

Chapter 1

They Sort Out Like Nuts and Bolts: A Scientific Biography of Guy G. Musser

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INTRODUCTION

“They sort out like nuts and bolts,” or similar wording, was an assertion that regularly arose in my conversations or correspondence with Guy over the past 40 years. The “they” in this statement are species of Indo-Australian rodents (Muroidea: Muridae: Murinae), a diverse and taxonomically complex Old World group that would dominate his research contributions and secure his professional reputation as one of the foremost systematic mammalogists of his generation. The statement carried an implicit comparative context: it referenced Guy’s formative experiences with a comparably complex group of New World rodents, deer mice of the genus *Peromyscus* (Muroidea: Cricetidae: Neotominae), research that comprised some of his earliest taxonomic works. The subtle features consulted to distinguish *Peromyscus* species served to sharpen his eye for specific discrimination whenever applied to other murid genera investigated thereafter, particularly *Rattus* and kin.

There is so much that needs to be done, so many groups [of Indo-Australian murids] that require good systematic revision, and just not enough time. *Melomys* is another example of a bottomless pit. . . All the previous work on the genus has been terrible.² We would not have had this problem if everyone had first worked and honed their skills on *Peromyscus*. (GGM, in litt., 31 March 1987)

How this innate, finely calibrated sense of discrimination as perfected through experi-

ences with New World cricetids would lead to sorting the nuts and bolts of Old World murines is a story that bears telling from the beginning, at least from the academic beginnings.

ACADEMIC AND MUSEUM FOUNDATIONS (1956–1966)

Inevitabilities of a life lived are a beginning and an end. (GGM, in litt., 23 September 1997, apropos the sudden death of Karl Koopman, longtime friend and colleague in the American Museum of Natural History)

Guy Graham Musser was born 10 August 1936 in Salt Lake City, Utah, and there attended elementary and secondary public schools until 1955. Like many of his contemporaries who entered the profession of mammalogy in the middle 1900s (e.g., see various autobiographies in Phillips and Jones, 2005), Guy recalls a boyhood compulsion to be outdoors and a preference for activities that indulged his enjoyment of the natural world. The family lived on the outskirts of Salt Lake City, from where he liked to take a bus, east to the foothills of the Wasatch Mountains or west to the Great Salt Lake Desert, hike around all day, and catch a returning bus in the evening. Other foothills nearer home harbored a cool mountain stream and the site of his earliest attempts at trout fishing, which was to become a lifelong pursuit, partly escapist recreation and partly ongoing education. He and friends

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² Not long afterward, rigorous taxonomic reviews of the genus appeared (Menzies, 1990, 1996).

used to scout *Microtus* runways and occasionally hand-capture a slow-footed vole that they would observe in an old washtub outfitted as a makeshift terrarium. Membership in the Boy Scouts afforded more opportunities for exploring different landscapes around Salt Lake City, including annual weeklong hikes into the Uinta Mountains, where he first experienced untramed wilderness away from human sign. Although undirected and diffusely experienced, such snatches of earliest memories presaged a deep attraction to and comfort with the outdoors.

Guy entered the University of Utah in the fall of 1955, having no predetermined field of matriculation, but his unabating curiosity about all things natural and a preference for being outdoors attracted him to a major in biology by his sophomore year. The university offered broad training in natural history and field biology, with many “-ology” courses—entomology and aquatic entomology, limnology, ichthyology, ornithology, mammalogy—that are no longer commonplace in today’s university curricula, even in universities with natural history museums (e.g., see Schmidly, 2005). Guy thrived in such courses and happily immersed himself in counting diatoms to assay water quality, learning fish anatomy to identify native minnows, or keying out dragonflies by the patterns of wing venation. The classes satisfied his inclination to gain a hands-on understanding of natural systems, while actually requiring field trips, specimen collection, and species identification as part of the coursework. Furthermore, they planted the idea that diversionary pastimes enjoyed aimlessly as a youngster might be pursued as an equally rewarding and legitimate vocation as an adult. While still an undergraduate, extracurricular work connected with his aquatic entomology class fortuitously led to participation in major collecting expeditions along the Colorado River (Glen Canyon) and Green River (Flaming Gorge), undertaken in anticipation of impoundments planned along the upper Colorado drainage. Angus M. Woodbury and Stephen D. Durrant, respectively an entomologist and mammalogist in the university’s Department of Zoology and Entomology, coordinated

these field surveys, and Guy’s responsibilities involved the collecting of aquatic insects and limnological data, not mammals. His first scientific article (1)³, published in 1960 with aquatic entomologist G.F. Edmunds, documented the mayfly fauna gathered along the Green River.

Guy took Durrant’s mammalogy course in his senior year. Durrant’s class emphasized practical aspects of field mammalogy and required that the students set traplines, prepare study skins (his first a *Peromyscus maniculatus*!), and identify specimens. Again, his boyhood experiences—hiking around different habitats and chasing rodents—served him well in the mammalogy course: trapping mammals seemed to come as if second nature. Perhaps the inherent mystery kindled by the setting of a trap and attendant curiosity over what small mammal might appear in the next day’s catch helped to shift his interest from insects to mammals. Equally or more pivotal were his interactions with M. Raymond Lee, a senior doctoral student of Durrant. Lee helped Guy with the identification of any unknowns captured in his traplines, discussed where to find and how to trap certain mammals, and shared the results of his own thesis research. By the close of the mammalogy course and after further consultation with Lee, Guy had decided to pursue systematic mammalogy and approached Durrant to accept him as a graduate student. After completing a bachelor of science degree in 1959, Guy thus remained at the University of Utah for postgraduate study (1959–1961). The composition and synergy of one’s graduate student cohort play an important role in our higher education, perhaps as influential as courses taken, favorite professors, and committee chairs. In both stages of Guy’s graduate study, first at the University of Utah (Ray Lee, Gary Ranck) and later at the University of Michigan (Jim Brown, Dave Klingener, Tim Lawlor), he enjoyed interactions with individuals who would become

³ To avoid duplication, numbers in parentheses correspond to Musser’s publications as enumerated chronologically and consecutively in appendix 1. Non-Musser citations are found in References.

dedicated and respected mammalogists in their own careers.

Guy's master's thesis entailed months of basic field survey, during which he honed his knowledge of where mammals lived and which traps and methods performed best to catch them. It also required much attendant curation in the department's expanding Museum of Zoology, processing and identifying his collections. The resulting faunal study on the "Mammals of the Tushar Mountains and Pavant Range in southwestern Utah" (M.S., 1961) was never published as such, but specimens from this fieldwork contributed to Guy's first papers on mammals, which involved new records of bat distribution (2) and description of a new subspecies of flying squirrel (3). Range extensions and subspecies descriptions were customary and respectable teething studies for a young systematic mammalogist coming of age during the middle 1900s.

Durrant had earned his doctorate at the University of Kansas (KU; Ph.D., 1950), under the direction of the preeminent mammalogist E. Raymond Hall. The Utah-Kansas academic connection offered a logical career path, for example, as was followed by Henry W. Setzer, one of Durrant's earlier master's students who relocated to KU to complete a doctoral thesis under Hall. Or, as encouraged by Durrant, Guy could stay at Utah and there continue a Ph.D. dissertation. He was uninterested, however, in conducting another "mammals of" faunal study, such as that undertaken for his M.S. degree. At some point during his master's study, Lee had enthusiastically shown him a paper by Emmet T. Hooper on the phallic anatomy of *Peromyscus* (Hooper, 1958). That study, along with Hooper's (1952) revision of Central American *Reithrodontomys*, indelibly impressed Guy for their thoroughness, taxonomic scope, and novel evolutionary insights. Hooper, together with William H. Burt, was a curator in the Museum of Zoology, University of Michigan (UMMZ), and the two were there developing a first-class graduate program in systematic mammalogy. Like Hall, Hooper and Burt were the academic progeny of Joseph Grinnell, curator and professor in the prestigious Museum of Vertebrate Zoology, University of Cali-

fornia, and both were devoted adherents to field-oriented, museum-based systematic research as inspired by the model of their major professor. Although remaining at Utah to study under Durrant was the comfortable choice, the prospects of a new university environment and different research challenges persuaded Guy to write Hooper and ask about possibilities of graduate study at the UMMZ. Following a summer spent collecting birds throughout Utah for William H. Behle, his ornithology professor at Utah, Guy drove his '59 Chevy pickup cross-country to the flat upper Midwest and entered the University of Michigan in the fall of 1961.

The move to the University of Michigan conferred an ideal wedding of the field-collecting enthusiasm of a young graduate student, pursued in the setting of a major university-based natural history museum, under the tutelage of a critically minded systematist. After a year of earning his keep as a teaching fellow, Guy served as research assistant to Hooper, initiating the research that led to their minor classics on *Peromyscus* classification and muroid interrelationships (4, 5). In 1962, Guy and fellow grad student Dave Klingener accompanied Hooper for fieldwork in Costa Rica. Here, Guy first experienced trapping in tropical forests, lowland and montane, and was introduced to a rodent fauna very different from that of the Intermountain West. At Michigan, Guy's field talents were legendary to the grad students of my generation. The symmetry and natural proportions of a Musser study skin are readily identifiable within a drawer of rats and were emulated as the embodiment of a properly prepared round skin. Even so reserved a person as Hooper frankly regarded Guy as the best field person with whom he had ever associated, and Durrant grudgingly acknowledged (fide Hooper) the superior trapping abilities of "that damned hippie" (well, it was the '60s).

