Biological Journal of the Linnean Society (1997), *61:* 385–408. With 4 figures

Systematics of *Maxomys* Sody, 1936 (Rodentia: Muridae: Murinae): DNA/DNA hybridization studies of some Borneo-Javan species and allied Sundaic and Australo-Papuan genera

LUIS A. RUEDAS

Museum of Southwestern Biology, University of New Mexico, Albuquerque NM 87131, U.S.A.

JOHN A. W. KIRSCH

University of Wisconsin Zoological Museum, 250 North Mills Street, Madison WI 53706, U.S.A.

Received 26 July 1996; accepted for publication 5 December 1996

We compared five species of the murine genus *Maxomys* and representatives of nine other murid genera in a complete 15 × 15 DNA-hybridization matrix. FITCH trees were calculated for the entire suite of taxa and for subsets including only the five *Maxomys* and these together with the four nearest outgroups. All trees were validated by 'bootstrapping' and by jackknifing, performing both single- and multiple-deletions of taxa. The full 15 × 15 data set indicated a sister-group relationship between *Maxomys* and two pairs of genera (*Sundamys-Rattus sensu stricto* and *Niviventer-Leopoldamys*) that are more closely related to each other than to *Maxomys*; addition of data on *Bandicota* and *Berylmys* from another recent DNA-hybridization study confirmed that these genera are successive sister-taxa to the *Sundamys-Rattus* pair. *Mus-Myomys* and *Uromys-Melomys* were each distinct lineages from the above grouping of *Rattus sensu lato* species, and from the putative outgroup sigmodontine *Peromyscus*, but the interrelations of the three murine clades were unresolved. Within *Maxomys, M. surifer* and *M. bartelsii* are a related pair, and *M. ochraceiventer* probably forms an unresolved trio with *M. rajah* and *M. whiteheadi*. Calibration of a tree generated from saturation-corrected distances against a likely divergence-date of 12.2 Mybp for the separation of *Mus* and *Rattus* confirms a high rate of single-copy DNA change in murids (2.1%/Myr); and suggests that Sigmodontinae and Murinae diverged at around 15.3 Mybp, that *Maxomys* and the group of six other *Rattus sensu lato* separated approximately 7.6 Myr ago, and that *Maxomys* began to diversify 4.8 Myr ago.

ADDITIONAL KEY WORDS:—biogeography – evolutionary rates – molecular evolution – Sunda Shelf.

Correspondence to: L. A. Ruedas. e mail: lruedas@sevilleta.umn.edu

0024–4066/97/070385 + 24 $25.00/0/bj960129

CONTENTS

INTRODUCTION

> "It is obvious that anatomical evidence can be conflicting when it is applied to the determination of intergeneric relationships." (Tate, 1951:214)

The rodent genus *Maxomys* was established by Sody (1936) for *bartelsii* (Jentink, 1910), which until then had been included in the genus *Mus* Linnæus, 1758, and the taxonomy of *Maxomys* has fluctuated ever since. Ellerman (1941) included *Maxomys* as a subgenus of *Rattus* Fischer, 1803, with a composition similar to that as currently understood, including: *surifer* (Miller, 1900), *rajah* (Thomas, 1894), *panglima* (Robinson, 1921), *moi* (Robinson & Kloss, 1922), *inflatus* (Robinson & Kloss, 1916), and *hellwaldii* (Jentink, 1878), but also *Rattus* [=*Niviventer*] *coxingi* (Swinhoe, 1864) from Taiwan. Ellerman also described *dollmani* (Ellerman, 1941) as a subspecies of *hellwaldii*. However, in a subsequent work, Ellerman & Morrison-Scott (1951) included in the (then) subgenus *Maxomys* only the aberrant Annamese species *moi* (as a subspecies of *Niviventer coxingi*), together with other species now included in *Niviventer*: *N. niviventer* (Hodgson, 1836), *N. fulvescens* (Gray, 1847), *N. huang* (Gray, 1847) [=*N. fulvescens*], and *N. cremoriventer* (Miller, 1900). The inclusion of *M. moi* undoubtedly makes this a paraphyletic group, although our understanding of these and related genera is still incomplete, and *Niviventer* clearly is phylogenetically allied to *Maxomys* (Musser & Newcomb, 1983; this paper). Misonne (1969:128) regarded *Maxomys* as "a very homogeneous group [whose] dental pattern is easily recognizable among all the other groups of this *Rattus* division." However, his *Maxomys* similarly included species now allocated to *Niviventer*: consisting of *N. huang*, *N. fulvescens*, *N. lepturus* (Jentink, 1879), *N. eha* (Wroughton, 1916), *N. andersoni* (Thomas, 1911), *N. niviventer*, and *N. (=Maxomys) bartelsii*. Additional species of what currently is construed to constitute *Maxomys* (Musser, Marshall & Boeadi, 1979) were placed in the subgenus *Lenothrix* Miller, 1903 of *Rattus* by Ellerman & Morrison-Scott (1951), along with *rajah*, *surifer* (as a subspecies of *rajah*) and the Sulawesian *musschenbroekii* (Jentink,

1878). A more detailed summary of the taxonomic history of *Maxomys* was provided by Musser *et al.* (1979) together with a coherent definition of the genus.

Musser *et al.*'s definition of *Maxomys*, however, focused on which species belonged in the genus; only a general sketch of the morphological limits of these species was included. Similarly, although the species were treated as monophyletic, there was no attempt to discern their interrelationships. Musser *et al.* (1979) also noted that species they listed might be composite [e.g. Indochinese *vs.* Sundaic populations of *surifer*, discussed by Musser *et al.* (1979) and by Musser & Carleton (1993)]. In addition, some of what now are considered *Maxomys* may not belong in that genus: for example, specimens of *moi* display unusual dental morphology compared to other *Maxomys* (Ruedas, unpublished data); indeed, *M. moi* is distinct enough for Ellerman (1941) to have remarked that, along with *inflatus* and *hellwaldii* (the latter a Sulawesian species), *moi* differed markedly from remaining *rajah*-group *'Rattus'*. Sulawesian *Maxomys* likewise may warrant separate generic status (Musser, pers. comm.).

Finally, with respect to zoogeographic relationships among the various areas comprising the Malay Archipelago in particular, and the Indo-Australian Region in general (as defined by Corbet & Hill, 1992), the distributions of the constituent species of *Maxomys* make this a genus of singular utility. The species of *Maxomys* are distributed from mainland southeast Asia, throughout much of the Malay Archipelago to Sulawesi, Borneo, and Palawan, as well as on several of the smaller islands of the Sunda Shelf. Many of the species display limited (some montane) distributions, including for example *hylomyoides* (Robinson & Kloss, 1916) and *inflatus* on Sumatra, and *ochraceiventer* (Thomas, 1894), *bœodon* (Thomas, 1894), and *alticola* (Thomas, 1888) in Borneo, with widespread species (more than likely 'superspecies') overlain on disjunct distributional patterns [e.g. of *rajah, surifer*, and *whiteheadi* (Thomas, 1894)]. Thus, *Maxomys* presents itself as a species-rich genus embracing a wide range of morphological, geographic, ecological, and altitudinal variation that is reflected in at least 17 known species, most still requiring rigorous definition. Besides the more widespread and diverse *Rattus*, *Maxomys* is the only terrestrial rodent genus containing numerous species that is distributed from mainland southeast Asia, over islands on the Sunda Shelf and its edge, to Sulawesi and the Philippines. In fact, *Maxomys* is more diverse than any other rodent genus on the Malay peninsula and Sunda Shelf and outlying islands (Musser & Newcomb, 1983; Musser & Holden, 1991).

The purpose of the present research was to recover the relationships among a limited number of *Maxomys* species from Borneo and Java in order to determine the potential of *Maxomys* as a test organism for the illumination of zoogeographic relationships among land masses in Sundaland and Wallacea. In particular, if *Maxomys* were to prove monophyletic, then by determining the phylogenetic relationships among *Maxomys* species, and those of *Maxomys* with allied genera, it would be possible to formulate more robust zoogeographic hypotheses for Sundaland and Wallacea.

We caution the reader, however, that all of the *Maxomys* examined in this study are Sunda Shelf species. Besides the aberrant Indochinese *M. moi*, there may exist sufficient evidence to warrant some level of distinctiveness—perhaps even at the generic level—between the Sundaic and Sulawesian species currently in *Maxomys* [Musser & Carleton (1993), and references therein]. Because we were unable to secure tissues of any Sulawesian *Maxomys*, it currently is unclear at what categorical level such a distinction would be made from a molecular perspective. Whether or

not such a distinction were to be made does not, however, preclude a useful role for *Maxomys* in zoogeographic studies of Malesia: indeed, such a dichotomy (or trichotomy, if one considers *M. moi*) may even enhance the role of *Maxomys* in elucidation of biogeographic relationships among Malesian areas.

MATERIAL AND METHODS

Specimens examined

Frozen soft-tissue samples from two individuals each of five *Maxomys* spp., *Sundamys muelleri* (Jentink, 1879), *Niviventer cremoriventer*, and *Leopoldamys sabanus* (Thomas, 1887) were provided by Mark D. Engstrom of the Royal Ontario Museum; ethanol-preserved livers and DNA extracts from the other six taxa [*Melomys cervinipes* (Gould, 1852), *Mus musculus* Linnaeus, 1758, *Peromyscus eremicus* (Baird, 1858), *Myomys verreauxii* (Smith, 1834), *Rattus fuscipes* Waterhouse, 1839, and *Uromys caudimaculatus* (Krefft, 1867)] were drawn from the tissue library of the University of Wisconsin Zoological Museum (UWZM) Molecular Systematics Laboratory. Catalogue numbers and provenances are listed below.

Maxomys bartelsii. – INDONESIA: West Java; Cibodas; Royal Ontario Museum (ROM), 101913, 101914. *M. whiteheadi.* – INDONESIA: West Kalimantan (Borneo); Bukit Soeharto Experimental Forest, 60 km South of Samarinda; ROM 101987, 101989. *M. rajah.* – INDONESIA: East Kalimantan (Borneo); Lalut Birai Reserve Station, Kayan Mentarang Nature Reserve; ROM 102004, 102005. *M. surifer.* – INDONESIA: East Kalimantan (Borneo); Lalut Birai Reserve Station, Kayan Mentarang Nature Reserve; ROM 102078, 102086. *M. ochraceiventer.* – INDONESIA: East Kalimantan (Borneo); Long Sungan, 8 km NW Puak; ROM 102212, 102241. *Sundamys muelleri.* – INDONESIA: East Kalimantan (Borneo); Lalut Birai Reserve Station, Kayan Mentarang Nature Reserve; ROM 102074, 102075. *Niviventer cremoriventer.* – INDONESIA: East Kalimantan (Borneo); Long Sungan, 8 km NW Puak; ROM 102214, 102215. *Leopoldamys sabanus.* – INDONESIA: East Kalimantan (Borneo); Long Sungan, 8 km NW Puak; ROM 102218, 102219. *Rattus fuscipes.* – AUSTRALIA: Queensland; Kuruanda; UWZM 2882, 2883. *Uromys caudimaculatus.* – AUSTRALIA: Queensland; UWZM 2879, 2880. *Melomys cervinipes.* – AUSTRALIA: Queensland; UWZM 2884. *Myomys verreauxii.* – SOUTH AFRICA; UWZM 2878. *Mus musculus.* – USA: Dane County, Wisconsin; UWZM 1869, 2582. *Peromyscus eremicus.* – USA: Arizona; UWZM 1969, 1970.

