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Anschriften der Verfasser: Dr. Eckhard Grimmberger, Steinstr. 58, DDR-2200 Greifswald; Doz. Dr. sc. Hans Hackethal, Museum für Naturkunde der Humboldt-Universität, Invalidenstr. 43, DDR-1040 Berlin; Zbibgniew Urbańczyk, Os.J.III. Sobieskiego 26 d/142, Polen – 60-683 Poznań

Phylogenetic relationships among four arvicolid genera

By Barbara R. Stein

Museum of Natural History, The University of Kansas, Lawrence, Kansas, USA

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Abstract

Appendicular myology and osteology in four genera of arvicolid rodents, *Clethrionomys, Eothenomys, Alticola* and *Synaptomys*, were evaluated for characters useful in constructing hypotheses of phylogenetic relationships. Postcranial morphological data, combined with information on karyology, biochemistry, stomach, glandular, and external morphology, support a close evolutionary relationship among these taxa. Myological characters supported the monophyly of *Clethrionomys, Eothenomys* and *Alticola* and indicated the apomorphic nature of *Alticola* relative to the other two genera. In no instance was myology alone sufficient to distinguish *Clethrionomys* from *Eothenomys*. In contrast, osteology identified derived characters among species of *Clethrionomys*, whereas the genus *Synaptomys* was apomorphic both osteologically and myologically. Postcranial morphological data also indicated that within *Clethrionomys* the species *gapperi, glareolus* and *rutilus* are closely related; *C. rufocanus* is distinctive and is considered primitive within the genus. The presence of rooted molars is regarded as a derived character among these taxa and represents a character reversal in the proposed phylogeny. Heterochrony is hypothesized as a mechanism that would explain this arrangement.

Introduction

Within the Arvicolidae (Honacki et al. 1982), a family comprising the voles (Microtini) and lemmings (Lemmini), the *Clethrionomys-Eothenomys-Alticola* group currently represents one of the most unstable areas of classification at the generic level (Corbet 1978). Although a close evolutionary relationship among these genera has long been hypothesized (Miller 1896), attempts to document this relationship have not produced a single, generally accepted classification.

Owing to the abundance of Pleistocene rodent fossils, many arvicolid classifications have relied predominantly on cranial and dental characters (Corbet 1978). However, Imaizumi (1957) noted great confusion in the classification of Japanese voles resulting from

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the use of these characters and numerous investigators subsequently have documented variation of these structures both within and between arvicolid populations (PERRIN 1978; ALIBHAI 1980; ABE 1973a, b, 1982; CORBET 1963, 1964; GUTHRIE 1965, 1971; HAITLINGER 1965; BATES and HARRISON 1980; AIROLDI and HOFFMANN 1984; MIYAO 1966; ZEJDA 1960; ZIMMERMANN 1965; PATTERSON 1983; ILYENKO and KRAPIVKO 1983).

Based on this evidence, I have examined appendicular myology and osteology in *Clethrionomys, Eothenomys* and *Alticola* (tribe Microtini) as alternative sets of characters on which to base a cladistic analysis of this group. The bog lemming, *Synaptomys*, was examined for purposes of comparison within the Arvicolidae, because this genus is considered the most generalized member of the more primitive arvicolid tribe, the Lemmini (HINTON 1926; ELLERMAN 1940). Postcranial myological characters should accurately reflect evolutionary relationships because it is possible to trace the innervation of muscles and, therefore, to establish their homologies (BRYANT 1945; KLINGENER 1964; WOODS 1972). Several studies also exist in which postcranial osteology in rodents has been examined. CARLETON's (1980) work on neotomine-peromyscine relationships employed postcranial osteology in a phylogenetic analysis. BATES and HARRISON (1980) attempted to identify interspecific variation using long bones. HECHT (1971) examined the scapula, humerus, femur and pelvis in four genera of rodents and drew attention to their morphological differences among species. BEST (1978) included postcranial measurements in his morphometric analysis of *Dipodomys*, as did COTHRAN (1983) in his ground squirrel study.

The study presented herein is not a phylogenetic assessment based solely on postcranial morphology. These data have been combined with information obtained from the literature on karyology, biochemistry, glandular, stomach and external morphology to produce a synthetic phylogeny of the taxa under consideration.

Material and methods

Separate sets of specimens were used for qualitative myological and osteological analyses. In the former, one side on each of 57 specimens representing 10 taxa was dissected. These taxa included five of the seven currently recognized species of *Clethrionomys*, specimens of *Eothenomys melanogaster, Alticola roylei* and *Synaptomys cooperi*. For osteological analyses four species of *Clethrionomys*, three of *Eothenomys* and one each of *Alticola* and *Synaptomys* were examined. Skeletons were compared under a magnifying lens and differences in morphology noted. The following specimens were examined:

Alcoholic specimens

Clethrionomys gapperi: CANADA: Manitoba: North Knife River, 5 KU; USA: New Hampshire: Coos Co., 1.25 mi N, 11.5 mi E Pittsburgh, 2 CM; Grafton Co., Franconia Notch State Park, 4.7 mi S, 3.5 mi E Franconia, 1 CM; Wisconsin: Douglas Co., Solon Springs, 3 FMNH; Wyoming: Fremont Co., 17 mi SW Lander, 1 KU; Lincoln Co., 13.5 mi N, 8 mi E Cokeville, 1 KU.

Clethrionomys californicus: USA: California: Humboldt Co., Cutteback, 1 MVZ; Mendocino Co., Mendocino City, 1 MVZ; Oregon: Jackson Co., 3 mi N, 11 mi E Ashland, 2 UMMZ.

Clethrionomys rex: JAPAN: Rishiri Island, 1 PSMNH.

Clethrionomys rufocanus: KOREA: central, 1 USNM; Hill 1468 m, 3 mi SSE Sumil-li, 1 AMNH; 3 mi E Rt. 33 on 22, 1 USNM; Pusan area, 1 USNM; PRC: No. Manchuria: Great Khingan Mts., Yalu Station, China E. Railway, 2 CAS.

Clethrionomys glareolus: CZECHOSLOVAKIA: Velky Tisy, 2 USNM; near Nymburk, 1 USNM; FINLAND: Uusimaa, near Helsinki, Sipoa, 3 UMMZ.

Clethrionomys rutilus: USA: Alaska: St. Michaels, 2 USNM; Tonzona, 1 USNM; Anchorage, 2 UMMZ; Yukon Hwy., mi 30, 1 UMMZ.

Clethrionomys sikotanensis: USSR: RSFSR, Sakhalinsk. Obl., Anivsk. rai., 3 KU.

