

Systematics of the Snub-nosed Monkey: *Rhinopithecus*

by

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INTRODUCTION

This paper will explore and summarize some of the published evidence for the systematic relationships of the colobine monkeys in the poorly known genus, *Rhinopithecus*. *Rhinopithecus* comprises four allopatric colobine species (or subspecies, see Groves, 1970, and below) that share a distinctive, turquoise-colored face and nose, the nose being characterized by a sharply upturned superior border with accessory flaps of skin, on the lateral nasal borders, that partially cover the nasal openings (Dollman, 1912; Milne-Edwards, 1870, 1872 [cited in Szalay & Delson, 1979]; Thomas, 1903). Their ecology and distribution will be briefly reviewed and an account of the history of their proposed taxonomic relations will be presented. Some locomotor characteristics of these monkeys will be (very briefly) evaluated to elucidate the relative primitiveness or specialization of these distinctive monkeys with respect to the eucatarrhine condition and other fossil and living forms.

ECOLOGY AND DISTRIBUTION

Three populations of golden monkeys (*Rhinopithecus roxellana*, *R. bieti*, and *R. brelichi*) occupy non-overlapping ranges in central and southern China, while a fourth, possibly extinct, species (*R. avunculus*) recently existed in North Vietnam, near the Chinese border (Groves, 1970; Happel & Cheek, 1986; Pan & Yong, 1985; Roonwal & Mohnot, 1977). Virtually nothing is known of the ecology or behavior of *R. avunculus* (Happel & Cheek, 1986; Pan & Yong, 1985).

The remaining three species occupy high elevation, temperate montane regions, distributed in different faunal habitats in disjunct elevational zones (see below). They are sexually dimorphic colobines, with body weight dimorphism of 63% to 69% (Jablonski & Pan, 1991). Adult males range from 13 kilograms (*R. brelichi*: Quan & Li, 1981--though this individual was ill; when healthy, it weighed 15 kg.) to over 21 kilograms (*R. roxellana*: Tenaza et al., 1988), while females range from 8 kilograms (*R. brelichi*: Chao, 1982) to between 6 and almost 13 kilograms (*R. roxellana*: Tenaza et al., 1988). Weights for fully mature *R. bieti* are not published, but they are purported to be larger than the other two species (e.g., Groves, 1970).

Only anecdotal evidence was found to support Fleagle's (1988) claim that some animals may reach 30 kg (Long, cited in Jablonski & Pan, 1991).

Davison (1982), noted convergence with terrestrial

cercopithecines by a captive pair of *R. roxellana* in limb proportions (e.g., intermembral indices range from 89 (Davison, 1982) to 96 (Groves, 1970)) and behavior (74% to 83% of the time was spent on the ground of the enclosure by the male and female, respectively). Most observations of wild populations, however, indicate that *R. roxellana* (Pan & Yong, 1985 and references therein; Happel & Cheek, 1986 and references therein) and *R. brelichi* (Quan & Xie, 1981) are highly arboreal, while *R. bieti* has been variously reported to be highly arboreal (Li et al., 1982), semiterrestrial (Yang, 1988), or primarily terrestrial (Wu et al., 1988)--the varied reports may relate to the proximity of *R. bieti* to the tree line, or age-specific differences in locomotor patterns (Jablonski et al., 1992).

The highest ranging nonhuman primate is the highly endangered Yunnan, or Dian, golden monkey, *R. bieti*; it ranges from 3200 to 4000 meters above sea level in Yunnan Province in southwestern China. It inhabits a mostly coniferous floral regime (Li et al., 1982; Yang, 1988).

The best known and most populous of the Chinese golden monkeys is the Sichuan golden monkey, *R. roxellana* (Poirier & Hu, 1983). *R. roxellana* is the only species that exhibits marked seasonal variation in group size--summer aggregations of 600 individuals have been reported (Hu et al., 1980, cited in Happel & Cheek, 1986)--and ranges from 1700 to 3000 meters above sea level in mixed coniferous and broadleaf forests of south-central China (Pan & Yong, 1985). A golden-colored

monkey encountered in India by Gee (1952), and attributed by him to *R. roxellana*, is widely held to have been the subsequently discovered golden langur (*Presbytis geei*) (e.g., Groves, 1970).

