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COCCIDIA (APICOMPLEXA), GENETIC DIVERSITY, AND ENVIRONMENTAL UNPREDICTABILITY OF FOUR CHROMOSOMAL SPECIES OF THE SUBTERRANEAN SUPERSPECIES *SPALAX EHRENBERGI* (MOLE-RAT) IN ISRAEL

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ABSTRACT: Forty-five mole-rats, representing 4 chromosomal species ($2n = 52, 54, 58, 60$) of the superspecies *Spalax ehrenbergi*, were collected from 12 localities in Israel in 4 distinct climatic regions. Feces were examined for coccidian oocysts and 41 (91%) were infected; 26 (63%) had multiple infections of up to 5 coccidian species, 4 of which are described here as new species. Sporulated oocysts of *Eimeria anzanensis* n. sp. were ellipsoidal $18.3 \times 12.5 \mu\text{m}$ ($14\text{--}22 \times 10\text{--}16$) and had elongate-oval sporocysts $7.3 \times 4.9 \mu\text{m}$ ($5\text{--}10 \times 3\text{--}7$); it occurred in 39 of 45 (87%) mole-rats, including all chromosomal species. Sporulated oocysts of *Eimeria spalacensis* n. sp. were ovoidal $23.4 \times 18.3 \mu\text{m}$ ($17\text{--}29 \times 12\text{--}21$) with ovoidal sporocysts $9.4 \times 6.8 \mu\text{m}$ ($6\text{--}12 \times 4\text{--}10$); it occurred in 7 of 45 (16%) mole-rats ($2n = 54, 58, 60$). Sporulated oocysts of *Eimeria carmelensis* n. sp. were subspheroidal to ellipsoidal $19.1 \times 16.5 \mu\text{m}$ ($14\text{--}25 \times 11\text{--}20$) and had sporocysts that were spheroidal to ellipsoidal $8.6 \times 6.2 \mu\text{m}$ ($6\text{--}13 \times 4\text{--}8$); it occurred in 5 of 45 (11%) mole-rats ($2n = 58, 60$). Sporulated oocysts of *Isospora spalacensis* n. sp. were ellipsoidal $14.6 \times 11.0 \mu\text{m}$ ($12\text{--}17 \times 9\text{--}14$) with ellipsoidal to ovoidal sporocysts $8.5 \times 4.5 \mu\text{m}$ ($7.5\text{--}11 \times 4\text{--}7$); it occurred in 5 of 45 (11%) mole-rats ($2n = 58, 60$). Twenty-five of 45 (56%) mole-rats (all 4 species) were infected with a previously described form, *Eimeria elliptica* Sayin, Dincer, and Meric, 1977. The genetic diversity of mole-rats in Israel is known to increase chromosomally ($2n = 52 \rightarrow 60$) and genically (heterozygosity $[H] = 0.035 \rightarrow 0.069$) as the environment becomes more demanding (i.e., increasingly warm, dry, and climatically unpredictable). At the same time, there is an increased diversity of coccidian parasites. This suggests correlation among host chromosomal variability, habitat, and increased prevalence of multiple infections, a pattern also seen in other fossorial rodents infected with coccidia.

Between 1988 and 1990, mole-rats of the *Spalax ehrenbergi* Nehring superspecies (see Nevo, 1985, 1991) were collected in Israel and examined for coccidian parasites. Members of this subterranean rodent superspecies are morphologically indistinguishable, yet constitute 4 chromosomally homozygous species that exhibit adaptive radiation associated with diverse climatic regions (Nevo, 1986, 1991). Although the genetics of *S. ehrenbergi* from Israel have been well studied (Nevo and Shaw, 1972; Nevo and Cleve, 1978; Wahrman et al., 1985), only 3 papers have been written about the parasites of these hosts (Costa and Nevo, 1969 [arthropods]; Wertheim and Nevo, 1971 [nematodes]; Fair et al., 1990 [a cestode]); there is no study to date on the coccidia that infect these chromosomal species.

Brooks (1979) proposed that coaccommodation and cospeciation between hosts and their parasites may be representative of mutual descent. Thus, we were interested in examining these

chromosomal species of *Spalax* to learn if there was any correlation between host chromosomal variability and parasite–host specificity or parasite–host climate dependency as further evidence of a coevolutionary trend. With this in mind, we looked at samples of the known chromosomal species from each climatic locality. Three new species of *Eimeria* and 1 of *Isospora* are described, *Eimeria elliptica* Sayin, Dincer, and Meric, 1980, is described for the first time from *S. ehrenbergi*, and the relationships of these coccidians to their hosts' genetic makeups and environments are discussed.

