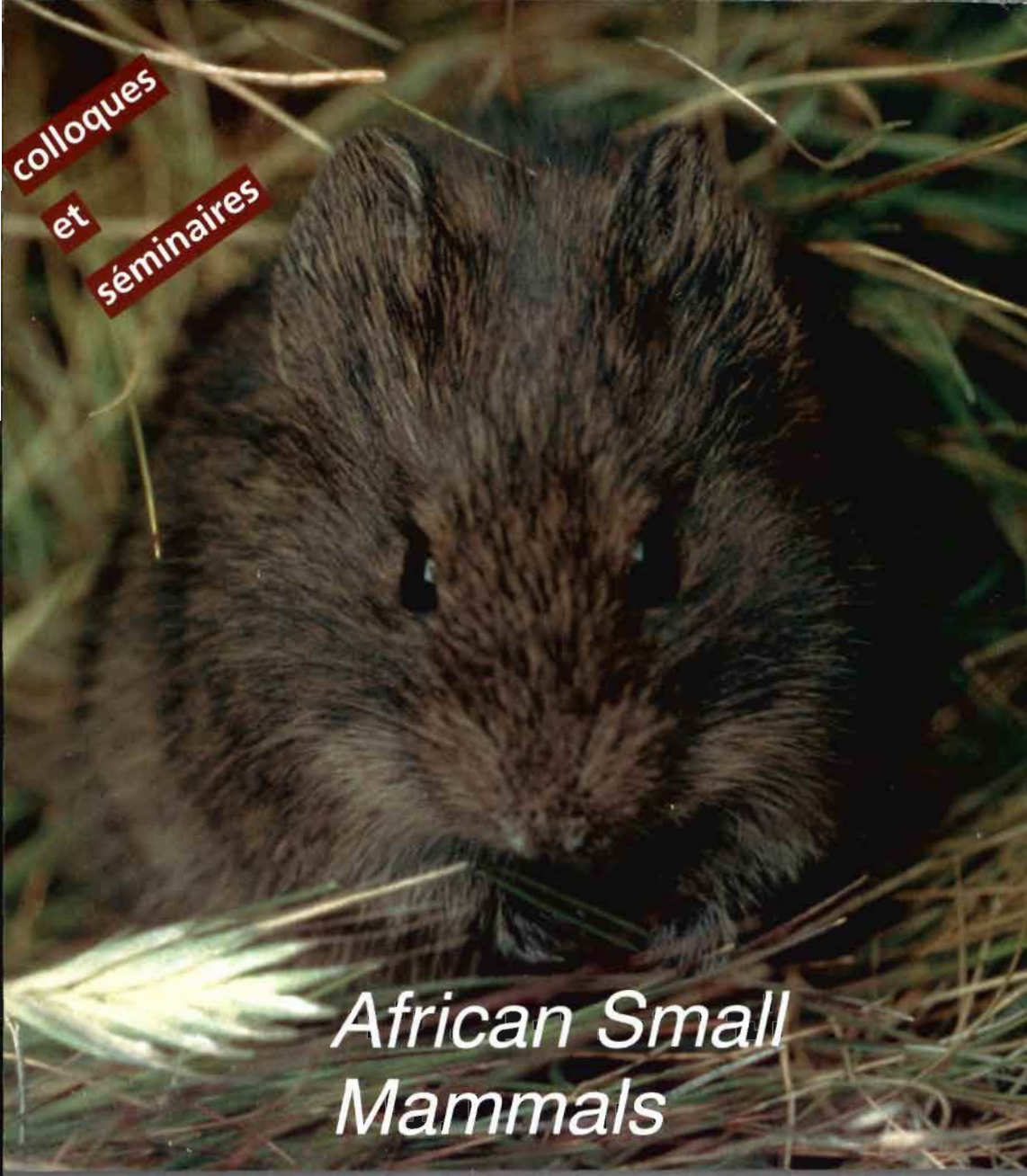

colloques et séminaires

African Small Mammals

Petits mammifères africains

Scientific editors
Éditeurs scientifiques

Christiane Denys
Laurent Granjon
Alain Poulet

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Introduction

Taken as comprising all species of less than 20 kg, the 10 orders (Bats, Lipotyphlans, Primates, Carnivores, Hyraxes, Artiodactyls, Rodents, Lagomorphs, Macroscelids and Pholidotes) of African small mammals represent more than 80% of the African mammalian diversity. Systematics and many aspects of the biology of the vast majority of these species are unknown or inadequately documented. Yet some of the most abundant and widespread species, particularly rodents, are agricultural pests and/or reservoirs for various diseases and are of considerable economic and sanitary importance. Knowledge of their systematics, geographic distributions, and ecologies is prerequisite to determining any possible measures undertaken to control their populations and reduce their negative impact on human activities and health. Habitat destruction, overhunting and other human-related activities threaten the survival of other species. Here again, knowing their taxonomical and geographical limits as well as their ecology in the broader sense is urgent to implement conservation strategies aimed at preserving their populations. Finally, the peculiar history of isolation and long-term presence of tropical climates that characterize Africa make African small mammals excellent candidates for use in research directed at answering questions related to mammalian evolutionary history not only on the continent but also on the planet.

The 8th International African Small Mammal Symposium held in Paris between 5-9 July 1999 provided an occasion to tackle these questions, thanks to the attendance of more than 120 biologists involved in research on African small mammals. The diversity of origin of the participants (25 countries), the significant number of students and the number and quality of the communications highlight the dynamic research efforts in this field. This volume of proceedings, though representing only a part of the materials presented during the Symposium, accurately reflects its coverage. All the main topics that were identified as headings of sessions are represented, and the volume is thus organized nearly in the same way as the Symposium proceeded.

Ten reports are devoted to "Taxonomy and classification": Alpha taxonomy using genetic methods to recognize shrew or rodent species in Ethiopia (BANNIKOVA *et al.*) and Mauritania (BÂ *et al.*) or to confirm a new rodent sub-family (CHEVRET *et al.*); morphometrical and

anatomical methods to recognize species in the group of rusty-spotted genets from southern Africa (CRAWFORD-CABRAL and FERNANDES), define the oldest representative of Carnivores for Africa (CROCHET *et al.*), construct identification keys in the genera *Genetta* (GAUBERT *et al.*) and *Praomys* (LECOMPTE *et al.*), or revise concepts in Gerbillid classification (PAVLINOV); morphological and morphometrical methods to help quantify species diversity in the rodent genus *Otomys* (TAYLOR and KUMIRAI) as well as study the origin and differentiation of the dental pattern in that genus (SENEGAS).

The section "Phylogeny and evolution" is introduced by a thorough and useful review of the role of cytogenetics in the study of African small mammal systematics (ROBINSON), followed by the presentation of early Eocene small mammal faunas from Algeria (TABUCE *et al.*) and their evolutionary consequences. The other contributions are based respectively on: functional morphology in *Cryptomys hottentotus* (BANKE *et al.*); comparative cranial anatomy in Tenrecomorpha (GIERE *et al.*); biogeography in chromosomally diverse Bathyergid rodents (KAWALIKA *et al.*; BURDA); reproductive biology to address the old question of hystricognath evolution (MESS); and molecular *vs.* morphological analyses to try determine the phylogenetic position of Gliridae, Anomaluridae and Pedetidae (MONTGELARD *et al.*).

Various aspects of "Behaviour" are the subject of five papers, from nutritional ecology of rodents pollinators of South African *Protea* (VAN TETS *et al.*) to reproductive behaviour in *Rhabdomys pumilio* (BENNETT and PILLAY) or *Heliophobius argentocinereus* (SUMBERA) via socioecology in the squirrel *Atantoxerus getulus* (GOUAT et YAHYAOUI) or swimming abilities in rodents from Senegal (DUPLANTIER and BÂ). Attached to this section is the paper by HAIM and AFIK on *Acomys cahirinus* responses to photoperiod manipulations, originally presented in a "Physiology and Reproduction" session.

Finally, nine contributions have been grouped in the "Ecology" section, which opens with a well-documented analysis of the major trends and perspectives in African small mammal ecology (HAPPOLD). Three inventories present new data on poorly known, high elevation places from various parts of Africa: Nyika plateau in Malawi (CHITAUKALI *et al.*), Mt Elgon in Uganda (CLAUSNITZER) and Adrar des Iforas Massif in Mali (DOBIGNY *et al.*). Specific studies concern spatiotemporal habitat use by *Mastomys* cf. *natalensis* in Uganda as revealed by radio-

tracking (HOFFMANN and KLINGEL), population dynamics of *Gerbillus nigeriae* on agricultural land in Niger (NOMAO and GAUTUN) and habitat preference of *Arvicanthis dembeensis* in Ethiopia (WUBE and BEKELE). A taphonomical study based on Eagle-Owl pellets in Algeria (LAUDET and HAMDINE) and a synthesis on the role of gerbils and jirds in desert rodent communities (SHENBROT *et al.*) conclude this chapter.

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Christiane Denys, Laurent Granjon et Alain Poulet

Introduction

Considérés comme comprenant toutes les espèces de moins de 20 kg, les dix ordres (Chiroptères, Lipotyphles, Primates, Carnivores, Hyracoïdes, Artiodactyles, Rongeurs, Lagomorphes, Macroscelides et Pholidotes) de petits mammifères africains représentent plus de 80 % de la diversité mammalienne d'Afrique. La systématique ainsi que de nombreux aspects de la biologie de la grande majorité de ces espèces sont inconnus ou incomplètement documentés. Pourtant, certaines parmi les plus abondantes et les plus largement réparties de ces espèces, en particulier chez les Rongeurs, sont nuisibles pour l'agriculture et / ou réservoirs de diverses maladies, et de ce fait ont une importance économique et sanitaire considérable. La connaissance de leur systématique, de leur distribution géographique et de leur écologie est un préalable à la mise en place de mesures visant à contrôler les populations de ces espèces afin de réduire leur impact négatif sur les activités et la santé humaine. Par ailleurs, la destruction de l'habitat, la chasse et d'autres activités liées à l'homme menacent la survie d'un certain nombre d'autres espèces. Connaître leurs limites en terme de systématique et de biogéographie, ainsi que leur écologie dans le sens le plus large est urgent dans le but de développer des stratégies de conservation de leurs populations. Enfin, le long isolement et la persistance de climats tropicaux qui caractérisent l'Afrique font des petits mammifères africains d'excellents candidats pour aborder des sujets de recherche liés à l'histoire évolutive des Mammifères, non seulement sur le continent mais également à l'échelle de la planète.

Le 8e Symposium international sur les petits mammifères africains qui s'est tenu à Paris du 5 au 9 juillet 1999 a été l'occasion d'aborder ces questions, grâce à la participation de plus de 120 biologistes impliqués dans des recherches sur les petits Mammifères africains. La diversité d'origine des participants (25 pays), le nombre significatif d'étudiants ainsi que le nombre et la qualité des communications illustrent bien les efforts de recherche dans ce domaine. Ce volume d'actes, bien que ne représentant qu'une partie de ce qui a été présenté pendant ce Symposium, n'en reflète pas moins assez fidèlement le contenu. Tous les thèmes majeurs qui avaient été retenus comme titres de sessions sont représentés, et ce volume est de ce fait

organisé à peu de chose près de la même façon que le Symposium s'est déroulé.

Dix textes sont consacrés au thème « Taxonomie et classification » : alpha-taxonomie grâce à des méthodes génétiques pour caractériser des espèces de musaraignes ou de Rongeurs en Éthiopie (BANNIKOVA *et al.*) et Mauritanie (BÂ *et al.*) ou pour confirmer la validité d'une nouvelle sous-famille de Rongeurs (CHEVRET *et al.*) ; méthodes morphométriques et anatomiques pour reconnaître les espèces du groupe des genettes tigrines d'Afrique du Sud (CRAWFORD-CABRAL et FERNANDES), définir le plus ancien Carnivore d'Afrique (CROCHET *et al.*), construire des clés d'identification dans les genres *Genetta* (GAUBERT *et al.*) et *Praomys* (LECOMPTE *et al.*), ou réviser les concepts de la classification des Gerbillidés (PAVLINOV) ; méthodes morphologiques et morphométriques pour aider à quantifier la diversité spécifique chez les Rongeurs du genre *Otomys* (TAYLOR et KUMIRAI) ou étudier l'origine et la différenciation des schémas dentaires dans ce genre (SENEGAS).

La section « Phylogénie et évolution » est introduite par une revue très complète et utile du rôle de la cytogénétique dans l'étude de la systématique des petits mammifères africains (ROBINSON). Suivent ensuite sept autres contributions, concernant respectivement la présentation d'une faune de l'Eocène d'Algérie (TABUCE *et al.*) ; la morphologie fonctionnelle chez *Cryptomys hottentus* (BANKE *et al.*) ; l'anatomie crânienne comparée chez les Tenrecomorpha (GIERE *et al.*) ; la biogéographie des Rongeurs Bathyergidés chromosomiquement diversifiés (KAWALIKA *et al.* ; BURDA) ; la biologie de la reproduction pour aborder la vieille question de l'évolution des Hystricognathes (MESS) ; et la confrontation d'analyses moléculaires et morphologiques pour tenter de préciser la position phylogénétique des Gliridés, Anomaluridés et Pedetidés (MONTGELARD *et al.*).

Le comportement est le sujet de cinq contributions, allant de l'écologie nutritionnelle des rongeurs pollinisateurs de *Protea* en Afrique du Sud (VAN TETS *et al.*) au comportement reproducteur de *Rhabdomys pumilio* (BENNETT et PILLAY) ou d'*Heliophobius argentocinereus* (SUMBERA) en passant par la socio-écologie de l'écureuil terrestre *Atlantoxerus getulus* (GOUAT et YAHYAOUI) et les performances natatoires de rongeurs du Sénégal (DUPLANTIER et BÂ). L'article d'HAIM et AFIK sur les réponses aux manipulations de la

photopériode, originellement présenté dans la session « Physiologie et Reproduction » a été rattaché à ce chapitre.

Enfin, neuf contributions ont été regroupée dans la section « Écologie », introduite par une analyse bien documentée des tendances majeures et des perspectives de la recherche en écologie sur les petits Mammifères africains (HAPPOLD). Trois inventaires présentent des données nouvelles sur des sites mal connus d'altitude : le plateau du Nyika au Malawi (CHITAUKALI *et al.*), le mont Elgon en Ouganda (CLAUSNITZER) et le Massif de l'Adrar des Iforas au Mali (DOBIGNY *et al.*). Des études plus spécifiques concernent l'utilisation spatio-temporelle de l'habitat par *Mastomys* cf. *natalensis* en Ouganda telle que révélée par radio-tracking (HOFFMAN et KLINGEL), la dynamique de population de *Gerbillus nigeriae* sur une zone agriculturale au Niger (NOMAO et GAUTUN) et les préférences d'habitat d'*Arvicanthis dembeensis* en Ethiopia (WUBE et BEKELE). Une étude taphonomique basée sur des pelotes de Grand-Duc en Algérie (LAUDET et HAMDINE) et une synthèse sur le rôle des gerbilles et mériones dans les communautés de rongeurs complètent ce chapitre (SHENBROT *et al.*).

Ce Symposium n'aurait pas été possible sans le soutien financier et logistique du Muséum national d'histoire naturelle, Paris. Le CNRS (Département des Sciences de la Vie) et l'IRD ainsi que le ministère des Affaires étrangères ont également aidé financièrement à cette organisation. Toutes ces institutions sont remerciée pour leur participation. La préparation et le contenu scientifique de cette réunion doivent beaucoup aux membres du Comité Scientifique, aux modérateurs des sessions et aux relecteurs des résumés et des manuscrits, qui ont toujours répondu à nos requêtes rapidement et efficacement. Nos plus chaleureux remerciements vont à Peter Andrews, Claude Baudoin, Afework Bekele, Janice Britton-Davidian, Chris Chimimba, Marc Colyn, Marco Corti, Edith Dempster, Fritz Dieterlen, Jean-Marc Duplantier, Guila Ganem, Jean-Pierre Gasc, Emmanuel Gheerbrant, Jean-Paul Gonzalez, Abraham Haim, David Happold, Jean-Louis Hartenberger, Barbara Herzig, Giora Heth, Graham Hickman, Rainer Hutterer, Farida Khammar, Leonid Lavrenchenko, Michel le Berre, Herwig Leirs, Thomas Martin, Jacques Michaux, Guy Musser, Françis et Germaine Petter, Neville Pillay, Duane Schlitter, Norbert Schmidt-Kittler, Bruno Sicard, Peter Taylor, Erik Van der Straeten, Erik Verheyen, Géraldine Véron et Peter Vogel.

Localement, de nombreuses personnes nous ont aidé à un moment ou à un autre de la préparation et de l'accomplissement de ce Symposium, et nous leur en sommes sincèrement reconnaissants : Bertrand Bed'hom, Evelyne Brémond-Hoslet, Marie Thérèse Broucksaux, Cécile Callou, Raphaël Cornette, Jacques Cuisin, Gauthier Dobigny, Jean-François Ducroz, Evelyne Granjon, Céline Houssin, Jean-Pierre Hugot, Ronan Kirsch, Emilie Lecompte, Suzanne Marchand, Sybile Moulin, Francis Petter, Jean-Philippe Reyftman, Christine Rollard, Michel Tranier, Vitaly Volobouev.

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Hommage à Francis Petter

Michel Tranier

Christiane Denys

Francis Petter est né le 28 juillet 1923 à Paris. Ses parents ont habité rue des Écoles, à deux pas d'un Muséum qui allait être une bonne partie de sa vie. Aîné de trois garçons également attirés par la nature et la science, il a été tout naturellement amené à fréquenter le Jardin des Plantes, et en particulier sa Ménagerie et son Vivarium. A propos du Vivarium, on peut dire que Francis en a été le fournisseur attitré pendant 50 ans ! Enfant, il s'est passionné pour l'élevage d'animaux divers, une passion qui allait se concrétiser dans une carrière de vétérinaire et de zoologiste.

Chose curieuse, c'est son frère cadet Jean-Jacques qui devait amener Francis au Laboratoire des mammifères et oiseaux ; c'est là que, pendant les années scolaires difficiles de la Seconde Guerre mondiale, Francis rencontra deux personnalités marquantes : le directeur du laboratoire Édouard Bourdelle, et le sous-directeur Jacques Berlioz. Le premier était vétérinaire et mammalogiste, le second était ornithologue ; dans le Muséum un peu étriqué de cette époque, les laboratoires étaient rarement composés de plus de trois chercheurs : on comptait généralement un ou deux assistants, un sous-directeur, et un directeur par service ; aux Mammifères et Oiseaux, une règle non écrite établissait l'alternance entre les grades : si le directeur était mammalogiste, le sous-directeur était ornithologue, et l'assistant mammalogiste.

Francis, qui fréquente assidûment le Muséum, ses galeries et le Jardin des Plantes, propose ses services de naturaliste en herbe ; surmontant le côté rébarbatif des collections, il s'émerveille des formes et des couleurs, rêve sur les provenances et les collecteurs, et va compléter sa formation en observant les animaux vivants à la Ménagerie et au

Vivarium. Les conversations qu'il a avec le personnel du laboratoire lui fixent peu à peu le profil de ce qu'était alors un zoologiste dans un grand musée. Décidément, Francis se dit qu'il sera un biologiste, mais à ce stade, il balance encore – et il va balancer longtemps ! – entre devenir médecin-vétérinaire ou zoologiste au Muséum. Il se passionne pour toute la nature, mais a un petit faible pour les mammifères ; à la fin de la guerre, il entre à l'École vétérinaire d'Alfort dont il sortira en 1949. À cette époque, entre 1945 et 1950, Francis complète sa formation à l'université, fait de l'aide et du remplacement chez un vétérinaire parisien, installé dans une clientèle prospère, qui va lui proposer l'association pendant une quinzaine d'années. Francis aime la pratique vétérinaire, il est doué pour les rapports avec la clientèle et pour le commerce (qui l'a vu marchander en Afrique me croira volontiers !), ce métier rapporte bien, mais pourtant, il préférerait travailler au Muséum, malgré les moyens et les salaires qu'il connaît dans cette institution.

En 1949, le sort lui offre une opportunité : Paul Rode, l'assistant du laboratoire, meurt prématurément : Jean Dorst, son condisciple à l'université et Jacques Berlioz qui, entre temps, est devenu le patron, lui proposent le poste pour s'occuper de mammalogie. Francis accepte, et 50 ans après, il est toujours là ; malgré cette longue fidélité, tout n'ira pas toujours si facilement dans sa carrière.

De 1950 à 1960, il mène de front trois grosses activités : d'abord rendre la collection mammalogique utilisable, ensuite préparer une thèse d'État, enfin s'occuper de la revue *Mammalia.*

La collection : quand Francis arrive au laboratoire, les petits mammifères, surtout des spécimens historiques, sont en tas littéralement abandonnés ; il lui faut trier les collections en vrac, où les spécimens sont rarement déterminés et presque jamais catalogués ; il va impulser un élan déterminant à la collection mammalogique, laquelle va s'accroître de 30 000 spécimens en 40 ans ; il fait inscrire les milliers de spécimens non enregistrés ; il participe à de nombreuses missions, collectant lui-même des centaines d'animaux ou se les faisant remettre par d'autres collecteurs, en particulier de l'Orstom et de l'Institut Pasteur.

La thèse : bien qu'il n'ait pas été très soutenu par son patron, Francis décide de préparer une thèse ; au laboratoire, il a remarqué un groupe difficile de Rongeurs, les gerbilles et leurs parents ; son épouse

Germaine, paléontologue, étudie les goniatites, Ammonoïdés du Devonien au Sahara ; Francis accompagne sa femme en Algérie, et étudie l'éthologie, l'écologie et la systématique des rongeurs sahariens. Les conditions initiales de la thèse sont assez épiques, et confinent au steeple-chase : Francis n'est autorisé à aller sur le terrain que pendant ses vacances ; il n'est autorisé à les prendre qu'en été, et bien sûr, tout cela est à ses frais, le Muséum à l'époque n'ayant pas les moyens de payer de telles missions. Peu à peu, Francis, qui n'est pas homme à se laisser abattre, va s'affranchir des contraintes, trouver de l'argent au CNRS, et élargir son champ d'exploration : vers la fin des années 1960, il a parcouru une vaste partie de la zone saharo-sindienne. Il en tirera une synthèse qui fera date.

L'étude des rongeurs Gerbillidés, entièrement inféodés aux paysages ouverts, steppiques ou désertiques a fait l'objet de la thèse d'état de Francis Petter, publiée en 1961 dans *Mammalia*. Les observations écologiques qu'il a effectuées sur le terrain, au Sahara, pendant plusieurs années de suite à partir de 1950, puis en Iran et en Irak, lui ont permis d'abord de reconnaître les espèces d'après leur mode de vie et leur habitus, puis d'en discerner au laboratoire les caractères morphologiques particuliers. Cela l'a amené progressivement à une révision des genres de cette famille, dont près des trois-quarts peuvent être établis, à la fois d'après des caractères dentaires et d'autres caractères morphologiques ou biologiques. De plus, cela a initié les travaux sur la signification de l'hypertrophie des bulles tympaniques et il a décrit le retour au gîte chez certains rongeurs ainsi que la structure des terriers des rongeurs fouisseurs. En plus de l'analyse morphologique, l'analyse des caractères chromosomiques a permis de préciser les limites des espèces et de leur distribution géographique. Incidemment, le passage devant lui d'un lièvre gris foncé, inconnu au Sahara, l'amène à reprendre de fond en comble la systématique des lièvres de toute l'Afrique, à l'aide des collections du British Museum de Londres où il se rend à de nombreuses reprises, et de nombreux autres musées qui lui envoient les leurs en prêt.

Sa thèse soutenue, Francis Petter estime que sa carrière doit prendre un tournant : ou le Muséum lui donne un poste de sous-directeur, ou il abandonne la recherche et s'installe en clientèle ; le patron du laboratoire a les données en mains, et sait que c'est un ultimatum sérieux :

il fait ce qu'il faut faire à l'époque, et Francis est nommé sous-directeur en 1961.

La décennie 1960-1970 est faste pour les postes au Muséum national : l'institution voit ses postes tripler en 10 ans. Grâce à ces recrutements massifs, Francis peut constituer une petite équipe de mammalogistes, et diversifier ses sujets d'intérêt. C'est l'époque où il s'attaque, en particulier, à la faune de Madagascar, et à celle de Centrafrique avec son assistante Huguette Genest. C'est aussi l'époque moins faste où le Muséum laisse tomber en ruines le Musée du duc d'Orléans et la Galerie de zoologie. Francis, à ce moment-là, est du petit nombre de ceux qui pensent que c'est une honte et que le Muséum devrait avoir une Galerie de Zoologie digne de lui. Toujours pendant cette décennie 1960-1970, Francis va nouer des liens professionnels très solides avec le père de la cytotaxonomie, le Suisse Robert Matthey ; l'austère lausannois et le parisien entreprenant vont s'entendre durablement pendant 15 ans et publier des dizaines de formules chromosomiques. Ainsi, pour la première fois, un spécialiste de la cytogénétique (technique peu répandue à l'époque) et un spécialiste de la morpho-anatomie et de l'éco-éthologie vont unir leur forces pour préciser la systématique des petits mammifères africains et asiatiques. Cette recherche très fructueuse conduira ainsi à une meilleure connaissance des *Arvicanthis, Taterillus, Praomys, Mastomys, Acomys* et, entre autres, ouvrira la voie à la systématique moderne au Laboratoire de Zoologie des mammifères et oiseaux du MNHN.

Pendant les deux décennies 1970-1990, Francis élargit ses centres d'intérêt, voyage beaucoup et décrit beaucoup. Il s'occupe toujours de la revue *Mammalia*. Pendant cette période, il va se montrer de plus en plus systématicien et de moins en moins écologiste : c'est aussi dans ces années qu'il « découvre l'Amérique », et qu'il va s'intéresser à la faune du Brésil et de la Guyane. De plus, il noue des collaborations étroites avec le laboratoire de Parasitologie du professeur Chabaud et participe, en Malaisie, avec Odile Bain en 1977 à la découverte d'une nouvelle espèce de filaire, tandis qu'une sous-espèce nouvelle de *Plasmodium vinckei* porte son nom.

Francis a décrit plusieurs espèces nouvelles comme, par exemple deux nouveaux rongeurs malgaches : *Macrotarsomys ingens* en 1959, et *Brachytarsomys albicauda villosa* en 1962, celui-ci reconnu comme une espèce en 2001. Il décrit aussi un nouvel insectivore du nord de

l'Assam *Anourosorex squamipes schmidi* en 1963. Il décrit encore en 1966 un genre inédit de rongeur de forêt de Brazzavile qu'il baptise *Dendroprionomys rousseloti* qui n'est encore connu que par trois spécimens. Parmi les nouvelles espèces il décrit encore une sarigue du Brésil, *Marmosa karimii* (1968), *Mus mattheyi* (1969), *Stenocephalemys griseicauda* et *Lophuromys melanonyx* en 1972, *Proechimys cuvieri* (1978), un rat pêcheur de Guyane française, *Daptomys oyapocki* (1978), un nouveau rat d'eau de Guyane française *Nectomys parvipes* en 1979, un *Isothrix* et un *Rhipidomys* nouveaux en Guyane, du Mt Oku (Cameroun) un nouveau Murinae *Lamottemys okuensis* en 1986.

Ne dédaignant pas la paléontologie F. Petter signera ainsi une étude sur les Léporidés du Pleistocène moyen de Corrèze ainsi que la description en collaboration avec M. Crusafont-Pairo du Murinae géant des îles Canaries *Canariomys bravoi* en 1964, et en unique auteur, la description de *Paraethomys filfilae* d'Algérie en 1968. Une espèce de rongeur fossile d'*Otomys* lui a été dédiée par l'un d'entre nous (C.D.) Parmi les rongeurs des milieux désertiques il a aussi pu valider la gerboise *Jaculus blanfordi* et *Meriones vinogradovi* en Iran.

Les travaux sur la révision de certains genres de rongeurs l'ont amené à se pencher sur les grandes lignes de la Classification des rongeurs. Ainsi, en collaboration avec Chaline et Mein, il propose en 1977 la suppression de la famille des Spalacidae et une révision du contenu de la famille des Cricetidae et des Muridae. Il a également défini la famille des Cricetomyidae. Même si ces regroupements ont été bousculés ultérieurement par d'autres anatomistes, par des découvertes paléontologiques ou par les analyses moléculaires, il est devenu la référence, souvent avec son complice Matthey, pour des taxons réputés difficiles. Ses révisions des genres *Gerbillus*, *Acomys*, *Praomys*, *Lepus*, *Nannomys* font date. Elles seront publiées dans la clé de détermination des petits mammifères africains de la Smithsonian Institution sous la responsabilité de Setzer, publiée de 1971 à 1977, qui reste d'actualité dans le domaine.

Outre l'aspect taxonomique, Francis Petter, par ses nombreux travaux de terrain ou ses travaux sur les collections, a permis de préciser l'aire géographique de certaines espèces de petits mammifères africains, ce qui représente une précieuse contribution biogéographique.

Passionné d'élevage, Francis Petter a contribué à l'acclimatation et à l'élevage de rongeurs africains, asiatiques et sud-américains au laboratoire dont il pense qu'on ne peut pas se passer pour en comprendre les parentés. Il a testé par ailleurs la validité de certaines espèces en faisant des croisements entre individus provenant de populations géographiques distinctes.

Enfin, c'est pendant ces années 1970-1990 que Francis mettra toute son énergie à faire sortir la Galerie de Zoologie du néant ; avec quelques autres motivés, comme Jean Dorst et Claude Lévi, ils obtiendront la construction de la Zoothèque dans les années 1980 (photo 1), et sa suite logique, l'inauguration de la Galerie de l'Évolution en 1994 qui marquera l'aboutissement de 25 ans d'effort.

Cette merveilleuse Galerie de l'Évolution nous a d'ailleurs phagocyté Francis, qui a été bien trop occupé par ce vaste projet pour continuer à faire de la systématique, au grand dam de ses amis et collègues. Il continue donc toujours à participer à des expositions au titre de conseiller scientifique bénévole.

Homme de terrain hors pair, bon naturaliste, bon zootechnicien et systématicien entraîné, Francis a fait plus de 150 publications et 20 descriptions de taxons nouveaux. Son caractère affable et son égalité d'humeur en ont fait un patron et un collègue très agréable. Il demeure à la fois un spécialiste incontesté de l'écologie des petits mammifères sahariens et de la systématique des petits Muridés des régions tropicales, ce qui lui a valu son surnom donné affectueusement par un de ses plus anciens collègues anglo-saxon de « roi des rongeurs ».

Liste chronologique des publications

PETTER F., 1950 —
La détermination expérimentale du sexe chez les Mammifères. *Mammalia*, 14, 49-77.

BOURDELLE et E. PETTER F., 1950 —
Note relative à un éléphant nain du Gabon. *Mammalia*, 14, 145-153.

JOUANIN C. et PETTER F., 1951 —
Contribution à l'étude de l'avifaune du sud-oranais. *Bull. Mus. Nat. Hist. Nat.*, 23, 616-620.

PETTER F., 1951 —
Contribution à l'étude du genre *Psammomys* Cretschmar (Rongeurs Muridés). *Mammalia*, 15, 39-46.

PETTER F., 1951 —
Note sur quelques rongeurs du Sahara occidental. *Mammalia*, 15, 69-72.

PETTER F., 1951 —
Étude d'une collection de rongeurs du Sahara nord-occidental. *Bull. Mus. Nat. Hist. Nat.*, 23, 483-488.

PETTER F., 1952 —
Note sur un type de F. Cuvier : *Gerbillus pygargus*, la Gerbille du Sénégal. *Mammalia*, 16, 37-39.

PETTER F., 1952 —
Note préliminaire sur l'éthologie et l'écologie de *Psammomys obesus* Cretzschmar. *Mammalia*, 16, 137-147.

PETTER F., 1952 —
Note sur la systématique de quelques rongeurs désertiques. *Proc. Internat. Symp. on Desert Research*, Jérusalem, 1-3.

PETTER F., 1952 —
Le Renard famélique. *Terre et Vie*, 190-193.

PETTER F. et ROCHE J., 1952 —
Étude de la collection de rongeurs du Tassili des Ajjers récoltée par J. Roche (mission 1951). Trav. Inst. Rech. Sahar. (série Tassili), 3, 127-132.

PETTER F., 1953 —
Étude d'une collection de Sciuridés du Cameroun. *Bull. Mus. Nat. Hist.*, 25, 433-436.

PETTER F., 1953 —
Remarques sur la signification des bulles tympaniques chez les mammifères. *C. R. Acad. Sciences*, 237, 848-849.

PETTER F., 1953 —
Une question d'actualité : myxomatose et acclimatation. *Terre et Vie*, 144-147.

PETTER F., 1953 —
Note préliminaire sur l'éthologie et l'écologie de *Meriones libycus* (Rongeurs, Gerbillidés). *Mammalia*, 17, 281-294.

SAINT-GIRONS M.C. et PETTER F., 1953 —
Notes sur quelques petits mammifères du Maroc Atlantique. *Mammalia*, 17, 318-321.

PETTER F., 1954 —
La systématique des formes de la souris d'après E. et H. Schwartz. *Mammalia*, 18, 124-126.

PETTER F., 1954 —
Nouvelle note biologique sur le Hérisson du désert. *Mammalia*, 18, 220-221.

PETTER F., 1954 —
Remarques biologiques sur des rats épineux du genre *Acomys*. Répartition au Sahara. *Mammalia*, 18, 389-396.

PETTER F., 1954 —
Méthode rapide de conservation des cadavres de petits mammifères sur les lieux de collecte. *Mammalia*, 18, 422-423.

PETTER F., 1954 —
Un rat du Sahara. *Sc. Nat.* 6, 25-27.

LARGOUIX J-P., PETTER F. et WISNER A., 1954 —
Étude de l'audition chez des mammifères à bulles tympaniques hypertrophiées. *Mammalia*, 18, 262-271.

WISNER A., LEGOUIX J.-P. et PETTER F., 1954 —
Étude histologique de l'oreille d'un rongeur à bulles tympaniques hypertrophiées : *Meriones crassus*. *Mammalia*, 18, 371-374.

PETTER F., 1955 —
Les terriers de *Meriones crassus* et de *Pachyuromys duprasi* (Rongeurs, Gerbillidae). *Mammalia*, 19, 325-334.

PETTER F., 1955 —
Contribution à l'étude de *Meriones vinogradovi* Heptner (Rongeurs, Gerbillidae). *Mammalia*, 19, 391-398.

PETTER F., 1955 —
Note sur l'estivation et l'hibernation observées chez plusieurs espèces de rongeurs. *Mammalia*, 19, 444-446.

PETTER F., 1956 —
Caractères comparés de *Gerbillus allenbyi* et de deux autres espèces du sous-genre *Gerbillus*. *Mammalia*, 20, 231-237.

PETTER F., 1956 —
Évolution du dessin de la surface d'usure des molaires de *Gerbillus*, *Meriones*, *Pachyuromys* et *Sekeetamys*. *Mammalia*, 20, 419-426.

PETTER F., 1956 —
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Remarques sur la systématique des *Rattus* africains et description d'une forme nouvelle de l'Aïr. *Mammalia*, 21, 125-132.

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Photo 1
Francis Petter (premier plan) et Philippe Taquet
à l'inauguration de la Zoothèque en février 1986.

Homage to Fritz Dieterlen

Rainer Hutterer

Fritz Dieterlen was born on 12 April 1929 in Rottweil (southern Württemberg), Germany. His father was a physician, his mother a technical assistant; both met each other at work. His father had been in the medical service of the German government in New Guinea between 1913 and 1915, a fact which later influenced the professional interests of Fritz.

Fritz graduated from high-school in 1949. At that time he was interested in animal-keeping and served seven-and-a-half months as a volunteer in the Frankfurt Zoo; he later returned for further six weeks. In April 1951 he began to study zoology, botany, geography, and geology at Freiburg University. There he developed a deep interest in behavioural science and in 1959 presented his thesis on the behaviour of the Syrian hamster, a work which also included Kaspar-Hauser experiments with rodents. His supervisor was Professor Otto Koehler, a leading ethologist in Germany at that time and editor of the "Zeitschrift fur Tierpsychologie". His scientific interests now displaced his plans in animal husbandry, and so he continued his studies on the behaviour and biology of small mammals, with emphasis on spiny mice of the genus *Acomys*.

At Freiburg University Fritz met another student of biology, Traute Jilly, and both married in 1959. They had four children, a son and three daughters born between 1961 and 1967.

Early in 1962 Fritz looked for a position in a foreign country. The best offer came from Dr Urs Rahm, at that time managing director of the "Institut pour la recherche scientifique en Afrique centrale" (Irsac) in the former Belgian Congo. With financial support of the Fritz-Thyssen-Foundation, he moved with his family to Mombasa, Kenya, and then drove by car to the eastern Congo, where Irsac had its office near Bukavu at the shore of Lake Kivu. Here they stayed

and worked until August 1967, when the civil war forced them to leave the country and to return to Europe.

From 1963 to 1965 Fritz studied the ecology and economical importance of rodents in the cultivated savannas west of Lake Kivu; after that he concentrated on the almost pristine mountain forest and the lowland forest around Irangi. He also travelled and collected mammals in Rwanda, Uganda, and Tanzania.

The Irsac institute was a major centre for tropical studies at that time. Well-known researchers as Chapin, Pirlot, Stephan, Rahm, and Dieterlen conducted mammal studies and left thousands of specimens in European and American museums for future studies. Fritz and his crew alone collected 16.000 small mammals which formed the basis for much of his future research. While studying the ecology of rodents he also came across taxonomic problems which sometimes led to the discovery of new species. As a result of his studies, he described *Dendromus kahuzienis* in 1969 and two new species of *Lophuromys* in 1974 and 1975.

As mentioned earlier, the civil war in the Congo forced all Europeans to leave the country in 1967. Fritz was offered a position as a mammal curator in the Museum Alexander Koenig at Bonn by the director Martin Eisentraut, who himself was highly interested in African mammals. Fritz took this position and worked in Bonn until 1969, before he changed for the Staatliches Museum für Naturkunde, Stuttgart, where he had applied for the position of a mammal curator. For the next 25 years until retirement he worked in the Stuttgart Museum. Most of his African collections have been deposited there, and under his care the mammal collection increased from about 10.000 to more than 40.000 specimens. It is now one of the most important collections of African small mammals in Germany.

Between 1971 and 1974 he returned to eastern Zaire six times, as the country was now called, and participated in a research program on tropical forest ecology. In 1972 they developed new methods for the study of the canopy of the rain forest based on African traditional knowledge. This pioneer work in canopy research has never gained the acknowledgement it deserves. Fritz returned again to the same area in 1992, 1993, and 1994 to continue his studies in the poorly investigated transition forest, but these attempts were abruptly terminated by another civil war in Rwanda in April 1994.

During his time in Stuttgart Fritz got into contact with some young and talented biologists interested in African mammals. Hans Rupp started co-operating with him in 1971 and Gerhard Nikolaus in 1974. Both collected together and separately in Ethiopia, Sudan, Kenya, and Tanzania. Due to their activities a number of new rodents were discovered and subsequently described, including *Megadendromus nikolausi*, *Praomys ruppi*, and *Grammomys minnae*. The sudden death of Hans Rupp in Kenya in 1979 terminated his career, but a wealth of new information on the rodents of Sudan and Ethiopia still remains to be published. It is hoped that Fritz will find the time to do so in the forthcoming years. He assembled further material and knowledge during three visits to the Sudan from 1980 to 1983 devoted to the study of rodents as pests in crops in central Sudan.

Museum curators have all kind of duties, the Stuttgart Museum being no exception. Fritz therefore had to participate in the museum education program, design new permanent and temporary exhibits, participate in local surveys, and so on. A major long-term project, "The mammals of Baden-Württemberg", for which he serves as editor, organiser, and author, absorbs much of his time since 1989 and will do so until the book will be published.

It is not easy to briefly summarize Fritz Dieterlen's research activities during the past 45 years. As mentioned before, he started as an ethologist, then became an ecologist, and later a taxonomist. African rodents were and are always the main object of his research. As an ethologist, he discovered unknown details of the social and reproductive system of rodents, for example the fact that young *Acomys* leave the nest just after birth, the first case discovered in a murid rodent. As an ecologist, he discovered the seasonality in the reproduction of rodents and shrews in the tropical rainforest near the Equator, and likewise the seasonality of flowering and seed production of trees in such forests. He also developed new methods for the quantitative study of small mammal communities, and for the study of the forest canopy. As a taxonomist, he discovered new and interesting rodents and presented revisions of some genera such as *Lophuromys*, *Colomys*, *Dendromus* and *Otomys*, always incorporating his biological and ecological observations on these rodents. Highlights will always be his description of the genus *Megadendromus*, his biological study of the African water rat *Colomys*,

Photo 1.
Fritz Dieterlen with his son and Congolese assistants during fieldwork at Lwiro, Eastern Congo, March 1965 (Photo by courtesy of F. Dieterlen).

or the study, together with Henri Heim de Balsac, of the ecology and taxonomy of the shrews of the Kivu region. The latter work is remarkable also for the fact that it is the only scientific paper known to me which was written and published partly in French and partly in German. The reader has to know both languages to understand the text, a wonderful example of French-German cooperation!

Finally, a few words about Fritz Dieterlen as a person. Museum curators are not always the easiest people to deal with, but he is one of the exceptions I have met in my life: always polite, helpful to the extreme, and always willing to share his broad knowledge. His personal interests are very diverse, and possibly because of his permanent curiosity he has remained the young man he is, despite of his age. I feel honoured to have had the privilege to work with Fritz, and I am happy that our small community of African small mammal researchers includes personalities like him.

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Taxonomy and Classification

thème 1

Molecular diversity of some *Crocidura* species (Insectivora, Soricidae) from Ethiopia

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Introduction

The rich and unique fauna of Ethiopia is associated with its extremely diverse geomorphology. At present, 277 mammalian species have been recorded from Ethiopia, 29 of which (10.5%) are endemic (YALDEN *et al.*, 1996). The small mammal fauna is particularly diverse. The family Soricidae is represented by 25 native species in Ethiopia, including 8 (32%) endemic ones. Local endemism may be rather high: of the 6 species known from the Bale Massif, 4 are endemic (HUTTERER and YALDEN, 1990). In view of the rapid habitat destruction in Ethiopia, taxonomic and evolutionary studies on Ethiopian small mammals are particularly important and urgent for identifying specific field conservation projects that are needed for endangered species. To improve our knowledge on the taxonomy, biodiversity, and phylogenetic relationships of Ethiopian shrews, we conducted a study using morphological, cytogenetical and DNA analyses. This paper presents a comparative study of repetitive DNA sequences in six species of shrews of the genus *Crocidura* from Ethiopia.

Material and methods

Species studied

All samples of shrews were collected by one of us (L. A. L.) during extensive trapping sessions in the framework of the Joint Ethio-Russian Biological Expedition (JERBE), from 1995 to 1998. The identification of specimens was kindly performed by Dr. R. Hutterer (Museum Alexander Koenig, Bonn). The specimens are deposited in the Zoological Museum of the Lomonosov Moscow State University (ZMMU). The localities of specimens used in this study are shown in table 1.

Species	n	Museum's catalogue numbers	Locality
C. glassi Heim de Balsac, 1966	3	S-164856 S-164853 S-164860	Eastern Plateau, Bale Mountains: mosaic grassland/forest habitats in the Dinsho area (3,170 m ASL, 7° 06′ N 39°47′ E)
C. thalia Dippenaar, 1980	3	S-165166 S-165165 S-164858	Eastern Plateau, Bale Mountains: Shawe River at *Aningeria* belt of the Harenna Forest (1,935 m ASL, 06° 38′ N 39° 44′ E)
Crocidura sp. B	2	S-165342 S-165343	Western Plateau: riverine variant of the humid afromontane Beletta Forest (1,900 m ASL, 07° 34′ N 36° 31′ E)
C. olivieri Lesson, 1827	1	S-166027	Western Plateau: *Acacia-Terminalia-Combretum* savanna and woodlands at the Middle Godjeb Valley (1,220 m ASL, 07° 15′ N 36° 47′ E)
C. macmillani Dollman, 1915	2	S-166029 S-166031	Western Plateau: *Acacia-Terminalia-Combretum* savanna and woodlands at the Middle Godjeb Valley (1,220 m ASL, 07° 15′ N 36° 47′ E)
C. parvipes Osgood, 1910	4	S-166030 S-166032 S-166033 S-166034	Western Plateau: *Acacia-Terminalia-Combretum* savanna and woodlands at the Middle Godjeb Valley (1,220 m ASL, 07° 15′ N 36° 47′ E)

Table 1
List of *Crocidura* shrew specimens used in the present study (n-number of specimens).

Crocidura glassi, *C. thalia* and *C. macmillani* are very similar in their morphology and were previously lumped under *C. fumosa* Thomas, 1904 (YALDEN *et al.*, 1976). *Crocidura olivieri* is morphologically very distinct, characterized by a large size. *Crocidura* sp. B is certainly a species new to science. A full description, diagnosis and nomenclature of this new species endemic to Ethiopia will be published elsewhere (LAVRENCHENKO and HUTTERER, in prep.).

The karyotype of all the species studied have been described. *Crocidura thalia*, *C. glassi* and *Crocidura* sp. B have 36 chromosomes (LAVRENCHENKO *et al.*, 1997; ANISKIN *et al.*, 1998) while *C. olivieri* and *C. parvipes* have 50 chromosomes. The diploid number of *C. macmillani* is 28 chromosomes. A detailed description of the karyotypes of these species will be published elsewhere (LAVRENCHENKO and HUTTERER, in prep.).

All these shrew species occupy different habitats on both sides of the Ethiopian Rift Valley. *Crocidura glassi* is a specialized moorland form, whereas *C. thalia* is a species of mountain grassland. *Crocidura* sp. B is a true forest species while *C. macmillani* and *C. parvipes* are inhabitants of woodlands and savannas. *Crocidura olivieri* is widely distributed throughout savanna and grassland habitats.

Restriction DNA analysis

Total DNA was extracted from ethanol fixed liver, testes and muscles by proteinase K digestion followed by phenol/chloroform extraction and ethanol precipitation according to a standard procedure (ARRIGHI *et al.*, 1968). We examined genomic DNA patterns of shrews with a specially optimized method of DNA repeated units detection called taxonomic DNA fingerprint or taxonprint (GRECHKO *et al.*, 1997; FEDOROV *et al.*, 1999). The difference between this approach and the traditional restriction DNA analysis (RFLP) is that we used short-cutting restriction endonucleases followed by phosphorous 32 end-labeling of the restriction fragments. This procedure has permitted to detect short fragments (30-300 bp) of repeated DNA sequences. The advantage of taxonprint analysis as a phylogenetic tool was described by GRECHKO *et al.* (1997) and FEDOROV *et al.* (1999). The main property of this approach is the intraspecific identity of band patterns, which enables to use small numbers of individuals (even only one

Taxon	Status of character
C. thalia	000000000001000101110000000010001100000000110110000000111110011101000000000001101001001111111111100101110
C. glassi	000000000001000101110011010010001100000000110110000000001110011101110111111001101001001010111100000101101
Crocidura sp. B	000000000101000101110000100110001110000000110110100000001110011101000000000001101001001011111110010101110
C. olivieri	011000101000110101011000001011101100100001101100000000000111111110010000001111101101100011000000000100
C. macmillani	000000000000000101010000000100011000000001000000100000000100111010000000000011010010010001100000000100
C. parvipes	100101000010000101011100001000001100001100100001000111000010011101000000000101111101101000110000000000100
S. murinus	000010010000001011010000000000011101010010100000001000000000010100000000000001001001000000110000001010100

Table 2
Complete character matrix for phylogenetic analysis of six *Crocidura* species and *Suncus murinus* as outgroup for MspI, HinfI, TaqI, BcnI and Eco130I restriction endonucleases. Total number of bands is 105.

for rare species) and does not require any intraspecific statistical analysis. Another property of electrophoretic bands of DNA repeats revealed by our technique is the hierarchical order of their organization which can be seen on a higher taxonomical level: bands can be common for a group of related species such as genus and family (BANNIKOVA *et al.*, 1996; FEDOROV *et al.*, 1999).

Conditions of experiment

Five restriction enzymes were used: MspI, HinfI, TaqI, BcnI, Eco130I. 0.5 microgram genomic DNA was incubated with 5 U of restriction endonuclease in 20 µl of its specific buffer for 4-12 h. Labeling the recessed 3′ termini of DNA restriction fragments (0.1 µg) was carried out in 10 µl of buffer (10 mM Tris-HCl /pH 7.5/, 10 mM $MgCl_2$, 50 mM NaCl) in the presence of 1 µCi of appropriate [α^{32}P]dNTP, 20 µm of each of the three remaining cold dNTPs, and 0.5 U of Klenow fragment for 15 min at 20 °C. The reaction was stopped by the addition of EDTA to 10 mM. Samples (2-3 µl) were subjected to electrophoresis in non-denaturing 10% polyacrylamide gels with

	C. thalia	*C. glassi*	*C. olivieri*	*Crocidura* sp. B	*C. macmillani*	*C. parvipes*
C. glassi	0,238					
C. olivieri	0,494	0,517				
Crocidura sp. B	0,136	0,247	0,500			
C. macmillani	0,344	0,385	0,375	0,355		
C. parvipes	0,500	0,525	0,418	0,506	0,333	
Suncus murinus	0,594	0,618	0,612	0,600	0,422	0,567

Table 3
Matrix of genetic distances according to the method of Nei and Li (1979).

1xTBE buffer at 800-1200 V for 4-5 h. After electrophoresis the gel was dried and autoradiographed for 16-48 h. pBR322 DNA fragments digested with MspI were used as molecular-weight markers.

Phylogenetic analysis

The number and distribution of bands corresponding to digested DNA fractions were examined in autoradiographs of the species tested. The lack or presence of a band with equal electrophoretical mobility was designated as "0" and "1", respectively. Thus the results of experiments with all endonucleases were presented in the form of a matrix composed of 0/1, reflecting the state of binary characters (tabl. 2). On the whole, 105 bands were detected across the 7 species tested, including the outgroup. This data set includes 92 variable characters, 26 of which are informative; 13 bands were common for all tested species. Phylogenetic analyses with *Suncus murinus* as an outgroup were carried out using neighbour-joining (NJ) and parsimony methods in TREECONW (VAN DE PEER and DE WACHTER, 1994) and Phylip version 3.5 (FELSENSTEIN, 1993) packages, respectively. Bootstrap analysis with 500 replicates was conducted to assess the reliability of branching patterns. The genetic distances in NJ tree based on a total of 105 characters were computed by the formula of NEI and LI (1979) (tabl. 3).

Results and discussion

The results of restriction nuclease analysis are shown in the 0/1 matrix (tabl. 2), in the table of genetic distances (tabl. 3) and on the NJ dendrogram (fig. 1) The topologies based on both NJ and parsimony methods appeared similar. Here we present only the NJ tree, which branch lengths correspond to genetic distances (following NEI and LI, 1979). The standard indicators of support of the inferred tree topology are high (consistency indices with uninformative characters included or excluded of 0.979 and 0.929, respectively).

According to our data the 36 chromosome species belong to the same monophyletic cluster with *Crocidura* sp. B and *C. thalia* being more closely related to each other than either is to *C. glassi*, which itself is equally divergent from *Crocidura* sp. B and *C. thalia*. *Crocidura olivieri* and *C. parvipes* joined into the same phyletic lineage. The 50 chromosome species and 36-chromosomal species appear to constitute a sister group of *C. macmillani* which forms a basal branch in both reconstructions, with poor bootstrap support.

Analysis of DNA divergence degree in different species was carried out by length comparison of appropriate branches of dendrogram. Both methods indicate strong differences in rates of DNA evolution between *C. macmillani* and other taxa. To confirm this hypothesis a modification of the relative rate test (SARICH and WILSON, 1967) was applied. The level of divergence from the outgroup of each terminal taxon was assessed as the fraction of bands (out of 105 characters) found in a given species but lacking in *Suncus murinus*. The comparison of estimates obtained on the basis of 2000 bootstrap replicates showed that *C. macmillani* is significantly less divergent ($p < 0.01$) from the outgroup than any other species studied. The relative rate test by TAKEZAKI *et al.* (1995) in the Phyltest program, version 2.0 (Kumar, 1995), was also applied. The difference of evolutionary rate in the lineage of *C. macmillani* is statistically significant, and the rate constancy is rejected at 5% level ($z = 8.694$).

Conversely, there is no significant difference of evolutionary rates between lineages of 36 and 50 chromosome species ($z = 0.224$). However, the differences accumulated along the stem of the 36 chromosome group is greater by a factor of 2.7. Eleven potential synapo-

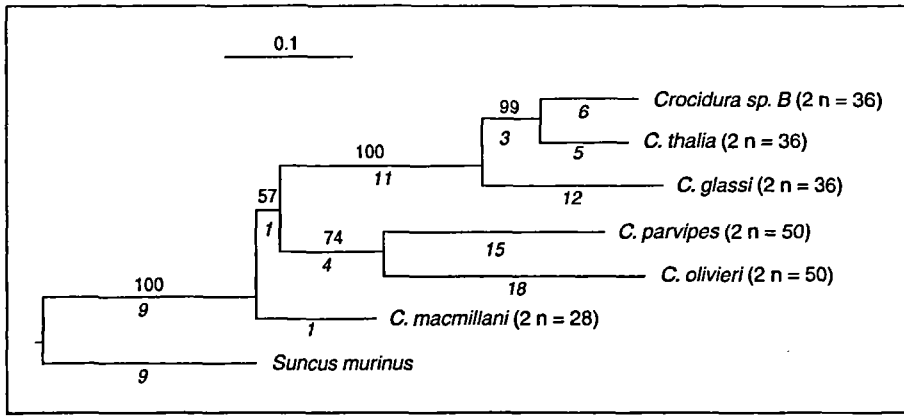

Figure 1
Neighbour joining dendrogram of the relationships of six *Crocidura* shrews from Ethiopia. Length of branches corresponds to Nei and Li (1979) genetic distances. The numbers under a line correspond to the number of changes observed along the branches of the maximum parsimony tree. Numbers above the branches show bootsrap support (% of 500 replications). *Suncus murinus* is used as an outgroup.

morphies (band gains) are revealed for the clade comprising the three 36 chromosome species while there are only 4 bands unique for the *parvipes-olivieri* clade (the difference is nearly significant, $p > 0.06$, Fisher criterion). If we assume a clocklike evolution for this part of the tree, the results can be regarded as an indication of a relatively recent divergence within the 36 chromosome clade. *Crocidura glassi* and *C. olivieri* have accumulated more changes than the other taxa while *C. macmillani* has acquired fewer differences.

Therefore the 36 chromosome species, 50 chromosome species and 28 chromosome *C. macmillani* form distinct phylogenetic lineages. It is clear that DNA repeated sequences evolution correlates well with chromosome number divergence of the species studied but not directly with morphological diversity. It is essential to note that except for *C. macmillani*, all cytogenetically studied endemic Ethiopian *Crocidura* species (including *C. bottegoides* HUTTERER and YALDEN, 1990; *C. harenna* HUTTERER and YALDEN, 1990; *C. lucina* DIPPENAAR, 1980) have 36 chromosomes (LAVRENCHENKO *et al.*, 1997). Although African *Crocidura* species are extremely numerous

and diverse (morphologically and cytogenetically), only two species with diploid numbers of 36 were found in the rest of Sub-saharan Africa (*C. obscurior* from Ivory Coast and *C. luna* from Burundi) (SCHLITTER *et al.*, 1999). Taking into account this evidence along with the results of our phylogenetic analysis, we may suppose that all 36 chromosomal species endemic to Ethiopia form a monophyletic group of a relatively recent origin.

DIPPENAAR and MEESTER (1989) believed that the five Ethiopian taxa (*C. macmillani*, *C. baileyi*, *C. glassi*, *C. lucina* and *C. thalia*) form a distinct group of closely related endemic species. Our phylogenetic analysis demonstrated that *C. macmillani* is phyletically distant from the group comprising the other Ethiopian endemics, although a moderate bootstrap value supports this branching pattern. The topology of the tree is congruent with chromosomal data. The former species can be hypothesized to be similar to the ancestor of at least several lineages of African *Crocidura*.

The essential differences among the species examined were reflected in DNA repeated units patterns, confirming that the Ethiopian *Crocidura* species form a group with a high level of both morphological and molecular divergence. Our data suggest that the fauna of Ethiopian endemic *Crocidura* has a complex origin and comprises both an ancient lineage and a group of closely related species that has undergone recent (and presumably adaptive) radiation.

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The Rusty-spotted genets as a group with three species in Southern Africa (Carnivora: Viverridae)

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Introduction

In Southern Africa, defined by ELLERMAN *et al.* (1953) as the whole of Africa south of the Democratic Republic of Congo and Tanzania, four species of *Genetta* G. Cuvier, 1816, were accepted in the second edition of the reference book *Mammal Species of the World*: *Genetta angolensis* Bocage, 1882, *Genetta genetta* (Linnaeus, 1758), *Genetta maculata* (Gray, 1830), and *Genetta tigrina* (Schreber, 1776) (WOZENCRAFT, 1993). With the exception of the Small-spotted genet (*G. genetta*), which is easily recognizable, among other features, by its white tipped tail, all other species had been mixed up and their systematics is far from settled.

The present paper concerns the Rusty-spotted genets, a group of forms that inhabits tropical Africa from the Volta River to Zululand, and which are considered subspecies of *G. maculata* by WOZENCRAFT (1993). They generally present rows of more rusty than black spots and stripes on each side of a median dorsal line, the spots being smaller and the stripes narrower than in *G. tigrina* (ROBERTS, 1951) and the hair length shorter than in *G. angolensis* (CRAWFORD-CABRAL, 1969). However, as result of a significant amount of individual and ecological variation, it is sometimes difficult to identify them, as their

characteristics sometimes fall into those typical of other species. Moreover, since there is no proof that these several forms are all conspecific, the colloquial name Rusty-spotted genet is used herein, instead of a scientific species name, until a conclusion can be drawn about the taxonomy and nomenclature of these animals. They were classified by SCHWARZ (1930) within *G. tigrina* (commonly mentioned under the colloquial name Large-spotted genet) as subspecies, a classification maintained by several authors until a very recent date (ANSELL, 1960; SMITHERS, 1971; WENZEL and HALTENORTH, 1972; COETZEE, 1977; KINGDON, 1977; SMITHERS, 1983; MEESTER *et al.*, 1986; KINGDON, 1997). For instance, PRINGLE (1977), based on the analysis of pelage coloration pattern of specimens from KwaZulu-Natal, stated that within this area hybridisation occurred between *G. tigrina* and a Rusty-spotted genet. However, *G. tigrina* has been regarded as specifically distinct from the Rusty-spotted genets by some other authors (ROBERTS, 1951; ELLERMAN *et al.*, 1953; CORBETT and HILL, 1980; CRAWFORD-CABRAL, 1980-81; HONACKI *et al.*, 1982; ANSELL and DOWSETT, 1988). Indeed, CRAWFORD-CABRAL and PACHECO (1992), using multivariate analysis of cranial measures, also concluded that the Rusty-spotted and the Large-spotted genets are separate species.

Meanwhile, two alternatives to the species name *G. tigrina* for the Rusty-spotted genets arose. One was to consider the forms of this group as conspecific with the Pardine genet. In this way, they were classified as subspecies of *Genetta pardina* I. Geoffroy, 1832 (CRAWFORD-CABRAL, 1969, 1970, 1973; ANSELL, 1978) or as subspecies of *G. maculata* (SCHLAWE, 1980, 1981; WOZENCRAFT, 1993), a difference that has only to do with the scientific name assigned to the Pardine genet. However, the sympatry that apparently occurs, at least in Nigeria (POWELL et VAN ROMPAEY, 1998), between *poensis* Waterhouse, 1838, a form generally considered as a morph of the Pardine genet and whose type locality is Fernando Po (= Bioko, Equatorial Guinea) (but see POCOCK, 1907 and ROSEVEAR, 1974) and a Rusty-spotted genet (possibly *fieldiana* Du Chaillu, 1860), seems to imply a non-conspecificity (CRAWFORD-CABRAL, 1980-81). The other alternative was to accept the Rusty-spotted genets as a separate species either from the Large-spotted or the Pardine genets and, following various authors (BOCAGE, 1882, 1889; HILL and CARTER, 1941; ROBERTS, 1951; ELLERMAN *et al.*,

1953) to name the Rusty-spotted genets *Genetta rubiginosa* Pucheran, 1855 (CRAWFORD-CABRAL, 1966, 1981; ANSELL and DOWSETT, 1988). Nevertheless, having in view that *G. rubiginosa* is the senior synonym of *Genetta thierryi* Matschie, 1902, as SCHLAWE (1981) ascertained, we have serious doubts in maintaining the name *rubiginosa* for the Rusty-spotted genet (CRAWFORD-CABRAL and FERNANDES, 1999).

With regard to the Southern African forms of this complex, ROBERTS (1951), on the basis of material in the Transvaal Museum, recognized five subspecies within the *G. rubiginosa* complex: the nominate *rubiginosa*, in Rustenberg and Zoutpansberg districts of North West Province – on the incorrect supposition that Pucheran's type came from southern « Bechuanaland », an area presently corresponding to northern Cape Province, when in fact that specimen came from Senegal and represents *G. thierryi* (SCHLAWE, 1981; CRAWFORD-CABRAL and FERNANDES, 1999); *letabae* Thomas and Schwann, 1906, in Mpumalanga Province; *zuluensis* Roberts, 1924, in Kwazulu-Natal; *zambesiana* Matschie, 1902, in Malawi (a form described from Boror, Mozambique); and *albiventris* Roberts, 1932, in northern Botswana and northern Namibia. In addition to considering *G. rubiginosa* a valid species, ROBERTS (1951), on the basis of specimens from Boror, Mozambique, also accepted *Genetta mossambica* Matschie, 1902, a form described from Mossimboa, northern Mozambique. The taxonomic position of G. *mossambica* has been controversial and it is still unresolved. It was regarded in some classifications (ELLERMAN *et al*, 1953; ANSELL, 1960; COETZEE, 1977) as more closely related to the forms described by ROBERTS (1951) in *G. rubiginosa*. Later, *G. mossambica* was considered by other authors (WENZELL and HALTERNOTH, 1972; SCHLAWE, 1980, 1981; WOZENCRAFT, 1993) as a synonym or subspecies of *G. angolensis*. However, a principal component analysis (PCA) by CRAWFORD-CABRAL and PACHECO (1992), that included the two specimens from Boror recognized by ROBERTS (1951) as *G. mossambica*, found that *mossambica* (but not *angolensis*) falls, at least craniometrically, within the phenotypic profile typical of the Rusty-spotted genets. In view of this result, which also supports the older classifications grouping *mossambica* with the *rubiginosa* forms (i.e. with the traditionally called Rusty-spotted genets), *mossambica* is included *a priori* in the present study as a Rusty-spotted genet.

Material and methods

The material upon which this study was based, is composed of ninety four specimens of *Genetta* from several parts of Southern Africa, housed in different museums, namely the Transvaal Museum, Pretoria, South Africa (TM); the Natural History Museum, London, England (BM); the Centro de Estudos of the former Instituto de Investigação Científica de Angola, at Lubango, today the Instituto Superior de Ciências e Educação, Angola (ISCED), and the Centro de Zoologia of the Instituto de Investigação Científica Tropical, Lisbon, Portugal (CZ). These specimens were examined many years ago, their skulls measured and the resulting measurements published (CRAWFORD-CABRAL, 1981). Sixty-six of these specimens represent forms regarded here as Rusty-spotted genets, therefore including, besides sixty-three « *rubiginosa* » specimens, three representatives of *G. mossambica*, and served to establish relationships between them; the remaining were seventeen specimens of *G. tigrina* and eleven specimens of *G. angolensis* used for comparison and to position these two species in regard to the forms of Rusty-spotted genets.

The following twelve cranial measurements were taken on the specimens with a dial calliper: x_1 – Condylo-basal length; x_2 – Braincase breadth; x_3 – Zygomatic breadth; x_4 – Intertemporal constriction; x_5 – Rostrum breadth; x_6 – Basion-inion height; x_7 – Greatest diameter of bullae; x_8 – Interpterygoid width; x_9 – Palate length; x_{10} – M^1- M^1 outside breadth; x_{11} – Upper tooth row C-M^2; x_{12} – Greatest diameter of P^4. All the cranial measurements that form the raw data of the present analyses are listed in a table (Quadro I) in CRAWFORD-CABRAL (1981), with the exception of a specimen of group MOZ (CZ n° 48.00941), the data of which were taken from CRAWFORD-CABRAL (1973).

With the purpose of performing a multiple group discriminant analysis (canonical analysis), the specimens were organized in groups, in accordance with their identification and geographical origin. The groups were defined in such a way as to produce taxonomic units with a level of geographic scale that seemed sensible and suitable for the questions that the study tries to address. The groups considered for the statistical analysis are described in table 1. The approximate

Group name	Group size	Geographical area	Identification and Type Locality	Museum
TRV	16	Mpumalanga Province, South Africa	*G. rubiginosa letabae (a); Klein Letaba, eastern Transvaal*	Transvaal
ZUL	8	KwaZulu-Natal Province, South Africa	*G. rubiginosa zuluensis (a); White Umfolozi, Zululand*	Transvaal
KAL	3	North West Province, South Africa; Botswana	*G. rubiginosa rubiginosa (a)*	Transvaal
NAM	4	North East Namibia	*G. rubiginosa albiventris (a); Maun, northern Botswana*	Transvaal
ZIM	9	Mt. Selinda and Salisbury, Zimbabwe		British; ISCED; Transvaal
ZAM	5	Southwestern Zambia	*G. rubiginosa albiventris (b); Maun, northern Botswana*	British
MOZ	8	Central Mozambique	*G. rubiginosa zambesiana (c); Boror, Mozambique*	British; CZ
ANG	10	Southwestern Angola	*G. rubiginosa gleimi (c); Luanda, Angola*	ISCED
BOR	3	Boror, Mozambique	*G. mossambica (a); Mossimboa, Mozambique*	Transvaal
KNY	17	Knysna, Cape Province, South Africa	*G. tigrina tigrina (a); Cape of Good Hope*	British; Transvaal
MUL	11	Mulundo, Angola	*G. angolensis angolensis (c); Caconda, Angola*	ISCED

Table 1
Arrangement of the groups for canonical analysis according to the geographical origin and identification of the specimens. The identification is founded on (a) Roberts, 1951, (b) Ansell, 1978, and (c) Crawford-Cabral, 1980-81.

locations for the groups of specimens and the geographical areas under study are displayed in figure 1.

For all the analyses we used *Statistica* version 5 software. For the discriminant function analysis the "forward stepwise with casewise deleted" (i.e. without missing values) method was used. The results, in the form of scatter plots of canonical scores for the two most

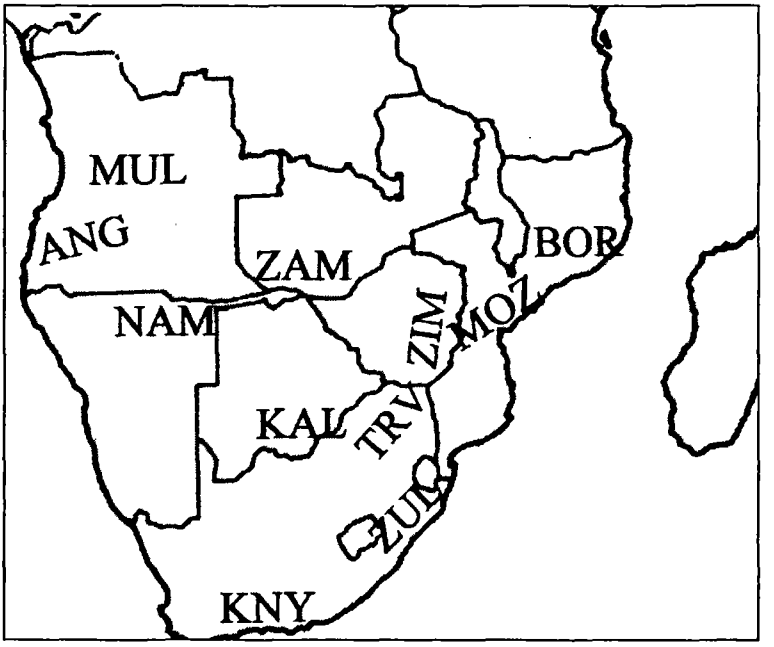

Figure 1
Map of Africa indicating the areas from where the groups considered in the present study originate

discriminant functions or canonical roots, were studied in order to screen those which were most informative and with the greatest statistical robustness. With this purpose the canonical roots were tested for significance using the Chi-Square test. The size of the Wilk's Lambda and the cumulative proportion of explained variance accounted for by each root were also taken into account.

Results

We present here only the results of the analyses, among all those which were undertaken, that allow a clear and synthetic description of the suggested taxonomic arrangement of the Rusty-spotted genets in Southern Africa, and their relationships with other genet species occurring in the same area.

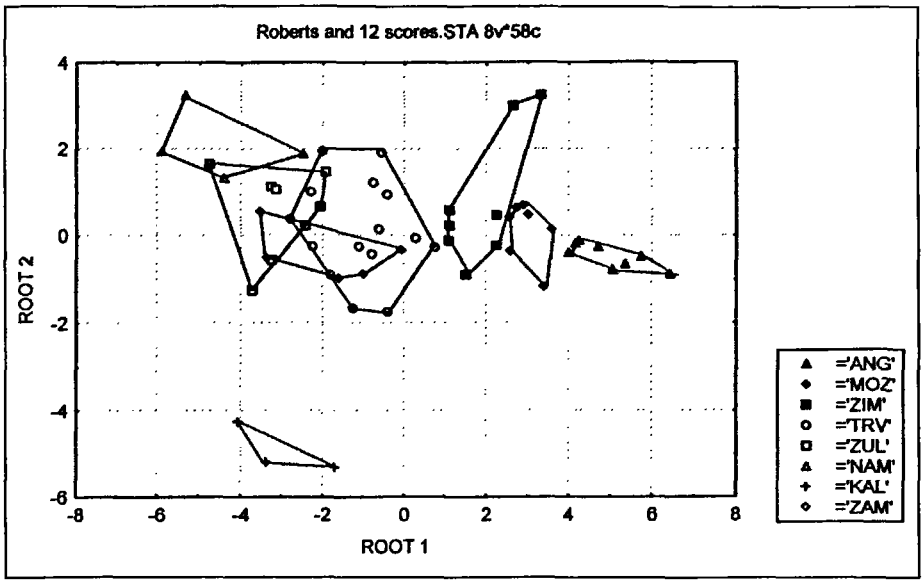

Figure 2
First analysis: projections of the groups ANG, MOZ, ZIM, TRV, ZUL, NAM, KAL and ZAM onto the plan of the first two canonical roots.

The purpose of the first analysis performed was to examine the taxonomic relationships of all the Southern African forms classically regarded as Rusty-spotted genets. It dealt not only with the forms accepted by ROBERTS (1951) as subspecies of *G. rubiginosa*, i.e. *letabae*, *zuluensis*, *albiventris*, *zambesiana* and the form of Botswana and western Transvaal considered by him as the topotypical *rubiginosa*, but also with a genet of southwestern Angola, that CRAWFORD-CABRAL (1969) regarded as a subspecies akin to *gleimi* Matschie, from Luanda. These forms were respectively represented by the groups TRV, ZUL, NAM, MOZ, KAL and ANG; the groups ZAM and ZIM were also included, the first one to test the statement of ANSELL (1960, 1978) that the population from SW Zambia would represent or incline towards *albiventris*, and the group ZIM to get an insight of the taxonomic relationships of populations in eastern Zimbabwe, which until now have been vaguely defined.

The graphic of the projections onto the plan of the first two canonical roots (fig. 2) reveals a fair separation of the groups, in spite of

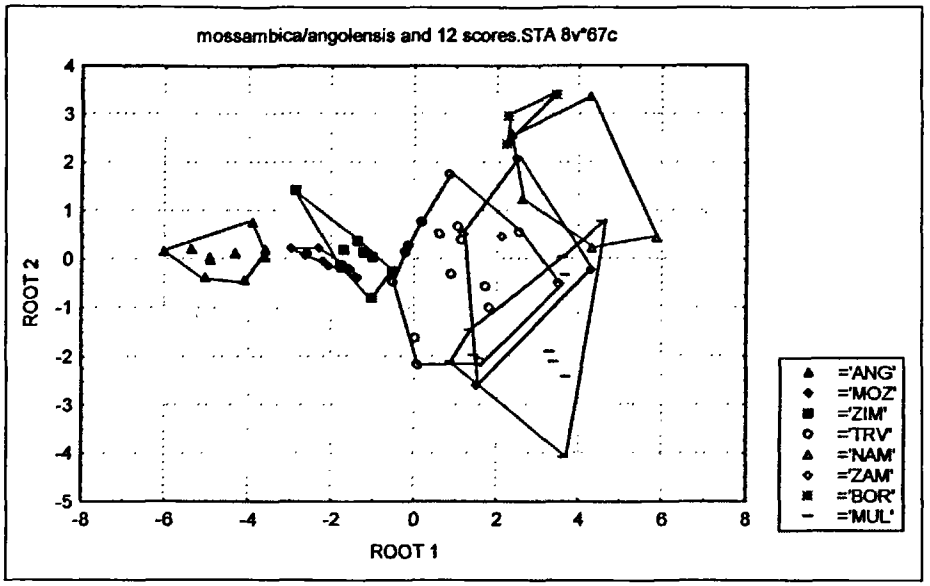

Figure 3
Second analysis: projections of the groups ANG, MOZ, ZIM, TRV, NAM, ZAM, BOR and MUL onto the plan of the first canonical roots.

some overlap that occurs between the groups NAM and ZAM, in the second case even more pronounced, with ZUL and TRV. It is possible to observe a clear separation between the groups ZIM, MOZ and ANG, which are projected on the positive side of the first canonical axis, and all other groups, which, with the only exception of two TRV specimens, are projected on the negative side of the same axis. The importance of skull size in the position of the groups along the first axis is obvious and reflected in the extreme positions of the small-sized *gleimi* (ANG) and the large-sized *albiventris* (NAM).

The aim of the second analysis was to evaluate the status of *mossambica* (BOR) as a Rusty-spotted genet, as suggested by PCA data (CRAWFORD-CABRAL and PACHECO, 1992), but now through the use of canonical analysis. As this form was already also regarded as conspecific with *angolensis* (WENZELL and HALTERNOTH, 1972; SCHLAWE, 1981; ANSELL and DOWSETT, 1988), the group MUL, which represents this species, was also included in the analysis. In

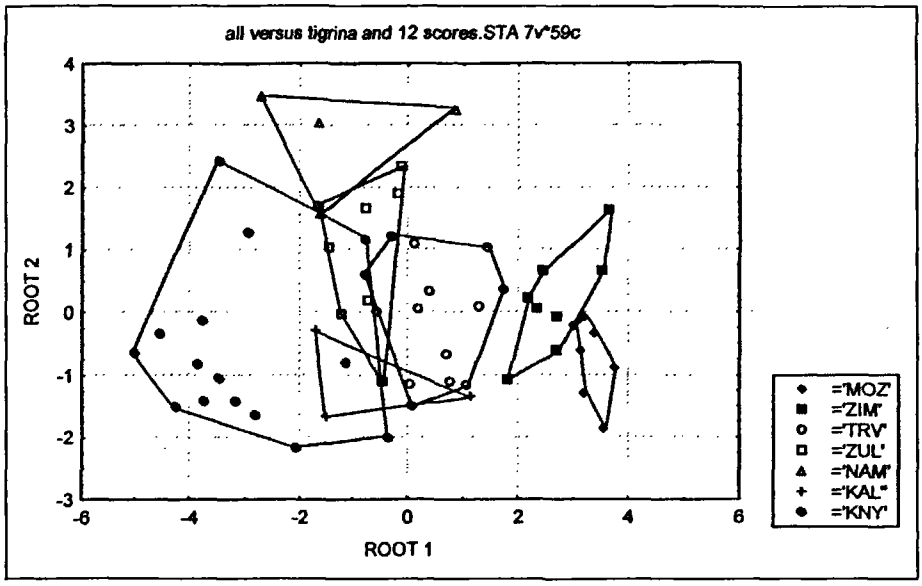

Figure 4
Third analysis: projections of the groups MOZ, ZIM, TRV, ZUL, NAM, KAL and KNY onto the plan of the first two canonical roots.

order to avoid the noise resulting from the redundant presence of too many groups giving the same kind of information that is not essential to understand the status of *mossambica*, the geographical range of the Rusty-spotted genet groups was restricted by the exclusion of the southernmost ones, i.e. KAL and ZUL.

In the scatter plot of canonical scores for the two first canonical roots that resulted from the analysis (fig. 3), it is possible to observe again a fairly clear separation between sets of groups along the first canonical axis. The groups BOR and MUL, both with positive scores in regard to the first root, have their projections distant from one another, BOR with positive scores and MUL mostly with negative scores in the second root.

The objective of the third analysis was to compare forms of Rusty-spotted genets with *G. tigrina* (represented by the group KNY), in order to evaluate the taxonomic relationships between them. In the resulting scatter plot (fig. 4) it is possible to observe that, in spite of

	Standardised Coefficients for Canonical Variables								
	First Analysis			Second Analysis			Third Analysis		
	Variable	Root 1	Root 2	Variable	Root 1	Root 2	Variable	Root 1	Root 2
	x1	- 0,96265	- 0,168368	x1	0,690000	0,420688	x1	- 0,736656	0,037981
	x11	0,05659	0,651040	x3	0,147741	- 0,695789	x4	- 0,567026	- 0,407739
	x3	- 0,26770	- 0,537422	x2	0,439402	- 0,393540	x8	0,107203	0,679333
	x8	0,13123	0,214076	x8	0,240528	0,056656	x12	- 0,184447	0,436636
	x4	- 0,56776	- 0,062913	x7	0,139792	0,081600	x9	- 0,262580	0,423312
	x2	- 0,38943	0,532763	x5	0,422499	0,323198	x2	- 0,372115	0,385000
	x12	- 0,27435	0,209025	x4	0,413720	- 0,265507	x11	- 0,159149	0,260220
	x10	0,20244	0,663861	x9	0,354046	0,427182	x10	- 0,279512	- 0,174369
	x5	- 0,52388	0,571895	x10	0,311606	- 0,252658	x3	- 0,179228	- 0,038186
	x6	- 0,138393	0,260378	x11	- 0,174002	- 0,003242			
Eigenvalue		10,00727	2,109977		8,822047	1,068085		5,254144	1,117620
Cumm. Prop. Variance		77%	93%		78%	88%		72%	87%

Table 2
Standardized coefficients for canonical variables, eigenvalues and cumulative proportions of explained variance for the two canonical roots.

a slight overlap of KNY with both KAL and ZUL, most of the *G. tigrina* specimens are projected as a well detached cloud onto the negative side of both canonical axes.

Table 2 lists, for all three analyses, the standardized coefficients for canonical variables, the eigenvalues and the cumulative proportion of explained variance accounted for by each root. In table 3, the Chi-Square tests and Wilks' Lambda are presented for the canonical roots for the three analyses. It is possible to observe, for any of the three analyses, a total variance of around 90% explained by the two first roots. The roots are significant in accordance with the Chi-Square tests, and the small Wilks' Lambda values indicate that they have a strong discriminatory power.

	Chi-Square Tests with Successive Roots Removed											
	First Analysis				Second Analysis				Third Analysis			
Roots Removed	Wilks' Lambda	Chi-Square	DF	p-level	Wilks' Lambda	Chi-Square	DF	p-level	Wilks' Lambda	Chi-Square	DF	p-level
0	0,012922	197,8712	63	0,000000	0,01545	235,6188	77	0,000000	0,034794	157,84120	54	0,000000
1	0,142237	88,7369	48	0,000321	0,151736	106,5372	60	0,000208	0,217604	71,67880	40	0,001555
2	0,442353	37,1119	35	0,371971	0,313803	65,4830	45	0,024761	0,460802	36,415	28	0,132474

Table 3
Chi-quare tests with successive roots removed for the three canonical analyses.

Discussion

All the analyses seem to indicate a clear separation between the forms represented by the groups ANG, MOZ and ZIM, i.e. *gleimi* and *zambesiana*, and those represented by TRV, ZUL, ZAM and NAM, i.e. *letabae*, *zuluensis* and *albiventris*. This is particularly visible in the scatter plot of canonical scores derived from the first analysis (fig. 2). Certainly, the position of these forms in different clusters is not a reason in itself to accept them as non-conspecific. The fact that ZIM has an intermediate position between MOZ and TRV could even be interpreted as the result of an intergradation between the two groups. However, all specimens in CZ (including flat skins examined for this study) collected in Mozambique from Mambone, south of the Save River, represent *letabae* (*zuluensis* in CRAWFORD-CABRAL, 1973), whereas those from localities from the Manica and Sofala Province, just north of the Save River, represent *zambesiana* (*rubiginosa* in CRAWFORD-CABRAL, 1973). In fact, *zambesiana* specimens are generally smaller, and with smaller and more numerous spots in the coat, than *letabae* individuals (CRAWFORD-CABRAL, 1973). But, even if we accept the presence of a continuous series of forms merging gradually into each others on the eastern part of the range of the southern African Rusty-spotted genet and then the hypothesis of a single species, the situation on the western part of the range is quite differ-

ent. Indeed, both the largest-sized *albiventris* and the smallest-sized *gleimi* occur in southern Angola, probably separated by the Cunene River as suggested by the examination of flat skins from both sides of this river, and without any signal of intergradation. So, the presence of geographical barriers like rivers separating populations from the two sets of groups opens the possibility that *G. rubiginosa* in Southern Africa might not be one but two separate taxa, possibly species.

This case seems to be an example of a "circle of species", where the intermediate forms appear as representing different stages of a polytypic species, but the extreme forms behave as separate species. In fact, circles of species are superspecies (MAYR and ASHLOCK, 1991), and most likely when referring to the forms included by Roberts (1951) in *rubiginosa* we are dealing not with a single species, but with a superspecies. If this is the case here, then *zambesiana* and *gleimi* may represent the same allospecies, to which the proposed name in the present paper is *G. zambesiana*, with *letabae*, *zuluensis* and *albiventris* being another allospecies, the name of which, according to the priority rule, should be *G. letabae*.

More difficult to interpret is the form represented by KAL, projected far from all other groups on the second canonical root, but with similar regression coefficients for the first root to TRV, ZAM, ZUL and NAM. It may represent a small population of southern Botswana, northern Cape Province and western Transvaal, to which the closest neighbour seems to be the eastern Transvaal (TRV) population. The most moderate taxonomic procedure would be to regard such a form as a subspecies of *G. letabae*, yet still innominate, in view that the name *rubiginosa*, as ascribed by ROBERTS (1951) to that form, should not be used for any Rusty-spotted genet (CRAWFORD-CABRAL and FERNANDES, 1999).

The second analysis suggests, considering the separate positions of their projections, that *mossambica* and *angolensis* are different species. Moreover, the projection of BOR is very far from MOZ and ZIM, which are their nearest geographical neighbours, which means, agreeing with ROBERTS' (1951) opinion, that *mossambica* and *zambesiana* are two quite different forms. On the other hand, the projection of *mossambica* near to *albiventris*, two forms with quite different external traits, may only reflect craniometrical similarity without taxo-

nomic value. The same can be said of the projection of *angolensis* near to *letabae* and *albiventris*.

By observing the scatter plot of canonical scores for the third analysis (fig. 4) where the majority of the projections of KNY are fairly isolated, in spite of some overlap with ZUL and KAL, no reasons are found to support *G. tigrina* and *G. letabae* as conspecific. The opinion that they are separate species is therefore maintained.

Conclusion

We can conclude that in Southern Africa there are three species of *Genetta* that can be considered under the colloquial name Rusty-spotted genets. The three species are: *G. letabae*, G. *zambesiana* and *G. mossambica*. The first two are parapatric and most likely constitute a superspecies, comprising all the forms placed by ROBERTS (1951) in *G. rubiginosa*. *Genetta mossambica* and *G. angolensis* are allopatric in relation to each other and both are sympatric with *G. zambesiana*. *Genetta tigrina* has an isolated distribution in the Cape Province and a plausible contact with *G. letabae* in Natal and Orange Free State.

Considering the overall picture in Southern Africa, it is quite probable that these five species of *Genetta*, all of them characterised by three to five longitudinal rows of rusty, black with rusty hairs or even deep black spots on each side of a mid-dorsal line and by 6 to 9 black tail rings, confluent to the always black tail tip, form a species-group (MAYR and ASHLOCK, 1991). It is also possible that the remaining forms, from other parts of Africa, normally accepted as Rusty-spotted genets, and even *G. pardina*, are part of such species-group.

Although consistent with the results obtained in this study, and also with accumulated evidence in the literature, it is clear that the conclusions that we draw here are still quite speculative and exploratory. For instance, and considering that the range of the Rusty-spotted genets is larger than the geographic scope of this study, it is necessary to perform a study concerning the entire area of the distribution before definite taxonomic conclusions may be put forward. Regarding the urgency of studying such a problematic group as the Rusty-spot-

ted genets with modern tools of taxonomic research, one of us (F. C.) has begun to investigate the internal structure of this complex of forms and its relationships with akin species, as part of a PhD on the phylogeny of cryptic species complexes within the genus *Genetta*, using molecular markers. Besides data coming from sequencing of specific mtDNA regions, it is obvious that information resulting from other kinds of molecular research, such as cytogenetical and biochemical ones, are also most welcome in the production of a more robust Rusty-spotted genets' taxonomy.

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An investigation of morpho-anatomical characters within the genus *Genetta* (Carnivora, Viverridae) with a remark on *Osbornictis*, the aquatic genet

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Introduction

The Viverrinae subfamily remains a controversial taxonomic group. Therefore, it has been subjected to many systematic reappraisals, mostly based on morpho-anatomical considerations (GRAY, 1864; MIVART, 1882; POCOCK, 1915; GREGORY and HELLMAN, 1939; WOZENCRAFT, 1989). Moreover, phylogenetic relationships within this group, although poorly considered, are liable to discussions and opposite scenarii have been proposed (POCOCK, 1915; GREGORY and HELLMAN, 1939; PETTER, 1969; KINGDON, 1977; CRAWFORD-CABRAL, 1993; VERON, 1995).

Some taxa (notably members of the genera *Genetta* and *Poiana*) are also subject to doubtful specific delimitations (ROSEVEAR, 1974;

SCHLAWE, 1981; CRAWFORD-CABRAL, 1981a and b; CRAWFORD-CABRAL and PACHECO, 1992; CRAWFORD-CABRAL, 1993; WOZENCRAFT, 1993; KINGDON, 1997), often due to a lack of diagnostic characters in their initial descriptions. As a consequence, the current Viverrinae classifications fail to propose similar taxa sets, both from quantitative or qualitative viewpoints (GRZIMEK, 1990; NOWAK, 1991; WOZENCRAFT, 1993; KINGDON, 1997).

We can easily imagine the headache that the Viverrinae –and especially the genets– may represent for people concerned by their identification and classification, that is to say naturalists and/or collection curators. With the aim to clarify interspecific limits within the genus *Genetta*, we undertook an exhaustive examination of morpho-anatomical characters. Although previous identification keys related to the genets do already exist (COETZEE, 1971; ROSEVEAR, 1974; CRAWFORD-CABRAL, 1981b), diagnostic characters which are proposed (craniometrical measures, coat colours, spots pattern, etc.) generally seem not easily applicable to species differentiation. Thus, two identification keys (one based on cranial characters and the other one based on coat characters) are here presented for the genus *Genetta*.

Material and methods

Most of the specimens used in the present study belong to the Paris Natural History Museum (MNHN) collections (Laboratoire de Zoologie: Mammifères et Oiseaux, and Laboratoire d'Anatomie comparée), but the Musée Royal de l'Afrique centrale of Tervuren (MRAC) and the London Natural History Museum (NHML) also allowed us to complete our taxonomic set.

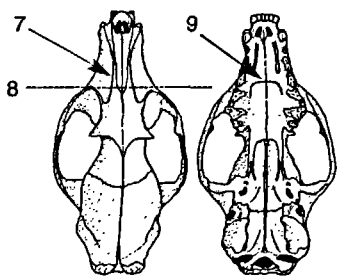
Characters taken into account to discriminate each taxon (skull and coat) were at first determined on non-ambiguously delimited species (the so-called « genet-like » species as *Osbornictis piscivora*, *Prionodon linsang* and *Prionodon pardicolor*, and also some genet species as *Genetta johnstoni*, *Genetta victoriae* and *Genetta thierryi*), and then applied to the other taxa.

Results

Identification keys

Cranial characters

1. *Foramen magnum:* – compressed ..... *G. johnstoni*
   – not compressed 2
2. *Fronto-nasal suture:* – bilobate ..... *G. thierryi*
   – unilobate 3
3. *Sagittal crest:* – absent 4
   – present 6
4. *Postorbital process:* – strong 5
   – weak 8
5. *Postero-accessory cusp (P_2):* – present ..... *G. abyssinica*
   – absent ..... *G. tigrina*
6. *Entotympanic bone:* – not inflated ..... *G. "rubiginosa"*
   – inflated 7
7. *Premaxillo-frontal contact:* – present ..... *G. pardina*
   – absent ..... *G. angolensis*
8. *Fronto-nasal suture:* – subsequent to the upper border of the lachrymal bone ..... *G. genetta*
   – at the level of the upper border of the lachrymal bone 9
9. *Maxillo-palatine suture:* – subsequent to the P^3 main cusp ..... *G. victoriae*
   – aligned with the P^3 main cusp ..... *G. servalina*



Coat characters

1. *Mid-dorsal line:* – clear in the middle and dark-bordered 2
   – discontinuous 3
   – continuous and down stroke 4

2. *Spots of the first latero-dorsal row:*
   – merged in a continuous line .....*G. abyssinica*
   – merged only in the back part .....*G. thierryi*

3. *Pair of wide median nuchal stripes:* – absent.....*G. servalina*
   – present .....*G. victoriae*

4. *Tip of the tail:* – clear.....*G. genetta*
   – dark.....5

5. *Upper labial spots*: – small and not very contrasting...*G. johnstoni*
   – wide and very contrasting.....6

6. *Upper part of the hind leg*: – poorly spotted .....*G. tigrina*
   – extensively spotted 7

7. *Width of the spots of the first latero-dorsal row*:
   – wider than the mid-dorsal line .....*G. "rubiginosa"*
   – equal to the mid-dorsal line 8

8. *Spots of the first latero-dorsal row:*
   – not merged .....*G. pardina*
   – merged only in the back part .....*G. angolensis*

Reconsideration of Osbornictis piscivora *(Allen, 1919) plantar pads description*

Our exhaustive examination of morpho-anatomical characters (applied to a large set of Viverrinae) allowed us to reconsider the plantar pads description of *Osbornictis piscivora*, as ALLEN (1924) did not mention the presence of the metatarsal pads (nomenclature from POCOCK, 1915) in his type-specimen illustration. The examination of the specimen 87-68-M1 (MRAC) permits to determine distinct metatarsal pads, even if they seem merged with the hairless plantar structure (fig.1).

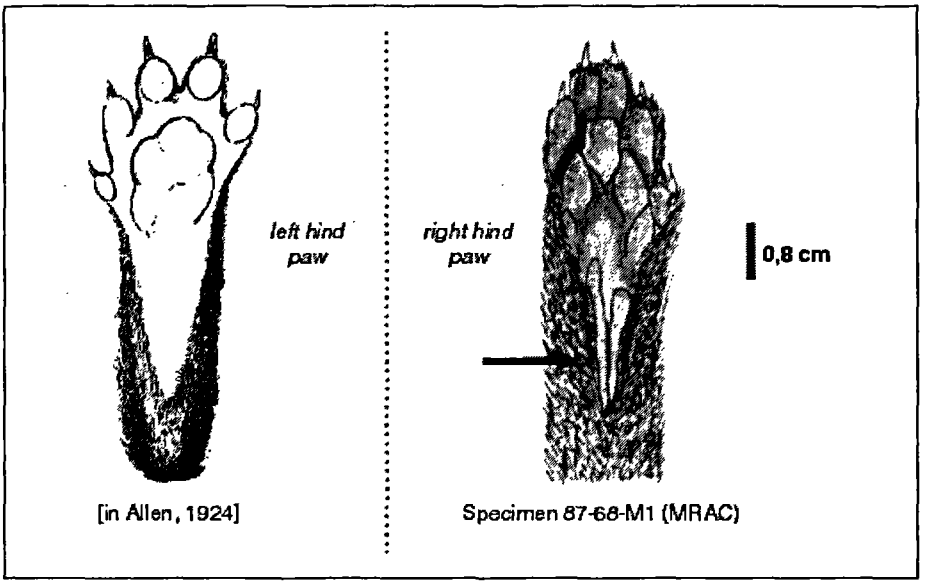


Figure 1
Allen illustration (left) (Allen, 1924 : by courtesy of the American Museum of Natural History) and new illustration (right) of the *Osbornictis piscivora* plantar pads.

Discussion

Regarding the genet "species" that occur in the identification keys, we must clarify some taxonomic points. Indeed, the observation of diverse characters led us to make associations and discriminations within some still status-debated taxa:

– no distinction between *Genetta genetta* (Linné, 1758), *Genetta felina* (Thunberg, 1811) and *Genetta senegalensis* (Fischer, 1829) was allowed on the basis of the observed qualitative characters (skull, teeth and skin). The same can be said in the case of *Genetta angolensis* Bocage, 1882 and *Genetta mossambica* Matschie, 1902. These conclusions disagree with those of several recent authors. *Genetta felina* and *Genetta genetta* are considered as distinct species by SCHLAWE (1981), as well as *Genetta genetta* and *Genetta senegalensis* by ROSEVEAR (1974), but the phenotypic differentiations on which these distinctions are based (colour variations and measurements) are

far less sufficient to definitely diagnose them as valid species, like it was suggested by the authors themselves. *Genetta mossambica* has been previously considered as a valid species, and COETZEE (1971) included it in his identification key of the genus *Genetta*. However, the characters used to discriminate *Genetta mossambica* from *Genetta angolensis* are obviously incorrect (for instance, respectively "spots small" and "large spots"; see SCHLAWE's photographs (1981) for illustrated arguments) and probably due to the scarcity of *Genetta mossambica* specimens in Museum collections. Their distinction is also suggested in the identification key of CRAWFORD-CABRAL (1981b), even if the author noticed the great similarity between the habitus of the two "forms".

– on the other hand, the case of *Genetta servalina* is inconclusive as no specimens of *Genetta cristata* Hayman, 1940 were included in this study.

– the distinction between *Genetta pardina* I. Geoffroy Saint Hilaire, 1832 and *Genetta "rubiginosa"* Pucheran, 1855 (see CRAWFORD-CABRAL, 1981a and b; CRAWFORD-CABRAL and PACHECO, 1992), both grouped in the single species *Genetta maculata* (Gray, 1830) by WOZENCRAFT (1993), is confirmed by an important divergence related to cranial characters (GAUBERT *et al.*, in prep.). These considerations, complicated by the fact that *Genetta rubiginosa* is the senior synonym of *Genetta thierryi* (SCHLAWE, 1981; CRAWFORD-CABRAL and FERNANDES, 1999), should involve further nomenclatural modifications (GAUBERT *et al.*, in prep.). But in order to keep the discussion clear, we have chosen to refer to the most commonly accepted nomenclature of the genus (CRAWFORD-CABRAL, 1981b; WOZENCRAFT, 1993).

Secondly, we must specify that some juvenile character states - even present in post-juvenile specimens- can interfere with the identification keys utilisation:

– (1) the sagittal crest is absent, that is to say temporal muscles insertion crests form quite a large area (a similar observation was noticed for the weasel (*Mustela nivalis*) by KING (1980)).

– (2) the curvature of the maxillo-palatine suture's anterior extension is elongated ahead, which can influence the alignment with the P^3 main cusp.

– (3) the coat is generally more densely spotted. Besides, the spots of the first two latero-dorsal rows are often merged so that they constitute two continuous stripes (observations on stillborn specimens of *Genetta servalina* (1996.318 and 319 - NHML)).

Furthermore, this type of observation permits to point out the morpho-anatomical divergence of *Genetta johnstoni* compared to the other genets characteristics, as its adult morphotype presents some juvenile character states like – among others – (1) and (3).

Finally, the *Osbornictis piscivora* metatarsal pads reconsideration shows that morphological observations are still of interest, especially in the Viverrinae subfamily, for which some accurate structure descriptions remain impossible on the basis of current Museum collections (perineal glands, rhinarium, claws recantation system, etc.). Moreover, the presence of distinct metatarsal pads in *Osbornictis* constitutes an additional evidence of its supposed terrestrial way of life (HART and TIMM, 1978; COLYN and GEVAERTS, 1986; VAN ROMPAEY, 1988; KINGDON, 1997), as the organisation and the morphology of its pads are very close to the structural plan of the genet-like taxa (VERON, 1999) and have suffered no important transformations caused by a hypothetical adaptation to aquatic life in river streams. The bare palms of the so-called Aquatic genet only suggest adaptation to fishing activities (HART and TIMM, 1978).

Conclusions and prospects

Although a special attention to "evident" characters has been paid in this determination work, we shall notice that no hand-made identification keys can pretend to resolve every encountered questions of identification. For instance, very similar species, such as *Genetta pardina* and *Genetta "rubiginosa"*, are hardly distinguishable on the basis of coat characters. However, the keys proposed here proved to be a powerful tool in the relabelling of the genets of the MNHN collections.

This preliminary study constitutes a preamble to a cladistic analysis applied to the Viverrinae subfamily, for which the phylogenetic usefulness of the whole character set observed (non reported here) will be tested.

Moreover, the intrageneric delimitation question within the genus *Genetta* will have to be dealt using coupled methods like genetic divergence, caryology, new determination of morpho-anatomical characters and ecological studies.

Acknowledgements

We are very grateful to Paula Jenkins (Natural History Museum of London) and Wim Van Neer (Musée royal d'Afrique centrale in Tervuren) for giving us access to their viverrine collections. Thanks are due to two anonymous reviewers for useful comments on earlier version of the manuscript. This is a contribution of E.A. 2586 "Systématique et évolution des vertébrés tétrapodes".

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Ancienneté des Carnivora (Mammalia) en Afrique

Jean-Yves Crochet

Stéphane Peigne

Mohamed Mahboubi

Jusqu'à présent, l'histoire de l'ordre des Carnivora (Mammalia) n'était documentée en Afrique qu'à partir du Miocène inférieur (SAVAGE, 1965, SCHMIDT-KITTLER, 1987). En effet, les preuves de leur présence plus ancienne dans le Paléocène du Maroc (CAPPETTA *et al.*, 1980) restaient conjecturales. En revanche, les Creodonta s'y sont développés et diversifiés au moins depuis l'Eocène inférieur (CROCHET, 1988), sinon depuis le Paléocène (CAPPETTA *et al.*, 1980). De plus, ces derniers restent majoritaires sur ce continent jusqu'à l'arrivée des carnivores modernes et ne disparaissent qu'au Miocène supérieur. Dans ce contexte, la dent d'un Carnivora au Glib Zegdou est une découverte importante pour l'histoire du groupe. Surtout, l'âge des plus anciens Carnivora nommés en Afrique s'en trouve considérablement vieilli. En effet, Glib Zegdou est une localité du Sahara algérien dont l'âge se situe entre l'Éocène inférieur terminal et l' Éocène moyen basal, sur la base des charophytes (GEVIN *et al.*, 1974) et des stades évolutifs des mammifères (VIANEY-LIAUD *et al.*, 1994 ; GODINOT and MAHBOUBI, 1994). Le site fossilifère est situé sur le flanc d'une butte-témoin entre les hamadas du Dra, du Guir et de la Daoura constituant un des Gour d'une hamada éocène en partie démantelée par l'érosion (MAHBOUBI, 1995).

Description

Une unique molaire inférieure gauche (longueur : 7,6 mm ; longueur du trigonide : 3,7 mm ; longueur du talonide : 3,9 mm ; largeur du trigonide : 4,45 mm ; largeur du talonide : 4,05 mm) a été découverte dans le niveau F du Glib Zegdou par l'un d'entre nous (M. M.). Malgré une fracture, cette dent est dans un excellent état de conservation. Les surfaces d'usure sont peu développées (fig. 1).

Le trigonide est moyennement élevé par rapport au talonide qui est plus long et moins large. Les cuspides sont relativement massives si on considère l'âge du spécimen.

Le protoconide est un peu plus haut que le paraconide et ce dernier dépasse le métaconide qui est particulièrement bas. Le paraconide, normalement cuspidé en position linguale, est situé à l'extrémité d'un paralophide très légèrement arqué. Le métaconide est légèrement postérieur au protoconide. L'ouverture linguale du trigonide est haute. Un précingulide, relativement large mais court, souligne la base de la partie la plus linguale du paralophide.

Le talonide est peu profond. L'hypoconide, l'hypoconulide et l'entoconide sont de hauteur comparable, l'hypoconulide étant en position axiale et plus postérieure. L'entocristide est basse avec un métastylide. La crête oblique remonte très légèrement sur la muraille postérieure du trigonide en direction de l'encoche située au milieu du protolophide. Un cingulide irrégulier ferme partiellement l'ectoflexide.

Les encoches carnassières sont nettes (paralophide, protolophide, entocristide entre le métastylide et l'entoconide, postcristide de part et d'autre de l'hypoconulide).

La hauteur du protoconide au-dessus du trigonide et celle du trigonide par rapport au talonide militent en faveur d'une désignation de ce spécimen comme une M/1. Mais l'importance de l'hypoconulide sur une postcristide bien arquée est un caractère qui serait plus propre à évoquer une dernière molaire. Un certain doute peut planer sur le rang de cette molaire. Cependant, dans les comparaisons qui suivent, les auteurs la considèrent comme une M/1.

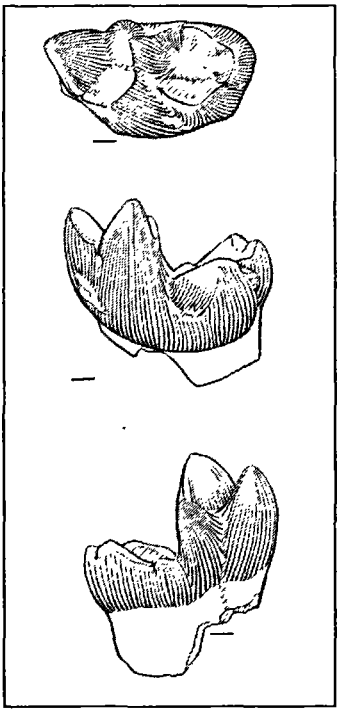

Figure 1
M/1 gauche, GZC 35, spécimen-type de *Glibzegdouia tabelbalaensis* n.g. n.sp. du site du Glib Zegdou (collections université d'Oran).
a : vue labiale ;
b : vue occlusale ;
c : vue linguale.

Le tiret correspond à 1 mm.

Comparaisons

La présence de nombreuses encoches sur les cristides indique un régime alimentaire de type carnassier. Des comparaisons ont été effectuées avec des Proteutheria (Palaeoryctidae, Pantolestidae...), des Condylarthra Mesonychidae, des Creodonta et des Carnivora.

Comparaisons avec divers mammifères du Tertiaire ancien

Le caractère aigu des cuspides des molaires inférieures des Palaeoryctidae s'oppose à la massivité relative du spécimen du Glib Zegdou. Le trigonide des Pantolestidae est toujours pincé antéro-postérieurement avec un faible paraconide. Les condylarthres

Mesonychidae possèdent une denture inférieure typiquement secodonte (SZALAY, 1969). Quant aux Creodonta, si leurs molaires inférieures augmentent généralement de taille vers l'arrière (caractère qui ne peut être jugé ici), la plus postérieure d'entre elles possède un talonide plus ou moins réduit (Oxyaenidae Oxyaeninae, Hyaenodontidae Proviverrinae) ou absent (Hyaenodontinae). Les Oxyaenidae Tytthaeninae et de nombreux Palaeonictinae montrent habituellement des M/2 un peu plus grandes que les M/1 avec des métaconides normalement développés, un talonide plus étroit que le trigonide et un hypoconulide dévié lingualement (GINGERICH, 1980 ; GUNNELL et GINGERICH, 1991). La dent examinée ne peut donc pas être attribuée à l'un de ces taxons d'ordre supérieur. Une attribution à l'ordre des Carnivora s'impose.

Comparaisons avec les Carnivora primitifs

Si à ce jour aucun représentant paléogène d'attribution certaine n'est décrit d'Afrique, l'ordre des Carnivora est représenté depuis le Paléocène en Amérique du Nord et en Eurasie par des espèces regroupées dans les familles des Viverravidae (incluant les Didymictidae de FLYNN et GALIANO, 1982) et des Miacidae. Ils disparaissent à la fin de l'Eocène mais perdurent peut-être jusqu'à l'Oligocène moyen en Asie (RUSSELL et ZHAI, 1987).

