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Species delimitation in the *Acomys cahirinus–dimidiatus* complex (Rodentia, Muridae) inferred from chromosomal and morphological analyses

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Our earlier chromosome banding studies of *Acomys cahirinus* and *Acomys dimidiatus* (the latter long considered to be a subspecies of the former) revealed that, despite very close diploid numbers (36 vs. 38), these taxa possess sharply different karyotypes and undoubtedly belong to different species. In this context, the taxonomic status and the relationship between the two chromosomal forms in Sinai ($2n = 36$) and Israel ($2n = 38$), chromosomally homozygous across a vast range except for a very narrow hybrid zone, remain poorly documented. Neither of these forms have previously been studied by chromosome banding; thus, the exact nature of chromosomal differences as well as the species to which these forms should be assigned remain unknown. Here, we present the data on comparative G-banding analysis and morphometrics of *Acomys* from Israel, Sinai, and Saudi Arabia, and a hybrid obtained in laboratory crosses between latter two. The analysis revealed that karyotype of *Acomys* from Israel is identical to that of *Acomys* from Saudi Arabia and both are different from that of *Acomys* from Sinai by one Robertsonian fusion. Therefore, karyotypically, all three are very different from *A. cahirinus*. It follows from the study that Sinai and probably Arabian peninsula and Minor Asia must be excluded from geographical distribution of *A. cahirinus*, which is limited from West Sahara to Egypt along Nile river (except Sinai). Furthermore, the synthesis of chromosomal and recent molecular data suggests a phylogeographical scenario explaining the modern distribution of *Acomys* in the Sinai and Arabian peninsulas and permits the update of the taxonomic status of these populations. *Biological Journal of the Linnean Society*, 2007, **91**, 203–214.

ADDITIONAL KEYWORDS: chromosomes – distribution – morphology – morphometrics – taxonomy.

INTRODUCTION

Different aspects of the systematics of spiny mice (genus *Acomys*) remain controversial particularly regarding the species composition, their distribution limits, and their phylogenetic affinities (Musser & Carleton, 1993 and references therein). The *cahirinus–dimidiatus* complex represents the most debated grouping within the genus: 17 taxa are included in this complex but, according to various authors, are considered to be either separate species, subspecies, or synonyms of either *Acomys cahirinus* or *Acomys dimidiatus* (Ellerman, 1941; Rosevear, 1969; Setzer, 1975; Petter, 1983; Harrison & Bates, 1991; Musser & Carleton, 1993). Additionally, the specific status of *A. dimidiatus* has not yet been recognized officially (Honacki, Kinman & Koeppl, 1982; Corbet & Hill, 1991; Musser & Carleton, 1993). Whatever their

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opinions, systematicists agree that the *cahirinus–dimidiatus* group may comprise several morphologically similar species (Petter, 1983; Janacek, Schlitter & Rautenbach, 1991; Musser & Carleton, 1993; Denys *et al*., 1994; Barome, Monnerot & Gautun, 1998, 2000).

Acomys cahirinus was described as *Mus cahirinus* in 1819 by Desmarest, based on a small sample of specimens brought from Cairo, Egypt, by Etienne Geoffroy Saint-Hilaire (Desmarest, 1819, cited by Rosevear, 1969). *Acomys dimidiatus* was described as *Mus dimidiatus* in 1826, by Cretzschmar, based on a specimen caught in the vicinity of Saint Catherine monastery in Sinai mountains by Rüppell (Cretzschmar, 1826, cited by Rosevear, 1969). Another subspecies of *A. dimidiatus* was subsequently described in Arabia, *A. d. homericus* Thomas, 1923. However, morphological studies of the *cahirinus–dimidiatus* group and other species (*Acomys cineraceus*, *Acomys spinosissimus*, and *Acomys wilsoni*) whose taxonomic status is debatable (Barome *et al*., 2000, 2001), has led to variable estimates of the number of species in the genus, from 38 (Ellerman, 1941) to 14 (Musser & Carleton, 1993), nine (Corbet & Hill, 1991), or even seven (Honacki *et al*., 1982). Apart from Ellerman (1941) and Denys *et al*. (1994), all these authors considered *A. dimidiatus* and its subspecies as subspecies of *A. cahirinus*.

By contrast to the limited contribution of morphoanatomical approaches, chromosome banding analysis has turned out to be a powerful tool for the discrimination of spiny mice species. In particular, comparison of chromosome banding patterns of *Acomys* cf. *A. dimidiatus* ($2n = 38$, $NF = 70$) from Taif (Saudi Arabia) and *A. cahirinus* ($2n = 36$, $NF = 68$) from Cairo (Egypt) (Volobouev, Tranier & Dutrillaux, 1991, Volobouev, Gautun & Tranier, 1996) with those of *A. airensis* ($2n = 42$, $NF = 68$) from Agadès (Niger) (Viegas-Péquignot *et al*., 1983; our data) revealed that their karyotypes show practically complete arm homology; however, apart from one metacentric pair common to *A. cahirinus* and *A. dimidiatus* (Kunze *et al*., 1999), they do not share any identical biarmed chromosomes due to different sequences of fusions of acrocentric chromosomes into metacentric ones. In addition to a large monobrachial homology, one tandem translocation distinguishes *A. cahirinus* and *A. airensis* from *A.* cf. *A. dimidiatus* that results in change of the number of chromosomal arms (*NF*) from 70 to 68. These studies indicate that, despite rather close diploid and fundamental numbers, these three taxa clearly possess different karyotypes and are strongly isolated cytogenetically from one another. This conclusion is in a good agreement with recent data on cytochrome *b* gene sequencing showing substantial nucleotide distances between these three species and their topology on the cladogram (Barome *et al*., 1998, 2000).

