Investigations on the Sciurid manus

I. Some new taxonomic characters and their importance in the classification of squirrels

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Introduction

The structure of the manus is important in the classification of the Sciuridae. Some of the characters of the manus that distinguish high taxonomic groups result perhaps from evolutionary convergence, but others are conservative and useful. Some trends in form of the manus are irreversible, and therefore reveal phylogenetic information.

The characters of the forefoot augment those of the teeth and baculum in sciurid classification.

Materials and methods

The forefoot of specimens in Nearctic *Eutamias (minimus* 32, *amoenus* 2, *dorsalis* 2, *merriami* 1, *ruficaudus* 1, *quadrivittatus* 2, *umbrinus* 9, *ruficaudus* 1), *Tamias striatus* 86, *Marmota (monax* 5, *flaviventris* 2), *Spermophilus (tridecemlineatus* 34, *spilosoma* 1, *mexicanus* 1, *franklinii* 5, *lateralis* 9, *tereticaudus* 3, *variegatus* 3, *armatus* 3, *richardsonii* 8, *beldingi* 1, *townsendii* 1, *washingtonii* 1, *beecheyi* 1, *undulatus* 1), *Ammospermophilus (leucurus* 1, *harrisii* 3), *Cynomys (leucurus* 3, *ludovicianus* 1), *Tamiasciurus (douglasii* 1, *hudsonicus* 70), *Sciurus (niger* 24, *carolinensis* 41), *and Glaucomys (sabrinus* 6, *volans* 22), as well as three Oriental species *(Petaurista lena* 1; *P. grandis* 1; *Sciurus lis* 1) and one South American species *(Sciurus granatensis 2)* was examined of preserved skins in the University of Wisconsin-Stevens Point Museum of Natural History. A skin of *Aplodontia rufa* was also examined. Representative skins obtained on loan of some genera of South American, African, and Asian squirrels were examined, including two *Microsciurus mimulus* (Colombia), two *Sciurotamias davidianus* (Wen Chuhn, China), two *Callosciurus caniceps* (Siam), two *Menetes berdmorei* (Viet Nam), one *Ratufa bicolor* (South Viet Nam), one *Reithrosciurus macrotis* (Borneo), two *Nannosciurus borneanus* (Borneo) one *Rhinosciurus laticaudatus tupaioides* (Malaya), two *Heliosciurus rufobrachium* (Ogouma, Africa), one *Myosciurus minutus* (Kamerun, Africa), two *Protoxerus stangeri* (Ogouma, Africa) and two *Epixerus wilsoni* (Pemba, Nyambi, Africa).

Results and discussion

Systematics of recent Sciuridae

The Sciuridae have received much attention from taxonomists and paleontologists (Pocock, 1922, 1923; Bryant, 1945; Moore, 1959; Wilson, 1960; Black, 1963; and others). *Sciurus* is usually considered a generalized, primitive form. Subfamilies listed in Black are Sciurinae and Petauristiae. The former includes the tribes Tamiini (chipmunks), Sciurini *(Sciurus, Tamiasciurus,* and other scansorial forms), Funambulini *(Myosciurus, Funambulus,* etc.), Callosciurini (numerous diverse genera such as *Callosciurus, Nannosciurus, Menetes, Sciurotamias),* Marmotini (holarctic ground

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squirrels and marmots), and Xerini (African ground squirrels). The Petauristinae contains a dozen genera of volant squirrels.

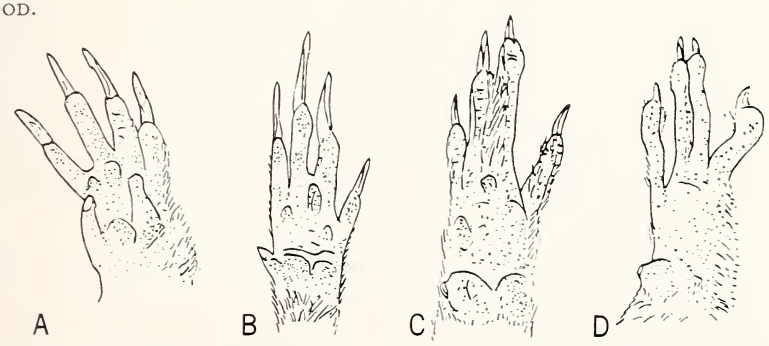
Many modern workers have removed *Tamiasciurus* from Sciurini (Moore, 1959) chiefly because its simple penis usually lacks a baculum. Moore arranged *Tamiasciurus* with *Sciurotamias,* but Black placed the latter in the Callosciurini. Black doubted that the Petauristinae is a natural group, and stated that the group arose from "tree squirrels", probably *Sciurus* and *Callosciurus.* The recent taxon closest in relationship to the Sciuridae is the exceptionally primitive Aplodontidae of the American Northwest.

Patterns and characters

Study of the sciurid forefoot reveals important patterns and new characters, some of which are phylogenetically irreversible.

