

**Pan troglodytes.** By Clyde Jones, Cheri A. Jones, J. Knox Jones, Jr., and Don E. Wilson

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**Pan Oken, 1816**

- Troglodytes* E. Geoffroy, 1812:87. Type species *Troglodytes niger* E. Geoffroy. Name preoccupied by *Troglodytes* Vieillot, 1806, a genus of birds.
- Pan* Oken, 1816:1230. Type species *Pan africanus* Oken. Name taken from an invalid work, but validated by the International Commission on Zoological Nomenclature (opinion 1368) with *Simia troglodytes* as the type species.
- Mimetes* Leach, 1820:104. Type species *Simia satyrus* Linnaeus (= *Simia troglodytes* Blumenbach, 1775). Name preoccupied by *Mimetes* Hubner, 1816, a genus of Lepidoptera.
- Theranthropus* Brookes, 1828:28. Type species *Theranthropus niger* Brookes (= *Troglodytes niger* E. Geoffroy).
- Chimpansee* Voigt, 1831:76. Type species *Simia troglodytes* Blumenbach, 1775.
- Anthropopithecus* Blainville, 1839:360. Type species *Anthropopithecus troglodytes* Blainville (= *Simia troglodytes* Blumenbach).
- Hylanthropus* Gloger, 1841:34. Type species *Hylanthropus troglodytes* Gloger (= *Simia troglodytes* Blumenbach).
- Satyrus* Mayer, 1856:281. Part; for gorillas, chimpanzees, and orangutans, collectively (not *Satyrus* Linnaeus 1760).
- Pseudanthropos* Reichenbach, 1862:191. Replacement name for *Troglodytes* E. Geoffroy.
- Pongo* Haeckel, 1866:cl. New name for *Troglodytes* E. Geoffroy, preoccupied. Not *Pongo* Lacepede, 1799, the orangutan.
- Engeco* Haeckel, 1866:275. Type species *Engeco troglodytes* Haeckel (= *Simia troglodytes* Blumenbach).
- Fsihego* DePauw, 1905:13. Type species *Fsihego ituriensis* Matschie.
- Bonobo* Tratz and Heck, 1954:97. Type species *Bonobo paniscus* (= *Pan satyrus paniscus* Schwarz).

**CONTEXT AND CONTENT.** Order Primates, Suborder Anthropoidea, Superfamily Hominoidea, Family Hominidae, Subfamily Ponginae. *Pan* includes two extant species, *P. troglodytes* and *P. paniscus* (Groves, 1993).

In adults, head and body length more than 70 cm, stocky build, face rounded with pink or black skin ..... *P. troglodytes*  
 In adults, head and body length 70 cm or less, slender build, face elongated with black skin ..... *P. paniscus*

***Pan troglodytes* (Blumenbach 1775)**

**Chimpanzee**

- Simia satyrus* Linnaeus, 1758:25. Type locality "Africa;" restricted to "Mayumba, French Congo," by Schwarz (1934:580). Suppressed by action of International Commission on Zoological Nomenclature, opinion 114.
- Simia troglodytes* Blumenbach, 1775:37. Type locality "Angola."
- Troglodytes niger* E. Geoffroy, 1812:87. Type locality "Coast of Angola."
- Pan africanus* Oken, 1816:1231. Type locality "Congo, Angola, Guinea, Sierra Leona." Invalid (International Commission on Zoological Nomenclature, opinion 417).
- Troglodytes leucoprymnus* Lesson, 1831:pl. 32. Type locality "Coast of Guinea."
- Anthropopithecus pan* Lesson, 1840. No locality given.
- Troglodytes tschego* Duvernoy, 1855:1. Type locality "West Coast of Africa."
- Satyrus lagaros* Mayer, 1856:282. No locality given.
- Satyrus chimpansee* Mayer, 1856:282. No locality given.

