Integrative systematics: the importance of combining techniques for increasing knowledge of African Murinae

Christiane Denys[1,*], *Emilie Lecompte*[1], *Laurent Granjon*[1,2], *Michel Baylac*[3], *Pedro Cordeiro*[1], *Raphaël Cornette*[1], *Gauthier Dobigny*[1], *Elisabeth Fichet-Calvet*[1], *Jean-Pierre Hugot*[1], *Cyril Meslage*[1], *Virginie Millien-Parra*[1], *Paola Petrillo*[1], *Vitaly Volobouev*[1] *and Marjorie Welz*[1]

[1]Museum National d'Histoire Naturelle, EA 2586, Laboratoire Mammifères et Oiseaux, 55 rue Buffon, 75005 Paris, FRANCE

[2]Laboratoire de Mammalogie (CBGP, UMR R022), Institut pour la Recherche et le Développement (IRD), BP 2528, Bamako, MALI

[3]Museum National d'Histoire Naturelle, Morphometric Working group and CNRS UPRES A 8043, 45 rue Buffon, 75005 Paris, FRANCE

*Corresponding author, email: denys@cimrs1.mnhn.fr

Abstract. The soft-furred rats of the *Praomys* group are of economic and health importance but represent one of the most difficult groups of the Murinae for systematics analyses due to a high degree of morphological similarity among species. Because neither morpho-anatomy nor morphometrics are 100% efficient, the use of cytotaxonomy and DNA sequencing is essential. We present together our recent results about taxonomy and biosystematics of the group. The distinction of two complexes, *P. jacksoni* and *P. tullbergi*, is here confirmed both by morpho-anatomy and geometric morphometrics, as well as by cytochrome b sequencing. It is also shown that the fronto-parietal crest disposition has a phyletic signal. However, these criteria cannot be applied to juvenile and very old specimens, which restricts its application. DNA sequencing of the mitochondrial cytochrome *b* gene also confirms the monophyly of the *Praomys* group. However, some incongruence is observed between molecules and morphology due to the paraphyly of the genus *Myomys*. This pattern points out the inaccuracy of external morphological characters taken as diagnostic criteria. In such a case, like in various other Murinae, the combination of different techniques appears necessary in order to better understand the taxonomy and biosystematics in the group. These results have important implications for epidemiological research.

Introduction

Systematics is the science devoted to discovery, identification, classification and interpretation of biological diversity. It is often divided into taxonomy (or description, naming and classification of taxa) and biosystematics (assessment of the evolutionary relationships between species, i.e. phylogeny). This distinction reflects different approaches and the frequent involvement of different groups of scientists. Nevertheless, the two disciplines share the phylogenetic approach and have the same fundamental aim: the production of stabilised classifications, allowing evolutionary inferences both for fundamental and applied biology. Systematics has recently benefited from a complete renewal, with the ongoing development of new methods and concepts, among them cladistics, morphometrics, molecular systematics and global genomics. The integrative application of all these tools to the same study models is now possible and this approach is developed in our research team. It provides a rich approach that leads to more complete and precise descriptions of biodiversity.

Tropical Africa supports very high micro-mammalian diversity, especially between African Murinae (Rodentia, Muridae). The soft-furred rats of the genus *Praomys* are widely distributed from West Africa (Senegal to Angola) to East Africa (Uganda to Malawi) and in both primary and secondary forest zones. The genus comprises 10 species whose geographical limits are still poorly known due to the low level of morphological differentiation among the species and a long history of confusion and misidentifications (Musser and Carleton 1993; Van der Straeten and Kerbis-Peterhans 1999). Until recently, the genus *Praomys* was broadly conceived and included members of such well recognised genera as *Mastomys*, *Hylomyscus* and *Myomys*. A revision of the genus *Praomys* also requires that we adopt a broader approach that includes these taxa, which together constitute the *Praomys* group. No phylogeny was formerly available, despite the fact that the entire group has economic and health importance (Lecompte et al., this volume). More specifically, *P. jacksoni* is a primary natural host of the arenavirus Mobala (Mills et al. 1997) and is probably a reservoir of Ebola virus (Morvan et al. 1999). Furthermore, some species of *Praomys* are almost unknown because they are restricted to some isolated montane forests. These species have special conservation importance.

Finally, the biodiversity of *Praomys* may be underestimated due to the probable existence of sibling species in various African Murinae, as suggested recently by Meester (1988) and Taylor (2000). A careful revision of

all members of the genus is required, but with special attention to *P. tullbergi*, the type species of the genus. In this paper, we have applied the integrative and comparative approach to the *Praomys* group, both at specific and generic levels, in order to solve some taxonomic problems. We will highlight the perspective brought by each technique, as well as the importance of comparing results and the implications of such an approach.

Material and methods

Voucher specimens from the collections of the Museum National d'Histoire Naturelle (MNHN; Paris, France), the Natural History Museum (London, England), and the Royal Museum for Central Africa (Tervuren, Belgium) have been used for morpho-anatomical, morphometric and phylogenetic analysis. Two taxonomic levels are considered in this study. First, the initial recognition of elementary taxonomic units (OTUs) is made both at genus and species level with the help of morphometric methods; and then, the analysis of relationships within *Praomys* is performed through phylogenetic methods and assessed for their consensus.

