Fig. I.21. Left hand of squirrel monkey, *Saimiri sciureus*, with ungula (nail) on thumb, tegulae on digits *II-IV*, and falcula (claw) on *V*. Pedal ungues are similar. Complete differentiation between claw and nail appears in individual variable. Opposability evolves with reduction of sharp, downwardly curved claw to a harmless nonprotruding nail present on digit *I*.

Fig. I.22. Left hind foot of tarsier, *Tarsius syrichta*, with claws of digits *II* and *III* specialized for grooming. Ungues of remaining digits are degenerate claws. The grooming claws project nearly at right angles to the digits, thus avoiding interference with other pedal functions.

Fig. I.20. Right hand of *Callithrix argentata*; all digits armed with protruding downwardly curved claws specialized for clinging and grappling; the claws preclude opposability.

erate claws. In turn, clawlessness is the result of a degenerative process often associated with reduction and loss of the terminal phalanx.

In *Tarsius*, extreme hypertrophy of the terminal phalangial touch pads of the hand is associated with a corresponding reduction and modification of the claws into nonfunctional splinters. On the foot, digits II and III are each armed with a short grooming claw of a primitive type which projects nearly at right angles above the touch pads (fig. I.22). The erect position of grooming claws averts interference with other digital functions. Pedal digits IV and V each bear a short pointed, flattened and keeled, nonprojecting tegula. The hallux bears the vestige of a nail or tegula.

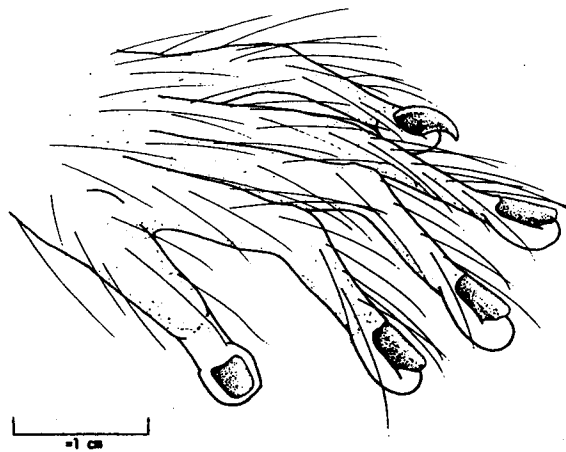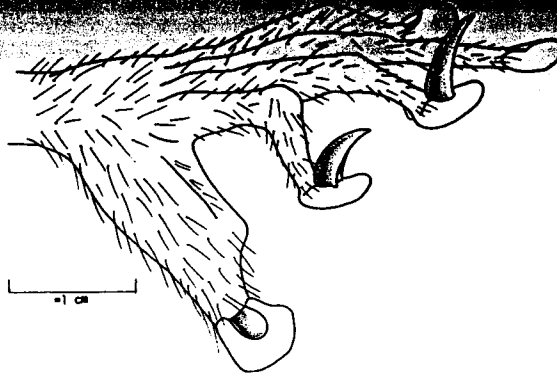In lemurs, hallux and pollex are nailed, and pedal digit

II is usually provided with a grooming claw. The remaining ungues are adpressed and nonprotruding tegulae, some flattened, others pointed and keeled; still others, as in *Microcebus* (figs. I.23, 24), may be obsolete. In galagos and lorises, the ungues, except the grooming claw of digit II, are well-defined nails. The unguis of the cebid pollex varies from tegula to nail, all remaining ungues are distinct tegulae except those of the squirrel monkey (*Saimiri*) digits V which persist as short recurved claws. In catarrhine monkeys and gibbons, pollex and hallux are nailed, the remaining digits tegulate, but in some species, particularly the more terrestrial ones, the tegulae are nearly naillike. A nail is present on all digits of man and higher apes except as noted.

Modification of ungues from falculae to tegulae and ungulae, and the ultimate obsolescence and disappearance of the latter are widespread among mammals. An opposable digit, whether in primates, marsupials, or rodents, either bears a nail or is inungulate. A sharp, protruding claw prevents or inhibits opposability. Well-developed digital touch pads in arboreal mammals, including many marsupials and rodents, are characterized

