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Description of a New Genus and Species of Rodent (Murinae, Muridae, Rodentia) from the Tower Karst Region of Northeastern Vietnam

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ABSTRACT

Tonkinomys daovantieni, a new genus and species of murid rodent in the *Dacnomys* Division, is described. It is represented by 14 adults collected from talus habitats in the forested tower karst landscape of the Huu Lien Nature Reserve of northeastern Vietnam. The combination of semispinuous, dense, grayish black fur covering upperparts; a dark gray venter; gray ears; a thick, bicolored tail considerably shorter than length of head and body; and large, extremely bulbous footpads is unlike any other species of Indomalayan murid. Body size and build of the new rat, along with some cranial features, are similar to the Thai *Leopoldamys neilli*, but other cranial traits coupled with molar occlusal patterns resemble morphology in species of the Indomalayan *Niviventer*, *Chiromyscus*, and *Saxatilomys*. The new species is petricolous, includes insects in its diet, and was found only in talus composed of large limestone blocks. Its distribution in the reserve is likely patchy. Whether this limestone rat is restricted to the extensive karst regions of northeastern Vietnam or also occurs in southern China and elsewhere in the northern karst landscapes of Indochina, and Vietnam in particular, will be known only by conducting surveys in limestone regions outside of northeastern Vietnam.

INTRODUCTION

During Paleozoic times, a succession of waterways covered what is now northern Vietnam. Lithification, followed by tectonic

deformation and uplift, and spurred by subsequent erosional processes, transformed those ancient tidal flows and marine landscapes into a spectacular terrestrial topography of tower karst riddled by fissures and

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Fig. 1. Tower karst landscape where we captured our series of *Tonkinomys daovantieni* within the Huu Lien Nature Reserve. Tropical moist deciduous forest covers the steep slopes, but the valley bottom has been cleared for agriculture. Photographed by D. P. Lunde, April 2004.

honeycombed with caverns. Beautiful cycad rosettes secured high on sheer limestone cliffs, and a forest cover in which many of the components are adapted to karstic habitats, are the living botanical link to those ancient seas. A dark gray rat, its fur coloration indistinguishable from the limestone, its lair concealed deep within fissured cliffs and limestone talus, is the zoological connection.

We discovered this limestone rat during a survey (April, 2004) of small mammals in a forested tower karst region that forms much of Lang Son Province in northeastern Vietnam (Głazek, 1966; Tuyet, 1998) (fig. 1). Our intent was to sample, using a variety of traps and other techniques, as many native species as possible. Our past field experience in Indochina had taught us that setting traps on the ground in regular lines would quickly sample the generalists of the more common terrestrial habitats but not those specialized for life on substrates above the forest floor or in unusual petricolic environments. With this

in mind we made special efforts to set a portion of our traps on tree limbs, woody vines looping through the understory, and on high limestone ledges. At one place, chunks of limestone had long ago fallen from two high forested towers, filling the space between them with huge blocks, their surfaces now partially covered with tropical vegetation, and riddled beneath with tunnels and fissures detectable at the surface only by small scattered openings (fig. 2). We set traps on top of this block pile, and also tied traps to lengths of rope and carefully lowered them through the openings to the bottom, to depths of at least 8 m. Unsure if we would catch anything different from the common rats already encountered in nearby different habitats—*Niviventer fulvescens*, *N. langbianis*, and *Rattus andamanensis*—we were very pleased, and somewhat surprised, to capture a dark gray rat on top of the rubble and two from deep within the labyrinth. Additional individuals were captured during the days that followed.



Fig. 2. Habitat where we trapped 13 of the 14 examples of *Tonkinomys daovantieni* showing large blocks of limestone overgrown with creeping vines (left) and a portion of the steep slopes of an adjacent karst tower (right). Our trail to the site is visible between these two structures. Photographed by D. P. Lunde, April 2004.

We knew nothing like this animal had ever been caught in Vietnam or elsewhere in Southeast Asia. Except for their fur coloration and short tails, the rats resembled species of *Leopoldamys*, but no member of that genus has dark gray fur and a tail shorter than head and body. Those two attributes also pointed to *Berylmys*, but none of them have dark gray underparts. We knew our sample of the limestone rat represented an undescribed species, but only after study in the museum did we confirm our suspicion that it could not be placed in any named genus.

Here we describe the limestone rat as a new genus and species, and summarize our limited observations about its natural history. We focus on describing the animal and comparing it to murines with which it is morphologically most similar, members of a cluster containing genera that Musser and Carleton (2005) refer to as the *Dacnomys* Division: extant species of the Indomalayan *Chiromyscus*, *Dacnomys*, *Leopoldamys*, and *Niviventer*; the Sri Lankan

Srilankamys; and the recently described Laotian *Saxatilomys* (Musser et al., 2005). We also contrast *Tonkinomys* with members of the *Dacnomys* Division represented by fossils recovered from Indochinese Plio-Pleistocene sediments: extinct species of *Leopoldamys* and *Niviventer*, and the extinct genera *Wushanomys* and *Qianomys*. Of these, the new rat requires close and careful comparisons only with *Leopoldamys*, *Niviventer*, *Chiromyscus*, *Saxatilomys* and the Plio-Pleistocene *Wushanomys* and *Qianomys*.

Descriptions of new taxa, and in particular those occurring in gradually diminishing tropical forest refuges, should be published as soon as possible. Phylogenetic inquiries take time—incorporating the new rat into phylogenetic analyses employing samples of all native Indochinese murines will be the subject of a future report.

Our discovery joins those of several other small-bodied mammals living in Indochina that have been discovered and described, with

little fanfare, during the past five years: two shrews, *Chodsgoia caovansunga* and *Crocidura kegoensis* (Lunde et al., 2003, 2004); three bats, *Hipposideros scutinares* (Robinson et al., 2003), *Rhinolophus steno microglobosus* (Csorba and Jenkins, 1998) and *Myotis annamiticus* (Kruskop and Tsytulina, 2001); and a rabbit, *Nesolagus timminsi* (Averianov et al., 2000; Can et al., 2001). These can be added to an assemblage of large mammals occurring in Vietnam, and some in nearby Laos, named and described as new within the last decade or so, but with attendant worldwide publicity: two primates, *Trachypithecus ebenus* and *Pygathrix cinerea* (summarized in Groves, 2001); three muntjacs, *Muntiacus truongsoneensis*, *M. vuquangensis*, and *M. puhoatensis* (see reviews in Amato et al., 2000; Groves and Schaller, 2000; Grubb, 2005); and the saola, *Pseudoryx nghetinhensis* (see review and references in Groves and Schaller, 2000).⁴ All are a testimony to the significant results derived from past biodiversity surveys, discoveries that provide compelling stimulus for zoologists to continue detecting the real diversity of small mammals in Vietnam.

MATERIALS AND METHODS

All 14 examples of the new rat were fixed in 10% formalin in the field and subsequently transferred to 70% ethanol for storage. Liver samples were collected prior to fixation and placed in lysis buffer in the field, and later stored in liquid nitrogen at the American Museum of Natural History (AMNH). Skulls were subsequently removed from 10 of 13 specimens (one of the 14 preserved is represented by only an ear with a bit of fur-covered skin attached, the only remnant left in the trap by a hungry predator) and cleaned by a dermestid colony, American Museum. The elements of each specimen are identified by a catalog number in the Department of Mammalogy, AMNH. Each liver sample was transferred to the American Museum Cryo Collection (AMCC), where it is registered

⁴ *Viverra zibetha*, another supposed newly discovered species living in Vietnam, was described by Sokolov et al. (1997). Its specific integrity, however, was questioned by Walston and Veron (2001), and the name is currently included in the synonymy of the large Indian civet, *Viverra zibetha* (Wozencraft, 2005).

under a second number in addition to its departmental catalog number. Some fluid-preserved specimens and accompanying skulls will be retained at AMNH; others will be returned to the Department of Zoology at the Institute of Ecology and Biological Resources in Hanoi.

Comparative material we consulted, primarily samples of *Leopoldamys*, *Niviventer*, *Chinomyscus*, and *Saxatilomys*, are in collections at AMNH; the Field Museum, Chicago; and the National Museum of Natural History, Washington, DC.

Values (in millimeters, mm) for total length, length of tail (LT), length of hind foot, including claw (LHF), and length of ear from intertragal notch to crown (LE) are those we obtained in the field and recorded in our field journals. Values for length of head and body (LHB) were determined by subtracting length of tail from total length. Weights were obtained in the field with a Pesola spring scale (300-gram capacity). The distal portion of the tail is white (unpigmented) in all specimens of the limestone rat. We measured the length of this white tip on the dorsal surface of each tail and calculated it as a percentage of total tail length. Values for cranial and dental measurements were obtained by Lunde using digital calipers accurate to the nearest 0.01 mm; however, values were rounded to the nearest 0.1 mm. The following cranial and dental dimensions (listed in the sequence they appear in tables) were measured; their limits are illustrated in figure 3 and defined in Musser and Newcomb (1983).

ONL	occipitonasal length (= greatest length of skull)
ZB	zygomatic breadth
IB	interorbital breadth
LR	length of rostrum
BR	breadth of rostrum
BBC	breadth of braincase
HBC	height of braincase
BZP	breadth of zygomatic plate
LD	length of diastema
LIF	length of incisive foramina
BIF	breadth of incisive foramina
LBP	length of bony palate (palatal bridge)
BBP	breadth across bony palate at first molars
PPL	postpalatal length
BMF	breadth of mesopterygoid fossa
LB	length of bulla
CLM1-3	crown length of maxillary molar row
BM1	breadth of first upper molar

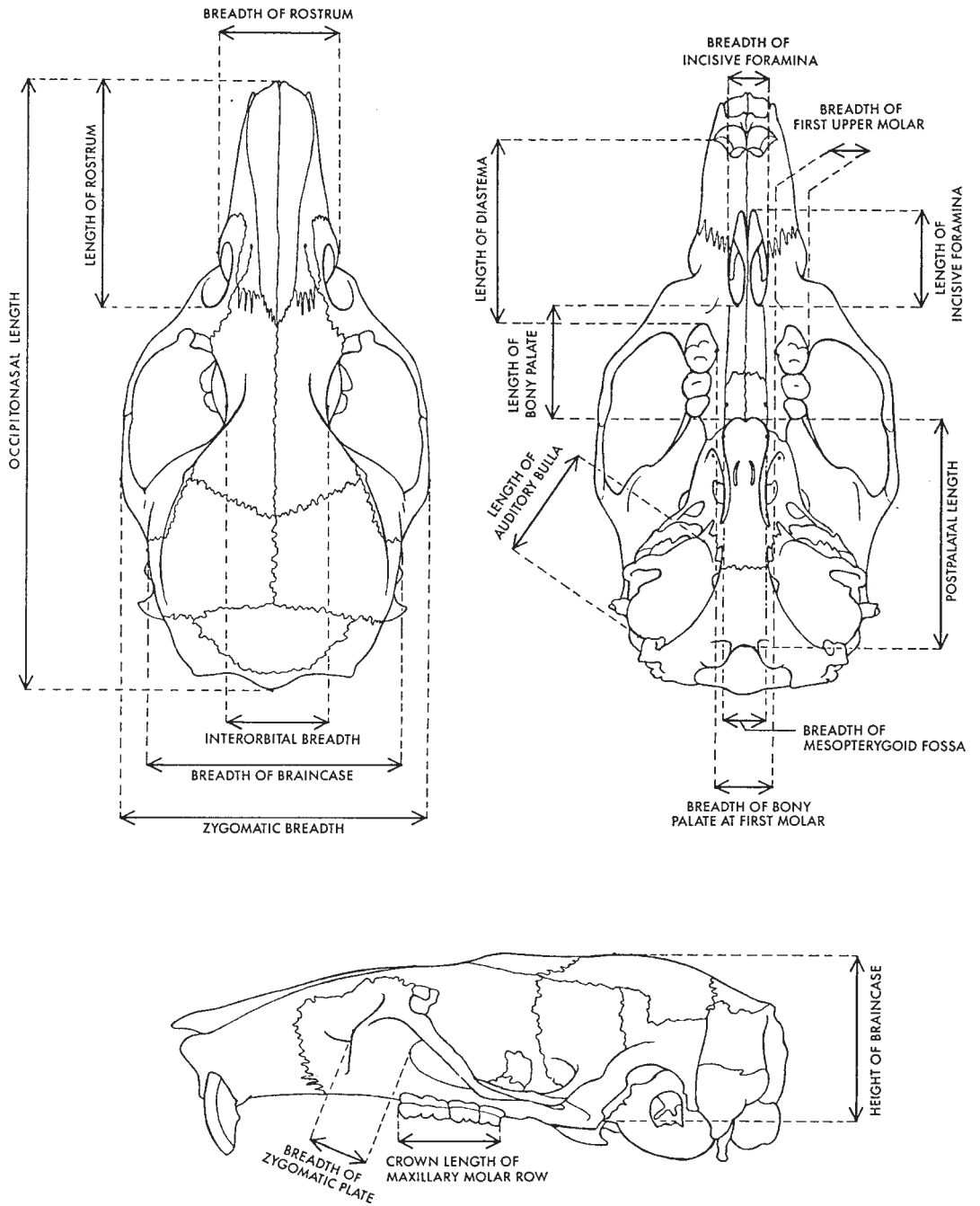


Fig. 3. Views of cranium and molars of an adult *Bunomys chrysocomus* showing limits of cranial and dental measurements. See text for abbreviations and additional information.

Old adults, adults, and young adults (as defined by Musser and Heaney, 1992: 5) were lumped as “adults” and measurements derived from them were used to calculate standard descriptive statistics (mean, standard deviation, and observed range). Small sample size dictated that we combine sexes in the analyses. Anatomical terminology follows Brown (1971) and Brown and Yalden (1973) for external features of the head and limbs; Bugge (1970) for the cephalic arteries; Wahlert (1985) for the cranial foramina; and Carleton (1980), Carleton and Musser (1984), Musser and Durden (2002), Musser and Heaney (1992), Musser et al. (1998), and Voss (1988) for cranial morphology. Names of cusps and cusplets of upper and lower molars are noted in figure 13; sources of this terminology are explained by Musser and Newcomb (1983: 332).

SYSTEMATIC DESCRIPTION OF THE NEW GENUS AND SPECIES

Tonkinomys, new genus

TYPE SPECIES: *Tonkinomys daovantieni*, the new species described below.

DIAGNOSIS: A genus of Muridae in the *Dacnomys* Division (Musser and Carleton, 2005) of the subfamily Murinae (as delimited by Carleton and Musser, 1984) that is set apart from all other described murid genera by the following combination of morphological traits: (1) fur covering head and body semispinous and grayish black, spattered with a white blaze on forehead in most individuals, underparts dark gray with white patch on the chest, ears gray, rhinarium and lips and chin unpigmented; (2) mystacial and superciliary vibrissae very long; (3) dorsal surfaces of front feet white, hind feet white with brown hairs on metatarsal region; (4) tail much shorter than length of head and body, thick and round in cross-section and well-haired, the proximal one-half to three-fourths of its dorsal and lateral surfaces dark brown, the distal one-fourth to one-half white (unpigmented); (5) palmar and plantar pads large, swollen, and set close together; (6) four pairs of teats; (7) robust skull with moderately long and wide rostrum, prominent postorbital and temporal ridges, sturdy zygomatic arches, and deep

occiput; (8) squamosal root of each zygomatic arch situated high on side of cranium where its posterior ridge-like portion runs horizontally just below posteroventral margin of the parietal and projects ventrad to form dorso-lateral side of cranium; (9) lateral cranial wall intact anterior to occiput, without large subsquamosal foramen; (10) narrow alisphenoid struts in most specimens; (11) wide and moderately long incisive foramina, their posterior borders located just before anterior margins of molar rows, even with them, or penetrating slightly between; (12) posteriorly divergent maxillary molar rows; (13) wide and long bony palate projecting beyond molars to form a wide platform; (14) moderately spacious sphenopalatine vacuities; (15) wide and shallowly excavated pterygoid fossae; (16) small ectotympanic bulla relative to skull size, incompletely covering periotic so that dorsal and slanting posterodorsal wall of carotid canal formed by periotic and not ectotympanic; (17) large foramen for stapedial artery, no sphenofrontal foramen or squamosoalisphenoid groove, indicating the widespread murine cephalic arterial pattern; (18) coronoid process of dentary small, condyloid and angular processes joined by shallow concave posterior margin of dentary, and alveolar incisor capsule only slightly evident on lateral surface of dentary; (19) upper incisors opisthodont relative to rostrum; (20) first upper molar with four large roots (anterior, two lingual, and posterior), second and third molars each with three roots (anterior, lingual, and posterior); (21) each lower molar with two roots; (22) molars brachydont, with cusp rows forming uncomplicated occlusal patterns resembling those in species of *Niviventer*, *Chiromyscus*, and *Saxatilomys*.

ETYMOLOGY: From *Tonkin*, used during the French colonial period (1883–1954) for the protectorate occupying the northern third of Vietnam, and the Greek *mys*, referring to mouse, or rat in this case. Although most often negatively associated with Vietnam’s dark French administration, the name *Tonkin* has an illustrious origin. It is derived from the Vietnamese *Don Kinh*, which means “eastern capital”, and was the name given to what is now Hanoi by Emperor Le Loi who, in 1427, along with his band of Vietnamese

TABLE 1
Summary Statistics for Cranial and Dental Measurements (mm) and Weight (m) of *Tonkinomys daovantieni* from Vietnam

(Mean, plus or minus one SD, observed range in parentheses, and number of specimens in each sample are listed for each measurement. Sample contains both sexes and a range in age from young to old adults. Individuals measured and weighed are identified in the footnote.)