- Troglodytes calvus* Du Chaillu, 1860:296. Type locality "Interior of Gaboon, south of Cape Lopez."
- Troglodytes kooloo-kamba* Du Chaillu, 1860:358. Type locality "Ashankolo Mts., upper Ovenga River, French Congo."
- Troglodytes vellerosus* Gray, 1862:181. Type locality "Cameroon Mountains, northern Cameroons."
- Troglodytes aubryi* Gratiolet and Alix, 1866:1. No locality given; probably Gaboon (Allen, 1939).
- Pseudanthropus fuliginosus* Schaufuss, 1870:345. Type locality "French Congo."
- Troglodytes angustimanus* Brehm, 1871.
- Troglodytes schweinfurthii* Giglioli, 1872:114. Type locality "Upper Uele drainage, Niam-niam country, northeastern Congo Belge." Now in Zaire.
- Anthropopithecus fuscus* Meyer, 1895:7. No locality given.
- Simia chimpansee* Matschie, 1904:67. No locality given.
- Fsihego ituriensis* DePauw, 1905:13. Type locality "Ituri and central Congo Belge." Both now in Zaire.
- Simia (Anthropopithecus) nahani* Matschie, 1912:118. Type locality "Banalia, Aruwimi River," Zaire.
- Simia (Anthropopithecus) ituricus* Matschie, 1912:121. Type locality "Makala-Avakubi road, Ituri basin," Zaire.
- Simia (Anthropopithecus) cottoni* Matschie, 1912:124. Type locality "Sassa (Ishasha) River, southeast of Lake Albert, western border of Uganda."
- Simia (Anthropopithecus) adolfi-friederici* Matschie, 1913:46. Type locality "Bugoi forest, northeast of Lake Kivu," Rwanda.
- (Anthropopithecus) ellioti* Matschie, 1914:327. Type locality "Near Bascho, North Cameroon."
- Anthropopithecus oertzeni* Matschie, 1914:327. Type locality "Near Bascho, northern Cameroons."
- Anthropopithecus reuteri* Matschie, 1914:328. Type locality "Mouth of Dume River, in the Kadei, southern Cameroons."
- Anthropopithecus ochroleucus* Matschie, 1914:329. Type locality "North of Sangmelima, upper Lobo River, southern Cameroons."
- Anthropopithecus purschei* Matschie, 1914:332. Type locality "Tchingogo forest, between Lakes Kivu and Luhondo," Rwanda.
- Anthropopithecus pfeifferi* Matschie, 1914:333. Type locality "East of Russissi on border of Urundi, near sources of the Akanjara," Rwanda.
- Anthropopithecus graueri* Matschie, 1914:333. Type locality "Eighty kilometers northwest of Boko, west shore of Lake Tanganyika," Zaire.
- Anthropopithecus calvescens* Matschie, 1914:334. Type locality "On road from Baraka to Kasongo, between Niembo and Kambambare, on the Luama River, west of Lake Tanganyika," Zaire.
- Anthropopithecus castanomale* Matschie, 1914:334. Type locality "Northeast shore of Lake Tanganyika," Burundi.
- Anthropopithecus schulzi* Matschie, 1914:335. Type locality "Between Kilo and Irumu, upper Ituri River, west of Lake Albert," Zaire.
- Anthropopithecus steindachneri* Lorenz, 1914:550. Type locality "Ituri forest near Moera, north of Beni," Zaire.
- Anthropopithecus schneideri* Matschie, 1919:75. Type locality "Fernan Vaz district, French Congo."
- Anthropopithecus pusillus* Matschie, 1919:76. Type locality probably "lower Ogowe, between Cape Lopez and lake Anengue, Gaboon" (Allen, 1939).
- Anthropopithecus papio* Matschie, 1919:80. Type locality "Barombi, Elephant Lake, Cameroons."

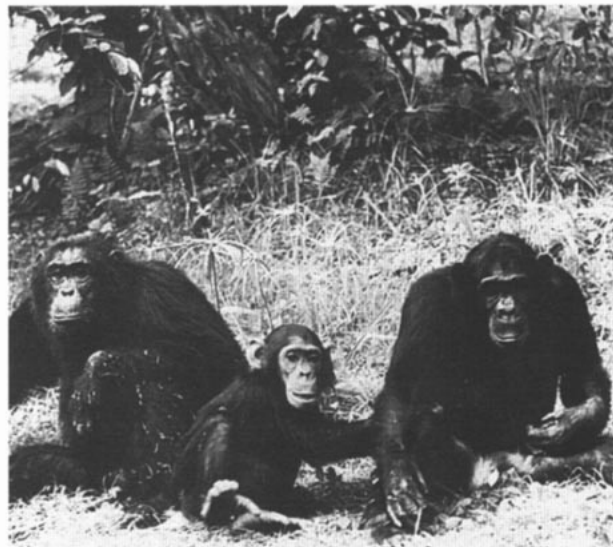


FIG. 1. Photograph of *Pan troglodytes*. Photograph reprinted by permission of Dr. Jane Goodall and Harvard University Press.

*Anthropopithecus hecki* Koch, 1932:100. Type locality "Hinterland of Cameroons."

**CONTEXT AND CONTENT.** As for the genus. There is considerable confusion with regard to the number of geographic races that warrant subspecific recognition. Three subspecies (*P. t. troglodytes*, *P. t. verus*, *P. t. schweinfurthii*) generally have been recognized (Hill, 1966; Napier and Napier, 1967; Reynolds and Reynolds, 1965; Vandebroek, 1959; Yerkes, 1943). The pygmy chimpanzee, or bonobo, *P. paniscus*, although considered as a subspecies of *P. troglodytes* by some authors, is not included herein because it currently is regarded as a distinct species (Groves, 1993; Thorington and Anderson, 1984). In accordance with Dandelot (1971), Hill (1969), and Tuttle (1986), four subspecies of *P. troglodytes* are recognized here. There is a problem, however, in that *t. koolokamba* is sympatric with *t. troglodytes*.

*P. t. koolokamba* Du Chaillu, 1860:358. See above.

*P. t. schweinfurthii* (Giglioli, 1872:114). See above (*marungensis*, *ituriensis*, *nahani*, *ituristicus*, *cottoni*, *adolffrederici*, *yambuyae*, *purschei*, *pfeifferi*, *graueri*, *calvescens*, *castanomale*, *schubolzi*, *steindachneri*).

*P. t. troglodytes* (Blumenbach, 1775:65). See above (*pongo*, *jocko*, *niger*, *leucopymnus*, *pan tshego*, *lagaros*, *chimpanse*, *calvus*, *vellerosus*, *aubryi*, *fuliginosus*, *angustimanus*, *fuscus*, *varipilosus*, *elliotti*, *oertzeni*, *reuteri*, *ochroleucus*, *schneideri*, *pusillus*, *papio*, *hecki*).

*P. t. verus* Schwarz, 1934:578. Type locality "Sanda Magbolonto chiefdom, Karima district, Sierra Leone." (? *schimpanse* a synonym, which, if true, would take precedence over *verus*).

Some of the complex problems with regard to systematic relationships, synonymies, and type localities of *P. troglodytes* were discussed by Allen (1939), Groves (1989), Hill (1966, 1969), Schwarz (1934), Simonetta (1957), and Stiles and Orleman (1927).