Guy's doctoral thesis (Ph.D., 1967) involved systematic study of a tree squirrel of northern Middle America: "A systematic study of the Mexican and Guatemalan gray squirrel *Sciurus aureogaster*, F. Cuvier (Rodentia, Sciuridae)." Many taxa now associated with this species—such as *griseoflavus*,

nelsoni, *poliopus*, and *socialis*—were formerly viewed as an intractable species complex whose populations exhibit exceptional variation in pelage color and pattern. Hooper had been intrigued by the problem, stimulated by his own Mexican fieldwork and specimen examination, and its resolution required the assembly of more material from regions undocumented by museum specimens, as well as the synthesis of extant museum holdings. Such needs suited his student's desire to return regularly to the field and see new environments, which Guy did in stints of 3–4 months over the years 1963–1965. The basic questions posed (Musser, 1968 [9]: 6) were “how many gene pools” are represented by *aureogaster* and related forms and “what are the morphological and ecological characteristics of these pools”? Pelage patterns of the nape, rump, and venter were meticulously quantified and collated geographically to infer intergradation among named forms and directions of gene flow; he concluded that the several names represent interbreeding populations of one immensely variable species, *S. aureogaster*, with only two broadly defined subspecies. The invocation of gene pools, directions of gene flow, and genetic isolation, as inferred from sample frequencies of chromatic traits, may sound anomalous when juxtaposed against gene sequencing, today's taxonomic tool of choice for understanding such population-level processes. Nevertheless, the terminology echoes the vocabulary and population thinking of the New Systematics and Evolutionary Synthesis, wherein the circumscription of definable geographic races (subspecies) presumably reflected underlying patterns of genetic discontinuity among populations and the potential evolution of nascent species. His dissertation represents a fine example of the subspeciation studies that unfolded in mid-century (e.g., Setzer, 1949; Hoffmeister, 1951; Anderson, 1956; Bowen, 1968).

Curiously, Guy's thesis on *Sciurus aureogaster* (9), with its emphases on intraspecific variation and infraspecific taxa, is atypical of the subsequent research that would characterize his prolific contributions on murine rodents of Asia and Indo-Australia. Instead, the reports on his field collections of *Peromyscus* made while at the UMMZ (6, 10)

and collaborations with Hooper on muroid phallic morphology (4, 5) better preview his future research methodology and its emphasis on taxonomic ranks at the species level and above. The interactions with and standards set by Hooper while at Michigan, whether in the curation of collections or the conduct of systematic research, proved transformative. He afterward acknowledged Hooper's professional example on many occasions and in different contexts, for instance, apropos the tedious review of a long, meandering paper:

It is not the kind of report Hooper would have allowed to see the light of day—either I am getting older and more mellow or I am just appreciating what I learned from him. I realize now that he allowed you to express your imagination and use innovation in preparing results but also insisted on rigorous documentation and clear presentation. (GGM, in litt., 31 March 1988)

Rigorous documentation and clear presentation would become hallmarks of his systematic contributions throughout the next phase of his career in the Department of Mammalogy at the American Museum of Natural History (AMNH).

The circumstances that brought Guy to the AMNH departed from today's usual hurdles of open competitive searches, short lists, and job seminars. While Guy was mired in analyzing data and writing his thesis, Burt and Hooper began nudging him to think about future job possibilities. Given his overriding interests in museum-based field investigation and having a somewhat loner personality, Guy never pictured himself teaching in an academic setting, surrounded by a stable of graduate students. Instead, he recalled the feelings of grand adventure instilled when, as a grad student at Utah, he first perused AMNH bulletins on the early Archbold New Guinea expeditions. Based on such stray recollections, Guy decided that the AMNH would be a neat place to work and enjoined Hooper to write Richard Van Gelder, then chairman of the AMNH Department of Mammalogy, and inquire about curatorial positions for a soon-to-graduate prospect. Hooper's first inquiry elicited a “Don't call us, we'll call you” response...and shortly afterward they did.

The impending retirement of Leonard J. Brass, Archbold Associate Curator and the chief botanist on the New Guinea expeditions, prompted Van Gelder to reconsider and contact Hooper about his student's qualifications and depth of interest. An abrupt trip to New York City, an introduction to the department and collections, and dinner with Van Gelder and Brass culminated with an on-the-spot job offer from Van Gelder. Although this serendipitous cascade of events nowadays borders on the unbelievable, history would judge that the individual's experience and talents preeminently suited the position's requirements and expectations.

AMERICAN MUSEUM OF NATURAL HISTORY (1966–2002)

Guy joined the Department of Mammalogy in 1966 before completing his Ph.D. thesis. Hooper afterward confessed a nagging worry that Guy's premature departure for a curatorial plum in an elite museum would erode or erase any initiative to finalize his doctoral research, thereby following the path of certain other Michigan graduate students in mammalogy (notably, C.O. Handley, Jr., an earlier Hooper student who left to become a curator in the U.S. National Museum in 1949, but did not finish his dissertation until 1955). Hooper's concern was misplaced. While Guy was familiarizing himself with his new AMNH colleagues and the extensive mammal collections, he diligently refined the *Sciurus aureogaster* study, returned to Michigan in 1967 to formally file his dissertation, and submitted it to the UMMZ series soon thereafter (9).

The AMNH position offered to Guy was that of Archbold Assistant Curator, a curatorship funded by one of the Museum's major benefactors, Richard Archbold. Archbold (1907–1976) was independently wealthy, the family's riches stemming from early ventures in Pennsylvania oil refineries, and throughout his lifetime he sought meaningful avenues to disperse that wealth, including geographic exploration and natural history discovery. In the 1930s, Archbold sponsored a series of AMNH expeditions, personally leading those to New Guinea but also supporting collectors in Sulawesi (Celebes)

and northern Australia, where the field teams broadly collected vertebrates, insects, and plants. As a research associate in the Department of Mammalogy (1931–1976), Archbold participated in many of the mammalian descriptions emanating from these expeditions, especially those authored in collaboration with George Tate, the expedition's lead mammalogist (e.g., Tate and Archbold, 1935). Archbold's scientific philanthropy was soon incorporated as the nonprofit Archbold Expeditions, a bountiful partnership that supported Museum fieldwork and personnel costs during the years 1937–1981. The titles in many of Guy's publications accordingly include the preface "Results of the Archbold Expeditions, No. x," and after Archbold passed away, he honored the man for his "patronage and commitment to indifferent inquiry" by naming a new genus of Philippine murid (*Archboldomys* Musser, 1982). Archbold's sister, Frances Archbold Hufty, continued as president of Archbold Expeditions after her brother's death, but financial support for the Museum dwindled and eventually ended in 1981. Guy nonetheless preferred to retain the honorary title of Archbold Curator until his retirement, the last of a distinguished line of AMNH Archbold curators.

TAXONOMIC THEMES AND RESEARCH APPROACH

When I began writing papers about rats it became very clear that what most of the literature on murid systematics lacked was stated context and reasons why the papers were necessary. The systematic sections are really very boring to most readers, even mammalogists. But, to put the results in some kind of context, either evolutionary or historical, adds significant dimension and, depending on the competence of the section, depth. I think that this combination of data analyses, results, and context is what defines scholarship. (GGM, in litt., 15 July 1998).

Guy's concept of scholarship is plainly evident in the 108 scientific papers that he has produced to date, a publication record notable for its uniformly high quality and steady productivity that features the regular

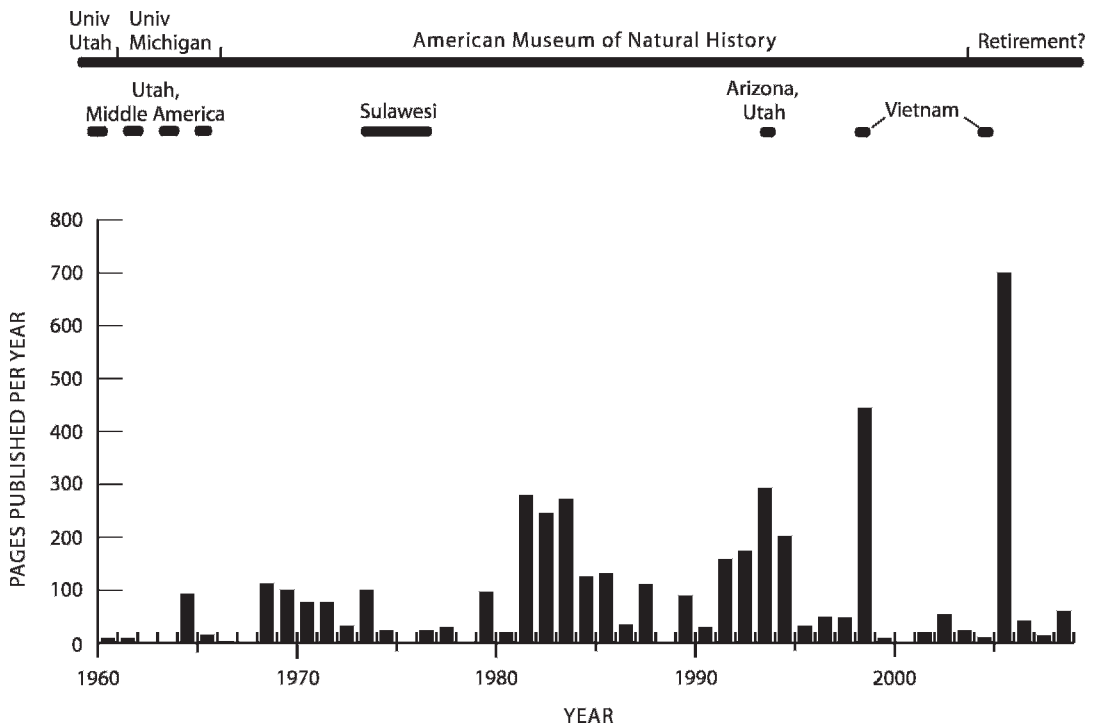


Fig. 1. Three perspectives that summarize broad aspects of Guy G. Musser's professional career. The top bar brackets institutional bases where he conducted his museum researches; the interrupted lower bar indicates general areas where fieldwork was periodically conducted. The histogram views his career productivity in terms of pages published per year (see appendix 1). From his earlier contributions that treated alpha taxonomic details of *Peromyscus* and *Rattus*, among others, his publications have trended toward larger, more synthetic revisions, monographs, and taxonomic catalogs.

appearance of monographic treatises (appendix 1, fig. 1). The majority of his papers (80 publications) involve taxonomic descriptions and revisions of muroid rodents, by far the most speciose superfamily of living mammals (e.g., Wilson and Reeder, 2005), and as a body of work, his contributions have substantially reordered our systematic understanding of these diverse rats and mice from the species to family ranks. Guy's research on Muroidea has emphasized genera and species of Old World muroids (Muridae: Murinae [61 publications]), pursuant to his responsibilities as an Archbold curator, and to a lesser extent certain New World groups (Cricetidae: Neotominae [6 publications] and Sigmodontinae [7 publications]) and higher-order classifications of the superfamily (5 publications). These broad taxonomic foci and the research effort dedicated among them are approximately reflected in the

impressive numbers of new mammalian taxa that Guy has described—including 2 subspecies, 39 species, 19 genera, 3 tribes, and 2 subfamilies—over the period from 1961 through 2009 (and counting; table 1). Such parameters outline the bare results of his lifelong researches but say little about their context and impact.