Fig. I.23. Volar surface of right hand (*above*) and right foot (*below*) of *Marmosa murina* (Didelphidae, Marsupialia), and *Microcebus murinus* (Lemuridae, Primates).
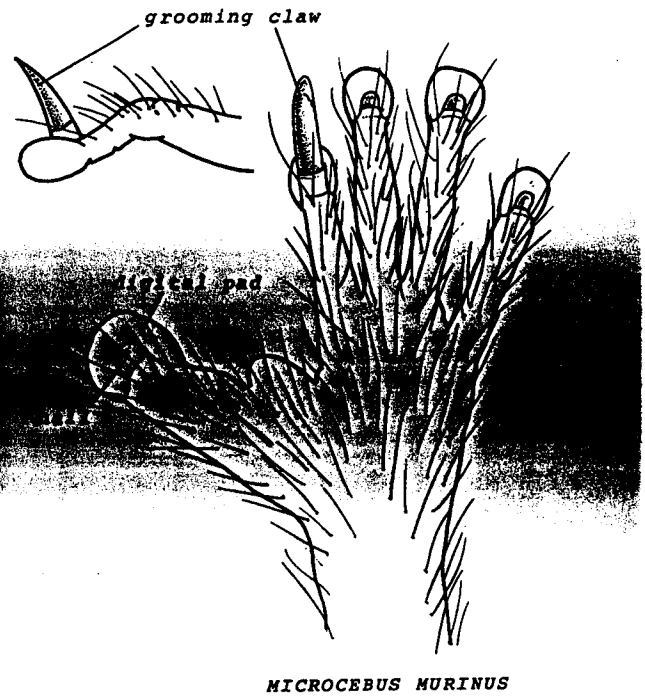

MICROCEBUS MURINUS

Fig. I.24. Right foot of *Microcebus murinus*, diagram of dorsal surface to show claw of digit *II* specialized for grooming but not effective in climbing, and degenerate ungues of digits *I, III–V* replaced by sensory digital pads.

by comparatively weak claws turned upward so they do not interfere with use of digits for grasping or sensing. As was previously noted, the upturned claws of prosimians and some other mammals, notably among marsupials, for example, *Dromicia*, are secondarily adapted for grooming. Degenerate and lost claws or nails are also common. Examples, in addition to the primates mentioned above, include the nailed or nailless flippers of manatees, the nail of the disappearing thumb of most rodents, the vestigial and lost claws of so-called clawless otters, and the complete loss of ungues in cetaceans.

The hallux of living tupaiids (fig. I.25) and the Paleocene *Plesiadapis* is provided with a well-developed claw. This character alone, although there are other trenchant ones, is evidence enough that neither animal group is Primate.

Opposable Pollex

A more-or-less opposable thumb is present in the vast majority of living primates. In *Ateles, Brachyteles*, and *Colobus*, the thumb is vestigial or absent (fig. II.14). The thumb is well developed but primitively nonopposable and provided with a distinct claw in the tarsier (*Tarsius*), aye-aye (*Daubentonia*), all callitrichids (Callitrichidae), and *Callimico*. The same must have been true of the pollex of the ancestral primate and most, if not all, early Tertiary primates. Evidently opposability was perfected in the great toe before it appeared in the thumb.

Opposability is the capacity of the first digit, pollex

or hallux, to seize an object and hold it securely against an opposing digit. The function evolved pari passu with degeneration of the primitively sharp protruding claw into a short nail which disappears in some forms. In primates with thumbs vestigial or lost, opposability is replaced by prehensility between digits II and III. Prehensility between one or more flexed digits and the palm characterizes all primates.

An early stage pollical opposability consists of a movement of adduction combined with digital flexion and some rotation at the carpophalangeal joint of the thumb. This simple form of opposability characterizes cebids. The tarsier's pollex performs the same movements, according to Haines (1958, p. 14), but Napier (1961; also Napier and Napier 1967), regard the tarsier pollex as nonopposable. These conclusions appear to qualify the Day and Napier (1963, p. 132) generalization that "there is a direct relationship between true opposability and the presence of a deep head to flexor pollicis brevis" in the tarsier, all cercopithecoids with thumbs, and the orang and man only (Day and Napier 1963, p. 128) among living hominoids.

In larger primates, increasing specialization of the hand for grasping larger branches is marked by a shift of the thumb from the primitive position of near alignment with the other digits to a more proximal position. The gap or cleft between base of thumb and index finger in most living prosimians allows a wider *power grip*, but no refinement of the *precision grip*, as defined by Napier (1960).

