CYTOGENETIC PROPERTIES OF NINE SPECIES OF GOLDEN MOLES (INSECTIVORA: CHRYSOCHLORIDAE)

GARY N. BRONNER

Department of Mammals, Transvaal Museum, P.O. Box 413, Pretoria, 0001, South Africa

Standard karyotypes and the location of nucleolar organizer regions are reported for nine species of chrysochlorids representing five genera (*Amblysomus, Calcochloris, Chlorotalpa, Chrysochloris,* and *Chrysospalax*). Intraspecific karyotypic variation is negligible except in *Amblysomus hottentotus,* which displays three allopatric cytotypes characterized by differences in diploid number (30, 34, 36) and fundamental number (56, 60, 62, 68) as well as the number and location of nucleolar organizer regions. With the exception of *Calcochloris,* a monotypic genus with 2n = 28, most genera display 2n = 30, but differ in fundamental number and locations of nucleolar organizer regions. Evidence that the three cytotypes in *A. hottentotus* represent distinct biological species is presented. Cladistic relationships based on chromosomal properties support the recognition of *Chlorotalpa* and *Calcochloris* as discrete genera and the subgeneric recognition of the taxon *Neamblysomus* for the species *A. (N.) gunningi* and *A. (N.) julianae.* Limited banding studies indicate that centric fissions, tandem fusions, pericentric inversions, and heterochromatic additions may have played a role in the chromosomal evolution of chrysochlorids. Karyotypic evolution in the Chrysochloridae appears to be similar in mode and tempo to that in other fossorial Insectivora, in contrast to subterranean rodents, which are characterized by greater chromosomal diversity and karyotypic orthoselection.

Key words: Chrysochloridae, cytogenetics, taxonomy, chromosomal evolution

Currently available data on the karyology of fossorial mammals pertain mostly to subterrestrial rodents (Bathyergidae—Nevo et al., 1986; Geomyidae—Patton and Sherwood, 1983; Spalacidae—Nevo et al., 1982; Savic and Nevo, 1990) that display karyotypic diversity, the marsupial mole (Calaby et al., 1974), and a single family of Insectivora (Talpidae) that is karyotypically conservative (Fillipucci et al., 1987; Meylan, 1966). With the exception of a recent report dealing with two species (Capanna et al., 1989), chromosomal data for the Chrysochloridae, the only other family of fossorial Insectivora, are lacking, primarily due to the difficulty of procuring live specimens. Such data potentially are valuable, not only for deciphering the problematic taxonomy of the family, but also because they may provide a more balanced perspective of the extent and mechanisms of chromosomal evolution in fossorial mammals.

The Chrysochloridae comprise 18 known species grouped in seven genera (Meester, 1974; Meester et al., 1986). Their relationships to other Insectivora are obscure, as fossil chrysochlorids show many of the morphological specializations found in extant taxa (Butler and Hopwood, 1957), specializations so varied and unique that ordinal status for the family has been proposed by several authors (Broom, 1915, 1916; Butler, 1972; Roberts, 1951; Roux, 1947). MacPhee and Novacek (1993) recently demonstrated that golden moles display no resemblances to other insectivores that cannot be explained as merely primitive retentions or convergences and argued that because chrysochlorids differ in many important respects from other Insectivora, this ought to be recognized in classification by assigning them to the distinct suborder Chrysochloromorpha. This proposal reiter-

ates my conclusions based on hyoid morphology (Bronner, 1991).

Although chrysochlorids occupy a wide geographic, climatic, and elevational spectrum of subterrestrial niches in sub-Saharan Africa, few species are common, and most are known only from scattered or localized populations. Fifteen species occur exclusively in southern Africa. Species differ markedly in size and color, but also display considerable structural homogeneity with both primitive and highly-specialized mammalian characters (Bronner, 1991; Bronner et al., 1990; Broom, 1915, 1916; Bugge, 1974; Forster Cooper, 1928; Hickman, 1990; Roux, 1947). Species boundaries are in most instances well defined, but generic relationships remain abstruse. Previous taxonomic studies of the family, based on only qualitative characters or univariate and bivariate analyses of morphological data, differed greatly in their treatment of *Amblysomus, Chlorotalpa,* and *Calcochloris,* which were either synonymized under *Amblysomus* (Petter, 1981), split further (Lundholm, 1955; Roberts, 1951), or recognized with differing species allocations (Meester, 1974; Meester et al., 1986; Simonetta, 1968).

Comprehensive analyses of alternative data suites, therefore, are needed to resolve generic relationships in the Chrysochloridae. Nicoll and Rathbun (1990), who included 13 chrysochlorid taxa in IUCN (International Union for the Conservation of Nature and Natural Resources) Threatened Species categories, stressed the need for chromosomal studies to assist in the resolution of taxonomic problems. This paper details the results of karyotypic analyses of nine species of chrysochlorids representing 12 currently recognized taxa belonging to five genera from South Africa, undertaken to augment current morphometric studies on systematic relationships within the family.

Materials and Methods

Eighty-nine golden moles from 31 localities in South Africa were karyotyped. Somatic metaphase spreads were obtained from bone-marrow preparations by a standard in-vitro method (Green et al., 1980), following yeast-stressing (Lee and Elder, 1980). G-banding was performed using a trypsin-digestion method modified from Wang and Federoff (1972), whereas C-bands were induced using the procedure of Baker and Qumsiyeh (1988). Nucleolar organizer regions (NORs) were detected by the $AgNO_3$ colloidal-developer method of Howell and Black (1980), with counter-staining in 4% Giemsa for 1 min to facilitate identification of the NOR-bearing chromosomes. A minimum of five spreads per individual were analyzed. Karyograms were prepared for each specimen by matching homologous chromosomes using relative lengths (expressed as percentages of the total haploid complement plus X) and centromeric indices determined from measurements taken (to the nearest 0.1 mm) on photomicrographs with Tesa Digit-Cal II calipers.

The karyotype of *A. h. hottentotus* was chosen for a standardized numbering system because this taxon displays a diploid number (30) found in most other taxa and samples (and, thus, confidence limits) were largest. Chromosomes were arranged and numbered according to relative length, with the two smallest acrocentrics last. In taxa displaying $2n > 30$, the additional chromosomal pairs were arranged in order of decreasing relative size after the two smallest autosomes. This numbering system, although unconventional in that only autosomes usually are enumerated, was used because it expedites interspecific comparisons and the identification of sex chromosomes when no male specimen of a species is available for study.

Interspecific comparisons were made only after the chromosomes of conspecifics were matched and their morphology was well known. Homology within and among taxa was determined using pairwise comparisons of both the photographed chromosomes and idiograms prepared using mean measurements calculated from a minimum of five karyograms per taxon. All specimens (Appendix 1) were karyotyped within 24 h of capture and were prepared as voucher specimens, and deposited in the Transvaal Museum mammal collection.

