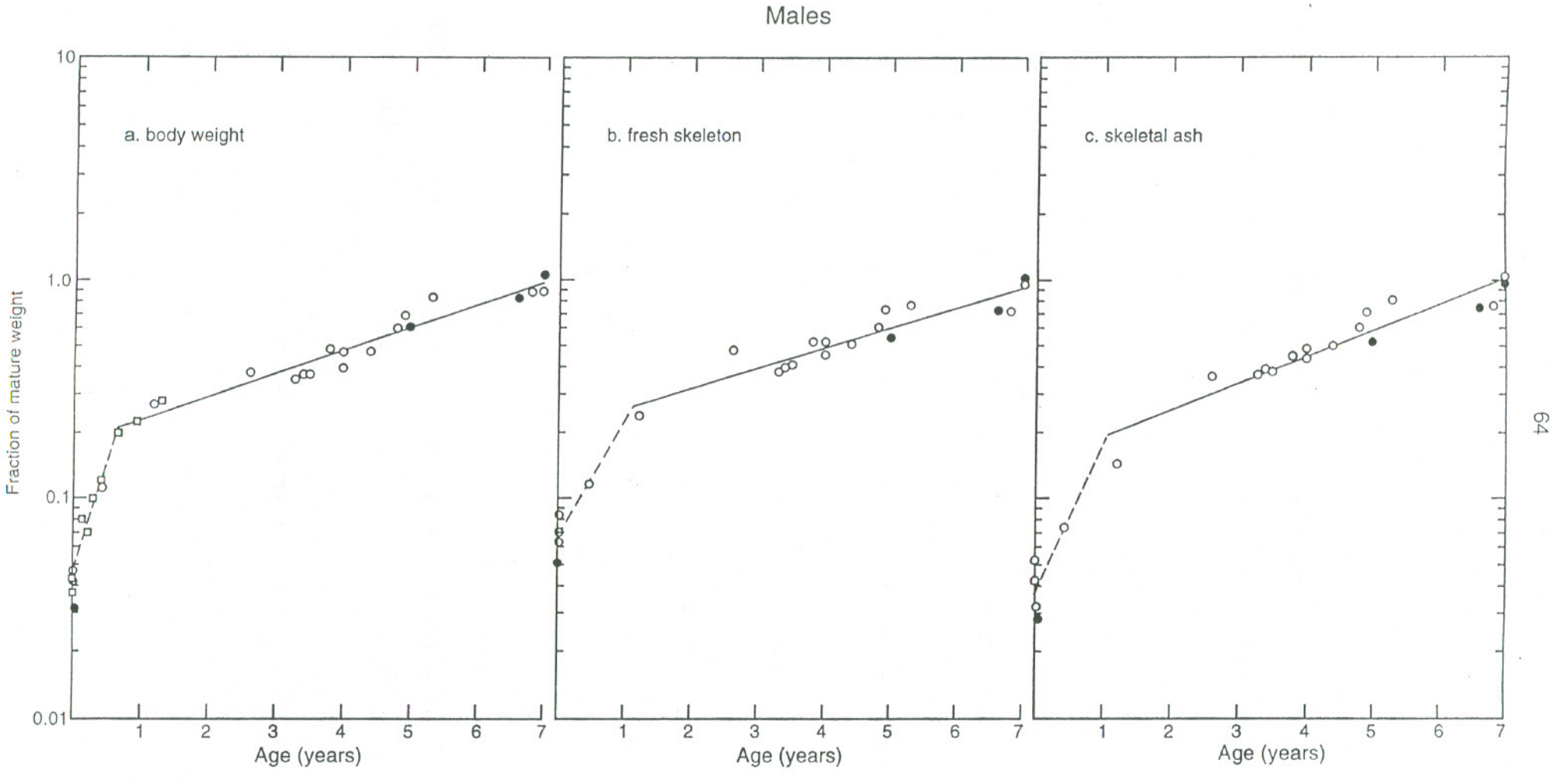

Figure 3. Males: Growth expressed as fraction of mature weight of (a) whole body, (b) fresh skeleton, (c) ashed skeleton. o-rhesus monkeys, ●-cynomolgus monkeys, □-sequential live weights of three to six rhesus monkeys. The paucity of data from very young monkeys makes the slopes of the rapid initial components of growth uncertain, and they are shown as dashed lines.

