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Leidyana migrator n. sp. (Apicomplexa: Eugregarinida: Leidyanidae) from the Madagascar hissing cockroach, *Gromphadorhina portentosa* (Insecta: Blattodea)

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Abstract. *Leidyana migrator* n. sp. (Apicomplexa: Eugregarinida) is described from the alimentary tract of the Madagascar hissing cockroach, *Gromphadorhina portentosa* (Insecta: Blattodea), taken from research colonies in Texas. This is the first species of *Leidyana* described from a cockroach, and the complete life cycle and development are presented. Although trophozoites and gamonts of *L. migrator* overlap morphometrically with those of the 2 most similar congeners, *L. erratica* and *L. oviformis,* each of the 3 species displays unique characters. The lanceolate epimerite of *L. oviformis* distinguishes this species from *L. migrator* and *L. erratica,* which possess a simple, globular epimerite. *Leidyana migrator* and *L. erratica* are separated by differences in their gametocysts, dehiscence, and oocysts. The gametocysts of *L. migrator* are elliptoid with an average length of 1,066 μm; they dehisce through 6 spore tubes, releasing dolioform oocysts measuring 8 μm by 4 μm. In contrast, the gametocysts of *L. erratica* are spherical and 260–350 μm in diameter; they dehisce through 1–12 spore tubes, releasing dolioform oocysts measuring 6 μm by 3 μm.

Additional key words: Gregarine, parasite, Sporozoa

Watson (1915) erected the genus *Leidyana* to comprise those gregarine species possessing a simple, globular epimerite, "solitary sporonts," gametocysts dehiscing by spore ducts, and dolioform oocysts. The phrase "solitary sporonts" indicates that trophozoites do not form extended associations; reproductive associations are formed only by mature gamonts just before syzygy and gametocyst formation begin. *Leidyana* comprises 27 species and is cosmopolitan. Species of *Leidyana* are parasites of insects and are reported from lepidopterans (Keilin 1918; H. Hoshide 1958; Geus 1966; Ormières 1967; Rabindra & Jayaraj 1981; Lipa & Martignoni 1984; Ghosh & Choudhury 1992), orthopterans (Dufour 1837; Watson 1915; Narain 1961; Corbel 1967a, 1968; Issi & Lipa 1968; Geus 1969; K. Hoshide 1973a,b, 1978; Haldar & Sarkar 1979; Hooger & Amoji 1986; Sarkar 1988), coleopterans (Braune 1930; Geus 1969; Patil & Amoji 1979; Roy 1989), trichopterans (Baudoin 1966, 1967; Geus 1969), and a single hymenopteran species (Bhatia & Setna 1924).

Gregarine infections were discovered in laboratory colonies of the Madagascar hissing cockroach, *Gromphadorhina portentosa* (Insecta: Blattodea). A study of the parasite's life cycle revealed the diagnostic characters of the genus *Leidyana.* The gregarine populations recovered from *G. portentosa* are morphologically distinct from all described species of *Leidyana,* and prompted the proposal of a new eugregarine species. This is the first report of a species of *Leidyana* parasitizing a cockroach.

Methods

Colonies of host cockroaches, *Gromphadorhina portentosa,* maintained by the Department of Entomology, Texas A&M University, were subcultured. The cockroaches were reared in plexiglass cubes (30 cm^3) on a substrate of heat-treated pine chips and given cardboard shelters. Dog kibble (Purina Dog Chow, Ralston Purina, Inc.) and water were provided *ad libidium.*

Cockroaches were killed with carbon dioxide gas. Their alimentary canals were dissected in insect muscle saline (Belton & Grundfest 1962) and teased open to release gregarines. Living specimens were prepared as wet mounts using insect muscle saline and examined under bright-field and phase-contrast microscopy. Smear preparations of host intestinal tissue were simultaneously fixed and stained for 2 min in Semi-

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chon's acetocarmine, dehydrated, cleared in xylene, and mounted in Damar balsam (Galigher & Kozloff 1971). Gametocysts were collected from the rectum, transferred into individual wells of a tissue culture plate and measured. Water was added to the margins of the culture plate to provide humidity and the gametocysts were held for maturation and dehiscence. Oocyst structure and dimensions were taken from fresh preparations of oocysts suspended in water or glycerin. Oocysts rotated freely in glycerin preparations and the full 3-dimensional structure was observed.