Laboratory protocols

Methods for purification of DNA, preparation of extracts for iodination and hybridization, and evaluation of hybrids were as outlined in earlier papers (Bleiweiss, Kirsch & Matheus, 1994; Kirsch *et al.*, 1990), except that the single-copy fractions were separated at a higher Equivalent-C_0t (2260 rather than 1130) and amounts of driver DNA were reduced to 25 from 50 μg. All 14 species were labelled (one of them twice), and over 1000 hybrids were prepared, with tracer:driver ratios of *c.* 1:500.

Matrices and corrections to the data

A 15 × 15 matrix comparing the 14 species (including two labeled individuals of *Maxomys ochraceiventer*) was assembled from two or more 'runs' of up to 25 hybrids with each of the 15 tracers, the Δs being calculated from 56° or 72°C with reference to 2–17 homoduplexes per label and indexed as ΔT_ms (median melting-temperatures of hybridized sequences). Due to the marked and variable low-temperature peak characteristic of murid hybrids (Brownell, 1983), modes were unrecoverable for most of the more distant comparisons, even when the starting-temperature was taken as 72°C. The table-wide average standard-deviation (SD) of ΔT_ms calculated from 56°C was about four times that of the SD on ΔT_m values calculated from the higher temperature, again reflecting the variance introduced by the low-temperature peak. Reciprocal values in the matrices were corrected for asymmetry by the method of Sarich & Cronin (1976) to obviate systematic experimental error [the 'compression effect' of Springer & Kirsch (1991)], which was severe only for the *Myomys* label due to poor preservation of the *Myomys* tissues. Such corrections were carried out separately for 15 × 15, 10 × 10, and 6 × 6 partitions of the data. Tables of ΔT_{50}Hs (median melting-temperatures corrected for percent hybridization) for all species and ΔT_{mode}s (peak melting-temperatures) for the nine more-closely related species also were compiled and analyzed in parallel with the ΔT_ms as noted below, but are not, for reasons of space, shown here; these tables and the corresponding results are available from either author.

Phylogenetic analyses and validation

Subsets of the data (15 × 15, 10 × 10, and 6 × 6) were analysed by FITCH (version 3.5c; Felsenstein, 1993), using the global branch-swapping, subreplicate, and Cavalli-Sforza & Edwards options, and varying the input-order of taxa 100 times except for the 6 × 6 subsets. Subdivision of the matrix was undertaken because of evidence that ingroup topology (especially among closely related species, as of *Maxomys*) may be affected by the choice of outgroups and small random variations in reciprocal ingroup-outgroup distances (Kirsch, Lapointe & Foeste, 1995). The fitted pathlengths on the FITCH trees were correlated with the original distances in order to obtain an estimate of how well the data conformed to the assumption of additivity. The 15- and 10-taxon trees were validated by Krajewski & Dickerman's (1990) adaptation of bootstrapping for distance data (a technique for exploring measurement error), generating a consensus of 1000 pseudoreplicate trees in each case; and by the jackknife for weighted trees of Lapointe, Kirsch & Bleiweiss (1994). For the 10-taxon sets, single- and all possible combinations of single- or multiple-deletions of taxa (847) were carried out; for the 15-taxon sets, 500 random- as well as all single-deletions were performed. In all cases, the pathlengths on the jackknife trees were compiled and FITCH trees calculated from the averages, minima and maxima observed. In addition, the 15-, 10-, and 6-taxon submatrices were tested for phylogenetic (or other) structure using an adaptation of the Mantel test (Dickerman, 1992). This test (providing a z-score) amounts to comparing the sums-of-squares of a large number of trees (here, 1000 for the 15- and 10- taxon sets; 500 for the 6 × 6 matrices) calculated from randomized data with that of a tree generated from the unrandomized matrix. Only column values are randomized and the diagonal

elements (homologous comparisons) are kept constant. The expectation is that the sum-of-squares for phylogenetically or otherwise structured data will lie two or more standard deviations from the mean for randomized information. Because outgroups may render this test too liberal by introducing large distances between the in- and outgroups, we carried out these tests on 6×6 submatrices of *Maxomys* spp. alone, as well as on the 15×15 and 10×10 subsets.

Finally, in an attempt better to understand the contribution of individual variation to differences among the trees, we conducted a partitioned analysis on the 10-taxon ΔT_m data calculated from 72°C: the data were divided into subsets corresponding, respectively, to comparisons involving only the *autologous* extracts (those that were labeled) or the second, *allologous*, individual of each species. FITCH trees were generated from each subset, and the submatrices were bootstrapped 1000 times and jackknifed both exhaustively and with single-deletions of taxa.

Rate-determination and dating of divergences

An empirical regression-equation relating ΔT_{50}Hs to ΔT_ms was determined to allow for inclusion of ΔT_m comparisons with *Bandicota bengalensis* (Gray & Hardwicke, 1833) and *Berylmys bowersi* (Anderson, 1879), taken from Chevret (submitted), in a matrix that served as the basis for estimation of divergence-dates; some additional measurements were added from Chevret *et al.* (1994). All ΔT_ms were converted to ΔT_{50}Hs using this equation; missing comparisons were estimated by the procedures of Landry, Lapointe & Kirsch (1996) and Lapointe & Kirsch (1995); and the data were further calibrated for percent sequence-divergence (Springer, Davidson & Britten, 1992) and corrected for multiple-hits (Jukes & Cantor, 1969). These manipulations result in more realistic estimates of longer distances (Springer & Krajewski, 1989), and begin with ΔT_{50}H-converted ΔT_ms in order to take into account any differences in percent hybridization among the taxa. Subreplicate numbers for estimated and reflected cells in the matrix were arbitrarily set equal to one in computing a FITCH tree from these 'ΔT_mH-C' distances [percent sequence-divergences (Catzeflis *et al.*, 1987]), the distances were correlated with the tree-fitted pathlengths, and the matrix was jackknifed with both single- and 500 random-deletions. Because this and all other trees displayed some apparent rate-non-uniformity, we then forced the FITCH ΔT_mH-C topology onto a KITSCH computation in order to obviate the effects of such variation. The KITSCH tree was initially calibrated against the putative *Mus-Rattus* separation-date of 10 Myrbp (Catzeflis *et al.*, 1987), as that is the figure usually employed for calibration of cladogenic events in murid molecular studies, and the resulting rate was used to determine other divergence-dates from the ultrametric pathlengths on the KITSCH tree. However, other estimates for the *Mus-Rattus* divergence suggest that this event occurred as at least as early as 12.2 Mybp (see Discussion). We therefore calculated dates based on both the 10 (for comparison with previous studies) and 12.2 Mybp calibration points.

RESULTS

Tables, randomization tests and figures

Table 1 presents the unsymmetrized ΔT_m data for all 14 species (calculated from 56°C), with the corrections (column-multipliers) for 10-, 15-, and 6-taxon subsets

TABLE 1. Unsymmetrized ΔT_ms among 14 species of Muridae, calculated from 56°C; total number of hybrids = 1028. First line of each cell gives average Δ, except that actual mean melting temperature of the homologue is provided as appropriate to allow comparison of label qualities. Second line gives standard deviation (SD) and number of replicates, separated by a slash. Columns are tracers, identified by first four letters of genus-name and first letter of specific epithet, given in rows, except for the two individuals of *Maxomys ochraceiventer* (designated *MaxoO1* and *MaxoO2*). Unweighted average SD for cells with more than one measurement = ±0.84°C for all 15 taxa, ±1.13°C for ten, and ±1.20°C for six. Corrections at bottom of table are column-multipliers used to effect symmetrization, which was performed separately for three subsets of the data. Asymmetry for 15 taxa before and after symmetrization = 8.62% and 3.46%, respectively; for ten taxa, 5.36% and 4.35%; for six, 10.03% and 4.09%. Abbreviation: na = not applicable

	PeroE	*MusMu*	*MyomV*	*MeloC*	*UromC*	*LeopS*	*NiviC*	*RattF*	*SundM*	*MaxoB*	*MaxoO1*	*MaxoO2*	*MaxoR*	*MaxoS*	*MaxoW*
Peromyscus	80.17	20.44	12.94	14.72	18.22	21.67	21.04	19.72	18.99	18.84	17.46	19.80	18.56	19.19	18.02
eremicus	0.75/2	0.47/2	0.16/2	0.57/2	0.06/2	0.13/2	0.04/2	0.06/2	0.28/2	0.49/2	0.74/2	na/1	0.12/2	0.01/2	0.21/2
Mus	19.03	82.84	8.68	13.23	14.12	16.41	16.48	16.21	16.45	16.17	13.79	15.59	15.30	16.31	14.97
musculus	0.07/2	0.30/3	0.55/2	2.05/2	0.45/2	1.17/2	0.22/2	0.44/2	1.77/2	0.05/2	0.23/2	0.09/2	0.33/2	0.65/2	0.68/2
Myomys	18.28	18.03	74.84	14.92	16.38	18.70	18.71	17.95	18.04	17.76	15.07	18.11	17.53	17.83	16.87
verreauxii	0.03/3	0.50/4	1.64/4	0.31/3	0.60/3	0.95/4	0.67/4	0.81/3	0.40/4	0.18/4	0.35/2	0.12/4	0.45/3	1.09/4	0.88/4
Melomys	18.77	17.85	9.82	77.35	5.65	16.67	17.38	17.70	17.45	16.71	14.63	16.84	16.45	16.97	15.68
cervinipes	0.07/4	0.82/4	0.52/3	3.42/4	0.60/4	1.36/4	0.41/4	0.97/4	1.43/4	0.34/4	0.30/2	0.49/4	0.43/4	0.89/4	0.70/4
Uromys	18.68	16.81	9.11	3.58	80.82	16.07	16.77	16.60	16.47	15.70	13.97	15.79	14.47	14.82	15.58
caudimaculatus	0.34/4	0.84/4	0.71/4	1.20/3	0.39/5	0.83/4	0.60/4	1.14/4	0.97/4	0.46/4	0.29/3	0.37/4	1.46/6	1.31/4	0.44/3
Leopoldamys	19.18	16.99	10.53	12.80	13.35	83.95	5.05	8.37	8.50	11.00	9.64	10.98	10.15	10.91	9.20
sabanus	0.20/3	0.90/3	0.11/3	0.15/3	1.19/4	0.99/4	1.13/4	1.38/4	1.41/4	1.08/7	0.82/3	0.50/3	1.78/4	1.31/4	0.91/4
Niviventer	18.88	16.89	9.11	13.13	15.20	5.28	82.79	8.53	8.49	11.28	10.16	11.19	9.27	11.02	10.21
cremoriventer	0.21/4	0.76/4	1.22/3	0.87/4	0.29/4	0.70/4	0.63/5	1.27/4	0.89/4	0.78/4	0.71/3	0.84/4	1.29/4	0.93/4	1.64/4
Rattus	18.66	17.28	10.32	14.15	15.21	9.34	9.69	81.72	4.62	11.92	10.52	12.02	10.90	11.65	10.56
fuscipes	0.05/4	0.80/4	0.23/3	0.78/4	0.50/3	0.95/4	1.13/4	0.58/5	1.99/4	0.69/4	1.04/3	0.68/4	1.49/4	0.73/4	1.58/3
Sundamys	18.95	17.83	10.80	13.14	15.70	8.17	8.50	4.41	81.47	11.17	11.04	11.27	9.73	10.93	10.56
muelleri	0.19/3	0.52/4	0.29/2	0.74/4	0.65/4	0.42/4	0.31/4	1.13/3	2.96/6	1.00/8	0.27/3	0.78/4	1.25/6	0.69/4	0.52/8
Maxomys	18.65	17.32	8.85	12.90	14.95	10.82	11.29	11.31	10.64	81.11	7.26	8.33	6.33	5.09	6.83
bartelsii	0.14/4	0.54/4	0.41/4	0.92/4	0.29/3	0.90/4	0.51/4	0.78/4	0.95/7	0.84/16	0.68/10	1.25/8	1.38/16	1.77/13	1.13/14
Maxomys	18.90	16.55	10.54	13.90	14.23	10.97	12.09	11.27	10.57	6.17	80.26	1.44	5.96	4.83	4.44
*ochraceiventer*1	0.15/2	0.66/2	0.14/2	na/1	0.70/2	0.63/2	0.89/2	1.91/2	1.89/4	1.42/7	0.74/9	0.82/7	0.88/7	1.63/7	0.43/6
Maxomys	18.37	16.17	9.17	14.41	14.78	10.82	11.19	12.42	10.44	7.68	1.73	82.19	6.99	7.53	6.87
*ochraceiventer*2	0.45/2	0.49/2	0.88/2	na/1	na/1	1.31/2	0.32/2	1.89/2	2.20/3	0.86/7	1.87/7	0.76/7	1.24/7	0.98/7	1.58/7
Maxomys	18.45	15.87	8.92	11.16	14.10	10.10	10.05	10.44	10.12	6.05	6.54	6.83	81.08	4.91	4.21
rajah	0.33/4	0.31/3	0.52/2	1.23/2	1.07/4	1.06/4	0.41/4	1.35/4	1.22/4	1.30/14	0.63/10	0.53/9	1.11/17	1.47/14	1.38/12
Maxomys	18.91	17.03	9.85	13.01	13.92	11.04	11.31	11.21	11.66	6.85	7.55	7.74	6.69	81.83	6.04
surifer	0.14/4	0.72/4	0.61/3	0.67/3	1.49/4	1.24/4	0.60/4	1.75/4	1.30/4	1.58/13	0.72/9	0.60/9	2.04/14	1.12/15	2.05/14
Maxomys	18.82	17.27	10.15	13.03	14.22	11.36	11.37	12.02	10.95	7.62	7.59	7.83	7.27	6.39	80.76
whiteheadi	0.09/4	0.59/4	0.49/3	0.86/4	1.51/3	0.85/3	0.94/3	1.83/4	1.92/6	1.68/14	0.77/10	0.36/8	2.20/13	2.37/13	1.07/15
Correction (15)	0.967	0.861	1.663	1.179	0.985	0.887	0.877	0.935	0.937	0.908	0.971	0.906	0.884	0.961	1.032
Correction (10)						0.959	0.951	1.013	0.999	0.973	0.936	0.977	0.939	1.078	1.171
Correction (6)										0.973	0.767	0.990	0.857	1.155	1.219