Eothenomys melanogaster: PRC: Yunnan: Mucheng, Salween, Drng, 5 AMNH; ROC (TAIWAN): Chuei-Feng, Nan Ton Tsien, 2 USNM.

Alticola roylei: AFGHANISTAN: Badakhshan Prov.: 15 m E of Eshkashem, 2 FMNH; PAKISTAN: Dir State: 16 mi No. Dir, 8400′, 1 USNM; 20.5 mi No. Dir., 10400′, 1 USNM.

Synaptomys cooperi: USA: Kansas: Atchison Co., Atchison Co. State Lake, 2 KU; Jefferson Co., Nelson Evironmental Study Area, 1 KU; Nebraska: Gage Co., 0.25 mi W Homestead Nat'l Mon., 3 KU.

Skeletal material

Clethrionomys gapperi: CANADA: Alberta: Fort McMurray, 1 MCZ; Quebec: Richmond Gulf, 1 MCZ; Bonaventure Co., 5.34 mi N, 2 mi E St. Elzear de Bonaventure, 3 CM; 5.67 mi N, 1 mi E St. Elzear de Bonaventure, 1 CM; 4.5 mi N, 0.5 mi E St. Elzear de Bonaventure, 1 CM; 4.5 mi N, 2 mi E St. Elzear de Bonaventure, 1 CM; USA: Idaho: Adams Co., 0.5 mi E Black Lake, 1 MVZ; 0.5 mi E Black Lake, 6800′, 2 KU; SW slope Smith Mt., 1 MVZ; 1 mi N Bear R. S., SW slope Smith Mt., 5400′, 1 KU; 3 mi W Payette L., 1 MVZ; Bannock Co., 1 KU; Bannock Co., Pocatello, 1 KU; Maine: Franklin Co., 3.7 mi NW Kingfield, 8 CM; Massachusetts: Middlesex Co., Pepperell, 4 MCZ; Michigan: Chippewa Co., Marquette National Forest, 1 KU; Marquette Co., Huron Mts., 10 FMNH; New Hampshire: Grafton Co., Franconia Notch State Park, 4.75 mi S, 3.5 mi E Franconia: 1 CM; Pennsylvania: Crawford Co., Pymatuning Swamp, Sedge Linesville, 1022′, 1 CM; Pymatuning Swamp, 4 mi W Linesville, 2 CM; Pymatuning Swamp, 4 mi W Linesville, 1000′, 1 CM; West Virginia: Randolf Co., Blister Pine Run, 1 mi SE Cheat Bridge, P. O. 3675′, 2 CM; Wyoming: Albany Co., 3 mi ESE Browns Peak, 3 KU.

Clethrionomys californicus: USA: California: Mendocino Co., 3 mi NW of Gualada, St. Orres Creek, 60′, 1 LACM; Trinity Co., White Rock Ranger Sta., 4800′, 1 MVZ.

Clethrionomys rutilus: CANADA: Northwest Territory: Tyrell Lake Region; 7 UMMZ; Beverly Lake Region, 2 UMMZ; Artillery Lake Region, 1 UMMZ; LAPLAND: I USNM; USA: Alaska: 1 UMMZ; Chandler Lake, 68°12′, 152°45′, 2900′, 3 KU; Glacier Bay Nat'l Mon., Torch Bay, 7 KU; Glacier Bay Nat'l Mon., Thistle Cove, 2 KU; Glacier Bay, 1 KU; St. Lawrence Island, Mt. Gambell, 2 PSMNH; St. Lawrence Island, 2 mi SW N. E. Cape, 1 USNM; Anakturuk Pass, 2 PSMNH; Paxson Lake, 1 UMMZ; Paxson, 1 USNM; Fairbanks, within 100 mi radius of, 2 USNM; Fairbanks region, Piled River Slough, 2 UMMZ; Seward Peninsula, Lava Lake, 5 USNM; Inmachuk River, 1 USNM; Kuzitrin Lake, 1 USNM; Tonzona, 1 USNM; Nulato River, 1 USNM; Cantwell, 2212′; Jack River 4 mi Camp, 2400′, 1 AMNH; Koalak River, 70° N, 3 MVZ; College University of Alaska, 1 PSMNH; Brooks Range, Anzktuvuk Pass, 1 PSMNH.

Clethrionomys rufocanus: FINLAND: Lappi District, Kilpisjarvi, 5 CM; JAPAN: Hokkaido: 6 PSMNH; Hokkaido: Toshina-Schicho, 1 PSMNH; Hokkaido: Toyotami, 1 PSMNH; Hokkaido: Yukomambetsu, 1 PSMNH; Rishiri Island: 3 PSMNH.

Clethrionomys rex: JAPAN: Rishiri Island: 8 PSMNH.

Clethrionomys centralis (= frater): USSR: 1 UMMZ.

Clethrionomys glareolus: AUSTRIA: Niederösterreich Prov.: I. I. A. S. A., Laxenburg, 1 MVZ; ENGLAND: Uttoxeter, 1 AMNH; Berkshire: Culham College, 2 mi SW Abingdon, 2 MVZ; Devonshire: Torrington, 3 AMNH; FINLAND: Hame District: 2 km N, 3.5 km E Iso-Evo, 6 CM; Oulo District: 4 km N, 4 km W Rukajawi, 2 CM; FRANCE: Cote d'Or, 1 USNM; USSR: Vyborg, 2 AMNH.

Eothenomys melanogaster: PRC: Szechwan: Kuan Shien, 8 USNM; Mupin, 2 USNM; Wan Shien, 1 USNM; Tseo-Jia-Geo, 1 USNM; THAILAND: top of Mt. Angka, 1 MCZ.

Eothenomys smithi (including *kageus*): JAPAN: Fukuoka Pref., 2 PSMNH; Honshu Island: Japanese Alps, 3 PSMNH; Yamanashi Pref., Mt. Fuji, 1 PSMNH.

Aschizomys (Eothenomys) andersoni (includes *imaizumi*): JAPAN: 1 PSMNH; Mt. Zaoh, 1 PSMNH; Tochigi Pref., 1 PSMNH; Yumagata Pref., Mt. Rao, 1 PSMNH; Honshu Island: Natchinotaki Falls, 1 PSMNH.

Alticola sp.: INDIA: Ladak, above Leh, 1 USNM.