No more than 10 individuals from each host were measured. Widths of protomerites and deutomerites were taken at the widest points. Measurements were taken on living specimens and are presented as means followed by range values and standard deviations in parentheses. Terminology for parasite ontogenetic stages follows Levine (1971). Terminology for shapes of planes and solids is consistent with that suggested by the Systematics Association Committee for Descriptive Biological Terminology (1962). Terms used for insect morphology follow Dailey & Graves (1976).

Drawings were made with the aid of a camera lucida. All observations were made using a Wild binocular compound microscope with 10× wide-field eyepieces and 10×, 20×, and 40× objectives. Color observations were made using a Nikon Alphaphot binocular compound microscope with 10× wide-field eyepieces, achromatic objectives, and a daylight filter.

Taxonomic Account

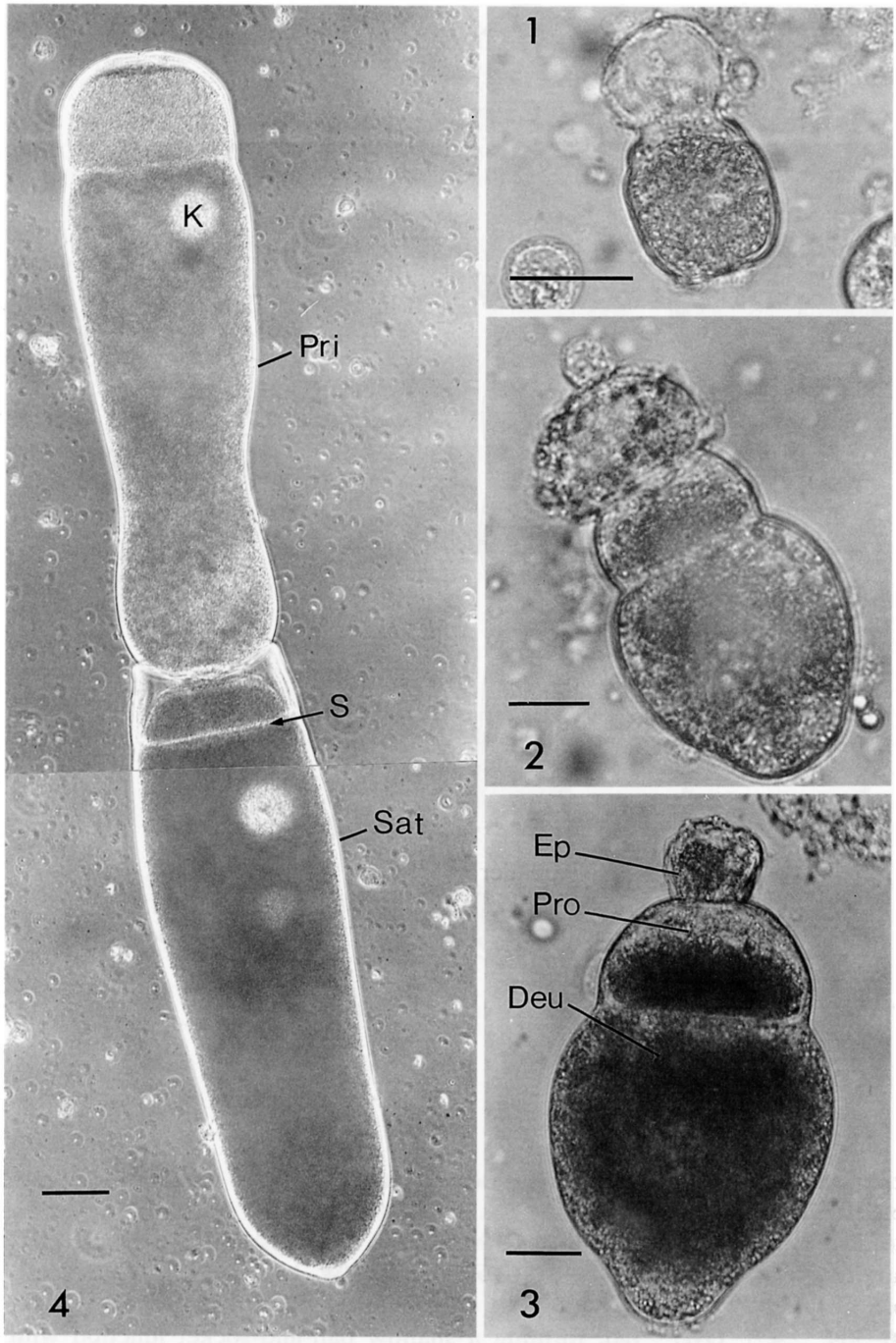
Order Eugregarinida Léger 1892
sensu stricto Levine et al. 1980
Suborder Septatina Lankester 1885
sensu stricto Levine et al. 1980
Superfamily Stenophoricae Levine 1984
sensu Solitaroidea Chakravarty 1960
Family Leidyanidae Kudo 1954
Genus *Leidyana* Watson 1915