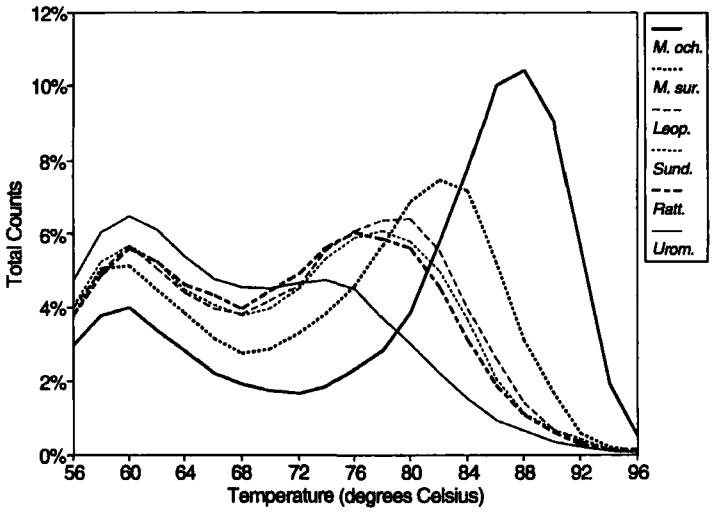

Figure 1. Representative stepwise thermal-elution curves of hybrids with labelled *Maxomys ochraceiventer*. Elutions at each temperature increment have been corrected for percent hybridization to indicate extent of reassociation as well as distribution of counts. Note the marked low-temperature (secondary) peak, which is higher for more distant hybrids. Abbreviations: *Leop.* = *Leopoldamys sabanus*; *M. och.* = *Maxomys ochraceiventer*; *M. sur.* = *Maxomys surifer*; *Ratt.* = *Rattus fuscipes*; *Sund.* = *Sundamys muelleri*; and *Urom.* = *Uromys caudimaculatus*.

used to ameliorate asymmetry listed at the bottom; the correction-factor for *Myomys* is unusually high, indicating severe compression of distances obtained with this label, because of the poor preservation of *Myomys* tissues mentioned above. Iterations of the Sarich-Cronin algorithm (that is, multiplication of column-values followed by recalculation of the row/column ratios) were repeated ten times or until there was no further reduction in percent asymmetry. Tables 2–4 are ΔT_ms calculated from 72°C for ten taxa (for the complete data, and for measurements partitioned among auto- and allologous extracts, respectively; there is of course some overlap between Tables 3 and 4 because of the inclusion of two labelled individuals of *M. ochraceiventer* —i.e., there were no allologous extracts for these tracers). Again, corrections for asymmetry are given beneath the columns in Tables 2–4. Table 5 shows the completed and corrected ΔT_mH-Cs for 17 taxa (folded; lower-left triangle), and the pathlengths between taxa on the KITSCH tree derived from these data (upper-right triangle). Table 6 lists some divergence-dates among Muridae based on our experiments and those of Chevret (submitted).

All of the z-scores on these data were significant at $P<0.01$. As expected, the scores were higher for subsets including more distant outgroups: those for six taxa (*Maxomys* only) ranged from 4.07 to 4.90; those for ten taxa (*Maxomys* and other *Rattus s. l.*), from 10.15 to 11.01; and that for 15 taxa was 13.80.

Figure 1 presents representative stepwise thermal-elution curves for a *Maxomys ochraceiventer* label. Individual values at each temperature increment have been corrected for percent hybridization to indicate the extent of reassociation. Note that all hybrids have a marked low-temperature peak. The secondary peak has been ascribed to poorly-matched paralogues (Fox & Schmid, 1980; Werman, Springer & Britten, 1990); this explanation is likely as in general the height (but not position)

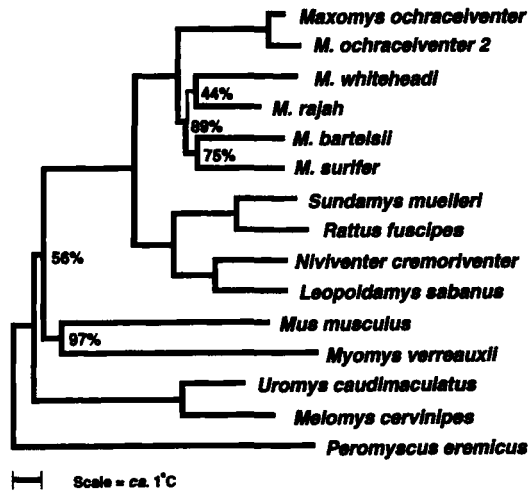

Figure 2. Best-fit FITCH tree of 15 murids, calculated from the symmetrized ΔT_m data of Table 1, with input order of taxa shuffled 100 times. Approximately to scale. Correlation of fitted branchlengths with original distances = 0.990. Numbers at nodes are bootstrap percentages (consensus of 1000 pseudoreplicate trees) when these were less than 100%. Thin lines indicate any discrepancies among the jackknives. Only the minimum-pathlengths single-deletion jackknife tree differed from the FITCH topology shown here for these ten taxa, placing *Maxomys whiteheadi* and *M. rajah* as successive sister-taxa to the *M. bartelsii-M. surifer* pair.

of that peak is directly correlated with the distance of a hetero- from a homoduplex. In the most distant comparisons (e.g. of *Maxomys* with *Peromyscus*) the mode could not be distinguished from the low-temperature peak; this is the reason we could not use ΔT_{mode}s for indexing comparisons among all fourteen species. In fact, the peak also contributed a great deal of variance to the ΔT_m comparisons (see table legends), such that calculations which excluded it (i.e. those calculated from 72°C; Tables 2–4) are more precise, having table-wide average standard-deviations (SDs) about one-fourth that of ΔT_ms calculated from 56°C.

Figures 2 and 3 are FITCH trees for several analyses of the ΔT_m data. For all of the trees shown the correlation of fitted branchlengths with the original distances is ≥ 0.990, indicating near-perfect additivity of the data. Bootstrap percentages (out of 1000 trials) are given at the nodes when these were less than 100%; branches not supported by all of the jackknives are depicted with thin lines (which index nodes that would collapse were a strict-consensus calculated). Note that in one case (Fig. 3B) the FITCH tree does not correspond exactly to the bootstrap consensus.

The regression equation relating mean ΔT_{50}Hs and mean ΔT_ms (Table 1) for 225 pairwise comparisons is $\Delta T_{50}H = 1.18 \times \Delta T_m$ ($r^2 = 0.97$). Transformation of ΔT_ms using this equation allowed inclusion of measurements among additional species represented in Chevret's (submitted) data, reported only as ΔT_ms, for the purposes of calibration and dating. Figure 4 shows the tree obtained after addition of these data and correction for sequence-divergence (Springer *et al.*, 1992) and saturation using the Jukes & Cantor (1969) one-parameter formula (Table 5, lower-left triangle; Figure 4 was calculated from the unfolded matrix). Missing comparisons were estimated by the procedures of Landry *et al.* (1996) and Lapointe & Kirsch (1995). Because the transformations were performed on mean Δs, the data could

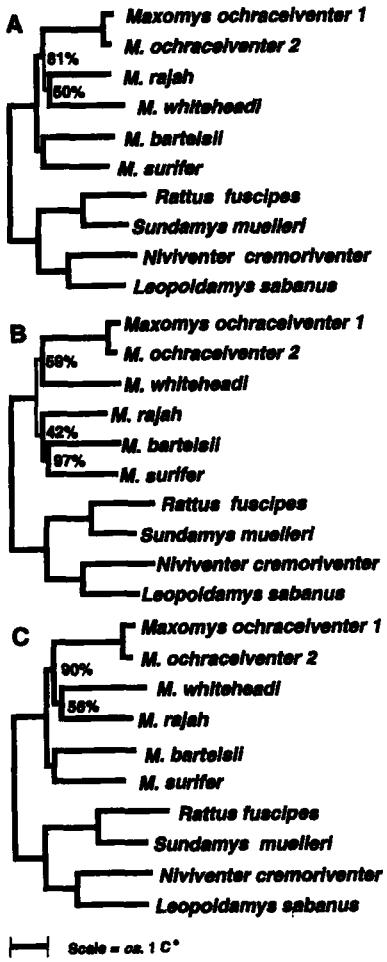

Figure 3. Best-fit FITCH trees of ten murines, calculated from the symmetrized ΔT_m data of Table 2–4, with input order of taxa shuffled 100 times. Approximately to scale. Numbers at nodes are bootstrap percentages (consensus of 1000 pseudoreplicate trees) when these were less than 100%. Thin lines indicate any discrepancies among the jackknives. A, tree from data of Table 2 (all measurements). Correlation of fitted branchlengths with original distances = 0.997. The average- and minimum- pathlengths single-deletion jackknife trees differed from the FITCH topology, placing *Maxomys whiteheadi* and *M. rajah* as successive sister-taxa to *M. ochraceiventer*, as did the minimum-pathlengths exhaustive-jackknive tree. B, tree from data of Table 3 (autologous comparisons only). Correlation of fitted branchlengths with original distances = 0.998. Note that the majority-rule bootstrap topology differed from the FITCH topology shown here, placing *Maxomys whiteheadi* and *M. rajah* as successive sister-taxa to *M. ochraceiventer* in 59% and 52% of the pseudoreplicate trees, respectively. The average- and minimum-pathlengths of both single- and exhaustive-jackknife trees matched the bootstrap consensus; while the maximum-pathlengths tree for single deletions was congruent with the FITCH topology, and that for exhaustive deletions put *Maxomys whiteheadi* and *M. rajah* together as a sister-taxon to *M. ochraceiventer*. C, tree from data of Table 4 (allologous comparisons only). Correlation of fitted branchlengths with original distances = 0.996. All jackknives were cogruent with the FITCH topology.

not be bootstrapped; but all jackknife trees (of either single- or 500 random-deletions) had the same topology as Figure 4. The correlation of pathlengths on this tree with the original distances is 0.983. A KITSCH version of Figure 4 provided the basis for rate-calibrations and estimates of divergence-dates among the 17 taxa (see below).

