Mammalian Reservoirs of Arenaviruses

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1 Introduction

Arenaviruses are negative-stranded RNA viruses that have been isolated from several species of mammals in various parts of the world. With two exceptions, these viruses have all been isolated from rodents of the family Muridae – sensu Musser and Carleton (1993). Tacaribe virus was originally isolated from fruit-eating bats of the genus *Artibeus*, while Sabiá virus has no known wild reservoir. Arenavirus infections in their rodent reservoirs are characterized by persistent shedding of infectious virus in the urine (Johnson 1970).

The history and classification of the virus species are treated elsewhere in this volume. Our purpose in this chapter is to present updated information on the identity of the various mammalian hosts of arenaviruses, reviewing aspects of their ecology, distribution, taxonomy, and systematics. In addition, we propose minimum standards we feel need to be considered when analyzing or reporting new species of viruses and their mammal hosts.

Because two serological groups of arenaviruses are recognized (Peters 1997), this chapter on their mammal hosts is divided accordingly.

1.1 Zoonoses and Reservoir Species

Zoonoses, diseases transmitted between animals and humans, are of great public health importance. Although most occur only sporadically, some have been responsible for important epidemics. Most zoonotic diseases are derived from natural hosts that are any of a number of species or groups of mammals. Ashford (1997) suggested that four mammal orders (Artiodactyla, Carnivora, Primates, and Rodentia) are the most significant sources for zoonotic diseases, although it is becoming evident that other groups (e.g., Chiroptera, the bats) are also important (Daszak et al. 2000).

Considerable contention currently surrounds the "proper way" of referring to the mammal host species from which a virus has been isolated; herein, we follow Benenson's recommendations and refer to these species as "reservoirs" (Benenson 1995). A reservoir of infection is best identified as an ecological system in which the infectious agent survives indefinitely. Where a vertebrate host or group of hosts is essential to such a system, these are termed reservoir host(s) (Ashford 1997).

Mammal reservoir species and their viruses are nowadays the subject of intense study and scrutiny. This is not so much the result of the realization that certain diseases are "coming back", as it is that new diseases and disease-causing viruses are being discovered on a regular basis. It is therefore our contention that the appraisal of the mammal reservoirs' systematics and taxonomy is in a difficult position in this regard as several – if not most – of the rodent genera known to carry arenaviruses have yet to be revised critically. The precise identities of many hosts are therefore uncertain, with dire consequences for epidemiology or any prospects of disease control.

2 Mammal Hosts of Arenaviruses

Two serological groups of arenaviruses are recognized. This division is also present in their mammal reservoir species as most Old World arenaviruses have been recovered from Old World murid rodents. In contrast, New World arenaviruses (i.e., the Tacaribe complex) are found primarily in rodents of the New World.

2.1 Old World Arenaviruses

The known diversity of arenaviruses in the Old World is about one-third of that of the New World forms. The forms included in this group are: Lymphocytic choriomeningitis (LCM), Lassa (LAS), Mopeia (MOP), Mobala (MOB), and Ippy (IPP) viruses.

2.1.1 Lassa Fever Virus

The best known of the African arenaviruses is Lassa fever virus, having been described in a series of articles in *The American Journal of Tropical Medicine and Hygiene* in 1970 (Buckley and Casals 1970; Frame et al. 1970; Leifer et al. 1970; Speir et al. 1970; Troup et al. 1970). It was 4 years later before a mammalian reservoir species (*Mastomys natalensis*) was associated with the disease (Monath et al. 1974). The disease currently affects 300,000–500,000 cases annually, causing approximately 5,000 deaths per annum.

The virus and the disease it causes have thus been known for over 30 years; however, the taxonomy and systematics of the host remain problematic. Indeed, the systematic status of the rodent genus *Mastomys* may be succinctly summarized as confused and in a state of flux. Even the intrafamilial taxonomic status of *Mastomys* may be in doubt: traditionally classified as a genus in the subfamily Murinae of the rodent family Muridae, recent work by Catzeflis, Chevret, and collaborators (Catzeflis and Denys 1992; Catzeflis et al. 1987, 1992; Chevret and Hänni 1994; Chevret et al. 1993a,b, 1994; Dubois et al. 1999; Furano et al. 1994; Hänni et al. 1995; Huchon et al. 1999; Usdin et al. 1995) has suggested that *Mastomys*, along with most African murids, may belong in a unique African subfamily of rodents allied to Murinae (see also Graur 1994).

Mastomys, described as a genus in 1915 by Oldfield Thomas, is currently thought to be constituted by eight species (Musser and Carleton 1993): *M. angolensis* (Angola and southern Zaire), *M. coucha* (South Africa, southern and western Zimbabwe, and central Namibia), *M. erythroleucus* (a disjunct population in Morocco, and sub-Saharan Africa to Zaire), *M. hildebrandtii* (sub-Saharan Africa to Zaire; this name antedates *huberti*, hence references to *huberti* are, more properly, references to a species which should be called *hildebrandtii*), *M. natalensis* (South Africa, Zimbabwe, central and northeastern Namibia, east-central Tanzania, and a disjunct population in Senegal), *M. pernanus* (southwestern Kenya,

northwestern Tanzania, and Rwanda), *M. shortridgei* (Okavango delta region between Botswana and Namibia), and *M. verheyeni* (Nigeria and Cameroun – and likely Chad – in the immediate vicinity of southern Lake Chad).

Lassa fever virus has been associated in the literature with the multimammate mouse, *M. natalensis* (Monath et al. 1974). Although generally found in fields, the species reputedly is broadly distributed in all habitats from South Africa to sub-Saharan Africa. However, taxonomic problems exist associated with the assignation of LAS to *M. natalensis*. In fact, *M. natalensis* does not occur in the two disjunct hotbeds of Lassa fever in West Africa: Nigeria on the one hand, and Guinea, Sierra Leone, and Liberia on the other. The species potentially occurs in Senegal, although the taxonomic status of the Senegal population (and other populations) should be carefully scrutinized (Wulff et al. 1977; Gordon 1978; Green et al. 1978; Granjon et al. 1996); Granjon et al. (1996) hypothesized that the Sénégal and South African populations are conspecific and part of a single, continuous, panmictic population, but this hypothesis requires additional data and specimens from intervening areas in order to be rigorously tested. On the strength of these facts, namely absence from the Lassa fever zone of endemism, Peters (1997) pointed out that it was more likely that the actual hosts of LAS were either *M. huberti* or *M. erythroleucus*; to our knowledge, there is no instance of a host with multiple arenaviruses, nor of multiple hosts with a single arenavirus (other than due to spillover, but see below).

Assignation of LAS to *M. huberti* and/or *M. erythroleucus* carries its own caveats, however. Indeed, like *M. natalensis*, these are more likely superspecies complexes, and constituted by a number of cryptic species. In fact, all *M. "huberti"* were, until recently, reported to have a diploid chromosome number ($2n$) of 32. However, Viegas-Péquignot et al. (1983) and Baskevich and Orlov (1993) reported on additional cytotypes, all $2n = 32$ but with radically differing fundamental numbers, which could not be considered conspecific with *M. huberti*. Thus, there exist (at least) four distinct $2n = 32$ cytotypes within *M. huberti*, no combinations of which should give rise to fertile F_1 hybrids given the nature of the chromosomal rearrangements between each possible pair. By the classical definition of species, failure to interbreed is *prima facie* evidence of non-conspecificity. These $2n = 32$ cytotypes, which may be considered full species, are distributed in Sénégal, Central African Republic, and the Central Ethiopian Rift Valley. Lyons et al. [(1977; "1978") – NB: Lyons et al. "1978" was seen cited in Gordon 1978 as "in press" in the journal *Heredity*; we have been unable to ascertain the existence of any such article in *Heredity* or any other journal; Lyons et al. 1977 mention that a "full report of the geographic distribution of the two species will appear at a later date (Lyons et al., in preparation)". It is possible that a manuscript circulated among certain individuals but was never published; we retain the citation herein for completeness] reported on additional chromosomal forms from Zimbabwe in what they considered *M. natalensis*, which they designate "species A" – $2n = 32$ – and "species B" – $2n = 36$. Based on chromosomal investigations undertaken at or near the type localities for some of these taxa (Green et al. 1978), it may be hypothesized that species A refers to a true *M. natalensis* type (as all *M. natalensis* are

reputed to have $2n = 32$; Matthey 1965; Viegas-Pequignot et al. 1983, 1987; Baskevich and Orlov 1993), while species B is assignable to *M. coucha*. To further complicate matters, *M. huberti* and *M. erythroleucus* have almost interchangeable ecologies, depending on geographic location: in West Africa, *M. huberti* is more aggressive, intra- and peridomestic, while in Central Africa, it is *M. erythroleucus* which takes over this role, relegating *M. huberti* to agricultural fields and forest edges.

The question of the taxonomic identity of the host of this disease, affecting 300,000–500,000 individuals annually, might have been satisfactorily resolved had the specimens upon which the Monath et al. (1974) report is based been properly archived. However, they were not: Monath (T.P. Monath, personal communication) indicated that they were identified by Setzer (fourth author of the Monath et al. article), then transferred to Colorado State University for histological analyses (DeMartini et al. 1975). Subsequent to the latter publication, the carcasses used as a basis for the DeMartini et al. article were discarded. The track of the remaining specimens is lost: M.D. Carleton, current curator of mammals at the Smithsonian, reported (M.D. Carleton, personal communication) that there are no *Mastomys* from the original collection at the US National Museum, and only four from Panguma, collected in 1981 by C.J. Krebs; the original Monath collection consisted of 109 *Mastomys* (of a total of 475 rodents). Had the specimens been available for examination, their identity within the current – or any subsequent – taxonomic framework for *Mastomys* could have been determined. As Mills and Childs (1998) stated, the imprecise taxonomy of the *Mastomys* species complex will result in "years before the geographic distributions of each species can be mapped and used to interpret the restricted distribution of Lassa fever".

2.1.2 Mobala

This arenavirus is relatively new, having been described in 1983 by Gonzalez et al. The host was reported by the authors as *Praomys* sp., which has since been restricted to *P. jacksoni* by Peters (1997). The rodents were identified based on data in the literature, most notably Rosevear's (1969) classic *Rodents of West Africa*, as well as data from Petter (1977) and Hubert et al. (1983).