Generic diagnosis. Association late; epimerite simple, globular, sessile; gametocysts dehiscing through sporoducts; oocysts dolioform, released in long chains.

Leidyana migrator n. sp.

Trophozoite (Figs. 1–3, 5): Attached to host ventricular and enteric caecal epithelium, solitary. In very young trophozoites, epimerite spherical; protomerite transverse oblong elliptoid; deutomerite broadly elliptoid. In older trophozoites (n = 50), epimerite simple, globular, broadly obovoid to very broadly obovoid; epimerite length (EL) 37 μm (24–64, ±9), epimerite width (EW) 45 μm (24–72, ±11), EW/EL 1.21 (0.90–1.75, ±0.22); lost with maturity, leaving a distinct omphalic or navel-like scar that is carried to syzygy. Protomerite broadly ovoid to depressed ovoid; protomerite length (PL) 49 μm (24–80, ±12), protomerite width (PW) 87 μm (56–136, ±15), PW/PL 1.83 (0.93–2.50, ±0.29); tapering anteriad to junction with epimerite, becoming ampulliform with maturity; with strong posteriad constriction at protomerite-deutomerite septum. Deutomerite obovoid to broadly obovoid, becoming distinctly obovoid in older trophozoites; deutomerite length (DL) 138 μm (72–252, ±37), deutomerite width (DW) 127 μm (68–168, ±24), DW/DL 0.94 (0.50–1.25, ±0.14); truncated anteriad at protomerite-deutomerite septum; young trophozoites broadly rounded posteriad, becoming obampulliform and finally obovoid with maturity. Total length excluding epimerite (TL) 187 μm (96–332, ±48); PL/TL 0.26 (0.14–0.31, ±0.03); DL/TL 0.74 (0.69–0.86, ±0.03); PL/DL 0.36 (0.17–0.45, ±0.05); PW/DW 0.69 (0.36–0.83, ±0.06). Nucleus spheroid to elliptoid; nucleus length (KL) 37 μm (24–48, ±5), nucleus width (KW) 38 μm (24–48, ±5), KW/KL 1.03 (0.75–1.25, ±0.10); placement roughly axial, equatorial; with 2–6 distinct nuclear endosomes, increasing in number with maturity, clearly revealed with acid carmine staining. Fresh trophozoites with endocyte granular when young, becoming opaque with maturity, epicyte clear. Color white under reflected light, brownish-orange under transmitted light. Variation in trophozoite morphology reflects both maturation (Figs. 1–3) and normal population variability (Fig. 5).