INDO-AUSTRALIAN MUROIDS (MURINAE): Upon Guy's arrival at the AMNH as a newly minted Archbold Assistant Curator, there already existed a rich collection of mammals from the Indo-Australian region that invited careful research, as well as a mechanism, the Archbold Expeditions, Inc., that encouraged pursuit of museum and field studies relating to them. From this stage, his research focus and publication theme are largely straightforward.

Guy's early years at the AMNH were spent learning the mammals, especially Ro-

TABLE 1

New Taxa (in boldface) described by Guy G. Musser and Colleagues

(Arranged chronologically and grouped by family and country or broad geographic region. † = fossil taxon; * = genus or species based on new material collected by Musser or coauthors; no symbol = genus or species based on old material reposing in collections from 20–100 years.)

| Taxon, Authorship, and Year | Geographic Domain |
|--|-------------------|
| Neotropical Sciuridae: | |
| * <i>Glaucomys sabrinus murinauralis</i> Musser, 1961 | United States |
| Neotropical Cricetidae: | |
| <i>Habromys</i> ^a Hooper and Musser, 1964b | Mesoamerica |
| <i>Isthomys</i> ^a Hooper and Musser, 1964b | Panama |
| <i>Osgoodomys</i> ^a Hooper and Musser, 1964b | Mexico |
| * <i>Peromyscus thomasi cryophilus</i> ^b Musser, 1964 | Mexico |
| * <i>Peromyscus chinanteco</i> Robertson and Musser, 1976 | Mexico |
| * <i>Daptomys peruviansis</i> ^c Musser and Gardner, 1974 | Peru |
| <i>Oryzomys tatei</i> Musser, Carleton, Brothers, and Gardner, 1998 | Ecuador |
| * <i>Oryzomys emmonsae</i> Musser, Carleton, Brothers, and Gardner, 1998 | Brazil |
| * <i>Oecomys sydandersoni</i> Carleton, Emmons, and Musser, 2009 | Bolivia |
| Indo-Australian Muridae: | |
| <i>Tateomys rhinogradoides</i> Musser, 1969b | Sulawesi |
| <i>Chiropodomys karlkoopmani</i> Musser, 1979 | Sumatra |
| <i>Komodomys</i> Musser and Boeadi, 1980 | Lesser Sundas |
| <i>Srilankamys</i> Musser, 1981a | Sri Lanka |
| <i>Margaretamys</i> Musser, 1981a | Sulawesi |
| * <i>M. elegans</i> Musser, 1981a | Sulawesi |
| * <i>M. parvus</i> Musser, 1981a | Sulawesi |
| <i>Anonymomys mindorensis</i> Musser, 1981a | Philippines |
| † <i>Papagomys theodorverhoeveni</i> Musser, 1981b | Lesser Sundas |
| † <i>Hooijeromys nusatenggara</i> Musser, 1981b | Lesser Sundas |
| † <i>Paulamys naso</i> ^d Musser, 1981b | Lesser Sundas |
| <i>Kadarsanomys</i> Musser, 1981c | Java |
| <i>Rhynchomys isarogensis</i> Musser and Freeman, 1981 | Philippines |
| <i>Crateromys paulus</i> Musser and Gordon, 1981 | Philippines |
| <i>Abditomys</i> Musser, 1982a | Philippines |
| <i>Crunomys rabori</i> ^e Musser, 1982c | Philippines |
| * <i>Crunomys celebensis</i> Musser, 1982c | Sulawesi |
| <i>Archboldomys luzonensis</i> Musser, 1982c | Philippines |
| * <i>Tateomys macrocerus</i> Musser, 1982c | Sulawesi |
| <i>Hydromys hussoni</i> Musser and Piik, 1982 | New Guinea |
| † <i>Rattus trinilensis</i> Musser, 1982d | Java |
| <i>Palawanomys furvus</i> Musser and Newcomb, 1983 | Palawan |
| <i>Sundamys</i> Musser and Newcomb, 1983 | Sunda Shelf |
| <i>Rattus osgoodi</i> Musser and Newcomb, 1985 | Vietnam |
| <i>Rattus tawitawiensis</i> Musser and Heaney, 1985 | Philippines |
| * <i>Crateromys australis</i> Musser, Heaney, and Rabor, 1985 | Philippines |
| † <i>Hadromys loujacobsi</i> Musser, 1987a | Pakistan |
| * <i>Bunomys prolatus</i> Musser, 1991 | Sulawesi |
| * <i>Maxomys watsi</i> Musser, 1991 | Sulawesi |
| <i>Rattus koopmani</i> Musser and Holden, 1991 | Sulawesi |
| <i>Tarsomys echinatus</i> Musser and Heaney, 1992 | Philippines |
| * <i>Batomys russatus</i> Musser, Heaney, and Tabaranza, 1998 | Philippines |
| <i>Sommeromys macrorhinos</i> Musser and Durden, 2002 | Sulawesi |
| * <i>Saxatilomys paulinae</i> Musser, Smith, Robinson, and Lunde, 2005 | Lao PDR |
| * <i>Tonkinomys daovantieni</i> Musser, Lunde, and Son, 2006 | Vietnam |
| <i>Leptomys paulus</i> Musser, Helgen, and Lunde, 2008 | New Guinea |

TABLE 1
(Continued)

| Taxon, Authorship, and Year | Geographic Domain |
|---|-------------------|
| <i>Leptomys arfakensis</i> Musser, Helgen, and Lunde, 2008 | New Guinea |
| <i>Coccymys kirrhos</i> Musser and Lunde, 2009 | New Guinea |
| <i>Brassomys</i> Musser and Lunde, 2009 | New Guinea |
| Muroidea: | |
| Delanymyinae Musser and Carleton, 2005 | Africa |
| Leimacomyinae Musser and Carleton, 2005 | Africa |
| Baiomyini Musser and Carleton, 2005 | North America |
| Ochrotomyini Musser and Carleton, 2005 | North America |
| Nyctomyini Musser and Carleton, 2005 | Middle America |
| Asian Soricidae: | |
| <i>Chodsigoa caovansunga</i> Lunde, Musser, and Son, 2003 | Vietnam |
| <i>Crocidura kegoensis</i> Lunde, Musser, and Ziegler, 2004 | Vietnam |
| Suckling lice (Anoplura): | |
| <i>Hoplopleura traubi</i> Durden and Musser, 1991 | Sulawesi |
| * <i>Polyplax melasmothrxi</i> Durden and Musser, 1992 | Sulawesi |
| <i>Hoplopleura sommeri</i> Musser and Durden, 2002 | Sulawesi |

^a Described as subgenus.

^b Elevated to species by Carleton (1989).

^c Now = *Neusticomys peruviansis* sensu Voss (1988).

^d *Paulamys* Musser (1986) was coined as a replacement name for *Floresomys* Musser, 1981.

^e Merged as a junior synonym of *Crunomys melanius* by Rickart et al. (1998).

dentia, of the region, and assessing the strengths and weaknesses of the collections. This education necessarily required much basic, hands-on curation, bringing a peromyscine yardstick of discrimination to the murine identifications and alpha taxonomies of Archbold and Tate. Guy also invested considerable curatorial effort in the important Indo-Malayan rodent series contained in the U.S. National Museum of Natural History (USNM), the repository of collections generated by W.C. Abbott and H.C. Raven, along with the numerous holotypes and type series of taxa described by Ned Hollister and Gerrit Miller in the early 1900s (e.g., Miller, 1900; Hollister, 1913; Miller and Hollister, 1921). In the late 1960s through early 1970s, Guy worked so often in the

USNM, commuting by rail between New York City and Washington, D.C., that the divisional technicians viewed him as the Mammal Division's fourth curator.⁴ Having improved the identification of material housed in North American collections as a dependable taxonomic resource, travel to European museums was the obvious next step. Those that contained critical series of Indo-Australian rats and mice—the British Museum of Natural History, London (BMNH); Rijksmuseum van Natuurlijke Histoire, Leiden; and the Museum National d'Histoire Naturelle, Paris—were visited in 1969, not as a routine museum trip of days to weeks in duration but a prolonged tour of five months.

The British Museum and the museum at Leiden are full of real treasures. Going through their collections is like being in the field and discovering new and interesting animals. (GGM, in litt., 2 February 1970)

Examination of holotypes and associated material, the bases of descriptions by early workers such as Oldfield Thomas, F.A.

⁴ In the late 1960s, curators in the USNM Division of Mammals included Charles O. Handley, Jr. (1949–2000), David H. Johnson (1941–1967), and Henry W. Setzer (1948–1978). By the early 1970s, Johnson had retired and the Division expanded to include Handley, Setzer, James Mead (Marine Mammal Program), and Richard Thorington (Primates Program). Technically, Guy would have been the “fifth” USNM curator over this period.

Jentink, and Alphonse Milne-Edwards, was necessary to resolve explicit nomenclatural problems and enlighten taxonomic suspicions. By the conclusion of the 1969 European trip, he had examined all of the types of rodent taxa known from Sulawesi. A three-month museum trip followed in 1971 to study collections in Indonesia, Malaya, Singapore, and Thailand.

