

## Revision of the Genus *Protomagalhaensia* and Description of *Protomagalhaensia wolfi* n. comb. (Apicomplexa: Eugregarinida: Hirmocystidae) and *Leidyana haasi* n. comb. (Apicomplexa: Eugregarinida: Leidyaniidae) Parasitizing the Lobster Cockroach, *Nauphoeta cinerea* (Dictyoptera: Blaberidae)

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**ABSTRACT:** *Protomagalhaensia wolfi* n. comb. and *Leidyana haasi* n. comb. were originally described as species of *Gregarina* parasitizing the lobster cockroach, *Nauphoeta cinerea*, in east Africa. Gamonts of *Protomagalhaensia* species are elongate and serpentine in general shape. Species within the genus are differentiated primarily by epimerite and oocyst morphology. Among described species of *Protomagalhaensia*, only *P. wolfi* possesses an obdeltoid epimerite. The oocysts of *P. wolfi* possess no apical spine or knob and are notably larger than oocysts of other species in the genus. Among the 33 species of *Leidyana*, only *L. haasi* and *Leidyana migrator* are reported from cockroaches (Dictyoptera). In general, gamonts of *L. migrator* are longer and more anisometric than those of *L. haasi*, the greater length reflecting notably longer deutomerites in *L. migrator*. The gamontic protomerites of *L. haasi* are longer but considerably narrower than those of *L. migrator* even though gamonts of *L. migrator* are larger overall. Both *L. migrator* and *L. haasi* are characterized by elliptoid oocysts that differ in relative morphology and overall size. The elliptoid gametocysts of *L. migrator* are ca. 3 times larger than those of *L. haasi*. We redescribe *P. wolfi* and *L. haasi* and refer them to genera other than *Gregarina*, establish neotype specimens, revise the diagnosis of *Protomagalhaensia* to reflect oocyst variation within the genus and distinguish it from the other 15 genera comprising Hirmocystidae, and discuss the fidelity of endemic gregarine faunas with their cockroach hosts despite global host dispersal.

**KEY WORDS:** Apicomplexa, Hirmocystidae, Leidyaniidae, Gregarine, *Leidyana haasi*, *Gregarina haasi*, *Protomagalhaensia wolfi*, *Gregarina wolfi*, *Nauphoeta cinerea*, lobster cockroach.

Cockroaches and their gregarines are readily and inexpensively obtained, easily maintained in culture, and amenable to experimental manipulation, providing effective host-parasite experimental models (e.g., Clopton and Smith, 2002; Smith and Clopton, 2003). Unfortunately, there are considerable impediments to their broader use and development as experimental models: gregarine biodiversity within cockroaches remains largely unknown and where taxa are known to exist, the generally abysmal state of cockroach-gregarine taxonomy precludes ready identification of the parasites. As part of a larger study of Nearctic gregarine biodiversity, we have undertaken a survey of gregarines parasitizing cockroaches in culture. Increasing knowledge of diversity within the group coupled with a robust taxonomy will significantly increase the utility of cockroach-gregarine host-parasite models in experimental parasitology.

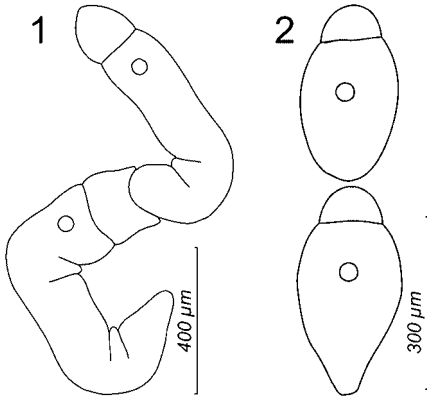
In the winter of 2004, we established cultures of the lobster cockroach, *Nauphoeta cinerea* (Olivier, 1789) (Dictyoptera: Blattaria: Blaberidae: Oxyhalinae: Nau-

phoetini) using stock material from Florida, U.S.A. Postmortem examination of lobster cockroaches maintained in colony revealed infections by 2 distinct gregarine species. Both are previously described from a small collection of nymphs of *N. cinerea* from east Africa (Geus, 1969), but the original descriptions are incomplete, providing little morphometric data and no observation of gametocyst or oocyst morphology. Although originally described as *Gregarina wolfi* Geus, 1969 and *Gregarina haasi* Geus, 1969, (Figs. 1, 2) our studies of their morphology and life cycle patterns demonstrate the original placements incorrect. Herein we revise the genus *Protomagalhaensia* Pinto, 1918; provide complete redescription and diagnosis of *G. wolfi* and *G. haasi*; refer these taxa to separate genera with the creation of *Protomagalhaensia wolfi* n. comb. and *Leidyana haasi* n. comb., respectively; and distinguish *P. wolfi* and *L. haasi* from existing members of their respective genera.

### MATERIALS AND METHODS

*Nauphoeta cinerea* breeding colonies were established using wild-caught stock from a private collector in Tampa, Florida, U.S.A., and maintained in 50-L plastic tubs with

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**Figures 1–2.** Gregarines described from *Nauphoeta cinerea* collected in Ndanda, Tanzania (after Geus, 1969). **1.** *Gregarina wolfi* Geus, 1969, association. **2.** *Gregarina haasi* Geus, 1969, association.

softwood bedding and cardboard egg-crate roosting habitat. Food (a mixture comprising equal parts coarsely ground commercial dry puppy food, dry kitten food, and rat chow) and water were provided ad libitum. Adult or late-instar nymphal *N. cinerea* were removed from the colony and examined for gregarine parasites. Cockroaches were held overnight in 0.6-L clear styrene containers to collect shed feces for gametocyst studies. Cockroaches were eviscerated and their alimentary canals dissected in insect muscle saline (Belton and Grundfest, 1962). Permanent microscope slide preparations were made using wet smears of gregarines and host gut tissues fixed by flotation on hot AFA (ethanol, formalin, and acetic acid), stained with either Semichon's acetocarmine (Semichon, 1924) or Harris' hematoxylin and eosin-xytol and mounted in Damar balsam (Clopton 1995, 1999, 2000, 2002, 2004a; Clopton and Nolte, 2002; Clopton et al., 2004; Hays et al., 2004). Subsamples of each gregarine species from each of 5 hosts were collected and pooled by species in groups of 100 individuals each. The DNA from each pooled sample was isolated using a protocol similar to that reported by Laird et al. (1991). Isolated DNA samples were re-suspended in nuclease free water and stored at  $-20^{\circ}\text{C}$  for future genetic analysis. Gametocysts were isolated from collected feces, triple-rinsed in insect muscle saline, photographed for morphometric analysis, surface sterilized in 0.1% formalin, triple-rinsed in 17-M $\Omega$  deionized water, dried briefly on filter paper, and transferred to 4 mm black cardstock disks previously sterilized in 0.1% formalin and placed in individual  $4 \times 12$  mm glass micro vials (BioQuip Products, Gardena, California, U.S.A.). After allowing the excess moisture to evaporate (ca. 45 min), vials were sealed with white silicon stoppers and gametocysts were held for maturation and dehiscence. Gametocysts were observed daily and any changes in structure, maturation or dehiscence noted. Oocyst structure and dimensions were taken from fresh preparations of oocysts in wet mounts and agar monolayer mounts (Clopton, 1999, 2000, 2002, 2004a; Clopton and Nolte, 2002; Clopton et al., 2004; Hays et al., 2004) prepared as follows. Molten agar (1.5% solution) was pipetted onto a clean glass slide, allowed to drain, and the slide was quickly chilled on a cold aluminum block to produce a thin, uniform layer of agar. Oocysts were placed

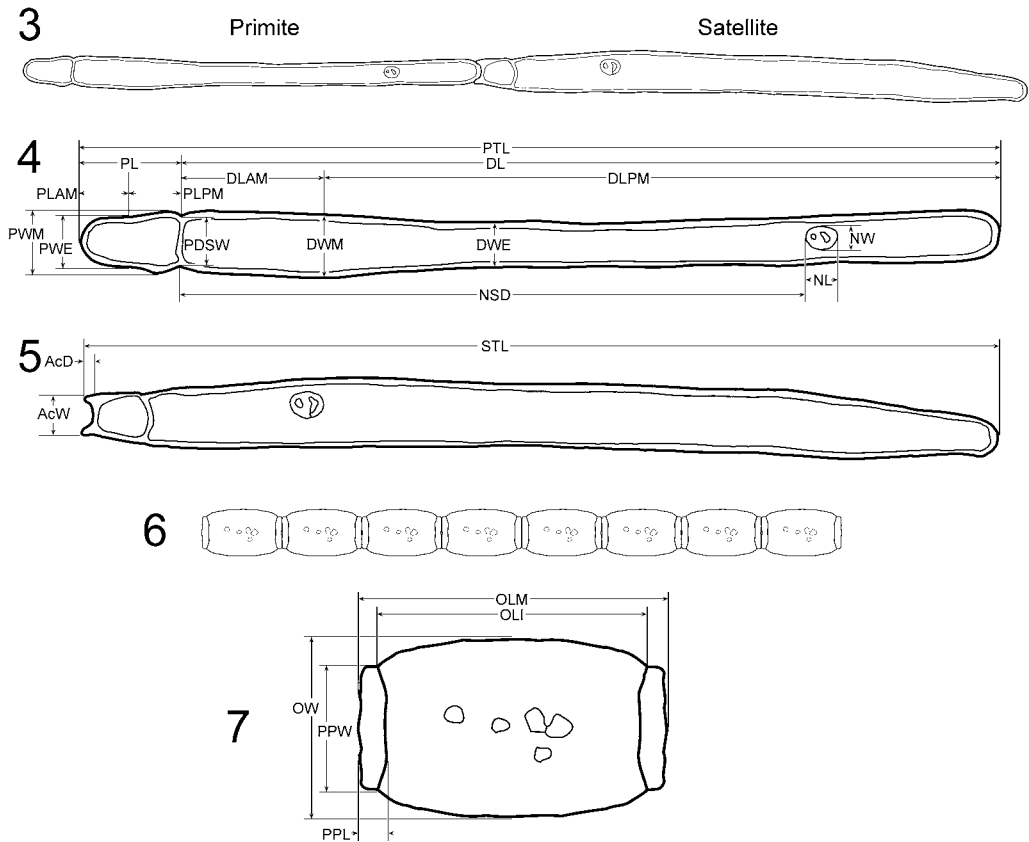
in a small (ca. 7  $\mu\text{l}$ ) drop of water on a 12 mm round cover glass (#0 thickness) and the agar slide was inverted to pick up the cover glass. The resulting preparation produced a monolayer of oocysts trapped between the agar layer and the cover glass, providing a uniform object plane for light microscopy.