By contrast to these findings which have clarified the specific distinction between *A. cahirinus* ($2n = 36$, $NF = 68$) from Egypt and *A.* cf. *A. dimidiatus* ($2n = 38$, $NF = 70$) from Arabia, the taxonomic status and the relationship between the two parapatric chromosomal forms ($2n = 36$ and $2n = 38$) of the Sinai and Israel remain poorly documented. These last two forms share the same $NF = 70$, but both have been referred to *A. cahirinus* (Zahavi & Wahrman, 1956; Wahrman & Goitein, 1972) following a generally accepted taxonomic arrangement (for references, see Musser & Carleton, 1993). On the basis of meiosis in the hybrids naturally occurring in the contact zone between these two forms, Wahrman & Goiten (1972) concluded that the two forms differed by one Rb fusion/fission rearrangement. However, because none of these forms have been studied with banding techniques, the exact nature of chromosomal differences as well as the species to which these forms should be assigned remain unknown. Similarly, no morphological or morphometrical study has yet been carried out on the *Acomys* taxa from these localities.

Due to confusion resulting from previous morphoanatomical and chromosomal treatments, the distributions of both *A. dimidiatus* and *A. cahirinus* remain to be precisely determined, as does the status of *Acomys* from Israel and Arabia. To answer these questions, we present data on comparative G-banding analyses of *Acomys* from Israel, *Acomys* from Sinai, *Acomys* from Saudi Arabia, and a hybrid obtained in laboratory crosses between two latter. We also present data on morphological and morphometrical analyses involving type specimens and those preliminary karyotyped and/or sequenced.

MATERIAL AND METHODS

Cytogenetic analysis

Three specimens of *A.* cf. *A. dimidiatus* were collected from Saudi Arabia: one male and one female were captured in the vicinity of Taif (1500 m a.s.l.) (21°15′N, 40°21′E), whereas a further male came from Abba, near the Yemen border (2000 m a.s.l.) (18°14′N, 42°31′E). Two additional specimens (male and female) of *Acomys* sp. were collected from Quorenit, approximately 50 km north-east of Haifa, Israel (32°48′N, 34°59′E) and two further specimens, *A. dimidiatus s.s.*, were collected from Sinai mountain, near Saint Catherine monastery (28°32′N, 33°59′E). One male, an F_1 hybrid between *Acomys* from Taif and *A. dimidiatus s.s.* from Sinai was obtained from a successfully hybridizing colony kept at the Mammifères et Oiseaux laboratory of the Paris Museum National

Table 1. List of voucher specimens used for DNA sequencing, cytogenetics and morphometrics

Species	Locality/country	Voucher number	Mor	Cyto	DNA
Acomys dimidiatus					
Topotype *dimidiatus*	Sinai, Egypt	NHM 76.3.7.2	x		
dimidiatus	Sinai, Egypt	NHM 94.7.20.1	x		
dimidiatus	Sinai, Egypt	MNHN-CG 1996-426	x	x	x
dimidiatus	Sinai, Egypt	MNHN-CG 1996-428	x		
d. dimidiatus	Sinai (breed)	MNHN-1996-427	x		
d. dimidiatus	Sinai, Egypt	MNHN-1996-424	x	x	x
d. dimidiatus	Sinai,St Catherine, Egypt	MNHN-1997-1368	x	x	
dimidiatus	Sinai, Egypt	MNHN-2001-15	x		
Holotype *dimidiatus*	Sinai, Egypt	SMNH 4321	x		
Paralectotype *dimidiatus*	Sinai, Egypt	SMNH 26199	x		
dimidiatus	Taif, Saudi Arabia	MNHN-CG 1996-443	x		
dimidiatus	Abha, Saudi Arabia	MNHN-CG 1996-433	x	x	
dimidiatus	Quorenit, Israel	MNHN-CG 2005-348	x	x	
dimidiatus	Israel (breed)	MNHN-CG 2001-1	x		
dimidiatus	Taif, Saudi Arabia	ISEM N213	x		
dimidiatus	Taif, Saudi Arabia	ISEM N206	x		
dimidiatus	Taif, Saudi Arabia	ISEM N212	x		
dimidiatus	Taif, Saudi Arabia	ISEM N210	x		
dimidiatus	Taif, Saudi Arabia	ISEM N214	x		
dimidiatus	Taif, Saudi Arabia	ISEM N188	x		
dimidiatus	Taif, Saudi Arabia	MNHN-CG 1991-331	x		
dimidiatus	Taif, Saudi Arabia	MNHN-CG 1997-1373	x	x	
dimidiatus	Taif, Saudi Arabia	MNHN-CG 2001-17	x		
dimidiatus	Taif, Saudi Arabia (breed)	MNHN-CG 1992-1811	x		
dimidiatus	Taif, Saudi Arabia (breed)	MNHN-CG 1992-1810	x		
Hybrid	Taif–Sinai	MNHN-CG 2004-155	x	x	
Hybrid	Taif–Sinai	MNHN-CG 2001-14	x		
Hybrid	Taif–Sinai	MNHN-CG 2001-13	x		
Hybrid	Taif–Sinai	MNHN-CG 2001-12	x		
Acomys cahirinus					
Paratype *cahirinus*	Cairo, Egypt	MNHN-CG 1989-24	x		
Holotype *cahirinus*	Cairo, Egypt	MNHN-CG 1989-23	x		
Paratype *cahirinus*	Cairo, Egypt	MNHN-AC7453	x		
Paratype *cahirinus*	Cairo, Egypt	MNHN-AC748	x		
cahirinus	Cairo, Egypt	MNHN-CG 1999-6	x	x	x
cahirinus	Cairo, Egypt	MNHN-CG 1996-432	x		
cahirinus	Cairo, Egypt	MNHN-CG 1996-431	x		
cahirinus	Cairo, Egypt	MNHN-CG 1996-430	x		

NHM, Natural History Museum (London); MNHN, Muséum National d'Histoire Naturelle (Paris); CG, Catalogue Général; SMNH, Senckenberg Museum,(Frankfurt); ISEM, Institut des Sciences de l'Evolution (Montpellier); Mor, Specimens examined in morphological analysis; Cyto, Specimens karyotyped; DNA, specimens from which cytochrome *b* has been sequenced by Barome *et al*. (2001).

d'Histoire Naturelle (MNHN) by one of us (C.D.). One male specimen of *A. cahirinus* was captured in the suburbs of Cairo, Egypt (30°03′N, 31°15′E). The skulls and skins of the studied specimens are preserved at the MNHN where they are currently catalogued in the MNHN collection (Table 1).

