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Taxonomy and distributional records of Oriental and European *Apodemus*, with a review of the *Apodemus-Sylvaemus* problem

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Abstract. Specimens of Oriental *Apodemus agrarius*, *A. chevrieri*, *A. latronum*, *A. draco*, *A. semotus*, *A. gurkha*, *A. peninsulae*, *A. speciosus*, and *A. argenteus* that are stored in four natural history museums are documented. Relevant taxonomic and distributional discussion is provided for each species account. Also recorded are series of *A. alpicola* housed in the American Museum of Natural History and the Field Museum of Natural History. Some of the biochemical and morphological data is evaluated that has been used to support elevating subgenus *Sylvaemus* to generic rank. We conclude that the species within the genus *Apodemus* can be separated into three groups rather than two: ***Apodemus* Group** (*A. agrarius*, *A. chevrieri*, *A. speciosus*, *A. peninsulae*, *A. latronum*, *A. draco*, *A. semotus*, *A. gurkha*); ***Sylvaemus* Group** (*A. sylvaticus*, *A. flavicollis*, *A. uralensis*, *A. mystacinus*, *A. fulvipectus*, *A. hermonensis*, *A. alpicola*, *A. arianus*, *A. hyranicus*, *A. ponticus*, *A. rusiges*, *A. wardi*); and ***Argenteus* Group** (*A. argenteus*). We further admonish that careful systematic revision of all the species, using biochemical and morphological data in which polarities are determined, is required to test the alternate hypotheses of whether *Apodemus* is monophyletic or polyphyletic.

Key words. Mammalia, Rodentia, Muridae, *Apodemus*, *Sylvaemus*, systematics, eastern Asia.

Introduction

In 1972, Martens & Niethammer reported on samples of two species of *Apodemus* they had collected in Nepal. One they identified as *A. sylvaticus wardi*, a form having phylogenetic affinities with species of the subgenus *Sylvaemus* that are found from central Asia to Europe, and in North Africa. *Apodemus gurkha*, the other species recognized, is allied to a group centered in eastern Asia, defined by Zimmermann (1962) as the subgenus *Alsomys*. A map of collecting localities and the few places of sympatry, careful morphological comparisons between samples of the two kinds, records of the material studied, and a discussion of the Oriental species of *Apodemus* and *A. gurkha*'s relationship to them constituted the core of their paper. Martens' and Niethammer's contribution was the first to carefully document the morphological and geographic delimitation of an eastern Asian species of *Apodemus* in a comparative context and to indicate the samples upon which their results were based. It remains the exception.

This fine publication was followed by Gemmeke & Niethammer's (1982), study of karyotypes of the two Nepalese species, along with results of electrophoretic analyses of proteins from samples of Nepalese *A. sylvaticus* and European *Apodemus*. One of their conclusions, that the samples of "*sylvaticus*" from Nepal probably

represented a different species than the European *A. sylvaticus*, but one related to it, provided new and significant insights into the phylogenetic relationships of Asian *Sylvaemus*.

Unfortunately, no general systematic revision of other Oriental species of *Apodemus* is available. Ellerman (1949, 1961), whose checklists relied upon collections in the British Museum, obscured the pattern of species-diversity in eastern Asia by trying to force most Asian species into subspecies of the European *A. sylvaticus* and *A. flavicollis*. Zimmermann (1962) refuted this view and correctly pointed out that none of the Oriental samples were part of the European species, but his study was not revisionary. The taxonomic reviews of *Apodemus* by Corbet (1978) and Corbet & Hill (1992), and the checklist by Musser & Carleton (1993), relied on museum collections, but the accounts are synoptic and undocumented by data analyses or specimens.

The American Museum of Natural History, Field Museum of Natural History, and National Museum of Natural History house large samples of *Apodemus* collected from eastern Asia, mostly China and Korea. Except for the Korean series at the National Museum reported by Jones & Johnson (1965), and a small portion of the Chinese material at the American Museum discussed by Allen (1940), the bulk of the collections were never recorded in the literature or even identified in the museums beyond "*Apodemus*," in spite of their accessibility to researchers since the 1930s, the era in which most Chinese specimens were obtained. The collections constitute a significant source of data for use in any systematic revision of *Apodemus*, particularly the eastern Asian species. Because catalogued specimens in institutional collections are a primary source of data for systematic studies that focus on delimiting boundaries of species and reconstructing evolutionary relationships, we use this opportunity to record our identifications (documented by collecting locality and museum catalog number) of the material in the three museums, as well as the Museum Alexander Koenig.

Our identifications involved several steps and actually began more than ten years ago when Musser curated, at a coarse level, the collection at the American Museum. For this report we first sorted the specimens into what we could discern as different morphological entities. We checked our results against Corbet's (1978: 133) excellent key as a starting point in identifying the correct scientific name to use for each group, and tested our conclusions against the comparative information provided by Corbet & Hill (1992) for Oriental *Apodemus*. The literature containing original descriptions of taxa was also consulted, and some holotypes were examined.

Our report consists of three parts. Identifications of Oriental samples form the first segment. The second is a record of specimens identified as *Apodemus alpicola* that are stored in United States museums and the Museum Alexander Koenig; we explain our reasons for this action in that account. Finally, we evaluate the evidence and review the merit of raising the subgenus *Sylvaemus* to generic rank, a usage already employed by some researchers. During the last few years, published results documenting genetic variation in *Apodemus* have revitalized an earlier assertion based on morphology that suggested *Apodemus* really consists of two monophyletic groups, or distinct genera, with separate evolutionary histories. Our results counter this interpretation. We can recognize three primary groups of species, not just two,

and recommend that all three be retained in the one genus *Apodemus* pending systematic revision of the entire complex within a framework of phylogenetic analyses.

We dedicate our contribution on *Apodemus* to Jochen Niethammer. His careful and thoughtful systematic studies have significantly enhanced our understanding of species-diversity within *Apodemus* and Asian mammals in general. His research efforts will be missed.

Museums, methods, maps, and gazetteers

Specimens: We identified and record here 4296 specimens of Oriental *Apodemus* and 90 European *Apodemus*. Several hundred additional examples of European species were used for character-state surveys but not recorded. All these specimens are stored in the American Museum of Natural History, New York City (AMNH); the Field Museum of Natural History, Chicago (FMNH); the National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM); and the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). We also examined a small sample, including holotypes, from the British Museum (Natural History), London (BMNH). The majority of the specimens had been prepared as conventional study skins with accompanying skulls, some were in the form of a skin only or skull only, and a few were preserved in fluid.

Measurements and Cusp and Root Surveys: Only measurements (recorded in millimeters) of three dimensions were used in analyses: length of head and body (derived by subtracting length of tail from total length [taken from skin tags]), length of tail (taken from skin tags), and crown length of maxillary molar row (CLM1-3; measured from the face of the first molar, excluding the anterior root, to the enamel back of the third molar) using dial callipers beneath a dissecting microscope. Molar occlusal patterns and lingual roots beneath first upper molars were also surveyed using a microscope.

We relied upon CLM1-3 as an index of body size to help discriminate between samples of *Apodemus agrarius* and *A. chevrieri*, and between series of *A. latronum* and *A. draco*. Shape and proportional contrasts may also exist between samples of these two sets of species but we could not quantitatively test any differences by univariate or multivariate analyses because the largest collections of all four are in the American Museum and the skulls are fragmentary (the result of improper preparation that was usual at the time the samples were received at the museum) and intractable for obtaining complete sets of measurements.

Maps and Gazetteers: We do not provide distribution maps here, but we did attempt to locate collecting places on maps and determine coordinates. Most of the specimens are from China and we relied on The Times Atlas of China (Geelan & Twitchett 1974), Atlas of the People's Republic of China (Sun 1989), two maps published by the National Geographic Society (1945, 1991), and a War Office map (1926). Maps published in expeditionary accounts were also consulted (Andrews 1932, for example). Unless indicated otherwise in the lists of localities and specimens, coordinates were taken from the United States Board on Geographic Names (abbreviated in the text as USBGN) for China (1990). A few were found in a computer generated gazetteer of Chinese collecting localities based upon specimens in the Field Museum of Natural History that was compiled by Julian Kerbis Peterhans and others. The printout was sent to us in late March, 1995; we reference it in the text as "Kerbis Peterhans 1995." We also consulted gazetteers in faunal accounts (Traylor 1967, for example), and estimated some coordinates directly from maps.

Collecting sites in other countries were identified on National Geographic Society maps (1960, 1991) and maps included as parts of published faunal surveys (Anthony 1941, for example). Coordinates were found in USBGN gazetteers for Japan (1955), North Korea (1963), South Korea (1965), and Burma (1966), and the Korean gazetteer in Jones & Johnson (1965).

The Times Atlas of the World, 9th Edition (Geelan & Lewis 1992) and archival material stored in the Department of Mammalogy at the American Museum of Natural History were important sources we frequently consulted.

In the lists of Localities and Specimens Examined, we first indicate the locality name that is currently used, and place the older usage — usually the name written on the skin tag — in parentheses. Most of our spellings for names of Chinese places conform to the Pinyin system: “Pinyin spellings are the official roman spellings used by the People’s Republic of China” (USBGN for China 1990: x).

Oriental *Apodemus*

Pertinent discussion covering taxonomy and geographic distributions, as well as lists of localities and specimens examined (each referenced by museum acronym and catalog number) that were collected at those places, are provided for the nine Far East species we have identified: *A. agrarius*, *A. chevrieri*, *A. latronum*, *A. draco*, *A. semotus*, *A. peninsulae*, *A. gorkha*, *A. speciosus*, and *A. argenteus*.

Apodemus agrarius

Remarks: The type species of the genus (Musser & Carleton 1993:569), *A. agrarius*, is easily recognized by its chunky body, brown dorsum broken by a narrow blackish or brown middorsal stripe, short tail relative to length of head and body, elongate skull with prominent supraorbital ridges and wide zygomatic plate (fig. 3), first upper molars anchored by four roots, second upper molars usually without cusp t3, and third molars reduced in size relative to others in the toothrow (fig. 4B-D). The species has been the subject of many reports focusing on geographic variation and its significance, age and sex variation, chromosomal and biochemical characteristics, and ecology. Pertinent to the Oriental populations are the taxonomic, chromosomal and morphometric studies of Korean samples by Jones & Johnson (1965), Kang & Koh (1976), Koh (1982, 1983, 1988, 1991), and reports on Chinese populations by Wang (1985), Zhao & Lu (1986), Liu et al. (1991), and Wang et al. (1993). Studies of the species in other parts of its geographic range are referenced by Musser & Carleton (1993).

The diagnostic middorsal stripe, so distinctive on mice in most samples, does vary in intensity of expression. Corbet and Hill (1992) mentioned that samples of *A. agrarius* from the southern portions of China had faint stripes while those from the north had the characteristic prominent stripe. Our specimens mirror those observations. The stripe is barely evident on our few specimens from Fujian Province. In 21 specimens from Hubin College, Hunan Province, the range of variation in pattern extends from blackish brown stripes, through brown to a pattern in which the upperparts are uniformly brownish buff broken only by a faint darkening along the mid-dorsal region.

Localities and specimens examined:

CHINA:

Heilongjiang (=North Manchuria) **Province:** **Yimianpo** (=Imienpo) district, near **Kazanseve Station of China Eastern Railway**, AMNH 80951; **Yimianpo** (=Imienpo, 45°03'N/128°04'E), USNM 199656–199661; near **Yimianpo**, USNM 201272–201277, 201279; **Songhua Jiang** (=Sungari River), FMNH 43417–43420; **N bank Songhua Jiang, 120 mi NE Yilan** (=San-si[ng], 46°19'N/129°34'E), USNM 201267–201271, 201278; **Xiaoling** (=Hsiaoling, 45°22'N/127°17'E), FMNH 45038.

Jilin Province: **20 mi SSE Chaoyang** (=Chao-yang-chen, 42°40'N/126°00'E), USNM 197795; **35 mi SSE Chaoyang**, USNM 197796; **Songhua Jiang, 60 mi SW Jilin** (43°53'N/126°35'E), USNM 197798–197803, 197805–197810, 197812, 197815, 197816, 197818; **180 mi up Yalu River**, USNM 199654.

Nei Mongol Autonomous Region: Da Hinggan Ling (Greater Khingan Mountains), **Yalu** (48°33'N/122°07'E), FMNH 44760; **Da Hinggan Ling, Yalu Station** (48°06'N/122°15'E; Kerbis Peterhans, 1995), FMNH 49911, 49912.

Hebei (=Chihli) Province: Eastern Tombs (=Tung Ling, 40°12'N/117°35'E), **80 mi NE Beijing** (=Peking), AMNH 56214, 56215, 56217 (Pope, 1932: 470–471, indicated that “Eastern Tombs” is more distant from Beijing but in the same general direction as “Hsinglungshan”, which is northeast of Peking as indicated on the map at the back of Andrews (1932) report on the American Museum Central Asiatic expeditions.); **Wuling Shan** (40°47'N/117°30'E), **75 mi N Beijing**, USNM 219238, 219239, 219241; **Hsin-lung-hsien** (=Xinglong Xian, 40°28'N/117°28'E), **65 mi NE Beijing**, USNM 219240, 219242.

Shandong Province: Changqing (=Chang Quing, 36°34'N/116°43'E), FMNH 128592, 128597; **Ming-shui** (=Ming Shui, 36°43'N/117°30'E), FMNH 128594, 128595, 128598–128601; **Chang Gin**, FMNH 128602, 128603; **Tao Shan** (this might be the same as T'ai Shan, 36°30'N/117°20'E), FMNH 128604; “**Shandong**” (no other information), FMNH 128593, 128596.

Jiangsu Province: Chang Jiang Valley, Zhenjiang (=Chinkiang, 32°13'N/119°26'E), USNM 218170, 219270; **near Nanjing** (=Nanking, 32°03'N/118°47'E), FMNH 28950, USNM 219266–219269, 219271. **Tianjin Municipality: near Tianjin** (=Tientsin, 39°08'N/117°12'E), USNM 219236, 219237.

Shaanxi (=Shensi) Province: Qin Ling Shandi (=Tsing Ling Mountains), **base of Taibai Shan** (=Tai Pai Shan, 33°57'N/107°45'E), 4600 ft, AMNH 56218, 56220–56232, 56235–56237, 56239, 56242–56253, 56255–56261, 56263, 56264, 56267, 56268, 56270–56281, 56284–56297, 59777, FMNH 32778, 32780, 32782–32784, 32786–32789; **45 mi S Fengxiang** (=Fengsiangfu, 34°32'N/107°23'E), 3600 ft, AMNH 32283–32290, FMNH 18929, 18930; **Yan'an Shi** (=Yenan-fu/[J]shih, 36°36'N/109°28'E), USNM 155065, 155066; **Liucun** (=Liu-tsuen=Liu-ts'un, 34°31'N/108°44'E), **15 mi S Xi'an** (=Sianfu, 34°16'N/108°54'E), USNM 155115–155118.

Gansu (=Kansu) Province: Jiuquan (=Tsu Chow, previously Suzhou or Suchow, 39°46'N/98°34'E), AMNH 84260, 84307; **Archuen**, AMNH 84248–84250, 84252–84256; **Maqu Xian** (=Ma Chu, 34°05'N/101°45'E), AMNH 84259 (“Ma Chu” is the only locality information on the field tag; Allen [1940:960] listed “Machu” as being in Kansu Province); **Mountains 30 mi SW Maqu Xian**, AMNH 84257, 84258.

Sichuan Province: Garzê (=Kanze, 31°38'N/100°01'E), AMNH 113587–113589; **Dawu Xian** (=Tao Fu Shien, 31°00'N/101°09'E), AMNH 113582–113586; **Yen-ching-kou**, **20 mi S Wanxian** (=Wanhhsien, 30°49'N/108°24'E), AMNH 56096–56118, 56120, 56122–56129, 56132–56136, 56139–56150, 56153–56184, 56186, 56187, 56189–56192, 56420, 59856–59861, 59863, 59864, 59866, 59867, 59869–59871, 59873–59890, 59892; **Yibin** (=Suifu, 28°46'N/104°34'E), USNM 241146, 241147, 252893, 253334–253337; **S of Yibin, Tseo-jia-keo/Yunnan border**, USNM 252891, 253771, 253772; **Chung Chiang Miao**, 29°03'N/103°23'E; Traylor 1967), **30 mi W Minjian** (=Mapienting, 28°48'N/103°39'E), FMNH 40908 (Most samples of *A. agrarius* and the other Oriental species listed in this report that are in the Field Museum were obtained by F. T. Smith during 1931 and 1932. Traylor (1967) provided a gazetteer of Smith's collecting localities in western China as well as a map and general description of the region in which he worked.); **Lu Erh Cheh**, FMNH 40906, 40907; **Lung Min Chiao** (“not found, 'near Chungking (Smith)”, Traylor 1967: 8; Chongqing [=Chungking] is at 29°34'N/106°35'E), FMNH 37360–37366; **Tao Kuo**, FMNH 37337–37347; **Tu Kan** (29°20'N/107°55'E; Traylor 1967), **on Wu Jiang** (=Wu River), FMNH 40910; **Fu Pa** (28°45'N/106°45'E; Traylor 1967), FMNH 37334, 37335; **Pu Hoo** (28°55'N/106°55'E; Traylor 1967), **65 mi SE Chongqing**, FMNH 37336; **Chen Chia Chang** (29°06'N/107°07'E; Kerbis Peterhans, 1995), FMNH 37348–37359; **7 mi S Kao Ku**, FMNH 40911–40914; **Kao Ku** (29°30'N/108°06'E; Kerbis Peterhans, 1995), **Wu Jiang** (=Wu River), FMNH 40909; **Ta Chi Ho** (29°39'N/107°30'E; Kerbis Peterhans, 1995), **Wu Jiang** (=Wu River), FMNH 40904; **Yang Ko Chih** (29°23'N/107°48'E; Kerbis Peterhans, 1995), **Wu Jiang**, FMNH 40905; **Chin Chuan Shan**, 29°40'N/103°06'E (Kerbis Peterhans, 1995), FMNH 45279–45317; **Hei Ngai Ping** (30°00'N/103°33'E; Kerbis Peterhans, 1995), **E Ya'an** (=Yachow, 29°59'N/103°05'E), FMNH 45318–45337; **Wanxian** (=Wan Hsien, 30°49'N/108°24'E), **Chang Jiang** (=Yangtze River), FMNH 32790–32796; **Guan Xian** (=Kuan Hsien, 31°00'N/103°37'E), **Upper Min Jiang** (=Min River), FMNH 40901; **Shan Tai Su** (28°46'N/104°42'E; Kerbis Peterhans, 1995), **7 mi E Yibin** (=Ipin=Suifu, 28°46'N/104°34'E), FMNH 40902, 40903.

Anhui Province: Chang Jiang (=Yangtze) **Valley, near Dangtu** (=Tai-ping-fu, 31°34'N/118°29'E), USNM 219272–219274.

Shanghai Province: Shanghai (31°06'N/121°22'E), USNM 239750.

Hubei (=Hupeh) Province: Yichang Xian (=Ichang Hsien, 30°48'N/111°20'E), AMNH 36886, 36887.

Hunan Province: Yueyang (=Yochow), Hubin (=Huping, 29°19'N/113°06'E) College, AMNH 56193, 56194, 56196, 56198, 56200, 56202–56208, 56210, 56212, 56213, 56476–56479, 56481, 56768; Yueyang (=Yochow, 29°23'N/113°06'E), FMNH 32762–32767; USNM 239540–239542, 239549–239553, 239555–239558, 239578, 239579, 239581–239583; **Chun San Island**, USNM 239536, 239543–239548; **Changshow Kai**, Hunan-Jiangxi border ("Changshow Kai" is probably Ch'ang-shou-chieh [=Chang-shoujie], 28°43'N/113°58'E), USNM 240205, 240206.

Guizhou Province: Shimenkan (=Shih men k'an, 28°41'N/106°48'E), USNM 259197; Guiyang (=Kweiyang, 26°35'N/106°43'E), USNM 279297–279299, 282626.

Fujian (=Fukien) Province: Chong'an Xian (=Chungan Hsien, 27°46'N/118°01'E), AMNH 84774; Shaowu (27°21'N/117°27'E), ZFMK 50.452, 50.455, 50.460.

Taiwan Province: USNM 283763, 283764, 330234; **T'aipei** (25°05'N/121°32'E), USNM 238146, 238147, 261049; **Waterworks**, USNM 283738, 283739; **5 mi NE Taichong** (=Taichung, 24°09'N/120°40'E), USNM 294208–294211; **Ho-ping [Xian?]**, **Taichong** (=Tai-chong), USNM 330235; **T'aipei Xian**, **Ali-lao** (25°17'N/121°36'E), USNM 330236–330241, 332980–332982; **T'aipei Xian**, **Ling kau**, USNM 358369. **NORTH KOREA:**

North Hamgyong Province: Tumen river valley, Musan (42°12'N/129°15'E), AMNH 34087, 34089, 34091, 34092; Hozando, AMNH 34094–34097, 34099–34101; Daichi-bei (also "Daichchei"), AMNH 34082. (R. C. Andrews, the collector, wrote that "these three localities are practically the same, being only a few miles apart and all in the Tumen river valley with no physical barriers separating them" [correspondence files in AMNH Department of Mammalogy].)