Synaptomys cooperi: USA: Kansas: Anderson Co., 6 mi S Garnett, 3 KU; Barber Co., 3 mi N, 1 mi E Sharon, 2 KU; Douglas Co., 6 KU; Lawrence, KU campus, 1 KU; 7 mi SW Lawrence, 3 KU; 7.5 mi SW Lawrence, 5 KU; 2.5 mi W Lawrence, 1 KU; 1 mi W Lawrence, 3 KU; 1 mi SW Lawrence, 1 KU; 1.67 mi W Lawrence, 1 KU; 2 mi W Lawrence, 4 KU; Lawrence, 1.5 mi N, 1.5 mi E courthouse, 4 KU; Meade Co., 14.5 mi SW Meade, 1 KU; 17 mi SW Meade, 1 KU; Nebraska: Dundy Co., 5 mi N, 2 mi W Parks, 2 KU.

AMNH = Amer. Mus. Nat. Hist., CAS = Calif. Acad. Sci., CM = Carnegie Mus. Nat. Hist., FMNH = Field Mus. Nat. Hist., KU = Univ. Kansas Mus. Nat. Hist., LACM = L. A. Co. Mus., MCZ = Mus. Comp. Zool. Harvard, MVZ = Mus. Vert. Zool. Berkeley, PSMNH = Puget Sound Mus. Nat. Hist., UMMZ = Univ. Mich. Mus. Zool., USNM = U. S. Nat'l. Mus.

A character-by-character analysis was employed in constructing the cladogram because I observed relatively little homoplasy among taxa. A computer analysis of the data set using the PAUP algorithm

(Swofford, 1984) confirmed the phylogram. The cricetine genera *Neotoma, Peromyscus, Sigmodon* and *Oryzomys* were examined for outgroup comparison and reference was made to Rinker's (1954) classic monograph of myology in these taxa. Conditions observed in these genera were considered plesiomorphic and, thus, determined the polarities of my characters (table).

Results

Myological characters

Although a great deal of individual variation was noted, the myology of *Eothenomys* was not found to differ from that of *Clethrionomys* in any identifiable way, nor was variation among species of *Clethrionomys* felt to have any systematic significance. Of the 110 muscles dissected, four in the forelimb and four in the hind limb did exhibit variation that I considered valuable for systematic analyses (fig. 1).

In the forelimb, the insertion of M. occipitoscapularis is confined to the cranial half of the vertebral border in *Clethrionomys, Eothenomys* and *Alticola* whereas in *Synaptomys* and in the cricetine genera the insertion extends along the scapular root to the base of the scapular spine. Second, the insertion of M. omocervicalis is confined to the metacromion process in *Clethrionomys, Eothenomys* and in the cricetines examined but it extends to include the acromion in *Synaptomys* and in *Alticola*. Third, *Synaptomys* and the cricetine genera possess a primarily radial insertion of M. biceps brachii versus an insertion that is primarily ulnar in *Clethrionomys* and in *Eothenomys* and one which is half radial and half ulnar in *Alticola*. Fourth, *Synaptomys* possesses only two points of insertion for M. abductor pollicis longus. All other genera examined, with the exception of *Sigmodon*, possess three points.

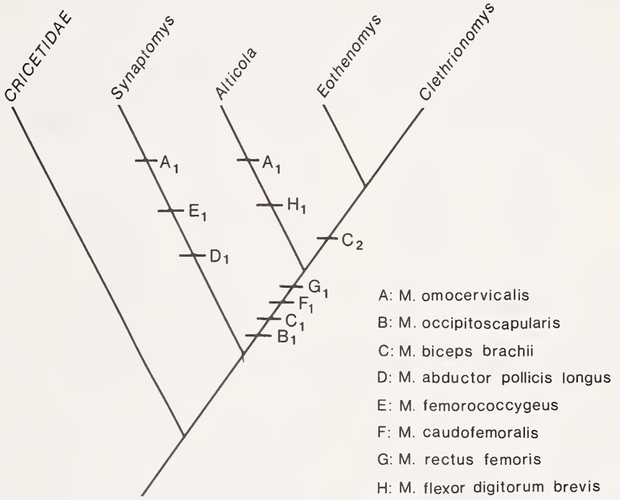

Fig. 1. Cladogram of the four arvicolid genera examined and their outgroup based on the results of myological dissections (from Stein 1986)

In the hind limb, the insertion of M. femorococcygeus is restricted to the knee joint capsule in *Synaptomys* and in the cricetine taxa but extends along the distal end of the posterior femoral shaft in *Clethrionomys, Eothenomys* and *Alticola*. In addition, the tendons of the two heads of M. rectus femoris are not well defined in *Clethrionomys* and *Eothenomys* but are distinct in *Synaptomys* and in the cricetine genera. Their condition in *Alticola* is intermediate between these two extremes. Third, in *Clethrionomys, Eothenomys* and *Alticola*, M. caudofemoralis arises from the deep surface of M. femorococcygeus. In *Synaptomys* and in the cricetines the muscle arises directly from the sacral and caudal vertebrae. Lastly, *Alticola* was the only genus examined that possesses a tendon from M. flexor digitorum brevis to Digit V. Complete muscle descriptions and figures for all muscles dissected are provided in Stein (1986).

Osteological characters

In contrast to the results of my dissections, several osteological characters served to identify individual species of *Clethrionomys*. *Clethrionomys glareolus*, which proved indistinguishable from *C. rutilus* in all other respects, had a greater trochanter of the humerus that was relatively larger than that noted for all other species examined (Bates and Harrison 1980). Additionally, the humerus of *C. rutilus* was recognized as having a relatively larger head than those in the other species although this difference was not outstanding. Moreover, the ridge of the humerus adjacent to the lateral condyle was square in outline as compared with a smoother profile in the remaining taxa. *Clethrionomys gapperi*, *C. glareolus* and *C. rutilus* were united in that all possessed a bifid spine of the axis vertebra compared to a thin, flattened spine observed in the other species examined. The one specimen of *Alticola* available to me also possessed a bifid spine, but this character must be examined in additional material before a definitive statement about its condition in that genus can be made.