Chromosome analysis was performed on preparations obtained from fibroblast cultures from tail biopsies. Mitotic chromosomes were studied with GTG-banding in accordance with Seabright (1971). For each specimen, at least 20 metaphase plates were analysed.

Morphological and morphometrics analyses

Morphometrics analyses have been performed on karyotyped specimens plus those collected at the same

times and in the same localities for which karyotyping failed. The holotypes and type-series of *A. cahirinus* and *A. dimidiatus* have been examined and, when possible, measured. The hybrid specimens obtained by breeding in captivity were also incorporated to the analyses (Table 1). Using results of karyotype and sequences identifications, principal component analysis (PCA) were performed on 40 specimens and on ten skulls measurements (*sensu* Denys *et al*., 1994) using XLSTAT, Version 5.2 (Addinsoft, Paris and New York).

RESULTS

Cytogenetic analysis

The karyotype of *Acomys* sp. from Moreshet (Israel) has $2n = 38$ and consists of 16 pairs of meta- to submetacentric and two pairs of acrocentric autosomes. Both sex chromosomes, a medium-sized X and a small Y, are acrocentric, thus resulting in $NF = 70$ (Fig. 1).

The chromosome set of *Acomys* from Sinai comprises 17 pairs of biarmed autosomes and acrocentric X and Y chromosomes ($2n = 36, NF = 70$); the sex chromosomes are similar in size to those of 38 chromosome *Acomys* from Moreshet (Fig. 2).

The karyotype of three specimens of *Acomys* from Arabia is identical to that of *Acomys* from Moreshet ($2n = 38$, $NF = 70$) (Fig. 3).

The chromosomal complement of a laboratory obtained F_1 hybrid between *Acomys* from Sinai ($2n = 36$) and *Acomys* from Arabia ($2n = 38$) comprised 17 pairs of autosomes one of which was composed of biarmed chromosome identical to pair 17 of *Acomys* from Sinai and two different acrocentrics corresponding to chromosomes 17 and 18 of *Acomys* from Arabia, thus resulting in $2n = 37$, $NF = 70$ (Fig. 3).

The karyotype of *A. cahirinus* ($2n = 36$, $NF = 68$) from Egypt contains 16 pairs of bi-armed and one pair of acrocentric autosomes, and two sex chromosomes similar in size and morphology to those of *Acomys* from Israel, Sinai, and Saudi Arabia (Fig. 4).

Comparison of G-banding patterns revealed that karyotypes of *Acomys* from Israel and *Acomys* from Arabia are identical ($2n = 38$, $NF = 70$) and both are different from that of Sinaitic form by one Rb rearrangement (Fig. 3). By contrast, the comparison of G-banding between *A. cahirinus*, on the one hand, and *Acomys* from Israel, Sinai, and Saudi Arabia, on the other hand, showed that, apart from one common pair 8 (Figs 3, 4), they do not share any identical bi-armed chromosome due to different sequence of fusions of acrocentric chromosomes into metacentric ones (for more details, see Volobouev *et al*., 1996).

Morphological and morphometric study

A morphological comparison between skulls of types of *A. dimidiatus* and karyotyped specimens of *Acomys* from Taif has been made earlier (Volobouev *et al*.,

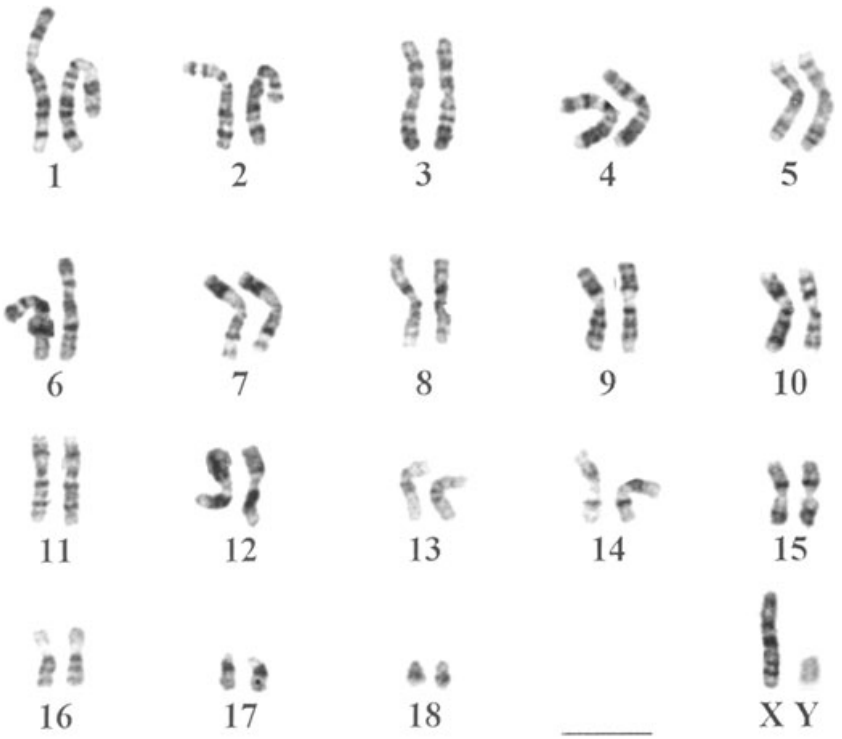

Figure 1. G-banded karyotype of male *Acomys* from Israel, $2n = 38$. Scale bar = 10 μm.