Praomys, described by Oldfield Thomas in 1915, is another very problematic genus like *Mastomys*. *Praomys* is hypothesized to be closely allied to *Mastomys*, which latter genus has at various times been included within *Praomys* (e.g., Davis 1965; Misonne 1974). In addition, at least one species formerly included at various times in *Praomys* and *Myomys* (*P. albipes*), has been excised from *Praomys* and placed in the Ethiopian endemic genus *Stenocephalemys* (Lavrachenko et al. 1999; these authors' data suggest that species limits in *Stenocephalemys* are problematic). *P. jacksoni* has variously been considered conspecific with *P. tullbergi*; however, as reviewed by Van der Straeten and Dieterlen (1987), *P. jacksoni* was excised from *P. tullbergi*. Although antibodies to Mobala have been found in humans as well as nonhuman mammals in the Central African Republic (Georges et al. 1985), there does not appear to be any human disease caused by this virus.

The problems associated with the taxonomy of *Praomys* are as monumental as those described in the foregoing section on *Mastomys*; Musser and Carleton (1993: p 642) summarize the situation as follows: "Not only do the contents of *Praomys* require careful systematic revision, but its phylogenetic relationships relative to *Mastomys*, *Myomys*, and *Hylomyscus* also needs resolution through revisionary studies". We further note that *P. jacksoni*, like most of the *Mastomys* species and, indeed, many of the remaining species of *Praomys*, likely is a composite that only will be defined through careful studies including morphology, karyology, and molecular data.

2.1.3 Ippy

Ippy virus first was described by Digoutte in 1970. However, it was not until 1985 that Swanepoel et al. identified Ippy as a virus in the Lassa fever group, closely followed by Meunier et al. (1985) who further cemented the association of Ippy as a LCM–LAS group virus. The host species was listed by Digoutte (1970) as *Arvicanthis* sp. from the Central African Republic. However, the Institut Pasteur CRORA database lists as additional hosts the African murid rodents *Lemniscomys striatus*, *Praomys* sp., and *Mastomys* sp. Furthermore, of the 22 isolates (all from the Central African Republic), 16 are from *Praomys*. Thus, although the initial isolate was from *Arvicanthis*, the primary host is more likely *Praomys*. Only Bishop (1990) lists *Praomys* as a potential host, citing unpublished data from Digoutte (likely data similar to that presently available in the Pasteur Institute's CRORA database). Other reviewers of arenaviruses (McCormick 1990: p 1246; Peters 1997: p 974) all restrict Ippy to *Arvicanthis*. Data derived from microcompliment fixation (as well as Digoutte, personal communication) are supportive of their being at least two distinct strains of Ippy virus which are not highly cross-reactive; it is possible that one of these is in *Arvicanthis*, while the other is from *Praomys*. Having discussed *Praomys* above (Mobala), we will restrict ourselves herein to *Arvicanthis*.

As currently understood (Musser and Carleton 1993), *Arvicanthis* is comprised of five species, only one of which, *A. niloticus*, is distributed throughout the Central African Republic; however, there have been at least 44 named species in the genus (Capanna et al. 1996). In their review of murids, Musser and Carleton (1993) further pointed out that more than one species likely is included in what is construed as *A. niloticus*. Ample chromosomal data exist in support of this hypothesis: for example, at least four distinct diploid numbers, with seven fundamental numbers (seven distinct karyotypes) have been documented within *A. niloticus*, some of which undoubtedly form panmictic populations, but others of which definitely cannot interbreed and therefore constitute distinct species (Capanna et al. 1996; Capanna and Civitelli 1988; Civitelli et al. 1995; Granjon et al. 1992; Matthey 1965; Viegas-Pequignot et al. 1983; Volobouev et al. 1988).

Molecular data derived from sequences of the mitochondrial cytochrome *b* gene (Ducroz et al. 1998) support the more extreme view of *Arvicanthis* as a

more speciose genus than currently understood, with perhaps an additional 11 undescribed species. Their data suggest that the status *A. niloticus* as a single, unique species is not concordant with biological reality. We reanalyzed their sequence data in order to assess branch lengths among taxa. The results of our somewhat cursory analyses are not fully concordant with theirs, but we feel that the *A. niloticus* they sampled is best divided into at least three species: one sampled in Sénégal, one sampled in Niger, and one sampled in Egypt; the latter would be the sister species to *A. dembeensis*, which likely is a valid species, Musser and Carlton (1993) and Ducroz et al. (1998) notwithstanding: Musser and Carleton (1993) relegate *A. dembeensis* to subspecific status within *A. niloticus*, albeit restricted to Ethiopia. Ducroz et al. (1998) consider that the genetic divergence between *A. dembeensis* and *A. niloticus* does not warrant recognition of the former, however, that genetic divergence is equal to that between other sister species in *Arvicanthis*, suggesting that *A. dembeensis* is in fact a valid, species-level taxon. At very least, further studies are indicated to definitively clarify this question.

2.1.4 Mopeia

Two strains of Mopeia have been described: Mopeia Mozambique (Wulff et al. 1977) and Mopeia Zimbabwe (Johnson et al. 1981). Although antibodies have been detected in humans (K.M. Johnson, unpublished data), there is no evidence of pathogenicity to humans. As to reservoirs of MOP, Wulff et al. (1977) merely present *M. natalensis* as the mammal host species for the Mozambique strain. Johnson et al. (1981) brought captured and field-identified *M. natalensis* specimens back to the laboratory where further identifications (and confirmation) were undertaken based on electrophoresis of hemoglobin proteins after Green et al. (1978). Swanepoel (2001) reported that the Wulff et al. (1977) specimens were supplied in 1972 by a "long since retired" member of the South African National Institute for Virology; no tissues for these animals can currently be found, although sera may exist (Swanepoel 2001). As for the animals reported in Johnson et al. (1981), these were supplied by Paul Taylor of the Zimbabwe Department of Health Blair Laboratory. Swanepoel (2001) indicates that the specimens upon which the research of Johnson et al. (1981) was based may be at the National Museum in Harare, Zimbabwe. Our efforts to locate them there have come to naught.

We have already stressed above (see Sect. 2.1.1) the uncertainties regarding the taxonomic identifications of animals in the genus *Mastomys*, most specifically *M. natalensis*. In the case of specimens hosting Mopeia, some were identified using biochemical techniques; however, even these identifications were undertaken without the benefit of comparisons to type material, that is to say, the "name-bearing" specimen upon which the name *M. natalensis* is based. Accordingly, even these identifications remain suspect until a thorough review of *Mastomys* and *Praomys* is undertaken, leading to a clear understanding of species boundaries in this complex group.

2.1.5 Lymphocytic Choriomeningitis

Identification of lymphocytic choriomeningitis as a viral disease (LCM) was first done by Charles Armstrong and R.D. Lillie, of the US Public Health Service, in 1934 and further detailed by Armstrong and Dickens in 1935. The disease as such had previously been thoroughly described by Arvid Wallgren in 1924. Wallgren (1924) noted, however, that cases likely referable to LCM were described in the literature as early as 1910, but none prior to 1906 (the nature of his method of citing precludes our investigation of the 1910 report). Apparently, identification of the disease as such, albeit not its viral association, was due to epidemics in France (1910–1913) and Scandinavia (1920–1923). Association of LCM with a mammal reservoir was reported soon thereafter: Traub (1935, 1936a,b) reported that LCM circulated in white laboratory mice. Armstrong and Sweet (1939) first incriminated wild (i.e., peridomestic) *Mus musculus* as the reservoir species of LCM.

Although the genus *Mus* itself contains numerous species of nebulous validity, *Mus musculus* had previously been thought to be the one Old World host of an arenavirus wherein little if any taxonomic uncertainty exists. However, there in fact do remain substantive gaps in our knowledge of these organisms (Boursot et al. 1993) which may have a vital impact on the epidemiology of LCM: over 150 scientific names have been used for house mice (133 listed in Berry and Bronson 1992; more complete listing in Appendix I of Marshall 1998). The current scientific name of the house mouse, *Mus musculus*, is ascribable to Linnaeus (1758). As with many of the species Linnaeus named, there is no holotype (vide Marshall 1977), that is to say, no specimen is available for examination and comparison as a basis for the nomenclature and taxonomy of *Mus musculus*. Although the genus *Mus* is clearly Asian in origin, *M. musculus* occurs worldwide, with a range habitually human abetted. The name *M. musculus*, as described by Linnaeus, refers to the taxon currently found in Sweden: *M. m. musculus*. Other former subspecies within *M. musculus* have been excised over time from that taxon, as the biological reality of their isolation has led to their recognition as a species distinct from *M. musculus*. Accordingly, our most recent understanding of the house mouse (Boursot et al. 1993; Marshall 1998) clearly indicates that the house mouse is a complex composed of at least three distinct valid species: *M. castaneus*, *M. domesticus*, and *M. musculus*.

The nominate subspecies of *M. musculus*, *Mus m. musculus*, ranges from far east Asia (Chukotskiy Peninsula) throughout Asia north of the Himalayas and Caucasus, to Central Europe, where it meets and hybridizes along a narrow band (30–40km) with *M. domesticus* (Boursot et al. 1993), the other potential host of LCM. *Mus domesticus* occurs in Western Europe, Africa, and the Middle East, including the Arabian Peninsula, to a band between the Persian Gulf and the Caspian Sea. The Caucasus forms the boundary between *M. musculus* and *M. domesticus* in this region, thereby affording little opportunity for hybridization. A broader zone of overlap, with some hybridization, exists in Asia between *M. musculus* and *M. castaneus*. This region of overlap and potential hybridization extends from the Sea of Okhotsk (Udskaya Guba, in Khabarovsk, Russia) to

approximately the Tibetan Plateau (near the type locality for *M. m. gansuensis*). Nominally, *M. m. musculus* only occurs from the zone of hybridization in Central Europe (Denmark, then Mecklenburger Bucht in NE Germany, south along the Elbe and Danube, through eastern Austria, central Slovenia, interior Croatia and Bosnia-Herzegovina, and through Yugoslavia perhaps as far south as Macedonia to Bulgaria and the Black Sea; figured in Boursot et al. 1993 and Marshall 1998) to the Ural Mountains in the East. East of the Urals, *M. m. wagneri* is found.

Given that the predominant species in Western Europe is *M. domesticus*, we suspect that the host of LCM is, therefore, *M. domesticus*. Several lines of evidence point to that trend. In terms of indirect inference, most human immigration into North America historically has been from Western Europe. One might assume, therefore, that ships leaving western European ports would be occupied with the locally predominant species of mouse, that is: *M. domesticus*.