The highly endangered Qian, or gray, golden monkey (*R. brelichi*) is restricted entirely to the primarily broadleaf forests of the Fanjing Shan reserve of northern Guizhou Province, in southern China (Pan & Yong, 1985; Sun et al., 1989).

It ranges from 1400 to 1800 meters above sea level (Pan & Yong, 1985).

HISTORY OF TAXONOMY

In 1870, Alphonse Milne-Edwards introduced the mountain-dwelling Chinese Golden monkey to Western science (Milne-Edwards, 1870). *Semnopithecus roxellana* was distinguished from its congeners by its very long and shaggy pelage, like a goat's; the hair on its head, back, limbs and the sides of the face was grey with yellow tips; the forehead had a mixture of brilliant red tints; the face was turquoise; and the hands and feet were brown. The superior border of the nose was well-developed and strongly turned up (i.e., a snub nose). Not mentioned by Milne-Edwards, but probably visible in the plate (missing in the only available copy), are the flanges of blue skin that dominate the lateral margins of the nose, and which characterize all members of this genus.

In 1872, Milne-Edwards (cited in Szalay & Delson, 1979) assigned the species to generic status under the name

Rhinopithecus. He also changed the name of the type species from *roxellana* to *roxellanae*, "for no apparent reason" (Tenaza et al., 1988, p. 1--but see Allen, 1938, p. 301, who describes the name change as a correction); this paper will use the designation *R. roxellana*, given its chronological precedence.

Rhinopithecus bieti was described and given full species status by Milne-Edwards in 1897 (as cited in Ellerman & Morrison-Scott, 1951, p. 202), though the chief difference between *R. bieti* and *R. roxellana* noted by Milne-Edwards (as summarized in Groves, 1970) was that *R. bieti* had a less brightly colored pelage.

R. brelichi was first described and named by Oldfield Thomas (1903) based on a single, headless skin of a female, purchased from a hunter by Henry Brelich. Thomas noted, among other things, that *R. brelichi* was larger than *R. roxellana* or *R. bieti* (this is not true), had a prominent white patch on the withers, had a longer tail than the other species, and lacked areas with particularly long hairs, shared by the other species.

R. avunculus was first described by Dollman (1912); the type was a female and he indirectly compared this specimen to several representatives of *R. bieti* via correspondence with a Frenchman, M. Trouessart, of the Paris Museum. This species, unlike the above three species, occupied the sub-montane rain forests of Tonkin (now North Vietnam), and had a longer tail than its congeners.

In 1924, Pocock raised *R. avunculus* to generic status, referring it to the new genus *Presbyticus* (Pocock, 1924), primarily on the basis of its longer phalanges. Subsequently, Ellerman and Morrison-Scott (1951), subsumed *R. roxellana*, *R. bieti*, and *R. brelichi* into one species, *R. roxellana*, stating that, "it is difficult to believe that three [allopatric] forms . . . differing . . . only in details of colouring . . . are good species" (Ellerman & Morrison-Scott, 1951, pp. 201-202).

These authors maintained the original species designations as the subspecific names, and split the genus into two subgenera: *Rhinopithecus* and *Presbyticus*. The above three subspecies were put into *R. (Rhinopithecus)* and, following Pocock (1924) *Presbyticus avunculus* was subsumed into *R. (Presbyticus) avunculus*.

In 1970, Groves sank the genus *Rhinopithecus* and genus/subgenus *Presbyticus* into *Pygathrix* on the basis of the following shared features (relative to *Nasalis larvatus* and *Nasalis (=Simias) concolor*: flaps of skin on lateral borders of nose (though, in *Pygathrix nemaeus* the nose is flat, not upturned); broad skulls; wide, square orbits; short faces; high interorbital distance; long braincase; robust mandibles with everted gonial angles; and short, imperfectly formed nasal bones (Groves, 1970). *Rhinopithecus* was retained by Groves as a valid subgenus. *Nasalis larvatus* and *Nasalis (=Simias) concolor* were viewed as being more similar to each other than *P. (Pygathrix)* to *P. (Rhinopithecus)*.

Rhinopithecus roxellana and *R. bieti* were subsumed into *Pygathrix (Rhinopithecus) roxellana* because, according to Groves, these animals are distinguished only by minor features of the pelage (color and hair length), body size, and hair patterns on the proximal part of the tail--only this last was considered by him to be possibly "of complex genetic origin" (Groves, 1970, p. 561). In both of these monkeys, the tail is shorter than the head plus body (86%-90%), they have long yellow guard hairs (120-160mm), the genital region is marked by a patch of white hair, and bregma is indented, posteriorly.