	Holotype ^a	Sample (with holotype) ^b
Length of head and body	213	204.6 ± 10.34 (184–217) 13
Length of tail	177	169 ± 7.0 (156–183) 13
Length of hind foot	40	39.0 ± 1.1 (37–41) 13
Length of ear	30	30.0 ± 0.8 (29–31) 14
Weight	160	171 ± 22.8 (140–205) 13
Occipitonasal length	51.2	50.0 ± 1.6 (47.1–52.4) 7
Zygomatic breadth	21.6	21.3 ± 0.2 (20.9–21.6) 7
Interorbital breadth	6.7	6.9 ± 0.2 (6.6–7.3) 7
Length of rostrum	17.7	17.1 ± 0.6 (15.9–17.7) 7
Breadth of rostrum	7.7	7.8 ± 0.4 (7.1–8.5) 7
Breadth of braincase	17.7	17.7 ± 0.2 (17.4–18.1) 7
Height of braincase	11.7	11.8 ± 0.2 (11.4–12.0) 7
Breadth of zygomatic plate	4.9	4.8 ± 0.1 (4.7–5.0) 7
Length of diastema	13.3	13.6 ± 0.5 (12.9–14.6) 7
Length of incisive foramina	9.1	9.5 ± 0.5 (8.9–10.2) 7
Breadth of incisive foramina	3.4	3.5 ± 0.2 (3.4–3.9) 7
Length of bony palate	10.7	10.5 ± 0.3 (10.0–10.7) 7
Breadth across bony palate at M1	9.6	9.6 ± 0.1 (9.5–9.8) 7
Postpalatal length	16.2	15.7 ± 0.6 (14.6–16.4) 7
Breadth of mesopterygoid fossa	3.9	3.8 ± 0.2 (3.5–3.9) 7
Length of bulla	6.2	6.3 ± 0.1 (6.2–6.5) 7
Crown length of M1-3	8.3	8.3 ± 0.2 (8.0–8.8) 7
Breadth of first upper molar	2.1	2.1 ± 0.1 (2.0–2.2) 7

^a AMNH 275618.

^b AMNH 275575-275577, 275586, 275593, 275602, 275618, 275627, 275644, 275688, 275692, 275711, and 275712.

rebels, expelled from Vietnam the repressive Ming occupiers. By the early 1800s, the capital was moved to Hue, and the Emperor Minh Mang renamed the “eastern capital” Hanoi, meaning “this side of the river”.

Tonkinomys daovantieni, new species

HOLOTYPE: AMNH 275618, an adult female collected by the authors (DPL 1706) on 17 April, 2004, in the vicinity of Lân Đốt Village (21°40'52"W/106°20'28"E), 150 m, Hưũ Liên Nature Reserve, Hưũ Liên Commune, Hưũ Luũ District, Lang Sơn Province, Vietnam. The specimen was fixed in 10% formalin for several days before being transferred to 70% ethanol for storage. A liver sample was collected prior to fixation and placed in lysis buffer before its ultimate transfer to the

American Museum Cryo Collection (AMCC 125060). The skull (figs. 10, 11) was later extracted and cleaned by dermestids in a colony at the American Museum.

REFERRED MATERIAL: In addition to the holotype, 13 additional adults of *T. daovantieni* were collected from the vicinity of Lân Đốt Village during April, 2004, on the days indicated (AMCC catalog numbers tied to liver samples are in brackets). **April 13:** AMNH 275575 [125016], male; 275576 [125017], male; 275577 [125018], male. **April 14:** 275586 [125027], female; 275593 [125034], male. **April 16:** 275602 [125044], male. **April 19:** 275627 [125069], male; 275644 [125086], male. **April 23:** 275688 [125130], male. **April 24:** 275692 [125134], male; 275693 [125135], ear with attached bit of furry skin only. **April 25:** 275711 [125153], male; 275712 [125154], female.



Fig. 4. A live *Tonkinomys daovantieni* (AMNH 275593). Note the unpigmented distal portion of the tail and the blaze of white on the forehead. Other external traits are described in the text. Photographed by D. P. Lunde, April 2004.

GEOGRAPHIC DISTRIBUTION: *Tonkinomys daovantieni* is currently known only from the type locality, but the species probably occurs in suitable forested habitats throughout the karst landscapes of northern Vietnam (identified as the “Vietbac Karst Zone” by Tuyet, 1998: 187; or the Caobang and Bacson regions by Głazek, 1966), and possibly in southern China (see the distributions of karst outcrops mapped in Tuyet, 1998, and Zhang, 1989).

DIAGNOSIS: Because *daovantieni* is the only known species of *Tonkinomys*, generic and specific diagnoses are the same.

ETYMOLOGY: We are honored to name this distinctive gray-furred and short-tailed limestone endemic after the late Đào Văn Tiển, who when he died on May 3, 1995, at the age of 78, was emeritus professor of biology at the National University of Hanoi. Our esteem for this Vietnamese scholar is reflected in the obituary prepared by Groves and Weitzel (1995: 15–16):

Professor Tien was educated in Hanoi under the French colonial Administration. He taught several generations of Vietnamese scientists and carried his Biology Faculty through the difficult years after his country gained its freedom. Though Professor Tien’s principal works and many of his papers were in mammalian zoology, his advice, his academic research, and most importantly his student support was never limited to this. Certainly, all senior biologists in northern Vietnam today gladly call Professor Tien their teacher. It is hard to calculate the importance of this gentle and thoughtful man in the history of Vietnam’s science. He was the father of his field in Vietnam. His loss was a great blow for us, though he left for the world an incalculable legacy of studies of the rich biology of Vietnam, and a scholarly tradition for those who will follow in his footsteps.

The biodiversity surveys undertaken in northern Vietnam during the past decade that have contributed so significantly to knowledge of mammalian diversity in that country can be viewed as extensions of earlier vertebrate surveys in northern Vietnam from 1957 to 1971 initiated and managed by Professor Tiển. His results generated large and important



Fig. 5. Underparts of *Tonkinomys daovantieni* (AMNH 275593). The dark grayish black dorsal coat merges gradually into the dark gray venter, which is broken by a white pectoral patch (found in ten other specimens of the sample of 13). Photographed by D. P. Lunde, April 2004.

collections of voucher specimens (currently housed at the University of Hanoi), and were summarized by him in 1985 (Đào, 1985). That body of field data and museum specimens, and the scientific results derived from them formed the foundation of “Checklist of Mammals in Vietnam” published nine years later (Đặng et al., 1994), which at the time stood as the finest and most comprehensive annotated list of Vietnam mammals, and today remains not only an important reference, but a tribute to Professor Tiên, his students, and his colleagues.

MORPHOLOGICAL DESCRIPTION: Large head and eyes, a stocky body, dark gray ears, short and bicolored tail, grayish black (gunmetal) upperparts, and dark gray underparts charac-

terize live *Tonkinomys daovantieni* (figs. 4, 5; table 1). Detailed descriptions of its external features, skull, and dentition are provided below.

External traits: The dense fur covering upperparts of head and body is grayish black with burnished highlights, and consists of three types of hairs. The soft underhairs (up to 12 mm long) are gray for their entire length. The overfur layer (up to 15 mm thick) is formed by wide, flexible, and grooved spines, each pale gray for most of its length and tipped with brown or black. Scattered guard hairs project 5–10 mm beyond the overhairs, the basal half of each is gray, the distal half black. The combination of hair types and their pigmented banding patterns imparts a thick and semispinous texture, and a burnished, grayish black tone to the upperparts. The dorsal pelage is less spiny along the sides of the body, appears especially soft and gray over the shoulders and hips, and gradually blends into the softer and shorter (up to 8 mm thick) dark gray fur covering the underparts. That coat is formed by soft underhairs mixed with soft, wide, and grooved spines; both kinds of hairs are gray for their entire lengths. Although paler than the dorsal coat because it has no dark brown guard hairs, no sharp demarcation exists between dorsal and ventral fur. A white patch (size ranges from 10 mm long and 5 mm wide to 30 mm by 12 mm) interrupts the dark gray fur over the chest in 11 of the 13 specimens; the other two lack this chest mark. On the forehead a blaze of white hairs (expression ranges from a few hairs to a patch 15 mm long and 5 mm wide) contrasting with surrounding dark fur is present in nine specimens; four, including the holotype, lack the blaze. Sides of the face and throat are dark gray; the lips, chin, and rhinarium are unpigmented. Fur covering the lower limbs is dark gray everywhere, but shorter than that on the torso.

Eyes, relative to head area, are large, proportionally similar to species of *Rattus*. A wide unpigmented ring surrounds each narrow and circular, dark brown eyelid. Beyond the eyes, the fur is dark gray covering this part of the head, and although somewhat more suffused with black, this darker tone does not define a facial mask.

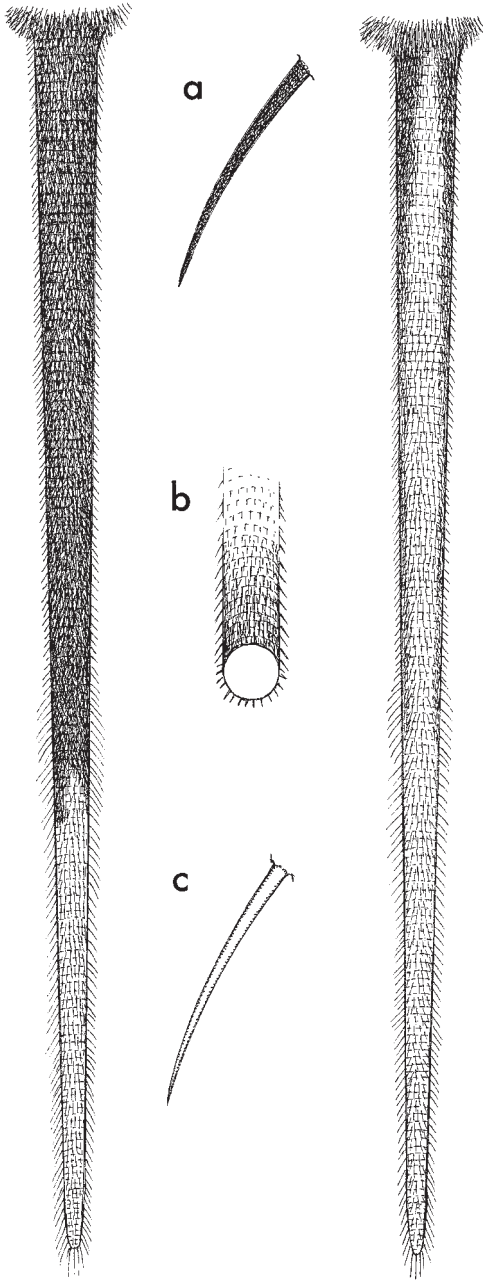


Fig. 6. Holotype of *Tonkinomys daovantieni*. Dorsal (left) and ventral (right) views of the tail. Note increasing length of scale hairs from base to tail tip. Basal two-thirds of dorsal and lateral surfaces of tail is dark brown, produced by brown pigment in both scales and scale hairs (a); scales and scale hairs (c) on underside and distal one-third of the tail are unpigmented. See text for discussion of pattern variation within the complete sample. Tail is round in cross-section (b).

The pinnae (external ears) are moderately large, but not disproportionately expansive relative to body size. They are dark gray, somewhat oval in outline, and rubbery in texture. Short brown hairs (visible only under magnification) are sparsely scattered over both outer and inner surfaces, but do not tint the gray background.

The mystacial vibrissae are either dark brown or unpigmented, fine, and very long (up to 75 mm); when laid against the head the longest projects up to 20 mm beyond the distal margin of each pinna. The longest in each pair of superciliary (or supraorbital) vibrissae (up to 60 mm long) also extend well past the pinna when appressed against the head. The short submental and interramal vibrissae are unpigmented. The few short (up to 25 mm) genal vibrissae are inconspicuous and unpigmented for most of their lengths. The base of the wrist supports four moderately long (up to 10 mm) unpigmented ulnar carpal vibrissae, and from the inside of each heel springs a longer (up to 15 mm) unpigmented tarsal vibrissa.

The tail is appreciably shorter than the length of head and body ($LT/LHB = 83\%$, average of 13 individuals) and it is thick (range in 13 specimens is 5.7 mm to 6.3 mm, measured laterally at midpoint of tail length) and round in cross section (table 1; fig. 6). The proximal one-half to three-fourths is dark brown on dorsal and lateral surfaces (produced by the brown pigment in scales and scale hairs). The ventral surface is white, as are all surfaces of the distal one-fourth to one-half (25%–44% of total tail length among the 13 specimens). In a few specimens, scattered scales in the unpigmented regions retain very pale brown pigment, which provides a slight speckling to the white portion, usually over the ventral surface. Scales in the overlapping annuli are moderately large (10 annuli of scales per centimeter, counted along basal one-third of the tail), and beneath each scale emerge three hairs. These are bristle-like and about as long as two scale annuli (1.0 mm) near the base of the tail, but those at the tail tip are softer and longer (5–6 mm); there is a gradual increase in hair length and texture from base to tail tip. Because the hairs are mostly longer than the scale annuli, the tail

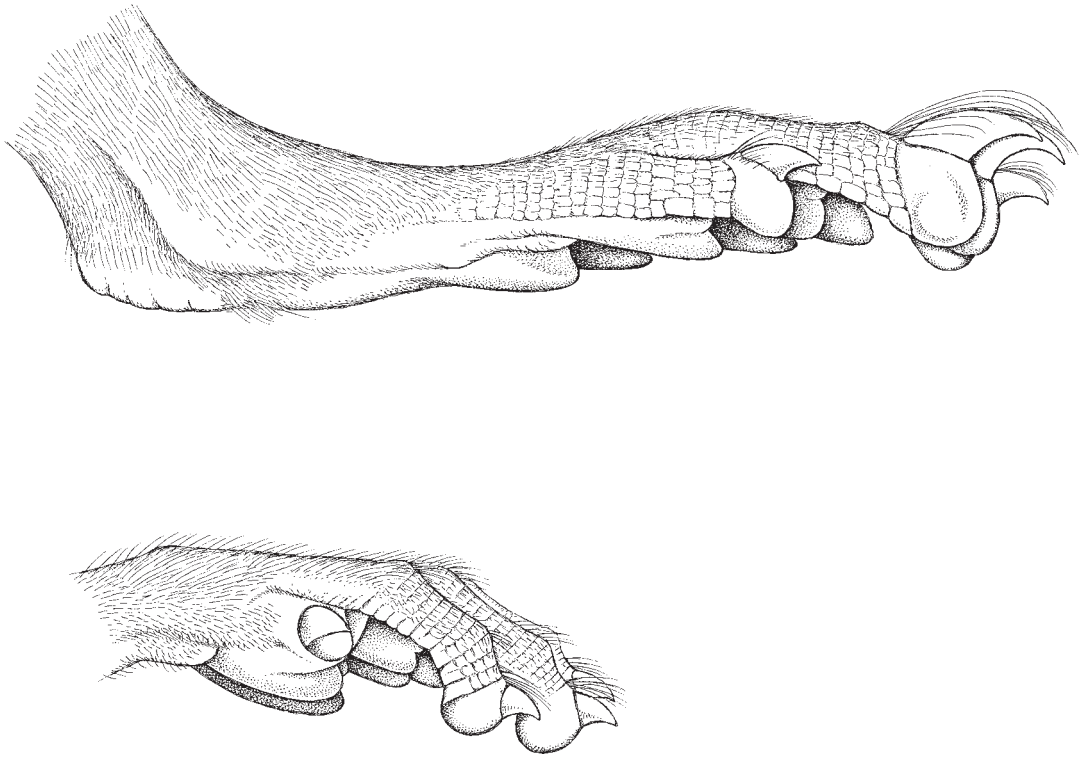


Fig. 7. Holotype of *Tonkinomys daovantieni*. **Top:** Lateral view of left hind foot. **Bottom:** Lateral view of left front foot. The bulbous palmar and plantar pads are clearly evident.

appears somewhat hairy, especially the distal half (fig. 6).

Claws are unpigmented, as are their thin covering of hairs (ungual tufts) and the digits of the front and hind feet. So too is the dorsal metacarpal and metatarsal integument, but an overlying covering of brown hairs imparts a diluted brown wash to these surfaces. Both front and hind claws are not unusually long, and are gently curved (fig. 7). Their covering unguis tufts either do not or only slightly project beyond the claw tips (fig. 8). Each palmar surface is naked and mostly unpigmented. Its topography is dominated by five huge and swollen pads: three interdigital, thenar, and hypothenar (fig. 8). Gray patches mark some of the pads, and the ventral surfaces of all are nearly smooth, exhibiting only traces of semicircular and transverse lamellae. The hind foot is moderately long and wide (table 1). Its naked plantar surface and some of the pads are dark gray. The anterior half of the plantar

surface is formed by six very large and swollen pads (tubercles) in a tight cluster: two inner interdigitals (2 and 3), two outer interdigitals nearly opposite each other (1 and 4), a large hypothenar (nearly as large as an interdigital) just behind and slightly overlapping the lateral interdigital, and an even larger thenar (fig. 8). Size and protuberance of the pads relative to plantar surface, and their contiguous positions resemble the conformation seen in arboreal murines like the Sulawesi species of *Margaretamys* (Musser, 1981: 279). They contrast with such terrestrial examples as Sundanese *Sundamys muelleri* and *Berlymys bowersii* (Musser and Newcomb, 1983: 357), *Rattus argentiventer* (Musser, 1973: 7), or Sulawesi *Maxomys* (Musser 1991: 27) whose pads are smaller relative to area of the plantar surface with the two outer interdigital mounds set well apart from the inner pair, and the hypothenar and thenar widely spaced from each other and the interdigitals.