The most advanced form of opposability, occurring in catarrhines, combines the thumb cleft and power grip
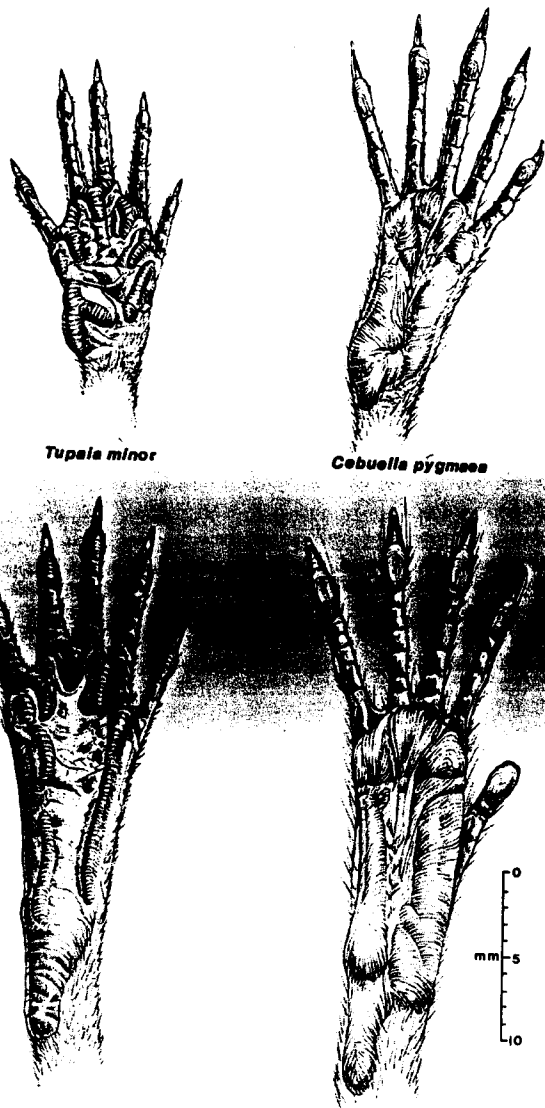
Tupaia minor   **Cebuella pygmaea**

Fig. I.25. Volar surface of right hand (*above*) and right foot (*below*) of *Tupaia minor* (*Insectivora*) and *Cebuella pygmaea* (*Callitrichidae*, Primates).

of prosimians, the carpophalangeal movement of platyr-rhines, and a new movement of rotation of the carpometatarsal joint. Catarrhine opposability, according to Napier (1961, pp. 116, 128, fig. 1) is derived from the cebid type. The latter, termed "pseudo opposability" by Napier is a comparatively primitive, or *semiopposable* form as compared with the more *advanced* prosimian type, and the highly evolved or *compound* catarrhine type. The bones alone (figs. I.26–29) hardly reflect the diversity and complexity of hand movements among the different kinds of primates.

Opposable Hallux

An opposable great toe provided with a nail (or inunguiculate) is characteristic of all primates, many marsupials, arboreal rodents, and almost certainly the hypothetical preprimates. Except for *Homo*, animals with nonopposable great toes are not primates. In *Homo* the original opposability of the great toe has been secondarily reduced or lost.

Volar Pads and Papillary Ridges

Cutaneous pads and ridges of palm and sole are modifications of the primitive scaly volar armor. Unmodified, nonimbricated scales or their vestiges are still preserved around the base of the pads in many species.

The primitive number of mammalian volar pads is 11. The plan consists of 5 digital (= phalangeal, terminal, touch, or nail) pads with one on the terminal phalanx of each digit, 4 postdigital (= interdigital or distal) pads, and 2 volar (= thenar and hypothenar) pads. With specialization, individual pads may become suppressed, fuse with a neighboring pad, or subdivide. New or accessory pads also may arise at new points of stress or sensitivity. The skin of the pads may be scaly, warty, pebbled, or ridged. The roughened surface enhances the locomotor, prehensile, and sensory capabilities of the cheiridia.

The primitive primate volar pad system (fig. I.30) is already specialized in its adaptations for arboreal locomotion and prehensile and tactile operations. Compared with those of primitive mammals, the pads are enlarged, more fleshy, richly innervated and vascularized, and distinguished by parallel and concentric cutaneous or papillary ridges arranged in unique patterns of whorls, loops, and arches. Sweat glands are also more profuse and active. The horny scales from which pads and ridges differentiated have virtually disappeared except for the minute warts of incomplete or discontinuous ridges and the scaly pebbling on the central volar area of the more primitive species (figs. I.23, XI.14). The number of pads may increase with specialization, accessory cushions are added to the thenar and hypothenar pads, and new pads appear on phalanges and the central volar surface between the primitive pads.

The tupaiid volar pad pattern (fig. I.25) regarded by Biegert (1963, p. 135) as a model for primitive primate types is essentially a specialized terrestrial type and highly variable. It may have originated from the same basal mammalian pattern that gave rise to primate designs, but it cannot be considered ancestral to them.