P. (R.) brelichi was given species status by Groves on the basis of their longer tails (133% of body head plus body length), absence of guard hairs, absence of white in genital region, lack of indentation at bregma, presence of the aforementioned white patch on the withers, presence of a white tip on the tail.

P. (R.) avunculus is differentiated from the above species by a much longer tail (143%-148% of head plus body length), shorter hair (45-50mm--the other species have hair length 50-80mm), and the possession of long, slender phalanges (the other species have short, stubby digits--first noted by Allen, 1938). It has a combination of the pelage features of its congeners: like *P. (R.) roxellana*, it has a white genital region and lacks a white patch on the withers; like *P. (R.) brelichi*, it lacks long, yellow guard hairs and has a white tip on the tail.

Delson (1975), in an extensive review of the evolutionary relationships of extinct and extant cercopithecids, stated that "Groves' [1970] interpretation of [modern colobines] can be generally supported, especially in linking *Pygathrix* with *Rhinopithecus* and *Nasalis* with *Simias*." (1975, p. 201). However, in light of cranial analyses not explicated beyond general remarks, Delson maintained that the *Nasalis/Simias* and *Pygathrix/Rhinopithecus* pairs are equally distinct; therefore, Delson resurrected *Simias* as a subgeneric classification. Szalay and Delson (1979), in their review of the primates, retained Groves' classification *in toto*, devoting a mere two sentences of text to the genus *Pygathrix*.

Though the translation (of an abstract) is poor, it seems that Peng, Ye, Zhang, and Liu (1985), examining morphology and ecology, agreed with Groves' (1970) classification, but asserted that *Nasalis* and *Simias* were more similar to *Mesopithecus*, therefore *P.* (*Rhinopithecus*), must be more derived. They then state that *Rhinopithecus* is "possibly the most advanced monkeys among Old World Monkeys [*sic*]" (Peng et al., 1985, p. 181). If the translation can be trusted, it seems that these authors invoke a *Scala Natura*, along which *Rhinopithecus* occupies the most advanced position in an inexorable evolution toward the hominoid condition.

Subsequently, Peng, Ye, Zhang, and Pan (1988), comparing morphological characters (unspecified in abstract), made the following enigmatic remark, "the divergence between *roxllanae*

[sic] and *bieti* are the earliest, then between *roxellana* and *brelichii* and the latest appeared between *bieti* and *brelichii*" (Peng et al., 1988, p. 247). Unfortunately, the available copy of the abstract is missing the original Chinese text, so resolution of this phylogenetic paradox in accordance with what the authors were really asserting is not possible. Clearly, good translations are needed before the Chinese contributions can be fairly assimilated.

More recently, Groves (1989), citing recent Chinese work (Li & Lin, 1983), resurrected *bieti* for the Yunnan golden monkey, but otherwise retained his earlier (1970) classification. The most compelling evidence for the subspecific status of these forms is the report of a successful captive birth, in 1970, of a female hybrid, from a *brelichii* mother and a *roxellana* father, who reached maturity and subsequently gave birth, in 1974, to a second-generation hybrid (Chao, 1982; Quan & Xie, 1981). Yet, by far the majority of workers accord full generic status to *Rhinopithecus* and full species status (*contra* Ellerman & Morrison-Scott, 1951) to the allopatric forms (e.g., Happel & Cheek, 1986; Jablonski, 1992; Li et al., 1982; Pan & Yong, 1985; Sun et al., 1989; Ye et al., 1989; Zhao et al., 1988).

EVALUATION OF TAXONOMIC RELATIONSHIPS

Few published data exist with which to evaluate the interrelationships of the Chinese snub-nosed monkeys. In terms of body size, relative length of tail, relative length of digits,

and thickness and length of body hair, the four species of *Rhinopithecus* clearly conform to Bergmann's Rule (Bergmann, 1847, as cited in Harrison et al., 1988; see Table I--the author is indebted to Ms. Kelly A. Cichy for this observation).