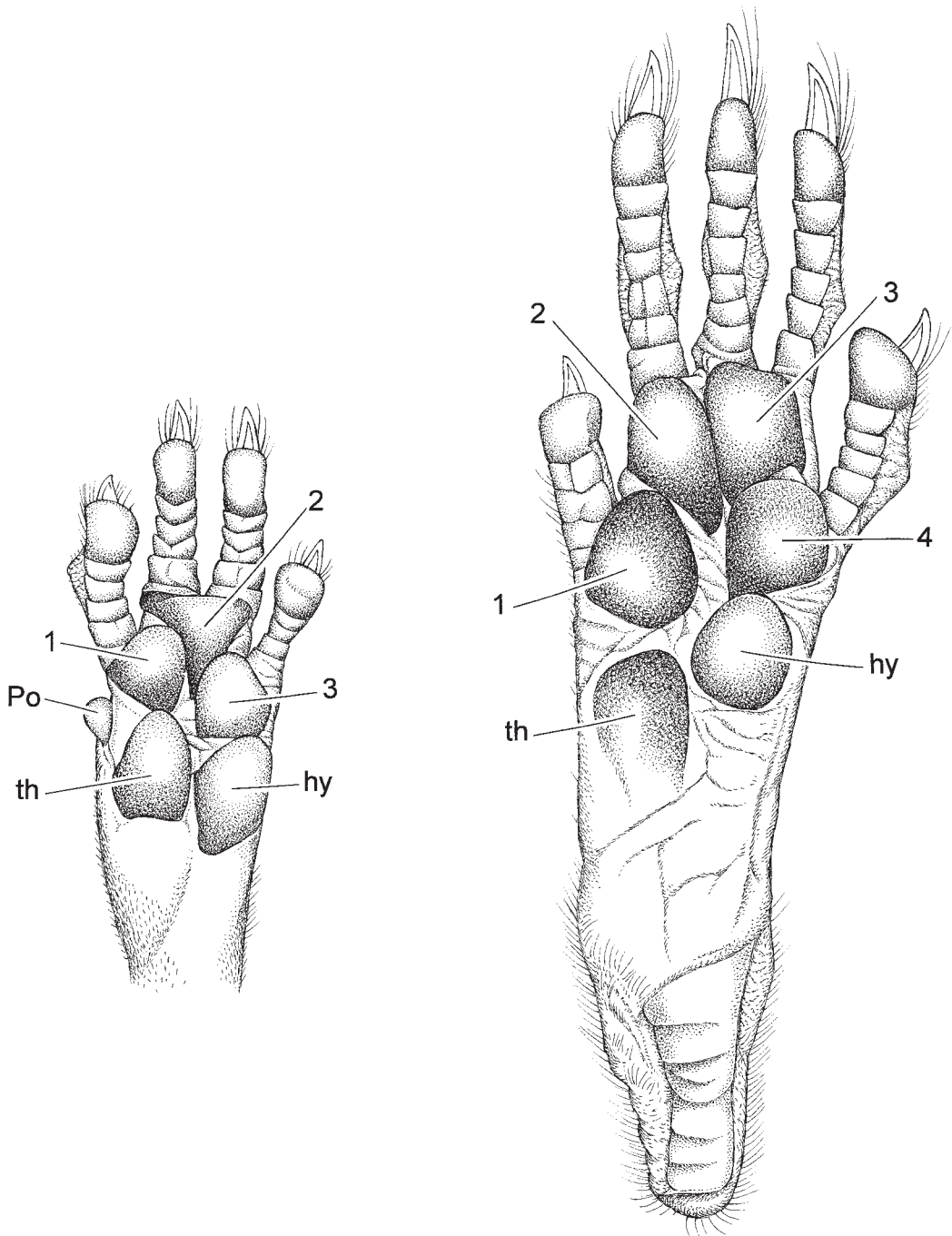


Fig. 8. Holotype of *Tonkinomys daovantieni*. **Left:** Palmar view of left front foot. **Right:** Plantar view of left hind foot (compare with the plantar views of *Chiromyscus*, *Niviventer*, and *Saxatilomys* in fig. 9). Abbreviations: **hy**, hypothenar pad; **po**, pollex; **th**, thenar pad; **1—4**, first through fourth interdigital pads.

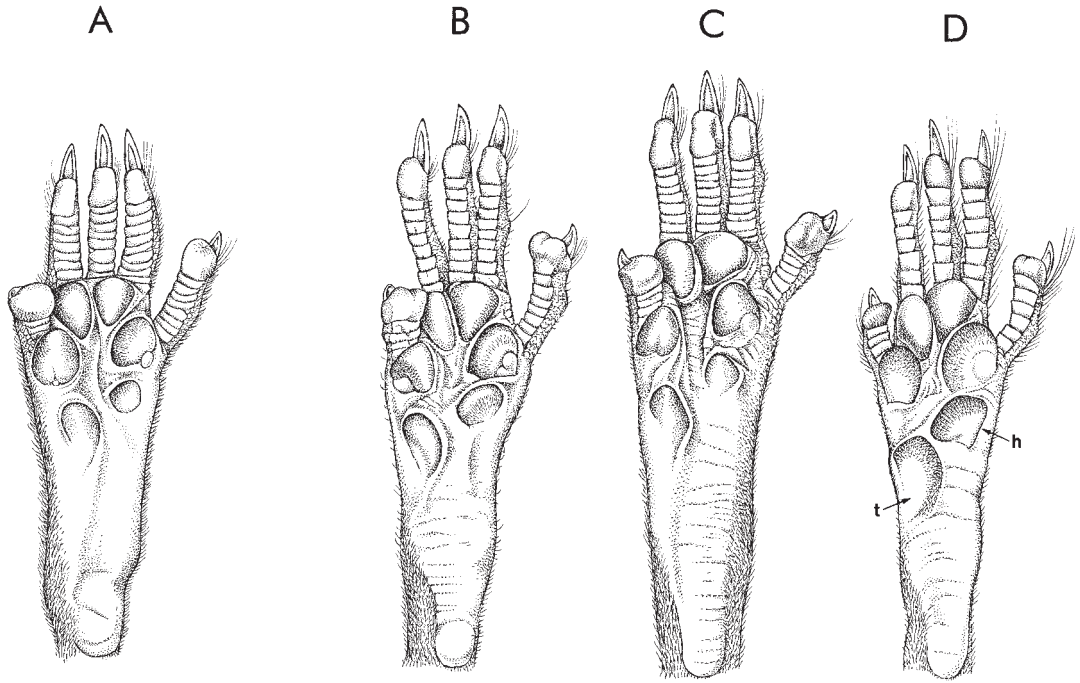


Fig. 9. Plantar views of left hind feet of adults of Indomalayan murines in the *Dacnomys* division. **A**, *Chiromyscus chiropus* (AMNH 268333, southern Vietnam). **B**, *Niviventer langbianis* (AMNH 272251, northern Vietnam). **C**, *N. fulvescens* (AMNH 272376, northern Vietnam). **D**, *Saxatilomys paulinae* (BMNH 2000.292, Lao PDR). The feet of the arboreal *C. chiropus* and *N. langbianis* are short and adorned with large and bulbous plantar pads compared with the longer foot and relatively smaller pads in the terrestrial/scansorial *N. fulvescens*. The four interdigital pads (at the bases of the digits), thenar (**t**), and hypothernar (**h**) of *S. paulinae* are set appreciably closer than in any of the other species, are more swollen, and larger, not only absolutely but relative to plantar surface, an overall plantar adornment resembling that exhibited by *Tonkinomys daovantieni* (fig. 8).

Each female in our sample has four pairs of mammae: one pectoral, one postaxillary, and two inguinal.

Skull: *Tonkinomys daovantieni* has an elongate skull, sturdy in appearance, the visual impression reflecting a long rostrum, narrow cranium, and robust zygoma. In dorsal view (fig. 10), the rostrum is moderately long and wide, its parallel sides dimpled by a small nasolacrimal capsule (just anterior to the anterior spine of each zygomatic plate). The distal portion of the rostrum is slightly tapered, the anterior margin of the nasals is triangular, and the adjacent premaxillaries project well beyond the posterior nasal-frontal suture. A moderately deep zygomatic notch is evident between the rostral wall and the projecting anterior spine of the zygomatic plate. The dorsal portion of each lacrimal

bone (in the anterolateral pocket of the orbit) is small, rectangular, and fused with the dorsal maxillary zygomatic root (no shared suture with the frontal). Dorsolateral margins of the interorbit, which is about as wide as the rostrum, are defined by high ridges that are prominent as they sweep back along the dorsolateral postorbital margins of the frontals; these ridges become weaker in expression and less pronounced where they extend (as temporal ridges) onto the parietal margins (accentuating dorsolateral rims of the cranium) to about the level of the posterior edge of the squamosal zygomatic root. Here the temporal ridge is barely discernable, and the parietal extends ventrally to form the dorsolateral cranial wall between the posterior margin of the zygomatic root and the lamboidal ridge; a bony swelling

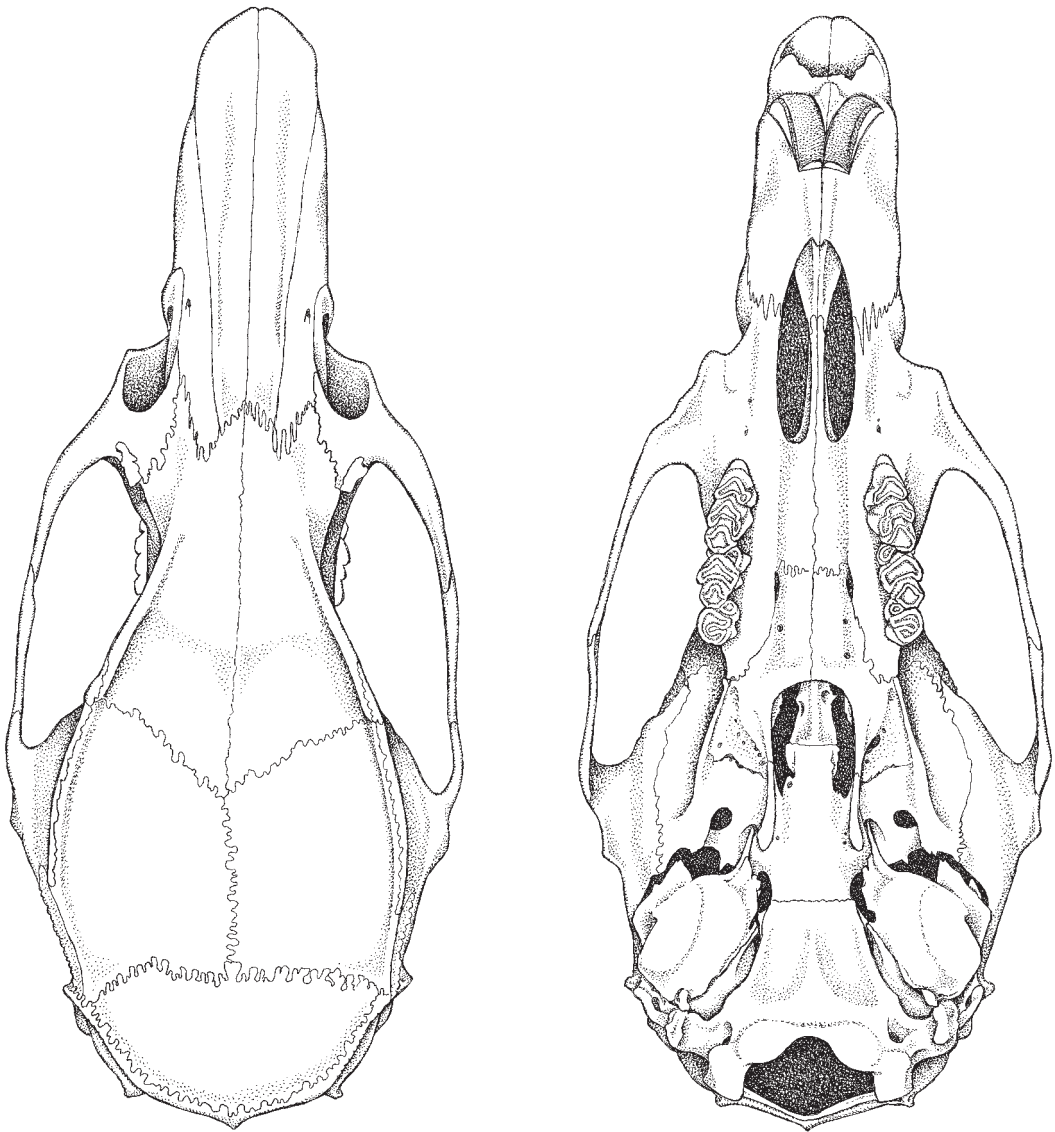


Fig. 10. Holotype of *Tonkinomys daovantieni*. Dorsal (left) and ventral (right) views of cranium. Measurements are listed in table 1.

outlines the parietal-squamosal connection all the way to the lamboidal ridge. The interparietal is long (in anterior-posterior plane) and moderately wide (its lateral margins are within the parietal and supraoccipital sutures, not extending to the parietal-squamosal suture) and its posterior two-thirds roofs a deep occiput with a slightly convex or chevron-shaped posterior margin. Zygomatic arches are robust and arranged nearly parallel to one

another; neither zygoma bows out far from the skull.

The skull appears long, low, and without significant basicranial flexion when viewed from lateral perspective (fig. 11). The rostrum is rectangular in side view, and extends slightly beyond the incisor faces to enclose the nasal aperture in a short tube in which nasals provide the roof and premaxillaries the sides. Much of the ventral maxillary root of each

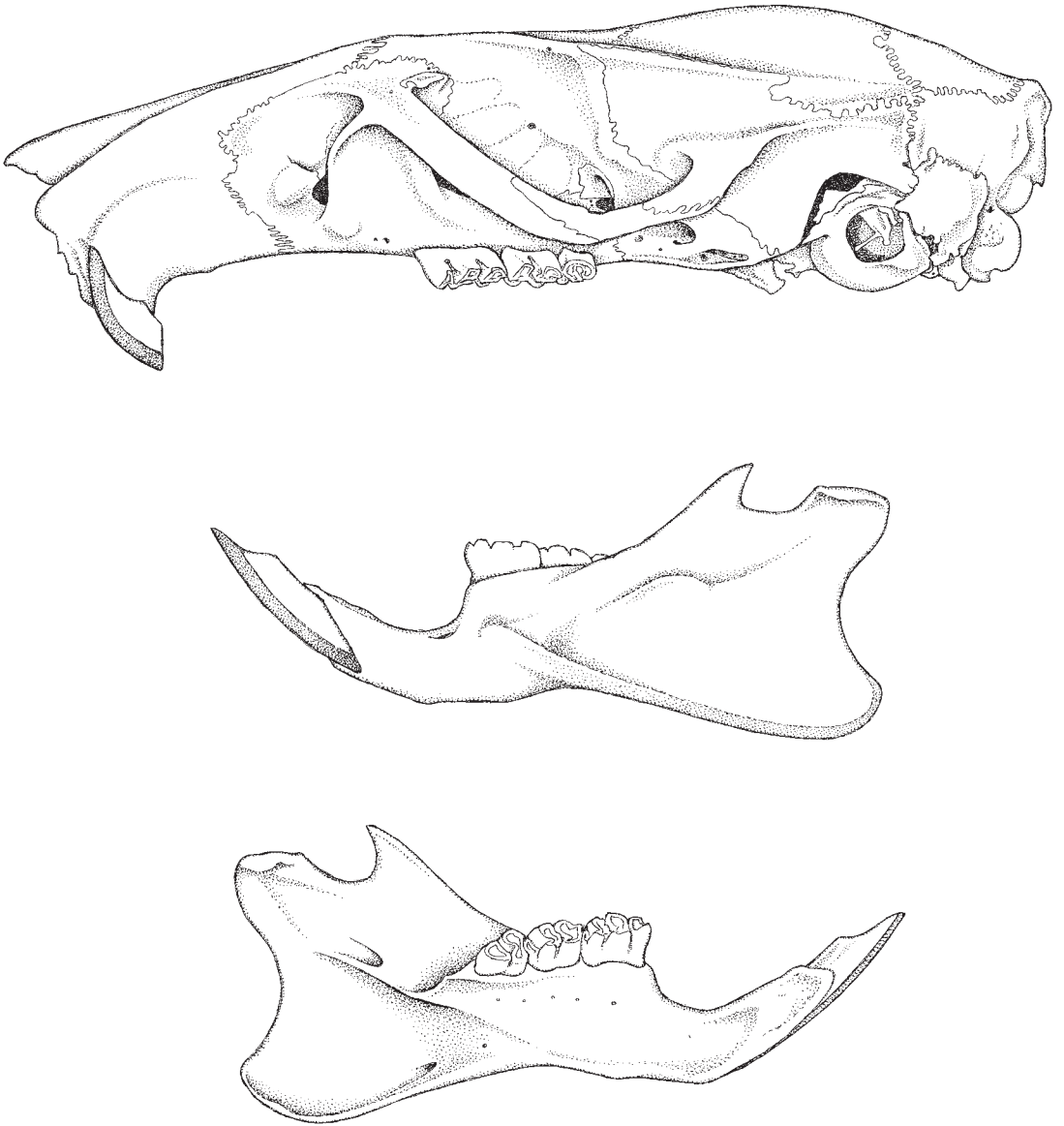


Fig. 11. Holotype of *Tonkinomys daovantieni*. **Top**: Lateral view of cranium. **Middle**: Lateral view of left dentary with incisor and molars. **Bottom**: Medial view of same dentary.

zygomatic arch lies anterior to the molar row, with the posterior margin of the zygomatic plate extending behind the front margin of the toothrow (0.5–1.0 mm is the range in our sample of skulls). The zygomatic plate is wide, its convex anterior margin projecting beyond the dorsal maxillary zygomatic root to form a moderately deep zygomatic notch (best seen in dorsal view). This anterior spine of the plate

does not project far enough forward to conceal the nasolacrimal capsule, which is small and only slightly inflated. Maxillary and squamosal zygomatic processes are joined by a long jugal to form a thick and robust zygomatic arch. The squamosal root of each arch is situated high on the side of the cranium where its posterior ridge-like portion extends horizontally just below the posteroventral