At the intraspecific level, 208 skulls of *P. tullbergi* from MNHN have been used for morphometric analyses (to be reported in detail elsewhere). Twenty skull and mandible measurements were taken using a caliper (0.01 mm precision). Principal component analysis (PCA) and canonical variable analysis (CVA) were done using log-transformed values. Outlines of dental rows were drawn using a binocular microscope with a camera lucida and digitised using a standard orientation after preliminary tests. A total of 194 dental-row outlines of *P. tullbergi* specimens from MNHN collections—86 females and 114 males, coming from Ivory Coast (N = 45), Cameroon (N = 2), Gabon (N = 94), Burkina Faso (N = 2), Central African Republic (N = 31), Senegal (N = 6) and Togo (N = 14)—were digitalised using TPSDig software (Rohlf 2001) and then analysed using specially devised MATLAB V.6. routines for Elliptic Fourier analysis (Kuhl and Giardina 1982). Coefficients of elliptic Fourier were calculated for normalised and orientated contours. Four landmarks at the junction of the teeth were taken in order to superimpose the outlines. Shape and size differences were analysed using PCA and CVA of Fourier coefficients.

Seven landmarks were taken on the left anterior half of the dorsal side of the skulls of different *Praomys* species (Figure 1). Landmarks were acquired using a charge coupled device (CCD) camera with a macrophotographic device and the Measurement TV software (version 1.92, Updegraff 1990). Thin-plate spline analyses were conducted using the thin-late splines relative warp (TPSRW) analysis software of Rohlf (2001) allowing superposition of landmarks and visualisation of shape deformations in function of variance.

On the basis of good taxonomical identifications, phylogenetic analysis can be performed. A preliminary morphological phylogeny (Lecompte et al. 2002a) was completed with new characters and increased samples within the *Praomys* group. The data matrix had 51 characters on 27 species, including 24 species of the *Praomys* group. Total genomic DNA was extracted from liver, heart or muscles preserved in 70% ethanol using a CTAB protocol (Winnepenninckx et al. 1993). Mitochondrial sequences containing the cytochrome b gene (1140 pb) were isolated via the polymerase chain reaction (PCR) and sequenced directly from purified PCR products with an automatic sequencer (CEQ2000; Beckman). The sequences were entered and manually aligned using the Bioedit software. Mutational saturation was studied for each codon position for transitions and transversions separately. Both for morpho-anatomical and molecular data, the phylogenetic relationships were analysed by the maximum parsimony (MP) method using PAUP 4.0 (Swofford 1998). Twenty species of the *Praomys* group, represented by one to six specimens, were treated with other Murinae species chosen as outgroups according to Lecompte et al. (2002b). The molecular and morphological trees were compared with Treemap 1.0 software (Page 1995).

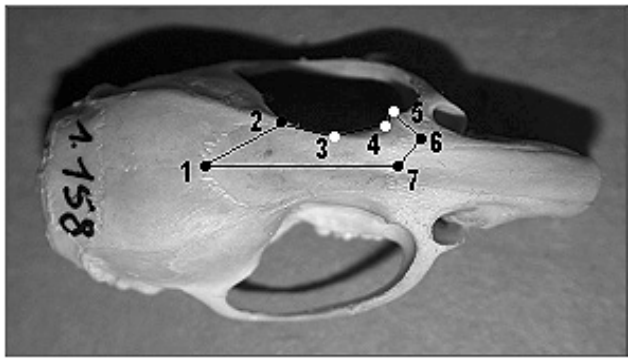

Figure 1. Dorsal view of a *Praomys* skull showing the landmarks used to analyse the shape of the frontal bone.

Results and discussion

OTU definition

Within the framework of the biological species concept of Mayr (1963), there is a need to define elementary taxonomic units (OTUs), especially when looking at 'non-natural' populations (issued from collections or systematic field inventories) where the critical tests of hybridisation cannot be made. It is also necessary in the case of sibling species (morphologically similar species but genetically structured and reproductively isolated; Mayr 1963). Classical morpho-anatomy or morphometric tools are well suited for morphospecies definition, however in the case of sibling species or a species complex, cytotaxonomic methods, especially using banding techniques, are better adapted.

Morpho-anatomy

The search for diagnostic characters is especially important for species identification. In the past, the diag-

nosis of species was based on external characters but this can lead to considerable confusion, especially in groups with high levels of morphological similarity and/or variability. In the *Praomys* group, most of the genera were long confused and even placed in the same genus (see Ellerman 1940–1941; Meester and Setzer 1971–1977). The first morphological revisions of the group grew out of Petter's (1965, 1975) and Rosevear's (1969) studies of skull and molar morphology, which provided some useful characters, both at the generic and specific levels. However, these authors each looked only at a few species of the genus. Around the same time, other authors reported some supplementary characters that allowed the discrimination of certain species, but comparisons were generally very limited. Our research group has, for the first time, examined all recognised species of *Praomys*, with samples of 15 to 100 specimens per species to accurately assess intraspecific variability. The selection of skull characters took into account the nature and extent of variability of the characters; all highly variable characters were rejected in devising the identification key.