The sciurid manus functions in digging, holding food, scampering, climbing, grooming and copulation. No generalizations seem to have been recorded regarding structure of the sciurid foot excepting comments on the elongation of the bones of the limb and manus in arboreal and flying squirrels (Piterka, 1936; Bryant, 1945) and an observation that some squirrels are "perissodactyl" in having the third digit longest whereas others are "artiodactyl" having the third and fourth nearly equal, the fourth slightly longer (Pocock, 1922). Pocock and others have mentioned that squirrels generally have a nail on the first digit, and Bryant stated that all Nearctic squirrels possess one excepting *Cynomys,* which has a stout claw.

Wood (1962) described the partially complete manus in several paramyid (= ischyromyid) fossils. In *Leptotomus* the thumb seemed "divergent", and the pattern of the digits was problematic though metacarpals III and IV were subequal. In *Ischyrotomus* IV was elongate but III possibly longer, and the thumb appeared robust. In *Pseudotomus* the "strongly divergent" thumb was robust and freely movable. The third digit was longest and IV was longer than II, which exceeded V in length. The elongate digit III is unlike that of modern arboreal squirrels. Probably some ancestral squirrels and certainly some ancestral rodents (ischyromyids) were semi-arboreal, showing some scansorial adaptations such as elongate tail according to Wood.



Manus in some sciuromorph rodents. A. *Aplodontia rufa;* B. *Spermophilus mexicanus;* C. *Sciurus carolinensis;* D. *Glaucomys volans*

Assuming semi-arboreal *Aplodontia rufa,* of the closely related and primitive Aplodontidae, has a primitive structure of the manus, then the ancestral sciurid foot was probably pentadactyl with the first digit functional and armed with a claw, the second digit longer than the fifth, and the third the longest (Fig.), as in *Pseudotomas.* This pattern is widespread in the Rodentia.

In burrowing ground squirrels and their allies (Marmotini) the first digit is extremely short, the third longest (perissodactyl), the second is longer than the fifth usually, and the small "nail" on the pollex is usually somewhat pointed (except in *Marmota)* (see Fig.). Fossorial mammals such as pocket gophers, badgers, and moles show a similar development of the second and third digits.

Tamias, Eutamias, Tamiasciurus, Sciurotamias, and *Rhinosciurus* have a generally artiodactyl pattern; the paired subequal digits (III, and IV, II and V) are not so specialized in elongation of the outermost digits as seen in the pattern of arboreal and volant species. All of these genera spend much time on the ground, and their taxonomic affinities with other sciurids are unknown. *Rhinosciurus* is extremely specialized for feeding on ants.

In the arboreal pattern, found also in the volant species, the fourth toe is markedly longer than the third. The rudimentary first digit bears a nail-like structure. The fifth toe, as well as the fourth, shows elongation, and they both ordinarily exceed the second in length (see Fig.).

The tendency to lengthen the lateral digits and relatively speaking to concomitantly suppress the inner ones is adaptive in a form which climbs vertical, cylindrical tree trunks. The arms and sharply clawed digits must encompass much of the curved surface to prevent the squirrel from falling backward.

Evolution of ancestral squirrels

The Sciuridae probably arose from the extinct Paramyidae (Bryant, 1945; Wilson, 1949; Black, 1963), now regarded by Black (1971) as the Ischyromyidae. They show close resemblance to recent *Sciurus* in the pattern of the molar teeth (Wood, 1962). Wilson (1960), Bryant (1945), and Black (1963) suggest that the ancestral (Oligocene) squirrels were ground forms, although Wilson has discussed the popular acceptance of *Sciurus* as primitive. Wood (1962) has shown semi-arboreal specializations in ischyromyids.

Evolution of ground squirrels

In North America *Tamias* is the oldest genus that survives today, closely related to *Protosciurus* (Black, 1963). *Spermophilus* appears in the record later, and *Marmota* even later. Our study of the manus shows *Marmota* to resemble *Spermophilus* and *Cynomys* in digital pattern, but the broad nail on the nearly vestigial pollex in marmots indicates some divergence from the spermophiles. The foot of *Cynomys* is advanced beyond that in *Spermophilus,* and this specialization is consistent with the hypothesis of Nadler et al. (1971) and Black (1963) that *Spermophilus* is the ancestor of *Cynomys.*

The marmots are interesting because their pattern of the manus resembles that of semi-fossorial *Spermophilus* and *Cynomys,* yet the pollex bears a broad "nail". *Marmota marmota* lacks the pollex and nail (Pocock, 1922). The nail suggests a surprising affinity with tree squirrels or, much more likely, a general preference for boulders and other rocky habitats (for example, in *Marmota flaviventris* of the Rocky Mountains). In any event, the broad nail reveals a significant divergence from the holarctic ground squirrels and *Cynomys.* Assignment of all these terrestrial squirrels to the Marmotini is based chiefly on a strong resemblance of the baculum (Pocock, 1923) and teeth (Black, 1963).

According to Pocock (1923) the African ground squirrels, Xerini, have the middle digit longest, although IV is slightly longer than II. Thus, surprising convergence with the ground dwellers' pattern in the Marmotini is evident.