Gamont: Free, located between host ventricular peritrophic membrane and ventricular epithelium, solitary (n = 62, except as noted). Epimerite absent, shed with maturity, marked by a distinct omphalic or navel-like scar. Protomerite broadly ovoid to depressed ovoid; PL 58 μm (36–88, ±13), PW 113 μm (44–228, ±44), PW/PL 1.89 (0.92–3.17, ±0.52); rounded anteriad; with strong thickening of the epicyte surrounding epimerite scar; with strong posteriad constriction at protomerite-deutomerite septum. Deutomerite narrowly obovoid to broadly obovoid, often with a shallow marginal sinus along each margin (narrowly panduriform); DL 294 μm (172–460, ±80), DW 188 μm (60–352, ±91), DW/DL 0.60 (0.28–0.82, ±0.18), truncated anteriad at protomerite-deutomerite septum, acuminate posteriad. TL 352 μm (220–536, ±91); PL/TL 0.17 (0.12–0.22, ±0.02); DL/TL 0.83 (0.77–0.88, ±0.02); PL/DL 0.20 (0.14–0.28, ±0.03); PW/DW 0.66 (0.51–1.78, ±0.19); DW across sinoid constriction 111 μm (28–240, ±76, n = 43). Nucleus ellipsoid to depressed ellipsoid (n = 43); KL 30 μm (12–44, ±8), KW 25 μm (10–48, ±9), KW/KL 0.83 (0.50–1.40, ±0.21); placement roughly abaxial in the anterior half

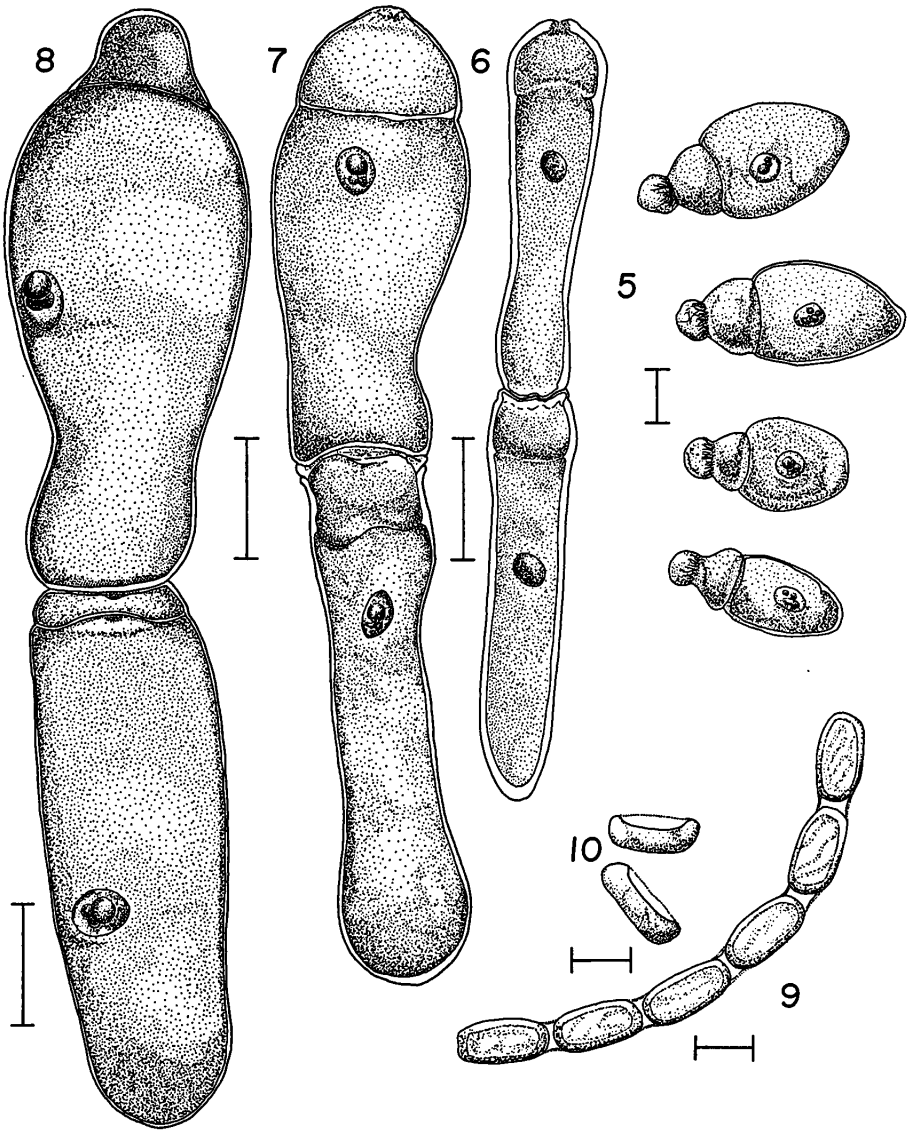


Figs. 1–4. Live specimens of *Leidyana migrator* n. sp. Phrase-contrast micrographs. **Figs. 1–3.** Young trophozoites; differences reflect varying maturity. Epimerite (Ep); protomerite (Pro); deutomerite (Deu). Scale bars, 25 μm. **Fig. 4.** Association. Nucleus (K), primite (Pri), septum (S), satellite (Sat). Scale bar, 50 μm.