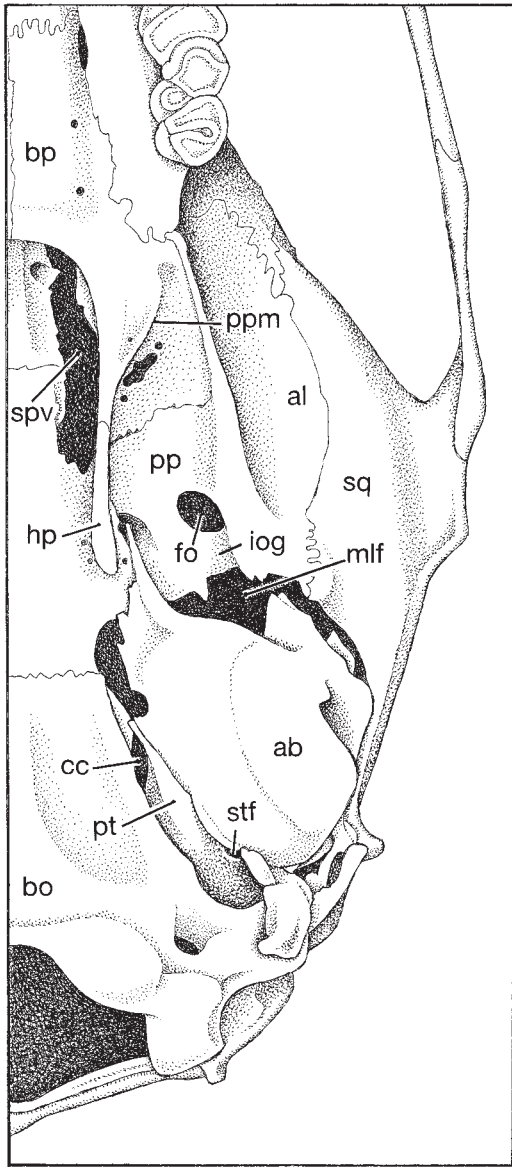


Fig. 12. Holotype of *Tonkinomys daovantieni* illustrating details in enlarged view of left basicranial region. Abbreviations: **ab**, auditory bulla; **al**, alisphenoid; **bo**, basioccipital; **bp**, bony palate; **cc**, carotid canal; **fo**, foramen ovale; **hp**, hamular process; **iog**, groove for the infraorbital artery; **mlf**, middle lacerate foramen; **pp**, pterygoid plate (its ventral surface is the pterygoid fossa); **ppm**, posterolateral palatal margin; **pt**, periotic; **spv**, sphenopalatine vacuity; **sq**, squamosal; **stf**, stapedial foramen.

margin of the parietal, which projects ventrad to form the dorsolateral side of the cranium. The low ridge of the squamosal zygomatic root disappears 10–15 mm anterior to the vertical ridge formed by the squamosal-exoccipital suture. The configuration is similar to, but not identical with, that documented for species of *Leopoldamys* (see Musser, 1981: fig. 18) and *Niviventer* (Musser et al., 2005: figs. 7 and 8). Dorsal to the auditory (ectotympanic) bulla and posterior to the squamosal zygomatic root, the squamosal forming the side of the cranium is intact except for a minute subsquamosal foramen at the prominent ridge formed by the squamosal-exoccipital suture. This foramen is the only landmark identifying where the squamosal and a wide hamular process of the squamosal have completely fused to form the solid cranial wall. A spacious postglenoid foramen that is confluent in some specimens with a wide postalar fissure (ventral to the postglenoid foramen) separates the squamosal margin from the periotic flange and dorsoanterior surface of the ectotympanic (auditory) bulla. That capsule is attached to the squamosal dorsally by the posteroventral portion of that bone, which represents the cranial wall fused with a wide hamular process. There is no anterior attachment, which is the usual pattern among most murines. An anterior flange of the periotic, the tegmen tympani, is present (and partly separates the dorsal postglenoid foramen from the ventral postalar fissure), but is separated by a narrow or moderately wide gap from the posterior margin of the squamosal in most specimens; there is no posterior suspensory process of the squamosal to which the tegmen tympani could attach (in some cricetid rodents, the tegmen tympani overlaps a posterior projection of the squamosal to form one of the suspensory attachments between ectotympanic capsule and squamosal; see the diagrams in Voss, 1993: 19). The moderately inflated mastoid is tightly sutured to squamosal and exoccipital. It is completely ossified, without the moderate or large fenestrae found in some murines (*Crunomys celebensis*, for example; Musser, 1982: 38) and sigmodontines (see Carleton and Musser, 1989: 34); only a very small opening penetrates the dorsal mastoid-exocci-

pital suture. The foramen magnum is directed caudad (which reflects the horizontal rather than arched axis of the skull—no significant basicranial flexion), and the deep occiput projects slightly beyond posterior surfaces of the occipital condyles. The ethmoid foramen within the orbit is tiny, and the optic foramen moderately large. The dorsal palatine foramen is separate from the sphenopalatine foramen, a configuration usual among Asian murines, with a few exceptions where the two foramina are coalesced (Musser, 1982: 22). Eight specimens have a bony alisphenoid strut (ranging from moderately wide to slender in the sample) on each side of the skull posterior to the orbit and dorsad to the pterygoid ridge (the lateral edge of the pterygoid plate). The strut separates the foramen ovale accessorius from the combined buccinator-masticatory foramen on the side of the cranium, and obscures the anterior opening of the alisphenoid canal. One specimen exhibits a strong strut on the left side, but only a bony thread on the right. Only one individual in our sample of skulls lacks struts (which are represented by only a dorsal nubbin on each side). In this specimen, the opening to the alisphenoid canal is evident, the foramen ovale accessorius and buccinator-masticatory foramina coalesce (basically disappear), and the course of the buccinator and masticatory nerves is marked by a shallow groove extending from the foramen ovale onto the side of the alisphenoid.

The short rostral tube anterior to faces of the incisors, wide rostrum, long incisive foramina and bony palate, diverging molar rows, moderately wide mesopterygoid fossa and pterygoid plates, and small bullae are the topographic highlights when the skull is studied from ventral perspective (figs. 10, 12). Just behind the incisors is a tiny interpremaxillary foramen, and beyond it the rostrum is perforated by long and spacious incisive foramina, their posterior rims situated slightly before (0.5 mm) anterior margins of the first molars, even with those molar surfaces, or projecting slightly (not more than 0.5 mm) between them. The bony palate is wide and long, extending 1.5–2.0 mm beyond the molar rows to form a broad platform with a slightly concave and smooth posterior

margin (up to 20% of the palate extends past the third molars) unmarked by any bony ridge in most specimens, slightly thickened in others. Each posterolateral margin of this shelf extends as a flat, bony surface onto the anterior portion of each pterygoid plate where its sharp diagonal border marks the antero-medial margin of each pterygoid fossa. The ventral surface of the bony palate is smooth except for a pair of oblong posterior palatine foramina (in the maxillary-palatine suture opposite the middle or posterior half of each second molar), a pair of shallow grooves, and small or minute nutrient foramina scattered over the palatal shelf. The mesopterygoid fossa is wide, and dorsolateral margins of its roof are perforated by long and moderately wide sphenopalatine vacuities. On each side of the pterygoid fossa, a robust hamular process of the pterygoid marks the boundary between the mesopterygoid fossa and each adjacent pterygoid plate, its ventral surface sculptured by a shallow pterygoid fossa. The bony pterygoid plate is breached by the large ventral opening of the foramen ovale in its posterior half; its anteromedial portion along the rim of the bony palatal extension is slightly fenestrated (irregular traces of the sphenopterygoid vacuity). A shallow trough (in which the infraorbital artery passes) scores the ventral margin of the pterygoid plate between the ventral opening of the foramen ovale and the middle lacerate foramen. Small relative to overall size of the skull, the globular and only slightly inflated ectotympanic (auditory) bulla does not conceal nearly all of the periotic as it does in some other murine groups, species of *Rattus*, for example. In *Tonkinomys daovantieni*, a wide, wedge-shaped segment of the periotic is exposed between the dorsal capsular margin and basioccipital, and this wedge of periotic extends anteriorly to form the dorsal and slanting posterodorsal wall of the carotid canal. The conformation resembles that illustrated by Carleton and Musser (1989: 33) for the sigmodontine, *Oligoryzomys*, and is unlike many other murid rodents in which a more inflated ectotympanic capsule covers most of the periotic and the anteromedial margin of this capsule meets the basioccipital, so the opening to the carotid canal is bounded by the ectotympanic capsule and adjacent basiocci-

pital (the condition in *Oryzomys palustris* depicted by Carleton and Musser, 1989: 33; and species of *Rattus* and its allies illustrated in Musser and Heaney, 1992: 99). Tapering rostrally from the ectotympanic capsule is a moderately short and wide bony eustachian tube. A spacious middle lacerate foramen separates the anterior slope of the ectotympanic capsule from posterior margin of the pterygoid plate.

The cephalic arterial pattern possessed by *Tonkinomys daovantieni* is not unique among members of Murinae (as that subfamily is delineated by Carleton and Musser, 1984; Musser and Carleton, 2005). As in all described species of *Niviventer*, *Chiromyscus*, *Saxatilomys*, and *Leopoldamys*, *T. daovantieni* lacks a sphenofrontal foramen and related squamosoalisphenoid groove, the petrotympanic fissure between bullar capsule and periotic is perforated by a spacious stapedial foramen continuous laterally with a deep groove on dorsal surface of the periotic, and there is a shallow but wide groove on the posterior ventral surface of the pterygoid plate (fig. 12). This set of osteological landmarks signals a cephalic arterial pattern in which the supraorbital branch of the stapedial artery is absent and the orbital circulation derives from the distal portion of the infraorbital branch. The infraorbital is a continuation of the stapedial artery, which passes over the dorsal groove in the periotic, through the middle lacerate foramen, continues in the shallow groove ventral to the posterior margin of the pterygoid plate to course through the alisphenoid canal, and emerges onto the orbital floor through the anterior alar fissure. Common to most murines (Carleton and Musser, 1984; Musser and Newcomb, 1983; Musser and Heaney, 1992), this pattern of vessels and associated osteological landmarks is also characteristic of some sigmodontine rodents (described and diagramed for *Oligoryzomys* by Carleton and Musser, 1989; pattern 2 in Voss, 1988), and is derived compared with the cephalic arterial pattern hypothesized to be primitive for muroid rodents (Bugge, 1985; Carleton, 1980).

Mandible: The sturdy dentary supports a delicate coronoid process, relative to extent of the deep ascending ramus, a moderately

deep sigmoid notch between coronoid and prominent condyloid processes, and a shallowly concave posterior margin connecting condyloid and angular processes (fig. 11). In contrast with the wide and conspicuous ventral masseteric ridge, the dorsal ridge is either undetectable or indicated by a shallow, elongate depression. Besides the ventral masseteric ridge, the only other significant structure that marks an otherwise smooth lateral dentary surface is a slight bulge below the anterior root of the coronoid process that in turn marks termination of the incisor alveolus within the bone. In no specimen did the incisor capsule extend farther caudad to project into the condyloid process (checked by shining a high-intensity light through the dentary) as it does in some other murines (Musser and Heaney, 1992: 84). Topography of the lingual dentary surface resembles that characteristic of most other murines, the primary landmarks being a prominent lingual ridge above which is the large mandibular foramen (as in *Papagomys armandvillei*, for example; see Musser et al., 1986: 5). The body of the dentary projects anteriorly beyond the molar row as a moderately short and stocky tube containing the incisor. Just in front of the molar row on the dorsolateral labial surface is a small mental foramen.

Dentition: Enamel faces of upper and lower incisors are pale orange and smooth, without grooves or shallow sulci. Thickness of the enamel relative to the dentine is similar to that in species of *Rattus* and many other murines (Musser and Heaney, 1992: 79). The upper incisors curve caudad after emerging from the rostrum (opisthodont conformation; see Thomas, 1919; Hershkovitz, 1962: 103). Gnawing edges of the uppers are at right angles to the long axis of the skull, so their combined tips form a straight cutting edge (as in species of *Rattus*; see Musser and Heaney, 1992: 79), not curved or V-shaped (as in some Philippine and Sulawesi endemics; see Musser and Heaney, 1992; Musser and Durden, 2002). The lower incisors are moderately long and curved, their cutting tips either straight or arcuate.

Alveolar patterns for roots of upper molars are distinctive. A large anterior root, two robust lingual roots, and a large posterior

holdfast anchor each first upper molar. No labial root is present between the large anterior and posterior anchors. Three roots hold the second and third molars in place: a large anterior and posterior, and small lingual. Two large roots anchor each lower molar. Except for the first upper molars, the pattern of roots in all our examples of *Tonkinomys daovantieni* is primitive for murines (Musser and Newcomb, 1983; Musser and Heaney, 1992).

Upper molar rows are moderately long (about 17% of occipitonasal length) and strongly diverge posteriorly (width of bony palate is considerably greater between third molars than between the first; see fig. 10). Occlusal surfaces of the brachydont (low-crowned) molars are simple in topography, consisting of tightly pressed rows exposing chunky chewing surfaces in the shapes of narrow chevrons and diamonds (fig. 14). Occlusal surface of each first upper molar consists of two anterior rows of cusps, each in the form of a tight chevron, and a large roughly diamond-shaped posterior surface. The most anterior chevron is comprised of cusps t1, t2, and t3; cusps t2 and t3 are so coalesced that their limits are obliterated, at least in adults. The blended cusps t4, t5, and t6 form the second chevron, although the labial and lingual cusps retain some definition. The large, chunky posterior third of the molar consists primarily of cusp t8 merged with a smaller, indistinct cusp t9 to form a roughly diamond-shaped chewing surface. On the occlusal surface of each second upper molar, the anterior chevron is represented by only a large cusp t1 forming the anterolingual portion of the tooth. In seven out of 10 specimens, a small cusp t3 sits on the anterolabial margin; in two others, the cusp is missing and the anterolabial border is marked by only an inconspicuous cingulum; and presence or absence of cusp t3 in the tenth specimen cannot be determined because the molars are too worn. The complete chevron and chunky posterior portion of the second molar, in size and shape, resembles comparable rows in the first molar. Each third molar has an occlusal pattern that is basically a compacted form of that characterizing the second molar: a conspicuous cusp t1; minute

cusp t3 (seen in young rats but unidentifiable in older animals with more worn chewing surfaces); a complete arcuate lamina derived from the total coalescence of cusps t4, t5, and t6; and small posterior chunk either diamond-shaped or oblong in outline (formed primarily of cusp t8; cusp t9 is either absent or unidentifiable due to its total incorporation into cusp t8). We could not detect a cusp t7 (on the lingual cingulum between cusps t4 and t8 when present; see Musser and Newcomb, 1983: 333), posterior cingulum (pressed against the posterior margin of cusp t8, if present; see Musser and Newcomb, 1983: 333), accessory cusplets, or longitudinal crests connecting the cusps to form a garland configuration ("stephanodonty"; see Schaub, 1938, and Misonne, 1969) on any of the upper molars. When present these structures provide complexity to the occlusal planes and in some murines significantly increase chewing surfaces.

Occlusal planes of the lower molars are also comprised of uncomplicated patterns (fig. 14). An anterolingual cusp coalesced with a smaller anterolabial forms the anteroconid, the most anterior cusp row, which is narrower than the lamina behind it. The second and third are in the shape of narrow chevrons and represent unions of protoconid-metaconid and hypoconid-entoconid, respectively. A roughly triangular posterior cingulum forms the entire posterior fourth of the molar. Except for lacking an anteroconid, occlusal cusp patterns of the second molar resemble patterns seen in the first. The anterior half of each third molar consists of a front chevron formed by union of protoconid and metaconid and behind that a large oblong structure likely representing the complete fusion of hypoconid and entoconid. Anterolabial cusps are absent from second and third molars in most specimens, but we are not certain about others in the sample because their molars are worn to a level such that, if present, these cusps are now indistinct because they have completely coalesced with the adjacent lamina; we did find evidence of a small anterolabial cusp on the third molar of the holotype (fig. 14). We had the same frustration determining the frequency of posterior labial cusplets on some specimens. This small cone is prominent and forms the

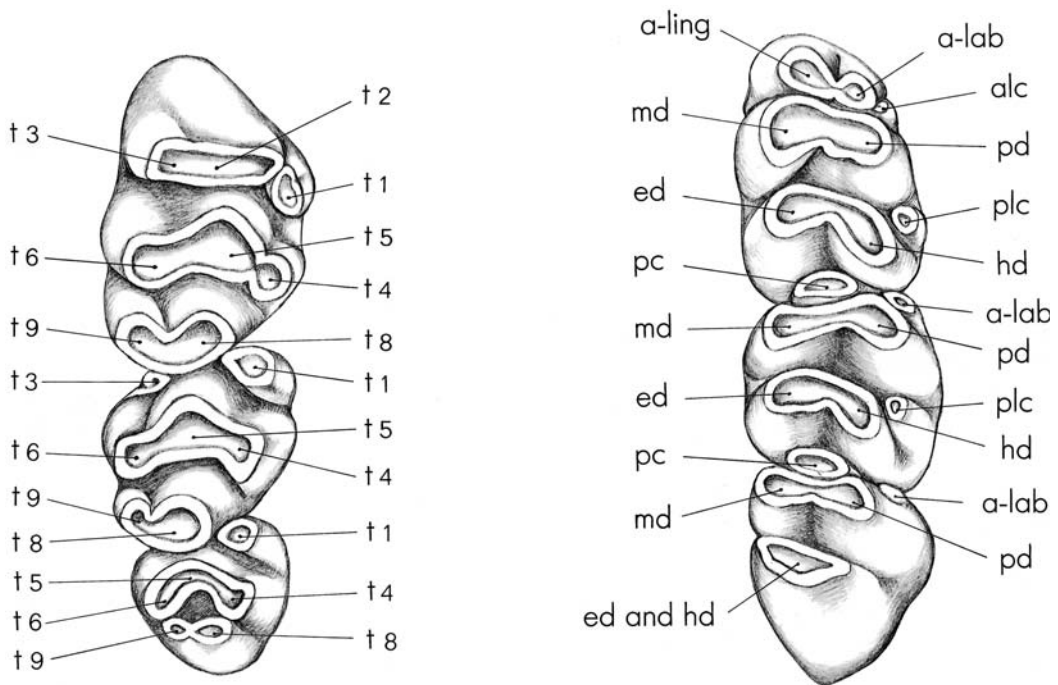


Fig. 13. Diagram of maxillary (left) and mandibular (right) molar rows from right side of *Bunomys chrysocomus* illustrating structural terms. **Maxillary molars:** cusps are numbered according to Miller's (1912) scheme and referred to in the text with the prefix "t". **Mandibular molars:** **a-lab**, anterolabial cusp; **a-ling**, anterolingual cusp; **alc**, anterior labial cusplet; **ed**, entoconid; **hd**, hypoconid; **md**, metaconid; **pc**, posterior cingulum; **pd**, protoconid; **plc**, posterior labial cusplet.

anterolabial margins of the posterior laminae of first and second molars in the holotype (fig. 14). The cusplets are present but inconspicuous on first and second molars in three other specimens (the laminar outline reflects the blending of a cusplet with the anterolabial laminar margin), and are either absent or undetectable in seven rats (because the cusplet has completely coalesced with the adjacent cusp). A posterolabial cusplet clearly does not occur on any third molar in any of the specimens at hand.