Volar pads of some arboreal rodents and marsupials (fig. I.23) may be no less specialized than those of primates. Papillary ridges may also attain as much complexity in some marsupials as in primates. Sensory ridges evolved independently in other mammals as well and are particularly refined in tupaiids, arboreal rodents, arboreal carnivores (especially *Potos* and *Bassaricyon*), some xenarthrans, and pinnipeds. For detailed accounts of mammalian volar pads see Whipple (1904), Kidd (1907), Dankmeijer (1938), Midlo and Cummins (1942), and Biegert (1961).

Digital Formulae

The relative degree of distal projection of each digit of hand and foot tends to be stable in mammals generally. The most projecting digit, however, is usually, but not necessarily, the longest. A long digit with a short metapodial is often less projecting than a shorter digit with a long metapodial (figs. I.26–29).

The following summary (table 2) of digital formulae, arranged by families, is based on the cheiridia described and figured by Biegert (1963), on complete hands and feet (not skeletons) of approximately five hundred museum-preserved callitrichids I examined, and on a rapid survey of the complete cheiridia of representatives of the nearly all other living primates and all tupaiid

Table 2. Formulae of Digital Distal Projection in Primates.

family	manus	pes
Tupaiidae [non-primate]	3-4-2-5-1	3 or 4-2-5-1
Lemuridae	4 or 3-2 or 5-1	4 or 3-2 or 5-1
Indriidae	4-3-5-2-1	3-4-5-2-1
Daubentoniidae	4-3-2-5-1	3 or 4-5-2-1
Galagidae	4-3-2 or 5-1	4-3-5-2-1
Lorisidae	4-3-5-2 or 1	4-3 or 5-2-1
Tarsiidae	3-2-4-5-1	4-3-2 or 5-1
Cebidae	3 or 4-5 or 2-1	3 or 4-2-5-1
Callimiconidae	3-4-2-5-1	4-3-5 or 2-1
Callitrichidae	3 or 4-2-5-1	3-4-5-2-1
Hylobatidae	3-2-4-5-1	3-2-4-5-1
Pongidae	3-2 or 4-5-1	3-2 or 4-5-1

genera preserved in the Field Museum. The digits are given in the order of most to least projecting. In a hand or foot where either of two digits sometimes projects more than the other, that digit is listed after the first. For example, in the formula 3 or 4-2-5-1, digit 4 is sometimes, but not usually, even with or slightly more projecting than digit 3.

The common digital formula of the hand is 3-4-2-5-1, with a strong tendency for digit 4 to be even with or project slightly beyond digit 3. Deviation from the 2-5-1 portion of the formula occurs in peculiarly specialized hands.

The most widely established digital formula of the foot is (4-3) or (3-4)-5-2-1. In some groups, digit 2 is more projecting than digit 5. As in the hand, most departures from the common formula occur in primates with very special forms of pedal locomotion. There is no correlation between digital length or projection and rate of phalangeal and metatarsal ossification (fig. I.31).

Functional Axis of the Hand

The functional axis of the manus in primates...

In a second type of hand, the functional axis extends through the grasping interval between digits 2 and 3. Here, digits 1 and 2 act together in convergence and in a scissorlike adduction with digit 3. Digit 1 has a nail, but its opposability is little more than incipient. This hand type was described by Pocock (1920; 1925a) as zygodactylous and shown to occur in the cebids Cacajao, Chiropotes, Alouatta, Lagothrix, Ateles, and Brachyteles. The term schizodactylous was proposed by Haines