In addition, most (but not all) of the stocks of laboratory mice apparently are derived from *M. domesticus* (Boursot et al. 1993); it is possible, however, that these laboratory strains may all have been derived from *M. domesticus*, but from distinct geographic regions within the range of the species, hence from distinct demes, or gene pools, constituting the species. Given that no tests have been carried out on the susceptibility and transmission dynamics of LCM in wild *M. domesticus*, and that *Mus* species are notoriously variable at the molecular and morphological levels, different laboratory mouse strains with different origins even within a single species (be it *M. domesticus* or *M. musculus*) may very well display differing degrees of resistance, infectivity, and other host characteristics to LCM. The initial assessments by Armstrong and Lillie (1934) and Traub (1935) of the presence of a virus during some epidemics were undertaken post hoc the epidemic in laboratory strains of *Mus* species. None of these mouse specimens have been archived for subsequent identification, but all were susceptible to varying degrees. No figures are available in Armstrong and Lillie (1934); however, Traub (1935) reported a 13%–40% fatality rate in laboratory mice (intracerebral inoculation), while Armstrong and Sweet (1939) reported a 100% fatality rate in mice also i.c. inoculated from a single infected mouse.

We point out as a cautionary note that certain populations of house mouse in the USA may indeed have a more likely origin in *M. musculus*, specifically *M. m. wagneri*. The tumbleweed, or Russian thistle (*Salsola* sp., generally *S. tragus* or *S. ibirica* or *S. kali*) has its origin in the Russian steppes east of the Urals. The invasion of *Salsola* is said to have been due to contaminated flax seeds brought to the USA (South Dakota) by Mennonite farmers (Tellman 1997), as well as in grain shipments from Russia. Given the current range of *Salsola* in Canada, México, and the USA, it would not be implausible to hypothesize that many populations of *Mus* in central and southwestern USA are derived not from *M. domesticus* (likely present in either coast), but rather from *M. m. wagneri* imported along with Russian grain shipments. Furthermore (and most critically), the epidemic of 1920–1923 took place in Scandinavia, where only *M. musculus* occurs. The 1910–1913 epidemic in France could have been due to either species, as both co-occur in parts of France.

Criteria to distinguish among the various species and subspecies have been established by Orsini et al. (1983), Gerasimov et al. (1990), Macholan (1996a,b), and most particularly Marshall (1998). The latter author particularly mentions (among pointed external differences) the difference in tail length between *M. domesticus* and *M. musculus*, and the difference in color of the underparts: white or whitish in *M. musculus* in contrast to the darker brownish-gray in *M. d. domesticus* (other subspecies of *M. domesticus* may have varying degrees of gray venter: from the brownish-gray of *M. d. domesticus*, through "sullied white" for Northern Mediterranean *M. d. brevirostris*, to white with gray bases in the Himalayan *M. d. humorous*, to the pure white North African, Middle Eastern, and Pakistani and Western Indian *M. d. praetextus*). Most populations of mice that we have observed in North America have had the gray or brown-gray venter characteristic of *M. d. domesticus*; careful and meticulous analysis nevertheless remains the order of the day. We have not touched upon the potential for *"bactrianus"* (Iran through India south of the Himalayas to Burma) being a valid species as well: Marshall (1998) considered *bactrianus* a synonym of *praetextus*, itself a subspecies of *M. domesticus*. However, genetic data from Bonhomme et al. (1984) indicate that it is almost certainly a distinct species, as *bactrianus* or *praetextus*, the latter being the oldest available name for the taxon.

From the foregoing discussion, it is clear that at present we simply do not nor cannot know what biological species of *Mus* constitutes the natural host of LCM. Association of an ongoing incidence of LCM to an indubitably identified host species is critical if we are to understand the dynamics of the disease. Accordingly, we recommend that specimens of *Mus* captured and tested in the course of LCM investigations should be deposited in museums (public, university, governmental, or private) and be identified by an expert in rodent taxonomy.

2.2 New World Arenaviruses

Members of this group are also known as members of the Tacaribe complex. This group includes the following viruses: Tacaribe (TCR), Junín (JUN), Machupo (MAC), Amaparí (AMA), Paraná (PAR), Tamiami (TAM), Latino (LAT), Pichindé (PIC), Flexal (FLE), Oliveros (OLV), Sabiá (SAB), Guanarito (GUA), Whitewater Arroyo (WWA), and Pirital (PIR), and Cupixi (CPX) (Tesh et al. 1999). One other virus (Pampa virus) is considered to be a strain of Oliveros (C.J. Peters, personal communication) and has as a putative reservoir an unrecognized species of *Bolomys* (Lozano et al. 1997). Consequently, we did not consider it further.

2.2.1 Tacaribe Virus

This virus was originally isolated by Downs et al. (1963) from tissues and salivary glands of two species of bats (*Artibeus lituratus palmarum* and *A. jamaicensis trinitatis*) captured between March 1956 and December 1958. Virus isolation from a mixed pool of mosquitoes collected in September 1956 was also reported.

No further isolation of virus from mosquito pools has been successful since although more than a million mosquitoes were processed in the ensuing 6 years; it is therefore unlikely that mosquitoes were ever involved in the circulation of Tacaribe.

The bat species reported by Downs et al. (1963) were identified by one of the most preeminent mammalogists of the first half of the century – G.G. Goodwin – who at the time was Associate Curator of Mammals at the American Museum of Natural History (AMNH). Voucher specimen numbers were reported in the original paper, and the voucher specimens are deposited in the collection of the Department of Mammalogy of that museum. In their monographic treatment of the bats of Trinidad and Tobago, Goodwin and Greenhall (1961) commented on the new viral strain isolated from these species.

The two bat subspecies *A. l. palmarum* and *A. j. trinitatis* are endemic to Trinidad and Tobago. The species *A. lituratus* and *A. jamaicensis*, however, range much more broadly*: A. jamaicensis* is distributed from Sinaloa and Tamaulipas (México) to Ecuador, Venezuela, the Greater and Lesser Antilles, and Trinidad and Tobago. *A. lituratus* ranges from Sinaloa and Tamaulipas (México) into southern Brazil, northern Argentina, and Bolivia. This species is also known from islands off the coast of South America (Trinidad and Tobago), the southern Lesser Antilles, and the Tres Marías Islands (Koopman 1993; Wilson 1991) off the Pacific coast of México.

These two species are among the most common bats of the tropical environments they inhabit. Primarily frugivores, they feed principally on fruits of trees of the genus *Ficus* (Handley et al. 1991). Both species exhibit a seasonal pattern in the timing of reproduction, which – at least in the case *of A. jamaicensis* – is highly coincident with the maximum abundance of fruit (Wilson 1979). Goodwin and Greenhall (1961) reported that both species shared roosting sites and dipteran streblid ectoparasites (*Pterellipis aranea*), as well as food items and general habits.

The fact that Tacaribe is the only arenavirus whose putative mammal host is not a rodent has provoked skepticism in the scientific community in light of recent works (e.g., Bowen et al. 1997; Mills et al. 1997) pointing to an appreciable degree of rodent–arenavirus co-evolution. At present, however, and based on the available evidence, Tacaribe remains known only from the aforementioned two species of bats. This is further supported by the fact that the virus was isolated from 11 animals collected over a span of 3 years (1956–1958), demonstrating that the virus was circulating in fruit-bats at least over that span of time.

Bats of the genera *Artibeus* and *Desmodus* infected with Tacaribe by inoculation in a laboratory setting did not circulate virus, and detectable antibodies were shown only in 1 of 39 bats studied (Downs et al. 1963). To our knowledge, no new attempts to isolate Tacaribe virus from other potential reservoirs have been undertaken since the original description of the virus in 1963.

2.2.2 Junín Virus

Junín virus, the etiological agent of Argentine hemorrhagic fever (AHF), has most commonly been isolated from the organs and body fluids of three species of rodents: *Calomys musculinus*, *C. laucha*, and *Akodon azarae*. In addition, the virus

has been isolated from other rodent species such as *Mus musculus* (Sabattini et al. 1977) and *Oligoryzomys flavescens* (Mills et al. 1991a). The vesper mouse, *Calomys musculinus*, is considered the primary reservoir because it was the most commonly trapped rodent in the endemic area, and because persistent viremia and virus shedding via saliva was found both in naturally and laboratory-infected animals (Carballal et al. 1986). Furthermore, in long-term studies of rodent populations in the greater risk area of AFH, Mills et al. (1991a) found that *C. musculinus* comprised the bulk of the antigen-positive trapped rodents, thus confirming this species as the principal reservoir. In another study, (Mills et al. 1992a) found 37 of 41 antigen-positive captures were individuals of *C. musculinus*, thereby lending support to the hypothesis that this species is the principal reservoir of JUN. Additional support comes from Mills et al. (1994), who found that 89% of JUN-seropositive animals in two mark-recapture grids in the epidemic area of AHF were *C. musculinus*.

The type locality of *C. musculinus* is Jujuy, Province of Jujuy, Argentina, at an elevation of 1,200m, nearly 700 miles north of the area of distribution of AHF. The type specimen is British Museum (Natural History) number BMNH 20.1.7.46; it remains housed at the Natural History Museum in London. *C. musculinus* can be distinguished from all other species of the genus on the basis of the following characters: body size moderate (total length including tail of adults generally 155–200mm); tail long, equal to or slightly longer than head and body length; dorsum sandy brown, frequently lined with black hairs, venter white, hairs gray at base; skull medium in size, greatest length of skull in adults generally 22–26mm; auditory bullæ slightly inflated; maxillary toothrow moderately long (3.4–3.8mm; Olds 1988).

As currently understood, this species ranges widely across South America, from central Bolivia at moderate to high elevations in the eastern slopes of the Andes (Anderson 1997), through the lowlands of central Argentina (in Chubut Province), to western Paraguay and possibly into Central Brazil. Obviously, such a variation in elevation and latitude encompasses a large number of habitats ranging from mesothermic valleys in southern Bolivia to subhumid tropical Chacoan forest in Paraguay and potentially Brazil.

Mills et al. (1991b) have summarized some ecological information for *C. musculinus* near to or in the endo-epidemic zone of AHF. These authors found *C. musculinus* abundant in agricultural areas, especially corn and wheat fields, although linear habitats (fencerows, roadsides, and railroads) were also commonly occupied. Population densities for this species were described as relatively high in the spring and remaining so through the summer and early autumn from November to April (Mills et al. 1991b). In another study, Mills et al. (1992a) found that most *C. musculinus* that had tested positive for JUN antigen were statistically associated with linear habitats (roadsides and fence lines). Similar results were found by Ellis et al. (1997), albeit contrasting with the results of Busch et al. (1997), who suggested that *C. musculinus* does not show habitat preference in any season, overlapping with both *C. laucha* and *Akodan azarae* in fields and linear habitats.