APPENDIX-CALCULATIONS:

I. Notation and abbreviations

The notation for bones and bone parts and abbreviations of measured properties of bone specimens shown in Appendix Table 3 were adopted for the calculations described in this section.

II. Accounting for missing skeletal parts

a. Paired bones: The ashed weight of the reserved right rib and right humerus (and any other member of a paired bone reserved for autoradiography) were assumed to equal the measured values for the left rib and the left humerus (and its subdivisions into ends and shaft), respectively. Left-right symmetry of the weights and nuclide content of long bones (intact or subdivided) was verified by the separate measurements of right and left leg bones of i.m. injected monkeys.

b. Sub-samples of bones: The calvarium (all of the parietal, most of the frontal, and some of the temporal bone of the skull) was defleshed, removed by saw cuts and divided by sawing at the midline into two nearly equal parts each of which were weighed wet. The right portion was reserved, and the left portion was ashed and radioanalyzed. The ashed weight of the reserved portion was calculated assuming that the concentration of mineral (afr) was the same in both portions.

After 1974, two central sternebrae were weighed wet and reserved. The remainder, which usually contained about two-thirds of the total wet weight, was ashed and radioanalyzed. The ashed weight of the reserved sternum sample was calculated assuming that afr was uniform for the whole sternum.

c. Lumbar vertebrae: The lumbar vertebrae of the monkey are complex individually and as a group. The LVB are composed chiefly of fine cancellous bone in red marrow enclosed in a thin cortical shell. The LVA of Macaques, presumably in response to the need for structural strength imposed by upright sitting posture, are composed of compact bone that encloses a variable

number of spaces filled with fatty marrow; the sizes of the fatty marrow spaces in the LVA are variable and generally of larger diameter than the intertrabecular spaces of the cancellous bone of the LVB.

Wet and ashed weights of LV increase progressively from LV1 to LV5 (in some cases, LV6); the wet weight of LV7 (in most cases also of LV6) is about the same as or less than that of the heaviest LV (usually LV5). The degree of mineralization of the LV (ash fraction, afr) decreases from LV2 to LV7. Based on measurements of intact LV from the 16 cynomolgus and 17 rhesus adult females , $\bar{a}$ fr(LV2) is (0.30 ± 0.030, and 0.29 ± 0.05, respectively and both are significantly greater than $\bar{a}$ fr(LV7), 0.27 ± 0.02, and 0.28 ± 0.04, respectively..

Before describing the trends in the structural parameters of the LV (arch fractions, wAfr and aAfr) and the composition parameters [afr (LVA) and afr(LVB)], it should be noted that some unavoidable variability was introduced by the process used to separate LVA and LVB. Even though best efforts were made to locate the saw cuts close to the lateral margins of the LVB (as shown in Fig. 1), both the bone saw and the LV were hand held (the LV was gripped with a large hemostat), and consequently, not all LV were divided at exactly the same location.

The arch fractions of the LV of the female monkeys, were generally larger for LV2 and LV4 than for LV5-LV7, $\bar{w}$ Afr(LV2)was almost the same as $\bar{w}$ Afr(LV4), and both were greater than $\bar{w}$ Afr(LV7). Similarly, $\bar{a}$ Afr(LV2) was not different from $\bar{a}$ Afr(LV4), but it was greater than $\bar{a}$ Afr(LV7), 0.589 ± 0.102.

The numbers of monkeys with divided LV were large enough to examine variations in $\bar{w}$ Afr, $\bar{a}$ Afr, $\bar{a}$ fr(LVA), and $\bar{a}$ fr(LVB) within individual monkeys (average parameters of the set of five divided LV for each monkey) and variations due to differences between monkeys. In all cases, the average standard deviation (% S.D.) was greater among monkeys than within monkeys. The ratios of the average deviations [(% S.D. among monkeys) (% S.D. within monkeys)$^{-1}$] were smaller for $\bar{a}$ fr(LVA) and $\bar{a}$ Afr than for $\bar{w}$ Afr and $\bar{a}$ fr(LVB). Grand averages of the structural and composition parameters of the LV and their parts were, therefore, substituted for

missing values only in the absence of any relevant data from the same animal. When it was necessary to substitute default values, the less animal-specific $\bar{a}$ fr(LVA) and $\bar{a}$ Afr were used.