Results and Discussion

Karyotypes and nucleolar organizer regions.—Six different karyotypes charac-

TABLE 1.—*Relative lengths of chromosomes (expressed as a percentage of the haploid karyotype + X chromosome) and centromeric indices for various chrysochlorid taxa, based on measurements taken from a minimum of five karyograms per taxon; RL = mean relative chromosome length ± 1 SE; ci = mean centromeric index ± 1 SE.*

Chromosome no.	*Amblysomus hottentotus hottentotus*		*A. hottentotus* (Wakkerstroom and Ermelo)		*A. hottentotus* (Dullstroom)		*Amblysomus julianae*	
	RL	ci	RL	ci	RL	ci	RL	ci
1	13.2 ± 0.6	23.4 ± 1.4	13.2 ± 1.0	23.0 ± 0.8	12.4 ± 0.1	24.9 ± 0.1	16.1 ± 1.3	22.5 ± 1.7
2	11.7 ± 0.4	24.1 ± 3.8	10.3 ± 0.2	27.5 ± 1.3	9.6 ± 0.1	27.0 ± 0.2	12.9 ± 0.6	24.2 ± 1.9
3	10.3 ± 0.4	29.3 ± 1.6	9.5 ± 0.8	13.5 ± 3.4	10.4 ± 0.1	13.6 ± 0.6	11.4 ± 0.5	29.2 ± 1.3
4	7.8 ± 0.2	42.8 ± 3.8	7.4 ± 0.4	41.2 ± 4.7	7.9 ± 0.1	42.8 ± 0.6	7.8 ± 0.5	45.6 ± 2.2
5	7.1 ± 0.3	31.1 ± 5.2	7.9 ± 0.1	26.3 ± 0.8	8.2 ± 0.7	28.8 ± 1.8	7.5 ± 0.5	30.7 ± 1.7
6	7.5 ± 0.3	27.7 ± 3.0	6.5 ± 0.3	23.5 ± 2.1	6.7 ± 0.2	22.9 ± 2.6	6.6 ± 0.2	23.4 ± 4.2
7	6.8 ± 0.3	26.8 ± 3.4	6.1 ± 0.6	17.3 ± 2.1	6.4 ± 0.1	17.8 ± 0.6	6.9 ± 0.3	21.1 ± 3.8
8	6.1 ± 0.7	42.6 ± 3.7	5.4 ± 0.1	42.5 ± 3.0	4.8 ± 0.1	36.3 ± 0.7	5.8 ± 0.4	43.3 ± 1.7
9	6.0 ± 0.6	33.5 ± 4.0	5.7 ± 0.2	39.4 ± 2.2	5.0 ± 0.1	32.6 ± 0.6	5.6 ± 0.6	29.5 ± 1.9
10 (X)	5.7 ± 0.2	42.5 ± 3.2	5.2 ± 0.3	39.2 ± 5.4	5.5 ± 0.1	39.7 ± 0.3	5.6 ± 0.3	42.9 ± 4.2
11	5.1 ± 0.2	39.5 ± 2.7	4.9 ± 0.2	33.1 ± 0.9	4.1 ± 0.1	32.1 ± 0.1	3.8 ± 0.4	21.8 ± 1.6
12	3.9 ± 0.2	30.8 ± 2.7	4.4 ± 0.4	35.1 ± 2.1	2.7 ± 0.1	29.5 ± 3.2	3.1 ± 0.3	31.7 ± 6.6
13	3.6 ± 0.2	45.6 ± 3.4	3.1 ± 0.2	46.7 ± 1.4	2.7 ± 0.2	47.0 ± 1.1	2.8 ± 0.6	45.0 ± 1.0
14	2.9 ± 0.2	<12.5	2.5 ± 0.2	<12.5	3.0 ± 0.1	<12.5	2.5 ± 0.3	<12.5
15	2.4 ± 0.3	<12.5	2.3 ± 0.1	<12.5	2.9 ± 0.1	<12.5	2.1 ± 0.5	<12.5
16			2.9 ± 0.1	<12.5	3.6 ± 0.3	24.2 ± 0.8		
17			2.6 ± 0.1	22.9 ± 0.8	3.1 ± 0.3	24.2 ± 2.1		
18					2.0 ± 0.3	27.1 ± 3.6		

Chromosome no.	*Amblysomus iris*		*Amblysomus gunningi*		*Chlorotalpa duthieae*		*Chlorotalpa sclateri*	
	RL	ci	RL	ci	RL	ci	RL	ci
1	15.0 ± 0.9	23.8 ± 1.6	16.6 ± 1.2	22.8 ± 0.6	15.7 ± 0.1	21.6 ± 0.4	14.4 ± 1.0	25.0 ± 1.8
2	12.0 ± 1.2	26.1 ± 3.7	15.0 ± 1.1	20.6 ± 2.1	12.6 ± 0.1	31.8 ± 0.4	12.5 ± 0.3	31.2 ± 2.1
3	12.3 ± 1.9	29.6 ± 3.9	11.9 ± 1.3	27.8 ± 3.3	12.2 ± 0.2	28.2 ± 5.7	11.4 ± 0.9	28.2 ± 0.9
4	8.3 ± 1.2	44.1 ± 3.0	8.0 ± 0.3	41.7 ± 3.3	8.1 ± 0.1	38.2 ± 2.2	7.5 ± 0.4	40.1 ± 1.6
5	8.0 ± 0.9	29.3 ± 1.8	7.6 ± 0.2	27.7 ± 1.0	7.8 ± 0.4	29.9 ± 2.3	7.6 ± 0.2	31.2 ± 1.8
6	7.6 ± 1.1	26.4 ± 1.9	6.8 ± 0.7	17.0 ± 2.4	6.8 ± 0.2	18.3 ± 3.6	6.9 ± 0.5	29.4 ± 3.2
7	6.8 ± 0.8	24.3 ± 6.0	5.8 ± 0.2	17.7 ± 1.6	6.7 ± 0.1	17.8 ± 4.4	6.2 ± 0.2	30.1 ± 4.8
8	6.3 ± 1.0	45.1 ± 2.8	5.1 ± 0.2	44.6 ± 2.2	4.9 ± 0.5	33.7 ± 0.9	5.6 ± 0.5	43.0 ± 4.9
9	6.4 ± 1.2	33.8 ± 2.3	5.3 ± 0.3	26.7 ± 3.8	5.0 ± 0.4	27.0 ± 1.1	5.2 ± 0.1	32.9 ± 3.7
10 (X)	5.8 ± 0.9	41.3 ± 2.6	4.8 ± 0.9	39.2 ± 5.7	5.0 ± 0.9	42.5 ± 2.1	4.9 ± 0.1	40.8 ± 2.5
11	5.8 ± 0.5	40.5 ± 6.0	3.7 ± 0.4	23.0 ± 0.7	3.0 ± 0.1	24.2 ± 3.9	4.4 ± 0.5	32.6 ± 2.3
12	4.0 ± 1.1	31.4 ± 4.8	2.8 ± 0.2	28.4 ± 4.4	3.8 ± 0.4	18.7 ± 0.4	3.5 ± 0.2	26.8 ± 2.6
13	3.5 ± 0.8	46.5 ± 3.8	2.4 ± 0.3	43.8 ± 2.3	3.4 ± 0.2	44.6 ± 5.5	3.5 ± 0.5	30.8 ± 5.1
14	3.0 ± 0.8	<12.5	2.2 ± 0.2	<12.5	2.8 ± 0.1	30.8 ± 1.8	3.5 ± 0.5	27.3 ± 2.0
15	2.6 ± 0.7	<12.5	1.8 ± 0.1	<12.5	2.6 ± 0.2	45.2 ± 2.9	2.8 ± 0.3	47.7 ± 2.0
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terized by combinations of four diploid numbers (28, 30, 34, 36), four fundamental numbers (56, 60, 62, 68), and four locations of NORs are shown by the nine species examined (Tables 1 and 2). Differences in diploid number occur at both the specific level (*A. hottentotus*, 2n = 30, 34, 36—Fig. 1) and between genera, whereas differences in fundamental numbers are evident mainly at the intergeneric level. In all taxa, the X chromosome is a medium-sized metacentric chromosome (corresponding to pair 10 ac-