Observations were made using an Olympus B-Max 50 compound microscope with 10X, 20X, 40X and 60X universal planapochromatic objectives with either phase contrast condensers or differential interference contrast prisms and an infinity-optics turret doubler. Digital photographs were taken with an Olympus DP-70 digital camera through the aforementioned microscope. Measurements were taken from the digitized images of preserved specimens using Image-Pro Express<sup>®</sup> v 4.0 and Image-Pro Discovery<sup>®</sup> v 4.0 image analysis software (Media Cybernetics, L.P., Silver Spring, Maryland, U.S.A.). Photographic plates were processed and assembled using Adobe<sup>®</sup> PhotoShop<sup>®</sup> 5.5 and Adobe<sup>®</sup> PhotoShop<sup>®</sup> 7.0.1 software (Adobe Systems Inc., San Jose, California, U.S.A.).

Extended morphometric character sets have been delineated for several gregarine genera including *Stictospora*, *Xiphocephalus*, *Amoebogregarina*, and *Clitellocephalus* (see Hays et al., 2004; Clopton, 1999; Kula and Clopton, 1999; and, Clopton and Nolte, 2002, respectively). These extended morphometric sets include standard mensural data and ratios common to all gregarine species but also include additional metrics particular to the genus of study. Extended character sets used herein for *Protomagalhaensia* and *Leidyana* are delineated in Figures 3–10.

The following metric characters and abbreviations are used herein: satellite acetabulum depth (AcD), satellite acetabulum width (AcW), length of deutomerite (DL), distance from protomerite-deutomerite septum to deutomerite axis of maximum width (DLAM), distance from posterior end of deutomerite to deutomerite axis of maximum width (DLPM), dehiscence plate length (DPL), dehiscence plate width (DPW), width of deutomerite at equatorial axis (DWE), maximum width of deutomerite (DWM), karyosome diameter (KD1), distance from nucleus to protomerite-deutomerite septum (NSD), length of nucleus (NL), width of nucleus (NW), interior oocyst length (OLI), maximum exterior oocyst length (OLM), oocyst width (OW), width of protomerite-deutomerite septum (PDSW), length of protomerite (PL), distance from anterior end of protomerite to protomerite axis of maximum width (PLAM), distance from protomerite-deutomerite septum to protomerite axis of maximum width (PLPM), polar plate length (PPL), polar plate width (PPW), total length of primate (PTL), width of protomerite at equatorial axis (PWE), maximum width of protomerite (PWM), total length of satellite (STL).

The shape and relative proportion of structures in mature trophozoites, particularly the epimerite, comprise an important diagnostic character suite. Although shape and relative proportion are useful, significant developmental variation within taxa precludes the use of absolute metrics taken from trophozoites (Filipponi, 1951; Watwood et al., 1997; Clopton, 1999). Separate description of primate and satellite ontogenic stages are provided to account for the sexual dimorphism commonly observed among the Gregarinicae (Filipponi, 1947, 1951, 1952c, 1954, 1955). Measurements are presented in  $\mu\text{m}$  as mean values followed by range values, standard deviations, and sample sizes in parentheses. Terminology for parasite ontogenic stages and anatomy largely follows that



**Figures 3–7.** Morphometric character set for gamonts and oocysts of *Protomagalhaensia* species. **3.** Primate and satellite of *Protomagalhaensia wolfi* in association. **4.** Generalized gamont characters mapped on a primate of *P. wolfi*. **5.** Specialized satellite characters of *P. wolfi*. **6.** Oocyst chain of *P. wolfi* showing placement of dehiscence plates. **7.** Oocyst characters of *P. wolfi*. (AcD, satellite acetabulum depth; AcW, satellite acetabulum width; DL, length of deutomerite; DLAM, distance from protomerite-deutomerite septum to deutomerite axis of maximum width; DLP, distance from posterior end of deutomerite to deutomerite axis of maximum width; DWE, width of deutomerite at equatorial axis; DWM, maximum width of deutomerite; NSD, distance from nucleus to protomerite-deutomerite septum; NL, length of nucleus; NW, width of nucleus; OLI, interior oocyst length; OLM, maximum exterior oocyst length; OW, oocyst width; PDSW, width of protomerite-deutomerite septum; PL, length of protomerite; PLAM, distance from anterior end of protomerite to protomerite axis of maximum width; PPL, polar plate length; PPW, polar plate width; PTL, total length of primate; PWE, width of protomerite at equatorial axis; PWM, maximum width of protomerite; STL, total length of satellite.)

proposed by Levine (1971). Terminology for shapes of planes and solids follows Clopton (2004b). Additional descriptive terminology is derived from Harris and Harris (1994).

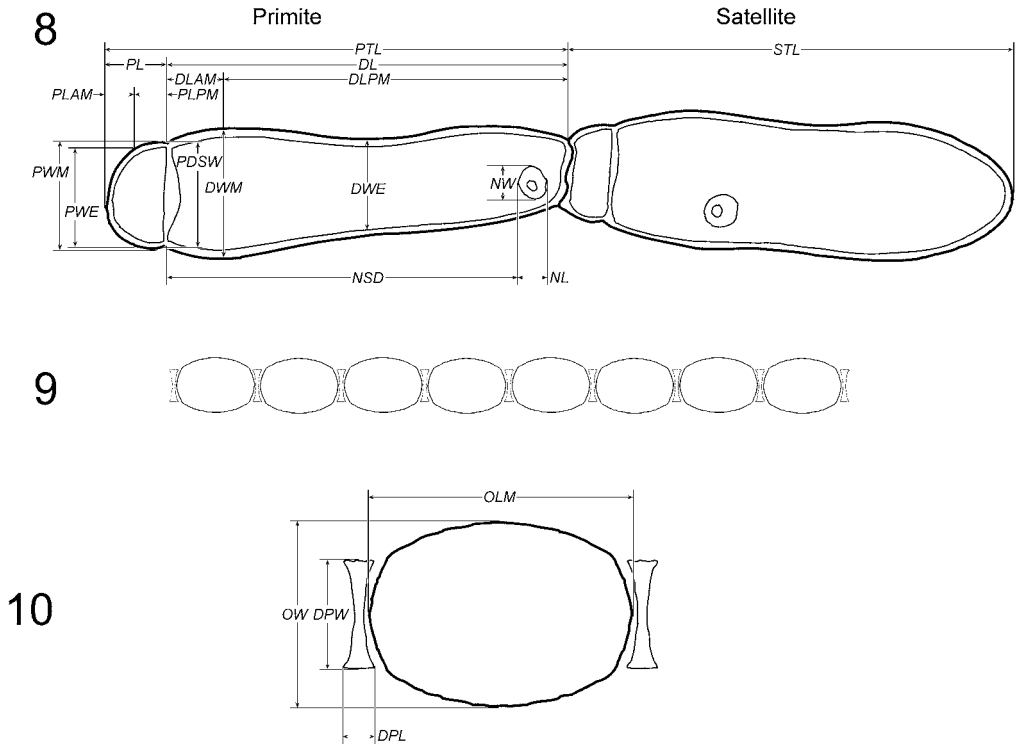
## RESULTS

### *Protomagalhaensia* Pinto, 1918 revised

#### Revised diagnosis

Order Eugregarinida Léger, 1892, sensu strictu Levine et al. (1980); Suborder Septatina Lankester, 1885, sensu strictu Levine et al. (1980); Superfamily

Gregarinicae, Chakaravarty, 1960 sensu Clopton (2002); Family Hirmocystidae Grassé, 1953 sensu Clopton (2002); Genus *Protomagalhaensia* Pinto, 1918 revised as follows: epimerite shallowly obovoid to shallowly obdeltoid, developed intracellularly within a single host intestinal epithelial cell, not retained in gamonts; trophozoites becoming elongate after association; association precocious, caudofrontal, association interface a shallowly semi-obpanduriform interlock in which the posterior end of the primate's deutomerite is constricted and clamped by an acetabulum formed from the anterior membranes



**Figures 8–10.** Morphometric character set for gamonts and oocysts of *Leidyana* species. **8.** Primate and satellite of *Leidyana haasi* in association. Generalized gamont characters are mapped on the primate only. **9.** Oocyst chain of *L. haasi* showing articulation of polar plates. **10.** Oocyst characters of *L. haasi*. (DL, length of deutomerite; DLAM, distance from protomerite-deutomerite septum to deutomerite axis of maximum width; DLPM, distance from posterior end of deutomerite to deutomerite axis of maximum width; DPL, dehiscence plate length; DPW, dehiscence plate width; DWE, width of deutomerite at equatorial axis; DWM, maximum width of deutomerite; NSD, distance from nucleus to protomerite-deutomerite septum; NL, length of nucleus; NW, width of nucleus; OLM, maximum exterior oocyst length; OW, oocyst width; PDSW, width of protomerite-deutomerite septum; PL, length of protomerite; PLAM, distance from anterior end of protomerite to protomerite axis of maximum width; PLPM, distance from protomerite-deutomerite septum to protomerite axis of maximum width; PTL, total length of primate; PWE, width of protomerite at equatorial axis; PWM, maximum width of protomerite; STL, total length of satellite.)

of the satellite’s protomerite; oocysts dolioform with or without spines or knobs at terminal apices, released in chains from gametocyst by simple rupture.

**Taxonomic summary**

*Type species: Protomagalhaensia serpentula* (de Magalhaes, 1900) Pinto, 1918 (=Gregarina serpentula de Magalhaes, 1900).