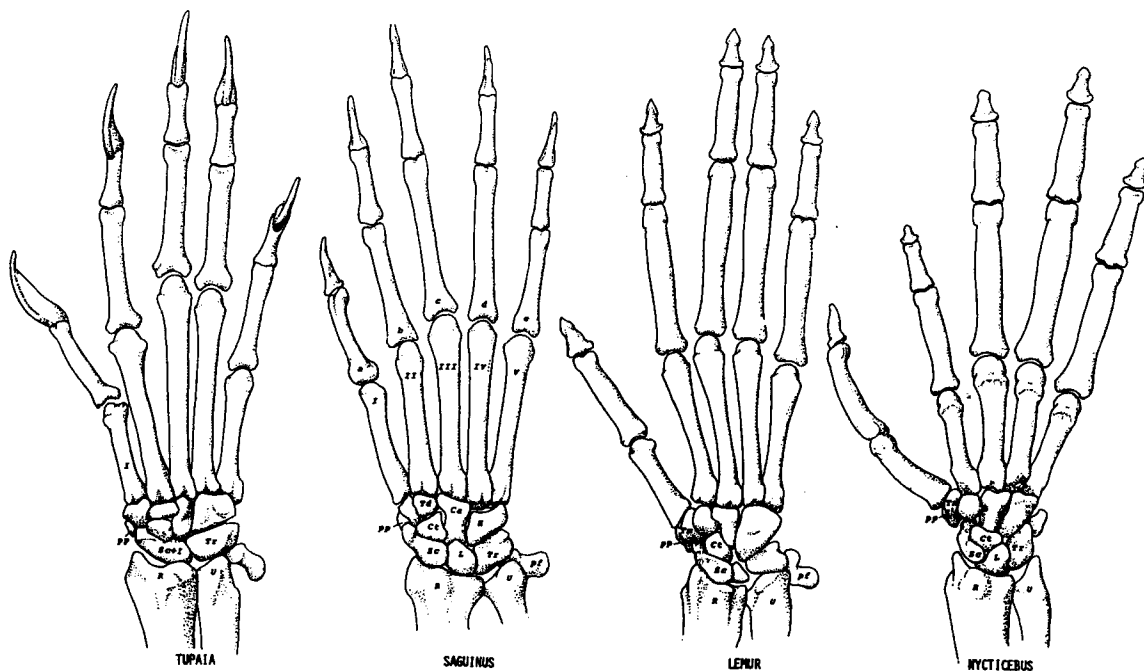

Fig. I.26. Right-hand skeleton of Tupaia, Saguinus, Lemur, and Nycticebus, all drawn to same size. Shape of terminal phalanx indicates form of its ungues. Forearm bones: R = radius, U = ulna. Carpal (wrist) bones: Sc = scaphoid (scaphoideum, naviculare, navicular, radial); L = lunate (lunatum, lunar, semilunar, intermediate); Sc + L = fused scaphoid and lunate; Tr = triquetrum (cuneiform, triangular, pyramidal, cubital, ulnar); Tm = trapezium (carpal 1, greater multangular, multangulum majus); Td = trapezoid (trapezoideum, carpal 2, lesser multangulum, multangulum minus); Ca = capitate (capitatum, carpal 3, magnum); H = hamate (hamatum, carpals 4-5, unciform, uncinate); Ct = central (os centrale, centrale, multangulum accessorium); pf = pisiform (pisiforme, subcarpal accessory, ulnar sesamoid); pp = prepollex (praepollex, radial sesamoid). Metacarpal (palmar) bones: I-V. Phalangeal (finger, digital) bones: a-e = proximal phalanges.
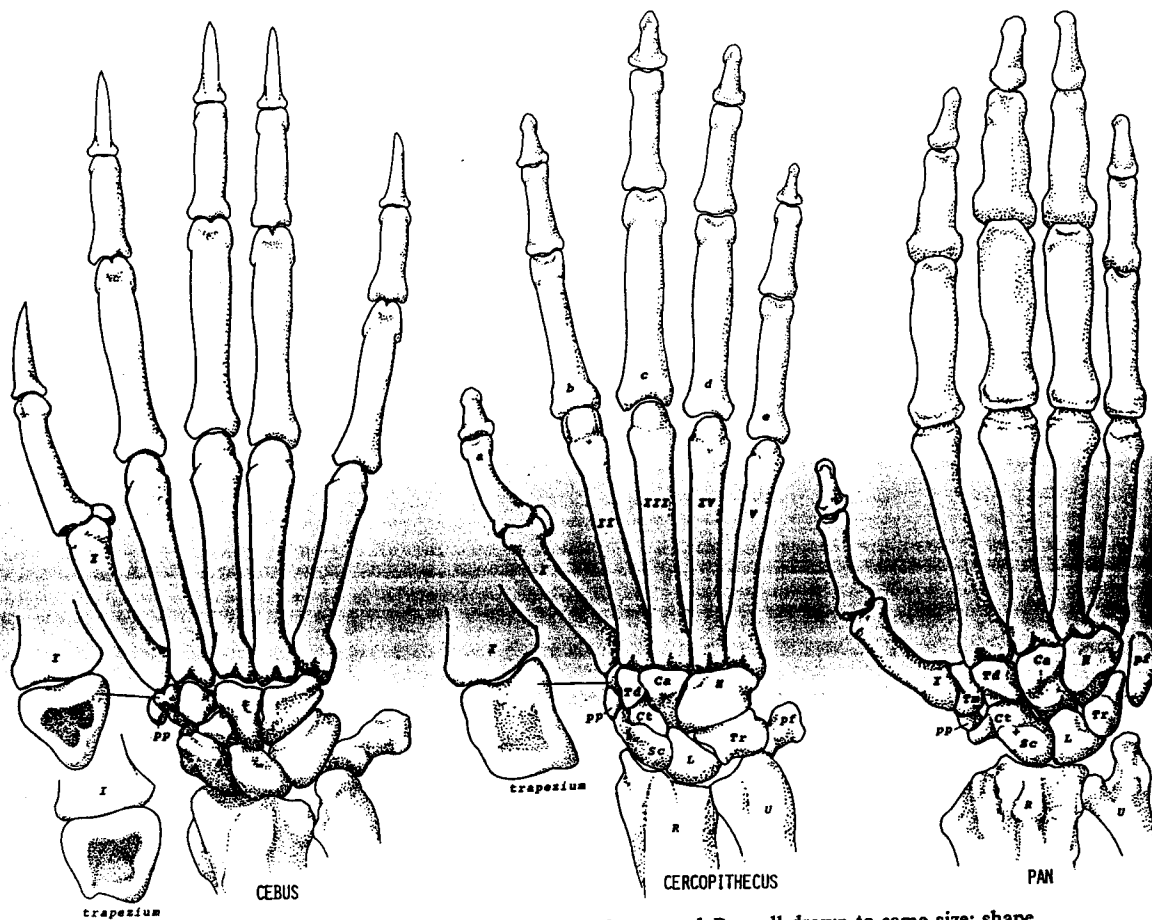
Fig. I.27. Right-hand skeleton of *Cebus, Cercopithecus,* and *Pan,* all drawn to same size; shape of terminal phalanges indicates form of its ungues; dorsoproximal aspect of trapezium enlarged to show transition from the triangular shape in platyrrhines (*Cebus*) to the subrectangular shape in catarrhines (*Cercopithecus*). *Ct + Sc =* fused central and scaphoid bones; for names of all wrist bones see fig. I.26.