The cranial characters selected for this identification key are illustrated in Figure 2. The only external character employed here is the mammary formula, because this was initially used by Thomas (1915) to separate the genera *Myomys*, *Mastomys* and *Praomys*. It is expressed as the total number of pectoral mammae and inguinal mammae. This character can be used only with adult females and consequently it is limited for purposes of species determination. We provide here an identification key for species of the genus *Praomys* (after Lecompte et al. 2001).

1. Supraorbital ridges absent or very weak (Figure 2, label a). 2.
   Supraorbital ridges present, more or less pronounced. 3.
2. Anterior limit of palatine bone extending to the level of the posterior part of M1 (Figure 2, h), nasal/frontal suture almost horizontal (Figure 2, f), zygomatic bone of the same breadth as malar process, mammary formula: 1 + 2 = 6. *P. morio*
   Anterior limit of the palatine bone extending to between M1 and M2 (Figure 2, i), nasal/frontal suture V-shaped (Figure 2, g), zygomatic bone very thin (half of the breadth of malar process), mammary formula: 2 + 2 = 8. *P. delectorum*
3. Supraorbital ridges beginning in the middle of frontals (Figure 2, b) 4.
   Supraorbital ridges very strong, straight, beginning in front of frontals (Figure 2, c) 7.
4. Posterior limit of anterior palatal foramina reaching anterior edge of first root of M1 (Figure 2, j). 5.
   Posterior limit of anterior palatal foramina reaching halfway between first and second roots of M1 (Figure 2, k). *P. hartwigi*
5. Proportions of the teeth normal (ratio of molar row length/maximum length of skull >15%) *P. tullbergi*
   Microdonty (ratio of molar row length/maximum length of skull <15%) 6.
6. Interorbital constriction gradual and amphora-shaped (Figure 2, d) *P. misonnei*
   Interorbital constriction more sharply angular in the middle of frontal (Figure 2, e) *P. rostratus*
7. Posterior limit of anterior palatal foramina reaching anterior edge of first root of M1 (Figure 2, j). *P. mutoni*
   Posterior limit of anterior palatal foramina reaching halfway between first and second roots of M1 (Figure 2, k). 8.
8. Four small accessory plantar pads, mammary formula: 1 + 2 = 6 *P. jacksoni*
   One or no small accessory pad, mammary formula: 2 + 2 = 8 *P. degraaffi*

Some characters must be handled carefully because of sex and/or age dependence. For instance, the 'supraorbital ridges' present some variation in relation to age—the ridges increasing in strength with the age of the animal. Thus, old *P. morio* can have similar ridges to young *P. tullbergi*, and the type of *P. morio*, a young adult, presents very weak ridges, which could be quite misleading. This illustrates the necessity of taking into account both sex

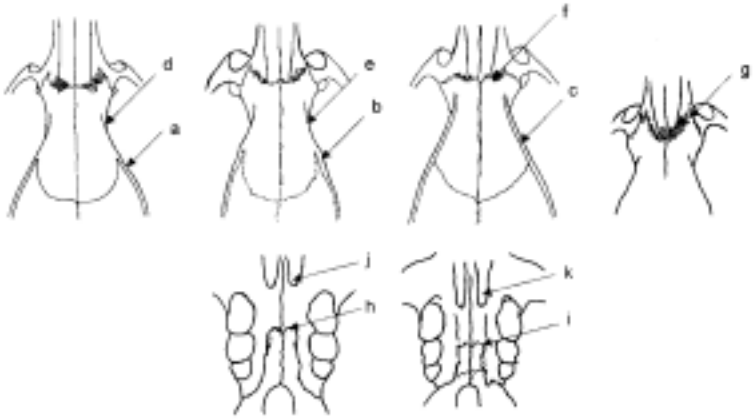

Figure 2. Morphological characters used in the identification key for *Praomys* species. See text for identification of morphological features.

and age influences on diagnostic morphological characters.

Molar teeth characters are useful for palaeontology and determination of remains in owl pellets (Denys 2002). *Praomys* teeth are characterised by an undifferentiated prelobe of the upper M1/, with t2 and t3 aligned and hardly distinguishable, low crowned teeth with well-fused cusps, a lack of deep valleys between cusps, and bunodonty of very narrow lower molars without developed cingula (Figure 3). In general, molar cusps are well united and there are few longitudinal crests.

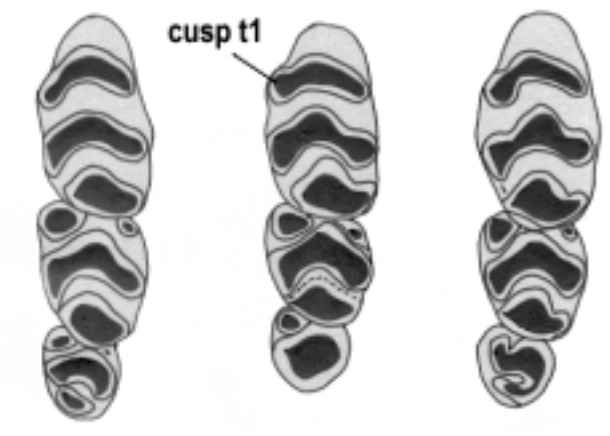

Figure 3. Variation in upper molar morphology among populations of *Praomys tullbergi*: left, Ivory Coast specimen; middle, Senegal specimen (notice the smaller size and that cusp t1 is better individualised); and right, Guinean specimen. All are left upper molar rows.