C. musculinus also appears to be relatively common in other habitats. For example, Gonnet and Ojeda (1998) found this species to be one of the two most dominant species in the Andean foothills of the Monte Desert of Argentina. In that study, *C. musculinus* preferred grassy microhabitats within the most complex habitat (or undisturbed thicket). Yahnke (1999) found that in the Paraguayan Chaco, *C. musculinus* occupied several habitats but showed a preference for microhabitats with low herbs and grassy vegetation.

The systematics of this species (and species-group) remains in need of a comprehensive revision. Our own work (Salazar-Bravo et al. 2001) has shown that this species is a member of the "mountain clade" of the genus and closely related *to C. lepidus* and *C. sorellus*. What is not yet clear is whether more than one biological species is present in what we now understand as the singular *C. musculinus*. The species has been characterized chromosomally across a wide range of habitats and appears to present a relatively conserved karyotype throughout it range. The diploid chromosome number $2n = 38$ has been found in specimens from Córdoba and Buenos Aires provinces (Argentina). However, some chromosomal polymorphism has been detected, both in the morphology of the autosomes, as well as in the size and position of the centromere in the Y chromosome (Ciccioli 1991; Ciccioli and Poggio 1993; Lisanti et al. 1996; Massoia et al. 1968). As a result, the fundamental number (FN) varies from 48 (Massoia et al. 1968) to 56 (Lisanti et al. 1996; Ciccioli 1991). Olds (1988) defined *C. musculinus* as present only in northwestern Argentina and southern Bolivia, and considered *C. murillus* a distinct species. However, in her concluding remarks (Olds 1988: p 149), she acknowledged the potential for conspecificity of *C. musculinus* and *C. murillus*. Salazar-Bravo et al. (2001) found no support for the recognition of *C. murillus*, although several specimens included in their analyses came from the province of Buenos Aires, and one from near the type locality of *C. murillus* (environs of La Plata).

2.2.3 Machupo Virus

Machupo virus, the etiological agent of Bolivian hemorrhagic fever (BHF), was isolated from the spleen, brain, and blood of a rodent species: *Calomys* cf. *callosus* (Kuns 1965; Johnson et al. 1966). Webb et al. (1967) reported that 4 or 5 specimens of *Proechimys brevicauda* from the environs of San Joaquín also tested positive for neutralizing antibodies; this was the area of the endo-epidemic of BHF in 1963. Subsequent to these isolations, several attempts to isolate Machupo virus from *P. brevicauda* failed (Johnson et al. 1966; Webb et al. 1975). This fact points to spill-over from *Calomys* as a contributing factor for the presence of Machupo in *Proechimys*.

The taxonomic status of *C.* cf. *callosus* remains nebulous (Salazar-Bravo et al., in preparation), but it now appears evident that this is a species separate from, yet morphologically similar to, *C. callosus* (*sensu stricto*). Following phylogenetic analysis based on genetic data (cytochrome *b* gene sequence of mitochondrial DNA), these authors suggested that *Calomys* spp. ex Beni (reservoir of MAC) is most closely related to *C. fecundus*, which is common to abundant in intermediate

elevations (500–2,800m) on the eastern flank of the Andes in southern Bolivia and northern Argentina.

The distribution of *C.* cf. *callosus* appears to match closely the distribution of savannas in the northeastern Bolivian department of El Beni. These savanna plains lie east of the Andes in the Amazon basin and have a mean elevation of about 200m. The prevailing vegetation type "is that of a grassland broken occasionally with 'islands' of forest and laced with tree-lined rivers and streams" (KUNS 1965). A complete analysis of the vegetation, geography, and overview of the ecology of the savannas in northeastern Bolivia was presented in HANAGARTH (1993). The westernmost record of *C.* cf. *callosus*. is near the town of Reyes (PATTERSON 1992) on the border between Beni and La Paz departments (Bolivia). Although most cases of BHF have been reported from only a handful of localities, *C.* cf. *callosus* has been collected in other areas of the savannas where BHF is endemic.

Little is known or published about the ecology of this species. KUNS (1965) reported *C.* cf. *callosus* as a pastoral species often collected in grasslands and along forest edges around the town of San Joaquín. He also remarked on the comensalism of this species with humans, as many individuals were trapped in and around houses. After the rodent control program was initiated in San Joaquín, almost 2,880 *C.* cf. *callosus* were recovered from the village, representing 96% of all rodents captured (KUNS 1965).

JUSTINES and JOHNSON (1970) summarized several years of data on laboratory rearing of this species. The colony, initiated with six animals, was still thriving after 5 years. Their report indicated that breeding was continuous throughout the year. Sexual maturity was attained at about 8 weeks, estrous cycle was 6 days, and gestation period was estimated as 21 days. Average litter size was approximately six, with high weaning ratios (ca. 97%).

2.2.4 Amaparí and Cupixi Virus

This arenavirus was originally isolated by PINHEIRO et al. (1966) from pools of tissues (liver, spleen, kidneys, and hearts) from spiny mice (*Neacomys guianae*), the rice rat (*Oryzomys* cf. *goeldi*), and a pool of mites ($n = 199$) combed from two infected *Oryzomys*. As suggested by BOWEN et al. (1998) it is likely that a second arenavirus (Cupixi) might have been responsible for the infection in *Oryzomys*, therefore here we follow their advice and treat Amapari as restricted to *Neacomys guianae*. The prototype strain of Amapari was isolated from an individual spiny mouse captured on 8 July 1964, near Serra do Navio in the northeastern Brazilian State of Amapa. Viruses were isolated only from one of seven animals tested. Later, PINHEIRO et al. (1977) reported on a long-term study during which the virus was isolated at the same locality from 145 *Neacomys* over a period of 7 years.

The spiny mouse (*Neacomys guianae*) is restricted to rainforest regions ranging throughout the Guianas and adjacent parts of northern Brazil, north of the Amazon and east of the Rio Negro (HUSSON 1978; EISENBERG and REDFORD 1999). As MUSSER and CARLETON (1993) stated, "traits for species recognition and distributional limits in this genus are poorly delineated". Furthermore, PATTON

et al. (2000) showed levels of diversity in this genus that had previously been unrecognized. *Neacomys guianae* is recognized by a smaller size and darker coloration (Ellerman 1941; Gyldenstolpe 1932) compared with other species in the genus. Little is known of the ecology of this species. Husson (1978) reported that this species preferred dense, humid forests, and Emmons and Feer (1999) reported that the animals favor areas of dense ground cover, travelling on the ground or on logs or vines near the ground. Guillotin (1982) working in Guiana trapped more spiny mice between March and May in disturbed sites than in July and August in pristine forest. Emmons and Feer (1999) reported that *N. guianae* is nocturnal, terrestrial, and solitary, and that the diet of this species was 60% insects and 40% fruit, seeds, and other plant material.

In contrast, successful isolation of an Arenavirus was accomplished from three individuals of *Oryzomys* cf. *goeldi* trapped between December 1964 and January 1965 at Sierra de Navio. Later, Pinheiro et al. (1977) reported on a long-term study during which the virus was isolated at the same locality from 127 *Oryzomys*. It has been suggested by Bowen et al. (1998) that this arenavirus is in fact different from Amapari and suggested the name Cupixi for it.

The species of *Oryzomys* implicated as a reservoir of Amaparí originally was identified as *O. goeldi*, although named *O. capito* in Pinheiro et al. (1977). This incongruence is not actually so. The systematic knowledge of the genus *Oryzomys* has advanced greatly with recent work (e.g., Musser et al. 1998; Voss and Carleton 1993; Weksler et al. 1999; Bonvicino and Martins 2001; Patton et al. 2000). Recently, Musser et al. (1998) considered the two species synonymous with *O. megacephalus*. We note that differences in DNA sequence (Patton et al. 1996, 2000; Bonvicino and Martins 2001) as well as chromosomal characters (summarized in Musser et al. 1998, Table 13) for geographic groups of populations (eastern vs. western Amazonian) point to the differentiation of *O. megacephalus* and *O. perennensis*, with *O. megacephalus* being restricted to eastern Amazonia.

But the problem with the identification of the reservoir of Cupixi does not end there. Sympatry and syntopy among three species of *Oryzomys* with similar morphological characteristics has been documented at Serra do Navio and the immediate area: *O. yunganus*, *O. megacephalus*, and *O. macconnelli* (cf. Musser et al. 1998). In the original publication describing Amaparí (Pinheiro et al. 1966), only one species of *Oryzomys* was mentioned: *O. goeldi*. In Pinheiro et al. (1977), two species were implicated: *O. capito* and *O. macconnelli*. If we accept the current taxonomy, both *O. capito* and *O. goeldi* are junior synonyms of *O. megacephalus*, and distinct from *O. yunganus*, a species also documented in the area. From which of these two species of *Oryzomys* was the virus isolated? Recent revisionary work on this group could easily allow us to answer that question. Unfortunately, we do not know which individual animals were the source of the virus. If we take the Pinheiro et al. (1977) report at face value, the updated species name of the reservoir of Amaparí should be *O. megacephalus* – a course of action followed herein because this species appears to be more abundant at that locality – cf. Musser et al. (1998). We note, however, that further inquiry into the viral laboratory records may shed light on the positive identity of the mammal reservoir species.

The species *O. megacephalus* is broadly distributed and "occurs primarily in tropical evergreen rainforest formations (which include riverine or gallery forest in the Brazilian Cerrado) in the Orinoco basin in southern Venezuela, the Guiana Region (including the tepuis of eastern Venezuela), the island of Trinidad, and drainage basin of the Amazon River" (Musser et al. 1998).

The ecology of this species has been extensively studied (e.g., Mares et al. 1989; Alho and Pereira 1985; Lacher et al. 1989; Guillotin 1982). One study (Guillotin 1982) reported this species (under the name *Oryzomys capito velutinus*) as nocturnal, terrestrial, found only in climax forest (not in secondary growth), and fairly abundant. She reported this species as the most abundant muroid rodent in the area.