MATERIALS AND METHODS

Mole-rats comprising 4 chromosomal species of the superspecies *S. ehrenbergi*, from 4 climatic regions in Israel, were live-caught by hand and fecal samples from the small intestine, cecum, and colon collected upon necropsy. Fecal samples were placed in separate vials containing 2% (w/v) aqueous potassium dichromate ($\text{K}_2\text{Cr}_2\text{O}_7$), mixed thoroughly, and stored at ambient temperature. Upon receiving the samples in Albuquerque, they were processed, and oocysts were stored, measured, and photographed as detailed by Duszynski et al. (1982). All measurements are given in micrometers with size ranges in parentheses following the means. Karyotypes of mole-rats from the different climatic regions were as described previously (see Wahrman et al., 1985). Host carcasses were preserved either in alcohol or frozen and are deposited at the Institute

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of Evolution, University of Haifa, Haifa, Israel (IEUH), under the name and collection number of the collector, along with the date of collection.

RESULTS

Forty-five mole-rats of the superspecies *S. ehrenbergi* were collected from 12 localities in Israel (Fig. 1) within 4 distinct climatic regimes and 41 (91%) were infected with 1–5 species of coccidians representing 4 species of eimerians and 1 species of isosporan (Table I). Of those infected, 26 (63%) had multiple infections (Table II) and 3 of the eimerian species and 1 isosporan species appear to be new. *Eimeria elliptica* is described for the first time from *S. ehrenbergi*, and the occurrence in Israel constitutes a new geographic record for this species.

Eimeria anzanensis n. sp.
(Figs. 2–4, 13)

Description

Oocyst ellipsoidal (Fig. 3), wall ~1.3, composed of 2 layers: outer layer smooth, pale yellow in transmitted light, ~½ of total thickness; inner layer transparent, smooth; micropyle and oocyst residuum absent, but small, refractile polar body sometimes present (19/50, 38%; Fig. 3); sporulated oocysts ($n = 50$) 18.3×12.5 ($14\text{--}22 \times 10\text{--}16$) with length:width ratio (=shape index, SI) 1.4 (1.05–1.9); sporocysts ($n = 50$) elongate-ovoidal, 7.3×4.9 ($5\text{--}10 \times 3\text{--}7$) with SI 1.5 (1.1–2.0); Stieda body present (Figs. 2, 4), but sub- and parastieda bodies absent; sporocyst residuum of granules that appear in clusters lying along center of sporocyst (Figs. 2, 4); sporozoites have large posterior refractile body.

Taxonomic summary

Type host: *Spalax ehrenbergi* Nehring ($2n = 60$).

Type locality: Anza, Israel, 55 km SE of Haifa.

Prevalence: Found in 39 of 45 (87%) *S. ehrenbergi* superspecies including 8 of 10 (80%) from chromosomal species $2n = 52$, 6 of 8 (75%) from species $2n = 54$, 13 of 15 (87%) from species $2n = 58$, and all 12 (100%) from species $2n = 60$.

Site of infection: Unknown, oocysts collected from feces.

Material deposited: Phototype (see Bandoni and Duszynski, 1988) of sporulated oocysts in the U.S. National Museum Parasite Collection, Beltsville, Maryland, (USNMPC) no. 82497; symbiotype (see Frey et al., 1992) in IEUH as catalogue number E. Nevo, #D-1500.

Etymology: The nomen triviale is derived from the locality from which the first infected animal occurred and -ensis (L., belonging to).

Remarks

Sporulated oocysts of *E. anzanensis* resemble in shape those of *Eimeria celebii* Sayin, 1980, from *S. ehrenbergi* collected in Turkey and those of *E. elliptica* and *Eimeria lalahanensis* Sayin, Dincer, and Meric, 1977, both from *Spalax leucodon* Nordmann, also found in Turkey. They differ from those of *E. celebii* by having