Phylogeny

The 15-taxon tree from ΔT_ms calculated beginning at 56°C (Fig. 2) displays three murine clades consisting of *Mus* with *Myomys*, *Melomys* with *Uromys*, and all others. The outgroup *Peromyscus* rooted that tree between *Melomys-Uromys* and the rest, but bootstrap support for the pairing of the other two murine groups was only 56%. Within the third murine clade, *Rattus* and *Sundamys* were paired, as were *Leopoldamys* and *Niviventer*; all four jointly were sister to *Maxomys*. Relationships among some species of the latter genus varied. For the FITCH and bootstrap trees, the two exemplars of *M. ochraceiventer* were the most distinct, with *M. surifer* and *M. bartelsii* paired and *M. whiteheadi* associated with *M. rajah* (with less than 50% bootstrap support) as the sister-taxon to *M. surifer* plus *M. bartelsii*. The average-consensus jackknife trees (whether for single- or random-deletions) did not differ from Figure 2, although the minimum-pathlengths single-deletion jackknife placed *M. whiteheadi* and *M. rajah* as successive sister-taxa to the *M. bartelsii-M. surifer* pair. Jackknife trees based on 500 random deletions were completely stable for both indices and again matched Figure 2 topologically. A validated tree calculated from ΔT_{50}Hs (not shown) differed from the ΔT_m-based tree mainly in resolving the basal murine trichotomy in favor of *Uromys-Melomys* as sister to *Rattus s. l.*

The FITCH tree founded on the 10-taxon subset of Table 1 (not shown) again placed *M. rajah* and *M. whiteheadi* with each other (but once more at a low bootstrap percentage: 39%) and together as sister to *M. bartelsii* plus *M. surifer* (with 73% support; *M. bartelsii* and *M. surifer* were paired with 80% bootstrap support); the node uniting *M. rajah* with *M. whiteheadi* was unstable in both the single- deletion and exhaustive jackknives. A tree based on the 6×6 subset of Table 1 (*Maxomys* spp.; not shown) joined *M. whiteheadi* and *M. rajah* not with each other but at nodes successive to that pairing the two *M. ochraceiventer* specimens, with *M. surifer* and *M. bartelsii* emanating from a separate point. Trees generated from ΔT_{50}H data for ten or six taxa were similar to those just described.

Thus, inclusion of ougroups did not materially affect *Maxomys* species-relationships, which were much the same in 15- and 10-taxon trees; but elision of the four other *Rattus s. l.* taxa did produce a distinct arrangement among *Maxomys* spp. alone. A strict consensus for analyses of trees generated from the three taxonomic subsets of Table 1 would therefore show a trichotomy among the paired *M. bartelsii* and *M. surifer*, *M. rajah*, and *M. whiteheadi*, with *M. ochraceiventer* sister to the other four *Maxomys* species.

However, as the average SDs of these data were rather high (± 0.84°C for all 15 taxa, ± 1.13°C for ten, and ± 1.20°C for six), we compiled ΔT_ms calculated from 72°C to reduce the variance caused by the low-temperature peak (Table 2). As anticipated, the average SDs for the data calculated from 72°C were much lower than those for Δs calculated starting at the lower temperature (± 0.23°C *vs.* ± 1.13°C, respectively, for ten taxa; and ± 0.29°C *vs.* ± 1.20°C, respectively, for six). Of course, elimination of the lower portions of the curves means that discrimination at greater distances is lost; for this reason we discuss analyses of these data only for *Maxomys* spp. alone and with their four nearest sister-taxa.

The resulting FITCH tree (Fig. 3A) calculated from Table 2 data for ten taxa gave a different placement of *M. rajah* and *M. whiteheadi* from that in Figure 2, with *M. rajah* and *M. whiteheadi* again paired (albeit with only 50% bootstrap support) but

TABLE 2. Unsymmetrized ΔT_ms among nine species of Murinae, calculated from 72°C; total number of hybrids = 641. Conventions as for Table 1. Unweighted average SD = ±0.23°C for all ten taxa; ±0.29°C for six. Asymmetry for ten taxa before and after symmetrization = 5.94% and 2.40%, respectively; for six, 7.37% and 4.13%

	LeopS	*NiviC*	*RattF*	*SundM*	*MaxoB*	*MaxoO1*	*MaxoO2*	*MaxoR*	*MaxoS*	*MaxoW*
Leopoldamys	85.54	3.89	5.80	6.52	7.45	6.66	7.15	6.73	7.26	6.57
sabanus	0.37/4	0.34/4	0.10/4	0.19/4	0.24/7	0.08/3	0.12/3	0.24/4	0.09/4	0.09/4
Niviventer	4.68	84.78	6.46	7.00	7.63	7.00	7.56	6.58	7.43	6.87
cremoriventer	0.24/4	0.40/5	0.09/4	0.10/4	0.41/4	0.30/3	0.38/4	0.68/4	0.26/4	0.37/4
Rattus	7.13	6.97	84.46	4.10	7.95	7.07	7.79	7.10	7.62	7.05
fuscipes	0.26/4	0.21/4	0.26/5	0.50/4	0.09/4	0.07/3	0.24/4	0.14/4	0.13/4	0.02/3
Sundamys	6.33	6.16	2.88	85.25	7.48	6.83	7.29	6.75	7.16	6.72
muelleri	0.15/4	0.07/4	0.34/3	0.36/6	0.14/8	0.03/3	0.06/4	0.16/6	0.23/4	0.11/8
Maxomys	7.88	7.72	7.40	8.11	84.44	4.48	5.02	4.32	4.13	4.54
bartelsii	0.21/4	0.08/4	0.23/4	0.14/7	0.42/16	0.22/10	0.25/8	0.29/16	0.20/13	0.33/14
Maxomys	7.98	7.87	7.15	8.01	5.14	83.83	0.79	4.24	4.67	4.42
*ochraceiventer*1	0.11/2	0.21/2	0.06/2	0.15/4	0.22/7	0.21/9	0.22/7	0.34/7	0.36/7	0.44/6
Maxomys	7.89	7.69	7.37	8.05	5.08	0.28	84.79	4.12	4.69	4.04
*ochraceiventer*2	0.23/2	0.01/2	0.15/2	0.28/3	0.28/7	0.25/7	0.28/7	0.24/7	0.23/7	0.37/7
Maxomys	7.73	7.49	7.15	7.82	4.79	4.15	4.64	84.06	4.23	3.78
rajah	0.30/4	0.03/4	0.14/4	0.24/4	0.28/14	0.25/10	0.20/9	0.42/17	0.21/14	0.34/12
Maxomys	7.79	7.52	7.26	7.89	4.72	4.35	4.78	4.03	84.43	4.29
surifer	0.29/4	0.13/4	0.11/4	0.14/4	0.16/13	0.27/9	0.21/9	0.25/14	0.32/15	0.30/14
Maxomys	7.97	7.80	7.37	8.16	5.31	4.35	4.93	4.38	4.63	83.72
whiteheadi	0.12/3	0.09/3	0.09/4	0.24/6	0.25/14	0.22/10	0.20/8	0.29/13	0.31/13	0.70/15
Correction (10)	0.897	0.974	1.063	0.885	0.955	1.090	0.965	1.052	1.001	1.110
Correction (6)					0.911	1.087	0.901	1.013	0.989	1.093

closer to *M. ochraceiventer* than to the *M. bartelsii-M. surifer* pair, and with varying results in both single- and exhaustive jackknives (see caption to Fig. 3). Trees (not shown) for just the *Maxomys* species had topologies consistent with the consensus for that including the four outgroups, and therefore also with the 6-taxon trees derived from the ΔT_ms calculated from 56°C. Trees based on ΔT_{mode}s (not shown) gave similar results, always placing *M. rajah* and *M. whiteheadi* with *M. ocraceiventer.*

Because some trees (also not shown) based on matrices including just one or the other of the two *M. ochraceiventer* labels suggested that individual variation might be a cause of the varying arrangements among *Maxomys* spp., we carried out two additional sets of analyses with data partitioned according to whether the measurements involved hybrids made with autologous or allologous extracts (the first type being those used to generate the tracers), again calculating FITCH trees and bootstrapping and jackknifing (with both single and exhaustive deletions) the 10-taxon submatrices (Tables 3 and 4); the resulting trees are shown in Figure 3B, C.

Interestingly, for the autologous comparisons the FITCH tree (Fig. 3B) placed *M. whiteheadi* with *M. ochraceiventer*, and *M. rajah* with *M. bartelsii-M. surifer*; but the bootstrap consensus put *M. whiteheadi* and *M. rajah* successively further from (but both closer to) *M. ochraceiventer.* There was only 52% support for this grouping of species, and these nodes were unstable in the jackknife analyses. On the other hand, FITCH (Fig. 3C) and all jackknives for allologous comparisons were consistent in pairing *M. rajah* and *M. whiteheadi* together as a sister-taxon to *M. ochraceiventer*, although bootstrap support for the union of *M. whiteheadi* with *M. rajah* was only 56%. Trees for *Maxomys* spp. by themselves, for either autologous or allologous

TABLE 3. Unsymmetrized ΔT_ms among nine species of Murinae, calculated from 72°C, for autologous extracts only; total number of hybrids = 379. Conventions as for Table 1. Unweighted average SD for cells with more than one measurement = ±0.19°C for all ten taxa; ±0.25°C for six. Asymmetry for ten taxa before and after symmetrization = 4.97% and 2.22%, respectively; for six, 6.68% and 3.89%