**DIAGNOSIS.** The geographic range of *P. troglodytes* has little or no overlap with that of the congeneric form, *P. paniscus* (Tuttle, 1986). However, if the two apes occur in sympatry, behavioral differences may prevent intermingling between the species (Tuttle, 1986). The chimpanzee is larger and more stocky than the smaller and more slender pygmy chimpanzee (Napier and Napier, 1967). Chimpanzees are smaller in size and lack the development of sagittal crests and corresponding musculature of the head and neck as prominent as those characteristic of gorillas (Napier and Napier, 1967). Chimpanzees (Fig. 1) are large arboreal and terrestrial anthropoid primates with flattened nails on all digits; pollex and hallux are opposable. In these apes, the tail is absent; there are no ischial callosities. The face is prominent and prognathous; the nasal region is catarrhine; there are no cheekpouches. The skull is longer than wide, with a tendency to develop bony crests,

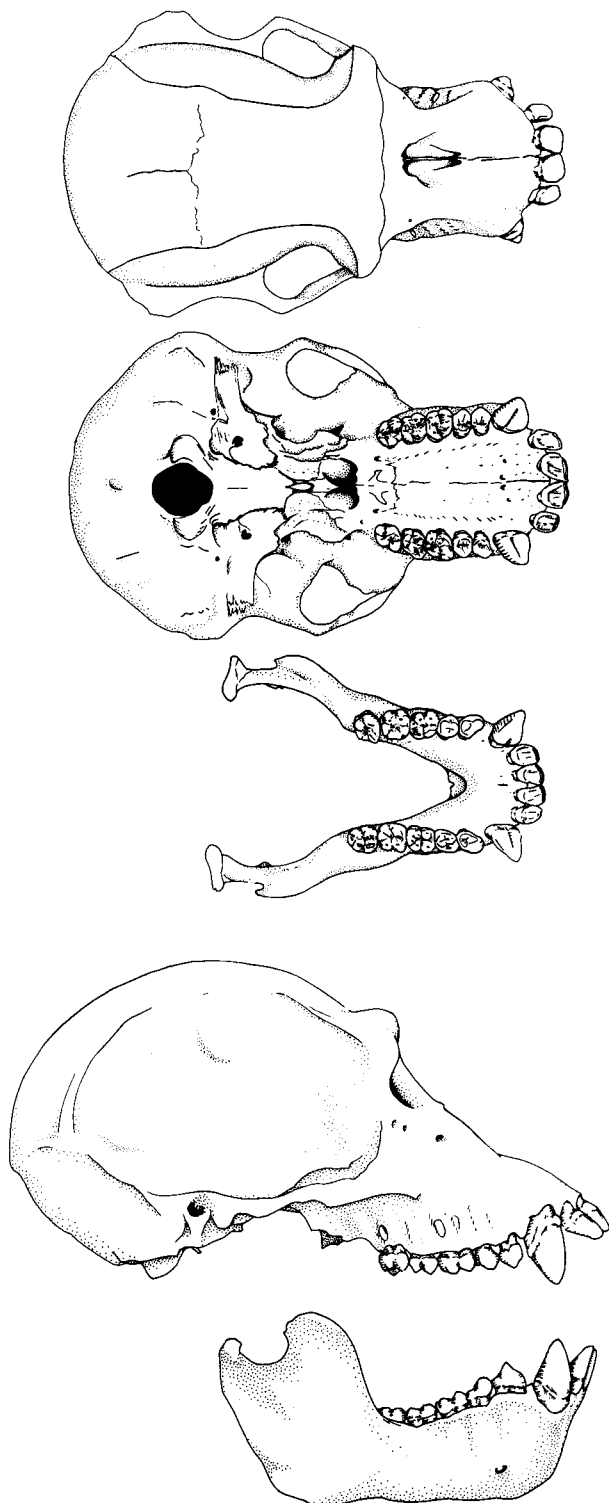


FIG. 2. Dorsal, ventral, and lateral views of the skull, and lateral and dorsal views of the lower jaw of *Pan troglodytes* (USNM 395820, male). Greatest length of skull, 206 mm. Drawings by Wilma Martin.

especially in old males (Napier and Napier, 1967). The dental formula is  $i \ 2/2$ ,  $c \ 1/1$ ,  $p \ 2/2$ ,  $m \ 3/3$ , total 32 (Fig. 2). The maxillary and occluding mandibular tooththrows generally are parallel, with teeth generally large, molars quadrangular, incisors broad, especially the first upper pair, and canines relatively large, especially in males. The premaxillae and symphyseal region of the mandible is considerably widened, with the symphyseal region strengthened by

a bony shelf (Swindler, 1976). The forelimbs are distinctly longer than the hind limbs. The brachial index (radius length  $\times$  100/humerus length) 87 to 100, crural index (tibia length  $\times$  100/femur length) 78 to 90, and the intermembral index (humerus + radius length  $\times$  100/femur + tibia length) 102 to 114 (Napier and Napier, 1967). The sternum is broad; centrale is absent. The thorax is widened transversely; the body is shortened due to reduction of the number of thoraco-lumbar vertebrae by incorporation of posterior lumbar into sacrum. The pelvis is lengthened, with an expanded ilium. The stomach is simple; a caecum is present, with vermiform appendix. There is no glans penis (all other anthropoids possess a glans penis). Details on these diagnostic features are found elsewhere (Anderson, 1967; Grasse, 1955; Napier and Napier, 1967; Thorington and Anderson, 1984).