Sans discuter des relations phylogénétiques et du devenir de ces deux familles réputées souches des deux sous-ordres des Carnivora (respectivement les Feliformia et les Caniformia), constatons qu'elles possèdent généralement deux molaires inférieures. Lorsque la présence d'une M/3 est constatée (notamment chez les Miacidae), elle est toujours de très petite taille et les talonides des M/2 et M/3 ne sont pas allongés.

Dans la famille des Viverravidae, les M/1 possèdent des cuspides aiguës, un trigonide généralement très haut au dessus du talonide, sans réduction du métaconide, et une postcristide non arquée avec éventuellement un faible hypoconulide. Exceptionnellement, cette postcristide peut être faiblement arquée avec un hypoconulide faible (GINGERICH et WINKLER, 1985, fig. 9) ou plus développé (*ibid.*, fig. 7).

Sur les dernières molaires (des M/2), le trigonide est peu élevé au dessus du talonide et le métaconide n'a pas régressé. Le talonide, plus long que le trigonide, est presque aussi large que ce dernier avec un hypoconulide projeté en arrière. La présence de ces caractères est constatée dès le Paléocène supérieur d'Amérique du Nord. Cependant, le trigonide de la dernière molaire est relativement plus élevé dans le genre *Simpsonictis* MacIntyre, 1962 (GINGERICH et WINKLER, 1985).

La molaire du Glib Zegdou se distingue nettement de cette morphologie par l'aspect relativement élevé des cuspides de son trigonide et la faible hauteur de son métaconide.

Comparaisons avec des Carnivora modernes

Des ressemblances morphologiques sont constatées avec les molaires de certains représentants miocènes et africains de l'ordre des Carnivora, en particulier avec *Legetetia nandii* Schmidt-Kittler, 1987, l'un des plus anciens Viverridae africains, provenant du Miocène inférieur du Kenya (sites de Legetet, Koru, Chamtwara et Songhor).

Si les hauteurs relatives du trigonide et du talonide des M/1 sont comparables, un certain nombre de caractères de l'unique molaire du Glib Zegdou (GZC 35) se retrouvent dans le même état ou dans un état différent chez *L. nandii*. Un métaconide plus bas que le paraconide (même état que GZC 35) s'observe sur le spécimen LG-789 de *L. nandii* (SCHMIDT-KITTLER, 1987, fig. 15) alors qu'il est d'égale hauteur sur SO-1379 et 1409 (*ibid.*, fig. 18) ou légèrement plus élevé (LG-755, *ibid.*, fig. 14). Le métastylide présent au Glib Zegdou ne se retrouve que sur un spécimen kenyan (*ibid.*, fig. 15). La postcristide de *L. nandii* est peu ou pas convexe et, dans ce cas, l'hypoconulide est très peu marqué. Parfois, il est plus développé (*ibid.*, fig. 15) mais sans atteindre la taille et la position très reculée qu'il présente sur GZC 35.

Entre la M/1 du Glib Zegdou et celles de *L. nandii*, des différences plus significatives sont notées. Les mensurations de GZC 35 sont plus importantes (7,6 x 3,9 mm contre 5,8-6,3 x 3,4 – 3,8). L'ouverture linguale du trigonide est singulièrement plus haute et le protoconide

domine plus nettement le trigonide. Sa crête oblique est en position moins linguale et ses encoches carnassières moins profondes.

Il est évident que la signification de ces comparaisons est atténuée par le fait que nous ne connaissons qu'un spécimen au Glib Zegdou alors qu'il y en a 7 dans les sites de l'Est africain.

Les M/2 de *L. nandii* ne se distinguent pas nécessairement par une taille plus petite que celle de la M/1. Mais la hauteur du trigonide par rapport au talonide, plus étroit, est faible et ce dernier est plus long que le premier avec une postcristide en arc de cercle supportant un fort hypoconulide axial rappelant ce qui est observable à ce niveau sur la molaire du Glib Zegdou.

Détermination

Le caractère le plus particulier de la molaire du Glib Zegdou est la petite taille relative du métaconide. Chez l'ensemble des mammifères carnivores, cette cuspide tend souvent à diminuer de taille. Cette diminution est associée à un allongement du trigonide par déplacement du paraconide en position plus labiale et à la formation d'un paralophide tranchant. Ces transformations permettent progressivement le passage d'une molaire tribosphénique à une molaire secodonte. C'est dire que les phénomènes de convergence sont fréquents et rendent les déterminations parfois délicates lorsque le matériel disponible est ancien, fragmentaire ou peu abondant.

La question de la position systématique du genre *Legetetia*, qui présente quelques traits communs avec la dent du Glib Zegdou, reste imprécise au sein des Viverridae (McKenna et Bell, 1997), alors que manifestement le genre *Kichechia* (Schmidt-Kittler, 1987) des mêmes sites montre déjà les principaux caractères qui permettent de reconnaître un Herpestidae moderne.

En conclusion, il apparaît que la dent du Glib Zegdou ne peut être présentement incluse dans le cadre systématique familial des Carnivora tel qu'il ressort des dernières synthèses, celle de McKenna et Bell (1997) en particulier. Pour cette raison, nous proposons la création d'un nouveau genre et d'une nouvelle espèce pour marquer l'origi-

nalité du matériel étudié. Selon nous, toute attribution à un sous-ordre (Feliformia ou Caniformia) ou à une famille existante semble prématurée.

Ordre Carnivora Bowdich, 1821
Sous-ordre et famille indéterminés
Glibzegdouia n. g.

Derivatio nominis : de Glib Zegdou, localité de l'espèce-type.
Espèce-type : *Glibzegdouia tabelbalaensis* n.sp.
Diagnose provisoire : celle de l'espèce-type.
Glibzegdouia tabelbalaensis n. sp.

Derivatio nominis : de Tabelbala, village situé à proximité du gisement-type. Cette espèce est dédiée à ses habitants pour l'hospitalité et l'aide qui ont largement contribué au succès des missions dans cette région.

Diagnose partielle et provisoire : espèce de Carnivora de taille petite à moyenne. Le trigonide de la M/1 surplombe nettement le talonide ; le métaconide est plus bas que le paraconide ; le talonide est à peine moins étroit que le trigonide et de même longueur. L'hypoconulide, aussi haut que les entoconide et hypoconide, leur est nettement postérieur.

Holotype et unique spécimen : une probable première molaire inférieure gauche, GZC 35, coll. Université d'Oran.

Gisement-type : Glib Zegdou, unique gisement connu (Eocène inférieur terminal à Eocène moyen basal du Sahara algérien).

Conclusion

L'ancienneté certifiée de l'ordre des Carvivora en Afrique est reculée de quelques 23 millions d'années. Leur rareté est à associer au petit nombre de gisements qui ponctuent cette période sur ce continent et, bien souvent, à des spectres fauniques peu fournis. Dans ce contexte, seul le site d'Adrar Mjorn 1 a livré une faune thanétienne diversifiée dans laquelle les carnivores sont représentés par trois-

formes attribuées dubitativement à des Créodontes (Proviverrinae ?) et à un « probable » Carnivore (miacidés ?) (GHEERBRANT, 1987).

La présence des seuls Creodonta est constatée dans les sites paléogènes d'Afrique : une espèce (*Koholia atlasense*) dans l'Eocène inférieur d'El Kohol en Algérie *in* CROCHET (1988) et 11 dans l'Oligocène inférieur du Fayum *in* BOWN *et al.* (1982) et 19 *in* HOLROYD (1994). Leur absence est peut-être provisoire dans d'autres sites éocènes comme ceux de Chambi (HARTENBERGER *et al.*, 1998) et de Nementcha (COIFFAIT *et al.*, 1984). Le Miocène inférieur du Kenya avait livré les plus anciens Carnivora africains : 15 espèces sont recensées par SAVAGE (1965) et SCHMIDT-KITTLER (1987). Elles sont associées dans les mêmes sites à 15 espèces de Creodonta. Après cette période, la diversité des Creodonta va diminuer et celle des Carnivora augmenter.

Les espèces concernées font donc partie de lignées endémiques africaines dont les souches ont pu émigrer vers l'Afrique au Tertiaire ancien (GHEERBRANT, 1987). Des auteurs ont évoqué des émigrations plus tardives, à l'Eocène inférieur par exemple. Cette originalité est appuyée par la présence constante d'Hyracoïdes dans ces gisements, de macroscélidés primitifs au Chambi et par l'étude des rongeurs (VIANEY-LIAUD *et al.*, 1994). Reste que le rôle joué par les Carnivora dans les écosystèmes africains a été fort discret jusqu'au Miocène pour des raisons qui nous échappent encore.

Ainsi et à titre d'hypothèse, *Glibzegdouia tabelbalaensis* pourrait représenter un stade ancien original (réduction du métaconide) d'une lignée africaine de Carnivora.

Remerciements

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Preliminary study on some rodents of southern Mauritania as reservoir of human pathogenic viruses

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Introduction

Rodents are being found to be involved as reservoirs in an ever growing number of human viral diseases, the vectors of which are usually Arthropods (see MILLS and CHILDS, 1998 for Americas and GRATZ, 1997 for Africa). In Africa, *Mastomys* and *Arvicanthis* are the two main genera concerned, but a number of other murids have also been found to host viruses potentially transmissible to Man (see SALUZZO *et al.*, 1986; GRATZ, 1997). Thus, a correct identification of these rodent species and a good knowledge of their ecology (and more importantly their relations to humans) are important prerequisites for an understanding of their role in the maintenance and spread of such viruses.

The occurrence of human cases of Rift Valley Fever in the region of Ayoun El Atroûss (South Mauritania) in September-October 1998 (following previous episodes in 1987 and 1993) prompted the organization of a field survey aiming, among other things, at evaluating the potential role of rodents as reservoirs in this disease. Previous studies in West Africa were not conclusive in this respect, with the presence of antibodies against this virus having been found only exceptionally (a few positive cases in *Mastomys* sp. and *Arvicanthis niloticus*, cf. SALUZZO *et al.*, 1987a; ZELLER *et al.*, 1997). The rodents caught in this study were also tested for the presence of various other viruses. Some of these viruses have already been found in nearby Senegal (Saboya and Gabek Forest, both isolated from rodents and phlebotomes, ROBIN *et al.*, 1968), or in other West African countries (Lassa, isolated from *Mastomys natalensis* in Nigeria and Sierra Leone, in SALUZZO *et al.*, 1986), whereas others (Puumala, Seoul and Hantaan), known to be harmful to humans, have not yet been identified in Africa.

Here we present the results on rodents captured during this survey, as well as the chromosomal data that have enabled us to unambiguously determine 2 of the species caught. The results of virological analyses are also presented. These data are discussed in terms of community composition and the potential risk associated with the presence of these rodents in this region of Mauritania.

Material and methods

Wire mesh live traps were used in domestic (inside houses and in cattle enclosures), peridomestic (small cultivated areas around villages) and natural habitats in and around 5 localities near Ayoun El Atroûss (16°40'50"N; 9°18'07"W; fig.1). Night drives (COSSON *et al.*, 1997) also enabled us to catch by hand some individuals. The rodents captured were sacrificed, and various samples were taken:

– pectoral muscle with ribs was put on culture medium and cell cultures were processed in the laboratory. Conventional karyotypes were obtained from dividing cells by the standard method.

– organs, brain, as well as blood were taken. Sera were tested at 1:100 dilution for IgG antibodies against Rift Valley Fever and Gabek

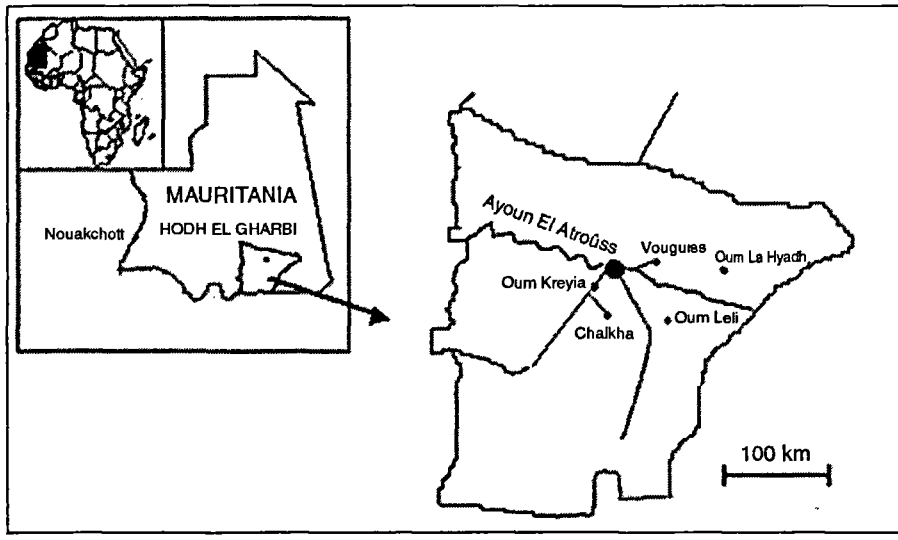

Figure 1
Map of the study region.

Forest (Phleboviruses), Saboya (Flavivirus), Hantaan, Puumala and Seoul (Hantaviruses) and Lassa (Arenavirus) inactivated viral antigens by an indirect Elisa. The conjugate was a peroxidase-labeled anti-mouse IgG.

Results

The rodent community

Seventy-three individuals of five species were caught (tabl. 1):

– *Gerbillus tarabuli* (Gerbillinae) was by far the dominant species caught and was present in both peridomestic and natural sandy habitats. An identical karyotype with 2 N = 40, NFa = 74 (fig. 2a) was found for 12 individuals. This karyotype is characteristic of this species which is well known in this region (GRANJON *et al.*, 1999) where it is morphologically very similar to *G. nigeriae*.

Locality	Vouguiss			Oum La Hyadh		Chalkha		Oum Lell		Oum Kreyia	Total
Habitat type	a	b	c	b	c	b	c	b	c	c	
trap nb	20	50		75	20	140	30	40	30	20	445
Acomys airensis	–			–	–	1	–	–	–	7	8
Arvicanthis niloticus	–			–	–	1	–	–	–	–	1
Gerbillus tarabuli	–	19		8	1	–	25 (3)	1	–	2	59
Desmodilliscus braueri			(1)								1
Jaculus jaculus			(3)						(1)		4
Total	–	19	4	8	1	2	28	1	1	9	73

a: domestic habitat ; b: peridomestic habitat ; c: natural habitat

Table 1
Rodents trapped at 5 localities near Ayoun El Atroûss.
Numbers between brackets refer to hand captures.

– A single individual of *Desmodilliscus braueri* (Gerbillinae) was caught by hand, as usual for this trap-shy species.

– *Acomys* cf. *airensis* (Acomyinae) was caught mainly in rocky habitats at one locality, but one individual was trapped in a garden. The karyotype of one specimen (2 n = 40, NFa = 66; fig. 2b) appears to be very close to what was known previously for specimens of *A. airensis* studied in other parts of the species range (VOLOBOUEV, pers. comm.), although small differences were observed that would deserve further analyses.

– *Arvicanthis niloticus* (Murinae) was trapped only once in peridomestic habitat.

– A few individuals of *Jaculus jaculus* (Dipodidae) were caught by hand, as usual for this trap-shy species, but numerous other individuals were seen during night drives.

Virological analyses

The serum of 51 rodents (16 males and 25 females *G. tarabuli*, 4 males *J. jaculus*, 1 male *D. braueri*, 1 female *A. niloticus*, 3 males and 1 female *A.*, cf. *airensis*) have been subjected to serological analyses against the 7 viruses cited above. All attempts to find antibodies against them were negative.

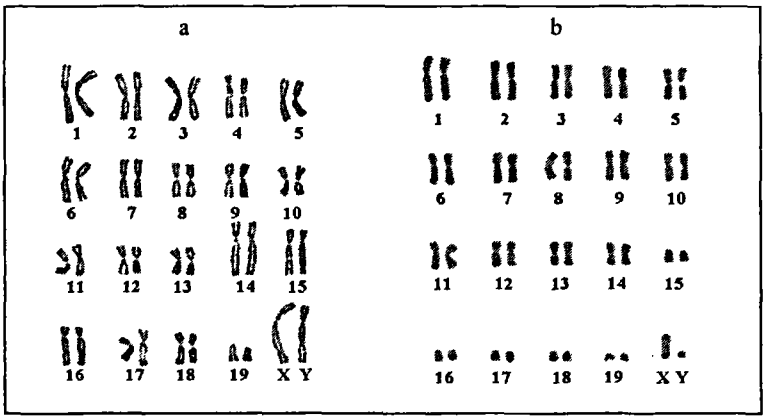

Figure 2
Standard karyotypes of **a**-a male specimen of *Gerbillus tarabuli*, and **b**-a male specimen of *Acomys* cf. *airensis* from the region of Ayoun El Atroûss.

Discussion – Conclusions

The species found in this study are typical of a saharo-sahelian sandy-clay environment (*J. jaculus*, *D. braueri*, *G. tarabuli*) with rocky outcrops (*A.* cf. *airensis*) and "enriched" by human settlements (*A. niloticus*). *Jaculus jaculus* and *G. tarabuli* are widespread species (GRANJON *et al.*, 1997), whereas *D. braueri* appears to be more localized (HUTTERER and DIETERLEN, 1986). *Acomys* cf. *airensis* is recorded for the first time in Mauritania, the only previous mention of *Acomys* in this country corresponds to the description of *A. chudeaui* from the Adrar Massif (KOLMANN, 1911). Further work is needed, including morphological and genetical analyses, to compare specimens from northern and southern Mauritania and check for their potential conspecificity. The presence of *A. niloticus* is probably associated with its commensalism, as natural habitats are probably too arid for this species (GRANJON *et al.*, 1997). Additional fieldwork should complete this inventory with the potential addition of other species of *Gerbillus*, *Taterillus* and possibly commensal *Mastomys*.

Many serological data exist for the Ayoun El Atroûss region, showing positive cases for RVF in both humans and domestic ungulates (SALUZZO

et al., 1987b). The relatively high densities of rodents found in peridomestic habitats confirms that contacts between rodents and humans are highly probable, opening an avenue for transmission of viruses to humans should the rodents be reservoirs. In this respect, the small number of individuals studied, as well as the near absence of *Arvicanthis* and *Mastomys*, which are the more regularly involved genera in such endozootics in the region, may explain the negative results of virological analyses. In Senegal, Saboya virus was found in *Tatera kempi* (= *T. gambiana*), *Mastomys* sp., *A. niloticus*, and *Mus musculus*) and Gabeck Forest virus in *T. kempi*, *Taterillus* sp. and *A. niloticus* (SALUZZO *et al.*, 1986). One individual of the latter species was also found to host Gabeck Forest virus in Mauritania (SALUZZO *et al.*, 1987a). As for RVF, and following the 1987 epidemic in Rosso (southern Mauritania), isolation attempts on 1478 individual rodents by SALUZZO *et al.* (1987a) were unsuccessful. In the same study, immunofluorescence tests on the serum of 268 *Mastomys* sp. only yielded 2 positive cases. Similarly, ZELLER *et al.* (1997) mentioned the presence of RVF antibodies in the serum of 2 out of 70 *A. niloticus* caught in March 1990 in the Senegal river delta of northwestern Senegal. In South Africa, evidence of natural infection by RVF virus was demonstrated in the murid rodent *Aethomys namaquensis* (PRETORIUS *et al.*, 1997).

Further studies are needed in other periods of the year (especially at periods of high vector – i.e. arthropods – densities) and including a larger sample of small mammal specimens to definitely define the role of these small mammals in the maintenance and transmission of pathogens in the region of Ayoun El Atroûss. As shown here, special care should be taken for an accurate determination of the species involved (particularly via chromosomal analyses) in such genera as *Gerbillus*, *Taterillus*, *Acomys* and *Mastomys* where morphologically similar species may coexist.

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"Acomyinae": new molecular evidences for a muroid taxon (Rodentia: Muridae)

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François Catzeflis

Johan R. Michaux

Introduction

Until the immunological study of SARICH (1985), *Acomys*, the spiny mouse, was included in the Murinae based on its morphology. More precisely it was considered as a close relative of *Mus* (JACOBS, 1978). Sarich's results raised questions about the taxonomic affinities of *Acomys*, and other immunological works came to similar conclusions. These distance-based analyses indicated that the immunological distance between *Acomys* and Murinae was as large as between Murinae and other non-murine rodents (HAMMER *et al.*, 1987; WILSON *et al.*, 1987; FRAGUEDAKIS-TSOLIS *et al.*, 1993). MONTGELARD (1992) furthermore indicated that another Murinae, *Uranomys* might be in the same taxonomic situation. Following these first immunological data, other molecular studies came to support the exclusion of *Acomys* from Murinae, and its association with at least 2 other "murines": *Uranomys* and *Lophuromys*, such as DNA/DNA hybridizations (CATZEFLIS, 1990; CHEVRET *et al.*, 1993), 12S rRNA sequences (HÄNNI *et al.*, 1995) and a study of LINE repeated elements (FURANO *et al.*, 1994; USDIN *et al.*, 1995). A morphological reexamination of the third upper molar (DENYS and MICHAUX, 1992) evidenced also

a peculiar morphology of that tooth shared by the three genera *Acomys*, *Uranomys* and *Lophuromys*. Thus, different biochemical, molecular and morphological evidences have recently indicated that *Acomys*, *Uranomys* and *Lophuromys* cannot be considered anymore as murine rodents (see CHEVRET and HÄNNI, 1994 for more details). HÄNNI *et al.* (1995) proposed the term « Acomyinae » for this group of muroids, without providing any morphological diagnosis. In order to precise the composition of the Acomyinae, the relations among them and with their closest relatives, we performed three different molecular analysis: we completed the data sets for the DNA/DNA hybridizations (CHEVRET *et al.*, 1993) and the 12S rRNA sequences (HÄNNI *et al.*, 1995) and we included new data of the LCAT nuclear gene.

Material and methods

Material

The list of genera involved in the three different analyses is presented on table 1. DNA samples were extracted from 95% ethanol-preserved tissues housed in the collection of Preserved Mammalian Tissues of the Institut des Sciences de l'Évolution, Montpellier (CATZEFLIS, 1991).

DNA/DNA hybridizations

This approach measures the global divergence between the scnDNA (single copy nuclear DNA) of two species. We used the same methods as described in our previous papers (CHEVRET *et al.*, 1993, 1994). The 21*21 matrices of distances (delta-Tm, delta-mode) include only labelled taxa but were still rather incomplete (41% of missing cells). Prior to any distance analysis, we completed the matrices following the procedures described by LANDRY *et al.* (1996) with the RECALL program, kindly provided by F. J. Lapointe. To ascertain the stability of topologies with regards to taxonomic sampling, we used the weighted jackknife performed through the MAJACK program (LAPOINTE *et al.*, 1994).

Subfamily	Genus	DNA/DNA hybridization	12S rRNA	LCAT analysis	Combined
Acomyinae	*Acomys*	+	+	+	+
	Uranomys	+	+	+	+
	Lophuromys	+	+	+	+
	Deomys	+	+	+	+
Murinae	*Arvicanthis*	+			
	Hylomyscus	+			
	Malacomys	+			
	Mastomys	+			
	Millardia	+			
	Mus	+ (3 sp.)	+	+	+
	Myomys	+			
	Praomys	+			
	Rattus	+ (2 sp.)	+	+	+
Gerbillinae	*Gerbillus*	+	+	+	+
	Tatera	+	+	+	+
Dendromurinae	*Steatomys*	+	+	+	+
	Dendromus		+	+	+
Otomyinae	*Otomys*	+			
Cricetomyinae	*Cricetomys*	+	+		
	Saccostomus		+	+	+
Nesomyinae	*Macrotarsomys*		+	+	+
	Nesomys		+	+	+
Mystromyinae	*Mystromys*		+	+	+
Cricetinae	*Mesocricetus*		+	+	+
	Cricetulus		+	+	+
Myospalacinae	*Myospalax*		+	+	+
Sigmodontinae	*Peromyscus*		+	+	+
Arvicolinae	*Clethrionomys*		+	+	+
	Microtus		+	+	+
Spalacinae	*Spalax*		+	+	+
Rhizomyinae	*Rhizomys*		+	+	+

Table 1
List of taxa involved in the different analyses. Additional informations (species, geographic origin, collector, voucher-specimen when available) can be obtained upon request from the senior author.

The distance analyses were done with FITCH and KITSCH programs from the Phylip package (version 3.5c, FELSENSTEIN, 1993). To propose divergence times, the delta-Tm values were then transformed into% base pair mismatch (bpm) estimates by the relation of 1 °C delta-Tm = 1.18% pbm (SPRINGER *et al.*, 1992). These estimates were finally transformed into percent nucleotide substitutions (% nucl. subst.) by the JUKES and CANTOR formula (1969), which corrects for

multiple substitutions. The% nucl. subst. values are then calibrated against the geological time provided by the fossil record, in our case the *Mus-Rattus* dichotomy estimated at *ca* 12 Ma (JACOBS and PILBEAM, 1980; JAEGER *et al.*, 1986; JACOBS and DOWNS, 1994).

Sequences

Mitochondrial DNA: complete 12S rRNA gene

We performed the amplifications of the complete 12S rRNA genes with the R1 and S2 primers (SOURROUILLE *et al.*, 1995) and realised a direct sequencing with the ^{33}P sequencing kit of Amersham, using similar sequencing primers as in previous 12S studies (SOURROUILLE *et al.*, 1995, HÄNNI *et al.*, 1995; DUBOIS *et al.*, 1996). The ten new sequences have been deposited in EMBL under accession numbers AJ 250349 to AJ250358.

The sequences were manually aligned using the ED program (MUST package, PHILIPPE, 1993), and the alignment was refined in order to minimize the number of indels (insertions-deletions) in stems. The hypervariable region (47 nucleotides, position 912 to 958) was excluded from all analyses, which were realized on a final alignment of 964 positions. In order to locate homoplasy, we searched for the evidence of saturation using the method of HASSANIN *et al.* (1998). This analysis shows the importance of multiple substitutions by comparing the pairwise numbers of observed versus inferred changes, as calculated by PAUP. This saturation was checked for 4 partitions (transitions and transversions in stems and loops). The values derived from this analysis were used in a weighted analysis via a stepmatrix procedure in PAUP. In order to test the possibility to estimate the divergence time from the 12S data set we compared the likelihood of the trees constructed with a clock and non-clock hypothesis as proposed by FELSENSTEIN (1981) and calculated with Puzzle 4.0 (STRIMMER and VON HAESELER, 1996).

Nuclear DNA: LCAT (Lecithin-Cholesterol Acyl-Transferase), exons 2 to 6 (804 bp).

Two fragments of the nuclear LCAT gene were amplified using the PCR primers designed by ROBINSON *et al.* (1997). Sequencing on

both strands was done using a dye terminator (Perkin Elmer) sequencing kit and a ABI 373 (Perkin Elmer) automatic sequencer.

Previously known sequences were extracted from GenBank and aligned with the new sequences using CLUSTALW (THOMPSON *et al.*, 1994) and the ED editor (MUST package, PHILIPPE, 1993). As for the 12S gene, in order to locate those substitutions which are the most prone to saturation, we searched for the evidence of saturation by comparing the pairwise numbers of observed versus inferred changes of each substitution type (transition, transversion) at each codon position. The new sequences will be presented elsewhere (MICHAUX and CATZEFLIS, 2000). As indicated in MICHAUX and CATZEFLIS (in press), a relative rate-test was performed with RRTree, version 1.0 (ROBINSON *et al.*, 1998), with Dipodidae as outgroup for the intra-Muridae phylogeny. This leads to the exclusion of the slowest-and fastest-evolving taxa.

Combined analysis

Combining both genes resulted in a data matrix of 22 taxa x 1768 nucleotidic sites. We performed a congruence test (program ARNIE, included in the Random Cladistics Package, SIDDALL, 1996) which indicated that both data sets were not in conflict, hence the combined analysis.

Phylogenetic analysis

On the three resulting data sets (12S, LCAT and 12S + LCAT), we realized analyses with distances (Neighbor-joining, SAITOU and NEI, 1987), Maximum Parsimony (PAUP 3.11, SWOFFORD, 1993, or Paup 4.0b, SWOFFORD, 1998) and Maximum Likelihood (Puzzle 4.0, STRIMMER and VON HAESELER, 1996). The robustness of the phylogenies was assessed by bootstrap for distance and parsimony, by the Bremer Support Index (BSI) (BREMER, 1988) for parsimony, and by reliability percentages for maximum likelihood. A stepmatrix procedure was also used with PAUP with the values deduced from the different saturation analyses. The molecular clock hypothesis was tested for both data sets with Puzzle 4.0 (STRIMMER and VON HAESELER, 1996) and RRTree 1.0 (ROBINSON *et al.*, 1998).

Results and discussion

DNA/DNA hybridizations

The average consensus tree resulting from 10000 jacknife with equiprobable deletions from 4 to 17 taxa (LAPOINTE *et al.*, 1994) on the delta-Tm matrix is presented figure 1. The raw 21*21 delta-matrices can be obtained upon request from the senior author. Except for one case (see below), all ancestral segments were retrieved in all (minimum, average, maximum) consensus trees (details of the jacknife procedure can be found in LAPOINTE *et al.*, 1994). The trees built with the delta-mode and consensus trees obtained with jacknife with single deletion (LANYON, 1985) gave similar results (data not shown). On this tree with 19 ingroup taxa, the association of *Acomys*, *Uranomys* and *Lophuromys* is evidenced, confirming the previous results of CHEVRET *et al.* (1993), which were based on a smaller set of taxa. The so-called « Acomyinae » group also comprises a Dendromurinae, *Deomys,* as previously suggested by a reduced data set (DENYS *et al.*, 1995). This group is clearly separated from the other subfamilies included in this study (Gerbillinae, Murinae), and from the outgroups represented by *Cricetomys* and *Steatomys.* Other molecular studies (see below) indicate that the genera *Cricetomys/ Steatomys* can be considered as a valid outgroup for rooting the Acomyinae/Murinae/ Gerbillinae. In the jacknife procedure with single deletions, the suppression of different taxa leads to an Acomyinae-Murinae (exclusion of *Uranomys* or *Tatera*) or a Acomyinae-Gerbillinae (exclusion of *Steatomys)* association. Thus, the clustering of Gerbillinae with Murinae is not robust, which suggests that our DNA hybridization data are best interpreted as an unsolved polytomy Acomyinae - Murinae – Gerbillinae. The divergence between the Murinae, Gerbillinae and Acomyinae can be estimated at around 14.5 My (with reference to *Mus/Rattus* dichotomy at 12 My), while the four different genera among the acomyine group diverged between 10 and 8.5 millions years ago, and *Tatera* and *Gerbillus* at 8.2 My.

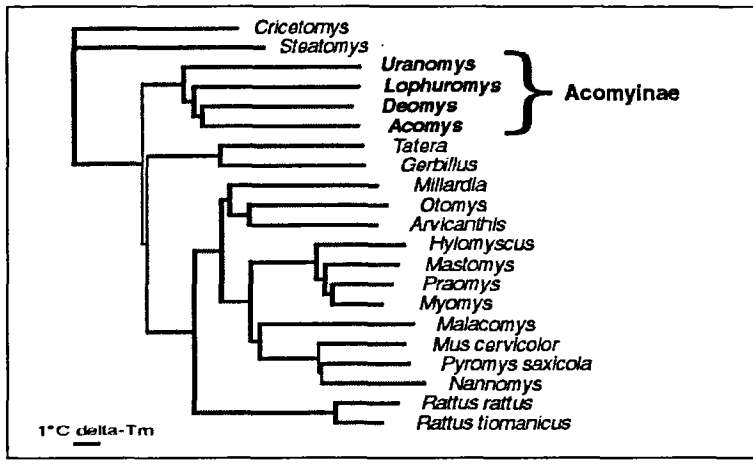

Figure 1
Average consensus tree derived from the 21*21 delta-Tm matrices produced with the weighted jacknife procedure (LAPOINTE *et al.*, 1994). Thin lines indicate two uncertainties: 1) the relationships between *Mus saxicola*, *M. cervicolor* and *Nannomys* were not retrieved in all jacknife combinations of the multiple-deletions procedure; 2) different branching patterns for Murinae - Gerbillinae - Acomyinae were observed in jacknife replications during the single-deletion procedure.

Sequences analysis

The results of the combined analysis of both genes are presented on the tree illustrated on figure 2. The supports for the main nodes for the different data sets and for the different phylogenetic analyses are indicated in table 2. These results do not change significantly when weighted analyses were performed (data not shown). As indicated in a previous study of the LCAT gene (ROBINSON *et al.*, 1997), *Spalax* and *Rhizomys* seem an appropriate outgroup for the rest of the murid taxa included in our analysis. Here again a robust association of the four Acomyinae (*Acomys*, *Uranomys*, *Deomys* and *Lophuromys*) is observed when both genes are concatenated. Nevertheless, the association of *Uranomys* with the three other Acomyinae is not robustly supported by the 12S rRNA data set alone, as in a previous analysis with a reduced 12S data set (see figs. 3 and 4 in HÄNNI *et al.*, 1995). Within Acomyinae, the combined analysis indicates that *Acomys* and *Deomys* are sister-taxa, followed by *Lophuromys* and *Uranomys*. The

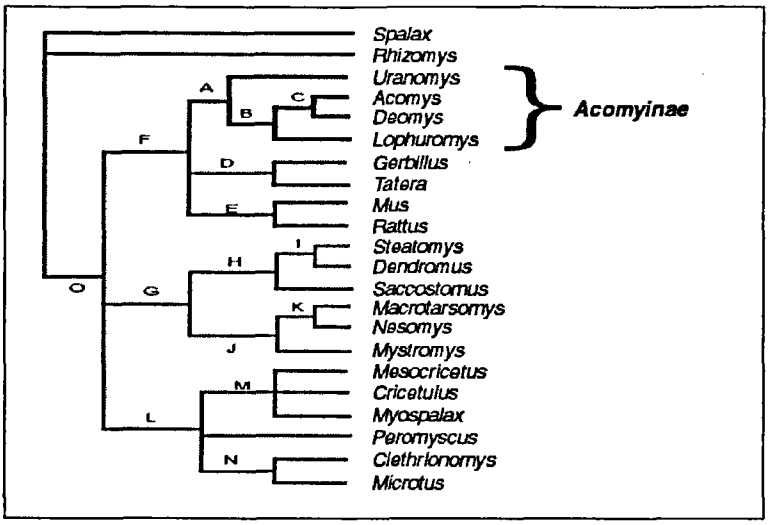

Figure 2
Consensus tree of the combined analysis of the 12S rRNA and LCAT genes using all events (TV + TS + indels) and all positions. When a node was not robustly supported or when there was desagreement between the different phylogenetic analyses, a polytomy is indicated. The different nodes are labelled A to O, the corresponding supports for the parsimony, distance and maximum likelihood analyses are indicated in table 2. Branch lengths are arbitrary.

results of the LCAT gene analysis inverse the position of *Lophuromys* and *Uranomys*, but the support of the *Uranomys/Acomys/Deomys* group is low (tabl. 2).

As with the DNA hybridization data, gene sequences were not able to precise the relationships between Acomyinae, Gerbillinae and Murinae. The different approaches lead either to a Murinae-Acomyinae or to a Acomyinae-Gerbillinae clades, with low supports in both cases. Consequently, we have depicted these three taxa as issued from an unsolved polytomy (fig. 2).

It appears that the mitochondrial 12S rRNA gene does not provide strong support for the oldest segments, such as nodes G, J, L, or M (fig. 1, tabl. 2), to the difference of the nuclear LCAT gene and the combined analysis. The association of these two genes provides the

Node	12S rRNA	LCAT	Combined analysis
A: Acomyinae	–	97/+8 99/81	96/+15 100/82
B: *Acomys/Deomys/Lophuromys*	74/+2 95/79	–	91/+9 96/94
C: *Acomys/Deomys*	–	94/+6 92/92	85/+6 61/97
D: Gerbillinae	100/+31 100/67	100/+8 99/88	100/+43 100/89
E: Murinae	85/+3 100/87	98/+11 98/91	100/+19 100/91
F: Murinae/Gerbillinae/Murinae	–	70/+4 69/<40	86/+11 72/53
G	–	40/+1 62/<40	57/+3 73/42
H	29/0 63/40	86/+7 93/76	96/+13 100/91
I	78/0 85/51	47/0 47/65	86/+6 87/75
J	–	88/+4 100/90	70/+4 92/78
K	86/+8 94/82	67/+3 67/80	95/+13 100/67
L	–	39/+1 70/69	57/+4 97/60
M	–	95/+6 99/70	83/+6 94/58
N	99/+10 100/85	100/+16 100/84	100/+27 100/85
O	100/+33 100/83	99/+14 99/99	100/+54 100/94

Table 2
Support values for ancestral segments of the phylogenetic tree of Figure 2. For each node labelled A to O: above line: Boostrap Percentage (BP parsimony) / Bremer Support Index (BSI parsimony); below line: Bootstrap Percentage (BP distance) / Reliability Percentage (RP maximum likelihood). These robustness values were obtained using all events (TV + TS + indels) and all positions: not supported at the 50% treshold.

best support for several nodes (for example, nodes F or H: fig. 1, tabl. 2), and some ancestral segments that are not robustly supported by separate analyses appear much stronger such as the African group (node G) or the association Cricetinae, *Peromyscus*, *Myospalax* and Arvicolinae (node L).

The tests of the molecular clock hypothesis lead to the rejection of the use of the 12S rRNA gene to determine the timing of divergence of our taxa, as the two Gerbillinae are some of the fastest-evolving sequences, as indicated by the RRTree analysis. Consequently gerbils should be excluded from molecular-clock tree. For the LCAT gene the same tests lead to the exclusion of Sigmondontinae, *Nesomys* and *Rhizomys*, but Gerbillinae, Acomyinae and Murinae can be used in a phylogeny constructed with a molecular clock hypothesis. This analysis, with the *Mus/Rattus* divergence at 12 My as reference, indicates that Acomyinae, Gerbillinae and Murinae diverged at 16.6 My, the four acomyines genera from 11.9 to 6.6 My, *Tatera* and *Gerbillus* at 8.7 My.

Molecules and morphology: support for the Acomyinae?

Both molecular approaches indicate the existence of an Acomyinae clade which comprises *Acomys*, *Deomys* and *Lophuromys* (for the 12S rRNA data sets) associated with *Uranomys* for the other data sets. The resolution of the different approaches are not equivalent. The 12S rRNA gene and the hybridization data sets provide less resolution for older divergences than the LCAT gene or the combined sequences. Other molecular data have also grouped some of these taxa. *Acomys* and *Uranomys* were associated by HÄNNI *et al.* (1995) and DUBOIS *et al.* (1999), but the supports for this group were low (fig. 4B, HÄNNI *et al.*, 1995; fig. 4, DUBOIS *et al.*, 1999). Other associations were also published, *Lophuromys* and *Deomys* (VERHEYEN *et al.*, 1996), *Acomys*, *Lophuromys* and *Deomys* (DENYS *et al.*, 1995), *Acomys*, *Uranomys* and *Lophuromys* (CHEVRET *et al.*, 1993). But this is the first study that clearly groups the four acomyine genera together, with the support of different molecular methods involving scnDNA hybridization, a mitochondrial and a nuclear gene.

If our data bring strong molecular support for the existence of the Acomyinae, morphological evidence uniting them is still lacking.

The four genera have been brought closer by different authors but only two at a time, with most evidences supporting an *Acomys-Uranomys* clade. *Acomys* and *Uranomys* have been effectively considered as closely related based on dental and cranial morphology since a long time (HELLER, 1911; HINTON, 1921; INGOLBY, 1929; ELLERMAN, 1941; HEIM DE BALSAC, 1963; MISONNE, 1969). More recently, HUTTERER *et al.* (1988) have associated *Acomys*, *Uranomys* and a fossil of the Canary Islands, *Malpaisomys*. This hypothesis was refuted by the immunological analysis of MONTGELARD (1992) which indicated that *Malpaisomys* was more closely related to *Mus* than to *Acomys* and *Uranomys*, without any further information concerning their relationships. DENYS *et al.* (1992), in a morphological analysis on dental characters in *Acomys*, *Uranomys* and other murid rodents, associated *Acomys* and *Uranomys*, considering them as an early offshoot of the Murinae. However, the re-examination of the third upper molar by the same authors (DENYS and MICHAUX, 1992) lead them to propose a morphological synapomorphy uniting *Acomys*, *Uranomys* and *Lophuromys*, and excluding them from the Murinae. Thus, some strong morphological support does exist for the association of these three genera, which also share precocious youngs, a fragile skin and tail, and a partially diurnal life.

Lophuromys and *Deomys* share similarities in the morphology of the zygomatic arch (ELLERMAN, 1941), but this author and DIETERLEN (1976) considered that this character state might be a convergence due to their similar diet (mostly insectivorous). A morphological re-examination of the eight living genera of Dendromurinae lead DENYS *et al.* (1995) to the conclusion that this taxon was not monophyletic. This interpretation is congruent with our results, which indicate that *Deomys* is within the Acomyinae, whereas *Dendromus* and *Steatomys* are more closely related to the Cricetomyinae (*Saccostomus* or *Cricetomys*, figs. 1 and 2). DENYS *et al.* (1995) also found that *Acomys* and *Lophuromys* are closely related, but without any close relationship with *Deomys*. Comparative morphology suggested that *Acomys* and *Lophuromys* were more closely related to Murinae than to Gerbillinae, as the morphology of the latter group appears very derived.

Thus, if the association of *Acomys*, *Uranomys* and *Lophuromys* is now supported by both molecular and morphological data, the problem of their morphological association with *Deomys* is neither explained

nor solved, as the latter genus appears completely distinct from the remaining Acomyinae.

Acomyinae within the Muridae

The sister-group of Acomyinae is either Murinae or Gerbillinae, but we cannot decide between both hypotheses. Morphology and paleontology would tend to associate Murinae and Acomyinae, notably due to the supposed derived morphology of their first upper molar which was considered a diagnostic feature of all Murinae (JACOBS *et al.*, 1989). Among Muridae, paleontologists very often associate Murinae, Dendromurinae, Gerbillinae and, sometimes, Cricetomyinae (FLYNN *et al.*, 1985; JAEGER *et al.*, 1986, 1985; TONG and JAEGER, 1993). Our results indicate that Murinae, Acomyinae and Gerbillinae are indeed sister-taxa, as proposed by TONG and JAEGER (1993). Cricetomyinae (here represented by *Saccostomus*) belong to a completely different group which comprises African (*Steatomys, Dendromus, Mystromys*) and Malagasy (*Nesomys, Macrotarsomys*) murids, which is a new phylogenetic hypothesis. The age of the divergence – 16 My – proposed by TONG and JAEGER (1993) for the Murinae/Gerbillinae split is not too different from our estimates: 16.6 (LCAT) and 14.5 My (scnDNA hybridation), considering that one of our dating (14.5 My) for such an old divergence is probably underestimated due to some DNA/DNA hybridization properties (SPRINGER and KIRSCH, 1991).

If the existence of Acomyinae and its composition might be difficult to explain morphologically, the relative position of the group within the Muridae seems more in agreement with traditional views.

Conclusion

Our data provide strong molecular support for an Acomyinae group comprising *Acomys, Uranomys, Lophuromys* and *Deomys*. If there is also some morphological support for an *Acomys, Lophuromys* and *Uranomys* clade based upon the morphology of the third upper molar (DENYS and MICHAUX, 1992), there is still no morphological evidence for the association of *Deomys* with this group. The molecular clade

Acomyinae thus raises questions concerning the definition of Dendromurinae and Murinae as based on comparative morphology, especially dental. Other morphological characters (cranial, post-cranial, internal soft anatomy) should be searched and analysed for testing our molecular findings. Additional species of *Acomys* and *Lophuromys* have now to be included in order to precise the relationships within this group. If we can propose the existence of an Acomyinae/Gerbillinae/Murinae cluster within Muridae, none of our methods can decipher clearly the relationships between these three subfamilies. The use of other molecules, especially slow-evolving protein-coding nuclear genes, the study of repeated elements and the use of other morphological data may be able to answer the question of their relationships.

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An identification key for species within the genus *Praomys* (Rodentia: Muridae)

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Introduction

Within the Murinae (Rodentia, Muridae), African rats of the genus *Praomys* Thomas, 1915 are widely distributed in the intertropical zone, from West (Senegal to Angola) to East Africa (Uganda to Malawi). They live in closed (primary forest) to semi-opened (secondary forest, fringes, gallery forest and fallow) biotopes.

According to MUSSER and CARLETON (1993), the genus *Praomys* comprises nine species. However, the number of species and their geographical limits are not well understood due to the low level of morphological differentiation between species, making it difficult to find specific diagnostic characters. As a result, the systematics of this genus is yet to be resolved, particularly in the light of new species being described. For instance, VAN DER STRAETEN and KERBIS PETERHANS (1999) recently described a tenth species, *Praomys degraaffi*. Other studies based on morphometric, morphological and chromosomal data also strongly suggest the existence of another new species, which has yet to be described (MATTHEY, 1970; WELTZ and VAN DER STRAETEN, unpublished data).

Based on morphometric studies, VAN DER STRAETEN and DIETERLEN (1987) and VAN DER STRAETEN and DUDU (1990) proposed that the genus *Praomys* be divided into three species complexes. The relationships within and among these complexes remain unknown. It is only recently that a comprehensive study of intrageneric relationships based on a cladistic analysis of morphological characters and including most species within the genus has been undertaken (LECOMPTE *et al.*, in press). From the large set of characters used for cladistic analysis, it was possible to select a series of diagnostic characters to devise the identification key proposed here, together with a synopsis of nine out of the ten currently recognised species within the genus. This key mainly provides diagnostic skull characters for each species and, when possible presents several character combinations to define them. Notes on geographic distribution, based both on literature and museum specimens observations, and chromosomal data available to date are also presented.

Praomys diversity

The genus *Praomys* was defined by THOMAS in 1915 as a subgenus of *Epimys* Trouessart by its mammary formula: 1+2 = 6 or 2+2 = 8. ELLERMAN (1941) classified it as a subgenus of *Rattus* with most of the other Murinae. Then, DAVIS (1965) elevated it at the generic rank.

Data on *Praomys* are presented according to the three species complexes defined by VAN DER STRAETEN and DIETERLEN (1987) and VAN DER STRAETEN and DUDU (1990) as follows.

The tullbergi-*complex*

The *tullbergi*-complex includes *P. hartwigi* Eisentraut, 1968, *P. misonnei* Van der Straeten and Dieterlen, 1987, *P. morio* (Trouessart, 1881), *P. rostratus* (Miller, 1900), *P. tullbergi* (Thomas, 1894). This species complex is supported by some morphological characters such as palatal ridges (9 instead of 7 in the other species of the genus), a large foramen ovale, and supraorbital ridges that originate from the middle of the frontals.

Praomys hartwigi Eisentraut, 1968

Synonyms: *obscurus* Hutterer *et al.*, 1992. This taxon was described as a subspecies from Nigeria. However HUTTERER *et al.* (1992) think about it as a full species and Van der Straeten also considers it as a good species (oral communication). This species occurs in mountain forests of Cameroon (lake Oku) and Nigeria (Gotel Mts) (EISENTRAUT, 1970; HUTTERER *et al.*, 1992).

Praomys misonnei Van der Straeten & Dieterlen, 1987

This species is found in Central and East Africa (Zaire and Kenya) (VAN DER STRAETEN and DIETERLEN, 1987; VAN DER STRAETEN and DUDU, 1990, DUDU *et al.*, 1997). Some specimens from Kenya, attributed to this species, are characterised by a diploid number of 2N = 36 (QUMSIYEH *et al.*, 1990), but MUSSER and CARLETON (1993) suggested that these specimens need to be re-examined to confirm their identity. Van der Straeten looked at these specimens and considers them as *P. misonnei* (pers. comm.)

Praomys morio (Trouessart, 1881)

Synonyms: *maura* (Gray, 1862). TROUESSART in 1881 renamed this species *morio* because it was preoccupied by *Mus maura* Waterhouse, 1839.

This species is restricted to Mount Cameroon and Bioko (EISENTRAUT, 1970). The species has a diploid number of 2N = 34 (MATTHEY, 1965). PETTER (1965) discussed about specimens from Central African Republic, which finally appeared to be another species, here called *Praomys sp.* (see further).

Praomys rostratus (Miller, 1900)

This species has been recorded in West Africa from Liberia, Guinea to Ivory Coast (VAN DER STRAETEN and VERHEYEN, 1981; GAUTUN *et al.*, 1986) and is characterised by a diploid number of 2N = 34 (GAUTUN *et al.*, 1986). It was first considered as subspecies of *P. tullbergi* until VAN DER STRAETEN and VERHEYEN (1981) separated them on the basis on morphometric data. GAUTUN *et al.* (1986) also recorded different ecological requirements for *rostratus* and *tullbergi*.

Praomys tullbergi (Thomas, 1894)

Synonyms: *burtoni* (Thomas, 1892). THOMAS renamed in 1894 this species because it was preoccupied by *Mus burtoni* Ramsay, 1887.

This species is widely distributed in West and West and Central Africa. Like *P. rostratus*, it also has a diploid number of 2N = 34 (MATTHEY, 1958).

The yet to be described, *Praomys sp.* from central Africa, called *P. morio* in PETTER (1965), and *P. cf. lukolelae* in PETTER (1975) and CHEVRET *et al.* (1994), is included in the *tullbergi*-complex, on the basis of morphometric data (WELTZ and VAN DER STRAETEN, unpublished data). This species corresponds with specimens from Central Africa evoked by MUSSER and CARLETON (1993) as an undescribed species. It is characterised by a diploid number of 2N = 42 (MATTHEY, 1965, 1970).

The jacksoni-*complex*

The *jacksoni*-complex includes *P. jacksoni* (de Winton, 1897), *P. minor* Hatt, 1934, *P. mutoni* Van der Straeten and Dudu, 1990 and the recently described *P. degraaffi* Van der Straeten and Kerbis Peterhans, 1999. This species-complex is also supported by some morphological characters such as strong and straight supraorbital ridges, a small foramen ovale and a distinct t3 on M^1.

Praomys jacksoni (de Winton, 1897)

Synonyms: *peromyscus* (Heller, 1909) described as full species; *montis* (Thomas and Wrougthon, 1910), described as full species; *viator* (Thomas, 1911), described as subspecies; *sudanensis* Setzer, 1956 described as subspecies. Some of these taxa are considered as full species by VAN DER STRAETEN and DUDU (1990).

This species occurs widely in East, Central and West Africa. Its karyotype is characterised by a diploid number of 2N = 28 and an autosomal fundamental number of NFa = 30 (MATTHEY, 1959). This species represents the most widely distributed one of *Praomys*.

Praomys minor Hatt, 1934

This species is only known from three specimens from the type-locality in central Zaire, which were not available for examination in this study. However, previous morphometric analyses (VAN DER STRAETEN and DIETERLEN, 1987; VAN DER STRAETEN and DUDU, 1990) have shown this species to be closely related to *P. jacksoni.*

Praomys mutoni Van der Straeten & Dudu, 1990

It is only known from the type-locality in Northern Zaire (VAN DER STRAETEN and DUDU, 1990; DUDU *et al.*, 1997).

Praomys degraaffi Van der Straeten & Kerbis Peterhans, 1999

It is a mountain species from the Albertine Rift in Burundi, Rwanda and Uganda (VAN DER STRAETEN and KERBIS PETERHANS, 1999; MADDALENA *et al.*, 1989). Its karyotype is characterised by a diploid number of 2N = 26 and NFa = 24 (MADDALENA *et al.*, 1989).

The delectorum-*complex*

The *delectorum*-complex only includes *P. delectorum* (Thomas, 1910). This species is characterised by a distinct t3 on M^1, weak supraorbital ridges, and a large foramen ovale as in the *tullbergi* species complex.

Praomys delectorum (Thomas, 1910)

Synonyms: *taitae* (Heller, 1912), described as full species; *octomastis* Hatt, 1940, described as subspecies; *melanotus* Allen and Loveridge, 1933, described as subspecies.

This species is distributed on high plateaus and isolated mountains from Malawi, Tanzania to Kenya. *Praomys taitae*, considered as a synonym of *P. delectorum* was found to possess a diploid number of 2N = 48 (MATTHEY, 1965).

Identification key of the species of the genus *Praomys*

The number of specimens examined range from N = 15 to N = 100 per species. The widely distributed species were represented by large series of specimens encompassing the distributional range of the species while the endemic species such as *P. hartwigi* and *P. morio* were represented by the smallest samples. The selection of skull characters took into account the nature and extent of variability of the

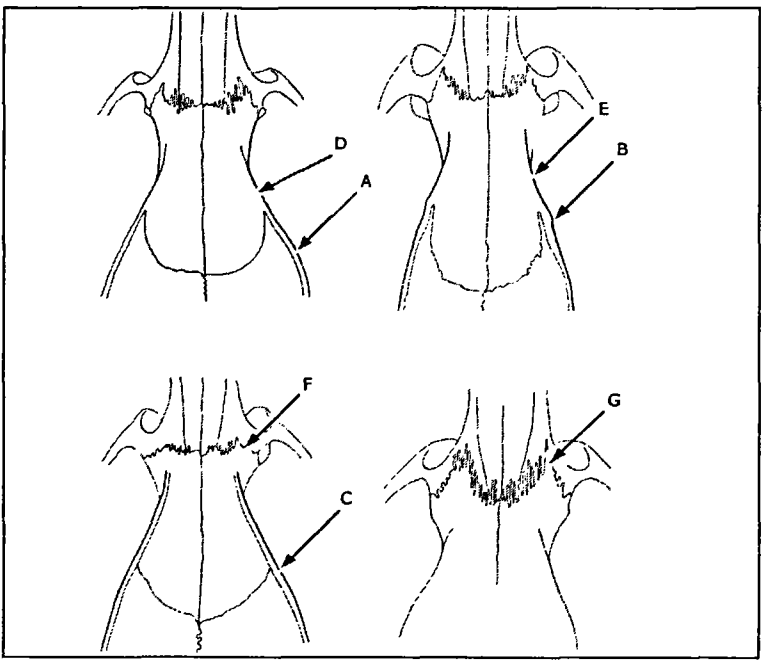

Figure 1
Dorsal views of the skull, showing the development of supraorbital ridges, interorbital constriction and the suture between nasals and frontals. The extent of development of the ridges, already used by PETTER (1965) can be absent or very weak (A), present, and originating from the middle of frontals (B), or very strong, prominent, straight, and originating in front of frontals (C). The interorbital constriction can be gradual and amphora-shaped (D) or more bold in the middle and as a broken line (E). The suture can be almost horizontal (F) or V-shaped (G).

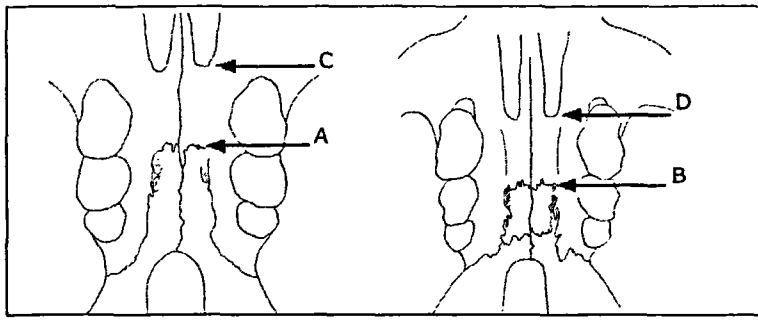

Figure 2
Ventral views of the skull, showing the limits of the palatine bone and the posterior limit of the anterior palatal foramina. The anterior limit of the palatine bone can extend to the level of the posterior part of M^1 (A), or between M^1 and M^2 (B). The posterior limit of the anterior palatal foramina can reach the front edge of the 1st root of M^1 (C) or reach the middle of the M^1, between its 1st and 2nd roots (D).

characters such the highly variable characters were not considered in devising the identification key.

The skull characters used in this identification key are illustrated in Figs. 1 and 2. The mammary formula was also included but may not be independently diagnostic, and is defined as the number of pectoral mammae plus the number of inguinal mammae on each side of the body. The mammary formula has previously been used to separate the genera *Myomys*, *Mastomys* and *Praomys* (THOMAS, 1915).

1. Supraorbital ridges absent or very weak (fig. 1 character 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 M^1 (fig. 2 character A), nasal/frontal suture almost horizontal (fig. 1 character 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 M^1 and M^2 (fig. 2 character B), nasal / frontal suture V-shaped (fig. 1 character 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 (fig. 1 character B)..... 4.

Supraorbital ridges very strong, straight, beginning in front of frontals (fig. 1 character C)..... 7.

Posterior limit of anterior palatal foramina reaching anterior edge of first root of M^1 (fig. 2 character C)..... 5.

4. Posterior limit of anterior palatal foramina reaching halfway between first and second roots of M^1 (fig. 2 character D)..... *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 (fig. 1 character D)..... *P. misonnei.*

   Interorbital constriction more bold in the middle of frontal and as a broken line (fig. 1 character E)..... *P. rostratus.*

7. Posterior limit of anterior palatal foramina reaching anterior edge of first root of M^1 (fig. 2 character C). ..... *P. mutoni.*

   Posterior limit of anterior palatal foramina reaching halfway between first and second roots of M^1 (fig. 2 character D)..... 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.*

The characters related to supraorbital ridges present some variation as a function of age, the ridges increasing with the age of the animals. It is thus important to be careful about the age of the specimens compared. For example, old *P. morio* can have ridges as young P. *tullbergi*, although they will generally not be so developed. The type of *P. morio*, a young adult, presents very weak ridges.

The characters related to posterior limit of anterior palatal foramina and anterior limit of the palatine bone used by ROSEVEAR (1969) also show some variation, but in a way which is compatible with their use as diagnostic characters.

To summarize, table 1 presents a list of the useful characters for each species.

	degraaffi	*delectorum*	*hartwigi*	*jacksoni*	*misonnei*	*morio*	*mutoni*	*rostratus*	*tullbergi*
Supraorbital ridges	prominent, beginning in front of frontals	very weak	beginning in the middle of frontals	prominent, beginning in front of frontals	beginning in the middle of frontals	very weak	prominent, beginning in front of frontals	beginning in the middle of frontals	beginning in the middle of frontals
anterior limit of palatine bone extending to	posterior part of M1	between M1 and M2	posterior part of M1	posterior part of M1	posterior part of M1	posterior part of M1	posterior part of M1	posterior part of M1	posterior part of M1
Naso-frontal suture	almost horizontal	V-shaped	almost horizontal	almost horizontal	almost horizontal	almost horizontal	almost horizontal	almost horizontal	almost horizontal
Breadth of the zygomatic bone	as malar process	very thin	as malar process	as malar process	as malar process	as malar process	as malar process	as malar process	as malar process
Posterior limit of anterior palatal foramina	between first and second roots of M1	between first and second roots of M1	between first and second roots of M1	between first and second roots of M1	anterior edge of the first root of M1	between first and second roots of M1	anterior edge of the first root of M1	anterior edge of the first root of M1	anterior edge of the first root of M1
Ratio of molar row length / maximum length of skull	> 15%	> 15%	> 15%	> 15%	< 15%	> 15%	> 15%	< 15%	> 15%
Interorbital constriction	very bold in front of the frontals	bold, as a broken line	bold, as a broken line	very bold in front of the frontals	gradual, amphora-shaped	gradual, amphora-shaped	very bold in front of the frontals	bold, as a broken line	bold, as a broken line

Table 1
List of useful cranial characters for each species.

Discussion

The previous identification key for *Praomys* species by MISONNE (1974) only included the following five species: *P. tullbergi, P. morio, P. hartwigi, P. jacksoni* and *P. delectorum.* Due to the absence of appropriate diagnostic morphological characters, the identification of *P. tullbergi* was only based on its geographic distribution, but the species is now known to be sympatric with *P. rostratus* (GAUTUN *et al.*, 1986). Moreover, *P. morio sensu* MISONNE (1974), included a combination of specimens of *P. morio* from Cameroon and of the species referred here in as *Praomys sp.* from central Africa. By the fact, "*Praomys morio*" was considered to have a diploid number of 2N = 42, which in fact represents the diploid number of the species referred here in as *Praomys sp.*, whereas the "true" *P. morio* from Cameroon has a diploid number of 2N = 34 (MATTHEY, 1965). Next, the characters used by MISONNE (1974) to define "*P. morio*" are also present in species of the *tullbergi*-complex such as *P. rostratus* and *P. misonnei.* Furthermore, *P. jacksoni* and *P. delectorum* were both defined by straight supraorbital ridges, which are not prominent in the latter species. The two species can also be distinguished by their mammary formula, which only applies to females, and therefore cannot be used alone.

Consequently, a new identification key for *Praomys* species based on other morphological characters became necessary. For a more practical identification, additional characters involving external features need to be identified, particularly for those species lacking diagnostic characters. In addition, once enough evidence is available, it will be possible to provide species descriptions. For example, *Praomys* sp. has been known from the literature since 1965. It was initially referred to *P. morio* (MATTHEY, 1965; PETTER, 1965), and subsequently to *P. lukolelae* (PETTER, 1975). However, the species is currently considered to be distinct from both *P. morio* and *P. lukolelae* (= *Malacomys lukolelae* in MUSSER and CARLETON, 1993), and has yet to be described. An attempt has been made here to define species limits and their characteristics, but there is an urgent need to refine the key by using alternative techniques, such as cytogenetics and DNA sequencing.

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Current concepts of Gerbillid phylogeny and classification

Igor J. A. Pavlinov

Introduction

Gerbillids constitute a moderately small group of about 20 genera (PAVLINOV *et al.*, 1990; MUSSER and CARLETON, 1993). This group attracted close attention of taxonomists in the 70s and 80s, when several hypotheses about its relations with other muroids and principal phylogenetic divisions were elaborated (CHALINE *et al.*, 1977; PAVLINOV, 1982; TONG, 1989; PAVLINOV *et al.*, 1990). All these studies were morphological and considered a very limited data set, mainly dental and bullar morphology. One of the most surprising matters in this respect is that very few biochemical and cytogenetical works have been made with gerbillids, when compared with their "neighbors" in the classification (murids, arvicolids, etc.).

I do not mean that morphological data exhausted themselves and are now outdated. Instead, they still provide quite interesting information about gerbillid affinities and phylogeny. So, below I shall consider some focal points in the phylogeny and taxonomy of gerbillids, as they are seen by a morphologist.

The protoconulid story

On the basis of dental morphology, gerbillids have been continuously placed within the Palaearctic cricetids or considered as an independent family or subfamily. However, in the 70s, a hypothesis of their possible relation to Miocene myocricetodontines was proposed by paleontologists (JAEGER, 1977; CHALINE *et al.*, 1977). That was a really sudden idea, because the genus *Myocricetodon* with its closest allies possessing at least some accessory murid cusplets on lower molars was traditionally considered as a member of Murinae (JACOBS, 1978). Contrary to this, no recent gerbillid genus was known at that time to possess such a murid feature; only the Miocene *Protatera,* presumably related to taterillines, has been reported to possess a protoconulid on the first lower molar (JAEGER, 1977).

However, at the present moment, the protoconulid, one of the murid cusplets, was found in several recent gerbillid genera (fig. 1) as in *Ammodillus* (PAVLINOV, 1981) or in Asian *Tatera* and South African *Desmodillus* (PAVLINOV, 1985). In all these taxa, this small cusplet is clearly visible on the unworn first lower molar and disappears with tooth wear.

The presence of a protoconulid is clearly a primitive condition for gerbillids. The more advanced morphotypes of the anterior part of M_1 are of two principal types, horseshoe and rhomboid ones (PAVLINOV, 1984). The first type is a characteristic feature of African taterillines, while the second is typical for *Gerbillus, Meriones* and their allies. In *Desmodillus*, it is possible to trace, in a set of teeth with various degrees of wear, the interrelations among these morphotypes. The protoconulid first becomes united with elements of the anteroconid to turn into the horseshoe type, and then the latter turns into the rhomboid type. If we take this ontogenetic transformation series as a kind of recapitulation, it could be supposed that the rhomboid type is a derivative of the horseshoe type, and the latter is a derivative of the type with an isolated protoconulid (PAVLINOV, 1984).

In this connection, one can note that the horseshoe type also occurs sometimes in *Gerbillus* (PETTER, 1956; PAVLINOV, 1984) for which the rhomboid type is typical. Following the above arguments, it is possible to consider such a condition as a kind of atavism. If this is

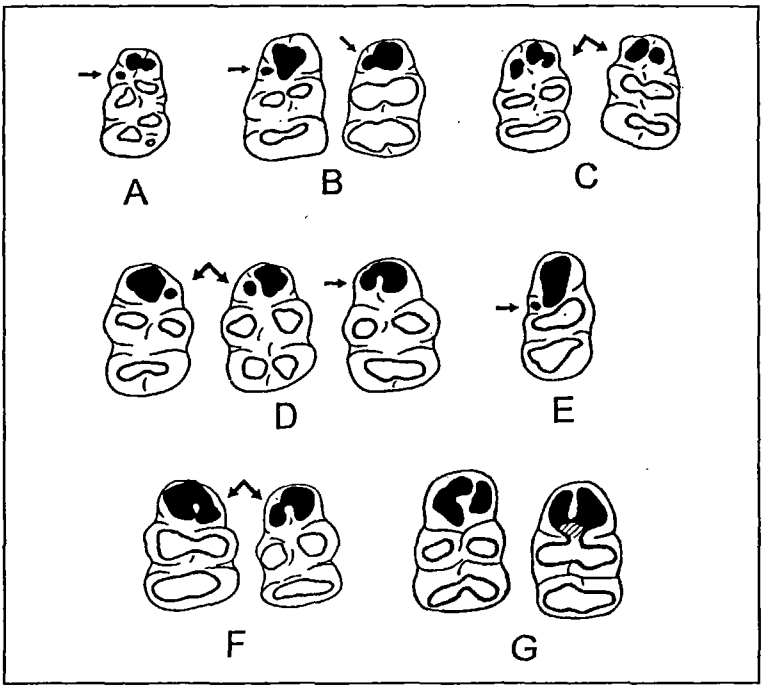

Figure 1
Dental crown pattern of minimally worn M_1 in some gerbillids and their allies to show the presence of protoconulid and anteroconid (both shown in black). A) *Myocricetodon*, B) *Protatera*, C) *Tatera indica*, D) *Desmodillus*, E) *Ammodillus*, F) *Gerbillurus*, G) *Gerbillus*. Arrows indicate the position of the protoconulid. A and B are after JAEGER (1977); others are from PAVLINOV (1984).

correct, then it can be supposed that the horseshoe type of anteroconid was a characteristic feature of direct ancestors of *Gerbillus*. And this can be taken as an indirect evidence that the protoconulid occurred in the ancestors of many gerbillid genera, and not only of those still retaining it.

One may conclude that the most recent ancestors of gerbillids did have an accessory "murid" cusplet, namely a protoconulid, on the first lower molar. On the basis of this conclusion alone, it seems clear that cricetids cannot be ancestors of gerbillids. The hypothesis of gerbillid affinities to myocricetodontines looks more plausible in the light of the anteroconid morphology.

However, it seems premature to unite these taxa in the same family, as CHALINE *et al.*, (1977) suggested. On the one hand, the myocricetodontines show no evolutionary trends in dental morphology common to "real" gerbillids. On the other hand, they still possessed a fairly "murid" mandible (as it was drawn in JAEGER, 1977), which suggests their auditory bulla was murid-like as well, that is without significant pneumatization.

As to the gerbillids themselves, the anteroconid morphology may witness about the following. The Ethiopian *Ammodillus* occupies an isolated position, as it is the only recent representative of the family possessing a separate protoconulid that does not join with the anteroconid proper. The South African *Desmodillus* and *Gerbillurus* are very similar with respect to dental morphology. They both display a primitive horseshoe pattern of anteroconid and, by this, could be related phylogenetically to the taterilline lineage. Finally, the Asian *Tatera indica* displays a more primitive anteroconid morphology as compared to its African relatives.

Mastoid morphology

The next structure to be discussed is the morphology of the mastoid portion of the auditory bulla. LAY (1972), PAVLINOV (1980), and PAVLINOV *et al.* (1990) showed that gerbillid taxa differ from each others by both the degree and, more importantly, the type of mastoid pneumatization (fig. 2).

Omitting the details, pneumatization of a primitive solid mastoid can be considered as resulting from the penetration of tympanic cavity into the mastoid. Two principal pathways of this penetration are supposed to occur in the gerbillids, i.e. anterior and ventral. In the first case, the tympanic cavity penetrates into the mastoid through the dorsal part of the bulla, just above of the ossicles and before the mastoid. This process produces morphotypes B to E. The ventral penetration occurs through the posterior part of the bulla, just ventral to the mastoid. To it, morphotypes F to H belong.

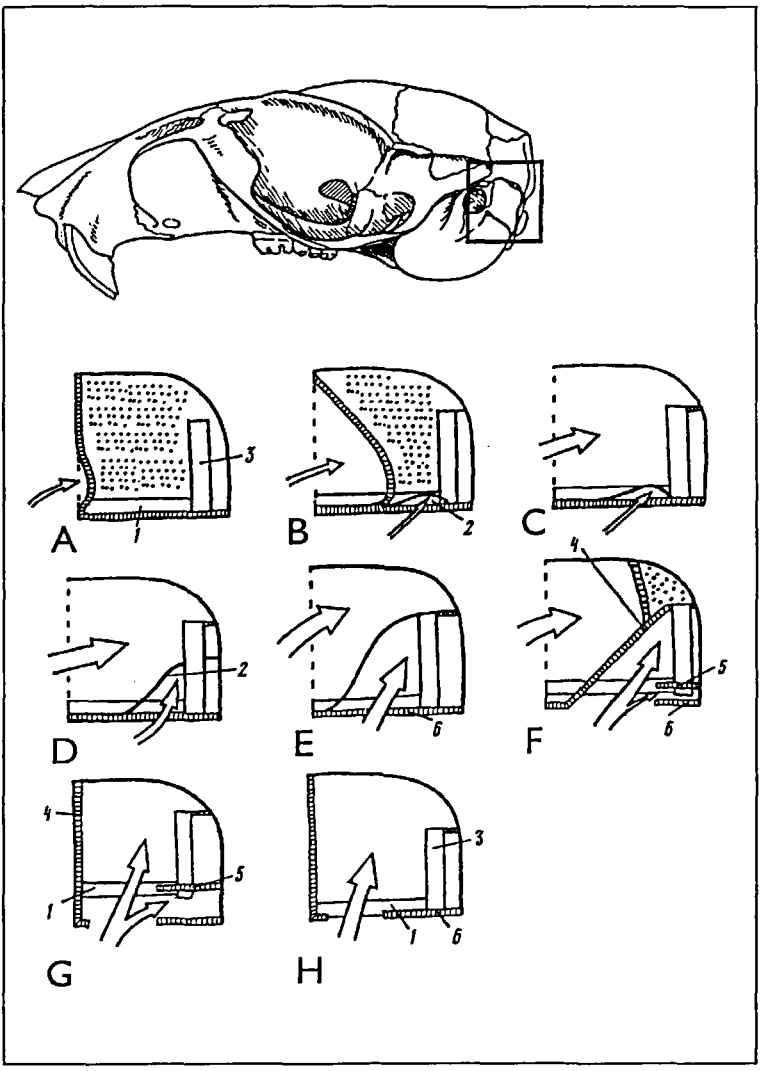

Figure 2
Principal morphotypes (A-H) of the mastoid in Gerbillidae (after PAVLINOV *et al.*, 1990). Schematic parasagittal section. Arrows indicate pathways of penetration of the tympanic cavity into the mastoid. Dashed line indicates an imaginary anterior border between tympanic and mastoid cavities (no bony septa separates them), dotted area indicates part of the lateral mastoid wall knitted with the paraflocculer fossa. Figures designate respective bony elements: 1, 3) semicircular channels; 2) inner mastoid septa; 4) mastoid septa; 5) caudal septa; 6) tympano-mastoid septa.

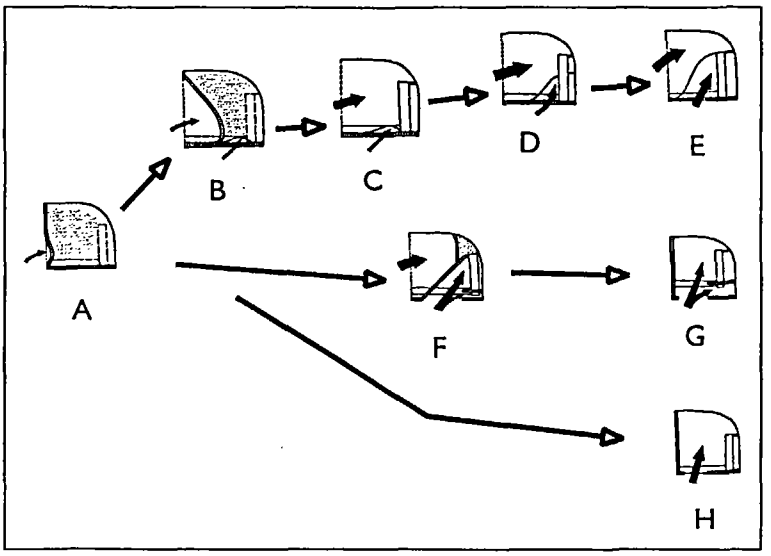

Figure 3
Transformation series indicating supposed evolutionary relations between mastoid morphotypes in Gerbillidae. Morphotype designations are the same as on fig. 2.

There is also a secondary ventral penetration occurring within the so-called anterior type. The resulting pattern of mastoid chambers may be superficially very similar to those displayed by primary ventral penetration (compare morphotypes E and F). However, the bony elements separating the respective mastoid chambers are not really homologous: the diagonal septa includes the horizontal semicircular channel in morphotype E and does not include it in morphotype F.

Thus, one may suppose that each of these two pathways is quite constrained morphogenetically. As such it seems highly improbable for one of them to "switch" into the other. On this basis, it is possible to reconstruct transformation series of gerbillid mastoid morphotypes (fig. 3). It is then reasonable to hypothesize that the type of mastoid pneumatization can be taken as the evidence of phylogenetic affinities of respective gerbillid taxa. The most interesting points in this respect are the following.

Among the taterillines, *Taterillus* is the most primitive (morphotype A) and the Asian *Tatera* is the most advanced (morphotype C).

African *Taterona* and *Gerbilliscus* belong to different lineages, each displaying the initial stage of anterior and ventral penetrations (morphotypes B and F, respectively).

As with dental morphology, *Desmodillus* and *Gerbillurus sensu lato* are again very similar in mastoid structure (morphotypes B and C, respectively). They belong to the same lineage and differ only by the degree of pneumatization, the least being in the subgenus *Progerbillurus* (morphotype B).

Desmodilliscus (morphotype G) does not belong to the same lineage as *Desmodillus,* so they cannot be considered as close relatives. Instead, *Desmodilliscus* resembles in this respect to *Gerbillus* and *Meriones* and their allies (all possess morphotypes F or G).

Mastoid pattern in the genus *Pachyuromys* (morphotype H) is peculiar. It belongs to the ventral type of pneumatization but can be derived from a very primitive condition only.

The cladogram

The resulting cladogram (fig. 4) has been produced (PAVLINOV, 1982; PAVLINOV *et al.*, 1990) without using any computer program. It reflects relations among recent genera derived mainly from the data on dental and bullar morphology. The following peculiarities are to be stressed.

Taking Gerbillidae as a family, two subfamilies can be defined, Taterillinae and Gerbillinae *sensu stricto.* The former contains also *Desmodillus* and *Gerbillurus* as closest relatives, the latter – the remainder genera, except probably *Ammodillus.*

At the tribal level, two presumably monophyletic taxa are recognized in Taterillinae and four in Gerbillinae *sensu stricto.* Their contents are evident from the cladogram, so my additional comment might only be that *Desmodilliscus* and *Pachyuromys* both constitute monotypical tribes of their own. Notice also that both the middle ear and dental morphology place *Sekeetamys* with Rhombomyini rather than with Gerbillini *sensu stricto.* (PAVLINOV *et al.*, 1990).

At nearly the same time, a paleontologist, TONG (1989), published a phylogenetic tree of Gerbillidae which appeared to be very similar

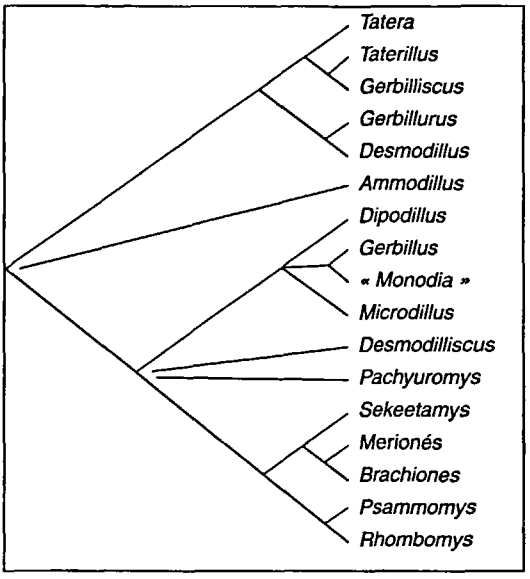

Figure 4
Cladistic relations among recent genera of Gerbillidae (after PAVLINOV *et al.*, 1990) derived mainly from dental and bullar morphology.

to that of mine (PAVLINOV, 1982; PAVLINOV *et al.*, 1990). The principal differences are the following.

The genera *Desmodillus, Ammodillus* and *Desmodilliscus* are placed by TONG (1989) together among the gerbillines proper. Based upon the morphological data described here, this suggestion seems to be incorrect. The patterns of bullar morphology in *Desmodillus* and *Desmodilliscus* belong to different types of pneumatization; these genera also have distinct dentitions. The position of *Ammodillus* remains unclear.

The genus *Pachyuromys* is placed by TONG (1989) close to *Brachiones,* which is improbable: the latter is just a specialized relative of *Meriones* (PAVLINOV *et al.*, 1990).

Among the questions regarding within-gerbillid affinities, of special interest are the relations among taterillines. Usually, *Tatera* proper, *Gerbilliscus* and *Taterona* are all considered congeneric, while *Taterillus* is given full generic rank. However, my data indicate that the Asian branch of this group represented by *Tatera sensu stricto* may be quite isolated from the African branch including the remainding taterillines. It is characterized by peculiar combination of a more

archaic dental pattern (initial stage of horseshoe anteroconid development) and a more advanced mastoid type. Contrary to this, *Gerbilliscus* and *Taterona* (together with *Taterillus*) possess the most advanced horseshoe anteroconid and a more primitive mastoid. The taxonomic conclusion might be that the genus *Tatera* is to be devoted to the Asian species only, while African taterans are to be included in a separate genus whose valid name should be *Gerbilliscus sensu lato.*

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Interpretation of the dental pattern of the South African fossil *Euryotomys* (Rodentia, Murinae, and origin of otomyine dental morphology

Frank Sénégas

Introduction

Otomyinae, the grooved toothed rats, include two genera: *Parotomys* and *Otomys*. Both are semi-hypsodont and their jugal teeth have plane occlusal surfaces characterized by transverse laminae. The third upper molar and the first lower one show a high number of laminae (3 to 10) in comparison to the other molars. Concerning *Parotomys*, 3 complete laminae and a posterior pillar constitute the third upper molar, the first lower one being composed by 4 laminae, the anterior two ones being linked together in a kidney shape structure. The number of transverse laminae is much more variable in *Otomys*: for the third upper molar it can vary from 4 to 10 and from 4 to 6 for the first lower molar. Otomyinae are exclusively African. *Parotomys* is restricted to the west of South Africa and Namibia; it inhabits semi-arid to arid environments while *Otomys* has a wider distribution, from savannas and mountain grasslands to semi-arid areas. Both are completely vegetarian with a diet mainly composed of seeds, grasses and shoots of shrubs (DE GRAAFF, 1981; SKINNER and SMITHERS, 1990).

For years, many authors (for example ELLERMAN, 1941; SIMPSON, 1945; MEESTER and SETZER, 1971; CHALINE and MEIN, 1979; DE GRAAFF, 1981; LAVOCAT and PARENT, 1985; MUSSER and CARLETON, 1993) have debated about the position of this group within the Muroids because of the particular characteristics of their skull and jugal teeth. The description of *Euryotomys pelomyoides* by POCOCK (1976) from the Mio-Pliocene locality of Langebaanweg (West of South Africa) brought evidence of a close relationship with the Murinae. The recently described *E. bolti* (SÉNÉGAS and AVERY, 1998) from the Early Pliocene locality of Waypoint 160 (Bolt's Farm area, Gauteng Province, South Africa) strengthened the hypothesis of a close affinity of otomyine rodents to Murinae, while several molecular investigations support similar conclusions (CHEVRET *et al.*, 1993; WATTS and BAVERSTOCK, 1995; DUCROZ, 1998). With the discovery of *E. bolti* which appears as a clear missing link between *Euryotomys pelomyoides* and the oldest *Otomys* species, it was confirmed (SÉNÉGAS and AVERY, 1998) that the Otomyinae should not be considered a subfamily but rather a tribe of the Murinae, the Otomyini.

The dental patterns of the jugal teeth of the two species of *Euryotomys* are clearly intermediate between the one of the murines and the peculiar one of the otomyines. *Euryotomys pelomyoides* has a less derived dental pattern than the one of *Euryotomys bolti* (fig. 1). *E. pelomyoides* has a Late Miocene or very Early Pliocene age and *E. bolti*, according to its stage of evolution is dated from Early Pliocene. In the former, there is a weak variability of crown morphology contrary to the latter. The most important characteristics of *E. bolti* are the weak development or the absence of the accessory cusps t1 and t3 on the second and third upper molars and the posterior cingulum (pc) on the first and second lower molars; the laminated pattern is also more developed, and the number of laminae of the third upper molar is variable (fig. 2). If DENYS (1990) has correctly emphasized the fact that there are few lineages of rodents recognized in South Africa, *Euryotomys* and the modern Otomyini nevertheless illustrate one good example of such a lineage. Basically, in murine jugal teeth, cusps are linked together by more or less developed transverse ridges but one can still observe the trace of the murine cusps even at pronounced wear stages. Cusps are much less individualized in the two *Euryotomys* species and, in *Otomys* and *Parotomys*, cusps have completely disappeared, the crown only showing transverse laminae.

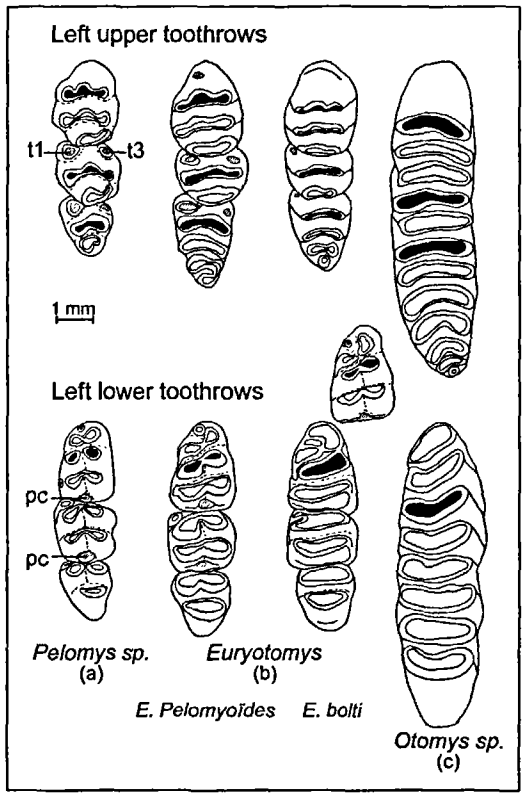


Figure 1
Dental pattern in Murinae (top: upper toothrows, bottom: lower toothrows).
a) cusp pattern of *Pelomys sp.*,
b) intermediate pattern of the two fossil species (*Euryotomys pelomyoides* and *Euryotomys bolti*),
c) laminar pattern of a true Otomyini (*Otomys sp.*)

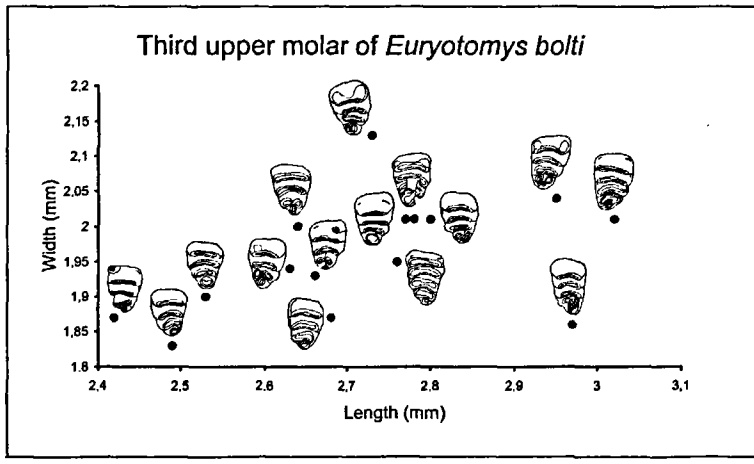


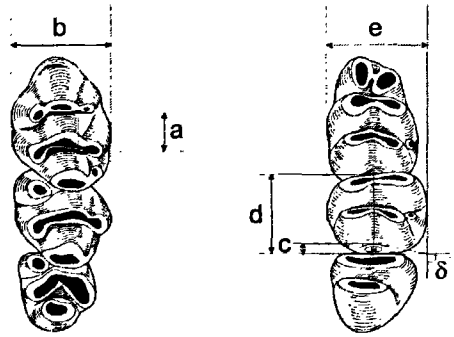
Figure 2
Morphological variability of the third upper molar in *Euryotomys bolti* (Waypoint 160) superimposed on a length and width diagram.

Some transformations of the dental pattern in rodents can be put in relation with an adaptation to a grazing diet, as for instance the development of hypsodonty and lamination (HERSHKOVITZ, 1962). This question has been recently assessed by VAN DAM (1997) for extant and fossil Murinae. This author used a morphometric analysis to describe and compare dental patterns in order to infer if the diet of extinct species involved grazing adaptation. Considering the above, our primary aim was to use such an approach to determine how the dental morphology of the two species of *Euryotomys* bridges the gap between the patterns of some Murinae already adapted to an abrasive diet and the more derived pattern of Otomyini.

Material and methods

An analysis has been conducted following VAN DAM's (1997) morphometric approach. Three indices are calculated to quantify differences in dental patterns for extant and extinct Murinae (fig. 3): 1) b/a: index of relative width of the first upper molar; 2) e/d: index of relative width of the second lower molar; 3) δ: the angle measuring the curvature of the chevrons. This latter index gives at the same time a measure of the degree of development of the posterior cingulum. Such a definition is more appropriate to this work. In VAN DAM's (1997) work, the material was composed by 5 first upper molars and 5 second lower molars for each species. The standardized calculated indices were treated by Principal Component Analysis (PCA). This is a method of graphic representation of the variables (here the indices), where the axes are recalculated in order to express the maximum of variation. In the present analysis, the first component explains more than 80% of the total variation. VAN DAM (1997) precised that this first component is calculated and used as a summary index. The latter analysis indicates that the diminution of relative size of the posterior cingulum associated with the increase of hypsodonty and with the straightening of the chevrons are a good indication of grazing in Murinae.

We are aware that the use of PCA on indices could reduce the amount of information get in processing the raw data. Nevertheless we did so in order to compare our data with those of VAN DAM (1997) who



Index of relative width of the first upper molar: b/a
Index of relative width of the second lower molar: e/d
Angle indicating the degree of development of the posterior cingulum : δ

Figure 3
Representation of the three indices used (e/d, b/a and 2δ) on upper and lower toothrows of *Aethomys sp.* (Murinae), according to Van Dam (1997).

published only indices. We have calculated the three indices for three extinct taxa: *E. pelomyoides*, *E. bolti* and the more recent *Otomys gracilis*. Our sample is as follows: *Euryotomys pelomyoides*, 8 unbroken first upper molars and 12 unbroken second lower molars; *Euryotomys bolti*, 11 unbroken first upper molars and 6 unbroken second lower molars; *Otomys gracilis*, 6 unbroken first upper molars and 5 unbroken second lower molars. A PCA was conducted using the program Statistica v. 4.3 (1993). Henceforth, we adopt the convention by which upper molar is represented by M and lower molar by m.

Results

The main results are summarized in table 1. Only the first principal axis is represented as it explains most of the variation (with the 3 new taxa included, it reaches 90%). In fig. 4, the score of the first principal component for each species is reported from the lowest to the highest. We note an increase of this value from *E. pelomyoides* to

species	locality	e/d	2δ	b/a	PC1
extant:					
Aethomys kaiseri	Wangeregeze Forest, Uganda	0,94	144	2,4	– 0.10
Apodemus mystacinus	Scalita, Turkey	0,96	130	2	– 0.68
Apodemus sylvaticus	Ethe, Belgium	0,94	131	2	– 0.71
Arvicanthis niloticus	Nakuru, Kenya	1,09	157	2,7	0.89
Daysmys incomtus	Chaya, Nr. Ruchuru	1,2	179	2,8	1.81
Grammomys dolichurus	Namaganga Forest, Uganda	0,95	130	2	– 0.71
Hybomys univittatus	Wangeregeze Forest, Uganda	0,97	129	2,5	– 0.28
Lemniscomys striatus	Queen Elizabeth Park, Uganda	1,11	146	2,7	0.69
Lenothrix canus	Kepong, Malaysia	0,88	120	2,2	– 0.99
Oenomys hypoxanthus	Namaganga Forest, Uganda	0,94	135	2,4	– 0.31
Thallomys paedulcus	Stampriet, Namibia	0,96	129	2,1	– 0.62
Thamnomys rutilans	Ghana	0,94	131	2,1	– 0.63
fossil:					
Apodemus gudrunae	Valdecebro 3, Spain	0,89	129	2,1	– 0.83
Huerzelerimys turoliensis	Concud 3, Spain	0,89	134	2,2	– 0.64
Huerzelerimys vireti	Puente Minero, Spain	0,96	137	2	– 0.51
Occitanomys adroveri	Los Mansuetos, Spain	0,99	152	2,5	0.32
Occitanomys alcalai	Valdecebro 3, Spain	0,97	139	2,3	– 0.20
Occitanomys sondaari	Tortajada A, Spain	0,96	142	2,3	– 0.16
Parapodemus barbarae	Los Mansuetos, Spain	0,94	129	2	– 0.76
Parapodemus lugdunensi	Lefkon, Greece (M1) and Crevillente 2, Spain (m2)	0,89	132	1,9	– 0.92
Progonomys cathalai	Masia del Barbo 2B, Spain	0,88	127	2,2	– 0.83
Progonomys hispanicus	Masia del Barbo 2B, Spain	0,93	137	2,2	– 0.45
Stephanomys donnezani	Layna, Spain	1,04	144	2,6	0.36
Stephanomys ramblensis	Valdecebro 3, Spain	1,01	143	2,5	0.17
Euryotomys pelomyoides	Langebaanweg, South Africa	1,17	143,54	2,98	1.03
Euryotomys bolti	Waypoint 160, Bolt's Farm, South Africa	1,35	166,68	3,21	2.29
Otomys gracilis	Bridge Cave, Bolt's Farm, south Africa	1,22	180	3,95	2.78

Table 1
Mean values for the 3 indices (e/d, 2δ and b/a) and their first principal component (PC1) for extant and fossil murines. The Van Dam sample (1997) is composed for each species of 5 M1 and 5 m2. For *Euryotomys pelomyoides* we had 8 M1 and 12 m2, for *E. bolti* 11 M1 and 6 m2 and for *Otomys gracilis* 6 M1 and 5 m2.

E. bolti and *O. gracilis* with the last two ones having the highest values of all the species studied. Such an increase is interpreted as indicating a diet including more and more grazing and we can associate to this changes in the modifications of the dental pattern in the lineage, the loss of accessory cusps and the disappearance of cusps within the laminae. It can be noted that 3 genera of the tribe Arvicanthini (*Dasymys*, *Arvicanthis* and *Lemniscomys*), thought to be the sister group of the Otomyini (DUCROZ, 1998) have also high values for the first component of the PCA.

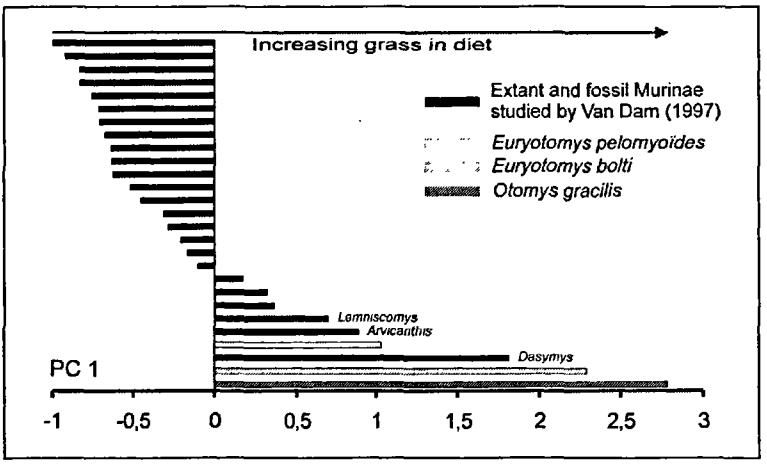


Figure 4
Ranked values of the first principal component of an analysis on the standardized indices (b/a, e/d and 2δ).

Discussion and conclusion

What drives the evolution towards the *Otomys* pattern? A classical interpretation would advocate an environmental determinism: an environment which became more open offered the opportunity to a murine pre-adapted to a relatively abrasive diet to go further in such a direction as it is shown by the above biometric analysis (fig. 4). As several authors have shown, there were some important climatic events in the period considered here. During the Late Miocene, there was a cooling (KENNETT, 1995), a drying and a progressive replacement of C3 by C4 plants (CERLING *et al.*, 1997). This climatic modification could have induced changes in the vegetation and a possible adaptation of the lineage to an abrasive diet through transformations in the dental pattern. Indeed, we know that the adaptation towards a more grazing diet can result at the dental level in several modifications, as observed in different groups of mammals in particular with the development of hypsodonty in ungulates (VRBA, 1978; JANIS, 1988), associated with a lamellar pattern in some small mammals including rodents (JANIS and FORTELIUS, 1988). Chronological data do not

contradict such an hypothesis: Langebaanweg with *Euryotomys pelomyoides* is Late Miocene or Early Pliocene, Waypoint 160 with *E. bolti* is younger but older than Makapansgat Member 1 (about 3.7-3.5 Ma) (PARTRIDGE, 1973; MC FADDEN and BROCK, 1984). Inferred dating based on molecular clock (TAYLOR *et al.*, 1989) indicated that the separation between the Arvicanthini and the Otomyini may have occurred between 8 and 9 Ma (DUCROZ, 1998) or around 7 Ma (CHEVRET *et al.*, 1993) and that the dichotomy (*Parotomys* + *Otomys unisulcatus*)/*Otomys* may have occurred between 5.5 and 6.4 Ma. So the early differentiation of the lineage leading to the Otomyini may have occurred during the Late Miocene. Based on the findings in the two sites of Langebaanweg and Waypoint 160 (Bolt's Farm area), we can also hypothesize that at least at one time, *Euryotomys* was widespread in a large portion of South Africa. Later, some populations could have been restricted to the more arid western part of South Africa. This could have stabilized the morphological variability and led to the group of *Parotomys*. The others, with a wider distribution, could have occupied a more diversified environment and led to the group of *Otomys*. In this case, the wider geographic distribution would have allowed a more important radiation.

We need, of course, more Early Pliocene sites both in West and in East of South Africa to appraise more precisely how this group was distributed during these periods and at what rhythm the dental morphology has changed. We also need more specimens for the different species considered in order to solve the problem of small sample sizes and intraspecific variability. We are now completing the sample for recent material; as for extinct material, we depend on the discovery of new fossils. We also lack fossil *Parotomys*. But the hypothesis we propose could be a basis of work to explain how the group of Otomyini has differentiated.

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Craniometric relationships between the Southern African Vlei rat, *Otomys irroratus* (Rodentia, Muridae, Otomyinae) and allied species from North of the Zambezi River

Peter J. Taylor

Albert Kumirai

Introduction

Fourteen species and two genera (*Parotomys* Thomas 1918 – two species, and *Otomys* Cuvier 1823 – 12 species) of laminate-toothed rats (Family Muridae; Subfamily Otomyinae) are currently recognized in Africa, although probably more unrecognized species occur as endemics associated with the isolated East African highlands and volcanoes (MUSSER and CARLETON, 1993). While the two recognized species of *Parotomys* are restricted to the arid and semi-arid regions of southern Africa, the genus *Otomys* includes 64 previously described forms, mostly tied to moist or montane habitats, and discontinuously distributed from the Cape to Mount Cameroun in the West and Ethiopia in the East (DENYS, 1989). Most species of *Otomys* have a uniform

vole-like external appearance, with shaggy, dark-brown pelage, and short tail, making taxonomic determination difficult. Moreover, the taxonomy of the group is highly unstable due to variability in diagnostic characters, usually involving the number of laminae in M^3 and M_1, grooving of the incisors, shape of the nasal bone and shape of the petrotympanic foramen (ALLEN and LOVERIDGE, 1933; BOHMANN, 1952; DE GRAAFF, 1981; DIETERLEN and VAN DER STRAETEN, 1992; LAWRENCE and LOVERIDGE, 1953; MEESTER *et al.*, 1986; MISONNE, 1974; THOMAS, 1918).

While species of southern African *Otomys* can for the most part be objectively delimited on morphological, cytogenetic and biochemical grounds (CONTRAFATTO *et al.*, 1992a-c; MEESTER *et al.*, 1992; TAYLOR *et al.*, 1993), the same is not true for West, East and central African taxa (MUSSER and CARLETON, 1993). Critical to delimiting the final number of extant species of *Otomys* is resolving the species and geographical limits of a key southern African species, *O. irroratus* Brants 1827, in relation to several East and West African forms that have in the past been included in this species. PETTER (1982) included *anchietae* Bocage 1882 (which includes *occidentalis* Dieterlen and Van der Straeten 1992, *lacustris* Allen and Loveridge 1933, *barbouri* Lawrence and Loveridge 1953), *tropicalis* Thomas 1902, *typus* Heuglin 1877 and *laminatus* Thomas and Schwann 1905 within a highly polymorphic and widely distributed *O. irroratus* species-complex or "rassenkreis". MISONNE (1974) considered *tropicalis* and *irroratus* together as being possibly conspecific, but distinct from the other above-mentioned species. DIETERLEN and VAN DER STRAETEN (1992), although describing West African *occidentalis* as a distinct species allied to the "*anchietae* group", nevertheless retained *tropicalis* as a synonym of *irroratus*. These authors further recognized *lacustris* (from East Africa) and *barbouri* (from Mount Elgon) to be distinct from *anchietae* (from Angola). Members of the "*anchietae* group" (*anchietae*, *lacustris*, *barbouri* and *occidentalis*) are characterized by having five laminae in M_1, as opposed to four or less in other species (with the exception of *O. laminatus* which has 7). While recognizing *occidentalis* to be a good species, MUSSER and CARLETON (1993) retained *lacustris* and *barbouri* in *anchietae*. Based on allozyme and cytogenetic evidence, LAVRENCHENKO *et al.* (1997) suspected that two distinct species should be recognized within *O.* cf. *typus* from the Bale Mountains in Ethiopia.

This paper addresses questions of conspecificity between *O. irroratus* and allied forms, and among members of the "*anchietae* group", using both principal component analysis and discriminant functions analysis based on craniometric data. Since not all the relevant types have been included here (see Appendix), this study is not a final systematic revision of the group in question but rather an evaluation of craniometric relationships which should facilitate a complete systematic revision in the near future. We summarize patterns of variation in dental and cranial diagnostic characters across the subfamily Otomyinae, in order to integrate qualitative and quantitative data. THOMAS (1918) suggested that skull shape would be a more useful feature for separating species of *Otomys* than highly variable key characters such as laminae number. While the present study uses a "traditional" craniometric approach based on linear measurements, further studies in progress are investigating cranial shape relationships between otomyine rodents based on the more recent approach of geometric morphometrics (TAYLOR, KUMIRAI and CONTRAFATTO, unpubl. data).

Materials and methods

Material examined

Quantitative and qualitative cranial measurements were obtained for 285 specimens from all currently recognized species of otomyine rodents except *O. maximus* Roberts 1924 which is not recognized by some authors (e.g., MISONNE, 1974; MEESTER *et al.*, 1986). Skulls were loaned from the following institutions: Amathole Museum (King William's Town), Durban Natural Science Museum, Museum National d'Histoire Naturelle (Paris), and the Natural History Museum (London). Additionally, descriptions and measurements of type specimens of certain species were obtained from the literature, e.g. *O. occidentalis* (DIETERLEN and VAN DER STRAETEN, 1992; type from Staatliches Museum für Naturkunde, Stuttgart - SMNS), *O. lacustris* (ALLEN and LOVERIDGE, 1933; type from Museum of Comparative Zoology, Harvard - MCZ) and *O. barbouri* (LAWRENCE and

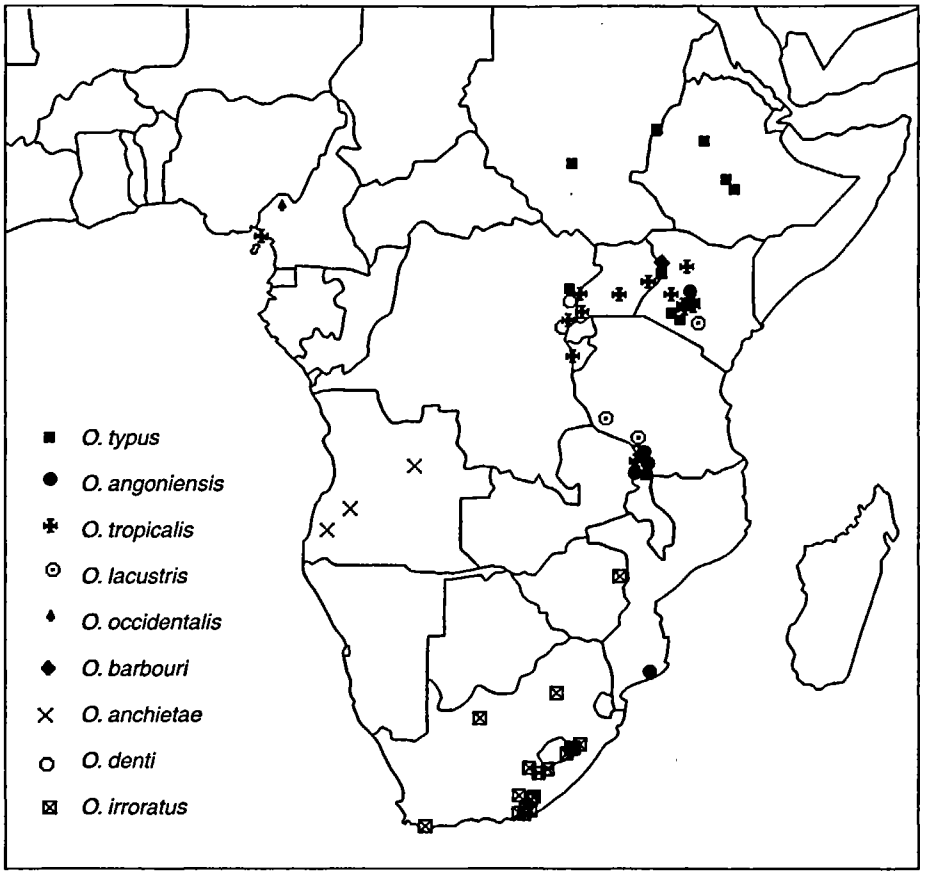

Figure 1
Map of Africa south of Sahara showing distribution of *Otomys irroratus* and related congeneric species occurring north of the Zambezi River, based on material examined.

LOVERIDGE, 1953; type from MCZ). The sample of *O. irroratus* ($n = 105$) was a representative subset of adult skulls (age class 4 and 5) from a larger sample used to analyse morphometric variation within this species (KUMIRAI, unpubl. data). The Appendix provides both a gazetteer of localities and a summary of material examined for each species. Fig. 1 shows the distribution of localities representing material examined for the several species of *Otomys* which were subjected to morphometric analysis, as outlined below.