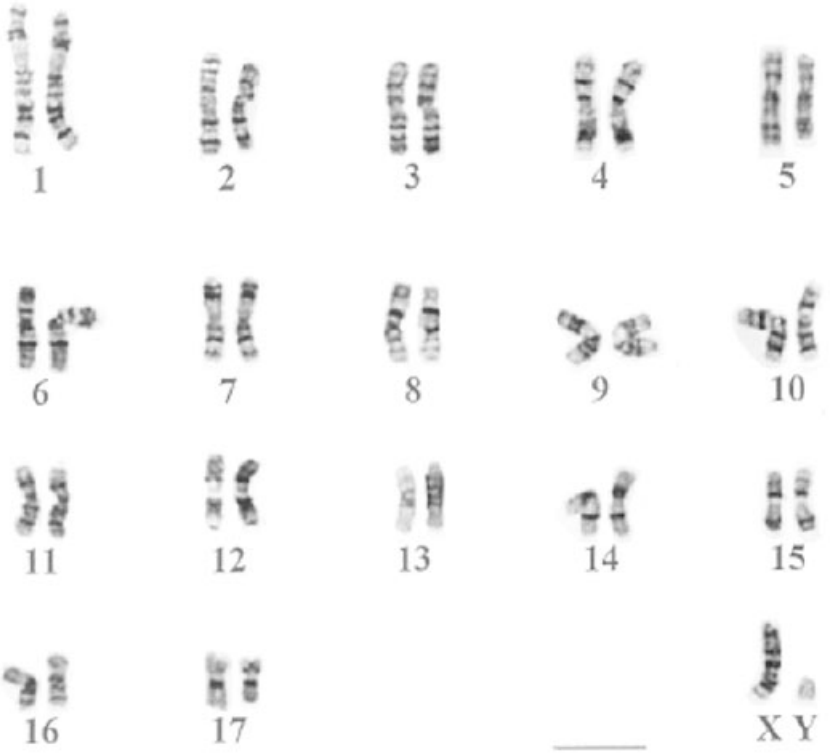

Figure 2. G-banded karyotype of male *Acomys* from Sinai, $2n = 36$. Scale bar = 10 μm.

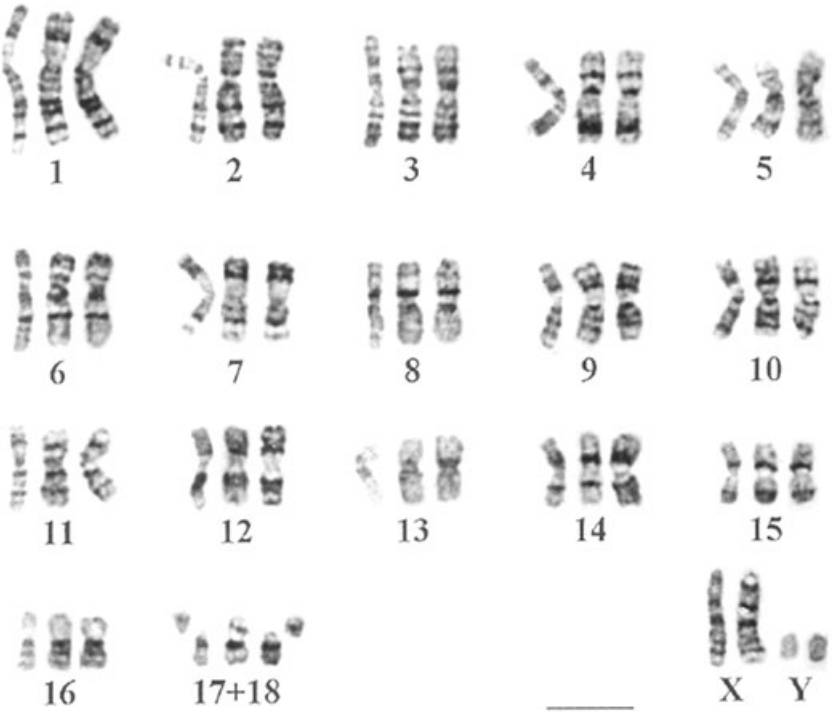

Figure 3. Comparison of G-banding patterns between *Acomys* from Israel, $2n = 38$ (left) and the F_1 hybrid (36 chromosome *Acomys* from Sinai X 38 chromosome *Acomys dimidiatus* from Saudi Arabia), $2n = 37$ (centre, right). Scale bar = 10 μm.

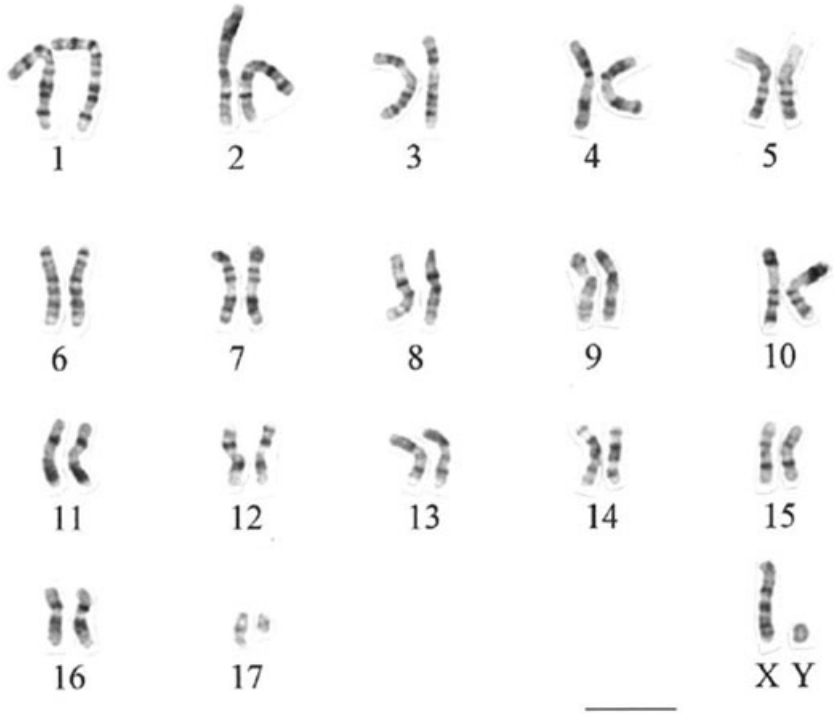

Figure 4. G-banded karyotype of male *Acomys cahirinus* from Egypt, $2n = 36$. Scale bar = 10 μm. Note that, except for pair 8, the arm composition of autosomes is different from that of *Acomys* from Israel, Sinai, and Saudi Arabia.