of the deutomerite, opaque; with 6–8 distinct nuclear endosomes, clearly revealed with acid carmine staining. Nucleus often obscured in late gamonts. Fresh gamonts granular to opaque, epicyte clear. Color white under reflected light, brownish-orange under transmitted light.

Association (Figs. 4, 6–8): Syzygy late, caudofrontal, syzygial pairs and gametocysts located between host ventricular peritrophic membrane and posterior ventricular epithelium (n = 60, except where noted). Fresh gamonts granular to opaque, epicyte clear. Color white under reflected light, brownish-orange under transmitted light. Differences in association morphology reflect normal population variation (Fig. 4, 6–8).

Primite. Protomerite broadly ovoid to depressed ovoid; PL 62 μm (40–96, ±15), PW 107 μm (68–160, ±24), PW/PL 1.78 (1.00–3.70, ±0.44); truncated anteriad, approaching hemispheroid; with strong thick-



Figs. 5–10. *Leidyana migrator* n. sp. **Fig. 5.** Trophozoites, differences reflect normal population variation. Scale bar, 50 μm. **Figs. 6–8.** Associations; differences reflect maturation and population variation. Scale bar, 100 μm. **Fig. 9.** Chain of oocysts, dorsal aspect. Scale bar, 5 μm. **Fig. 10.** Oocysts, lateral aspect. Scale bar, 5 μm.

ening of the epicyte surrounding epimerite scar; with strong posteriad constriction at protomerite-deutomerite septum. Deutomerite narrowly obovoid to broadly obovoid, often with a shallow marginal sinus along each margin (narrowly panduriform); DL 389 μm (248–520, ±69), DW 145 μm (76–304, ±43), DW/DL 0.38 (0.21–0.78, ±0.12); truncated anteriad at protomerite-deutomerite septum, rounded posteriad. TL 447 μm (296–568, ±74); PL/TL 0.14 (0.09–0.22, ±0.03); DL/TL 0.87 (0.78–0.92, ±0.03); PL/DL 0.16 (0.10–0.28, ±0.04); PW/DW 0.77 (0.45–1.76, ±0.21); DW across sinoid constriction 134 μm (48–280, ±47, n = 56). Primite TL/satellite TL 1.12 (0.85–1.43, ±0.16). Nucleus ellipsoid to depressed ellipsoid (n = 54); KL 28 μm (20–44, ±6), KW 37 μm (26–48, ±6), KW/KL 1.35 (0.81–2.40, ±0.32); placement roughly abaxial in the anterior half of the deutomerite, opaque; nuclear endosomes indistinct, often obscured with maturity and the onset of syzygy.

Satellite. Protomerite transverse oblong elliptoid; PL 37 μm (16–64, ±11), PW 114 μm (72–160, ±22), PW/PL 3.30 (1.69–10.00, ±0.16); crateriform anteriad, forming a shallow ball-and-socket junction with primite; truncated posteriad at protomerite-deutomerite septum. Deutomerite narrowly elliptoid to broadly elliptoid; DL 373 μm (192–496, ±69), DW 142 μm (68–276, ±40), DW/DL 0.39 (0.24–0.79, ±0.02); truncated anteriad at protomerite-deutomerite septum, acuminate posteriad. TL 404 μm (220–548, ±73); PL/TL 0.09 (0.04–0.15, ±0.01); DL/TL 0.92 (0.85–0.99, ±0.01); PL/DL 0.10 (0.04–0.15, ±0.01); PW/DW 0.83 (0.47–1.13, ±0.16). Satellite TL/Primite TL 0.91 (0.70–1.18, ±0.13). Nucleus ellipsoid to depressed ellipsoid (n = 53); KL 36 μm (20–50, ±7), KW 30 μm