(1958), for the same hand. This *schizaxonic* hand (fig. I.33) intergrades morphologically and functionally with the primitive mesaxonic hand.

The schizaxonic hand is functionally interchangeable with the mesaxonic in situations when the latter is of little avail in gaining support on slender branches or vines. Rothe (1972) demonstrated this optional function in the case of *Callithrix jacchus.* Cartmill (1974b, p. 75) believes that the schizaxonic or schizodactylous hand is primitive for primates. This hand, however, does not appear as a morphological specialization except in certain higher platyrrhines and prosimians with cheiridia most highly specialized for clutching.

With evolution of pollical opposability, the functional axis of the hand shifted to a line running between interdigital pads 1 and 2 in the grasping interval between digits 1 and 2. This advanced type, the telaxonic hand, is found in the majority of living primates including lorisoids (fig. I.34), where digit 2 tends toward obsolescence. Digit 1 is provided with a nail, digits 2–5 are tegulate or ungulate. The telaxonic type grasp may shift to or combine with a weak schizaxonic grasp.

The functional axis of the primitive mammalian foot was probably mesaxonic. The tupaiid foot is not far removed. With evolution of an opposable hallux in primates, marsupials, and rodents, the axis became telaxonic by shifting to a position between thenar and hypothenar

pads proximally and interdigital pads 1 and 2 distally in the grasping interval between digits 1 and 2. In some more-or-less terrestrial primates, the pedal axis may seem to have shifted back toward the middle digit. Thus, Morton (1935, p. 36) depicts the "functional" axis of the pedal skeleton of *Lepilemur* and *Macaca* as running through digit 3. Perhaps he intends to show the morphological rather than the functional axis. In any case, Lessertisseur and Jouffroy (1974, p. 144) define the morphological axes of primate feet as follows:

Mesaxonic: Axis through digit III (pongids).
Ectaxonic: Axis through digit IV (prosimians including *Tarsius,* some platyrrhines—notably *Aotus, Tupaia*).
Entaxonic: Axis through digit II (man only).
Paraxonic: Axis between III and IV (many platyrrhines and cercopithecoids).

Ancestral Primate Cheiridia

A hypothetical model of cheiridia constructed by Biegert (1961, p. 134) from which hands and feet of modern primates could be derived, has the following characters.