Eight osteological characters, in addition to four myological ones, supported the monophyly of *Clethrionomys*, *Eothenomys* and *Alticola* (fig. 2). The ventral tip of the atlas in these three taxa was vertical, whereas in *Synaptomys* and in the cricetines it was angled posteriorly (fig. 2a, b). The shape of the clavicle and the acromion process of the scapula

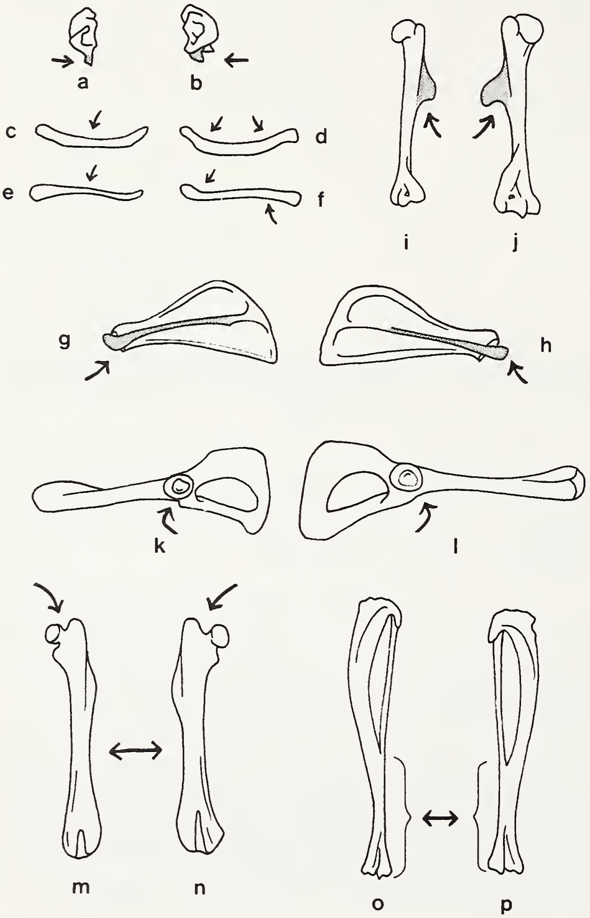

Fig. 2. Eight osteological characters which support the monophyly of *Clethrionomys*, *Eothenomys* and *Alticola*. a: ventral tip of the atlas vertical; c, e: clavicle relatively straight; g: acromion process of scapula hook-like; i: deltoid crest of humerus smooth and round in profile; k: notch formed by pubic ramus; m: head of the femur tipped towards the greater trochanter and shaft of the femur relatively thin; o: tibia/fibular fusion relatively more extensive. Figures b, d, f, h, j, l, n and p show the corresponding plesiomorphic conditions were also distinctive in these genera. The clavicle was relatively straight, curving slightly at the ends in all three, whereas in *Synaptomys* and in the cricetines it curved both in anterior/posterior and in dorsal/ventral planes, appearing to twist along its course (fig. 2c–f). In general, the acromion process of the scapula curved gently like a hook at the distal end in the Microtini, whereas in *Synaptomys* it appeared spatulate (fig. 2g, h). The deltoid crest of the humerus in the former three genera was smooth and round in profile contrasting with a larger, more "beak-like" curvature in *Synaptomys* and in the cricetines (fig. 2i, j).

In the hind limb osteological differences were noted in several elements. The majority of variation in the pelvis related to differences in shape between males and females. Overall, sexual dimorphism is not considered significant in this family with the exception of pelvic shape differences (Rossolimo 1962; Aimi 1980; Ognev 1950; Moskvitina and Suchkova 1976; Kaneko 1968, 1969; Brown and Twigg 1969) and my observations support this hypothesis. A notch formed by the public ramus was distinct in most species but was relatively weak in many specimens of *C. rufocanus* and *Eothenomys* and in some individuals of *C. rutilus* (fig. 2 k, l). The head of the femur was angled more towards the greater, versus the lesser, trochanter of that bone and extended above it in *Clethrionomys*, *Eothenomys* and *Alticola* (fig. 2m, n). In *Synaptomys* and in the cricetines the head was tipped towards the lesser trochanter and the greater trochanter extended above it. The shaft of the femur was thinner in the former three genera relative to its condition in the other taxa examined. Lastly, the degree of fusion of the distal ends of the tibia and fibula was most extensive in the Microtini (fig. 2o, p). Carleton (1980) recognized this character to be significant phylogenetically in his study of neotomine-peromyscine relationships.

The genus *Synaptomys* was apomorphic for a number of osteological, as well as myological, characters (fig. 3). The transverse processes of the atlas were unusually large and protruding relative to the other genera and the dorsal surface of that bone was distinctly notched (fig. 3a, b). The carotid tubercle on the ventral surface of the sixth cervical vertebra curved posteriorly as a smooth shaft which tapered distally, in contrast to the more angular-shaped tubercles of the other genera (fig. 3c, d). For most individuals of *Synaptomys* examined, the height of the scapula was small relative to the overall length, with the bone tending to be square in outline, the borders thickened (fig. 3e, f). This condition contrasted sharply with all other species which had deep scapulae, domed cranially and with delicate borders.

The only other difference in the forelimb of *Synaptomys* was noted in the shape of the nail. In this genus the nail was wedge-shaped rather than rounded, and the tip of the pollex bulbous as though the digital pad had been repositioned distally. No functional explanation for this phenomenon is obvious at the present time.

In the hind limb of *Synaptomys* only one outstanding apomorphy was noted. The ischial tuberosity of the pubis was a large, flattened triangular area whereas in all other genera it was relatively indistinct. The medial and lateral flanges of the tibia seemed reduced in this genus as well but the difference was not dramatic (fig. 3g, h).

I do not report any variation in the shape or size of the calcaneum among these genera because the distal extremities were lacking in a majority of the specimens I examined. I expect that some interspecific or intergeneric differences do exist within this group based on the work of Carleton (1980) and Stains (1959). The latter author found this bone to be particularly important taxonomically within the Rodentia. Specifically, within the Arvicolidae, he found variation not only in size but also in the position of the trochlear process, in a peculiar enlargement and twisting of the calcaneal body, and in the presence of an anterior articular surface for the astragalus. He did not, however, specify what these differences were for the genera he examined.