**GENERAL CHARACTERS.** Length of head and body ranges from 770 to 925 mm in males and from 700 to 850 mm in females; body mass averages 48.9 kg for males and 40.6 kg for females (Napier and Napier, 1967). Hands are longer than feet; hand length index (total length of hand  $\times$  100/humerus + radius + hand length) is 29 to 31, phalangeal index (phalangeal length  $\times$  100/hand length) is 48 to 52, thumb length index (thumb length  $\times$  100/total hand length) is 33 to 35, and opposability index (thumb length  $\times$  100/index ray length) is 38 to 44 (Napier and Napier, 1967). The head is rounded; ears are small, rounded, and without lobes. The zygomatic arches are wide, eyes are directed forward, and lips are protrusive. The skin pigmentation of the face ranges from pale to mottled to darkly pigmented (Fig. 1), the amount increasing with age (Napier and Napier, 1967). The face is sparsely haired, palmar surfaces, plantar surfaces, and ears are naked; pelage of the body generally is black, but white hairs grow on chins of adults of both sexes, and adults have gray hairs in the lumbar region and on the thighs; and juveniles have white tufts of hairs in the anal region. The pelage is generally coarse; hairs on the forearms grow toward the elbow (Napier and Napier, 1967). The placenta is a single disc, deciduous, and hemochorial. The vertebral formula is 7 C, 12–13 T, 3–5 L, 3–8 S, and 2–3 Ca, total 27–36. Genital swelling is especially prominent. A baculum is present (Graham and Bradley, 1972; Napier and Napier, 1967).

**DISTRIBUTION.** The geographic range of the species is included within an area between about 10°N to 8°S and 15°W to 32°E (Fig. 3). Isolated populations of chimpanzees are known from the Sudan and Tanzania, as well as in the West African forest block (Vandebroek, 1959). However, some of these populations may be extinct (Tuttle, 1986). Elevational range is from sea level in West Africa to about 2,750 m in the Ruwenzori Mountains on the Congo-Uganda border. The ecologic range is tropical. General discussions and details of geographic distributions and zoogeographic relationships of *P. troglodytes* were presented by Booth (1954, 1958a, 1958b), Bournonville (1967), Dandelot (1971), and Reynolds (1965, 1967). Geographic distributions of the subspecies are: *P. t. koolokamba*, high level forests in southern Cameroon, Gabon, and Congo; *P. t. schweinfurthi*, forest block between the Oubangui and Congo Rivers, eastward to Sudan and western Uganda, and southward as far as both shores of Lake Tanganyika; *P. t. troglodytes*, forest block south of the Sanaga River, eastward to the Central African Republic, and southward to the Congo; *P. t. verus*, forests in Guinea, Sierra Leone, Liberia, and Ivory Coast, as well as Togo, Dahomey, and west of the Niger River in Nigeria (Tuttle, 1986).

**FOSSIL RECORD.** *Dryopithecus africanus*, known from several sites in Kenya, would have dentition similar to that of *P. troglodytes* if there were a loss of cingula and further hypertrophy of incisors in *Dryopithecus* (Simons and Pilbeam, 1972). Based on dentition and similarities of the forelimb, these authors regarded *D. africanus* as the possible ancestor of the chimpanzee. However, other authors have concluded that ancestors of extant apes cannot be discerned precisely (Tuttle, 1986).

**FORM.** In the skull, the calvarium is rounded. The internasal suture is fused. Supraorbital ridges are pronounced. The articulation of the pterion is between the frontal and temporal bones. The postglenoid process is long and well developed. The foramen ovale is located entirely within the temporal bone. Spinous processes of the vertebrae are long. There are 13 pairs of ribs; seven reach the sternum directly. Of all Hominoidea, *Pan* has the narrowest sternum (Swindler and Wood, 1973). The scapula has a long vertebral

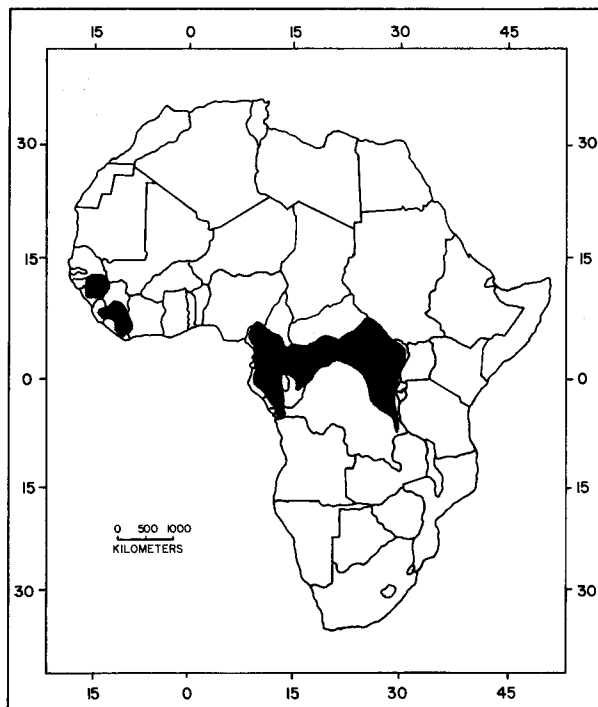


FIG. 3. Original, known distribution of *Pan troglodytes*. Map modified from those of Goodall (1986) and Tuttle (1986). For information on the current distribution of the species and subspecies, see the section on distribution, as well as comments by Goodall (1986) and Tuttle (1986).