COMPARISONS

The morphological attributes of *Tonkinomys daovantieni* place it in the Dacnomys Division of Musser and Carleton (2005), which contains the Indomalayan *Chiromyscus* (one species), *Dacnomys* (one), *Leopoldamys* (six), and *Niviventer* (17); Sri Lankan *Srilankamys* (one); and the recently

described Lao PDR *Saxatilomys* (one species). Musser (1981), Musser and Newcomb (1983), Musser and Heaney (1992), Musser and Carleton (2005), and Musser et al. (2005) have chronicled the geographic distributions of these genera, along with their taxonomies, descriptions of morphologies, and postulated phylogenetic relationships. In conformation of body and limb proportions, and in characteristics of skull and teeth, *T. daovantieni* most closely resembles species of *Leopoldamys*, *Niviventer*, *Chiromyscus*, and *Saxatilomys*. Our comparisons contrast *Tonkinomys* first with extant examples of *Leopoldamys*, then with *Niviventer* and *Chiromyscus*, and finally with *Saxatilomys*.

A large body of literature has accumulated over the past two decades reporting fossil murines, mostly isolated molars and incisors, which have been recovered from Pliocene, Pleistocene, and Holocene sediments in the Indomalayan region. Some material has been

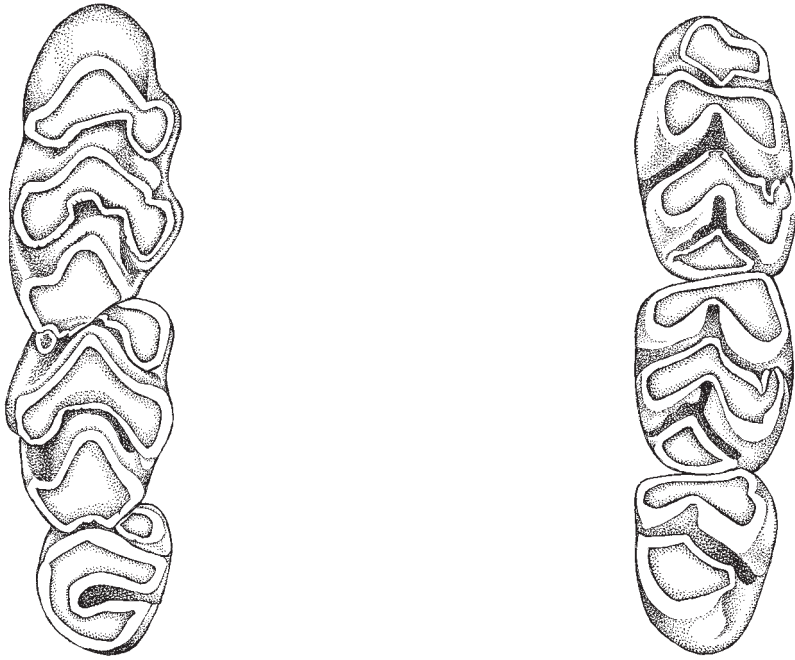


Fig. 14. Occlusal views of maxillary (left) and mandibular (right) molar rows from right side of the holotype of *Tonkinomys daovantieni* (CLM1-3 = 8.3 mm, CLm1-3 = 8.3 mm). See figure 13 for terminology of cusps and cusplets.

described as new taxa whose diagnostic traits identify them as members of the *Dacnomys* Division, and other samples have been regarded as examples of extant members of that group. We examined pertinent publications to determine whether any of the new taxa that are based on fossils represent examples of *Tonkinomys*. The significance for nomenclature is obvious. Equally important is the zoogeographic context. If some samples of fossils that have been identified as either extinct or extant species are actually examples of *Tonkinomys*, or close phylogenetic relatives, they would provide a window through which could be glimpsed the past distribution of this unique limestone rat, and the geologic depth of its evolutionary history.

***Leopoldamys*:** The smallest extant member of the six currently recognized species of *Leopoldamys* (Musser and Carleton, 2005) is the Thai *L. neilli* (only the extinct *L. minutus* is smaller, described from samples recovered from late Pliocene–early Pleistocene fissure and cave sediments; Chaimanee, 1998), and the head and body proportions, body size,

weight, and posture of the live animal closely resemble *Tonkinomys daovantieni* (Marshall, 1988: 485, provided a photograph of a live *Leopoldamys*). Although the two species are similar in body size (table 2), they are strikingly dissimilar in other particulars of external morphology. *Leopoldamys neilli* has: (1) short, sleek brown fur over upperparts of head and body that is sharply demarcated from white underparts (long, semispinous, grayish black fur over the dorsum and dark gray venter in *T. daovantieni*); (2) slightly smaller external pinnae, both absolutely and relative to head and body length; (3) a long, slender, tapered tail that is much longer than length of head and body, LT/LHB = 124% on average, and similar to an inverted U in cross-section—flat ventral surface and arched across sides and top (less tapered in *T. daovantieni*, chunky and much shorter than head and body, LT/LHB = 83%, and round in cross-section); (4) a very slender, pointed tail tip that is covered with short scale hairs no longer than 1–2 mm (tip of tail is stubby in *T. daovantieni*, covered by much longer hairs, 5–7 mm, and brush-like in

TABLE 2

Summary Statistics for Cranial and Dental Measurements (mm), and Tail-to-Body Ratio of *Tonkinomys*, *Leopoldamys*, and *Niviventer* Selected to Demonstrate Contrasts in Relative Tail Length, and Size of Body, Skull, and Maxillary Molar Row^a

(Mean, observed range in parentheses, and number of specimens are listed for each measurement; values for *L. neilli* means derived from a sample of 12. LT/LHB expressed as %.)

	<i>T. daovantieni</i> (Vietnam)	<i>L. neilli</i> ^b (Thailand)	<i>N. andersoni</i> ^c (Sichuan, Yunnan)	<i>N. confucianus</i> ^c (Sichuan)
LHB	204.6 (184–217) 13	217	171.6 (150–198) 46	143.2 (125–170) 24
LT	168.9 (156–183) 13	270	229.7 (194–269) 44	182.7 (160–204) 23
LT/LHB	83	124	134	128
LHF	39.0 (37–41) 13	42	35.1 (31–40) 47	29.8 (28–32) 20
LE	30.0 (29–31) 13	27	26.4 (22–28) 19	21.0 (20–23) 24
ONL	50.0 (47.1–52.4) 7	51.9	41.7 (38.7–45.7) 37	36.9 (33.9–40.5) 25
CLM	8.33 (8.0–8.8) 7	8.3	7.3 (6.9–7.5) 18	5.8 (5.3–6.3) 59

^a *Leopoldamys neilli* is the smallest in body size of any extant *Leopoldamys*, *N. andersoni* is among the largest within *Niviventer*, and *N. confucianus* represents most species in the genus in body size, along with body and tail proportions.

^b Values are from Marshall (1988: 485), and are means derived from 12 adults.

^c Lengths of head and body, tail, hind foot, ear, and ONL are from Musser and Chiu (1979: 584); lengths of maxillary molar rows are unpublished summaries by Musser and Lunde (ms.) derived from AMNH samples collected in China.

appearance); and (5) swollen plantar tubercles situated in distal two-thirds of plantar surface, as seen in *Tonkinomys* (figs. 9, 10), but slightly smaller relative to plantar area—the thenar pad, for example, forms about 17% of plantar surface (*T. daovantieni* has relatively more expansive plantar pads—the thenar constitutes about 20% of plantar surface). Short, sleek fur with the coat that covers upperparts of the head and body strikingly contrasting with the ventral covering is characteristic of all extant species of *Leopoldamys*. Also common to all extant species in that genus is a very long and tapered tail, with its cross section resembling an inverted U, and its tip covered by very short bristles. Elongate hind feet are common to all *Leopoldamys*, as are the number of plantar tubercles, their size relative to plantar surface, and distribution in the distal two-thirds of the plantar surface.

The skull of *L. neilli* is similar to that of *T. daovantieni* in overall size (table 2), and the two are remarkably alike when viewed from a dorsal perspective (compare the cranial photographs of *Leopoldamys* in Musser, 1981: 259, and the drawing on p. 264, with the renditions in fig. 10). In ventral view, however, the two species are strikingly dissimilar. Compared with the Vietnam species, *L. neilli* (and all other extant species of *Leopoldamys*) has: (1) significantly shorter

incisive foramina, their posterior margins well anterior to faces of first upper molars (longer in *T. daovantieni*, the posterior edges located just before anterior margins of first molars, even with them, or slightly projecting between the first molars); (2) a much shorter bony palate, its posterior margin aligned somewhere between the middle or end of each third upper molar, depending upon the species and variation within each sample (longer in *T. daovantieni*, extending beyond the molar rows to form a wide platform); (3) longer postpalatal length, which reflects the shorter bony palate (much shorter in *T. daovantieni*); (4) wider, chunky molars relative to size of skull, which is correlated with an absolutely narrower bony palate (smaller, gracile molars relative to size of skull, and an attendant absolutely wider bony palate in *T. daovantieni*); (5) molar rows that barely diverge posteriorly (molar rows diverge appreciably along anterior-posterior axis in *T. daovantieni*); (6) a small, moderately inflated ectotympanic bulla relative to size of the skull (more inflated capsule in *T. daovantieni*, and absolutely larger in most examples); and (7) a very long, bony eustachian tube, especially contrasted with the small bulla (much shorter eustachian tube in *T. daovantieni*). These differences also separate *T. daovantieni* from specimens we examined representing the other five species of

Leopoldamys. Our study of those comparative samples also reveals that *L. neilli* and the other species of *Leopoldamys* have wider and sturdier alisphenoid struts relative to skull size, and these struts are present in every individual of each species (relatively weaker struts in *T. daovantieni*, and absent from some specimens).

Patterns of roots beneath certain molars that are characteristic of *T. daovantieni* are dissimilar to those exhibited by species of *Leopoldamys*. Both extant samples (material in AMNH and USNM; also see Musser, 1981: 260) of *Leopoldamys* and those represented by fossils (Chaimanee, 1998; Zheng, 1993) have four-rooted upper molars: large posterior, single large lingual (we have never encountered a specimen with two lingual roots), large anterior, and a small labial, which is sometimes divided (also four roots in *T. daovantieni*, but there are two large lingual holdfasts instead of one, and no labial root). All *Leopoldamys* have a second upper molar that is anchored by either three or four roots (only three roots in all our *T. daovantieni*). Both *Leopoldamys* and *Tonkinomys* have three-rooted third upper molars. All species of *Leopoldamys* have four-rooted first lower molars: two large anterior and posterior anchors, and smaller labial and lingual holdfasts (all examples of *T. daovantieni* have only two roots, an anterior and posterior coequal in size). Second and third lower molars in *Leopoldamys* have two roots (large anterior and posterior), which is also the pattern in *T. daovantieni*.

In addition to the marked contrasts in robustness and width of molars between *Leopoldamys* and *Tonkinomys*, occlusal patterns of molars are different (compare illustrations of molar rows for *Leopoldamys* in Musser, 1981: 262, with those of *Tonkinomys* in fig. 14). Coronal surfaces of maxillary molars are characterized by simple patterns in both genera (no cusp t7 or posterior cingulum on any molar, no accessory cusplets, no longitudinal crests connecting the primary cusps), but the conformations of laminae forming the occlusal surfaces are dissimilar. The anterior lamina of the first molar in *Leopoldamys* consists of a nearly horizontal segment, formed by the complete fusion of

cusps t2 and t3, and a discrete cusp t1 on its posterolingual margin. The second lamina is not as straight but gently arcuate. These are diagnostic molar traits for *Leopoldamys*. In contrast, the two comparable laminae in *Tonkinomys* are tight chevrons—cusps t1 and t3 are opposite each other in the first lamina, as are cusps t4 and t6 in the second. Furthermore, cusps t4 and t6 in *T. daovantieni*, although coalesced with the central cusp t5, are large relative to overall dimensions of the lamina, and retain part of their identity as cusps. Comparable cusps in the second lamina in *Leopoldamys* are relatively smaller and so broadly merged with cusp t5 that their boundaries are not determinable. The large chunky posterior lamina in *Leopoldamys* is wider than long, but roughly diamond-shaped in *Tonkinomys*. Contrasts in second upper molars are similar to those seen in the first. The third upper molars in *Leopoldamys* have a stretched, ridge-like cusp t4 compared with the shorter version in *Tonkinomys*; otherwise, the occlusal patterns in the two genera are similar.

Cusps form either nearly straight or gently arcuate lamina in the lower (mandibular) molars of *Leopoldamys*. The posterior cingula are wide and elliptical in cross-section in all members of that genus, prominent posterior cusplets adorn the labial margin of the first and second molars, and two nearly straight laminae form the occlusal surface of each third molar (see the illustrations in Musser, 1981: 260). In parallel with the upper molars of *Tonkinomys*, the two cusps forming the laminae of its lower molars are diagonally oriented so that after wear they form chevrons in which the arms are very close, the posterior cingula are roughly triangular, labial cusplets are indistinct or not present on most specimens (prominent only in the holotype), and the occlusal surface of the third molar is formed by a distinct anterior chevron-shaped lamina and a posterior oblong chunk.

***Niviventer* and *Chiromyscus*:** We examined samples of all 17 of the currently recognized species of *Niviventer* and the single species of *Chiromyscus* (taxonomy and geographic distributions for both genera are summarized in Musser and Carleton, 2005; specimens forming the comparative samples we utilized are

listed in the Appendix by Musser et al., 2005). We preface our comparisons by explaining that the present contents of *Chiromyscus* and *Niviventer* will likely be altered after careful systematic revision of these genera. Musser (1981) characterized them, provided provisional diagnoses and contents, but his exposition was more of a taxonomic summary and meant to be a working hypothesis, not a systematic revision. That kind of study has yet to be realized. Most species will remain in *Niviventer*, but two sets may eventually be differently allocated. Except for its nail-like claw on the hallux, shelf-like ridges bordering dorsolateral margins of the postorbital region and braincase, pattern of roots beneath the first upper molar (table 3), color pattern of the dorsal pelage, and large and very bulbous plantar pads set close together, other external and most cranial and dental characteristics of the arboreal *C. chiropus* are similar to those features in the species of *Niviventer*, particularly *N. langbianis* (Musser, 1981; Musser and Lunde, ms.). The latter is also arboreal (observations by Lunde and Musser derived from trapping surveys in Vietnam), and shares with *C. chiropus* comparable prominent postorbital and temporal ridges, the number of roots anchoring each first upper molar, a nail-like claw on the hallux, a pelage color pattern that does not match in details but is similar, and equal expression of plantar pads. A revisionary inquiry may either move *N. langbianis* to *Chiromyscus*, or *C. chiropus* will be subsumed within *Niviventer* (that name would then be a synonym of the older *Chiromyscus*).

Niviventer andersoni and *N. excelsior* form another set now allocated to *Niviventer* that will probably be removed. Musser (1981) described a suite of cranial and dental traits held by these two species that contrast with the characters common to the other species in *Niviventer*. Should information from other anatomical systems, and that derived from chromosomal and biochemical surveys, support the cranial and dental distinctions, he (p 328) noted "... that the phylogenetic relationship between *Niviventer* and the *N. andersoni* division [would be] better expressed by excluding the latter from *Niviventer* and placing *N. andersoni* and *N. excelsior* in a genus of their own."

We accept the current, although provisional, contents of *Niviventer* for our comparative context. We will also refer only to "*Niviventer*", understanding that the contrasts between species in that genus and *Tonkinomys* are much the same as between the latter and *C. chiropus*.

While the body conformation of *Tonkinomys daovantieni* recalls small-bodied *Leopoldamys*, no such resemblance exists between the Vietnamese animal and any species of *Niviventer*. Among the largest species of *Niviventer* in body size is *N. andersoni*, which is still appreciably smaller than *T. daovantieni* (table 2). In all species of *Niviventer*, dorsal head and body fur ranges from buffy or brownish gray through brown to reddish brown (Musser, 1981). *Niviventer brahma* and *N. eha* have grayish white underparts (Musser, 1970), *N. hinpoon* has a buffy pale gray venter (Marshall, 1988), but all other species have white venters. No example of *Niviventer* has *Tonkinomys*'s unique dorsal and ventral pelage coloration. Some species of *Niviventer*, however, do have semispinous pelage similar in texture to that possessed by *T. daovantieni* (*N. fulvescens* and *N. tenaster* are good examples). The conformation of tail and proportional relationship between lengths of tail and body in *Tonkinomys* (stocky, with a stubby tip, and significantly shorter than combined head and body length) does not occur in any species of *Niviventer*. The tail is tapered to a pointed tip and gracile in appearance in all species of *Niviventer*, and much longer than length of head and body in all species except *N. hinpoon*, in which the tail is equal to or slightly longer than head and body length (table 2; Marshall, 1988; Musser, 1970, 1973, 1981; Musser and Chiu, 1979; Lunde and Son, 2001). The plantar pads of *Tonkinomys* are larger, closer together, and more swollen relative to plantar surface than in any terrestrial or scansorial species of *Niviventer*, including *N. hinpoon*, which is thought to be closely associated with limestone cliff habitats (Marshall, 1988), or even the arboreal *N. langbianis* and *Chiromyscus chiropus* (fig. 9); *N. fulvescens* (fig. 9) exhibits the configuration of plantar pads that is common to most species of *Niviventer*.