Cytotaxonomy

It has been shown recently that, in the case of African murids, cytogenetic variations provide some of the most reliable diagnostic criteria (karyospecies concept, Dobigny et al. 2002a,b). Unfortunately, cytogenetic information is lacking for some of the 10 recognised *Praomys* species. A preliminary survey of all published data indicates the existence of species complexes and of potential sibling species, especially in the *tullbergi* group, where two morphologies are known for the sexual chromosomes (Matthey 1958; Capanna 1996) (Table 1). No banding techniques have yet been applied to verify the taxonomic status of these forms. Molecular taxonomy, in this context, can also help to understand relationships within taxa and perhaps reveal cryptic species.

Morphometrics

Morphometrics is the quantitative description of size and shape of organisms (Rohlf and Marcus 1993). Initially based on distance measurements (classical morphometrics), it has been recently renewed with the use of thin-plate spline (TPS) and Fourier analysis methods which allow the analysis of shape of organisms (geometric morphometrics: Bookstein1991). Morphometric techniques are appropriate in taxonomy for species discrimination but can also help to find useful morphological characters for phylogenies or to analyse the evolution of shape by mapping onto cladograms. Classical morphometric techniques (canonical analyses) have been applied successfully to distinguish between *Praomys* taxa. For example, Van der Straeten and Verheyen (1981), Van der Straeten and Dieterlen (1987) and Van der Straeten and Dudu (1990) used these methods to define species complexes within *Praomys* and to justify the naming of new *Praomys* species. Discriminant analyses of distances have also been applied in studies of other African Murinae, both to investigate geographical patterns within species and to search for cryptic species (Taylor et al. 1993; Chimimba 1994). We present here the results of various morphometric analyses performed at different taxonomic levels, reflecting the fact that, in the case of *Praomys*, even the generic boundaries still need to be defined.

Table 1. Chromosomal data available to date for *Praomys* species (2N = diploid number of chromosomes; NFa = fundamental chromosome number; X = sex chromosome X; Y = sex chromosome Y; SM = submetacentric; M = metacentric; A = acrocentric).

Species	Chromosomal data	References
P. taitae	2N = 48, NFa = 54; X = SM	Matthey 1965
P. degraaffi	2N = 26, NFa = 24	Maddalena et al. 1989
P. jacksoni	2N = 28, NFa = 26; X = SM	Matthey 1959
P. misonnei	2N = 36, NFa = 46	Qumsiyeh et al. 1990
P. morio	2N = 34, NFa = 32; X = SM; Y = M	Matthey 1970
P. rostratus	2N = 34, NFa = 32	Gautun et al. 1986
P. tullbergi	2N = 34, NFa = 32; X = A; Y = A or X = M	Matthey 1958; Capanna 1996
Praomys sp.	2N = 42, NFa = 62; X = SM; Y = A	Matthey 1965

Morphometric methods were first applied at the population level in order to test whether the chromosomal variability observed by Matthey (1958) and Capanna et al. (1996) in *P. tullbergi* has any morphological basis (Figure 4) or if any geographical substructure occurs within the species. In Figure 4, the first canonical variate separates out *P. tullbergi* from Ivory Coast, while the second canonical variate sets Guinea and Senegal populations apart from the others. The major difference between the Ivory Coast and other populations is size—especially size of the molars. This geographical difference was also investigated by using geometrical techniques of outline reconstructions, specifically to see if changes in dental size were accompanied by any changes in their shape. Elliptical Fourier analysis shows effectively that, in addition to size, there are shape differences in upper molar outline between the Guinean and Senegal populations of *P. tullbergi* (Figure 5). These results indicate a possible taxonomic differentiation within the *tullbergi* species group for the

more western part of tropical Africa. Concerning the chromosomal difference between specimens from the Central African Republic and from the Ivory Coast, the morphometrics analyses confirm some differences but much more sampling is required to investigate this problem thoroughly.

At a higher taxonomic level, there is confusion in the literature with the type of *P. lukolelae* from Central Africa. This taxon was placed in synonymy with *Malacomys* (Musser and Carleton 1993). TPS analysis using landmarks on the dorsal part of the skull confirms the distinction between the two species complexes of *Praomys* and suggest placement of *M. lukolelae* among the *P. tullbergi* complex. Combined with traditional skull and dental analysis, this strongly suggests by a quantitative method that the taxon *lukolelae* does not belong in *Malacomys* (Figure 6). Fronto-parietal crest disposition, as well as shape of the frontal part of the skull, helped to firm up the qualitative characters of Petter (1975). However, in all cases presented here, morphometrics never provided full discrimination between species or populations, hence other techniques are now required for OTU determination.