Hyesan Province: P'ot'ae-nodongjagu (=Potaidon, 41°43'N/128°20'E; USBGN Korea, 1963; Jones & Johnson 1965: 403, give approximate coordinates of 41°43'N/128°22'E for "Potai-dong"), AMNH 34084, 34086 (R. C. Andrews, the collector, referred to this locality as a village in a tributary valley of the Yalu River [correspondence files in AMNH Department of Mammalogy]); **Pochong**, AMNH 34104 (R. C. Andrews mentioned that Pochong is about 25 miles from Potaidon in a connecting river valley [correspondence files in the Department of Mammalogy]. Jones & Johnson 1965: 403, could not exactly locate Pochong, but gave approximate coordinates at 41°31'N/128°18'E.).

Chagang Province: Chonggang-up (=Chungkang-chin, 41°46'N/126°52'E), AMNH 34105.

North Korea: (Province not determinable), 150 mi up Yalu River, USNM 199655.

"Korea": (Province not located), **Kuksa-bong** (Jones & Johnson 1965: 402, commented about this locality: "not exactly located, but probably the mountain by that name at 38°05'N 126°37'E." These coordinates place the locality in North Korea.), USNM 298158, 198159.

SOUTH KOREA:

North Ch'ungch'ong Province: 7 mi W Ch'ungju, 36°58'N/127°56'E), 100 m: USNM 299546–299550; 4 mi W Ch'ungju, 100 m, USNM 298984.

South Kyongsang Province: Ulsan (35°32'N/129°21'E), AMNH 34106, 34107; **Pusan area** (35°08'N/129°04'E), USNM 298164–298167; 5 mi ENE Pusan, 2 m, USNM 299187–299202.

Kyonggi Province: Unsan-ni (38°04'N/127°13'E), 100 m: USNM 299532, 299533; **Ori-dong** (38°03'N/126°58'E), USNM 298131–298138; **Soul-t'ukpyolsi**, **Soul** (=Seoul, 37°30'N/127°00'E), AMNH 170103, 170104, FMNH 91365–91369, 90420–90427; **Soul-t'ukpyolsi**, 10 mi NE Soul, USNM 283675; **Soul-t'ukpyolsi**, 6 mi E Soul, USNM 299534–299545, 299555–299558, 299584; 5 mi E Soul, USNM 298975, 298976; **Soul-t'ukpyolsi**, NE Soul, **Mosug-ri Station**, USNM 283639, 283640; **Soul-t'ukpyolsi**, **Soul**, **King's Palace**, USNM 298149–298152; **Soul**, **CS-2360**, USNM 299603–299611; **Chang-ni** (37°31'N/126°49'E), USNM 298130; **Nam San** (37°33'N/126°59'E), USNM 283638; **Central National Forest**, 15–18 mi NE Seoul, USNM 298153–298157; **Central National Forest**, near **Pup'yong-ni** (37°44'N/127°12'E), 100–200 m, USNM 299110, 299111, 299527, 299529, 299551, 299552; **Yonch'on** (38°06'N/127°04'E), USNM 294676–294678, 294680, 298141–298145; 4 mi S **Yonch'on**, USNM 294679, 294699; 5 mi SSE **Yonch'on**, USNM 294692; 2 mi E **Songdong-ni** (38°01'N/127°16'E), 95 m, USNM 299108, 299109; **Munsan-ni** (37°51'N/126°47'E), 50 ft, USNM 300449–300451; 2 mi S **Suwon** (37°16'N/127°01'E), 27 m, USNM 299114–299127, 299629; 1/2 mi N **T'ongjin** (37°43'N/126°33'E), USNM 298993, 298994; 3 mi S **Osan** (37°09'N/127°04'E), 17 m, USNM 299128–299142; **Songu-ri** (37°50'N/127°09'E), USNM 294681–294683, 298160–298162; **Toktun-ni** (37°58'N/127°07'E), USNM 294693, 298163; **Chongong-ni** (Jones & Johnson 1965, spell the name as "Ch'onsong-ni" in the text [p. 385] and "Chon'gong-ni" in their gazetteer [p. 402]; coordinates they provide are 38°01'N/127°04'E, which are the same given by USBGN Korea, 1963, for Chongong-ni.), USNM 294687–294691, 298116–298122.

Kangwon Province: 3 mi NW Chip'o-ri, 145 m, USNM 299105; Chip'o-ri (38°08'N/127°19'E), USNM 294667, 294668, 294670–294675, 298109–298115, 299528; Tokkum-ni (38°09'N/127°06'E), AMNH 170069; Kumhwa (38°17'N/127°28'E), USNM 294694, 294695, 298126–298129; 10 mi S Kumhwa, USNM 294697, 294698; 15 mi S Kumhwa, USNM 294696; Sinsul-tong (=Sinsul-li, 38°10'N/127°25'E), USNM 298139, 298140; 3 mi SW Yanggu (38°06'N/128°00'E), 450 m, USNM 298977, 298978; 1 mi NW Oho-ri (38°20'N/128°32'E), 6 m: USNM 298990; 1 mi N Oho-ri, 1–2 m, USNM 298979, 298980, 298991, 298992; 3 mi SSE Sumil-li (38°02'N/127°30'E), 1468 m, USNM 299106, 299107; 3 mi SE Kangnung (37°45'N/128°54'E), 6 m, USNM 298987–298989; 8 mi SW Kangnung, 550 m, 298985, 298986; 1 mi W Tangjonggok (38°11'N/128°19'E), 425 m: USNM 298981–298983; Tokkum-ni (38°09'N/127°06'E), 110 m: USNM 298995, 298996; Ch'ongyang-ni (38°15'N/127°23'E), USNM 294684–294686, 298123–298125.

North Cholla Province: 8 mi SW Kunsan (35°59'N/126°43'E), 10 m, USNM 299143–299160, 299161 (holotype of *Apodemus agrarius pallescens*), 299162–299171.

South Cholla Province: 5 mi W Kwangju (35°09'N/126°55'E), 13 m, USNM 299172–299186.

Cheju Province, Cheju do (=Quelpart Island): 6 mi NNE Sogwi-ri (33°15'N/126°34'E), 460 m, USNM 299216, 299223, 299224; 10 mi NE Mosulp'o (33°13'N/126°15'E), USNM 299203, 299204 (holotype of *Apodemus agrarius chejuensis*), 299205, 299206, 299626; 6 mi NE Mosulp'o, 200 m, USNM 299207–299214, 299627; 4 mi E Mosulp'o, 100 m, USNM 299215, 299217–299219; 2 mi SE Mosulp'o, 3 m, USNM 299220–299222.

“KOREA” (no other locality data): USNM 283676, 283677.

Apodemus chevrieri

Remarks: Originally described as a species by Milne-Edwards in 1872, *chevrieri* was arranged as a subspecies of *Mus sylvaticus* by Barrett-Hamilton (1900: 418), retained as a species in Thomas' (1912) report on Chinese mammals and in Ellerman's (1941) checklist, and until recently was treated as a subspecies of *A. agrarius* (Allen 1940; Ellerman 1949; Ellerman & Morrison-Scott 1951; Corbet 1978). In 1962, however, Pen et al. reported that both species were found in Omei Shan, *A. chevrieri* at higher altitudes and *A. agrarius* lower. Citing that report and other information, Xia (1985) contended that *A. chevrieri* should be regarded as a species because it and *A. agrarius* occur together in parts of Sichuan and Guizhou provinces, an assertion independently supported by Wang's (1985) study of *A. chevrieri* and *A. agrarius*, which also indicated sympatry between the two species.

The status of *chevrieri* as a distinct species of *Apodemus* whose closest living relative is *A. agrarius* is now accepted (Corbet & Hill 1992; Musser & Carleton 1993).

Besides lacking a middorsal stripe, examples of *A. chevrieri* are larger than those of *A. agrarius*, as indicated by lengths of head and body, hind feet, greatest length of skull, and length of maxillary molar row (see Table 227 in Corbet & Hill 1992: 357). Toothrow measurements are useful in distinguishing series of the two species. The difference in means of toothrow length between our samples of 208 *A. agrarius* and 320 *A. chevrieri* is statistically highly significant (table 1).

Corbet & Hill (1992: 357) indicated the lingual (medial in their terminology) root beneath each first upper molar to vary in form between the two species. It is, according to them, divided into two elements in specimens of *A. agrarius* but single in all examples of *A. chevrieri*. Each of the 331 specimens of *A. agrarius* that we surveyed does have two lingual roots. However, so do nearly all examples of *A. chevrieri* examined for this trait (table 2): out of 190 individuals from Yunnan, 97 % have double roots, and out of 431 specimens from Sichuan, 89 % have two clear lingual roots. A minority of specimens of *A. chevrieri* from those provinces either have one root or a single structure that is creased by a vertical furrow.

Table 1: Comparisons between AMNH Chinese samples of *Apodemus agrarius* and *A. chevrieri* in crown length of maxillary molar row (mm). The mean plus or minus one SD, range (in parentheses), and number of specimens are listed for each sample. P is the significance probability derived from a table of cumulative Student's *t* distribution; any value less than .05 is considered significant enough to reject the hypothesis that means of the two samples were drawn from the same population.

Province	<i>A. agrarius</i>	P	<i>A. chevrieri</i>
Fujian	3.8 ± 0.00 1		—
Hunan	4.0 ± 0.16 (3.7—4.3) 17		—
Sichuan	3.9 ± 0.13 (3.6—4.2) 120	.02—.01	4.2 ± 0.12 (3.9—4.6) 178
Yunnan	—		4.3 ± 0.15 (3.9—4.6) 142
Gansu	3.7 ± 0.16 (3.5—4.0) 8		—
Shaanxi	3.9 ± 0.14 (3.6—4.1) 57		—
Hubei	4.1 ± 0.00 2		—
Hebei	3.9 ± 0.07 (3.8—3.9) 2		—
Heilongjiang	3.9 ± 0.00 1		—
TOTALS	3.9 ± 0.14 (3.5—4.3) 208	.01—001	4.2 ± 0.14 (3.9—4.6) 320

Table 2: Variation (expressed in number of specimens) in configuration of the lingual root beneath each first upper molar: comparisons between AMNH and FMNH samples of *Apodemus agrarius* and *A. chevrieri* from provinces in China.

Species and Province	Form of Root		
	Single	Single but creased by vertical furrow	Double
<i>A. agrarius</i> Fujian, Hunan, Sichuan, Gansu, Shaanxi, Hubei, Hebei, Jiangsu, Heilongjiang	0	0	331
<i>A. chevrieri</i> Sichuan	20	29	382
Yunnan	1	5	184

That examples of *A. chevrieri* average larger in body size than do those of *A. agrarius*, as indicated by the comparisons in Table 227 (p. 357) provided in Corbet & Hill (1992), is evident from our visual observations comparing crania of each species, side-by-side.

Sympatry between *A. agrarius* and *A. chevrieri* has been asserted (Wang 1985; Xia 1985; Corbet & Hill 1992), but supporting evidence has never been documented by publishing catalog numbers and localities for actual specimens upon which distributional records are based. We have identified samples of the two species collected from the same localities in Sichuan: 1) Chung Chiang Miao, 30 mi W Minjian; 2) Lu Erh Cheh; 3) Hei Ngai Ping, E Ya'an; 4) Guan Xian, upper Min Jiang; and 5) Nguluko (see Localities and Specimens Examined). Whether altitudes or microhabitats were common to samples of both species from each locality is unknown. These data would illuminate whether the two species are syntopic or parapatric.

Certain morphological traits shared by *Apodemus chevrieri* and *A. agrarius* indicate these species are phylogenetically closer to each other than to other species of *Apodemus*. Both have prominent supraorbital ridges that outline the interorbit and sweep back along lateral margins of the parietals. In other *Apodemus* that have supraorbital ridges, they are confined to the lateral margins of the frontals (fig. 3). In both species, a posterior cingulum on the first upper molar is either absent or small (see fig. 4B and the frequencies listed for *A. agrarius* in table 5). The majority of specimens in any sample of each species lack a cusp t3 on the second upper molar (fig. 4; table 5). The third molars are smaller relative to the others in the row than in any other species of *Apodemus*; cusp t8 is frequently missing or coalesced with cusp t5 (fig. 4; table 5). Finally, samples of *A. agrarius* we surveyed and most specimens of *A. chevrieri* have a divided lingual root beneath the first upper molar (table 2). Among muroid rodents, these character states are derived (Musser & Newcomb 1983), and their combination is uniquely shared by *A. agrarius* and *A. chevrieri* among species of *Apodemus*.

Localities and specimens examined:

CHINA:

Sichuan Province: Qionglai Shan (=Chien Lliang Shan Range), 30 mi W Miansi (=Wenchwan, 31°22'N/103°33'E), 9500 ft, AMNH 111841, 111842, 111843–111851, 111868, 111869, 111875, 111878, 256449, 256450 ("Wenchwan", the town that Carter, Sage, and Sheldon used as a reference point for their collecting localities during the AMNH Sage West China Expedition, is probably not "Wenquan" as determined by Lawrence [1982]. The only Gazetteer listing for Wenquan is in eastern Sichuan at 31°22'N/108°27'E. "Wenchuan Xian" [previously Wenchuan Hsien] or "Weizhou" [previously Wenchuan hsien] are both better choices. According to USBGN, China, 1990, Weizhou is a PPL [populated place] and Wenchuan Xian is an ADM3 [third-order administrative division]; both are located at 31°28'N/103°35'E, significantly closer to the expedition route, as reproduced on Gioiosa's map in Sheldon [1975]. However, Weizhou [Wenchuan] seems to correspond to the "Wei-chou" on Gioiosa's map, both on topological and coordinate bases. The current locality which we believe to be the "Wen-chu-an" of Gioiosa's map is Miansi [previously Miansizhen] at 31°22'N/103°33'E. But, if "Wen-chu-an" of Gioiosa's map is the same as "Wenchwan" of the field localities, then all distances are overestimated.); Chengou (also "Chenggou" or "Chengo") Forks, 30 mi W Miansi, 7600 ft, AMNH 112529, 112540, 112541, 112546, 112557, 112574, 112601, 112602, 256460; Chengou Creek, Cheng Wei, 25 mi W Miansi, 7000–10,000 ft, AMNH 112025, 112027, 112028, 112030–112033, 112035, 112039, 112042, 112044–112047, 112049, 112050, 112053, 112054, 112057, 112058, 112060, 112061, 112063–112067, 112068, 112073–112076, 112078, 112081–112089, 112091–112094, 112099, 112100, 112103–112107, 112121, 112125, 112126, 112128, 112129,

112133–112136, 112142–112145, 112153, 112156, 112158, 112159, 112164, 112167, 112185, 112191, 112198, 112205, 112206, 112215–112220, 112222–112224, 112230, 112232, 112233, 112236–112239, 112241–112243, 112245, 112256, 112259–112267, 112269, 112270, 112272–112274, 112276–112278, 112287–112291, 112294, 112296, 112308–112311, 112327, 112328, 112336, 112342–112345, 112350, 112359, 112360, 112362–112364, 112370, 112375, 112378, 112380, 112381, 112383, 112391, 112392, 112398, 112401, 112409, 112416, 112434, 112441, 112455, 112456, 112482, 256454; **Chengou Creek**, **Tsa Pei**, 20 mi W Miansi, 6200 ft, AMNH 112019; **Chengou Creek**, 10 mi W Miansi, 5000 ft, AMNH 112484; **South slope Tsao Po ridge**, 20 mi SW Miansi, 5000 ft, AMNH 112016; **Tsao Po**, 15 mi SW Miansi, 5000 ft, AMNH 111910, 111923, 111924, 111932, 111933, 111940, 111947, 111949, 111950, 111957, 111958, 111960–111962, 111964, 111968, 111969, 111976, 111977, 111981, 111991, 112005; 6000 ft, 111950; **Wa Shan** (possibly Wanshan, 30°22'N/106°07'E), 7000 ft, AMNH 36891; **Kuan Shien**, (=Guanjian, 29°59'N/105°59'E), USNM 258119, 258120; **Chung Chiang Miao** (29°03'N/103°23'E; Traylor 1967), 30 mi W Minjian (=Mapienting, 28°48'N/103°39'E), S of Dadu He (=Tung River), FMNH 40698, 40699; **Goan Shih Dwe** (31°00'N/103°36'E; Kerbis Peterhans 1995), FMNH 45100, 45147, 45379–45385, 45387, 45389, 45390, 45615; **Lu Erh Cheh**, FMNH 40697; **Nai Su Chen**, FMNH 44924, 44926, 44930, 44932, 44934, 44935, 44945, 44948–44953, 44960, 44969, 44971, 44972, 44975, 45341–45364, 45366–45378, 45440, 45446; **Ta Cho Fu** (29°12'N/103°20'E; Traylor 1967), 30 mi NW Minjian (=Mapienting), just S Dadu He (=Tung River), FMNH 40659, 40662, 40664, 40665, 40667, 40668, 40670–40672, 40679, 40682, 40684, 40685, 40918; **Ta Tsai Tsu** (31°28'N/103°40'E; Traylor 1967), NE Wen Chuan Hsien, FMNH 44916, 44918, 45338–45340; **Hei Ngai Ping** (30°00'N/103°33'E; Kerbis Peterhans 1995), E Ya'an (=Yachow, 29°59'N/103°05'E), FMNH 44979–44981; **Hsiao Yang Chi** (29°06'N/103°21'E), 27 mi W Minjian (=Mapienting), S Dadu He (=Tung River), FMNH 40701, 40704, 40706; **Guan Xian** (=Kuan Hsien, 31°00'N/103°37'E), upper Min Jiang (=Min River); FMNH 40711, 40716, 40722, 40727, 40742, 40757, 40762, 40775, 40781, 40801, 40803, 40808, 40810, 40824, 40844, 40860, 40862, 40885–40887, 40894, 40896, 40897; **Chou Tsen Goh**, near Pin Yang Goh (30°25'N/102°36'E; Kerbis Peterhans 1995), FMNH 45072–45079, 45233–45235, 45237, 45240, 45532; **Dun Shih Goh** (30°25'N/102°51'E; Kerbis Peterhans 1995), above Baoxing (30°23'N/102°50'E), FMNH 37370–37373, 37375, 37377–37396, 37438, 37453, 37474, 37490, 37499, 37503, 37521, 37527, 37820; **Fi Shan Kwan** (30°03'N/103°06'E; Kerbis Peterhans 1995), FMNH 37406–37418, 37553, 40655, 40657; **Baoxing** (=Paohing=Mupin, also spelled Mouping, 30°23'N/102°50'E), FMNH 36413–36417, 37367–37369, 37397–37405, 37542, 37549; **Pin Yang Goh** (30°25'N/102°36'E), W Baoxing, FMNH 44983, 44986, 44990, 44994, 44996, 44997, 45001–45006, 45008, 45010, 45012, 45013, 45016–45018, 45022–45024, 45029, 45031–45039, 45041, 45042, 45044, 45045, 45048–45051, 45054–45060, 45062, 45065, 45067, 45070, 45244, 45245, 45258, 45259, 45261, 45263–45267, 45270, 45271, 45273, 45275, 45276, 45479; **Sha Kuan Zu** (30°15'N/103°00'E; Traylor 1967), SE Baoxing, FMNH 36419, 36420; **Shan Tai Su** (28°46'N/104°42'E; Kerbis Peterhans 1995), 7 mi E Yibin (=Ipin=Suifu, 28°46'N/104°34'E), FMNH 40658; **Mi-Li**, FMNH 33144; **Gang Yang Go** (30°21'N/102°30'E; Kerbis Peterhans 1995), 20 mi WSW Baoxing, FMNH 36382, 36383, 36396, 36397, 36399–36402, 36408, 36409; **Luan Shih Go** (30°15'N/102°22'E; Kerbis Peterhans 1995), 20 mi SW Gang Yang Go, upper Dadu He (=Tung River), FMNH 36410–36412; **Chin Chuan Shan**, 29°40'N/103°06'E; Kerbis Peterhans 1995), FMNH 44978; “Sichuan” (no other locality data), FMNH 36407.