The dividends from this initial phase of museum investigation started to appear in papers produced from 1969 to 1973 (appendix 1). The majority of these focused on taxa described from Sulawesi and most involved reparatory taxonomic and nomenclatural issues: providing diagnoses and comparisons for obscure taxa; resurrecting epithets long buried in *Rattus* infraspecific taxonomy to valid species; reassigning subjective synonyms among species judged to be valid, especially the allocation of poorly known forms with the correct species of commensal *Rattus*; emending definitions of taxa based on composite holotypes, designating lectotypes, and restricting type localities. In one exceptionally contorted case (17), the type series of *Mus callitrichus* Jentink, 1879, proved to be a mixture of five divergent species (*Taeromys callitrichus* proper plus *Bunomys chrysocomus*, *B. fratorum*, *Pauromys dominator*, and *Rattus hoffmani*). Only one new taxonomic description appeared in this period (*Tateomys rhinogradoides* Musser, 1969), but "Results of the Archbold Expeditions. No. 91" was a beefy *Novitates* (12) that portended the succession of insightful AMNH reports and monographs on Indo-Australian murids. Hooper chuckled that only Guy could write a 41-page article based on a single specimen. Of course, the paper covered much more than an exacting morphological description of *Tateomys* (which it certainly contained), but it also broadly addressed evolutionary origins and possible relationships among the shrew rats of Sulawesi and the Philippines and began to consolidate the rodent genera endemic to Sulawesi. Those uninitiated to the arcana of murine nomenclature may find such papers tortuous to read, yet together they constituted the building stones of an objective foundation that would impel a fresh look at the diversification of murine rodents across

the Indo-Australian region. A crucial aspect of any fresh look would depend upon renewed biological survey.

Spent a week with Musser at AMNH. Good for the soul. The museum thinks he will be gone for a year. He thinks 3 years. (D.J. Klingener, in litt., 5 July 1973)

And three years it was: from June 1973 to September 1976, Guy lived in the forests of Sulawesi and accumulated a superb collection of small mammals, especially rodents. As a Michigan grad student at the time, I kept writing to AMNH to inquire when Musser would return from Sulawesi, only to learn that he had extended his fieldwork for still another six months in view of the exciting discoveries being made. Van Gelder and Sydney Anderson, departmental chairs during those years, didn't seem to mind his prolonged absence in view of the shipments of well-preserved small mammals that periodically emerged from somewhere in the forests of Sulawesi, with runners porting specimens out and carrying supplies in as required, all shipped via Jakarta. Guy purposefully situated his base camps in primary forests of the interior, away from human settlements, and concentrated his field surveys in the central highlands of Sulawesi. Detailed altitudinal transects from lowland evergreen rainforest through upper montane rainforest were regularly established to delimit altitudinal ranges and ecological occurrences (e.g., see Musser and Holden, 1991 [71]: table 18). The value of his Sulawesi collections is enhanced not only by the quality of the specimen preparations but, for the era, their variety—yes, the traditional skins and skulls, but also fluids, skeletons, and chromosomal preparations ("I can now run rats through the chromosome mill and that required a whole different suite of junk that I am unused to taking into the field."—GGM, in litt., 5 June 1973). Reams of ecological, reproductive, and dietary information were recovered and habitats and live animals were photographed in order to document the natural history of the specimens collected. The latter kinds of data were typically absent from the scanty descriptive literature with which Guy had to contend, but they would be profusely integrated throughout his subsequent generic and specific revisions.

I don't think that I could stand to do something else like this [1979 study of *Chiropodomys*] for a while, but then these papers always start out innocently and innocuously; I am still perplexed why this one grew into a monster. (GGM, in litt., 19 April 1978)

At a girth of merely 69 pages, the *Chiropodomys* revision (35) would prove to be only a dwarf Godzilla compared with the monographic monsters that were soon to hatch. The continuing dissemination of results from Guy's museum sleuthing, now supplemented by the abundant new material collected during his Sulawesi expedition, would yield a fertile second phase of publication on murine systematics (1979–1987; appendix 1, fig. 1). The majority of his murine descriptions, 11 genera and 20 species, appeared during this period (table 1), which included five substantial *Bulletins*, many weighty *Novitates*, and some of the longest "notes" ever published in *Journal of Mammalogy* before the journal abandoned that subdivision of articles. Such numbers of taxa new to science pale against the lifetime output of a C. Hart Merriam (U.S. Biological Survey) or Oldfield Thomas (BMNH), but one must appreciate that Guy's mammalian discoveries transpired in the latter 1900s, a century after the inception of directed survey collecting and correlative eruption of taxonomic description (e.g., Kohler, 2006). For someone whose command of the Eurasian and Indo-Australian murid faunas was now so expert, new species or genera were relatively simple to spot in a drawer of specimens (though proper documentation of those novelties was never a simple task). More taxonomically complicated and excruciating to document were the many groups extricated from the nebulous construct and bloated synonymy of Indo-Australian *Rattus* that prevailed in the middle 1900s (e.g., Chasen, 1940; Ellerman, 1941, 1961; Simpson, 1945; Ellerman and Morrison-Scott, 1951; Tate, 1951; Laurie and Hill, 1954). Genera such as *Limnomys* (34), *Maxomys* (37), *Leopoldamys* and *Niviventer* (40), *Apomys* (46), and *Berylmys*, *Bullimus*, and *Bunomys* (52) had to be differentiated from *Rattus* and from one another, their morphological diagnoses recrafted, and their specific contents and distributions redefined.

Guy's contributions to the systematics of Indo-Australian murines have steadily continued from 1990 onward (appendix 1), but not with the concentrated flourishes that characterized the two earlier periods. Preoccupation with new research interests competed for his time and energy. Noteworthy over this latter period was the 1992 monograph of Musser and Heaney on native Philippine murines (74). Though not a quantitative phyletic analysis per se, the authors systematized the character variation among the 18 native genera as evidence of three major divisions and developed phylogenetic and biogeographic hypotheses to account those divisions. A recent molecular study (Jansa et al., 2006) has broadly supported their ideas, particularly with regard to Old Endemic and New Endemic groupings, although disagreeing (naturally) over details. Guy twice returned to the field in the Indo-Australian region, in 1998 and 2004, after a lapse of 22 years since the productive expedition to Sulawesi. Field trips of 1–2 months duration were conducted to Vietnam, under the auspices of the AMNH Center for Biodiversity and Conservation, and uncovered new species of shrews and a new genus and species of rodent (96, 99, 104; table 1). Guy coordinated the first Vietnam trip, but Darrin Lunde, a frequent collaborator and AMNH Collection Manager of Mammals, handled all logistics for the second, with Guy tagging along as earnest field hand (fig. 2).

He knew I was going to Vietnam and after I had already made the necessary arrangements, Guy mentioned that he really missed going into the field He just wanted to trap Needless to say he was one of the most amazing field assistants anyone ever had, and it was a role he seemed to fill with great humor. I remember him gloating every time I had . . . to deal with permits or any number of other unpleasanties you need to take care of in the field. He would just pick up some traps to head off into the forest with what seemed an almost gleeful smile. (D.P. Lunde, in litt., 25 September 2008)

Guy's studies of Indo-Australian murines feature twin subtexts that are threaded among the bare bones of his taxonomic findings and amended synonymies. One was the need to disentangle truly indigenous



Fig. 2. Twenty-two years after his fieldwork in Sulawesi (see frontispiece), Guy returned to fieldwork in Indo-Malayan forests, this time for shorter surveys conducted in Vietnam in 1998 and 2004. Guy is pictured here with a live individual of the new genus and species *Tonkinomys daovantieni* Musser, Lunde, and Son, 2006 (photograph by Darrin P. Lunde, 2004). When a live animal was captured, Guy often retained it in the trap in order to observe its behavior and to test reactions to various foodstuffs.

species from those forms associated with human peregrinations and agricultural activities. Credible identification of the latter (commensal) species was hindered by an overburden of scientific names, particularly for *Rattus*, and the consequent nomenclatural morass obscured real biogeographic commonalities or differences among the murine faunas of Sulawesi, the Philippines, and Sunda Shelf (fig. 3). The 1973 paper on *Rattus argentiventer* (28), the ricefield rat once considered to be an ecological subspecies of *R. rattus*, signaled his emerging perception of the microdistributional dichotomy between indigenous murines (mainly confined to pristine environments) and introduced species (limited to anthropogenic settings), and other reports followed to

solidify this pattern (33, 52, 63, 71). Other researchers had appreciated such a division, albeit on a local basis (e.g., Barbehenn et al., 1972–1973, for the Philippines). Guy grounded his morphological understanding of commensal species through actual examination of type specimens; periodically updated the growing list of synonyms, many described and long disguised as endemic species (especially see 33, 52); and achieved a fresh picture of their distributions throughout the Indo-Australian region. These dogged efforts revealed a surprisingly diverse suite of species that are never encountered in primary forest (apart from the usual triumvirate of *Rattus rattus*, *R. norvegicus*, and *Mus musculus*), and whose presence on the Sunda Shelf or across Indo-Australian island groups had resulted