Cursory analysis of the data presented by Ye, Peng, and Zhang (1989), on the places of insertion and origin of 56 muscles in specimens of the three Chinese species, reveals no simple relationship between elevation and differences between the taxa. Of the 56 muscles examined, eleven exhibited differences among the taxa in presence, or place of origin and insertion; fourteen differences were noted in the eleven muscles (see Table II). Of these fourteen differences, eleven were so distributed that two of the three species shared place or span of origin or insertion of these muscles; in two cases, presence of a muscle or portion thereof (cleido-occipital portion of the m. Sternocleidomastoideus and m. Epitrochleo-anococeus) was shared by two of the three species; and one muscle (the capital portion of m. Longissimus) differed in insertion between all three species.

Since five of the thirteen shared features (38.5%) were between *R. bieti* and *R. brelichi*, which occupy opposite poles of an elevational continuum, no strong elevational influence on the places of origins or insertions, or presence or absence of muscles, is immediately evident. Of the remaining eight pairs of shared muscular traits, five were shared between *R. roxellana* and *R. brelichi* (38.5%), while three were shared

between *R. roxellana* and *R. bieti* (23.0%). The origin of the m. Longissimus capitis differs among the three, but not in accordance with the simple elevational gradient discussed above. More detailed, functional analysis might reveal differences secondarily related to elevation, for example: the shared features in the tail muscles of shorter-tailed, higher elevation species (items 27 and 28 in Table II), but given the small sample sizes and mixed-sex composition of the sample (see Table II), little can be stated with confidence.

In sum, based on the clinally distributed features set forth in Table I, it seems reasonable to characterize the higher-ranging taxa as more derived, with the shorter tails, digits, and certain features of the pelage comprising secondary derivations within Colobinae, since *Rhinopithecus* shares many of the classic colobine traits: sacculated stomachs, wide interorbital septum, wide supramalar face, short infraborbital face, short nasals, M₃ hypoconulid, etc. (Delson, 1975; Delson & Andrews, 1975; Groves, 1970; Strasser & Delson, 1987; Szalay & Delson, 1979; Vogel, 1968). However, interpretation of possible relationships with fossil forms requires a (very) brief review of reconstructions of the catarrhine ancestor.

THE CATARRHINE ANCESTOR

Until recently, the standard reconstruction of the catarrhine ancestor (Delson, 1975; Delson & Andrews, 1975; Strasser & Delson, 1987; Szalay & Delson, 1979; Vogel, 1968)

had, among other features, a short face, wide across the orbits, wide interorbital septum, short nasal bones; was, in short, more "colobine-like" than "cercopithecine-like." Benefit and McCrossin (1991; McCrossin & Benefit, 1992), assessing the significance of the facial and ischial morphology of the middle Miocene cercopithecoid *Victoriapithecus*, have challenged that reconstruction. *Victoriapithecus* (whose close relationship is based, in part, on its retention of the primitive upper molar *crista obliqua* combined with an advanced bilophodont pattern) possesses: "a moderately long muzzle and midfacial region. . . a deep cheek region relative to facial height . . . [and] a narrow interorbital septum" (Benefit & McCrossin, 1991, p. 5268). The face of *Victoriapithecus*, in short, "differs in almost every respect from the *Colobus*-like face predicted for ancestral cercopithecoids" (Benefit & McCrossin, 1991, p. 5268).

The significance of this work for the systematics of *Rhinopithecus* is that the polarities of the morphoclines for many characters in the heretofore dominant reconstructions of the catarrhine ancestor are effectively reversed; this permits a re-evaluation of the relevance of fossil colobines to *Rhinopithecus* taxonomy.

SOME FOSSIL COLOBINES

The only fossil colobine confidently attributed to *Rhinopithecus* is a middle Pleistocene juvenile cranium, two

maxillary fragments, and a mandibular fragment attributed by Matthew and Granger (1923) to *Rhinopithecus tingianus*, sp. nov.

Colbert and Hooijer (1953) later subsumed the specimens into *R. roxellana* as a subspecies, citing the fact that, *contra* Matthew and Granger (1923), the cranium and teeth were no larger than a typical male juvenile *R. roxellana* at the same stage of development. Though the fossil was found well east of the range of extant *R. roxellana*, and quite close to the very restricted range of *R. brelichi*, Colbert and Hooijer (1953) felt that the specimens probably represented the former much larger geographical range of the type species of *Rhinopithecus*.