Yunnan Province: **Zhongdian** (=Chung Tien), Song-Pa, 8000 ft, AMNH 43960; **Tomulang**, 10,000 ft, AMNH 43870, 43871, 43955, 43959, 44920, 44925, 44930 (we located Tomulang on a U.S. War Office map [1926]; it appears to be just north of „Tu-gan-sha”); **Tuguncun** (=Tu-gan-sha, previously known as T'u-kuan-ts'un), 20 mi S Zhongdian (27°22'N/100°00'E), 10,000 ft, AMNH 43500, 44942; **Hoa Shan**, 30 mi S Zhongdian, AMNH 43767, 43863; **Fire Mountain**, 30 mi S Zhongdian, AMNH 43861, 43862, 43965; **Phete Mountain**, 10,000 ft, AMNH 43968; **Phete Mountains**, 30 mi S Zhongdian, 10,000 ft, AMNH 43966; **Phete Mountain**, 40 mi S Zhongdian, 8000 ft, AMNH 43770; **Ha-pa**, 20 mi N Taku Ferry, 10,000 ft, AMNH 43972, 43973 (We cannot update Ha-pa or Taku; Andrews & Andrews 1918, apparently referred to this locality as “Habala;” their route map shows Taku Ferry and Habala as roughly equidistant between Xiaozhongdian [27°35'N/99°48'E] and “Snow Mountain;”); **Jinsha Jiang** (=Yangtze River), W bank of Taku Ferry, 6000 ft, AMNH 43624, 43676, 43791, 43792, 43873, 43874, 43969, 43970; **Lijiang** (=Lichiang), **Yolungxue Shan** (=Snow Mountain), 12,000 ft, AMNH 43821; **Pes-hsui**, 10,000 ft, AMNH 43520, 43522, 43705, 43706, 43826, 43827; **Ssu Shan Mountain**, 12,000 ft, AMNH 43884; **Ssu Shan Chang**, 9000 ft, AMNH 43518, 43577, 43578, 43584, 43648, 43686, 43830–43848, 43908, 43909, 43911–43915, 43917–43919, 44805–44808, 44826, 44827, 44944, 44951; **Jinsha Jiang**, **Chi-tien**, 6400 ft, AMNH 43674, 43675, 43876; **Lijiang** (26°48'N/100°16'E), 8200 ft, AMNH 43516, 43626, 43646, 43647,

43684, 43685, 43716, 43717, 43920–43934, 43990, 44028–44030, 85043; **Jinsha Jiang, La-sa-ku** (just N “Shih-ku”), 6000 ft, AMNH 43505, 43696, 43697; **Jinsha Jiang, Shigu** (=Shih-ku, 26°52'N/99°57'E), 6000 ft, AMNH 43504, 43793; **Jinsha (=Yangtze)-Lancang (=Mekong) drainage, Litien**, 10,000 ft, AMNH 43951, 43952 (Litien is on our U.S. War Office Map [1926]; it lies halfway between Weixi [=Weihsi] and Judian [=Kütien]; inferred coordinates are 27°20'N/99°20'E); **Lancang Jiang (=Mekong River), Chung-ba**, 6000 ft, AMNH 43860, 43947; **Lancang Jiang, Hsiao-tien**, 6500 ft, AMNH 43507, 43632, 43690; **Lancang Jiang, Hsiao-ke-la**, 8000 ft, AMNH 43601, 43945; **Lancang Jiang, Yin-pan-kai**, 9000 ft, AMNH 43672, 43691, 43852, 43950 (There is a Yin-pan-kai at 26°27'N/99°09'E, which is just off Andrews & Andrews' 1918 published route map, but is most likely the same place); **Lancang Jiang, La-chu-wei**, 9000 ft, AMNH 43859; **Lancang Jiang drainage, Chiang-wei**, 8000 ft, AMNH 43508, 43688, 43689, 43786, 43857, 43858, 43935–43939 (“Chiang-wei” lies between the Pei-ping and “Yang-tsen” localities); **Lancang Jiang drainage, Sha-sung-shao**, 7500 ft, AMNH 43509, 43785, 43940 (Sha-sung-shao is probably the same as Gongguoqiao, 25°36'N/99°20'E); **Lancang Jiang drainage, Yang-tsen**, 9000 ft, AMNH 43494; **Er Hai (=Tali Lake) drainage, Nui-kai**, 7500 ft, AMNH 43695; **Er Hai, Yuhu** (=Langchiung hsien, 26°07'N/99°57'E), 7000 ft, AMNH 43680, 43681, 43694, 43866–43868, 43985; **Er Hai, Shan Kuan**, 6500 ft, AMNH 43506, 43865, 43984; **Nu Jiang (=Salween River) drainage, Mu-cheng**, 7000 ft, AMNH 43512, 43978 (our inferred coordinates of “Mu-cheng” are 23°45'N/99°12'E); **Wuding** (=Wu Ting Hsien), **Longjie** (=Lung Kai, 24°41'N/100°48'E), AMNH 84965, 84966, 84968, 84977, 84987, 84992; **Kunming** (=Yunnan Fu), **Kao Chiao Temple**, AMNH 84963, 84976, 84979 (according to Granger, 1932: 532, Kao Chiao Temple is on the western shore of “Kun-yang-hai” [=Dian Chi]); **15 mi SW Kunming** (25°04'N/102°41'E), USNM 279293; **Meti Long, near Muli**, 7700 ft, FMNH 32535; **Lijiang (=Dayan), Lijiang Range**, 9300 ft, FMNH 33190; **Lijiang (=Dayan), Lijiang Ridge**, 9000 ft, FMNH 28961, 28962; **Lijiang (=Dayan), 45 mi N Lijiang** (26°48'N/100°16'E), FMNH 32534; **Nguluko** (27°03'N/100°12'E; Kerbis Peterhans 1995), FMNH 33164, 33166–33174, 33176–33179, 33187–33189; **Nguluko**, 9500 ft, FMNH 33162, 33163; **S Yongning** (=Yungning, 27°50'N/100°40'E), 9000 ft, FMNH 33195–33197; **Guizhou Province: Guiyang** (=Kweiyang, 26°35'N/106°43'E), USNM 279294–279296.

Apodemus latronum

Remarks: This species was originally named as a subspecies of *A. speciosus* by Thomas (1911: 49), who succinctly diagnosed it as a large brown mouse with a short tail and long ears; an amplified description was provided a year later (Thomas 1912). The distinctive traits of *latronum* were evident to some investigators who thought they defined a valid species, but not to others who continued to view it as a subspecies of either *A. speciosus* or some other species of *Apodemus*. Osgood (1932), for example, recognized *latronum* as a species, noting that its large body size and big blackish ears distinguish it from *A. speciosus*; he thought it might instead be related to the European *A. flavicollis*, which is also characterized by large body size. In his report on mammals collected in China and Mongolia, Allen (1940: 950) concurred, noting that although *latronum* had originally been “described as a race of *A. speciosus* by Thomas, there is no doubt that this represents a species quite distinct” (p. 952). He agreed with Osgood that the Chinese form may prove to be allied to *A. flavicollis* but explained that “until a complete revision of the group can be made ... it seems as well to use the binomial, awaiting a more accurate determination of its relationship” (p. 952).

During the next few decades this Oriental endemic lost its identity as a species. In 1941, Ellerman followed Thomas in recognizing *latronum* as a subspecies of *A. speciosus*. By 1949, Ellerman had concluded that *latronum* represented an eastern subspecies of *A. flavicollis*, and it was later listed this way by Ellerman & Morrison-Scott (1951) and Ellerman (1961).

The specific recognition of *latronum*, as a member of a distinct group of eastern *Apodemus* unrelated to the European *A. flavicollis* and *A. sylvaticus*, was supported by Zimmermann in 1962. In his taxonomic review of Palearctic mammals, Corbet (1978) followed Zimmermann and also provided key traits that distinguish *A. latronum* from other species, especially *A. draco* with which it occurs sympatrically and syntopically. The identity of *latronum* has remained intact to the present (Corbet & Hill 1992; Musser & Carleton 1993; Xia 1984, 1985) except for the report by Feng et al. (1986), who considered it a subspecies of *A. draco*.

Our records of the species are from the mountains of Sichuan and northern Yunnan. Feng et al. (1986) identified specimens as *A. draco latronum* from eastern Xizang (Tibet), and Corbet & Hill (1992: 358) included northern Burma in the range. We do not know the source (publication or specimens?) upon which this Burmese segment is based; our large series of *Apodemus* from northern Burma are all *A. draco*.

Allen (1940) provided a good description of *A. latronum*. It closely resembles *A. draco* in fur color and chromatic pattern as well as cranial and dental morphology. *Apodemus latronum* is larger, has a much longer molar row (table 3; fig. 1), three pairs of mammae instead of two (Corbet & Hill 1992: 357; we have verified this pattern with AMNH specimens), and longer fur that is silky to the touch (shorter and more velvety in *A. draco*).

Difference in body size is a primary trait distinguishing examples of *A. latronum* from series of *A. draco*. Other than size and number of mammae, the two species are closely similar in characters associated with fur and appendages. A similar cranial conformation is shared by both — the skull of *A. latronum* appears to be a larger version of that in *A. draco*, based on our visual comparisons.

The geographic range of *A. latronum* overlaps those of several other species of *Apodemus*. Corbet & Hill (1992) as well as Xia (1985) noted that *A. latronum* and *A. draco* are found together over “much” of their geographic range. Among our samples, we found no localities in Sichuan where both species were collected together, but we do have samples in the American Museum from Yunnan (Tomulang, Tuguncun, Ha-pa, Lijiang, Ssu Shan Mountains, and Ssu Shan Chang; see lists of Localities and specimens examined) that contain examples of both species collected at the same localities, altitudes, and time periods.

Small samples of both *A. latronum* and *A. peninsulae* were collected at two localities in western Sichuan (see the account of *A. peninsulae* below).

Apodemus chevrieri has also been taken with *A. latronum*. Corbet & Hill's (1992: 358) map indicates that the ranges of these two species do not overlap, but the American and Field Museums have samples of both species obtained from northwestern Yunnan at Tomulang, Tuguncun, Ha-Pa, Lijiang, Ssu Shan Mountains, Ssu Shan Chang, 45 mi N Lijiang, Yin-pan-kai, Yang-tsen, and Nguluko (see Localities and specimens examined).

Localities and specimens examined:

CHINA:

Sichuan Province: 20 miles N of Litang (30°02'N/101°21'E), AMNH 113683 (J. T. Young, the collector, who was in W Sichuan in 1934, listed the Litang area and all of his other localities [Hekou, Wolongshi, Yalung Jiang, Gongga Shan] as being within the “Sikong District”. Sikang was an administrative district

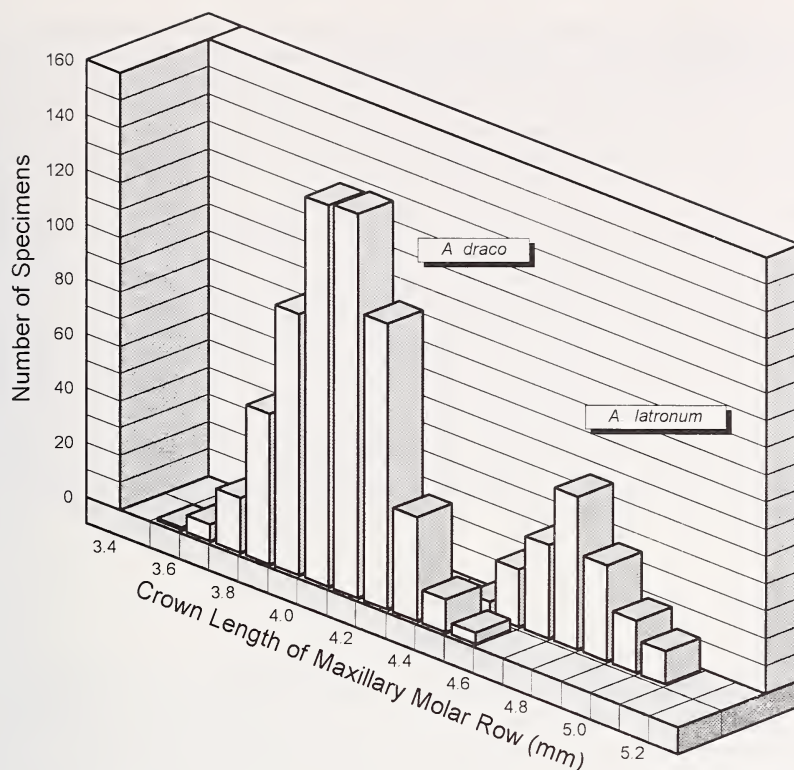


Fig. 1: Frequency distributions of values for crown length of maxillary molar row obtained from Chinese samples of *Apodemus draco* (n = 618) and *A. latronum* (n = 182). Summary statistics for the samples are listed in table 3.

that no longer exists; it has been divided, with the eastern portion [where Young collected] annexed to Sichuan Province, and the western part associated with Xizang Zizhiqu [Tibet Autonomous Region].; **Hekou** (=Hokow, 30°02'N/101°02'E), 9400 ft, AMNH 113626; **Wolongshi** (=Wo-lung-shih 30°03'N/101°21'E), AMNH 113626, 113686, 113687; **Yalung Jiang** (=Yalung Jiang), AMNH 113628, 113629 (Yalung Jiang is a river flowing through the areas in which J. T. Young worked. We were unable to pinpoint the localities at which the specimens were collected.); **Gongga Shan** (=Minya Konka 29°34'N/101°53'E), **Konka Gumpa**, AMNH 113630, 113631, 113633, 113638–113641, 113645, 113646, 113648–113650, 113652–113656, 113660–113662, 113664–113667, 113688; 10,000 ft, AMNH 113622; **Gongga Shan, Mu-chu Valley**, AMNH 113647, 113651, 113663; **Gongga Shan, Tze Mei**, AMNH 113632, 113634–113637, 113657–113659; 9000 ft, 113668–113677 (Stevens, 1930: 354, identified a “Tzumei” which is about 30 mi SSW of “Minya Konka” [approximately 29°17'N/101°58'E]; if this is Young’s Tze Mei, then there is no guarantee that the other specific locations for “Minya Konka” [Konka Gumpa and Mu-chu Valley] are necessarily close to the mountain.); **Chu Lung Shien, Da Pu Tze**, 7000 ft, AMNH 113623 (J. T. Young’s collecting locality, Chu lung Shien, is a mystery, but there is a “Dapuzi” at 28°12'N 101°24'E, which is a bit south of the other collecting sites); **Ta chiao**, AMNH 36890; **Tang-gu** (=Tanggo, 29°06'N/101°27'E), USNM 255924; **near Gieu-long Shien** (=Gulung), USNM 255923; **Yu-long-shi Gorge**, USNM 255927, 255951 (this could be Yulong, 31°05'N/103°30'E, Wo-long-shih [locality used by J.T. Young], or neither one); **Ku-lu** (=Ku-lo=Gulung, 30°53'N/99°52'E), USNM 259521; **Wuxi** (=Wu-chi, 31°28'N/109°36'E), USNM 259522; **Chong ku, near Lucheng** (=K'angting, 30°03'N/102°02'E), USNM 267660; **Ku-Lu** (this may be the same as Gulung, which is the same as Ku-lo, 30°53'N/99°51'E), FMNH

33200–33203, 33205–33211; **Nien Yuen Fu**, FMNH 32530; **Wuxi** (=Wu-Chi or Wu-ch'i, 31°28'N/109°36'E), FMNH 33147, 33212–33220, 33222–33231; **Chao-Loo** (29°56'N/101°33'E; Kerbis Peterhans 1995), 13,600 ft, FMNH 33148; **Che-Lo** (30°03'N/101°38'E; Kerbis Peterhans 1995), FMNH 33149, 33150.

Yunnan Province: Zhongdian (=Chung Tien), **Tomulang**, 10,000 ft, AMNH 43495, 43503, 43958 (see note in *A. chevrieri* section); **Tuguancun** (=Tu-gan-sha; previously T'u-kuan-ts'un), **20 mi S Zhongdian** (27°22'N/100°00'E), 10,000 ft, AMNH 43496–43499, 43692, 43961, 43962; **Ha-pa**, **20 mi N Taku**, AMNH 43677; **Chang Jiang**, **10 mi E Taku Hills**, 9000 ft, AMNH 43790, 43975, 43976 (see note in section on *A. chevrieri*); **Lijiang, Yolongxue Shan** (=Snow Mountain, 27°07'N/100°10'E), 12,000 ft, AMNH 43528, 43530, 43533, 43540, 43543, 43545–43549, 43552, 43698, 43699, 43820, 43881, 43882, 43885, 43910, 43992, 43993; 13,000 ft (timber line), AMNH 43536–43539, 43877–43879; **Pes-hsui**, 10,000 ft, AMNH 43525, 43492, 43521, 43524, 43527, 43899, 43900, 43902, 43566, 43567, 43569, 43650, 43687, 43707, 43710, 43711, 43828, 43829, 43904–43907, 43991; **Ssu Shan Mountains**, 12,000 ft, AMNH 43493, 43534, 43535, 43553–43557, 43560, 43561, 43563, 43701, 43822, 43886–43894, 43896–43898, 43994; **Ssu Shan Chang**, 9000 ft, AMNH 43571–43573, 43575, 43580–43583, 43585–43590, 43649, 43712, 43713, 43916 (see note in section on *A. chevrieri*); **Lijiang, 25 mi N** (27°00'N/100°17'E; Kerbis Peterhans 1995), FMNH 32532; **Lijiang, 45 mi N** (27°29'/100°17'E; Kerbis Peterhans 1995), 10,500 ft, FMNH 32542, 32533; **Lancang Jiang, Yin-pan-kai**, 9000 ft, AMNH 43605 (see note in section on *A. chevrieri*); **Yang-tsen, Lancang Jiang Drainage**, 9000 ft AMNH 43941; **Nguluko** (27°03'N/100°12'E; Kerbis Peterhans 1995), FMNH 33165, 33175, 33180–33182, 33184–33186, 33192, 33582; **Jinsha Jiang** (=Yangtse River), **Big Bend** (27°27'N/100°14'E; Kerbis Peterhans 1995), 10,600 ft, FMNH 33191, 33193, 33194.

Apodemus draco

Remarks: Barrett-Hamilton (1900: 418) described *draco* and designated it a subspecies of *Mus sylvaticus*; the type series was collected at Kuatun in the northwestern part of Fujian Province. The association of *draco* with the European *A. sylvaticus* was accepted by most authors (Allen 1940; Ellerman 1941, 1949; Ellerman & Morrison-Scott 1951) until 1962, when Zimmermann separated *draco* as a species and aligned it with other Oriental *Apodemus* in the subgenus *Alsomys*.

By 1978, Corbet had summarized the key features distinguishing *draco* as a species, and treated *orestes* (Thomas, 1911, which included *ilex* Thomas, 1922) as a valid subspecies of *A. draco*. Earlier, Allen (1940) had considered both *draco* and *orestes* to be subspecies of *A. sylvaticus*, with *draco* distributed in eastern China and *orestes* in the western portion of that country. Both Anthony (1941), writing about the mammals collected in northern Burma by members of an American Museum expedition, and Lu et al. (1964), in a report on mammals from the Lin-Tsang region of western Yunnan, recognized *orestes* as a subspecies of *A. sylvaticus*.

Allen (1940), Ellerman & Morrison-Scott (1951), and Corbet (1978) erroneously included the names *argenteus* and *badius* as synonyms of *A. draco*. Both names were attributed to Swinhoe (1870), but each was actually proposed by someone else and Swinhoe had simply used them to identify specimens from China.

Corbet's (1978) diagnosis of *A. draco* is clear. Specimens can be unambiguously determined as *A. draco* or some other species by using his identification key. Xia (1984, 1985), in a report on Chinese *Apodemus*, also accepted Corbet's evaluation and treated *draco* as a species and recognized two subspecies: *A. d. draco* in north-eastern and southeastern China, and *A. d. orestes* in western China. Feng et al. (1986) identified their material from Xizang (Tibet) as *A. draco orestes*. The Oriental *draco* is also one of the species of *Apodemus* listed by Musser & Carleton (1993).

Table 3: Contrasts between Chinese samples of *Apodemus draco* and *A. latronum* in crown length of maxillary molar row (mm). The mean plus or minus one SD, range (in parentheses), and number of specimens are listed for each sample. P is the significance probability derived from a table of cumulative Student's t distribution; any value less than .05 is significant enough to reject the hypothesis that means of the two samples were drawn from the same population. Samples of *A. draco* are in AMNH, those of *A. latronum* are in AMNH and FMNH.

Province	<i>A. draco</i>	P	<i>A. latronum</i>
Fujian	3.8 ± 0.22 (3.5—4.1) 5		—
Gansu	4.2 ± 0.00 1		—
Hebei	3.9 ± 0.12 (3.8—4.1) 17		—
Hubei	4.0 ± 0.00 1		—
Shaanxi	3.9 ± 0.00 2		—
Sichuan	4.1 ± 0.16 (3.6—4.5) 415	<.001	4.7 ± 0.15 (4.4—5.0) 62
Yunnan	3.9 ± 0.14 (3.6—4.4) 177	<.001	4.7 ± 0.14 (4.4—5.0) 120
TOTALS	4.0 ± 0.16 (3.5—4.5) 618	<.001	4.7 ± 0.13 (4.4—5.0) 182

Recently, in their review of Indomalayan mammals, Corbet & Hill (1992) have modified the definition of *A. draco*, extracting *orestes* from it, and recognizing that form as a separate species. In their view, *A. draco* (in which they would include, with question, *semotus* from Taiwan and *ilex* from Yunnan) ranges from Assam and northern Burma to southern China (Yunnan, Hubei, and Fujian provinces), possibly Taiwan and north into the provinces of Sichuan, Gansu, Shanxi, and Hebei; *Apodemus orestes* occurs in the mountains of Sichuan, Yunnan, northern Burma, and Assam (see their map on p. 359). Corbet & Hill (1992: 360) also contended that *A. orestes* “is sympatric (or possibly parapatric) with forms referable to *A. draco* in Sichuan, mainly at higher altitudes. It is clearly distinguishable by darker colour and very long tail (usually over 120 % of head and body).” Thomas, who originally described *orestes* and named it as a subspecies of *A. speciosus* in 1911, had pointed out in 1912 (p. 137) that *orestes* differed from *draco* “by its larger size, longer tail, and less rufous tone.” Other than the difference in tail length and fur tone, samples of *orestes* and *draco* are virtually indistinguishable from one another in body size, coloration of pelage, number of mammae, and dental and cranial morphology, judged by the traits Corbet & Hill list in their Table 227 (p. 357) to distinguish the species of *Apodemus*.

We studied large series of *draco/orestes* from China and northern Burma to deter-

mine if we could distinguish two species. Paula Jenkins also loaned us a reference series from the British Museum: two examples of *orestes* (BMNH 11.9.8.92 and 11.9.8.98) from the type series collected on Mount Omei Shan in Sichuan, one from 8000 ft, the other from 12,000 ft; a specimen of *draco* (BMNH 97.6.6.11) from the type series obtained at Kuatun in Fujian Province; another example of *draco* (BMNH 11.9.8.90) from Mount Omei Shan obtained at 6000 ft; and a specimen of *draco* (BMNH 11.2.1.147) from Wenhsien in southern Kansu Province. According to Paula, all these specimens had been studied by Corbet. (Musser had previously examined holotypes of *Mus sylvaticus draco*, BMNH 98.11.1.20, and *Apodemus speciosus orestes*, BMNH 11.2.1.170.)