Evolution of rock squirrels

The hoof-like form of the pollex in *Ratufa* indicates a preference for a hard stony substrate, but this squirrel is strictly arboreal, with arboreal digits. Perhaps the Ratufini paralleled the rock and tree hyraxes in form and function of the manus. Another possibility is that the pollex of *Ratufa* is adapted to standing on the main branches of trees, even more so than of *Sciurus*. The rock squirrel *(Spermophilus variegatus)* shows a moderately broad claw on the pollex. *Sciurotamias* also prefers rocky ground and possesses a fairly broad nail. Marmots often live in rocky habitat, and most of them possess a robust "nail" or hoof. The broad nail is apparently an adaptive, inconstant character in the Sciuridae.

Evolution of tree squirrels and flying squirrels

Tree squirrels appeared as fossils in the Miocene (Dawson, 1967; Black, 1963) and their record is only fair (see also Mein, 1970). The arboreal pattern of the digits is seen in Asia, Africa, Europe and the Americas and is highly correlated to scansorial habits.

Reithrosciurus resembles *Sciurus* in general form, structure of the manus, and even of the baculum (see Pocock, 1923, p. 214), but in its habits this squirrel has apparently returned to the ground (Walker, 1964, p. 677). The fossil record for volant squirrels is also poor, although one is known from the Miocene (but see Black, 1963, p. 239). The volant squirrels possibly arose polyphyletically. Piterka (1936) showed numerous arboreal-volant homologies, and Black (1963) suggested that some genera arose from *Sciurus* and other from *Callosciurus*. The structure of the manus in *Glaucomys* and *Petaurista* is similar to that of *Sciurus* and other arboreal squirrels, except that *Petaurista* is advanced in loss of the pollex.

The Petauristines show amazing diversity in bacular form (Pocock, 1923, p. 244—248) as well as in characters of the tail and flight membrane. *Eoglaucomys* ist most markedly divergent, though its baculum is possibly derived from the *Sciurus* pattern. The penis bone in *Petaurista* and *Hylopetes* though differing greatly could have developed from the pattern in *Sciurus*. The slender bone in *Glaucomys* is not formed usually as figured by Pocock, and resembles somewhat the bone in *Sciurus*.

Summary and conclusions

Our study of the manus and consideration of other characters (tail, cheek pouches, penis, teeth) suggest that the Marmotini, as recognized by Black (1963) is as well differentiated as (or more so than) the Petauristinae. Although Petauristines are probably polyphyletic, with nevertheless a high degree of evolutionary homodynamy, the manus shows that their origin lies in arboreal squirrels probably taxonomically near *Sciurus*. The baculum in its diversity reflects nonetheless a *Sciurus* pattern. The holarctic ground squirrels *(Spermophilus, Cynomys,* and their close relatives) differ significantly from marmots in the form of the pollex. However, in anal glands and pattern of the digits of the manus the two groups show close relationship. *Ratufa* is distinctive in the Sciurinae in structure of the manus, and of the baculum (Pocock, 1923). *Rhinosciurus* seems highly divergent from the arboreal and gliding squirrels in dental and cranial characters, and the foot shows little resemblance to them. *Petaurista, Rhinosciurus, Menetes, Myosciurus,* and *Nannosciurus* lack a pollex and are ruled out as ancestors of any of the other genera examined. *Nannosciurus* and *Menetes* resemble *Callosciurus* in bacular form (Pocock, 1923, p. 220) and

apparently are descended from it or a close relative. New world chipmunks, *Tamiasciurus, Sciurotamias,* and *Rhinosciurus* neither resemble the arboreal forms nor the Marmotini in structure of the manus, and are somewhat intermediate in form of the manus. None of them should be arranged with the Sciurini in our opinion.

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Zusammenfassung

Untersuchungen an der Hand von Sciuriden. I. Einige neue taxonomische Merkmale und ihre Bedeutung für die Klassifikation der Hörnchen

Die Ausbildung der Vorderfußzehen wurde an einer großen Zahl von Sciuriden vergleichend untersucht und in ihrer taxonomischen Bedeutung erörtert. Bei grabenden Formen ist die 3., bei baumlebenden die 4. Zehe die längste. Zwischen beiden Gruppen vermitteln wenig spezialisierte, „artiodactyle" Arten, bei denen 3. und 4. Finger gleich lang sind *(Tamias, Eutamias, Tamiasciurus, Sciurotamias* und *Rhinosciurus).* Unter den Marmotini nehmen amerikanische Arten durch den Besitz eines Nagels am Pollex eine Sonderstellung ein. Ein Daumen fehlt aber bei *Marmota marmota* wie auch bei manchen Baum- und Flughörnchen: *Petaurista, Rhinosciurus, Menetes, Myosciurus* und *Nannosciurus.* Im übrigen unterscheiden sich hinsichtlich der Finger die Marmotini von den anderen Sciurinae mehr als die Baumhörnchen von den Flughörnchen.

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