In conclusion, objective identification of OTUs requires attentive observation of large series of specimens in order to see the variability and eliminate the age differences. Good skeletal preparations and knowledge of anatomy are necessary. The discrimination methods can be applied locally with some specific identification success or at the generic level. However, in the case of *Praomys*, other molecular and karyological techniques are now needed to solve the problem of OTU definition within this group.

Phylogeny and classification

Phylogeny retraces the sister relationships of a species or a group of species. The genealogy obtained is shown graphically as a tree where the topology represents an hypothesis corresponding to the inferred evolutionary relationships between taxa. Congruent phylogenetic trees produced from different types of characters can form the basis for stable classifications (build the tree of life). Robust monophyletic groups allow us to make hypotheses about the history of characters and distributions. Phylogenetic relationships within the *Praomys* group were inferred using both morphological (Lecompte et al. 2002a) and molecular data (Lecompte et al. 2002b). By comparing the results of these analyses (Figure 7), several points of incongruency are given emphasis.

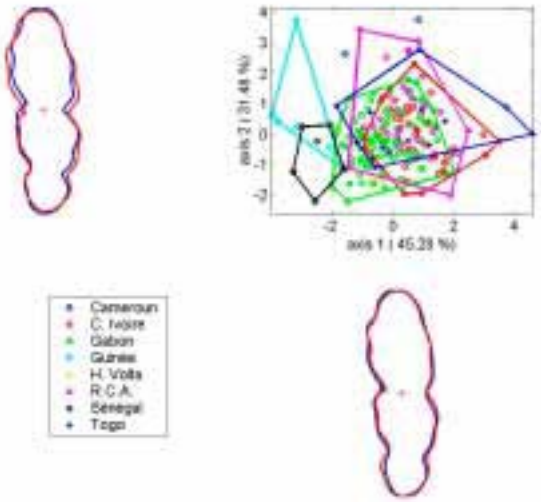

Figure 5. Canonical variable analysis (CVA) on upper molar row outlines and the representation of extreme shapes on each axis. The first canonical variable shows mainly a size difference and the second one a shape asymmetry especially on upper M1/.

A new maximum parsimony analysis is presented here for all members of the *Praomys* group. The morphology-based consensus tree displayed in Figure 7 (left), shows that the *Praomys* group is monophyletic and further confirms that the genus *Praomys* can be divided into two complexes, the *jacksoni* complex and the *tullbergi* complex. The crest character, first qualitatively identified by Petter (1975) and assessed quantitatively here (Figure 6), appears to have a robust phylogenetic value insofar as it provides an unambiguous synapomorphy for the *jacksoni* complex. The divergence between the *tullbergi* and *jacksoni* complexes is supported by a total of 13 synapomorphies. Species within

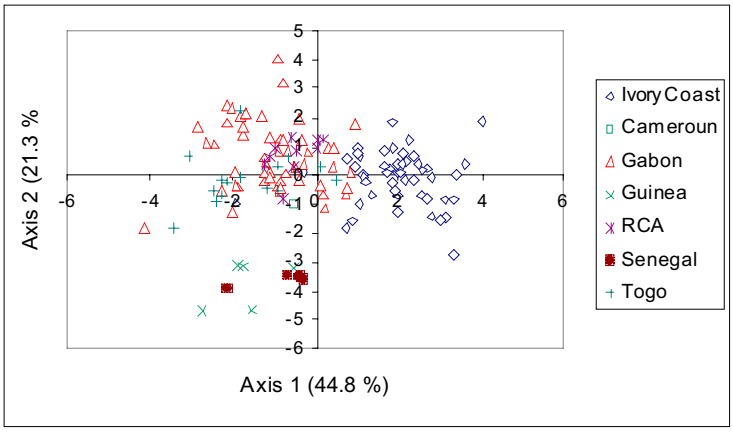

Figure 4. Results of the canonical variable analysis (CVA) based on 20 skull log-transformed measurements for 208 specimens of *P. tullbergi* from West Africa (axes 1 and 2) (RCA = Central African Republic).

the *tullbergi* group are distinguishable by up to six synapomorphies but there is no autapomorphy to define this entire group. Generally, some characters provide good local synapomorphies but they show convergence at the total *Praomys* group scale.

DNA sequencing is an important and objective source of characters usable in phylogeny (Figure 7, right). For the cytochrome b gene, the *Praomys* group is found to be monophyletic, as in the morphological tree. On the contrary, *Praomys*, *Myomys* and *Stenocephalemys* are this time paraphyletic. The cytochrome b sequences within the *P. tullbergi* group suggest the existence of a complex of species since *P. tullbergi* itself is divided into three paraphyletic units (E. Lecompte, unpublished). This pattern is consistent with previous geometric morphometrics and cytogenetic results.