Table 2. Summary of cytogenetical, biometrical (average values in mm) and morphological differences between *Acomys dimidiatus* and *Acomys cahirinus*

Characters	*Acomys dimidiatus*	*Acomys cahirinus*
Karyotype	$2n = 36$–38, $NF = 70$	$2n = 36$, $NF = 68$
Skull length	27.00–34.56 mm ($N = 24$)	27.35–30.25 mm ($N = 6$)
Head and body length	112 mm (85–129 mm, $N = 11$)	103 mm (101–105 mm, $N = 2$)
Tail length	103 mm (88–117 mm, $N = 5$)	116 mm ($N = 1$)
Upper molar row	4.58 mm ($N = 27$)	3.96 mm ($N = 8$)
Lower molar row	4.26 mm ($N = 26$)	3.82 mm ($N = 7$)
Upper first molar M/1	T3 posterior to t2	T3 at the same level as t2
Lower M/1	Tma incorporated into the prelobe	Tma very small or absent, not linked to prelobe
Cusps	Linked with crests	Poorly linked, more bunodont

1991). The type skull of *A. dimidiatus* is in poor condition, but molar characters can still be observed (Fig. 5, Table 2). The type of *A. cahirinus* belonged to a very young animal (wear stage 2 for the upper molar row and stage 3 to the lower one). The skull and mandible are different sizes, and the type may be a composite mismatched specimen (Fig. 6). Comparisons with *A. dimidiatus* are made through the use of two topotypes at same wear stage and some differences can be specific, such as the generalized presence of anteromedian tubercle (tma) on the lower M1 of *A. dimidiatus* and the more aligned t3 and bunodont cusps of *A. cahirinus*, as already suggested by Setzer (1959) and Osborn & Helmy (1980) on Egyptian collections. Most of the skull and external measurements are larger in *A. dimidiatus* than *A. cahirinus*. Lengths of upper molar rows of *A. cahirinus* and *A. dimidiatus* do not overlap (Table 3).

Principal components analysis of the *A. cahirinus*–*dimidiatus* specimens shows a size gradient along axis 1 (93% of the variance was explained). We interpreted this axis as size because all variables are positively correlated with it (Fig. 7). Axis 2 separates the two $2n = 38$ specimens of Taif-Israel on one side from the $2n = 36$ population from Sinai. The two DNA sequenced specimens are outliers along this axis.

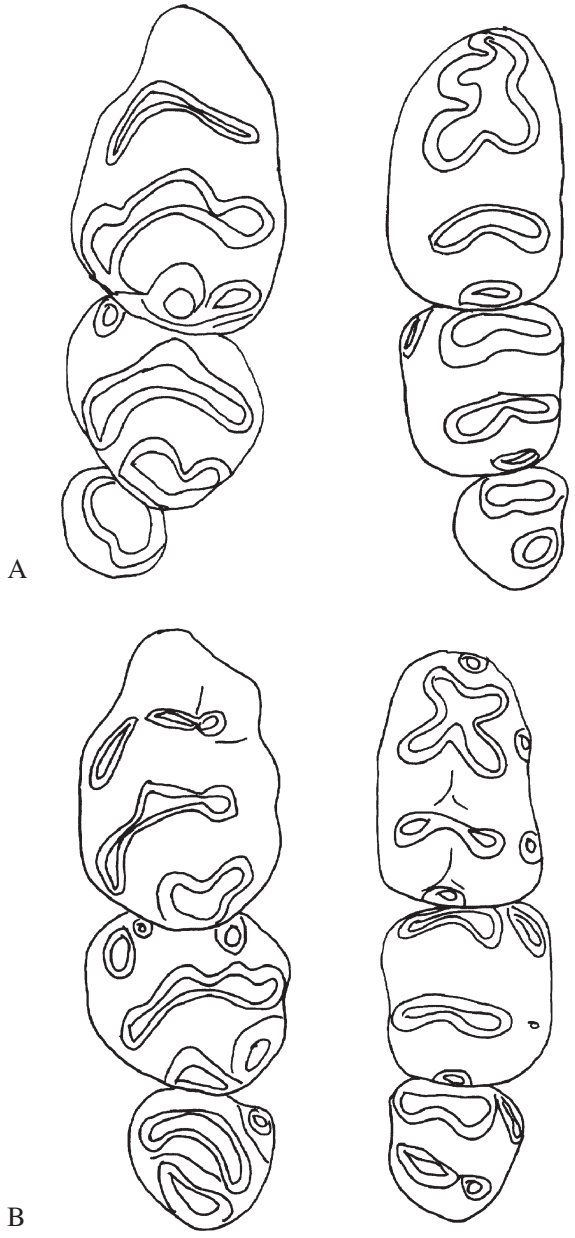

Figure 5. A, *Acomys dimidiatus*: type specimen SMNH 4321 upper and lower molars. B, *Acomys dimidiatus*: CG MNHN 1991-331 from Taif (karyotyped) (× 18).