Qualitative and quantitative measurements

The following qualitative cranial key characters were scored on 285 skulls representing 13 species of *Otomys*:

1) Number of laminae in M^3

2) Number of laminae in M_1

3) Angle of lateral edge of nasal bone at its point of anteriormost expansion – this was scored subjectively as being closest to 90°, 120° or 150°

4) Shape of petrotympanic foramen - slit-like or round

5) Grooving on lower incisors - absent (0), single groove (1), single groove with trace of second (1'), one deep and one faint groove (1+), or two deep grooves (2)

Using Mitutoyo digital calipers with 0.01 mm accuracy, twelve quantitative cranial measurements were taken on the same sample of skulls as mentioned above; however only data from seven species are analysed in the present study, representing southern African *O. irroratus* and extralimital species which have in the past been included in this species. Measurement details are as follows (based on TAYLOR *et al.*, 1993):

GLS - Greatest length of skull measured dorsally (A-B, fig. 2)

PL - Palatal length, from anterior edge of premaxillae to anteriormost point on posterior edge of palate (G-W, fig. 2)

APF - maximum length of anterior palatal foramen (Q-R, fig. 2)

NAW - Nasal width, greatest width across nasals (J-K, fig. 2)

ZYW - Zygomatic width, greatest distance between the outer margins of the zygomatic arches (E-F, fig. 2)

IOC - Interorbital constriction, least distance dorsally between the orbits (C, fig. 2)

BUL - Greatest length of bulla along the longitudinal axis (D, fig. 2)

BUW - Bulla diameter, greatest width of bulla at right angles to main axis of skull (H, fig. 2)

MXTRL - Maxillary tooth row length, distance from anterior edge of first maxillary tooth to posterior edge of last maxillary tooth (I-M, fig. 2)

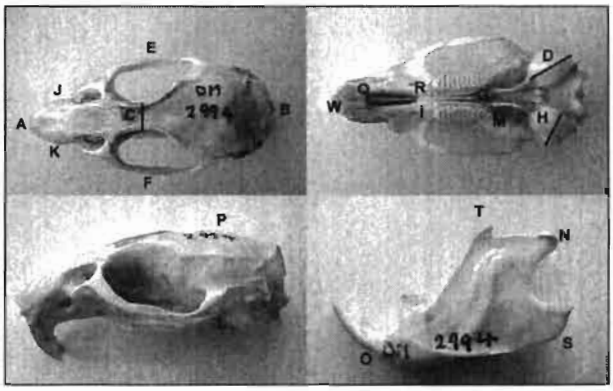

Figure 2
Skull of *Otomys* indicating reference points of 12 cranial variables measured from morphometric analysis. See text for descriptions.

BCD - Depth of braincase measured vertically at basioccipital (L-P, fig. 2)

GLM - Mandible length, greatest length of the mandible excluding teeth (N-O, fig. 2)

MDH - Mandible height from ventral surface of mandibular ramus to dorsal surface of coronoid process (S-T, fig. 2)

Age variation

Every skull was assigned to a relative age class based on skull size and shape, suture development and tooth wear as follows (after Taylor *et al.* 1993, fig. 3):

Class 1: Occlusal surface of maxillary tooth row sloping in lateral view (higher at M^1 than M^3), lamellae separate; braincase pear-shaped, smooth; tooth wear minimal, with dentine not exposed across full labio-lingual width of molars; fronto-parietal, naso-frontal, naso-maxillary, parieto-interparietal and interparieto-occipital sutures open, distinct; skull conspicuously small (condylobasal length < 30 mm).

Class 2: Occlusal surface of maxillary tooth row as above in lateral view, although one or two anterior lamellae may not be completely separated; braincase oval, interorbital region smooth or slightly ridged; tooth wear either as above, or dentine may be exposed across full labio-lingual width of molars; sutures open; skull noticeably larger (condylobasal length > 30 mm).

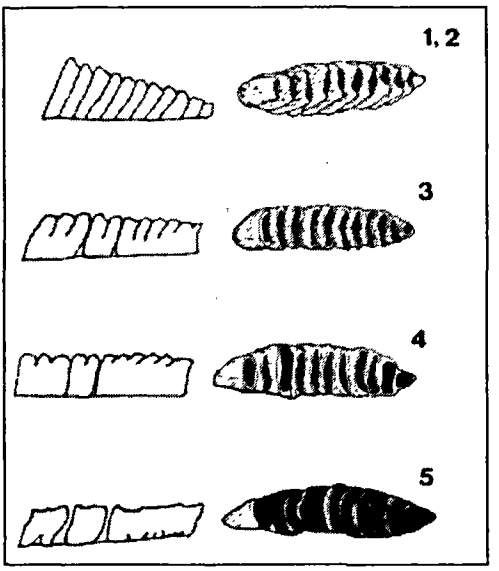

Figure 3
Diagrammatic representation of lateral (left) and occlusal (right) views of upper toothrows of five recognized age classes of *Otomys*. See text for description of toothwear criteria for each class.

Class 3: Occlusal surface of maxillary tooth row almost horizontal in lateral view, molars clearly defined in lateral view but with lamellae of individual molars not fully separated (i.e. divisions extending to over half of the distance from the crown to the cingulum); braincase oval and conspicuously ridged with interorbital and occipital ridges; tooth wear moderate with dentine exposed across full occlusal width of molars, but with enamel faces of lamellae still visible in occlusal view; sutures distinct or becoming indistinct.

Class 4: Occlusal surface of maxillary tooth row horizontal in lateral view, divisions between lamellae extending only to less than half the distance from the crown to the cingulum; braincase oval, sharply ridged; toothwear moderate, with enamel faces of lamellae no longer clearly visible in occlusal view; sutures indistinct.

Class 5: Occlusal surface of maxillary tooth row horizontal, crown-cingulum height much reduced, lamellar divisions no longer visible in lateral view; braincase oval, very strongly ridged; tooth wear severe, with flat occlusal surface composed of exposed dentine and thin transverse enamel bridges, enamel side walls eroded; sutures indistinct or not visible.

Statistical analysis

Due to the broken nature of many skulls and the small sample sizes available for some of the more rarely collected species, principal component analysis of *O. irroratus* and six related East and West African forms (*anchietae*, *lacustris*, *barbouri*, *occidentalis*, *typus* and *tropicalis*) was performed using only five robust, functionally important and commonly used cranial variables: GLS, NAW, IOC, MXTRL and BUL. Nevertheless, for two-group discriminant analyses involving combinations of the above-mentioned species, in which statistical re-sampling was performed (n = 100 randomizations), 12 or 10 variables were included wherever sample sizes permitted. Multivariate craniometric analysis was restricted only to *O. irroratus* and the six species or forms which have in the past been included in this species.

For most of the species, small sample sizes prohibited detailed non-geographic analysis to investigate the effects of variation due to age and sexual dimorphism. However, a separate study of *O. irroratus* in the Western Cape Province of South Africa (TAYLOR *et al.*, 1993) revealed that, although males tend to have larger crania than females, these differences were generally non-significant, while age classes 3-5 could be considered "adult". Thus, in the present study, males and females were combined and age classes 1 and 2 were not considered for statistical analyses.

Complete discussions of multivariate procedures used in this study can be found in BLACKITH and REYMENT (1971), SNEATH and SOKAL (1973), PIMENTEL (1979), and NEFF and MARCUS (1980). Principal component analysis was performed using NTSYSpc Version 2.01h (ROHLF, 1997). Two-group discriminant analysis, with statistical re-sampling (n = 100 replications), was performed using the programme LINDA (LINear Discriminant Analysis) and Comparison of Multivariate Samples with Randomization Tests, version 5.12; CAVALCANTI, 1999). Hotelling's T-squared, and Wilks Lambda coefficients were calculated, and variance-ratio (F) tests and chi-squared tests respectively were used to test for significant differences between mean vectors.

Results and discussion

Qualitative characters

Table 1 summarises variation in dental and cranial key characters, based on the sample of 285 individuals. The number of laminae in M_1 varied from 3-4 (*Parotomys*) to 7 (*O. laminatus*), but was generally 4, with the exception of members of the "*anchietae* group" which typically have 5 (although this number varied from 4 to 6 in *anchietae*, and a single *O. barbouri* was found to have 4). Laminae number in M^3 varied from 4 (*Parotomys*) to 10 (*O. laminatus*), but was highly variable in both the "*anchietae* group" and *O. typus*. Within the "*anchietae* group", the modal number varied from 6 (*lacustris*) to 7 (*anchietae, barbouri*) to 8 (*occidentalis*), suggesting that this character might prove useful in the future for separating these forms. Within *O. typus* the number of laminae in M^3 appeared to vary geographically, with 6 laminae being recorded from Uganda, 7 from Kenya and Malawi, and 8 or 9 from Ethiopia. In a sample of *O.* cf. *typus* analysed from Bale Mountains in Ethiopia, LAVRENCHENKO *et al.* (1997) noted 6 laminae in M^3 of "*Otomys* sp. A" with a diploid chromosome number of 56, but 7-8 laminae in M^3 of "*Otomys* sp. B" (2n = 57 – 58).

DENYS (1989) surmised that a relatively low number of 5-6 laminae in M^3 was present in ancestral *Otomys* species, as evidenced by the extinct *O. gracilis* in South Africa (from 1-3.5 Myr deposits), and extinct *O. petteri* from East Africa (from 0.6 - 2 Myr deposits), with a subsequent trend towards an increasing number of laminae in time reflected in extant species. On the basis of a relatively low number of laminae (6), DENYS (1989) assumed *O. saundersiae* Roberts 1929 to be primitive to other extant species of this genus, while "*irroratus - tropicalis*" was said to have 7-8 laminae. Tabl. 2 shows that, while *O. tropicalis* has either 7 (73 individuals) or 8 (10 individuals) laminae, *O. irroratus* invariably possesses 6 (115 out of 116 individuals). Thus, M^3 laminae number appears to provide strong evidence for specific separation between *O. irroratus* and *O. tropicalis*, and *O. irroratus* appears more primitive than presumed by DENYS (1989).

The angle at which the anterior portion of the nasal joins the posterior is highly variable. In most species of *Otomys* the angle is close

	No. of laminae in lower M1					No. of laminae in upper M3							Nasal angle			Petrotympanic		No. grooves in lower incisor				
	3	4	5	6	7	4	5	6	7	8	9	10	90°	120°	150°	Hole	Slit	0	1	1'	1+	2
O. anchietae	-	1	2	4	-	-	-	1	4	1	-	-	-	6	-	5	-	-	4	1	-	-
**O. barbouri*	-	1	7	-	-	-	-	-	6	2	-	-	7	1	-	8	-	-	8	-	-	-
**O. lacustris*	-	-	4	-	-	-	-	3	1	-	-	-	1	3	-	4	-	-	4	-	-	-
O. occidentalis	-	-	7	-	-	-	-	-	2	5	-	-	-	-	-	-	-	-	6	-	-	-
O. angoniensis	-	10	-	-	-	-	-	2	8	-	-	-	3	4	3	-	6	-	-	5	1	-
O. denti	-	2	-	-	-	-	1	1	-	-	-	-	-	2	-	2	-	-	1	1	-	-
O. tropicalis	-	84	-	-	-	-	-	-	73	10	-	-	8	61	14	72	-	-	5	60	11	-
O. typus	-	38	-	-	-	-	-	4	9	15	10	-	32	6	-	36	-	-	-	1	-	28
O. irroratus	-	116	-	-	-	-	-	115	1	-	-	-	74	36	-	116	-	-	-	11	1	-
O. laminatus	-	-	-	-	1	-	-	-	-	-	-	1	1	-	-	1	-	-	-	1	-	-
O. saundersiae karoensis	-	5	-	-	-	-	-	5	-	-	-	-	-	5	-	5	-	-	1	4	-	-
O. unisulcatus	-	2	-	-	-	-	2	-	-	-	-	-	-	-	2	2	-	2	-	-	-	-
O. sloggetti	-	2	-	-	-	1	1	-	-	-	-	-	-	-	2	-	1	2	-	-	-	-
P. brantsii	-	2	-	-	-	3	-	-	-	-	-	-	-	-	3	-	-	1	1	-	-	-
P. littledalei	1	-	-	-	-	1	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-
O. gracilis (E)	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
O. petteri (E)	-	x	-	-	-	-	4%	90%	5%	-	-	-	-	-	-	-	-	-	-	x	-	-

Table 1
Table showing variation of craniodental qualitative characters in laminate-toothed rats of the genera *Otomys* and *Parotomys*, based on specimens examined (Appendix), and from Denys (1989) for the extinct (E) species. Forms marked with asterisks are currently included in the species, *O. anchietae*.

Variable	Species						
	O. irroratus (n=105)	*O. tropicalis* (n=52)	*O. typus* (n=19)	*O. anchietae* (n=5)	**O. barbouri* (n=8)	**O. lacustris* (n=3)	*O. occidentalis* (n=4)
GLS	41.0 ± 2.5 32.6 - 45.9	39.0 ± 2.7 29.0 - 43.5	39.1 ± 3.2 34.3 - 45.9	49.4 ± 3.1 46.2 - 52.8	36.6 ± 2.2 32.4 - 39.0	38.6 ± 1.6 36.8 - 39.9	34.9 ±1.9 32.7 - 36.9
BCD	12.1 ± 0.8 9.5 - 14.0	11.2 ± 0.6 9.2 - 12.4	11.4 ± 0.7 10.5 - 13.1	15.4 ± 1.1 14.6 - 16.6	11.3 ± 0.6 10.5 - 11.8	— (n=2) 10.8 - 12.0	— (n=1) 9.7
MDH	14.8 ± 1.2 10.6 - 17.6	13.5 ± 1.1 9.2 - 16.9	14.0 ±1.3 (25) 12.2 - 16.4	20.0 ± 0.9 (4) 18.9 - 20.9	12.8 ± 0.7 (5) 11.8 - 13.5	— (n=1) 14.6	— (n=1) 10.8
GLM	27.2 ± 2.1 21.7 - 31.5	24.9 ±1.5 20.5 - 28.7	25.6 ± 2.2 22.0 - 30.2	34.4 ± 2.5 31.8 - 37.5	24.4 ± 1.7 21.2 - 27.0	24.6 ± 2.0 22.3 - 25.8	— (n=1) 21.9
APF	7.6 ± 0.8 5.4 - 9.0	6.9 ±0.7 4.5 - 8.4	7.2 ± 0.7 5.8 - 8.6	8.4 ± 0.8 7.3 - 9.3	7.0 ± 0.6 5.9 - 7.7	7.3 ± 0.5 6.6 - 7.9	— (n=2) 5.7 - 6.9
MXTRL	9.7 ± 0.5 8.5 - 11.5	9.2 ± 0.4 8.4 - 10.4	9.6 ±1.0 8.1 - 11.6	12.0 ± 0.5 11.3 - 12.5	8.9 ± 0.2 8.6 - 9.3	8.8 ± 0.3 8.6 - 9.1	8.8 ± 0.5 8.4 - 9.6
NAW	8.0 ± 0.7 6.2 - 9.9	7.0 ± 0.6 4.8 - 7.9	7.0 ± 0.8 6.2 - 9.2	8.8 ± 0.6 8.1 - 9.6	6.6 ± 0.5 5.7 - 7.3	6.5 ± 0.4 6.0 - 6.8	6.2 ±0.2 6.0 - 6.6
IOC	4.6 ±0.2 4.1 - 5.1	4.5 ± 0.2 4.1 - 5.0	4.1 ± 0.3 3.7 - 4.7	5.5 ± 0.4 5.0 - 5.9	4.2 ± 0.3 3.6 - 4.6	4.3 ± 0.1 4.2 - 4.4	4.3 ±0.2 4.1 - 4.4
ZYW	20.5 ± 2.5 (n = 104) 16.8 - 24.1	19.0 ± 1.1 15.0 - 21.8	19.4 ± 1.7 (27) 15.8 - 22.8	26.5 ± 1.5 (4) 25.0 - 28.0	18.5 ±1.0 (10) 16.5 -19.7	— (n=1) 18.9	— (n=1) 17.5
PL	22.8 ± 1.8 18.1 - 27.6	20.7 ± 1.5 15.3 - 24.4	20.8 ± 1.9 17.4 - 24.9	27.1 ± 2.0 25.0 - 29.2	19.6 ± 1.7 16.7 - 21.7	20.2 ± 1.2 18.4 - 21.0	— (n=2) 18.2 - 18.7
BUL	7.0 ± 0.5 5.9 - 8.7	7.6 ± 0.5 6.5 - 9.7	7.6 ± 0.6 6.8 - 8.5	8.8 ± 0.6 7.9 - 9.3	6.7 ± 0.3 6.1 - 7.1	7.0 ± 0.8 6.6 - 7.9	7.1 ± 0.7 6.1 - 7.5
BUW	6.9 ± 0.5 5.8 - 8.4	7.5 ± 0.7 5.5 - 8.8	8.0 ± 0.6 6.8 - 8.9	10.1 ± 0.6 9.2 - 10.9	7.2 ± 0.6 6.1 - 8.0	— (n=2) 7.1 - 8.2	– (n=2) 6.2 - 6.6

Table 2
Summary statistics for craniometric variables in seven species of *Otomys*.
Values represent means ± standard deviation, followed by minimum and maximum values.
Forms marked with asterisks are currently included in the species *O. anchietae*.
Where sample size varies from the value shown under each species name, this is indicated in parentheses.

to 90° or 120°. However, this angle is more obtuse (150°) in species of *Parotomys*, and in *O. unisulcatus* Cuvier 1829, *O. sloggetti* Thomas 1902, and *O. saundersiae karoensis*. In 17% of *O. tropicalis*, the nasal angle is 150°, while the modal character state for this species is 120°, as opposed to 90° in *O. irroratus*, providing further support for specific separation of these two species (tabl. 2). DIETERLEN and VAN DER STRAETEN (1992) distinguished *O. occidentalis*, *barbouri* and *lacustris* from "*irroratus*" (= *tropicalis*), based on a more obtuse nasal angle in the latter.

The shape of the petrotympanic foramen is less variable than dental characters and nasal angle, being slit-like in *O. angoniensis* and *O. sloggetti* and consistently round in all other species.

Grooving of lower incisors is absent in *Parotomys* and two species of *Otomys*, *O. unisulcatus* and *O. sloggetti*. Cladistic analyses of allozyme (TAYLOR *et al.*, 1989) and immunoblot data (CONTRAFATTO *et al.*, 1994) provide further support for this clade, and hence for the paraphyly of the genus *Otomys* as currently understood. The presence of two distinct grooves in the lower incisors is diagnostic for *O. typus*. In the present study, this character was relatively consistent, although one individual classified as *O. typus* had an indistinct second groove. Members of the *O. anchietae* group are distinctive in showing generally no trace of a second groove in the lower incisor, a key feature normally used in the identification of *O. denti* Thomas 1906 (MISONNE, 1974), but found in only one of two individuals of *O. denti* examined here (tabl. 1).

Multivariate analysis of craniometric characters

Based on principal component analysis of five cranial variables (fig. 4), the large-skulled *O. anchietae* (see tabl. 2) separates completely from all other species, including other much smaller members of the "*anchietae*-group", *barbouri*, *lacustris* and *occidentalis*. *Otomys irroratus* shows limited or no overlap with the other species with which it has previously been included. Based on variable loadings on each of the

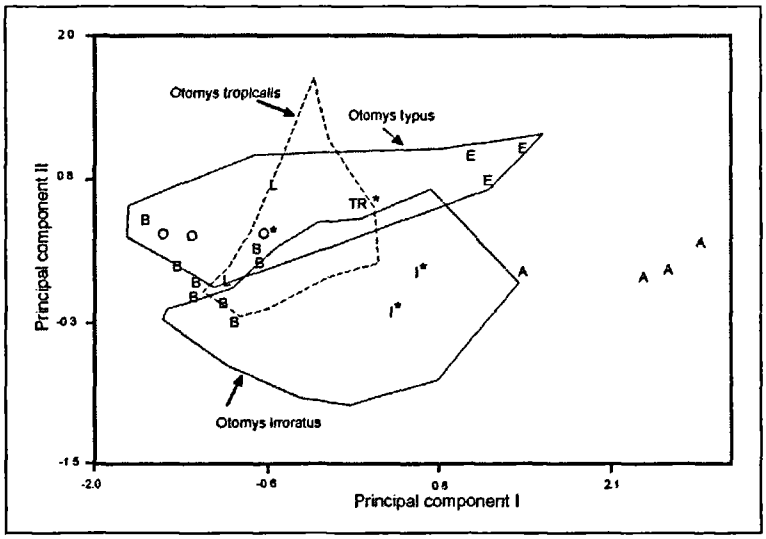

Figure 4
Principal component analysis of five cranial variables in 181 specimens representing seven species of *Otomys*. The first component explained 57.9% of variation, the second 19.2%. Polygons enclose all individuals within the three large species-samples, *O. irroratus*, *O. tropicalis* and *O. typus*. Type specimens of *O. irroratus coensis* from Kuruman, South Africa (I), *O. tropicalis* from Mount Kenya (TR), and *O. occidentalis* from Mount Oku, Cameroon (measurements from literature) are indicated by asterisks. Individuals of the 5-laminate forms are indicated as "A" (*anchietae*), "B" (*barbouri*), "L" (*lacustris*), and "O" (*occidentalis*). Outlying (large) specimens of *O. typus* from Lake Tana in Ethiopia are indicated by "E".

first three principal components (tabl. 3), which cumulatively explain 91.5% of the variation, the first component is influenced by overall size (positive high loadings for all variables), while the second component is a "shape axis" contrasting bulla length with nasal and interorbital widths (high scores represent individuals having relatively inflated bulla and narrow nasals and interorbital region). The third component contrasts interorbital constriction (negative) with nasal width; since it explains only 14.4% of the variation, it is not regarded further. Clearly, *O. irroratus* is distinguished mostly from its allies on the basis of the second principal component, in having proportionately

Variable	PC 1	PC 2	PC 3
Greatest skull length (GLS)	0.93	0.06	0.14
Maxillary toothrow length (MXTRL)	0.89	0.07	0.14
Nasal width (NAW)	0.83	-0.30	0.33
Interorbital constriction (IOC)	0.54	-0.47	-0.69
Bulla length (BUL)	0.50	0.80	-0.30

Table 3
Standardized coefficients from five-variable, principal components analysis of seven species of laminate-toothed rats, *Otomys*. The first three components explained 57.9%, 19.2% and 14.4% respectively of the total variation.

smaller bullae and wider nasals and interorbital region. The extreme range in size variation (first component) in *O. typus* is due to the presence of three outlying, large specimens from Lake Tana in Ethiopia (marked as "E" in fig. 2). As noted above, Ethiopian specimens typically have nine laminae in M^3, as opposed to 6 to 8 further south, confirming the observation of larger size. It is likely that this species probably represents a composite of two or more species. Generally, individuals of this species plot towards the left of the first component (small skulls) and higher on the second component (larger bullae and narrower nasals and interorbital region).

Two-group discriminant analyses involving the same species as mentioned above generally resulted in limited overlap (low percentage of misclassifications) and significant differences between species mean vectors (based on both Hotelling's T-squared and Wilk's Lamda tests) (tabl. 4).

A 12-variable discriminant analysis of *O. irroratus* and *O. tropicalis* resulted in misclassification of 15.4% of *O. irroratus* and only 3.8% of *O. tropicalis*. The three variables showing the greatest percentage contribution to the total multivariate distance (i.e. greatest relative importance) were palatal length (38%), and bulla length (32%) and width (13%). From summary data (tabl. 2), *O. tropicalis* tends to be slightly smaller than *O. irroratus* in most cranial dimensions but to have disproportionately larger bullae and a disproportionately shortened palate.

Species	Number of variables	Hotelling T-squared	Wilks Lambda	% mis-classified	Variables contributing strongly (> 20% contribution)
irroratus (n = 105) vs. *tropicalis* (n = 52)	12	259.9**	0.37**	15.4; 3.8	PL, BUL
irroratus (n = 105) vs. *typus* (n = 19)	10	237.8**	0.34**	2.9; 5.3	BUW, PL, IOC
irroratus (n = 105) vs. *anchietae* (n = 5)	10	382.7**	0.22**	0.0; 0.0	BUW, GLM, MXTRL
irroratus (n = 105) vs. *barbouri* (n = 8)	10	102.9**	0.52**	1.9; 0.0	GLS, NAW
anchietae (n = 5) vs. *occidentalis* (n = 4)	5	102.2	0.06*	0.0; 0.0	MXTRL, NAW
anchietae (n = 5) vs. *barbouri* (n = 8)	10	1903*	0.01**	0.0;0.0	GLS, GLM
occidentalis (n = 4) vs. *barbouri* (n = 12)	5	10.8	0.56	25.0; 16.7	BUL, NAW
barbouri (n = 12) vs. *lacustris* (n = 3)	5	28.2*	0.32*	0.0; 0.0	GLS
tropicalis (n = 52) vs. *typus* (n = 19)	10	65.9**	0.51**	11.5; 21.1	IOC, APF

Table 4
Results of selected two-group discriminant analyses, with re-sampling (*n* = 100 randomizations), to test conspecificity between *O. irroratus* and related species-groups, and between members of the "*anchietae* - group". Asterisks indicate statistical significance (** – $p < 0.01$; * – $p < 0.05$)) of Hotelling T-squared and Wilks Lambda coefficients based on variance ratio (F) and Chi-squared tests respectively.

A 10-variable discriminant analysis of *O. irroratus* and *O. typus* resulted in misclassification of 2.9% of *O. irroratus* and 5.3% of *O. typus* (tabl. 4). Bulla width contributed most strongly to this separation (41%), followed by palatal length (26.2%) and interorbital constriction (25.7%). As also reported for *O. tropicalis*, *O. typus* has a cranium which is smaller in overall size compared to *O. irroratus*, but with disproportionately inflated bullae and shortened palate (tabl. 2). As would be predicted from the above, *O. tropicalis* and

O. typus show greater morphometric overlap (11.5% of *O. tropicalis* and 21.1% of *O. typus* misclassified) than when either species is compared with *O. irroratus*. However, craniometric differences between these two species are still significantly different in multivariate space (tabl. 4).

As was evidenced from the principal component analysis (fig. 2), the much larger (tabl. 2) *O. anchietae* separates clearly in two-group discriminant analysis from both *O. irroratus* (0% misclassified), as well as additional forms previously included in the "*anchietae*-group" such as *O. occidentalis* and *O. barbouri* (0% misclassified; tabl. 4). Greater morphometric overlap occurs between the smaller members of the "*anchietae*-group" (*barbouri, lacustris, occidentalis*). For example, differences between mean vectors of *O. occidentalis* and *O. barbouri* are not statistically significant ($p > 0.05$), and 18.8% of individuals are misclassified.

Conclusions

The hypothesis put forward by PETTER (1982), that *O. irroratus* comprises a highly polymorphic species with Pan African distribution, including the forms *anchietae, occidentalis, lacustris, barbouri, tropicalis*, and *typus*, can be refuted based on the craniometric results presented here. *Otomys irroratus* can be reliably separated from all of the above East and West African forms, using discriminant analysis of cranial variables. Furthermore, in spite of the plasticity of some cranial and dental qualitative characters, *O. irroratus* can be convincingly separated from *O. tropicalis* based on the consistent occurrence of 6 laminae in M^3 in *O. irroratus*, as opposed to 7 or 8 in *O. tropicalis*, as well as by the acute angle of the nasal bone in *O. irroratus*, compared to a much less acute angle in *O. tropicalis* (see also THOMAS, 1918). *Otomys typus* can be clearly separated from all other species, including *O. irroratus*, due to the unique and consistent presence of two grooves in the upper incisor (present in 28 out of 29 skulls examined), thus validating the usefulness of this key character for this species.

The situation regarding the 5-laminate-M_1 "*anchietae* - group" (*anchietae*, *barbouri*, *occidentalis* and *lacustris*) is less clearcut. While *anchietae* from Angola separates very clearly from all other otomyines in its much larger cranial size (GLS > 46 mm), the smaller forms (hereafter termed "*lacustris* - group") show varying degrees of morphometric overlap. These forms tend to be restricted to isolated mountain chains, e.g. *occidentalis* to the Gotel Mts and mont Oku in West Africa, *O. barbouri* to Mount Elgon in Uganda/Kenya, and *O. lacustris* to the Uzungwe Mts, Ukinga Mts, Ufipa Plateau and Poroto Mts in Tanzania, and the Aberdare Range in Kenya. Based on the information presented above, and given the disjunct nature of the distribution of these taxa, it is best to follow the example of VAN DER STRAETEN and DIETERLEN (1992), and to recognize *anchietae*, *barbouri*, *lacustris* and *occidentalis* as full species pending a thorough review.

Further studies including all the relevant type specimens, and using morphometric, cytogenetic and molecular characters, are required before the correct number of species of *Otomys* can be finally established. Cytogenetic, biochemical or molecular data are available for *O. barbouri*, *O. tropicalis*, and *O. typus* from Mount Elgon (TAYLOR, KUMIRAI, CONTRAFATTO and CAMPBELL, unpubl. data), *O. typus* from Ethiopia (LAVRENCHENKO *et al.*, 1997), and many of the southern African otomyine taxa (CONTRAFATTO *et al.*, 1992a-c; MEESTER *et al.*, 1992; RAMBAU *et al.*, 1997; ROBINSON and ELDER, 1987; S. MAREE in litt.), but are urgently required for most species occurring north of the Zambesi River.

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Appendix

Gazetteer of localities and summary of material examined from nine species of *Otomys*. Type localities are indicated; in most case type specimens were examined in the collection of the Natural History Museum, London. Location, descriptions and/or measurements of type specimens of *O. occidentalis*, *O. lacustris* and *O. barbouri* were obtained from the literature (DIETERLEN and VAN DER STRAETEN, 1992; ALLEN and LOVERIDGE, 1933; and LAWRENCE and LOVERIDGE 1953, respectively). Acronyms for museums are explained in the text. Acronyms for South African province names as follows: ECP (Eastern Cape), GTP (Gauteng), KZN (KwaZulu-Natal), NWP (Northwest).

Species	Locality	Coordinates	Specimens examined
Otomys anchietae	Angola: Alto Chicapa	10° 56'S 19° 12'E	BM (5)
Otomys anchietae	Angola: Caconda (TYPE)	13° 42; S 15° 03'E	? Not seen
Otomys anchietae	Angola: Huila (incl. P. Campana?)	15° 06'S 13° 33'E	MNHN (2)
Otomys angoniensis	Kenya: Menengai (East) – 2333 m	0° 12'S 36° 46'E	MNHN (3)
Otomys angoniensis	Malawi: Nthungwa	11° 42'S 33° 50'E	BM (1)
Otomys angoniensis nyikae	Malawi: Nyika Plateau (TYPE)	10° 6'S 33° 42'E	BM (1)
Otomys angoniensis	Malawi: Matipa Forest, 2100 m (= M'Kombhuie) (TYPE)	9° 39'S 33° 26'E	BM (2)
Otomys angoniensis rowleyi	Mozambique: « Coguus » (= Coguna), Inhambane (TYPE)	24° 23'S 34° 32'E	BM (1)
Otomys barbouri	Uganda: Kaburomi, Mt Elgon, 3150 m (TYPE)	1° 14'N 34° 31'E	MCZ—not seen
Otomys barbouri	Uganda: Mount Elgon: Mission Delomo	1° 10'N 34° 29'E	MNHN (8)
Otomys barbouri	Uganda: Mude Cave Camp, Mt Elgon, 3600 m	1° 10'N 34° 29'E	DM (5)
Otomys denti	Uganda: Ruwenzori E, Mubuku Valley, 1800 m (TYPE)	0° 22'N 30° 02'E	BM (1)
Otomys denti kempi	Rwanda: Burunga, Mt Mikeno, 1800 m (TYPE)	1° 29'S 29° 21'E	BM (1)
Otomys irroratus	South Africa: ECP: Albany, Grahamstown	33° 18'S 26° 30'E	KM (8), DM (1)
Otomys irroratus	South Africa: ECP: 37.5 km west of Alexandria	33° 40'S 26° 00'E	KM (4)
Otomys irroratus	South Africa: ECP: 2.1 km west of Alexandria	33° 45'S 26° 23'E	KM (4)
Otomys irroratus	South Africa: ECP: Alice	32° 47'S 26° 50'E	DM (5), KM (1)
Otomys irroratus	South Africa: ECP: Aliwal North	30° 42'S 26° 42'E	KM (2)
Otomys irroratus	South Africa: ECP: Barkly East, Tushielaw	30° 47'S 27° 57'E	KM (1)
Otomys irroratus	South Africa: ECP: 23 km west of Barkly	31° 02'S 27° 21'E	KM (1)
Otomys irroratus	South Africa: ECP: Bathurst State Forest	33° 32'S 26° 47'E	KM (5)
Otomys irroratus	South Africa: ECP: Bedford, Lyndock	32° 31'S 26° 01'E	KM (1)

Otomys irroratus	South Africa: ECP: 8.1 km west of Bredasdorp	34° 32'S 19° 57'E	KM (2)
Otomys irroratus	South Africa: ECP: Hogsback	32° 36'S 27° 01'E	DM (8)
Otomys irroratus	South Africa: GTP: Rietvlei Nature Reserve	25° 49'S 28° 32'E	DM (2)
Otomys irroratus	South Africa: KZN: Garden Castle Nature Reserve	29° 45'S 29° 13'E	DM (3)
Otomys irroratus	South Africa: KZN: Kamberg Nature Reserve	29° 24'S 29° 40'E	DM (5)
Otomys irroratus	South Africa: KZN: Karkloof Forest	29° 10'S 30° 05'E	DM (37)
Otomys irroratus	South Africa: KZN: Loteni Nature Reserve	29° 27'S 29° 32'E	DM (3)
Otomys irroratus	South Africa: NWP: Kuruman	27° 27'S 23° 26'E	DM (5)
Otomys irroratus	Zimbabwe: Nyanga Mts	18° 12'S 32° 40'E	KM (10)
Otomys lacustris	Kenya: Aberdares	0° 20'S 36° 37'E	BM (1)
Otomys lacustris	Tanzania: Madehani, Ukinga Mts (TYPE)	9° 20'S 34° 01'E	MCZ—not seen
Otomys lacustris	Tanzania: Mbizi Forest, Ufipa Plateau	7° 52'S 31° 43'E	BM (3)
Otomys lacustris	Tanzania: Poroto Mts, E. of Mbeya	9° 00'S 33° 44'E	BM (1)
Otomys occidentalis	Cameroon: Mt Oku, 2700-2900m (TYPE)	6° 12'N 10° 31'E	SMNS—not seen, MNHN (3)
Otomys tropicalis	Burundi: Tora	3° 42'S 29° 33'E	MNHN (45)
Otomys tropicalis	Burundi: Ntentamaza	?	MNHN (12)
Otomys tropicalis	Kenya: Aberdares	0° 20'S 36° 37'E	BM (5)
Otomys tropicalis nubilis	Kenya: Jambeni (TYPE)	0° 20'N 35° 50'E	BM (1)
Otomys tropicalis	Kenya: Kangaita, 6mi N Kerugoy	0° 25'S 37° 15'E	BM (4)
Otomys tropicalis	Kenya: Mt Kenya, W slope, 3000 m (TYPE)	0° 10'S 37° 10'E	BM (1)
Otomys tropicalis	Kenya: Mt Kinangop, 2700 m	0° 37'S 36° 42'E	MNHN (1)
Otomys tropicalis	Kenya: Mt Kenya, 4000 m	0° 10'S 37° 10'E	MNHN (1)
Otomys tropicalis vivax	Kenya: Mt Nyiru (TYPE)	2° 10'N 36° 50'E	BM (1)
Otomys tropicalis	Kenya: Solai, Mt Kenya	0° 05'S 37° 14'E	BM (3)
Otomys tropicalis	Malawi: Nyika Plateau	10° 36'S 33° 42'E	BM (1)
Otomys tropicalis burtoni	Nigeria: Onyanga, E. Mt Cameroon (TYPE)	4° 14'N 9° 10'E	BM (1)
Otomys tropicalis	Uganda: Bumasola, Mt Elgon	1° 11'N 34° 23'E	DM (1)
Otomys tropicalis	Uganda: Gitebe	1° 21'S 29° 15'E	MNHN (1)
Otomys tropicalis	Uganda: Kagambah, 1600 m	0° 49'S 30° 10'E	BM (1)
Otomys tropicalis	Uganda: Kampala	0° 19'N 32° 34'E	MNHN (1)
Otomys tropicalis	Uganda: Ruwenzori	0° 22'N 30° 02'E	MNHN (1)
Otomys typus	Ethiopia: Arussi, Albasso	7° 49'N 39° 13'E	BM (2)
Otomys typus fortior	Ethiopia: Dangila, Lk Tana (TYPE)	11° 17'N 34° 56'E	BM (11)
Otomys typus	Ethiopia: Dinsho	7° 06'N 39° 46'E	MNHN (11)
Otomys typus	Ethiopia: Gojjam, Debra Marcos	10° 20'N 37° 42'E	BM (1)
Otomys typus	Ethiopia: Shoa Province (TYPE)	9° 00'N 29° 30'E	?—not seen
Otomys typus thomasi	Kenya: Mt Kinangop, Aberdares (TYPE)	0° 37'S 36° 42'E	BM (1)
Otomys typus percivali	Kenya: Naivasha (TYPE)	0° 43'S 36° 26'E	BM (2)
Otomys typus jacksoni	Kenya/Uganda: Mt Elgon, 3960 m (TYPE)	1° 10'N 34° 29'E	BM (1)
Otomys typus uzungwensis	Malawi: Chelinda, Nyika Plateau (TYPE)	10° 36'S 33° 48'E	BM (3)
Otomys typus	Uganda: Mude Cave Camp, Mt Elgon, 3600 m	1° 10'N 34° 29'E	DM (1)
Otomys typus dartmouthi	Uganda: Ruwenzori East, 3750 m (TYPE)	0° 22'N 30° 00'E	BM (3)

Phylogeny and Evolution

thème 2

The Comparative Cytogenetics of African Small Mammals in Perspective

Status, Trends, and Bibliography

Terence J. Robinson

I Introduction

The choice of topic caused me some concern - had this been comparative cytogenetics in mammals, or even simply African Mammals (both large and small), I would have felt more at ease. But African Small Mammals is focused indeed and, to emphasize certain trends in the field I will, of necessity, draw on data from species that may defy the size restriction (20 kg C. DENYS, pers. comm.), and are most certainly not endemic. The transgression will, however, be slight.

The period included in this review covers the twenty-odd years spanning 1978 to present. The reasons are two fold. First, 1978 saw the publication by Lynn ROBBINS and Robert BAKER of a bibliography on karyotypic data for African mammals (both large and small). This paper (ROBBINS and BAKER, 1978) covered the pre-banding era and much of what could be regarded as the "hay day" of classical comparative cytogenetics (studies which rely on conventional banding protocols) - in essence, the 10 years from about the early 70s to the early 80s.

Secondly, it was from about this time that mapping by *in situ* hybridization started to play a significant role in the physical localization of

genes and DNA sequences (initially using radioactively labelled probes and culminating in FISH and the utilization of flow sorted chromosome libraries and custom made whole chromosome painting probes). This approach has provided powerful methods to identify homologous chromosome segments among species. These developing technologies took both cytogenetic expertise and grant money with them leaving classical comparative cytogenetics very much the poor relative. In other words, comparative cytogenetics, like so many scientific endeavours, has not escaped the molecular revolution.

In this review I will examine what has held the attention of mammalogists and other practitioners of comparative cytogenetics in the past two decades. I will touch on the problems that face us when attempting to place the cytogenetic data into a phylogenetic framework, and how comparative genomics and cross species chromosome painting has identified conserved chromosome segments and whole chromosomes across deep evolutionary divisions. This has allowed a first glimpse at the ancestral mammalian karyotype.

Historical perspective

Comparative cytogenetics, which led to the tracing of evolutionary changes in the chromosomal complement, advanced rapidly in the 1970-80s through the application of chromosome banding. It was a time of cytogenetic ferment. It was the era of the Mammalian Chromosomes Newsletter edited by T. C. HSU at the MD ANDERSON Cancer Center, and the Atlas of Mammalian Chromosomes (edited by T. C. HSU and K. BENIRSCHKE). The latter was published in a series of volumes from about 1967 through about 1977 and included hundreds of conventionally stained karyotypes and their description, a simple taxonomy, the source of the karyotypes (e.g., fibroblast cultures from zoo animals, gifts from contributors) and, where possible, collection localities and a bibliography. Some of the later volumes even included banded karyotypes. It was a time when it was unusual not to find several comparative chromosome papers in each issue of specialist journals such as *Chromosoma, Cytogenetics* (currently *Cytogenetics and Cell Genetics*), *Experientia, Caryologia, Hereditas*

and the *Journal of Heredity* in addition to those with a more generalized zoological focus. It was a time of large, active research groups, many of them led by human cytogeneticists and people whose primary research focus was in medicine.

Research outputs 1979-1999

Twenty years on and to what extent have we, who work predominantly with African Small mammals, progressed beyond that? With the help of colleagues it was possible to gather a bibliography comprising approximately 160 research articles, theses and dissertations which detail cytogenetic data on African Small Mammals most of which have been on rodents although lagomorphs, bats, insectivores, primates, hyraxes and some of the miniature antelope are also included. While the partitioning of the outputs into discrete topics is clearly subjective, and although there are undoubtedly omissions in the bibliography (but these are probably random in terms of topic), it was possible to group the outputs into six categories. These serve loosely to illustrate where the effort has been placed these past 20 years.

Studies where the focus was in recognizing karyotypic diversity within recognized forms (i.e. "cryptic species") predominated forming approximately 40% of the research output. Next were papers with more of a phylogenetic bent but associations were made without using outgroup comparisons - only about 5% of papers in the period under review actually subjected the chromosomal data to the rigors of cladistic analysis. Multidisciplinary studies (in which cytogenetics was only one of the parameters used) and review articles were the next most numerous category followed by "other" (meiosis, synaptonemal formation, multiple sex chromosome systems, characterization of C-band repeats). Lastly, and somewhat surprisingly given the international trends in comparative cytogenetics, comparative genomics – used here as a catch-all for works that had included molecular cytogenetic aspects such as cross-species chromosome painting – was represented by a mere 8% of papers.

What motivated these cytogenetic studies?

From the analysis of outputs it would appear that we are purposely using the techniques to document "genetic biodiversity" i.e. the search for cryptic and previously undescribed species. If this were true, I would suggest that there are other more cost effective and sensitive approaches (in terms of providing greater resolution) to doing this.

As part of the justification for the use of karyotyping for "biodiversity" assessment it could be argued that in recently diverged taxa, chromosomal change often appears to predate divergence by other markers. This certainly appears to be the case in the house mouse (BRITTON-DAVIDIAN *et al.*, 1989; NACHMAN *et al.*, 1994; NACHMAN and SEARLE., 1995 and references therein), but the mouse is an exception in many aspects of its genome evolution. Moreover, if we assume that the fixation of structural rearrangements in mammalian populations requires extremely small populations (a hypothesis proposed by BUSH *et al.* (1977) and which is still widely regarded as having some foundation), it is precisely under these conditions of restricted founders that mitochondrial DNA is most sensitive (AVISE, 1994 and references therein).

Chromosomes and phylogenetic discontinuities

That phylogeographic discontinuities are often delimited by chromosomal differences is certainly true (DUCROZ *et al.*, 1997, 1998; MATTHEE and ROBINSON, 1997). By way of example, mitochondrial DNA was used together with comparative cytogenetics to examine the evolutionary history and taxonomic status of the springhare (*Pedetes capensis*). Mitochondrial phylogeographic structure showed that the majority of the southern African populations (*P. c. capensis*) are characterized by unique but closely related maternal lineages. This is an observation in keeping with a relatively recent range expansion from smaller source populations. In contrast, however, the east African populations (*P. c. surdaster*) appear more structured and are distinguished from those in southern Africa by an average sequence

divergence of 5.52% (±1.4%; MATTHEE and ROBINSON, 1997). This marked divergence is concordant with results of the cytogenetic study: Specimens from southern Africa have 2n = 38 and those in eastern Africa 2n = 40 (MATTHEE and ROBINSON, 1997).

Importantly, however, the converse also holds - there have been numerous examples of species which show marked mtDNA phylogenetic structure but which are karyotypically invariant (in other words, where the two markers are discordant but with mtDNA showing greater resolution). African examples include the rock hyrax (*Procavia capensis*; PRINSLOO and ROBINSON, 1992), the red rock rabbit (*Pronolagus rupestris*; MATTHEE and ROBINSON, 1996) and, in the case of larger species, both the roan and sable antelope are deeply structured in parts of their continental ranges (the roan in west Africa, the sable in east Africa) when using the control region sequences (MATTHEE and ROBINSON, 1999), but are karyotypically identical (ROBINSON and HARLEY, 1995). Simply put, it could be argued that chromosomes may not be the most effective genetic marker if one is looking to uncover hitherto undescribed taxonomic units of biodiversity.

In fact, if our brief was indeed to survey genetic variation on a continental scale – leaving the relative merits of the various approaches aside – a justification for mtDNA (or other DNA based approaches) could be made simply on ease of sampling. Those of us that have attempted karyotyping under primitive field conditions, yeast stressing mice that die hours before starting with bone marrow extractions, the thick layer of cytoplasm that almost invariably covers the chromosomes (which is simply an anathema to good G-band resolution), the generally short and widely splayed chromatids, poor spreading and the low mitotic index can all vouch for the fact that simply placing a piece of tissue in a DMSO-NaCl or ethanol solution is much less frustrating. It takes away the need for access to refrigeration and freezers in remote areas, and removes the costs incurred in transporting and keeping live animals should the decision be taken to do the analysis in the comfort of one's own laboratory. Most importantly, it allows for the analysis of sample sizes far in excess of what could be catered to in karyotyping and in so doing highlights a fundamental weakness of the karyological approach. Conventionally, karyotype descriptions have been based on few specimens, frequently drawn from the same or geographically closely allied populations, with these

data often extrapolated to the species as a whole on the premise that the taxon comprises a single cytotype. No thought is given to possible intraspecific (geographic) chromosomal variation, an assumption increasingly being challenged by accumulating data in both small and large mammals (see ROBINSON and ELDER, 1993 and references therein). The detection of novel cytotypes in other regions of a species' range (often equated with the detection of "new cryptic species") clearly becomes questionable under this scenario.

Cytogenetics simply as a tool in species identification

If contributing to studies on African biodiversity is not the stimulus that drives comparative cytogenetics in African small mammals, then what is? Perhaps it is that in most instances we use cytogenetics simply as a tool in species identification and the detection of new cryptic species and cytotypes (and by extension geographic genetic partitioning in what appears to be continuously distributed species) is simply a result of this. In other words, we are not using cytogenetics to address "genetic" questions, or those of evolutionary relationships. We are using the methods primarily for correct assignment of species, especially in cases where species are not well delimited on morphological grounds. In fact, if one analyses the outputs contained in the bibliography, many papers have essentially been descriptions of new karyotypes, serendipitously discovered and often based on standard karyotypes or sub-optimal banding comparisons. But this is really to deprecate the usefulness of comparative cytogenetic data. Why, almost 20 years after banding studies were firmly established and the detection of homologous segments had become routine, have there been so few attempts at resolving phylogenetic relationships chromosomally and, in particular, subjecting the data to the rigors of cladistic analysis (only 5% of papers)? Is it a problem inherent with this type of data? Or has it to do with the fact that use of mammalian chromosomal data in phylogeny reconstruction has been limited by our inability to correctly identify homologous chromosomes (or chromosome regions) between species and, perhaps more debilitating, to compare these to appropriate outgroup taxa?

Cytogenetics in phylogeny reconstruction

Cladistics

The cladistic method dictates that two species are considered closely related if they share one or more derived character states. Derived conditions are distinguished from primitive ones by analysis of appropriate out-groups and parsimony (HILLIS *et al.*, 1996). The underlying assumption in this approach is that a character state possessed by both ingroup and outgroup taxa represents the primitive condition for the ingroup. However, conclusions on chromosomal homology, whether the character is primitive (plesiomorphic) or derived (apomorphic), and the direction of evolutionary change can only be made if the chromosomes/chromosome segments can be unequivocally identified as homologous, and, in turn, if these can be identified across ingroup as well as outgroup species to the specific assemblage. And it is the precise detection of homologous chromosomes or chromosome segments which, I believe, has been central to chromosomes' poor performance in inferring phylogenetic relationships.

In fact, it could be argued that interspecific homologies based on conventional banding are only reliable between species which have experienced few chromosomal rearrangements. This is reflected in the papers contained in the bibliography. While there have been relatively few papers that employ rigorous outgroup criteria and analyze the data in a cladistic framework (e.g. BRITTON-DAVIDIAN *et al.*, 1995; QUMSIYEH *et al.*, 1987), there have been a great deal more attempts to infer evolutionary relationships from presumed ancestral karyotypes which have been derived using only the patterns reflected by ingroup taxa. In many instances, these did not have full taxon representation (e.g. ROBINSON *et al.*, 1981).

The selection of an appropriate outgroup is not a trivial exercise. For example, data from New and Old world monkeys, pro-simians and species from other mammalian orders such as carnivores and ungulates were essential in constructing the ancestral primate karyotype (WIENBERG and STANYON, 1997). Part of the need to have such broad

outgroup representation has to do with eliminating errors that may be introduced by confusing convergence with homology.

Convergence of character states

A pattern, tentative as it may be, is that convergent rearrangements (rearranged chromosomes that have arisen independently in two or more species) do occur and are certainly not uncommon. For example, the single pair of NOR bearing "marker chromosomes" in the Hylobatidae and old world monkeys (Cercopithecidae) were long held to be homologous (STANYON *et al.*, 1995). This suggestion would have placed the lesser apes phylogenetically together with the monkeys rather than the great apes (and man), an hypothesis that persisted even after the introduction of chromosome banding. However, cross species chromosome painting showed that the NOR chromosomes in lesser apes and monkeys were not homologous and although HSA 22 was part of the NOR bearing chromosomes in all Old World monkeys this was not the case for the gibbons (STANYON *et al.*, 1995). In other words, the "marker chromosomes" in these species showed no homology outside of the NOR itself. The point is that classical banding studies are often unable to distinguish between convergence and true homology of bands. This is important since, in reality, one band looks much like another, and it is frequently possible only to detect conserved banding patterns in relatively large regions (GRAVES, 1998).

Additional complications in respect of convergence are related to the type of chromosome change. In lineages where chromosomal evolution has been predominantly through Robertsonian change, chromosomes have proved to be of limited utility when analyzed cladistically, especially if no other supporting data are present (QUMSIYEH *et al.*, 1987). I believe that in part, this is a reflection of the limited segregational difficulties often encountered with centric fusions. Therefore, it is quite likely that lineages which are prone to this type of chromosomal evolution may be characterized by brachial combinations which are essentially random and contribute little in phylogenetic studies beyond "noise". This appears to be the situation in some rodents, for example *Tatera* and *Gerbillurus* (QUMSIYEH *et al.*, 1987) as well as the Bovidae (GALAGHER and WOMACK, 1992; GALAGHER *et al.*, 1994). In spite of the large numbers of centric

fusions found in these taxa, many appear to be *de novo* changes involving the same chromosomes, and comparative cytogenetics has had limited success in detecting synapomorphies for use in determining phylogenetic relationships among species.

While it can be argued that more complex arrangements may be less prone to reversals (and thus are not a source of homoplasy), their detection by G-banding is often tenuous. In reality, the only recourse open to investigators working with species where chromosomal rearrangements have led to extensive genome rearrangement, and who are intent on determining chromosomal homologies, may be through chromosome painting.

Fluorescence *in situ* hybridization (FISH)

FISH, using probes derived from flow sorted or microdissected chromosomes has provided a means whereby gross sequence homology across chromosomes of different species can be established (chromosome painting). In other words, a chromosome paint comprises a mixture of DNA which hybridizes to the entire chromosome of origin and corresponding sequences in other taxa. While this approach was originally restricted to painting across species using human chromosome paints (Zoo-FISH), recent developments in chromosome microdissection and DOP-PCR (PCR amplification of DNA using degenerate oligonucleotide primers which ensure that all the sequences contained within the source DNA are represented) have simplified the production of chromosome specific paints (see FERGUSON-SMITH, 1997). This has opened up direct high resolution comparisons (not using the human as common denominator) between closely as well as distantly related species.

A particularly vivid example of the power of cross-species chromosome painting is that of the white-cheeked gibbon, *Hylobates concolor*, by SCHRÖCK *et al.* (1996). The karyotypes of most Old world primates, including man, are distinguished by few translocations; they are chromosomally conservative and chromosomal syntenies have been maintained intact (WIENBERG and STANYON, 1997). However, the

hylobatids (gibbons and siamang) are an exception to this and conventional chromosome banding revealed few homologies between the lesser apes and those of other primates (WIENBERG and STANYON, 1995) reflecting the extensive genomic reorganization that delimits them. Spectral karyotyping by SCHRÖCK *et al.* (1996) using all 24 human chromosome specific painting probes allowed for the detection of at least 60 different segments in the gibbon genome resulting from a series of translocations and complex intrachromosomal rearrangements that have occurred since divergence from their last common ancestor (WIENBERG and STANYON, 1995, 1997).

Of course one does not have to go to primates, and extralimital ones at that, to find species which show extensive karyotype reshuffling between closely related species. In terms of African small Mammals, the Otomyinae provide a good example of this. In spite of *O. irroratus* and *O. unisulcatus* having identical diploid numbers (2N = 28) conventional banding studies were unable to detect G-band homologies between them (ROBINSON and ELDER, 1978). These authors extended their comparisons to include the chromosomes of the rat (*R. norvegicus*) and a North American *Peromyscus* species (*P. melanophrys*) and, although several of the *unisulcatus* chromosomes could be convincingly matched to chromosomes of these species, no homologies were evident with the *O. irroratus* chromosomes.

More recently, cross species chromosome painting using two commercially available mouse chromosome paints (corresponding to MMU2 and MMU6) uncovered homologies that were not detected by G-band patterns in the past (RAMBAU *et al.*, 1997). FISH showed that sequences corresponding to MMU2 are conserved as a single chromosome in *O. irroratus* but are found on two separate chromosomes in *O. unisulcatus* and the whistling rat, *P. brantsii*; mouse sequences corresponding to chromosome 6 are conserved as single chromosomes in all three species. In fact, the split signal detected in some of the Otomyinae is even more interesting when viewed against the recent cross species painting between rat and mouse (GRÜTZNER *et al.*, 1999; GUILLY *et al.*, 1999; STANYON *et al.*, 1999). Mouse chromosome paint 2 hybridizes to a single chromosome in the rat (number 3) mirroring the situation in *irroratus*. So in spite of its extensively rearranged genome *irroratus* has retained this chromosome in an unaltered state (probably ancestral) while it has been rearranged in the two other species.

Mouse: rat reciprocal painting studies

Since so much of the cytogenetic work on African small mammals is on rodents allow me to dwell on these comparisons for a few moments. Thirteen mouse chromosomes have sequence homology to single chromosomes or chromosome segments in the rat (MMU 2, 3, 4, 6, 7, 9, 12, 14, 15, 16, 18, 19, X); in contrast, the painting probes for the remaining seven chromosomes (1, 5, 8, 10, 11, 13, and 17) produce split hybridization signals on the rat (GRÜTZNER *et al.*, 1999). Moreover, reciprocal chromosome painting shows that the evolutionary rate of chromosome translocations between these two rodents is about 10 times faster than that found between human and cats (STANYON *et al.*, 1999). Out-group comparison reveal that the mouse karyotype is more extensively rearranged than that of the rat, and that many of the mouse chromosomes are evolutionarily derived.

In summary, the reciprocal painting studies clearly underscore how strikingly different the mouse and rat karyotypes are, especially for species from the same subfamily (Murinae). There are at least 14 translocations separating the genomes of these two rodents (STANYON *et al.*, 1999). Emphasizing that many/most of the segmental homologies defy resolution by conventional banding is not to overstate the case.

FISH is not a panacea

In spite of the obvious power of cross species chromosome painting, I do not believe that comparative FISH is a panacea to all the problems one encounters in identifying homologies and retrieving phylogenetic information from the karyotype. It, like conventional banding, suffers from significant shortcomings, the most important being that it does not provide insights into intrachromosomal rearrangements (gene order) within conserved blocks, and consequently a whole class of potentially informative rearrangements will be missed unless subregional markers are also used.

The point to be emphasized is that G-bands alone may be poor indicators of true homology, and these data may often be in conflict with one of the basic assumptions underpinning phylogenetic analysis - that of true character homology (SWOFFORD *et al.*, 1996). One can

question whether in addition to the tendency for Robertsonian changes (particularly fusions) to show high levels of homoplasy, phylogenetic resolution may also be confounded by assessments of homology, and whether in many instances these data (G-bands) lend themselves to robust phylogenetic analysis at all.

Comparative cytogenetics and abilities to detect deeper phylogenetic relationships

The early comparisons based on conventional banding indicated (with few exceptions i.e. NASH and O'BRIEN, 1982; DUTRILLAUX and COUTURIER, 1983) extensive genome scrambling between mammalian ordinal groups effectively sidelining chromosomal data in studies of this nature. However, chromosome painting across mammalian orders has shown that the mammalian genome is highly conserved - allowing the identification of conserved large blocks and even whole chromosomes between ungulates, carnivores and primates. Nowhere is this conservatism more striking than in the detection of whole chromosomes that have survived intact not only within primates, but also among other orders of mammals. For example, of the 23 human chromosomes 16 show homology with single cat chromosomes and the remaining seven are represented, in most instances, by two interrupted blocks (RETTENBERGER *et al.*, 1995; O'BRIEN *et al.*, 1997). Conservation of entire chromosomes appears also to extend to other orders. For example HSA4 maintains whole chromosome synteny in the pig, the harbor seal, mink and cat (CHOWDHARY *et al.*, 1998) while HSA 17 appears to be intact in carnivores (cat and seal), artiodactyls (pig and cattle), cetaceans (dolphin) and even insectivores (shrews; GRAVES, 1998 and references therein). The X chromosome is considered conserved within all eutherians.

Somewhat puzzlingly, the picture of conserved synteny appears inconsistent with the evolutionary distance between species. For instance, most Old World primates are generally chromosomally conservative

and syntenies have been maintained intact while in another closely related group, lesser apes (most notably the gibbons), multiple rearrangements delimit the various karyotypes (WIENBERG and STANYON, 1997). Similarly, even with the paucity of dog genes that have been mapped, the degree of synteny shown with human is considerably less than is evident with the highly conserved cat genome thus highlighting marked differences within carnivores (GRAVES, 1998). Yet another pattern to emerge is that rodent maps are generally fragmented in comparison to human maps. It was initially thought that this break down of synteny merely reflected the increased evolutionary distance between rodents and primates - the greater the time since common ancestry, the greater the chance for chromosome rearrangements to have occurred. However, the hamster genome shows considerably more synteny with human than what mouse does (GRAVES, 1998).

So why do we have patterns of extreme genome rearrangement in some lineages and not in others? Certainly differences in populations structure, isolation, selection and drift - the classical circumstances thought to promote chromosomal evolution - are probably applicable in some way or another (ELDER and HSU, 1988). Perhaps certain lineages contain novel DNA sequences which predispose to chromosomal rearrangements. In the past, studies of natural hybrids have demonstrated elevated chromosome mutation rates that are presumably precipitated by the hybridization event with transposable elements possibly mediating the rapid and large scale changes in the genome composition (BUSH, 1981; ELDER and HSU, 1988; O'NEILL *et al.*, 1998). These and other observations beg the question whether something happens to destabilize the genome in a particular lineage and, if so, how is stability reinstated?

We still have no real data on these basic questions which are all central to chromosome evolution. In fact, in spite of the plethora of molecular data (ARIGA *et al.*, 1990; WICHMAN *et al.*, 1992; O'NEILL *et al.*, 1998 and others) and the myriad new techniques available, we have not progressed beyond ELDER and HSU's (1988) view... "that in some ancestral populations both genomic and population conditions were right for reorganization to occur. In other populations these conditions were not right or at least have not been right to this point in their evolution."

Mammalian ancestral karyotype

What is clear, however, is that our ability to detect homologous chromosomes and chromosome segments across ordinal divisions holds promise for the eventual description of the ancestral mammalian karyotype. These data should finally put an end to the debate which has had authors postulating an increase in diploid number as the overriding trend in mammalian chromosome evolution, and others arguing that a decrease in 2n is more characteristic. Traditionally, three hypothesis for the primitive condition have been proposed (RETTENBERGER *et al.*, 1995). Ohno's fusion model posits a 2N = 96 acrocentric complement (OHNO, 1970), TODD (1970) held that fission was the driving force with 2N = 14 metacentric and submetacentric chromosomes representing the ancestral karyotype, whereas Matthey's modal hypothesis (MATTHEY, 1973) favoured the midpoint with 2N = 40-56 as the ancestral eutherian condition.

On the basis of conserved chromosomes blocks observed in eight species analysed so far (man, pig, cattle, muntjak, horse, cat, mink, seal) the putative karyotype of the common ancestor of primates, carnivores, perissodactyls, and artiodactyls most probably had a chromosome number of 48 (CHOWDHARY *et al.*, 1998 but see RETTENBERGER *et al.*, 1995); CHOWDHARY and co-workers (1998) have suggested a tentative ancestral chromosome complement corresponding to the human equivalents of HSA 1p, 1q, 2pter - q13, 2q13-qter, (3/21), 4, 5, 6, 7, 8, 9, 10, 11, (12/22 part), 13, (14/15), (16q/19q), 16p, 17, 18, 19p, 22(part), X and Y. Obviously, it is to be expected that with the availability of more comparative Zoo-FISH karyotypes spanning other orders, this rather preliminary view of the primitive mammalian condition will improve.

Future trends

First, the idea that good banding continues to be effective in resolving relationships among groups where there has not been wholesale rearrangement is probably valid. This is particularly true for species where karyotypes can be related by simple Robertsonian fusions and

fissions. That said however, it may be simplistic to assume that the genomes of these "constrained" groups could not have been subjected to subtle rearrangement which fall beyond the resolution of conventional banding and this clearly questions whether banding data, used in isolation, lend themselves to phylogenetic analysis. The real power of cross chromosome species painting is that it provides an effective means of confirming the accuracy of homologies suggested by conventional banding; the real power of *good* G-banding is that it can often reveal intrachromosomal rearrangements which are obscured by chromosome painting. In summary, although it may not be necessary to resort to FISH in every instance, the need for its application is only likely to be resolved on a case by case basis.

Secondly, I think it will be unavoidable that much of what we do in the context of mammalian cytogenetics in next 10 years will, unavoidably, be shaped by developments in comparative genomics. Chromosomal painting in highly rearranged genomes such as those of the hylobatids and pro-simians (WIENBERG and STANYON, *1995*; SCHRÖCK *et al.*, 1996) some of the Otomine species (RAMBAU *et al.*, *1997*), and taxa such as the donkey and the horse (RAUDSEPP and CHOWDHARY, 1999) has clearly shown that chromosomal homologies previously established on the basis of banding were not reliable, and that cytogenetic phylogenies should, ideally, be substantiated by both conventional banding and molecular data.

Thirdly, there are at least nine orders of mammals for which there is little or no comparative genomic data (mapping or, importantly in the context of the present paper, cross species painting) - these include the Chiroptera, Pholidota, Pinnipeds, Proboscidea, Hyracoidea, Sirenia, Dermoptera, Scandentia and Xenartha (O'BRIEN *et al.*, 1997). These data will be critical to discerning the major features of genome evolution. Quite clearly, there is a lot to do.

Conclusion

It seems likely that as comparative maps of species representing the 20 modern orders of mammals are gradually assembled, the opportunity to use precise chromosomal and segmental homologies for

comparative and phylogenetic studies will become a reality. However, whether these data do turn out to "represent the most powerful suite of phylogenetic (cladistic) characters available for resolving the precise hierarchy of mammalian evolution" (O'BRIEN *et al.*, 1997) remains to be seen.

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Knowledge of the evolution of African Paleogene mammals

Contribution of the Bir El Ater locality (Eocene, Algeria)

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Introduction: The Early African Paleogene mammals

The African fossil record of therians begins with the Early Cretaceous of the Middle Atlas (Morocco) (SIGOGNEAU-RUSSELL, 1991); however, the modern mammalian orders appear only during the early Tertiary in North Africa (figure 1A).

The Paleocene and Ypresian localities from the Ouarzazate Basin (Morocco) have yielded mammalian faunas with possible creodonts, « insectivores » (paleoryctids, todralestids and adapisoriculids) (GHEERBRANT, 1992, 1994, 1995), the oldest representative of euprimates (SIGÉ *et al.*, 1990) and archaic ungulates (SUDRE *et al.*, 1993). Recently, the discovery of *Phosphatherium* (Proboscidea) in

	Ypresian	Early to middle eocene				Middle eocene		Middle to late eocene	Late eocene	
	N'Tagourt 2 (Morocco)	El Kohol (Algeria)	Glib Zegdou (Algeria)	Gour Lazib (Algeria)	Chambi (Tunisia)	In Tafidet and Tamaguilelt (Mali)	M'Bodione (Senegal)	Bir el Ater (Algeria)	Dor el Talha "Evaporit Unit" (Libya)	Qasr el Sagha (Fayum, Egypt)
Metatheria					*Kasserinotherium tunisiense*					
Creodonta		*Koholia atlasense*						gen. et sp. indet		*Apterodon Hyaenodon*
Carnivora			*Glibzegdouia tabelbalaensis*							
Condylarthra	Condylarthra indet.						Condylarthra indet.			
Artiodactyla										cf. Bothriogenys sp.
Proboscidea	*Khamsaconus bulbosus*	*Numidotherium koholense*				*Moeritherium indet.*	*Moentherium indet.*	*Moeritherium sp.*	*Barytherium grave Moeritherium lyonsi Phiomia indet.*	*Barytherium grave Moeritherium lyonsi*
HYRACOIDEA		*Seggeurius amourensis*	*Titanohyrax mongereaui*	*Megalohyrax gevini Bunohyrax or Megalohyrax indet. Microhyrax lavocati*	*Titanohyrax tantulus*			*Bunohyrax matsumotoi*	Hyracoidea indet.	Pliohyracidea indet.
Macroscelidea					*Chambius kasserinensis*			*Nementchatherium senarhense*		

	Ypresian	Early to middle eocene				Middle eocene		Middle to late eocene	Late eocene	
"Insectivora"	*Afrodon tagourtensis* *cf. Palaeoryctes minimus* *Todralestes butleri* *Didelphodontinae* *Adapisoriculidae* *?Tinerhodon disputatum*	*Garatherium mahboubi* *Insectivora indet.*	Palaeoryctes sp.	Palaeoryctes sp.	*Chambilestes foussanensis*			"Insectivora" indet.		
Rodentia			*Glibemys algeriensis* *Glibia pentalopha* *Glibia tetralopha* *Zegdoumys lavocati*		*Zegdoumys sbeitlai*			*Protophiomys algeriensis* *Nementchamys lavocati*		
Chiroptera					*Dizzya exsultans* *Rhinolophoidea indet.* *Chiroptera indet.*					
Primates			*Algeripithecus minutus* *Tabelia hammadae* *Primates indet.*	*Azibius trerki*	*Djebelemur martinezi*			*Biretia piveteaui cf. Algeripithecus* *Oligopithecidae indet.* *Primates indet.*		
Mammalia Incertae sedis	Mammalia indet.		Mammalia indet.	*Heliosus insolitus*	Mammalia indet (Primates or Condylarthra?)		Mammalia indet.	Mammalia indet.	Mammalia indet.	

phosphatic deposits of the Ouled Abdoun Basin (Morocco), documents the first occurrence of modern ungulates (GHEERBRANT *et al.*, 1996).

These mammalian orders radiated during the Eocene times (table 1). New proboscideans appear, *Numidotherium* (MAHBOUBI *et al.*, 1984) at El Kohol (Algeria) and *Moeritherium* in Mali, Senegal and Libya. As for the primates, *Djebelemur* from Chambi (Tunisia) is considered as an adapiform (HARTENBERGER and MARANDAT, 1992) and *Algeripithecus* from Glib Zegdou (Algeria) as the earliest African anthropoid (GODINOT and MAHBOUBI, 1992). These Early-Middle Eocene Algerian localities and that of Chambi have also yielded new cosmopolitan orders like rodents (VIANEY-LIAUD *et al.*, 1994) or endemic ones: the oldest macroscelid is known from Chambi (HARTENBERGER, 1986), and several genera of hyraxes have been described (SUDRE, 1979; MAHBOUBI *et al.*, 1986; COURT and HARTENBERGER, 1992).

These fossils suggest the occurrence of several paleogene terrestrial interchanges between the African continent and the North-Tethyan regions (MAHBOUBI *et al.*, 1997 for an overview). The paleoryctid and adapisoriculid « insectivores » from Morocco record faunal exchanges between Europe and Africa around the K/T boundary (GHEERBRANT, 1987). GHEERBRANT (1990) considered the possible hyaenodontid creodonts and the omomyid primate from this country as strong arguments in favor of interchanges with Europe (and perhaps Asia) at the Paleocene/Eocene boundary. The zegdoumyid rodents from Gour Lazib (Algeria) (VIANEY-LIAUD *et al.*, 1994) and the macroscelid from Chambi (HARTENBERGER, 1986) indicate also North-South communications between Africa and the Holarctic continents. Then, if the Eocene period is globally characterized by an endemic evolution with the diversification of endemic lineages – such as Proboscidea and Hyracoidea –, these results suggest that the Arabo-

Table 1 *(previous page)*
Fossil terrestrial mammals known from faunas assigned to the Eocene in Africa. After ARAMBOURG *et al.* (1951), CROCHET *et al.* (this volume), GHEERBRANT *et al.* (1998), HARTENBERGER *et al.* (1997), MAHBOUBI *et al.* (1986), SUDRE (1979), VIANEY-LIAUD *et al.* (1994) and WIGHT (1980). The locality of Kpogame-Hahotoe (Togo) has yielded indeterminable remains of land mammals.

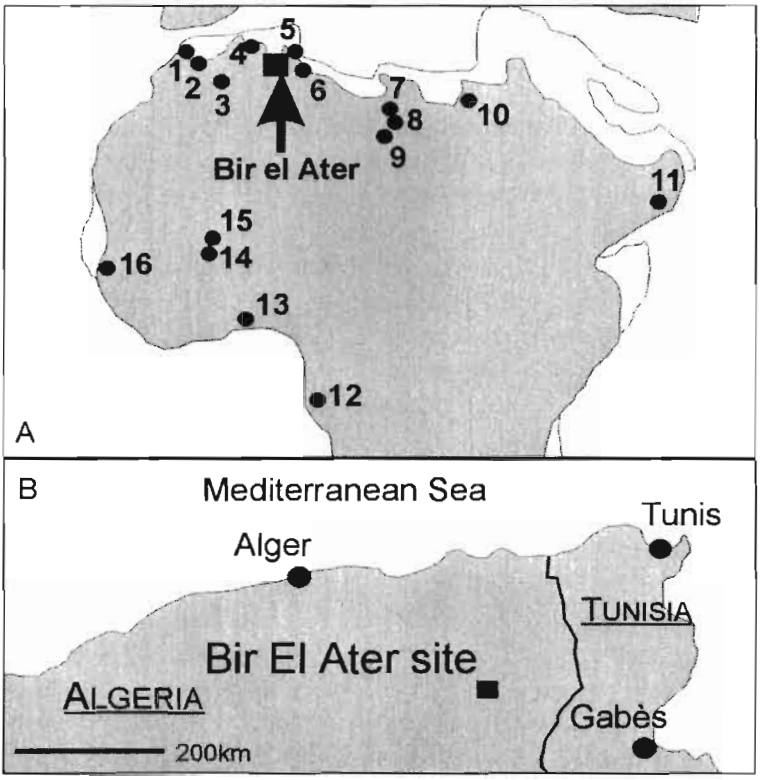

Figure 1
A, Location of the Bir El Ater site relative to the other Paleogene terrestrial mammal localities of Africa (reconstitution of the paleo-coastlines during the Early Paleogene, modified from Smith *et al.* 1994): 1 Ouled Abdoun Basin (Morocco); 2 Ouarzazate Basin (Morocco); 3 Gour Lazib/Glib Zegdou (Algeria); 4 El Kohol (Algeria); 5 Chambi (Tunisia); 6 Jebel Bou Gobrine (Tunisia); 7 Zella (Libya); 8 Dor El Talha (Libya); 9 Jebel Hasanawah (Libya); 10 Fayum (Egypt); 11 Taqah and Thaytiniti (Oman); 12 Malembe (Angola); 13 Kpogame-Hahotoe (Togo); 14 In Tafidet (Mali); 15 Tamaguilelt (Mali); 16 M'bodione Dadere (Senegal).
B, Location map of the Bir El Ater site, Easthern Algeria.

African continent was not a completely isolated land mass in the Early Paleogene; it is only during the Oligocene that Africa was strictly isolated. Several localities in the Fayum depression (Egypt) (see HOLROYD, 1994) and two Oman sites (THOMAS *et al.*, 1989) document well this period.

Geological setting of Bir El Ater site

The Nementcha Mountains constitute the oriental end of the Algerian Saharan Atlas. In these massifs the Early Eocene is strictly marine and phosphatic. The presence of the continental Eocene was revealed by COIFFAIT *et al.* (1984) in deposits close to Bir El Ater in the south of the Jebel Abiod (figure 1B). These deposits yielded a composite fauna of continental and marine vertebrates in which the authors identified some rodents, several primates, a proboscidean, a hyracoid, a macroscelid as well as insectivores. Only the rodents (JAEGER *et al.*, 1985) and an anthropoid primate (de BONIS *et al.*, 1988) have been described.

In the stratigraphic section, the marine Cretaceous limestone is overlain in concordance by the Ypresian (limestone with marl intercalations) and by an other marine succession composed of marls and gypsum with mollusks and Lutetian ostracods (FAID, 1999). The vertebrate fauna was found in a detritic basal layer of a sandy fluvio-deltaic member overlaying discordantly these marine deposits. The discordance seems to represent the Lutetian tectonic Atlasic event. These Middle to Late Eocene deposits are immediately overlain by the continental Miocene.

These stratigraphic data permitted to consider the Bir El Ater locality as post Lutetian and ante Neogene in age (COIFFAIT *et al.*, 1984). The much more primitive phiomyid rodents compared to those of the Early Oligocene from the Jebel El Qatrani (Fayum, Egypt) also indicate a Middle-Late Eocene age (JAEGER *et al.*, 1985).

Comments on the mammalian fauna from Bir El Ater

This part presents the reassessment of the mammals from Bir El Ater, while insisting on the phylogenetic and paleobiogeographic conclusions. Except for the many dental remains of *Moeritherium* (Proboscidea), the whole of the material refers to small mammals (figure 2).

"Insectivora"

An « insectivore » known from only one molar trigonid is still undetermined. This specimen (figure 2A) shares with the Palaeoryctidae from the Thanetian-Ypresian of Morocco a minute, sharp and prominent trigonid with a small paraconid. But the lack of other characters, the existence of undescribed « insectivores » from the Early-Middle Eocene of Algeria (El Kohol, Gour Lazib and Glib Zegdou) and their absence (taphonomic biases?) in the Early Oligocene of the Fayum and Oman cannot allow a systematic assignment.

Macroscelidea

A new genus of elephants-shrew (Tabuce *et al.*, 2001), documented by some lower and upper cheek teeth, is attributed to the Herodotiinae. This subfamily is composed of two monospecific genera, *Chambius* from the Early-Middle Eocene of Chambi (HARTENBERGER, 1986) and *Herodotius* from the Early Oligocene of the Fayum (SIMONS *et al.*, 1991). Like these two genera (BUTLER, 1995), the new genus from Bir El Ater seems to have close relationships with the archaic ungulates ("condylarths"), and especially with one Hyopsodontidae Louisininae from the Paleogene of Europe.

Rodentia

The rodents are the most abundant fossils of the locality, with dozens of isolated teeth. When the Bir El Ater locality was found, *Nementchamys lavocati* Jaeger *et al.*, 1985 (Anomaluridae) and *Protophiomys algeriensis* Jaeger *et al.*, 1985 (Phiomyidae) were the oldest representatives of the order in Africa.

Since then, the discovery of the Zegdoumyidae permitted to reconsider the uncertain position of the Anomaluridae. It seems that this family is rooted in the zegdoumyids from the Early-Middle Eocene of Chambi and Glib Zegdou. This African group, the European Gliridae and the North American Sciuravidae would be related to the Ischyromyoids (VIANEY-LIAUD *et al.*, 1994). *Protophiomys algeriensis* remains the first occurrence of the Phiomyidae and shares several derived characters with the Asiatic Eocene Chapattimyidae (JAEGER *et al.*, 1985).

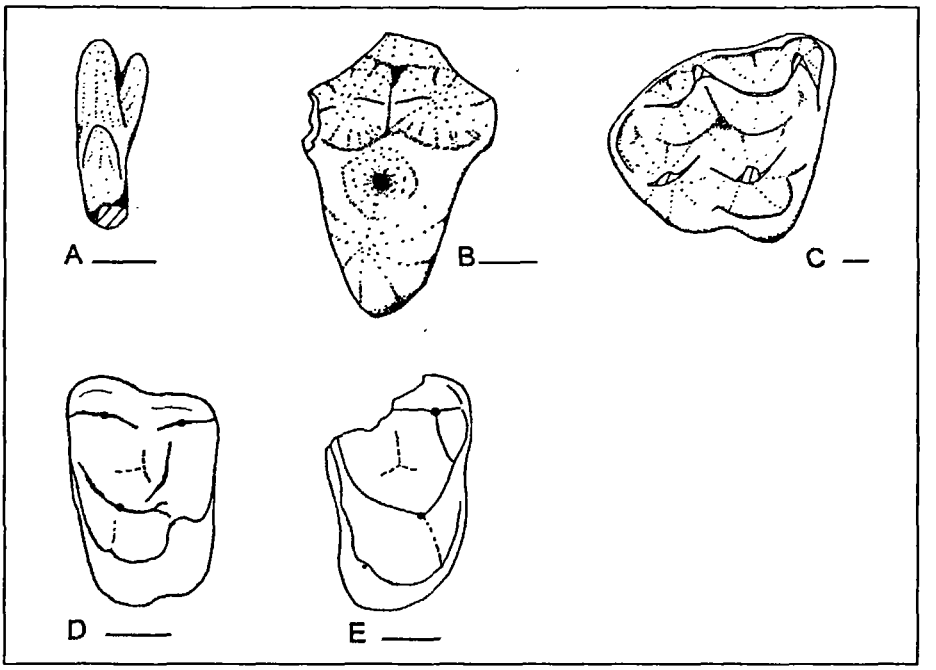

Figure 2
Mammals from Bir El Ater (scale bar 1 mm):
A, « Insectivora ». indet. UON 362, trigonid of a right lower molar in lingual view;
B, Carnivora or Creodonta indet. UON 360, right M^{1or2} in occlusal view;
C, *Bunohyrax matsumotoi* UON 372, right M^3 in occlusal view;
D, cf. *Algeripithecus* UON 364, left M^{1or2} in occlusal view;
E, Oligopithecidae indet. UON 366, right M^{1or2} in occlusal view.

Carnivora or Creodonta

Two teeth are related to a carnivore or a creodont. This assumption is supported by several characters: on the tritubercular M^{1-2} (fig. 2B), the paracone and the metacone are connected, the postmetacrista is broken but probably elongated, the parastyle is weakly cuspidate and anterior to the rest of the crown, the trigon basin is narrow with strong preprotocrista and postprotocrista, and the buccal area is well developed. This tooth shares with the creodont *Masrasector* from the Fayum

and Oman (SIMONS and GINGERICH, 1974; CROCHET *et al.*, 1990; HOLROYD, 1994) similar measurements, the mesio-distal narrowness of the protocone and the fact that the hypocone and the lingual cingulum are lacking. A tritubercular P^3 without well developed buccal cusp recalls some European forms like *Paracynohyaenodon* (hyaenodontid creodont). However, all these characters are plesiomorphic and inappropriate to relate our taxa to the creodonts rather than to the carnivores.

Hyracoidea

This order is documented by a complete upper molar and by several lower trigonids and talonids (figure 2C). COIFFAIT *et al.* (1984) attributed this hyrax to *Bunohyrax* (Pliohyracidae). This assignment is suggested by the bunodont to bunoselenodont molar morphology, the great asymmetry between the buccal and lingual cusps, the hypocristid not linked with the cristid obliqua, the parastyle and the mesostyle distally compressed, the lingual cingulid which surrounds the protocone but not the hypocone, and by a spur on the mesial base of the protocone. *Bunohyrax* is known by two species from the Jebel El Qatrani Formation (Fayum, Egypt): B. *major* and *B. fayumensis*. The small size of the Algerian fossil and the weak development of its protocone spur exclude this taxon to belong to these Egyptian species (Tabuce *et al.*, 2000). Our fossil could be related to a small size species of *Bunohyrax* distinguished by RASMUSSEN (1989) in the Green Hill Locality of the Fayum. This species was neither described nor figured, therefore it was not possible to establish detailed comparisons.

Anthropoid primates

The origin of Anthropoids is a very controversial question. The low number of known Eocene species, their fragmentary status and the importance of homoplasy make the problem very complex. The last decade has witnessed great advances in our knowledge of early anthropoidean primates in Africa and Asia (see SIMONS and RASMUSSEN, 1994 and DUCROCQ, 1998 for an overview). From Bir El Ater, three anthropoids have been discovered.

Biretia piveteaui de BONIS *et al.*, 1988

Until now, *Biretia* is the only primate described from Bir El Ater. It was considered as the oldest Catarrhini (Anthropoidea) and it could fill the gap between the Omomyid Tarsiiformes and the Catarrhini (de BONIS *et al.*, 1988). However, KAY and WILLIAMS (1994) relate *Biretia* to another anthropoid group – the Parapithecidae – and especially to the species *Quatrania wingi* from the Fayum.

cf. *Algeripithecus*

Two upper molars from Bir El Ater (figure 2D) share with *Algeripithecus* from Glib Zegdou a great degree of bunodonty, the lingual expansion of the paracone, sharpened preparacrista and postmetacrista, and the protocone-pericone link. However, our primate from Bir El Ater cannot be related to the species *A. minutus* because of its twice larger size, a paraconule-preparacrista link and a small hypocone.

Algeripithecus is considered as a primitive Parapithecidae by GODINOT (1994). According to that anthropoid assumption, cf. *Algeripithecus* from Bir El Ater would be a representative of a primitive lineage of *Algeripithecus*, contemporaneous to its sister group (the true Egyptian parapithecids). However, *A. minutus* and the other « African small bunodont simians » are rather considered by HARTENBERGER *et al.* (1997) as cercamoniine adapiforms with European affinities. Our fossil shares evident characters with these primates; anyway the Anthropoid assumption or the Adapid one could be validated only with more complete material.

Oligopithecidae indet

An upper molar (figure 2E) can be clearly related to the Oligopithecidae by a similar size (especially with *Catopithecus*), a distinct hypoparacrista, a crestiform hypocone, a lack of conules and pericone, a lingual expansion of the protocone, a strong pre- and postprotocrista and a well-marked disto-lingual cingulid.

The Oligopithecidae with the Propliopithecidae from Africa (Fayum and Oman) and the Amphipithecidae from the Middle-Late Eocene of South-Asia constitute the three Paleogene families of the Catarrhini. According to JAEGER *et al.* (1998), the greater antiquity of Asian taxa

suggests an Asian origin of catarrhines, and/or an ancient dichotomy between African and Asian catarrhines. This dichotomy could be the result of Eocene faunal exchanges between North Africa and Asia which are also documented by rodents (COIFFAIT *et al.*, 1984), artiodactyls (DUCROCQ, 1997) and carnivores (HOLROYD and MAAS, 1994). The discovery of a catarrhine anthropoid in the Middle-Late Eocene of Bir El Ater contributes to the debate because it is the oldest stratigraphic occurrence of the Oligopithecidae. In the current state of our knowledge, we can propose two hypothesis: either it represents the witnesses of an Asian Middle Eocene immigration, or it documents an unknown older African lineage to date.

Conclusion

The mammalian fauna from Bir El Ater appears to be one of the most diversified from the African Eocene; the majority of the terrestrial eutherian orders, known during the Paleogene in Africa, are represented. African endemic lineages are documented by Proboscidea, Hyracoidea, Macroscelidea, Anomaluridae and Phiomyidae rodents. The diversity of primates is also notable with three anthropoids and at least one undeterminate prosimiiform.

These African Paleogene fossils are important in terms of higher rank taxa systematic and phylogeny. An increased knowledge of these mammals becomes necessary, not only to identify the continent where the anthropoids originate, but also to solve the palaeontological problem of the molecular Afrotheria clade (STANHOPE *et al.*, 1998). Although the « African molecular clade » suggests a common origin for the African endemic groups (Proboscidea, Hyracoidea, Macroscelidea, Tubulidentata, Tenrecidae and Chrysochloridae), no current morphological or palaeontological data agree with that assumption.

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Functional morphology of the rostral head region of *Cryptomys hottentotus* (Bathyergidae, Rodentia)

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Introduction

The African rodent family Bathyergidae (mole-rats) is characterized by a fossorial lifestyle (TULLBERG, 1899/1900; STARCK, 1995). As digging tools mole-rats use the strong gnawing teeth and the forehand (SHERMAN *et al.*, 1991). Previous, morphological studies concerning fossorial adaptations of the Bathyergidae in an evolutionary and, simultaneously, phylogenetic context, have only dealt with external features of the forehand (ADE and ZIEKUR, 1999). Though morphological examinations of several mole-rat species were conducted in recent studies of the rhinarium (ADE, 1998) and the nasal skeleton (MESS, 1997, 1999) of rodents, as well as the facial musculature of mammals (GAMBARYAN, 1989), a comprehensive picture of the rostral head region, including the spatial relations between integument, skeleton and musculature, was not available. Thus, the present study concentrates on the morphology of the rostral nasal and oral region, with special reference to the gnawing teeth, the external rhinarium, the cartilaginous rostral nasal skeleton, the upper *inflexa pellita*, and the associated facial musculature. Based on the presented morphological characters, function is inferred to get an idea

of the organismical context of the rostral head region with regard to the fossorial lifestyle of *Cryptomys*. We have chosen the common mole-rat *Cryptomys hottentotus* (Lesson 1826), because it is regarded as a representative of the Bathyergidae exhibiting the largest number of plesiomorphic characters (MAIER and SCHRENK, 1987; ADE, 1998).

Material and methods

The study is based on the combination of macroscopic and microscopic examinations (tabl. 1). Macroscopic observations and dissection were carried out under a stereomicroscope. Microscopic examination is based on transverse serial sections (40 µm) which were stained according to standard histological techniques (AZAN after Heidenhain). Microscopic drawings, made with the aid of an occular-grid or camera lucida, were used to produce a 3-dimensional graphic reconstruction of the cartilaginous rostral nasal skeleton, i.e., the cupula nasi anterior. The material is part of the collection at the Museum für Naturkunde, Berlin and the Smithsonian Institution, Washington, D.C.

Methodology and terminology

The scope of the present study covers external features and skeletal structures as well as the associated facial musculature. From a functional perspective the discussion elucidates the biological role of the respective structures with regard to fossorial lifestyle. However, it has to be noted that a consideration of the facial musculature in greater detail is beyond the scope of the present paper. For detailed descriptions of the mimetic muscles, the reader is referred to BANKE (1999).

In terms of nomenclature, the description of the rhinarium follows ADE (1998), that of the nasal skeleton MESS (1997, 1999). Terminology of the mimetic muscles is based on MEINERTZ (1942*a-d*,

Material	Methods	Investigated structures
*C. hottentotus** (alcohol-preserved juvenile specimen, HL 35 mm, CRL 97 mm)	macroscopic examination dissection	external features mimetic musculature
*C. hottentotus*** (head of a juvenile specimen, embedded in celloidin, HL 32 mm)	microscopic examination	rostral nasal skeleton, mimetic musculature

* Museum für Naturkunde zu Berlin
** Smithsonian Institution, Washington, D.C.

Table 1
Material and methods (CRL: crown-rump-length; HL: head-length)

1951) and SABAN (1970). Since the homology of the various portions of the *M. naso-labialis profundus* is not analysed within rodents (MEINERTZ, 1942, 1951), the applied terminology functionally refers to the origin of portions.

Results

Strong, rostrally orientated (proodont) incisors form the rostral pole of the head (figure 1A, B). Immediately behind the upper incisors the rostral nasal region exhibits a broad, hairless integument differentiation, i.e., the *Regio rhinarica* (figure 1A). This forms an almost vertically orientated plate that extensively surrounds the small nares. The *Regio rhinarica* continues gradually into the normal hairy skin and is therefore not precisely delimitable. Medially, the *Regio rhinarica* is divided by a vertical *sulcus medianus* (figure 1A) that runs from the supranaric to the supralabial part of the *Regio rhinarica*. The internaric region exhibits two indistinct triangular elements between the *sulcus medianus* and the dorsomedial margin of the nares (fig. 1A). Surface patterns, i.e., rhinoglyphs, are absent. The *regio supralabialis* possesses two integument folds that continue ventrocaudally into the oral region (figure 2B). They pass beside the protruding upper incisors and accompany the palatal rugae caudally. Since the ventral

margin of the *Regio supralabialis* turns directly into the gingiva (figure 1A, 2B), the area above the upper gnawing teeth lacks a hairy lip portion and the gingiva takes a prominent, rostral position.

The central aspect of the *Regio rhinarica* is supported by the cartilaginous rostral nasal skeleton, i.e., the *cupula nasi* anterior (figure 1C). The rostral aspect of the *cupula nasi* anterior is characterized by the lack of an anterior wall and the well-developed processus cupularis at the rostroventral margin of the cupula (figure 1C). Two portions of the *M. naso-labialis profundus* originate on the ventral margin as well as on the medial side of this processus (see below). The area between the processus cupularis and the dorsal margin of the cupula nasi anterior corresponds with the internaric region of the *Regio rhinarica.* Because the cupula has a small lateral extension (figure 1C), it only encloses the area immediately around the nares. Thus, the integument beside and above the nares (figure 1A), i.e., the supralabial and supranaric part of the *Regio rhinarica* is movable. Moreover, the cupula has a restricted rostral extension (figure 1C). Thus, the cupula is ventrally almost completely stabilized by the premaxilla and, instead of the nose tip, the proodont incisors form the rostral pole of the snout (figures 1C, 2C).

In *Cryptomys* the facial musculature of the nasal region consists of: 1) the *M. naso-labialis superficialis* associated with the skin of the *dorsum nasi*; 2) the rostrally directed *M. naso-labialis* and *M. maxillo-labialis*, which are characterized by a bony origin and an insertion on the rostrum surrounding skin behind the *Regio rhinarica*; and 3) numerous portions of the caudally directed *M. naso-labialis profundus* (figure 1B) that originate on the *cupula nasi anterior* (cna, portion 1-3; figure 1C), the adjacent skin of the nasal opening (no, portion 1-2; figure 1B), and the rostrolateral tip of the premaxilla (p, portion 1-3; figure 1C). The *M. dilatator nasi* is lacking in *Cryptomys.* According to their insertion the previously mentioned muscles can be divided in *dorsum nasi-movers* (dnm) and *upper lip-movers* (ulm). Subsequently, within both groups it is possible to distinguish between *for-* and *backward-movers* of the *dorsum nasi* or the upper lip with regard to the caudally or rostrally directed course of fibres. It has to be noted that the *M. naso-labialis profundus* is the only muscle of the nasal region, which is directly associated with the *cupula nasi anterior* and the nasal openings (figure 1B). Therefore, the *M. naso-*

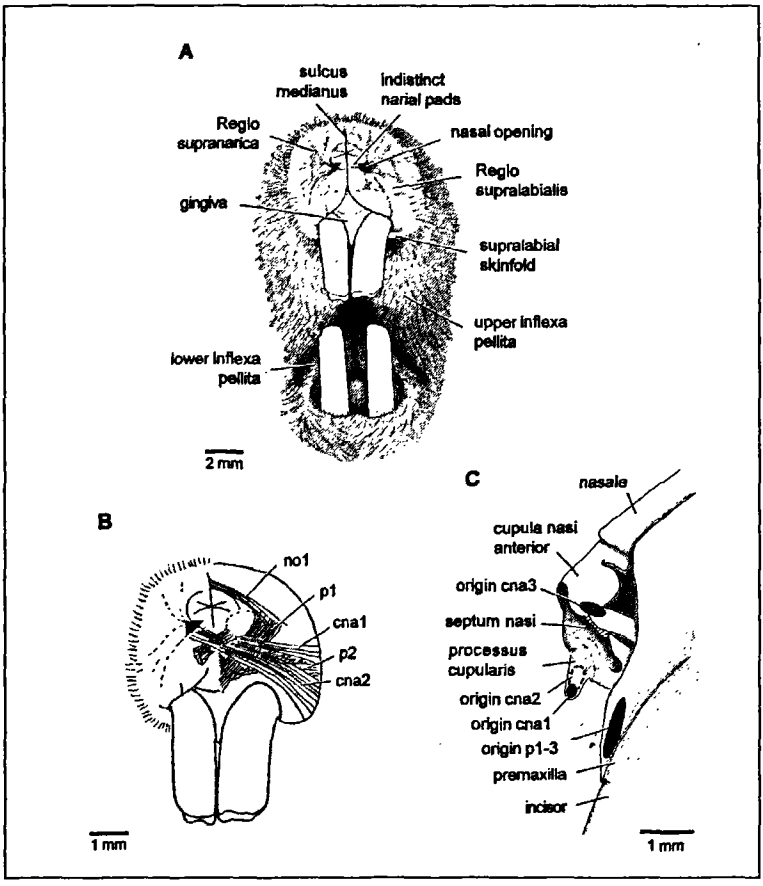

Figure 1
The rostral nasal region of *Cryptomys hottentotus*, rostral view. A, external rostral aspect of the snout; B, *Regio rhinarica* with halfsidely dissected superficial portions of the *M. naso-labialis profundus*, rostral view; C, reconstruction of the rostral nasal skeleton on the base of transverse serial sections, including origins of the *M. naso-labialis profundus*, rostrolateral view.

labialis profundus is not only a *dorsum nasi*- and upper lip-mover, but at the same time a *cupula nasi anterior*- and nasal opening-mover.

The labial complex is strongly developed in *Cryptomys*. Both the upper and lower lip possess the so called *inflexa pellita* (SCHULZE, 1912), i.e., hairy skinfolds that continue medially into the mouth

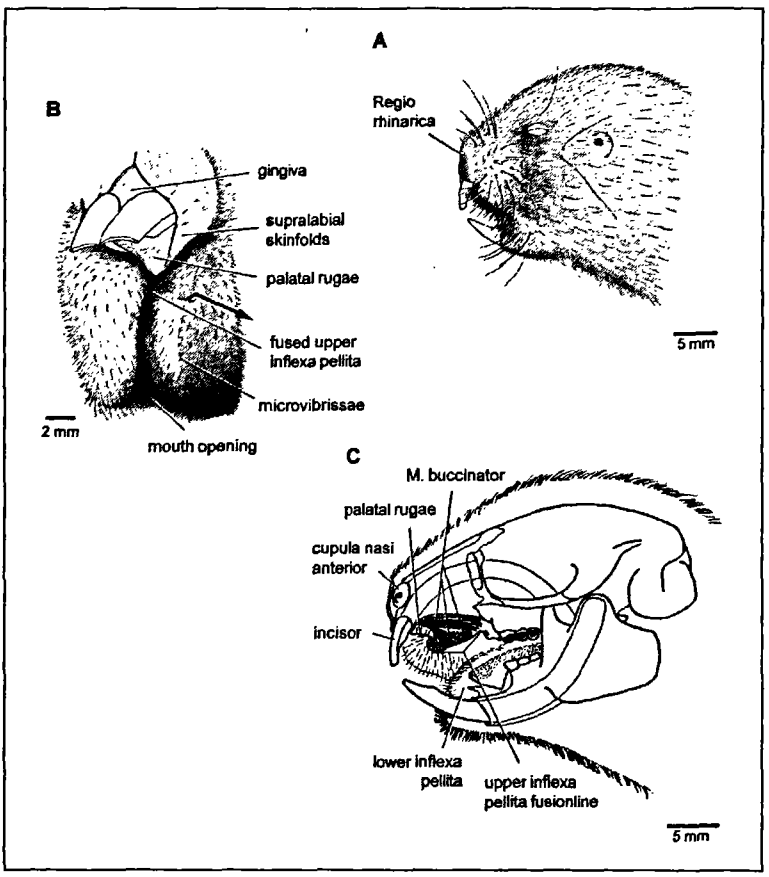

Figure 2
The oral region of *Cryptomys hottentotus*. A, external aspect of the head, lateral view, B, external aspect of the fused upper *inflexa pellita*, rostrolateral view, C, internal aspect of the mouth cavity, lateral view.

cavity (figure 1A). In *Cryptomys* the *inflexa pellita* are situated behind the incisors. Thus, the gnawing teeth occupy an extraoral position and the actual mouth opening is situated behind them. Externally the *inflexa pellita* exhibit microvibrissae (figure 2B) crossing each other when the mouth opening is closed. The upper inflexa are especially prominent in *Cryptomys* (figure 2B). They are fused behind the incisors (figure 2B) and occupy the broad diastemal space completely (figure 2C).

Internally, the upper *inflexa pellita* are associated with facial musculature. For the most part it belongs to the *M. buccinator* (figure 2C), which originates along the fusion line of the upper *inflexa pellita* and on the ventral side of the premaxilla, immediately behind the upper incisors. Furthermore, the *M. bucco-naso-labialis* and the *Platysma myoides pars buccalis* insert inside the upper *inflexa pellita*. The former originates on the lateral side of the premaxilla. The latter originates on the skin of the neck region. According to the course of fibres, within these *upper inflexa pellita-movers* (uipm) the *M. bucco-naso-labialis* and the *Platysma myoides pars buccalis* have to be regarded as mouth cavity-openers, while the *M. buccinator* is a mouth cavity-closer. Also inside the lower *inflexa pellita* facial musculature exists that consists of numerous portions of the *M. buccinator* and the *M. mandibulo-labialis*.

Discussion and conclusions

In the rostral head region of *Cryptomys* the gnawing teeth form a suitable digging tool, because of their extraoral and prominent rostral position (comp. BOLLER, 1970). The *Regio rhinarica* and the underlying *cupula nasi* anterior are situated behind the gnawing teeth. As the latter therefore come into contact with the substrate more often than the rostrum, the incisors also seem to be an important rostral instrument for gathering tactile information from the environment (comp. ADE, 1999). This is most likely the reason that the narial pads, i.e., tactile elements of the nose tip of rodents, are hardly represented in the examined juveniles of *Cryptomys*. That the indistinct pairy elements in the internaric region have to be regarded as narial pads at all is finally supported by ADE (1998), who provides ontogenetic evidence for narial pads in *Cryptomys mechowi*.

In *Cryptomys* the *Regio supralabialis* is continuous with the oral region. In the sense of a broad contact, the supralabial skinfolds of the *Regio rhinarica* can therefore be regarded as a link between the external nose tip and the oral region. Most likely, secretions produced by the nasal glands are transported to the oral region along these supralabial skinfolds. Though such a link has been never mentioned

as explicitly as in the present paper, it is indirectly confirmed by photographs and illustrations of further representatives of the Bathyergidae (STARCK, 1957; ADE, 1998).

The facial musculature of the nasal region enables *Cryptomys* both to modify the entrance of the nasal opening and to move the skin of the rostrum backwards and forwards, i.e., the *dorsum nasi* including the adjacent supranaric part of the *Regio rhinarica* and the upper lip together with the lateral aspect of the *Regio supralabialis*. Two more aspects are probably important with regard to moving the nasal region. Firstly, due to the absence of an anterior wall of the *cupula nasi anterior*, which is regarded as an apomorphic character within hystricognath rodents occurring in all Bathyergidae investigated so far (MESS, 1997, 1999), the dorsal margin of the nasal opening is shifted upwards. Secondly, the lack of the *M. dilatator nasi* in *Cryptomys* most likely causes a high flexibility of the *dorsum nasi* in rostral direction. To date, a comparable condition is only known for the naked mole-rat *Heterocephalus glaber*, where the *M. dilatator nasi* is either strongly reduced or lacking (MEINERTZ, 1951). Taken together, these aspects indicate that the rostral protrusion of the *dorsum nasi* is unlikely to be without influence on the nares, i.e., the forward-movement of the *dorsum nasi* seems to be a covering mechanism of the nasal openings. This mechanism is interpretated as protecting the nasal cavity from penetration by the substrate while digging. This hypothesis is supported by behavioural observations of the naked mole-rat, which is able to cover the nares by an integument fold (STARCK, 1957; HILL *et al.*, 1957).

In *Cryptomys* the *cupula nasi anterior* is ventrally almost completely supported by the premaxilla. It is interpretated as a stabilizer of the rostral nasal cartilage. During digging powerful mechanical forces are transmitted to the top of the head making stabilization necessary.

The upper *inflexa pellita* are fused behind the gnawing teeth and the associated facial musculature consists of mouth cavity-openers and -closers. Thus, in *Cryptomys* the *inflexa pellita* form a very mobile oral instrument that allows a tight closure of the mouth cavity while digging with the gnawing teeth. Due to this, the oral region is protected from penetrating substrate. In this context the external microvibrissae also keep out substrate. The possession of *inflexa pellita* is primitive for rodents (ADE, 1998; FRAHNERT, 1997). It is most likely that

fused upper *inflexa pellita* have to be regarded as an apomorphic character within rodents, based on the distribution of this feature within them (TULLBERG, 1899/1900). However, it is yet to be determined if this fusion is either an autapomorphic character of *Cryptomys* or a mole-rat defining condition within hystricognath rodents.

In conclusion, with regard to fossorial lifestyle the gnawing teeth form a suitable digging tool in the rostral head region, particularly due to their extraoral position. Based on the flexible *dorsum nasi* and the differentiation of the cartilaginous nasal skeleton, the nares can be almost completely closed during digging. The *inflexa pellita* form a mobile oral instrument that protects the actual mouth cavity from irritating substrate during digging.

Prospectively, further examinations within the Bathyergidae and the Rodentia are necessary, especially with regard to the distribution of the following character states: 1) indistinct narial pads; 2) continuation of the *Regio supralabialis* into the oral region; 3) lack of an anterior wall of the *cupula nasi anterior*; 4) lack of the *M. dilatator nasi*, and 5) fusion of the upper *inflexa pellita*. Moreover, future research should be aimed at homologizing the various portions of the *M. nasolabialis profundus* within rodents in order to allow phylogenetic interpretations.

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Comparative craniological systematics of the "Tenrecomorpha" (Mammalia: Insectivora)

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Anke C. Schunke

Ulrich Zeller

Introduction

Insectivore systematics has long been of special interest for mammalogists in the belief that a member of this group represents the ancestral eutherian stock. Despite this attention, the establishment of a phylogenetic classification based on shared derived characters proved to be difficult due to the heterogeneity of the group and the paucity of such characters (cf. BUTLER 1988, MACPHEE and NOVACEK 1993). In part, this is also true for the taxa identified within the Insectivora. Here, a closer look will be taken at the "Tenrecomorpha", consisting of the Malagasy tenrecs and the central and west African otter shrews.

Based mainly on palaeontological data, BUTLER (1972) distinguished the "Tenrecomorpha" from the Erinaceomorpha, Soricomorpha and Chrysochlorida. Due to a misidentification of the original material, this division of the insectivores was abandoned (BUTLER 1988), and both tenrecs and otter shrews are now subsumed under the Soricomorpha (BUTLER 1988; cf. MACPHEE and NOVACEK 1993; MCKENNA and BELL 1997). The label "Tenrecomorpha" is used here to facilitate denoting tenrecs and otter shrews and could be used inter-

changeably with "Tenrecidae" as in HUTTERER (1993) or "Tenrecoidea" as in MCKENNA and BELL (1997). It is *not* used here to distinguish the tenrecs and otter shrews as a higher level taxon to be separated from other insectivore higher taxa.

The two genera of otter shrews, *Potamogale* and *Micropotamogale* are generally placed within the Tenrecidae (e.g. CABRERA 1925; MCDOWELL 1958; CORBET 1971; HUTTERER 1993; MCKENNA and BELL 1997). This classification stems from morphological similarities of *Micropotamogale* with rice tenrecs, Oryzorictinae, (HEIM DE BALSAC and BOURLIÈRE 1955; GUTH *et al.* 1959; 1960) and tenrecs *sensu stricto*, Tenrecinae (cf. CORBET 1971). It is striking, however, that little emphasis was given to distinguishing between plesiomorphic and apomorphic character states (MCKENNA 1975). Here, ontogenetic data of members of the "Tenrecomorpha" are reviewed and, in conjunction with new data, are used for comparison with data from other insectivore, eutherian and metatherian taxa in order to discuss their polarity.

Material and methods

Serial histological frontal sections (6-100 µm distance between sections) of five tenrec and otter shrew species of various ontogenetic stages were studied, together with *Erinaceus europaeus*, *Tupaia belangeri*, and *Monodelphis domestica* as out-groups for the Insectivora, Eutheria and Metatheria, respectively (table 1). Histological sections were used in order to include soft tissue data that otherwise is lost in studies of macerated museum material, whereas ontogenetic series (available to varying extent in most species studied) offered the opportunity to identify temporary and changing characters.