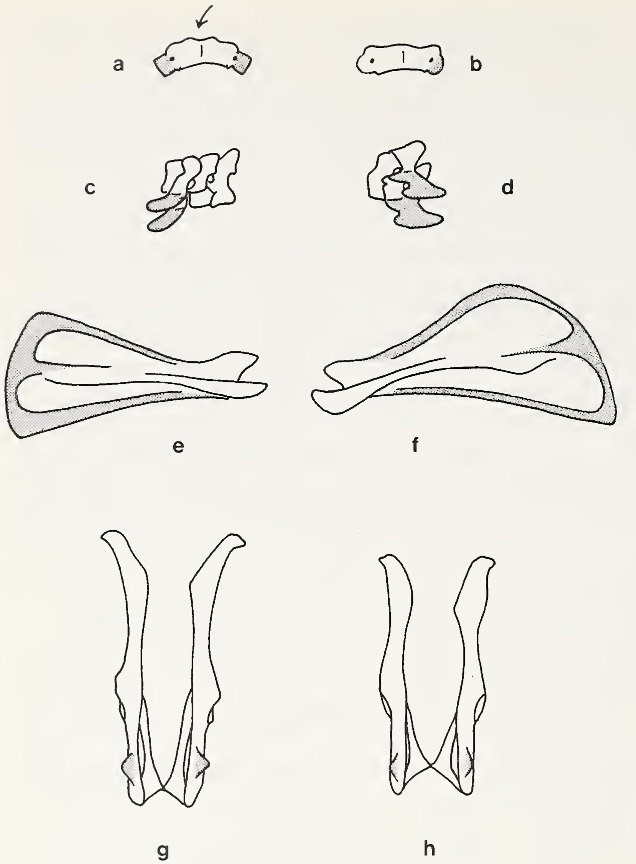

Fig. 3. Characters exhibiting an apomorphic condition in *Synaptomys.* a: transverse processes of atlas large and dorsal surface of atlas distinctly notched; c: carotid tubercle of 6th cervical vertebra smooth in outline and tapering distally; e: height of scapula small relative to overall length, with thickened borders, square in outline; g: ischial tuberosity of pubis large, flat and triangular in shape. Figures b, d, f and h show the corresponding plesiomorphic conditions

Discussion

Information gleaned from the literature pertaining to karyology, biochemistry, stomach, glandular and external morphology have been added to the myological and osteological characters which I observed in order to produce a phyologenetic hypothesis which I feel should closely approximate the evolutionary history of this subgroup of rodents (fig. 4, and table). Descriptions and/or figures of bacula for all groups except *Alticola* were found. However, sufficient controversy surrounds the nature of this structure as a reliable phylogenetic character within the family that I have not emphasized it greatly (Burt 1936; Hamilton 1946; Dearden 1958; Anderson 1960; Hooper and Hart 1962; Hooper and Musser 1964; Hershkovitz 1966; Morris 1972; Long and Frank 1968; Aimi 1980; Jameson 1961; Ognev 1950; Didier 1954). In addition, mammae number does not vary much among these taxa except within the genus *Eothenomys* (see below), and anatomy of the middle ear has been described only for some Nearctic genera (Hooper 1968).

In addition to four myological characters (table) (13–16) and eight osteological characters (20–27), *Clethrionomys, Eothenomys* and *Alticola* are united in possessing a bony palate terminating as a thin, transverse shelf and lacking a median bridge sloping dorsally to join the midpoint of the pterygoid fossa (Hinton 1926) (18). Moreover, all three genera possess an intermediate grade I glandular zone of the stomach (Carleton 1981) (19) and, compared with *Synaptomys,* all have a lower incisor that extends posteriorly in the jaw to a

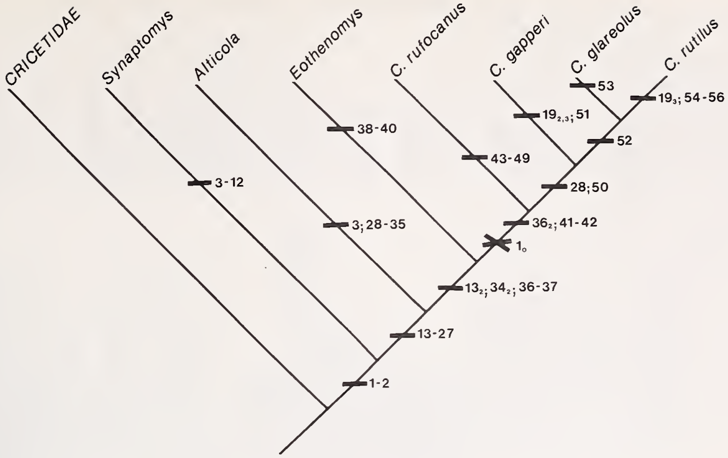

Fig. 4. Final cladogram. See table for a list of characters and their derived states

point distal and labial to m_3 (Ellerman 1940) (17). *Eothenomys* closely resembles *Clethrionomys* externally as well as in the shape of the skull (Ellerman 1940; Allen 1940; Jameson 1961), and one author even proposed the genus as a possible antecedent to *Clethrionomys* (Allen 1940). However, the two may be distinguished by the complete absence of rooted molars in *Eothenomys,* even in animals of very old age (Hinton 1926; Ellerman 1940), as opposed to their presence in *Clethrionomys* (1). *Alticola* is similar to *Clethrionomys* in most respects but differs in the presence of slender and elongate cheek teeth (Corbet 1978) (30) and a body form that is not modified externally for fossoriality (Ellerman 1940). Its close relationship to *Eothenomys* has been recognized by several authors (Ellerman and Morrison-Scott 1951; Allen 1940), one of whom postulated that it was a rock-dwelling version of this woodland vole (Allen 1940).

All members of the genus *Clethrionomys* possess a bright, rufous pelage (41), rooted molars (1), a large single, rather than double, opening at the base of the alisphenoid (Carleton 1985) (42) and an increase in size, but a decrease in number of Meibomian (= tarsal) glands compared to *Eothenomys* (Quay 1954) (36). Within this genus, however, *C. rufocanus* has differentiated morphologically, ecologically and biochemically (Ognev 1950; Graf 1982). The species is distinguished by its large body size (46) and by late rooting of its molars (Hinton 1926) (43). Ognev (1950) also noted that its ear ossicles differed appreciably (44) from those of other species in the genus and that its penis (47) was relatively long and narrow. The postorbital process of the skull is well developed in *rufocanus* (Miller 1900) (48) and the root of the third lower molar lies in a separate capsule lingual to the incisor root (Hinton 1926) (45). The distinctive nature of this species is supported further by its displaying lower allozymic affinities to *C. rutilus* and *C. glareolus* than these species share with one another and by its possession of two unique allozyme alleles and two minor hemoglobin (Hgb) bands, one of which is unique (Nadler et al. 1978) (49). Nadler et al. (1978) have hypothesized that *rufocanus* diverged from the *rutilus-gapperi* stock prior to 13,000 years ago, perhaps in response to the same Pleistocene events that led to the divergence of other mammalian groups such as the long-tailed ground squirrels. Because of its distinctive nature, *C. rufocanus* has been variously assigned to the genera *Craseomys* and *Aschizomys* but, most recently, it has been retained within the genus *Clethrionomys* (Aimi 1980).