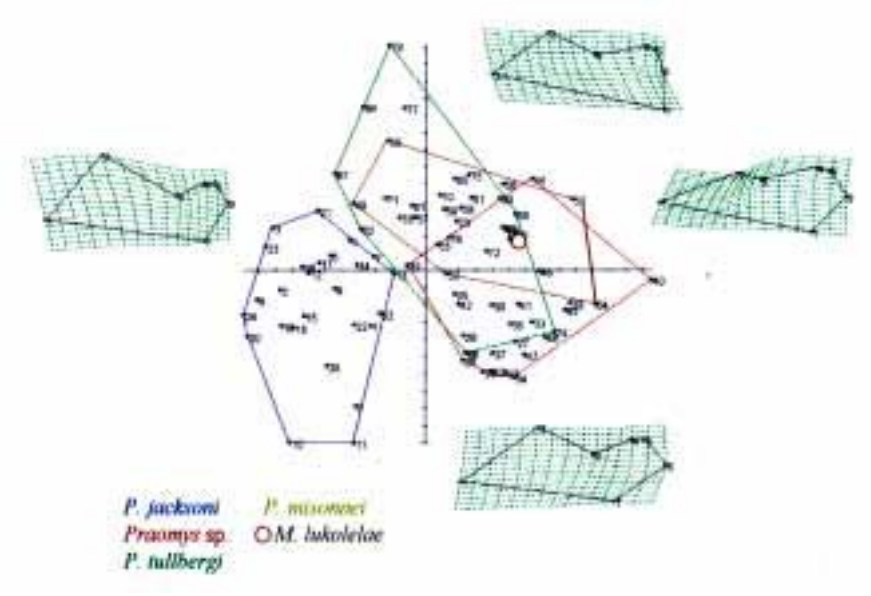

Figure 6. Thin-plate splines relative warp (TPSRW) analysis of variation in the dorsal outline of the frontal bone of different *Praomys* species. The results demonstrate the distinction of *P. jacksoni* on axis 1 and the similarity of the type of '*Malacomys*' *lukolelae* to members of the *P. tullbergi* complex.

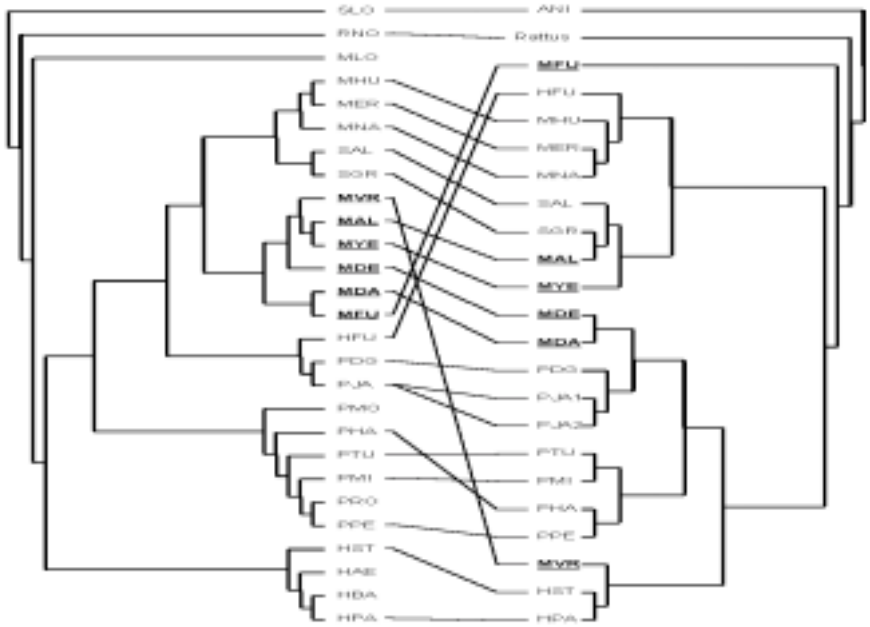

Figure 7. Morphological (left) and molecular (right) phylogenies of the *Praomys* group (after Lecompte et al. 2002a), showing the incongruence between these analyses. *Praomys* species are identified by acronyms beginning with P; *Hylomyscus* with H; *Stenocephalemys* with S; *Mastomys* are MER, MHU and MNA; *Heimyscus* is HFU; and the *Myomys* species are underlined.

In a recent article, Hillis and Wiens (1999) summarised the advantages and disadvantages of molecular versus morphological data for phylogenetic analysis. Both methods can provide useful information, especially when a range of different techniques is applied. Here, the comparison of the two trees with Treemap shows that the discrepant points are made by the *Myomys* species whose position in both the morphological and molecular trees is neither stable nor congruent. As a consequence, the morphological and molecular phylogenies are once again in conflict, especially in basal nodes and the monophyly/paraphyly of the genus *Myomys*. This conflict suggests that the genus *Myomys* is a possible cause of the wider confusion in the *Praomys* group. One classical criterion used to distinguish *Myomys* from *Praomys* or *Mastomys* species, is the number of mammae (10 in *Myomys* species), but the phylogenetic significance of this character is challenged by the molecular data that fail to support *Myomys* as a valid biological OTU. Similarly, the condition of a pure white belly may not be of phylogenetic value since this character is shared by *M. daltoni* and *M. fumatus*, which are highly divergent phylogenetically.