TABLE 1.—*Continued.*

Chromosome no.	*Calcochloris obtusirostris*		*Chrysochloris asiatica*		*Chrysospalax trevelyani*	
	RL	ci	RL	ci	RL	ci
1	15.0 ± 0.7	36.0 ± 3.6	15.0 ± 0.8	24.0 ± 3.2	14.9 ± 0.4	23.5 ± 0.7
2	11.1 ± 0.4	28.0 ± 2.1	13.4 ± 0.6	25.4 ± 1.7	12.9 ± 1.1	25.9 ± 0.8
3	13.4 ± 0.6	37.8 ± 1.7	11.3 ± 0.9	36.2 ± 1.7	10.7 ± 0.4	29.9 ± 0.6
4	8.2 ± 1.0	41.1 ± 3.0	7.4 ± 0.9	47.4 ± 3.4	7.6 ± 0.4	42.4 ± 3.1
5	8.4 ± 0.7	32.9 ± 2.2	7.4 ± 0.5	32.0 ± 1.9	8.0 ± 0.4	30.9 ± 2.7
6	7.5 ± 0.5	29.0 ± 2.3	5.5 ± 0.4	20.3 ± 1.9	5.9 ± 0.4	25.8 ± 2.9
7	5.7 ± 0.2	21.6 ± 0.8	5.6 ± 0.3	<12.5	5.9 ± 0.3	<12.5
8	6.4 ± 0.4	34.6 ± 1.9	5.5 ± 0.3	43.6 ± 2.2	5.9 ± 0.3	37.1 ± 2.1
9	5.6 ± 0.3	28.2 ± 4.9	5.5 ± 0.3	29.7 ± 4.3	5.6 ± 0.2	33.4 ± 2.4
10 (X)	5.4 ± 0.5	41.6 ± 5.5	4.6 ± 0.7	40.5 ± 2.5	5.3 ± 0.1	47.1 ± 0.5
11	3.6 ± 0.2	32.9 ± 1.6	4.2 ± 0.6	34.2 ± 6.3	4.1 ± 0.3	31.3 ± 2.7
12	4.0 ± 0.6	22.6 ± 0.3	5.1 ± 0.6	26.6 ± 5.8	3.6 ± 0.4	22.7 ± 5.6
13	3.3 ± 0.6	44.9 ± 1.2	3.5 ± 0.4	44.7 ± 1.6	3.4 ± 0.1	38.1 ± 4.7
14			3.0 ± 0.4	<12.5	3.5 ± 0.3	<12.5
15	2.3 ± 0.6	45.9 ± 0.5	2.6 ± 0.2	39.9 ± 1.9	3.1 ± 0.3	45.4 ± 0.5
16						
17						
18						

cording to the relative-size criterion used) that constitutes 5.3 ± 0.4% of the haploid genome. The Y chromosome is a small metacentric or submetacentric chromosome in all taxa except *C. duthieae* in which it appears to be a small acrocentric chromosome. As no male *A. iris* was analyzed, the morphology of the sex chromosomes could not be unambiguously assessed. However, the 10th largest chromosome pair is similar

TABLE 2.—*Summary of karyotypic properties for 14 chrysochlorid taxa. Fundamental number includes sex elements. Chromosomal nomenclature used follows Levan et al. (1964): M = metacentric; SM = submetacentric; ST = subtelocentric; A = acrocentric. Designations of nucleolar organizer regions (NORs) refer to chromosome number and location on the short (S) and long (L) arms.*

Taxon	2n	FN	Chromosome no.						NORs
			1	3	7	11	14	15	
Calcochloris obtusirostris	28	56	SM	M	ST	SM		M	12S13S
Chrysochloris asiatica	30	56	ST	SM	A	SM	A	M	12L13S
Chrysospalax trevelyani	30	56	ST	SM	A	SM	A	M	12S13S
Chlorotalpa sclateri	30	60	ST	SM	SM	SM	SM	M	12S13S
Chlorotalpa duthieae	30	60	ST	SM	ST	SM	SM	M	12S13S
Amblysomus julianae	30	56	ST	SM	ST	ST	A	A	12S13S
Amblysomus gunningi	30	56	ST	SM	ST	ST	A	A	12S13S
Amblysomus iris iris	30	56	ST	SM	ST	M	A	A	8S11S
Amblysomus iris corriae	30	56	ST	SM	ST	M	A	A	8S11S
Amblysomus hottentotus hottentotus	30	56	ST	SM	ST	M	A	A	8S11S
Amblysomus hottentotus marleyi	30	56	ST	SM	ST	M	A	A	8S11S
Amblysomus hottentotus devilliersi	30	56	ST	SM	ST	M	A	A	8S11S
Amblysomus hottentotus (Ermelo and Wakkerstroom)	34	62	ST	ST	ST	SM	A	A	8S9S11S
Amblysomus hottentotus (Dullstroom)	36	68	ST	ST	ST	SM	A	A	8S9S11S

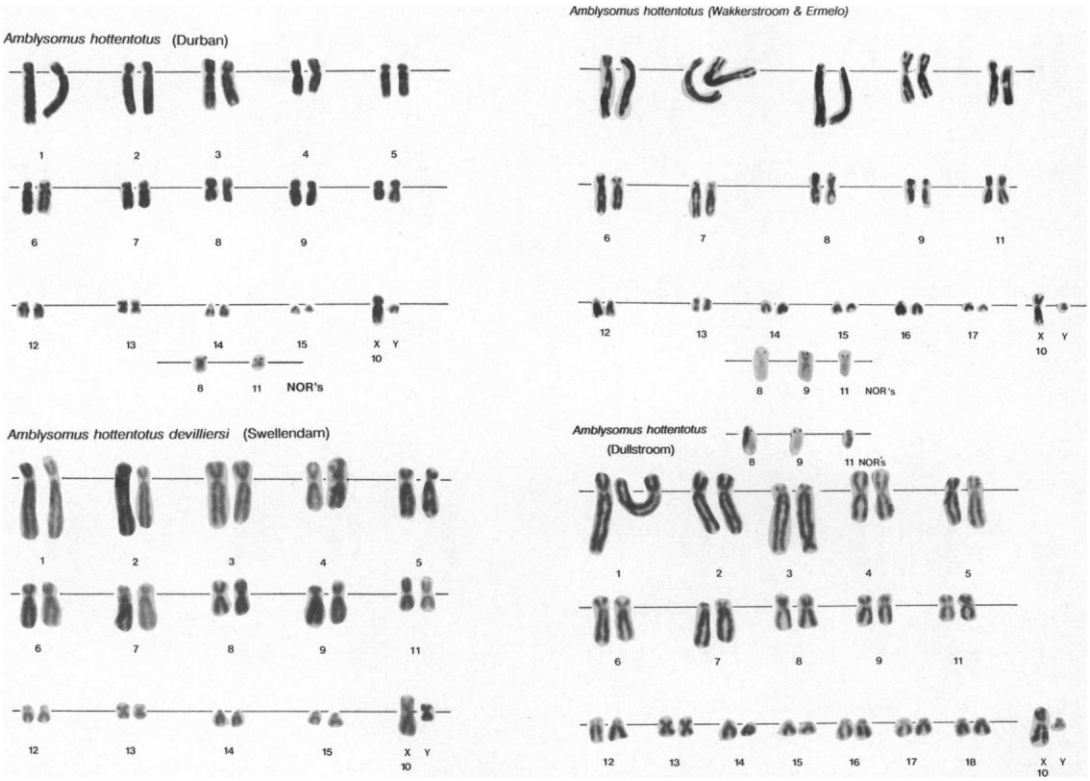

FIG. 1.—Karyotypes and nucleolar chromosomes of male *Amblysomus hottentotus hottentotus, A. h. devilliersi, A. hottentotus* cytotype 2n = 34 from Wakkerstroom and Ermelo, and *A. hottentotus* cytotype 2n = 36 from Dullstroom.

in size (RL = 5.8 ± 0.9) and centromeric index (ci = 41.3 ± 2.6) to that of the X chromosomes in other taxa, suggesting that it represents the XX pair.