FIGURE 1. Distribution of 4 chromosomal species ($2n = 52, 54, 58, 60$) of *Spalax ehrenbergi* superspecies in Israel. Numbers in open circles indicate the 4 chromosomal species; small numbers next to closed circles indicate the 12 collection localities used in this study. 1, Maalot; 2, Kerem Ben Zimra; 3, Kiryat Shemona; 4, Hermon; 5, Quneitra; 6, El-Al; 7, Kabri; 8, Zipori; 9, Afik; 10, Anza; 11, Carmel; 12, Lahav.

a stouter oocyst (SI 1.4 vs. 1.6) with ovoidal (vs. ellipsoidal) sporocysts, and in the presence of a prominent refractile body in each sporozoite, which is missing in *E. celebii*. They differ from those of *E. elliptica* by lacking 2 prominent polar bodies and in having larger sporocysts (9.4×6.8 vs. 8.2×5.1), which are ovoidal rather than ellipsoidal, with a residuum composed of multiple granules vs. 3–5 small granules. They differ from those of *E. lalahanensis* by having smaller oocysts with fewer polar bodies, in sporocyst shape, and in the size and shape of the sporocyst residuum.

Eimeria elliptica Sayin, Dincer, and Meric, 1977
(Fig. 5)

Description

Oocyst ellipsoidal with 2 walls of uniform thickness, ~1.0: outer wall smooth, pale yellow, ~½ of total thickness; inner wall smooth, transparent; micropyle and oocyst residuum absent, but 1 (common) to 2 (rare) large, refractile polar bodies present; sporulated oocysts

TABLE I. Coccidian species found in 45 blind mole-rats, *Spalax ehrenbergi* superspecies, collected from 12 localities in 4 climatic regions in Israel.

Climatic region Host population*	Number infected/ number examined (%)	Number of chromosomes (2n)	Coccidian species†
Cool-humid			
Maalot (1)	3/4 (75%)	52	I, II
Kerem Ben Zimra (2)	1/2 (50%)	52	I
Kiryat Shemona (3)	4/4 (100%)	52	I, II
Cool-semidry			
Hermon (4)	2/2 (100%)	54	I, II
El-Al (6)	1/1 (100%)	54	II
Quneitra (5)	5/5 (100%)	54	I, II, III
Warm-humid			
Kabri (7)	2/2 (100%)	58	I, V
Zipory (8)	2/2 (100%)	58	I, II, V
Carmel (11)	6/7 (86%)	58	I, II, IV, V
Afiq (9)	3/4 (75%)	58	I, II, III, IV
Warm-dry			
Lahav (12)	2/2 (100%)	60	I, II, III, IV, V
Anza (10)	10/10 (100%)	60	I, II, III, IV
Total 12 localities	41/45 (91%)	4 species	5 species

* Numerals refer to geographic localities shown in Figure 1.

† I, *Eimeria anzanensis*; II, *Eimeria elliptica*; III, *Eimeria spalacensis*; IV, *Eimeria carmelensis*; V, *Isospora spalacensis*.

(n = 50) 15.3 × 10.6 (11–24 × 7–13) with SI 1.45 (1.0–2.0); sporocysts (n = 50) ovoidal, 6.0 × 4.0 (4–8 × 3–5) with SI 1.5 (1.2–2.5); Stieda body present, but sub- and parastieda bodies absent; sporocyst residuum present, composed of small granules that lie in narrow band along center of sporocyst, between sporozoites; sporozoites each with large, posterior refractile body.

Taxonomic summary

Prevalence: Found in 25 of 45 (56%) *S. ehrenbergi* superspecies including 3 of 10 (30%) from chromosomal species 2n = 52, 4 of 8 (50%) from species 2n = 54, 10 of 15 (67%) from species 2n = 58, and 8 of 12 (67%) from species 2n = 60.

Site of infection: Unknown, oocysts collected from feces.

Remarks

This eimerian species was first described from the herbivorous mole-rat, *S. leucodon*, collected in Turkey by Sayin et al. (1977). The oocysts we saw differ from the original description only by having 2 walls vs. 1 in the original description, but the total wall thickness is the same. Other than minor differences in size, the oocysts we saw otherwise were identical to those described by Sayin et al. (1977) as *E. elliptica*.

***Eimeria spalacensis* n. sp.**
(Figs. 6, 7, 12)

Description

Oocyst ovoidal with 2 obvious walls, ~1.6: outer wall smooth, but appears slightly striated under trans-

TABLE II. Infection patterns of coccidians in blind mole-rats, *Spalax ehrenbergi*, as host genetic diversity increases (2n = 52 → 60) toward more unpredictable environmental extremes (cool/humid → dry/hot).