	LeopS	*NiviC*	*RattF*	*SundM*	*MaxoB*	*MaxoO1*	*MaxoO2*	*MaxoR*	*MaxoS*	*MaxoW*
Leopoldamys	85.55	3.92	6.04	6.56	7.67	6.69	7.23	7.06	7.44	6.99
sabanus	0.45/3	0.07/2	0.04/2	0.22/2	0.19/3	0.10/2	na/1	0.01/2	0.01/2	0.16/2
Niviventer	4.50	84.97	6.64	6.99	8.12	7.16	7.87	7.33	7.79	7.58
cremoriventer	0.22/2	0.41/3	0.15/2	0.11/2	0.30/2	0.18/2	0.13/2	0.02/2	0.11/2	0.20/2
Rattus	7.06	7.27	84.62	3.89	8.12	7.10	7.64	7.28	7.70	7.48
fuscipes	0.37/2	0.07/2	0.09/3	0.35/2	0.15/2	0.08/2	0.01/2	0.15/2	0.18/2	na/1
Sundamys	6.22	6.29	2.94	85.26	7.60	6.84	7.33	6.98	7.40	7.07
muelleri	0.01/2	0.04/2	na/1	0.43/4	0.16/4	0.04/2	0.08/2	0.15/4	0.33/2	0.04/4
Maxomys	7.75	7.87	7.39	8.15	84.62	4.35	5.08	4.45	4.35	4.82
bartelsii	0.20/2	0.05/2	0.12/2	0.16/4	0.30/9	0.16/5	0.12/3	0.27/9	0.23/7	0.25/7
Maxomys	7.98	8.06	7.30	8.02	5.32	83.83	0.79	4.40	4.81	4.83
ochraceiventer1	0.11/2	0.21/2	0.06/2	0.15/4	0.22/7	0.21/9	0.22/7	0.34/7	0.36/7	0.44/6
Maxomys	7.89	7.87	7.52	8.06	5.26	0.28	84.79	4.28	4.83	4.45
ochraceiventer2	0.23/2	0.01/2	0.15/2	0.28/3	0.28/7	0.25/7	0.28/7	0.24/7	0.23/7	0.37/7
Maxomys	7.85	7.69	7.21	7.74	4.88	4.29	4.70	84.22	4.34	4.21
rajah	0.44/2	0.00/2	0.06/2	0.13/2	0.22/7	0.08/5	0.25/4	0.14/10	0.27/7	0.27/5
Maxomys	7.77	7.74	7.43	7.97	4.89	4.49	4.82	4.19	84.57	4.72
surifer	0.18/2	0.21/2	0.05/2	0.19/2	0.12/7	0.28/4	0.30/4	0.22/7	0.17/8	0.26/7
Maxomys	8.07	7.98	7.55	8.10	5.39	4.42	4.90	4.51	4.80	84.13
whiteheadi	na/1	0.13/2	0.03/2	0.39/2	0.16/7	0.27/5	0.26/3	0.29/7	0.27/7	0.40/9
Correction (10)	0.922	0.992	1.056	0.903	0.943	1.108	0.983	1.034	1.001	1.053
Correction (6)					0.909	1.112	0.929	1.019	0.997	1.031

comparisons, were like those described above for the 6-taxon subsets of Tables 1 and 2.

In sum, results of the partitioning of ΔT_ms calculated from 72°C were largely consistent in uniting *M. ochraceiventer*, *M. rajah*, and *M. whiteheadi*, but differed from trees based on the ΔT_m data for 15 or ten taxa calculated from 56°C, which placed *M. rajah* and *M. whiteheadi* nearer to the *M. bartelsii-M. surifer* pair and therefore all four jointly as sister to *M. ochraceiventer*. However, *M. bartelsii* and *M. surifer* were consistently associated throughout the analyses (Figs 2 and 3), as of course were the two exemplars of *M. ochraceiventer*. A strict-consensus for the relationships among *Maxomys* spp. inferred from *all* FITCH, bootstrap, and jackknife trees would therefore depict a quadrichotomy amongst *M. ochraceiventer*, *M. rajah*, *M. whiteheadi*, and the *M. bartelsii-M. surifer* pair.

Calibration and dating

Figure 4 shows the relationships among the taxa we have studied, with the addition of information on *Bandicota* and *Berylmys* taken from Chevret (submitted). Because this tree includes all outgroups and was ultimately based on ΔT_ms calculated from 56°C, relationships among *Maxomys* spp. correspond more closely to those of Figure 2 than to those of Figure 3. Table 5 (upper-right triangle) presents the ultrametric pathlengths among all pairs of taxa shown in Figure 4 when the FITCH

TABLE 4. Unsymmetrized ΔT_ms among nine species of Murinae, calculated from 72°C, for allologous extracts only; total number of hybrids = 366. Conventions as for Table 1. Unweighted average SD for cells with more than one measurement = ±0.21°C for all ten taxa; ±0.30°C for six. Asymmetry for ten taxa before and after symmetrization = 7.84% and 3.01%, respectively; for six, 9.60% and 4.67%

	LeopS	*NiviC*	*RattF*	*SundM*	*MaxoB*	*MaxoO1*	*MaxoO2*	*MaxoR*	*MaxoS*	*MaxoW*
Leopoldamys	85.54	3.78	5.49	6.46	7.20	6.61	7.11	6.33	7.06	5.93
sabanus	na/1	0.48/2	0.04/2	0.24/2	0.30/4	na/1	0.14/2	0.25/2	0.13/2	0.04/2
Niviventer	4.84	84.51	6.20	6.99	7.09	6.68	7.25	5.75	7.06	5.94
cremoriventer	0.04/2	0.21/2	0.03/2	0.12/2	0.11/2	na/1	0.13/2	0.08/2	0.01/2	0.07/2
Rattus	7.20	6.58	84.24	4.29	7.73	7.03	7.94	6.86	7.52	6.42
fuscipes	0.21/2	0.28/2	0.29/2	0.66/2	0.01/2	na/1	0.28/2	0.20/2	0.11/2	0.03/2
Sundamys	6.45	5.94	2.70	85.22	7.32	6.82	7.25	6.41	6.90	6.17
muelleri	0.08/2	0.02/2	0.47/2	0.34/2	0.10/4	na/1	0.00/2	0.17/2	0.08/2	0.11/4
Maxomys	8.02	7.47	7.34	8.06	84.22	4.60	4.99	4.13	3.88	4.05
bartelsii	0.12/2	0.11/2	0.19/2	0.14/3	0.46/7	0.22/5	0.32/5	0.33/7	0.11/6	0.37/7
Maxomys	7.97	7.59	6.92	7.97	4.92	83.83	0.79	4.00	4.51	3.80
ochraceiventer1	0.11/2	0.21/2	0.06/2	0.15/4	0.22/7	0.21/9	0.22/7	0.34/7	0.36/7	0.44/6
Maxomys	7.89	7.41	7.14	8.02	4.86	0.28	84.79	3.88	4.53	3.41
ochraceiventer2	0.23/2	0.01/2	0.15/2	0.28/3	0.28/7	0.25/7	0.28/7	0.24/7	0.23/7	0.37/7
Maxomys	7.61	7.20	7.01	7.88	4.65	4.02	4.59	83.82	4.10	3.15
rajah	0.13/2	0.05/2	0.16/2	0.35/2	0.33/7	0.30/5	0.16/5	0.58/7	0.16/7	0.40/7
Maxomys	7.80	7.21	7.01	7.79	4.50	4.24	4.74	3.80	84.27	3.66
surifer	0.47/2	0.01/2	0.17/2	0.08/2	0.20/6	0.23/5	0.14/5	0.29/7	0.39/7	0.35/7
Maxomys	7.91	7.55	7.13	8.16	5.18	4.28	4.95	4.20	4.44	83.09
whiteheadi	0.11/2	na/1	0.14/2	0.19/4	0.30/7	0.16/5	0.19/5	0.30/6	0.39/6	0.59/6
Correction (10)	0.862	0.953	1.073	0.859	0.965	1.060	0.931	1.072	0.992	1.216
Correction (6)					0.906	1.040	0.853	1.004	0.968	1.211

topology was forced onto a KITSCH computation. Assuming an approximately 10-Mybp separation between *Mus* and the group including *Rattus s. s.*, the rate of single-copy DNA change is 2.6% nucleotide sequence-divergence per million years—very close to that of 2.5%/Myr calculated by Catzeflis *et al.* (1987) from study of a different suite of muroid rodents. This rate, when divided into the pathlengths of Table 5, suggests that the *Maxomys*-other *Rattus s. l.* clade shared a common ancestor at about 6.1 Mybp, while *Maxomys* spp. diversified at 3.9 Mybp. The separation of the three major murine lineages from *Peromyscus* would have occurred at 12.4 Mybp. Using an earlier *Mus-Rattus* separation at 12.2 Mybp (see Discussion) to calibrate Figure 4 gives a rate of 2.1%/Myr; the inferred divergence-dates are then 7.6 (*Maxomys*-other *Rattus s. l.*), 4.8 (*Maxomys* spp.), and 15.3 Mybp (Sigmodontinae-Murinae). These and additional dates based on both calibration points, and using our and Chevret's (submitted) data, are given in Table 6.

DISCUSSION

Monophyly and context of Maxomys

Our aim in this study was to resolve relationships among species of the southeast Asian genus *Maxomys*, in part with a view to addressing problems of Sunda Shelf biogeography. The first question that must be asked, however, is whether *Maxomys* is indeed monophyletic: our results are quite clear that it is, at least insofar as the

TABLE 5. Symmetrized and weighted average ΔT_mH-Cs among sixteen species of Muridae (lower left-hand triangle), and fitted pathlengths from the KITSCH version of Figure 7 (upper right-hand triangle) calculated from these measurements before folding the data matrix. Naming conventions for columns as for Table 1. Asymmetry before symmetrization (unfilled cells only) = 8.03%; after symmetrization (all cells), 2.97%. Data after conversion of the ΔT_ms of Table 1 and with addition of measurements from Chevret (1994, submitted) for *Bandicota* and *Berylmys*

	PeroE	*MusMu*	*MyomV*	*MeloC*	*UromC*	*LeopS*	*NiviC*	*RattF*	*SundM*	*MaxoB*	*MaxoO1*	*MaxoO2*	*MaxoR*	*MaxoS*	*MaxoW*	*BandB*	*BeryB*
Peromyscus eremicus	0	32.19	32.19	32.19	32.19	32.19	32.19	32.19	32.19	32.19	32.19	32.19	32.19	32.19	32.19	32.19	32.19
Mus musculus	32.45	0	25.04	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91
Myomys verreauxii	34.47	25.04	0	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91
Melomys cervinipes	31.80	27.02	29.43	0	7.61	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91
Uromys caudimaculatus	32.11	24.63	26.48	7.61	0	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91	25.91
Leopoldamys sabanus	33.97	25.28	29.60	25.59	23.15	0	6.93	11.44	11.44	15.97	15.97	15.97	15.97	15.97	15.97	11.44	11.44
Niviventer cremoriventer	32.72	25.06	27.13	26.37	25.31	6.93	0	11.44	11.44	15.97	15.97	15.97	15.97	15.97	15.97	11.44	11.44
Rattus fuscipes	32.48	26.07	29.49	29.11	26.33	12.75	13.00	0	5.34	15.97	15.97	15.97	15.97	15.97	15.97	5.34	6.86
Sundamys muelleri	32.28	26.86	30.14	27.57	26.59	11.95	12.08	6.42	0	15.97	15.97	15.97	15.97	15.97	15.97	5.34	6.86
Maxomys bartelsii	31.45	25.76	26.25	26.07	24.57	15.86	16.21	17.40	16.22	0	10.16	10.16	8.94	8.53	8.94	15.97	15.97
Maxomys ochraceiventer1	31.19	23.58	27.55	25.56	23.14	15.25	16.37	16.74	16.55	10.00	0	2.20	10.16	10.16	10.16	15.97	15.97
Maxomys ochraceiventer2	31.66	23.99	27.58	26.93	24.39	15.80	16.14	18.20	16.16	11.38	2.20	0	10.16	10.16	10.16	15.97	15.97
Maxomys rajah	30.62	23.18	25.81	23.76	22.10	14.28	13.41	15.57	14.22	8.48	9.07	9.53	0	8.94	8.94	15.97	15.97
Maxomys surifer	32.79	26.09	29.15	27.52	23.61	16.40	16.54	17.67	17.40	8.53	9.52	11.09	8.12	0	8.94	15.97	15.97
Maxomys whiteheadi	32.79	26.22	29.93	27.28	25.79	15.69	16.61	18.13	17.23	10.87	9.81	11.06	8.31	9.55	0	15.97	15.97
Bandicota bengalensis	30.28	19.74	28.54	26.49	24.84	9.13	11.04	5.06	4.60	15.15	15.12	16.15	12.60	15.83	15.81	0	6.86
Berylmys bowersi	28.36	19.03	25.37	30.78	28.33	9.11	10.63	6.82	7.46	17.02	15.21	17.23	12.38	15.59	12.41	6.69	0