**Remarks**

Pinto (1918) erected the genus *Protomagalhaensia* to recognize differences in gametocyst dehiscence and oocyst morphology between *P. serpentula*, described from *Blatella orientalis* Linnaeus, 1758

(Dictyoptera: Blattaria: Blaberidae), and the remaining members of *Gregarina* Dufour, 1828. (The original description of *Protomagalhaensia*, Pinto [1918], is 1 of a series of published preliminary meeting reports. These preliminary notes are incorporated into a larger more comprehensive work, Pinto [1922], which includes a more complete description of *Protomagalhaensia* with comparisons to *Gregarina*.) Oocysts of *P. serpentula* were described as dolioform with terminal corner spines: their gametocysts dehisce by simple rupture (Pinto, 1922). In contrast, the oocysts of *Gregarina* species range from dolioform to spherical and their gametocysts dehisce through spore tubes (Clopton, 2002).

The genus remained monotypic until Filipponi (1952a) described *Protomagalhaensia marottai*

Filipponi, 1952 from adults and larvae of *Scaurus striatus* (Coleoptera: Tenebrionidae), although he noted reservations about the generic diagnosis in the original description, (“L’attribuzione della specie al genere *Protomagalhaensia* Pinto 1918 è solo provvisoria”). Within the year, Théodoridès (1952) synonymized *P. marottai* with *Gregarina cavalierina* Blanchard, 1905 and presented a case for the synonymy of *Gregarina* and *Protomagalhaensia* based largely on trophozoite and gamont structure and interpretation of oocyst structure. Filipponi (1952b, 1952c, 1953) maintained the separate and unique status of *P. marottai* through a series of studies on the relative canalization of morphometric characters in the taxon, but the opinion of Théodoridès (1952) prevailed and is reflected in the most recent checklist of the Eugregarinorida (see Levine, 1988). Our observations using differential interference microscopy confirm the hypothesis of Théodoridès (1952) that the terminal corner spines reported from the oocysts of species of *Protomagalhaensia* can be the result of optical refraction artifacts rather than real structure. The generic diagnosis is revised herein to reflect these new oocyst observations.

Despite efforts focused on morphometric differentiation of trophozoites and gamonts among *Protomagalhaensia* and *Gregarina*; these differences are systematically moot given the family-level differences between the genera. Gregarinidae Labbé, 1899 includes genera of Septatina with precocious association whose gametocysts dehiscence through multiple spore tubes. Hirmocystidae Grassé, 1953 comprises genera of Septatina with precocious association whose gametocysts dehiscence by simple rupture. Although the arrangement of Chakravarty (1960) failed to recognize differences in gametocyst dehiscence among genera of Septatina, the more recent arrangements of Levine (1979, 1988) and Clopton (2002) reflect this distinction. Species of *Protomagalhaensia* are characterized by precocious association and gametocyst dehiscence by simple rupture and thus the generic diagnosis should distinguish *Protomagalhaensia* from genera within Hirmocystidae rather than Gregarinidae.

Hirmocystidae was erected to comprise genera whose gametocysts dehiscence by simple rupture rather than through sporoducts. The type genus was originally based on the multiple associations formed by trophozoites in the group (Labbé, 1899). The state and position of the family has been the topic of some debate. Watson (1916, 1922) placed *Hirmocystis* within the Gregarinidae. Grassé (1953) erected the family Hirmocystidae to comprise *Hirmocystis*, *Didymophyes*, and 5 related genera. This arrangement was accepted and

clarified by Chakravarty (1960) who placed the members of Hirmocystidae Grassé with Didymophyidae Léger and declared Hirmocystidae a junior synonym. However, these arrangements failed to recognize differences in gametocyst dehiscence among member genera. Levine (1979) resurrected Hirmocystidae to comprise the 9 genera of Didymophyidae sensu Chakravarty (1960) whose gametocysts dehiscence by simple rupture. Levine (1985) revised Hirmocystidae sensu Grassé to include general trends in epimerite structure. Although this arrangement is reflected by Levine (1988) and Clopton (2002), Vivier and Desportes (1990) adopted Hirmocystidae sensu Grassé.

Hirmocystidae comprises *Protomagalhaensia* among 15 other genera (Clopton, 2002): *Hirmocystis* Labbé, 1899; *Dumbellicephalus* Bala and Kaur, 1988; *Neohirmocystis* Ghose, Ray, and Haldar, 1986; *Tettigonospora* Smith, 1930; *Eliptocystis* Sengupta, Ghosh, and Haldar, 1991; *Acanthogregarina* Kalavati, Narasimhamurti and Vnidyllatadevi, 1988; *Retractocephalus* Haldar and Chakraborty, 1976; *Hyalospora*, Schneider, 1875; *Quadruhyalodiscus* Kundu and Haldar, 1984; *Liposcelius* Sarkar and Haldar, 1980; *Arachnocystis* Levine, 1979; *Euspora* Schneider, 1875; *Pintospora* Carini, 1944; *Tintinospora* Hoshide, 1959; and *Endomycola* Théodoridès, Desportes, and Jolivet, 1972. Hirmocystid genera are defined by unique suites of non-unique characters or, in the case of many monotypic genera, by putatively unique characters for which the states are unknown in other genera. This is a trend within the septate gregarines and demonstrates the need for comprehensive evaluation of generic-level character sets. Table 1 presents a summary of re-evaluated states of the common cardinal characters of genera within Hirmocystidae. *Protomagalhaensia* is distinguished with the family by oocyst shape. Alone among the genera comprising Hirmocystidae, species of *Protomagalhaensia* possess dolioform oocysts with a depressed oblong polar plate at each end and, in some species, with spines or knobs at the terminal apices. Trophozoites of species belonging to both *Protomagalhaensia* and *Tettigonospora* are characterized by epimerites that are obdeltoid in shape, but species of *Tettigonospora* possess orbicular rather than dolioform oocysts. Three hirmocystid genera are characterized by species in which the association interface creates an interlock: *Protomagalhaensia*, *Hyalospora*, and *Acanthogregarina*. Species constituting *Protomagalhaensia* and *Hyalospora* are characterized by a convex association interlock in which the posterior margin of the primate's deutomerite is constricted and clamped by an acetabulum formed from the anterior membranes of the

**Table 1. States of the common cardinal characters of the 16 genera comprising the family Hirmocystidae Grassé, 1953.**

Taxon	Oocyst shape*	Epimerite		Association interface	
		Shape*	Coronate	Shape*	Polarity†
<i>Protomagalhaensia</i> <sup>1</sup>	Dolioform	Deeply Obdeltoid	0	Shallowly Semi-obpanduriform	Convex‡
<i>Hyalospora</i> <sup>2</sup>	Elliptoid	Orbicular§	0	Semi-lomentiform	Convex‡
<i>Hirmocystis</i> <sup>3</sup>	Elliptoid	Deltoid	0	Very Depressed Obovoid	Unbiased
<i>Quadruhyalodiscus</i> <sup>4</sup>	Elliptoid	0	1	Very Depressed Obdeltoid	Unbiased
<i>Liposcelius</i> <sup>5</sup>	Hesperidiform	Orbicular	1¶	Very Depressed Obovoid	Unbiased
<i>Tintinospora</i> <sup>6</sup>	Lomentiform#	Orbicular	0	Very Depressed Obovoid	Convex
<i>Acanthogregarina</i> <sup>7</sup>	Oblong	Orbicular	1**	Very Broadly Pyriform	Concave‡
<i>Retractocephalus</i> <sup>8</sup>	Oblong to Narrowly Quadrate	Orbicular§	0	Very Depressed Obovoid	Convex
<i>Dumbellicephalus</i> <sup>9</sup>	Orbicular	Orbicular	0	Very Depressed Obovoid†	Convex
<i>Tetragonospora</i> <sup>10</sup>	Orbicular	Deeply Obdeltoid	0	Very Depressed Obovoid	Convex
<i>Eliptocystis</i> <sup>11</sup>	Orbicular	Deltoid	0	Very Depressed Obovoid	Convex
<i>Neohirmocystis</i> ‡‡,‡,‡ <sup>12</sup>	Orbicular	Unknown	Unknown	Very Depressed Obovoid	Convex
<i>Euspora</i> ‡‡,‡ <sup>13</sup>	Pentagonal Column	Unknown	Unknown	Shallowly Obpyriform	Convex‡
<i>Arachnocystis</i> ‡‡,‡ <sup>14</sup>	Rhomboid	Orbicular	0	Unknown	Unknown
<i>Endomycola</i> ‡‡,‡ <sup>15</sup>	Unknown	Orbicular	0	Unknown	Unknown
<i>Pintospora</i> ‡‡,‡ <sup>16</sup>	Unknown	Unknown	Unknown	Unknown	Unknown

\* Shape nomenclature follows Clopton (2004b).

† Deflection of posterior margin of primate deutomerite.

‡ Deutomerite of primate forming a mechanical interlock with the satellite protomerite.

§ Epimerite capable of retraction into protomerite.

|| Coronate with 4 hyaline suckers.

¶ Coronate with longitudinal sulci.

# With dehiscence plate.

\*\* Coronate with narrow spines.

†† Satellite protomerite with distinct pad or rolled margin at interface with primate.

‡‡ Incertae cedis (existing data and records are so incomplete that cardinal generic characters cannot be assessed for constituent species).

<sup>1</sup> Data from de Magalhaes (1900), Pinto (1918, 1922), Théodoridès (1952), Geus (1969), and Peregrine (1970).

<sup>2</sup> Data from Schneider (1875); Tuzet (1953), Tuzet and Ormières (1954, 1956), Larsson et al. (1992), Shailaja and Amoji (1992), and Hoshide and Sacho (1994).

<sup>3</sup> Data from Labbé (1899), Hall (1907), Hoshide (1951), Halder and Chakraborty (1979, 1981), Théodoridès (1980), Kundu and Halder (1981), Roy (1989), and Saha et al. (1995).

<sup>4</sup> Data from Kundu and Halder (1984).

<sup>5</sup> Data from Sarkar and Halder (1980) and Kalavati (1995).

<sup>6</sup> Data from Hoshide (1959a, 1959b).

<sup>7</sup> Data from Kalavati et al. (1988).

<sup>8</sup> Data from Halder and Chakraborty (1976), Kalavati and Krishna Murty (1989), Pushkala et al. (2000), and Halder et al. (1982).