The major karyotypic differences observed between and within taxa involve six elements, chromosomes 1, 3, 7, 11, 14, and 15 (Table 2). In *C. obtusirostris* (the only taxon with 2n = 28 and FN = 56), the elements corresponding to chromosome pair 14 in other taxa appear to be absent (Fig. 2). Pair 1 is submetacentric, and pair 3 metacentric; in other taxa, these elements are subtelocentric and subtelocentric-submetacentric, respectively. *Chrysochloris* and *Chrysospalax* are the only genera in which pair 7 is acrocentric (Fig. 3), whereas *Chlorotalpa* is the only genus in which pair 14 is biarmed. The smallest autosomes (pair 15) are acrocentric in *Amblysomus,* but metacentric in the other genera. Chromosome 11 is submetacentric in *Chrysochloris, Chrysospalax, Calcochloris,* and *Chlorotalpa*; however, in *Amblysomus,* it is either subtelocentric (*A. julianae, A. gunningi*) or metacentric (*A. iris, A. hottentotus* cytotype 2n = 30).

Interpopulational variation in karyotypic properties is negligible in most species, and was not assessed in *C. duthieae* because specimens from only a single locality were analyzed. The only species characterized by appreciable geographic variation is *A. hottentotus,* in which three cytotypes with apparently allopatric distributions occur. Whereas *A. hottentotus* from KwaZulu-Natal, Southwestern Cape, and the Eastern Cape Province have identical karyotypes

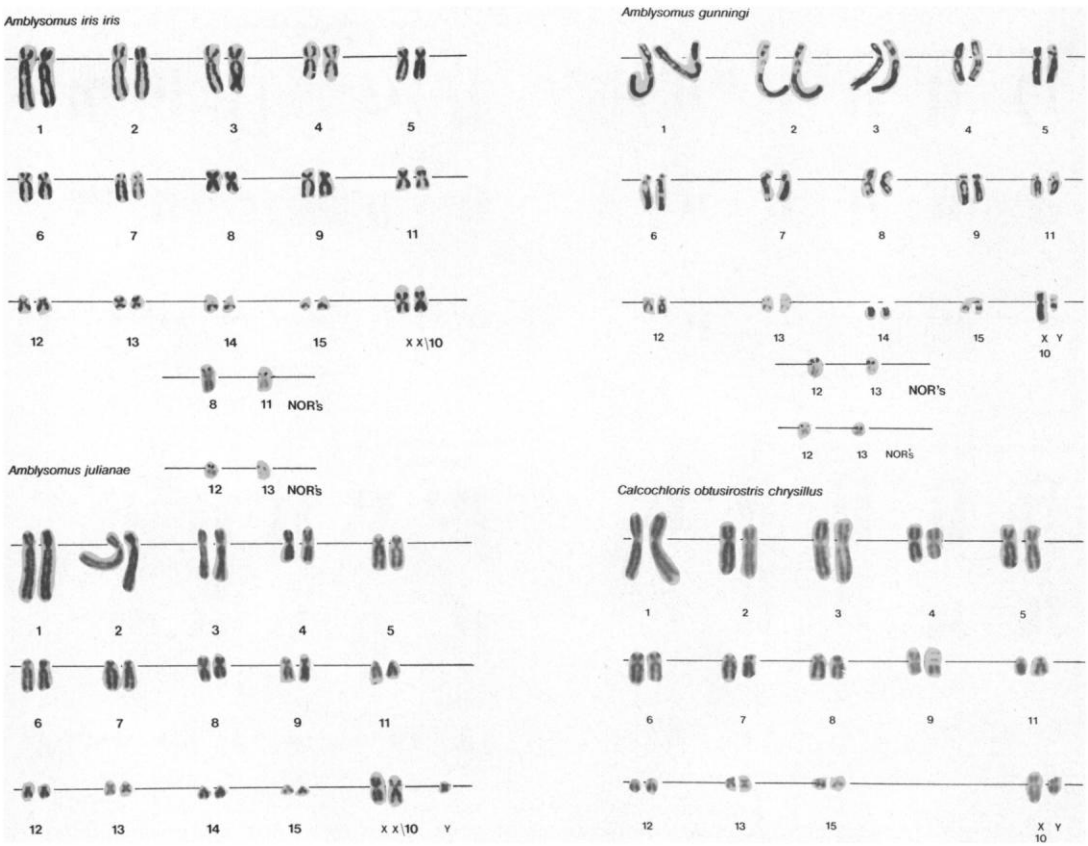

FIG. 2.—Karyotypes and nucleolar chromosomes of *Amblysomus iris, Amblysomus julianae, Amblysomus gunningi,* and *Calcochloris obtusirostris.* Pair 10 possibly corresponds to the X-pair in *A. iris.*

with 2n = 30 and FN = 56, two populations from the southeastern Transvaal highveld (Wakkerstroom and Ermelo) show 2n = 34 and FN = 62, and a montane population from the eastern highveld (Dullstroom) is characterized by 2n = 36 and FN = 68 (Fig. 1). These differences are due to the presence of an extra acrocentric and subtelocentric pair in the cytotype 2n = 34, and three extra pairs of submetacentrics-subtelocentrics in the cytotype 2n = 36. Chromosome pairs 3 and 7 in these populations are characterized by centromeric indices of <14 and <18, respectively, markedly lower than those for homologues (ci = 29.3 ± 1.6 and 26.8 ± 3.4, respectively) in nominotypical *A. hottentotus.* The cytotypes 2n = 34 and 2n = 36 also are distinguished by three NORs on pairs 8, 9, and 11, in contrast to the two NORs located on either the short arms of chromosomes 8 and 11 (*A. hottentotus* cytotype 2n = 30 and *A. iris*), the short arms of elements 12 and 13 (*A. gunningi, A. julianae, Calcochloris, Chlorotalpa,* and *Chrysospalax*), or the long and short arms of pairs 12 and 13 (*C. asiatica*).