The species *Clethrionomys gapperi, C. glareolus* and *C. rutilus* are considered to be closely related within the genus because each species has a bifid spine on the axis vertebra

Table

List of characters used to construct the cladogram in figure 4

Character	State	Source
1. Molar growth	0: rooted 1: rootless	Hinton 1926; Ellerman 1940
2. Molar configuration	0: cuspidate 1: prismatic	Hinton 1926
3. M. omocervicalis	0: metacromial insertion 1: acromial and metacrom. inser.	Stein 1986
4. M. abd. poll. long.	0: 3 pts. of insertion 1: 2 pts. of insertion	Stein 1986
5. Nail of pollex	0: rounded 1: wedge-shaped, bulbous	Stein 1986
6. M. femorococcygeus	0: insert. post. femur 1: insert. prim. at patella	Stein 1986
7. Atlas, trans. proc.	0: small 1: large and protrud. past facets	this paper
8. Atlas, middorsum	0: wide band 1: notched	this paper
9. Carotid tubercle	0: angular 1: curved smoothly	this paper
10. Scapula	0: wide, smooth outline 1: narrow, square outline	this paper
11. Ischial tuberosity	0: weakly developed 1: flat, triangular	this paper
12. Tibial flanges	0: large 1: reduced	this paper
13. M. biceps brachii	0: prim. radial insertion 1: 1/2 radial, 1/2 ulnar 2: prim. ulnar insertion	Stein 1986
14. M. occipitoscap.	0: scap. spine insertion 1: no insertion on spine	Stein 1986
15. M. caudofemoralis	0: prim. vertebral origin 1: origin from M. femorococc.	Stein 1986
16. M. rectus femoris	0: 2 heads distinct 1: 2 heads not distinct	Stein 1986
17. Lower incisor	0: extends to m3 lingually 1: extends past m3 labially	Ellerman 1940
18. Bony palate	0: w/ med. ridge, lat. pits 1: thin, trans. shelf post.	Hinton 1926
19. Stomach, gland. zone	0: hemiglandular 1: intermed. grade I 2: intermed. grade II 3: intermed. grade III	Carleton 1981
20. Atlas	0: vent. proc. tipped ant. 1: vent. proc. vertical	this paper
21. Clavicle	0: curved in 2 planes 1: relatively straight	this paper
22. Scapula, acromion	0: spatulate 1: hook-like	this paper
23. Humerus, delt. crest	0: hook-like 1: smooth in profile	this paper
24. Pubic ramus	0: notch absent 1: notch present	this paper
25. Femur, trochanters	0: sm. angle btw. head & lesser 1: sm. angle btw. head & great.	this paper
26. Femur, shaft	0: rel. broad 1: rel. narrow	this paper
27. Tib/fib fusion	0: less 1: rel. more extensive	Carleton 1980; this paper
28. Axis	0: spine flattened 1: spine bifid	this paper
29. M. flex. dig. brev.	0: no tendon to Digit V 1: tendon to Digit V	this paper
30. Molars	0: rel. broad 1: slender & elongate	Corbet 1978
31. Pollex	0: developed 1: rudimentary	Hinton 1926
32. Tail	0: short, one color 1: long, sharply bicolored	Roberts 1977; this paper
33. Malleus	0: laminal border complete 1: laminal border emarginate	Ognev 1950

34. Stomach, incis. ang.	0: shallow 1: intermed. depth 2: deep	Carleton 1981
35. Stomach, bord. fold	0: smooth 1: emarginate	Carleton 1981
36. Meibomian glands	0: small, numerous 1: inc. size, dec. number 2: further inc. size, dec. no.	Quay 1954
37. Glans penis	0: group I type 1: group II type	Hooper and Hart 1962
38. Mammae	0: 4–8 1: 4–6	Hooper and Hart 1962
39. 6th plantar pad	0: position rel. ant. 1: position rel. post.	Tokuda 1955; Imaizumi 1957
40. Squamosal crests	0: weakly developed 1: well developed	Ellerman 1940
41. Pelage color	0: grey or dullish 1: rufous	this paper
42. Alisphenoid	0: base w/ double opening 1: base w/ single opening	Carleton 1985
43. Molars	0: root early in life 1: root late in life	Hinton 1926
44. Auditory ossicles	0: malleus, sht, ant. proc. 1: malleus, lg, thin proc.	Ognev 1950
45. Lower m3	0: root labial to incisor rt. 1: root lingual to incisor rt.	Hinton 1926
46. Body size	0: relatively small 1: relatively large	Hinton 1926
47. Penis	0: rel. short, rounded base 1: long & narrow, base flat	Ognev 1950
48. Postorbital proc.	0: weakly developed 1: well developed	Miller 1900
49. Allozymes	0: none unique 1: 2 unique & 2 minor Hgb	Nadler et al. 1978
50. Chromosomes	0: no G-banding of 1 and 9 1: G-banding of 1 and 9	Gamperl 1982
51. Baculum	0: med. process w/o spine 1: lat. proc. w/o vanes	Hamilton 1946; Anderson 1960
52. Y-chromosomes	0: telocentric 1: metacentric	Borodkin and Khlyabova 1980
53. Humerus, gr. tuber.	0: normal size 1: rel. larger	Bates and Harrison 1980
54. Baculum	0: shaft ave. diameter 1: shaft part. slender	Ognev 1950
55. Humerus, head	0: normal size 1: rel. larger	this paper
56. Humerus, lat. cond.	0: outline smooth 1: outine squared	this paper

(28) and distinctive G-banding of chromosomes one and nine (Gamperl 1982) (50). Indeed, Ellerman and Morrison-Scott (1951) considered these species difficult to define because characters, and the species themselves, seemed to grade into one another when all forms were taken into consideration. *Clethrionomys gapperi* and *C. rutilus* are morphologically similar and chromosomally identical, their close taxonomic relationship being reflected in the large number of serum proteins they share in common (Canham and Cameron 1972). Bee and Hall (1956) even suggested that these two taxa were conspecific. Alternately, indistinguishable chromosome-banding patterns link *C. rutilus* from Eurasia to *C. glareolus* (Nadler et al. 1976) and the presence of a metacentric Y-chromosome (52) in these species is absent in all other members of the genus (Borodkin and Khlybora 1980; Rausch and Rausch 1975). However, reexamination of Eurasian populations of these genera has revealed intraspecific polymorphisms for this character at the subspecific level (Vorontsov et al. 1978), a factor that requires additional investigation. Hinton (1926) was unable to identify a single character which successfully distinguished all forms of *gapperi* from all forms of *glareolus*, leading him to designate *gapperi* as an additional subspecies of *glareolus*. Moreover, several studies have discussed the status of these genera as semispecies (Grant 1974) and as conspecific taxa (Matthey 1956; Corbet 1978). Examination of postcra-

nial myology and osteology among species of *Clethrionomys* was unable to resolve this controversy. As a result, I regard the proposed resolution of this trichotomy (fig. 4) as merely a tentative framework within which to test alternative hypotheses as additional characters become available.