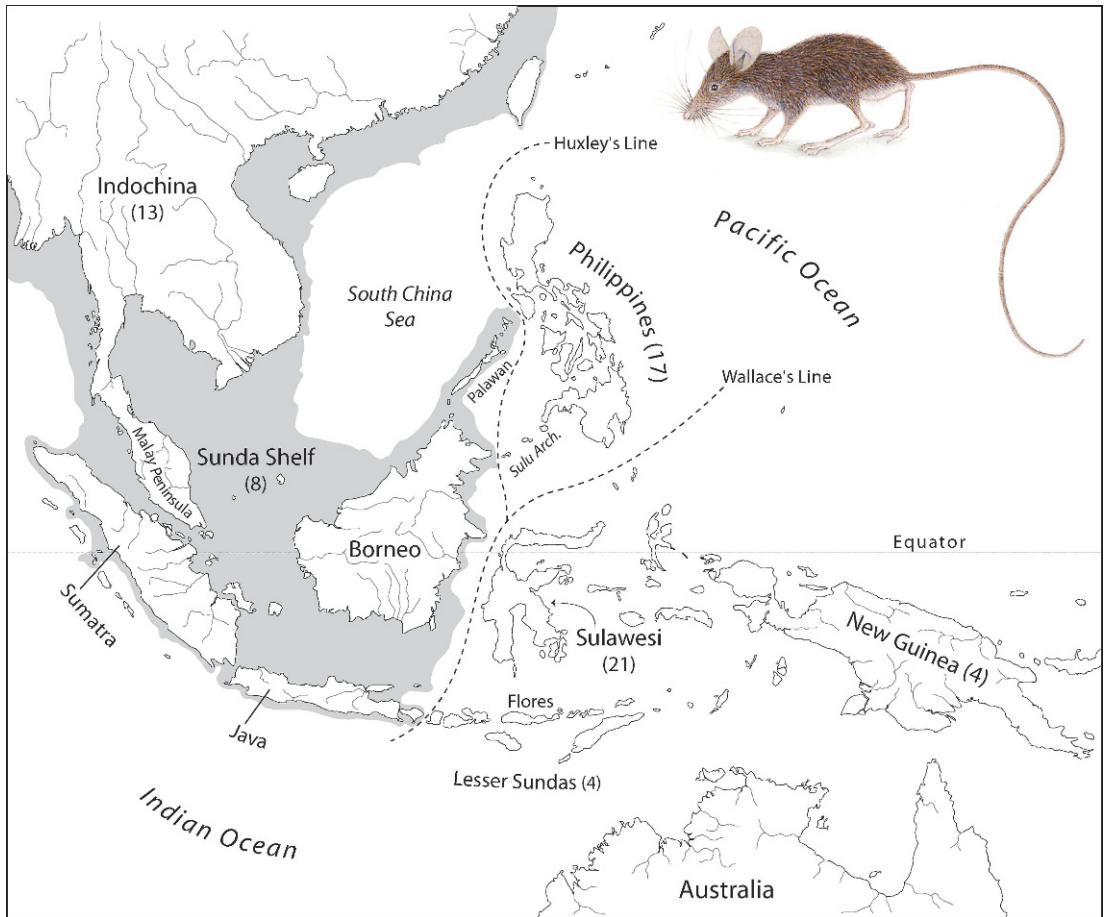


Fig. 3. The Indo-Australian region formed the dramatic geographic backdrop to Guy G. Musser's systematic studies of Murinae. Sulawesi, where Guy spent three years in the field (1973–1976), was the centerpiece of his contributions to murine systematics, but substantial research was necessarily devoted to nearby islands, archipelagos, and Indochina to clarify the taxonomy, evolutionary relationships, and biogeography of rats and mice that inhabit the region (numbers in parentheses next to island groups or geographic feature signify the number of publications that principally address taxa in those areas). Color inset: *Sommeromys macrorhinus* Musser and Durden (2002), one of the many endemics described from Sulawesi (drawing by Patricia Wynne). (Figure adapted from Musser, 1981[40].)

from human-mediated introductions (i.e., *R. argentiventer*, *R. exulans*, *R. nitidus*, *R. tanezumi*, *Bandicota indica*, *B. bengalensis*, *Mus caroli*, *M. cervicolor*, and *M. terricolor*). Coincidentally, the degree of endemism recorded for indigenous rodents was substantially enhanced at both specific and generic ranks. The taxonomic lists and endemism tallies for various Indo-Malayan island groups presented in a recent article on the “Diversity, distribution, and conservation of endemic island rodents” readily attest to the

magnitude of Guy's alpha-taxonomic labors (Amori et al., 2008; also see, Corbet and Hill, 1992).

The second interwoven subtext concerned the need for a morphologically credible, monophyletic construct of the genus *Rattus*. The heterogeneous, waste-basket composition of the genus handed down from the era of Chasen, Ellerman, and Simpson defied objective diagnosis, and its apparently expansive occurrence across the Indo-Australian region posed distributional enigmas that misled past

zoogeographers. Misonne (1969) began to unravel this view of *Rattus* by excluding genera endemic to Africa, but little headway had been accomplished with Indo-Malayan rodents when Guy started to work with the Archbold collections. His approach to the problem was direct and methodical: sorting out clearly definable, morphological clusters; describing new genera (table 1) or resurrecting genus-group taxa uncritically lumped under *Rattus* (e.g., 37, 39, 52); and contrasting all of these with regional forms of true *Rattus*. Most generic changes were accompanied by detailed enumerations of differentiating traits and/or tabulations of primitive versus derived character states (such as, 39, 52, 71, 74). By the close of his second phase of murine investigations in 1987, Guy could record that the indigenous murines on Sulawesi consisted of 14 genera and 36 species, four of them in *Rattus* (63); in contrast, Laurie and Hill (1954) had recognized six genera and 35 species, 29 of them in *Rattus*. Although the process was operationally phenetic, the ultimate goal was phylogenetic. His taxonomic amendments typically raised evolutionary questions that invite testing and identified explicit means to reject or accept his proposals. Recent molecular studies of murine phylogeny appear to offer broad support for his redrawn limits of genera and notions of relationship vis-à-vis *Rattus* (e.g., Steppan et al., 2005; Jansa et al., 2006; Lecompte et al., 2008; Rowe et al., 2008). Forms such as *Apomys*, *Maxomys*, and *Sundamys* decidedly fall outside the clade of *Rattus* proper, and the polyphyletic burden of the genus sensu Ellerman and others has been appreciably and irrevocably reduced. Throughout his ongoing murine investigations, Guy had obviously formulated a working diagnosis of *Rattus* sensu stricto and intended one day to punctuate his many alpha-taxonomic projects with a proper phylogenetic delineation of the genus. As sometimes happens, one's ambitions run out of lifetime to fulfill them.

Guy would not style himself as a biogeographer, but his research arguably holds its greatest relevance within the arena of Indo-Australian biogeography. Still, encamping for three years in the forests of Sulawesi speaks an awareness of biogeographic insights that could unfold from intense field-

work there. Sulawesi is a large island found immediately east of Wallace's line (fig. 3), where so many abrupt faunal and floral changes are recorded compared with islands of the Sunda Shelf and the Philippines, and is situated at the nexus of colliding tectonic plates and complex geomorphic changes. The study group of choice, murine rodents, also conveys a deliberate calculation in view of their low vagility, the ample opportunities for fine-grained speciation across such a geologically volatile region, and the general want of rigorous revision since the descriptive era. Yet only a couple of his papers overtly address murine biogeography of the region (33, 63). Instead, most remarks on the topic are relayed incidentally within his revisions and descriptions, which also consider the biogeographic ramifications of the proposed taxonomic changes and summarize the altered picture of faunal associations and endemism patterns. A noteworthy example was the description of *Rattus osgoodi* from southern Vietnam (56), a paper that highlighted the Annamite Mountains as an area of endemism before the biogeographic excitement they sparked apropos the discovery of new ungulates (Dung et al., 1993; Giao et al., 1998). His studies of fossil and subfossil murines (late Pliocene–Holocene) from Sulawesi and various Lesser Sunda Islands have supplied another important window to understanding the paleogeography of the region (40, 48, 53, 90, 91).

In the context of assessing rates of extinction and colonization in southeastern Asia, Heaney (1986) pleaded "for research of the most fundamental sort. All of these [biogeographic] studies are predicated on the availability of accurate taxonomic data, and yet the distributions and systematic relations of many, if not most, insular mammals are poorly known, especially in the tropics. Theoretical advances in island biogeography are currently impeded by insufficient empirical data." In effect, Guy's career of thoughtfully crafted systematic essays was undertaken with just those inadequacies foremost in mind. Looking back, the conceptual landscape that existed when Guy initiated his researches on Indo-Australian rodents resembled, in geographic and taxonomic scale, the state of sigmodontine

taxonomy as direly assessed by Ellerman (1941: 327): “But directly Panama is passed, an enormous list of names described for the most part binomially, and in appalling chaos, is reached.” If one rephrased this as “But directly the Malay Peninsula is passed,” Ellerman’s words would capture the systematic confusion that greeted the young Archbold Assistant Curator in 1966.

NEW WORLD MUROIDS (NEOTOMINAE AND SIGMODONTINAE): Among the small mammals collected in the Tushar Mountains of southwestern Utah, Guy was certainly drawn to the variety of native murid rodents (Neotominae) and intrigued by the difficulties in supplying specific determinations. He developed a fondness for woodrats and fleetingly considered *Neotoma* as a research focus, but the move to UMMZ cemented his interest in the systematics of *Peromyscus*. Presented with the opportunity to work with an eminent “peromyscologist,” how could it have happened otherwise? When not hunting for tree squirrels in southern Mexico (1963–1965), Guy managed to set and run traplines, yielding catches of interesting *Peromyscus*. These specimens provided the impetus for important reports on the taxonomy and distribution of a wide array of Neotropical groups, notably those of *P. (Megadontomys) thomasi* (6), *P. (Osgoodomys) banderanus* (10), the *P. (Habromys) lepturus* complex (10, 32), and the *P. mexicanus* group (6, 10, 20). Undoubtedly the most influential of his *Peromyscus* researches was the 1964 collaboration with his major professor (5). “Notes on Classification” expanded upon Hooper’s (1958) application of male reproductive anatomy to evaluate interspecific relationships and formal groupings within the genus, and together they conceived the most substantive reclassification into species groups and subgenera (some newly described; see table 1) since Osgood’s (1909) classic work. The 1964 paper set the stage for Hooper’s (1968) deft review of *Peromyscus* classification, and together they have animated four decades of fruitful and penetrating research, drawing upon a variety of data, analytical tools, and research methodologies (e.g., see many articles cited in Carleton, 1989, and in Musser and Carleton, 2005 [103]). To judge from recent issues of *Journal of Mammalogy*,

the discussion continues (Bradley et al., 2007; Miller and Engstrom, 2008).

You know I have always enjoyed working with *Peromyscus*, especially groups that are so diverse, like the *mexicanus* bunch. Sometimes I feel like chucking *Rattus* and going back to Mexico and Central America. (GGM, in litt., 6 October 1977)

The unrelenting tug to first complete his Indo-Australian projects effectively stifled such passing yearnings for a taxonomic first love.