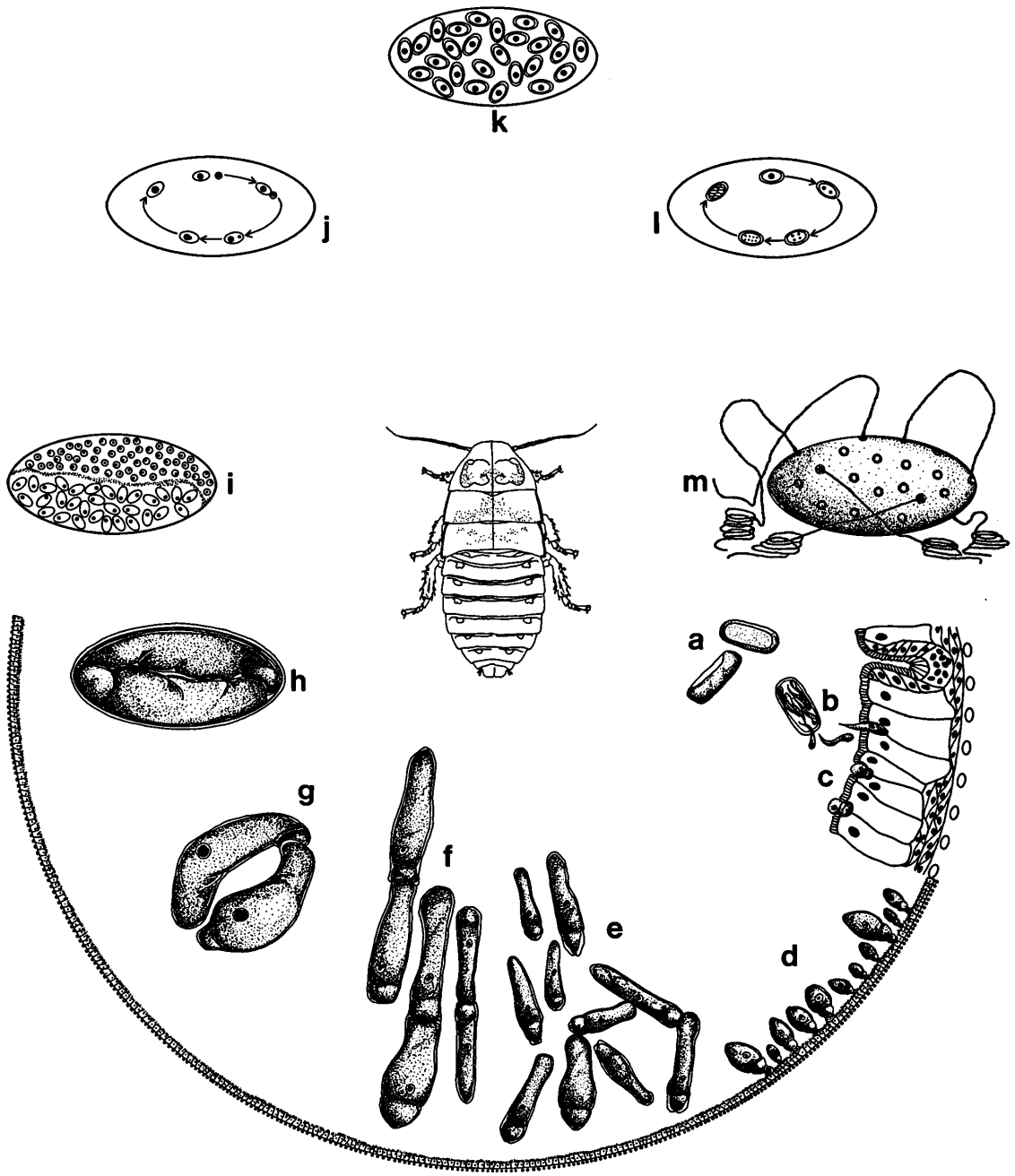


Fig. 11. Life cycle and development of *Leidyana migrator* in *Gromphadorhina portentosa.* Oocysts in the environment (a) are consumed by a hissing cockroach. Enclosed sporozoites activate in the host gut, escape the oocyst sheath, and migrate to the intestinal epithelium (b). Sporozoites establish themselves between the cells of the intestinal epithelium and undergo an intercellular development phase (c). Gregarine trophozoites (d) remain attached to the host epithelium by an epimerite during the lumenal growth phase. Mature trophozoites (e) detach from the host epithelium, form reproductive associations (f), and undergo syzygy (g) to produce a reproductive gametocyst (h) that is shed with host feces. Gametogony (i), fertilization, and zygote formation (j) occur in the exogenous gametocyst. Each zygote forms a protective oocyst envelope (k) and undergoes sporogony (l), producing 8 sporozoites. Gametocysts dehisce when mature (m), releasing infective oocysts into the environment to continue the cycle.

Table 1. Comparison of gamont morphometric data from 3 species of *Leidyana*[1].

	L. erratica[2]	*L. migrator*	*L. oviformis*[3]
Total Length (TL)	395 (290–500)	352 (220–536)	292 (243–350)
Protomerite Length (PL)	65 (50–80)	58 (36–88)	53 (44–65)
Deutomerite Length (DL)	330 (240–420)	294 (172–460)	239 (199–285)
Protomerite Width (PW)	75 (50–100)	113 (44–228)	66 (49–88)
Deutomerite Width (DW)	110 (60–160)	188 (60–352)	112 (69–169)
PL/TL	0.16	0.16	0.18
DL/TL	0.84	0.84	0.82
PL/DL	0.20	0.20	0.22
PW/PL	1.15	1.95	1.24
DW/DL	0.33	0.64	0.47
PW/DW	0.68	0.66	0.59

[1] Measurement values (μm) are means with ranges in parentheses. Ratio values are means.
[2] Data from Watson (1916).
[3] Data from K. Hoshide (1978).

(16–48, ±7), KW/KL 1.28 (0.58–2.5, ±0.39); placement roughly abaxial in the anterior half of the deutomerite, opaque; nuclear endosomes indistinct, often obscured with maturity and the onset of syzygy.