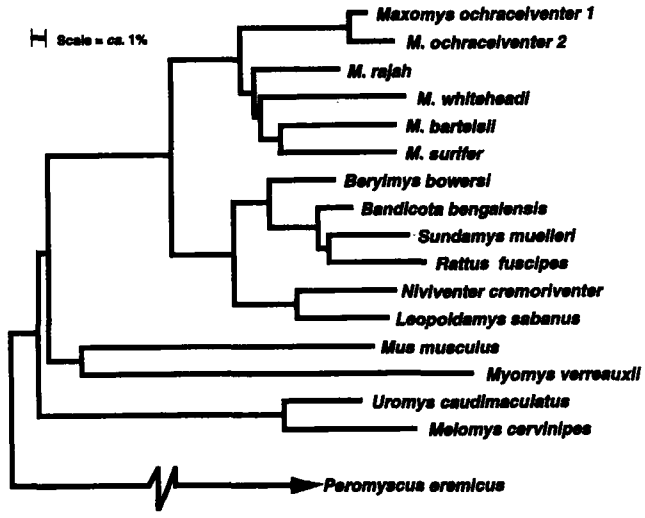

Figure 4. Best-fit FITCH tree of 17 murids, calculated from the ΔT_mH-C data of Table 5 (lower left-hand triangle; tree was calculated from unfolded matrix), with input order of taxa shuffled 100 times. Approximately to scale, but distance from murine root to *Peromyscus eremicus* (19.2%) has been truncated to fit page. Correlation of fitted branchlengths with original distances = 0.983. All jackknives were congruent with the FITCH topology. Other variants of the reconstruction algorithm [e.g. ultrametric estimation (Lapointe & Kirsch, 1995)] gave qualitatively similar results, but with less jackknife support for the topology of *Maxomys* spp. depicted herein.

TABLE 6. Comparison of some divergence-dates inferred from the data in the present study and in Chevret (submitted, table 7), calibrated against two proposed times for the separation of the *Mus* and *Rattus* lineages (10.0 and 12.2 Mybp). Dashes represent comparisons not made

	This paper		Chevret (subm)	
Calibration Dates (Myrbp)	10.0	12.2	10.0	12.2
Rates (%/myr)	2.6	2.1	1.8	1.4
Peromyscus-Murinæ	12.4	15.3	–	–
*Rattus sensu stricto-(Leopoldamys-Niviventer)**	4.4	5.4	5.4	6.6
Rattus-Sundamys	2.1	2.5	–	–
Rattus-Bandicota	2.1	2.5	2.5	3.0
Rattus-Berylmys	2.6	3.3	3.7	4.5
Leopoldamys-Niviventer	2.7	3.3	3.4	4.1
Rattus-Maxomys	6.1	7.6	6.7	8.2
M. rajah-M. whiteheadi	3.4	4.3	4.2	5.1
Diversification of *Maxomys*	3.9	4.8	–	–

* (*Rattus s. s.* plus *Berylmys*)-(*Leopoldamys* plus *Niviventer*) in Chevret (submitted).

species we examined are concerned. From an analytical point of view, documenting the monophyly of any taxon necessarily involves inclusion of a number of subdivided outgroups (Smith, 1994), and special caution must be exercised in the choice of outgroup taxa in studies of murines in particular. For example, there are numerous studies supportive of the use of *Lenothrix canus* Miller, 1903 as outgroup to more derived murines (e.g. Misonne, 1969; Medway & Yong, 1976; Musser, 1981a,b;

Musser & Newcomb, 1983). However, there are also biochemical (Chan, Dhaliwal & Yong, 1978) and chromosomal (Gadi & Sharma, 1983) data supportive of a relationship between *Lenothrix* and *Niviventer*, while dental morphology associates *Lenothrix* with *Pithecheir* Cuvier, 1838 (Musser & Carleton, 1993). The most extreme example of conflicting evidence on murid relationships may be the case of *Acomys*, 'obviously' a murine on the basis of dental anatomy (Jacobs, 1978), but almost certainly representative of a distinct higher taxon if several biochemical studies are correct (e.g. Sarich, 1985; Chevret *et al.*, 1993; Hänni *et al.*, 1995).

Thus we chose to use a broad sampling of murids as outgroup taxa, as the relationships among all murine clades still are far from clear. Accordingly, our results with these taxa have implications beyond demonstrating the monophyly of and interspecific relationships within *Maxomys*, especially for the affinities of southeast Asian with Australo-Papuan rodents. The present study confirms the association of *Rattus s. l.*; topologically our arrangement of the four outgroup taxa nearest to *Maxomys* (*Leopoldomys*, *Niviventer*, *Rattus s. s.*, and *Sundamys*) is therefore of some interest, agreeing entirely with that of Chevret (1994, submitted), whose study likewise was based on DNA hybridization. Addition of data on two genera examined by Chevret but unavailable to us also confirms the association of *Bandicota* and *Berylmys* with *Rattus-Sundamys*, *Bandicota* being closer to these two genera than is *Berylmys*. In the broader context, relationships we have recovered among the murid outgroups are also consistent with previous hybridization and immunological studies (e.g. Dickerman, 1992; Chevret *et al.*, 1994; Watts & Baverstock, 1994, 1995), although the dichotomous arrangement among the three murine clades remains unresolved in our investigation. However, consideration of the temporal dimension implied by our trees requires justification of the basis for our determination of divergence-dates.

The timing of murid evolution

Chronological estimates of murid cladogenesis inferred from molecular data are usually based on a *Mus-Rattus* divergence at 10 mybp, a date generally ascribed to Catzeflis *et al.* (1987). Those authors did not intend their date to be a hard-and-fast figure, however. Rather, they cited Jacobs (1978), Flynn, Jacobs & Lindsay (1985), and Jaeger *et al.* (1985) as justification for a range of *c.* 8–11 mybp; a personal communication from L.J. Flynn is suggestive that the earlier date (11 Mybp) probably is closer to the actual event. Furthermore, Jacobs, Flynn & Downs (1989) maintain that early murines can be divided into the *Progonomys* Schaub, 1938 and *Karnimata* Jacobs, 1978 groups, a species of *Progonomys* having given rise to *Mus* and allies, while species of *Rattus* and related genera were derived from within *Karnimata*. *Progonomys* ranges in the Asian Miocene from 12.1 to 7.1 Mybp, and in France is found possibly as early as 12.5 Mybp (Aguilar, Calvet & Michaux, 1991), although this estimate probably is too early (L.J. Flynn, *in litt.*, suggests that, as part of faunal zone MN 8, it may be as young as 11 Mybp); *Karnimata* ranges from 10.6 to 5.5 Mybp (Jacobs *et al.*, 1989; Flynn *et al.*, 1990, 1995: Jacobs & Downs, 1994). If this is so, then the estimate of 10 Mybp for the split between *Mus* and *Rattus* clades becomes untenable, as the latest that there then could have been an ancestor common to both *Mus* and *Rattus* would be before 12.1 Mybp (=earliest Asian record of *Progonomys*). However, there is a complication: Jacobs *et al.* (1990) regard *Micromys* Dehne, 1841 as also a modern descendant of a common ancestor shared with

Progonomys, and at least two molecular studies (Chevret, 1994; Furano *et al.*, 1994) demonstrate *Micromys* to be the sister-taxon to a group that includes *both Mus* and *Rattus*. Thus, if Jacobs *et al.* (1990) are correct in deriving *Micromys* as well as *Mus* from a *Progonomys*-like form, the latter must be paraphyletic with respect to *Karnimata* and hence *Rattus*, and the temporal provenance of *Progonomys* is less critical in determining the date of divergence between *Mus* and *Rattus*. However, an alternative suggested to us by F.M. Catzeflis (pers. comm.) is that *Micromys* was derived from the still-older fossil *Antemus* Jacobs, 1977, separately from the *Progonomys-Mus* and *Karnimata-Rattus* lineages.

Nevertheless, it does seem likely that the *Mus* and *Rattus* lineages are older than 10 Myr. An estimate of 12 ± 2 Mybp was used by Watts & Baverstock (1995) on the strength of a review by Catzeflis, Aguilar & Jaeger (1992) and additional data from Jacobs & Pilbeam (1980). Given the data of Flynn *et al.* (1995), we also support a date greater than 12.1 Mybp. Accordingly, we advocate use of at least 12.2 Mybp for calibration, and have cited divergence estimates based on this (probably more accurate) date of separation between *Mus* and *Rattus* as well as on the more commonly used 10 Mybp date (Table 6). Use of the earlier date has the effect of reducing our rate-determination from 2.6%/million years to 2.1%/million years, which is more in line with the figure of 2%/million years proposed by Dickerman (1992). In turn, the slower rate implies earlier dates for other dichotomies: that between *Maxomys* spp. and other *Rattus s. l.* becomes 7.6 Mybp, and the initial divergence among *Maxomys* species is placed at 4.8 Mybp. Implicit in all such estimates, of course, is that the rate of single-copy DNA evolution has been more or less regular through time. This presumption cannot be verified on the basis of a single calibration-point, and it also seems likely that even with application of a saturation-correction that the earliest divergences (e.g. between Sigmodontinae and the murine lineages) may be somewhat underestimated.

What is nonethless of great interest from a technical standpoint is the close correspondence of our dates with those of Chevret (submitted). Chevret calculated somewhat slower rates of 1.75% and 1.45% per Myr (based respectively on 10 and 12 Mybp dates for the *Mus-Rattus* divergence), largely because she did not correct her data for percent. hybridization (hence her Δs are smaller than ours). Even so, Chevret's estimates of divergence-dates are remarkably similar to ours, probably because the equivalent Δs in her and our studies are mainly within the range where distances remain linear. In particular, we note that the means for six common comparisons in corresponding pairs of columns in Table 6 differ by just 0.8 Myr. The dates in that table thus provide some constraints on the interpretation of the DNA-hybridization trees in the context of other studies of southeast Asian murid evolution.

We also note with gratification the close correspondence of our dates estimated for major cladogenic events (Table 6) with those of major tectonic events in the region. It has recently been pointed out that there have been two regionally important periods of tectonic change during the past 50 Mybp (Hall, 1996). The most recent of these, at 5 Mybp, was the collision of the Philippine Arc with the Eurasian continental margin, which "appears to be a key to the recent tectonics of the region" (Hall, 1996:153) and led to major deformations concentrated between the Banda Sea and Taiwan, precisely the area of focus in the present report. The 5 Mybp events in turn were driven by northward movement of the Australian continent, and its collision with the Philippine Sea plate are 25 Mybp. Several cladogenic and

zoogeographic events of note are congruent with the 5 Mybp date: our data for the initial diversification of *Maxomys* is suggestive of cladogenesis at *c.* 4.8 Mybp, as is the diversification of the *Rattus s. l.* group as witnessed by the cladogenesis of the *Niviventer-Leopoldamys* clade from the *Rattus-Sundamys-Bandicota-Berylmys* clade, *c.* 5.4 Mybp (Figure 5). The 5 Mybp event also agrees with the proposed date for the invasion of Australia by *Rattus*, and the beginning of the last pre-Pleistocene faunal interchange between Australia and New Guinea (*c.* 4.7 Mybp) based on biochemical evidence from albumin immunological data [Aplin *et al.*, 1993; *contra* Simpson (1961), Tate (1951), and Taylor & Horner (1973), all of whom advocated, based on scant morphological data, a Pleistocene or even Holocene date for the Australo-Papuan interchange and invasion of Australia by *Rattus*].