1. Digital formula of manus and pes, 3–4–2–5–1.
2. Functional axis, manus and pes, mesaxonic.
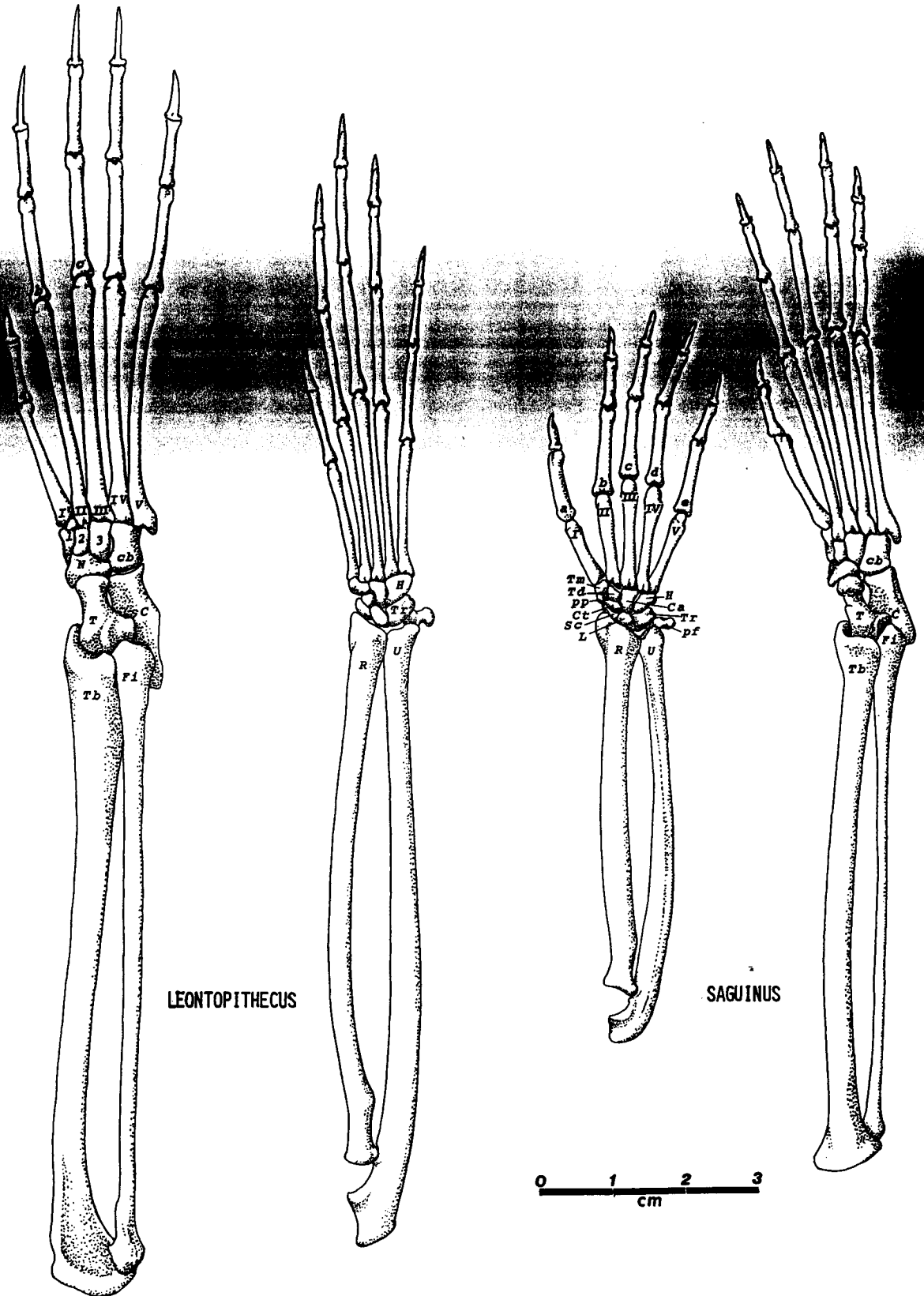3. All digits provided with claws.