border, the result of an extension of the scapula in a craniocaudal direction. The humerus is longer than the radius. The humeral head is directed medially, with the trochlea and capitulum separated by a prominent keel. The olecranon process is short, the head of the radius is rounded, and the shaft bowed. The os centrale usually is fused to the scaphoid in the hand of adult animals. Phalanges are curved and grooved ventrally. Terminal phalanges are broad, flat, and slightly concave on the palmar surfaces. The femur is robust, with antero-posterior curvature. The malleolus of the tibia is long; however, the process is usually straight and ungrooved. The interosseous margin of the fibula is elevated in a keel-like fashion for attachment of the interosseous membrane. The hallux is long and stout (Swindler and Wood, 1973). When compared to carpal bones, those of the tarsus are larger and show a greater diversity of size. The gluteal surface of the ilium has a craniocaudal concavity extending from the iliac crest to the corpus of the ilium and bounded by a bony elevation along the dorsal border of the ilium. Acetabula are directed dorsolaterally. Ischial tuberosities are lacking (Swindler and Wood, 1973).

Of the facial muscles, the platysma lacks much of the nuchal-noto portion. The temporalis craniomandibular muscle is powerful and usually attaches to a well-developed sagittal crest, especially in adult males. The masseter muscle is divided into superficial and deep strata in the posterior portion; frequently there is an aponeurotic sheet separating the two parts. The angle of the chin is considerable (Hershkovitz, 1970).

The maxillary teeth present a rectangular or U-shaped outline. A diastema is present between the lateral incisor and canine, and the central incisor is broader than the lateral one. Lingual surfaces of the incisors are characterized by raised enamel marginal ridges, with a concavity forming a shovel-shaped fossa. Canines are prominent, especially in males. Premolars have a buccal and a lingual cusp; these teeth usually are equal in size in their buccal-lingual dimensions. The molars are quadrilateral, with conical cusps. Of all living pongids, chimpanzees have molars with absolute sizes that approximate most closely those of *Homo* (Swindler, 1976). The outline of the mandibular dental arch is similar to that of the maxillary arch. Central incisors usually are smaller than lateral incisors. Lower canines are long and powerful, but there is less sexual dimorphism than exhibited by the maxillary canines. Premolars are het-

eromorphic in that the first premolars are enlarged and compressed to form a cutting platform for the upper canines. Molars have five cusps, including a hypoconulid, but lack the talonid heel (Gregory, 1916; Hellman, 1928; Swindler, 1976).

The vertex of kyphosis (angle between the presellary skull base and the postsellary skull base) is situated in the presphenoid (Hofer, 1969), similar to *Homo*. Cranial capacity ranges from 320 to 480 cc, with a mean of 410 (Noback and Montagna, 1970). The deltoid prominence on the lateral side of the shaft of the humerus is located on the distal portion of this bone (Sonntag, 1923b). There often is fusion between the deltoid and pectoralis major muscles of the chimpanzee. The brachial artery is superficial to the nerve (Sonntag, 1924). The deep flexor muscle of the forearm arises from the proximal shaft of the ulna. This muscle terminates in two tendons, a large one to the index finger and a small one to the thumb. The long abductor of the thumb is a large muscle with a double insertion into the trapezoid and base of the first metacarpal. A sesamoid bone is present in the tendon. In the hand, the distal transverse flexure line lies proximal to digits 3, 4, and 5, and passes obliquely across the entire palm. This is referred to as the "simian line." The hand exhibits primitive pentadactylism. The basic phalangeal formula is 3, 4, 2, 5, 1. The third digit is the functional axis of the hand (Sonntag, 1923a; Swindler and Wood, 1973; Tuttle, 1986).

The levator scapulae attaches to the first four or five cervical vertebrae and passes to the vertebral border of the scapula. The rhomboid muscle is a single, undivided muscle sheet. There is a muscle passing from the transverse process of the third cervical vertebra to the transverse process of the atlas. Sonntag (1923a) described this muscle and thought that it probably represented an individual peculiarity. However, Swindler and Wood (1973) found this muscle present in all specimens they examined. There usually are 13 thoracic nerves in the chimpanzee, compared to 12 in most other primates. The structure of the heart of *Pan* is similar to that of *Homo* (Frick, 1960).

The tongue is long and narrow with a blunt apex. It bears a number of conical papillae (with points directed backwards) and some fungiform papillae. The esophagus has a thick stratified epithelium, underpinned by connective tissue and containing a two-layered muscularis mucosae. The stomach consists of the cardiac region, fundus, body, antrum, and pylorus; it has a characteristic long, curved shape, and is simple and capacious. As in *Homo*, there is secondary support for the jejunum and ileum in the form of a mesentery that extends from the duodenojejunal flexure to the ileocecal junction. The mesentery contains the vessels passing to and from the intestine (Swindler and Wood, 1973). The ascending and descending parts of the colon may be fixed to the dorsal body wall. The sigmoid portion of the colon includes a mesocolon. The liver has four lobes (right, left, caudate, quadrate) and is invested by an incomplete tunica serosa. The duodenum is composed of horizontal, descending, and ascending parts. There is a well-defined duodenojejunal flexure. The jejunum and ileum are 3.5 m in length. The colon is 1.2 m in length, sacculated, and possesses many appendices epiploicae. Three teniae coli are present. The cecum is a blind pouch, 75 mm in length, situated below the ileocolic valve; it connects directly with the colon. The vermiform appendix of *Pan* usually is longer than that of *Homo*, and frequently has several coils (Swindler and Wood, 1973). The rectum and anal canal are 1.5 m in length.