The skull of *Tonkinomys* is appreciably larger (as indexed by occipitonasal length) and more robust than all species of *Niviventer*, even *N. andersoni*, which has the largest skull among the species in the genus (table 2). The skull of *Tonkinomys*, however, is not a giant version of *Niviventer*; compared with *Niviventer*, *Tonkinomys* has: (1) insignificant basicranial flexion (most species of *Niviventer* display marked basicranial flexion); (2) maxillary molar rows that are situated farther forward relative to posterior margin of the zygomatic plate (front of molar row either even with back of zygomatic plate or well behind it in most specimens of *Niviventer*); (3) the squamosal root of the zygoma originating higher on side of the braincase (set lower in *Niviventer*, particularly *N. andersoni* and *N. excelsior*); (4) more slender alisphenoid struts relative to size of skull, with some specimens lacking struts (relative to skull size, alisphenoid struts are more substantial in all species of *Niviventer*, and present in all specimens we examined); (5) strongly posteriorly diverging molar rows (parallel or only slightly diverging in *Niviventer*); (6) a bony palate projecting appreciably beyond posterior margins of third molars to form a wide platform (posterior margin of bony palate ends about 0.5 mm anterior to posterior surfaces of upper third molars, even with them, or no more than about 0.5 mm beyond in all species of *Niviventer*); (7) a posterior margin of the bony palate that is smooth or only slightly thickened (the palatal border is defined by a prominent and thick bony ridge in *Niviventer*); and (8) a thick, bony, and flat posterolateral projection of the bony palate covering the anteromedial portion of each pterygoid plate, its sharp diagonal border (**ppm** in fig. 12) defining the anteromedial edge of the pterygoid fossa (no such conformation in any species of *Niviventer*). Other than the larger size of each dentary in *Tonkinomys*, we did not detect any significant differences with those of *Niviventer* in overall shape; positions of foramina; expanse of coronoid, condyloid, and angular processes relative to body of the dentary; expression of masseteric and lingual ridging; or position of the posterior terminus of the incisor capsule.

Shapes of the upper and lower incisors in *Tonkinomys*, their enamel color and thickness, and the opisthodont conformation of the uppers resemble the incisors in all species of *Niviventer*. The larger size of these structures in *Tonkinomys* provides the obvious contrast. Reflecting the much greater skull dimensions of *Tonkinomys* when compared with species of *Niviventer* are the elongate molar rows of the former, which are much longer than even the largest-bodied species of *Niviventer* (table 2). Occlusal patterns of the upper molars fit within the range of variation we observed among most species of *Niviventer*, except that cusps t4 and t6 on the second lamina of the first molar in *Tonkinomys* tend to retain more of their identity, and cusp t9 is smaller and indistinct relative to the huge central cusp t8. The anterior lamina on the first upper molar in *N. andersoni* and *N. excelsior* resembles the shape in *Leopoldamys*, and contrasts with the comparable chevron-shaped lamina in *Tonkinomys*, but those two species also differ from most other species of *Niviventer* in this trait. Coronal patterns of lower molars in *Tonkinomys* are also closely similar to those in the species of *Niviventer*.

While occlusal patterns on upper and lower molars in our sample of *Tonkinomys* fall within the range of variation of the patterns we observed among the species of *Niviventer*, the number of roots anchoring most of those molars do not—this set of structures by themselves identifies *Tonkinomys* as the representative of a monophyletic group separate from *Niviventer*, a position only strengthened by the external and cranial contrasts between the two genera already described. Except for the first upper molar, which has four roots, *Tonkinomys* exhibits the primitive number of roots anchoring upper (three per tooth) and lower (two per tooth) molars. All species of *Niviventer*, in contrast, have multi-rooted molars (table 3; also see Chaimanee, 1998, and Zheng, 1993). First upper and lower molars can be used as examples. Most species of *Niviventer* have five-rooted first upper molars: large anterior, two smaller lingual, large posterior, and small labial (some specimens have one or more labial rootlets in addition to the primary labial anchor). In *N. langbianis*, and also in *Chiromyscus chiropus*,

TABLE 3

Number of Roots on M1 and m1 in Selected Species of *Niviventer*, and the Species of *Chiromyscus* and *Saxatilomys*

(Number opposite species indicates specimens examined. Symbol key: **4/4**, M1 with large anterior, single lingual, and posterior roots, and a small labial root; **m1** with large anterior and posterior roots, and small labial and lingual roots. **5/4**, M1 with large anterior and posterior roots, two lingual, and a small labial root; **m1** with large anterior and posterior roots, and small labial and lingual anchors. **5/2**, M1 with large anterior and posterior roots, two lingual, and a small labial root; **m1** with a large anterior root and large posterior root. Specimens surveyed are in AMNH, BMNH, FMNH, and USNM.)^a

Species	Roots (M1/m1)		
	4/4	5/4	5/2
<i>N. andersoni</i> (China: Sichuan, Yunnan)	—	46	—
<i>N. excelsior</i> (China: Sichuan)	—	12	—
<i>N. brahma</i> (northern Myanmar)	—	7	—
<i>N. eha</i> (northern Myanmar)	—	17	—
<i>N. langbianis</i> (Vietnam)	40	—	—
<i>N. cremoriventer</i> (Sunda Shelf)	—	53	—
<i>N. hinpoon</i> (Thailand)	—	15	—
<i>N. confucianus</i> (China, northern Myanmar)	—	53	—
<i>N. tenaster</i> (China: Hainan, Vietnam)	—	55	—
<i>N. conninga</i> (Taiwan)	—	53	—
<i>N. rapit</i> (northern Borneo)	—	6	—
<i>N. fraternus</i> (Sumatra)	—	20	—
<i>N. lepturus</i> (Java)	—	21	—
<i>N. cameroni</i> (Malay Peninsula)	—	42	—
<i>C. chiropus</i> (Vietnam)	2	—	—
<i>S. paulinae</i> (Lao PDF)	—	—	11

^a Labial roots are divided into two or more rootlets on some upper and lower molars, but we did not count these projections as independent roots. In some specimens, the posterior root on the lower molar is furrowed down the middle suggesting separate posterolingual and posterolabial anchors, but we scored this configuration as one large root. The sample of *S. paulinae* consists of two whole animals and fragments recovered from owl pellets, so the count is derived from 3 first upper molars and 8 first lower molars. Sample sizes for all the other species are based on complete specimens.

four roots anchor each molar: large single lingual, large anterior and posterior roots, and small labial. *Tonkinomys* also possesses four roots beneath each first upper molar, but the pattern is different from that in *N. langbianis* and *Chiromyscus*. No specimen in our sample

of *Tonkinomys* has a labial anchor, and the four-rooted pattern is formed by large anterior and posterior roots along with two prominent lingual roots. A small labial root, not a divided lingual, forms the fourth root in *N. langbianis* and *Chiromyscus*. Although our survey results for second and third upper molars are not summarized in table 3, we also determined that second upper molars in *Niviventer* have four roots (three in *Tonkinomys*), and third upper molars have three (as in *Tonkinomys*, which is the usual number for the third molar in most murines, even when the first and second molars have more than three roots).

Four roots (large anterior and posterior, smaller labial and lingual) anchor each first lower molar in all species of *Niviventer* (and *Chiromyscus*), but only two are present in the Vietnamese limestone rat. Two to four is the range in number of roots anchoring each second lower molar among species of *Niviventer*, and each third lower molar has either two or three roots (two roots beneath second and third molars of *Tonkinomys*).

***Saxatilomys*:** Described from two whole animals along with 14 individuals represented by cranial, mandibular, and dental fragments recovered from owl pellets, *S. paulinae* has been recorded only from the Khammouan Limestone National Biodiversity Conservation Area in Lao PDR (Musser et al., 2005).

Body size, build, and proportions of limbs, pinnae, and tail that are characteristic of *S. paulinae* resemble most species of *Niviventer*; “*S. paulinae* simply looks like a *Niviventer* and not like any other species in any other genus” (Musser et al., 2005: 20). That Lao species strikingly contrasts with the large-bodied and short-tailed Vietnamese animal. *Tonkinomys daovantieni* is more robust in build and much larger in body size than *S. paulinae* (range in length of head and body is 184–217 mm for 13 examples of *T. daovantieni* versus 144–150 mm for two *S. paulinae*). Its thick, stubby tail is shorter than head and body length (LT/LHB = 83%, average of 13 specimens) compared with the slim, tapered, and gracile tail of *S. paulinae* that is appreciably longer than body length (LT/LHB = 112%–116% for two individuals). The tail of both species is bicolored, but the dark brown and white pattern is different in each. In *T. daovantieni*,

the tail is dark brown except for the ventral surface, which is white, and the distal one-fourth to one-half, which is white on all surfaces; the tail of *S. paulinae* is dark brown on dorsal and lateral surfaces from base to tip, and white (with slight speckling) over only its ventral surface. Both species have dense and dark gray fur covering upperparts and underparts of the head and body. *Saxatilomys paulinae*, however, lacks a white forehead blaze and white pectoral patch, a pattern exhibited by most examples of *T. daovantieni*, and its venter is lightly frosted in contrast to the total gray of the Vietnamese animal. *Tonkinomys* and *Saxatilomys* do share bulbous plantar pads that are very large relative to plantar surface and arranged in a tight cluster (compare the plantar surface of *T. daovantieni* in fig. 8 with that of *S. paulinae* in fig. 9).

Tonkinomys and *Saxatilomys* possess an elongate skull, wide zygomatic plate relative to cranial size, narrow alisphenoid struts present in most specimens, bony palate projecting past the third molars to form a broad shelf with either a smooth or slightly thickened (not ridged) posterior margin, strongly divergent maxillary molar rows, and a similar mandibular conformation (compare figs. 10 and 11 with the views of *Saxatilomys* in Musser et al., 2005: fig. 6).

The two species differ in size and some qualitative traits. *Tonkinomys* has a more robust and larger skull (occipitonasal length, for example, ranges from 47.1 to 52.4 mm in seven *T. daovantieni*, and 40.3 to 40.5 mm for the two intact skulls of *S. paulinae*). Size of the gracile skull in the Lao genus resembles the larger-bodied species of *Niviventer* (the Indochinese *N. tenaster*, for example; compare the values listed in tables 1 and 4 of Musser et al., 2005, with those presented in table 1). *Tonkinomys* further contrasts with *Saxatilomys* by having a less tapered rostrum (when viewed from dorsal or ventral aspect), significantly less basicranial flexion (marked flexion in *Saxatilomys*; see fig. 6 in Musser et al., 2005), and spacious incisive foramina (not the narrow slits of *Saxatilomys*).

Three other qualitative features provide marked contrasts between the two genera. In *Tonkinomys*, the squamosal root of the zygo-

matic arch is situated high on the side of the cranium where its ridge-like portion runs horizontally just below the posteroventral margin of the parietal, which projects ventrad to form the dorsolateral side of the braincase; the low ridge of the squamosal root disappears 10–15 mm anterior to the vertical ridge formed by the squamosal-exoccipital suture (fig. 11). The configuration is similar to that characteristic of *Leopoldamys* and *Niviventer*. The squamosal root of each arch in *Saxatilomys* also originates high on the side of the cranium, but is oriented diagonally so that its posterior ridge-like portion extends diagonally to merge with the squamosal-parietal suture (which forms the temporal ridge) well anterior to the vertical ridge created by the squamosal-exoccipital suture (see figs. 6 and 8 in Musser et al., 2005). The parietal does not drop below the temporal ridge, and the upper portion of the braincase consists only of the squamosal.

Tonkinomys daovantieni and *S. paulinae* have a wide and long bony palate that projects beyond the molar rows to form a broad platform. In *Tonkinomys*, the posterolateral edges of this shelf extends as a flat, bony surface onto the anterior portion of each pterygoid plate where its sharp diagonal border (**ppm** in fig. 12) marks the anteromedial margin of each pterygoid fossa. No such conformation exists in *S. paulinae* (or in any species of *Niviventer*).

The globular and only slightly inflated ectotympanic (auditory) bulla of *Tonkinomys* does not conceal all of the periotic. A wide, wedge-shaped segment of that bone is exposed between the dorsal capsular margin and basioccipital, and this wedge of periotic extends anteriorly to form the dorsal and slanting posterodorsal wall of the carotid canal (fig. 12). The conformation is primitive among murines and closely resembles the morphology depicted by Carleton and Musser (1989: 33) for the sigmodontine, *Oligoryzomys*, and by Musser and Heaney (1992: 99) for some of the Philippine Old endemic murines. By contrast, the globular ectotympanic capsule exhibited by *Saxatilomys* covers all but a narrow wedge of the periotic, and the anteromedial margin of the capsule meets the basioccipital, so that it is the

ectotympanic (or auditory capsule) that forms the posterior wall of the opening into the carotid canal. This structural relationship between ectotympanic and periotic is specialized, and is particularly well illustrated in Carleton and Musser (1989: 33) for the sigmodontine *Oryzomys palustris*. Species of *Rattus* and its allies have a comparable pattern (Musser and Heaney, 1992: 99).

Primary dental differences between *Tonkinomys* and *Saxatilomys* involve size, one proportional feature, and pattern of molar roots. *Tonkinomys* has larger upper and lower incisors than does *Saxatilomys*, but otherwise pigmentation and thickness of enamel, their shapes, and opisthodont configuration of the uppers relative to the rostrum are similar. *Tonkinomys* also has longer molar rows (as indexed by lengths of maxillary rows: 8.0–8.8 mm in 7 specimens of *Tonkinomys*, 7.2–7.3 mm for three *Saxatilomys*); length of maxillary row relative to occipitonasal length for the two genera, however, is, on average, not significantly different (the ratio, CLM1-3/ONL, using mean values from each generic sample, is 17% for *Tonkinomys* and for *Saxatilomys*). In contrast to molar length, the individual molars in *Tonkinomys* are not significantly wider than are the molars of *Saxatilomys* (using breadth of the first upper molar as a guide, the mean is 2.1 mm for 7 examples of *Tonkinomys* and for 3 specimens of *Saxatilomys*; contrast the values listed in table 1 with those figs. in table 4 in Musser et al., 2005: 21), indicating significantly narrower molars relative to length of the maxillary row (the ratio, BM1/CLM1-3, using mean values from each generic sample, is 25% for *Tonkinomys* and 29% for *Saxatilomys*). Two roots (large anterior and posterior) anchor each lower molar in all specimens examined of *Tonkinomys* and *Saxatilomys*, but the root patterns for the first and second maxillary molars are dissimilar in the two genera. In *Tonkinomys*, the first maxillary molar has four roots (anterior, posterior, and divided lingual), the second has three. *Saxatilomys* has five-rooted first molars (table 3) and four-rooted second molars; in samples of both *Tonkinomys* and *Saxatilomys*, three roots anchor each third molar.

Tonkinomys and *Saxatilomys* (along with most species of *Niviventer*) share similar maxillary and mandibular molar occlusal patterns. Distinctions between the Vietnamese and Lao limestone rats are present but not spectacular (contrast fig. 14 with the occlusal views of *Saxatilomys* in Musser et al., 2005: fig. 10); compared with *Saxatilomys*, cusps t4 and t6 on the second lamina of the first maxillary molar in *Tonkinomys* tend to retain more of their identity (less distinct in *Saxatilomys* and in most species of *Niviventer*), second and third mandibular molars lack anterolabial cusps in most specimens (most species of *Niviventer* also lack these cusps, but they are present in *Saxatilomys*), and the cusps on upper and lower molars form more distinct and tighter chevrons (cusp rows more arcuate, with greater space between arms of each chevron in *Saxatilomys*).

Other genera: We also compared examples of *Dacnomys* and *Srilankamys*, other Indomalayan members of the *Dacnomys* Division, with our sample of *Tonkinomys*. *Dacnomys* is a giant version of *Niviventer*, especially *N. andersoni*, in its external and cranial traits, as well as root patterns of the molars (see description and illustrations in Musser, 1981). Those molars, however, are large, chunky, and hypsodont, with complicated cuspidate occlusal patterns, and strikingly contrast with the brachydont and gracile molars with their simple occlusal patterns possessed by all species of *Niviventer*. *Tonkinomys* bears no close resemblance to *Dacnomys* in external, cranial, or dental traits.

A combination of traits, some of which recall features in *Niviventer*, others that resemble *Maxomys*, and some that are unique, characterizes the morphological definition of *Srilankamys* (see the description and illustrations in Musser, 1981). Its membership in the *Dacnomys* Division is provisional, pending reassessment of its phylogenetic relationships by additional morphological characters in combination with molecular data (Musser and Carleton, 2005). *Srilankamys* shares the same pattern of molar roots with *Tonkinomys*, but otherwise its diagnostic external and cranial traits, along with molar occlusal patterns, are unlike those of *Tonkinomys*.

Musser and Carleton (2005) included the Philippine Mindoran endemic *Anonymomys mindorensis* in the *Dacnomys* Division. Its placement there, however, is very provisional. Some morphological traits of *Anonymomys* recall those of genera in the *Dacnomys* Division, particularly *Niviventer*, but others suggest a closer affinity to Bornean and Sulawesian *Haeromys*, a member of the *Micromys* Division of Musser and Carleton (2005). *Tonkinomys* is morphologically distant from *Anonymomys* and requires no comparisons with it.

Our comparative study also included the Indomalayan *Maxomys*, although that genus is not contained within the *Dacnomys* Group (Musser and Carleton, 2005). Species of *Maxomys* are prominent members of the Indochinese murine fauna (Corbet and Hill, 1992), and some share with *Tonkinomys* the same number of roots anchoring each molar (Musser et al., 1979). Any close similarity ends with that character complex. No species of *Maxomys* has the pelage coloration possessed by *Tonkinomys*, or the thick, short tail, or the crowded, fleshy palmar and plantar pads. Additionally, all *Maxomys* have short, wide incise foramina that have the outline of an inverted heart, a bony palate ending well anterior to posterior margins of the molar rows, a very long postpalatal region, and other cranial attributes, as well as molar occlusal patterns (see descriptions and illustrations in Musser, 1991) that are not shared with *Tonkinomys*. We found no derived characters that identified *Tonkinomys* as either a member or close relative of *Maxomys*.