All the data for weights of individual LV, LVA, and LVB were examined together, and the following conclusions were reached: i) The structural (wAfr, aAfr) and composition [afr(LVA), afr(LVB)] parameters of adult female cynomolgus and rhesus monkeys are indistinguishable. ii) The similarities in structure and composition of the first four LV of the monkeys permit the use of data from any one of them to be substituted for missing data from the others without introducing serious errors, however, because LV1 most closely resembles LV2, and LV3 resembles both LV2 and LV4, data from the adjacent LV were substituted whenever possible.

The following procedure was adopted to account for missing ashed weights of LV1 and LV3 that were reserved for autoradiography. LV2 had been taken from each monkey (LV2 of several monkeys in was divided into LV2A and LV2B). It was thoroughly defleshed, weighed wet and ashed; similar data were available for LV4 (divided) from the 33 monkeys killed after 1974. The reserved LV1 and LV3, were defleshed and weighed wet. If ashed weight was available only for LV2, the ashed weights [a(LV1), a(LV3)] were calculated from the measured wet weights, [w(LV1), w(LV3)] and the measured values of afr(LV2), where a(LV1) = w(LV1) afr(LV2). If data were also available from LV4, a(LV1) was calculated as above, and a(LV3) was calculated from the numerical average of afr of LV2 and LV4.

III. Estimation of wet weights of incompletely defleshed bones

a. Teeth. Extraction of wet monkey teeth is difficult and time consuming; it is also often incomplete, when broken roots are left in place. However, both crowns and roots can be quantitatively removed from the alveolar bone after ashing. All teeth were extracted wet from the skull and mandible of three monkeys at autopsy, and upper canine teeth were routinely extracted from male monkeys. The extracted teeth were weighed wet and ashed, yielding $\bar{a}$ fr(teeth), 0.69 $\pm$ 0.01. Skull and mandible (with their normal complements of teeth) were weighed wet and ashed. The tooth roots were carefully removed from the ashed bone (the crowns usually

separated during ashing and fell to the bottom of the ashing beaker); the ashed upper teeth, lower teeth, skull, and mandible were weighed separately. The weights of fresh teeth were calculated from the average afr(teeth), and those weights were subtracted from the appropriate sample wet weight (upper teeth from skull, lower teeth from mandible) to obtain edentulous wet weights.

b. Hand and foot bones. The many small bones of the hands and wrists and feet and ankles of monkeys are difficult and time consuming to disarticulate and completely deflesh. The hand and foot bones of most of the monkeys in these studies were not disarticulated and were only partly defleshed; all hand and foot bones of many of the monkeys were combined as a hands-plus-feet sample. Separate ashed weights of hand and foot bones eventually became available from 52 monkeys. Separate wet weights of disarticulated and completely defleshed hand and foot bones were accumulated from 22 Macaques of both species and sex . There were no statistically significant differences in the hands fractions [(hand bones) (hand-plus-foot bones)$^{-1}$] of the wet or ashed weights . The combined results are as follows: hands fraction of total wet weight, 0.36 $\pm$ 0.03; hands fraction of total ashed weight, 0.35 $\pm$ 0.03. The hands fraction of total wet and ashed weight and nuclide content of the hands-plus-feet samples are all nearly the same, and a general hands fractions 0.35 $\pm$ 0.04 (144 measurements), was used to partition the weights and nuclide content of the combined hands-plus-feet samples between hand bones and foot bones.

Based on the wet and ashed weights of 22 sets of disarticulated and completely defleshed Macaque hand bones and foot bones, ash fractions [$\bar{a}$ fr(hands), $\bar{a}$ fr(feet)] were obtained for four species-sex groupings . There were no statistically significant differences attributable to either species or sex, and the combined $\bar{a}$ fr were 0.30 $\pm$ 0.03 and 0.32 $\pm$ 0.03 for hand and foot bones, respectively, and those values were used to calculate wet weights from the measured ashed weights of hand and foot bones, either separated or combined.