Graphic reconstructions or plate models of entire skulls or parts thereof were available for *Hemicentetes semispinosus* (14 mm headlength [hl]; SCHUNKE and ZELLER, in prep.); *Potamogale velox* (20 mm hl; BEHRENS 1998); *Erinaceus europaeus* (13 mm hl, 18 mm hl, adult; GIERE and ZELLER 1998, and unpublished data) and *Tupaia belan-*

Classification	*Species*	Approximate, inferred headlength
Insectivora: "Tenrecomorpha"	*Echinops telfairi*	18 mm
Insectivora: "Tenrecomorpha"	*Echinops telfairi*	32.8 mm [1?]
Insectivora: "Tenrecomorpha"	*Hemicentetes semispinosus*	14 mm
Insectivora: "Tenrecomorpha"	*Hemicentetes semispinosus*	23 mm
Insectivora: "Tenrecomorpha"	*Tenrec ecaudatus*	48 m [1?]
Insectivora: "Tenrecomorpha"	*Micropotamogale lamottei*	8.5 mm
Insectivora: "Tenrecomorpha"	*Potamogale velox*	20 mm
Insectivora: "Tenrecomorpha"	*Potamogale velox*	25 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	6.5 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	8.7 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	13 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	18 mm [2]
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	25.5 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	18 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	23.5 mm
Insectivora: Erinaceomorpha	*Erinaceus europaeus*	n/a [1]
Scandentia: Tupaiidae	*Tupaia belangeri*	several [3]
Marsupialia: Didelphidae	*Monodelphis domestica*	15.5 mm

1. Adult specimen; 2. specimen incomplete; 3. Cf. Zeller 1987.

Table 1
Species and specimens examined.

geri (cf. ZELLER 1983; 1987). Models aided in the positional interpretation of the cranial characters involved, whereas graphic reconstructions were mainly used to examine skull details, e.g. the paraseptal cartilage (unpublished data).

Results and discussion

Prior to the description of morphological data available from the study of histological sections, a brief review of representative diagnostic characters (as presently used) for each tenrecs and otter shrews species and the "Tenrecomorpha" is given. In various recent classifications of (African) insectivores, resolution ends at the family level and excep-

tions for sub-families from the characters given for the Tenrecidae are noted (McDowell 1958; Findley 1967; Lawlor 1976; Yates 1984). Only an identification manual for African mammals (Meester and Setzer 1971) differed in providing a separate entry for Potamogalinae (Corbet 1971) in the chapter on Tenrecidae (Genest and Petter 1971). A similar approach is taken here in not distinguishing between Geogalinae, Oryzorictinae and Tenrecinae when looking at "tenrecs" as opposed to otter shrews. This, however, does not imply a supposed underlying phylogeny.

Recent tenrecs are diagnosed as possessing a clavicle and completely free or webbed hind toes, whereas otter shrews lack a clavicle and have second and third hind toes that are joined basally (Cabrera 1925; Guth *et al.* 1960). Cranial diagnostic characters for the otter shrews include an osseous auditory bulla with a large contribution of the basisphenoid (Heim de Balsac 1954, Guth *et al.* 1959) and the presence of a condyloid canal not found in other tenrecs (McDowell 1958). According to Heim de Balsac (1954), tenrecs do not possess a bulla similar to that of the Potamogalinae. This view is not entirely shared by MacPhee (1981), who can only see minor differences in his phylogenetic interpretation of bullar characters. Unfortunately, no published interpretation on the postcranial characters could be found. Nevertheless, a multiple origin can be assumed for the reduction of the Clavicula and the development of syndactyl toes (e.g. Carnivora and Macropodidae, respectively).

A character identified by the histological approach in an embryo of *Potamogale velox* is the absence of a nasolacrimal duct (Behrens 1998) which was also found to be missing in *Micropotamogale lamottei* in this study. This reduction of the canal linking the eye with the nasal cavity may be considered apomorphic for otter shrews since the duct is present in *Hemicentetes semispinosus* (Schunke and Zeller, in prep.), *Tenrec ecaudatus*, *Erinaceus europaeus* and *Tupaia belangeri* (own observation; Zeller 1983). These data suggest the presence of a nasolacrimal duct in the insectivore morphotype, which, nevertheless, needs to be verified with data of the other Insectivore taxa.

The reduction of the nasolacrimal duct in a semi-aquatic animal might be regarded as an adaptation to the limnic habitat. However, in other semi-aquatic animals such as beavers (*Castor fiber* and *Castor*

canadensis), this canal is present (FRAHNERT 1998), which questions this interpretation.

Another cranial character visible only on frontal histological sections was found by SCHUNKE and ZELLER (1996) for the Tenrecinae: *Hemicentetes semispinosus* and *Tenrec ecaudatus* possess, being macrosmatic animals (cf. STEPHAN *et al.* 1991), a *Recessus ethmoturbinalis* that is extended caudally if compared to otter shrews and other insectivores. This results in a lateral displacement and a dorsal extension of the *Cavum epiptericum*, which then forms a recessus lateral to the posterior part of the *Paries nasi* (SCHUNKE and ZELLER 1996). This ventral recessus of the *Cavum epiptericum* houses the sphenopalatine ganglion besides the second branch of the trigeminal nerve. SCHUNKE and ZELLER (1996) considered this to be an autapomorphic character for the tenrecs, a hypothesis that is supported for the Tenrecinae by the comparative data available in the present study. Judging from brain characteristics (STEPHAN *et al.* 1991), it can be assumed that both Oryzorictinae and Geogalinae possess a caudally extended *Recessus ethmoturbinalis* and thus a structure of the *Cavum epiptericum* similar to that of the tenrec species examined.

BUTLER (1972) based his new taxon "Tenrecomorpha" mainly on the long infraorbital canal present in otter shrews and a fossil tenrec, which, however, turned out to be based on a misidentified erinaceid (BUTLER 1988). Other cranial characters shared by tenrecs and otter shrews include zalambdodont molars ("pseudo-dilambdodont" in *Potamogale velox*; cf. GUTH *et al.* 1959; 1960), an incomplete zygomatic arch (jugal reduced), a modified entoglenoid process and the structure of the auditory bulla (FINDLEY 1967; YATES 1984). Zalambdodont teeth, which have long been used for classification (e.g. GILL 1889; VAN VALEN 1967), also occur in Solenodontidae and Chrysochloridae within the Insectivora as well as in *Notoryctes* (Metatheria: Notoryctidae) and BUTLER (1972) critically discusses the phylogenetic relevance of this character. No information on the remaining characters was found.

Histological sections provide some additional information in the examination of the "Tenrecomorpha". SCHUNKE and ZELLER (in prep.) found a missing connection between the paraseptal cartilage and the *Lamina transversalis anterior* in both tenrecs and otter shrews in their extensive histological study of these taxa. However, in the older spec-

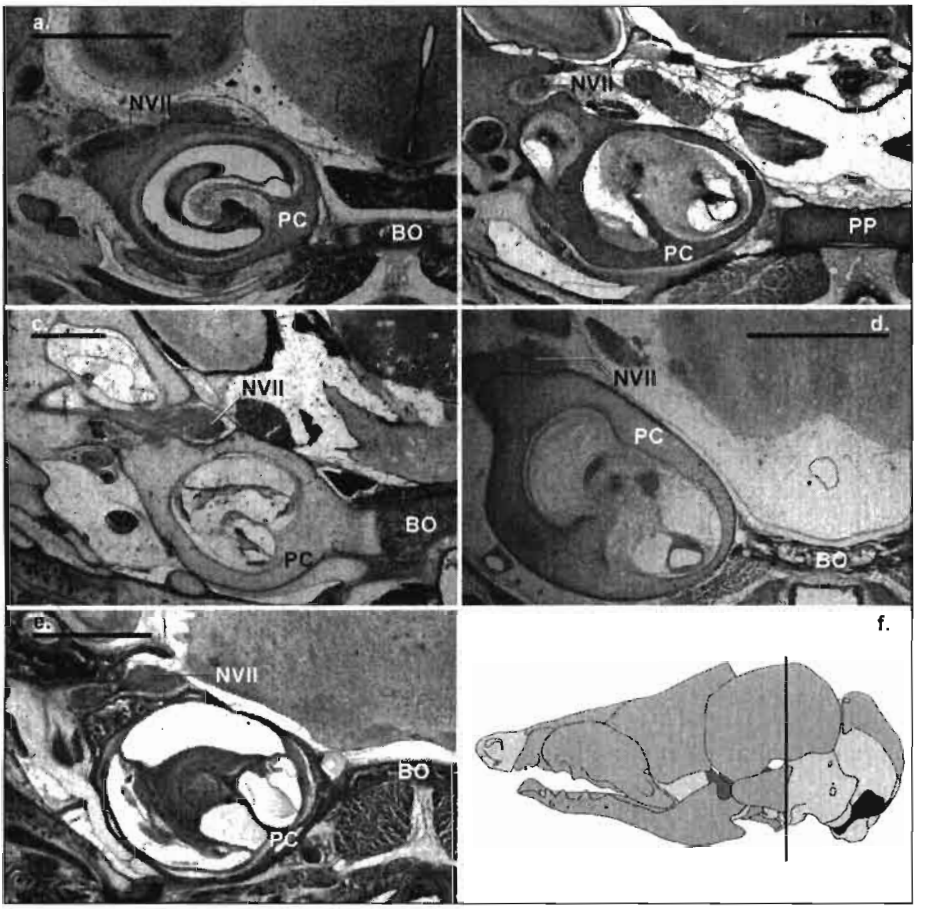

Figure 1
Frontal sections through the *Pars cochlearis* of the auditory capsule of:
a. *Hemicentetes semispinosus*;
b. *Potamogale velox*;
c. *Erinaceus europaeus*;
d. *Tupaia belangeri*;
e. *Monodelphis domestica*; Horizontal bars equal 1 mm;
f. Lateral view of a reconstruction of *Hemicentetes* (modified after Schunke and Zeller 1996), vertical bar indicates approximate plane of sections at the internal opening for the *Nervus facialis*.
Abbreviations:
PC: *Pars cochlearis;*
PP: parachordal plate;
BO: Basioccipitale;
NVII: *Nervus facialis*.

imen of *Potamogale velox*, these cartilaginous structures are joined (SCHUNKE and ZELLER, in prep.). Viewed in the light of the greater ontogenetic database available for the erinaceids in this study (prenatal and postnatal stages including the adult), this character is recognized as undergoing substantial changes during ontogeny, i.e. in *Erinaceus europaeus*, the paraseptal cartilage is linked to the *Lamina transversalis anterior* during embryogenesis and is separated in the adult. Thus, it must be cautioned that unless it is clear that the characters concerned do not change during ontogeny, only ontogenetic stages which are at a similar developmental level may be compared when analyzing embryonic data.

Nevertheless, further evidence was found for the "Tenrecomorpha" in the sectioned material. In all tenrec and otter shrew specimens examined, the *Pars cochlearis* of the ear capsule formed a low angle with the parachordal plate / Basioccipitale, resulting in an almost horizontal position of this structure (figure 1). This character was retained throughout ontogeny. In addition, the medio-ventral side of the *Pars cochlearis* maintains the angle given by the ventral side of the parachordal plate, a character that is obscured in macerated material. This character was found in all specimens except *Echinops telfairi*. In all species used as out-groups, the *Pars cochlearis* is angled against the horizontal plane and the medio-ventral side of this structure forms an angle with the parachordal plate. Thus, these characters can be regarded as apomorphies for the "Tenrecomorpha", assuming a similar composition of the inner ear in the Oryzorictinae and Geogalinae.

Concluding from the evidence compiled here, despite the ontogenetic apomorphies presented and several shared (but not necessarily) derived characters, not much evidence for the "Tenrecomorpha" is found. This corresponds partly to the results of a recent study on tenrecid phylogeny, where some tree topologies failed to indicate monophyly of the Tenrecidae (ASHER 1999). A cladistic review of the characters originally used to link otter shrews and tenrecs is necessary to establish the monophyly of the "Tenrecomorpha" as used here. For the Insectivora, this was achieved by BUTLER (1988) and, more explicitly, by MACPHEE and NOVACEK (1993). However, the morphological evidence is scanty and more characters are needed, which may be supplied by studies of serially sectioned specimens. This is necessary in the light of recent molecular studies of eutherian phylogeny

(SPRINGER *et al.* 1997; STANHOPE *et al.* 1998; EMERSON *et al.* 1999) that question insectivore monophyly by separating Tenrecidae and Chrysochloridae into a newly established clade, the "Afrosoricida" (STANHOPE *et al.* 1998). Unfortunately, neither of the molecular studies included data from otter shrews, thus no molecular evidence for the "Tenrecomorpha" is available.

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Was Zambia a cradle of the genus *Cryptomys* (Bathyergidae, Rodentia)?

A further new ancestral (?) species of *Cryptomys* from Zambia

Mathias Kawalika

Hynek Burda

Diana Brüggert

Introduction

African mole-rats of the genus *Cryptomys* Gray, 1864, (Bathyergidae), are subterranean rodents occurring from semi-arid to mesic habitats in different soil types over a wide geographic range from Ghana to the Cape Province in South Africa. Pronounced polymorphism in body size, coloration and many cranial features makes taxonomic treatment of this genus very difficult. Accordingly, different authors recognised different numbers of species. Thus for instance, 44 to 49 species of *Cryptomys* have been named by ALLEN (1939) or ELLERMANN (1940), respectively, whereas only three have been considered by NOWAK (1991). It has been repeatedly demonstrated (ROSEVEAR, 1969; ANSELL, 1978; WILLIAMS *et al.*, 1983; NEVO *et al.*, 1986, 1987; HONEYCUTT *et al.*, 1987, 1991; JANECEK *et al.*, 1992) that classical morphological qualitative and quantitative traits are not sufficient for the species diagnosis in *Cryptomys*, and additionally, cytology, serology, and molecular genetics should be considered.

Taking these aspects into account, HONEYCUTT *et al.* (1991) have recognised seven species: *Cryptomys bocagei* (De Winton, 1897); *Cryptomys damarensis* (Ogilby, 1838); *Cryptomys foxi* (Thomas, 1911); *Cryptomys hottentotus* with subspecies *C. h. hottentotus* (Lesson, 1826); *C. h. natalensis* (Roberts, 1913), *C. h. darlingi* (Thomas, 1895); *C. h. amatus* (Wroughton, 1907); *C. h. whytei* (Thomas, 1897); *Cryptomys mechowi* (Peters, 1881); *Cryptomys ochraceocinereus* (Heuglin, 1864); *Cryptomys zechi* (Matschie, 1900). However, the authors had studied *Cryptomys* mole-rats originating from the Southern African Subregion and had no molecular or karyologic data on more northern populations. Based on the relative uniformity of *Cryptomys* from South Africa they considered also the common mole-rats from subequatorial central Africa to belong mainly to the *C. hottentotus* species. Subsequent karyological studies demonstrated, however, that *Cryptomys darlingi* and *Cryptomys amatus* should be considered distinct species (AGUILAR, 1993; MACHOLÁN *et al.*, 1998). Besides that, our allozyme and karyotype studies (FILIPPUCCI *et al.*, 1994, 1997; BURDA *et al.*, 1999) identified two additional species within the small form of *Cryptomys* in Zambia: *C. anselli* and *C. kafuensis*. Furthermore, we showed that *Cryptomys* from the Malawian Nyika, characterised by the karyotype 2n = 46 should be considered a distinct species which we call here (on the grounds of geographical vicinity to the type locality of *C. hottentotus whytei*) *C. whytei* (CHITAUKALI *et al.*, this volume).

In this paper we report finding of another population of *Cryptomys* from Kasama, Zambia, which constitutes a distinct species and the karyotype of which may provide new insight into (chromosomal) speciation of *Cryptomys*.

Material and methods

Two mole-rats were obtained from Kasama, Zambia, (S 10: 16; E 31: 0; altitude about 1 500 m). The habitat is characterised by cultivated fields within savanna woodland (miombo), with an average annual rainfall of 1 073 mm (monthly range 1-2 750, with 4 virtually rain-

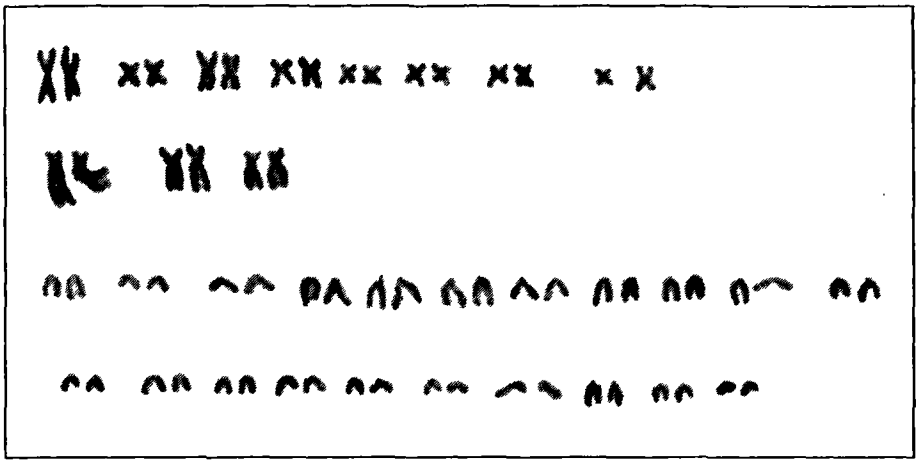

Figure 1
The karyotype of a female *Cryptomys* from the locality Kasama, Zambia.

less months per year) and mean temperatures (monthly averages) varying between 22-24°C (October) and 16-18 °C (July).

Chromosome preparations were obtained from one adult female (body weight 100 g), directly from the bone marrow of long bones using the standard method (LEE, 1969; LEE and ELDER, 1977).

Results

The karyotype of the female *Cryptomys* from Kasama was 2N = 64 (NF = 86) and consisted of 11 biarmed (four metacentic, six submetacentric, and one subtelocentric) and 21 acrocentric chromosome pairs (figure 1). The largest chromosome pair was subtelocentric, three other distinctly large pairs were biarmed, submetacentric. Two submetacentric pairs differed in their arm ratio: the length of the arms was fairly similar in one pair, whereas it was distinctly different in the other. A biarmed pair of medium size was submetacentric, the

Table 1
Characteristics of known karyotypes (representing different species) of *Cryptomys*.
M – metacentric,
SM – submetacentric,
ST – subtelocentric,
A – acrocentric,
NF – fundamental number of chromosome arms in a female karyotype.

Species	Occurrence	Karyotype (2n)	Autosomes M, SM	Autosomes A, ST	Sex chromosomes X	Sex chromosomes Y	Arms (NF) a NF	Arms (NF) NF (XX)	Authors
C. mechowi	Zambia (Copperbelt Province)	40	18	1	M/SM	SM	76	80	MACHOLÁN *et al.* 1993
C. whytei	Malawi (Nyika)	46	15 M, 8 A					92	BURDA, CHITAUKALI, BRÜGGERT (unpubl.)
C. amatus	Zambia (Central Province)	50	22	2	M	A	92	96	MACHOLÁN *et al.* 1997
C. h. hottentotus	South Africa (Transvaal)	54	25	1	SM	?	102	106	NEVO *et al.* 1986
C. h. natalensis	South Africa (Natal)	54	24	2	SM	A	100	104	NEVO *et al.* 1986
C. darlingi	Zimbabwe	54	14	12	A	M	80	82	AGUILAR 1993
C. kafuensis Zambia	(Southern Province)	58	9	19	M	dot	74	78	BURDA *et al.* 1999
KASAMA Zambia	(Northern Province)	64	11 M, 21 A					86	present paper
C. foxi	Cameroon	66 (70)	26 (28)	6	SM	M	116 (124)	120 (128)	WILLIAMS *et al.* 1983
C. anselli	Zambia (Lusaka Province)	68	5	28	M	A	76	80	BURDA *et al.* 1999
C. damarensis	Namibia	78	8	30	M	SM	92	96	NEVO *et al.* 1986

remaining four biarmed pairs were metacentric. The acrocentric chromosomes formed an array with continually diminishing size. The largest acrocentric chromosomes were similar in size to the medium-sized submetacentric pair.

Discussion

Earlier studies of bathyergid karyotypes indicated, in contrast to the situation in many other subterranean rodents (particularly spalacids and ctenomyids) remarkable chromosome stability and conservatism. Thus, only one karyotype (2N = 60, GEORGE, 1979) was described in the eusocial naked mole-rat (*Heterocephalus glaber*), the distribution of which covers 14 latitude degrees. Two karyotypes (2N = 60, GEORGE, 1979; 2N = 62, SCHARFF, 1999) are known in solitary *Heliophobius argenteocinereus*, distributed across 18 latitude degrees, and three chromosome species of *Cryptomys* were defined in the Southern African Subregion, covering about 17 latitude degrees: 2N = 78 (or 74) in *C. damarensis* and 2n = 54 in *C. hottentotus* (NEVO *et al.*, 1986), and 2N = 54 in *C. darlingi* (AGUILAR, 1993).

Contrary to those earlier findings on bathyergids from other regions of Africa, within a relatively narrow belt covering 3 latitude degrees in Zambia, we have already identified five distinct karyotypes, representing five different species of *Cryptomys*: 2N = 40 (MACHOLÁN *et al.*, 1993), 2N = 50 (MACHOLÁN *et al.*, 1998), 2N = 58 and 2N = 68 (BURDA *et al.*, 1999), 2N = 64 (present study). Since only few populations were studied within the given belt and since Zambia itself extends from north to south over ten latitude degrees, many more karyotypes are expected to occur there. Systematic faunistic, taxonomic and ecological study of *Cryptomys* in Zambia may be thus of high interest for an assessment of chromosomal evolution in this "hotspot" region and its historical/ecological causes, compared to the relative stability in the Southern Africa Subregion.

Among the karyotypes of *Cryptomys* known to date, only *C. anselli*, *C. damarensis*, *C. kafuensis* and *Cryptomys*-Kasama have markedly more acrocentrics than metacentrics in their karyotypes (Table 1,

anselli	*damar.*	*kafuens.*	Kasama	*darlingi*	*whytei*	*mecho.*	*amatus*	*natal.*	*hottent.*	*foxi*
										X
									X	X
								X	X	X
								X	X	X
							X	X	X	X
							X	X	X	X
							X	X	X	X
							X	X	X	X
							X	X	X	X
						X	X	X	X	X
						X	X	X	X	X
						X	X	X	X	X
						X	X	X	X	X
						X	X	X	X	X
					X	X	X	X	X	X
				X	X	X	X	X	X	X
				X	X	X	X	X	X	X
				X	X	X	X	X	X	X
				X	X	X	X	X	X	X
			X	X	X	X	X	X	X	X
		X	X	X	X	X	X	X	X	X
	X	X	X	X	X	X	X	X	X	X
	X	X	X	X	X	X	X	X	X	X
	X	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	X	X
V	V	V	V	V	V	V	V	V	V	V
V	V	V	V	V	V		V	V		V
V	V	V	V	V	V					V
V	V	V	V	V	V					V
V	V	V	V	V	V					V
V	V	V	V	V	V					V
V	V	V	V	V	V					V
V	V	V	V	V	V					
V	V	V	V	V						
V	V	V	V							
V	V	V	V	V						
V	V	V	V	V						
V	V	V	V	V						
V	V	V	V	V						
V	V	V	V	V						
V	V	V	V	V						
V	V	V	V	V						
V	V		V							
V	V									
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V	V									
	V									

Table 2
Schematic representation of known karyotypes of *Cryptomys*.
X - metacentric and submetacentric chromosomes;
V - subtelocentric and acrocentric chromosomes.

table 2). Assuming that different chromosomal fusions might have taken place in the evolution of individual lineages we suggest that the named species form an ancestral clade. Interestingly, they all occur in Zambia along a SW-NE axis, eastwards of the Muchinga Escarpment, along the presumed site of the "arid corridor". We suggest that the other karyotypes (species): *C. amatus, C. mechowi, C. darlingi, C. hottentotus, C. whytei*, and the supraequatorial (Central and West African) *Cryptomys* descended from the above named lineage.

We are aware that chromosomal evolution of *Cryptomys* may have involved also rearrangements other than fusions (fissions, pericentric inversions). Unless banded karyotypes are available and compared, the above suggestion remains a hypothesis which should be tested. Nevertheless, our scenario suggesting that *C. anselli, C. damarensis, C. kafuensis*, and *Cryptomys* Kasama (all with more acrocentrics than metacentrics) represent an ancestral clade from which other species have separately evolved is more parsimonious with respect to the geographical distributional pattern and paleoecological (course of the arid corridor) aspects.

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Determinants of the distribution and radiation of African mole-rats (Bathyergidae, Rodentia)

Ecology or geography?

Hynek Burda

Introduction

The African endemic rodent family Bathyergidae includes five genera of subterranean mole-rats exhibiting different social behaviour: three genera (*Bathyergus*, *Georychus* and *Heliophobius*) comprise animals of solitary habits, two genera, *Heterocephalus* and *Cryptomys* are characterized by highly social habits. Whereas four genera are monotypic (or with no more than two species recognised), karyotypically rather conservative, and their distribution is clearly delimitated, the genus *Cryptomys* is polytypic with at least 14 distinguishable species having distinctly different karyotypes, and widely distributed in sub-Saharan Africa (table 1). Particularly the unique social biology (eusociality) of the naked mole-rat (*Heterocephalus glaber*) and the common mole-rat (*Cryptomys* spp.) has triggered the interest in the family, with the consequence that both genera rank currently to the most thoroughly studied and best known African rodents (cf. BURDA *et al.*, 1999, 2000; HONEYCYUTT, 1991; HONEYCUTT *et al.*, 1992; SHERMAN *et al.*, 1991).

Many sociobiologists linked sociality of mole-rats to ecological factors (SHERMAN *et al.*, 1991; JARVIS *et al.*, 1994, 1998; BENNETT and FAULKES, 2000). This fact tends to be simplified by the authors of

secondary or tertiary texts on mole-rats who then consider the (eu)social species to be typical inhabitants of harsh arid climates, while solitary species are assumed to occupy mesic regions and be ecologically precluded from living in semi-deserts. The determinants of the social system and of the distribution of a particular species are generally considered to be of ecological nature (food resources, precipitation, soil characteristics).

Here, I challenge this broadly adopted view on two points:

1. Hitherto, ecological correlations are too rough and have been oversimplified. So far, only selected data and not the whole geographical range of species-relevant data have been sampled. Data on animals from selected study sites were taken as representative for the whole distribution area of a given species. This fact can be exemplified through correlation with precipitation data. It should be noted that soil characteristics and food resources may vary even on a much smaller scale, and for many widely distributed species it is almost impossible, at the current state of knowledge, to cover the whole spectrum of these habitat characteristics.

2. Geographical (geomorphological) determinants of the distribution pattern of bathyergids have never been considered.

Material and methods

Sources of locality records

Data on localities of a particular species of bathyergid mole-rats were obtained from the literature and my own published and unpublished data. Only unambiguously defined localities were considered to which geographic coordinates were provided or could be allocated. The sources for locality records are given in Table 1 (in some cases, when the localities were revisited several times, only one source is given):

Species mapping

Localities of species were attributed to (and defined by) quarter-degree square loci which correspond to the 1:50,000 map sheets and were numbered in the same way (cf. ANSELL, 1978; ANSELL and DOWSETT,

Species (Descriptor)	Type locality	2n (NF/2n)	Country	Sources for proved locality records
Cryptomys amatus (Wroughton, 1907)	Chibale (Zambia)	50 (1.92)	ZAM	Macholan *et al.* (1998)
Cryptomys anselli (Burda *et al.*, 1999)	Lusaka (Zambia)	68 (1.18)	ZAM	Burda *et al.* (1999)
Cryptomys bocagei (De Winton, 1897)	Hanha (Angola)	58 (1.45)	ANG, NAM	Aguilar (pers. comm), Allen (1939), Ferdinando (pers. comm.)
Cryptomys damarensis (Ogilby, 1838)	Damaraland (Namibia)	74/78 (1.2-1.4)	NAM, BOT, SAR, ZAM, ZIM	Aguilar (pers. comm.), Allen (1939), Honeycutt *et al.* (1987), Janecek *et al.* (1992), Lovegrove and Knight-Eloff (1988), Nevo *et al.* (1987), Smithers (1968)
Cryptomys darlingi (Thomas, 1895)	Harare (Zimbabwe)	54 (1.52)	ZIM	Aguilar (1993)
Cryptomys foxi (Thomas 1911)	Panyam (Nigeria)	66/70 (1.82)	CAM, NIG	Allen (1939), Williams *et al.* (1983)
Cryptomys hottentotus (Lesson, 1862)	Paarl (South Africa)	54 (1.96)	SAR	Allen (1939), Janecek *et al.* (1992), Nevo *et al.* (1987)
Cryptomys kafuensis (Burda *et al.*, 1999)	Itezhi-Tezhi (Zambia)	58 (1.34)	ZAM	Burda et al. (1999)
Cryptomys "Choma" formally not yet described	Kalomo (Zambia)	50 (1.52)	ZAM	Aguilar (pers. comm.)
Cryptomys Kasama formally not yet described	Kasama (Zambia)	64 (1.34)	ZAM	Kawalika *et al.* (this volume)
Cryptomys mechowi (Peters, 1881)	Malange (Angola)	40 (2.00)	ANG, ZAM, CON	Allen (1939), Ansell (1978), Ansell and Dowsett (1988), Burda and Kawalika (1993, unpubl.), Hill and Prior (1941), Macholan *et al.* (1993), Palata (pers. comm.), Scharff (1998)
Cryptomys ochraceocinereus (Heuglin, 1864)	Bahr-el-Ghazal (Sudan)	?	SUD, CAR	Allen (1939)
Cryptomys Nyika (= *C. whytei*? -Thomas, 1897)	Nyika (Karonga) (Malawi)	46 (2.0)	MAL	Chitaukali *et al.* (this volume)
Cryptomys zechi (Matschie, 1900)	Kete-Krachi (Ghana)	?	GHA	Allen (1939)

Table 1

Continued on next page.

Species (Descriptor)	Type locality	2n (NF/2n)	Country	Sources for proved locality records
Common (small-sized) *Cryptomys* of uncertain taxonomic status			BOT, SAR, ZIM, ZAM, MAL, MOZ, TAN	Allen (1939), Allen and Loveridge (1933), Ansell (1978), Ansell and Dowsett (1988), *Burda (unpubl.)*, Davies and Jarvis (1986), Dhliwayo (pers. comm.), Roberts (1917), Smithers (1968).
Bathyergus janetta (Thomas and Schwann, 1904)	Port Nolloth (South Africa)	54 (2.00)	SAR	Allen (1939), Davies and Jarvis (1986), De Graaff (1981), Janecek *et al.* (1992), Nevo *et al.* (1987).
Bathyergus suillus Schreber, 1782)	(Cape of Good Hope (South Africa)	56 (1.89)	SAR	
Georychus capensis (Pallas, 1778)	Cape of Good Hope (South Africa)	54 (1.92)	SAR	
Heliophobius argenteocinereus (Peters, 1846)	Tete (Mozambique)	60-62 (1.90-1.97)	KEN, TAN, MAL, ZAM MOZ	Allen (1939), Ansell (1978), Ansell and Dowsett (1988), Chitaukali *et al.* (this vol.), De Graaff (1981), George (1979), Janecek *et al.* (1992), Kingdon (1974), Peters (1852), Scharff (1998), Thomas (1917)
Heterocephalus glaber (Rüppel, 1842)	Shoa (Ethiopia)	60	ETH, KEN, SOM	Allen (1939), Faulkes *et al.* (1997), George (1979), Hill (1953), Hill *et al.* (1957), Hollister (1919), Jarvis and Bennett (1991), Kingdon (1974), Nurhusien (pers. comm.), Porter (1957), Senna (1915), Sherman *et al.* (1991), Starck (1957), Thomas (1885, 1903, 1904).

Table 1 *(suite)*
The list of currently distinguished species of Bathyergidae, their descriptors, type localities, karyotype characterististics, distribution across countries, and sources of proved locality records. 2n = diploid chromosome number. The ratio betwen 2n and NF (fundamental number of chromosome arms as established in a female) gives information on the proportion of biarmed (metacentric) chromosomes (high ratio) and uniarmed (acrocentric) chromosomes (low ratio) in the karyotype. Descriptors of karyotypes and the country where the karyotyped specimens came from are pointed out. ANG = Angola, BOT = Botswana, CAM = Cameroon, CAR = Central African Rep., CON = Democratic Rep. Congo, ETH = Ethiopia, GHA = Ghana, KEN = Kenya, MAL = Malawi, MOZ = Mozambique, NAM = Namibia, NIG = Nigeria, SAR = South Africa, SOM = Somalia, SUD = Sudan, TAN = Tanzania, ZAM = Zambia, ZIM = Zimbabwe.

1988). In figures 1 and 2, distribution of species were plotted by full-degree square loci, for the purpose of clarity.

Correlation with climatic data

For each quarter-degree square in which mole-rats were recorded, the nearest (within a radius of about 30 km) climatic station was identified according to the Global Historical Climatological Network database: <http://www.ncdc.noaa.gov/ol/climate/research/ghcn/ghcn.html>. Monthly precipitation data were retrieved from the database and mean values were counted for particular months. Altogether 179 climatic stations were considered. For each station there were on average 55 (SD 22, 10-136) year recordings (i.e., monthly data for about 55 years). All available monthly records for each station were averaged. If there were more climatic stations within the given radius of a mole-rat locality their mean precipitation data were averaged, so that eventually only one set of climatic data was related to each quarter-degree square. In a further step, means of precipitation parameters of quarter-degree squares were averaged to get a mean value characterizing the respective full-degree square. Eventually, "species-characteristic means" and standard deviations were counted from average values of all full-degree-squares in which a particular mole-rat species was recorded. In other words, mean values were counted as weighed means in a process of subsequent averaging steps. Besides that, the real climatic relevance of the precipitation station for a given locality was checked using a detailed climate-atlas (WALTHER and LIETH, 1967).

Results and discussion

Geographical pattern of the distribution

Although in many areas (at least within full-degree squares) up to three species of mole-rats live sympatrically, generally, there is an obvious geographical pattern in distribution of mole-rats along the main NE-SW-axis. *Heterocephalus glaber* is the only genus and

species to occur in NE Africa (Somalia, Ethiopia, Kenya). Apparently, it has not crossed the main and the Eastern branch of the Rift Valley, so that the East African Horn can be considered as the centre of origin of this monotypic genus. This conclusion is supported by the fossil records (DENYS, 1999). More southwards (southern Kenya, Tanzania), it is replaced by *Heliophobius*. In fact, the area of (original) distribution of this (also monotypic?) genus seems to be confined by both branches of the Rift Valley, the Muchinga Escarpment, mountains at the Kenya-Tanzania borders to the North, and the Zambezi river to the South. A number of *Cryptomys* species diversified in central subequatorial Africa, i.e., on the west "bank" of the Rift Valley (its western branch and Muchinga Escarpment). Further southwards, *Cryptomys* diversified along two parallel streams: The western branch (Zambia, Botswana, Namibia) is represented by *C. damarensis*, while the eastern branch (South Africa) comprises two subspecies of *C. hottentotus*: *C. h. hottentotus* (westwards) and *C. h. natalensis* (eastwards). Between the Zambezi and the Limpopo rivers (in Zimbabwe), only one *Cryptomys* species, *C. darlingi*, has been identified so far. On the southern tip of the continent, mainly in coastal regions, two genera, *Georychus* and *Bathyergus* with two species in the latter genus, have diversified. In west Africa north of the Equator apparently only isolates of *Cryptomys* occur.

The published maps of distribution of mole-rats (HONEYCUTT, 1992; HONEYCUTT *et al.*, 1991; JARVIS *et al.*, 1994) indicate usually only outer limits of distribution. The current method of plotting only proved records by degree squares, as is usual in faunistic studies, provides a clearer picture and a solid basis for further testing and complementary studies. It is apparent from figures 1 and 2 that the current distribution of bathyergids is geographically continuous, and well outlined in most species (rather than consisting of intermingled isolates of different species) and can be well explained on the ground of geographical (geomorphological) data.

From the current (geographical) point of view, the absence of *Cryptomys* in Tanzania and Kenya is not surprising. Concordantly, the absence of *Cryptomys* from fossil sites in East Africa (all of them are on the east side or within the Rift Valley) is not surprising (DENYS, 1999). It can also be easily understood that it has been *Cryptomys* (whose centre of origin lies out of the area confined by the Rift Valley)

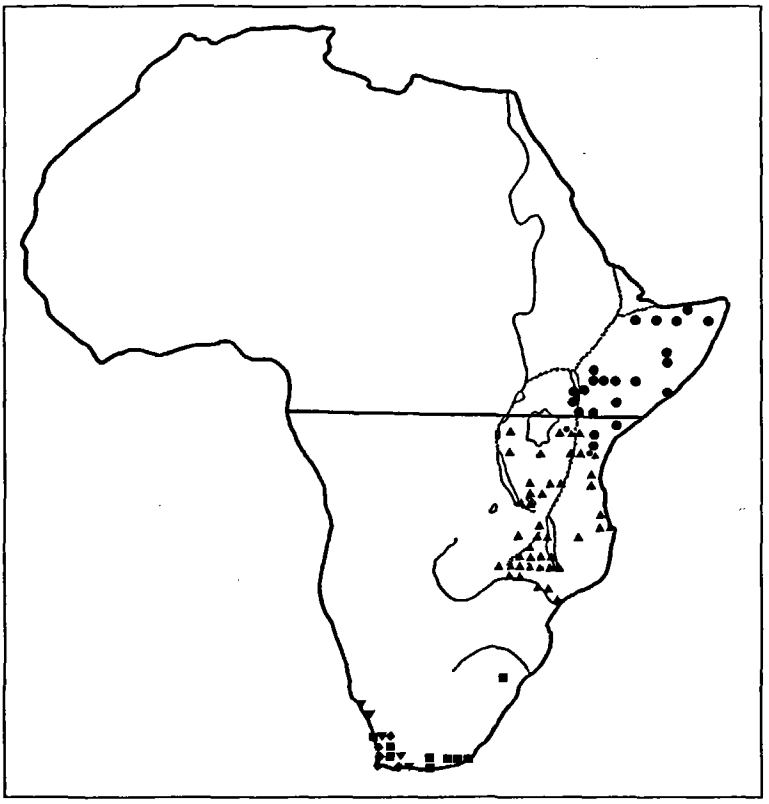

Figure 1
Distribution of Bathyergidae of the genera: *Heterocephalus* (circles), *Heliophobius* (triangles), *Bathyergus* (down pointing triangles and diamonds), and *Georychus* (squares) in Africa. Indicated is the course of the Great River Valley and Muchinga Escarpment, great African lakes, the Zambezi and the Limpopo rivers.

which could widely spread throughout Africa, and not e.g., *Heterocephalus* or *Heliophobius*. Northern and southern populations of *Cryptomys* have been apparently separated by expanding rain forest in the Congo Basin during the interglacial and/or postglacial times, or before, in the Pliocene (BROMAGE and SCHRENK, 1999). It should be tested whether the patchy distribution (particularly in west Africa) or apparent absence of *Cryptomys* (in central and east Africa) reflect a real situation or our limited knowledge.

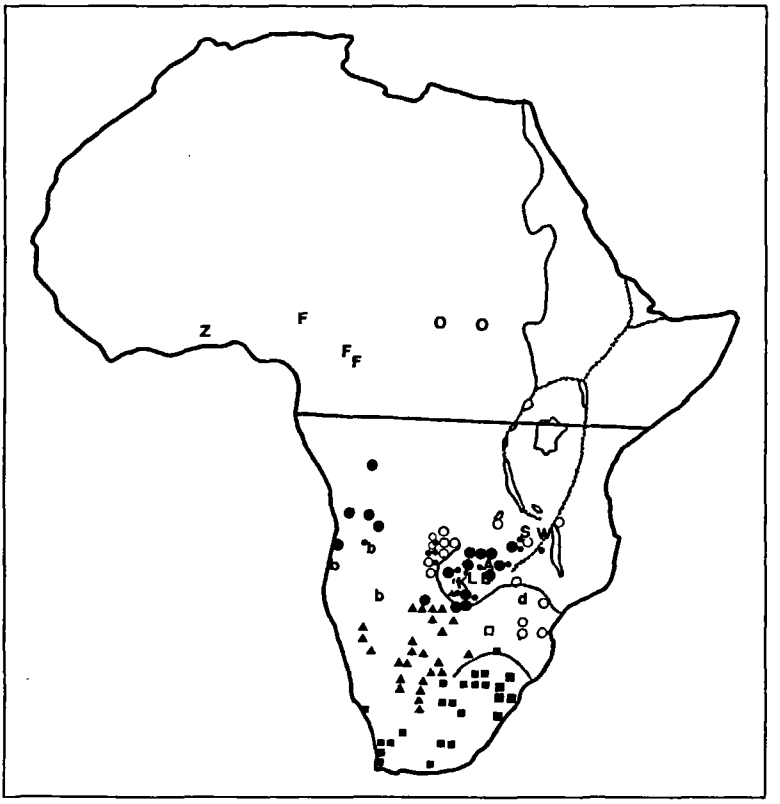

Figure 2
Distribution of the genus *Cryptomys* (Bathyergidae) in Africa: *Cryptomys damarensis* (triangles), *C. hottentotus hottentotus* (small squares), *C. h. natalensis* (large squares), *C. h. nimrodi* (empty squares), *C. darlingi* (d), *C. bocagei* (b), *C. mechowi* (full circles), common (small) *Cryptomys* of uncertain status (empty circles), *C. kafuensis* (K), *C. anselli* (L), *C. amatus* (A), *C.* Kasama (S), *C.* Nyika (= *C. whytei?*) (W), *C. ochracinereus* (O), *C. foxi* (F), *C. zechi* (Z). Indicated is the course of the Great River Valley and Muchinga Escarpment, great African lakes, the Zambezi and the Limpopo rivers.

The species diversity is particularly high in the fifteen-degree square outlined by 10°-20° S and 25°-35° E., i.e. in the very centre of the Zambezian Region (WHITE, 1983). The diversification of mole-rats in this area should be mapped in detail and the reasons (historical and/or ecological) for this speciation should be further examined. It

can be expected that even more sibling species of *Cryptomys* will be identified in the given region by biochemical, karyological and molecular methods. One of the possible factors triggering high speciation rate may be a high degree of rainfall unpredictability (uneven distribution of precipitation throughout the year) characterizing this region (table 2 and 3). High speciation of mole-rats in this region may reflect ecological changes in the past due to periodic closure (partition/fragmentation) and opening of the drought corridor running across what is now Zambia (BROMAGE and SCHRENK, 1999). Since mole-rats are typical inhabitants of savanna/savanna-woodland habitats, and as all small and particularly subterranean mammals have restricted vagility, it can be expected that they had to be most affected by the fragmentation of the savanna habitats and vicariance. Unfortunately, there are no fossil sites known from that region (DENYS, 1999). In this way, the current diversification of mole-rats is a powerful indirect means to study and understand paleoecology of the Zambezian Region.

Precipitation variables

The weighted means (averaged step by step), standard deviations and ranges of precipitation characteristics of habitats of particular mole-rat species are provided in Table 2.

There is no clear relationship between social structure and aridity as characterized by the rain amount (tables 2 and 3). While the critical aridity limit (annual rainfall less than 350 mm) favouring evolution of eusociality (JARVIS and BENNETT, 1991) may apply for selected study sites and/or years, it does not apply for average habitat requirements of given eusocial species, i.e., for the whole area of distribution and long-term records. Thus, only 20% and 27% of full-degree squares in which eusocial species, *Heterocephalus glaber* and *Cryptomys damarensis*, respectively, were recorded are characterized by a mean annual rainfall less than 350 mm. Also, 37% of the distribution area of the social *C. h. hottentotus* and 100% of the distribution area of the solitary *Bathyergus janetta* have a similarly low rainfall. Similarly, eusocial *C. mechowi* experiences seven rainless or dry months (April to October: 23, 4, 0, 0, 1, 1, 19 mm) per year in Kabwe (Zambia) but only two to three dry months in Kinshasa (Dem. Rep. Congo).

species	2n	annual rainfall (mm)					monthly rainfall (mm)				<25	<350
		mean	SD	range	n	c.v.	mean	SD	range	c.v.	(%)	(%)
B. janetta	54	179			1		15	9	4-28	60	92	100
B. suillus	56	320	200	73-611	6	62	27	12	10-45	44	50	84
C. h. hottentotus	54	453	171	179-707	8	38	38	6	26-48	16	8	37
C. damarensis	74,78	502	195	190-960	15	39	42	44	1-113	105	42	27
C. h. nimrodi	54	595			1		50	52	0-134	104	50	0
H. glaber	60	602	299	112-1,358	25	51	50	37	17-131	74	42	20
G. capensis	54	632	219	228-888	12	35	53	4	47-58	7	0	17
C. kafuensis	58	787			1		66	81	0-199	123	58	0
C. anselli	68	817			1		68	85	0-213	125	58	0
C. h natalensis	54	824	153	571-982	4	19	69	42	15-124	61	25	0
C. darlingi	54	860			1		72	78	1-202	108	42	0
H. argenteo-cinereus	60,62	988	275	555-1,686	37	27	83	72	8-185	87	42	0
C. mechowi	40	1,055	255	243-1,418	29	24	87	94	0-226	108	42	4
C. bocagei		1,074	265	887-1,262	2	25	89	81	0-198	91	42	0
C. amatus	50	1,133			1		94	110	0-269	117	50	0
C. Kasama	64	1,288			1		107	120	0-275	112	50	0
C. Nyika	46	1,415			1		118	122	4-340	103	42	0
C. zechi	1,437				1		120	80	15-241	67	17	0
C. foxi	66,70	1,591	30	1,570-1,613	2	2	133	112	2-283	84	33	0

Table 2
Precipitation variables (weighed mean values)
for areas of distribution of particular mole-rat species.
2n = diploid chromosome number (karyotype);
n = number of full-degree squares
with occurrence records and precipitation data,
c.v. = coefficient of variation (%);
< 25 = part of the year with little rain (under 25 mm/month);
< 350 = part of the area of occurrence
with annual rainfall less than 350 mm.
(No climatic data are available
for localities of *C. ochraceocinereus*.)

Table 3
Mean aridity and rainfall unpredictability characteristics (divided into four categories) of distribution areas of particular mole-rat species. (No climatic data are available for localities of *C. ochraceocinereus*.)

	Mean annual rainfall (mm)		number of months with little rain (< 25 mm/month)		variation of precipitation through the year (coeff. variation in%)	
I. (arid)	<350	*B. janetta, B. suillus*	9-12	*B. janetta*	> 100	*C. anselli, C. kafuensis, C. amatus, C.* Kasama, *C. mechowi, C.* Nyika *C. darlingi, C. h. nimrodi,* C. damarensis
II.	350-700	*C. h. hottentotus, C. damarensis, C. h. nimrodi, H. glaber, G. capensis*	6-9	*C. anselli, C. kafuensis, C. amatus, C.* Kasama, *C. h. nimrodi, B. suillus*	80-100	*C. bocagei, H. argenteocinereus, C. foxi*
III.	700-1,050	*C. kafuensis, C. anselli, C.h.natalensis, C. darlingi, H. argenteocinereus*	3-6	*C. h. hottentotus, C. mechowi, H. glaber, C.* Nyika, *C. bocagei, H. argenteocinereus, C. darlingi, C. foxi, G. capensis, C. damarensis*	60-80	*H. glaber, C. h. natalensis, B. janetta, C. zechi*
IV. (mesic)	> 1,050	*C. mechowi, C. bocagei, C. amatus, C.* Kasama, *C. whytei, C. zechi, C. foxi*	< 3	*C. h. natalensis, C. zechi*	40-60	*G. capensis, B. suillus, C. h. hottentotus*

The distribution of rains throughout the year (expressed here as coefficient of variation) does not indicate any clear correlation between the unpredictability of the rain and social system either (tables 2 and 3). Similarly, the number of months with less than 25 mm of rain counted (on the basis of mean full-degree-square data sets) for the whole distribution area of a particular species cannot be correlated with the social system (table 2s and 3; see also above).

It would be a simplification to define ecological potency of particular species just on the basis of their social systems and current ecological characteristics of habitats. One should take into account that it may have been just historical reasons (geomorphological barriers) and not ecological barriers in combination with behavioural ecology, which have prevented some genera or species from occupying some regions and which are determining the current distribution pattern.

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Evolutionary differentiation of placental organisation in hystricognath rodents

Andrea Mess

Introduction

Hystricognathi is an infraordinal rodent taxon that is widely accepted as monophyletic (LUCKETT, 1985; LUCKETT and HARTENBERGER, 1985, 1993; NEDBAL *et al.*, 1994, 1996; CATZEFLIS *et al.*, 1995; HUCHON *et al.*, 1999, 2000). Their fossil record starts before the Eocene/Oligocene boundary in Africa and South America as part of the earliest rodent fauna of both continents (JAEGER *et al.*, 1985; WYSS *et al.*, 1993). Recent South American Hystricognathi include about 200 species of 14 families with very different life styles, whereas there are only 4 families of these rodents on the African continent (WOODS, 1993). To try find explanations of the radiation or decrease of a taxon it is of special importance to find characters which may have influenced their evolutionary differentiation. Particularly the character complex of early ontogeny and placentation was successfully used in phylogenetic studies of Hystricognathi, i.e. to support their monophyly (LUCKETT, 1985; LUCKETT and HARTENBERGER, 1985, 1993). Although we therefore must assume that reproduction plays an important role in the evolutionary history of Hystricognathi, less is known about its evolutionary and functional significance.

In general, reproductive biology is often discussed as an important point in the ecological relationships of organisms (BEGON *et al.*, 1991). In mammalian species two generations, i.e. mother and offspring, are linked by placentation and postpartum care (cf.

EISENBERG, 1981). The degree of development of the newborn, i.e. altricial or praecocial, seems to be an important characterization of mammalian reproduction (PORTMANN, 1965). Hystricognathi usually have praecocial youngs that are born with open eyes, well furred and are locomotory active (cf. DIETERLEN, 1963; EISENBERG, 1981; BURDA, 1989). The development at birth depends to a high degree on the feto-maternal communication during the intra-uterin phase, an interaction on which the placental organization as well as the maternal and fetal blood vessels inside the placenta may provide information. Therefore, the morphology of the placenta and its vessels within Hystricognathi is considered below. The study focuses on the placental organization with particular reference to the late placenta. Additionally, an evolutionary interpretation of these data is presented and as far as possible, the placental characteristics of the hystricognath stem species pattern (i.e. morphotype) will be reconstructed. Nevertheless, a cladistic analysis based on placental characters in regard to the phylogenetic relationships within Hystricognathi is far beyond the scope of this paper, because the information available at present is too scanty.

Methodology

Since investigations of the mammalian placenta usually require time-consuming methods, data are often available only from very few species and ontogenetic stages. Here, new results from hystricognath species are presented. Special attention is drawn to the African *Petromus typicus* (Petromuridae) and the South American *Octodon degus* (Octodontidae), because the placental morphology in these families were unknown so far. Further original investigations include the African *Thryonomys swinderianus* (Thryonomyidae) and *Atherurus africanus* (Hystricidae) as well as the South American *Cavia porcellus* (Caviidae). As out-groups *Rattus norvegicus* (Muridae, Rodentia, on the basis of my own investigations) and *Echinosorex gymnura* (Insectivora, on the basis of literature data according to MEISTER and DAVIES, 1953) were chosen. Furthermore, published data were considered to check for the distribution of placental characters on a larger sample. Usually published data do not consider the

Species	Material and method	Placental stage	Holding
Petromus typicus	histological sections	undated, late placenta	MfN Berlin
Thryonomys swinderianus	macroscopic preparation	undated, late placenta	MfN Berlin
Atherurus africanus	macroscopic preparation	undated, late placenta	MfN Berlin
Octodon degus	histological sections	late placenta, 84 day	MfN Berlin
Cavia porcellus	histological sections	undated, late placenta	Utrecht
Rattus norvegicus	histological sections	undated, late placenta	MfN Berlin

Table 1
Material and methods, and origin of the specimens housed in Museum für Naturkunde, Berlin, and Hubrecht Collection, Utrecht.

morphological structure of the whole placenta, but are based on single histological cross-sections from the middle part of the placenta. Therefore, the present examination is also restricted to comparable information on single slides in terms of phylogenetic interpretation. The cross-sections run along the mesometrial-antimesometrial direction and include the beginning of the umbilical cord. The present study will contribute to reconstruct the stem species pattern or morphotype of Hystricognathi. Therefore, placental characteristics that occur in all recognized members of Hystricognathi are regarded as characters that belong to the hystricognath stem species pattern.

Material and methods

They are described in table 1.

Results

The placenta of *Petromus typicus* is differentiated into two regions (figure 1, MESS, 1999): a central labyrinthplacenta and an outer ectoplacenta. Both regions differ fundamentally in regard to the general

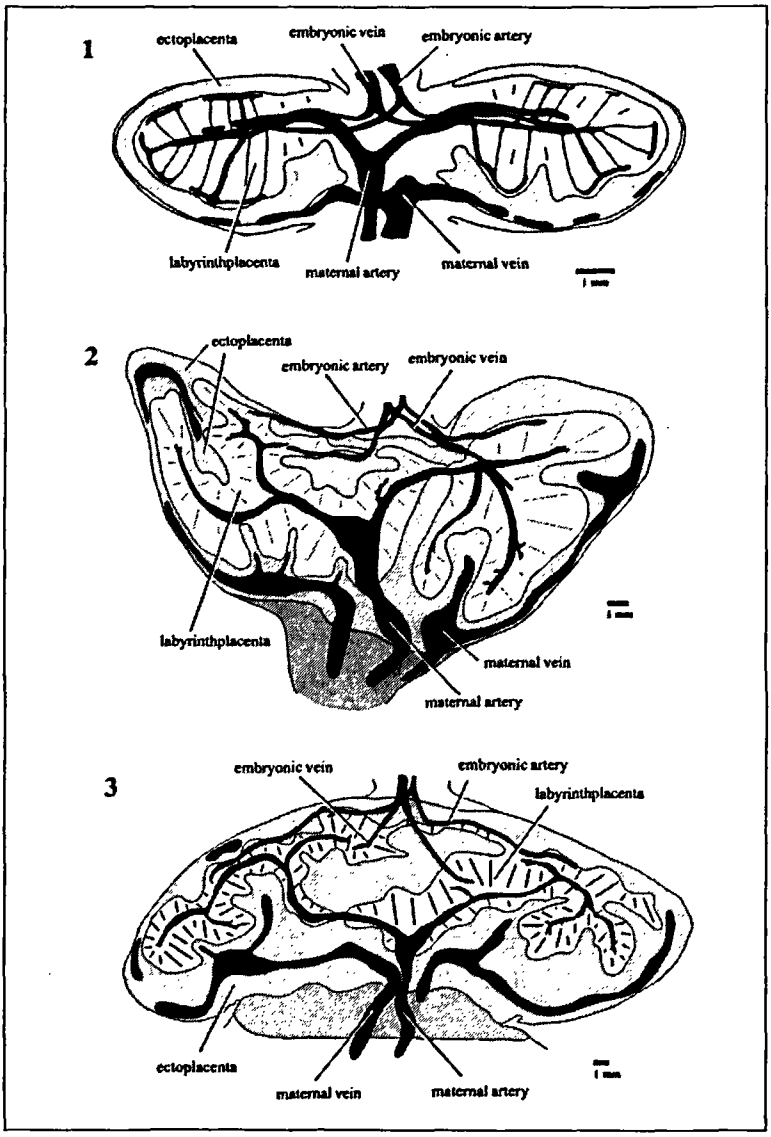

Figure 1
The chorioallantoisplacenta of *Petromus typicus.*

Figure 2
The chorioallantoisplacenta of *Thryonomys swinderianus.*

Figure 3
The chorioallantoisplacenta of *Atherurus africanus.*

morphological organization and the blood vessels inside: Embryonic vessels are restricted to the labyrinthplacenta. The labyrinthplacenta is characterized by the close topographical interaction between maternal blood chambers and placental tissue which includes the embryonic vessels. In contrast, the ectoplacenta contains a spongy structure of placental tissue without embryonic vessels. Beneath this morphological organization, the placenta is only poorly lobulated in *Petromus* (figure 1).

The fetal and maternal blood systems are developed in the following manner: The embryonic umbilical artery branches off centrally inside the labyrinthplacenta (figure 1). Smaller arteries pass through the labyrinthplacenta. At the boundary between labyrinth- and ectoplacenta, they branch off. Starting from this boundary, capillary vessels pass through the labyrinthplacenta in an opposite direction to the above mentioned arteries (figure 1). Judged from their course, the blood in the capillary vessels flows into the centrally situated embryological veins and leaves the placental disc to nourish the embryo (figure 1). The maternal system is established by arteries and veins of the mesometrium. Inside the placenta the central maternal artery, or blood chamber, branches off and runs through the labyrinthplacenta (figure 1). According to a haemochorial placental type, the blood of these supplying vessels pours into the placenta. The maternal blood flows through the placenta in an opposite direction to the embryonic capillaries. It is collected in the spongy structure of the ectoplacenta. Maternal veins on the outer surface of the placenta collect the blood and return it to the mother's body (figure 1).

In *Thryonomys swinderianus* (figure 2), *Atherurus africanus* (figure 3) and *Cavia porcellus* (figure 5), the placenta is much more lobulated than in the previously mentioned species. However, a similar organization is present: The maternal arteries are situated centrally in each lobe of the labyrinthplacenta (figures 3, 4, 5). Moreover, in *Thryonomys* (figure 2) and *Atherurus* (figure 3), the ectoplacenta encircles the placenta, whereas in *Cavia* it is only nearly circular with regard to the whole placenta (figure 5). However, in all species each lobe of the labyrinthplacenta is surrounded by ectoplacental tissue, comparably to the organization of the poorly lobulated placentae of *Petromus* and *Octodon*.

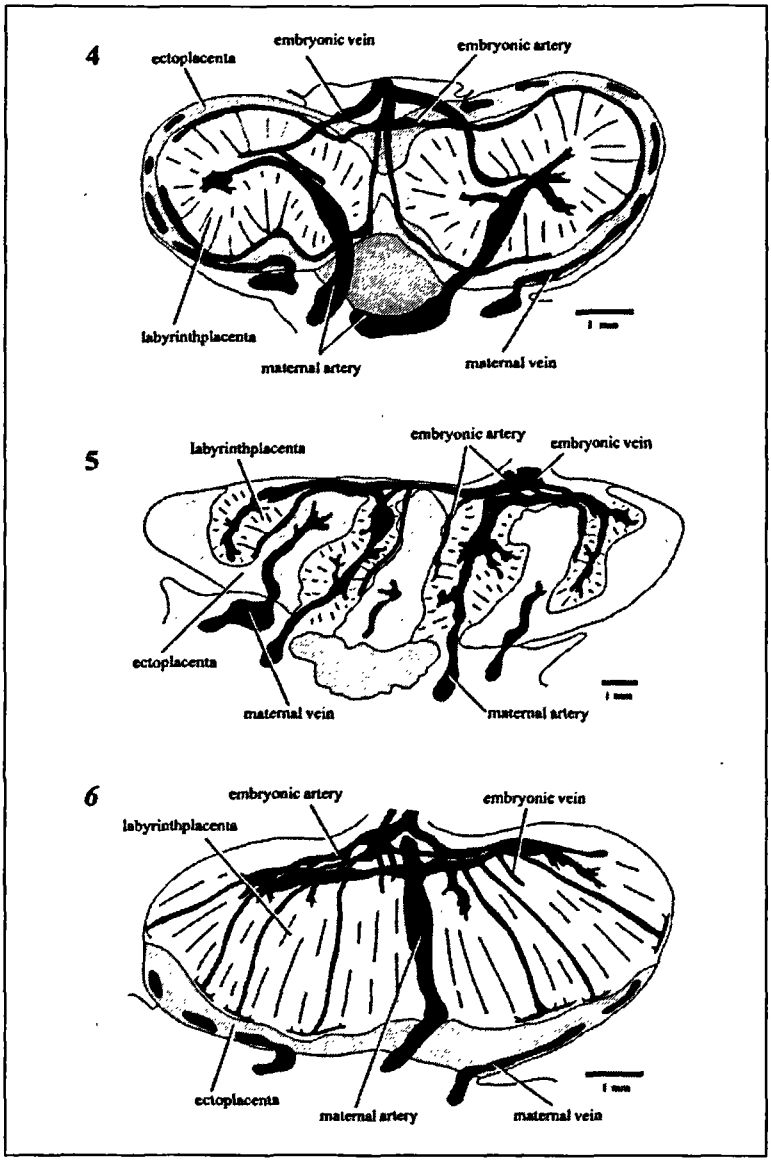

Figure 4
The chorioallantoisplacenta of *Octodon degus.*

Figure 5
The chorioallantoisplacenta of *Cavia porcellus.*

Figure 6
The chorioallantoisplacenta of *Rattus norvegicus.*

Likewise, in *Octodon degus* only the inner part of the placenta, the labyrinthplacenta, is interspersed by embryonic capillaries, whereas the ectoplacenta is not capillarized (figure 4). The placenta in *Octodon* is only poorly lobulated, although the labyrinthplacenta is a little bit more prominent than in *Petromus*. However, like in *Petromus*, the maternal arteries are situated centrally in the labyrinthplacenta and the blood pours out in a starshaped or radial pattern. The ectoplacenta encircles the inner part of the placenta (figure 4).

In *Rattus norvegicus*, a non-hystricognathous Rodent, a clear distinction between ectoplacenta and labyrinthplacenta with the same internal characteristics than in Hystricognathi also occur (figure 6). However, the general organization according to the arrangement of these regions differs fundamentally in comparison to Hystricognathi. In contrast to the species mentioned before, the ectoplacenta is restricted to the maternal part of the placenta (figure 6). The maternal arteries or blood chambers are situated at the fetal side (figure 6). Therefore, the maternal blood must flow through the labyrinthplacenta in only one direction, i.e. from the fetal side towards the maternal side of the placenta. Nevertheless, an opposite direction of maternal and fetal blood flow inside the labyrinthplacenta is established in *Rattus*, like in the labyrinthplacentae of *Petromus* and other Hystricognathi.

Discussion and conclusion

Placental characters in the stem species pattern of Hystricognathi

According to the distribution of placental characters in table 2, a circular ectoplacenta (even surrounding the lobes of the labyrinthplacenta as in *Cavia*) occurs in all investigated Hystricognathi (own obs., STARCK, 1959; HILLEMANN and GAYNOR, 1961; LUCKETT and MOSSMAN, 1981; ODUOR-OKELO and GOMBE, 1982; MOSSMAN, 1987). Moreover, the distributional data (table 2) indicate that centrally situated maternal arteries or blood chambers are characteristics of all Hystricognathi (own obs., STARCK, 1959; HILLEMANN and GAYNOR,

1961; LUCKETT and MOSSMAN, 1981; ODUOR-OKELO and GOMBE, 1982; MOSSMAN, 1987). Therefore, a circular ectoplacenta as well as maternal arteries that are centrally situated inside the placenta are regarded as being part of the hystricognath stem species pattern. These characteristics are setting Hystricognathi apart from most other rodents: In contrast to Hystricognathi, the ectoplacenta is restricted to the maternal side of the chorioallantoisplacenta and the maternal arteries are situated on the fetal side of the chorioallantoisplacenta in *Rattus* and *Echinosorex* (MEISTER and DAVIES, 1953). Additionally, the character conditions of the latter two taxa are developed in most other non-hystricognath Rodentia investigated so far (MOSSMAN and WEISFELDT, 1939; STARCK, 1959; MOSSMAN, 1987), and can be detected in other eutherian taxa, e.g. Insectivora (cf. STARCK, 1959; MOSSMAN, 1987). Therefore it is assumed that an ectoplacenta restricted to the maternal side of the placenta and maternal arteries situated on the fetal side of the placenta are plesiomorphic for Rodentia. Thus, the circular extension of the ectoplacenta and the centrally situated maternal arteries inside the labyrinthplacenta are regarded to be apomorphic within Rodentia. This indicates an evolutionary transformation of this character complex along the stem lineage of Hystricognathi. However, it belongs to future research on morphology and cladistic analysis to reveal if they are autapomorphic characters of Hystricognathi or if they support a larger taxon within Rodentia including Hystricognathi.

Within the taxa sample of Hystricognathi (see table 2), non-lobulated or poorly lobulated placentae occur in *Petromus* and *Octodon*, whereas highly lobulated placentae are present in all other hystricognath taxa (own obs., STARCK, 1959; HILLEMANN and GAYNOR, 1961; LUCKETT and MOSSMAN, 1981; ODUOR-OKELO and GOMBE, 1982; MOSSMAN, 1987). In regard to the occurrence of both character conditions within Hystricognathi, it is not possible to reveal the stem species pattern without further assumptions. However, the phylogenetic systematics or classification of Hystricognathi are unresolved or controversial in many cases, or the studied species differ from the ones investigated for placental studies (cf. NEDBAL *et al.*, 1994, 1996; CATZEFLIS *et al.*, 1995; HUCHON *et al.*, 1999, 2000; MCKENNA and BELL, 1995). Thus, no reconstruction on the basis of existing trees can be carried out. Nevertheless, a placenta without a marked degree of lobulation, as demonstrated for *Rattus*, is widespread in non-hystri-

Taxon	Ectoplacenta	Maternal arteries	Lobulation	Citation
Petromus typicus	Circular	Centrally	Poorly	Own obs., MESS, 1999
Thryonomys swinderianus	Circular, in lobes	Centrally	Highly	own obs., ODUOR-OKELO and GOMBE, 1982
Atherurus africanus	Circular, in lobes	Centrally	Highly	own obs.
Hystrix africaeaustralis	Circular, in lobes	Centrally	Highly	LUCKETT and MOSSMAN, 1981
Bathyergus janettta	Circular	Centrally	Highly	LUCKETT & MOSSMAN, 1981
Octodon degus	Circular	Centrally	Poorly	own obs.
Myocastor coypus	Circular, in lobes	—	Highly	HILLEMANN and GAYNOR, 1961
Cavia porcellus	Circular, in lobes	Centrally	Highly	own obs., STARCK, 1959; MOSSMAN, 1987
Rattus norvegicus	Maternal side	Fetal side	Poorly	own obs., STARCK, 1959; MOSSMAN, 1987
Echinosorex gymnura	Maternal side	Fetal side	poorly	MEISTER & DAVIES, 1953

Table 2
Character distribution with particular reference to Hystricognathi.

cognath rodents, and occurred in *Echinosorex* and other Insectivora (own. obs., MOSSMAN and WEISFELDT, 1939; MEISTER and DAVIES, 1953; STARCK, 1959; MOSSMAN, 1987). This gives an indication that even in the stem species pattern of Hystricognathi a low degree of lobulation is likely and that the highly lobulated placental structure may be evolved within this clade.

Functional interpretation of the hystricognath stem species pattern

According to the interpretation above, the stem species pattern of Hystricognathi is at least characterized by a circular ectoplacenta and centrally situated maternal arteries or blood chambers. These characteristics are most likely the result of an evolutionary transformation towards the stem lineage of Hystricognathi. Most likely, the

starshaped or radial flow of maternal blood through the labyrinthplacenta is not possible without a circular ectoplacenta that collects the blood in the outer part of the placenta. Obviously, there is a functional dependence of these features.

In summary, the data presented here reveal that the internal structure of the placenta differs fundamentally within Rodentia in regard to the establishment of the fetomaternal blood system, e.g. *Petromus* versus *Rattus*. The labyrinthplacenta seems to be of particular importance for the fetomaternal substance exchange, because only in this placental region embryonic blood vessels are present and the maternal blood gets into close contact to embryonic capillaries. Because of the radial organization, the placenta seems to be a more effective exchange organ in Hystricognathi than in other Rodentia: The labyrinthplacenta enables exchanges by using two directions and shorter length of vessels in Hystricognathi (the labyrinthplacenta is nearly equal in dimensions in *Petromus* and *Rattus* for example). Since according to MOSSMAN (1965) the extension of the exchange region of the labyrinthplacenta can be used as an approximation of the length of the exchange vessels, the capillaries in Hystricognathi are half as long than in other rodents. The current rate of blood flow inside the embryonic capillaries and the maternal blood spaces is therefore double the strength (according to the law of Hagen-Poiseuille, cf. VOGEL, 1988; SCHMIDT and THEWS, 1995). Thus, the placental organization in Hystricognathi should enhance the placental blood flow and the related effectiveness of exchange according to a given diameter of the placenta. This is especially the case for liquid soluble substances, e.g. O_2 and CO_2 (SCHMIDT and THEWS, 1995). Additionally, it seems likely that placental lobulation could have occurred as a second step within the evolution of Hystricognathi to increase the effectiveness of placental exchange, because it expands the region of exchange by producing a larger area with close interaction of the maternal and fetal blood systems due to surface enlargement.

Conclusion and ecological interpretation

The described placental character complex must have evolved before the radiation of Hystricognathi in Africa and South America, i.e. it must have been developed in Eocene times at least. It should be

mentioned that in *Petromus* for example, young are born at the beginning of the rainy season (SKINNER and SMITHERS, 1990). According to its precocial reproductive strategy with a gestation period of about 3 months (MESS, 2000), substantial parts of the pregnancy must take place in the dry season. Thus, to enable pregnancy under conditions with low production of plant food sources, a more effective placental organisation would be helpful or even necessary. In contrast, the beginning of pregnancy is correlated or initialized by the start of the rainy season in many muroid or other rodents (HAPPOLD, 1983; SKINNER and SMITHERS, 1990). If this interpretation can be confirmed by further analysis, it would indicate that Hystricognathi could have been adapted to such ecological conditions. However, the relation of the placental characters to the periods of reproduction as well as an analysis of their phylogenetic significance will be the subject of future work. Moreover, a deeper understanding must be achieved by a more detailed analysis of the placental complex with regard to its functional histology. Further research should particularly consider the 3 dimensional organization and volumetric extension of placental vessels with regard to the whole placenta, as well as the interactions between the embryonic capillaries, the separating tissue and the maternal blood chambers in high resolution.

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Molecular phylogeny of the sciurognath rodent families Gliridae, Anomaluridae and Pedetidae

Morphological and paleontological implications.

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Introduction

Tullberg's classification (1899) of rodents was based on the angle of the lower jaw and included two suborders: Sciurognathi and Hystricognathi. Since that time, the monophyly of Hystricognathi, which includes 18 Recent families (WILSON and REEDER, 1993), has received increasing support from palaeontological data (LUCKETT and HARTENBERGER, 1985; JAEGER, 1988; WYSS *et al.*, 1993; HARTENBERGER, 1998), anatomical (LAVOCAT and PARENT, 1985; BUGGE, 1985; LUCKETT, 1985; WOOD, 1985), and molecular (CATZEFLIS *et al.*, 1995; NEDBAL *et al.*, 1996; HUCHON *et al.*, 1999, 2000). On the other hand, neither morphological nor molecular data provide support to the Sciurognathi clade and phylogenetic relationships among the diverse "non-Hystricognathi" families are obscure

and hotly debated. The suborder Sciurognathi includes 11 families (WILSON and REEDER, 1993): Aplodontidae, Sciuridae, Castoridae, Geomyidae, Heteromyidae, Dipodidae, Muridae, Anomaluridae, Pedetidae, Ctenodactylidae, and Gliridae. Among them, we focus here on three taxa: Gliridae (dormice), Anomaluridae (scaly-tailed squirrels) and Pedetidae (springhare). Gliridae includes three subfamilies: the Eurasian Leithiinae (four genera) and Glirinae (three genera) and the African Graphiurinae (one genus). Anomaluridae (three genera) and Pedetidae (one genus) are two African families, for which LUCKETT and HARTENBERGER (1985) stated that their affinities "are among the most obscure of all rodents".

We were before all interested to test the morphological and palaeontological hypotheses (VIANEY-LIAUD and JAEGER, 1996) having stated that *Graphiurus*, [which exhibits many peculiar traits relative to other glirids; see BENTZ and MONTGELARD, 1999 for a review] could be more closely related to the African Anomaluridae than to the remaining Gliridae. On the other hand, Anomaluridae is grouped with Pedetidae by some anatomical characters, such as middle-ear features (LAVOCAT and PARENT, 1985) or the carotid arterial pattern (BUGGE, 1985). Conversely, some palaeontological (JAEGER, 1988) and morphological data based on enamel incisor microstructure (MARTIN, 1995) do not corroborate this hypothesis. No molecular study has yet included Anomaluridae and the papers of NEDBAL *et al.* (1996) and MATTHEE and ROBINSON (1997), which include *Pedetes* only, do not identify a possible sister group for this species. In our study, the taxonomic sampling appears relevant to test these various hypotheses and the molecular study is based on two mitochondrial (cytochrome *b* and 12S ribosomal RNA) and one nuclear (LCAT: Lecithin Cholesterol Acyl Transferase) genes.

Molecular analysis

The whole molecular analysis was performed on 18 taxa among which 14 species represent five sciurognath rodent families. The study included six of the eight extant genera of Gliridae: *Dryomys nitedula* and *Eliomys quercinus* for the Leithiinae subfamily; *Glis glis*,

	Genus	Species	Family	Geographic origin	Collector/Donator
T-1787	*Anomalurus*	*sp.*	Anomaluridae	Cameroon: Djoum	J.-C. Gautun (V-804)
T-0768	*Dryomys*	*nitedula*	Gliridae	Georgia: north-west Caucasus	M. Baskevitch (0-22)
T-1110	*Glaucomys*	*volans*	Sciuridae	Audubon Zoo, New Orleans, USA	R.M. Zink & D. Reynolds
T-1715	*Glirulus*	*japonicus*	Gliridae	Japan	H. Suzuki (HS 443)
T-0472	*Graphiurus*	*murinus*	Gliridae	Burundi: Buagaramu	T. Maddalena (IZEA 2702)
T-1728	*Idiurus*	*macrotis*	Anomaluridae	Ivory Coast	M. Colyn (R-24210)
T-1451	*Muscardinus*	*avellanarius*	Gliridae	Switzerland: Lausanne	P. Vogel (IZEA 4927)
T-1701	*Pedetes*	*capensis*	Pedetidae	South Africa: Willem Pretorius Nature Reserve	C. Matthee (DMSO-2)

Table 1
Origin of the animals sequenced for the LCAT gene (EMBL accession numbers AJ401283 to AJ401297)
Tissue numbers (T-) are those from the Collection of Mammalian Tissues of Montpellier. Numbers in parenthesis are specimen's references from collectors or donators.

Muscardinus avellanarius and *Glirulus glirulus* for the Glirinae, and *Graphiurus murinus* for the Graphiurinae. Other sciurognath rodents are represented by two Anomaluridae (*Anomalurus sp.* and *Idiurus macrotis*), one Pedetidae (*Pedetes capensis*), three Muridae (*Mus musculus*, *Rattus norvegicus* and *Spalax ehrenbergi*), and two Sciuridae (*Sciurus aestuans* or *griseus* and *Glaucomys volans*). Two representatives of Hystricognathi (*Cavia porcellus* and *Octodon lunatus* or *O. degus*) were also included and two primates (*Papio anubis* or *P. hamadryas* and *Homo sapiens*) were used as outgroups. Eight new sequences are here presented for the LCAT gene of *Graphiurus*, *Glirulus*, *Muscardinus*, *Dryomys*, *Glaucomys*, *Pedetes*, *Anomalurus* and *Idiurus*, and were deposited at the EMBL database with accession numbers AJ401283 to AJ401297; Table 1 indicates the biological origin for these new data. However, exon 6 (about 500 pb) from *Pedetes* was not successfully amplified. Other LCAT sequences are from ROBINSON *et al.* (1997). References for cytochrome *b* and 12S rRNA sequences can be found in BENTZ and MONTGELARD (1999) and in writing to the senior author.

Saturation analysis

Analysis of gene saturation was performed using maximum parsimony reconstruction, according to the procedure of PHILIPPE *et al.* (1994) and HASSANIN *et al.* (1998): the observed differences from pairwise comparisons are plotted against the corresponding number of substitutions inferred from a parsimony analysis. The slope (S) of the linear regression is used to estimate the level of saturation, S decreasing towards zero as the level of saturation increases. Calculations were performed with PAUP 3.1.1 (SWOFFORD, 1993) using the option "patristic distance".

As commonly observed (figure 1), more homoplasy is detected for the cytochrome *b* (A: S = 0.31) than for the 12S rRNA (C: S = 0.47). Saturation in the cytochrome *b* is much reduced when positions 1 and 2 only are considered (B: S = 0.75). Coding sequences of the nuclear gene LCAT (concatenation of exons 2 to 6) appear the least saturated (D:S = 0.68) and also show the least scatter in points (R = 0.93). In order to diminish DNA sequence homoplasy (due to multiple substitutions at the same site), the most saturated sites (position 3 of the cytochrome *b* and LCAT introns) and sites with alignment ambiguities (indels of the 12S rRNA and LCAT introns) were excluded from analyses. The combined analysis was then performed on 2495 sites (1062 Variable and 738 Informative characters) including: (1) 760 positions (272 V, 185 I) for the first and second positions of cytochrome *b*, (2) 875 positions (424 V, 325 I) for the 12S rRNA when indels are omitted, (3) 860 positions (366 V, 228 I) for exons 2 to 6 of LCAT when introns are excluded. Homogeneity between the three partitions was evaluated with PAUP*4.0 (option HOMPART, 1000 replicates) using the test ILD (FARRIS *et al.*, 1995) on variable sites only. This test indicates that there is no statistical incongruence between the three genes ($P = 0.41 > 0.05$).

Phylogenetic results

Phylogenetic reconstructions were performed in Maximum Parsimony (MP) with PAUP 3.1.1 using informative sites equally weighted, and in Maximum Likelihood (ML) using the quartet puzzling approach (PUZZLE 4.0; STRIMMER and VON HAESELER, 1996) with the Tamura-

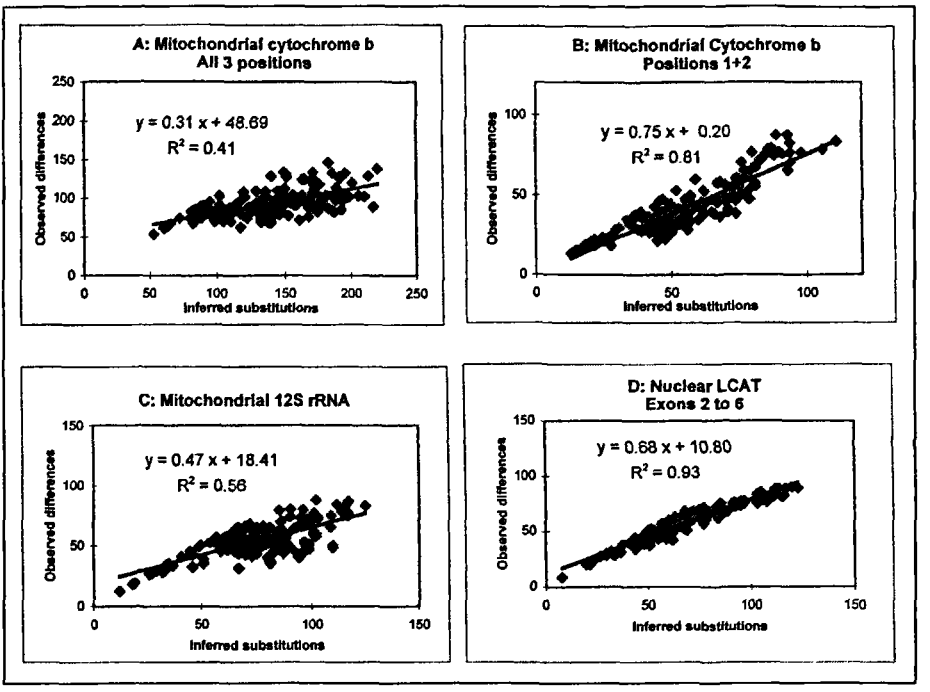

Figure 1
Graphic estimation of the level of saturation according to the procedure of HASSANIN et al (1998): pairwise numbers of observed nucleotide differences are plotted against the corresponding number of substitutions inferred from the maximum parsimony tree. Inferred distances were obtained with PAUP using 529 Informative sites for the whole cytochrome *b* (A) and 185 I when position 3 is excluded (B), 325 I for the 12S rRNA (C), and 228 I for LCAT (D). Equation of the linear regression and correlation coefficient are indicated.

Nei model and a gamma distribution with eight categories for substitution rates. In MP, robustness of the nodes was assessed with bootstrap percentages (BP) after 1000 replicates and with the decay index (DI; BREMER, 1988). With ML, robustness was estimated by Reliability Percentages (RP) with 1000 puzzling steps.

Results from the three genes in combination are presented in Figure 2. In parsimony, only one MP tree is recovered (L = 1219, CI = 0.467, RI = 0.473). The sole difference between ML and MP trees concerns

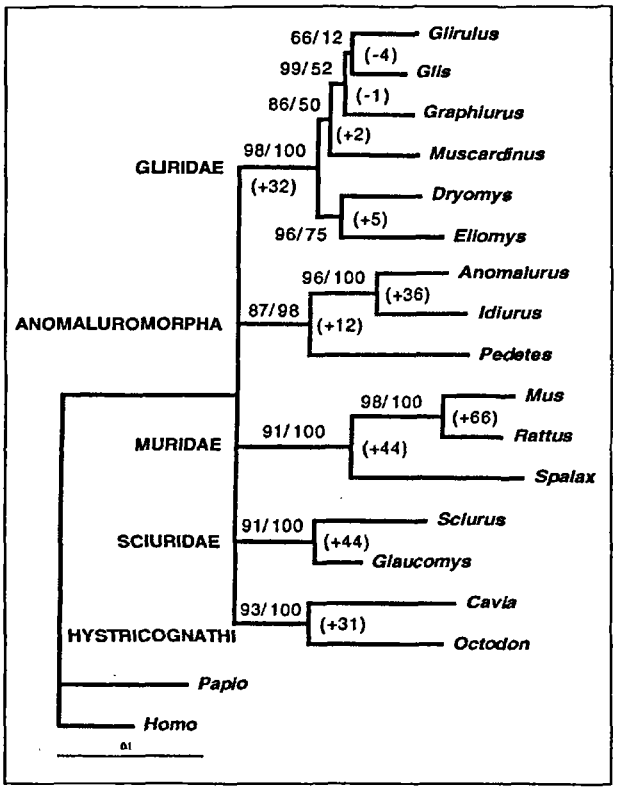

Figure 2
Maximum likelihood quartet puzzling tree from the combined cytochrome *b* (codon positions 1 and 2), 12S rRNA (excluding indels), and LCAT (exons 2 to 6) genes. Numbers above branches refer to reliability percentages (1000 quartet puzzling steps with PUZZLE) in likelihood analysis on the left, and to bootstrap percentages in maximum parsimony (1000 replicates with PAUP) on the right. Decay indexes [numbers of extra steps to break (+) or to build (–) a grouping] are indicated in parentheses.

the branching pattern of *Glis* which clusters with *Muscardinus* in the MP tree, with *Graphiurus* in the bootstrap tree in parsimony (BP = 37%) and with *Glirulus* in the puzzling tree (RP = 66%). Otherwise, the molecular analysis reveals that *Graphiurus* is clearly a member of the Gliridae (98% in ML, 100% in MP, DI = + 32). The monophyly of Leithiinae (here represented by *Dryomys* and *Eliomys*) appears well supported (96%, 75%, + 5), whereas there is no support for the subfamily Glirinae which should have included, according to WAHLERT *et al.* (1993), *Glis*, *Glirulus* and *Muscardinus*. The African *Graphiurus* appears nested among Glirinae, with affinities for the Eurasian *Glirulus* and *Glis* genera. However, these associations are strongly supported in ML (86% and 99%, respectively), but very weakly in MP (50% and 52%). Such a discrepancy between reconstruction methods was already reported by CAO *et al.* (1998) who

mentioned that the quartet puzzling approach can sometimes give reliability values misleadingly high as compared to bootstrap resampling.

The Anomaluridae family, here represented by the two genera *Anomalurus* and *Idiurus*, (the third genus, *Zenkerella*, is lacking) is very well defined (96%, 100%, + 36). The other strong result of this molecular analysis is the robust relationship between the two African Anomaluridae and Pedetidae families (87%, 98%, + 12). This relationship appears equally supported by each gene separately (data not shown): cytochrome *b* (89%, 78%, + 2), 12S rRNA (76%, 59%, + 3) and LCAT (58%, 62%, + 1). In the latter case, the support may be weakened due to the lack of exon 6 for *Pedetes*. In the combined analysis, the association between Anomaluridae and Pedetidae appears almost as strongly supported as are other rodent families, such as Sciuridae, Gliridae or Muridae.

Discussion

About the Gliridae, adding the nuclear LCAT gene allows to corroborate and reinforce previous results obtained with the two mitochondrial genes only (BENTZ and MONTGELARD, 1999). That is, the combined analysis confirms that *Graphiurus* belongs to the Gliridae family and strengthens the monophyly of the Leithiinae clade (*Dryomys* and *Eliomys* in this study). *Graphiurus* appears nested among Glirinae but the association *Glis-Graphiurus-Glirulus* is supported only in ML (99%). Thus, the systematic position of *Graphiurus* among Glirinae does not appear fully resolved, suggesting a possible multi-lineages radiation within this subfamily. This result should be validated by including additional *Graphiurus* representatives as only one species is considered here out of the 14 recognized in WILSON and REEDER (1993).

The position of *Graphiurus* among Gliridae contrasts with the palaeontological hypothesis of a *Graphiurus*-Anomaluridae relationship (VIANEY-LIAUD and JAEGER, 1996). Moreover, the molecular analysis reveals a close relatedness between the two African Anomaluridae and Pedetidae families. These two lineages thus appear as a natural

clade among sciurognath rodents, and are included in the suborder Anomaluromorpha. This clade was defined 25 years ago by BUGGE (1974) on the basis of the carotid arterial pattern and is also supported by middle-ear features (PARENT, 1980; LAVOCAT and PARENT, 1985). This relationship remains at odds with some palaeontological data (FLYNN *et al.*, 1986; JAEGER, 1988) as well as with conclusions derived from the study of incisor enamel microstructure, which clusters Pedetidae among a clade including Hystricognathi as well as Recent and fossil Ctenodactyloidea (MARTIN, 1995). However, Ctenodactylidae were proposed as a possible sister group to Hystricognathi by several morphological and palaeontological studies (LUCKETT and HARTENBERGER, 1985; BRYANT and MCKENNA, 1995). Such a hypothesis was recently corroborated by molecular data (HUCHON *et al.*, 2000) on the basis of nuclear vWF sequences, defining the clade Ctenohystrica. In this study, the clusterings of Pedetidae as sister group to Hystricognathi or Ctenodactylidae are statistically rejected. Thus, although our own study does not include ctenodactylid representatives, the possibility of a Ctenodactylidae-Pedetidae relationships remains unlikely. The two points of discordance (palaeontological data and enamel microstructure) raised by the association between Pedetidae and Anomaluridae are developed in the following discussion.

Palaeontological data

If the present African distribution of Pedetidae (southern Africa) and Anomaluridae (western and central Africa) appears consistent with their close relationships, a rather different picture emerges when paleontological data only are considered.

The Anomaluridae lineage can be traced back until the late Eocene (42 Myr) in Algeria where *Nementchamys lavocati* is described as the oldest known fossil of Anomaluridae (JAEGER *et al.*, 1985). More recent anomalurid fossils were attributed to the genera *Paranomalurus, Anomalurus,* and *Zenkerella* in early and middle Miocene (13-20 Myr) deposits from Kenya (DENYS and JAEGER, 1992; WINKLER, 1992; LAVOCAT, 1973). Moreover, the fossil family Zegdoumyidae described from the late early Eocene (45-50 Myr) of Tunisia and Algeria, was considered as the ancestral stock of the Anomaluridae

(VIANEY-LIAUD *et al.*, 1994). So, until now, the fossil history of the anomalurid lineage is restricted to Africa.

Concerning Pedetidae, the fossil record is sparse and represented in Africa by *Megapedetes pentadactylus* (MACINNES, 1957) from Kenya and *Parapedetes namaquensis* from Namibia (STROMER, 1926), both from the early Miocene (20 Myr). Besides Africa, *Megapedetes aegaeus* (SEN, 1977) is described from the Middle Miocene (12-13 Myr) of Western Anatolia (Turkey). *Diatomys* found in middle Miocene (18-19 Myr) of China (LI, 1974) and Thailand (MEIN and GINSBURG, 1985) has been proposed as a possible ancestor for *Pedetes*, thus suggesting an Asiatic origin for Pedetidae. However, this hypothesis was recently challenged (MEIN and GINSBURG, 1997) because new fossils of *Diatomys* found in Thailand do not present the jumping adaptation which was already achieved in Pedetidae from the lower Miocene. A plausible ancestor for *Diatomys* is represented by the ctenodactyloid genus *Fallomus* from the Miocene of Baluchistan (FLYNN *et al.*, 1986; MEIN and GINSBURG, 1997), but the relationship between the Asiatic *Fallomus-Diatomys* and the African *Parapedetes*-Pedetidae lineages remains to substantiate. Therefore, the pre-Miocene (beyond 20 Myr) fossil history and the origin of Pedetidae stays unknown (HARTENBERGER, 1998).

Finally, a close relationship between pedetids and anomalurids appears not congruent with palaeontological data mainly because of the gap between the record of fossil Pedetidae (not older than 20 Myr) and the long history of the Anomaluridae lineage (42 Myr). Thus, a common ancestor to Anomaluromorpha would have to be searched in the early Tertiary, possibly from ischyromyoids (BUGGE, 1974), an early Eocene fossil family from which several sciurognath rodents could be issued.

As our molecular data do not evidence a rate constancy among the different lineages (data available upon request), we refrain from applying the molecular clock concept. Thus, no attempt of dating the different molecular dichotomies was done, pending a better sampling of sciurognath and hystricognath families for applying various local molecular clocks.

Implications for the microstructure of incisor enamel

In rodents, three basic types of incisor enamel microstructure (Hunter-Schreger Bands = HSB) are described and used as a phylogenetic tool at the familial or suprafamilial levels (review in MARTIN, 1997). The first type, called pauciserial, characterizes the most primitive rodents and represents the ancestral condition for the Rodentia (see figure 3). The two other types, uniserial and multi-serial HSB, are derived states. Recent Ctenodactylidae, Hystricognathi and Pedetidae show the multi-serial condition which was therefore considered as a synapomorphy for this group (MARTIN, 1997). The uniserial condition characterizes all other sciurognath lineages and this state is thought to have evolved several times independently in some rodent lineages derived from the extinct Ischyromyoidea (MARTIN, 1993).

If, as suggested by molecular data and some morphological characters, Pedetidae and Anomaluridae are related, how then to interpret the multi-serial condition of Pedetidae as opposed to the uniserial type of Anomaluridae? Two hypotheses can be advanced:

– Hypothesis A in Figure 3: As stated by MARTIN (1995), the multi-serial condition is a synapomorphy of Ctenodactylidae, Hystricognathi and Pedetidae, inherited from Paleogene ctenodactyloid ancestors. Under this hypothesis, the uniserial condition of Anomaluridae could have evolved from the pedetid multi-serial condition. However, according to MARTIN (1995, p. 696), "there is no way that uniserial HSB can evolve from the derived multi-serial condition". Moreover, Zegdoumyidae, considered as the ancestral stock of anomalurids, show HSB that are transitional from the ancestral pauciserial to the derived uniserial condition (MARTIN, 1993). This hypothesis is clearly not consistent with the Pedetidae-Anomaluridae relationships because at the present time no palaeontological data supports the assumption of any ctenodactyloid origin for the anomalurid lineage.

– Hypothesis B in Figure 3: The multi-serial condition in Pedetidae has been achieved convergently with that of Ctenodactylidae and Hystricognathi. As convergent evolution has been described for the uniserial HSB, we may assume that the multi-serial condition also appeared independently in two lineages. Recently, MARTIN (1999) found that several representatives of the Paleogene fossil family

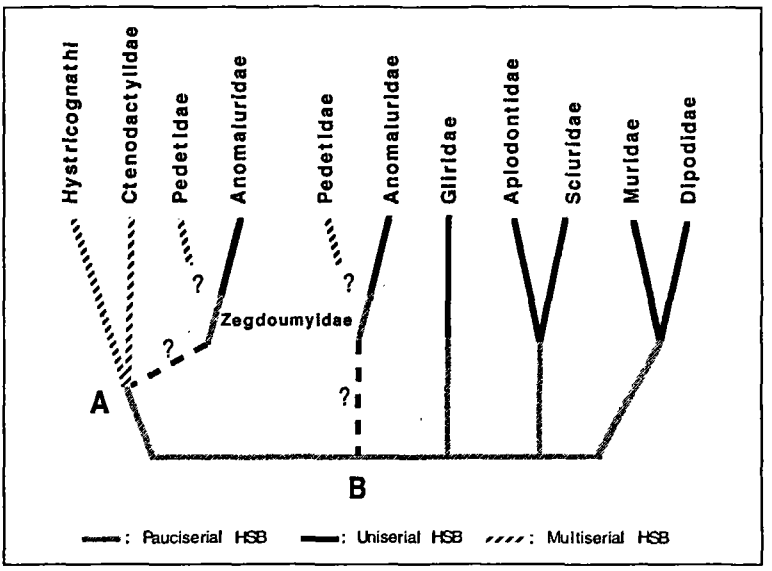

Figure 3
Evolution of incisor enamel microstructure: two hypotheses (A and B, see text) to interpret, on the basis of a Pedetidae-Anomaluridae relationship, the uniserial condition (in black) of Anomaluridae, and the multi-serial HSB (hachured) of Pedetidae. Incisor enamel data are from MARTIN (1993), and phylogenetic relationships are from LUCKETT and HARTENBERGER (1985) and VIANEY-LIAUD *et al.* (1994) for the fossil family Zegdoumyidae.

Theridomyidae were characterized by a pseudo-multiserial HSB. If this condition does not indicate a close phylogenetic relationships with Ctenodactylidae or hystricognath rodents (MARTIN, 1999), it nevertheless suggests that parallel evolution does exist for the multi-serial state. Under the assumption of independent origin, multi-serial HSB can then be considered as homologous in the clade Hystricognathi-Ctenodactylidae, but not for the Pedetidae lineage. Consequently, Pedetidae inherited their multi-serial HSB from ancestors which are presently unknown because even the possible relative genera *Fallomus* and *Diatomys* already present the mutiserial state (FLYNN *et al.*, 1986; MARTIN, 1995).

In conclusion, the molecular analyses performed on three genes (two mitochondrial and one nuclear markers) provide strong support for

the inclusion of *Graphiurus* in the Gliridae family, and for the clade Anomaluromorpha uniting the two African families Anomaluridae and Pedetidae. This relationship clearly contradicts the hypothesis of a unique appearance of the multi-serial state of incisor enamel microstructure but does not appear really in conflict with palaeontological interpretations because of the lack of fossil data for Pedetidae. It is clear that the acquisition of more molecular data (other genes and all sciurognath lineages) as well as the finding of fossils documenting the ancestral lineage for Pedetidae will greatly improve our understanding of the relationships between Anomaluridae and Pedetidae.

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Behaviour, Physiology and Reproduction

thème 3

The nutritional ecology of rodent pollinators of *Protea* in South Africa

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Introduction

Many African mammals feed on flowers. Many rodents eat flowers or flower-parts and even large mammals such as springbok, *Antidorcas marsupialis*, and giraffe, *Giraffa camelopardalis*, rely heavily on flowers as food at certain times of the year (SAUER, 1983; NAGY and KNIGHT 1994). In most cases, flower-feeding by African mammals is destructive and is of little or no benefit to the plant. However, in the fynbos biome in southwestern South Africa, rodents are important pollinators of a number of *Protea* species (family Proteaceae) which bear cryptic inflorescences close to the ground (ROURKE & WIENS, 1977; WIENS *et al.*, 1983) and there is increasing evidence that rodents are also important pollinators in the succulent Karoo biome (S.D. JOHNSON, pers. comm.). Although pollination by non-flying mammals is not a uniquely African phenomenon, the degree to which it occurs in the fynbos is exceptional and matched only in Australia, where the plants involved are usually from the Proteaceae or Myrtaceae (ROURKE & WIENS, 1977; REBELO and BREYTENBACH, 1987; CARTHEW and GOLDINGAY, 1997). Non-flying mammal pollination in the fynbos (unlike Australia) is carried out by generalist

rodent species, such as *Rhabdomys pumilio* and *Aethomys namaquensis*, which also occur in many parts of the southern African subcontinent where such flowers are absent (WIENS *et al.*, 1983). However, the plants themselves often appear specialised for mammal pollination (REBELO and BREYTENBACH, 1987).

Flower-feeding mammals, regardless of their status as pollinators or predators, visit the flowers to obtain nutrition from flower parts and products. For small mammalian pollinators, the flowers may provide a substantial proportion of their diet (VAN TETS and WHELAN, 1997). However, there has been very little study to date on the nutritional benefits or the physiological difficulties associated with flower-feeding.

The African rodents involved in the pollination of *Protea* species are seasonal nectarivores, feeding on foliage and seeds for most of the year. The main food rewards, nectar and pollen, are available to them in winter, when energy requirements of small rodents are high. More predaceous flower-feeders which eat entire flowers will also extract energy and various nutrients from petals, bracts and other flower parts, and rodent pollinators sometimes consume the bracts of *Protea* inflorescences (ROURKE and WIENS, 1977; I.G. VAN TETS, unpubl. data). Nectar is a dilute sugar solution, while pollen has protein-rich cytoplasm encased within a thick multi-layered cell wall. Both these food sources present a number of physiological challenges that the flower-feeder must be capable of overcoming. For nectar feeders the sugar concentration and composition will be important. Choice of flowers is likely to be influenced by sugar preferences that may well in turn be related to the animal's physiological capabilities. Pollen feeders must be able to extract the protein-rich cytoplasm from the surrounding cell wall, and their ability to utilise the pollen protein will be strongly affected by its amino acid composition.

Nectar

The nectar of *Protea* is unusual in that it contains the pentose sugar xylose (VAN WYK and NICOLSON, 1995). The concentration of xylose ranges from 0-36% of total sugar in the 46 species of *Protea* for which data are available, and tends to be higher in mammal-pollinated species

than in bird-pollinated species (NICOLSON and VAN WYK, 1998). Within the Proteaceae, this sugar is restricted to the closely related genera *Protea* and *Faurea*, and it is not known from any other floral nectars. Physiological studies related to xylose consumption by pollinating rodents are described below. Variation in nectar sugars at the plant level was examined in two mammal-pollinated species of *Protea:* in both *P. amplexicaulis* and *P. humiflora*, variation in sugar composition between inflorescences and between plants was less than that within an inflorescence (NICOLSON and VAN WYK, 1998).

The nectar of rodent-pollinated *Protea* species has a higher sugar concentration than that of bird-pollinated species (WIENS *et al.*, 1983; S.W. NICOLSON, unpubl. data). This may be correlated with the greater proportion of sucrose (as well as xylose) in the rodent-pollinated species. Regardless of whether the nectar concentration averages 20.7% or 36.1% (four bird-pollinated and three mammal-pollinated species respectively; WIENS *et al.*, 1983), the pollinator obtaining its energy requirements from large volumes of sugar solution faces osmoregulatory challenges, especially if the nectar is diluted by winter rainfall. Hummingbirds and sunbirds are subject to chronic diuresis (BEUCHAT *et al.*, 1990; LOTZ and NICOLSON, 1999). We have investigated the urine diluting ability of two rodent pollinators, the striped field mouse (*Rhabdomys pumilio*) and the Namaqua rock mouse (*Aethomys namaquensis*). When these mice were fed 0.1 M sucrose solution, equivalent to 3.5% (w/w), their urine osmolalities dropped to 30.5 ± 12.0 mOsm. kg^{-1} (mean ± SE) and 37.2 ± 9.5 mOsm. kg^{-1} respectively (I.G. VAN TETS, C.A. BEUCHAT & S.W. NICOLSON, in prep.). In contrast, the same individuals, when deprived of water and fed rat chow only, were able to concentrate their urine to 4915 ± 595 and 3416 ± 79 mOsm. kg^{-1} respectively. These nectarivorous rodents are thus both good concentrators and good dilutors, and indeed they may be subject to both water stress and water deprivation in their natural environment: although seasonal nectar feeders in the fynbos biome, they are also widespread in southern Africa, including desert regions. Our data do not support the suggestion by BADDOURI *et al.* (1987) that the diluting ability of desert rodents may be compromised by their good concentrating ability.

Sunbirds and sugarbirds show a strong aversion to the xylose in *Protea* nectar (JACKSON *et al.*, 1998a). We tested the sugar prefer-

ences of *Aethomys namaquensis*, using pairwise combinations of 30% (w/w) solutions of sucrose, glucose, fructose, xylose, and a mixture of equal parts of glucose and fructose (JOHNSON *et al.*, 1999). The tests were designed to control for side biases which are evident in nectarivorous birds (JACKSON *et al.*, 1998a) and also in the mice. The mice preferred sucrose to hexoses and hexoses to xylose but, unlike the birds, they were willing to drink pure xylose solutions. The order of sugar preferences corresponded to the relative proportions of the sugars in rodent-pollinated *Protea* species (NICOLSON and VAN WYK, 1998). The only previous study of the sugar preferences of non-flying mammalian pollinators is that of LANDWEHR *et al.*, (1990) on Australian possums, which do not encounter xylose-containing nectars.

The efficiency of xylose absorption and metabolism in *A. namaquensis* was assessed by measuring dietary intake, blood xylose levels, and output in urine and faeces (JOHNSON *et al.*, 1999). Table 1 shows data obtained over a two day period, during which the mice ingested a large amount of xylose (approx. 1 g per day). The apparent absorption efficiency can be calculated from dietary intake and urinary output as approximately 97%. This is comparable with the high absorption efficiencies of sucrose, glucose and fructose in a variety of nectarivorous birds (JACKSON *et al.*, 1998b). The high value in *A. namaquensis* contrasts with the xylose absorption efficiency of 53% measured previously in the Cape sugarbird (*Promerops cafer*) fed with a xylose / glucose mixture (JACKSON *et al.*, 1998b). The mice are therefore able to utilise the xylose in *Protea* nectar.

The xylose may be metabolised by intestinal bacteria (as occurs in ruminants), or it may be absorbed and then metabolised by the mice themselves. This latter possibility is supported by the observation of extremely low levels of xylose in both faeces and blood (Table 1). If hindgut fermentation is the primary method of xylose breakdown, a much higher level of faecal xylose would be expected, as faecal material that did not pass through the caecum should still contain xylose. Furthermore, if *A. namaquensis* itself is unable to metabolise absorbed xylose, then a much higher blood xylose level would be expected. Xylose is readily absorbed across the gut wall of rodents (SALEM *et al.*, 1965; ALVARADO, 1966). Its absence from the blood, coupled with the low level in the urine, suggests that it has been metabolised or converted into another chemical form after absorbtion. However, further work is necessary to truly distinguish between these two possibilities.

		DAY 1	DAY 2
Food	Xylose consumed (mg)	979 ± 82	855 ± 189
Urine	Xylose excreted (mg)	31 ± 7.2	25 ± 10.5
Faeces	Xylose excreted (mg)	0.43 ± 0.16	0.29 ± 0.08
Blood	Xylose concentration (mg / ml)	0.20 ± 0.04	No data

Mice were provided with 30 % (w/w) sucrose and rat chow.
All values are mean ± SE. n = 8 (except faeces on day 2: n = 4).

Table 1
Data used to calculate xylose absorption efficiency in *Aethomys namaquensis*.

It has previously been assumed that mammals other than ruminants absorb xylose but are unable to metabolise it: this is the basis of the xylose absorption test (ZILVA and PANNALL, 1984). Metabolism of nectar xylose has wider significance, because xylans (xylose polymers) are major components of the hemicellulose in plant cell walls and this pentose sugar could be an important metabolite for herbivorous rodents.

Pollen

WIENS *et al.* (1983) disregarded pollen as a reward for small mammals visiting *Protea* inflorescences, assuming that it was ingested during grooming. Pollen is often overlooked in studies of pollinator nutrition for a number of reasons. The pollinator may not ingest enough to gain a significant nutritional benefit, the pollen may be deficient in one or more essential amino acids (MARTÍNEZ DEL RIO, 1994), and the tough cell wall may render it indigestible (STANLEY and LINSKENS, 1974). However, it seems that these three objections do not apply to mammalian pollinators of Proteaceae in either Australia (LAW, 1992; VAN TETS and WHELAN, 1997; VAN TETS and HULBERT, 1999) or South Africa (VAN TETS, 1997; HUTCHINGS, 1997; VAN TETS *et al.*, 2000) and that the pollen of Proteaceae is a potentially useful source of nitrogen and protein for small mammals. It is also probable that rodents feeding destructively on flowers would also gain protein from this source.

Analysis of the faeces of four small mammalian species captured in mountain fynbos near Cape Town revealed that all were capable of digesting *Protea* pollen (VAN TETS, 1997). The samples were taken from Namaqua rock mice, *Aethomys namaquensis*, and Edward's elephant shrews, *Elephantulus edwardsii*, at a site where *Protea humiflora* was flowering, and from striped field mice, *Rhabdomys pumilio*, and pygmy mice, *Mus minutoides*, from a site with *P. subulifolia* flowers. Staining with cotton blue lactophenol resulted in a dark blue protoplast but left the cell wall unstained, and the percentage of grains from which the protoplast had been removed, even if only partially, was counted using a light microscope. Samples of pollen were also taken directly from the pollen presenters of *P. humiflora* and *P. subulifolia* and assessed in a similar manner. In the faeces, the mean percentage of empty or partially empty pollen grains ranged from 49-83% in the four mammal species, but less than 1% of the pollen grains taken directly from the flowers fell into this category.