2.2.5 Paraná Virus

Webb et al. (1970) isolated this arenavirus from the kidneys of rodents collected in southern Paraguay, in the environs of the town of San Francisco, in the Department of Misiones. The virus was isolated from three specimens (of four collected) of *Oryzomys buccinatus*. No catalogue or accession numbers are presented in the paper, although it is likely that at least some of the specimens collected are now at the US National Museum (Webb et al. 1970: p 380).

Musser et al. (1998) discussed the systematics and nomenclatural history of *O. buccinatus*, concluding that the name *O. angouya* has priority and should be used rather than *O. buccinatus*. According to these authors, the species *O. angouya* also includes *O. ratticeps*. Thus, the reservoir species of Paraná virus, as currently understood, is distributed from eastern Paraguay and northeastern Argentina to southeastern Brazil (Musser et al. 1998; Redford and Eisenberg 1992).

Not much has been published on the ecology of this species, but Myers (1982) found it in the interface between forest and secondary vegetation. Olmos (1991) during a 13-month capture–recapture study in the Atlantic forest in southern São Paulo found *O. ratticeps* in a 0.5-ha trapping-grid established within an old second growth forest. He also reported this species as terrestrial, but with the ability to climb well and exploit arboreal vegetation. The capture pattern suggested a general decrease in numbers towards the end of the year; reproduction appeared to occur outside winter (May–August).

2.2.6 Tamiami Virus

Calisher et al. (1970) originally described this virus by isolating it from the heart tissue of an adult hispid cotton rat (*Sigmodon hispidus*) collected 5 January 1965 from Mahogany Hammock (latitude 26°17′N, longitude 81°05′W), Everglades National Park, Florida, USA. Further isolations were made from cotton rats collected just north of the park in or near the Big Cypress Seminole Indian Reservation in January 1964 and 1965. In addition, Wellings et al. (1972) reported isolation of Tamiami virus from rice rats (*Oryzomys palustris*), and Bigler et al. (1975) reported antibodies in 4 of 27 rice rats (*O. palustris*) sampled from

throughout Florida. Nevertheless, hispid cotton rats, *S. hispidus*, are considered the primary rodent host (cf. also Kosoy et al. 1996).

Cotton rats are distributed from about latitude 41° north (in Iowa and Nebraska) throughout most of the southern, southeastern, and southwestern USA, through Mexico and Central America, to northern South America. Hall (1981) mapped the ranges of all recognized subspecies within the taxon in his monumental work on North American mammals. Based on his maps, the specimens collected by Calisher et al. (1970) are referable to the subspecies *S. hispidus spadicipygus*, originally described from Cape Sable, Florida, some 50miles southwest of the locality whence Tamiami virus was described (Mahogany Hammock).

The systematics of *Sigmodon* has received renewed attention since the early 1990s. Voss (1992), in reviewing the South American species of the genus, suggested that *S. hispidus* formed a morphologically cohesive group (including North American representatives in his study for comparison as well); but he also suggested that other methods of analysis be brought to bear to the study of this species. Peppers and Bradley (2000) analyzed several populations of hispid cotton rats from throughout the range of the species using sequence data from the cytochrome *b* gene. Their analyses showed that within the taxa sampled, at least three potential groups of species constituted the nominal "hispid group": *S. hispidus*, *S. toltecus*, and *S. hirsutus*. These authors confirmed the genetic identity of *spadicipygus* as a subspecies of *S. hispidus*, thus reinforcing the hypothesis that *S. hispidus* (*sensu stricto*) is the primary reservoir species of Tamiami.

The ecology of *S. hispidus* has been thoroughly studied since the pioneering work of Bangs (Bangs 1898). A summary of the ecological and life history aspects of the species is presented in Cameron and Spencer (1981). Only reports associated with *S. hispidus* (*s.s.*) are included herein.

S. hispidus exhibits bimodal population fluctuations annually in Texas and Georgia, with maximum densities occurring in the autumn and secondary peaks in the spring. Densities fluctuate depending on the study, with records of 25 animals/ha in Florida and 69/ha in Georgia to 10/ha and 8/ha at the low end, respectively. In the northern part of the range (Kansas), population densities were unimodal, with peaks in the autumn (20/ha) and lows in the spring (minimum densities 0.02/ha). Individual populations for which expectations of further life (average duration of local residence for all individuals) have been calculated indicate an average of 2 months for both sexes with longest periods of residence at 9.5 months (average for both sexes). This species prefers habitat dominated by grasses, mixed grass, and shrubs, or old fields in early stages to secondary succession. The diet is almost restricted to grasses but on occasion may include insects. Average home ranges for adults is 0.39ha for males and 0.22ha for females, although females have exclusive home ranges. Dispersal of *S. hispidus* is positively correlated with density, and the sex ratio and age structure of dispersers were similar to those of the source population. Males move longer distances within a day than females (17m vs. 6.6m on average), and reproductive males tend to move longer distances than nonreproductive males. Cotton rats are active at all hours of the day and night in coastal Texas, with two peaks of activity identified around 0900 and 1900 hours. Field and

laboratory studies showed that *S. hispidus* are practically inactive between 2300 and 0500 hours. Although mostly ground-dwellers, they have also been caught along vines up to 2.7m above ground. *S. hispidus* is a solitary species as males build prolonged social contact (up to several days) only with females (depending on their reproductive status). This social contact is accompanied by frequent physical contact (i.e., sleeping, huddling, and mutual grooming), but males always remain dominant over females in these pairs.

2.2.7 Latino Virus

This virus has not been properly described, or at least not to the standards set in descriptions of remaining arenaviruses. Most of what has been recorded on the biology and reservoir of this virus was presented in Webb et al. (1973). Later, Webb et al. (1975) added some information on the subject. Webb et al. (1973: p 315) referred to a paper to be published shortly thereafter where they intended to fully describe Latino virus; to our knowledge, that paper was never published. For our purposes however, Webb et al. (1973) contains enough information on the rodent reservoir's geographic origin and putative identification.

Animals from localities in eastern Bolivia (towns of Juan Latino, San Ignacio) and neighboring Brazil (Corumbá) yielded 18 strains of Latino virus. It is unknown how many animals were tested or what proportion of all animals tested were positive. In the experimental work upon which these authors subsequently reported, a colony was founded with two breeding pairs captured in the town of Juan Latino (Santa Cruz Dept., Bolivia). These animals were free of virus as they were killed and tested after the second generation of breeders had matured.

Webb et al. (1973) reported that the animals had been identified to the species level as *Calomys callosus* by Ronald H. Pine, then of the Smithsonian Institution. Chromosomal analysis on these animals was undertaken by Robert J. Baker at Texas Tech University. Some unpublished photographs of the karyotypes were later sent to Nancy Olds from the American Museum of Natural History in New York, and material based on this work were included in her unpublished PhD dissertation (Olds 1988). However, Pine (R. Pine, personal communication) was following Hershkovitz (1962) in including within *C. callosus* all medium-sized species of *Calomys* with posteriorly divergent supraorbital regions.

Molecular analyses in our laboratory (Salazar-Bravo et al., in preparation) show that members of this population (and those of the semideciduous forest of southeastern Bolivia, extreme southwestern Brazil, western Paraguay, and northeastern Argentina) cluster outside the clade that includes other well differentiated taxa (e.g., *C. venustus*, *C. fecundus*, *Calomys* spp. ex Beni). This information helps to elucidate the biological properties of the virus-reservoir dynamics described by Webb et al. (1973).

The proper name for the mammal reservoir species of Latino virus is therefore *C. callosus* (*s.s.*), the oldest name available for this clade. Recently, Bonvicino and Almeida (2000) presented evidence that *C. expulsus* may have been confused in some instances with *C. callosus* in the literature on the ecology of small mammals in

central Brazil. Thus, some of the information collated below may include aspects on the ecology of the former. Since most ecological studies fail to secure voucher specimens, it is impossible to confirm the identification of the species in these reports.

Several aspects of the ecology of *C. callosus* have been published. This species is found in thickets at the edge of pastures, ravines, and forest roads in the Pantanal of Brazil (Schaller 1983), in Caatinga, Cerrado (Mares et al. 1985, 1989; Engel and Mello 1993; Alho and Pereira 1985; Alho et al. 1986), but not in Cerrado gallery forest of Brazil (Nitikman and Mares 1987; Mares and Ernest 1995), in second growth habitats in mesic forested areas, such as stream areas, road cuts, old fields, grassy areas, sugar cane fields, and river banks of Chacoan thorn scrub, abandoned fields of Brazil (Mares et al. 1981a), and the Chaco of Paraguay (Myers 1982). In the northeast of Brazil, Karimi and Petter (1976) and Mares et al. (1981b) found this species in piles of dried grass and later stages of oldfield succession in the Caatinga Baixa. *C. callosus* has been reported as rare in abandoned fields and the Caatinga Baixa of Brazil (Mares et al. 1981b); never in large numbers in Caatinga (Streilein 1982b), at low density in Pernambuco, Brazil (less than 1.7% of all rodents trapped in the study area in a 4 year period; Karimi and Petter 1976), low numbers in the Pantanal of Brazil (Schaller 1983), common in the Cerrado of Brazil and in Salta Province, Argentina (Alho and Pereira 1985; Engel and Mello 1993; Mares et al. 1981a).

Mello (1980) found a population peak of *C. callosus* in July 1975, then another in August to November 1976, in the northern part of the state of Goias, Brazil. Out of a total of 963 captured rodents, individuals of *C. callosus* comprised about 41% (398/963) over 2.5 years; 44.2% were female and 55.8% male. Many of the females were immature. Density has been reported as 3–4 individuals per hectare (Alho et al. 1986). Home range is about 100–1000m^2 according to Alho et al. (1986).

The species is nocturnal and feeds on arachnids and seeds, moths, and beetles (Karimi and Petter 1976; Streilein 1982a). Contradictory reports on the arboreality of this species exist: *C. callosus* has been reported as not appearing to climb, but as an agile, active climber that uses its tail as a climbing aid, showing a tendency toward arboreal activity in the laboratory (Streilein 1982b; Mares et al. 1981b). Streilein (1982a) also noted that adults were capable of vertical leaps of 0.7–0.8m.

Nests have been described as made of dried grass (Karimi and Petter 1976) and as being spherical and made of "finely shredded, interwoven plant material found in depressions hollowed in the ground, camouflaged with twigs and leaves" (Alho et al. 1986: p 453). Nests are generally above the ground in clumps of grass or in branches of dead trees (Mello 1984). Streilein (1982a) found that nests in the laboratory were spherical, made of finely shredded, interwoven plant material, while those in the field were simple depressions hollowed in the ground 10–15cm deep and wide camouflaged with leaves. He noted that caches of seeds were occasionally found near the nests.