c. Bones of the spinal column. Wet and ashed weights of disarticulated completely defleshed segments of the spinal column were eventually obtained from Macaques of both species and sex. No statistically significant differences related either to species or sex were found for the $\bar{a}$ fr

of the five spinal segments [CV(1-7), TV(1-12), LV(1-7), sacrum, tail], and grand average values were computed as follows: $\bar{a}$ fr(CV), 0.289± 0.07, 36 monkeys; $\bar{a}$ fr(TV), 0.28 ± 0.04, 36 monkeys; $\bar{a}$ fr(LV), 0.28 ± 0.03, 50 monkeys; $\bar{a}$ fr(sacrum), 0.25 ± 0.03, 45 monkeys; $\bar{a}$ fr(tail), 0.282± 0.04, 18 monkeys. The $\bar{a}$ fr(CV), $\bar{a}$ fr(TV), $\bar{a}$ fr(LV), and $\bar{a}$ fr(tail) were not significantly different from each other, but $\bar{a}$ fr(sacrum) was significantly less than $\bar{a}$(LV) . A grand average, $\bar{a}$ fr(V), 0.28 ± 0.05 (140 measurements), was used to calculate wet weight of poorly defleshed segments of the spine (CV, TV, LV, tail) from their measured or estimated ashed weights. The $\bar{a}$ fr(sacrum) was used to calculate sacrum wet weight from measured or estimated ashed weight.

IV. Partitioning weights of grouped or undivided bones

a. Sternum-plus-costal cartilages. Before 1973, the interpretive value of the nuclide concentration in specimens of nearly pure cancellous bone was not fully appreciated and sternum (st) was not separated from the costal cartilages (cc). The mineralized cores of the cc are poorly vascularized, and only the mineral-cartilage interface is accessible for deposition of bone-seeking elements (As52). The cc contribute more than one-half of the mineral ash of the combined sample (st + cc), but the cc usually contain much less than one-half of the Am or Pu content of the combined sample. The net result is that the nuclide content of (st + cc) is about 20% more than that of st, but the nuclide concentration in the combined ash, is less than one-half that in st ash.

Separate wet and ashed weights of st and cc were eventually accumulated for 24 adult cynomolgus monkeys of both sexes and 27 adult rhesus monkeys of both sexes. There were no statistically significant sex or species-related differences in the weight relationships of st and (st + cc), and data were combined as follows:

$\bar{a}$ fr(st): 0.14 ± 0.03,

wet weight ratio, w(st) $w(st + cc)^{-1}$: 0.43 ± 0.06,

ashed weight ratio = a(st) $a(st + cc)^{-1}$ = 0.39 ± 0.09 (cynomolgus),

= 0.51 ± 0.10 (rhesus) .

Estimates of wet and ashed weights and nuclide content of the cc were obtained by difference.

b. Partitioning undivided LV into arch and body. It was noted in section II.c that the arch fractions of the seven LV and the ash fractions of their LVA and LVB varied less within monkeys than among monkeys. As far as possible, structural, and composition data from one of the first four LV of the same animal were used to partition its undivided LV. Measurements of wAfr were frequently unavailable, and based on measurements of wAfr and aAfr of LV2 and/or LV4 of 23 cynomolgus and 24 rhesus monkeys, the average ratio of wAfr $aAfr^{-1}$, 0.85 ± 0.08, was used to calculate wAfr from aAfr.

i) When LV4 through LV7 and either LV2 or LV3 were divided at autopsy, measurements of wAfr, and aAfr of an adjacent LV were used to partition the undivided LV.

ii) When LV4 through LV7 were divided at autopsy, values of wAfr(LV4) and aAfr(LV4) were substituted.

iii) LV3, salvaged intact from the alcohol-fixed reserved bone material of five cynomolgus and 19 rhesus monkeys was divided into arch and body, ashed, and radioanalyzed. The measured values of aAfr(LV3) were used to partition LV1 and LV2, and wAfr was calculated from aAfr(LV3).

iv) Alcohol-fixed remnants of LV1A and LV1B, available from three cynomolgus and 15 rhesus monkeys represented more than 20% of their total wet weights; they were ashed and radioanalyzed, providing reasonably reliable measurements of afr(LVA) and afr(LVB), from which the total ash weights could be estimated..

c. Partitioning lower lumbar spine and sacrum. For 22 cynomolgus monkeys and 25 rhesus monkeys, LV(3-7) [in six cases, LV(4-7)] had been combined with the sacrum and the ashed weight of the combined sample [sacrum + LV(3-7)] was measured. The ashed weight of LV(1,2) or LV(1-3) were first added to those of the [sacrum + LV(3-7)] sample to obtain the ashed weight of the sacrum and entire lower spine [sacrum + LV(1-7)]. The sacrum fraction of the ashed weight of the lower spine and the ratio of the ashed weight of sacrum and LV(1,2) were later determined for 23 cynomolgus and 37 rhesus monkeys (both sexes), respectively, whose sacrum and

lumbar vertebrae were disarticulated, thoroughly defleshed, and weighed, separately. The fractional sacrum ashed weights were 0.19 ± 0.02, and 0.17 ± 0.02 for cynomolgus and rhesus monkeys, respectively.