Analysis of the amino acid composition of *P. humiflora* and *P. subulifolia* pollen using HPLC (HUTCHINGS, 1997) demonstrated that the amino acid deficiencies seen in the pollen of hummingbird-pollinated flowers in North America (MARTÍNEZ DEL RIO, 1994) were not apparent. For the North American flowers, methionine and lysine were typically absent or present only in very low quantities. *Protea* humiflora pollen contains 2.0% methionine and 5.5% lysine (percentage of total amino acids, in moles per mole) and *Protea subulifolia* 2.1% and 6.4% respectively. These values compare favourably with those of good protein sources (MOIR, 1994). It should be noted that only small quantities of amino acids are present in *Protea* nectar, whether from bird-pollinated or mammal-pollinated species (WIENS *et al.*, 1983).

To test the ability of these rodents to use pollen as a source of nitrogen, we conducted feeding trials on *Aethomys namaquensis* using commercially available *Eucalyptus* pollen, with a similar amino acid profile to the two *Protea* species, and casein (HUTCHINGS, 1997; VAN TETS *et al.*, 2000). The mice were fed diets in which varying amounts of the protein source – either pollen or casein – were suspended in an agar gel enriched with sucrose, fructose and glucose. At the end of each trial, the faeces were collected, dried and weighed, as was any uneaten food. Urine was collected under paraffin to prevent evap-

oration, and Kjeldahl analysis was used to determine the nitrogen levels in the food, urine and faeces.

From these data we were able to measure a number of digestive parameters. These included the apparent digestibility of the nitrogen (the proportion of the dietary nitrogen intake that was not lost as faeces), the biological value (the percentage of the absorbed nitrogen that is retained by the animal and not lost in the urine), and the maintenance nitrogen requirement (the nitrogen intake required to maintain nitrogen balance).

The apparent digestibility of the pollen nitrogen was, not surprisingly, significantly less than that of the purified protein (75.6 *vs.* 58.4% for pollen, $P < 0.05$, t-test). The amino acids in a purified protein are exposed to digestion much more readily than those bound in or protected by complex biological structures. However, on all other parameters the mice did significantly better on pollen than on casein. The biological value of pollen was 49% as opposed to 39% for casein ($P < 0.05$, t-test) and the dietary maintenance nitrogen requirements were 84 mg N. day^{-1} on pollen and 161 mg N. day^{-1} on casein. This is equivalent to 700 mg of pollen per day and is consistent with the expected nitrogen requirements for an animal of this size on a natural diet (VAN TETS *et al.*, 2000).

Conclusions

The nutritional ecology of the mammalian pollinators in the Western Cape has many similarities to that of the mammalian pollinators in similar ecosystems in Australia. It is difficult to compare the sugar preferences of pollinators in the two regions as xylose is not present in the nectar of Australian Proteaceae, but both *Aethomys namaquensis* in South Africa and *Tarsipes rostratus* in Western Australia exhibit preferences that reflect the sugar composition of the flowers on which they feed (LANDWEHR *et al.*, 1990; JOHNSON *et al.*, 1999). In both regions, pollen was once assumed to be eaten only as the result of accidental ingestion during nectar feeding or grooming (WIENS *et al.*, 1983) and to be of little or no nutritional significance (SMITH, 1982). However, it is now clear that not only is it eaten directly by many

small mammals while feeding on flowers (RICHARDSON *et al.*, 1986; VAN TETS pers. obsv.), but that it is also, regardless of the motivation behind ingestion, a potentially valuable protein source for small mammals. This includes those, such as the rodent pollinators of *Protea*, which are not specialist flower feeders. Not only do mammalian pollinators digest a large proportion of the pollen they ingest but, in at least four instances, they can meet their nitrogen requirements on a relatively small quantity of pollen (LAW, 1992; VAN TETS, 1998; VAN TETS *et al.*, 2000). The importance of pollen as a dietary item for vertebrate pollinators is increasingly being recognised (GRANT, 1996; HERRERA & MARTÍNEZ DEL RIO, 1998).

These seasonal flower visitors have provided unexpected insights into general rodent physiology. We are now aware that rodents can digest xylose, a hitherto overlooked but presumably important source of energy for herbivorous rodents, and we have investigated the possible links between diluting and concentrating ability in small mammals. Flower products are clearly an important element of the diet of many rodents in the Western Cape and should not be overlooked in nutritional and dietary studies dealing with small mammals in other parts of Africa.

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Responses of male *Rhabdomys pumilio* to urine of females in different reproductive states

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Introduction

Olfactory signals are commonly used to indicate the reproductive status of female mammals, and may have highly specific effects on the sexual behaviour of males, such as attraction or eliciting sexual behaviour (FERKIN and JOHNSTON, 1995; JOHNSTON, 1983). For example, odour of a female during oestrus is one of the primary stimuli indicating her receptivity to males (EISENBERG and KLEIMAN, 1972). In many rodents, such as house mice *Mus musculus* (FERON and BAUDOIN, 1992), brown lemmings *Lemmus sibiricus* (HUCK and BANKS, 1984), woodrats *Neotoma lepida lepida* (FLEMING *et al.*, 1981), Djungarian hamsters *Phodopus campbelli* (LAI *et al.*, 1996) and rats *Rattus norvegicus* (NYBY, 1982), males spend greater time sniffing odours of oestrous than non-oestrous females.

Preference for oestrus over non-oestrus females is not universal, however. Male golden hamsters *Mesocricetus auratus* show no preference for odour of oestrous to dioestrous female conspecifics, but prefer odours of oestrous females to those of pregnant females (JOHNSTON, 1980). In some mammals, for example Djungarian

hamsters *P. campbelli* (LAI *et al.*, 1996), males are particularly attracted to the scent of postpartum oestrus females. This attraction is probably consistent with the situation in nature, since many mammals go through cycles of pregnancy rather than through repeated oestrous cycles (BRONSON, 1985).

In a recent study, BENNETT (1999) showed that male striped mice *Rhabdomys pumilio* are more attracted to the smell of urine than other odour sources (i.e. body and facial odour, saliva and vaginal secretions) of oestrous females. Nothing is known about whether male striped mice show differential preference of urinary odour over a variety of female reproductive states, which was the objective of the present study. In order to facilitate mating, receptive females are likely to produce substances in the urine which are attractive to males. Hence, it is predicted that male striped mice would prefer urine of receptive females (i.e. oestrus, postpartum oestrus) to non-receptive females (i.e. dioestrus and pregnant).

Rhabdomys pumilio is widely distributed in southern Africa (SKINNER and SMITHERS, 1990), occurring in high population densities in suitable habitats (WILLAN and MEESTER, 1989). It is a seasonal breeder, producing litters averaging around five pups (PERRIN, 1980; WILLAN and MEESTER, 1989). During the breeding season, adult females are intrasexually territorial with a limited home range size, and adult males occupy larger home ranges that overlap those of several females (PILLAY, 1999; SKINNER and SMITHERS, 1990). Mature females have a spontaneous oestrous cycle of four days, in which they are receptive for one day (oestrus; BENNETT, 1999). Females also have postpartum oestrus, mating within a day or two of parturition (PILLAY, 2000).

Materials and methods

Rhabdomys pumilio individuals were derived from wild caught parents from Alice, Eastern Cape Province (32° 48' S; 26° 52' E), South Africa. Thirty-two adult male and 38 adult female *R. pumilio* were used in the study. All animals were sexually experienced. They were housed

individually in Labotec® cages, under partially controlled environmental conditions at a temperature of approximately 25°C, rH = 30-50%, and a light regime of 14L; 10D (lights on between 05.00 and 19.00), thereby approximating summer in the southern hemisphere and hence optimal breeding conditions. Animals were fed ad libitum Epol® mouse cubes (containing 18% protein), and were provided twice weekly with maize and sunflower seeds. Water was available at all times.

Stimulus samples (urine) were collected from donor females in five different reproductive states: i) oestrus (cycling, receptive females); ii) dioestrus (cycling, non-receptive females); iii) mid-pregnancy (females in their second week of pregnancy, approximately mid-term of the 23-day gestation period); iv) late-pregnancy (2-3 days before parturition); v) postpartum oestrus (12-48 hours after parturition). Vaginal smears were taken to establish postpartum oestrus as well as the stage of oestrus of cycling females. Mated females were assessed for pregnancy by means of vaginal smears and palpation.

Urine samples from females in the different reproductive states were presented to test males in seven different treatments in two-choice tests: i) dioestrus vs oestrus; ii) dioestrus vs mid-pregnant; iii) dioestrus vs late pregnant; iv) dioestrus vs postpartum oestrus; v) oestrus vs mid-pregnant; vi) oestrus vs late pregnant; and vii) oestrus vs postpartum oestrus. Twelve replicates of each treatment were performed. Before conducting experiments, 12 control tests were carried out, where males were offered a choice of two clean cotton buds. This was done to expose any potential bias in test equipment.

Of the 32 males used in experiments, four were initially tested per treatment and the control. Males were then re-used twice more in treatments or control tests. No male was exposed to the same treatment or the control more than once, and they were never exposed to the urine of a particular female more than once. The allocation of males to the experiments was done randomly. Males were allowed a rest period of three days between consecutive tests.

Tests were carried out by first collecting urine from two scent donor females by wiping a clean cotton bud over the female's clitoris as she produced urine. The cotton buds (with the urine samples) were then placed into clean petri dishes, covered with gauze, and placed into a two-choice chamber. The choice chamber comprised three linearly

arranged compartments. The stimulus samples were randomly placed into the two outer compartments, while the test male was initially placed in the centre compartment. During experiments, he had access to the urine samples by means of interconnecting passages; a complete description and illustration of the choice chamber is provided in PILLAY *et al.* (1995).

The behaviour of the male was then recorded using a Sony TR880E video camera. All tests were conducted during the light phase of the light-dark cycle, since *R. pumilo* is diurnal.

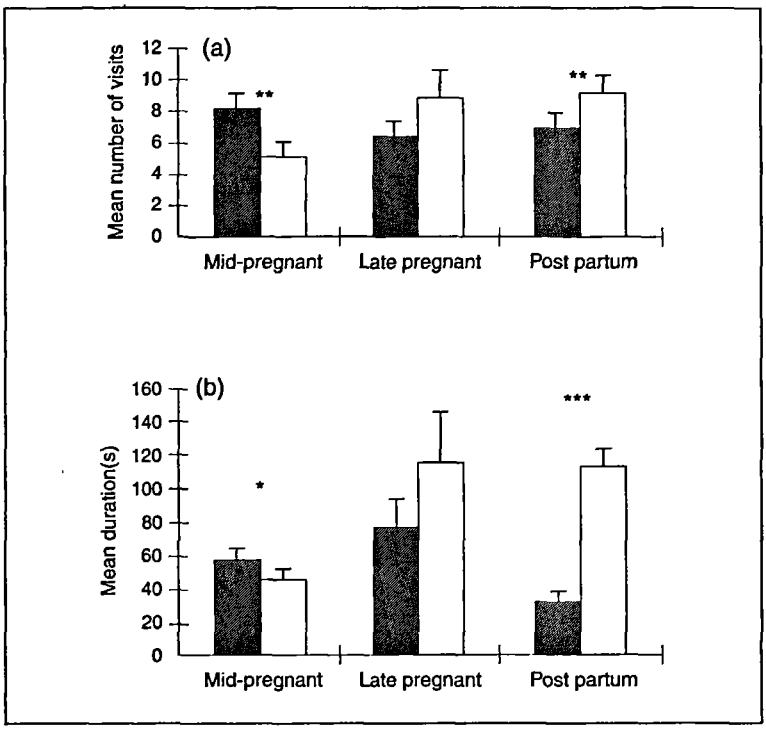
Immediately after the male made contact with either one of the urine samples, the total time he spent at each urine sample, and number of times he visited each urine sample were recorded for 20 min. The mean duration of time spent at each urine sample and the mean number of visits to each urine sample were calculated per combination of reproductive states. Data were analysed using a two-tailed paired-t test to establish whether males displayed a directional preference in each treatment and in the control (ZAR, 1996).

Results

Males spent an equal duration at both left and right control samples ($p > 0.05$; paired t-test), suggesting no bias in test equipment.

In experiments involving choice between dioestrous and oestrous female urine samples, the frequency of visits by males to dioestrous ($X \pm SE = 7.50 \pm 1.02$) and oestrous (7.30 ± 0.98) samples did not differ significantly ($p > 0.05$, paired t-test). Males spent equivalent amounts of time at oestrous (54.00 ± 6.96 s) and dioestrous (49.20 ± 8.24 s) female urine samples ($p > 0.05$; paired t-test).

The mean number of visits and the duration of visits of males to dioestrous female urine samples versus those from females in different stages of pregnancy or postpartum oestrus are shown in Figure 1. Males did not show a clear preference between urine of dioestrous females and that of females in late pregnancy, but preferred dioestrus

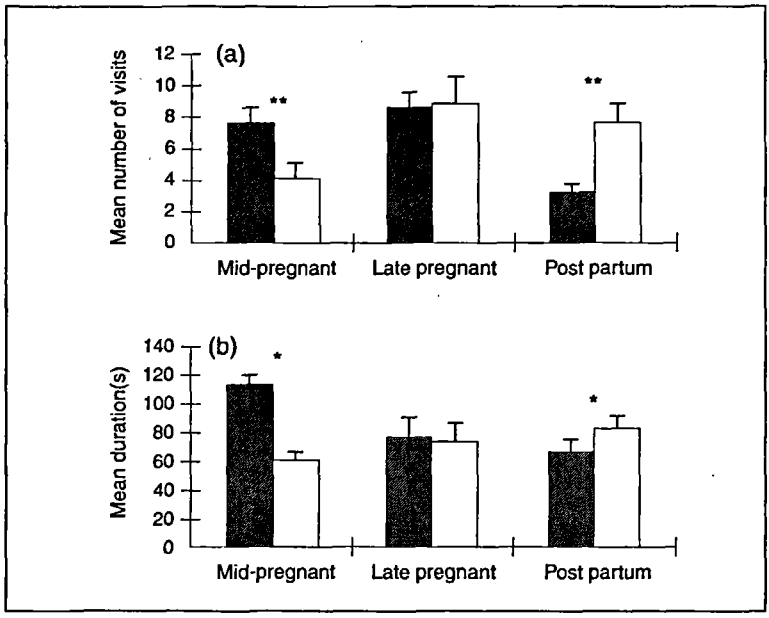


*p < 0.05; **p < 0.01; ***p < 0.001.

Figure 1
Mean number of visits (a) and mean duration (b) displayed by male *R. pumilio* in respect of urine samples from dioestrous females (black bars) versus those from females in other reproductive stages (open bars).
Error bars = 1SE of the mean.

to mid-pregnant female urine (fig. 1). Males clearly preferred urine of postpartum oestrous females to urine of dioestrous females (fig. 1).

Figure 2 gives the number of visits and the duration of visits that males made to urine from oestrous females to those in different stages of pregnancy and postpartum oestrus. Males significantly preferred the urine of oestrous females to that of mid-pregnant females. Postpartum oestrous female odour was preferred to oestrous female odour (fig. 2).



*p <0.05, **p < 0.01.

Figure 2
Mean number of visits (a) and mean duration (b) displayed by male *R. pumilio* in respect of urine samples from oestrous females (hatched bars) versus those females in other reproductive stages (open bars). Error bars = 1SE of the mean.

Discussion

The prediction that male *R. pumilio* would prefer receptive to non-receptive females was only partially supported in this study. On the one hand, males showed equal preference for dioestrous and oestrous female urine, and for cycling females and those in late pregnancy. On the other hand, urine from cycling females was preferred to that of females in mid-pregnancy. In addition, postpartum oestrous female urine was highly attractive to *R. pumilio* males, significantly more so than urine from cycling females.

The literature on rodent olfactory communication shows both similarities and differences to the results obtained in the present study.

Male golden hamsters *M. auratus* showed no preference for odours of dioestrous or oestrous females, but preferred the odours of oestrous females over those of pregnant or lactating females (golden hamsters do not have a postpartum oestrus; JOHNSTON, 1980). Male Djungarian hamsters *P. campbelli* were more attracted to urine from females in postpartum oestrus than that of dioestrous females, but showed no preference for urine from females the day before parturition (late-pregnancy) or from dioestrous females (LAI *et al.*, 1996). In meadow voles *Microtus pennsylvanicus,* male attraction to female scent increased greatly just after parturition when females were in post-partum oestrus (FERKIN & JOHNSTON, 1995).

The lack of preference between the urine of dioestrous females and oestrous females urine by male striped mice should be interpreted with caution, since such a situation could imply either an inability to discriminate between the scents or an equal interest in both urine samples. In recent experiments (PILLAY unpubl. data), however, male *R. pumilio* were sexually aroused by the presence of oestrous females and not dioestrous females, displaying more mounting and nasal-anal behaviours in the presence of oestrous females. Hence, males can discriminate between the two reproductive states. This does raise the possibility that a preference for oestrous females would occur when a greater number of signals is available. In our study, males could potentially evaluate the stimuli with the sense of smell (olfactory and vomeronasal) only, but other cues could elicit differential responses in the male; for example, ultrasonic calls or lordotic posture of females (TAYLOR & DEWSBURY, 1990).

LAI *et al.* (1996) suggest that some pregnant female rodents might produce a "stay away" signal that males find unattractive. Similarly, the reduced interest in mid-pregnant female urine corresponds with the time when females are furthest away from receptivity. It is intriguing therefore that the urine of females in late pregnancy (a few days away from receptivity) was as attractive to males as the urine of both dioestrous and oestrous females. These results may be explained by the social and population biology of *R. pumilio.*

Striped mice occur at high densities during the breeding season, and male-male competition for breeding females is apparently intense (WILLAN & MEESTER, 1989). Females are receptive within two days of both dioestrous and late pregnancy (2-3 days before parturition in

the present study). Thus, it would be advantageous for males to be equally attracted to females in dioestrous and late-pregnancy, as they are to oestrous females, and remain near these females shortly before receptivity (DEWSBURY *et al.*, 1986; JOHNSTON, 1980).

The preference for the urine of postpartum females over that of cycling females is consistent with the reproductive biology of the species. Free-living *R. pumilio* reproduce at a high rate (BROOKS, 1982; PERRIN, 1980; WILLAN and MEESTER, 1989) which means females would be pregnant or in postpartum oestrus throughout the breeding season. Females would therefore go through cycles of pregnancy rather than oestrous cycles, and males are more likely to encounter postpartum oestrous females than cycling females.

Further studies involving chemical analysis of *R. pumilio* urine should be done to evaluate the changes in components and/or concentrations of components that may exist between various female reproductive stages.

Acknowledgements

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Swimming ability in six West-African rodent species under laboratory conditions

Evaluation of their potentialities to colonize islands

Jean-Marc Duplantier

Kalilou Bâ

Introduction

Swimming ability has already been tested in different groups of rodents to examine the role that water bodies (rivers or sea-arms) may play as barriers to dispersal, mainly as an attempt to explain the observed distributions of various continental populations or species (HAFNER and HAFNER, 1975; SAVIDGE, 1973; GIANNONI *et al.*, 1994), less frequently to assess different species' potential to invade islands (CARTER and MERRITT, 1981). Similarly, a large number of studies on this topic have concerned European and North American rodents and strangely enough mainly subterranean rodents (see HICKMAN, 1988, for a review), yet only one study has been devoted to above-ground African species (HICKMAN and MACHINÉ, 1986).

Several field studies in Senegal allowed us to study island populations in two very different contexts: the rocky Madeleine Island off the coast of Dakar on the one hand, and the sandy islands of the Saloum Delta (DUPLANTIER, 1988; GRANJON, 1987; GRANJON and DUPLANTIER, 1989) on the other hand. The rodent community on an

island can be either the remnant of an original mainland community, subsequently isolated, or the result of immigrations, or the resultant of the two processes. It is generally accepted that islands are colonized by the most abundant species from the nearest mainland and/or by species commensal with humans (MAC ARTHUR and WILSON, 1967). This general pattern corresponds to the situation we observed on Madeleine Island: the only species occurring on the island, *Mastomys erythroleucus*, is the most abundant species on the mainland, indoors as well as outdoors. Conversely, three other rodent species were encountered on the Saloum islands. The black rat, *Rattus rattus*, is indeed a commensal species, yet the other two, *Mastomys huberti* and *Tatera gambiana* are not, nor are they the most abundant species on the nearby mainland. Therefore, they must have arrived on these islands by their own means. It thus appeared interesting to compare swimming ability of the main species on the mainland in an effort to understand the present community on these islands.

Material and methods

Five species of Muridae (*Arvicanthis niloticus, Mastomys huberti, Mastomys erythroleucus, Myomys daltoni* and *Dasymys rufulus)* and one Gerbillidae (*Tatera gambiana*) were used in this study. Ten individuals of each species (5 males and 5 females) were tested under identical conditions, except for *Myomys daltoni* for which only 3 males and 3 females were studied. All individuals were adults captured in nature and maintained in captivity for several weeks prior to the tests. Only individuals showing no wounds (in particular with a complete and intact tail) were used.

Tests were carried out in a plastic aquarium 100 cm long, 50 cm wide and 40 cm high, filled with fresh water up to 22 cm high. Water temperature was 22 °C. Animals were tested individually and each test lasted 10 minutes. Each individual was weighed before and after the test, and also after one, three and five minutes in the water, to assess water uptake by the fur relative to time spent in the water.

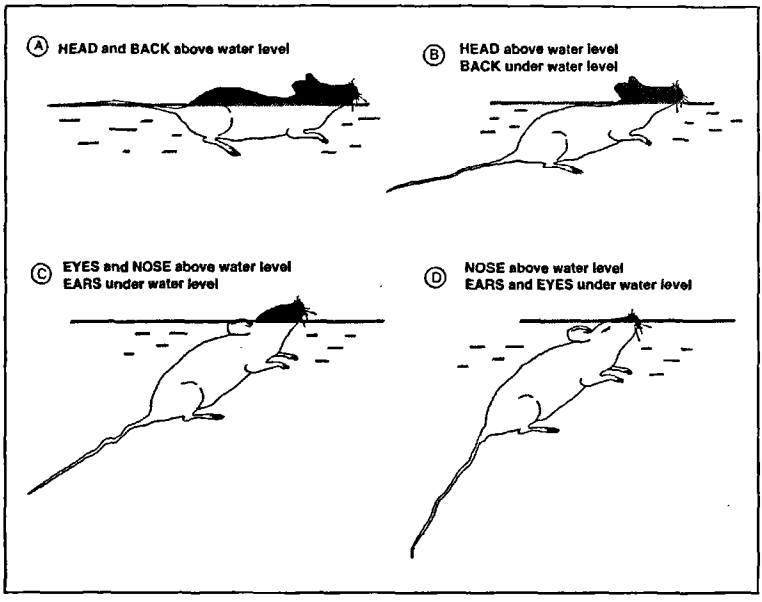

Figure 1
Different body positions in water, recorded during the tests.

During the tests, we recorded the following activities, swimming, floating, sinking, and diving by two-second sequences: that is to say that activities lasting less than 2" were not taken into account and those lasting more were divided in 2" units. Swimming refers to the animal moving by means of the limbs and / or the tail. Floating refers to the animal keeping its limbs immobile while maintaining its body stable in the water. Sinking refers to the body going under water by the rear with or without tail or limb movements and with the nose under water level. When more than ten sinking sequences occurred within one minute, or when a rodent displayed difficulty in surfacing again after sinking with signs of drowning, it was immediately retrieved from the water and the test was stopped for that individual. Diving refers to the animal swimming under the water, head first, towards the bottom of the aquarium. At the end of each minute, the position of the body in the water was recorded (fig. 1).

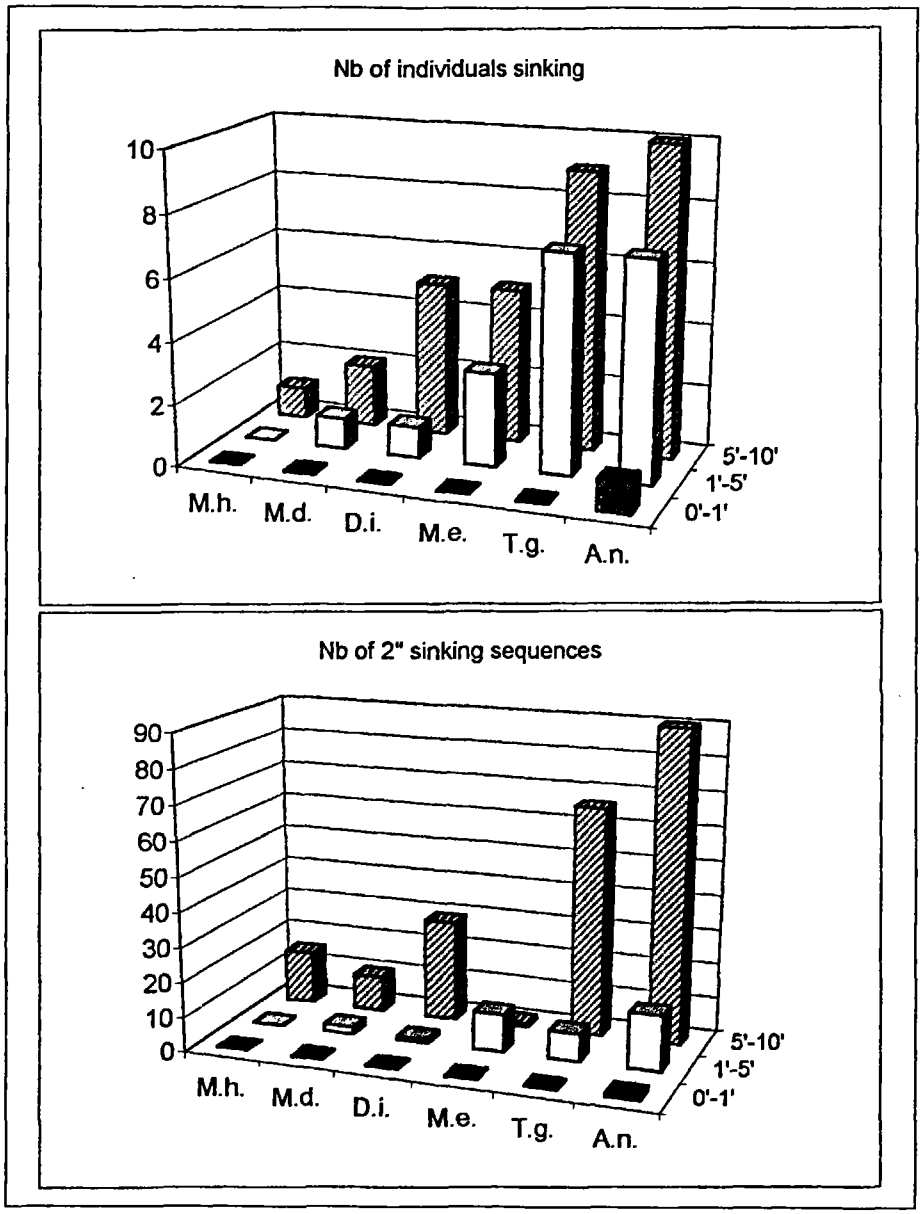

Figure 2
Importance of sinking according to time spent in water, for the six species tested (A.n. = *Arvicanthis niloticus*, D.i. = *Dasymys rufulus*, M.d. = *Myomys daltoni*, M.e. = *Mastomys erythroleucus*, M.h. = *Mastomys huberti*, T.g. = *Tatera gambiana*).

Results

Overall results and sinking

In three species, *D. rufulus, M. huberti* and *M. daltoni*, all individuals passed the 10-minute test. In contrast, only 7 out of 10 individuals in *A. niloticus* and *T. gambiana*, and 6 out of 10 in *M. erythroleucus* succeeded. In *T. gambiana*, the individuals that failed were the lightest (1 male and 2 females). Three *A. niloticus* females were eliminated with no apparent relation to their weight (they ranked 3rd, 7th and 10th by decreasing weight).

Three *M. erythroleucus* females and one male were eliminated with no relation to weight either (1st, 4th, 7th and 10th by decreasing weight). But the 6 remaining individuals presented the lowest number of sinking sequences (fig 2). All *A. niloticus* individuals and 9/10 *T. gambiana* individuals sank at least once during the experiment, against only one *M. huberti.*

Water uptake by the fur

With the exception of *M. daltoni*, there was extensive individual variability for this parameter in all species, as denoted by important standard deviations (fig 3). Increase in body weight peaked after one minute in the water, except for *M. huberti*. This species always displayed the lowest average values regardless of time spent in the water. Conversely, *D. rufulus* always displayed the highest averages. After 10 minutes the average increase in body weight was significantly larger in *D. rufulus* than in *M. huberti* (Mann-Whitney U test, $p < 0.05$). For five species we did not detect any correlation between initial (dry) weight of individuals and the magnitude of water uptake at the end of the test. In *D. rufulus*, however, this correlation was negative: the heaviest individuals displayed the lowest relative water uptake (% of initial weight, $r = -0.8526$, $p > 0.01$). We did not observe any significant difference between males and females within a given species. Finally, the individuals that had to be removed from the water before the end of the experiment did not display the highest water uptake: the 3 *T. gambiana* that were eliminated ranked 3rd, 4th and

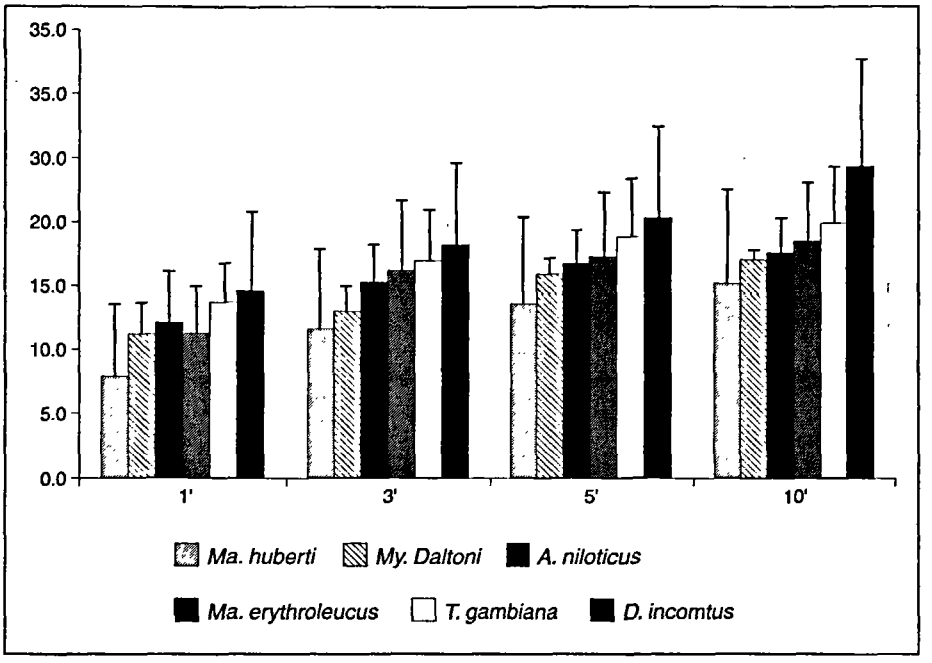

Figure 3
Water uptake by the fur according to time spent in water (mean and standard deviation, expressed as percentage of the initial weight).

10th by decreasing water uptake. The 4 eliminated *M. erythroleucus* similarly ranked 1st, 4th, 6th and 8th; and the 3 eliminated *A. niloticus* ranked 4th, 6th and 8th.

Position in the water

M. huberti and *D. rufulus* were the only species which individuals were still horizontal after ten minutes of test. In these two species as in *M. erythroleucus*, there was great individual variations however. In *D. rufulus* the three individuals that were in position A after 10 minutes were all males, whereas of the 5 individuals in position D there were 4 females and 1 male. In *M. huberti* the two individuals that were in position A at the end of the test were males, two other males were in position B and the fifth was in position D. In *M. erythroleucus*, 3 females were eliminated, 1 was in position C and 1 in position D.

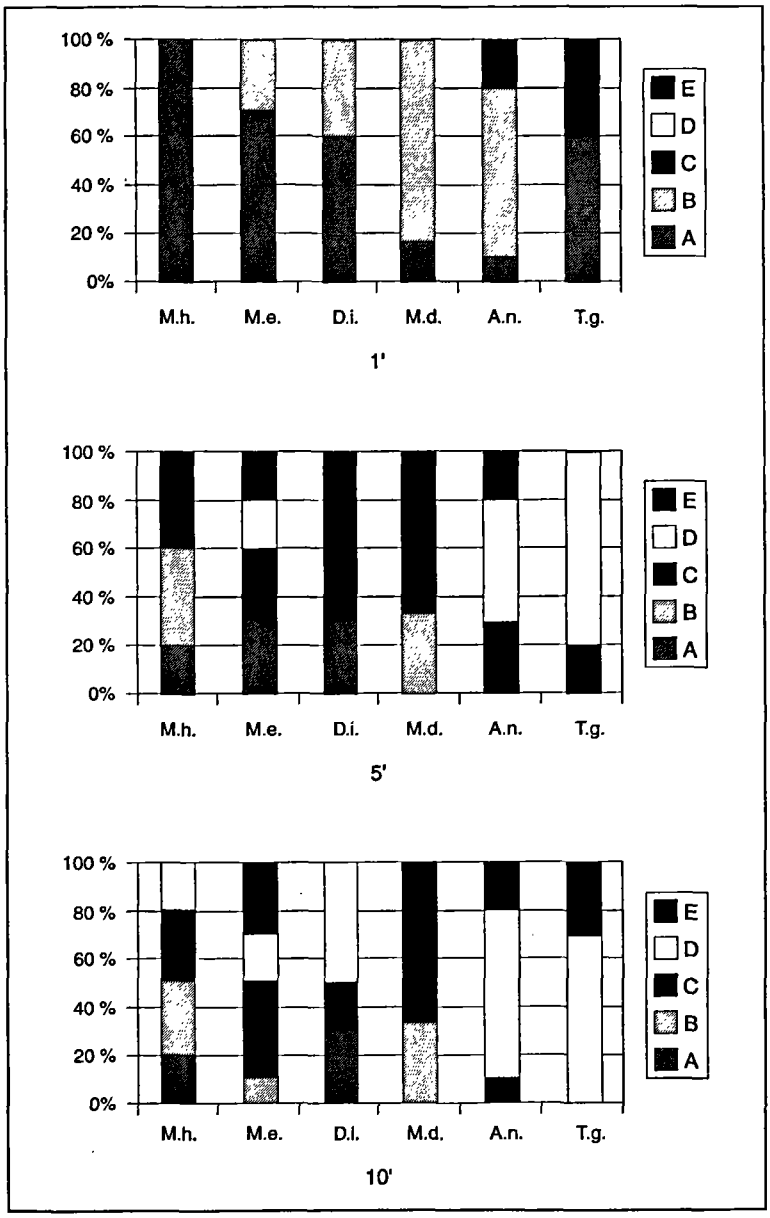

Figure 4
Percentage of individuals in the different "body position in water" (see fig 1), according to time for each species:
A, B, C and D = body positions;
E = number of individuals eliminated.

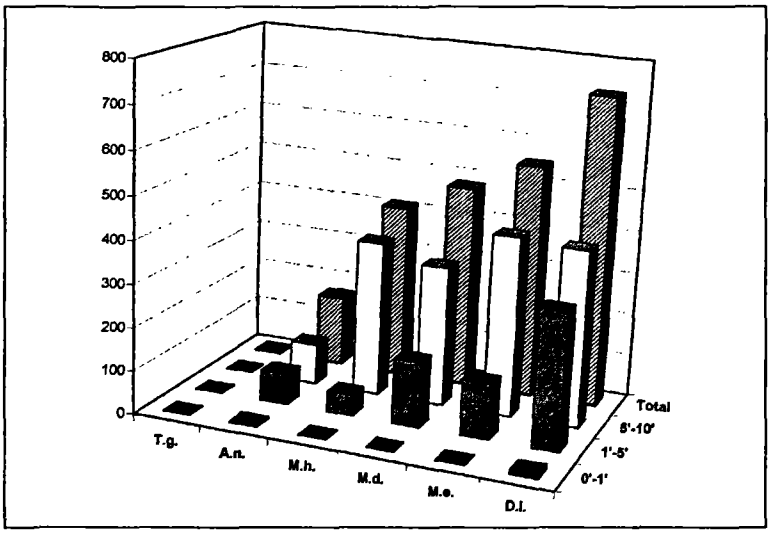

Figure 5
Number of floating periods according to species and time spent in water.

Conversely, after the first five minutes in the water, all *M. daltoni* individuals were in an intermediate position, and *A. niloticus* and *T. gambiana* were heavily slanting backwards.

Floating

Only one *T. gambiana* individual managed to float for 2 seconds. This behaviour concerned the majority or all individuals in the other species. The number of floating periods was null or very low in all species during the first minutes spent in the water. It increased between 1 and 5 minutes except for *M. huberti* and *A. niloticus.* It increased considerably beyond 5 minutes in *M. huberti* and remained stable in *A. niloticus.*

Diving

This behavior was recorded in four species only. One *D. rufulus* dived twice, one *M. erythroleucus* and one *T. gambiana* 4 times each. Three *A. niloticus* dived, among which one individual did it twice.

Discussion

One of the main findings from these tests is the extensive individual variability observed for the majority of the parameters recorded. Yet within-species behavior is rather homogeneous in three species: *M. huberti, M. daltoni* and *T. gambiana.* A small fraction of individuals displayed better abilities than their conspecifics in *A. niloticus* and weaker abilities in *D. rufulus*. Finally, in *M. erythroleucus*, the individuals tested were evenly distributed among good and poor swimmers. Considering these facts it is possible to rank the different species from good to poor swimmers.

Mastomys huberti

We have shown (DUPLANTIER and GRANJON, 1988) that *M. huberti* is a characteristic wetland species; therefore it is not surprising that it ranks first in this classification. All the individuals reached the end of the test and presented the lowest occurrence of sinking. Water uptake by the fur was the lowest regardless of the time spent in water. Eight of ten individuals had at least the eyes and the nose above water level at the end of the test.

Myomys daltoni

All the individuals reached the end of the experiment and presented one of the lowest rate of sinking. All the individuals had at least the eyes and the nose above water level at the end of the test. This species is considered to be semi-arboreal; it is sometimes commensal, but only rarely inhabits wetlands. Its ecology and distribution thus cannot explain its good performances. However, its morphology may play an important role: this species has the longest tail in our sample and the importance of this organ in swimming has already been demonstrated (HICKMAN and MACHINÉ, 1986).

Dasymys rufulus

All the individuals reached the end point of the experiment. Water uptake by the fur was greater than in other species, yet this sample

presented the highest number of floating sequences. This species is commonly called the swamp rat or the shaggy rat, which adequately illustrates its ecological and morphological attributes. *Dasymys rufulus* usually has a shaggy fur with a very dense and thick undercoat relatively impermeable to water. However, NOWAK and PARADISO (1983) noted that individuals with long and straight fur can be found. These individuals could have been moulting and their changing fur would have been less impermeable. This could explain the weaker performances and greater water uptake that we observed in lighter individuals.

Mastomys erythroleucus

As opposed to its congeneric *M. huberti*, this species falls into two groups: some individuals displayed good abilities whereas others did not at all. Four of ten individuals had to be removed from water before the end of the test, but the 6 others presented the lowest occurrence of sinking. Half of the individuals had at least the eyes and the nose above water level at the end of the test.

Arvicanthis niloticus

Three of ten Nile rats had to be removed from the water, and the remaining individuals presented the highest occurrence of sinking. Only one individual had at least the eyes and the nose above water level at the end of the test. The poor performances observed in the individuals we tested are somewhat surprising. The Nile rat is a diurnal species that often lives by the water and on several occasions we observed individuals swimming in the Senegal river valley.

Tatera gambiana

Three of ten gerbils had to be removed from the water and the remaining individuals presented among the highest occurrences of sinking. After 6 mn in the water, all these individuals had only the nose above water level. All tested animals seemed unable to float and had to swim constantly. These poor results corroborate the observations by HICKMAN and MACHINÉ (1986) on another species of the same genus,

namely *T. leucogaster*. Moreover, the fur of *T. gambiana* was found to be more absorbent than that of Muridae and this may represent a heavy handicap in this species characteristic of arid habitats.

With respect to the ability to reach islands, these test results are in accordance with the distributions observed in the field. *Mastomys erythroleucus* displays poor performances and its presence on Madeleine Island can be explained both by its abundance on the neighbouring mainland and by the fact that it is a commensal species. Madeleine Island was isolated from the mainland 8000 years ago and traces of human settlements are documented back to 1000 years BP (DESCAMPS, 1982). The present occurrence of *M. erythroleucus* can thus be explained both by lower extinction risks as compared to other mainland species (diversified diet, very high fertility, DUPLANTIER, 1988) and by numerous opportunities for passive immigration with humans in the course of several hundreds of years.

In the Saloum Delta, *R. rattus* was found only on islands with permanent human settlements, whereas only *T. gambiana* and *M. huberti* live on uninhabited islands (GRANJON and DUPLANTIER, 1989). Due to temporary human presence (camps of fishermen) or permanent settlements on all these islands, we can assume that *M. erythroleucus* has had repeated opportunities for colonization. Its inability to establish permanent populations in these islands can be explained by two factors. First, it is probably out-competed by the black rat inside human dwellings, as we have shown on the mainland (DUPLANTIER *et al.*, 1997). Second, it seems unable to adapt to the lack of fresh water characteristic of these sandy islands covered with halophilous vegetation, contrarily to *M. huberti* (GRANJON *et al.*, 1994; GANEM *et al.*, 1995).

As for *T. gambiana* and *M. huberti*, two different contexts must be considered. The two species cohabit on large islands (over 3000 ha in area) separated from the mainland by narrow channels (25 to 50 meters wide on average, only a few meters at some points). On smaller islands located more than 200 meters from the nearest large island or mainland, *M. huberti* is the only species present. This shows that *T. gambiana*, an arid-habitat species, can perfectly adapt to such salty habitats contrarily to other species on the mainland that are either more abundant (*A. niloticus*) or best swimmers (*M. daltoni, D. rufulus*), yet its poor swimming abilities prevent it from reaching the most remote islands.

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Reproductive period and group structure variety in the Barbary ground squirrel *Atlantoxerus getulus*

Preliminary results

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Introduction

Socioecology is the comparative study of social structure in relation to ecology (CROOK, 1970). Its main focus is to gain insight on how social structures and contrasts in ecology are correlated, by way of comparisons between closely related species (CROOK, 1965; CROOK and GARTLAN, 1966; JARMAN, 1974).

This comparative approach has been efficiently used in North American ground dwelling squirrels (MURIE and MICHENER, 1984). Ground squirrels (i.e. marmots, prairie dogs and spermophiles) occupy a wide variety of habitats in North America, from Arctic tundra to desert, and they display different social structures. MICHENER (1983) described five grades of social structure which form a continuum of sociality from asocial to egalitarian polygynous harems. ARMITAGE (1981) concluded, from a comparative study of 18 species of ground dwelling squirrels, that the more social species are characterized by a large body size combined with a short growing season and that sociality has evolved through the formation of groups of related females.

The comparison of different species nevertheless raises several statistical problems (see review in GITTLEMAN and DECKER, 1994). An alternative approach is to compare only two closely related species living in different habitats as suggested by FELSENSTEIN (1985). This method has been applied in two species of ground squirrels of the *Spermophilus Ictidomys* sub-genus and has emphasized behavioral adaptations to desert environment (LIVOREIL *et al.*, 1993; YAYHAOUI *et al.*, 1995; GOUAT *et al.*, 1996; MANDIER and GOUAT, 1996). It is also possible to study the variability in social structure between different populations of a given species. General rules established through inter-specific comparisons may explain intraspecific differences (BARASH, 1973; 1974, but see ARMITAGE, 1977). Intraspecific variations in the social structure of wild vertebrates in relation with habitat differences proved to be an heuristic approach in different species (LOTT, 1984; WAAS, 1990; FERRON, 1991). Intuitively, species occupying a large range of habitats are thought to be the most appropriate species to explore the relationships between ecological constraints and social behaviour.

The Barbary ground squirrel, *Atlantoxerus getulus* (Linnaeus, 1758), is an endemic species from Morocco and Algeria. If the presence of rocky shelters is a requisite to make a site convenient for occupation, the Barbary ground squirrel occupies a wide variety of habitats from alpine meadows (up to 3000 m a.s.l.) to desert (SAINT GIRONS and PETTER, 1965; AULAGNIER and THÉVENOT, 1986). In order to determine if the Barbary ground squirrel is a suitable species for socioecological studies, this paper presents preliminary results on the reproductive period and on the group structure among sites scattered on the species geographical range in Morocco.

Methods

Location of the sites

Sites are classified according to their location on the three principal mountain ranges of Morocco: High Atlas, AntiAtlas and Middle Atlas (fig. 1).

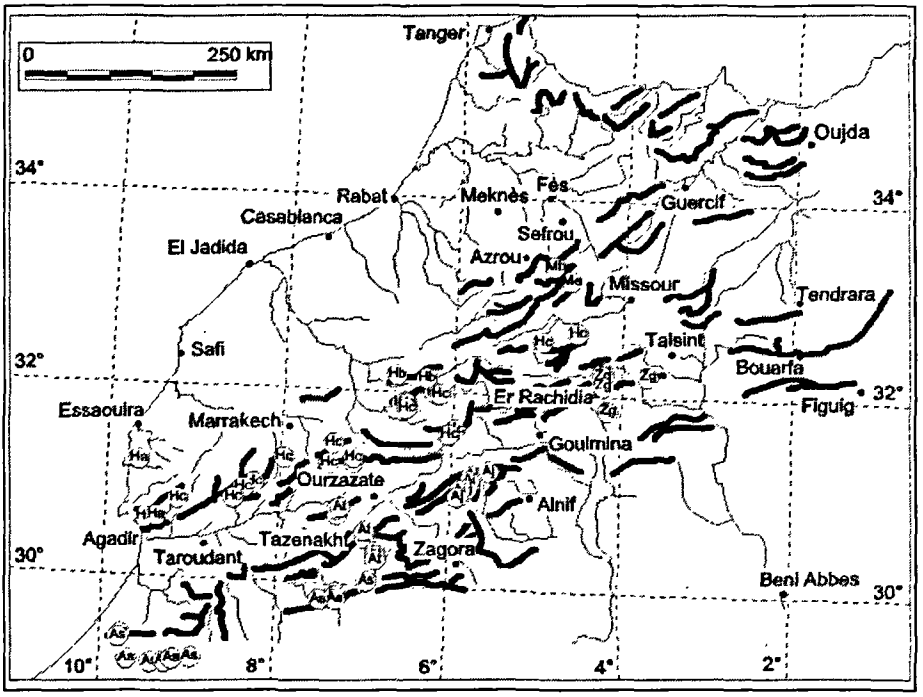

Figure 1
Distribution of the observation sites in Morocco. Sites are located by open circles and two letters according to the different regions. Ha: Atlantic range of High Atlas; Ha: central part of High Atlas; Hb: Bin el Ouidane region; Mb: Boulemane region of Middle Atlas, Me: Enjil region of Middle Atlas; Zg: lower part of wadis Ziz and Guir; As: South-western part of AntiAtlas, At: Tazenakht region of Anti-Antlas; Aj: Jbel Sahro region of AntiAtlas.

Inside High Atlas sites, three sub-units have been distinguished. Central High Atlas encompassed 19 sites, with elevation ranging from 1000 m to 2000 m a.s.l. Snow is usually present during winter. The two other sub-units are composed of low-elevation sites located near the Atlantic coast or in a more central place (Bin el Ouidane). These sites are characterized by the presence of *Euphorbia resinifera* and the absence of snow during winter.

On the eastern part of the High Atlas, two important "wadis" flow to the South and to the Sahara desert, wadi Ziz and wadi Guir, crossing the eastern range of the AntiAtlas. Four sites were located in the lower parts of these two wadis.

Sites of the AntiAtlas have been divided into three sub-units. Sites of the South-West and Tazenakht regions are located in desert habitat. The third sub-unit is located in Jbel Sahro, a volcanic and high-elevated massif. Due to the scarcity of precipitation, snow is rare during winter, but minimum temperatures fall below zero at that period.

Barbary ground squirrels are not abundant in the Middle Atlas. Only two sites have been observed, both of them located in the eastern part of the Middle Atlas.

Data collection

In order to collect data on the social structure of the Barbary ground squirrel, we have prospected sites during five different periods of the year:

- May: from May 1st to May 6th 1991.
- December: from December 26th 1991 to January 2nd 1992.
- April: from April 18th to May 4th 1994.
- March: from March 11th to March 30th 1995.
- July: from July 11th to August 10th 1996.

All sites were not observed at each of the five periods (tabl. 1).

Group composition was assessed by direct observation using binoculars (10 x 50) or a telescope (20-50 x 63). Depending on the site, observation lasted from 2 hours up to a complete diurnal period. Using this method, one can recognize adults from young animals of less than three months of age. Among adults, lactating females, females at the end of gestation, and sometimes males when tests are in a scrotal position may be identified.

		Nb of sites	Altitude in m min. – max.	December	March	April	May	July
ANTI-ATLAS	South-West	12	525 – 950	–	–	young	–	–
	Tazenakht	8	720 – 1700	adults	preg. fem.	young	adults	adults
	Jbel Sahro	7	1390 – 2400	–	adults	–	adults	young
ZIZ and GUIR	Lower part	4	900 – 1300	–	–	young	adults	adults
HIGH ATLAS	Atlantic	3	150 – 340	adults	–	adults	–	–
	Bin El Ouidane	2	860 – 870	adults	–	young	–	–
	Central	19	1020 – 2080	adults	–	adults	adults	young
MIDDLE ATLAS	Boulemane	1	1590	–	–	–	–	young
	Enjil	1	1850	young	–	–	–	–

Table 1
Presence of young on sites of different regions as observed during the five periods.
Number of sites and minimum and maximum elevations are given for each region.
Young: lactating females and young were observed at least in one site;
preg. fem.: no young was observed, and a pregnant female was observed at least in one of the sites;
adults: only adults were observed on all sites of a given region;
– : no observation was made in this region at that period.

Results

Reproductive period

Data are summarized by geographic sub-regions in table 1. The reproductive period was assessed by the presence of young animals in at least one of the sites observed at a given period. The presence of a pregnant female was unambiguous in only one observation at a site of the Tazenakht region in AntiAtlas on March 26th. Five males were courting this female and were chasing each others. This observation tends to prove that a post-partum oestrus occurs in the Barbary ground squirrel and that two successive litters are possible in a same reproductive season. Nevertheless, the presence of young animals does not last for a long period. In the most regularly investigated Tazenakht

	ANTI - ATLAS			ZIZ and GUIR	HIGH ATLAS	MIDDLE ATLAS	
	South-West	Tazenakht	Jbel Sahro	Lower part	Central	Boulemane	Enjil
1 female and young	2	2	1		2		1
2 females and young	2	2		1	1		
Colony of families	1						
Males, females, young				1		1	
1 adult	2	1		1			
2 adults or more	2	2					

Table 2
Group composition during the reproductive period. The number of sites per region in which each type of group was observed is given.

region, young animals were observed only in April. A similar result was found in the central High Atlas but young were observed in July only. Reproduction appears to be highly seasonal but seems to occur at two different periods according to the geographic location. In high altitude sites of the High Atlas (central part) and of the AntiAtlas (Jbel Sahro), young were observed in July, while in lower altitude sites of AntiAtlas (South-West region and Tazenakht region) as in the wadis Ziz and Guir sites and Bin El Ouidane sites in High Atlas, reproductive period occurred in April.

In the Middle Atlas the situation is far less clear and more data are needed. In the Boulemane site, youngs were observed in July, while in Enjil juveniles were observed in December. According to their body mass, these juveniles may have been born in mid-autumn.

Group composition

During the reproductive period, group composition differs greatly, even between sites of a given region (tabl. 2). The most simple family unit is composed of a single female with her young. The next step occurs when two females share their litters in a common rocky shelter. At the time of our observations, young had already emerged from the

natal nest and were able to move around independently. We have no direct observation of two females sharing a common natal nest, even if two females were observed together just before the reproductive season. These family units may form colonies. In two sites, the social group was more complex and included several lactating females (at least three) with their young, and at least one male.

Discussion

These preliminary results revealed that the Barbary ground squirrel displays a high variability in reproductive period and group composition.

The period of reproduction differs dramatically according to the elevation of the site. In the high-altitude sites, both in High Atlas and AntiAtlas, reproduction occurs in summer while in other sites reproduction takes place in spring. Our fragmented data may give a distorted vision of the variability, and reproductive period variation may occur within a continuum. Nevertheless, such a range of intraspecific variability is unusual. For example, in the gundi, *Ctenodactylus gundi*, a diurnal rodent living in similar habitats (GOUAT and GOUAT, 1982; 1983), the range of variation in reproductive period between high-altitude and desert colonies does not exceed one month (GOUAT, 1985; 1988; 1991). In non-hibernating rodents, seasonal breeding is thought to be mainly determined by day-length variation. In the Barbary ground squirrel, temperature and food availability, primarily insects, may be key factors to initiate reproduction.

Variability in group composition during the reproductive season is high, but contrary to the reproductive period, no clear link with habitat was revealed by our data. The difference between sites of a given region may cover the complete range of variation observed. This social variety may contribute to the ecological success of this species as is shown by the diversity of habitats occupied. Proximal factors, both social and ecological, may explain variations in social structures as shown in the yellow-bellied marmot (ARMITAGE, 1973; 1975; 1977; 1982; ANDERSEN *et al.*, 1976; FRASE and ARMITAGE, 1984). Longitudinal observations are clearly needed to determine the key

factors of this variability. As in other species of ground squirrels, the formation of groups of females appears to be basis of an increase in the level of sociality (MICHENER, 1983). The range of variability observed in *Atlantoxerus getulus* however, exceeds what is described in each of the other ground-dwelling squirrel species (FERRON, 1991).

The Barbary ground squirrel has been found to occupy a wide variety of habitats. In addition, a substantial variety of social structures was observed in this species. The relationships between ecological constraints and social structures are far from being understood; *Atlantoxerus getulus* however, already appears to be a suitable biological model for further socioecological studies.

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The mating behaviour of the Silvery mole-rat

(*Heliophobius argenteocinereus*)

Radim Sumbera

Introduction

Subterranean rodents in general, and solitary subterranean rodents in particular, do not reproduce easily in captivity. Although most of subterranean rodents are solitary, the available data on reproduction and reproductive behaviour refer mostly to social species representing just three genera: *Heterocephalus glaber* (JARVIS, 1991), *Cryptomys damarensis* (BENNETT and JARVIS, 1988b; BENNETT, 1994), *Cryptomys hottentotus* (HICKMAN, 1982; BENNETT, 1989), *Cryptomys anselli* (BURDA, 1989; BEGALL and BURDA, 1998), *Cryptomys darlingi* (BENNETT *et al.*, 1994), *Cryptomys mechowi* (BURDA and KAWALIKA, 1993; BENNETT and AGUILAR, 1995; SCHARFF *et al.*, 1999), *Spalacopus cyanus* (BEGALL *et al.*, 1999). Solitary forms are territorial, xenophobic and aggressive, so that even observations of their mating are rare. There are reports on mating behaviour in *Georychus capensis* (BENNETT and JARVIS, 1988a), *Spalax ehrenbergi* (NEVO, 1969; SHANAS *et al.*, 1995; GAZIT *et al.*, 1996), *Cannomys badius* (EISENBERG and MALINIAK, 1973), *Thomomys talpoides* (ANDERSEN, 1978), and *Ctenomys mendocinus* (CAMÍN, 1999). It is apparent that any further comparative data on mating behaviour in (particularly solitary) subterranean rodents would

be of interest, in order to be able to establish phylogenetically conserved and ecologically adaptive components of relevant behavioural patterns.

The African mole-rats (Bathyergidae) involve two genera of social and three genera of solitary rodents. Although this African endemic family is one of the best examined taxa of subterranean mammals, reproduction and reproductive behaviour of solitary forms remain still largely unknown. In particular the reproductive biology of the monotypic genus *Heliophobius* has been enigmatic, although among all the mole-rat species, *H. argenteocinereus* is the most widely distributed. This paper provides the first description of the mating behaviour in this species.

Materials and methods

Animals and housing

Altogether 17 wild-captured adult silvery mole-rats (*Heliophobius argenteocinereus*, Bathyergidae) were studied. Animals were kept individually in plastic cages (49 × 30 × 20 cm), or in a Plexiglas maze, or in pairs in a glass terrarium, on a shallow litter of horticultural peat. They were fed with carrots, potatoes, lettuce, and other seasonal vegetables. General activity and mating behaviour was monitored and videotaped continuously. Each mating was assessed qualitatively and quantitatively.

Encounter experiments

Two females and three males captured in Zambia (Lubalashi area, 1996) and Malawi (Nyika, Blantyre, Mulanje, 1996-1998) were used in the study. Mate choice was ascertained in an apparatus (constructed according to SHANAS *et al.*, 1995) consisting of four cross-connected Plexiglas tubes. The tubes were connected with the home cages of three males, while a wire barrier prevented the males entering the maze. The fourth tube leading to the female cage was opened, enabling

the female to enter the system. The female and male that spent the most time at partition were considered as being the most interested in each other. These animals were relocated into another system consisting of two interconnected equal-sized cages, divided by a movable wire barrier. During encounters of animals at partition, the barrier was lifted up carefully and this allowed them physical contact. Both animals were given the opportunity to meet each other for several weeks up to three months.

Mating behaviour

Twelve animals captured from February to April 1999 in Mulanje (Malawi) were repeatedly combined into heterosexual pairs. The contact ended either aggressively, and the animals had to be separated, or the animals were amicable to each other and sexual activity could be recorded. Copulation was observed in three pairs, in which the following parameters were recorded: Courtship behaviour (duration and initiator), intromissions and thrusting (duration and frequency), frequency of marking behaviour (number of incidences of urinating on the cage walls during periods of male activity with copulation versus periods of male activity with no copulation).

Results

Encounters experiments

In spite of long-term (over six months) intensive observations no signs of seismic (vibrational, knocking) communication were observed in animals housed individually, separated by a partition or living in pairs, or living in tubes, boxes and open cages.

When the partition was removed, the animals interacted with each other with open mouths and protruding incisors, and the threat behaviour (fig. 1a) resulted subsequently in sparring. If the animals attacked each other seriously, they were separated. In some cases, a couple spent several hours in interconnected territories without any

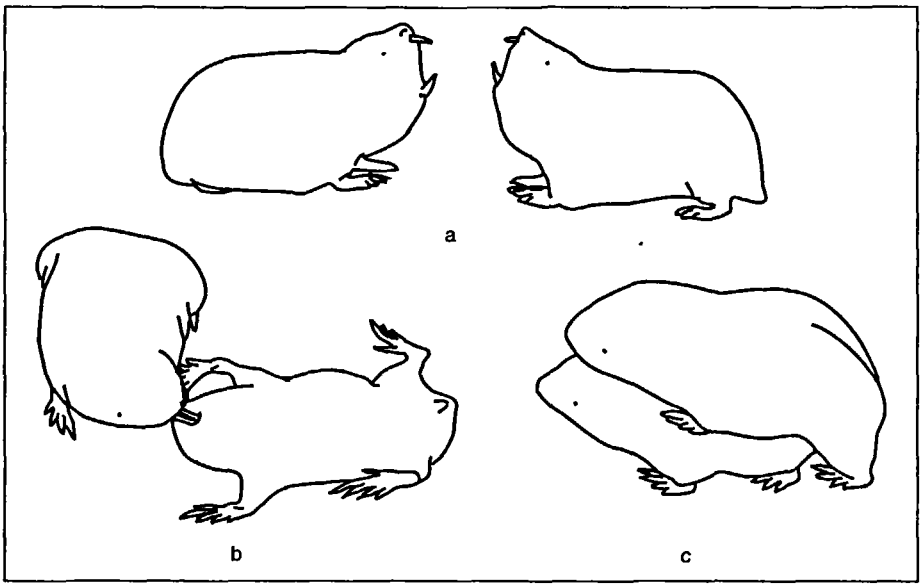

Figure 1
Postures of *Heliophobius argenteocinereus*: (a) agressive encounter, (b) lying on the back during courtship, (c) mounting.

confrontation. Frequent and repeated contacts gradually reduced aggressiveness. Nevertheless, in most cases, the encounters eventually resulted in fighting. During highly aggressive encounters, both partners exhibited (usually simultaneously) short, fast and repeated drumming with the forelimbs.

The females used the opportunity of interconnected territories to steal the food from male boxes (in 62 from 77, i.e., 80.5%, of encounters).

Mating behaviour

Courtship behaviour was initiated by the male which followed the female and sometimes sniffed at her anogenital region. Both partners were vocal, but vocalisation was pronounced in females. Then the animals faced each other frontally, nibbled each other gently, and locked incisors. Alternatively, one of them lied on its back (fig. 1b).

There was no difference between both sexes in the frequency of showing the "back-up" (normal posture) or "belly-up" (supine) position ($\chi^2_{(1)} = 0.391$, $p < 0.531$). Contacts eventually resulting in copulation were mostly initiated by males. However, soliciting behaviour and lordosis posture of a female with no response by the male was frequent. The courtship behaviour of animals lasted for about 2 minutes (ranging 40 to 241 s, n = 11) and resulted in copulation (10 out of 11).

Copulation started when a male mounted a female (fig. 1c). Initial mounting attempts were sometimes interrupted by the female which did not stay still, yet the male continued and remounted the female. Lordosis of a female was a prerequisite for successful intromisions. The male thrusted at a high rate of 7.3 per s (range 4.5-9.5, n = 29 intromissions) for 10-30 s. Copulation ended with deep thrusting during which the female vocalized intensively. First-time copulations and copulations occurring after a longer abstinence culminated, apparently, with ejaculation. The male then fell down from the female, lay on its side or back with his limbs jerking. In the case of more frequent copulations, the ejaculation was less prominent. Nevertheless, sperm found in the female vagina provided evidence that ejaculation still took place. Repeated copulations were very rare. No aggressive behaviour was noted after ejaculation. Males urinated on the vertical walls of the terrarium. The urinating intensified during mating ($U = 27.0$, $p < 0.001$ Mann–Whitney U-test).

Discussion

Encounter experiments

The absence of seismic communication is rather surprising. It has been assumed that this form of communication is widely distributed among solitary subterranean mammals (HETH *et al.*, 1987; RADO *et al.*, 1987; BURDA *et al.*, 1990; NARINS *et al.*, 1992). Seismic communication is relevant not only for mating but also in territorial context, and knocking and drumming (e.g. in *Spalax*) can be recorded and elicited in captive animals outside the reproductive season (cf. HETH *et al.*, 1991). *Georychus, Spalax*, and *Bathyergus* drum even in arti-

ficial maze when separated only by a perforated or unperforated partition (HETH *et al.*, 1987; 1991; RADO *et al.*, 1987; BENNETT and JARVIS, 1988a; BENNETT and JARVIS, 1991; NARINS *et al.*, 1992). Seismic communication in *Heliophobius* was not recorded even in cases when both animals were separated by two partitions 40 cm apart. Nevertheless, I have not performed any specific experiment to test for the absence/presence of seismic communication in *H. argenteocinereus*.

Mutual attacking after removal of the partition indicates that the animals were not motivated to mate, although at the same time some were sexually active. The reasons for this remains unknown. Solitary subterranean rodents studied so far (*Spalax, Bathyergus, Georychus, Thomomys, Geomys*) are seasonal breeders (NEVO, 1979; JARVIS and BENNETT, 1991). Seasonality of reproduction guarantees synchronised reduction of aggressiveness and territoriality of putative partners. There is indication that reproduction in *H. argenteocinereus* may also be season-dependent (JARVIS and BENNETT, 1991; BURDA and CHITAUKALI, pers. comm.). If so, it may be that some (so far unidentified) environmental stimulus triggering sexual activity was missing in our experimental setting. The nature of such a putative stimulus is, however, unknown for any seasonally breeding mammal with long pregnancy living in the tropics (GOODMAN, 1998). It can be only speculated that some factors linked to changes in precipitation which represent the most fundamental seasonal change may play a role.

Mating behaviour

Mating behaviour in diverse subterranean rodents of solitary habits *Spalax ehrenbergi* (NEVO, 1969; SHANAS *et al.*, 1995; GAZIT *et al.*, 1996), *Cannomys badius* (EISENBERG and MALINIAK, 1973), *Thomomys talpoides* (ANDERSEN, 1978), and *Georychus capensis* (BENNETT and JARVIS, 1988a) is similar in several aspects. The male initiates courtship and/or is the more active partner, or both partners are equally active like in *Spalax* (NEVO, 1969; SHANAS *et al.*, 1995) and *Ctenomys* (CAMÍN, 1999). In social species, mating is usually initiated by a female and female appeal is considered a characteristic

mating pattern of social species (BENNETT and JARVIS, 1988b). In *Cryptomys anselli* and *C. mechowi* female soliciting is common in non-familiar pairs, whereas in established pairs it is usually the male who starts mating (BURDA, 1989; SCHARFF *et al.*, 1999). Initiation by male was also recorded in *Cryptomys h. hottentotus* (BENNETT, 1989). The alternative lying on the back observed in partners of silvery mole-rat can be considered a ritualised form of agonistic behaviour. The same behaviour was observed during aggressive encounters when the animals attacked from supine position. Posting on the back during mating was observed also in female *Spalax* (NEVO, 1969) and both partners in *Ctenomys* (CAMÍN, 1999).

Copulation in solitary subterranean rodents involves pelvic thrusting and multiple intromissions, during which the female adopts lordosis posture, and deep thrusts before withdrawal. Apart from few exceptions, *H. argenteocinereus* appears to conform to this pattern. Short average duration of courtship may be due to the habituation involving familiarity between partners. Repeated intromissions in *H. argenteocinereus* (10-30 s) resemble the situation in *C. badius* (< 22 s, EISENBERG and MALINIAK, 1973), and are longer than in the social common mole-rat *C. hottentotus* (5 s, HICKMAN, 1982), *H. glaber* (< 15 s, LACEY *et al.*, 1991), *S. cyanus* (< 15 s, BEGALL *et al.*, 1999), yet they are shorter than in solitary *C. mendocinus* (up to 5.5 min, CAMÍN, 1999), *S. ehrenbergi* (up to several min, Nevo 1969), or *T. talpoides* (up to 15 min, ANDERSEN, 1978). *Heliophobius* is unique among all subterranean rodents studied to date in the high frequency of thrusting: 7.3 per s in *Heliophobius*, 2-4 in *C. h. hottentotus* (BENNETT, 1989), 3-4 in *C. damarensis* (BENNETT and JARVIS, 1988b), 1-2 in *C. mechowi* (BENNETT and AGUILAR, 1995), 2-3 in *G. capensis* (BENNETT and JARVIS, 1988b), 0-1 in *T. talpoides* (ANDERSEN, 1978) and 1-5 in *C. mendocinus* (CAMÍN, 1999). However, it is difficult to interpret these phenomena.

Urinating on vertical surfaces (both in own or female's territory) was common in mating males. Similar behaviour was noted in *Spalacopus cyanus* (KLEIMAN, 1974) and *Ctenomys mendocinus* (CAMÍN, 1999). One possible assumption is that urine provides the female with some information on male's reproductive state (KLEIMAN, 1974).

Mating behaviour in different rodent taxa

Sciurognatha versus Hystricognatha

DEWSBURY (1972) classified copulatory behaviour in mammals into 16 categories according to the absence or presence of four traits: lock during copulation, pelvic thrusting during insertion, multiple intromissions with no sperm transfer, and multiple ejaculation within an hour of the first ejaculation. Based on these categories there are conspicuous differences between sciurognath and hystricognath rodents (YOUNG and GRUNT, 1951; BIGNAMI and BEACH, 1968; KLEIMAN, 1974), although they are not absolute (DEWSBURY, 1975). Two patterns are typical for the Hystricognatha: no lock, thrusting during intromission, few intromissions, single (pattern 10) or multiple ejaculations (pattern 9) (KLEIMAN, 1974). Single intromission and one ejaculation (pattern 12) was reported for *Cavia porcellus* (YOUNG and GRUNT, 1951), *Ctenomys mendocinus* (CAMÍN, 1999), and *Spalacopus cyanus* (Begall *et al.*, 1999). Sciurognatha display a much more variable copulatory behaviour. The typical pattern (pattern 13) for most sciurognaths involves multiple intromission with multiple ejaculations, and no lock or thrusting after penetration (DEWSBURY, 1972). Thrusting is a trait typical for hystricognaths (KLEIMAN, 1974) and atypical for most sciurognaths (DEWSBURY, 1972). Copulation in *H. argenteocinereus* is characterised by intravaginal thrusts, multiple intromissions, and absence of any lock. The next copulation and ejaculation follows after a long interval, so that *Heliophobius* conforms to basic hystricognath pattern (pattern 10). The same pattern can be ascribed also to *Cryptomys hottentotus* (HICKMANN, 1982; BENNETT, 1989). The descriptions for other bathyergids are not complete with missing data on the number of intromissions and ejaculations. As typical representatives of hystricognath rodents they display thrusting and it can be assumed that their pattern is not basically different from the hystricognath patterns.

Subterranean versus supraterranean rodents

Supraterranean rodents display short precopulatory interval (incl. courtship) and very short intromissions (i.a. YOUNG and GRUNT, 1951;

BEACH and RABEDAEU, 1959; BIGNAMI and BEACH, 1968; KUEHN and ZUCKER, 1968; DEWSBURY, 1972; GRAY and DEWSBURY, 1973; KLEIMAN, 1974; DEWSBURY and HODGES, 1987). The copulation of subterranean sciurognath rodents markedly resembles those of the especially solitary bathyergids through their longer precopulatory interval, prolonged intromissions lasting up to several minutes, and thrusting (Nevo, 1969; EISENBERG and MALINIAK, 1973; ANDERSEN, 1978; GAZIT *et al.*, 1996). Following DEWSBURY (1975) the displayed pattern is 10 (*Spalax*, *Cannomys*), or, in the case of multiple ejaculations, pattern 9 (*Thomomys*). Detection of ejaculation is difficult, however. Longer mating sequence may reflect higher safety of the subterranean ecotope (ANDERSEN, 1978; BENNETT and JARVIS, 1988a).

Social versus solitary subterranean rodents

Courtship of solitary species *Ctenomys* (1-65 min, CAMÍN, 1999), *Spalax* (8-55 min, NEVO, 1969) *Cannomys* (EISENBERG and MALINIAK, 1973) and *Thomomys* (ANDERSEN, 1978) is much longer than in the social mole-rat *C. hottentotus* (max 3 min, BENNETT, 1989). Solitary territorial rodents have first to reduce aggression of any intruders, irrespective of sex (NEVO, 1969; BENNETT *et al.*, 1991; *Shanas et al.*, 1995; GAZIT *et al.*, 1996). The other characteristic feature, short intromissions in social subterranean rodents, has been attributed to disturbance by other inhabitants of the burrow system (HICKMANN, 1982; JARVIS, 1991). The difference is conspicuous in species with the same copulation pattern, like in solitary *Ctenomys mendocinus* and social *Spalacopus cyanus*, both representatives of the same family, Octodontidae. Whereas the intromission in *C. mendocinus* can last up to six minutes (CAMÍN, 1999), it takes no more than 15 s in *S. cyanus* (BEGALL *et al.*, 1999).

In conclusion, the mating pattern of solitary subterranean silvery mole-rats (recorded here for the first time) reflects both their subterranean way of life and their hystricognath affinities.

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Thermoregulatory and metabolic responses to photoperiod manipulations in a mesic population of the common spiny mouse, *Acomys cahirinus*

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Introduction

In the Levant the common spiny mouse, *Acomys cahirinus* (*Acomys dimidiatus*) is widely distributed in rocky habitats of dry and warm desert as well as in mesic areas (HARRISON and BATES, 1991). Several biological aspects have been studied in this species. Among others, a comparative ecophysiological study was carried out, where individuals from arid and mesic environments were compared (WEISSENBERG and SHKOLNIK, 1994). This study revealed differences in thermoregulation, metabolisme as well as in kidney morphology and functions between populations, occurring in different environments. Individuals from the arid environment could cope better with dry and warm conditions.

Many rodent species use the changes in photoperiod as an environmental signal for seasonal acclimatization of thermoregulatory and metabolic systems (LYNCH, 1970; HAIM and FOURIE, 1980; HELDMAIER *et al.*, 1981; HAIM, 1982). The daily rhythms of body temperature (T_b) in rodents is well documented (ASCHOFF, 1982; HELDMAIER *et al.*, 1989). Seasonal acclimatization of T_b daily rhythms were revealed in common spiny mice from a mesic population (HAIM and RUBAL, 1994). Such changes in the temporal organization of T_b are assumed to be associated with control of energy balance (HAIM *et al.*, 1995). So it makes sense to assume that a change in the T_b daily rhythm could reflect a change in energy intake, which is also photoperiod responsive (HAIM and LEVI, 1990). Therefore, the aim of the present research was to study the thermoregulatory and metabolic responses of a mesic population of common spiny mice to photoperiod manipulation, in order to assess the use of photoperiodic cues by this species for seasonal acclimatization of its thermoregulatory system.

Material and methods

Eight adult males with a body mass of (56.9 ± 2.6 g) were taken from our breeding colony at Oranim, Kiryat Tivon. The ancestors of these mice were captured on Mount Carmel, Israel. Mice were acclimatized for two weeks at least, to an ambient temperature of 26 ± 1 °C, first under a short day (SD) photoperiod (lights were on between 08:00-16:00h) and then, after measurement of different variables, to a long day (LD) photoperiod (lights were on between 06:00-22:00h). Food trials started only after two weeks of acclimatization and body mass was measured at the beginning of each trial. During the light period, neon lights (800 lx) and dim red lights (40 lx) were on, while during the dark period only the dim light was on. Each mouse was kept separately in a cage and sawdust was used for bedding. During the period of acclimatization, mice were maintained on rodent chow *ad libitum* with fresh carrots and cucumbers served as a water source.

Daily rhythms of body temperature

These were recorded at the end of the acclimatization period. Measurements continued for 48h at intervals of 4h. Body (rectal) temperature was measured by using a copper-constantan thermocouple connected to a Wescor (Logan, UT, USA) TH65 digital TC thermometer. The thermocouple was inserted 3 cm into the rectum of the tested mouse for a period less than 30 sec. During the measurement the tested mouse was kept inside a cotton bag (HAIM *et al.*, 1994).

Food, water and energy consumption

Food consumption was measured as apparent Digested Dry Matter Intake, DDMI (the difference in mass, between Apparent Dry Matter Intake ADMI and the dry faeces outlet). Tested mice were kept separately in cages with filter paper as bedding, on a diet of dried (Memmert 60°C) rat pellets (20% protein, Koffolk Ltd., Israel) and fresh cucumbers (containing 96% water) throughout the measurements. Fifty grams (Sartourius, 1900 MPS) of dried rat pellets were provided once a week, while fresh weighed cucumbers were added every two days. Measurements went on for two weeks at each photoperiod regime and at the end of this period food leftovers, faeces and cucumber leftovers were dried at 60°C and separated from each others (HAIM, 1987). Water intake could be calculated from cucumber consumption assuming that cucumbers contain 96% water.

Energy consumption was measured as Gross Digestible Energy Intake GDEI, the difference between the measured caloric contents of the food consumed and of the faeces. The energy contents of samples of dried rat pellets, cucumber and faeces were determined by a computerized bomb calorimeter (PARR 1261, Parr instruments Co.). Digestibility was calculated as the ratio DDMI /ADMI (in percent), (HAIM *et al.*, 1994).

Statistics analysis

All results are given as means ± S.D. Students *t* test was used for determination of significant ($p \leq 0.05$) differences between means.

Results

A difference in the T_b daily rhythm was noted between SD- and LD-acclimatized mice. While under SD-acclimatization T_b values were high between 19:00 and 03:00h ($p < 0.05$, compared with T_b at 11:00h). Under LD-acclimatization, high T_b values were recorded at 23:00 and 03:00h ($p < 0.01$; compared with T_b at any other time). However, the values at 03:00h were significantly ($p < 0.01$) higher than those obtained at 23:00h. Under LD-acclimatization a sharp decrease in T_b was noted at 07:00h, while in SD-acclimatized mice, the decrease was moderated (Fig 1).

Body mass decreased significantly ($p < 0.05$) under SD-acclimatization, while under LD-acclimatization it did not change. Water consumption was significantly higher in LD-acclimatized mice ($p < 0.05$), compared with SD-acclimatized mice. However, in all food and energy consumption variables, the values obtained for SD-acclimatized mice were significantly higher than those of LD-acclimatized ones ($p < 0.05$; Table 1).

Discussion

The common spiny mice population on Mount Carmel, Israel, is exposed to seasonal changes where the cold and wet season is short (four months) and the dry and warm season is long (eight months). The change in ambient temperature (D = 10-15 °C) takes place in a very short period, a few days. Therefore, rodent species such as the broad-toothed wood-mice *Apodemus mystacinus* were found to use changes in photoperiod (which occur before the changes in ambient temperature) as a major cue for seasonal acclimatization of their thermoregulatory system (HAIM and YAHAV, 1982).

The results of our study show that common spiny mice inhabiting Mount Carmel, can use photoperiod cues for seasonal acclimatization of their thermoregulatory system. Body temperature is an outcome of the relation between heat production (metabolism) and heat

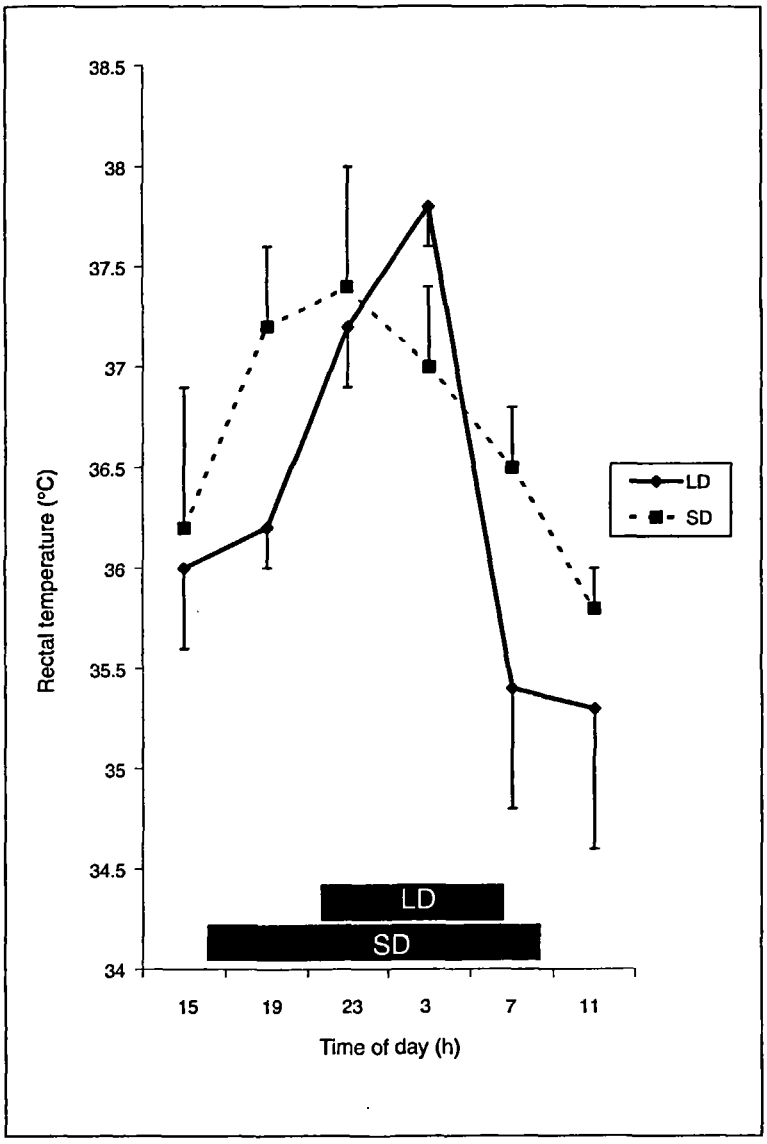

Figure 1
Body temperature (T_b °C) of daily rhythms of common spiny mice Acomys cahirinus (Acomys dimidiatus) from Mount Carmel, Israel. Mice were acclimatized to two different photoperiod regimes at an ambient temperature of 26 ± 1 °C. Mice acclimatized to short day (SD, 8L:16D), mice acclimatized to long day (LD, 16L:8D). Each point is a mean value + S.D., for n = 8.

	Short Day	Long Day	t	P <
ADMI g/100 g W_b.day	5.3 ± 0.28	4.4 ± 0.33	4.28	0.01
DDMI g/100 g W_b.day	4.6 ± 0.37	3.9 ± 0.34	4.77	0.01
GEI Cal./g.day	226.2 ± 20.2	194.5 ± 14.0	3.41	0.05
DEI Cal./g.day	195.0 ± 22.1	168.5 ± 13.5	2.80	0.05
Water Consumption GH_2O/100 g W_b.day	12.3 ± 0.9	13.6 ± 0.7	3.02	0.05
W_b before g	56.9 ± 2.6	52.8 ± 4.4	4.425	0.05
W_b after g	50.8 ± 1.8	52.0 ± 3.8	4.425	0.05

Table 1
Food, energy and water variables of common spiny mice *Acomys cahirinus* (*Acomys dimidiatus*) from Mount Carmel, Israel, acclimatized to two different photoperiod regimes (short day SD - 8L:16D, long day LD - 16L:8D) at an ambient temperature of 26 ± 1 °C.
ADMI - Apparent Dry Matter Intake, DDMI - Digestible Dry Matter Intake, GEI - Gross energy intake, DEI - Digestible Energy Intake, Wb - Body mass before and after acclimatization to each photoperiod regime. All variables are means ± S.D. for n = 8 mice. For establishing statistical differences, Student t-test was used. Values are significantly different at $p < 0.05$.

dissipation (conductance or insulation). Therefore, a further question that can be asked is: "what mechanism is affected by the photoperiodic changes"? For a species with a body mass of about 50 g the change will mainly depend on heat production mechanisms rather than on heat dissipation, as seasonal changes of insulation in small mammals are of minor significance (HART, 1956). Our food and energy consumption results (Table 1) support this idea.

The role of photoperiodicity in the control of T_b rhythms was discussed by HELDMAIER *et al.* (1989) and the results they used were obtained mainly from mesic or cold adapted species. Acclimatization to SD in such species decreased the time in the 24h cycles in which T_b was

kept at high values. Such a change in T_b temporal organization results in energy conservation. However, in desert adapted rodents as the fat jird *Meriones crassus* (HAIM and LEVI, 1990) and the golden spiny mouse *A. russatus* (HAIM *et al.*, 1994) a different pattern was observed, where SD acclimatization resulted in higher T_b values for a longer period each day. The results obtained in this study for the common spiny mouse, although of a mesic population, agree with those of the desert-adapted species rather than mesic adapted ones (Fig. 1).

Photoperiod and ambient temperature are two environmental parameters that are seasonally dependent, and the changes in ambient temperature follow those of photoperiod. The response of food and energy intake, in rodents from different habitats to long and short photoperiod acclimatization were summarized by HAIM and RUBAL (1993). They found a difference between desert and mesic species. While under short photoperiod acclimatization, an increase in food and energy intake was noted, such differences were not revealed in species of a mesic origin. An increase in food and energy intake under short photoperiod acclimatization, were also noted in the golden spiny mice from extreme arid habitats (HAIM *et al.*, 1994). The results of our study show that SD-acclimatized *A. cahirinus,* also increased food and energy intake as compared with LD-acclimatized ones (Table 1).

This increase in energy intake of SD-acclimatized mice, was accompanied by a decrease in body mass, while in LD-acclimatized mice body mass did not change. Such a decrease in body mass was not revealed in SD-acclimatized *A. russatus* (HAIM *et al.*, 1994). The results obtained for *A. cahirinus* show that LD-acclimatized mice, increased water consumption relatively to SD-acclimatized mice. This increase contrasts with the results obtained for *A. russatus* (HAIM *et al.*, 1994). *Acomys cahirinus*, depends on water evaporation through the skin for cooling (SHKOLNIK and BORUT, 1969), therefore, it may be assumed that the increase in water consumption of LD-acclimatized mice, could be an outcome of summer seasonal acclimatization of peripheral blood vessels.

The results of our study suggest that the metabolic and thermoregulatory seasonal changes in *A. cahirinus* from a mesic population are at least partly a response to the changes in photoperiod. Therefore, it may be concluded that seasonal acclimatization of these systems are

photoperiod- dependent and that the changes in day length can be used as a cue. Although this species inhabits mesic habitats in the Mediterranean ecosystem (HARRISON and BATES, 1991), it retains several physiological characteristics which are typical for African desert adapted species.

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Ecology

thème 4

Ecology of African Small Mammals

Recent research and perspectives

D. C. D. Happold

Introduction

In the early years of the century, most papers on African small mammals were descriptions of new species, and lists of the species at selected localities. Since then, new ideas and theories about ecology, and an increase in basic knowledge about African small mammals, have provided new ecological insights into how individuals, communities and species integrate with the environment. Such studies have been at local, regional and pan-African levels, and hence it is now possible to take a more holistic view of small mammals than was possible previously. Early studies on rodents were primarily on habitat preferences, demography, the use of tooth wear to indicate population structure, the influence of burning on populations, and reproduction (DELANY, 1972, 1986). These studies showed that, in many aspects of their life-histories, African rodents are capable of great flexibility and adaptability in relation to the short- and long-term changes in their environment. In contrast, the other "small mammals" – lagomorphs, bats, insectivores and elephant-shrews – have been studied to a much lesser extent. This paper surveys some of the most recent studies on small mammals and shows how these studies have provided African examples for some of the principal disciplines within ecology.

Order	Number of species	% of small mammals	% of total mammalian fauna of Africa *
Insectivora	173	22.2	16.2
Chiroptera	200	25.6	18.7
Rodentia	380	48.7	35.6
Lagomorpha	11	1.5	1.0
Macroscelidea	15	1.9	1.4
TOTAL	779	100.0	72.9

* = 1068

Table 1
The Numbers of Small Mammals in Africa
(Insectivora, Chiroptera, Rodentia, Lagomorpha, Macroscelidea).

How many species are there?

It comes as a surprise to many people that there are so many species of small mammals on the African continent (including the islands of the continental shelf). The five orders of small mammals comprise 73% of all mammals in Africa (Table 1; HAPPOLD, unpubl.). The most numerous are the rodents with 380 species, followed by the bats with 200 species. Such data does not tell anything about the numbers of each species, nor the geographical extent of each species; but it does serve to emphasise the huge species richness of the continent. The species richness of some orders of small mammals is far greater than for the larger better known species, for example the Artiodactyla (92 spp.), Carnivora (70 spp.) and Primates (99 spp.) (HAPPOLD, unpubl.). To place these numbers in context, the species richness in North America (from the far north to Panama, plus the Greater and Lesser Antilles) is (about) 54 species of Insectivora, 403 species of rodents, 192 species of bats and 25 species of Lagomorpha (calculated from data in HALL, 1981); thus Africa has about the same number of species of bats and rodents as North America, more Insectivora and fewer Lagomorpha.

Are African small mammals important?

The answer to this question obviously depends on your point of view. In terms of size, biomass, and the capacity to earn revenue for a country, they are not as important as the larger better known mammals. However, the sheer number of species, and the large population numbers of some of these species, deserve some measure of recognition. Small mammals are particularly important because of their multiple functional roles in the ecosystem. They occur in virtually all habitats, their feeding habits include grass-eaters, seed-eaters, carnivores, insectivores and fruit-eaters, their activities result in recycling of nutrients, they have many beneficial interactions with plants such as seed dispersal, seed germination and pollination of flowers, they modify local environments («ecological engineering») by their burrowing activities, and they provide food for many predators. Some species are reservoir hosts for micro-organisms which cause diseases in humans and domestic animals, and others are pests in agriculture and stored products. Bats are of value as predators of insects, and some species of rodents are utilised as food by humans. Thus small mammals have roles in most ecological systems and in all habitats, and many of their activities impinge on other animals, including humans (see HAPPOLD, 1995).

Recent studies on African small mammals

During the last decade or so, new biological techniques especially in relation to cladistics, cytogenetics and DNA analysis have resulted in many papers which investigate the genetical and evolutionary relationships within and between species and higher taxa. In order to get a rough idea of the main focus of research during the last five years (1994-1998 inclusive), the papers published in 10 journals were analysed in respect of taxonomic group(s) (orders, families) and subject.

Taxonomic categories	% of papers	Category as % of all small mammals
INSECTIVORA	7.5	22.2
Soricidae	4.8	
Chrysochloridae	2.7	
Erinaceidae	0	
CHIROPTERA	19.8	25.6
Megachiroptera	13.4	
Microchiroptera	6.4	
RODENTIA	59.8	48.7
Sciuridae	1.1	
Anomaluridae	1.1	
Muridae	39.0	
Bathyergidae	14.4	
Ctenodactylidae	0.5	
Hystricidae	2.7	
Thryonomidae	0.5	
Pedetidae	0.5	
LAGOMORPHA	1.1	1.5
MACROSCELIDEA	10.7	1.9
SEVERAL ORDERS*	1.6	1.6

* Papers where two or more of the above Orders are considered.

Table 2
Publications on African Small Mammals – analysis of 187 papers published in ten Journals** (1994-1998) by taxonomic categories.

The journals selected were those which historically have published a wide range of papers on African small mammals. The largest number of papers considered the Rodentia (especially Muridae), followed by Chiroptera and Macroscelidea (Table 2). The number of papers for each taxon is not in proportion to the numbers of species in the taxa, e.g. the Rodentia is represented by more papers than justified by its numbers, and the Chiroptera and Insectivora by fewer papers.

Likewise, analysis by subject shows that ecological studies of various sorts comprise the majority of papers (Table 3). Field studies on single species and communities form the largest category (29%),

** *Acta Theriologica, African Journal of Ecology, Biodiversity and Conservation, Journal of Mammalogy, Journal of Tropical Ecology, Journal of Zoology* (London), *Mammal Review, Mammalia, South African Journal of Zoology, Zeitschrift für Säugetierkunde.*

Subject	% of papers
Autecology	15
Community Ecology	14
Reproductive Ecology	17
Geographical ecology/surveys	8
Conservation Ecology	4
Behavioral Ecology	6
Taxonomy/systematics	6
Cytogenetics	10
Physiology	10
Morphology	10

Table 3
Publications on African Small Mammals – analysis of 187 papers published in ten Journals (see note of Table 2) (1994-1998) by subject. Papers on Feeding ecology are included in Autecology and Reproductive Ecology.

followed by reproduction (17%). Taxonomy and cytogenetics form 16%. Surveys and biogeographical studies appear to have declined in number in recent years, and there are few papers on conservation of small mammals.

Ecological studies

The remainder of this paper surveys some of the recent (and not so recent) ecological studies, and considers only some of the categories identified in the analysis given above. The ecological studies may be considered under six subdisciplines: autecology, community ecology, feeding ecology, reproductive ecology, geographical ecology and conservation ecology. The other categories in Table 3 are not considered in detail in this paper.

A word of caution is needed regarding the names of African small mammals. Ecological studies are often hampered by doubt as to the correct name, especially at the species level, of the animals under investigation. There are many examples of where a « single » species is now considered a complex of species (e.g. within the genera *Mastomys, Praomys* and *Hylomyscus*). The contrary situation also creates difficulties because what is actually a single species has been

described, in the past, under a plethora of names, each one from a separate locality. A glance at the names of African mammals in WILSON and REEDER (1993) shows that synonymy is a very common occurrence. The ecologist, therefore, may have real difficulty in knowing the correct name(s) of the animals being studied. The problem may be overcome, to some extent, by placing specimens in a museum (so their identity can be re-assessed at a later date) and by pointing out the difficulties of nomenclature, if such exist, for the «species». Hopefully, these difficulties will be minimised in the future as a result of new methods of taxonomic analysis.

Autecology

Autecological studies are valuable in that they provide detailed information on a single species, perhaps in several parts of its range. The notable studies on selected bathyergids by JARVIS, BENNETT and their co-workers have provided detailed information on reproduction, colony structure and behaviour, and have shown how different members of this family vary in their characteristics according to sociality and location (e.g. BENNETT, 1994; BENNETT and JARVIS, 1995; BENNETT *et al.*, 1994; O'RIAIN and JARVIS, 1998). Likewise studies of *Praomys albipes* in Ethiopia (BEKELE, 1995; 1996), several species of *Gerbillus* (SHENBROT *et al.*, 1994, 1997), several species of elephant-shrews (KERLEY, 1995; LEIRS *et al.*, 1995; FITZGIBBON, 1997), *Beamys hindei* (FITZGIBBON *et al.*, 1995) *Saccostomus mearnsi* (KEESING, 1998a), *Mastomys natalensis* (LEIRS *et al.*, 1996, 1997), several species of gundis (GOUAT, 1985; GOUAT and GOUAT, 1987), and *Pipistrellus nanus* (HAPPOLD and HAPPOLD, 1996) – to name a few – have added to knowledge of these particular species. Most autecological studies have tended to be on species which are common and relatively easy to study. Lacking are studies of the less common and less widespread species about which we know practically nothing.

Community ecology

In recent years, studies on communities of animals living in one place have provided particularly valuable information on how different species have different habitat preferences, life-history strategies, demographic parameters, and reproductive strategies. These differ-

	Habitats				
	Grassland	Miombo	Mopane	Talus	Thicket
Number of species	8	8	4	4	2
Commonest species	*Mastomys natalensis*	*Tatera leucogaster*	*Aethomys chrysophilus*	*Aethomys namaquensis*	*Tatera leucogaster*
Species richness (hot wet – cool dry)	1.6 – 3.7	2.2 – 4.3	0.8 – 1.3	1.8 – 3.0	0.8 – 1.0
Species Diversity (hot wet – cool dry)	0.83 – 0.92	0.86 -1.39	1.25 - 0.54	0.56 – 0.86	0.65 – nd
Density (#/ha) (low- high)	0.2 – 36.7	2.1 – 10.0	1.6 – 33.0	8.2 – 32.1	0.8 – 4.1
Density ratio	1:183	1:5	1:20	1:4	1:5

Hot wet (Nov 1992-Apr 1993) — cool dry (May-Jul 1993) — nd : no data.

Table 4
Some characteristics of community structure of small mammals (data excludes *Paraxerus cepapi* which occured in all habitats except grassland) in Zimbabwe (data from LINZEY and KESNER 1997a, b).

ences are related to their different evolutionary histories and relationships, but show that there are many ways of survival under a particular set of environmental conditions, and that different localities may support quite different sets of species. Here, I will illustrate these ideas using some recent papers on rodents and on bats.

At the Sengwa Wildlife Research Area in Zimbabwe, there are five major plant habitats (Table 4). By studying the small mammals in each of these simultaneously, LINZEY and KESNER (1997a, b) were able to show that there were marked seasonal differences in the number of species, abundance and community structure in each of these habitats. Eleven species of rodents were recorded (excluding the sciurid *Paraxerus cepapi*), although there were only 2-8 species in each habitat. A single species occupied 1-4 habitats, although each species tended to prefer only one habitat. Comparison of habitats showed that each had a different species which was the most abundant species (except for miombo and thicket), different species richness and species diversity, and different densities. When population numbers increased (the timing of this varied slightly between species), maximum numbers

for any particular species were attained in the habitat where it occurred when its numbers were low, i.e. as numbers increased a species did not invade a previously unoccupied habitat. Temporal variation (as measured by minimum and maximum numbers) was greatest in the riverine grasslands (as a result of the large numbers of *Mastomys natalensis*) and least in miombo, talus and thicket (where *M. natalensis* did not occur). The advantage of studying several habitats at the same time highlights the differences and variations between habitats and their mammalian faunas; what happens in one habitat is not necessarily (or usually) what happens in a neighbouring habitat. These findings are consistent with studies in other savanna habitats (HAPPOLD and HAPPOLD, 1990a, 1991) and illustrate a general pattern for small mammals in savannas.

Where the ranges of a number of species overlap, these species form a community. In theory, all species whose ranges overlap form a community; thus a millepede, a mouse, an antelope and an elephant form a community but since each of these species is so different to each other, most ecologists would regard this as stretching the meaning of "community" too far. However, a number of related species of rodents, or bats, or antelopes show a number of similarities due to their evolutionary relationships and each species may compete for resources with other species. So how do the species in a community fit together? Are there any rules which determine how many, and what sort of, species can co-exist? BROWN (1975) examined the communities of rodents in various deserts of SW America, and showed that in any one desert each species of rodent differed in weight (and many other characteristics); hence each species had slightly different requirements and abilities. Moreover, each of the communities showed the same pattern although the species involved were different.

An analysis of the 26 species of bats (HAPPOLD and HAPPOLD, unpubl.) living in Liwonde National Park in Malawi show a similar separation for within genus groups (Fig. 1) as did Brown's rodents. For example, there are five species of *Rhinolophus;* all vary in weight (by at least a factor of 1.2 as predicted by "Hutchinson's Rule"). The same is true for the other genera. Although some species have the same weights as other species, such similarity is only between species of different genera. Although weight is a very simple measure, different weights imply differences in size, wing area, wing loading, flight

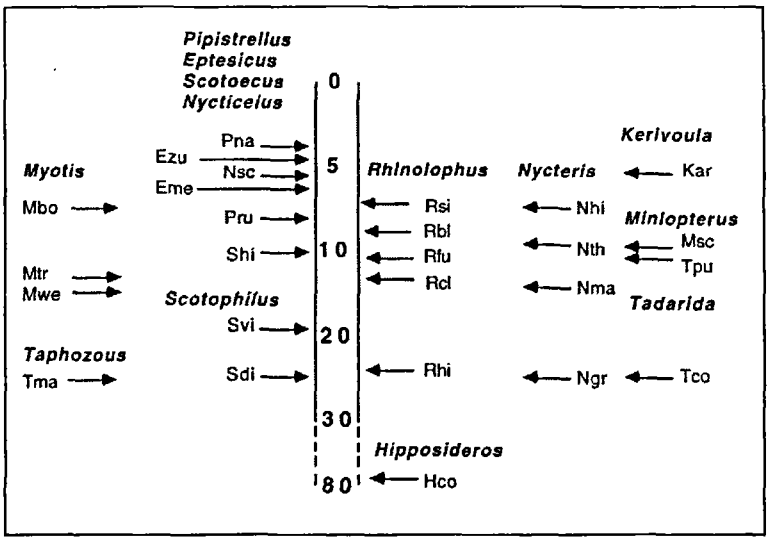

Figure 1
Community structure of insectivorous bats in Liwonde National Park, Malawi (as indicated by mean weight in grams) (M. and D. C. D. HAPPOLD, unpubl.).
Mbo = *Myotis bocagei*, Mtr = *M. tricolor*, Mwe = *M. welwitschii*, Tma = *Taphozous mauritianus*, Pna = *Pipistrellus nanus*, Pru = *P. rueppellii*, Ezu = *Eptesicus zuluensis*, Eme = *E. melchorum*, Nsc = *Nycticelus schlieffenii*, Shi = *Scotoecus hirundu*, Svi = *Scotophilus viridis*, Sdi = *S. dinganii*, Rsi = *Rhinolophus simulator*, Rbl = *R. blasii*, Rfu = *R. fumigatus*, Rcl = *R. clivosus*, Rhi = *R. hildebrandtii*, Hco = *Hipposideros commersoni*, Nhi = *Nycteris hispida*, Nth = *N. thebaica*, Nma = *N. macrotis*, Ngr = *N. grandis*, Kar = *Kerivoula argentata*, Msc = *Miniopteris schreibersii*, Tpu = *Tadarida pumila*, T. co = *T. condylura*.

characteristics, mouth size, and potential food. Thus the large number of species in this community can co-exist because of the many genera, and the differences between species within each genus and between genera. The bats of Kruger National Park (see ALDRIDGE and RAUTENBACH, 1987) are equally diverse, for the same reasons as given above. More information on other communities of bats in Africa, especially where there are many species, is required to confirm whether this is a general feature of African bats.

Genera [number of species]	Western Ghana [5]	Ghana [6]	Gambari Forest W. Nigeria [7]	M'passa Forest Gabon [8]	Irangi Kivu [9]	Mayanja Forest Uganda [13]
Praomys	***tullbergi***	***tullbergi***	***tullbergi***	*tullbergi*	***jacksoni***	*morio*
Malacomys	*edwardsi*	*edwardsi longipes*	*edwardsi*		*longipes*	*longipes*
Hybomys	*trivirgatus*	*trivirgatus*	*trivirgatus*	*trivirgatus*	*univittatus lunaris*	*univittatus*
Hylomyscus	*stella*	*stella*	*stella*	***stella*** *parvus*	*alleni*	*stella*
Lophuromys	*sikapusi*		*sikapusi*	*sikapusi*	*flavopunctatus*	*sikapusi* ***flavopunctatus***
Grammomys				*rutilans*		*dolichurus*
Stochomys		*defua*	*longicaudatus*			
Deomys				*ferrugineus*	*ferrugineus*	
Heimyscus				*fumosus*		
Aethomys						*kaiseri*
Lemniscomys					*striatus*	*striatus*
Mus						*triton minutoides*
Tatera						*valida*
Oenomys						*hypoxanthus*

Sources: JEFFREY 1977 (Ghana); COLE 1975 (Ghana); HAPPOLD 1977 (W. Nigeria); DUPLANTIER 1989 (Gabon); DIETERLEN 1985 (Kivu); DELANY 1971 (Uganda).

Table 5
Species of small rodents in selected rainforests to illustrate variation in species richness, species replacement and subsets.
The most abundant species in each rainforest is in **bold** print

Analyses of communities of rodents illustrate other aspects of how communities are structured. After surveying many communities of rodents (primarily in North America and Australia), Fox (FOX and BROWN, 1993; BROWN, 1995) suggested a series of «assembly rules» which were applicable to all communities. The three principal rules are: (a) different communities show character convergence (in contrast to "character displacement" within the community), (b) there is usually

Locality (number of species)	Abundance (%)				
	1st	2nd	3rd	4th	n
Gambari, Nigeria (7) [1]	75	10	3	2	482
Ghana (6) [2]	37	23	11	11	270
Ghana (5) [3]	57	20	14	5	194
Gabon (8) [4]	58	12	11	11	549
Ituri, Zaire (4) [5]	35	32	30	3	60
Kivu, Zaire (8) [6]	25	22	14	13	3541
Mayanja, Uganda (13) [7]	51	28	6	4	818
Mean values	48	21	13	7	

[1] HAPPOLD 1977; [2]; COLE 1975; [3] JEFFREY 1977; [4] DUPLANTIER 1989; [5] GUBISTA 1999; [6] DIETERLEN 1985; [7] DELANY 1971.

Table 6
The four most abundant species of terrestrial rodents in primary rainforests expressed as the percentage of all individuals.

only one species per genus and a new genus is added to the community in preference to a second or third species within a genus, and (c) communities in different localities within region or biome consist of a series of nested subsets in which common abundant species are found in all communities and rare species occur only in certain communities where they are additional to the common species. Do these « assembly rules » apply to African rodents? Rainforests contain 5-13 species according to locality (Table 5); individuals of the single commonest species comprises about one half of the community and the two commonest species comprise about 70% of the community (Table 6). The remainder (i.e. 3 -11 spp.) comprise the remaining 30% and hence are uncommon or rare. Communities of small mammals within each of the forest « blocks » in rainforest zone of Africa (i.e. Western, West Central, East Central, South Central; see HAPPOLD, 1996) are unique in respect of their species composition (although there is greater similarity at the genus level), but nevertheless the functional characteristics of each community appear to be similar. Lists of species show that each genus is usually represented by only one species, and that certain genera and/or species are widespread

Locality (number of species)	Abundance (%)				
	1st	2nd	3rd	4th	n
Olokomeji, Nigeria (8) [1]	57	33	4	3	606
Igbo-Oro, Nigeria (6) [2]	62	10	10	8	48
Foro, Ivory Coast (10) [3]	47	24	10	10	3 900
Uganda (10) [4]	40	18	15	12	349
Kenya (9) [5]	77	7	7	3	1456
Liwonde, Malawi (7) [6]	47	19	18	8	106
Zimbabwe (11) [7]	35	31	14	5	313
Mean values	52	20	11	7	

[1] ANADU 1973; [2] HAPPOLD 1975; [3] GAUTUN 1975]; [4] CHEESEMAN 1975; [5] KEESING 1998a; [6] HAPPOLD and HAPPOLD 1990a; [7] LINZEY and KESNER 1997a.

Table 7
The four most abundant species of terrestrial rodents in natural savanna expressed as the percentage of all individuals.

while others are very restricted (Table 5). For example, individuals of one species of the genus *Praomys* (*tullbergi, jacksoni* or *morio*) are always the most numerous or the second most numerous comprising 75-28% of all rodents, and individuals of the genus *Malacomys* (*longipes* or *edwardsi)* comprise 23-2.7% in the five forests where they occur. Some species (of the genera *Stochomys*, *Deomys*, *Oenomys*) are always rare if they occur at all. The abundance of *Lophuromys* (*sikapusi* or *flavopunctatus*) varies greatly according to the availability of damp grassy patches within the forest, in much the same way as the abundance of *Malacomys* depends on the availability of swampy areas. In savanna localities, there are 6-10 species and the most abundant species comprises 35-77% of individuals (Table 7). However, compared with the rainforest (Table 6), there are a greater number of species which may comprise the most numerous species; according to the locality, it may be *Lemniscomys* spp., *Myomys daltoni*, *Saccostomus* spp., *Acomys spinossisimus*, *Tatera leucogaster* or *Aethomys chrysophilus*.