The suprarenal glands become smaller with age. These glands receive more blood per gram of mass than any other organ in the body (Bourne and Golarz de Bourne, 1972). The gall bladder is pear-shaped, and lies on the interior surface of the liver. The pancreas is composed of a head, a body, and a tail, and there is an additional process that extends a short distance along the portal vein. As in *Homo*, the left lung is divided into upper and lower lobes; the right lung is separated into upper, middle, and lower lobes, but does not seem to have an azygos lobe. The kidneys are located in the posterior part of the abdomen, situated one on either side of the vertebral column; the right kidney seems to be a little higher than the left one (Bourne and Golarz de Bourne, 1972; Swindler and Wood, 1973).

It practically is impossible to distinguish between the placentae of *Pan*, *Gorilla*, *Pongo*, and *Homo* (Ludwig and Baur, 1971). In the chimpanzee, the uterus is pisiform in outline and is extremely muscular. The long axis of the uterus is inclined ventrally only slightly from the direction taken by the vagina. The clitoris is es-

pecially well developed. The prostate gland is well developed, and it unites anteriorly, although the ventral lobe is small. The penis is long, narrow, and tapers toward the tip. A small os penis, about 6 mm in length and 1 mm in diameter, lies dorsally over the urethra, and extends from the distal extremity of the corpus cavernosum almost to the tip of the penis; other anthropoids, except *Homo*, possess an os penis (Benton and Gavan, 1960; Graham and Bradley, 1972).

The phalangeal formula of the foot is 3, 4, 2, 5, 1, with the third digit forming the functional axis. The plantar surface has an area characterized by alternating ridges and sulci, which form definite configurations termed dermatoglyphics. The superficial fascia on the sole of the foot contains much fat embedded in the dense fibrous tissue. The tendon of the peroneus longus muscle extends across the sole of the foot from lateral to medial, and attaches to the base of the metatarsal of the great toe (Hill, 1957; James, 1960; Schultz, 1930, 1961, 1969; Sonntag, 1924; Swindler and Wood, 1973).

**FUNCTION.** The scapula can be rotated to a considerable degree allowing elevation of the front limb to the fullest extent (Oxnard, 1968). There is a relatively wide range of movement at the metacarpophalangeal joint contributing to opposability of the thumb. Because of ridges and sulci of the palmar integuments, friction is increased during locomotion and prehension, and there is the additional function of tactile sensibility. The skin over the dorsum of the hand and foot can be manipulated and slipped in any direction. The power grip is mostly by digits and palmar surfaces. Precision grip is mostly prevented between the tips of the thumb and index finger, but does occur between the index and adjacent fingers. The principle grip used during locomotion is hook-like. The center of gravity is displaced forwardly, as reflected by the conspicuous anteroposterior shortening of the proximal and intermediate tarsal bones. The pelvis can be rotated freely, as is typical of many terrestrial quadrupeds. The thigh is rotated laterally when the animal is moving forward in a typical bent-knee gait (Oxnard, 1968; Swindler and Wood, 1973).

The complexity of facial muscles is associated with functions of facial expressions (movements of lips, eyes, and eyelids) that are characteristic of this species. The degree of kyphosis permits greater elevation of the head in relation to erect bipedal locomotion. Several explanations are available concerning the function of the laryngeal sac, including the addition of resonance to vocalizations and mechanical assistance in the support of the heavy jaws, as well as some functions related to mostly herbivorous diets (Swindler and Wood, 1973). Abnormal development of the central and lateral air sacs has been described (Yerkes, 1943).

Studies of the brain of chimpanzees, relative to some of their unique capabilities, are extensive (Noback and Montagna, 1970; Zingesser, 1973). With regard to intelligence, mental traits, evidence of insight, and vocalizations in association with food, other chimpanzees, and other animals, the capabilities of *Pan* frequently have been compared with those of *Homo* (Oxnard, 1984; Yerkes and Learned, 1925). Innovations in behavior probably set *Pan* apart from other monkeys and apes (Rumbaugh, 1971). In addition, postural characteristics, structure and function of the head in relation to posture, and individual differences in postures and positions among chimpanzees have been studied and documented (Riesen and Kinder, 1952). Comparisons of chimpanzees with advanced terrestrial (gorilla) and specialized arboreal (orangutan) apes elucidate the arboreal-terrestrial and locomotion-manipulation specialities of chimpanzees. Chimpanzees share anatomical structures with gorillas, which are especially adapted to knuckle-walking and plantigrade posturing of the hands and feet. Like orangutans, chimpanzees have hand features that may be related to proficient suspensory posturing, such as the elongation and palmar curvature of the second to fifth manual rays and the double-locking mechanism of the fingers (Tuttle, 1986).

**ONTOGENY AND REPRODUCTION.** The period of gestation varies from 196 to 260 days (Keeling and Roberts, 1972). Chimpanzees reach menarche at approximately 8 yrs of age (Vagtborg, 1968). The menstrual cycle for adults is about 36 days in duration. Swelling of the sexual skin may be marked, with an increase up to 1,400 cc in volume caused by accumulation of intercellular fluids. Usually the maximal swelling is reached at about day 15 of the cycle, and it subsides about 11 days before menstru-

ation begins; detumescence is rapid, occurring within about 48 hr. The maximal swelling coincides with or just precedes the period of greatest estrogen excretion in the urine (Asdell, 1964; Graham, 1977; Vagtborg, 1968).

Copulation usually occurs on the ground in a dorso-ventral posture, but sometimes is ventro-ventral (Goodall, 1986; Tuttle, 1986). Mating patterns of chimpanzees are variable. Promiscuity, including gang sex, is common, but there also are consortships and possessive matings by high-ranking males (Tuttle, 1986).