Gametocyst: White to ivory, elliptoid (n = 48); length 1,066 μm (620–1,400, ±195), width 656 μm (420–860, ±120), width/length 0.62 (0.48–0.81, ±0.06); hyaline coat uniform, opalescent, narrow, width about 20 μm, observed on gametocysts in the host rectum but indistinct on exogenous gametocysts. Gametocysts mature and dehisce through short spore tubes (4–8, usually 6) within 60–72 hr. Oocysts are extruded in coiled chains. No epispore or packet membrane was observed.

Oocyst (Figs. 9, 10): Dolioform in dorsal aspect (Fig. 9), very uniform in size and shape, no variation within the limits of accuracy of measurement (n = 30): length 8 μm, width 4 μm; botuliform in lateral aspect (Fig. 10), terminal height 4 μm; median height 2 μm; terminal ends roughly squared by enclosing membrane.

Type host: *Gromphadorhina portentosa* (SCHAUM) (Insecta: Blattodea), Madagascar hissing cockroach.

Host Records: Nymphs and adults of *Gromphadorhina portentosa.*

Type locality: Research colonies maintained by the Department of Entomology, Texas A&M University, College Station, Texas, USA.

Specimens deposited: Two type slides were deposited in the United States National Parasite Collection (USNPC), Biosystematic Parasitology Laboratory, Beltsville, Maryland. The holotype is a trophozoite on slide USNPC No. 84555 and is marked by an etched circle. The remaining trophozoites, gamonts, and associations (USNPC No. 84555, 84556) are paratypes. Six slides were deposited in the Harold Manter Laboratory for Parasitology (HWML), Division of Parasitology, University of Nebraska State Museum, Lincoln, Nebraska. Trophozoites, gamonts, and associations in HWML 38218 (4 slides) and HWML 38219 (2 slides) are paratypes. Trophozoites, gamonts and associations on slides REC950036–REC950057, REC950063–REC950071, and REC950087–REC950091 are paratypes retained in the author's personal collection. One specimen of *G. portentosa* was deposited as voucher specimen TAMU-614 in the Systematics Research Collection, Department of Entomology, Texas A&M University, College Station, Texas.