Similarly, morphologically divergent taxa like *Stenocephalemys* are found to be sister groups of certain *Myomys* species, and in this the new phylogeny confirms previous works by Lavrenchenko et al. (1999) and Fadda et al. (2001). The two phylogenies are congruent on the paraphyly of the genus *Praomys* (forest species): some *Myomys* (savannah species) are closer to *P. jacksoni* than to *P. tullbergi*. Interestingly, both *Praomys* species are hosts of arenaviruses (e.g. Mobala, Ippy, probably Ebola). The taxonomic results suggest that research on these viruses among related savannah taxa might prove of great interest from an epidemiological perspective.

Conclusion

In the *Praomys* group, it is now demonstrated that traditional diagnostic external morphological characters are far from effective in species identification. By combining cytogenetic, morphometric and molecular approaches in taxonomy, an accurate and stable classification can be achieved. Good species identification is still fundamental for applied research in agriculture and health. Furthermore, robust classifications that reflect the evolutionary history of the group may help in predicting the distributions of viruses and in discovering new species of potential hosts. The *Praomys* group has yielded numerous sibling species, especially in *Praomys* and *Mastomys* groups (Lecompte et al., this volume) and the biodiversity of the group is probably very much underestimated for these taxa. A similar conclusion can probably be inferred for most other genera of African Murinae. There is an urgent need to collect numerous specimens and tissues, spanning the entire geographical distributions of species within these genera. This is particularly pressing for some of the poorly known species that are under threat from drastic reduction of their primary and mountainous forest habitats.

References

Bookstein, F.L. 1991. Morphometric tools for landmark data: geometry and biology. New York, Cambridge University Press, 435 p.

Capanna, E., Codjia, J.T.C., Chrysostome, C. and Civitelli, M.V. 1996. Les chromosomes des Rongeurs du Bénin (Afrique de l'Ouest): 3 Murinae. Atti della Accademia dei lincei classe di scienze fisiche matematiche e naturali rendiconti lincei scienze fisiche e naturali, serie 9, 8, 25–37.

Chimimba, C. 1994. Non-geographic variation in *A. chrysophilus* (de Winton, 1897) and *A. namaquensis* (A. Smith, 1834) (Rodentia: Muridae) from southern Africa. South African Journal of Zoology, 29, 108–117.

Denys, C. 2002. The problem of species identification in palaeontology and biology: the case of *Mastomys* (Mammalia: Rodentia) and its dental variability. In: Baylac, M., Klingenberg, C.P., Fermon, Y. and Bailly, N., ed., Morphométrie multivariable, systématique et evolution: concepts, méthodes et applications. Paris, Muséum National d'Histoire Naturelle–Institut de Recherche pour le Développement (MNHN–IRD) Editions (in press).

Dobigny, G., Baylac, M. and Denys, C. 2002a. Geometric morphometrics and diagnosis of sibling species: the complex of west African *Taterillus* (Rodentia, Gerbillinae). Biological Journal of the Linnean Society (in press).

Dobigny, G., Granjon, L., Aniskine, V., Ba, K. and Volobouev, V. 2002b. A new sibling *Taterillus* species from West Africa. Mammalian Biology (in press).

Ellerman, J.R. 1940–1941. The families and genera of living rodents. London, British Museum (Natural History), 690 p.

Fadda, C., Corti, M. and Verheyen, E. 2001. Molecular phylogeny of *Myomys*/*Stenocephalemys* complex and its relationships with related African genera. Biochemical Systematics and Ecology, 29, 585–596.

Gautun, J.C., Sankhon, I. and Tranier, M. 1986. Nouvelle contribution à la connaissance des rongeurs du massif guinéen des monts Nimba (Afrique occidentale). Systématique et aperçu quantitatif. Mammalia, 50, 205–217.

Hillis, D.M. and Wiens, J.J. 1999. Molecules versus morphology in systematics. Conflicts, artefacts, and misconceptions. In: Wiens, J.J., ed., Phylogenetic analysis of morphological data. Washington D.C., Smithsonian Institution Press, 1–19.

Kuhl, F.P. and Giardina, G.R. 1982. Elliptic Fourier features of a closest contour. Computer Graphics and Image Processing, 18, 236–258.

Lavrenchenko, L.A., Milishnikov, A.N., Aniskin, V.M. and Warshavsky, A.A. 1999. Systematics and phylogeny of the genus *Stenocephalemys* Frick, 1914 (Rodentia, Muridae): a multidisciplinary approach. Mammalia, 63, 475–494.

Lecompte E., Denys, C. and Granjon, L. 2001. An identification key of the *Praomys* species (Rodentia: Muridae). In: Denys, C., Granjon, L. and Poulet, A., ed., African small mammals. Collection colloques et séminaires, Institut de Recherche pour le Développement (IRD) Editions, 127–140.

Lecompte, E., Granjon, L. and Denys, C. 2002a. The phylogeny of the *Praomys* complex (Rodentia: Muridae) and its phylogeographic implications. Journal of Zoological Systematics and Evolutionary Research, 40, 8–25.

Lecompte, E., Kerbis-Peterhans, J., Granjon, L. and Denys, C. 2002. Cytochrome-b based phylogeny of the *Praomys* group (Rodentia, Murinae): A new African radiation? Comptes Rendus de l'Académie des Sciences, Paris, Serie III (in press).