Growth and development of chimpanzees is depicted by recognized standard age classes (Tuttle, 1986): infant, up to 5 years; juvenile, 5–7 years; adolescent, 7–10 years (females), 7–12 years (males); subadult, 10–13 years (females), 12–15 years (males); adult, >13 years (females), >15 years (males). Life spans of *P. troglodytes* may exceed 50 years (Tuttle, 1986).

**ECOLOGY.** Throughout most of the geographic range, chimpanzees inhabit either tropical rain forest (Richards, 1952) or tropical closed forest (Clark, 1967). In West Africa, *P. troglodytes* inhabits mature lowland and upland rain forests in several stages of succession (Booth, 1958b; Gartlan and Struhsaker, 1972; Jones and Sabater Pi, 1971; Kortlandt, 1962, 1966; Rahm, 1967; Sabater Pi and Jones, 1967; Struhsaker and Hunkeler, 1971). This ape occurs in savanna, scrub forest, gallery forest, and park forest in Guinea (Bournonville, 1967). In East Africa, chimpanzees occur in deciduous woodlands, savannas, dense rain forests, riverine forests, bamboo forests, and in mosaic vegetation at all elevations (Ghiglieri, 1984; Goodall, 1965, 1986; Izawa, 1970; Izawa and Itani, 1966; Nishida, 1968; Reynolds, 1965; Suzuki, 1969). Preferred habitats of *P. troglodytes* vary somewhat in accordance with seasonal and daily activities (Goodall, 1968, 1986; Sabater Pi and Jones, 1967; Tuttle, 1986). In general, chimpanzees are omnivorous and a frugivorous diet probably is most common throughout the geographic range of the species (Goodall, 1968, 1986). However, these animals exhibit herbivorous, insectivorous, and carnivorous diets, at least in certain seasons and in some geographic localities (Goodall, 1965, 1968, 1986; Jones, 1972; Jones and Sabater Pi, 1969; Struhsaker and Hunkeler, 1971; Teleki, 1973a, 1973b). Chimpanzees capture and kill prey, and consume meat (Goodall, 1986; Kawanaka, 1982; Teleki, 1973b). Cannibalism among chimpanzees has been reported in some areas; infanticide is committed by both males and females (Goodall, 1986; Tuttle, 1986).

Predation by humans on chimpanzees for food is common in some parts of the range (Bournonville, 1967; Jones and Sabater Pi, 1971; Kingdon, 1971; Kortlandt, 1966; Reynolds, 1967; Suzuki, 1969). Populations of *P. troglodytes* in some areas are exploited for sale and exportation (Harrisson, 1971). Chimpanzees are captured most easily by shooting adult females and taking young animals. For each live young chimpanzee that is acquired, it is estimated that at least four to six other animals are removed from wild populations (Harrisson, 1971). Leopards occur sympatrically in some parts of the range and could be predators on both young and adults (Albrecht and Dunnett, 1971; Byrne and Byrne, 1988; Goodall, 1968; Izawa and Itani, 1966; Kortlandt, 1962, 1966). Other possible threats to chimpanzees are from pythons (*Python sabae*) and martial eagles (*Poleamaetus bellicosus*), but there is no direct evidence of predation (Goodall, 1968).

*Pediculus schaeffi* (Pediculidae: Anoplura) was described from *P. troglodytes* and also has been recorded from *P. paniscus* (Kim and Emerson, 1968). Intestinal helminths (*Strongyloides*, *Oesophagostomum*, *Trichurus*, *Streptopharagus*) and trematodes occur in chimpanzees (Jessee et al., 1970). Ketosis, or acetonemia, syndrome in *P. troglodytes* is a metabolic disorder considered a pathological oddity because only one animal of 21 necropsied exhibited the condition (Seibold, 1969).

**BEHAVIOR.** The behavior of chimpanzees is as complex as that of other great apes and humans, and has been well documented under natural conditions by Goodall (1965, 1968, 1986). Chimpanzees frequently travel from place to place on the ground, usually by walking or galloping on all four limbs, but often walk bipedally for short distances. They commonly stand upright to look over vegetation when searching for other animals and when carrying objects in both hands (Goodall, 1968, 1986).

Chimpanzees climb trees with ease, mostly by placing the hands on either side of the trunk and pushing up the tree with the hind limbs. These animals walk along large branches by gripping

them with the hands and feet. Brachiation is common; when moving slowly from one tree to another, a chimpanzee either walks or brachiates along a branch until the branch bends under its weight and it can reach a lower branch. Animals that are excited sometimes leap from one branch to another; occasionally, chimpanzees have been seen to dive from a tree limb to a lower branch (Goodall, 1968, 1986).

Under natural conditions, chimpanzees spend much of their time either feeding or traveling from one food source to another. From 6 to 8 h each day are expended in feeding activities. After feeding on one kind of food for an hour or so, the animals move on to feed elsewhere within the home range of a group. In this way, groups of animals may move from 1 to 16 km/day. Chimpanzees usually feed intensively for at least 2 h in early morning, feed, rest, and wander during the middle part of the day, and feed intensively again in late afternoon before making nests for the night (Goodall, 1965, 1968, 1986).