Infection site: Trophozoites and gamonts were observed in the anterior enteric caeca and descending ventriculus. Associations were observed in the posterior coiled ventriculus, anterior to the ileum and the attachment of the Malpighian tubules. All endogenous life-cycle stages were observed between host ventricular peritrophic membrane and ventricular epithelium. Trophozoites were attached to the ventricular epithelium.

Etymology: *Leidyana migrator* is an obligate parasite of *Gromphadorhina portentosa,* an animal whose New World distribution is limited to laboratory colonies. The specific epithet is taken from the Latin *migrator* ("wanderer") and is given to mark the migration of the protistan ("Leidy's wanderer") with its host.

Discussion

Leidyana erratica (CRAWLEY 1907) WATSON 1915 and *Leidyana oviformis* K. HOSHIDE 1978 resemble *L. migrator* more closely than other described species of *Leidyana.* Individuals of *L. oviformis* are smaller than those of *L. erratica* and *L. migrator,* but gamonts of all 3 species overlap morphometrically (Table 1). Despite these similarities, all 3 species possess unique characters. The epimerite of *L. erratica* is simple and globular (Watson 1916), like that of *L. migrator.* In contrast, the epimerite of *L. oviformis* is lanceolate (K. Hoshide 1978). This character separates *L. migrator* and *L. erratica* from *L. oviformis. Leidyana migrator* and *L. erratica* are separated by differences in their gametocysts, dehiscence, and oocysts. The gametocysts of *L. migrator* are elliptoid with an average length of 1,066 μm. When mature they dehisce

through 6 spore tubes, releasing dolioform oocysts measuring 8 μm by 4 μm. In contrast, the gametocysts of *L. erratica* are spherical and 260–350 μm in diameter (Watson 1915; Issi & Lipa 1968; K. Hoshide 1973b). When mature they dehisce through 1–12 spore tubes, releasing dolioform oocysts measuring 6 μm by 3 μm (Watson 1915). In addition, the gametocysts of *L. erratica* possess a hyaline epicyst 30 μm thick (Watson 1916; K. Hoshide 1973b), not present on the gametocysts of *L. migrator.*

The diagnostic characters of *Leidyana* (a simple, globular epimerite, "solitary sporonts," gametocyst dehiscence by spore ducts, and dolioform oocysts) represent 4 distinct ontogenetic stages (trophozoites, gamonts, mature gametocysts, and oocysts, respectively). Therefore, the complete life cycle and development of any putative species of *Leidyana* must be observed in order to confidently ascribe that species to the genus (Corbel 1967b). An unfortunate indication of the taxonomic instability of many member species is that developmental details are known for only 17 of the 27 species that currently constitute *Leidyana.* This study of the life cycle and development of *L. migrator* (Fig. 11), in which all of the diagnostic characters of the genus *Leidyana* have been observed, brings the total to 18 well-documented species of the 28 in the genus *Leidyana.*

Ball et al. (1995) reported heavy gregarine infections in wild hissing cockroaches imported from Madagascar. Although a complete description was not provided, the gregarines they reported strongly resemble *L. migrator.* Gregarines are regarded as highly host-specific parasites, generally restricted to a single host species (Levine 1988). In light of the host-specific nature of eugregarines, the reports of Ball et al. (1995) suggest that *L. migrator* was probably introduced into the New World in association with *G. portentosa.* Ball et al. (1995) associated lethal disease with heavy gregarine infections in *G. portentosa,* but I have observed no lethal pathology in hissing cockroaches infected with *L. migrator.*

Leidyana migrator is the first species of *Leidyana* reported from a cockroach. Although less than half of named *Leidyana* spp. are reported from orthopteroids, *L. erratica* and *L. oviformis* are both reported from gryllids (*Gryllus* spp. and *Pteromenobius* spp., respectively) (Watson 1915; Issi & Lipa 1968; K. Hoshide 1973b, 1978). No phylogenetic or biogeographical inference can be drawn from this pattern, but it does suggest a common relationship among species of *Leidyana* that infect orthopteroids. These phylogenetic and biogeographical patterns will be addressed as we expand our knowledge of the diversity, distribution, and host relationships of *Leidyana.*

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