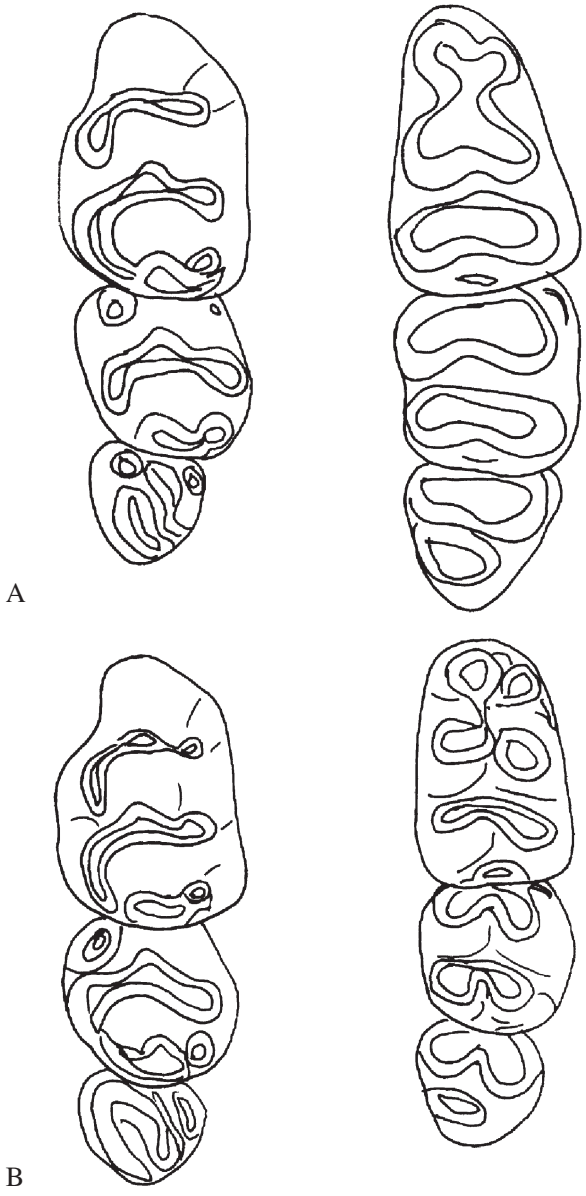

Figure 6. A, *Acomys cahirinus*: type specimen CG MNHN 1989-24 upper and lower molars (from Cairo, Egypt). B, *Acomys cahirinus* paratype from Cairo CG MNHN 1989-23 (× 18).

The PCA performed only on the *A. dimidiatus* sample, including the Taif–Sinai hybrids, shows no clear distinction between specimens with $2n = 36$ and $2n = 38$ on axes 1 and 2 (Fig. 8). The hybrids have the largest variability and the karyotyped one, a young individual, makes a strong contribution to axis 1. As shown in Figure 7, the two sequenced samples from Sinai are opposed along axis 2 and illustrate the low level of differences between the two cytotypes.

DISCUSSION

SPECIES LIMITS BETWEEN *A. DIMIDIATUS* AND *A. CAHIRINUS*

As established earlier, the 36 (Sinai) and 38 (Israel) chromosomal forms of *Acomys* freely hybridize in the contact zones and produce fertile hybrids (Wahrman & Goiten, 1972). Although we have karyotyped only one F_1 hybrid between *Acomys* from Arabia and *Acomys* from Sinai, a hybridization between F_1 and hybrids of further generations was also successful (C. Denys,

Table 3. Standard statistical parameters for skull and external measurements of *Acomys cahirinus* and *Acomys dimidiatus*

	LGT	WZYG	CIO	LNAS	WNAS	LS13	LBT	LI13	LMDB	HMDB	HB	TL	HF	E
Acomys cahirinus														
N	6	7	7	6	7	8	7	7	6	6	2	1	2	2
Minimum	27 350	11 000	4320	9140	3220	3790	4830	3590	16 770	6530	101 000	116 000	19 000	18 000
Maximum	30 250	13 680	4990	11 410	3590	4140	6000	4490	18 880	8270	105 000	116 000	20 000	19 000
Mean	29 117	12 853	4663	10 815	3379	3956	5580	3821	18 353	7212	103 000	116 000	19 500	18 500
CV	0 040	0 079	0048	0 078	0040	0029	0074	0079	0 043	0082	0 027	0 036	0 038	
SD	1 067	0 943	0207	0 769	0124	0109	0380	0280	0 719	0540	2 000	0 000	0 500	0 500
Acomys dimidiatus														
N	24	26	27	18	21	27	19	26	18	17	11	5	11	11
Minimum	27 020	12 570	4600	10 250	2700	4310	5150	3960	16 390	5860	85 000	88 000	19 000	18 000
Maximum	34 560	16 060	6100	13 830	4380	4840	6610	4710	21 390	7830	129 000	117 000	22 000	22 000
Mean	31 171	14 423	4974	12 407	3619	4576	5843	4256	19 390	7206	112 182	103 200	20 545	20 000
CV	0 062	0 063	0057	0 085	0128	0035	0070	0043	0 073	0074	0 103	0 130	0 059	0 062
SD	1 881	0 887	0279	1 024	0452	0157	0397	0181	1 383	0518	11 052	11 957	1 157	1 187

N, Number of specimens measured; minimum–maximum, minimum and maximum values of the measurement (mean is the average value); CV, coefficient of variation (SD/mean); SD, standard deviation; LGT, total length of the skull; WZYG, width of zygomatic arches; CIO, width of interorbital constriction; WNAS, width of nasal bones in the anterior part of the rostrum; LS13, length of upper molar row; LBT, maximum length of tympanic bullae; Ll13, length of lower molar row; LMDB, length of the mandible; HMDB, height of the mandible; HB, head and body length; TL, tail length; HF, hindfoot length; E, ear length.