	Makokou district Gabon (1)		Liwonde N. P. Malawi (2)		Kruger N.P. South Africa (3)	
	Genera	Species	Genera	Species	Genera	Species
Rodentia	22	31	11	11	19	20
Chiroptera	20	34	14	27	15	29

Sources: (1) HAPPOLD 1996 (based on Brosset 1966, 1969, 1988; DUBOST 1968, b; EMMONS *et al.* 1983). (2) ANSELL and DOWSETT 1988, HAPPOLD and HAPPOLD 1990b, D. C. D. & M. HAPPOLD unpubl. (3) PIENAAR *et al.* 1980.

Table 8
The numbers of genera and species of rodents and bats at three localities.

There are few localities where both rodents and bats together have been studied in detail. However where such data are available, such as at Makokou, Liwonde and Kruger (Table 8), bat communities have a greater species richness (and usually genus richness), and therefore greater complexity than do rodent communities. Rodents seem to conform more to the second of the assembly rules than do bats; the ratio of genus: species for rodents is 1:1 for Liwonde and Kruger and 1:1.4 for Makokou, but 1:1.7 and 1:1.9 for bats. Thus bat communities are able to accommodate more species per genus than rodents. The reasons for this are unclear although the larger pool of species and the three-dimensional environment of bats may be contributory reasons. The number of genera and species are a measure of the complexity of the habitat.

Thus, these « rules » are partially correct for African small mammals. Certainly there is character convergence at the genus and functional level for rainforest rodents and, likewise, for savanna rodents. Within the rodent communities of rainforest and savanna there is generally only one species for each genus, although in some situations there may be two species per genus, and the communities which contain only a small number of species are usually a subset (at the generic level) of communities with larger numbers of species. In contrast, the rodents of the northern (Sahara) and southern (Namib) desert and semidesert regions show a contrary community structure: each has its unique fauna, with no overlap in species composition although

functionally they are similar. Within each fauna, there is character displacement; for example, the species of *Gerbillus* in the Sahara are the ecological equivalents of *Gerbillurus* in the Namib.

African bats, for the most part, do not conform to these « rules ». The limited evidence suggests that different communities exhibit character convergence, and in the larger communities there are many species per genus. Hence, each species shows strong character displacement. No conclusions can be made about nested subsets for bat communities; however, a study on bat communities in Tanzania (COCKLE *et al.*, 1998 – see later) suggest that they are not organised as subsets.

Feeding ecology

Analyses of stomach contents and faecal pellets has provided a lot of data on the diet of rodents. Many species of rodents have been shown to feed a wide variety of green vegetation and seeds, each being fairly specific in what it eats; others are omnivorous, some tend towards insectivory and carnivory. All tend to vary their diet on a seasonal basis in response to what is available. Regular sampling can provide a very detailed picture of the main constituents of the diet and the adaptability of a species. One example will suffice to illustrate a general trend in rodents. The Nile Rat *Arvicanthis niloticus* is a widespread species in moist savanna habitats. A study by RABIU and FISHER (1989) recognised four food categories – monocotyledons, dicotyledons, animal matter, and seeds (including grains); all four categories formed some part of the diet in most months, but the proportional contribution of each varied according to month and season (Fig. 2). During two dry seasons, monocotyledons and dicotyledons formed the main part of the diet (monocotyledons 51.7 and 38.9%, dicotyledons 32.5 and 41.2%). During the wet season, the proportion of monocotyledons and dicotyledons declined and the proportion of animal matter (27.7 and 31.7%) and seeds (15.7 and 39.9%) increased. This suggests that the rats show a preference for animal matter and seeds when available but eat a greater proportion of vegetation during the dry season when animal matter and seeds are less available. Although the pattern between the two successive years was similar, animal foods and seeds formed a smaller propor-

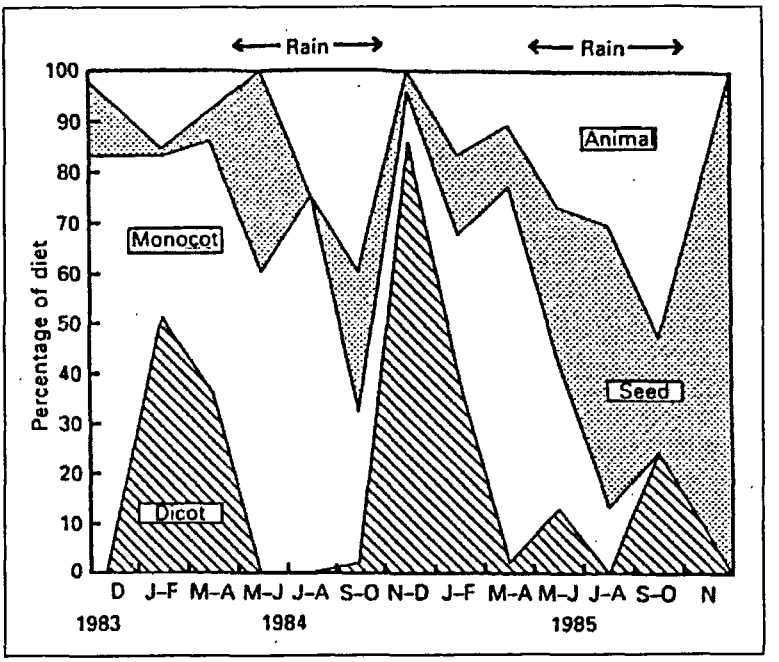

Figure 2
The diet of *Arvicanthis niloticus* in Kenya (RABIU and FISHER, 1989).

tion during the first year when rainfall was lower than during the second. The diet of Nile rats in Kenya (DELANY and MUNRO, 1986) showed a similar pattern in relation to wet and dry seasons, even though the length and timing of wet and dry seasons in Kenya are quite different to that in Nigeria. Flexibility of diet in relation to the timing and length of wet and dry seasons, and to variation between years, appears to be a general characteristic of small rodents. The Nile rat and other widespread species owe their success, in part, to their omnivorous and opportunistic feeding habits. In contrast, specialist feeders are less widespread and less successful.

Even within such broad categories as those given above, rodents need to be selective in order to maximise the amount of energy from their food. Because of their small size and relatively high metabolic rates, small rodents (and other small mammals) can not afford to spend time looking for and eating foods which provide only small amounts

of energy. The Optimal Foraging Theory suggests that optimal diet maximises energy gain, and that mammals (small ones in particular) must select those foods, and parts of foods, that are high in energy. In addition, the energy (and time) spent in foraging and « handling » must be less than the energy gained from the food. Such ideas have rarely been tested on African small mammals. However, KERLEY and ERASMUS (1991) showed that *Gerbillus paeba*, *Mus minutoides* and *Mastomys natalensis* were selective when presented with 11 types of seeds. The rodents chose those seeds, or parts of seeds, which allowed the highest rate of energy intake and which required the least amount of « handling time ». For larger seeds, they ate only those parts of the seed which were high in energy. The smallest species, *Mus minutoides*, preferred seeds which could be eaten with the minimum of wastage, and avoided larger seeds which required long handling times.

The importance of food selection is provided by an experimental study on *Gerbillus henleyi* (mean wt 10g) and *Meriones crassus* (mean wt 73g) which live in the deserts of northern Africa (KHOKHLOVA *et al.*, 1997). Both species gained the majority of their energy intake from the millet seeds, but some energy (and water) was obtained from the saltbush (*Hammada salicornica*). However, gerbils ate only the young buds, located in the stem nodes, which are rich in energy; in contrast *Meriones* ate all parts of the plant including the fibrous stems. By careful selection of the buds, the gerbil maximises its energy and water intake from its plant food by selection of the most nutritious parts. These studies illustrate how experimental and laboratory studies are useful for understanding observations in the field.

Rodents show the same principles of food selection (although on a much smaller scale) as do the Artiodactyla (see JARMAN, 1974); large species (such as buffaloes and cane rats) can eat large amounts of food which may not necessarily be nutritious, but small species (such as duikers and small murids) must select only those parts of a plant, such as new shoots, fruits and seeds which are highly nutritious.

Shrews, elephant shrews and microbats are insectivorous, but there are few detailed studies on the precise nature of their diets. However, a study in the Namib desert showed that the diet of three species of shrews (*Crocidura fuscomurina*, *C. cyanea* and *C. hirta*) was primarily invertebrates (64.9 – 82.9% of the diet) but also included small lizards (DICKMAN, 1995). All three species were generalist insectivores, but

each species selected a slightly different range of prey. *Crocidura fuscomurina* ate proportionally more Chilopoda, Araneidae, Coleoptera, Orthoptera and larvae, and fewer Collembola and Formicidae, than was expected from the frequency of these prey in the habitat; *C. cyanea* had a similar diet but with more Isoptera than expected and fewer Coleoptera, while *C. hirta* had a diet similar to *C. fuscomurina* but with fewer Orthoptera and more Isoptera. Thus each species had a diet composed of a different mixture of the available food items reflecting, in part, species-specific food selection and differences in the abundance of different food items in the habitats where each species foraged. Elephant shrews have traditionally been thought of as insectivores, although recent studies (KERLEY, 1995; SPINKS and PERRIN, 1995) show that many species are omnivores and include herbage in their diet. For example, *Elephantulus rufescens* has an almost entirely insectivorous diet (99% insects, 1% herbage), whereas herbage constitutes 18-49% of other species which have been investigated. The amount of herbage varies according to the time of year and the locality (KERLEY, 1995). Microbats, like shrews, are purely insectivorous although one species, *Nycteris grandis*, feeds also on small vertebrates (FENTON *et al.*, 1981). Each species of insectivorous bat shows careful food selection in respect of size and hardness of its insect prey, the location of the prey, and its flight characteristics. There are several classic papers on the diet of microbats which provide details on the diet of a number of species (e.g., FENTON *et al.*, 1977; VAUGHAN, 1977; ALDRIDGE and RAUTENBACH, 1987; FINDLEY, 1993). These examples of rodents, shrews, elephant shrews and bats indicate that small mammals select their food carefully and utilise many resources.

Reproductive ecology

Research on reproduction of African rodents had resulted in many papers; these have covered topics as varied as length of gestation, litter size, growth of young, variations in reproduction in relation to environment change, the relationship between reproduction and demography, and environmental stimuli for reproductive activity. Needless to say, the large species richness of rodents and the very

1.	All species have a species-specific well-defined period of reproduction, with a period of maximum reproductive activity. Period of reproduction may be short or long.
2.	Seasonal and yearly variations in rainfall and food at a single locality result in changes in the onset and termination of the reproductive period.
3.	Species with a large biogeographical range show flexibility in the timing and length of the reproductive period (from seasonal to aseasonal).
4.	Each species at a single locality has a different reproductive strategy, resulting in differing effects on the demography of the community.
5.	The reproductive period is mainly controlled by changes in climate (especially rainfall) and food availability and quality (especially proteins and oestrogenic compounds). Daylength and temperature are of lesser importance at lower latitudes than at higher latitudes.
6.	Females of most species are polytocous (2-10+ young/litter) and polyoestrous; have a post-partum oestrus, and a period of anoestrus.

Table 9
Reproduction in African small rodents.

varied habitats and climates of Africa have resulted in a wealth of different methods of reproduction. However, the number of species for which there is detailed knowledge is limited; species which were well studied in recent years include *Mastomys natalensis* (DUPLANTIER *et al.*, 1996; FIRQUET *et al.*, 1996; LEIRS *et al.*, 1994), *Tatera leucogaster* (NEAL and ALIBHAI, 1991; NEAL, 1996), *Arvicanthis niloticus* (RABIU and FISHER, 1989), several species in the Sahel (SICARD and FUMINIER, 1996), and several species of bathyergids (e.g. BENNETT, 1994; BENNETT *et al.*, 1994). A few generalisation may be made from all this variety (Table 9).

Reproductive ecology in African rodents has been studied in two main ways: (a) field studies which record the times when adults are in reproductive condition and when young individuals enter a population, and (b) the effect of supplemental food on wild populations. There are many studies which have recorded the times of reproductive maturity and pregnancies for a range of species (see Table 2 in NEAL, 1991). All the features listed in Table 9 have a common goal: to maximise fecundity and to increase the chances of survival for the young. In rainforest, reproductive activity is strongly related to the seasonal pattern of rainfall which, by and large, is regular and predictable. For example, in Uganda and Zaire near the Equator where

the wet season is extensive, reproduction may occur throughout the year (but with seasonal peaks of births) (e.g. DELANY, 1971; HAPPOLD, 1977). In West Africa, where the wet season is shorter, reproduction is mostly at the end of the wet season and the early part of the dry season (HAPPOLD, 1978, 1996). In savannas and semi-arid habitats where grasses and herbs are the principal foods, the months when conditions are good may be less predictable and rodents have to show more flexibility and opportunism. The period of reproduction may be limited to certain months when quality food and water are available (most species), but where food and water are not limited reproduction may be continuous (e.g. *Mastomys huberti* in flooded and riverine habitats (SICARD and FUMINIER, 1996)). In arid and semi-arid regions, reproduction is restricted to a few months (or weeks) when quality food and water are available, and temperatures are not too cold. There is considerable variation between different species at a single locality, and likewise species with a wide geographical range exhibit variations in their reproduction at different localities.

A particularly fruitful field of investigation has been the relationship between diet and reproduction. One of the best-studied genus in this respect is *Mastomys*. Various studies have shown that reproduction slows and stops during the dry season and that food *per se* does not necessarily initiate reproduction (Kenya: TAYLOR and GREEN (1976); Tanzania: LEIRS *et al.*, 1994; Senegal: HUBERT *et al.*, 1981). However, it seems very likely that new shoots from germinating seeds (as occurs at the beginning of the wet seasons) may be more important as a stimulant to reproduction than just the amount that is available (LEIRS *et al.*, 1994). Several studies on *Mastomys* (e.g. LEIRS *et al.*, 1994, MONADJEM and PERRIN, 1998; NEAL and ALIBHAI, 1991) have shown that supplemental food results in higher body weights. In southern Africa, supplemental food also resulted in higher densities of animals probably due to immigration and an increase in the number of males with scrotal testes, but did not stimulate reproductive activity in females (MONADJEM and PERRIN, 1998). As FIELD (1976) suggested long ago, quality is often more important than quantity. High quality food rich in protein and oestrogenic compounds is necessary for reproductive activity in both sexes, and does not usually become available until after the wet season begins. Hence it is not surprising that FIRQUET *et al.* (1996), LEIRS *et al.* (1994) and MONADJEM and PERRIN (1998) showed a correlation, for *Mastomys natalensis*, between

reproductive activity and the rainfall one or two months previously. It is highly likely that such a correlation is a widespread occurrence and underlies the control of reproduction in many species; the variations on this basic theme are dependent on the amount and pattern of rainfall, absence of extreme heat or cold, and the time taken to produce quality food (whether germinating seeds, fruits or insects). Although photoperiod is considered an important environmental factor controlling reproduction in temperate environments, it is not considered of much importance in the tropics where annual differences in photoperiod are very slight. A full discussion on this topic may be found in DELANY (1986).

Development and growth of young rodents is also very varied. NEAL (1990) analysed the reproductive characteristics of many species of murid rodents, and showed that weight at birth (and many other reproductive characteristics) is strongly correlated with the adult body weight. The principal dichotomy in development and growth is between species which have precocial young and those which have altricial young. Precocial species (such as *Otomys* and *Acomys* spp.) have a longer gestation and fewer young in a litter, the young are heavier at birth and they have a slower postnatal growth rate than in altricial species. Most interestingly, altricial species living in arid and semi-arid regions (e.g. *Gerbillus* spp.), and arboreal folivores (e.g. *Thamnomys*) also have lower growth rates, perhaps due to an inadequate supply of high quality foods. Species within a subfamily often show similar characteristics; for example species of Dendromurinae and Gerbillinae tend to have shorter gestations and the young have lower birth weights than species in other subfamilies of equivalent weight. Studies such as this provide an interesting insight into how the various evolutionary lines of rodents have evolved. It would be interesting to look at other families of rodents in these respects, and to investigate the Lifetime Reproductive Success (LRS) of African rodents. Very little is known about longevity, fecundity, and survivorship of African small mammals and how LRS affects demography and abundance. One clue, as suggested by DUPLANTIER *et al.* (1996), is that species which are very fecund have the greater potential to expand their distribution compared with species with a lower fecundity; for example the higher fecundity of *Mastomys erythroleucus* in Senegal allows this species to spread more rapidly than *M. huberti* and *M. natalensis* which have lower fecundity.

Information on reproduction of bats is not as extensive as for rodents. Bats, like rodents, need to produce their young at a time which provides the best chance of survival for the young. An additional constraint is that female bats must remain aerodynamically efficient at all stages of pregnancy and while carrying new-born young. There is great diversity in the reproductive strategies: HAPPOLD and HAPPOLD (1990b) recognised 10 strategies based on the timing of parturition in relation to season, the presence or absence of reproductive synchrony, the number of pregnancies per year, and the presence or absence of post-partum oestrus. Several features of bat reproduction are worth mentioning:

(1) Most African microchiroptera have only one young/litter, and many have only one litter per year. Hence the annual productivity is low (contrary to most rodents). Whether this is compensated for by greater survival and greater longevity is uncertain.

(2) Usually, more than one strategy occurs within a geographical locality. In Malawi, for example, five strategies (Restricted Seasonal Monoestry, Extended Seasonal Monoestry, Seasonal Bimodal Polyoestry, Aseasonal Polyoestry, and Seasonal Multimodal Polyoestry) have been recorded in the 15 species for which there is adequate data.

(3) Some species of bats can change their chronology of reproduction by altering the interval between copulation and parturition; this may be achieved by sperm storage and delayed fertilisation (e.g. *Pipistrellus nanus* [BERNARD *et al.*, 1997]), delayed implantation (e.g. *Miniopterus schreibersi* [BERNARD *et al.*, 1996]), or retarded embryonic development (e.g. *Scotophilus borbonicus* [VAN DER MERVE *et al.*, 1988]).

(4) Most species in temperate regions and dry regions of Africa are monoestrous, although polyoestry is possible in those tropical regions where rain falls for most months of the year and insects are abundant for most of the year.

Geographical ecology

In contrast to many of the studies mentioned above which describe species or communities in a clearly defined locality, geographical ecology deals with the patterns and trends throughout the range of a

species, a genus, a family or an order. It also seeks to understand how communities are structured, and how and why a taxon may change in abundance at different places within its range. BROWN (1995) has termed this subdiscipline « macroecology » implying that it is the large-scale patterns of distribution, rather than the fine detail, that enable a better understanding of the biogeography of animals.

There are many distribution maps for African mammals (Fig. 3); some record collecting and sighting localities (e.g. SETZER, 1956 for Sudan, HAPPOLD, 1987 for Nigeria) and others indicate presence/absence in quarter-degree squares (e.g. TAYLOR (1998) for Kwa-Zulu Natal, ANSELL and DOWSETT (1988) for Malawi, MONADJEM (1998) for Swaziland). A third method indicates the approximate range by shading or colour (e.g. SMITHERS (1983) for southern Africa, DORST and DANDELOT (1970) for Africa) but may include some areas where the species does not occur because the habitat is unsuitable. Whatever the range may be, it is a representation of various aspects of the ecology of the species and portrays an area where the vegetation, temperature, water availability and landscape ecology are within the tolerance of the species. Beyond this area, one or more « limiting factors » exceed the tolerance of the species preventing its permanent occupancy. Maps (on a fine and coarse scale) also indicate short-term historical and long-term evolutionary changes in distribution. The importance of good locality records (as provided by surveys and museum specimens) can not be over-emphasised. However, there are many species (and many countries) for which there are very little data. It may be too late to obtain reliable biogeographical data on some species because of the widespread destruction of many habitats in recent years.

When good data are available for many species in a region or a country, it is then possible to produce layer maps and identify « hotspots » of biological diversity. Good examples of this are recent studies in Namibia (Fig. 4; GRIFFIN, 1998) and in South Africa (GELDERBLOM *et al.*, 1995; GELDERBLOM and BRONNER, 1995; MUGO *et al.*, 1995) which clearly show that some areas contain greater species richness than others. Such hotspots are usually associated with high plant productivity and/or high plant diversity. Some ecologists have coined the terms « warmspots » and « coolspots » implying areas of lower biodiversity. Of course, areas of lower diversity (« coolspots ») may contain species and assemblages which do not occur in a hotspot, as

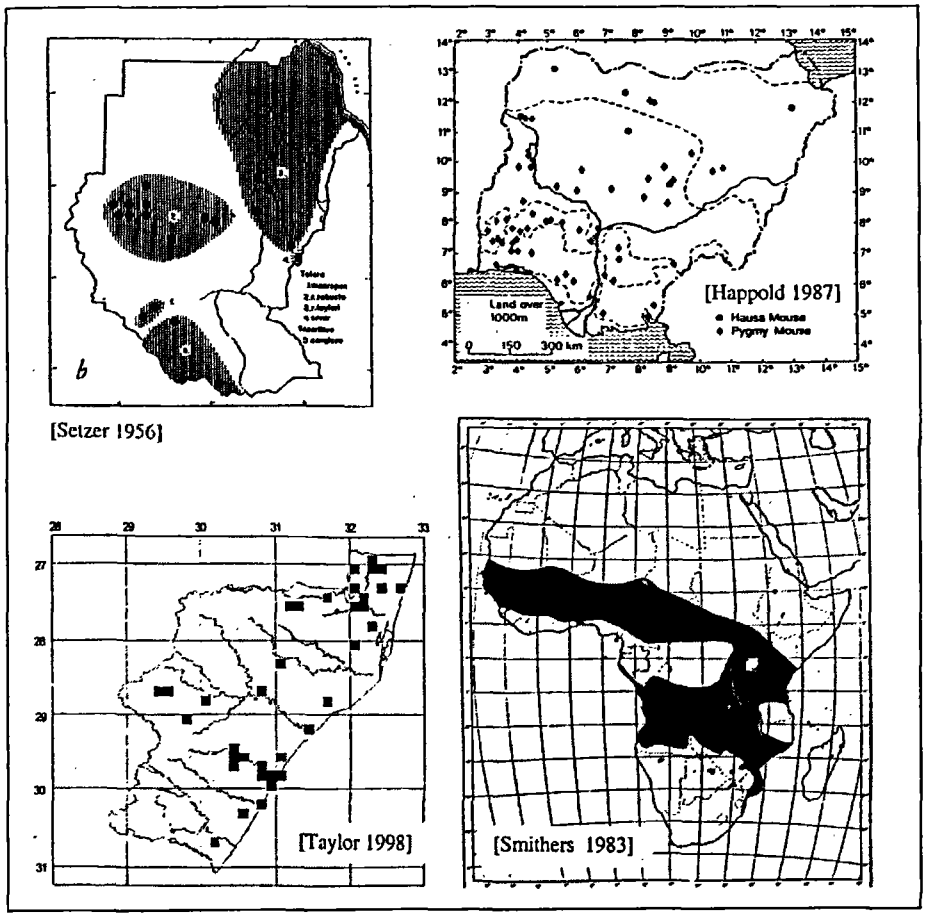

Figure 3
Examples of distribution maps for small mammals in Africa.
Top left: locality records and presumed distribution (SETZER, 1956);
top right: locality records only (HAPPOLD, 1987);
bottom left: presence in quarter degree squares (TAYLOR, 1998);
bottom right: general distribution without locality records (SMITHERS, 1983).

well as endemic species; such areas also require special conservation especially if they are not within a reserved area (GELDERBLOM and BRONNER, 1995). Thus knowledge of hotspots and of the distribution of species is necessary to identify localities of biological interest and conservation value.

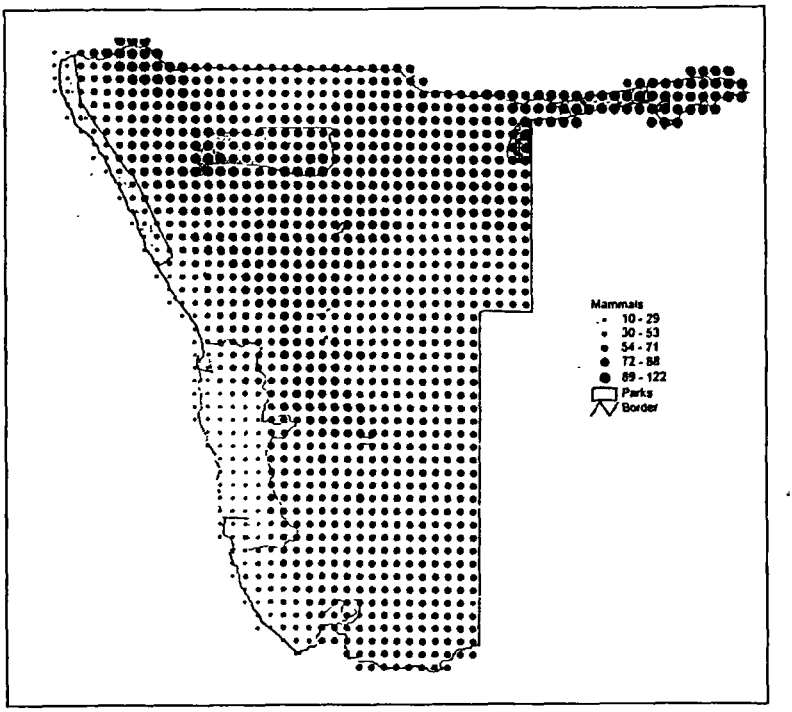

Figure 4
The number of species in quarter degree squares indicating variations in species richness – an example from Namibia (from GRIFFIN, 1998).

It is well known that different parts of the continent contain different assemblages of mammals. Travelling from east to west and north to south, from low altitudes to high altitudes, and from one vegetation type to another, there are slight (or major) discontinuities in the fauna. Species, genera and families decline in abundance, and other taxa take their place. Such changes can be analysed numerically (see e.g. HAPPOLD, 1987, and Fig. 5). For example, in Nigeria the number of species of rodents declines from south (rainforest zone) to north (Sahel savanna) whereas the Carnivora show the opposite trend, and the Artiodactyla have more species in the Guinea savanna than in the rainforest and Sahel savanna zones. Many situations in other parts of Africa could be analysed in a similar way. A different form of macrogeographical analysis is to look at the numbers of species of, for example, ungulates, carnivores, etc., in different regions of the conti-

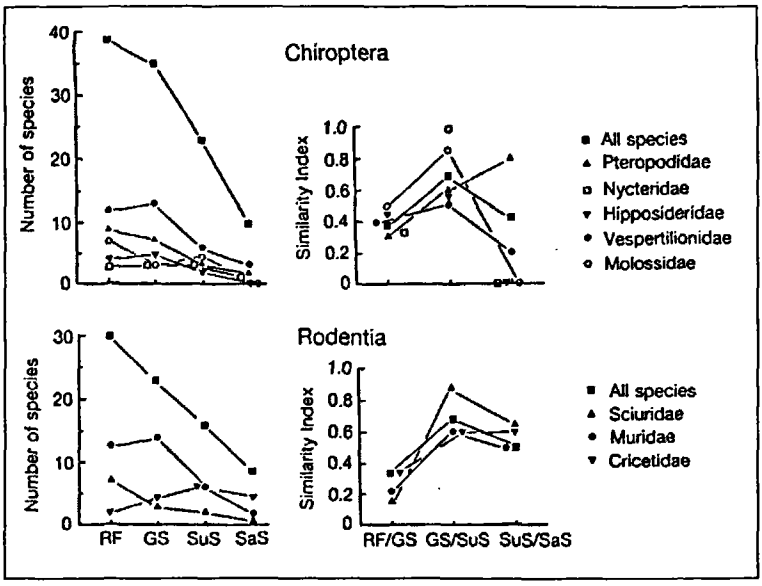

Figure 5
The number of species (left) and Similarity Index (right) of Chiroptera (top) and Rodentia (bottom) in Nigeria. *Number of species: numerals indicate species numbers;* RF = Rainforest, GS = Guinea savanna, SuS = Sudan savanna, SaS = Sahel savanna. Similarity Index: numerals indicate similarity *between pairs of vegetation zones. 0 = no similarity, 1.0 = exact* similarity. RF/GS = comparison between rainforest and Guinea savanna mammals, GS/SuS = comparison between Guinea *savanna and Sudan savanna mammals, SuS/SaS = comparison* between Sudan savanna and Sahel savanna mammals (from HAPPOLD, 1987).

nent (TURPIE and CROWE, 1994). Such analysis shows that the patterns of distribution correspond with the major vegetational biomes, and that the richness in each biome depends on the taxon. Different taxa attain their greatest species richness in different biomes: for Primates it is the central rainforests, for ungulates it is the east African savannas, and for carnivores it is the east and southern savannas. In general, richness is greatest close to the Equator, declining towards the higher latitudes. The complexity of distribution depends on the taxa; the ungulates have the greatest complexity (and hence the continent is divided into more regions each with its representative species) and the primates and carnivores have lesser complexities. The patterns

for endemism do not necessarily follow the pattern for richness because endemism is a reflection of the past climates and vegetation (e.g. the Somali Arid Subregion has a high proportion of endemics in relation to its richness and area). There is great scope for similar studies on small mammals.

Another aspect of geographical ecology considers the distribution of communities, their likenesses and their differences. Bat communities tend to be more complex than rodent communities because of their greater species richness, and hence there is a greater degree of species packing (i.e. the niche for each species is narrower and more precise, and a greater number of species co-exist). An interesting example is provided by the bats living in the coastal forests of northern Tanzania (COCKLE *et al.*, 1998). Each of the 16 forests which were surveyed is fairly small (from a few tens of hectares to a few square kilometres); all are less than 600 m elevation, and the rainfall varies from under 1000 to about 2000 mm/year. A total of 46 species were recorded, but no more than 15 species were found in any one forest. For each of the eight forests which were surveyed in greatest detail, the number of species was 6-15, but why there were such differences is uncertain. Some forests tended to be dominated by rhinolophid bats, others by hipposiderid bats. The number of forests in which each species was recorded was also very varied: 20 species were caught in only one forest, 12 species were caught in two forests, and only two species were really widespread (*Hipposideros ruber* in 12 forests, and *Epomophorus wahlbergi* in 11 forests). The distribution of all 46 species is extremely patchy and does not seem to show any easily recognised pattern. Analysis of several other communities of African bats (HELLER and VOLLETH, 1995) showed that each varied in its species richness, and each had a mixture of morphological types (as indicated by aspect ratio and wingtip ratio). In some respects, the community structure was similar at each locality although there was great variation in the species composition. There are several important conclusions from these studies:

(1) Species richness and community structure of bats are extremely varied, and each species of bat may be associated with a different assemblage of bats at different localities.

(2) There are real and significant differences between neighbouring localities (clearly shown in the Tanzanian study) due to differences

in their ecology and/or evolutionary history. High species richness can occur at both a regional and a local level. Such richness at the local level has also been recorded in several other localities in Africa, such as in the Kruger National Park (PIENAAR *et al.*, 1980), at Masalani in Kenya (O'SHEA and VAUGHAN, 1980) and in Liwonde National Park in Malawi (Fig. 1) (see also HELLER and VOLLETH, 1995). High species richness and diversity may be the «normal» situation for bat communities in Africa.

(3) There is similarity in the community structure at different localities (despite differences in richness and composition) which suggests that the «rules» which govern bat communities are universal (perhaps with some exceptions?).

(4) The patterns of regional and local community structure has important implications for the conservation of bats.

Conservation ecology

In recent years, conservation of mammals in Africa has concentrated, correctly, on the larger species whose numbers have fallen rapidly and whose habitats are being destroyed and reduced in area. The decline in habitats and populations of many species is due, ultimately, to the increasing numbers of humans and the exploitation of the land for food production and resource exploitation (HAPPOLD, 1995). Conservation of small mammals is not usually considered as an important issue, in much the same way that conservation of large species was rarely considered in the first half of the 20th century. Nevertheless, there are many changes in land use which are equally adverse to small mammals as to large mammals (Table 10); many of these are interconnected. Any change in land use alters the desirability of the habitat for small mammals: most changes are deleterious (e.g. large scale agriculture and ranching, subsistence farming, removal of tree cover). Less well-known are the effects of plantations in former mixed woodlands and reforestation (where plantations replace grasslands – see ARMSTRONG and VANHENSBERGEN, 1996) because monocultures do not provide the variety of habitats and food which supported the original populations (HAPPOLD, 1987). Similarly, fragmentation of habitats from a large continuous areas to a series of isolated pockets reduces overall population numbers, isolates one population from

1	Increase in the numbers of humans and domestic animals.
2	Agricultural methods.
3	Timber extraction; reduction of forests.
4	Plantations of exotic trees.
5	Fragmentation of habitats.
6	Loss of specialised habitats.
7	Increased incidence of fires.

Table 10
Ecological factors which have adverse effects on small mammals in Africa.

another, and prevents movement of individuals between populations (see e.g. SAUNDERS *et al.*, 1987, USHER, 1987). A few species of small mammals have benefited from human activities however; for example *Mastomys natalensis* (which flourishes in agricultural fields and food stores), some species of *Tadarida* (which roost in human dwellings), and *Pipistrellus nanus* (which lives in furled banana leaves). It is wise to look ahead now and think about what measures may be taken to ensure adequate conservation of small mammals (Table 11).

Although African countries, in general, have a good record of established reserved areas (the average is about 7% [range 0 – 30%] of the landmass of each country), about 90% of the land is without any formal protection. WESTERN (1989) has pointed out that more attention must be given to conservation outside National Parks and Game Reserves, where in fact the majority of most populations of animals are living. Hence there needs to be better landscape management, i.e. promotion of vegetation along streams, reforestation with natural woodlands on slopes, protection of grasslands, and reduction of fragmentation by planting corridors to link fragments. The natural fauna (both mammals and other animals) will benefit by restoration of land to its former natural state by removal of exotic plants and animals, by elimination or reduction of humanized activities which gradually degrade the land, and by replanting with indigenous vegetation. Some of these initiatives are occurring in some African countries for more pragmatic reasons (such as improving water quality, preventing erosion and spread of weeds) than conserving small

1	More attention to be given to the 90% of land outside reserved areas.
2	Better landscape management.
3	Managed woodlands – natural and planted.
4	Restoration of habitats.
5	Exclosures.
6	Changes in burning policy.

Table 11
Initiatives for the conservation of small mammals in Africa.

mammals. Such initiatives should be applauded because, indirectly, they increase the biodiversity of the ecosystem and help to conserve small mammals. The suggestions made here must be co-ordinated within a total landscape policy which includes intensive agriculture, forestry, grazing lands and urban development.

Even in National Parks, simple procedures could enhance populations of small mammals. Most reserved areas were gazetted to protect the larger mammals, and anything else that lived or grew there was an added bonus. As far back as 1972, DELANY commented that populations of small mammals were lower in habitats which were overgrazed and overbrowsed by large mammals. Small mammals require a certain amount of cover, whether it be growing grass, presence of shrubs and thickets, leaf- and grass-litter, or fallen trees – and hence overgrazing and burning (NEAL, 1970; CHEESEMAN and DELANY, 1979) cause temporary reductions in populations. Protection of habitats by enclosures can form «mini-reserves» for smaller species; a good example of the effectiveness of enclosures is shown by KEESING (1998b) in Kenya who demonstrated that populations of *Saccostomus mearnsi* were twice as numerous inside enclosures, where there was no grazing pressure by wild ungulates and domestic cattle, than outside; other species showed similar trends but not so significantly. Protection within an enclosure also reduced episodic reductions of population numbers which were evident outside the enclosures. Reductions in the frequency of burning, to promote larger areas of unburnt grass and shrubs, will also encourage the increase in the numbers of small mammals.

Since each species responds differently to perturbations and protection, a mosaic of habitats with different levels of protection and management will promote the greatest diversity of small mammals both in reserved areas and in unprotected areas such as farmlands (HAPPOLD and HAPPOLD, 1997), forests (HALL, 1998) and ranches.

Future research

Although the last decade has produced many interesting ecological studies, research has been very uneven in respect of the species and countries. There are masses of studies on common and widespread species, and absolutely nothing on other species. Likewise, many studies originate in some countries, and very few in others. This discrepancy needs to be addressed, although it will be difficult because of the political instability, poor economy and lack of security in some countries. In many African countries, researchers have not been able to obtain modern equipment, or to have the chance to learn modern methodologies. One hopes that this will change in the near future. However, «simple» methods are still of great value, but they need better standardization so that studies at different localities (in the same and in different countries) are comparable. Ideally, research during the next decade should continue present initiatives and should focus on the following:

(1) Detailed surveys of communities with greater attention to structure, rather than just presence/absence. Such surveys may be at the local or regional level, and should be organised so that the results are comparative with other surveys.

(2) More information is required on the less common species and those with restricted biogeographical ranges. Likewise, collection of data and surveys of faunas should be encouraged in those countries which have not been extensively studied in the past. This will necessitate granting of funds and personnel by the richer well-endowed countries.

(3) There should be greater emphasis on experimental work to augment ecological studies, e.g. manipulation of habitats, addition of resources, and removal of species and individuals, followed by monitoring of

community composition, movements of individuals and other biological parameters. Such studies can determine the role of supposed «limiting factors» and provide evidence not obtainable by other means. Adequate replication is essential.

(4) Initiation of long-term studies which can follow complete cycles of demographic and ecological change. Some demographic cycles are short (e.g. rodents), but others are long (e.g. bats); such studies are essential for a proper understanding of the relationship between populations and their environments.

(5) Conservation-oriented research on rare and uncommon species, and on communities; identification of hotspots and habitats of special significance; the effects of habitat change on populations; formulation and implementation of methods to restore and increase the biogeographical ranges and populations numbers of species of small mammals.

(6) Analyses of pan-African or regional trends which help in an understanding of species and communities: their evolution, variations in biological characteristics in different environments, their current biogeographical ranges, and their interactions with other species.

Many of these suggestions for future research are not strictly ecological, but will involve physiologists, ethologists, taxonomists and geneticists. Such collaboration will enable a much more holistic view of the small mammals of Africa.

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On small mammals of the Nyika Plateau, Malawi

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Introduction

A characteristic topographical feature of eastern Africa is the chain of isolated mountain groups that runs parallel to the Indian Ocean coast from Ethiopia in the north to the Drakensberg Mountains in the south. These high plateaux are separated by lowland savannas and woodlands and form, from a biogeographical point of view, one of the most famous continental island archipelagos of the world. They contain some of the biologically most diverse and endemic-rich montane ecosystems in the world (WHITE, 1981; HAPPOLD and HAPPOLD, 1989).

The Nyika Plateau in the northern region of Malawi is probably one of the more important yet also the least known of these mountain islands. Its average altitude is 2,300 (600 - 2,600) m above sea level and it includes many of the habitats found throughout Malawi. The most characteristic feature of the Nyika Plateau, however, is the rolling hills covered by grasses. The Nyika Plateau became Malawi's first National Park in 1968. It covers 3,134 sq km and is largely uninhabited and inaccessible (ANSELL and DOWSETT, 1988; HAPPOLD and HAPPOLD, 1989). Although it represents the type locality for several species and subspecies of mammals (some of which bear the name "*nyikae*"), it has remained relatively unstudied from a mamma-

logical point of view. Our knowledge of the mammalian fauna of the Nyika Plateau is mainly based on incidental records.

Material and methods

Two surveys (trapping, mist-netting, digging, collecting remnants of dead animals) of small mammals were conducted in several remote sites on the Nyika Plateau at altitudes ranging from 1,530 - 2,250 m. The first survey was in March-April 1997 (three weeks at the end of the rainy season) and covered the localities Nganda and Mondwe (see below). During the second survey in July 1998 (two weeks in the middle of the dry season), localities Nganda, Chipome and Sawi were visited.

Chipome Valley (S10.20, E33.50, altitude about 1,530 m). *Brachystegia* woodland, tall grasses, shrubs at the river banks.

Mondwe Valley (S10.24, E33.50, altitude 1,760 m). *Brachystegia* woodland, tall grasses, shrubs at the river banks.

Nganda on the South-West Nganda slopes (S10.26, E 33.51, altitude 2,200-2,300 m). Alpine meadows with shrub patches at the river banks.

Sawi River at Bunthukwa Msisya village (S10.20, E33.53; altitude about 1,500 m). High grasses and shrubs at the river banks.

Live traps (Sherman, Longworth and small cage traps) were baited with peanut butter mixed with canned fish-oil. The number of trap nights was 475 in 1997 and 370 in 1998. Mist-netting was performed only incidentally at some suitable places where bats were sighted.

Reference specimens are deposited in the Senckenberg Museum, Frankfurt am Main, Germany. Chromosome preparations were obtained in the field, directly from the bone marrow of long bones using the standard method (LEE, 1969; LEE and ELDER, 1977), and are deposited at the Department of General Zoology, Faculty of Biosciences, University of Essen, Germany. Authorship and publication dates of rodent species are given in Table 1, otherwise quoted in the text.

Results

The mammals recorded during our surveys include two species of macroscelids (*Rhynchocyon cirnei* and *Elephantulus brachyurus*) from Nganda and Chipome respectively, four species of shrews: *Crocidura luna* (Chipome, Nganda, Mondwe), *C. nigrofusca* (Nganda), *C. occidentalis* (Nganda), and *C. hirta* (Nganda, new record for Nyika) and new records of bats for the Nyika Plateau (see below). We also recorded 20 species of rodents out of the 39 currently known to occur on the Nyika Plateau (our results being included, cf. table 1).

Noteworthy species records

Crocidura hirta hirta Peters, 1852: New for the Nyika Plateau and montane regions of northern Malawi in general.

Epomops dobsonii (Bocage, 1889): Previously known from few Malawi localities only, this species is recorded for the first time from the Nyika Plateau in Chipome Valley. Its presence here may be seasonal in dependence of available food sources.

Plerotes anchietae (Seabra, 1900): Details of this addition to the Malawi fauna have been published by KOCK *et al.* (1998).

Rhinolophus simulator Andersen, 1904: A single specimen obtained at Nganga Hill, is of dimensions comparable to other specimens of *R. simulator* from this part of central Africa (HAPPOLD *et al.*, 1988). A horseshoe bat only doubtfully referred to *R. simulator* was colleted by ANSELL and ANSELL (1973: postscript) on the Zambian Nyika Plateau. That specimen is clearly larger and its specific identity remains to be confirmed.

Pipistrellus nanus (Peters, 1852): Of this species widely distributed in Malawi, two males from Chelinda, 2,300 m, represent the first record on the Nyika Plateau. These specimens do not possess paired glands on the tail. Such glands were found by HAPPOLD and HAPPOLD (1996) in thatch-roosting *P. nanus*, whereas leaf-roosting individuals

	Rodentia recorded in Nyika	1997	1998	Localities	note
1	*Heliosciurus mutabilis* (PETERS 1852)	-	-		
2	*Paraxerus lucifer* (THOMAS 1897)	-	-		
3	*Paraxerus cepapi* (A. SMITH 1836)	-	-		
4	*Tatera boehmi* (NOACK 1887)	-	-		
5	*Cricetomys gambianus* WATERHOUSE 1840	-	-		
6	***Saccostomus campestris* PETERS 1846**	-	1	C	nrN
7	*Beamys major* DOLLMAN 1914	-	-		
8	***Dendromus nyikae* WROUGHTON 1909**	-	3	N	
9	*Dendromus melanotis* A. SMITH 1834	-	-		
10	*Dendromus mesomelas* BRANTS 1827	-	-		
11	*Dendromus mystacalis* HEUGLIN 1863	-	-		
12	***Steatomys pratensis* PETERS 1846**	-	1	C	nrN
13	***Acomys spinosissimus* PETERS 1852**	-	14	C,S	nrN
14	*Pelomys fallax* (PETERS 1852)	-	-		
15	***Mylomys dybowskii* (POUSARGUES 1893)**	1	-	N	nrM
16	*Lemniscomys rosalia* (THOMAS 1904)	-	-		
17	***Rhabdomys pumilio* (SPARRMAN 1784)**	21	8	N	
18	***Zelotomys hildegardeae* (THOMAS 1902)**	2	3	C, N	
19	*Dasymys incomtus* (Sundevall 1847)	-	-		
20	*Grammomys cometes* (THOMAS & WROUGHTON 1908)	-	-		
21	**Grammomys ibeanus (OSGOOD 1910)**	22	7	M, N, S	nrM
22	***Mus triton* (THOMAS 1909)**	14	14	C, M, N, S	
23	*Mus minutoides* A. SMITH 1834	-	-		
24	***Lophuromys flavopunctatus* THOMAS 1888**	17	10	N	
25	***Praomys delectorum* (THOMAS 1910)**	1	1	C, N	
26	***Mastomys natalensis* (A. SMITH 1834)**	2	1	C	
27	***Aethomys chrysophilus* (DE WINTON 1897)**	-	7	C, S	
28	***Aethomys nyikae* (THOMAS 1897)**	1	-	N	
29	***Rattus rattus* (LINNAEUS 1758)**	1	-	Chelinda	
30	*Otomys angoniensis* WROUGHTON 1906	-	-		
31	*Otomys denti kempi* DOLLMAN 1915	-	-		
32	***Otomys typus uzungwensis* LAWRENCE & LOVERIDGE 1953**	-	1	N	
33	*Graphiurus murinus* (DESMAREST 1822)	-	-		
34	***Graphiurus microtis* (NOACK 1887)**	2	2	C, N	
35	*Graphiurus kelleni* (REUVENS 1890)	-	-		
36	***Cryptomys whytei* (THOMAS 1897)**	1	-	M	
37	***Heliophobius argenteocinereus angonicus* THOMAS 1917**	2	1	N	
38	*Thryonomys gregorianus* (THOMAS 1894)	-	-		
39	***Hystrix africaeaustralis* PETERS 1852**	1	-	M	

Table 1
Comparison of the results (species and numbers of specimens of Rodentia obtained) of our recent survey in 1997 and 1998 with the complete list of rodent species reported from Nyika until present (as summarized by ANSELL and DOWSETT 1988, HANNEY 1965, CRITCHLOW in press, results of our surveys being incorporated). Conventional taxonomy is followed. The number of caught specimens is given, nrM = new records for Malawi, nrN = new records for Nyika. Localities: C = Chipome, M = Mondwe, N = Nganda, S = Sawi.

do not have these glands. Pending further generic revisions, the older name *P. africanus* (Rüppell, 1842) is not used here.

Saccostomus campestris elegans Thomas, 1897: Records from northern Malawi are rather rare and the finding of this species in Chipome Valley is new for the Nyika and montane regions in general (ANSELL and DOWSETT, 1988). In regard of the chromosomal variability of neighbouring populations, we assign the single specimen collected to the subspecies *elegans*, described from Karonga at Lake Malawi.

Steatomys pratensis Peters, 1846: Known mainly from southern Malawi, a single specimen has been collected in Chipome Valley, for the first time on the Nyika and in montane regions of northern Malawi in general.

Mylomys dybowskii (Pousargues, 1893): This species is new to the Malawi fauna. Our finding apparently documents an isolated population. The nearest known occurrences of this species are in the Mahali Mts. on the western side of Lake Tanganyika, eastern Tanzania (ROSEVEAR, 1969) and in southern Kenya (KINGDON, 1974). Compared to specimens from the west side of Lake Kivu, NE-Zaire, the present specimen is smaller in external dimensions (probably due to age), but no characters were observed in coloration or skull features to distinguish between the two populations.

Grammomys ibeanus (Osgood, 1910): Although MUSSER and CARLETON (1993) quote ANSELL and DOWSETT (1988, under *G. cometes*) for the occurrence of this species in Malawi, it is here formally listed for the first time in Malawi. ANSELL & DOWSETT (1988) quote specimens and records of *G. cometes* (THOMAS and WROUGHTON, 1908) from the Nyika Plateau, but it has not been confirmed if these are indeed *G. ibeanus* or belong to G. *dolichurus* (SMUTS, 1832), the latter being known from the Zambian part of the Nyika as well as from its Malawian part (INGLES, 1965; HAPPOLD and HAPPOLD, 1989).

Acomys spinosissimus (Peters, 1852): While THOMAS (1898) recorded this species (as *A. selousi* De Winton, 1896) from the Nyika Plateau at 6-7,000 ft., and LAWRENCE and LOVERIDGE (1953) confirmed its occurrence, based on specimens from above Nchenachena, 7,500 ft., no spiny mice were obtained by HANNEY (1962). Consequently ANSELL (1964) noted that the occurrence of this species on the Nyika

Plateau was unconfirmed, and finally HANNEY (1965) stated *Acomys* to be absent from the Nyika. The above material confirms *A. spinosissimus selousi* to be present.

Elephantulus brachyrhynchus (A. Smith, 1836): This elephant shrew was recorded from the Nyika by THOMAS (1898), but ANSELL (1978) thought it likely that this occurrence was below the true montane part. No substantiation coming forth, ANSELL and DOWSETT (1988) and ANSELL (1989) stated that *E. brachyrhynchus* is not found in montane zones of the Nyika Plateau. The present specimen, being collected on the Sawi River, 1,500 m, demonstrates the species to be at least fringing the montane region of the Nyika.

Remarks on nomenclature

Crocidura occidentalis (Pucheran, 1855): Used since *C. olivieri* (Lesson, 1827) is a *nomen dubium* (see HEIM DE BALSAC & BARLOY, 1966). The neotype fixation by CORBET (1978) is based on a bibliographical reference only and therefore *C. olivieri* is validated by this act and has to be quoted from CORBET (1978). However, *C. olivieri* is antedated by *C. flavescens deltae* Heim de Balsac & Barloy, 1966 (with identical neotype as *C. olivieri*). If conspecifity of the giant shrew from Lower Egypt with the West African shrew of similar size, *C. occidentalis*, is assumed, the latter name has priority.

Crocidura nigrofusca nyikae Dollman, 1915: This is the *C. zaodon* Osgood, 1910 of ANSELL and DOWSETT (1988).

Cryptomys whytei (Thomas, 1897): Described from Karonga, on the NW-shore of Lake Malawi, was considered a subspecies of *C. hottentotus* by subsequent authors. Other specimens from the same collection, but from a different collecting site, the top of the Nyika Plateau, were referred to the same taxon (THOMAS, 1897, 1898). Although we have ourselves not examined mole-rats from the type locality, we have studied karyotypes of single individuals from Kasama (ref. grid 1031-A) (KAWALIKA *et al.*, this volume) and from Malawian Nyika (ref. grid 1033-B) (BURDA and CHITAUKALI, unpubl. data). Animals from both localities are chromosomally clearly distinct from each other and from all other *Cryptomys* Gray 1864, and particularly from

C. hottentotus (Lesson, 1826) studied to date. Consequently we designate the Nyika specimen provisionally as *C. whytei* on the basis of geographical vicinity to Karonga and since it is clearly distinct from *C. hottentotus* from South Africa, from which it is also geographically widely separated by intervening species, again clearly different.

Preliminary karyological, morphological and morphometrical data suggest that several species differ significantly from the taxa they have been conventionally identified with. They possibly represent taxa until present undefined and may need to be described as new forms: thus *Mus* (2n = 18), *Cryptomys* (2n = 46), *Heliophobius* (2n = 56-58), *Lophuromys* (2n = 60-68), *Grammomys* (2n = 44-48) and *Graphiurus* (2n = 52) possess undescribed karyotypes. Detailed analyses will be published elsewhere.

Discussion

Although several mammalogical surveys have been made on the Nyika Plateau already, the studies cannot be easily compared. W.F.H. ANSELL and some other authors (cf. ANSELL and DOWSETT, 1988) collected mostly on the Zambian side of the Nyika Plateau or in less remote areas (as e.g. near Chelinda settlement). Data which would enable quantitative comparison of ecological parameters were usually not provided by earlier authors. Only two more recent surveys (OVERTON and NURSAW, 1972; HAPPOLD and HAPPOLD, 1989) can be partly compared. In Table 2 we have extracted available data referring to comparable methods and comparable habitats.

One has to be cautious when comparing quantitative (maybe even qualitative) aspects of the above studies. They have been made in different localities, in different years, partly in different seasons, and had different durations. They also used partly different types of traps. Trapping success ranged a great deal according to the particular sites, and seemed to be independent of the period of the year. Since the low mean trapping success in some studies has been compensated by the intensity of trapping, at the end all four studies resulted in comparable numbers of specimens caught. The numbers of specimens caught as well as the spectrum of the most frequently caught species

Locality	Date	Season	Trap nights	Specimens	Mean trap success (%)	Species	Specimens / species	Authors
diverse localities	July-Sept. 1972	dry	1,325	98	7.5	12	8.2	OVERTON & NURSAW 1971
Chelinda	April - May 1985	rainy-dry	525	74	14.1	5	14.8	HAPPOLD & HAPPOLD 1989
Nganda, Mondwe	March-April 1997	rainy	475	83	17.5	10	8.3	present report
Nganda, Chipome, Sawi	July 1998	dry	370	82	22.2	16	5.1	present report

Table 2
Comparison of trapping studies of small mammals performed in Nyika montane grasslands. Only small mammals caught by means of trapping in comparable habitats (montane grasslands with bracken at an altitude of about 1,500-2,300 m) are considered. Trapping success represents a mean value.

(*Lophuromys flavopunctatus*, *Grammomys ibeanus*, *Rhabdomys pumilio*, *Mus triton*) were rather comparable in all four studies. It may be of interest that the number of species recorded in remote areas (present study and study of OVERTON and NURSAW, 1972) was more than twice as high as in the survey of the fauna near the Chelinda settlement (HAPPPOLD and HAPPOLD, 1989). Although one is tempted to speculate whether this may be the effect of human-induced disturbance in the montane habitats, we point out that it would be premature to make such conclusions at the present state of knowledge and further studies are necessary.

The seasonal effect on the community of small mammals is apparent from the comparison of the results of the two surveys using the same method at the very same place, SE slope of Mt. Nganda (tabl. 3). In each season eight species (*Rhabdomys pumilio*, *Grammomys ibeanus*, *Lophuromys flavopunctatus*, *Mus triton*, *Zelotomys hildegardae*, *Praomys delectorum*, *Crocidura luna* and *C. nigrofusca*) were constantly recorded, with three additional species (*Graphiurus microtis*, *Aethomys nyikae*, *Mylomys dybowskii*) being trapped during the rainy season and four additional species (*Crocidura hirta*, *C. occidentalis*, *Dendromus nyikae*, *Otomys typus unzungwensis*) in the dry

		Rainy season 1997				Dry season 1998				Total
		M	F	juv	%	M	F	juv	%	%
1	*Rhabdomys pumilio*	8	8	5	25.9	8	0	0	15.7	22.0
2	*Grammomys ibeanus*	7	7	7	25.9	4	3	0	13.7	21.2
3	*Lophuromys flavopunctatus*	9	6	2	21.0	9	1	0	19.6	20.4
4	*Mus triton*	4	7	2	16.0	3	0	8	21.6	18.2
5	*Zelotomys hildegardeae*	2	0	0	2.5	2	0	0	3.9	3.0
6	*Crocidura luna*	1	0	0	1.2	2	1	0	5.9	3.0
7	*Crocidura nigrofusca*	1	0	0	1.2	2	1	0	5.9	3.0
8	*Dendromus nyikae*	0	0	0	0	1	1	1	5.9	2.3
9	*Graphiurus microtis*	0	1	1	2.5	0	0	0	0	1.5
10	*Praomys delectorum*	1	0	0	1.2	0	0	1	2.0	0.7
11	*Aethomys nyikae*	1	0	0	1.2	0	0	0	0	0.7
12	*Mylomys dybowskii*	0	1	0	1.2	0	0	0	0	0.7
13	*Otomys typus unzungwensis*	0	0	0	0	1	0	0	2.0	0.7
14	*Crocidura hirta*	0	0	0	0	1	0	0	2.0	0.7
15	*Crocidura occidentalis*	0	0	0	0	1	0	0	2.0	0.7
	total specimens	34	30	17	100	34	7	10	100	100
		81				51				

Table 3
Comparison of trapping surveys at the same locality (SE slope of Nganda, S10.26, E33.51, altitude about 2,250 m; alpine meadows with shrub patches and the river bank) during the rainy season (March/April 1997) and the dry season (July 1998).

season. Despite the fact that fewer specimens (51) were caught during the dry season (the number of trap nights was lower) than in the rainy season (81), the species spectrum was a little richer during the dry period (note, however, that only two seasons were compared).

Rhabdomys pumilio, *Grammomys ibeanus*, *Lophuromys flavopunctatus*, and *Mus triton* were dominant species in both seasons, and contributed to about 80% of all the catches. Within the habitat generally designed as "montane grasslands", *R. pumilio* and *M. triton* seemed to prefer the open grassland, *L. flavopunctatus* was trapped usually on mesic sites close to swamps and river banks, and *G. ibeanus* was found mostly near bracken and shrubs. Our data do not support

the conclusion by HAPPOLD and HAPPOLD (1989) that there is a competitive exclusion of smaller *M. triton* by larger *R. pumilio*. Whereas in all the rodent species, both sexes and different age/weight classes (including pregnant and lactating females) were trapped during the rainy season, the sex ratio was significantly biased in favour of adult males during the dry period. Indeed, apart from *G. ibeanus* and *Dendromus nyikae*, catches of all other species consisted (almost) only of adult males, indicating their high dispersing activity during the dry season which contrasted with the lowered activity and/or trappability of females and absence of juveniles during this time.

Of a total of 55 species of rodents (according to conventional taxonomy) recorded so far from Malawi, 40 (73%) have been found on the Nyika Plateau. *Otomys typus* and *Mylomys dybowskii* are known in Malawi only from the Nyika Plateau, as is *Plerotes anchietae* (KOCK *et al.*, 1997). For about 15 further species of rodents, the Nyika represents one of altogether only two to ten known localities of occurrence in Malawi. Of a total of 56 species of bats recorded from Malawi, at least 13 (24%) occur on the Nyika, all four species collected during our surveys being new records.

All these aspects demonstrate the species richness, uniqueness, and conservation value of the Nyika Plateau and its importance as an evolutionary theatre where speciation, divergence and adaptive radiation and/or refuge of small mammals have taken place. At the same time the need for further research (both faunistic survey and ecological studies) is apparent.

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Rodents of the afro-alpine zone of Mt. Elgon

Viola Clausnitzer

Introduction

"The mountains are Africa's Galápagos Islands" (KINGDON, 1989). The flora and fauna of these montane islands differ from the surrounding lowlands, bearing a number of endemics and species with highly disjoint distribution, as well as having developed a number of unique life forms. Some of these conspicuous elements can be found on virtually all of the East African mountains. Although montane forests formed a migration belt in the last ice age, no evidence for continuous afro-alpine environments was found so far (HAMILTON, 1982).

The isolated mountains in East Africa have never attracted the same degree of scientific attention as their neighbouring savanna biomes. Few studies on the afro-alpine rodent communities have been carried out, e.g. in the Simien Mts., focusing on the population ecology of *Arvicanthis abyssinicus* (MÜLLER, 1977). This report will concentrate on the four most common species in the afro-alpine grasslands of Mt. Elgon: *Rhabdomys pumilio, Lophuromys flavopunctatus, Otomys barbouri* and *O. typus.*

Taxonomic note

Nomenclature follows MUSSER and CARLETON (1993), except for the Mt. Elgon endemic *Otomys barbouri.* This species was described by LAWRENCE and LOVERIDGE (1953), later considered as a subspecies of *O. anchietae* and only recently rehabilitated

(DIETERLEN and VAN DER STRAETEN, 1992), a position followed by TAYLOR and KUMIRAI (2001).

Study site

Mt. Elgon (4321 m a.s.l.) is an isolated massif of volcanic origin straddling the Kenya-Uganda border (0°54'-1°25'N and 34°14'-34°45'E), which was deglaciated about 12000 years BP. The volcano rises from a plateau lying at 1850-2000 m a.s.l. to the east and 1050 - 1350 m a.s.l. to the west; the longest north-south distance is about 80 km, the longest east-west distance 50 km.

The montane vegetation and the extension of the different vegetation belts are influenced for long by human impacts, e.g. grazing and burning, and by climate degradation. Moorlands and tussock-grasslands extend down to 3200 m a.s.l. due to frequent burning. Ericaceous forest is only found in small patches and along valleys. Downwards, *Hagenia* and *Rapanea* forests are mixed with bamboo patches terminating in montane forest.

The study sites were situated on the western slopes of Mt. Elgon, between 3650 and 3800 m a.s.l., near the Dirigana Valley. During the study period the precipitation at that elevation was 911 mm per year, April and September were the wettest months, and the average temperature was 5,4° C.

Methods

Three 1 ha grids were laid out for a mark-recapture study. Each of these grids consisted of 11 parallel lines, 10 m apart. The lines had trapping stations with two traps every 10 m, resulting in 121 trapping stations and 242 traps per grid. Trapping was done with Sherman live traps (Large and Extra Large) baited with a peanut-cassava flour mixture for four days each month from October 1996 to November 1997. Since the *Otomys* species were not attracted by any

bait the traps were placed directly in their surface runway system. The difficulties in catching *Otomys* were described before by various authors (e.g. KINGDON, 1974; SHORE and GARBETT, 1991).

Additionally rodents were surveyed along an elevation gradient on the western side of Mt. Elgon. The transect covered representative vegetation formations of different altitudes between 2900 and 4200 m a.s.l. Sampling was done for two consecutive nights every two month between October 1996 and October 1997. The traps were placed in three trap-lines (N-S direction) 40 m apart. Trap stations were set at 20-m intervals with one small and one large break-back trap baited with a peanut-cassava-oil mixture. The traps were laid in surface runways if possible, to increase the trapping success for *Otomys*. Voucher specimens from this study are deposited in the Naturkunde Museum Schloß Rosenstein, Stuttgart, Museum Alexander Koenig, Bonn and the Zoology Museum of the Makerere University, Kampala.

The animals from the mark-recapture grids were individually marked by toe-clipping, weighed to the nearest gram, measured and the sexual condition and ectoparasites were recorded. The vegetation was mapped for all three grids, the vertical structure measured using the point-intercept method; all plants were identified (WESCHE, 2000). Invertebrates were trapped with six pitfalls at the same time as each trapping session on the mark-recapture grids, weighed and identified at least to the order.

Faeces of individuals of *Otomys barbouri* and *O. typus* were collected on the mark-recapture grids from the traps and later analysed using a microscope. For identification of the cell fragments in the pellets a cell catalogue was prepared from sampled plant species. Some of the cell fragments could be identified up to species level. The diet of *Lophuromys flavopunctatus* was analysed from the stomachs of animals caught in the trap-lines.

Individuals of *Otomys typus* and *O. barbouri* were radio-tracked for several days, using a TRX-10002 receiver (Widlife Materials, Canada) and MD-2C transmitters (Holohil Systems, Canada).

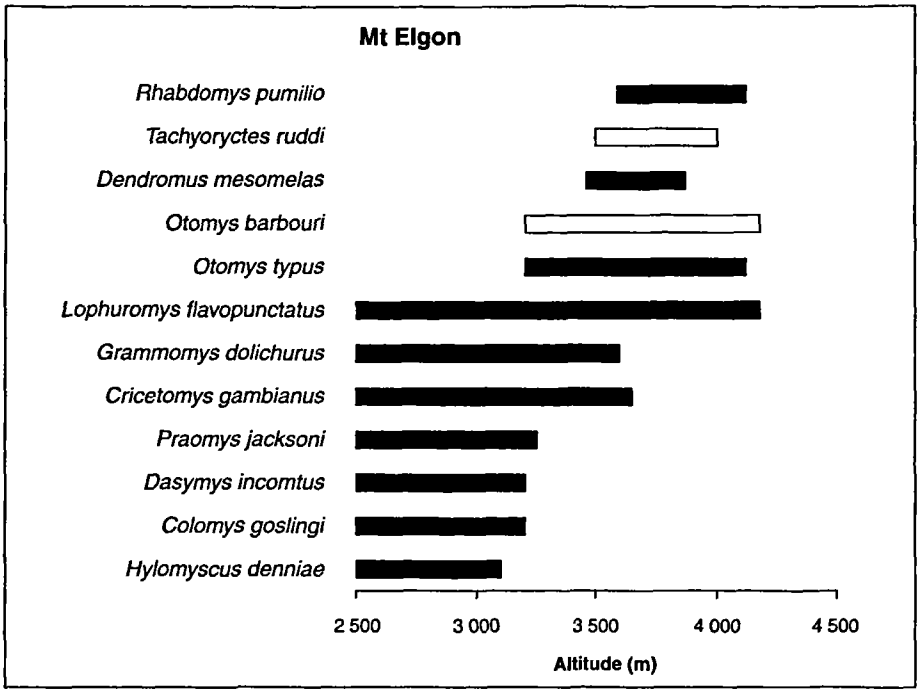

Figure 1
Vertical distribution of rodents on the western slopes of Mt. Elgon; white bars indicate endemics.

Results and discussion with notes on selected species

A total of 384 rodents consisting of 13 species were caught in 4200 trap-nights. A clear change in species composition on Mt. Elgon occurs at about 3200 m a.s.l., which coincides with the present upper limit of the montane forest (fig. 1).

Endemic rodents are only found in the afro-alpine zone, where they inhabit ericaceous vegetation, moorlands and tussock grasslands ranging between 3300 - 4300 m a.s.l. The moorlands and tussock-grasslands above 3700 m a.s.l. on Mt. Elgon are permanently inhabited by 9 rodent species, 8 of them belonging to the Muridae (table 1).

MURIDAE	
Cricetomys gambianus Waterhouse, 1840	
Dendromus mesomelas (Brants, 1827)	X
Grammomys dolichurus (Smuts, 1832)	
Lophuromys flavopunctatus Thomas, 1888	X
Otomys barbouri Lawrence and Loveridge, 1953	X
Otomys typus Heuglin, 1877	X
Rhabdomys pumilio (Sparrman, 1784)	X
Tachyoryctes ruddi Thomas, 1909	X
GLIRIDAE	
Graphiurus murinus (Desmarest, 1822)	

Table 1
Rodents of Mt. Elgon above 3700 m a.s.l.; the most common ones are underlined; x: abundant in grassland habitats.

Lophuromys flavopunctatus *Thomas, 1888*

Lophuromys flavopunctatus is one of the most numerous rodents in the moister areas of East Africa, inhabiting a wide range of different habitats over a large geographical zone. For example in the Ruwenzori Mts. it occurs from lowland forests at about 500 m a.s.l. to the afro-alpine zone reaching well above 4200 m a.s.l. (MISONNE, 1963). Its opportunistic abilities to colonize also less favourable habitats, e.g. the ericaceous belt and montane moorlands, makes *L. flavopunctatus* one of the most successful rodents (MISONNE, 1969).

Lophuromys flavopunctatus has specialized on invertebrates and vertebrates (e.g. small frogs) and is highly dependent on this protein rich diet. HANNEY (1964) reported that *L. flavopunctatus* kept in captivity would not survive for over a week unless fed with worms, frogs or insects. DIETERLEN (1976) could keep individuals on a meat-free diet for several months, feeding them with nuts and sun-flower seeds, but such animals would loose weight drastically and would not reproduce. Compared to mainly vegetarian rodents, the time *Lophuromys* species spend feeding is very short (KINGDON, 1974). In many rodent communities representatives of the genus *Lophuromys* are the only entomophagous species (e.g. VERSCHUREN *et al.*, 1983).

The food particles found in stomachs of *Lophuromys flavopunctatus* belonged largely to the following categories: 1. invertebrates, 2. plant material, and 3. mosses. Vertebrates were not considered since these were most often snap-trapped conspecifics, nor were roots and earth, occasionally found in the stomachs and probably ingested accidentally while searching for and consuming soil-dwelling invertebrates.

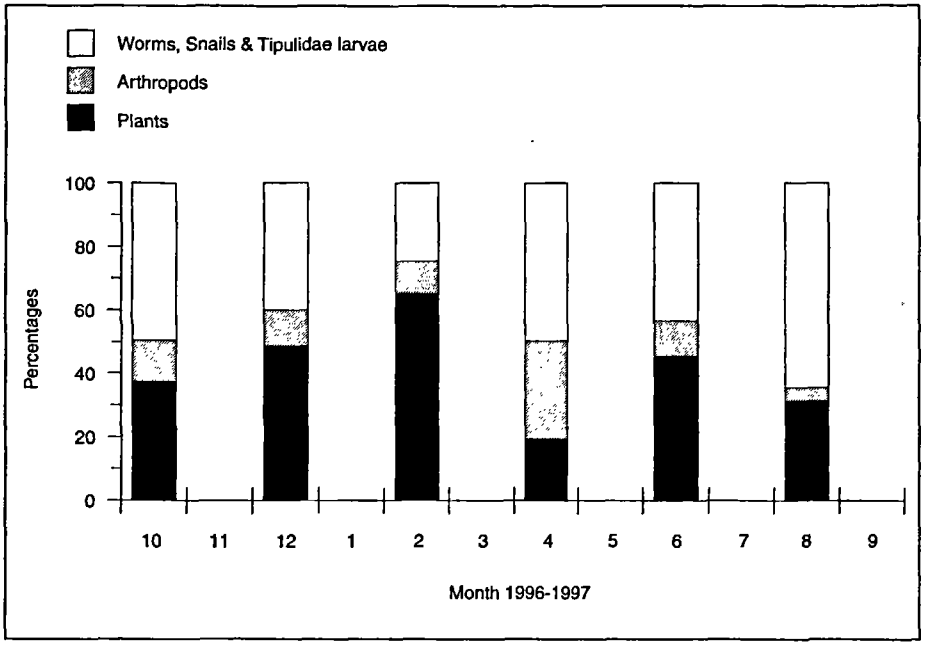

Figure 2
Seasonal changes in the diet of *Lophuromys flavopunctatus.*

Vascular plants were mainly parts of monocotyledons, with only few dicotyledons. A part of them may also have been ingested accidentally with invertebrates.

Figure 2 shows the seasonal changes in the diet of *Lophuromys flavopunctatus* caught in afro-alpine grasslands 3800 m a.s.l. The major food items are soil-dwelling invertebrates, namely earthworms, snails, and insect larvae (Tipulidae). Plants are also a food source, but not necessarily the first choice. In the driest month, February, the plant proportion reached a maximum with over 50%. In April and August, the wettest months, the stomachs contained the highest invertebrate portion, mainly earthworms and *Tipula* larvae. These subterranean invertebrates are rare and difficult to get in the dry season. The total weight of invertebrates from the pitfalls correlates significantly with rainfall (fig. 3), (Mann-Whitney U Test; $n_{weight} = 12$; $n_{prec.} = 12$; one-tailed $p = 0.0002$).

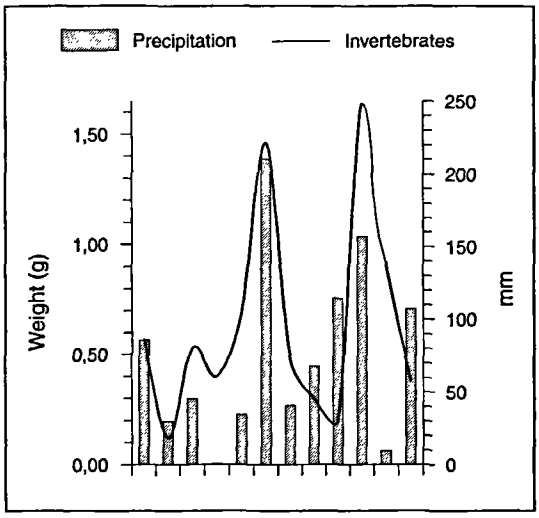

Figure 3
Correlation of the total weight of invertebrates from pitfalls and the monthly precipitation.

Similar positive correlations between the consumption of insects and rainfall have been observed for some rodent species in Africa, e.g. *Rhabdomys pumilio* in South Africa (PERRIN, 1980), *Lemniscomys striatus* in Uganda (FIELD, 1975), *Arvicanthis niloticus* in Kenya (TAYLOR and GREEN, 1976) and *Mastomys natalensis* in Tanzania (LEIRS, 1995).

Otomys barbouri *Lawrence and Loveridge, 1953 and* O. typus *Heuglin, 1877*

Species belonging to the genus *Otomys* were widespread and common in grassland biomes in Africa during the Plio-Pleistocene (DENYS and JAEGER, 1986; DENYS, 1989). Fossils of the whole subfamily Otomyinae predominate in southern African Pleistocene deposits (BRONNER *et al.*, 1988). The present distribution of *Otomys* is disjoint, mainly restricted to montane habitats in tropical Africa and to South African grasslands. This distribution pattern seems to be the result of climatic changes and competition with Murinae, which invaded Africa in the early Pliocene (DENYS and JAEGER, 1986; DENYS, 1989).

Otomys typus and *O. barbouri* are the most common rodents in the afro-alpine zone of Mt. Elgon. They have been recorded at densities

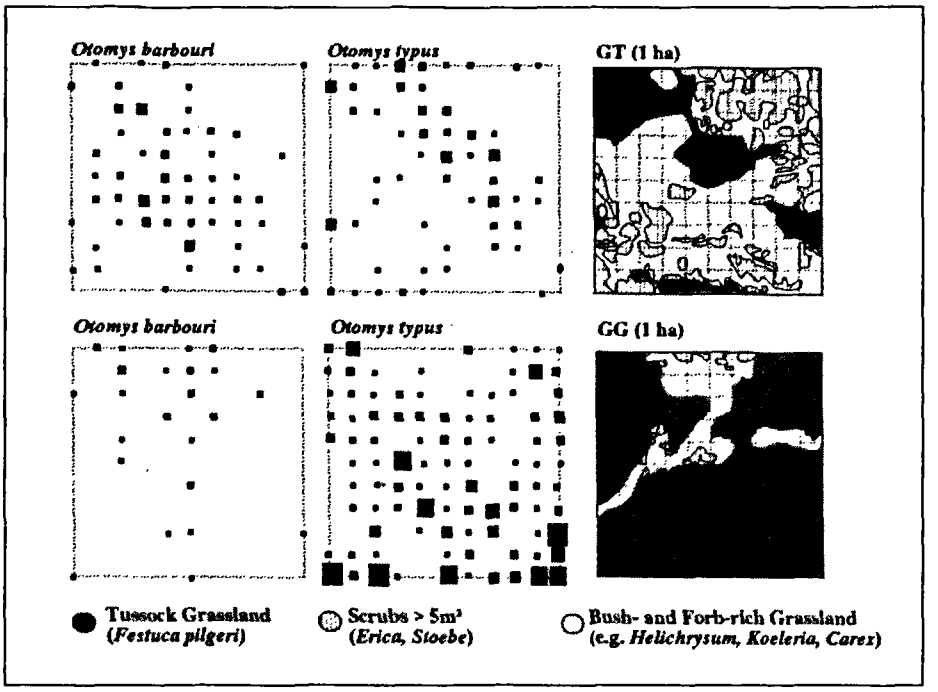

Figure 4
Comparison of two trapping grids, upper line at 3650 m elevation, lower line at 3750 m. Black squares symbolize numbers of individuals of a given species caught at a trap station. Data for a full year summarized. Drawings on the right indicate the corresponding vegetation structure.

of 32 (*O. typus*) and 23 (*O. barbouri*) individuals per hectare, making up a biomass of 3,200 and 2,200 g per ha, respectively.

A total number of 87 *O. barbouri* and of 177 *O. typus* were marked individually on the three grids. The overall recapture rates were 67% for *O. barbouri* and 72% for *O. typus*. In the second half of the study the proportion of recaptured animals in each monthly capture session was at least 80%.

Microhabitat use

Both *Otomys* species coexist sympatrically in large areas on Mt. Elgon, but they show significant differences in their microhabitat use

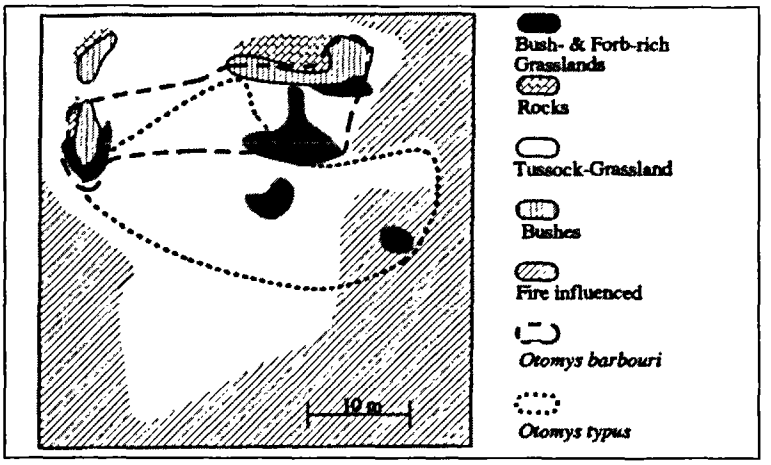

Figure 5
Home range sizes for *Otomys barbouri* and *O. typus* based on a one year mark-recapture study at about 3700 m a.s.l. on Mt. Elgon (100% convex polygons).

(fig. 4). The local distribution of each species depends on vegetation composition and structure and plant species richness. The distribution of *O. barbouri* on structured and species-rich grasslands and of *O. typus* on *Festuca pilgeri*-dominated tussock grasslands was significant ($\chi 2$-test: n = 53, p = 0.018).

Figure 4 compares the abundance (on trapping grids) of the Elgon endemic *O. barbouri* with that of the more widely distributed *O. typus*, in relation with vegetation structure. *Otomys barbouri* prefers patchy grasslands or those rich in shrubs, whereas pure tussocks are avoided. In contrast, *O. typus* avoids patchy vegetation and prefers tussock grasslands. Dense scrub is inhabited by none of the species. The lower grid is a much more uniform grassland where the endemic species is rare, whereas *O. typus* is abundant. The relatively small home ranges, as calculated with the 100% convex polygon method (fig. 5), make such microhabitat analysis sensible. The home-range sizes for both species did not vary between males and females.

Figure 6 illustrates the habitat preferences of the 2 *Otomys* species on Mt. Elgon. Radio-tracked *O. typus* (n = 4) moved only within the

Figure 6
Habitats of *Otomys*; *O. typus* is mainly found in the *Festuca pilgeri* grasslands shown in the foreground, *O. barbouri* in the *Helichrysum* and *Dendrosenecio* thicket in the back; Mt. Elgon, 3600 m a.s.l.

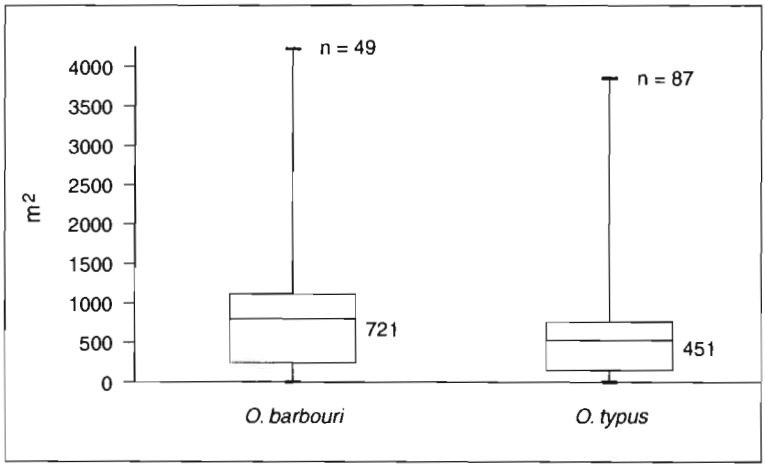

Figure 7
Ranges (mean and variation interval) of male *Otomys barbouri* and a male *O. typus* (28. 2. - 5. 3.1999); Mt. Elgon, 3600 m a.s.l.

Festuca pilgeri grassland, while individuals of *O. barbouri* (n = 3) spent most of their time in the *Helichrysum* and *Dendrosenecio* bushes.

The maximum duration one individual could be followed up during the radio-tracking was 9 days. All radio-tracked individuals (n = 15) moved a total maximum distance of 35 m, most often to and from the same areas. Both species occurred in the same areas, but used different microhabitats (fig. 6) or have different range sizes (fig. 7).

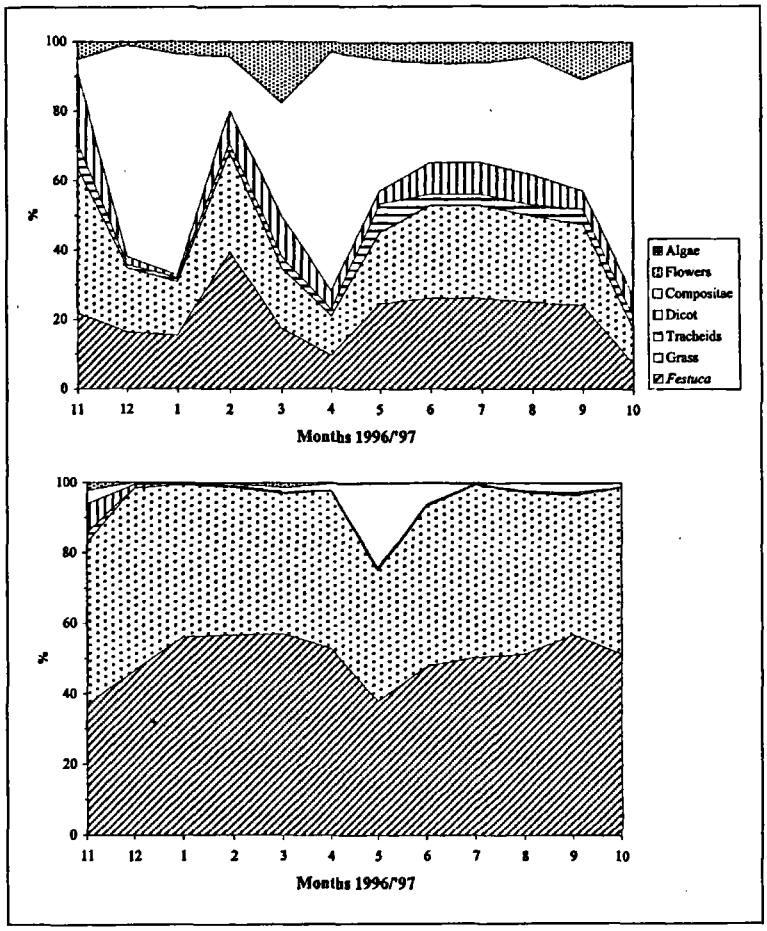

Figure 8
Faecal analyses, based on monthly collected pellets on Mt. Elgon, 3670 m a.s.l. for *Otomys barbouri* (top) and *O. typus* (bottom).

Although being very unsociable, which is the case in most *Otomys* species (e.g. DAVIS, 1972; DIETERLEN, 1967; VERMEUEN and NEL, 1988), the study animals did not establish territories, and their home ranges overlapped strongly, whatever the sex or species. When animals met in the field, they used to give a warning call and normally each moved away. Fights were not observed in the study. Additionally no evidence for fights, like wounded ears or tails was found.

Diet composition

The faecal analyses showed no significant fluctuation in diet composition over the year (fig. 8). The diet of *O. typus* consisted mainly of grasses of which *Festuca pilgeri* made 50%. In the pellets of *O. barbouri* all grasses together totalled about 50%, the other cell fragments were from dicotyledons, mainly parts of Compositae inflorescence.

The genus *Otomys* is a highly adapted herbivore, which relies exclusively on grass and herbs (PERRIN and CURTIS, 1980). The two species studied on Mt. Elgon were strictly herbivorous, *O. typus* feeding mainly on grasses, *O. barbouri* on grasses and dicotyledons. Food, specially grasses, is not a limiting factor for these species on Mt. Elgon. Plant phenology is not markedly seasonal (WESCHE, 2000) and flowers, a preferred food of *O. barbouri*, are supplied throughout the year.

Although one might think that the climatic conditions in the afro-alpine zone have a strong influence on the rodents, *O. barbouri* and *O. typus* did not show any seasonality in the parameters studied. Reproduction, population fluctuations or weight gain or loss did not correlate with climatic variations. Both species reproduce all year round and no evidence for unfavourable seasons could be found.

Rhabdomys pumilio *(Sparrmann, 1784)*

Rhabdomys pumilio is widely distributed in South Africa and has isolated populations in montane grasslands in Tanzania and Kenya. The Mt. Elgon population is the most northern and western one. I regard this western limit of the present disjoint distribution of *R. pumilio* in East Africa as a climatic one, the mountainous areas west of Lake Victoria being probably too humid for this species.

The abundance (MNA) estimates for *R. pumilio* fluctuate in a parallel patterns on the mark-recapture grids (fig. 9). No significant difference between monthly population sizes exist between the two plots (Friedman test: $n = 9$, $\chi 2 = 2.78$, $p = 0.1$). On both mark-recapture grids the populations experienced a total population breakdown, which started with the rainy season in April 1997. The populations did not recover and the plots were not recolonized during the study period.

The population size estimates of *Rhabdomys pumilio* are negatively correlated with rainfall. The most often described pattern of popula-

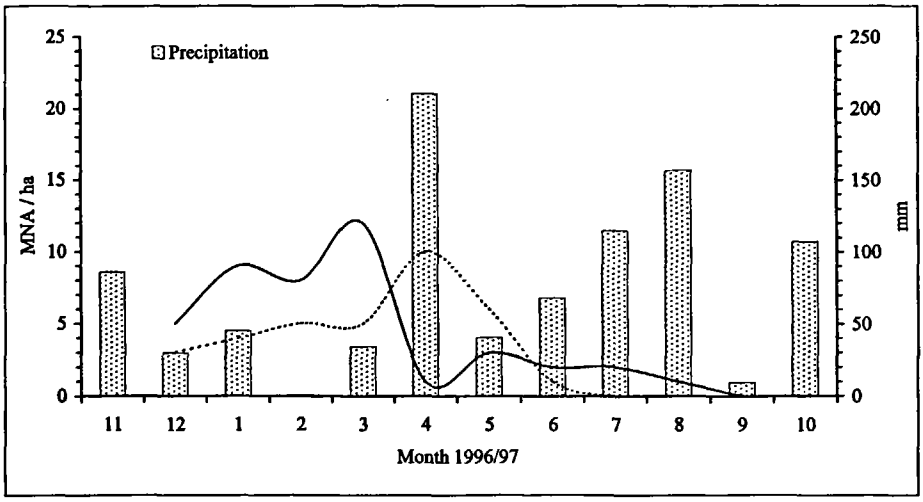

Figure 9
Population size estimates (Minimum Number Alive) for *Rhabdomys pumilio* on the two mark-recapture grids BG and GG in about 3700 m a.s.l. on Mt. Elgon from November 1996 to October 1997. The columns give the monthly precipitation measured near the grids.

tion fluctuation in African rodents is an increase in the rainy season and a decrease in the dry season (e.g. NANDWA, 1973; OGUGE, 1995). Such a pattern is generally correlated with the availability of higher nutritious food in the rainy season (e.g. FIELD, 1975; LEIRS, 1995; TAYLOR and GREEN, 1976). This relationship has been observed for *R. pumilio* as well (e.g. PERRIN, 1980) and TAYLOR and GREEN (1976) even found an increased reproduction activity when nutritive food was added experimentally.

The population fluctuations observed for *R. pumilio* on Mt. Elgon are exactly at the opposite to all other studies. There is an increase in the population size in the dry season (fig. 9), during which breeding occurs, then the population goes down again with the start of the rainy season. Food seems not to be a major trigger for *R. pumilio* reproduction on Mt. Elgon. The amount of invertebrates is significantly positively correlated with the rainfall, thus one would expect breeding and increase in population size in the rainy season. All the results for *R. pumilio* on Mt. Elgon point to a strong climatic influence

on the population dynamics of this species, which is in fact highly affected by cold and humid weather conditions. For instance, the animals died very fast once they got wet (CLAUSNITZER, 2000). *Rhabdomys pumilio* probably undergoes very strong population fluctuations on Mt Elgon, with increase in dry years and strong decrease in wet years, as on the mark-recapture grids in 1997. In other areas *R. pumilio* occurred throughout the study period, its most preferred habitat being areas with open soil. Such places probably develop a good microclimate, less humid and heating up faster than places with very dense vegetation.

Fire as an important factor in landscape formation

The different grassland formations in the afro-alpine zone of Mt. Elgon, which I have discussed as important habitats for *Otomys barbouri*, *O. typus* and *R. pumilio* are the result of a long fire history. The importance of fires in afro-alpine ecosystems is well known and was described in detail by HEDBERG (1964). Mt. Elgon is mentioned as a particularly human-affected highland (HEDBERG, 1951; BECK *et al.*, 1987). The impact of fire on the ericaceous and grassland communities on Mt. Elgon was directly observed (WESCHE *et al.* in press). Fires, which are all man-made, appear to be the major agent in replacing the natural ericaceous vegetation by the grassland communities. Without fires the upper ericaceous belt up to about 4000 m a.s.l. on Mt. Elgon would naturally consist of dwarf *Erica* forest, with more open and shrubby communities only in bogs or on shallow rocky soils. Megaherbivores probably had a large impact on the vegetation, leaving open areas of different successions and size. Today relics of unburned ericaceous vegetation mainly survive in fire-safe rocky sites.

Both *Otomys* species and *Rhabdomys pumilio* benefit from the fire-induced changes from ericaceous forest towards dominating grasslands. *Otomys barbouri* prefers vegetation mosaics such as those created by rare fires. With increasing fire frequency the vegetation is converted into pure tussock grasslands, which are avoided by

O. barbouri, but inhabited in high densities by *O. typus* and *R. pumilio*. A high fire frequency results in patchy grasslands with open soil, providing optimal conditions for *R. pumilio*. This species is sensible to humid conditions in dense grasslands and seeks more open vegetation with a better microclimate. Without any fire, all three species would be very limited in their distribution, with scattered occurrences in naturally open or patchy vegetation in a dense ericaceous forest.

Acknowledgements

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The Mammals of Adrar des Iforas (Mali), with special emphasis on small mammals

Systematic and Biogeographical Implications

Gauthier Dobigny

Raphaël Cornette

Sibyle Moulin

Ehya Ag Sidiyène

Introduction

The Adrar des Iforas (or Adagh des Ifoghas) Massif covers about 150.000 km^2 in Northern Mali (fig. 1). Like for most of the other Central Saharan massifs, data concerning its fauna are very sparse, and on the whole quite poor. AG SIDIYÈNE and TRANIER (1990) put forward a history and gave an up to date list of mammals known in the area. Unfortunately, information collected on small mammals remained very fragmentary. In order to complete the inventory initiated by these authors, we went to the Adrar des Iforas in February-March 1999 with the aim of focusing our efforts on small mammal collection and identification.

We here present a commented list of the mammalian fauna we met, with special emphasis on small mammals (mainly Rodentia and Insectivora) which species are still poorly known in Northern Mali. The different taxa were identified on a morphological basis when-

ever it was possible unambiguously. As for Rodents however, and because sibling species are frequent in West African genera (e.g. *Arvicanthis*: VOLOBOUEV *et al.*, 1987, 1988; *Gerbillus*: LAY, 1983; TRANIER and JULIEN-LAFERRIÈRE, 1988), chromosomal analyses were performed in order to characterise without any ambiguity some of the specimens collected.

These findings led to the addition of new species for the Adrar des Iforas and the finding of new chromosomal forms in the genera studied. Then, the analysis of the updated mammalian fauna of this massif allows us to propose a biogeographical scenario in order to explain the coexistence there of Saharan and typically Sahelian species.

Material and methods

Because of the extent of the Adrar des Iforas area, and of the difficulty to move along, we did not inventory the whole massif. We focused on the Western part of it, from south of Kidal (18°26'N/ 1°24'E) up to the latitude of Aguelhok (19°28'N/0°51'E) (fig. 1). We sampled different types of habitats, namely fallen granite rocks and caves in the Edjerir (18°12'N/1°24'E) and Humoum (Adrar Timejelalin, 18°58'N/ 1°02'E) valleys and in Adrar Ichoualen (19°07'N/1°12'E), sandy depressions in the valleys of Edjerir, Ibdeken (18°45'N/1°20'E) and Ouertejach (Adrar Tirharhar, around 19°30'N/1°16E), sandy wadis in Tararabat (Adrar Ichoualen, 19°24'N/1°14'E), and anthropised areas like gardens (dates, tomatoes), grain stores (corn powder) and straw huts in Tararabat and in the city of Kidal.

The inventory was based on the analysis of raptors pellet and nest remains, on trapping results (wire mesh traps, Sherman traps, and hand captures), but also on direct (night drives or walks, stalking) and indirect observations (spoors, faeces and skeletons), often confirmed by discussions with nomad Tuaregs living in the area.

Karyotypes were obtained from fibroblast cell cultures established from biopsies made on animals brought back to the laboratory. Cells were maintained in metaphase with colchicine at 0.4% one hour before harvest. Cellular membranes were burst by a hypotonical solution

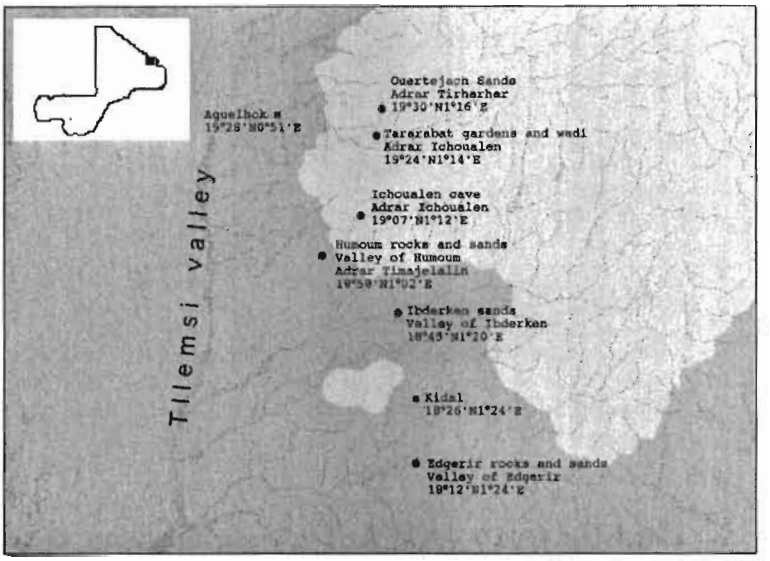

Figure 1
Map of the different trapping localities, in the Adrar des Iforas.

containing bidistilled water, KCl (0.075/M) and new-born calf serum (proportions 5:6:1), then the cells were fixed (methanol and acetic acid, 3:1) and stained with standard Giemsa. On a few occasions, femoral bone marrow cells were used for karyotyping, the hypotonical solution being then composed only of KCl (0.075/M). Diploid numbers (2n) and autosomal fundamental numbers (NFa) could be determined.

Results

Chiroptera

A living specimen of *Rhinopoma* was captured by hand in the cave of Ichoualen. Furthermore, some skulls of *R. hardwickei* and *Asellia tridens* (TAYLOR, pers. comm.) were found in rejection pellets from fallen granite rocks in the Edjerir valley. The former species has never been mentioned before in the Adrar des Iforas, nor in Mali, but was

Presumed species	TRL (mm)	CH (mm)
C. cf. *somalica* (n = 6)	7.38 – 8.24 **7.89** ± 0.36	4.85 – 5.32 **5.06** ± 0.19
C. cf. *lusitania* (n = 3)	5.87 – 6.17 **5.99** ± 0.16	3.81 – 3.9 **3.84** ± 0.05
C. cf. *pascha* (n = 10)	4.32 – 4.92 **4.75** ± 0.17	2.44 – 2.88 **2.7** ± 0.12

Table 1
Measurements of mandibles of *Crocidura* found in nest remains. TRL and CH are respectively for Tooth Row Length and Coronoid Height. The range observed (first line), the mean (in bold) and the standard deviation for each presumed species and each measure are given.

known at the same latitude, from Mauritania and Niger (POULET, 1970; review in LE BERRE, 1990). *Asellia tridens* has already been reported by AG SIDIYÈNE and TRANIER (1990) and was known from Senegal and Chad (KOOPMAN, 1993).

Insectivora

Many tracks of hedgehogs were followed, but no specimen could be observed directly. So, it is impossible to precise the number and identity of the species inhabiting the area. The only indications may be derived from the comparison with the neighbouring Aïr massif in Niger, where *Atelerix albiventris* and *Hemiechinus aethiopicus* have been described (LE BERRE, 1990). The latter species is also known from Mauritania (GRANJON *et al.* 1997). Further prospections will be necessary to confirm the systematic status of the hedgehogs from the Adrar des Iforas.

Around one hundred rejection pellets of a nocturnal raptor, most probably the barn owl *Tyto alba*, were found in granite rocks of the Edjerir valley. Moreover, the cave soil was covered with nest remains, in which at least 13 different mammal taxa were recovered, among which dozens of skulls and mandibles belonging to 3 species of *Crocidura* (HUTTERER, pers. comm.). Using mandible measurements (tabl. 1), 3 groups could be distinguished, and may be referred to *C. somalica*, *C. lusitania* and *C. pasha* (HUTTERER, pers. comm.). *Crocidura lusitania* and *C. somalica* have already been trapped and described in

the Adrar des Iforas (AG SIDIYÈNE, 1989; HUTTERER *et al.*, 1992, respectively). Nevertheless, the specimens of *C. lusitania* are rather small, and may represent a local form (HUTTERER, pers. comm.). On the other hand, *C. pasha* represents a new record for Mali and for West Africa (HUTTERER, pers. comm.), being only known from Sudan and Ethiopia to date (HUTTERER, 1993).

It is interesting to notice the absence of *Crocidura* in our trapping results or night observations, which contrasts with their abundance in pellets and nest remains where they seem to constitute a major part of the raptor preys. This underlines the interest of that kind of material for faunistic inventory purposes.

Lagomorpha

Many hares were seen at night, and some during the day, in many places. But these observations were too transient for a precise identification. It may be *Lepus capensis*, as roughly proposed in a large-scale distribution map in LE BERRE (1990), but no reliable data are available about Lagomorpha in Northern Mali yet.

Rodentia

This Order has the most important specific diversity, as thirteen species belonging to five different families were identified. Captures (by traps and/or hands) allow us to confirm the presence of *Massoutiera mzabi* (Ctenodactylidae), *Jaculus jaculus* (Dipodidae) and to give the first mention of *Desmodilliscus braueri* (Muridae, Gerbillinae) which Heim de Balsac found in rejection pellets from west of the Tilemsi (cf. fig. 1) and which is here at the Northern edge of its distribution area (see AG SIDIYÈNE and TRANIER, 1990).

Direct observations were performed of *Xerus erythropus* (Sciuridae), thus supporting the findings of AG SIDIYÈNE (1989) and AG SIDIYÈNE and TRANIER (1990). This paleotropical species seems to survive in different Saharan massifs, and has even a relictual population in Morocco (HOFFMAN *et al.*, 1993; review in LE BERRE, 1990). Quills and tracks of *Hystrix cristata* (Hystricidae) were found, as expected given the fact that porcupines are present in the Mauritanian Adrar, in Aïr and in Maghreb up to Asia Minor and Southern Europe (WOODS, 1993; review in LE BERRE, 1990).

Chromosomal analyses enabled us to specifically determine non-ambiguously most of the specimens of *Gerbillus* (Muridae, Gerbillinae) captured in the different sites. All of them are new mentions for this region: *G. campestris* (Edjerir; n = 2; 2n = 56; NFa = 68), *G. nanus* (Edjerir, Tararabat and Ouertijach; n = 4; 2n = 52; NFa = 58), *G. tarabuli* (Edjerir; n = 2; 2n = 40; NFa = 74) and *Gerbillus* sp. (Ouertijach; Tararabat; n = 3; 2n = 38, NFa = 72, which may correspond to *Gerbillus pyramidum* known in Egypt and Sudan (GRANJON *et al.*, 1999). On the other hand, karyotype studies also allow us to confirm that the unstriped grass rats captured were referable to *Arvicanthis niloticus* (Muridae, Murinae) (Edjerir and Tararabat; n = 5; 2n = 62; NFa = 62), as suspected by AG SIDIYÈNE (1989), and that the spiny mice were tentatively referable to *Acomys* cf. *airensis* (Muridae, Acomyinae) (Edjerir; n = 2; 2N = 44 and 46; NFa = 66). Finally, the capture of *Myomys daltoni* (Muridae, Murinae) (Kidal; n = 1; 2n = 36) in the city of Kidal represents the northernmost mention for the genus and the species on the African continent. All these cytogenetical results and their systematic implications are detailed elsewhere (DOBIGNY *et al.*, 2001).

The analysis of raptor nest remains and rejection pellets confirmed the occurrence of *Desmodilliscus braueri*, *Jaculus jaculus*, *Arvicanthis niloticus*, and added *Mus* (subgenus *Nannomys*) sp. (DENYS, pers. comm.), as a first mention in the Adrar des Iforas. The systematics of this subgenus needs thorough revision (MUSSER and CARLETON, 1993), nevertheless its presence in the Adrar des Iforas constitutes the northernmost point of its currently known distribution.

From an ecological point of view, some interesting observations were realised. Indeed, the captures of *Arvicanthis niloticus*, *Acomys* cf. *airensis* and *Myomys daltoni*, and also *Gerbillus* cf. *pyramidum* and *G. nanus* in gardens, store houses and straw huts in the valley of wadi Tararabat or in Kidal city (*Myomys*) show that these species can dwell near human settlements. Some direct observations in stores and discussions with tuaregs indicate that they can even become a real pest for stored foodstuff. On the other hand, all these species, except *Myomys daltoni*, have also been trapped or observed in other valleys (Humoum, Edjerir, Ouertejach, Ibdeken) where human influence is very weak.

Moreover, we could notice several cases of sympatry, as in the Edjerir valley where *G. nanus* and *G. tarabuli* are coexisting in bushy and

sandy beds. The same was observed in stores and gardens in Tararabat where *G. nanus* and *G.* cf *pyramidum* were caught in the same trap lines. It would be interesting to conduct further ecological studies to understand the way these species live together and share the available resources.

Discussion

Of course, this inventory may not be exhaustive, first because the Adrar des Iforas is a large massif, some habitats of which we did not study, second, because some species may have been missed by us. For example, AG SIDIYÈNE and TRANIER (1990) found a specimen of *Gerbillus gerbillus*, a species we did not record during our own study. However, the techniques used to survey this small mammal community (rejection pellets and raptor nest remains, hand captures, trapping, direct or indirect observations and chromosomal analyses) appear complementary (tabl. 2).

Data about the fauna of Central Saharan massifs are rather sparse, especially concerning small mammals. Among these massifs, the Adrar des Iforas one has been one of the least studied by scientists during this century. Consequently, many of the observations reported here represent first mentions for the region (Chiroptera: *Rhinopoma hardwickei*; Insectivora: *Crocidura pasha*; Rodentia: 4 species of the genus *Gerbillus*, *Myomys daltoni*, *Acomys airensis*, *Desmodilliscus braueri*, *Mus* (*Nannomys*) sp.). From there, it is possible to update the list of mammal species recorded in the Adrar des Iforas during the last century (see Appendix). Many of these taxa, especially the medium-sized and larger ones, have become extinct during the last decades, mainly because of the advance of the desert, human pressure, and the appearance of fire arms and vehicles which have intensified hunting pressure (AG SIDIYÈNE and TRANIER, 1990). Part of the remaining mammalian fauna of this region of Mali seems to be really endangered and, without any accurate protection, many species may disappear before being really known.

From the species list compiled here (see Appendix), one can distinguish two faunas, according to their biogeographical origin. The first

Species	Chromosomal Analysis	Rejection pellets, nest remains	Trapping (wire mesh and sherman traps)	Hand captures	Direct observations	Indirect observations (tracks, faeces, skeletons, quills, etc.)
Acomys airensis	+	?	?			
Arvicanthis niloticus	+	?	?		?	
Myomys daltoni	+		+			
Nannomys sp.		+	?			
Gerbillus sp.	+	?	?		?	?
G. campestris	+	?	?	+	+	?
G. nanus	+	?	?		?	?
G. tarabuli	+	?	?		?	?
Desmodilliscus braueri		+		+	+	
Jaculus jaculus		+		+	+	+
Massouteria mzabi			+			
Euxerus erythropus					+	
Hystrix cristata						+
Lepus sp.					+	+
Crocidura lusitania		+				
C. pasha		+				
C. somalica		+				
Asellia tridens		+		+	+	
Rhinopoma hardwickel		+		+	+	

Table 2
Means of inventory for each small mammal species encountered.
"?" means that the determination only by this mean is ambiguous.

one is composed of Saharan or Saharo-Sahelian species, like the Trident Leaf-nosed bat *Asellia tridens*, gerbils (genus *Gerbillus*), the jerboa (*Jaculus jaculus*) or the gundi (*Massoutiera mzabi*). The second one groups typically Sahelian to Sudano-Sahelian species like *Arvicanthis niloticus*, *Myomys daltoni*, *Desmodilliscus braueri*, *Taterillus* sp. (AG SIDIYÈNE, unpubl. data, specimen n°1991-1033 in MNHN, Paris), *Hystrix cristata* or *Xerus erythropus*. This is confirmed when looking at medium-sized and larger mammals, with e.g.