The ashed weight of the sacrum was estimated from those relationships and a(LV1-7) was obtained by difference.

d. Partitioning lower lumbar spine, sacrum, and tail. The tails of the earliest autopsied monkeys (seven cynomolgus, 13 rhesus) were not detached from the lower spine, and the ashed weights of the combined sample [sacrum + LV(3-7) + tail] were measured.

For the rhesus monkeys, estimates of the ashed weights of [sacrum + LV(1-7)] could also be obtained from the relationships between the ashed weights of the lower spine [sacrum + LV(1-7)] and those of the upper spine [CV + TV], which was measured in all monkeys. The [sacrum + LV(1-7)] fraction of the ashed weight of the entire spinal column, determined for 30 monkeys, was 0.16 ± 0.03, and

$$a[\text{sacrum} + \text{LV}(1\text{-}7)] = 1.60\ a[\text{CV} + \text{TV}] \quad .$$

First, the measured ashed weights of LV(1,2) was added to those of the measured [sacrum + LV(3-7) + tail] sample. Estimates of a[sacrum + LV(1-7)] were then obtained using the measured values of a[CV + TV). Those values were partitioned between sacrum and LV(1-7) to yield a second set of estimates of a(sacrum), and a(LV(1-7)), n(sacrum). The values of the sums, a[sacrum + LV(1-7)] were subtracted from the measured ashed weight of the combined sample [sacrum + LV(1-7) + tail] to obtain separate estimates of a(tail). The tail of the rhesus monkey is short, the fraction contributed by the tail to fresh and ashed weight, while somewhat more variable than those of the LV(1-7) and sacrum segments, is sufficiently consistent to permit the use of average weight fractions to partition total sample weight into the weight of the individual segments. Weight fractions of the three lower spine segments were calculated from data from 15 adult and late adolescent female rhesus monkeys whose lower spinal columns had been completely disarticulated and defleshed and individual bones weighed and radioanalyzed.

Estimation of the ashed weights of the three lower spine segments was accomplished, as follows: Measured ashed weights of LV(1,2) and [LV(3-7) + sacrum + tail] were summed to obtain the total a[LV(1-7) + sacrum + tail] for those monkeys whose lower spine had been managed as a combined sample. The following ashed weight fractions were used to estimate the separate ashed weights: LV(1-7), 0.70 $\pm$ 0.03, sacrum, 0.16+ 0.01;and tail, 0.14 + 0.02.

e. Partitioning (long bones – humerus) into arm and leg bones. Except for the humerus, the long limb bones of 19 adult female cynomolgus monkeys were divided into ends and shaft, which were then combined to constitute two large samples, long bone ends and long bone shafts. The ends and shaft samples, thus, consisted of the proximal and distal ends and shafts of the two lower arm bones (radii-ulnae) and the three leg bones (femora-tibiae-fibulae). In order to compute total weights of the upper and lower limbs separately, those combined samples were partitioned by calculation into radii-ulnae ends and shafts and leg bone ends and shafts. Weights (wet and ashed) of all the individual long bones (separated into ends and shaft) were eventually available from 19 adult female monkeys. The fractions of the total wet and ashed weights of the combined radii-ulnae-femora-tibiae-fibulae ends (shafts) samples contributed by the radii-ulnae ends (shafts) that were used to compute the separate contributions of the arm bones are as follows:

wet weight fractions

$$w[(\text{radii-ulnae})\text{ends}] = (0.22 \pm 0.02)\, w[(\text{long bones} - \text{humerus})\text{ends}] \quad ,$$

$$w[(\text{radii-ulnae})\text{shafts}] = (0.30 \pm 0.02)\, w[(\text{long bones} - \text{humerus})\text{shafts}] \quad ,$$

ashed weight fractions

$$a[(\text{radii-ulnae})\text{ends}] = (0.24 \pm 0.02)\, a[(\text{long bones} - \text{humerus})\text{ends}] \quad ,$$

$$a[(\text{radii-ulnae})\text{shafts}] = (0.31 \pm 0.02)\, a[(\text{long bones} - \text{humerus})\text{shafts}] \, .$$

Weights of the combined leg bone ends and shafts were obtained by difference.