In a laboratory colony in Pernambuco, Brazil, Petter et al. (1967) found the number of embryos ranged from 1 to 10, the newborn weight was 1.3–2.5g, more males were born than females (1.22:1), the gestation period was 19–22 days, adults

weighed 35–45g, eyes opened in 7–8 days, the lower incisors erupted after 6–7 days, and the upper incisors erupted after 7–8 days. The dorsal pelage is gray by the third day and is about 2mm in length. Mello (1978) reported the average litter size to be 4.5 (range 2–9) and the length of gestation to be 21.8 days, with a range of 20–23 days. The ratio at birth of males to females was 1.05:1. The eyes opened 6–7 days after birth, weaning occurred 15–17 days after birth, and pelage cover was complete on the sixth day.

Mello (1980) reported gestation to require 21.8 days in the laboratory, intervals between matings to be 30–50 days, and the average number of embryos per litter to be 4.5. Animals were sexually mature at 22–23g, embryos were present in June (8 in a female), September (4 and 2, in two females), October (one female with 4), November (two females, both with 4), January (one female with 3), and April (two females, 4 and 7). She further noted that the reproductive periods were coincident with the end of the rainy season. The average litter size in field studies in Brazil was 4.4, and the range was 2–8 (Streilein 1982a). Reproductive information from his study included a lactating female in September, two lactating females in October, one pregnant and one lactating female in November, two lactating females in February, one lactating female in April, and one female showing no reproductive activity in May. Little is known about the dispersal and population responses to disturbance and seasonal climate changes in this species.

2.2.8 Pichindé Virus

This virus, described by Trapido and SanMartin (1971), was isolated from two species of sigmodontine rodents (*Oryzomys albigularis* and *Thomasomys fuscatus*) and from mites and ticks from viremic *O. albigularis*. This latter is considered the reservoir species because Pichindé was isolated from *T. fuscatus* only once and because *O. albigularis* showed the highest seroprevalence: 54 of 271 animals sampled from four different localities were positive for the virus. Interestingly, over a period of 2 years (March 1967 to December 1969), the authors isolated Pichindé several times from pools of mites of the species *Gigantolaelaps inca* and ticks of the species *Ixodes tropicalis* obtained from viremic *O. albigularis*. Moreover, virus isolation was successfully undertaken from a pool of four *I. tropicalis* individuals that had been maintained alive at ambient temperature 5–8 days after being recovered from an *O. albigularis*.

The range of *O. albigularis* as the species is currently understood from a taxonomic perspective (Musser and Carleton 1993) includes the montane forests of north and western Venezuela, easternmost Panamá, Andes of Colombia and Ecuador, to northern Peru. The taxonomy of the species has recently been updated by the works of Aguilera et al. (1995) and Marquez et al. (2000). However, these two reports are based exclusively on specimens from Venezuela and did not include animals from Ecuador (wherein is the type locality) or from Colombia, where Pichindé was described. In an earlier report (Gardner and Patton 1976), animals were karyotyped from the same locality as those that had proven to be virulent in the valley of the Pichindé River. In that report, the karyotype of *O. albigularis* is

presented as $2n = 66$, FN = 94. Gardner and Patton (1976) correctly argued that until chromosomal information of animals from the type locality is reported, the name *albigularis* likely was applicable to this chromosomal form. Trapido and SanMartin (1971) argued that the identification of *O. albigularis* was warranted by the "distinctiveness" of this species. Although their report includes several individual rodent field numbers (e.g., HTC 1338, HTC 1341, etc. – probably Harold Trapido's field numbers) no reference in the paper is made as to where the voucher specimens were sent for identification, or where (and if) those animals are stored now. It is interesting that the more than 1,350 animals entered in their Table 4 are identified to the species level (representing 24 species), a fact implying that the specimens were handled and identified by a professional. It is possible that the specimens ensuing from this work were deposited in the Colección de Mamíferos of the Universidad del Valle.

The ecology of this species has been studied by Barnett (1999) in Ecuador and by Diaz De Pascual (1994) and Aagard (1982) in Venezuela. Ectoparasite associations of this species have been reported by Timm and Ashe (1987) and Ashe and Timm (1995). *O. albigularis* is among the largest rodent in the ecosystem in which it occurs (weighing up to 79g, total length of 330mm; Barnett 1999). In Ecuador, specimens of *O. albigularis* were trapped only in cloud forest, a habitat preference also reported by Handley (1976), Ashe and Timm (1987), and Eisenberg and Redford (1999). The species appears to prefer dense cover. Durant and Diaz (1995) reported that this species was at its lowest density during the wet season. Such seasonal fluctuations may explain why it was reported by Zuñiga et al. (1983) as being the rarest species in northwest facing montane forest sites between 1,000 and 2,500m while Pefaur and Diaz De Pascual (1985) reported *O. albigularis* as the numerically dominant species.

At Monte Zerpa's cloud forest in Mérida (Venezuela), Diaz De Pascual (1994) trapped *O. albigularis* with seven other species of rodents: *Microryzomys minutus*, *Aepeomys lugens*, *Thomasomys laniger*, *Rhipidomys venustus*, *Chilomys instans*, *Ichthyomys hydrobates*, and *Akodon urichi*. According to this author, *O. albigularis* lives in patchy environments which vary in space and time. Major inter- and intra-annual variation in relative abundance of this species was observed, potentially related to the availability of preferred food items for this species. It was suggested that *O. albigularis* are spatially structured as metapopulations, with food availability being the main factor determining dispersal between demes. Aagard (1982) reported no significant seasonal differences in captures for this species in Mérida, Venezuela, and at the same time showed that most animals were trapped on the ground. Males were larger and heavier than females independently of season, and males were reproductively active all year round. A breeding peak in the wet season was indicated.

2.2.9 Flexal Virus

Flexal virus was presented in a paper by Pinheiro et al. (1977) as a new type of arenavirus from a locality 212km S of Itaituba, in the Brazilian state of Pará. The

authors made passing mention to the three specimens of *Oryzomys* from which the virus was isolated and that were captured between October and December 1975. No mention is made of field numbers identifying the rodent specimens nor whether the animals were sent to specialists for identification. As a consequence, the identification of the reservoir species of this virus remains highly suspect; we submit that the identity of the reservoir is not justified even at the generic level. In the text, the authors stated that "No antibodies were found in the sera of 3 *Oryzomys* that yielded the virus nor in the sera of the 8 *Oryzomys oecomys* [sic] captured in the area, including the two from which the virus was isolated" (Pinheiro et al. 1977: p 179). This passage appears to suggest the reservoir is *O. oecomys*; however, that name combination does not exist (cf. Musser and Carleton 1993). Both *Oryzomys* and *Oecomys* are distinct and equally valid taxa of genus level within the tribe Oryzomyini (Voss and Carleton 1993). Therefore, and since no voucher specimens exist with which to confirm identifications, we recommend that the reservoir of this arenavirus be restricted to a member of the Oryzomyini, with no specification as to generic identification. That being said, a cursory analysis of the primary and secondary literature suggests that the general area in which the Flexal virus was found harbors nowadays at least two species of *Oryzomys* and three to four species of *Oecomys* (Voss and Emmons 1996; Eisenberg and Redford 1999). Virologists and mammalogists working in that area would provide a great service by collecting and vouchering specimens of the Oryzomyini and having them tested for Flexal in order to identify the reservoir of this arenavirus properly.

2.2.10 Oliveros Virus

This arenavirus was characterized by Mills et al. (1996) and its phylogenetic relationships explored by Bowen et al. (1997). It was noted in central Argentina, a region described as "an area of intensive agriculture and cattle production" where "crop fields are bordered by fence lines, roadsides and railroads rights-of-ways" (Mills et al. 1996). It is also one of the most populated areas in Argentina.

Although several species of sigmodontine rodents occur in the area (*Bolomys obscurus*, *Calomys musculinus*, *C. laucha*, *Akodon azarae*, and *Oligoryzomys flavescens*, as well as the murine *Mus musculus*), Mills et al. (1996) concluded that *B. obscurus* was the reservoir of Oliveros because the virus was extracted from individuals of this species, and because about 25% of all *B. obscurus* were seropositive as opposed to none or very few individuals from other species in the area.

The taxonomy of the genus *Bolomys* is currently in a state of flux. Massoia and Pardinas (1993) suggested that *Necromys* is a senior synonym of *Bolomys*, an assertion that has received little support by most mammalogists (e.g., Anderson 1997; Salazar-Bravo and Yates, in preparation). On the other hand, Galliari and Pardinas (2000) recently suggested that the Argentine Pampa is populated by *B. benefactus*, while populations in Uruguay and SE Buenos Aires province in contrast are referable to *B. obscurus*. Thus, based on geographic information and the identification of several specimens from the Mills et al. collections by one of us

(JSB), we suggest that the reservoir of Oliveros virus be restricted to *B. benefactus* rather than *B. obscurus*.

Several aspects of the ecology of *B. benefactus* have been studied extensively (Mills et al. 1991b; Fornes and Massoia 1965, and references therein). The species appears to be restricted to the Pampa habitat of Argentina (Galliari and Pardinas 2000).

Ellis et al. (1997) found that *B. benefactus* (reported under the name of *B. obscurus*) primarily inhabited the more stable, weedy borders of cultivated fields, and Mills et al. (1991b) showed peaks in relative densities in late autumn and early winter, with numbers more evenly distributed throughout the year. Also, Mills et al. (1992b) reported that the breeding season – as assessed by pregnancies – was September or October through April or May. Although several reports (Reig 1987, and references therein) suggest that the species is mostly insectivorous, Ellis et al. (1994, 1998) found that the diet corresponded more closely to that of an omnivorous species, with leaves forming a relatively minor proportion of the diet (average 16% for *Bolomys*) throughout the year. This species also consumed higher quantities of seeds (35%–60% of stomach volume) than arthropods (30%–35%) during the autumn and winter but switched to higher quantities of arthropods (30%–53%) in the spring and summer. No information is available on dispersal patterns.

2.2.11 Sabiá Virus

Coimbra et al. (1994) described this virus from the Brazilian state of Saõ Paulo in a fatal case of hemorrhagic fever initially thought to be yellow fever. Antigenic and molecular analyses showed that this was a new arenavirus which they named Sabiá after the community wherein the index case was staying when she became ill. Sabiá is a small community in the southeastern part of the state. Several species of potential hosts occur in the area.