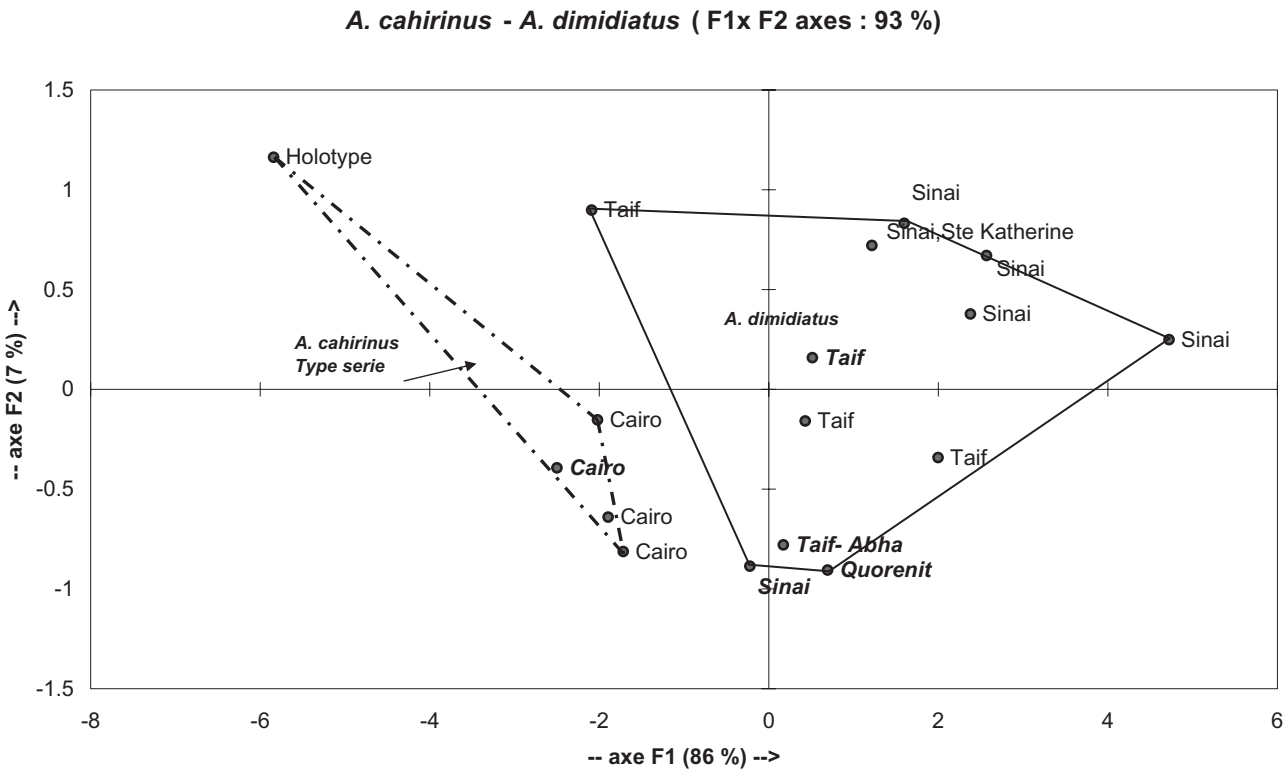

Figure 7. Graph of the first two principal component axes of karyotyped *Acomys cahirinus–dimidiatus* specimens (40 individuals, 15 skull measurements). Karyotyped or sequenced specimens are shown in bold.

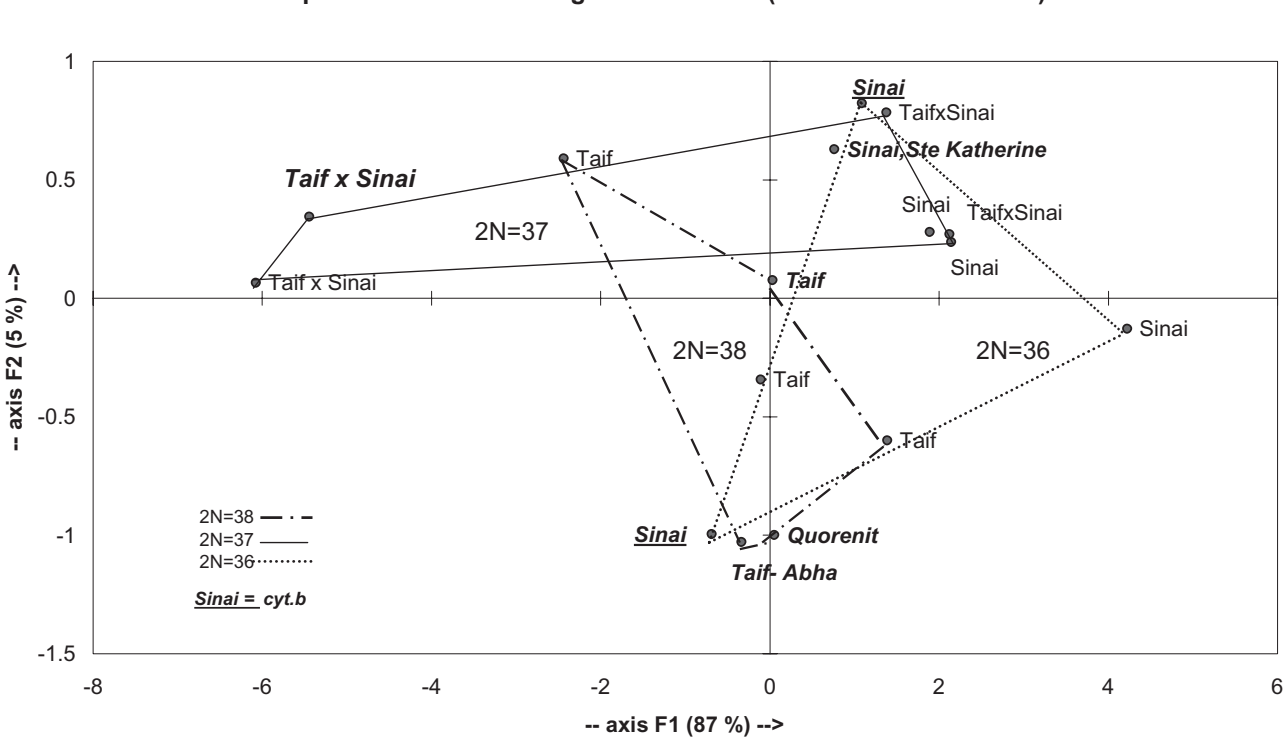

Figure 8. Graph of the first two principal component axes of *Acomys dimidiatus* specimens only (15 specimens, 15 skull measurements). Karyotyped specimens are underlined: sequenced (cytochrome *b*) specimens are shown in bold.