Fig. I.28. Lower right hind limb and lower right forelimb of *Leontopithecus* and *Saguinus*. Shape of terminal phalanx indicates form of its ungues. Arm and leg bones: *Fi* = fibula; *Tb* = tibia; *R* = radius; *U* = ulna. Carpal (wrist) bones: *Sc* = scaphoid (scaphoideum, naviculare, navicular, radial); *L* = lunate (lunatum, lunar, semilunar, intermediate); *Tr* = triquetrum (cuneiform, triangular, pyramidal, cubital, ulnar); *Tm* = trapezium (carpal 1, greater multangular, multan-
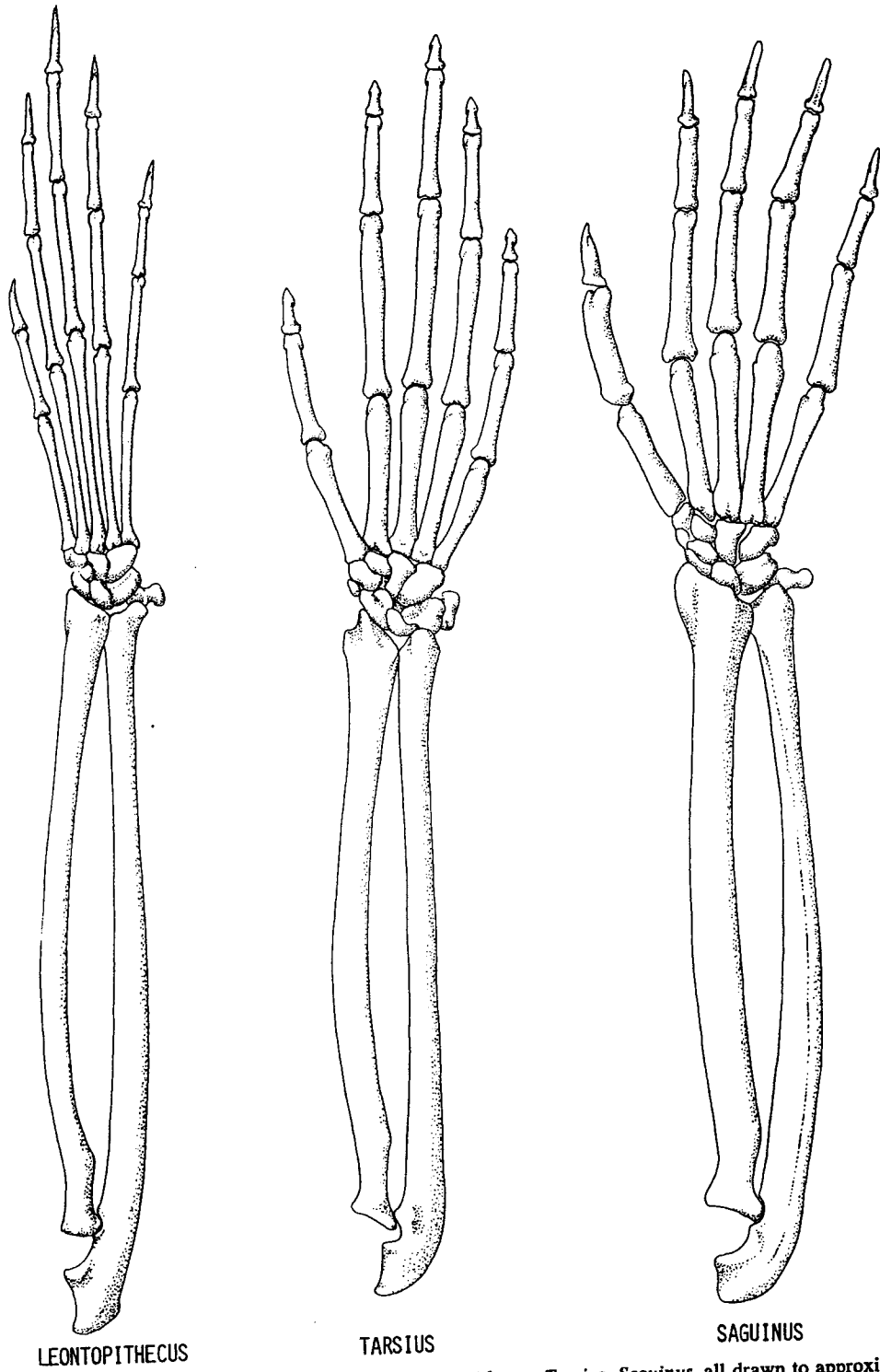
LEONTOPITHECUS   TARSIUS   SAGUINUS

Fig. I.29. Skeleton of right forelimb of *Leontopithecus, Tarsius, Saguinus*, all drawn to approximately same size. Note similarities between *Tarsius* and *Leontopithecus* in certain proportional bone lengths and greater similarities between *Tarsius* and *Saguinus* in proportional bone breadths.

gulum majus); Td = trapezoid (trapezoideum, carpal 2, lesser multangulum, multangulum minus); Ca = capitate (capitatum, carpal 3, magnum); H = hamate (hamatum, carpals 4–5, unciform, uncinate); Ct = central (os centrale, centrale, multangulum accessorium); pf = pisiform (pisiforme, subcarpal accessory, ulnar sesamoid); pp = prepollex (praepollex, radial sesamoid). Tarsal (ankle) bones: T = talus; C = calcaneum; N = navicular; 1 = entocuneiform; 2 = mesocuneiform; 3 = ectocuneiform; cb = cuboid. Metacarpal (palm) and metatarsal (sole) bones: I-V. Phalangeal (finger and toe) bones: a-e = proximal phalanges.