Climatic region (karyotype, 2n)	Number infected/ number examined (%)	Coccidian species present*	Infection pattern†
Cool-humid (2n = 52)	8/10 (80)	I, II	2 (0), 5 (I), 3 (I, II)
Cool-semidry (2n = 54)	8/8 (100)	I–III	3 (I), 2 (II), 2 (I, II), 1 (I, III)
Warm-humid (2n = 58)	13/15 (87)	I–V	2 (0), 2 (I), 6 (I, II), 1 (I, V), 2 (I, II, V), 1 (I–IV), 1 (I–III, V)
Warm-dry (2n = 60)	12/12 (100)	I–V	2 (I), 5 (I, II), 2 (I, III), 2 (I–IV), 1 (I–V)

* I, *Eimeria anzanensis*; II, *Eimeria elliptica*; III, *Eimeria spalacensis*; IV, *Eimeria carmelensis*; V, *Isospora spalacensis*.

† Number of mole-rats followed by coccidian species present in parentheses.

FIGURES 2–11. Photomicrographs of sporulated oocysts obtained from the feces of *Spalax ehrenbergi* superspecies in Israel. 2–4. *Eimeria anzanensis* n. sp. 5. *Eimeria elliptica*. 6, 7. *Eimeria spalacensis* n. sp. 8, 9. *Eimeria carmelensis* n. sp. 10, 11. *Isospora spalacensis* n. sp. Scale bar = 10 μ m for all figures. Abbreviations: S, Stieda body; sr, sporocyst residuum; pb, polar body; *, refractile body of sporozoite.

FIGURES 12–15. Composite line drawings of sporulated oocysts of coccidia collected from feces of *Spalax ehrenbergi* superspecies from Israel. 12. *Eimeria spalacensis*. 13. *Eimeria anzanensis*. 14. *Eimeria carmelensis*. 15. *Isospora spalacensis*. Scale bar = 10 μ m.

mitted light (Figs. 6, 7), $\sim 1/2$ – $2/3$ of the total thickness; wall is not of uniform thickness, thinning slightly at the pointed end of oocyst; micropyle and oocyst residuum absent, but 1–3 large, refractile polar bodies (1.5×3) are present (Fig. 7); sporulated oocysts ($n = 50$) 23.4×18.3 (17 – 29×12 – 21) with SI 1.3 (1.0 – 1.7); sporocysts ($n = 50$) ovoidal, 9.4×6.8 (6 – 12×4 – 10) with SI 1.4 (1.1 – 1.9); Stieda body present (Figs. 6, 7), but sub- and parastieda bodies absent; sporocyst residuum consists of large coarse granules that lie in band across center of sporocyst (Figs. 6, 7); sporozoites with 1 large posterior refractile body.

Taxonomic summary

Type host: *Spalax ehrenbergi* Nehring ($2n = 60$).

Type locality: Anza, Israel, 55 km SE of Haifa.

Prevalence: Found in 7 of 45 (16%) *S. ehrenbergi* superspecies including 1 of 8 (12.5%) from chromosomal species $2n = 54$, 1 of 15 (7%) from species $2n = 58$, and 5 of 12 (42%) from species $2n = 60$.

Site of infection: Unknown, oocysts collected from feces.

Material deposited: Phototypes of sporulated oocysts in USNMPC, no. 82499; symbiotype in IEUH no. E. Nevo, #D-1640.

Etymology: The nomen triviale is derived from the generic name of the host and *-ensis* (L., belonging to).

Remarks

Sporulated oocysts of this eimerian species are the largest of the 4 species found in *S. ehrenbergi* from Israel. Of all the eimerians described from species of *Spalax*, oocysts of this form are similar in size and shape only to those of *Eimeria oytuni* Sayin, 1980, described from *S. ehrenbergi* in Turkey, but they differ by lacking a micropyle, by having polar bodies, and by the size and shape of the sporocyst, its Stieda body, and residuum.