Maddalena, T., Van der Straeten, E., Ntahuga, L. and Sparti, A. 1989. Nouvelles données et caryotypes des rongeurs du Burundi. Revue Suisse de Zoologie, 96, 561–570.

Matthey, R. 1958. Les chromosomes et la position systématique de quelques Murinae africains (Mammalia–Rodentia). Acta Tropica, 15, 97–117.

Matthey, R., 1959. Formules chromosomiques de Muridae et de Spalacidae. La question du polymorphisme chromosomique chez les Mammifères. Revue Suisse de Zoologie, 66, 175–209.

Matthey, R. 1965. Etudes de cytogénétique sur les Murinae africains appartenant aux genres *Arvicanthis*, *Praomys*, *Acomys* et *Mastomys* (Rodentia). Mammalia, 29, 228–249.

Matthey, R. 1970. Caryotypes de Muridés et de Dendromuridés originaires de République Centrafricaine. Mammalia, 34, 459–466.

Mayr, E. 1963. Animal species and evolution. Cambridge, Harvard University Press.

Meester, J. 1988. Chromosomal speciation in southern African small mammals. South African Journal of Science, 84, 721–724.

Meester, J. and Setzer, H.W. 1971–1977. The mammals of Africa. An identification manual. Washington D.C., Smithsonian Institution Press.

Mills, J., Bowen, M. and Nichol, S. 1977 African arenaviruses—coevolution between virus and murid host. Belgian Journal of Zoology, 127, 19–38.

Morvan, J.M.M., Deubel, V., Gounon, P., Nakouné, E., Barrière, P., Murri, S., Volchov, V., Perpète, O., Selekon, B., Coudrier, D., Gautier-Hion, A. and Colyn, M. 1999. Identification of Ebola virus sequences present as RNA or DNA in organs of terrestrial small mammals of the Central African Republic. Microbes and Infection, 1, 1192–1201.

Musser, G.G. and Carleton, M.D. 1993. Family Muridae. In: Wilson, D.E. and Reeder, D.M., ed., Mammal species of the world: a taxonomic and geographic reference. Washington D.C., Smithsonian Institution Press, 501–755.

Page, R.D.M. 1995. Parallel phylogenies: reconstructing the history of host–parasite assemblage. Cladistics, 10, 155–173.

Petter F. 1965. Les *Praomys* d'afrique centrale. Zeitschrift für Säugetierkunde, 30, 54–60.

Petter F. 1975. Les *Praomys* de la République Centrafricaine (Rongeurs, Muridés). Mammalia, 39, 51–56.

Qumsiyeh, M.B., King, S.W., Arroyo-Cabrales, J., Aggundey, I.R., Schlitter, D.A., Baker, R.J. and Morrow, K.J. 1990. Chromosomes and protein in morphologically similar species of *Praomys* sensu lato (Rodentia, Muridae). Journal of Heredity, 81, 58–65.

Rohlf, F.J. 2001. TPSRW. Stony Brook, New York, Department of Ecology and Evolution, State University of New York.

Rohlf, F.J. and Marcus, L.F. 1993. A revolution in morphometrics, Trends in Ecology and Evolution, 8, 129–132.

Rosevear, D.R. 1969. The rodents of West Africa. London, Trustees of the British Museum (Natural History), 604 p.

Swofford D.L. 1998. PAUP: phylogenetic analysis using parsimony. Champaign, Illinois, Natural History Survey, 177 p.

Taylor, P.J. 2000. Patterns of chromosomal variation in southern African rodents. Journal of Mammalogy, 81, 317–331.

Taylor, P.J., Meester, J. and Kearney, T. 1993. The taxonomic status of Saunder's vlei rat, *Otomys saundersiae* Roberts (Rodentia : Muridae: Otomyinae). Journal of African Zoology, 107, 6, 571–596.

Thomas, O. 1915. List of mammals collected on the Upper Congo by Christy for the Congo Museum, Tervueren. Annals and Magazine of Natural History, Series 8, 16 , 465–481.

Updegraff, G. 1990. Measurement TV. Version 1.92. Data Crunch.

Van der Straeten, E. and Dieterlen, F. 1987. *Praomys misonnei*, a new species of Muridae from Eastern Zaïre (Mammalia). Stuttgarter Beiträge zur Naturkunde, serie A (Biologie), 402, 1–11.

Van der Straeten, E. and Dudu, A. M. 1990. Systematics and distribution of *Praomys* from the Masako Forest Reserve (Zaire), with the description of a new species, In: Peters, G. and Hutterer, R., ed., Vertebrates in the tropics. Bonn, Museum Alexander Koenig, 72–83.

Van der Straeten, E. and Kerbis-Peterhans, J.C. 1999. *Praomys degraaffi*, a new species of Muridae (Mammalia) from central Africa. South African Journal of Zoology, 34, 80–90.

Van der Straeten, E. and Verheyen, W. 1981. Etude biométrique du genre *Praomys* en Côte d'Ivoire. Bonner Zoologishe Beitrräge, 32, 249–264.

Winnepenninckx, B., Backeljau, T. and De Wachter, R. 1993. Extraction of high molecular weight DNA from molluscs. Trends in Genetics, 9, 407.