Fossils: Reports covering murines recovered from late Pliocene to Pleistocene sediments in caves and limestone fissures in Thailand and China contain descriptions of samples identified as species of *Leopoldamys*, *Niviventer*, and related extinct genera. The bulk of the material is comprised of isolated molars; a few samples contain cranial and mandibular fragments. Only some of the publications contain information pertinent to our inquiry.

In her detailed and comprehensive treatise on the Plio-Pleistocene rodents of Thailand, Chaimanee (1998) described samples representing extant species of *Leopoldamys* (*L.*

sabanus) and *Niviventer* (*N. fulvescens*) and new species in those genera that are extinct and represented only by fossils (*L. minutus* and *N. gracilis*). Judged from her descriptions, measurements, and illustrations, all these samples are correctly allocated to genus; none represents *Tonkinomys*.

Pleistocene samples from Guangxi Province in southern China were determined by Chen et al. (2002) to contain examples of *Niviventer* and *Leopoldamys*, but no identifications to species were provided. Zheng et al. (1997) reported the extant *Niviventer confucianus* and extinct *N. preconfucianus* from Plio-Pleistocene fissure fillings in Shandong Province. Measurements and drawings of molar occlusal patterns presented in these reports convince us their generic attributions are correct.

Zheng (1993) has provided perhaps the most comprehensive and thorough survey of fossil murines recovered from late Pliocene and Pleistocene cave and fissure fillings. All come from the northern margin of the Yunnan-Guizhou Plateau within an area bounded by 104° to 110°E and 26° to 31°N in the provinces of Sichuan and Guizhou. By clear descriptions and a wealth of measurements, Zheng meticulously documented those parts of the samples representing extant *Leopoldamys edwardsi* and extinct *L. edwardsioides*; extant *Niviventer fulvescens*, *N. confucianus*, *N. andersoni*, and possibly *N. excelsior*; and the extinct *N. preconfucianus*. His descriptive and quantitative data, along with clear illustrations, provide unquestionable support for his identifications.

Zheng (1993) also described three new species in two new genera that seem morphologically similar to *Niviventer* and other members of the *Dacnomys* Division. *Wushanomys brachyodus* is represented by a large cranial fragment containing intact molar rows, dentary fragments with complete or partial molar rows, and numerous isolated upper and lower molars. The fossils come from sediments thought to be no older than 2.5 million years ago, and no younger than 1.0 million years ago. Judged by length of upper (9.30 mm, 1 specimen) and lower (8.80–9.20 mm, 5 specimens) molar rows, this extinct species is much larger than *Tonkinomys daovantieni* (uppers, 8.03–8.78 mm, 7 specimens; lowers, 7.64–

8.52 mm, 10 specimens). Range in measurements of first upper (4.00–4.90 mm by 2.14–2.66 mm, 85 examples) and lower (3.40–3.95 mm by 1.90–2.20 mm, 97 specimens) molars of *W. brachyodus* overlaps with those of *T. daovantieni* (table 4), but average longer and wider (see Zheng, 1993: 190). Most of the first upper molars in *W. brachyodus* have three roots, but Zheng noted that some molars have a divided lingual (see Zheng, 2004: 175), which is the pattern in *T. daovantieni*. First lower molars have two roots, the primitive pattern that is also typical of the Vietnamese limestone rat.

Molar occlusal patterns of *Wushanomys* are unlike those of *Tonkinomys*. The anterior lamina on the first upper molar in *Wushanomys* consists of a straight segment formed by the complete fusion of cusps t2 and t3, and a posteriorly offset cusp t1; the second lamina is arcuate in outline; and cusp t9 is distinct in the posterior part of the tooth (see the illustration in Zheng, 1993: 192). These occlusal outlines are strongly dissimilar to the strong, tight chevrons formed by the two front laminae on the first upper molar in *Tonkinomys* (fig. 14) and its cusp t9, so coalesced with the large central cusp t8 that it resembles a low ridge. Lamina outlines on lower molars of *Wushanomys* are also nearly straight or form wider-armed chevrons, a contrast with the tight chevrons in *Tonkinomys*.

The cranial and mandibular fragments of *W. brachyodus* provide additional comparative information. Zheng did not illustrate the specimen, but described it as having very long incisive foramina that terminate 1.7 mm posterior to anterior faces of first molars, a bony palate extending about 0.7 mm beyond the molar rows to form a short platform, a very narrow interorbit (6 mm), especially for what seems to be a large skull judging from lengths of molar rows, and a flat, wide zygomatic plate (no measurement listed). Zheng did include a drawing of a partial dentary (the body of the ramus behind the molar row is gone, p. 204). The portion anterior to the molar row, along with the incisor, is long and slender, and the dorsal outline from anterior margin of the molar to incisor tip is gently concave. This conformation usually accompanies a long rostrum, and the mandibular

configuration recalls that typical of the long-nosed Sulawesi murines, *Bunomys prolatulus* and *B. chrysocomus* (Musser, 1991: 12–13). In *Tonkinomys*, posterior margins of the incisive foramina end just in front of anterior faces of the first molars, even with them, or extend only slightly beyond (no more than 0.5 mm); the bony palate extends 1.5–2.0 mm beyond the molar rows forming a much more expansive platform, and the interorbit is wide (6.6–7.3 mm; table 1), which is the usual proportion in skulls the size of *Tonkinomys* (and other murines, *Leopoldamys neilli*, for example). The bony projection containing the lower incisor in the dentary of *Tonkinomys* is shorter and thicker, and the dorsal outline from molar row to incisor tip is more deeply concave, a shape common to species of *Niviventer*, *Leopoldamys*, and other murines with less specialized dentaries (Musser, 1981: 272; Zheng, 1993: 204).

Zheng's description of the cranial traits in *Wushanomys brachyodus* tantalizingly resembles the conformation in other extinct murines, such as the Canary Islands *Malpaisomys insularis*, which was likely adapted to living and climbing about in the crevicular system of lava fields (Boye et al., 1992; Hutterer et al., 1988). Perhaps *W. brachyodus* lived and climbed about in karstic fissures, had a long rostrum, and included invertebrates in its diet. Whatever its habitat and habits, the summation of morphological traits characterizing the complement of fossil remains identifies, in our view, a monophyletic group (at the level of genus) separate from that represented by *Tonkinomys daovantieni*; other than *Wushanomys* likely being a member of the *Dacnomys* Group, there seems no closer phylogenetic link between *Wushanomys* and *Tonkinomys*.

Zheng (1993) described a second species of *Wushanomys*, *W. hypsodontus*, based on a few isolated molars that are high-crowned, have slightly more complex occlusal surfaces, and greater dimensions than found in *W. brachyodus*. The time span in which the fossils lie is 2.0 to 1.8 million years ago.

Zheng's other new genus and species, *Qianomys wui*, is based on a small series of dentary fragments containing full or partial molar rows, an isolated first lower molar, and

two upper molars. These were recovered from sediments thought to be late Pleistocene, 400,000 to about 200,000 years ago. The two upper molars (4.40 mm and 4.60 mm long) fall within the high end and slightly beyond the range of variation in molar length we recorded for *Tonkinomys daovantieni*, but they are much wider (2.35 mm and 2.40 mm) than the molars of *T. daovantieni* (table 4). The occlusal pattern does not match that of *Tonkinomys*, and five roots are present. The uppers are not examples of the Vietnamese limestone rat. Even Zheng noted their close similarity to *Niviventer* in crown outline and number of roots, and suggested they may not be correctly associated with the lower molars, to which the generic and specific name is nomenclaturally attached. We agree. For us, Zheng's diagram (p. 199) of a first upper molar closely resembles *N. andersoni* in occlusal pattern; however, the size is slightly outside the range of variation we obtained from our sample of that species (table 4) and that which Zheng derived from his material of *N. andersoni* (p. 181).

The three intact lower molar rows of *Qianomys* for which measurements are provided (8.60, 9.40, and 9.43 mm) are appreciably longer than those in *Tonkinomys* (7.64–8.52 mm, 10 specimens) as are length and width dimensions of the first lower molars (3.66–4.20 mm by 2.10–2.34 mm, 8 specimens of *Qianomys*; 3.40–3.50 mm by 1.90–2.00 mm in *Tonkinomys*, table 4). If molar dimensions are any indication of skull and body size, *Q. wui* was a much larger rat than *T. daovantieni*. *Qianomys* and *Tonkinomys* share the same primitive root pattern, two beneath each lower molar. Occlusal patterns formed by the rows of laminae fall within the range of patterns exhibited by *Tonkinomys* as well as species of *Niviventer*. Zheng, however, claimed that none of the molars he assigned to *Qianomys* have anterolabial cusps on the second and third molars or posterolabial cusplets on any molar, features, in addition to number of roots, which he used to distinguish *Qianomys* from *Niviventer*. Comparable cusps do occur on the lower molars of *T. daovantieni*. An illustration of a partial dentary (Zheng, 1993: 204) indicates the portion anterior to the molar row to be similar in shape to that of

Tonkinomys, *Niviventer*, *Leopoldamys*, and *Saxatilomys*.

Qianomys wui is certainly a different species than *Tonkinomys daovantieni*. Whether the gross similarities between the two in molar occlusal patterns signal close phylogenetic relationship or convergence cannot be determined until we can compare the fossils directly with our extant samples, and until cranial material representing *Qianomys* is recovered and described. Resolving the ambiguous association between the present sample of upper molars and lowers allocated to *Qianomys* is also critical. That genus would resemble only *Saxatilomys* among members of the *Dacnomys* Division if the five-rooted first upper molars with their *Niviventer*-like occlusal patterns actually belong to *Qianomys* with its two-rooted lower molars.

A recent report by Zheng (2004) documents identities of rodents, represented mostly by isolated molars, collected from sedimentary layers in Longgudong Cave (30°39'14.9"N/110°04'29.1"E), the "Jianshi Homind Site" in western Hubei Province of central China. Geological age was given as Early Pleistocene, but correlation between the 11 sedimentary layers sampled and the geomagnetic polarity timescale indicated a range extending from the Olduvai Event of the Matuyama Chron (the Pleistocene/Pliocene boundary) back to earlier than 2.15 million years before the present, reflecting initial deposition during the Late Pliocene (see Flynn et al., 1997, and Qiu, 1989, for illuminating expositions of Chinese geochronology at the end of the Neogene). Among the murines recovered were three species in the *Dacnomys* Division. One is the extinct *Niviventer preconfucianus*, which Zheng himself had named and described in 1993, and another is represented by isolated molars identified only as an undetermined species of *Leopoldamys*. The third is a new species of the extinct *Wushanomys*, *W. ultimus*, described from molars recovered from all but the top two layers of the cave sediments, most from layers dated between 1.95 to earlier than 2.15 million years before the present (Late Pliocene). Molars from *W. ultimus* are intermediate in size between the earlier described *W. brachyodus* and *W. hypsodontus* (Zheng, 1993), express greater hypsodonty, and differ

slightly in coronal patterns. Ranges in length and breadth values for first upper (3.90–4.92 mm by 2.20–2.65 mm, 22 examples) and lower (2.90–4.30 mm by 1.98–2.30 mm, 18 specimens) molars of *W. ultimus* (see Zheng, 2004: 173) overlap with those of *Tonkinomys daovantieni* (table 4), but average slightly longer and wider. Each first lower molar of *W. ultimus* has two roots, the pattern common to the other two species of *Wushanomys*, but first upper molars have either four (anterior, divided lingual, posterior) or five roots (a small labial holdfast or nubbin in addition to the four primary roots). The pattern of the four primary roots beneath the first upper molars and two anchoring first lower molars also characterizes *Tonkinomys daovantieni*, but molars of that Vietnamese rat are not hypsodont, and although the extinct and extant species share molars similar in size, their occlusal patterns are dissimilar. The occlusal cusp patterns characteristic of *W. ultimus* resemble, except for minor details, those in *W. brachyodus* and differ from *T. daovantieni* in the configurations we previously described contrasting *W. brachyodus* and the Vietnamese species.

These new samples of the *Dacnomys* Division recovered from the Jianshi Hominid Site provide additional information on Late Pliocene geographic distributions of *Niviventer* and *Leopoldamys*. The geographic range of *Wushanomys* is also expanded as is the diversity of species in that genus. Judged from Zheng's (2004) descriptions, measurements, and illustrations, none of the identified fossil molars represent the Vietnamese *Tonkinomys*.

Our final survey of fossils assesses the identification of murines recovered from Pleistocene sediments in Ma U'Oi cave in northern Vietnam, south of Hanoi (Bacon et al., 2004). One mandible containing a complete molar row was identified as *Niviventer fulvescens*; an upper first molar and a lower first molar were attributed to *N. andersoni*; and a dentary containing all molars, and isolated first and second molars, were determined as *Leopoldamys sabanus*. The molars were identified by comparing them with Chaimanee's (1998) treatise on fossil Plio-Pleistocene Thai rodents. Unfortunately, we are not treated to

drawings of molar occlusal cusp patterns, or to measurement values for the sample of *N. fulvescens*.

We cannot verify the identification of *N. fulvescens*. That species is common in northern Vietnam and in many places occurs together with *N. tenaster* (results of our trapping surveys in several different regions of northern Vietnam), which is somewhat larger in dimensions of body and skull, as well as length of molar row and breadths of molars (Musser and Lunde, ms.). *Niviventer tenaster* also occurs in northern Thailand (Musser and Carleton, 2005), but Chaimanee (1998) did not include it in her report. The material reported by Bacon et al. (2004) should be reexamined to determine whether it is really *N. fulvescens* or possibly *N. tenaster*.

Measurements listed by Bacon et al. (2004) for two first lower molars of *Leopoldamys* (4.0 by 2.6 mm and 4.7 by 2.8 mm) fall within the range of variation for the larger species of that genus (Chaimanee, 1998; Zheng, 1993), and well outside the range for our sample of *Tonkinomys* (table 4). The lower second and third molars that were identified as *Leopoldamys* are also large and likely represent that genus. But these fossil molars may not belong to *L. sabanus*. *Leopoldamys* requires taxonomic revision because more species exist than are usually recognized (four were listed by Musser and Carleton, 1993, and six by Musser and Carleton, 2005, which still underestimates the number of species), and the situation in northern Vietnam is especially complex. At least two species occur there. One may be *L. edwardsi*, the other is usually identified as *L. sabanus*, but is actually a different species (Gorog et al., 2004; Musser and Carleton, 2005).

An upper first molar and lower first molar were identified as *Niviventer andersoni* in Bacon et al. (2004). Ma U'Oi cave is far south of the present geographic distribution of *N. andersoni*, which extends from eastern Xizang (Tibet) through northern Yunnan, western Sichuan, and northern Ghizhou to southern Shaanxi, and over an altitudinal range from 6000 to 10,000 ft (Musser and Chiu, 1979; Musser and Carleton, 1993, 2005). We sought to determine whether these two fossil molars belong to *Tonkinomys*. Dimensions of the first

TABLE 4

Summary Statistics for Lengths and Breadths (mm) of First Upper and Lower Molars of *Niviventer andersoni* (China, Yunnan and Sichuan), *N. excelsior* (China, Sichuan), *N. tenaster* (Vietnam), Pleistocene First Molars Identified as *N. andersoni* by Bacon et al. (2004), and *Tonkinomys daovantieni* (Vietnam)

(Mean, plus or minus one SD, and observed range in parentheses are listed for each measurement. Samples consist entirely of AMNH specimens except those reported by Bacon et al., 2004.)

	<i>N. andersoni</i>	<i>N. excelsior</i>	<i>N. tenaster</i>	Bacon et al.	<i>T. daovantieni</i>
	(<i>N</i> = 45)	(<i>N</i> = 13)	(<i>N</i> = 16)	(<i>N</i> = 1)	(<i>N</i> = 7)
Length of M1	3.7 ± 0.1 (3.5–4.0)	3.3 ± 0.1 (3.1–3.6)	3.2 ± 0.1 (3.0–3.6)	3.7	4.2 ± 0.1 (4.1–4.5)
Breadth of M1	2.1 ± 0.1 (2.0–2.2)	1.9 ± 0.1 (1.8–2.0)	1.7 ± 0.1 (1.6–1.8)	2.0	2.1 ± 0.1 (2.0–2.2)
Length of m1	3.3 ± 0.1 (3.1–3.5)	3.0 ± 0.1 (2.8–3.2)	2.8 ± 0.1 (2.7–3.1)	4.1	3.5 ± 0.1 (3.4–3.5)
Breadth of m1	1.8 ± 0.1 (1.7–1.9)	1.7 ± 0.1 (1.6–1.9)	1.6 ± 0.1 (1.5–1.7)	2.5	2.0 ± 0.1 (1.9–2.0)

upper molar (3.7 by 2.0 mm) do fall within the range of variation of our values (table 4) and those tabulated by Zheng (1993: 181) for large sample sizes of *N. andersoni*. Breadth of the fossil molar fits within our observed range for first upper molars of *Tonkinomys*, but the length is much too short—based on these data, the molar did not come from the Vietnamese limestone rat. However, it may not represent *N. andersoni*. The width, for example, matches our range of values for *N. excelsior*, and the length is only 0.1 mm shorter (table 4). *Niviventer excelsior* is a close relative of *N. andersoni* that presently occurs only in high mountains north of the Yangtze River (Musser and Chiu, 1979). For *N. excelsior* to have once occurred in northern Vietnam, however, seems as implausible to us as the presence of *N. andersoni* there, especially because all the fossils of other mammals found in situ in the Ma U’Oi cave define “... a relatively modern fauna ...” (Bacon et al., 2004: 312). *Niviventer tenaster* currently lives in northern Vietnam in forest habitats. Lengths and breadths of first upper molars from this species in our sample from that country nearly embrace dimensions of the fossil molar (table 4), and that tooth just might be from a large individual of *N. tenaster*. Both *N. andersoni* and *N. excelsior* can easily be distinguished from *N. tenaster* by occlusal patterns. In the former pair, the anterior lamina on the first upper molar

consists of a nearly straight segment, formed by the coalescence of cusps t2 and t3, and a posteriorly displaced lingual cusp t1 (see figs. in Musser, 1981, and Zheng, 1993). The comparable lamina has an arcuate outline on the upper molar in *N. tenaster*, similar to that found in *N. confucianus* (Musser, 1981). The fossil molar needs to be reexamined; it is not an example of *Tonkinomys*, and we question its identity as *N. andersoni*.