***Eimeria carmelensis* n. sp.**
(Figs. 8, 9, 14)

Description

Oocyst subspheroidal to ellipsoidal (Figs. 8, 9) with wall ~ 1.1 , composed of 2 layers: outer layer smooth,

$\sim 1/3$ of total thickness; inner layer transparent, smooth; micropyle, oocyst residuum, and polar body absent; sporulated oocysts ($n = 50$) 19.1×16.5 (14 – 25×11 – 20) with SI 1.2 (1.05 – 1.4); sporocysts ($n = 50$) spheroidal to ellipsoidal 8.6×6.2 (6 – 13×4 – 8) with SI 1.4 (1.0 – 1.9); Stieda body present (Fig. 9), but difficult to see in most oocysts due to tight packing of sporocysts (Fig. 9), sub- and parastieda bodies absent; sporocyst residuum a mass of large granules covering center of sporocyst (Figs. 8, 9); sporozoites with large, posterior refractile body.

Taxonomic summary

Type host: *Spalax ehrenbergi* Nehring ($2n = 58$).

Type locality: Carmel, Israel, Mukhraka Monastery, 20 km SE of Haifa.

Prevalence: Found in 5 of 45 (11%) *S. ehrenbergi* superspecies including 2 of 15 (13%) from chromosomal species $2n = 58$ and 3 of 12 (25%) from species $2n = 60$.

Site of infection: Unknown, oocysts collected from feces.

Material deposited: Phototypes of sporulated oocysts in USNMPC, no. 82498; symbiotype in IEUH no. E. Nevo, #G-943.

Etymology: The nomen triviale is derived from the general locality in Israel from which the first infected animal was examined and *-ensis* (L., belonging to).

Remarks

Oocysts of this species most closely resemble those of *Eimeria tuzdii* Sayin, Dincer, and Meric, 1977, described from *S. leucodon* in Turkey, in size and shape of their oocysts. They differ, however, by the lack of a striated oocyst outer wall, by not having 2 polar bodies, and by the size and shape of the sporocysts and their Stieda bodies.

***Isospora spalacensis* n. sp.**
(Figs. 10, 11, 15)

Description

Oocyst ellipsoidal (Fig. 10) with wall ~ 0.8 , composed of 2 layers: outer layer smooth, pale yellow, $\sim 1/3$ of total thickness; inner layer transparent, smooth; mi-

cropyle and oocyst residuum absent, but 1–2 polar bodies present (Fig. 10), ~ 1.5 ; sporulated oocysts ($n = 25$) 14.6×11.0 ($12\text{--}17 \times 9\text{--}14$) with SI 1.3 (1.1–1.7); sporocysts ($n = 25$) ellipsoidal to ovoidal, 8.5×4.5 ($7.5\text{--}11 \times 4\text{--}7$) with SI 1.95 (1.6–2.3); Stieda body present, difficult to see due to tight packing of sporocysts in oocyst (Figs. 10, 11), but sub- and parastieda bodies absent; sporocyst residuum of small granules in narrow band across middle of sporocyst; sporozoites with larger, posterior refractile body (Figs. 10, 11).

Taxonomic summary

Type host: *Spalax ehrenbergi* Nehring ($2n = 58$).

Type locality: Kabri, Israel, 28 km NE of Haifa.

Prevalence: Found in 5 of 45 (11%) *S. ehrenbergi* superspecies including 4 of 15 (27%) from chromosomal species $2n = 58$ and 1 of 12 (8%) from species $2n = 60$.

Site of infection: Unknown, oocysts collected from feces.

Material deposited: Phototypes of sporulated oocysts in USNMPC, no. 82500; symbiotype in IEUH no. E. Nevo, #G-910.

Etymology: The nomen triviale is derived from the generic name of the host and *-ensis* (L., belonging to).

Remarks

Only 1 isosporan, *Isospora anatolicum* Sayin, Dincer, and Meric, 1977, has been described from mole-rats; it was found in only 1 of 96 (1%) *S. leucodon* from Turkey. Neither the oocysts nor sporocysts of the form reported here resemble those of *I. anatolicum*.

DISCUSSION

Mole-rats are truly subterranean rodents that can be distinguished from all others by the absence of external openings for their eyes, though small eyes are present beneath the skin. They do not live in true deserts, but they can inhabit any type of soil, except sand dunes, that receives > 100 mm of annual precipitation. They are primarily herbivorous, feeding on the underground parts of plants (i.e., corms, bulbs, roots), and they rarely venture above ground. Elaborate tunnel systems, used mainly in the search for food, may be tens of meters long, and in their eastern Mediterranean range these rodents are considered serious agricultural pests. Each burrow system has several chambers used for various purposes (e.g., nesting, storing food) including 1 or more chambers used only for defecation (Nevo, 1961).