Clethrionomys gapperi has several autapomorphic characters. The glandular zone of its stomach is characterized by an intermediate grade of I, II or III (CARLETON 1981) (19) whereas only grade I has been observed in two of the other three species. Its baculum is also distinctive (51) in that the lateral processes lack vanes whereas the median process shows a definitive spine (ANDERSON 1960; HAMILTON 1946).

Clethrionomys glareolus, regarded as a primitive member of the genus (HINTON 1926), exhibited only one autapomorphy among the characters examined. It may be diagnosed by the greater tuberosity of the humerus which seems relatively larger in this species (53) than in all others within the genus (BATES and HARRISON 1980). The distinction, however, is quite fine.

The Holarctic species *C. rutilus* has been considered a derivative of *C. glareolus* adapted to more northern habitats (HINTON 1926). However, it exhibits several autapomorphic traits. Only the fundic portion of its stomach is glandular (ORLOV 1968; VORONTSOV 1961), associated with an intermediate grade III type of stomach (CARLETON 1981) (19), and the distal end of its bacular shaft is particularly slender (OGNEV 1950) (54). I observed that the head of the humerus was relatively larger (55) than that of the other species within the genus and that the ridge along the distal end of the shaft of the humerus connecting to the lateral condyle was square in outline (56).

Crosses of *C. glareolus* and *C. rutilus* have been attempted in the laboratory. ZIMMERMANN (1965) found that the resulting offspring exhibited slight hybrid vigor with respect to litter size, birth weight and growth. However, crosses made by RAUSCHERT (1963) and SPANHOFF (1960) produced sterile offspring. GRANT (1974) concluded that this sterility resulted from the development of reproductive isolating mechanisms between these species in the absence of geographic isolation. His hypothesis was borne out by crosses of *C. gapperi* and *C. glareolus* (GRANT 1974) which produced fertile offspring. Accordingly, he concluded that geographic allopatry in these two species did not encourage the evolution of such mechanisms and he predicted that a state of contiguous allopatry would result in reproductive isolation between these species over time. Specific distinction between *gapperi* and *glareolus* also is supported by biochemical differences (JOHNSON 1968) although cytological evidence at first indicated that the two species might be conspecific (MATTHEY 1956).

Clethrionomys rex was recognized as a distinct species by IMAIZUMI (1971) based on its large size, small auditory bullae, the incomplete lateral bridges of the palatine and several dental characters. AIMI (1980) reexamined the same specimens employing IMAIZUMI's criteria and found extensive variation of these characters among individuals. This caused him to question the validity of *rex* as a distinct species and to designate it as a form of *rufocanus* that exhibits insular gigantism. Increase in body size among insular forms is a well-recognized phenomenon (HEANEY 1978; LAWLOR 1982) and one which has been documented in voles by several investigators who have noted variation in coat color and in dental patterns as well (STEVEN 1953; CORBET 1963, 1964; COUTTS and ROWLANDS 1969). I observed no character differences in *rex* that would warrant giving it specific status. Because no skeletal material of *C. sikotanensis* was available to me and because no myological differences were observed among species of *Clethrionomys,* I am unable to discuss the placement of this taxa in the present analysis.

Members of the genus *Eothenomys* are grey and dullish in color and inhabit montane regions of northern Thailand, China, Korea and the islands of Japan and Taiwan. *Eothenomys* closely resembles *Clethrionomys* but is distinguished by the presence of rootless molars throughout its life (HINTON 1926; ALLEN 1940; ELLERMAN 1940) (1).

However, the two are united as sister taxa by several synapomorphies. In both genera, M. biceps brachii has an insertion that is primarily ulnar (13) in contrast to the condition noted for *Alticola* wherein the insertion is half radial, half ulnar and that recorded for *Synaptomys* and four genera of cricetine rodents in which the insertion is fully radial (Stein 1986). The incisura angularis of the stomach is deep (34) in both *Clethrionomys* and *Eothenomys* (Carleton 1981) and the glans penis in these taxa belongs to the group 2 type (Hooper and Hart 1962) (37). *Clethrionomys* and *Eothenomys* also exhibit a further increase in size and decrease in number of Meibomian glands relative to the other genera examined (Quay 1954) (36). *Eothenomys* itself has well-developed squamosal crests on the skull (Ellerman 1940) (40) and the position of the sixth plantar pad on the pes is posterior relative to its condition in *Clethrionomys* (Imaizumi 1957; Tokuda 1955) (39).

The allocation of species within this genus has been the subject of continuing controversy among investigators (Tokuda 1955; Imaizumi 1957, 1960; Jameson 1961; Miyao et al. 1964; Miyao 1967; Aimi 1967, 1980; Tanaka 1971) and has centered often on the number of mammae present within each taxon. Most species of *Eothenomys* possess four to six mammae (38), a decrease in number from the primitive arvicolid condition in which eight mammae are present (Hooper and Hart 1962); only *E. andersoni* possesses the primitive number.

Several authors have shown that number of mammae may vary both intra- and interspecifically within a genus. Miyao (1967) reported that mammae counts in *E. smithi* and in *E. kageus* exhibited clinal variation, such that the number of glands decreased in more southern populations. He also noted that the hind-foot length and tail length exhibited a similar trend. Niethammer (1972) observed that a reduction in the number of mammae in arvicolids was always correlated with small litter sizes and occurred near the southern edge of the animals' distribution. Because similar variation in mammae number within a genus has been documented for other rodents as well (Hill 1937; Avry 1974), I believe that it constitutes a poor diagnostic character at the specific level. Therefore, until more conclusive evidence is available, I recognize *kageus* as a synonym of *E. smithi* and *imaizumi* as a synonym of *E. andersoni* (Aimi 1980).

Alticola roylei, although not remarkably different from *Eothenomys* (Ellerman 1940), is autapomorphic for a number of traits. Myologically, there is a tendon from the belly of M. flexor digitorum brevis on the sole of the foot to the ring tendon on Digit V (Stein 1986) (29). It also exhibits the derived state for M. omocervicalis (3), a condition observed in *Synaptomys* as well. Osteologically, the axis spine is bifid (28), a condition present in three species of *Clethrionomys.* Although not enough is currently known about the ecology of these voles to appraise this variation accurately, I hypothesize possible differences in muscle attachment at this site from those voles possessing a flattened spine. In *Alticola* the nature of the axis may relate to its habitation of talus slopes where it primarily utilizes rock crevices for shelter rather than burrowing in soils as do the other taxa.