We focused on the American Museum collection and first surveyed skulls. Nearly all the crania are broken or incomplete, the result of improper technique used when the material was cleaned in the 1930s and 1940s, so our survey was not quantitative but inspectional. Other than noticing obvious size differences associated with age classes, we could not sort the skulls into two groups that might represent two species; these results paralleled those obtained from our study of the British Museum reference series.

We then surveyed fur color and relative tail length in adults, the only features used to distinguish *draco* from *orestes* (Thomas 1912; Corbet & Hill 1992). We are not impressed with the color difference. All our specimens from Burma, collected from altitudes spanning 4200 to 9000 ft, have dark brown upperparts, whether long-tailed or short-tailed. Nearly all of the Chinese samples also have dark brown fur. Those from Tsao Po at 5000 ft in Sichuan Province are slightly brighter with more buff overtones than are those collected at higher altitudes in Sichuan, but the difference is subtle and wide overlap exists in the range of variation observed among the samples. Finally, the American Museum series from Chong'an Xian, in the mountains of Fujian Province, close to Kuatun, the type locality of *draco*, and topotypes stored in Washington and Bonn, are just as dark as those specimens in samples from Sichuan obtained at elevations between 7000 and 11,000 ft (the Miansi region). Mice in the Fujian sample have shorter coats than do those at high altitudes in Sichuan but differences in tone or hue are not apparent.

Similar results came from our study of the British Museum reference series. Fur of the *draco* from Kuatun is just as dark as coats on the two examples of *orestes* from Mount Omei Shan; difference in pelage thickness was the only contrast.

Because the type localities of *draco* and *orestes* are in China, we surveyed primarily the American Museum Chinese material to test the validity of tail length as a diagnostic trait. We only included specimens in full adult pelage, used the measurements recorded on skin labels, and examined the distribution of percentages obtained from the ratio "length of tail/length of head and body". Our data comes from samples collected at Chong'an Xian in Fujian Province and Eastern Tombs (Tung Ling) in Hebei Province (FMNH examples from here were included), specimens that morphologically match typical *draco* from Kuatun; and from material obtained in Sichuan at altitudes extending from 5000 to 11,000 ft in the Miansi region (various localities 10–40 mi W Miansi, and Tsao Po, 15 mi SW Miansi), which certainly represents *orestes* at the higher altitudes and should include *draco*, particularly from lower places. The utility of relative tail length as a

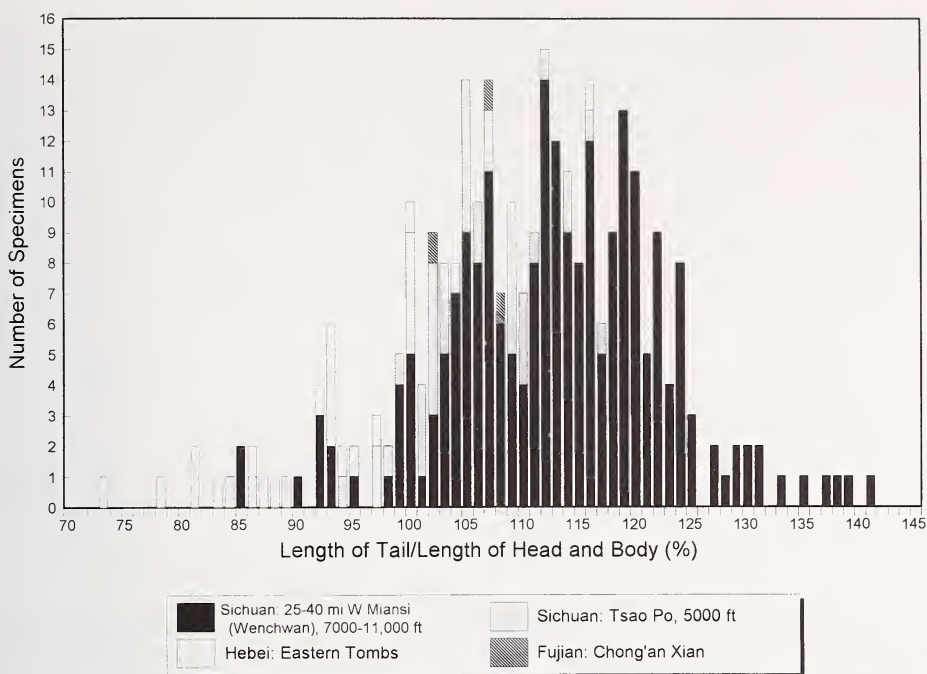


Fig. 2: Frequency distribution of values derived from the ratio, Length of Tail/Length of Head and Body and obtained from Chinese samples representing “*draco*” and “*orestes*” Samples are from Sichuan Province, Miansi region ($n = 223$, mean = 115 %), Sichuan Province, Tsao Po ($n = 46$, mean = 104 %), Hebei Province ($n = 19$, mean = 91 %), and Fujian Province ($n = 3$, mean = 106 %). Note the apparent lack of bimodality. See text for discussion.

distinguishing character should be revealed in the frequency distribution of ratio values: either a unimodal or bimodal profile.

The frequency distribution of values we obtained appears unimodal (fig. 2). Values from the high-altitude series from 7000–11,000 ft by themselves form a nearly symmetrical unimodal distribution. Those from specimens collected at 5000 ft, the small series from Fujian, and the sample from Hebei are mostly scattered throughout the left portion of the frequency profile but a few points extend to the right half of the distribution. The range in values obtained from four out of the five specimens in the British Museum reference series (the specimen from Kuatun lacks measurements) is 115–127, which clusters in the right side of the frequency distribution. If more than one species exists in these samples, they cannot be confidently separated by relative tail length.

Nor is there any suggestion of bimodality in the histogram of molar row length for samples of *draco* from the Chinese provinces of Fujian, Gansu, Hebei, Hubei, Shaanxi, Sichuan, and Yunnan ($N=618$, fig. 1). Furthermore, we did not find statistically significant differences among means of molar row length in samples from which the histogram in figure 2 (depicting distribution of relative tail lengths)

Table 4: Comparisons among AMNH Chinese samples of *Apodemus draco* in crown length of maxillary molar row (mm). Number of specimens (N), mean plus or minus one standard deviation ($M \pm SD$), and observed range (OR) are listed for each sample. Data are from the same samples from which the histogram in fig. 2 was derived. No statistically significant differences ($P = <.05$) were found between means of any of the six possible comparisons.^a

Locality	N	$M \pm SD$	OR
FUJIAN			
Chong'an Xian	4	3.9 ± 0.13	3.8—4.1
HEBEI			
Eastern Tombs	17	3.9 ± 0.12	3.8—4.1
SICHUAN			
Tsao Po, 5000 ft	87	4.0 ± 0.15	3.6—4.3
25—40 mi W Miansi (Wenchwan), 7000—11,000 ft	258	4.1 ± 0.13	3.7—4.5

^aP values are: Eastern Tombs vs. Chong'an Xian, .6—; Eastern Tombs vs. Tsao Po, >.9; Eastern Tombs vs. Miansi, .2—; Chong'an Xian vs. Tsao Po, .5—; Chong'an Xian vs. Miansi, .2—; Tsao Po vs. Miansi, .2—.

was derived (table 4). Species of muroid rodents that closely resemble each other in body size and morphology typically can be distinguished by a significant difference in length of toothrow (*A. agrarius* and *A. chevrieri*, for example, table 1).

We did not find evidence supporting the separation of *orestes* as a species separate from *draco*, at least based upon our study of the specimens listed here as well as the British Museum reference sample. There does seem to be geographic variation in tail length within the species that may be significant. Mice obtained from lower elevations and from regions to the southeast and northeast of Sichuan tend to have shorter tails relative to head and body length.

Localities and specimens examined:

CHINA:

Hebei (=Chihli) Province: Eastern Tombs (Tung Ling), 80 mi NE Beijing, AMNH 56423—56428, 56431—56433, 56435, 56437, 56439—56441, 56443—56447, 85287, 85289, FMNH 32768—32771 (see comments about this locality in section on *A. agrarius*).

Shaanxi (=Shensi) Province: Qin Lin Shandi (=Tsing Ling Mountains), Taibai Shan (=Tai Pai Shan, 33°57'N/107°45'E), 10,000 ft, AMNH 56405, 56406, 56790; Taibai Shan (=Tai-pei-shan), 80 mi WSW Xi'an (=Sianfu, 34°16'N/108°54'E), 2000 and 3000 ft, USNM 200876, 200878; Taibai Shan, 90 mi WSW Xi'an, 9000 ft, USNM 200877; Liucun (=Liu-tsuen=Liu-tsun, 34°31'N/108°44'E), 15 mi S Xi'an (=Sianfu), USNM 155120, 155121 (see comment in *A. agrarius* section).

Gansu (=Kansu) Province: Maqu Xian (=Ma Chu, 34°05'N/101°45'E), AMNH 84305, 84306 (see note in *A. agrarius* section).

Sichuan Province: Da Bei Hsui Gou (also "Dabieshuigo"), 40 mi W Miansi (=Wenchwan, 31°22'N/103°33'E), 11000 ft, AMNH 112615 (see the note about "Wenchwan" in the section on *A. chevrieri*); Qionglai Shan (=Chien Lliang), 30 mi W Miansi, 9500 ft, AMNH 111852, 111854—111866, 111870—111874, 111876, 111877, 111879—111895; Mao Mo Gou (includes "Mamago"), 30 mi W Miansi, 8600 ft, AMNH 112488—112490, 112492—112519, 256457, 256458; Chengou (includes "Chenggou," "Chengo") Forks, 30 mi W Miansi, 7600 ft, AMNH 112520—112528, 112530—112539, 112542—112545, 112547—112556, 112558—112573, 112575—112600, 112603—112609, 112610—112612, 112614, 256459, 256461; 8000 ft, 112613; Chengou Creek, Cheng Wei, 25 mi W Miansi, 7000—10,000 ft, AMNH 110920, 112034, 112055, 112070—112072, 112080, 112096—112098, 112101, 112102, 112108, 112109, 112112—112118,

112120, 112122–112124, 112131, 112137–112141, 112146, 112148–112152, 112154, 112155, 112157, 112161–112163, 112165, 112166, 112169–112175, 112177–112180, 112183, 112184, 112186–112190, 112192–112196, 112200, 112201, 112204, 112207, 112209, 112210, 112212, 112213, 112226–112228, 112246, 112248, 112251, 112254, 112258, 112271, 112279–112281, 112283–112286, 112292, 112293, 112295, 112297–112301, 112303–112307, 112312, 112314–112319, 112321–112323, 112326, 112329–112335, 112337–112340, 112346–112348, 112351–112357, 112361, 112366, 112369, 112372, 112373, 112376, 112379, 112384, 112386–112390, 112393–112396, 112399, 112400, 112402, 112404–112408, 112411–112415, 112417–112419, 112422, 112423, 112426–112432, 112436, 112438, 112439, 112443, 112445, 112446, 112452–112454, 112457–112462, 112464, 112466, 112468–112470, 112473–112476, 112478, 113012, 256452–256456, 256462–256465 (The range “7000–10000” ft is written on many of the field labels, “7000” ft on some; many field tags are missing; “7000” ft is noted on nearly all the museum skin labels.); **Chengou Creek, Tsa Pei, 20 miles W Miansi**, 6200 ft, AMNH 112020, 112021; **Chengou Creek, 10 mi W Miansi**, 5000 ft, AMNH 112485–112487; **Tsao Po ridge, 20 mi SW Miansi**, south slope, 8700 ft, AMNH 112017; **Tsao Po, 15 mi SW Miansi**, 5000 ft, AMNH 111896–111909, 111911–111922, 111925–111930, 111934–111939, 111941–111946, 111948, 111951–111956, 111959, 111963, 111965–111967, 111970–111973, 111975, 111978–111980, 111982–111986, 111988, 111989, 111992–112004, 112006–112015, 111376, 256451; **Wa Shan** (possibly Wanshan, 30°22'N/106°07'E), 7000 ft, AMNH 36889; **Chu Lung Shien, Da Pu Tze**, AMNH 113678–113680 (see the note about J. T. Young's collecting localities under the “Litang” entry in the *A. latronum* section); **Zhongdian** (= Chung Tien), **Song Pa**, 8000 ft, AMNH 43668, 43794 (Andrews and Heller, the collectors, did not travel all the way to Zhongdian [see route map in Andrews & Andrews 1918]. The northern extent of their route passed through “Hsiao Chung Tien,” now Xiaozhongdian [xiao is a diminutive Pinyin prefix], a smaller town which lies to the south of Zhongdian. Xiaozhongdian is located at 27°35'N/99°48'E; Song Pa is probably very near.); **Wenchuan, Wolong Nature Reserve** (21°20'N/103°48'E), AMNH 232376–232378; **Uen Dhuan**, USNM 240394; **near Washan**, USNM 241284; **Yibin** (=Suifu, 28°46'N/104°34'E), USNM 252892, 253333; **Ya'an** (=Yachow, 29°59'N/103°05'E), USNM 253794; **Yu-long-shi valley**, USNM 255925, 255928; **Yu-long-shi gorge**, USNM 253926, 253929, 253930 (D. C. Graham, collector; see note in section on *A. latronum*); **Li Tio**, USNM 255972; **near Li Tio**, USNM 256118; **Kuan Shien**, USNM 258121 (see note in list of *A. chevrieri*); **Baoxing** (=Mupin, also spelled Mouping, 30°23'N/102°50'E), USNM 258367–258380, 258382, 258384–258391, 258393–258401; **Weizhou** (=Wei Chow, 31°28'N/103°35'E), USNM 258546–258548; **Wen Chuan**, 258709, 259364 (see discussion of Wenchuan in section on *A. chevrieri*); **Shimian Xian, 17 km SSE Xinmian** (=Shimian, 29°15'N/102°23'E), **along Daho**, USNM 574336–574354, 574411–574457, 574471–574473; **Chu Mar, 21 mi SW Tze Ta Tee**, FMNH 32536; **Goan Shih Dwe**, FMNH 45080–45099, 45101–45146, 45148–45212, 45386, 45388, **Lu Erh Cheh**, FMNH 40688–40696; **Nai Su Chen**, FMNH 44922, 44923, 44925, 44927–44929, 44931, 44933, 44936–44944, 44946, 44947, 44954–44959, 44961–44968, 44970, 44973, 44976, 44977, 45365, 45394, 45396; **Ta Cho Fu** (29°12'N/103°20'E; Traylor 1967), **30 mi NW Minjian** (=Mapienting, 28°48'N/103°39'E), **just S Dadu He** (=Tung River), FMNH 40660, 40661, 40669, 40677, 40680, 40681, 40683, 40686, 40687; **Hsiao Yang Chi** (29°06'N/103°21'E; Kerbis Peterhans 1995), **27 mi W Minjian, S Dadu He**, FMNH 40700, 40707, 40708; **Yueh Li Tsai**, FMNH 44902; **Ta Tsai Tsu** (31°28'N/103°40'E; Traylor 1967), **NE Wen Chuan Hsien**, FMNH 44903–44915, 44917, 44919–44921; **Shan Wan Kun** (29°01'N/103°28'E; Kerbis Peterhans 1995), FMNH 40673–40676; **Guan Xian** (=Kuan Hsien, 31°00'N/103°37'E), **upper Min Jiang** (=Min River), FMNH 40712–40715, 40717–40721, 40723–40726, 40728–40741, 40743–40756, 40758–40761, 40763–40771, 40773, 40774, 40776–40780, 40782–40800, 40802, 40804–40807, 40811–40823, 40825–40843, 40845–40855, 40857–40859, 40861, 40863–40884, 40888–40893, 40895, 40898–40900; **Chou Tsen Goh, near Pin Yang Goh** (30°25'N/102°36'E; Kerbis Peterhans 1995), FMNH 44982, 45071, 45229–45232, 45236, 45238, 45239; **Dun Shih Goh** (30°25'N/102°51'E; Kerbis Peterhans 1995), **above Baoxing** (30°23'N/102°50'E), FMNH 37374, 37376, 37421–37433, 37435–37437, 37439–37447, 37449–37452, 37454–37473, 37475–37489, 37491–37498, 37500–37502, 37504–37520, 37522–37526, 37528–37541; **Fi Shan Kwan** (30°03'N/103°06'E; Kerbis Peterhans 1995), FMNH 40656; **Baoxing** (=Paohing=Mouping, 30°23'N/102°50'E), FMNH 37419, 37543–37548; **Pin Yang Goh** (30°25'N/102°36'E; Kerbis Peterhans 1995), **W Baoxing**, FMNH 44985, 44987, 44989, 44991–44993, 44995, 44998–45000, 45007, 45009, 45011, 45014, 45015, 45019–45021, 45025–45028, 45030, 45040, 45043, 45046, 45047, 45052, 45053, 45061, 45063, 45064, 45066, 45068, 45069, 45242, 45246–45257, 45260, 45262, 45269, 45272, 45274, 45277, 45278, 45398; **I-Tze**, FMNH 33145; **Mi-li**, FMNH 33141–33143, 33198, 33199; **N Hlagong**, FMNH 33146; **Gang Yang Go** (30°21'N/102°30'E; Kerbis Peterhans 1995), **20 mi WSW Baoxing**, FMNH

36384–36394; **Lu Ting Shan** (30°15'N/102°22'E; Kerbis Peterhans 1995), FMNH 36252–36344, 36346–36381 (6650–6850 ft), 36377–36381 (6650–7600 ft), 36395, 36505; “**Sichuan**” (no other data), FMNH 36404–36406.

Yunnan Province: **Zhongdian** (=Chung Tien), **Tomulang**, 10,000 ft, AMNH 43502, 43666, 43667, 43795, 43953, 43954, 43956 (see the note about this locality in the section on *A. latronum*); **Tuguancun** (=Tu-gan-sha, previously T'u-kuan-tsun), **20 mi S Zhongdian** (27°22'N/100°00'E), 10,000 ft, AMNH 43501, 43619, 43664, 43665, 43872, 43963, 43964, 44919, 44926, 44932, 44954, 44956 (see note in *A. latronum* section); **Hoa Shan**, **30 miles S Zhongdian**, AMNH 43654–43657, 43765–43767; **Phete** (also “**Pe-ti**” or “**Peh-ti**”) **Mountain**, AMNH 43660; 10,000 ft, AMNH 43774; **Phete Mountains**, **30 mi S Zhongdian**, 10,000 ft, AMNH 43618, 43653, 43661–43663, 43771–43773, 43864, 44923, 44963; **Phete Mountains**, **40 mi S Zhongdian**, 8000 ft, AMNH 43617, 43658, 43768, 43769; **Ha-pa**, **20 mi N Taku Ferry**, 10,000 ft, AMNH 43678, 43679, 43971 (see the note in section on *A. chevrieri*); **Lijiang**, **Yolungxue Shan** (=Snow Mountain), 12,000 ft, AMNH 43532, 43541, 43542, 43544, 43550, 43551, 43880, 43883; **Pes-hsui**, 9000 ft, AMNH 43715; 10,000 ft, AMNH 43519, 43523, 43526, 43564, 43565, 43568, 43651, 43652, 43703, 43704, 43708, 43709, 43824, 43825, 43851; **Ssu Shan Mountains**, 12,000 ft, AMNH 43531, 43558, 43559, 43562, 43700, 43823, 44800, 44933, 44957; **Ssu Shan Chang**, 9000 ft, AMNH 43570, 43574, 43576, 43591, 43714, 43849, 43850, 44809, 44813, 44817, 44822, 44922, 44936, 44937, 44948, 44952 (see note in *A. chevrieri* section); **Lancang Jiang** (=Mekong River), **Hsiao-tien**, 6500 ft, AMNH 43948; **Lancang Jiang**, **Hsiao-ke-la**, 8000 ft, AMNH 43597–43600, 43603, 43673, 43781, 43855, 43942–43944, 43946, FMNH 39406; **Lancang Jiang**, **Yin-pan-kai**, 9000 ft, AMNH 43604, 43775–43777, 43779, 43853, 43854, 43949, FMNH 39407 (see note in *A. chevrieri* section); **Lancang Jiang**, **La-chu-wei**, 9000 ft, AMNH 43669, 43670, 43782; **Lancang Jiang drainage**, **Pei-ping** (also “**Pi-ping**” or “**Peti-ping**”), 8000 ft, AMNH 43671, 43783, 43784, 43987, 43988 (Andrews and Heller collected in the “Mekong River drainage” after their expedition turned away from the Lancang Jiang but before they reached Jianchuan [=Chau-chuan chou, 26°28'N/99°52'E]. Our inferred coordinates of Pei-ping are 26°40'N/99°30'E.); **Lancang Jiang-Jinsha Jiang** (=Mekong-Yangtze Rivers) **Divide** (27°30'N/98°40'–99°20'E), 8000–9000 ft, FMNH 28959; **Lancang Jiang-Jinsha Jiang Valley** (28°00'N/98°40'–99°20'E), 7000 ft, FMNH 28960; **Ho-mu-shu Pass**, 8000 ft, AMNH 43593, 43796–43802, 43804–43809, 43811, 43813, 43815, 43816, 43986, 44062, 44870, FMNH 39413–39415; **Longchuan Jiang** (=Shiveli River), **Tai-ping-pu**, 7000 ft, AMNH 43788, 43789; 8000 ft, AMNH 43787 (“**Tai-ping-pu**” is between “**Ho-mu-shu**” and **Tengchong** [=Teng-yueh, 25°02'N/98°28'E]); **Nu Jiang** (=Salween River) **drainage**, **Mu-cheng** (23°45'N/99°11'E; Kerbis Peterhans 1995), AMNH 43513, 43719, 43720; 6000 ft, AMNH 43682, 43749, 43751–43756, 43758, 43760, 43762–43764, FMNH 39408–39410; 7000 ft, AMNH 43510, 43511, 43514, 43515, 43683, 43721–43724, 43726, 43727–43735, 43737–43748, 43979–43981, 43983, 44876, 44879–44884, 44886, 44894, 44946, 44953, 83972, FMNH 39411, 39412; **Nanding He** (=Namting River), **Burma Border**, AMNH 44872.