However, Guy’s research sights did turn once more to New World rodents, this time drawn to the impressive radiation of South American cricetids (Sigmodontinae). Besides presenting the opportunity to work with a valued colleague, the description of a new ichthyomyine species (31) with Al Gardner dovetailed with Guy’s planned revision of the ichthyomyine group, a project earlier initiated by Hooper and continued by Guy when he relocated to the AMNH. Aware that he could never finish a thorough review as his Indo-Australian projects proliferated, Guy returned his ichthyomyine loans in 1977. Another UMMZ student of a successive generation would carry forth investigation of the group and resoundingly close a circle of sorts (Voss, 1988). More taxonomic attention was devoted to another tribe of Sigmodontinae, the Oryzomyini (55, 64, 65, 85, 89, 107). The genesis of these papers stemmed from basic curation of the large oryzomyine holdings in the AMNH and USNM, a task that exposed the glaring inadequacies of species definitions and generic limits as then recognized (notably, Goldman, 1918; Hershkovitz, 1960; Cabrera, 1961; Handley, 1976). The impediments to improve understanding of oryzomyine diversity somewhat paralleled the situation that Guy encountered when first grappling with Indo-Australian murines: an abundance of names used inconsistently for decades and lack of a phylogenetic diagnosis of *Oryzomys* sensu stricto. The deconstruction of the polyphyletic mishmash that so long characterized *Oryzomys* was precipitated by the watershed karyotypic paper of Gardner and Patton (1976), advanced by the studies of Carleton and Musser (1989 [65]) and Musser et al. (1998 [89]), and completed

by the syncretistic investigations of Weksler (2006; Weksler et al., 2006). During the years of reidentifying oryzomyine specimens, Guy predictably called upon those same discriminatory abilities acquired through his early *Peromyscus* examinations, as exemplified by his remarks on researching the *Oligoryzomys* addendum to our *Microryzomys* revision (65).

It has been very rewarding. *Oligoryzomys* turns out to be much like *Peromyscus* and once you adjust the neurons to *Peromyscus* receptors, the species of *Oligoryzomys* jump out at you. I am wondering why others did not see the patterns earlier. (GGM, in litt., 25 January 1989)

MUROID RODENT CLASSIFICATION AND RELATIONSHIPS: Guy's interest in relationships among muroid lineages was whetted by his experience as research assistant to Hooper in the early 1960s. Their morphological survey of "The glans penis in Neotropical cricetines" formed a framework for reassessing relationship, in this case higher levels of kinship among neotomine-peromyscines (Neotominae), South American cricetines (Sigmodontinae), and major assemblages of Muroidea (4). The 1964 study of Hooper and Musser immediately drew sharp criticism from Hershkovitz (1966) for recklessly drawing broad phylogenetic conclusions based on a single organ (Karl Koopman occasionally tweaked Guy by reciting one of Hershkovitz's more colorful lines—namely, that their study was "insistently and unremittingly phallic and typological," a quotation punctuated by Karl's peals of laughter). Notwithstanding Hershkovitz's caustic disapproval, the 1964 report (4) has stimulated vigorous and abundant follow-up research, including taxonomically broad surveys of other organ systems (Carleton, 1973; Voss and Linzey, 1981) and phylogenetic studies using morphological characters (Carleton, 1980; Steppan, 1995). In particular, their diagrams of possible relationships, at the generic and family level (e.g., see fig. 4), were sufficiently explicit to provoke testing by that new information base for phylogenetic inference, DNA sequences (e.g., Engel et al., 1998; Smith and Patton, 1999; Michaux et al., 2001; D'Elia 2003; Bradley et al., 2004; Jansa and Weksler, 2004; Steppan et al., 2004). True, Hooper and Musser did not supply an OTU by

character-state matrix, branch-support statistics, or consensus trees, but their diagrams did depict evolutionary lines of descent and hierarchies of relationship. Viewed against the long sweep of muroid classifications, from Gill (1872) to Musser and Carleton (2005 [103]), the innovative studies of Hooper and Musser (4, 5) served as conceptual stepping stones between the evolutionary taxonomy of Mayr and Simpson and the phylogenetic systematics of Hennig and its various quantitative phyletic applications.

The 1984 review of muroid rodents (54) unfolded from Anderson's appeal to Guy for recommendations of authors who could assume responsibility for orphaned chapters from the first edition (Anderson and Jones, 1967). Although our collaboration was faulted for equivocation over the issue of Cricetidae versus Muridae (Hershkovitz, 1993), a reclassification of Muroidea was never the chapter's purpose (Carleton and Musser, 1984 [54]: 300): "Consequently...our arrangement of the groups as equivalent subfamilies of Muridae reflects not our conviction that this is the preferred nomenclature, but rather our uncertainty of the hierarchical pattern and our desire to focus upon the distinctive and richly varied geographic and biological properties of the groups comprising the Muroidea." Based on extensive specimen examination and literature search, traits used to diagnose muroid groups were evaluated as primitive versus derived character states, amplified, and discussed in terms of the evidence for monophyly, patterns of relationship, and support for past classifications. With regard to these more modest aims, the chapter succeeded and provided the family-group rationale adopted in Guy's subsequent contributions on the superfamily (78, 87).

When Don Wilson became Chair of the American Society of Mammalogists Checklist Committee in 1990, he initiated important format changes for preparation of the next editions of *Mammal Species of the World* (Wilson and Reeder, 1993, 2005). Foremost, it was agreed that individual authors would be recognized for each family, rather than buried among some 150 contributors in a forgotten preface as was done for the first edition (Honacki et al., 1982). This change

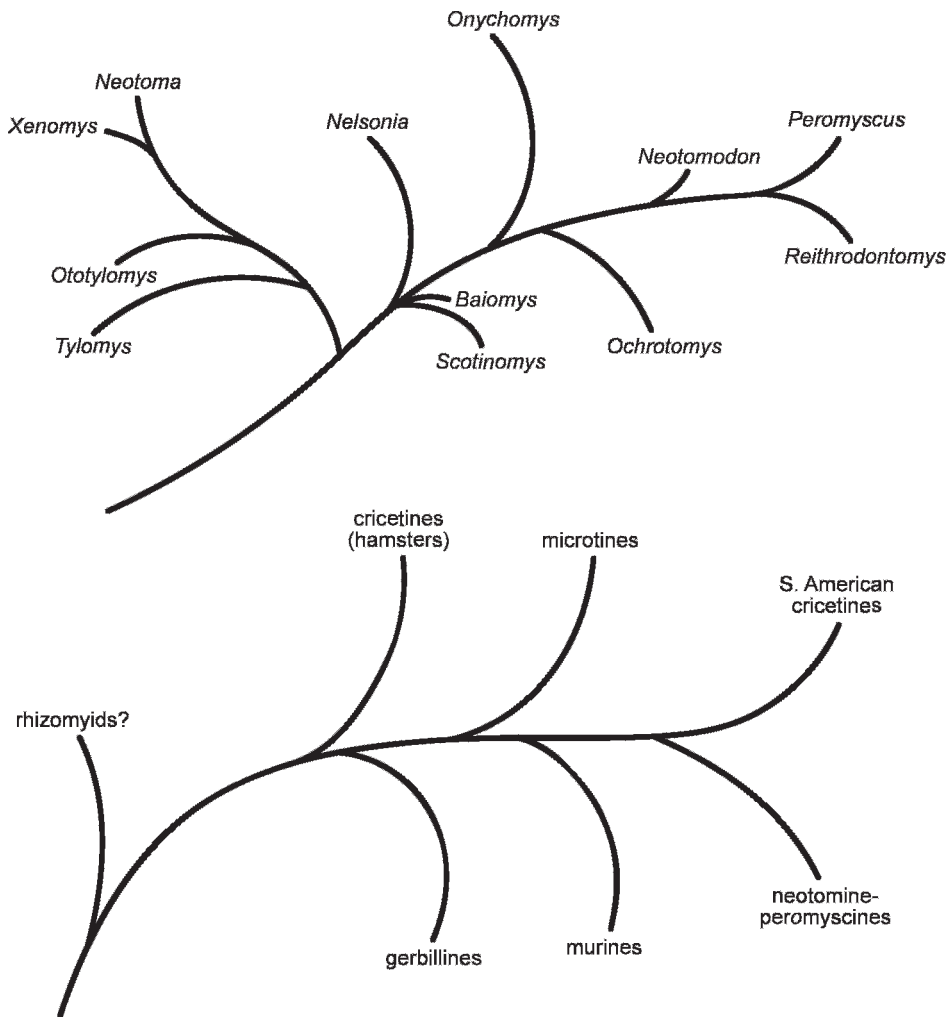


Fig. 4. Two diagrams of possible relationships developed by Hooper and Musser as based on their morphological surveys of the glans penis in various assemblages of muroids. **Top**, hypothesized phyletic affinity among genera of neotomine-peromyscines (Neotominae); **bottom**, hypothesized relationships among several groups (subfamilies) of Muroidea (after Hooper and Musser, 1964[4]: figs. 8 and 9). Such clearly depicted lines of descent precipitated vibrant waves of systematic study using successively more sophisticated methods and information bases for judging relationship and inferring phylogenies.

appealed to Guy's preference for personal accountability for one's ideas and control (more or less) over content and secured his involvement in our next joint ventures with the superfamily (78, 103). In preparing the 1993 chapter and especially its 2005 successor, we were staggered by the voluminous literature that had appeared since Honacki et al. (1982), particularly because many specific and generic accounts were informed not simply by literature compilation but also

through specimen examination, insofar as possible (availability of specimens) or practical (availability of time). For example, the specific and generic accounts of African murines and assorted "archaic" muroids were extensively upgraded, compared with contemporary standards (Misonne, 1974; Honacki et al., 1982; Corbet and Hill, 1991), based on inspection of the large African series in the AMNH and USNM, supplemented by trips to or loans from the

Field Museum of Natural History and Museum of Comparative Zoology, and nomenclaturally grounded on Guy's prior studies of BMNH types. I thought that we had pushed the envelope on the amount of specimen examination in researching the 1993 edition, but museum documentation, as cited within distributions and comments, grew appreciably in the 2005 edition (as appreciated by Solari and Baker, 2007, in their review). As I reviewed Guy's first drafts of various murines, one reason for the difference became apparent: with retirement fast approaching, the third edition of MSW represented the last opportunity to record incidental results accumulated during his many years of specimen examination in European and Asian museums. Whereas the 1984 and 1993 murid contributions were never intended to be formal family-group classifications, the six-family arrangement presented in the 2005 chapter was, and it broke with the recent classificatory habit to place all subfamilies under one huge Family Muridae (e.g. Corbet and Hill, 1991; Musser and Carleton, 1993 [78]; McKenna and Bell, 1997). The 2005 classification drew upon our 1984 synthesis of morphological and paleontological information (54), historically influential arrangements of the superfamily, and the fresh insight to those past classifications supplied by the rapidly proliferating, taxonomically broad molecular investigations (that of Michaux et al., 2001, was pivotal). During the years of composing the 1993 and 2005 contributions, a lively correspondence transpired, as much to bolster one another's sagging enthusiasm to persevere as to exchange ideas.