<sup>9</sup> Data from Bala and Kaur (1988).

<sup>10</sup> Data from Smith (1929, 1930).

<sup>11</sup> Data from Sengupta et al. (1991).

<sup>12</sup> Data from Ghose et al. (1986).

<sup>13</sup> Data from Schneider (1875), Allison (1969), Geus (1969), and Théodoridès et al. (1972).

<sup>14</sup> Data from Devdhar and Gourishankar (1971), Devdhar and Amoji (1978), and Levine (1979).

<sup>15</sup> Data from Théodoridès et al. (1972).

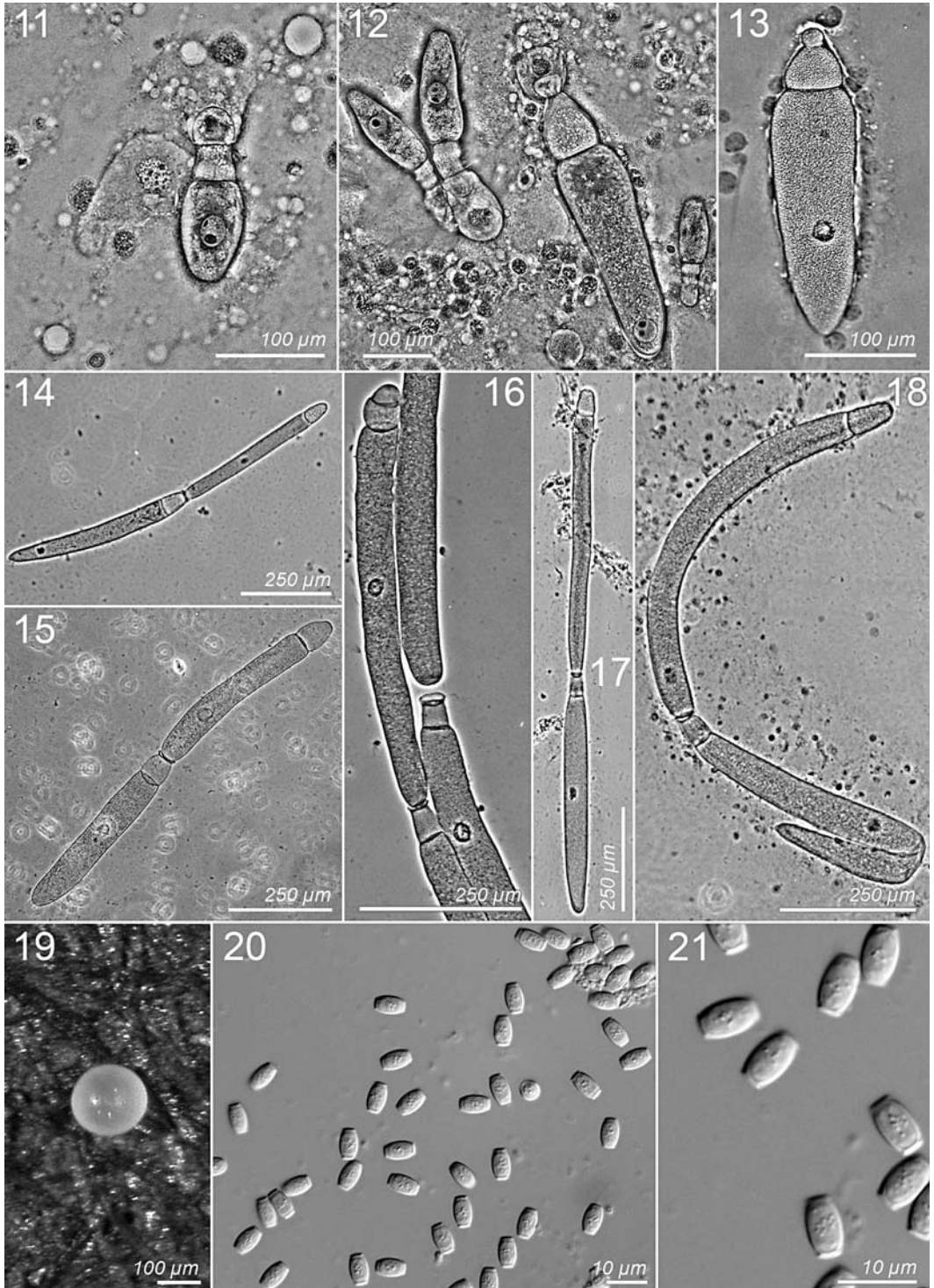
<sup>16</sup> Data from Carini (1944).

satellite's protomerite. In contrast, species constituting *Acanthogregarina* are characterized by a concave association interlock, the anterior margin of the satellite's protomerite is constricted and clamped by an acetabulum formed from the posterior membranes of the primate's deutomerite. *Protomagalhaensia* and *Hyalospora* are differentiated by the shape of the convex association interlock, which is shallowly semi-obpanduriform in species constituting *Protomagal-*

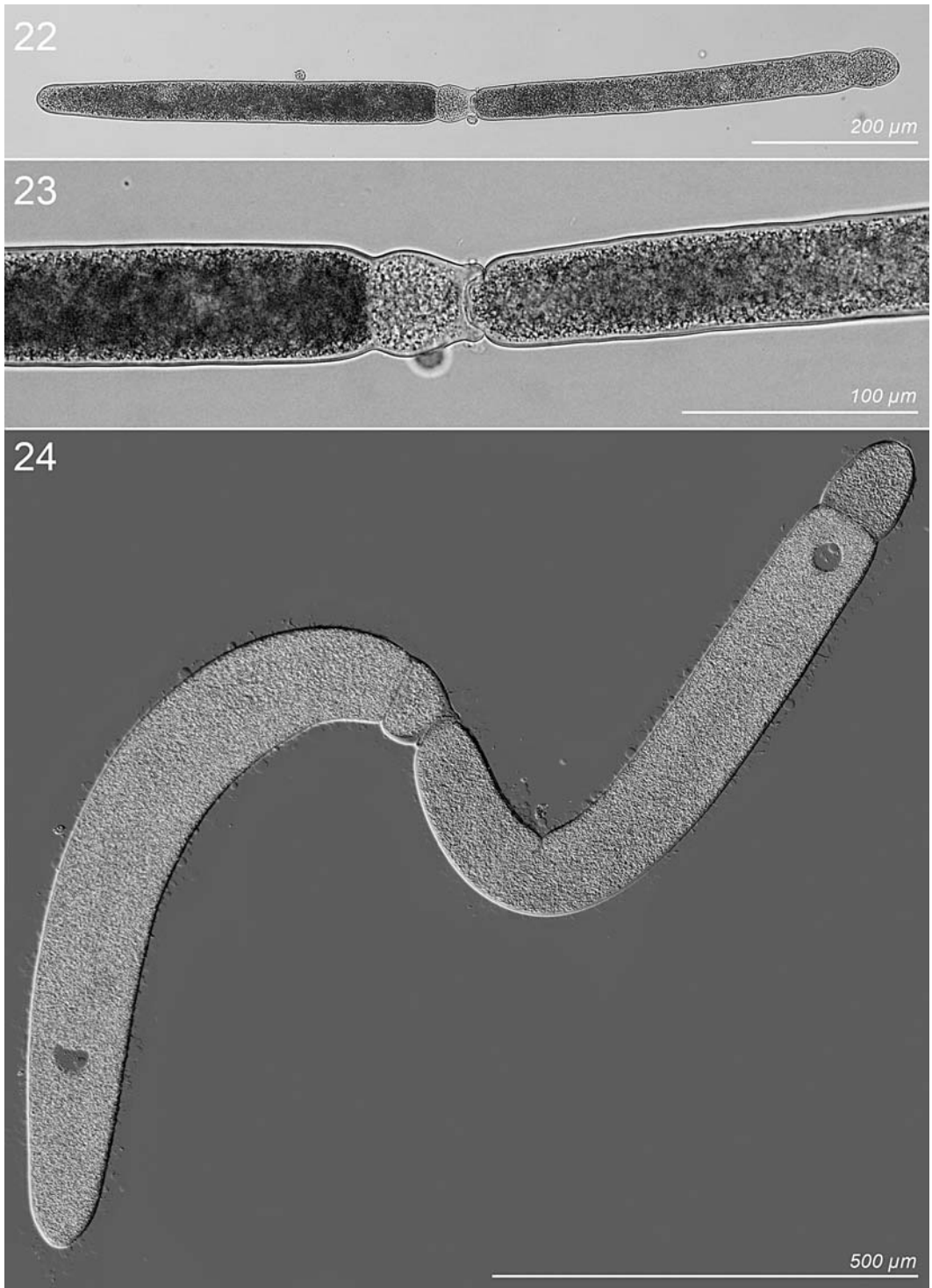
*haensia*, but semi-lomentiform in those constituting *Hyalospora*.

***Protomagalhaensia wolffi* (Geus, 1969)  
Hays and Clopton, 2006, n. comb.  
(Figures 11–24)**

*Young solitary trophozoites:* Young trophozoites solitary, extracellular forms attached to host ventricular epithelium. Holdfast a simple epimerite



**Figures 11–21.** *Protomagalhaensia wolfi* n. comb. 11–12. Young trophozoite. 13. Older trophozoite. 14–15. Young associations. 16–17. Associations showing the association interface and satellite acetabulum. 18. Mature gamonts in association. 19. Gametocyst. 20–21. Oocysts. (Figs 11–18, Harris' hematoxylin and eosin-xytol, phase contrast; Fig 19, live; Figs 20–21, agar monolayer mount, differential interference contrast.)



**Figures 22–24.** *Protomagalhaensia wolfi* n. comb. **22.** Young association (live, phase contrast). **23.** Association interface (live, phase contrast). **24.** Mature association (live, differential interference contrast).



developing intracellularly in a single host epithelial cell. Epimerite very broadly ovoid in young solitary trophozoites, becoming obdeltoid to narrowly obdeltoid in older solitary trophozoites. Protomerite very shallowly ovoid in young solitary trophozoites, becoming broadly ovoid in older solitary trophozoites. Deutomerite obdeltoid in young solitary trophozoites, becoming narrowly obdeltoid in older solitary trophozoites. Nucleus orbicular with 1 or 2 distinct, smooth-margined karyosomes.