Appendix Table 1. Weights of whole skeleton and major skeletal units of adult wild-caught female rhesus monkeys housed at LBNL or UR (13.3 ± 4.2 y, 6.4 ± 1.5 kg, n=35).

	Wet weight (g)	Ash weight (g)	a/w (%)	Wet bone/skeleton (%)	Bone ash/skeletal ash (%)
	mean ± SD	mean ± SD	mean ± SD	mean ± SD	mean ± SD
Head[a]	140 ± 20	58 ± 8.4	41 ± 3.2	19 ± 2.1	22 ± 2.6
Upper limbs	120 ± 21	49 ± 11	42 ± 3.6	16 ± 1.1	18 ± 1.3
Lower limbs	180 ± 30	70 ± 15	38 ± 3.3	24 ± 1.6	26 ± 1.9
Spine[b]	160 ± 34	40 ± 8.7	26 ± 3.8	22 ± 3.9	15 ± 1.4
Thorax[c]	82 ± 21	25 ± 5.4	31 ± 3.8	11 ± 1.4	10 ± 1.0
Pelvis	66 ± 12	23 ± 4.6	35 ± 3.9	9.0 ± 1.1	9.0 ± 0.8
Skeleton	750 ± 120	260 ± 48	35 ± 2.8	*12 ± 2.1*[d]	*4.0 ± 0.7*[d]

[a]Excludes teeth. [b]Excludes tail. [c]Includes costal cartilages. [d]Skeleton weight/body weight (%) (shown in italics).

Appendix Table 2. Weights of whole skeleton and major skeletal units of wild caught adult female rhesus monkeys housed at Yale (15.4 ± 4.8 y, 8.3 ± 1.4 kg, n=16).

	Wet weight (g)	Ash weight (g)	a/w (%)	Bone/skeleton (%)	Bone ash/skeleton ash (%)
	mean ± SD	mean ± SD	mean ± SD	mean ± SD	mean ± SD
Head[a]	150 ± 36	60 ± 14	40 ± 4.2	20 ± 2.5	21 ± 2.4
Upper limbs	120 ± 27	52 ± 12	43 ± 2.6	16 ± 0.8	18 ± 1.0
Lower limbs	180 ± 44	72 ± 17	40 ± 1.6	24 ± 1.1	26 ± 0.9
Spine[b]	160 ± 43	44 ± 12	28 ± 0.1[c]	20 ± 1.6	16 ± 1.1
Thorax[d]	88 ± 21	28 ± 6.3	32 ± 3.5	12 ± 1.1	9.9 ± 0.8
Pelvis	68 ± 19	25 ± 6.8	37 ± 3.7	8.8 ± 0.6	9.0 ± 0.6
Skeleton	770 ± 179	280 ± 65	37 ± 2.0	*9.4 ± 2.4*[e]	*3.5 ± 0.9*[e]

[a]Excludes teeth. [b]Excludes tail. [c]Five monkeys with well-cleaned vertebrae. [d] Includes costal cartilages. [e]Skeleton weight/body weight (%) (shown in italics).

Appendix Table 3. Notation and abbreviations used in calculations of weights of missing bones and bone parts and to partition weights of grouped bones into their components.

Item and definition	Abbreviation[a]	Unit
lumbar vertebra intact	LV	
lumbar vertebral arch	LVA	
lumbar vertebral body	LVB	
combined LV1 and LV2	LV(1,2)	
combined LV4 through LV7	LV(4-7)	
sternum	st	
costal cartilages	cc	
sternum and costal cartilages combined	(st + cc)	
wet weight	w	g
ashed weight	a	g
ash fraction, a w^{-1}	afr	
arch fraction of vertebra wet, wA wLV^{-1}	wAfr	
arch fraction of vertebra ashed, aA aLV^{-1}	aAfr	

[a]Abbreviations of properties, added as prefixes, refer to that property of a specific bone or bone part, also abbreviated and enclosed in ( ). For example, wet weight of sternum is w(st); ashed weight of costal cartilages is a(cc); ash fraction of LV2 is wAfr(LV2); arch fraction of LV2 ashed is aAfr(LV2).