Hubei (=Hupei) **Province:** **Fan Xian** (=Fang Hsien, 32°04'N/110°47'E), 8500 ft, AMNH 36888.

Fujian (=Fukien) **Province:** **Chong'an Xian** (=Chungan Hsien, 27°46'N/118°01'E), AMNH 84751, 84754, 84757, 84758, 84760, 84763, 84768, 84770; **Kuatun**, 2000 m, ZFMK 50.445–50.447, 50.449, 50.451; **Kuatun**, USNM 141484, 252183–252185. (All these specimens from Fujian are topotypes or near-topotypes of *A. draco*.)

BURMA:

Kachin State: **Imaw Bum** (26°10'N/98°28'E), 9000 ft, AMNH 115324–115337, 115477–115481; **Nyetmaw River** (approximately 26°10'N/98°30'E), AMNH 115339 (9000 ft), 115340–115356, 115482–115486 (8600 ft); **Vijawlaw** (approximately 26°11'N/98°06'E), **5 mi NE Kangfang**, 6000 ft, AMNH 115314, 115315; **Kangfang** (=Gangfang, 26°08'N/98°35'E), 5200 ft, AMNH 115260–115276, 115278, 115279, 115282–115292, 115294, 115297, 115298, 115302–115313, 115316–115321, 115495, 115544, 115553; **above Tsonma** (26°09'N/98°34'E), **1 mi W Kangfang**, 8300 ft, AMNH 115357, 115487; **Tangtung** (26°04'N/98°35'E), **S of Kangfang**, 5077 ft, AMNH 115375, 115376; **Pawahku** (26°11'N/98°40'E), 7400 ft, AMNH 115358, 115373, 115374, 115490; **Chimeli Pass road** (approximately 26°12'N/98°41'E), AMNH 115359–115363, 115366, 115367, 115370, 115488, 115489 (10,000 ft), 115364, 115365, 115368, 115369, 115371, 115372 (9800–10,800 ft); **Hpinmaw** (26°01'N/98°37'E), 7600 ft, AMNH 115377–115383, 115395; **Hpinmaw road**, **SE Hpinmaw**, 9000 ft, AMNH 115384–115394, 115396, 115397; **Black Rock** (approximately 26°01'N/98°32'E), AMNH 115399; **Hpinlawshka** (=Hpinlaw River, approximately 26°00'N/98°25'E), 4200 ft, AMNH 115491; **Htawgaw**, 5600 ft, AMNH 115461, 115492, 115258, 115259, 115400, 115401, 115494; **Luksuk** (approximately 25°54'N/98°24'E), 5200 ft, AMNH 115402, 115403; **Hpare** (25°50'N/98°25'E), 6000 ft, AMNH 115404, 115438–115454, 115459, 115460; **Hpare Pass Camp** (approximate

mately 25°46'N/98°27'E), 8500 ft, AMNH 115455–115458; **Hpare-Saulang road**, 8200 ft, AMNH 115428–115436; **Saulang** (25°42'N/98°21'E), 6500 ft, AMNH 115405–115408, 115425–115427; **Changy-inku** (25°35'N/98°21'E), 7000 ft, AMNH 115409–115424; **Nam Kui Mts, Adung Valley** (28°10'–15°N/97°40'E), FMNH 40967–40975 (6000 ft), 40971–40983 (8000 ft), 40984–40994 (12,000 ft). (We relied on Anthony's reports, both unpublished [1939] and published [1941] for information about localities in Kachin State where American Museum specimens were collected; the map provided by Anthony [1941] was particularly helpful. Coordinates indicated as “approximately” were inferred from Anthony's map, the others are from the Burma Gazetteer [USBGN Burma, 1966].)

Chin State: Mount Victoria (21°14'N/93°55'E; from USBGN Burma, 1966), AMNH 163692 (2200 m), 163663–163683, 163685, 163686, 163688–163691 (2600 m), 163687 (2800 m).

INDIA:

Arunachal Pradesh: Miao, Upper Camp (27°15'N/96°52'E), 2500 m, USNM 564493.

Apodemus semotus

Remarks: Originally described as a species of *Apodemus* by Thomas (1908), *semotus* was later listed as a subspecies of *A. sylvaticus* (Ellerman 1949; Ellerman & Morrison-Scott 1951). Corbet (1978: 137) treated it as a species, an action followed by Musser & Carleton (1993), but Corbet also noted that the “form is close to *A. draco* and could be conspecific with it.” Corbet & Hill (1992) did include *semotus* within *A. draco* but questioned the association. In its morphology, the specimens of *semotus* in the American Museum and National Museum of Natural History are more similar to examples of *draco* than to any other mainland species represented by our samples; its relationship to mainland *A. draco* will have to be resolved in the context of a critical systematic revision of *A. draco*, as well as *A. semotus*, in which the extent of individual and geographic variation in and among mainland and island samples is addressed.

Apodemus semotus is a montane endemic, most commonly found between 1400 and 3700 m, but rarely below or above those altitudes. The only other species of *Apodemus* occurring on Taiwan is *A. agrarius*, which is found only below 1000 m (Yu 1994).

Localities and specimens examined:

CHINA:

Taiwan Province: Chia-i Xian, Ali Shan (=Mount Ali, Mount Arisan, 23°32'N/120°48'E), AMNH 247647 (2200 m), USNM 261050–261059, 283740, 283741, 295128, 332993–333025; **Chia-i Xian, Ali Shan Station**, USNM 358371–358375; **2 km W Ali Shan Station**, USNM 358370, 358376–358380; **Nan-t'ou Xian, Chuei Feng**, USNM 332983–332992, 333027, 333032–333034; **Nan-t'ou Xian, Wu-she** (=Wu-sheh, 24°02'N/121°08'E), USNM 333026, 333028–333031; **Nan-t'ou Xian, Ho Huan Shan** (24°09'N/121°16'E), USNM 358381–358396.

Apodemus peninsulae

Remarks: Jones (1956) carefully reviewed the taxonomic history of *A. peninsulae*, from its original description by Thomas (1907) as a subspecies of *Micromys speciosus*, through the stage during which it was recognized as a separate species (Allen 1940; Hollister 1913; Miller 1914), to its submersion as a subspecies of *A. flavicollis* (Ellerman 1949; Ellerman & Morrison-Scott 1951). He also enumerated the traits distinguishing *A. flavicollis* and *A. peninsulae* and described a new subspecies of the latter, *A. p. sowerbyi*, from northern China.

Subsequent reports on *Apodemus* or Asian faunal assemblages have reinforced the species-integrity of *peninsulae* as a member of the palearctic fauna (Zimmermann 1962, 1964; Jones & Johnson 1965; Vorontsov et al. 1977; Corbet 1978; Xia 1984, 1985; Pavlinov & Rossolimo 1987; Mezhzherin & Zikov 1991; Feng et al. 1983, 1986; Martens & Niethammer 1972; Musser & Carleton 1993). Museum records listed here are within the recorded geographic range of *A. peninsulae*, which consists of a northern segment and two southern arms (see the map in Corbet 1978: 252). The northern range extends through southern Siberia from the Altai Mountains in the west to the Ussuri region in the east (Vorontsov et al. 1977; Bekasova et al. 1980), as well as the island of Sakhalin in the Russian Federation and the northern Japanese island of Hokkaidō. Based upon our records, an eastern arm drops south through eastern Mongolia and northeastern China through the provinces of Heilongjiang, Jilin, Liaoning, Hebei, E Nei Mongol, covers the Korean Peninsula, then extends westward through northern China in the provinces of Shanxi, Shaanxi, southeastern Gansu to southeastern Qinghai, then drops south through western Sichuan. Feng et al. (1983) recorded the species from southwestern Sichuan and eastern Xizang (Tibet), and Allen (1940) referred to a specimen from northwestern Yunnan. There are no records south of that region of Yunnan, and none west of about 92° east longitude. Musser & Carleton (1993) incorrectly included the Chinese province of Xinjiang within the range of *A. peninsulae*, but only *A. agrarius* and *A. uralensis* (recorded as *A. sylvaticus tscherga*) are known from that region (Ma et al. 1987).

Apodemus peninsulae and *A. draco* are superficially similar in their morphologies, leading Corbet (1978: 137) to suggest they are conspecific. Corbet & Hill (1992), however, recognized both species. Some American Museum series of *A. draco* were originally identified as *A. peninsulae*, and we found samples of each in other museums misidentified as either *A. peninsulae* or *A. draco*. Examples of Chinese *A. peninsulae* contrast most conspicuously with specimens of *A. draco* in ear and molar traits: the buffy pinnae of *A. peninsulae* are the same color as the rest of the dorsal fur, and lack a swatch of dark hairs at their anterior bases; cusp t7 on each first upper molar is conspicuously smaller than the anterior lingual cusps t1 and t4 and usually occurs as a spur or narrow ridge off the central cusp t8 (fig. 5C). Ears of *A. draco* are blackish brown, the anterior base of each partially covered with a preauricular tuft of long black hairs; both dark preauricular tuft and ears provide vivid contrast with the general dorsal color of the upperparts. Cusp t7 in *A. draco* is much larger, subequal in size to cusps t1 and t4, and forms a distinct cusplet off the central cusp t8 (fig. 5B). These discriminating features were pointed out by Allen (1940), who also noted the close general resemblance between the two species.

Our inspection revealed other traits that seem to distinguish samples of the two species. *Apodemus draco* has absolutely larger pinnae, relatively longer incisive foramina, usually reaching the level of, or sometimes penetrating between, the anterior root of the first upper molars, as compared to terminating short of the roots in *A. peninsulae*. The zygomatic plate and hind feet seem narrower in *A. draco* than seen in *A. peninsulae*.

Apodemus peninsulae occurs primarily in northern latitudes, *A. draco* ranges mainly to the south and west of *A. peninsulae*, and their distributions slightly overlap in northern China (northern Hebei and southern Shaanxi), judged by the specimens

recorded in our report. Although they overlap, we have no evidence from our material, nor from published documentation, that both species occur at the same locality. Jones (1956: 342) mentioned twelve specimens from 65–75 miles northeast of Beijing that were originally identified as *A. peninsulae*, four of which he retained as that species, but reallocated the rest to *A. draco*. We studied the same series in the National Museum and determined all 12 to be *A. peninsulae* based on characters discussed above. Both species are similar in body size and morphology. If they also have similar diets they might not be able to utilize resources at the same place and may not be syntopic but perhaps parapatric.

In western Sichuan, examples of *A. peninsulae* and *A. latronum* have been collected together at two places: 20 mi N Litang, and in the Mu-chu Valley of the Gongga Shan (see lists of Localities and specimens examined). *Apodemus latronum* is much larger in body size than *A. peninsulae*.

The American Museum and National Museum series of *A. peninsulae* illustrate what may be significant geographic variation in body size that was formally defined by Jones (1956) when he described Chinese samples under the name *sowerbyi*, a distinctive subspecies of *A. peninsulae*. Jones pointed out that his samples from Korea, northern Manchuria (=Heilongjiang), and Siberia contained specimens that are basically larger and brighter than examples from China obtained at about 40° latitude and south of there to possibly northeastern Sichuan. His table of measurements (1956: 344) clearly illustrates the size difference. Our specimens from northern China (Heilongjiang, Jilin, and Liaoning), Mongolia, Russian Federation, North and South Korea (also identified by Jones & Johnson 1965: 387, as typical *peninsulae*), and the Japanese island of Hokkaido are noticeably larger (as judged by size of skull) and have brighter fur than do examples from farther south in China (Hebei, southern Nei Mongol, Shanxi, Shaanxi, SE Gansu, SE Qinghai, and W Sichuan). The contrast between the two sets of samples is striking and, except for Jones' astute observations, has been overlooked or unremarked in reports dealing with *A. peninsulae* (Corbet 1978, for example). A careful study of geographic variation in samples now identified as *A. peninsulae* is needed to test the alternative hypotheses that the geographic variation reflects the presence of two species, possibly parapatric in distribution, or just north-south clinal variation in body size within one species. If no morphological or genic evidence of intergradation between northern and southern samples can be demonstrated, the central and southern Chinese segment should be recognized as *A. sowerbyi*. One probable synonym of *sowerbyi*, whether treated as species or subspecies, is *qinghaiensis*, a subspecies of *A. peninsulae* described by Feng et al. (1983) based upon samples from southwestern Sichuan and eastern Xizang (Tibet).

Samples identified as *A. peninsulae* need to be reassessed in the context of a careful systematic study to determine 1) the significance of morphological variation within and among series, 2) the actual geographic range of the species, and 3) its phylogenetic relationship to *A. draco* and the extent and details in overlap of geographic distributions. Study of our specimens and those of other species listed here indicates that the morphology of *A. peninsulae* is distinctive compared with all other species of *Apodemus*.

Localities and specimens examined:

CHINA:

Heilongjiang (=North Manchuria) **Province: Xiaoling** (=Hsiaoling, 45°22'N/127°17'E), AMNH 120445, FMNH 44759; **Yimianpo** (=I-mien-po, 45°03'N/128°04'E), USNM 199668–199671; near **Yimianpo**, USNM 199666, 199667, 201280–201293; **Shuanghe**, USNM 544446.

Jilin Province: Songhua Jiang (=Sungaree River), **60 mi SW Jilin** (=Chilin=Kirin, 43°53'N/126°35'E), USNM 197784–197791, 197794 (holotype of *Apodemus praetor*), 197793, 197794; **Hang-Tao-Hetzu**, FMNH 44757, 44758.

Hebei (=Chihhi) **Province: 100 mi NE Beijing**, AMNH 45460–45463, 56449, 56451–56458, 56465, 56468–56471, FMNH 32772–32775; **Hsin-lung-shan**, **65 mi NE Peking**, USNM 219224–219233, 219235; **Wuling Shan** (40°47'N/117°30'E), **75 mi NE Peking**, USNM 219234.

Nei Mongol Autonomous Region (=N. Shansi): **Hohhot** (=Kwei hua cheng, 40°47'N/111°37'E), AMNH 45385–45387, 56473; **mountains 30 mi W Hohhot**, USNM 175521, 175522, 175523 (holotype of *Apodemus peninsulae sowerbyi*), 175525 (“mountains” not included in locality designated in description of the subspecies); **Da Hinggan Ling** (=Great Khingan Mountains, 49°00'N/122°00'E), **Yalu** (48°33'N/122°07'E), FMNH 44351; **Yalu Station, China East Railway**, FMNH 49910, USNM 270438, 270439.

Liaoning Province: Fengtien, **20 mi SSE Chiao-yang-chen**, USNM 197783; **Fengtien**, “**35 mi SW SSE**” **Chiao-yang-chen**, USNM 197782 (We found coordinates for both of these localities, but they don't match the relationships as described. Shenyang [Fengtien, 41°48'N/123°27'E] and Chaoyang [Ch'ao-yang-chen, 41°33'N 120°25'E]).

Jiangxi Province: Yichun (=I-ch'un), **Cenyang** (=Hsing'an, 28°25'N/117°35'E), ZFMK 59.329.

Shanxi (=Shansi) **Province: Lung-wang-shan**, **20 mi E Taiyuan** (=Tai-yuan-fu, 37°52'N/112°33'E), 4000 ft, AMNH 36894, 36895; **He-shuin**, AMNH 45389; **mountains 50 mi NW Taiyuan** (=T'ai-yuan-fu, 37°52'N/112°33'E), USNM 172559–172562; **Chiao-cheng-shan**, **90 mi W Taiyuan**, USNM 155068–155071; **18 mi W Taiyuan**, USNM 155067; **Longwang** (=Lung-wang-shan, 37°20'N/113°13'E), **20 mi E Taiyuan**, USNM 172506, 172508–172515, 172558.

Shaanxi (=Shensi) **Province: 45 mi S Fengxiang** (=Fengsiangfu, 34°32'N/107°23'E), 3600 ft, AMNH 32281, 32282; **12 mi S of Yan'an** (=Yenan-fu, 36°36'N/109°28'E), USNM 155072–155075.

Gansu (=Kansu) **Province: Mountains 10 mi SW Jonê** (=Choni, 34°35'N/103°32'E), AMNH 84289, 84292, 84294–84302; FMNH 32777; **Jonê** (34°35'N/103°32'E), FMNH 36072–36076, 36093; **Archuen**, AMNH 34285, 34286, 34288, 34290, 34291, FMNH 32776; **mountains 15 mi S Lanzhou** (=Lanchow, 36°03'N/103°41'E), USNM 155171; **40 mi SE Xincheng** (=Taochou, 34°43'N/103°35'E), 11,000 ft, FMNH 19076, 19077; **10 mi SE Xincheng** (=Taochou), 8000, 8500 ft, FMNH 19078, 19079.

Qinghai Province: Yushu Zangzu Zizhizhou, **Nangqên Xian** (32°15'N/96°13'E), **Bei Zha Forestry Station**, USNM 449148–449150, 449174, 449175.

Sichuan Province: 10 mi N Dawu Xian (=Tao Fu Shien, 31°00'N/101°09'E), 10,500 ft, AMNH 113624; **20 mi N Litang**, AMNH 113681, 113682; **26 mi E Litang**, 15,000 ft, AMNH 113625, 113685; **Litang**, 30°02'N/101°21'E, 14,000 ft, AMNH 113684; **Gongga Shan** (=Minya Konka), **Mu Chu Valley** (29°34'N/101°53'E), AMNH 113642–113644 (see note in *A. latronum* section).

RUSSIAN FEDERATION:

W Siberia: Krasnoyarsk Kray, Khakassia Republic (=Khakas-skaya A.O.), **Abakan** (53°43'N/91°25'E), USNM 254967.

Siberia: Altay Kray: 25 mi SE of Biysk (=Biisk, 52°35'N/85°16'E), **Altai Mountains, Tepucha**, USNM 175164 (holotype of *Apodemus nigrilis*); **Eastern Siberia, Tandy** (49°18'N/81°18'E), USNM 257373–257381.

Southern Siberia, Chita Oblast': Sretensk (52°15'N/117°52'E), AMNH 178835; **Transbaikalia, vicinity of Sretensk**, AMNH 87092.

Amurskaya Oblast': Svobodnyy Rayon (51°24'N/128°05'E), USNM 448224, 448225.

Khabarovsk Kray: Amur River, Nanke, **75 mi N Khabarovsk**, AMNH 85470; **Nelta River, 60 mi N Khabarovsk**, AMNH 85469; **Monoma River, 80 mi E Troitskoye** (=Troitskoy, 49°25'N/136°32'E), AMNH 85422.

Gorno-Altay Republic: Dapucha, Altai, USNM 175163, 175168–175171.

MONGOLIA:

15 mi N Ulaanbaatar (=Urga, 47°54'N/106°52'E), AMNH 45842, 45843.

NORTH KOREA:

North Hamgyong Province: Tumen river valley, Musan (42°12'N/129°15'E), AMNH 34066, 34067; Hozando, AMNH 34052, 34062, 34065, 34093 (see note in *A. agrarius* section); Tumen river valley, 18 mi SW Nonsatong, AMNH 34053, 34056, 34058, 34061; 43 mi SW Nonsatong, AMNH 34068 (Nojido is actually written on the skin tags, but Andrews wrote that Nojido and Nonsatong "are synonyms, being simply the Japanese and Korean names of the same place." He also noted that this locality is in the Tumen river valley, 50 miles away from Musan, but he doesn't reveal in which direction it lies from Musan [correspondence files in AMNH Department of Mammalogy]. USOG for Korea, 1963, listed a "Nongsa-dong" at 42°03'N/129°59'E, almost exactly 50 mi SE of Musan, very close to the sea of Japan; that place, however, is not in the Tumen river valley.).

Hyesan Province: P'ot'ae-nodongjagu (=Potaidon, 41°43'N/128°20'E; USBGN for Korea, 1963; Jones & Johnson 1965: 403 give approximate coordinates of 41°43'N/128°22'E for "Potai-dong"), USNM 197974, 197975.

"Korea": Kuksa-bong (apparently in North Korea; see comment in list of *A. agrarius*), USNM 198177.

North Korea: (Province not determinable), 150 mi up Yalu River, USNM 199662–199664.