C- and G-banding.—Owing to low mitotic indices, only limited success was achieved with C- and G-banding analyses. Satisfactory C-bands were obtained for *A. julianae, A. i. iris, C. asiatica,* and *C. trevelyani* (Fig. 4), which show similar patterns with the constitutive heterochromatin locat-

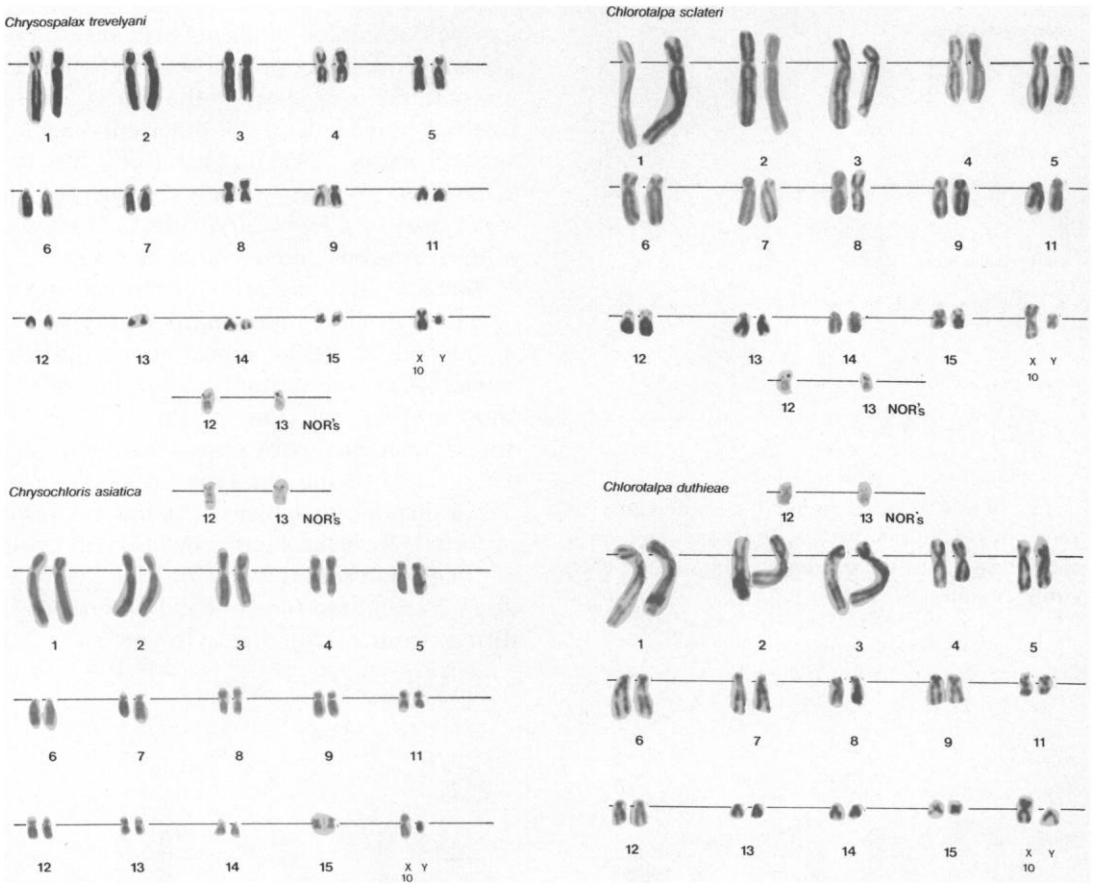

FIG. 3.—Karyotypes and nucleolar chromosomes of male *Chlorotalpa sclateri, Chlorotalpa duthieae, Chrysospalax trevelyani,* and *Chrysochloris asiatica.*

ed mainly in the centromeric region of most chromosomes. In *A. iris, C. asiatica,* and *C. trevelyani,* heterochromatic blocks also appear to extend along the long arms (pairs 3 or 4), the short arms (pair 7), and both arms (pairs 8 and 10) of some chromosomes, and the small metacentric pair 12 is almost entirely heterochromatic. Heterochromatin also occurs along the arms of the large acrocentric chromosomes (pair 7) in *C. asiatica* and *C. trevelyani,* unlike the pericentromeric bands in the *Amblysomus* species.

G-banding was not successful for *C. duthieae* or the *A. hottentotus* cytotype 2n = 36. Even in the other taxa G-bands of comparable quality were limited to the larger chromosomes, the sequences on smaller elements being indistinct or ambiguous. Of the six elements for which G-band homologies could be identified (Fig. 5), major differences among species and genera involve chromosome pairs 1 and 3 in *C. obtusirostris,* pair 7 in *C. asiatica* and *C. trevelyani,* and pairs 3 and 7 in the *A. hottentotus* cytotype 2n = 34. These differences correspond with disparities in relative lengths and centromeric indices (Table 1), and seem to be the result of both Robertsonian changes (fusions or fissions) and pericentric inversions.

The large acrocentric chromosomes (pair 7) in *C. asiatica* and *C. trevelyani* correspond with the long arms of homologues in other taxa. *Chrysochloris* and *Chrysospalax*

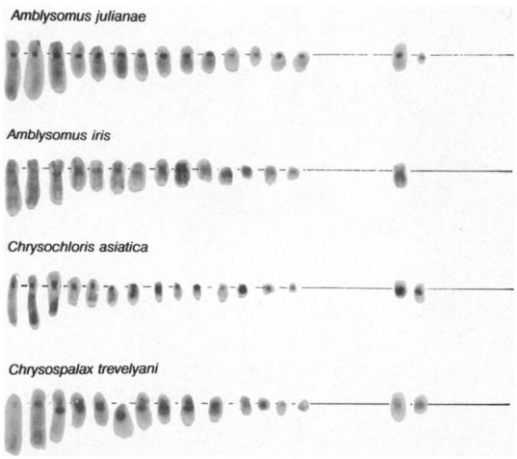

FIG. 4.—C-banded haploid complements of four chrysochlorid species. Presumed sex chromosomes are at the extreme right side of each complement.

can be considered outgroups because these genera show many primitive morphological characters, suggesting that they have evolved independently of other chrysochlorids (Roberts, 1951). Therefore, the biarmed morphology of pair 7 observed in *Amblysomus, Chlorotalpa,* and *Calcochloris* must be considered synapomorphic.

Whereas the long arms of chromosomes 3 and 7 in the *A. hottentotus* cytotypes 2n = 30 and 2n = 34 appear to be directly homologous, the terminal sequences of the short arms in the cytotype 2n = 30 correspond with the extra chromosomes (pairs 16 and 17) of the cytotype 2n = 34 (Fig. 6a), indicating that fusions or fissions have occurred. Because short arms are still present in chromosomes 3 and 7 of the cytotype 2n = 34, and the fundamental number (62) differs from that of the cytotype 2n = 30