Erythrocebus patas and *Mellivora capensis* on the one hand, *Gazella dorcas*, *Ammotragus lervia*, *Vulpes zerda* on the other hand (AG SIDIYÈNE and TRANIER, 1990; KINGDON, 1997; this study). Similarly, bird (S. MOULIN, unpubl. data) and plant species (AG SIDIYÈNE, 1996) show the same trend.

At the end, some of the taxa encountered showed great adaptive capacities and to be very opportunistic. In particular, commensalism may be an especially efficient survival strategy in this harsh environment. From a general point of view, our observations lead to the conclusion that the Adrar des Iforas massif constitutes a Sahelian refuge in the middle of the Sahara desert. Its rather high altitude reaching 850 metres may have contributed to make it a real climatic and ecological island during the last Southward progression of the desert which started around 6.000 bp. That would explain the cohabitation between desert species and Sudano-Sahelian ones (AG SIDIYÈNE and TRANIER, 1990): the Malian Adrar could have been colonised by the latter for example during the last interglaciary episode (around 9.000 bp). It would then have acted as an "ecological trap" during the last Southward progression of the Sahara. This kind of pattern has already been emphasized about the fauna of the neighbouring Aïr massif in Niger (POILECOT, 1996), another Saharan massif belonging to the same geological complex. Molecular analyses would be of great interest for evaluating the genetic divergence between individuals from the Adrar des Iforas and conspecifics from Sahel, and then for dating the different events of colonisation. On that basis, and as it may be the same pattern in the other Saharan massifs (e.g. Aïr, POILECOT, 1996), biogeographical studies should allow to propose a global scenario for the history of Central Sahara faunas.

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Appendix

Review of the species of mammals from Adrar des Iforas (for the last century).

Species	Status	References
Hippotragus equinus	Extinct	Ag Sidiyène and Tranier 1990
Damaliscus lunatus	Extinct	Ag Sidiyène and Tranier 1990
Giraffa camelopardalis	Extinct	Ag Sidiyène and Tranier 1990
Alcelaphus buselaphus	Extinct	Ag Sidiyène and Tranier 1990
Gazella dorcas	Endangered	Ag Sidiyène and Tranier 1990 Le Berre 1990 This study
Gazella rufifrons	Extinct	Ag Sidiyène and Tranier 1990
Gazella dama	Extinct	Ag Sidiyène and Tranier 1990
Addax nasomaculatus	Extinct	Ag Sidiyène and Tranier 1990
Ammotragus lervia	Endangered	Ag Sidiyène and Tranier 1990 Le Berre 1990 This study
Oryx dammah	Extinct	Ag Sidiyène and Tranier 1990
Phacochoerus aethiopicus	Extinct	Chudeau 1920 Ag Sidiyène and Tranier 1990
Orycteropus afer	Extinct	Ag Sidiyène and Tranier 1990
Erythrocebus patas	Endangered	Ag Sidiyène and Tranier 1990 This study
Panthera leo	Extinct	Chudeau 1920 Ag Sidiyène and Tranier 1990
Panthera pardus	Extinct	Ag Sidiyène and Tranier 1990
Lycaon pictus	Extinct	Sayer 1977 Ag Sidiyène and Tranier 1990
Vulpes zerda	Insufficiently known	Ag Sidiyène and Tranier 1990 This study Le Berre 1990
Vulpes pallida	Insufficiently known	Ag Sidiyène and Tranier 1990 This study
Vulpes rueppelli	Presence suspected	Ag Sidiyène and Tranier 1990
Canis aureus	Insufficiently known	Ag Sidiyène and Tranier 1990 This study Le Berre 1990

Species	Status	References
Canis adustus	Insufficiently known	Ag Sidiyène and Tranier 1990
Hyaena hyaena	Insufficiently known	Blanguernon 1955 (*In Le Berre 1990*) Ag Sidiyène and Tranier 1990 This study
Crocuta crocuta	Extinct	Chudeau 1920 Ag Sidiyène and Tranier 1990
Acinonyx jubatus	Endangered	Sayer 1977 Ag Sidiyène and Tranier 1990
Felis sylvestris libyca	Insufficiently known	Ag Sidiyène and Tranier 1990
Caracal caracal	Endangered	Ag Sidiyène and Tranier 1990
Felis serval	Insufficiently known	Ag Sidiyène and Tranier 1990
Ictonyx striatus	Presence suspected	Ag Sidiyène and Tranier 1990
Poecilictis libyca	Presence suspected	Le Berre 1990 Ag Sidiyène and Tranier 1990
Mellivora capensis	Abundant	Happold 1984 (In Le Berre 1990) Ag Sidiyène and Tranier 1990 This study
Procavia capensis	Insufficiently known	Seurat 1934
Rhinopoma hardwickei	Insufficiently known	This study
Nycteris thebalca	Insufficiently known	Ag Sidiyène and Tranier 1990
Asellia tridens	Insufficiently known	Ag Sidiyène and Tranier 1990 This study
Nycticeius schlieffeni	Insufficiently known	Ag Sidiyène and Tranier 1990
Crocidura lusitania	Insufficiently known	Ag Sidiyène 1989 Ag Sidiyène and Tranier 1990 This study
Crocidura somalica	Insufficiently known	Hutterer *et al.* 1992 This study
Crocidura pasha.	Insufficiently known	This study
Hedgehog (undetermined)	Insufficiently known	This study
Arvicanthis niloticus	Abundant	Ag Sidiyène 1989 This study
Myomys daltoni	Insufficiently known	This study
Acomys airensis	Abundant	This study
Mus nannomys sp.	Insufficiently known	This study
Gerbillus gerbillus	Insufficiently known	Petter 1961 Ag Sidiyène and Tranier 1990

Species	Status	References
Gerbillus campestris	Abundant	Petter 1961 This study
Gerbillus nanus	Abundant	Petter 1961 This study
Gerbillus tarabuli	Abundant	This study
Gerbillus sp.(cf. *pyramidum*?)	Abundant	(Petter 1961?) (Ag Sidiyène and Tranier 1990?) This study
Desmodilliscus braueri	Insufficiently known	This study
Taterillus sp.	Presence suspected	Ag Sidiyène unpublished
Psammomys obesus	Presence suspected	Petter 1961
Pachyuromys duprasi	Presence suspected	Ag Sidiyène and Tranier 1990
Meriones crassus	Presence suspected	Petter 1961 Ag Sidiyène and Tranier 1990
Massoutiera mzabi	Insufficiently known	Ag Sidiyène and Tranier 199 Le Berre 1990 This study
Jaculus jaculus	Abundant	Misonne 1986 (In Le Berre 1990) Ag Sidiyène and Tranier 1990 This study
Xerus erythropus	Abundant	Ag Sidiyène 1989 Ag Sidiyène and Tranier 1990 This study
Hystrix cristata	Insufficiently known	Chudeau 1920 This study
Lepus sp. (cf. *capensis*)	Abundant	This study (Le Berre 1990)

Spatial and temporal patterns in *Mastomys* cf. *natalensis* (Smith, 1834) as revealed by radio-tracking

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Hans Klingel

Introduction

Mastomys natalensis (Smith 1834) is a common rodent species in Africa and has been extensively studied (e.g. VEENSTRA, 1958; COETZEE, 1975; NEAL, 1977; TELFORD, 1989; LEIRS, 1995; OGUGE, 1995; MONADJEM, 1998). However, knowledge of its spatial and temporal patterns of activity is still scanty. Until now home range sizes of this species have been determined using the capture-mark-release method (CMR) (CHEESEMAN, 1975; LEIRS, 1995; CHRISTENSEN, 1996) except for one investigation that used radio-tracking, in fallow fields in Tanzania (LEIRS *et al.*, 1996). Previous investigations of activity patterns were carried out mainly in the laboratory (VEENSTRA, 1958, DELANY AND KANSIIMERUHANGA, 1970; CHEESEMAN, 1975; DUPLANTIER AND GRANJON, 1990) and little information is available from the field (DELANY, 1964; NEAL, 1970). In this study radio-tracking was used to elucidate home range size, home range utilization and activity pattern of *M.* cf. *natalensis* in its natural habitat. The data presented here are part of a larger study of the ecology of these populations (HOFFMANN, 1999). The name *Mastomys* cf. *natalensis* is given here to highlight the fact

that the specimens under study may not belong to *M. natalensis*. Indeed, Volobouev *et al.* (2001) have shown the presence of a 38-chromosome species in the immediate vicinity of the study site, a karyotype that may be closer (although not identical) to the one of *M. erythroleucus*.

Methods and materials

Study area

The investigation took place in the Queen Elizabeth National Park (00°15'S, 30°00'E), in south-west Uganda. From 1995 to 1997 the ecology of small mammals in different grassland communities was studied using live trapping methods (CMR) throughout the year (HOFFMANN, 1999). For the radio-tracking experiment two live trapping plots of 1 ha each, about 2.5 km apart and with different vegetation types, were selected in the crater region. Radio-tracking was done at the start of the rainy seasons in March (plot 1) and in August (plot 2) and extended over periods of 2 weeks. Plot 1 was in the *Imperata-Cymbopogon* grassland (grass height 150 cm). Plot 2 was in the bushland-grassland-mosaic with 6-8 *Capparis-Euphorbia* bush patches (10-20 m in diameter) per ha, within the *Bothriochloa-Themeda-Chloris* grassland (grass height 70 cm). In plot 2, 6% of the area was covered with those bushes. It was used more frequently by big game than plot 1. Annual fires occurred in both plots.

Selection of individuals

Only adult males and females were selected, which had been resident on the plots for at least 2 consecutive trapping sessions, i.e. for at least 6 weeks. As both home range sizes and activity patterns were to be investigated, it was necessary to take the fixes at short intervals. This limited the number of individuals to be radio-tracked simultaneously to 5.

Fitting the collar

The animals were equipped with radio-collars with TW-4 transmitters (BIOTRACK, UK) of about 2.5 g, which represented 5-7% of the individuals' body weight. This was within the commonly recommended value of less than 10% (KENWARD, 1987). The collars were fitted in the laboratory. Subsequently the animals were kept for a few hours under observation and then released at their original trap sites.

Locating the animals

Generally the signal could be detected at up to 90 m. The position of each animal was determined by the homing-in-technique (WHITE AND GARROTT, 1990) within a 5 x 5 m grid using marker posts. The rats were located within the live trapping grid of 1 ha and beyond. Tracking started in the evening before the animals left their nests and ended in the morning after they had returned. The animals were radio-tracked in each area for 9-10 nights. To check for possible diurnal activity some day fixes were also taken.

Analysis

Size and shape of the home ranges were calculated using the software program RANGES V (KENWARD AND HODDER, 1995) and the Minimum-Convex-Polygon-Method. The latter was found to be adequate as it allows for comparison with our CMR-results and with previous studies (JONES AND SHERMAN, 1983). To minimize the influence of "occasional excursions" (BURT, 1943), the home range sizes were calculated disregarding 5% of the outermost fixes. The core areas were defined as encompassing 60% of the inner fixes.

For comparison, the home range sizes based on recapture data were calculated for all radio-tracked individuals. For this purpose, data from several trapping sessions were pooled. The CMR home range results so calculated are based on 4-9 different trapping locations for each individual over periods of 2-11 months.

Habitat utilization in plot 2 was assessed using all fixes of the 3 individuals when outside the nest. The activity status was determined by

the changes of location of a particular individual during its activity period. In plot 1 fixes were taken at 30 min interval. In plot 2 the larger home ranges of the residents required longer walks and therefore longer lapses between the fixes. This also minimized encounters with lions (*Panthera leo*) and elephants (*Loxodonta africana*). In plot 1 an individual was considered resting after 3 consecutive fixes at the same location, in plot 2 after 2 consecutive fixes. Those nocturnal resting bouts counted still for the active period.

Results

Seven individuals were successfully radio-tracked, providing a total of 1.375 fixes, 121 to 289 for each individual. In 3 more individuals the transmitter failed (n = 1) and the animals disappeared (n = 2).

Spatial patterns derived by telemetry

Imperata-Cymbopogon grassland

One female (F1) and 3 males (M1, M2, M3) were radio-tracked successfully in plot 1. All home ranges were located to a large extend within the trapping grid and they were overlapping. Home range sizes (at 95%) were found to range from 0.119 - 0.255 ha (tabl. 1). F1 and M2 made few excursions, which is expressed by the large differences between the home range sizes calculated from 100% and 95% of the fixes (tabl. 1). During one excursion however, M2 moved 130 m away from his den, but came back to his home range after 1.5 hours.

The sleeping sites were in the central part of the individuals' home ranges. F1 and M3 had their dens in termite structures (*Odontotermes* sp.), M2 in a hole in the ground, and M1 used a den at the base of a grass tussock. With few exceptions, the animals returned to the same dens in the morning and used these sites also for resting bouts during activity phases. The sleeping sites of M1 and F1 were situated in the overlapping zone of their 100% home ranges. Twice during the experiment, both used the same den, once that of the male, once that of the female.

	Radio-Tracking					CMR		
Indiv.	Period	Fixes n	HR (ha) 100%	95%	60%	Period	Capture n	HR (ha) 100%
Plot 1								
F1	03/96	287	0.315	0.163	0.073	02/96-07/96	9	0.120
M1	03/96	289	0.291	0.255	0.068	02/96-03/96	5	0.135
M2	03/96	265	0.603	0.201	0.064	02/96-05-96	4	0.043
M3	03/96	166	0.153	0.119	0.021	02/96-03/96	6	0.090
Plot 2								
F2	08/96	121	1.018	0.840	0.246	09/95-09/96	6	0.293
F3	08/96	123	0.765	0.701	0.338	09/95-09/96	2	—
M4	08/96	124	0.726	0.656	0.164	09/95-09/96	8	0.275

M = Male, F = Female.

Table 1
Home range sizes (HR) of *M.* cf. *natalensis* in both plots, revealed by radio-tracking and CMR. For F3, an estimate based on CMR results was not possible due to low trapping success.

Bushland-grassland-mosaic

Two females (F2, F3) and 1 male (M4) were successfully radio-tracked. Their home range sizes (at 95%) ranged from 0.656 - 0.840 ha (tabl. 1) and were on average 4 times larger than those in plot 1. The animals moved far outside the trapping grid and used dens at the periphery of their home ranges, up to 70 m from the edge of the grid. M4 and F2 used dens in different *Capparis-Euphorbia* bushes, F3 used a hole in the ground in the open grassland.

In the mornings the animals returned to their dens. But in contrast to the inhabitants of plot 1, they never came back to their dens during the activity period. Instead, hides in *Capparis-Euphorbia* bushes were used for resting bouts. While home ranges of M4 and F3 overlapped, these individuals met only twice and only briefly during the radio-tracking periods. In total the animals spent about the same amount of time in the grassland and in the bushes (fig. 1). Considering that the bush patches cover only 6% of the area, *M.* cf. *natalensis* actually utilized 94,4% of the corresponding surface.

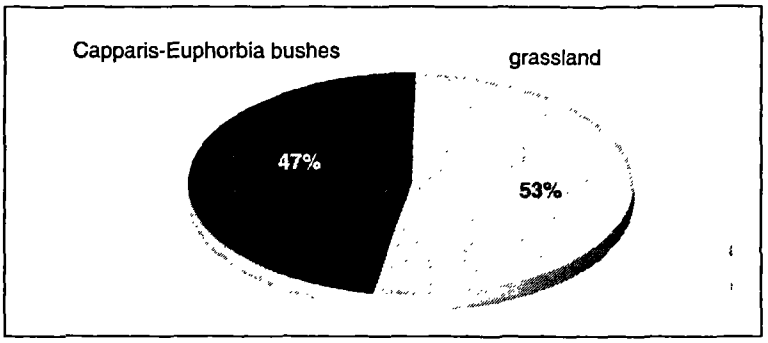

Figure 1
Habitat utilization of *M.* cf. *natalensis* [%] in the bushland-grassland-mosaic. Total fixes (n = 230) outside the nests of all individuals (n = 3) are pooled.

Spatial patterns derived by CMR-method

Home range sizes derived from the CMR-method were considerably smaller than those assessed by radio-tracking (tabl. 1). The CMR home ranges are about the size of the core areas (60%) as revealed by telemetry.

Activity patterns derived by telemetry

In both plots *M.* cf. *natalensis* was strictly nocturnal. The animals left their dens after dusk and returned to them before dawn. But their activity rhythms were different. In plot 1 all animals showed two distinct activity peaks, whereas in plot 2 they had just one (fig. 2). The mean activity patterns of the 2 plots are significantly different (Mann-Whitney U = 40, Z =-2.283, n = 13, p = 0.022)

In plot 1 the first peak of activity was about 1 hour after dusk, the second one 1 hour before dawn. In comparison with plot 1, activity in plot 2 started later and the one and only peak was delayed by about 1 hour, then the activity declined more or less continuously until dawn. On average the animals in plot 2 returned to their nest sites about 2 hours earlier than those in plot 1. In total, the activity period in the bushland-grassland-mosaic (plot 2) was almost 3 hours shorter

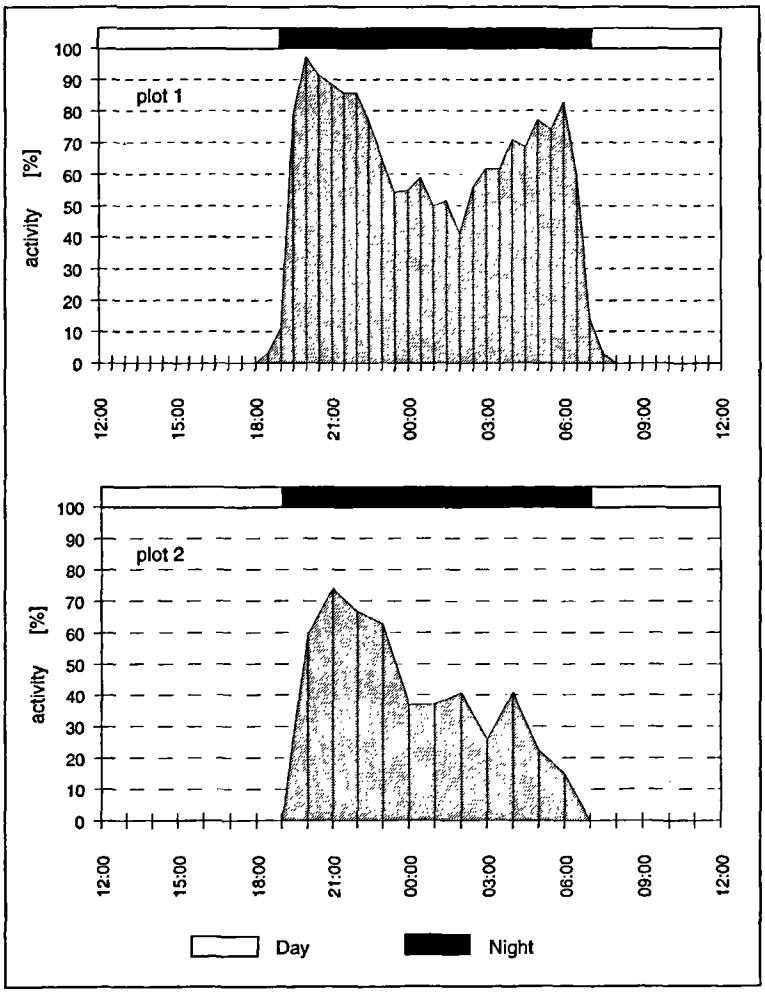

Figure 2
Activity records for *M. cf. natalensis* in both plots.
Fixes (N) of all individuals (n) in each plot are pooled:
plot 1 (n = 4, N = 959), plot 2 (n = 3, N = 377).

than in the *Imperata-Cymbopogon* grassland (plot 1). The activity period in the bushland-grassland-mosaic was on average 8.5 ± 1.3 h (n = 26) vs 11.2 ± 0.4 h (n = 25) in the *Imperata-Cymbopogon* grassland (HOFFMANN, 1999).

Discussion

Home range size and utilization

Home range sizes of *M.* cf. *natalensis* determined by radio telemetry in different vegetation types vary considerably, from 0.022 ha in a Tanzanian fallow field (LEIRS *et al.*, 1996), to 0.840 ha in a bushland-grassland-mosaic (this study, plot 2). Our plot 1 results and those of CHEESEMAN (1975) from the same *Imperata-Cymbopogon* grassland are intermediate. Home range sizes are likely to be correlated with density: in the fallow field of Tanzania an enormous density of up to 401 ind./ha was found (LEIRS *et al.*, 1996), vs 25 in the *Imperata-Cymbopogon* grassland (CHEESEMAN, 1975; HOFFMANN, 1999), and only 7 in the bushland-grassland-mosaic (HOFFMANN, 1999). These findings suggest that high densities are associated with reduced mobility. Home range overlap suggests a non-territorial range utilization pattern, which supports the conclusions of LEIRS *et al.* (1996).

Home range sizes calculated using the CMR-technique were very much smaller than those revealed by radio-tracking. This was also found by LEIRS *et al.* (1996).

Our sample is not large enough for assessing a possible correlation between spatial or temporal patterns of activity and sex or sexual activity. Home range sizes found with the CMR-method (HOFFMANN, 1999) suggest, for both plots, that the home ranges of males are on average larger than those of females. This is in contrast with the results of CHEESEMAN (1975) and LEIRS *et al.* (1996). Sexually active individuals of both sexes were found to have larger ranges than inactive ones (LEIRS *et al.*, 1996; HOFFMANN, 1999). Seasonal variations in home range sizes could not be found in this species (OGUGE, 1995; CHRISTENSEN, 1996; LEIRS *et al.*, 1996; HOFFMANN, 1999).

Activity patterns

The strictly nocturnal activity of the radio-tagged individuals substantiates previous trapping results (DELANY, 1964; NEAL, 1970). In the laboratory *M.* cf. *natalensis* has been found to exhibit short bouts of activity during the day (VEENSTRA, 1958; CHEESEMAN, 1975;

DUPLANTIER AND GRANJON, 1990), which may have been caused by the laboratory conditions. In our study an activity peak was found about 1 hour after dusk, whereas a second peak before dawn was not always distinct. The causes for the shorter activity period in plot 2 (fig. 2) are not clear. It may be because the quality and quantity of food available in the bushes were sufficiently high, so that feeding took less time than in plot 1. There, the animals spent less time resting during the nocturnal activity period. These differences can also be explained by differences of habitat use. The smaller home ranges in plot 1 (tabl. 1) may allow the animals additional time for e.g. exploration and foraging, after the main mid-night resting bout, which they spent in their nearby dens. In plot 2 the animals used bushes intensively (fig. 1). As the distances between the frequently used bushes were quite large (up to 80 m), returning to their nest sites for a short resting bout during the activity period would not be economical. The intensive use of the bushes and the reduced activity period in plot 2 should also result in reduced predation. Possibly the patchiness of food resources and shelters in plot 2 does not allow for high population density.

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Differential representation of gerbilids in European eagle owl (*Bubo bubo ascalaphus*) pellets from Southwestern Algeria

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Introduction

Nocturnal raptor pellets analyses are useful for different kinds of scientific purposes. For ecological and zoological studies, undigested prey remains sometimes constitute a useful source of data for small mammal taxa which could have not been observed/trapped in the field. They also allow diet analysis for predator-prey relationship studies. In these cases, preys are mainly identified and counted from skull/teeth material. Studies on skeletal material recovered from pellets are also undertaken in order to understand the origin and the paleoecological signification of small mammal fossil assemblages (MAYHEW, 1977; KORTH, 1979; DODSON and WEXLAR, 1979; DENYS, 1985, 1986; HOFFMAN, 1988; KUSMER, 1990; ANDREWS, 1990; DENYS *et al.*, 1996; SAAVEDRA and SIMONETTI, 1998). This kind of approach, i.e. taphonomic analysis, consists essentially in counting the skeletal elements representation and assessing their degradations (breakage and digestion) by different kinds of raptor species. It aims to outline criteria for recognizing predators and hence evaluate their consequences on fossil accumulation (ANDREWS, 1990; FERNANDEZ-JALVO *et al.*, 1998).

However, different raptors are able to reject several pellets within 24 hours: some are regurgitated during the day and concentrated at the roost, while others are randomly rejected and spread throughout the hunting territory during nocturnal foraging activities. Indeed, raptor roost pellets only represent a part of the diet (GUÉRIN, 1928; KORTH, 1979; GÉROUDET, 1984). Different studies have also indicated that a same meal can be rejected among several successive pellets. For instance, LOWE (1980) has noted that some bones have been kept in a tawny owl stomach during two days. CARPENTIER (1934) mentioned the simultaneous rejection of three pellets by the eagle owl, which has conducted GUÉRIN (1934) to propose that a heavy meal is rather rejected within several pellets. In fact, such observations are frequently noted for largest preys remains by those who study owls diet (e.g. BAUDVIN *et al.*, 1995; GANEY, 1992; SOUTHERN, 1954), but there is still no quantification of this pattern. In almost all studies dealing with pellets, this loss of skeletal parts is neglected for a number of skeletal elements or prey number calculation. Indeed, when the whole rejected pellets can not be examined, how is this loss of pellets and multirejection of preys likely to affect the representation of skeletal elements data for both ecological or taphonomic analyses? This pellet study is the first attempt to evaluate this problem of prey multirejection and its consequences for diet or taphonomic bias estimations.

Material and methods

Thirty pellets of *Bubo bubo ascalaphus* have been selected for their perfect preservation state from a sample of 300 pellets. They have been recovered in December 1997 in several sites of the palm grove of Krouaa (Beni Abbès region, SW Algeria). The diet of this owl in this region is essentially composed of Gerbilids (genera *Meriones* and *Gerbillus*), which are found by one to three individuals per pellet.

The skeletal content of each pellet has been sorted manually and separated from those of other pellets. The main elements have been counted: long bones (humerus, tibia, femur, radius, ulna), flat bones (scapula and pelvis), molars and incisors, maxilla and mandibles. A skull is considered to be present if more than half of its parts is present

within a pellet, and intact if at least the different parts from nasals to frontals are joined. Teeth digestion intensity has been noted according to FERNANDEZ-JALVO and ANDREWS (1992).

Rodent remains have been separated and counted according to two different size classes: adult/subadult *Meriones* and jerboa (g. *Jaculus*) in class 1 (80-140g) and gerbils (*Gerbillus* spp.) and young *Meriones* (of which small postcranial elements could have been mistaken for gerbil ones) in class 2 (20-60g).

Because only 10% of the whole pellets have been sorted, the probability that one individual was recovered within several of the selected pellets (i.e. that different bones of the same prey was spread over different pellets) was very low. Indeed, the total number of preys is the sum of the number of preys counted from each pellet, whatever the latters are identified by a complete skeleton or one single bone. Relative rates of representation (relative completeness percentage), Ri, have been calculated for each element: they correspond to the total number of elements divided by the number of these elements expected if whole prey skeleton was regurgitated (i.e. 12 for molars, 4 for incisors, 2 for maxilla, mandibles, long and flat bones). Two rates of representation have been calculated: R1, calculated from the minimum number of each kind of preys (R1a for class 1 and R1b for class 2), and R2, according to the number of rejected prey (s) in the pellet (R2a for one prey per pellet, R2b for more). The mean relative representation for each skeletal element, calculated from the number of whole preys is noted Pr. Pr2 is the mean representation calculated from the most numerous elements (which gives the minimum number of individuals, or MNI), as it is usually made from a fossil bone or a pellet assemblage.

Results

Distribution of taxa

The content of each pellet is listed in table 1. The remains of 47 rodents have been recovered (46 gerbilids and one jerboa). Sixteen of these rodents have been rejected alone in a single pellet, 11 pellets contained the remains of two individuals and the last three, of three.

Table 1
Distribution of skeletal parts in each pellet according to the size class of rodents.

	Class 1 rodents																							Class 2 rodents											TOTAL
	one individual/pellet															1-3 preys/pellet								1 prey/p		1-3 preys/pellet									
N°/Pellet	1	3	5	6	7	8	11	12	14	15	16	17	22	28	9	10	21	29	2	4	26	27	19	25	13	18	20	21	24	30	3	4	26	27	30
Humerus	1	2	1	2	2			2	2	2		2	2	1	2	4	2	2	1		1	2	1	2	5	1	2	4	4	1	1	2	1	3	60
Tibia	2	2	2	2	2	1	1	2	2	2	2	2	2	1		1	2	2	1	2	2	2		2	6	2	2	1	4	2	2	2		4	64
Femur	2	2	2	2	2	2	1	1	2	2	2	2	1	2		2	3	2	1	2	2	2	1	1	6	3	3	4	4	3	2	2	2	4	74
Radius	2	2	1	2	2		1	2	2	2		2	2	1	3	4	3	3		1	1	2	1	2	3	1	2	3	4	1	1	1	2	4	63
Ulna	2	2	1	2	2	1		2	2			2	2	1	3	4	3	3	1	1		2		2	5	1	2	5	4	2		2	1	4	64
Scapula	1	2		2	1	2		2	1	1		2	1	1	2	3	3	3	2	2	2			1	2	1	2	2	3		1	1	1	3	50
Pelvis	1	2	2	2	2			2	2	2	2	2	2	1	1	2	3	2	2	2	1	2		2	6	3	2	2	4	3	2	1	1	4	67
Maxilla	2	2	2	2	2	2	2	1	2	2	2		2	2	4	2	2	4	2		1		2	2	4	2	2	1	4	3		2	2	2	66
Mandible	2	2	1	2	2	2	2	2	2	2	2		2	2	4	2	3	4	2		1		1	2	4	1	2	1	3	3		1	2	2	63
up. molars	*6*	*6*	*6*	*6*	*6*	*6*	*6*	*3*	*6*	*6*	*6*		*6*	*6*	*12*	*6*	*6*	*12*	*6*		*3*		*4*	*6*	*8*	*2*	*6*	*2*	*9*	*6*		*1*	*3*	*3*	170
low. molars	*6*	*6*	*3*	*6*	*6*	*6*	*6*	*6*	*6*	*6*	*6*		*6*	*6*	*12*	*6*	*8*	*11*	*6*		*3*		*3*	*5*	*10*	*1*	*6*	*1*	*9*	*6*		*4*	*3*	*6*	175
total molars	12	12	9	12	12	12	12	9	12	12	12		12	12	24	12	14	23	12		6		7	11	18	3	12	3	18	12		5	6	9	345
up. incisor	2	2	2	2	2	2	2	1	2	2	2		2	2	4	2	2	4	2		1		1	2	3	2	2	2	4	3		2	2	2	65
digested	*2*	*2*		*2*	*2*	*2*	*1*	*2*		*2*				*1*															*2*			*2*			20
low. incisor	2	2	1	2	2	2	2	2	2	2	2		2	2	4	2	3	4	2		1		1	2	3	1	2	1	4	3		1	2	2	63
digested				*2*	*2*	*1*	*2*																												7
total incisors	6	6	3	6	6	6	5	5	4	6	4		4	5	8	4	5	8	4		2		2	4	6	3	4	3	10	6		5	4	4	135
skull	1	1	1	1	1	1	1	1	1	1	1	0	1	1	2	1	1	2	1	0	1	0	1	1	2	1	1	1	2	1	0	1	1	1	34
complete skull	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*0*	*1*	*1*	*1*	*0*	*1*	*0*	*2*	*0*	*1*	*2*	*1*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*1*	*0*	*1*	*0*	*0*	*0*	*0*	*0*	*19*
N/class 1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	1	1	1	1									*1*	*1*	*1*	*1*	26
N/class 2																			*1*	*1*	*1*	*2*	1	1	3	2	2	3	2	2	1	1	1	2	21
total rodent(s)/pellet	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*1*	*2*	*2*	*2*	*2*	*2*	*2*	*2*	*3*	*1*	*1*	*3*	*2*	*2*	*3*	*2*	*2*	*2*	*2*	*2*	*3*	47

	Rodent size :				Number of prey/pellet :				TOTAL		
	Class 1		Class 2		1 prey/pel.		> 1 preys/pel.				
element	N	R1a	N	R1b	N	R2a	N	R2b	N	Pr	Pr2
Humerus	33	63,5	27	64,3	22	68,8	38	61,3	60	63,8	81,1
Tibia	37	71,2	27	64,3	27	84,4	37	59,7	64	68,1	86,5
Femur	39	75,0	35	83,3	27	84,4	47	75,8	74	78,7	100,0
Radius	38	73,1	25	59,5	24	75,0	39	62,9	63	67,0	85,1
Ulna	36	69,2	28	66,7	21	65,6	43	69,4	64	68,1	86,5
Scapula	33	63,5	17	40,5	17	53,1	33	53,2	50	53,2	67,6
Pelvis	37	71,2	30	71,4	24	75,0	43	69,4	67	71,3	90,5
total postcr.	253	69,5	189	64,3	162	72,3	280	64,5	442	67,2	85,3
Maxilla	40	76,9	26	61,9	29	90,6	37	59,7	66	70,2	89,2
Mandible	41	78,8	22	52,4	28	87,5	35	56,5	63	67,0	85,1
upper molar	120	76,9	51	40,5	85	88,5	85	45,7	170	60,3	76,6
lower molar	121	77,6	53	42,1	83	86,5	92	49,5	175	62,1	78,8
total molars	241	77,2	104	41,3	168	87,5	177	47,6	345	61,2	77,7
upper incisor	40	76,9	25	59,5	28	87,5	37	59,7	65	69,1	87,8
digested up. inc.	16	40,0	4	16,0	16	57,1	4	10,8	20	30,8	27,0
lower incisor	41	78,8	22	52,4	28	87,5	35	56,5	63	67,0	85,1
digested low. inc.	7	17,1	0	0,0	7	25,0	0	0,0	7	11,1	9,5
total incisors	81	77,9	47	56,0	56	87,5	72	58,1	128	68,1	86,5
digested incisors	23	28,4	4	8,5	23	41,1	4	5,6	27	21,1	36,5
Skull	21	80,8	13	61,9	15	93,8	19	61,3	34	72,3	91,9
MNP/MNI	26 / 21		21 / 18		16 / 15		31 / 24			47	37

Table 2
Representation of the different skeletal parts according to the size (class 1 and 2 : R1a and R1b) and the number of prey per pellet (1 and 2-3 : R2a and R2b).

Twenty-six rodents have been classified in class 1. The remains of 14 of them have made up the content of a similar number of single-prey pellets. Nineteen preys of the class 2 were concentrated in 10 2/3-prey pellets, *vs* two in a single-prey pellet.

Bone and teeth representation

Rates of representation according to size class and number of prey per pellets are detailed in table 2.

Skull and teeth

Thirty-four skulls have been recovered (72% of the total preys). Among them, 21 belong to the 26 class 1 rodents (R1a = 81%), and 15 belong to single-prey pellets out of 16 (R2a = 94%). Only 13 skulls belong to the 21 detected class 2 rodents (R1b = 62%) and 19 to the 31 preys found in pellets with remains of 2 or 3 individuals (R2b = 61%).

Nineteen skulls were found intact: 11 recovered from the 16 single-prey pellets, and 17 being from class 1 rodents. Few maxilla or mandibles have lost their teeth: the consequences are a best molar representation in single-prey pellets (R2a = 87.5%) compared with 2/3- prey pellets (R2b = 47.6%), as well as for class 1 (largest) rodents (R1a = 77.2%) compared with class 2 rodents (R1b = 41.3%).

Incisors are slighlty more numerous than molars, particularly for class 2 rodents (R1b = 56%) and several-prey pellets (R2b = 58.1%), but the best representation remains for class 1 incisors (R1a = 77.9%) and within single-prey pellets (R2a = 87.5%).

Postcranial elements

The discrepancies of the mean representation values according to the kind of preys and pellets are less important for whole postcranial bones than teeth: R1a = 69.5% against 64.3% for R1b, but the single-prey pellets have provided 72.3% of the expected number of bones against 64.5% for the others (tabl. 2). The variation of skeletal element representation according to the size of preys is especially important for radius (R1a = 73.1%, R1b = 59.5%) and scapula (R1a = 63.5%, R1b = 40.5%). According to the number of preys per pellet, the discrepancies are important for tibia only (R2a = 84.4%, R2b = 59.2%).

Femurs are the best represented elements in all cases (Pr = 78.7%). The lowest rate of completeness is that of the scapula (between 40.5%

and 63.5%, Pr = 53.2%). Other bones are represented from around 60% to 75% of their theorical number.

Completeness of individuals

When the whole skeleton is considered, the representation of individuals is very variable according to the preys and the number of preys within the pellets.

– In single-prey pellets, 11 prey skeletons have only lost 23 postcranial bones (15% of total), one maxilla and two mandibles (7%). Only one individual is represented by all its postcranial parts without the skull (pellet 17), and 4 are mainly represented by their cranial parts, with three or six long or flat bones out of 14 (pellets 8, 11, 16 and 19).

– In several-prey pellets, three of class 1 rodents have no skull, but the main part of their postcranial bones (pellets 4, 10, 27). One prey is represented by its skull with only two long bones (pellet 9), and a case is intermediate (one mandible with 5 postcranial bones: pellet 23). Seven preys out of the 19 class 2 rodents in these pellets are only represented by their postcranial bones (pellets 2, 13, 18, 12, 21, and 27) and one by one maxilla and mandible with a pelvis (pellet 30). The smallest gerbils (*Gerbillus nanus*, 3 individuals) are represented in two cases by only one femur (pellet n° 20 and 30) with one broken maxilla and a mandible (pellet 30). Other gerbils are represented by a femur and a broken pelvis in one case (pellet 18), and by a single ulna in another one (pellet 21).

Digestion

Twenty-seven incisors show digestion traces (Pr = 21.1%). Among them, 23 are from class 1 rodents in single-prey pellets. Twenty are upper incisors (74.1%). Indeed, 40% of class 1 upper incisors are digested (n = 16) *vs* only 16% of class 2 incisors (n = 4). All digested lower incisors are those of class 1 rodents (R1a = 17,1%).

The digestion intensity is very light (grade 1), except for three teeth (grade 2 and 3). No molar shows any digestion.

Discussion

These results outline that losses of bones/skulls follow a peculiar pattern. The most important loss of elements is either due to the absence of skull (11 cases) or the absence of more than 50% of postcranial bones, while the skull is present (4 cases). Four individuals are represented by less than 3 bones alone in the pellets. Only one case is intermediate (with both high loss of cranial and postcranial bones). So, this absence of skull or postcranial parts is not due to digestion because bones are not particularly digested, except in two cases when two postcranial bones are the only remains of a single individual.

Selective decapitation observed in several raptor preys may sometimes explain this lack of skulls, but it concerns essentially the largest preys. *Bubo bubo ascalaphus* prey decapitation has been noted when feeding owlets: adults consume the head and let the body to their youngs. But in this case, pellets are mainly constituted by prey skulls (VEIN and THÉVENOT, 1978).

Indeed, a frequent multirejection of prey skeletal elements seems to be the most logical explanation. Two/three-prey pellets are particularly affected, and this deficiency in skulls underestimates the presence of the smallest preys if calculations are made from the dental/cranial material only: 13 preys are counted against 21 from postcranial elements (-33%), while this underestimation is less than 20% for the largest rodents (21 preys against 26). Adult *Meriones* and other large preys could be sufficiently large to be eaten one by one and digested in consequence. On the contrary, other preys are too light to constitute a unique meal alone: so, several preys have to be eaten to constitute a sufficient meal for the owl. As the skeletal volume of several small preys is more important than that of a large prey, a part of such small prey could then be rejected within a second pellet.

The volume of the skull is relatively important when compared with postcranial bones, and this could lead to an easy separation of the skull from the other bones when a second pellet must be elaborated by the owl. This can explain the major pattern observed in our samples (loss of the skull or postcranial elements). The rejection of different pellets is not necessarily simultaneous: the two cases where only a few bones identified an individual (pellets 18 and 20), they were more

heavily digested than other intact preys in the same pellet, certainly because of a retention in the stomach and a longer digestion.

The same law of rejection could apply if a prey is too large (e.g. pellet 11). As rodents are often decapitated when they are too large to be swallowed, one may think that if the skull and the skeleton form a too large volume for a single potential pellet, part of the bones would remain in the stomach to be rejected with the next pellet (with or without another prey). Data about *Tyto alba* largest preys in South Africa tend to confirm these observations (LAUDET, 2000). Additionally, because their skull seems to be more resistant than that of other preys (COETZEE, 1963; DENYS *et al.*, 1996), gerbilids could be particularly affected by these kinds of bias.

We can also note that teeth from single-prey pellets are more frequently digested than others: perhaps this ideal size of prey (or digestible parts) would favour prey digestion.

Consequences of these observations and hypotheses that can be drawn from them are multiple:

1) Counting preys from skull elements only is not exhaustive. The fact that different kinds of prey are not rejected in the same way can affect significantly their relative frequencies in the diet, if calculated from skulls only. The error will be dependent on the completeness of the pellets recovering. For instance, the diet of our owl (s) calculated from skulls is 62% of class 1 (n = 21) and 38% (n = 13) of class 2 rodents, while the same rates, calculated from postcranial elements pellet by pellet are 55% (n = 23) and 45% (n = 21), respectively. If the different postcranial elements are mixed and considered as a whole, the proportion of preys is quite similar to the precedent one: 54% (n = 21) of class 1 and 46% of class 2 (35 femurs, n = 18).

2) These results could also affect data in usual taphonomic analyses. Until now, taphonomic data on pellets are relatively rare, and most analyses have been made on small samples of pellets (generally around 30-50 pellets, ANDREWS, 1990), recovered from natural settings for which the number of swallowed preys is unknown. Our results show that losses of skeletal elements are not only due to digestion – which rate is useful for recognizing predators – but can vary according to the kind of preys and the quality of the recovering. Multirejection of prey hypothesis suggests that most teeth are rather lost by non-recov-

Localities	Beni Abbès	Qatar (1)	Honaine (2)	Aflou (2)	Igli (2)	Kerzaz (2)
Humerus	81,1	98,1	43,4	57,4	31,5	18,2
Tibia	86,5	67,3	44,9	100	100	100
Femur	100,0	94,2	50	98,6	84,4	66,4
Radius	85,1	88,5	14,2	20,4	9,5	7,3
Ulna	86,5	90,4	15,2	31,7	17,5	10
Scapula	67,6	80,8	8,2	16,7	5,9	3,6
Pelvis	90,5	86,6	42,2	86,8	64,4	48,2
Total postcranial	85,3	86,6	31,2	58,8	44,7	36,2
Maxilla	89,2	82,4	48,7	47,4	40,6	31,8
Mandible	85,1	80,8	99,9	83,4	99,6	99,1
Molar	77,7	23,1				
Incisor	86,5	32,7				
MNI	37	26	548	442	341	130

Table 3
Representation (in %) of skeletal parts from *Bubo bubo ascalaphus* pellets. The minimum number of individuals (MNI) was calculated from the most abundant recovered bone elements.
(1) from ANDREWS (1990), (2) from DENYS *et al.* (1996).

ering of pellets (where skulls or bones have been rejected), than by digestion only. For example, our sample has been subjected to a mean loss of 33% of bones and 39% of molars: these high losses are mainly due to the lack in our sample of the pellets where these missing cranial or postcranial parts have been "multirejected". Indeed, these results could explain the important differences observed between taphonomic studies dealing with raptors preys, and particularly *Bubo bubo ascalaphus* ones (tabl. 3).

Additional analyses should be performed to have a better idea of potential biases associated with preys and skeletal elements within pellets. These biases appear more complex than previously thought. The relative size of a predator and its preys could be the main factor explaining the distribution of skeleton parts within pellets. The size of the first prey eaten will also determine the choice of hunting for a second prey or not (thus increasing or not the probabilities of rejec-

tion of a second pellet). This also means that timing and locations of foraging activities of preys are also important factors.

In conclusion, if these observations are confirmed by further studies, they could help precise diet estimations and ecological conclusions in bringing correction factors for prey species representation. Also, they will enable to better predict taphonomic biases in fossil rodent assemblages. However, we encourage the use of postcranial bones per pellet to accurately estimate the number of preys eaten, particularly when studying small samples taken in owl roosts, and if the size spectrum of preys is relatively large.

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Dynamique de l'abondance et reproduction de la population de *Gerbillus nigeriae* (Rodentia, Gerbillinae) dans la ferme de Kolo (Niger)

Adamou Nomao

Jean-Claude Gautun

Introduction

Dans le Sahel, les cultures de céréales pluviales comme le mil ou le sorgho fournissent la base de l'alimentation des populations rurales. Le bon déroulement du cycle végétal de ces cultures vivrières revêt donc une importance primordiale. Dans les conditions de leur culture en milieu paysan, les rendements de ces céréales sont ordinairement très faibles et se situent aux environs de 200 à 300 kg / ha en moyenne sur les 3,2 millions d'hectares de mil cultivés au Niger (BEZANÇON *et al.*, 1995). De ce fait, chaque facteur réduisant les rendements de ce vivrier est ressenti comme une forte pénalisation par le paysan. Parmi l'ensemble des contraintes sahéliennes limitant la production agricole pluviale certaines, telles les conditions climatiques, sont incontrôlables par l'homme. En revanche d'autres, telles les contraintes phytosanitaires, peuvent être plus ou moins contrôlées par les paysans,

à conditions que ces derniers soient formés et informés. Parmi ces contraintes phytosanitaires, on peut mentionner les mauvaises herbes (dont le *Stiga*), les maladies (virus et champignons parasites), les Insectes (foreurs des tiges, punaises, criquets), les Oiseaux (surtout les *Quelea*) et les Rongeurs (Murinae, Gerbillinae et Dipodidae).

Concernant les rongeurs sahéliens et pour l'ensemble de la zone comprise entre le Tchad et le Sénégal, GAUTUN (1994) et SICARD *et al.* (1995) mentionnent la nature et le type de dégâts observés sur le mil, principalement des dégâts sur les semis dans les poquets. Les auteurs en sont *Desmodilliscus braueri, Gerbillus* sp. et *Jaculus jaculus.*

Pour le Sénégal, des informations sont rapportées par HUBERT (1979), POULET (1983), POULET *et al.* (1979), POULET and DUPLANTIER (1983), qui mentionnent la présence de Gerbillinae, essentiellement *Taterillus* sp., dans et aux alentours des campements, des greniers et des champs de mil. Au Burkina Faso des observations similaires ont été faites par GAUTUN *et al.* (1985) et SICARD *et al.* (1988) concernant les Gerbillinae dans le nord-est du pays. Au Tchad, FISCHER and MURPHY (1987) se sont intéressés à la part des différents groupes qui jouent un rôle dans les contraintes phytosanitaires sur le mil. L'impact des rongeurs y est assez faible (2 %) par suite de la seule prise en compte des dégâts sur les épis alors que les dégâts les plus importants sont faits sur les semis comme l'a signalé BROOKS (1992).

Au Niger, LEWIS et BAROCH (1979), dans leur étude sur les rongeurs nuisibles aux cultures dans la région de Tahoua, rapportent des dégâts dus aux gerbilles (*Gerbillus agag, Taterillus gracilis*) et aux gerboises (*Jaculus jaculus*) au moment des semis, si importants qu'ils impliquent de semer à nouveau, quelquefois à plusieurs reprises. D'après les résultats d'expérimentations réalisées à Kornaka et à Ouallam, BELKO (1996) précise que les principaux rongeurs impliqués dans la destruction des semis de mil sont des Gerbillinae appartenant aux genres *Desmodilliscus* (*D. braueri*) et *Gerbillus* (*G. nigeriae, G. henleyi, G. nancillus*). Dans la partie la plus aride de la zone de culture du mil, la destruction des semis est aussi due aux Gerboises (*Jaculus jaculus*). Mais quelle que soit la localité choisie dans la zone de culture du mil, l'espèce de rongeur constamment présente et la plus abondante est *Gerbillus nigeriae.*

C'est dans l'appui à cette démarche de lutte paysanne que se place notre étude dont l'objectif est de mieux connaître la biologie et l'écologie des rongeurs sahéliens nuisibles afin d'aider à réduire leurs dégâts, de façon la plus efficace et la moins onéreuse possible.

Pour déterminer les paramètres biologiques et écologiques nécessaires à un contrôle efficace, nous avons entrepris, entre juin 1997 et mai 1999, le suivi d'une population pilote de *Gerbillus nigeriae* dans la ferme de Kolo, aux environs de Niamey.

Le site d'étude

Localisation

La ferme de Kolo (13°15'N et 2°18'E) est un domaine de 50 ha à 35 km à l'est de Niamey. Elle est située dans la vaste zone agro-écologique propice à la culture du mil qui couvre la partie du Niger au sud de l'isohyète 250 mm. Les sols de la ferme de Kolo sont des sols sableux faiblement argileux qui conviennent particulièrement bien à la culture du mil.

Climat

La ferme de Kolo est située dans la zone climatique sud-sahélienne (SAADOU, 1990). La température moyenne varie de 24 à 34 °C durant l'année. Les précipitations sont en moyenne comprises entre 400 et 650 mm et la saison des pluies d'une durée de 4 à 5 mois s'étend de mai à septembre. La saison sèche qui couvre le reste de l'année peut être découpée en :

– une période humide et chaude entre octobre et novembre, avec des températures minimale moyenne de 21,3 °C et maximale moyenne de 37,1 °C;

– une période sèche et fraîche entre décembre et février, avec des températures minimale moyenne de 17,2 °C et maximale moyenne de 33,6 °C;

– une période sèche et chaude entre mars et mai, avec des températures minimale moyenne de 25,2 °C et maximale moyenne de 40,4 °C.

Pour ce qui concerne plus particulièrement la période de notre étude, entre 1997 et 1999, la pluviométrie et les saisons humides y ont été très variables en intensité et en durée :

– l'année 1997, avec 326,8 mm de pluies réparties sur 4 mois, 3 mois humides en juin, juillet et août 1997, mais un seul mois à pluviométrie réellement excédentaire par rapport au diagramme ombrothermique, doit être considérée comme une année sèche à très fort déficit pluviométrique ;

– l'année 1998, avec 848,5 mm de pluies réparties sur 5 mois et les mêmes 5 mois humides, doit être considérée comme une année humide à très fort excédent pluviométrique. Il convient de noter que le très fort excédent pluviométrique provient surtout de pluies anormalement fortes observées fin août et début septembre ;

– le début de l'année 1999 qui seul intéresse notre étude, est caractérisé par l'apparition de pluies assez précoces en mai (30,8 mm).

Matériel et méthodes

Le suivi de la dynamique de la population de *Gerbillus nigeriae* a été fait selon un protocole classique de capture-marquage-recapture (CMR). De forme rectangulaire, la grille de piégeage mesure 190 m x 150 m et couvre une surface brute de 2,85 ha. Elle se compose de 13 lignes espacées de 12,5 m comportant chacune 39 postes de piégeage espacés de 5 m dotés chacun d'un piège-couloir grillagé. Les paramètres retenus pour la construction de cette grille de piégeage ont été définis au cours d'une expérimentation comparant l'efficacité de dispositifs de piégeage différant en taille, forme, disposition des lignes et concentration de pièges. Nous avons retenu le dispositif qui nous a permis d'obtenir le pourcentage de captures / recaptures le plus élevé avec des sessions de piégeage de durée minimale et un nombre de pièges compatible avec les possibilités du laboratoire. La durée de 4 jours de piégeage (4 fois 24 heures) permet la capture de plus de 90 % des nouveaux individus qui composent l'échantillon mensuel de la population de *Gerbillus nigeriae*.

Les pièges utilisés sont des pièges-couloirs grillagés à socle en bois de dimensions 33 x 8 x 8,5 cm. Ils sont appâtés avec une gousse d'arachide enrobée de pâte d'arachides grillées. Ils restent tendus durant 4 jours consécutifs et ils sont contrôlés et appâtés de nouveau chaque matin si nécessaire. Une nouvelle application générale de pâte d'arachide est faite dans l'après-midi du second jour du piégeage. De juin 1997 à mai 1999, nous avons effectué 24 sessions mensuelles de piégeage. L'effort total de piégeage a été de 44 368 jours-pièges.

À chaque session de piégeage, les nouveaux individus non marqués ou les premières recaptures des individus marqués les mois antérieurs sont anesthésiés à l'éther avant d'être pesés et mesurés. Le sexe et le développement sexuel externe sont enregistrés. Les nouveaux individus sont numérotés par amputation de phalanges (au maximum une phalange par main ou pied). Lorsque les rongeurs sont des recaptures des jours précédents de la même session de piégeage, ils ne sont pas anesthésiés mais seulement identifiés par leur numéro. Chaque rongeur est ensuite relâché à son poste de capture d'où il est suivi visuellement jusqu'à l'entrée dans son terrier afin de le protéger des attaques fréquentes de rapaces.

L'abondance de la population de *G. nigeriae* a été estimée par deux méthodes différentes :

– selon la méthode du « Lincoln-Index » modifiée par Schnabel, citée par SEBER (1973) et analysée sur le Campagnol par MEUNIER et SOLARI (1979) ;

– selon la méthode du calendrier de présence ou « Minimum Number Alive (MNA) » de KREBS *et al.* (1966) qui prend en compte le nombre de rongeurs effectivement capturés au cours de la session de piégeage, augmenté du nombre d'individus supposés présents dans la grille. Ces derniers sont des anciens individus qui ne sont pas repris au cours de la session de piégeage considérée mais qui seront recapturés au cours des sessions suivantes.

Le classement des individus selon les classes adulte ou jeune, tient compte des résultats sur la reproduction obtenus en élevage et des observations faites sur les individus capturés à Kolo. Les femelles sont adultes vers l'âge de 2 mois, elles atteignent alors un poids corporel de 17 g (poids des plus jeunes femelles trouvées gestantes). Les mâles sont adultes également vers l'âge de 2 mois, ils atteignent alors

un poids corporel de 15 g (testicules bien développés en position scrotale *et* vésicules séminales bien développées et remplies de liquide vésiculaire).

Les données précises sur la reproduction ont été recueillies lors de l'autopsie de spécimens capturés en dehors, mais à proximité, de la grille de marquage. Les femelles actives sont des femelles adultes gestantes, les mâles actifs sont des mâles adultes dont les testicules ont une surface de 100 mm^2 et les vésicules séminales ont une surface de 40 mm^2.

Résultats

Résultat du piégeage et nature du peuplement de rongeurs

Au cours de la période d'étude qui va de juin 1997 à mai 1999, nous avons capturé dans la grille de piégeage 731 rongeurs, soit un rendement de 16,5 rongeurs / 1 000 jours-pièges. Si l'on tient compte des rongeurs collectés sur la ferme de Kolo mais en dehors de la grille de piégeage, le peuplement de rongeurs se compose de 9 genres et d'au moins 9 espèces. Les Muridae sont représentés par 6 genres dont trois sont des Murinae (*Mastomys, Myomys* et *Nannomys*) qui représentent 61 spécimens (14,3 % des captures totales) et trois sont des Gerbillinae (*Desmodilliscus, Gerbillus* et *Taterillus*) qui représentent 352 spécimens (82,6 % des captures totales). Les autres individus capturés appartiennent à trois familles, les Sciuridae (5 individus de *Xerus erythropus* et 1,2 % des captures), les Cricetomyidae (1 individu de *Cricetomys gambianus* et 0,2 % des captures) et les Myoxidae (7 individus de *Graphiurus* sp. et 1,5 % des captures). Les *Graphiurus* ont été capturés dans les toits des poulaillers désaffectés, les *Xerus erythropus* et le *Cricetomys gambianus* ont été capturés au cours de battues.

Le rongeur qui domine largement le peuplement est la gerbille commune du Nigeria, *Gerbillus nigeriae* avec 347 individus (81,5 % des captures). La détermination spécifique de cette gerbille est faite sous réserve des résultats de l'analyse des caryotypes en banding. En

effet, différents auteurs dont VOLOBOUEV *et al.* (1988) et MÉRIGUET (1999), ont constaté que sur son aire de répartition (de la Mauritanie au Niger), *G. nigeriae* présente une si grande variabilité dans son caryotype (2 n compris entre 62 et 74 chromosomes et Nfa compris entre 120 et 144) qu'elle peut faire douter de l'unicité spécifique de ce genre.

À Kolo, les spécimens de *G. nigeriae* sont de teinte ocre-orangé pâle à la partie supérieure et blanc pur de la bouche à l'anus, à la partie ventrale. La longueur moyenne tête et corps (T + C) varie de 90 à 110 mm, la longueur moyenne de la queue, sans le pinceau terminal, varie de 110 à 130 mm (120 % de T + C), la longueur moyenne du pied (avec griffes), dont la sole plantaire est poilue, varie de 23 à 26 mm, la longueur moyenne de l'oreille varie de 13 à 15 mm. Le poids moyen des adultes varie entre 20 et 35 g. Les spécimens de Kolo possèdent une formule chromosomique à 2 n compris entre 70 et 74 chromosomes et Nfa compris entre 136 et 144.

Variation de l'abondance de Gerbillus nigeriae

Estimées par l'une ou l'autre des deux méthodes mentionnées ci-dessus, les deux séries de valeurs représentant l'abondance mensuelle sont fortement corrélées (R de Spearman = 0,93 ; $p < 10^{-3}$). Sauf en mars 1998, la valeur moyenne de l'abondance mensuelle calculée par la méthode de Schnabel est toujours supérieure à celle obtenue par le calendrier de présence. Par la méthode de Schnabel, l'estimation globale est en moyenne 34 % plus élevée avec un intervalle de variation compris entre 15 % et 51 %. À l'exception, d'une part, des mois de juillet, novembre et décembre 1997 et, d'autre part, des mois de janvier à mai 1999, pour lesquels la correction des dénombrements mensuels bruts par la reprise postérieure d'anciens marqués n'a pas pu être faite par suite de la disparition presque totale de la population entre septembre et novembre 1998 (pourcentages d'anciens dans l'échantillon de décembre 1998 + janvier 1999 = 16 %, contre 67 % en 97 / 98 et 62 % en 1999/2000), l'estimation faite par le calendrier de capture se situe toujours dans l'intervalle de confiance de l'estimation faite par la méthode de Schnabel.

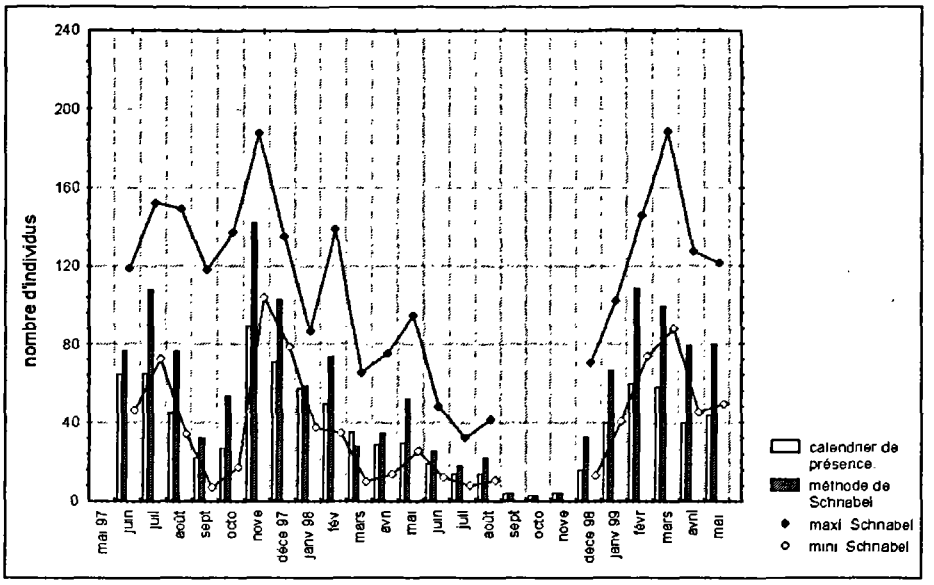

Figure 1
Abondance mensuelle de la population de *Gerbillus nigeriae* à Kolo, estimée par la méthode de Schnabel et par le calendrier de présence.

Malgré ces différences, nous avons maintenu l'estimation par le calendrier de présence, d'une part parce que cela nous permet de vérifier la cohérence des estimations obtenues avec la méthode de Schnabel et d'autre part parce que cela nous permet de détecter d'éventuelles périodes où les *G. nigeriae* se montreraient réfractaires au piégeage (cas de la période de septembre à novembre 1998 et dans une certaine mesure de mars 1998), lorsque l'alimentation naturelle, disponible en très grande quantité, concurrence fortement les appâts des pièges ou bien lorsque les conditions environnementales (températures trop élevées de fin de saison sèche et chaude, travaux de nettoyage des résidus de récolte ou labours avant les semis) affectent les déplacements et conduisent au confinement des rongeurs dans leur terrier.

Pendant la période de juin 1997 à mai 1999 (fig. 1), le niveau d'abondance de la population de *G. nigeriae,* estimé par la méthode de Schnabel, a présenté de grandes variations, intra-annuelles et inter-annuelles, dont les caractéristiques sont les suivantes :

– de hauts niveaux d'abondance entre juin et août 1997 avec un pic à 107 individus en juillet (intervalle de confiance 72 à 152), puis une nouvelle période d'abondance entre octobre 1997 et février 1998 avec en novembre 1997 un pic à 142 individus (intervalle de confiance 104 à 188). En 1998, on constate une seule période d'abondance entre avril et mai avec un pic en mai 1998 à 52 individus (intervalle de confiance 25 à 95). En 1999, on note une période d'abondance qui couvre la période allant de janvier à mai 1999 avec un pic à 106 individus (intervalle de confiance 74 à 146);

– des faibles niveaux d'abondance, dont l'un ponctuel en septembre 1997 avec 32 individus (intervalle de confiance 7 à 118), un autre ponctuel en mars 1998 avec 28 individus (intervalle de confiance 10 à 66) puis une grande période de faible abondance entre juin et décembre 1998 où le minimum de 2 à 3 individus (estimé par le calendrier de présence) s'est maintenu durant les mois de septembre à novembre 1998.

Même si on ne met pas en évidence de périodicité strictement reproductible du cycle d'abondance, on peut préciser une tendance vers les plus fortes abondances durant la saison sèche avec un glissement du début vers la fin de la saison sèche (novembre à février 1997-98 et janvier à mai 1998-99) et une tendance vers les plus faibles abondances en fin de saison des pluies avec aussi un glissement vers le début de la saison sèche (septembre 1997 et septembre à novembre 1998).

Modalités de la reproduction de G. nigeriae

Activité reproductrice des femelles et production de jeunes

Les femelles de *G. nigeriae* ont des périodes de reproduction dont le démarrage se fait durant la saison des pluies et dont la durée et l'intensité sont variables selon les années (fig. 2). En 1997, la saison de reproduction a débuté en août / septembre et s'est s'achevée, après avoir duré 4 mois, en novembre. En 1998, la saison de reproduction a également commencé en septembre, elle est restée très forte en décembre et s'est prolongée à un niveau soutenu jusqu'en avril 1999,

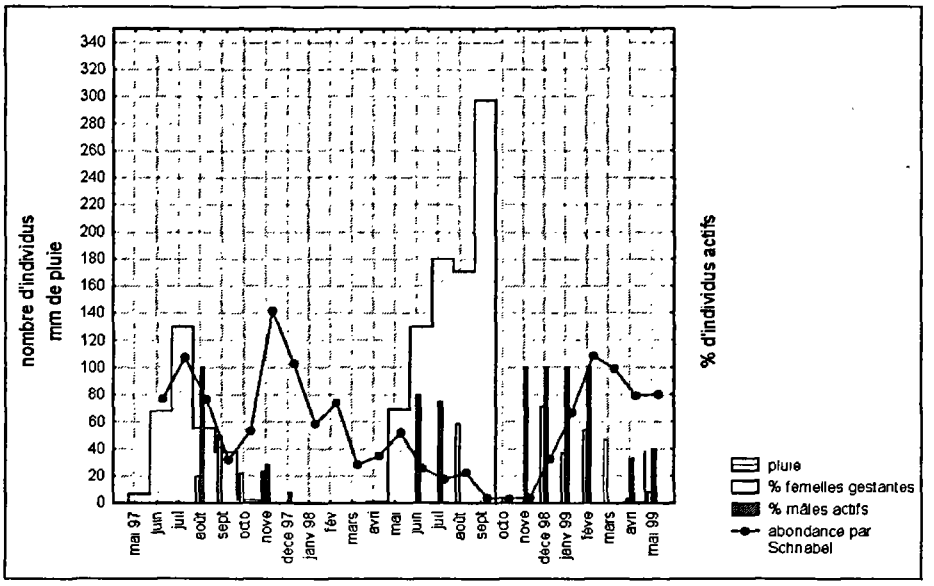

Figure 2
Évolution mensuelle de l'activité sexuelle des mâles, de la reproduction des femelles et de la proportion de jeunes de *Gerbillus nigeriae*, en liaison avec les saisons des pluies.

puis faible en mai 1999. La saison de reproduction 1998 a été nettement plus longue que celle de 1997 puisqu'elle a été effective durant 7 mois. Notons que la raréfaction de *G. nigeriae* entre octobre et décembre 1998 ne nous a pas permis de savoir si des femelles adultes étaient actives durant cette période.

L'apparition périodique de jeunes individus dans les échantillons mensuels confirme la discontinuité de l'activité de reproduction chez les femelles. Les jeunes qui sont présents dans les échantillons mensuels de novembre 1997 à mars 1998 correspondent à la saison de reproduction observée entre août et novembre 1997. Les jeunes qui sont présents dans les échantillons mensuels de janvier à mai 1999 correspondent à la période de reproduction observée à partir de décembre 1998.

L'absence de jeunes dans les échantillons mensuels de novembre à décembre 1998 n'infirme pas le pic de reproduction en août 1998, elle s'explique par la disparition de la population de *G. nigeriae* durant cette période, consécutivement aux très fortes pluies de fin août –

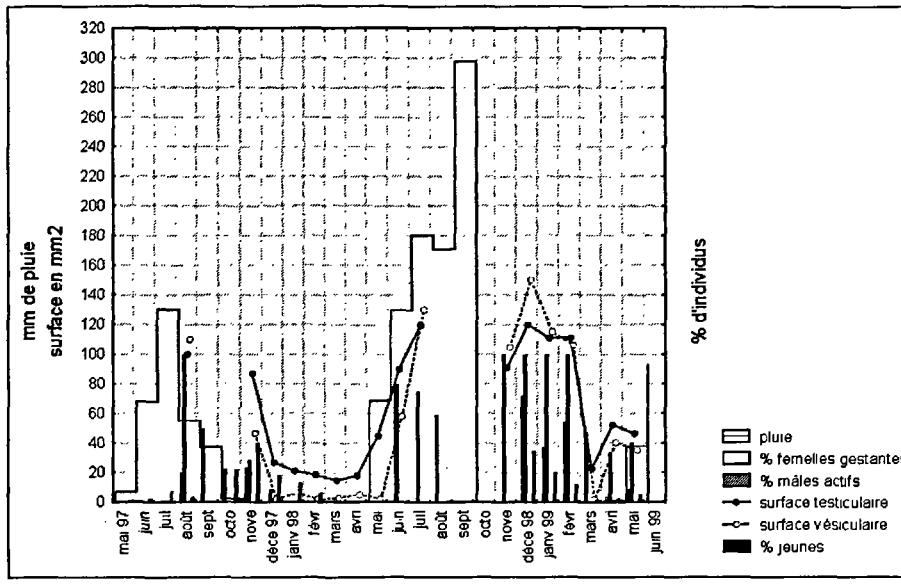

Figure 3
Évolution de l'abondance et de l'activité reproductrice de *Gerbillus nigeriae* en liaison avec les saisons des pluies.

début septembre. En revanche, la présence de jeunes individus dans les trois premières sessions de piégeage (juin – août 1997) nous conduit à faire l'hypothèse que des femelles ont été en reproduction au cours de la période d'avril à juin 1997 et donc que comme en 1999, la saison de reproduction 1996-1997 a pu se prolonger jusque dans la saison sèche et chaude.

Activité sexuelle des mâles

L'absence de données en juillet, août, octobre et novembre 1997, puis en septembre, octobre et novembre 1999, nous empêche de conclure aussi formellement que pour les femelles pour ce qui concerne le déroulement global de l'activité sexuelle des mâles de *G. nigeriae* durant la période d'étude. Comme pour les femelles, on constate que cette activité sexuelle n'est pas permanente, qu'elle présente des périodes de forte activité sexuelle et des périodes de repos sexuel (fig. 3).

Les périodes où l'on rencontre des mâles en activité sexuelle se situent en août et en novembre 1997 avec probablement, si l'on tient compte de la présence de femelles gestantes sans discontinuité durant la même période, une continuité de l'activité en septembre et octobre, puis en juin et juillet 1998, puis de novembre 1998 à février 1999. Les périodes de repos sexuel chez les mâles se situent entre décembre 1997 et mai 1998, puis en mars 1999.

Discussion

Sans présenter une nette saisonnalité, nous avons pu constater que l'abondance de la population de *G. nigeriae* n'est ni stable au cours de l'année ni régulière d'une année à l'autre. Cette constatation est classique lorsque l'on étudie des populations de rongeurs sahéliens en situation non commensale, comme cela a déjà été mentionné par POULET (1981) ou HUBERT (1982) au Sénégal, par GAUTUN (1985) ou SICARD (1987) au Burkina Faso, par MCDONALD et MCDONALD (1992) au Tchad, et que ce soit à propos des Murinae (*Arvicanthis niloticus, Mastomys* sp., *Acomys* sp.) ou des Gerbillinae (*Taterillus* sp. ou *Gerbillus nigeriae*).

A Kolo, on a constaté que les *G. nigeriae* présentent un cycle annuel d'abondance biphasique et déséquilibré, avec une première période d'abondance moins intense en niveau et en durée, calée en fin de saison sèche / début de saison des pluies (juin / juillet 1997 ou mai 1998), puis une seconde période d'abondance plus intense, en niveau et en durée, calée au milieu de la saison sèche (entre novembre 1997 et février 1998 avec le pic d'abondance en novembre / décembre 1997, puis entre janvier et avril 1999 avec le pic en février / mars). Pour la même espèce, dans les milieux dunaires du nord du Burkina Faso, SICARD (1987) a observé que la courbe d'abondance y était monophasique avec un pic calé sur le début de saison des pluies en juin / juillet. Comme à Kolo, il a aussi constaté qu'en année à pluviométrie exceptionnelle, la phase de forte abondance peut se prolonger jusque dans la saison fraîche.

Chez un autre Gerbillinae du Sénégal, *Taterillus pygargus*, POULET (1981) a constaté que le cycle d'abondance est monophasique, avec un pic en saison sèche, la plupart du temps en février (années 1975-1977).

Une première tentative d'explication de la dynamique de l'abondance de la population de *G. nigeriae* a consisté à mettre en évidence des corrélations statistiques entre l'abondance, la reproduction et la proportion de jeunes piégés. La simple comparaison statistique par un test R de Spearman, entre les des différents paramètres comparés pour les mêmes mois, ne fait pas apparaître de corrélation significative entre l'évolution de l'abondance et le déroulement de la reproduction mâle ou femelle.

Si l'on fait l'hypothèse que l'abondance de la population pour un mois donné est pour partie la conséquence de la reproduction qui s'est produite durant les mois antérieurs, on doit comparer le paramètre mensuel de la reproduction avec celui représentant l'abondance mensuelle mais décalée de un, deux ou trois mois. Avec un mois de décalage de la variable « pourcentage de femelles gestantes », il n'apparaît toujours pas de corrélation significative, mais décalée de deux mois, la série de valeurs devient très fortement corrélée avec les estimations d'abondance selon Schnabel ($R = 0,54$; $p = 0,009$) ou du calendrier de présence ($R = 0,46$; $p = 0,03$). Un décalage de 3 mois de la même variable ne fournit pas de résultat plus significatif.

Ainsi, en tenant compte du temps nécessaire aux embryons trouvés dans les femelles gestantes pour devenir de jeunes *G. nigeriae* émancipés et capables de se faire piéger (intervalle de 2 mois, au moins), on constate que l'évolution de l'abondance de la population de *G. nigeriae* est fortement corrélée avec l'intensité de la reproduction des femelles.

La corrélation entre l'évolution du pourcentage de femelles gestantes et le pourcentage de jeunes dans l'échantillon mensuel, fournit des résultats à la limite de la significativité à 5 % lorsque la série des valeurs des femelles reste décalée de 2 mois. Il est probable que les mouvements migratoires des jeunes perturbent cette analyse.

Par ailleurs, il apparaît une corrélation significative entre l'évolution du pourcentage de femelles gestantes et l'évolution du pourcentage de mâles actifs ($R = 0,48$; $p = 0,047$).

Comme l'ont fait les chercheurs cités plus haut, on peut tenter de mettre en évidence des relations entre d'une part l'abondance et la reproduction et d'autre part l'abondance, la reproduction et la qualité des saisons des pluies (précocité, régularité et longueur) qui conditionnent la survie des animaux et probablement le cycle de reproduction *sensu lato.* Notre période de suivi de la population de *G. nigeriae* à Kolo qui est trop courte au regard de la très grande variabilité inter-annuelle des saisons des pluies, rend difficile la mise en évidence de corrélations simples. Une période d'au moins 5 années consécutives serait nécessaire pour obtenir la quantité d'observations permettant de faire une telle étude. De fait, la simple comparaison statistique de la série de données caractérisant les saisons des pluies et celle caractérisant l'abondance ne met pas en évidence de relations directes entre ces variables.

En revanche, on note une très forte corrélation négative entre les pluies et l'abondance ($R = -0,52$; $p = 0,009$ pour le calendrier de présence et $R = -0,51$; $p = 0,011$ pour l'estimation par la méthode de Schnabel). Cette corrélation négative est conforme avec l'analyse de la figure 3 où l'on a constaté que les principales périodes d'abondance se situent en saison sèche.

Si l'on fait l'hypothèse que l'abondance de la population de *G. nigeriae* (en terme de survie des individus) peut-être, en partie, en relation avec la qualité de la saison des pluies précédente, on peut comparer les deux séries de données en décalant vers l'antériorité celle qui caractérise l'abondance. Le coefficient R de Spearman ne devient significatif ($R = 0,41$; $p = 0.045$ pour le calendrier de présence et $R = 0,45$; $p = 0.025$ pour l'estimation avec Schnabel) que lorsque le décalage atteint un laps de temps de 8 mois entre les deux séries de paramètres.

Les causes probables du très faible niveau d'abondance observé entre septembre et novembre 1998, peuvent avoir deux origines climatiques différentes. D'une part le faible niveau de population observé durant la première période d'abondance de 1998 (110 individus en août 1997 et 20 individus en août 1998) pourrait être la conséquence de la très mauvaise saison des pluies 1997 (1 seul mois de pluie efficace en juillet 1997 et presque 10 mois de saison sèche entre mi-août 1997 et mi-mai 1998. Le maintien du très bas niveau d'abondance en octobre et novembre (140 individus en novembre 1997 et

2 individus en novembre 1998) peut être en outre la conséquence d'une forte mortalité consécutive aux pluies exceptionnelles de 1998, en août (171 mm) et surtout au début de septembre (298 mm) qui ont inondé le terrain et éboulé les terriers avec les nouveau-nés à l'intérieur.

Considérant les niveaux de densités brutes (abondance rapportée à la surface brute de la grille de piégeage soit 2,85 ha), nous observons, pour la première période d'abondance à Kolo, des valeurs qui sont du même ordre de grandeur que celles observées par SICARD (1987) dans les dunes du nord-est burkinabè. A Oursi, les fortes densités situées en début de saison des pluies sont comprises entre 30 et 50 rongeurs par hectare chez *Gerbillus nigeriae*. A Kolo nous obtenons des valeurs de l'ordre de 38 individus à l'hectare en juillet 1997 et 80 individus en mai 1999.

Concernant les relations entre l'activité des mâles, l'activité reproductrice des femelles, la production de jeunes et les saisons des pluies, la seule relation trouvée concerne la corrélation négative ($R = -0,44$; $p = 0.025$) entre le pourcentage de jeunes et les saisons des pluies. Cette corrélation est évidemment logique puisque c'est plutôt en fin de saison des pluies, lorsque l'alimentation est disponible en grande quantité que l'on rencontre les jeunes. Dans les conditions de sols dunaires du nord du Burkina Faso, (SICARD, 1987) la production de jeunes *G. nigeriae*, en année normale, se situe plutôt durant la saison des pluies ce qui est différent de ce que l'on trouve à Kolo où notre dispositif de piégeage est installé dans une parcelle cultivé en mil.

Conclusions

L'étude de la dynamique d'une population de *Gerbillus nigeriae* entre juin 1997 et mai 1999 au Niger nous a permis de confirmer le choix de la méthodologie de piégeage CMR et la représentativité du site de Kolo. Les principales caractéristiques de l'évolution de l'abondance et de l'organisation de la reproduction font que l'une et l'autre ne sont ni des paramètres dont les niveaux sont constants dans l'année, ni des paramètres dont la reproductibilité est régulière selon les saisons.

Le fait que l'abondance de la population, qui semble présenter un cycle biphasique, passe par un maximum en fin de saison sèche / début de saison des pluies, est particulièrement contraignant pour les paysans dont les dates de semis de leurs champs de mil coïncident exactement avec ce pic d'abondance, à une période où la végétation naturelle n'existe plus et où les graines sauvages tombées sur le sol ont pratiquement toutes été consommées, en particulier par les fourmis.

Il semble que la reproduction des femelles soit également un phénomène à activité biphasique, mais les observations dont nous disposons ne couvrent pas une période suffisamment longue pour nous permettre de conclure avec certitude.

Pour prévoir la gravité annuelle des dégâts chroniques qui seront infligés aux semis de mil, nous souhaitons pouvoir préciser les corrélations existant entre les conditions climatiques et les niveaux des pics d'abondance, surtout pour ce qui concerne la période de coïncidence avec la saison des semis de mil. Mais compte tenu de la très grande variabilité des années climatiques, il nous faudra intégrer les résultats d'un suivi portant sur une période de temps assez longue et nous envisageons une période de 5 ans pour pouvoir prendre en compte efficacement les particularités climatiques de chaque année étudiée.

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Habitat preference of the African grass rat, *Arvicanthis dembeensis* (Rodentia, Muridae) in Koka, Central Ethiopia

Tilaye Wube

Afework Bekele

Introduction

A number of studies have been carried out on the ecology of African small mammals. These studies were more inclined towards the understanding of their breeding biology, activity pattern, population dynamics, feeding behaviour and interactions (CHAPMAN *et al.*, 1959; SOUTHERN and OLIVER, 1963; DELANY 1964a; COETZEE, 1965; OKIA, 1973; HAPPOLD, 1974; MULLER, 1977; NEAL, 1977, 1981, 1986; CHIDUMAYO, 1980; SWANEPOEL, 1980; GHOBRIEL and HODIEB, 1982; LEIRS *et al.*, 1990, 1993; FISHER, 1991; PERRIN *et al.*, 1992; SICARD *et al.*, 1994; AFEWORK BEKELE and LEIRS, 1997). However, studies on habitat use and distribution patterns of African small mammals seem to be neglected. There are only very few investigations carried out on these areas (SENZOTA, 1982; BOND *et al.*, 1980). Fragmentary information is available in the literature as introductory or supplementary part of reports which usually concentrate on any of the above mentioned ecological features (e.g. TAYLOR and GREEN, 1976; DELANY and MONRO, 1985).

Arvicanthis is a genus distributed in tropical Africa all the way from Senegal to Somalia and along the Nile basin from Egypt to Tanzania.

It is an opportunistic breeder which reaches an outbreak population size during maximum reproduction. The genus is usually associated with grassland habitats. It feeds on a wide variety of food items ranging from grasses and seeds to animal matter, particularly insects (NEAL, 1970; DELANY, 1964b; CHEESEMAN 1977; SICARD *et al.*, 1994; RABIU and FISHER, 1989). Presently, the number of species recognized for the genus reaches the maximum number of 6 (CORTI and FADDA, 1996). On the other hand, some investigators have also lumped all the taxa into one species i.e. *Arvicanthis niloticus* (MISONNE, 1971; HONACKI *et al.*, 1982). The variation in the number of species described for the genus suggests that there is a need for further taxonomical investigation. However, there is a common understanding that populations from the Nile delta and West Africa belong to *A. niloticus* while those from East Africa and the Horn belong to any one of the six species *A. blicki, A. abyssinicus, A. dembeensis, A. somalicus, A. nairobae,* and *A. testicularis* (CORBET and HILL, 1991; MUSSER and CARLETON, 1993).

VOLOBOUEV *et al.* (1988) provisionally grouped populations of *A. niloticus* into three cytotypes. Populations of *A. dembeensis* have been observed to be similar to the ANI -1 cytotype (CORTI *et al.*, 1996). Following this, it is strongly believed that *A. dembeensis* is a geographical variant of *A. niloticus* (CAPANNA *et al.*, 1996).

This paper is an attempt to add to the already existing few studies on habitat use of African small mammals. It is also targeted to initiate further research in this area so that a balance could be maintained between the various fields of ecological research on small mammals. Habitat use in *Arvicanthis* has not been studied in such details as in other small mammals. The present study is an initiative to fill some of the existing gaps in this knowledge.

Materials and methods

The study was carried out in the Koka Dairy Farm Enterprise located near Koka town, Central Ethiopia (08° 25' N, 39° 02' E) at an altitude of 1700 m a.s.l. The vegetation of the area represents a typical

degraded savanna woodland. The farm compound, however, incorporates various modified habitats as a result of plantations of various vegetation like reeds, sisal, maize, and pastoral grass species. These provided the opportunity to investigate the habitat use of *Arvicanthis* in both natural and modified habitats.

Fifteen quadrats, each with an area of 15 x 15 m, were selected to represent the study sites. A number of vegetation parameters that could influence rodents were considered while selecting the quadrats. These were: plant species composition; ground vegetation cover; aerial vegetation cover.

A minimum of 100 m distance was maintained between the sites to secure independent catch records. The fifteen sites were labeled "A" to "O". The field data collection was carried out from February 1997 to February 1998 on a six month interval. Consequently, three trapping periods were covered i.e. February 1997 (1st dry season), August 1997 (wet season) and February 1998 (2nd dry season).

Trapping was carried out using Victor mouse traps. Peanut butter was used as bait. The trapping stations were established at 3 m intervals along four trapping lines. Consequently, a total of 16 trap stations were established in each site. Traps were set late in the afternoon (3:00-4:00 p.m.) and kept for three consecutive days and nights. Seven of the sites were trapped for the first three days and nights and then the remaining 8 were trapped for the same duration. The animals were retrieved early in the morning (6: 00-8: 00 a.m.) and in the late afternoon (4: 00-6: 00 p.m.). The captured specimens were sexed, weighed and measured. Then, they were categorized into their age groups based on their weight and reproductive condition. Individuals which weighed < 26 g were considered as juveniles, between 26 and 60 as subadults and > 60 g as adults.

The habitat structure of each site was thoroughly described during each trapping session (table 1). Major plant species were collected from each site and identified at the National Herbarium, Biology Department, Addis Ababa University (table 2). Catch records of each site were compared using two-way ANOVAs ($P = 0.05$) and Critical Difference (C.D.) analyses.

Sites	Description
A	Thick bushes, about 1.5 m high, dominated by sisal plants (*Agavae sisalina*) and other shrubs and scrubs. The ground cover within the range of 1-20 cm height was scanty. The bush was continuous on both right and left hand sides while the back and the front sides were open grass fields.
B	Thick bush, about 1.75 m high, entirely dominated by *Achyranthus aspera* with well covered ground. However, there was no ground vegetation in the form of hedges and grass strips. Almost at the center of the site there was a big *Ficus* tree whose branches shade the entire site. The very ground is covered with dried, broad leaves which fall down from the *Ficus* tree.
C	Relatively open bush, about 1 m high, with ground well covered by dried grasses, about 30 cm high. It was dominated by *Solanum* spp. The front and back sides were fairly open while left and right sides were continuous about 10 m on both sides.
D	Extremely dense bush, about 2 m high, with a number of shrub, scrub and grass species. The ground was also very thick and dark. On each of its four corners it was surrounded by fields of cut grasses. It appeared like an island of thick bush.
E	Had fairly thick ground cover, about 40 cm high, provided by dried grasses. It was full of dried unbranched, leafless Castor oil trees (2.3 m high). However, they didn't provide any good aerial cover.
F	Except its species composition, it had quite similar vegetation structure as site B. The ground was devoid of any growth but only dried fallen leaves. It was surrounded by acacia trees (about 4 m high) and bushes (about 1.5 m high), part of an extensive bush system composed of shrubs and scrubs.
G	A fallow land with bare ground. There were only few individuals of herb species. It was well exposed.
H	Totally covered with grasses. However, the grass cover was fairly spaced. The aerial cover was non-existent. The total vegetation canopy was about 70 cm high.
I	An open field similar to site G. The ground was covered with sand grains. Some stations, however, were fairly shaded with grasses (about 60 cm high) which form a nest like harbour. Further out of the site, along these fairly shaded stations, there was a dense bush. Opposite to this end of the site there was a pile of harvested waste of maize.
J	It was part of an extensive acacia bush. The average height of the vertical growth was 2.5 m. The ground was covered with dense grasses where ever there was an acacia tree. But on those spots where the acacia trees were not present, the ground was bare.
K	Extremely thick bush dominated by very tall grasses (about 2 m high). Both the ground and aerial cover were provided by the grasses. There were also orange trees which bore fruits (about 3 m high).
L	Dominated by the grass which was also found in site K. But the thickness was reduced in L. The aerial cover was very thick which was made by reed plants.
M	It was a harvested maize field composed of dried, falling maize plants and grasses. The ground was covered by these dried grasses and maize plants. The aerial cover was very poor.
N	An open field of cut grasses. No ground or aerial cover was present.
O	Quite similar with site B both with regard to vegetation structure and species composition. However, the *Ficus* trees were absent in O.

Table 1
Habitat description of each trapping sites.

Sites	Plant species
A	*Gloriosa simplex, Agavae sisalina,*
B	*Cynodon dactylon, Achyranthus aspera, Bidens pilosa, Ficus sur*
C	*Tagetus minuta, Cynodon dactylon, Solanum incum*
D	*Ehretia cymosa, Vernonia leoploidii, Cynodon dactylon, Sesbania sesban*
E	*Amaranthus hybridus, Cynodon dactylon, Solanum marginatum, Solanum incum, Racinus comunis*
F	*Abutilion bidentatum, Leucas abyssinica, Balanites aegyptica, Cynodon dactylon, Solanum shimperi, Eheretia cymosa*
G	*Commeline bengalensis, Datura sramonium*
H	*Eheretia cymosa, Cynoglossum geometricum, Cyathula cylindrica, Crotalaria laburnifolia, Dactylectenium aegypticum, Cynodon dactylon, Sporobolus pyramidalis*
I	*Flaveria trinervia*
J	*Eheretia cymosa, Capparis tomentosa, Cenchrus setigerus, Acacia albida*
K	Sterile grass species, *Citrus sinensis*
L	Sterile grass species, *Achyranthus aspera*
M	*Zea mays*
N	*Eheretia cymosa, Cynodon dactylon*
O	*Bidens pilosa, Ipomoea cairica*

Table 2
Major plant species identified from the fifteen sites.

Results

Four rodent and one insectivore species were caught in the entire trapping sessions. A total of 365 individuals were caught. Of these, 174 (47.7%) were *Mastomys erythroleucus*, 161 (44.1%) *Arvicanthis dembeensis*, 17 (4.7%) *Tatera robusta*, 9 (2.5%) *Crocidura olivieri* and 4 (1.1%) *Rattus rattus* (table 3). The catch distribution of *Arvicanthis dembeensis* in each site is given in table 4 where data were combined for the February 1997 and 1998 trapping periods.

Species	1st dry season	2nd dry season	Wet season
Arvicanthis	98	43	20
Mastomys	78	41	55
Tatera	2	11	4
Crocidura	6	3	–
Rattus	2	1	1
Total	186	99	80

Table 3
Number of small mammals caught in each season.

This was done because both periods represent the dry season, with similar vegetation structure for each site. The August 1997 trapping data, however, are presented separately as the habitats changed during this period owing to the climatic change.

The catch records of the 15 sites were significantly different ($P < 0.05$) for both seasons. However, since the wet season sample size was very small, the corresponding data were not analyzed further. Consequently, the C.D. analysis was conducted only for the dry seasons. We have compared the means of the three day captures recorded for each site from the ANOVA table. Figure 1 shows the mean values for each site. Based on the C.D. analyses, it was possible to rank the sites as favoured (high catch records) and disfavoured (low catch records) (table 5). The sites which belonged to the 1st rank recorded from 21 to 32 individuals, 2nd rank 14, 3rd rank 13, 4th rank 8, 5th rank 3-5 and 6th rank 0-1.

Discussion

The present data show that habitat selection of *Arvicanthis dembeensis* is more influenced by the vegetation structure than by its species composition. This is in agreement with what BOND *et al.* (1980) found. Habitats that possessed dependable cover yielded high catch values.

Sites	Dry seasons	Wet season
A	21	1
B	14	–
C	13	2
D	8	–
E	1	2
F	5	2
G	–	–
H	–	3
I	8	–
J	1	1
K	32	2
L	21	–
M	3	–
N	–	2
O	14	5
Total	141	20

Table 4
Catch distribution of *Arvicanthis* among the 15 sites.

On the other hand, those that did not have fairly thick vegetation were not preferred. In fact, there is an apparent explanation for these observations. *Arvicanthis* is a diurnal rodent. Rodents in general are highly vulnerable to predators, particularly birds as observed in the study area. They can not afford an extended stay in exposed habitats as they will be picked up by the birds. Consequently, their survival is highly dependent on the presence of shelter. In addition, well covered habitats provide them with good nesting sites. The observed catch distribution in the selected habitat types is in good agreement with this simple habitat selection strategy. Those sites which fall in the 1st rank (K, A, and L) had thick bushes with dependable cover. The same was true with those which belonged to the 2nd (B and O) and 3rd ranks (C). However, all these sites were different in their species composition (table 2). These observations could lead one to inquire about food. Does *Arvicanthis* consume whatever plant species is available, or does it completely depend on sources of food other than the vegetation profile? Studies showed that *Arvicanthis* is mainly herbivorous (DELANY and MONRO, 1986; SENZOTA, 1982). However, it also

1st rank	2nd rank	3rd rank	4th rank	5th rank	6th rank
K	B	C	D	F	E
A	O	–	I	M	G
L	–	–	–	–	H
–	–	–	–	–	J
–	–	–	–	–	N

Table 5
The rank of each trapping site (A - O) based on the C.D. analyses.

includes animal matter, particularly insects, in its diet (RABIU and FISHER, 1989). In the study area, it has been observed feeding on the larvae of termites (casual observations). It also feeds upon grasses, seeds, fruits, and cereals when found near agricultural areas (TAYLOR and GREEN, 1976; RABIU and FISHER, 1989). It is an opportunistic feeder. However, indigestible woody vegetation can not be used as food. All the major vegetation types which were found in our trapping sites fall under these categories. *A. dembeensis* may not use the major plant species as a source of food. Instead, the food source could be insects, small blades of grasses, weeds and fallen leaves which were widely distributed almost among all the sites. It could also be possible that the rats pay short visits to nearby areas with potential food sources and return back to their permanent residence. In fact, the catch record observed in site I could truly illustrate this. The site was a rather exposed area with regard to both aerial and ground cover, and was hardly favoured by rodents. However, along one side of the site, there existed a thick bush which can possibly harbour a good population of rodents. The 8 individuals caught in site I were probably residents of this bush which pay short visit to the nearby site, which in turn was located near a pile of the waste components of harvested maize.

Although most of our results support the idea that vegetation structure is the most important factor determining habitat selection, some of the catch records showed inconsistencies. For example, the catch record of site D was much less than what was expected. It was an extremely thick, well protected and diverse habitat. However, as

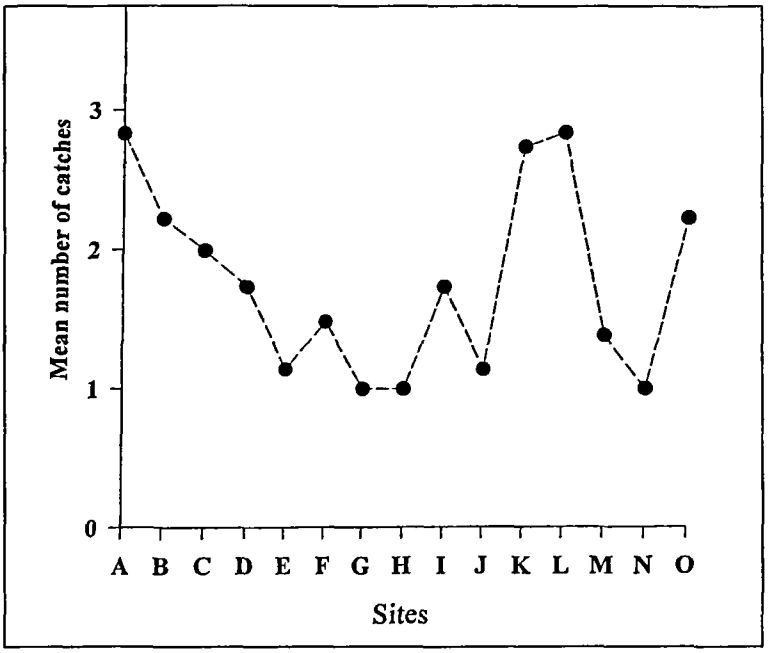

Figure 1
Mean catch values of each site used in the C.D. analyses.

SENZOTA (1982) found out, the site might have discouraged colonization. SENZOTA (1982) observed low catch records (67 individuals/ha) in habitats with 40% bush cover, against 320 individuals/ha in habitats which had 10% bush cover. Probably the rats are discouraged by congested habitats due to lack of free space for movement. The low catch records observed in sites E, H, and J were also surprising. Site E had dense ground cover of dried grasses. However, its poor aerial cover may have made it quite exposed and unfavourable for colonization. Site H, too, had a good vegetation cover dominated by grasses. But, once again it lacked good aerial cover. SENZOTA (1982) also observed little capture values on pure grassland habitats. Such habitats are exposed to predators and provide poor nesting sites. It becomes even more difficult to explain J's case. Both the aerial and ground vegetation were dependable. The *Acacia* bushes of the site had very thick and spreading branches which protected the ground

like an umbrella. The ground was covered with dense grasses which provided good nesting sites and hiding places. One may hypothesize that the area was not fully colonized by *Arvicanthis* yet because it was distantly isolated at the northern boundary of the enterprise's enclosure.

In summary, we emphasize the importance of vegetation structure as the governing factor of habitat selection by *Arvicanthis dembeensis*. Most of our data support this assumption. However, since the number of trapping sessions we have employed was very limited, some observed apparent inconsistencies between catch records and vegetation structure in some of the sites could result from chance. From there, it becomes apparent that detailed micro-habitat studies are required to better understand the habitat selection of *Arvicanthis*.

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Geographic variation in the role of gerbils and jirds (Gerbillinae) in rodent communities across the Great Palaearctic Desert Belt

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Introduction

The Great Palaearctic Desert Belt is the largest desert area in the world, extending from the Atlantic coast of northwest Africa in the west to northeastern China in the east. Environmental conditions (including climate, landscape and vegetation types) of different parts of this belt differ significantly both due to their distinct geographic positions and as a result of unique geological histories (PETROV, 1973). Consequently, significant faunal changes take place along the belt (for rodent biogeography of the Palaearctic desert belt, see SHENBROT *et al.*, 1999). The Gerbillinae is the only rodent taxon represented across the whole belt, although its species richness and species composition varies geographically. In many deserts of the Old World, gerbils and jirds are important components of ecosystems and in some cases they can be agricultural pests and reservoirs of

dangerous diseases such as plague and cutaneous leishmaniasis (PAVLINOV *et al.*, 1990).

The aim of this paper is to review and quantify patterns of geographic variation in the relative importance of Gerbillinae across the Great Palaearctic Desert Belt using both biogeographic and ecological approaches.

Material and methods

Biogeography

We restricted our analysis to the species that we consider to belong to desert faunas and we analyzed the distribution of these species within the borders of the Palaearctic desert zone only. We considered a species as a desert species if its geographical range is either entirely or mostly located in the desert and if it occupies zonal desert habitats rather than intrazonal ones (mountains, river valleys and lake shores). The taxonomic composition for different rodent groups followed PAVLINOV *et al.*, (1990) for Gerbillinae, SHENBROT *et al.*, (1995) for Dipodoidea and WILSON and REEDER (1993) for other rodents. In total, we analyzed the distribution of 109 rodent species in Palaearctic deserts. For each of these species we compiled a geographic range map based on data published in the following regional monographs: North Africa - RANCK (1968), OSBORN and HELMY (1980), LE BERRE (1990), and KOWALSKI and RZEBIK-KOWALSKA (1991); Southwest Asia - LAY (1967), HASSINGER (1973), ROBERTS (1977), HARRISON and BATES (1991), CORBET and HILL (1992), SHALMON (1993), and QUMSIYEH (1996); Central Asia (former USSR) - BOBRINSKY *et al.* (1965), SLUDSKY *et al.* (1969, 1977, 1978), YANUSHEVICH *et al.* (1972), and GROMOV and ERBAJEVA (1995); Mongolia and China - BANNIKOV (1954), SOKOLOV and ORLOV (1980), and MA *et al.* (1987). Finally, we divided each map of a species distribution by a 2° by 2°grid, and compiled a list of rodent species for each grid cell.

Ecology

Analysis of community composition requires a preliminary ecological classification of all the species in the community. Such a classification is meaningful if it is based on those characters and features that facilitate resource partitioning among coexisting species. Thus, ecological classification has to be based on the type of resources that are used (diet composition) and on the conditions of resource acquisition in space (habitat distribution) and time (activity patterns).

Our ecological data were obtained over the last twenty years in the course of studying desert rodent communities. Data were collected in 1980-1982 and 1989-1990 in the Kyzylkum Desert (Uzbekistan), in 1984-1988 in the Gobi Desert (Mongolia), in 1989 in the Thar desert (India) and in 1992-1999 in the Negev Desert (Israel). Rodents were trapped on 1-ha plots that were chosen to represent main substrate and vegetation gradients. The number of sampled plots was 24 in the Southern Kyzylkum (39°33'-39°41'N, 64°35'-64°43'E), 22 in South-Western Kyzylkum (39°37'-40°38'N, 62°31'-64°00'E), 26 in Northern Gobi (44°46'-47°31'N, 92°23'-100°59'E), 18 in Western Gobi (42°50'-44°23'N, 96°36'-100°15'E), 26 in Eastern Gobi (42°34'-44°52'N, 104°19'-111°07'E), 15 in Thar (26°-28°N, 73°-75°E), 24 in central Negev (30°22'-30°52'N, 34°27'-35°03'E) and 24 in northern Negev (30°52'-31°17'N, 34°17'-34°49'E). Each plot was sampled for three consecutive days using 50 Sherman live-traps or Museum Special snap-traps placed in a grid of 5 x 5 stations with two traps per station and an interval of 20 m between stations. Jerboas were caught with a net at night using a searchlight. Large jirds (*Psammomys*, *Rhombomys* and some *Meriones*) and ground squirrels (*Spermophilus* and *Spermophilopsis*) which usually avoid traps were counted in the morning using binoculars. Each trapped animal was sexed, weighed and either marked by toe-clipping and released or collected to analyze reproductive condition and stomach content and for subsequent museum deposition.

To analyze relationships between rodent distribution and abundance and parameters of the environment, we described a set of environmental variables around each trap station. To make analyses of the spatial structure of rodent communities from different deserts as comparable as possible, our approach was standardized by measuring almost the same set of environmental variables in each study area.

The total number of measured or derived variables varied from 18 to 24 in the different deserts. Three of these variables described the mechanical composition of the soil, six the abundance and composition of annual plants and geophytes, and the remainder characterized the structure of the perennial vegetation. The last mentioned group of environmental variables comprised cover by perennial grasses, aphyllous, microphyllous and succulent shrubs and the volume of shrub crowns in 4 or 5 vertical layers.

We classified our sample plots into habitat types using both similarities in environmental parameters and in rodent species composition. Details of analysis were published earlier (KRASNOV *et al.*, 1996; SHENBROT *et al.*, 1999). Species were considered as habitat specialists if they occurred in only one or two similar (e.g. stabilized and semi-stabilized sand dunes) habitats and as habitat generalists in other cases.

Diet was identified using stomach content analysis. Stomach content was examined under a stereoscopic dissection microscope, and food remains were divided into four categories, namely seeds, green parts of vegetation, underground parts of vegetation (bulbs and roots) and animal remains. The amount of each food category in each stomach was estimated visually as a percentage of the total volume with 5%-accuracy. We classified species by their diets as granivorous or folivorous if the primary food types (seeds or green parts of vegetation, respectively) comprised not less than 80% of diet by volume. Otherwise, a species was classified as omnivorous (if all food types were represented in its diet more or less equally) or mixivorous (if the diet was the mixture of two or three food types).

Results and discussion

Biogeography

The results of zoogeographical analysis demonstrate that the Gerbillinae are represented in all Palaearctic deserts. The greatest number of coexisting gerbil and jird species (11-13 species) is observed

in the relative narrow strip along the Mediterranean coast of North Africa (fig. 1). High Gerbillinae species richness (9-10 species) is recorded in the northern and central parts of the Sahara Desert, and moderate species richness (7-8 species) is typical for most other parts of the Sahara, central parts of Arabian Peninsula and Iranian deserts. Species richness decreases slightly towards the southern borders of the North African and Arabian deserts and much more sharply in a northeastern direction within Asian deserts.

Gerbil and jird species richness varies within Palaearctic deserts from 1 to 13 species, whereas general rodent species richness in this region varies from 5 to 22 species (SHENBROT *et al.*, 1999). Due to this, patterns of geographic variation of the proportion of Gerbillinae in Palaearctic desert rodent faunas generally match the patterns of Gerbillinae species richness (fig. 2). Gerbillines comprise the largest fraction of the entire rodent fauna (50-70%) in most parts of the Sahara and in eastern Arabia. This fraction decreases to the south, to the north-west and to the north-east, comprising 30-50% of all rodents in the peripheral parts of the Sahara and in the deserts of the Horn of Africa, Arabia, Iran and Sind, 10-30% in Turanian deserts and less than 10% in the Gobi desert. These patterns can be explained mainly by the history of Gerbillinae: their origin and early stages of radiation took place in Africa, whereas their Asian history is much shorter (PAVLINOV *et al.*, 1990).

Community structure

Quantitative community parameters

The results of estimations of quantitative parameters for some Palaearctic desert rodent communities based on our data are presented in table I. In the Negev and Thar communities, gerbils and jirds dominate both in relative abundance (the Gerbillinae fraction represents 86-96% of all rodent individuals) and in relative biomass (89-98% of all rodent biomass). Nevertheless, the fraction of Gerbillinae in these faunas is not especially high (62-64% in the Negev and 40% in the Thar Desert). Thus, the important role of Gerbillinae in the Negev and Thar communities in terms of relative abundance and biomass is determined by the fact that most gerbil and jird species

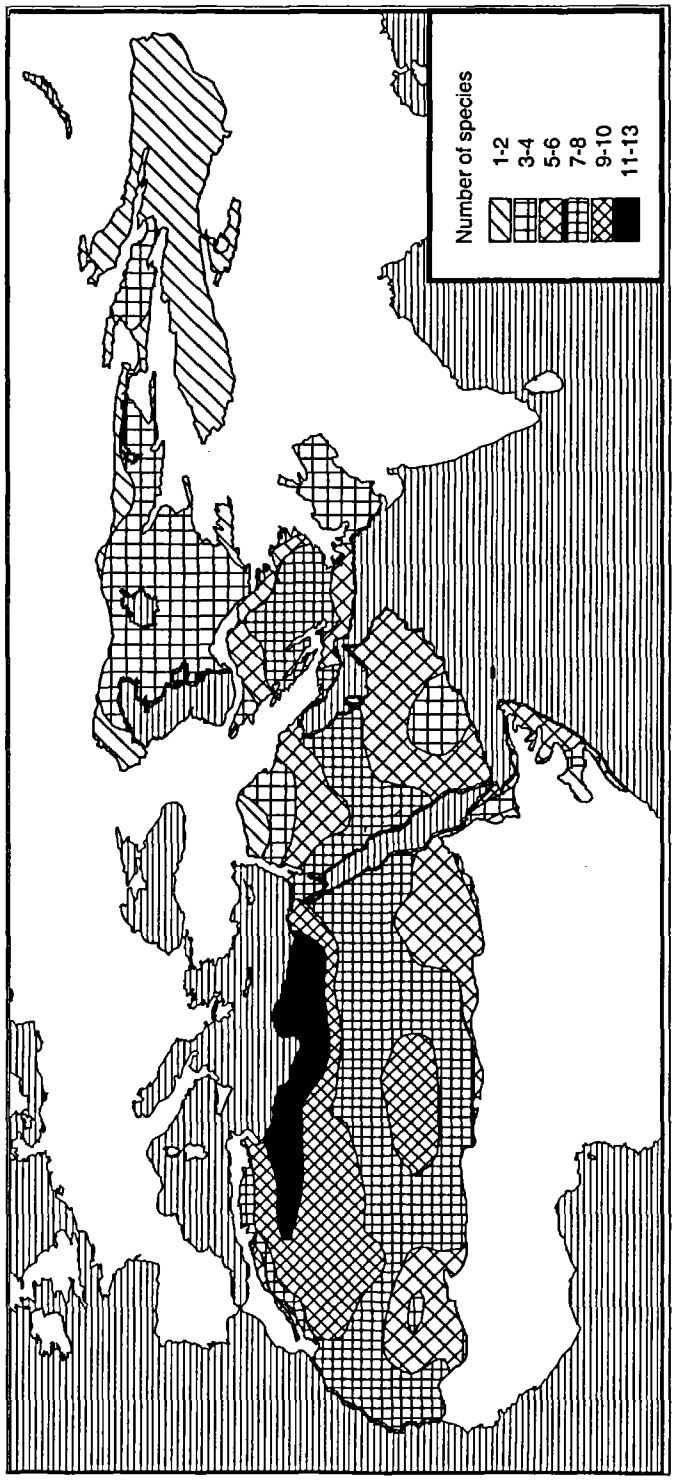

Figure 1
Species richness of Gerbillinae in Palaearctic deserts.