The taxonomy of this host group has not been resolved. Honacki et al. (1982) placed the mole-rats in their own family (Spalacidae) containing only *Spalax* with 3 species (also see Anderson and Jones, 1984), whereas Nowak (1991) separated the mole-rats into 3 genera (*Spalax*, *Nannospalax*, *Myospalax*) containing 14 species.

Karyological studies have demonstrated the existence of about 30 chromosomal species of *S. leucodon* (= *Nannospalax leucodon*) in the Balkans, Russia, and Asia Minor (Savic and Nevo, 1990), as well as 4 of *S. ehrenbergi* in Israel; the latter 4 chromosomal races are known now to be distinct species, all closely related (Nevo and Bar-El, 1976; Nevo et al., 1982, 1988; Nevo, 1985, 1991; Savic and Nevo, 1990). This complex of biological species is relatively young (Pleistocene in age), and in all previous molecular and organismal analyses (see Nevo [1991] for review) the $2n = 52$ and 54 are the older pairs, whereas the $2n = 58$ and 60 are the younger pairs.

Prior to our work, there were already 16 coccidian species described from mole-rats: Veisov (1975) described 3 eimerian species from *S. leucodon* in what was the U.S.S.R.; Sayin et al. (1977) described 5 eimerian species and 1 isosporan species from 96 *S. leucodon* collected in Turkey; and Sayin (1980) described 7 eimerian species from 41 *S. ehrenbergi*, also from Turkey. Whatever the actual number of species of mole-rats, given the prevalence, intensity, and variety of infection with coccidians in only the 2 nominal species (and 4 chromosomal species) examined for coccidia to date, it appears that the chance of discovery of additional species is high as more mole-rats are studied.

Speciation of the *S. ehrenbergi* complex of mole-rats in Israel into 4 chromosomal species ($2n = 52, 54, 58, 60$) has been studied in great detail and is known to be intimately associated, and statistically correlated, with both the macro- and microclimatic structure of the country as follows: $2n = 52$ primarily in the cool-humid upper Galilee Mountains; $2n = 54$ in the cool-semidry Golan Heights; $2n = 58$ in the warm-humid lower Galilee Mountains and central coastal plain; and $2n = 60$ in the warm-dry southern coastal plain and northern Negev Desert (Nevo, 1985, 1986, 1991; also see Table II). This ecological speciation of *S. ehrenbergi* into increasingly arid environments involves climatically coadapted genomic and organismal adaptations (Nevo, 1991).

Genetic diversity of *S. ehrenbergi* is known to increase progressively southward and eastward in Israel, toward the desert. This increased diversity can be measured both chromosomally ($2n = 52 \rightarrow 58 \rightarrow 60$ southward and $2n = 52 \rightarrow 54$ eastward [Nevo, 1985, 1991]) and genically (heterozygosity $[H] = 0.035, 0.037, \text{ and } 0.069$ for $2n = 52, 58, \text{ and } 60$, respectively [Nevo and

Cleve, 1978]). This trend of increasing genetic diversity toward climatically unpredictable environments (i.e., increased heat and drying) is shared by many plants and animals in Israel (Nevo, 1983; Nevo and Beiles, 1988) and seems to be correlated positively with both parasite prevalence and parasite success in these hosts. Using percentage of infected mole-rats as a measure of infectivity, data from 2 previous parasite surveys (Costa and Nevo, 1969 [ectoparasites]; Wertheim and Nevo, 1971 [nematodes]) were reexamined in a recent study on class II major histocompatibility complex (Mhc) molecules (Nevo and Beiles, 1992). The results showed that both mite and nematode infections increased with the climatic index, i.e., with both humidity and temperature; both infections correlated positively with the H of 2 class II Mhc genes; and that H was highest in the regions of most infection, occupied by the $2n = 58$ species. The conclusion drawn was that the evolutionary forces responsible for the Mhc class II 2 gene polymorphisms include selection for increased H as a defense strategy against ecto- and endoparasite infections.