pers. commun.). Therefore, karyological and hybridization data indicate that the Israeli, Sinaitic and Arabian *Acomys* forms undoubtedly belong to the same biological species. Because of the earliest description from Sinai by Cretzschmar (Cretzschmar, 1826, cited by Rosevear, 1969), this species must be named *A. dimidiatus* and is characterized by a karyotype with $2n$ in the range 36–38 and invariable $NF = 70$. Despite sharply different karyotypes, few morphological differences clearly distinguish *A. dimidiatus* from *A. cahirinus*, except fur colour, which is grey in the *A. cahirinus* specimens that are available. This result is confirmed by PCA on skull measurements and by DNA studies (Barome *et al*., 1998, 2000). However, the length of the molar row allows good discrimination between the two species and is not age-dependant. The tail length of the young type of *A. cahirinus* is longer than the older specimens of *A. dimidiatus* and suggests specific allometry. Therefore, cytogenetics, DNA sequencing, morphology, and morphometrics are in a good agreement for the exclusion of populations from the Sinai, and probably Arabian peninsula, and from Minor Asia from the geographical distribution of *A. cahirinus*, which is limited from the western Sahara to the Nile River in Egypt. The Israeli 36 and 38 chromosome forms of *A. dimidiatus* are conspecific.

In addition, in two previous studies (Volobouev *et al*., 1991; Denys *et al*., 1994), we showed that karyological differences between *A. cahirinus* from Cairo and *A. dimidiatus* from Israel and Arabia were sustained by differences in dental patterns, which are reconfirmed here by including for the first time the *A. dimidiatus* type specimen. Moreover, compared with work carried out by Denys *et al*. (1994), some morphological characters allowing species identification are identified. In conclusion, we consider that *A. cahirinus* is the valid name for the species inhabiting at least the lower Nile Valley, and that *A. dimidiatus* is the valid name for this species of the *cahirinus–dimidiatus* group encountered east of the Suez Canal.

Evolutionary scenario of *A. dimidiatus* differentiation

Recent molecular studies have provided further, more precise insight into phylogeny and geographical distribution patterns of *Acomys* (Barome *et al*., 1998). These data indicate that the emergence of the *A. cahirinus–dimidiatus* group took place somewhere in eastern Africa between 2.8 and 2 Mya. Most of the taxa included in the group moved westwards (during a cold event) whereas *A. dimidiatus* migrated to the Arabian Peninsula, most probably just before the opening of the Red Sea, during the Upper Pliocene (Tchernov, 1992). According to cytochrome *b* sequences analysis, the colonization passed through Abba, Taif, the Levant, and Sinai. Therefore, Sinaitic *A. dimidiatus* with $2n = 36$ could be considered as the final step of the migration wave and thus a derivative from *A. dimidiatus* from Taif and Abba with $2n = 38$ in the result of one Rb fusion and not fission, as was suggested by Nevo (1985). It is well known that, by itself, this chromosomal difference is not sufficient to create an effective reproductive barrier. In this context, chromosomal homozygosity across the ranges of the Israeli and Sinaitic forms, except for a narrow hybrid zone, raises questions concerning their taxonomic status, the origin of this secondary contact, and the factors responsible for the vicariance of the originally continuous distribution. During its period of isolation, *Acomys* from western Sinai must have acquired and fixed the final Rb rearrangement resulting in $2n = 36$. Were the factors responsible for this vicariance event climatic and/or ecological in nature? Is it possible that *A. russatus*, a much older inhabitant of Arabia and Sinai that is sharply different genetically and chromosomally (Barome *et al*., 1998, 2000; Volobouev *et al*., 2002) and is a strong ecological competitor of *A. dimidiatus*, could have promoted this isolation? It is possible that the diurnal way of life of *A. russatus*, which contrasts with the typical nocturnal condition found in all other *Acomys*, could be the result of this competition? Whatever the origin of this isolation event, it follows from the molecular data that it occurred relatively recently in time. Thus, it cannot be excluded that the secondary contact zone is simply the beginning of introgressive hybridization. The low genetic distances between chromosomal forms found by biochemical (Nevo, 1985) or more precise sequencing analyses (Barome *et al*., 1998) do not contradict this possibility. On the other hand, although a chromosomal difference comprising one Rb rearrangement is not an obstacle for hybridization, a varying degree of negatively heterotic effects of this rearrangement in heterozygous carriers has been observed in a range of domestic and wild species (cattle, Gustavsson, 1969; mice, Gropp & Winking, 1981; Harris, Wallace & Evans, 1986; blue foxes, Mäkinen & Lohi, 1987). Unfortunately, no natural or laboratory hybrids of *Acomys* have been studied in this respect. It follows that the conclusion of Nevo (1985; 1989) regarding the incipient speciation within *A. dimidiatus* (*A. cahirinus* in these papers) cannot be rejected a priori. Thus, we may conclude that the question remains open and needs a more thorough examination. The detailed cytogenetic and molecular study of the hybrid zone between Israeli and Sinaitic *Acomys*, as well as studies of the ecological and ethological characteristics of *A. russatus* and chromosomal forms of *A. dimidiatus* within and outside their zone of sympatric occurrence, may constitute an interesting

research project that would allow one to choose between two possible explanations.

CONCLUSION

The present study confirms the karyological and morphological differences between *A. cahirinus* and *A. dimidiatus*. The available chromosomal, morphological, and molecular data provide compatible evidence indicating that the Israeli and Sinaitic *Acomys* and their hybrids belong to the same species, which is *A. dimidiatus* and not *A. cahirinus*. The absence of the latter in the distribution area of *A. dimidiatus* is most probably related to its later arrival in north-eastern Africa when the Red Sea and the Bitter Lakes rift were already open. From that time onward, the regions neighbouring the Red Sea and Bitter Lakes formed an impassable ecological barrier to *Acomys* in both directions. The occurrence of *A. cahirinus* in Suez region is most probably related to its transport by man.

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