Back to the list (last night I dreamed of sorting rats and typing entries). (GGM, in litt., 10 October 1991)

The four species of *Petromyscus* are diagnosed by such clear qualitative and quantitative traits, and by geography and habitat, that someone should have sorted them out long ago instead of continuing the same old bad taxonomy in current lists... Back to Murinae—Argh! (GGM, in litt., 22 October 1991)

Spent 3 days or more on *Mus musculus*, what a nightmare, but interesting... I think the Murinae may increase by as much as a third of the past edition, which will probably make [Don] Wilson see red. There is no way I can finish

everything by January 1. (GGM, in litt., 6 December 2001)

Just about to leave for home... Spent most of the day sorting out our [AMNH] *Eothenomys* specimens to be sure my accounts were accurate. (GGM, in litt., 7 February 2002)

I dread the library these days—every new pertinent paper seems a chore. (GGM, in litt., 28 February 2002)

That should clear up Arvicolinae. Let us hope that somebody does not publish anything else between now and when we submit it to Don [Wilson] and DeeAnn [Reeder]. I don't want to see any more vole literature. The next time I see a *Microtus pennsylvanicus* at the campground I will step on it. (GGM, in litt., 18 July 2002)

I guess I am becoming cranky and disinterested in these problems as the last of the checklist nears completion [editors had extended the literature cutoff to 30 June]. I just want to get the damn thing done, but in the right way of course. (GGM, in litt., 24 March 2003)

Although my prejudice is justifiably suspect, I thought that we did it the "right way," or as right as one could achieve for Mammalia's richest clade, from the species to family ranks, with due attribution of the classic and recent literature on extant and extinct muroids, and constrained to the format of a "species checklist."

RESEARCH APPROACH: "Sorting" is a fundamental method mentioned in many of Guy's papers, usually in the context of defining the taxonomic problem, as in: "I have sorted the specimens into five lots, each defined and distinguished from the others by a combination of features... I judge that each lot represents a species" (Musser, 1979 [35]: 388); or, "Sorting and studying museum specimens... has allowed us to document the morphological and distributional limits of 10 Neotropical species" (Musser et al., 1998 [89]: 5). To sort, according to the sense intended here, is to "arrange systematically or according to type, class, etc.; separate and put into different sorts" (Oxford English Dictionary, II 6). The dictionary definition intimates that "types" and "classes" are somehow preexisting, that the activity is little more than a casual shuffling of specimens into already defined groups based on self-evident characteristics. To the contrary, sorting is an

investigational tool in its own right, an objective means to discern natural units of meaningful biological significance, or as the method was aptly characterized by Kohler (2006: 227): “The act of sorting and categorizing is as theoretically creative as any scientific act.” In a storage cabinet in the UMMZ mammal range, Hooper maintained a stack of specimen examination boards, cut from eighth-inch masonite sheets into various rectangular sizes, from ca. 8×12 to 12×20 inches, and spray-painted a flat black to accentuate the osseous white of mammal skulls. Generic identifications of a new collections accession could be reliably ascertained based on features of the skin, but when specific determinations in problematic genera such as *Peromyscus* or *Reithrodontomys* were required, out came the examination boards. Skulls were first aligned by occipitonasal length, dorsal side up, to uncover possible assortment of gender with size and to judge interorbital configuration, zygomatic spread, and rostral proportion in relation to size. Skulls would then be flipped over, ventral side up, to appreciate possible correspondence of molar wear (age) to increasing size and to view conformation of incisive foramina, robustness of molar rows, and relative bullar inflation. Series of specimens of known species from nearby localities might be arrayed on the examination boards, together with the unknowns, and extensive comparisons, dorsal and ventral, would be repeated. This iterative routine, patiently and skillfully applied, was keenly sensitive to appraising subtle variational patterns in cranial size and shape and to disclosing specific gaps in those patterns. Sorting, as practiced by the best of our predecessors, was essentially a forerunner of multivariate factor analysis, minus the digital data, covariance matrices, and variable loading coefficients. Guy was—is—among the best, so it is little wonder that species and genera of the unrevised Indo-Australian murid fauna would, for him, “sort out like nuts and bolts” (“I still hear his [Hooper’s] voice in my ear and feel his presence over my shoulder every time I lay out a string of skulls.”—GGM, in litt., 2 August 1992). With the advent of molecular bar-coding as the first approximation of specific identification, sort-

ing of specimens, like the “-ology” courses, may pass into obscurity.

The extended field sabbatical in Sulawesi (1973–1976), following years of studying specimens in museums, conforms to a recurring theme of Guy’s systematic approach, the interplay of field versus museum perspectives and the reciprocal illumination that each brings to the other. A tropical forest can be bewildering to comprehend, with its infinite variety and immense complexity, but a rodent caught in a trap deliberately placed by the investigator supplies a concrete bit of information—the first hypothesis tested. The requisite next question to ask is what scientific name should be applied to the specimen, an antithetical hypothesis elaborated through recourse to the comparative material and type specimens contained in the world’s museums. Guy variously highlighted the contrapuntal theses of forest and museum in conveying his taxonomic conclusions, such as: “My experiences in the forests of Celebes gave reality to a picture that I had formed while I was working in museums” (Musser, 1977 [33]: 1); or, “Our report represents only a beginning, an understanding in the museum of the first lesson in the forest” (Musser et al., 1998 [89]: 324). The length of Guy’s fieldwork in Sulawesi, three years, also underscores key aspects of his work habits: a drive to get it right and pertinacity to resolve as many taxonomic questions as possible, without regard to the practical time constraints that truncate the research aspirations of most of us. Guy is relentlessly methodical and thorough, which are useful compulsions for good scientific research in general, but his uncompromising adherence to these qualities is exceptional and surpassed by few other mammalogists in my experience. His papers decidedly evince a preference for working at a tangible empirical level and eschew abstract theorizing. He does not dither over species concepts from paper to paper; instead his specific descriptions and amendments are abundantly accompanied by enumeration and illustration of differentiating traits. Primary source materials, vouchered specimens and the distributional data associated with them, form the core of his taxonomic studies and anchor any commentary on biogeography and phylogeny.

The diagnostic traits of a Musser publication—replete historical and biological context, detailed morphological description, exhaustive taxonomic comparison, and elegant illustration—coalesced during Guy's second phase of murine publications (1979–1987). The AMNH has always liberally supported the illustrational needs of its scientists, and Guy just as liberally availed himself of those artistic talents and funds. He has an artful knack for judging the illustrational needs required to tell a paper's story. Assembling the figures, maps, and tables is, for him, just as critical to communicating results of one's study as is composing the text ("I really see the need to have illustrations and a simple diagram of terms. I can picture the tooth in my head but readers will have a tough time."—GGM, in litt., 12 December 1988). Although some may find the description overmuch and the illustration excessive, Guy's reason for this approach is difficult to assail: to consolidate at one time and place the involved nomenclatural histories, empirical specimen-based data scattered amongst the world's museums, and all character information on which his own taxonomic results are based. An overarching motivation has been to spare future systematists the time and effort that he was forced to expend in trying to comprehend the taxonomic pronouncements of his predecessors. He reflected on these points as an aside when reviewing one of my papers.

There are probably some persons who would have you cut the paper in half but that would necessitate removing the analyses of the data and thus would not allow readers to know how you arrived at your conclusions.... I have faced this problem from the time I began to write about rats and mice of the Far East. Faced with a mountain of dogmatic literature based on opinions and with no hard data, I have had to carefully document every damn change in the taxonomy of murids. The process results in longer papers that have to be put into context.... Readers know what questions I am asking and why they are important and can see the data for themselves and the reasons I formed my conclusions. (GGM, in litt., 27 May 1978)

His words may sound like banal truisms measured by today's standards of systematic research (though not always the practice).

However, the quotation must be understood from the perspective of a new Archbold Assistant Curator, grappling with a daunting body of systematic literature set forth by luminaries such as Thomas, Miller, and Ellerman, and judged against the meagre documentation that accompanied the far-reaching biogeographic and phylogenetic implications of their specific and generic taxonomies.

A MUSEUM CONSCIENCE THAT JOSEPH GRINNELL WOULD APPROVE

CHAIRMAN AND COLLECTION DUTIES: When Guy joined the AMNH Department of Mammalogy in 1966, his responsibility was mostly confined to research, as departmental roles were delineated by Van Gelder. Promotions to Archbold Associate Curator (1970) and Archbold Curator (1976) followed mainly in recognition of his research output and extensive fieldwork. Guy was early on immersed in collections curation, although such activities were then related to his immediate research projects—foremost Indo-Australian murids of the Archbold collections, to a lesser degree the extensive holdings of South American cricetids acquired by Anthony and Tate in the early 1900s. Inside-the-case experiences with the latter gave Guy a sobering glimpse of the curatorial needs of the department as a whole.

Well, this gives you some idea of the curatorial headache we have with the South American cricetines [Sigmodontinae]. A lot of real good stuff, but much has never been identified—literally whole cabinets full. And the fluid-preserved material is another whole mess. (GGM, in litt., 1 November 1972)

Guy became chairman of the department in 1981, following the terms of Van Gelder (1959–1974) and Anderson (1975–1981), and launched a long (1981–1993), concerted program to upgrade the physical storage and curatorial order of the entire mammal holdings, which had been sadly neglected for decades. Guy was successful in securing several NSF collection support grants (1981–1990), which allowed purchase of new cases for decompression of overcrowded cases and wholesale reorganization of large, heavily

utilized orders, such as marsupials, carnivores, and primates. The dust-covered, unidentified jars of fluid specimens were removed from the back stairwells and arranged taxonomically within a new alcohol range that featured compactor shelving. Ungulate skeletons scattered throughout attics and other wings of the museum were consolidated and recurated to become again accessible to visitors. Storage and arrangement of large, tanned skins were improved. Attention was also devoted to upgrading the physical plant, including plastering and painting of the ranges and offices and the installation of air conditioners to exclude the dust and soot that permeated the collections when windows were opened during the summer months. Guy's involvement in these improvements included supervisory oversight as well as much hands-on curation, verifying identifications so that groups could be properly rearranged into new trays and cases. At the halfway point of his chairmanship, Guy assessed the status of the collections as follows.