When our results are considered in light of this previous work on the same host model, other interpretations also may be possible. In addition to increasing environmental unpredictability contributing to elevated genic and chromosomal diversity, such an environment also should be more stressful physiologically to the hosts that live there, and this stress apparently makes them more susceptible to coccidial infection in at least 2 ways: the number of individuals in the population that harbor an infection (prevalence) is increased, and the number of coccidian species found in these hosts also is increased. Thus, we found 5 coccidian species in our $2n = 58$ and $2n = 60$ species, whereas only 2 eimerian species were found in $2n = 52$ mole-rats and 3 eimerian species in the $2n = 54$ species. Also, mole-rats that live in warm climates, i.e., the species with $2n = 58$ and $2n = 60$, were more often infected with 2–5 coccidian species concurrently (21/27, 78%), whereas those with $2n = 52$ and $2n = 54$ had fewer multiple infections (6/18, 33%).

A parallel observation was made earlier on the coccidial burdens of another subterranean rodent, the tuco-tuco (*Ctenomys* spp.), in Bolivia, South America (Gardner and Duszynski, 1990). Most species of *Ctenomys* are highly subterranean, exhibit low vagility, occur in relatively low population densities, and, as a group, exhibit the

highest known chromosomal variation for all mammals (Cook et al., 1990). The 7 tuco-tuco species examined for coccidia by Gardner and Duszynski (1990) occurred in 4 habitat types in Bolivia: warm-humid, a palm-nut/savanna region of east-central Bolivia (*Ctenomys boliviensis* Waterhouse, 1848; *Ctenomys steinbachi* Thomas, 1907); warm-dry, a lowland dry Chaco thorn forest (*Ctenomys conoveri* Osgood, 1946); cool-moist, a montane/grassland habitat (*Ctenomys frater* Thomas, 1902); and cold-dry, the high altitude ($>4,000$ m)/puna habitat of the Altiplano (*Ctenomys leucodon* Waterhouse, 1848; *Ctenomys lewisi* Thomas, 1926; *Ctenomys opimus* Wagner, 1848). Tuco-tucos in the harshest of these environments, the Altiplano (essentially a cold desert), had higher prevalences of infection (80%) than tucos in the other 3 habitat types (33%, 33%, and 27%, respectively). Also, the tucos on the Altiplano were infected by 4 species of *Eimeria*, and nearly half of those with coccidia (49%) were infected with multiple species, whereas no tuco (0% of 88 infected animals) in the other 3 environments was infected with more than 1 eimerian (*Eimeria opimi* Lambert, Gardner, and Duszynski, 1988).

The pattern seen in the above studies on subterranean rodents in some ways is counterintuitive. For example, it is known that parasites evolve with their hosts over evolutionary time and often reach compromises along the way; thus, evolutionarily older hosts (e.g., $2n = 52$ and 54 mole-rats), especially those that are genically conservative (e.g., moles, rabbits), might support more parasites than evolutionarily younger hosts undergoing rapid genic change (e.g., many mice species). This should apply especially for intracellular parasites that are closely tied to the genome of their host as are the coccidia; i.e., the parasites simply have a chance to “catch up” to changes in their environment (their hosts’ epithelial cells), to adapt accordingly, and eventually to speciate. Such is certainly true for the moles (Insectivora) examined to date for coccidians: of 195 moles in 8 species and 6 genera from England, Japan, and the U.S.A., 183 (94%) were infected with coccidia and 153 (84%) of those infected had oocysts from 2 to 8 coccidian species in their feces when examined (Duszynski, 1989). Rabbits also are known to be heavily infected with many species of coccidia almost all the time (Duszynski and Marquardt, 1968), whereas many mammals that speciate more frequently (mice, bats, etc.) tend to have lower prevalences of in-

fection and seldom harbor more than 1 or 2 coccidian species at a time (Duszynski, 1986).

However, a different mechanism, or more likely a combination of several factors, seems to regulate coccidial infections in subterranean rodents. In addition to living a rather solitary existence in their burrow systems, the ctenomyids in South America and the spalacids in southeast Europe both seem to approach unpredictable environments (deserts, cold, and hot respectively) with increased genetic diversity and, for whatever reasons, this increased genetic diversity is accompanied both by increased infection prevalences and by more frequent infection with multiple coccidial species, especially in the most inhospitable environments. This is certainly a topic that deserves more study.

Another topic that deserves attention is the mechanism of transmission of oocysts among subterranean rodents in hot and cold deserts. Clearly, the burrow provides moisture and protection from ultraviolet radiation, both conditions that would be conducive to oocyst development and longevity; however, tucos and mole-rats are mostly solitary individuals that do not share burrows with others of their species and the question of how so many of them can be infected, and with so many species, in such environments remains to be answered.

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