*Association:* Gamonts anisomorphic, association precocious, association interface a shallowly semi-obpanduriform interlock in which the posterior end of the primate's deutomerite is constricted and clamped by an acetabulum formed from the anterior membranes of the satellite's protomerite, becoming less prominent with maturity; PTL/STL 1 (0.8–1.3,  $\pm 0.13$ , 30).

*Primate:* Epimerite absent; protomerite very narrowly panduriform; PL 77.1 (53–101,  $\pm 11.61$ , 30), PWE 41.8 (29.1–56.5,  $\pm 6.5$ , 30), PWM 46.8 (33.1–61.7,  $\pm 6.82$ , 30), PLAM 57 (40.1–82.1,  $\pm 11.6$ , 30), PLPM 20.3 (10–32.1,  $\pm 5.93$ , 30), PDSW 43.6 (29–65.4,  $\pm 8.16$ , 30), PL/PWE 1.9 (1.3–2.7,  $\pm 0.31$ , 30), PL/PWM 1.7 (1.2–2.4,  $\pm 0.25$ , 30), PL/PDSW 1.8 (1.4–2.4,  $\pm 0.26$ , 30), PLAM/PL 0.7 (0.6–0.9,  $\pm 0.08$ , 30), PLAM/PLPM 3.1 (1.3–5.7,  $\pm 1.21$ , 30), PWM/PWE 1.1 (1–1.4,  $\pm 0.07$ , 30). Deutomerite elongated, very narrowly to linearly obpanduriform; DL 459.4 (303.8–756.7,  $\pm 112.54$ , 30), DWE 45.9 (21.3–60,  $\pm 8.23$ , 30), DWM 55.5 (32.2–80.8,  $\pm 9.06$ , 30), DLAM 70 (20.7–219.6,  $\pm 50.55$ , 30), DLPM 390.4 (242.5–614.3,  $\pm 99.77$ , 30), DL/DWE 10.3 (5.2–16.6,  $\pm 3.05$ , 30), DL/DWM 8.5 (4.6–15.5,  $\pm 2.5$ , 30), DLAM/DL 0.2 (0–0.4,  $\pm 0.1$ , 30), DLAM/DLPM 0.2 (0.1–0.8,  $\pm 0.17$ , 30), DWM/DWE 1.2 (1–1.5,  $\pm 0.13$ , 30), PTL 533.3 (394.6–835.6,  $\pm 111.79$ , 30). Indices: PTL/PL 7.1 (4.1–10.5,  $\pm 1.69$ , 30), DL/PL 6.1 (3.2–9.5,  $\pm 1.69$ , 30), DWM/PWM 1.2 (1–1.4,  $\pm 0.09$ , 30), PTL/DL 1.2 (1.1–1.3,  $\pm 0.05$ , 30). Nucleus broadly elliptoid with a single, eccentricly placed orbicular karyosome; NL 25 (15.3–32.1,  $\pm 4.33$ , 30), NW 19.9 (12.6–25.3,  $\pm 3.47$ , 30), NDS 211.4 (29.6–575.6,  $\pm 126.51$ , 30), KD1 9.4 (6–13.6,  $\pm 1.65$ , 30), NL/NW 1.3 (0.8–1.8,  $\pm 0.21$ , 30), NDS/NL 8.8 (1–23.8,  $\pm 5.43$ , 30), DL/NDS 3.5 (1.1–13.6,  $\pm 3.18$ , 30), NL/KD1 2.7 (2–3.7,  $\pm 0.48$ , 30).

*Satellite:* Protomerite oblong to narrowly oblong, anterior membranes forming a cup-shaped acetabulum; PL 61.5 (35.3–86.2,  $\pm 13.06$ , 30), AcW 35.1

(20.6–48.3,  $\pm 6.78$ , 30), AcD 10.3 (6.4–14.2,  $\pm 2.09$ , 30), PWE 42.6 (26.2–62.2,  $\pm 8.3$ , 30), PWM 47.1 (30–67.2,  $\pm 8.64$ , 30), PLAM 41.7 (24.2–63.8,  $\pm 9.59$ , 30), PLPM 19.5 (1.3–34.4,  $\pm 7.4$ , 30), PDSW 43 (23.4–59.3,  $\pm 8.92$ , 30), AcW/AcD 3.5 (2–7.4,  $\pm 1$ , 30), AcW/PWM 0.7 (0.6–1,  $\pm 0.09$ , 30), AcD/PL 0.2 (0.1–0.3,  $\pm 0.05$ , 30), PL/PWE 1.5 (1.1–2.3,  $\pm 0.24$ , 30), PL/PWM 1.3 (0.9–1.9,  $\pm 0.21$ , 30), PL/PDSW 1.4 (1.1–2,  $\pm 0.19$ , 30), PLAM/PL 0.7 (0.4–0.8,  $\pm 0.08$ , 30), PLAM/PLPM 3.1 (0.9–26.6,  $\pm 4.5$ , 30), PWM/PWE 1.1 (1–1.3,  $\pm 0.07$ , 30). Deutomerite elongated, very narrowly dolioform; DL 471.8 (288–792.1,  $\pm 138.66$ , 30), DWE 54.4 (32.7–69.2,  $\pm 9.01$ , 30), DWM 61.5 (34–75.3,  $\pm 10.83$ , 30), DLAM 117.7 (33.9–359.2,  $\pm 81.41$ , 30), DLPM 346.5 (83.8–603.5,  $\pm 102.97$ , 30), DL/DWE 8.7 (6–13.4,  $\pm 2.03$ , 30), DL/DWM 7.8 (5.1–12.5,  $\pm 2.01$ , 30), DLAM/DL 0.2 (0.1–0.5,  $\pm 0.11$ , 30), DLAM/DLPM 0.4 (0.1–1,  $\pm 0.23$ , 30), DWM/DWE 1.1 (1–1.3,  $\pm 0.08$ , 30), STL 535 (338.5–859.3,  $\pm 138.81$ , 30). Indices: STL/PL 9.1 (5.3–17.6,  $\pm 3.22$ , 30), DL/PL 8.1 (4.4–16.3,  $\pm 3.15$ , 30), DWM/PWM 1.3 (1–1.8,  $\pm 0.2$ , 30), STL/DL 1.1 (1.1–1.2,  $\pm 0.05$ , 30). Nucleus broadly elliptoid with a single, eccentricly placed orbicular karyosome; NL 26.5 (16.5–39.7,  $\pm 5.92$ , 30), NW 20.1 (13.1–26.7,  $\pm 3.56$ , 30), NDS 249.7 (61.6–697.8,  $\pm 166$ , 30), KD1 10.2 (6–14.3,  $\pm 1.92$ , 30), NL/NW 1.3 (0.8–1.9,  $\pm 0.28$ , 30), NDS/NL 9.5 (2.4–20.2,  $\pm 5.68$ , 30), DL/NDS 2.8 (1.1–6.5,  $\pm 1.91$ , 30), NL/KD1 2.6 (1.9–3.5,  $\pm 0.44$ , 30).

*Gametocysts:* Opaque, irregularly orbicular in outline, diameter 177.0 (126.4–206.3  $\pm 21.68$ , 32). Thirty-eight gametocysts were collected and stored under moist conditions, dehiscing by simple rupture in 96–120 hr.

*Oocysts:* Dolioform with a depressed oblong polar plate at each end; OLM 9.2 (8.7–9.6,  $\pm 0.2$ , 30), OLI 7.5 (7.2–8,  $\pm 0.22$ , 30), OW 5.5 (5.1–5.8,  $\pm 0.18$ , 30), PPW 3.4 (3–3.7,  $\pm 0.19$ , 30), PPL 0.8 (0.6–1.1,  $\pm 0.15$ , 30), OLM/OLI 1.2 (1.2–1.3,  $\pm 0.03$ , 30), OLI/OW 1.4 (1.3–1.5,  $\pm 0.07$ , 30), OLM/OW 1.7 (1.6–1.8,  $\pm 0.06$ , 30), PPW/PPL 4.2 (2.9–6,  $\pm 0.88$ , 30).

### Taxonomic summary

*Type host:* *Nauphoeta cinerea* (Olivier, 1789) (Dictyoptera: Blattaria: Blaberidae: Oxyhalinae: Nauphoetini), nymphs and adults.

*Type locality:* Ndanda, Tanzania.

*Symbiotype:* Five symbiotype specimens (authors' specimens REC05042–REC05046) are deposited in

**Table 2. Comparative association morphometrics of *Protomagalhaensia serpentula*, *Protomagalhaensia granulosa*, *Protomagalhaensia blaberae*, and *Protomagalhaensia wolfi* n. comb.**

	<i>P.</i> <i>serpentula</i> *	<i>P.</i> <i>granulosa</i> †	<i>P.</i> <i>blaberae</i> †	<i>P.</i> <i>wolfi</i>
Primate				
PL	50	87	74	77
DL	350	563	481	460
PTL	400	650	555	533
PL:PTL	8	7.5	7.5	7.1
PWM:DWM	1.3	1.03	1.09	1.2
Satellite				
PL	50	62	55	62
DL	350	488	505	472
STL	400	550	560	535
PL:STL	8	8.85	10.2	9.1
PWM:DWM	1.3	1.02	1.04	1.3
PTL:STL	1	1.18	0.99	0.99

\* Data from de Magalhaes (1900) and Pinto (1918, 1922).

† Data from Peregrine (1970).

the Sam Houston State University Insect Collection (SHSUC), Department of Biology, Sam Houston State University, Huntsville, Texas. Individual accession numbers are not assigned by SHSUC.

*Site of infection:* Trophozoites and gamonts were collected from the ventriculus posterior to the intercecal region. Trophozoites primarily located in and immediately posterior to the intercecal region. Associations primarily located in the ileum. Gametocysts were collected from the host hindgut, rectum, and feces.

*Prevalence:* Prevalence in colony approaches 100%.

*Records:* *Nauphoeta cinerea*, nymphs, Ndanda, Tanzania (type locality); *Nauphoeta cinerea*, nymphs and adults, Research colonies, Peru State College, Peru, Nebraska, U.S.A.