SOUTH KOREA:

Kyonggi Province: Soul-t'ukpyolsi, Soul (=Seoul, 37°30'N/127°00'E), AMNH 170067, 170068, 170099–17102; Soul-t'ukpyolsi, 6 mi S Yongdungp'o, USNM 299554; Soul-t'ukpyolsi, 6 mi E Soul, 45 m, USNM 299526, 299612; Central National Forest, 15–18 mi NE Soul, USNM 298169–298173, 299585; Central National Forest, Pup'yong-ni (37°44'N/127°12'E), USNM 299113, 299236, 299239, 299240, 300651; Central National Forest, near Pup'yong-ni, 200 m, USNM 299112, 299230–299235, 299237, 299238, 299530, 299531, 299553, 299559, 300650; 4 mi S Yonch'on (38°06'N/127°04'E), USNM 294719; 7 mi SSE Munsan-ni (37°51'N/126°47'E), USNM 302913; Toktun-ni (37°58'N/127°07'E), USNM 294707, 294708.

Kangwon Province: Chip'o-ri (38°08'N/127°19'E), USNM 294669, 294700–294705; Kumbwa (38°17'N/127°28'E), USNM 294709–294712; 8 mi SW Kangnung (37°45'N/128°54'E), 550 m, USNM 298972–298974; 3 mi SSE Sumil-li (38°02'N/127°30'E), 1468 m, USNM 299229; Ch'ongyang-ni (38°15'N/127°23'E), USNM 294706.

JAPAN:

Hokkaidō: Sapporo (43°05'N/141°21'E), USNM 281679, 281680.

Apodemus gurkha

Remarks: This very distinctive Nepalese species was named and first described by Thomas in 1924, but later relegated as a subspecies of *A. flavicollis* by Ellerman (1949, 1961) and Ellerman & Morrison-Scott (1951). Martens & Niethammer (1972) extracted *gurkha* from synonymy, documenting its morphological limits and geographic distribution based on 44 specimens. They concluded that particular morphological traits of the skin, skull, and dentition allied *A. gurkha* with Oriental species of *Apodemus* in the subgenus *Alsomys* rather than *A. sylvaticus* and its allies in the subgenus *Sylvaemus*, which supported Zimmermann's (1962) premise. Chromosomal evidence also seemed to affirm a link between *A. gurkha* and the Oriental group (Gemmeke & Niethammer 1982). *Apodemus gurkha* is now recognized as a unique endemic of Nepal (Corbet 1978; Corbet & Hill 1992; Musser & Carleton 1993).

Localities and specimens examined:

NEPAL:

Myagdi District: Dhorpatan (28°33'N/83°05'E), FMNH 142105 (8950 ft), ZFMK 84.1092–84.1099 (3000 m); Dhorpatan, Uttar-Ganga Valley, 2950 m, ZFMK 84.1100, 84.1101, 84.1113–84.1155, 92.138–92.146, 92.152; Bobang, S Dhorpatan, 2450 m, ZFMK 84.1102–84.1109; Thankur, N Dhorpatan, 3350 m, ZFMK 84.1156–84.1159, 92.147; Ghustung Khola, trail from Dhorpatan to Tarakot, 2900 m, ZFMK 84.1110, 84.1111.

Mustang District: Thakkola, Chadziou Khola, 2600 m, ZFMK 84.1069–84.1072, 84.1074–84.1076;

Thakkola, Meristi Khola, 3450 m, ZFMK 84.1073; **Thakkola, Tukche, Thaksang**, 3150 m, ZFMK 84.1077, 84.1078, 84.1081—84.1088, 84.1164—84.1172; **Thakkola, Lake Titi**, 2700 m, ZFMK 84.1079; **Thakkola, Lethe**, 2450—2600 m, ZFMK 84.1080, 92.151; **Thakkola, Purano Marpha**, 3200 m, ZFMK 84.1175; **Kali Gandaki valley, above Marpha**, 3100 m, ZFMK 84.1176.

Parbat District: Gorapani pass, 2850 m, ZFMK 84.1089–84.1091.

Dolpo District: Barbung Khola, Gompa near Tarakot (28°53'N/82°59'E), 3250 m, ZFMK 84.1160—84.1163; **Dolpa, Ringmo/Phoksumdo lake**, 3750 m, ZFMK 84.1112.

Manang District: Marsiyandi valley (=Marsiyandi), **Thimang**, 3000 m, ZFMK 84.1173, 84.1174.

Gortha District: Chhyul-Wang Valley, Meme Kharka, 3400 m, ZFMK 84.1177.

District undetermined: Maharigaon (29°21'N/82°23'E), 10,375 ft, FMNH 142106; **Sathar Hill**, FMNH 82938; **Sottidanda**, 12,000 ft, FMNH 82939; “Nepal” (no other data), ZFMK 92.148, 92.149.

Apodemus speciosus

Remarks: *Apodemus speciosus* occurs on the four primary and other smaller islands of Japan (Saitoh et al. 1989; Corbet 1978; Musser & Carleton 1993), and has been restricted to the archipelago from at least Middle Pleistocene and certainly earlier (Kawamura 1989). It occurs together with *A. peninsulae* on the Japanese island of Hokkaido and is considered by some researchers to be closely related to that species (Bekasova et al. 1980; Saitoh et al. 1989; Xia 1985). *Apodemus speciosus* is morphologically and phylogenetically distant from *A. argenteus*, the only other *Apodemus* endemic to Japan (Saitoh et al. 1989).

Musser & Carleton (1993) and Kawamura (1989) provided references reviewing the taxonomic history of *A. speciosus*. Numerous samples of the species, mostly molars, are available from Middle and Late Pleistocene, as well as Holocene deposits. These have been analyzed in great detail by Kawamura (1989: 57), who also noted that “the temporal morphological changes since the Middle Pleistocene are generally slight in...” *A. speciosus*.

Localities and specimens examined:

JAPAN:

Hokkaido: Sapporo, Ishiyama (=Ishkiri-yama, 42°58'N/141°20'E), USNM 299426—299428; **Tarumae-san** (=Tarumai-dake, 42°41'N/141°23'E), USNM 299424—299425; **Jozankei** (42°58'N/141°10'E), SW of Sapporo, USNM 299429, 299430.

Honshū: Myagi-ken, Onagawa, USNM 290614—290621, 291745—291748; **Myagi-ken, Sendai** (38°16'N/140°52'E), **Ojojihara**, USNM 294422, 294423, 299361—299365, 299390—299394, 299592; **Myagi-ken, Sendai, Fukanuma**, USNM 299367; **Sado Island, 2.5 mi SE Shinmachi**, USNM 300318; **Nagano-ken, Inamachi**, 700 m, AMNH 148556; **Nagano-ken, Karuisawa** (36°21'N/138°38'E), USNM 260877—260881.

Shizuoka-ken, foothills at base of Mount Fuji (35°25'N/138°42'E), AMNH 232455; **Shizuoka-ken, Fuji**, USNM 299401—299410; **Shizuoka-ken, Fuji Yama**, USNM 355904; **Shizuoka-ken: Fuji-san** (=Mount Fuji), **SE slope** (35°22'N/138°44'E), USNM 356066—356070; **Fuji-san, SE slope, North Camp**, USNM 356016—356065; **Kanagawa-ken, Koajiro** (=Koajoro), USNM 123669; **Kanagawa-ken, Miura** (35°08'N/139°37'E), USNM 115306—115309 (Some combination of the names “Koajiro Miura Misaki, Koajiro Misaki Miura, and Koajiro Sagami [prov.]” are on skin tags of these four specimens. They misleadingly appear to have been collected at different localities, with several confusing place names, but Sagami is the gulf, Koajiro is the bay in the gulf, Misaki is the peninsula that juts out into the bay that is in the gulf, and Miura is the town on the peninsula, the actual origin of all four animals.); **Kyōto-ken, Kyoto** (35°02'N/135°45'E), FMNH 44376; **Hyōgo-ken, Sasayama** (35°03'N/135°12'E), FMNH 44375; **Hyōgo-ken, Kobe** (34°40'N/135°12'E), USNM 148774; **Yamanashi-ken, Yamanaka-ko** (=Lake Yamanaka, 35°25'N/138°52'E), FMNH 47011, 47012, USNM 260882—260887, 266936—266938; **Yamanashi-ken, Fuji**, USNM 299395—299400; **Tōkyō-ken, Tōkyō** (35°40'N/139°45'E), USNM 121270, 121271; **Gifu-ken, Naka-chō** (35°24'N/136°50'E), **Camp Gifu**, USNM 355907—355909; **Yamagata-ken, Gawa Mogami** (=Mogami River), USNM 279403; **Yamagata-ken, Tateoka** (38°29'N/140°23'E), USNM 294424, 294425,

299352–299360, 299366; **Tochigi-ken** (=Totigi or Totiai), **Yumoto** (37°01'N/140°51'E), FMNH 47013, USNM 266941; **Hiroshima-ken**, **Hiwa-machi**, **Hiba-gun**, 420 m, ZFMK 58.257.

Shikoku: **Shimizu** (=Shimidzu, 32°46'N/132°57'E or 32°57'N/132°48'E), AMNH 31637–31643; **Tokushima**, **Awaikeda**, USNM 299411–299423.

Kyūshū: **Amakusa Shimo-shima**, **Hondo** (32°28'N/130°12'E), AMNH 119646, 119647; **Hakata** (this may be Hakata-kō, 33°37'N/130°23'E, or Hakata-nai-kō, 33°36'N/130°24'E; both are described as harbor/basin), USNM 294420, 294421; **Kumamoto-ken**, USNM 299368–299376, **Kumamoto-ken**, **Owaga** ("=Ozawa"), **Aso-gun**, USNM 399106; **Ōita-ken**, **Beppu** (33°18'N/131°30'E), USNM 299377–299389; **Nagasaki-ken**, **Tsushima**, **Izuhara** (34°128'N/129°17'E), USNM 399107.

Apodemus argenteus

Remarks: This distinctive forest mouse has not been confused with other species of *Apodemus* from the time it was named in 1844 (see Barrett-Hamilton 1900; Corbet 1978; Kawamura 1989; Musser & Carleton 1993). It occurs on Hokkaidō, Honshū, Shikoku, Kyūshū, and other smaller islands in the Japanese archipelago where it has “flourished” since the Middle Pleistocene. “Because even the Middle Pleistocene fossils of *A. argenteus* are hardly different from the living animals, this species possibly arose from its ancestor in the periods earlier than the Middle Pleistocene” (Kawamura 1989: 86).

Localities and specimens examined:

JAPAN:

Hokkaidō: **Sapporo**, **Ishiyama** (=Ishikiri-yama, 42°58'N/141°20'E), USNM 299450–299452; **Jōzankei** (42°58'N/141°10'E), **SW of Sapporo**, USNM 299453, 299454.

Honshū: **Miyagi-ken**, **Onagawa** (38°26'N/141°27'E), USNM 291744; **Niigata-ken**, **Akakura**, 1500 ft, FMNH 28948; **Tochigi-ken** (=Totigi-ken=Totiai-ken), **Yumoto** (37°01'N/140°51'E), FMNH 47014, 47015, USNM 266939, 266940; **Nagano-ken**, **Yatsuga-take Pk**, **Meiji** (35°58'N/138°22'E for Yatsuga-take), FMNH 28949; **Tōkyō**, **Asakawa District**, **Tōkyō** (35°40'N/139°45'E), 200 m, AMNH 148567; **Shizuoka-ken**, **Fuji**, USNM 299432–299448; **Shizuoka-ken**, **Fuji-san** (=Mount Fuji), **SE slope** (35°22'N/138°44'E), USNM 356092–356128; **Fuji-san**, **SE slope**, **North Camp**, USNM 356071–356078, 356088–356091, 356129; **Fuji-san**, **SE slope**, **Jig area**, USNM 356079–356087; **Hyōgo-ken**, **Kōbe** (34°40'N/135°12'E), AMNH 119645, FMNH 44377, 44378; **Wakayama-ken**, **Nachi Falls**, 300 m, AMNH 184578; **Yamanashi-ken**, **Fuji**, USNM 299449, 355905; **Hiroshima-ken**, **Hiwa-machi**, **Hiba-gun**, 420 m, ZFMK 58.255.

Kyūshū: **Ōita**, **Beppu** (33°18'N/131°30'E), USNM 299431; **Fukuoka**, **Hiko-san** (=Mount Hiko, 33°29'N/130°56'E), USNM 399108; **Amakusa Shimo-shima**, **Hondo** (32°28'N/130°12'E), AMNH 119644.

Shikoku: **Kōchi-ken**, **Lu-Chu Islands**, **Okino-shima** (32°43'N/132°32'E), FMNH 48816 (50 ft), 48817 (100 ft), 48818 (300 ft).

European Apodemus

European species of *Apodemus* are well represented in the American Museum of Natural History, the Field Museum of Natural History, the National Museum of Natural History, and the Museum Alexander Koenig. Most series consist of *A. sylvaticus*, *A. flavicollis*, and *A. mystacinus*. We do not list these specimens because the morphologies and geographic distributions of the species have been more fully documented compared with the published records available for the Oriental group (see the references in Niethammer & Krapp 1978a, and Musser & Carleton 1993).

We record here only information about *A. alpicola*. It is not generally known that the American Museum of Natural History houses a large number of specimens, including the holotype (Lawrence 1993: 137), upon which Heinrich (1951) formulated

his description of *alpicola*, originally named *alpinus*, or that examples are also held by the Field Museum of Natural History and the Museum Alexander Koenig. These samples are available for study and form a potentially important source of morphometric data that could be used in a thorough systematic revision of *Apodemus*.

Apodemus alpicola

Remarks: In 1951 Gerd Heinrich described what he thought was a distinctive montane population of *Apodemus flavicollis*, calling it *A. f. alpinus*. His sample consisted of 82 specimens (Heinrich 1951: 114) and initially he sent fourteen of these to the American Museum of Natural History; subsequently Heinrich sent the holotype and 26 additional specimens from his personal collection to New York, and six examples to Chicago.

The name *alpinus*, Heinrich (1952: 260) discovered, had already been used for a population of *A. sylvaticus* so he proposed *alpicola* to replace it. That is not all that would change; in 1989, Storch & Lütt compared samples of *alpicola* with those of *A. flavicollis* and *A. sylvaticus* and carefully documented a suite of morphological traits that set *alpicola* apart as a species — not subspecies — from the other two kinds of *Apodemus*. Storch & Lütt also noted that the three species occurred together in the same forest.

Subsequent studies of *A. alpicola* have been undertaken in a biochemical context. To test the assertion of Storch & Lütt (1989), which was derived from study of morphology, Vogel et al. (1991) analyzed allozyme variation at 27 loci in samples of *A. alpicola*, *A. flavicollis*, and *A. sylvaticus*. At one level, their results confirmed the conclusion reached by Storch & Lütt and simply added biochemical traits to the morphological attributes that defined *alpicola* as a distinct species; at another, their determinations of genetic distance revealed *A. alpicola* to be more closely related to *A. sylvaticus* than to *A. flavicollis*.

The specific identity of *alpicola* was also reinforced by Filippucci's (1992) study of allozymic variation at 28–33 loci in samples of *A. agrarius*, *A. flavicollis*, *A. sylvaticus*, *A. alpicola*, *A. microps*, *A. hermonensis*, and *A. mystacinus*. Although Filippucci substantiated the validity of *alpicola* as a species, her analyses of allozyme variation portrayed a different configuration of relationships than that suggested by Vogel et al. (1991). Among the seven species, Filippucci obtained the smallest genetic distances between *A. microps* and *A. alpicola*, and between *A. flavicollis* and *A. hermonensis*, with a lower mean value of genetic distance between these two species-pairs than between any other set of groupings. To Filippucci, such results implied a recent separation of the four species from a common ancestor, a split that "occurred in the last 600,000 years" (p. 213).

The postulated close genetic relationship between *A. alpicola* and *A. microps* invites further inquiry. The species that was known as *microps* is currently called *A. uralensis*; it is found in eastern Europe and Turkey, extends east to the Altai Mountains and northwestern China (Xinjiang), and south into the Caucasus (see references in Musser & Carleton 1993).

Both the geographic range of *A. uralensis* and the scientific names associated with it are in revision, largely a result of biological exploration in the field and of in-

investigators critically studying and reidentifying specimens already in museums and other institutions. Until recently, for example, the range of *A. uralensis* in Eastern Europe was not known to include the Baltic region (Steiner 1978, documented under *microps*), but Zagorodnyuk & Mezhzherin (1992) have recorded it from Estonia, Latvia, northern Lithuania and Belorussia, and the adjacent area of the Russian Federation. Their records are based on original data and specimens previously stored in museum collections.

Another new record for the species was given by Kyselyuk (1993, under *microps*) from the high altitudes of the Carpathian range in extreme southwestern Ukraine.

Finally, Zagorodnyuk (1993) has altered the range of *A. uralensis* and transferred one of its former synonyms to another species. Specimens from the eastern Ukraine, particularly those east of the Dnepr River, that had been historically identified as *charkovensis*, which was considered to be a form of *A. uralensis* (see references in Musser & Carleton 1993: 574), are actually examples of *A. sylvaticus*, according to Zagorodnyuk's reidentifications of museum specimens and freshly collected material. He contends that *charkovensis* is the easternmost subspecies of *A. sylvaticus*, not *A. uralensis*.

A critical survey of North American and European museums will probably uncover additional examples of *A. uralensis*. Such material could be used in revisionary studies of *Apodemus* to more rigorously define the morphological and geographic boundaries of *A. uralensis* and to provide data for testing Filippucci's (1992) sister-group hypothesis between *A. uralensis* and *A. alpicola*.

Localities and specimens examined:

GERMANY:

Bayern: Allgäuer Alpen, Kempten (=Allgäu), **Osterach-Tal**, 1100 m, AMNH 145921 (holotype of *A. flavicollis alpinus*), 163201, 163202, 163204, 181893–181898, 181902–181906, 181966–181969, FMNH 66238–66241, ZFMK 49.20–49.25; **Pfannenhölzer**, 1800 m, AMNH 181899, 181900; **Hinterstein**, 1000 m, AMNH 163203, 181901; **Bayerische Alpen, Berchtesgaden**, 1100–1300, and 1700 m, AMNH 162916, 162917, 162923, 162924, 162927, 162928, 181880–181883; FMNH 63844, 63841 (*A. flavicollis*, AMNH 162914, 162915, 162918–162922, 162925, 162926, was also collected at Berchtesgaden during the same months of 1947).

AUSTRIA:

Steiermark: Admont, Kaiserau, 1000 and 1300 m, AMNH 163329, 181884, 181917–181921, 181928–181931 (*A. flavicollis*, AMNH 181923–181926, was also collected here at the same elevations and during 1950, but on different days); **Kreutenstein**, AMNH 181922.

LIECHTENSTEIN:

Silum, ZFMK 56.1025; **Saminatal**, ZFMK 62.69–62.74.

ITALY:

Piemont: P. N. Gran Paradiso, ZFMK 73.181, 73.183–73.185, 73.197, 73.199, 73.207.

Species-groups or genera?

In addition to *Apodemus*, five other genus-group names have been proposed, based upon morphological traits, for certain species or clusters of species: *Sylvaemus*, *Nemomys*, *Alsomys*, *Petromys*, and *Karstomys*. *Sylvaemus* (Ognev 1924), as a genus, and *Nemomys* (Thomas 1924), as a subgenus, have the same type-species, *Mus sylvaticus*. Dukelski (1928) erected *Alsomys* as a subgenus of *Mus* with *Mus major* (= *Apodemus peninsulae*) as the type-species. He also recognized Ognev's "*Sylvimus*" as a subgenus of *Mus*. *Apodemus mystacinus* was used by Martino (see

references in Ellerman & Morrison-Scott 1951; Corbet 1978) for *Petromys*, which, because it was preoccupied, was replaced by *Karstomys*. *Nemomys* is a synonym of *Sylvaemus*, and *Karstomys* has not been generally accepted (Corbet 1978; Niethammer & Krapp 1978, who also cite exceptions that employ the subgenus) because *A. mystacinus*, although a distinctive species, is related to *A. sylvaticus* and its allies (Niethammer & Krapp 1978b).

Eventually Zimmermann (1962) formalized the interspecific classification of *Apodemus* by arguing for the retention of three subgenera: *Apodemus*, containing *A. agrarius*; *Sylvaemus*, comprising *A. mystacinus*, *A. flavicollis*, *A. sylvaticus*, and *A. microps* (= *uralensis*); and *Alsomys*, including *A. speciosus*, *A. latronum*, *A. peninsulae*, *A. gurkha*, *A. draco*, and *A. geisha* (= *argenteus*). This tripartite arrangement, defined by morphology and geography, was accepted by Niethammer & Krapp (1978b: 305) but not by Corbet (1978: 132), Pavlinov & Rossolimo (1987), nor Corbet & Hill (1992: 357), all of whom acknowledged only *Apodemus* and *Sylvaemus* as subgenera.

During the 1980s and early 1990s, several groups presented genic relationships among species of *Apodemus* (European, Israeli, Transcaucasian, and North African samples) by electrophoretically analyzing allozyme variation at particular gene loci and began to test the interspecific relationships among *Apodemus* as indicated by morphology. Several papers are preminent (others are cited in these reports): Gemmeke (1980; 11 loci in samples of *A. sylvaticus*, *A. flavicollis*, *A. mystacinus*, and *A. agrarius*), Iskandar (1984; also reported in Bonhomme et al. 1985, Iskandar & Bonhomme 1984; 24 loci from the same species used by Gemmeke 1980), Gill et al. (1987; 21–24 loci from Yugoslavian samples of *A. sylvaticus*, *A. flavicollis*, and *A. agrarius*), Britton-Davidian et al. (1990; 20 loci from the same species analyzed by Gemmeke 1980), Filippucci (1992; 28–33 gene loci from samples of *A. agrarius*, *A. flavicollis*, *A. sylvaticus*, *A. alpicola*, *A. microps*, *A. hermonensis*, and *A. mystacinus*), Hartl et al. (1992; 30 loci from samples of *A. agrarius*, *A. sylvaticus*, *A. flavicollis*, and *A. microps*), and Mezhzherin et al. (1992; 37 gene loci from *A. sylvaticus*, *A. flavicollis*, *A. microps*, *A. falzfeini*, *A. mystacinus*, and three unnamed samples).