2.2.12 Guanarito Virus

Early reports on the etiology and characterization of Venezuelan hemorrhagic fever (VHF) implicated two rodents as reservoirs (Tesh et al. 1993): *Zygodontomys brevicauda* and *Sigmodon alstoni*. As early as 1996, the possibility that two different arenaviruses were circulating in these two species of wild rodents in the same general area in Venezuela had been advanced. Fulhorst et al. (1997) described a second arenavirus from *S. alstoni* (cf. below) and experimental work by Fulhorst and colleagues (1999) clearly identified *Z. brevicauda* as the reservoir species of Guanarito, the etiological agent of VHF.

The taxonomic status of *Z. brevicauda* as well as some aspects of the natural history of this species were summarized in Voss (1991). This species ranges widely below 1,500m from the "Pacific littoral and foothills of eastern Costa Rica, through Panamá, Colombia (except the valleys of the upper Rio Cauca, Rio Patía and Rio Dagua), Venezuela, Guyana, Surinam, French Guiana, and Brazil north of the Amazon Basin". Voss (1991) further reported that *Z. brevicauda* inhabits a wide

variety of lowland habitats with the exception of mature, closed-canopy rain forest. The species is nocturnal and terrestrial. In the agricultural and pastoral areas of the western Llanos of Venezuela, Utrera et al. (2000) found that most habitat types, especially relatively uniform areas of mechanized agriculture, were numerically dominated by two rodents, *S. alstoni* and *Z. brevicauda*. The latter species has been said to be omnivorous (Einsenberg 1989), but Martino and Aguilera (1993) found that it is chiefly insectivorous (70.6%), although they also suggested that diet was dependent on resource availability. Voss (1992) found that captive-bred litters typically consist of four or five pups each weighing 3–4g at birth. Adults 20–40 weeks old average 60–80g with some sexual dimorphism. Females are sexually mature at 3–4 weeks of age, males at 6–8 weeks. Ovulation is spontaneous, and gestation lasts 25 days. In the field, reproduction in *Z. brevicauda* appears to be continuous and aseasonal. Several reports indicated that *Z. brevicauda* are among the most abundant rodents in the areas where they occur. Densities reported for this species vary from "not very abundant" (Martino and Aguilera 1993) to 40/ha or even 100/ha (summarized in Voss 1992).

2.2.13 Whitewater Arroyo Virus

In 1996, Kosoy et al. reported an unexpectedly high level of prevalence of antibodies to arenaviruses in rodents from the southwestern USA, providing the first published evidence that these viruses infect individuals of the North American sigmodontine genus *Neotoma* (packrats). The same year, Fulhorst et al. (1996) isolated and characterized three strains of Whitewater Arroyo virus from two individuals of *N. albigula* from Whitewater Arroyo in McKinley County, New Mexico. Other species of sigmodontine rodents also found to be antibody-positive to WWA were: *N. fuscipes*, *Peromyscus boylii*, *P. californicus*, *P. eremicus*, *P. maniculatus*, and *Reithrodontomys megalotis* (Bennet et al. 2000).

N. albigula is nearly ubiquitous in western North America, occupying several habitat types throughout its geographic range (Hall 1981). It is found from southeastern California and southeastern Utah to central Texas, northeastern Michoacán, and Hidalgo, México (Macedo and Mares 1988). The species is primarily found in arid regions and prefers areas where prickly pear (*Opuntia*) and piñon-juniper habitat are abundant. Shelter-site selection is influenced by the quantity of ground-level vegetation available for cover. *N. albigula* is nocturnal and terrestrial, although it has been trapped above the ground and been seen climbing in bushes and trees.

The species is chiefly herbivorous. Dial (1988) showed that in sympatry with congeners, *N. albigula* was found selectively to forage on *Yucca* while *N. devia* specialized on *Ephedra epidermis*, and *N. stephensi* on *Juniperus*. Macedo and Mares (1988) reported that early accounts of the diet of this species showed up to 44% of the annual diet composed of cacti. Home-range estimates in this species vary with habitat but have been estimated to be $161 \pm 19 m^2$ in Cholla-forest habitat. Nests are defended, but home ranges overlapped, at times by as much as 100% (Boggs 1974). Whitford (1976) found that in southern New Mexico, *N. albigula* maintained stable and nearly constant population densities in a 4-year study at

about 2/ha with a significant increase at the end of the third year. In analyzing 4 years of data from central New Mexico, Parmenter et al. (1999) showed that *N. albigula* presented two distinct density patterns. In Placitas (at 2,200–2,300m in the foothills of the Sandia Mountains, Sandoval Co., north-central New Mexico), densities remained constant at 1–2/ha, whereas in the Sevilleta National Wildlife Refuge (high desert, 1,600–1,700m in central New Mexico) densities varied from 1–10/ha with population peaks in the late autumn. Serrano (1987) showed that population densities in northern México varied from 10–46/ha in preferred habitat (*Opuntia* fields). Brown and Heske (1990) showed that at their study site in Arizona, *N. albigula* densities were relatively constant throughout their 10-year study period (~10/ha). Macedo and Mares (1988) reported that reproduction occurred continuously through the year, gestation lasted 30–38 days, and pups were weaned at about 20–25 days.

2.2.14 Pirital Virus

This virus was isolated by Fulhorst et al. (1997) from 10 of 46 *Sigmodon alstoni* rodents tested from the Venezuelan state of Portuguesa, a study subsequently expanded upon by Fulhorst et al. (1999). These latter authors confirmed that *S. alstoni* is the reservoir of Pirital virus. No voucher specimens or museum names (where the animals may have been identified or are now deposited) are mentioned in the text.

S. alstoni is common throughout unforested and deforested habitats below about 1,300m elevation east of the Andes and south of the coastal cordilleras, including all of the Llanos, some isolated savannas in the Venezuelan state of Amazonas, deforested regions in the northeastern Venezuelan highlands, the Gran Sabana in southeastern Venezuela, the savannas of the upper Rio Branco in Brazil, the Rupununi savannas of Guyana, the coastal and interior savannas of Suriname, and contiguous savannas in the upper Rio Parú drainage of the Brazilian state of Pará (Voss 1992). The species is said to be diurnal and nocturnal, and terrestrial.

Ibañez and Moreno (1982, cited in Voss 1992) concluded that this species is herbivorous based on the examination of stomach contents. Voss (1992) reported pregnancies throughout the annual cycle of flooding and drought that characterizes this extremely seasonal environment, but reproductive activity may be least in the dry season, based on autopsies of over 150 animals; the number of embryos counted *in utero* ranged from 2 to 8, with a mean of 4.4. Vivas (1986) suggested that females of this species are reproductively active all year round in the Llanos of Venezuela.

3 A Synthesis of the Evolutionary History of Murid Rodents

The most obvious generalization that can be made about the mammal reservoir species of arenaviruses is that (with the exception of Tacaribe) they are all

members of two groups (currently classified at the subfamilial level) of rodents in the family Muridae. These two groups (sometimes also treated as families) are the Murinae and Sigmodontinae. Primarily African and Asian, murine rodents are the ecological counterparts of the sigmodontine rodents of the Western Hemisphere. With close to 300 genera and over 1,300 species, murid rodents are the most speciose family of mammals (Musser and Carleton 1993). This diversity is increasing at an accelerated pace: for example, Patterson (2000) has shown that 22 new species of murid rodents have been described in South America alone from 1992 to 1998. A detailed analysis of the evolution of murid rodents is beyond the scope of this chapter, but the following summary may contribute to an enhanced understanding of the evolutionary setting of Muridae–Arenavirus coevolution.

Hartenberger (1998) proposed that the lower Eocene (ca. 55Mya) form from Siberia, *Ivanantonia efremovi*, might represent the first murid rodent. Although the evolutionary history of murid rodents is probably more complex than the fossil record indicates, there appear to have been three major temporal climatically driven episodes that have defined the ecological success of this group. The first event probably occurred at the boundary between the Eocene and Oligocene, characterized by a dramatic climate change with a tendency to a major latitudinal zonation, an increase in seasonality, and a major faunal turnover, which has been designated in Asia as the Mongolian remodelling (Meng and McKenna 1998), in Europe (e.g., Cuenca and Canudo 1992) as the "Grande Coupure", and even extended into North America by Hartenberger (1998). The most dramatic cooling episode was at 33.5Mya, slightly subsequent to the Eocene/Oligocene boundary, and was characterized by a severe drop in mean annual temperature and changes in vegetation from Eocene dense forests to more open country during the Oligocene. In Mongolia and Europe, mammal faunae changed to be dominated by rodents and lagomorphs. This is the time of the split of the major groups of muroid rodents. At about the same time, hystricognath rodents (cavies, porcupines, and their allies) arrived in South America (Flynn and Wyss 1998). As a result of these faunal turnovers, murid rodents arrive in Europe from Asia. Several forms may have made it to North America as well but went extinct ca. 16Mya [e.g., Eucricetodontinae, Eumyinae (Flynn et al. 1985)].

The second major event is concurrent with the beginning of the Miocene (~23Mya) when the connections between Africa and Europe and North America and Asia were reestablished due to a reduction of sea level (Hamilton 1983). Ruedas and Kirsch (1997) presented a constructive discussion of the timing and players of the murine evolution in Asia, and Denys (1999) presented a complete analysis for Africa. The latter author suggested that the first true murine rodent from Africa is an undetermined *Praomys*-like genus from Chorora, Ethiopia (~10Mya) and *Karnimata* from Namibia (8–9Mya). In North America, the fossil record of ~16Mya is dominated by the presence of *Copemys*, a genus with obscure relationships to Old World forms that may have given rise to most contemporary genera of the tribal-level group Peromyscini (i.e., *Neotoma*, *Ochrotomys*, *Osgoodomys*, *Peromyscus*, etc.). Although current systematic treat-

ments consider this tribe as part of the subfamily Sigmodontinae (cf. Musser and Carleton 1993), recent molecular analysis (Engel et al. 1998) suggests that this subfamily may be polyphyletic. In this work, members of the North American Peromyscini and the (mostly) South American Sigmodontini are not sister to each other, indicating that they may have originated from separated lineages. Baskin (1986) suggested that *Abelmoschomys* (from the Clarendonian of Florida, ~9Mya) is the first true sigmodontine. Czaplewski (1987) further recorded several forms assigned to Sigmodontinae from Arizona (ca. 4.5–5Mya), including members of the now exclusively South American tribe Akodontini and *Sigmodon* proper.