*Specimens deposited:* No specimen from the original type series is known. The neotype slide is deposited in the Harold W. Manter Laboratory for Parasitology (HWML), Division of Parasitology, University of Nebraska State Museum, Lincoln, Nebraska. The neotype slide HWML 48314 (authors' slide REC050107j) is a hapantotype containing multiple trophozoites, gamonts, and associations. The neotype slide is one of a series of 34 slides containing trophozoites, gamonts, and associations: HWML48271 (CMR050065f); HWML48274 (CMR050067d, f, j, l); HWML48277 (REC050105e); HWML48280 (REC050106d-f); HWML48283 (REC050107h, REC050107k, l); HWML48285 (REC050108b,

d); HWML48287 (JJH040022b); HWML48290 (JJH040023h, j, t); HWML48293 (JJH040024a, b, g-j); HWML48296 (JJH040025f, i); HWML48300 (JJH040027e, f); HWML48305 (JJH040030c, h); and, HWML48312 (JJH040033a-c). No specimen from the neotype series is retained by the authors. An additional series of 52 voucher slides containing trophozoites, gamonts, and associations of both species redescribed herein is deposited with the neotype series: HWML48270 (CMR050065c, e); HWML48273 (CMR050067a, g, k); HWML48276 (REC050105a, c, d, f, g); HWML48279 (REC050106g); HWML48282 (REC050107i); HWML48284 (REC050108a, c); HWML48289 (JJH040023a, d, e, g, k, q, r, s, v); HWML48292 (JJH040024f, k); HWML48295 (JJH040025e, g); HWML48299 (JJH040027a); HWML48302 (JJH040028b-f); HWML48304 (JJH040030d-f, JJH040030j, p, q); HWML48307 (JJH040031e); HWML48309 (JJH040032f-j); and, HWML48311 (JJH040033d, f-k).

## Remarks

The genus *Protomagalhaensia* comprises 4 species, all described from cockroaches: *P. wolfi* from *N. cinerea*; *P. serpentula*, (the type species), from *B. orientalis*; *Protomagalhaensia blaberae* Peregrine, 1970 from *Blaberus boliviensis* Princis, 1946; and, *Protomagalhaensia granulosa* Peregrine, 1970 from *Blaberus discoidalis* Serville, 1839. No type or permanent specimen of *P. serpentula* or *P. wolfi* is known. The type series of *P. granulosa* (Register number: 1970.333 and 1970.334, British Museum of Natural History [BMNH] Cromwell Road, London SW7 5BD, United Kingdom,) and *P. blaberae* (BMNH register number 1970.333) were examined and neotype specimens of *P. wolfi* were deposited.

The overall morphology of all 4 species is similarly elongate and serpentine (Table 2). They differ primarily in epimerite and oocyst morphology. Among described species of *Protomagalhaensia*, only *P. wolfi* is characterized by a divergent epimerite shape. The epimerite of *P. wolfi* is characteristically obdeltoid in young trophozoites and broadens to become orbicular in older trophozoites. In contrast, the epimerites of *P. granulosa* and *P. blaberae* are narrowly deltoid to narrowly pyriform and pyriform to broadly pyriform, respectively (Peregrine, 1970). The epimerite of *P. serpentula* is a very shallowly to depressed ovoid, but is not well studied (Pinto, 1922). Oocyst morphology and relative morphometrics also distinguish species of *Protomagalhaensia*. All 4 species possess dolioform oocysts. Oocysts of *P.*

*granulosae* and *P. serpentula* also possess apical corner spines or knobs (de Magalhaes, 1900; Pinto, 1918, 1922; Peregrine, 1970) that are absent in the oocysts of *P. wolfi* and *P. blaberae*. Only the oocysts of *P. wolfi* possess polar plates, but the oocysts of *P. granulosae* possess a lateral depression unique among members of the genus. The oocysts of *P. wolfi* are notably larger (OLM, 9.2; OW, 5.5) than those of *P. granulosae* (OLM, 6.8; OW 4.4, [Peregrine, 1970]), *P. blaberae* (OLM, 6.8; OW 4.4, [Peregrine, 1970]), or *P. serpentula* (OLM, 7.5; OW 2.8, [de Magalhaes, 1900]).

***Leidyana haasi* (Geus, 1969)  
Hays and Clopton, 2006 n. comb.  
(Figures 25–40)**

**Trophozoites:** Trophozoites solitary, extracellular forms attached to epithelium of host pyloric caecae. Holdfast a simple epimerite. Epimerite orbicular. Protomerite shallowly to very shallowly ovoid. Deutomerite obdeltoid in young trophozoites, becoming obovoid in older trophozoites. Nucleus orbicular with 3 or more distinct karyosomes.

**Association:** Gamonts anisomorphic; association caudofrontal, late, associations forming just prior to syzygy, association interface linear; PTL/STL 1 (0.8–1.1,  $\pm 0.1$ , 30). Cytoplasm of satellite notably denser/darker than cytoplasm of primate.

**Primate:** Epimerite absent, protomerite shallowly ovoid; PL 66.4 (37.2–81.7,  $\pm 11.39$ , 30), PWE 73 (42.3–99.8,  $\pm 12.65$ , 30), PWM 78.9 (49.6–109.4,  $\pm 13.3$ , 30), PLAM 43.6 (21.7–58.5,  $\pm 10.75$ , 30), PLPM 23.5 (13.4–39.9,  $\pm 7.82$ , 30), PDSW 76.9 (50.3–106.5,  $\pm 12.77$ , 30), PL/PWE 0.9 (0.7–1.1,  $\pm 0.13$ , 30), PL/PWM 0.8 (0.6–1,  $\pm 0.12$ , 30), PL/PDSW 0.9 (0.6–1,  $\pm 0.13$ , 30), PLAM/PL 0.7 (0.4–0.8,  $\pm 0.11$ , 30), PLAM/PLPM 2.1 (0.8–3.9,  $\pm 0.81$ , 30), PWM/PWE 1.1 (1–1.2,  $\pm 0.03$ , 30). Deutomerite narrowly obpanduriform; DL 300.4 (112.9–412.1,  $\pm 65.47$ , 30), DWE 78.9 (48.1–104.8,  $\pm 13.76$ , 30), DWM 99.1 (60.4–136.3,  $\pm 16.8$ , 30), DLAM 61.3 (27.5–77.2,  $\pm 12.96$ , 30), DLPM 239.9 (87–349.1,  $\pm 54.65$ , 30), DL/DWE 3.9 (1.4–4.9,  $\pm 0.83$ , 30), DL/DWM 3.1 (1.3–3.8,  $\pm 0.62$ , 30), DLAM/DL 0.2 (0.1–0.2,  $\pm 0.03$ , 30), DLAM/DLPM 0.3 (0.2–0.3,  $\pm 0.04$ , 30), DWM/DWE 1.3 (1.1–1.5,  $\pm 0.13$ , 30), PTL 360.6 (148.3–480.4,  $\pm 73.59$ , 30). Indices: PTL/PL 5.4 (4–7,  $\pm 0.77$ , 30), DL/PL 4.5 (3–6,  $\pm 0.73$ , 30), DWM/PWM 1.3 (1.2–1.5,  $\pm 0.09$ , 30), PTL/DL 1.2 (1.2–1.3,  $\pm 0.04$ , 30). Nucleus orbicular, karyosome number variable but usually 7; NL 28.7 (18.4–36.1,

$\pm 5.07$ , 30), NW 26.9 (14.5–34.1,  $\pm 5.14$ , 30), NDS 114.5 (5.9–359.9,  $\pm 92.08$ , 30), NL/NW 1.1 (0.9–1.3,  $\pm 0.12$ , 30), NDS/NL 3.8 (0.3–11.8,  $\pm 2.99$ , 30), DL/NDS 5.9 (1.1–19.1,  $\pm 5.41$ , 30). Cytoplasm granulated.