Origins of the Australo-Papuan rodent fauna

The origins of the Australo-Papuan rodents have been, if not controversial, at least nebulous. Alston (1876) first distinguished a group of such genera which was maintained (with varying compositions) by Ellerman (1941), Tate (1951), and Simpson (1945), as well as by others since. Of particular interest in light of our experiments, the dichotomy between *Rattus* and *Uromys-Melomys* was accentuated by Simpson (1961), who explicitly separated the Australian Rodentia into four groups: *Rattus*, Old Papuan genera, Old Australians ('Pseudomyinae'), and 'Hydromyinae.' For Simpson, the Old Papuan genera were comprised of "the '*Uromys* group' ": *Uromys, Melomys, Xenuromys* Thomas, 1889, and *Pogonomelomys* Rummler, 1936. While acknowledging the distinctness of these genera, Simpson hypothesized that they "could well have been derived within New Guinea from a single ancestry in or near *Rattus*" (Simpson, 1961:433).

Although we did not include a broad sampling of Australian taxa, a negative judgement on Simpson's conclusions can nevertheless be drawn from our study. The Figure 2 tree is best regarded as showing a trichotomy amongst the three murine clades, given the low bootstrap support for the position of *Mus-Myomys* as sister to *Rattus s. l.* (cf. Fig. 4). No doubt this uncertain resolution is due in part to the difficulty of resolving distantly-related murid lineages separated by short internodes, as has been remarked by Catzeflis (1990), but the inconsistency itself (together with the lengthy internode segregating the *Rattus s. l.* lineage) demonstrates that Australo-Papuan rodents clearly show no especially close relationship with *Rattus*. In this respect, our data support the results of the albumin microcomplement-fixation analyses performed by Watts & Baverstock (1994, 1995). Australo-Papuan genera therefore probably represent the descendants of a very early radiation of murid rodents; the timing indicated by our data for separation of the *Uromys-Melomys* group is suggestive of an origin for these Papuan genera as early as that for *Mus* and *Rattus*. This date may also be construed as supportive of Aplin, Baverstock & Donnellan's (1993) hypothesis of a dispersal of the common ancestor of Old Papuan genera into New Guinea *c.* 10–12 Mybp, but presumably from a northern rather than southern source.

The southeast Asian Murinae

Our timing of the Sundaic-southeast Asian murid radiation (i.e. that giving rise to the *Maxomys* and other *Rattus s. l.* clades) at about 7.6 Mybp is similarly congruent

with other molecular and fossil evidence. In particular, it is quite close to Watts & Baverstock's (1995) estimate of 8 ± 1 Mybp for the major early radiations within southeast Asia. We further suggest that *Maxomys* (as represented by the five species we studied) began to diversify about 4.8 Myr ago and other *Rattus s. l.* genera about half a million years earlier. Although the emergence of the lineage giving rise to *Rattus* may be taken as being in the *Karnimata* group [with a horizon of 10.6 to 5.5 Mybp (Flynn *et al.*, 1990, 1995; Jacobs *et al.*, 1989; Jacobs & Downs, 1994)], the oldest *Rattus* fossil dates from the Pinjor Formation of India (Gaur, 1986), which is probably later Pliocene (Jacobs *et al.*, 1989). This date is roughly consistent with our estimate of an origin for *Rattus s. s.*, based on its divergence from *Sundamys*, of *ca.* 2.5 Mybp (although we caution that 'What is *Rattus*?' remains a burning question). Such a date would be consistent with a relatively recent invasion by *Rattus s. s.* of Australo-Papua, the estimated timing of which is again closely congruent with the albumin immunological evidence of Aplin *et al.* (1993) suggesting a faunal interchange between 2.7 and 4.7 Mybp.

Interspecific relationships among Maxomys

Determination of relationships among species of *Maxomys*—the central aim of our study—proved more difficult than demonstration of the genus' monophyly or relationships *vis-à-vis* other southeast Asian genera. Resolution of close affinities (and hence short internodes), as those among congeners are likely to be, is problematic for any molecular technique but particularly so for one which, like DNA hybridization, is subject to some experimental error which may especially confound ingroup relationships (Kirsch *et al.*, 1995). A high degree of replication, attention to possible individual variation, and tests with varying taxonomic subsets of the data are all necessary in order to arrive at accurate estimates of topology and internodal lengths (Kirsch *et al.*, 1993, 1995); choice of the most precise index of distance also is desirable. Having largely met these requirements, we believe that some conclusions are justified even on the basis of our restricted taxonomic sample.

First, the two individuals of *M. ochraceiventer* always paired, as might be hoped, showing both that single labels were sufficient for our purposes and that individual variation (at least for these *Maxomys* species) does not overlap differences among species. Second, *M. bartelsii* and *M. surifer* always associated, no matter which index was employed or which starting-temperature was used for calculating the ΔT_ms. Third, there was a suggestion of a similar pairing between *M. rajah* and *M. whiteheadi.* However, this linkage was rarely supported in more than 50% of the bootstrap trees, and often was vulnerable to jackknifing. Furthermore, the joint association of those two species with either *M. ochraceiventer* or the paired *M. bartelsii* and *M. surifer* varied across the analyses. Notwithstanding, if the relative precision of the ΔT_ms calculated from 56°C and 72°C is any guide, then the association of *M. rajah* and *M. whiteheadi* with *M. ochraceiventer* is to be preferred, as this affiliation was found in trees based on ΔT_ms calculated from 72°C, which had SDs one-fourth of those based on the lower starting temperature. In addition, the ΔT_ms partitioned according to individual tended to give the same association (i.e. with *M. ochraceiventer*), whether based on autologous or allologous comparisons. As well, the ordering of nodes in trees based on 6×6 subsets of all treatments of the data (i.e. matrices including only *Maxomys* spp.) were consistent with the FITCH trees calculated from 72°C, but not

with those of 15×15 or 10×10 subsets of ΔT_m data calculated from 56°C. Of course, the 6-taxon trees are unrooted, but it may be significant that *M. whiteheadi* always joined the network at a node next to that uniting the two *M. ochraceiventer* specimens. That is, the alternative placement of *M. whiteheadi* nearer *M. bartelsii* and *M. surifer* (and separated from *M. ochraceiventer* by *M. rajah*) in some jackknife trees based on indices calculated from 56°C was not supported by *any* 6-taxon topology. We note also that trees based on ΔT_{50}Hs or ΔT_{mode}s for ten or six taxa conformed closely to the corresponding ΔT_m-based results calculated from 72°C.

Thus we favour an arrangement of *Maxomys* spp. that recognizes two species-groups: one consisting of an unresolved trichotomy among *M. ochraceiventer*, *M. rajah*, and *M. whiteheadi* (albeit suggestive of a closer relationship between *M. rajah* and *M. whiteheadi*), and another pairing *M. bartelsii* and *M. surifer* as the sister-group to the other three species; we estimate the divergence-date of *M. bartelsii* and *M. surifer* to be about 4 Mybp. Therefore, with respect to the hypothesis that *rajah* and *surifer* are conspecific [the latter being a subspecies of the former (e.g. (Ellerman, 1955; Ellerman & Morrison-Scott, 1951; Harrison, 1957, 1966)], our molecular data concur with the morphological, chromosomal, and biochemical information of Yong (1972), the anatomical data of Musser *et al.* (1979), and the immunological results of Watts & Baverstock (1994): there can remain no doubt that both *rajah* and *surifer* are distinct species.

Finally, as one goal of our study was to assess the utility of *Maxomys* in Sundo-Wallacean zoogeographic studies, it is gratifying to remark that, based on the results presented herein, *Maxomys* clearly will fulfill a key role in this respect. For example, our specimens of *M. bartelsii* were from Java (where the species is endemic), but consistently displayed closest affinity to *M. surifer*, the only other *Maxomys* species present on Java, despite the fact that our *surifer* were collected on Borneo. While morphological consistency may not necessarily be congruent with zoogeographic logic, this result is nevertheless pleasing. Further analysis of members of Malesian *Rattus* in concert with *Maxomys* will undoubtedly yield fine-resolution answers to zoogeographic questions, as well as to the question of the circumscription of *Rattus* intimated by Corbet & Hill (1992:336): "Most [. . .] work has been on too local a scale to adequately resolve the [taxonomic] problems [in *Rattus*] . . ." Although we have begun to document phylogenetic trends within *Maxomys*, much work remains to be done on this fascinating genus. Sixteen years later, the words of Musser (1981a: 318) largely still ring true: "Most species of *Maxomys* require careful taxonomic revision; the phylogenetic relationships among them all need to be determined."

ACKNOWLEDGEMENTS

This work would not have been possible without the assistance of personnel of the University of Wisconsin Zoological Museum's Molecular Systematics Laboratory (UWZMMSL), particularly Brandon Brunner, Lin-Ling Changchien and James Hutcheon. LAR's stay at the University of Wisconsin was supported by the 'Linkages' Program of the University of Wisconsin Graduate School under the administration of Mercile Lee, whom we most particularly thank, and by indirect funds from the Howard Hughes Foundation to the University of Puerto Rico (Cayey College) Department of Biology; the cost of the experiments was partially defrayed by private

donations. We are particularly indebted to Mark Engstrom of the Royal Ontario Museum for the gift of murine tissues; and to him as well as to François Catzeflis, Pascale Chevret, and Lawrence J. Flynn for critical comments on the manuscript. This is Contribution No. 34 from the UWZMMSL.

REFERENCES

Aguilar JP, Calvet M, Michaux, J. 1991. Présence de *Progonomys* (Muridae, Rodentia, Mammalia) dans une association de Rongeurs de la fin du Miocène moyen (Castelnou 1B; Pyrènées-Orientales, France). *Geobios* **24:** 503–508.

Alston ER. 1876. On the classification of the Order Glires. *Proceedings of the Zoological Society, London* **1875:** 61–98.

Aplin KP, Baverstock PR, Donnellan SC. 1993. Albumin immunological evidence for the time and mode of origin of the New Guinean terrestrial mammal fauna. *Science in New Guinea* **19:** 131–144.

Bleiweiss R, Kirsch JAW, Matheus JC. 1994. DNA-DNA hybridization evidence for subfamily structure among hummingbirds. *Auk* **111:** 8–19.

Brownell E. 1983. DNA-DNA hybridization studies of muroid rodents: symmetry and rates of molecular evolution. *Evolution* **27:** 212–216.

Catzeflis FM. 1990. DNA hybridization as a guide to phylogenies: raw data in muroid rodents. In: Nevo E, Reig OA, eds. *Evolution of subterranean mammals at the organismal and molecular levels.* New York: Wiley-Liss, 317–345.

Catzeflis FM, Aguilar J-P, Jaeger J-J. 1992. Muroid rodents: phylogeny and evolution. *Trends in Ecology and Evolution* **7:** 122–127.

Catzeflis FM, Sheldon FH, Ahlquist JE, Sibley CG. 1987. DNA-DNA hybridization evidence of the rapid rate of rodent DNA evolution. *Molecular Biology and Evolution* **4:** 242–253.

Chan KL, Dhaliwal SS, Yong HS. 1978. Protein variation and systematics of three subgenera of Malayan rats (Rodentia: Muridae, genus *Rattus* Fischer). *Comparative Biochemistry and Physiology* **64B:** 329–337.