The beginning of the Pliocene was punctuated by the development of open environments which were apparently driven by a CO_2 starvation phenomenon (Cerling et al. 1997, 1998) documented in the tropical regions at around 8–7Mya. As a result, the number of rodent groups and genera increased, and most current-day associations were formed at that time. The connection of South America to North America with the establishment of the isthmus of Panama occurs at 3.5–7Mya, setting the scene for a full-scale Great American Biotic Interchange (GABI) that filtered representatives of South American forms from proceeding north while allowing the incursion of numerous northern taxa into South America. It is postulated, however, that the oldest sigmodontine rodent in South America (*Auliscomys formosus* from Argentina, ~4.5Mya) may predate the GABI (Pardinas and Tonni 1998). Two lines of evidence are helpful to understand this conundrum. First, Knowlton and Weigt (1998) proposed that the closure of the isthmus was gradual and may have started up to 7Mya before complete closure. Secondly, molecular phylogenies have proposed that the radiation of the Sigmodontinae may have been earlier than the fossil record suggests (Salazar-Bravo et al. 2001; Smith and Patton 1999).

Of the major groups of murid rodents (murines, cricetines, arvicolines, and sigmodontines), only two are known to be reservoirs for arenavirus.

Considering that Murinae and Sigmodontinae are not sister taxons (cf. Dickerman 1992; Engel et al. 1998; Conroy and Cook 1999), it is tempting to suggest that early muroid rodents (like *Ivanantonia* or later forms) may have harbored arenaviruses or arenavirus-like forms well before the 30Mya figure mentioned elsewhere (e.g., Bowen et al. 1997). Such a scenario results in a testable hypothesis: if arenaviruses had infected earlier forms, then all remaining murid subfamilies (cf. Musser and Carleton 1993) should have genera that currently also harbor arenaviruses. Africa is the place to test this hypothesis as many subfamilies of Muridae – albeit not overly speciose – presently occur there. An alternative conclusion would suggest that arenaviruses might have infected the immediate ancestor of both Sigmodontinae and Murinae (which are not, however, each other's closest relatives). Since this putative ancestor must perforce also be ancestral to the Cricetinae, this latter subfamily must also have lineages infected with arenaviruses. A similar scenario has been proposed for hantaviruses (Hjelle and Yates 2001). These are all testable hypotheses and as such constitute a rich field for future research.

4 Ecological and Geographic Generalities of the Mammalian Reservoirs of Arenaviruses

A final important aspect to be considered is that, for the most part, the genera (and sometimes species) of rodents that are involved are among the most diverse and abundant elements of the ecosystems that occupy. *Oryzomys*, *Calomys*, *Mastomys*, *Bolomys*, *Arvicanthis*, etc. are highly abundant and considered by many to be akin to pest species. As Ashford (1997) suggested, the main population factor favoring a reservoir role are high density and longevity sufficient to provide a habitat for the parasite during any season or period of nontransmission (i.e., the ability of serving as "viral" refugia). Most rodent reservoirs identified thus far conform to this requisite.

Furthermore, there are some data that tend to indicate a certain level of "correlation" between population abundance and viral infection (or at least seroprevalence). In most epidemiological work ensuing from outbreak responses, rodent trapping usually results (depending on the geographic location) in the capture of one or two species of rodents in rather abundant numbers and a few more with lower levels of abundance. Usually, one of the more abundant species is also the reservoir species. In some extreme cases, if there are two "more abundant" species, each may harbor a different arenavirus (e.g., *Zygodontomys*/*Sigmodon* and Guanarito/Pirital or *Calomys*/*Bolomys* and Junín/Oliveros). There are, however, several other cases where even in relatively diverse and heterogeneous habitats (e.g., mountain forests in Colombia) and even after a large number of mammal species have been tested, only one (the most abundant) tests positive for the virus (e.g., Pichindé).

Another pattern is that most arenaviruses appear to use as reservoirs species that inhabit low to middle elevations. Certainly, no arenaviruses are known from elevations above 2,500m in the New World; Pichindé set the record, as it has been isolated from *O. albigularis* collected from a forest patch at Munchique (2,500m). In the Old World, with one possible exception, none of the mammal host species of arenaviruses occur above 2,000m. The one possible exception is *Mus domesticus*. This species can inhabit high elevations and does so in particular in the Pamir region of Pakistan and Kashmir, as well as in the Caucasus. However, as noted in the foregoing section on LCM, we cannot know with any degree of certainty whether it is *M. domesticus* or *M. musculus* (or both) which definitively hosts that virus. We might make a case, based on our hypothesis that if it is only species restricted to the lower elevations which host arenaviruses, that it is unlikely that *M. domesticus* is the host for LCM, which then would be restricted to *M. musculus*. This is a testable hypothesis that merits further investigation. Two further caveats conflate a tidy picture: (1) the most likely source for the émigré populations in the New World, that is Western Europe, is predominantly inhabited by *M. domesticus*; and (2) there exist populations of *M. musculus* in the Pamir (e.g., *M. m. theobaldi*, *M. m. pachycercus*) which also exist at high elevations. We suspect that the full

extent of the biodiversity at present collectively amalgamated into *M. domesticus* and *M. musculus* far underdescribes the biological reality of their taxonomic distinctiveness.

The pattern holds even if species in arenavirus-infected genera are also "available" at higher elevations. For example, *Calomys lepidus* and *C. sorellus* are closely related to *C. musculinus* (Salazar-Bravo et al. 2001), yet to date, no arenavirus has been described from either of the former species. Is this a sampling artifact? Perhaps. We submit that virologists should make use of phylogenetic analyses of those mammal genera known to serve as arenavirus reservoirs and test associated taxa for potential new species of arenaviruses.

It could be argued, moreover, that the patterns discerned here will change when and if more data are available. At present, it is clear that most arenaviruses have been discovered in the aftermath of outbreaks and therefore in a haphazard manner. A more systematic pursuit of arenaviruses in the freezers of mammalogists the world over will eventually show results one way or the other.

Lastly, one phenomenon evident in all of the species of disease-causing arenaviruses known to date is that there is an incomplete pattern of overlap between the distribution of the mammal species reservoir and that of the endo-epidemic zone of infection. This pattern is congruent with Pavloskii's concept of natural nidality (Pavloskii 1966). Pavloskii's definition is interpreted here as a dynamic process wherein several members (i.e., virus, reservoir, vectors) of an ecosystem in a particular geographic location (or biopathocenose) interact to promote the continuous circulation of the disease agent. Humans in the Pavloskii sense would then act as "sentinels" of these localized diseases. In Pavloskii's definition, the distribution of the disease does not necessarily correspond to the distribution of any element of the biopathocenose, a phenomenon distinctly observable in mammal host–arenavirus distributions.

5 Concluding Remarks and Recommendations

The underlying theme of the foregoing sections is uncertainty: there cannot be full knowledge of a zoonotic virus without knowledge of its reservoir; measures to attenuate the effects of viruses from a public health standpoint are doomed to failure if the host is unknown or, worse yet, if the host is misidentified. The basic alpha-level taxonomy of the mammalian hosts of arenaviruses is fluctuating so that at times a probable arenavirus host is subsumed as a subspecies within a broadly distributed species (although the virus itself may be geographically restricted). Other times, the taxonomy may be better known from a molecular or chromosomal perspective, but characters amenable to field identification of the mammal host species are few or nonexistent. The critical problem here is not so much the lack of a fundamental taxonomic framework for African or American murid rodents (although this does impede progress) as the lack of specimens upon which to

undertake the research. Often, the initial research is undertaken, the animals given a cursory identification, and the specimens then disappear. The tools used by mammalogists to identify and further study the phylogenetic relationships of murid rodents are diverse. A perfunctory review of the current literature shows that characters ranging from general skull morphology and chromosomes to protein analyses and DNA sequencing are used to that effect. Thus, it is imperative that as much information as possible be obtained from the potential reservoirs. A potential – yet by no means exhaustive – list of ancillary material that should be obtained includes: chromosomes, cell suspensions, endoparasites, ectoparasites, stomach contents, tissues stored in alcohol and frozen, eye lenses, detailed information on habitat, trapping effort, etc. in addition to the voucher specimens, which usually consist of skins, skulls, whole body skeletons, or alcohol-preserved bodies. All of the ancillary materials need to be traceable to each other and to the voucher specimen by the assignation of an unique number that can serve as a link between them all. One such method is the New Mexico kryovoucher (NK) system used at the University of New Mexico. In this system, each specimen is assigned a unique NK number in the field at the beginning of the processing procedure. A wide variety of information is recorded on the NK data sheet, including the type of specimen prepared and the kind and amount of other materials (e.g., chromosomes, cell suspensions, tissues, parasites, etc.) that were taken from the specimen. Use of a single unique numbering system for tracking associated materials with a traditional voucher in the field has the advantage of allowing specimens to be given a number as soon as they are removed from the field. As a result, each worker in the process can label associated materials (e.g., parasites, tissues, etc.) with the same number and thus reduce confusion and errors that might occur using individual collector or preparator numbers. Such a system also has advantages for the storage and retrieval of these materials once they are in the collection. Because ancillary materials are stored numerically by NK number, the problem of wasted storage space common to taxonomically arranged collections is eliminated. Such a system is particularly valuable when ancillary materials and voucher specimens are deposited at different institutions. It also saves time once the collection is returned to the repository, because ancillary materials can be installed immediately without the need for ''recataloguing'' (Yates et al. 1996).

Deposition of specimens and their ancillary materials in a museum – where subsequent taxonomic work may be undertaken and the taxonomy constantly updated – is therefore more than a mere exercise in academic minutiae; rather, it is a *sine qua non* requirement of a research program wherein the outcome, human life and death, hangs in the balance.

N.B. While the manuscript was in revision, several papers pertinent to the ecology of mammalian reservoirs of Arenaviruses were published. Among them is the description of a new species of Arenavirus dubbed Allpahuayo by Moncayo et al. (2001). This virus was isolated from two species of arboreal rice rats of the genus *Oecomys*. Although the authors refer to their identifications as preliminary, some of the original virus isolates were identified by field number (e.g., CLHP 2098, CLHP 2472), and being deposited at the Natural Science Research Laboratory of

the Museum of Texas Tech are thus widely available for further taxonomic work. This Arenavirus was called PC-242 by Tesh et al. (1999).

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