The first lower molar determined to be *N. andersoni* in Bacon et al. (2004) is large (4.1 by 2.5 mm), and its dimensions fall far outside the range of variation in our samples of *Tonkinomys*, *Niviventer andersoni*, *N. excelsior*, and *N. tenaster* (table 4). The tooth is actually about the same size as the two first lower molars (4.0 by 2.6 mm, 4.7 by 2.8 mm) they identified as *Leopoldamys*. The values are either misprints, or the molar does belong to *Leopoldamys*; it, and the first upper molar assigned to *N. andersoni*, warrants restudy.

Summary: There would have been an elegant symmetry in discovering ancient, fossilized remnants hidden in limestone fissures that represented the same murine species living today in crevicular habitats within the tower karst landscape forming northern Vietnam. Unfortunately, we cannot unambiguously tie any published identifications of fossilized fragments representing Indochinese murines to the extant *Tonkinomys daovantieni*.

Its past distribution and phylogenetic alliance to extinct taxa, as might have been illuminated by fossils, remain a mystery.

Unresolved also is the phylogenetic position of *Tonkinomys* with respect to *Leopoldamys*, *Niviventer*, and *Saxatilomys*, the three extant genera with morphologies most like that of *Tonkinomys*. The differences enumerated above between *Tonkinomys daovantieni* on one hand and species of *Leopoldamys* and *Niviventer* on the other reflect a combination of primitive and derived features. Relative to the pelage coloration, shape of tail, and its length relative to length of head and body in *Leopoldamys* and *Niviventer*, the contrasting condition in *Tonkinomys* is derived. Also representing specializations in *Tonkinomys* are the position of the squamosal zygomatic roots high on the sides of the braincase, slender or no alisphenoid struts, its long incisive foramina, a very long bony palate that projects beyond the molar rows to form a broad shelf, posteriorly diverging maxillary molar rows, simple molar occlusal patterns, and a divided lingual root beneath the first upper molar. Presence of three roots beneath each second and third molar, and two roots anchoring each lower molar represent the primitive condition in *Tonkinomys* compared with the derived state in *Leopoldamys* and *Niviventer*. *Tonkinomys daovantieni* resembles the Indochinese *Leopoldamys neilli* in body size, and it along with the other Indomalayan species of *Leopoldamys* in general cranial conformation and a few cranial particulars (position of the squamosal zygomatic roots, for example); with *Niviventer*, *Tonkinomys* shares long incisive foramina, comparable inflation of the auditory bulla relative to the underlying petiotic bone, and similar molar occlusal patterns. Other traits exclude *T. daovantieni* from each of those genera as they are currently diagnosed (Musser, 1981). No species of *Leopoldamys* or *Niviventer* (or *Chiromyscus*), whether occurring in Indochina or on the islands on the Sunda Shelf, has *Tonkinomys*'s combination of dark grayish black upperparts and dark gray underparts; thick tail with a stubby tip that is much shorter than length of head and body; large, bulbous, and contiguous plantar pads; bony palate projecting well beyond the third molars

to form a shelf with a smooth posterior margin; strongly diverging (along the anteroposterior axis) maxillary molar rows; derived root pattern for the first upper molar coupled with the primitive root patterns underlying the other uppers and all the lower molars.

Both *Tonkinomys daovantieni* and *Saxatilomys paulinae* are associated with forested karstic habitats. Both genera display dark gray pelage, large and swollen plantar tubercles, a bony palate that projects beyond the molar rows to form a broad platform, maxillary molar rows that appreciably diverge posteriorly (along the anterior-posterior axis) and are long relative to length of skull, and two-rooted mandibular molars. All but the root pattern are specialized traits. This combination of attributes is not combined in any species of either *Leopoldamys* or *Niviventer* (or *Chiromyscus*). We do not know whether the morphological specializations shared by *T. daovantieni* and *S. paulinae* phylogenetically link these species closer to each other than to species of *Leopoldamys* and *Niviventer*, or rather reflect independent evolutionary adaptations to forested karstic environments in the Indochinese tropics. In opposition to the shared specializations, external morphology of *Tonkinomys* (except for relative length of tail) recalls a small-bodied *Leopoldamys*, while that of *Saxatilomys* resembles most species of *Niviventer*. Overall cranial form in *Tonkinomys* also resembles *Leopoldamys*, and except for those cranial traits that distinguish *S. paulinae* from species of *Niviventer* (comparisons are enumerated by Musser et al., 2005), the general cranial conformation of *Saxatilomys* is not unlike most species of *Niviventer*. Inferring the phylogenetic relationship of *Tonkinomys* among species now allocated to the *Dacnomys* Division in general, and especially to species of *Leopoldamys*, *Niviventer* (including *Chiromyscus*), and *Saxatilomys* will rest on results derived from future phylogenetic analyses of information derived from both morphological and molecular sources.

HABITAT AND HABITS

The Dao village of Lan Dat lies within a spectacular tower karst landscape, its houses

and adjoining agricultural clearings scattered over flat depressions nestled among high limestone hills with steep sides and sheer, expansive cliffs. The area epitomizes the classic description of karst landforms: "Karstic terrain is commonly characterized by closed depressions, subterranean drainage and caves" (Gillieson, 1996: 59). The climate is monsoonal, with most of the year's rain concentrated from April to October. Average annual rainfall (measured at Lang Son over 50 years) is 1395 mm, and even though cold temperatures dominate from November through March, humidity remains high, the annual relative humidity averaging 81% (Điêu, 1995).

Most of the flat areas, once supporting tropical moist deciduous forest, have been cleared by the Dao for rice cultivation and shifting agriculture. Forest remains at the base of the cliffs, in ravines between the high towers, and on the steep slopes, and it is not unlike Whitmore's (1984: 174) description: "... limestone slopes have a dense, irregular forest with trees clinging precariously, their roots penetrating to great depths in crevices ..." The forest consists of a low canopy (up to 15 m high) with taller (up to 25 m or more) emergents scattered over the steep slopes. Most trees are small (1–3 ft in diameter near the base), except in places allowing accumulation of sufficient soil where huge emergents are able to grow. Here and there a grove of emergent species forms a small area of high canopy. Palms and bamboo clumps are scattered through the understory, strangler figs are uncommon, and woody vines drape over high limestone ledges and form tangles beneath the forest canopy. The limestone towers are densely forested except for the sheer cliffs. Clumps of *Pandanus* are common at the base of these walls, and sometimes grow higher where they can obtain purchase in joints and fissures. We did not encounter cycads in the forest, and saw them only high on the vertical cliffs. Isolated clumps of bamboo remain in some of the clearings, and dense bamboo forest covers the steep slopes and tops of some limestone towers.

Most of the hillsides support primary forest, old and tall secondary growth covers hillsides

close to houses and fields, and scrub habitats dominate clearings not utilized for crops (fig. 1). Forest once growing on the few flat or gently sloping places above the valley and between limestone towers has been either removed or thinned. The primary forest cover is also not undisturbed by human activity. Trails cut through the understory usually lead to remnants of a huge emergent tree felled and processed for lumber. Natural disturbance in the form of treefalls and landslips is eventually covered by shrubs and then taller second-growth.

The day we broke camp and climbed out of the valley our usual trail chatter was silenced by a loud rumble, which had been generated by a massive rockslide. This is a periodic, unpredictable event, according to the villagers, and potentially dangerous. Weathering of the high cliff faces through the combined forces of water dissolving the limestone, differences in temperature, and pressure from large tree roots eventually dislodge chunks of cliff wall, some small, others huge. Such an event formed the habitat in which we trapped most of the limestone rats. Above the valley floor, a wide ravine between two contiguous limestone towers had been filled by a chunk of cliff wall the size of a small house along with smaller pieces—basically a talus of large blocks between the towers. The openings among the pieces were eventually enlarged, mostly by water flowing into the rubble pile from the top, and underneath it along the bottom of the old ravine. The result is a honeycomb of passageways, some extending vertically to small openings on top of the rubble, others opening to an uncovered section of the ravine. Walls of the labyrinth are wet and the air is cool. Shrubs, vines, and moss cover the surface of the rubble, hill forest persists at the cliff bases of each tower, and small trees are scattered over the talus (fig. 2). The surface of the rubble is difficult to negotiate. Rain has sculpted the limestone into small depressions surrounded by knife-sharp edges; small to large openings are everywhere, some as deep as 8 meters that expand into large cavities; and some openings are concealed by loose limestone fragments that shift underfoot.

Thirteen of the *T. daovantieni* were caught in this talus. Two were trapped on the surface, one beneath a shrub, the other one at the margin of the rubble beneath a rotting trunk. Five were taken in traps set at the bottom of the ravine beneath the main overhanging limestone chunk (the configuration resembled a small cave, but was really only a low passage beneath the straddling rock). Another was captured on a moss-covered ledge just outside of this cave-like passage. Five others were caught in traps lowered by ropes through small and large holes in the talus surface to the bottom of the labyrinth, which ranged from 4 to 8 m, depending on how close the vertical passages were to sides of the ravine. In these situations, most live and snap-traps were placed directly on the passageway floors. Traps placed on limestone ledges above this rubble near bases of the towers, or in the dense forest covering steep slopes away from the talus, yielded only *Niviventer fulvescens* and *N. langbianis*.

Tonkinomys daovantieni was not the only inhabitant of this talus. We captured a *Rattus andamanensis* and a *Niviventer fulvescens* at the mouth of the cave-like passage, an *N. fulvescens* on the surface, and one at the bottom of the deepest chamber.

The only limestone rat not trapped in or on the talus was taken in mature second growth hillside forest behind camp, which is at the other end of the valley from the rubble where all the others were caught. Here between the massive cliffs and valley floor is a steep middle region of limestone talus, formed of small to massive chunks that broke away from the cliff above. This is the only talus-like structure we encountered here. While soil has filled in most of the spaces among the blocks, apparently enough interstices and underground extensions exist to provide the proper habitat for *T. daovantieni*. Either that or the animal wandered from places on the tower we did not survey. The forest covering the talus is dense and festooned with woody vines. *Niviventer fulvescens* and the boreal *N. langbianis* were common.

Populations of *T. daovantieni* apparently have a patchy distributional pattern. Despite our sampling efforts on other hillsides, where traps were placed beneath rocky outcrops, on ledges, at the bottom of deep fissures in cliffs,

and on the forest floor, we did not encounter any *T. daovantieni*. A large cave was accessible, but it was being used as a corral for cattle; the interior was dry, and mostly scrub and young secondary forest persisted near the entrance. Traps placed on ledges inside the cave and outside near the entrance yielded nothing. We also set traps in a small, wet cave used as a roosting site by bats. No limestone rats were caught. Caves occur throughout the area, but the openings to most are high in the cliffs and inaccessible to us.

Certainly more field study is required to assess the habitat requirements of *T. daovantieni*, but our trapping experience suggests this forest species to be petricolous. It seems to require large areas of rock debris or talus that provides sufficient passageways and chambers for protected den sites, and a cool, damp environment. Long vibrissae; large, bulbous palmar and plantar pads; and a tail that is considerably shorter than head and body, that is thick and stubby-tipped, and that has a well-haired distal half and tip are adaptations important in a crevicular environment. The vibrissae monitor the cracks and walls for prey, surface information, and passage width; the fleshy pads provide purchase on rock surfaces; and the tail is used for balance as the rat scurries up and over the rocks and through the crevices and passageways, or as a fifth appendage when pressed against the limestone (the hairs would aid in purchase by pressing against the rough surface). We see similar adaptations in other petricolous murid rodents. The bushy-tailed woodrat, *Neotoma cinerea*, for example, is a North American cricetid analog to the Vietnamese murid, *T. daovantieni*. This species of *Neotoma* dens in caves, fissures in high cliffs, and deep in talus slopes (Finley, 1958; Grayson, 1999; Musser's trapping experience). Size and fleshiness of its footpads relative to foot size, length of tail relative to head and body length, and even overall body size is closely similar to these qualities in the limestone rat (see measurements provided by Finley, 1958: 322–325).

A cool and damp environment of crevices and larger passageways may be important to the diet of *T. daovantieni* because the diversity and numbers of arthropods is probably higher

there than in dry situations. Of two limestone rats kept captive, one devoured two kinds of cockroaches: a large-bodied species caught at the talus, and a smaller species collected in village houses and at camp. This rat refused offers of corn, manioc, snails, earthworms, grasshoppers, beetles, and small frogs. Our other captive rejected cockroaches offered during daytime, but headless bodies we piled in its cage were gone by morning. We are not sure whether they were dragged away by insects or eaten by the rat. We extracted stomach contents from two rats. In one, the stomach was distended with bait (mixture of peanut butter, bacon pieces, oatmeal, and raisins) in which were scattered pieces of very small beetles, which were likely on the bait and inadvertently ingested by the rat. The stomach of the other was partly full, containing fragments of sclerites intermingled with soft unidentifiable animal tissue. *Tonkinomys daovantieni* includes insects in its diet, but other components remain to be discovered.

The limestone rat is probably nocturnal, but may also be active at times during the day. We were drawn to the talus because during one late morning Lunde had glimpsed a large, dark gray rodent scurrying across the limestone and disappearing into the rubble. Results from the first night's traps revealed the rodent to be the limestone rat. We kept our traps in place during day and night, and often checked them in the evening, but never caught any rats during the day.

CLOSING OBSERVATIONS

Other species of Indochinese murids live in the tropical forests of karst regions but, except for *Saxatilomys paulinae*, none have any of the diagnostic morphological attributes of *Tonkinomys daovantieni* and none are so ecologically tied to the kind of crevice habitat in which we discovered the Vietnamese species. Two Thai murids are generally considered closely associated with limestone. *Leopoldamys neilli* is documented by a few specimens captured on the upper sections of forested limestone cliffs in Saraburi Province and adjacent Kanchanaburi Province in southwestern Thailand (Marshall, 1988; specimens in AMNH and USNM). Wiles (1981:

49), however, captured three individuals in lowland bamboo forest in a different part of Kanchanaburi Province. The trap sites averaged 115 m from the base of the nearest limestone mountain, and *L. neilli* was not encountered in the other habitat types Wiles surveyed, indicating the species to prefer lowland bamboo forest, which "... challenges the belief that *L. neilli* is strictly a cliff-dwelling rat."

Niviventer hinpoon is apparently endemic to the Korat Plateau in Saraburi Province of southern Thailand (Marshall, 1988; specimens in AMNH and USNM). One sample, which includes the holotype, was collected halfway up the face of a forested limestone cliff outside the entrance to a cave. Another series came from "... high above the valley floor, in scrubby vegetation at the base of vertical limestone cliffs" (Marshall, 1988: 459). Other species of murids were captured in the forested stream valley below the cliffs, but not *N. hinpoon*. Marshall (1988) also noted that one individual had been taken inside a limestone cave at a different locality. Whether *N. hinpoon* dens in clefts in cliffs or in talus is not recorded. Except for its tail, which is equal to or slightly longer than length of head and body, its buffy gray underparts, and its smaller body size (Marshall, 1988), the morphological traits of *N. hinpoon* are similar to those of *N. fulvescens*; our multivariate analyses of morphometric cranial and dental data place it closer to *N. fulvescens* than to any other species (Musser and Lunde, ms.). Relative to palmar and plantar areas, the pads are no larger or set no closer together than in *N. fulvescens* (see fig. 9) or any of the other species of *Niviventer*. Nothing in the morphology of *N. hinpoon* points to an obligate limestone cliff-dweller. We need to learn details of its actual microhabitat and other aspects of its life history.

Nothing comparable to the Vietnamese *Tonkinomys*, or to the Lao *Saxatilomys*, in morphology or habits has so far been found in the karst landscapes of Thailand.

Whitmore (1984: 148) noted that karst landscapes covered only a small part of tropical Asia. In Indochina they occur in southern China, north and central Vietnam, central Lao PDR, southern Cambodia,

Thailand, and northeastern Burma (Middleton and Waltham, 1986; Zhang, 1989; Tuyet, 1998; also see the references cited in Whitmore, 1984). Except for the large limestone plateau in southern China, karst landscapes in Indochina are small in area, scattered over the region, and constitute isolated geological islands (see the informative distribution maps in Middleton and Waltham, 1986). They are difficult places in which to work, and most Indochinese karst habitats have been inadequately sampled for murid rodents.

Saxatilomys paulinae and *Tonkinomys daovantieni* are the only petricolous Indochinese murines that to date have been found to be endemic to tropical karstic environments. The Khammouan Limestone in central Lao PDR defines the known distribution of *S. paulinae*. That tower karst landscape is part of the Quy Dat massif (or Kebang karst block; Tuyet, 1998: 189), which extends eastward at the same latitude into Bienh Tri Thien Province of north-central Vietnam. In the Lao segment, *S. paulinae*, the gymnure, *Hylomys megalotis*, and the hystricomorph rodent, *Laonastes aenigmamus* form a small community that may be restricted to forested, rocky habitats within the extensive and massive karst landscape; this same mammalian assemblage may also occur in the Vietnamese segment of the Quy Dat massif (Musser et al., 2005). The Quy Dat outcrop forms a karstic island approximately 475 km south of the expansive Vietbac tower karst region in northern Vietnam where *Tonkinomys daovantieni* occurs. That limestone rat, isolated on a geological island separate from the one on which *S. paulinae* was found, has been recorded only from the type locality in northeastern Vietnam but may have a wider geographic distribution in forested habitats throughout the karst landscapes of northern Vietnam and adjacent southern China. Unlike the Khammouan Limestone region, no other petricolous mammalian limestone endemics have been discovered in the same landscape occupied by *T. daovantieni*.

We have asked ourselves if the Vietnamese and Lao limestone rats are the only murine components of a pattern reflecting evolutionary adaptation of ancestral murines to forest-

ed karstic environments, or if other karstic islands in Indochina support different and unique murine endemics. Surveys for small mammals, such as ours that yielded *Tonkinomys*, would uncover the mammalian diversity in these extraordinary isolated landscapes and provide an answer to our question.

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