Trees with adequate height, foliage, and supple branches usually are selected by chimpanzees as sites in which to construct nests. Members of foraging parties generally nest together, sometimes splitting into smaller lodging groups. Independent males tend to lodge away from groups of females and young, which usually construct beds close together. Throughout the geographic range of *P. troglodytes*, most beds are located 4 to 50 m above the ground (Goodall, 1986; Tuttle, 1986). Nests rarely are made on the ground. New beds usually are made each night, but old nests may be reused on consecutive nights. New nests sometimes are constructed on consecutive nights in the same trees containing old beds (Goodall, 1968; Jones and Sabater Pi, 1971).

Chimpanzees usually use their hands to transfer food to their mouths, although small fruits and blossoms may be picked from branches with the lips while the plant is held to the mouth with a hand. Animals occasionally gather and eat fallen fruits from the ground. Individual feeding mannerisms vary considerably. Chimpanzees frequently hold a wad of food pulp in the mouth, sucking and chewing on it for considerable periods of time. *Pan troglodytes* eats insects throughout the geographic range (Goodall, 1965, 1968, 1986; Jones and Sabater Pi, 1969). Chimpanzees are known to use a variety of tools (Goodall, 1986; Tuttle, 1986), although use of specific tools varies geographically and seasonally (Struhsaker and Hunkeler, 1971). Probes and levers are used to open termite mounds and ant hills, sops and wipes are used to obtain fluids and remove materials from the body, and stones are used for cracking nuts and fruits. In addition, sticks, stones, and debris may be used as clubs and missiles during various displays (Goodall, 1986; Jones and Sabater Pi, 1969; Struhsaker and Hunkeler, 1971; Tuttle, 1986).

**GENETICS.** The diploid number of chromosomes is 48. Of the autosomes, 34 are metacentric and 12 are acrocentric. The acrocentric autosomes have satellites on the short arms. The X chromosome is metacentric. The Y chromosome is acrocentric and occasionally metacentric (Hsu and Benirschke, 1967). Only blood groups O and A exist in chimpanzees (Weiner and Moor-Jankowski, 1969). Variant transferrins of the iron-binding G-globulin are found (Barnicot, 1969). However, polymorphism for the group-specific (Gc) component, widespread in humans and other primates, has not been detected in *Pan*. The complete primary structure of hemoglobin includes alpha, beta, gamma, and delta chains, and some polymorphic variation occurs (Barnicot, 1969). Infrequent occurrence of antigenic polymorphism in the 2-macroglobulin serum proteins has been demonstrated (Lichter, 1969).

**REMARKS.** *Pan* refers to the mythical Greek god of forests, flocks, and shepherds, represented with the head, chest, and arms of a man and the legs and sometimes horns and ears of a goat. The species name *troglodytes* is a Greek word and refers to one who creeps into holes or a cave dweller (Jaeger, 1955). The vernacular name chimpanzee is a Bantu word used originally in northern Angola and the Congo to refer to these apes (Yerkes and Yerkes, 1929).

In this account, we present coverage of representative publications on general biology and field studies of *P. troglodytes*. Discussions of the biomedical literature and studies of captive animals are found elsewhere (Bourne, 1969, 1970a, 1970b, 1971, 1972, 1973; Rohles, 1972), as are historical (Yerkes and Yerkes, 1929) and modern (Baldwin and Teleki, 1978; Reynolds, 1967; Szalay and Delson, 1979; Tuttle, 1986) reviews of the development of

knowledge about *P. troglodytes* and other apes. Also, the Laboratory Primate Newsletter and reports from the primate research centers provide information about research on chimpanzees, as well as other primates.

There has been some debate with regard to the appropriate scientific names for the chimpanzee. *Pan* Oken, 1816, was made available as the appropriate generic name in 1985 by Opinion 1368 of the International Commission on Zoological Nomenclature. The specific epithet *troglydytes* was credited to Gmelin (1788) by Simonetta (1957); however, we follow Groves (1993) who dated the name from Blumenbach (1775). Also, we follow Groves (1989, 1993) with regard to the higher classification of the chimpanzees.

Since the discovery of the chimpanzee, as well as other great apes, there has been considerable interest in systematic relationships between them and humans. Studies of classification of higher primates have increased in recent years as reflected in the proliferation of scientific literature on this subject. For example bone marrow, blood chemistry, cerebrospinal fluid, urine, feces, and semen have been compared between great apes and humans (McClure et al., 1973). Development of the chondrocranium and osteocranium in a fetal chimpanzee has been compared with that in humans (Starck, 1973). Some data on statics and mechanics of the upper extremities of both species were provided by Preuschoft (1973). Comparisons of selected primate chromosomes with those of humans using general and regional banding methods indicated that *P. troglodytes* probably is not as closely related to *Homo* as is *Gorilla* (Miller, 1977). Quantitative comparisons of morphological distances of body shapes between chimpanzees and humans show that morphological differences between *Pan* and *Homo* are large in relation to structural gene differences between the two species (Cherry et al., 1978). However, recent studies (Nozawa et al., 1982) have indicated a rather close relationship between *Pan* and *Homo*. In addition, phylogenetic analyses of nucleotide sequences by the parsimony method indicate that humans and chimpanzees are more closely related to each other than either one is to other great apes (Miyamoto et al., 1987).

*Pan troglodytes* is listed as endangered wherever found in the wild and threatened wherever found in captivity (U.S. Fish and Wildlife Service, 1992). *Pan troglodytes* is listed as vulnerable and *P. t. verus* is considered endangered by the IUCN (Groombridge, 1993). The species is considered as endangered in some areas, protected in other areas, and probably extinct in some places (Tuttle, 1986). In the early 1980s, it was estimated that only about 35,000 animals still may survive in all known potential habitats (Koebner, 1982). However, there are no precise data with regard to the status of most populations of chimpanzees in the wild.

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