Externally, *Alticola* differs from *Clethrionomys* and *Eothenomys* in that it is not specialized for fossoriality (Ellerman 1940). Its pollex is rudimentary and may or may not support a nail (Hinton 1926) (31). Its tail is long and varies from sharply bicolored to all white (Roberts 1977; pers. obs.) (32). This contrasts with the tails of species in the other genera examined, all of which are relatively short and some of which are only weakly bicolored. The molars of *Alticola* are slender and elongate relative to those of the other genera examined (Corbet 1978) (30). Although no description was given, illustrations of ear ossicles (Ognev 1950) indicate that the inferior laminal border of the malleus is emarginate (33) in *Alticola* as compared with *Clethrionomys* and *Eothenomys.* The incisura angularis of its stomach is intermediate in type (34) and the bordering fold of its stomach is emarginate (Carleton 1981) (35).

In figure 4 I have summarized the relationships among these voles based on the characters discussed above. The only reversal on this tree is a dental character (1). I believe that the presence of rootless molars is a derived character state which is known to have evolved independently in other rodent lineages such as the Geomyidae. Moreover, its placement at the base of the tree and its reversal in the genus *Clethrionomys* is the most parsimonious allocation of the characters among these taxa. Independent derivation of rootless molars in *Synaptomys, Alticola* and in *Eothenomys* would require a greater number of steps. Alternately, to unite these taxa on the basis of rootless molars derived from the primitive molars in *Clethrionomys* would be the least parsimonious decision owing to the large number of characters which support this phylogeny.

The evolution of rooted molars which this character reversal requires is easily interpreted if heterochrony is hypothesized. Change in the relative time of appearance of a structure is exactly what occurs in *Clethrionomys rufocanus.* In this species rooting occurs so late in life that at the time of death many individuals still exhibit rootless molars (HINTON 1926). Because *C. rufocanus* is believed to be the most primitive member of the genus, this condition may represent an intermediate evolutionary stage between *Eothenomys, Alticola* and *Synaptomys* which exhibit rootless molars throughout life, and the more advanced *Clethrionomys* species which have evolved fully rooted molars in adult members.

Two other characters examined are homoplastic. M. omocervicalis possesses an insertion that is apomorphic in both *Alticola* and in *Synaptomys* whereas the bifid shape of the axis spine represents the derived state of this character in *Alticola* and in three species of *Clethrionomys.* However, additional studies that might elucidate functional benefits accrued by such variations or the examination of additional taxa within this family would be useful in confirming the hypothesis proposed herein that these conditions have evolved independently in several lineages.

Conclusion

Postcranial myological and osteological characters have provided valuable data for use in constructing a phylogenetic classification in a subgroup of arvicolid rodents, *Clethrionomys, Eothenomys* and *Alticola.* These data were combined with other types of morphological characters to produce a phylogeny that supports a close evolutionary relationship among these taxa.

This study, while contributing to a better understanding of the relationships among some members of the Arvicolidae, highlights the need for more extensive studies which would incorporate many more taxa within the family. In particular, an examination of other members of the Lemmini might offer insight into the appropriateness of use of *Synaptomys* as a generalized member of this tribe given the large number of apomorphic characters that I observed in that genus. This study also underscores the need for detailed ecological studies of these voles so that differences in myology and osteology may be understood more clearly within the context of ecology and function.

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Zusammenfassung

Phylogenetische Beziehungen zwischen vier Arvicoliden-Gattungen

Muskeln und Skelett von Rumpf und Extremitäten von den Arvicoliden-Gattungen *Clethrionomys, Eothenomys, Alticola* und *Synaptomys* wurden verglichen. Diese und andere Merkmale wurden dazu benutzt, die phylogenetischen Beziehungen der Gattungen zu erörtern. Enger verwandt sind *Clethrionomys, Eothenomys* und *Alticola,* und hier stehen sich wiederum *Clethrionomys* und *Eothenomys* besonders nahe. Das Aufzweigungsschema ergab sich allein schon aus einer Reihe von Autapomorphien und Apomorphien für mehrere Gattungen aus Muskel- und Skelettmerkmalen. Schließlich weisen diese Merkmale auch auf die Sonderstellung von *Clethrionomys rufocanus* in ihrer Gattung hin. Die bewurzelten Molaren bei *Clethrionomys* müssen nach dem Prinzip der Sparsamkeit als apomorph angesehen werden. Entgegen der allgemeinen Tendenz bei den Arvicoliden, von bewurzelten zu wurzellosen Backenzähnen fortzuschreiten, handelt es sich hier also um eine Umkehr der Evolutionsrichtung.

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Author's address: Dr. Barbara Stein, University of California, Museum of Vertebrate Zoology,
2593 Life Sciences Building, Berkeley, CA 94720, U.S.A.

The hystricomorphy of the Bathyergidae, as determined from ontogenetic evidence

By W. Maier and F. Schrenk

Zentrum der Morphologie, Dr. Senckenbergische Anatomie, Frankfurt/Main

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Abstract

Two younger fetuses of *Bathyergus janetta* and *Georychus capensis* showed small bundels of the anterior zygomatico-mandibular muscle penetrating the infraorbital canal. This infraorbital muscle is missing in adult bathyergids with the exception of *Cryptomys hottentotus*. It is an old and as yet unsettled question whether the bathyergids are primarily 'protrogomorphous' or 'hystricomorphous' rodents. The transitory embryonic relics of infraorbital muscles described in this study seem to favour the latter opinion. Our results support the position that the Bathyergidae should be grouped together with the other hystricognathous and hystricomorphous rodents.

Introduction

The relationship of African 'hystricomorphous' rodents is one of the major open questions of the phylogenetic systematics of rodents (Luckett and Hartenberger 1985). Within this context the status of the Bathyergidae (mole-rats) is of considerable relevance. With the exception of *Cryptomys*, all genera of this family show relatively small infraorbital foramina which are not penetrated by a portion of the anterior zygomatico-mandibular (or anterior medial masseter) muscle; there is an old and as yet unsettled debate whether this 'protrogomorphy' is a primitive or derived character state. Tullberg (1899), Ellerman (1940), Morlok (1983) and Wood (1985) adhere to the position that the Bathyergidae primarily possess a small infraorbital foramen, and that *Cryptomys* is showing a secondary specialization; according to Wood (1985) *Cryptomys* demonstrates the evolutionary development of 'hystricomorphy' in statu nascendi and "may currently be about to do the same thing" as did the Miocene *Bathyergoides* and many other rodents in parallel. The

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