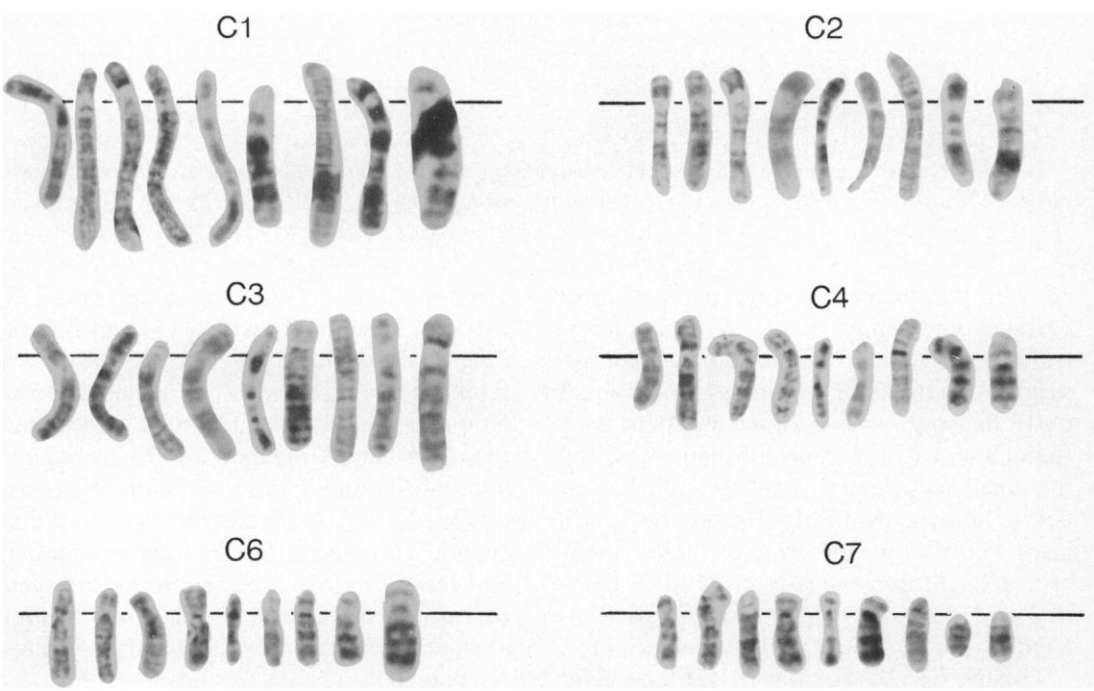

FIG. 5.—Haploid G-banded chromosomes (pairs 1–4 and 6–7) of (from left to right) *Calcochloris obtusirostris, Amblysomus hottentotus hottentotus* (2n = 30), *A. hottentotus* (2n = 34), *Amblysomus iris, Amblysomus gunningi, Amblysomus julianae, Chlorotalpa sclateri, Chrysochloris asiatica,* and *Chrysospalax trevelyani.*

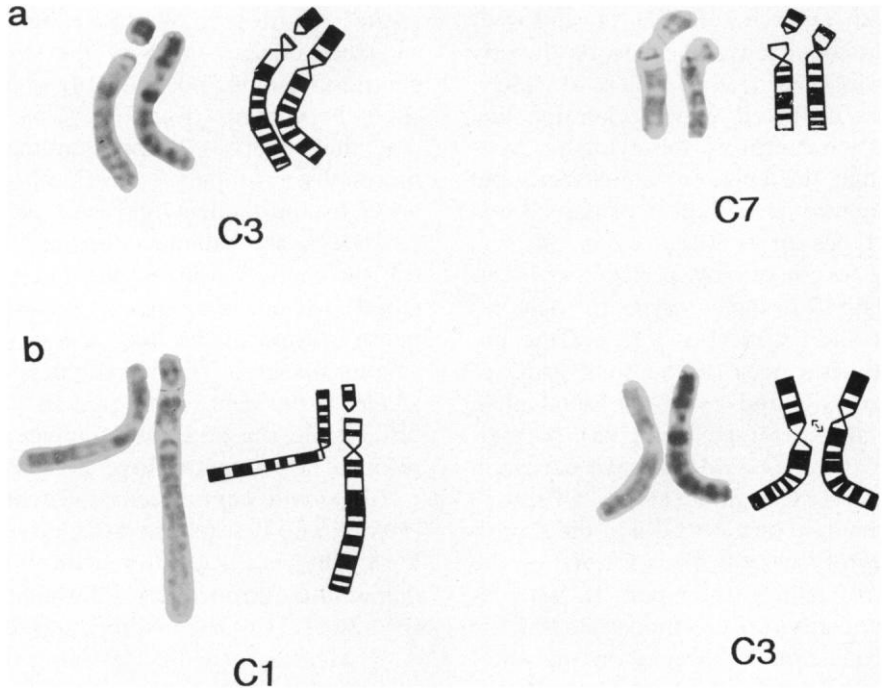

FIG. 6.—Comparison of homologous elements and idiograms of: a, chromosomes 3 and 7 of the *Amblysomus hottentotus* cytotypes 2n = 34 (left) and 2n = 30 (right); b, chromosomes 1 and 3 of *Calcochloris obtusirostris* (left) and *A. hottentotus* cytotype 2n = 30 (right).

(56), it superficially appears that two tandem fusions may have occurred, leading to a reduction in both diploid and fundamental number. However, the G-banding sequences on the short arm of chromosome 3 of the cytotype 2n = 30 are similar to those of the outgroups (*C. asiatica* and *C. trevelyani*), indicating that the subtelocentric morphology of pair 3 in the cytotype 2n = 34 represents a derived condition. Furthermore, examination of the C-banded karyotypes of *A. hottentotus* published by Capanna et al. (1989) reveals that the short arms of chromosomes 3, 7 (their pair no. 6), and 17 in the cytotype 2n = 34 are entirely heterochromatic, whereas in the cytotype 2n = 30, the heterochromatic blocks extend only partially along the short arms of pairs 3 and 7. These data support an alternative hypothesis; namely that the differences between the cytotypes 2n = 30 and 2n = 34 are the result of two fissions (involving pairs 3 and 7), leading to an increase in diploid number; followed by heterochromatic additions to chromosomes 3, 7, and 17, causing a change in fundamental number. Although comparable G-bands for the *A. hottentotus* cytotype 2n = 36 were not obtained, chromosomes 3 and 7 closely resemble those in the cytotype 2n = 34, suggesting that the subtelocentric morphology of these elements can be considered synapomorphic, and that the cytotype 2n = 36 may have evolved from the karyotype 2n = 34.

Capanna et al. (1989:8) speculated that the apparent differences in the absolute lengths of chromosome pair 1 in the cytotypes 2n = 30 and 2n = 34 (mean lengths = 12.1 ± 2.4 μm and 14.2 ± 2.1 μm, respectively) could be the result of euchromatic additions or deletions, depending on assumed evolutionary polarity. The present data do not support this speculation. Relative lengths of these chromosomes are sim-

ilar in both cytotypes (Table 1), and their G-banding sequences appear to be directly homologous (Fig. 5). Capanna et al. (1989: 5, 8) were mistaken also in claiming that pair 17 is telocentric in the cytotype 2n = 34, and that the apparent equal sizes but different centromeric indices of pairs 3 and 7 of cytotypes 2n = 30 and 2n = 34 "... are easily explained by pericentric inversions." Pair 17 in the cytotype 2n = 34 has a distinct short arm (Fig. 1), and the euchromatic sequences of the long arms of chromosomes 3 and 7 appear identical in the respective cytotypes (Fig. 6a), so pericentric inversions could not have occurred. Furthermore, Capanna et al. (1989:5) claimed that one of the NORs in the *A. hottentotus* cytotype 2n = 30 is located on the long arm of pair 8 (their pair 9), whereas my data unequivocally demonstrate that the NOR in question is located on the short arm. These discrepancies can be attributed to the small samples (n = 4 and n = 1 for the cytotypes 2n = 30 and 2n = 34, respectively) analyzed by Capanna et al. (1989) and their reliance on nondifferentially stained karyotypes, which do not allow accurate determination of genetic homology or the type and number of chromosomal rearrangements that may have occurred (Baker et al., 1987).