Chevret P. 1994. Étude évolutive des Murinae (Rongeurs: Mammifères) africains par hybridation ADN/ADN. Comparaisons avec les approches morphologiques et paléontologiques. Unpublished Ph.D. dissertation, Université Monpellier II.

Chevret P, Denys C, Jaeger J-J, Michaux J, Catzeflis FM. 1993. Molecular evidence that the spiny mouse (*Acomys*) is more closely related to gerbils (Gerbillinae) than to true mice. *Proceedings of the National Academy of the United States of America* **90:** 3433–3436.

Chevret P, Granjon L, Duplantier J-M, Denys C, Catzeflis FM. 1994. Molecular phylogeny of the *Myomys* complex (Rodentia, Murinae): a study based on DNA/DNA hybridization experiments. *Zoological Journal of the Linnean Society* **112:** 425–442.

Corbet GB, Hill JE. 1992. *The mammals of the Indomalayan region.* New York: Natural History Museum Publications and Oxford University Press.

Dickerman AW. 1992. Molecular phylogeny of some New World rodents. Unpublished Ph.D. dissertation, University of Wisconsin-Madison.

Ellerman JR. 1941. *The families and genera of living rodents. Volume II. Family Muridae.* London: British Museum (Natural History).

Ellerman JR. 1955. *Checklist of Palearctic and Indian mammals (second edition).* London: British Museum (Natural History).

Ellerman JR, Morrison-Scott TCS. 1951. *Checklist of Palearctic and Indian mammals.* London: British Museum (Natural History).

Felsenstein J. 1993. *PHYLIP, phylogenetic inference package, program and documentation, version 3.5c.* Seattle: University of Washington.

Flynn LJ, Barry JC, Morgan ME, Pilbeam D, Jacobs LL, Lindsay EH. 1995. Neogene Siwalik mammalian lineages: species longevities, rates of change, and modes of speciation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **115:** 249–264.

Flynn LJ, Jacobs LL, Lindsay EH. 1985. Problems in muroid phylogeny: relationships to other rodents and origin of major groups. In: Luckett WP, Hartenberger J-L, eds. *Evolutionary relationships among rodents: a multidisciplinary analysis.* New York: Plenum Press, 589–616.

Flynn LJ, Pilbeam D, Jacobs LL, Behrensmeyer AK, Kappelman JW. 1990. The Siwaliks of Pakistan: time and faunas in a Miocene terrestrial setting. *Journal of Geology* **98:** 589–604.

Fox GM, Schmid CW. 1980. Related single copy sequences in the human genome. *Biochimica Biophysica Acta* **609:** 349–363.

Furano AV, Hayward BE, Chevret P, Catzeflis F, Usdin K. 1994. Amplification of the ancient murine Lx family of long interspersed repeated DNA occurred during the murine radiation. *Journal of Molecular Evolution* **38:** 18–27.

Gadi IK, Sharma T. 1983. Cytogenetic relationships in *Rattus, Cremnomys, Millardia, Nesokia,* and *Bandicota* (Rodentia: Muridae). *Genetica* **61:** 21–40.

Gaur R. 1986. 1st report on a fossil *Rattus* (Murinae, Rodentia) from the Pinjor formation of Upper Siwalik of India. *Current Science* **55:** 542–544.

Hall R. 1996. Reconstructing Cenozoic SE Asia. In: Hall R, Blundell DJ, eds. *Tectonic evolution of Southeast Asia.* London: Geological Society Publishing House, 153–184.

Hänni C, Laudet V, Barriel V, Catzeflis FM. 1995. Evolutionary relationships of *Acomys* and other murids (Rodentia, Mammalia) based on complete 12S rRNA mitochondrial gene sequences. *Israel Journal of Zoology* **41:** 131–146.

Harrison JL. 1957. Habitat studies of some Malaysian mammals. *Proceedings of the Zoological Society, London* **128:** 1–21.

Harrison JL. 1966. *An introduction to the mammals of Singapore and Malaya.* Singapore: Tien Wah Press, Malayan Nature Society, Singapore Branch.

Jacobs LL. 1978. Fossil rodents (Rhizomyidae and Muridae) from Neogene Siwalik deposits, Pakistan. *Museum of Northern Arizona Press Bulletin* **ser. 52:** 1–104.

Jacobs LL, Downs WR. 1994. The evolution of murine rodents in Asia. In: Tomida Y, Li Ck, Setoguchi T, eds. *Rodent and lagomorph families of Asian origins and diversification.* Tokyo: National Science Museum Monographs, No. 8, 149–156.

Jacobs LL, Flynn LJ, Downs WR. 1989. Neogene rodents of Southern Asia. In: Black CC, Dawson MR, eds. *Papers on fossil rodents in honor of Albert Elmer Wood. No. 33, Science Series.* Los Angeles: Natural History Museum of Los Angeles County, 157–177.

Jacobs LL, Flynn LL, Downs WR, Barry JC. 1990. Quo vadis, *Antemus*? The Siwalik muroid record. In: Lyndsay EH, Fahlbusch V, Mein P, eds. *European Neogene mammal chronology.* New York: Plenum Press, 573–586.

Jacobs LL, Pilbeam D. 1980. Of mice and men: fossil based divergence dates and molecular 'clocks'. *Journal of Human Evolution* **9:** 551–555.

Jaeger JJ, Tong H, Buffetaut E, Ingavat R. 1985. The first fossil rodents from the Miocene of northern Thailand and their bearing on the problems of the origin of the Muridae. *Review of Paleobiology* **4:** 1–7.

Jukes TH, Cantor CH. 1969. Evolution of protein molecules. In: Munro, HM, ed. *Mammalian protein metabolism.* New York: Academic Press, 21–123.

Kirsch JAW, Bleiweiss RE, Dickerman AW, Reig OA. 1993. DNA/DNA hybridization studies of carnivorous marsupials. III. relationships among species of *Didelphis. Journal of Mammalian Evolution* **1:** 75–97.

Kirsch JAW, Lapointe F-J, Foeste A. 1995. Resolution of portions of the kangaroo phylogeny (Marsupialia: Macropodidae) using DNA hybridization. *Biological Journal of the Linnean Society* **55:** 309–328.

Kirsch JAW, Springer MS, Krajewski C, Archer M, Aplin K, Dickerman AW. 1990. DNA/DNA hybridization studies of carnivorous marsupials. I: the intergeneric relationships of bandicoots (Marsupialia: Perameloidea). *Journal of Molecular Evolution* **30:** 434–448.

Krajewski C, Dickerman AW. 1990. Bootstrap analysis of phylogenetic trees derived from DNA hybridization distances. *Systematic Zoology* **39:** 383–390.

Landry P-A, Lapointe F-J, Kirsch JAW. 1996. Estimating phylogenies from lacunose distance matrices: additive is superior to ultrametric estimation. *Molecular Biology and Evolution* **13:** 818–823.

Lapointe F-J, Kirsch JAW. 1995. Estimating phylogenies from lacunose distance matrices, with special reference to DNA hybridization data. *Molecular Biology and Evolution* **12:** 266–284.

Lapointe F-J, Kirsch JAW, Bleiweiss R. 1994. Jackknifing of weighted trees: validation of phylogenies reconstructed from distance matrices. *Molecular Phylogenetics and Evolution* **3:** 256–267.

Medway Lord, Yong H-S. 1976. Problems in the systematics of the rats (Muridae) of Peninsular Malaysia. *Malaysian Journal of Science* **4(A):** 43–53.

Misonne X. 1969. African and Indo-Australian Muridae. Evolutionary trends. *Annales du Musée Royal d'Afrique Centrale, Tervuren* **172:** 1–219.

Musser GG. 1981a. Results of the Archbold Expeditions. No. 105. Notes on the systematics of Indo-Malayan murid rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. *Bulletin of the American Museum of Natural History* **168:** 225–334.

Musser GG. 1981b. The giant rat of Flores and its relatives east of Borneo and Bali. *Bulletin of the American Museum of Natural History* **169:** 67–176.

Musser GG, Carleton MD. 1993. Family Muridae. In: Wilson DE, Reeder DAM, eds. *Mammal species of the world a taxonomic and geographic reference, 2nd ed.* Washington, D.C.: Smithsonian Institution Press, 501–755.

Musser GG, Holden ME. 1991. Sulawesi rodents (Muridae: Murinae): Morphological and geographical boundaries of species in the *Rattus hoffmani* Group and a new species from Pulau Peleng. *Bulletin of the American Museum of Natural History* **206:** 322–413.

Musser GG, Marshall, JT Jr, Boeadi. 1979. Definition and contents of the Sundaic genus *Maxomys* (Rodentia, Muridae). *Journal of Mammalogy* **60:** 592–606.

Musser GG, Newcomb C. 1983. Malaysian murids and the giant rat of Sumatra. *Bulletin of the American Museum of Natural History* **174:** 327–598.

Sarich VM, 1985. Rodent macromolecular systematics. In: Luckett WP, Hartenberger J-L, eds. *Evolutionary relationships among rodents: a multidisciplinary analysis.* New York: Plenum Press, 423–452.

Sarich VM, Cronin JE. 1976. Molecular systematics of the primates. In: Goodman M, Tashian RE, eds. *Molecular anthropology, genes, and proteins in the evolutionary ascent of the primates.* New York: Plenum Press, 141–170.

Simpson GG. 1945. Principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* **85:** 1–350.

Simpson GG. 1961. Historical zoogeography of Australian mammals. *Evolution* **15:** 431–446.

Smith AB. 1994. Rooting molecular trees: problems and strategies. *Biological Journal of the Linnean Society* **51:** 279–292.

Sody HJV. 1936. Seventeen new generic, specific, and subspecific names for Dutch East Indian Mammals. *Natuurkundig Tijdschrift voor Nederlandsch-Indië* **96:** 42–55.

Springer MS, Davidson EH, Britten RJ. 1992. Calculation of sequence divergence from the thermal stability of DNA heteroduplexes. *Journal of Molecular Evolution* **34:** 379–382.

Springer MS, Kirsch JAW. 1991. DNA hybridization, the compression effect, and the radiation of diprotodontian marsupials. *Systematic Zoology* **40:** 131–151.

Springer MS, Krajewski C. 1989. DNA hybridization in animal taxonomy: a critique from first principles. *Quarterly Review of Biology* **64:** 291–318.

Tate GHH. 1951. Results of the Archbold Expeditions. No. 65. The rodents of Australia and New Guinea. *Bulletin of the American Museum of Natural History* **97**(4): 183–430.

Taylor JM, Horner BE. 1973. Results of the Archbold Expeditions. No. 98. Systematics of native australian *Rattus* (Rodentia, Muridae). *Bulletin of the American Museum of Natural History* **150**(1): 1–130.

Watts CHS, Baverstock PR. 1994. Evolution in some south-east Asian Murinae (Rodentia) assessed by microcomplement fixation of albumin, and their relationships to Australian murines. *Australian Journal of Zoology* **42:** 711–722.

Watts CHS, Baverstock PR. 1995. Evolution in the Murinae (Rodentia) assessed by micro-complement fixation of albumin. *Australian Journal of Zoology* **43:** 105–118.

Werman SD, Springer MS, Britten RJ. 1990. Nucleic Acids I: DNA-DNA hybridization. In: Hillis DM, Moritz C, eds. *Molecular systematics.* Sunderland, Massachussetts: Sinauer Associates, Inc., 204–249.

Yong HS. 1972. The Gunong Benom Expedition 1967. 7. The systematic status of Malayan *Rattus rajah* and *Rattus surifer. Bulletin of the British Museum (Natural History), Zoology* **23**(6): 155–163.