Groves (1970) attributed these specimens to *P. (R.) brelichi* because the fossils were found only 110 miles NNE from "Van Gin Shan" (=Fanjing Shan) and were therefore probably ancestral to the living species. He provisionally classed *tingianus* as a subspecies of *brelichi* for the foregoing reason and that bregma did not seem to be posteriorly-indented (from an examination of the drawing in Colbert and Hooijer, 1953).

Examination of that drawing and the original photographs in Matthew and Granger (1923) reveals a distinct indentation of the vault at bregma, but it is not possible to determine exactly what Groves meant by, "bregma indented posteriorly" (1970, p. 567).

"No Pliocene or Early Pleistocene fossil colobines are known from Asia" (Delson, 1975, p. 201). The two fossil candidates with the strongest claims to close relationship with

the living Asian colobines hail from Europe and the Near East.

The middle Pliocene southern European colobine, *Dolichopithecus*, differs from modern colobines, *inter alia*, in its extreme adaptation to terrestriality, long nasal bones, deep infraorbital malar region, only slightly enlarged gonial, and a suite of limb features that were characterized by Szalay and Delson as "convergences toward a 'baboon-like' locomotor pattern" (1979, p. 413); these features include: posteriorly-oriented humeral medial epicondyle, prominent trochlear flange, large olecranon process, etc. Delson has asserted that, while a "dentally typical" colobine, *Dolichopithecus* "evidences facial lengthening and concomitant changes at least to the degree seen in *Nasalis larvatus*" (1975, p. 198). It should be stressed that, among living colobines, *Nasalis* evidences these facial features in the highest degree (Groves, 1970; Vogel 1968).

The late Miocene/early Pliocene colobine, *Mesopithecus*, comprises two species, *M. pentelici* and *M. monspessulanus*, from southern and central Europe, southeastern England, and Iran (Szalay & Delson, 1979). Numerous workers have noted affinities between this ancient colobine and *Nasalis*. Szalay and Delson pointed out that, "in its cranium and dentition, *Mesopithecus* reveals mostly colobine features" (1979, p. 409) and maintained that in numerous features (e.g., expanded gonial region, strongly expressed P³ protocone, etc.) it resembles *Nasalis*; but, since they believed all colobine-like traits were

necessarily primitive, and therefore, *Nasalis* to be secondarily derived relative to other colobines toward a more macaque-like and terrestrially-adapted morphology, they stated that the only shared features with living colobines were sympleisiomorphic.

Radinsky (1974) noted that a natural endocast of *Mesopithecus pentelici* demonstrated very strong affinities with living colobines, rather than cercopithecines, in several sulcal patterns: the anterolateral curvature of the intraparietal sulcus, narrow angle of the sulcus rectus relative to the orbital border of the frontal lobe, open limbs of the arcuate sulcus, caudal position of the lunate sulcus, and dimpling of the occipital lobe by two secondary sulci. But Radinsky interpreted these features as pleisiomorphic, therefore, "not positive evidence of colobine affinities for *Mesopithecus*" (1974, p. 26).

If the ancestral catarrhine morphotype was more cercopithecine-like than colobine-like, even in additional features not discussed by Benefit and McCrossin (1991; McCrossin & Benefit, 1992)--such as cerebral pattern, substrate preference, pedal functional axis, etc. (from Strasser & Delson, 1987, their Table 1)--then, obviously, many of the multitudinous shared features of modern colobine taxa must be synapomorphic, not primitive. If this view is correct, then both *Dolichopithecus* and *Mesopithecus* are very handy ancestors for at least some of the living colobines. For example, the "mostly

colobine" *Mesopithecus*, rather than beginning to converge "toward a more terrestrial, macaque-like way of life" (Szalay & Delson, 1979, p. 411), would be more parsimoniously viewed as evolving away from a generalized terrestrial adaptation and toward increased arboreality. Though somewhat beyond the scope of this paper, yet, nevertheless indicative of a potentially fruitful line of inquiry, if this interpretation is correct, then the coincidence of this increasingly arboreal lifeway for (at least some of) the nascent colobines with the decline of the plethora of generalized Miocene apes has obvious implications for the interpretation of the Asian colobine radiation and subsequent specializations.