Two insights distilled from the above results are important here. First, the investigations that sampled *A. mystacinus* (Gemmeke 1980; Britton-Davidian et al. 1990; Filippucci 1992; Mezhzherin et al. 1992) concluded the species is allied with members of *Sylvaemus*. Although a large genetic distance separated *A. mystacinus* from other members of *Sylvaemus*, the genic data still did not support the isolated phylogenetic position of *A. mystacinus* implied by its lone inclusion in a subgenus (*Karstomys*). This relationship is best exemplified by Filippucci (1992: 211), who analyzed samples of more species of *Sylvaemus* than any of the other investigators. In her UPGMA dendrogram summarizing genetic relationships, *A. sylvaticus*, *A. flavicollis*, *A. hermonensis*, *A. alpicola*, and *A. microps* form a cluster in which the mean values of genetic distances among them were less than 0.2. *Apodemus mystacinus* was separated from that group by a mean distance of 0.405, and *A. agrarius* by 1.23. The biochemical evidence reinforced the views of other researchers who, while allying *A. mystacinus* with members of *Sylvaemus* based on morphological traits, also pointed out the combination of characters that distinguished it from other members of that subgenus: blueish gray dorsal coat, relatively short

and oblique anterior spine on the zygomatic plate, prominent posterior cingulum on second upper molar, two pairs of metacentric autosomal chromosomes (Zimmermann 1962; Soldatović et al. 1969; Niethammer 1978; Bekasova et al. 1980).

Second, all studies containing samples of *A. agrarius* concluded that the genetic relationships among the species reveal two groups. One consisted of *A. agrarius* (subgenus *Apodemus*), the other contained *A. sylvaticus* and all other species sampled (subgenus *Sylvaemus*). Genetic distances among species of *Sylvaemus* corresponded to those expected between both slightly or well-differentiated species, but the very high distance value between the subgenera *Apodemus* and *Sylvaemus* resembled those found among different rodent genera. Some investigators (Iskandar 1984; Bonhomme et al. 1985) asserted that *Apodemus* “did not appear to be more closely related to *Sylvaemus* than to other murids” (Filippucci 1992: 214), and called for a taxonomic revision of the genus as well as the possible elevation of the two subgenera to generic rank, an action already taken by Bonhomme et al. (1985). Britton-Davidian et al. (1991) and Filippucci (1992), however, cautioned that “it would be imperative that biochemical data be collected for species belonging to the third subgenus (*Alsomys*) in order to correctly establish the evolutionary relationships within the *Apodemus* complex” (Britton-Davidian et al. 1991: 32).

Two species of *Alsomys* have already been analyzed. Mezhzhherin & Zikov (1991) sampled the genetic variability of 36 presumed loci in five species of *Sylvaemus* (*A. sylvaticus*, *A. flavicollis*, *A. microps*, *A. falzfeini*, and *A. ponticus*), in *Apodemus agrarius*, and in two species that Zimmermann (1962) assigned to *Alsomys* (*A. peninsulæ*, the type-species of *Alsomys*, and *A. speciosus*). In their results, the two species of *Alsomys* formed a cluster that included *A. agrarius* and was separated from species of *Sylvaemus* by a large genetic distance, a magnitude too great in their view to be expected in one genus. Mezhzhherin & Zikov promptly recognized *Sylvaemus* and *Apodemus* (including *Alsomys*) as separate genera.

Hartl et al. (1992) extended their analyses farther than other investigators and derived a different and enlightened perspective of the phylogenetic relationships within *Apodemus*. They included samples of *Mus*, *Rattus*, arvicolines, and *Cricetus* in their project. According to their rooted dendrogram of genetic distances, species of *Mus* and *Rattus* appeared more closely related to the three species of *Sylvaemus* sampled than was *A. agrarius* (subgenus *Apodemus*). Genetic relationships estimated in the studies cited above were also presented as dendrograms, and, like those researchers, Hartl et al. (p. 368) concluded that “according to the rooted dendrogram . . . *A. agrarius* should be excluded from the other wood mice and given separate genus rank.”

But Hartl et al. next reanalyzed their allelic data cladistically and produced a different phylogeny among the species of *Apodemus* and the outgroups (*Mus*, *Rattus*, voles, *Cricetus*). No such analysis was attempted, or at least reported, by other investigators. In Hartl's et al. reanalysis, *A. agrarius* was shown to have many autapomorphic character states that were “. . . due to fixed alleles rather than to a high extent of polymorphism” (p. 367). The cladogram (p. 368),

“ignoring variable numbers of autapomorphic character states for the formation of branching patterns, connects *A. agrarius* with the other investigated species of *Apodemus* by some synapomorphic alleles. Moreover, no alleles were found for

supporting the formation of a cluster of *A. agrarius* and either *Mus* or *Rattus*. Although the cladogram leaves open the possibility for considering *A. agrarius* as a separate genus, it demonstrates clearly that the topology of the rooted tree [the dendrogram] . . . does not indicate a phylogenetically more distinct position of *A. agrarius* from all other *Apodemus* species investigated than either *Mus* or *Rattus*. It is rather the case that the very high number of autapomorphic character states [in *A. agrarius*] is the result of an accelerated rate of enzyme evolution, making numerical (especially rooted) dendrograms inappropriate for inferring the phylogenetic situation."

"As a consequence of unequal rates of allozyme evolution among taxa, use of both numerical and cladistic approaches for the evaluation of phylogenies is emphasized" (Hartl et al. 1992: 363).

To determine if we could identify different monophyletic groups within *Apodemus*, concordant with the biochemical results, we surveyed morphological characters and other data in the literature that had been used to diagnose subgeneric clusters or distinguish species. Our direct survey of specimens covered only selected traits seen in museum skins and skulls, and included only samples of species accessible to us.

Our indirect survey included published comparative studies of the male reproductive tract, but we did not find the results helpful in assessing generic status of various groups of species. Study of the glans penis of Croatian samples of *A. agrarius*, *A. flavicollis*, *A. sylvaticus* (including *krkensis*), and *A. mystacinus* by Williams et al. (1980), for example, revealed variation among species in absolute size and shape, density of epidermal spines, morphology of such traits as dorsal ridge and urethral process, and presence or absence of various grooves. Each species could be recognized by a unique combination of traits, but no characters supported separation of an *A. agrarius* cluster from a group containing all the other species. Their results identified *A. mystacinus* as the most divergent member of the five taxa examined. Yang & Fang (1988) surveyed phallic morphology in Chinese samples of murines that included species of *Rattus*, *Niviventer*, *Mus*, *Micromys*, and *Apodemus* (*A. agrarius*, *A. chevrieri*, *A. peninsulae*, and *A. draco*). They listed traits that characterized each genus and found differences among species within genera, but did not identify characters suggesting their sample of *Apodemus* consisted of more than one genus. They did indicate that *A. agrarius* and *A. chevrieri* had dorsal papilla and urethral lappets that differed slightly in morphology from that seen in the other two species of *Apodemus*.

Our evaluation of data from other selected sets of characters (based upon our survey of specimens) has led us to identify three groups of species, which we briefly discuss below.

***Apodemus* Group:** *A. agrarius*, *A. chevrieri*, *A. speciosus*, *A. peninsulae*, *A. latronum*, *A. draco*, *A. semotus*, and *A. gorkha*.

Some expression of supraorbital ridges (as illustrated by the examples of *A. agrarius*, *A. peninsulae*, and *A. speciosus* in fig. 3) is the one morphological trait we found that unites all these species; comparable ridges are not present in any of the other species of *Apodemus*. Presence of supraorbital ridges or shelves is likely a derived condition in muroid rodents (Musser & Newcomb 1983). In this group are

Table 5: Occurrence of certain cusps on upper molars (expressed in number of specimens) in AMNH samples of subgenus *Apodemus*, represented by type-species *A. agrarius*, and subgenus *Sylvaemus*, represented by type-species *A. sylvaticus*.

Expression of Cusp ^a	<i>A. agrarius</i> (China)	<i>A. sylvaticus</i> (England, Ireland, Germany, Italy)
Posterior cingulum on M1		
not present	57	0
tiny-small	58	0
medium-large	19	126 ^b
Cusp t3 on M2^c		
not present	121	0
tiny-small	9	1
medium-large	1	126
Cusp t8 on M3^d		
not present	18	0
tiny-small	71	20
medium-large	42	105

^aExplanation of categories: **not present**, cusp either absent or merged with adjacent part of tooth to a degree that we could not detect it; **tiny-small**, detectable as a cingular nubbin to a larger but still inconspicuous mound well below the coronal surface; **medium-large**, a conspicuous element forming a prominent part of the occlusal surface. ^bIn 91 specimens, the posterior cingulum was integrated within the ridge between cusps t8 and t9, but identifiable as a cusp in 35 individuals. ^cThese results are comparable to those reported in the literature. For example, in a survey of Polish samples, Ruprecht (1978) found cusp t3 on M2 in only 3.9 % of 3228 specimens of *A. agrarius*, but in 99.9 % of 4911 skulls of *A. sylvaticus*. ^dIn specimens where cusp t8 is either absent or undetectable because it has coalesced with cusp t5, or tiny-small, the occlusal surface of the molar appears to be formed of two rows of cusps rather than three (fig. 4C, D).

Table 6: Occurrence of cusp t3 on M2 (expressed as number of specimens) in AMNH and USNM samples of four species of *Apodemus* referred to the subgenus *Alsomys*.

Species and Country	Expression of Cusp t3 on M2		
	Not present	Tiny-small	Medium-large
<i>A. peninsulae</i> ^a China, Mongolia, Korea, Russian Federation	0	16	38
<i>A. draco</i> China	4	62	34
<i>A. latronum</i> China	0	5	41
<i>A. speciosus</i> ^b Japan	58	25	22

^aType-species of subgenus *Alsomys*. ^bOut of 294 second molars of *A. speciosus* from Pleistocene and Recent samples, Kawamura (1989: 39) found that cusp t3 was “completely absent” from 77, “represented as a cingulum” in 128, “moderately developed” in 82 (these two categories correspond to our “tiny-small”), and “well developed” (our “medium-large”) in only 7. His figures for *A. argenteus*, obtained from 266 Pleistocene and Recent second molars, were 6, 31, 172, and 57, respectively, clearly underscoring another difference between the two Japanese endemics.

Table 7: Variation (expressed as number of specimens) in configuration of the lingual root beneath each first upper molar: comparison of samples in AMNH, FMNH, USNM, and ZFMK among selected species.

Species and Country	Form of Root		
	Single	Single but creased by vertical furrow	Double
APODEMUS GROUP			
<i>A. agrarius</i> China	0	0	331
<i>A. chevrieri</i> China	21	34	566
<i>A. latronum</i> China	107	63	34
<i>A. draco</i> China, Burma	1158	114	20
<i>A. semotus</i> Taiwan	48	16	0
<i>A. gurkha</i> ^a Nepal	107	1	1
<i>A. peninsulae</i> Mongolia, China, Japan, North Korea, Siberia	159	27	2
<i>A. speciosus</i> ^b Japan	109	3	0
SYLVAEMUS GROUP			
<i>A. sylvaticus</i> Iceland, Denmark, Italy, Ireland, England, Germany, Austria, Belgium, France, Sweden, Crete, Greece	0	0	327
<i>A. flavicollis</i> Germany, Austria, Norway, Sweden	0	0	76
<i>A. alpicola</i> Austria, Germany	0	1	51
<i>A. uralensis</i> Russian Federation, Georgia, Kazakhstan, Turkey, Turkmenistan	0	5	159
<i>A. mystacinus</i> Crete, Greece, Turkey, Iran, Yugoslavia, Georgia, Syria, Lebanon	0	4	74
ARGENTEUS GROUP			
<i>A. argenteus</i> Japan	2 ^c	0	157 ^c

^a Martens and Niethammer (1972) noted that one of the traits distinguishing *A. gurkha* from the Nepalese *A. sylvaticus* was the three roots anchoring each first molar of the former and the four roots of the latter. ^b Kawamura (1989: 26), after examining "thousands of specimens" of first upper molars of *A. speciosus* from Middle Pleistocene to Recent samples, reported that "three roots are almost always present" (meaning all molars have a single lingual), and found only one tooth in which the lingual root was divided into two elements. ^c These figures include Kawamura's (1989: 72) counts. Out of 128 first upper molars of *A. argenteus* from Middle Pleistocene to Holocene samples, Kawamura (1989: 72) recorded that two had three roots (single lingual) and 126 had four roots (divided lingual; 14 of these also had an additional lingual rootlet).

also the species in which cusp t3 on the second upper molar is either absent from most specimens in any sample (*A. agrarius*, table 5, and *A. chevrieri*), reduced in size (*A. gorkha*, Martens & Niethammer 1972), or occurs at a low frequency (*A. speciosus*, table 6). And all but one of the species in the group has four pairs of mammae rather than three (Martens & Niethammer 1972; Corbet & Hill 1992: 357, also verified by our survey).

Biochemical evidence, interpreted as a dendrogram of genetic distances, supports the unification of *A. agrarius*, *A. peninsulae*, and *A. speciosus* (Mezhzherin & Zykov (1991), although the data needs to be analyzed cladistically to test the results. Data from analyses of restriction sites in ribosomal DNA suggests that *A. semotus* and *A. agrarius* are closely related, but also indicates that *A. speciosus* or *A. peninsulae*, the only other species of our group that were sampled, is as phylogenetically distant from *A. semotus*/*A. agrarius* as from *A. sylvaticus*/*A. flavicollis* (Suzuki et al. 1990).

We include all the species that Zimmermann (1962) had placed in *Alsomys*, an eastern Asian group, and agree with Corbet (1978: 132) who noted that the traits Zimmermann used to define *Alsomys* “do indeed seem valid for the recognition of species but there seem to be no characters sufficiently invariable amongst the eastern group to justify uniting them as a distinct subgenus.”

Supraorbital ridges, usually four pairs of mammae, cusp t3 on second upper molar reduced or large, first and second upper molars each with a single root, and third upper molar not reduced in size were Zimmermann's (1962: 201) defining traits for *Alsomys*. None is diagnostic. Zimmermann had included *A. argenteus*, which does not have supraorbital ridges or single lingual molar roots. A reduced or absent cusp t3 on the second upper molar is also diagnostic of subgenus *Apodemus*. An unreduced third upper molar, comparable in size with *A. agrarius*, is also characteristic of species in the subgenus *Sylvaemus*. Most members of *Alsomys* have four pairs of mammae, but *A. latronum* has three; eight mammae are common to *A. agrarius* and six to *A. sylvaticus* and allies. Finally, samples of most species Zimmermann included in *Alsomys* have a single lingual root, but except for our samples of *A. speciosus* and *A. semotus*, we found specimens of all other species that had either two lingual roots or a single root creased by a vertical groove (table 7).

Except for *A. agrarius*, which has a European and Asian geographic range, the species in our *Apodemus* Group are found only in eastern Asia. This pattern had already been noticed by Xia (1984: 98), who studied Chinese *Apodemus* in the context of assessing their relationship to Japanese species, and asserted that *A. draco*, *A. peninsulae*, *A. latronum*, *A. chevrieri*, and *A. agrarius* “all occur in Hengduan Mountains, i.e. the area including western Sichuan, eastern Xizang and Yunnan. I think this area may be one of the places of origin of the present genus.” This is an idea that certainly should be pursued by additional study.

***Sylvaemus* Group:** *A. sylvaticus*, *A. flavicollis*, *A. uralensis*, *A. mystacinus*, *A. fulvipectus*, *A. hermonensis*, *A. alpicola*, *A. arianus*, *A. hyranicus*, *A. ponticus*, *A. rusiges*, *A. wardi* (these are the species listed by Musser & Carleton 1993; see their discussions of the taxonomic problems associated with some of them — the *arianus-rusiges-wardi* complex, for example).

Table 8: Occurrence of posterior cingulum on M2 (expressed as number of specimens) in AMNH and USNM samples of selected species.

Species and Country	Expression of posterior cingulum on M2		
	Not present	Tiny-small	Medium-large
APODEMUS GROUP			
<i>A. agrarius</i> China, North Korea	118	1	0
<i>A. chevrieri</i> China	126	37	13
<i>A. latronum</i> China	119	13	0
<i>A. draco</i> China, Burma	156	11	4
<i>A. peninsulae</i> China, North Korea, Mongolia	93	10	0
<i>A. speciosus</i> ^a Japan	145	44	39
SYLVAEMUS GROUP			
<i>A. sylvaticus</i> England, Italy, Germany	123	3	2
<i>A. flavicollis</i> Germany, Austria	47	6	3
<i>A. alpicola</i> Germany, Austria	31	1	2
<i>A. uralensis</i> Russian Federation, Georgia, Turkmenistan, Kazakhstan	18	0	0
<i>A. mystacinus</i> Crete, Turkey, Yugoslavia	1	4	36
ARGENTEUS GROUP			
<i>A. argenteus</i> ^b Japan	0	0	234

^a Data are from Kawamura's (1989: 40) survey of 228 second upper molars from *A. speciosus*; he scored the posterior cingulum as "undeveloped" (our "not present"), "intermediate" (our "tiny-small"), and "developed" (our "medium-large"). ^b We consulted Kawamura (1989) again. He had available 234 second upper molars of *A. argenteus* and noted that "... the posterior cingulum is always well-developed ..." and shaped like "... an elongated ellipse in occlusal view."

Members of this cluster contrast with all species in the *Apodemus* Group only by absence of supraorbital ridges. The interorbital region, from dorsal perspective, is shaped like an hourglass and its lateral margins are not defined by ridges (illustrated by *A. sylvaticus* and *A. mystacinus* in fig. 3). Genic traits of the few species analyzed indicate a closer relationship among the species in this group than to *A. agrarius* and

two others in the *Apodemus* Group (Mezhzherin & Zykov 1991; Hartl et al. 1992, for example). Study of restriction sites in ribosomal DNA among several species of *Apodemus* revealed a close tie between *A. sylvaticus* and *A. flavicollis* and a distant relationship to the other species sampled: *A. semotus*, *A. agrarius*, *A. argenteus*, *A. speciosus*, and *A. peninsulae* (Suzuki et al. 1990).

The *Sylvaemus* cluster can also be characterized by a combination of other morphological traits, but none is restricted to it. We did not survey samples of all species listed above, but those we checked have traits that are found in *A. sylvaticus*: three pairs of mammae, a posterior cingulum on the first upper molar, large cusp t3 on the second upper molar, an unreduced third upper molar with three rows of cusps, and two lingual roots beneath first upper molars (tables 5, 7). Some of these characters are also found in members of the *Apodemus* and *Argenteus* groups. Without surveying more morphological and biochemical traits, and analyzing them within a phylogenetic context, it is difficult to characterize the *Sylvaemus* Group except by saying that it fits nowhere else. Their one uniting characteristic, an interorbit shaped like an hourglass, is likely primitive.

The *Sylvaemus* Group is the only cluster that cannot be diagnosed by a unique trait or set of traits, unless the derived alleles shared by *A. sylvaticus*, *A. flavicollis*, and *A. microps* (= *uralensis*) (Hartl et al. 1992) prove common to the other species we include in the *Sylvaemus* Group and not shared by any species in the other two groups. The *Apodemus* Group can be defined by at least one derived trait, supra-orbital ridges, and all the species with cusp reduction or loss (which are derivations) are members of that cluster. As discussed below, the *Argenteus* Group is also defined by unique characters. In order to test the reality of a *Sylvaemus* Group, broader character survey of more species within the framework of a rigorous phylogenetic analysis is required.

***Argenteus* Group: *A. argenteus*.**

Zimmermann (1962) placed the Japanese *A. argenteus* in the subgenus *Alsomys*, but unlike other species he had included there, *A. argenteus* has an interorbital region shaped like an hourglass (fig. 3) and first upper molars with two lingual roots (table 7). These traits recall *A. sylvaticus*, and the skull of *A. argenteus* superficially resembles that species, a similarity that has impressed other researchers. Barrett-Hamilton (1900: 421) thought *A. argenteus* to be “a local development from a *sylvaticus*-like stock, in which the skull has not altered from that of the type,” and Corbet (1978: 136), writing nearly eight decades later, remarked that “of the eastern Asiatic *Apodemus* this species [*A. argenteus*] most closely resembles the western *A. sylvaticus*.”

Conformation of the interorbital region in *A. argenteus* and *A. sylvaticus* is primitive (see Musser & Newcomb 1983, and references cited there), the double lingual molar roots shared by both is a derived condition, but this feature also characterizes *A. agrarius*, most examples of *A. chevrieri*, and a few specimens in samples of other species in the *Apodemus* Group. In this context, neither interorbit nor root configuration is informative about possible phylogenetic relationships between *A. argenteus* and the *Sylvaemus* Group.

Apodemus argenteus does have four pairs of mammae (Corbet 1978: 133), a count

also shared by most members of Zimmermann's (1962) *Alsomys* as well as *A. agrarius* and *A. chevrieri* (Corbet & Hill 1992: 357). However, eight mammae might represent the ancestral state among muroid rodents (Carleton 1980: 71, and reference he cites), and mammae number may just be a primitive feature shared by the Japanese endemic and the species in our *Apodemus* Group.