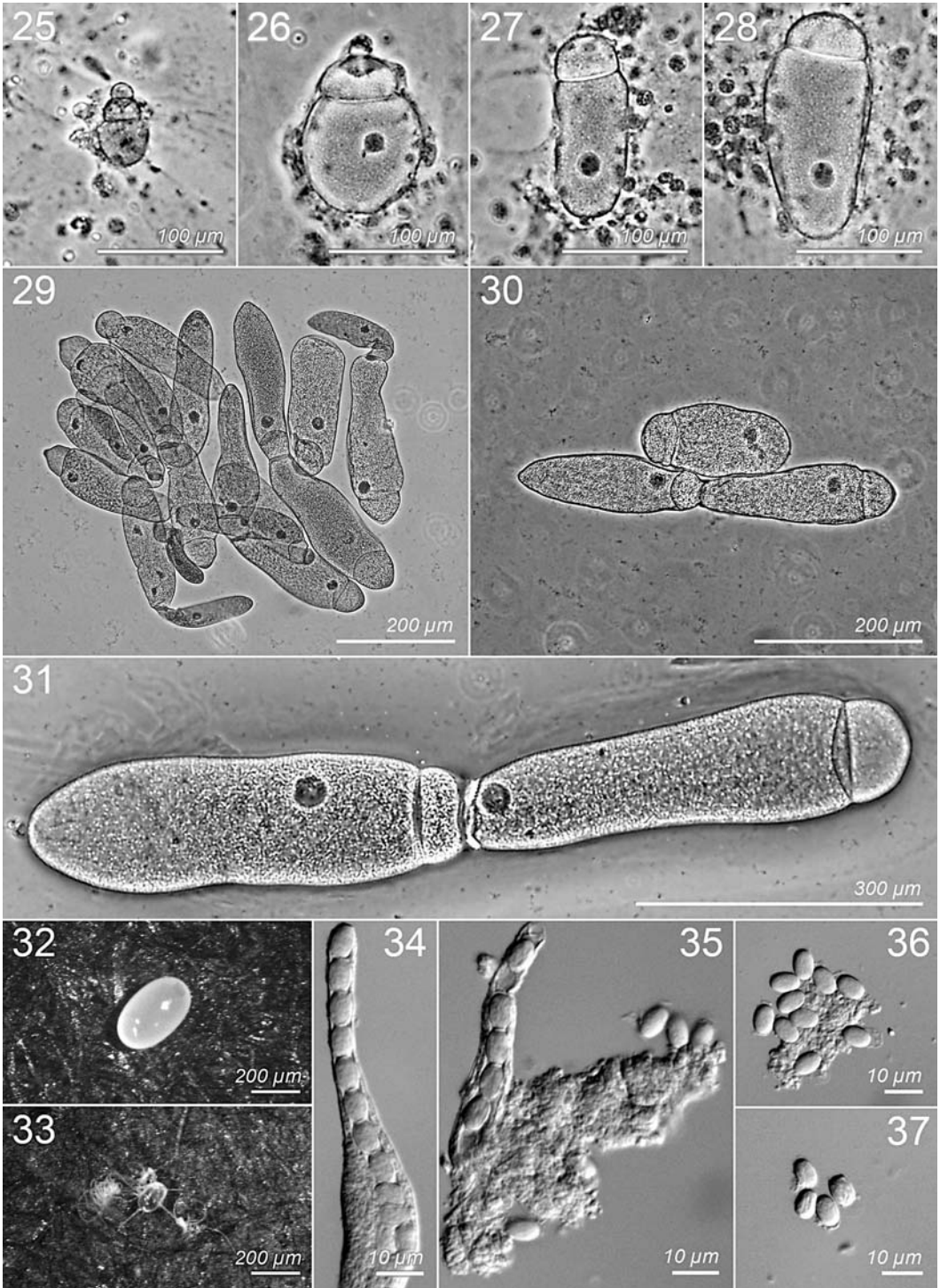
**Satellite:** Protomerite shallowly oblong; PL 58.4 (40.1–90,  $\pm 12.71$ , 30), PWE 71.5 (52.8–102.3,  $\pm 12.09$ , 30), PWM 78.9 (55.7–102.3,  $\pm 10.66$ , 30), PLAM 36.7 (16.3–54,  $\pm 9.71$ , 30), PLPM 22.2 (11.3–39.1,  $\pm 7.48$ , 30), PDSW 80.5 (57–101.1,  $\pm 9.36$ , 30), PL/PWE 0.8 (0.5–1.4,  $\pm 0.23$ , 30), PL/PWM 0.7 (0.5–1.1,  $\pm 0.18$ , 30), PL/PDSW 0.7 (0.5–1.1,  $\pm 0.16$ , 30), PLAM/PL 0.6 (0.4–0.8,  $\pm 0.1$ , 30), PLAM/PLPM 1.8 (0.7–3.2,  $\pm 0.68$ , 30), PWM/PWE 1.1 (1–1.2,  $\pm 0.06$ , 30). Deutomerite narrowly panduriform to narrowly lomentiform; DL 322.1 (134–417.1,  $\pm 67.08$ , 30), DWE 84.2 (55.9–133.6,  $\pm 17.53$ , 30), DWM 98.1 (75.5–142,  $\pm 16.24$ , 30), DLAM 60.2 (41.2–99.7,  $\pm 13.33$ , 30), DLPM 256.5 (67.6–316,  $\pm 62.98$ , 30), DL/DWE 3.9 (1.6–4.9,  $\pm 0.77$ , 30), DL/DWM 3.3 (1.5–3.8,  $\pm 0.62$ , 30), DLAM/DL 0.2 (0.1–0.3,  $\pm 0.05$ , 30), DLAM/DLPM 0.3 (0.1–0.6,  $\pm 0.11$ , 30), DWM/DWE 1.2 (1–1.4,  $\pm 0.13$ , 30), STL 369.2 (164.1–459.8,  $\pm 71.7$ , 30). Indices: STL/PL 6.4 (3.3–8.9,  $\pm 1.3$ , 30), DL/PL 5.6 (2.7–8,  $\pm 1.24$ , 30), DWM/PWM 1.2 (1.1–1.5,  $\pm 0.15$ , 30), STL/DL 1.2 (1.1–1.2,  $\pm 0.03$ , 30). Nucleus orbicular, karyosome number variable but usually 7; NL 30.1 (22.5–43.5,  $\pm 5.75$ , 30), NW 29.5 (17.2–40.8,  $\pm 5.44$ , 30), NDS 46.5 (25.4–102.7,  $\pm 20.28$ , 30), NL/NW 1 (0.9–1.3,  $\pm 0.12$ , 30), NDS/NL 1.6 (0.8–2.9,  $\pm 0.61$ , 30), DL/NDS 7.6 (4.1–11.8,  $\pm 2.38$ , 30). Cytoplasm granulated, distinctly more dense in satellite than in primate.

**Gametocysts:** Opaque, shallowly elliptoid in outline, length 316.6 (226.0–369.0,  $\pm 38.78$ , 32), width 190.1 (152.0–218.0,  $\pm 21.68$ , 32), width/length 0.60 (0.55–0.73,  $\pm 0.05$ , 32). Forty-six gametocysts were collected and stored under moist conditions, dehiscing by multiple spore tubes in 96–120 hr.

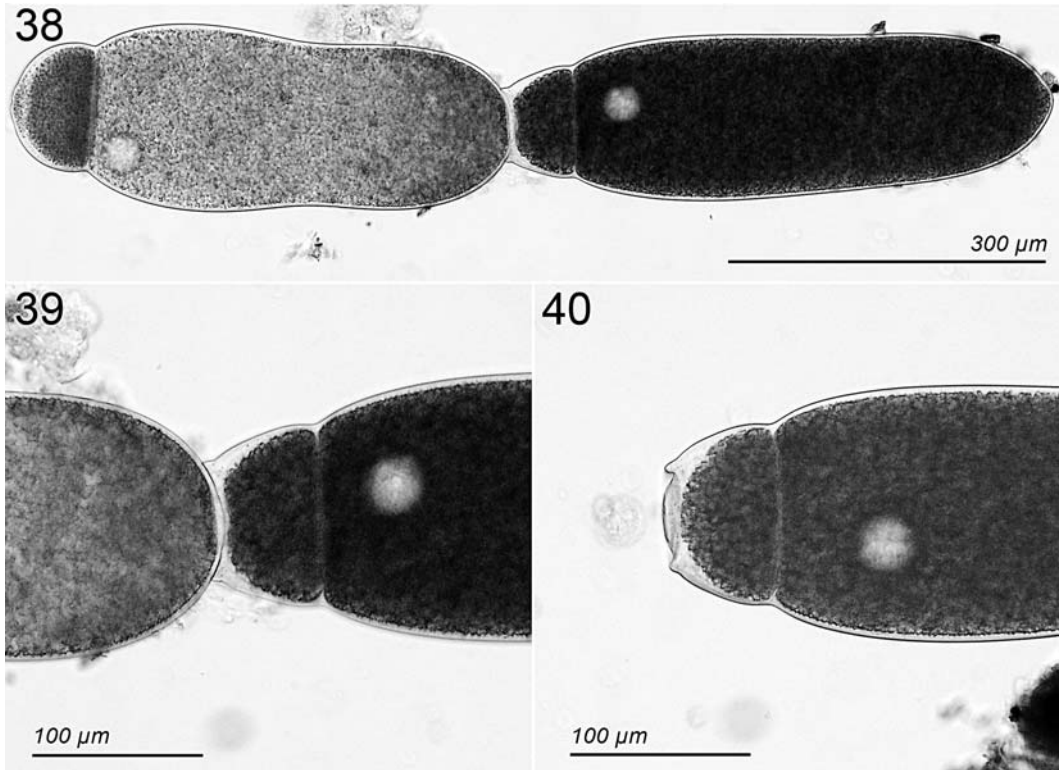
**Oocysts:** Elliptoid; OLM 8.7 (8.1–9.2,  $\pm 0.27$ , 32), OW 5.7 (5.4–6.3,  $\pm 0.23$ , 32), OLM/OW 1.5 (1.4–1.7,  $\pm 0.07$ , 32); with terminal but unattached very narrowly concavo-concave dehiscence plate; DPW 3 (2.2–3.5,  $\pm 0.32$ , 32), DPL 0.6 (0.4–0.9,  $\pm 0.11$ , 32).

**Taxonomic summary**

**Type host:** *Nauphoeta cinerea* (Olivier, 1789) (Dictyoptera: Blattaria: Blaberidae: Oxypalae: Nauphoetini), nymphs and adults.



**Figures 25–37.** *Leidyana haasi* n. comb. **25–28.** Young trophozoite. **29–31.** Mature gamonts in association. **32.** Gametocyst. **33.** Gametocyst after dehiscence with spore tubes and coiled oocyst chains. **34–35.** Spore tubes with oocysts. **36–37.** Oocysts. (Figs. 25–31, Harris' hematoxylin and eosin-xytol, phase contrast; Figs. 32, 33, live; Figs. 36–37, agar monolayer mount, differential interference contrast.)



**Figures 38–40.** *Leidyana haasi* n. comb. 22. Mature association (live, phase contrast). 39–40. Association interface (live, phase contrast).

*Type locality:* Ndanda, Tanzania.

*Symbiotype:* Five symbiotype specimens (authors' specimens REC05042–REC05046) are deposited in the Sam Houston State University Insect Collection (SHSUIIC), Department of Biology, Sam Houston State University, Huntsville, Texas. Individual accession numbers are not assigned by SHSUIIC.

*Site of infection:* Trophozoites and gamonts were collected from the pyloric caecae and intercecal region of the ventriculus. Associations primarily located in the intercecal region and sporadically in the ileum. Gametocysts were collected from the host hindgut, rectum, and feces.

*Prevalence:* Prevalence in colony approaches 100%.

*Records:* *Nauphoeta cinerea*, nymphs, Ndanda, Tanzania (type locality); *Nauphoeta cinerea*, nymphs and adults, Research colonies, Peru State College, Peru, Nebraska, U.S.A.