SUMMARY AND CONCLUSIONS

Groves (1970) noted that the odd-nosed monkeys shared, besides their unusual nasal morphology, very high intermembral indices (90-98). The relevance of the foregoing discussion to the systematics of *Rhinopithecus*, is the implication that *Rhinopithecus*, with its typical colobine adaptation to folivory and arboreality, and close craniofacial relationship to *Presbytis* (e.g., Peng et al., 1985; Szalay & Delson, 1979), is that *Rhinopithecus* may have independently converged on the limb proportions of *Nasalis*, if we assume the high intermembral index in *Nasalis* to be conservative. If this is the case, then Delson's (e.g., 1975) portrayal of *Nasalis* as the sister group to a *Pygathrix* (including *Rhinopithecus*)/*Presbytis* clade

stands, but not because *Nasalis* is autapomorphic in many features relative to the "primitive" colobine ancestor; rather, *Presbytis*, *Pygathrix*, and *Rhinopithecus* are synapomorphic in derived, "typical" colobine features, and *Rhinopithecus* has independently converged on the limb proportions of *Nasalis* (presaged in *Mesopithecus*: intermembral index = 88 (Groves, 1970) and, presumably, primitive for cercopithecoids (see above)). Jablonski, Pan, and Wu (1992) noted that the *Rhinopithecus* shoulder girdles "were reminiscent of those of brachiating primates" (1992, p. 94), yet *Rhinopithecus* also possesses skeletal traits indicative of cyclical, strong compression (robust limb shafts), not seen in *Presbytis* or other arboreal forms (e.g., Groves, 1970)--they reported a juvenile phase marked by a high degree of suspensory locomotor behavior relative to the much heavier adults.

Since it seems entirely reasonable to posit that the ancestral *Rhinopithecus* was smaller than the living forms and that increased body size in the living forms is an adaptation to the stresses of higher elevation habitats, then their degree of terrestriality should be correlated with elevation, and their limb proportions might be secondarily derived relative to *Nasalis*.

Table I

Relationships between elevation, hair length, and extremities in *Rhinopithecus*
(see text for references).

Species	Elevation (meters)	Max. Weight ♂ (kilograms)	Tail Length (% of head + body)	Digit Length (Short/Long)	Hair Length (milli- meters)	Presence of Guard Hairs (120-160mm)
<i>R. bieti</i>	3200-4000	largest	86-90	short	50-80	present
<i>R. roxellana</i>	1700-3000	21	86-90	short	50-80	present
<i>R. brelichi</i>	1400-1800	15	133	short	70-80	absent
<i>R. avunculus</i>	sub-monta ne	smallest	143-148	long	45-50	absent

Table II

Differences in complement, origins, and insertions in three *Rhinopithecus* species
(data from Ye et al. 1989).

Muscle	<i>R. roxellana</i> (3 females)	<i>R. bieti</i> (1 male)	<i>R. brelichi</i> (2 males)
1 Sternocleidomastoideus (cleido-occipital)	Present	Absent	Absent
8a L. colli inf. obliq.	1st 3 thor. verts.	1st 2 thor. verts.	1st 2 thor. verts.
8b L. colli vert. obliq.	Cerv. verts. 2-4	Cerv. verts. 2-5	Cerv. verts. 2-5
13 Serratus post. sup.	2nd-6th ribs	2nd-7th ribs	2nd-6th ribs
14 Serratus post. inf.	6th rib	5th rib	6th rib
17a Longissimus cervicis	1st 6 thor. verts.	1st 5 thor. verts.	1st 6 thor. verts.
17b L. capitis origin	Last 3 cerv. verts.	Last 6 cerv. verts.	Last 4 cerv. verts.
17c Longissimus capitis insertion	6th thor. vert.	5th thor. vert.	6th thor. vert.
18 Semispinalis capitis (medial)	2 intersections	2 intersections	1 intersection
19 Pectoralis minor (origin)	2nd-5th costal cart.	2nd-4th costal cart.	2nd-4th costal cart.
27 Pubocaudalis	3rd caudal vert.	3rd caudal vert.	3rd-5th caud. verts.
28 Iliocaudalis	4th-5th caud. verts.	4th-5th caud. verts.	3rd-5th caud. verts.
30 Coraco-brachialis	Middle 1/3 humerus	Middle 1/5 humerus	Middle 1/3 humerus
33 Epitrochleo-ancoceus	Absent	Present	Present

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