The autosomal part of the karyotype of *A. argenteus* is composed of mostly telocentric (=acrocentric) chromosomes and three pairs of small metacentrics (Bekasova et al. 1980; Saitoh et al. 1989). A pattern of mostly telocentric pairs along with a few metacentric pairs was thought to characterize species in the subgenera *Alsomys* (Martens & Niethammer 1972) and *Apodemus* (Vujosevic et al. 1984; Britton-Davidian 1991; see references in those reports) and to exclude them from members of the subgenus *Sylvaemus*, in which most species have only telocentric chromosomes.

Within our *Apodemus* Group, *A. agrarius*, *A. speciosus*, and *A. gurkha* do have such a chromosomal composition (Gemmeke & Niethammer 1982; table and references in Bekasova et al. 1980), but *A. peninsulae* does not. That species has all telocentric pairs; a variable number of metacentric supernumerary or B-chromosomes are present in some samples, depending upon their geographic origin (Bekasova et al. 1980). Autosomes are all telocentric within *Sylvaemus* except for *A. mystacinus*, which differs from the other species of *Sylvaemus* sampled in that it has two pairs of small metacentric chromosomes in addition to an otherwise telocentric complement (Soldatovic et al. 1969; Niethammer 1978). This distribution of metacentric chromosomes among what was considered three subgenera prompted Bekasova et al. (1980: 40) to remark on the heterogeneity of *Alsomys* and its intermediate position between what they considered the two most chromosomally divergent subgenera, *Apodemus* and *Sylvaemus*. So the occurrence of metacentric autosomes in the karyotype is not unique to species of *Apodemus*, does not correspond meaningfully to a particular cluster of species, and does not seem to be a character useful in detecting close relatives of *A. argenteus*.

Among species of *Apodemus*, *A. argenteus* is set apart by its zygomatic plate and molar characters. The zygomatic plate is narrow, such that its anterior margin either does not project beyond the dorsal anterior margin of the zygomatic arch or barely does (fig. 3), a configuration also noted by Corbet (1978: 133). The plate projects forward beyond the anterior margin of the zygomatic arch in all other species (see the examples in fig. 3).

Both first and second upper molars of *A. argenteus* have a thick and elongate posterior cingulum that projects anterolabially to touch cusp t9 (fig. 5D; Kawamura 1989: 65) and forms an appreciable portion of the occlusal surface. After only slight wear, the anterior margin of the posterior cingulum coalesces with the posterior margin of cusp t9. The presence of a posterior cingulum on first and second molars is primitive, but its very large size relative to occlusal surface of each tooth and contact with cusp t9 are likely specialized.

The posterior cingulum on the first upper molar in other species of *Apodemus* is either absent, as in some *A. agrarius* (table 5; fig. 4B, D), or much less prominent than the conformation in *A. argenteus*, and constitutes a relatively negligible part of the occlusal surface. Typically, the cusp is similar in size and shape to that seen in

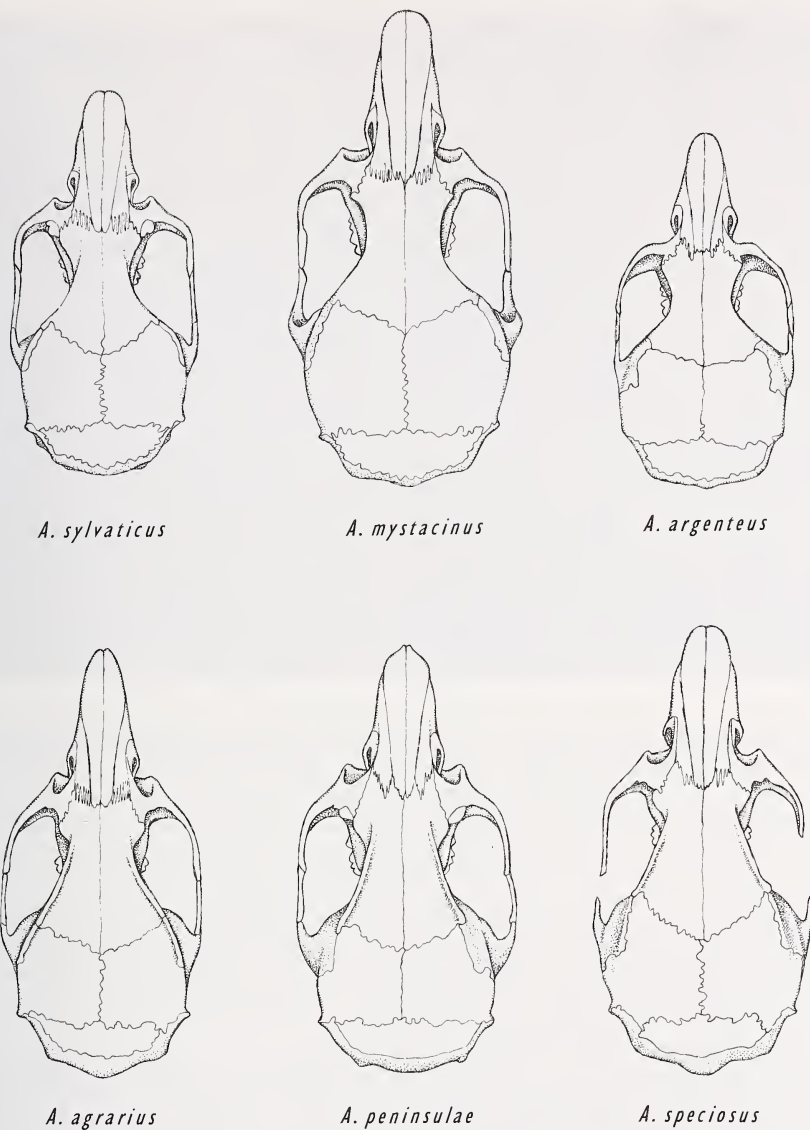


Fig. 3: Dorsal views of crania illustrating conformation of the interorbital region. Diagrams are based on the following specimens: *A. sylvaticus*, AMNH 181976, Germany; *A. mystacinus*, AMNH 147551, Crete; *A. argenteus*, AMNH 119644, Japan; *A. agrarius*, AMNH 56293, China; *A. peninsulae*, AMNH 85422, China; *A. speciosus*, AMNH 31637, Japan. X3. The shape of the interorbit of *A. sylvaticus* and *A. mystacinus* is also shared by the other species in our *Sylvaemus* Group. An interorbit defined by ridges is common to species in our *Apodemus* Group. Note that *A. argenteus*, the only member of our *Argenteus* Group, lacks supraorbital ridges.

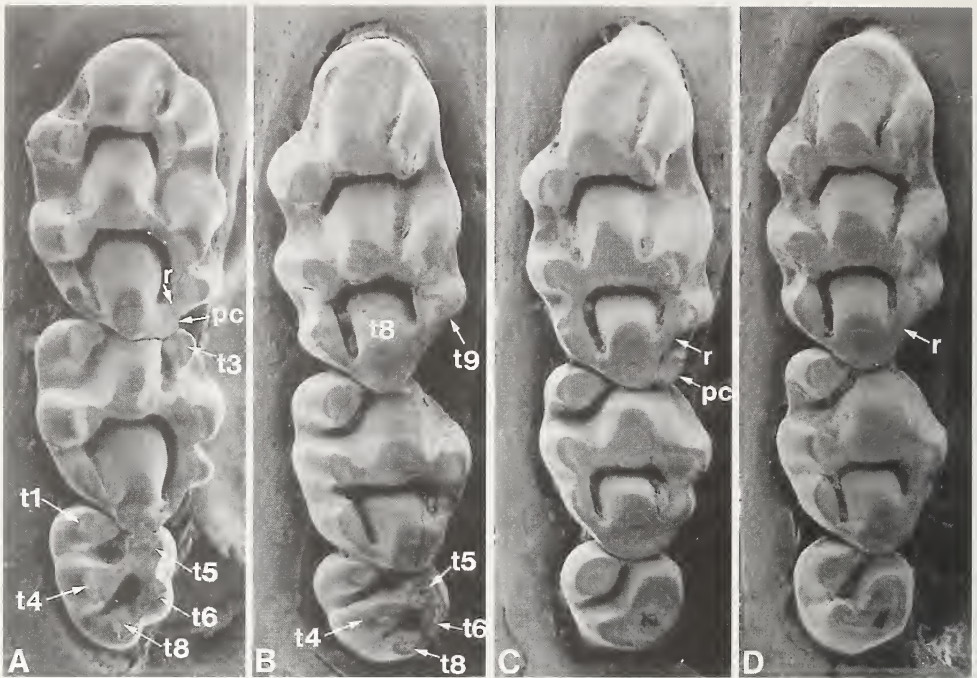


Fig. 4: Occlusal views (scanning electron micrographs) of left upper molar rows. **A**, *Apodemus sylvaticus* (AMNH 70928, England, CLM1-3 = 3.5 mm); **B**, *Apodemus agrarius* (AMNH 56252, China, CLM1-3 = 3.9 mm); **C**, *A. agrarius* (AMNH 56239, China, CLM1-3 = 4.0 mm); **D**, *A. agrarius* (AMNH 56186, China, CLM1-3 = 4.0 mm).

Note that cusp t3 is large and prominent on M2 of *A. sylvaticus*, but not present on most *A. agrarius* (see table 5). Compared with *A. sylvaticus*, *A. agrarius* has a smaller M3 relative to M1 and M2 that consists of what appears to be only two rows of cusps in most specimens (C and D; also table 5), but three rows (comparable to the three rows and same cusps seen in *A. sylvaticus*) in some (B; also table 5). The first row is formed by cusp t1, the second row by cusps 4, 5, and 6, and the last row by the single cusp t8, as labelled. The molar appears to have only two rows in C and D because one element is the oblong cusp t1 and the second row is formed by fusion of cusps t5, t6, and t8 into a single structure; cusp t8 does not occur on a few specimens in any large sample (table 5).

A posterior cingulum (pc) is absent or not detectable on M1 and M2 in most *A. agrarius* (B and D), but present on M1 of a few (C; also see table 5). The ridge (r) connecting cusps t8 and t9 is sometimes mistaken for a posterior cingulum. The posterior cingulum in *A. sylvaticus* is attached only to cusp t8 and free of the ridge connecting cusps t8 and t9 in some specimens (similar to the pattern of *A. agrarius* in C), but coalesced with that ridge in other specimens (the configuration shown in A).

A. sylvaticus (fig. 4A), *A. latronum* (fig. 5A), and *A. peninsulae* (fig. 5C). Rarely is the posterior cingulum long enough to contact cusp t9 as in the unusual specimen of *A. draco* (fig. 5B).

The posterior cingulum is usually absent from the second upper molar in most specimens of each sample of nearly all other species of *Apodemus* (table 8; figs. 4, 5). A minority of individuals in any sample will have either a weakly developed or

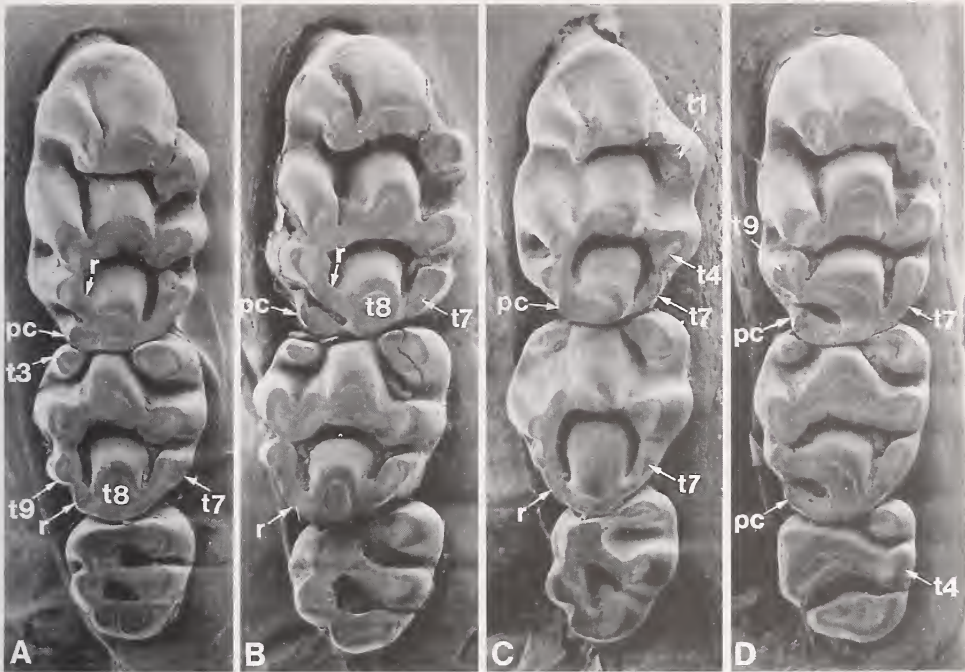


Fig. 5: Occlusal views (scanning electron micrographs) of right upper molar rows. **A**, *Apodemus latronum* (AMNH 43589, China, CLM1-3 = 4.6 mm); **B**, *A. draco* (AMNH 111927, China, CLM1-3 = 3.9 mm); **C**, *A. peninsulae* (AMNH 84294, China, CLM1-3 = 3.9 mm); **D**, *A. argenteus* (AMNH 119645, Japan, CLM1-3 = 3.6).

Note that cusp t3 is large and prominent on each M2 of *A. latronum*, *A. draco*, and *A. argenteus*, but reduced in size in this example of *A. peninsulae* (see also table 6 and Kawamura 1987).

Cusp t7 is a short narrow ridge off cusp t8 and much smaller than lingual cusps t1 and t4 on the M1 and M2 of *A. peninsulae*, but large and about the same size as cusps t1 and t4 in *A. draco*. The posterior cingulum (pc) at the back of each M1 may be mostly merged with the ridge (r) connecting cusp t9 and t8 (*A. peninsulae*), larger but partly merged with the ridge (*A. latronum*), or free of the ridge and connected only to cusp t8 (*A. draco*). This range in expression of the posterior cingulum on M1 can be found in each of these three species, although the conformation in B is uncommon. A posterior cingulum is not present, or at least not developed and normally undetectable, at the back of each M2 in most specimens in every sample (see table 8). The ridge connecting cusp t8 with cusp t9 in A-C resembles a posterior cingulum but is not that cusp. In *A. speciosus*, which is related to the species shown in A-C, Kawamura (1978: 36) surveyed 378 Pleistocene and Recent first molars and found the posterior cingulum “undeveloped” in 32, “intermediate” (resembling A and D) in 185, and “developed” (similar to B) in 161; out of 228 second molars, he noted that the posterior cingulum was “undeveloped” in 145, “intermediate” in 44, and “developed” in 39.

Apodemus argenteus has a very large and elongate posterior cingulum on both M1 and M2 that is connected to cusp t8 and touches cusp t9, merging with that cusp after a little wear. Kawamura (1987) found this pattern to be present in all the first and second molars of *A. argenteus* he surveyed from Pleistocene and Recent samples. The configuration formed by the posterior cingulum on M1 and M2 seen in *A. argenteus* is not found in any other species of *Apodemus*. Note the M3 in *A. argenteus*, in which most cusps have fused to form two primary horizontal rows of cusps that resemble laminae. This laminar-like pattern is enhanced by the absence of cusp t3 from the anterolabial margin of the tooth. Kawamura (1989: 76) examined 127 third upper molars of *A. argenteus* and found cusp t3 missing from all but seven of them.

a large posterior cingulum (table 8); if prominent, the cusp is usually smaller than its counterpart on the first molar. *Apodemus mystacinus* is an exception. All but one of the specimens we examined have a posterior cingulum on each second upper molar (table 8) that, although smaller than its counterpart on the first molar, is a prominent structure; this trait has been used to help characterize the species (Niethammer 1978: 306). However, the posterior cingulum is round or oblong, still small relative to occlusal surface of the molar and does not contact cusp t9 or even come close.

The occlusal surface of each third upper molar in *A. argenteus* consists of a large anterolingual cusp t1 and two nearly horizontal laminae (fig. 5D; Kawamura 1989: 65). The anterior lamina is composed of a small cusp t4 fused to elongated cusps t5 and t6. The posterior lamina represents either one elongate cusp or two smaller ellipsoidal cusps fused together. The cuspidate origins of the laminae are sometimes evident in unworn teeth, but are obscured in the horizontal lophs after only moderate wear. This tendency towards lamination is probably derived. In other species of *Apodemus*, the second and third rows of cusps are usually tilted posterolingually (in occlusal view), and are prominently cuspidate rather than laminar (see examples in figs 4 and 5).

Phylogenetic relationships of *A. argenteus* are obscure. The combination of smooth interorbit, configuration of zygomatic plate in relation to anterior margin of zygomatic arch, two lingual roots anchoring first upper molars, unique upper molar occlusal patterns, four pairs of mammae, and karyotype consisting of mostly telocentric with some metacentric chromosomes make it difficult to place *A. argenteus* into any group of *Apodemus* other than its own.

Biochemical evidence does not illuminate affinities. In a study of genetic relationships between samples of *A. speciosus*, *A. giliacus* (= *A. peninsulae*), and *A. argenteus*, Saitoh et al. (1989: 1016) noted that the average genetic distance value "between *A. argenteus* and the lineage of *speciosus-giliacus* is comparable to the values observed between different species or closely related genera of many other animals, and therefore . . . *A. argenteus* may be remote to some extent in its affinity from the lineage of *speciosus-giliacus*." Analyses of differentiation of restriction sites in ribosomal DNA among certain species of *Apodemus* indicated only that *A. argenteus* was equally distant from *A. sylvaticus*/*A. flavicollis*, *A. semotus*/*A. agrarius*, *A. speciosus*, and *A. peninsulae* (Suzuki et al. 1990).

Apodemus argenteus needs to be compared with other species in the genus within a revisionary study that focuses on phylogenetic analyses of morphological and biochemical characters before we can identify its nearest phyletic affinity. Molar occlusal patterns and zygomatic plate conformation, for example, are certainly unique to *A. argenteus*, but their phylogenetic significance in the context of ancestral versus derived conditions and their shared pattern with other species are unresolved. Until analysis of that kind is performed, we are left with the assessment by Kawamura (1989: 85), who after studying numerous teeth and some skull fragments of *A. argenteus* obtained from Middle and Late Pleistocene sediments as well as Holocene and Recent material, suggested that the "species is relatively primitive in dental morphology and possibly near to ancestral forms of the genus *Apodemus*."

Conclusion

The elevation of *Sylvaemus* to generic rank coordinate with *Apodemus* is difficult to justify based upon the biochemical evidence analyzed outside of a methodology that identifies the primitive-derived polarities of alleles. The same misgivings apply to chromosomal and morphological data mustered to date. We continue to view *Apodemus* as a single genus, not because to break it up would be “excessive splitting” (Corbet 1978: 132), but because no careful systematic inquiry is available that identifies character polarities and tests monophyly of the subgenera, or even of *Apodemus* itself, by critical phylogenetic analyses. Furthermore, biochemical and morphological data need to be obtained from more species and analyzed within a wider taxonomic framework of species comparisons, within *Apodemus* as well as among other Murinae. Samples of *A. argenteus*, for example, are usually contrasted only with other Japanese species of *Apodemus*, not with the mainland Asian and European groups. Traits that seem to define some clusters — such as *A. agrarius* and *A. chevrieri*, or those that isolate *A. argenteus* — should be viewed within an analysis inclusive of all the species to determine if their distinctive features are only autapomorphies, traits not as useful in inferring relationships as those based on shared-derived characters. Our rough groupings and review of the characteristics that define them are intended to formulate hypotheses of monophyly to be tested by future careful systematic revisionary effort.

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Zusammenfassung

Das in den Naturhistorischen Museen von Bonn, Chicago, New York und Washington vorhandene Material der ostasiatischen Nagetierarten *Apodemus agrarius*, *A. chevrieri*, *A. latronum*, *A. draco*, *A. semotus*, *A. gurkha*, *A. peninsulae*, *A. speciosus* und *A. argenteus* wird dokumentiert. Für jede Art werden relevante taxonomische und geographische Aspekte erörtert. Darüberhinaus werden die Sammlungsbestände von *A. alpicola* im American Museum of Natural History, im Field Museum und im Museum Alexander Koenig dokumentiert. Biochemische und morphologische Daten, die benutzt wurden, um den generische Rang von *Sylvaemus* zu begründen, werden kritisch evaluiert. Wir kommen zu dem Ergebnis, daß die gegenwärtig im Genus *Apodemus* zusammengefaßten Arten in drei statt wie bisher in zwei Gruppen aufgeteilt werden können, die wie folgt definiert werden: *Apodemus*-Gruppe (*A. agrarius*, *A. chevrieri*, *A. speciosus*, *A. peninsulae*, *A. latronum*, *A. draco*, *A. semotus*, *A. gurkha*); *Sylvaemus*-Gruppe (*A. sylvaticus*, *A. flavicollis*, *A. uralensis*, *A. mystacinus*,

A. fulvipectus, *A. hermonensis*, *A. alpicola*, *A. arianus*, *A. hyranicus*, *A. ponticus*, *A. rusiges*, *A. wardi*); und *Argenteus*-Gruppe (*A. argenteus*). Wir sind weiterhin der Ansicht, daß für alle Arten sorgfältige systematische Revisionen unter Berücksichtigung biochemischer und morphologischer Daten mit klar determinierten Polaritäten erforderlich sind, bevor die alternativen Hypothesen, ob *Apodemus* monophyletisch oder polyphyletisch ist, getestet werden können.

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