I am trying to finish departmental work just in case [the Director ends my appointment as Chair]. This means working on our archives (library, records, and other items), curating the carnivores and marsupials, and other odd jobs. I am getting a little tired of shifting cases and scrounging for this and that, and recurating; six years of this has worn all of us out but there is more to be done. And I thought we could finish everything in two years or so. Turns out none of us had any idea of the magnitude of the lousy shape parts of the collection were in. There are still years worth of minor recuration but at least the big tasks will be done. (GGM, in litt., 12 October 1987)

The curatorial achievements owed much to a dedicated support staff, in particular Helmut Sommer, who long worked (1959–1997) as technician in the Mammalogy Department. Rescued from the museum's defunct taxidermic unit, Helmut was delighted and inspired to see the multifaceted attention being devoted to the mammal collections after Guy became chairman. The two developed an effective working bond and collaborated to correct specimen identifications uncovered during Helmut's curation of marsupials (72). Guy considered him to be a museum-based member of the Archbold

Sulawesi Expedition and acknowledged his reliance on Helmut's wide-ranging capabilities in naming a new genus of Sulawesi rodent (*Sommeromys* Musser and Durden, 2002). Another focus of recuration was the type collection, along with revision of the type catalog, which projects Guy entrusted to Marie Lawrence. The two amended a taxonomic oversight discovered during Marie's curation (66), and after her unexpected death in 1992, Guy assumed the final editing chores that brought her first draft of the type catalog to publishable form (Lawrence, 1993). Any long-term user of the AMNH mammal collections readily appreciates the many and vast improvements he effected during his tenure as chairman.

Hooper was a student of Grinnell and reverently absorbed his professor's short commentary (1922) on "The Museum Conscience." Hooper observed Grinnell's dual essentials of a scientific museum—order and accuracy—in his assiduous care and curation of the UMMZ mammal collection, standards of excellence that were surely impressed upon Guy during his graduate years at Michigan. In closing his essay, Grinnell (1922: 63) remarked that "My visits to the larger museums have left me with the unpleasant and very distinct conviction that a large portion of the vertebrate collections in this country . . . are in far from satisfactory condition with respect to the matters here emphasized." Reading between the lines, it seems probable that his remarks on "larger museums" were directed, in part, at the AMNH and USNM. That a second-generation, academic descendent of Grinnell would begin to redress unsatisfactory conditions of the AMNH mammal collection was somehow fitting.

In spite of the substantial progress in collection improvement, Guy considered that his most important accomplishment as chair was to give Karl Koopman free rein to concentrate solely on his bat research. Under previous chairs, Karl was the curatorial specialist of Chiroptera, which, in addition to research, involved such tasks as pulling specimens for loans and answering information requests. Among the curators in the Mammalogy Department when Guy arrived, he and Karl developed a special friendship although they seldom collaborated on scien-

tific matters (49, 83). Guy twice acknowledged Karl's intellectual breadth and contributions to systematic biology in describing new murine species (*Chiropodomys karlkoopmani* Musser 1979; *Rattus koopmani* Musser and Holden 1991) and regularly sought his input as reviewer of presubmission drafts. When Karl started to mutter about the unseemly increase of murid genera and species, Guy would thereafter present a manuscript along with a tray of rat skins and skulls so that Karl could verify the traits mentioned in diagnoses and comparisons. The muttering stopped.

OTHER PROFESSIONAL ACTIVITIES AND HONORS: Guy has had little formal involvement in academia and the matriculation of future mammalogists, partly given his position in an independent museum and partly due to his conviction that research and curation in a huge collection are by themselves fulltime endeavors. Nevertheless, Guy has influenced many graduate students through his curatorial efforts to make the AMNH mammal collections accessible for their research, sponsorship of short-term visitor awards, and encouragement of collection internships under which graduate students could simultaneously conduct their own specimen examinations and recurate a portion of the mammal collection. He regularly participated in the Susan Greenwall Foundation, administered by the AMNH, and involved graduate students as collaborators in his own research projects (52, 56, 59, 61). Guy has shown especial willingness to review the manuscripts of graduate students or younger colleagues and has volunteered detailed and thoughtful, sometimes hard-nosed but always constructive, advice on how to write a systematic paper, frame a species description, or develop a taxonomic revision ("You need more illustrations!" was a familiar urging). In this informal capacity, his involvement in the education of systematic mammalogists has been generous and substantial, benefiting the professional development of most contributors to this volume among many others.

Guy's professional activities in the American Society of Mammalogists (ASM) included turns as editor for General Notes (1971) and editor for Feature Articles (1972–1973) for the society's journal and membership on

various standing committees (Bibliography Committee, 1978–1980, which compiled the now-discontinued Recent Literature sections of the journal; Nomenclature Committee, 1978–1982; and the Checklist Committee, 1983–present, essentially responsible for producing revised editions of *Mammal Species of the World*). Guy is by nature a private individual, tends to shun gregarious settings like scientific meetings, and is uninterested in the prestige of holding societal offices. Given the usual constraints of budgets and time, he has preferred writing papers over giving talks, visiting museums over attending meetings. Notwithstanding his infrequent attendance at annual meetings, the ASM has bestowed two of its highest honors upon Guy. In 1992, he received the C. Hart Merriam Award, established primarily to give recognition to mammalogists with a stellar record in scientific research and singling out "his seminal contributions to understanding the systematics of murid rodents and because he is internationally recognized as an outstanding systematist." In 2004, two years into retirement, he was elected to honorary membership in the ASM, an esteemed honor bequeathed for a distinguished record of achievement in the science of mammalogy.

Several mammalian species have been named to honor Guy, including a shrew (*Crocidura musseri* Ruedi, 1995) and, naturally, several species of muroid rodents (*Microhydromys musseri* Flannery, 1989; *Archboldomys musseri* Rickart, Heaney, Tabaranza, and Balete, 1998; *Neacomys musseri* Patton, da Silva, and Malcolm, 2000; *Coryphomys musseri* Aplin and Helgen, in press). A surprising number of invertebrate patronyms have been named, reflecting Guy's encouragement of such researchers to use the Sulawesi collections and glean parasites (fleas—*Neopsylla musseri* Beaucournu and Durden 1999; a suckling louse—*Hoplopleura musseri* Durden 1990; a fur mite—*Listrophoroides musseri* Bochkov and O'Connor 2005; and a nematode—*Heligmonoides musseri* Hasegawa and Syafruddin 1994); the collegiality formed with one of those specialists, Lance A. Durden, led to their fruitful collaborations on suckling lice of Murinae (70, 73, 80, 81, 93). The present volume

appropriately continues this honorific mode: *Crocidura guy* Jenkins, Lunde, and Moncrieff; *Reithrodontomys musseri* Gardner and Carleton; and *Musseromys* Heaney, Balete, Rickart, Veluz, and Jansa.

CURATOR EMERITUS (2002–PRESENT)

Adjusting to retirement away from the museum has taken more time than anticipated. There are still days when I get the knee-jerk reaction to commute into the museum. On the other hand, once I left the building...I felt liberated. However, the pressure and stress to keep working on research projects is greater than it was during my employment. It was certainly time to leave and I have no regrets. (GGM, in litt., 11 December 2002)

Guy retired from the AMNH on 11 September 2002, and he, his spouse Mary Ellen (Holden, herself a systematic mammalogist and occasional collaborator), and family of three moved to South Carolina in November, to be nearer her family and the children nearer to their grandparents. Although formally retired, he has managed a very active research program (fig. 1, appendix 1), in spite of the isolation from a world-class scientific library and immense museum collection. At the time of his retirement, he was mired in the composition of chapters for *Mammal Species of the World* (101–103), which were not completed until he had relocated to South Carolina. Thanks to the internet, he has maintained collaborative projects and continued his studies on Sulawesi murines (100, 104, 106, 108; and others in preparation), Sulawesi squirrels (in preparation, with L.A. Durden), and oryzomyines (107). In view of Guy's ongoing projects, this scientific biography is necessarily incomplete and must end abruptly.

Yesterday I abandoned SCIENCE and FAMILY and escaped to the tidal creeks to catch red drum and watch kingfishers dive, white ibis stand nearby, and little blue herons mess around. Since I am supposed to be retired, I can act irresponsible sometimes. (GGM, in litt., 19 November 2003)

The participants in this festschrift, and undoubtedly others who have known Guy

personally or professionally through his research, will happily excuse such occasional flights of irresponsibility and heartily wish him more of them. His internal sense of responsibility may not be so approving.

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Alfred L. Gardner, Lawrence R. Heaney, Darrin P. Lunde, and Robert S. Voss critically reviewed the manuscript and offered their perspectives on Guy and his research. I especially appreciate the reflections of Darrin Lunde (AMNH), who accompanied Guy during fieldwork in Vietnam and who permitted reproduction of the photograph in figure 2.

I count myself privileged to have coauthored several publications with Guy, and in a sense, this biographical sketch is yet another collaboration as I have attempted to interweave a first-person perspective throughout the text. For this former UMMZ student, Guy's encouragement to publish my results and timely advice offered along the way proved pivotal in orienting my mammalogical career. Over the years, he has functioned as a senior graduate student counselor, à la M. Raymond Lee, an unofficial adjunct committee member, professional colleague, and friend.

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APPENDIX 1

SCIENTIFIC PUBLICATIONS OF GUY G. MUSSER

(Arranged by year to accentuate the pace and evolving research focus of his publications; this data formed the basis for the graphical summary in fig. 1. Numbers at the left-hand margin correspond to those used in the text to reference Musser's publications.)

1. Edmunds, G.F., and G.G. Musser. 1960. The mayfly fauna of Green River in the Flaming Gorge Reservoir Basin, Wyoming and Utah. In Angus Woodbury et al. (eds.), "Ecological studies of the flora and fauna of Flaming Gorge Reservoir Basin, Utah and Wyoming." University of Utah Anthropology papers, No. 48, Upper Colorado Series, No. 3: 125–131.
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