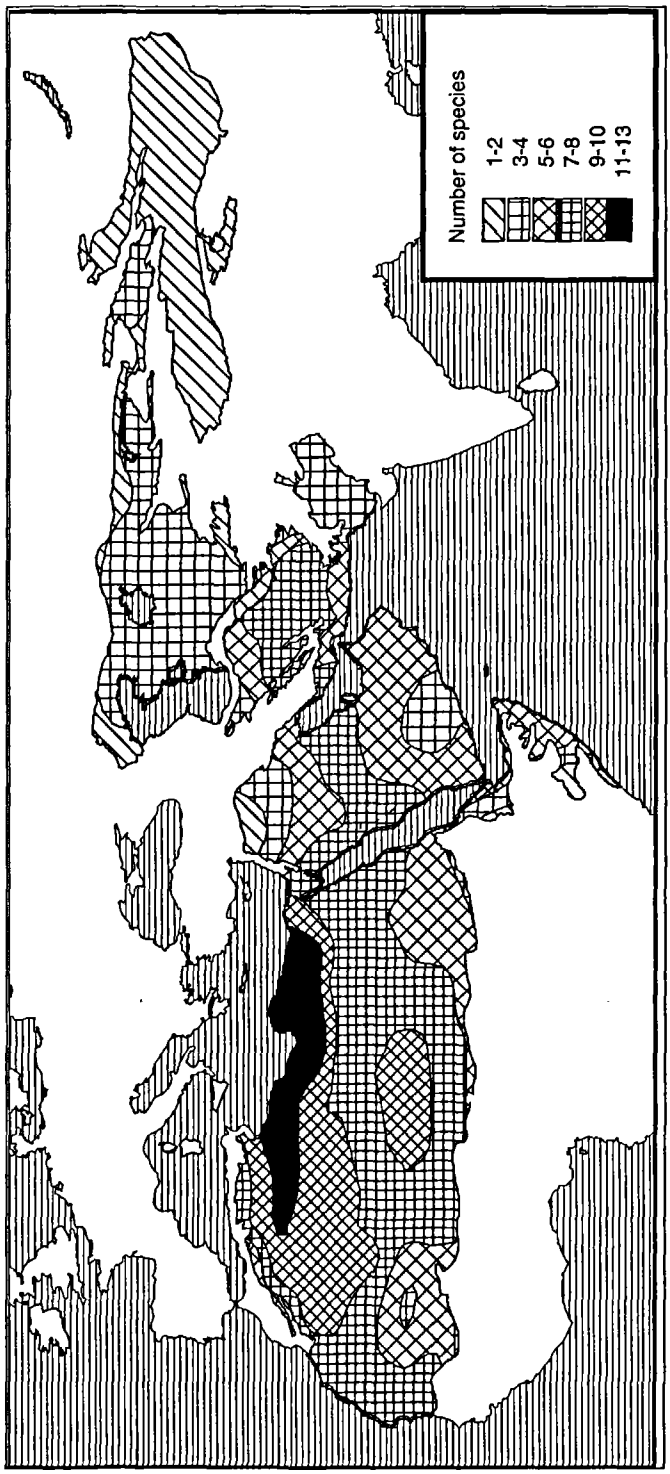

Figure 2
Fraction of Gerbillinae *species in taxonomic* composition of Palaearctic desert *rodent faunas.*

are numerous and also that jirds have relatively large body mass. Unfortunately, there are no comparable data on Saharan desert rodent communities (with density and biomass estimations of all rodents including jerboas and ctenodactylids and taking into account the whole spectrum of habitats at a place). Provisional analysis of data on the specimens composition in local samples and in owl pellets published in regional monographs (e.g. KOWALSKI and RZEBIK-KOWALSKA, 1991) showed that relative Gerbillinae abundance in the Sahara varies in most cases within limits of 80-90%. Considering the above data and faunal composition, it is possible to hypothesize that the pattern that was revealed for the Negev and Thar deserts would be typical for the entire Saharo-Sindian desert region.

The role of Gerbillinae in Palaearctic desert rodent communities decreases in a northeastern direction. Gerbillinae continue to be the dominant rodent group in Turan deserts (Kyzylkum) both in terms of relative abundance and biomass (58-72% and 55-73%, respectively) despite comprising relatively little (21-23%) of the community taxonomic composition. Further to the east, in the Gobi Desert, Gerbillinae become a minor fraction of rodent communities in terms of all estimated parameters. This is especially true for the eastern Gobi (table 1).

Qualitative community composition

The diet of Gerbillinae in Thar, Kyzylkum and Gobi deserts is presented in table II. Based on these data, we can classify *Gerbillus gleadowi* and *G. nanus indus* as granivores, *Meriones hurrianae*, *M. erythrourus*, *M. meridianus*, and *Tatera indica* as mixivores, and *Rhombomys opimus* as a folivore. Unfortunately, we have no comparable data on the diet of Gerbillinae in the Negev desert. However, available information (BAR *et al.*, 1984; DEGEN *et al.*, 1986, 1988; KHOKHLOVA *et al.*, 1995), as well as our observations on gerbil feeding in captivity suggest that *Gerbillus gerbillus* and *G. henleyi* are granivores, *Gerbillus andersonii*, *G. pyramidum*, *G. dasyurus*, *Meriones crassus*, and *M. sacramenti* are mixivores, *Sekeetamys calurus* is an omnivore, and *Psammomys obesus* is a folivore. Thus, there are two types of feeding mode among Gerbillinae in each of the rodent communities of Kyzylkum, Gobi and Thar deserts. In the communities of the Negev desert gerbillines are more diverse with respect to

Region	Species richness		Rodent density (ind/ha)	Relative Gerbillinae abundance (in %)	Rodent biomass (kg/ha)	Relative Gerbillinae biomass (in %)
	All rodents	Gerbillinae				
N. Negev	13	8	13.3	89.9	1.54	88.5
C. Negev	11	7	11.7	85.9	1.31	95.8
Thar	10	4	55.5	95.8	5.88	98.3
S. Kyzylkum	13	3	16.9	72.2	1.39	73.0
S.W. Kyzylkum	14	3	15.4	58.4	1.24	54.6
N. Gobi	17	3	13.3	33.5	1.20	38.9
W. Gobi	14	2	13.5	16.0	1.06	23.2
E. Gobi	14	2	18.9	9.0	1.56	13.3

Table 1
Quantitative parameters of some rodent communities of Palaearctic deserts

diet (three types of feeding mode in the northern Negev and four types of feeding mode in the central Negev).

There are two main groups of desert rodents in terms of habitat selection, namely habitat generalists and habitat specialists. In turn, habitat specialists can be subdivided into three subgroups, namely psammophiles (specialist sand dwellers), petrophiles (specialist rock dwellers) and sclerophiles (specialist occupants of open plains with hard clay substrate). Some habitat generalists with extensive geographic ranges narrow their habitat distribution towards the periphery of their range where they demonstrate habitat specialisation (for a review, see SHENBROT *et al.*, 1999). Table 3 provides a summary of our data on habitat selection of Gerbillinae in the studied Palaearctic desert rodent communities (see SHENBROT, 1992; ROGOVIN *et al.*, 1994; SHENBROT *et al.*, 1994; ROGOVIN and SHENBROT, 1995; SHENBROT and ROGOVIN, 1995; KRASNOV *et al.*, 1996; KRASNOV and SHENBROT, 1998; SHENBROT *et al.*, 1999 for details). No sclerophilous species and only one petrophilous species (*Sekeetamys calurus*, Negev Desert) were found among gerbils and jirds. Most Gerbillinae species are habitat generalists. The fraction of psammophiles varies from three species in the northern Negev to one species in the central Negev and Thar deserts. There are no psammophilous jirds in Kyzylkum Desert. *Rhombomys opimus*, which is

Species	Region	Sample size	Food type				Source
			Insects	Seeds	Bulbs	Green	
T. indica	Thar	122	10.83	18.75	47.08	23.33	2
G. gleadowi	Thar	9	0	93.75	0	6.25	1
G. n. indus	Thar	6	0	93.00	0	7	1
M. hurrianae	Thar	172	5.83	34.17	36.25	23.75	2
M. erythrourus	Kyzylkum	64	6.64	48.67	2.81	41.87	1
M. meridianus	Kyzylkum	71	4.51	60.992	0.70	33.80	1
M. meridianus	Gobi	63	7.70	67.22	3.17	21.90	1
R. opimus	Kyzylkum	24	1.67	3.33	13.54	81.46	1
R. opimus	Gobi	15	2.15	4.76	11.32	81.77	1

Table 2
Diet composition (percentages by fresh volume) of Gerbillinae in some Palaearctic deserts. Sources of information: 1 – our data, 2 – PRAKASH, 1993.

a strict sand dweller in the Gobi desert but occupies diverse habitats in the Kyzylkum Desert, represents a typical case of habitat generalist with peripheral decrease in habitat breadth. Thus, there are three types of habitat selection among Gerbillinae in the central Negev, two types in the northern Negev and Thar and only one type in the Kyzylkum and Gobi deserts.

One jird species with diurnal activity always exists in each desert rodent community, whereas all other species are nocturnal. Such diurnal species are *Psammomys obesus* in the Negev Desert, *Rhombomys opimus* in the Kyzylkum and Thar deserts and *Meriones hurrianae* in the Thar Desert. It is important to note that these diurnal jird species construct more complex and extensive burrow systems than nocturnal species. In desert rodents diurnal activity usually correlates with sociality. So, existence of such complex burrow systems can be explained by its additional function to provide enough room for family groups together with other common functions (place for nest and food storage, safe access to aboveground food resources, refuges from predators, etc.) (SHENBROT *et al.*, 1999). These burrows provide a specific environment and refuge for a number of invertebrate and small vertebrate species and can be considered as sites of "environmental engineering".

Region	Type of habitat selection			
	Habitat generalists	Psammophyles	Petrophyles	Sclerophyles
Negev	*Gerbillus dasyurus* *Gerbillus henleyi* *Meriones crassus* *Meriones tristrami* *Psammomys obesus* 1 Myoxidae sp. 1 Dipodidae sp. 1 Muridae sp.	*Gerbillus andersoni* *Gerbillus gerbillus* *Gerbillus pyramidum* *Meriones sacramenti*	*Sekeetamys calurus* 2 Muridae sp.	1 Dipodidae sp.
Thar	*Tatera indica* *Gerbillus nanus* *Meriones hurrianae* 1 Sciuridae sp. 3 Muridae sp.	*Gerbillus gleadowi*	2 Muridae sp.	
Kyzylkum	*Meriones erythrourus* *Meriones meridianus* *Rhombomys opimus* 2 Sciuridae sp. 2 Dipodidae sp. 1 Arvicolidae sp. 1 Cricetidae sp. 1 Muridae sp.	3 Dipodidae sp.		3 Dipodidae sp.
Gobi	*Meriones meridianus* 1 Sciuridae sp. 4 Dipodidae sp. 2 Arvicolidae sp 4 Cricetidae sp.	*Rhombomys opimus* 2 Dipodidae sp.	1 Arvicolidae sp. 1 Cricetidae sp.	2 Dipodidae sp.

Table 3
Types of habitat selection
in some Palaearctic desert rodent communities.

Combining the above three classifications, we calculated the final ecological classification of the Gerbillinae. Local communities of gerbils and jirds consist of five ecological groups in the central Negev, four groups in the northern Negev and Thar Desert, and two groups in the Kyzylkum and Gobi deserts (table 4).

Region	Habitat generalists				Psammophyles			Petrophyles
	Nocturnal		Diurnal		Nocturnal		Diurnal	Nocturnal
	Granivores	Mixivores	Mixivores	Folivores	Granivores	Mixivores	Folivores	Omnivores
N. Negev	*G. henleyi* *M. tristrami*	*G. dasyurus* *M. crassus*		*P. obesus*		*G. andersoni* *G. pyramidum* *M. sacramenti*		
C. Negev	*G. henleyi*	*G. dasyurus* *M. crassus*		*P. obesus*	*G. gerbillus*			*S. calurus*
Thar	*G. nanus*	*T. indica*	*M. hurrianae*		*G. gleadowi*			
Kyzylkum		*M. meridianus*		*R. opimus*				
Gobi		*M. meridianus*					*R. opimus*	

Table 4
Composition of ecological groups of Gerbillinae in some Palearctic local rodent communities.

Considering taxonomic composition of rodent faunas, it is possible to hypothesize that the presence of four-five ecological groups in communities of Gerbillinae should be typical for the whole Saharo-Sindian part of the Palaearctic desert belt, whereas two ecological groups of jirds should be common in communities of the Turano-Gobian deserts. The simplification of Gerbillinae community structure in Turano-Gobian deserts is the result of the absence of granivorous and omnivorous species. It has been suggested that in most rodent phylogenetic lineages (including Gerbillinae), such forms are evolutionarily most primitive (VORONTSOV, 1967). Thus, their absence in the Turano-Gobian deserts may be explained by the late penetration of Gerbillinae into this region (PAVLINOV *et al.*, 1990) when ecological niches of small granivores and omnivores were already occupied by endemic species (jerboas and hamsters).

In addition, species composing an ecological group differ substantially in their size. For example, the group of nocturnal mixivorous habitat generalists of the Negev Desert consists of two species, *Gerbillus dasyurus* and *Meriones crassus*, with a threefold difference in body mass (22 and 72 g, respectively). The group of nocturnal mixivorous psammophiles of the northern Negev is composed of *Gerbillus andersoni*, *G. pyramidum* and *Meriones sacramenti*, with a 1.5-3-fold difference in body mass (24, 38 and 120 g, respectively). The group of nocturnal mixivorous habitat generalists of the Kyzylkum

Desert consists of two species, *Meriones meridianus* and *M. erythrourus*, with about two-fold difference in body mass (42 and 77 g, respectively). Such differences are typical for desert rodent communities and can be explained as a mechanism facilitating coexistence of ecologically-similar species (BROWN, 1995).

Among-variable statistical interactions

There was a very strong positive correlation between relative abundance and relative biomass of gerbils and jirds ($r = +0.96$, $P < 0.001$). The relationships between relative abundance and relative biomass of Gerbillinae and their fraction in rodent communities are also positive but not linear (fig. 3). These relationships are best fitted by regression equations $Rab = 1.233 + 0.477*Ln\ (Fr)$ and $Rbm = 1.243 + 0.478*Ln\ (Fr)$, where *Rab* is relative abundance, *Rbm* is relative biomass and *Fr* is fraction of Gerbillinae in a rodent community. Both regression equations are statistically significant ($R^2 = 0.796$ and 0.791, respectively; $P < 0.005$ in both cases). Such a pattern means that the ecological significance of Gerbillinae increases faster than their taxonomic importance. Gerbils and jirds become the dominant components of rodent communities (in terms of abundance and biomass) as soon as they comprise approximately one quarter of all rodent species only. This result can be considered as evidence of the evolutionary success of the taxon. The observed patterns can be discussed also in terms of the species abundance – body size concept. It has been shown that the relationship between body size and population abundance is negative, but the proportion of variance in abundance explained by body size is always low and plots of the relationship tend to be polygonal (BLACKBURN *et al.*, 1993; BROWN, 1995). If so, a linear relationship between relative abundance and relative biomass may be observed only if Gerbillinae represent the modal size class of a rodent community, or if they are equally distributed among all size classes. The former is found in the Turano-Gobian communities, whereas the latter is observed for those in the Thar and Negev communities. Nonlinearity of the relationships between relative abundance and relative biomass of Gerbillinae and their fraction in rodent communities may be explained by differences between Turano-Gobian and Saharo-Sindian rodent communities in species distribution within abundance

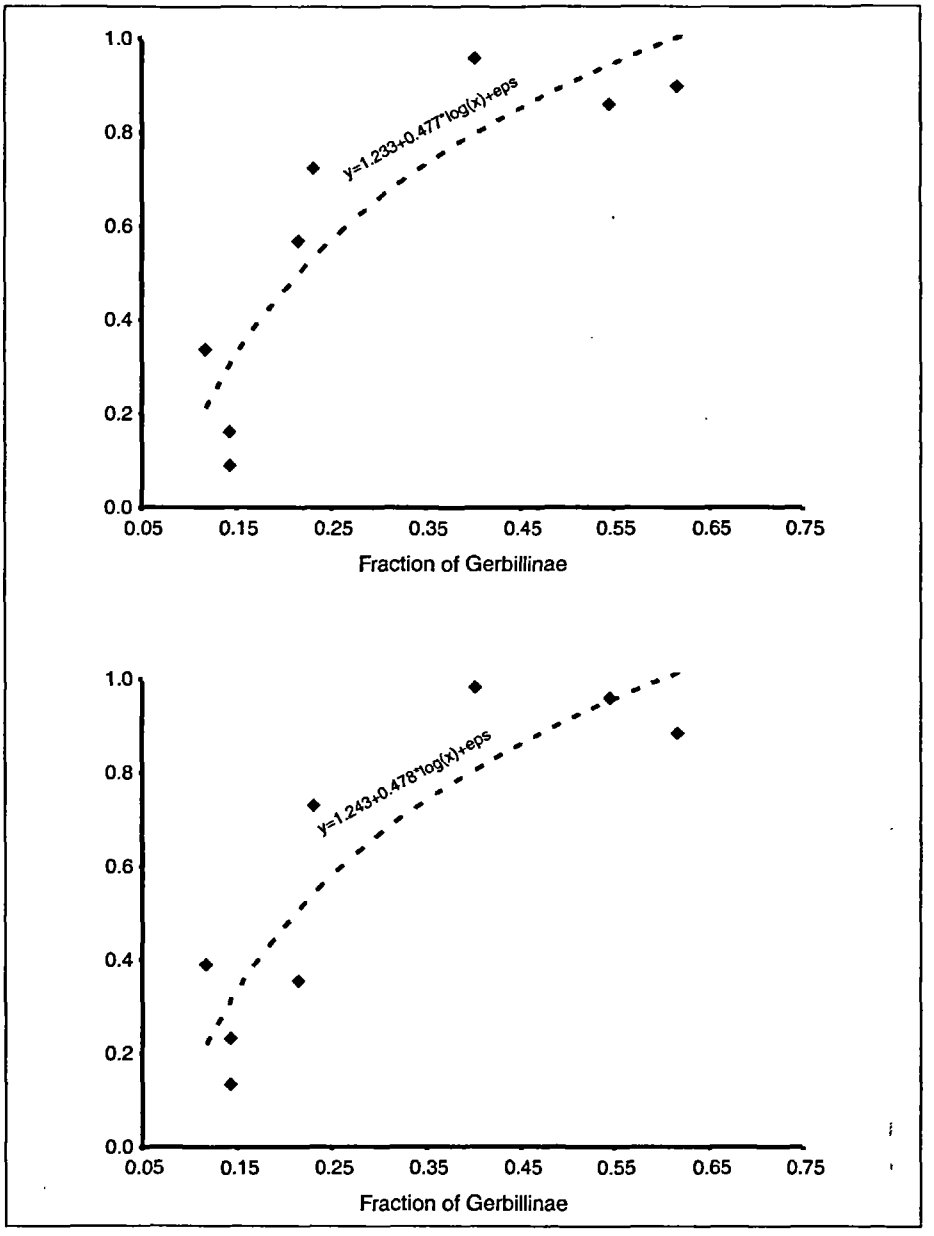

Figure 3
Relationships between relative abundance (top), relative biomass (low) and the proportion of Gerbillinae in taxonomic composition of Palaearctic desert rodent communities.

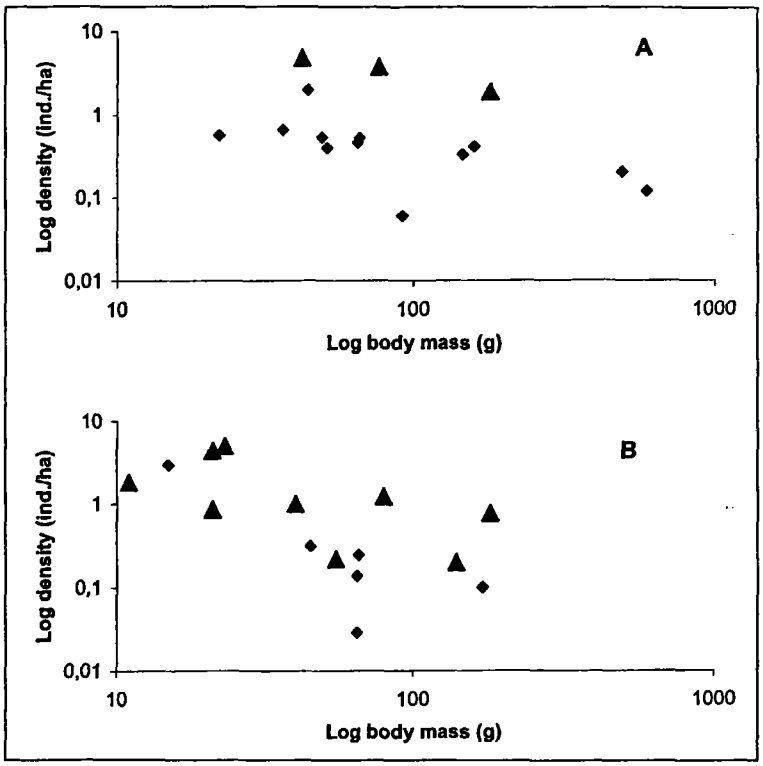

Figure 4
Relationships between body mass and abundance in rodent communities of the Negev Desert (A) and the Kyzylkum Desert (B). Gerbillinae species are denoted by the large triangles, non-gerbillinae species by small diamonds.

– body size polygons. Few jird species of the Turano-Gobian communities occupy the upper part of these polygons (fig. 4A). It means that Gerbillinae are represented here by species of the modal size class but with high densities. In such a case, a small increase in the Gerbillinae fraction in a community will lead to a rapid growth of their relative abundance and biomass. Conversely, numerous gerbil and jird species of the Thar and Negev communities occupy abundance – body size polygons evenly (fig. 4B), demonstrating their diversity of body size classes and density levels. The well-known positive relationship between species abundance and geographic range size among groups of closely related species (BROWN, 1995; GASTON

et al., 1997), suggests that any increase in the Gerbillinae fraction of a community will most likely occur as a result of the addition of relatively rare species with narrow geographic ranges. In such a case, even a significant increase in the Gerbillinae fraction of a community will provide only a slow growth of their relative abundance and relative biomass.

There is a strong positive correlation ($r = +0.88$, $P < 0.005$) between the number of Gerbillinae species and the number of their ecological groups. This pattern reflects an increasing level of ecological diversification with growth in the number of coexisting species. It should be noted that this pattern is demonstrated for Asian communities only, in the absence of appropriate data on Saharan communities. Nevertheless, one may expect that a similar pattern will be revealed within Saharan rodent communities. However, the relative morphological uniformity of Gerbillinae should put an upper limit to the number of their potential ecological groups. A working hypothesis for future ecological studies of the Saharan desert rodent communities might be that the relation between the number of Gerbillinae species and the number of their ecological groups should be positive but non-linear. The number of ecological groups should attain an upper limit at some moderate species richness. Additional increases of species richness from moderate to high values should produce an ecological diversification within each ecological group by subdividing it into different size classes.

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Abstracts

Taxonomy and classification

A. Bannikova, L. Lavrenchenko, A. Lomov, B. Mednikov: "Molecular diversity of some *Crocidura* species (Insectivora, Soricidae) from Ethiopia"

A comparative study of repetitive DNA elements was undertaken in six species of *Crocidura* of Ethiopia: *C. glassi* (2n = 36), *C. thalia* (2n = 36), *Crocidura* sp. B (2n = 36), *C. macmillani* (2n = 28), *C. parvipes* (2n = 50) and *C. olivieri* (2n = 50). Tree topologies based on parsimony and neighbour-joining methods appear to be similar. The 50-chromosomeal species and 36-chromosomeal species are sister groups. *C. macmillani* forms a basal branch with a moderate bootstrap support. *Crocidura* sp. B is closer to *C. thalia* rather than to *C. glassi.*

Keywords: *Crocidura* — Ethiopia — DNA — Molecular taxonomy — RFLP.

J. Crawford-Cabral, C. Alberto Fernandes: "The Rusty-spotted genets as a group with three species in Southern Africa (Carnivora: Viverridae)"

The Rusty-spotted genets are a group of forms included by some authors in *Genetta tigrina* (Schreber, 1776), by others in *Genetta maculata* (Gray, 1830) (or *Genetta pardina* I. Geoffroy, 1832), and yet accepted by others as a separate species – *Genetta rubiginosa* authors *nec* Pucheran, 1855. However, at least concerning Southern Africa, the results from canonical analyses of craniometrical data point to the Rusty-spotted genets as being not one, but three different species. The southernmost one, characterized by a larger size, includes "*rubiginosa*" *sensu* Roberts, *letabae* Thomas & Schwann, 1906, *zuluensis* Roberts, 1924, and *albiventris* Roberts, 1932. We propose *Genetta letabae* as the name to be given to this species. The second species corresponds to *zambesiana* Matschie, 1902 and includes *gleimi* Matschie, 1902. It occurs in central and northern Mozambique, Malawi, Zambia and Angola. The third species is known from specimens in the

Transvaal Museum collected at Boror, Mozambique and identified by Roberts as *Genetta mossambica* Matschie, 1902, a form described from Mossimboa, Mozambique. The results also suggest that *Genetta angolensis* Bocage, 1882, and *G. tigrina* are, although akin, specifically distinct from any of the Rusty-spotted genets. However, they probably form with them a species-group where *G. zambesiana* and *G. letabae* constitute a superspecies.

Keywords: *Genetta* — Rusty-spotted genets — Southern Africa — Cranial morphometrics — Taxonomy.

P. Gaubert, G. Véron, M. Tranier: "An investigation of morpho-anatomical characters within the genus *Genetta* (Carnivora, Viverridae), with a remark on *Osbornictis*, the aquatic genet"

Through an exhaustive observation of morpho-anatomical characters related to some Viverrinae (genets and « genets-like » taxa), two identification keys based on cranial and coat characters are proposed for the genus *Genetta*. Such a survey also allows us to reconsider the plantar pads description of the poorly known species *Osbornictis piscivora*.

Keywords: Viverrinae — Genets — Morpho-anatomical characters — Identification keys — Interspecific delimitation.

J.-Y. Crochet, S. Peigné, M. Mahboubi: "Ancientness of the carnivora (mammalia) in Africa"

The ante Oligocene African faunas are of primeval importance for a better understanding of mammalian history. In this paper, we describe and provide an interpretation of a carnivorous mammal first lower molar which predates by some 23 million years the first record of the order Carnivora in Africa. This fossil has been collected at the Glib Zegdou site, located between the Dra, Gir and Daoura Hammadas (Algerian Sahara). A late Early to Middle Eocene age has been proposed on charophyte evidence for the fossiliferous level or Early Eocene according to the mammalian evolutionary stages. This tooth is morphologically of tribosphenic structure and it shows narrow and deep notches on the crests. This feature evokes the carnassial trend of the mammal diet.

The hypoconulid is median and bent backward. But the most remarkable feature of this tooth is the relatively small size of its metaconid. This character is considered as apomorphic in all the representatives of the carnivorous mammals. Comparisons with Early Tertiary carnassial mammals belonging to various orders, particularly with the order Carnivora are not conclusive. It is not possible to refer the Glig Zegdou tooth to any primitive family of the Carnivora: Viverravidae and Miacidae, known during the Palaeocene and the Eocene in which the trigonid is much higher with regard to the talonid. A reduced metaconid can be observed on the first lower molar of *Legetetia nandii* (Carnivora, Viverridae from the Lower Miocene of Kenya, described by Schmidt-Kittler, 1987, when the second (and last) molar shows a flat trigonid. However, a reference to this family is therefore excluded for the algerian tooth due to many other differences. It is impossible to assess the Glib Zegdou form to any known Carnivora family and the authors here propose the creation of a new genus (*Glibzegdouia)* and species *(tabelbalaensis)* that they refer to a suborder and indeterminate family in the Carnivora.

Keywords: Carnivora — Eocene — Algeria — Tooth — Morphology.

K. Bâ, C. Mathiot, M. Diallo, P. Nabeth, L. Lochouarn, Y. Kane, M. Abdalahi, L. Granjon: "Preliminary study on some rodents of southern Mauritania as reservoirs of human pathogenic viruses"

In December 1998, 73 rodents belonging to 5 species (*Gerbillus tarabuli, Desmodilliscus braueri, Arvicanthis niloticus, Acomys* cf. *airensis* and *Jaculus jaculus*) were captured in natural, peridomestic or domestic habitats in and around 4 localities near Ayoun El Atroûss (southern Mauritania). The identity of *G. tarabuli* (2N = 40, NFa = 74) and *A.* cf. *airensis* (2N = 42, NFa = 66), was confirmed based on chromosomal data. IgG serologies were done by immunoenzymatic techniques against the following viruses: Rift Valley Fever, Lassa, Hantaan, Puumala, Seoul, Saboya and Gabek Forest. None of the 7 viruses searched for was found on any of the 51 individuals tested.

Keywords: Rodents — Viruses — Mauritania — Karyology.

P. Chevret, F. Catzeflis, J. R. Michaux: "'Acomyinae': new molecular evidences for a muroid taxon (Rodentia: Muridae)"

The taxonomic position of the spiny mouse (genus *Acomys*) within the Murinae (Rodentia) was first challenged by the immunological data of SARICH (1985). Subsequent molecular data have also excluded *Acomys* from the murine rodents, in association with two murine genera (*Uranomys* and *Lophuromys)* and a "dendromurine" *Deomys*; this group was designed as "Acomyinae". We present here complementary DNA/DNA hybridization results, mitochondrial gene sequences (12S rRNA) and nuclear gene sequences (LCAT), which confirm the existence of an "Acomyine" clade, that comprises *Acomys, Uranomys, Lophuromys* and *Deomys*. But there is still no morphological synapomorphy that can define this group. We also evidenced that the Murinae, Gerbillinae and Acomyinae are sister groups but we were not able to decipher their relationships.

Keywords: Acomyinae — scnDNA hybridization — 12S rRNA — LCAT — combined analysis.

E. Lecompte, C. Denys, L. Granjon: "An identification key for the species within the genus *Praomys* (Rodentia: Muridae)"

An identification key for African soft-furred rats of the genus *Praomys* Thomas, 1915, based on morpho-anatomical characters on skull is proposed. The key provides for the identification of nine of the ten currently recognised species, namely: *P. degraaffi* Van der Straeten & Kerbis Peterhans, 1999, *P. delectorum* (Thomas, 1910), *P. hartwigi* Eisentraut, 1968, *P. jacksoni* (de Winton, 1897), *P. misonnei* Van der Straeten & Dieterlen, 1987, *P. morio* (Trouessart, 1881), *P. mutoni* Van der Straeten & Dudu, 1990, *P. rostratus* (Miller, 1900) and *P. tullbergi* (Thomas, 1894). A synopsis of the currently recognised species, their geographical distribution and the available chromosomal data are also presented.

Keywords: Murinae — *Praomys* — Identification — Morphology — Systematics.

I. J. A. Pavlinov: "Current concepts of Gerbillid phylogeny and classification"

Under brief consideration are morphological backgrounds of predominating concepts in the phylogeny and classification of the family Gerbillidae. Two key structures are considered: protoconulid of the first lower molar and mastoid portion of the auditory bulla. Presence of the protoconulid in some gerbillids favors their myocricetodontine affinities. Two basic types of mastoid pneumatization support the recognition of two subfamilies, Taterillinae and Gerbillinae *sensu.stricto.*; genus *Ammodillus* takes having uncertain position. Within the first subfamily, the tribes Taterillini *sensu stricto* and Gerbillurini (with genera *Gerbillurus* and *Desmodillus*) are recognized. Among taterillines proper, the Asian *Tatera indica* is likely to be the a sister group of an African cluster including *Taterona, Gerbilliscus*, and *Taterillus*. Within the subfamily Gerbillinae, four tribes are recognized: the polytypical Gerbillini *sensu. stricto.* (*Gerbillus* and allies) and Rhombomyini (*Meriones* and allies), and the monotypical Desmodilliscini and Pachyuromyini.

Keywords: Gerbillidae — Rodents — Phylogeny — Classification — Morphoanatomy.

F. Sénégas: "Interpretation of the dental pattern of the South African Murinae *Euryotomys* (Rodentia, Muridae) and origin of otomyine dental morphology"

Euryotomys bolti recently described from the locality Waypoint 160 (Bolt's Farm area, Gauteng Province, South Africa) provides additional palaeontological evidence for the reassessment of the relationship between Murinae and Otomyinae. As molecular data are congruent with palaeontological ones, the sub-family Otomyinae must be considered simply as a tribe – Otomyini – within the Murinae. *Euryotomys pelomyoides* from the Mio-Pliocene locality of Langebaanweg in the west of South Africa, and the more evolved *Euryotomys bolti* (an Early Pliocene age is advocated for this species) document a new phyletic lineage, an interesting fact as few rodent lineages are up to now recognized in the Plio-Pleistocene of South Africa. Following Van Dam's (1997) approach of the dental

morphology in murine rodents, biometric analyses in *Euryotomys* demonstrate that the two known species, first fill the gap between a murine pattern already adapted to a grazing diet and the most derived ones seen in *Otomys* and *Parotomys*, and second, that *Otomys* and *Parotomys* have the most derived dental pattern to be expected for Murinae adapted to an abrasive diet.

Keywords: *Euryotomys bolti* — Early Pliocene — South Africa — Phyletic lineage — Diet modification.

P. J. Taylor, A. Kumirai: "Craniometric relationships between the Southern African Vlei rat, *Otomys irroratus* (Rodentia, Muridae, Otomyinae), and allied species from north of the Zambezi river"

Based on principal component analysis and discriminant analysis of craniometric data, as well as variation in dental and cranial qualitative characters, this study considers *Otomys irroratus* in relation to species of *Otomys* from north of the Zambezi River, several of which have in the past been included in this species. The hypothesis of Petter (1982) that *O. irroratus* is a widely distributed and polymorphic species encompassing several Pan African forms, is refuted. Compared with other species, *O. irroratus* has proportionately smaller bullae and wider nasals and interorbital region. In particular, *Otomys tropicalis* (north of the Zambezi River) and *O. irroratus* (south of the Zambezi River) show minimal craniometric overlap, and can be separated reliably on dental characters (6 laminae in M^3 in *irroratus*, 7 or more in *tropicalis*). Further, *O. anchietae*, by its larger cranium, is shown to separate clearly from all other species of *Otomys*, including forms comprising the "*anchietae* - group", which will probably be shown by further study to be afforded species rank.

Keywords: Otomyinae — Principal component analysis — Discriminant analysis — Skull Morphometry.

Phylogeny and Evolution

T. J. Robinson: "The comparative cytogenetics of African small Mammals in perspective: Status, trends, and bibliography"

Internationally, the field of comparative cytogenetics advanced rapidly in the 70s and 80s through the application of chro-

mosomal banding studies and the tracing of evolutionary changes in the chromosomal complement. Now, almost 30 years later, it is possible to reflect on the use of chromosomes in studies of African small mammals. While there have been significant advances in karyotypically evaluating numerous species, phylogenetic interpretation of the findings has lagged considering the new technologies currently available. In many instances, work on African taxa has been descriptive and has been based on either standard karyotypes or sub-optimal banding comparisons. Since these potential shortcomings can suggest false homologies, it is likely that they have contributed, in part, to the generally weak performance of banding studies in retrieving phylogenies and to the paucity of attempts to place chromosomal data in cladistic frameworks. It is suggested that the application of fluorescent *in situ* hybridization (FISH) technology is an essential adjunct for the accurate identification of chromosomal character states for phylogenetic inference, particularly in taxa characterized by highly rearranged karyotypes as is found in many rodents. Methodological improvements in chromosome painting are likely to continue to drive comparative cytogenetics and work on African small mammals will increasingly reflect this.

Keywords: Cytogenetics — Small mammals — Banding — FISH — Phylogeny — Karytoype.

R. Tabuce, B. Coiffait, P. E. Coiffait, M. Mahboubi, J-J. Jaeger: "Contribution of the Bir El Ater locality (Algeria) to the knowledge of the evolution of African Paleogene mammals"

The Early Paleogene African fossil record of eutherian mammals is very scarce. However, several localities from Morocco, Tunisia and Algeria have largely contributed to our knowledge of the first placental mammals from the Arabo-African area. This work presents the faunal lists of most African Eocene localities. It also summarizes the preliminary study of the new Middle-Late Eocene mammals from Bir El Ater. Except for teeth of *Moeritherium* (Proboscidea), the whole of the material refers to small mammals. A carnivore or a creodont and an "insectivore" are undeterminate. A hyracoid (*Bunohyrax*) might represent a new species. A new genus of

elephant-shrew represents one of the two oldest representatives of this order and testifies the condylarthran relationships of the group. The primates are represented by four taxa. The genus *Algeripithecus* from Glib Zegdou (Algeria) is identified and an Oligopithecidae represents the oldest occurrence of this catarrhine group in Africa.

Keywords: Africa - Algeria - Eocene - Endemic mammals - Primates.

J. Banke, A. Mess, U. Zeller: "Functional morphology of the rostral region of *Cryptomys hottentotus* (Bathyergidae, Rodentia)"

Based on a morphological examination of the rostral head region, the fossorial rodent *Cryptomys hottentotus* is chararacterized as follows: 1) the proodont incisors take a permanent extraoral position, 2) the actual mouth opening is situated behind the incisors and the oral region is characterized by fused *upper inflexa pellita*, 3) the *Regio rhinarica* is situated behind the incisors, and is provided with indistinct narial pads and supralabial skinfolds, 4) the underlying cartilaginous rostral nasal skeleton lacks an anterior wall and is ventrally stabilized by the premaxilla, and 5) movement of the nasal and oral region is enabled by facial musculature that is associated with the dorsum nasi, the nasal opening, the cupula nasi anterior, the upper lip and the *inflexa pellita*. From a functional viewpoint relating to the fossorial lifestyle of *Cryptomys*, the gnawing teeth form a suitable digging tool in the rostral head region. Due to a covering mechanism of the nares via the flexible *dorsum nasi* and the differentiation of the *inflexa pellita*, the nasal as well as the oral cavity can be protected from irritating substrate during digging.

Keywords: Rodentia — Bathyergidae — Rostral head — Morphology — Fossorial lifestyle.

P. Giere, A. C. Schunke, U. Zeller: "Comparative craniological systematics of the "Tenrecomorpha" (Mammalia: Insectivora)"

Departing from diagnostic characters for the "Tenrecomorpha" (otter shrews and Malagasy tenrecs), characters that usually are derived from taxidermized specimens, the scope of available information on this taxon is enlarged by considering

morphological data from histological sections. Various members of the "Tenrecomorpha" as well as other Insectivora, Eutheria and Metatheria were compared for determination of character polarity. Only little new evidence from the auditory region was found for the "Tenrecomorpha".

Keywords: "Tenrecomorpha" — Tenrecidae — Potamogalinae — Systematics — Cranial Morphology.

M. Kawalika, H. Burda, D. Bruggert: "Was Zambia a cradle of the genus *Cryptomys* (Bathyergidae, Rodentia)? A further new ancestral (?) species of *Cryptomys* from Zambia"

A new karyotype of *Cryptomys* from Kasama, Zambia, characterised by of 2N = 64 chromosomes is described. The karyotype consists preliminarily of acrocentric (21 or 23 pairs) and fewer biarmed (8 or 11 pairs) chromosomes. We suggest that the Kasama *Cryptomys* belongs to an ancestral lineage of *Cryptomys* mole-rats which diversified along the so-called arid corridor in subequatorial central Africa.

Key words: *Cryptomys* — Bathyergidae — Chromosome speciation — Karyotype.

H. Burda: "Determinants of the distribution and radiation of African mole-rats (Bathyergidae, Rodentia): Ecology or geography?"

The pattern of the distribution of African bathyergid mole-rats, as revised on the basis of the available records, seems to be determined primarily by geographical (geomorphological) features. The Great Rift Valley represents an important barrier separating the centres of origin and distribution areas of *Cryptomys* westwards, *Heterocephalus* eastwards, and *Heliophobius* enclosed by both branches of the Rift Valley, mountains on the Kenya-Tanzanian borders and the Zambezi river. Chromosomal differentiation of bathyergids eastwards of the Great Rift Valley and southwards of the Zambezi River is low. Current ecological parameters cannot be used for a clear definition of the habitat preferences and delimitation of distribution areas of the any particular species. However, highly uneven distribution of precipitation throughout the year, as well as paleoecological and paleoclimatic factors may have

been responsible for vicariance and the high speciation rate of *Cryptomys* in the central subequatorial Africa (i.e. the Zambezian Region involving Zambia and Malawi).

Key words: African mole-rats — Bathyergidae — Zoogeography — Rodents.

A. Mess: "Evolutionary differentiation of placental organisation in hystricognath rodents"

The study presents an analysis of the placenta in hystricognath rodents. On focus are the general morphological organisation of placenta as well as the courses of maternal and fetal vessels with particular reference to the late placenta. According to the results presented, the degree of placental lobulation differs within Hystricognathi. However, in all Hystricognathi the placenta is characterized by a circular situated ectoplacenta as well as centrally located maternal arteries or blood chambers. The latter character conditions belong to the stem species pattern of Hystricognathi and has to be the result of an evolutionary transformation along their stem lineage. This character must have evolved before the radiation of Hystricognathi in Africa and South America took place, i.e. in Eocene times. The profound differences with regard to the outgroup taxa indicates an important meaning of the placenta to in the evolutionary history of Hystricognathi. The results indicate that future research should focus on a deeper understanding of the phylogenetic, evolutive and functional significance of this character complex.

Keywords: Rodentia — Hystricognathi — Evolution — Placentation — Reproductive biology.

C. Montgelard, S. Bentz, C. Douady, J. Lauquin, F. Catzeflis: "Molecular phylogeny of the sciurognath rodent families Gliridae, Anomaluridae and Pedetidae: morphological and palaeontological implications"

The combined molecular analysis between two mitochondrial (cytochrome *b* and 12S rRNA) and one nuclear (LCAT: Lecithin Cholesterol Acyl Transferase) genes was performed on several sciurognath rodent families with special emphasis

on Gliridae, Anomaluridae and Pedetidae. This study confirms that the genus *Graphiurus* is clearly a member of the Gliridae family and reveals a strong affinity between Anomaluridae and Pedetidae. These two African families appear as a new lineage (suborder Anomaluromorpha) among sciurognath rodents as previously suggested by some morphological characters. This molecular result clearly contradicts morphological relationships deduced from the evolution of incisor enamel microstructure. Implications of molecular and morphological results are discussed in the light of paleontological data.

Keywords: Rodents — Classification — Molecular phylogeny — Palaeontology — Incisor enamel.

Behaviour, Physiology and Reproduction

I. G. Van Tets, S. W. Nicolson: "The nutritional ecology of rodent pollinators of *Protea*"

The nutritional ecology of rodent pollinators of *Protea* species in South Africa is reviewed. Sugar preferences of *Aethomys namaquensis* are correlated with the sugar composition of rodent-pollinated species of *Protea* and xylose, a pentose sugar found in *Protea* nectar, is more willingly consumed by the mice than by bird pollinators. The ability of *A. namaquensis* to metabolise xylose is an exciting new finding. At least two species of these seasonal nectarivores are capable of producing both remarkably dilute urine and highly concentrated urine in response to variation in water intake, and *A. namaquensis* is able to meet its nitrogen requirements on small quantities of pollen. *Protea* flowers are likely to be an important food resource for these animals in winter.

Keywords: *Protea* — Rodent — Nectar — Pollen — Pollination.

L. N. Bennett, N. Pillay: "Responses of male *Rhabdomys pumilio* to urine of females in different reproductive states"

The behavioural responses of male striped mice *Rhabdomys pumilio* to urine of cycling (dioestrus, oestrus), pregnant (mid- and late pregnancy), and postpartum oestrous females were studied in two-stimulus preference tests. It was predicted that males would prefer urine of receptive females to that of non-

receptive females. Males demonstrated equal preference for urine of females in dioestrus and oestrus, preferred urine of cycling females to that of females in mid-pregnancy, and did not show a clear preference between urine of females in late pregnancy and that of cycling females. Urine of females in postpartum oestrus was preferred significantly more than urine of cycling females. Male *R. pumilio* are clearly attracted to females that will be receptive soon (i.e. dioestrus and late pregnancy) rather those furthest away from receptivity (i.e. mid-pregnancy). Preference for postpartum oestrus over cycling females is consistent with events in nature since females go through cycles of pregnancy rather than oestrous cycles.

Keywords: *Rhabdomys pumilio* — Reproduction — Behaviour — Oestrus — Odour.

J-M. Duplantier, K. Bâ: "Swimming ability in six West-african rodents species under laboratory conditions: evaluation of their potentialities to colonize islands"

In order to estimate their natural potentialities of dispersing to islands, swimming tests were realized in laboratory conditions for five murids and one gerbil rodent species. Ten adults (5 males and 5 females) per species were tested in an aquarium during 10 minutes maximum. In *Dasymys rufulus, Mastomys huberti* and *Myomys daltoni*, all the individuals reached the end of the test whereas 3 *Arvicanthis niloticus* and *Tatera gambiana*, and 4 *Mastomys erythroleucus* had to be removed from the water. The highest values for water intake by the fur were observed in *D. rufulus*: after 10 mn in the water, their weight was increased by an average of 25% on average. For the other species the weight increase ranged from 15% to 20%. Despite this, *D. rufulus* presented the highest number of floating sequences. Conversely *T. gambiana* seemed unable to float and had to swim constantly. The best performances were observed for a species living in humid areas (*M. huberti*), but also more surprisingly for *M. daltoni*, and whereas the worse swimming times were by *A. niloticus* and above all by the gerbil *T. gambiana*. These results are consistent with the rodent distribution observed in the Saloum Delta: if *T. gambiana* is the most abundant species in large islands

connected from time to time with the mainland, *M. huberti* is the only species living in small, completely isolated islands.

Keywords: Rodents — Swimming — Island colonization — Laboratory experiments.

P. Gouat, I.E. Yahyaoui: "Reproductive period and group structure variety in the Barabary ground squirrel *Atlantoxerus getulus*: preliminary results"

The Barbary ground squirrel, *Atlantoxerus getulus*, is an endemic species from Morocco and Algeria. This species occupies a wide variety of habitats from alpine meadows to desert. Preliminary results on the reproductive period and the group structure are presented in our this paper. In high-altitude sites, both in High and Anti-Atlas, reproduction occurs in summer while in other sites reproduction takes place in spring. During the reproductive period, group composition differs greatly, even among sites of a given region.

Keywords: *Atlantoxerus getulus* — Sciuridae — Rodents — Ethology — Reproductive period — Morocco.

R. Sumbera: "The mating behaviour of the silvery mole-rat (*Heliophobius argenteocinereus*)"

The Silvery mole-rat Heliophobius argenteocinereus is a solitary subterranean rodent occurring in eastern Africa. As generally applicable to all solitary subterranean rodents, its reproductive biology is still obscure. I provide the first data on mating behaviour of this species as displayed in the laboratory, and compare the observed patterns with those patterns described for systematically related versus non-related (Hystricognatha v. Sciurognatha) and ecologically convergent versus divergent (subterranean v. supraterranean, solitary v. social) rodents.

Keywords: Bathyergidae — Behavioural convergence — *Heliophobius* — Mating behaviour — Subterranean mammal.

A. Haim, D. Afik, U. Shanas: "Thermoregulatory and metabolic responses to photoperiod manipulations in a mesic population of the common spiny mouse, *Acomys cahirinus*"

Photoperiod and ambient temperature are environmental variables which show seasonal changes. In the Mediterranean ecosystem the change in photoperiod occurs before that of temperature. The Mediterranean ecosystem on mount Carmel, Israel, is characterized by seasonal asymmetry, with a long dry and warm season and a short wet and cold season. One of the rodent species that exist in this ecosystem is the common spiny mouse *Acomys cahirinus*, of African origin. The aim of this research was to study the metabolic and thermoregulatory responses of a rodent population to changes in photoperiod, in order to assess whether this species uses photoperiod changes, as a cue for seasonal acclimatization of its metabolic and thermoregulatory systems. For this purpose mice were kept under two photoperiod regimes (16L: 8D and 8L: 16D) at a constant ambient temperature. The results of our study show that the metabolic and thermoregulatory systems of *A. cahirinus* respond to changes in photoperiod. Under short day acclimatization, food and energy consumption increased, compared to long day acclimatization. Body temperature daily rhythms also changed in response to photoperiod manipulations. Although the studied individuals were from a mesic population the patterns observed were similar to those of desert rodent species. Therefore, it is suggested that this population of *A. cahirinus (A. dimidiatus)* can use photoperiod cues for seasonal acclimatization.

Keywords: *Acomys cahirinus* — Thermoregulation — Metabolic response — Photoperiod manipulations — Food — Energy and water consumption.

Ecology

D. Happold: "Ecology of African small Mammals – recent research and perspectives"

This review describes recent research on the ecology of African small mammals (Insectivora, Chiroptera, Rodentia, Lagomorpha and Macroscelidea). The paper begins with consideration of the numbers of species, the importance of

small mammals, and an analysis of papers published in 1994-1998. Six subdisciplines of ecology (autecology, community ecology, feeding ecology, reproductive ecology, geographical ecology and conservation ecology) are described and illustrated with examples from recent publications. The review ends with suggestions for the conservation of small mammals and recommendations for future research.

Keywords: Ecology — Small mammals — Africa — Review.

W. N. Chitaukali, H. Burda, D. Kock: "On small mammals of the Nyika Plateau, Malawi"

During two short-term surveys of small mammals in montane grasslands of remote parts of the Nyika National Park in Malawi, two species of macroscelids, four *Crocidura* species, four species of Chiroptera, and 20 rodent species were recorded. Among them, *Plerotes anchietae*, *Mylomys dybowskii*, and *Grammomys ibeanus* are new records for Malawi, while *Crocidura hirta*, *Epomops dobsonii*, *Rhinolophus simulator*, *Pipistrellus nanus*, *Acomys spinosissimus*, *Steatomys pratensis* and *Saccostomus campestris* are new records for the Nyika Plateau. The latter two species also represent new records for montane regions in general. New, previously undescribed, karyotypes have also been found in several species of rodents. Some ecological aspects are discussed.

Keywords: Nyika Plateau — Malawi — Rodents — Chiropteres — Macroscelididae — Crocidurinae

V. Clausnitzer: "Rodents of the Afro-alpine zone of Mt. Elgon"

The ecology of montane grassland rodents was studied on Mt. Elgon, Uganda at elevations above 3500 m a.s.l. between October 1996 and November 1997 and additionally in March 1999. The moorlands and afro-alpine vegetation in these altitudes are inhabited by 8 rodent species; in wooded patches 5 additional species are found. The most common species are *Lophuromys flavopunctatus*, *Rhabdomys pumilio* and two *Otomys* species: the endemic *O. barbouri* and the disjunct distributed *O. typus*. Distribution and density of *Rhabdomys pumilio* and *Otomys* species correlate with

vegetation structure, humidity and floral composition. *Otomys typus* and *Rhabdomys pumilio* are associated with extensive tussock-grasslands, dominated by *Festuca pilgeri*. *Otomys barbouri* avoids pure stands of this tussock-grass and favours more diverse habitats in respect of vegetation structure and species diversity. *Lophuromys flavopunctatus* shows no distinctive habitat preferences, which coincides with its diet of snails, worms and Tipulidae-larvae, whichthat are common all over the mountain. The present distribution and density of the afro-alpine rodents on Mt. Elgon are strongly influenced by the fire- induced vegetation patterns. A moderate fire regime results in a much higher rodent density, but not in a higher diversity, when compared to "natural" vegetation patterns. A high fire frequency decreases the rodent diversity, leaving a high density of grassland species.

Keywords: Ecology — Uganda — Rodents — *Otomys*.

G. Dobigny, R. Cornette, S. Moulin, E. Ag Sidiyène: "The mammals of Adrar des Iforas (Mali), with special emphasis on small mammals: Systematics and biogeographical implications"

An inventory of the mammals (especially small mammals) from the Adrar des Iforas (Mali) was undertaken, in order to complete the list of species of this poorly known area of central Sahara. Various technics methods enabled to testify for the non ambiguous presence of several small mammals species never mentioned before in the Adrar des Iforas, and belonging to orders Rodentia (4 species of *Gerbillus*, *Desmodilliscus braueri*, *Acomys airensis*, *Myomys daltoni*, *Mus* subgenus *Nannomys* sp.), Chiroptera (*Rhinopoma hardwickei*, *Asellia tridens*) and Insectivora (*Crocidura pasha*). The presence of many other species was confirmed. We then propose an up-to-date list of mammals, based on our data and those from the literature. This compilation enables to distinguish two kinds of faunas, according to their biogeographic affinities, thus suggesting a biogeographical scenario for the colonization of the Adrar des Iforas.

Keywords: Adrar des Iforas — Mali — Sahara — Taxonomy — Biogeography — Mammals.

F. Laudet, W. Hamdine: "Differential representation of gerbilids in European eagle owl (*Bubo bubo ascalaphus*) pellets from Southwestern Algeria"

A taphonomic analysis has been performed on 30 pellets of the European Eagle Owl (*Bubo bubo ascalaphus*) recovered in the region of Beni-Abbès (SW Algeria). Remains from 47 rodents (46 gerbillids and one jerboa) have been identified. Skull material presence varies according to prey size: largest preys (*Meriones* and the jerboa), which represent the major part of single-prey pellets, have supplied 77.2% of their theorical number of teeth, while small preys (gerbils), which are rather rejected in 2 or 3-preys pellets, have only supplied 44.2% of their teeth. However, incisors of rodents rejected alone are more frequently digested than others (41.1% against 5.6%). The elaboration of several pellets when one or several digested preys exceeds a certain volume, including the separation of skull from the rest of the skeleton, could explain such observations. Consequences on rodent representation in both modern or fossil pellet assemblages are discussed.

Keywords: *Owl pellets* — Taphonomy — Rodent — Multirejection — *Bubo bubo ascalaphus* — Algeria.

A. Hoffmann, H. Klingel: "Spatial and temporal patterns in *Mastomys* cf. *natalensis* (Smith, 1834) as revealed by radio-tracking"

Radio-tracking of *Mastomys* cf. *natalensis* was carried out in the grasslands of the Queen Elizabeth National Park in Uganda. Home range sizes calculated by Ranges V "using the Minimum-Convex-Polygon-Method (at 95%) were on average 4 times larger in the bushland-grassland-mosaic than those in the *Imperata-Cymbopogon* grassland. An inverse relation between home range size and population density was found. In both grasslands the species was strictly nocturnal but showed different activity rhythms. The activity period in the bushland-grassland-mosaic was considerably shorter than in the *Imperata-Cymbopogon* grassland.

Keywords: *Mastomys* cf. *natalensis* — Home range — Activity — Radio-tracking — Rodent.

A. Nomao, J.-C. Gautun: "Dynamics of abundance and reproduction in the population of *Gerbillus nigeriae* (Rodentia, Gerbillinae) from the farm of Kolo (Niger)"

This study concerns a population of *Gerbillus nigeriae* from a farm in Kolo, near Niamey (Niger), that was submitted to a Capture-Mark-Release program on a trapping grid. Monthly trapping sessions were performed between June 1997 and May 1999. During this period, rainfall was especially low in 1997, and especially high in 1998. Among the Murinae and Gerbillinae rodents present on the site, *Gerbillus nigeriae*, the main predator on millet seedlings, was by far the most abundant species, representing 82.6% of the total captures. The dynamics of abundance of this population of *G. nigeriae* showed periods of minimal abundance at the end of the rainy season, and periods of maximal abundance during the first half of the dry season. Reproductive activity, as characterized by the size development of male genitals (testes and seminal vesicles) and by the presence of pregnant females, also displayed temporal variations. In males, sexual activity starts in June and lasts until December, i.e. during the rainy season and the first part of the dry season. In females, reprodctive activity starts in September and lasts until December at least, i.e. from the end of the rainy season to the middle of the dry season. For males as well as for females, the reproductive season may go on later in the dry season, as in 1998-1999.

Keywords: *Gerbillus nigeriae* — Sahel — Niger — Abundance — Reproduction.

T. Wube, A. Bekele: "Habitat preference of the African grass rat, *Arvicanthis dembeensis* (Rodentia, Muridae) in Koka, Central Ethiopia"

A habitat preference study was carried out on the African grass rat, *Arvicanthis dembeensis*, in Koka, Central Ethiopia from February 1997 to February 1998. Trapping was carried out consecutively for two weeks on a six month interval to accommodate both dry and wet seasons. Fifteen habitats, which mainly differed by qualitative vegetation parameters, were used as study sites. A total of 365 small mammals, which belonged to four Rodent and one Insectivorous species were

captured. A two way ANOVA showed that the catch records of the 15 sites were significantly different. Using Critical Difference (C.D.) analyses, the sites were ranked based on catch records. Habitats with moderately dense vegetation recorded high catches while those which were open fields and extremely dense bushes were less inhabited by the rats.

Keywords: *Arvicanthis* — Rodentia — Ethiopia — Habitat preference — Koka — Vegetation.

G. Shenbrot, B. Krasnov: "Geographic variation of the role of gerbills and jirds (Gerbillinae) in rodent communities across the Great Palaearctic Desert Belt"

Gerbillinae represents one of the most important components of rodent communities in the North African and Asian deserts. The number of co-existing species of gerbils and jirds reaches the maximum (13 species) in the northern part of the Sahara Desert and declines both southward (4-5 species at the southern border of Sahara) and eastward (2 species in Gobi Desert). In terms of species composition, gerbillines comprise the largest fraction of the entire rodent fauna (approximately 70%) in the North African and Arabian deserts. This fraction decreases to the northeast, reaching about 20% of all rodents in the Turan and less than 10% in the Gobi desert. Gerbils usually are abundant desert rodents and can attain high population densities (more than 50 individuals per ha). As a result, the role of gerbillines in desert rodent communities in terms of relative individual's abundance is higher than in terms of relative species richness. Gerbillines comprise 95% of all individuals of rodents in the Thar Desert, 85% of all individuals in the Negev Desert and 57-72% of all individuals in the Turan Desert. Only in the Gobi desert does the fraction of jirds decrease significantly, comprising 35% and 9% of all individuals in the Northern Gobi and in the Eastern Gobi, respectively. Being mainly medium-size rodents (body mass 25-300 g) gerbillines comprise even more massive fraction of rodent communities in terms of relative biomass. The relative biomass of gerbillines comprises 95-98% of all rodent biomass in the Negev and Thar deserts, 60-70% of rodent biomass in the Turan Desert, 40% of rodent biomass in the Northern Gobi

and only in the Eastern Gobi it decreases down to 14% of all rodent biomass. In gerbil-poor communities of Turan and Gobi deserts gerbillines are represented by folivorous and foli-granivorous habitat generalists. In gerbil-rich communities of Saharo-Sindian deserts gerbillines are more diverse both in terms of feeding modes (granivores, omnivores, folivores) and in terms of habitat specialization (habitat specialists and generalists). Diversity of habitat specialization types among gerbillines is highest in deserts around the Red Sea.

Keywords: Gerbillinae — Rodentia — Diversity — Biogeography — Community composition.

Résumés

Taxonomie et classification

A. Bannikova, L. Lavrenchenko, A. Lomov, B. Mednikov : « Diversité moléculaire de quelques espèces de *Crocidura* (Insectivores, Soricidae) d'Éthiopie »

Une étude comparative des éléments répétés ADN a été effectuée sur six espèces de *Crocidura* d'Éthiopie : *C. glassi* (2n = 36), *C. thalia* (2n = 36), *Crocidura* sp. B (2n = 36), *C. macmillani* (2n = 28), *C. parvipes* (2n = 50) et *C. olivieri* (2n = 50). Trois topologies semblables ont été obtenues à partir d'arbres de parcimonie et de « Neighbour-joining ». Les espèces à 50 et 36 chromosomes forment un groupe frère. *C. macmillani* représente une branche basale avec un support de bootstrap modéré. *Crocidura* sp. B est plus proche de *C. thalia* que de *C. glassi.*

Mots clés : *Crocidura* — Éthiopie — ADN — Taxonomie moléculaire — RFLP.

J. Crawford-Cabral, C. A. Fernandes : « Les genettes tigrines (Carnivora, Viverridae) d'Afrique centrale forment un groupe de trois espèces en Afrique australe »

Les genettes tigrines d'Afrique centrale forment un groupe inclus par certains auteurs dans *G. tigrina* ou *G. maculata* (ou *G. pardina*) et encore accepté par certains auteurs comme une espèce séparée *G. rubiginosa*. Cependant, au moins en ce qui concerne l'Afrique du Sud, les résultats de l'analyse canonique des données craniométriques montre ce groupe de genettes comme étant composé de trois espèces différentes. La forme la plus australe, caractérisée par une grande taille que nous proposons d'appeler *letabae*, comprend *rubiginosa* sensu Roberts, *letabeae* Thomas & Schwann 1906, *zuluensis* Roberts 1924 et *albiventris* Roberts 1932. La seconde espèce correspond à *zambeziana* Matschie 1902 et inclut *gleimi* Matschie 1902. Elle vit au Mozambique central et septentrional, au Malawi, en Zambie et en Angola. La troisième

espèce est connue par des spécimens du Transvaal Museum collectés à Boror (Mozambique) et identifiés par Roberts comme *Genetta mossambica* décrite de Mossimboa, Mozambique. Ces résultas suggèrent également que *G. angolensis* Bocage 1882 et *G. tigrina* sont, bien que proches, distinctes au niveau spécifique de toutes les genettes tigrines d'Afrique centrale. Cependant, elles constituent avec ces dernières un complexe d'espèces ou *G. zambesiana* et *G. letabae* constituent des super-espèces.

Mots clés : *Genetta* — Genettes tigrines — Afrique du Sud — Morphométrie crânienne — Taxonomie.

P. Gaubert, G. Véron, M. Tranier : « Une recherche des caractères morpho-anatomiques du genre *Genetta* (Carnivora, Viverridae) avec une remarque sur *Osbornictis*, la genette aquatique »

Une observation exhaustive des caractères morpho-anatomiques de quelques Viverrinae (genettes et apparentés) a permis de proposer deux clefs d'identification basées respectivement sur les caractères crâniens et sur le pelage pour le genre *Genetta*. Ce travail permet de reconsidérer la description des coussinets plantaires du très mal connu *Obsornictis piscivora*.

Mots clés : Viverrinae – *Genetta* – Morpho-anatomie – Clé d'Identification – Délimitation d'espèce.

J.-Y. Crochet, S. Peigné, M. Mahboubi : « Ancienneté des Carnivora (Mammalia) en Afrique »

L'étude des faunes africaines ante-oligocènes est primordiale pour une meilleure compréhension de l'histoire des mammifères. La découverte d'une molaire inférieure ayant appartenu à un nouveau représentant des Carnivora au Glib Zegdou (Sahara algérien) recule de quelques 23 millions d'années la présence attestée de cet ordre de mammifères en Afrique. Un âge éocène inférieur terminal à éocène moyen basal a été proposé pour le niveau fossilifère sur la base des charophytes ou éocène inférieur d'après les stades évolutifs des mammifères. Morphologiquement, cette dent est remarquable par la petite taille de son métaconide, caractère apomorphe chez

l'ensemble des carnassiers. Il s'agit très probablement d'une première molaire inférieure. Les comparaisons effectuées avec les mammifères carnassiers du Tertiaire ancien appartenant à divers ordres, en particulier celui des Creodonta, ne sont pas concluantes. Il n'est pas possible d'attribuer la dent du Glib Zegdou à l'une des familles primitives de Carnivora, Viverravidae et Miacidae, connues au cours du Paléocène et de l'Éocène : la hauteur du trigonide par rapport au talonide est beaucoup trop importante chez ces dernières. Une réduction du métaconide est parfois constatée sur la première molaire inférieure de *Legetetia nandii* (Carnivora Viverridae du Miocène inférieur du Kenya décrit par Schmidt-Kittler, 1987). Toutefois, devant l'impossibilité d'intégrer la forme du Glib Zegdou dans une famille de Carnivora, les auteurs proposent la création d'un nouveau genre et une nouvelle espèce *: Glibzegdouia tabelbalaensis*, inclus dans un sous-ordre et une famille indéterminés de Carnivora.

Mots clés : Carnivora — Eocène — Algérie – Dent — Morphologie.

K. Bâ, C. Mathiot, M. Diallo, P. Nabeth, L. Lochouarn, Y. Kane, M. Abdalahi, L. Granjon : « Étude préliminaire de quelques rongeurs réservoirs de virus pathogènes pour l'homme en Mauritanie du Sud »

En décembre 1998, 73 rongeurs appartenant à 5 espèces (*Gerbillus tarabuli, Desmodilliscus braueri, Arvicanthis niloticus, Acomys* cf. *airensis* et *Jaculus jaculus)* ont été capturés dans des habitats naturels, péri-domestiques ou domestiques dans 4 localités près d'Ayoun El Atrouss (Sud Mauritanie) ainsi que dans leurs alentours. L'identité de *G. tarabuli* (2N = 40, NFa = 74) et d'*A.* cf. *airensis* (2N = 42, NFa = 66) a été confirmée grâce aux données chromosomiques. Les sérologies IgG ont été faites par techniques immunoenzymatiques contre les virus suivants : fièvre de la vallée du Rift, Lassa, Hantaan, Puumala, Seoul, Saboya et Gabek Forest. Aucun des 7 virus cherchés n'a été trouvé dans les 51 individus testés.

Mots clés : Rongeurs — Virus — Mauritanie — Karyologie.

P. Chevret, F. Catzeflis, J. R. Michaux : « "Acomyinae" : nouvelle évidence moléculaire pour un taxon muroide (Rodentia : Muridae) »

La position taxonomique du rat épineux *Acomys* au sein des Murinae (Rodentia) a déjà été remise en question par les données immunologiques de Sarich (1985). Les données moléculaires ont par la suite exclu *Acomys* des Murinae, et en association avec deux murinae (*Uranomys* et *Lophuromys*) plus un dendromurinae *Deomys*, ce groupe a été baptisé « Acomyinae ». Nous présentons ici des résultats complémentaires d'hybridation ADN / ADN, de séquençage du gène mitochondrial 12s et du gène nucléaire LCAT qui confirment l'existence d'un clade Acomyinae comprenant *Acomys, Uranomys, Lophuromys* et *Deomys*. Il n'y a toujours pas de synapomorphie pour définir ce groupe. Nous montrons également dans ce travail que les Murinae, Gerbillinae et Acomyinae sont des groupes frères mais nous n'avons pas pu déchiffrer leurs relations de parenté.

Mots clés : Acomyinae — scnADN hybridation — 12 S rRNA — LCAT — Analyse combinée.

E. Lecompte, C. Denys, L. Granjon : « Une clef d'identification des espèces du genre *Praomys* (Rodentia : Muridae) »

Une clef d'identification pour les rats africains à fourrure douce du genre *Praomys* Thomas, 1915, basée sur des caractères morphoanatomiques du crâne, est proposée dans ce travail. La clef permet d'identifier neuf des 10 espèces reconnues actuellement : *P. degraaffi* Van der Straeten & Kerbis Peterhans, 1999, *P. delectorum* (Thomas, 1910), *P. hartwigi* Eisentraut, 1968, *P. jacksoni* (de Winton, 1897), *P. misonnei* Van der Straeten & Dieterlen, 1987, *P. morio* (Trouessart, 1881), *P. mutoni* Van der Straeten & Dudu, 1990, *P. rostratus* (Miller, 1900) *et P. tullbergi* (Thomas, 1894). Un résumé des espèces reconnues, leur distribution géographique et les données chromosomiques disponibles accompagnent cette clef.

Mots clés : Murinae — *Praomys* — Identification — Morphologie — Systématique.

I. J. A. Pavlinov : « Concepts courants de la phylogénie et de la classification des Gerbillidae »

Ce travail concerne les fondements morphologiques de la phylogénie et de la classification de la famille des Gerbillidae. Deux

structures morphologiques sont considérées comme fondamentales : la présence d'un protoconulide individualisé sur la première molaire inférieure et le type de pneumatisation de la partie mastoïde de la bulle tympanique. La présence d'un protoconulide chez certaines gerbilles est en faveur de leurs affinités myocriceétodontes. Deux types fondamentaux de pneumatisation mastoïde permettent la reconnaissance de deux sous-familles, Taterillinae et Gerbillinae *sensu stricto*, le genre *Ammodillus* ayant une position incertaine. Dans la première sous-famille on reconnaît les tribus des Taterillini *sensu stricto* et des Gerbillurini (avec les genres *Gerbillurus* et *Desmodillus*). Parmi les taterilles proprement dits, *Tatera indica* est vraisemblablement un groupe frère du groupe africain qui comprend *Taterona*, *Gerbilliscus* et *Taterillus*. Dans la sous-famille des Gerbillinae, on reconnaît quatre tribus : les tribus polytypiques des Gerbillini *sensu. stricto*. (*Gerbillus* et formes alliées) et des Rhombomyini (*Meriones* et formes alliées), et les tribus monotypiques des Desmodilliscini et des Pachyuromyini.

Mots clés : Gerbillidae — Rongeurs — Phylogénie — Classification — Morphoanatomie.

F. Sénégas : « Interprétation du patron dentaire des *Euryotomys* fossiles sud africains (Rodentia, Murinae, Otomyini) et origine de la morphologie dentaire otomyine »

Euryotomys bolti récemment décrit de la localité de Waypoint 160 (Bolt's Farm area, Gauteng Province, South Africa) apporte une évidence paléontologique supplémentaire des relations Otomyinae-Murinae. Les données moléculaires étant concordantes avec celles de la paléontologie, la sous-famille des Otomyinae devient une simple tribu, les Otomyini, au sein des Muridae. *Euryotomys pelomyoides* de la localité Plio-Pléistocène de Langebaanweg à l'Ouest de l'Afrique du Sud et *E. bolti* le plus évolué (début du Pliocène) forment une nouvelle lignée évolutive, ce qui présente un grand intérêt car il en existe très peu reconnues à présent pour le Plio-Pléistocène d'Afrique du Sud. En suivant l'approche de Van Dam (1997), l'analyse biométrique des molaires d'*Euryotomys* démontre que les deux espèces connues remplissent l'espace morphologique entre un murinae adapté à une diète herbivore et un schéma plus avancé d'*Otomys* et de *Parotomys*, ces derniers

représentant le patron dentaire le plus dérivé pour des Murinae adaptés à un régime alimentaire abrasif.

Mots clés : *Euryotomys bolti* — Pliocène — Afrique du Sud — Lignée évolutive — Modification de régime alimentaire.

P. Taylor, A. Kumirai : « Relations crâniométriques entre les rats du veld sud-africains, *Otomys irroratus* (Rodentia, Muridae, Otomyinae) et les espèces proches du nord du fleuve Zambèze »

L'étude de la variation qualitative et quantitative des caractères crâniens et dentaires d'*Otomys irroratus* permet, grâce à l'analyse en composante principale et à l'analyse discriminante, de considérer les relations de cette espèce avec les *Otomys* du nord du fleuve Zambèze, dont plusieurs avaient été inclues auparavant dans *O. irroratus*. L'hypothèse de Petter (1982) qu'*O. irroratus* est une espèce polymorphe à grande distribution géographique incluant plusieurs formes panafricaines est réfutée. Comparée aux autres espèces, *O. irroratus* a proportionnellement une plus petite bulle tympanique, ainsi que des nasaux et une région inter-orbitaire plus larges. Plus particulièrement, *O. tropicalis* (nord du fleuve Zambèze) et *O. irroratus* (sud du Zambèze) montrent peu de recouvrement des valeurs crâniométriques et peuvent être séparées sur des caractères dentaires fiables (6 lames sur la M3 / d'*O. irroratus* contre 7 ou plus chez *O. tropicalis*). De plus, *O. anchietae* par son crâne plus grand se sépare clairement des autres espèces d'*Otomys*, y compris d'autres formes du groupe d'*O. anchietae*.

Mots clés : Otomyinae — Analyse en composante principale — Analyse discriminante — Morphométrie crânienne.

Phylogénie et évolution

T. J. Robinson : « Perspectives de la cytogénétique comparative des petits mammifères africains : statut, tendances et bibliographie »

Internationalement, le champ de la cytogénétique comparative a évolué rapidement dans les années 1970 et 1980 grâce à l'utilisation des techniques chromosomiques en bandes et à la recherche des changements évolutifs dans ces dernières. Actuellement, il est possible de faire le point sur les études cytogénétiques effectuées sur les petits mammifères africains.

Bien qu'il y a eu beaucoup d'avancées significatives sur l'évolution karyotypique des espèces, l'interprétation phylogénétique de ces découvertes a stagné lorsque l'on considère les nouvelles technologiques disponibles en ce domaine. Dans beaucoup de cas, le travail est resté descriptif et a été basé soit sur les karyotypes standards soit sur des comparaison optimales de bandes. Ces méthodes pouvant suggérer de fausses homologies, il est heureux qu'elles n'aient contribué qu'en faible partie aux études phylogénétiques basées sur le banding pour placer les chromosomes dans un cadre cladistique. Il est suggéré ici que l'application des techniques d'hybridation fluorescente *in situ* est essentielle pour obtenir une identification précise des états des caractères chromosomiques pour les inférences phylogénétiques, en particulier pour les taxons caractérisés par des karyotypes hautement remaniés comme ceux trouvés chez de nombreux rongeurs. Les améliorations méthodologiques de la peinture chromosomique vont bénéficier à la cytogénétique comparative, et ceci devrait se refléter de plus en plus dans les travaux concernant les petits mammifères africains.

Mots clés : Cytogénétique — Petits mammifères — Banding — FISH — Phylogénie — Karytoype.

R. Tabuce, B. Coiffait, P.-E. Coiffait, M. Mahboubi, J.-J. Jaeger : « Contribution de la localité de Bir el Ater (Eocène, Algérie) à la connaissance des faunes mammaliennes du Paléogène d'Afrique »

L'enregistrement fossile des mammifères euthériens du Paléogène ancien est très sporadique sur le continent africain. Seuls quelques sites au Maroc, en Tunisie et en Algérie ont contribué à notre connaissance des premiers mammifères placentaires du continent arabo-africain. Ce travail présente une liste faunique actualisée de la plupart des gisements mammaliens de l'Eocène africain, et résume l'étude préliminaire des mammifères inédits de Bir El Ater (Eocène moyen à supérieur, Algérie). Hormis les restes dentaires de *Moeritherium* (Proboscidea), l'ensemble du matériel se rapporte à des mammifères de petite taille. Un carnivore ou un créodonte ainsi qu'un « insectivore » restent indéterminés. Un hyracoïde (*Bunohyrax*) semble représenter une nouvelle espèce. Un nouveau genre de macroscélididé étaye l'origine condylarthre

du groupe et constitue l'un des deux plus anciens représentants de l'ordre. Enfin, la diversité des primates est notable avec au moins quatre formes reconnues. Le genre *Algeripithecus* du Glib Zegdou (Algérie) est identifié et un Oligopithecidae constitue la plus ancienne occurrence de ce groupe de catarrhinien en Afrique.

Mots clés : Afrique — Algérie — Eocène — Mammifères endémiques — Primates.

J. Banke, A. Mess, U. Zeller : « Morphologie fonctionnelle de la région rostrale de la tête chez *Cryptomys hottentotus* (Bathyergidae, Rodentia) »

À partir de l'examen morphologique de la région rostrale de la tête, le rongeur fouisseur *Cryptomys hottentotus* est caractérisé comme suit : 1) Les incisives proodontes prennent une position extrorale permanente, 2) l'ouverture de la bouche est située derrière les incisives et la région orale est caractérisée par les *inflexa pellita* supérieures fusionnées, 3) la région *rhinarica* est située en arrière des incisives et elle est pourvue de bourrelets nasaux indistincts et de plis de peau supralabiaux, 4) le cartilage rostral nasal sous jacent manque de cloison nasale antérieure et est stabilisé ventralement par le prémaxillaire, et 5) les mouvements des régions nasales et orales sont permis grâce à la musculature faciale qui est associée au *dorsum nasi*, l'ouverture nasale, la cupule nasale antérieure, la lèvre supérieure et l'*inflexa pellita*. D'un point de vue fonctionnel lié au mode de vie fouisseur de *Cryptomys*, les incisives forment un outil de fouissage dans la région rostrale de la tête. Grâce à un mécanisme recouvrant les narines via le *dorsum nasi* flexible et la différentiation de l'*inflexa pellita*, les nasaux ainsi que la cavité orale sont protégés du substrat pendant le creusement.

Mots clés : Rongeurs — Bathyergidae — Rostre — Morphologie — Vie fouisseuse.

P. Giere, A. C. Schunke, U. Zeller : « Systématique et craniologie comparative des "Tenrecomorpha" (Mammalia, Insectivora) »

Mis à part les caractères diagnostiques du groupe des « Tenrecomorpha » traditionnellement recherchés sur des spécimens taxidermisés, le champ des observations est considérablement

étendu lorsqu'on ajoute l'étude des données morphologiques provenant de coupes sériées histologiques. De nombreux représentants des tenrecomorphes ainsi que d'autres Insectivores, Eutheriens et Metatheriens ont été comparés pour déterminer la polarité des caractères. Peu de caractéristiques de la région auditive soutiennent le clade des tenrecomorpha.

Mots clés : Tenrecomorphes — Tenrecidae — Potamogalinae — Systématique — Morphologie crânienne.

M. Kawalika, H. Burda, D. Bruggert : « La Zambie, berceau du genre *Cryptomys* (Bathyergidae, Rodentia). Une nouvelle espèce ancestrale (?) de *Cryptomys* de Zambie »

Un nouveau karyotype de Kasama, Zambie, caractérisé par 2N = 64 chromosomes est décrit. Le karyotype consiste de façon préliminaire en 21 paires de chromosomes acrocentriques plus 11 paires de chromosomes à deux bras. Nous suggérons que le *Cryptomys* de Kasama appartient à une lignée ancestrale de rats-taupes qui se sont diversifiés le long de ce qui a été appelé le corridor aride de l'Afrique centrale subtropicale.

Mots clés : *Cryptomys* — Bathyergidae — Spéciation chromosomique — Karyotype.

H. Burda : « Déterminants de la distribution et de la radiation des rats-taupes africains (Bathyergidae, Rodentia) : écologie ou géographie ? »

Les patrons de distribution des rats-taupes bathyergidae africains, révisés sur la base des données disponibles, semblent être déterminés principalement par des traits géographiques (géomorphologiques). La vallée du Rift représente une barrière importante séparant les centres d'origine et les aires de distribution de *Cryptomys* vers l'ouest, *Heterocephalus* vers l'est et *Heliophobius* encerclé par les deux branches de la vallée, les montagnes des frontières kenyo-tanzaniennes et le fleuve Zambèze. Les paramètres écologiques courants ne peuvent pas être utilisés pour une définition claire des préférences d'habitat et la délimitation des aires d'aucune espèce en particulier. Cependant, la distribution hautement irrégulière des précipitations annuelles, ainsi que les facteurs paléoécologiques et

paléoclimatiques, pourraient être responsables de la vicariance et du fort taux de spéciation de *Cryptomys* en Afrique centrale subéquatoriale (c'est-à-dire la région zambézienne incluant la Zambie et le Malawi).

Mots clés : Rats-taupes africains — Bathyergidae — Zoogéographie — Rongeurs.

A. Mess : « Différentiation et évolution de l'organisation placentaire chez les rongeurs hystricognathes »

Cette étude présente une analyse du placenta des rongeurs hystricognathes et plus particulièrement de l'organisation morphologique de ce dernier ainsi que du trajet des vaisseaux maternels et fœtaux avec une référence particulière au placenta de fin de développement. Selon les résultats présentés, le degré de lobulation du placenta diffère chez les Hystricognathi. Cependant, tous les placenta du groupe sont caractérisés par un ectoplacenta circulaire ainsi que par des artères maternelles localisées au centre ou chambres sanguines. Cette dernière condition correspond au groupe basal du patron hystricognathes et est le résultat d'une transformation le long d'une lignée souche. Ce caractère pourrait avoir évolué avant la radiation des hystricognathes en Afrique et en Amérique du Sud, c'est-à-dire à l'Eocène. Les différences profondes par rapport au groupe externe indiquent une signification importante du placenta dans l'histoire évolutive des hystricognathes. Ce résultat montre que la recherche future devra se concentrer sur une meilleure connaissance de la signification phylogénétique, évolutive et fonctionnelle de ce complexe de caractères.

Mots clés : Rongeurs — Hystricognathes — Évolution — Placentation — Biologie de la reproduction.

C. Montgelard, S. Bentz, C. Douady, J. Lauquin, F. Catzeflis : « Phylogénie moléculaire des rongeurs sciurognathes de la famille des Gliridae, Anomaluridae, Pedetidae. Implications morphologiques et paléontologiques »

L'analyse moléculaire combinée entre deux gènes mitochondriaux (cyt b et 12SRNA) et un gène nucléaire (LCAT) a été effectuée sur plusieurs familles de rongeurs sciurognathes avec un regard spécial sur les Gliridae, Anomaluridae et les

Pedetidae. Cette étude confirme que le genre *Graphiurus* appartient bien aux Gliridae et qu'il y a une relation forte entre Anomaluridae et Pedetidae. Ces deux familles africaines constituent une nouvelle lignée (sous-ordre Anomaluromorpha) parmi les rongeurs sciurognathes, ce qui avait déjà été suggéré par des caractères morphologiques. Ce résultat moléculaire contredit les relations morphologiques déduites de l'évolution de la microstructure de l'émail des incisives. Les implications des résultats morphologiques et moléculaires sont discutées à la lueur des données paléontologiques.

Mots clés : Rongeurs — Classification — Phylogénie moléculaire — Paléontologie — Émail — Incisives

Comportement, physiologie et reproduction

I. G. Van Tets, S. W. Nicolson : « L'écologie nutritionnelle des rongeurs pollinisateurs de *Protea* en Afrique du Sud »

L'écologie nutritionnelle des rongeurs pollinisateurs de *Protea* en Afrique du Sud est passée en revue. Les préférences en sucres d'*Aethomys namaquensis* sont corrélées avec la composition en sucres des espèces de *Protea* pollinisées par les rongeurs, et le xylose, un pentose trouvé dans le nectar des *Protea*, est plus volontiers consommé par les rongeurs que par les oiseaux pollinisateurs. La capacité d'*A. namaquensis* à métaboliser le xylose est une découverte intéressante. Au moins deux espèces de nectarivores saisonniers sont capables de produire une urine soit très diluée, soit très concentrée, en réponse à la quantité d'eau consommée, et *A. namaquensis* peut subvenir à ses besoins en azote à partir de petites quantités de pollen. Les fleurs de *Protea* sont ainsi susceptibles de représenter une ressource alimentaire importante pour ces animaux en hiver.

Mots clés : *Protea* — Rongeurs — Nectar — Pollen — Pollinisation.

L. N. Bennett, N. Pillay : « Réponses de mâles de *Rhabdomys pumilio* à l'urine de femelles à différents états reproducteurs »

Les réponses comportementales de mâles de *Rhabdomys pumilio* à l'urine de femelles à différents stades de leur cycle reproducteur (di-œstrus, œstrus, milieu et fin de gestation, œstrus

post-partum) ont été étudiées lors de tests de préférence à 2 stimulus. L'hypothèse de départ était que les mâles préféreraient l'urine de femelles réceptives à celle de femelles non réceptives. Les mâles ont montré une réponse équivalente à l'urine de femelles en di-œstrus et en œstrus, une préférence pour l'urine de femelles en cours de cycle par rapport à l'urine de femelle en milieu de gestation, mais pas de préférence nette entre l'urine de femelles en fin de gestation et celle de femelles cyclées. L'urine de femelles en œstrus post-partum a été préférée significativement à celle de femelles cyclées. Les mâles de *R. pumilio* sont clairement plus attirés par des femelles prêtes à être réceptives (i.e. en di-œstrus ou fin de gestation) que par celles qui ne seront réceptives qu'un certain temps plus tard (i.e. en milieu de gestation). La préférence pour les femelles en œstrus post-partum par rapport aux femelles cyclées est conforme à ce qui se passe dans la nature où les femelles sont plutôt sujettes à des alternances de gestations que de cycles œstriens.

Mots clés : *Rhabdomys pumilio* — Reproduction — Comportement — Œstrus — Odeur.

J.-M. Duplantier, K. Bâ : « Capacité natatoire chez six espèces de rongeurs d'Afrique de l'Ouest au laboratoire : évaluation de leur potentiel de colonisation des îles »

Afin d'estimer leurs capacités d'envahir les îles par leurs propres moyens, des tests de natation ont été réalisés en laboratoire sur 5 espèces de rongeurs Murinés et une de Gerbillinés. Dix individus adultes (5 mâles et 5 femelles) ont été testés dans un aquarium durant 10 mn au maximum. Pour les espèces, *Dasymys rufulus, Mastomys huberti* et *Myomys daltoni*, tous les individus ont atteint la fin du test tandis que 3 sur 10 des *Arvicanthis niloticus* et des *Tatera gambiana*, ainsi que 4 sur 10 des *Mastomys erythroleucus* ont du être retirés de l'eau avant la fin. Les plus fortes augmentations de poids, dues à l'absorption d'eau par le pelage, ont été observées chez *D. rufulus* : après 10 mn dans l'eau son poids augmente en moyenne de 25 %, alors que cette augmentation n'est que de 15 % à 20 % pour les autres espèces. Malgré cela *D. rufulus* présente le plus grand nombre de séquences de flottaison. À l'opposé,

T. gambiana semble incapable de flotter et doit nager en permanence pour ne pas se noyer. Les meilleures performances ont été observées chez une espèce vivant dans les milieux humides (*M. huberti*), mais aussi de façon plus surprenante chez *M. daltoni*, les plus mauvaises par *A. niloticus* et surtout par le Gerbilliné *T. gambiana*. Ceci concorde assez bien avec la répartition des rongeurs observée dans le delta du Saloum (Sénégal) : si *T. gambiana* est l'espèce la plus abondante dans les grandes îles connectées de temps à autre avec le continent, *M. huberti* est la seule espèce présente sur les petites îles isolées en permanence.

Mots clés : Rongeurs — Nage — Colonisation des îles — Expérimentation en laboratoire.

P. Gouat, I-E. Yahyaoui : « Résultats préliminaires sur la variabilité de la période de reproduction et la structure des groupes chez l'écureuil terrestre de Barbarie *Atlantoxerus getulus* »

L'écureuil terrestre de Barbarie, *Atlantoxerus getulus*, est endémique du Maroc et d'Algérie. L'espèce occupe une large gamme d'habitats depuis les prairies alpines jusqu'au désert. Des résultats préliminaires sur la période de reproduction et la structure des groupes sont présentés. Dans les sites de haute altitude du Haut-Atlas et de l'Anti-Atlas, la reproduction a lieu en été alors que dans les autres sites, elle a lieu au printemps. Pendant la période de reproduction, la composition des groupes varie de façon importante, même entre sites d'une région donnée.

Mots clés : *Atlantoxerus getulus* — Sciuridae — Rongeurs — Éthologie — Période de reproduction — Maroc.

R. Sumbera : « Le comportement d'accouplement du rat-taupe argenté (*Heliophobius argenteocinereus*) »

Le rat-taupe argenté *Heliophobius argenteocinereus* est un rongeur souterrain solitaire d'Afrique de l'Est. Comme souvent chez les rongeurs souterrains solitaires, sa biologie reproductive est encore mal connue. Sont présentées ici les premières données sur le comportement d'accouplement de cette espèce tel qu'observé au laboratoire. Les résultats obtenus sont comparés avec ceux décrits pour des espèces de

rongeurs apparentées ou non (Hystricognathes vs Sciurognathes) et écologiquement convergentes ou non (souterrains vs épigés, solitaires vs sociaux).

Mots clés : Bathyergidae — Convergence — Comportement — *Heliophobius* — Accouplement — Mammifères souterrains.

A. Haim, D. Afik, U. Shanas : « Réponses thermorégulatrice et métabolique à des manipulations de la photopériode dans une population de rat épineux commun, *Acomys cahirinus* »

La photopériode et la température sont des variables environnementales qui montrent des changements saisonniers. Dans l'écosystème méditerranéen, le changement de photopériode intervient avant celui de température. Sur le Mont Carmel (Israël), cet écosystème est caractérisé par une asymétrie saisonnière, avec une longue saison sèche et chaude, et une courte saison humide et froide. Une des espèces de rongeurs vivant dans cet écosystème est le rat épineux commun *Acomys cahirinus* (*Acomys dimidiatus*), d'origine africaine. Le but de ce travail est d'étudier les réponses thermorégulatrice et métabolique dans une population de cette espèce aux variations de la photopériode, afin d'évaluer ses capacités à utiliser les changements de photopériode comme un signal permettant l'acclimatation de ses systèmes métabolique et thermorégulateur. Dans cette optique, des rats épineux ont été maintenus sous deux régimes photopériodiques (16L : 8D et 8L : 16D), à température ambiante constante. Les résultats montrent que les systèmes métabolique et thermorégulateur d'*A. cahirinus* répondent aux changements de photopériode. Sous acclimatation en jours courts, la consommation de nourriture et d'énergie est plus importante que sous acclimatation en jours longs. Le rythme journalier de température corporelle change aussi en réponse aux manipulations de photopériode. Bien que les individus étudiés provenaient d'une population de milieu relativement humide, les résultats obtenus ont été similaires à ceux d'espèces de rongeurs désertiques. Cela suggère donc que cette population d'*A. cahirinus* peut utiliser des signaux photopériodiques pour son acclimatation saisonnière.

Mots clés : *Acomys cahirinus* — Thermorégulation — Réponse métabolique — Manipulations de photopériode — Nourriture — Énergie et consommation d'eau.

Écologie

D. Happold : « L'écologie des petits mammifères africains : recherches récentes et perspectives »

Cette revue décrit les recherches récentes sur l'écologie des petits mammifères africains (Insectivora, Chiroptera, Rodentia, Lagomorpha and Macroscelidea). Elle commence par des considérations sur le nombre d'espèces, l'importance des petits mammifères, et une analyse des articles publiés entre 1994 et 1998. Six sous-disciplines de l'écologie (autécologie, écologie des communautés, écologie alimentaire, écologie reproductive, écologie géographique et écologie de la conservation) sont décrites et illustrées par des exemples tirés de publications récentes. Cette revue se termine par des suggestions pour la conservation des petits mammifères et des recommandations pour des recherches futures.

Mots clés : Écologie — Petits mammifères — Afrique — Revue.

W. N. Chitaukali, H. Burda, D. Kock : « Les petits mammifères du plateau Nyika, Malawi »

Au cours de deux missions d'étude des petits mammifères dans les prairies de montagne de parties reculées du parc national du Nyika au Malawi, deux espèces de Macroscélidés, quatre espèces de Crocidures, quatre espèces de Chiroptères et 20 espèces de Rongeurs ont été trouvées. *Plerotes anchietae*, *Mylomys dybowskii* et *Grammomys ibeanus* représentent des espèces nouvelles pour le Malawi, tandis que *Crocidura hirta*, *Epomops dobsonii*, *Rhinolophus simulator*, *Pipistrellus nanus*, *Acomys spinosissimus*, *Steatomys pratensis* et *Saccostomus campestris* sont nouveaux pour le plateau du Nyika. Ces deux derniers représentent également des ajouts à la faune des régions de montagne en général. Des caryotypes non décrits précédemment ont aussi été trouvés chez plusieurs espèces de Rongeurs. Quelques aspects écologiques sont discutés.

Mots clés : Nyika Plateau — Malawi — Rongeurs — Chiroptères — Macroscelididae — Crocidurinae

V. Clausnitzer : « Les rongeurs de la zone afro-alpine du mont Elgon »

L'écologie des rongeurs des prairies de montagne a été étudiée à des altitudes supérieures à 3 500 m entre octobre 1996 et novembre 1997, puis en mars 1999 sur le mont Elgon, Ouganda. Les landes et les zones de végétation afro-alpine de ces altitudes sont habitées par 8 espèces de rongeurs ; dans les parties boisées, 5 espèces additionnelles sont trouvées. Les espèces les plus communes sont *Lophuromys flavopunctatus*, *Rhabdomys pumilio* et deux espèces d'*Otomys* : l'endémique *O. barbouri* et *O. typus*. La distribution et la densité de *R. pumilio* et des *Otomys* sont corrélées avec la structure de la végétation, l'humidité et la composition florale. *Otomys typus* et *R. pumilio* sont associés aux grandes touffes d'herbes où domine *Festuca pilgeri*. *Otomys barbouri* évite ces formations et préfère des habitats plus variés en terme de structure de végétation et diversité spécifique. *Lophuromys flavopunctatus* ne montre pas de préférence d'habitat marquée, ce qui coïncide avec son régime alimentaire d'escargots, vers et larves de Tipulidae qui sont communs partout sur la montagne. La distribution actuelle et la densité des rongeurs afro-alpins sur le mont Elgon sont fortement influencées par la distribution de la végétation telle qu'induite par les feux. Un régime de feux modéré résulte en une densité de rongeurs bien supérieure, mais pas en une diversité supérieure, par rapport aux zones à végétation « naturelle ». Une fréquence élevée de feux réduit la diversité en rongeurs, en favorisant de fortes densités chez les espèces de prairie.

Mots clés : Écologie — Ouganda — Rongeurs — *Otomys*.

G. Dobigny, R. Cornette, S. Moulin, E. Ag Sidiyène : « Les mammifères de l'Adrar des Iforas (Mali), avec mention spéciale aux petits mammifères : implications systématiques et biogéographiques »

Un inventaire des mammifères (particulièrement des petits mammifères) de l'Adrar des Iforas (Mali) a été entrepris, afin de compléter la liste des espèces de cette zone mal connue du Sahara central. Différentes méthodes ont permis de confirmer de façon non ambiguë la présence de plusieurs espèces jamais mentionnées auparavant dans l'Adrar des Iforas, et appartenant aux Rongeurs (4 espèces de *Gerbillus*, *Desmodilliscus*

braueri, *Acomys airensis*, *Myomys daltoni*, *Mus* subgenus *Nannomys* sp.), Chiroptères (*Rhinopoma hardwickei*, *Asellia tridens*) et Insectivores (*Crocidura pasha*). La présence de nombreuses autres espèces a été confirmée. À partir de là, nous proposons une liste actualisée des mammifères, sur la base de nos données et celles de la littérature. Cette compilation permet de distinguer deux types de faunes, en fonction de leurs affinités biogéographiques, suggérant ainsi un scénario biogéographique de colonisation de l'Adrar des Iforas.

Mots clés : Adrar des Iforas – Mali – Sahara – Taxonomie – Biogéographie – Mammifères.

F. Laudet, W. Hamdine : « Représentation différentielle des gerbillinés dans les pelotes de Grand Duc ascalaphe (*Bubo bubo ascalaphus*) d'Algérie du Sud-Ouest »

Une analyse taphonomique a été réalisée sur un lot de 30 pelotes de Grand-Duc ascalaphe (*Bubo bubo ascalaphus*) récoltées dans la région de Beni-Abbès (sud-ouest de l'Algérie). Les restes de 47 rongeurs (46 gerbillinés et une gerboise) ont été identifiés. On observe une variation de la représentation du matériel dentaire et crânien en fonction de la taille des proies : les mérions et la gerboise, qui forment l'essentiel des taxons au sein des pelotes où les restes d'une seule proie sont rejetés, présentent 77,2 % du nombre de dents théorique, alors que les petites proies (gerbilles), qui sont majoritairement rejetées par deux ou trois, n'en présentent que 44,2 %. En revanche, les incisives des rongeurs rejetés seuls sont beaucoup plus fréquemment digérées que les autres (41,1 % contre 5,6 %). L'élaboration de plusieurs pelotes quand la ou les proies digérées dépassent un certain volume, incluant la séparation du crâne d'avec le reste du squelette, pourrait expliquer de telles observations. Les conséquences sur les calculs de représentation des rongeurs d'un assemblage actuel ou fossile issu d'une accumulation de pelotes sont discutées.

Mots clés : Pelotes de rapaces — Taphonomie — Multiréjection — Rongeur — *Bubo bubo ascalaphus* — Algérie.

A. Hoffmann, H. Klingel : « Caractéristiques spatiales et temporelles chez *Mastomys* cf. *natalensis* (Smith, 1834) révélées par radio-pistage »

Une étude par radio-pistage a été menée chez *Mastomys* cf. *natalensis* dans les prairies du Queen Elizabeth Park en Ouganda. Les domaines vitaux calculés par Ranges V avec la méthode des Polygones convexes minimum (à 95 %) étaient en moyenne 4 fois plus grands dans la zone de végétation mosaïque à buissons que dans la prairie à *Imperata-Cymbopogon*. Une relation inverse a été trouvée entre la taille du domaine vital et la densité de population. Dans les deux types d'habitats, l'espèce était nocturne, mais avec des rythmes d'activité différents. La durée d'activité dans la mosaïque de prairie à buissons était beaucoup plus courte que dans la prairie à *Imperata-Cymbopogon*.

Mots clés : *Mastomys* cf. *natalensis* — Territoire — Activité — Radio-pistage – Rongeur.

A. Nomao, J.-C. Gautun : « Dynamique de l'abondance et de la reproduction de la population de *Gerbillus nigeriae* (Rodentia, Gerbillinae) dans la ferme de Kolo (Niger) »

Cette étude concerne une population de *Gerbillus nigeriae* vivant dans la ferme de Kolo, près de Niamey au Niger. Le suivi de la population a été fait par capture-marquage-recapture sur une grille de piégeage. Les piégeages réalisés selon une fréquence mensuelle se sont déroulés entre juin 1997 et mai 1999. Cette période de 2 ans comporte une année de pluviométrie très déficitaire (1997) et une année à pluviométrie fortement excédentaire (1998). Parmi le peuplement identifié qui se compose de Murinae et de Gerbillinae dont *Gerbillus nigeriae*, le principal déprédateur des semis de mil, qui est le rongeur le plus abondant avec 82,6 % des captures. Concernant la dynamique de l'abondance de cette population de *Gerbillus nigeriae*, on a constaté la présence de périodes où l'abondance passe par un niveau minimum en fin de saison des pluies et d'autres où l'abondance passe par un maximum qui se place dans la première moitié de la saison sèche. L'activité reproductrice de *Gerbillus nigeriae*, caractérisée par le développement en taille des organes génitaux mâles (testicules et vésicules séminales) et par la présence de femelles

portant des embryons, présente également des variations d'intensité selon des périodes de l'année. Chez les mâles, l'activité sexuelle s'installe en juin et se poursuit jusqu'en décembre, soit durant la saison des pluies et la première partie de la saison sèche. Chez les femelles, l'activité reproductrice s'installe à partir de septembre et se poursuit au moins jusqu'en décembre, soit de la fin de la saison des pluies au milieu de la saison sèche. La saison de reproduction peut, aussi bien chez les mâles que chez les femelles, se prolonger largement durant la saison sèche comme cela a été le cas en 1998-1999.

Mots clés : *Gerbillus nigeriae* — Sahel — Niger — Abondance — Reproduction.

T. Wube, A. Bekelé : « Préférence d'habitat chez *Arvicanthis dembeensis* (Rodentia, Muridae) à Koka, Éthiopie centrale »

Une étude des préférences d'habitat d'*Arvicanthis dembeensis* a été menée entre février 1997 et février 1998 à Koka, en Éthiopie centrale. Des piégeages de deux semaines ont été effectués tous les 6 mois, pour prendre en compte les saisons sèches et humides. Quinze habitats, différant surtout par des paramètres de végétation qualitatifs ont été échantillonnés. Un total de 365 petits mammifères, appartenant à 4 espèces de Rongeurs et une espèce d'Insectivores, ont été capturés. Une analyse de variance à deux facteurs a montré que les résultats de capture étaient significativement différents entre les 15 sites. À partir d'analyses critiques de différences, les sites ont été classés sur la base des résultats de capture. Les habitats avec une densité de végétation modérément dense ont enregistré les taux de capture les plus importants, alors que les habitats les plus ouverts et ceux à buissons denses étaient beaucoup moins occupés par les Rongeurs.

Mots clés : *Arvicanthis* — Rongeurs — Éthiopie — Préférence d'habitat — Koka — Végétation.

G. Shenbrot, B. Krasnov : « Variation géographique du rôle des gerbilles et des mériones (Gerbillinae) dans les communautés de rongeurs des déserts paléarctiques »

Les Gerbillinae représentent un des composants les plus importants des communautés de Rongeurs des déserts d'Afrique du

Nord et d'Asie. Le nombre d'espèces sympatriques de gerbilles et de mériones atteint un maximum (13 espèces) dans la partie nord du Sahara et diminue vers le sud (4-5 espèces au sud du Sahara) et vers l'est (2 espèces dans le désert de Gobi). En termes de composition spécifique, les gerbillinés représentent la part principale des faunes de rongeurs (environ 70 %) dans les déserts d'Afrique du Nord et d'Arabie. Cette part décroît vers le nord-est, jusqu'à 20 % dans le désert de Turan et moins de 10 % dans le désert de Gobi.

Les gerbilles sont généralement abondantes, pouvant atteindre des densités de populations élevées (plus de 50 individus par hectare). De ce fait, leur rôle dans les communautés de rongeurs désertiques en termes d'abondance individuelle relative est plus important qu'en termes de richesse spécifique relative. Les gerbillinés représentent 95 % de l'ensemble des individus de rongeurs dans le désert de Thar, 85 % dans le Negev et de 57 à 72 % dans le Turan. C'est seulement dans le Gobi que le pourcentage représenté par les mériones décroît significativement, avec 35 % et 9 % dans le nord et l'est du Gobi, respectivement. Comprenant essentiellement des rongeurs de taille moyenne (entre 25 et 300 g), les gerbillinés représentent une fraction encore plus importante des communautés de rongeurs en termes de biomasse relative : 95 % à 98 % de toute la biomasse de rongeurs dans le Negev et le Thar, 60 % à 70 % dans le Turan, 40 % dans le nord du Gobi, et seulement 14 % dans l'est du Gobi. Dans les communautés pauvres en gerbilles des déserts de Turan et de Gobi, les gerbillinés sont représentés par des folivores et des folivores-granivores généralistes au niveau de leurs préférences d'habitat. Dans les communautés riches en gerbilles des déserts saharo-sindiens, les gerbillinés sont plus divers dans leur régime alimentaire (granivores, omnivores, folivores) et leur sélection d'habitat (spécialistes et généralistes). La diversité des types de spécialisation d'habitat parmi les gerbillinés est la plus importante dans les déserts autour de la mer Rouge.

Mots clés : Gerbillinae — Rongeurs — Diversité — Biogéographie — Structure des communautés.

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Small mammals constitute about 80 % of the African mammalian diversity and they occur in all environments. Despite the fact that many small mammal species are of great economical and medical importance, many aspects of their systematics and biology are still not well known.
This volume attempts to fill some of these gaps by presenting recent studies on taxonomy, phylogeny, classification, eco-ethology and ecology of various insectivores, carnivores and rodents from different African countries. Moreover, inventories for scarcely explored regions provide new data on African biodiversity. This volume highlights the most recent advances in fundamental and applied research concerning African small Mammals.

Africa – Mammals – Systematics – Phylogeny – Ecology – Physiology – Ethology – Biogeography

Les petits mammifères représentent environ 80 % de la diversité mammalienne africaine et on les rencontre dans tous les environnements. Malgré leur intérêt économique et médical, de nombreux aspects de leur systématique et de leur biologie restent encore mal connus.
Ce volume présente des travaux récents sur la taxonomie, la phylogénie, la classification, l'éco-éthologie et l'écologie d'insectivores, carnivores et rongeurs de différentes régions d'Afrique. De plus, quelques inventaires effectués dans des régions peu explorées éclairent notre connaissance de la biodiversité africaine. Les aspects les plus récents de la recherche fondamentale et appliquée sur les petits mammifères africains sont exposés dans cet ouvrage.

Afrique – Mammifères – Systématique – Phylogénie – Écologie – Physiologie – Éthologie – Biogéographie

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