The long arms of pair 1 in *C. obtusirostris* correspond directly with those of *C. asiatica* and *C. trevelyani,* but with only the proximal euchromatic sequences in *Amblysomus* and *Chlorotalpa.* Because C-bands are located pericentromerically in *Amblysomus* and both outgroups (*C. asiatica* and *C. trevelyani*; Fig. 4), differences in the long arms of these taxa cannot be ascribed to heterochromatic additions. This implies that euchromatic additions to pair 1 have occurred during the karyotypic evolution of *Amblysomus* and *Chlorotalpa.* The precise rearrangements involved, however, cannot be ascertained from the limited banding data available.

The proximal sequences of the short arm in *C. obtusirostris* also appear to correspond with those in other taxa, but the distal sequences match those of the small acrocentric chromosome (pair 14) observed in *A. h. hottentotus* (Fig. 6b). This suggests that the reduced 2n and submetacentric morphology of pair 1 in *C. obtusirostris* arose by the tandem fusion of pairs 1 and 14, which are subtelocentric and acrocentric, respectively, in all the other species. Good G-band homology is evident for the major portion of the long arm of pair 3 in *C. obtusirostris.* The proximal portion adjacent to the centromere and its short arm differ from the other taxa, apparently as a result of a pericentric inversion (Fig. 6b).

Taxonomic implications.—Capanna et al. (1989), who first reported the karyotypes of the cytotypes 2n = 30 and 2n = 34 in *A. hottentotus,* erroneously referred the cytotype 2n = 34 to the taxon *A. iris,* despite J. A. J. Meester's (in litt.) warning that positive identification of the single skull available was not possible because these species are cranially indistinguishable. Although the cytotype 2n = 34 occurs at Wakkerstroom, the type locality of *A. i. septentrionalis* Roberts, 1913, my morphometric analyses unequivocally indicate that *A. iris* is a purely coastal taxon whose range does not extend inland to the southern Transvaal highveld. All of the specimens collected at Wakkerstroom during the present study have 2n = 34 and associate with the types of *A. h. drakensbergensis* Roberts, 1946, and *A. i. septentrionalis* in multivariate morphometric analyses, indicating that they represent the same species. Roberts (1913, 1946), therefore, was mistaken in referring *Amblysomus* from this region to two different species.

Given the apparent lack of intraspecific karyotypic variation in most of the taxa analyzed, the existence of three geographical cytotypes in *A. hottentotus* is taxonomically important. The rearrangements that occurred during the differentiation of these cytotypes cannot, however, necessarily be regarded to have caused genetic divergence. The role of chromosomal rearrangements in

speciation and evolution is controversial, and it is becoming increasingly apparent that such changes often do not have severe negative heterotic effects (Baker, 1981; Sites and Moritz, 1987; Yates and Moore, 1990). However, differences in number and locations of NORs in the cytotypes 2n = 30 and 2n = 34–36 strongly suggest functional genome divergence. NORs correspond with clusters of rRNA cistrons, which play an important role in the inner organization of chromosomes; thus, differentiation of NORs probably affects gene expression and plays an active role in species divergence (Yoshida, 1983).

The karyotypic differences among the cytotypes are correlated with morphological and ecological differences. Overall size increases markedly with the change from the karyotypes 2n = 30 to 2n = 34 and 2n = 36. This variation is associated with increasing elevation and vegetation differences. The cytotype 2n = 30 occurs in a variety of forest, macchia, and grassland habitats at lower elevations (0–1,200 m) in southeastern Africa and shows a clinal pattern of increase in size in relation to elevation in Natal, whereas the other cytotypes are known from only "Near-Highland Sourveld" (veld type 57b—Acocks, 1988) at elevations of 1,600–1,800 m in the southeastern Transvaal escarpment (2n = 34), or elevations of 2,000–2,150 m in the eastern Transvaal highveld (2n = 36—Bronner, 1990). Multivariate analyses of skull measurements indicate that the three cytotypes also differ diagnostically in cranial configuration, to the extent that there is no overlap of discriminant-score ranges along the first two canonical-variate axes, and individuals are assigned to their correct a priori cytotype groups with 100% accuracy (pers. obser.). The three cytotypes, thus, differ phenotypically, cytogenetically, and ecologically and can be considered to represent cryptic but distinct biological species. The cytotype 2n = 34, which Capanna et al. (1989) erroneously referred to *A. iris,* thus, represents the species *A. septentrionalis* Roberts, 1913. This name has priority over *A. drakensbergensis* Roberts, 1946, which becomes the first synonym. No name is yet available for the new species (currently being described) represented by the cytotype 2n = 36.

Cladistic analysis of karyotypic properties distinguish six groupings within the chrysochlorids studied (Table 2, Fig. 7), of which three correspond with recognized genera, whereas the others are members of *Amblysomus.* The chromosomal data presented here, although equivocal, clearly differentiate *Amblysomus* from *Chlorotalpa* and *Calcochloris.* Karyotypic data, thus, support Meester's (1974) recognition of *Chlorotalpa* and *Calcochloris* as discrete genera, in contrast to Simonetta (1968) and Petter (1981) who synonymized these taxa with *Amblysomus.* Chromosomal data also are congruent with hyoid data (Bronner, 1991) in suggesting that *A. gunningi* and *A. julianae* should be distinguished taxonomically (in the subgenus *Neamblysomus*—Roberts, 1924) from other *Amblysomus.* The relatively greater karyotypic variability of *Amblysomus* is correlated with a richer diversity of species that, although cranially similar, are characterized by quite marked differences in size and color. This genus exhibits many advanced karyotypic and morphological features, suggesting that it is still in the process of diverging from other taxa of chrysochlorids.

Comparison with other subterranean mammals.—Capanna et al. (1989) remarked that the nondifferentially stained karyotypes of golden moles resemble those of certain Madagascan Tenrecidae, which often are regarded as being the closest extant relatives of chrysochlorids. Such comparison is meaningless, because standard karyotypes do not allow accurate assessment of genetic homology (Baker et al., 1987) and there is no morphological evidence favoring a close relationship between tenrecs and chrysochlorids (Butler, 1972; MacPhee and Novacek, 1993). Until complete G-banded karyotypes of both families