*Specimens deposited:* No specimen from the original type series is known. The neotype slide is

deposited in the Harold W. Manter Laboratory for Parasitology (HWML), Division of Parasitology, University of Nebraska State Museum, Lincoln, Nebraska. The neotype slide HWML 48313 (authors' slide REC050107c) is a hapantotype containing multiple trophozoites, gamonts, and associations. The neotype slide is one of a series of 84 slides containing trophozoites, gamonts, and associations: HWML48269 (CMR050065a, b, d, g); HWML48272 (CMR050067b, c, e, h, i, n); HWML48275 (REC050105b); HWML48278 (REC050106a-c); HWML48281 (REC050107a, b, d-g); HWML48286 (JJH040022a, JJH040022c, d-h, j-n); HWML48288 (-b, -f, -i, -l-p, u); HWML48291 (JJH040024d, -e); HWML48294 (JJH040025a-d, j); HWML48297 (JJH040026a-f); HWML48298 (JJH040027b-d); HWML48301 (JJH040028g, h); HWML48303 (JJH040030a, b, g, i, k-o); HWML48306 (JJH040031a-d, f, g); HWML48308 (JJH040032a-e, k-n); and, HWML48310 (JJH040033e). No specimen from the neotype series is retained by the authors. An additional series of 52 voucher slides containing trophozoites, gamonts, and associations of both *P. wolffi* and *L. haasi*

**Table 3. Comparative association morphometrics of *Leidyana migrator* and *Leidyana haasi* n. comb.**

	<i>L. migrator</i> *	<i>L. haasi</i>
Primate		
PL	62	66.4
PWM	107	78.9
PL/PWM	0.56	0.8
DL	389	300.4
DWM	145	99.1
DL/DWM	2.63	3.1
PTL	447	360.6
PTL/PL	7.14	5.4
PTL/DL	1.15	1.2
DL/PL	6.25	4.5
DWM/PWM	1.3	1.3
NL	28	28.7
NW	37	26.9
NL/NW	0.74	1.1
Satellite		
PL	37	58.4
PWM	114	78.9
PL/PWM	0.3	0.7
DL	373	322.1
DWM	142	98.1
DL/DWM	2.56	3.3
STL	404	369.2
STL/PL	11.11	6.4
STL/DL	1.09	1.2
DL/PL	10	5.6
DWM/PWM	1.2	1.2
NL	36	30.1
NW	30	29.5
NL/NW	0.78	1
PTL/STL	1.12	1

\* Data from Clopton (1995).

is deposited with the neotype series: HWML48270 (CMR050065c, e); HWML48273 (CMR050067a, g, k); HWML48276 (REC050105a, c, d, f, g); HWML48279 (REC050106g); HWML48282 (REC050107i); HWML48284 (REC050108a, c); HWML48289 (JJH040023a, d, e, g, k, q, r, s, v); HWML48292 (JJH040024f, k); HWML48295 (JJH040025e, g); HWML48299 (JJH040027a); HWML48302 (JJH040028b-f); HWML48304 (JJH040030d-f, JJH040030j, p, q); HWML48307 (JJH040031e); HWML48309 (JJH040032f-j); and, HWML48311 (JJH040033d, f-k).

### Remarks

The genus *Leidyana* comprises 33 species reported from 5 insect orders: Orthoptera (Dufour, 1837; Watson, 1915; Narain, 1961; Théodoridès and Echar, 1962; Corbel, 1967a, 1967b, 1968; Issi and Lipa, 1968; Geus, 1969; Hoshide, 1973a, 1973b, 1978, Haldar and Sarkar, 1979; Hooger and Amoji,

1986; Sarkar, 1988; Pushkala and Muralirangan, 1998; Johnny, et al., 1999; Haldar and Patra, 2000; Johnny, et al., 2000; Lange and Cigliano, 2004), Lepidoptera (Keilin, 1918; Tuzet and Ormières, 1956; Hoshide, 1958; Geus, 1966; Ormières, 1967; Rabindra and Jayaraj, 1981; Lipa and Martignoni, 1984; Ghosh and Choudhury, 1992; Clopton and Lucarotti, 1997), Coleoptera (Braune, 1930; Finlayson, 1950; Geus, 1969; Patil and Amoji, 1979; Golemansky and Duhlińska, 1982; Roy, 1989), Trichoptera (Baudoin, 1966, 1967), Hymenoptera (Bhatia and Setna, 1924), and Dichtyoptera (Clopton, 1995). Only *Leidyana migrator* Clopton, 1995 and *L. haasi* are reported from cockroaches (Dichtyoptera).

Comparative association morphometrics for *L. migrator* and *L. haasi* are reported in Table 3. In general, gamonts of *L. migrator* are longer and more anisometric than those of *L. haasi* (mean PTL, STL, and PTL/STL of 447, 404, and 1.12, respectively, for *L. migrator*; 361, 369, and 1.00, respectively, for *L. haasi*). The greater gamontic length observed for *L. migrator* is a function of notably longer deutomerites. The gamontic protomerites of *L. haasi* are actually longer but considerably narrower than those of *L. migrator* even though gamonts of *L. migrator* are larger overall (see Table 3, compare mean PL and PWM for primites and satellites among species). Both species share a similar overall morphology that is similarly proportioned in breadth (mean DWM/PWM is 1.3 for primites and 1.2 for satellites of both species), but not length (mean DL/PL for primites and satellites of *L. migrator* are 6.25 and 10, respectively; but 4.5 and 5.6, respectively, for *L. haasi*). Both *L. migrator* and *L. haasi* have shallowly elliptoid gametocysts (mean width/length 0.62 and 0.60, respectively) but the gametocysts of *L. migrator* are ca. 3 times larger than those of *L. haasi* (mean length 1,066 and 316.6, respectively). Both *L. migrator* and *L. haasi* are characterized by elliptoid oocysts that differ in relative morphology (mean OLM/OW 2.0 and 1.5, respectively) and overall size (mean OLM 8.0 and 8.7, respectively; mean OW 4.0 and 5.7, respectively).

### DISCUSSION

*Nauphoeta cinerea* was originally described from specimens taken on Mauritius in the Mascarene Islands of the Indian Ocean. East African in origin, *N. cinerea* populations were apparently disseminated along global trading routes by sailing vessels: first throughout the Malagasy region by Arab traders and then to the Philippines and the Orient by Portuguese and Spanish vessels in the 16<sup>th</sup> and 17<sup>th</sup> centuries

(Rehn, 1945; Cornwell, 1968). New World colonies in Brazil, Mexico and the Caribbean were probably disseminated by Portuguese traders in goods brought from the Philippines (Rehn, 1945). Their proclivity for facultative parthenogenesis has made *N. cinerea* popular as a laboratory research model (e.g., Clark et al., 1997; Corley et al., 1999; Moore and Moore, 1999; Harris and Moore, 2005). *Nauphoeta cinerea* is frequently used as a colonized live prey item in the captive reptile trade where it is also called the "Madeira," "cinereous," "Tampa," "Tanzanian," "Speckled," or "marble" cockroach. The relative ease with which this species is domesticated, shipped, and maintained in colony for various purposes has undoubtedly facilitated worldwide dissemination of the species, which is now circumtropical in distribution (Atkinson and Koehler, 1990). Wild populations of *N. cinerea* are ecologically associated with domiciliary structures and feed mills: the species is apparently peridomestic rather than truly domiciliary or feral (Gresham, 1952; Cornwell, 1968; Grandcolas et al., 1996). New world records include Cuba, Hispaniola, Mexico, Brazil, and the Galapagos Islands (Atkinson and Koehler, 1990; Peck et al., 1998). Pacific records include the Malaysia (Vythilingam et al., 1997); Thailand (Asahina and Hasegawa, 1981; Tawatsin et al., 2001); Hawaiian Islands (Jamieson, 1999); Philippines, Sumatra, Australia, and New Caledonia (Princis, 1965). East African records extend from Egypt through the Sudan to Tanzania, the Transvaal and Natal (Princis, 1965). It also occurs on Madagascar and Mauritius (Princis, 1965). First reported from the U.S.A. around feed manufacturing mills near Tampa, Florida in 1952 (Gresham, 1952), *N. cinerea* now appears to be endemic throughout southern Florida (Pratt, 1988).

As an appendix to his monograph on the gregarines of central Europe, Geus (1969) provided the original descriptions of *P. wolfi* (= *G. wolfi*) and *L. haasi* (= *G. haasi*) from a small sample of nymphs of *N. cinerea* collected from the Holy See's Territorial Abbey at Ndanda, Tanzania (each species epithet honors a monk of the Benedictine Order). Although his descriptions are incomplete, his figures are consistent with the redescrptions provided herein. *Nauphoeta cinerea* arose in the general region of east Africa and thus the Geus (1969) descriptions suggest a generally east African origin for *P. wolfi* and *L. haasi*. Although now distributed throughout much of the world, *N. cinerea* has maintained its endemic gregarine fauna intact. This apparently robust host-parasite fidelity in gregarine-cockroach systems is not unique.

*Leidyana haasi* is the 1 of only 2 species of

*Leidyana* known from dictyopteran hosts. Clopton (1995) described *L. migrator* from colonies of the Madagascar Hissing Cockroach, *Gromphadorhina portentosa*, that had been maintained in culture for nearly 2 decades. These colonies were subcultures of colonies maintained for a least a decade in New York, U.S.A., reportedly established from laboratory cultures of unknown origin. Adults and nymphs of *G. portentosa* are commercially available and our surveys of individuals from commercial biological supply houses invariably confirm infection by *L. migrator*. Ball et al. (1995) reported septate gregarines conforming to *L. migrator* from a breeding colony of *G. portentosa* originating from wild stock in Madagascar, London, U.K. The gregarine assemblages of both *N. cinerea* and *G. portentosa* have remained intact despite broad distribution, multiple emigration events, and serial subculture. This host-parasite fidelity suggests that many more such gregarine-cockroach experimental models await discovery and their eventual diversity may provide significant opportunities for comparative studies of dispersal and co-evolution.

## ACKNOWLEDGMENTS

It is a pleasure to acknowledge the Peru State College Foundation, who generously provided stipend support for JJH in 2004. We especially thank the Dean of Arts & Science at Peru State College, Dr. Stephen Sylvester, for his unwavering support of faculty and undergraduate research, providing facilities and resources to support this work, and for running tactical interference with those who do not happily cohabit with colonies of exotic cockroaches.

This material is based upon work supported by the National Science Foundation through grant NSF DEB 0340774. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

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