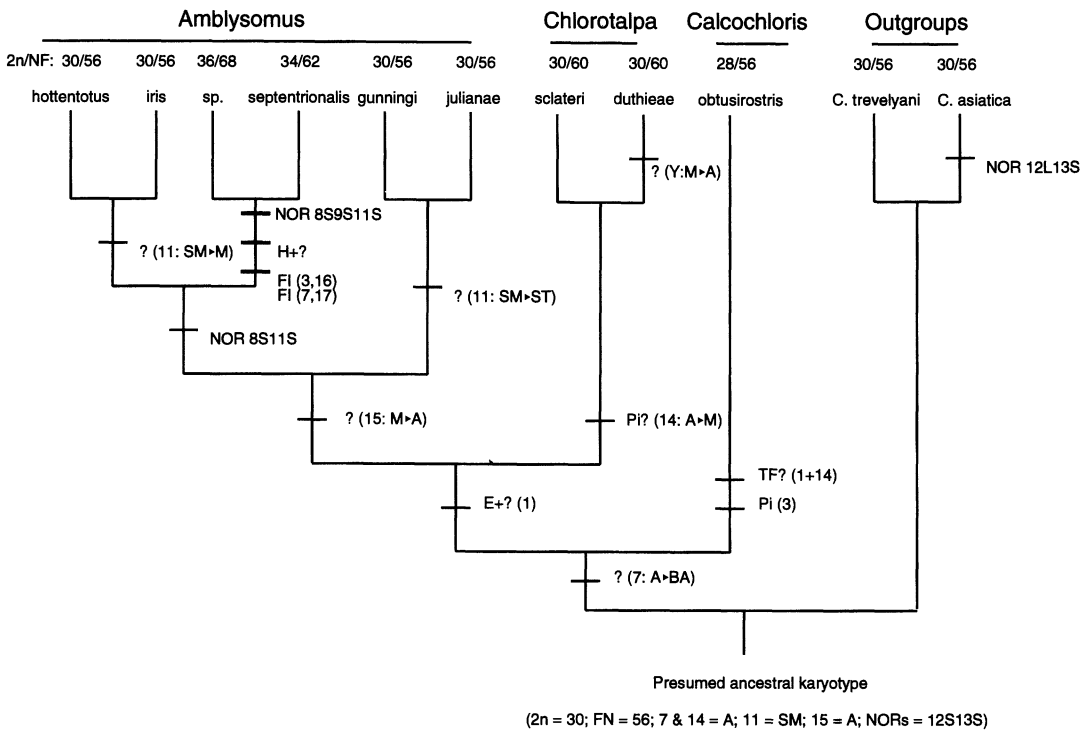

FIG. 7.—Cladistic relationships among the chrysochlorid taxa studied, based on chromosomal data, with *Chrysochloris asiatica* and *Chrysospalax trevelyani* used as outgroups. A = acrocentric; BA = biarmed; ST = subtelocentric; SM = submetacentric; M = metacentric; E+ = euchromatic addition; Pi = pericentric inversion; H+ = heterochromatin addition; TF = tandem fusion; FI = centric fission; NOR = location of the nucleolar organizer regions on the long (L) or short (S) arms of chromosomes. Question marks denote unidentified rearrangements that have led to changes in standard karyotypes.

are available for comparison, the degree of cytotaxonomic affinity among these taxa cannot be decisively addressed.

Although only a few chromosomal rearrangements have been identified here, it appears that centric fissions, tandem fusions, pericentric inversions, heterochromatic additions, and alterations in the number and location of the NORs may have played a role in the chromosomal evolution of chrysochlorids. As in the Talpidae, there does not appear to be any overt pattern to the fixation of rearrangements whereby the occurrence of one type of change affects the likelihood of the same kind of mutation occurring in a particular lineage again (Yates and Moore, 1990). Chromosomal variability in the Chrysochloridae, although sufficiently marked to be taxonomically useful, thus, is similar in extent and nature to that of the karyotypically conservative talpids and does not appear to be the result of chain processes involving multiple changes of a particular kind. This is in contrast to the chromosomal diversity and prominent role of karyotypic orthoselection charactizing many fossorial rodents (Patton and Sherwood, 1983; White, 1978).

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APPENDIX 1

Specimens examined.—Taxonomic designations follow Meester et al. (1986), and province names follow regional designations in the 1993 Constitution of the Republic of South Africa.

Amblysomus gunningi, n = 2. Northern Transvaal: De Hoek State Forest, Magoebaskloof, 2.4 km N, 13.6 km W Tzaneen, 23°50′S, 30°02′E.

Amblysomus hottentotus devilliersi, n = 3. Southwestern Cape Province: Grootvadersbosch Forest Reserve, 5.5 km N, 10 km W Heidelberg, 34°01′S, 20°47′E; Jonkershoek Nature Conservation Headquarters, 6.4 km S, 6.5 km E Stellenbosch, 34°00′S, 18°58′E.

Amblysomus hottentotus hottentotus, n = 33. Eastern Cape Province: Palm Springs Resort, Kidds Beach, 20 km S, 15 km W East London, 33°09′S, 27°42′E; Kwazulu-Natal: Balgowan, Michaelhouse Golf Course, 29°24′S, 30°03′E; Botanic Gardens, University of Natal sports grounds, and Durban Country Club, central Durban, 29°50′S, 31°01′E; Dukuduku Forest Reserve, 7.5 km N, 15 km W Mtubatuba, 28°22′S, 32°21′E; Umtamvuma Nature Reserve, 9 km N, 9 km W Port Edward, 31°02′S, 30°12′E; Wyford Farm, 4 km S, 4.8 km E Van Reenen, 28°24′S, 29°25′E; Eastern Transvaal: Ermelo Dam, 7 km W Ermelo, 26°28′S, 28°57′E; Graskop town, 24°56′S, 30°50′E; Tafelkop Farm, 7.2 km N, 12 km E Wakkerstroom, 27°21′S, 30°09′E; Verloren-Vallei Nature Reserve, 26.4 km N, 3.2 km E Dullstroom, 25°13′S, 30°08′E.

Amblysomus hottentotus marleyi, n = 1, Kwazulu-Natal: Goudhoek Farm, 10 km N, 10 km W Babanango, 28°17′S, 30′54′E.

Amblysomus iris iris, n = 6. Kwazulu-Natal: Hazelmere Dam, 6 km N, 2 km W Verulam, 29°36′S, 31°01′E; Dukuduku Forest Reserve, 7.5 km N, 15 km W Mtubatuba, 28°22′S, 32°21′E.

Amblysomus iris corriae, n = 3. Southwestern Cape Province: Natures Valley Township, 33°59′S, 23°33′E; Saasveld Forest Research Station, 6 km E George, 33°58′S, 22°31′E.

Amblysomus julianae, n = 11. Northern Transvaal: Nylsvley Nature Reserve, 14.4 km S, 2.4 km W Naboomspruit, 24°40′S, 28°43′E; Eastern Transvaal: Pretoriuskop Rest Camp, Kruger National Park, 25°11′S, 31°17′E; PWV (Pretoria-Vereeniging-Witwatersrand) Province: Shere and Tierpoort smallholdings, 15.2 km S, 20 km E Pretoria, 25°45′S, 28°24′E.

Chlorotalpa duthieae, n = 3. Southwestern Cape Province: Natures Valley Township, 33°59′S, 23°33′E.

Chlorotalpa sclateri, n = 6. Southwestern

Cape Province: Mountain View Camp, Karoo National Park, 14 km N, 4 km W Beaufort West, 32°15′S, 22°32′E; Orange Free State: Agricultural Showgrounds, Ficksburg, 28°53′S, 27°53′E.

Calcochloris obtusirostris chrysillus, n = 11. Kwazulu-Natal: Kwazulu Department of Health Camp, Kosi Lake, 26°57′S, 32°49′E; Lalanek Inspection Quarters, 6 km N, 4.5 km E Manzengwenya, 27°13′S, 32°46′E.

Chrysochloris asiatica, n = 6. Southwestern Cape Province: Kirstenbosch Gardens, Cape Town, 33°58′S, 18°28′E; Jonkershoek Nature Conservation Headquarters, 6.4 km S, 6.5 km E Stellenbosch, 34°00′S, 18°58′E; Algeria Forest, 21 km S, 16 km E Clanwilliam, 32°22′S, 19°02′E.

Chrysospalax trevelyani, n = 5. Eastern Cape Province: Nqadu Forest, 19 km N, 2.5 km W Umtata, Transkei, 31°26′S, 28°46′E; Kologha Forest, 5 km N, 6 km W Stutterheim, 32°32′S, 27°15′E.